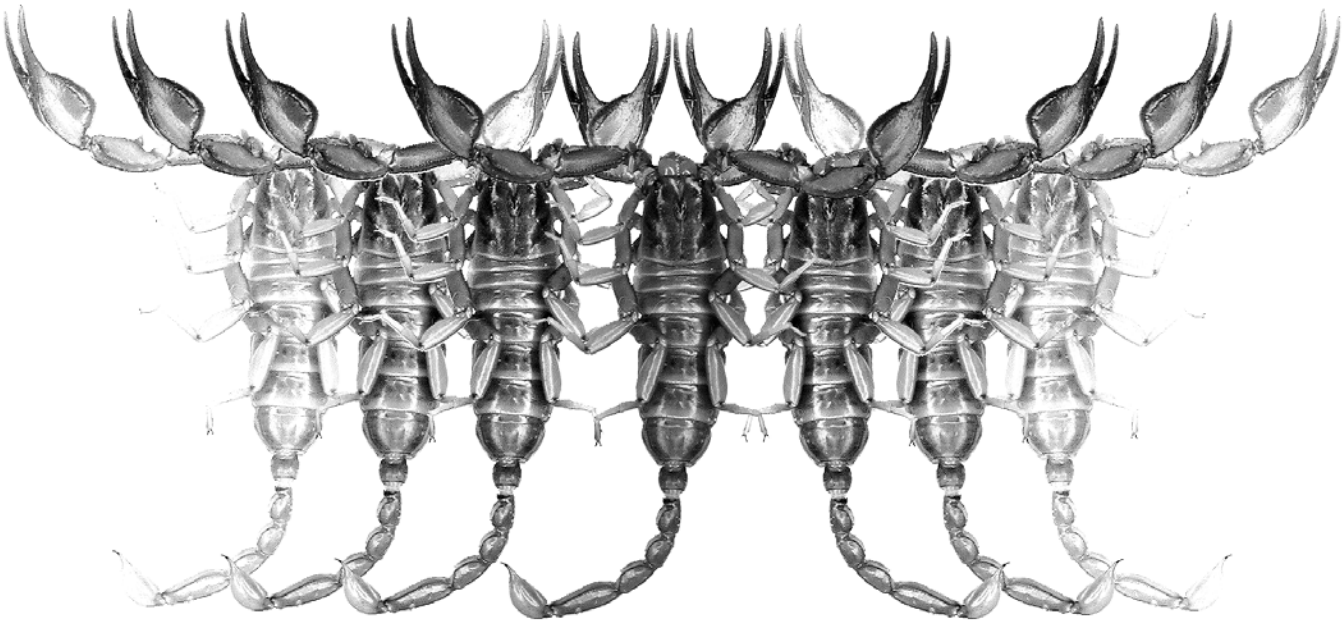
Euscorpius

Occasional Publications in Scorpiology



Vestigial Serrula in Scorpion Genera *Paravaejovis*, *Paruroctonus*, *Smeringurus* and *Vejovoidus* (Scorpiones: Vaejovidae)

Victor Fet, Michael E. Soleglad, Michael S. Brewer, David P. A. Neff and Michael L. Norton

December 2006 – No. 49

Euscorpius

Occasional Publications in Scorpiology

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

Derivatio Nominis

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

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

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

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

---

Publication date: 22 December 2006

Euscorpius — Occasional Publications in Scorpiology. 2006, No. 49

Vestigial serrula in scorpion genera *Paravaejovis*, *Paruroctonus*, *Smeringurus* and *Vejovoidus* (Scorpiones: Vaejovidae)

Victor Fet [1], Michael E. Soleglad [2], Michael S. Brewer [1], David P. A. Neff [3] and Michael L. Norton [3]

[1] Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755, USA
[2] P.O. Box 250, Borrego Springs, California 92004, USA
[3] Department of Chemistry, Marshall University, Huntington, West Virginia 25755, USA

Summary

The presence of vestigial serrula on the ventral edge of the cheliceral movable finger is established for vaejovid genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus*. Detailed descriptions and SEM images illustrating the various manifestations of this interesting cheliceral structure are provided for many species of these four genera. A brief systematic overview of this structure as it exists in Recent scorpions is also presented.

Introduction

Surprisingly, the reporting of cheliceral serrula in Recent scorpions has been somewhat sporadic, its primary references, when present, occurring in the families Vaejovidae and Superstitioniidae. However, in family Vaejovidae, presence (or absence) of serrula was not consistently reported by many scorpion systematists (see Graham & Fet, 2006, for a detailed history of these reports).

Since Stockwell's (1989) unpublished Ph.D. dissertation, the consensus has been that serrula is absent in the related vaejovid genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus.* Stockwell (1989: 91) states: "… Among the Vaejovinae and Syntropinae, the genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* lack a serrula. …"; and, consistent with this statement, Stockwell (1992: 408) further states that "… *Vejovoidus* shares several potential synapomorphies with *Paruroctonus* … (*Smeringurus*) … and *Paravaejovis* … the absence of ventral serrula on the movable finger of the chelicera…" His key to the families and genera of North American scorpions (Stockwell, 1992: 416) says in the second part of couplet 11: "… inferior surface of movable finger of chelicera lacking a serrula ...," which delineates, in part, the four genera *Vejovoidus*, *Paruroctonus*, *Paravaejovis*, and *Smeringurus* (couplets 17 to 19). Since Stockwell (1989: figs. 251, 257) hypothesized the presence of serrula to be a plesiomorphic character of Vaejovidae, the "apparent" loss of serrula in these four related genera was considered to be synapomorphic. This issue is discussed later in this paper.

Contrary to current opinions being held today, however, we demonstrate in this paper that the four listed genera do indeed exhibit vestigial serrula, and in some cases even well developed serrula. And yet, in other cases, we see a very reduced serrula, if it is present at all. Although serrula, as illustrated in this paper, has been detected in all four subject genera, its occurrence is surprisingly sporadic in some species, where we see no serrula, serrula with reduced tines (i.e. "teeth"), and even serrula exhibiting a single tine. Therefore, it is not surprising that serrula has not been reported before in these four genera due to its somewhat sporadic occurrence as documented herein.

Although a detailed survey using SEM microscopy of serrula as it occurs in Recent scorpions is presently being conducted (Brewer et al., in progress), this paper will concentrate only on serrula as it exists in four related vaejovid genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus*. Therefore, this effort is a continuation of the evaluation and systematic revision of scorpion family Vaejovidae (see previous publications in this ongoing analysis: Soleglad & Fet, 2003, 2005, 2006; Fet et al., 2006a, 2006b; Graham, 2006).

Methods & Material

The presence of serrula in these four genera was discovered using SEM microscopy, which is crucial for the detection of this small delicate structure in some of

the studied species. In those species where serrula is more developed, in particular in the genus *Smeringurus*, the structure was detectable using a regular dissection microscope. For this study 80 SEM images were studied spanning 16 species of the four subject genera.

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).

SEM microscopy

To investigate scorpion serrula, the structures were sonicated in water, and then 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 Scanning Electron Microscope at Marshall University, Huntington, 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

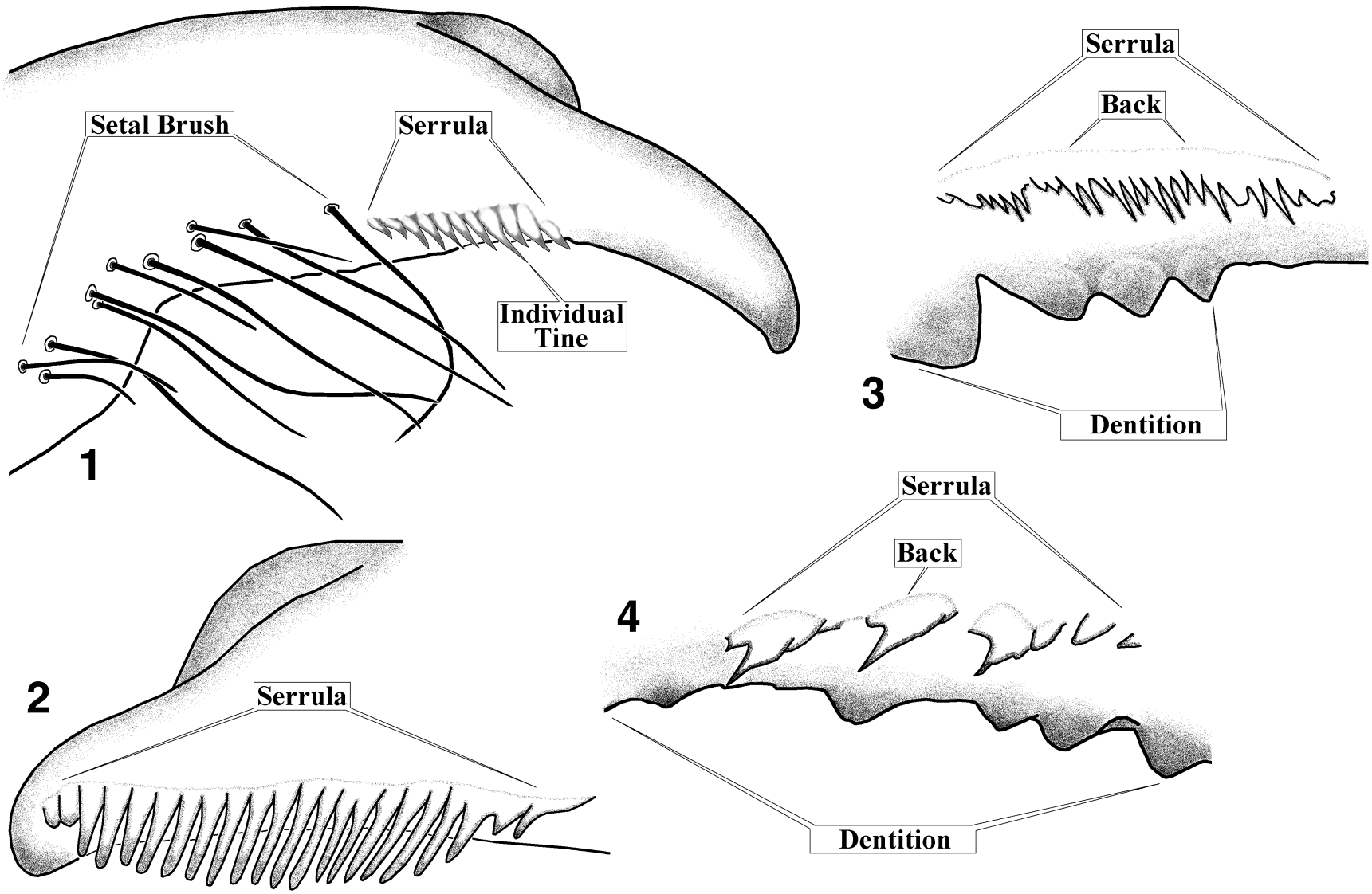
The following vaejovid material was examined for analysis, SEM microscopy, and/or illustrations provided in this paper.

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 gracilior* (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 vaejovid 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).

Serrula: its location and structure

Serrula is located on the ventral surface of the cheliceral movable finger. It is a comb-like structure emanating directly from the cuticle. It is aligned essentially parallel to the ventral edge of the movable finger and, depending on the species, can extend for most of the length of the ventral edge or just exist only on the distal one-third (or less) of the finger. Serrula



Figures 1–4: Cheliceral movable finger, partial ventral view, showing different serrula configurations in family Vaejovidae. **1.** *Vaejovis*, showing in-line orientation of serrula with respect to setal brush. Note the sharpness distally of each tine. **2.** *Pseudouroctonus*, showing a significantly developed serrula with elongated but distally blunted tines. **3.** *Smeringurus*, showing a well developed serrula with somewhat reduced but distally sharp tines. **4.** *Paruroctonus*, showing a very reduced serrula with widened individual backs of the tines, which are quite sharp distally. Note, in Figs. 3-4, a well developed dentition on the ventral edge of the finger, commonly found in these two genera.

(Figs. 1–4) is composed of two components, the *back* which emanates directly from the cuticle and extends along the finger edge, and the *tines* which form "spike-" or "tooth-like" structures extending perpendicularly from the back towards the finger edge and slanting slightly towards the distal aspect of the finger. The tines do not touch the finger surface but instead angle outwards from the finger/back juncture (roughly 30 ° in *Stahnkeus subtilimanus*; see Graham & Fet, 2006, fig. 4), the distal tips of the tines being the farthest from the finger surface.

As can be seen in Figures 1–5, the size and form of the back and tine structure, as well as the number of tines, vary considerably depending on the scorpion group, genus, and/or species. In addition, as we show in this paper for the first time, the serrula structure is variable within a species (even within a specimen), especially where it is very vestigial, as in some of the genera discussed here.

When the serrula tines are sparse (i.e., not forming a contiguous structure), their individual backs become larger and wider, and the tines also are wider at the base and then quickly narrow to a sharp distal tip (Figs. 4–5). Typically, if the tines are contiguous they also are longer and narrower at the base (Figs. 1–3, 5).

Serrula in genera *Paravaejovis, Paruroctonus, Smeringurus,* and *Vejovoidus*

We have documented serrula in the four genera discussed in this paper; however, the consistency of its presence, its form, its degree of preservation, and number of tines can vary considerably (see Table 1 for a complete set of statistical data on serrula presence and absence). However, common to all four genera is the unique *single line* of setae, which we call a *setal brush* (Fig. 1, 6, 8, 10–11, 14, 18–19, 21, 24, 26, 28, 30–38, 40, 42, 44, 46, and 49) that is located on the basal half of the cheliceral movable finger and extends distally towards and *in line* with the proximal end of the serrula. Generally, individual seta are directed towards the distal denticle of the movable finger. Depending on the species, this setal brush can be quite sparse exhibiting only two or three setae. We discuss this in more detail below for the individual genera.

***Paravaejovis*:** Serrula in *Paravaejovis* (Figs. 5, 6–9) is weakly developed, exhibiting 3–6 tines. The serrula begins proximally, at the middle of the movable finger and, depending on the number of tines, extends to the distal one-fifth of the finger, just before the distal denticle abruptly curves. Tines are situated sparsely within the serrula, with approximately one tine width space between them. The individual tines are variable in shape, depending on their density. In the individual with six tines (Figs. 6–7), the tines are somewhat elongated, the back forming a wider and rounded connection to the finger surface. In the individual with only three tines (Figs. 5, 8–9), the tines are shorter and their base wider, accommodating the expanded back. Due to the wide back and shorter tine, the tine abruptly narrows to a sharp distal point. The basal setal brush is limited to a few setae (five shown in Fig. 6), though directly in line with the serrula, and does not extend close to the proximal end of the serrula.

***Paruroctonus*:** A great variability in the density of serrula tines exists in the genus *Paruroctonus* (Figs. 1, 5, 10–25), ranging from zero to seven tines (based on the examination of ten species). Serrula was not observed in *P. gracilior* (three specimens, five chelicerae) or *P. boreus* (three specimens, five chelicerae). Two tines, located distally just before the curving of the distal denticle, were detected in *P. luteolus* (Figs. 5, 19), one considerably smaller than the other. The larger tine, though somewhat small, was elongated and sharp. Accompanying these tines is a very reduced setal brush comprised of two setae which was situated quite basally on the finger edge. In *P. ventosus* (Fig. 18) and *P. silvestrii* (Fig. 21), we identified two tines, in both cases located just before the curving of the distal denticle. In *P. silvestrii*, the setal brush is somewhat extensive, comprised of eleven setae, and terminates close to the proximal end of the serrula. In *P. becki* (Figs. 5, 14–17), we detect 0–5 tines, and in *P. utahensis* (Fig. 24–25), three tines, again located distally just before the curving of the distal denticle. The tines in both these species are sparsely populated with spacing roughly half the width of a tine. The tines in *P. becki* shown in Figs. 14–17 exhibit very wide backs and abruptly taper into very fine sharp points. The setal brushes in these two species extend somewhat close to the proximal end of the serrula. In *P. arnaudi* we located five blunted tines obviously showing some wear. The setal brush on this species was well developed, comprised of 14 setae terminating quite close to the proximal end of the serrula. Seven tines were detected in *P. surensis* (Figs. 5, 20) and *P. stahnkei* (Figs. 22–23), in both cases located distally just before the curving of the distal denticle. The tines in *P. surensis* were closely arranged into two clusters separated by a gap approximately the width of four tines. The majority of these tines were elongated, thin, and sharp, and presented the most developed example of serrula so far detected in *Paruroctonus*. Seven tines in *P. stahnkei* were also positioned in close proximity, but were considerably worn down, in general only the backs were observable. See Table 1 for a complete list of the number of tines detected for each species of *Paruroctonus*.

***Smeringurus*:** Serrula in the genus *Smeringurus* is by far the most developed among the four genera studied in this paper so that the term "vestigial" may be an overstatement. The setal brush in this genus is also more

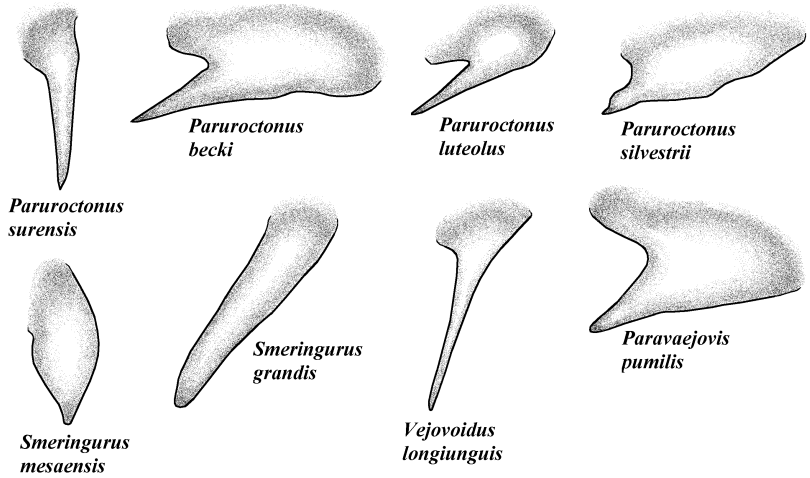


Figure 5: Examples of serrula tines in genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* showing the great variety in their overall structure. Note that all tines slant towards the distal aspect of the cheliceral movable finger, and, in these examples, their distal tips are not blunted or broken.

developed, exhibiting up to 28 setae in the material examined. These setae are sometimes aligned in two or more rows basally, but usually occur as a single row from mid-finger on, in line with the serrula. *Smeringurus grandis* (Figs. 5, 26–33) has a relatively developed serrula with tine numbers ranging 4–15 and in general closely positioned. As in other species in our study group, in serrula with a smaller number of tines, the tines are shorter, with wider backs, and sparsely positioned. For example, the specimen with 15 tines (Figs. 26–27) exhibits narrower backs and longer, thinner tines. In *S. mesaensis* (Figs. 5, 42–45) we see a moderately developed serrula, showing 1–10 closely arranged tines. The tines in these examples are somewhat blunted due to wear. *Smeringurus aridus* (Figs. 34–39) and *S. vachoni immanis* (Figs. 40–41) exhibit the most developed serrulae of the four studied genera. In these two species, we documented generally closely arranged tines numbering as high as 21 for *S. aridus* and 24 for *S. vachoni immanis*. In all cases where the tines were not worn or blunted, they were elongated with narrow backs.

***Vejovoidus*:** For genus *Vejovoidus* (Figs. 5, 46–49) the term "vestigial" may be an understatement because the majority of specimens examined, involving two localities, adults, subadults and juveniles, lacked serrula completely. Only in one specimen (out of eleven) was serrula located, with one tine on one chelicera, and two tines on another. These tines were long and thin, with relatively narrow backs (Figs. 46–48). In Fig. 49 we illustrate a chelicera without serrula which should be compared to Fig. 46 where one tine is visible. It is interesting to note that the setal brush is significantly more developed on the specimen without serrula (showing sixteen setae) and they extend over the area where serrula is usually found, to the point where the distal denticle begins to curve.

Serrula development in Vaejovidae

Tables 1 and 2 provide statistical data on serrula presence in the four subject genera of this paper. Table 1 provides a list of all specimens examined using SEM microscopy (50 specimens and 80 chelicera in total), detailing exactly how many tines per serrula were observed on each chelicera, if any. These data were discussed in general terms above under the individual genera.

Table 2 introduces a "metric" for determining the relative development of a serrula. As is apparent from the discussion of individual serrula development in the four genera provided above, the degree of development is quite variable, anywhere from a single tine to a complete contiguous line of tines exceeding 20 in number. We propose to quantify the serrula development with a *Serrula Development Quotient* (SDQ). The SDQ is based both on the *density* of tine placement within the serrula as well as the number of tines. We define density as the percentage of area occupied by the tines in the serrula, as measured on a SEM image. If the tines are contiguous (i.e., there are no gaps between tines), the SDQ = 1.0. The most developed serrula under this scheme, would be a serrula with all tines positioned contiguously (i.e., a density of 1.0). Thus, a SDQ value is reduced if the density is less than one.

Table 2 shows that genus *Smeringurus* has a reasonably well developed serrula; of our eight examples shown in this table, six have contiguous tine placement. The number of tines is also the largest found in four studied genera, especially in *S. aridus* and *S. vachoni immanis*, where numbers range 13–24, and tines are also contiguous (i.e., density of 1.0). Genus *Paruroctonus*, though exhibiting considerable variability within species, has weak but usually present serrula. In general, the tines in this genus are not contiguously positioned, density ranging from 0.653–1.0 (average 0.855) and the number of tines ranging from 2–7 (based on eight species where serrula were detected). Genus *Paravaejovis* exhibits a reduced serrula with 3–6 tines occupying less than half of the serrula length (average density 0.467). Genus *Vejovoidus* exhibits the least developed serrula where in the only example where more than one tine was present (two were detected), they

	Specimen #, Age / Gender	Locality *	Tines
Paravaejovis pumilis	1, male	Ciudad Constitución	-/6
	2, male	Ciudad Constitución	3/-
Vejovoidus longiunguis	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/-
Smeringurus aridus	1, male	ABDSP, California	22/21
	2, male	ABDSP, California	17/-
	3, juvenile	ABDSP, California	13/8
	4, juvenile female	ABDSP, California	8/12
Smeringurus grandis	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
Smeringurus mesaensis	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/-
Smeringurus v. immanis	1, female	1000 Palms, California	24/-
Paruroctonus arnaudi	1, male	El Socorro	5/3
	2, juvenile	El Socorro	3/-
Paruroctonus becki	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
Paruroctonus boreus	1, male	Warland, Wyoming	0/-
	2, male	Warland, Wyoming	0/0
	3, male	Warland, Wyoming	0/0
Paruroctonus gracilior	1, male	Cuatro Ciénegas	0/0
	2, male	Cuatro Ciénegas	0/-
	3, juvenile	Lordsberg, New Mexico	0/0
Paruroctonus luteolus	1, female	ABDSP, California	2/2
Paruroctonus silvestrii	1, male	ABDSP, California	2/2
Paruroctonus stahnkei	1, female	Mesa, Arizona	7/-
Paruroctonus surensis	1, male	Las Bombas	7/-
Paruroctonus utahensis	1, male	Kermit, Winkler Co., Texas	0/-
	2, female	Kermit, Winkler Co., Texas	3/-
	3, male	Kermit, Winkler Co., Texas	6/7
Paruroctonus ventosus	1, male	El Socorro	2/-

Table 1: Serrula development in genera *Paravaejovis, Vejovoidus*, *Smeringurus*, and *Paruroctonus* (16 species, 50 specimens, 80 individual chelicerae screened by SEM). * See **Material Examined** section for exact locality data.

	Density*Number of Tines = SDQ
Paravaejovis pumilis	0.464*3 = 1.39 0.469*6 = 2.82
Vejovoidus longiunguis	0.364*2 = 0.73
Smeringurus aridus	1.0*13 = 13 1.0*21 = 21
Smeringurus grandis	0.840*4 = 3.36 0.738*6 = 4.43 1.0*15 = 15
Smeringurus mesaensis	1.0*6 = 6 1.0*10 = 10
Smeringurus v. immanis	1.0*24 = 24
Paruroctonus arnaudi	0.953*5 = 4.76
Paruroctonus becki	0.782*3 = 2.35
Paruroctonus luteolus	1.0*2 = 2.0
Paruroctonus silvestrii	0.725*2 = 1.45
Paruroctonus stahnkei	0.882*7 = 6.17
Paruroctonus surensis	0.653*7 = 4.57
Paruroctonus utahensis	0.846*3 = 2.54
Paruroctonus ventosus	1.0*2 = 2
Pseudouroctonus andreas	1.0*22 = 22
Stahnkeus subtilimanus	1.0*37 = 37
Serradigitus gertschi	1.0*27 = 27
Serradigitus joshuaensis	1.0*21 = 21
Serradigitus minutis	1.0*22 = 22
Uroctonites huachuca	1.0*31 = 31
Vaejovis confusus	1.0*11 = 11
Vaejovis globosus	0.918*10 = 9.18
Vaejovis gravicaudus	1.0*21 = 21
Vaejovis intrepidus	1.0*15 = 15
Vaejovis magdalensis	1.0*19 = 19
Vaejovis puritanus	1.0*16 = 16
Vaejovis viscainensis	1.0*15 = 15

Table 2: Serrula Development Quotient (SDQ). Density = space occupied by tines / serrula length (i.e., longitudinal distance along cheliceral movable finger). A density equal 1.0 implies that the tines are contiguously aligned in the serrula without gaps. Samples with only one tine are excluded from this table. Data presented on genera *Paravaejovis*, *Vejovoidus*, *Smeringurus*, and *Paruroctonus* based on Figures 6–49.

were separated from each other by more than three tine widths. This genus, based on the limited data, had the smallest density (0.364).

It is important to demonstrate here that serrula is indeed less developed (i.e. "vestigial") in the four discussed genera than in other Vaejovidae. Table 2 provides a good representation of other vaejovid genera as well as *Vaejovis* groups, which generally have contiguous tine placement and a considerably higher tine number, especially in those genera and groups that have been characterized by "well developed serrula" (see Soleglad & Fet, 2005: 5–6; Graham & Fet, 2006). We also observe a trend in closely related species (i.e., members of the same genus or *Vaejovis* group) where the larger species have higher numbers of tines than smaller species. For example, in tribe Stahnkeini, a large species *Stahnkeus subtilimanus* has 37 tines, whereas smaller species in its sister genus *Serradigitus* have lower tine numbers, e.g. *S. joshuaensis* and *S. minutis* with 21 and 22, respectively, (these are some of the smallest species in Vaejovidae). At the same time, *Serradigitus gertschi*, a larger species than the former two, has 27 tines. Two closely related species, a larger *Uroctonites huachuca* and a smaller *Pseudouroctonus andreas*, have 31 and 22 tines, respectively. The number of tines found in the *"eusthenura"* and *"punctipalpi"* groups of *Vaejovis* is smaller than in the genera just discussed, which is again consistent with the characterization of their serrula as "moderately developed."

Observations on Serrula Evolution

Stockwell (1989) has presented the only cogent cladistic analysis incorporating the cheliceral serrula in Recent scorpions. Stockwell (1989: 148–149, figs. 251, 256, 257) modeled serrula in Recent scorpions with three characters (37–39), together forming an additive binary complex. Character-37 represented the derivation of serrula, occurring twice in Stockwell's cladogram (1989: fig. 251) for the clades **Superstitioniidae** + **(Iuridae** (= Iuroidea) + **Vaejovidae)** and **Chactidae**. Characters 38–39 represented independent loses of serrula for clades **(*Caraboctonus* + *Hadruroides*)** + **(*Hadrurus* + *Anuroctonus*** [the latter now placed in Chactidae]**)**, members of Iuroidea, and ***Paravaejovis*** + **(*Smeringurus* + *Vejovoidus* + *Paruroctonus*)**, members of Vaejovidae, the subject of this paper.

The evolutionary picture of serrula in Recent scorpions is more complicated now since Stockwell's (1989) original analysis: (1) the recently discovered relict scorpion *Pseudochactas* Gromov, 1998, basal to all Recent scorpions, exhibits serrula (Soleglad & Fet, 2003: fig. 49; Graham & Fet, 2006: fig. 1); (2) genus *Chactopsis*, which exhibits serrula (Soleglad & Sissom,

2001: figs. 134, 140), is now placed in family Euscorpiidae; (3) genus *Anuroctonus*, which does not exhibit serrula, is now placed in family Chactidae; (4) superfamily Iuroidea (= Iuridae sensu Stockwell, 1989) is now considered basal to superfamilies Scorpionoidea and Chactoidea in parvorder Iurida (Soleglad & Fet, 2003: fig. 114); and (5) related vaejovid genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* exhibit vestigial serrula, as reported in this paper.

Based on the current classification of Recent scorpions, as established in Soleglad & Sissom (2001: fig. 211) and Soleglad & Fet (2003: fig. 114), the most parsimonious scenario of serrula evolution would be as follows. Serrula could be either plesiomorphic in all Recent scorpions and then lost at the Buthida node (i.e., *Pseudochactas* inherits ancestral serrula), or serrula absence could be plesiomorphic in all Recent scorpions, and derived independently in *Pseudochactas*. From this point in the phylogeny, serrula evolves independently in family Iuridae and in superfamily Chactoidea; serrula is then lost in family Euscorpiidae and in genus *Anuroctonus* (Chactidae); and finally serrula is derived in genus *Chactopsis* (Euscorpiidae) — a total of six steps if serrula evolution is modeled as a single two-state derivation, exhibiting high homoplasy (i.e., CI = 0.167). If three independent derivations of serrula are modeled as separate characters, or as separate states if one character, (a reasonable hypothesis since these derivations occur in three separate superfamilies, Pseudochactoidea, Iuroidea, and Chactoidea), the homoplasy is reduced and restricted only to Chactoidea. In Stockwell's (1989) interpretation, if we model the serrula character as a single two-state derivation (not as three characters as proposed by Stockwell), we have four steps (CI = 0.250). One has to remember, comparing these two examples, that at the time of Stockwell's (1989) analysis, *Pseudochactas* had not yet been discovered and the presence of vestigial serrula in related genera *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus* was not known.

As a final note, it is important to stress here that the over generalized characterizations of serrula development as "vestigial," "moderately developed," or "well developed" must be replaced with more detailed and precise quantifications. We believe that the breakdown of the serrula into back and tine structure, number of tines, and their density is a beginning to a further refinement of this delicate structure. In line with this, we also suggest (as hypothesized by Soleglad & Fet, 2004: 84) that the setal brush occurring basally on the ventral aspect of the cheliceral movable finger is related closely to serrula development in Recent scorpions and must be factored into the study of serrula. These issues are currently undergoing further analysis (Brewer et al., in progress).

Acknowledgments

We thank Graeme Lowe, Matthew Graham, Douglas Gaffin, and Elizabeth Fet for the generous gift of specimens used for SEM study. We also extend our gratitude to Matthew Graham and František Kovařík for reviewing this paper.

References

FET, V. & M. E. SOLEGLAD. 2005. Contributions to scorpion systematics. I. On recent changes in high-level taxonomy. *Euscorpius*, 31: 1–13.

FET, V., M. E. SOLEGLAD, M. S. BREWER. 2006a. Laterobasal aculear serrations (LAS) in scorpion family Vaejovidae (Scorpiones: Chactoidea). *Euscorpius*, 45: 1–19.

FET, V., M. E. SOLEGLAD, M. S. BREWER, D. P. A. NEFF & M. L. NORTON. 2006b. Constellation array in scorpion genera *Paruroctonus*, *Smeringurus*, *Vejovoidus*, and *Paravaejovis* (Scorpiones: Vaejovidae). *Euscorpius*, 41: 1–15.

GRAHAM, M. R. 2006. Redescription and lectotype designation of *Vaejovis lapidicola* Stahnke, 1940 (Scorpiones: Vaejovidae). *Euscorpius*, 46: 1–6.

GRAHAM, M. R. & V. FET. 2006. Serrula in retrospect: a historical look at scorpion literature (Scorpiones: Orthosterni). *Euscorpius*, 48: 1–19.

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

SOLEGLAD, M. E. & V. FET. 2004. The systematics of scorpion subfamily Uroctoninae (Scorpiones: Chactidae). *Revista Ibérica de Aracnología*, 10: 81–128.

SOLEGLAD, M. E. & V. FET. 2005. A new scorpion genus (Scorpiones: Vaejovidae) from Mexico. *Euscorpius*, 24: 1–13.

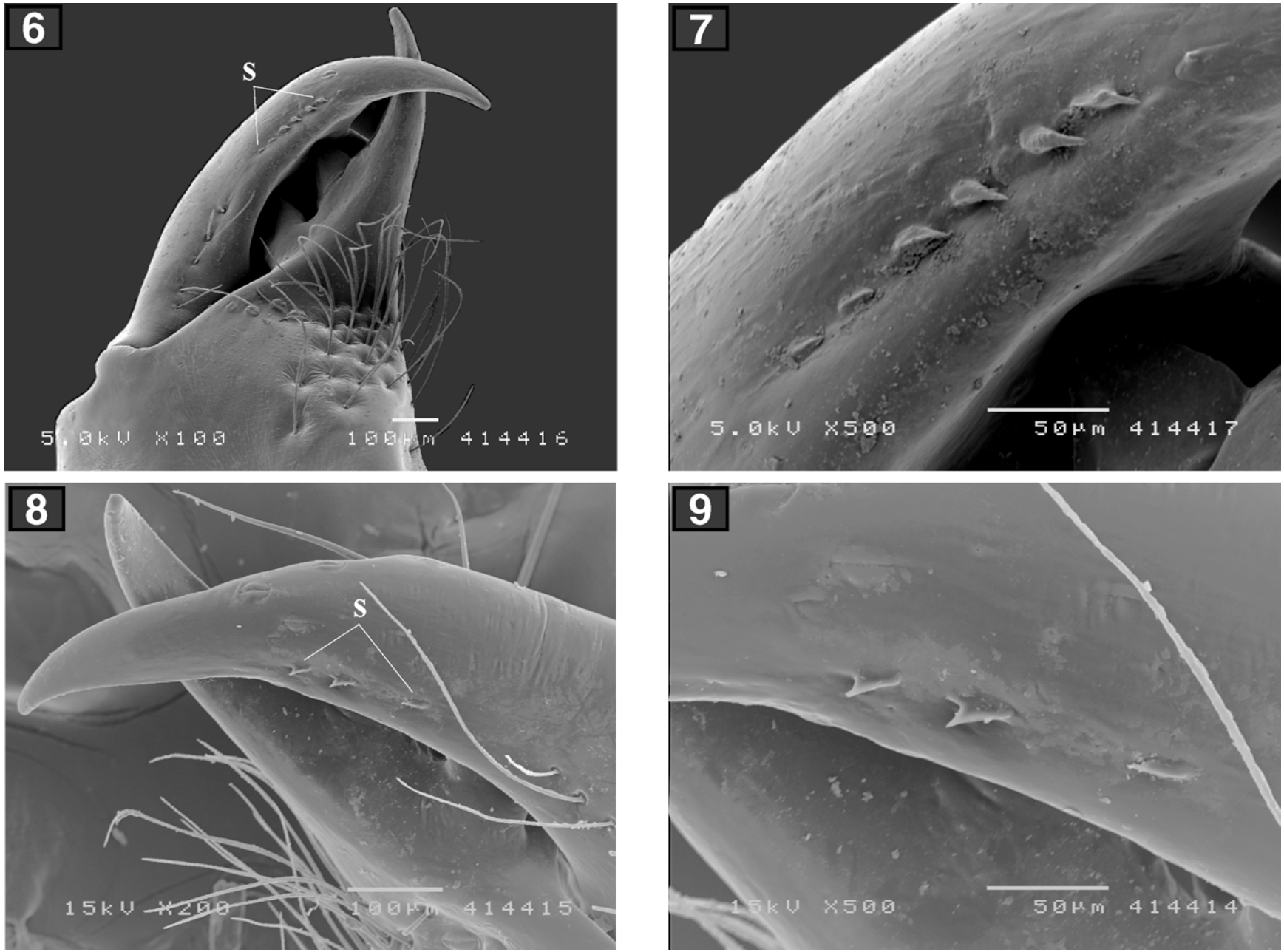
SOLEGLAD, M. E. & V. FET. 2006. Contributions to scorpion systematics. II. Stahnkeini, a new tribe in scorpion family Vaejovidae (Scorpiones: Chactoidea). *Euscorpius*, 40: 1–32.

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

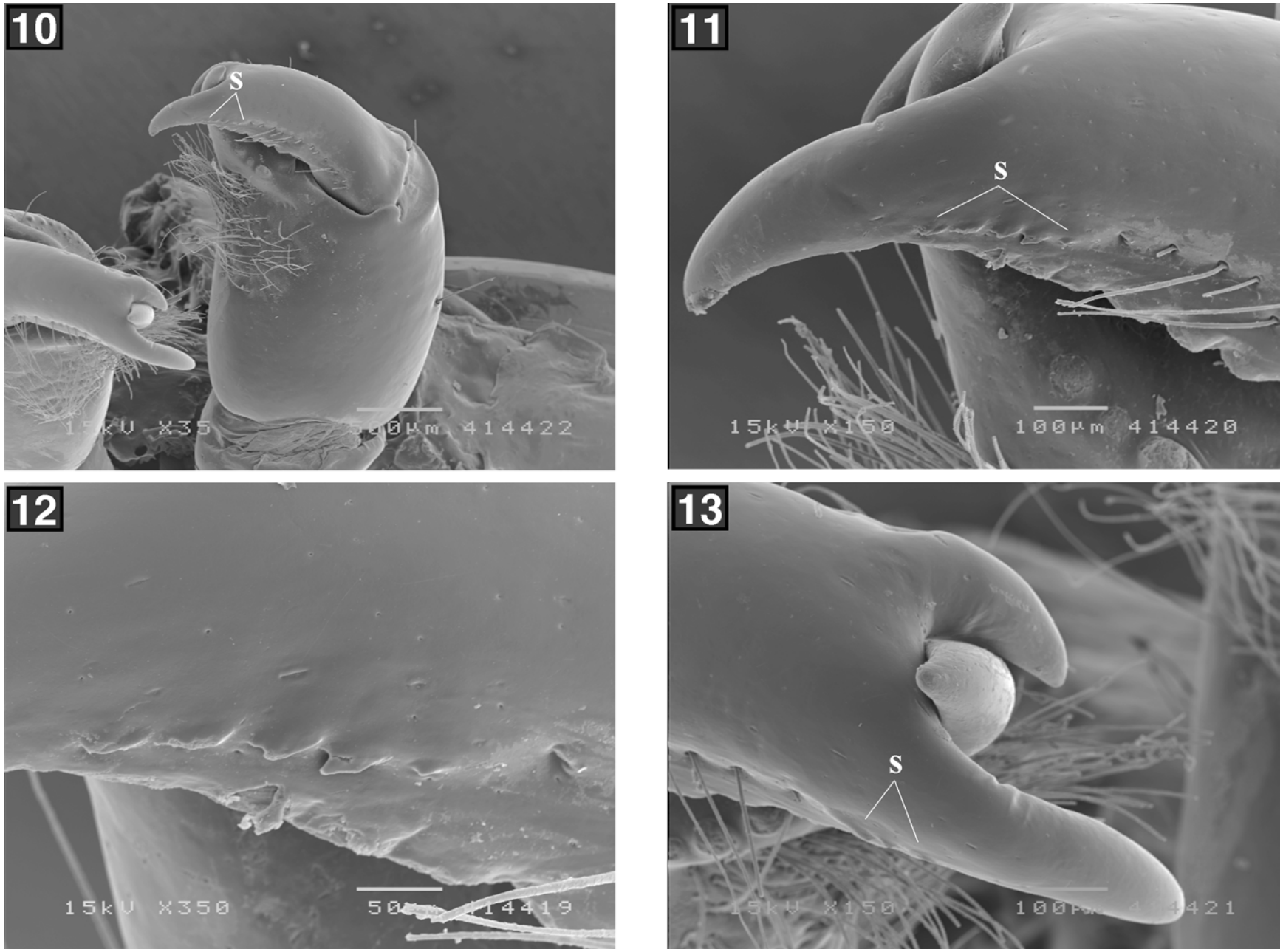
A. Polis. Burnham Beeches, Bucks: British Arachnological Society.

STOCKWELL, S. A. 1989. *Revision of the Phylogeny and Higher Classification of Scorpions (Chelicerata)*. Ph.D. Thesis, University of Berkeley, Berkeley, California. 319 pp. (unpublished). University Microfilms International, Ann Arbor, Michigan.

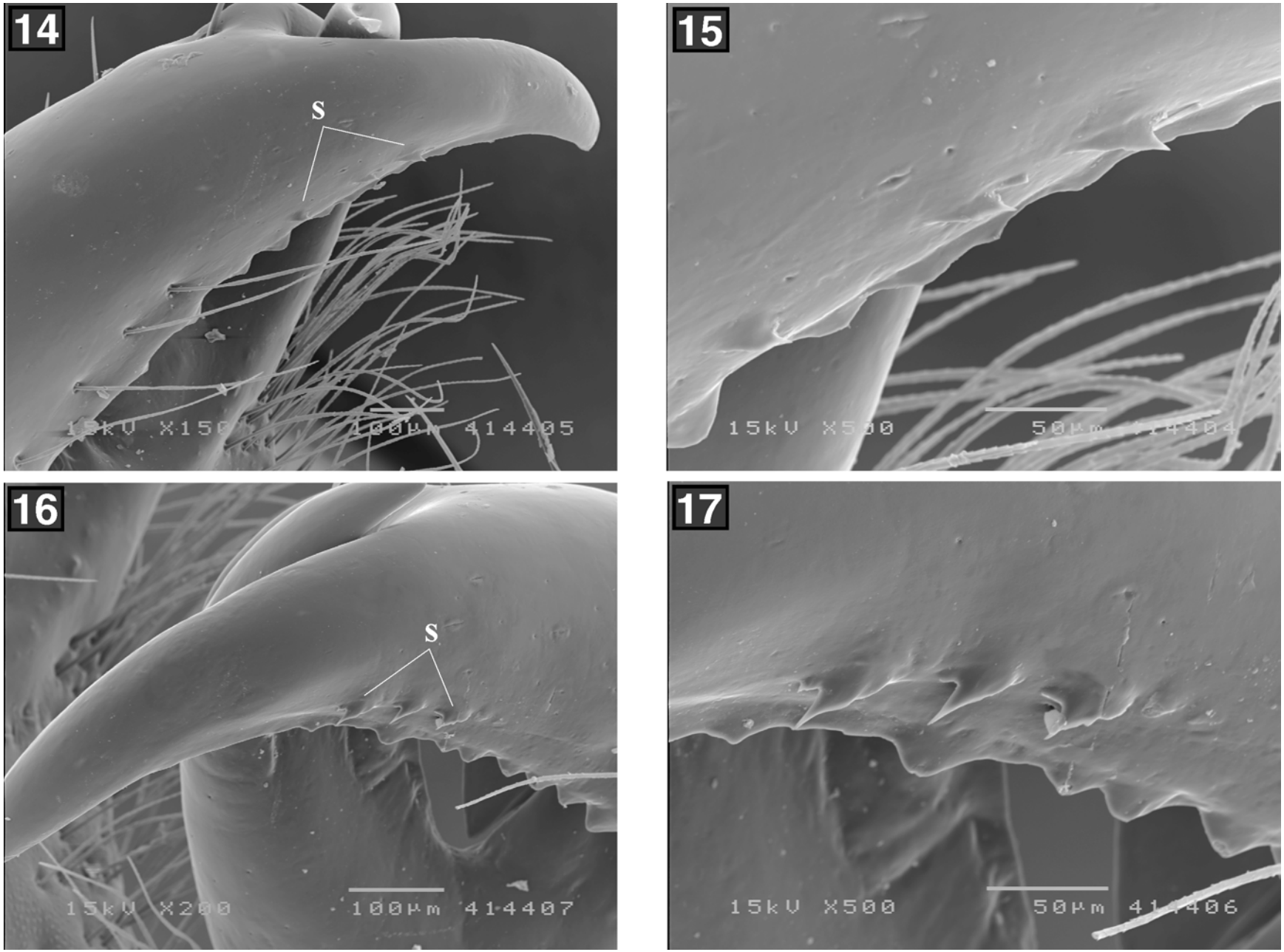
STOCKWELL, S. A. 1992. Systematic observations of North American Scorpionida with a key and checklist of the families and genera. *Journal of Medical Entomology*, 29(3): 407–422.



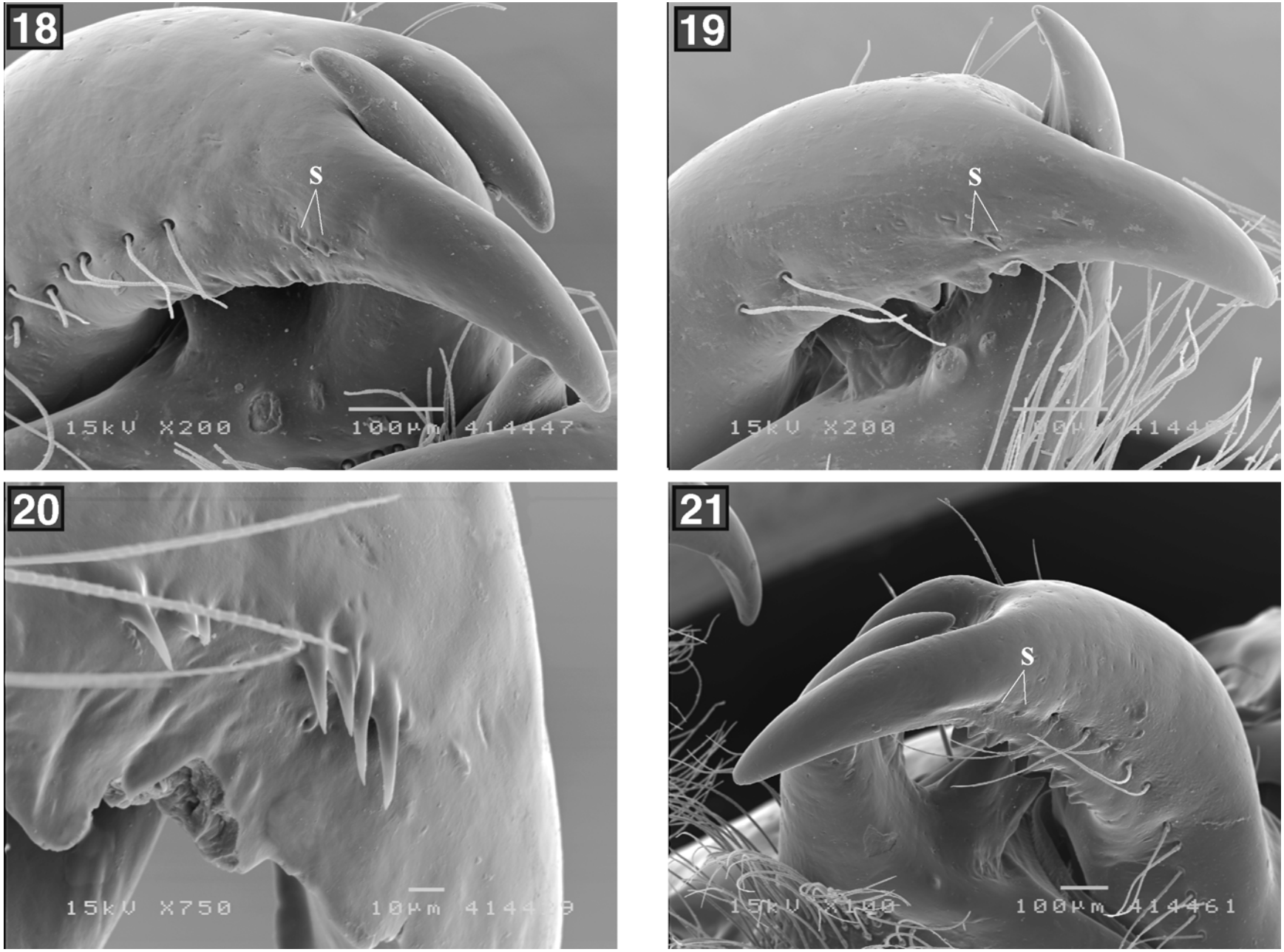
Figures 6–9: Cheliceral movable finger, ventral view, showing serrula in *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. **6 & 7.** Male-1, chelicera and closeup of serrula, showing six tines. Note the reduced setal brush on finger base. **8 & 9.** Male-2, chelicera and closeup of serrula, showing three tines; "s" indicates serrula.



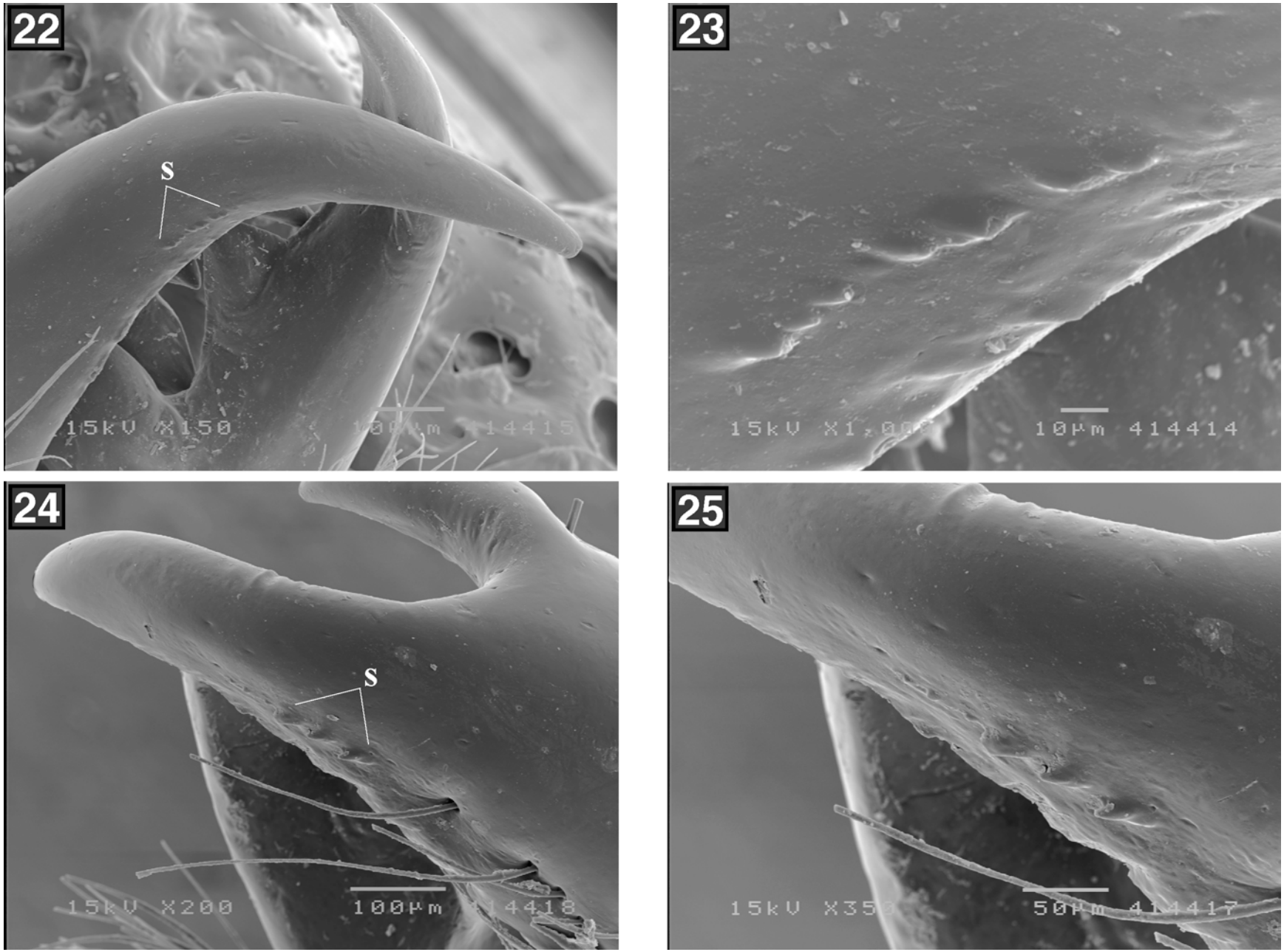
Figures 10–13: Cheliceral movable finger, ventral view, showing serrula in *Paruroctonus arnaudi*, male, El Socorro, Baja California, Mexico. **10–12.** Shows successive closeups of serrula on left chelicera with five tines. Note that serrula occurs distally in line with the row of setal brush. **13.** External view of right chelicera showing profile of distal serrula at base of distal denticle; "s" indicates serrula.



Figures 14–17: Cheliceral movable finger, ventral view, showing serrula in *Paruroctonus becki*, female, San Bernardino Co., California, USA. **14 & 15.** Shows successive closeups of serrula on right chelicera with three tines. Note that serrula occurs distally in line with the row of setal brush. **16 & 17.** Shows successive closeups of serrula on left chelicera with three tines; "s" indicates serrula.



Figures 18–21: Cheliceral movable finger, ventral view, showing serrula in the genus *Paruroctonus*. **18.** *Paruroctonus ventosus*, female, El Socorro, Baja California, Mexico, showing two tines. **19.** *Paruroctonus luteolus*, female, Palo Verde Wash, ABDSP, California, USA, showing two tines. Note an extremely reduced setal brush. **20.** *Paruroctonus surensis*, male, Las Bombas, Baja California Sur, Mexico, showing seven tines. **21.** *Paruroctonus silvestrii*, male, Chihuahua Road, ABDSP, California, USA, showing two tines; "s" indicates serrula.



Figures 22–25: Cheliceral movable finger, ventral view, showing serrula in the genus *Paruroctonus*. **22 & 23.** *Paruroctonus stahnkei*, female, Mesa, Arizona, USA, chelicera and closeup of serrula, showing seven blunted tines. **24 & 25.** *Paruroctonus utahensis*, female, Kermit, Winkler Co., Texas, USA, chelicera and closeup of serrula, showing three tines; "s" indicates serrula.