

	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. marksii</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>Vejovoidus 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 *Vejovoidus*, 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 Vaejovidae (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 Vaejovidae 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 Vaejovidae. 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>Vejovoidus</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 (3.0) 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 *Vejovoidus* 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. arm-andentis*, 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 hypothesis 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 Söleglad 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

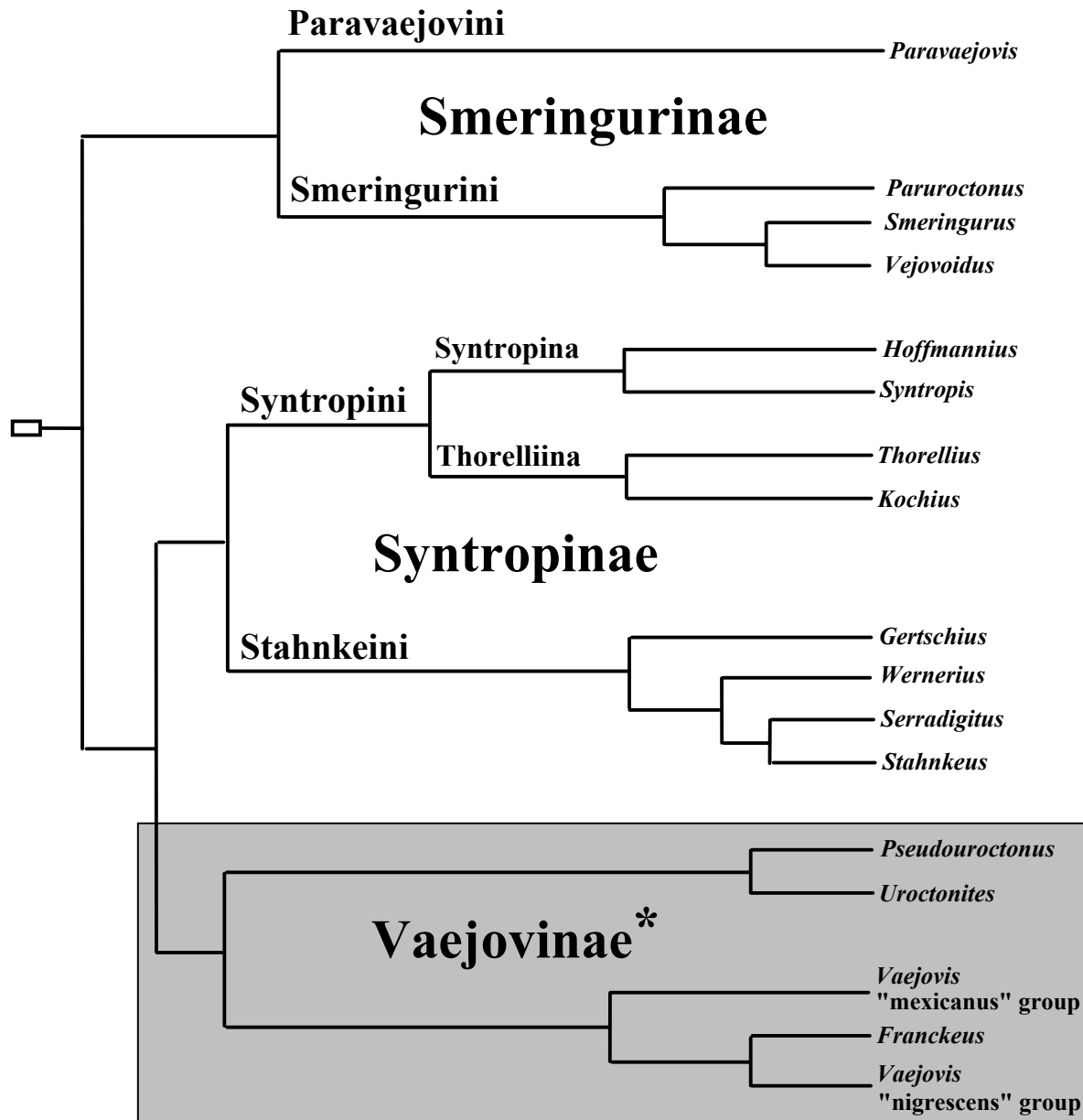


Figure 196: Phylogram showing the three current subfamilies of family Vaejovidae based on the results of this study. * Note, subfamily Vaejovinae (shaded), the default nominotypic subfamily for Vaejovidae, has not yet been revised and therefore only reflects the remaining taxa and their relationships 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. marksii 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. pecos</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>
Syntropinae	Stahnkeini		<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>Vejovoidus</i>	<i>V. longitunguis</i>
	Syntropini		<i>Gertschius</i>	<i>G. agilis</i> , <i>G. crassicornus</i>
			<i>Serradigitus</i>	<i>S. adcocki</i> , <i>S. armadentis</i> , <i>S. baueri</i> , <i>S. bechtlei</i> , <i>S. calidus</i> , <i>S. dwyeri</i> , <i>S. gertschi gertschi</i> , <i>S. gertschi striatus</i> , <i>S. giganteaensis</i> , <i>S. gramenestris</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. polisi</i> , <i>S. subtilimanus</i>
			<i>Wernerius</i>	<i>W. mumai</i> , <i>W. spicatus</i>
	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. viscaianensis</i> , <i>H. vittatus</i> , <i>H. waeringi</i> , <i>H. waueri</i>
			<i>Syntropis</i>	<i>S. aalbui</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. kovarikii</i> , <i>K. magdalenis</i> , <i>K. punctipalpi punctipalpi</i> , <i>K. punctipalpi barbatus</i> , <i>K. punctipalpi cerraalvensis</i> , <i>K. russelli</i> , <i>K. sonorae</i>
Vaejovinae			<i>Thorellius</i>	<i>T. atrox</i> , <i>T. cisnerosi</i> , <i>T. cristimanus</i> , <i>T. inrepidus</i> , <i>T. occidentalis</i> , <i>T. subcristatus</i>
			<i>Franceus</i>	<i>F. kochi</i> , <i>F. minckleyi</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. chicano</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. rufidus</i> , <i>P. sprousei</i> , <i>P. williamsi</i>
			<i>Uroctonites</i>	<i>U. giulianii</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. فرانкеи</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. mayarti</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).

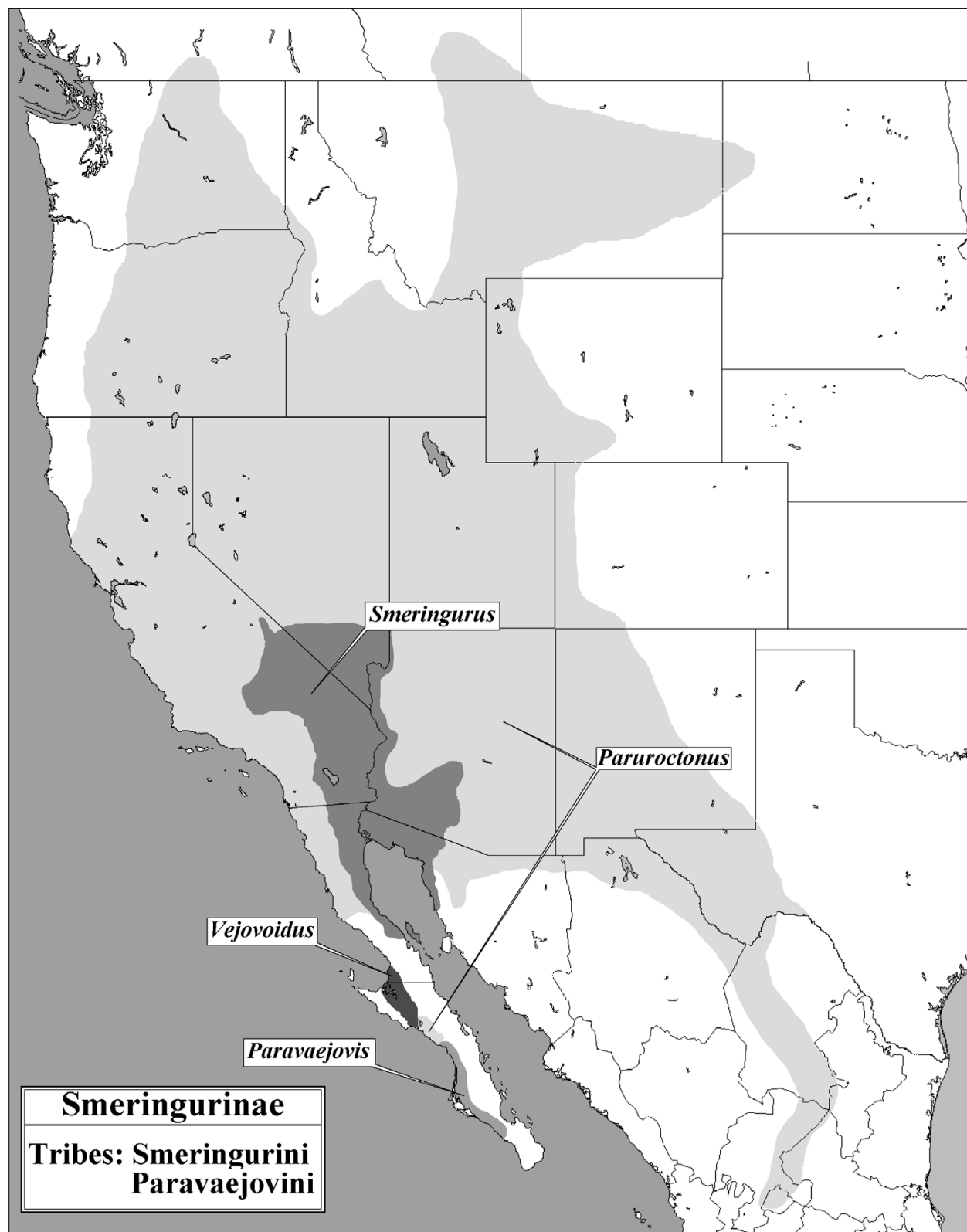


Figure 197: General distribution of scorpion subfamily **Smeringurinae** in North America with the ranges of genera *Paravaejovis* (tribe **Paravaejovini**) and *Smeringurus*, *Paruroctonus*, and *Vejovoidus* (tribe **Smeringurini**) delineated.

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 *Hoffmanniellus* 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 seta 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; Sologlad & 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 epitarsus (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 Sologlad et Fet, trib. nov.

Type Genus. *Paravaejovis* Williams, 1980.

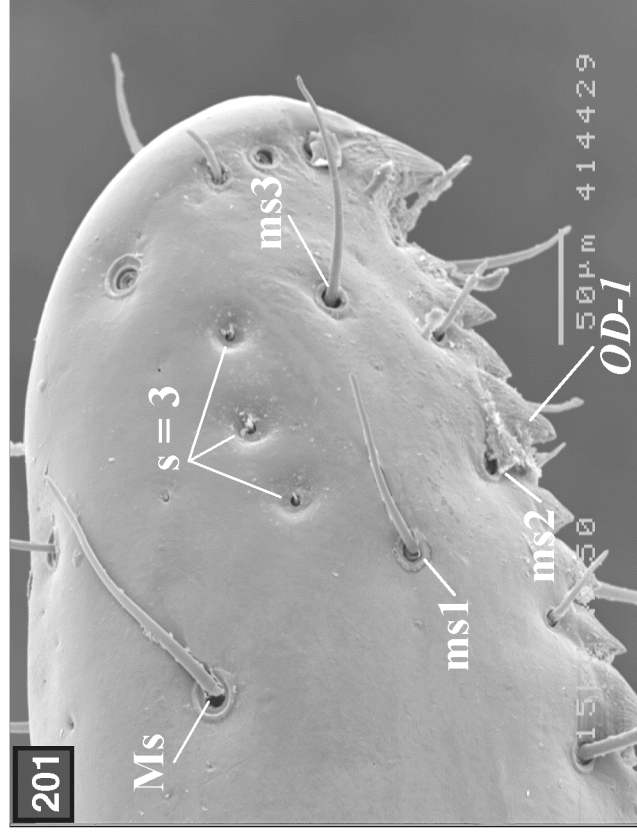
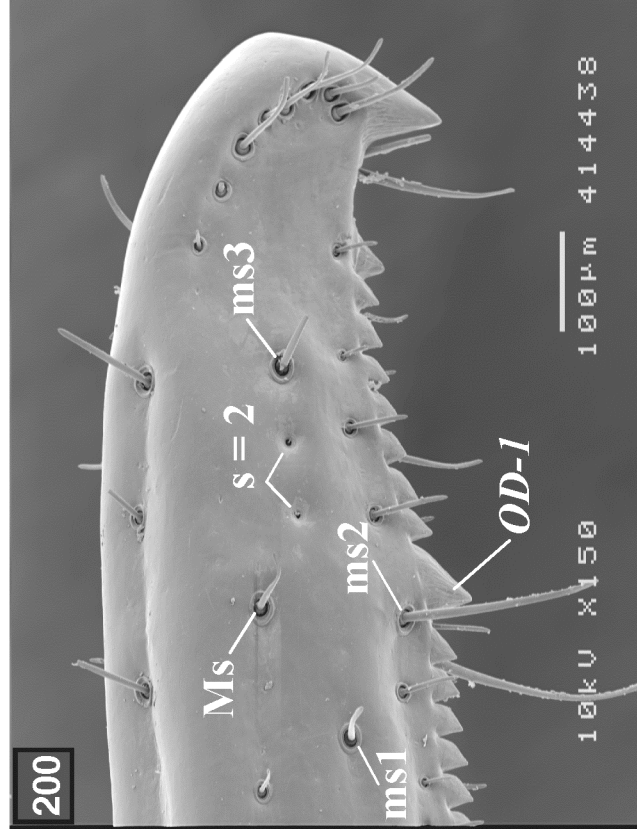
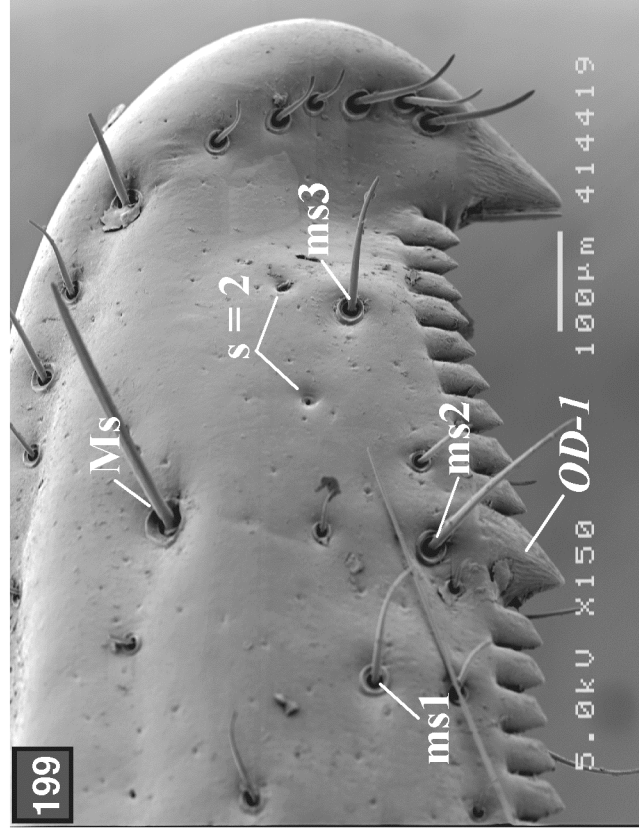
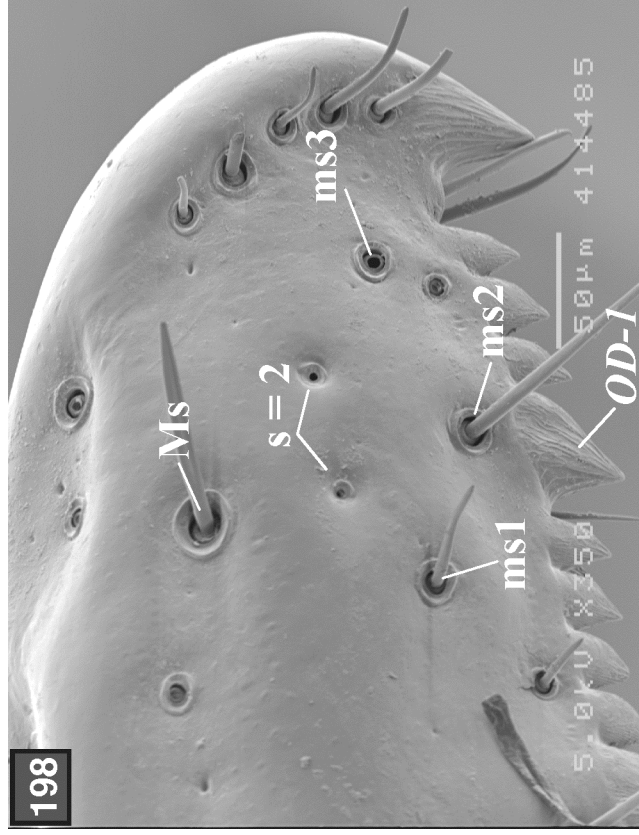
Composition. This monotypic tribe, established here, includes the genus *Paravaejovis*.

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 mesaensis*, male, ABDSP, California, USA. **200.** *Vejovaldus longiunguis*, female, Las Bombas, Baja California Sur, Mexico. **201.** *Paravaeiovus pumilis*, male, Ciudad Constitución, Baja California Sur, Mexico. Note that genus *Paravaeiovus* 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 *Vejovis 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 *V₂–V₃* distance approximately same as *V₁–V₂*; 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 hemispermaphore 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).

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

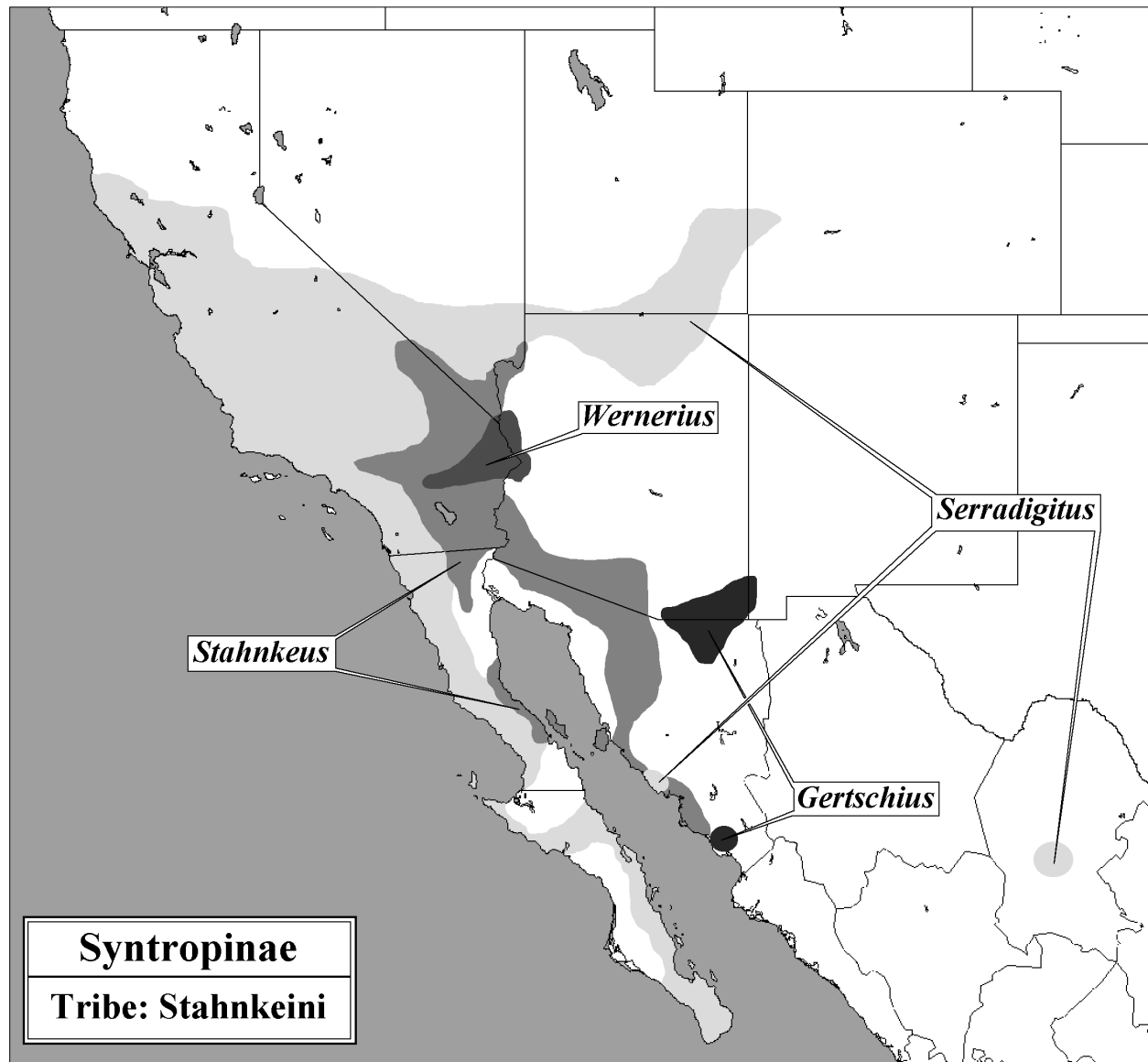


Figure 202: General distribution of scorpion subfamily **Syntropinae** (tribe **Stahnkeini**) in North America with the ranges of genera *Stahnkeus*, *Serradigitus*, *Gertschius*, and *Wernerius* delineated.

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 times).

Discussion. See discussion of genera below.

Subtribe Syntropina Kraepelin, 1905, new rank

Type Genus. *Syntropis* Kraepelin, 1900.

References:

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

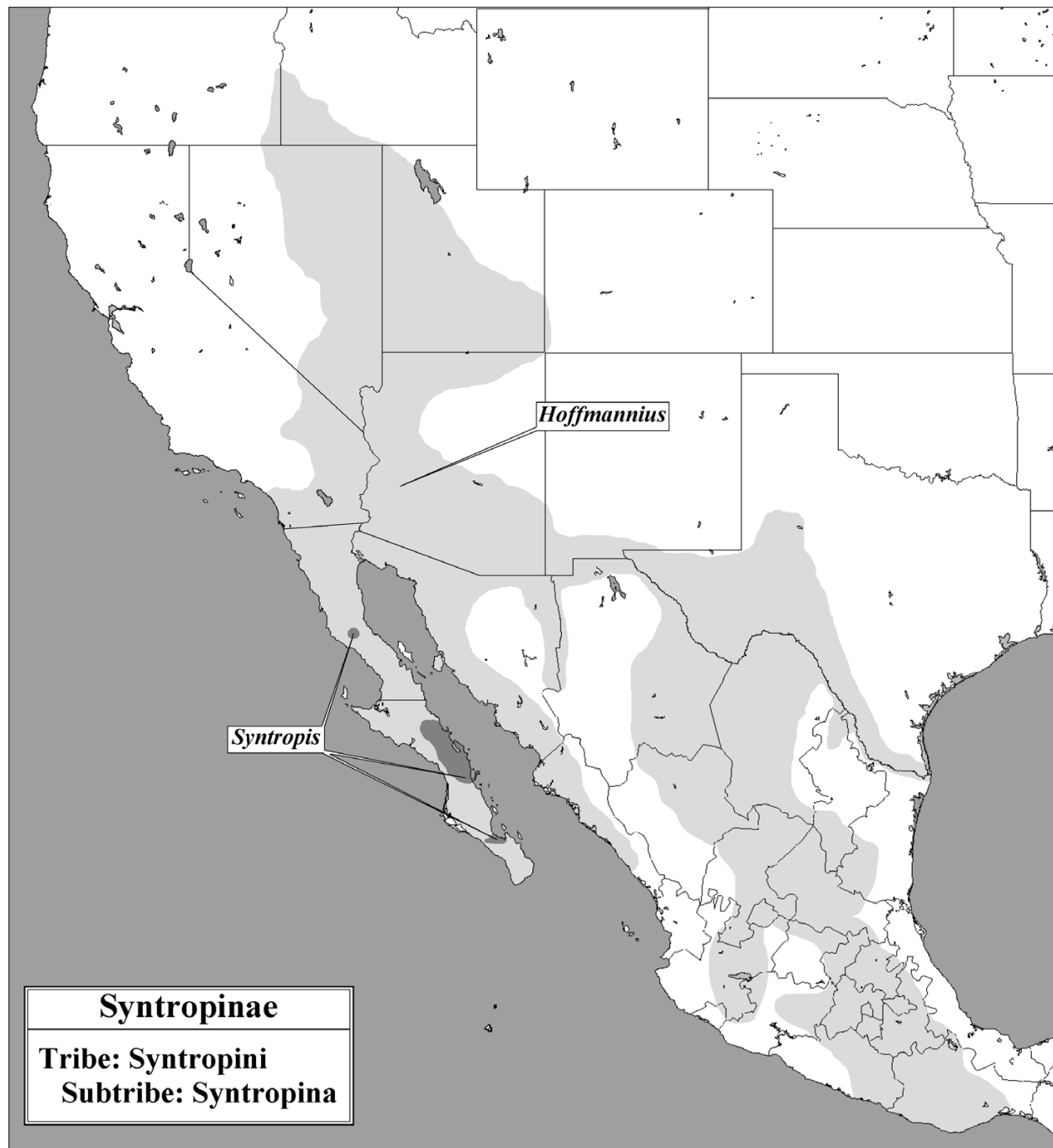


Figure 203: General distribution of scorpion subfamily **Syntropinae** (tribe **Syntropini**, subtribe **Syntropina**) in North America with the ranges of genera *Hoffmannius* and *Syntropis* delineated.

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. sonorae (Williams, 1971), **comb. nov.**

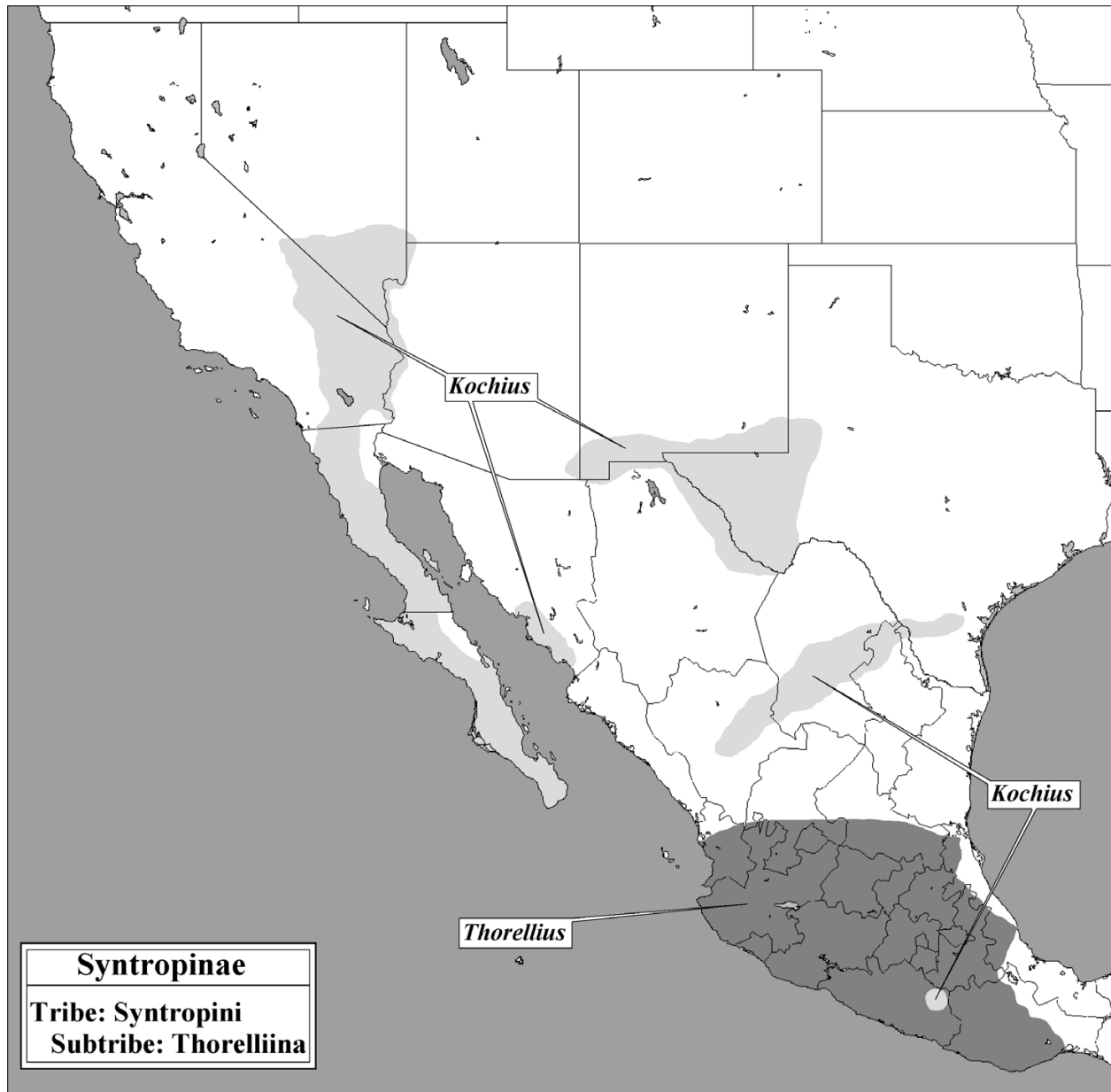


Figure 204: General distribution of scorpion subfamily **Syntropinae** (tribe **Syntropini**, subtribe **Thorelliina**) in North America with the ranges of genera *Kochius* and *Thorellius* delineated.

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. sonoreae*, 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* Soleglad 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 Teodor Thorell (1830–1901), one of the prominent scorpion taxonomists of the 19th century, and the author of many scorpion taxa, including family Vaejovidae.

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 crassicornus* 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: hemispermaphore 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.

Vejovinae (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; hemispermatophore 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. Vaejovid 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.

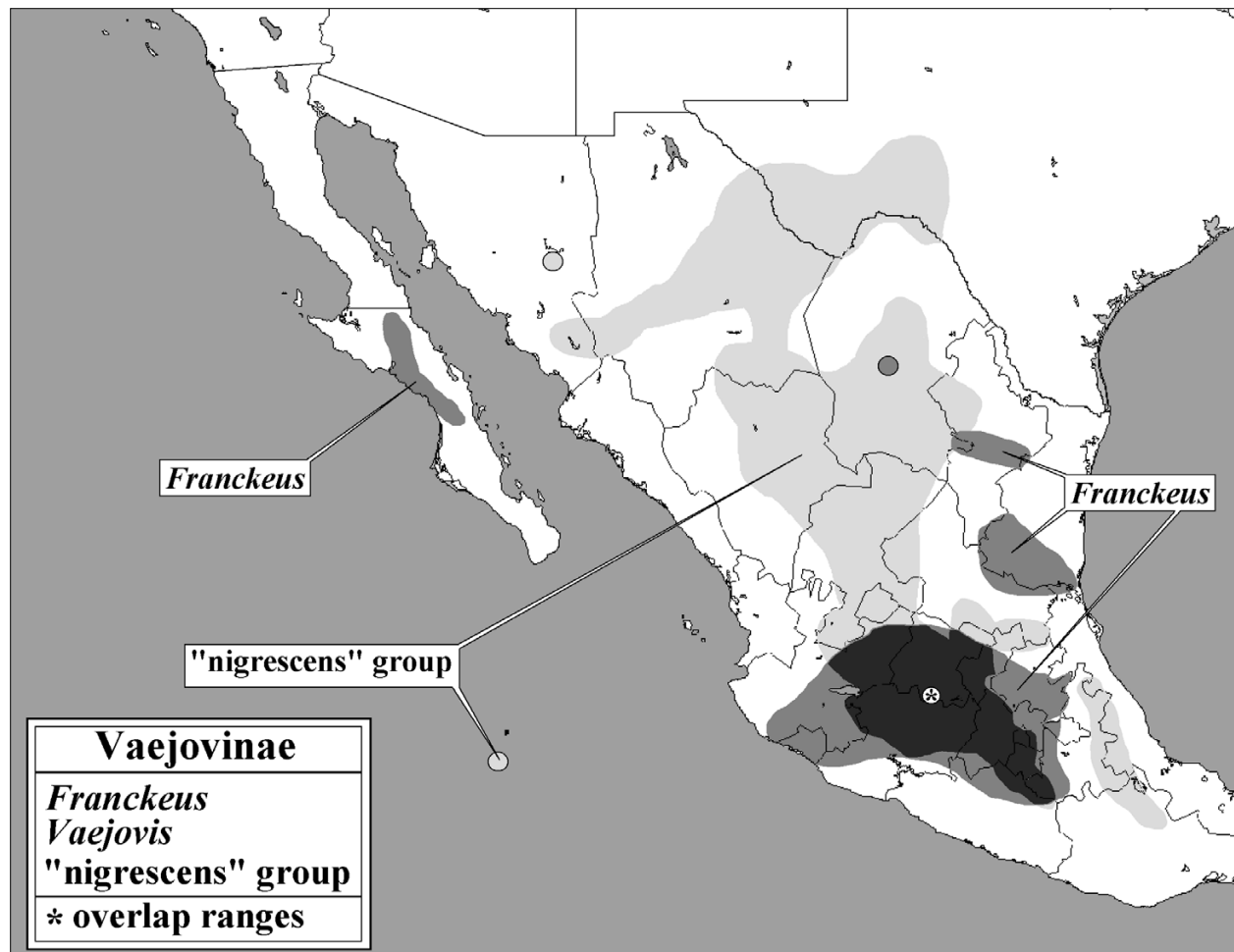


Figure 205: General distribution of scorpion subfamily **Vaejovinae** in North America with the ranges of genera *Franckeus* and *Vaejovis* “nigrescens” group delineated.

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. glimpei* occurring just south in Monterey and Mendocino Counties. Several *Pseudouroctonus* species occur in southern California (*P. angelenus*, *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. monterei (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. monterei*), 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).

Vejois: 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-Frias, 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

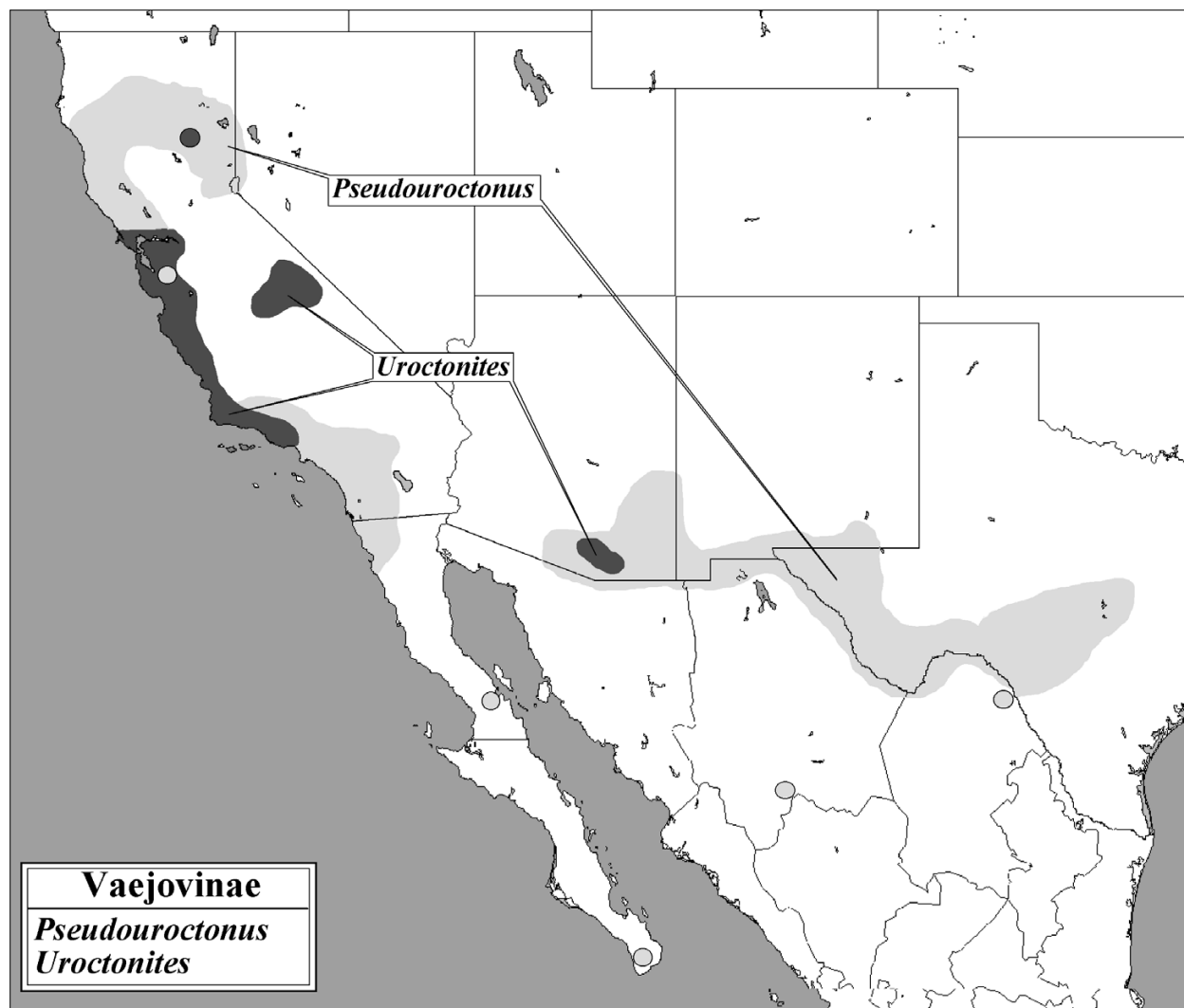


Figure 206: General distribution of scorpion subfamily **Vaejovinae** in North America with the ranges of genera *Pseudouroctonus* and *Uroctonites* delineated.

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.*

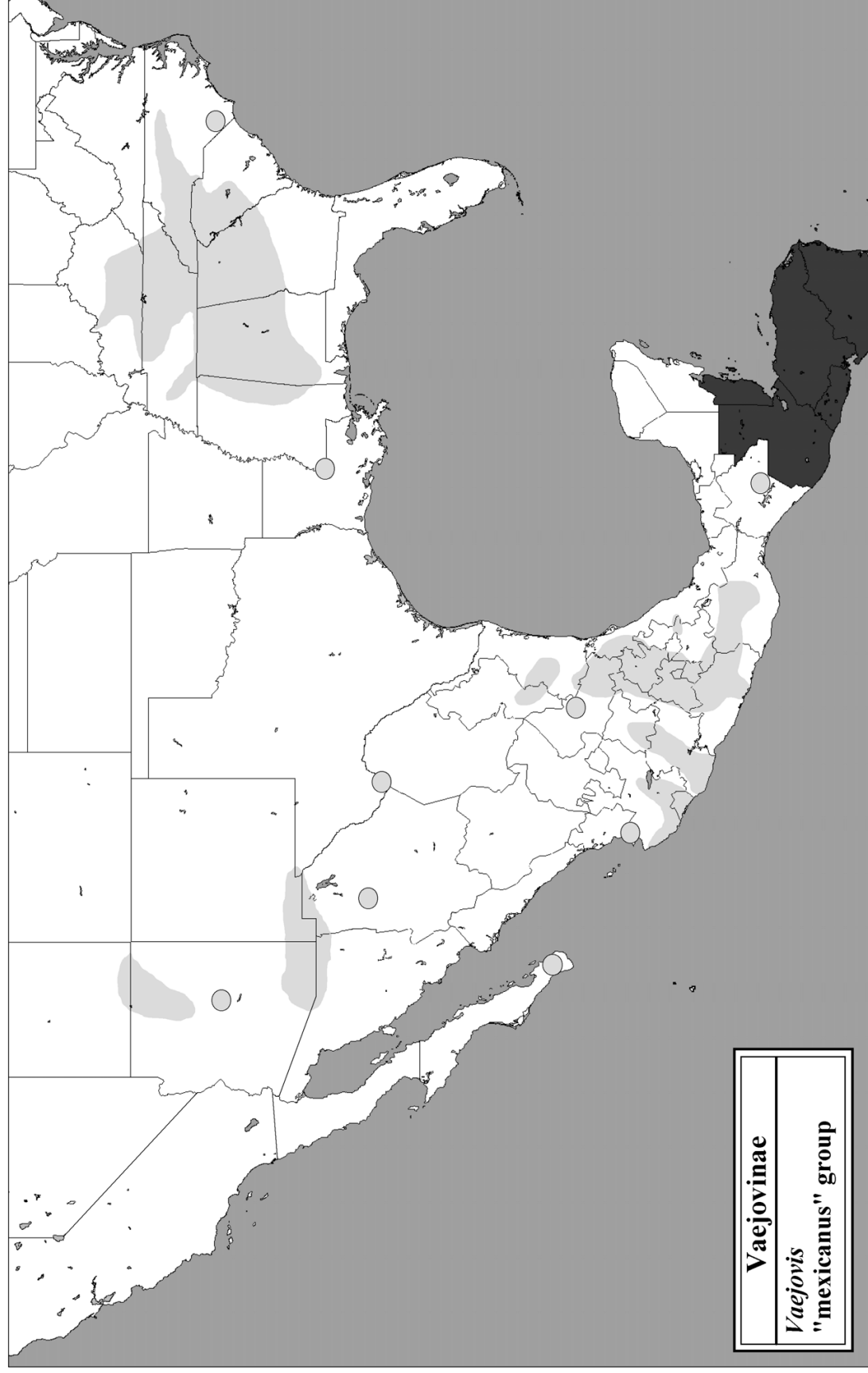


Figure 207: General distribution of scorpion subfamily *Vaejovinae* in North America with the ranges of genus *Vaejovis* "mexicanus" group delineated.

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. Hemispermaphore 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

■ Hemispermaphore 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 *Vejoivoidus*

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; chelal 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 (*D1*) 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 (*D1*) 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. Hemispermatophore 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**

■ Hemispermatophore 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 **Franckus**

■ 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 *OD*s 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.

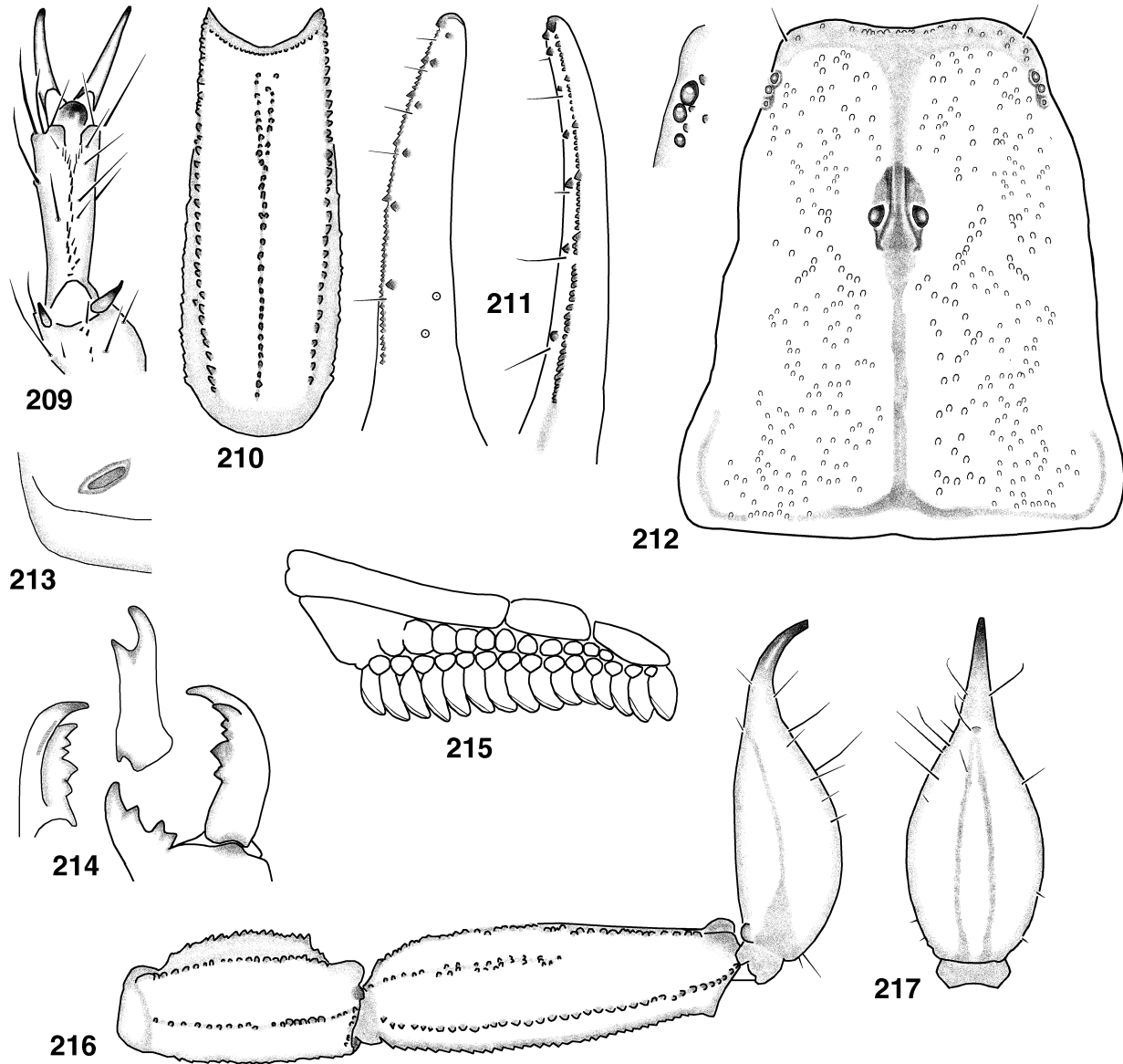
TELSON (Fig. 216–217). Somewhat elongated, with average sized aculeus, with 4/4 denticles in the latero-basal aculear serrations (LAS; Fet et al., 2006b). Ventral vesicle surface smooth, with scattered elongated setae on distal half; basal dorsal aspect with vesicular “tabs” terminating in two small 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*)

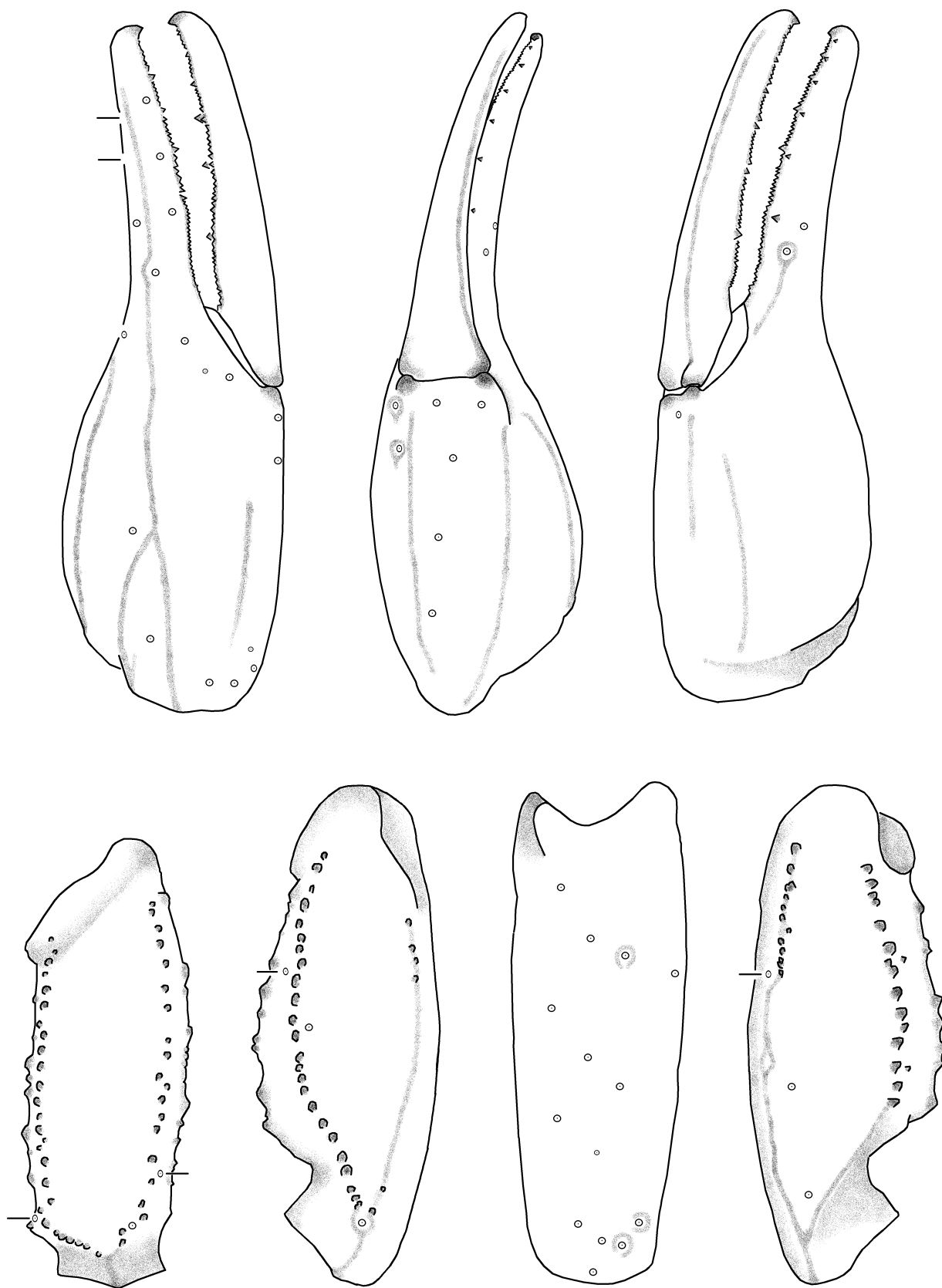


Figure 218: Trichobothrial pattern of *Kochius kovariki*, **sp. nov.**, female holotype, Durango, Durango, Mexico.

<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
Movable Finger Length	5.05
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 *v*₃ located on external surface, proximal of trichobothrium *et*₃. 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 *V*₁ and *V*₂ approximately same as *V*₂ and *V*₃; 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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