

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

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

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

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

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

## Chelicerae

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

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

#### **Dentition**

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

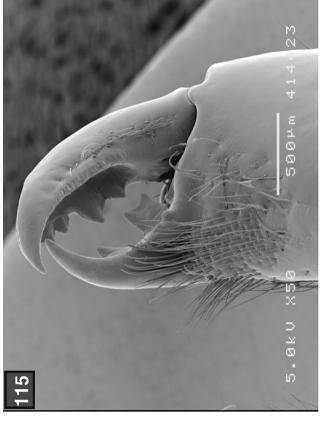
denticles exhibit considerable variability from quite large heavily pigmented denticles as seen in *Smeringurus* species (Fig. 117), to delicate non-pigmented denticles as seen in *Paruroctonus becki* (Fig. 118). In some cases, when the denticles are considerably wornout, or vestigial in development,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

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

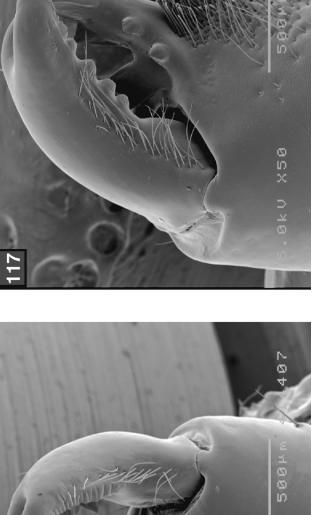
**Syntropinae.** Syntropine species lack dentition on the ventral edge of the movable finger and protuberances are lacking on the fixed finger ventral surface.

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

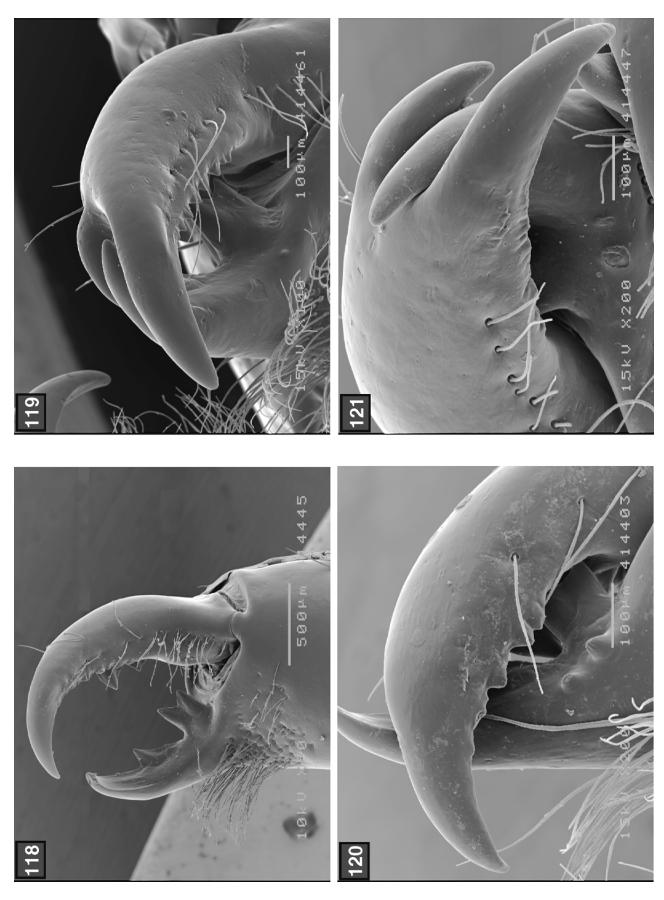




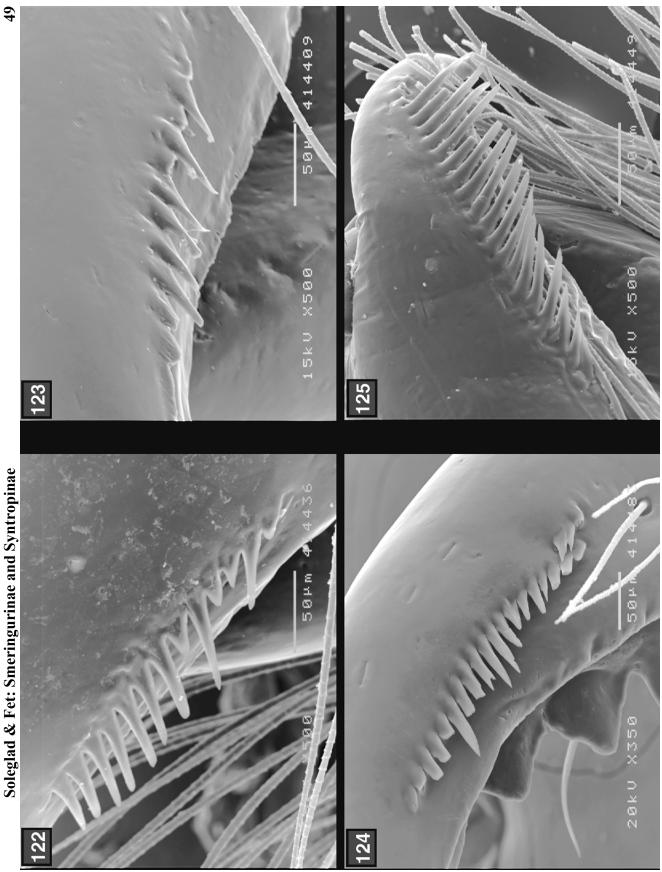




Figures 114–117: Chelicera, ventral view. 114. Paruroctonus gracilior, male, Cuatro Ciénegas, Coahuila, Mexico. White arrow points to reduced ventral carina of fixed finger. 115. Paruroctonus utahensis, male, Kermit, Winkler Co., Texas. 116. Vejovoidus longiunguis, female, Vizcaino Desert, Baja California,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



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



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

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

**Table 3:** Serrula Development Quotient (SDQ) for subfamily Syntropinae. Note the considerably larger number of tines in tribe Stahnkeini, 21–37, from the smallest to largest species as compared to 10–26 for tribe Syntropini. Correlating the number of tines to the species adult length emphasizes the significant difference in serrula based on species size. This comparison exhibits well over a factor of three difference. Density = space occupied by tines / serrula length (i.e., longitudinal distance along cheliceral movable finger). A density equal 1.0 implies that the tines are contiguously aligned in the serrula without gaps. \* Total length of adult female.

### Serrula

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

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

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

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

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

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

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

## **Carapace**

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

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

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

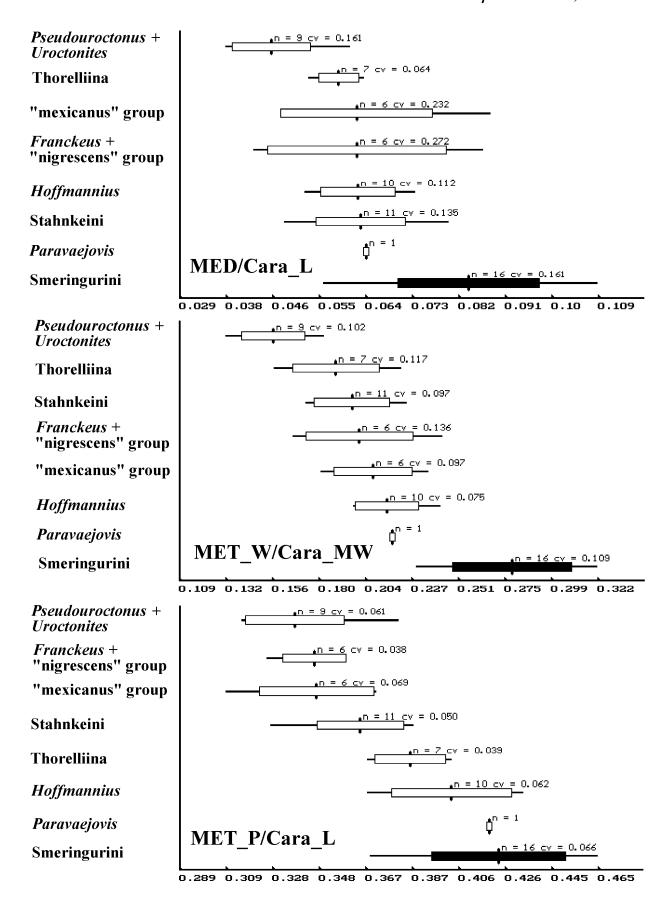
overlap. It is also interesting to note that the median eye is quite small in *Pseudouroctonus* + *Uroctonites*. The middle histogram in Fig. 126 shows complete standard deviation range separation from tribe Smeringurini and the other aggregates of Vaejovidae; tribe Paravaejovini (genus *Paravaejovis*)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

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

# Chelal Carinae

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

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



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

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

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

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

#### Metasoma Carinae

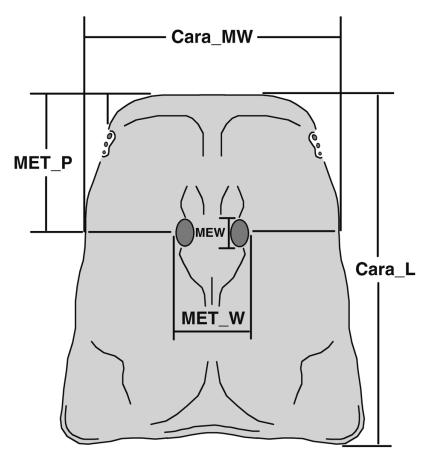
**Diagnostic value:** Metasoma carinae development is used to differentiate vaejovid subfamilies, in part, and genera of tribe Syntropini.

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

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

## Telson

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



**Figure 127:** Method of measurements for carapace. Cara\_L = carapace length; Cara\_MW = carapace median width; MET\_W = median eye tubercle width; MET\_P = median eye tubercle position; and MED = median eye diameter.

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

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

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

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

### **Morphometrics**

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