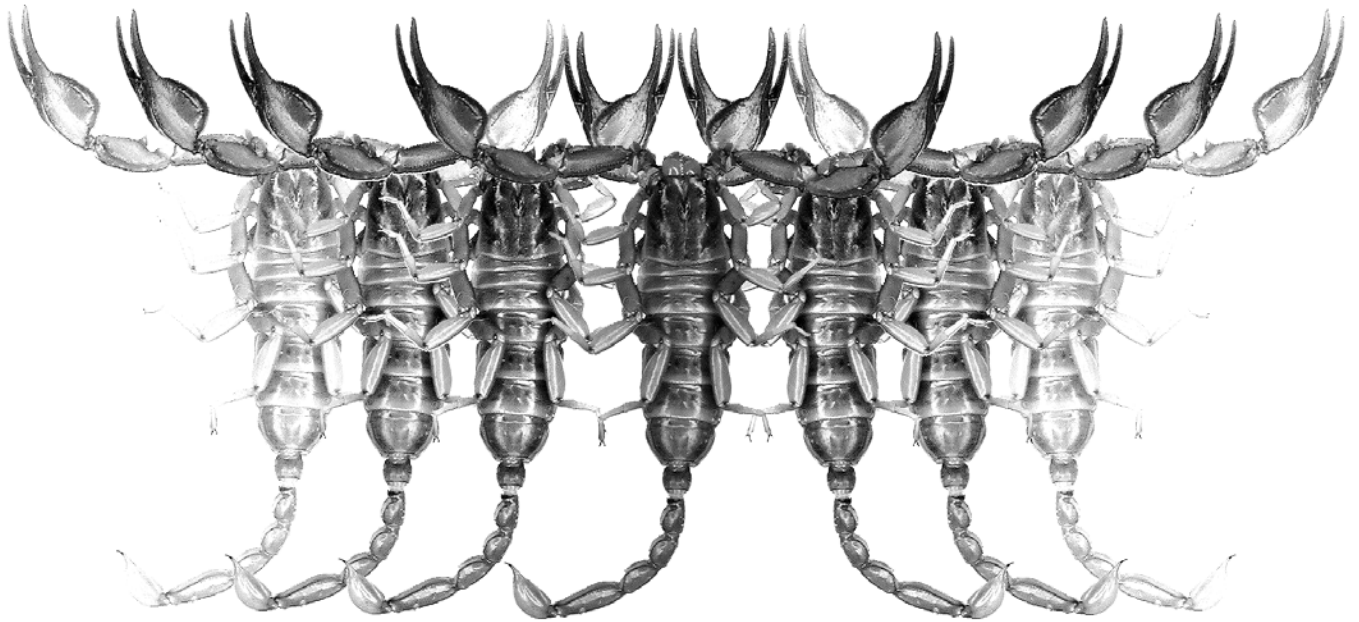


Euscorpilus

Occasional Publications in Scorpiology



**Contributions to Scorpion Systematics. III.
Subfamilies Smeringurinae and Syntropinae
(Scorpiones: Vaejoidea)**

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Contributions to scorpion systematics. III. Subfamilies Smeringurinae and Syntropinae (Scorpiones: Vaejovidae)

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Summary

Stockwell (1989), in an unpublished revision, suggested splitting the family Vaejovidae in two subfamilies, introducing also four tribes and four new genera. These results have not been reevaluated for 20 years. Here, we establish a new subfamily Smeringurinae, **subfam. nov.**, with two tribes, four genera, and 40 species and subspecies. The subfamily Smeringurinae includes two tribes: Smeringurini, **trib. nov.** and Paravaejovini, **trib. nov.** The tribe Smeringurini includes three genera: *Paruroctonus* Werner, 1934; *Smeringurus* Haradon, 1983; and *Vejovoidus* Stahnke, 1974. The tribe Paravaejovini includes the genus *Paravaejovis* Williams, 1980. We restore from synonymy the subfamily Syntropinae Kraepelin, 1905, and significantly expand its scope to include two tribes, two subtribes, eight genera, and 75 species and subspecies. The subfamily Syntropinae includes two tribes: Stahnkeini Soleglad et Fet, 2006, and Syntropini Kraepelin, 1905. The tribe Stahnkeini includes four genera: *Gertschius* Graham et Soleglad, 2007; *Serradigitus* Stahnke, 1974; *Stahnkeus* Soleglad et Fet, 2006; and *Wernerius*, **gen. nov.** The tribe Syntropini includes two subtribes, Syntropina Kraepelin, 1905, and Thorelliina, **subtrib. nov.** The subtribe Syntropina includes two genera, *Syntropis* Kraepelin, 1900 and *Hoffmannius*, **gen. nov.** The subtribe Thorelliina includes two new genera, *Thorellius*, **gen. nov.** and *Kochius*, **gen. nov.** Four new genera accommodate species from the former “eusthenura,” “intrepidus,” “punctipalpi,” and “spicatus” groups of *Vaejovis*. One new species from Durango, Mexico is described, *Kochius kovariki* Soleglad et Fet, **sp. nov.** *Thorellius cristimanus*, **stat. nov.** and *T. atrox*, **stat. nov.** are elevated to species from subspecies level. Our results confirm, in part, the phylogeny proposed by Stockwell (1989), with its further splitting of the overly inflated genus *Vaejovis*. The remaining default nominotypic subfamily, Vaejovinae Thorell, 1876, still unrevised at this time, is reduced to 66 species and subspecies, grouped in four genera, *Franckeus*, *Pseudouroctonus*, *Uroctonites*, and *Vaejovis* (the latter being divided into the “mexicanus” and “nigrescens” groups). Phylogenetic relationships within subfamilies Smeringurinae, Syntropinae, and Vaejovinae are discussed. As a result of the current revision, the family Vaejovidae now includes three subfamilies, four tribes, two subtribes, and 15 genera, with a total of 181 species-group taxa.

Introduction

A brief taxonomic history of the scorpion family Vaejovidae has been outlined by Sissom (2000). The family name was first introduced by Thorell (1876), based on the North American type genus *Vaejovis* C. L. Koch, 1836 (later, incorrect spellings *Vejojovidae* and *Vejojovis* have been widely used). During many decades of changing its taxonomic rank and scope, Vaejovidae included a number of genera now placed in separate families or even superfamilies. Kraepelin (1905) recognized five subfamilies in his *Vejojovidae*: Syntropinae, *Vejojovinae*, Caraboctoninae, *Iurinae*, and *Scorpiopsinae*. Stahnke (1974) revised the high-level systematics of this family: his *Vejojovidae* included *Iurinae*, *Hadrurinae*, *Caraboctoninae*, *Scorpiopsinae*, *Syntropinae* (two genera, *Syntropis* and *Vejojovoidus*), and *Vejojovinae* (six genera, *Paruroctonus*, *Physoctonus*,

Pseudouroctonus, *Serradigitus*, *Uroctonus*, and *Vejojovis*). In the decades to follow, vaejovids shrunk considerably in taxonomic scope. Francke & Soleglad (1981) separated the family *Iuridae* (now *Iuridae* and *Caraboctonidae*; Soleglad & Fet, 2003b), which also absorbed *Hadrurinae*. Stockwell (1992) elevated *Scorpiopsinae* to a family level (now subfamily of *Euscorpidae*; Soleglad & Sissom, 2001).

Sissom (2000) included ten North American genera in *Vaejovidae* (*Paravaejovis*, *Paruroctonus*, *Pseudouroctonus*, *Serradigitus*, *Smeringurus*, *Syntropis*, *Uroctonites*, *Uroctonus*, *Vaejovis*, *Vejojovoidus*). Compared to Stahnke (1974), this content corresponded to subfamilies *Syntropinae* and *Vaejojovinae*; one genus was removed (spurious *Physoctonus*, demonstrated to be a buthid; see Francke, 1977; Lourenço, 2007) and three new genera added: *Paravaejovis* Williams, 1980; *Smeringurus* Haradon, 1983; and *Uroctonites* Williams

et Savary, 1991. Sissom (2000: 504) commented that “it is not practical at this point to recognize subfamilies, and a cladistic analysis of the vaejoivid genera is necessary before this can be accomplished.” This referred to the subfamilies Syntropinae and Vaejovinae, which, however, remained formally valid at this time. We (Soleglad & Fet, 2003b) moved genus *Uroctonus* to Chactidae (see also Soleglad & Fet, 2004), leaving Vaejoividae with nine genera. We also formally synonymized subfamily Syntropinae with Vaejoividae (Soleglad & Fet, 2003b: 109), thus leaving Vaejoividae without any recognized subfamilies. No other family-group taxa (i.e. tribes or subtribes) have been ever proposed in Vaejoividae.

Sissom (2000) stated that “...the phylogenetic relationships of the [vaejoivid] genera are still obscure, and it is not possible at this time to recognize subfamilies or tribes. Vaejoivid phylogeny is under investigation by several authorities, and it is likely that such a classification will be a reality before long.” Sissom (2000) also mentioned that the largest genus, *Vaejovis* was not considered monophyletic. Two largest vaejoivid genera, *Vaejovis* and *Paruroctonus*, for many years have been subdivided into species-groups with no formal taxonomic status and unclear phylogenetic relationships; these traditional groups were listed in Sissom (2000).

Stockwell (1989), in an unpublished dissertation, made sweeping changes in the North American Vaejoividae, introducing two subfamilies (Vaejovinae and Syntropinae, the latter with four tribes) and 13 genera (including three new ones). Stockwell’s analysis provided the first modern glance into the vaejoivid phylogeny, including the unwieldy structure of its largest genus, *Vaejovis*. These changes, however, were never formally published and thus are not valid (ICZN, 1999a). Other taxonomic changes later published by Stockwell (1992) did not include his proposed changes in Vaejoividae (except elevation of *Smeringurus* to genus rank). Diagnoses and names for two of Stockwell’s unpublished genera (“*Sissomius*” and “*Lissovaejovis*”) were reproduced by Ponce Saavedra & Beutelspacher (2001: 88). However, these names are not available: they cannot be considered published by Ponce Saavedra & Beutelspacher, since these authors neither designated type species nor fixed type specimens (ICZN, 1999a).

Stockwell’s (1989) detailed phylogenetic analysis of Vaejoividae was never reevaluated, although his work on other scorpion families became a major modern foundation for phylogenetic analyses (Soleglad & Fet, 2003b).

Recent studies published by our research group allowed to analyze further complicated relationships within Vaejoividae. A new genus *Franckeus* was described that included a few species from the former “nitidulus” group of *Vaejovis* (Soleglad & Fet, 2005). A

new tribe Stahnkeini was established (Soleglad & Fet, 2006), which included *Serradigitus* and a new genus *Stahnkeus*. Finally, a new genus *Gertschius* was added to the tribe Stahnkeini (Graham & Soleglad, 2007).

Here, we present a further analysis, based on, but significantly expanding, the original ideas of Stockwell (1989), in which we establish a new subfamily, Smeringurinae, and reestablish subfamily Syntropinae. We explain and illustrate, in detail, the character sets involved in those new changes, and present formal diagnoses of all subfamilies, tribes, subtribes, and genera that we recognize within family Vaejoividae. No subgenera are currently recognized for any of vaejoivid genera. Our character analysis allowed to isolate diagnostic features, which, in our opinion, are sufficient to justify subfamilies Smeringurinae and Syntropinae as well as introduce other taxonomic changes at the levels of tribe, subtribe, and genus. An additional cladistic analysis will be published in a separate contribution.

Other vaejoivid assemblages, such as *Pseudo-uroctonus* + *Uroctonites*, *Vaejovis* “mexicanus” group, and *Franckeus* + *Vaejovis* “nigrescens” group, are proving to be less closely related to Smeringurinae and Syntropinae. These issues will be the subject of other upcoming contributions in the near future.

In this paper, among other detailed characters, we illustrate for the first time full trichobothrial patterns of 12 vaejoivid species, 23 hemispermaphores, and 13 extracted mating plugs. Several new SEM micrographs are presented in this paper highlighting various scorpion structures. A detailed key is provided for family Vaejoividae, spanning subfamilies, tribes, subtribes, and genera.

The subfamily systematics presented herein is supported, in part, by Soleglad & Fet (2003b: Appendix B, fig. B-2), DNA analysis of 16S mtDNA, which shows clades corresponding to subfamilies Smeringurinae and Syntropinae, with the latter further separated into clades corresponding to tribes Stahnkeini and Syntropini. Of course, this partial analysis was limited only to 16 vaejoivid species, and did not include members of subfamily Vaejovinae.

Methods & Material

Terminology and conventions

The systematics adhered to in this paper is current and therefore follows the classification as established in Fet & Soleglad (2005) and as modified by Soleglad & Fet (2006), Graham & Soleglad (2007), Fet & Soleglad (2007), and Soleglad et al. (2007). Terminology describing pedipalp chelal finger dentition follows that described and illustrated in Soleglad & Sissom (2001), that of the sternum follows that in Soleglad & Fet (2003a), and the metasomal and pedipalp carination, and

leg tarsus armature follows that described in Soleglad & Fet (2003b). Much of the information concerning the structure of the hemispermatophore of Vaejovidae, with the construction of the mating plug terminus in particular, is based on Stockwell's (1989) doctoral dissertation. Although we have verified many of the generalized statements made by Stockwell (1989) for many species, they have not been confirmed for *all* species. Our maps (Figs. 197, 202–207), which show only generalized distributions at the genus level, are based on many sources, including material examined and locality data and maps contained in the following major references: Hoffmann (1931), Gertsch & Allred (1965), Gertsch & Soleglad (1966, 1972), Hjelle (1972), Johnson & Allred (1972), Anderson (1975), Williams (1980), Williams & Savary (1991), Shelley (1994), Beutelspacher (2000), Hendrixson (2001), Ponce Saavedra & Beutelspacher (2001), Soleglad & Fet (2005, 2006), Graham & Soleglad (2007), and many other sources. Taxonomic history of genera relies, in part, on Sissom (2000).

SEM microscopy

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

Abbreviations

List of depositories: BH, Personal collection of Blaine Hébert; AMNH, American Museum of Natural History, New York, New York, USA; CAS, California Academy of Sciences, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MHNG, Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland; USNM, United States National Museum, Smithsonian Institution, Washington, D.C., USA; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; WDS, Personal collection of W. David Sissom, Canyon, Texas, USA.

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

Material

The following chactid and vaejovid material was examined for analysis and/or illustrations provided in this paper. The list of material reflects the taxonomic changes established in this paper (see **Systematics** section below).

Chactidae: subfamily Uroctoninae

Anuroctonus phaiodactylus (Wood, 1863), Garrison, Millard Co., Utah, USA, 3 ♂ (MES); *Anuroctonus pococki bajae* Soleglad et Fet, 2004, Chihuahua Road, ABDSP, California, USA, 3 ♂ (MES); *Anuroctonus pococki pococki* Soleglad et Fet, 2004, San Dimas Canyon, Los Angeles Co., California, USA, ♀ (AMNH), Santee, San Diego Co., California, USA, 2 ♂ (MES); *Uroctonus mordax mordax* Thorell, 1876, Weott, Humboldt Co., California, USA, ♂ (MES), Big Meadow, Yosemite National Park, Mariposa Co., California, USA, ♂ (MES), Foresta, Yosemite National Park, Mariposa Co., California, USA, ♂ (MES); *Uroctonus mordax pluridens* Hjelle, 1972, Santa Clara, California, USA, ♂ (MES).

Vaejovidae: subfamily Smeringurinae

Tribe Paravaejovini. *Paravaejovis pumilis* (Williams, 1970), Ciudad Constitución, Baja California Sur, Mexico, ♂ ♀ (MES).

Tribe Smeringurini. *Paruroctonus arenicola nudipes* Haradon, 1984, Kelso Dunes, San Bernardino Co., California, USA, ♂, juv. (GL); *Paruroctonus arnaudi* Williams, 1972, El Socorro, Baja California, Mexico, ♂ topotype (MES); *Paruroctonus bantai saratoga* Haradon, 1985, Death Valley, Inyo Co., California, USA, juv. (GL); *Paruroctonus becki* (Gertsch et Allred, 1965), San Bernardino Co., California, USA, ♂ (VF), Joshua Tree National Monument, California, USA, ♂ (MES); *Paruroctonus boreus* (Girard, 1854), Mercury, Nevada, USA, ♂ (MES); *Paruroctonus borregoensis borregoensis* Williams, 1972, Palo Verde Wash, ABDSP, California, USA, ♂ (MES); *Paruroctonus gracilior* (Hoffmann, 1931), New Mexico, USA, ♂ (MES), Cuatro Ciénegas, Coahuila, Mexico, ♂ ♀ (MES), Lajitas, Brewster Co., Texas, USA ♂ (GL); *Paruroctonus hirsutipes* Haradon, 1984, Algodones Dunes, Imperial Co., California, USA juv. (GL); *Paruroctonus luteolus* (Gertsch et Soleglad, 1966), Palo Verde Wash, ABDSP, California, USA, ♂ (MES); *Paruroctonus silvestrii* (Borelli, 1909), Chihuahua Road, ABDSP, California, USA, ♀ ♂ (MES); *Paruroctonus stahnkei* (Gertsch et Soleglad, 1966), Mesa, Maricopa Co., Arizona, USA, ♂ (MES), La Paz Co., Arizona, ♂ (VF); *Paruroctonus surensis*

Williams et Haradon, 1980, Las Bombas, Baja California Sur, Mexico, ♂ (MES); *Paruroctonus utahensis* (Williams, 1968), Samalayuca, Chihuahua, Mexico, ♂ (MES), Bluff, Utah, USA, ♂ (MES); *Paruroctonus ventosus* Williams, 1972, El Socorro, Baja California, Mexico, ♀ topotype (MES); *Paruroctonus xanthus* (Gertsch et Soleglad, 1966), Algodones Dunes, Imperial Co., California, USA, ♂ (GL); *Smeringurus aridus* (Soleglad, 1972), Palo Verde Wash, ABDSP, California, USA, ♂ ♀ (MES); *Smeringurus grandis* (Williams, 1970), Oakies Landing, Baja California, Mexico, ♂ ♀ (MES); *Smeringurus mesaensis* (Stahnke, 1957), Palo Verde Wash, ABDSP, California, USA, ♀ (MES), Borrego Springs, California, USA, ♂ (MES); *Smeringurus vachoni immanis* (Soleglad, 1972), 1000 Palms, Riverside Co., California, USA, ♀ ♂ (MES); *Vejovoidus longiunguis* (Williams, 1969), Las Bombas, Baja California Sur, Mexico, 2 ♂ ♀ (MES).

Subfamily Syntropinae

Tribe Stahnkeini. *Gertschius crassicornus* Graham et Soleglad, 2007, Navojoa, Sonora, Mexico, holotype ♀ paratype ♂ (MES); *Serradigitus adcocki* (Williams, 1980), Isla Cerralvo, Baja California Sur, Mexico, ♀ (CAS); *Serradigitus armadentis* (Williams, 1980), Isla Santa Cruz, Baja California Sur, Mexico, ♂ holotype (CAS); *Serradigitus baueri* (Gertsch, 1958), West San Benito Island, Baja California, Mexico, ♂ (CAS); *Serradigitus bechteli* (Williams, 1980), Isla Las Animas, Baja California Sur, Mexico, ♀ holotype (CAS); *Serradigitus calidus* (Soleglad, 1974), Cuatro Ciénegas, Coahuila, Mexico, ♀ paratype (MES); *Serradigitus dwyeri* (Williams, 1980), Isla Danzante, Baja California Sur, Mexico, ♂ holotype (CAS); *Serradigitus gertschi gertschi* (Williams, 1968), Chariot Canyon, ABDSP, California, USA, ♀ (MES); *Serradigitus gigantaensis* (Williams, 1980), San Jose de Comondú, Baja California Sur, Mexico, ♂ holotype (CAS); *Serradigitus gramenestris* (Williams, 1970), Travertine Spring, Death Valley, California, USA, ♀ ♂ paratopotypes (CAS); *Serradigitus haradoni* (Williams, 1980), Los Aripes, Baja California Sur, Mexico, ♂ paratype (CAS), Isla Santa Catalina, Baja California Sur, Mexico, 2 ♀ (CAS); *Serradigitus hearnei* (Williams, 1980), Loreto, Baja California Sur, Mexico, ♂ paratype (CAS); *Serradigitus joshuaensis* (Soleglad, 1972), Indian Gorge, ABDSP, California, USA, 2 ♀ (MES); *Serradigitus littoralis* (Williams, 1980), Isla Danzante, Baja California Sur, Mexico, ♀ (CAS); *Serradigitus minutis* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES), Cabo San Lucas, Baja California Sur, Mexico, ♀ (VF); *Serradigitus pacificus* (Williams, 1980), Isla Cedros, Baja California, Mexico, ♀ CAS); *Serradigitus torridus* Williams et Berke, 1986, Nine Mile Canyon Rd., Kern Co., California, USA, ♀ (GL); *Serradigitus*

wupatkiensis (Stahnke, 1940), Wupatki National Monument, Coconino Co., Arizona, USA, 2 ♀ 2 ♂ topotypes (MES); *Stahnkeus deserticola* (Williams, 1970), Saratoga Springs, Death Valley, California, USA, 3 ♀ (MES); *Stahnkeus harbisoni* (Williams, 1970), Puertocitos, Baja California, Mexico, ♀ (MES), Oakies Landing, Baja California, Mexico, ♂ ♀ (MES), Isla Smith, Baja California, Mexico, ♀ (VF); *Stahnkeus subtilimanus* (Soleglad, 1972), Borrego Springs, California, USA, ♀ (VF); Split Mountain, ABDSP, California, USA, ♂ (MES).

Tribe Syntropini. *Hoffmannius coahuilae* (Williams, 1968), Cuatro Ciénegas, Coahuila, Mexico, ♂ (MES); *Hoffmannius confusus* (Stahnke, 1940), Mesa, Maricopa Co., Arizona, USA, ♂ (MES); *Hoffmannius diazi diazi* (Williams, 1970), Ciudad Constitución, Baja California Sur, Mexico, ♀ (MES); *Hoffmannius eusthenura* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♂ ♀ (MES); *Hoffmannius globosus* (Borelli, 1915), Zacatecas, Zacatecas, Mexico, ♀ (MES); *Hoffmannius gravicaudus* (Williams, 1970), Santa Rosalía, Baja California Sur, Mexico, ♀ (MES); *Hoffmannius hoffmanni hoffmanni* (Williams, 1970), Rancho Tablón, Baja California Sur, Mexico, ♂ (MES); *Hoffmannius punctatus punctatus* (Karsch, 1879), Acatlán, Puebla, Mexico, ♂ ♀ (MES); *Hoffmannius puritanus* (Gertsch, 1958), Jasper Trail, ABDSP, California, USA, ♂ ♀ (MES); *Hoffmannius spinigerus* (Wood, 1863), Alamos, Sonora, Mexico, ♀ (MES); *Hoffmannius viscaínensis* (Williams, 1970), Las Bombas, Baja California Sur, Mexico, ♂ ♀ (MES); *Hoffmannius vittatus* (Williams, 1970), Cabo San Lucas, Baja California Sur, Mexico, ♂ (MES); *Hoffmannius waeringi* (Williams, 1970), Indian Gorge Canyon, ABDSP, California, USA, ♂ (MES); *Hoffmannius waueri* (Gertsch et Soleglad, 1972), Big Bend National Park, Brewster Co., Texas, USA, 2 ♀ (MES); *Kochius bruneus loretoensis* (Williams, 1970), Loreto, Baja California Sur, Mexico, ♂ (MES); *Kochius cazieri* (Williams, 1968), Cuatro Ciénegas, Coahuila, Mexico, ♂ (MES); *Kochius hirsuticauda* (Banks, 1910), Indian Gorge Canyon, ABDSP, California, USA, ♀ ♂ (MES); *Kochius kovariki* Soleglad et Fet, **sp. nov.**, Durango, Durango, Mexico, holotype ♀ (MES); *Kochius punctipalpi punctipalpi* (Williams, 1971), Los Aripes, Baja California Sur, Mexico, ♀ ♂ (MES), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Kochius russelli* (Williams, 1971), Deming, Luna Co., New Mexico, USA, ♀ (MES); *Syntropis aalbui* Lowe, Soleglad et Fet, 2007, Cataviña, Baja California, Mexico, holotype ♀ (MHNG); *Syntropis macrura* Kraepelin, 1900, Isla Carmen, Baja California Sur, Mexico, ♀ (WDS); *Syntropis williamsi* Soleglad, Lowe et Fet, 2007, Los Aripes, Baja California Sur, Mexico, holotype ♀ ♂ (MHNG); *Thorellius atrox* (Hoffmann,

1931), Colima, Colima, Mexico, ♀ (MES); *Thorellius cristimanus* (Thorell, 1876), Autlán, Jalisco, Mexico, 2 ♂ 2 ♀ (MES); *Thorellius intrepidus* (Thorell, 1876), Tepic, Nayarit, Mexico, ♀ (MES), ♀ (GL), Mexico, ♂ (VF); *Thorellius occidentalis* (Hoffmann, 1931), Acapulco, Guerrero, Mexico, ♀ (MES).

Subfamily Vaejovinae

Franckeus minckleyi (Williams, 1968), Cuatro Ciénegas, Coahuila, Mexico, ♂ ♀ (CAS); *Franckeus peninsularis* (Williams, 1980), San Raymundo, Baja California Sur, Mexico, ♂ ♀ paratypes (CAS); *Franckeus platnicki* (Sissom, 1991), Tampico, Mexico, paratype ♀ (USNM); *Pseudouroctonus andreas* (Gertsch et Soleglad, 1972), Chariot Canyon, ABDSP, California, USA, ♂ ♀ (MES); *Pseudouroctonus angeleus* (Gertsch et Soleglad, 1972), Ventura Co., California, USA, ♂ (BH); *Pseudouroctonus apacheanus* (Gertsch et Soleglad, 1972), Pinaleno Mt., Arizona, USA, ♀ (VF); *Pseudouroctonus iviei* (Gertsch et Soleglad, 1972), Little French Creek, Trinity Co., California, USA, ♀ ♂ (MES); *Pseudouroctonus minimus castaneus* (Gertsch et Soleglad, 1972), Vista, California, USA, ♂ (MES); *Pseudouroctonus minimus thompsoni* (Gertsch et Soleglad, 1972), Santa Cruz Island, Santa Barbara Co., California, USA, ♀ ♂ (GL); *Pseudouroctonus reddelli* (Gertsch et Soleglad, 1972), Gem Cave, Comal Co., Texas, USA, ♀ ♂ (MES); *Pseudouroctonus williamsi* (Gertsch et Soleglad, 1972), Santa Ysabel Reserve, California, USA, 2 ♀ 2 ♂ (MES); *Uroctonites giulianii* Williams et Savary, 1991, Lead Canyon, Inyo Co., California, USA, ♂ ♀ (CAS); *Uroctonites huachuca* (Gertsch et Soleglad, 1972), Huachuca Mountains, Cochise Co., Arizona, USA, ♀ ♂ (MES); *Uroctonites montereyus* (Gertsch et Soleglad, 1972), Hastings Natural History Reservation, Monterey Co., California, USA, ♂ (MES); *Vaejovis carolinianus* (Beauvois, 1805), Haralson Co., Georgia, USA, ♀ (MES), Athens, Georgia, USA, ♂ (MES); *Vaejovis curvidigitus* Sissom, 1991, Cuernavaca, Morelos, Mexico, paratype ♀ (USNM); *Vaejovis davidi* Soleglad et Fet, 2005, Cuetzalan, Puebla, Mexico, ♀ holotype (AMNH); *Vaejovis decipiens* Hoffmann, 1931, Chínipas, Chihuahua, Mexico, ♀ (MES); *Vaejovis feti* Graham, 2007, Meadow Creek, Grant Co., New Mexico, USA, 3 ♀ (MES); *Vaejovis granulatus* Pocock, 1898, Hidalgo, Mexico, ♀ (MES); *Vaejovis janssi* Williams, 1980, Isla Socorro, Mexico, ♂ ♀ (MES); *Vaejovis jonesi* Stahnke, 1940, Sedona, Coconino Co., Arizona, USA, ♀ (MES); *Vaejovis lapidicola* Stahnke, 1940, Williams, Coconino Co., Arizona, USA, ♂ (MES); *Vaejovis mexicanus* (C. L. Koch, 1836), Aculco, Distrito Federal, Mexico, ♀ (MES); *Vaejovis nigrescens* Pocock, 1898, Pachuca, Hidalgo, Mexico, ♀ (MES); *Vaejovis paysonensis* Soleglad, 1973, Payson, Arizona, USA, ♀

topotype (MES); *Vaejovis pococki* Sissom, 1991, Rioverde, San Luis Potosí, Mexico, ♂ (MES); *Vaejovis solegladi* Sissom, 1991, Cuicatlán, Oaxaca, Mexico, ♀ (MES); *Vaejovis vorhiesi* Stahnke, 1940, Huachuca Mountains, Cochise Co., Arizona, USA, ♀ topotype (MES).

Character Analysis

In this section, we discuss the diagnostic characters referenced in the **Systematics** section. In general, these discussions pertain to subfamilies Smeringurinae and Syntropinae, the subject of this study. However, information, if relevant at a subfamily level, is also provided for subfamily Vaejovinae. It must be noted that the systematics as established in this paper (subfamilies, tribes, subtribes, genera) is used in these character descriptions; see **Systematics** section for a formal statement of these emendations.

Trichobothria

Diagnostic value: Trichobothrial patterns are used to differentiate subfamilies and tribes in Vaejovidae.

Trichobothrial patterns in family Vaejovidae are of Type C (Vachon, 1974), in most cases orthobothriotaxic. Neobothriotaxy, if present, is limited to a small number of accessory trichobothria in genus *Franckeus*, *Paruroctonus ammonastes*, *Pseudouroctonus bogerti*, and *P. williamsi* (see Fig. 13 in this paper; Soleglad & Fet, 2003b: figs. 66, 80; Soleglad & Fet, 2005: fig. 6). Only genus *Paravaejovis* has a large number of accessory trichobothria on its chelal ventral surface. Therefore, in general, trichobothria-based diagnostic characters in Vaejovidae discussed in this paper deal with differences in the relative locations of certain trichobothria. Cladistically, we have isolated no less than 19 characters based on trichobothria positions for vaejovid scorpions (Soleglad and Fet, in progress). This set of characters *alone* is sufficient to define subfamilies Smeringurinae and Syntropinae recognized in this paper. Full trichobothria patterns are presented for the first time in this study for 12 species of Vaejovidae.

Trichobothria positions. In this study we find that the following trichobothria are important in diagnosing, in part, the subfamilies and tribes of family Vaejovidae: chelal V_1 – V_4 , Db , Dt , ib – it , db – dt , and eb – et alignments, and femoral d and i .

V_1 – V_4 . In subfamily Smeringurinae (*Paravaejovis* is not determinable due to neobothriotaxy) the spacing between chelal palm trichobothria V_2 – V_3 is considerably larger than V_1 – V_2 , roughly twice as large, whereas in the other subfamilies, Vaejovinae and Syntropinae, the spacing is roughly equal. This spacing difference was first reported by Soleglad & Fet (2003b: fig. 66). This

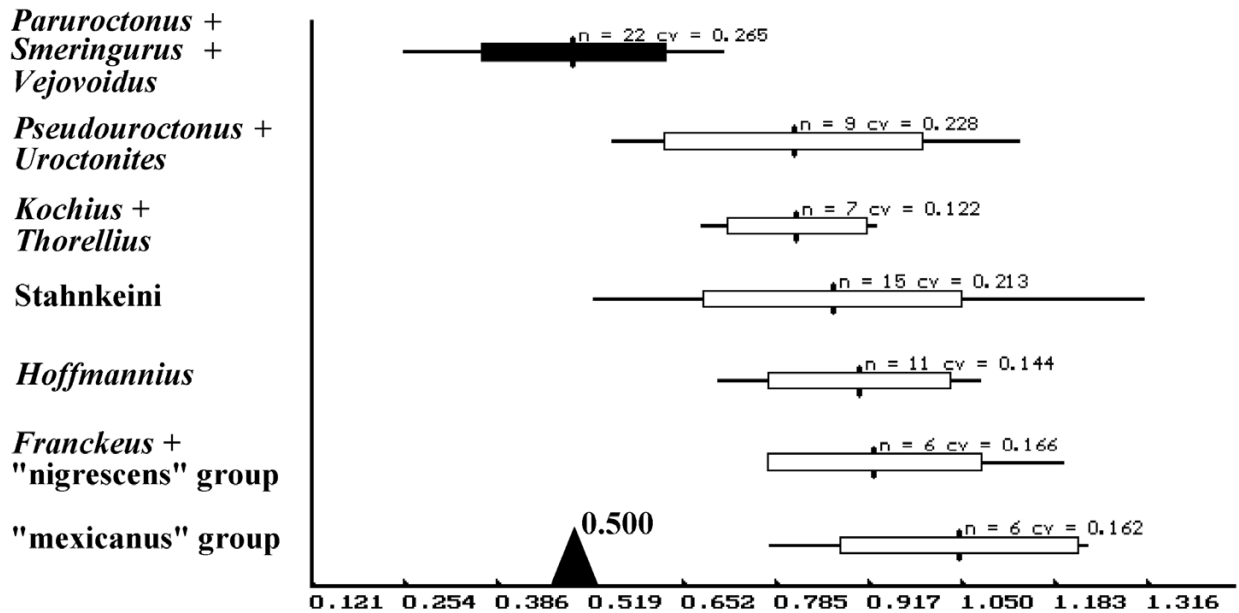


Figure 1: Histogram comparing chelal trichobothria distances between V_1 and V_2 , and V_2 and V_3 for family Vaejoidea (ratio = $V_1|V_2 / V_2|V_3$). It is clear from these data that in subfamily Smeringurinae the distance between trichobothria V_2 and V_3 is on average more than twice as great than that between V_1 and V_2 (mean = 0.497: note that genus *Paravaejovis* is excluded from these data due to major neobothriotaxy found on the ventral surface of the chelal palm). In the other vaejoid assemblages representing subfamilies Syntropinae and Vaejovinae, the distance between V_2 and V_3 is not considerably greater than that between V_1 and V_2 , exhibiting means from 0.812 to 1.049, i.e. the distances are typically subequal. In addition, Smeringurinae exhibits nearly standard error separation from the other vaejoid aggregates. Thin horizontal bar: minimum and maximum, heavy horizontal bar: standard error range (mean-SD/mean+SD), and vertical bar: mean; n = number of samples, cv = coefficient of variability (SD/mean).

relationship of ventral trichobothria spacing is quite apparent in the histogram presented in Fig. 1 where we see general separation of the standard deviation ranges in the genera and species groups in Syntropinae and Vaejovinae from that in Smeringurinae. Figures 2–6 show this spacing in several species and genera in subfamily Smeringurinae as compared to members of Syntropinae and Vaejovinae (Figs. 8–16). The unusual orientation of these trichobothria in Smeringurinae appears to be based on two derivations: V_2 moving closer to V_1 and V_3 moving more proximal on the palm, the two events together contributing to the conspicuous spacing. Of particular interest, note the basal shifting in the unusual species *Paruroctonus hirsutipes* (Fig. 3) of ventral trichobothria V_2 – V_4 , the latter quite close to the *Eb* series.

***db–dt* and *eb–et*.** The fixed finger trichobothria *db–dt* series is located more proximal to the *eb–et* series in Smeringurinae than it is in subfamily Syntropinae and Vaejovinae. In particular, trichobothria *dsb* and *dst* are proximal to *esb* and *est*, respectively, in Smeringurinae whereas in the other two subfamilies they are usually adjacent if not distal to *esb* and *est*. This is illustrated in all four smeringurine genera (Figs. 2–7). Figs. 8–16 illustrate the distal position of these trichobothria for

several species in subfamilies Syntropinae and Vaejovinae.

***Dt*.** The position of trichobothrium *Dt* is important at the subfamily level in Vaejoidea. In Figure 17 we present a histogram showing the relative position of trichobothrium *Dt* across 101 species of Vaejoidea as contrasted to *Uroctonus* and *Anuroctonus*, genera of subfamily Uroctoninae (Chactidae; Soleglad & Fet, 2003b). We can see that Uroctoninae has a very basal positioning of *Dt*, more proximal than any vaejoid. For Uroctoninae, multiple specimens of both subspecies of *U. mordax* and all three species and subspecies of *Anuroctonus* were included. In Vaejoidea, we can see that subfamily Smeringurinae has a very basal *Dt*. Only genus *Paravaejovis* is a conspicuous exception, its *Dt* is positioned distal to midpalm. In subfamily Vaejovinae, *Dt* is proximal of the palm midpoint, with genus *Uroctonites* exhibiting the most basal position. In subfamily Syntropinae, *Dt* is located at or beyond the palm midpoint: in *Gertschius* and *Wernerius* (tribe Stahnkeini) it is slightly proximal of midpoint, and in *Thorellius*, *Dt* is considerably distal of palm midpoint. Except for genera *Gertschius* and *Wernerius*, there is standard error separation between subfamilies Syntropinae and Vaejovinae.

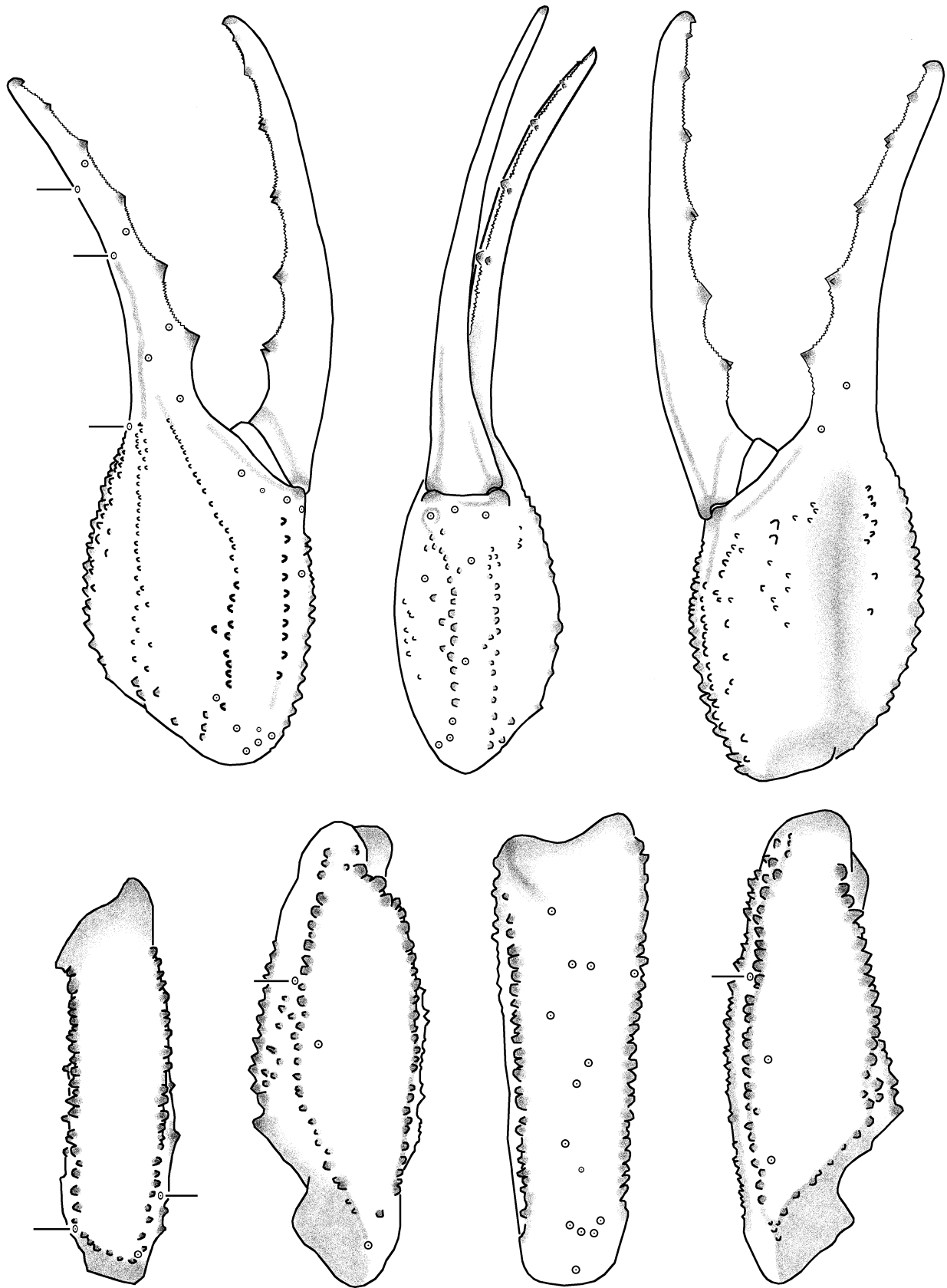


Figure 2: Trichobothrial pattern of *Paruroctonus xanthus*, male, Algodones Dunes, Imperial Co., California, USA.

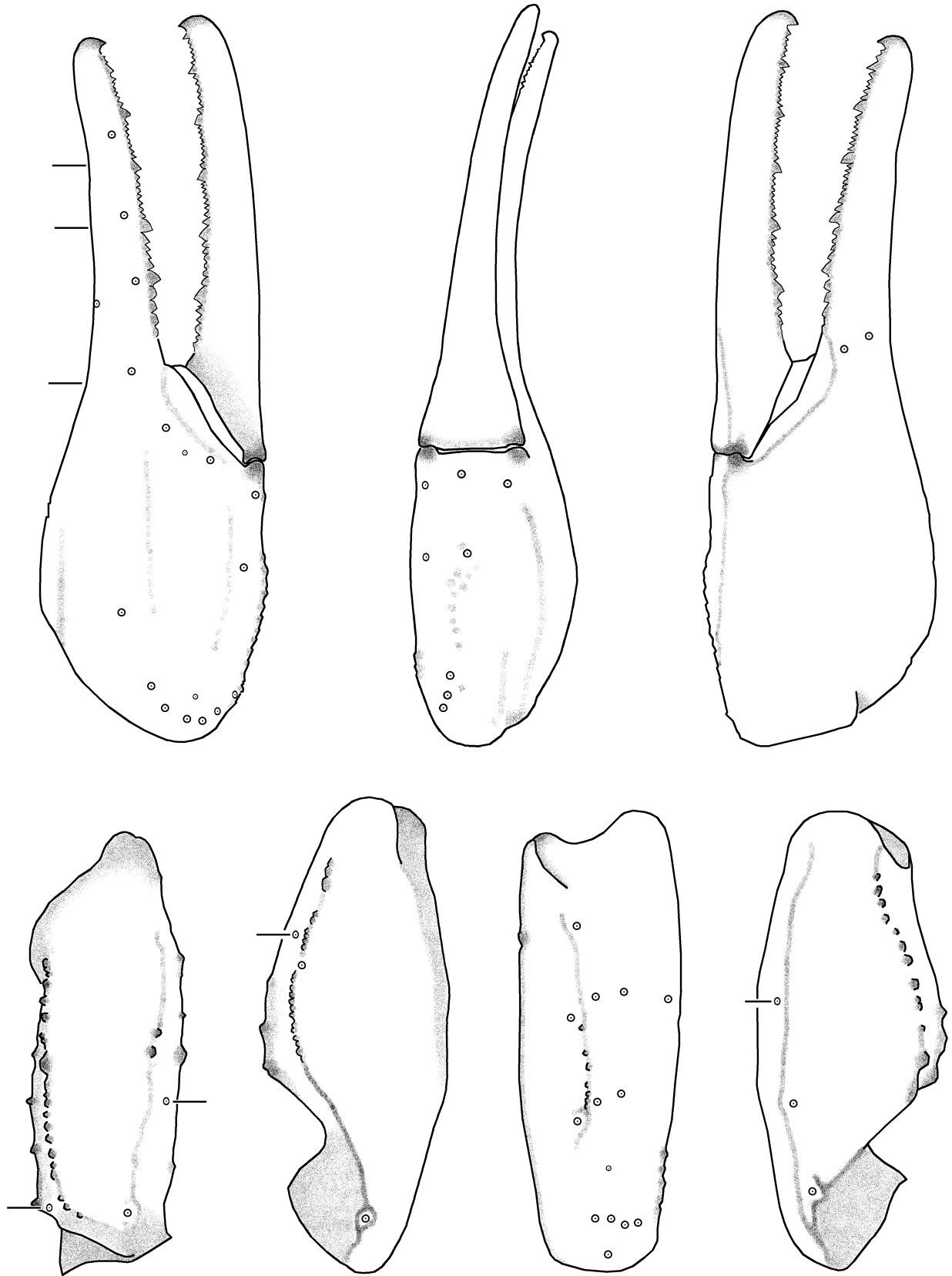


Figure 3: Trichobothrial pattern of *Paruroctonus hirsutipes*, female, Algodones Dunes, Imperial Co., California, USA.

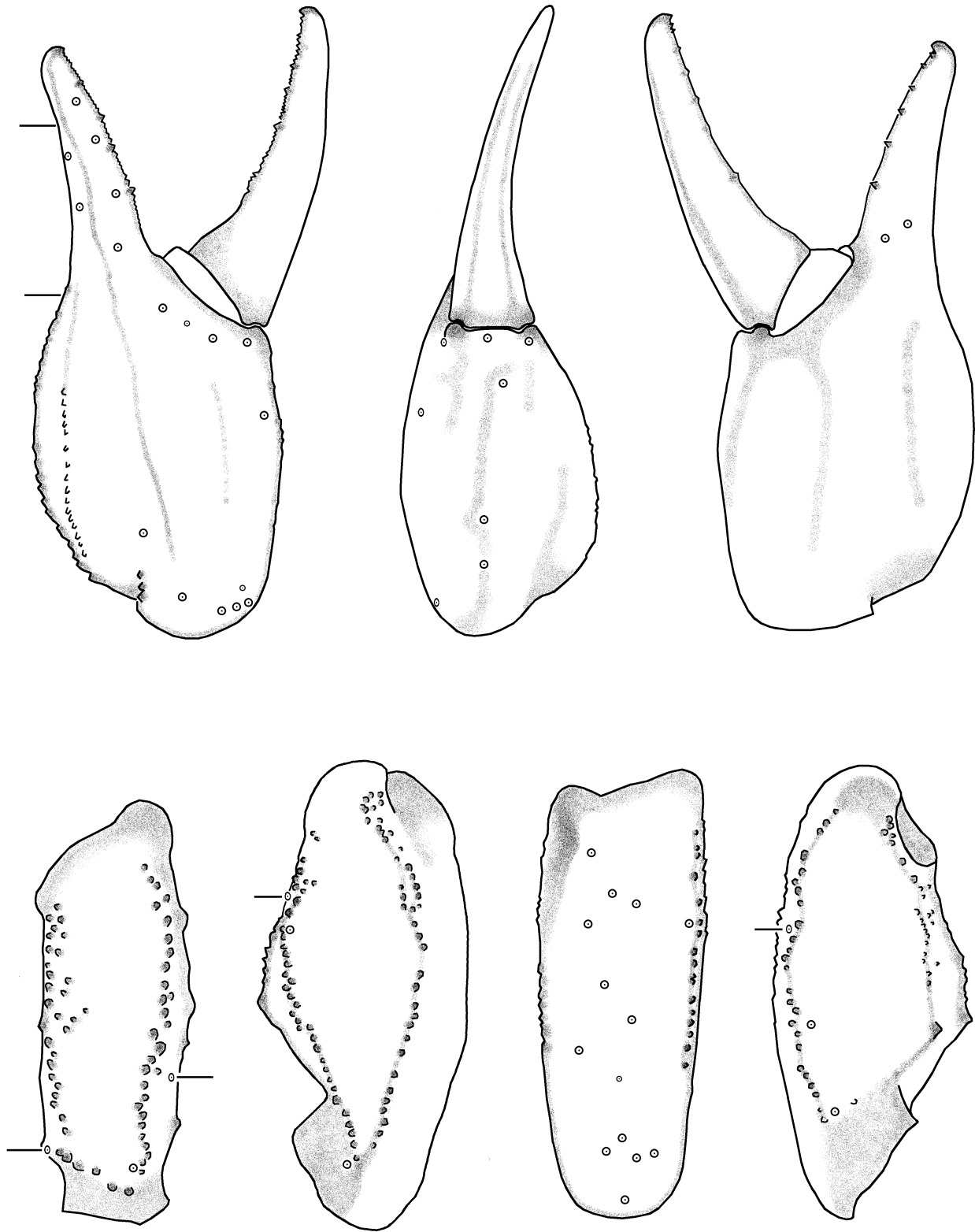


Figure 4: Trichobothrial pattern of *Paruroctonus surensis*, male, Las Bombas, Baja California Sur, Mexico.

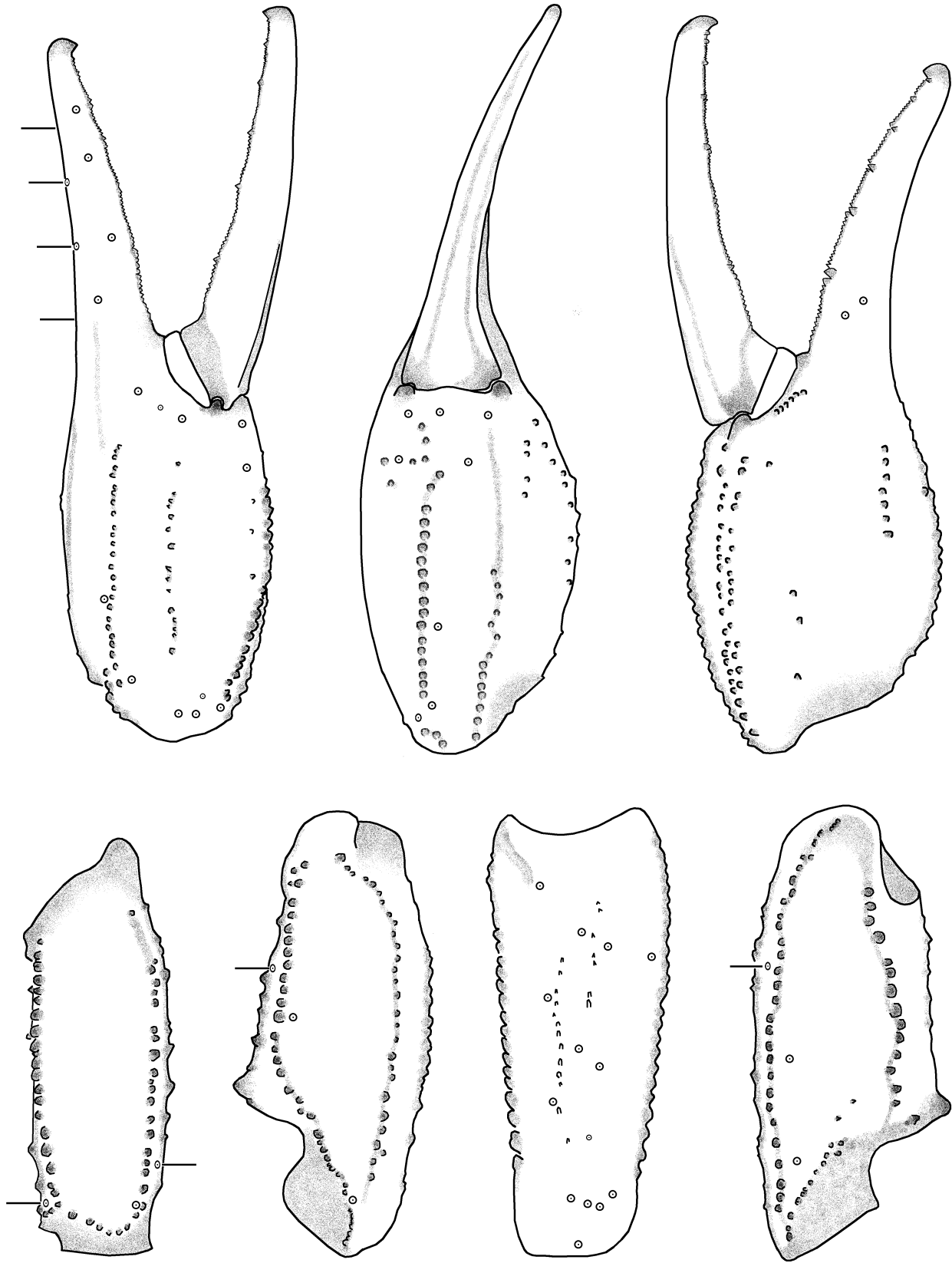


Figure 5: Trichobothrial pattern of *Smeringurus grandis*, female, Oakies Landing, Baja California, Mexico.

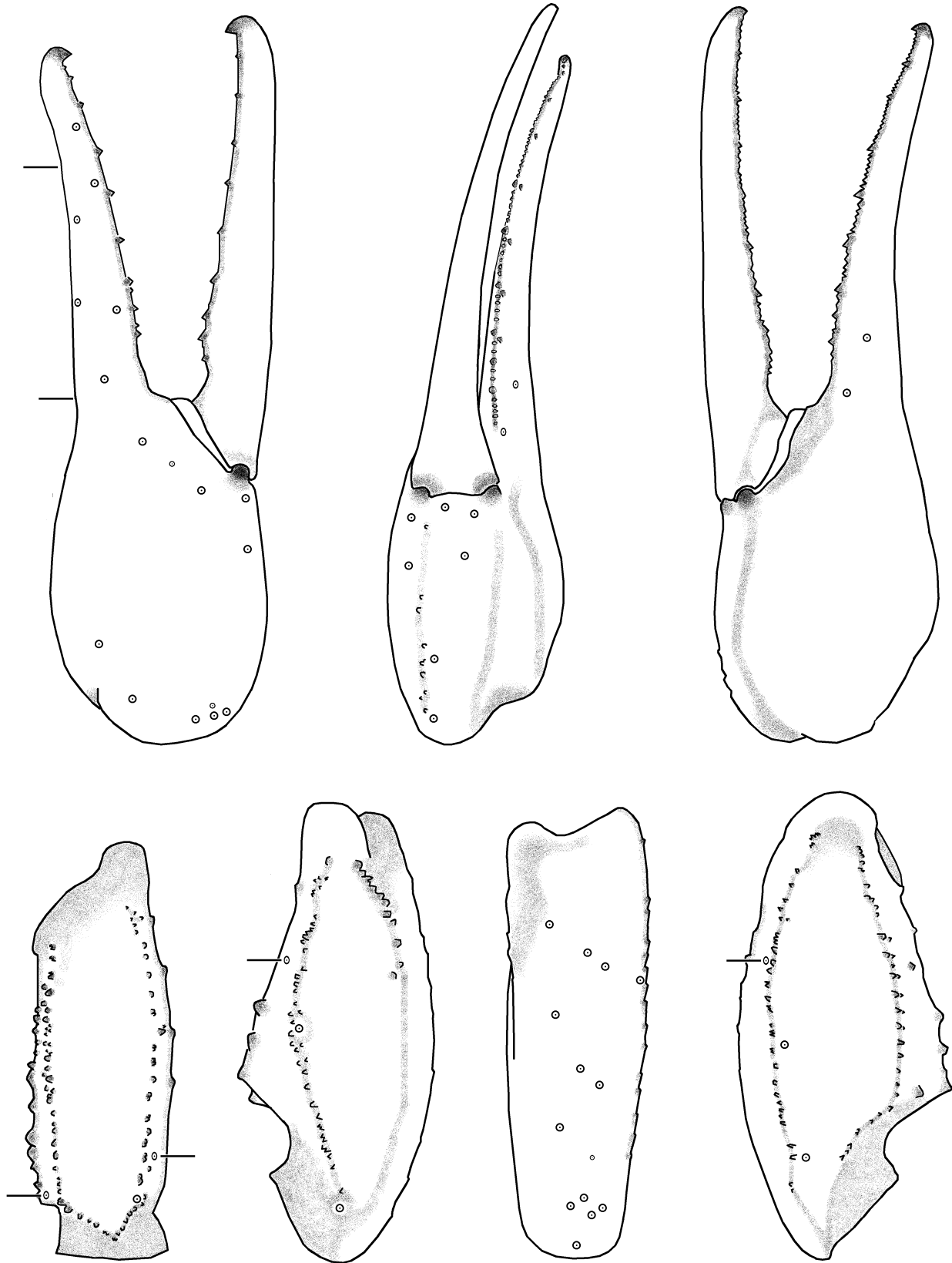


Figure 6: Trichobothrial pattern of *Vejovoidus longiunguis*, female, Las Bombas, Baja California Sur, Mexico.

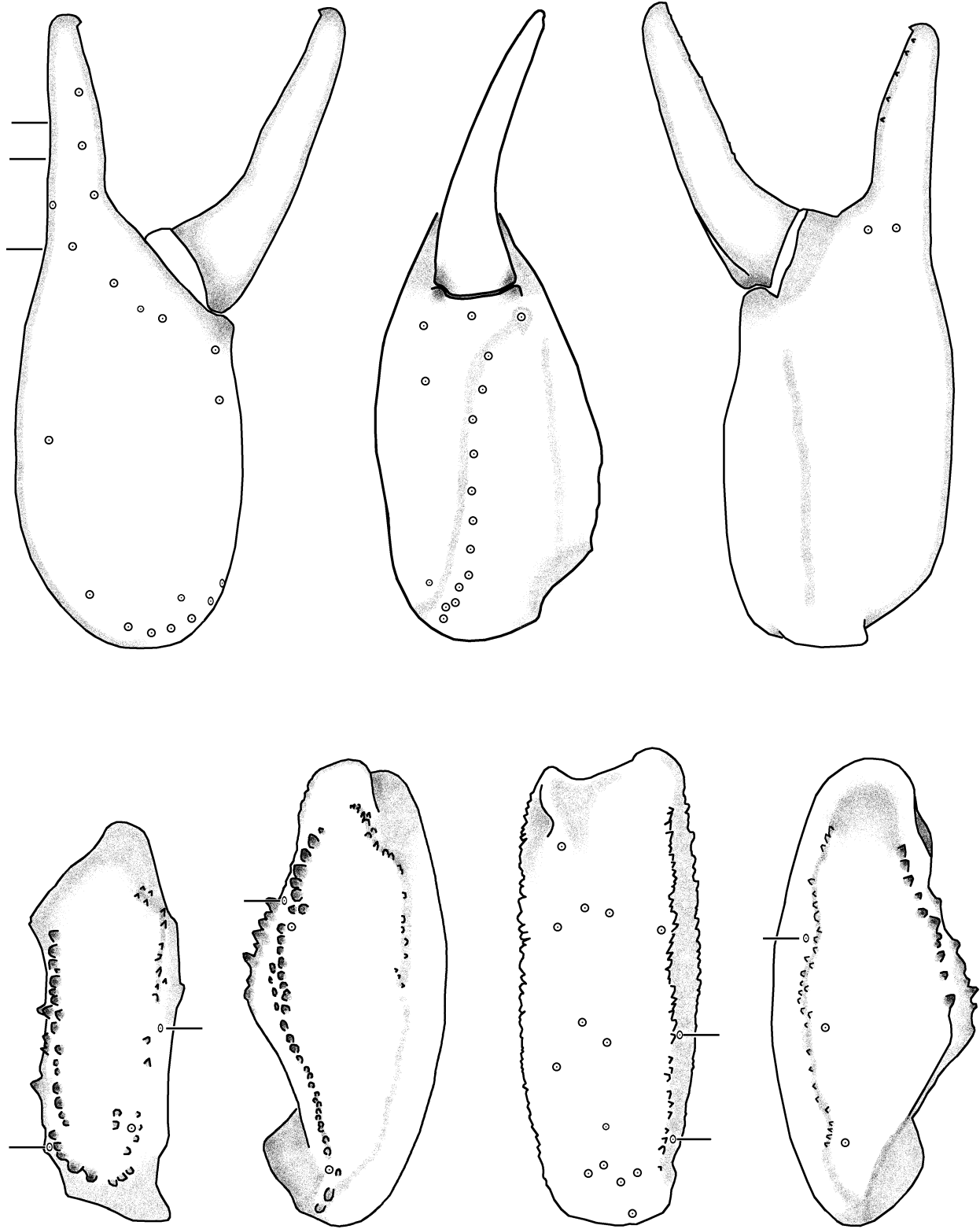


Figure 7: Trichobothrial pattern of *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico.

Db. The location of trichobothrium *Db* as it relates to the digital (*DI*) carina of the palm is an important diagnostic character, relevant at the subfamily and tribe levels. In subfamily Smeringurinae, it is usually located ventral of this carina (based on 22 species). In subfamily Syntropinae, the two tribes differ in this character: in tribe Stahnkeini, *Db* is located ventral of carina *DI* (although *Gertschius* is an exception with *Db* situated essentially on *DI*); in tribe Syntropini, *Db* is definitely positioned dorsal to *DI* (Figs. 9–12, 140–151). In subfamily Vaejovinae, there is more variability in the placement of *Db*. Genera *Pseudouroctonus* (Fig. 13) and *Uroctonites* have *Db* situated dorsal (i.e., “above”) of carina *DI*; in other taxa such as *Franckeus* and most of the *Vaejovis* “mexicanus” group, including the “vorhiesi” subgroup, *Db* is ventral of the *DI* carina (Figs. 14 and 16). In the *Vaejovis* “nigrescens” group, the placement of *Db* is variable (Fig. 15).

ib-it. The position of the chelal internal trichobothria *ib-it* is important in diagnosing the subfamilies in Vaejovidae. These trichobothria are always found on the fixed finger, never on the palm next to the movable finger articular membrane — a position where *ib-it* are located in all Chactidae (see Soleglad & Fet, 2003b: figs. 67–78, 81–90), a major differentiating character between these two chactoid families. In Smeringurinae, *ib-it* are usually located just proximal of the basal inner denticle (*ID*) (Figs. 2–7), sometimes quite basal, as seen in *Paravaejovis* (Fig. 7). In subfamily Vaejovinae, trichobothria *ib-it* are located at the extreme base of the finger (Figs. 13–16). This configuration was originally identified for the “mexicanus” group of *Vaejovis* by Soleglad (1973b). Recently, Fet & Soleglad (2007) illustrated the basal position of *ib-it* for the designated neotype of *Vaejovis mexicanus* C. L. Koch, 1836, the type species of *Vaejovis* (also shown in this paper, Fig. 14). Other authors have illustrated the basal position of the *ib-it* trichobothria for many species of Vaejovinae (selected references): genus *Franckeus*: *F. kochi*, *F. platnicki*, and *F. rubrimanus* (Sissom, 1991: figs. 18, 38, 58), *F. peninsularis* (Soleglad & Fet, 2005: fig. 18; also shown in this paper, Fig. 16); *Vaejovis* “nigrescens” group: *Vaejovis gracilis* (Gertsch & Soleglad, 1972: fig. 83), *V. curvidigitus*, *V. mitchelli*, *V. pococki*, and *V. solegladi* (Sissom, 1991d: figs. 8, 28, 48, 68), *V. janssi* (Soleglad & Fet, 2005: fig. 28; also shown in this paper, Fig. 15); *Vaejovis* “mexicanus” group: *V. granulatus* (Sissom, 1989: fig. 9), *V. dugesi* (Sissom, 1990b: fig. 1F); “vorhiesi” subgroup, *V. paysonensis* (Soleglad, 1973b: fig. 26), *V. vorhiesi*, *V. cashi*, and *V. feti* (Graham, 2007: figs. 6, 19, 32). In subfamily Syntropinae, the *ib-it* location is dependent on the tribe, although they are never found on the base of the finger as in Vaejovinae. Tribe Syntropini has *ib-it* located close to the basal inner denticle (*ID-6*) (Figs. 9–12). This location is quite

consistent, even in the lithophilic genus *Syntropis*, whose fingers are extremely slender (Fig. 10). In this genus (also see Soleglad et al., 2007: figs. 6, 23), the bases of the fingers are lengthened, so that the *OD* denticles occur on the distal half of the fingers. This lengthening of the base is also reflected by the position of the fixed finger trichobothria, in particular, *ib-it*, which are in close proximity of *ID-6*. In tribe Stahnkeini, *ib-it* positions are variable, based on the adult size: for smaller species such as *Serradigitus littoralis* or *S. joshuaensis*, they are located somewhat proximal, whereas in larger species such as *Serradigitus wupatkiensis* (Fig. 8), *S. adcocki*, or *Stahnkeus subtilimanus*, trichobothria *ib-it* may be positioned midfinger (see Soleglad & Fet, 2006: 19–20; tab. 5, for a detailed discussion).

Other trichobothria. The alignment of trichobothria on the external aspect of the patella also shows promise in further diagnosing certain assemblages in Vaejovidae. It must be noted, however, that there is frequent vertical dislocation of trichobothria on this patellar surface, therefore a consensus must be made using both pedipalps and multiple specimens. The relative position of trichobothrium v_3 with respect to et_3 shows certain trends in some vaejovid species: in subfamily Smeringurinae, v_3 is positioned proximal to et_3 (Figs. 2–7); it also provides a distinction between the tribes in subfamily Syntropinae: in tribe Stahnkeini, v_3 is distal to et_3 (Fig. 8) whereas in Syntropini, v_3 is positioned proximal to et_3 (Figs. 9–12). In subfamily Smeringurinae, trichobothria eb_2 – eb_5 essentially form a horizontal line, none in close proximity to eb_1 , which is evident in all smeringurine illustrations shown in this paper (Figs. 2–7). In other vaejovid groups, these trichobothria do not form a horizontal line, eb_4 angles proximally, somewhat in close proximity to eb_1 (e.g., in *Serradigitus wupatkiensis*, Fig. 8, and *Thorellius* species, Figs. 23–26).

Paravaejovini. In *Paravaejovis*, the chelal palm trichobothrium *Dt* is located slightly distal of the palm midpoint, in strong contrast to its position in Smeringurini, where it is positioned significantly basal on the palm (see histogram in Fig. 1). On the femur of *Paravaejovis*, the trichobothrium *d* is distal of *i*, whereas in Smeringurini it is proximal of *i*, as is the case for all other vaejovids. In Fig. 18, the relative distal position of trichobothrium *d* exhibited in *Paravaejovis* as compared to *i* is apparent in both the histogram and the diagrammatic comparison to other smeringurine species. Trichobothrium *e* in *Paravaejovis* is located slightly proximal of the femur midpoint, considerably more distal than it is in Smeringurini (or any other vaejovid). Again, this is apparent in Fig. 18 from both the diagrammatic comparisons and ratio histograms. Williams (1980: 29–30) created this genus based primarily on its major neobothriotaxy found on the

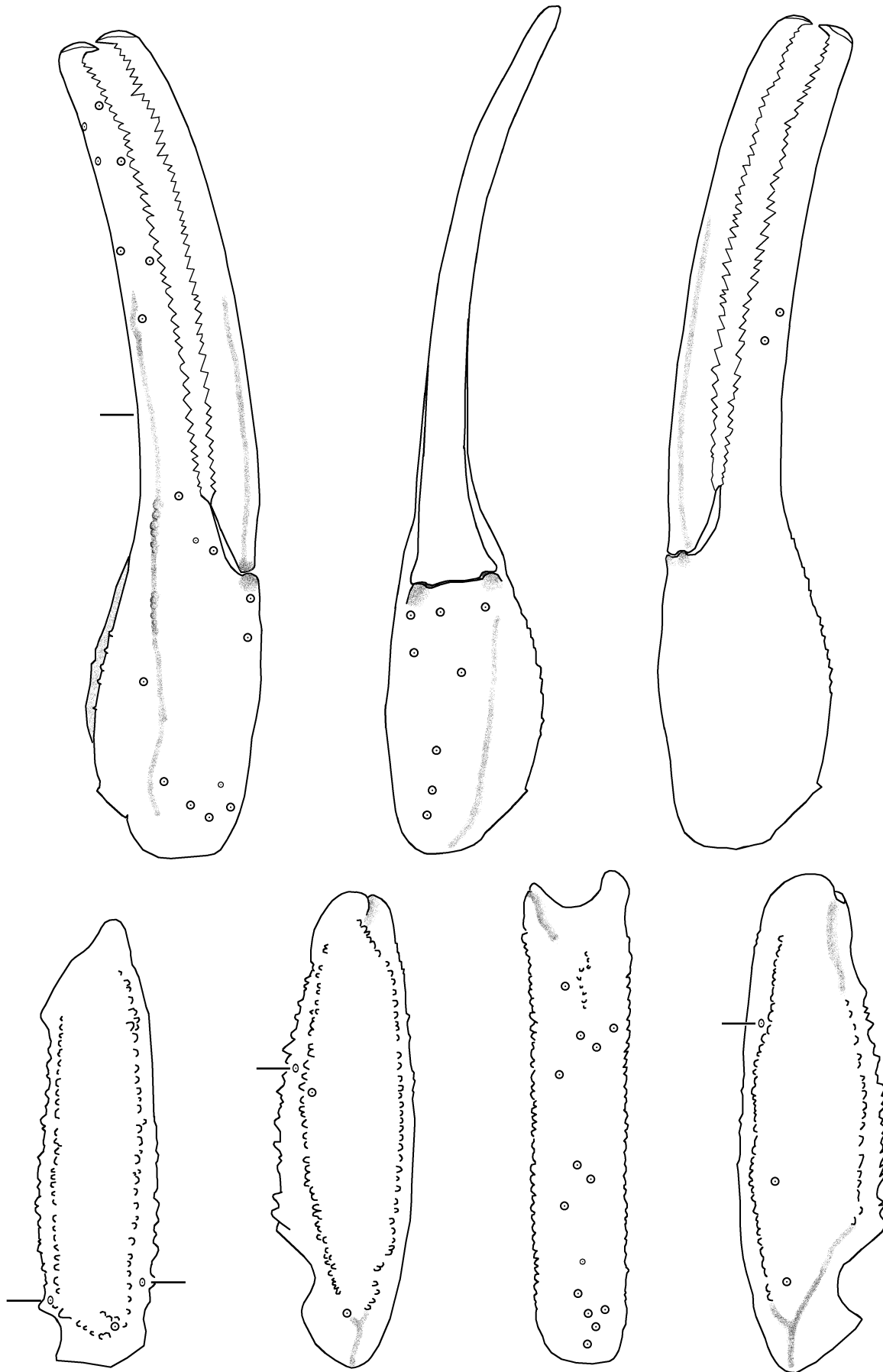


Figure 8: Trichobothrial pattern of *Serradigitus wupatkiensis*, female, Wupatki Ruin, Wupatki National Monument, Coconino Co., Arizona, USA.

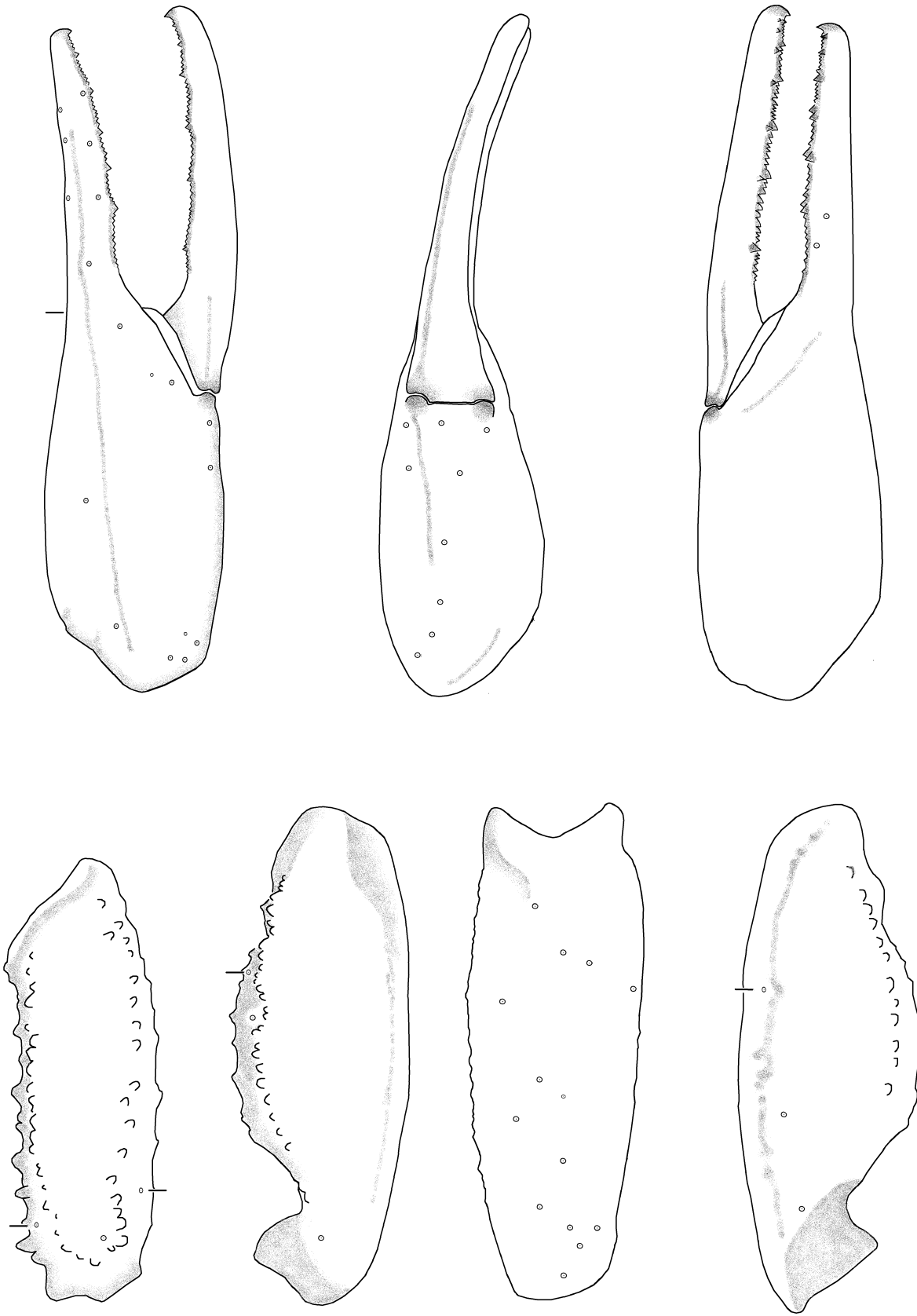


Figure 9: Trichobothrial pattern of *Hoffmannius eusthenura*, male, Cabo San Lucas, Baja California Sur, Mexico.

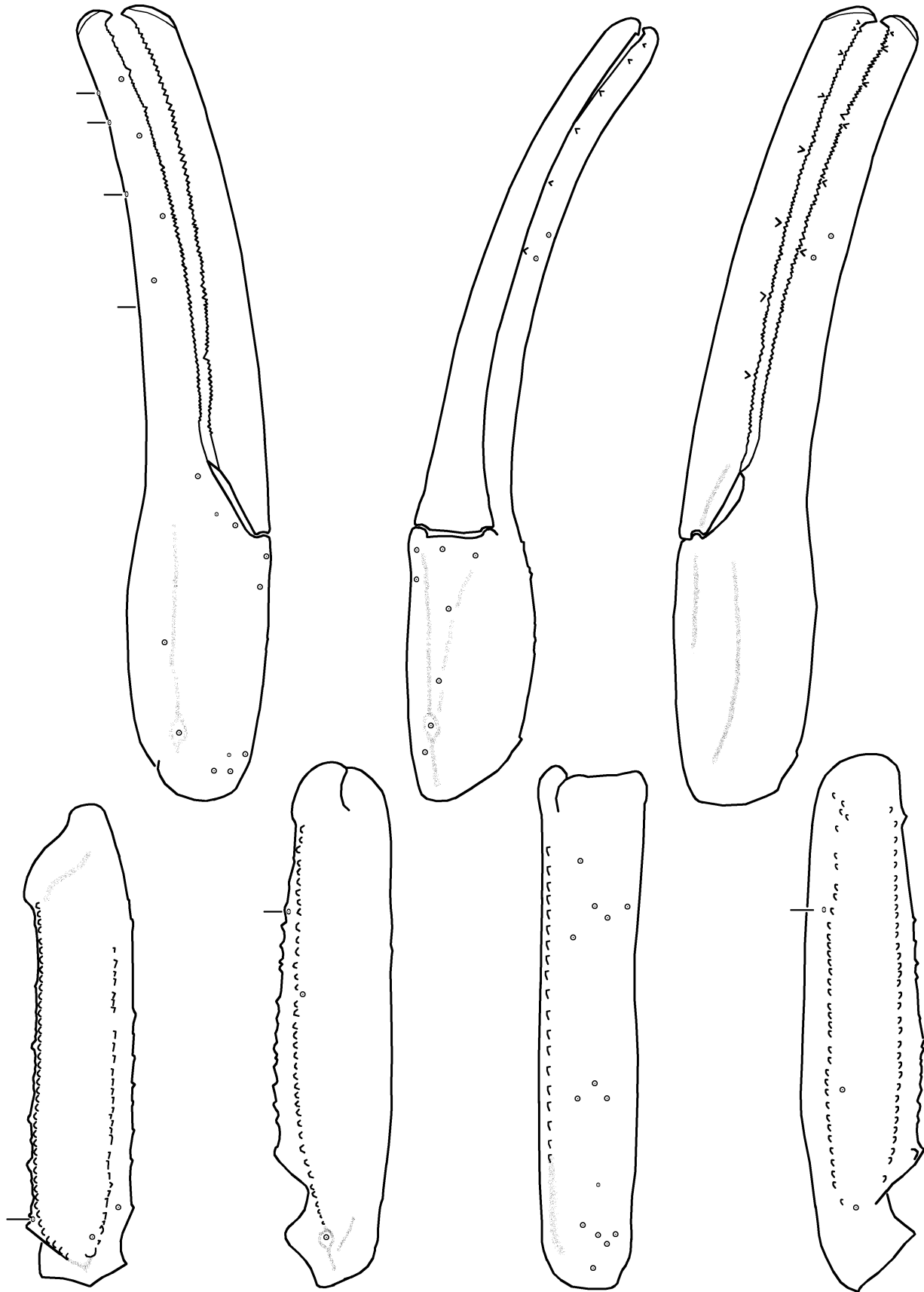


Figure 10: Trichobothrial pattern of *Syntropis williamsi*, female holotype, Los Aripes, Baja California Sur, Mexico (after Sogleglad et al., 2007: fig. 15).

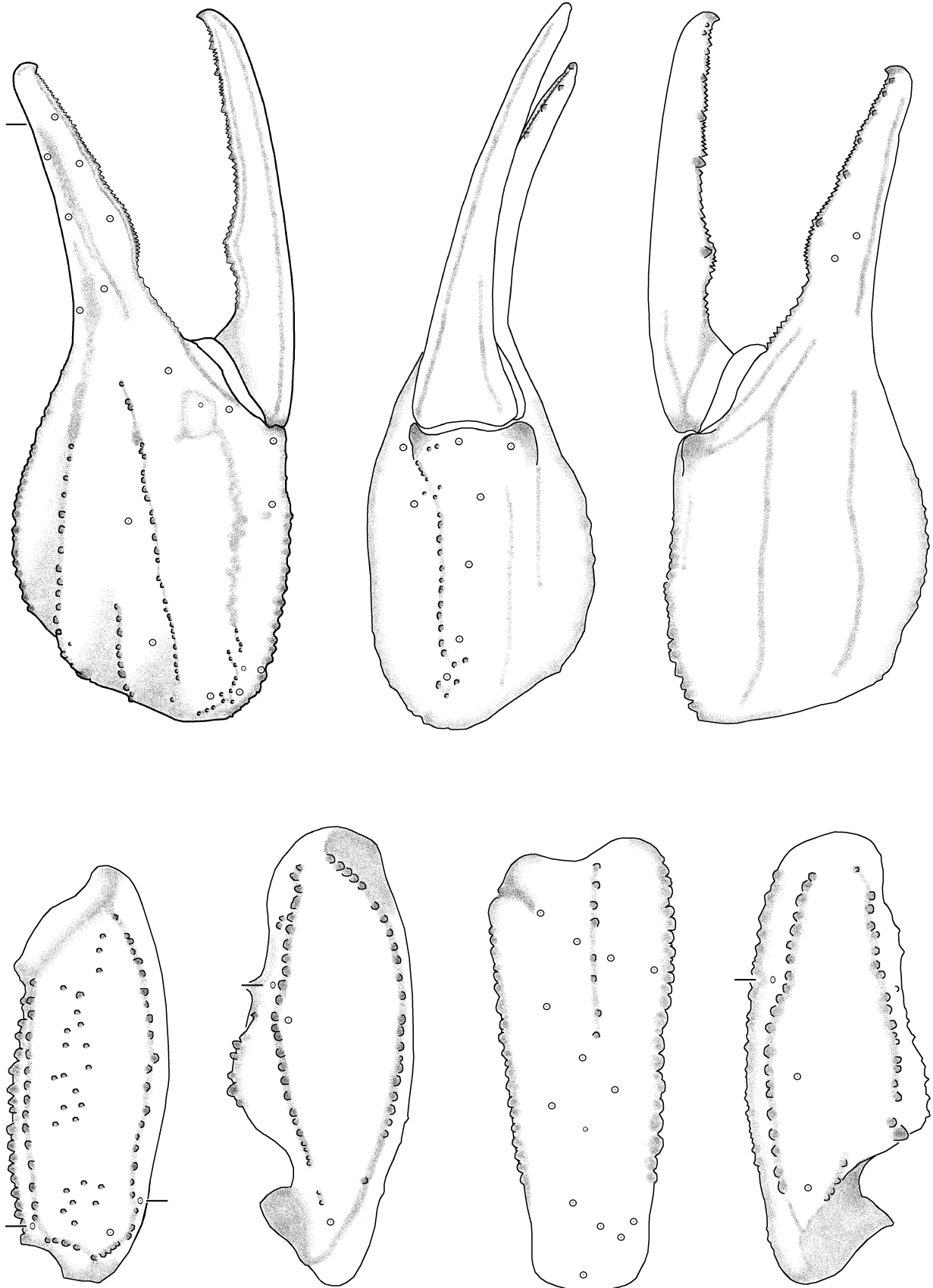


Figure 11: Trichobothrial pattern of *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico.

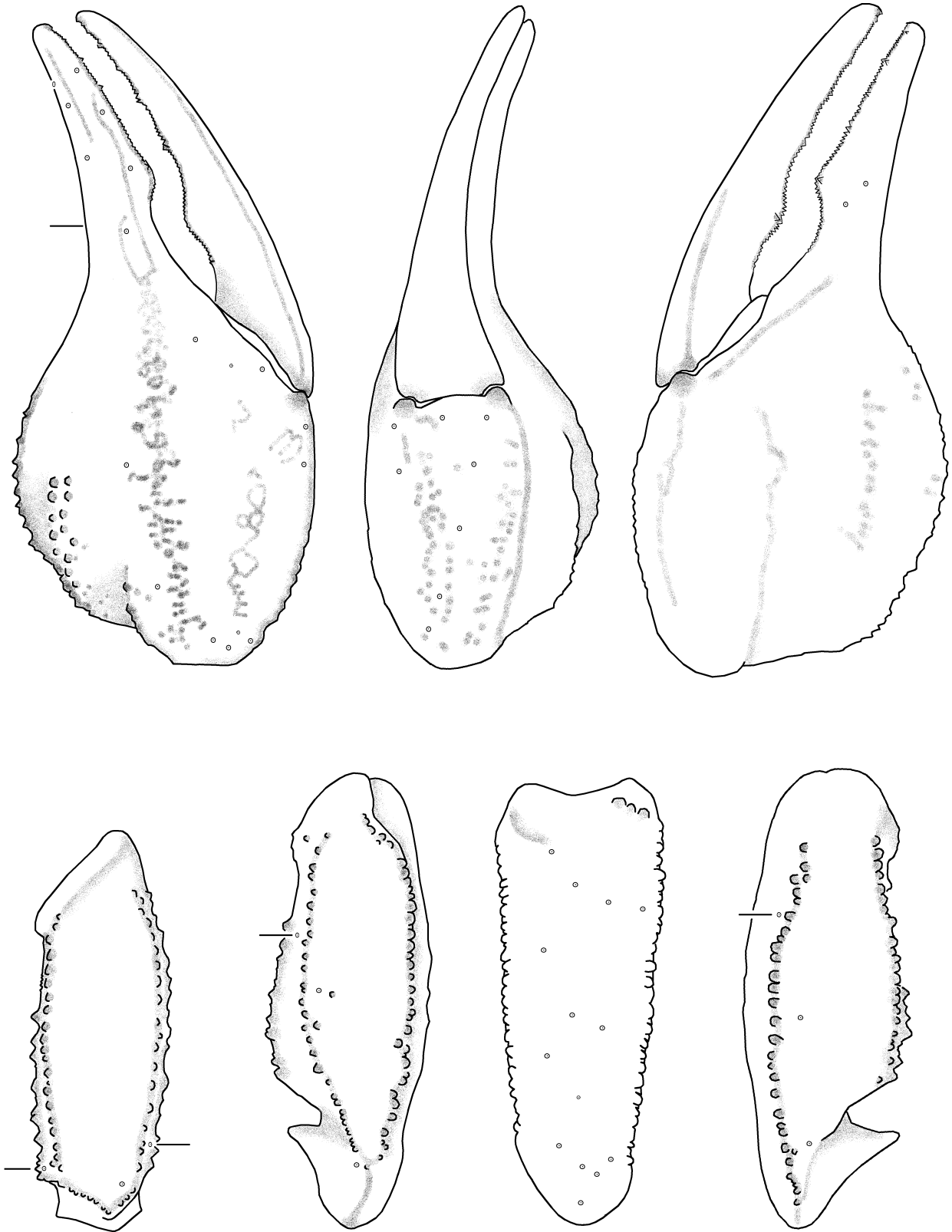


Figure 12: Trichobothrial pattern of *Thorellius intrepidus*, male, Mexico.

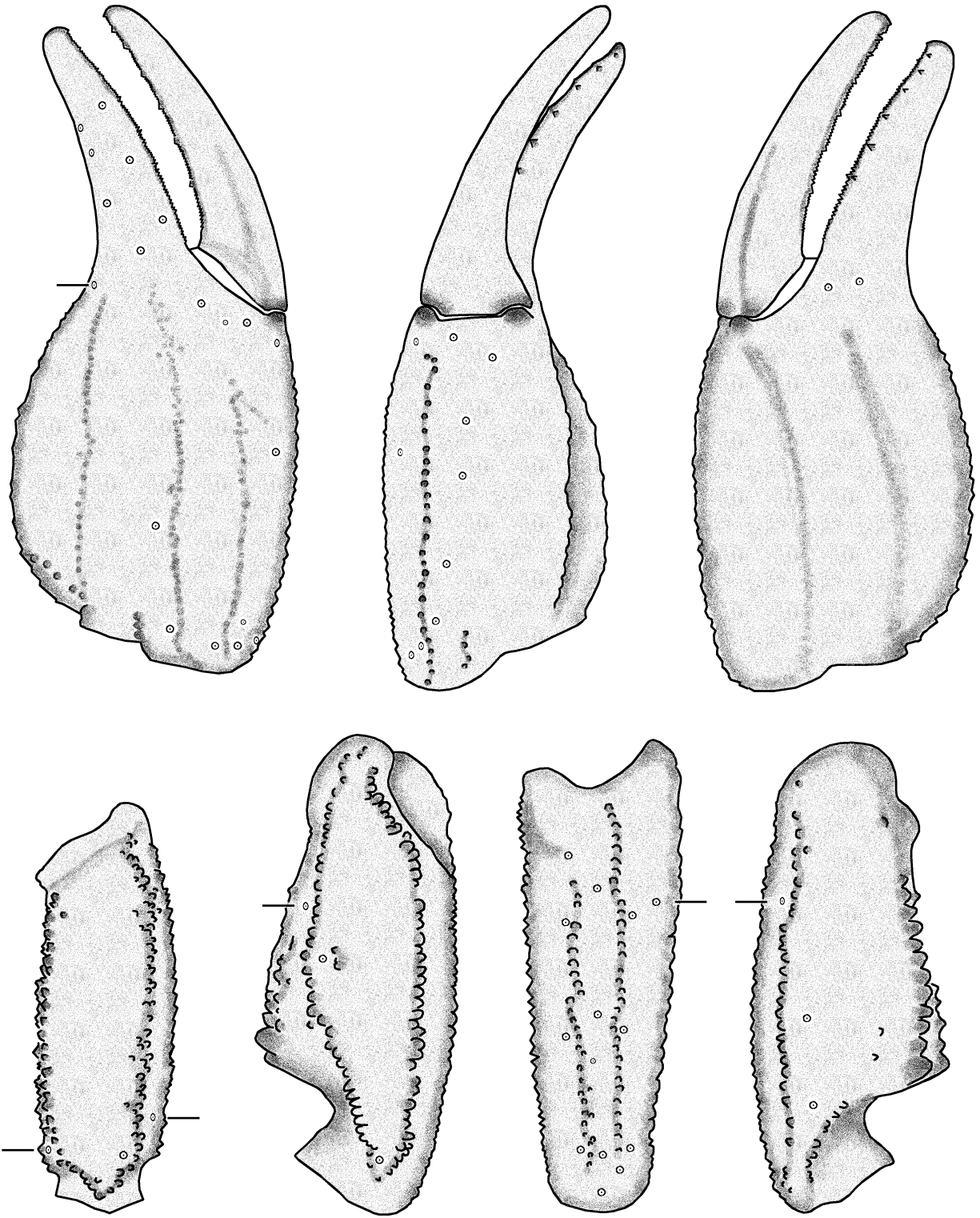


Figure 13: Trichobothrial pattern of *Pseudouroctonus williamsi*, male, Santa Ysabel Reserve, San Diego Co., California, USA.

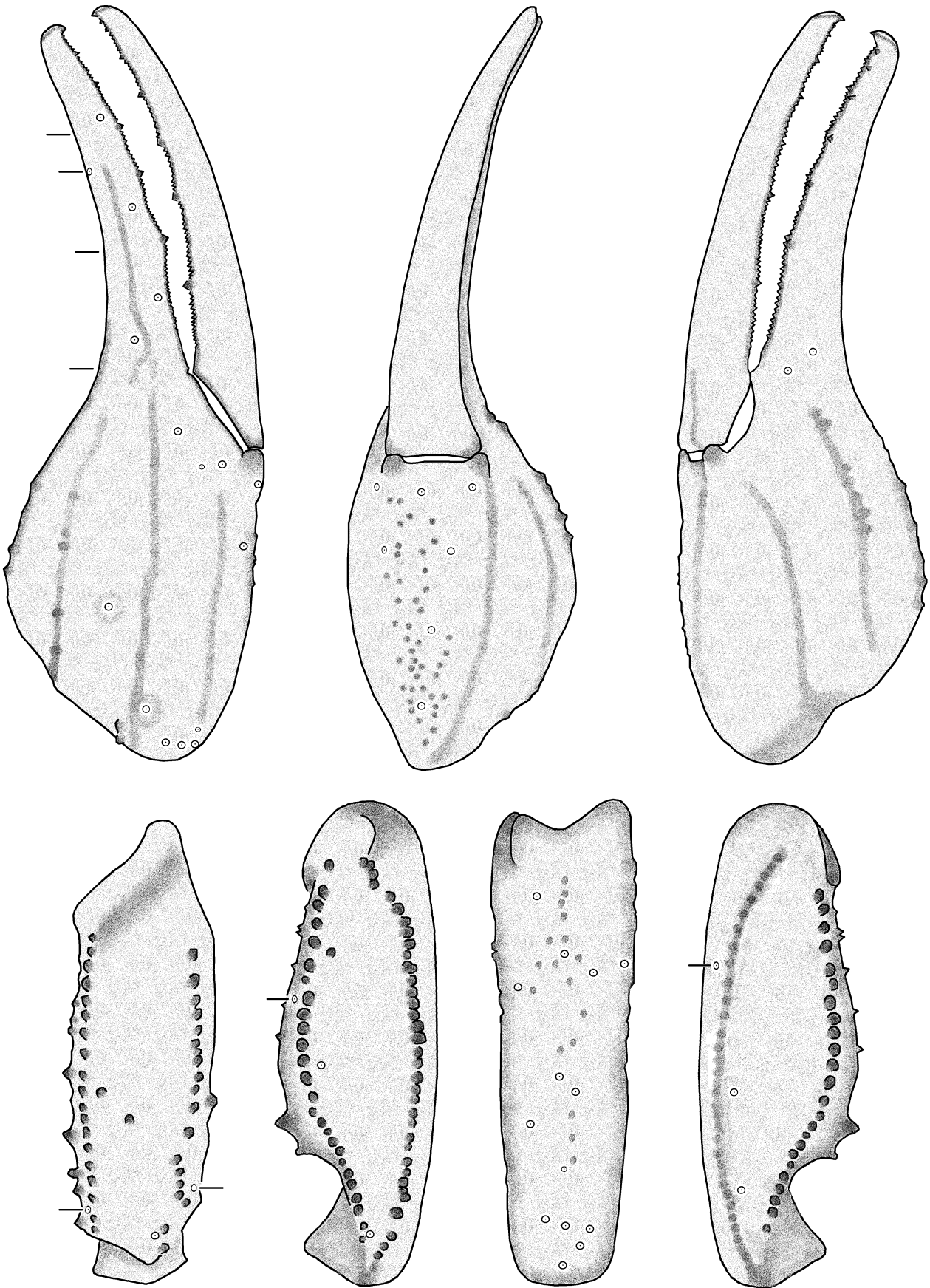


Figure 14: Pedipalp trichobothrial pattern of *Vaejovis mexicanus*, female neotype, Mexico City, Mexico (after Fet & Soleglad, 2007: fig. 7).

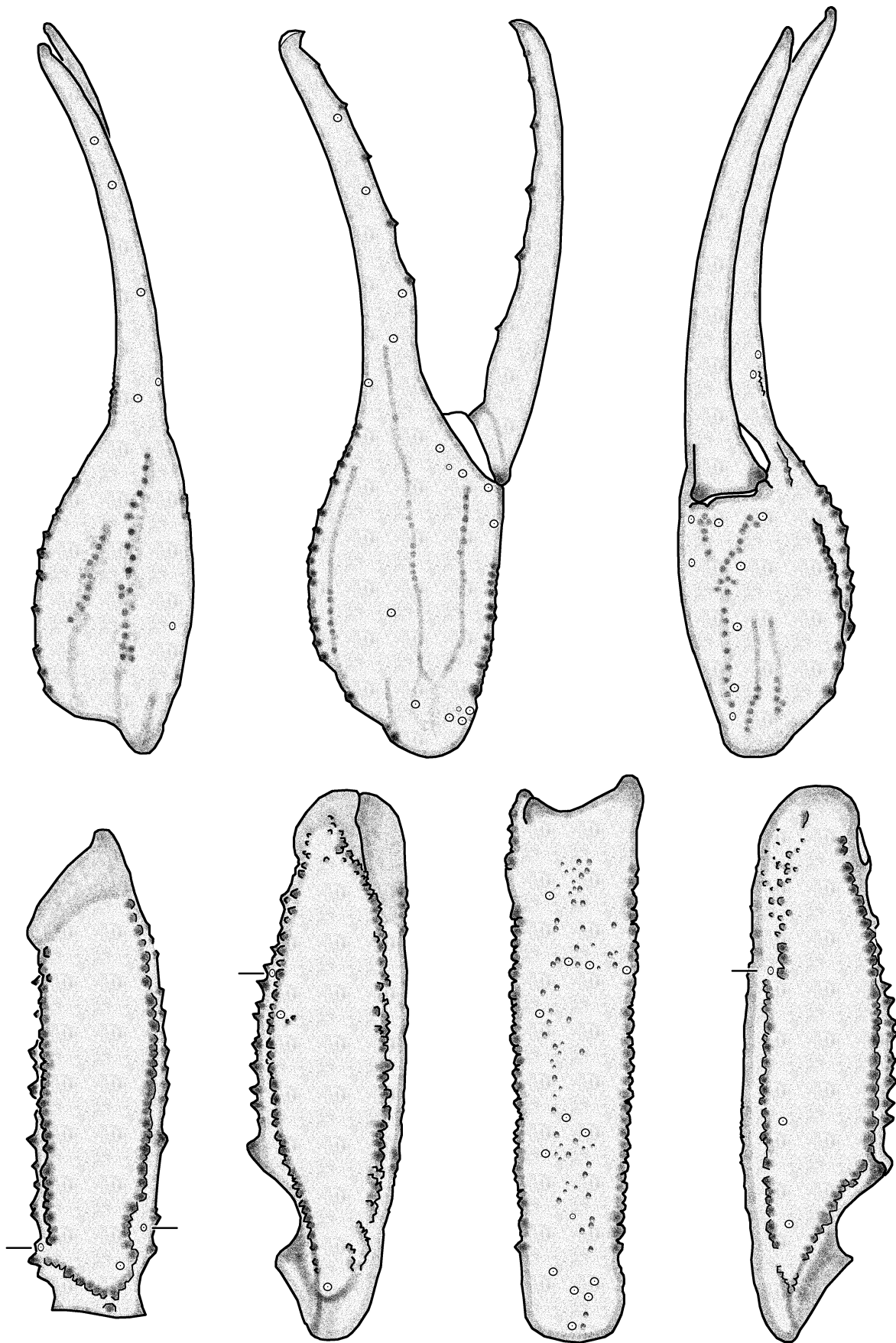


Figure 15: Trichobothrial pattern of *Vaejovis janssi*, male, Isla Socorro, Mexico (after Soleglad & Fet, 2005: figs. 20–26, in part).

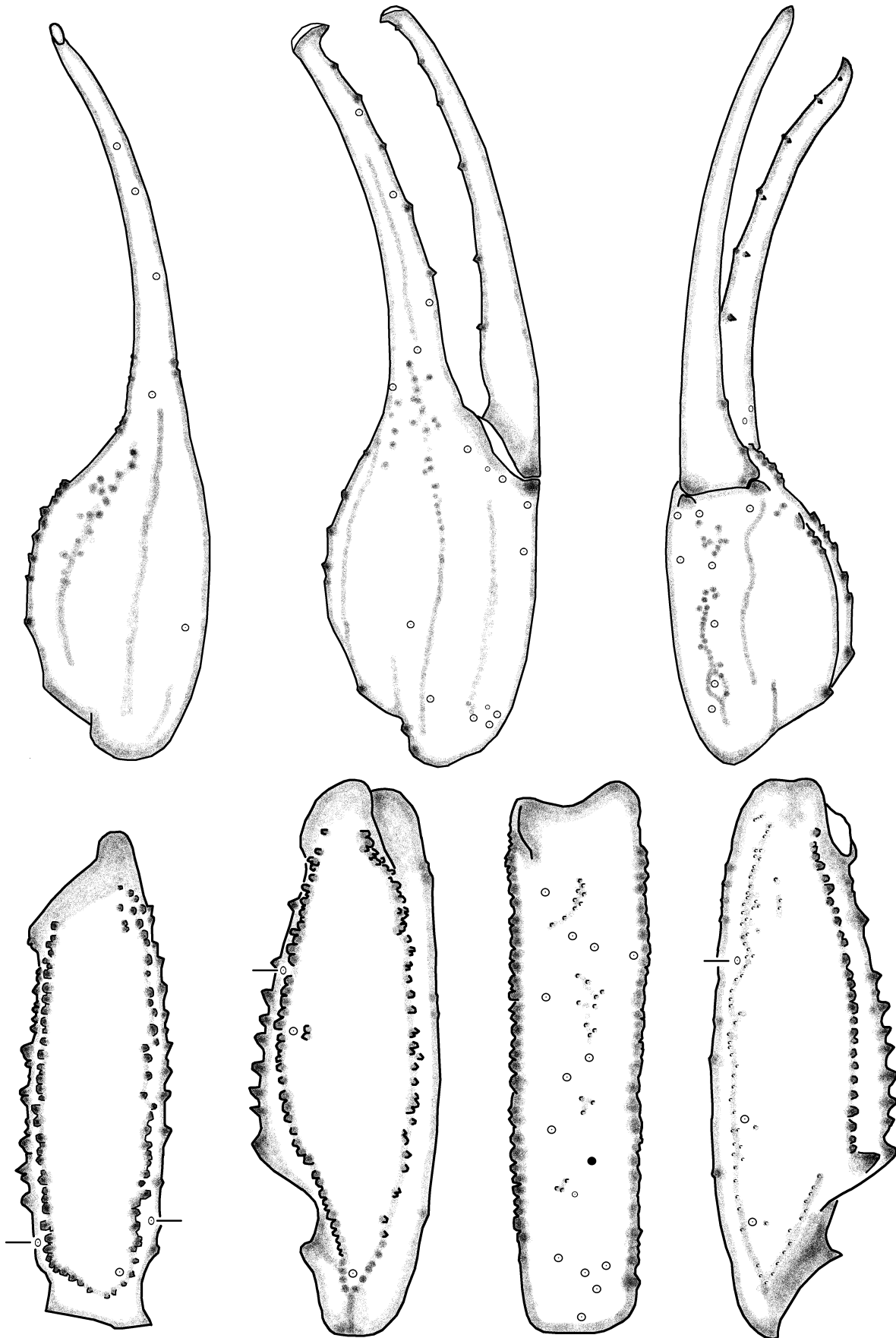


Figure 16: Trichobothrial pattern of *Franckeus peninsularis*, male, San Raymundo, Baja California Sur, Mexico (after Soleglad and Fet, 2005: figs. 10–16, in part). Solid circle shown in patella is an *accessory* trichobothrium depicting neobothriotaxy in the *esb* series.

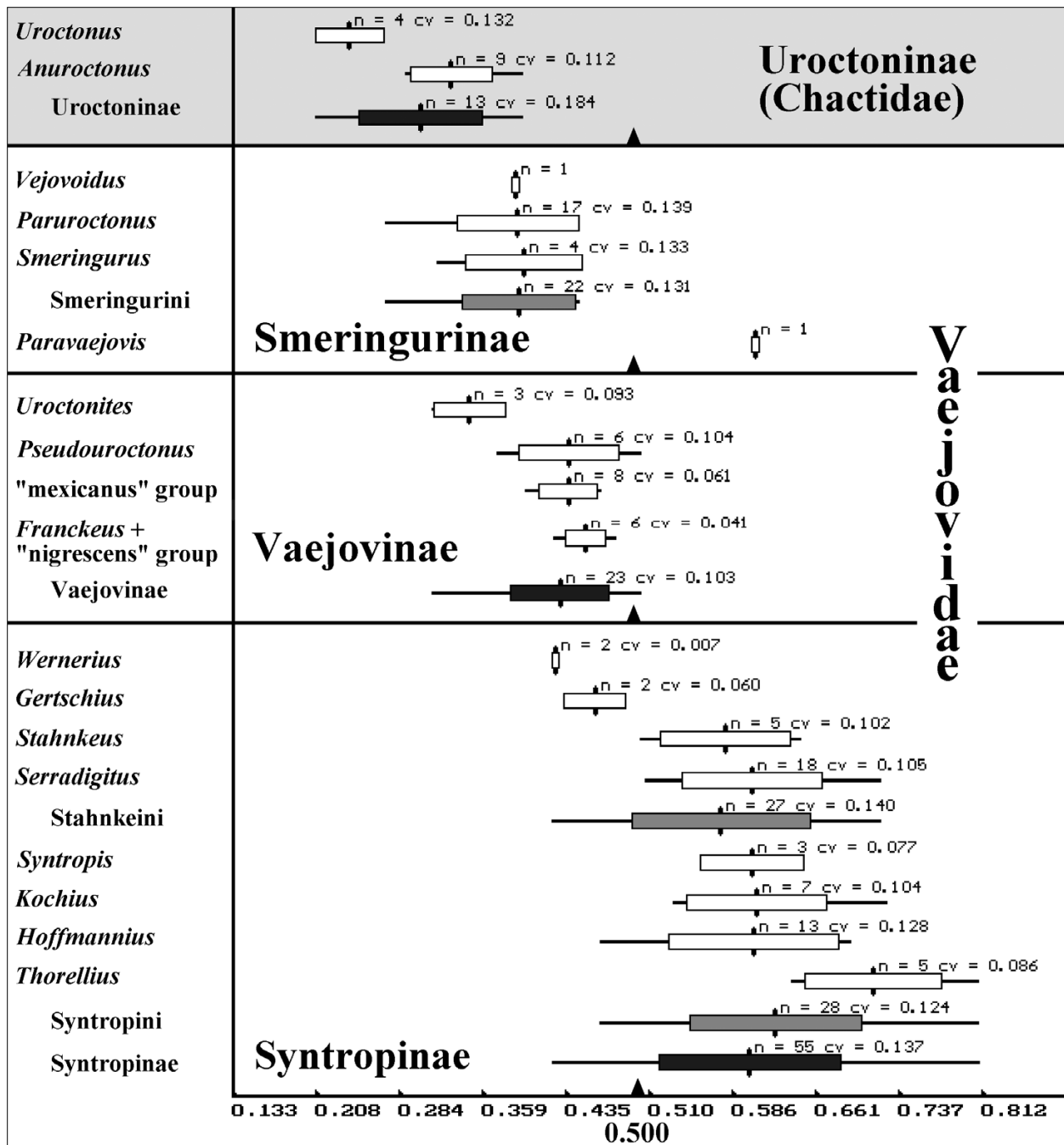


Figure 17: Histogram showing position of chelal trichobothrium *Dt* in relation to the palm length ($Dt_pos/Palm_L$: Dt_pos measured from palm base). More than 100 species and subspecies of family Vaejoidea and subfamily Uroctoninae (Chactidae) are represented. The extreme basal position of *Dt* in Uroctoninae is shown in contrast with Vaejoidea since at one time genus *Uroctonus* was considered a vaejovid. Vertical arrow indicates palm midpoint (i.e., ratio = 0.500). See Fig. 1 for explanation of histogram components.

ventral surface of the chela. This neobothriotaxy, which is shown in Figs. 7 and 19, extends onto the external aspect of the chelal palm in line with the trichobothrial series Eb_1-Eb_3 . The number of accessory trichobothria on chela is variable, as reported by Soleglad & Sissom (2001: table 3), 11–14 (12.256) [117], which includes the four ventral trichobothria, V_1-V_4 .

Patellar trichobothria in genus *Thorellius*. Hoffmann (1931: 377–388), in his discussion of species corresponding to our *Thorellius intrepidus*, *T. cristimanus*, and *T. atrox*, reports neobothriotaxy on the patella extern for the latter two species: 19 trichobothria for *T. cristimanus* and 20 for *T. atrox*. For *T. intrepidus*, Hoffmann (1931) reports 14 trichobothria, which un-

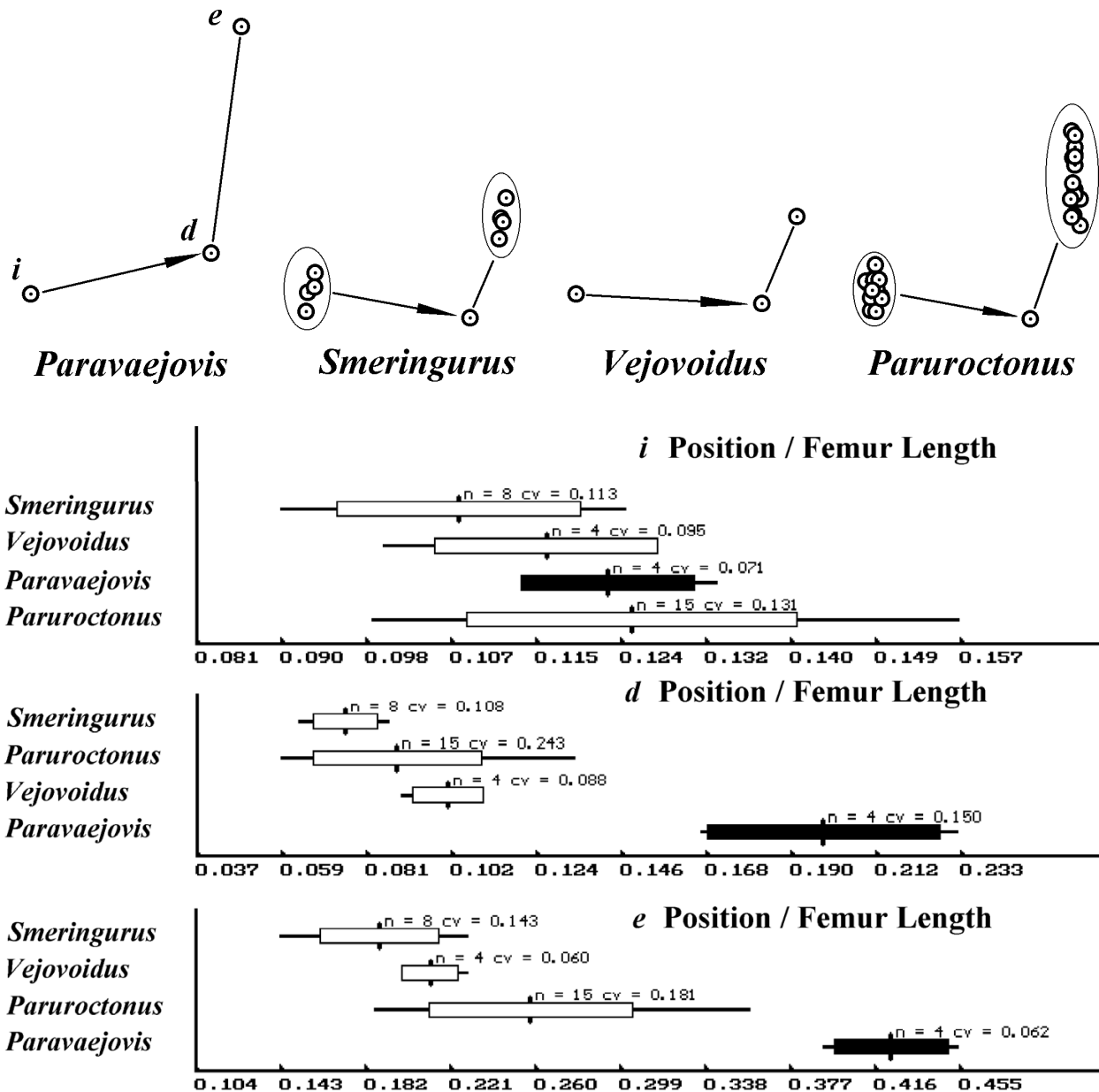
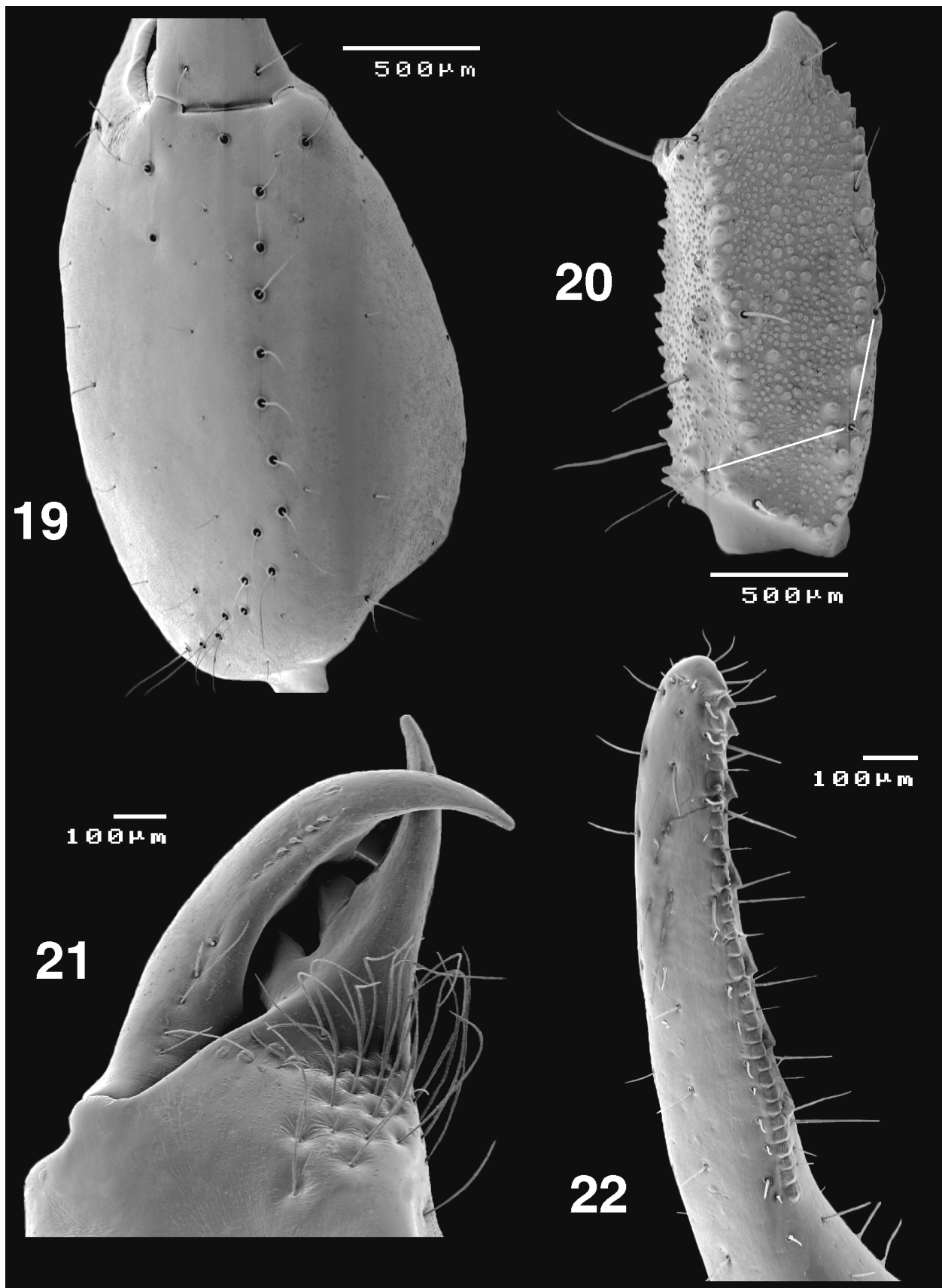


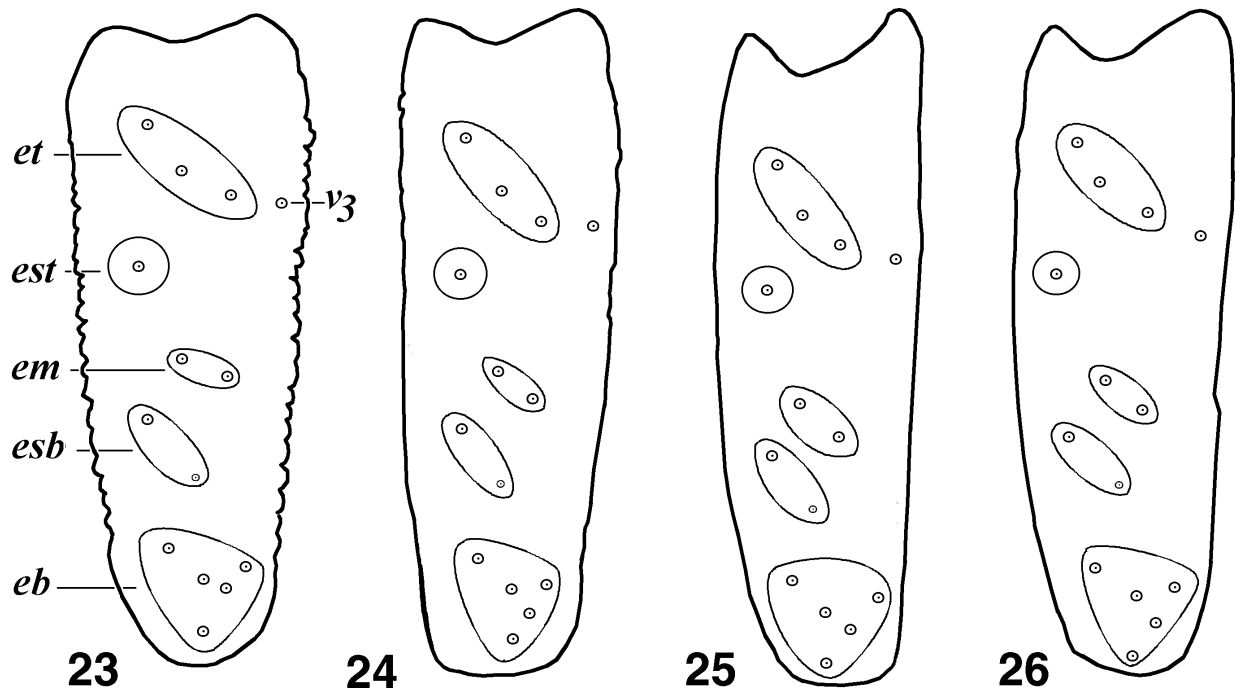
Figure 18: Pedipalp femur trichobothrial configurations for subfamily Smeringurinae. **Top figure** shows each configuration clustered, anchored at trichobothrium *d*, the other trichobothria clusters are plotted from this trichobothrium. All species of *Paravaejovis*, *Smeringurus*, and *Vejovoidus* are shown; 15 species of *Paruroctonus* are included. In genus *Paruroctonus*, we see some variability in the placement of trichobothrium *e*, the more distal locations seen in species *P. hirsutipes*, *P. surensis*, *P. luteolus*, *P. borregoensis*, and *P. ventosus*. In *Smeringurus* and *Vejovoidus*, the configurations are nearly identical. **Bottom figure** presents histograms showing femoral trichobothria positions with respect to femur length. Multiple specimens were measured in *Smeringurus*, *Vejovoidus*, and *Paravaejovis*. The trichobothrium *i* relative position is clearly the same for all four genera; however, trichobothria *d* and *e* are considerably more distal on the femur in *Paravaejovis*. In *Paruroctonus*, *Smeringurus*, and *Vejovoidus*, trichobothrium *d* is clearly proximal to *i*, whereas in *Paravaejovis*, it is distal. Distance to trichobothria measured from femur base. Abbreviations of trichobothria: *i* = internal; *d* = dorsal; *e* = external. See Fig. 1 for explanation of histogram components.

doubtedly included v_3 (thus the pattern is orthobothriotaxic, 13 external and one ventral trichobothria). We examined the material in our possession (four species, multiple specimens for two) and could not

isolate accessory trichobothria on the external surface of the patella. Figures 23–26 illustrate the external trichobothrial pattern of the patella for four species, including the two reported as neobothriotaxic. We



Figures 19–22: *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico, showing diagnostic characters. **19.** Chela, ventral view, showing neobothriotaxy. **20.** Femur, dorsointernal view, showing trichobothria configuration, note midsegment position of *e* and *d* located distal to *i* (trichobothria connected by white lines). **21.** Chelicera, ventral view, showing serrula and lack of ventral dentition on ventral edge of movable finger. **22.** Chelal movable finger denticle edge, showing seven *ID* denticles and enlarged *MD* denticles approximating size of *OD* denticles.



Figures 23–26: Trichobothrial pattern of pedipalp patella, external view, of genus *Thorellius* showing orthobothriotaxy. **23.** *T. intrepidus*, male, Mexico. **24.** *T. cristimanus*, male, Autlán, Jalisco, Mexico. **25.** *T. atrox*, female, Colima, Colima, Mexico. **26.** *T. occidentalis*, female, Acapulco, Guerrero, Mexico. Abbreviations of trichobothria: *eb* = external basal; *esb* = external suprabasal; *em* = external median; *est* = external subterminal; *et* = external terminal; *v*₃ = ventral trichobothrium number 3.

suspect that irregularities or pits on the patellar surface, and/or enlarged setae contributed to Hoffmann's error. Unfortunately, the patella trichobothrial pattern is not shown for *T. cisnerosi* by Ponce Saavedra & Sissom (2004), where only the chela is illustrated. Among these figures (their fig. 8) one can see nine trichobothria illustrated for the *db–dt* and *eb–et* series. Since the authors report orthobothriotaxy for this species, clearly this is a mistake in the illustration since eight trichobothria are found in these series.

Genital Operculum

Diagnostic value: Genital operculum of the female is used to differentiate subfamilies in Vaejoidea.

Williams (1972: 2), as he reinstated *Paruroctonus* as a genus (elevating it from subgenus status), was the first to delineate genera and/or species groups in Vaejoidea, in part, by the structure of the female genital operculum. Hjelle (1972: 22, 24), in the diagnoses of *Paruroctonus boreus* and *P. silvestrii* (then placed in *Vaejovis*), also made this distinction. Williams (1972) writes: "... *Paruroctonus* differs from *Vaejovis* ... having the two valves of female genital operculum not completely fused together longitudinally along their posterior one-fifth (these valves completely fused together in *Vaejovis*) ...". However, as pointed out by Soleglad (1973b: 351), when he defined the

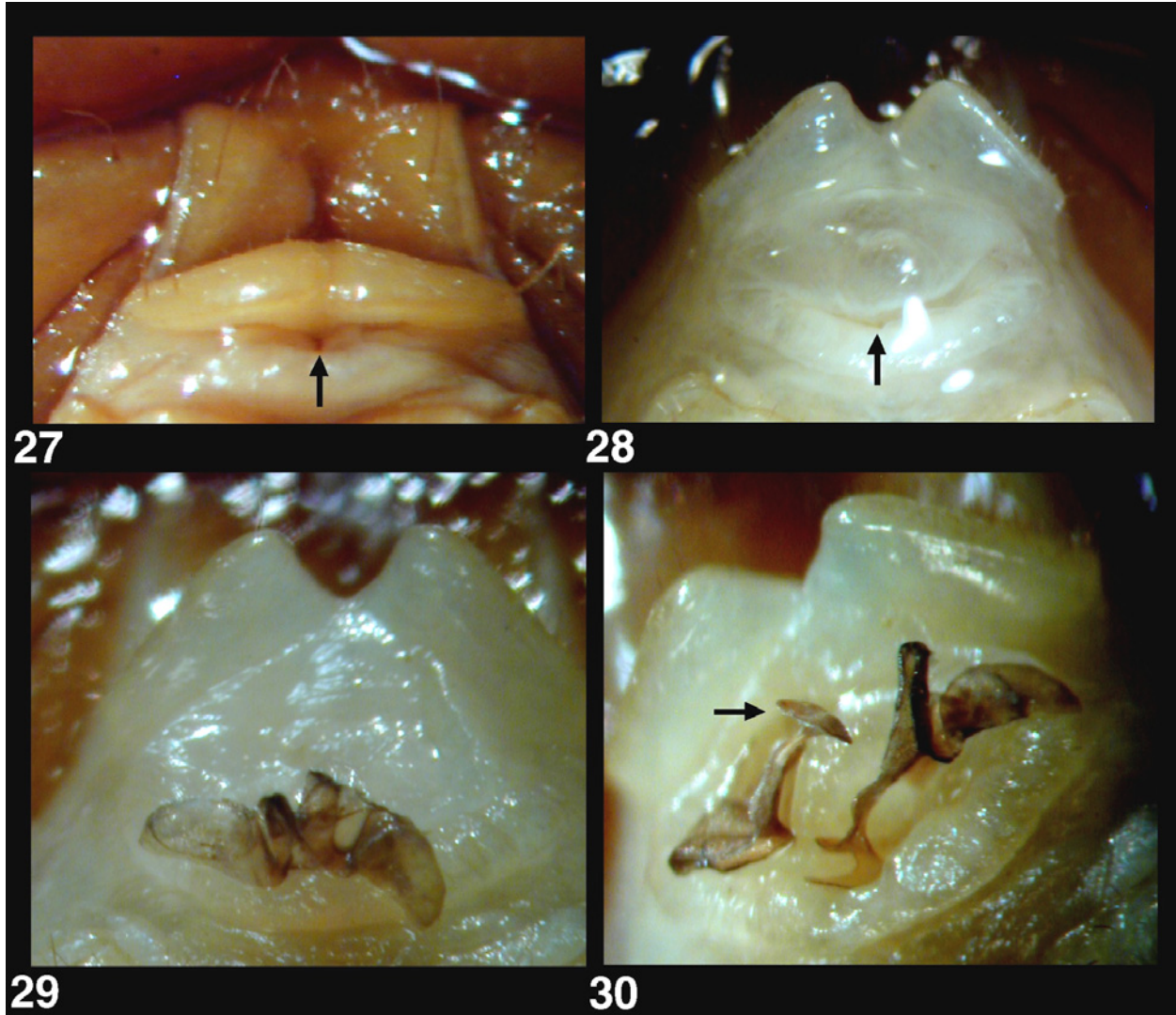
"mexicanus" group of *Vaejovis*, "... species of *Vaejovis* ... I have isolated a group of species that do not have a completely fused genital opercula on the female ... this group, the Mexicanus group ... Eusthenura, Wupatkiensis, and Punctipalpi groups of *Vaejovis* ... distinctly have completely fused genital opercula on the female ...". It is clear when Williams (1972) made statements about a fused genital operculum in *Vaejovis*, he was referring to these three groups of *Vaejovis* (defined by Williams). We might add here that in the chactid subfamily Uroctoninae, comprised of genera *Uroctonus* and *Anuroctonus*, the sclerites of the female genital operculum are separated *completely* to their anterior edge, a condition not present in any known vaejovid.

We have studied the female genital operculum in family Vaejoidea and can now classify this structure into two categories, one divided into two subcategories:

1) the genital operculum sclerites operate separately, their posterior one-half inner margins are separated, and the sclerites are connected to the mesosoma on the anterior half (44 to 55 % of sclerite) – subfamily Smeringurinae;

2) the genital operculum sclerites operate as a single unit and the sclerites are connected to the mesosoma on the anterior one-third (17 to 37 % of sclerite):

2a) the plates are fused for all or most of their inner margins, the fused plates are connected to the mesosoma at the extreme anterior of the operculum edge (17 to 27 % of sclerite) – subfamily Syntropinae;



Figures 27–30: Photographs of female genital operculi with sclerites raised from mesosoma exposing genital aperture and the internal structure beneath the plates. *Arrow* indicates aperture in Figs. 27–28. 27. *Syntropis aalbui*, holotype, Cataviña, Baja California, Mexico. Sclerites, raised 90°, are connected at the extreme posterior margin and show no medial separation. 29–30. *Pseudouroctonus williamsi*, Santa Ysabel Reserve, San Diego Co., California, USA. 28. Sclerites, raised 135°, are separated considerably at the posterior margin. 29. In this specimen (collected in a pit trap) post-insemination spermatophore mating plugs were found protruding from the genital aperture, only the plug bases are visible. 30. Mating plugs extracted from aperture, *arrow* points to smooth distal barb of one plug.

2b) the plates' posterior inner margins are separated 20 to 40 % – subfamily Vaejovinae.

In *Syntropis aalbui* these plates are connected (Fig. 27) and operate as a single unit, which is representative of members of subfamily Syntropinae (note that plates are positioned perpendicular to the mesosoma). Fig. 28 shows the posterior separation from an internal perspective in *Pseudouroctonus williamsi*, characteristic of subfamily Vaejovinae.

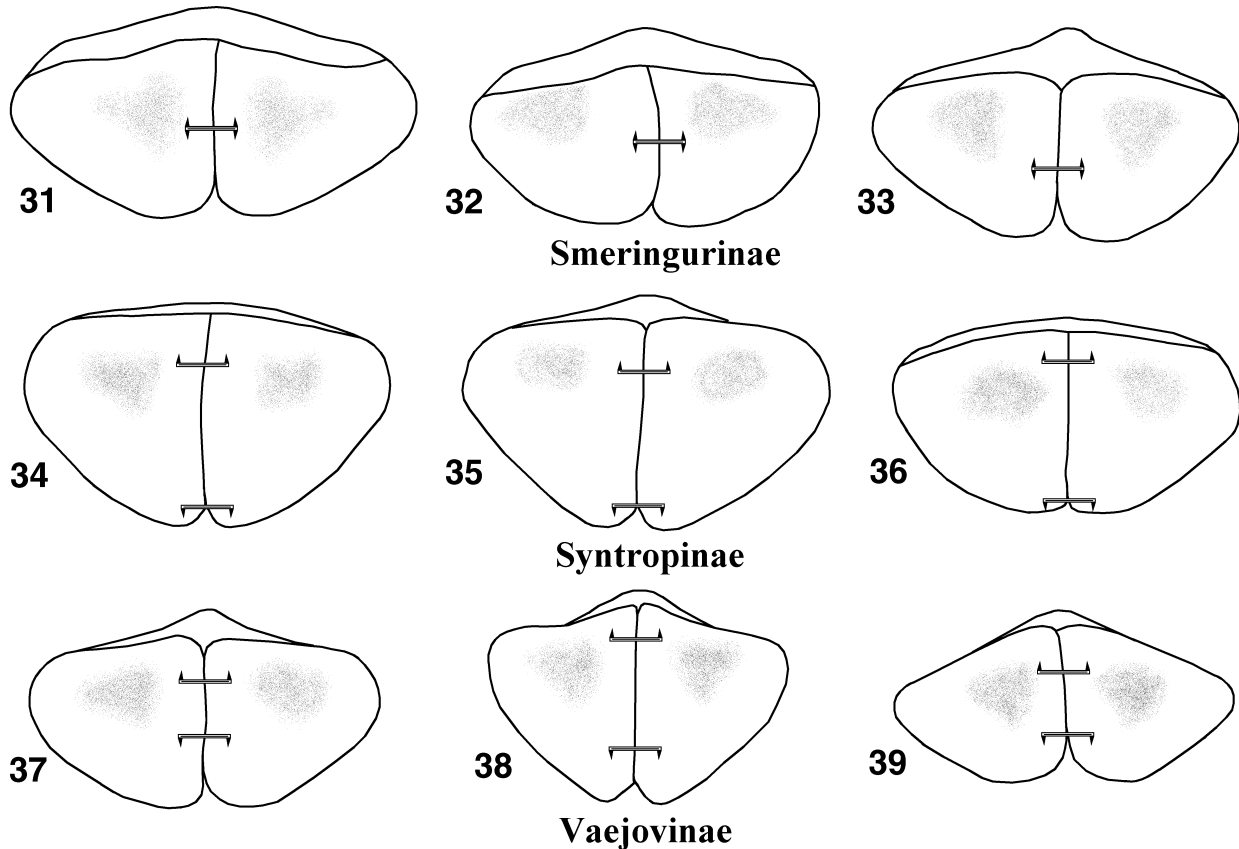
Table 1 details morphometrics of several species spanning all three vaejovid subfamilies. It is clear from these data that members of Smeringurinae have their plates connected roughly at the sclerite midpoint

whereas the plates are connected more anteriorly in the other two subfamilies. The posterior separation in Smeringurinae is more substantial than in Vaejovinae, roughly twice the distance.

In Figures 31–39 we illustrate several female genital opercula in family Vaejovidae. In these figures we observe that the membrane situated just anterior of the genital operculum is heavier, extending more vertically as well as further horizontally across the sclerites anterior edge in subfamily Smeringurinae. Also, at the extreme posterior inner margin, the sclerites are separated in all subfamilies, this is due to the rounded tips of the sclerites. This should not be confused with

	GOL	GOLI	SD	GOLI/GOL	SD/GOL
<i>Smeringurus aridus</i>	0.95	0.5	0.5	0.526	0.526
<i>Smeringurus mesaensis</i>	1.0	0.5	0.5	0.500	0.500
<i>Paruroctonus arnaudi</i>	1.2	0.6	0.6	0.500	0.500
<i>Paruroctonus arenicola nudipes</i>	0.85	0.45	0.45	0.529	0.529
<i>Paruroctonus gracilior</i>	1.15	0.6	0.6	0.522	0.522
<i>Paruroctonus silvestrii</i>	1.15	0.5	0.5	0.435	0.435
<i>Paruroctonus utahensis</i>	0.8	0.45	0.45	0.563	0.563
<i>Vejovoidus longiunguis</i>	0.85	0.4	0.4	0.471	0.471
<i>Paravaejovis pumilis</i>	0.6	0.325	0.325	0.542	0.542
Smeringurinae				0.435–0.563 (0.510)	0.435–0.563 (0.510)
<i>Gertschius crassicornis</i>	0.65	0.5	0.0	0.769	-
<i>Stahnkeus subtilimanus</i>	1.05	0.8	0.0	0.762	-
<i>Serradigitus wupatkiensis</i>	0.9	0.75	0.0	0.833	-
<i>Syntropis aalbui</i>	1.2	1.0	0.0	0.833	-
<i>Hoffmannius eusthenura</i>	1.0	0.8	0.0	0.800	-
<i>Hoffmannius spinigerus</i>	1.1	0.8	0.0	0.727	-
<i>Kochius kovariki</i>	1.2	0.875	0.0	0.729	-
<i>Kochius punctipalpi</i>	1.1	0.9	0.0	0.818	-
<i>Thorellius atrox</i>	1.2	0.9	0.0	0.750	-
<i>Thorellius cristimanus</i>	1.6	1.2	0.0	0.750	-
<i>Thorellius occidentalis</i>	1.05	0.85	0.0	0.810	-
Syntropinae				0.727–0.833 (0.780)	-
<i>Vaejovis carolinianus</i>	0.85	0.7	0.2	0.824	0.235
<i>Vaejovis curvidigitus</i>	0.9	0.7	0.275	0.778	0.306
<i>Vaejovis granulatus</i>	0.75	0.5	0.175	0.667	0.233
<i>Vaejovis mexicanus</i>	0.85	0.6	0.25	0.706	0.294
<i>Vaejovis vorhiesi</i>	0.6	0.4	0.175	0.667	0.292
<i>Vaejovis solegladi</i>	1.05	0.75	0.3	0.714	0.286
<i>Franckeus minckleyi</i>	0.9	0.6	0.2	0.667	0.222
<i>Franckeus platnicki</i>	0.475	0.3	0.15	0.632	0.316
<i>Pseudouroctonus minimus castaneus</i>	0.9	0.75	0.25	0.833	0.278
<i>Pseudouroctonus reddelli</i>	1.2	0.9	0.5	0.750	0.417
<i>Pseudouroctonus williamsi</i>	1.2	0.8	0.25	0.667	0.208
<i>Uroctonites huachuca</i>	0.8	0.6	0.2	0.750	0.250
Vaejovinae				0.632–0.833 (0.721)	0.208–0.417 (0.278)

Table 1: Measurements (mm) of female genital operculum of select species in family Vaejovidae. GOL = genital operculum vertical length (excluding anterior membrane); GOLI = internal to anterior membrane; SD = posterior separation length (excluding extreme posterior “tips” in subfamily Syntropinae).



Figures 31–39: Genital operculum of female of select species in family Vaejovidae. The *arrowed bar pointing upward* indicates position where sclerites are internally connected to the mesosoma; the *arrowed bar pointing downward* indicates anterior point of sclerite separation. Also note that in subfamily Smeringurinae the more developed membrane adjacent to the anterior edge of the sclerites. Subfamily **Smeringurinae**. **31.** *Smeringurus mesaensis*, Palo Verde Wash, ABDSP, California, USA. **32.** *Smeringurus aridus*, Palo Verde Wash, ABDSP, California, USA. **33.** *Paruroctonus silvestrii*, Chihuahua Road, ABDSP, California, USA. Subfamily **Syntropinae**. **34.** *Stahnkeus subtilimanus*, Borrego Springs, San Diego Co., California, USA. **35.** *Thorellius cristimanus*, Autlán, Jalisco, Mexico. **36.** *Kochius punctipalpi punctipalpi*, Cabo San Lucas, Baja California Sur, Mexico. Subfamily **Vaejovinae**. **37.** *Pseudouroctonus reddelli*, Comal Co., Texas, USA. **38.** *Pseudouroctonus minimus castaneus*, Vista, San Diego Co., California, USA. **39.** *Vaejovis mexicanus*, Aculco, Mexico, Mexico.

actual separation where the sclerites meet medially as exhibited in subfamilies Smeringurinae and Vaejovinae.

Hemispermatothore

Diagnostic value: Hemispermatothore structure is used to define subfamilies in Vaejovidae, tribes in subfamilies Smeringurinae and Syntropinae, and certain genera in subfamily Vaejovinae.

It is interesting to point out that the four parvorders established by Soleglad & Fet (2003b), which correspond to the four unique orthobothriotic types of Recent scorpions, are also defined by four unique hemispermatothore types. Until Stockwell (1989), Recent scorpion hemispermatothore types were divided into flagelliform for the buthoids (parvorder Buthida), and lamelliform for the other scorpion superfamilies

(parvorder Iurida) (see Sissom, 1990a: 76–77). Stockwell (1989: 202–203) presented a convincing argument for a third type of hemispermatothore, *fusiform*, for the genus *Chaerilus* (parvorder Chaerilida). This type was also illustrated by Lourenço (2002: figs. 19–21) for an unknown species of *Chaerilus*. Recently, Prendini et al. (2006: figs. 41–44) described and illustrated the unique hemispermatothore for the relict scorpion *Pseudochactas ovchinnikovi* Gromov, 1998 (parvorder Pseudochactida), a considerably tiny and unique looking structure.

The first hemispermatothores illustrated for family Vaejovidae (lamelliform type) were by Francke & Soleglad (1981; note that all analysis and illustrations of this structure were provided by Francke), for *Paruroctonus utahensis*, *Vaejovis spinigerus*, and *Pseudouroctonus apacheanus*. Interestingly, in the illustration of *V. spinigerus*, the toothed barb of the

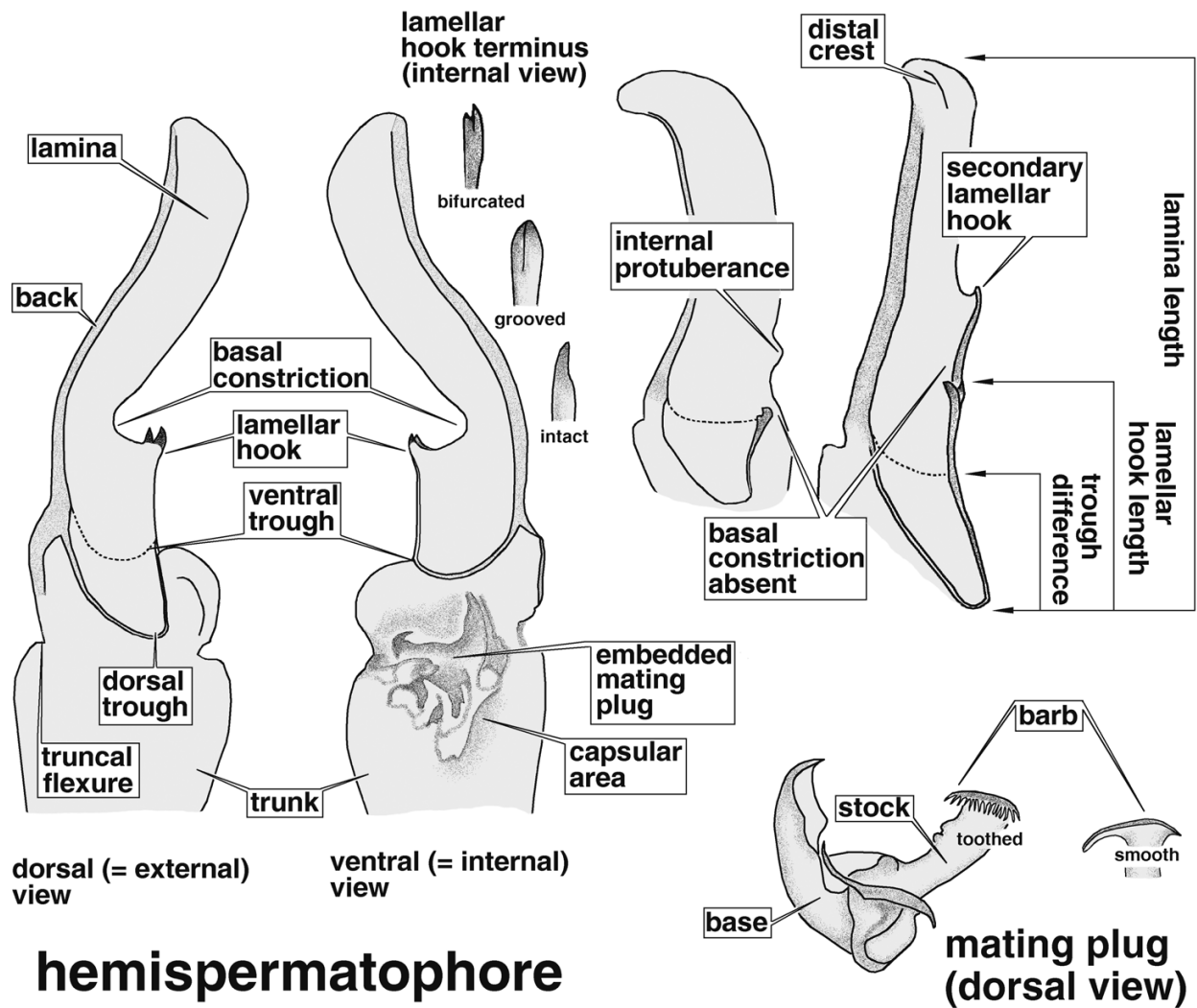
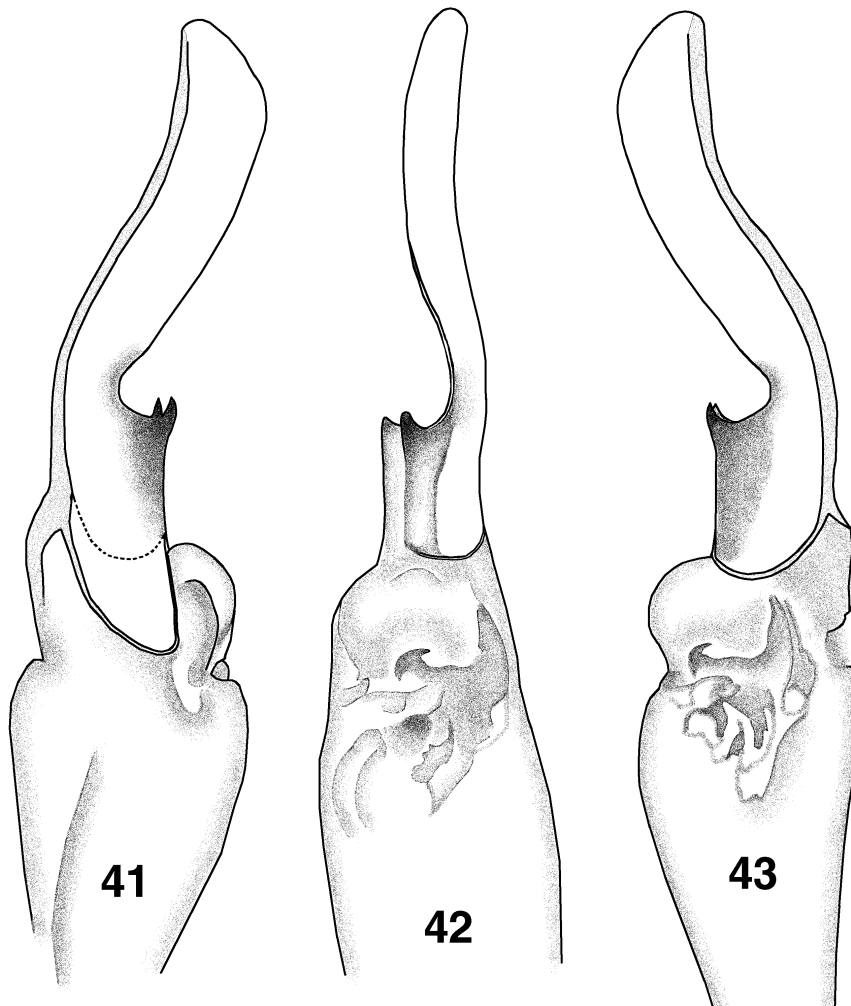


Figure 40: Hemispermatochore terminology and methods of measurement for family Vaejoidea (from a right hemispermatochore perspective). Dotted line depicts position of ventral trough from the dorsal side.

mating plug, characteristic of tribe Syntropini, is shown in part, though not discussed in the paper. The first serious attempts to describe the hemispermatochore of family Vaejoidea were by Sissom (see multiple references below), Stockwell (1989) in his unpublished PhD thesis, and Williams & Savary (1991). In his important work, Stockwell (1989) described and illustrated the hemispermatochores of important vaejoiid taxa *Syntropis macrura*, *Paravaeiovus pumilis*, *Paruroctonus utahensis*, and *Uroctonites montereus*. Of particular importance, Stockwell (1989) illustrated the mating (= sperm) plugs of *Syntropis* and *Paruroctonus*. From this point on, most authors illustrated the hemispermatochore, if available, for new species and/or redescrptions. In particular, W. D. Sissom made a considerable contribution in this area. Here is a list of all vaejoiid hemispermatochores illustrated to date: *Paruroctonus utahensis*, *Vaejovis spinigerus*, and

Pseudouroctonus apacheanus (Francke & Soleglad (1981); *Syntropis macrura*, *Paravaeiovus pumilis*, *Paruroctonus utahensis*, and *Uroctonites montereus* (Stockwell, 1989); *Vaejovis granulatus*, *V. maculosus*, *V. rossmani*, and *V. monticola* (Sissom, 1989a); *Thorrellius occidentalis* and *T. subcristatus* (Sissom, 1989b); *Vaejovis curvidigitus*, *V. intermedius*, *V. nigrescens*, *V. solegladi*, *V. mitchelli*, *V. nitidulus*, and *V. pococki* (Sissom, 1991); *Stahnkeus allredi*, *S. polisi*, *Serradigitus yaqui*, and *Gertschius agilis* (Sissom & Stockwell, 1991); *Uroctonites montereus*, *U. huachuca*, *U. giulianii*, *Pseudouroctonus lindsayi*, *P. minimus minimus*, *P. rufulus*, *P. andreas*, *P. cazieri*, *P. bogerti*, *P. angelenus*, *P. iviei*, and *P. glimpei* (Williams & Savary, 1991); *Wernerius spicatus* (Sissom, 1993); *V. mauryi* (Capes, 2001); *V. pequeno* (Hendrixson, 2001); *V. chisos* (Jarvis et al., 2004); *V. norteno* (Sissom & González Santillán, 2004); *V. sprousei* (González Santillán et al.,



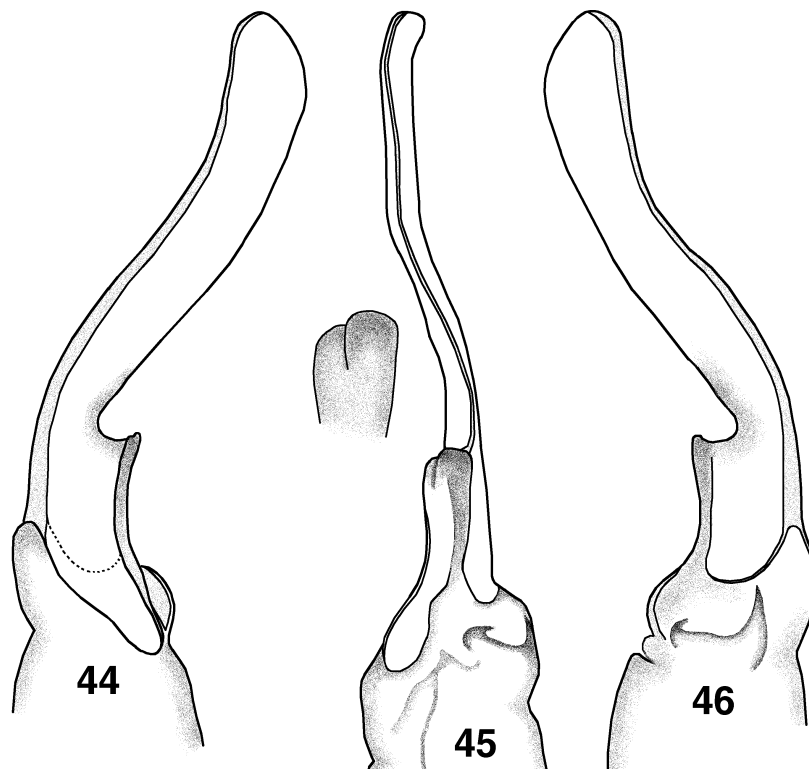
Figures 41–43: Right hemispermaphore of *Thorellius cristimanus*, Autlán, Jalisco, Mexico. **41.** Dorsal view; dotted line indicates position of ventral trough, see Fig. 43. **42.** Internoventral view showing partial view of embedded mating plug. **43.** Ventral view showing embedded mating plug partially visible on distal aspect, barb on left pointing inwards into capsular area. See Fig. 75 for extracted mating plug, dorsal view (barb pointing outward), showing toothed (16 teeth) distal barb.

2004); *Thorellius cisnerosi* (Ponce Saavedra & Sissom, 2004); *Vaejovis kuarapu* (Francke & Ponce Saavedra, 2005); *Hoffmannius glabrimanus* (Sissom & Hendrixson, 2005); *Pseudouroctonus sprousei* (Francke & Savary, 2006); *Kochius atenango* (Francke & González Santillán, 2007); and *Gertschius crassicornis* (Graham & Soleglad, 2007). In this paper we illustrate for the first time the hemispermaphore of 23 vaejovid species including 13 extracted mating plugs.

Hemispermaphore structure. The hemispermaphore of family Vaejovidae, classified as lamelliform, is moderately sclerotized in the distal aspects of the trunk and lamina. The lamina is elongated, blade-like, with a sclerotized back (located on the external edge of a right hemispermaphore, as illustrated in Fig. 40), whereas its internal edge is quite thin and delicate. The base of the lamina is supported by two concaved “troughs”, termed the dorsal and ventral troughs. The edges of these troughs are formed by the delicate darkened edges from the extensions of the sclerotized lamina back. The lamellar hook located on the internal edge is an

extension of the dorsal trough, and sometimes, ventral trough, as they extend distally curving towards the lamina tip. The small spacing between these trough extensions on the internal edge sometimes creates a groove or even a bifurcation at the extreme tip of the lamellar hook. If a basal constriction is present on the lamina’s internal edge, the lamellar hook projects outward conspicuously. Generally the dorsal trough is located somewhat proximal to the ventral trough which is situated just above the capsular area on the ventral surface. The capsular area is where the paraxial organ attaches, and the sperm duct and mating plug are located.

In this analysis, we consider the following hemispermaphore structures of taxonomic importance (see Fig. 40 for an idealized view of the hemispermaphore and mating plug defining the terminology and methods of measurement used in this study): the presence or absence of a basal constriction and, if present, its degree of development; the development of the lamellar hook, which can be formed



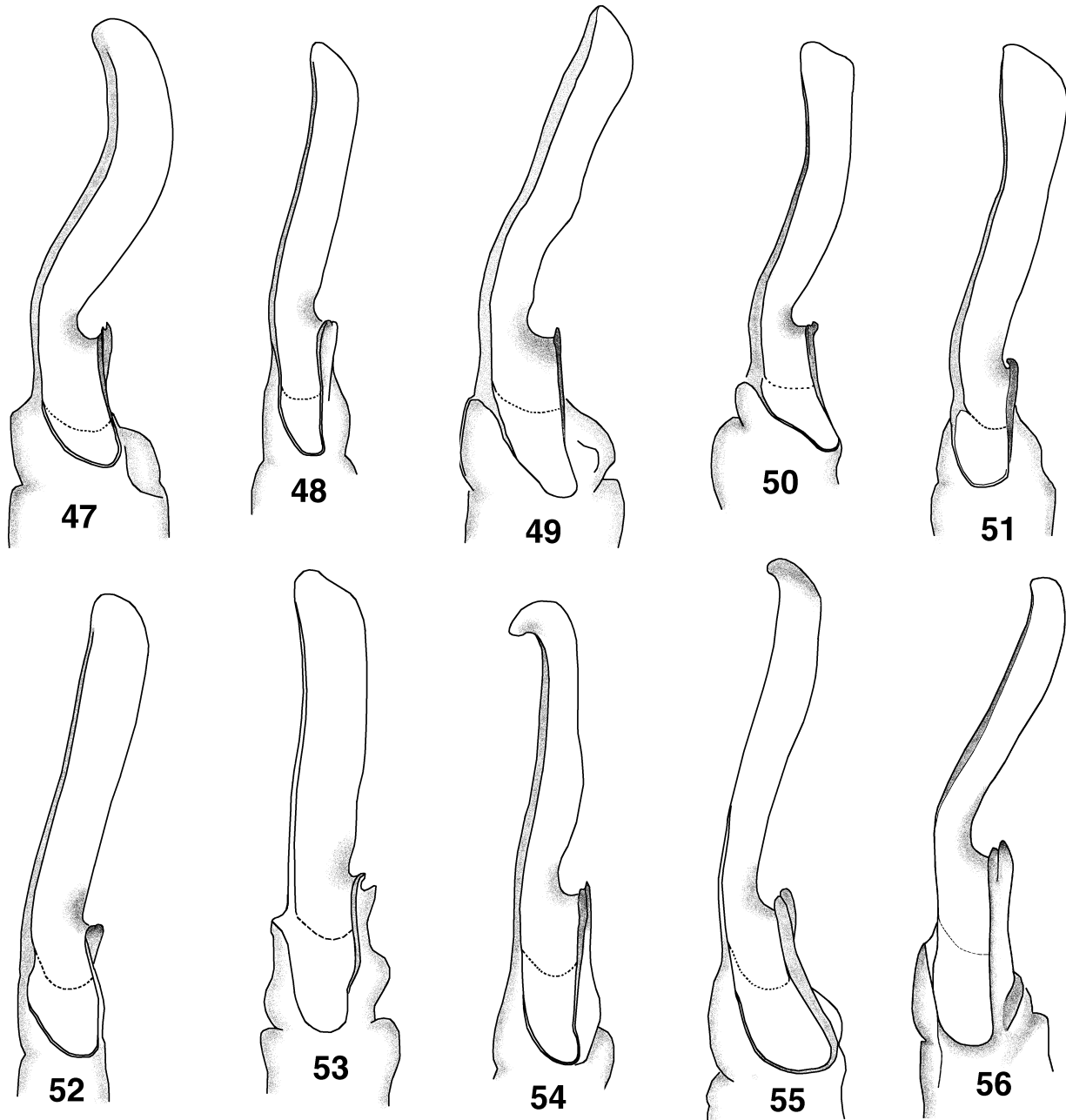
Figures 44–46: Right hemispermatophore of *Kochius punctipalpi punctipalpi*, Los Arripes, Baja California Sur, Mexico. **44.** Dorsal view; dotted line indicates position of ventral trough, see Fig. 46. **45.** Internal view showing partial view of embedded mating plug and close-up of bifurcated lamellar hook. **46.** Ventral view showing embedded mating plug partially visible on distal aspect, barb on left pointing inwards into capsular area. See Fig. 76 for extracted mating plug, dorsal view (barb pointing outward), showing toothed (12 teeth) distal barb.

by both troughs or just the dorsal trough; its length and degree of sclerotization and terminus arrangement (intact, grooved or bifurcated); the position of the lamellar hook with respect to the ventral trough; the relative ratio of the lamellar hook length compared to the lamina length; the presence or absence of a secondary lamellar hook; the presence or absence of a internal protuberance on the lamina base; and the composition of the mating plug barb, which can be smooth or toothed. Of secondary importance is the shape of the lamina terminus: blunted clip-like, narrow and curved, or exhibiting a slight groove (i.e., a distal crest). As to the orientation of the hemispermatophore, we opted to use the terms dorsal and ventral as opposed to external and internal.

Syntropinae. Figures 41–43, 44–46, 47–56 illustrate several hemispermatophores of seven genera in subfamily Syntropinae (see Sissom, 1993, figs. 12–14, for an example of the *Wernerius* hemispermatophore). Figures 41–43 and 44–46 illustrate three views of a hemispermatophore showing some detail of the capsular area for species *Thorellius cristimanus* and *Kochius punctipalpi*, respectively. In these figures we can see that the formation of the lamellar hook is derived from both the dorsal and ventral troughs, characteristic of this subfamily. All of these hemispermatophores have an enlarged lamellar hook whose distal tip is exaggerated

by a conspicuous basal constriction of the lamina. In most cases, the distal tip of the lamellar hook is at least partially bifurcated if not completely separated forming two hooks (Figs. 41–42, 45, 47, 50, 53–56). The ratio constructed from the lamellar hook length / lamella length (using the dorsal trough as the proximal base of both measurements) ranges from 0.292 – 0.450 (0.366), based on 21 species (see Table 2). Thus we can see that it is well developed exhibiting considerable length, roughly one-third of the lamina length. Also of importance is that the distal tip is considerably distal of the ventral trough, as indicated in Table 2, where the trough difference as compared to the hook length is 0.241–0.508 (0.426).

Comparing hemispermatophores of subtribe Thorelliina (represented by *Thorellius cristimanus*, *T. intrepidus*, *Kochius punctipalpi*, *K. hirsuticauda*, and *K. cazieri*; Figs. 41–43, 44–46, 47–49) with those of subtribe Syntropina (represented by *Hoffmannius eusthenura*, *H. waeringi*, *H. puritanus*, and *Syntropis macrura*; Figs. 50–53), we see little difference in the shape of the lamina terminus, and a general consistency in the strong development of the lamellar hook. For tribe Stahnkeini (represented by *Serradigitus wupatkiensis*, *Stahnkeus subtilimanus*, and *Gertschius crassicornus*; Figs. 54–56), the lamina appears to be slightly thinner with the distal tip sometimes curving externally, but



Figures 47–56: Right hemispermaphore, dorsal view, of genera of subfamily Syntropinae showing well developed lamellar hook. Dotted line indicates position of ventral trough. Tribe **Syntropini**: **47.** *Kochius hirsuticauda*, Indian Gorge Canyon, ABDSP, California, USA. **48.** *Kochius cazieri*, Cuatro Ciénegas, Coahuila, Mexico. **49.** *Thorellius intrepidus*, Mexico. **50.** *Hoffmannius eusthenura*, Cabo San Lucas, Baja California Sur, Mexico. **51.** *Hoffmannius waeringi*, Vallecito Creek, Carrizo Badlands, ABDSP, California, USA. **52.** *Hoffmannius puritanus*, Jasper Trail, ABDSP, California, USA. **53.** *Syntropis macrura* (after Stockwell, 1989: fig. 218, in part). Tribe **Stahnkeini**: **54.** *Serradigitus wupatkiensis*, Wupatki Ruins, Wupatki National Monument, Arizona, USA. **55.** *Stahnkeus subtilimanus*, Vallecito Creek, Carrizo Badlands, ABDSP, California, USA. **56.** *Gertschius crassicornus*, paratype, Navojoa, Sonora, Mexico (after Graham & Soleglad, 2007: fig. 10, in part).

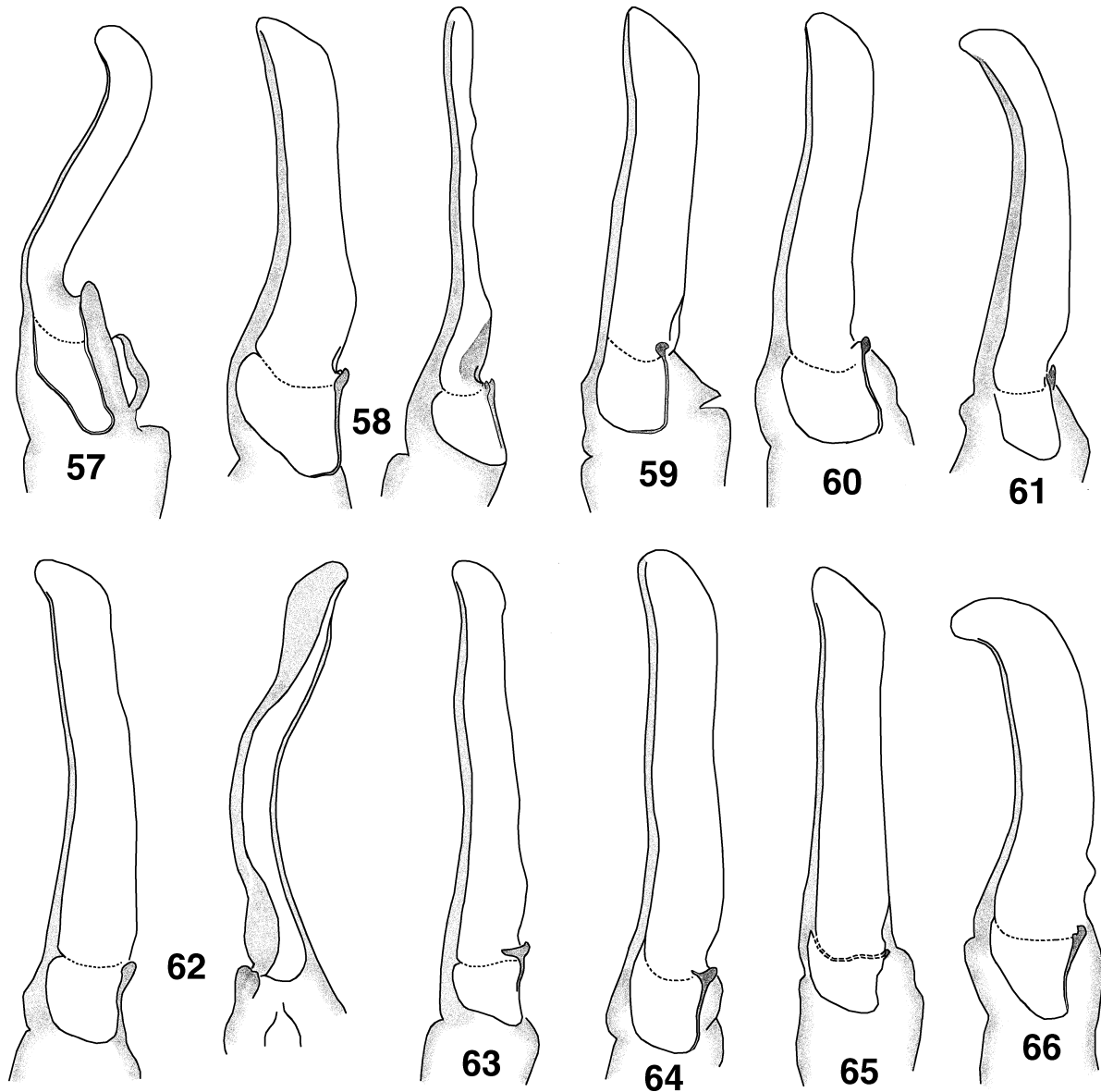
generally the lamellar hook development and strong basal constriction are consistent with those in sister tribe Syntropini.

Sissom (1991: 26–27, 1993: 68) was the first to report this well developed lamellar hook (*broad flange* in his terminology) where he correctly attributed it to

Serradigitus (now tribe Stahnkeini) and the three *Vaejovis* groups now comprising subfamily Syntropinae (as illustrated in Figs 41–43, 44–46, 47–56). Sissom (1991) contrasted this hemispermaphore with that of seven species in the “nigrescens” group of *Vaejovis*. Although the lamellar hook/lamella ratio is smaller in

	Hook L / Lamella L	Trough D / Hook L	Basal Constriction	Lamellar Hook Terminus	Secondary Lamellar Hook	Mating Plug Barb
<i>Gertschius</i>	0.340–0.450 (0.395) [2]	0.406–0.434 (0.420) [2]	Strong	Bifurcated	Absent	Smooth
<i>Serradigitus</i>	0.385 [1]	0.468 [1]	Strong	Bifurcated	Absent	Smooth
<i>Stahnkeus</i>	0.360–0.397 (0.381) [3]	0.462–0.474 (0.470) [3]	Strong	Bifurcated	Absent	Smooth
<i>Wernerius</i>	0.433 [1]	Not available	Strong	Bifurcated	Absent	Smooth
<i>Stahnkeini</i>	0.340–0.450 (0.393) [7]	0.406–0.474 (0.453) [6]	Strong	Bifurcated	Absent	Smooth
<i>Kochius</i>	0.321–0.400 (0.348) [4]	0.267–0.412 (0.355) [3]	Strong	Bifurcated	Absent	Toothed
<i>Hoffmannius</i>	0.292–0.409 (0.331) [4]	0.452–0.518 (0.490) [3]	Strong	Bifurcated	Absent	Toothed
<i>Syntropis</i>	0.345 [1]	0.580 [1]	Strong	Bifurcated	Absent	Toothed
<i>Thorellius</i>	0.323–0.441 (0.376) [5]	0.241–0.505 (0.355) [4]	Strong	Bifurcated	Absent	Toothed
<i>Syntropini</i>	0.292–0.441 (0.353) [14]	0.241–0.580 (0.412) [11]	Strong	Bifurcated	Absent	Toothed
Syntropinae	0.292–0.450 (0.366) [21]	0.241–0.508 (0.426) [17]	Strong	Bifurcated	Absent	Variable
<i>Paravaejovius</i>	0.366 [1]	0.616 [1]	Strong	Whole	Absent	Toothed
<i>Paravaejovini</i>	0.366 [1]	0.616 [1]	Strong	Whole	Absent	Toothed
<i>Paruroctonus</i>	0.210–0.242 (0.219) [4]	0.680–0.782 (0.748) [4]	Absent	Whole	Absent	Smooth
<i>Smeringurus</i>	0.138–0.169 (0.162) [4]	0.857–1.000 (0.872) [4]	Absent	Whole	Absent	?
<i>Vejovoidus</i>	0.221 [1]	0.833 [1]	Absent	Whole	Absent	?
<i>Smeringurini</i>	0.138–0.242 (0.194) [9]	0.680–1.000 (0.813) [9]	Absent	Whole	Absent	Smooth (?)
Smeringurinae	Variable	0.616–1.000 (0.793) [10]	Variable	Whole	Absent	Variable
<i>Franckeus</i>	0.237 [1]	Not available	Absent	Bifurcated	Absent	Smooth
<i>Pseudouroctonus</i>	0.269–0.527 (0.422) [12]	0.360–0.603 (0.474) [12]	Absent	Bifurcated	Present, in part *	Smooth
<i>Uroctonites</i>	0.038–0.076 (0.057) [3]	Not applicable	Medium	Whole	Absent	Non-sclerotized ***
<i>Vaejovius “mexicanus”</i>	0.121–0.458 (0.242) [9]	0.375–0.769 (0.576) [6]	Variable	Variable	In part (?) **	Variable
<i>Vaejovius “nigrescens”</i>	0.200–0.314 (0.257) [10]	0.500–0.654 (0.577) [2]	Absent	Bifurcated	Absent	Smooth
Vaejovinae	Variable	Variable	Variable	Variable	Present, in part	Smooth

Table 2: Hemispermatothore characteristics and morphometrics for family Vaejovidae based on, in part, 66 species. See Fig. 40 for terminology and method of measurement. Hook L = lamellar hook length (distal tip to dorsal trough), Lamella L = lamella length (distal tip to dorsal trough), Trough D = vertical distance between dorsal and ventral troughs, P = present, A = absent, n = number of samples. Based on specimens examined and illustrations from literature. * Present in species *P. williamsi*, *P. angelinus*, *P. bogerti*, *P. tyvei*, and *P. glimpei*. ** Some species (e.g., *Vaejovius chisos*, Jarvis et al., 2004: figs. 1–2) exhibit a non-sclerotized cleft on the internal edge of the lamellae. This cleft is probably not homologous to the secondary lamellar hook seen in some *Pseudouroctonus* species. *** After Williams & Savary (1991).

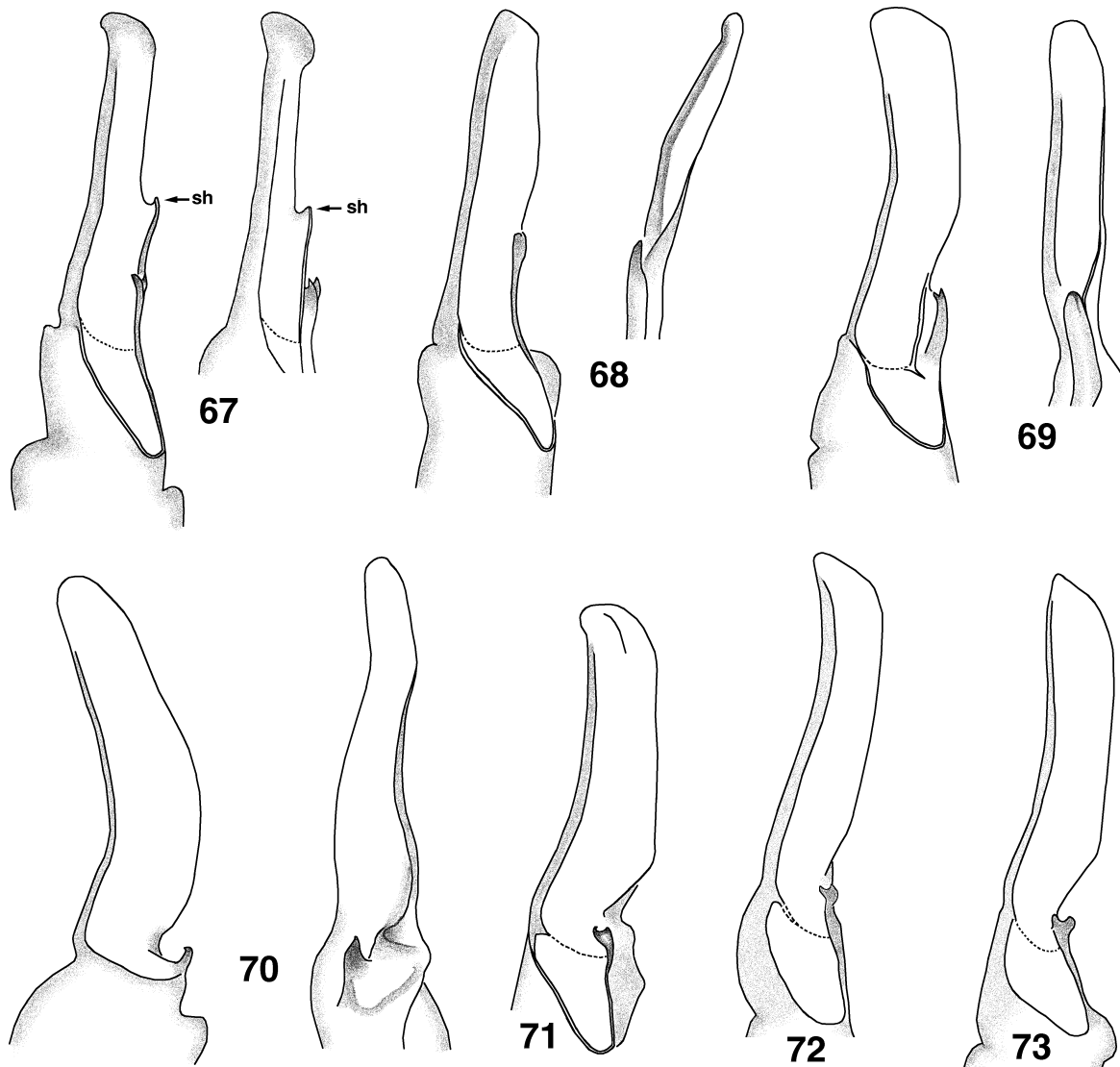


Figures 57–66: Right hemispermaphore, dorsal view, of genera of subfamily Smeringurinae. Dotted line indicates position of ventral trough. Tribe **Paravaejovini:** 57. *Paravaejovis pumilis*, Ciudad Constitución, Baja California Sur, Mexico. Tribe **Smeringurini:** 58. *Paruroctonus boreus*, Mercury, Nevada, USA, dorsal and dorsoexternal views. 59. *Paruroctonus gracilior*, Lajitas, Brewster Co., Texas, USA. 60. *Paruroctonus silvestrii*, Chihuahua Road, ABDSP, California, USA. 61. *Paruroctonus utahensis*, Bluff, Utah, USA. 62. *Smeringurus mesaensis*, Borrego Springs, California, USA, dorsal and internoventral views. 63. *Smeringurus aridus*, Palo Verde Wash, ABDSP, California, USA. 64. *Smeringurus vachoni immanis*, 1000 Palms, California, USA. 65. *Smeringurus grandis*, Oakies Landing, Baja California, Mexico. 66. *Vejovoidus longiunguis*, Las Bombas, Baja California Sur, Mexico.

the “nigrescens” group (0.200–0.314 (0.257) [10], see Table 2), it is our opinion that the basal constriction contributes considerably to the exaggerated lamellar hook seen in Syntropinae, whereas in the “nigrescens” group (see our Fig. 73 of *Vaejovis janssi*; Sissom, 1991: figs. 71–84) this constriction is essentially absent. The vertical distance between the dorsal and ventral troughs

is also significant in Syntropinae, roughly 40 % of the lamellar hook length.

This well developed lamellar hook with a conspicuous basal constriction is also illustrated by other authors for species *Thorellius occidentalis* and *T. subcristatus* (Sissom, 1989b: figs. 1–4), *Kochius atenango* (Francke & González Santillán, 2007: fig. 1), and



Figures 67–73: Right hemispermatophore of genera of subfamily Vaejovinae. Dotted line indicates position of ventral trough. **67.** *Pseudouroctonus williamsi*, Santa Ysabel Reserve, San Diego Co., California, USA, dorsal and dorsoexternal views. Note secondary lamellar hook (sh) (indicated by arrow). **68.** *Pseudouroctonus minimus castaneus*, Vista, San Diego Co., California, USA, dorsal and internal views. **69.** *Pseudouroctonus reddelli*, Gem Cave, Comal Co., Texas, USA, dorsal and internal views. **70.** *Uroctonites huachuca*, Huachuca Mountains, Cochise Co., Arizona, USA, dorsal and internal views. **71.** *Vaejovis lapidicola*, Williams, Coconino Co., Arizona, USA, dorsal view. **72.** *Vaejovis carolinianus*, Athens, Georgia, USA. **73.** *Vaejovis janssi*, Isla Socorro, Mexico.

Hoffmannius glabrimanus (Sissom & Hendrixson, 2005: fig. 9).

Smeringurinae. The hemispermatophore structure is quite interesting in subfamily Smeringurinae. In the tribe Paravaejovini (Fig. 57), lamellar hook is well developed, exaggerated by a conspicuous basal constriction, and its distal tip is considerably distal of the ventral trough, essentially identical to the hemispermatophore seen in Syntropinae. In stark contrast, tribe Smeringurini exhibits a very reduced lamellar hook whose distal tip is essentially in line with the ventral trough exhibiting roughly only 20 % of the lamina length (see Table 2). A basal constriction is essentially

absent in this tribe. The hook itself is quite small and weakly sclerotized and is formed by the dorsal trough. The reduction in the lamellar hook length is further emphasized when the hook length is compared to the dorsal and ventral trough distance, roughly 80 % of its length. Figures 58–65 show that the hemispermatophores are very similar across the two genera: *Paruroctonus*, as illustrated in species *P. boreus*, *P. gracilior*, *P. silvestrii*, and *P. utahensis*, and *Smeringurus*, species *S. mesaensis*, *S. aridus*, *S. vachoni immanis*, and *S. grandis*. The lamina itself is straight, with its distal aspect somewhat blunted. In the genus *Vejovoidus* (Fig. 66), the lamina is a little heavier,

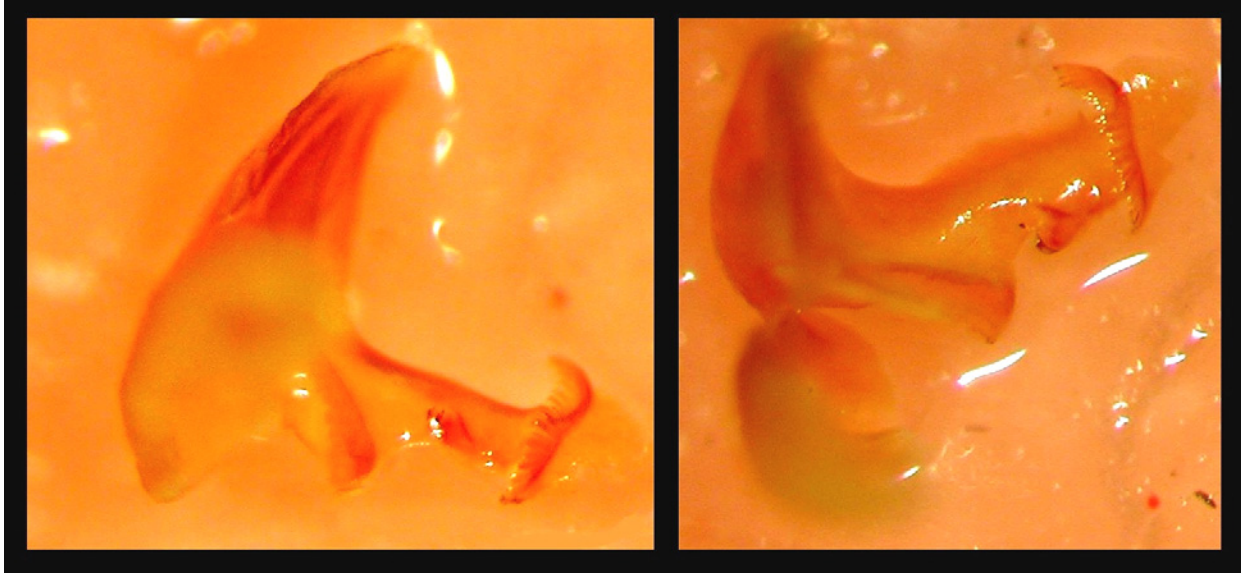


Figure 74: Photographs of hemispermatophore mating plug of *Thorellius cristimanus*, Autlán, Jalisco, Mexico. Distal barb is seen on right side of images, showing delicate curved teeth which face inwards when embedded in the hemispermatophore capsular area, the ventral side.

shorter, and distally curved. In addition, on the internal base of the lamina there is a slight protuberance (this was observed in two specimens), although its lamellar hook is marginally developed and is adjacent to the ventral trough typical of the tribe.

Other hemispermatophores of subfamily Smeringurinae were illustrated by Francke & Soleglad (1981: figs. 50–52) for *Paruroctonus utahensis*, and Stockwell (1989: figs. 220–221, 222–223) for *Paravaejovis pumilis* and *P. utahensis*.

Vaejovinae. There is a lot of diversity in the construction of the hemispermatophore in subfamily Vaejovinae. In our Figures 67–73, which illustrate species in three vaejovine genera and both groups of *Vaejovis*, we observe three basic types:

- (1) a distally placed highly reduced lamellar hook formed from the dorsal trough only, usually moderately bifurcated, that barely extends from the lamina internal edge as emphasized by an essentially obsolete basal constriction, genus *Pseudouroctonus* (Figs. 67–69);
- (2) a very short, proximally positioned lamellar hook, non-bifurcated, emphasized by a mediumly developed basal constriction in genus *Uroctonites* (Fig. 70); and
- (3) a medium length lamellar hook, usually bifurcated, with a weak basal constriction, in genera *Franckeus* and *Vaejovis* (Figs. 71–73), exhibited in both the “mexicanus” and “nigrescens” groups.

Sissom (see the many references above) illustrated the hemispermatophore of many species of genus *Vaejovis*

and *Franckeus*. Most of these illustrations are consistent with those illustrated in our Figures 71–73, representing species *V. lapidicola*, *V. carolinianus* (both members of “mexicanus” group), and *V. janssi* (member of “nigrescens” group). Comparison of morphometrics (Table 2) shows that the length of lamellar hook in *Vaejovis* and *Franckeus* is roughly 25 % of the lamina length (based on 20 samples). This length is intermediate between the very short hook exhibited in tribe Smeringurini (19 % of lamina length) and the long lamellar hook of subfamily Syntropinae (37 % of lamina length). This intermediate position shown by *Vaejovis* and *Franckeus* is also supported by the percentage of the trough difference when divided by the lamellar hook length, 58 % as compared to 81 % in tribe Smeringurini and 43 % in subfamily Syntropinae.

Williams & Savary (1991) contrasted the hemispermatophores of their new genus *Uroctonites* with, at that time, the “minimum” group of *Vaejovis* (now placed in genus *Pseudouroctonus*). They made the important observation that the lamellar hook was situated more basally in *Uroctonites* than in *Pseudouroctonus* species, whose hook is positioned considerably distally on the lamella, roughly at midpoint (0.269–0.527 (0.422) [12], see Table 2). Common to both genera, however, is a weakly developed lamellar hook, construction similar to that seen in Smeringurini, and the lack of a conspicuous basal constriction. Our Figure 67 of *Pseudouroctonus williamsi* demonstrates that a *secondary lamellar hook* is present, situated above the major lamellar hook, which is bifurcated, and is formed by the ventral trough. This secondary hook is also visible in the illustrations provided by Williams & Savary (1991: figs. 26–29) for

Pseudouroctonus bogerti, *P. angeleus*, *P. iviei*, and *P. glimmei*. The secondary hook may be of taxonomic importance since it is clear that some of these species are closely related, especially *P. williamsi*, *P. bogerti*, and *P. angeleus*, which also share other unique characters (e.g., neobothriotaxy of the chela, see Fig. 13).

Other, less defined tendencies in the hemispermaphore morphology are apparent in the shape and width of the lamina in subfamily Syntropinae: the lamella is quite curved in genera *Kochius* and *Thorellius* with a rounded distal tip (Figs. 41–43, 44–46, 47–49), in contrast to *Hoffmannius* with a more straight lamina and a wider blunted distal tip (Figs. 50–52); the lamella appears thinner with a sharper tip in tribe Stahnkeini (Figs. 54–55). Species of *Pseudouroctonus* also exhibit a blunted distal tip (Figs. 67–69). However, there are exceptions to many of these trends. Many more species need to be investigated to see if these more localized characteristics are consistent and therefore diagnostic.

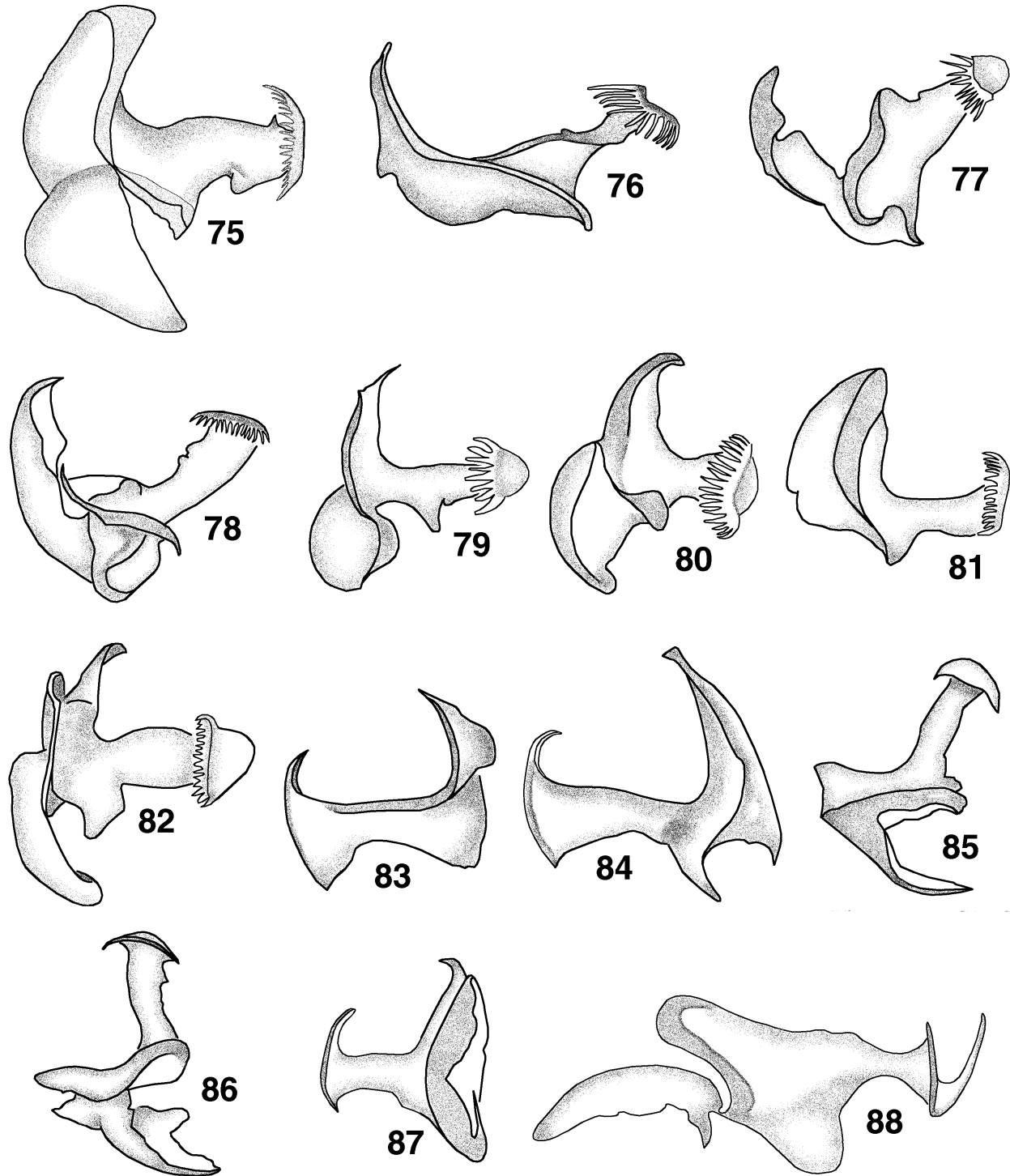
Mating plug composition. Stockwell (1989) first illustrated the mating (= sperm) plug of several species of scorpions, including *Syntropis macrura* (replicated in this paper, Fig. 82). Interestingly, Stockwell's (1989: fig. 228) illustration of *Syntropis* shows an extracted mating plug thus exposing the somewhat complicated base of the plug. Similar illustrations of extracted mating plugs were published for *Stahnkeus* and *Serradigitus* (Sissom & Stockwell, 1991), *Wernerius spicatus* (Sissom, 1993), *Vaejovis pequeno* (Hendrixson, 2001), and *Pseudouroctonus sprousei* (Francke & Savary, 2006). Figures 74, 75–88 illustrate several extracted mating plugs across all three subfamilies, although most are from Syntropinae genera where they are relatively large and sclerotized. In Figs. 29–30 we show post-insemination mating plugs as they protrude from the genital aperture of a female *Pseudouroctonus williamsi*.

This tiny structure has a complex arrangement of partially sclerotized components: the *base*, *stock*, and *barb* (see Fig. 40). The base of the mating plug is quite complex being composed of irregularly attached asymmetric highly convex/concave petal-like thin plates. The appearance of this complicated base is completely different depending on the angle and/or perspective viewed. For example, in Fig. 74, two slightly different perspectives of the mating plug of *Thorellius cristimanus* are shown. Note the significant differences in the base in these two views. Emanating from the base is a somewhat thick asymmetric stock, with or without smaller protuberances present. The stock, which is roughly as long as the base is wide, terminates into the barb. The barb is a thin component which is situated perpendicular to the stock and is asymmetric, folding lengthwise over to one side. Its length is roughly twice that of the thickness of the stock. With an embedded mating plug, the sharp edge of the barb faces into the hemispermaphore capsular area when viewed from the

ventral aspect (see Figs. 42–43 and 45–46 where the mating plug is embedded in the hemispermaphore). The sharp edge of the barb can be smooth or it can be lined with long delicate curved “teeth”. The toothed condition is sometimes referred to as the “crown”. The number of “teeth” on the barb varies, probably based on the species, but this has not been established. In our extracted mating plugs (Figs. 74, 75–82) that exhibited “teeth”, we counted 10–16 teeth. This toothed barb itself is similar in appearance to the terminus of the ental channel found in the euscorpoid genera *Euscorpium* and *Megacormus* (see Soleglad & Sissom, 2001: figs. 119–122; Fet & Soleglad, 2002: 37–38, figs. 65–67). This structure in *Euscorpium flavicaudis*, with its “crown” lacking “teeth”, is similar to the smooth mating plug barb. However, the ental channel is a substantial structure that emanates from the hemispermaphore base, thus much larger and located in a different area than the much smaller mating plug of the vaejovids. Whether these two structures are homologous between the two families remains to be seen.

As of now, the barb is the only taxonomically important component of the mating plug in Vaejovidae: is it either *smooth* or *toothed*. This distinction has proven to be an excellent diagnostic character for subfamily Syntropinae, where tribe Stahnkeini has a smooth barb (Figs. 83–84) and tribe Syntropini, a “toothed” barb (Figs. 75–82). So far, based on the species examined and reported in literature, there are no exceptions. The “toothed” barb appears to be derived for tribe Syntropini since it has only been reported in one other vaejovid genus, *Paravaejovis*, a member of Smeringurinae (Stockwell, 1989; see note below). We suspect that the base of the mating plug, with its complex structure, may also provide diagnostic characters. Figures 83–84 show that the base appears to be less complicated in Stahnkeini than it is in Syntropini, and highly complicated in vaejovine genus *Pseudouroctonus* (or at least for *P. williamsi*, Fig. 88) but this must be carefully examined; exact images of the mating plug base must be taken from several perspectives in order to adequately quantify its structure.

In subfamily Smeringurinae, the dichotomy of “toothed” versus “smooth” is also present. Stockwell (1989: fig. 221) shows that the mating plug barb of *Paravaejovis pumilis* is toothed. In tribe Smeringurini, it appears that the barb is smooth based on Stockwell's cladistic analysis and our preliminary results. Our preliminary investigations (Soleglad & Fet, in progress) have verified that genus *Paruroctonus* has a smooth mating plug barb; see Figs. 85–86 for *Paruroctonus boreus* and *P. silvestrii* and Stockwell's (1989: fig. 229), illustration of *P. utahensis*. However, many more species need to be investigated, and, as Stockwell (1989) states, the mating plug can be “greatly reduced, or absent,” making this determination all the more difficult.



Figures 75–88: Representative hemispermatochore mating plugs of subfamilies Syntropinae, Smeringurinae, and Vaejovinae. Tribe **Syntropini**, note *toothed* terminus. **75.** *Thorellius cristimanus*, Autlán, Jalisco, Mexico. **76.** *Kochius punctipalpi punctipalpi*, Los Arípes, Baja California Sur, Mexico. **77.** *Kochius hirsuticauda*, Indian Gorge Canyon, ABDSP, California, USA. **78.** *Kochius cazieri*, Cuatro Ciénegas, Coahuila, Mexico. **79.** *Hoffmannius eusthenura*, Cabo San Lucas, Baja California Sur, Mexico. **80.** *Hoffmannius puritanus*, Jasper Trail, ABDSP, California, USA. **81.** *Hoffmannius confusus*, Mesa, Arizona, USA. **82.** *Syntropis macrura* (after Stockwell, 1989: fig. 228, in part). Tribe **Stahnkeini**, note *smooth* terminus. **83.** *Serradigitus wupatkiensis*, ventral view, Wupatki Ruins, Wupatki National Monument, Arizona, USA. **84.** *Stahnkeus subtilimanus*, ventral view, Vallecito Creek, Carrizo Badlands, ABDSP, California, USA. Tribe **Smeringurini**, note *smooth* terminus. **85.** *Paruroctonus silvestrii*, Chihuahua Road, ABDSP, California, USA. **86.** *Paruroctonus boreus*, Mercury, Nevada, USA. Subfamily **Vaejovinae**, note *smooth* terminus. **87.** *Pseudouroctonus minimus castaneus*, Vista, San Diego Co., California, USA. **88.** *Pseudouroctonus williamsi*, Santa Ysabel Reserve, San Diego Co., California, USA.

In subfamily Vaejovinae, only a smooth barb has been reported for those species exhibiting a sclerotized mating plug (see Figs. 87–88), primarily in genus *Franckeus* and the “nigrescens” group of *Vaejovis* (Sissom, 1991: figs. 72, 74, 76, 78, 80, 82, 84). Stockwell (1989) stated that species in the “mexicanus” group (in part, and referred to as *Vaejovis* in his unpublished revision) do not have a sclerotized mating plug, which instead is gelatinous (see his cladistic character 117).

Note: Stockwell (1989: 204), in a diagnosis of his (unpublished) tribe “Paruroctonini”, which included genera *Paruroctonus*, *Smeringurus*, *Vejooidus*, and *Paravaejovis*, stated “... sclerotized mating plug of hemispermaphore well developed, greatly reduced, or absent; distal barb margin bearing teeth ...”. With respect to the “distal barb ... teeth” phrase, Stockwell (1989: tab. 6, fig. 257) contradicts this statement in his cladistic analysis, which reflects only *Paravaejovis* of this assemblage with a toothed barb. This is also shown in his cladograms where the toothed barb (character 119) is derived twice, once for *Paravaejovis* and once for our tribe Syntropini.

Leg Basitarsus and Tarsus

Diagnostic value: Leg basitarsus and tarsus setal and spinule configurations are used to differentiate subfamilies in Vaejovidae, tribes in subfamily Syntropinae, and genera (in part) in subfamily Vaejovinae.

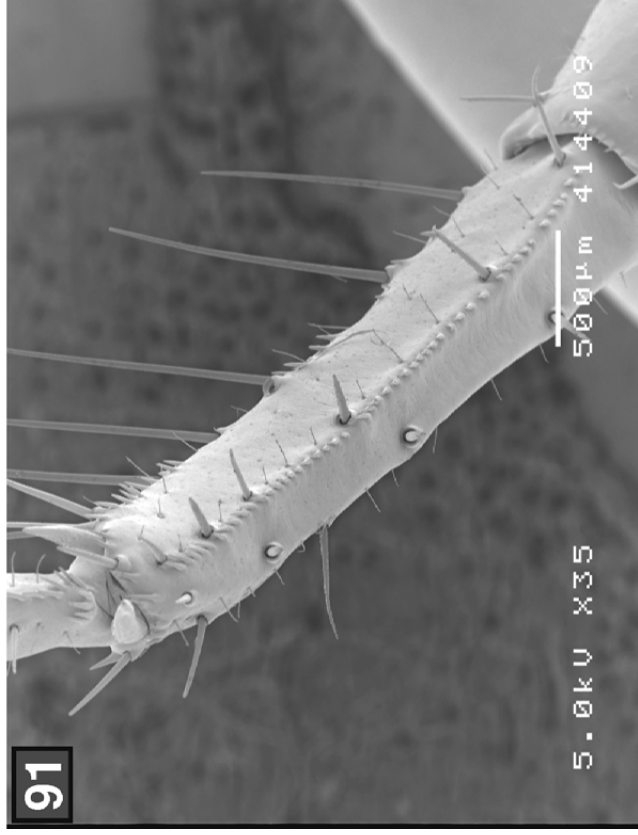
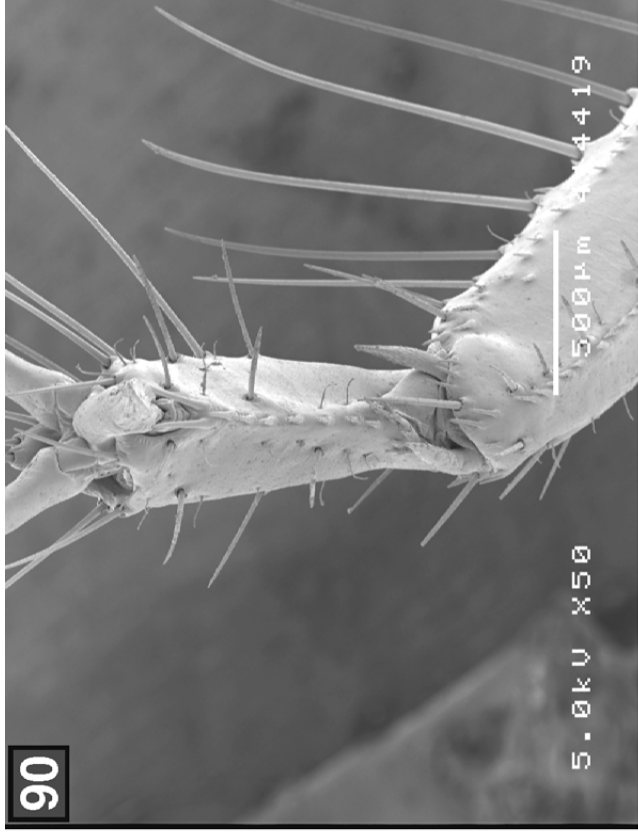
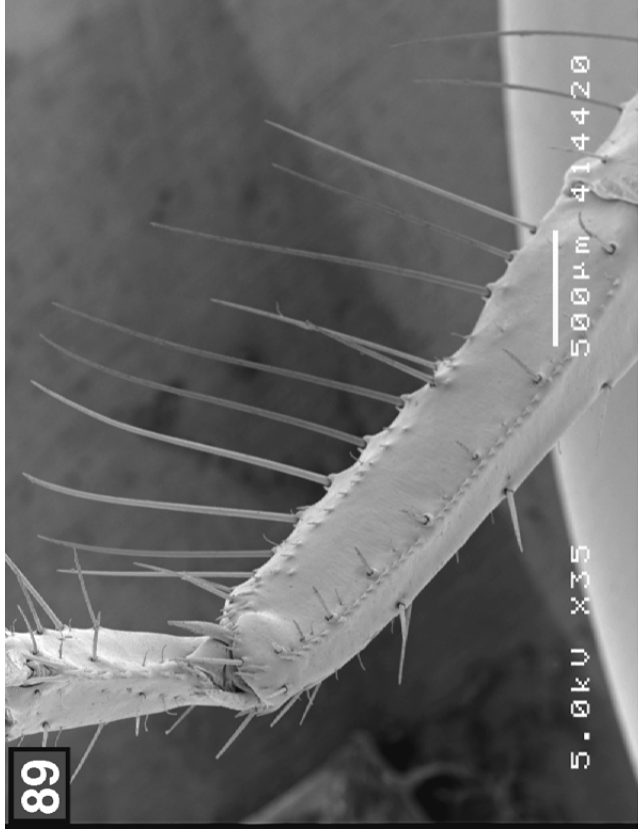
We (Soleglad & Fet, 2003b) categorized the setal and spinule configurations of the ventral surface of the leg tarsus for Recent scorpions into five types, combining parvorders Buthida and Chaerilida as type 2. Since then, after having examined additional species of *Chaerilus*, Fet et al. (2004: 17–18) expanded on type 2 indicating that the chaerilids tarsus configuration was different from Buthida, breaking them into types 2a and 2b. Superfamily Chactoidea, which includes Vaejovidae, is assigned to type 5: two lateral rows of small to medium setae with small sockets and a median row of spinules. Family Vaejovidae conforms to the chaetoid type 5, exhibiting both irregular seta pairs and a median spinule row on the leg tarsus. Note, in contrast, that in some chactids, namely subfamily Brotheinae, the median ventral spinule row is vestigial and the lateral setal rows are more developed forming distinct parallel rows (see Soleglad & Fet, 2003b: 39). Both the leg basitarsus and tarsus are of diagnostic value for the subfamilies in Vaejovidae.

Smeringurinae. In the subfamily Smeringurinae we find a “setal comb” on the dorsal margin of the basitarsus. A “setal comb” is an evenly arranged series of somewhat elongated setae located on dorsal margin of the leg basitarsus, most exaggerated on legs I–III.

Haradon (1983, 1984a, 1984b, 1985) used the configuration of the “setal comb” (which he termed *superior setae*) on the basitarsus extensively in his diagnoses of species in *Smeringurus* and the several “infra-” and “microgroups” defined for genus *Paruroctonus*. Stockwell (1989: fig. 257) considered the “comb-like” configuration of the dorsomarginal setae of the basitarsus a synapomorphy (his character 99) for his tribe Paruroctonini (= subfamily Smeringurinae). Figures 89–92, 93–96, 97, and 100 illustrate several setal combs spanning all four genera of Smeringurinae. It is interesting to see the difference in the density of the individual setae in these combs, presumably based on the species degree of adaptation as a psammophile (Fet et al., 1998). Our Figs. 89–92 illustrate two species of *Smeringurus*, *S. mesaensis*, an ultrapsammophile, and *S. grandis*, a fossorial species. *Smeringurus mesaensis* exhibits about twice as many setae than *S. grandis*. Similarly, for genus *Paruroctonus* (Figs. 93–94), the psammophile *P. utahensis* has more proportionally longer setae in the comb than the fossorial species *P. silvestrii*. Genus *Paravaejovis* (Fig. 97) is also equipped with a well developed setal comb on the basitarsus, the setae being extremely long compared to the leg basitarsus. The ultrapsammophile genus *Vejooidus* is equipped with an extraordinary array of setal arrangements (Figs. 100–102): the setal comb on the basitarsus is very well developed with elongated setae, and the tarsus is covered laterally and ventrally with a large cluster of setae essentially obscuring its ventral row of spinules.

The ventral surface of the leg tarsus in subfamily Smeringurinae has a ventral median row of spinules along its surface terminating distally with a single pair of spinules. Figures 90, 92, 94, 96, 99, 102 illustrate this single ventral spinule pair for all four genera. In genera *Paravaejovis*, *Paruroctonus*, and *Smeringurus*, the spinules are well developed and stout, the distal spinule pair straight and usually longer than the spinules in the median row. In genus *Vejooidus* (Fig. 102), the ventral median spinule row and distal pair of spinules is difficult to detect due to the high density of the setal cluster covering the ventral surface; therefore, in Fig. 102 the spinules are indicated with arrows, (black for the median row spinules and white for the distal pair). The distal pair is quite elongated, as in the other smeringurine genera.

Syntropinae. The dorsomarginal setae of the leg basitarsus are not arranged into a comb-like configuration in subfamily Syntropinae. The spinule configuration of the leg tarsus ventral surface, however, is diagnostic for the two tribes comprising this subfamily. As in Smeringurinae, tribe Stahnkeini has a single distal spinule pair on the leg tarsus, as shown in Figs. 111–113 for species *Serradigitus wupatkiensis*, *S. adcocki*, and *Stahnkeus subtilimanus*. This pair of



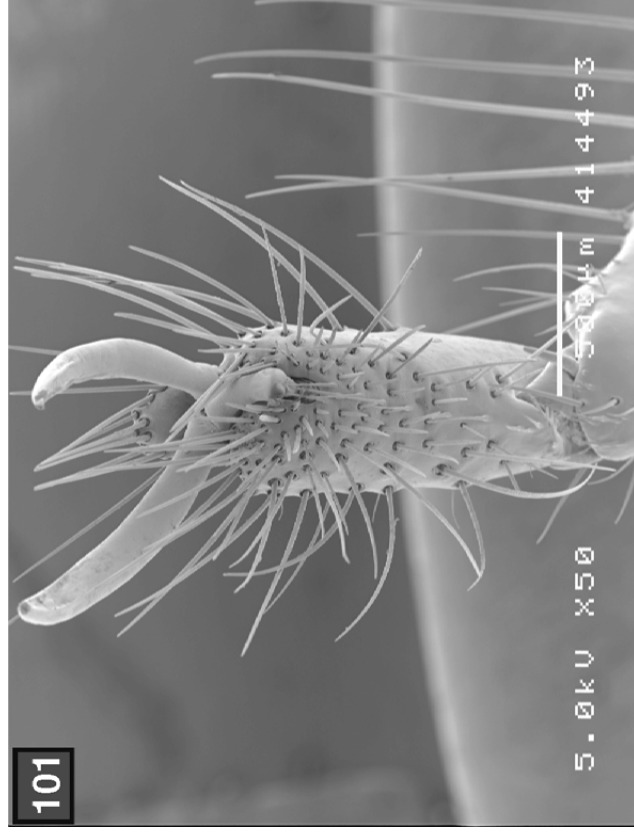
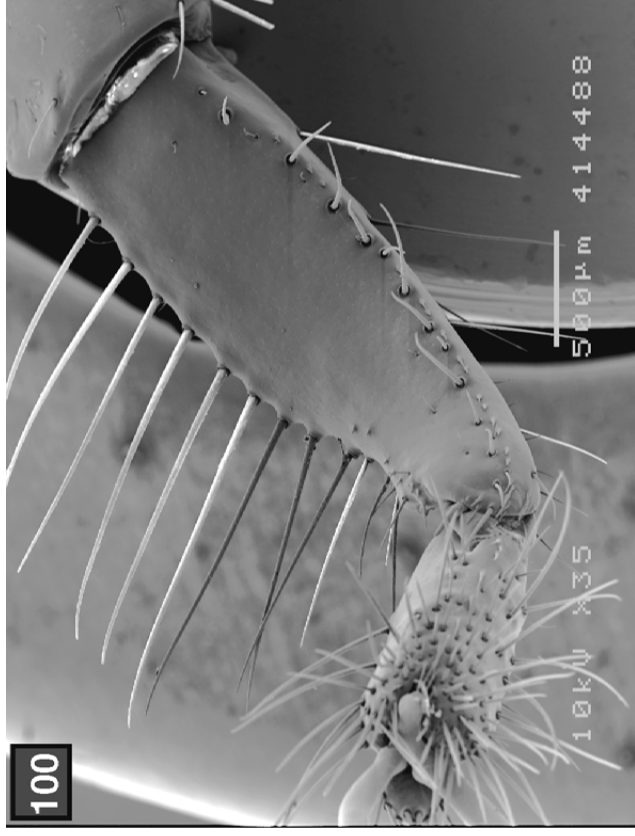
Figures 89-92: Leg III of *Smeringurus* species. **89 & 90.** *Smeringurus mesaensis*, female, Palo Verde Wash, ABDSP, California. **89.** Ventral view of basitarsus showing “setal combs”. **90.** Ventral view of tarsus showing median spinule row and single pair of distal spinules. **91 & 92.** *Smeringurus grandis*, male, Oakties Landing, Baja California, Mexico. **91.** Ventral view of tarsus showing median spinule row and single pair of distal spinules. **92.** Ventral view of basitarsus showing “setal combs”.



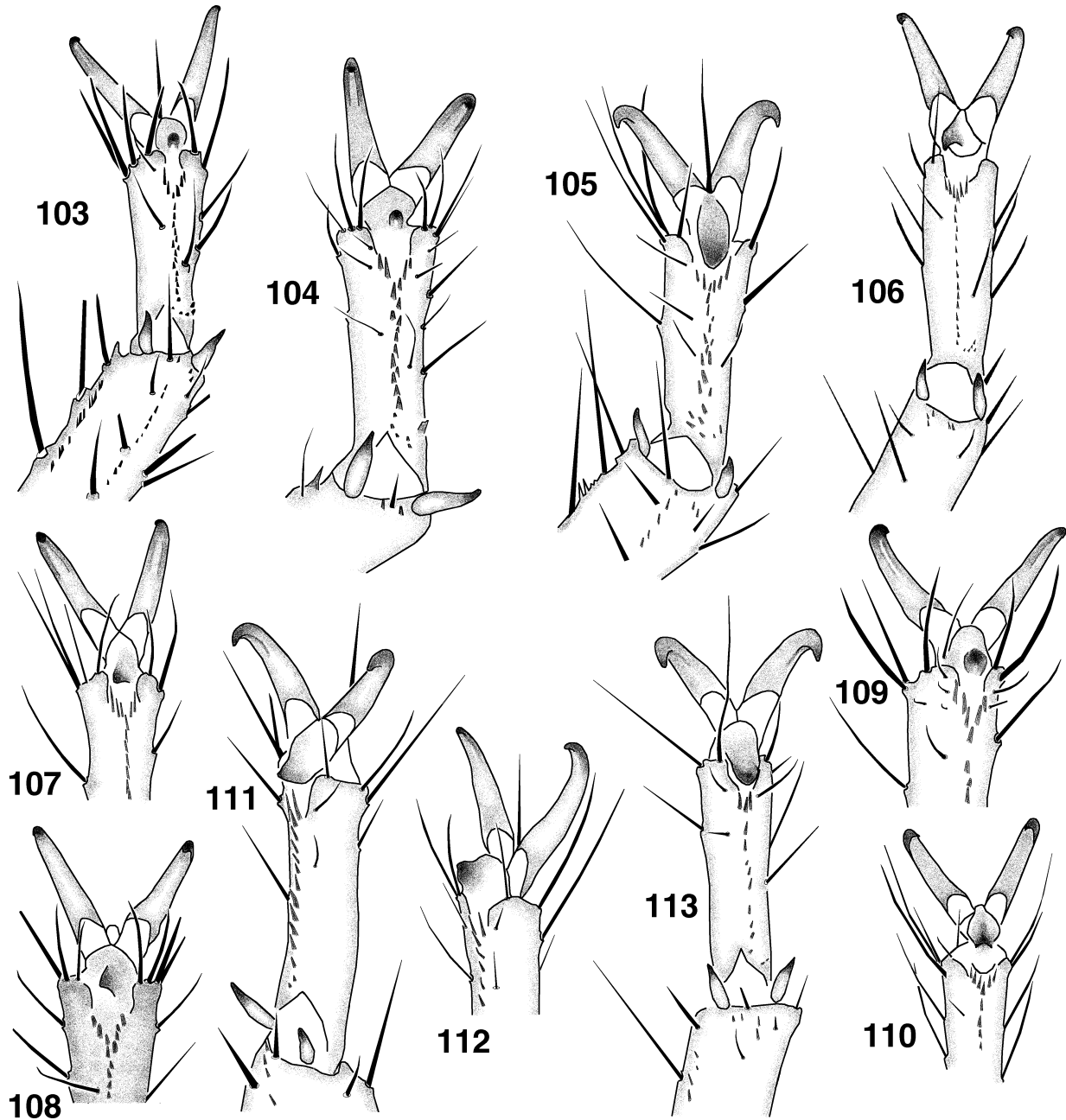
Figures 93–96: Leg III of *Paruroctonus* species. **93 & 94.** *Paruroctonus utahensis*, male, Kermit, Winkler Co., Texas. **93.** Ventral view of basitarsus and tarsus, showing “setal combs” on basitarsus. **94.** Ventral view of tarsus showing median spinule row and single pair of distal spinules. **95 & 96.** *Paruroctonus sierrae*, male, Chihuahua Road, ABDSP, California. **95.** Ventral view of basitarsus and tarsus, showing “setal combs” on basitarsus. **96.** Ventral view of tarsus showing median spinule row and single pair of distal spinules.



Figures 97–99: Right leg III of *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. **97.** Ventral view of basitarsus, tarsus, and epitarso, showing “setal combs” on basitarsus. **98.** Lateral view of tarsus showing median spinule row and single pair of distal spinules. **99.** Ventral view of tarsus showing median spinule row and single pair of distal spinules.



Figures 100–102: Right leg III of *Vejovoidus longiunguis*, female, Vizcaino Desert, Baja California, Mexico. **100.** Ventral view of basitarsus, tarsus, and epitarso, showing “setal combs” on basitarsus. **101.** Ventral view of tarsus and epitarso showing highly populated cluster of elongated curved setae on tarsus, the elongated asymmetric ungues of the epitarso, and the reduced somewhat blunted unguicular spine. **102.** Close-up of ventral view of tarsus showing setal cluster and median spinule row. Note that spinule median row and single pair of distal spinules are hidden in the setal cluster, median spinules indicated by *black* arrows and single distal setal pair indicated by *white* arrows.



Figures 103–113: Leg tarsus, ventral view, of select Syntropinae species. Tribe **Syntropini**, exhibiting multiple distal spinule pairs. **103.** *Kochius punctipalpi punctipalpi*, female, right leg III. **104.** *Thorellius cristimanus*, male, right leg IV. **105.** *Hoffmannius eusthenura*, male, right leg III. **106.** *Syntropis williamsi*, female holotype, right leg IV (after Soleglad et al., 2007: fig. 8, in part). **107.** *Kochius cazieri*, male, right leg III. **108.** *Thorellius atrox*, female, right leg III. **109.** *Hoffmannius gravicaudus*, female, right leg III. **110.** *Syntropis albuli*, female holotype, leg IV (after Soleglad et al., 2007: fig. 20, in part). Tribe **Stahnkeini**, exhibiting a single distal spinule pair. **111.** *Serradigitus wupatkiensis*, female, right leg III. **112.** *Serradigitus adcocki*, female, right leg III. **113.** *Stahnkeus subtilimanus*, female, right leg III.

spinules is slightly longer than the spinules comprising the median ventral row. In tribe Syntropini, we see 2–4 pairs of distal spinule pairs, as illustrated in Figures 103–110 for multiple species of all four genera. Of the

four genera, subtribe Thorelliina appears to have the larger number of distal spinule pairs, usually 3–4 pairs, as illustrated for species *Kochius punctipalpi* (Fig. 103), *K. cazieri* (Fig. 107), *Thorellius cristimanus* (Fig. 104),

and *T. atrox* (Fig. 108). Subtribe Syntropina species usually have 2–3 distal spinule pairs, as shown for species *Hoffmannius eusthenura* (Fig. 105), *H. gravicaudus* (Fig. 109), *Syntropis williamsi* (Fig. 106), and *S. aalbui* (Fig. 110). The presence of these multiple spinule pairs is a derived character for tribe Syntropini.

Vaejovinae. As in Syntropinae, scorpions in Vaejovinae lack a “setal comb”. The tarsal spinule configuration is similar to that in Syntropinae, species aggregates exhibiting multiple distal spinule pairs as well as a single pair. Genera *Pseudouroctonus* and *Uroctonites* have 3–4 spinule distal pairs on the ventral aspect of the tarsus (see Soleglad & Fet 2003b: fig. 36, for *Pseudouroctonus reddelli*). Genus *Franckeus* and the “nigrescens” group of *Vaejovis* have a single pair of distal spinules. The majority of the species in the “mexicanus” group of *Vaejovis* also exhibit a single spinule pair, but there are exceptions such as the type species *V. mexicanus*, *V. smithi*, and *V. jonesi*, which have two pairs. The “vorhiesi” subgroup of the “mexicanus” group which currently includes species *V. vorhiesi*, *V. cashi*, *V. feti*, and *V. paysonensis*, exhibits a single pair of distal spinules (Graham, 2007: 6, 9, 12).

Chelicerae

Diagnostic value: Cheliceral dentition is used to differentiate subfamilies in Vaejovidae, in part, and tribes in subfamily Smeringurinae.

The chelicerae include a number of important diagnostic characters, spanning phylogenetic levels as high as parvorders (see Soleglad & Fet, 2003b for detailed discussion). Vachon (1963) was the first to quantify and develop a terminology for the individual cheliceral denticles across scorpion families, terminology still currently being used. The vaejovids typically have two subdistal (*sd*) denticles and one basal denticle (*b*) on cheliceral movable finger dorsal edge; the ventral distal denticle (*vd*) is longer than its dorsal counterpart (*dd*); the ventral edge can be smooth, serrated, or with well developed accessory denticles (*va*); the fixed finger median (*m*) and basal (*b*) denticles are cojoined on a common trunk; and the presence of ventral accessory denticles (*va*) are variable. Serrula is present to one degree or another in Vaejovidae, from heavily developed to vestigial (essentially absent).

Dentition

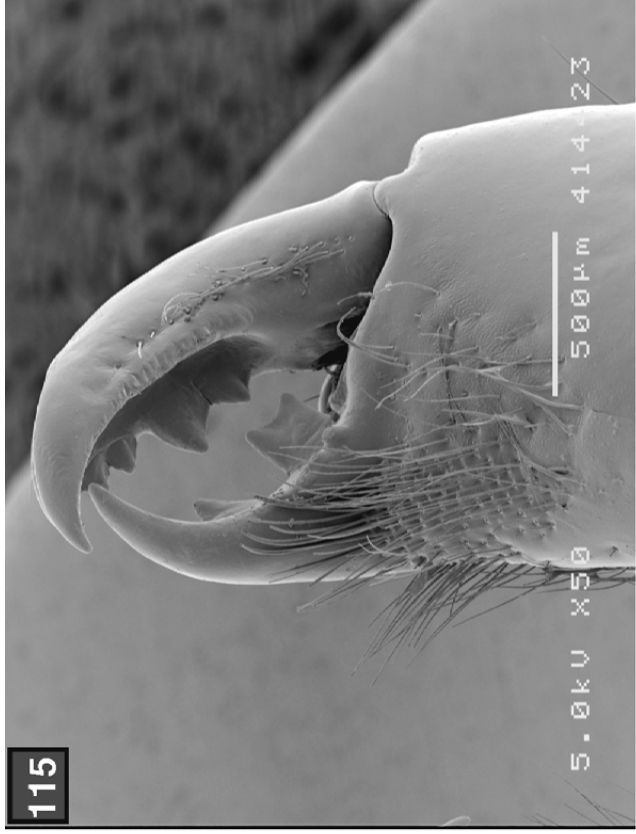
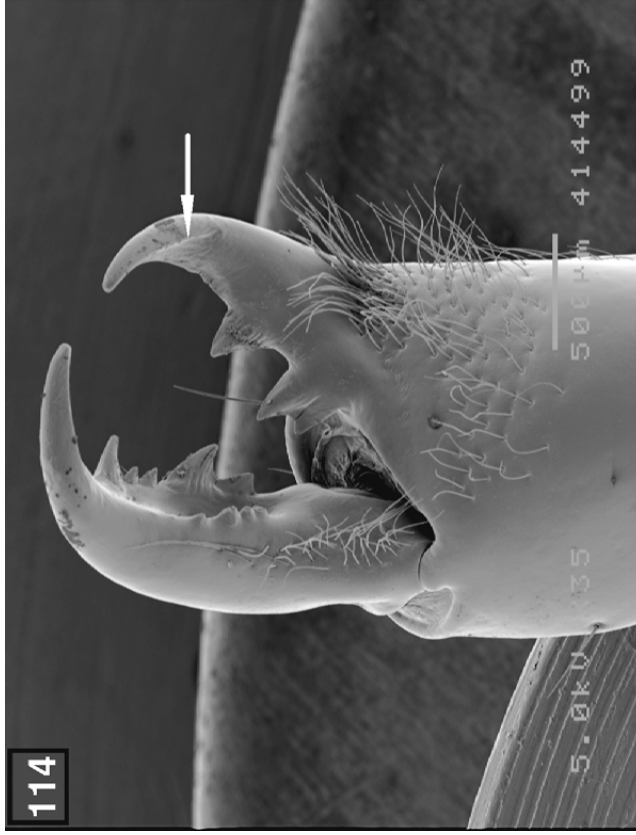
Smeringurinae. Tribe Smeringurini is equipped with well developed dentition on the ventral edge of the cheliceral movable finger, considered a synapomorphy for this tribe. In contrast, tribe Paravaejovini is lacking this dentition (Fig. 21). The development of these

denticles exhibit considerable variability from quite large heavily pigmented denticles as seen in *Smeringurus* species (Fig. 117), to delicate non-pigmented denticles as seen in *Paruroctonus becki* (Fig. 118). In some cases, when the denticles are considerably worn-out, or vestigial in development, the ventral edge of the movable finger may look somewhat crenulated, as seen in *Vejovoidus* (Fig. 116) and in other species, where denticles are sometimes apparent, *P. utahensis* (Fig. 115) and *P. ventosus* (Fig. 121). This dentition for *P. gracilior*, first illustrated by Hoffmann (1931: fig. 42), is somewhat unusual, the denticles are clustered closely on the basal one-third of the finger edge (Fig. 114). This condition is also found in *P. stahnkei* (see Gertsch & Soleglad, 1966: fig. 36).

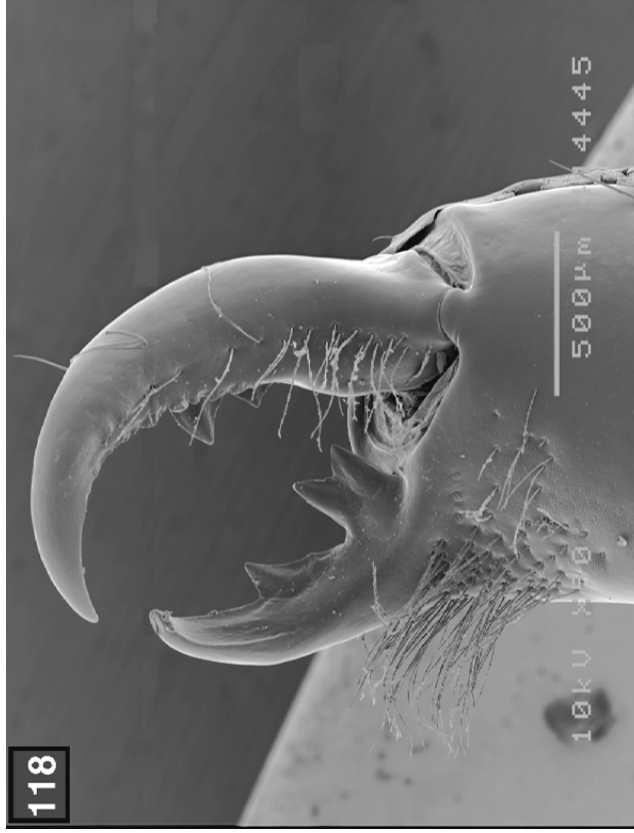
The fixed finger ventral edge, shaped as a subtle carina, has one to four protuberances, sometimes pigmented, in tribe Smeringurini, also considered a synapomorphy for this tribe. As with the ventral dentition of the movable finger, tribe Paravaejovini is lacking these denticles (Fig. 21). These protuberances are quite conspicuous in genera *Smeringurus* (Fig. 117) and *Vejovoidus* (Fig. 116) as well as in most *Paruroctonus* species, except for *P. gracilior* (Fig. 114) and *P. stahnkei* (Gertsch & Soleglad, 1966: fig. 36), *P. williamsi*, *P. pecosi*, and *P. coahuilanus* (after Haradon, 1985: 38). The absence of the protuberances in these species is interesting and possibly is due to the weak or marginally developed ventral carina of the fixed finger. Haradon (1985: 21) used this weakly developed carina as one of the diagnostic characters for his “gracilior” infragroup, in which *P. gracilior* is the sole member. He referenced the figure in Gertsch & Soleglad (1966: fig. 33). In *P. gracilior*, the carina only exists on the distal tine of fixed finger (this is also clear in our Figure 114). Further, Haradon (1985) classified other assemblages of *Paruroctonus* as to whether the ventral carina extends to the distal aspect of the bicuspid fixed finger denticles (denticles *m* and *b*), or beyond towards the base of the finger. In *P. stahnkei*, this carina only extends to the distal aspect of the bicuspid. Based on these observations by Haradon (1985), we suggest here that the protuberances may only occur on the ventral carina in the area of close proximity of the bicuspid.

Syntropinae. Syntropine species lack dentition on the ventral edge of the movable finger and protuberances are lacking on the fixed finger ventral surface.

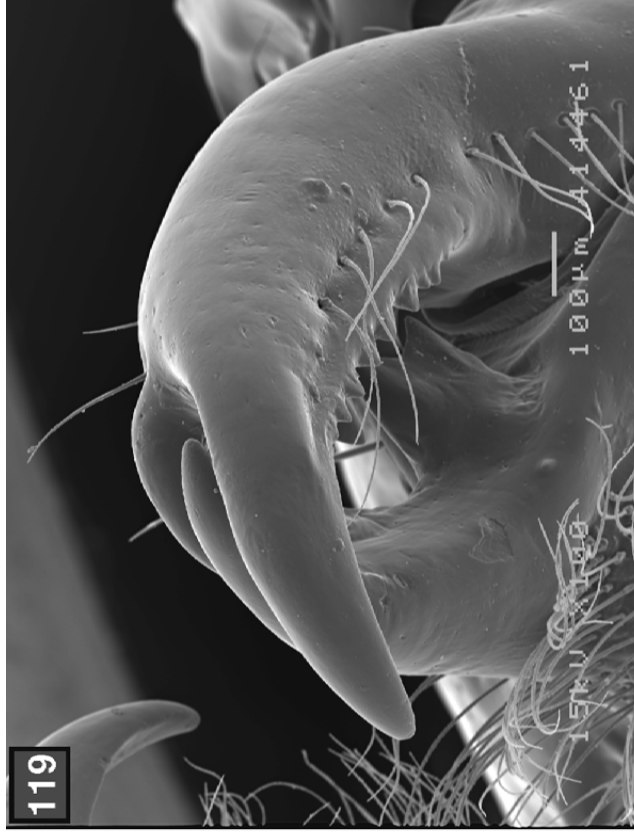
Vaejovinae. Vaejovinae species movable finger dentition is variable, usually smooth in most genera except for *Pseudouroctonus* and *Uroctonites*, which possess from well defined denticles to serrated or smooth ventral edges. Protuberances of the fixed finger are present in some species of *Pseudouroctonus*, the most exaggerated in the two closely related species *P. reddelli* and *P. sprousei*.



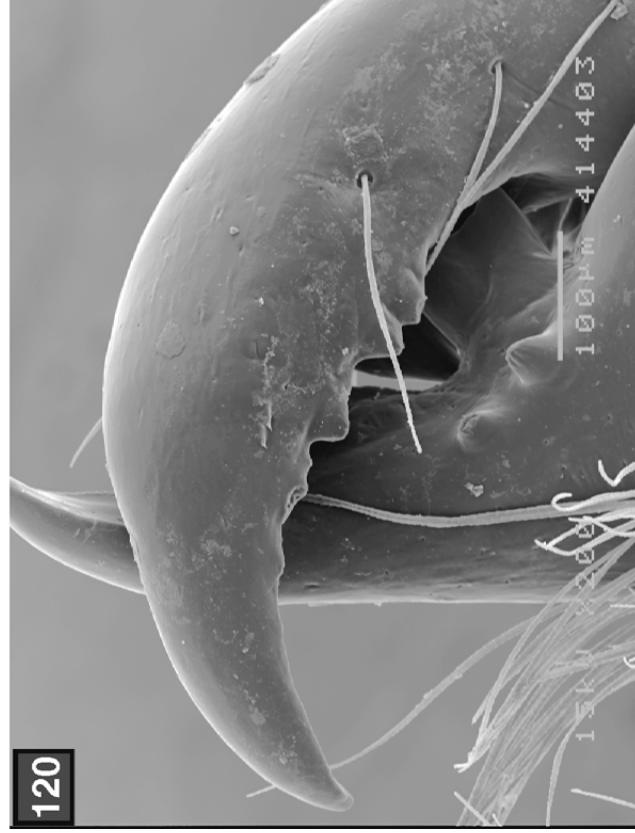
Figures 114–117: Chelicera, ventral view. **114.** *Paruroctonus gracilior*, male, Cuatro Ciénegas, Coahuila, Mexico. *White arrow* points to reduced ventral carina of fixed finger. **115.** *Paruroctonus utahensis*, male, Kermit, Winkler Co., Texas. **116.** *Vejovoidius longiunguis*, female, Vizcaino Desert, Baja California, Mexico. **117.** *Smeringurus grandis*, male, Oakies Landing, Baja California, Mexico.



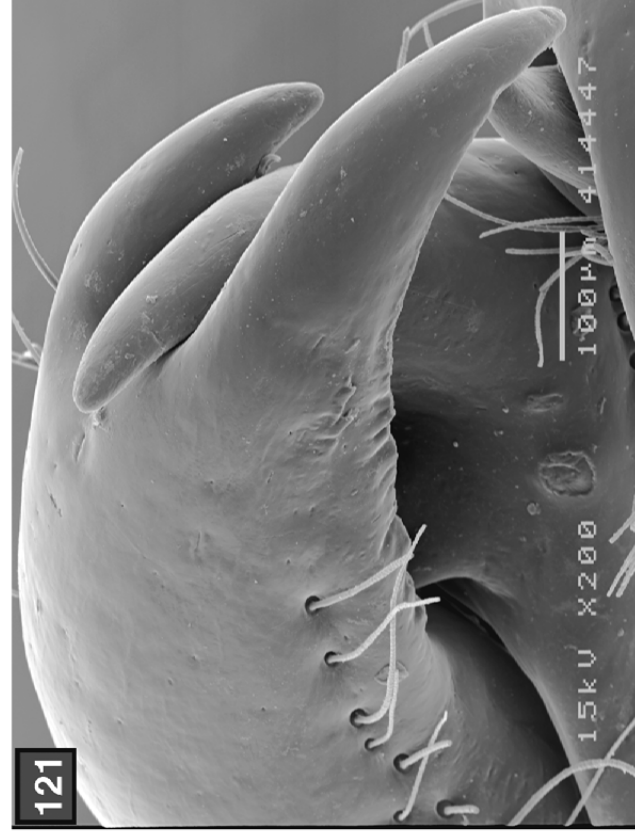
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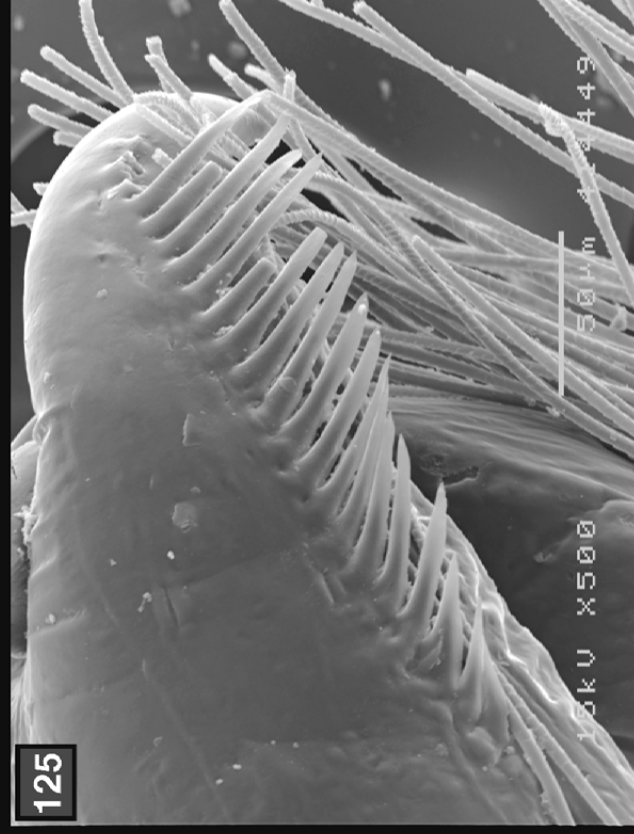
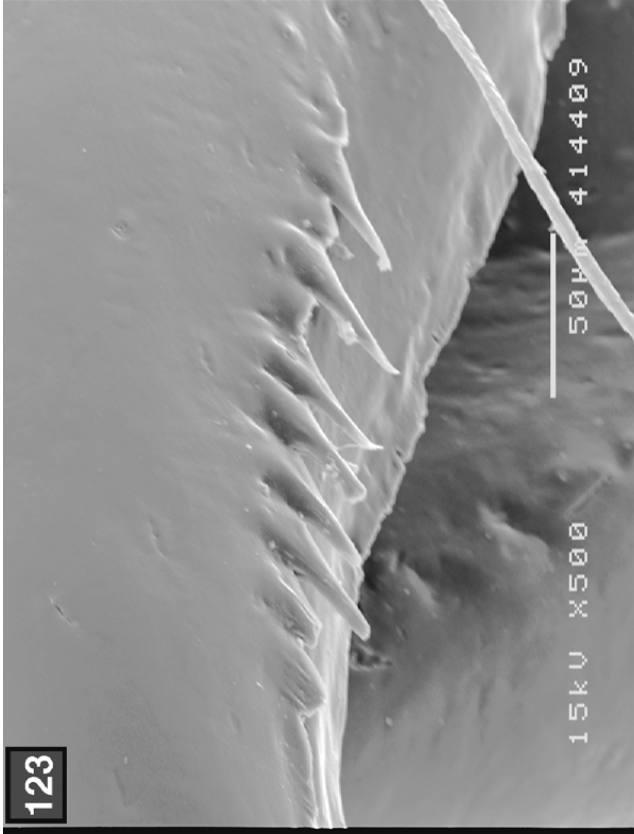
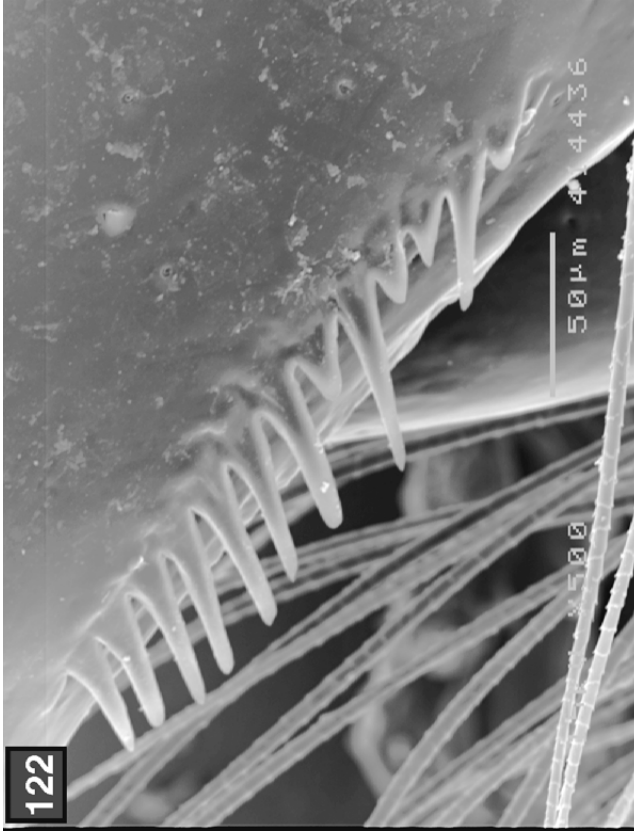


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Figures 118–121: Chelicera, ventral view. **118.** *Paruroctonus becki*, female, San Bernardino Co., California, USA. **119.** *Paruroctonus silvestrii*, male, Chihuahua Road, ABDSP, California, USA. **120.** *Paruroctonus luteolus*, female, Palo Verde Wash, ABDSP, California, USA. **121.** *Paruroctonus ventosus*, female, El Socorro, Baja California, Mexico.



Figures 122–125: Serrula of representative genera of subfamily Syntropinae. Tribe **Syntropini**: **122.** *Hoffmannius viscainetis*, male, Las Bombas, Baja California Sur, Mexico. **123.** *Hoffmannius confusus*, male, San Bernardino Co., California, USA. **124.** *Kochius punctipalpi*, male, Los Aripes, Baja California Sur, Mexico. Tribe **Stahnkeini**: **125.** *Serradigitus joshuaensis*, female, Indian Gorge Canyon, ABDSP, California, USA.

	Density*Number of Tines = SDQ	Adult Length */ Number of Tines
<i>Gertschius crassicornus</i>	1.0*27 = 27	25/27 = 0.926
<i>Serradigitus adcocki</i>	1.0*33	40/33 = 1.212
<i>Serradigitus calidus</i>	1.0*27	24/27 = 0.889
<i>Serradigitus gertschi</i>	1.0*27 = 27	25/27 = 0.926
<i>Serradigitus joshuaensis</i>	1.0*21 = 21	23/21 = 1.095
<i>Serradigitus minutis</i>	1.0*22 = 22	18/22 = 0.818
<i>Serradigitus torridus</i>	1.0*29	33/29 = 1.138
<i>Stahnkeus deserticola</i>	1.0*32	45/32 = 1.406
<i>Stahnkeus harbisoni</i>	1.0*35	51/35 = 1.457
<i>Stahnkeus subtilimanus</i>	1.0*37 = 37	48/37 = 1.297
Stahnkeini	21–37 (29.0)	0.818–1.457 (1.116)
<i>Hoffmannius confusus</i>	1.0*11 = 11	47/11 = 4.273
<i>Hoffmannius globosus</i>	0.918*10 = 9.18	33/10 = 3.333
<i>Hoffmannius gravicaudus</i>	1.0*21 = 21	65/21 = 3.095
<i>Hoffmannius punctatus</i>	1.0*15 = 15	55/15 = 3.667
<i>Hoffmannius puritanus</i>	1.0*16 = 16	55/16 = 3.438
<i>Hoffmannius viscainensis</i>	1.0*15 = 15	49/15 = 3.267
<i>Hoffmannius waeringi</i>	1.0*13 = 13	54/13 = 4.154
<i>Syntropis williamsi</i>	1.0*14 = 14	70/14 = 5.000
<i>Kochius cazieri</i>	1.0*17 = 17	56/17 = 3.294
<i>Kochius hirsuticauda</i>	1.0*14 = 14	36/14 = 2.571
<i>Kochius kovariki</i>	1.0*18 = 18	50/18 = 2.778
<i>Kochius punctipalpi</i>	1.0*19 = 19	59/19 = 3.105
<i>Thorellius cristimanus</i>	1.0*20 = 20	69/20 = 3.450
<i>Thorellius intrepidus</i>	1.0*26 = 26	81/26 = 3.115
Syntropini	10–26 (16.357)	2.571–5.000 (3.467)

Table 3: Serrula Development Quotient (SDQ) for subfamily Syntropinae. Note the considerably larger number of tines in tribe Stahnkeini, 21–37, from the smallest to largest species as compared to 10–26 for tribe Syntropini. Correlating the number of tines to the species adult length emphasizes the significant difference in serrula based on species size. This comparison exhibits well over a factor of three difference. 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. * Total length of adult female.

Serrula

The reporting of serrula has been sporadic at best in family Vaejovidae (for a detailed review see Graham & Fet, 2006), some authors ignoring it altogether, others including it in their species descriptions. Recently, Fet et al. (2006d) discovered vestigial serrula development in subfamily Smeringurinae, an assemblage of species thought to have no serrula. This further quantification of serrula, “vestigial,” added to its lexicon of “mediumly developed serrula” and “highly developed serrula.” These three distinctions are utilized in this study, assigning subfamily Smeringurinae with “vestigial serrula,” subfamily Syntropinae with “medium to highly developed serrula,” and Vaejovinae with “highly developed serrula.”

Of taxonomic interest here is that “mediumly” and “highly” developed serrula are confined exclusively to tribes in the subfamily Syntropinae: tribe Syntropini has a “mediumly developed serrula” and tribe Stahnkeini, a

“highly developed serrula.” Figures 122–125 illustrate serrula in subfamily Syntropinae, showing three genera, *Hoffmannius* (represented by *H. viscainensis* and *H. confusus*) and *Kochius punctipalpi* of tribe Syntropini, and *Serradigitus joshuaensis* of tribe Stahnkeini. It is clear that in *S. joshuaensis*, a very small species, the serrula is considerably more developed than in the other two genera. This difference in development manifests itself both in the length of the individual tines as well as the number of tines. In Syntropinae, the serrula tines are usually contiguously configured whereas in subfamily Smeringurinae, the vestigial serrula tines are usually separated with gaps (Fet et al., 2006d: table 2).

In Table 3, we show a representation of Syntropinae species serrula development. An important observation made by Fet et al. (2006d) was that the number of tines contained in serrula seemed to be related to the size of scorpion species, with larger species exhibiting a larger number of tines. This is the case across the entire subfamily Syntropinae (Table 3), spanning “highly

developed serrula” and “mediumly developed serrula”. The delineation between “highly developed” and “mediumly developed” is well illustrated: the former with 21–37 tines and the latter with 10–26 tines. The difference between the smallest number of serrula tines in Stahnkeini, 21 for *Serradigitus joshuaensis*, and the largest in Syntropini, 26 for *Thorellius intrepidus*, is only 5, a 23.8 % difference, whereas the difference in adult size of these two species is 252 %!

For details on the vestigial serrula found in subfamily Smeringurinae refer to Fet et al. (2006d) where numerous SEM images and statistics are presented spanning many species and all four genera of this subfamily. For all genera, serrula development ranges from almost obsolete in genus *Vejovoidus* to very vestigial in *Paravaejovis*, vestigial to weak in *Paruroctonus*, and weak to medium development in *Smeringurus*.

In subfamily Vaejovinae, all species appear to have well developed serrula, approaching that found in syntropine tribe Stahnkeini. Fet & Soleglad (2007: 259) reported well developed serrula for *Vaejovis mexicanus*, the type species of Vaejovinae.

Carapace

Diagnostic value: Carapace structure is used to differentiate subfamilies in Vaejoidea and, in part, genera of tribe Syntropini.

Smeringurinae. We studied the variety of carapaces found in family Vaejoidea as well as constructed three morphometric ratios. Figure 126 shows three histograms contrasting morphometric ratios of major taxonomic assemblages in Vaejoidea: the median eye diameter compared to the carapace length; the median eye tubercle width compared to the carapace width at that point; and the median eye tubercle position compared to the carapace length. Before going into detailed analysis of these three ratios, it is interesting to point out that for all three, *Pseudouroctonus* + *Uroctonites* and Smeringurinae (= Paravaejovini + Smeringurini) form the end-points of these histograms. That is, *Pseudouroctonus* + *Uroctonites* (subfamily Vaejovinae) have the smallest median eyes, smallest median tubercle, and the most anteriorly advanced median eye position in the family Vaejoidea, whereas Smeringurinae has the largest median eyes, median tubercles, and least advanced anteriorly median eye position. See Fig. 127 for method of measurement.

The top histogram in Fig. 126 illustrates the large median eyes found in tribe Smeringurini, showing standard deviation range separation from most vaejoidean aggregates, except for *Franckeus* + “nigrescens” group and “mexicanus” group, which have less than 50 %

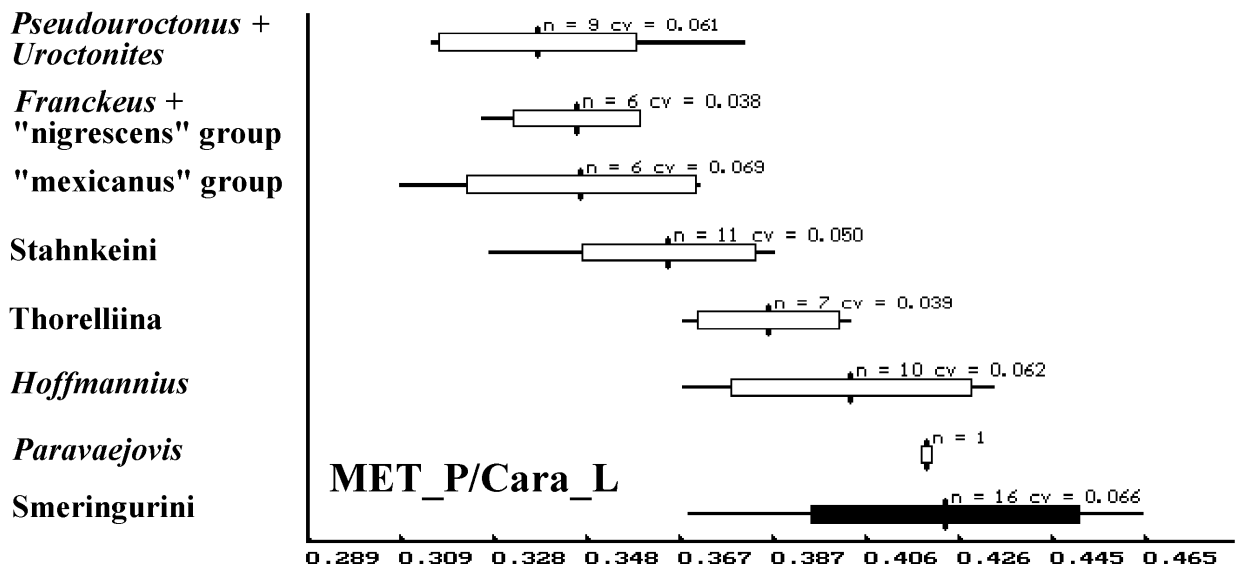
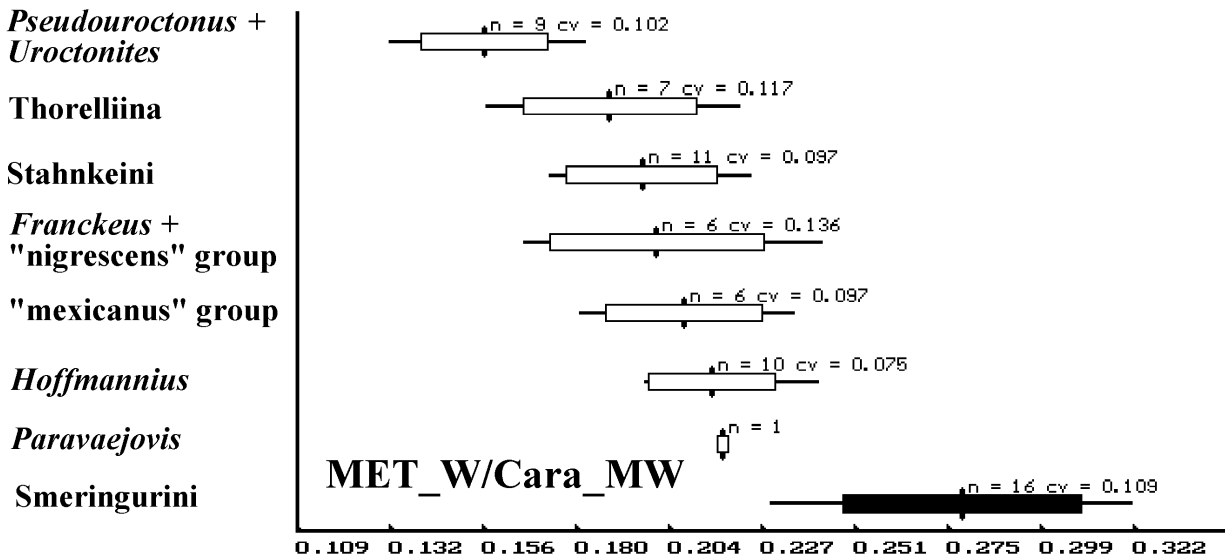
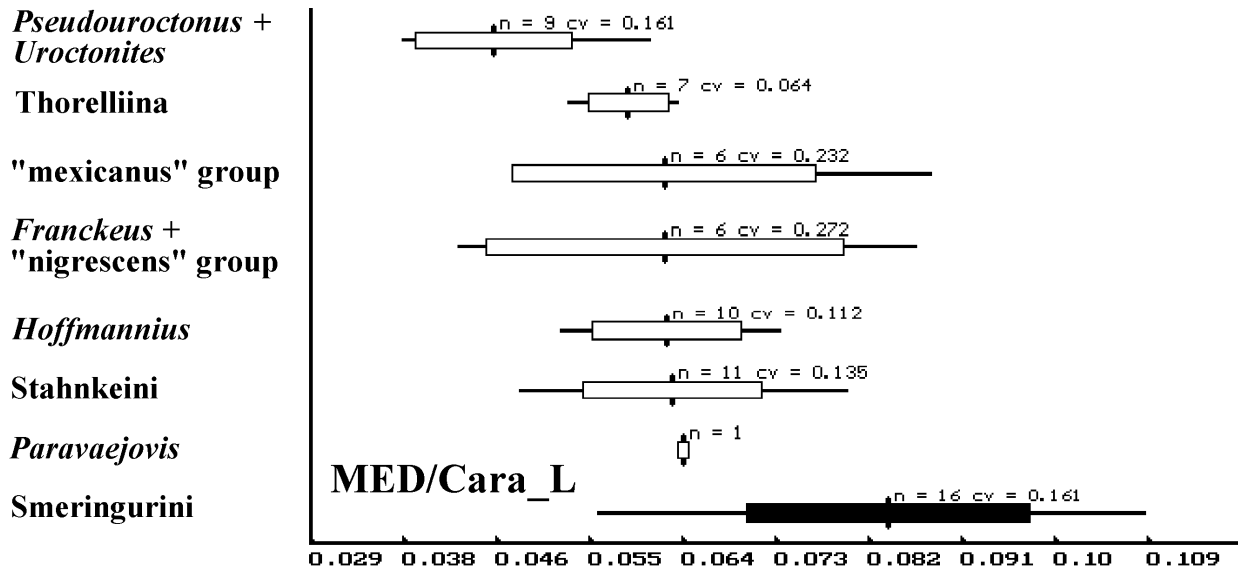
overlap. It is also interesting to note that the median eye is quite small in *Pseudouroctonus* + *Uroctonites*. The middle histogram in Fig. 126 shows complete standard deviation range separation from tribe Smeringurini and the other aggregates of Vaejoidea; tribe Paravaejovini (genus *Paravaejovis*) exhibits the second widest median tubercle though it is considerably separated from that in its sister tribe Smeringurini. Again, the aggregate *Pseudouroctonus* + *Uroctonites* shows the smallest median eye tubercle within Vaejoidea which is consistent with it also having relatively the smallest median eyes in the family. Although the bottom histogram in Fig. 126 shows a continuous sequence of standard error range overlap, the end-points of these data illustrate the more medially positioned median tubercle in subfamily Smeringurinae, in contrast to *Pseudouroctonus* + *Uroctonites* assemblage, where median tubercle is located on the distal one-third of the carapace. In addition, aggregates *Franckeus* + “nigrescens” group and “mexicanus” group also exhibit a forward positioned median tubercle close to that of *Pseudouroctonus* + *Uroctonites*, roughly at the one-third position of the carapace, thus indicating a trend for subfamily Vaejovinae.

Syntropinae. The carapace of genus *Kochius* is quite distinct. A well defined, but subtle, anterior emargination is present, extending to the lateral eyes (Figs. 128–133). In addition, a small shallow median indentation is present. In genus *Thorellius* (Figs. 134–135), the anterior emargination does not continue to the lateral eyes, but tapers off before reaching the eyes. Although the anterior edge in *Thorellius* is subtly concaved, there is no distinct small median indentation. In genera *Hoffmannius* (Figs. 136–138) and *Syntropis* (Fig. 139), the anterior edge of the carapace is essentially straight or sometimes slightly convexed or concaved. The anterior emargination is limited to the medial area, never reaching the lateral eyes. Narrow median indentations as exhibited in *Kochius* are not found in *Hoffmannius* or *Syntropis*.

Chelal Carinae

Diagnostic value: Chelal carinae development is used to differentiate, in part, genera and subtribes of tribe Syntropini.

An important diagnostic character separating subtribes Syntropina and Thorelliina is the development of the subdigital (*D2*) carina. Figs. 140–145 show that *D2* is well developed in genera *Kochius* and *Thorellius*, sometimes extending distally to almost 40 % of the palm length (see *K. hirsuticauda* in Fig. 141). In contrast, the species of *Hoffmannius* and *Syntropis* have essentially a vestigial *D2* carina (Figs. 146–151), usually represented



by a small granule or two. In Figs. 152–159 we show a diagrammatic view of the chelal palm illustrating the highly scalloped profile formed by the *D1–D5* carinae in *Kochius* and *Thorellius*. In addition, the location of *D2* is approximately mid-distance between carinae *D1* and *D3*.

Besides the subdigital (*D2*) carina development, the two subtribes of tribe Syntropini can be distinguished by the overall development of the other chelal carinae. Scorpions in subtribe Thorelliina have well developed carinae, especially in genus *Kochius*, whereas the members of subtribe Syntropina essentially exhibit carinae that are vestigial to smooth. This is apparent in Tables 4 and 5 where we show the development of the nine carinae of the chelae, spanning eight “grades”, from obsolete (a value of “0”) to serrated (a value of “8”). In genus *Kochius*, chelal carinae in general are developed from granulate to crenulate (values “3 to 6”), with only species *K. kovariki* having smooth (albeit well developed) carinae. Species of the genus *Thorellius* exhibit well developed carinae but their degree of granulation is more variable, vestigial to smooth in the southern species *T. subcristatus*, *T. occidentalis*, and *T. cisnerosi*, and strong and marbled in northern species *T. intrepidus*, *T. atrox*, and *T. cristimanus*. The marbling of the carinae (i.e., the partial fusing of the granules into irregular aligned carinae) in the latter species, especially the digital (*D1*), external (*E*), ventroexternal (*VI*), and

ventromedian (*V2*), is quite apparent (Figs. 144–145). In subtribe Syntropina, the chelal carinae development spans obsolete to smooth-granular, but on an average they are between obsolete to vestigial-smooth (values “0 to 1”). Also see section below on granulation quotients.

Metasoma Carinae

Diagnostic value: Metasoma carinae development is used to differentiate vaejovoid subfamilies, in part, and genera of tribe Syntropini.

In subfamily Smeringurinae, the dorsal (*D*) carinae of metasomal segments I–IV (especially segments I–III) terminate posteriorly in a somewhat rounded terminus with a small granule, not straight or flared dorsally exhibiting an elongated spine as in subfamilies Syntropinae and Vaejovinae. This terminus is illustrated in Figs. 160–163. Genus *Vejovoidus* (Fig. 162) is an exception to this where we see an exaggerated terminus spine, considered a synapomorphy for the genus, probably representing one of many derivations caused by its adaptation to sand environment (*Vejovoidus* is an ultrapsammophile). Similarly, in Smeringurinae, the terminus of the dorsolateral (*DL*) carinae of metasomal segment IV is also reduced, essentially terminating at the articulation condyle, whereas this terminus is highly flared in species of subfamilies Syntropinae and Vaejovinae (also illustrated in Figs. 164–169). The articulation condyle, a mechanism located between metasomal segments IV and V, was first described in detail by Soleglad & Fet (2003b: 11; figs. 8–9).

As was the case for chelal carinae, the two subtribes of tribe Syntropini can be differentiated, in part, by the degree of development of the ventromedian (*VM*) carinae of the metasoma. In Tables 4–5, the *VM* carinae of segments I–IV are depicted for all species of *Kochius*, *Thorellius*, and *Hoffmannius*. As in the chelal carinae, the *VM* carinae are significantly more developed in subtribe Thorelliina than in *Hoffmannius*. In genus *Kochius* the *VM* carinae are in general granulate to crenulate, in *Thorellius* they are generally smooth to granulate but well developed. Only *T. cisnerosi* has obsolete *VM* carinae on all four segments, which is considered an autapomorphy for this species. In contrast (Table 5), roughly half the species in genus *Hoffmannius* have obsolete *VM* carinae, and many other species have vestigial to smooth carinae. Species *H. waeringi*, *H. confusus*, *H. globosus*, and *H. viscainensis* exhibit the most developed *VM* carinae, smooth to granular. Also see section below on granulation quotients.

Telson

Diagnostic value: The shape and morphometrics of the telson are used to differentiate, in part, the genera of

← **Figure 126:** Morphometric ratios comparing carapace components for major assemblages of family Vaejoidea. **Top:** diameter of the median eye compared with the carapace length. These data illustrate the large median eyes found in tribe Smeringurini, showing standard error range separation from most vaejovoid aggregates except for *Franckeus* + *Vaejovis* “nigrescens” group and *Vaejovis* “mexicanus” group, where we see less than 50 % overlap. It is also interesting to note that the median eye is quite small in *Pseudouroctonus* + *Uroctonites*. **Middle:** width of the median eye tubercle compared with the carapace median width. These data show complete standard error range separation from tribe Smeringurini and the other aggregates of Vaejoidea; tribe Paravaejovini exhibits the second widest median tubercle though is considerably distant from its sister tribe Smeringurini. Again, the aggregate *Pseudouroctonus* + *Uroctonites* shows the smallest median eye tubercle within Vaejoidea which is consistent with it also having relatively the smallest median eyes in the family. **Bottom:** position of the median eye tubercle compared with the carapace length. Although we see a continuous sequence of standard error range overlap, the end-points of these data illustrate the more medially positioned median tubercle in subfamily Smeringurinae, in contrast to *Pseudouroctonus* + *Uroctonites* whose median tubercle is located on the distal third of the carapace. In addition, aggregates *Franckeus* + “nigrescens” group and “mexicanus” group also exhibit a forward positioned median tubercle. Cara_L = carapace length; Cara_MW = carapace median width; MET_P = median eye tubercle position; MET_W = median eye tubercle width; MED = median eye diameter. See Fig. 127 for method of measurements.

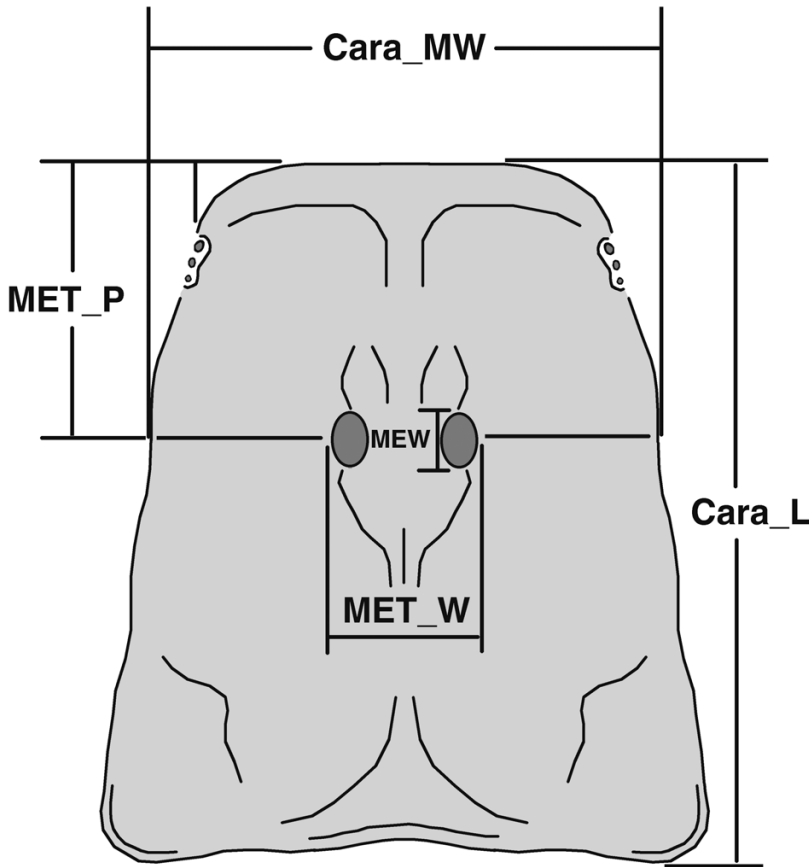


Figure 127: Method of measurements for carapace. Cara_L = carapace length; Cara_MW = carapace median width; MET_W = median eye tubercle width; MET_P = median eye tubercle position; and MED = median eye diameter.

tribe Syntropini; the armament of the vesicular tabs is used, in part, to differentiate genera in subfamily Smeringurinae.

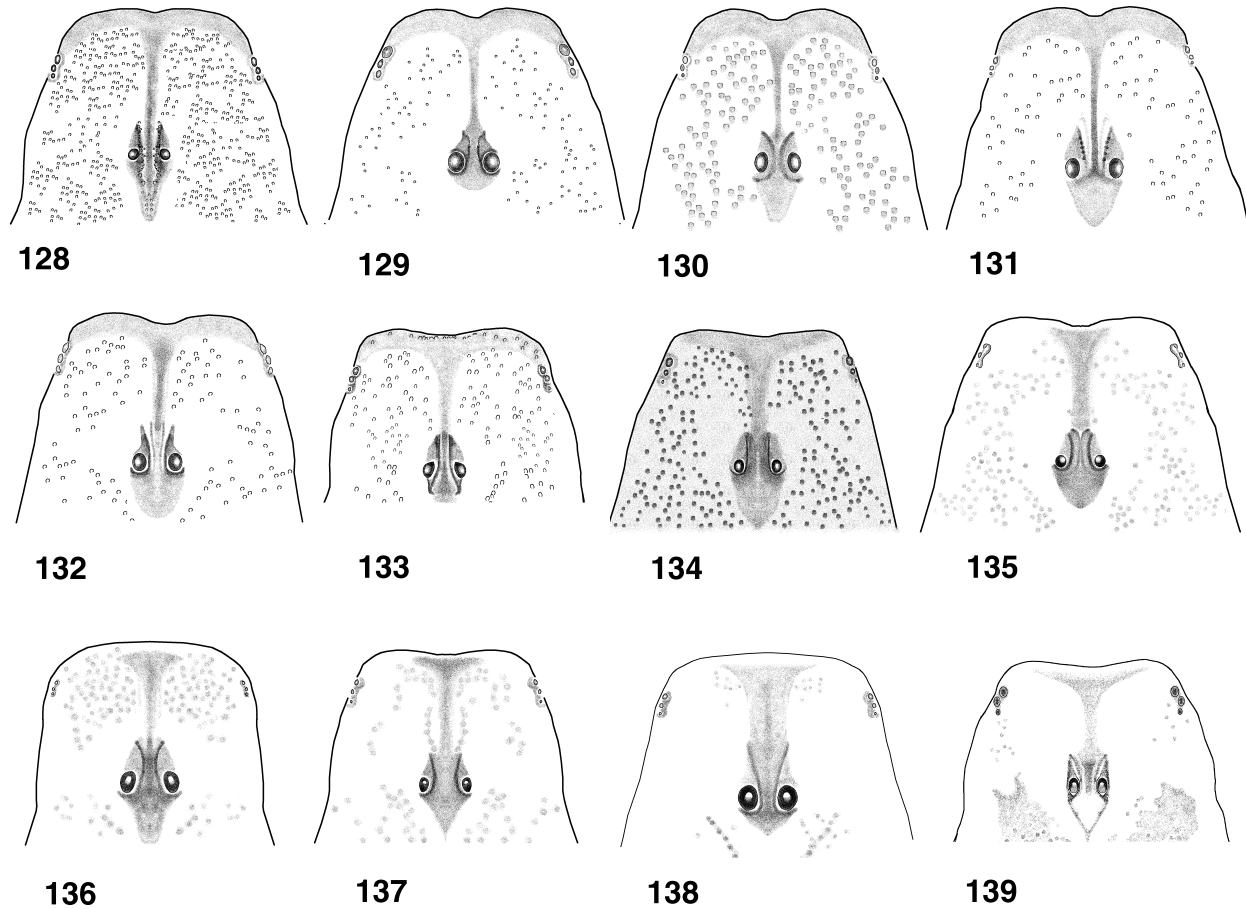
Syntropini. Figures 170–181 illustrate the lateral view of the telson of several species in tribe Syntropini spanning all four genera. The vesicle of genus *Hoffmannius* (Figs. 178–179) is quite enlarged basally, abruptly tapering towards the aculeus; that is, the thickest portion of the vesicle is proximal of its midpoint (measured from proximal base to the subaculear granules). In the other genera, the vesicle is more symmetrical laterally, the thickest point essentially located at the vesicle midpoint. In addition, telson morphometrics discussed elsewhere in this paper also support the enlargement of the vesicle base in *Hoffmannius*. The histograms in Figs. 192–193 show significant separation of *Hoffmannius* from genera *Thorellius* and *Kochius* for ratios involving the chelal palm depth as compared to the vesicle width and depth. Although the heavy chelate species of *Thorellius* and *Kochius* contributed to this ratio difference, the telson width and depth in *Hoffmannius* was equally a factor (see discussions below).

Smeringurinae. The development of the vesicular tabs is illustrated in Figs. 182–190 for species spanning both subfamilies Syntropinae and Smeringurinae. In particular, the development of the tab terminus is diagnostic in adults for genera of Smeringurinae.

The terminus of the vesicular tab is equipped with a slightly hooked spine, sometimes with additional subordinate granules at its base (e.g. in *Hoffmannius waeringi*, Fig. 182). In genus *Paruroctonus*, the terminal hooked spine is present, as illustrated for three species: *P. becki*, *P. silvestrii*, and *P. luteolus* (Figs. 185–187). For genera *Smeringurus*, *Paravaejovis*, and *Vejovoidus* (Figs. 188–190) the vesicular tab is very reduced and is lacking the terminal hooked spine in adults. In these three genera, the telson is more slender and/or elongated than that in most *Paruroctonus* species, which is possibly related to the reduced vesicular tab.

Morphometrics

Diagnostic value: Morphometrics are used to differentiate genera, in part, of subfamily Smeringurinae and tribe Syntropini.



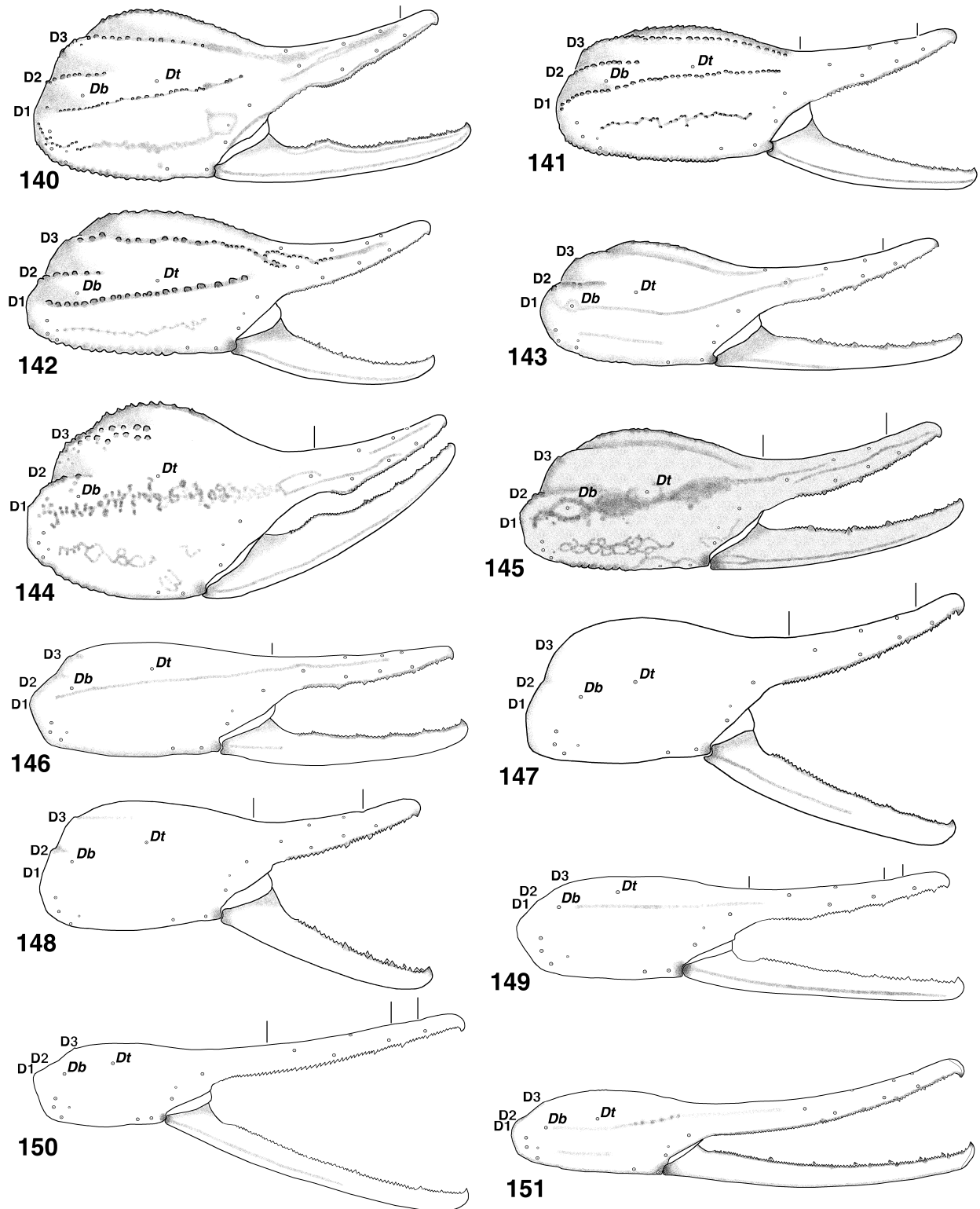
Figures 128–139: Carapace, anterior half, of representative Syntropini species, emphasizing differences in the *anterior emargination* and *median indentation*. **128.** *K. punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **129.** *K. bruneus loretoensis*, male, Loreto, Baja California Sur, Mexico. **130.** *K. hirsuticauda*, female, Indian Gorge Canyon, ABDSP, California, USA. **131.** *K. cazieri*, male, Cuatro Ciénegas, Coahuila, Mexico. **132.** *K. russelli*, female, Deming, New Mexico, USA. **133.** *K. kovariki*, female holotype, Durango, Durango, Mexico. **134.** *T. atrox*, female, Colima, Colima, Mexico. **135.** *T. cristimanus*, male, Autlán, Jalisco, Mexico. **136.** *H. eusthenura*, male, Cabo San Lucas, Baja California Sur, Mexico. **137.** *H. gravicaudus*, female, Santa Rosalia, Baja California Sur, Mexico. **138.** *H. globosus*, female, Zacatecas, Zacatecas, Mexico. **139.** *Syntropis aalbui*, holotype female, Cataviña, Baja California, Mexico (after Soleglad et al., 2007: fig. 17, in part).

Smeringurinae. Haradon (1983) defined a new subgenus *Smeringurus* comprised of five species and subspecies, with the type species *S. vachoni* (Stahnke, 1961). This subgenus was differentiated from *Paruroctonus* by the numerous irregularly placed setae occurring between the ventral median (*VM*) carinae of metasomal segments I–IV and having a significantly more slender metasoma. Stockwell (1992) established *Smeringurus* as a genus.

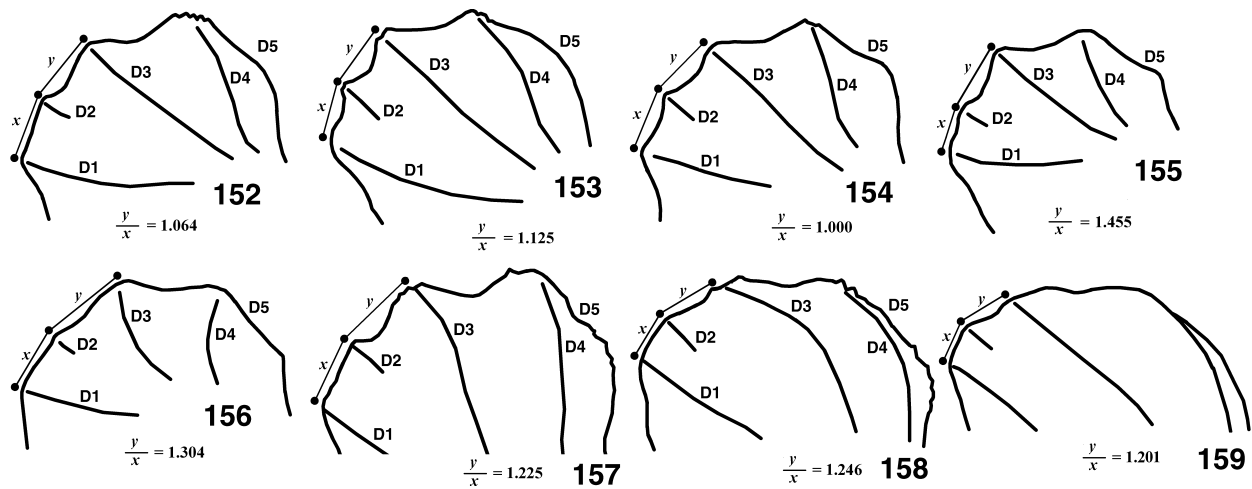
The slender metasoma found in *Smeringurus* is significant, in our opinion, and represents a valid diagnostic character. This is clear from the histograms presented in Fig. 191 showing morphometrics of metasomal segments I–IV (width-to-length ratios). In these data, where all genera and all species are represented, males and females are *combined*. This further illustrates the very slender metasoma of

Smeringurus as compared to the other three genera in Smeringurinae. Not only do we see complete separation of the standard deviation ranges, but the absolute ranges are separate as well. Mean value differences range from 150 to 300 % and resulting p-values from variance analysis are negligible exhibiting 13–14 fractional digits of significance. These data also show that genera *Vejovoidus* and *Paravaejovis* in general have the stockiest metasoma.

For genera *Smeringurus*, *Vejovoidus*, and *Paravaejovis*, additional specimens were measured, albeit most of the ratios were calculated from published data. In addition to material examined, the following references were used: Gertsch & Allred (1965), Gertsch & Soleglad (1966), Williams (1968b, 1969, 1970a, 1970b, 1972, 1980, 1987), Williams & Hadley (1967), Soleglad (1972), Sissom & Francke (1981), Hjelle



Figures 140–151: Chela, external view, of representative *Kochius*, *Thorellius*, *Hoffmannius*, and *Syntropis* species, showing carination and trichobothria pattern. In particular note the well developed subdigital (*D2*) carina, the mid-palm position of trichobothrium *Dt*, and location of *Db* dorsal of the digital (*D1*) carina. **140.** *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **141.** *K. hirsuticauda*, female, Indian Gorge Canyon, ABDSP, California, USA. **142.** *K. bruneus loretoensis*, male, Loreto, Baja California Sur, Mexico. **143.** *K. russelli*, female, Deming, New Mexico, USA. **144.** *Thorellius intrepidus*, male, Mexico. **145.** *T. atrox*, female, Colima, Colima, Mexico. **146.** *Hoffmannius eusthenura*, male, Cabo San Lucas, Baja California Sur, Mexico. **147.** *H. gravicaudus*, female, Santa Rosalia, Baja California Sur, Mexico. **148.** *H. globosus*, female, Zacatecas, Zacatecas, Mexico. **149.** *H. puritanus*, male, Jasper Trail, ABDSP, California, USA. **150.** *H. viscaianensis*, female, Las Bombas, Baja California Sur, Mexico. **151.** *Syntropis williamsi*, male paratype, Los Aripes, Baja California Sur, Mexico (after Soleglad et al., 2007: fig. 13, in part).



Figures 152–159: Diagrammatic view of chelal palm, proximal aspect, showing digital carinae (*D1–D5*). In particular, this perspective shows the profiled development of the subdigital (*D2*) carina and its relative position with respect to *D1* and *D3*. See Figs. 140–145 for lateral view of *D2* carina showing its relative length as compared to chelal palm length. **152.** *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **153.** *K. brunus loretoensis*, male, Loreto, Baja California Sur, Mexico. **154.** *K. hirsuticauda*, female, Indian Gorge Canyon, ABDSP, California, USA. **155.** *K. cazieri*, male, Cuatro Ciénegas, Coahuila, Mexico. **156.** *K. russelli*, female, Deming, New Mexico, USA. **157.** *Thorellius intrepidus*, male, Mexico. **158.** *T. cristimanus*, male, Autlán, Jalisco, Mexico. **159.** *T. atrox*, female, Colima, Colima, Mexico. *D1* = digital carina, *D2* = subdigital carina, *D3* = dorsosecondary carina, *D4* = dorsomarginal carina, *D5* = dorsointernal carina.

(1982), Haradon (1984a, 1984b, 1985), Sissom & Henson (1998).

Tribe Syntropini. Williams (1980: 49–55), in his key to the species groups of genus *Vaejovis* found in Baja California, Mexico, contrasts the heavily developed chela found in *Kochius* (referred to as the “punctipalpi” group) to the more slender chela found in *Hoffmannius* (referred to as the “eusthenura” group):

“... 16 (1). Pedipalp palm greatly swollen, ratio of movable-finger length to palm width 1.8 or less -----
---- 17

Pedipalp palm not greatly swollen, ratio of movable-finger length to palm greater than 1.8 ----- 30
[this isolates Williams’s “eusthenura” group which now is genus *Hoffmannius*] ...”.

In addition, Williams (1980) uses the relatively thin metasoma found in *Kochius* to differentiate it from another, also heavy chelate group now placed in genus *Pseudouroctonus*:

“...17 (16). Pectine teeth 15 or fewer in males, 14 or fewer in females; ratio of metasoma length to width of metasomal segment V equal to or less than 7.5; metasomal segment II as wide as or wider than long; metasomal segment IV with ratio of length to width 1.5 or less ----- 18 [this isolates species now placed in genus *Pseudouroctonus*]

Pectine teeth 16 or more in males, 15 or more in females; ratio of metasoma length to width of metasomal segment V greater than 7.5; metasomal

segment II longer than wide; metasomal segment IV with ratio of length to width greater than 1.5 -----
22 [this isolates Williams’s “punctipalpi” group now placed in genus *Kochius*] ...”.

Although we agree in general with Williams’s (1980) characterizations of these two assemblages of species, it is difficult to quantify these differences across all species to be used as “discrete” characters in a cladistic analysis. In order to fully understand these characterizations and others that may be present, we studied all morphometrics of these two genera along with genus *Thorellius*, the sister genus of *Kochius*.

Maximized ratios. We extracted a full set of measurements for a subset of species in genera *Hoffmannius* and *Kochius* where all possible morphometric ratios were compared: 300 resulting ratios based on 25 morphometrics. Each component of a ratio (i.e., its numerator and denominator) was analyzed as to its effect on the comparison between the two species sets. The measurements having the most effect across all ratio comparisons are considered measurements of potential diagnostic importance. To fully realize this, measurements having the most effect from *both* species sets must be combined in a ratio in order to *maximize* the ratio’s effect as diagnostic (see Fet & Soleglad, 2002: 5, for an explanation of this technique).

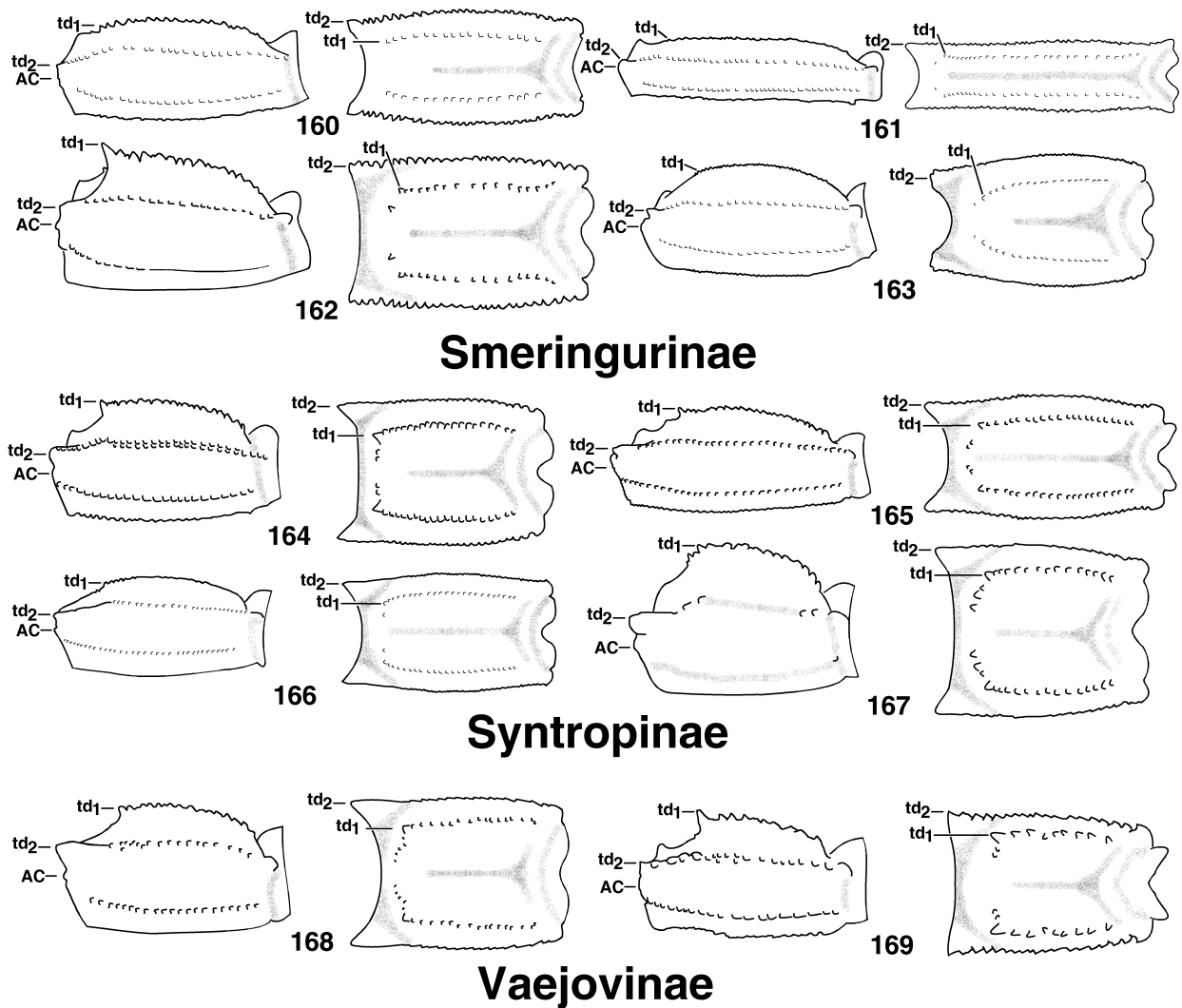
For genus *Kochius* two morphometrics dominated the ratio comparisons, the chelal palm depth and palm width. The palm depth dominated in all ratios (24 in all) and the palm width dominated in 23 ratios. For genus *Hoffmannius* five morphometrics dominated in most of

	Metasoma (L/W)										PD/ V_W	PD/ IV_W	PD/ TeIW	PD/ TeID	PW/ V_W	1/3M (I-IV) Carinae	Chela Carinae *
	I		II		III		IV		V								
<i>K. sonorae</i>	♂	0.947	1.176	1.375	1.800	2.400	-	-	1.333	1.818	2.222	1.133	8,8,8,8	4,4,4,4 x,x,x x			
	♀	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>K. russelli</i>	♂	0.960	1.130	1.217	1.682	2.429	1.000	0.955	1.313	1.500	1.500	0.905	2,2,6,6	3,3,4,4,4 6,x,x 1			
	♀	0.960	1.122	1.229	1.583	2.298	1.000	0.979	1.306	1.621	1.621	0.787	2,2,6,6	-			
<i>K. kovariki</i>	♂	-	-	-	-	-	-	-	-	-	-	-	-	-			
	♀	0.925	1.109	1.190	1.607	2.483	0.983	0.934	1.118	1.425	1.425	0.879	0,0,2,4	2,2,2,2,2 2,2,2 2			
<i>K. crassimanus</i>	♂	-	-	-	-	-	-	-	-	-	-	-	-	-			
	♀	1.000	1.194	1.257	1.706	2.625	1.188	1.118	1.357	1.462	1.462	1.125	3,7,7,7	3,3,3,3,3 3,3,3 3			
<i>K. punctipalpi</i>	♂	1.000	1.226	1.333	1.893	2.643	1.464	1.464	2.050	2.412	2.412	1.179	2,3,6,7	6,6,6,6 6,x,x 3			
	♀	0.923	1.108	1.286	1.875	2.594	1.531	1.531	2.227	2.579	2.579	1.188	2,3,6,7	-			
<i>K. atenango</i>	♂	1.000	1.206	1.375	1.871	2.759	1.069	1.000	0.969	1.632	1.632	1.000	1,3,3,7	4,?,4,4,4 ?,4,4 4			
	♀	0.944	1.083	1.294	1.844	2.594	0.938	0.938	1.034	1.364	1.364	1.000	-	-			
<i>K. cazieri</i>	♂	1.000	1.259	1.462	2.000	2.917	1.250	1.250	1.500	1.667	1.667	1.208	6,6,6,6	5,5,5,5,5 6,x,x,x 3			
	♀	1.000	1.242	1.303	1.781	2.677	1.290	1.250	1.429	1.819	1.819	1.226	6,6,6,6	-			
<i>K. bruneus</i>	♂	0.963	1.160	1.250	1.909	2.714	1.429	1.364	1.875	2.308	2.308	1.333	7,7,7,7	6,6,6,6,6 6,x,x,x 4			
	♀	1.000	1.226	1.379	1.926	2.920	1.440	1.333	1.800	2.250	2.250	1.360	7,7,7,7	-			
<i>K. insularis</i>	♂	1.000	1.250	1.391	1.818	2.750	1.350	1.227	1.688	2.250	2.250	1.250	8,8,8,8	4,4,4,4,4 x,x,x,x x			
	♀	0.933	1.286	1.357	1.846	2.792	1.417	1.308	1.889	2.429	2.429	1.250	8,8,8,8	-			
<i>K. magdalensis</i>	♂	1.000	1.292	1.391	1.955	2.762	1.333	1.273	2.000	2.333	2.333	1.143	3,3,3,7	5,5,5,5,5 x,x,x,x x			
	♀	0.929	1.231	1.360	1.875	2.773	1.364	1.250	2.000	2.500	2.500	1.182	3,3,3,7	-			
<i>K. hirsutaicauda</i>	♂	1.136	1.500	1.722	2.235	3.333	1.867	1.647	2.800	2.800	2.800	1.800	8,8,8,8	-			
	♀	1.100	1.444	1.706	2.333	3.462	1.769	1.533	2.556	2.556	2.556	1.538	8,8,8,8	6,6,6,6,6 6,x,x,x 4			
<i>T. atrox</i>	♂	-	-	-	-	-	-	-	-	-	-	-	-	-			
	♀	0.776	0.933	1.056	1.444	2.056	0.913	0.824	1.135	1.355	1.355	0.826	2,2,3,6	b,b,b,b,b b,b,b b			
<i>T. cristimanus</i>	♂	0.771	0.928	1.023	1.395	1.978	1.026	1.000	1.290	1.481	1.481	0.872	2,2,3,3	b,b,b,b,4 b,b,b,4 b			
	♀	0.717	0.846	0.953	1.313	1.913	1.318	1.261	1.526	1.871	1.871	0.909	1,1,3,6	-			
<i>T. intrepidus</i>	♂	0.990	1.173	1.245	1.734	2.250	1.383	1.327	1.625	1.711	1.711	1.064	2,2,2,3	b,4,4,4,4 b,b,b,4 b			
	♀	0.840	1.093	1.191	1.637	2.397	1.400	1.373	1.667	1.750	1.750	1.000	2,2,3,6	-			
<i>T. cisnerosi</i>	♂	0.986	1.192	1.222	1.586	2.197	1.091	1.029	1.469	1.714	1.714	0.848	0,0,0,0	1,1,1,1,1 1,1,1,1 1			
	♀	0.956	1.191	1.233	1.524	2.115	1.038	0.964	1.209	1.421	1.421	0.846	0,0,0,0	-			
<i>T. occidentalis</i>	♂	0.674	0.864	0.911	1.364	1.841	-	-	-	-	-	-	1,2,2,6	2,x,1,1,1 2,1,1 1			
	♀	0.833	0.957	1.014	1.296	1.912	0.743	0.703	1.040	1.238	1.238	0.629	2,2,2,5	2,1,2,2,2 b,2,2 1			
<i>T. suberistatus</i>	♂	0.906	1.094	1.194	1.600	2.333	1.067	1.067	1.280	1.524	1.524	0.917	1,1,1,2	1,1,1,1,1 1,1,1 1			
	♀	0.824	1.000	1.097	1.500	2.200	0.900	0.900	0.964	1.227	1.227	0.733	-	-			

Table 4: Select characters of genera *Kochius* and *Thorellius*. Ratios calculated from measurements taken from specimens examined, Gertsch & Allred (1965), Williams (1968, 1970, 1971a, 1971b), Stahnke (1973), Sissom (1989), Ponce Saavedra & Sissom (2004), Francke & González Santillán (2006). Order of species based on gross metasomal proportions, the more stocky metasoma first. Carinae codes: x = information not available, 0 = obsolete, 1 = vestigial-smooth, 2 = smooth, 3 = smooth-granular, 4 = granular, 5 = granular-crenulate, 6 = crenulate, 7 = crenulate-serrate, 8 = serrate, a = weak-marbled, b = strong marbled. * $D1-D5|V1-V3|E$.

	Metasoma (L/W)										PD/ V_W	PD/ IV_W	PD/ TeW	PD/ TeD	PW/ V_W	VM (I-IV) Carinae	Chela Carinae *
	I	II	III	IV	V												
<i>H. waueri</i>	♂ 0.818	-	0.818	1.238	1.714	-	0.524	0.733	0.917	-	0.476	0,0,0,0	1,1,1,1,1,1,1,1				
<i>H. bilineatus</i>	♂ 0.667	0.833	1.000	1.304	2.000	0.864	0.826	1.188	1.356	0.727	0.643	0,0,0,0	1,1,1,1,1,1,1,1				
<i>H. gravicaudus</i>	♂ 0.804	0.933	0.978	1.261	1.783	0.800	0.674	0.838	1.107	0.652	0.482	0,0,0,0,0,0,0,0	0,0,0,0,0,0,0,0				
<i>H. punctatus</i>	♂ 0.742	0.860	0.900	1.151	1.625	0.900	0.500	0.609	0.848	0.721	0.697	0,0,0,0	0,0,0,0,0,0,0,0				
<i>H. spinigerus</i>	♂ 0.772	0.900	0.967	1.279	1.869	0.885	0.885	1.350	1.742	0.721	0.697	-	-				
<i>H. vittatus</i>	♂ 0.743	0.838	0.925	1.235	1.818	0.848	0.824	0.982	1.333	0.667	0.667	0,0,0,0	0,0,0,0,0,0,0,0				
<i>H. eusthenura</i>	♂ 0.769	0.882	0.955	1.265	1.826	0.655	0.735	0.943	1.136	0.654	0.556	0,0,0,1	0,0,0,0,0,0,0,0				
<i>H. diazi</i>	♂ 0.882	0.828	0.929	1.250	1.852	0.731	0.607	0.950	1.267	0.625	0.577	0,0,1,2	0,0,0,0,0,0,0,0				
<i>H. hoffmanni</i>	♂ 0.815	0.938	1.031	1.438	1.969	0.635	0.688	0.778	1.158	0.542	0.577	0,0,0,0	0,0,0,0,0,0,0,0				
<i>H. coahuilae</i>	♂ 0.833	0.962	1.080	1.400	2.000	0.622	0.640	0.727	0.889	0.607	0.577	-	-				
<i>H. waeringi</i>	♂ 0.941	0.971	1.029	1.343	2.088	0.897	0.800	1.000	1.217	0.857	0.794	0,3,3,7	1,1,1,1,1,1,1,1				
<i>H. globosus</i>	♂ 0.880	1.088	1.152	1.529	2.094	0.531	0.500	0.630	0.810	0.438	0.526	2,2,2,3	2,1,3,3,3,2,2,2,1				
<i>H. confusus</i>	♂ 0.833	0.958	1.043	1.455	2.318	0.579	0.783	0.947	1.125	0.818	0.727	3,3,6,7	1,1,1,1,1,1,1,1				
<i>H. galbus</i>	♂ 0.958	1.200	1.200	1.538	2.115	0.818	0.818	0.818	1.000	0.538	0.571	1,2,3,6	1,1,1,1,1,1,1,1				
<i>H. glabrimanus</i>	♂ 0.944	0.970	1.061	1.371	1.800	0.629	0.629	0.688	0.957	0.720	0.720	-	-				
<i>H. puritanus</i>	♂ 0.895	1.125	1.167	1.565	2.125	0.667	0.696	0.842	1.067	0.583	0.583	1,1,1,1	0,0,0,0,0,0,0,0				
<i>H. viscaïnensis</i>	♂ 1.071	1.038	1.120	1.440	2.080	0.840	0.840	0.913	1.167	0.923	0.923	1,1,1,3	1,1,1,1,1,1,1,1				
	♂ 1.034	1.286	1.407	1.885	2.833	0.942	0.560	0.778	0.933	0.500	0.583	-	-				
	♀ 1.029	1.265	1.364	1.813	2.406	0.813	0.813	0.897	1.083	0.719	0.719	1,1,1,2	1,1,1,1,1,1,1,1				
	♀ 0.895	1.053	1.167	1.571	2.364	0.636	0.600	0.636	0.808	0.606	0.606	-	-				
	♂ 1.071	1.308	1.423	1.920	2.792	0.583	0.560	0.778	0.933	0.500	0.583	2,2,3,4	1,1,1,1,1,1,1,1				
	♀ 1.034	1.286	1.407	1.885	2.833	0.667	0.615	0.727	0.889	0.583	0.583	-	-				

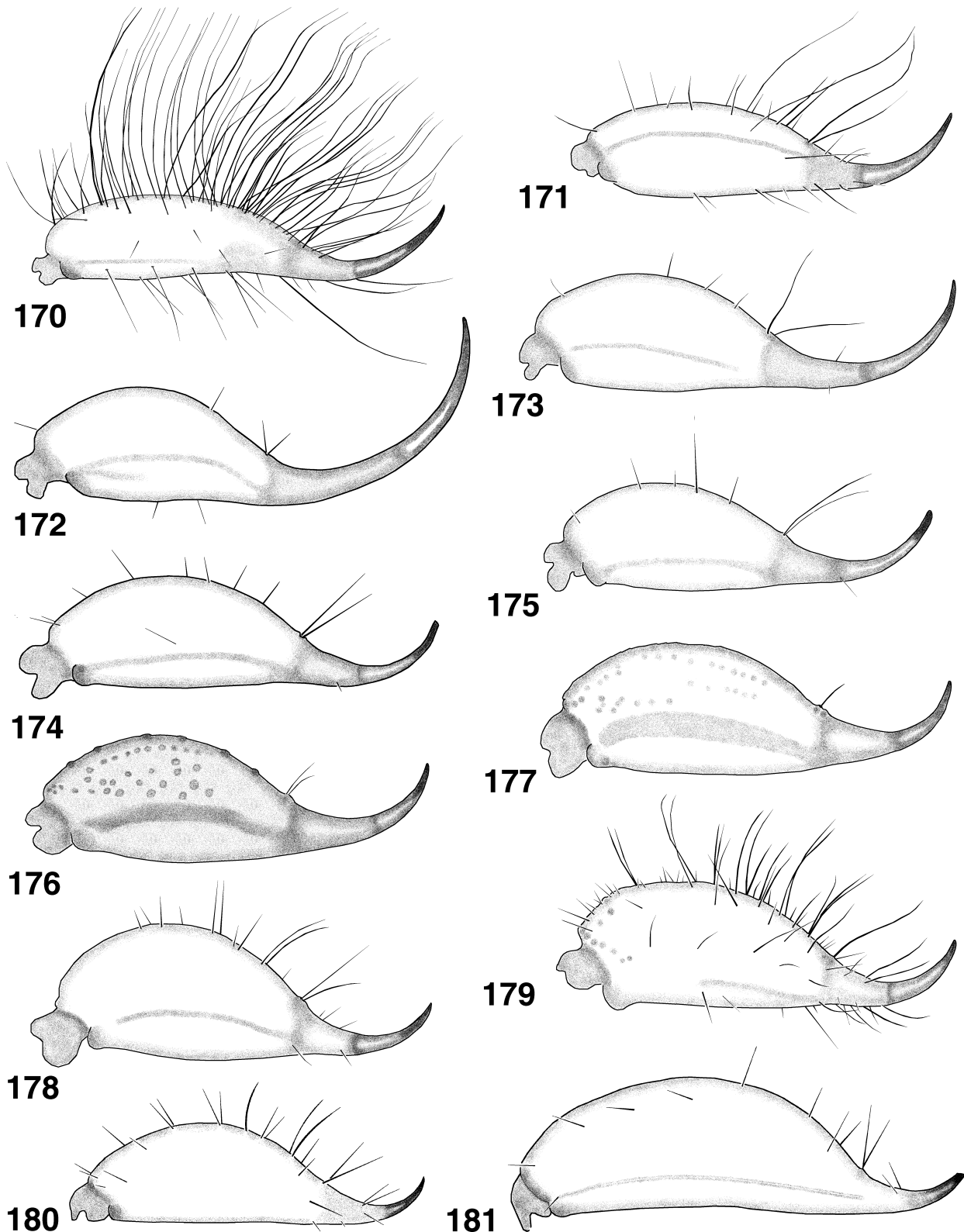
Table 5: Select characters of genus *Hoffmannius*. Ratios calculated from measurements taken from specimens examined, Hoffmann (1931), Gertsch (1958), Gertsch & Allred (1965), Gertsch & Soleglad (1972), Williams (1970c, 1970d, 1986), Yahia & Sissom (1996), Sissom & Hendrixson (2005). Order of species based on gross metasomal proportions, the more stocky metasoma first. Carinae codes: x = information not available, 0 = obsolete, 1 = vestigial-smooth, 2 = smooth, 3 = smooth-granular, 4 = granular, 5 = granular-crenulate, 6 = crenulate, 7 = crenulate-serrate, 8 = serrate. * D_{I-D5}/V_{I-V3E} .



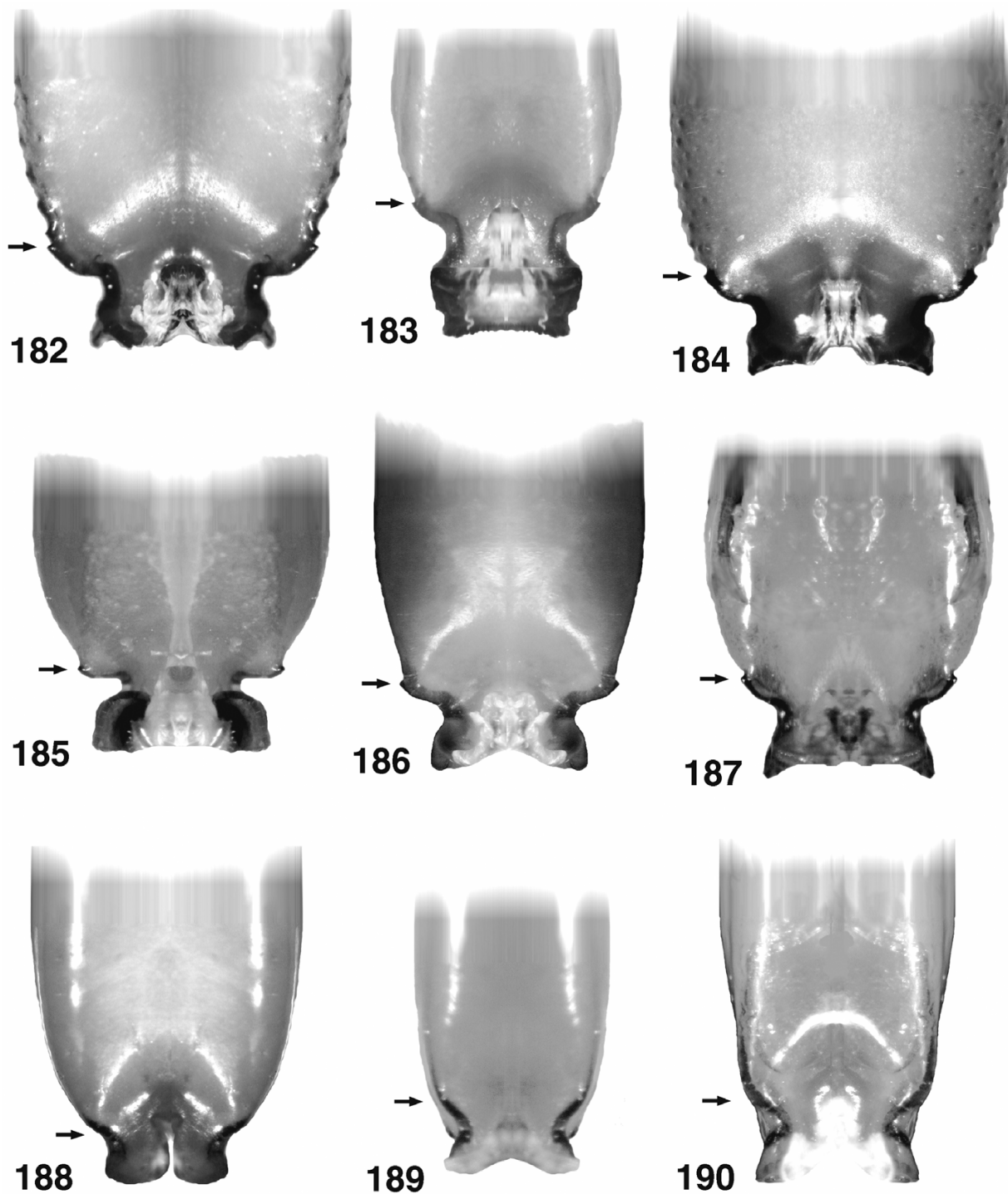
Figures 160–169: Metasomal segment IV, lateral and dorsal views, showing development of the terminus of the dorsal (*D*) and dorsolateral (*DL*) carinae for the three subfamilies of Vaejoidea. Subfamily **Smeringurinae**: **160.** *Paruroctonus stahnkei*, male, Mesa, Arizona, USA. **161.** *Smeringurus aridus*, male, ABDSP, California, USA. **162.** *Vejovoides longiunguis*, male, Las Bombas, Baja California Sur, Mexico. **163.** *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. Subfamily **Syntropinae**: **164.** *Stahnkeus subtilimanus*, ABDSP, California, USA. **165.** *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **166.** *Hoffmannius viscaïnensis*, male, Las Bombas, Baja California Sur, Mexico. **167.** *Hoffmannius gravicaudus*, female, Santa Rosalia, Baja California Sur, Mexico. Subfamily **Vaejovinae**: **168.** *Vaejovis solegladi*, female, Cuicatlan, Oaxaca, Mexico. **169.** *Pseudouroctonus reddelli*, male, Comal Co., Texas, USA. AC = articulation condyle, td₁ = terminal denticle of dorsal carina, td₂ = terminal denticle of dorsolateral carina. After Soleglad & Fet (2003b), in part.

the ratios in which they were involved: the width of metasomal segment V (all 24 ratios) and segment IV (21 ratios), and the telson vesicle width (23 ratios), depth (22 ratios) and telson length (19 ratios). These results, in part, are not surprising, when reflecting on diagnostic descriptions and keys of Williams (1970d, 1980) discussing the “punctipalpi” and “eusthenura” groups, in particular, the large robust chela in *Kochius* and the heavy metasoma in *Hoffmannius*. Our results did, however, uncover the relatively large telson exhibited in *Hoffmannius* as compared to *Kochius* (and *Thorellius*, see below), a character not previously disclosed.

Interestingly, the other three metasomal segment widths in *Hoffmannius* also dominated in the majority of the ratios in which they were involved but not as significantly as in segments V and IV: segment III, 18 out of 24 ratios, segment II, 17 ratios, and segment I, 16 ratios. This dominance of the metasoma segment’s width definitely implies that the metasoma in *Hoffmannius* is significantly wider than in *Kochius*. Similarly, consistent with the heavy chelal palm, the chela length in *Kochius* also dominated in its ratios, 22 out of 24. To further emphasize a thinner metasoma in *Kochius*, ratio comparisons for segment II–V lengths dominated in this



Figures 170–181: Telson, lateral view, of representative Syntropini species. **170.** *Kochius hirsuticauda*, female, Indian Gorge Canyon, ABDSP, California, USA. **171.** *K. bruneus loretoensis*, male, Loreto, Baja California Sur, Mexico. **172.** *K. punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **173.** *K. punctipalpi punctipalpi*, male, Los Aripes, Baja California Sur, Mexico. Note the significant sexual dimorphism in this species. **174.** *K. cazieri*, male, Cuatro Ciénegas, Coahuila, Mexico. **175.** *K. russelli* female, Deming, New Mexico, USA. **176.** *Thorellius atrox*, female, Colima, Colima, Mexico. **177.** *T. cristimanus*, male, Autlán, Jalisco, Mexico. **178.** *Hoffmannius globosus*, female, Zacatecas, Zacatecas, Mexico. **179.** *H. eusthenura*, male, Cabo San Lucas, Baja California Sur, Mexico. **180.** *Syntropis williamsi*, female holotype, Los Aripes, Baja California Sur, Mexico. **181.** *S. macrura*, female, Isla Carmen, Baja California Sur, Mexico. (Figs. 180, 181 after Soleglad et al., 2007, in part).



Figures 182–190: Base of telson vesicle, dorsal view, showing development of vesicular “tabs” (pointed to by *arrow*) in subfamilies Syntropinae and Smeringurinae. Note the reduced tabs, the sharp granules essentially obsolete, in *Smeringurus*, *Paravaejovis*, and *Vejovoidis*, whereas in *Paruroctonus* and subfamily Syntropinae, the spine is distinct and well developed. **182.** *Hoffmannius waeringi*, male, Indian Gorge Canyon, ABDSP, California, USA. **183.** *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico. **184.** *Stahnkeus subtilimanus*, female, Split Mountain, ABDSP, California, USA. **185.** *Paruroctonus becki*, male, Cottonwood Springs, Joshua Tree National Monument, California, USA. **186.** *Paruroctonus silvestrii*, Chihuahua Road, ABDSP, California, USA. **187.** *Paruroctonus luteolus*, male, Palo Verde Wash, ABDSP, California, USA. **188.** *Smeringurus mesaensis*, female, Palo Verde Wash, ABDSP, California, USA. **189.** *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. **190.** *Vejovoidis longiunguis*, female, Las Bombas, Baja California Sur, Mexico.

genus (whereas *widths* dominated in *Hoffmannius*) ranging from 13 to 17 ratios out of 24.

Based on this analysis, we constructed ten morphometric ratios for all species, including both

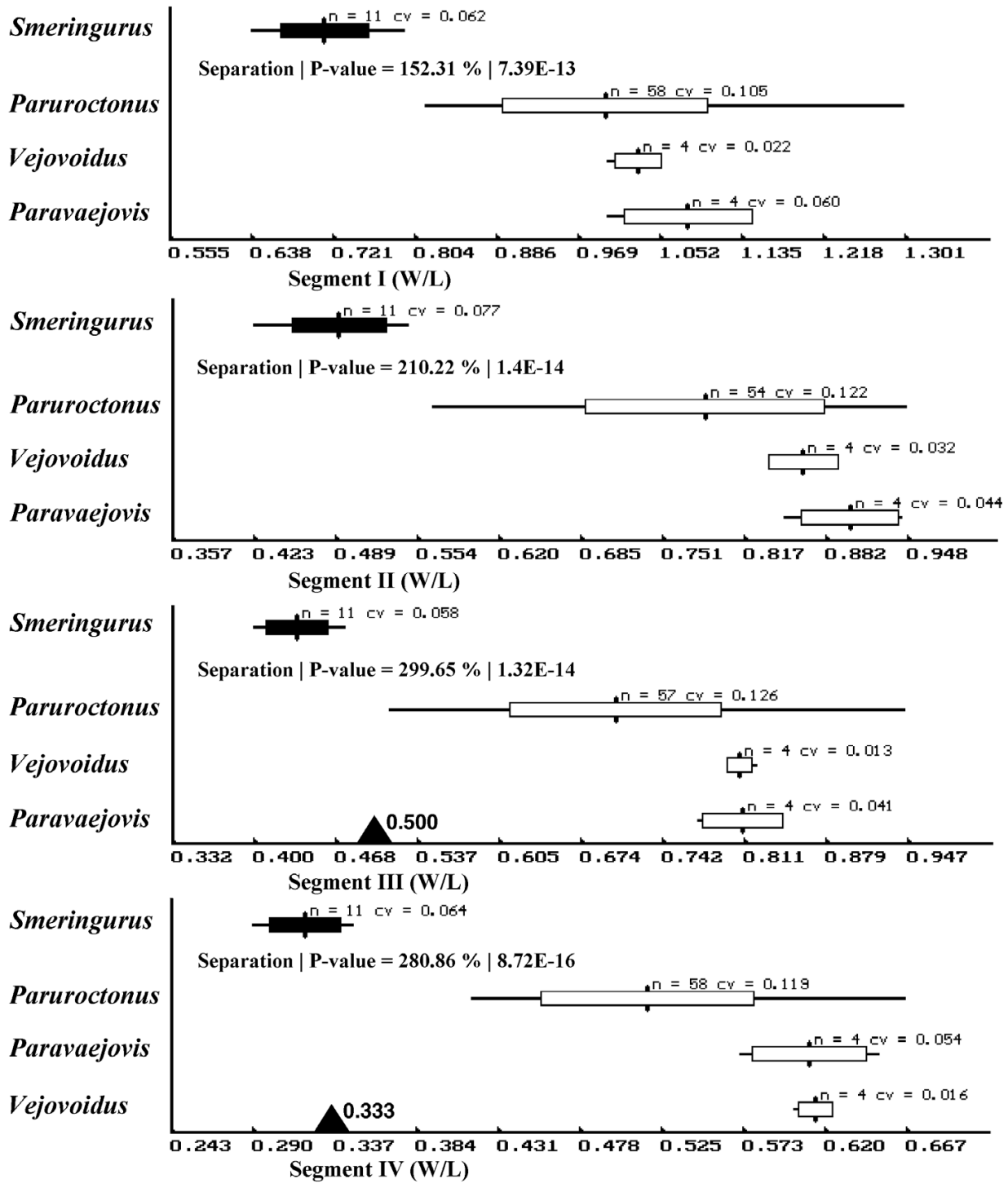


Figure 191: Metasomal segment (I–IV) proportions for subfamily Smeringurinae (ratios = segment width / segment length). Data include both adult males and females combined. These data show that *Smeringurus* segments are significantly thinner than in the other three genera, not only showing complete separation between standard error ranges, but for all data points. Statistical difference between *Smeringurus* and *Paruroctonus* is indicated by significant standard error separation and the negligible variance analysis value (p-value). In addition, segment III is at least twice as long as wide (indicated by 0.500 triangle marker) and segment IV is in general three times as long as wide (indicated by 0.333 triangle marker). The other genera cluster together, with *Vejovoidus* and *Paravaejovis* exhibiting the most stocky metasoma. The data, which encompass all species currently defined in Smeringurinae, were gathered from measurements calculated in this study as well as published measurements, primarily from those sources where the species were originally described (i.e., most measurements are from type specimens). See Fig. 1 for explanation of histogram components.

		<i>Kochius</i>		<i>Thorellius</i>		<i>Hoffmannius</i>	
PD/	♂	1.00 – 1.87 (1.344) (±0.249) [9]	1.03 – 1.38 (1.142) (±0.163) [4]	0.53 – 0.94 (0.723) (±0.134) [16]			
V_W	♀	0.94 – 1.77 (1.292) (±0.268) [10]	0.74 – 1.40 (1.052) (±0.257) [6]	0.50 – 0.85 (0.678) (±0.109) [16]			
PD/	♂	0.95 – 1.65 (1.279) (±0.214) [9]	1.00 – 1.33 (1.105) (±0.150) [4]	0.50 – 0.96 (0.716) (±0.134) [16]			
IV_W	♀	0.93 – 1.53 (1.217) (±0.223) [10]	0.70 – 1.37 (1.004) (±0.260) [6]	0.52 – 0.84 (0.673) (±0.103) [16]			
PD/	♂	0.97 – 2.80 (1.779) (±0.517) [9]	1.28 – 1.62 (1.416) (±0.164) [4]	0.63 – 1.35 (0.925) (±0.205) [16]			
TelW	♀	1.03 – 2.56 (1.672) (±0.502) [10]	0.96 – 1.67 (1.257) (±0.279) [6]	0.61 – 1.00 (0.788) (±0.124) [16]			
PD/	♂	1.50 – 2.80 (2.125) (±0.431) [9]	1.48 – 1.71 (1.608) (±0.122) [4]	0.79 – 1.74 (1.136) (±0.248) [16]			
TelID	♀	1.36 – 2.58 (2.000) (±0.510) [10]	1.23 – 1.87 (1.477) (±0.271) [6]	0.79 – 1.33 (0.999) (±0.161) [16]			
PD/	♂	0.42 – 0.93 (0.650) (±0.172) [9]	0.47 – 0.59 (0.520) (±0.057) [4]	0.23 – 0.52 (0.359) (±0.078) [16]			
TelL	♀	0.39 – 0.70 (0.532) (±0.088) [10]	0.40 – 0.64 (0.499) (±0.099) [6]	0.25 – 0.47 (0.344) (±0.060) [15]			
PW/	♂	0.90 – 1.80 (1.217) (±0.253) [9]	0.85 – 1.06 (0.925) (±0.097) [4]	0.44 – 0.92 (0.653) (±0.134) [16]			
V_W	♀	0.79 – 1.54 (1.154) (±0.221) [10]	0.63 – 1.00 (0.824) (±0.130) [6]	0.48 – 0.79 (0.613) (±0.089) [16]			
PW/	♂	0.86 – 1.59 (1.156) (±0.207) [9]	0.80 – 1.02 (0.897) (±0.095) [4]	0.41 – 0.94 (0.647) (±0.134) [16]			
IV_W	♀	0.77 – 1.33 (1.087) (±0.178) [10]	0.59 – 0.98 (0.785) (±0.131) [6]	0.48 – 0.77 (0.609) (±0.085) [16]			
PW/	♂	0.91 – 2.70 (1.607) (±0.491) [9]	1.10 – 1.25 (1.147) (±0.072) [4]	0.52 – 1.20 (0.832) (±0.179) [16]			
TelW	♀	1.00 – 2.22 (1.482) (±0.393) [10]	0.79 – 1.19 (0.987) (±0.141) [6]	0.59 – 0.96 (0.713) (±0.105) [16]			
PW/	♂	1.36 – 2.70 (1.918) (±0.398) [9]	1.26 – 1.33 (1.304) (±0.032) [4]	0.67 – 1.42 (1.022) (±0.212) [16]			
TelID	♀	1.27 – 2.22 (1.777) (±0.397) [10]	1.00 – 1.29 (1.162) (±0.116) [6]	0.71 – 1.17 (0.904) (±0.129) [16]			
PW/	♂	0.39 – 0.90 (0.588) (±0.165) [9]	0.40 – 0.45 (0.422) (±0.024) [4]	0.20 – 0.44 (0.323) (±0.068) [16]			
TelL	♀	0.37 – 0.57 (0.475) (±0.065) [10]	0.32 – 0.45 (0.393) (±0.046) [6]	0.22 – 0.39 (0.311) (±0.048) [15]			

Table 6: Statistical data for genera *Hoffmannius*, *Kochius*, and *Thorellius* based on maximized morphometric ratios. The data show that genus *Kochius* exhibits the larger mean value in all cases as does *Hoffmannius* the smallest, showing differences ranging from 53.3 % to 112.4 % between the two. *Thorellius* is always intermediate. Shaded data denote complete absolute separation of ranges. See Figures 192–193 for histograms of these data and variance analysis p-values. Data = minimum–maximum (mean) (± standard deviation) [number of samples]. PD = palm depth; PW = palm width; V_W = metasomal segment V width; IV_W = metasomal segment IV width; TelL = telson length; TelW = telson width; TelID = telson depth.

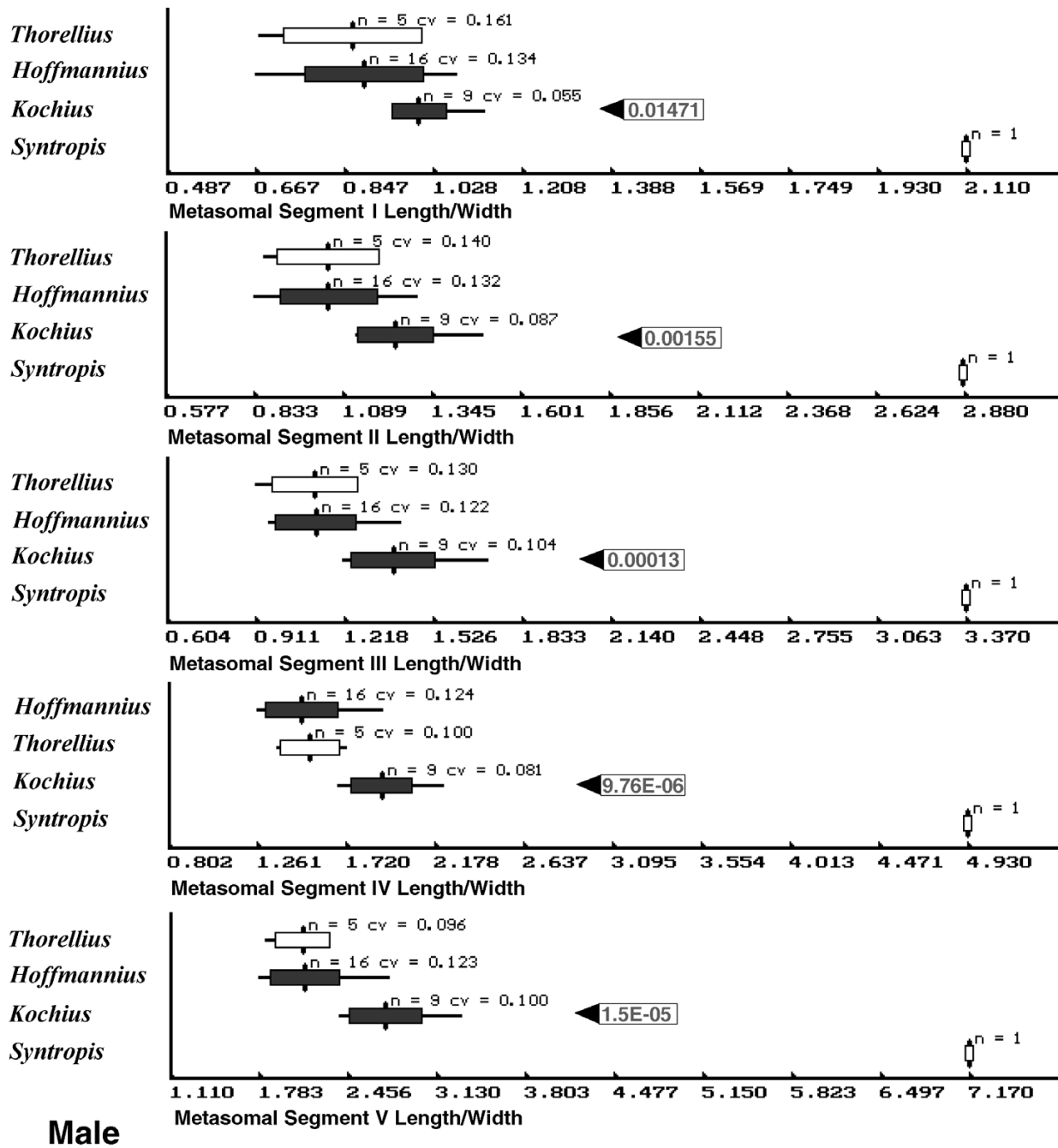


Figure 194: Morphometric ratios contrasting metasomal segments (length/width) for species in tribe Syntropini (male). Variance analysis p-values depicted in rectangles, *Hoffmannius* as compared to *Kochius*. Statistically significant p-values (i.e., very small) indicated with black arrow. See Fig. 1 for explanation of histogram components.

to Guerrero. Species *K. cazieri*, from Coahuila, Mexico, and *K. crassimanus* from southern Texas, are intermediate in these ratios.

In genus *Thorellius*, the species with generally the higher ratio values are *T. intrepidus* and *T. cristimanus*. Both of these species have very robust chelae. Species *T. subcristatus* and *T. occidentalis* exhibit less robust

chelae and therefore show lower ratio values. *T. cisnerosi* and *T. atrox* are intermediate. It is interesting to point out that the ratio values for *T. intrepidus* and *T. cristimanus* are lower than those that dominate in *Kochius* species, such as *K. hirsuticauda*. This is due to the heavier metasoma (see below) and larger telson found in genus *Thorellius*.

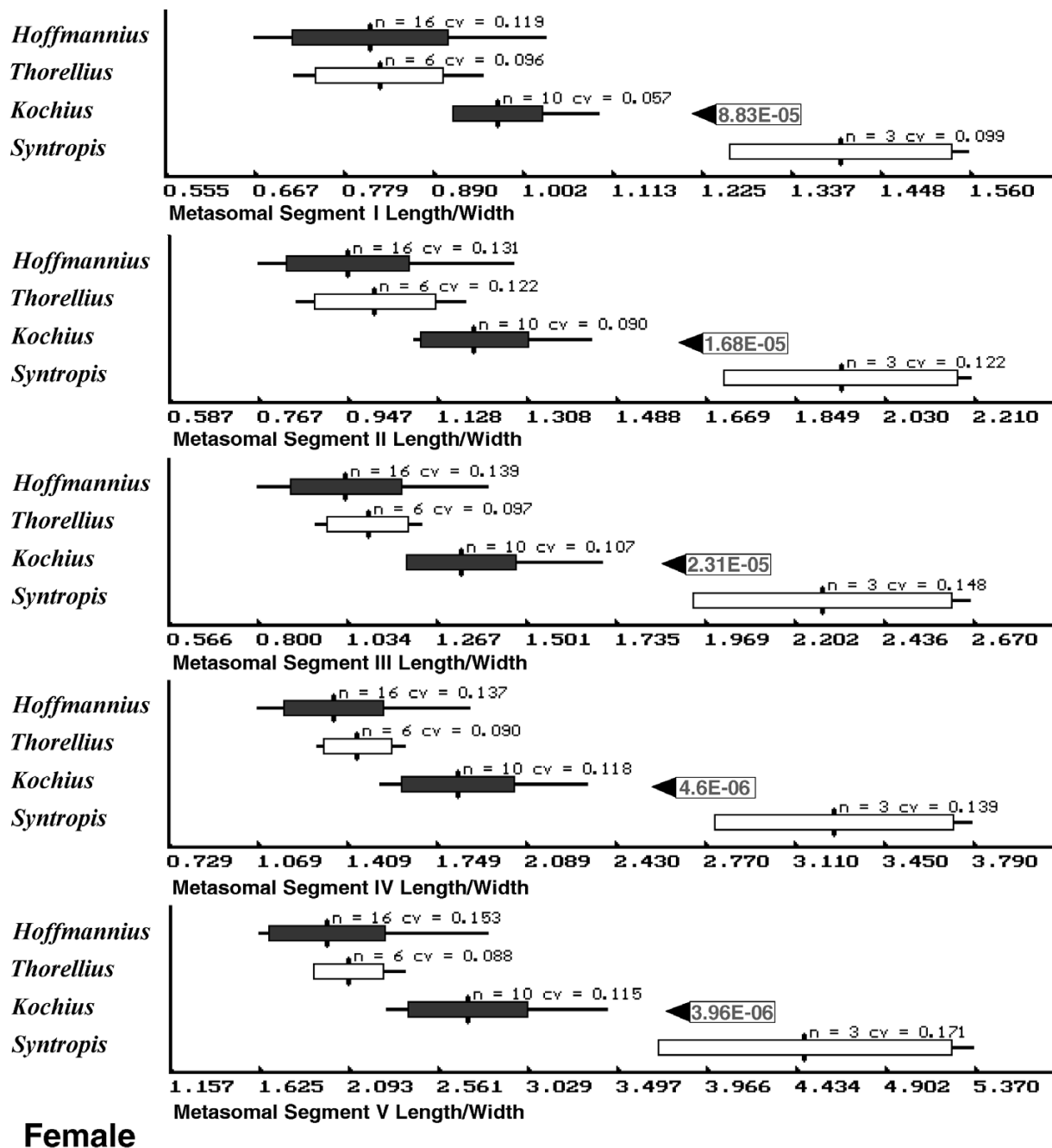


Figure 195: Morphometric ratios contrasting metasomal segments (length/width) for species in tribe Syntropini (female). Variance analysis p-values depicted in rectangles, *Hoffmannius* as compared to *Kochius*. Statistically significant p-values (i.e., very small) indicated with black arrow. See Fig. 1 for explanation of histogram components.

For genus *Hoffmannius*, there is a great variability in these ratio values, caused in most part by several species exhibiting somewhat heavy chelae, whereas others have longer and thinner chelae; all, however, have wide robust metasomas and telsons. Since dominant morphometrics for *Hoffmannius* form the denominator in the ratios, species with the smallest ratio values are typical of this genus. These species include *H. waeringi*,

H. gravicaudus, and *H. waueri*. In *H. puritanus*, *H. glabrimanus*, and *H. coahuilae*, ratio values are somewhat large due to their relatively thin metasoma (see below).

Metasoma ratios. We also analyzed the relative heaviness of the metasomal segments where we formed ratios for each segment, length divided by its width. Tables 4–5 show these data on a species and gender

basis, and Figures 194–195 show histograms for both genders of all four genera comprising tribe Syntropini.

The proportional differences in the metasoma for tribe Syntropini provide excellent diagnostic characters for its four genera. Figures 194–195 shows histograms of all five metasomal segments for the four genera. First and foremost, genus *Syntropis* has a very slender metasoma for both genders. All five segments are longer than wide, segment five, on average, is well over four times longer than wide, whereas in the other genera, the average is well under three times longer. Genus *Kochius* exhibits the next most slender metasoma, showing significant standard error differences in segments III–V, exhibiting very small p-values as compared to *Hoffmannius*, ranging from 0.00013 to 3.96E-06. The mean value difference between segments III–V for the two genera with the most slender metasomas, *Syntropis* and *Kochius*, are very significant: 71–166 %, 78–159 %, and 65–161 % percentage of difference (includes both male and female), thus further emphasizing a very slender metasoma of *Syntropis*. Genera *Hoffmannius* and *Thorellius* metasomal morphometrics are essentially the same, as seen in the histograms, standard deviation ranges essentially overlapped.

Of particular interest is a comparison between genera *Kochius* and *Hoffmannius*. Although we observe essential separation of standard deviation ranges for segments III–V, exhibiting a 24–29 %, 28–34 %, and 28–37 % percentage of difference between the mean values (includes both male and female), the two genera do overlap in some “end-point” species (i.e., an overlap between the most slender *Hoffmannius* and the most stocky *Kochius*). In Tables 4–5 (where the taxa are roughly ordered from the stockiest to thinnest metasomas), *H. puritanus* and *H. viscainensis*, the species with the thinnest metasoma in *Hoffmannius*, overlap with *Kochius sonoreae* and *K. russelli*, the more stocky members of *Kochius*. At the other extreme, if we compare the mean value difference between the thinnest male *Kochius* (*K. hirsuticauda*) and the stockiest *Hoffmannius* (*H. gravicaudus*), we see a 87 % percent difference for segment V. Therefore, with the significant mean value differences exhibited and the standard error separation, we consider these differences in metasomal segment morphometrics to be significant and therefore a legitimate diagnostic character. Although we see these trends for all five metasomal segments, we only establish segments III–V as significant since they exhibit standard error range separation. It must be pointed out, however, that, although the metasomal segments III–V provide important diagnostic characters, they do not show the absolute range separation as exhibited in some of the maximized ratios discussed above.

The morphometrics presented in this effort were gathered primarily from literature but several specimens were measured when necessary. The following ref-

rences provided morphometric data: Hoffmann (1931), Gertsch & Allred (1965), Gertsch & Soleglad (1972), Williams (1968a, 1970a, 1970b, 1971a, 1971b, 1980, 1986), Stahnke (1973), Sissom (1989b), Ponce Saavedra & Sissom (2004), Sissom & Hendrixson (2005), and Francke & González Santillán (2006).

Pectines

Diagnostic value: Pectinal tooth counts are used to differentiate tribes in subfamily Syntropinae.

Syntropinae. Soleglad & Fet (2003b: 61–65, figs. 110–113) discussed the number of pectinal teeth as it related to the mature size of the scorpion species, in particular, contrasting the four chactoid families, Chactidae, Euscorpiidae, Superstitioniidae, and Vaejovidae. In is interesting to point out here that this analysis by Soleglad & Fet (2003b) was based on the original observation of Soleglad (1973b: figs. 13–14) that within closely related species sets (e.g., a genus) the number of pectinal teeth is proportional to the scorpion species adult size; that is, larger species in a related species set will exhibit a larger pectinal tooth count than a smaller species in that same set. And, important to taxonomic analysis, the ratios derived from these comparisons differ across different species sets, thus providing a gross diagnostic indicator at the genus level or higher. In their analysis, based primarily on published data, Soleglad & Fet (2003b) demonstrated that pectinal tooth numbers in the family Vaejovidae is considerably higher than that found in the other three chactoid families, exhibiting, on average, an increase exceeding well over 100 % (i.e., as it relates to the species mature size). Consequently, a character was established in their cladistic analysis (character 103), where the more developed pectines was shown to be a synapomorphy for family Vaejovidae. See Soleglad & Fet (2003b: appendix D) for details and assumptions used in their analysis.

In this analysis, the data were recalculated to include all vaejovid species where the information was available (149 species). In particular, we use this metric to establish a significant difference in pectinal tooth numbers between the two tribes of subfamily Syntropinae, with that of tribe Stahnkeini being considerably higher (i.e., the ratio value is smaller) than that found in Syntropini. This was also discussed in Soleglad & Fet (2006).

The Total Length (TL)/Pectinal Tooth Count (PTC) ratios (female only) by genus are as follows (min–max (mean) (sdev) (sdev-range) [n]):

$$Gertschius = 1.517–1.923 (1.720) [2]$$

$$Serradigitus = 1.429–2.484 (1.942) [15]$$

	Pectinal Tooth Counts		Ratio
	♂	♀	♂/♀ *
<i>Paravaejovis pumilis</i>	12-16	7-8	1.867
<i>Paruroctonus ammonastes</i>	19-21	12-16	1.429
<i>P. arenicola</i>	23-29	17-22	1.333
<i>P. arnaudi</i>	26-31	21-25	1.239
<i>P. baergi</i>	18-23	14-15	1.414
<i>P. bajae</i>	19-22	14	1.464
<i>P. bantai</i>	23	17	1.353
<i>P. becki</i>	24-29	17-21	1.395
<i>P. boquillas</i>	23-28	17-23	1.275
<i>P. boreus</i>	25-31	18-23	1.366
<i>P. borregoensis</i>	15-18	9-11	1.650
<i>P. coahuilanus</i>	18-22	-	-
<i>P. gracilior</i>	25-31	17-20	1.514
<i>P. hirsutipes</i>	26-27	13-15	1.893
<i>P. luteolus</i>	16-19	11-15	1.346
<i>P. maritimus</i>	24-27	18-20	1.342
<i>P. marksi</i>	23-28	17-21	1.342
<i>P. nitidus</i>	-	17-18	-
<i>P. pecos</i>	20-22	13-15	1.500
<i>P. pseudopumilis</i>	17-18	9-10	1.842
<i>P. shulovi</i>	19-20	13-15	1.393
<i>P. silvestrii</i>	25-29	18-24	1.286
<i>P. simulatus</i>	18-24	12-17	1.448
<i>P. stahnkei</i>	20-23	14-15	1.483
<i>P. surensis</i>	17-19	8-9	2.118
<i>P. utahensis</i>	27-31	17-21	1.526
<i>P. variabilis</i>	25-31	21-25	1.217
<i>P. ventosus</i>	17	11-13	1.417
<i>P. williamsi</i>	19-23	14	1.500
<i>P. xanthus</i>	-	21-22	-
<i>Paruroctonus</i>, non-shaded	Mean = 1.402		
<i>Paruroctonus</i>, shaded	Mean = 1.951		
<i>Smeringurus aridus</i>	33-36	23	1.500
<i>S. grandis</i>	30-35	22-26	1.354
<i>S. mesaensis</i>	31-39	21-27	1.458
<i>S. vachoni vachoni</i>	33-36	23-27	1.380
<i>S. vachoni immanis</i>	31-34	21-26	1.383
<i>Smeringurus</i>	Mean = 1.415		
<i>Vejevovoidus longiunguis</i>	28-35	24-31	1.145

Table 7: Pectinal tooth counts of subfamily Smeringurinae. * Based on linear midpoint of respective ranges. Shaded species indicate female gender with considerably less pectinal teeth, ratio greater than 1.800, showing a 38 % difference when comparing the means. Also note that the pectinal tooth counts of genders quite close numerically in *Vejevovoidus*, exhibiting a ratio of 1.145. In *Smeringurus*, ratio value is in-line with that of the non-shaded *Paruroctonus*. All data extracted from literature.

Stahnkeus = 1.667–2.217 (2.041) [5]
Wernerius = 1.573–2.227 (1.900) [2]
 tribe **Stahnkeini** = 1.429–2.484 (1.941) (± 0.351)
 (1.590–2.292) [24]

Hoffmannius = 2.083–4.583 (3.134) [16]
Syntropis = 2.800–3.286 (2.992) [3]
Kochius = 2.355–4.071 (3.172) [10]
Thorellius = 2.703–3.767 (3.236) [6]
 tribe **Syntropini** = 2.083–4.583 (3.150) (± 0.602)
 (2.548–3.753) [35]

We can see that there is a 62.3 % difference in the mean values between the two tribes as well as complete separation of the standard error range. It is also important to point out that, except for four small species in genus *Hoffmannius* (i.e., *H. waueri*, *H. bilineatus*, *H. vittatus*, and *H. hoffmanni*), which had the smallest ratio values in Syntropini, there is no overlap in the absolute ranges between the two tribes. For completeness, we provide these data for the other vaejovid genera:

Paruroctonus = 1.851–3.586 (2.548) [27]
Smeringurus = 2.917–3.600 (3.214) [4]
Vejovoidus = 2.182–2.182 (2.182) [1]
Paravaejovis = 3.200–3.200 (3.200) [1]
 subfamily **Smeringurinae** = 1.851–4.118 (2.747)
 [33]

Pseudouroctonus = 2.444–4.909 (3.459) [12]
Uroctonites = 3.684–5.333 (4.531) [4]
Franckeus = 1.786–2.800 (2.442) [6]
Vaejovis “nigrescens” = 2.353–4.200 (2.992) [11]
Vaejovis “mexicanus” = 1.586–3.059 (2.137) [24]

Smeringurinae. Haradon’s (1984b) observation of similarities of sexual dimorphism between genus *Paravaejovis* and members of his “borregoensis” microgroup, as discussed elsewhere in this paper, is reflected in the large differences in the pectinal tooth counts between genders. In Table 7 we present a comparison of the pectinal tooth counts between genders for all species of subfamily Smeringurinae. Except for three species in the “borregoensis” microgroup, *Paruroctonus* and *Smeringurus* pectinal tooth numbers are approximately 1.4 times higher in the male. For species *P. hirsutipes*, *P. pseudopumilis*, and *P. surensis*, the female pectinal tooth numbers are somewhat smaller, the male exhibiting almost twice as many pectinal teeth (mean = 1.951). Similarly, in genus *Paravaejovis*, the pectinal tooth number in males almost doubles that in females (ratio = 1.867). However, we must point out that most members of the “borregoensis” microgroup do not fall into the range of *Paravaejovis*, but instead are consistent with other species in *Paruroctonus*, i.e., *P. luteolus*, *P. borregoensis*, *P. ventosus*, *P. bajae*, and *P.*

ammonastes. Finally, in genus *Vejovoidus* the difference in pectinal tooth counts between the genders is minimal, only 1.145 times higher in the male.

Granulation quotients

Granulation “quotients” deal with the degree of development of carinae: whether they are vestigial, smooth, irregularly granulate, serrate, etc. In general, as is the case with morphometrics, granulation is usually considered a “species-level” diagnostic character. That is, for any genus with a large set of species, the entire spectrum of degrees of granulation can be expected. Granulation quotients assume the existence of a carina, even if it is designated as “obsolete” by a researcher. The actual existence or absence of a carina is a much more significant event with respect to the evolution of a taxon than its degree of granulation (i.e., smooth, granular, or crenulate.) For example, the ventromedian (*VM*) carinae of the metasomal segments I–IV, where we can observe singular or paired carinae, is a somewhat high-level derivation as seen throughout Recent scorpions. The existence of two *VM* carinae on segment V as seen in both species of the relict scorpion family Pseudochactidae is unprecedented in Recent scorpions, all others exhibiting a single carina. A lesser carinal consideration than the previous two just mentioned is the more developed subdigital (*D2*) carina as seen in syntropine subtribe Thorelliina. This development, however, as with the other examples, is more significant than the simple observation or classification of a carina’s granulation quotient.

We have tabulated the granulation quotient for every species currently placed in family Vaejoidea (see Table 8). This quotient includes both the ventromedian (*VM*) carinae of metasomal segments I–IV and the dorsal carinae, *D1*, *D3*, *D4*, and *D5*, of the chelae. The subdigital (*D2*) carina is excluded from the quotient calculation since it is vestigial in most vaejovid species, thus its state as smooth, granulate, crenulate, etc. is not determinable (only genera *Kochius* and *Thorellius* exhibit a well developed *D2* carina, see discussion elsewhere in this paper). The *VM* carinae of the metasoma exhibit the most variability in Vaejoidea and therefore these carinae are the best candidate for potentially categorizing species assemblages. Similarly, the chelal dorsal carinae also reflect high variability and, important to these calculations, were usually characterized by numerous scorpologists who described and investigated many species from Vaejoidea. Some of this data is presented in Tables 4 and 5 at a species level for the syntropine genera *Hoffmannius*, *Kochius*, and *Thorellius*. In this section, we discuss these granulation quotients for the entire family. In general, as reflected in Tables 4, 5, and 8, the *VM* carina granulation quotient increases from the basal segments to the terminal

	Ventromedian (<i>VM</i>) Carinae (I–IV)	Chelal Carinae (<i>D1–D5</i> *)
Smeringurinae: Smeringurini		
<i>Paruroctonus</i> (29)	0–3 (1.00), 0–3 (1.55), 0–4 (1.86), 0–5 (3.00) QUO = 1.85 [smooth]	1–5 (3.79), 1–5 (3.79), 1–5 (3.83), 1–5 (3.83) QUO = 3.81 [granular]
<i>Smeringurus</i> (4)	0–4 (2.25), 2–4 (3.25), 2–4 (3.25), 4–5 (4.25) QUO = 3.25 [smooth to granular]	4–5 (4.75), 4–5 (4.75), 4–5 (4.75), 4–5 (4.75) QUO = 4.75 [granular to crenulate]
<i>Vejooidus</i> (1)	0 (0.00), 0 (0.00), 1 (1.00), 3 (3.00) QUO = 1.00 [vestigial to smooth]	3 (3.00), 3 (3.00), 3 (3.00), 3 (3.00) QUO = 3.00 [smooth to granular]
Smeringurinae: Paravaejovini		
<i>Paravaejovis</i> (1)	1 (1.00), 2 (2.00), 3 (3.00), 3 (3.00) QUO = 2.25 [smooth]	0 (0.00), 0 (0.00), 0 (0.00), 0 (0.00) QUO = 0.00 [obsolete]
Syntropinae: Stahnkeini		
<i>Gertschius</i> (2)	0 (0.00), 0 (0.00), 0–3 (1.50), 2–3 (2.50) QUO = 1.00 [vestigial to smooth]	2 (2.00), 2 (2.00), 4 (4.00), 4 (4.00) QUO = 3.00 [smooth to granular]
<i>Serradigitus</i> (18)	0–6 (2.28), 0–6 (2.94), 0–7 (3.67), 0–7 (4.22) QUO = 3.28 [smooth to granular]	0–3 (1.89), 0–3 (1.89), 0–4 (2.61), 0–4 (2.61) QUO = 2.25 [smooth]
<i>Stahnkeus</i> (5)	1–4 (2.80), 1–7 (3.80), 1–7 (4.80), 3–7 (5.80) QUO = 4.30 [granular]	2–4 (2.40), 2–4 (2.80), 2–4 (3.00), 2–4 (3.00) QUO = 2.80 [smooth to granular]
<i>Wernerius</i> (2)	3–5 (4.00), 6–7 (6.50), 7 (7.00), 7–8 (7.50) QUO = 6.25 [crenulate]	2 (2.00), 3 (3.00), 3 (3.00), 3 (3.00) QUO = 2.75 [smooth to granular]
Syntropinae: Syntropini		
<i>Hoffmannius</i> (17)	0–3 (0.65), 0–3 (0.88), 0–6 (1.24), 0–7 (2.12) QUO = 1.22 [vestigial to smooth]	0–2 (0.59), 0–3 (0.65), 0–3 (0.65), 0–3 (0.65) QUO = 0.64 [obsolete to vestigial]
<i>Syntropis</i> (3)	1 (1.00), 2 (2.00), 2–3 (2.33), 3–4 (3.67) QUO = 2.25 [smooth]	2 (2.00), 2 (2.00), 3 (3.00), 3 (3.00) QUO = 2.50 [smooth to granular]
<i>Kochius</i> (11)	0–8 (4.36), 0–8 (5.00), 2–8 (5.82), 4–8 (6.82) QUO = 5.50 [granular to crenulate]	2–6 (4.36), 2–6 (4.45), 2–6 (4.45), 2–6 (4.45) QUO = 4.43 [granular]
<i>Thorellius</i> (6)	0–2 (1.33), 0–2 (1.42), 0–3 (1.92), 0–6 (3.75) QUO = 2.11 [smooth]	1–b (3.67), 1–b (3.25), 1–b (2.92), 1–b (2.92) QUO = 3.19 [smooth to granular]
Vaejovinae		
<i>Franckeus</i> (5)	0–3 (0.83), 0–4 (1.00), 0–4 (1.33), 0–4 (1.50) QUO = 1.17 [vestigial to smooth]	1–4 (2.17), 1–4 (2.50), 3–4 (3.17), 3–4 (3.17) QUO = 2.75 [smooth to granular]
<i>Pseudouroctonus</i> (14)	2–5 (4.79), 5 (5.00), 5–8 (5.21), 5–8 (5.21) QUO = 5.05 [granular to crenulate]	2–4 (2.93), 2–4 (3.14), 3–4 (3.50), 3–4 (3.71) QUO = 3.32 [smooth to granular]
<i>Uroctonites</i> (4)	5 (5.00), 5 (5.00), 5 (5.00), 5 (5.00) QUO = 5.00 [granular to crenulate]	2–4 (2.50), 4 (4.00), 4 (4.00), 4 (4.00) QUO = 3.63 [granular]
<i>Vaejovis</i> “mexicanus” (28)	1–8 (3.32), 1–8 (4.25), 1–8 (4.61), 1–8 (4.86) QUO = 4.26 [granular]	1–4 (1.86), 1–4 (2.04), 1–4 (2.43), 1–4 (2.79) QUO = 2.28 [smooth]
<i>Vaejovis</i> “nigrescens” (12)	0–5 (1.25), 0–5 (1.92), 0–5 (2.25), 0–5 (2.50) QUO = 1.98 [smooth]	1–4 (2.58), 1–4 (2.83), 1–4 (3.08), 2–4 (3.25) QUO = 2.94 [smooth to granular]

Table 8: Granulation quotients for ventromedian (*VM*) carinae of metasomal segments I–IV and dorsal carinae (*D1*, *D3*, *D4*, *D5*) of pedipalp chela for family Vaejovidae. Data, which represent all species currently defined for Vaejovidae, are based on specimens examined and literature. Number accompanying genus name is number of species included. Per carina: minimum – maximum (mean). QUO = quotient (mean of segments I–IV or carinae *D1–D5*). Carinae codes: 0 = obsolete, 1 = vestigial-smooth, 2 = smooth, 3 = smooth-granular, 4 = granular, 5 = granular-crenulate, 6 = crenulate, 7 = crenulate-serrate, 8 = serrate, a = weak-marbled, b = strong marbled (note in the calculations, a and b are mapped to values 5 and 6). * *D2* (sub-digital) not included.

segment, segment IV usually having the highest quotient. For the chelal dorsal carinae, the internal carinae, *D4* and *D5* are usually granulate to some degree, except for those few species that do not exhibit carinae at all.

Smeringurinae. In Table 8 we see that the granulation quotient for the *VM* carinae for the smeringurines is somewhat low, ranging from vestigial–

smooth to smooth–granular. Monotypic genus *Vejooidus* exhibits a very weak *VM* carina throughout segments I–III, whereas genus *Smeringurus* shows the most developed *VM* carinae, with segments II–III at least smooth in development. *Paruroctonus*, the genus with the most species in this subfamily, shows the most variability: Species *P. nitidus*, *P. variabilis*, and *P. bajae* exhibiting very weak *VM* carinae, whereas *P. marksii*, *P.*

coahuilanus, and *P. stahnkei* with well developed *VM* carina, all at least smooth if not granulate.

In contrast to the somewhat low granulation quotient for the *VM* carinae, we see in Smeringurinae a high quotient for the chelal dorsal carinae, in particular genera *Paruroctonus* and *Smeringurus*. For these two genera we have a granulation quotient ranging from granular to granular-crenulate. The scorpions of these two genera are heavy chelate species, and most exhibit well defined carinae with granulation. Notable exceptions to this in *Paruroctonus* are *P. nitidus* with vestigial to smooth carinae and *P. arnaudi* and *P. hirsutipes* with smooth carinae. Genera *Vejovoidus* and *Paravaejovis* show weaker chelal carination, especially *Paravaejovis* whose palm is shiny and smooth, without any traces of carinae.

Syntropinae. In tribe **Stahnkeini** we see a very weak development of the *VM* carinae in *Gertschius*, vestigial-smooth. This is in stark contrast with the other three genera whose *VM* carinae quotient ranges from smooth-granular to crenulate. In particular, these carinae are very well developed in *Wernerius*. In *Serradigitus*, the largest genus in the tribe, we see the complete spectrum of *VM* development: *S. giganteensis*, *S. dwyeri*, and *S. minutis* with essentially obsolete-vestigial development, to *S. gertschi*, *S. joshuaensis*, *S. armandensis*, and *S. littoralis* with *VM* carinae granulate to crenulate. In genus *Stahnkeus*, the *VM* carinae are well developed, granular to crenulate-serrate, with *S. harbisoni* exhibiting the weakest carinae, smooth-granular.

The dorsal chelal carinae seen in tribe Stahnkeini are well developed, though not crenulate, but generally smooth-granular. Genus *Serradigitus* has the smoothest dorsal carinae with species *S. baueri* exhibiting essentially obsolete carinae and *S. bechteli* and *S. adcocki* with vestigial carinae. Species *S. wupatkiensis*, *S. gramenestris*, *S. littoralis*, and *S. torridus* show the most granulated dorsal carinae, smooth to granular.

In tribe **Syntropini**, *Hoffmannius* exhibits by far the least developed *VM* carinae, its granulation quotient vestigial-smooth. Roughly half of its species (see Table 5) have obsolete-vestigial quotients, such as, *H. bilineatus*, *H. spinigerus*, *H. hoffmanni*, etc. Species with the most developed *VM* carinae, ranging from smooth to smooth-granular, are represented by *H. coahuilae*, *H. confusus*, and *H. viscainensis*. *H. globosus* has the most developed *VM* carinae, all at least granular with the terminal segments crenulate. *Kochius* species, in contrast with *Hoffmannius*, have very well developed *VM* carinae, with a large majority exhibiting smooth-granular to serrate quotients (see Table 4). The smoothest *VM* carinae are seen in species *K. kovariki* and *K. atenango*. Genera *Syntropis* (*VM* singular) and *Thorellius* show smooth *VM* carinae throughout most of its species set. For *Thorellius*, species *T. subcristatus*

and *T. cisnerosi* exhibit the weakest development, the latter with obsolete *VM* carinae.

As was the case with the *VM* carinae, *Hoffmannius* has by far the least developed chelal dorsal carinae in tribe Syntropini, with a obsolete-vestigial quotient. In Table 5 we see no less than ten species with obsolete dorsal carinae (*H. spinigerus*, *H. diazi*, *H. galbus*, *H. eusthenura*, etc.) and six other species with obsolete-vestigial carinae (*H. confusus*, *H. puritanus*, etc.). *H. waeringi* shows the most developed chelal dorsal carinae, smooth to smooth-granular. Subtribe Thorelliina (i.e., genera *Kochius* and *Thorellius*), have the most developed chelal dorsal carinae in tribe Syntropini, with smooth-granular to granular quotients. These well developed carinae contribute to the heavy chelate appearance of these scorpions. As was the case for the *VM* carinae, *Kochius* exhibits the most developed dorsal carinae, especially in the species from Baja California (*K. punctipalpi*, *K. bruneus*, etc.), with a quotient ranging from granular to crenulate. In *Thorellius*, *T. intrepidus*, *T. cristimanus*, and *T. atrox* have the more stronger developed carinae whereas *T. subcristatus* and *T. cisnerosi* have vestigial to smooth carinal development. *Syntropis* species chelal dorsal carinae are moderately developed, smooth-crenulate.

Vaejovinae. Genera *Pseudouroctonus* and *Uroctonites* have very well developed *VM* carinae, granular-crenulate, by far the most developed in subfamily Vaejovinae. All species in these two genera comply, showing no variability. The “mexicanus” group of *Vaejovis* also exhibits well developed *VM* carinae with a granular quotient. This group, however, shows some variability with species *V. granulatus*, *V. setosus*, and *V. franckei* with vestigial-smooth carination of the basal segments, and *V. kuarapu* reflecting this condition for all four metasomal segments. Otherwise, the species in the “mexicanus” group are granular to crenulate. Related assemblages, *Franckeus* and the “nigrescens” group of *Vaejovis*, exhibit a less developed *VM* carinae, vestigial to smooth, though there is some variability present. In *Franckeus*, *F. rubrimanus* has granular *VM* carinae and in the “nigrescens” group species *V. norteno*, *V. davidi*, and *V. gracilis* all exhibit granulate to crenulate carinae.

Genera *Uroctonites* and *Pseudouroctonus* are heavy chelate species and their dorsal carination contributes to this appearance, exhibiting a smooth to granular quotient. Again, as with the *VM* carinae, these two genera do not show significant variability within the species. *Franckeus* and the “nigrescens” group of *Vaejovis* have smooth-granular chelal dorsal carinae, with species *F. platnicki* and *V. pococki* showing less developed carinae, vestigial-smooth. The “mexicanus” group of *Vaejovis* has the least developed chelal dorsal carinae in Vaejovinae with a quotient of smooth with several species with only vestigial carinae, *V.*

granulatus, *V. kuarapu*, *V. nayarit*, *V. pattersoni*, and *V. tessellatus*.

Summary. In Table 8 we summarize the granulation quotients of all genera and species groups for the family Vaejovidae. Incorporating this Table with the detailed discussion above that considered the variability within these assemblages, we can make the following observations: 1) Since, in general, except for genus *Hoffmannius*, we see at least smooth quotients for all taxa groups for both the *VM* carinae and the chelal dorsal carinae, we can hypothesize that the overall reduction in carinal development seen in *Hoffmannius* is derived. In line with this, we suggest those few species in *Hoffmannius* that exhibit more development of these carinae are also derivations from the less developed state show in the genus as a whole; 2) the heavy chelate scorpions of *Pseudouroctonus* and *Uroctonites*, accented by well developed dorsal carinae, is a derivation within the subfamily Vaejovinae. These modified chelae are further emphasized by the reduction of the ventromedian (*V2*) carina, also considered a derivation for these closely related genera. The heavily developed *VM* carinae of *Pseudouroctonus* and *Uroctonites* is also considered a potential derivation for this assemblage within Vaejovidae; 3) the exaggerated carinal development of the chelal as seen in subtribe Thorelliina can be considered a derivation within the subfamily Syntropinae.

Systematics

In this section, we present a formal set of diagnoses detailing the family, subfamilies, tribes, subtribes, and genera of Vaejovidae. In particular, subfamilies Smeringurinae and Syntropinae are discussed in detail. The general distribution and list of species are presented for all three subfamilies. Note that any exceptions exhibited by taxa to any of the diagnostic characters stated below are considered to be derivations of these taxa. A detailed key follows to subfamilies, tribes, subtribes, and genera.

Order **SCORPIONES** C. L. Koch, 1850
 Suborder Neoscorpiones Thorell et Lindström, 1885
 Infraorder Orthosterni Pocock, 1911
 Parvorder Iurida Soleglad et Fet, 2003
 Superfamily Chactoidea Pocock, 1893

Family Vaejovidae Thorell, 1876

Type Genus. *Vaejovis* C. L. Koch, 1836.

Composition. The family Vaejovidae, as accepted in this paper, includes three subfamilies: Smeringurinae, Syntropinae, and Vaejovinae.

Distribution. North America: Canada (southwest, only *Paruroctonus boreus*), USA (northwest, southwest, southeast), Mexico.

Subfamily Smeringurinae is found in the United States and Baja California peninsula (Mexico), but is essentially absent from mainland Mexico (except for a few species found on the United States-Mexico border, and the solitary species *Paruroctonus gracilior* which is found as far south as the Mexican state of Aguascalientes (see map in Fig. 197)).

Subfamilies Syntropinae and Vaejovinae occur in the United States and throughout mainland Mexico (see maps in Figs. 202–207). In subfamily Syntropinae, the distribution of tribe Stahnkeini (see map in Fig. 202) is similar to that of Smeringurinae, its species primarily occurring in the United States and Baja California peninsula, with isolated representation in the northern Mexican states of Sonora and Coahuila. Tribe Syntropini (see maps in Figs. 203–204) is widespread throughout United States and Mexico (including Baja California peninsula). In subtribe Syntropina (Fig. 203), genus *Hoffmannius* occurs throughout this range, having the largest range of any vaejovid genus, while the small genus *Syntropis* is endemic to Baja California. Subtribe Thorelliina (Fig. 204) is represented in portions of southern United States and Baja California by genus *Kochius*, and in southern mainland Mexico by genus *Thorellius*.

Subfamily Vaejovinae occurs predominantly in mainland Mexico, with major disjunct parts of its range in southeastern United States (the solitary species *Vaejovis carolinianus*), southwestern United States, and Baja California peninsula.

Diagnosis. Scorpions in the family Vaejovidae can be distinguished by the following characters: The trichobothrial pattern of the chelal fixed finger *est-esb-eb* juncture angles towards the fixed finger edge, *eb* angles towards the dorsal edge; *ib-it* pair is located on the finger, not on the palm; *V1-V4* series extends most of the palm length and *V1-V2-V3* juncture is straight, not angled towards the internal condyle; patellar trichobothrium *v3* is located on the external surface; femoral trichobothrium *d* is located next to the dorsoexternal carina and is proximal of trichobothrium *i*; laterobasal aculear serrations (LAS; Fet et al., 2006b) are present at the base of the telson aculeus; ventromedian (*VM*) carina of metasomal segment V is continuous and well developed posteriorly, exhibiting no significant irregularities, bifurcations, or the presence of a ventral transverse carina (*VTC*); chelal finger median (*MD*) denticle row groups are aligned in a straight line; inner accessory (*IAD*) and outer accessory (*OAD*) denticles are not present; genital operculum of the female is not separated its entire length, but instead is connected at least for the anterior half; the pedipalp patellar *DPS_c* carina is well developed; the terminus of the dorsolateral (*DL*) carina is flared, not coinciding with the articulation condyle; hemispermatophore lamellar hook present; total length / pectinal tooth count ratio

mean value of female is under 3.00, ranging from 2.8 to 2.9.

Discussion. The phylogram in Fig. 196 shows the basic topology of family Vaejovidae with all subfamilies, tribes, subtribes, and genera delineated. Table 9 shows the taxonomy down to the species and subspecies level. See below for taxonomic history of all subordinate family-group and genus-group taxa.

**Subfamily Smeringurinae Soleglad et Fet,
subfam. nov.**

Type Genus. *Smeringurus* Haradon, 1983.

Composition. This subfamily, established here, includes the tribes Smeringurini and Paravaejovini.

Distribution. North America: Canada (southwest), Mexico (north, Baja California), USA (northwest, southwest).

Diagnosis. Scorpions in the subfamily Smeringurinae can be distinguished by the following characters: genital operculum sclerites of female divided on posterior two-fifths to one-half, operating separately, not connected to mesosoma on extreme distal aspect, but more midpoint; *ib-it* positioned proximal to basal inner denticle (*ID*), but never basally on finger; chelal trichobothria V_2-V_3 distance approximately twice as long as V_1-V_2 ; fixed finger trichobothria *dsb* and *dst* positioned proximal of *esb* and *est*, respectively; leg tarsus with one pair of ventral distal spinules; setal combs present on legs; number of constellation array sensilla low, exhibiting 2–3 sensilla; cheliceral ventral edge of movable finger usually with denticles or serrations; serrula vestigial to non-contiguous, weakly developed; dorsal carinal terminus of metasomal segments I–III rounded, not terminating with an enlarged denticle; dorsolateral carinae of metasomal segment IV not flared at the terminus, essentially coinciding with articulation condyle; carapace anterior edge variable, from straight to a conspicuously convexed; median eye tubercle and eyes enlarged, 21–30 % as wide as carapace at that point.

Discussion. See discussion of genera below.

Tribe Smeringurini Soleglad et Fet, trib. nov.

Type Genus. *Smeringurus* Haradon, 1983.

Composition. This tribe, established here, includes the genera *Paruroctonus*, *Smeringurus*, and *Vejovoidus*.

Distribution. North America: Canada (southwest), Mexico (north, Baja California), USA (northwest, southwest).

Diagnosis. Hemispermaphore lamellar hook minimal, not extending beyond ventral trough; basal constriction essentially absent; mating plug barb is smooth; chelal trichobothrium *Dt* positioned quite proximal of palm midpoint; femoral trichobothrium *d* proximal to *i*,

and *e* positioned proximally on segment; major neobothriotaxy absent on the ventral aspect of the palm; usually with two constellation array sensilla; chelicerae with denticles on the ventral edge of the movable finger and protuberances usually found on the ventral surface of the fixed finger.

Discussion. See discussion of genera below.

Genus *Paruroctonus* Werner, 1934

Type Species. *Uroctonoides gracilior* Hoffmann, 1931 [= *Paruroctonus gracilior* (Hoffmann, 1931)].

Synonyms:

Uroctonoides Hoffmann, 1931: 405; a junior homonym of *Uroctonoides* Chamberlin, 1920 (= *Teuthraustes* Simon, 1878: Scorpiones, Chactidae).

Hoffmanniellius Mello-Leitão, 1934: 80; a replacement name for *Uroctonoides* Hoffmann, 1931 (see Sissom, 2000: 505).

References (selected):

Paruroctonus: Werner, 1934: 283, fig. 363 (a replacement name for *Uroctonoides* Hoffmann, 1931); Williams, 1972: 1–3 (in part); Stahnke, 1974: 119, 136 (in part); Williams, 1974: 15 (in part); Williams, 1980: 31–34, figs. 35–37 (in part); Sissom, 1990a: 110, 114 (in part); Stockwell, 1992: 408, 409, 416, 419, figs. 12, 37, 39, 58; Kovařík, 1998: 143; Sissom et al., 1998: 17–19; ICZN, 1999b: 209–210; Beutelspacher, 2000: 56, 65, 152 (in part); Sissom, 2000: 505–514; Soleglad & Fet, 2003b: 88.

Vejovis (*Paruroctonus*): Gertsch & Allred, 1965: 4 (in part); Williams, 1970c: 277 (in part); Gertsch & Soleglad, 1972: 4 (in part); Hjelle, 1972: 26 (in part).

Paruroctonus (*Paruroctonus*): Haradon, 1983: 256; Haradon, 1984a: 205–209; Haradon, 1984b: 317–318; Haradon, 1985: 19–21.

Composition. This genus includes the following 33 species and subspecies:

- P. ammonastes* Haradon, 1984
- P. arenicola arenicola* Haradon, 1984
- P. arenicola nudipes* Haradon, 1984
- P. arnaudi* Williams, 1972
- P. baergi* (Williams et Hadley, 1967)
- P. bajae* Williams, 1972
- P. bantai bantai* (Gertsch et Soleglad, 1966)
- P. bantai saratoga* Haradon, 1985
- P. becki* (Gertsch et Allred, 1965)
- P. boquillas* Sissom et Henson, 1998
- P. boreus* (Girard, 1854)
- P. borregoensis borregoensis* Williams, 1972
- P. borregoensis actites* Haradon, 1984

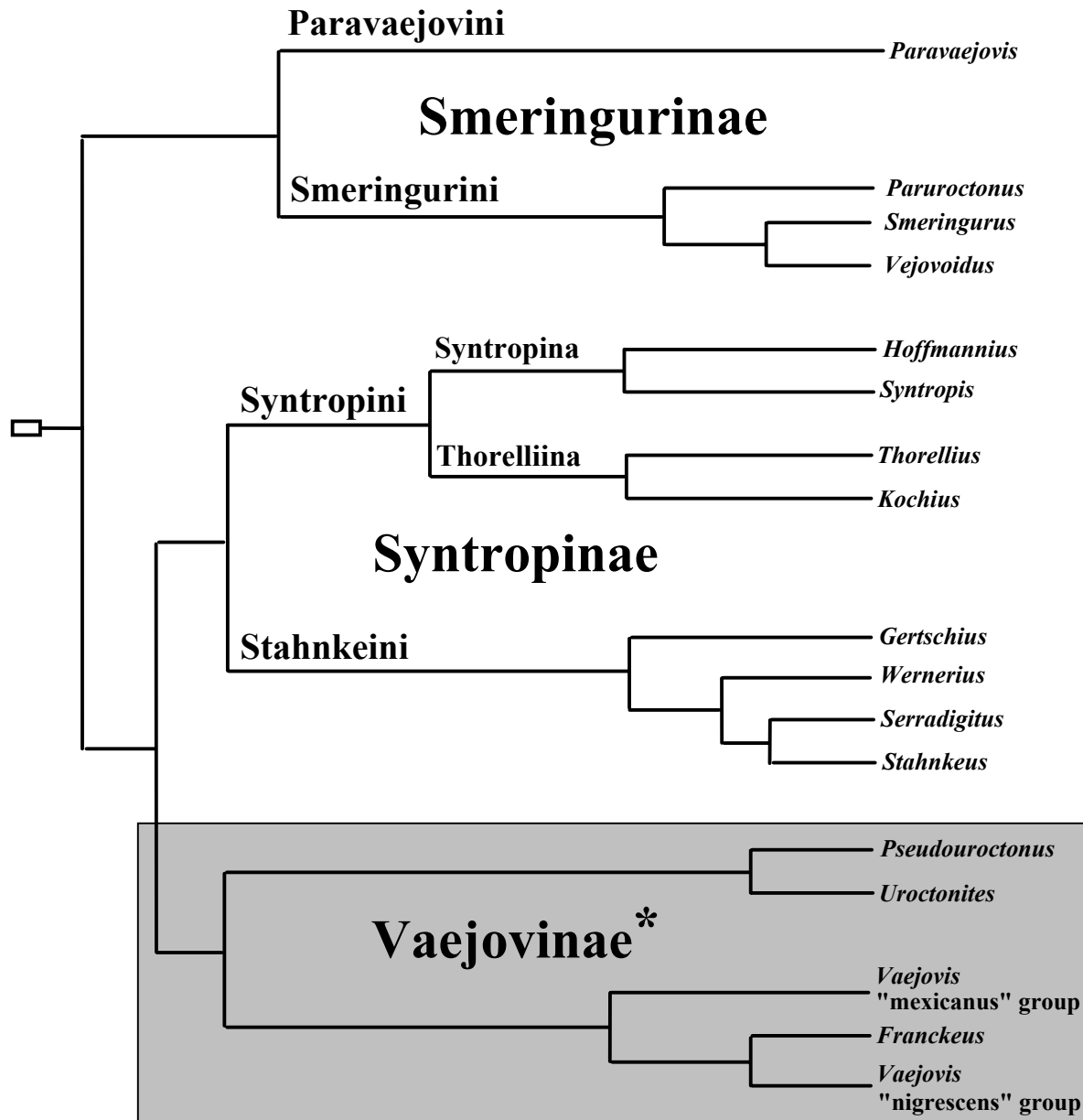


Figure 196: Phylogram showing the three current subfamilies of family Vaejovidae based on the results of this study. * Note, subfamily Vaejovinae (shaded), the default nominotypic subfamily for Vaejovidae, has not yet been revised and therefore only reflects the remaining taxa and their relationships as suggested by Stockwell (1989) and/or Soleglad & Fet (2005).

P. coahuilanus Haradon, 1985
P. gracilior (Hoffmann, 1931)
P. hirsutipes Haradon, 1984
P. luteolus (Gertsch et Soleglad, 1966)
P. maritimus Williams, 1987
P. marksi Haradon, 1984
P. nitidus Haradon, 1984
P. pecos Sissom et Francke, 1981
P. pseudopumilis (Williams, 1970)
P. shulovi shulovi (Williams, 1970)

P. shulovi nevadae Haradon, 1985
P. silvestrii (Borelli, 1909)
P. simulatus Haradon, 1985
P. stahnkei (Gertsch et Soleglad, 1966)
P. surensis Williams et Haradon, 1980
P. utahensis (Williams, 1968)
P. variabilis Hjelle, 1982
P. ventosus Williams, 1972
P. williamsi Sissom et Francke, 1981
P. xanthus (Gertsch et Soleglad, 1966)

Subfamily	Tribe	Subtribe	Genus	Species	
Smeringurinae	Paravaejovini		<i>Paravaejovis</i>	<i>P. pumilis</i>	
	Smeringurini		<i>Paruroctonus</i>	<i>P. ammonastes</i> , <i>P. arenicola arenicola</i> , <i>P. arenicola nudipes</i> , <i>P. arnaudi</i> , <i>P. baergi</i> , <i>P. bajae</i> , <i>P. bantai bantai</i> , <i>P. bantai saratoga</i> , <i>P. becki</i> , <i>P. boquillas</i> , <i>P. boreus</i> , <i>P. borregoensis borregoensis</i> , <i>P. borregoensis actites</i> , <i>P. coahuilanus</i> , <i>P. gracilior</i> , <i>P. hirsutipes</i> , <i>P. luteolus</i> , <i>P. maritimus</i> , <i>P. marksi</i> , <i>P. nitidus</i> , <i>P. peccos</i> , <i>P. pseudopumilis</i> , <i>P. shulovi shulovi</i> , <i>P. shulovi nevadae</i> , <i>P. silvestrii</i> , <i>P. simulatus</i> , <i>P. stahnkei</i> , <i>P. surensis</i> , <i>P. utahensis</i> , <i>P. variabilis</i> , <i>P. ventosus</i> , <i>P. williamsi</i> , <i>P. xanthus</i>	
			<i>Smeringurus</i>	<i>S. aridus</i> , <i>S. grandis</i> , <i>S. mesaensis</i> , <i>S. vachoni vachoni</i> , <i>S. vachoni immanis</i>	
		<i>Vaejovoidus</i>	<i>V. longiunguis</i>		
	Syntropinae	Stahnkeini		<i>Gertschius</i>	<i>G. agilis</i> , <i>G. crassicornis</i>
				<i>Serradigitus</i>	<i>S. adcocki</i> , <i>S. armadentis</i> , <i>S. baueri</i> , <i>S. bechteli</i> , <i>S. calidus</i> , <i>S. dwyeri</i> , <i>S. gertschii gertschii</i> , <i>S. gertschii striatus</i> , <i>S. giganteus</i> , <i>S. gramenstris</i> , <i>S. haradoni</i> , <i>S. hearnei</i> , <i>S. joshuaensis</i> , <i>S. littoralis</i> , <i>S. minutis</i> , <i>S. pacificus</i> , <i>S. torridus</i> , <i>S. wupatkiensis</i> , <i>S. yaqui</i>
			<i>Stahnkeus</i>	<i>S. alfredi</i> , <i>S. deserticola</i> , <i>S. harbisoni</i> , <i>S. polsi</i> , <i>S. subtilimanus</i>	
			<i>Wernerius</i>	<i>W. mumai</i> , <i>W. spicatus</i>	
		Syntropini	Syntropina	<i>Hoffmannius</i>	<i>H. bilineatus</i> , <i>H. coahuilae</i> , <i>H. confusus</i> , <i>H. diazi diazi</i> , <i>H. diazi transmontanus</i> , <i>H. eusthenura</i> , <i>H. galbus</i> , <i>H. glabrimanus</i> , <i>H. globosus</i> , <i>H. gravicaudus</i> , <i>H. hoffmanni hoffmanni</i> , <i>H. hoffmanni fuscus</i> , <i>H. punctatus punctatus</i> , <i>H. punctatus spadix</i> , <i>H. punctatus variegatus</i> , <i>H. puritanus</i> , <i>H. spinigerus</i> , <i>H. viscainensis</i> , <i>H. vittatus</i> , <i>H. waeringi</i> , <i>H. waneri</i>
	Vaejovinae	Thorellina		<i>Syntropis</i>	<i>S. aalbei</i> , <i>S. macrura</i> , <i>S. williamsi</i>
			<i>Kochius</i>	<i>K. atenango</i> , <i>K. bruneus bruneus</i> , <i>K. bruneus loretoensis</i> , <i>K. bruneus villosus</i> , <i>K. cazieri</i> , <i>K. crassimanus</i> , <i>K. hirsuticauda</i> , <i>K. insularis</i> , <i>K. kovariki</i> , <i>K. magdalenis</i> , <i>K. punctipalpi punctipalpi</i> , <i>K. punctipalpi barbatus</i> , <i>K. punctipalpi cerralvensis</i> , <i>K. russelli</i> , <i>K. sonorae</i>	
		<i>Thorellius</i>	<i>T. atrox</i> , <i>T. cisnerosi</i> , <i>T. eristimanus</i> , <i>T. intrepidus</i> , <i>T. occidentalis</i> , <i>T. subricostatus</i>		
		<i>Franekeus</i>	<i>F. kochi</i> , <i>F. mineckleyi</i> , <i>F. nitidulus</i> , <i>F. peninsularis</i> , <i>F. platnicki</i> , <i>F. rubrimanus</i>		
		<i>Pseudouroctonus</i>	<i>P. andreas</i> , <i>P. angelenus</i> , <i>P. apacheanus</i> , <i>P. bogerti</i> , <i>P. cazieri</i> , <i>P. chicoano</i> , <i>P. glimmeri</i> , <i>P. iviei</i> , <i>P. lindsayi</i> , <i>P. minimus minimus</i> , <i>P. minimus castaneus</i> , <i>P. minimus thompsoni</i> , <i>P. reddelli</i> , <i>P. rufulus</i> , <i>P. sprousei</i> , <i>P. williamsi</i>		
		<i>Uroctonites</i>	<i>U. giuliamii</i> , <i>U. huachuca</i> , <i>U. montereus</i> , <i>U. sequoia</i>		
		<i>Vaejovis</i>	"mexicanus" group <i>V. acapulco</i> , <i>V. carolinianus</i> , <i>V. cashi</i> , <i>V. chamelaensis</i> , <i>V. chiapas</i> , <i>V. chisos</i> , <i>V. digesi</i> , <i>V. feti</i> , <i>V. franckei</i> , <i>V. granulatus</i> , <i>V. jonesi</i> , <i>V. lapidicola</i> , <i>V. kuarapu</i> , <i>V. maculosus</i> , <i>V. mexicanus</i> , <i>V. monticola</i> , <i>V. nayarii</i> , <i>V. nigrofemoratus</i> , <i>V. pattersoni</i> , <i>V. paysonensis</i> , <i>V. pusillus</i> , <i>V. rossmani</i> , <i>V. setosus</i> , <i>V. smithi</i> , <i>V. sprousei</i> , <i>V. tessellatus</i> , <i>V. vaquero</i> , <i>V. vorhiesi</i> "nigrescens" group <i>V. curvidigitus</i> , <i>V. davidi</i> , <i>V. decipiens</i> , <i>V. gracilis</i> , <i>V. intermedius</i> , <i>V. janssi</i> , <i>V. mauryi</i> , <i>V. michelli</i> , <i>V. nigrescens</i> , <i>V. norteno</i> , <i>V. pococki</i> , <i>V. solegladi</i>		

Table 9: Taxonomy of Family Vaejovidae (Parvorder Iurida, Superfamily Chaetoidea).

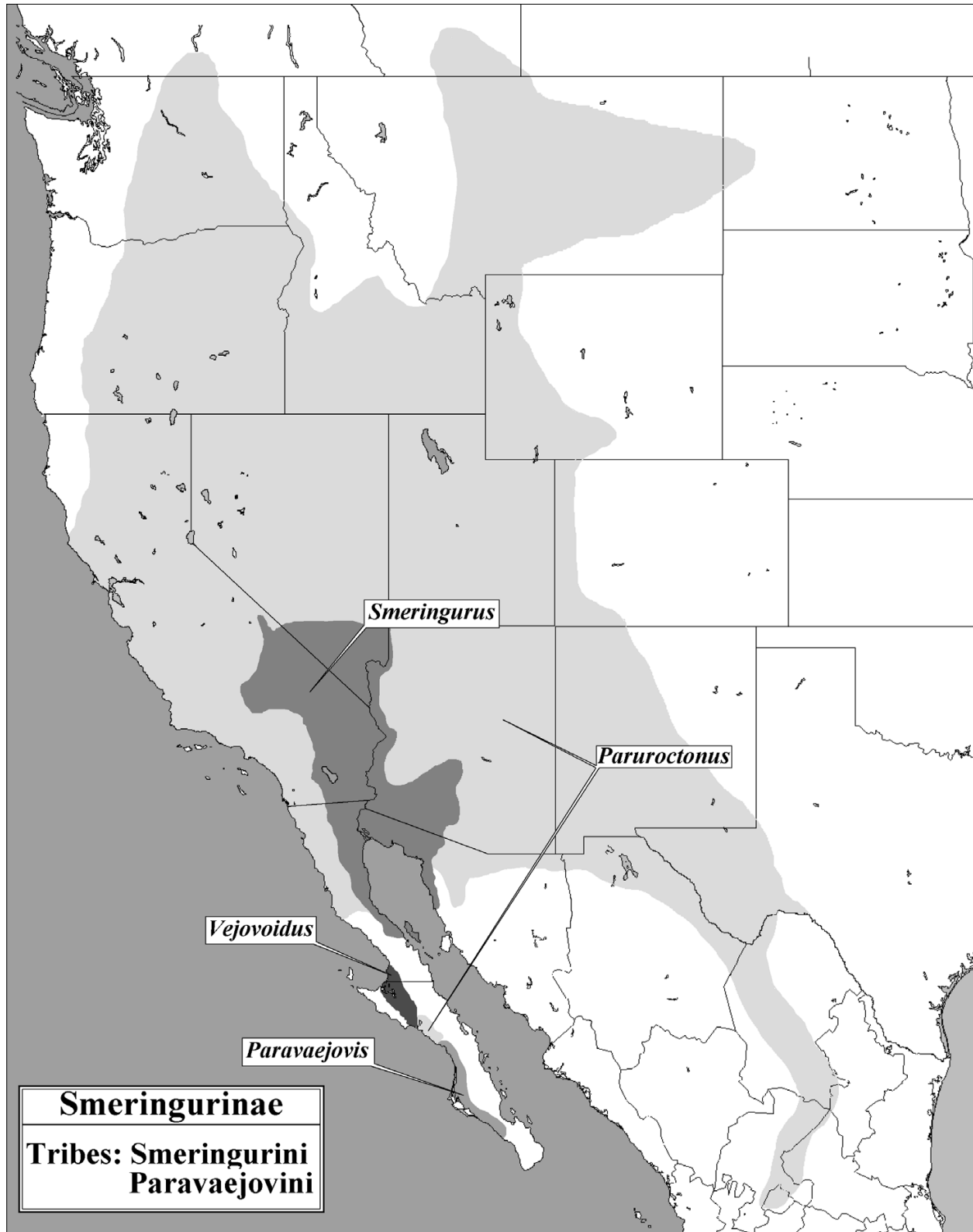


Figure 197: General distribution of scorpion subfamily **Smeringurinae** in North America with the ranges of genera *Paravaejovis* (tribe **Paravaejovini**) and *Smeringurus*, *Paruroctonus*, and *Vejovoidus* (tribe **Smeringurini**) delineated.

Distribution. Canada (southern edges of Alberta and British Columbia, only *P. boreus*), Mexico (Aguascalientes, Baja California, Baja California Sur, Chihuahua, Coahuila, Sonora, Zacatecas), USA (Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, South Dakota, Texas, Utah, Washington, Wyoming).

This genus is one of the most widely spread in family Vaejovidae (see map in Fig. 197), but most of this is due to the very large range of species *P. boreus*, which extends from southern Nevada to the extreme southwestern parts of Canada. Only species *P. gracilior* extends any distance into mainland Mexico, its type locality being Tepezalá, Aguascalientes. Genus *Paruroctonus* has a disjunct range in Baja California, Mexico; only two species are found in Baja California Sur, *P. pseudopumilis* and *P. surensis*, both isolated in the Vizcaino Desert. The closest most southern species in Baja California are *P. arnaudi*, *P. ventosus*, *P. silvestrii*, and *P. luteolus*; none are found beyond El Rosario on the east or Luis Gonzaga on the west. *P. arnaudi* and *P. ventosus* are psammophiles found in isolated inland sand dunes on the Pacific side of the peninsula.

Diagnosis. Metasomal segments I–IV with a pair of ventromedian (*VM*) carinae; metasomal segment I usually as wide as long in male and wider than long in female, segment III never twice as long as wide, segment IV never three times longer than wide; setal pairs found on ventromedian (*VM*) carinae of segments I–IV, intercarinal area of *VM* carinae without setation; lamina of hemispermatophore with squared or rounded distal tip, inner base of lamina without small protrusion; vesicular tabs well developed, equipped with conspicuous distal granule.

Taxonomic history. Two names, *Paruroctonus* Werner, 1934 and *Hoffmanniellius* Mello-Leitão, 1934 were proposed as replacement names for *Uroctonoides* Hoffmann, 1931, a subjective junior homonym of *Uroctonoides* Chamberlin, 1920 (= *Teuthraustes* Simon, 1878: Scorpiones, Chactidae). The name *Paruroctonus* was conserved by the International Commission on Zoological Nomenclature in 1999 due to its prevalent usage (Sissom et al., 1998; ICZN, 1999b). *Paruroctonus* was treated for some time as subgenus of *Vaejovis* until reinstated as genus by Williams (1972). The genus was revised by Haradon (1983, 1984a, 1984b, 1985) who established two subgenera (*Paruroctonus* and *Smeringurus*). Stockwell (1992) elevated *Smeringurus* Haradon, 1983 to the genus level (see below). No subgenera are currently recognized in *Paruroctonus*, although several informal assemblages of species (“infragroups” and “microgroups”) exist (Haradon, 1984a, 1984b, 1985; Sissom, 2000).

Discussion. In a series of detailed papers, Haradon (1984a, 1984b, 1985) presented a complete revision of

the genus *Paruroctonus*, defining, informally, no less than three “infragroups” and eight “microgroups” (also see Sissom, 2000). In these contributions ten species and subspecies were defined. Although many diagnostic characters were used in these treatments, the emphasis and most illustrations were placed on the setation of the pedipalp and the leg basitarsus and tarsus. Consequently, the question arises: do these setal patterns exhibit consistency across the various groups in *Paruroctonus* such that these groups can be elevated to separate genera?

After studying the three papers, we see that Haradon (1984a, 1984b, 1985) utilized landmark seta (*lms*) for the pedipalp (femur and patella [addressed as tibia]), and leg III (basitarsus and tarsus). These were, in a sense, defined at a group level and therefore appear to be potential synapomorphies for these groups. However, except for the leg, the utilization of *lms* character set by Haradon was minimal (i.e., in the pedipalp), and did not encompass many species. In addition, *lms* were not always illustrated in all pedipalp femur figures, and for the patella, *lms* were never identified (albeit, the standard trichobothria were shown in all cases). Therefore, we limit this discussion to only leg III; in Table 10 we summarize the setation for both the basitarsus and tarsus (referred to as the telotarsus in Haradon), as were illustrated and/or discussed by Haradon (1984a, 1984b, 1985). Utility of setation (beyond trichobothria) remains largely unexplored in scorpion systematics; see some preliminary information of pedipalp finger landmark setae in our recent work on constellation array in Smeringurinae (Fet et al., 2006c).

For the leg III *basitarsus* three distally positioned *lms* were identified by Haradon in contrast to the superior row of large elongated setae, or the “setal combs” of Stockwell (1989); the arrangement and number of latter is considered diagnostic (Graeme Lowe informed us that this was an excellent species-level diagnostic character, pers. comm. 2007). Haradon illustrated the basitarsus III for 14 species and supplied additional information on four species in the text. We consider the number of superior setae to be a species-level character and therefore do not necessarily believe they are of importance at the group level (except, maybe, if stated as a range). It does appear that the three *lms* of the basitarsus are consistently placed and numbered, providing a potential diagnostic character for the genus *Paruroctonus*, though, of course, not germane at lower group levels.

For the leg III *tarsus*, Haradon identified five categories of setae: superinterminal (*st*), a large seta, which he always designated as *lms*; retrosuperior (*rs*) (i.e., the “setal combs” of Stockwell, 1989); retromedial (*rm*); retroinferior (*ri*); and retroinferior terminal (*rit*). As seen in Table 10, all these setal groups are designated as landmark groups in one context or another, depending

		Tarsus III (<i>lms</i> context dependent)				Basitarsus III (<i>lms</i> = 3)	
		<i>rs</i> #	<i>rm</i> #	<i>ri</i> #	<i>rit</i> #	Superior #	<i>mrs</i> #
“boreus”	<i>P. arnaudi</i>						
	<i>P. bantai</i>						
	<i>P. boreus</i>						
	<i>P. maritimus</i>						
	<i>P. silvestrii</i>						
	<i>P. variabilis</i> ***						
“baergi”	<i>P. arenicola</i>	4 (1 small)	2	2 <i>lms</i>	2 <i>lms</i>	9–10	0–1
	<i>P. baergi</i>	4	1	2 <i>lms</i>	2 <i>lms</i>	9	1
	<i>P. boquillas</i> **	4	1	2 <i>lms</i>	2 <i>lms</i>	?	1 *
	<i>P. marksii</i>	2	2	2 <i>lms</i>	2 <i>lms</i>	7	1
	<i>P. utahensis</i>	4	2	2 <i>lms</i>	2 <i>lms</i>	8	1
1	<i>P. becki</i>						
2	<i>P. xanthus</i>	6–7 *	?	?	?	?	?
3	<i>P. gracilior</i>	2 *	2 *	1 *	1 *	5 *	1 *
4	<i>P. stahnkei</i>	?	?	?	1 *		
“borregoensis”	<i>P. ammonastes</i>	4	2 <i>lms</i>	2 <i>lms</i>	2 <i>lms</i>	8	1
	<i>P. bajae</i>	3 *	?	?	?	6 *	?
	<i>P. borregoensis</i>	3	2 <i>lms</i>	2 <i>lms</i>	2 <i>lms</i>	7	1
	<i>P. hirsutipes</i>	6	2 <i>lms</i>	2 <i>lms</i>	2 <i>lms</i>	9	1
	<i>P. luteolus</i>	2	2 <i>lms</i>	2 <i>lms</i>	2 <i>lms</i>	6	1
	<i>P. nitidus</i>	3 *	?	?	?	6 *	?
	<i>P. pseudopumilis</i>	2 *	?	?	?	7	1
	<i>P. surensis</i>	4 (1 small) *	?	?	?	8	1
	<i>P. ventosus</i>	4 *	?	?	?	8 *	?
“shulovi”	<i>P. shulovi</i>	2 <i>lms</i>	2 <i>lms</i>	2	2	7	1
	<i>P. simulatus</i>	2 <i>lms</i>	2 <i>lms</i>	1	1	6	1
“williamsi”	<i>P. coahuilanus</i>	?	?	2 *	?	8	1
	<i>P. pecos</i>	?	?	2 *	?	6	1
	<i>P. williamsi</i>	?	?	2 *	?		

Table 10: *Paruroctonus* setae analysis of the tarsus and basitarsus of leg III based on Haradon (1984a, 1984b, 1985). Species are grouped by assigned infra- and microgroups. Data from illustrations and/or text. *lms* = landmark setae, *rs* = retrosuperior, *rm* = retromedial, *ri* = retroinferior, *rit* = retroinferior terminal, *mrs* = mid-retrosuperior. * not illustrated, data from text. ** after Sissom & Henson (1998: fig. 7). *** after Hjelle, 1982, no seta data provided. ¹ “becki” microgroup, ² “xanthus” microgroup, ³ “gracilior” infragroup, ⁴ “stahnkei” infragroup, others are microgroups.

on the microgroup. I.e. the “baergi” and “borregoensis” microgroups both declare *ri* and *rit* setal groups as *lms*, and the “shulovi” and “borregoensis” microgroups stipulate the *rm* setal group as *lms*. Therefore, it is clear

that the *lms* designation was independently based on species subsets, and therefore, providing no consistency across the genus. For example, in the “boreus” microgroup, *lms* are not utilized at all in the diagnosis of

its species set. Similarly, landmark setae were not declared for the “williamsi” microgroup. We also see the same number of setae in setal groups across different microgroups where the setal group is or is not declared *lms*. For example, *P. marksi*, of the “baergi” microgroup, has two *rs* and *rm* setae, the same number of setae as in the “shulovi” microgroup where these setal groups are designated as *lms*; *P. shulovi*, of the “shulovi” microgroup, has two *ri* and *rit* setae, the same number as in the “borregoensis” and “baergi” microgroups where these same setal groups are declared as *lms*. Finally, species *P. luteolus*, of the “borregoensis” microgroup, *P. marksi*, of the “baergi” microgroup, and *P. shulovi*, of the “shulovi” microgroup, all exhibit two setae each in the *rs*, *rm*, *ri*, and *rit* setal groups. In fact, based solely on these setal groups, the only difference between these three species, assigned to three separate microgroups each, is one less superior seta on the basitarsus in *P. luteolus*. Clearly, other diagnostic characters must be used to differentiate these three species and the groups they occupy. This is reflected in the keys provided by Haradon (1984a, 1984b, 1985) where all *lms* characters are combined with other diagnostic characters such as pectinal tooth counts, coloration, metasomal setation, morphometric ratios, etc.

Based on these data, where we only consider the setation of the leg III basitarsus and tarsus, it appears that the *lms* as used in Haradon’s infra- and microgroup definitions do not provide, by themselves, useful cladistic characters for the further breakdown of the genus *Paruroctonus*. Possibly, using a combination of many characters may provide a basis for these group definitions.

Genus *Smeringurus* Haradon, 1983

Type Species. *Paruroctonus vachoni* Stahnke, 1961 [= *Smeringurus vachoni* (Stahnke, 1961)].

References (selected):

Paruroctonus (*Smeringurus*): Haradon, 1983: 255–256.

Smeringurus: Stockwell, 1992: 409, 416, 419, figs. 59–60; Kovařík, 1998: 146; Sissom, 2000: 524–526; Soleglad & Fet, 2003b: 88.

Composition. This genus includes the following five species and subspecies:

- S. aridus* (Soleglad, 1972)
- S. grandis* (Williams, 1970)
- S. mesaensis* (Stahnke, 1957)
- S. vachoni vachoni* (Stahnke, 1961)
- S. vachoni immanis* (Soleglad, 1972)

Distribution. Mexico (Baja California, Sonora), USA (Arizona, California, Nevada).

The genus has a somewhat compact range (see map in Fig. 197). *Smeringurus mesaensis*, a psammophile, is found in sandy areas in central Arizona, into the Colorado Desert of California and northeastern Baja California, and north into the Mojave Desert of California. *S. grandis* essentially replaces *S. mesaensis* where the Colorado Desert ends and the volcanic regions of the Sierra San Pedro Mártir occur on the eastern coast of the peninsula. Species *S. vachoni* and *S. aridus* both are fossorial; *S. vachoni* occurs in the Mojave Desert in California and southern Nevada, and along the Colorado River; and *S. aridus*, further south in the Colorado Desert in California, its range extending south towards Baja California.

Diagnosis. Metasomal segments I–IV with a pair of ventromedian (*VM*) carinae; metasomal segments I–IV always longer than wide in both genders, segment III more than two times longer than wide, segment IV three times longer than wide; setal pairs lacking on ventromedian (*VM*) carinae of segments I–IV, instead they are located between the *VM*; lamina of hemispermatophore with squared or rounded distal tip, inner base of lamina without small protrusion; vesicular tabs reduced and rounded, distal granule vestigial to obsolete in adults.

Taxonomic history. Haradon (1983) described *Smeringurus* as a subgenus of *Paruroctonus* Werner, 1934. Stockwell (1992) elevated *Smeringurus* to the genus level. Sissom (2000: 505) noted, regarding the status of *Smeringurus*, that “the situation requires further study.” Beutelspacher (2000) ignored existence of this genus-group name. The name *Paruroctonus* is still widely (and incorrectly) used in non-taxonomic literature for *Smeringurus* species, especially for *S. mesaensis*.

Discussion. This genus contains some of the largest scorpions in family Vaejovidae. A female *Smeringurus vachoni vachoni* was reported by Gertsch & Soleglad (1966: table 3) to be 98 mm in length and a female *S. aridus* 84 mm in length was reported by Soleglad (1972: table 1) (note, one must add in the telson length in both of these references). Matthew Graham recently informed us he has a live *S. v. vachoni* that is 111.5 mm in length (pers. comm., 2008), clearly the largest reported for this genus to date. Williams (1980) reports that *S. mesaensis* and *S. grandis* reach sizes of 70 and 80 mm, respectively.

Smeringurus mesaensis, the only psammophile in this small genus, is found sympatrically with both *S. vachoni* in the Mojave Desert and with *S. aridus* in the Anza-Borrego Desert State Park in the Colorado Desert. Interestingly, the first author has encountered *S. mesaensis* with both *S. vachoni immanis* and *S. aridus*; in each case, *S. mesaensis* was occupying the soft sand of a desert wash while a few feet away, *S. v. immanis* in

one case and *S. aridus* in the other were both found on the hard soil forming the banks of the wash.

Genus *Vejovoidus* Stahnke, 1974

Type Species. *Syntropis longiunguis* Williams, 1969 [= *Vejovoides longiunguis* (Williams, 1969)].

References:

Vejovoidus: Stahnke, 1974: 120–122; Williams, 1980: 112–113, fig. 50, 108A, C, D, 109–111; Sissom, 1990a: 110, 114; Stockwell, 1992: 409, 416, figs. 56, 57; Fet et al., 1998: 613, 614, figs. 1, 8; Kovařík, 1998: 148; Beutelspacher, 2000: 55; Sissom, 2000: 552; Soleglad & Fet, 2003b: 88.

Vaejovoidus: Nenilin & Fet, 1992: 10.

Composition. This monotypic genus includes the single species, *V. longiunguis* (Williams, 1969).

Distribution. Mexico (Baja California, Baja California Sur).

This genus, with its sole ultrapsammophile species, is endemic of the Vizcaino Desert including both Baja California on the extreme southern edge and Baja California Sur to Laguna San Ignacio (see map in Fig. 197).

Diagnosis. One ventromedian (*VM*) carina present on metasomal segments I–IV; unguis of legs elongated and asymmetric; ventral aspect of leg tarsus clothed in an exaggerated cluster of elongated curved setae scattered over its entire surface; lamina of hemispermatophore with pointed and hooked distal tip, inner base of lamina with small protuberance; terminus of dorsal carinae (*D*) of metasomal segments I–III with exaggerated sharp elongated spines; vesicular tabs reduced and rounded, distal granule vestigial to obsolete in adults.

Taxonomic history. Originally, Williams (1969) placed the sole species of this genus in *Syntropis*, but Stahnke (1974) established a new genus, which remains monotypic. Stahnke (1974), however, placed *Vejovoidus* in subfamily Syntropinae along with *Syntropis*, and no changes in this placement were ever published. Here, we place *Vejovoidus* in subfamily Smeringurinae.

Discussion. This unique monotypic genus has gone through a very interesting taxonomic history during a relatively short time (40 years) since it was originally defined. The single ventromedian (*VM*) carina occurring on metasomal segments I–IV, somewhat unique in Recent scorpions, was considered important enough by Williams (1969) to place this taxon in genus *Syntropis*, albeit this taxon and its sister species, *S. macrura*, appeared structurally quite different. Stahnke (1974), emphasizing the vast differences between the two species, created a new genus *Vejovoidus* for this species, *V. longiunguis*. However, Stahnke recognized Kraepelin's (1905) subfamily Syntropinae and placed both *S.*

macrura and *V. longiunguis* as its only members, thus endorsing, to some extent, the original grouping of Williams (1969). Not until Stockwell's (1989) unpublished PhD thesis did the close taxonomic relationships between *Vejovoidus* and the other members of subfamily Smeringurinae defined herein become apparent. Only at this time was the close taxonomic connection between *Vejovoidus* and *Syntropis* dispelled.

We suggest here that many of the derived characters defining this very unique scorpion are the product of its adaptation to a sand-only environment as a true ultrapsammophile (Fet et al., 1998). The modified leg epitarso (i.e., the highly asymmetric unguis), the heavy and exaggerated cluster of setae covering the ventral surface of the leg tarsus (see Fig. 101), the very narrow and streamlined telson, all confer possible advantages for moving in the sands of the Vizcaino Desert in Baja California.

The first author has encountered this genus in the sand dune areas of Las Bombas, Baja California Sur, which dominated the scorpion population along with species *Hadrurus concolorous* Stahnke, 1969, and *Hoffmannius viscainensis*. In a similar scenario, a “trio” of similarly related species are also commonly found in the sandy areas of southern California, *Smeringurus mesaensis*, *Hadrurus arizonensis* Ewing, 1928, and *Hoffmannius waeringi*.

Tribe Paravaejovini Soleglad et Fet, trib. nov.

Type Genus. *Paravaejovis* Williams, 1980.

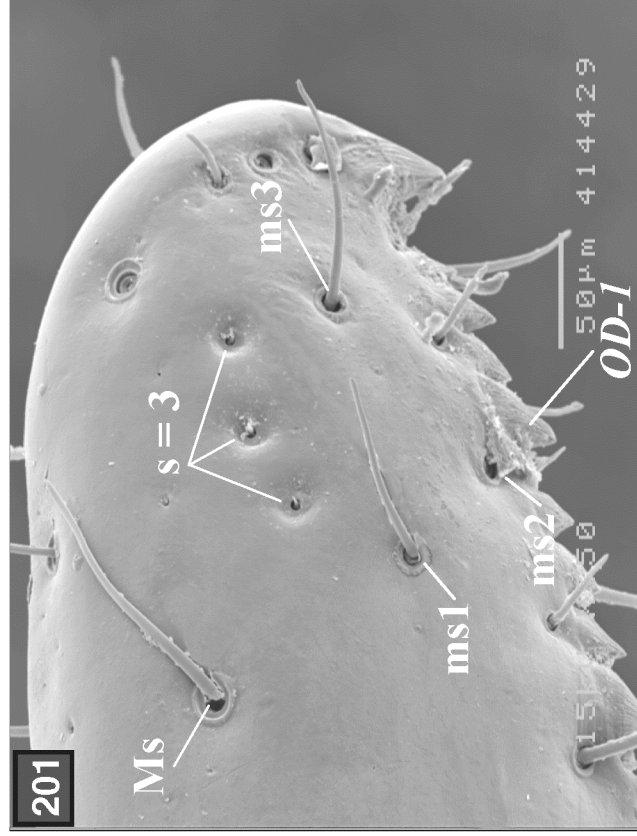
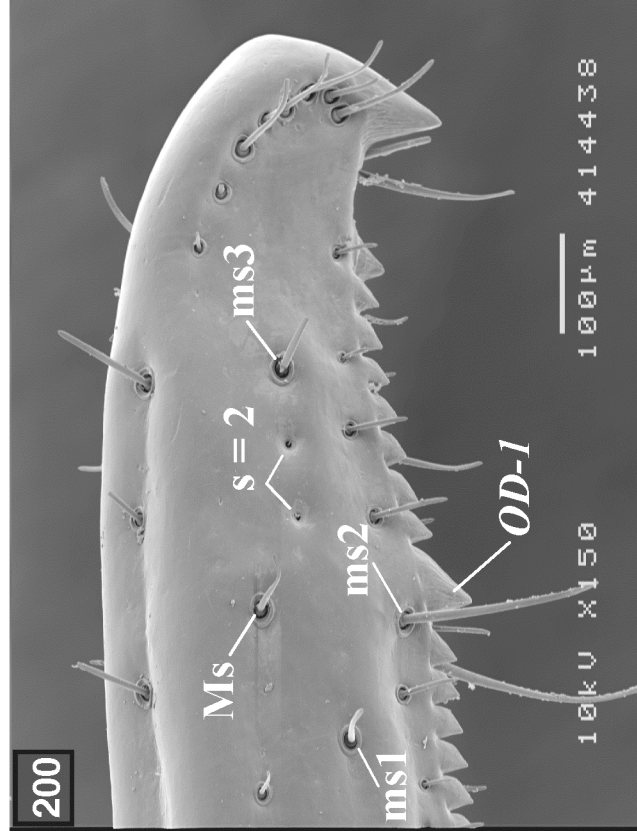
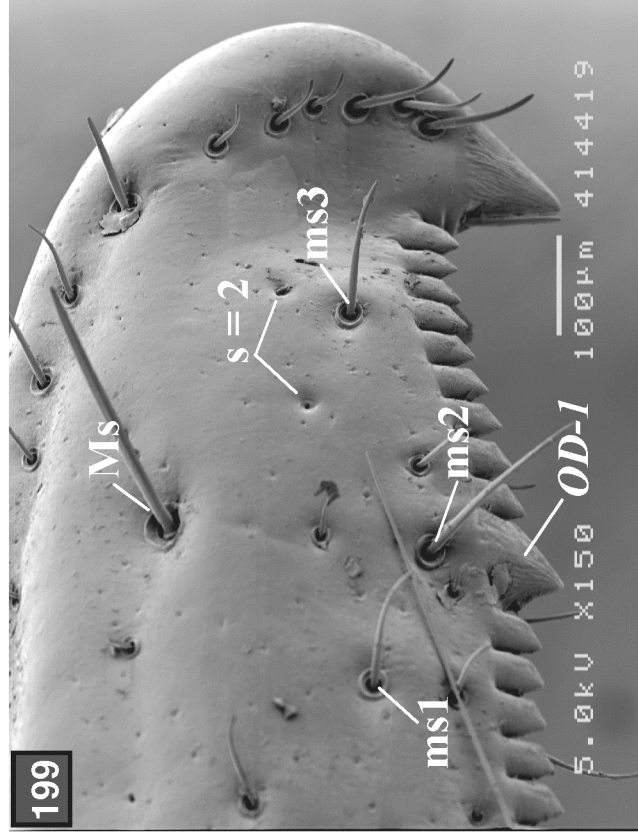
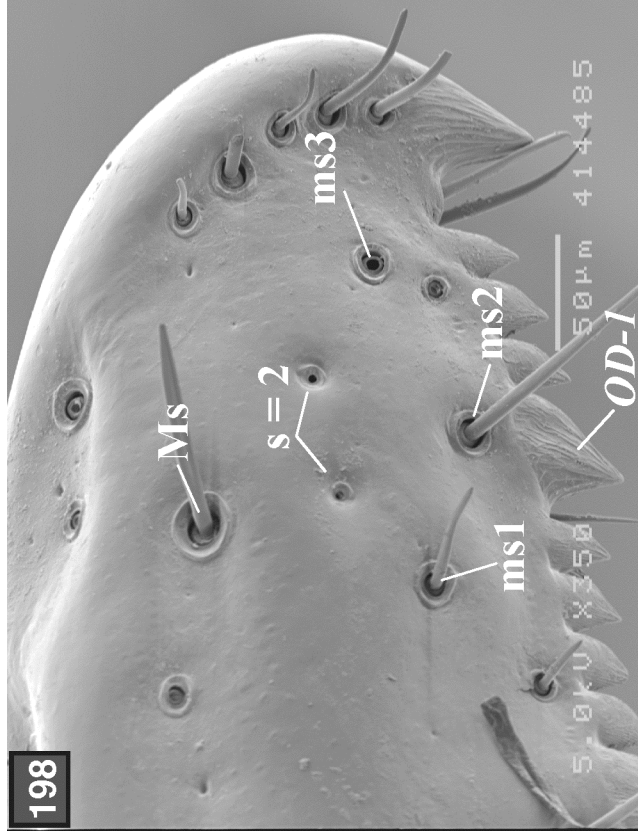
Composition. This monotypic tribe, established here, includes the genus *Paravaejovis*.

Distribution. Mexico (Baja California Sur).

The monotypic genus *Paravaejovis* is endemic of the central-western and southwestern regions of Baja California Sur, and is the most southern taxon of subfamily Smeringurinae found in Baja California peninsula (see map in Fig. 197). The range of this genus is essentially disjunct from other members of its subfamily except for the two isolated species of *Paruroctonus* found in the Vizcaino Desert.

Diagnosis. Hemispermatophore lamellar hook well developed, extending well distal of the ventral trough, exaggerated by conspicuous basal constriction; mating plug barb toothed (after Stockwell, 1989); chelal trichobothrium *Dt* positioned distal of palm midpoint; femoral trichobothrium *d* distal to *i*, and *e* positioned near midsegment; major neobothriotaxy present on ventral aspect of the palm; *three* constellation array sensilla; chelicerae without denticles on the ventral edge of the movable finger or protuberances on the ventral aspect of the fixed finger; vesicular tabs reduced and rounded, distal granule vestigial to obsolete in adults.

Discussion. See discussion of genus below.



Figures 198–201: Orientation of constellation array sensilla with respect to landmark setae for four smeringurine genera. **198.** *Paruroctonus luteolus*, male, ABDSP, California, USA. **199.** *Smeringurus mesacensis*, male, ABDSP, California, USA. **200.** *Vejoivodus longiunguis*, female, Las Bombas, Baja California Sur, Mexico. **201.** *Paravaeiovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. Note that genus *Paravaeiovis* is unique in these configurations, exhibiting *three* sensilla (not two). **s** = sensilla; **Ms** = major seta; **ms1–3** = minor setae 1–3; **et** = external terminal trichobothrium; **OD-1** & **2** = outer (OD) denticles 1 & 2; **MD** = distal median (MD) denticles. After Fet et al. (2006c), in part.

Genus *Paravaejovis* Williams, 1980

Type Species. *Vaejovis pumilis* Williams, 1970 [= *Paravaejovis pumilis* (Williams, 1970)].

References:

Paravaejovis: Williams, 1980: 29–30, figs. 32A–D; Haradon, 1984b: 319; Sissom, 1990a: 110, 114; Stockwell, 1992: 409, 416, figs. 62–63; Kovařík, 1998: 143; Beutelspacher, 2000: 56, 63, 151; Sissom, 2000: 504–505; Soleglad & Fet, 2003b: 88.

Composition. This monotypic genus includes the single species, *P. pumilis* (Williams, 1970).

Distribution. Mexico (endemic of Baja California Sur); see tribe.

Diagnosis. Same as for tribe.

Taxonomic History. The genus *Paravaejovis* was established by Williams (1980: 29–30) for a single, very unique little scorpion species originally described as *Vaejovis pumilis* also by Williams (1970c: 297–302).

Discussion. Along with *P. pumilis*, Williams (1970b) also described another smeringurine species from Baja California Sur, *Paruroctonus pseudopumilis*, which was then assigned to his “pumilis” group of *Vaejovis*. Later, this species was placed in the “borregoensis” microgroup of *Paruroctonus* by Haradon (1984b). Haradon (1984b), in his discussion of the “borregoensis” microgroup, states: “... carapace, metasoma, pectines, pedipalps and legs, and sexual dimorphism shown by *Paravaejovis*, indicate to me that this taxon is most closely related, if not subordinate, to the borregoensis group ...”. In his discussion, Haradon (1984b) questioned the importance of neobothriotaxy exhibited in *Paravaejovis* because it was not exclusively found in this genus in Vaejovidae. This is indeed true, but the examples provided by Haradon (1984b), involving a single accessory trichobothrium, are, in our opinion, different in their evolutionary and taxonomic significance from the major neobothriotaxy found in *Paravaejovis*. Also in agreement with Haradon’s (1984b) observation on sexual dimorphism, we point out in the section on the pectines (see above), the major difference in pectinal tooth counts between the genders in *Paravaejovis*, which is also found in three other species of the “borregoensis” microgroup of *Paruroctonus*. And if the only character differentiating *Paravaejovis* from the other Smeringurine species were neobothriotaxy, then we would agree with Haradon (1984b), since it clearly is autapomorphic. However, several other characters unique to *Paravaejovis* clearly separate it from tribe Smeringurini, including all its genera, among them the “borregoensis” microgroup of *Paruroctonus*. Fet et al. (2006c) presented a comprehensive analysis of the constellation array in Smeringurinae, showing that *Paravaejovis* exhibited three sensilla whereas Smeringurini have two (see our

Figures 198–201). Fet et al. (2006c) also suggested that constellation array sensilla are being lost in Smeringurinae since it exhibits the smallest number known in Vaejovidae (and in scorpions in general). This would imply that two sensilla condition seen in Smeringurini is derived from three as seen in Paravaejovini, the number three being a synapomorphy for the subfamily Smeringurinae, since in the other subfamilies, there are usually a larger number of sensilla (Fet et al., 2006a, in progress). As stated in the diagnosis, *Paravaejovis* is quite distinct from the other smeringurines with the unusual placement of the *d* and *e* trichobothria of the pedipalp femur, distal placement of chelal trichobothrium *Dt*, and the hemispermatophore, whose lamellar hook is well defined by a conspicuous basal constriction, placed well above the ventral trough, and the toothed condition of the mating plug barb (after Stockwell, 1989).

The geographic range of Paravaejovini is largely separated from that of its sister tribe Smeringurini, except for two isolated *Paruroctonus* species in the Vizcaino Desert, *P. pseudopumilis* and *P. surensis* (members of the “borregoensis” microgroup), whose range abuts the north edge of *Paravaejovis* range. Their geographic proximity to endemic *Paravaejovis*, combined with similar trends in pectinal tooth gender ratios (see above in “Pectines” section), might deserve further investigation.

Subfamily Syntropinae Kraepelin, 1905

Type Genus. *Syntropis* Kraepelin, 1900.

References:

Syntropinae: Kraepelin, 1905: 340; Birula, 1917a: 163, 184, 191; Birula, 1917b: 57; Werner, 1934: 281; Mello-Leitão, 1945: 118; Gertsch, 1958: 14; Stahnke, 1974: 112, 113 (in part).

Composition. This subfamily, as defined here, includes two tribes: Stahnkeini and Syntropini.

Distribution. Mexico (Baja California, Baja California Sur, and most of mainland Mexico), USA (Arizona, California, Idaho, Nevada, New Mexico, Texas, Utah).

This large subfamily is distributed over most of southwestern United States, Baja California peninsula, and mainland Mexico; see maps in Figs. 202–204 and discussions below for individual tribes, subtribes, and genera.

Diagnosis. Scorpions in the subfamily Syntropinae can be distinguished by the following characters: Genital operculum sclerites of female connected their entire length, operating as a single unit, connected to mesosoma on extreme distal aspect, 0.727–0.833 (0.780) of sclerite separate from mesosoma; hemispermatophore lamellar hook is well developed with conspicuous basal constriction, distally usually conspicuously bifurcated or

with slight cleft, and extends at least 30 percent of the length of the lamella from dorsal trough 0.292–0.450 (0.366) [21]; mating plug well developed and sclerotized, distal barb either smooth or toothed; chelal trichobothrium *Dt* positioned close to or distal of palm midpoint, never basally; *ib–it* positioned adjacent to basal inner denticle (*ID*) to midfinger, never considerably proximal of basal *ID*; chelal trichobothria $V_2–V_3$ distance approximately same as $V_1–V_2$; fixed finger trichobothria *dsb* and *dst* positioned adjacent to or distal of *esb* and *est*, respectively; setal combs absent on legs; cheliceral ventral edge of movable finger without denticles or serrations; serrula medium to well developed, never vestigial; carapace anterior edge straight or with small shallow median indentation, never widely or deeply indented; dorsal carinal terminus of metasomal segments I–III essentially straight (not rounded) terminating with an enlarged denticle; dorsolateral carinae of metasomal segment IV conspicuously flared at the terminus, not coinciding with articulation condyle.

Taxonomic history. Subfamily Syntropinae was established by Kraepelin (1905) as a monotypic taxon for a large, distinct genus *Syntropis*. The subfamily remained monotypic until Stahnke (1974) included here also genus *Vaejovoidus*. Vaejovoid subfamilies were last defined by Stahnke (1974). Due to further removal of Iurinae, Scorpiopsinae, and Hadrurinae from this family (Francke & Soleglad, 1981; Stockwell, 1992), two formally remaining subfamilies of Vaejovidae were Syntropinae (with *Syntropis* and *Vaejovoidus*) and Vaejovinae. Sissom (2000: 504) listed Syntropinae as a synonym of Vaejovidae, noting that “it is not practical at this point to recognize subfamilies.” Soleglad & Fet (2003b) formally synonymized Syntropinae with Vaejovidae. Here, we restore subfamily Syntropinae from synonymy and revise its diagnosis and scope; we also establish a new subfamily Smeringurinae. The nominotypic subfamily Vaejovinae is now also valid by default, albeit in a dramatically reduced scope. This subfamily so far remains unrevised; it includes only four genera: *Franckeus*, *Pseudouroctonus*, *Uroctonites*, and a considerably reduced *Vaejovis* (see below).

Discussion. See discussion of genera below.

Tribe Stahnkeini Soleglad et Fet, 2006

Type Genus. *Stahnkeus* Soleglad et Fet, 2006.

References:

Stahnkeini: Soleglad & Fet, 2006: 24–25; Graham & Soleglad, 2007: 11–12; Soleglad et al., 2007: 134.

Composition. This tribe, as defined here, includes the genera *Gertschius*, *Serradigitus*, *Stahnkeus*, and *Wernerius*.

Distribution. Mexico (Baja California, Baja California Sur, Coahuila, Sonora), USA (Arizona, California, Nevada, New Mexico, Utah).

The tribe Stahnkeini is distributed primarily in the southwestern United States, Baja California peninsula, and extreme northern areas of mainland Mexico; see map in Fig. 202 and discussions of genera below.

Diagnosis. Basal pectinal teeth (1 to as many as 4) of female lacking sensorial areas; median denticles (*MD*) of chelal fingers serrate; *MD + OD* denticle density quotient low, 30–42 (37); mating plug barb of hemispermatophore smooth; one ventral distal spinule pair on leg tarsus; chelal trichobothrium *Db* located on or ventral of digital (*DI*) carina; position of fixed finger trichobothria *ib–it* variable, from midfinger to slightly proximal of basal inner denticle (*ID*), based on species adult size; patellar trichobothrium v_3 positioned distal to *et_3*; ventral edge of cheliceral movable finger with well developed contiguous serrula (21–37 tines).

Taxonomic history. The tribe was recently established by Soleglad & Fet (2006) for vaejovoid genera *Serradigitus* and *Stahnkeus*. At that time, the tribe was not formally assigned to any subfamily. Graham & Soleglad (2007) added the genus *Gertschius* to tribe Stahnkeini. Here, we formally place Stahnkeini in subfamily Syntropinae, which is reestablished here from synonymy, along with the nominotypic tribe, Syntropini, established here. We also add a new genus, *Wernerius*.

Discussion. See discussion of genera below.

Genus *Gertschius* Graham et Soleglad, 2007

Type Species. *Gertschius crassicornus* Graham et Soleglad, 2007.

References:

Gertschius: Graham & Soleglad, 2007: 1–12, figs. 1–13.

Composition. This genus includes two species:

G. agilis (Sissom et Stockwell, 1991)

G. crassicornus Graham et Soleglad, 2007

Distribution. Mexico (Sonora), USA (Arizona, New Mexico).

This small genus (see map in Fig. 202) has a disjunct distribution, *G. agilis* being found in the extreme southern continuous areas of Arizona, New Mexico, and northern Sonora. *G. crassicornus*, based on type locality, is found in southern coastal Sonora (see discussion below of “*Vaejovis*” *pequeno*).

Diagnosis. Modification to basal pectinal teeth of female marginalized, missing sensorial area reduced to one or two teeth, not particularly swollen or elongated and showing some distal angling; outer denticles (*OD*) not serrated, all observable the entire length of both chelal fingers; distal denticle not overly elongated or hook-like, “whitish patch” minimal or absent altogether; inner accessory denticles (*IAD*) absent; subaculear

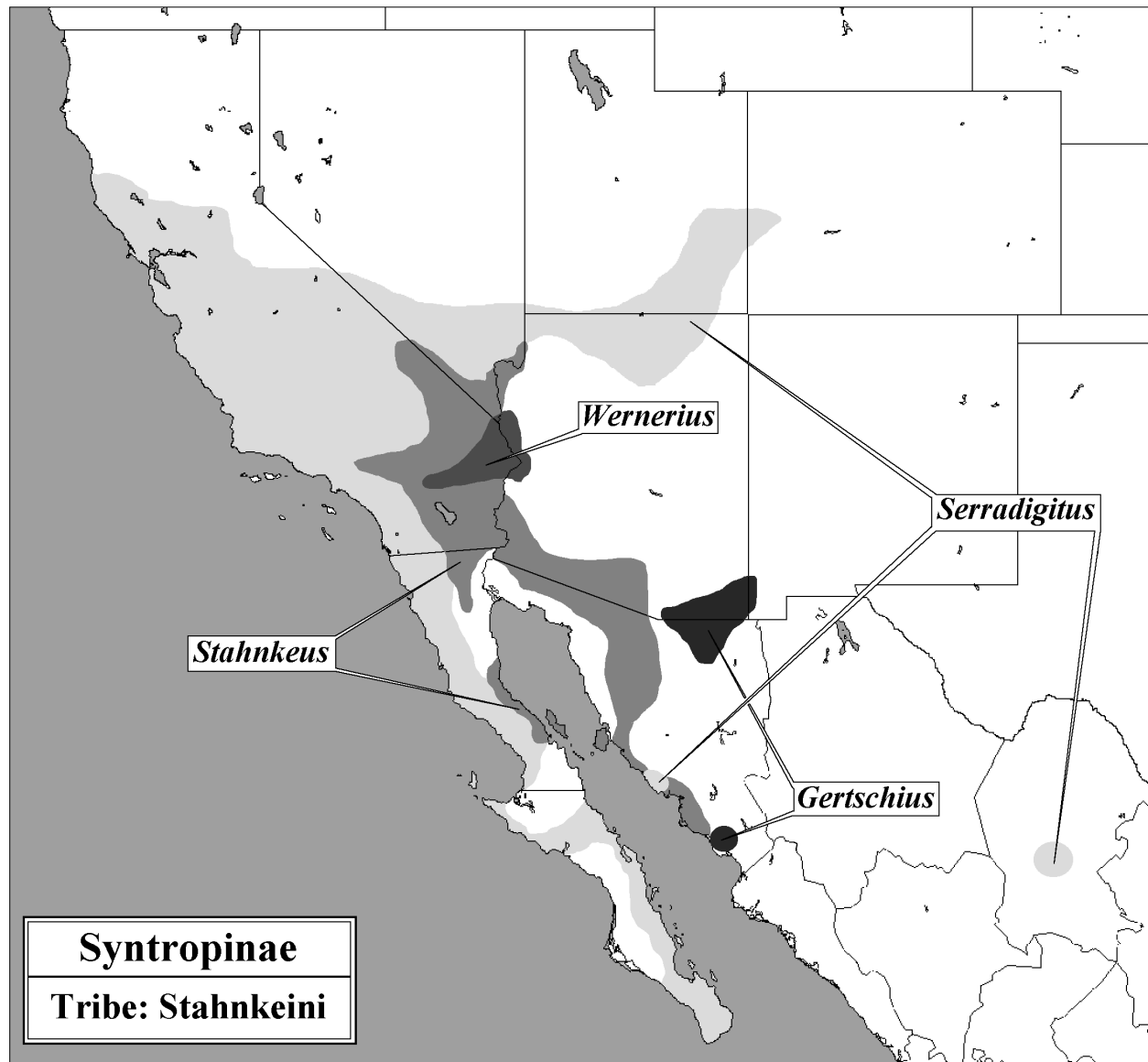


Figure 202: General distribution of scorpion subfamily *Syntropinae* (tribe *Stahnkeini*) in North America with the ranges of genera *Stahnkeus*, *Serradigitus*, *Gertschius*, and *Wernerius* delineated.

spinoid tooth not present; ventromedian (*VM*) carinae of metasomal segments I–II obsolete.

Taxonomic history. Graham & Soleglad (2007) established the genus *Gertschius* describing one new species and moving another (*G. agilis*) from *Serradigitus*. The genus was placed in tribe *Stahnkeini*.

Discussion. *Gertschius* was characterized by Graham & Soleglad (2007) as a “primitive taxon of tribe *Stahnkeini*.” By “primitive” the authors were referring to the less expressed modification of the basal pectinal teeth in the female where the loss of sensilla is limited to one or two teeth, some distal angling still present, and there is no swollenness and/or elongation as seen in many species in core genera of this tribe, *Serradigitus*

and *Stahnkeus*. Similarly, the serration of the chelal finger denticles in *Gertschius* is limited to the median row, the outer denticles (*OD*) are not serrated and readily visible the entire finger length. At the same time, in *Serradigitus* and *Stahnkeus* *OD* are highly serrated and are indistinguishable from the *MD* denticles medially and proximally on the finger. Finally, the distal denticle of each chelal finger in *Gertschius* is not overly elongated with a “whitish” patch, this condition either expressed only slightly or absent altogether. Geographically, the range of *Gertschius* (southern Arizona and Sonora, Mexico) is somewhat removed from the bulk of species found in California and throughout Baja California (see map in Fig. 202).

Genus *Serradigitus* Stahnke, 1974

Type Species. *Vaejovis wupatkiensis* Stahnke, 1940 [= *Serradigitus wupatkiensis* (Stahnke, 1940)].

References (selected):

Serradigitus: Stahnke, 1974: 130–132, figs. 6C, 6D (in part); Williams & Berke, 1986: 351 (in part); Sissom, 1990a: 114 (in part); Sissom & Stockwell, 1991: 197–214; Stockwell, 1992: 409, 416, figs. 19, 40, 42 (in part); Kovařík, 1998: 145 (in part); Sissom, 2000: 518–524 (in part); Soleglad & Fet, 2003b: 88 (in part); Soleglad & Fet, 2006: 26–27, 29, figs. 1–5, 12–14, 17–29, 33–40, 46; Graham & Soleglad, 2007: fig. 13.

Composition. This genus includes the following 19 species and subspecies:

S. adcocki (Williams, 1980)
S. armadentis (Williams, 1980)
S. baueri (Gertsch, 1958)
S. bechteli (Williams, 1980)
S. calidus (Soleglad, 1974)
S. dwyeri (Williams, 1980)
S. gertschi gertschi (Williams, 1968)
S. gertschi striatus (Hjelle, 1970)
S. gigantaensis (Williams, 1980)
S. gramenestris (Williams, 1970)
S. haradoni (Williams, 1980)
S. hearnei (Williams, 1980)
S. joshuaensis (Soleglad, 1972)
S. littoralis (Williams, 1980)
S. minutis (Williams, 1970)
S. pacificus (Williams, 1980)
S. torridus Williams et Berke, 1986
S. wupatkiensis (Stahnke, 1940)
S. yaqui Sissom et Stockwell, 1991

Distribution. Mexico (Baja California, Baja California Sur, Coahuila, Sonora), USA (Arizona, California, Nevada, Utah).

The range of the genus *Serradigitus* is disjunct (see map in Fig. 202): it includes the southwestern United States and Baja California peninsula, and mainland Mexico. Mexico represents its primary disjunction, with a small representation in central coastal Sonora; *S. yaqui*, and *S. calidus* found in Coahuila, Mexico. The most northern species are the type species *S. wupatkiensis* ranging into central Utah and *S. gertschi striatus*, found as far north as Mendocino County, California. The most southern species occur in Baja California Sur: *S. minutis*, *S. adcocki*, *S. bechteli*, *S. armadentis*, *S. haradoni*, and *S. gigantaensis*. The majority of *Serradigitus* species are found throughout Baja California, accounting for 12 endemic species (out of 19 species and subspecies); several species are limited to islands on

both the Pacific and the Sea of Cortez, *S. baueri*, *S. dwyeri*, *S. bechteli*, and *S. armadentis*.

Diagnosis. Modification to basal pectinal teeth of female usually significant, lacking sensorial area variable, affecting 1–4 teeth, blunted and ovoid to swollen and elongated, with little or no distal angling; *OD* denticles serrated, indistinguishable after *OD-3*; distal denticle elongated and hook-like with “whitish patch”; inner accessory denticles (*IAD*) absent; subaculear spinoid tooth not present.

Taxonomic history. Stahnke (1974) established the genus *Serradigitus* based on former “wupatkiensis” group of *Vaejovis*. Williams (1980) synonymized this genus back to *Vaejovis*, but later (Williams & Berke, 1986) reinstated it in reduced scope. Sissom & Stockwell (1991) provided a detailed study of Sonoran species. Beutelspacher (2000), without any reasoning, synonymized *Serradigitus* back to *Vaejovis*. Soleglad & Fet (2006) separated five species of *Serradigitus* as a new genus *Stahnkeus*, and included both genera in their new tribe Stahnkeini.

Discussion. Species in *Serradigitus* are small to medium in size, ranging from the smallest, *S. minutis*, *S. dwyeri*, *S. gigantaensis*, *S. joshuaensis*, and *S. haradoni*, 18–22 mm in length, to *S. pacificus*, *S. adcocki*, and *S. wupatkiensis*, 40 mm.

Serradigitus and its sister genus *Stahnkeus* exhibit the most exaggerated form of the modified basal pectinal teeth in the female and the serrated condition of the chelal fingers. Except for the occurrence of *S. calidus* in Coahuila and *S. yaqui* in coastal Sonora, this genus occurs primarily in California and Baja California and all species appear to be lithophilic.

Genus *Stahnkeus* Soleglad et Fet, 2006

Type Species. *Vaejovis harbisoni* Williams, 1970 [= *Stahnkeus harbisoni* (Williams, 1970)].

References:

Stahnkeus: Soleglad & Fet, 2006: 29–30, figs. 6–5, 15–16, 30–32, 41–48; Graham & Soleglad, 2007: 1, 3, 12; Soleglad et al., 2007: 134.

Composition. This genus includes five species:

S. allredi (Sissom et Stockwell, 1991)
S. deserticola (Williams, 1970)
S. harbisoni (Williams, 1970)
S. polisi (Sissom et Stockwell, 1991)
S. subtilimanus (Soleglad, 1972)

Distribution. Mexico (Baja California, Sonora), USA (Arizona, California, Nevada).

This genus (see map in Fig. 202) has a disjunct range with two parts, one in southern California, Nevada, and Arizona (*S. subtilimanus*, *S. deserticola*, *S. allredi*) and extending into Sonora, Mexico (*S. polisi*),

and the other isolated in central Baja California (*S. harbisoni*).

Diagnosis. Modification to basal pectinal teeth of female usually significant, lacking sensorial area variable, affecting 1–4 teeth, blunted and ovoid to swollen and elongated, with little or no distal angling; *OD* denticles serrated, indistinguishable after *OD-3*; distal denticle elongated and hook-like with “whitish patch”; inner accessory denticles (*IAD*) present; subaculear spinoid tooth not present.

Taxonomic history. The genus was separated from *Serradigitus* by Soleglad & Fet (2006), and the tribe *Stahnkeini* was established at the same time.

Discussion. Species in *Stahnkeus* are the largest in tribe *Stahnkeini*, *S. harbisoni* and *S. subtilimanus* reaching lengths of at least 50 mm. These two species and *S. deserticola* are closely related, showing a distribution extending from the Mojave Desert to central Baja California. The other two taxa, *S. polisi* and *S. allredi*, are smaller species, occurring in southern Arizona and coastal Sonora, Mexico.

This unique genus in *Stahnkeini* is defined by the presence of inner accessory denticles (*IAD*) found on both the fixed and movable fingers of the chela. This is the only example of *IAD* in the family *Vaejovidae*. As reported by Soleglad & Fet (2006: table 6), the number of *IAD* increases as a specimen progressively reaches maturity. *Stahnkeus harbisoni* may have as many as 20 *ID* + *IAD* denticles on the movable finger.

Genus *Wernerius* Soleglad et Fet, **gen. nov.**

Type Species. *Vaejovis spicatus* Haradon, 1974 [= *Wernerius spicatus* (Haradon, 1974), **comb. n.**].

Composition. This genus, established here, includes the following two species:

W. mumai (Sissom, 1993), **comb. nov.**

W. spicatus (Haradon, 1974), **comb. nov.**

Distribution. USA (Mojave Desert of Arizona and California).

This rare genus (see map in Fig. 202) has a limited range based so far on the few specimens collected. *W. spicatus* has been found in the south-central area of the Joshua Tree National Monument in California. *W. mumai* has been collected on the Arizona side of the Colorado River, between Kingman and Parker, Arizona. Both species appear to be somewhat adapted to rocky outcrops, similar to the microhabitats of many small *Serradigitus* species.

Etymology. The new generic name (masculine) is a patronym honoring Austrian zoologist Franz Werner (1867–1939), author of an encyclopedic treatise on scorpions (Werner, 1934).

Diagnosis. Modification to basal pectinal teeth of female marginalized, missing sensorial area reduced to one or two teeth, not particularly swollen or elongated and showing some distal angling or ovoid; *OD* denticles not serrated, all observable the entire length of both chelal fingers; distal denticle not overly elongated or hook-like, “whitish patch” minimal or absent altogether; inner accessory denticles (*IAD*) absent; conspicuous subaculear spinoid tooth present; ventromedian (*VM*) carinae of metasomal segments I–II granular to serrate.

Discussion. In the original species descriptions of *W. spicatus*, Haradon (1974), and *W. mumai*, Sissom (1993), certain diagnostic characters used in our current study are not outlined. However, by combining the two descriptions of these closely related species, both inhabiting the Mojave Desert of California and Arizona and sharing a distinct spinoid subaculear tooth (unusual in the vaejovids, see discussion below), we can establish most of the missing data. For example, the genital operculum, chelicerae and leg tarsus armature are not discussed by Sissom (1993) for *W. mumai* but they are, in part, for *W. spicatus*: Haradon (1974: 23–24) states the genital operculum is “completely fused medially” and the cheliceral movable finger has “serrula along smooth inferior margin, not extending to apex”. Neither author discusses the distal spinule pairs of the leg tarsus, but McWest (2000, in his unpublished Master thesis) states there are three spinules on *W. mumai*, which we will interpret here as a single pair. Haradon (1974) does not describe the hemispermatophore of *W. spicatus* (only females were available) nor does he state the condition of peg sensilla on the basal pectinal teeth. Sissom (1993: 65, figs. 12–14), however, nicely illustrates the hemispermatophore and mating plug of *W. spicatus* and reports that the basal pectinal tooth of the female *W. mumai* is ovoid and lacks sensilla. Both authors do illustrate the trichobothrial pattern which are identical in the key positions discussed in this study: fixed finger trichobothria *dsb* and *dst* are distal to *esb* and *est*, respectively; distance between chelal ventral trichobothria $V_1|V_2$ and $V_2|V_3$ are roughly the same ($V_2|V_3$ slightly shorter); trichobothrium *Dt* is located slightly proximal of palm midpoint, 0.424–0.429; *Db* is positioned ventral of digital (*DI*) carina; *ib-it* are located just proximal of basal inner denticle (*ID*); and patella trichobothrium v_3 is distal of *et_3*. In Sissom’s illustrations of the chelae, the “whitish patch” is shown though it is not mentioned specifically in the text. Although the chelal finger distal denticles are not reported enlarged or elongated by Sissom (1993: figs. 5, 10), the female illustrated by Haradon (1974: figs. 1, 3, 6) appears to have enlarged distal denticles. Sissom’s (1993) illustration of the hemispermatophore of *W. spicatus* conforms to that exhibited in *Syntropinae* (see Figs. 47–56): a well developed, slightly bifurcated, lamellar hook exaggerated by a conspicuous basal con-

striction. Though the ventral trough is not indicated, it is clear that the distal aspect of the lamellar hook is situated well distal of the former. The mating plug barb is smooth and the overall appearance of the base is quite similar to that found in tribe Stahnkeini (Figs. 83–84).

Sissom (1993: 68) discusses the taxonomic placement of these two taxa stating that "... In light of the structure of the hemispermaphore, the earlier interpretation of *V. spicatus* as a member of the *Vaejovis nitidulus* group now seems inappropriate. *V. spicatus* and *V. mumai* seem more properly allied to *Serradigitus* (but not included therein) ...". We agree with this assessment, especially if the genital operculum of the female is fused medially as reported by Haradon (1974). It is clear that these two species belong in subfamily Syntropinae, based on the genital operculum of the female, the shape of hemispermaphore, trichobothrial pattern, in particular, the non-basal placement of the chelal *ib-it* trichobothria. Based on the lack of sensilla on the basal tooth of the female pectines, the smooth barb of the mating plug, the single pair of ventral distal spinules of the leg tarsus, and well developed serrula, these species belong to tribe Stahnkeini where they share, in part, characters common to the genus *Gertschius*. Of course, genus *Wernerius* is unique with its spinoid subaculear tubercle, considered here a synapomorphy for the genus. Until detailed analysis of the chelal finger dentition of these two species is conducted, especially the number of *MD* and *OD* denticles, exact nature of *MD* development, etc. The exact placement of *Wernerius* within Stahnkeini remains somewhat unclear (see phylogram in Figure 196).

Other vaejovids with subaculear tubercles. Francke & Ponce Saavedra (2005) named a new species of *Vaejovis*, *V. kuarapu*, from Michoacán, Mexico. Of particular interest, this species exhibited a distinct subaculear tooth on the telson. Francke & Ponce Saavedra (2005) discussed their new species in context with other vaejovids reported with a subaculear tubercle, spanning all of North America: *Wernerius spicatus*, *W. mumai*, Mojave Desert, USA; *Vaejovis pattersoni*, Baja California Sur, Mexico; *V. chamelaensis*, Jalisco, Mexico; *V. acapulco*, Guerrero, Mexico; and *V. nayarit*, Nayarit, Mexico. They also mentioned *Serradigitus joshuaensis* from Mojave and Sonora Deserts, USA, which exhibits a small subaculear tubercle (see Fet et al., 2006b: fig. 1). Interestingly, since Haradon (1974) originally compared *W. spicatus* with *S. joshuaensis*, Sissom (1993) contrasted the subaculear tubercles between the two, *S. joshuaensis* having a tubercle but not a spinoid tooth as seen in *W. spicatus* and *W. mumai*. To add further to this distinction, Francke & Ponce Saavedra (2005) contrasted the subaculear tubercle on *V. kuarapu* (and *V. acapulco* and *V. nayarit*) as a spinoid tooth and *W. spicatus* and *W. mumai* as having a conical tooth.

Originally, Williams (1980: 65–66) placed *Vaejovis pattersoni* in the "eusthenura" group, as he also did the species *V. chamelaensis* (Williams, 1986). After viewing specimens Sissom (2000) moved *V. pattersoni* to the "mexicanus" group. Francke & Ponce Saavedra (2005: fig. 12) show that trichobothria *ib-it* in *V. chamelaensis* are situated quite basal on the fixed finger, not adjacent to the basal inner denticle (*ID*), a characteristic of subfamily Vaejovinae. Also, the ventromedian (*VM*) carinae of metasomal segments I–IV in *V. chamelaensis* are granular, unusual for the genus *Hoffmannius* (i.e., the "eusthenura" group). Consequently, we place *V. chamelaensis* in subfamily Vaejovinae. We agree with Francke & Ponce Saavedra (2005) that the Mexican species exhibiting the subaculear tubercle may be related. Based on their descriptions alone, all should tentatively be placed in subfamily Vaejovinae along with *V. pattersoni*. As far as a definite *Vaejovis* group affiliation, if any, we will defer on this until actual specimens are available for examination, but for this study they are placed in the "mexicanus" group.

Tribe **Syntropini** Kraepelin, 1905

Type Genus. *Syntropis* Kraepelin, 1900.

References:

Syntropinae: Kraepelin, 1905: 340 (as subfamily).

Composition. This tribe, established here by Principle of Coordination (ICZN, 1999a, Article 36.1), includes the subtribes Syntropina and Thorelliina.

Distribution. Mexico (Baja California, Baja California Sur, and most of mainland Mexico), USA (Arizona, California, Idaho, Nevada, New Mexico, Texas, Utah).

This large tribe is distributed over most of southwestern United States and Mexico, see maps in Figs. 203–204 and discussions below for individual subtribes and genera.

Diagnosis. Basal pectinal teeth of female with sensorial areas; median (*MD*) and outer denticles (*OD*) of chelal fingers not serrate, *MD* + *OD* denticles density quotient medium, 51–74 (58); mating plug barb of hemispermaphore toothed; 2–4 ventral distal spinule pairs on leg tarsus; chelal trichobothrium *Db* located on or dorsal of digital (*DI*) carina; fixed finger trichobothria *ib-it* adjacent to basal inner denticle (*ID*); ventral edge of cheliceral movable finger with medium developed contiguous serrula (10–21 tines).

Discussion. See discussion of genera below.

Subtribe **Syntropina** Kraepelin, 1905, **new rank**

Type Genus. *Syntropis* Kraepelin, 1900.

References:

Syntropinae: Kraepelin, 1905: 340 (as subfamily).

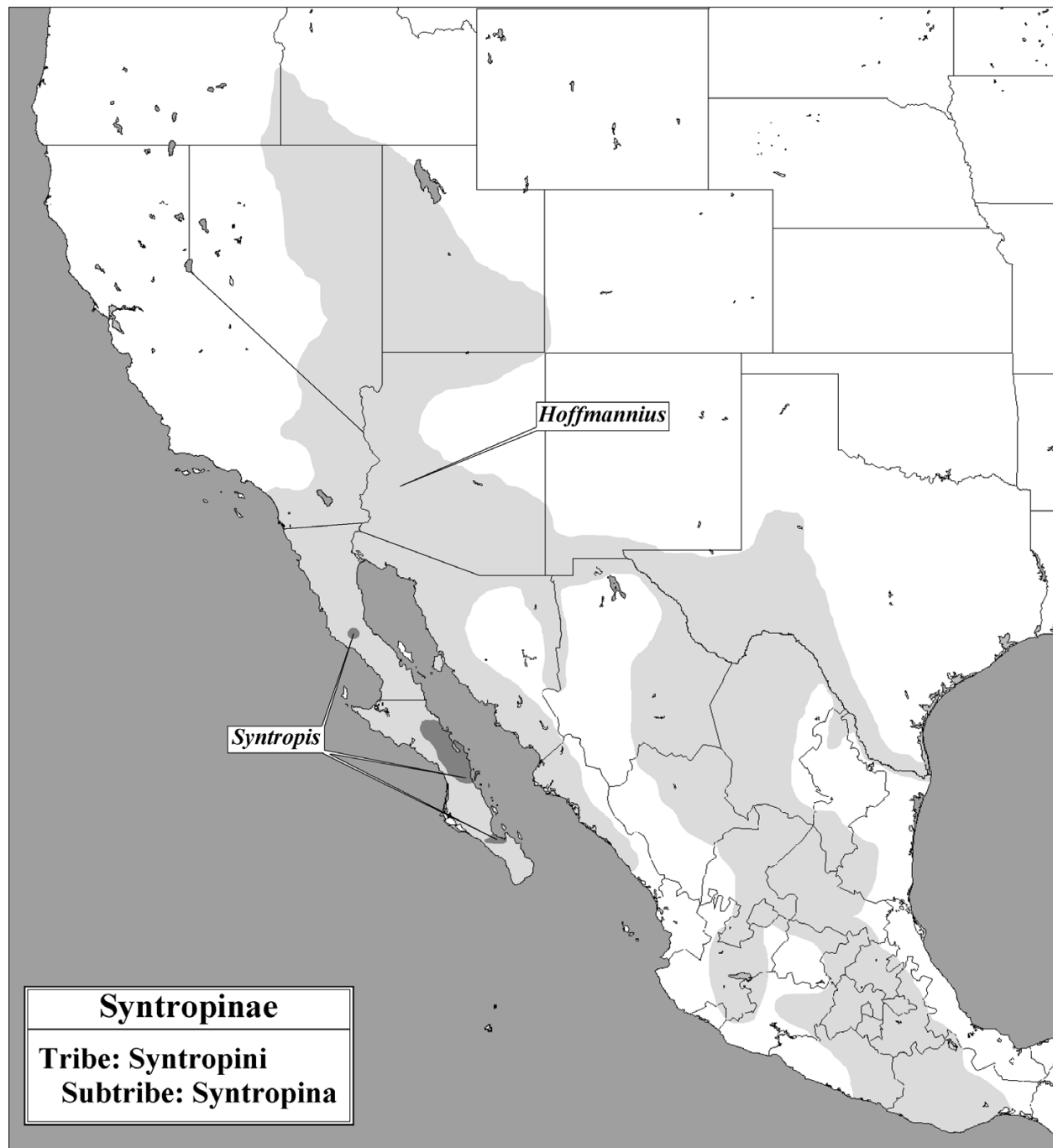


Figure 203: General distribution of scorpion subfamily **Syntropinae** (tribe **Syntropini**, subtribe **Syntropina**) in North America with the ranges of genera *Hoffmannius* and *Syntropis* delineated.

Composition. This subtribe, established here by Principle of Coordination (ICZN, 1999a, Article 36.1), includes the genera *Hoffmannius* and *Syntropis*.

Distribution. Mexico (Baja California, Baja California Sur, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Zacatecas), USA

(Arizona, California, Idaho, Nevada, New Mexico, Texas, Utah).

Diagnosis. Chelae with obsolete to reduced carination; subdigital (*D2*) carina vestigial, not in strong profile; *D2* carina positioned much closer to *D1* than *D3*; ventrolateral and ventromedian carinae of metasomal segments I–IV obsolete to smooth, some carination, never fully crenulate or serrate.

Discussion. See discussion of genera below.

Genus *Hoffmannius* Soleglad et Fet, **gen. nov.**

Type Species. *Buthus eusthenura* Wood, 1863 [= *Hoffmannius eusthenura* (Wood, 1863), **comb. nov.**]

Composition. This genus, established here, includes the following 21 species and subspecies:

- H. bilineatus* (Pocock, 1898), **comb. nov.**
H. coahuilae (Williams, 1968), **comb. nov.**
H. confusus (Stahnke, 1940), **comb. nov.**
H. diazi diazi (Williams, 1970), **comb. nov.**
H. diazi transmontanus (Williams, 1970), **comb. nov.**
H. eusthenura (Wood, 1863), **comb. nov.**
H. galbus (Williams, 1970), **comb. nov.**
H. glabrimanus (Sissom et Hendrixson, 2005), **comb. nov.**
H. globosus (Borelli, 1915), **comb. nov.**
H. gravicaudus (Williams, 1970), **comb. nov.**
H. hoffmanni hoffmanni (Williams, 1970), **comb. nov.**
H. hoffmanni fuscus (Williams, 1970), **comb. nov.**
H. punctatus punctatus (Karsch, 1879), **comb. nov.**
H. punctatus spadix (Hoffmann, 1931), **comb. nov.**
H. punctatus variegatus (Pocock, 1898), **comb. nov.**
H. puritanus (Gertsch, 1958), **comb. nov.**
H. spinigerus (Wood, 1863), **comb. nov.**
H. viscainensis (Williams, 1970), **comb. nov.**
H. vittatus (Williams, 1970), **comb. nov.**
H. waeringi (Williams, 1970), **comb. nov.**
H. waueri (Gertsch et Soleglad, 1972), **comb. nov.**

Distribution. Same as for subtribe.

This genus is widespread in North America (see map in Fig. 203), extending north to the southern edge of Idaho (*H. confusus*), is distributed in all areas of Baja California, Mexico. Its most northern species are *H. puritanus* and *H. waeringi*, and the extreme southern, *H. eusthenura*, *H. galbus*, and *H. vittatus*. Eastward the genus extends into Arizona (*H. confusus* and *H. spinigerus*), New Mexico and Texas (*H. coahuilae*, *H. globosus*, and *H. waueri*). Most of mainland Mexico is occupied by this genus, northern states such as Sonora (*H. spinigerus*), Chihuahua and Coahuila (*H. coahuilae*, *H. bilineatus*, and *H. globosus*), and central and southern states, as far south as Oaxaca (*H. punctatus*). Its highest diversity occurs in Baja California, Mexico with no less than nine out of 16 species, many endemic to the peninsula including the unusual species *H. viscainensis*, isolated in the Vizcaino Desert.

Etymology. The new generic name (masculine) is a patronym honoring Mexican zoologist Carlos C. Hoffmann (1876–1942), one of the prominent scorpion

researchers of the 20th century, the author of the first systematic revision of Mexican scorpions (Hoffmann, 1931, 1932).

Diagnosis. Metasomal segments I–IV with paired ventromedian carinae; chelal fingers variable in length, but never extremely elongated, basal *OD* denticles located basally or suprabasally on fingers; chelal trichobothria *ib–it*, *db–dt* and *eb–et* positioned evenly over the fixed finger, not on the distal half; metasomal segments medium to heavy, segments I–II usually as wide or wider than long, length-to-width ratio 0.67–1.08 (0.889) and 0.83–1.31 (1.051) for the male, and 0.67–1.03 (0.813) and 0.77–1.29 (0.949) for the female; dorsal and dorsolateral carinae of metasomal segments I–IV flared posteriorly, distal denticle noticeably larger than other denticles.

Taxonomic history. Scorpions of this genus were previously placed in the informal “eusthenura” group of *Vaejovis*, first defined by Williams (1970d); see Sissom (2000: 530–537).

Discussion. The majority of species in *Hoffmannius* are medium in size, averaging 45–55 mm in length, the smallest species are: *H. waueri*, 25 mm, *H. bilineatus*, 34 mm, and *H. vittatus*, 35 mm, and the largest: *H. spinigerus*, 68 mm, *H. gravicaudus*, 65 mm, and *V. punctatus*, 61 mm. Most species are clear yellow in color and lack patterns, but there are many exceptions to this, such as *H. spinigerus*, *H. gravicaudus*, and *H. vittatus* whose tergites are mottled with dark patterns and faint dark stripes are found on the ventral metasomal carinae, and *H. puritanus*, which exhibits color races from clear yellow to a darker yellow-orange with subtle variegated patterns.

Metasomal segments of this genus are in general somewhat heavy, significantly so in the terminal segments IV–V, as discussed in detail elsewhere in the section on morphometrics. The telson vesicle of *Hoffmannius* (Figs. 178–179) is large basally and tapers noticeably towards the aculeus. Again, the width and depth of the *Hoffmannius* vesicle is relatively the largest in tribe Syntropini. Carination of the ventral aspect of metasoma and the chelal palm is also quite reduced in *Hoffmannius*, Tables 4–5 compare this carinal development between *Hoffmannius* and subtribe Thorelliina genera *Thorellius* and *Kochius*. Roughly half of the species in *Hoffmannius* lack ventromedian carinae and the chelal carinae are in general obsolete to vestigial and smooth. At the same time, in *Kochius* and *Thorellius* many of the species exhibit granulate to serrate ventromedian carinae, especially in the former, and the chelal carinae are always present, with many being granulate to crenulate.

Genus *Syntropis* Kraepelin, 1900

References (selected):

Syntropis: Kraepelin, 1900: 16–17; Birula, 1917a: 163; Birula, 1917b: 57; Werner, 1934: 281;

Stahnke, 1974: 113–120; Williams, 1974: 15 (in part); Williams, 1980: 47; Sissom, 1990a: 110; Stockwell, 1992: 408, 419, fig. 44; Beutelspacher, 2000: 55, 70, 152; Sissom, 2000: 526; Soleglad & Fet, 2003b: 88; Soleglad et al., 2007: 119–136, figs. 1–37.

Type Species. *Syntropis macrura* Kraepelin, 1900.

Composition. This genus includes the following three species:

S. aalbui Lowe, Soleglad et Fet in Soleglad et al., 2007

S. macrura Kraepelin, 1900

S. williamsi Soleglad, Lowe et Fet, 2007

Distribution. Mexico (Baja California, Baja California Sur).

This genus is endemic to Baja California peninsula, Mexico (see map in Fig. 203). Its three species exhibit disjunct ranges, consistent with current theories of two vicariant events in the peninsula, between northern and southern Baja peninsula, and the La Paz Strait (Soleglad et al., 2007).

Diagnosis. Metasomal segments I–IV with single ventromedian carina; chelal fingers extremely elongated, basal OD denticles located at finger midpoint; chelal trichobothria *ib–it*, *db–dt*, and *eb–et* positioned on distal half of fixed finger; metasomal segments thin, all longer than wide in both genders, dorsal and dorsolateral carinae of metasomal segments I–IV not overly flared posteriorly and terminal denticle only slightly larger than other denticles.

Taxonomic history. This interesting and rare genus was first described by Kraepelin (1900), and was considered monotypic until recently when Soleglad et al. (2007) named two additional species.

Discussion. Males of *Syntropis macrura* approach 100 mm in length (i.e., Stahnke, 1965, reported the type male specimen to be 98 mm), which makes this species one of the longest in family Vaejovidae. Coloration varies from clear yellow without patterns in *S. williamsi*, to reddish yellow-brown, *S. aalbui* and *S. macrura*, and to dark red chelal fingers in *S. macrura*.

Syntropis is a very unique and rarely encountered genus exhibiting two or more discrete synapomorphies, which differentiates it from its sister genus *Hoffmannius*: it has a single ventromedian (*VM*) carina on metasomal segments I–IV, somewhat rare in Recent scorpions and only matched in Vaejovidae by the smeringurine genus *Vejovoidus*. The genus is quite slender and elongated in the metasoma and pedipalps (see histograms in Figs. 194–195), the latter probably contributing to the second synapomorphy of *Syntropis*, the midfinger to distal placement of trichobothrial series *ib–it*, *db–dt*, and *eb–et*. In addition, a potential third synapomorphy, the basal

outer denticle (*OD*) of the fixed finger is also located midfinger (see trichobothrial pattern for *S. williamsi* in Fig. 10). As suggested by Soleglad et al. (2007) one or more of these synapomorphies may be a product of the considerable adaptation of *Syntropis* to its microhabitat, mostly rock crevices (i.e., the genus is lithophilic to ultralithophilic).

Subtribe Thorelliina Soleglad et Fet, subtrib. nov.

Type Genus. *Thorellius* Soleglad et Fet, **gen. nov.**

Composition. This subtribe, established here, includes the new genera *Kochius* and *Thorellius*.

Distribution. Mexico (Aguascalientes, Baja California, Baja California Sur, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Veracruz, Zacatecas), USA (Arizona, California, Nevada, New Mexico, Texas).

Diagnosis. Chelae heavily carinated; subdigital (*D2*) carina well developed and in strong profile, sometimes spanning one-third of the palm length; *D2* carina positioned roughly equidistant between *D1* and *D3*; ventrolateral and ventromedian carinae of metasomal segments I–IV smooth to crenulate, sometimes serrate.

Discussion. See discussions under genera.

Genus **Kochius** Soleglad et Fet, **gen. nov.**

Type Species. *Buthus punctipalpi* Wood, 1863 [= *Kochius punctipalpi* (Wood, 1863), **comb. nov.**]

Composition. This genus, established here, includes the following 15 species and subspecies:

K. atenango (Francke et González Santillán, 2006), **comb. nov.**

K. bruneus bruneus (Williams, 1970), **comb. nov.**

K. bruneus loretoensis (Williams, 1971), **comb. nov.**

K. bruneus villosus (Williams, 1971), **comb. nov.**

K. cazieri (Williams, 1968), **comb. nov.**

K. crassimanus (Pocock, 1898), **comb. nov.**

K. hirsuticauda (Banks, 1910), **comb. nov.**

K. insularis (Williams, 1971), **comb. nov.**

K. kovariki Soleglad et Fet, **sp. nov.**

K. magdalensis (Williams, 1971), **comb. nov.**

K. punctipalpi punctipalpi (Wood, 1863), **comb. nov.**

K. punctipalpi barbatus (Williams, 1971), **comb. nov.**

K. punctipalpi cerralvensis (Williams, 1971), **comb. nov.**

K. russelli (Williams, 1971), **comb. nov.**

K. sonora (Williams, 1971), **comb. nov.**

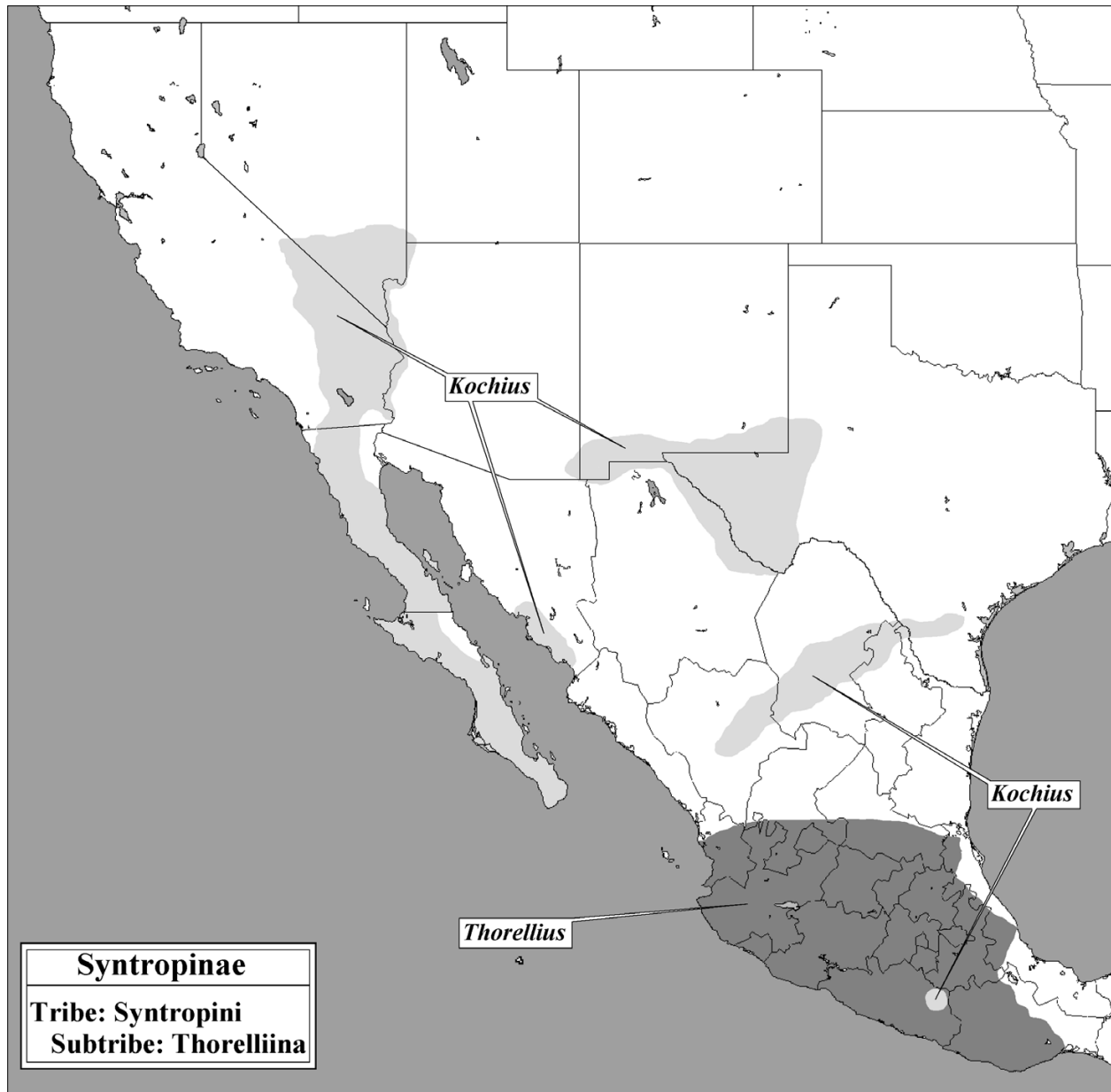


Figure 204: General distribution of scorpion subfamily **Syntropinae** (tribe **Syntropini**, subtribe **Thorelliina**) in North America with the ranges of genera *Kochius* and *Thorellius* delineated.

Distribution. Mexico (Baja California, Baja California Sur, Chihuahua, Coahuila, Durango, Nuevo León, San Luis Potosí, Sonora), USA (Arizona, California, Nevada, New Mexico, Texas).

Genus *Kochius* range is represented by several disjunct parts (see map in Fig. 204). The core group of species is found in southern California, Nevada, and Arizona (*K. hirsuticauda*), and the Baja California peninsula (*K. hirsuticauda*, *K. bruneus*, *K. magdalensis*, *K. insularis*, and *K. punctipalpi*). The second disjunct part of the range involves species *K. russelli* found in southeast Arizona, and southern New Mexico and Texas.

The third disjunct part, is interesting, involving three species, *K. crassimanus*, *K. cazieri*, and *K. kovariki* (albeit, there is some dispute concerning the type locality of *K. crassimanus*), in southern Texas, Durango, Coahuila, and Nuevo León, Mexico. The last isolated locations for *Kochius* is that of *K. sonorae*, from southwestern Sonora, and *K. atenango* from extreme southern Guerrero, Mexico. One would assume that additional collecting in the northern states of Mexico will fill in, or at least narrow, some of these disjunctions.

Etymology. The new generic name (masculine) is a patronym honoring German arachnologist Carl Ludwig

Koch (1778–1857), one of the prominent early scorpion researchers of 19th century, and the author of many scorpion taxa, including genus *Vaejovis*.

Diagnosis. Carapace anterior edge with conspicuous continuous emargination originating from the lateral eyes, with a small median indentation; metasomal segments IV–V length-to-width ratio 1.7–2.2 (1.91) and 2.4–3.3 (2.75) for males, and, 1.5–2.3 (1.83) and 2.3–3.5 (2.72) for females; metasomal segments I–III ventromedian (*VM*) carinae usually granular to crenulate; chelal carinae usually granular to crenulate.

Taxonomic history. Scorpions of this genus were previously placed in the informal “punctipalpi” group of *Vaejovis*, a group first defined by Williams (1971b); see Sissom (2000: 548–551).

Discussion. Species of *Kochius* are small to averaged sized scorpions (35–65 mm), mostly pale yellow in color, exhibiting little patterns, except for, in general, reddish pigmented chelal fingers. The largest species is *Kochius punctipalpi* and the smallest is *K. sonorae*. In general these scorpions are quite granular, the chelal and metasomal carinae are distinct, at least smooth, and usually granulate to serrate. The carapace anterior edge is very unique with its well defined emargination extending across to the lateral eyes and the narrow median indentation. The metasoma in these species are somewhat thin as compared to their sister genus *Thorellius*. The histograms in Figs. 194–195, for both the male and female, clearly show that, in general, metasoma in *Kochius* is thinner for each segment than in *Thorellius*. In particular, segments IV and V show significant differences: Histograms in Figs. 194–195 show complete standard error range separation, male and female. The differences in the mean values, based on all known species, are significant ranging 24 to 30 %.

As discussed elsewhere in the section on morphometrics for genus *Kochius*, species *K. hirsuticauda*, *K. punctipalpi*, *K. bruneus*, *K. insularis*, and *K. magdalenensis* in general have the heavier chelae across the genus. These species are all primarily found in Baja California, Mexico. The species *K. russelli*, *K. kovariki*, and *K. atenango* have a somewhat thinner chela than is normally exhibited in the genus. It is also interesting to point out that these species are found in western Mexico from Sonora and Durango, to Guerrero. Species *K. cazieri*, from Coahuila, Mexico, and *K. crassimanus* from southern Texas, are intermediate with respect to heavy chelae.

Francke & González Santillán (2007) described *K. atenango* from Guerrero, by far the most southern example of this genus. The authors placed *K. atenango* in the “punctipalpi” group of *Vaejovis*. We attempted to verify this placement of this species in *Kochius* from their description and illustrations. However, there is no mention of the female genital operculum so we cannot verify this important subfamily level character. The

hemispermaphore and mating plug barb are consistent with Syntropinae and tribe Syntropini. The carapace as illustrated is also consistent with the carapace found in a typical *Kochius* species. The degrees of carination of the chelal palm and the metasomal ventromedian carinae are less developed than normally seen in *Kochius*, only matched in species *K. crassimanus* and *K. kovariki*. Since only two views of the chela were illustrated, verification of key trichobothrial positions became impossible. In addition, we noticed that no less than three bogus trichobothria were shown in their figures 5–6, while four others were missing altogether; therefore, we consider this partial information completely unreliable.

Genus *Thorellius* Sölgglad et Fet, gen. nov.

Type Species. *Vaejovis intrepidus* Thorell, 1877 [= *Thorellius intrepidus* (Thorell, 1877), **comb. nov.**]

Composition. This genus, established here, includes the following six species (two of which are elevated from subspecies):

T. atrox (Hoffmann, 1931), **stat. nov., comb. nov.**

T. cisnerosi (Ponce Saavedra et Sissom, 2004), **comb. nov.**

T. cristimanus (Pocock, 1898), **stat. nov., comb. nov.**

T. intrepidus (Thorell, 1877), **comb. nov.**

T. occidentalis (Hoffmann, 1931), **comb. nov.**

T. subcristatus (Pocock, 1898), **comb. nov.**

Distribution. Mexico (Aguascalientes, Colima, Guerrero, Guanajuato, Hidalgo, Jalisco, Mexico, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Veracruz, Zacatecas).

Genus *Thorellius* distribution is contiguous, exhibiting no disjunctions (see map in Fig. 204). The most northern species, *T. intrepidus*, is found as far north as Nayarit, and species *T. cristimanus* and *T. atrox* occur in Jalisco and Colima. Hoffmann (1931) also reported *T. intrepidus* from Veracruz. Species *T. cisnerosi*, *T. occidentalis*, and *T. subcristatus* occur the furthest south in Mexico, the latter two species reported for states Guerrero and Puebla.

Etymology. The new generic name (masculine) is a patronym honoring Swedish arachnologist Tord Tamerlan Thorell (1830–1901), one of the prominent scorpion taxonomists of the 19th century, and the author of many scorpion taxa, including family Vaejoidea.

Diagnosis. Carapace anterior edge lacking conspicuous emargination, if present never extending to lateral eyes, median area either straight or with wide subtle indentation; metasomal segments IV–V length-to-width 1.4–1.7 (1.54) and 1.8–2.3 (2.12) for males, and, 1.3–1.6 (1.45) and 1.9–2.4 (2.10) for females; meta-

somal segments I–III ventromedian (*VM*) carinae usually smooth to granular; chelal carinae usually smooth to strongly marbled.

Taxonomic history. Scorpions of this genus were previously placed in the informal “intrepidus” group of *Vaejovis*; see Sissom (2000: 537–538).

Discussion. Genus *Thorellius* contain some of the largest species in family Vaejovidae. *T. intrepidus* has been reported up to 94 mm (Sissom, 2000: 537); only *Syntropis* or *Smeringurus* species may be slightly longer albeit much more slender. The smallest species in *Thorellius* are *T. occidentalis* and *T. subcristatus*, though both reach 50 mm. Unlike its sister genus *Kochius*, *Thorellius* may exhibit dark pigmentation and patterns; one species, *T. atrox*, is almost completely black in color.

As discussed above for genus *Kochius*, the metasoma of *Thorellius* is much thicker, approaching that seen in genus *Hoffmannius*. The heavy chelae, common to both *Kochius* and *Thorellius*, have their carinae less granular in *Thorellius*, but instead the carinae are irregular and “marbled” in appearance (see the digital (*DI*) carina in Figs. 144–145 for *T. intrepidus* and *T. atrox*). The carapace anterior edge (Figs. 134–135) in *Thorellius* does not exhibit an emargination extending to the lateral eyes and the narrow median indentation is not present as seen in *Kochius* (Figs. 128–133).

Ponce Saavedra & Sissom (2004) described species *T. cisnerosi* from Michoacán, Mexico. The authors were reluctant to place this species into one of the established *Vaejovis* groups stating: “... *Vaejovis cisnerosi* is very unique in morphology, rendering its placement in established species group ... difficult. ... is unlike all other species of *Vaejovis* ... carinae of the dorsal and lateral surfaces of the metasoma greatly reduced ... smooth ... metasomal setation is highly reduced ... lowest setal counts of any species in genus ... features are autapomorphic”. Clearly the hemispermatophore, with its well developed lamellar hook, the mating plug with its toothed barb, and the multiple pairs of ventral distal spinules of the leg tarsus imply this species is a member of tribe Syntropini. The chelal and metasomal carination of this species is unique (see Table 4) where the former exhibits vestigial to smooth carinae and the ventral carinae of the latter are obsolete. The existence of carinae on the chelae, though smooth, and the somewhat robust chelae imply this species is a member of subtribe Thorelliina. The carapace in *T. cisnerosi* lacks the anterior emargination extending to the lateral eyes as seen in *Kochius* and the placement of chelal trichobothrium *Dt* is well distal of the palm midpoint, indications of genus *Thorellius* (see histogram in Fig. 17). Finally, of somewhat less importance, the large size of this species, its large pectinal tooth count (20–22 for males and 20–21 for females), and its geographical distribution also indicates genus *Thorellius*.

Thorellius cristimanus, **stat. nov.** and *T. atrox*, **stat. nov.** are elevated here to species rank. These two taxa have been previously listed as *Vaejovis intrepidus* subspecies (Hoffmann, 1931: 378–385; Sissom, 2000: 538). The largest of the three species, *T. intrepidus*, has a much thinner metasoma than species *T. cristimanus* and *T. atrox*. In Table 4 we see that metasomal segments II–III are longer than wide in both genders in *T. intrepidus* whereas segment II is wider than long and segment III is approximately as wide as long in *T. cristimanus* and *T. atrox*. To further quantify these differences, we compared two female *T. intrepidus* specimens from Tepic, Nayarit against two females of *T. cristimanus* from Autlán, Jalisco. Comparing morphometric ratios for each metasomal segment (length / width, averaged for the two female specimens per species), we found the following percentage differences: segment I = 17.2 %, segment II = 29.2 %, segment III = 25.0 %, segment IV = 24.7 %, and segment V = 25.3 %, showing that segments II–IV are 25 % thinner in *T. intrepidus* than in *T. cristimanus*. We found similar percentage differences between the male of these two species (one *T. intrepidus* from Mexico and two *T. cristimanus* from Autlán, Jalisco): segment I = 28.4 %, segment II = 26.4 %, segment III = 21.7 %, segment IV = 24.3 %, and segment V = 13.8 %. The metasomal segment proportions are essentially the same in *T. cristimanus* and *T. atrox*. However, the chelae in *T. atrox* are thinner than in *T. intrepidus* and *T. cristimanus*. In the female, comparing the length to the palm depth, we see a ratio of 2.882 in *T. atrox* versus 2.379 in *T. cristimanus*, a 21.1 % difference. The chela in *T. intrepidus* is even more robust, exhibiting a ratio of 2.160 for the female, showing a 33.4 % difference from *T. atrox*. This difference in the chela proportions is quite visible in Figs. 144–145. Finally, *T. atrox* is a very dark scorpion, almost black, while *T. intrepidus* and *T. cristimanus* are much lighter, exhibiting a rich mahogany color with contrasting reddish carinae on the pedipalps and metasoma. The pectinal tooth numbers are slightly larger in *T. intrepidus*, 22–25 and 21–22 for male and female respectively, versus 21–24 and 19–21, and 19–20, for *T. cristimanus* and *T. atrox* (female only), respectively (data based on specimens examined and Hoffmann, 1931).

“*Incertae sedis*” members of subfamily Syntropinae

Two species, currently placed in genus *Vaejovis* (Sissom, 2000), are clearly members of subfamily Syntropinae: *Vaejovis flavus* Banks, 1900 and *Vaejovis pequeno* Hendrixson, 2001. These species, however, cannot be placed in a genus with certainty for the reasons detailed below: for *V. flavus*, the true identity of the type specimen of *V. flavus* is still in question, although Soleglad (1973a) redescribed *V. flavus* from a

type specimen obtained from MCZ; for *V. pequeno*, interpretation of some characters as reported needs to be reevaluated.

“Vaejovis” flavus. Soleglad (1973a) redescribed *V. flavus* from a presumed type specimen obtained from MCZ. At that time both W. J. Gertsch and H. W. Levi were of the opinion that this was indeed Banks type specimen. Soleglad (1973a: 168–169) placed *V. flavus* in the “eusthenura” group of *Vaejovis* although noting discrepancies both when compared with Banks’s (1900) original key (the only place that *V. flavus* was described) and with Williams’ (1970d) description of the group. In particular, the chelal palm carinae were well defined (see Soleglad, 1973a: fig. 5), the ventromedian carinae of the metasomal are crenulate, and a somewhat large pectinal tooth count for a female (22/21) was present.

Sissom (2000: 532) writes: “... The identity of this species, briefly described in a key couplet by Banks (1900), has long been problematic. Soleglad (1973a) redescribed the species, based on a specimen in the MCZ presumed to be the type. This specimen is apparently not the type (J. Bigelow, pers. comm.), and the true type is in the USNM. The specimens are not conspecific. Until *V. flavus* is redescribed from the USNM material, its identity cannot be known with certainty; Bigelow (pers. comm.) indicates, however, that it is a member of the eusthenura group. The MCZ specimen belongs to an undescribed species in the punctipalpi group.

Nothing matching either the original description or Soleglad’s redescription has subsequently been collected in the Albuquerque area (or anywhere else in New Mexico), despite extensive efforts (Sissom, unpublished). A specimen I believe to be conspecific with that in the MCZ was found as part of the type series of *V. punctipalpi* in the USNM (Cokendolpher & Peck, 1991). Whether this specimen was actually part of the original type series cannot be confirmed; if it was, then this species would occur in Baja California Sur. ...”

If, as suggested by Bigelow (see above), the USNM specimen is definitely in genus *Hoffmannius* (i.e., the “eusthenura” group), then it would be closer to Banks’s (1900) “one-line description” than the MCZ specimen, thus can be designated as the lectotype. It was also suggested (C. Baptista, 2008, pers. comm.) that the USNM specimen may be Stahnke’s *Hoffmannius confusus*, further complicating the situation. The USNM specimen was not available for examination for this study.

For the MCZ specimen, we tend to agree with Sissom’s (2000) assessment, in part, as to group affiliation, certainly the crenulated palm and metasomal ventromedian carinae would be consistent with his suspicion. However, the high pectinal tooth count for a female is considerably out of the range of any known

Kochius species, female or male, and therefore possibly its sister genus *Thorellius* is a better match. In *Thorellius* we have no less than three species with pectinal teeth in the range of the MCZ specimen. In either case, this specimen is a member of subtribe *Thorelliina*, probably a new species, and its locality is most likely incorrect. If our suspicion of a *Thorellius* match is correct, then the MCZ specimen is clearly an immature and probably originated from central Mexico.

“Vaejovis” pequeno. Hendrixson (2001) described *Vaejovis pequeno*, an interesting little scorpion from Sonora, Mexico, a species he did not place in any existing *Vaejovis* group. Hendrixson (2001) was quite meticulous in his description accounting for almost every important diagnostic character (albeit, the structure of the female genital operculum was not described and some trichobothria data were missing). This species was also discussed by Graham & Soleglad (2007) and compared to their new species *Gertschius crassicornis* since they were similar “looking” and occupied the same geographic area in Sonora, Mexico. Based on Hendrixson’s (2001) description, *Vaejovis pequeno* clearly belongs to subfamily Syntropinae and tribe Stahnkeini: hemispermatophore with well developed lamellar hook, extending well beyond the ventral trough, with a conspicuous basal constriction; mating plug barb is smooth; chelal trichobothria *ib–it* not found on extreme finger base; dorsal carinae of metasomal segments I–IV straight proximally terminating with enlarged denticle; leg tarsus with a single distal spinule pair; cheliceral movable finger with well developed serrula; and the Total Length (TL) / Pectinal Tooth Count (PTC) ratio for the female is 1.463, well within the range of Stahnkeini (1.429–2.484 (1.941), see discussion elsewhere). Although there is no information on the spacing of chelal ventral trichobothria and the construction of the female genital operculum is not known, we feel comfortable that this species is not a member of subfamilies Smeringurinae or Vaejovinae. Therefore this species does not belong in genus *Vaejovis*, whose definition is now restricted considerably by the results of this paper.

The placement of *Vaejovis pequeno* into one of the four Stahnkeini genera recognized here is problematic. *Wernerius* can be eliminated because *V. pequeno* does not have a subaculear tubercle. Similarly, *Serradigitus* and *Stahnkeus* can be excluded since *V. pequeno* does not exhibit the exaggerated modified female pectines, highly serrated finger *MD* and *OD* denticles with elongated distal tips, and inner accessory denticles (*IAD*) are lacking. Genus *Gertschius* is the closest taxon to *V. pequeno*, but this can’t be decided until certain details of key structures are ascertained. We believe the real questions to this issue are the interpretations by Hendrixson of “modified basal pectinal teeth” and what constitutes a “serrated” denticle edge. Soleglad & Fet

(2006) quantified these characters in great detail breaking them up into substructures. They also chronicled the history of these characters over time as described by authors dealing with species in genera *Serradigitus* and *Stahnkeus*. Interestingly, many authors did not view or described these diagnostic characters in the same fashion, and their interpretations changed over time. Many authors lumped several “subcomponents” of these characters (as defined by Soleglad & Fet, 2006) and if one or more subcomponents were missing, the structure was interpreted differently. *Gertschius crassicornus* is a species where the serrated condition is reduced to only the median denticles (*MD*), the outer denticles (*OD*) are not serrated. In addition the elongated distal tooth, usually accompanied by a “whitish patch” was reduced or absent in this genus. The latter is probably due to the fact that *G. crassicornus* appears not to be lithophilic. The lack of sensilla on the basal pectinal teeth of the female is restricted to the basal tooth in *G. crassicornus*, and the tooth is not particularly enlarged or ovoid. However, the number of *MD* + *OD* denticles is considerably reduced, conforming to the density quotient established for *Stahnkeini* by Soleglad & Fet (2006: tab. 1). These characters need to be reevaluated in *V. pequeno* before genus placement can be determined.

Subfamily Vaejovinae Thorell, 1876

Type Genus. *Vaejovis* C. L. Koch, 1836.

References:

Vejovoidae: Thorell, 1876: 10 (as family, in part).
 Vejovini (as subfamily, in part): Kraepelin, 1894: 7, 181–183; Laurie, 1896: 130.
 Vaejovinae (in part): Kraepelin, 1905: 340; Birula, 1917a: 162, 163; Birula, 1917b: 57; Werner, 1934: 281–282; Mello-Leitão, 1945: 118; Stahnke, 1974: 113, 118–120.

Vaejovinae (in part): Nenilin & Fet, 1992: 9.

Composition. This subfamily, as defined here, includes the genera *Franckeus*, *Pseudouroctonus*, *Uroctonites*, and *Vaejovis*.

Distribution. USA, Mexico.

Diagnosis. Scorpions in the subfamily Vaejovinae can be distinguished by the following characters: Genital operculum sclerites of female separate on posterior one-fifth to two-fifths, operating as a single unit, connected to mesosoma on distal aspect; *ib-it* positioned basal on finger, considerably proximal of last inner denticle (*ID*); chelal trichobothria *V₂-V₃* distance approximately same as *V₁-V₂*; fixed finger trichobothria *dsb* and *dst* positioned distal of *esb* and *est*, respectively; hemispermaphore without conspicuous basal constriction; setal combs absent on legs; serrula well developed; dorsal carinal terminus of metasomal segments I–III essentially straight (not rounded) terminating with an

enlarged denticle; dorsolateral carinae of metasomal segment IV conspicuously flared at the terminus, not coinciding with the articulation condyle.

Taxonomic history. Vaejovoid subfamilies were last defined by Stahnke (1974). Due to further removal of Iurinae, Scorpiopsinae, and Hadrurinae from this family (Francke & Soleglad, 1981; Stockwell, 1992), the only two subfamilies of Vaejovidae that remained were Syntropinae and the nominotypic Vaejovinae. Sissom (2000: 504) listed Syntropinae as synonym of Vaejovidae, noting that “it is not practical at this point to recognize subfamilies.” Soleglad & Fet (2003b) formally synonymized Syntropinae with Vaejovidae. Here, we restored subfamily Syntropinae from synonymy and revised its scope (see above); we also established a new subfamily Smeringurinae. The nominotypic subfamily Vaejovinae is now also valid by default, albeit in dramatically reduced volume. This subfamily, however, so far remains unrevised; at this time, it includes four valid genera: *Franckeus*, *Pseudouroctonus*, *Uroctonites*, and a considerably reduced *Vaejovis* (see below).

Discussion. Since this subfamily was not revised, we do not provide diagnoses or discussions of its various taxonomic components. However, in the key provided below, the genera are defined with detailed diagnostic characters.

Genus *Franckeus* Soleglad et Fet, 2005

Type Species. *Vaejovis nitidulus* C. L. Koch, 1843 [= *Franckeus nitidulus* (C. L. Koch, 1843)].

References:

Franckeus: Soleglad & Fet, 2005: 1–9, figs. 2–3, 5, 9–19; Soleglad et al., 2007: 134.

Composition. The genus includes the following six species:

F. kochi (Sissom, 1991)
F. minckleyi (Williams, 1968)
F. nitidulus (C. L. Koch, 1843)
F. peninsularis (Williams, 1980)
F. platnicki (Sissom, 1991)
F. rubrimanus (Sissom, 1991)

Distribution. Mexico (Baja California Sur, Coahuila, Distrito Federal, Hidalgo, Mexico, Nuevo León, Querétaro, San Luis Potosí).

The range of genus *Franckeus* exhibits several disjunct parts (see map in Fig. 205), the most conspicuously isolated is *F. peninsularis* occurring in the northern half of Baja California Sur. The most northern species in mainland Mexico are *F. minckleyi* in Coahuila, *F. rubrimanus* in Nuevo León, and *F. platnicki* in San Luis Potosí. Species *F. nitidulus* and *F. kochi* form the largest disjunct part of the range, occurring in southern states of Mexico and Hidalgo.

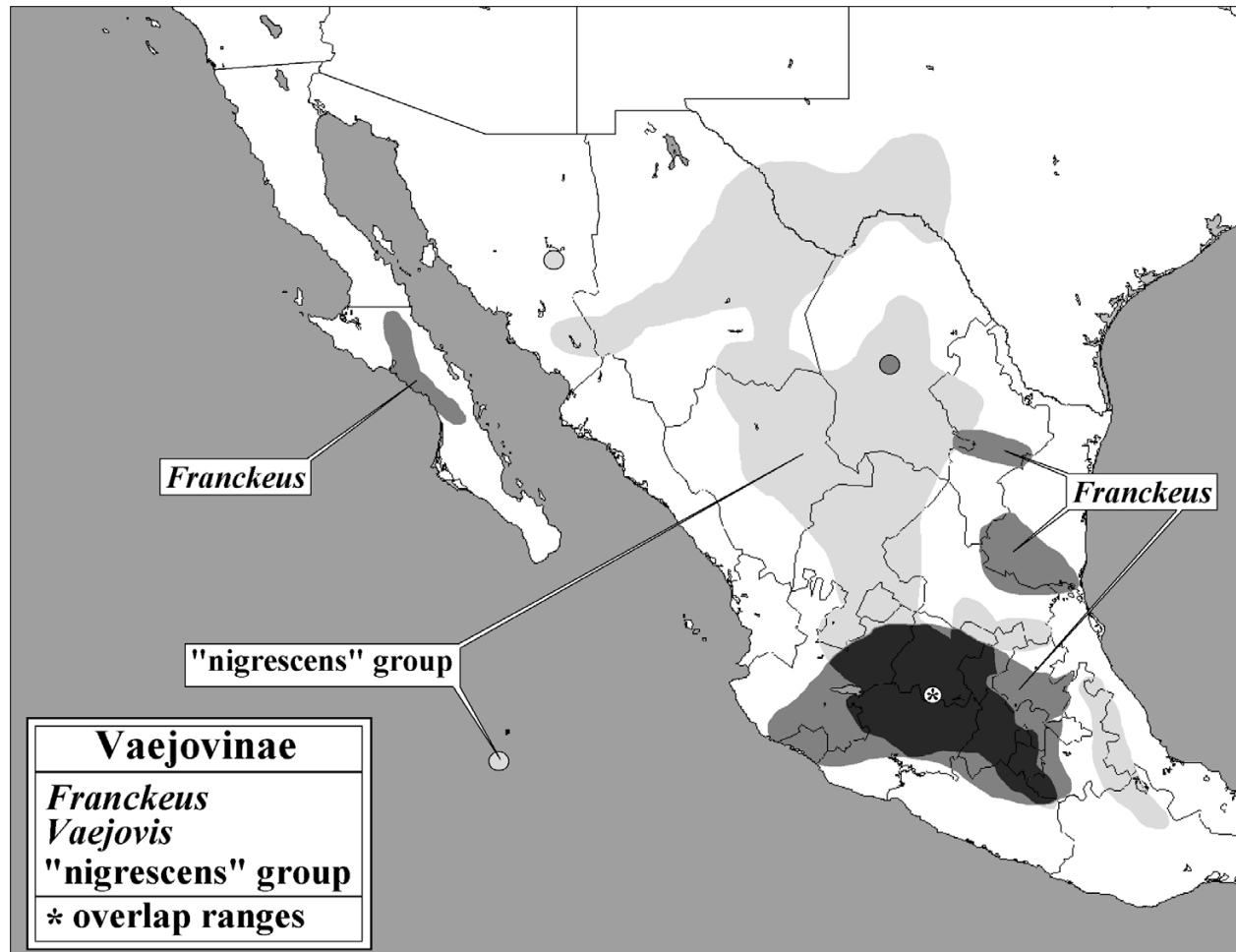


Figure 205: General distribution of scorpion subfamily **Vaejovinae** in North America with the ranges of genera *Franckeus* and *Vaejovis* "nigrescens" group delineated.

Except for *F. peninsularis* in Baja California Sur, *Franckeus* species distribution in general follows the range of the *Vaejovis* "nigrescens" group.

Taxonomic history. The genus *Franckeus* was recently established by Soleglad & Fet (2005). Scorpions of this genus were previously part of the informal "nitidulus" group of *Vaejovis*, established by Sissom & Francke (1985); see Sissom (2000: 544–547). The remaining species of this group have been placed by Soleglad & Fet (2005) in the informal "nigrescens" group of *Vaejovis*, closely related to *Franckeus*.

Genus *Pseudouroctonus* Stahnke, 1974

Type Species. *Vaejovis reddelli* Gertsch et Soleglad, 1972 [= *Pseudouroctonus reddelli* (Gertsch et Soleglad, 1972)]

References (selected):

Pseudouroctonus: Stahnke, 1974: 119, 132, fig. 7E, 9A–B; Sissom, 1990a: 114; Stockwell, 1992:

409–410, 416, 419; Kovařík, 1998: 144; Sissom, 2000: 514–518; Soleglad & Fet, 2003b: 88.

Composition. The genus includes the following 16 species and subspecies:

- P. andreas* (Gertsch et Soleglad, 1972)
- P. angelenus* (Gertsch et Soleglad, 1972)
- P. apacheanus* (Gertsch et Soleglad, 1972)
- P. bogerti* (Gertsch et Soleglad, 1972)
- P. cazieri* (Gertsch et Soleglad, 1972)
- P. chicano* (Gertsch et Soleglad, 1972)
- P. glimmei* (Hjelle, 1972)
- P. iviei* (Gertsch et Soleglad, 1972)
- P. lindsayi* (Gertsch et Soleglad, 1972)
- P. minimus minimus* (Kraepelin, 1911)
- P. minimus castaneus* (Gertsch et Soleglad, 1972)
- P. minimus thompsoni* (Gertsch et Soleglad, 1972)
- P. reddelli* (Gertsch et Soleglad, 1972)
- P. rufulus* (Gertsch et Soleglad, 1972)

P. sprousei Francke et Savary, 2006
P. williamsi (Gertsch et Soleglad, 1972)

Distribution. Mexico (north, Baja California), USA (southwest).

The range of this genus forms three primary disjunct parts in addition to three other isolated ranges based on solitary species (see map in Fig. 206). The most northern species, *P. iviei*, is distributed throughout northern California, with *P. glimmei* occurring just south in Monterey and Mendocino Counties. Several *Pseudouroctonus* species occur in southern California (*P. angeleus*, *P. bogerti*, *P. williamsi*, and *P. minimus*), or in southern California and northern Baja California, Mexico (*P. andreas* and *P. rufulus*). The third major part of the disjunct range of *Pseudouroctonus* includes southern Arizona, New Mexico, Texas, and extreme northern edges of Sonora, Chihuahua, and Coahuila, Mexico (*P. apacheanus*, *P. reddelli*, and *P. sprousei*). Separate, disjunct ranges are exhibited by species *P. cazieri* (southern Baja California), *P. lindsayi* (extreme southern Baja California Sur), and *P. chicano* (southern Chihuahua, Mexico).

Taxonomic history. The genus was established by Stahnke (1974), initially with only one species. Stockwell (1992) transferred here the species formerly placed in the “*minimus*” group of the overly inflated *Vaejovis*. Beutelspacher (2000), without any reasoning, synonymized *Pseudouroctonus* back to *Vaejovis*.

Genus *Uroctonites* Williams et Savary, 1991

Type Species. *Uroctonites giulianii* William et Savary, 1991.

References (selected):

Uroctonites: Williams & Savary, 1991: 273; Stockwell, 1992: 409, 416, 419, fig. 54; Kovařík, 1998: 145; Sissom, 2000: 526–527; Soleglad & Fet, 2003b: 88.

Composition. The genus includes the following four species:

U. giulianii William et Savary, 1991
U. huachuca (Gertsch et Soleglad, 1972)
U. montereus (Gertsch et Soleglad, 1972)
U. sequoia (Gertsch et Soleglad, 1972)

Distribution. USA (Arizona, California).

The range of the small genus *Uroctonites* exhibits three primary disjunct parts (see map in Fig. 206): coastal central California (*U. montereus*), west-central California (*U. giulianii* and *U. sequoia*; the latter also occurring in northern California), and southeastern Arizona (*U. huachuca*).

Taxonomic history. The genus and its type species were described by Williams & Savary (1991) who also

transferred to it three other species first described under *Uroctonus* by Gertsch & Soleglad (1972).

Genus *Vaejovis* C.L. Koch, 1836

Type Species. *Vaejovis mexicanus* C. L. Koch, 1836.

Synonyms:

Parabroteas Penther, 1913: 244–245, fig. 5; type species by monotypy *Vaejovis mexicanus* C. L. Koch, 1836, as *Parabroteas montezuma* Penther, 1913; a junior homonym of *Parabroteas* Mrázek, 1902 (Crustacea); see Fet & Soleglad (2007) for taxonomic history and nomenclature.

Pentheria Francke, 1985: 3, 11, 16, 19; a replacement name for *Parabroteas* Penther, 1913; synonymized by Sissom, 2000: 529–530. Type species: *Vaejovis mexicanus* C. L. Koch, 1836, as *Parabroteas montezuma* Penther, 1913; for details, see Fet & Soleglad (2007).

References (selected):

Vaejovis: C.L. Koch, 1836: 51; Pocock, 1898: 400; Pocock, 1902: 9; Ewing, 1928: 7, 9–10, 12 (in part); Williams, 1974: 15 (in part); Williams, 1980: 48–55 (in part); Sissom, 1990a: 110, 114 (in part); Stockwell, 1992: 419, figs. 4, 11, 23, 26, 36, 38, 41, 43, 45, 46, 50 (in part); Kovařík, 1998: 146 (in part); Beutelspacher, 2000: 56, 73, 152 (in part); Sissom, 2000: 529–552 (in part); Soleglad & Fet, 2003b: 88 (in part); Soleglad & Fet, 2005: 1–12, figs. 1, 4, 7, 20–29 (“*nigrescens*” group); Fet & Soleglad, 2007: 251–263, figs. 1–7 (“*mexicanus*” group).

Vejovis: Thorell, 1876: 10 (in part); Kraepelin, 1894: 182, 198 (in part); Kraepelin, 1899: 183–185 (in part); Birula, 1917a: 163 (in part); Birula, 1917b: 57 (in part); Hoffmann, 1931: 346 (in part); Werner, 1934: 282 (in part); Gertsch & Soleglad, 1972: 553, 557, 559, 564, 593 (in part); Soleglad, 1973b: 351–360 (“*mexicanus*” group); Stahnke, 1974: 132–136 (in part).

Composition. The genus, currently comprised of 40 species, is divided into two informal groups, the “*mexicanus*” group, comprised of 28 species, and “*nigrescens*” group, comprised of 12 species:

“*mexicanus*” group :

V. acapulco Armas et Martín-Frías, 2001
V. carolinianus (Beauvois, 1805)
V. cashi Graham, 2007
V. chamelaensis Williams, 1986
V. chiapas Sissom, 1989
V. chisos Sissom, 1990
V. dugesi Pocock, 1902
V. feti Graham, 2007
V. franckei Sissom, 1989

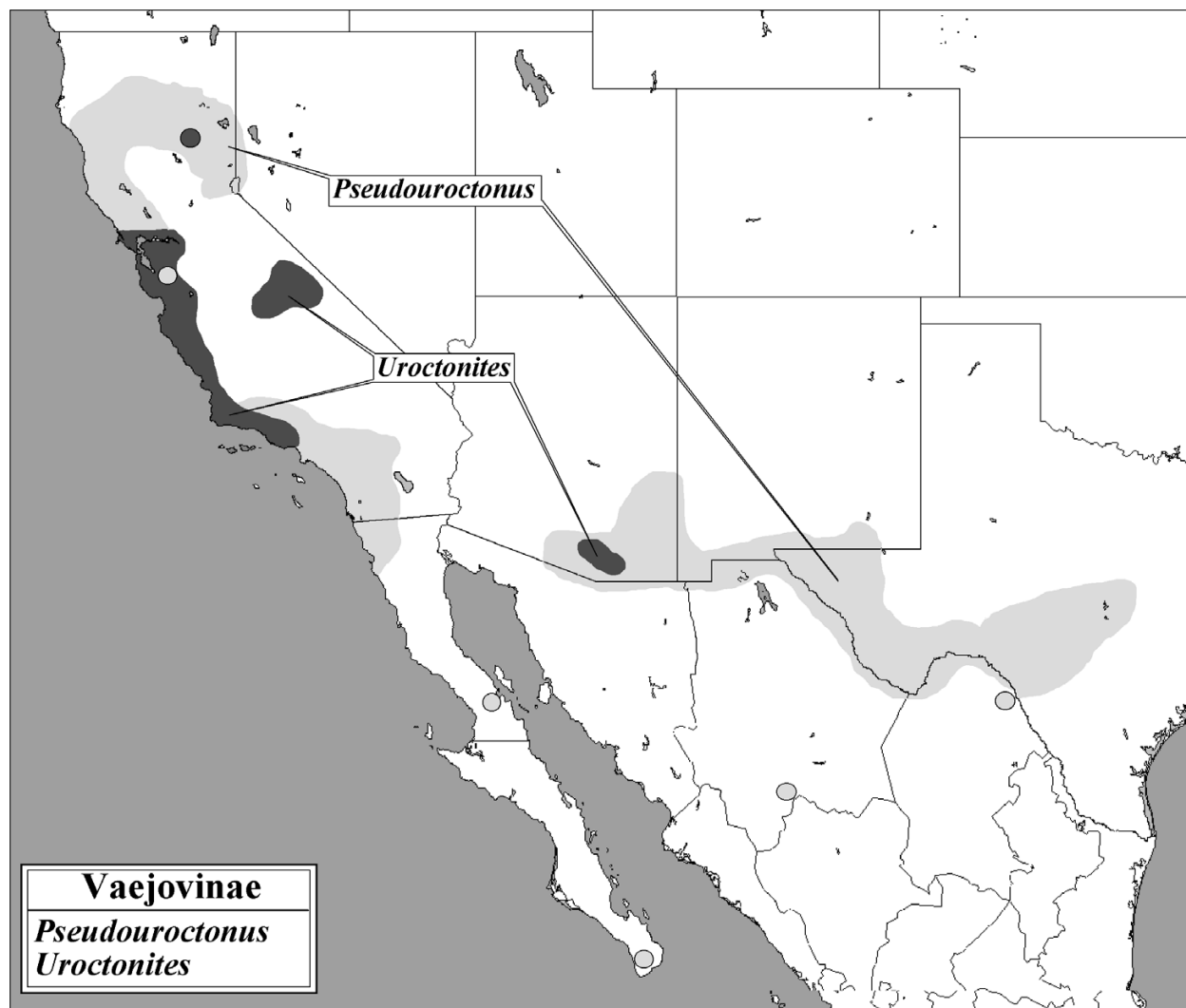


Figure 206: General distribution of scorpion subfamily *Vaejovinae* in North America with the ranges of genera *Pseudouroctonus* and *Uroctonites* delineated.

- V. granulatus* Pocock, 1898
- V. jonesi* Stahnke, 1940
- V. lapidicola* Stahnke, 1940
- V. kuarapu* Francke et Ponce Saavedra, 2006
- V. maculosus* Sissom, 1989
- V. mexicanus* C. L. Koch, 1836
- V. monticola* Sissom, 1989
- V. nayarit* Armas et Martín-Frías, 2001
- V. nigrofemoratus* Hendrixson et Sissom, 2001
- V. pattersoni* Williams, 1980
- V. paysonensis* Soleglad, 1973
- V. pusillus* Pocock, 1898
- V. rossmani* Sissom, 1989
- V. setosus* Sissom, 1989
- V. smithi* Pocock, 1902
- V. sprousei* Sissom, 1990
- V. tessellatus* Hendrixson et Sissom, 2001
- V. vaquero* Gertsch et Soleglad, 1972
- V. vorhiesi* Stahnke, 1940

Distribution. Mexico (Chiapas, Chihuahua, Coahuila, Colima, Distrito Federal, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas), USA (Alabama, Arizona, Georgia, Kentucky, Louisiana, Mississippi, New Mexico, North Carolina, South Carolina, Tennessee, Texas, Utah, Virginia).

The range of the “mexicanus” group of *Vaejovis* exhibits three primary disjunct parts (see map in Fig. 207): Arizona, Utah, and New Mexico (species *V. jonesi*, *V. lapidicola*, *V. paysonensis*, *V. vorhiesi*, *V. cashi*, and *V. feti*); southeastern United States (*V. Carolinianus*); and southern Mexico from San Luis Potosí to Chiapas, where the bulk of the species occur, including *V. mexicanus* (the type species of *Vaejovis*), *V. smithi*, *V. granulatus*, *V. pusillus*, and others (see list above). Separate, individual disjunct ranges also exist for *V. pattersoni* (extreme southern Baja California Sur), *V.*

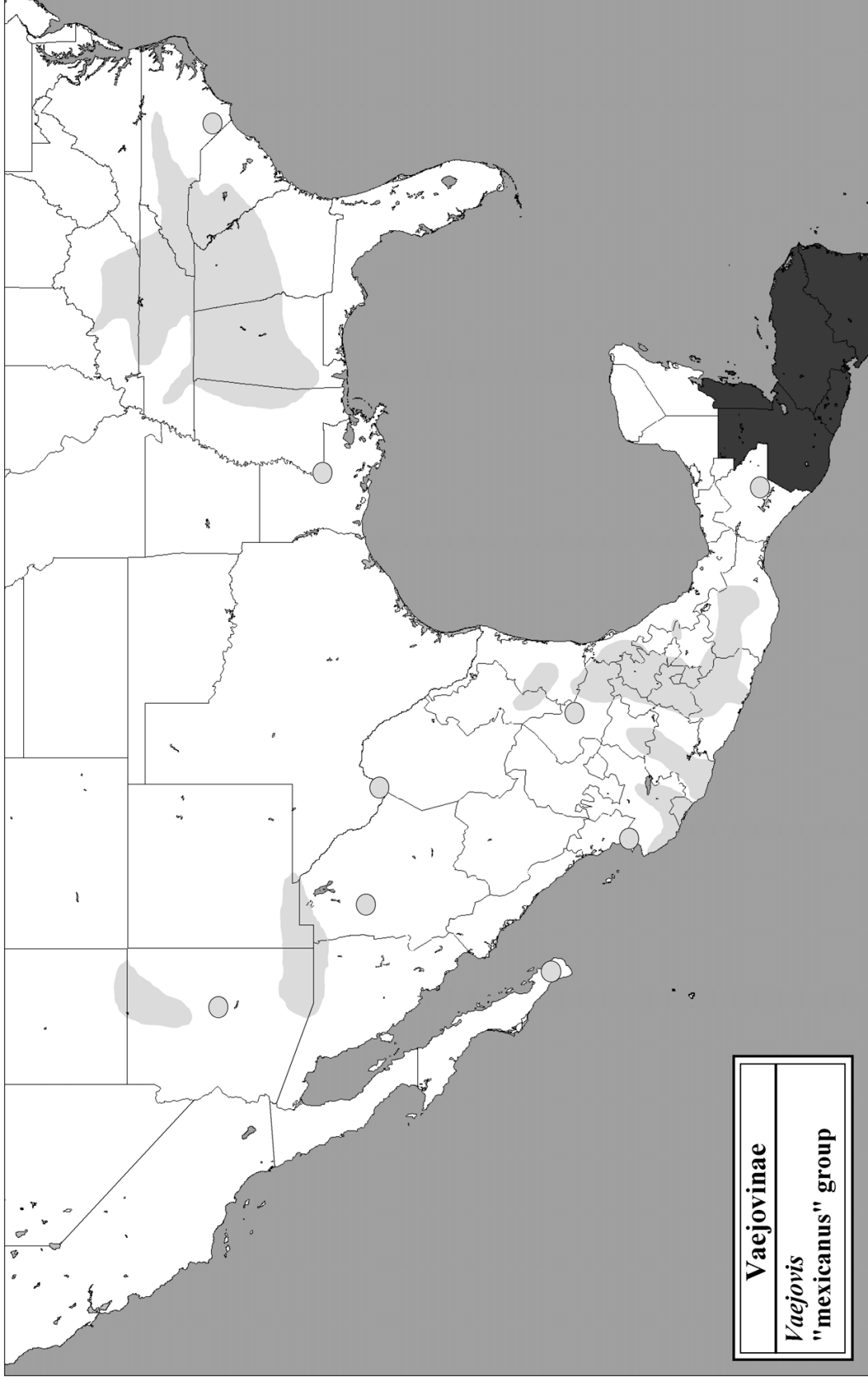


Figure 207: General distribution of scorpion subfamily Vaejovinae in North America with the ranges of genus *Vaejovis* "mexicanus" group delineated.

vaquero (central Chihuahua), *V. chisos* (border of Texas, Chihuahua and Coahuila), and *V. sprousei* (Nuevo León and Tamaulipas).

“nigrescens” group :

- V. curvidigitus* Sissom, 1991
- V. davidi* Soleglad et Fet, 2005
- V. decipiens* Hoffmann, 1931
- V. gracilis* Gertsch et Soleglad, 1972
- V. intermedius* Borelli, 1915
- V. janssi* Williams, 1980
- V. mauryi* Capes, 2001
- V. mitchelli* Sissom, 1991
- V. nigrescens* Pocock, 1898
- V. norteno* Sissom et González Santillán, 2004
- V. pococki* Sissom, 1991
- V. solegladi* Sissom, 1991

Distribution. Mexico (Aguascalientes, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Veracruz, Zacatecas), USA (Texas).

The range of the “nigrescens” group of *Vaejovis* exhibits four disjunct parts (see map in Fig. 205): *V. janssi* is found on the tiny Isla Socorro in the Pacific Ocean, *V. mauryi* in central Sonora, *V. gracilis* in Veracruz, and the majority of species found from as far north as Texas, Chihuahua, Coahuila, and Durango (*V. intermedius*) to Oaxaca (*V. solegladi*).

Taxonomic history. The nominotypic genus *Vaejovis* has been an “umbrella name” for many vaejovid taxa for well over 100 years (just like *Buthus* for Buthidae). Most notably, genera *Pseudouroctonus* Stahnke, 1974 and *Serradigitus* Stahnke, 1974 have been separated from *Vaejovis*; and, more recently, *Franckeus* Soleglad et Fet, 2005 and *Gertschius* Graham et Soleglad, 2007. The genus *Vaejovis* is further reduced here as a result of current revision, as we establish four new genera, *Hoffmannius*, *Kochius*, *Thorellius*, and *Wernerius*, which absorb the species from informal “eusthenura,” “intrepidus,” “punctipalpi,” and “spicatus” groups of *Vaejovis*.

**Key to subfamilies, tribes, subtribes,
and genera of family Vaejovidae**

1. Genital operculum sclerites of female operate separately, divided on posterior two-fifths to one-half, not connected to mesosoma on extreme distal aspect but more midpoint; chelal trichobothria *ib-it* positioned proximal to basal inner denticle (*ID*), but usually not on finger base; chelal trichobothria V_2-V_3 distance approximately twice as great as V_1-V_2 ; fixed finger trichobothria *dsb* and *dst* positioned proximal of *esb* and

est, respectively; leg tarsus with one pair of ventral distal spinules; setal combs present on legs; number of constellation array sensilla 2–3; serrula vestigial to weakly developed with non-contiguous tines; dorsal carinal terminus of metasomal segments I–III rounded, not terminating with an enlarged denticle; dorsolateral carinae of metasomal segment IV not conspicuously flared at the terminus, essentially coinciding with articulation condyle; median eye tubercle and eyes enlarged, 21–30 (27.6) % as wide as carapace at that point. ... (subfamily **Smeringurinae, subfam. nov.**) ... 2

■ Genital operculum sclerites of female operate as a single unit, either connected their entire length or divided on posterior one to two-fifths, connected to mesosoma on distal quarter; chelal trichobothria *ib-it* position variable, from base of fixed finger to finger midpoint; chelal trichobothria V_2-V_3 distance approximately same as V_1-V_2 ; fixed finger trichobothria *dsb* and *dst* positioned adjacent to or distal of *esb* and *est*, respectively; leg tarsus with 1–4 pairs of ventral distal spinules; setal combs absent on legs; number of constellation array sensilla 3–7; serrula medium to highly developed; dorsal carinal terminus of metasomal segments I–III flared, terminating with an enlarged denticle; dorsolateral carinae of metasomal segment IV conspicuously flared at the terminus, not coinciding with articulation condyle; median eye tubercle and eyes not enlarged, 12–23 (19.0) % as wide as carapace at that point. 5

2. Hemispermatophore lamellar hook minimal, not extending beyond ventral trough, basal constriction essentially absent; mating plug barb smooth; chelal trichobothrium *Dt* positioned quite proximal of palm midpoint; femoral trichobothrium *d* proximal to *i*, and *e* positioned proximally on segment; major neobothriotaxy absent on ventral aspect of palm; number of constellation array sensilla usually 2; chelicerae with denticles on the ventral edge of the movable finger, and protuberances usually found on the ventral aspect of fixed finger; vesicular tabs variable, either well developed with hooked spine, or reduced and rounded (tribe **Smeringurini, trib. nov.**) 3

■ Hemispermatophore lamellar hook well developed, extending well beyond the ventral trough, exaggerated by conspicuous basal constriction; mating plug barb toothed (after Stockwell, 1989); chelal trichobothrium *Dt* positioned distal of palm midpoint; femoral trichobothrium *d* distal to *i*, and *e* positioned near mid-segment; major neobothriotaxy present on ventral aspect of palm; number of constellation array sensilla 3; chelicerae without denticles on the ventral edge of the movable finger or protuberances on the ventral aspect of fixed finger; vesicular tabs reduced and rounded, distal granule vestigial to obsolete in adults. (tribe **Paravaejovini, trib. nov.**) genus **Paravaejovis**

3. Two ventromedian (*VM*) carinae present on metasomal segments I–IV; hemispermatophore lamina terminus with squared or rounded distal tip, inner base of lamina lacking small protuberance; unguis of legs not elongated or highly asymmetric; ventral aspect of leg tarsus surface lacking a cluster of elongated curved setae; dorsal carinae (*D*) of metasomal segments I–III terminus without sharp elongated spines; vesicular tabs variable, either well developed with hooked spine, or reduced and rounded 4

■ One ventromedian (*VM*) carina present on metasomal segments I–IV; hemispermatophore lamina terminus pointed with hooked distal tip, inner base of lamina with small protuberance; leg unguis elongated and highly asymmetric; ventral aspect of leg tarsus clothed in an exaggerated cluster of elongated curved setae; dorsal carinae (*D*) of metasomal segments I–III terminus with exaggerated sharp elongated spines; vesicular tabs reduced and rounded, distal spine vestigial to obsolete in adults genus *Vejovoidus*

4. Metasomal segment I usually as wide as long in male and wider than long in female, segment III never twice as long as wide, segment IV never three times longer than wide; setal pairs found on ventromedian (*VM*) carinae of segments I–IV, intercarinal area of *VM* carinae without setation; vesicular tabs well developed, equipped with conspicuous distal spine genus *Paruroctonus*

■ Metasomal segments I–IV always longer than wide in both genders, segment III more than two times longer than wide, segment IV three times longer than wide; setal pairs lacking on ventromedian (*VM*) carinae of segments I–IV, instead are located between the *VM*; vesicular tabs reduced and rounded, distal spine vestigial to obsolete in adults genus *Smeringurus*

5. Genital operculum sclerites of female connected their entire length, operating as a single unit; hemispermatophore lamellar hook usually conspicuously bifurcated or with slight cleft is well developed with conspicuous basal constriction, and extends at least 30 % of the length of the lamella from dorsal trough; mating plug well developed and sclerotized, distal barb either smooth or toothed; chelal trichobothrium *Dt* positioned at or beyond palm midpoint; *ib–it* positioned adjacent to basal inner denticle (*ID*) to midfinger, never considerably proximal of basal *ID*; cheliceral ventral edge of movable finger without denticles or serrations; serrula medium to well developed, never vestigial..... (subfamily **Syntropinae**) 6

■ Genital operculum sclerites of female separate on posterior one-fifth to two-fifths, operating as a single unit; hemispermatophore lamellar hook development is weak to medium with obsolete to minimal basal constriction, positioned basally to lamina midpoint;

mating plug well developed either gelatinous or sclerotized, if sclerotized distal barb is smooth; chelal trichobothrium *Dt* positioned basally; *ib–it* positioned basal on finger, considerably proximal of basal inner denticle (*ID*); cheliceral ventral edge of movable finger variable, smooth, serrated, or with distinct denticles; serrula well developed.. (subfamily **Vaejovinae**) 13

6. Basal pectinal teeth of female with sensorial areas; median (*MD*) and outer denticles (*OD*) of chelal fingers not serrate, *MD + OD* denticles density quotient medium, 51–74 (58); mating plug barb of hemispermatophore toothed; 2–4 ventral distal spinule pairs on leg tarsus; chelal trichobothrium *Db* located on or dorsal of digital (*D1*) carina; fixed finger trichobothria *ib–it* adjacent to basal inner denticle (*ID*); patellar trichobothrium *v₃* positioned proximal to *et₃*; ventral edge of cheliceral movable finger with medium developed contiguous serrula (10–21 times).. (tribe **Syntropini**) ... 7

■ Basal pectinal teeth (1 to as many as 4) of female lacking sensorial areas; median denticles (*MD*) of chelal fingers serrate; *MD + OD* denticle density quotient low, 30–42 (37); mating plug barb of hemispermatophore smooth; one ventral distal spinule pair on leg tarsus; chelal trichobothrium *Db* located on or ventral of digital (*D1*) carina; position of fixed finger trichobothria *ib–it* variable, from midfinger to slightly proximal of basal inner denticle (*ID*), based on species adult size; patellar trichobothrium *v₃* positioned distal to *et₃*; ventral edge of cheliceral movable finger with well developed contiguous serrula (21–37 times).... (tribe **Stahnkeini**).....10

7. Chelae with obsolete to reduced carination; subdigital (*D2*) carina vestigial, not in strong profile; *D2* carina positioned much closer to *D1* than *D3*; ventrolateral and ventromedian carinae of metasomal segments I–IV obsolete to smooth, sometimes with some carination, never fully crenulate or serrate (subtribe **Syntropina**) 8

■ Chelae heavily carinated; subdigital (*D2*) carina well developed and in strong profile, sometimes occurring one-third the palm's length; *D2* carina positioned roughly equidistant between *D1* and *D3*; ventrolateral and ventromedian carinae of metasomal segments I–IV smooth to crenulate, sometimes serrate (subtribe **Thorelliina**, **subtrib. nov.**) 9

8. Metasomal segments I–IV with paired ventromedian carinae; chelal fingers variable in length, but never extremely elongated, basal *OD* denticles located basally or suprabasally on fingers; chelal trichobothria *ib–it*, *db–dt* and *eb–et* positioned evenly over the fixed finger, not on the distal half; metasomal segments medium to heavy, segments I–II usually as wide or wider than long, length-to-width ratio 0.67–1.08 (0.89) and 0.83–1.31 (1.05) in males, and 0.67–1.03 (0.81) and 0.77–1.29

(0.95) in females; dorsal and dorsolateral carinae of metasomal segments I–IV flared posteriorly, distal denticle noticeably larger than other denticles genus **Hoffmannius**, **gen. nov.**

■ Metasomal segments I–IV with single ventromedian carina; chelal fingers extremely elongated, basal *OD* denticles located at finger midpoint; chelal trichobothria *ib-it*, *db-dt* and *eb-et* positioned on distal half of fixed finger; metasomal segments thin, all longer than wide in both genders, dorsal and dorsolateral carinae of metasomal segments I–IV not overly flared posteriorly and terminal denticle only slightly larger than other denticles genus **Syntropis**

9. Carapace anterior edge with conspicuous continuous emargination originating from the lateral eyes, with a small median indentation; metasomal segments IV–V length-to-width ratio 1.7–2.2 (1.91) and 2.4–3.3 (2.75) in males, and, 1.5–2.3 (1.83) and 2.3–3.5 (2.72) in females; metasomal segments I–III ventromedian (*VM*) carinae usually granular to crenulate genus **Kochius**, **gen. nov.**

■ Carapace anterior edge lacking conspicuous emargination, if present never extending to lateral eyes, median area either straight or with wide subtle indentation; metasomal segments IV–V length-to-width 1.4–1.7 (1.54) and 1.8–2.3 (2.12) in males, and, 1.3–1.6 (1.45) and 1.9–2.4 (2.10) in females; metasomal segments I–III ventromedian (*VM*) carinae usually smooth to granular; chelal carinae usually smooth to strongly marbled. genus **Thorellius**, **gen. nov.**

10. Modification to basal pectinal teeth of female significant, lacking sensorial area in 1–4 teeth, blunted and ovoid to swollen and elongated, with little or no distal angling; *OD* denticles serrated, indistinguishable after *OD-3*; distal denticle elongated and hook-like with “whitish patch” 11

■ Modification to basal pectinal teeth of female marginalized, lacking sensorial area only in 1–2 teeth, not particularly swollen or elongated and showing some distal angling, or ovoid; *OD* denticles not serrated, all observable the entire length of both chelal fingers; distal denticle not overly elongated or hook-like, “whitish patch” minimal or absent 12

11. Inner accessory denticles (*IAD*) on chelal fingers absent genus **Serradigitus**

■ Inner accessory denticles (*IAD*) on chelal fingers present genus **Stahnkeus**

12. Spinoid subaculear tooth absent; ventromedian (*VM*) carinae of metasomal segments I–II obsolete to smooth genus **Gertschius**

■ Spinoid subaculear tooth present; ventromedian (*VM*) carinae of metasomal segments I–II granular to serrate genus **Wernerius**, **gen. nov.**

13. Dorsal Patellar Spur carina (*DPS_c*) reduced, low profiled and composed of a few granules; chelal palm somewhat “flat” in appearance due to reduction of dorsosecondary (*D3*) and/or ventromedian (*V2*) carinae; leg tarsus with 2–4 ventral distal spinule pairs; carapace anterior edge with conspicuous indentation; chelal trichobothrium *Db* dorsal of digital (*DI*) carina; median eye tubercle and eyes reduced, 12–16 % as wide as carapace at that point; pectinal tooth numbers reduced with respect to species adult size, TL/PTC = 2.44–5.33 (3.73) 14

■ Dorsal Patellar Spur (*DPS_c*) carina well developed; chelal palm not “flat” in appearance, carinae *D3* and *V2* well developed; leg tarsus with 1–2 ventral distal spinule pairs; carapace anterior edge variable, either with conspicuous to wide indentation or straight; chelal trichobothrium *Db* on or ventral of digital (*DI*) carina; median eye tubercle and eyes medium in size, 17–23 % as wide as carapace at that point; pectinal tooth numbers medium with respect to species adult size, TL/PTC = 1.59–4.20 (2.41) 15

14. Hemispermaphore lamellar hook bifurcated, positioned quite close to lamina internal edge and well distal of lamina base, basal constriction absent; leg tarsus setal pairs on ventral aspect not particularly stout genus **Pseudouroctonus**

■ Hemispermaphore lamellar hook formed as a small non-bifurcated hook, positioned at lamina base, with a moderately developed basal constriction; leg tarsus setal pairs on ventral aspect somewhat stout genus **Uroctonites**

15. Neobothriotaxy present on patella external surface, one *accessory* trichobothrium positioned near trichobothrium *esb₂*; trichobothria series *em₁–em₂* angles towards the distal aspect of segment; leg tarsus with one ventral distal spinule pair; carapace with wide median indentation genus **Franckeus**

■ Neobothriotaxy not present on patella external surface; trichobothria series *em₁–em₂* angles towards the proximal aspect of segment; leg tarsus with 1–2 ventral distal spinule pairs; carapace anterior edge variable, either with conspicuous indentation or straight genus **Vaejovis**

Description of a New Species***Kochius kovariki* Soleglad et Fet, sp. nov.**

(Figs. 208–218, Table 11)

Holotype. Female, Durango, Durango, Mexico, November 1965 (collector unknown) (MES).**Diagnosis.** Medium sized species for its genus, reaching 50 mm in adult females. Overall coloration a pale yellow lacking patterns, chelal fingers not pigmented. Pectinal tooth counts 15 in females, males unknown. Chelal carinae well developed and conspicuous but smooth, showing no granulation. Basal outer (*OD*) denticle missing, 4 and 5 *ODs* present on fixed and movable fingers, respectively. Ventromedian carinae of metasoma obsolete on segments I–II and weak to smooth on III. Ventromedian carina of segment V serrate with distal aspect narrowly bifurcated.

K. kovariki can be differentiated from its closest relative *K. crassimanus* as follows (based solely on redescription of Williams, 1971a): All chelal carinae in *K. kovariki* are smooth, exhibiting no granulation and the ventromedian carinae of metasomal segments I–III are obsolete in I–II and obsolete to smooth in III. In *K. crassimanus* the chelal carinae exhibit some granulation and the ventromedian carinae of segment I–III are smooth to crenulate on I and crenulate to serrate on II–III. The chelae and movable finger in *K. kovariki* are shorter than in *K. crassimanus* exhibiting the following morphometric ratio percentage (%) differences on the following structures: “*structure*” / *chela length*|*movable finger length*: carapace length = 13.6|12.6 %; metasomal segment III length = 10.7|9.7 %; metasomal segment V length = 11.3|10.3 %; telson width = 18.3|17.2 %; pedipalp femur length = 12.2|11.2 %; pedipalp patella length = 16.9|15.8 %. The chelal fingers of *K. kovariki* are yellow, the same color as the palm, whereas in *K. crassimanus* they are reddish.

Distribution. Only known from type locality, Durango, Durango, Mexico.**Etymology.** Named after our colleague and friend František Kovářik (Prague, Czech Republic), who has contributed considerably to the knowledge of scorpion systematics.**FEMALE.** Description based on holotype female. Locality of holotype is Durango, Durango, Mexico. Metasoma is detached at segment I. Measurements of holotype specimen is presented in Table 11. See Figure 208 for a dorsal view of the female holotype.**COLORATION.** Basic color dark yellow. No patterns visible, chelal fingers same color as palm. Eyes and eye

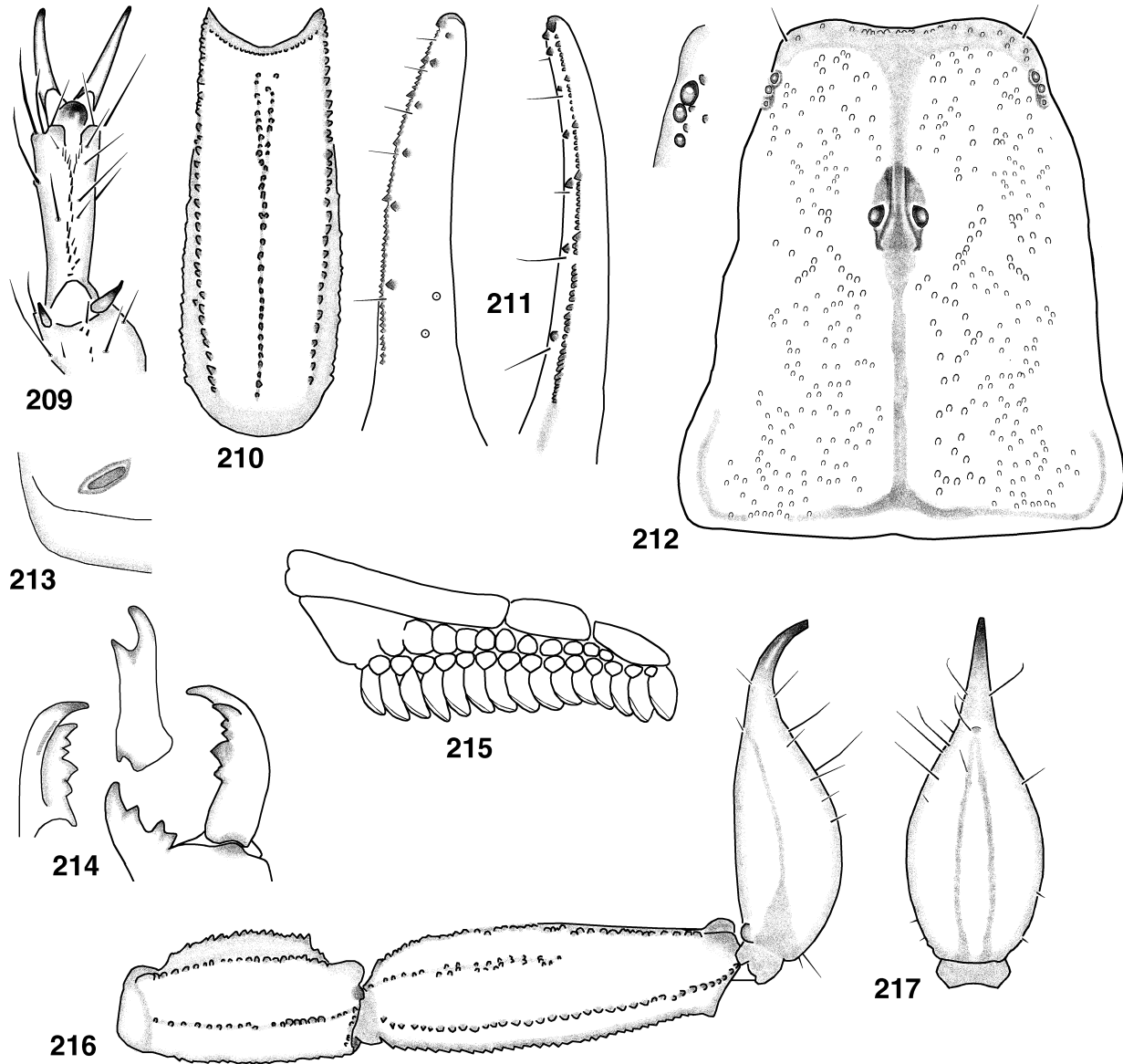
tubercles black. Telson aculeus and articulation condyles of legs dark reddish brown.

CARAPACE (Fig. 212). Anterior edge with emargination along its entirety, with narrow median indentation; interocular area covered with medium sized granules, bisected by a well developed indentation; posterior lateral aspects covered with medium to large granules. Posterior portion with deep medial groove, forming two conspicuous lateral posterior convexed lobes. Lateral eyes number three, decreasing in size posteriorly. Median eye tubercle positioned anteriorly of middle with the following length and width formulas: 255|665 (anterior edge to median tubercle middle|carapace length) and 85|465 (width of median tubercle including eyes|width of carapace at that point).**MESOSOMA (Fig. 213).** Tergites I–VI rough at 10x, extreme posterior edges with minute granules; tergite VII rough with two pairs of delicately crenulate carinae. Sternites smooth and lustrous; one pair of weak ventral lateral carinae present on segment V, rough to crenulate; median pair absent. Stigmata (Fig. 213) are long and slit-like.**METASOMA (Figs. 210, 216).** Segments II–IV longer than wide, segment I slightly wider than long. Segments I–IV: dorsal and dorsolateral carinae serrate, dorsal (I–IV) and dorsolateral (I–III) carinae terminate with enlarged spine; lateral carinae crenulate on I, crenulate on proximal 25 % of II–III, and obsolete on IV; ventrolateral weakly granulate on I–II and crenulate on III–IV; and ventromedian carinae obsolete on I–II, weak to smooth on III, and granulate on IV. Dorsolateral carinae of segment IV terminus conspicuously flared, not terminating at articulation condyle. Segment V: dorsolateral carinae rounded and granulate; lateral carinae irregularly granulated for 50% of anterior aspect; ventrolateral and ventromedian carinae serrate, ventromedian carina narrowly bifurcated on distal one-fifth (Fig. 210). Anal arch (ventral aspect) lined with minute granules. Intercarinal areas smooth. Ventral setal formulae (I–IV): 3|4|4|4.**TELSON (Fig. 216–217).** Somewhat elongated, with average sized aculeus, with 4/4 denticles in the latero-basal aculear serrations (LAS; Fet et al., 2006b). Ventral vesicle surface smooth, with scattered elongated setae on distal half; basal dorsal aspect with vesicular “tabs” terminating in two small hooked spines.**PECTINES (Fig. 215).** Moderately developed exhibiting length|width formula 391|170 (length taken at anterior lamellae|width at widest point including teeth). Sclerite construction complex, three anterior lamellae and 11/12 bead-like middle lamellae; fulcra of medium deve-



Figure 208: *Kochius kovariki*, sp. nov., female holotype, dorsal view. Metasoma is detached.

lopment. Teeth number 15/15 (note right pecten missing distal tooth, but its presence is indicated by fulcrum). Sensory areas developed along most of tooth inner length on all teeth, including basal tooth. Basal piece



Figures 209–217: *Kochius kovariki*, sp. nov., female holotype. **209.** Leg III tarsus, ventral view, showing median spinule row and four pairs of distal spinules. **210.** Metasomal segment V, ventral view, showing narrowly bifurcated ventromedian carina. **211.** Chelal movable fingers showing dentition pattern and position of trichobothria *ib-it*, fixed finger left and movable finger right. **212.** Carapace with close-up of lateral eyes. **213.** Stigma. **214.** Chelicerae, ventral, external, and dorsal views. **215.** Pecten. **216.** Metasomal segments IV–V and telson, lateral view. **217.** Telson, ventral view.

large, with deep indentation along anterior one-third, length|width formula 125|165.

GENITAL OPERCULUM. Sclerites connected for entire length, operating as a single unit, connection to body at extreme anterior edge.

STERNUM. Type 2, posterior emargination present, well-defined convex lateral lobes, apex visible but not

conspicuous; slightly wider than long, length|width formula 155|175; sclerite tapers anteriorly.

CHELICERAE (Fig. 214). Movable finger dorsal edge with two subdistal (*sd*) denticles; ventral edge smooth; with weak to medium developed serrula with 18 short contiguous tines, terminating just before distal tip. Ventral distal denticle (*vd*) longer than dorsal (*dd*) counterpart. Fixed finger with four denticles, median (*m*)

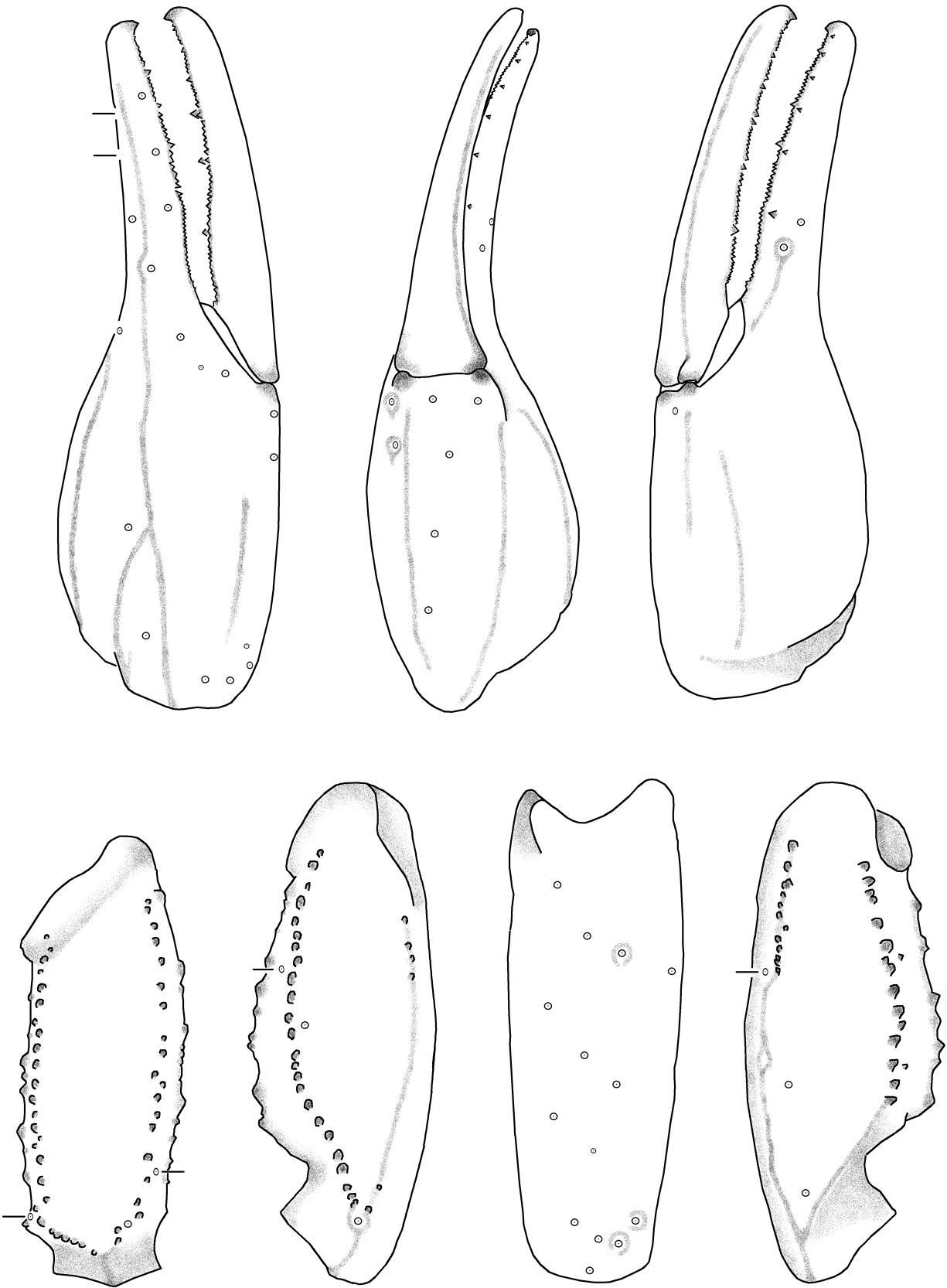


Figure 218: Trichobothrial pattern of *Kochius kovariki*, **sp. nov.**, female holotype, Durango, Durango, Mexico.

<i>Kochius kovariki</i> sp. nov.	
	Female Holotype
Total Length	49.85
Carapace Length	6.65
Mesosoma Length	14.20
Metasoma Length	22.50
Metasomal Segment I Length/Width	3.10/3.35
Metasomal Segment II Length/Width	3.55/3.20
Metasomal Segment III Length/Width	3.75/3.15
Metasomal Segment IV Length/Width	4.90/3.05
Metasomal Segment V Length/Width	7.20/2.90
Telson Length	6.50*
Vesicle Length/Width/Depth	4.30/2.55/2.00
Pedipalp length	18.75
Femur Length/Width	4.75/1.70
Patella Length/Width	5.40/2.00
Chela Length	8.70
Palm Length/Width/Depth	4.10/2.55/2.85
	5.05
Movable Finger Length	
Sternum Length	1.55
Anterior/Posterior Width	1.55/1.75
Pectinal Basal Plate Length/Width	1.25/1.65
Pectinal Teeth	15 15
Middle lamellae	11 12

Table 11: Measurements (in mm) of *Kochius kovariki* sp. nov. from Durango, Durango, Mexico. Extrapolated, aculeus tip missing.

and basal (*b*) denticles conjoined on common trunk; no ventral accessory denticles present.

PEDIPALPS (Figs. 211, 218). Medium to heavy chelate species, no scalloping on chelal fingers. Movable finger shorter than carapace, telson and metasomal segment V. **Femur:** Dorsointernal, dorsoexternal and ventrointernal carinae serrate, ventroexternal rounded to obsolete. Dorsal and ventral surfaces smooth, internal and external surfaces with line of large granules. **Patella:** Dorsointernal and ventrointernal serrate, dorsoexternal, and ventroexternal carinae irregularly granulate; Dorsal Patellar Spur (*DPS_c*) carina present with line of about 6–7 granules; exteromedian carina obsolete. All surfaces smooth; internal surface with remnants of a *DPS* and Ventral Patellar Spur (*VPS*), each represented by a small

solitary granule accompanied by a seta. **Chelal carinae:** all nine carinae well developed and smooth; subdigital (*D2*) carina rounded but in profile. **Chelal finger dentition (Fig. 211):** median denticle (*MD*) row groups aligned in straight line, numbering 5 and 6 (counting the distal single *MD* denticle as a group on the movable finger); 6/6 and 7/7 internal denticles (*ID*) and 4/4 and 5/5 outer denticles (*OD*) on fixed and movable fingers, respectively. No accessory denticles present. Number of *MD* denticles on movable finger is 54. Distal tips of both fingers lacking conspicuous “whitish” patch. **Trichobothrial patterns (Fig. 218):** Type C, orthobothriotaxic. Femur: trichobothrium *d* located next to dorsoexternal carina and proximal to *i*. Patella: ventral trichobothrium *v₃* located on external surface, proximal of trichobothrium *et₃*. Chela: trichobothrium *Dt* located at palm midpoint and *Db* positioned dorsal of *D1* carina; *ib–it* situated adjacent to the sixth inner denticle (*ID-6*) of fixed finger, *ib* proximal of and *it* adjacent to *ID-6*; spacing between trichobothria *V₁* and *V₂* approximately same as *V₂* and *V₃*; trichobothrium *dst* adjacent to *est*.

LEGS (Fig. 209). Both pedal spurs present, tibial spur absent. Tarsus with single median row of spinules on ventral surface, terminating distally with four spinule pairs.

Specimens examined: Adult female holotype, Durango, Durango, Mexico, November 1965 (collector unknown), (MES).

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