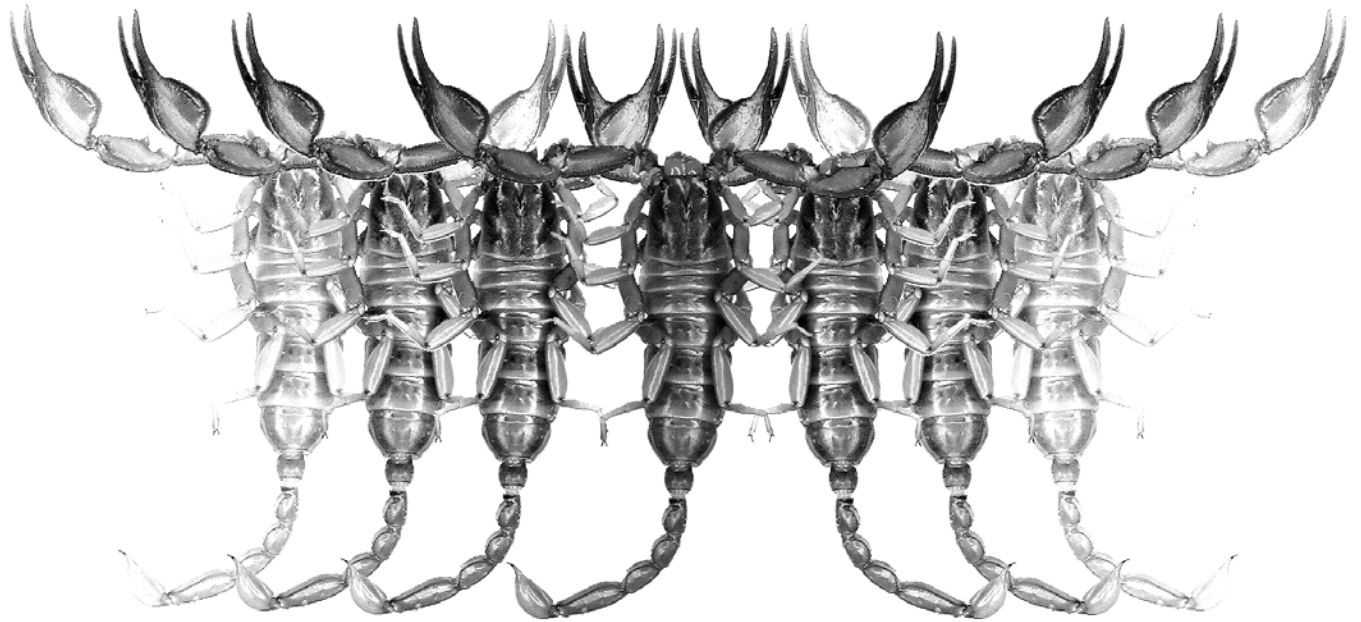


Euscorpius

Occasional Publications in Scorpiology



**Serrula in Retrospect: a Historical Look at Scorpion
Literature (Scorpiones: Orthosterni)**

Matthew R. Graham and Victor Fet

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Euscorpius

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- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway

Serrula in retrospect: a historical look at scorpion literature (Scorpiones: Orthosterni)

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Summary

Serrula, a small comb-like structure on the ventral aspect of cheliceral movable finger in scorpions, has often been overlooked or ignored. Scorpion genera that are currently known to possess serrula belong to six families: Chactidae, Euscorpiidae, Iuridae, Pseudochactidae, Superstitioniidae, and Vaejovidae. All relevant literature on scorpion serrula is reviewed, and serrula of representative scorpion taxa is illustrated by SEM images. We suggest that the inconsistency in reporting serrula is based on several factors (or combination thereof): (a) serrula tines can quite often be broken off partially or completely, especially in adults; (b) serrula can be vestigial and hardly visible under a dissection microscope; and (c) serrula can be obscured by long, dense setae.

Introduction

Serrula, a comb-like structure found on the ventral aspect of cheliceral movable finger in some scorpions, has been overlooked or ignored in many studies. The record of serrula in scorpion literature has been somewhat erratic, and relatively few authors have used this structure for taxonomic studies. Here, we discuss the history of the documentation of serrula in literature, list the taxa which possess the structure, and suggest some clues to why it has been often omitted even in the studies of scorpion groups where it was known to occur.

Material and Methods

This paper is based on an extensive analysis of literature, and is illustrated by a selection of original SEM images. Below, we list material and methods used for producing those images. All specimens are in the private collection of the second author. Taxonomy after Soleglad & Fet, 2003, 2006; Fet & Soleglad, 2005.

Material

Parvorder Iurida, superfamily Chactoidea, family Chactidae: *Belisarius xambeui* Simon, 1879, ♀, Fogars de Monclus, Barcelona Province, Spain; *Brotheas gervaisii* Pocock, 1893, ♀, Martinique; *Chactas reticulatus* Kraepelin, 1912, ♀, Colombia; *Uroctonus mordax* Thorell, 1876, ♀, California, USA; family Superstitioniidae: *Superstitionia donensis* Stahnke, 1940, ♀, San Diego, California, USA; family Vae-

jovidae: *Pseudouroctonus andreas* (Gertsch et Soleglad, 1972), ♀, Anza-Borrego Desert State Park, California, USA; *Stahnkeus subtilimanus* (Soleglad, 1972), ♀, Anza-Borrego Desert State Park, California, USA; superfamily Iuroidea, family Iuridae: *Iurus dufourei* (Brullé, 1832), juv. ♂, Crete, Greece. Parvorder Pseudochactida, superfamily Pseudo-chactoidea, family Pseudochactidae: *Pseudochactas ovchinnikovi* Gromov, 1998, juv. ♀, Akmachit, Babatag Mountains, Surkhandarya Region, Uzbekistan.

Microscopy

Scorpions were preserved in 70% or 96% ethanol. Chelicerae were removed from the animals and sonicated for 1 minute in 50% ethanol, after which they were dehydrated in an ethanol series (75, 95, and two changes of 100 %) before being air dried and coated with gold/palladium (ca. 10 nm thickness) in a Hummer sputter coater. SEM images were acquired with a JEOL JSM-5310LV at Marshall University, West Virginia, USA. 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. Digital SEM images were taken at magnifications from 75x to 350x.

What is a Serrula?

The term “serrula” (literally, “a small saw”) in arachnology is limited to a specific comb-like structure found on chelicera or pedipalp coxa in several orders of

arachnids such as spiders (e.g. Platnick & Ubick 2001; Maddison & Hedin, 2003) and schizomids (e.g. Rowland & Reddell, 1979). Cheliceral serrula is probably best known in pseudoscorpions (e. g. Chamberlin, 1932; Harvey, 1992), where it is found in the same location as in scorpions.

In scorpions, where it has been documented only in some taxa, the serrula is a comb-like structure that emanates from a longitudinal ridge on the ventral surface of the cheliceral movable finger, with tines directed downward. Each comb consists of a number of tines (sometimes over 30), lined up in a row. These tines vary in size with the smallest on the distal and proximal ends, tapering to longer tines in the middle. Serrula tines are so thin that they have been rarely adequately illustrated in literature; the only SEM micrographs were published by Williams & Savary (1987, fig. 4) for *Uroctonites giulianii* and Lourenço (1998a, figs. 25–26) for *Belisarius xambeui*. Representative serrulae of various degrees of development and preservation are illustrated here in Figs. 1–8. Serrula is angled relatively to the ventral surface of the movable finger (e.g. at approximately 30° in *Stahnkeus subtilimanus*, Fig. 4), which is illustrated here for the first time using SEM microscopy. This angling has been schematically illustrated by Mitchell (1968, figs. 6–7, 27–28; *Typhlochactas*); Vachon (1971, fig. 8; *Calchas*); Sissom (1985a, fig. 230; *Vaejovis*); and Soleglad & Sissom (2001, fig. 134; *Chactopsis*).

In some scorpions the serrula is greatly reduced, and the tines of such vestigial serrula are very small or appear as a row of crenulations (Fet et al., 2006). Furthermore, the entire length of the serrula can vary as well. Serrula can be as small as a single tine or as large as three-fourths of the cheliceral movable finger on which it is located. Some of the largest serrulae are probably found on the troglotic genera *Alacran*, *Sotanochactas*, *Troglotayosicus*, and *Typhlochactas* (Superstitioniidae).

According to our observations (Brewer et al., in progress), quite often, especially among adult specimens, some or even all of the tines can be broken off at the base (Figs. 1, 5–7). The remaining “serrula stubs” are barely visible under the regular dissection microscope, and cannot be adequately documented without SEM.

Which Scorpions have Serrula?

At this moment, in the following seven families of extant scorpions (using classification of Soleglad & Fet, 2003) serrula was never documented: Bothriuridae, Buthidae, Caraboctonidae, Chaerilidae, Hemiscorpidae, Microcharmidae, and Scorpionidae. It is present in relict families Pseudochactidae (monotypic family with one genus, *Pseudochactas*; Fig. 1) and Iuridae (two genera,

Calchas and *Iurus*; Fig. 2). Serrula is present also in all four families of the superfamily Chactioidea but its distribution is uneven. Among Euscorpidae, it is found only in *Chactopsis*. All genera of Superstitioniidae have serrula (Fig. 5) and the same is probably true for almost all Chactidae (except *Anuroctonus*) (Figs. 6–8). Finally, according to the most recent data, almost all genera of Vaejovidae appear to have at least a vestigial serrula (Fet et al., 2006) (Figs. 3–4).

History of Serrula Discovery and Observations

As far as we can tell, no authors prior to 1944 ever noticed scorpion serrula, even in well-studied groups which possess this structure. Such prominent scorpologists of the late 19th–early 20th century as Simon, Karsch, Thorell, Birula, Pocock, Kraepelin, Borelli, and Banks never documented a serrula in Vaejovidae, Chactidae, or Iuridae, although many new species and genera belonging to these families were described or redescribed by these authors, sometimes in great detail. Surprisingly, it was not mentioned in the very detailed descriptions of *Calchas* by Birula (1917a, 1917b). Hoffmann (1931) never mentioned serrula in his detailed study of the scorpions of Mexico, even though he examined many Vaejovidae that have this structure. Serrula was not mentioned in the definitive scorpion treatise of Werner (1934) either.

It was not until two almost coincidental publications by Mulaik & Higgins (1944) and Vachon (1945) that serrula was actually recognized in scorpions. These two very disparate papers, one American and one French, both described serrula but in different ways, and it is unlikely that their authors even knew about each other’s work. Both taxa at this time were placed in Chactidae.

Mulaik & Higgins (1944) (November issue of *Entomological News*) were the first to describe and illustrate serrula in scorpions. They published a remarkably detailed, for that time, description of a new North American chactoid genus and species they called *Diplops desertorum*. These authors illustrated not just the right chelicera and serrula (fig. 1) but also the strongly magnified images of individual setae and even noticed “minute oval fissures”; which we now know as sensory slit organs! The serrula is described by Mulaik & Higgins as “a comb of twelve bristles.” However, the short two-paragraph description of *Superstitionia donensis* by Stahnke (1940) took precedence, and *Diplops desertorum* was synonymized by Stahnke (1949). The scrupulous work of Mulaik & Higgins has been seldom addressed since that time. Stahnke (1939, 1940, 1949) never mentioned serrula in *Superstitionia*. Moreover, in his 1939 doctoral dissertation, Stahnke (1939) wrote that the inferior (ventral) surface of the

cheliceral movable finger in *Superstitionia donensis* was “entirely smooth and devoid of any crenulation, serration or denticulation.”

The simultaneous study by Vachon (1945) (date on the cover 1944; published February 15, 1945) described and illustrated serrula on the right chelicera for *Belisarius xambeui*, a blind, relict chactoid species from the Pyrenees. This was the first time the term “serrula” was used in scorpion literature. At this time, Vachon also worked with pseudoscorpions, the field from which he carried the term “serrula” over to scorpions. In his *Belisarius xambeui* redescription, Vachon illustrated a serrula (fig. 2) and described it (p. 299) as

“Face inférieure de la chélicère ornée de longues soies barbues, l’extrémité distale du doigt fixe est dépourvue de telles soies mais, par contre, possède une série de soies courtes et aplaties formant un peigne ou *serrula* en tous points semblable à celle des chélicères des Pseudoscorpions” (“Inferior aspect of the chelicera decorated with long barbed bristles, the distal end of the immovable [*sic!* – M.G.R. & V.F.] finger lacks such bristles but, on the contrary, has a series of short or flattened bristles forming a comb or *serrula* very similar to that on the chelicera of pseudoscorpions”).

Note that while in the text Vachon (1945) erroneously placed serrula on the *fixed* cheliceral finger, his legend to fig. 2 correctly says “doigt mobile” (“movable finger”). Vachon also added that serrula was not present in the scorpion genera *Euscorpis* or *Buthus*. Thus, serrula has been first documented for two different, monotypic chactoid genera: *Superstitionia* (now Superstitioniidae; Fig. 5) and *Belisarius* (now Chactidae; Fig. 6).

When nearly two decades later Vachon (1963) produced an important order-wide treatment of cheliceral dentition, in which he must have seen serrula, he did not mention it at all. Vachon must have considered serrula to be too localized a character to use in systematics, compared to cheliceral dentition and, especially, to trichobothria which were being actively studied at this time. It is also unclear whether Vachon by that time actually saw serrula in any other genus than *Belisarius*. No other studies of cheliceral dentition occurred until Francke & Soleglad (1981). Meanwhile, in 1940s–1960s serrula remained non-documented for other scorpion taxa, including North American Vaejovidae and South American Chactidae.

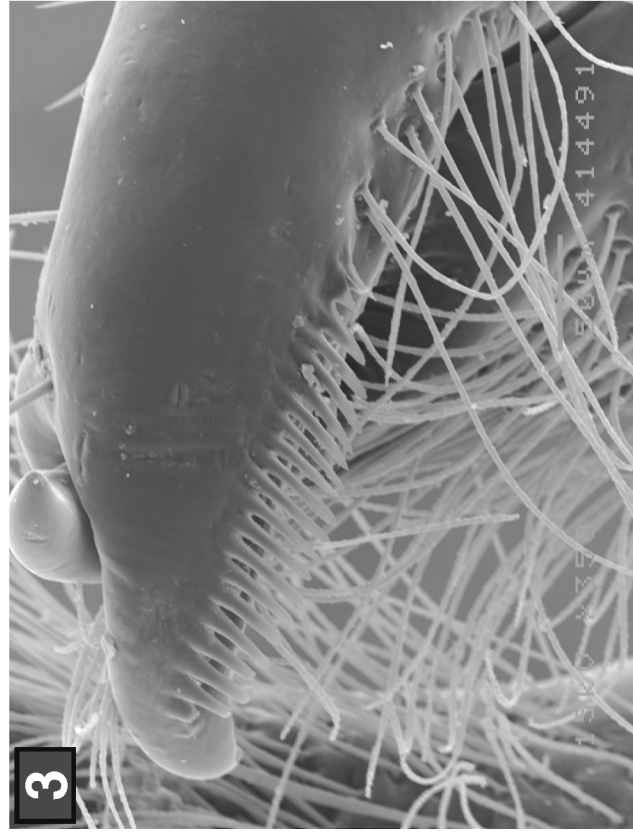
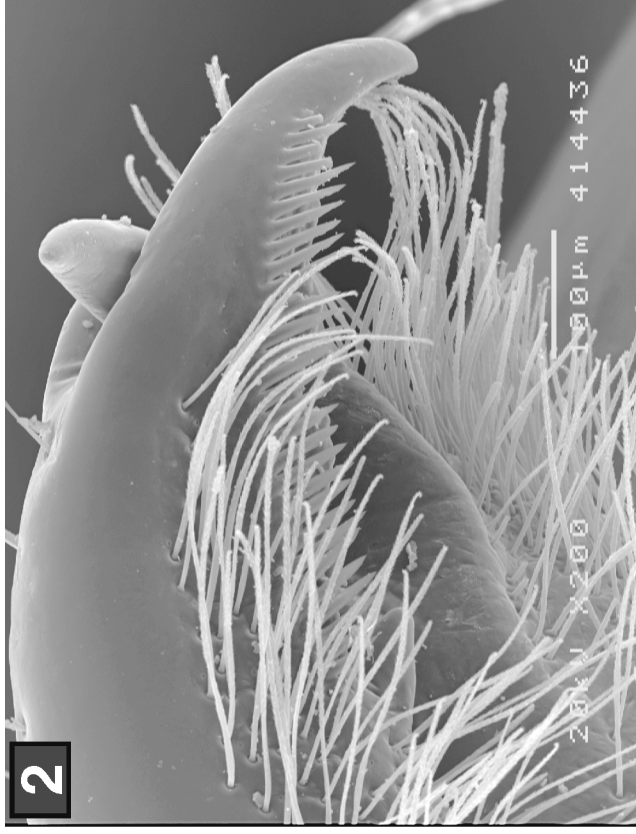
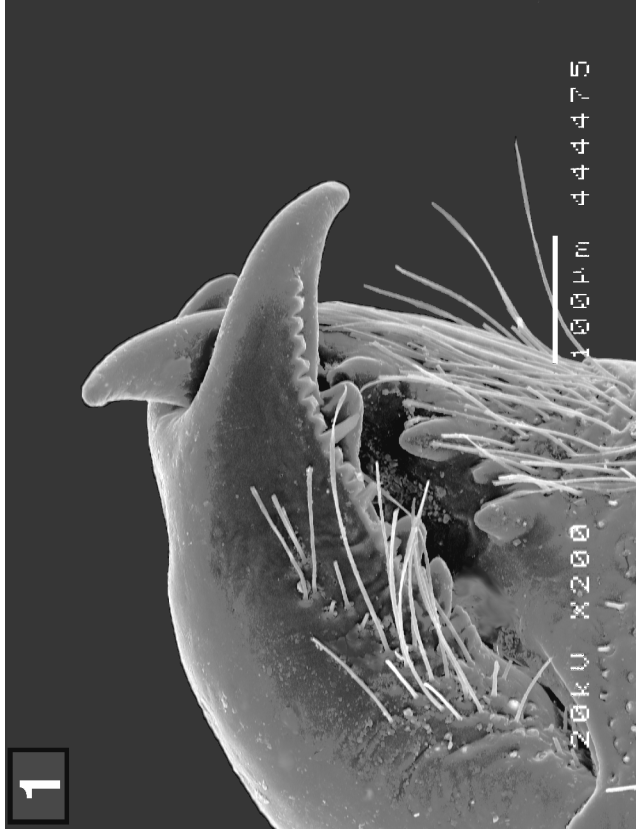
In his large monograph on all known South American scorpions, Mello-Leitão (1945) did not mention serrula for any Chactidae. Herbert L. Stahnke, very familiar with vaejovid scorpions of North America already by the 1940s (see Stahnke, 1939, 1940), never mentioned serrula in his work of 1940s–1960s, e.g. in a detailed study of the type specimen of *Syntropis macrura* (Stahnke, 1965). Willis J. Gertsch collaborated

in his spider studies with Stanley Mulaik, the discoverer of scorpion serrula (see e.g. Gertsch & Mulaik, 1940), and could have been aware of its existence in *Superstitionia*. However, in their scorpion papers published before 1972, Gertsch and his coauthors did not mention serrula in vaejovid species which possess it (Gertsch, 1958; Gertsch & Allred, 1965). In part, they dealt at this time with vaejovid species now placed in *Paruroctonus* and *Smeringurus* (Gertsch & Allred, 1965; Gertsch & Soleglad, 1966), in which, as we now know, serrula is heavily reduced (Fet et al., 2006). Serrula was also not mentioned by Vachon (1966) in his important and nicely illustrated paper on genus *Iurus* (Iuridae), although this paper even had schematic drawings of movable cheliceral finger (figs. 17–18).

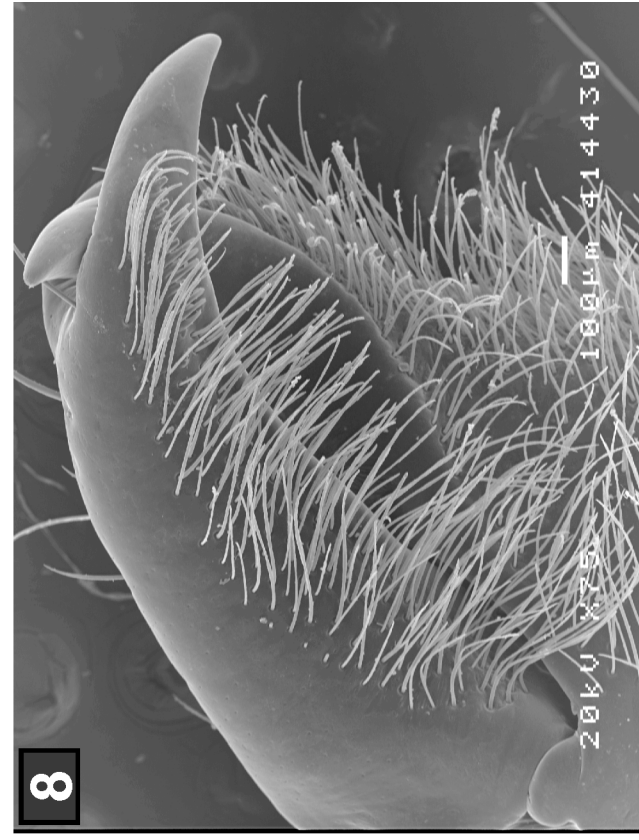
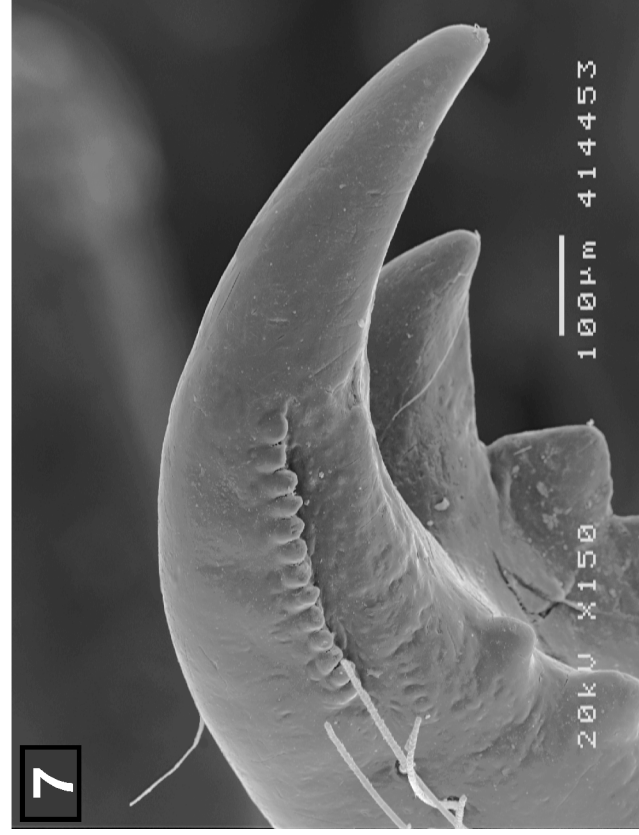
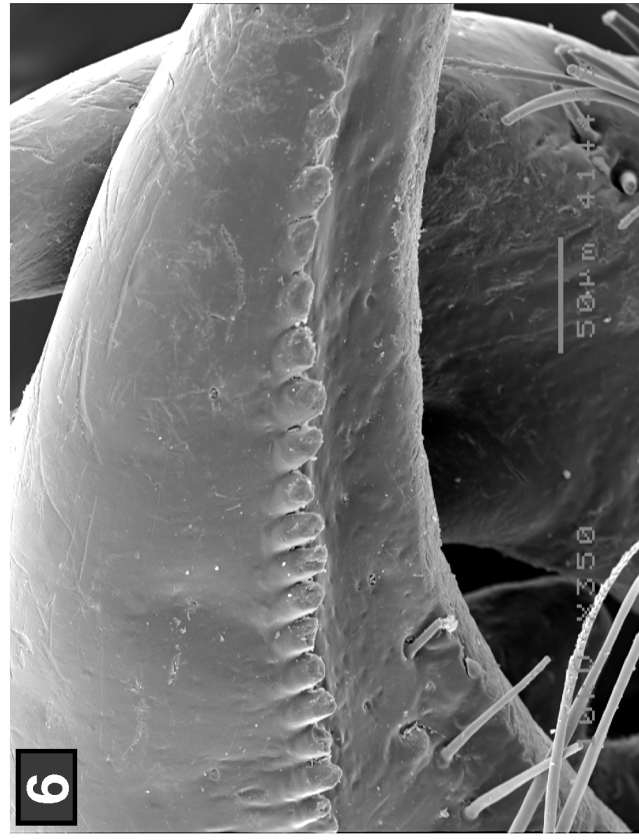
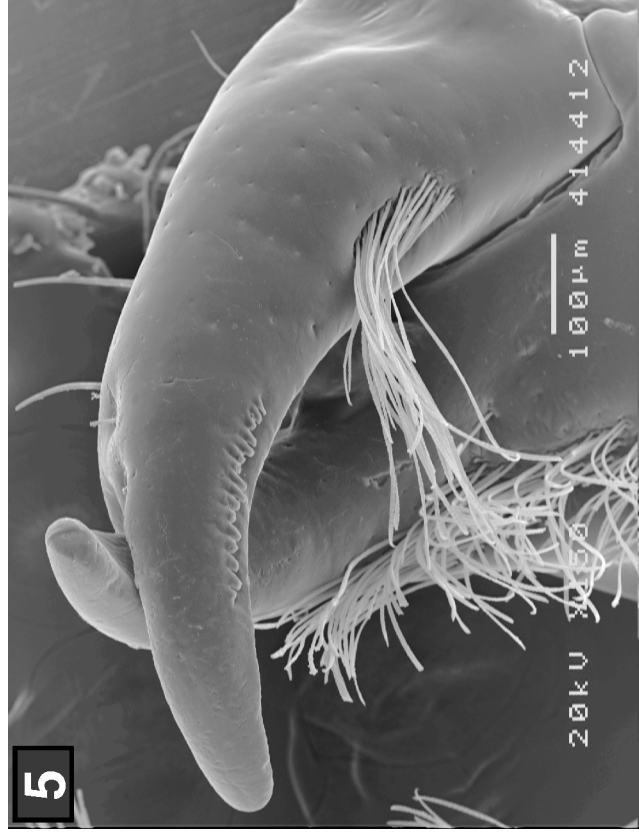
Only in 1968 serrula was mentioned in scorpion literature again, this time in a well-circulated paper by Robert W. Mitchell (1968). Based on a faunistic study of two Mexican caves, one in Tamaulipas and the other in Veracruz, Mitchell described two new chactoid species, *Typhlochactas rhodesi* and *T. reddelli* (now in Superstitioniidae). For these species, the serrula are described as “present on distal one-half of venter of movable finger” as well as illustrated ventrally, medially, and laterally (Mitchell, 1968, figs. 4, 6–8, 24, 26–28). Mitchell was very aware of Vachon (1945) and mentions that both *Belisarius* (which also happens to lack eyes!) and *Typhlochactas* possess serrula, indicating a potential relationship between the two (which is currently not confirmed; see Soleglad & Fet, 2003).

Further work on *Typhlochactas* usually documented presence of a serrula. Two more papers by Mitchell described new Mexican troglobites, *Typhlochactas elliotti* (Mitchell, 1971; now *Sotanochactas elliotti*) and *T. sylvestris* (Mitchell & Peck, 1977), both of which were noticed to possess serrula. For both species, Mitchell (1971, fig. 6) and Mitchell & Peck (1977, fig. 6) illustrated serrula and described it as “present on venter of movable finger, extending three-fourths length of finger.” Further work on *Typhlochactas* always recorded serrula. Francke (1986) described *Typhlochactas cavicola* with “serrula well developed.” Sissom (1988: 369) mentioned serrula in his description of *Typhlochactas mitchelli*: “Distinct serrula present on ventrodiscal two-thirds of movable finger.” Sissom & Cokendolpher (1998: 287) in their description of *Typhlochactas granulatus* wrote: “Distinct serrula present on ventrodiscal half of movable finger.” Both Sissom (1988) and Sissom & Cokendolpher (1998) also mentioned surrounding setation in the following terms: “Dense array of long, thin setae present on medial and ventral surfaces of fixed finger; a few longer hairlike setae situated on ventral aspect of movable finger (proximal to serrula).”

In addition to *Typhlochactas*, Mitchell (1968) mentioned that he also had an undescribed species of



Figures 1-4: Cheliceral movable finger, ventral view, showing examples of serrula in Recent scorpions representing the three superfamilies where it occurs. **1.** *Pseudochactas ovchinnikovi*, subadult female, Babatag, Uzbekistan (Pseudochactoidea), showing well developed serrula with severely broken tines. **2.** *Jurus difourei*, juvenile male, Crete, Greece (Luroidea), showing well developed serrula, middle to basal tines covered by setal brush. **3.** *Pseudouroctonus andreas*, male, California, USA (Chactoidea), showing well developed serrula. **4.** *Stahnkeus subtilimanus*, female, California, USA (Chactoidea), showing well developed serrula from a distal denticle perspective. Note how the serrula angles away from finger surface.



Figures 5-8: Cheliceral movable finger, ventral view, showing examples of serrula in Recent scorpions (Chactioidea). **5.** *Superstitonia donensis*, female, San Diego, California, showing well developed serrula with severely broken tines. **6.** *Belisarius xambeui*, female, Barcelona Province, Spain, showing a well developed but broken serrula. **7.** *Urocrionus mordax*, female, California, showing a well developed but broken serrula. **8.** *Chactas reticulatus*, female, Colombia, showing well developed serrula covered with heavy setal brush.

Vaejovidae from central Texas caves, which was not cave-adapted but *also had serrula*. This was the first time a vaejovid was mentioned as having serrula.

Subsequent to the publication of Mitchell (1968), the attention to serrula in scorpion literature became more prominent. Vachon (1971) published a redescription of enigmatic *Calchas nordmanni* Birula (now in Iuridae), where serrula was noted and even illustrated from internal aspect (Vachon, 1971, fig. 8). This paper was published first in Russian and then was translated into English. Vachon (1971) referred both to *Belisarius* and *Typhlochactas* when he acknowledges importance of serrula in the following discussion:

“It is also important to indicate the presence on the apex of the immobile [error: should be “movable”! - M.R.G. & V.F.] digit of a serrula consisting of an extension of a row of small chaetae forming a very short crest (Fig. 8). A similar crest occurs in the blind scorpion *Belisarius xambeui* Simon (Vachon, 1944:300, Fig. 2), in *Typhlochactas rhodesi* Mitchell (1968, Fig. 4, b, 7) and in *Typhlochactas reddelli* (Mitchell, 1968, Figs. 24, 26, 27).”

By some reason, the English translation of this paragraph (p. 407) incorrectly places serrula on the *fixed* finger, while the Russian original (p. 715) correctly has “podvizhnogo” (“movable”). The caption to fig. 8 in the Russian original also indicates movable finger.

The paper of Vachon (1971) was little known to Gertsch and Soleglad (M.E. Soleglad, pers. comm.) who at this time published a detailed study of several North American species then included under genera *Uroctonus* and *Vaejovis* (Gertsch & Soleglad, 1972). This paper, among other new species, described the cave vaejovid mentioned by Mitchell (1968) as *Vaejovis reddelli* (now *Pseudouroctonus reddelli*), with its serrula illustrated in fig. 39; its description (p. 597) documented “Serrulae present on lower edge of movable finger” (since the term “serrula” refers to the entire tine row, it seems more correct to use “serrula” in singular rather than “serrulae” in plural when referring to one comb).

For the genus *Uroctonus* (under which they listed taxa currently placed in *Uroctonus*, *Uroctonites*, and *Pseudouroctonus*), Gertsch & Soleglad (1972: 559) stated: “A constant feature of the lower margin of the movable finger is a row of fine serrulae along the distal part.” Serrula was illustrated by Gertsch & Soleglad (1972) for *Uroctonus mordax* (fig. 29), *U. cazieri* (now *Pseudouroctonus cazieri*) (fig. 31), *Uroctonus grahami* (fig. 33), *U. williamsi* (now *Pseudouroctonus williamsi*) (fig. 35), and *U. monterei* (now *Uroctonites monterei*) (fig. 37). These illustrations were made by Gertsch (M.E. Soleglad, pers. comm.), who not only knew the work of Mitchell (1968) but also discussed its discovery of *Typhlochactas* as “a notable event” and also mentioned *Belisarius* (Gertsch & Soleglad, 1972: 557).

A “row of delicate serrulae on lower edge of tip of movable finger” was mentioned in the description of *Uroctonus huachuca* (now *Uroctonites huachuca*) (p. 573). The description of *Uroctonus chicano* (now *Pseudouroctonus chicano*) said (p. 577): “lower margin of movable finger smooth except for line of serrulae.” Their description of *Vaejovis gracilis* stated again “Lower edge smooth, with delicate growth of serrulae” (p. 604). A “row of delicate serrulae” was also listed for *Vaejovis waueri* (p. 607). Serrula, however, was not explicitly mentioned in the descriptions of, or illustrated for, *Uroctonus apacheanus* (now *Pseudouroctonus apacheanus*), *U. bogerti* (now *Pseudouroctonus bogerti*), *U. rufulus* (now *Pseudouroctonus rufulus*), *U. lindsayi* (now *Pseudouroctonus lindsayi*), *U. andreas* (now *Pseudouroctonus andreas*), *U. angelenus* (now *Pseudouroctonus angelenus*), *U. sequoia* (now *Uroctonites sequoia*), *U. iviei* (now *Pseudouroctonus iviei*), *Vaejovis minimus* (now *Pseudouroctonus minimus*), and *Vaejovis vaquero*. Gertsch & Soleglad (1972) were thus the first to describe and illustrate serrula for three genera of Vaejovidae (*Vaejovis*, *Pseudouroctonus*, and *Uroctonites*) and genus *Uroctonus* (Chactidae).

Hjelle (1972) did not mention serrula in his descriptions of *Uroctonus glimmei* (now *Pseudouroctonus glimmei*) and *Vaejovis gertschi striatus* (now *Serradigitus g. striatus*) or in redescription of *Uroctonus mordax*, all of which possess this structure. Serrula also was not mentioned by Johnson & Allred (1972) in their key for *Superstitionia*, although they mentioned the setae on the “medioventral margin” of movable cheliceral finger (a conspicuous clump; see our Fig. 5).

Michael E. Soleglad documented serrula in Vaejovidae consistently through the 1970s (Soleglad, 1972b, 1973a, 1973b, 1974, 1975). He described and illustrated serrula for *Vaejovis paysonensis* (Soleglad, 1973a: 368, fig. 21), and noticed its presence in *Vaejovis flavus* (Soleglad, 1973b: 166), *V. subtilimanus* (now *Stahnkeus subtilimanus*) and *V. joshuaensis* (now *Serradigitus joshuaensis*) (Soleglad, 1972b: 185, 193), *V. calidus* (now *Serradigitus calidus*) (Soleglad, 1974: 112), and *V. davidi* (as *V. gracilis*; Soleglad, 1975: 115; Soleglad & Fet, 2005). Soleglad (1972a) did not comment on absence or presence of serrula in *Paruroctonus* (now *Smeringurus*).

Following the discovery of Gertsch and Soleglad (1972), Haradon (1974) reported “serrula along smooth inferior margin, not extending to apex” in *Vaejovis spicatus*; and Francke (1977) reported that serrula was “lacking” in *Vaejovis globosus*. Stahnke mentioned serrula only briefly in his large revision of the family Vaejovidae *sensu lato* (Stahnke, 1974: 111, 118) referring to it as to a significant character in Vaejovinae (now Vaejovidae). However, serrula was not mentioned in his redescription of *Vaejovis subcristatus* (Stahnke, 1973). Serrula was also completely ignored by the most

prolific vaejovoid systematist of the 1960s–1980s, Stanley Williams, even after it was documented in vaejovids by Gertsch & Soleglad (1972). For example, in his description of *Vaejovis gertschi* (now *Serradigitus gertschi*), Williams (1968b: 319) addresses the ventral aspect of movable cheliceral finger as “completely lacking denticles” but does not mention either presence or absence of serrula. Williams and his colleagues published 18 papers containing vaejovoid descriptions where serrula was never mentioned (Williams, 1968a, 1968b, 1969, 1970a, 1970b, 1970c, 1970d, 1970e, 1971a, 1971b, 1972, 1974, 1976, 1980, 1986a, 1986b, 1987a; Williams & Hadley, 1967). Only twice, already in the 1980s, its presence in *Serradigitus* was acknowledged as a “setal comb” for *S. torridus* (Williams & Berke, 1986: 353) and *S. wupatkiensis* (Williams, 1987b: 366).

Sissom & Francke (1981) did not comment on absence or presence of serrula in *Paruroctonus* from Texas and New Mexico, although they paid special attention to the dentition of inferior (ventral) margin of the cheliceral movable finger, an important diagnostic feature in this vaejovoid genus. Absence or presence of serrula also was not mentioned by Hjelle (1982) for *Paruroctonus*. Furthermore, Haradon (1983, 1984a, 1984b, 1985) did not discuss serrula in *Paruroctonus* (including his new subgenus *Smeringurus*).

Francke & Soleglad (1981) in their study of the family Iuridae illustrated serrula for *Calchas nordmanni* (fig. 20) following Vachon (1971). They also for the first time illustrated it for *Iurus dufourei* (fig. 19) although it was not mentioned in Francke (1981b) paper on *Iurus* systematics. Serrula is also listed by Francke & Soleglad (1981: 254) as one of the important diagnostic characters separating subfamilies Iurinae (which has serrula; now Iuridae) and Caraboctoninae (which lacks serrula; now Caraboctonidae). Absence of serrula was also earlier indicated by Francke & Soleglad (1980: 5, 10) for *Hadruroides*.

At the same time, Lourenço (1981b: 650) mentioned serrula in his diagnosis of the peculiar chactoid troglobitic genus *Troglotayosicus* from Los Tayos cave in Ecuador (now Superstitioniidae) (“présence d'une serrula sur la face ventrale du doigt mobile”) and illustrated it (fig. 45) in his description of its only known species, *Troglotayosicus vachoni*. This holotype-based description and illustration of serrula was reproduced later by Lourenço (1998a, fig. 13; 2006, fig. 4).

In yet another troglobite description, Francke (1982) documented a “well developed” serrula in a peculiar chactoid *Alacran tartarus* (now Superstitioniidae), collected from depths between 750 and 820 m below entrances of four caves in Oaxaca, Mexico. For *Alacran*, serrula was described as “present, extending about one-half the length of movable finger” (Francke, 1982: 55). Francke (1982: 57) also used serrula, along with other

characters, to suggest a sister group relationship between *Superstitionia* and typhlochactines; serrula was listed as a diagnostic character in the amended diagnosis of the subfamily Superstitioninae (now family Superstitioniidae) (Francke, 1982: 53, 60: “movable finger of chelicera with distinct ventral serrula.”). Also, (Francke, 1982: 57) noted that serrula is a common feature between Superstitioninae and *Belisarius*, but suggested rather the affinity between the latter and South American chactids; the most recent studies confirmed this hypothesis (Soleglad & Fet, 2003).

Thus, while between 1968 and 1987 the use of serrula in scorpion literature became more prominent, it was not yet a commonly recorded character and was mentioned rather sporadically.

The doctoral dissertation of Sissom (1985a) contained the most detailed treatment of cheliceral serrula at the time. In his systematic study of the *nitidulus* group of *Vaejovis*, Sissom (1985a: figs. 229–230) illustrated a serrula in the lateral view of the cheliceral movable finger of the species later published by Sissom (1991) as *Vaejovis mitchelli*. A “well developed serrula” was mentioned by Sissom & Francke (1985) in their detailed redescriptions for *Vaejovis nitidulus* (now *Franckeus nitidulus*) (p. 247), *V. nigrescens* (p. 252), *V. intermedius* (p. 256), and *V. decipiens* (p. 261) but not for *V. minckleyi* (now *Franckeus minckleyi*). Sissom (1985a, 1991) explicitly used serrula as a diagnostic character for the *nitidulus* group and characterized it in the following way (Sissom, 1985a: 246): “The cheliceral serrula is a small comb-like structure apparently composed of small, stiff, teeth which occurs on the ventrodorsal aspect of the cheliceral movable finger...” Sissom (1991: 4) stated that all members of “*Vaejovis nitidulus*” group possessed “a well developed serrula”; this statement was later repeated by Capes (2001).

Further discussing serrula, Sissom (1985a: 246) also commented that “[i]n the Vaejovidae it is restricted to *Uroctonus*, *Pseudouroctonus*, and the *mexicanus*, *minimus*, *nitidulus*, and *wupatkiensis* groups of *Vaejovis*” (the latter is now placed in genera *Serradigitus* and *Stahnkeus*). He hypothesized (Sissom, 1985a: 248) that serrula is a synapomorphic character for those taxa. A similar statement was published by Sissom (1985b) in the abstract titled “Phylogeny of the Vaejovidae (Arachnida: Scorpiones): preliminary synthesis” that listed “possession of a serrula” as one of the two common characters for “*mexicanus*, *minimus*, *nitidulus*, and *wupatkiensis* groups of *Vaejovis* ... *Uroctonus* and *Pseudouroctonus* clearly belongs to this group as well. The second group includes the *eusthenura*, *punctipalpi*, and *intrepidus* groups.”

Sissom (1985a: 246) also acknowledged the presence of serrula in “some Chactinae” (after González-Sponga, 1978), Iurinae, and Superstitioninae (now

Chactidae, Iuridae, and Superstitionidae), suggesting that in those groups it has “apparently arisen independently.”

In some subsequent works of Sissom and his collaborators on Vaejovidae (e.g. Sissom, 1986, 1991; Sissom & Stockwell, 1991; Capes, 2001; Hendrixson, 2001) serrula was mentioned briefly as “well developed” but was never illustrated. Sissom & Stockwell (1991: 198) in their work on *Serradigitus* (formerly the *wupatkiensis* group of *Vaejovis*) noted that all its species “have a well developed, comblike serrula on the ventrodiscal aspect of the cheliceral movable finger.” In other works on Vaejovidae by Sissom, the presence or absence of serrula was not mentioned (Sissom, 1989a, 1989b, 1990b, 1993; Yahia & Sissom, 1996).

Serrula did not appear in the index of the monumental 1990 book, *The Biology of Scorpions*, and was not mentioned in its systematic chapter under description of morphological characters of chelicerae (Sissom, 1990a: 65). It was not used in Sissom’s keys to distinguish any other chactoids but he mentioned that, in combined Chactidae and Vaejovidae, “the movable finger often has a serrula on the ventral aspect” (Sissom, 1990a: 107). Serrula was, however, used in Sissom’s key for Vaejovidae (p. 111) as one of several characters used in a couplet to distinguish *Uroctonus*, in which it was considered “always present,” from *Vaejovis*, where it is “absent in some species groups.” Presence of serrula was overlooked in his diagnoses of Iuridae and its subfamilies (Sissom, 1990a: 127, 130). Serrula was also omitted by Sissom (1990a) from the illustrations of ventral aspect of chelicera in *Superstitionia donensis* (fig. 3.1C), *Vaejovis* sp. (fig. 3.1H), and *Uroctonus mordax* (fig. 3.19H).

Numerous new data on serrula were presented in the pioneering and important doctoral dissertation of Stockwell (1989) on the higher classification of scorpions, which remained largely unpublished. In a very detailed discussion, Stockwell (1989: 91–92) recognized the presence of serrula in all Superstitioninae (now Superstitioniidae), all Chactinae (now Chactidae), *Nullibrotheas*, *Uroctonus* (then in Vaejovidae), *Belisarius* (then in Euscorpiinae), *Calchas* (as *Paraiurus*), and *Iurus*. Among Vaejovidae, Stockwell (1989) listed serrula as present in *Pseudouroctonus*, *Serradigitus*, *Syntropis*, *Uroctonites*, and the *mexicanus*, *nitidulus*, *punctipalpi*, and *eusthenura* groups of *Vaejovis*. He also listed other groups which, according to his count, lacked serrula. Among non-chactoids (*sensu* Soleglad & Fet, 2003) these were: fossil *Palaeopisthacanthus* (Palaeopisthacanthidae), Buthidae, Bothriuridae, Chaerilidae, Ischnuridae (now Hemiscorpiidae), Diplocentridae (now Diplocentrinae), Scorpionidae, and New World Iuridae (*Caraboctonus*, *Hadruroides*, *Hadrurus*; now Caraboctonidae). Among chactoids, Stockwell (1989) listed as lacking serrula: Mega-

cominae, Scorpiopsidae (now Scorpiopsinae), Syntropinae, *Anuroctonus*, *Euscorpius*, *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus*. Absence or presence of serrula was coded in Stockwell’s cladistic analysis (p. 148, characters 37–39), and he suggested possible evolutionary scenarios for its gain and loss. Absence of serrula was included by Stockwell (1989) in diagnoses of Euscorpiidae (p. 185), Scorpiopsidae (p. 186; now Scorpiopinae), Caraboctoninae (p. 194), Hadrurinae (p. 194; now a synonym of Caraboctoninae), all Scorpionoidea (p. 207). Presence of serrula was included by Stockwell (1989) in his updated diagnoses of Chactidae (p. 184), Superstitioniidae (p. 188; “a well developed ventral serrula is always present”), Iuridae (p. 192; including Caraboctonidae; “a ventral serrula is sometimes present on the movable finger of the chelicera, but is never well developed”), Iurinae (p. 193); Vaejovidae (p. 195; “a variably developed ventral serrula may be present on the movable finger of the chelicera.”) Defining his two vaejovid subfamilies Vaejovinae and Syntropinae (both of which are currently not recognized), Stockwell (1989: 196) diagnosed Vaejovinae as having “a well developed ventral serrula” but Syntropinae (p. 197) as more variable, having “ventral serrula of movable finger of the chelicera absent or variably developed.” Within his Syntropinae, Stockwell established four tribes. Tribe Syntropini, with “ventral serrula of movable finger of the chelicera variably developed, but always present” (p. 197), included *Syntropis*, *Serradigitus*, and two new genera based on the *punctipalpi* and *eusthenura* groups of *Vaejovis* named “*Franckeus*” and “*Lissovaejovis*” (these names remained unpublished and never became available; *Franckeus* Soleglad et Fet, 2005 refers to another taxon, see below). Tribe Uroctonini, with “ventral serrula of movable finger of the chelicera well developed and conspicuous” (p. 202), included *Pseudouroctonus*, *Uroctonus*, and *Uroctonites*. Stockwell’s tribe “Paruroctonini” (unavailable name), “completely lacking a serrula” (p. 204), included *Paravaejovis*, *Paruroctonus*, *Smeringurus*, and *Vejovoidus*. Finally, tribe “Sissomini” (unavailable name) was characterized by “a well developed, conspicuous, ventral serrula”; this tribe included the new genus “*Sissomius*,” with type species *Vaejovis nitidulus*, which makes this (unavailable) name equivalent to *Franckeus* Soleglad et Fet, 2005). Serrula figured prominently in Stockwell’s key to scorpion higher taxa (pp. 216–231), which followed the abovementioned diagnoses. Stockwell (1989) also illustrated serrula for the right chelicera of *Typhlochactas reddelli* (fig. 54), *Uroctonus grahami* (fig. 59), *Brotheas* sp. (fig. 59), *Iurus dufourei* (fig. 60), *Vaejovis hirsuticauda* (fig. 63), and *Vaejovis crassimanus* (fig. 64). He also documented absence of serrula in his illustrations of *Chaerilus granulatus* (fig. 52), *Scorpio maurus* (fig. 55),

Centruroides vittatus (fig. 56), *Anuroctonus phaiodactylus* (figs. 57, 62), and *Bothriurus bonariensis* (fig. 61).

Only small subset of the data first presented in the unpublished work of Stockwell (1989) was published and briefly discussed in his key to scorpions of North America (Stockwell, 1992). This important paper documented serrula in all genera of Superstitioniidae and several genera of Vaejovidae (including *Uroctonus*, now placed in Chactidae) as well as *Nullibrotheas* (Chactidae); it also documented absence of serrula in North American Euscorpiidae (*Megacormus*, *Plesiochactas*) and genus *Anuroctonus* (which Stockwell placed in Iuridae). Stockwell (1992: 408) stated that “*Vejoividus* shares several potential synapomorphies with *Paruroctonus* (*Paruroctonus*) Werner, 1934, *Paruroctonus* (*Smeringurus*) Haradon, 1983, and *Paravaejovis* Williams, 1980... These include the ... absence of a ventral serrula on the movable finger of the chelicera.” His vaejovid key distinguished this group of genera from other Vaejovidae, which are said to have “a serrula of variable development” (figs. 11, 50–51). Genus *Vaejovis* was characterized as having “a moderate to very weak serrula” while *Uroctonus*, *Uroctonites*, and *Pseudouroctonus* were said to have “a long, well-developed serrula” (p. 416). Stockwell (1992) also transferred *Nullibrotheas* to Chactinae (now Chactidae) stating that it “appears more closely related to the Chactinae by virtue of its cheliceral serrula (not present in Scorpionsinae, Megacorminae, or *Euscorpius*) (Stockwell, 1992: 409); these two groups were separated in his key (p. 416) as having “a conspicuous serrula” (*Nullibrotheas*) and lacking serrula (*Megacormus*). In total, Stockwell (1992) illustrated serrula for the following four North American chactoid genera: *Sotanochactas* (fig. 10), *Vaejovis* (figs. 11, 50), *Nullibrotheas* (fig. 14), and *Uroctonus* (fig. 51). In his drawings, we also can see documented absence of serrula in the following North American scorpion taxa: *Centruroides* sp. (fig. 8), *Diplocentrus* sp. (fig. 9), *Paruroctonus* (fig. 12), *Hadrurus* sp. (fig. 13), and *Megacormus* sp. (fig. 14).

Williams & Savary (1991, fig. 4), in their description of the new vaejovid genus *Uroctonites*, published an excellent SEM micrograph of the ventral aspect of the right chelicera of *U. giulianii*. The image shows a distinct serrula comprising about 27 tines, more than one-fourth of which are broken. Although the authors focused on the “weak crenulations on the ventral margin of the movable finger” illustrated in this image, they never mention the conspicuous serrula anywhere in the paper.

Ponce & Beutelspacher (2001: 98, figs. 9a, 9b), in their key of scorpions of Michoacán, Mexico, stated that a “serrula bien desarrollada” separates *Vaejovis pusillus* from eight other *Vaejovis* species, which are reported to

have “serrula muy débilmente desarrollada pero siempre presente.” Both character states are also listed by Ponce & Beutelspacher (2001: 88) in their “diagnoses of two new genera” proposed by Stockwell (1989: 200, 206), namely “*Sissomius*” (“well-developed serrula”) and “*Lissovaejovis*” (“very weakly developed but always present serrula”). These statements, which have been copied from the unpublished work of Stockwell (1989), indicate that the degree of serrula development could be used to distinguish species-groups of *Vaejovis*, which could also have generic status. Figures 9a and 9b showing serrula in Ponce & Beutelspacher (2001: 99) are unacknowledged reproductions of published figs. 50 and 51 from Stockwell (1992: 415). [Two generic names mentioned above are *not available* since they were never published by Stockwell. These names are also not available under the authorship of Ponce & Beutelspacher (2001) since these authors did not explicitly designate type species (Soleglad & Fet, 2003: 109) as required by ICZN Article 13.3.]

Hendrixson (2001) and Sissom & Hendrixson (2005) also indicated that the degree of serrula development could potentially be useful in species-group systematics of *Vaejovis*. Discussing problematic placement of his new species *Vaejovis pequeno*, Hendrixson (2001: 49) noted that “[a]lthough superficially similar to *V. waueri*, a member of the *eusthenura* group as defined by Williams (1970b), *V. pequeno* clearly does not belong to that group based on the chelicerae possessing a strongly pronounced serrula...[as well as other characters].” His species diagnosis of *Vaejovis pequeno* included an explicit statement on “the chelicerae with a strongly developed serrula (rather than a weakly developed serrula)” (Hendrixson, 2001: 48). At the same time, Sissom & Hendrixson (2005: 1088), describing *Vaejovis glabrimanus*, listed “cheliceral serrula weak or absent” as one of the diagnostic characters of *Vaejovis eusthenura* group, into which they placed this new species.

Recently, a “well developed serrula” was mentioned by Francke & Ponce Saavedra (2005) for *Vaejovis kuarapu*, and by Graham (2006) for *V. lapidicola*. Francke & Savary (2006) mentioned “a distinct serrula” for *Pseudouroctonus sprousei* but omitted it from their illustration (fig. 4).

Soleglad & Fet (2005a: 6), in their discussion of the new vaejovid genus *Franckeus* and its relationship to *Vaejovis* species groups, noted that having “a well developed serrula on the ventrodorsal aspect” was diagnostic but not necessarily synapomorphic for both *Franckeus* (previously *nitidulus* group of *Vaejovis*) and “*Vaejovis nigrescens*” group. They wrote: “Only the related genera *Paruroctonus*, *Smeringurus*, *Vejoividus* and *Paravaejovis* are excluded by this character. If “well developed” is emphasized, then some members of the

“*eusthenura*” and “*punctipalpi*” groups may be partially excluded as well. Again, *Serradigitus*, *Pseudouroctonus*, *Uroctonites* and the “*Vaejovis mexicanus*” group have well developed serrulae.” A “well developed serrula” was also listed as a diagnostic (not synapomorphic) character by Soleglad & Fet (2006: 24) for the new vaejovid tribe Stahnkeini (which includes genera *Serradigitus* and *Stahnkeus*).

However, in a number of other recent descriptions and redescrptions of vaejovid species serrula was not mentioned at all, e.g. for *Vaejovis pusillus*, *V. nigrofemoratus*, and *V. tessellatus* (Hendrixson & Sissom, 2001), *V. acapulco* and *V. nayarit* (Armas & Martín-Frías, 2001); *V. cisnerosi* (Ponce Saavedra & Sissom, 2004), *V. norteno* (Sissom & González Santillán, 2004), and *V. sprousei* (González Santillán et al., 2004). Serrula was not mentioned by Sissom & González Santillán (2004) in their key to 17 Mexican species of *Vaejovis nitidulus* group, or by Sissom & Hendrixson (2005) in their key to the vaejovids of Northeastern Mexico. Thus, attention to serrula in Vaejovidae has been, and remained, rather inconsistent.

Serrula of non-vaejovid scorpions has been mentioned in literature much less often than that of Vaejovidae. In Chactidae, this character received very little attention. Williams (1974) did not mention serrula when he described the new genus *Nullibrotheas* from Baja California (then in Vaejovidae), or in its brief redescription (Williams, 1980). According to Stockwell (1989), serrula is present in *Nullibrotheas* as well as in all South American chactid genera. However, serrula was hardly ever mentioned in numerous descriptions of chactid species belonging to *Auyantepuia*, *Brotheas*, *Broteochactas*, *Chactas*, *Guyanochactas*, *Hadrurochactas*, *Neochactas*, *Teuthraustes*, and *Vachoniochactas* from South America (e.g. Kjellesvig-Waering, 1966; González-Sponga, 1980, 1982, 1984a, 1984b, 1992, 1996a, 1996b, 1997, 2004; Francke & Boos, 1986; Matthiesen & González-Sponga, 1989; Lourenço, 1983, 1994c, 1995a, 1995b, 1996, 1997, 1999, 2003b; Lourenço & Pinto-da-Rocha, 2000; Lourenço & Dastych, 2001; Monod & Lourenço, 2001; Pinto-da-Rocha et al., 2002; Lourenço & Molteni Machado, 2004; Rojas-Runjaic, 2004). Neither did serrula appear in descriptions of new chactid genera from South America such as *Taurepania* (González-Sponga, 1978), *Auyantepuia* (González-Sponga, 1978), *Cayyoca* (González-Sponga, 1996b), *Guyanochactas* (Lourenço, 1998b), and *Neochactas* (Soleglad & Fet, 2003). Lourenço (1983: 781, 784) mentioned serrula for *Auyantepuia fravalae* (p. 781) and *A. gaillardi* (p. 784) but not for *Brotheas*, *Broteochactas*, or *Hadrurochactas*. Francke & Stockwell (1987: 28) confirmed serrula presence in *Chactas exsul*, and Lourenço (1997: 599), in *Broteochactas kelleri* (now *Neochactas kelleri*). Soleglad & Sissom (2001: 101) listed serrula for

Teuthraustes [oculatus] and *Brotheas [granulatus]* (as well as *Iurus*, *Belisarius*, and *Chactopsis*). The genus *Auyantepuia* was synonymized by Francke & Boos (1986) to *Broteochactas*, reestablished by Lourenço & Araújo (2004), and again synonymized by Soleglad & Fet (2005b) to *Neochactas*. Lourenço & Araújo (2004: 5) mentioned a “faible serrula” (“weak serrula”) in their diagnosis of *Auyantepuia* but without any comparison to other chactid genera.

Since Vachon (1945) mentioned absence of serrula in *Euscorpius*, most authors working with various taxa now included in Euscorpiidae, did not comment on this structure. Soleglad (1976) acknowledged absence of serrula in Megacorminae (now in Euscorpiidae). Francke (1981a) described a new genus *Troglocormus* (now in Euscorpiidae) with two Mexican troglobite species, *T. willis* and *T. ciego*, specifically characterizing them as “without serrula.” Soleglad & Sissom (2001) used presence or absence of serrula in their cladistic analysis (p. 101, character 7) while confirming its absence in all Euscorpiidae except *Chactopsis* (p. 59). The genus *Chactopsis*, traditionally placed in Chactidae, has been transferred by Soleglad & Sissom (2001) to Euscorpiidae, thus becoming the only genus of this family that has serrula [illustrated schematically in Soleglad & Sissom (2001) for *C. amazonica* (figs. 134, 140)]. Although Lourenço (2003a) considered this transfer controversial, he did not mention the possession of serrula in *Chactopsis* as the character that this genus indeed has in common with Chactidae rather than Euscorpiidae. Serrula in *Chactopsis* was not mentioned by Lourenço & Francke (1986). The first author to notice it was Stockwell (1989: 186) who listed *Chactopsis* in Chactidae who also commented on a trichobothrial character that this genus shared with Scorpiopsidae (now subfamily Scorpiopinae of Euscorpiidae).

Lourenço (1998a) offered some hypotheses on biogeography of troglobitic scorpions, in particular discussing a possible relationship between *Belisarius* and *Troglotayosicus* as well as Mexican Superstitioniidae. As a diagnostic character for his “family Troglotayosidae” he stated (Lourenço, 1998a: 137): “chélicères avec la présence d’une importante serrule sur la face ventrale du doigt mobile” (see below on critical discussion by Soleglad & Fet, 2003: 108). Serrula of *Troglotayosicus* was illustrated by Lourenço (1998a, fig. 13), reproducing the line drawing from Lourenço (1981, fig. 45). Lourenço (1998a, figs. 25–26) also published (although with a poor quality) the first two SEM micrographs of *Belisarius* serrula, one of the whole comb at 160x and one a closeup of six times (two of which are broken) at 450x.

Pecereaux (2004), in an unpublished thesis manuscript, used serrula in his cladistic analysis of Chactidae and related genera; serrula (character 22) was

coded simply as either present or absent. Of interest in his matrix of characters (Pecreux, 2004: 35) is that serrula was coded as *absent* in several chactoid taxa, namely: *Belisarius xambeui* (despite the evidence of Vachon, 1945; Lourenço, 1998a; Stockwell, 1989, 1992; see also our Fig. 6), *Superstitionia donensis* (despite the evidence of Mulaik & Higgins, 1944; Stockwell, 1989, 1992; see also our Fig. 5), *Anuroctonus phaiodactylus*, *Euscorpis flavicaudis*, and the following Chactidae: *Auyantepuia fravalae* and *A. gaillardi* (despite the evidence of Lourenço, 1983), *A. sissomi*, *Brotheas gervaisii*, *B. granulatus* (despite the evidence of Soleglad & Sissom, 2001), *B. paraensis*, *Guyanochactas gonzalezspingai*, *Chactopsis insignis*, and *Taurepania vestigialis*. At the same time, serrula was coded as *present* by Pecreux (2004) for the following chactoids: *Pseudouroctonus reddelli*, *Vaejovis punctatus*, *V. mexicanus*, *Broteochactas delicatus*, *B. laui*, *Chactas reticulatus*, *C. rubrolineatus*, *Hadrurochactas schaumii*, *Nullibrotheas allenii*, *Sotanochactas elliotti*, *Teuthraustes amazonicus*, *T. atramentarius*, *T. glaber*, *T. witti*, *Typhlochactas rhodesi*, *Uroctonus mordax*, and *Vachoniochactas ashleae*. Presence of serrula was listed under question mark in *Vaejovis punctipalpi* and *Cayyoca venezuelensis*. Statements of Pecreux (2004) on *absence* of serrula in some South American Chactidae are interesting but we feel that his observations (all of which were done from actual material, including not less than nine specimens of *Belisarius*) have to be confirmed since some of them are clearly questionable. Absence of serrula in all Scorpionoidea was stated by Prendini (2000).

Soleglad & Fet (2003, fig. 49) for the first time illustrated (but did not discuss) serrula in the relict non-chactoid Central Asian genus *Pseudochactas* (Pseudochactidae), which was not documented in its original description (Gromov, 1998). In addition, Soleglad & Fet (2003, fig. 55) illustrated serrula in the Mexican genus *Nullibrotheas* (Chactidae). Commenting on the statement of Lourenço (1998a) that a “significant serrula” is diagnostic for “Troglotayosidae”, Soleglad & Fet (2003: 108) wrote that “[t]he presence of serrulae is quite common in the chactoids (including *Superstitionia*, *Typhlochactas*, many vaejovids) and also is known from in the Old World iuroid, *Calchas*.”

In their recent revision of subfamily Uroctoninae (Chactidae), Soleglad & Fet (2004) stated:

“The presence of serrula (likely an adaptive grooming device) in Recent scorpions is quite curious at best due to its apparent “randomness” of occurrence, providing no real consistency within phylogenetic lineages. For example, we find serrula in the primitive scorpion *Pseudochactas* (family Pseudochactidae; Soleglad & Fet, 2003b: fig. 49), but it is missing from the buthoids and the chaeriloids; it is present in the Old World iuroids

(family Iuridae, genera *Calchas* and *Iurus*), but absent in the New World iuroids (family Caraboctonidae, subfamilies Caraboctoninae and Hadrurinae); it is present in genus *Chactopsis* (Soleglad & Sissom, 2001: Fig. 140), but absent in the other ten euscorpoid genera; it is present in most vaejovids but absent in related genera *Paruroctonus*, *Smeringurus*, and *Vejovoides*; and it is not reported for any of the scorpionoids. We (Fet et al., in progress) are examining the microstructure of serrula in all Recent scorpion groups using SEM micrography, attempting to determine if this curious structure can be analyzed for further diagnostic purposes...”

Last but not least, serrula was completely overlooked in a recent, very detailed study of *Pseudochactas* morphology by Prendini et al. (2006), even though its presence was reported previously by Soleglad & Fet (2003: fig. 49, 2004). When enlarged 300x to 400x in Adobe Acrobat 7.0 Professional™, fig. 15 in Prendini et al. (2006; PDF version), where ventral view of both chelicerae is presented, reveals unequivocal existence of a long “ridge” of stubs that belong to an obvious, completely broken serrula (compare to our Fig. 1 and also to Figs. 5–7).

Why the Inconsistency?

The inconsistent documentation of serrula in scorpion literature is likely the result of several confounding factors. Most obviously, some authors, such as those that predominantly study Buthoidea or Scorpionoidea, simply never encountered this character. Others, especially those working on Chactoidea groups, must have encountered serrula all the time, but could discern no pattern of variation and therefore chose not to deal with it. Another possibility is that some researchers may have thought serrula to be a character too specific for a certain taxon and therefore deemed it interesting but not important systematically (e.g. Vachon, 1945, 1971; Gertsch & Soleglad, 1972; Sissom & Stockwell, 1991).

Probably the foremost cause of the intermittent treatment of serrula was an insight we gained during SEM analysis, which was thus the impetus for this study; that serrula can be *broken* (Figs. 1, 5–7). Serrula is already hard to see with a standard dissecting scope, and a broken serrula in any of these states would require higher magnification, such as provided by SEM, to observe.

Unbroken serrula tines typically range from 50 to 100 µm in length, which is just within the maximal magnification range (ca. 60x) of a regular dissecting microscope. The stubs of broken serrula, on the other hand, typically range from 18 to 23 µm and under a dissecting microscope at most appear as a ridge, if visible at all.

In the case of a reduced or vestigial serrula, its tines also fall within this size range, and therefore were not visible to many researchers. For example, the vaejovid genera *Smeringurus* and *Paruroctonus* have been traditionally thought to be lacking serrula (Stockwell, 1989; Sissom, 1990; Soleglad & Fet, 2004), as opposed to other Vaejovidae. We now know, however, that all *Smeringurus* and most *Paruroctonus* actually do possess serrula (Fet et al., 2006), just an extremely small, reduced version of it. In some species, serrula is so reduced that it comprises only one or two small tines, comparable in size to the abovementioned “stubs” of broken serrula (Fet et al., 2006).

Another reason for inconsistency in observations is that serrula is sometimes obscured by dense long setae, present on the ventral aspect of the movable cheliceral finger, especially in Chactidae (Fig. 4). These tufts are sometimes abundant or angled forward so that they would cover up small and especially broken serrula.

Considering all these factors, that serrula can be reduced, broken, vestigial, or obscured by setae, it is not surprising that many authors never reported a serrula. This obviously calls for reevaluation of this character in those scorpion taxa, first of all among Chactoidea, where it either was not documented or was reported to be missing. Further SEM studies will undoubtedly shed more light on this interesting scorpion character and its possible phylogenetic importance.

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