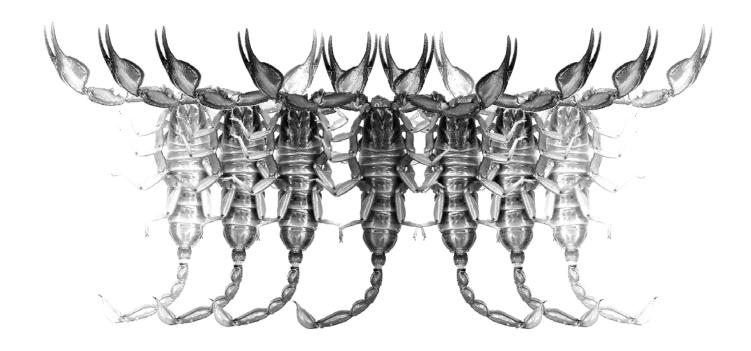
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Constellation Array in Scorpion Genera *Paruroctonus*, Smeringurus, Vejovoidus, and Paravaejovis (Scorpiones: Vaejovidae)

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Constellation array in scorpion genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* (Scorpiones: Vaejovidae)

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Summary

The constellation array (a recently discovered sensory structure on the fixed finger of pedipalp; Fet et al., 2006) is analyzed for a large set of species belonging to four genera in the family Vaejovidae: *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis*. It is shown that this structure is an important taxonomic character. Two distinct configurations are identified, a two-sensilla array for *Paruroctonus* + *Smeringurus* + *Vejovoidus* and a three-sensilla array for genus *Paravaejovis*, both differing from other vaejovid configurations so far investigated. The topology of these two array configurations are analyzed using *landmark setae* identified in this study.

Introduction

Fet et al. (2006) reported a sensory constellation array found on the external aspect of chelal fixed finger in scorpions, a curious array of tiny sensilla never described before. They described and illustrated this array for all major Recent scorpion groups: all four parvorders, all six superfamilies and 12 out of 13 families (only Microcharmidae was not represented) spanning 23 genera and 28 species. In addition, based on very limited sampling, the arrays were shown to be consistent in the number of sensilla and their configuration between genders as well as during ontogenetic growth, both qualities desired for a useful diagnostic character. As shown in this paper, the constellation array is proving to be important from a systematics perspective as well. We see overall consistency of the constellation array in its numbers of sensilla and their overall topology as determined by special "landmark setae" described in this paper.

Soleglad & Fet are currently involved in a major systematic revision of the family Vaejovidae (Soleglad & Fet, 2003, 2005, 2006, and in progress). Key to this revision is the identification of new diagnostic characters to be employed in their ongoing cladistic analysis. As stated above, we have reasons to believe that the constellation array could provide legitimate diagnostic characters. Therefore, this structure is investigated for a large related set of species in family Vaejovidae, the subject of this paper: *Paravaejovis* + (*Paruroctonus* +

Smeringurus + Vejovoidus), a topology originally suggested by Stockwell (1989). We demonstrate herein that this clade exhibits two unique constellation array topologies, both different from other vaejovid arrays so far studied. Of particular interest, these two topologies are congruent with the above clade, one topology seen in Paravaejovis, a three-sensilla configuration, and the other in Paruroctonus + Smeringurus + Vejovoidus, a two-sensilla configuration, thus providing additional evidence that Paravaejovis is distant from the three other more closely related genera. In addition, great consistency is shown in these two array configurations for the species so far examined, 15 species of Paruroctonus, 5 species and subspecies of Smeringurus (all taxa in this genus), and both species of the monotypic genera Vejovoidus and Paravaejovis. This observation is based on the analysis of over 80 digital SEM images of the four subject genera.

Methods & Material

Terminology and conventions

The systematics adhered to in this paper is current and therefore follows the classification as established in Fet & Soleglad (2005) and as modified by Soleglad & Fet (2006). Terminology describing the constellation array follows that described in Fet et al. (2006) and pedipalp chelal finger dentition follows that described and illustrated in Soleglad & Sissom (2001).

SEM microscopy

To investigate the chelal fingers, the structures were dehydrated in an ethanol series (50, 75, 95, and two changes of 100%) before being dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. Digital SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia. Acceleration voltage (10–20 kV), spot size, and working distance were adjusted as necessary to optimize resolution, adjust depth of field, and to minimize charging.

Abbreviations

List of depositories: GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA.

Other: ABDSP, Anza-Borrego Desert State Park, San Diego and Riverside Counties, California, USA.

Material examined

The following vaejovid material was examined for analysis and/or illustrations provided in this paper.

Genera Paravaejovis, Paruroctonus, Smeringurus, and Vejovoidus (40 specimens): Paravaejovis pumilis (Williams, 1970), Ciudad Constitución, Baja California Sur, Mexico, 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 & Allred, 1965), San Bernardino Co., California, USA, & (VF); Paruroctonus boreus (Girard, 1854), Mercury, Nevada, USA, & (MES); Paruroctonus borregoensis Williams, 1972, Palo Verde Wash, ABDSP, California, USA, & (MES); Paruroctonus gracilior (Hoffmann, 1931), New Mexico, USA, 3 (MES), Cuatro Cienegas, Coahuila, Mexico, (MES), Lajitas, Brewster Co., Texas, USA & (GL), Lordsburg, Hidalgo Co., New Mexico, USA, & (GL), Big Bend National Park, Brewster Co., Texas, USA, (VF); Paruroctonus hirsutipes Haradon, 1984, Algodones Dunes, Imperial Co., California, USA juv. (GL); Paruroctonus luteolus (Gertsch et Soleglad, 1966). Palo Verde Wash, ABDSP, California, USA, 3 (MES); Paruroctonus silvestrii (Borelli, 1909). Chihuahua Road, ABDSP, California, USA, ♀ (MES); Paruroctonus stahnkei (Gertsch et Soleglad, 1966), Mesa, Maricopa Co., Arizona, USA, ♂ (MES), La Paz

Co., Arizona, ♂ (VF); Paruroctonus surensis Williams et Haradon, 1980, Las Bombas, Baja California Sur, Mexico, ♂ (MES); Paruroctonus utahensis (Williams, 1968), Samalayuca, Chihuahua, Mexico, & (MES), Kermit, Winkler County, Texas, USA, $\mathcal{Q} \mathcal{O}$ (VF); Paruroctonus ventosus Williams, 1972, El Socorro, Baja California, Mexico, ♀ topotype (MES); Paruroctonus xanthus (Gertsch & Soleglad, 1966), Algodones Dunes, Imperial Co., California, USA, & (GL); Smeringurus aridus (Soleglad, 1972), Palo Verde Wash, ABDSP, California, USA, ♂ ♀ (MES); Smeringurus grandis (Williams, 1970), Oakies Landing, Baja California, Mexico, & (MES); Smeringurus mesaensis (Stahnke, 1957), Palo Verde Wash, ABDSP, California, USA, 3 ♀ (MES); Smeringurus vachoni immanis (Soleglad, 1972), 1000 Palms, Riverside Co., California, USA, ♀ (MES); Smeringurus vachoni vachoni (Stahnke, 1961), San Bernardino Co., California, USA, ♀ (VF); Vejovoidus longiunguis (Williams, 1969), Las Bombas, Baja California Sur, Mexico, $3 \circlearrowleft$, $2 \circlearrowleft$ (MES).

Additional comparative material (14 specimens): Pseudouroctonus andreas (Gertsch et Soleglad, 1972), Penasquitos Carmel Mtn. Rd., San Diego Co., California, USA, juv. 3 (VF); Pseudouroctonus reddelli (Gertsch et Soleglad, 1972), Travis Co., Texas, USA, ♀ (VF); Serradigitus gertschi gertschi (Williams, 1968), San Diego, California, USA ♀ (VF); Serradigitus joshuaensis (Soleglad, 1972), Borrego Springs, San minutis (Williams, 1970), Cabo San Lucas, Baia California Sur, Mexico, ♀ (VF); Stahnkeus subtilimanus (Soleglad, 1972), Borrego Springs, San Diego Co., California, USA, ♀ (VF); Vaejovis carolinianus (Beauvois, 1805), Tishomingo State Park, Mississippi, USA, ♀ (VF); Vaejovis confusus (Stahnke, 1940), San Bernardino Co., Arizona, USA, & (VF); Vaejovis eusthenura (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (VF); Vaejovis hirsuticauda (Banks, 1910), ABDSP, California, USA, ♀ (VF); Vaejovis punctipalpi (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (VF); Vaejovis puritanus Gertsch, 1958, ABDSP, California, USA, & (VF); Vaejovis viscainensis Williams, 1970, Las Bombas, Baja California Sur, Mexico, ♀ (VF); Vaejovis vittatus Williams, 1970, Cabo San Lucas, Baja California Sur, Mexico, $\mathcal{O}(VF)$.

Results and Discussion

Constellation array: the sensillum

The tiny sensillum of the constellation array has a somewhat complex structure: there is an outer areola which is formed as a small shallow depression in the cuticle with a low profile outer lip and sometimes

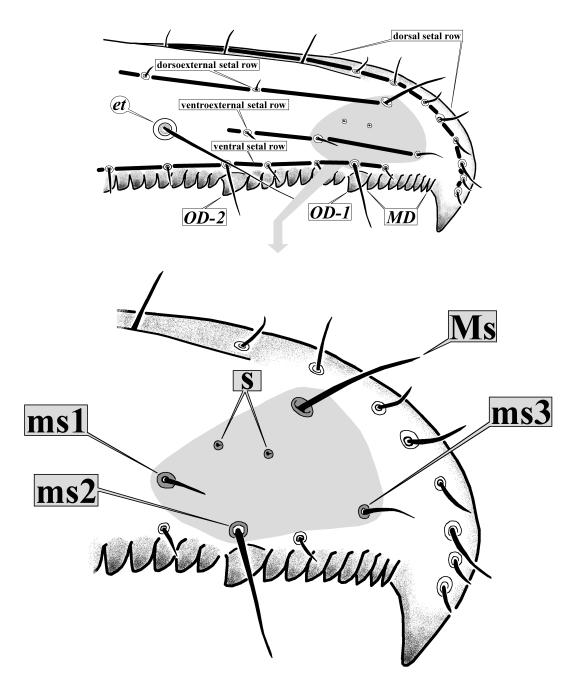


Figure 1: Distal one-third of chelal fixed finger, external view, of *Paruroctonus becki* showing general layout of constellation array sensilla, setal rows, *landmark* setae, trichobothria, and finger denticles. In **top** figure the four setal rows are identified (setae of each row are connected with black lines) as well as trichobothria and finger denticles of importance. Constellation array and landmark setae region are indicated by a gray polygon. In **bottom** figure the constellation array sensilla and landmark setae region (with darkened areolae for emphasis) are shown in closeup and identified. $\mathbf{s} = \text{sensilla}$; $\mathbf{Ms} = \text{major seta}$; $\mathbf{ms1} - \mathbf{3} = \text{minor setae } 1 - \mathbf{3}$; et = external terminal trichobothrium; OD-1 & 2 = outer (OD) denticles 1 & 2; MD = distal median (MD) denticles.

exhibiting additional subtle concentric rings in its concavity (Figs. 23–26, 28–30). Within this outer areola is an even smaller deeper areola located at its center, its diameter roughly one-third that of the outer areola. Internally the second areola is composed of successive concentric ridges extending into the areola. Extending

from this second areola is a short, stout, highly tapered seta, its external length being less than the diameter of the outer areola. At the base of some seta we see the evidence of striations, which is commonly found on leg setae. Table 1 provides measurements of sensillar size for 21 studied species.

Constellation array topologies

Constellation array fixed finger orientation. As shown in Figure 1, the constellation array is located on the extreme distal aspect of the chelal fixed finger external surface (see Fet et al., 2006 for an illustrated survey of this array across the entire scorpion order). To precisely determine the location of the sensilla as well as conduct comparative studies of their topology, we have identified a set of "landmarks" on the fixed finger comprised of both setae and outer (OD) denticles. In order to state exactly the location of the four landmark setae for the four genera studied in this paper we have divided the external surface of the fixed finger into four regions, each region occupied by a setal row extending along the finger:

dorsal setal row is located on the dorsal edge of the finger beginning at the dorsoexternal aspect of the distal tip, following the curve of the distal tip, and continuing along the dorsal edge, inline with trichobothrium dt — contains no landmark setae;

dorsoexternal setal row is located on the dorsoexternal surface, dorsal of trichobothrium et and the constellation array sensilla — contains landmark seta Ms;

ventroexternal setal row is located on the ventroexternal surface of the finger, ventral of trichobothrium et and the constellation array sensilla — contains two landmark setae, ms1 and ms3;

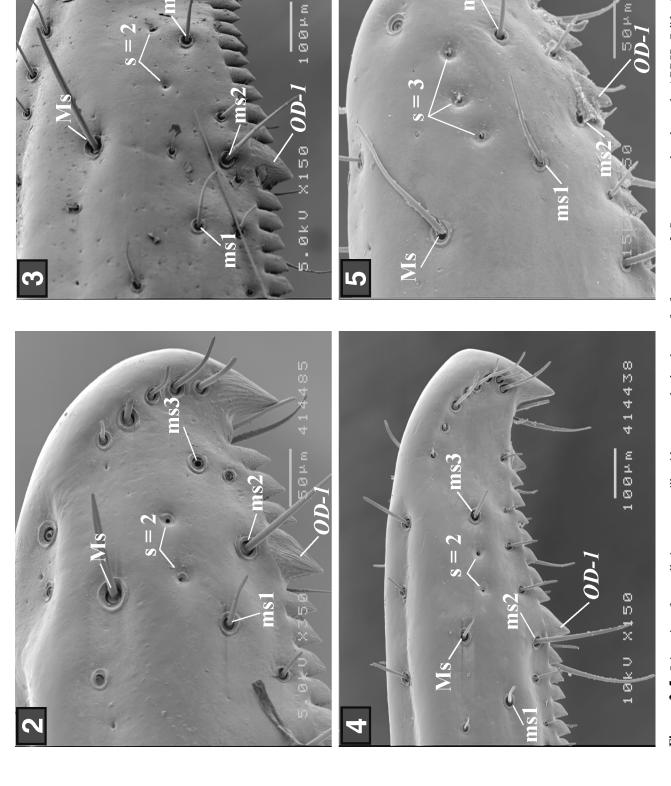
ventral setal row is located on the extreme ventroexternal surface, just above the finger denticle edge; in this row the single seta located above OD denticles is larger than those setae found above median (MD) denticles — contains landmark seta ms2, which is situated adjacent to the OD-1 denticle base.

We establish four setae as landmarks for sensilla charting (Fig. 1), all distal of the most distal trichobothrium et and ventral of the dorsal trichobothrium dt. The major seta (Ms) is a large isolated seta situated on the dorsal half of the fixed finger, being the largest and most distal seta in the dorsoexternal setal row. The minor seta-2 (ms2) is positioned close to the denticle edge in the ventral setal row, adjacent to the base of outer (OD) denticle-1. The minor seta-1 (ms1) is positioned just proximal of ms2 in the ventroexternal setal row, angling more dorsally on the finger. Finally, the minor seta-3 (ms3) is the most distal seta in the ventroexternal setal row, aligned horizontally with ms1, and is situated just proximal of several dorsal setal row setae arranged in a curved line along the distal denticle tip. The three minor setae are usually larger than other setae in the vicinity of the finger denticle edge but not as large as **Ms**. These four landmark setae, when connected, form an irregular four-sided polygon, essentially enclosing the constellation array sensilla thus providing a means for evaluating their position. The exact positions of these landmark setae are, of course, genus- and species-specific and do show some variability even within a species. Figures 2–5 specifically identify these landmark setae in the four genera discussed in this paper, but they are quite visible in the other figures as well, representing a large number of species.

Constellation array configurations. Figures 2–5, 7–22, 27 show the constellation arrays of 13 species of *Paruroctonus* and all species and subspecies of genera *Smeringurus*, *Vejovoidus*, and *Paravaejovis*. In these figures, we see two basic configurations of sensilla in our vaejovid study group: assemblage *Paruroctonus* (Figs. 2, 7–18) + *Smeringurus* (Figs. 3, 19–22, 27) + *Vejovoidus* (Fig. 4) with two sensilla, and genus *Paravaejovis* (Fig. 5) with three sensilla. In addition, we also see positional differences within these two configurations with respect to the landmark setae.

Figure 6 presents constellation array topology charts where the fixed finger denticle edge is aligned horizontally to the plane thus allowing consistent positional analysis of the sensilla with respect to landmark setae and outer denticles. In genus Paruroctonus (Fig. 6, showing charts of 15 species), sensilla are always proximal of ms3, usually inline vertically with Ms and ms2. Within this configuration, we see alignment differences that appear to be related to the number of distal MD denticles which is also, in part, a function of the species adult size: in species with small numbers of distal MD denticles (i.e., 2–3 MD denticles), such as P. surensis (Fig. 7), P. borregoensis (Fig. 9) and P. luteolus (Fig. 2), Ms is positioned slightly proximal of ms2 and the sensilla are either proximal of ms2, or if not both, then the most basal sensillum is situated proximally. As the number of distal MD denticles increases (i.e., 4-6), we see Ms distad of ms2, and both sensilla usually distal of ms2 as well. In species with large numbers of distal MD denticles, P. gracilior and P. xanthus (i.e., 10-11), we see the sensilla are considerably distal of Ms and ms2. Only species P. becki (Fig. 17) with MD = 8 violates this trend. Since these topology differences seem to be related, in part, to the species size, we are hesitant at this time to attach systematic importance to these observations.

In the assemblage *Smeringurus + Vejovoidus* (Fig. 6, showing charts of five species) the sensilla are placed considerably distad of **ms2**. This more distal placement of the sensilla may be due to the larger number of distal MD denticles (i.e., 6–13), similar to that seen in *Paruroctonus arnaudi*, *P. xanthus*, and *P. gracilior*. In



Figures 2–5: Orientation of constellation array sensilla with respect to landmark setae for four genera. 2. Paruroctonus luteolus, male, ABDSP, California, USA. 3. Smeringurus mesaensis, male, ABDSP, California, USA. 4. Vejovoidus longiunguis, female, Las Bombas, Baja California Sur, Mexico. 5. Paravaejovis pumilis, male, Cuidad Constitucion, Baja California Sur, Mexico. Note that genus Paravaejovis is unique in these configurations, exhibiting three sensilla (not two). See Fig. 1 for definition of annotations.

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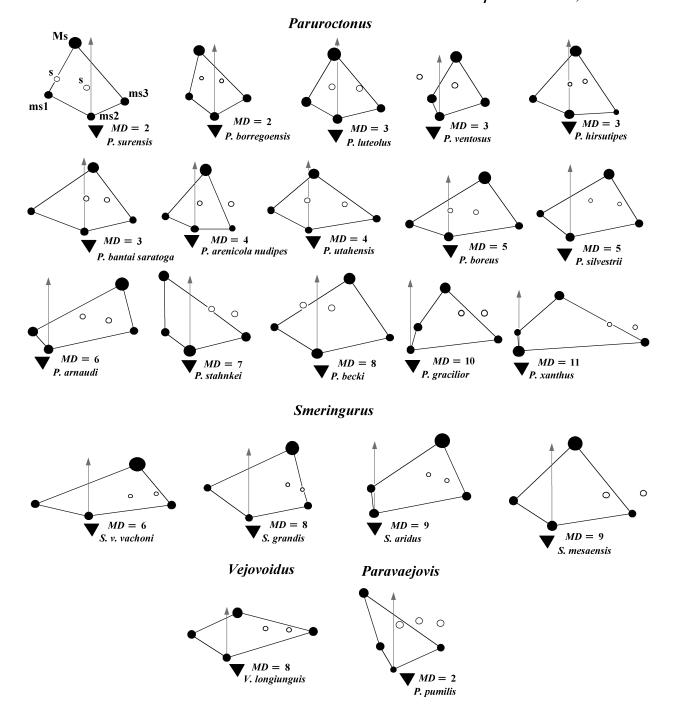


Figure 6: Constellation array **topology charts** for vaejovid genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis*. Open circles depict sensilla, closed circles depict major and minor landmark setae (connected by black lines) and the triangle depicts outer (*OD*) denticle-1. Vertical arrow provides alignment perspective for landmark setae **ms2** and **Ms**, and the sensilla. Individual charts within genera are ordered by increasing number of distal median (*MD*) denticles (i.e., the number of *MD* denticles located between *OD-1* and the distal denticle tip of the chelal fixed finger). It is important to note here in these charts (unlike those images show in figures Figs. 2–5, 7–22, 27) the fixed finger denticle edge is aligned horizontally, therefore perpendicular to the vertical arrow.

genus *Vejovoidus* we see an unusual, somewhat elongated distal tip on the fixed finger (Fig. 4) where the distal *MD* denticles do not extend completely to the distal denticle. In general, however, the topologies are strikingly similar in *Smeringurus* and *Vejovoidus*.

The constellation array in genus *Paravaejovis* (Fig. 6) is quite distinct from the other three genera, exhibiting *three sensilla* rather than two. In addition, the three sensilla are positioned on the dorsal one-third of the fixed finger, whereas in the other three genera the