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New Microanatomical Characters for Scorpion Taxonomy (Arachnida: Scorpiones)

Michael Brewer

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**NEW MICROANATOMICAL CHARACTERS FOR SCORPION TAXONOMY
(ARACHNIDA: SCORPIONES)**

Thesis submitted to The Graduate College of
Marshall University

In partial fulfillment of the requirements for the degree of
Master of Science
Biological Sciences

Submitted by
Michael Brewer
Marshall University, Department of Biological Sciences
May 3, 2007

Abstract

Morphological characters used in scorpion systematics are limited to a few reliable structures. The most recent high-level, comprehensive revision of scorpion phylogeny, 38 of the 105 morphological characters were based on trichobothria – socketed mechanosensory seta (Soleglad & Fet, 2003). Other microstructures such as granules, setae, spines, etc. have been found in scorpions but their use for taxonomy was limited. In an effort to better understand the complex relationships among these ancient but similar looking animals, we attempted to first locate new microstructures and then assess their reliability and variability thus determining the levels at which they are diagnostic. The initial surveys were conducted on representatives of each of the twelve extant families using scanning electron microscopy (SEM). After identifying a new structure, comparisons between the families were made, and statistics were applied when warranted. The constellation array, found on the distal end of the fixed chelal finger in all scorpions, can be examined by counting the number of sensilla present and morphometric analysis. The laterobasal aculear serrations (LAS) were found to be a synapomorphy of the family Vaejoidea and exhibited too much intraspecific variability to be diagnostic at lower levels. In a number of families, including Vaejoidea, serrula was found in groups that were documented as lacking the structure. The limited resolution of dissecting microscopes and three-dimensional nature of these structures make the use of a SEM essential to the advancement of scorpion, as well as other arthropod, systematics and to our overall understanding of biodiversity.

Dedication

I would like to dedicate this to my family for all their support and encouragement: my father M. Scott Brewer, Sr., my mother Linda L. Brewer, and my brother Tory D. Brewer. Also, I dedicate this work to Dr. Victor Fet for all the time he has spent guiding me towards the goals I am now beginning to accomplish.

Acknowledgments

I would like to recognize those who have helped me along the way: Dr. Victor Fet, Michael Soglead, Dr. Suzanne Strait, Dr. F. Robin O'Keefe, Matthew Graham, David P. A. Neff, Elizabeth Fet, Cassie York, Nicholas Smith, the NASA Space Grant Foundation, and all those who have been gracious enough to help me the last few years.

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Index of Abbreviations

ABDSP = Anza-Borrego Desert State Park (depository of specimens, San Diego and Riverside Counties, California, USA)

AMNH = American Museum of Natural History (depository of specimens, New York, NY, USA)

BH = Blaine Hebert (collector)

BMNH = British Museum of Natural History (depository of specimens, London, England)

CAS = California Academy of Sciences (depository of specimens, San Francisco, California, USA)

DDSP = Dorsal Distal Setal Pair

FMNH = Field Museum Natural History (depository of specimens, Chicago, Illinois, USA)

GL = Graeme Lowe (collector)

LAS = Laterobasal Aculear Serrations

MES = Michael E. Sologlad (collector)

MHNG = Museum d'Histoire Naturelle de Geneve (depository of specimens, Geneva, Switzerland)

μm = micrometer

mm = millimeter

N = Number of specimens examined

NHMW = Naturhistorisches Museum Wien (depository of specimens, Vienna, Austria)

nm = nanometer

SD or SDEV = Standard Deviation

SEM = Scanning Electron Microscopy or Scanning Electron Microscope

sp. = When preceded by the name of a genus, this indicates a specimen that either has no valid name or cannot be distinguished as a member of a valid species.

USNM = United States National Museum (depository of specimens, Smithsonian Institution, Washington D.C., USA)

VDSP = Ventral Distal Setal Pair

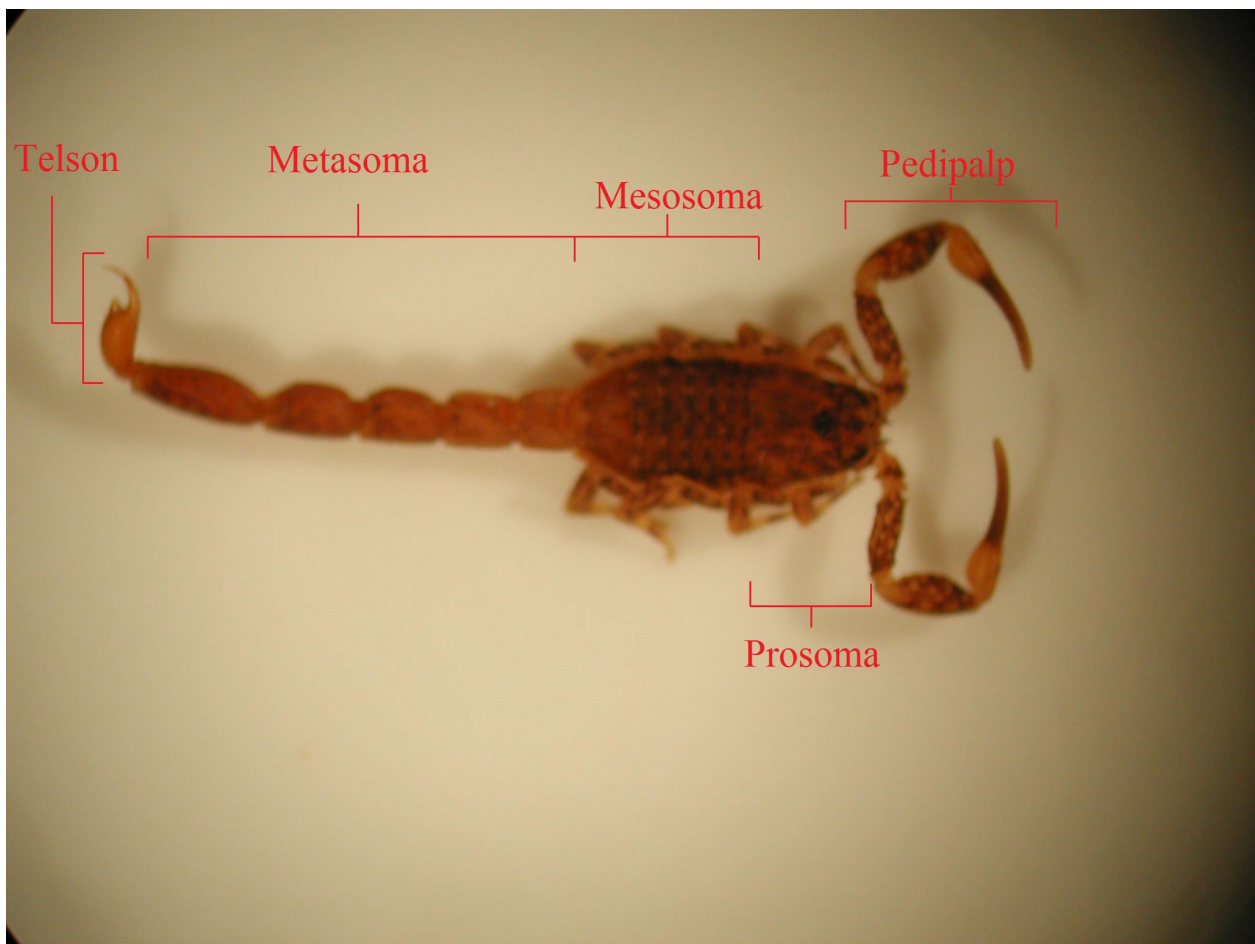
VF = Victor Fet (collector)

WDS = W. David Sissom (collector)

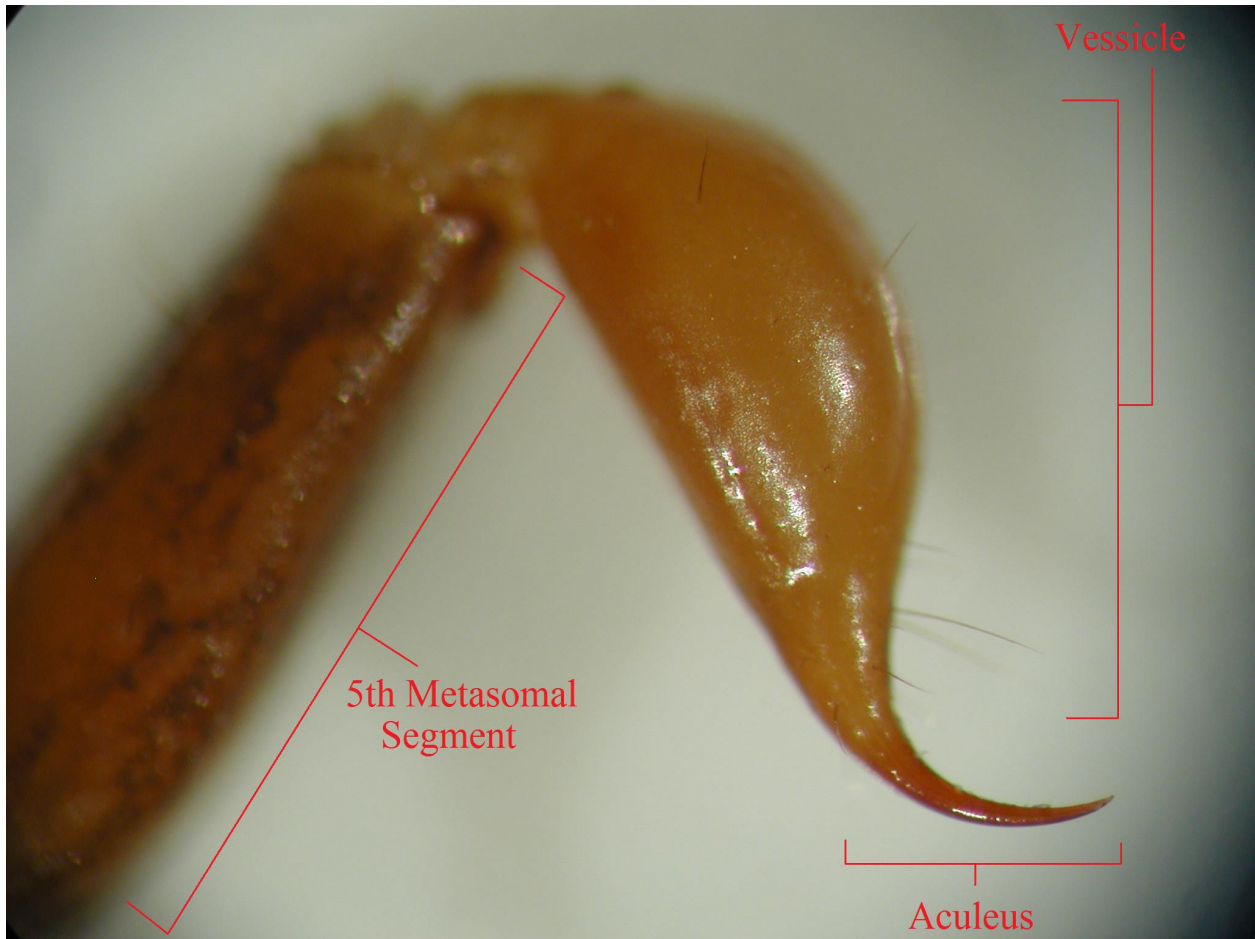
Chapter I: Introduction

Scorpion Morphology

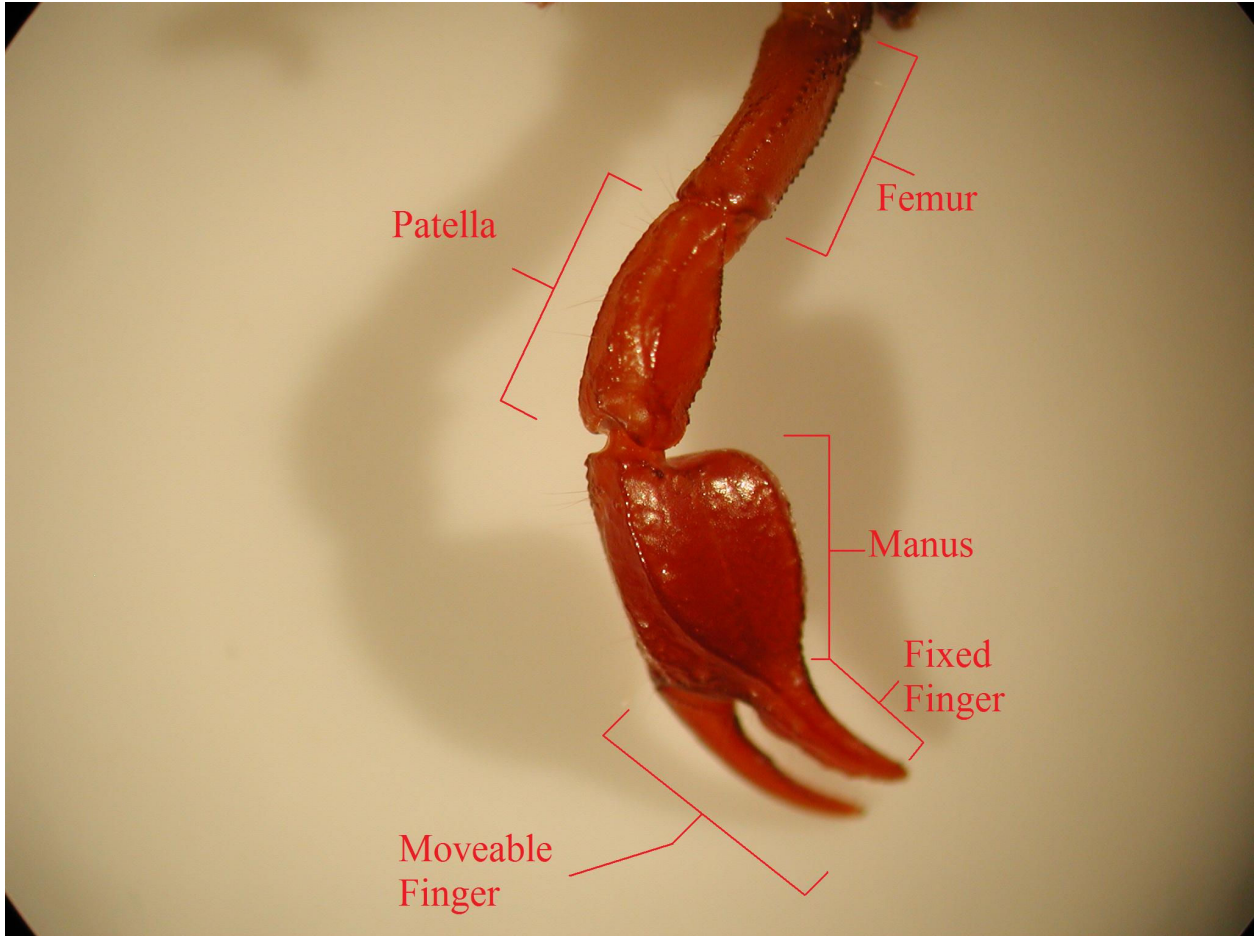
Scorpions have existed relatively unchanged since the middle Silurian (~450 million years ago) (Polis, 1990). The Recent scorpions all have a greatly conserved body pattern and general morphology (Figure 1.1-1.6).



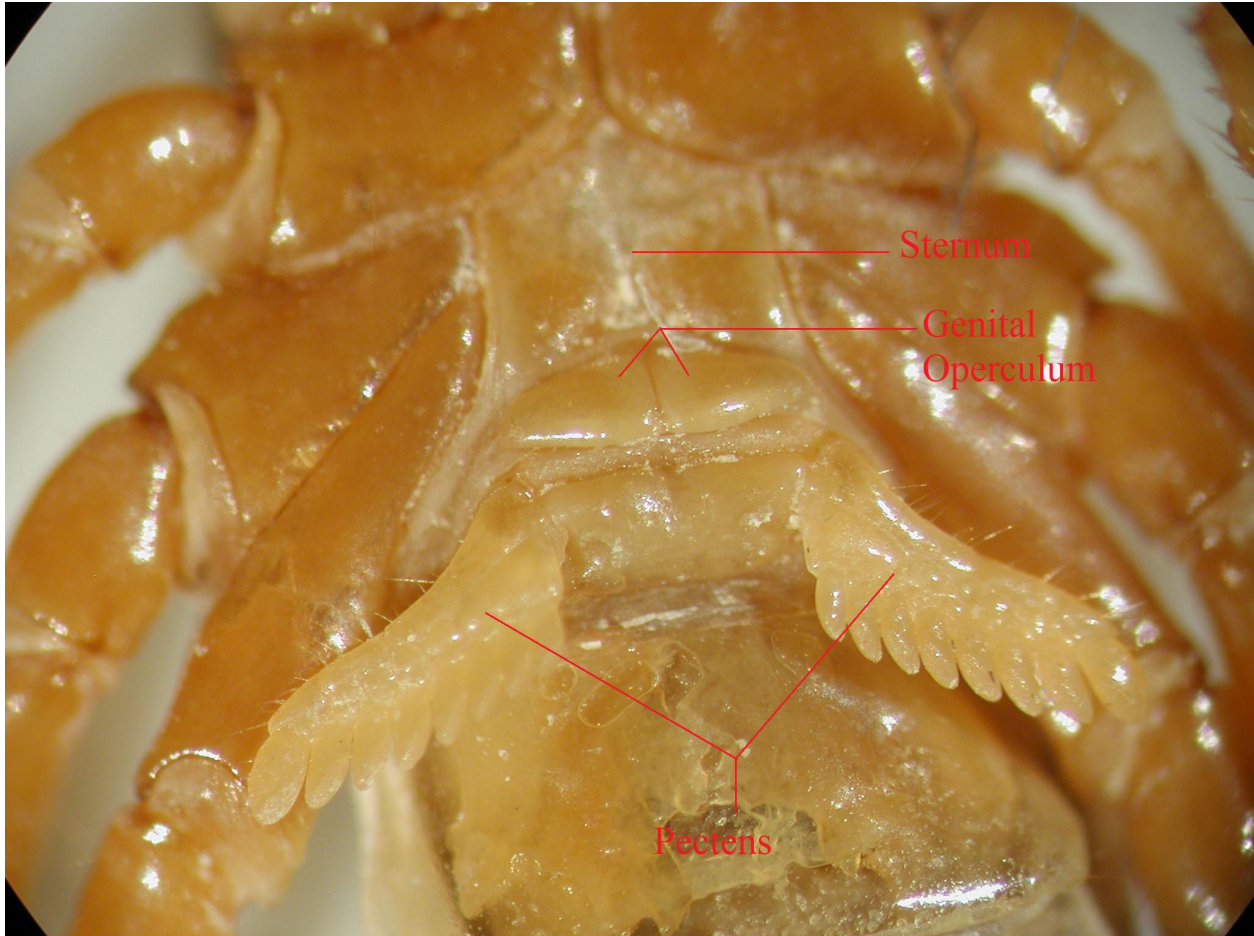
1 **Figure 1.1:** General scorpion body regions illustrated on *Microtityus fundorai*. (Dorsal view).



2 **Figure 1.2:** External telson anatomy illustrated on *Euscorpilus* sp. (Lateral view).



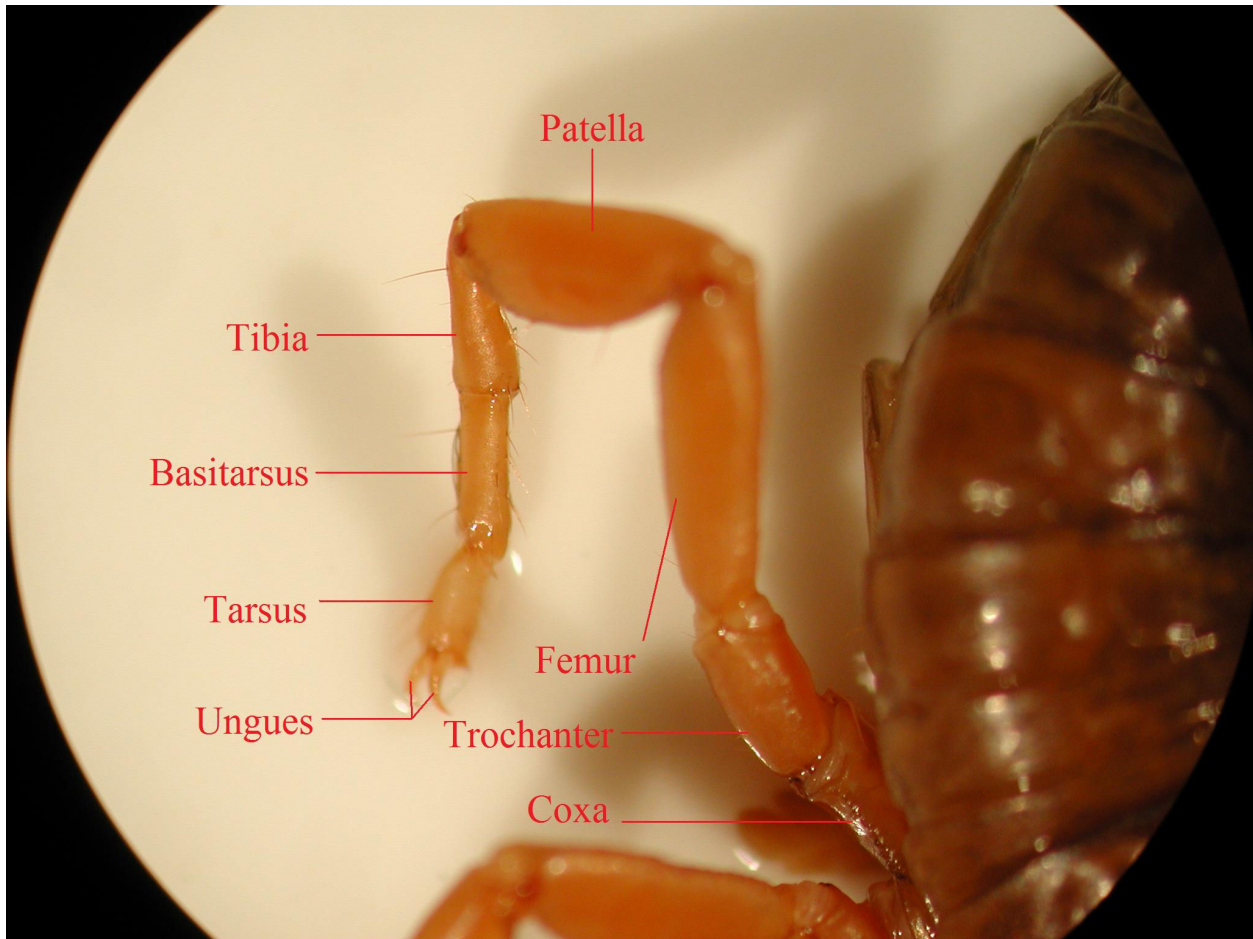
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4 **Figure 1.4:** Sternal region and related external anatomy shown on *Euscorpium* sp. (female) (Ventral view).



5 **Figure 1.5:** Sternal region and related anatomy shown on *Euscorpium* sp. (male) (Ventral view).



6 **Figure 1.6:** Leg anatomy of *Euscorpilus* sp. (Dorsal view, Posterior at top).

Scorpion Morphology in Systematics

These anatomical components have revealed several taxonomically important characters but few that can be easily examined using the naked eye. The genus *Euscorpilus* (Family: Euscorpilidae) recently underwent a morphological revision using many characteristics of the body regions listed below and general morphometric analysis (Soleglad and Fet, 2002). The chelicerae have a rather constant pattern of dentition, but the movable finger proves to be variable between families and is easily seen (Vachon, 1956, 1963). Trichobothrial patterns and numbers also prove to be very useful in systematic investigations, as proven by Vachon (1973), and can be viewed with the aid of only a dissecting microscope when dealing with adults. The patterns and

positions of trichobothria on each aspect of the femur, patella, and tibia of the pedipalp (manus and fixed finger) are used in Vachon's system. Another area of interest taxonomically is the coxosternal region (see Soleglad and Fet, 2003). Two variable structures in this area have been shown to be systematically diagnostic: the shape of the coxapophyses and the shape of the sternum. The shape of the coxapophyses of the first leg distinguishes the family Chaerilidae from all others. The anterior margin is very broad resulting in anterior "lobes" (Pocock, 1900). In other families, the margins are rounded. The sternal shape is always one of three types: subpentagonal, subtriangular, or broadly slitlike. The subpentagonal sternum is found in most taxa and at least one genus in each family. This type, however, is rarely found in Buthidae or Bothriuridae. The subtriangular sternum is found only in the family Buthidae and the slitlike sternum only in Bothriuridae. All first instar buthids have a subpentagonal sternum resulting in the hypothesis that it is the primitive condition. The slitlike shape of the sternum in some bothriurids appears to in fact be just a subpentagonal sternum modified by folding (Petrunkevitch, 1953). One other area of systematic interest is the leg, specifically the spination thereof. The presence or absence of tibial and pedal spurs has been used successfully in higher level systematics (Pocock, 1893a; Birula, 1917a; Vachon, 1952; Mitchell, 1968). Morphology of these spurs is useful at the generic or specific levels in many cases but much more so in buthids and bothriurids, in which they split and may contain setae. One final area of interest is the telson. Excluding the internal anatomy of the venom glands, the subaculear tooth is the most reliable diagnostic character on the telson. Most families share a general shape, but buthids exhibit much variability in the tooth (Polis, 1990). The pectens may also yield relevant data through the density of sensilla found on each tooth. Each of these characters may be useful at higher levels or only within certain lower taxa, but the number of characters available in most groups remains lacking.

Use of Scanning Electron Microscopy in Scorpiology

The use of microscopy is essential to the extrapolation of most pertinent data in the structures listed above and therefore necessary for the best understanding of

scorpion systematics. Microanatomical characters in scorpion systematics are somewhat few and far between, and, therefore, all available methods and tools to pioneer new characters must be explored. One of the most promising is the scanning electron microscope (SEM). This tool provides images at magnitudes and of such clarity and contrast that no other tool can provide. New regions of the animal can be explored with relative ease and great efficiency while existing characters may be verified and put under greater scrutiny, perhaps yielding new, even more informative characters while refining those already in use. The SEM has been used in the past for various projects in scorpology, including examination of sensory structures such as trichobothria, pectinal sensilla, and many others. As a systematic tool, the SEM projects have been fewer in number. The fact that many regions of the body of scorpions remain unexplored leaves one to believe that many discoveries have yet to be made.

Taxonomic Conventions

The taxonomy in this thesis, and each work detailed within, follows Soleglad and Fet, 2003; Soleglad and Fet, 2005; and Fet and Soleglad, 2005.

Chapter II: Methods and Materials

Specimen

Our specimens were obtained from a variety of sources. The natures of the works discussed here require material from all over the world and spanned the entire diversity of the scorpion order (12 families). A comprehensive list of the material examined in Appendixes A-C.

Scanning Electron Microscopy

All scorpions were preserved in 70% or 96% ethanol. Parts to be analyzed were removed from the specimen and sonicated for one minute in each of five consecutive ethanol solutions: 50%, 75%, 95%, 100%, and 100% again. This process helps to further dehydrate the anatomy and eases the transition to the SEM by reducing the amount of outgasing and therefore the time required to create a proper vacuum.

Before being inserted into the microscope's chamber, the material must be coated with a layer of approximately 10 nm thick gold/palladium in a Hummer sputter coater to make it more conductive thus allowing proper electron beam behavior. This act also reduces the amount of distortion viewed on the image as a result of charging, the accumulation of primary electrons as a result of poor surface conductivity.

The samples were then mounted on small mounting stubs designed specifically for the SEM. These were placed into a specific holding device that both holds up to four stubs and has a dove-tail groove on the underside that attaches to a site on the internal, movable stage in the SEM's sample chamber. After the chamber was closed and evacuated of air, current was supplied to the filament, thus initializing the electron beam. To further reduce charging, the acceleration voltage of the electron gun was adjusted accordingly. Digital images of 75X to 10,000X were taken and the spot size,

alignment of the electron gun, contrast, brightness, and focus were adjusted to optimize image clarity and focus. All images were captured in slow record speed by a PC with a digital capture card (see Appendix E for procedure), saved to a ZIP disk, and transported to another PC for editing by Photoshop and analysis. Measurements were taken using ImageJ (Rasband, 1997-2006) or by hand with a ruler and recorded.

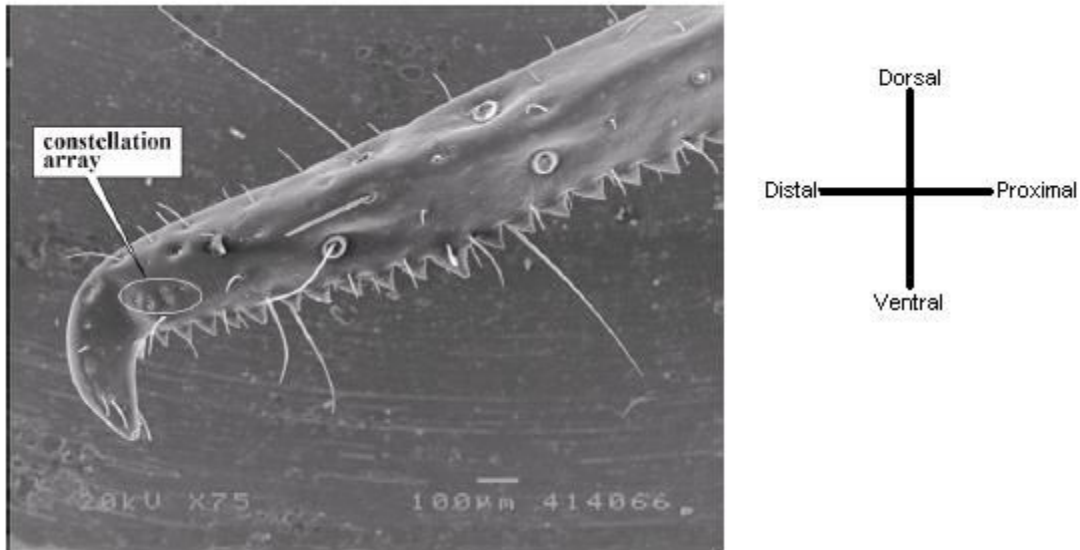
Chapter III: Constellation Array

Introduction

The constellation array is a sensory organ previously unknown in scorpions documented for the first time in this work (Fet *et al.*, 2006a). It is found on the anterior side of the distal end of the fixed chelal finger of both pedipalps and is below the visual threshold of the human eye. The organ exists as an array of microscopic sensilla arranged in various, and perhaps taxonomically conservative, patterns. In fact, the organ cannot be seen with a dissecting microscope of any power available at Marshall University (i.e. below 70X), and the chelal finger itself is too thick to be viewed under a compound light microscope without the implementation of microtoming. This size and unpigmented nature of the array requires that any practical analysis of its anatomy and orientation be done with electron microscopy. The SEM allows us to view the topology of chela and the orientation of the array in relation to surrounding structures such as sensilla and/or denticle rows and the fine structure of the organ.

Materials and Methods

Specimen, mostly females, from all four parvorders, all six superfamilies, all 12 families, 22 genera, and 27 species of extant scorpions (taxonomy after Soleglad & Fet, 2003; Soleglad *et al.* 2005; Fet & Soleglad, 2005) were examined in the initial pilot analysis. One species of the family Buthidae was examined from a SEM micrograph in literature: *Isometrus garyi* (Lourenco *et al.* Huber, 2002). In the Family Vaejovidae, we concentrated on the group of genera *Paruroctonus*, *Smeringurus*, *Vaejovis*, and *Vejovoidus*. These specimens were examined using the procedure outlined in the Chapter II. For a complete list of specimen examined, refer to Appendix A.



7 **Figure 3.1:** Constellation array placement and orientation (adapted from Fet *et al.*, 2006a and modified by M. Brewer).

Results and Discussion

All species observed had the array in some form or another on the external distal aspect of the fixed finger of the chela. The number and arrangement of sensilla varied greatly between taxa. The range of number of sensilla was from one in *Vejovoidus* (Vaejovidae) to 15 in *Calchas* (Luridae) with a mean of approximately six \pm three. The overall size of the array, from distal to proximal sensilla, ranged from 18 μm in a juvenile *Isometrus garyi* (Buthidae) to ca. 500 μm in *Euscorpius italicus* (Euscorpiidae) and averaged to be approximately 203 μm \pm 127 μm . Initial data obtained from *Calchas nordmanni* (Luridae), with fifteen sensilla, and *Euscorpius tergestinus* (Euscorpiidae), with six sensilla, indicate juveniles show no variation in number of sensilla between first instar juveniles and adults. As a result of studying mostly females, not many data on sexual dimorphism were collected. However, after examining males of *Euscorpius tergestinus* and *E. gamma* (Euscorpiidae) and comparing those data to those from females of each species, no discrepancies in the number of sensilla were observed. No

correlation between size of the animal and size of the array can be drawn as several small and large species had relatively the same size array.

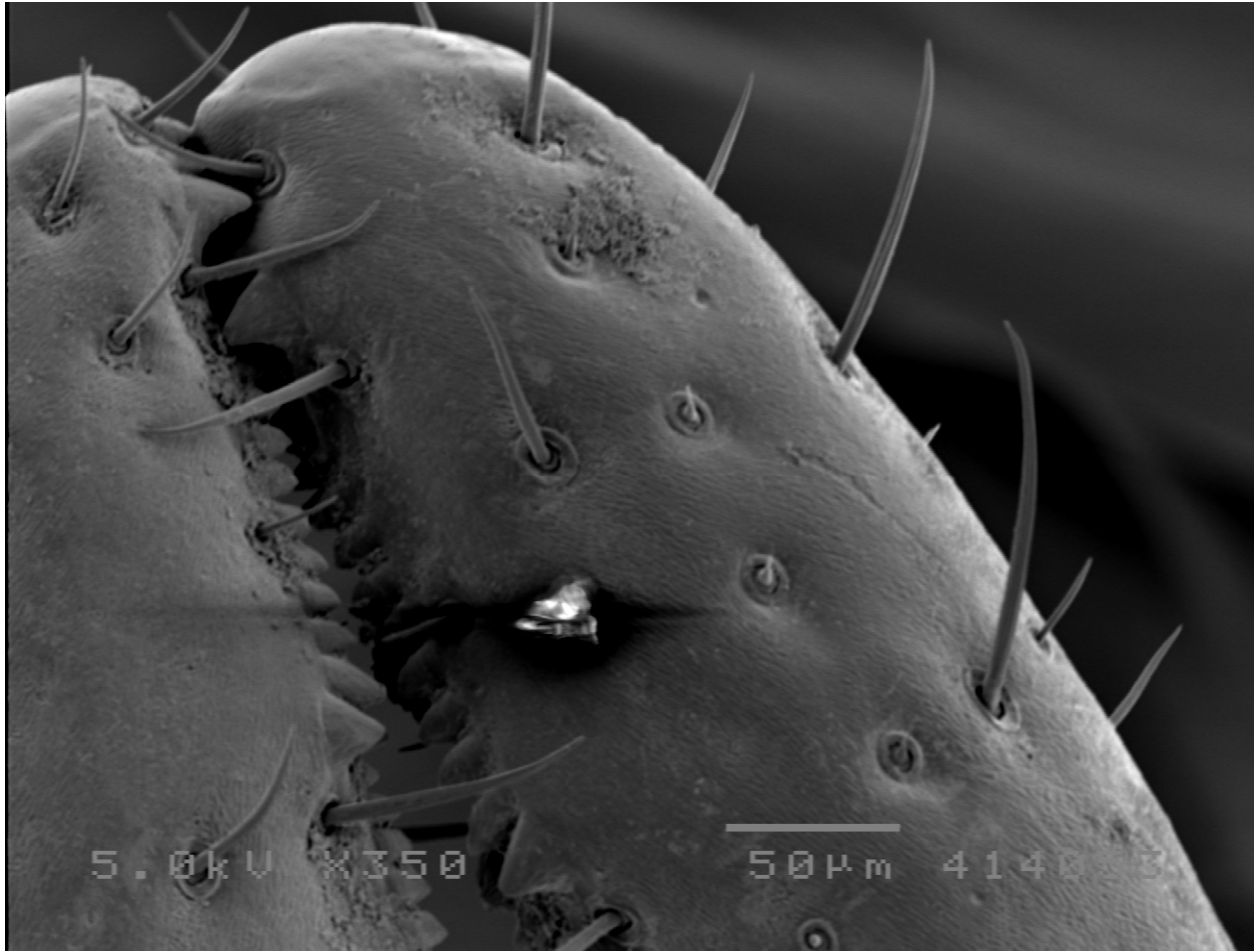
1 Table 3.1: Number and size data of the constellation array (adapted from Fet *et al.*, 2006a and modified by M. Brewer).

Family	Species	Number of sensilla	Size of constellation Array (maximal distance between sensilla), μm
Buthidae	<i>Centruroides hentzi</i>	5	32
	<i>Isometrus garyi</i> juvenile	6	18
	<i>Lychas mucronatus</i>	10	50
	<i>Mesobuthus caucasicus</i>	5	58
	<i>Mesobuthus eupeus</i>	5	36
Bothriuridae	<i>Centromachetes pocockii</i>	4	338
Caraboctonidae	<i>Hadrurides charcasus</i>	8	294
	<i>Hadrurus obscurus</i>	4	238
Chactidae	<i>Belisarius xambeui</i>	4	200
	<i>Broteas gervaisii</i>	14	364
	<i>Nullibrotheas allenii</i>	2	50
	<i>Uroctonus mordax</i>	4	144
Chaerilidae	<i>Chaerilus celebensis</i> juvenile	6	138
Euscorpiidae	<i>Euscorpius gamma</i> female	6	240
	<i>Euscorpius gamma</i> male	6	281
	<i>Euscorpius italicus</i>	5	517
	<i>Euscorpius tergestinus</i> female	6	432
	<i>Euscorpius tergestinus</i> juvenile	6	200
Hemiscorpiidae	<i>Hadogenes bicolor</i>	7	344
Iuridae	<i>Calchas nordmanni</i> female	15	263
	<i>Calchas nordmanni</i> juvenile	15	142
Pseudochactidae	<i>Pseudochactas ovchinnikovi</i>	4	173
Scorpionidae	<i>Bioculus comondae</i>	4	188
Superstitioniidae	<i>Superstitionia donensis</i>	4	356
Vaejovidae	<i>Serradigitus g. gertschi</i>	5	100
	<i>Serradigitus joshuaensis</i>	5	113
	<i>Serradigitus subtilimanus</i>	5	162
	<i>Smeringurus mesaensis</i>	2	308
	<i>Vaejovis carolinianus</i>	4	138
	<i>Vaejovis eusthenura</i>	5	183
	<i>Vejovoidus longiunguis</i>	1	not applicable
Mean \pm SD		$\sim 6 \pm 3$	203 ± 127

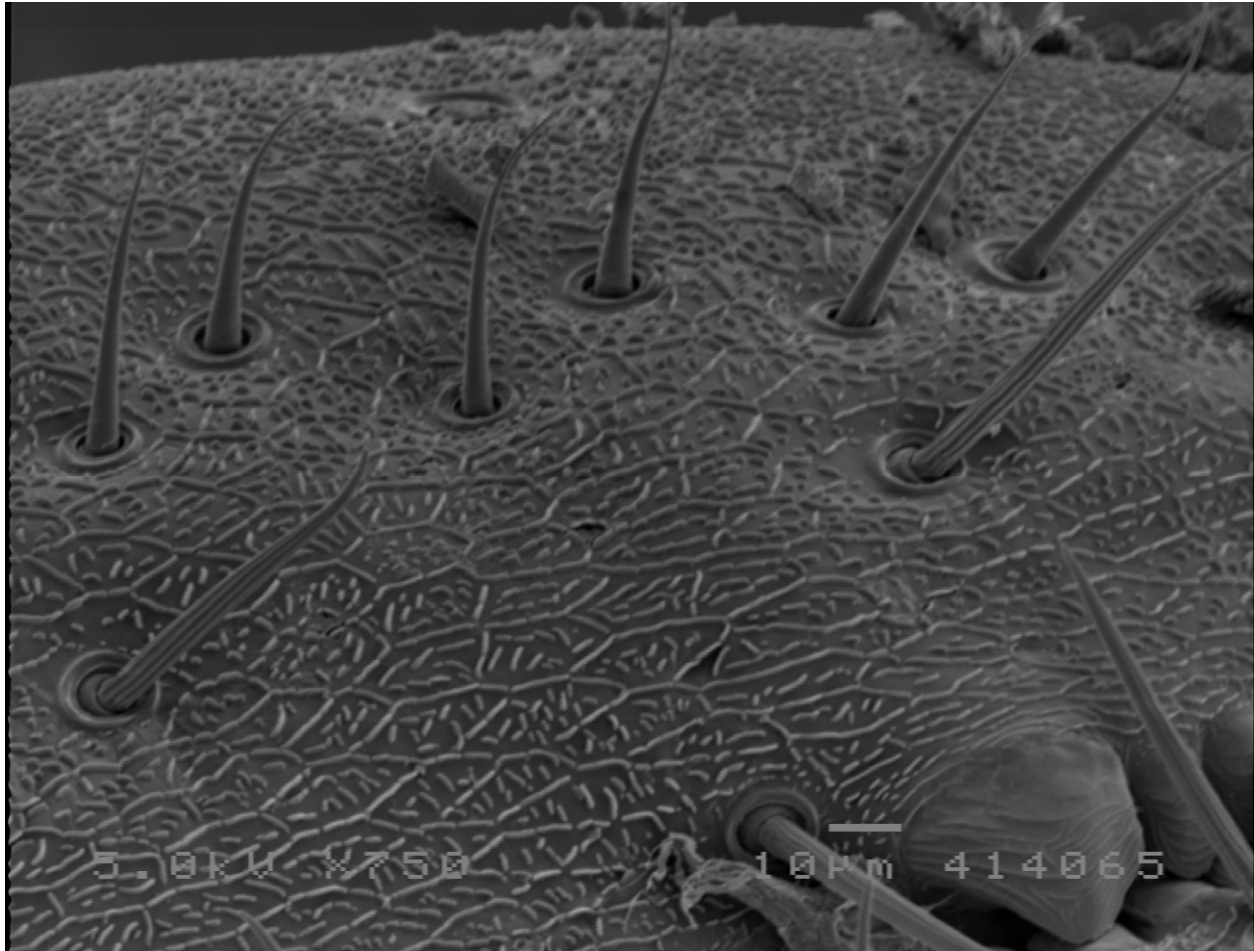
The family Buthidae appears to have very small size ranges for its members, about 30 to 50 μm . Juveniles did have smaller size ranges than adults of the same species in all cases observed.

The physiology and function of the organ have yet to be determined but this appears to be another example of antennalization, the placement of sensory organs on distal portions of the animal in an attempt to safely and effectively survey the environment. Scorpions are well known for this because they do not have proper antennae like many other arthropods. The discovery of the constellation array across all scorpion families shows that it is a very conserved and ancestral feature, a synapomorphy for the entire order. The number and position of sensilla also varies greatly between taxa indicating the possibility of a diagnostic character at several taxonomic ranks but extensive work in this area has yet to be done, however, the initial observations are very encouraging.

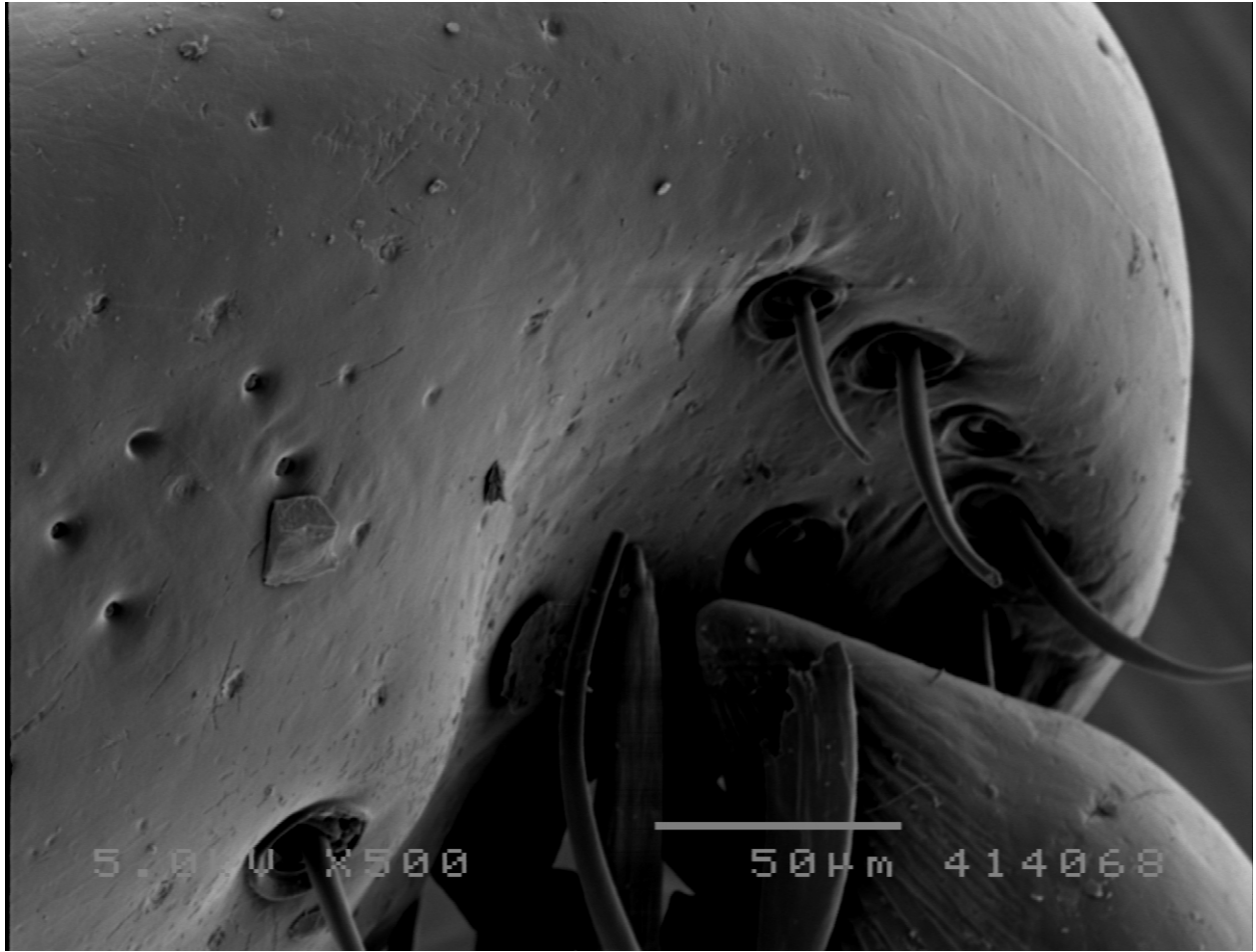
An attempt at using the organ as a systematic tool was attempted by a group, including myself, (Fet *et al.*, 2006b) for the vaejovid genera tentatively referred to as a tribe or subfamily (Fet *et al.*, in progress). *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis*. The orientation of setae and the constellation array's sensilla were diagnosed using landmark setae and chelal finger dentition, number of sensilla, sensillum diameter, distance from the most distal sensillum to the tip of the finger, and the distance between the sensillum centers (the two most proximal in the genus *Paravaejovis*). The data collected were very preliminary and limited to too few specimen and taxa, but some trends did arise, the most prevalent of these being the reduction of the number of sensilla in the genera examined as opposed to other, less closely related genera. The homology of sensilla between various groups also proved to be too complex to decipher given the amount of time and data available at the time of this work.



8 **Figure 3.2:** Constellation array of *Pseudochactas ovchinnikovi* (juvenile) showing four sensilla (Parvorder: Pseudochactidae).



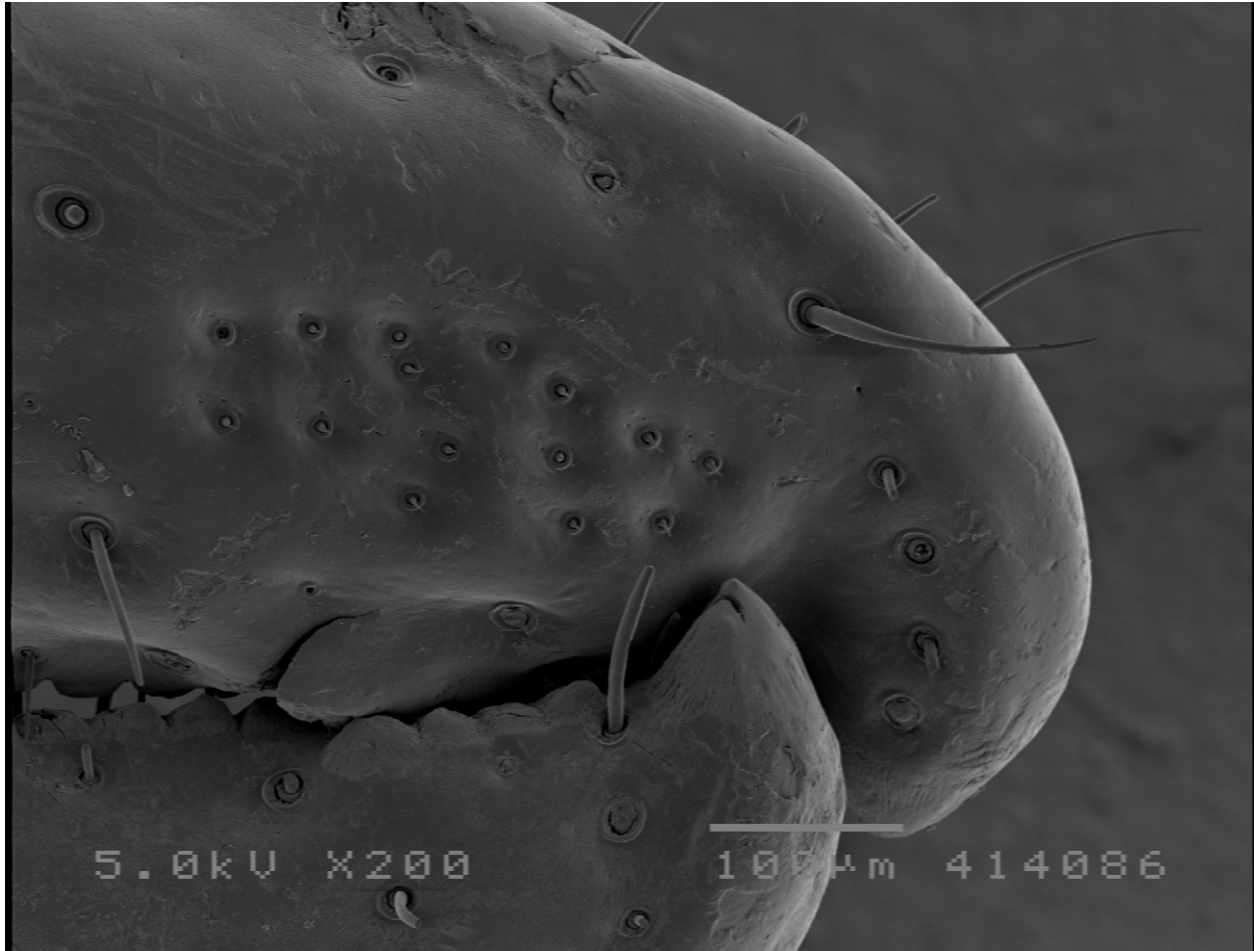
9 **Figure 3.3:** Constellation array of *Chaerilus celebensis* (juvenile) showing six elongated sensilla (Parvorder: Chaerilida).



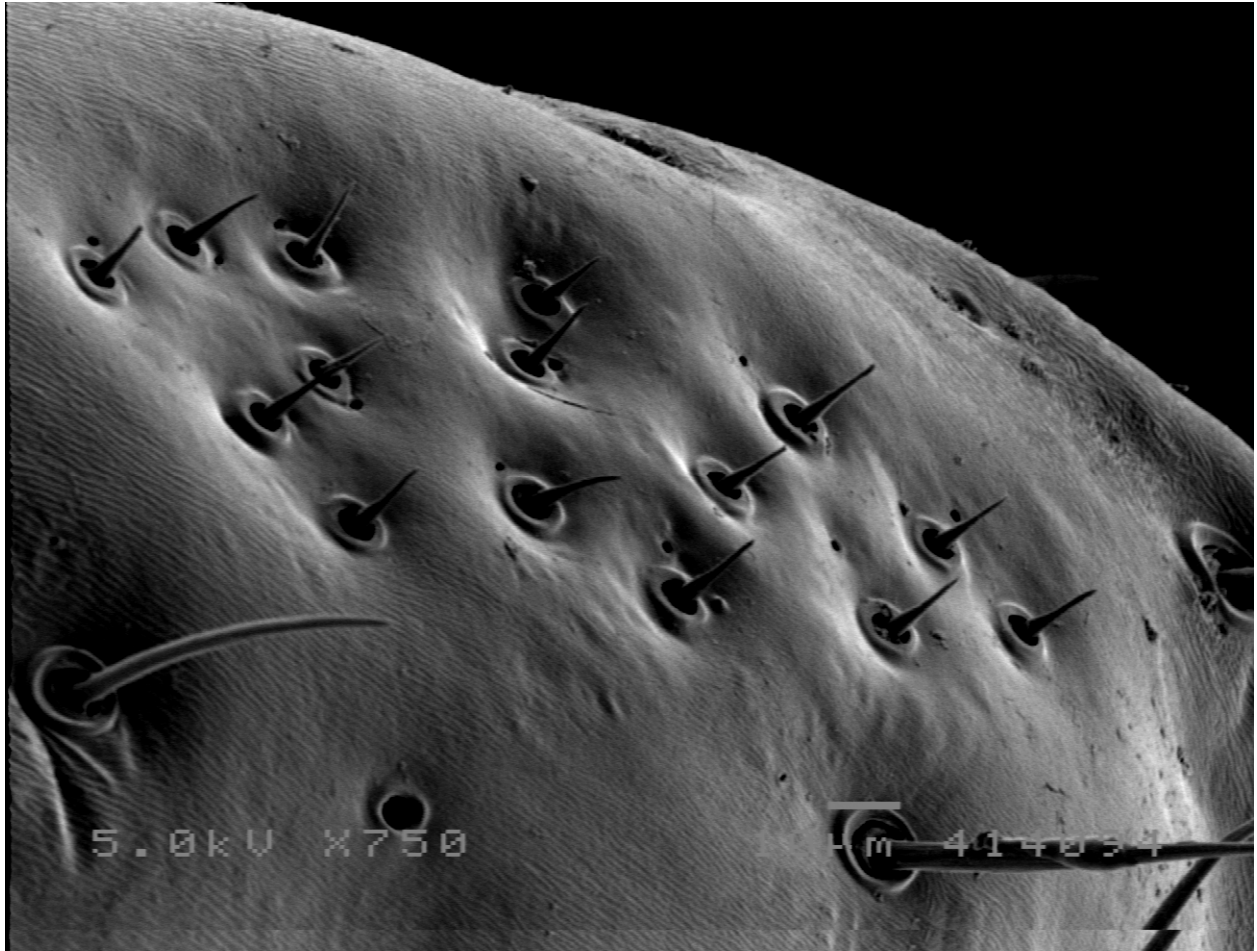
10 **Figure 3.4:** Constellation array of *Mesobuthus eupeus* showing five sensilla (Parvorder: Buthida).



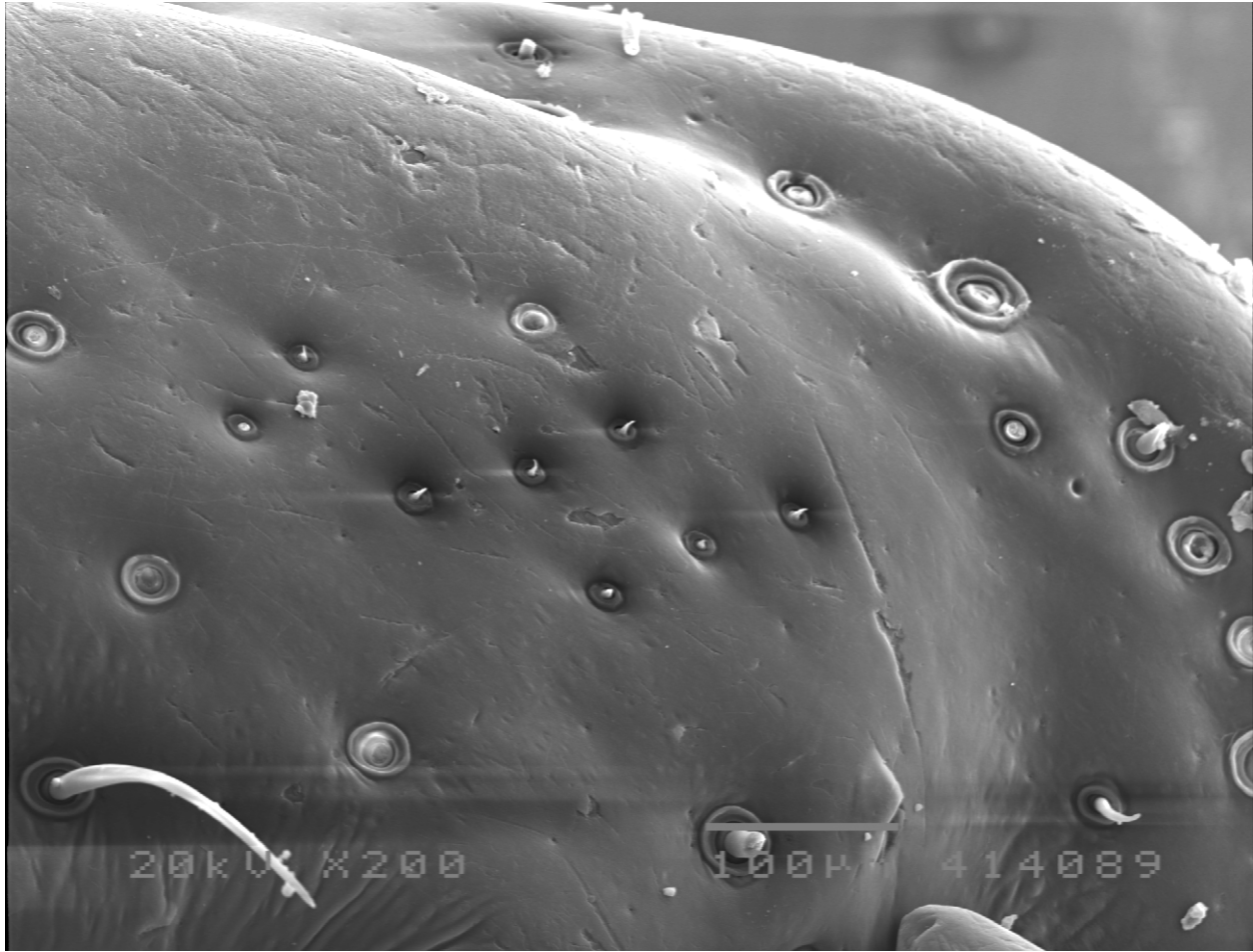
11 **Figure 3.5:** Constellation array of *Lychas mucronatus* showing ten sensilla (Parvorder: Buthida).



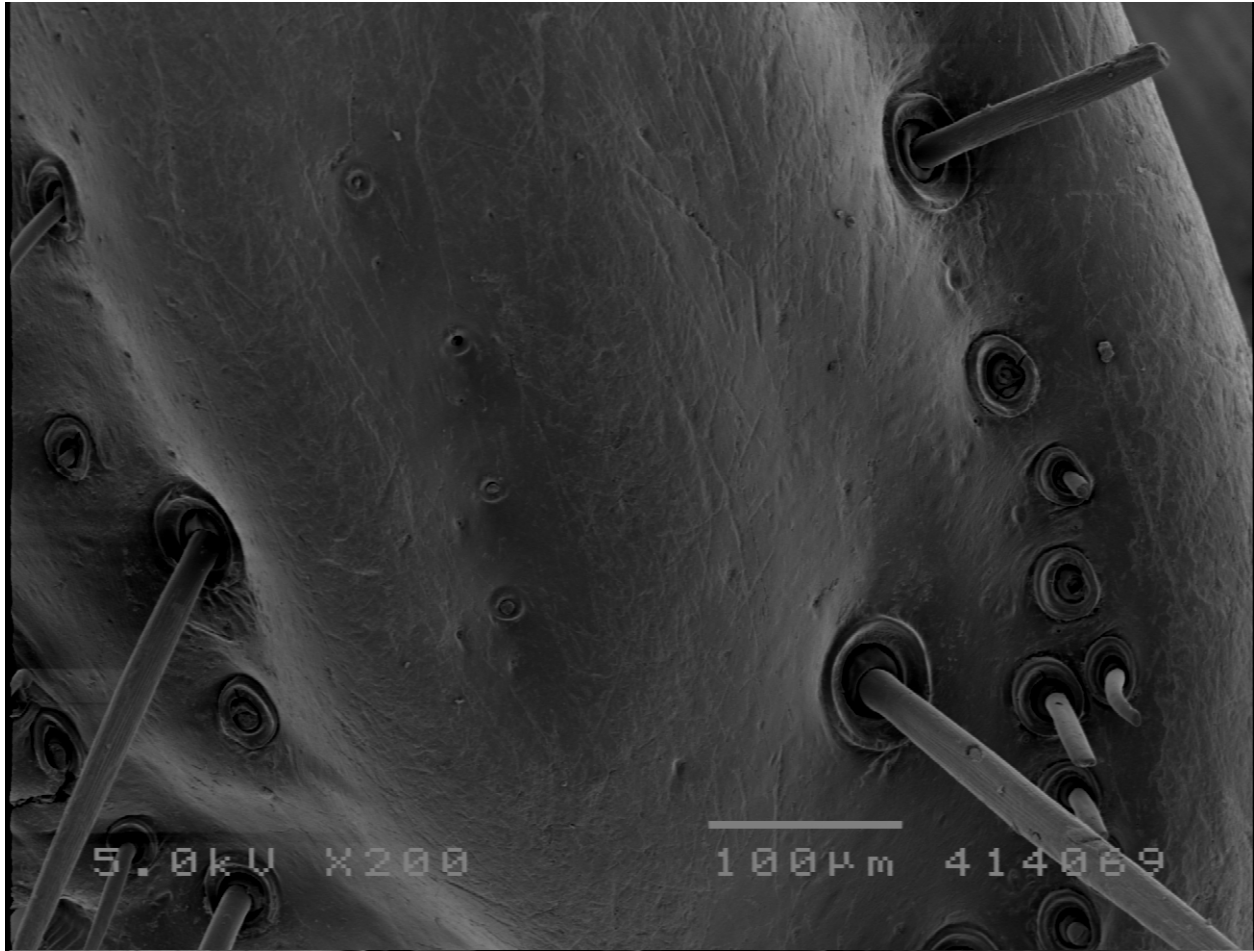
12 **Figure 3.6:** Constellation array of *Calchas nordmanni* (adult female) showing 15 sensilla (Parvorder: Iurida, Superfamily: Iuroidea).



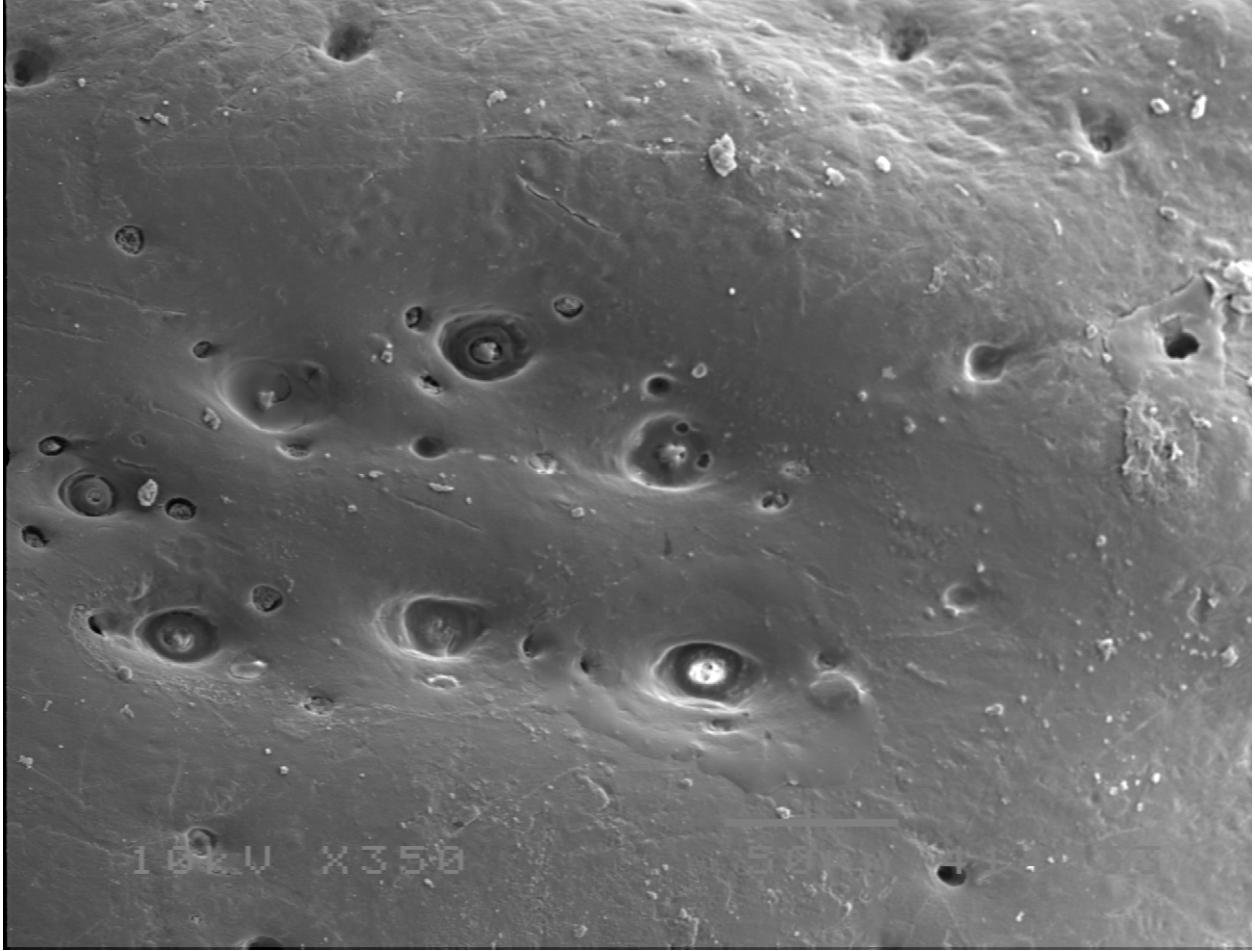
13 **Figure 3.7:** Constellation array of *Calchas nordmanni* (juvenile) showing 15 sensilla (Parvorder: Iurida, Superfamily: Iuroidea).



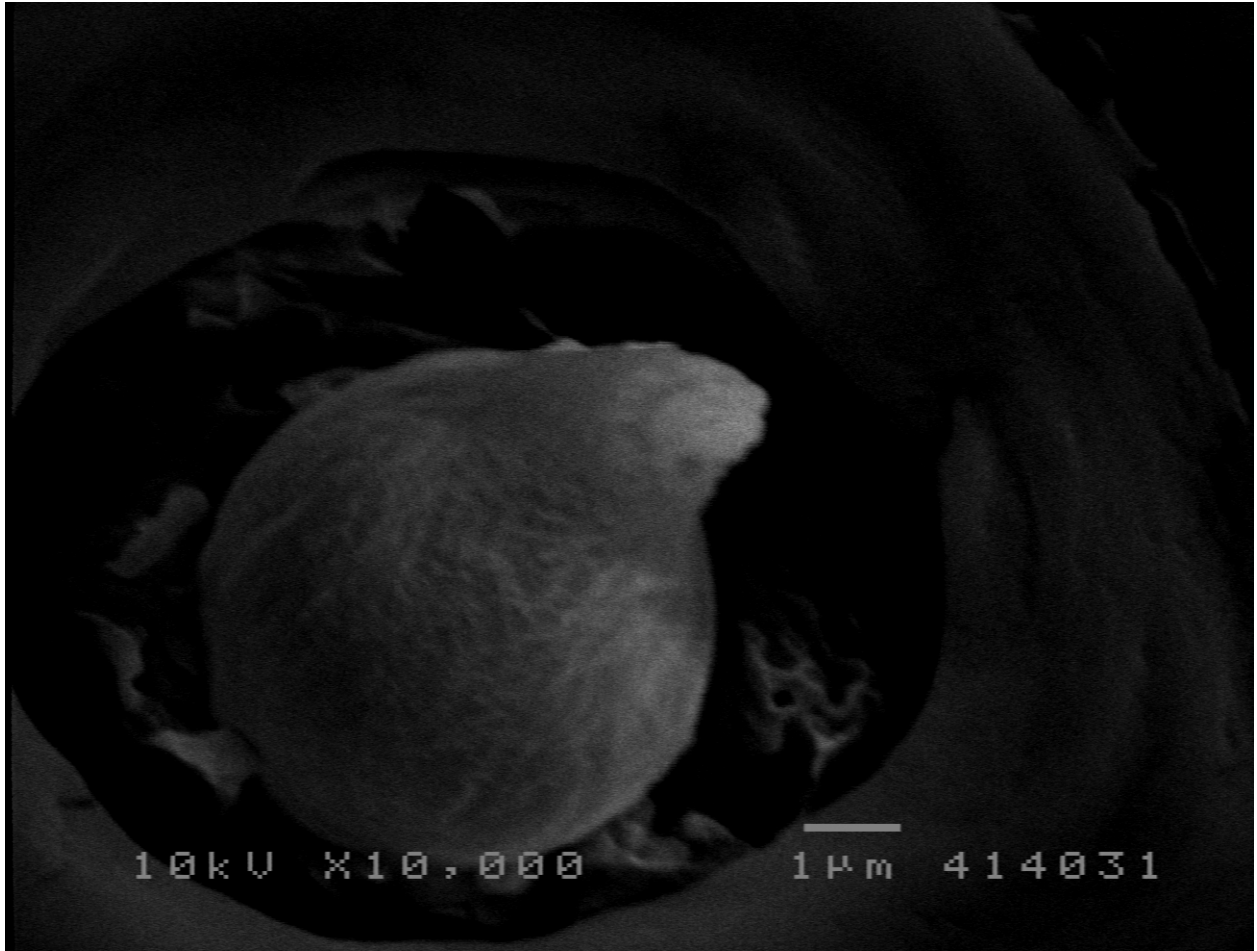
14 **Figure 3.8:** Constellation array of *Hadruroides charcasus* showing eight sensilla (Parvorder: lurida, Superfamily: luroidea).



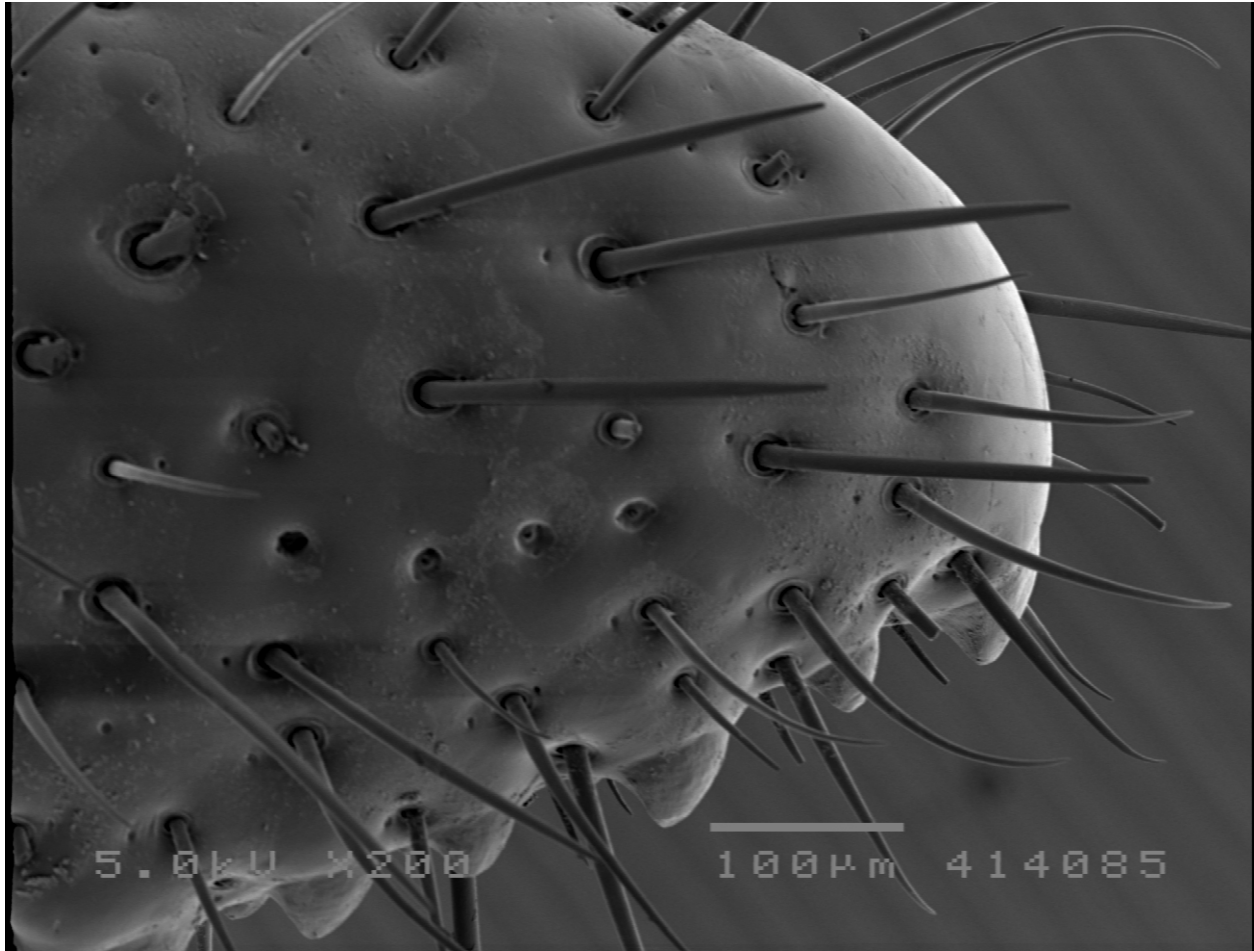
15 **Figure 3.9:** Constellation array of *Hadrurus obscurus* showing four sensilla (Parvorder: Iurida, Superfamily: Iuroidea, Family: Carboctonidae).



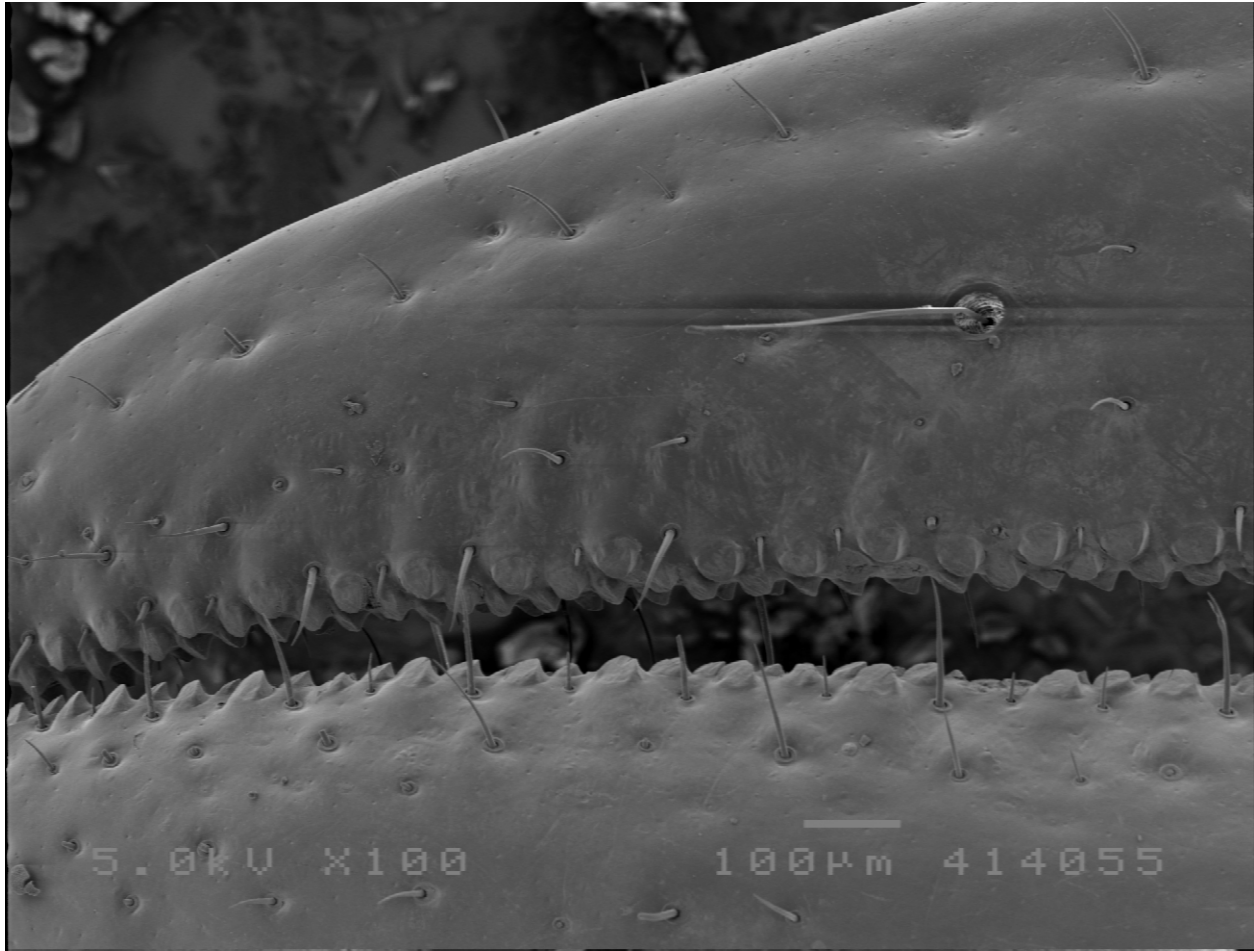
16 **Figure 3.10:** Constellation array of *Hadogenes bicolor* showing seven sensilla (Parvorder Iurida, Superfamily: Scorpionoidea, Family: Hemiscorpiidae).



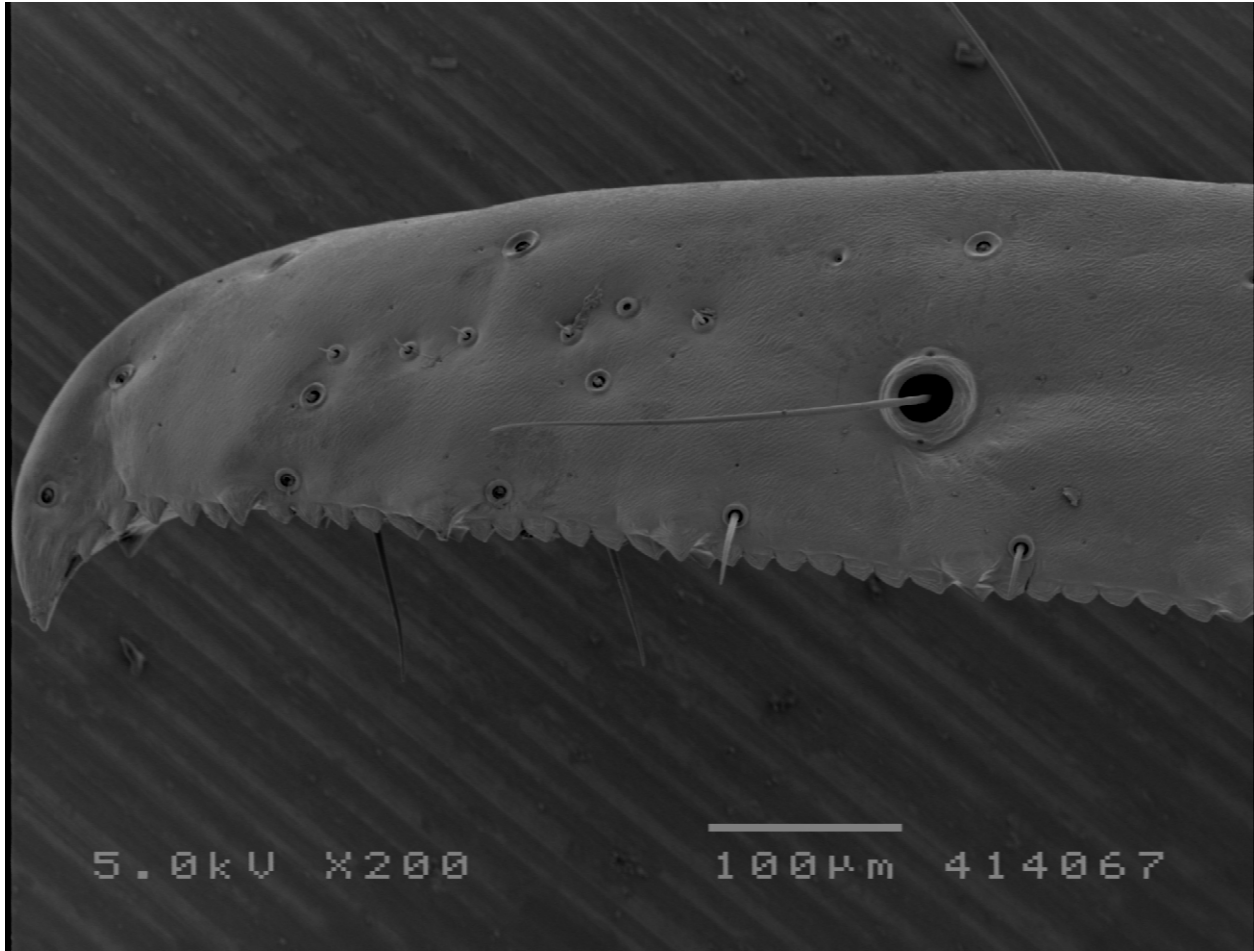
17 **Figure 3.11:** Close-up of a single sensillum of *Hadogenes bicolor*.



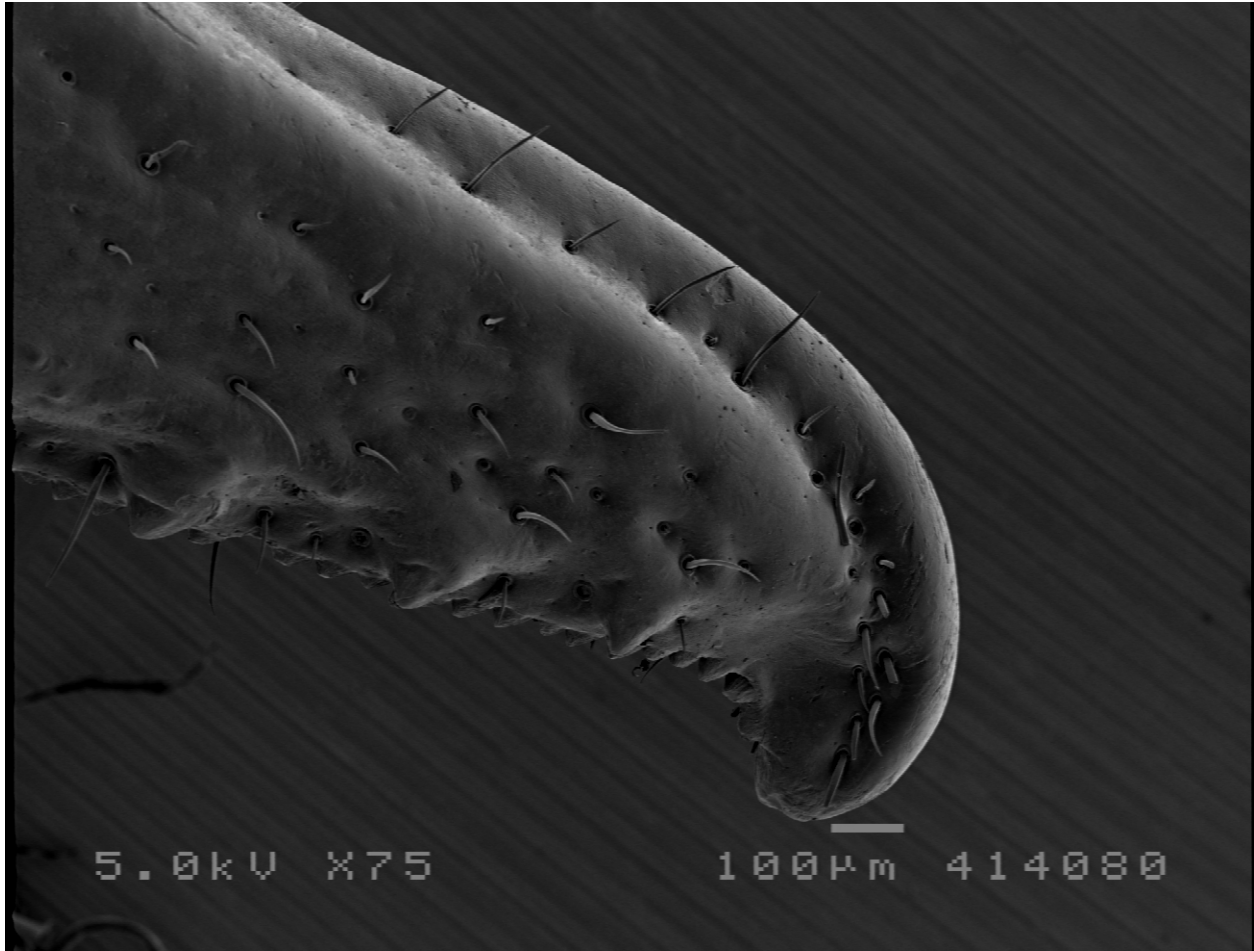
18 **Figure 3.12:** Constellation array of *Bioculus comondae* showing four sensilla.



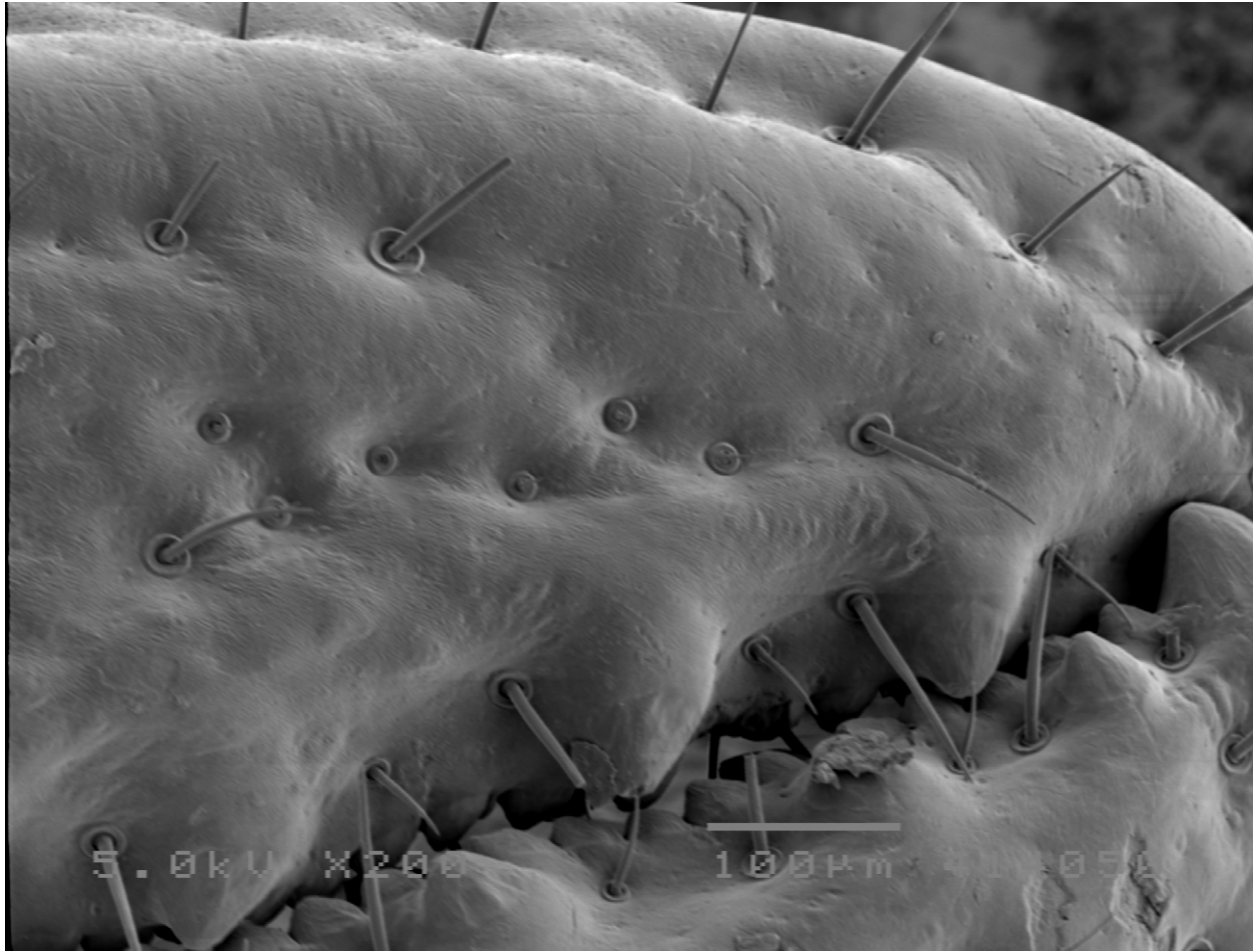
19 **Figure 3.13:** Constellation array of *Centromachetes pocockii* showing four sensilla (Parvorder: Iurida, Superfamily: Scorpionoidea, Family: Bothriuridae).



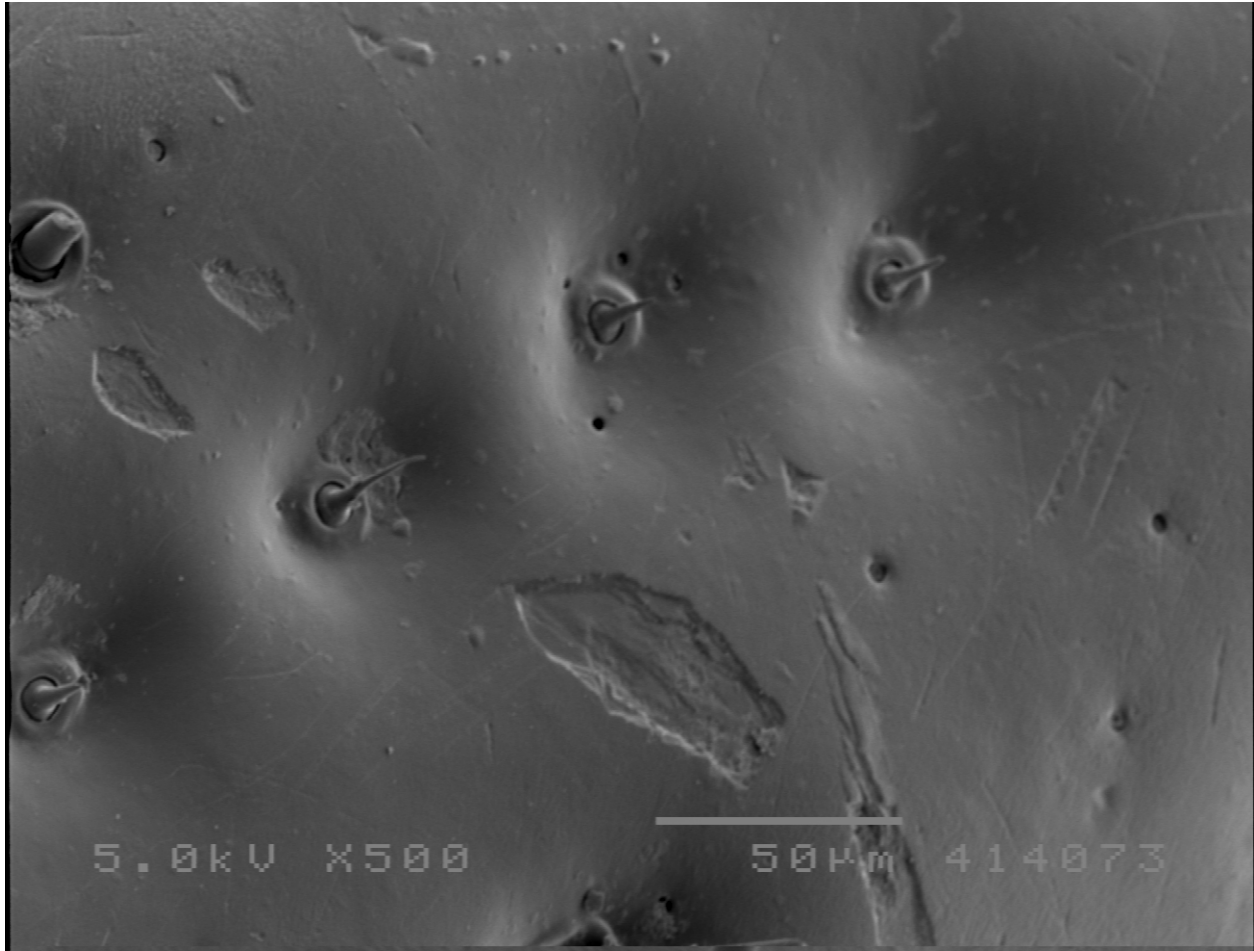
20 **Figure 3.14:** Constellation array of *Euscorpis tergestinus* (juvenile) showing six sensilla (Parvorder Iurida, Superfamily: Chactoidea, Family: Euscorpiidae).



21 **Figure 3.15:** Constellation array of *Euscorpius italicus* showing five sensilla (Parvorder Iurida, Superfamily: Chactoidea, Family: Euscorpiidae).



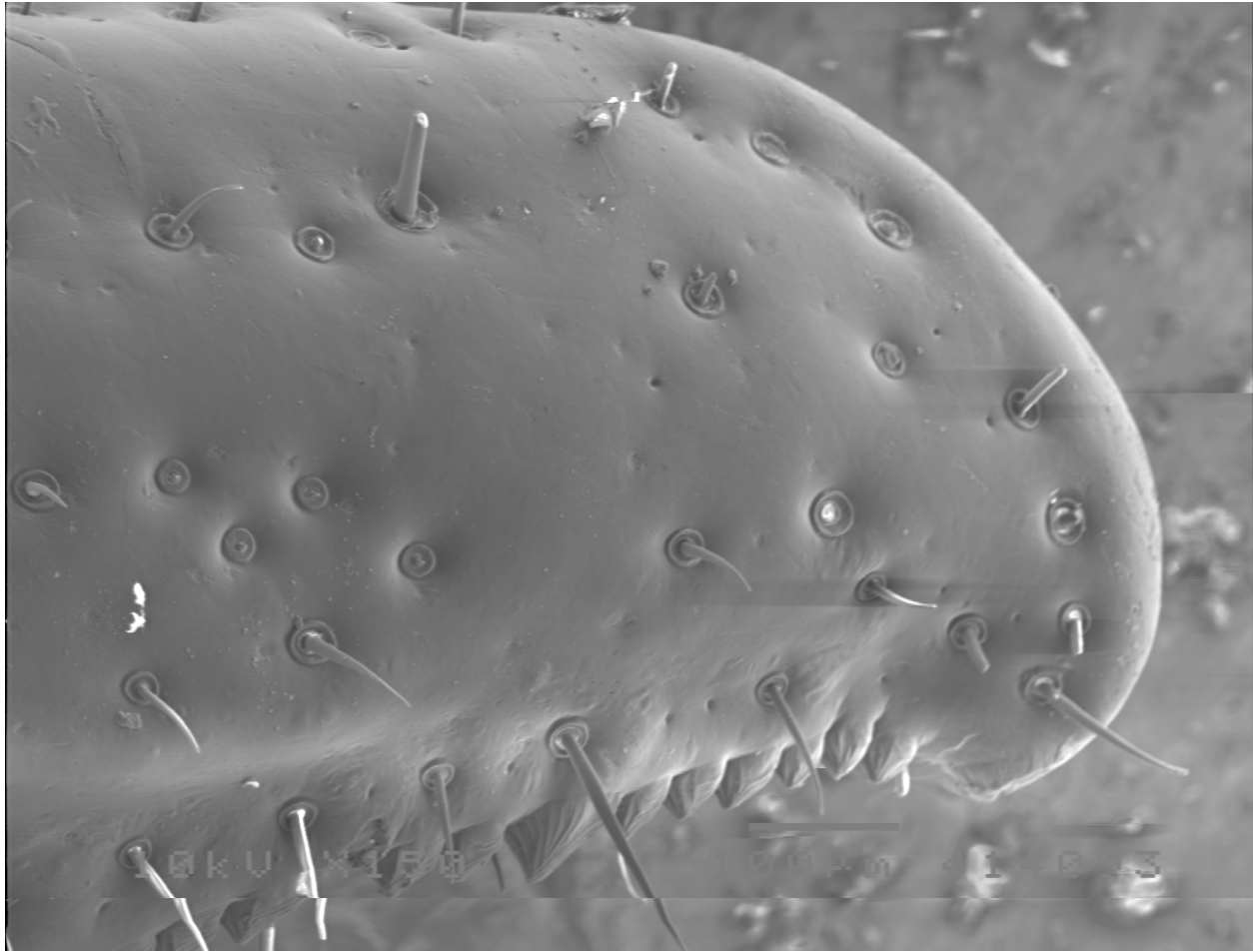
22 **Figure 3.16:** Constellation array of *Euscorpius gamma* showing six sensillum (Parvorder Iurida, Superfamily: Chactoidea, Family: Euscorpiidae).



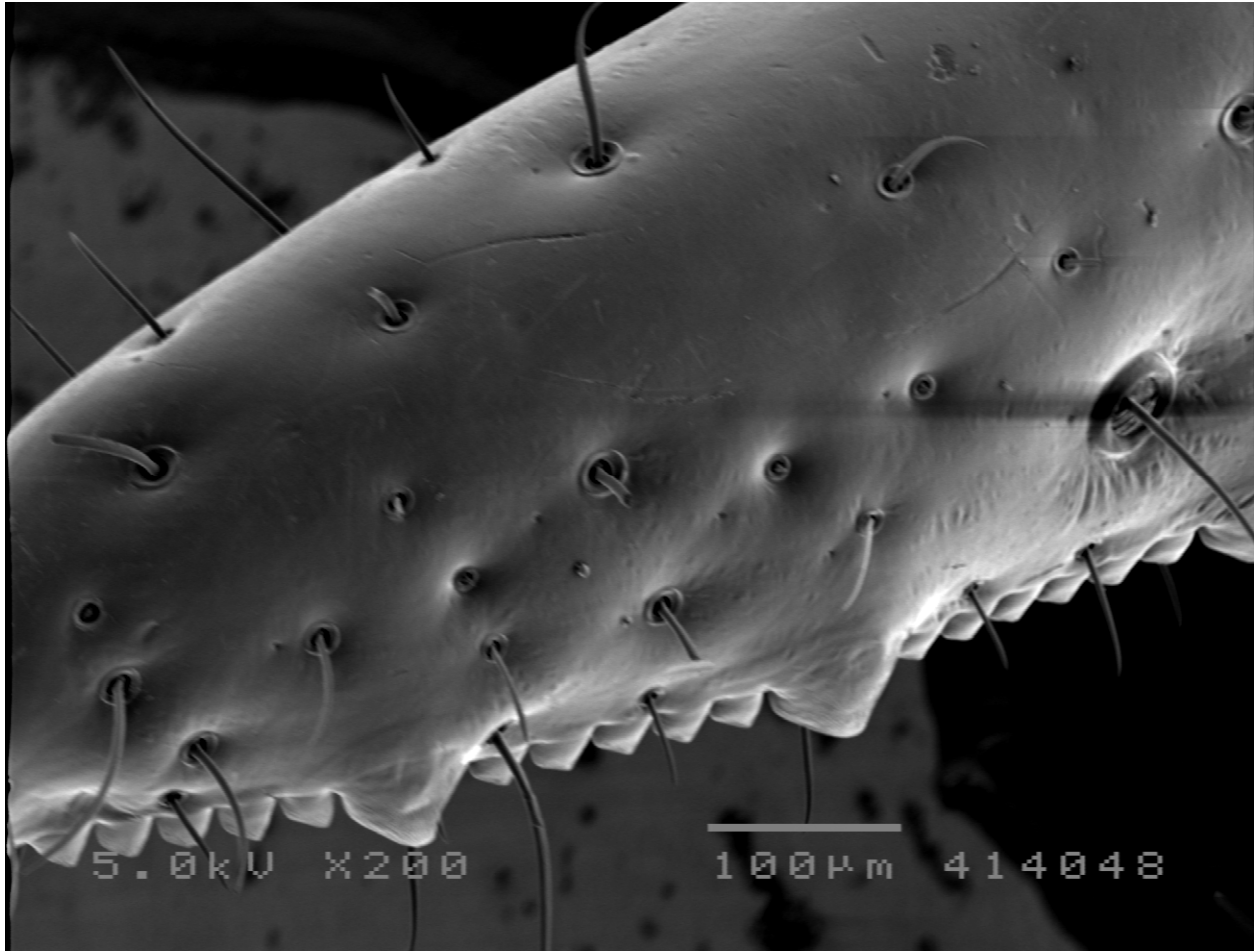
23 **Figure 3.17:** Constellation array of *Belisarius xambeui* showing four sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family: Chactidae).



24 **Figure 3.18:** Constellation array of *Nullibrotheas allenii* showing two sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family Chactidae).



25 **Figure 3.19:** Constellation array of *Uroctonus mordax* showing four sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family: Chactidae).



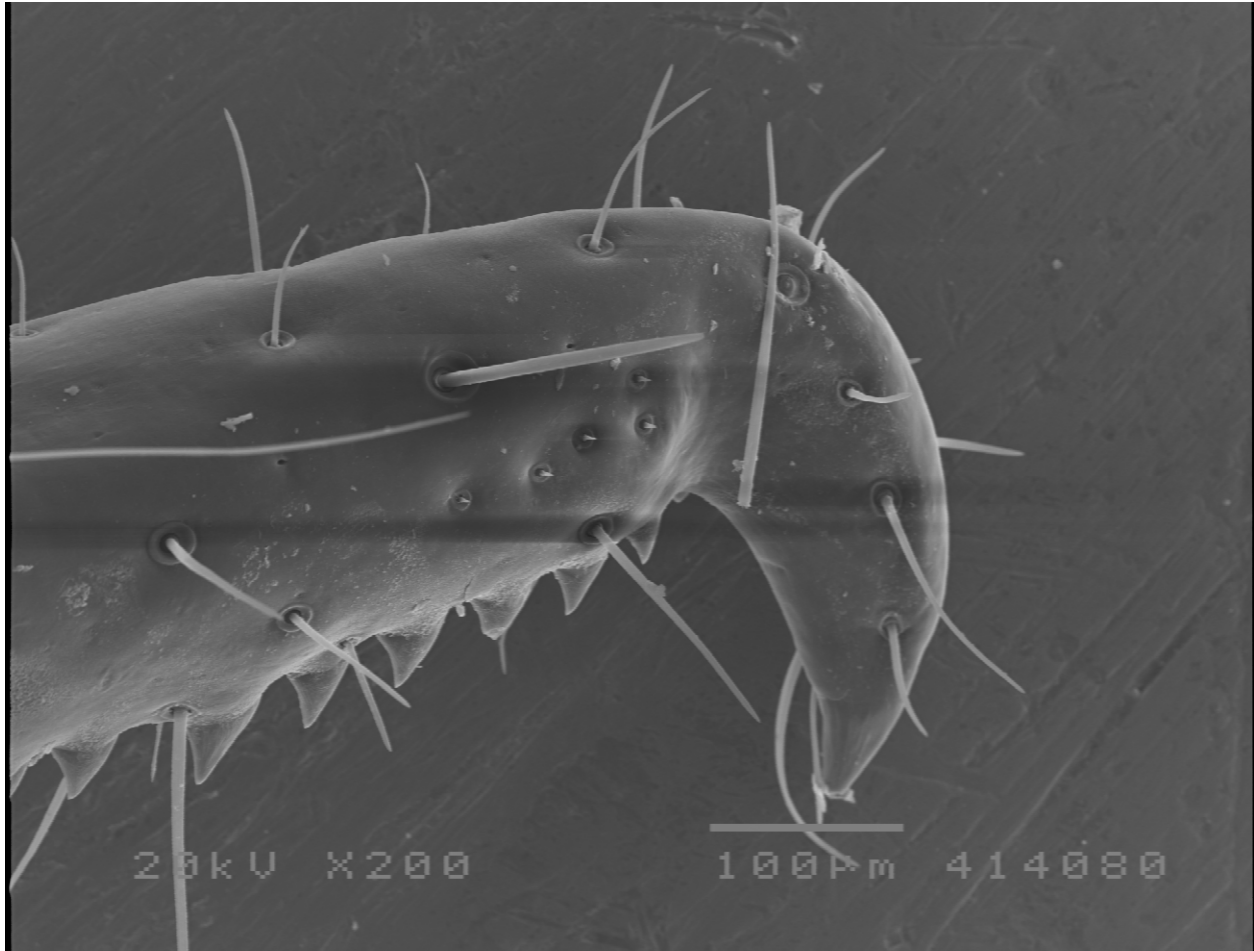
26 **Figure 3.20:** Constellation array of *Superstitionia domensis* showing four sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family: Superstitioniidae).



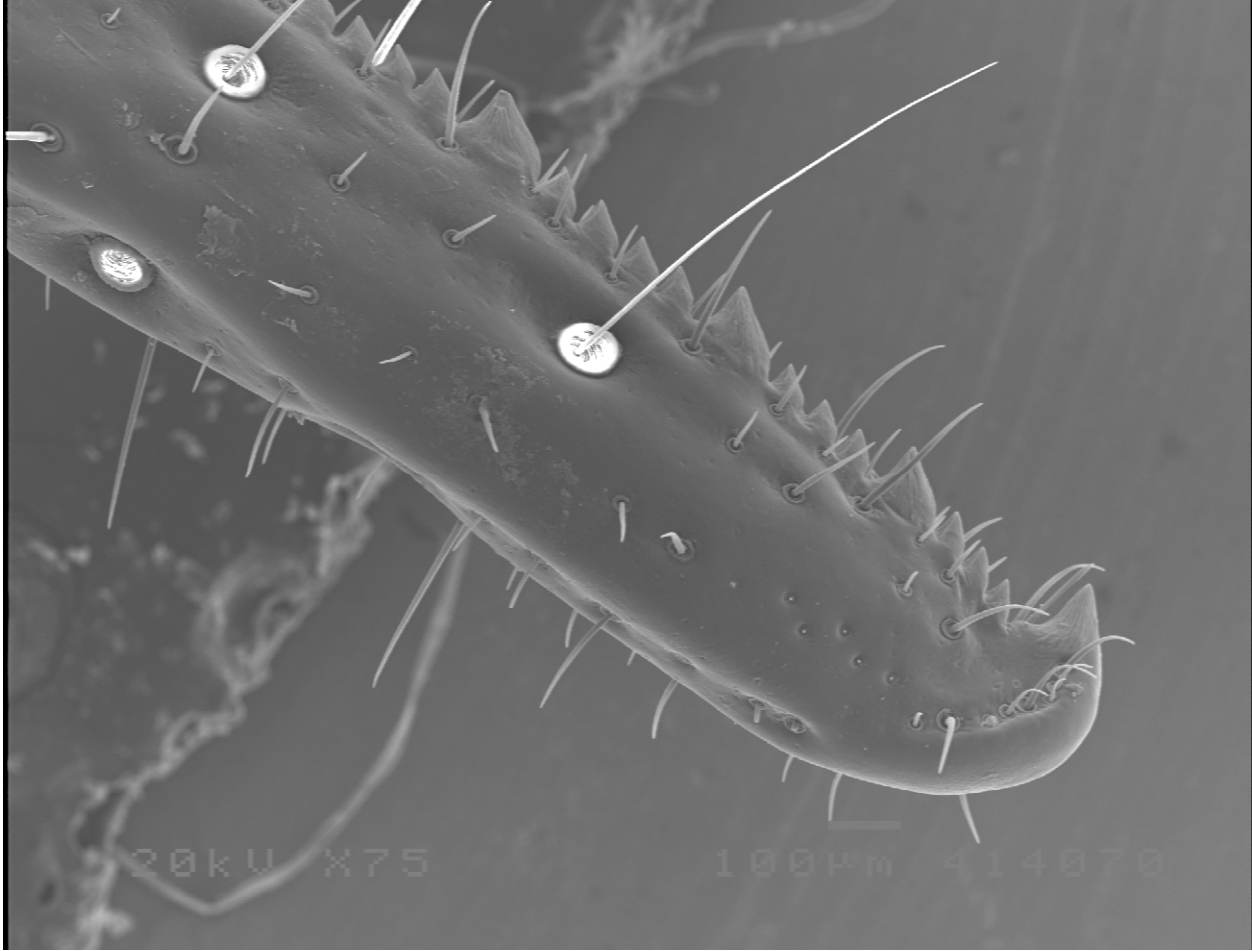
27 **Figure 3.21:** Constellation array of *Smeringurus mesaensis* showing two sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family Vaejovidae).



28 **Figure 3.22:** Constellation array of *Vejovoidus longiunguis* showing one sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family Vaejovidae).



29 **Figure 3.23:** Constellation array of *Serradigitus joshuaensis* showing five sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family Vaejovidae).



30 **Figure 3.24:** Constellation array of *Vaejovis eusthenura* showing five sensilla (Parvorder: Iurida, Superfamily: Chactoidea, Family Vaejovidae) (Position is inverted from convention).

Chapter IV: Laterobasal Aculear Serrations

Introduction

The aculeus (“stinger”) of scorpions has always been of great interest to biologists as well as a curious site to anyone who as ever given it a glance. Better known as the “stinger”, the aculeus is located posteriorly to the vesicle, where the toxin glands are housed. It is the device that delivers the toxin to prey or enemies of the scorpion. Many studies have concentrated on the area and various discoveries have resulted. The studies of toxic gland anatomy (Pavlovsky, 1913) and male glands in *Hadrurus* and *Hoffmannihadrurus* (Williams, 1970) have been non-systematic in nature but yielded other important information. The use of the aculeus as a systematic character has been outlined by Sissom (1990) to include characters such as granulation, carination, coloration, setation patterns, size and shape of the telson, vesicle/aculeus ratio, and aculeus curve. Sexual dimorphism exists in telson anatomy as male members Euscorpidae and Hemiscorpioninae (Scorpionoidea) have enlarged vesicles. Now a new and minute structure has been identified, the Laterobasal Aculear Serrations (LAS) in the family Vaejovidae.

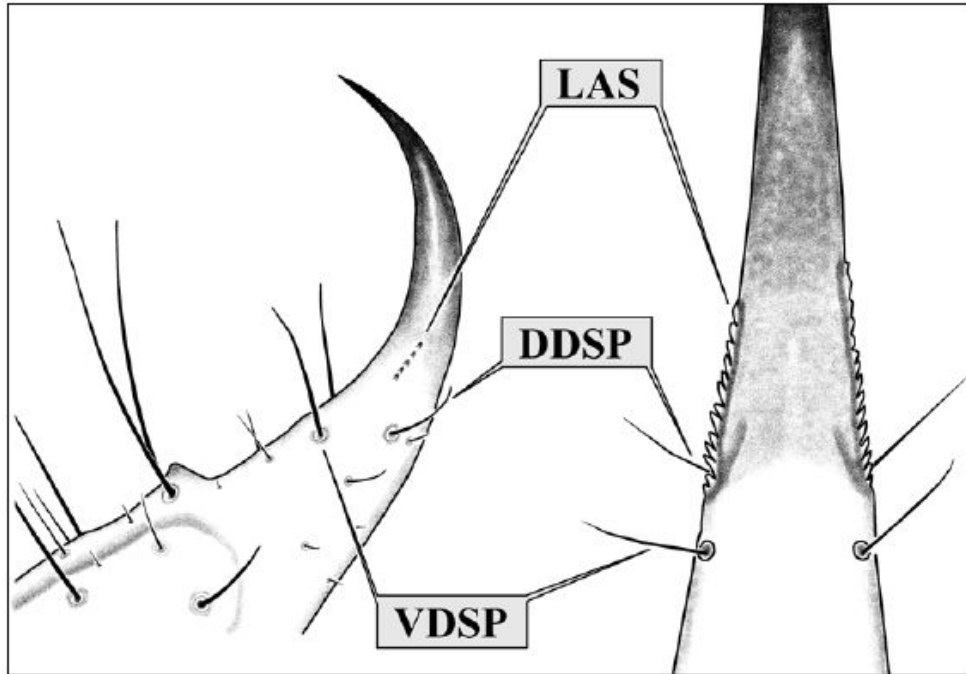
Materials and Methods

We examined eighty species representing all genera in the family Vaejovidae, including all groups in *Vaejovis*, with several multiples of species within a genus and of specimens within a species. Using SEM and a dissecting microscope, we described and compared the structure both within and between various taxonomic levels within the family and documented the absence of LAS in all other families. The material examined is outlined in Appendix B. Images were taken using the procedure for SEM use outlined

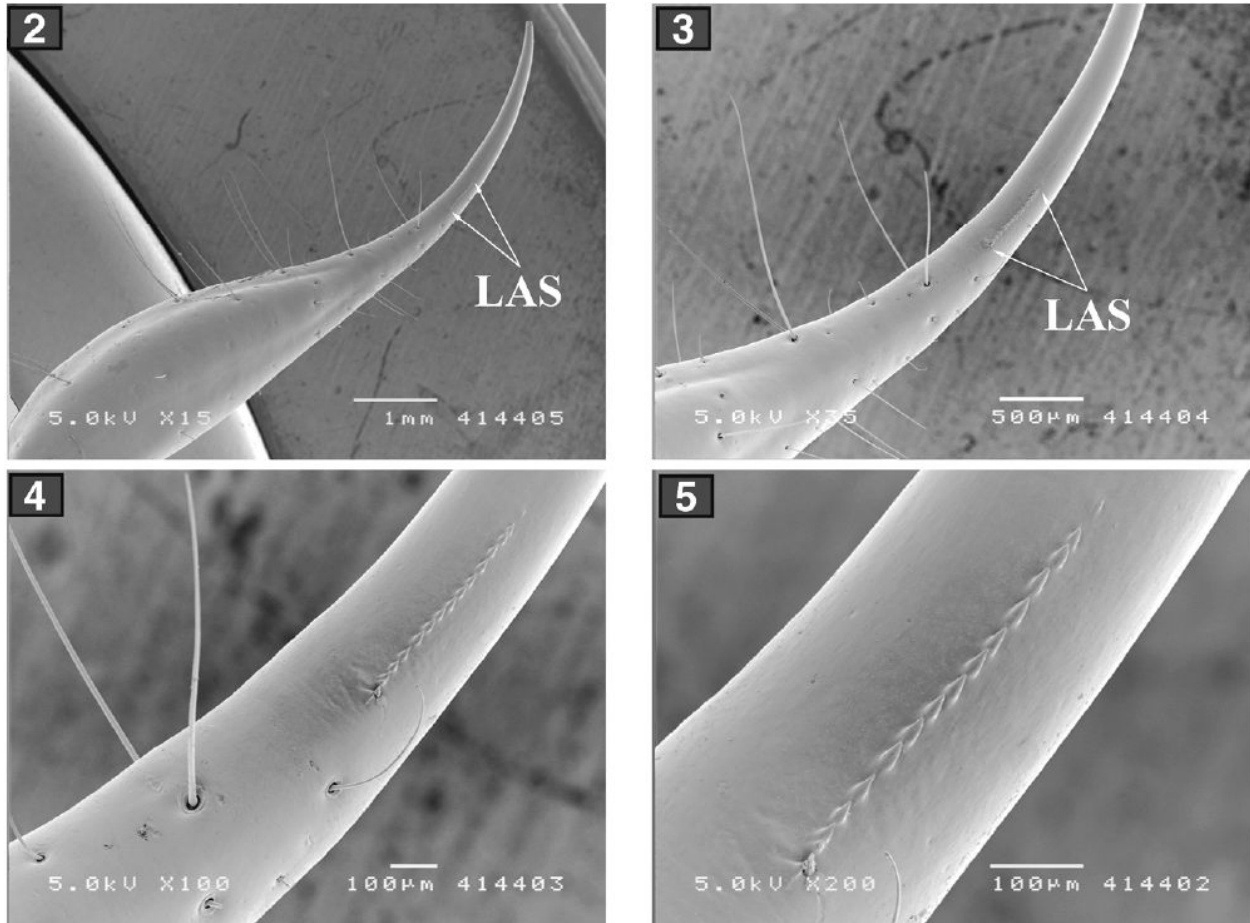
previously using the telson, occasionally with the fifth segment of the metasoma still attached. Lateral and ventral views were preferred to others to optimize views of the rows. Much of the data used in the statistical analysis presented were obtained using a dissecting microscope because the pigmentation of the LAS and its size make observation at 40 – 60X magnification possible. Landmark setae were chosen that proved to be consistent between taxa to provide points of reference. These landmarks were designated as the ventral distal setal pair (VDSP) and the dorsal distal setal pair (DDSP) (Figure 3.1).

Results and Discussion

The LAS is made up of two rows of symmetrically located denticles on the lateral sides of the telson. The rows are found on the basal portion of the aculeus where the telson starts narrowing and fading to a darker color just distal to the VDSP and DDSP and an area of wrinkling in the cuticle. In terms of number and strict position, they are not symmetrical, but instead vary greatly between individuals and even on a single individual between the left and right sides, an example of fluctuating asymmetry. The denticles are situated in a row that extends posteriorly along the telson in the same direction as the aculeus. The denticles are quite small themselves ranging from 17 μm to 37 μm in length and are angled toward the tip of the aculeus. The longest single row was found in *Vejooides longiunguis* (Figures 4.2 -4.5); its row of 14 denticles was still less than 0.5 mm in length.



31 **Figure 4.1:** Location and position of the LAS in relation to the ventral distal setal pair (VDSP) and dorsal distal setal pair (DDSP) and telson anatomy (adapted from Fet *et al.* 2006c).



32 **Figures 4.2 – 4.5:** LAS in lateral views of *Vejovoidus longiunguis* (female, Viscaïno Desert, Baja California, Mexico) showing the position of the denticles at various, descending magnifications (adapted from Fet *et al.*, 2006c).

The orientation of the rows varies greatly. Some rows are densely arranged, while others are quite spread out. In some cases, the spacing gradually changes from dense at the base to more spread out on the distal portion of the row. Some cases of very irregular doubling of denticles were documented in *Paruroctonus ventosus*. The exact location of the LAS is dependent on the area of narrowing and darkening, but this is not necessarily the same position in every taxon, especially those with elongated aculei in which the LAS tend to be more distal near the middle of the aculeus. Those with a highly curved aculeus tend to have their LAS nearer to the distal tip of the telson.

The structure is present on males, females, and juveniles, including instar-2, in taxa that express the trait. Our data does not indicate that the number of denticles changes as the animal matures. In *Smeringurus mesaensis*, denticle numbers as high as ten were found in both adults and instar-2 juveniles. The structure appears to be more conspicuous in juveniles and sometimes is less visible in adults of the same species. Trends in denticle number are difficult to detect as the number between species and even individuals tends to vary considerably (Table 3.1). Also, many individuals exhibit asymmetry between the number and position of denticles on each side of the telson. The number asymmetry has been recorded with variation as high as five denticles in *Vaejovis viscainensis* (7/12). The large standard deviations and high coefficients of variability further demonstrate the variable nature of the structure in many taxa. Males tend to express higher numbers of denticles (14.6% to 35.0% higher) than females of the same species (Table 4.2).

The largest number of denticles observed in a single specimen was in *Vejovoidus longiunguis*, which had numbers of 19/21, but the species averaged only 11.833 denticles per row. The number of denticles does not appear to be determined by the size of the animal as relatively high numbers have been found in smaller taxa such as *Paruroctonus surensis* (11/10 and 8/12) and *P. ventosus* (14/10). Some small species do exhibit smaller numbers of denticles such as *Pseudouroctonus andreas* with an average of 3.643.

When attempting to use the LAS as a systematic character, the trends in variation do little to distinguish taxa at levels lower than the family level. Single species of many genera of all other families of scorpions were surveyed, excluding family Superstitioniidae, and none had the LAS (Table 3.3). The structure appears to be a strict synapomorphy of the North American family Vaejovidae that has been lost several times in unrelated taxa within the family, but some of those lacking the structure are thought to be closely related and share many taxonomically important characters, such as the *Vaejovis* “*mexicanus*” and “*nigrescens*” groups. This homoplasy leads one to

believe that the structure is of little use at the species level, but some trends at the generic level can be seen within and between the genera in many well-supported groups. Some vaejovids appear to lack the LAS, but, in some cases, the number of individuals examined was too low to make a definitive conclusion. For example, *Paruroctonus hirsutipes* was the only member of its genus found to lack the structure, but we only examined one specimen due to a lack of material. Before a final conclusion regarding the designation of the LAS as a synapomorphy of the family is made, more specimens must be examined. The *Vaejovis* “nigrescens” and “mexicanus” groups and the genera *Pseudouroctonus* and *Uroctonites* are the taxa that require further examination. The statistics and evidence prove that the structure does not appear randomly, but is variable in number throughout the family.

Other members of the superfamily Chactoidea bear other distinctive structures in the same area as the LAS in Vaejovids. The genera *Troglocormus*, *Euscorpiops*, and *Alloscorpiops* (Euscorpiidae) all share an “annular ring” that is found on both males and females (Soleglad and Sissom, 2001, p. 67, figs. 189-191). In addition, *Anuroctonus* (Chactidae) has an enlarged “bulb” in males (Soleglad and Fet, 2004, fig 20). This bulb and the LAS are hypothesized to have similar functions. They could be designed to stop the aculeus from entering the target of the sting too far (a “sting-stopper”) thus impairing the scorpions ability to defend itself or allowing the aculeus to be broken off. The denticles are not socketed, appear uninnervated, but appear to be strategically placed. Transmission Electron Microscopy (TEM) analysis needs to be done to determine whether or not the structure is innervated. If innervated, perhaps the LAS is a stretch or pressure receptor that relays information on the amount of stress on the aculeus while the scorpion stinging. There is definitely not much selection against it as it appears in so many groups and is rarely lost in the family Vaejovidae.

2 Table 4.1: Complete statistical analysis of LAS numbers for all 80 vaejovoid species examined. From a ventral view denticle numbers are represented as right/ left. * Indicates a large sample size which underwent statistical analysis. Statistical grouping = min/max (mean) [number of samples N]. (S) indicates results were verified by SEM (adapted from Fet *et al.* 2006c).

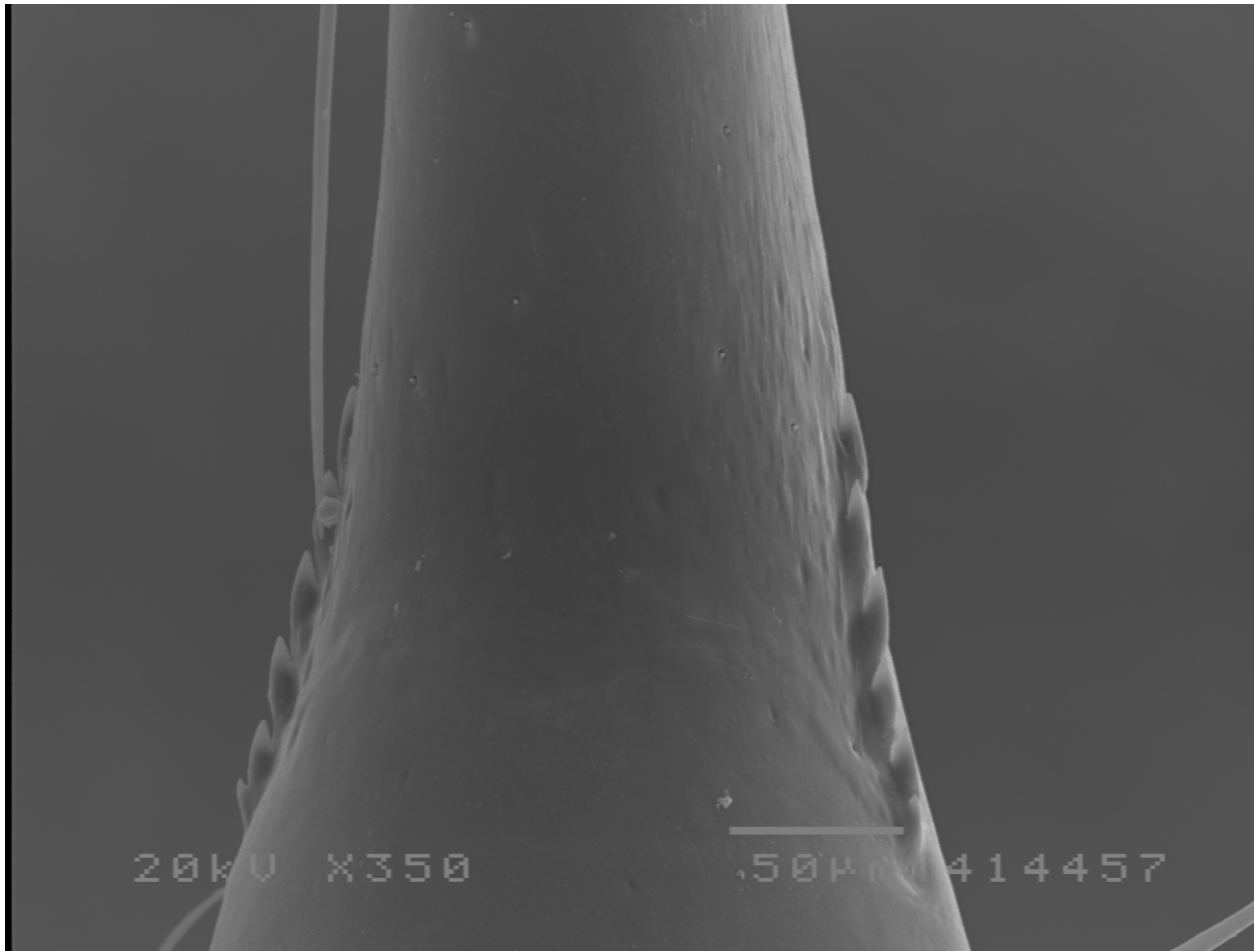
Vaejovidae Species	LAS: Right/Left	Vaejovidae Species	LAS: Right/Left
<i>Vejovoidus, Smeringurus, Paruroctonus, Paravaejovis</i>		<i>Vaejovis</i> “eusthenura” group and <i>Syntropis</i>	
<i>Vejovoidus longiunguis</i> * (S)	9–21 (11.833) [24]	<i>Vaejovis coahuilae</i>	4/6
<i>Smeringurus aridus</i> (S)	traces of 2	<i>V. confusus</i> (S)	9/7
<i>S. grandis</i>	1/1, 2/2, 3/3, 3/3	<i>V. diazi</i> (S)	6/5, 7/6, x_6
<i>S. mesaensis</i> * (S)	4–10 (7.406) [32]	<i>V. eusthenura</i> (S)	8/7, 5/6
<i>S. v. immanis</i>	4/x	<i>V. globosus</i> (S)	6/4, 2/3
<i>Paruroctonus arnaudi</i> (S)	9/11, 12/11, 13/12	<i>V. gravicaudus</i> (S)	8/9, 3/4
<i>P. arenicola nupides</i>	6/6	<i>V. hoffmanni</i>	6/5, 6/7, 4/7
<i>P. bantai saratoga</i>	2/2, 3/3	<i>V. punctatus</i> * (S)	2–8 (4.727) [33]
<i>P. becki</i> (S)	5/5, 8/8	<i>V. puritanus</i> * (S)	3–12 (7.714) [28]
<i>P. boreus</i> (S)	4/4, 7/x	<i>V. spinigerus</i> (S)	4/x, 5/3, 7/5, x/3
<i>P. borregoensis</i>	7/8	<i>V. viscaimensis</i> * (S)	6–15 (9.385) [26]
<i>P. gracilior</i> * (S)	4–9 (6.240) [25]	<i>V. vittatus</i> (S)	7/x
<i>P. hirsutipes</i>	ABSENT	<i>V. waeringi</i> (S)	6/11, 5/7
<i>P. luteolus</i> (S)	7/6, 6/7	<i>Syntropis macrura</i>	5/6, 10/8, 6/7, 3/3
<i>P. silvestrii</i> * (S)	1–10 (6.643) [28]	<i>Franckeus</i> and <i>Vaejovis</i> “nigrescens” group	
<i>P. stahnkei</i>	6/7	<i>Franckeus minckley</i>	9/8, 7/5, 6/5
<i>P. surensis</i> (S)	9/8, 11/10, 8/12	<i>F. pennisularis</i>	8/7, 3/4, 5/6, 3/3
<i>P. ventosus</i> (S)	14/10, 10/11	<i>Vaejovis davidi</i>	ABSENT
<i>P. utahensis</i> (S)	5/6, 3/4	<i>V. decipiens</i>	ABSENT
<i>P. xanthus</i>	1/1	<i>V. janssi</i>	x/2, 3/5, 5/4, 7/6, 7/9, 2/4
<i>Paravaejovis pumilis</i> * (S)	1–7 (4.306) [36]	<i>V. nigrescens</i>	traces of 2
<i>Stahnkeus</i> and <i>Serradigitus</i>		<i>V. pococki</i>	ABSENT
<i>Stahnkeus deserticola</i>	4/x	<i>V. solegladi</i>	ABSENT
<i>S. harbisoni</i>	2/5	<i>Vaejovis</i> “mexicanus” group	
<i>S. subtilimanus</i>	1/1, 4/3	<i>Vaejovis carolinianus</i>	2/x
<i>Serradigitus adcocki</i>	2/1	<i>V. granulatus</i> (S)	3/2
<i>S. baueri</i>	5/6	<i>V. jonesi</i>	5/5, 4/5
<i>S. calidus</i>	5/4	<i>V. lapidicola</i>	3/3
<i>S. gertschi</i> (S)	7/6, 10/11	<i>V. mexicanus</i>	ABSENT
<i>S. joshuaensis</i> * (S)	3–8 (5.409) [22]	<i>V. paysonensis</i>	7/5, 8/7, 4/5
<i>S. littoralis</i> (S)	3/3, 4/4	<i>V. vorhiesi</i> *	1–7 (5.000) [14]
<i>S. minutis</i>	6/7	<i>Pseudouroctonus</i> and <i>Uroctonites</i>	
<i>S. torridus</i>	4/4, 5/5	<i>Pseudouroctonus andreas</i> * (S)	2–5 (3.643) [14]
<i>S. wupatkiensis</i>	5/5	<i>P. angelenus</i>	2/x
<i>Vaejovis</i> “punctipalpi” group		<i>P. apacheanus</i> (S)	ABSENT
<i>V. bruneus</i>	6/7	<i>P. iviei</i>	ABSENT
<i>V. cazieri</i> (S)	4/4, 4/5	<i>P. minimus castaneus</i>	traces x/3
<i>V. hirsuticauda</i> (S)	7/9, 8/x	<i>P. minimus thompsoni</i>	3/2, 4/3, 3/3
<i>V. intrepidus</i>	4/7, 4/5	<i>P. reddelli</i>	3/x
<i>V. magdalenensis</i> * (S)	4–8 (5.357) [14]	<i>Uroctonites guiliani</i>	ABSENT
<i>V. occidentalis</i>	ABSENT	<i>U. huachuca</i> (S)	ABSENT
<i>V. punctipalpi</i>	4/5	<i>U. monterus</i>	ABSENT
<i>V. russelli</i>	8/10		

3 Table 4.2: Statistical data for males and females of 12 representative vaejovid species from major genera. Statistical grouping = minimum-maximum (mean) (\pm standard deviation) [Number of specimen examined] {mean-SDEV – mean+SDEV} \rightarrow coefficient of variability or SDEV/mean (adapted from Fet *et al.* 2006c).

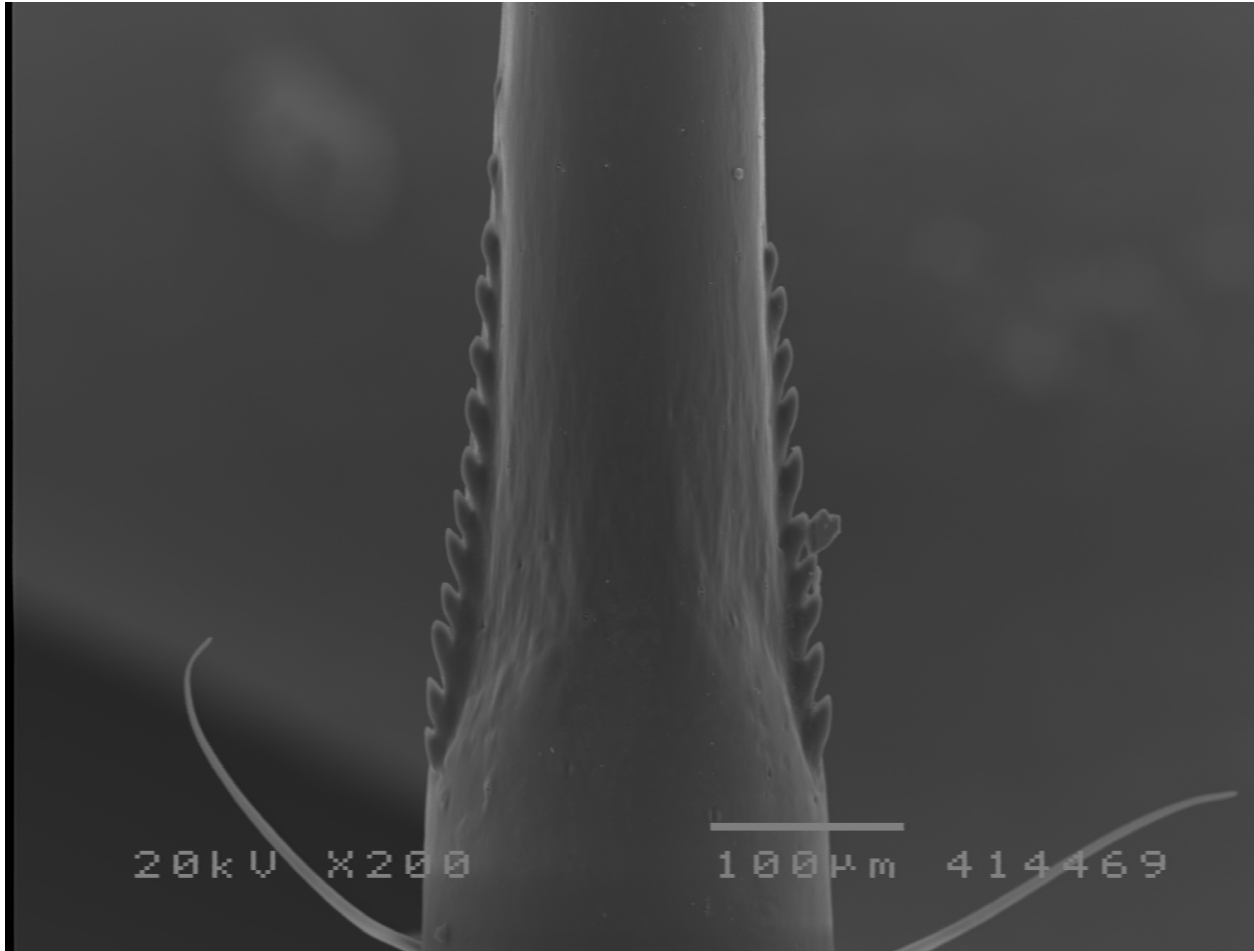
Species/Genders	Number of Denticles in LAS
<i>Paravaejovis pumilis</i>	1-7 (4.306) (\pm 1.238) [36] {3.068-5.544} \rightarrow 0.288
Males	2-7 (4.500)
Females	1-4 (3.333)
<i>Vejovoidus longiunguis</i>	9-21 (11.833) (\pm 3.031) [24] {8.802-14.865} \rightarrow 0.256
Males	10-21 (13.500)
Females	9-16 (11.000)
<i>Smeringurus mesaensis</i>	4-10 (7.406) (\pm 1.720) [32] {5.686-9.126} \rightarrow 0.232
Males	5-10 (7.944)
Females	4-9 (6.875)
<i>Paruroctonus gracilior</i>	4-9 (6.240) (\pm 1.332) [25] {4.908-7.572} \rightarrow 0.213
Males	4-9 (6.261)
Females	6 (6.000)
<i>Paruroctonus silvestrii</i>	1-10 (6.643) (\pm 2.264) [28] {4.379-8.907} \rightarrow 0.341
Males	1-10 (6.350)
Females	5-8 (7.375)
<i>Vaejovis viscainensis</i>	6-15 (9.385) (\pm 2.210) [26] {7.174-11.595} \rightarrow 0.236
Males	6-15 (9.944)
Females	6-12 (8.125)
<i>Vaejovis punctatus</i>	2-8 (4.727) (\pm 1.506) [33] {3.222-6.233} \rightarrow 0.319
Males	2-8 (5.190)
Females	2-6 (3.917)
<i>Vaejovis puritanus</i>	3-12 (7.714) (\pm 1.630) [28] {6.085-9.344} \rightarrow 0.211
Males	3-12 (7.579)
Females	9-10 (9.500)
<i>Vaejovis magdalensis</i>	4-8 (5.357) (\pm 1.277) [14] {4.080-6.635} \rightarrow 0.238
Males	4-8 (5.357) [14]
Females	-
<i>Serradigitus joshuaensis</i>	3-8 (5.409) (\pm 1.368) [22] {4.041-6.777} \rightarrow 0.253
Males	-
Females	3-8 (5.409)
<i>Vaejovis vorhiesi</i>	1-7 (5.000) (\pm 1.569) [14] {3.431-6.569} \rightarrow 0.314
Males	5-7 (5.500)
Females	1-7 (4.800)
<i>Pseudouroctonus andreas</i>	2-5 (3.643) (\pm 0.745) [14] {2.898-4.388} \rightarrow 0.204
Males	2-5 (3.583)
Females	4 (4.000)

4 **Table 4.3:** Taxa examined from 11 non-vaejovoid families and found to lack the LAS (72 genera; 86 species). (S) – indicates taxon absence verified by SEM (adapted from Fet et al. 2006c).

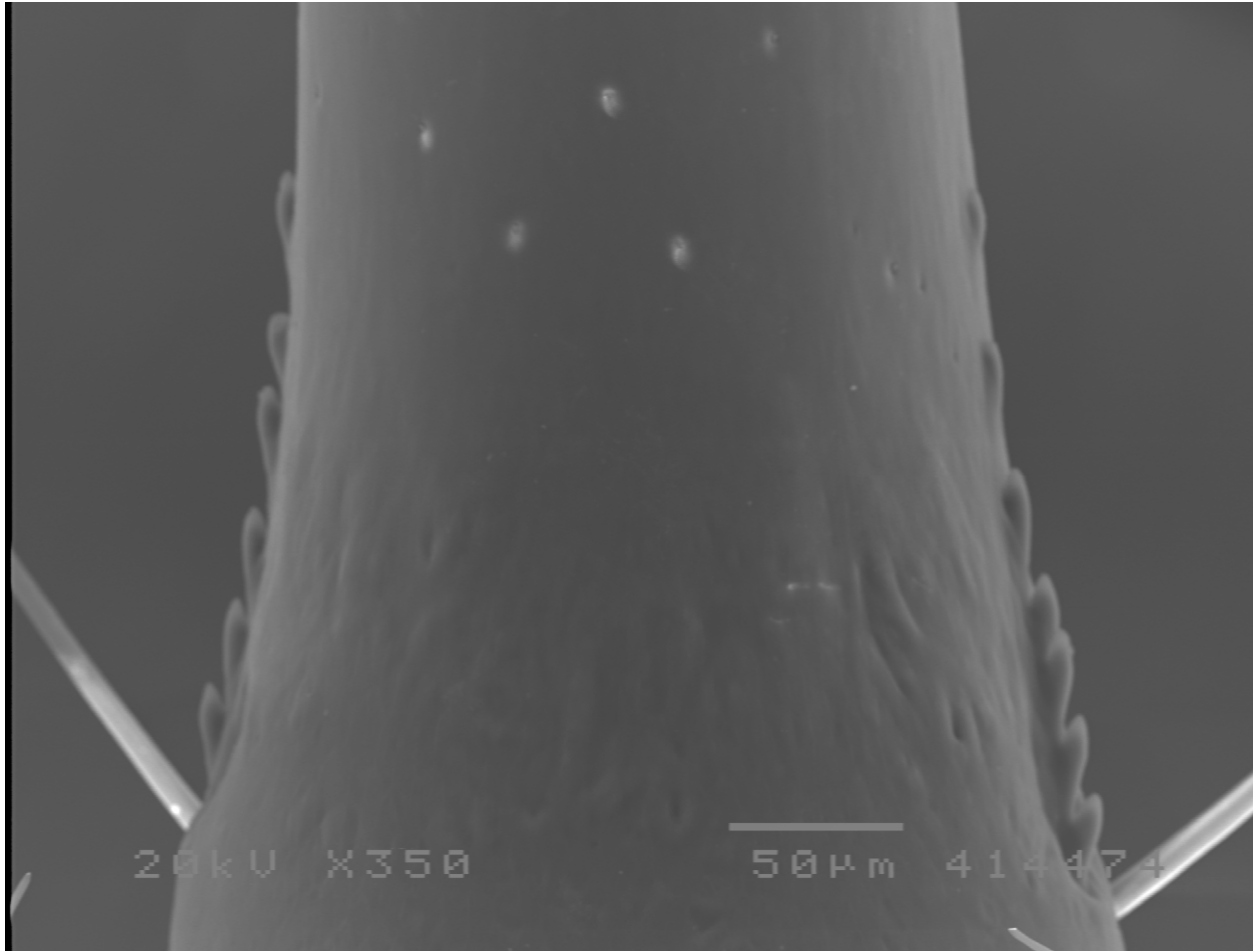
Pseudochactida: Pseudochactoidea	<i>Opisthophthalmus wahlbergi</i>
Pseudochactidae: <i>Pseudochactas ovchinnikovi</i> (S)	<i>Pandinus imperator</i>
Buthida: Buthoidea	<i>Scorpio maurus</i> (S)
Buthidae: <i>Alayotityus nanus</i>	<i>Urodacus manicatus</i>
<i>Androctonus bicolor</i>	Hemiscorpiidae: <i>Cheloctonus</i> sp.
<i>Anomalobuthus rickmersi</i>	<i>Liocheles australasiae</i> (S)
<i>Buthacus yotvatensis</i>	<i>Liocheles karschii</i>
<i>Buthus occitanus</i>	<i>Hadogenes troglodytes</i>
<i>Centruroides exilicauda</i>	<i>Heteroscorpion goodmani</i>
<i>Centruroides suffusus</i> (S)	<i>Opisthacanthus lepturus</i>
<i>Compsobuthus matthiesseni</i>	Bothriuridae: <i>Bothriurus araguayae</i> (S)
<i>Grosphus hirtus</i>	<i>Bothriurus burmeisteri</i>
<i>Hottentotta minax</i>	<i>Brachistosternus ehrenberghii</i>
<i>Isometrus maculatus</i>	<i>Centromachetes pocockii</i>
<i>Leiurus quinquestriatus</i> (S)	<i>Cercophonius squama</i>
<i>Liobuthus kessleri</i>	<i>Lisposoma josehermana</i>
<i>Lychas</i> sp.	<i>Phoniocercus pictus</i>
<i>Lychas mucronatus</i> (S)	<i>Urophonius paynensis</i>
<i>Mesobuthus caucasicus</i>	Iurida: Chactoidea
<i>Mesobuthus eupeus</i> (S)	Chactidae: <i>Anuroctonus pococki bajae</i> (S)
<i>Microbuthus</i> sp.	<i>Anuroctonus pococki pococki</i>
<i>Microtityus jaumi</i>	<i>Belisarius xambeui</i>
<i>Orthochirus gromovi</i> (S)	<i>Brotheas granulatus</i>
<i>Parabuthus</i> sp.	<i>Broteochactas porosus</i>
<i>Polisius persicus</i>	<i>Chactas exsul</i>
<i>Razianus zarudnyi</i>	<i>Hadrurochactas schaumii</i>
<i>Rhopalurus junceus</i> (S)	<i>Neochactas delicatus</i>
<i>Tityus nematochirus</i>	<i>Nullibrotheas allenii</i> (S)
<i>Uroplectes vittatus</i>	<i>Teuthraustes oculatus</i>
Microcharmidae: <i>Microcharmus hauseri</i>	<i>Uroctonus m. mordax</i> (S)
Chaerilida: Chaeriloidea	<i>Uroctonus m. pluridens</i>
Chaerilidae: <i>Chaerilus celebensis</i> (S)	<i>Vachoniochactas</i> sp.
<i>Chaerilus variegatus</i>	Euscorpiidae: <i>Alloscorpiops lindstroemii</i>
Iurida: Iuroidea	<i>Chactopsis insignis</i>
Caraboctonidae: <i>Caraboctonus keyserlingi</i>	<i>Euscorpiops</i> sp.
<i>Hadruroides charcasus</i>	<i>Euscorpius flavicaudis</i>
<i>Hadruroides maculatus</i>	<i>Euscorpius gamma</i> (S)
<i>Hadrurus concolorous</i>	<i>Euscorpius italicus</i>
<i>Hadrurus obscurus</i>	<i>Euscorpius mingrelicus</i>
<i>Hoffmannihadrurus aztecus</i>	<i>Euscorpius sicanus</i> (S)
Iuridae: <i>Calchas nordmanni</i>	<i>Megacormus gertschi</i>
<i>Iurus dufourensis</i>	<i>Neoscorpiops tenuicauda</i>
Iurida: Scorpionoidea	<i>Plesiochactas dilutus</i>
Scorpionidae: <i>Bioculus comondae</i> (S)	<i>Scorpiops</i> sp.
<i>Didymocentrus leseurii</i>	<i>Troglacormus willis</i>
<i>Heterometrus longimanus</i>	Superstitioniidae: <i>Superstitionia donensis</i> (S)
<i>Nebo hierichonticus</i>	Vaejovidae: (see Table 1)



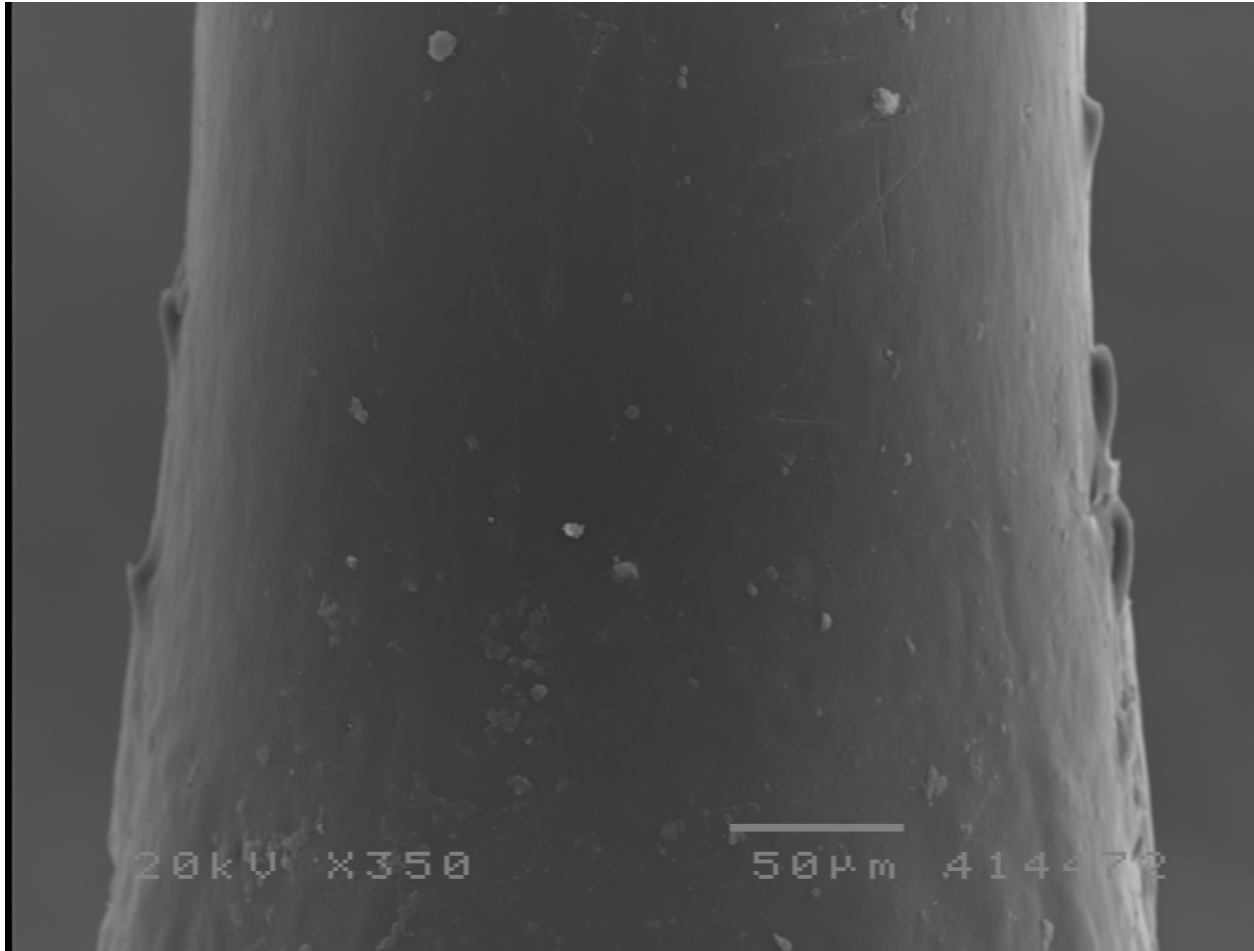
33 **Figure 4.6:** LAS in ventral view of *Paravaejovis pumilis* (male, Ciudad Constitucion, Baja California, Mexico).



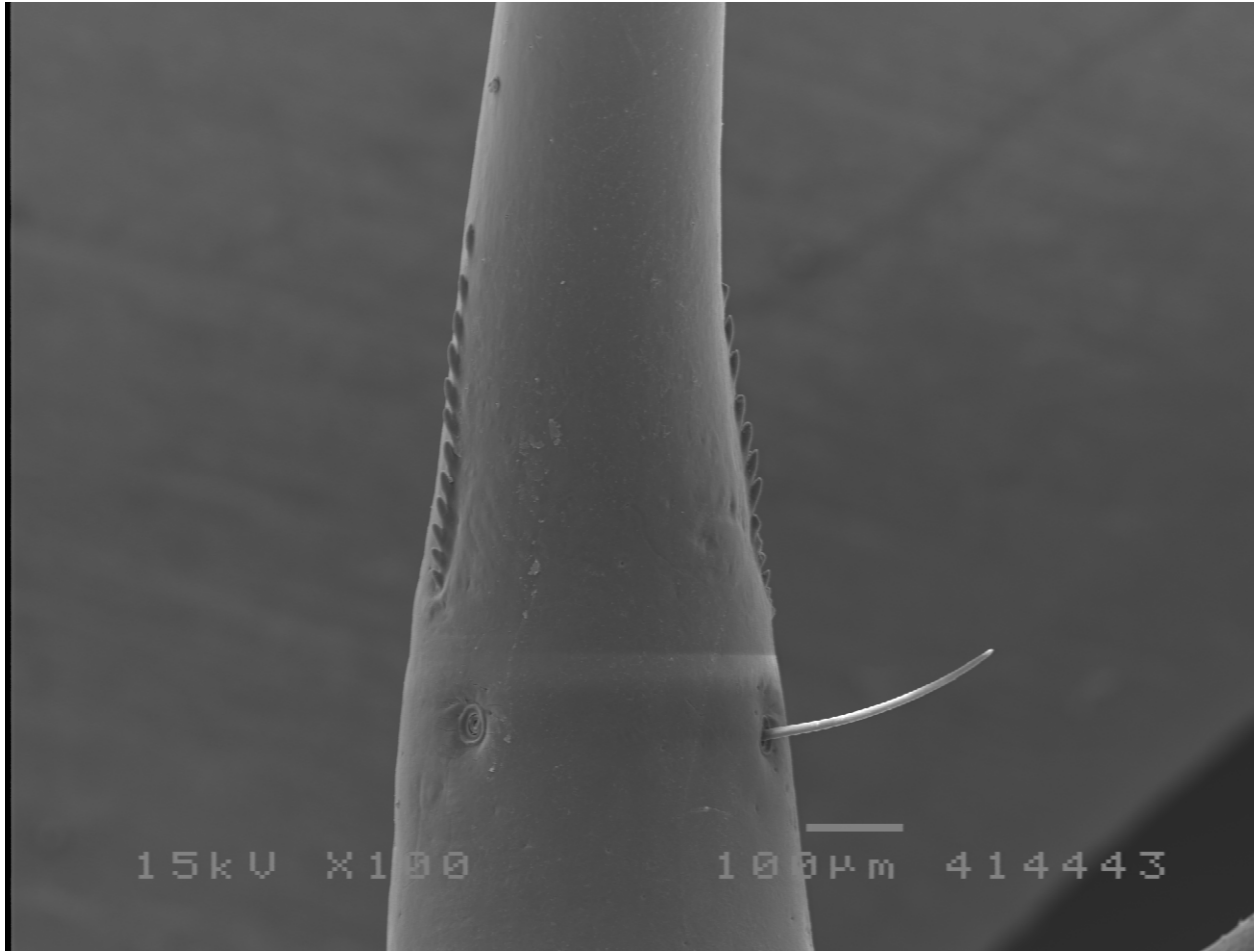
34 **Figure 4.7:** LAS in ventral view of *Vejovoidus longiunguis* (female, Viscaïno Desert, Baja California, Mexico).



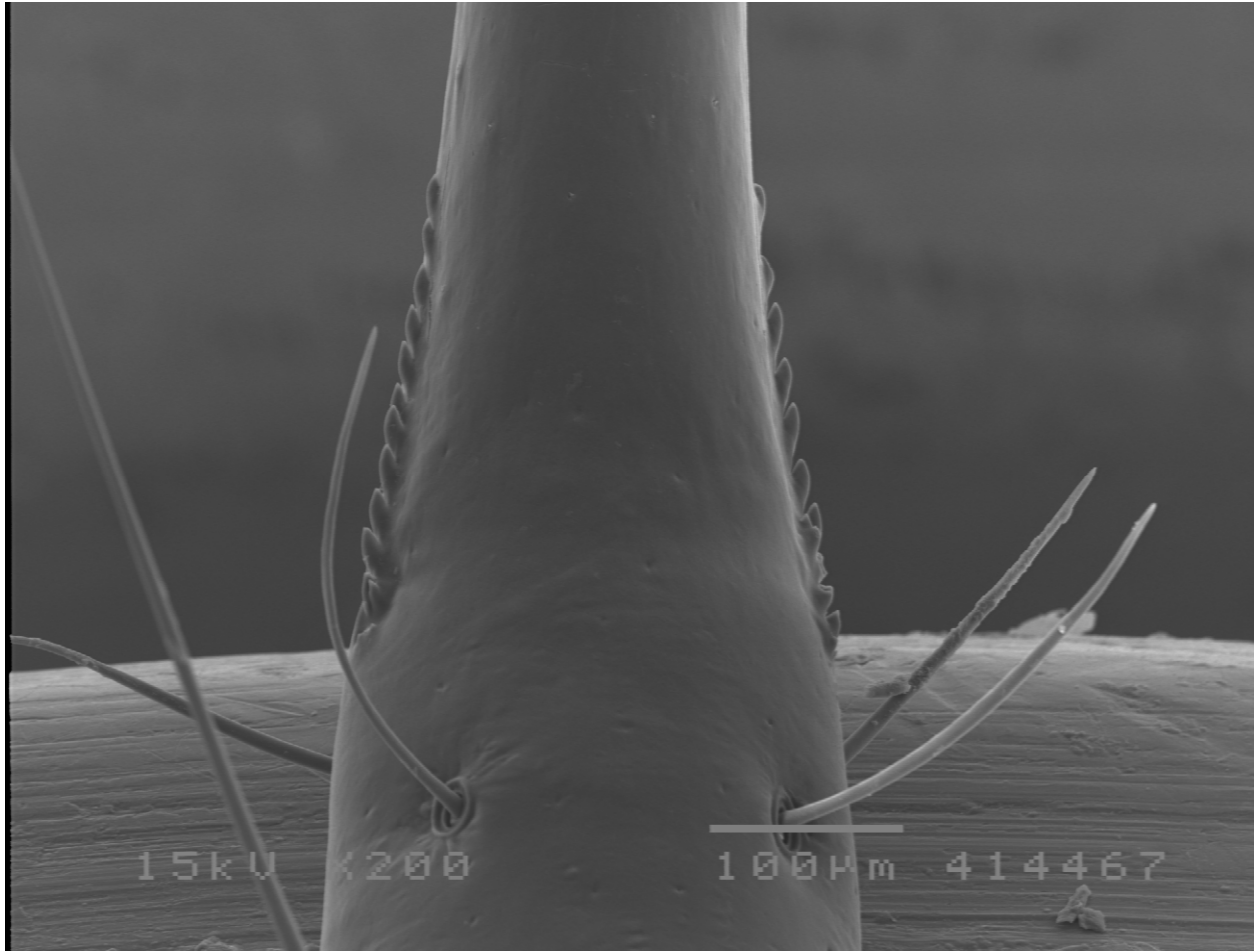
35 **Figure 4.8:** LAS in ventral view of *Paruroctonus boreus* (male, Worland, Wyoming).



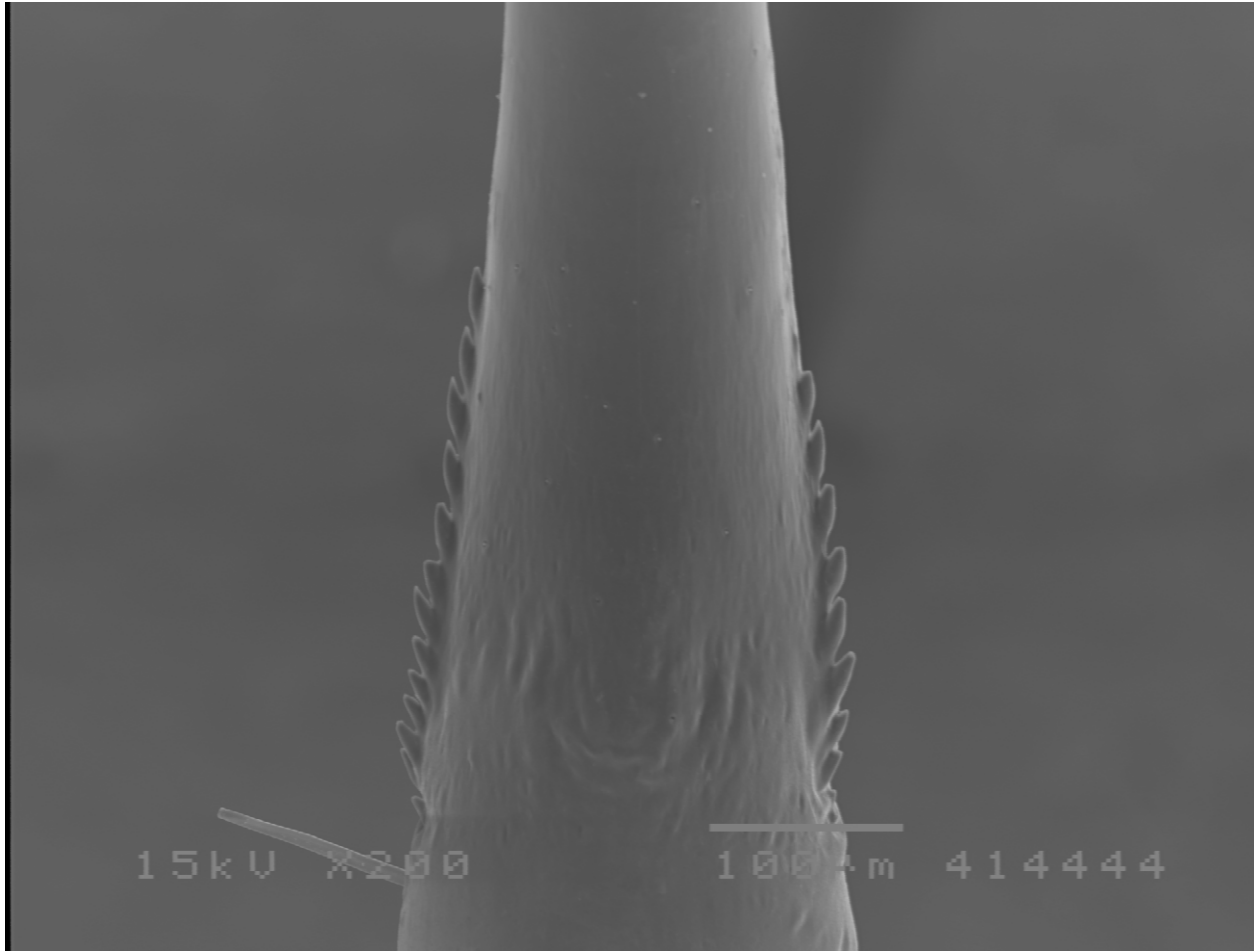
36 **Figure 4.9:** LAS in ventral view of *Smeringurus mesaensis* (female, Palo Verde Wash, ABDSP, California, USA).



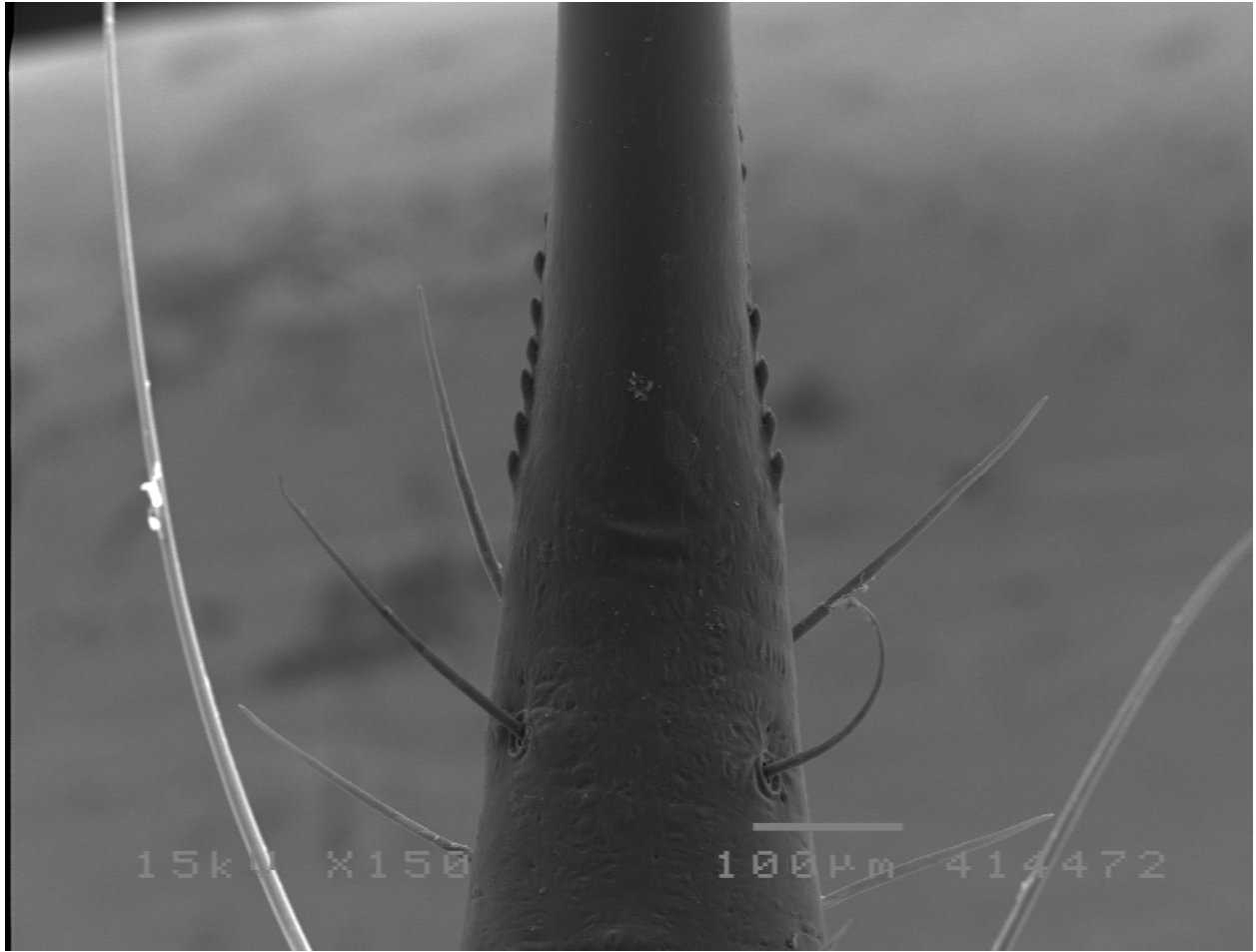
37 **Figure 4.10:** LAS in ventral view of *Paruroctonus arnaudi* (male, El Socorro, Baja California, Mexico).



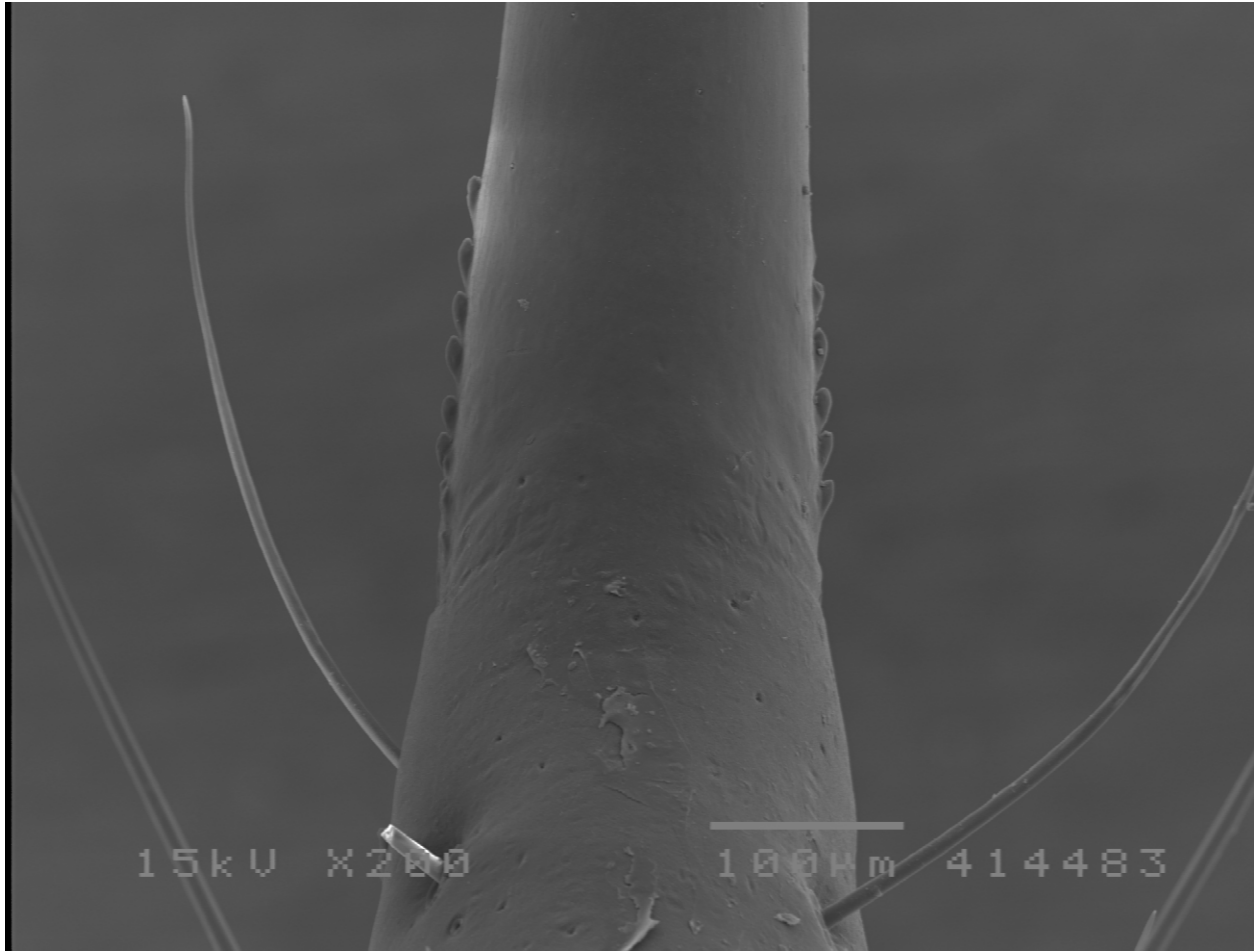
38 **Figure 4.11:** LAS in ventral view of *Paruroctonus ventosus* (female, El Socorro, Baja California, Mexico).



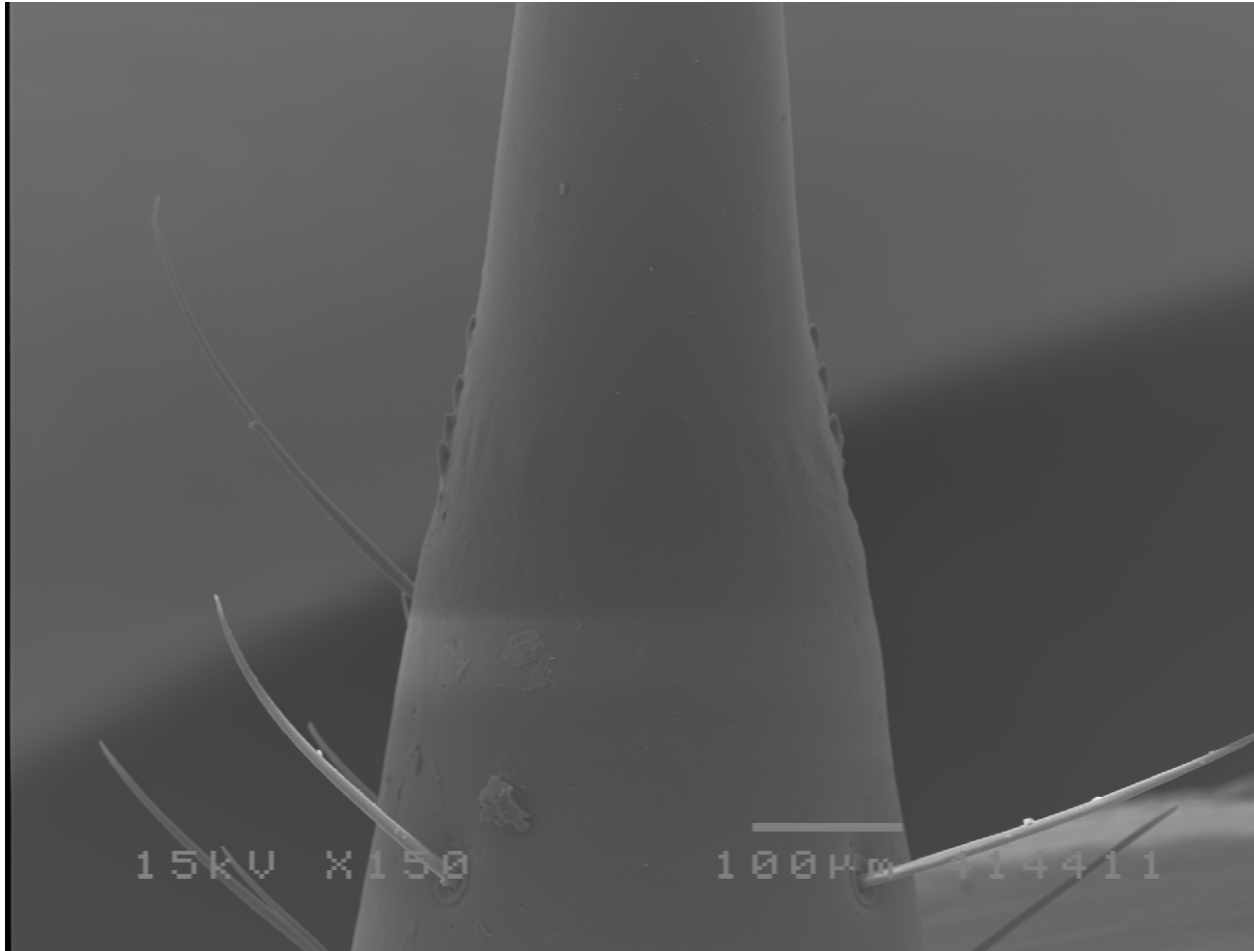
39 **Figure 4.12:** LAS in ventral view of *Paruroctonus surensis* (male, Las Bombas, Baja California Sur, Mexico).



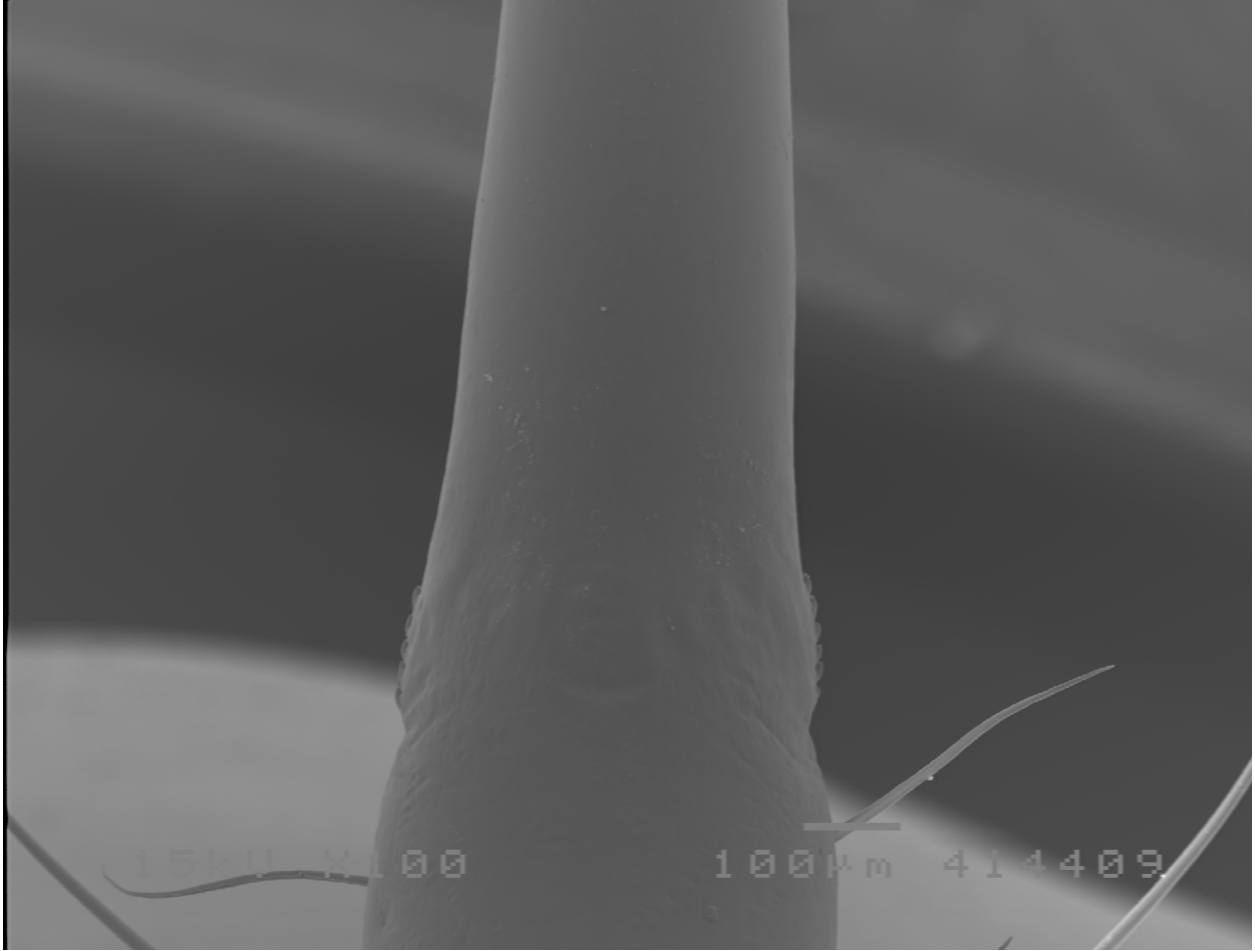
40 **Figure 4.13:** LAS in ventral view of *Paruroctonus luteolus* (female, Palo Verde Wash, ABDSP, California, USA).



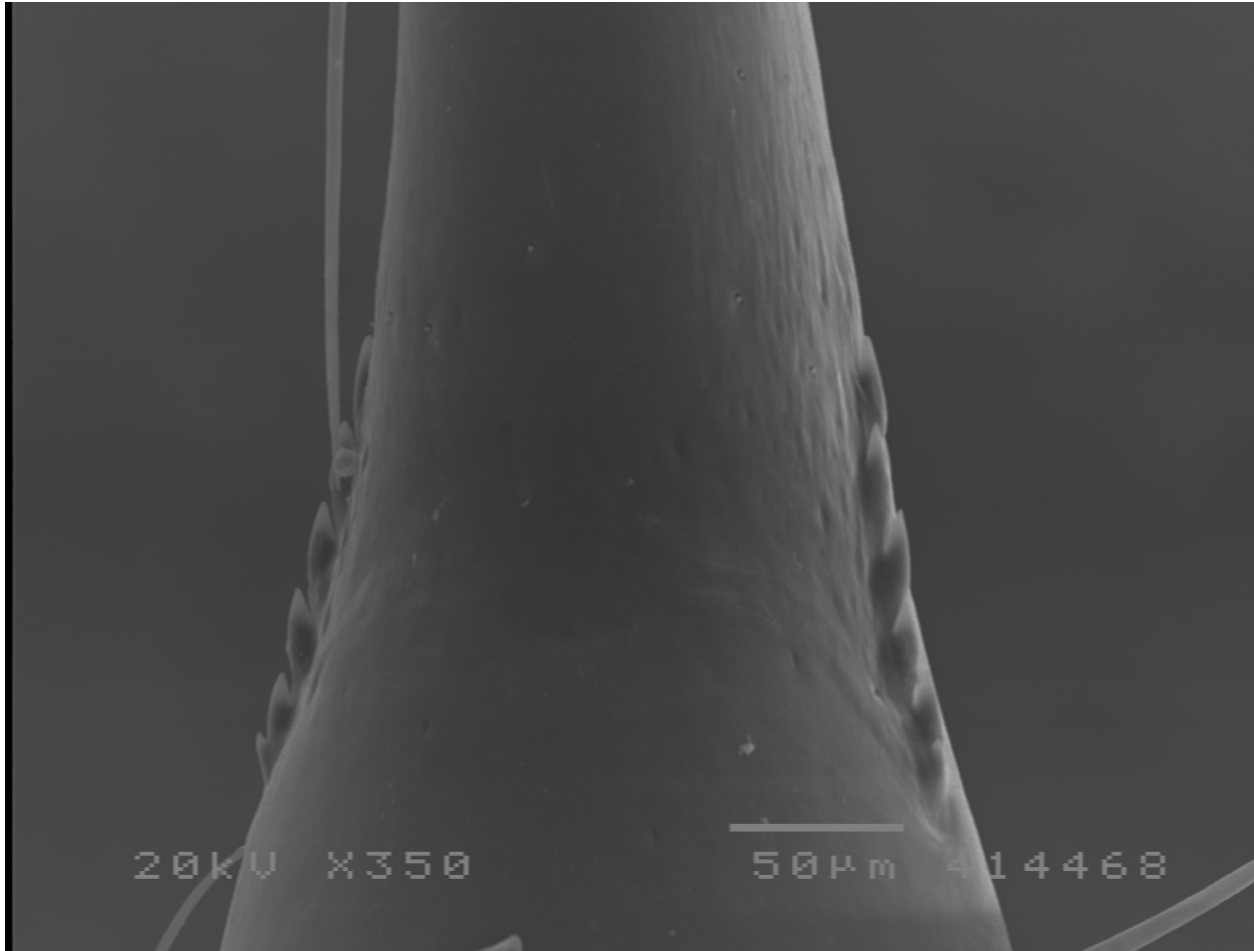
41 **Figure 4.14:** LAS in ventral view of *Vaejovis waeringi* (female, ABDSP, California, USA).



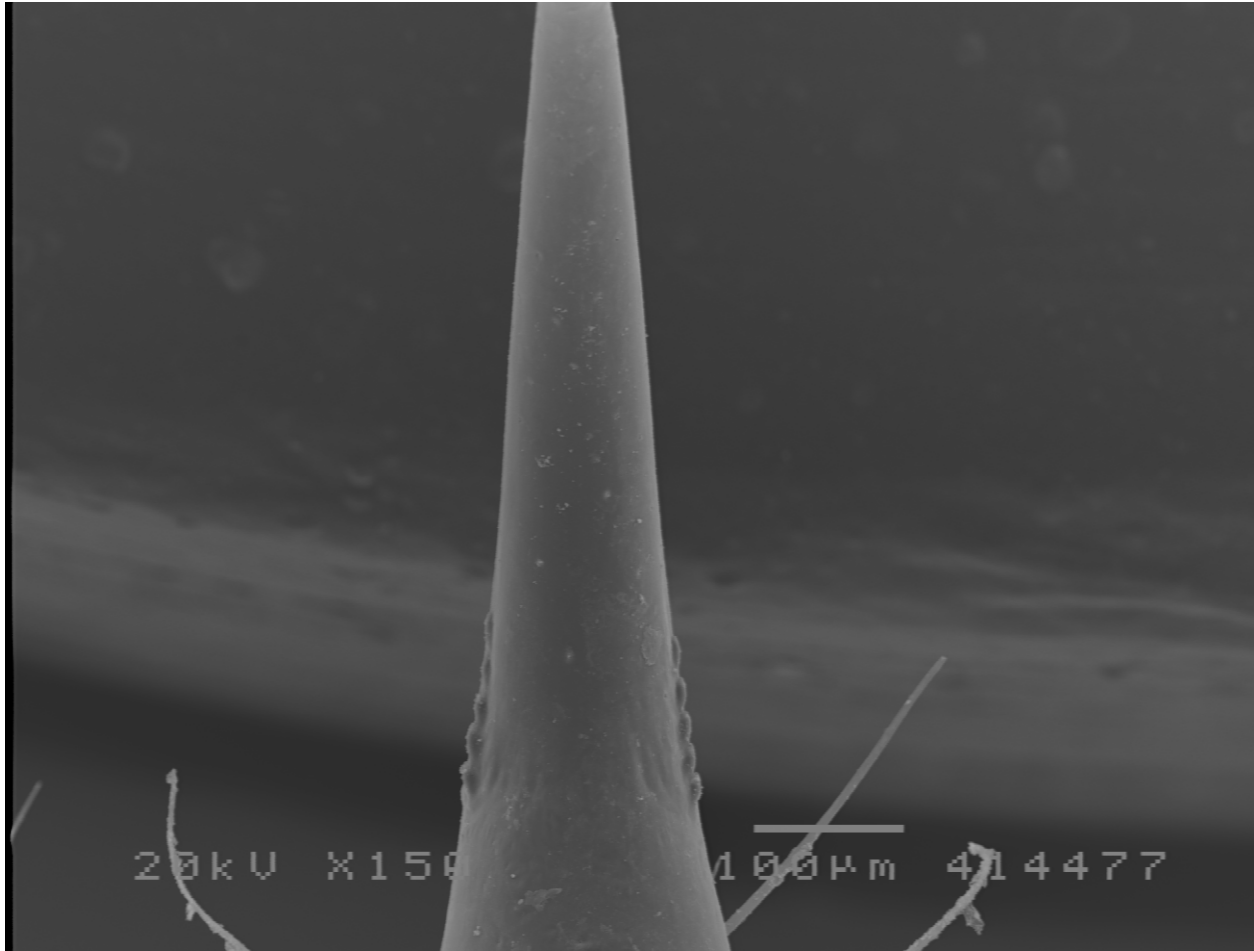
42 **Figure 4.15:** LAS in ventral view of *Vaejovis gravicaudis* (female, Santa Rosalia, Baja California Sur, Mexico).



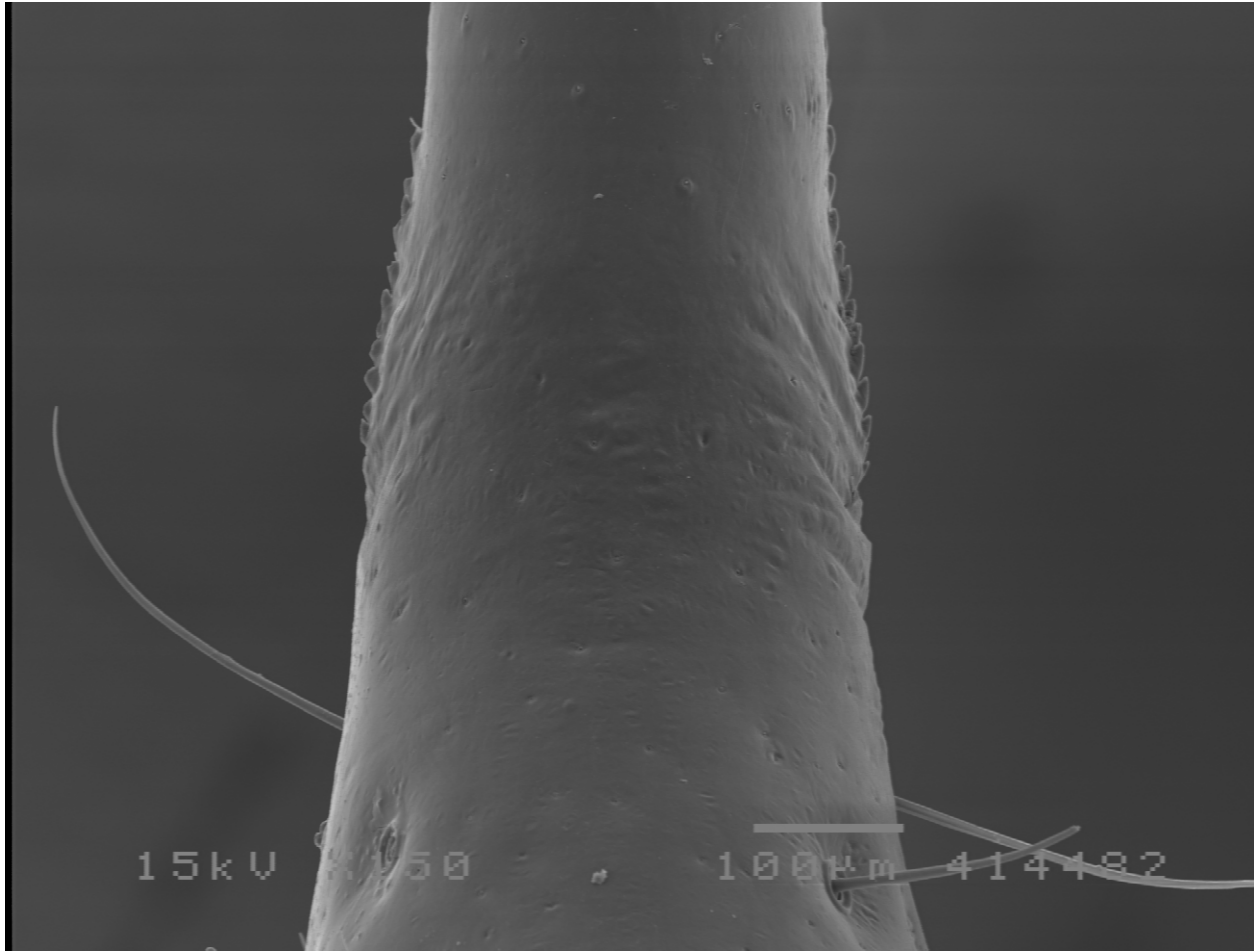
43 **Figure 4.16:** LAS in ventral view of *Vaejovis punctatus* (male, Acatlan, Puebla, Mexico).



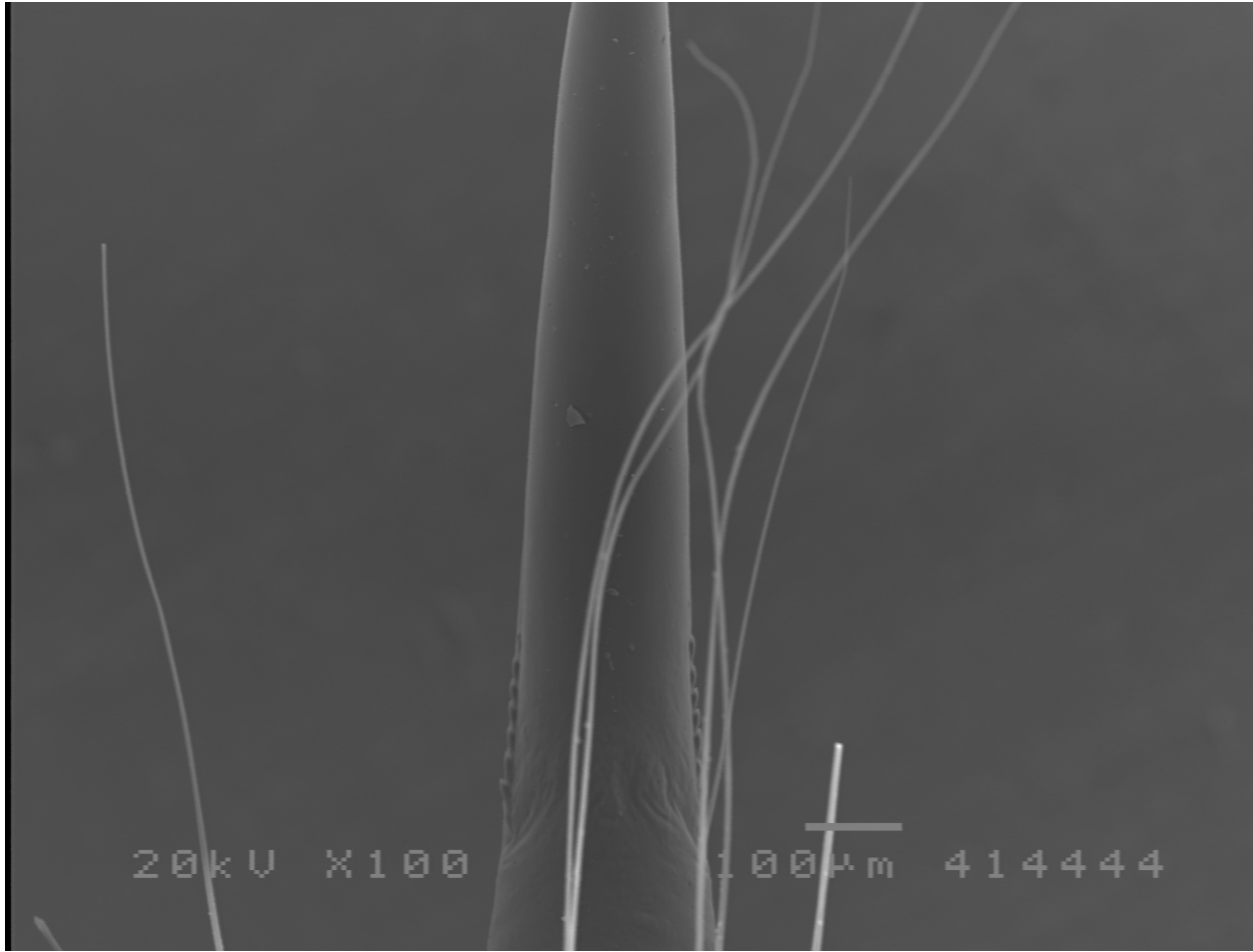
44 **Figure 4.17:** LAS in ventral view of *Vaejovis vittatus* (female, Cabo San Lucas, Baja California Sur, Mexico).



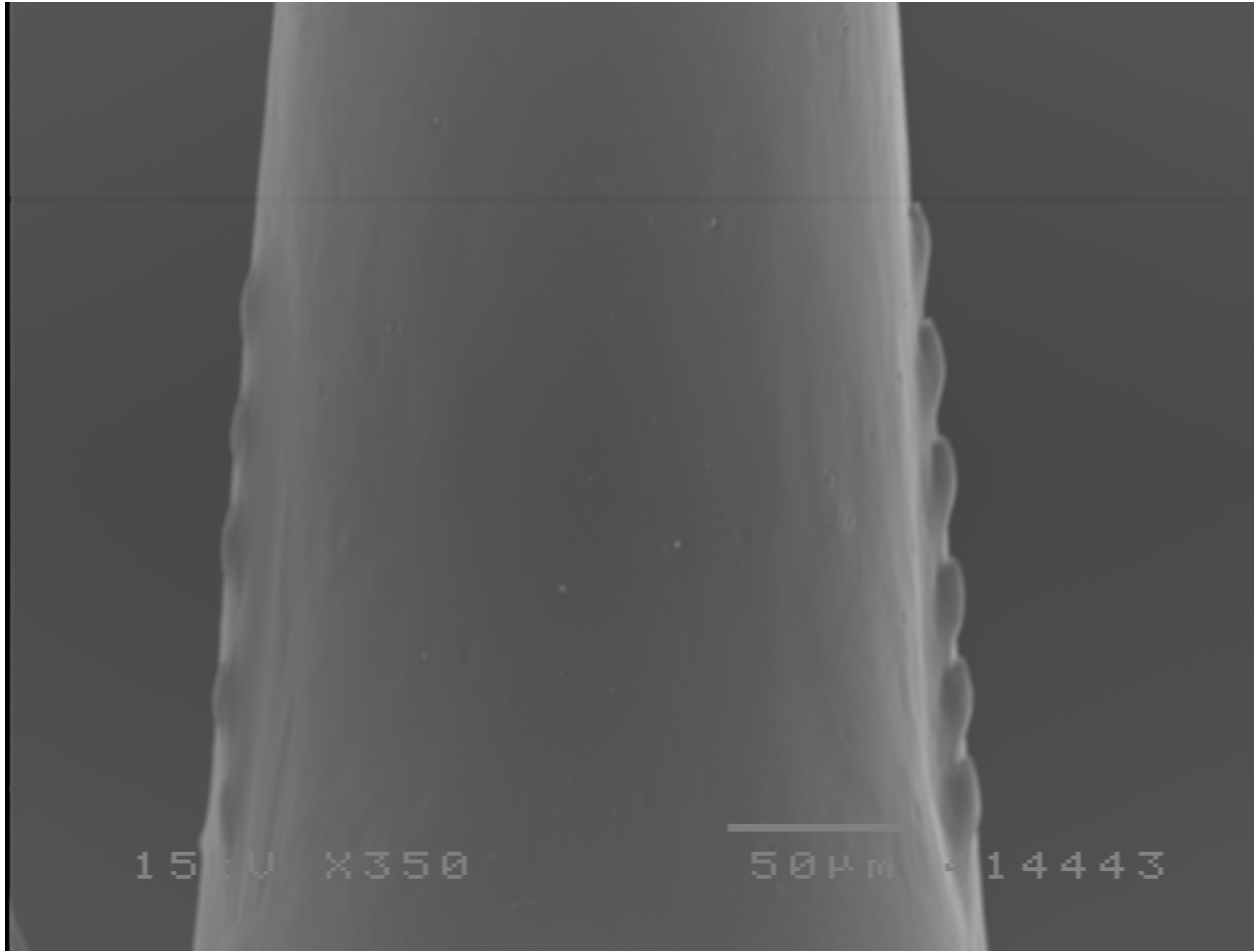
45 **Figure 4.18:** LAS in ventral view of *Serradigitus joshuaensis* (female, ABDSP, California, USA).



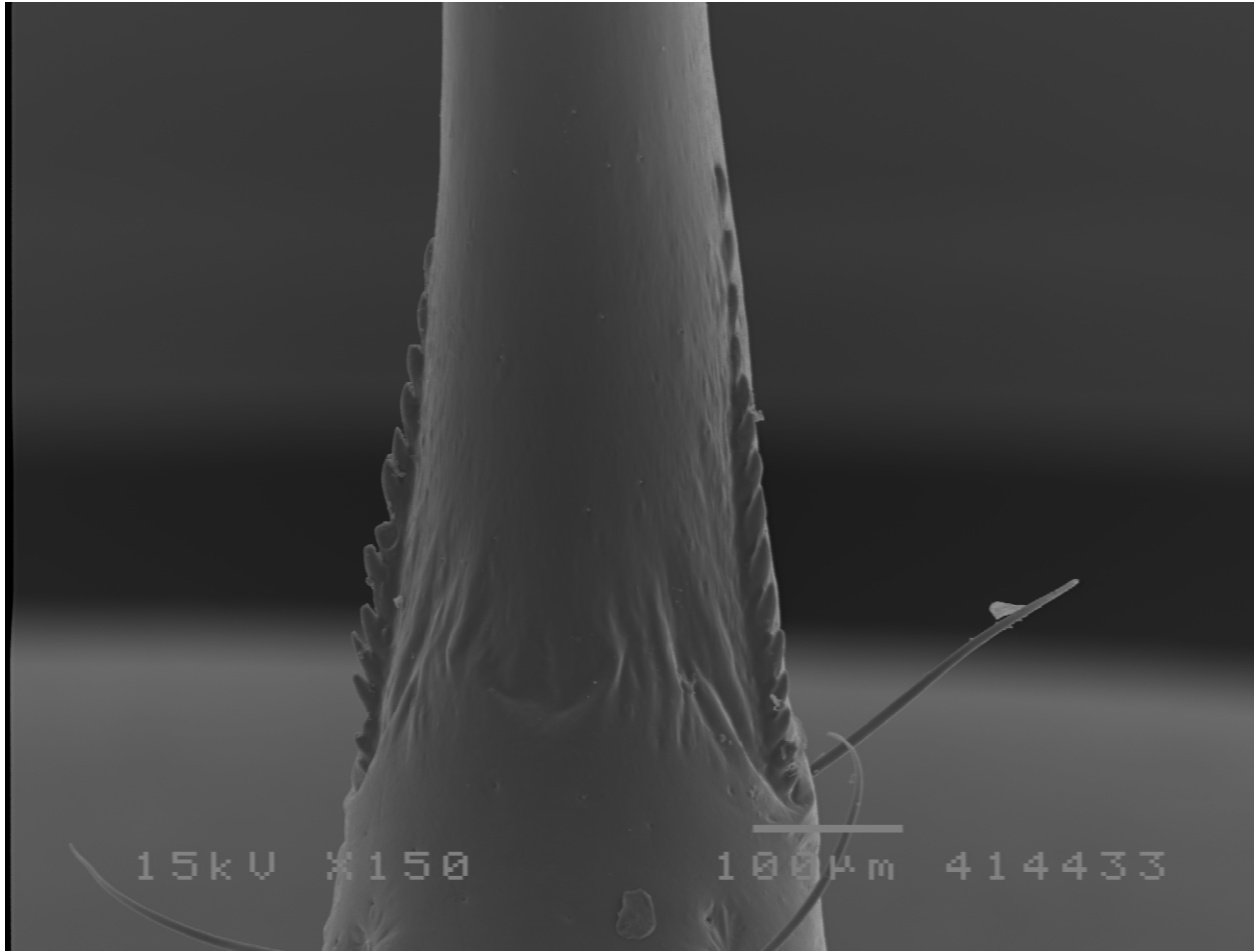
46 **Figure 4.19:** LAS in ventral view of *Serradigitus gertschi* (female, San Diego, California, USA).



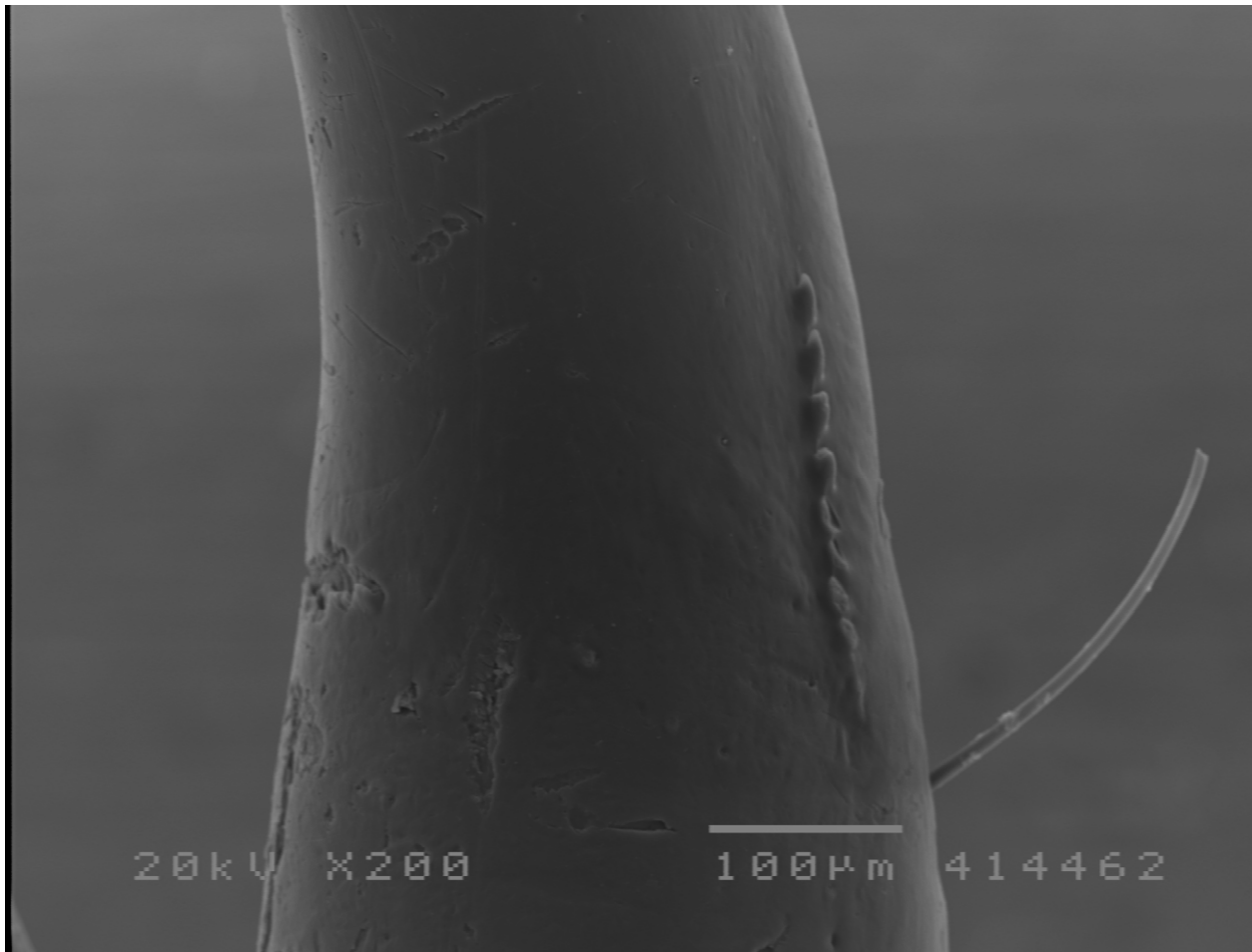
47 **Figure 4.20:** LAS in ventral view of *Vaejovis hirsuticauda* (female, ABDSP, California).



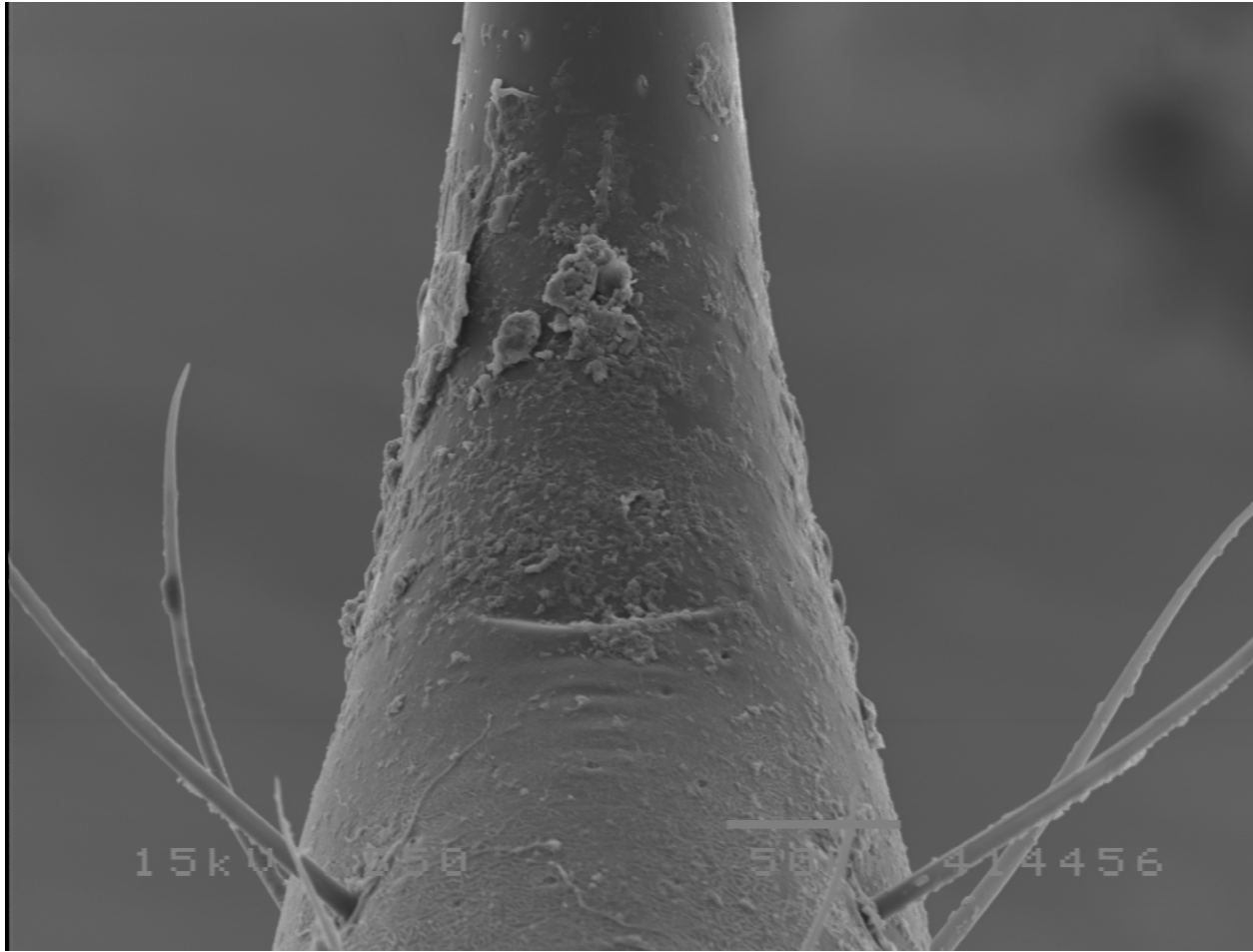
48 **Figure 4.21:** LAS in ventral view of *Vaejovis magdalensis* (male, Los Aripes, Baja California Sur, Mexico).



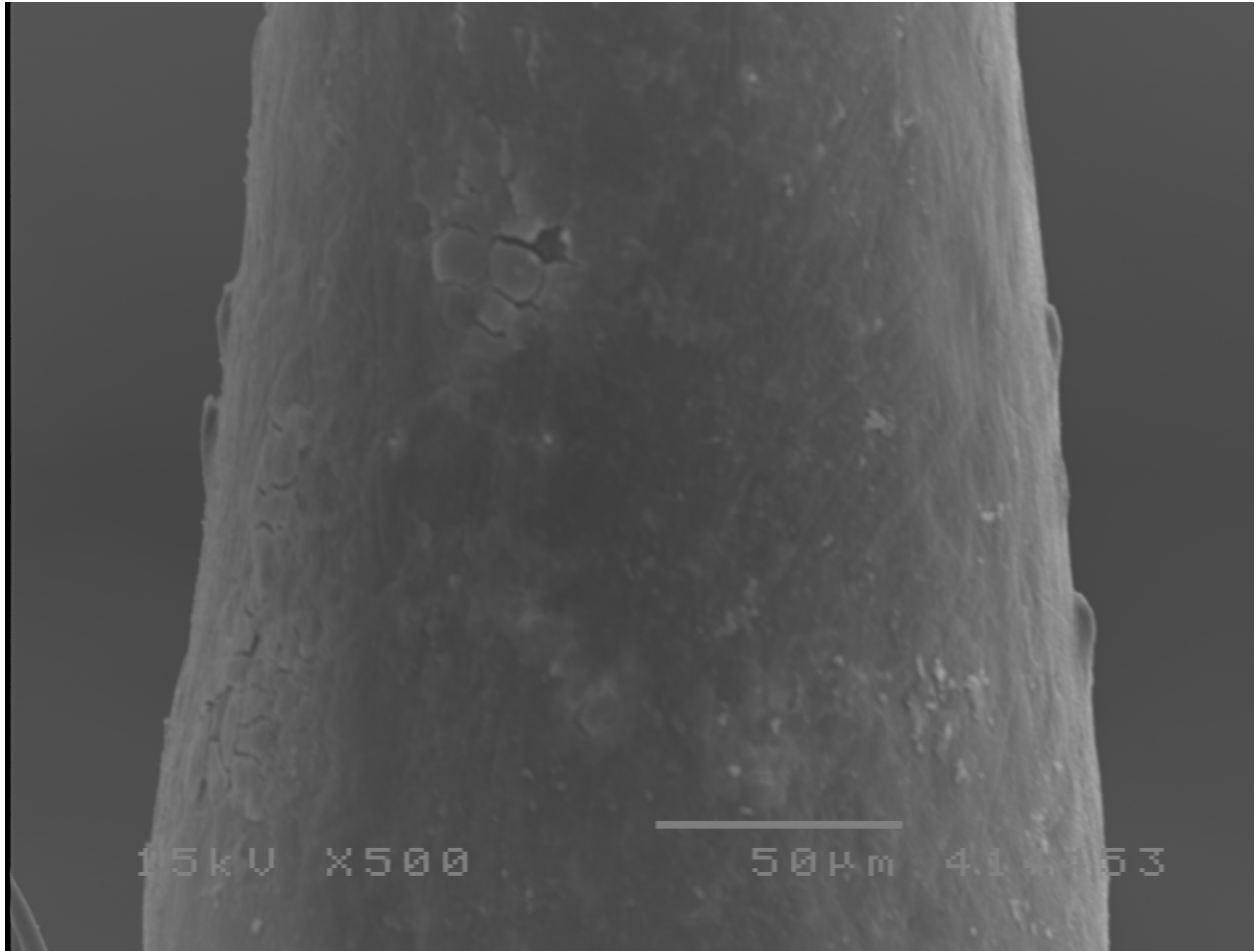
49 **Figure 4.22:** LAS in ventral view of *Vaejovis viscainensis* (male, Las Bombas, Baja California Sur, Mexico).



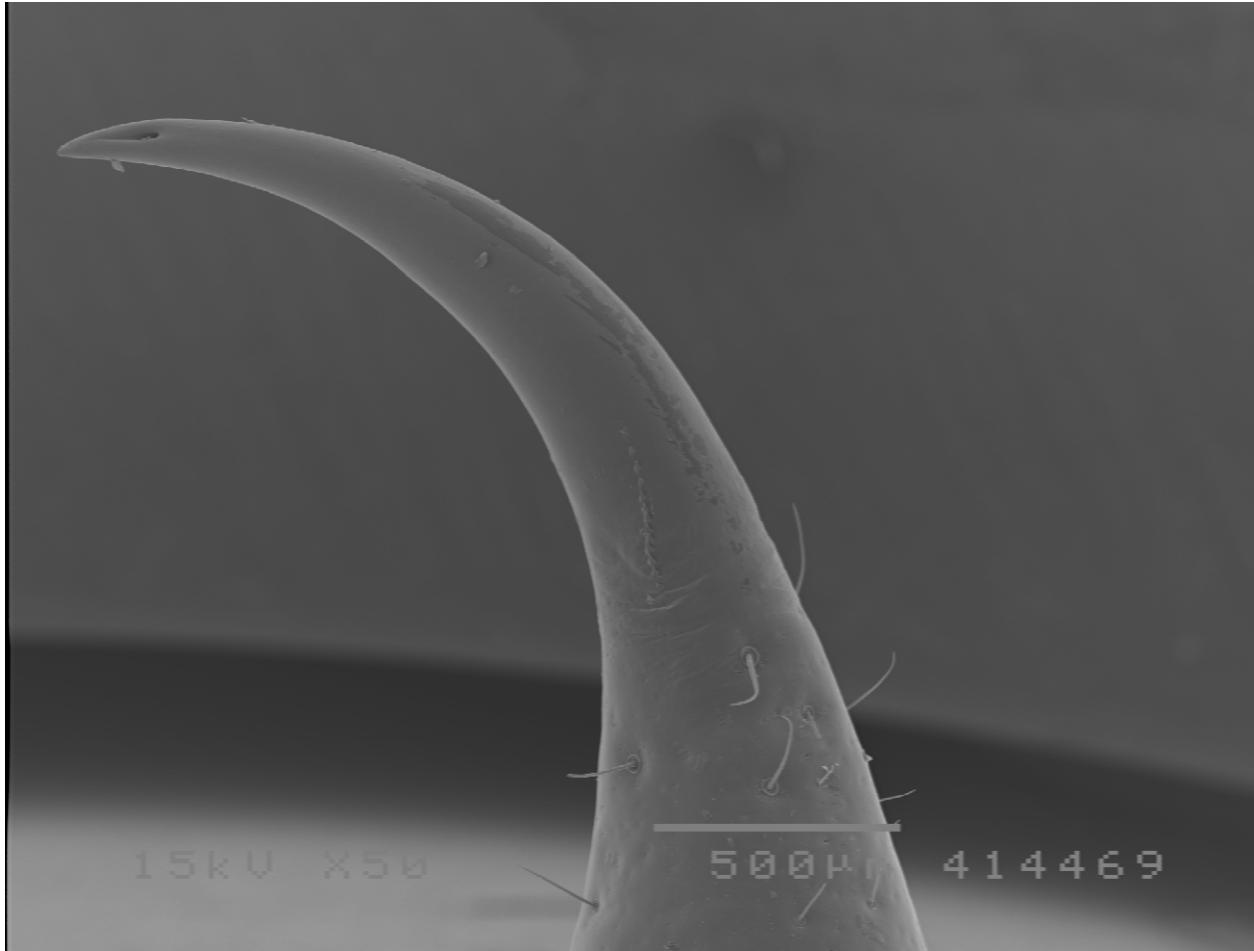
50 **Figure 4.23:** LAS in ventral view of *Vaejovis puritanus* (male, ABDSP, California, USA).



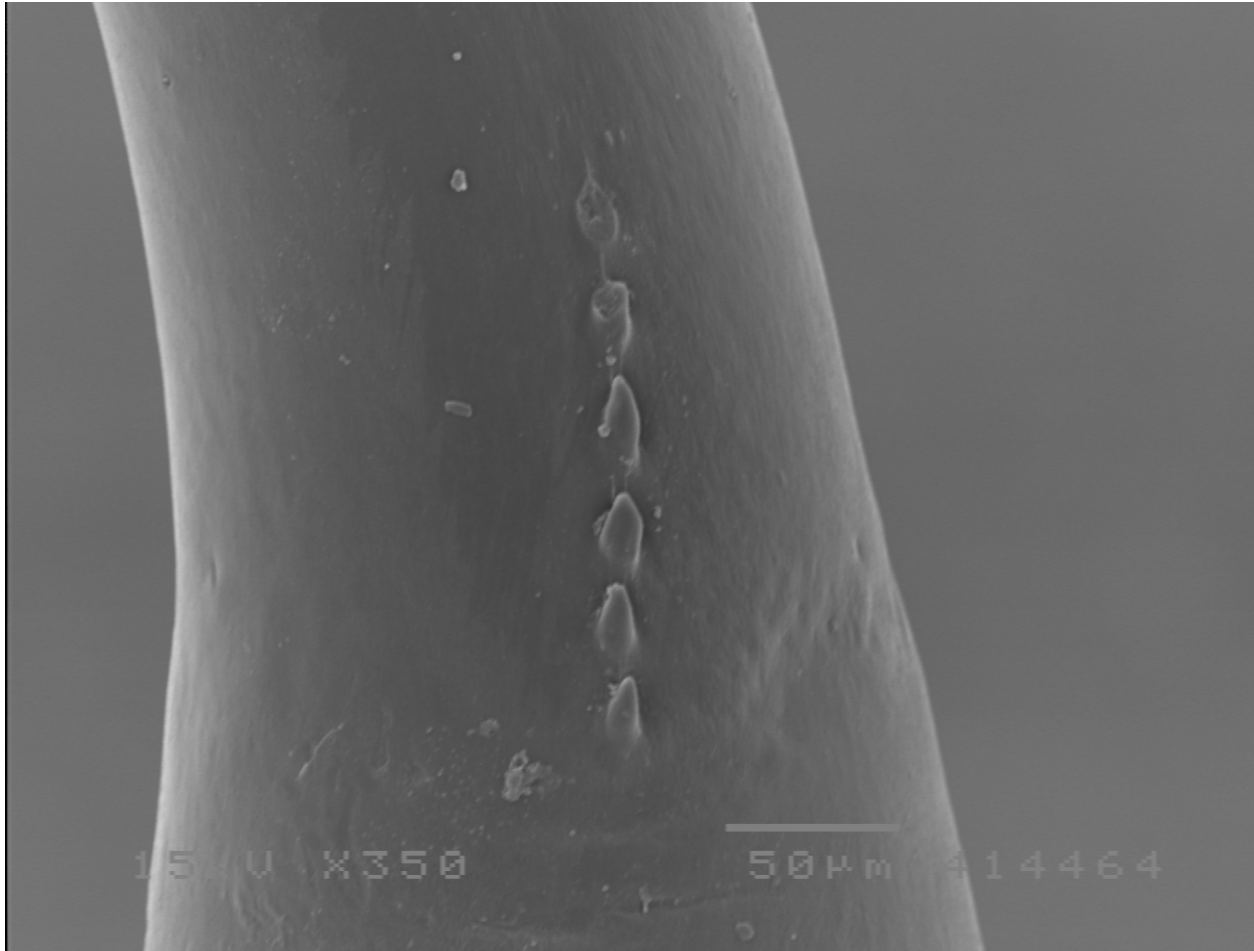
51 **Figure 4.24:** LAS in ventral view of *Pseudouroctonus andreas* (male, Chariot Canyon, ABDSP, California, USA).



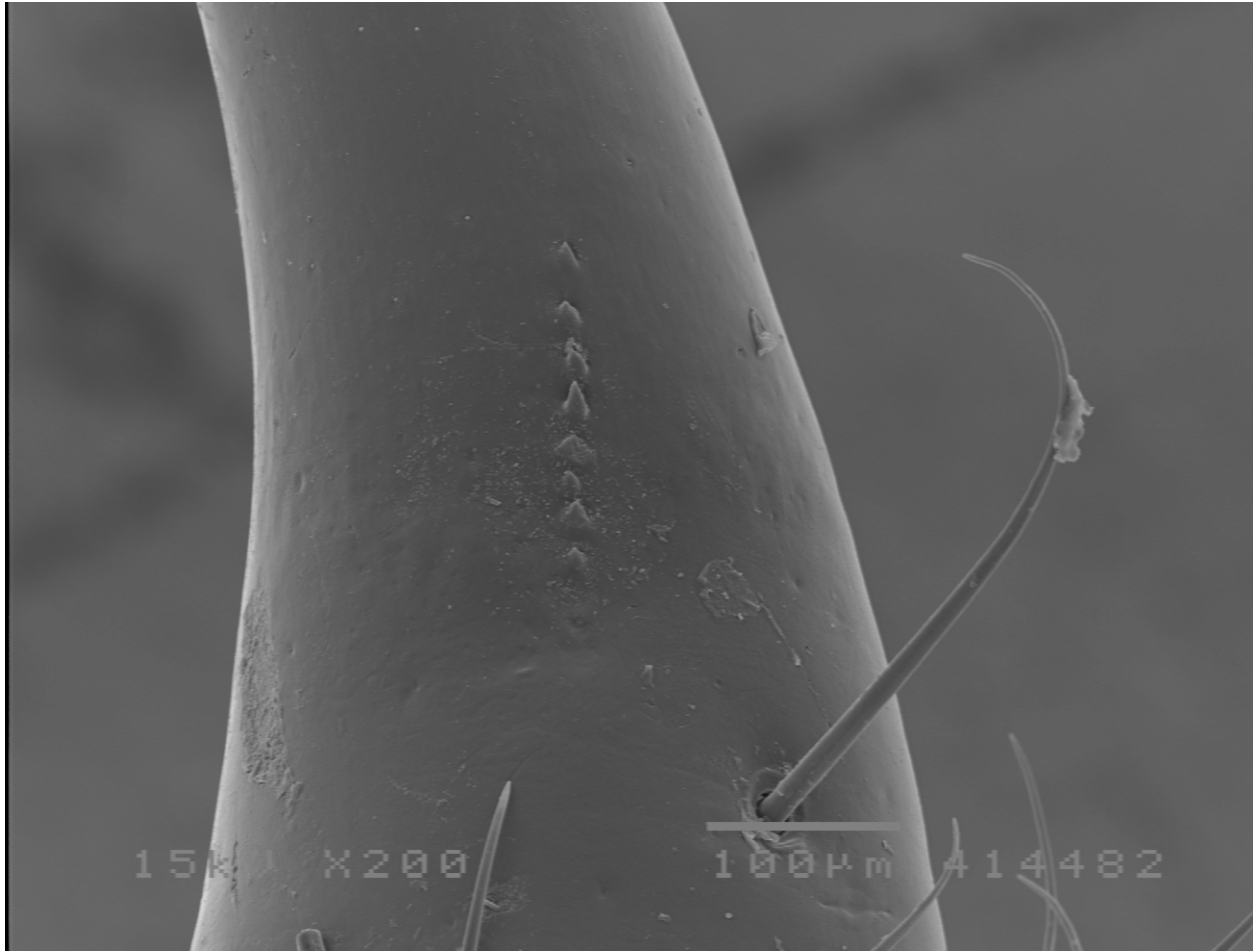
52 **Figure 4.25:** LAS in ventral view of *Vaejovis granulatus* (unknown sex, Pachuca, Hidalgo, Mexico).



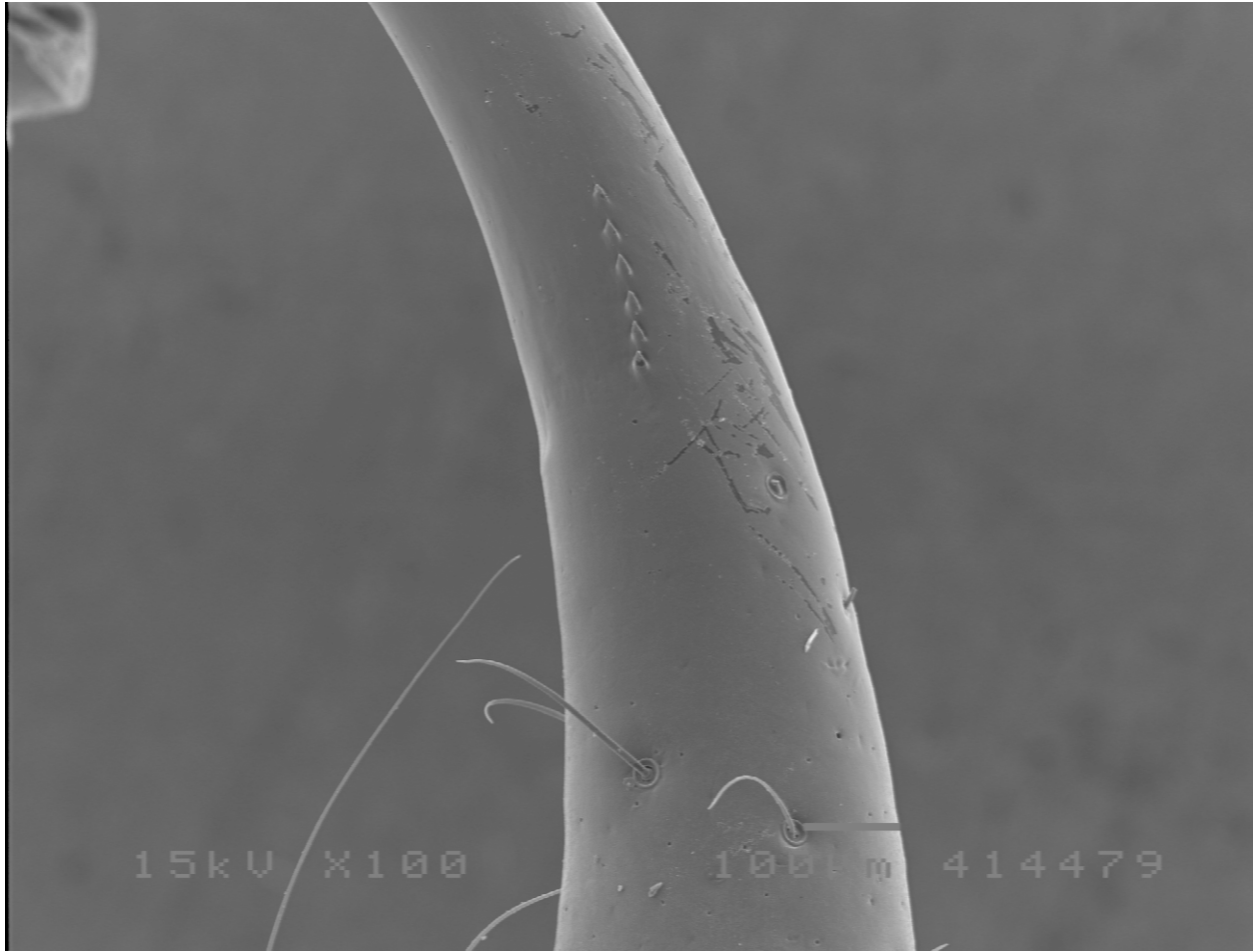
53 **Figure 4.26:** LAS in lateral view of *Vaejovis waeringi* (male, Indian Gorge Canyon, ABDSP, California, USA).



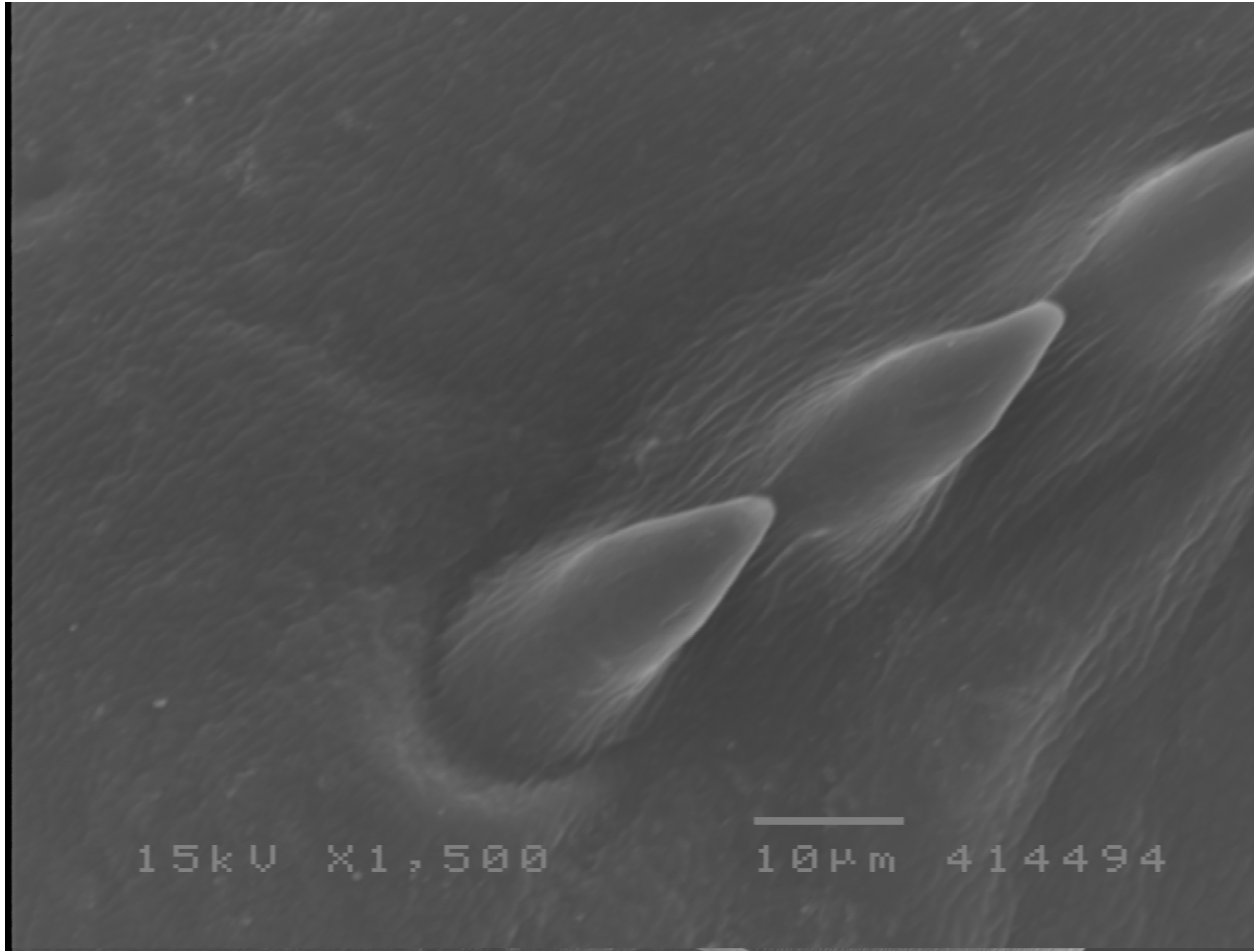
54 **Figure 4.27:** LAS in lateral view of *Serradigitus gertschi striatus* (female, Coloma, California, USA).



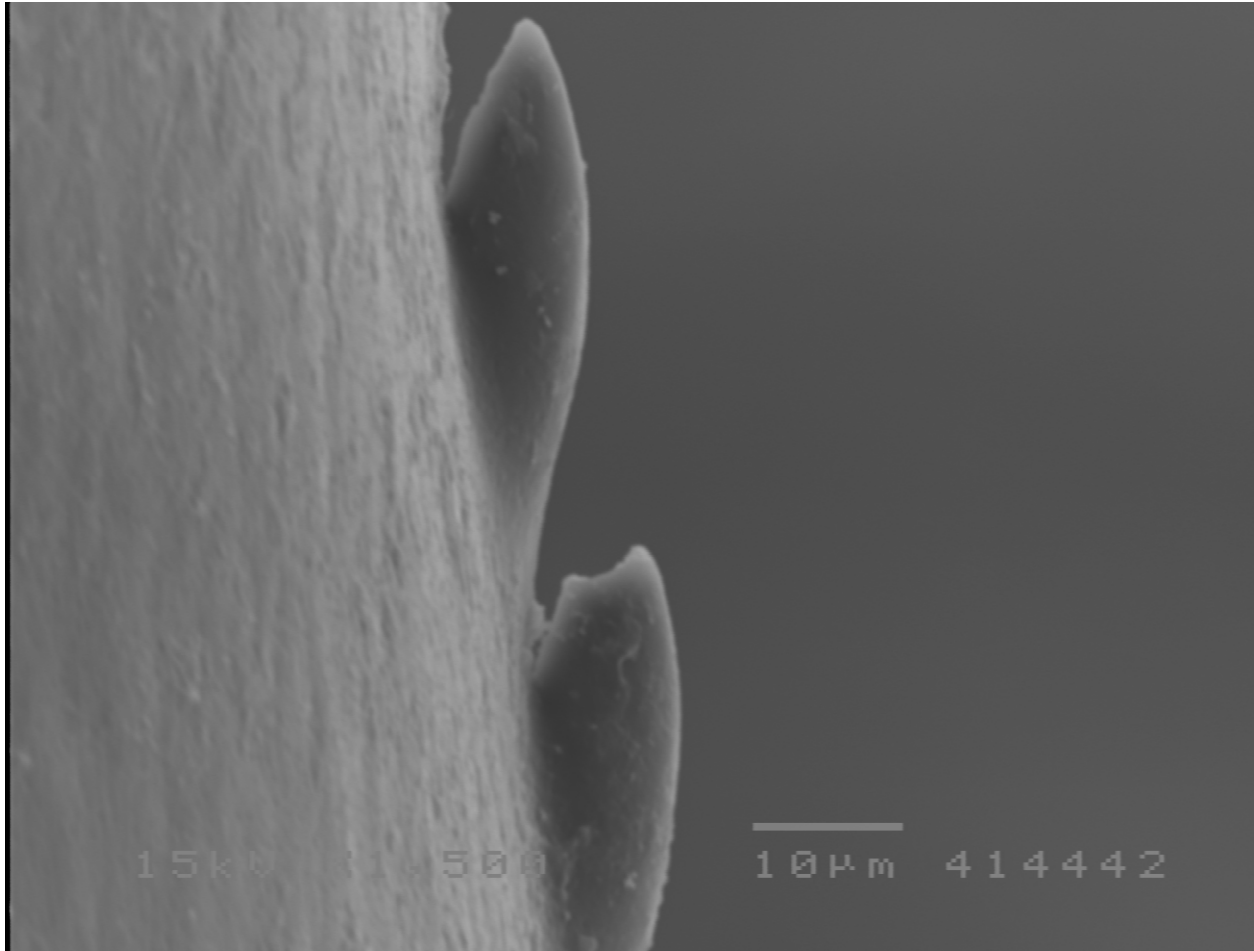
55 **Figure 4.28:** LAS in lateral view of *Vaejovis globosus* (female, Zacatecus, Zacatecus, Mexico).



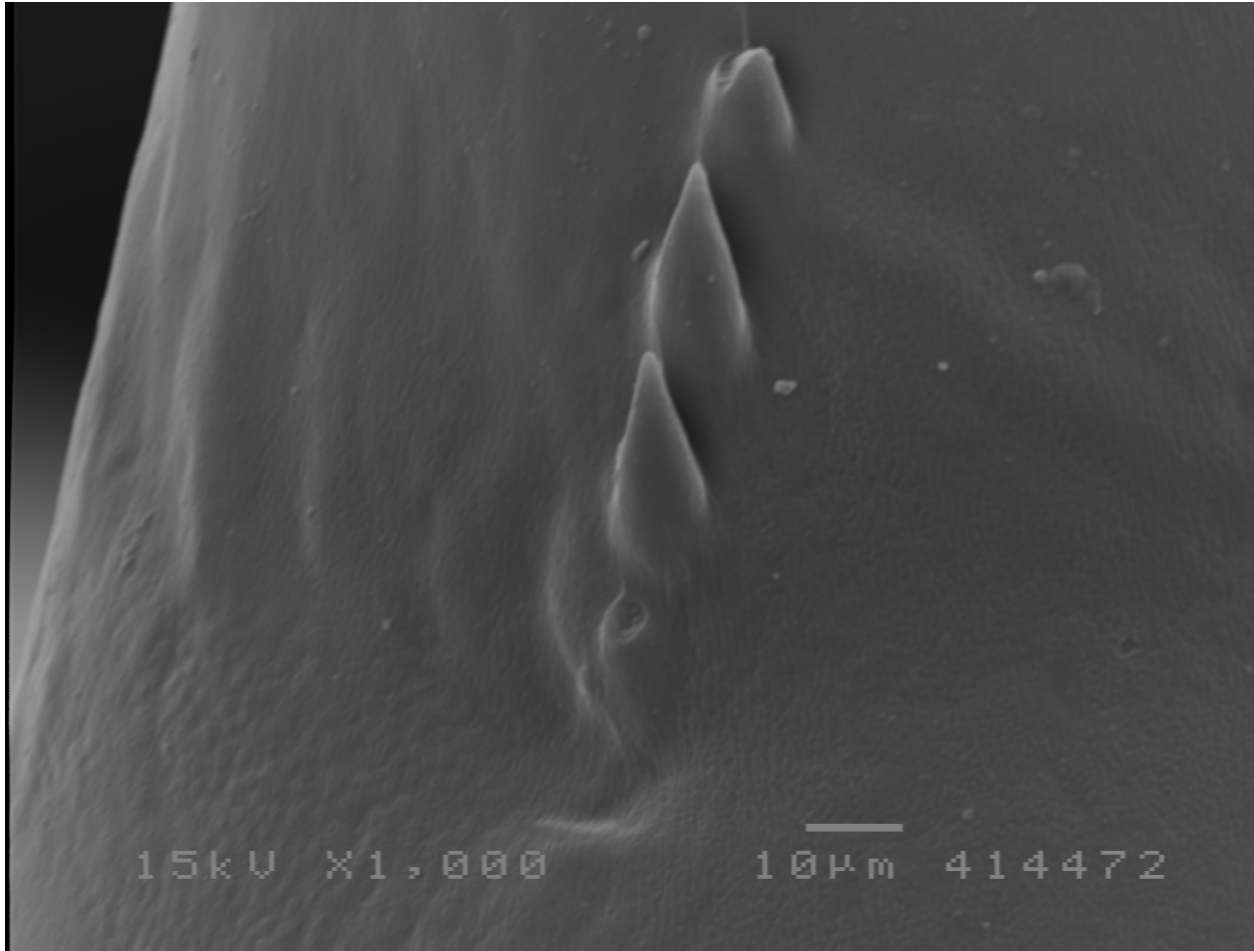
56 **Figure 4.29:** LAS in lateral view of *Vaejovis magdalensis* (male, Los Aripes, Baja California Sur, Mexico).



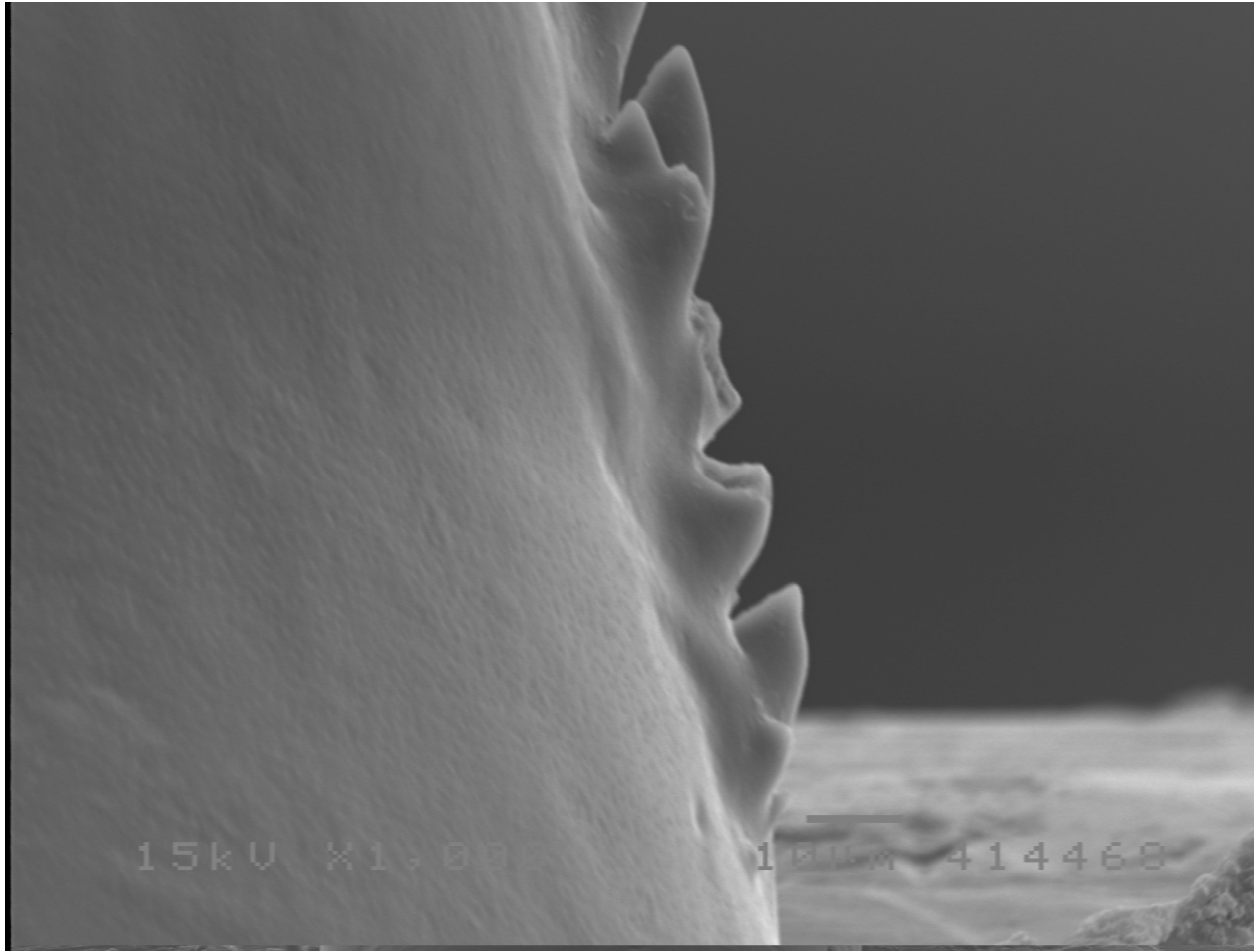
57 **Figure 4.30:** LAS in lateral view (close-up) of *Paruroctonus boreus* (male, Worland, Wyoming, USA).



58 **Figure 4.31:** LAS in ventral view (close-up) of *Paruroctonus arnaudi* (male, El Socorro, Baja California, Mexico).



59 **Figure 4.32:** LAS in lateral view (close-up) of *Serradigitus joshuaensis* (female, ABDSP, California, USA).

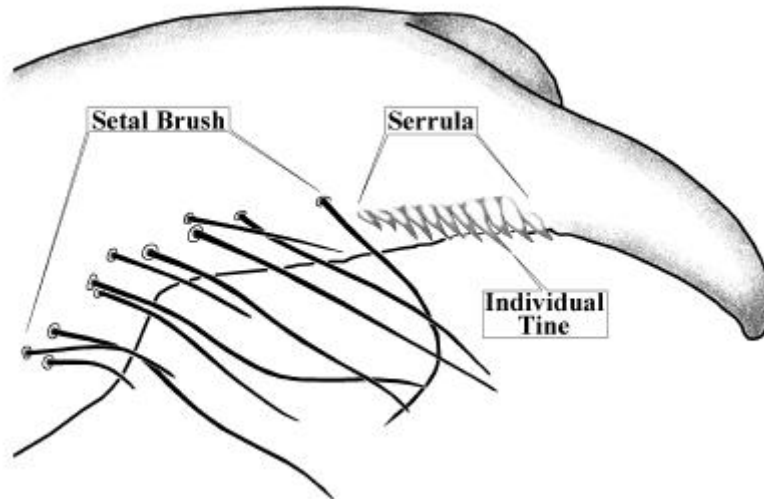


60 **Figure 4.33:** LAS in ventral view (close-up) of *Paruroctonus ventosus* (female, El Socorro, Baja California, Mexico) showing the doubling of some denticles.

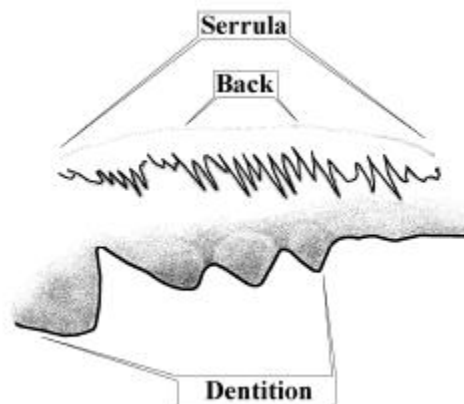
Chapter V: Serrula of Four Genera in the Family Vaejovidae

Introduction

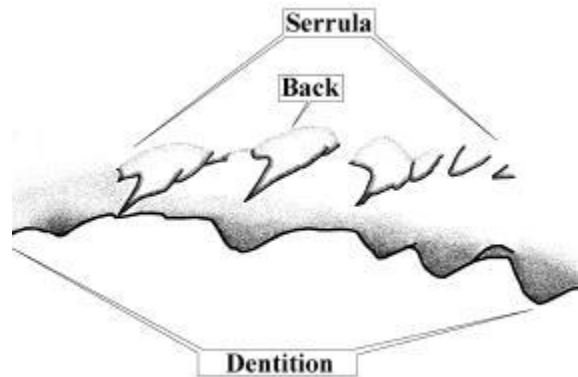
The structure known as serrula is found on the movable cheliceral finger of many scorpions (Figure 5.1), and serves an, as of yet, unknown function. In 2006, there was a paper written that fully explored the history of the structure upon which this chapter is based (Graham and Fet, 2006), and its misdiagnosis by many scorpion systematists for various reasons. Researchers dealing with the superfamilies Buthoidea and Scorpionoidea never recorded this structure. Those working in the superfamily Chactoidea see the organ often but may not be able to quantify any patterns and may disregard it. Others have deemed the organ too specific for certain taxa and ignored it (Vachon, 1945, 1971; Gertsch & Soleglad, 1972; Sissom and Stockwell, 1991). The organ itself has been mainly observed in the families Vaejovidae and Superstitioniidae, but its presence, or lack thereof, has been grossly misinterpreted. Stockwell (unpublished Ph.D. dissertation, 1989) stated that serrula were absent in the genera, all of which are presumed related, *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* and his key to families and genera of North America states lack of serrula as a key character for these four genera. Since then, the *lack* of serrula in these four genera has been considered a synapomorphy of the clade.



61 **Figure 5.1:** Location of pertinent morphology of the movable cheliceral finger showing the setal brush, serrula, and their arrangements in the genus *Vaejovis* (adapted from Fet *et al.*, 2006d).



62 **Figure 5.2:** Representation of serrula in the genus *Smeringurus* showing the tines, their backs, and the dentition of the movable, cheliceral finger (adapted from Fet *et al.*, 2006d).



63 **Figure 5.3:** Representation of serrula in the genus *Paruroctonus* showing the tines, their backs, and the dentition of the movable, cheliceral finger (adapted from Fet *et al.*, 2006d).

Materials and Methods

Over 80 SEM images of 16 species of the genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* were examined in this study. Highly developed serrula, such as those in the genus *Smeringurus*, can be examined using only a dissecting microscope, but the SEM is necessary for thorough investigation of the organ in all taxa. In addition, we documented the development of serrula in other Vaejovids as well as members of the families Iruidae, Chactidae, Superstitioniidae, and Pseudochactidae. For a complete list of the material examined, see Appendix C.

Results and Discussion

The presence of serrula was first documented in the genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* of the family Vaejovidae in this study. Some important observations made in this work include: despite the serrula being present in all of these, and other, genera, the form, consistency, number of tines, and degree of preservation are considerably variable. In addition, a single row of setae

located basally to the serrula was observed that we termed the “setal brush” (Fig. 5.1). The degree of setation in the brush area varies greatly, as low as two setae to almost completely covered, but is always present in these four genera. See Table 5.1 for a complete breakdown of the numbers of tines in all specimens examined.

In the genus *Paravaejovis* the serrula appear weakly developed, with species having only three to six tines. The row begins at about the middle of the movable, cheliceral finger and extends distally to the last one-fifth just before the finger curves. Tines are spaced relatively wide with enough space between the tines to fit another. The shape of the tines appears to depend on the density of the row. Those with a higher density tend to have long, thin tines, while those with a less dense row have shorter and broader tines that abruptly taper to a sharp point. The setal brush is quite sparse with few tines and is in line with but does not extend to the basal portion of the serrula.

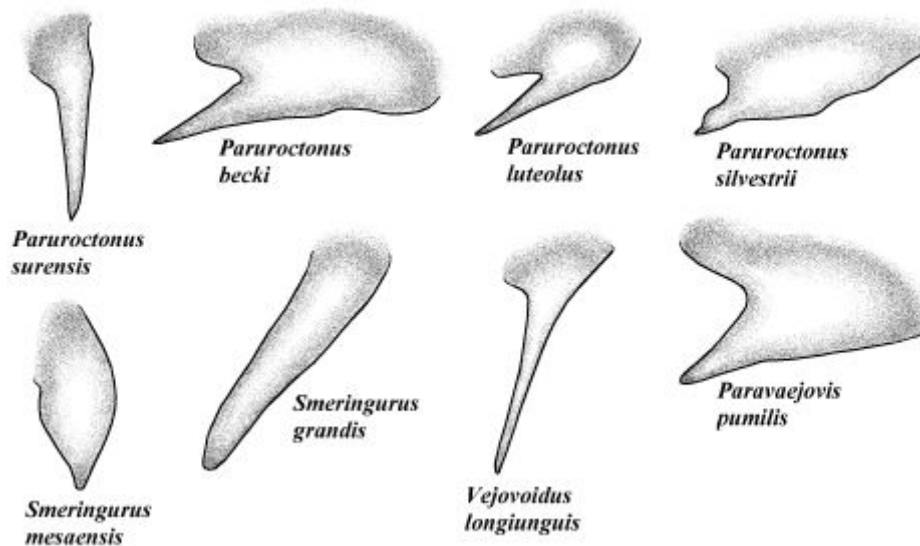
The genus *Paruroctonus* shows great variability regarding density of tines, zero to seven tines based on ten examined species. *P. gracilior* and *P. boreus* showed no observable tines in the three specimens examined of each species. Two distal tines were observed in *P. luteolus*, with one much smaller than the other and a very reduced setal brush comprised of two setae located basally. *P. silvestrii* had two tines located distally with an extensive setal brush that ended close to the proximal end of the serrula. *P. ventosus* also had two tines. *P. becki* had tine numbers ranging from zero to five tines, and *P. utahensis* had three tines. Both of these species had wide spacing between the tines. *P. arnaldi* had five worn tines and a very well developed setal brush that ended close to the serrula. *P. surensis* and *P. stahnkei* both had seven tines. The serrula in *P. surensis* was arranged in two groups of tines with wide spacing between them and exhibited the most developed example of serrula in *Paruroctonus*. The tines of *P. stahnkei* were very close in proximity and greatly worn.

5 Table 5.1: Number of serrula tines observed in all specimens examined for four genera and 16 species of the family Vaejovidae (adapted from Fet *et al.*, 2006d).

	Specimen #, Age / Gender	Locality *	Tines
<i>Paravaejovis pumilis</i>	1, male	Ciudad Constitución	-/6
	2, male	Ciudad Constitución	3/-
<i>Vejovoidus longiunguis</i>	1, female	Vizcaino Desert	0/0
	2, subadult female	Vizcaino Desert	1/2
	3, female	Las Bombas	0/0
	4, subadult male	Vizcaino Desert	0/0
	5, subadult female	Las Bombas	0/0
	6, subadult male	Las Bombas	0/0
	7, subadult male	Las Bombas	0/0
	8, juvenile	Las Bombas	0/0
	9, juvenile	Las Bombas	0/0
	10, subadult female	Las Bombas	0/0
	11, female	Vizcaino Desert	0/-
<i>Smeringurus aridus</i>	1, male	ABDSP, California	22/21
	2, male	ABDSP, California	17/-
	3, juvenile	ABDSP, California	13/8
	4, juvenile female	ABDSP, California	8/12
<i>Smeringurus grandis</i>	1, male	Oakies Landing	6/-
	2, female	Bahia de Los Angeles	15/13
	3, juvenile male	Oakies Landing	4/4
	4, juvenile female	Oakies Landing	6/8
<i>Smeringurus mesaensis</i>	1, female	ABDSP, California	3/-
	2, juvenile	San Bernardino Co., California	1/-
	3, juvenile	San Bernardino Co., California	10/-
	4, juvenile	San Bernardino Co., California	6/-
<i>Smeringurus v. immanis</i>	1, female	1000 Palms, California	24/-
<i>Paruroctonus arnaudi</i>	1, male	El Socorro	5/3
	2, juvenile	El Socorro	3/-
<i>Paruroctonus becki</i>	1, female	San Bernardino Co., California	5/-
	2, female	San Bernardino Co., California	3/3
	3, juvenile	Joshua Tree, California	1/-
	4, female	Joshua Tree, California	4/3
	5, female	San Bernardino Co., California	2/2
	6, female	San Bernardino Co., California	0/0
	7, female	San Bernardino Co., California	1/2
	8, juvenile	San Bernardino Co., California	3/1
<i>Paruroctonus boreus</i>	1, male	Warland, Wyoming	0/-
	2, male	Warland, Wyoming	0/0
	3, male	Warland, Wyoming	0/0
<i>Paruroctonus gracilior</i>	1, male	Cuatro Ciénegas	0/0
	2, male	Cuatro Ciénegas	0/-
	3, juvenile	Lordsberg, New Mexico	0/0
<i>Paruroctonus luteolus</i>	1, female	ABDSP, California	2/2
<i>Paruroctonus silvestrii</i>	1, male	ABDSP, California	2/2
<i>Paruroctonus stahnkei</i>	1, female	Mesa, Arizona	7/-
<i>Paruroctonus surensis</i>	1, male	Las Bombas	7/-
<i>Paruroctonus utahensis</i>	1, male	Kermit, Winkler Co., Texas	0/-
	2, female	Kermit, Winkler Co., Texas	3/-
	3, male	Kermit, Winkler Co., Texas	6/7
<i>Paruroctonus ventosus</i>	1, male	El Socorro	2/-

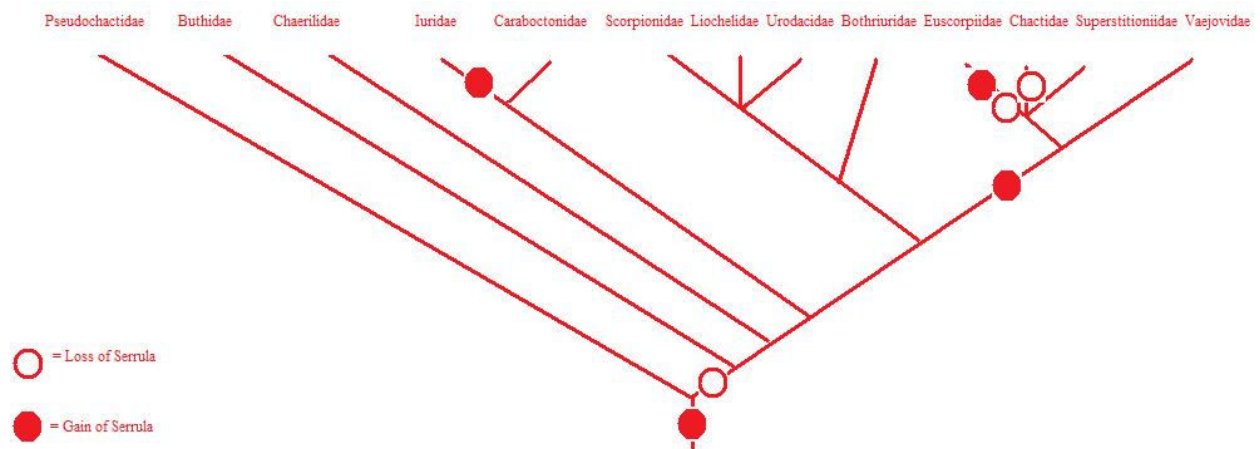
In the genus *Smeringurus*, the serrula is by far the most developed of the four genera examined; therefore the term vestigial may not be accurate. The setal brush is also much more developed, having up to 28 setae sometimes in multiple rows. *S. grandis* had between four and fifteen tines that were positioned closely. Again, the lower the density of tines, the shorter and broader the tines were. *S. mesaensis* had between one and ten tines that were closely arranged and reduced by what we determined to be wearing. *S. aridus*, 21 tines, and *S. vachoni immanis*, 24 tines, have by far the most developed serrula that, in both cases, were not worn but instead long with narrow backs.

The genus *Vejovoidus* may have the most underdeveloped serrula of all. Out of the eleven specimens examined of *V. longiunguis*, only one specimen had any serrula at all. This specimen had one tine on one chelicera and two on the other. The tine was very long and thin with a narrow back. Those specimens lacking serrula had very well developed setal brushes that were much more prominent than the specimen with serrula.



64 **Figure 5.4:** Examples of serrula tines in the Vaejovid genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* (adapted from Fet et al., 2006d).

The evolution of serrula within the order can be viewed in two ways that meet the rule of parsimony. Either serrula is plesiomorphic in all Recent scorpions and lost at the Buthida node and was inherited by the primitive scorpion *Pseudochactas* or lack of serrula is ancestral and arose independently in *Pseudochactas*. If the latter is true, the serrula would have to have evolved independently in the family Iuridae and the superfamily Chactoidea, be lost in the family Euscorpiidae and the genus *Anuroctonus* (Family: Chactidae), and then evolve again in the genus *Chactopsis* (Family: Euscorpiidae). This would require a total of six steps. If the derivation of serrula in the three separate instances is treated as distinct characters, homoplasy is restricted to only the superfamily Chactoidea. If the evolution of serrula is modeled as a two state character instead of the three proposed by Stockwell (1989) in his unpublished thesis, recognizing the advancements in the understanding of scorpion systematics since his work, then the number of steps is reduced to four. It has also been hypothesized that the setal brush may in fact replace the serrula in function as well as position. Perhaps it is even a different state of the same cladistic character. Until the full functionality of the serrula is determined, we will be unable to make this determination.

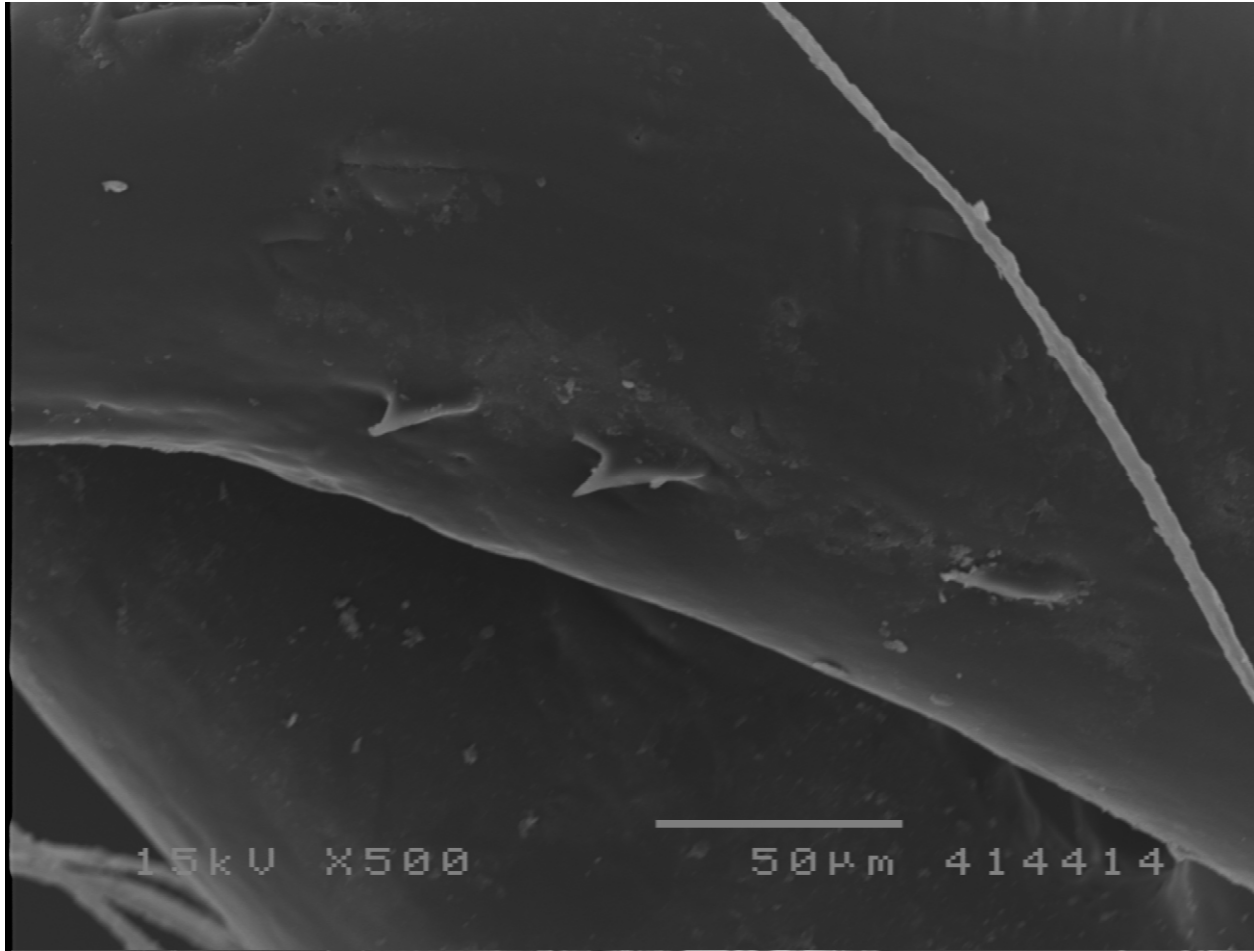


65 **Figure 5.5:** Cladogram showing the losses and gains of serrula as a character in the currently accepted scheme of scorpion relationships (hierarchy from Soleglad & Fet, 2003).

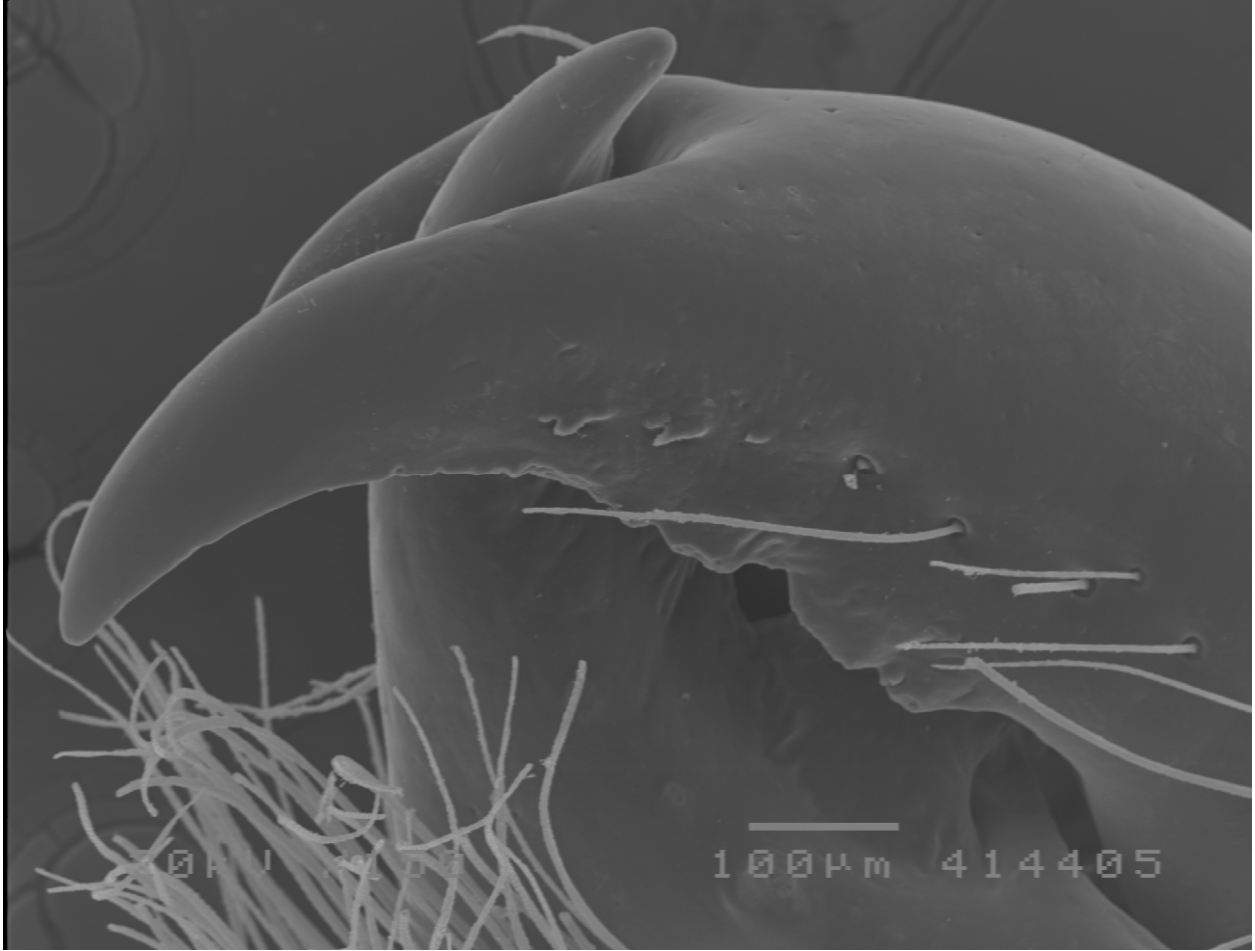
The function of serrula is hypothesized to be of a grooming nature. The feeding hairs around the chelicera become covered in the undigestible remains of the prey that has been masserated by the chelicera as a part of the external digestive processes of scorpion feeding. The comb-like anatomy of the serrula would provide a means of removing the debris that would accumulate in the area. Also, the broken nature of the tines in many cases shows a very mechanical use must be implemented in order to cause the damage seen.



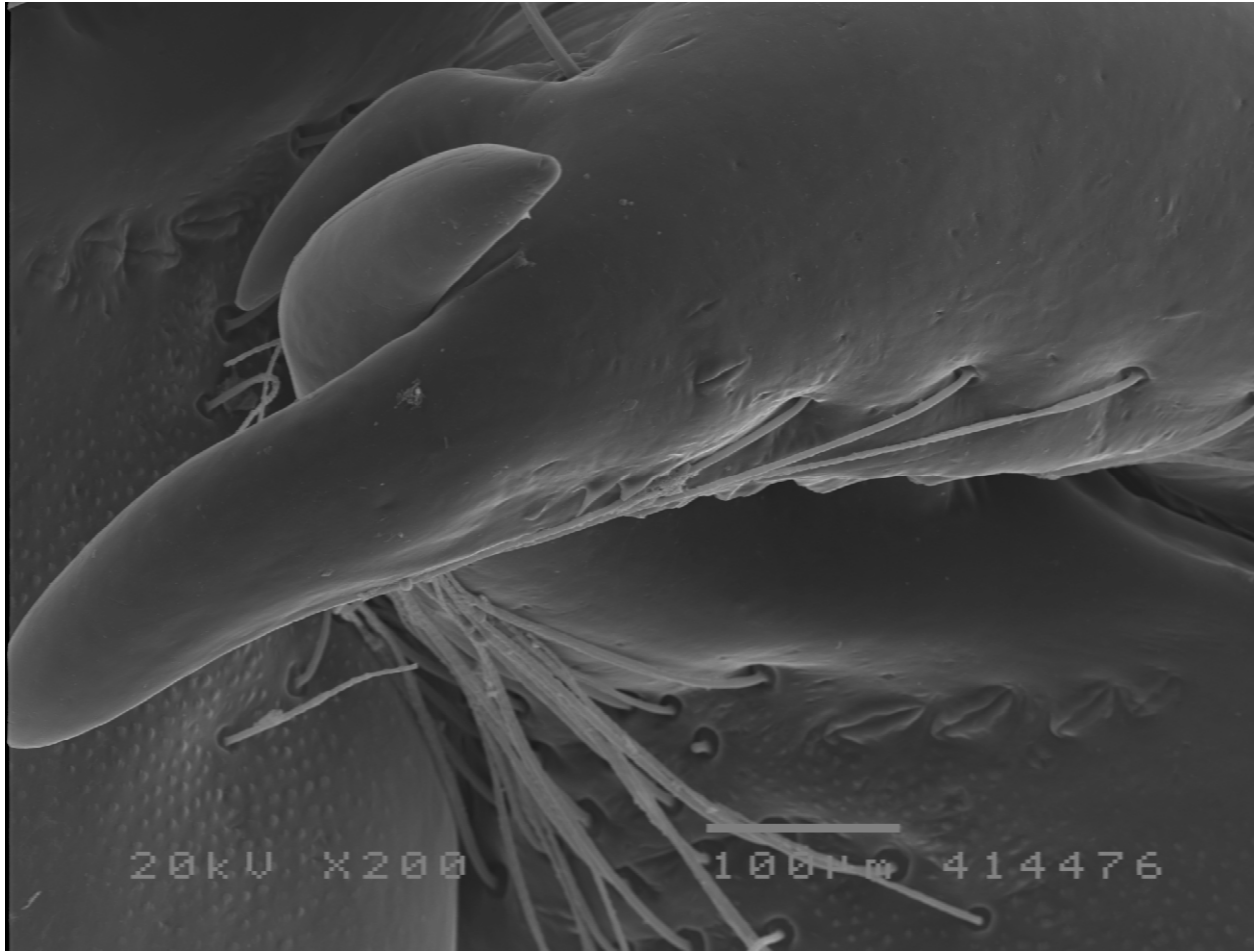
66 **Figure 5.6:** Movable cheliceral finger of *Paravaejovis pumilis* showing three tines of the serrula (male, Ciudad Constitucion, Baja California Sur, Mexico).



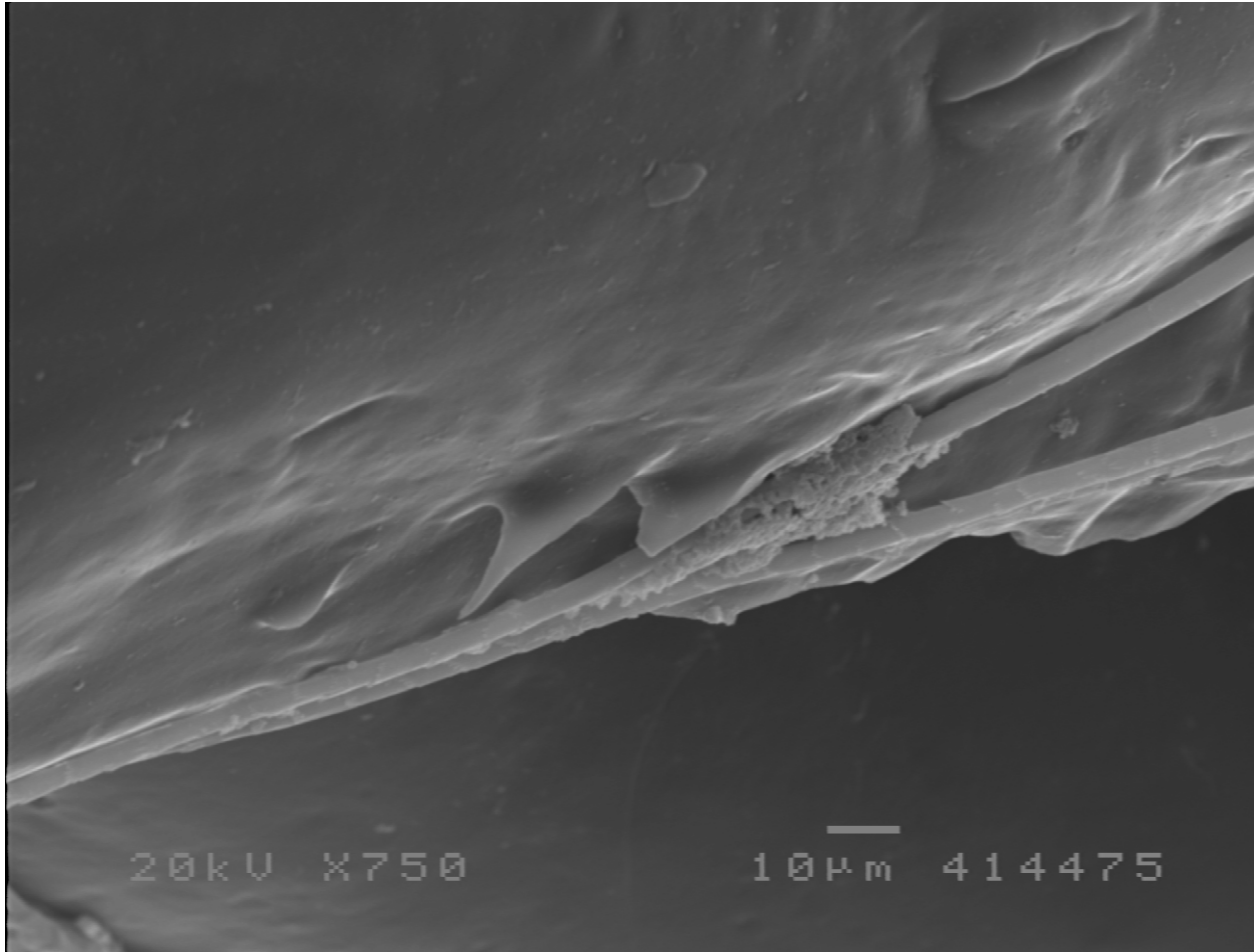
67 **Figure 5.7:** Movable cheliceral finger of *Paravaejovis pumilis* showing three tines of the serrula (male, Ciudad Constitucion, Baja California Sur, Mexico) (close-up).



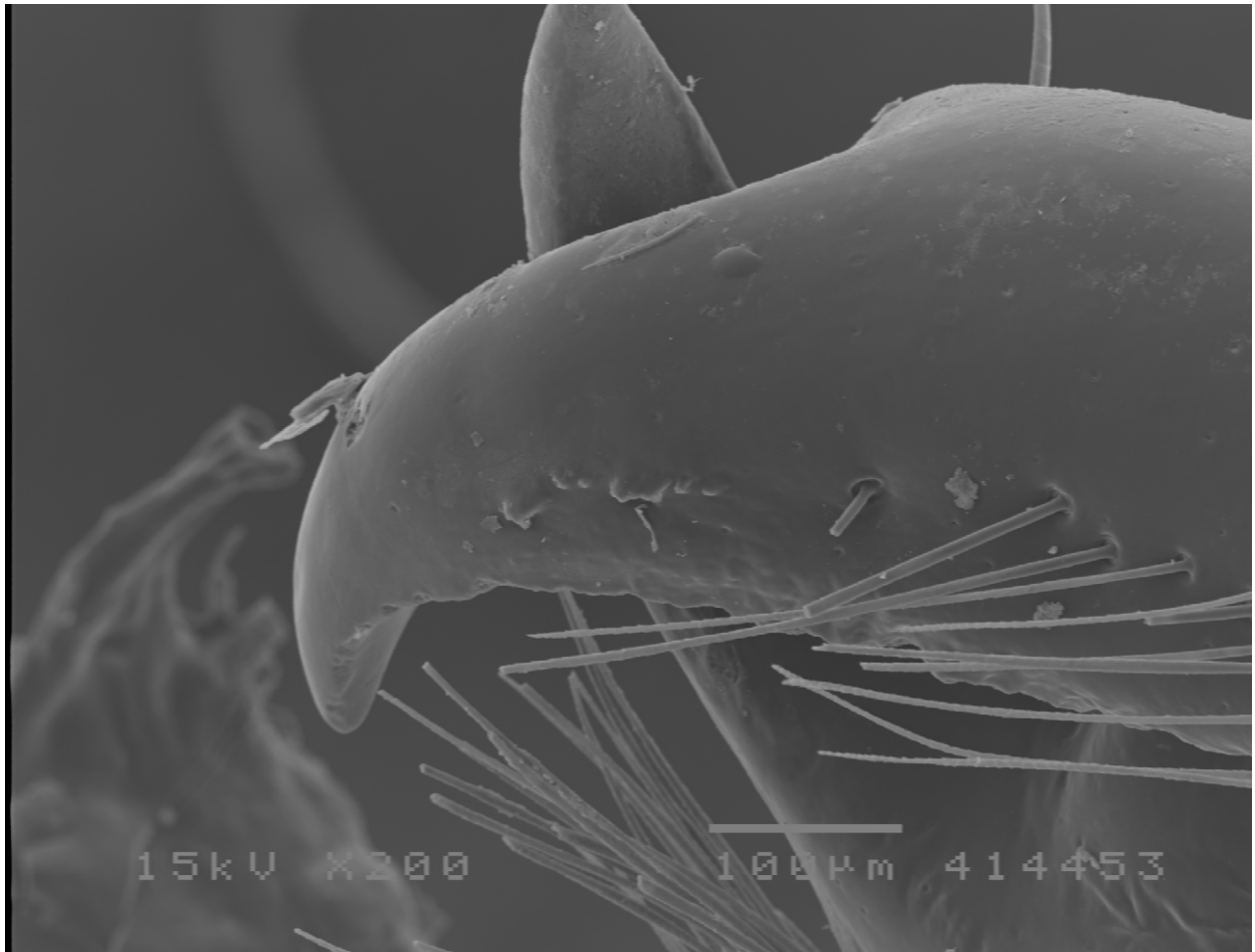
68 **Figure 5.8:** Movable cheliceral finger of *Paruroctonus araudi* showing three tines of the serrula (male).



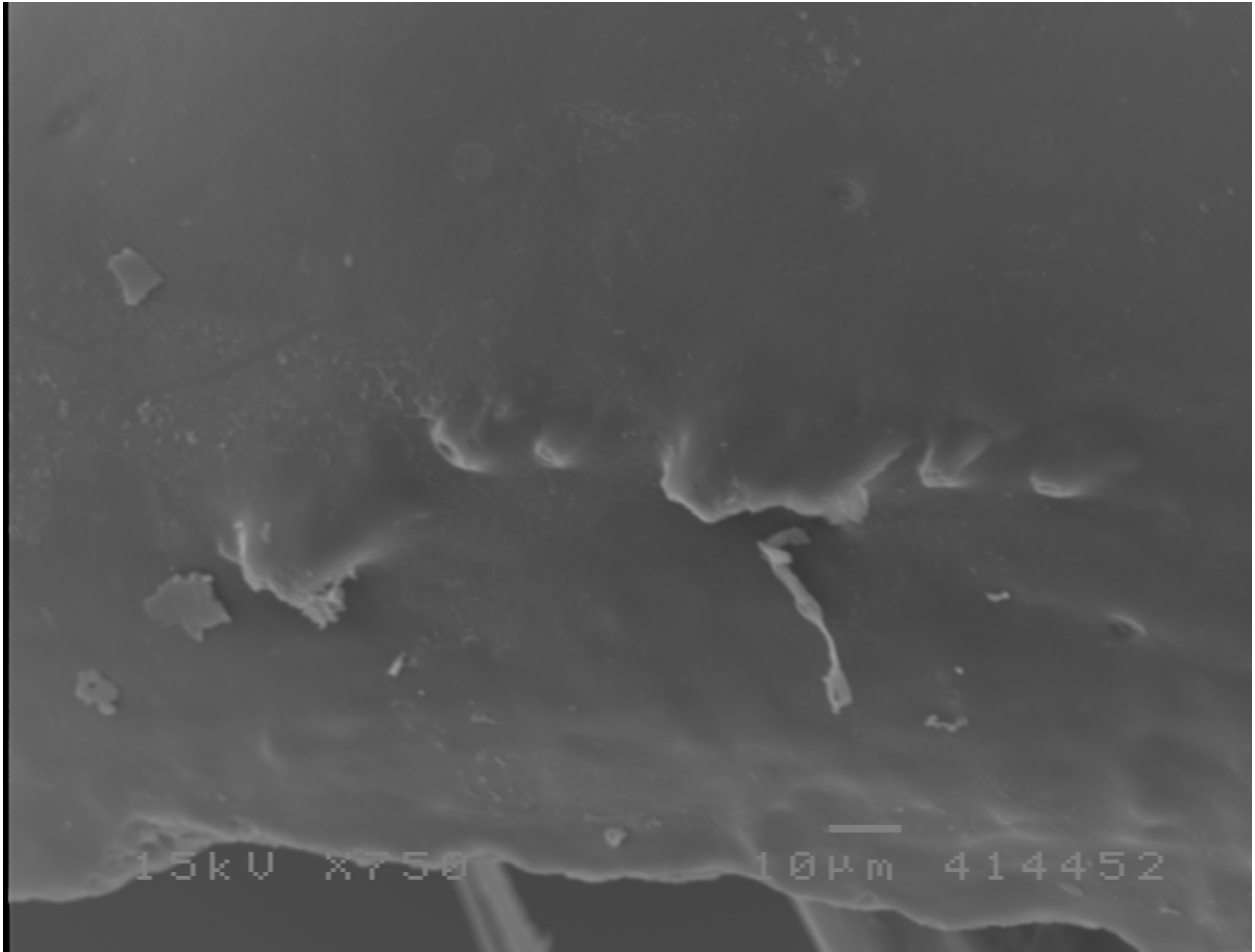
69 **Figure 5.9:** Movable cheliceral finger of *Paruroctonus becki* showing two tines of the serrula.



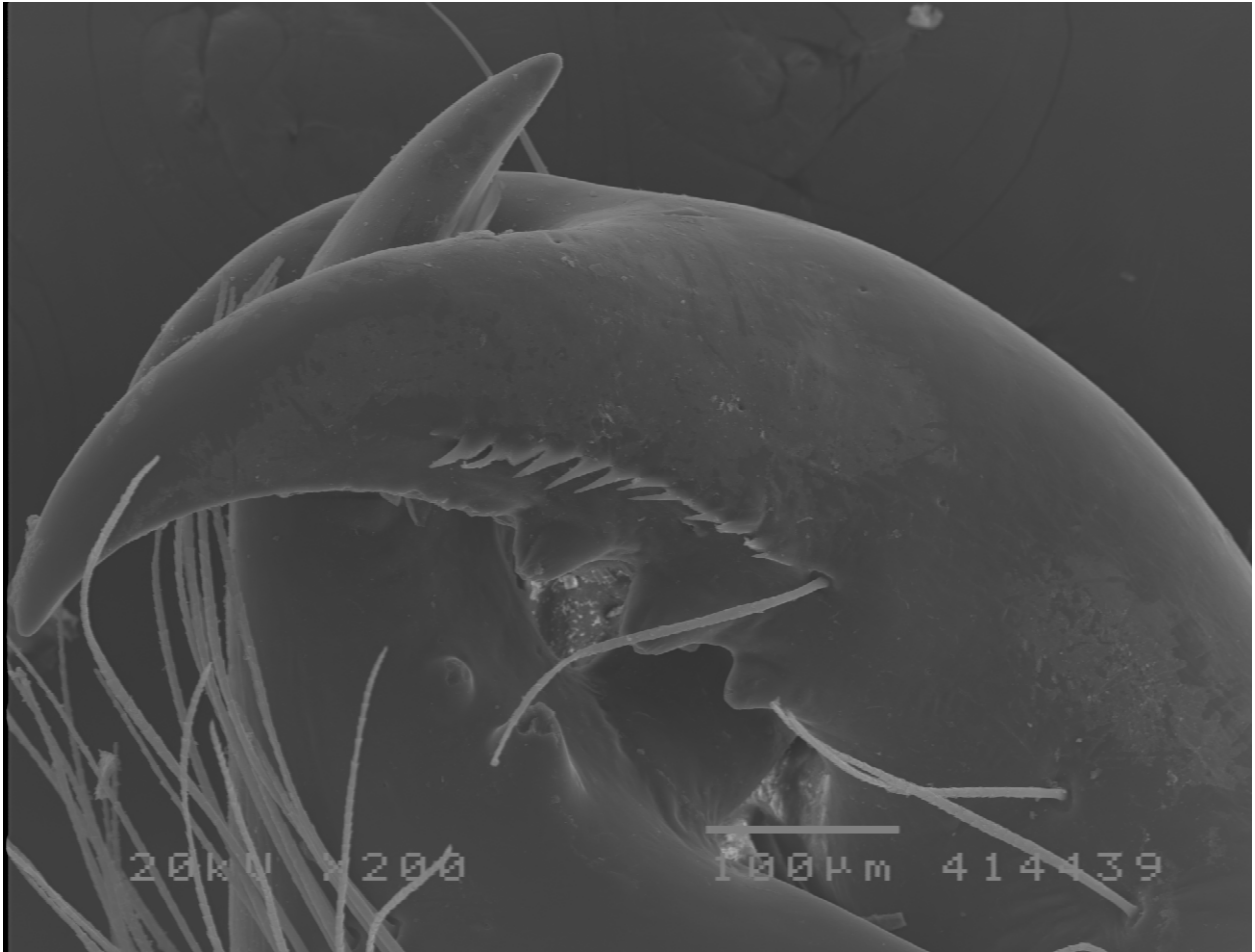
70 **Figure 5.10:** Close-up of specimen shown in Figure 5.9 showing two tines of the serrula in *Paruroctonus becki*.



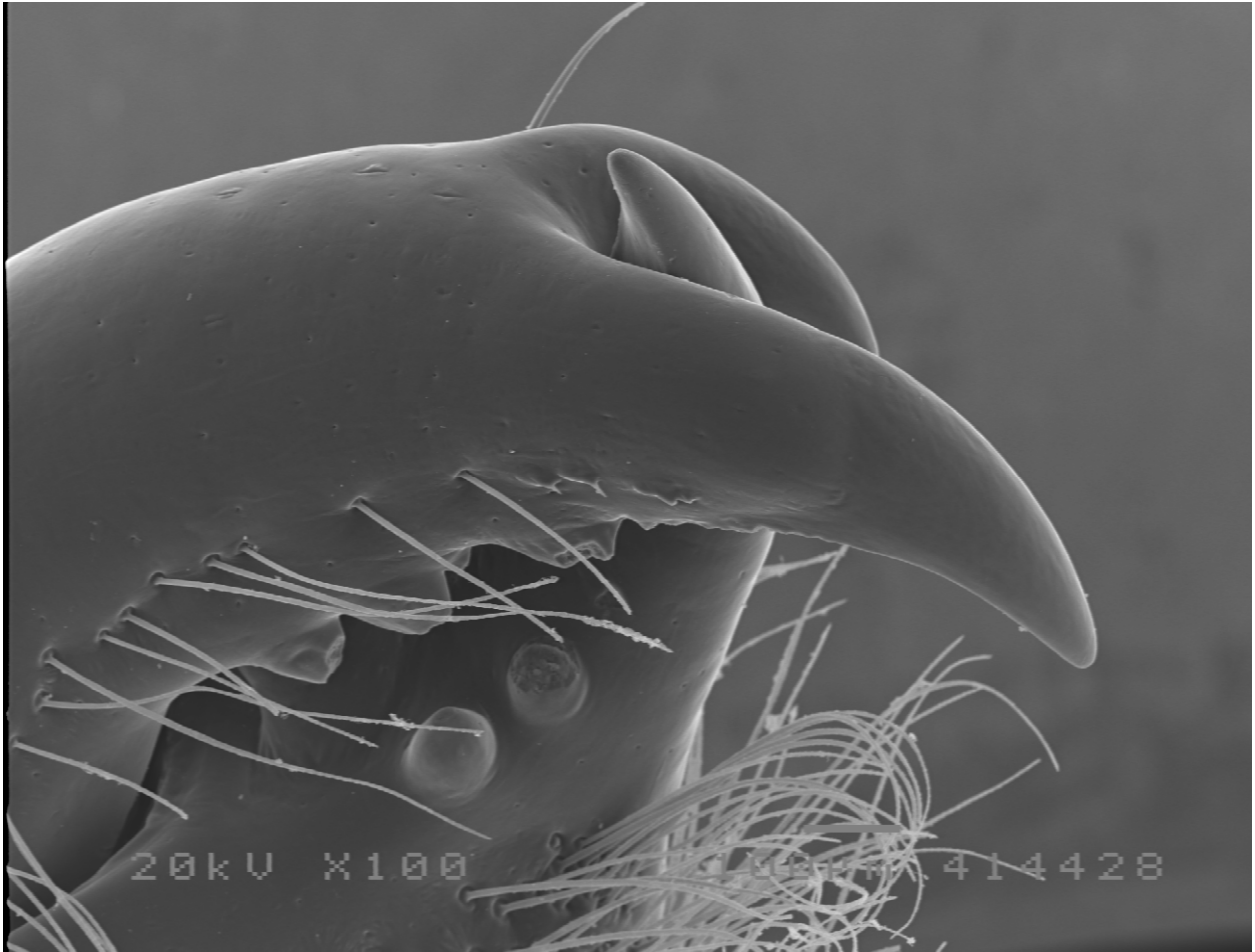
71 **Figure 5.11:** Movable cheliceral finger of *Paruroctonus utahensis* showing heavily worn or reduced tines of the serrula.



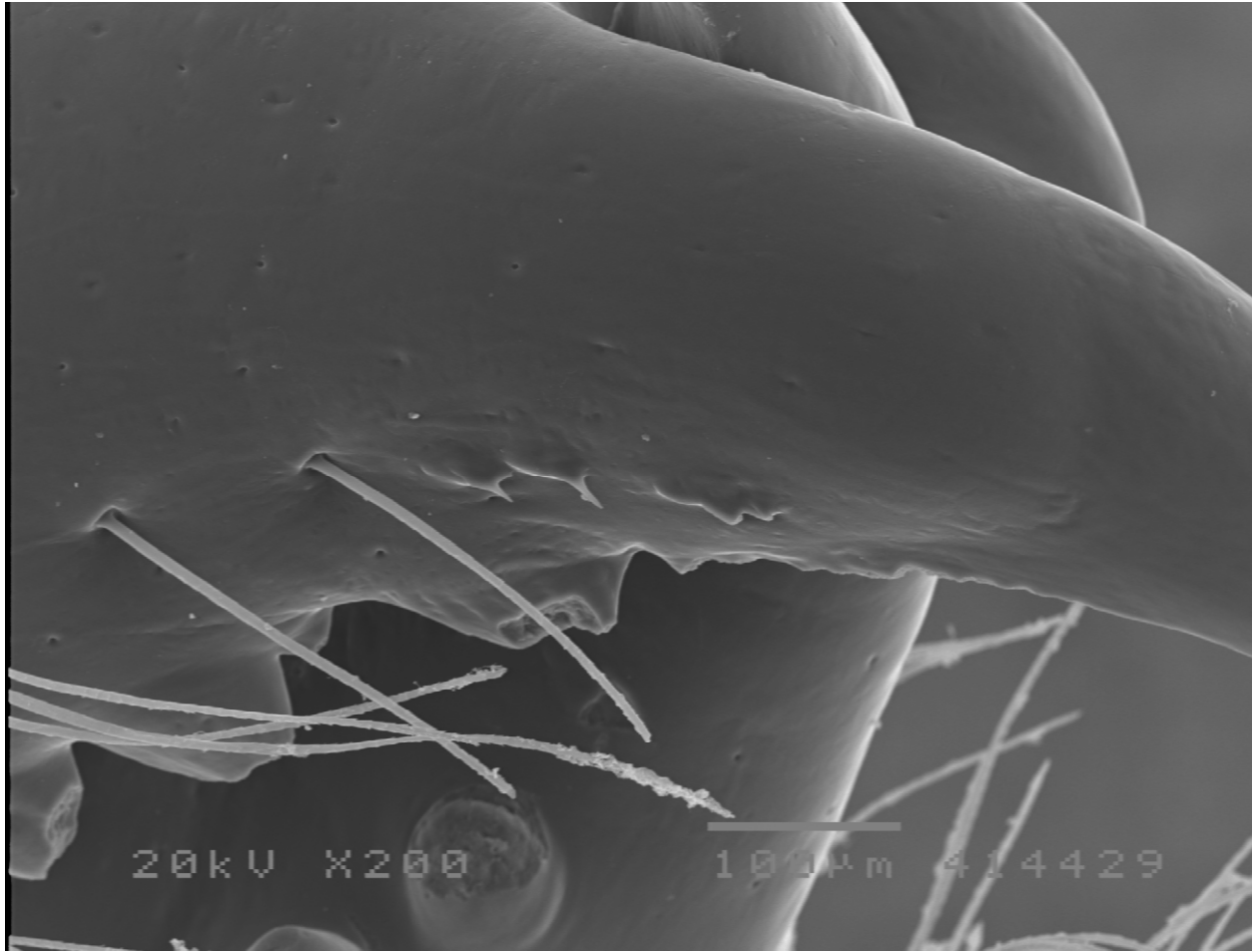
72 **Figure 5.12:** Close-up of specimen shown in Figure 5.11 showing serrula of *Paruroctonus utahensis*.



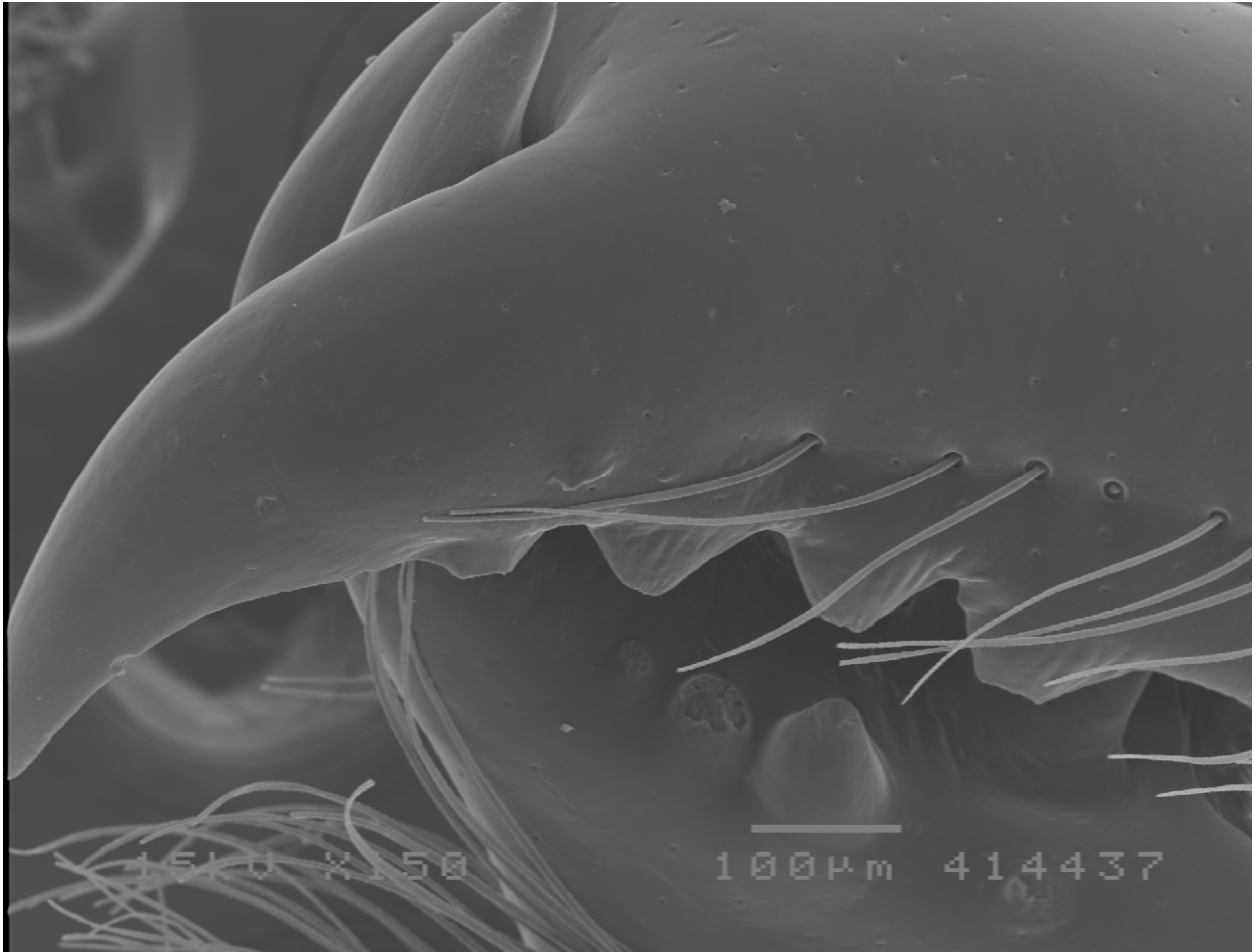
73 **Figure 5.13:** Movable cheliceral finger of *Smeringurus aridus* showing thirteen, sharp tines of the serrula (juvenile).



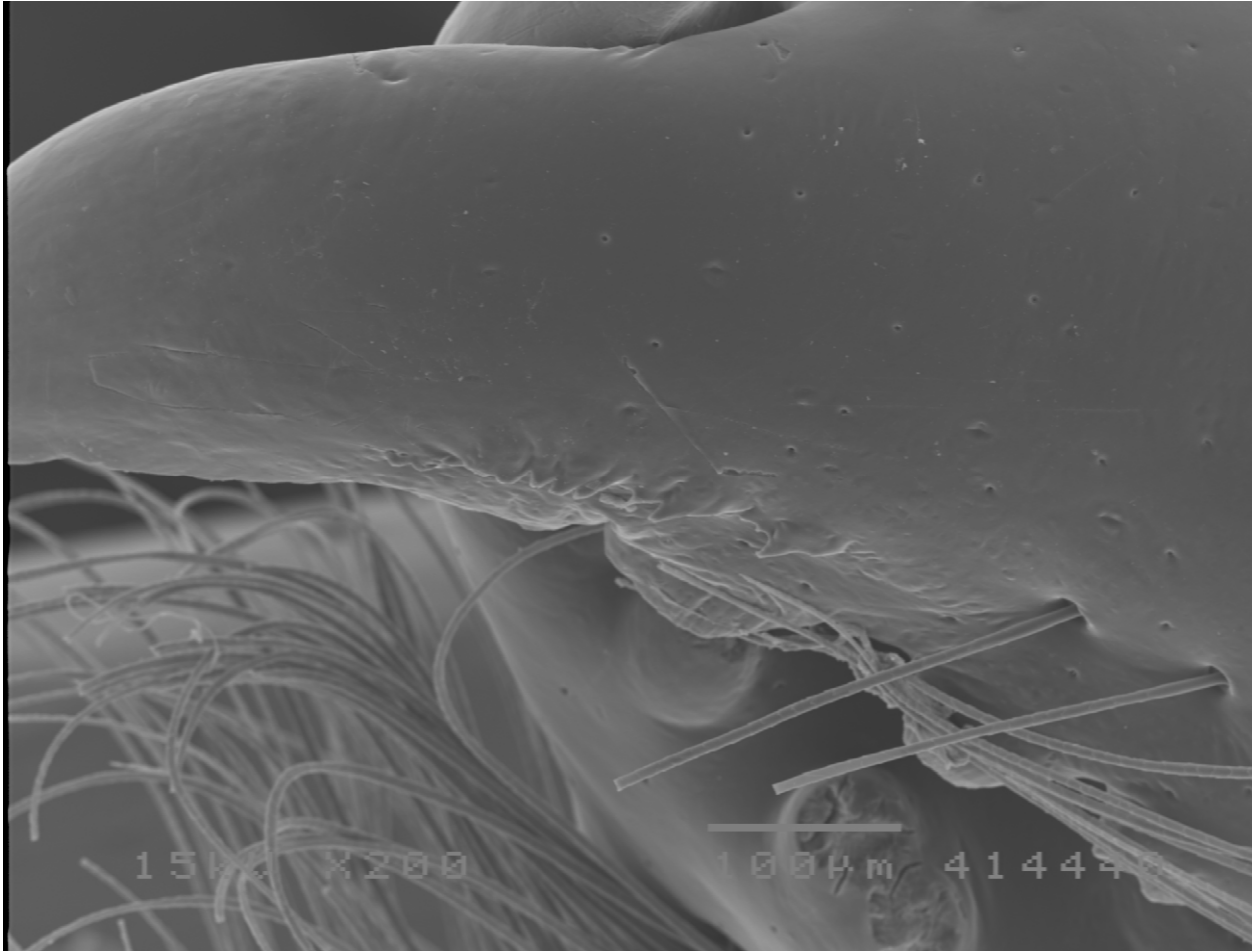
74 **Figure 5.14:** Movable cheliceral finger of *Smeringurus grandis* showing four tines of the serrula (juvenile male).



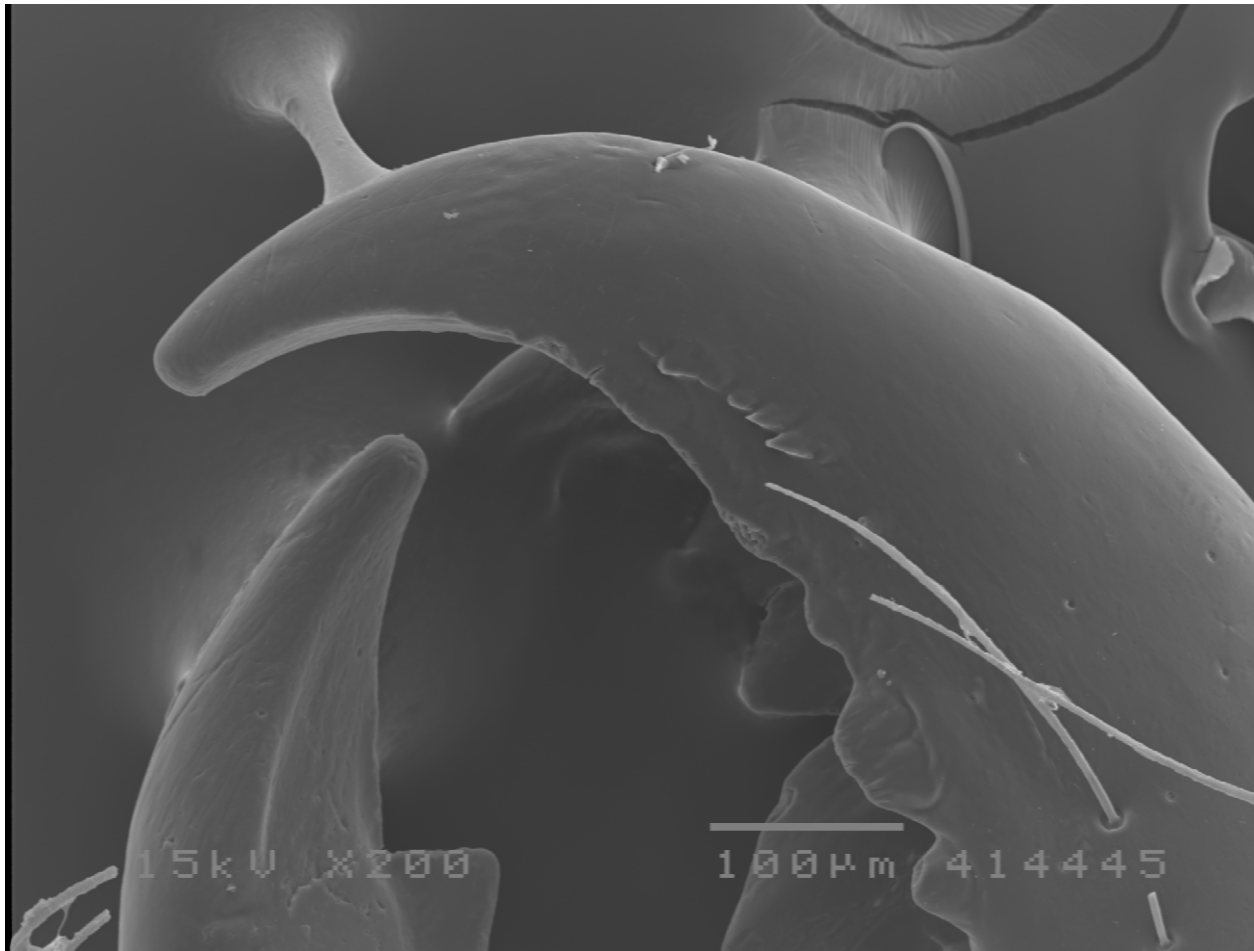
75 **Figure 5.15:** Close-up of specimen shown in Figure 5.14 showing serrula of *Smeringurus grandis* (juvenile male).



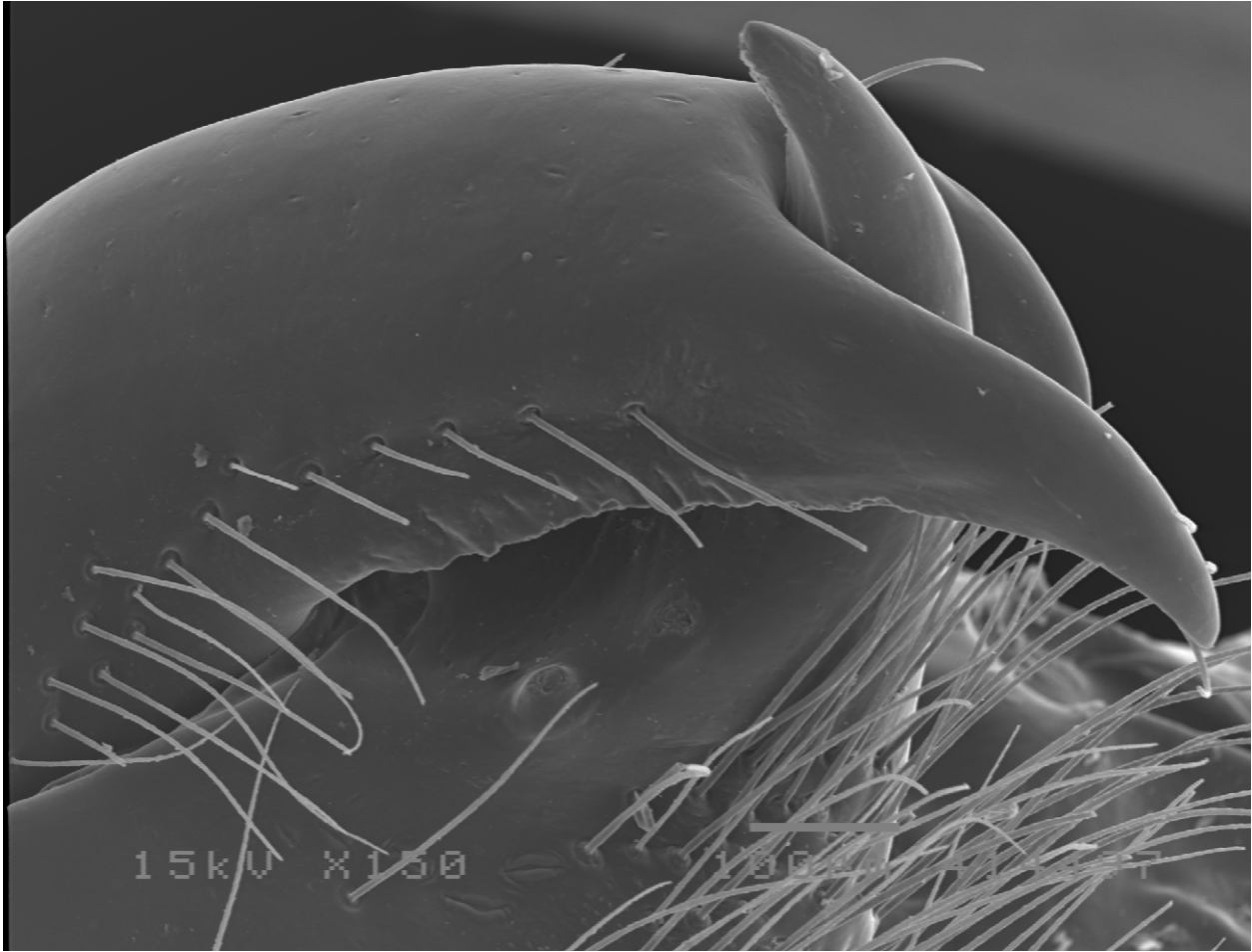
76 **Figure 5.16:** Movable cheliceral finger of *Smeringurus mesaensis* showing a single, blunted tine of the serrula (juvenile).



77 **Figure 5.17:** Movable cheliceral finger of *Smeringurus mesaensis* showing ten irregular tines of the serrula (juvenile).



78 **Figure 5.18:** Movable cheliceral finger of *Smeringurus mesaensis* showing six blunted tines of the serrula (juvenile).



79 **Figure 5.19:** Movable cheliceral finger of *Vejovoidus longiunguis* showing no serrula but an elongated setal brush that extends through the area normally occupied by the serrula instead (subadult male).

Chapter VI: General Conclusions

Even though the order Scorpiones has been studied heavily over the years, new discoveries are waiting to be made. The three structures outlined in this work are prime examples that animals as big as scorpions still need to be examined under the scrutiny of microscopy to fully understand their physiology and anatomy. These examinations may not only yield new anatomy but also may create new anatomical characters for systematics. The constellation array has been documented in all scorpions examined and shows promising variation trends, the LAS appear to be a synapomorphy of the family Vaejovidae, and serrula is now confirmed in all members of the superfamily Chactoidea. The variability between different levels viewed in each of these structures could prove to be of systematic importance if someone were to find a way to reliably diagnose and quantify it. Each of these structures was found on very different parts of the animal (the chelicera, telson, and pedipalps) and many areas have still not been examined.

What I have done could be viewed as the beginnings of an microanatomical atlas of the entire scorpion that must be continued by others and, most likely, finished by still others. Lastly, the discovery of these new structures implies unknown functions. The constellation array may be a thermosensor according to pilot data obtained by Dr. Douglas Gaffin at the University of Oklahoma, the LAS may be a “sting-stopper” of sorts, and the serrula could provide a means of grooming the feeding hairs in and around the gullet of the scorpion. The determination of the functions can only be achieved by others with the means to do behavioral, physiological, and TEM studies of living or new material and the continuation of my atlas-like work in more taxa and individuals of those already examined. This would provide a greater sample size and determinations of variability at more levels (species, population, etc.) and between ages, sexes, and individuals.

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Appendixes

Appendix A: Constellation Array Material Examined

(taxonomy after Sologlad & Fet, 2003; Sologlad et al. 2005; Fet & Sologlad, 2005)

Parvorder Buthida, superfamily Buthoidea, family Buthidae: *Centruroides hentzi* (Banks, 1910), female, Alachua Co., Florida, USA; *Lychas mucronatus* (Fabricius, 1798), female, Hanoi, Vietnam; *Mesobuthus caucasicus* (Nordmann, 1840), female, Repetek, Karakum Desert, Turkmenistan; *Mesobuthus eupeus* (C.L. Koch, 1839), female, Repetek, Karakum Desert, Turkmenistan.

Parvorder Chaerilida, superfamily Chaeriloidea, family Chaerilidae: *Chaerilus celebensis* Pocock, 1894, juvenile, Mapur Island, Indonesia.

Parvorder Iurida, superfamily Chactoidea, family Chactidae: *Belisarius xambeui* Simon, 1879, female, Fogars de Monclus, Barcelona Province, Spain; *Brotheas gervaisii* Pocock, 1893, female, Kaw, French Guiana; *Nullibrotheas allenii* (Wood, 1863), female, Cabo San Lucas, Baja California Sur, Mexico; *Uroctonus mordax* Thorell, 1876, male, Kalmiopsis Wilderness, Siskiyou National Forest, Oregon, USA; **family Euscorpiidae:** *Euscorpius gamma* (Caporiacco, 1950), male and female, Planinsko Polje, Slovenia; *Euscorpius italicus* (Herbst, 1800), male, Epirus, Greece; *Euscorpius tergestinus* (C. L. Koch, 1837), female and juvenile, Sežana, Slovenia; **family Superstitioniidae:** *Superstitionia donensis* Stahnke, 1940, female, San Diego, California, USA; **family Vaejovidae:** *Serradigitus gertschi gertschi* (Williams, 1968),

female, San Diego, California, USA; *Serradigitus joshuaensis* (Soleglad, 1972), female, Anza-Borrego Desert State Park, California, USA; *Serradigitus subtilimanus* (Soleglad, 1972), female, Anza-Borrego Desert State Park, California, USA; *Smeringurus mesaensis* (Stahnke, 1957), female, Anza-Borrego Desert State Park, California, USA; *Vaejovis carolinianus* (Beauvois, 1805), *Vaejovis eusthenura* (Wood, 1863), female, Cabo San Lucas, Baja California Sur, Mexico; *Vejovoidus longiunguis* (Williams, 1969), female, Vizcaino Desert, Baja California Sur, Mexico; **superfamily Iuroidea, family Raboetonidae:** *Hadrurides charcasus* (Karsch, 1879), female, Peru; *Hadrurus obscurus* Williams, 1970, male, Anza-Borrego Desert State Park, California, USA; **family Iuridae:** *Calchas nordmanni* Birula, 1899, juvenile, Megisti (=Kastelorizo) Island, Greece; female, Anamur, Turkey; **superfamily Scorpionoidea, family Bothriuridae:** *entromachetes pocockii* (Kraepelin, 1894), Lebu, Chile; **family Hemiscorpiidae:** *Hadogenes bicolor* Purcell, 1899, female, South Africa; **family Scorpionidae:** *Bioculus comondae* Stahnke, 1968, male, La Paz, Baja California, Mexico.

Parvorder Pseudochactida, superfamily Pseudochactoidea, family

Pseudochactidae: *Pseudochactas ovchinnikovi* Gromov, 1998, juvenile female, Akmachit, Babatag Mountains, Surkhandarya Region, Uzbekistan

Appendix B: LAS Material Examined

Superfamily Pseudochactoidea

Pseudochactidae: *Pseudochactas ovchinnikovi* Gromov, 1998, Babatag, Uzbekistan, 2 ♀ (VF).

Superfamily Buthoidea

Buthidae: *Alayotityus nanus* Armas, 1973, El Cobre, Santiago de Cuba Province, Cuba, ♀ (VF); *Androctonus bicolor* Ehrenberg, 1828, Lhav, Israel, ♂ (MES); *Anomalobuthus rickmersi* Kraepelin, 1900, Bukhara, Uzbekistan, 1 ♂ 1 ♀ (VF); *Buthacus macrocentrus* (Ehrenberg, 1828), Abu Dhabi, United Arab Emirates, ♂ (VF); *Buthus occitanus* Amoreux, 1789, Casablanca, Morocco, (MES); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Centruroides suffusus* (Pocock, 1902), Durango, Mexico, ♂ (VF); *Compsobuthus matthiesseni* (Birula, 1905), Baghdad, Iraq, ♀ (VF); *Grosphus hirtus* Kraepelin, 1901, Tamatave Province, Perinet, Madagascar, ♀ (MES); *Hottentotta minax* (L. Koch, 1875), Eritrea, ♂ (VF); *Isometrus maculatus* (DeGeer, 1778), Vaite Pava, Makatea, French Polynesia, ♂ (USNM); *Leiurus quinquestriatus* (Ehrenberg, 1828), Saudi Arabia, ♀ (VF), Negev, Israel, ♀ (VF); *Liobuthus kessleri* Birula, 1898, Chardara, Kazakhstan, ♀ (VF); *Lychas* sp., Indonesia, ♀ (VF); *Lychas mucronatus* (Fabricius, 1798), Hanoi, Vietnam, ♀ (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Chardara, Kazakhstan, ♀ (VF); *Mesobuthus eupeus* (C.L. Koch, 1839), Kzyl-Orda, Kazakhstan, ♀ (VF); *Microbuthus* sp., Rusail, Oman, ♂ (GL); *Microtityus jaumei* Armas, 1974, San Juan Botanical Garden, Santiago de Cuba Province, (VF); *Orthochirus gromovi* Kovařík, 2004,

Repetek, Turkmenistan, ♀ (VF); *Parabuthus* sp., Kenya, ♀ (VF); *Polisius persicus* Fet, Capes et Sissom, 2001, Zahedan, Iran, ♂ (USNM); *Razianus zarudnyi* (Birula, 1903), Gachsaran, Fars, Iran, ♀ (USNM); *Rhopalurus junceus* (Herbst, 1800), Sibanicú, Camagüey, Cuba, ♀ (VF); *Tityus nematochirus* Mello-Leitão, 1940, Bucaramango, Colombia, ♂ (MES); *Uroplectes vittatus* (Thorell, 1876), Doddiebum, Zimbabwe, ♂ (VF).

Microcharmidae: *Microcharmus hauseri* Louren-ço, 1996, Lokobe Natural Reserve, Île Nosy Be, Madagascar, holotype ♂ (MHNG).

Superfamily Chaeriloidea

Chaerilidae: *Chaerilus variegatus* Simon, 1877, Indonesia, ♂ (MES); *Chaerilus celebensis* Pocock, 1894, Mapur Island, Indonesia, juvenile ♀ (VF).

Superfamily Iuroidea

Caraboctonidae: *Caraboctonus keyserlingi* Po-cock, 1893, Chile, ♂ (MES); *Hadruioides charcasus* (Karsch, 1879), Peru, ♀ (MES); *Hadruioides maculatus* (Thorell, 1876), Huancayo, Peru, ♀ (MES); *Hadrurus concolorous* Stahnke, 1969, Santa Rosalía, Baja California Sur, Mexico, ♀ (MES); *Hadrurus obscurus* Williams, 1970, Pinyon Mountain, ABDSP, California, USA, ♂ (MES); *Hoffmannihadrurus aztecus* Pocock, 1902, Tehuacán, Puebla, Mexico, ♂ (MES).

Iuridae: *Calchas nordmanni* Birula, 1899, Anamur, Turkey, ♂ (NHMW); *Iurus dufourei* (Brullé, 1832), Turkey, ♂ (MES).

Superfamily Scorpionoidea

Bothriuridae: *Bothriurus araguayae* Vellard, 1934, Minas Gerais, Brazil, ♀ (VF); *Bothriurus burmeisteri* Kraepelin, 1894, Gobernador Costa, Chubut, Argentina, ♂ (VF); *Brachistosternus ehrenbergii* (Gervais, 1841), Lima, Peru, ♀ (VF); *Centromachetes pocockii* (Kraepelin, 1894), Lebu, Arauco, Chile, ♀ (VF); *Cercophonius squama* (Gervais, 1843), Engadine, Sidney, Australia, ♀ (VF); *Lisposoma josehermana* Lamoral, 1979, Waterberg, Namibia, subadult ♀ (CAS); *Phoniocercus pictus* Pocock, 1893, Valdivia, Ñancul, Fundo El Linque, Chile, ♀ (VF); *Urophonius granulatus* Pocock, 1898, Chile, (VF).

Hemiscorpiidae: *Cheloctonus* sp., St. Lucia, Kwazulu, Natal, South Africa, ♀ (VF); *Hadogenes troglodytes* (Peters, 1861), Johannesburg, South Africa (MES); *Heteroscorpion goodmani* Lourenço, 1996, Reserve Naturelle Integrale d'Andohahela, Toliara Province, Madagascar, ♂ paratype (FMNH); *Liocheles australasiae* (F., 1796), Bangor, Java, Indonesia, ♀ (VF); *Liocheles karschii* (Keyserling, 1885), Guadalcanal, Solomon Islands, ♂ (MES); *Opisthacanthus lepturus* (Beauvois, 1805), Aguacate, Panama, ♀ (MES).

Scorpionidae: *Bioculus comondae* Stahnke, 1968, Loreto, Baja California Sur, Mexico, ♂ (MES), La Paz, Baja California Sur, Mexico, ♂ (VF); *Didymocentrus leseurii* (Gervais, 1844), Martinique, ♀ (VF); *Heterometrus longimanus* (Herbst, 1800), Mindanao, Philippines, ♂ (MES); *Nebo hierichonticus* (Simon, 1872), Haifa, Israel, ♀ (VF); *Opisthophthalmus wahlbergii* (Thorell, 1876), Kalahari Gemsbock Park, Twee Rivieren, South Africa, ♂ (VF); *Pandinus imperator* (C. L. Koch, 1841), ♀ (MES); *Scorpio maurus* Linnaeus, 1758, Tel-Yezucham, Israel, ♀ (MES), Agadir, Morocco, ♀ (VF); *Urodacus manicatus* (Thorell, 1876), Australia, (VF).

Superfamily Chactoidea

Chactidae: *Anuroctonus pococki pococki* Soleglad et Fet, 2004, San Dimas Canyon, Los Angeles County, California, USA ♀ (AMNH); *Anuroctonus pococki bajae* Soleglad

et Fet, 2004, ABDSP, California, USA, ♂ (MES), ♂ (VF); *Belisarius xambeui* Simon, 1879, Vall d'en Bas, Girona, Catalunya, Spain, ♀ (VF); *Broteochactas porosus* Pocock, 1900, Mt. Roraima, Venezuela, ♂ paratype (BMNH); *Brotheas granulatus* Simon, 1877, Grande Île, French Guiana, ♂ (MES); *Chactas exsul* (Werner, 1939), Darién, Panama, ♂ (MES); *Hadrurochactas schaumii* (Karsch, 1880), Petite Île, French Guiana, ♂ (MES); *Neochactas delicatus* (Karsch, 1879), Grande Île, French Guiana, ♂ (MES); *Nullibrotheas allenii* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, (MES); *Teuthraustes oculatus* Pocock, 1900, Latacunga, Ecuador, ♀ (WDS); *Uroctonus mordax mordax* Thorell, 1876, Yosemite National Park, California, USA, 1 ♂ 1 ♀ (MES), Weott, California, USA, ♂ (MES); *Uroctonus mordax pluridens* Hjelle, 1972, Santa Clara Co., California, USA, ♂ (MES); *Vachoniochactas* sp., Alto Rio Mavaca, Amazonas, Venezuela, ♂ (CAS).

Euscorpiidae: *Alloscorpiops lindstroemii* (Thorell, 1889), Tak Province, Umphang, Thailand, ♀ (CAS); *Chactopsis insignis Kraepelin*, 1912, Loreto, Peru, ♀ (MNHN); *Euscorpiops* sp. Doi Sutep, Thailand, ♀ (WDS); *Euscorpius flavicaudis* (DeGeer, 1778), Banyuls, France, ♀ (MES); *Euscorpius gamma* Caporiaco, 1950, Postojna, Slovenia, ♀ (VF); *Euscorpius italicus* (Herbst, 1800), Agarone, Ticino, Switzerland, ♂ (MES); *Euscorpius mingrelicus* (Kessler, 1874), Batumi, Georgia, ♂ (MES); *Euscorpius sicanus* (C. L. Koch, 1837), Spilia, Mt. Ossa, Greece, ♀ (VF); *Megacormus gertschi* Díaz Nájera, 1966, Las Vigas, Veracruz, Mexico, ♂ (MES); *Neoscorpiops tenuicauda* (Pocock, 1894), Maharashtra, Bhimashankar, India, ♂ (CAS); *Plesiochactas dilutus* (Karsch, 1881), Portillo Nejapa, Oaxaca, Mexico, ♂ (AMNH); *Scorpiops* sp., Landeur, India, ♀ (USNM); *Troglocormus willis* Francke, 1981, Cueva de la Llorona, Yerbabuena, Tamaulipas, Mexico, ♀ (WDS).

Superstitioniidae: *Superstitionia donensis* Stahnke, 1940, Chariot Canyon, ABDSP, California, USA, ♀ (MES).

Vaejovidae: *Franckeus minckleyi* (Williams, 1968), Cuatro Ciénegas, Coahuila, Mexico, 1 ♂ 2 ♀ (CAS); *Franckeus peninsularis* (Williams, 1980), San Raymundo, Baja

California Sur, Mexico, 3 ♂ 1 ♀ paratypes (CAS); *Paravaejovis pumilis* (Williams, 1970), Ciudad Constitución, Baja California Sur, Mexico, 16 ♂ 3 ♀ (MES); *Paruroctonus arenicola nudipes* Haradon, 1984, Kelso Dunes, San Bernardino Co., California, USA, ♂, juv. (GL); *Paruroctonus arnaudi* Williams, 1972, El Socorro, Baja California, Mexico, ♂ topotype (MES); *Paruroctonus bantai saratoga* Haradon, 1985, Death Valley, Inyo Co., California, USA, juv. (GL); *Paruroctonus becki* (Gertsch et Allred, 1965), San Bernardino Co., California, USA, 1 ♀ 1 ♂ (VF); *Paruroctonus boreus* (Girard, 1854), Mercury, Nevada, USA, ♂ (MES); *Paruroctonus borregoensis* Williams, 1972, Palo Verde Wash, ABDSP, California, USA, ♂ (MES), ♀ (VF); *Paruroctonus gracilior* (Hoffmann, 1931), Cuatro Ciénegas, Coahuila, Mexico, 12 ♂ 1 ♀ (MES); *Paruroctonus hirsutipes* Haradon, 1984, Algodones Dunes, Imperial Co., California, USA, juv. (GL); *Paruroctonus luteolus* (Gertsch et Soleglad, 1966), Palo Verde Wash, ABDSP, California, USA, ♂ (MES); *Paruroctonus silvestrii* (Borelli, 1909), Chihuahua Road, ABDSP, California, USA, 10 ♂ 4 ♀ (MES), ♂ (VF); *Paruroctonus stahnkei* (Gertsch et Soleglad, 1966), Mesa, Maricopa Co., Arizona, USA, ♂ (MES), ♀ (VF), La Paz Co., Arizona, USA, ♂ (VF); *Paruroctonus surensis* Williams et Haradon, 1980, Las Bombas, Baja California Sur, Mexico, 2 ♂ (MES); *Paruroctonus utahensis* (Williams, 1968), Samalayuca, Chihuahua, Mexico, ♂ (MES), Kermit, Winkler County, Texas, USA, 1 ♀ 1 ♂ (VF); *Paruroctonus ventosus* Williams, 1972, El Socorro, Baja California, Mexico, ♀ topotype (MES); *Paruroctonus xanthus* (Gertsch et Soleglad, 1966), Algodones Dunes, Imperial Co., California, USA, ♂ (GL); *Pseudouroctonus andreas* (Gertsch et Soleglad, 1972), Chariot Canyon, ABDSP, California, USA, 6 ♂ 1 ♀ (MES); *Pseudouroctonus angelenus* (Gertsch et Soleglad, 1972), Ventura Co., California, USA, ♂ (BH); *Pseudouroctonus apacheanus* (Gertsch et Soleglad, 1972), Pinaleno Mt., Arizona, USA, ♀ (VF); *Pseudouroctonus iviei* (Gertsch et Soleglad, 1972), Little French Creek, Trinity Co., California, USA, 1 ♀ 1 ♂ (MES); *Pseudouroctonus minimus castaneus* (Gertsch et Soleglad, 1972), Vista, California, USA, ♂ (MES); *Pseudouroctonus minimus thompsoni* (Gertsch et Soleglad, 1972), Santa Cruz Island, Santa Barbara Co., California, USA, 2 ♀ 2 ♂ (GL); *Pseudouroctonus reddelli* (Gertsch et Soleglad, 1972), Gem Cave, Conal Co., Texas, USA, 2 ♀ 2 ♂ (MES); *Serradigitus adcocki* (Williams, 1980), Isla Cerralvo,

Baja California Sur, Mexico, ♀ (CAS); *Serradigitus baueri* (Gertsch, 1958), West San Benito Island, Baja California, Mexico, ♂ (CAS); *Serradigitus calidus* (Soleglad, 1974), Cuatro Ciénegas, Coahuila, Mexico, ♀ paratype (MES); *Serradigitus gertschi gertschi* (Williams, 1968), Chariot Canyon, ABDSP, California, USA, 2 ♀ (MES); *Serradigitus gertschi striatus* (Hjelle, 1970), Coloma, California, USA, ♀ (VF); *Serradigitus joshuaensis* (Soleglad, 1972), Indian Gorge, ABDSP, California, USA, ♀ (MES), Cottonwood Springs, Joshua National Monument, California, USA, 11 ♀ topotypes (MES); *Serradigitus littoralis* (Williams, 1980), Isla Danzante, Baja California Sur, Mexico, ♀ (CAS), Isla Smith (Coronado), Baja California, Mexico, ♀ (VF); *Serradigitus minutis* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Serradigitus torridus* Williams et Berke, 1986, Nine Mile Canyon Rd., Kern Co., California, USA, 2 ♀ (GL); *Serradigitus wupatkiensis* (Stahnke, 1940), Wupatki National Monument, Coconino Co., Arizona, USA, ♀ topotype (MES); *Smeringurus aridus* (Soleglad, 1972), Palo Verde Wash, ABDSP, California, USA, 1 ♂ 1 ♀ (MES); *Smeringurus grandis* (Williams, 1970), Oakies Landing, Baja California, Mexico, ♂ (MES); *Smeringurus mesaensis* (Stahnke, 1957), Palo Verde Wash, ABDSP, California, USA, 5 ♀ 11 ♂ (MES); *Smeringurus vachoni immanis* (Soleglad, 1972), 1000 Palms, Riverside Co., California, USA, ♀ (MES); *Smeringurus vachoni vachoni* (Stahnke, 1961), San Bernardino Co., California, USA, ♀ (VF); *Stahnkeus deserticola* (Williams, 1970), Saratoga Springs, Death Valley, California, USA, ♀ (MES); *Stahnkeus harbisoni* (Williams, 1970), Oakies Landing, Baja California, Mexico, ♀ (MES); *Stahnkeus subtilimanus* (Soleglad, 1972), Split Mountain, ABDSP, California, USA, 2 ♀ (MES); *Syntropis macrura* Kraepelin, 1910, Los Aripes, Baja California Sur, Mexico, 1 ♂ 3 ♀ (MHNG); *Uroctonites giulianii* Williams et Savary, 1991, Lead Canyon, Inyo Co., California, USA, 1 ♂ 2 ♀ (CAS); *Uroctonites huachuca* (Gertsch et Soleglad, 1972), Huachuca Mountains, Cochise Co., Arizona, USA, 1 ♀ 1 ♂ (MES); *Uroctonites montereus* (Gertsch et Soleglad, 1972), Hastings National History Reservation, Monterey Co., California, USA, ♂ (MES); *Vaejovis bruneus* Williams, 1970, Loreto, Baja California Sur, Mexico, ♂ (MES); *Vaejovis carolinianus* (Beauvois, 1805), Haralson Co., Georgia, USA, 5 ♀ (MES); *Vaejovis cazieri* Williams, 1968, Cuatro Ciénegas, Coahuila,

Mexico, ♂ (MES); *Vaejovis coahuilae* Williams, 1968, Cuatro Ciénegas, Coahuila, Mexico, ♂ (MES); *Vaejovis confusus* Stahnke, 1940, Mesa, Maricopa Co., Arizona, USA, ♂ (MES); *Vaejovis davidi* Soleglad et Fet, 2005, Cuelzalan, Puebla, Mexico, ♀ holotype (AMNH); *Vaejovis decipiens* Hoffmann, 1931, Chínipas, Chihuahua, Mexico, ♀ (MES); *Vaejovis diazi* Williams, 1970, Ciudad Constitución, Baja California Sur, Mexico, ♀ (MES); *Vaejovis eusthenura* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♂ (MES), ♀ (VF); *Vaejovis globosus* Borelli, 1915, Zacatecas, Zacatecas, Mexico, ♀ (MES); *Vaejovis granulatus* Pocock, 1898, Hidalgo, Mexico, ♀ (MES); *Vaejovis gravicaudus* Williams, 1970, Santa Rosalía, Baja California Sur, Mexico, ♀ (MES); *Vaejovis hirsuticauda* Banks, 1910, Indian Gorge Canyon, ABDSP, California, USA, ♀ (MES), Indian Gorge Canyon, ABDSP, California, USA, ♀ (VF); *Vaejovis hoffmanni* Williams, 1970, Rancho Tablón, Baja California Sur, Mexico, 1 ♂ 2 ♀ (MES); *Vaejovis intrepidus cristimanus* Thorell, 1876, Acatlán, Jalisco, Mexico, 2 ♂ (MES); *Vaejovis janssi* Williams, 1980, Isla Socorro, Mexico, 3 ♂ 1 ♀ (MES), 2 ♂ 2 ♀ 4 juv. (CAS); *Vaejovis jonesi* Stahnke, 1940, Sedona, Coconino Co., Arizona, USA, 2 ♀ (MES); *Vaejovis lapidicola* Stahnke, 1940, Williams, Coconino Co., Arizona, USA, ♂ (MES); *Vaejovis magdalensis* Williams, 1971, Los Aripes, Baja California Sur, Mexico, 7 ♂ (MES); *Vaejovis mexicanus* (C. L. Koch, 1836), Aculco, Distrito Federal, Mexico, 2 ♀ (MES), Tlaxcala, Tlaxcala, Mexico, 2 ♂ 2 ♀ (MES); *Vaejovis nigrescens* Pocock, 1898, Pachuca, Hidalgo, Mexico, 2 ♀ (MES); *Vaejovis occidentalis* Hoffmann, 1931, Acapulco, Guerrero, Mexico, ♀ (MES); *Vaejovis paysonensis* Soleglad, 1973, Payson, Arizona, USA, 3 ♀ topotypes (MES); *Vaejovis pococki* Sissom, 1991, Rioverde, San Luis Potosí, Mexico, ♂ (MES); *Vaejovis punctatus* Karsch, 1879, Acatlán, Puebla, Mexico, 11 ♂ 6 ♀ (MES); *Vaejovis punctipalpi* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Vaejovis puritanus* Gertsch, 1958, Jasper Trail, ABDSP, California, USA, 13 ♂ 1 ♀ (MES); *Vaejovis russelli* Williams, 1971, Deming, Luna Co., New Mexico, USA, ♀ (MES); *Vaejovis solegladi* Sissom, 1991, Cuicatlán, Oaxaca, Mexico, 2 ♀ (MES), Teotitlán, Oaxaca, Mexico, 2 ♀ (MES); *Vaejovis spinigerus* (Wood, 1863), Alamos, Sonora, Mexico, ♀ (MES); *Vaejovis viscainensis* Williams, 1970, Las Bombas, Baja California Sur, Mexico, 8 ♂ 4 ♀ (MES); *Vaejovis vorhiesi* Stahnke, 1940,

Huachuca Mountains, Cochise Co., Arizona, USA, 2 ♂ 5 ♀ topotypes (MES); *Vaejovis waeringi* Williams, 1970, Indian Gorge Canyon, ABDSP, California, USA, ♂ (MES); *Vejovoidus longiunguis* (Williams, 1969), Las Bombas, Baja California Sur, Mexico, 4 ♂ 8 ♀ (MES).

Appendix C: Serrula Material Examined

Genera Paravaejovis, Paruroctonus, Smeringurus, and Vejovoidus: *Paravaejovis pumilis* (Williams, 1970), Ciudad Constitución, Baja California Sur, Mexico, 2 ♂ (MES); *Paruroctonus arnaudi* Williams, 1972, El Socorro, Baja California, Mexico, 1 ♂ 1 juv. topotypes (MES); *Paruroctonus becki* (Gertsch et Allred, 1965), Joshua Tree National Monument, California, 1 ♀ 1 juv. (MES), San Bernardino Co., California, USA, 5 ♀ 1 juv. (VF); *Paruroctonus boreus* (Girard, 1854), 3 ♂, Worland, Wyoming (VF); *Paruroctonus gracillior* (Hoffmann, 1931), Cuatro Ciénegas, Coahuila, Mexico, 2 ♂ (MES), Lordsburg, Hidalgo Co., New Mexico, USA, ♂ (GL); *Paruroctonus luteolus* (Gertsch et Soleglad, 1966), Palo Verde Wash, ABDSP, California, USA, ♀ (MES); *Paruroctonus silvestrii* (Borelli, 1909), Chihuahua Road, ABDSP, California, USA, ♂ (MES); *Paruroctonus stahnkei* (Gertsch et Soleglad, 1966), Mesa, Maricopa Co., Arizona, USA, ♀ (MES); *Paruroctonus surensis* Williams et Haradon, 1980, Las Bombas, Baja California Sur, Mexico, ♂ (MES); *Paruroctonus utahensis* (Williams, 1968), Kermit, Winkler County, Texas, USA, 1 ♀ 2 ♂ (VF); *Paruroctonus ventosus* Williams, 1972, El Socorro, Baja California, Mexico, ♂ topotype (MES); *Smeringurus aridus* (Soleglad, 1972), Palo Verde Wash, ABDSP, California, USA, 2 ♂ 1 ♀ 1 juv. (MES); *Smeringurus grandis* (Williams, 1970), Oakies Landing, Baja California, Mexico, 2 ♂ 1 ♀ (MES), Bahia de Los Angeles, Baja California, Mexico, ♀ (VF); *Smeringurus mesaensis* (Stahnke, 1957), Palo Verde Wash, ABDSP, California, USA, ♀ (MES), San Bernardino Co., California, USA, 3 juv. (VF); *Smeringurus vachoni immanis* (Soleglad, 1972), 1000 Palms, Riverside Co., California, USA, ♀ (MES); *Vejovoidus longiunguis* (Williams, 1969), Las Bombas, Baja California Sur, Mexico, 3 ♂ 2 ♀ 2 juv. (MES), Vizcaino Desert, Baja California Sur, Mexico, 1 ♂ 2 ♀ (VF).

Additional vaejovoid comparative material: *Pseudouroctonus andreas* (Gertsch et Soleglad, 1972), Chariot Canyon, ABDSP, California, USA, ♂ (MES); *Serradigitus gertschi gertschi* (Williams, 1968), Chariot Canyon, ABDSP, California, USA, ♀ (MES);

Serradigitus joshuaensis (Soleglad, 1972), Indian Gorge, ABDSP, California, USA, ♀ (MES); *Serradigitus minutis* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Stahnkeus subtilimanus* (Soleglad, 1972), Split Mountain, ABDSP, California, USA, ♀ (MES); *Uroctonites huachuca* (Gertsch et Soleglad, 1972), Huachuca Mountains, Cochise Co., Arizona, USA, ♂ (MES); *Vaejovis confusus* Stahnke, 1940, San Bernardino Co., California, USA, ♂ (VF); *Vaejovis globosus* Borelli, 1915, Zacatecas, Zacatecas, Mexico, ♀ (MES); *Vaejovis gravicaudus* Williams, 1970, Santa Rosalía, Baja California Sur, Mexico, ♀ (MES); *Vaejovis intrepidus cristimanus* Thorell, 1876, Acatlán, Jalisco, Mexico, ♀ (MES); *Vaejovis magdalensis* Williams, 1971, Los Aripes, Baja California Sur, Mexico, ♂ (MES); *Vaejovis puritanus* Gertsch, 1958, Jasper Trail, ABDSP, California, USA, ♂ (MES); *Vaejovis viscainensis* Williams, 1970, Las Bombas, Baja California Sur, Mexico, ♂ (MES).

Appendix D: Curriculum Vitae

Name: Michael Brewer
Birth Date: April 10, 1983
Birth Place: Amarillo, TX
Current Residence: Huntington, WV

Present Positions

Graduate student and researcher, Department of Biological Sciences, Marshall University, Huntington, WV.

Lab instructor, Department of Biological Sciences, Marshall University, Huntington, WV.

Education

B.S. in Biological Sciences, Marshall University, Huntington, WV.

M.S. in Biological Sciences, Marshall University, Huntington, WV.

Teaching Experience

Lab instructor, General Biology BSC 104, Marshall University, 2005

Lab instructor, Human Biology BSC 105, Marshall University, 2006

Lab instructor, Human Anatomy BSC 227, Marshall University, 2006

Lab instructor, Principles of Genetics BSC 324, Marshall University, 2007

Lab instructor, Human Anatomy BSC 227, Marshall University, 2007

Research Grants

NASA Space Grant research grant, 2005 & 2006

Awards and Achievements

Undergraduate: John Marshall Scholarship (full tuition and fee waver with stipend)

Phi Eta Sigma honor society member

Graduated *Magna Cum Laude* with University Honors

NASA Space Grant Scholar, 2005

Graduate: Honorary member of the American Association for the Advancement of Science (AAAS), 2006-2007

NASA Space Grant Scholar, 2006

Publications

Fet, V., M.E. Soleglad & M.S. Brewer. 2006. Laterobasal aculear serrations (LAS) in scorpion family Vaejoidea (Scorpiones: Chactioidea). *Euscorpius*, 45, pp. 1–19.

Fet, V., M.E. Soleglad, M.S. Brewer, D.P.A. Neff & M.L. Norton. 2006. Constellation array in scorpion genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* (Scorpiones: Vaejoidea). *Euscorpius*, 41, pp. 1–15.

Fet, V., M.E. Soleglad, M.S. Brewer, D.P.A. Neff & M.L. Norton. 2006. Vestigial serrula in scorpion genera *Paravaejovis*, *Paruroctonus*, *Smeringurus* and *Vejovoidus* (Scorpiones: Vaejoidea). *Euscorpius*, 49, pp. 1–20.

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Posters

Brewer, M., V. Fet, V., E.V.Fet, J. O. Rein & M. Colombo. 2005. New mitochondrial DNA data for the phylogeny of the Balkan and Aegean *Euscorpius* (Scorpiones: Euscorpiidae). *American Arachnological Society 29th Annual Meeting*, Akron, Ohio, 26-30 June 2005.

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Website I created about constellation array: <http://users.marshall.edu/~brewer30>

Brewer, M., M. Graham, V. Fet, M. Soleglad. 2007. Scorpion serrula: an enigmatic structure under SEM (Arachnida: Scorpiones). *West Virginia Academy of Sciences Annual Meeting*, Huntington, West Virginia, 30-31 March 2007.