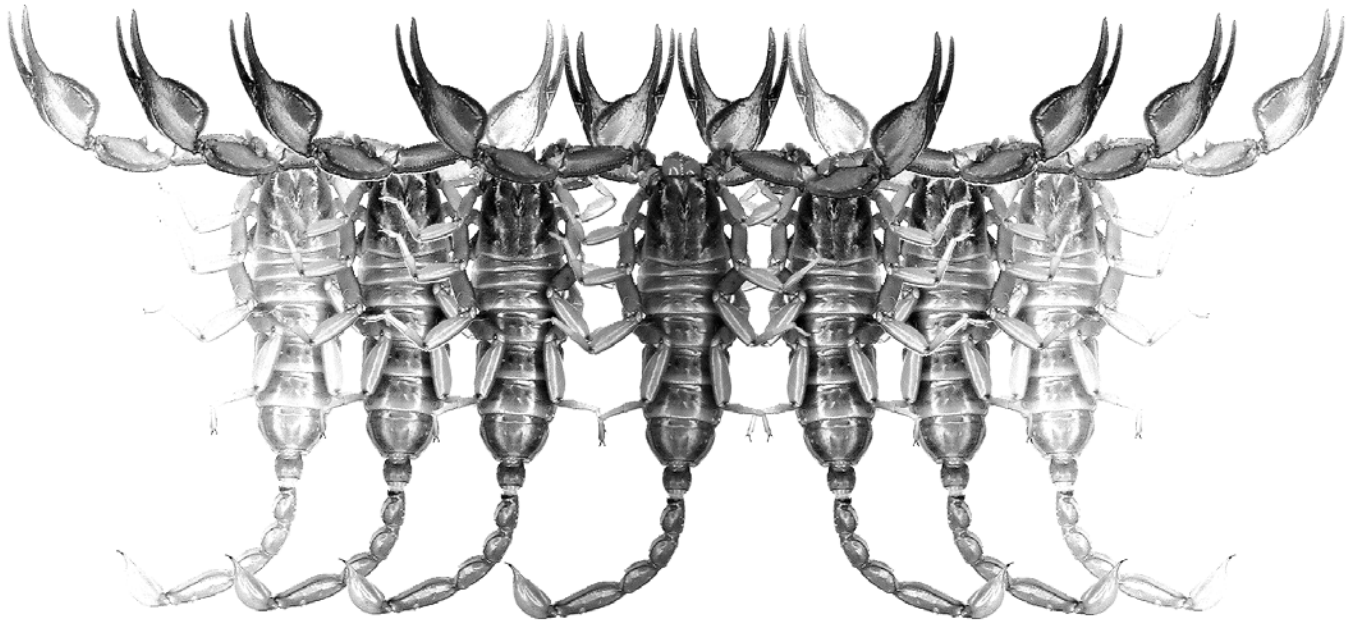


Euscorpius

Occasional Publications in Scorpiology



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

Michael E. Soleglad & Victor Fet

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EDITOR: Victor Fet, Marshall University, 'fet@marshall.edu'

ASSOCIATE EDITOR: Michael E. Soleglad, 'soleglad@la.znet.com'

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

Michael E. Soleglad¹ and Victor Fet²

¹ P. O. Box 250, Borrego Springs, California 92004, USA

² Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510, USA

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Stockwell (1989), in an unpublished revision, suggested splitting the family Vaejovidae in two subfamilies, introducing also four tribes and four new genera.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 *Vejovidae* and *Vejovis* 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 Vejovidae: Syntropinae, Vejovinae, Caraboctoninae, Iurinae, and Scorpionsinae. Stahnke (1974) revised the high-level systematics of this family: his Vejovidae included Iurinae, Hadrurinae, Caraboctoninae, Scorpionsinae, Syntropinae (two genera, *Syntropis* and *Vejovoidus*), and Vejovinae (six genera, *Paruroctonus*, *Physoctonus*,

Pseudouroctonus, *Serradigitus*, *Uroctonus*, and *Vaejovis*). 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 Scorpionsinae to a family level (now subfamily of Euscorpiidae; Soleglad & Sissom, 2001).

Sissom (2000) included ten North American genera in Vaejovidae (*Paravaejovis*, *Paruroctonus*, *Pseudouroctonus*, *Serradigitus*, *Smeringurus*, *Syntropis*, *Uroctonites*, *Uroctonus*, *Vaejovis*, *Vejovoidus*). Compared to Stahnke (1974), this content corresponded to subfamilies Syntropinae and Vaejovinae; 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 vaejovid 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 Vaejovidae with nine genera. We also formally synonymized subfamily Syntropinae with Vaejovidae (Soleglad & Fet, 2003b: 109), thus leaving Vaejovidae without any recognized subfamilies. No other family-group taxa (i.e. tribes or subtribes) have been ever proposed in Vaejovidae.

Sissom (2000) stated that “...the phylogenetic relationships of the [vaejovid] genera are still obscure, and it is not possible at this time to recognize subfamilies or tribes. Vaejovid 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 vaejovid 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 Vaejovidae, 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 vaejovid 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 Vaejovidae (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 Vaejovidae 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 Vaejovidae. 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 Vaejovidae. No subgenera are currently recognized for any of vaejovid 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 vaejovid 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 vaejovid 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 Vaejovidae, 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 vaejovid 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 hemispermaphore 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 crassicornis* 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* (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 angelenus* (Gertsch et Soleglad, 1972), Ventura Co., California, USA, ♂ (BH); *Pseudouroctonus apacheanus* (Gertsch et Soleglad, 1972), Pinaleno Mt., Arizona, USA, ♀ (VF); *Pseudouroctonus iviei* (Gertsch et Soleglad, 1972), Little French Creek, Trinity Co., California, USA, ♀ ♂ (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 montereus* (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), Acapulco, 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

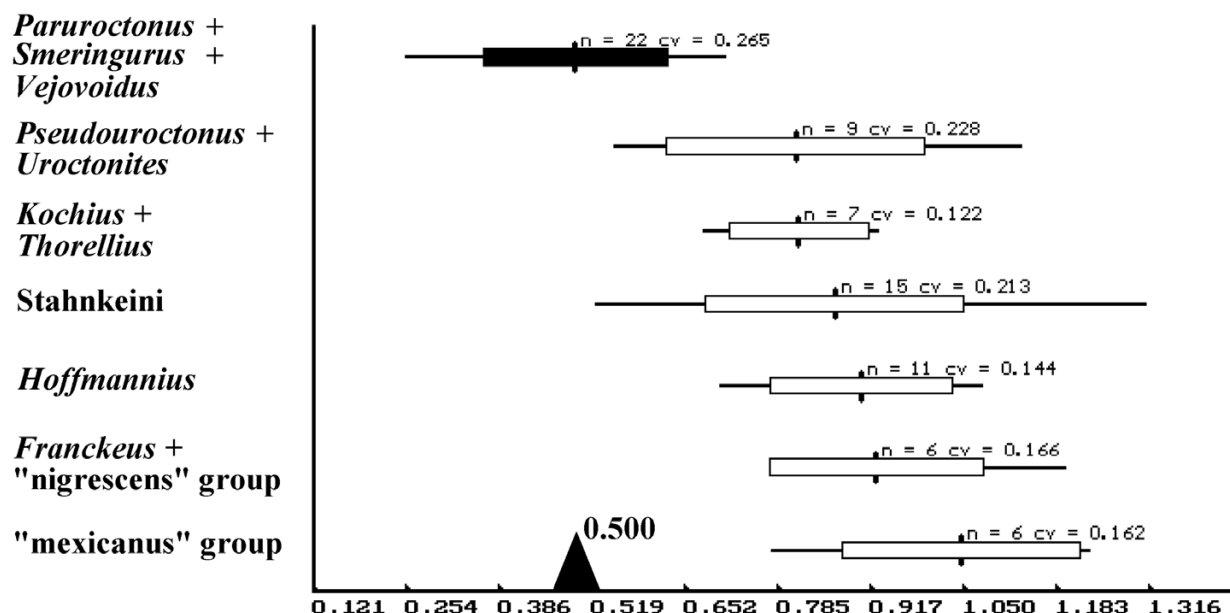


Figure 1: Histogram comparing chelal trichobothria distances between V_1 and V_2 , and V_2 and V_3 for family Vaejovidae (ratio = $V_1|V_2 / V_2|V_3$). It is clear from these data that in subfamily Smeringurinae the distance between trichobothria V_2 and V_3 is on average more than twice as great than 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 vaejovid 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 vaejovid 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 Vaejovidae. In Figure 17 we present a histogram showing the relative position of trichobothrium *Dt* across 101 species of Vaejovidae 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 vaejovid. For Uroctoninae, multiple specimens of both subspecies of *U. mordax* and all three species and subspecies of *Anuroctonus* were included. In Vaejovidae, 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.

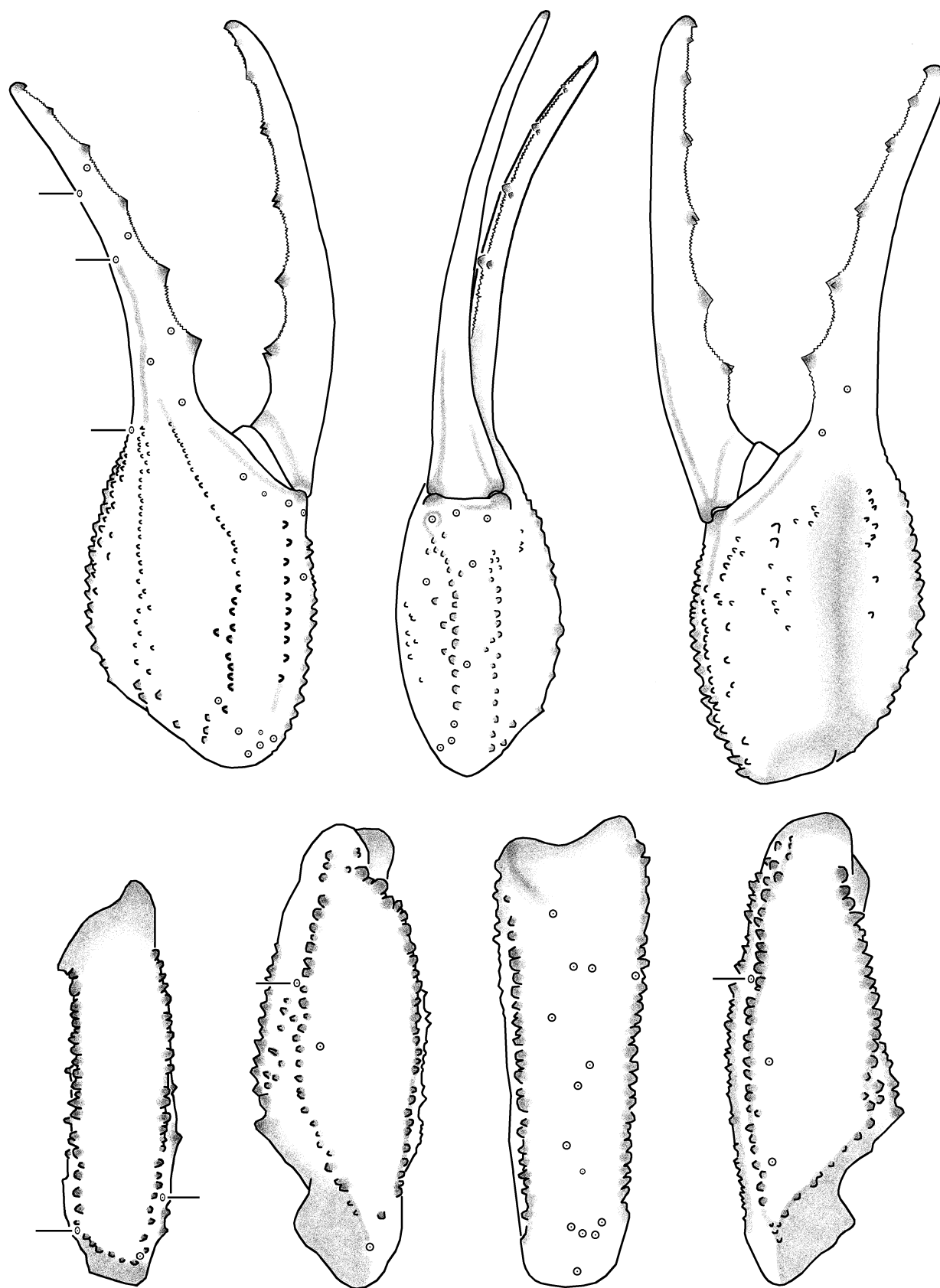


Figure 2: Trichobothrial pattern of *Paruroctonus xanthus*, male, Algodones Dunes, Imperial Co., California, USA.

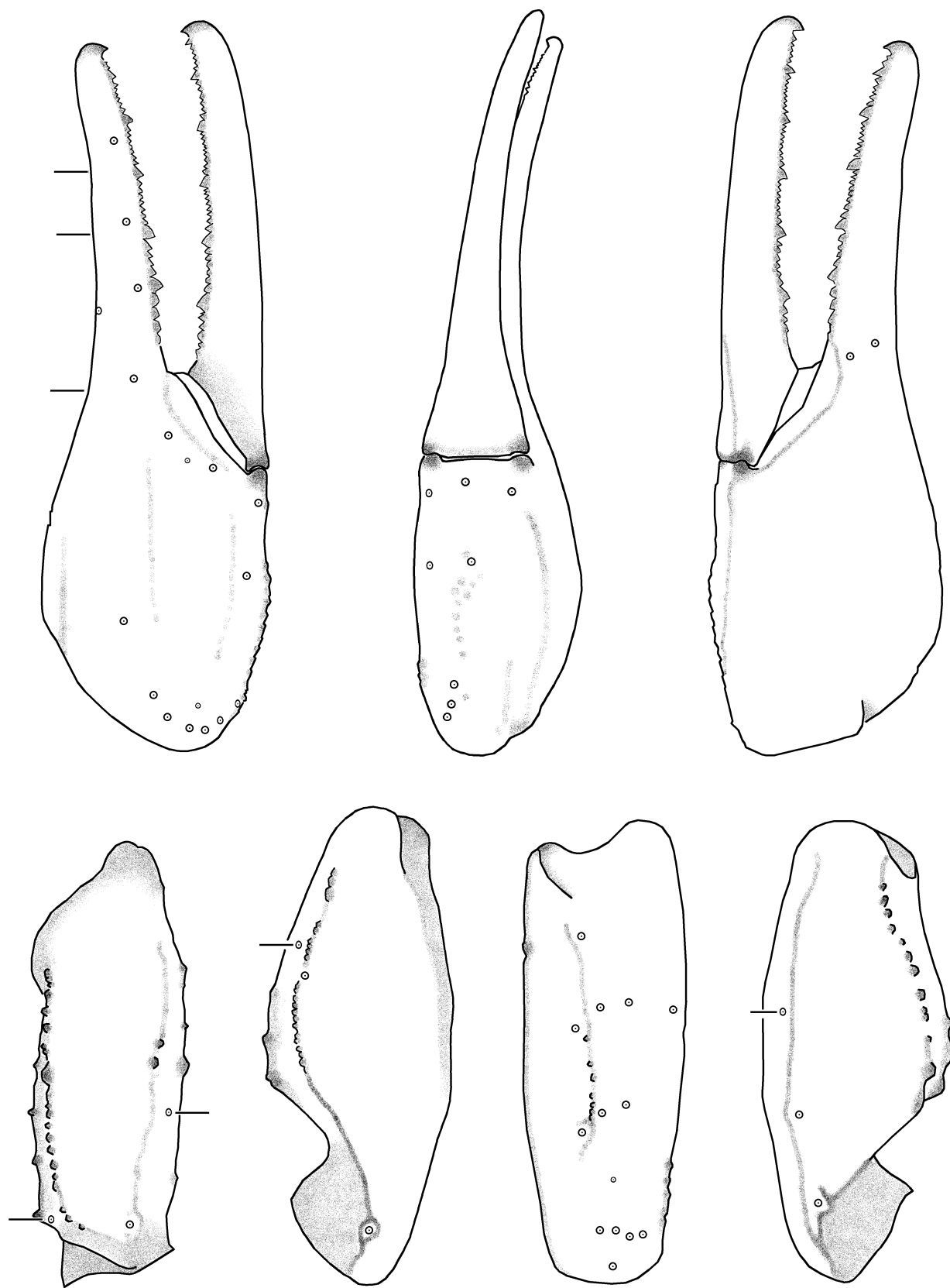


Figure 3: Trichobothrial pattern of *Paruroctonus hirsutipes*, female, Algodones Dunes, Imperial Co., California, USA.

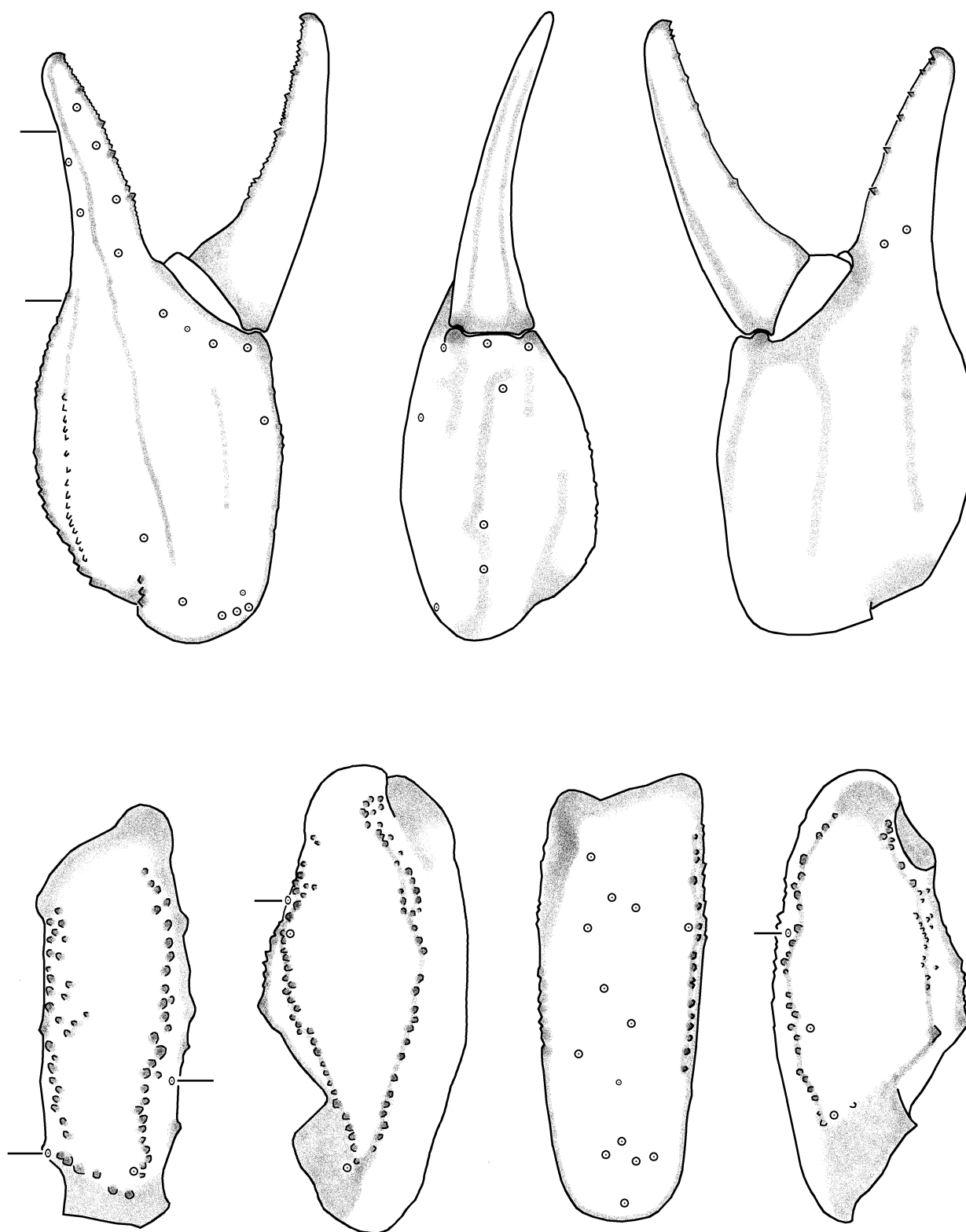


Figure 4: Trichobothrial pattern of *Paruroctonus surensis*, male, Las Bombas, Baja California Sur, Mexico.

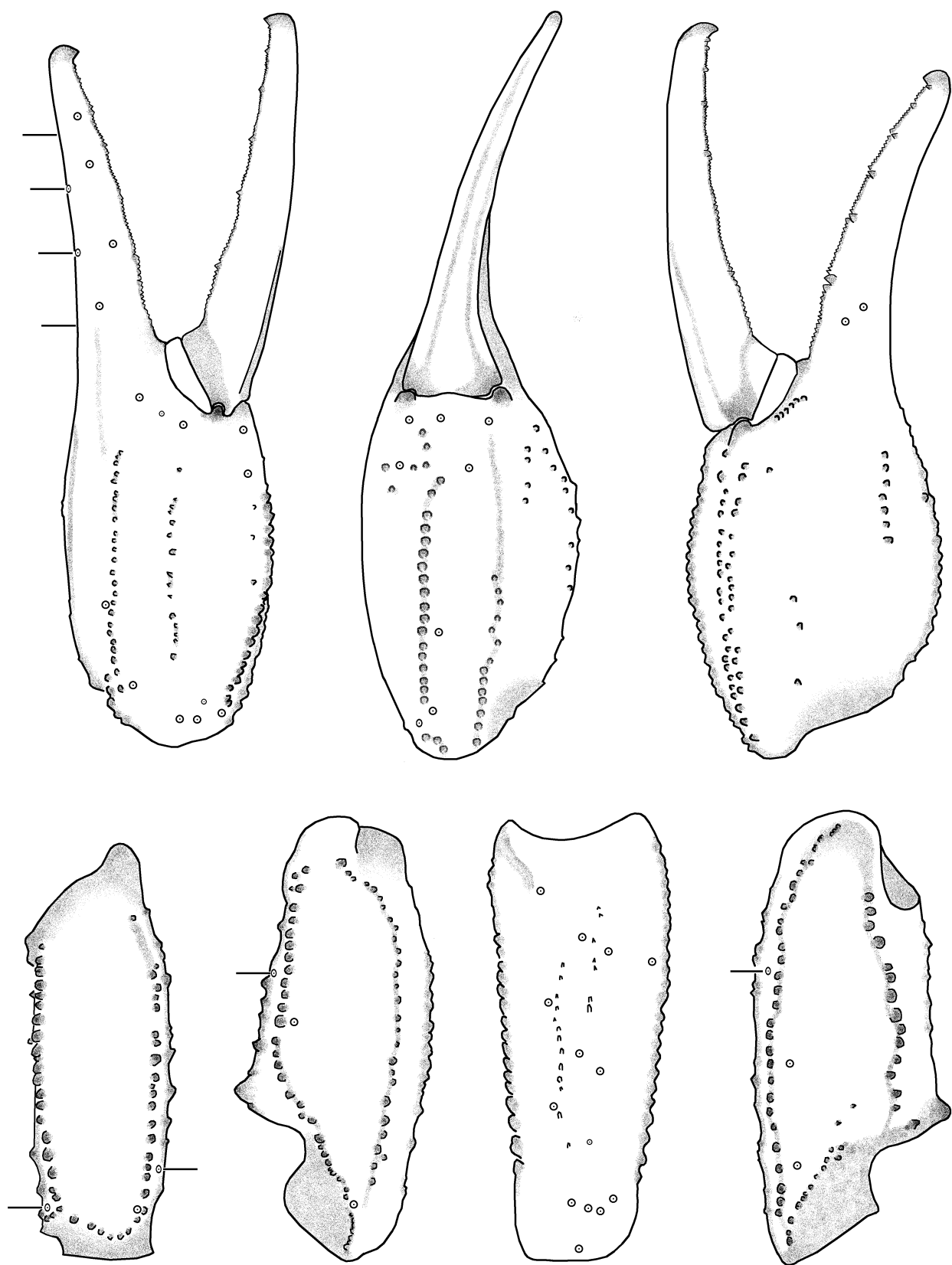


Figure 5: Trichobothrial pattern of *Smeringurus grandis*, female, Oakies Landing, Baja California, Mexico.

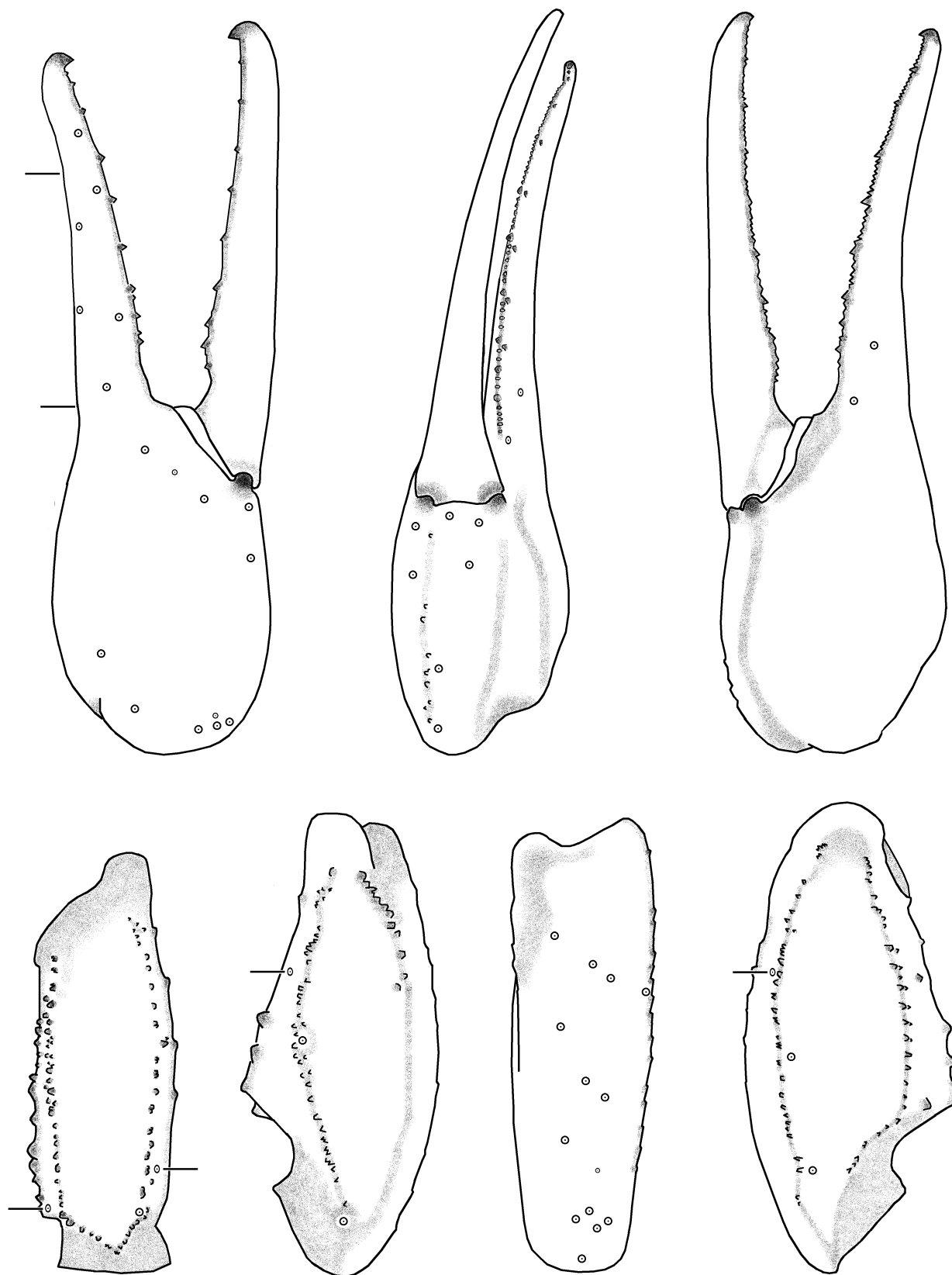


Figure 6: Trichobothrial pattern of *Vejovoidus longiunguis*, female, Las Bombas, Baja California Sur, Mexico.

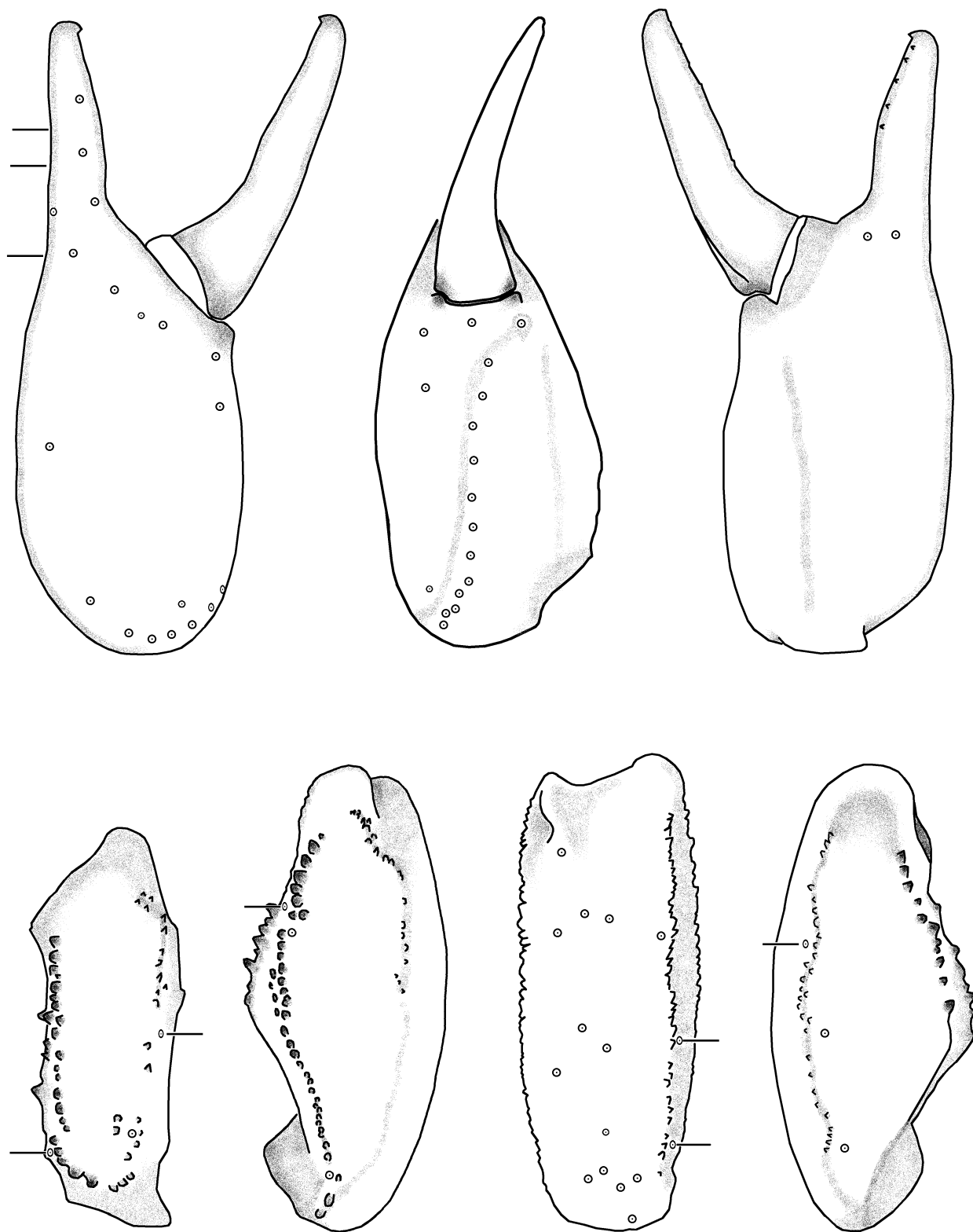


Figure 7: Trichobothrial pattern of *Paravaejovis pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico.

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. curvigitus*, *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 *v₃* with respect to *et₃* shows certain trends in some vaejovid species: in subfamily Smeringurinae, *v₃* is positioned proximal to *et₃* (Figs. 2–7); it also provides a distinction between the tribes in subfamily Syntropinae: in tribe Stahnkeini, *v₃* is distal to *et₃* (Fig. 8) whereas in Syntropini, *v₃* is positioned proximal to *et₃* (Figs. 9–12). In subfamily Smeringurinae, trichobothria *eb₂–eb₅* essentially form a horizontal line, none in close proximity to *eb₁*, 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, *eb₄* angles proximally, somewhat in close proximity to *eb₁* (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

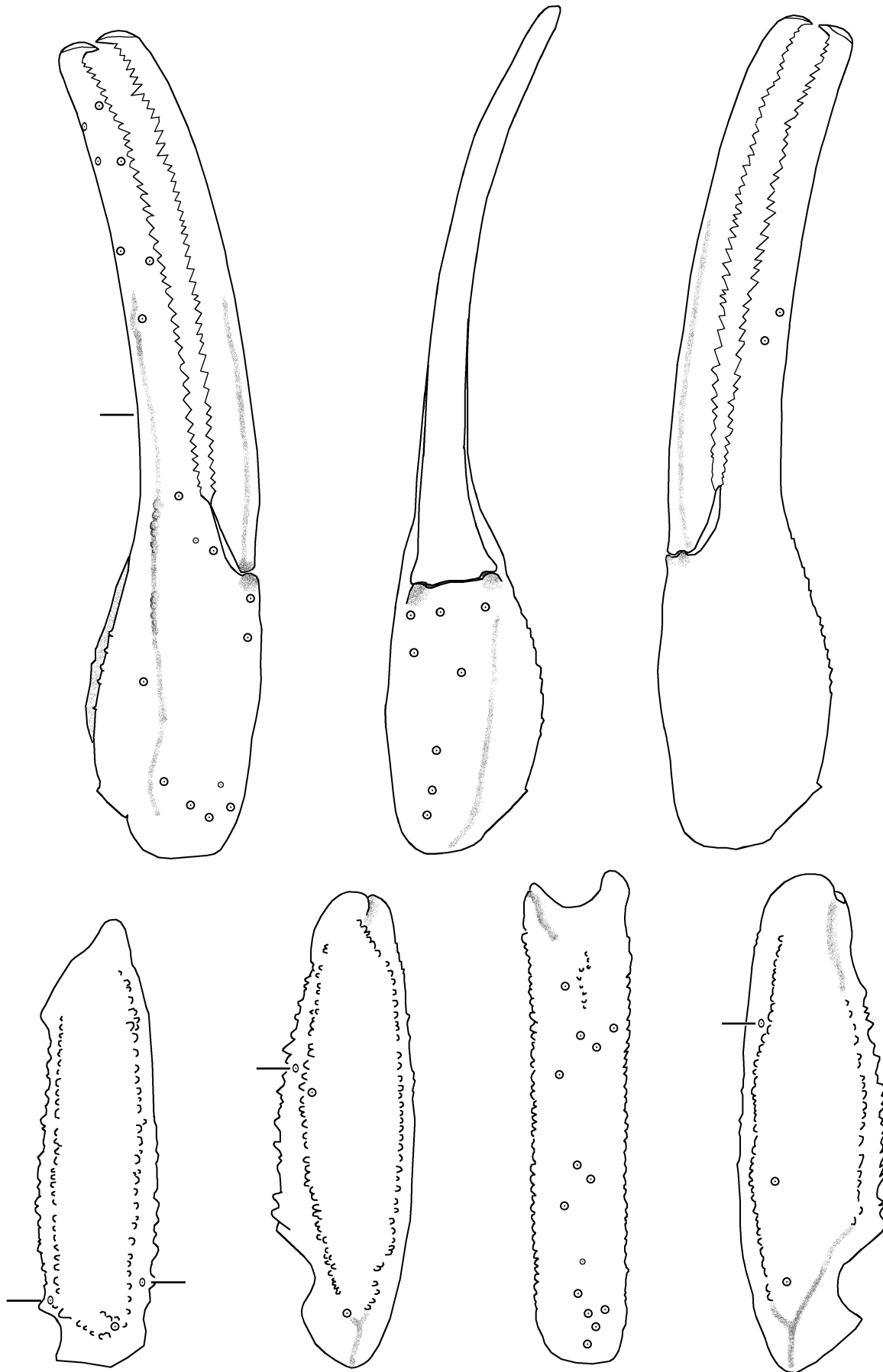


Figure 8: Trichobothrial pattern of *Serradigitus wupatkiensis*, female, Wupatki Ruin, Wupatki National Monument, Coconino Co., Arizona, USA.

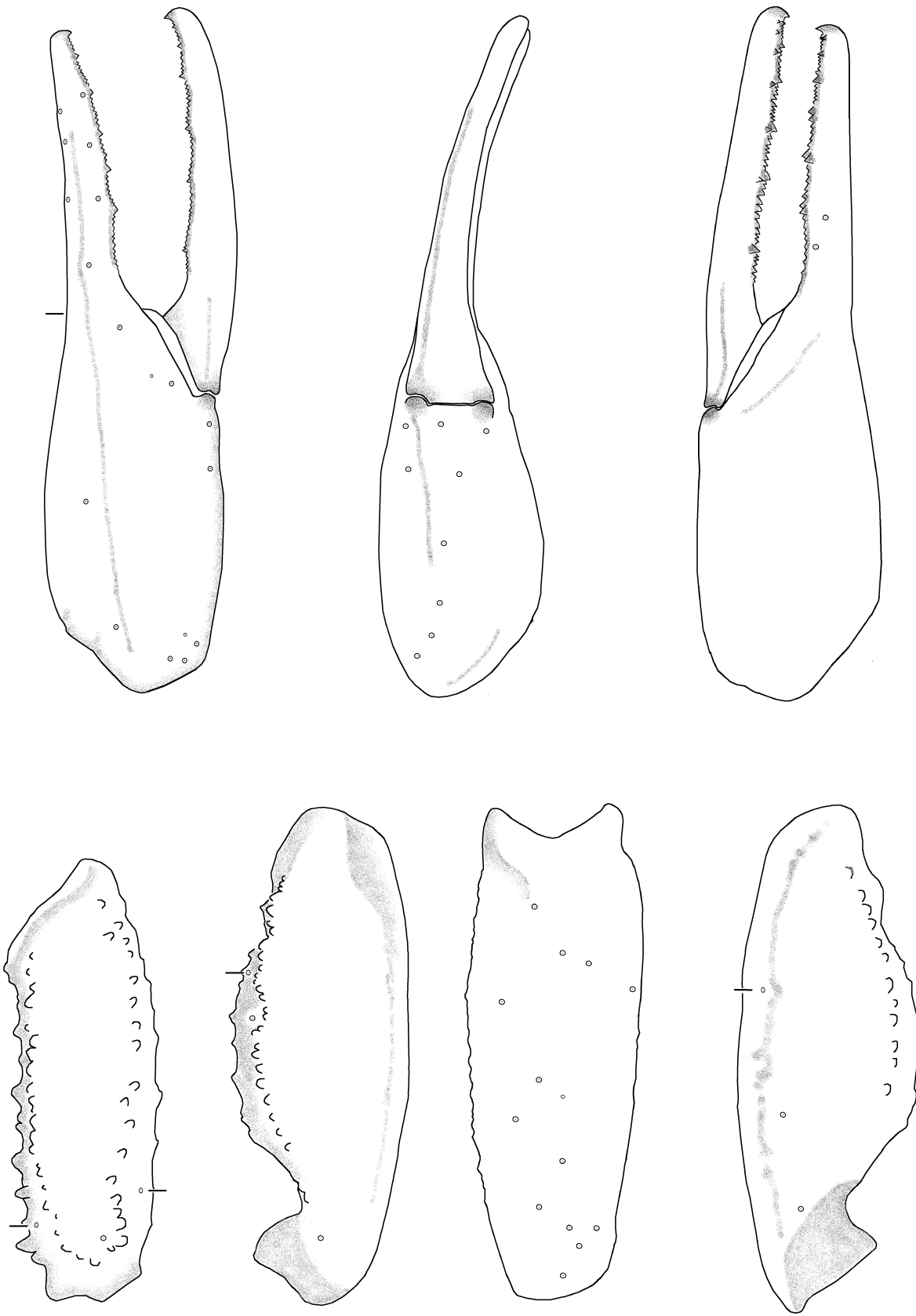


Figure 9: Trichobothrial pattern of *Hoffmannius eusthenura*, male, Cabo San Lucas, Baja California Sur, Mexico.

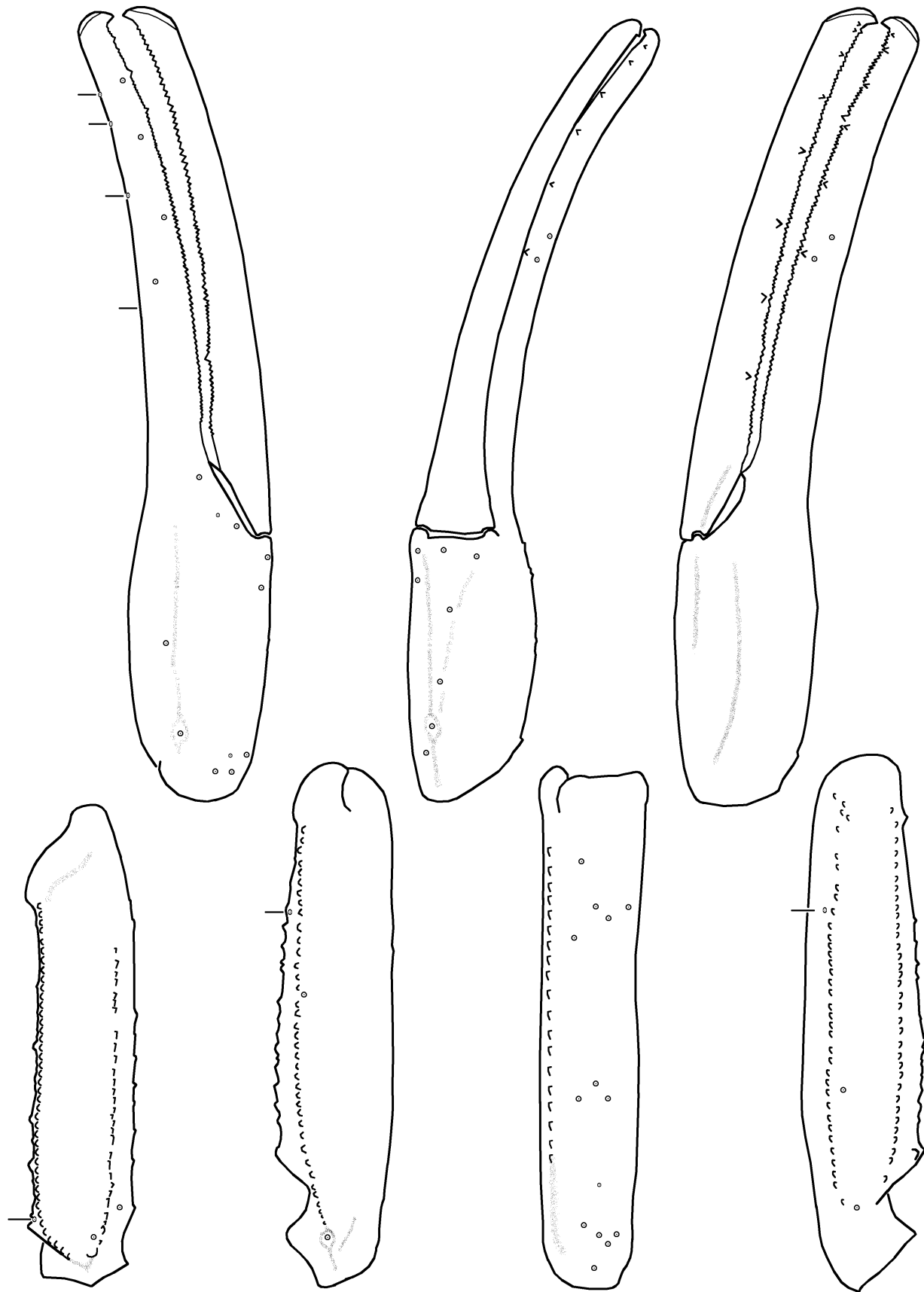


Figure 10: Trichobothrial pattern of *Syntropis williamsi*, female holotype, Los Aripes, Baja California Sur, Mexico (after Soleglad et al., 2007: fig. 15).

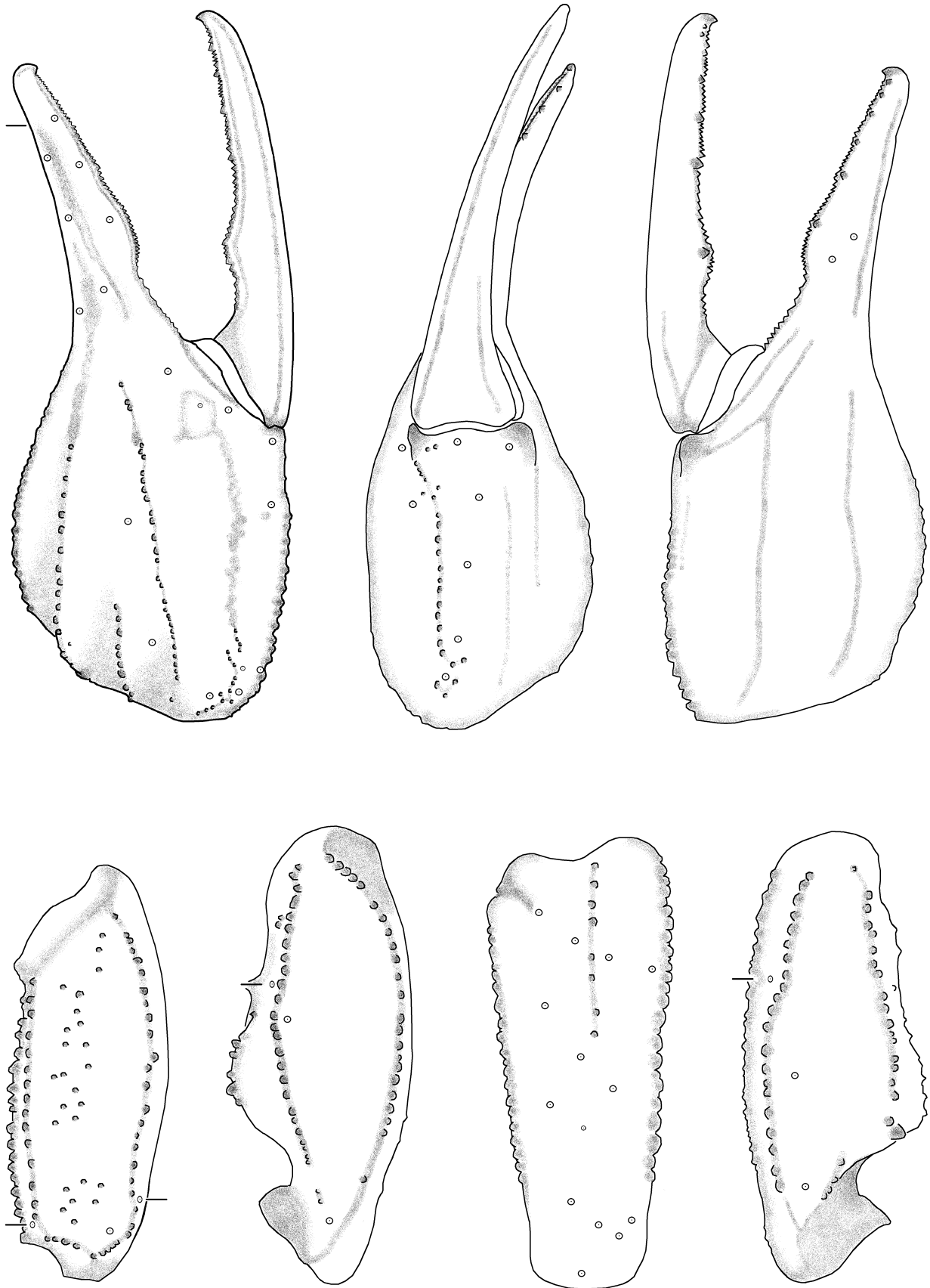


Figure 11: Trichobothrial pattern of *Kochius punctipalpi punctipalpi*, female, Cabo San Lucas, Baja California Sur, Mexico.

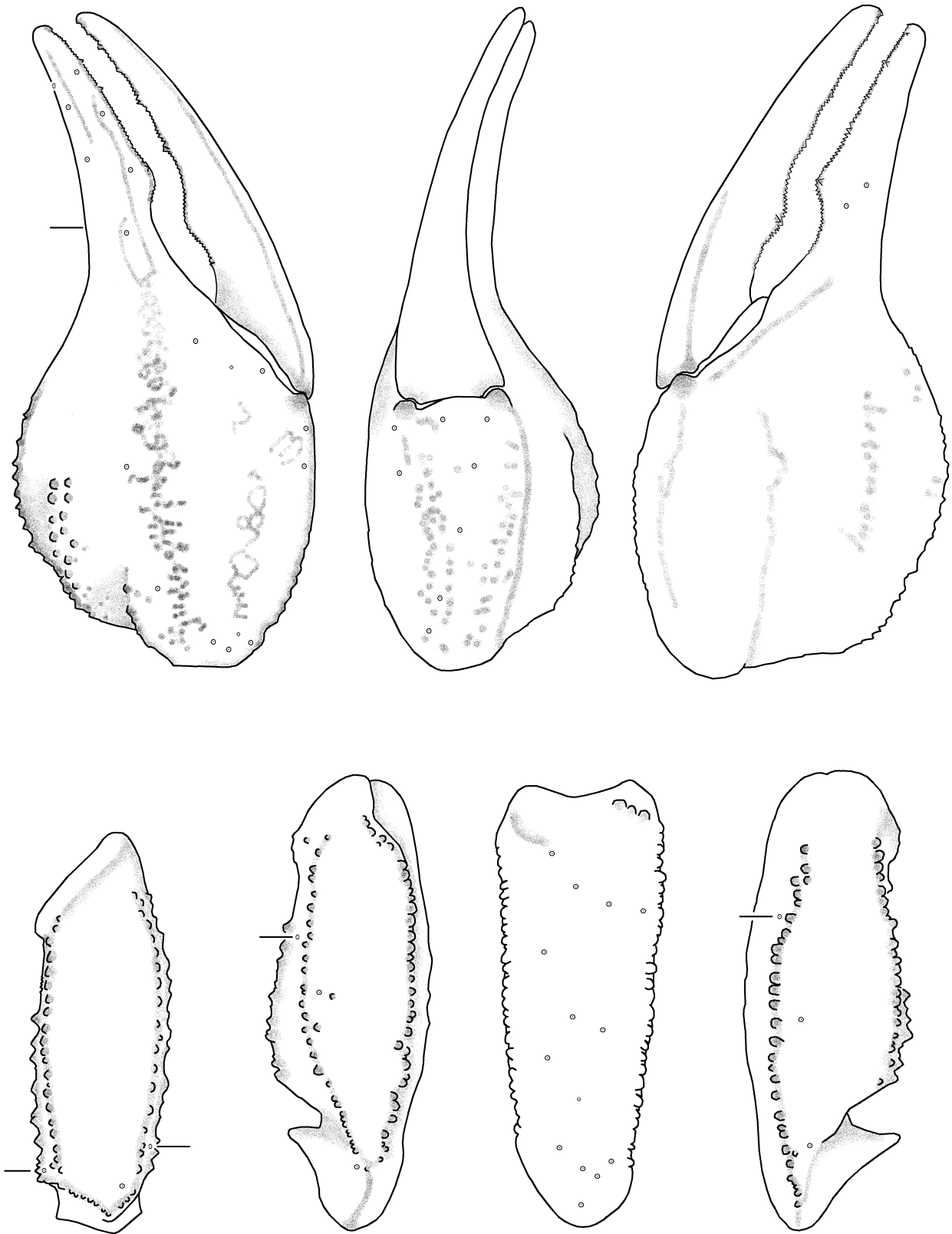


Figure 12: Trichobothrial pattern of *Thorellius intrepidus*, male, Mexico.

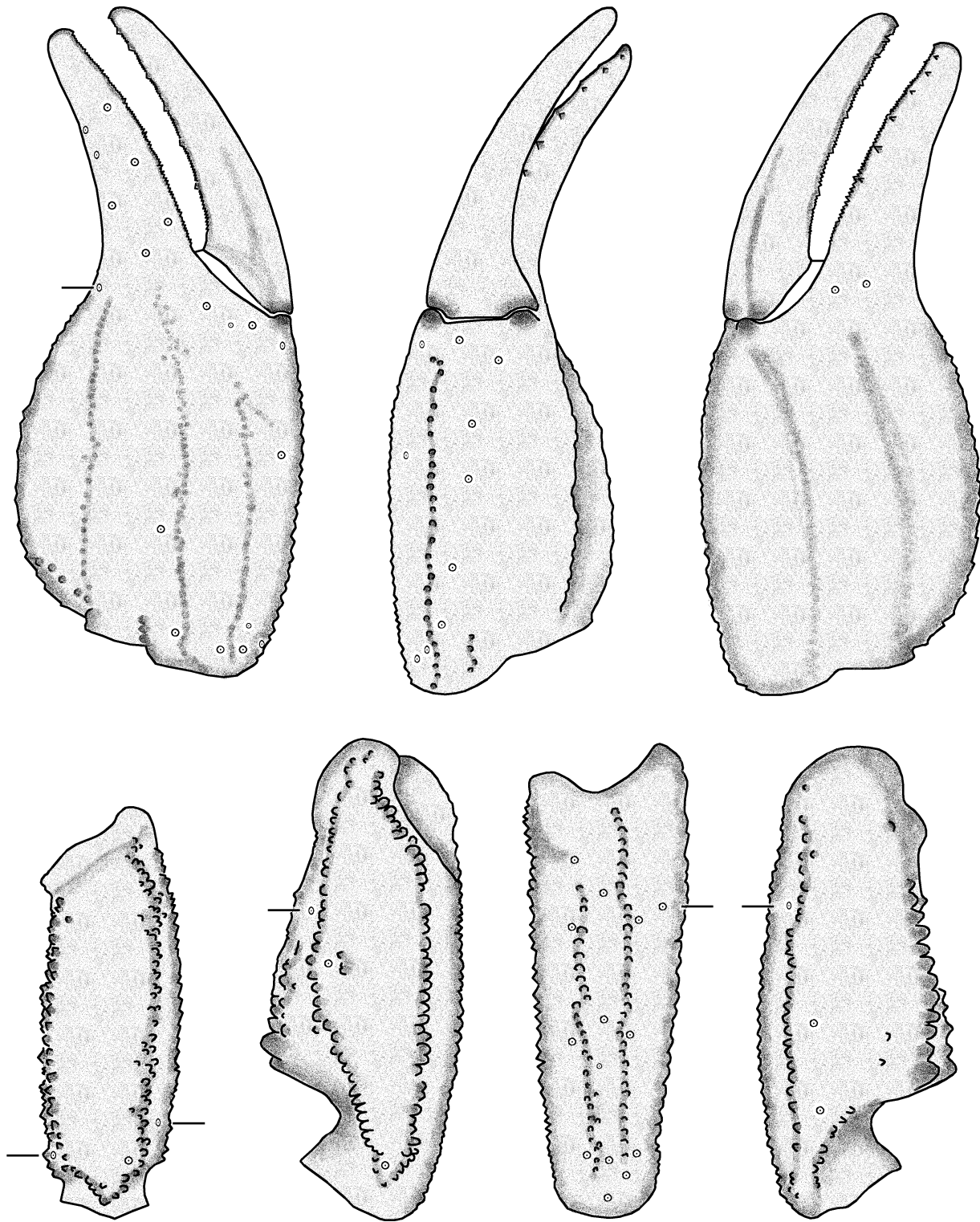


Figure 13: Trichobothrial pattern of *Pseudouroctonus williamsi*, male, Santa Ysabel Reserve, San Diego Co., California, USA.

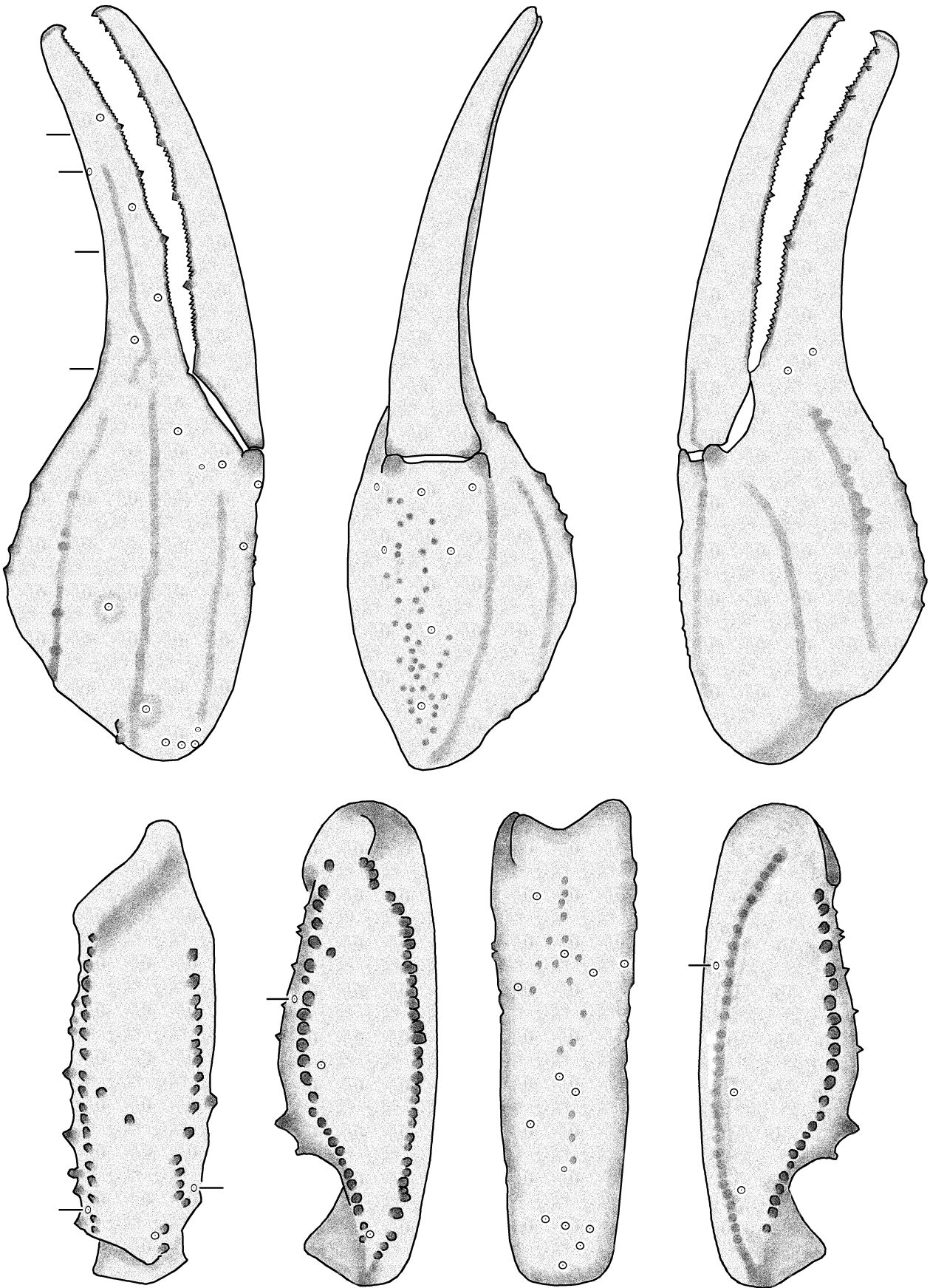


Figure 14: Pedipalp trichobothrial pattern of *Vaejovis mexicanus*, female neotype, Mexico City, Mexico (after Fet & Soleglad, 2007: fig. 7).