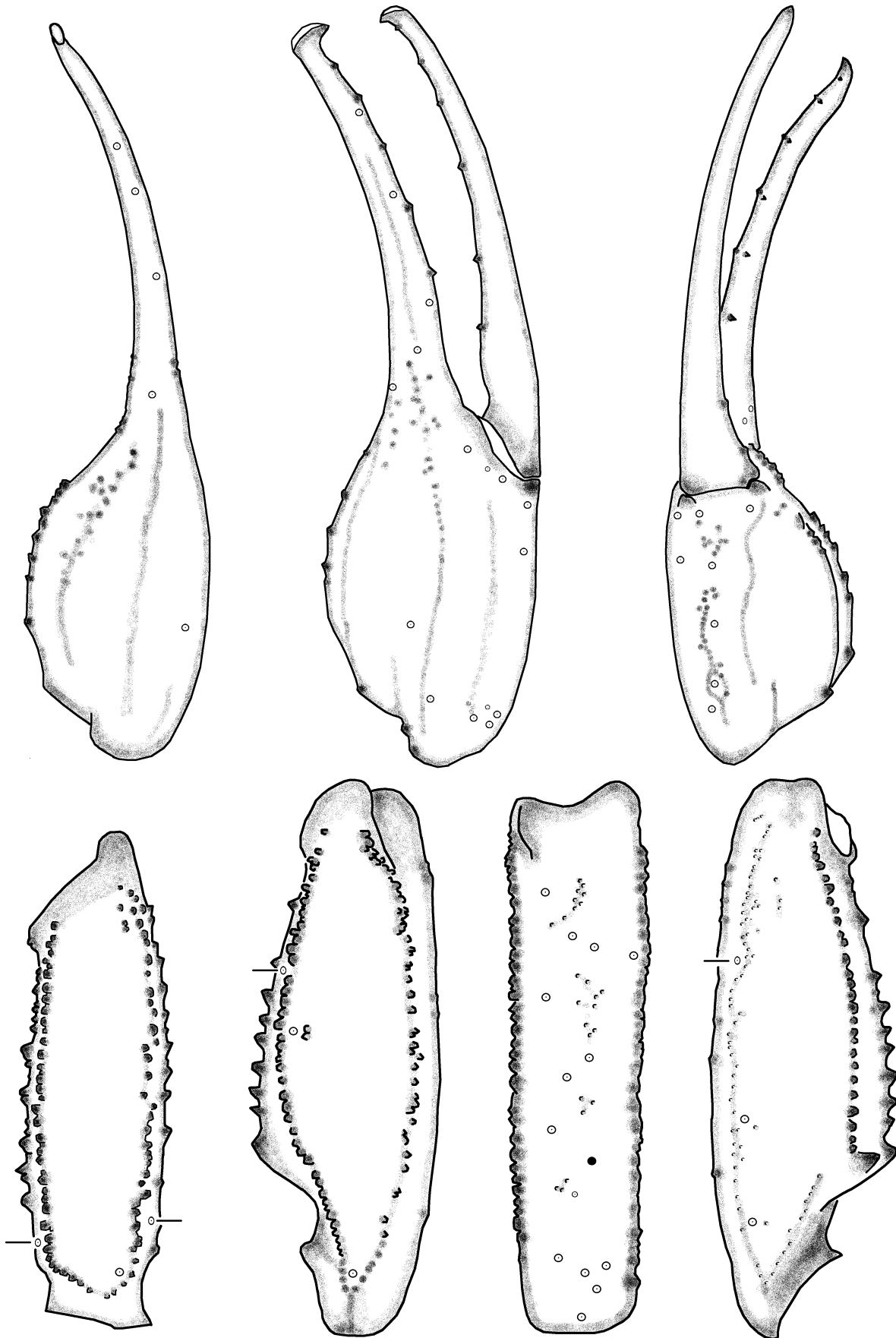
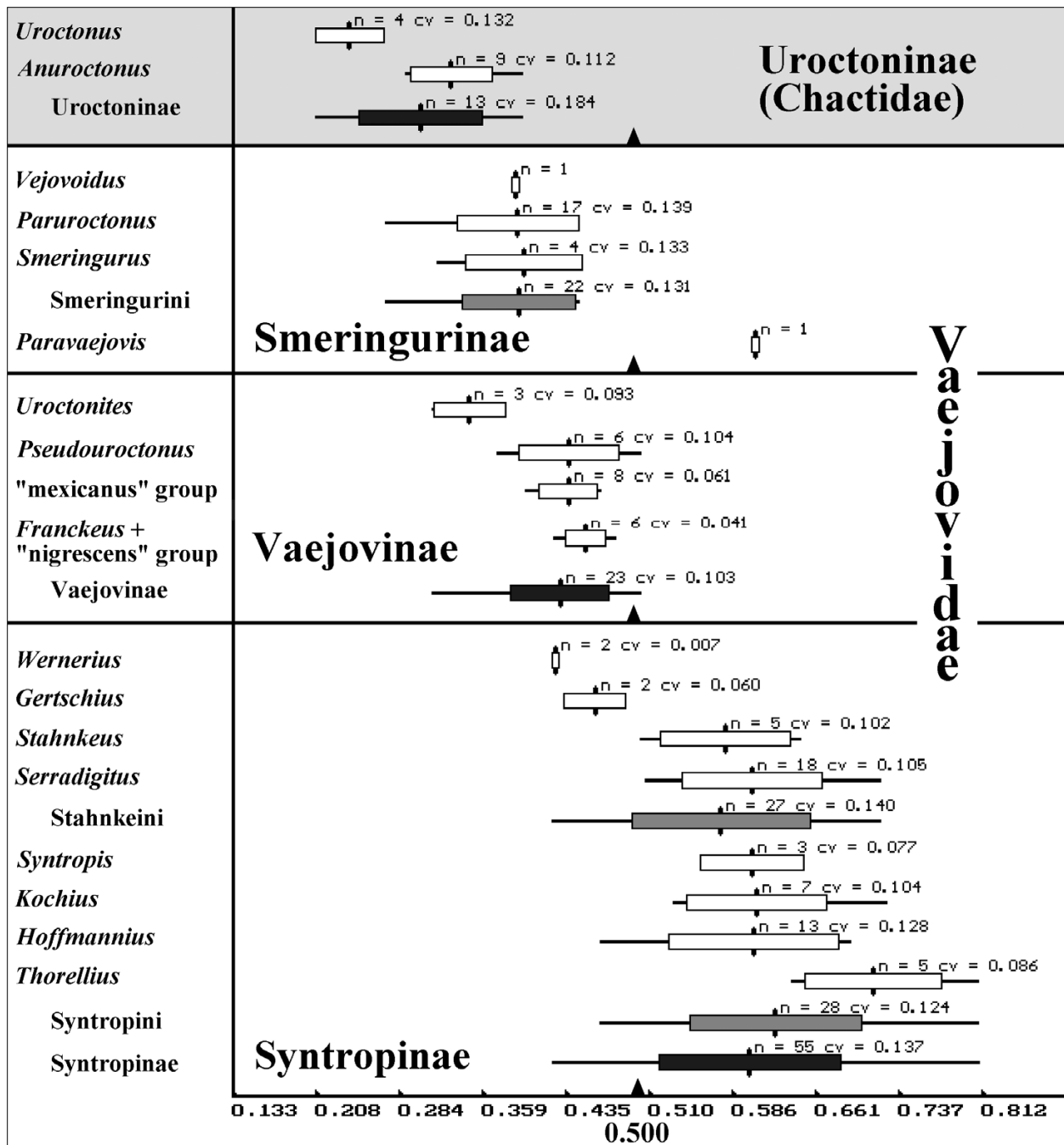


**Figure 15:** Trichobothrial pattern of *Vaejovis janssi*, male, Isla Socorro, Mexico (after Soleglad & Fet, 2005: figs. 20–26, in part).



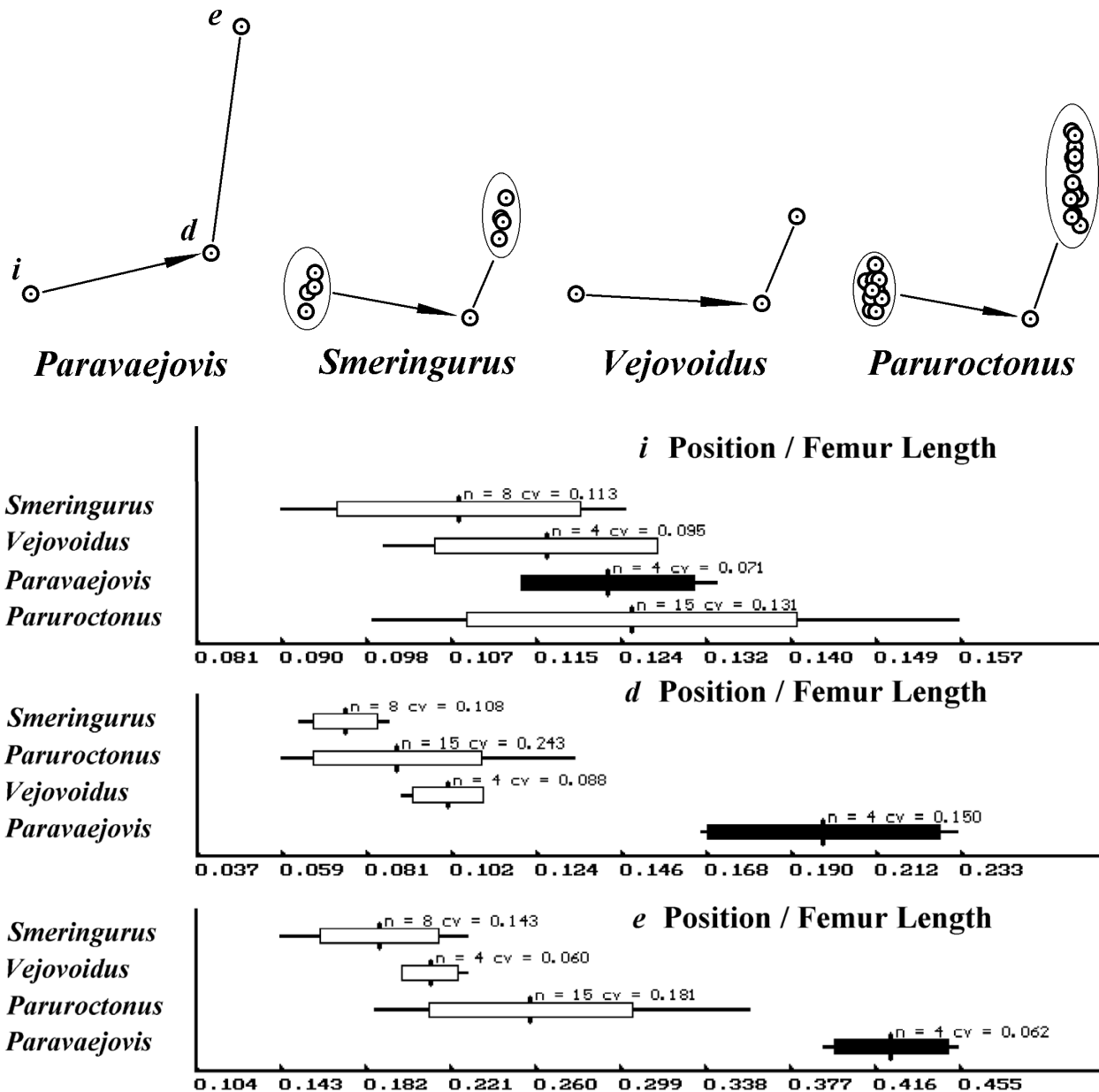
**Figure 16:** Trichobothrial pattern of *Franckeus peninsularis*, male, San Raymundo, Baja California Sur, Mexico (after Soleglad and Fet, 2005: figs. 10–16, in part). Solid circle shown in patella is an *accessory* trichobothrium depicting neobothriotaxy in the *esb* series.



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

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

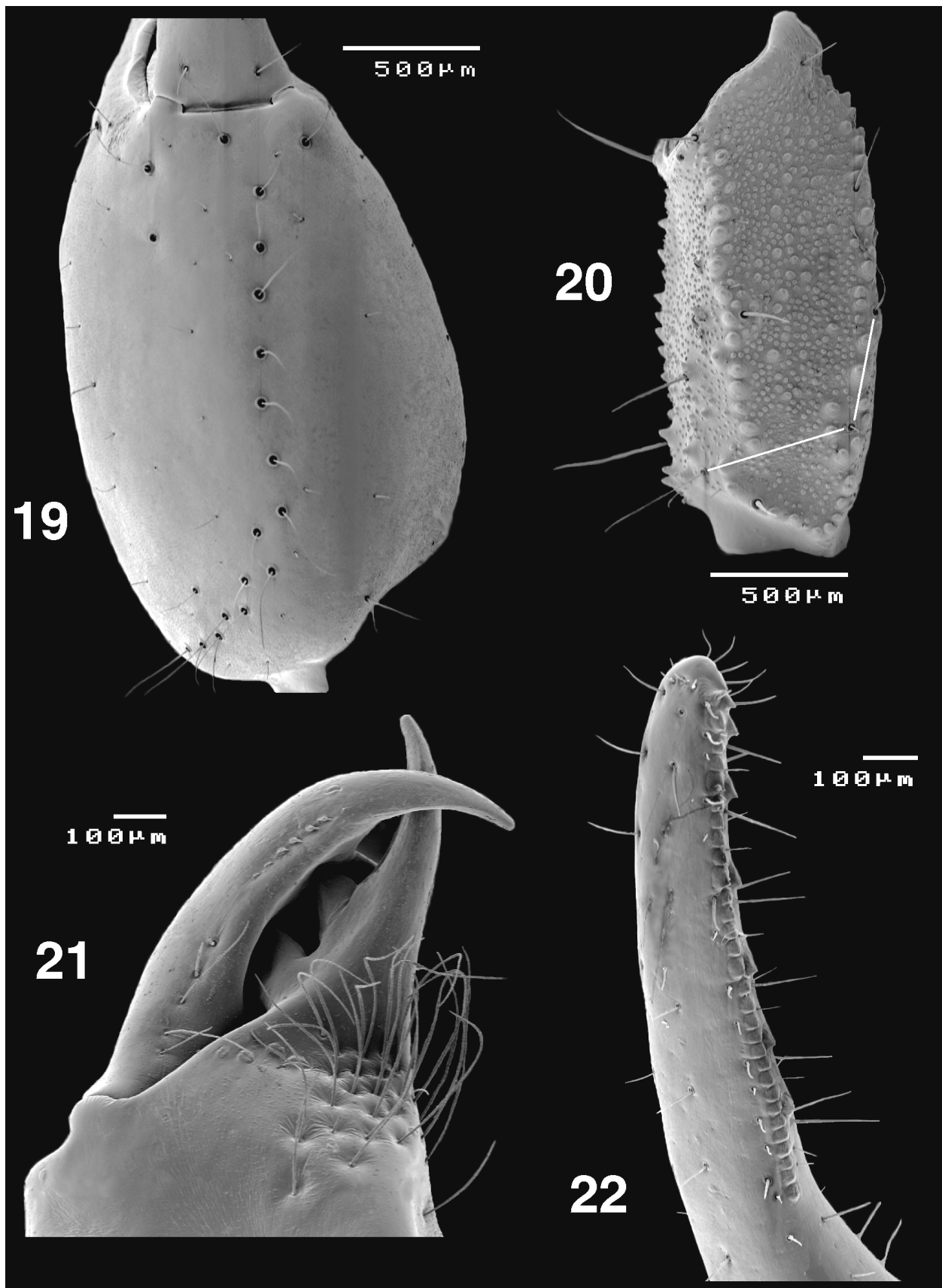
**Patellar trichobothria in genus *Thorellius*.** Hoffmann (1931: 377–388), in his discussion of species corresponding to our *Thorellius intrepidus*, *T. cristimanus*, and *T. atrox*, reports neobothriotaxy on the patella extern for the latter two species: 19 trichobothria for *T. cristimanus* and 20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



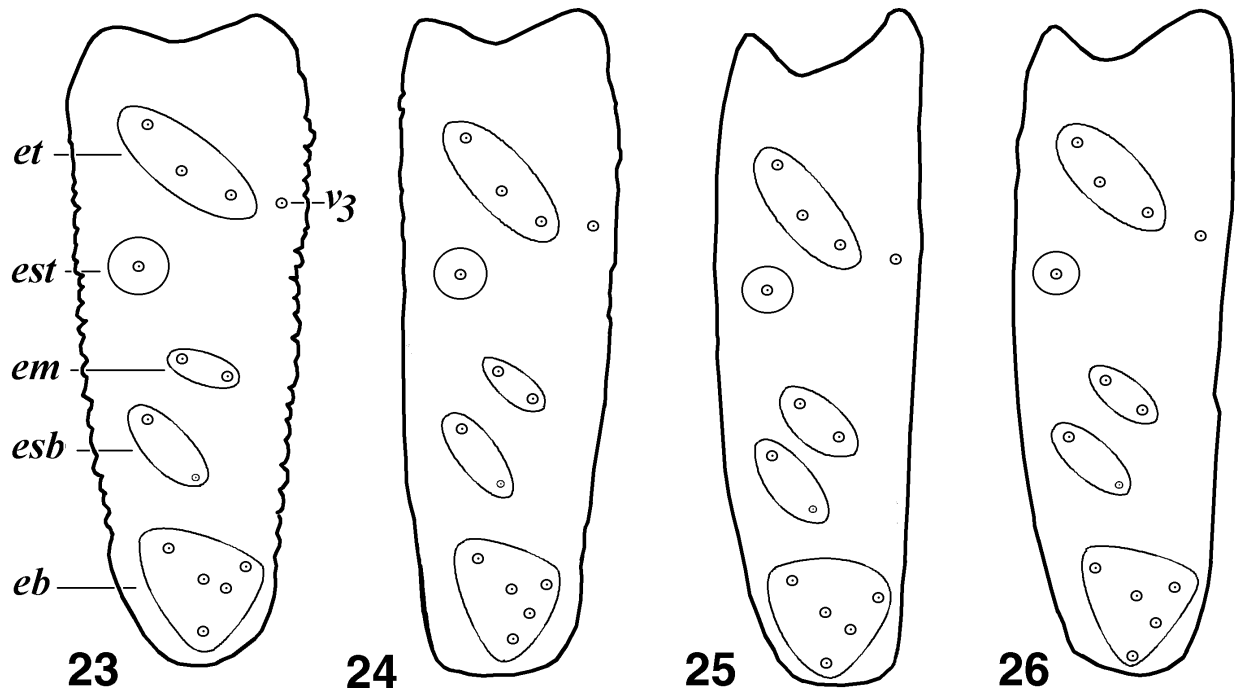
**Figure 18:** Pedipalp femur trichobothrial configurations for subfamily Smeringurinae. **Top figure** shows each configuration clustered, anchored at trichobothrium *d*, the other trichobothria clusters are plotted from this trichobothrium. All species of *Paravaejovis*, *Smeringurus*, and *Vejovoidus*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

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

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



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



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

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

### Genital Operculum

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

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

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

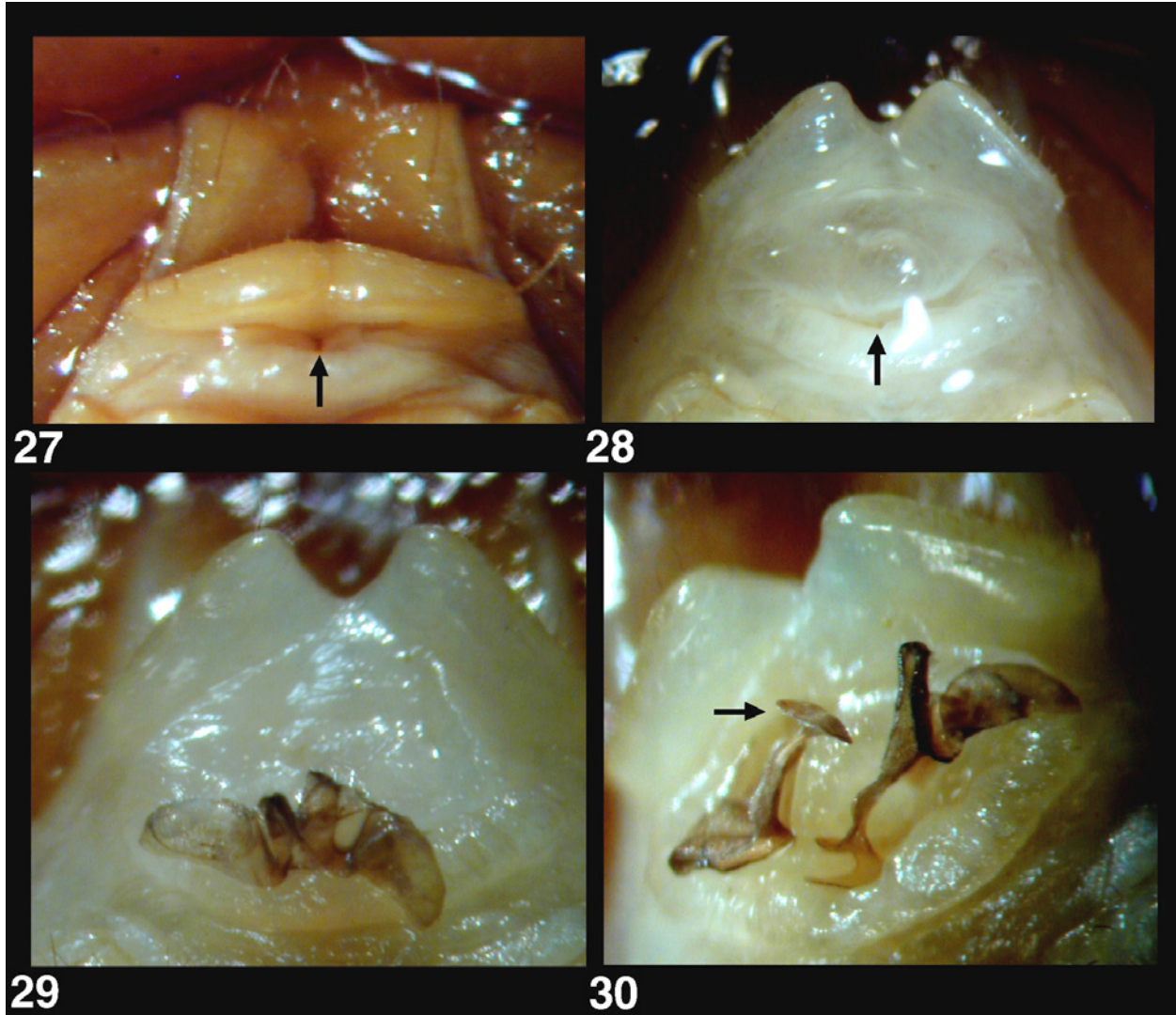
We have studied the female genital operculum in family Vaejoidea and can now classify this structure into two categories, one divided into two subcategories:

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

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

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





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

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

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

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

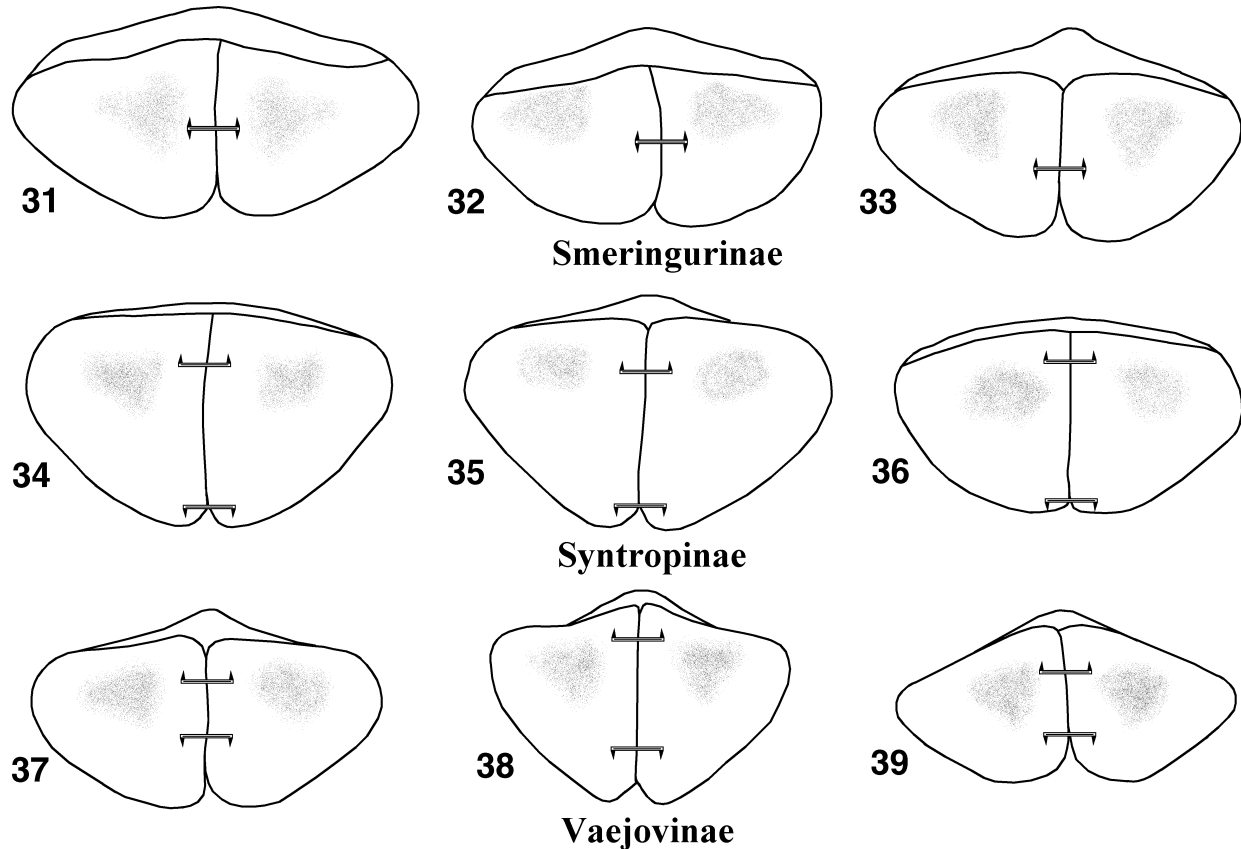
whereas the plates are connected more anteriorly in the other two subfamilies. The posterior separation in Smeringurinae is more substantial than in Vaejovinae, roughly twice the distance.

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

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

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





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

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

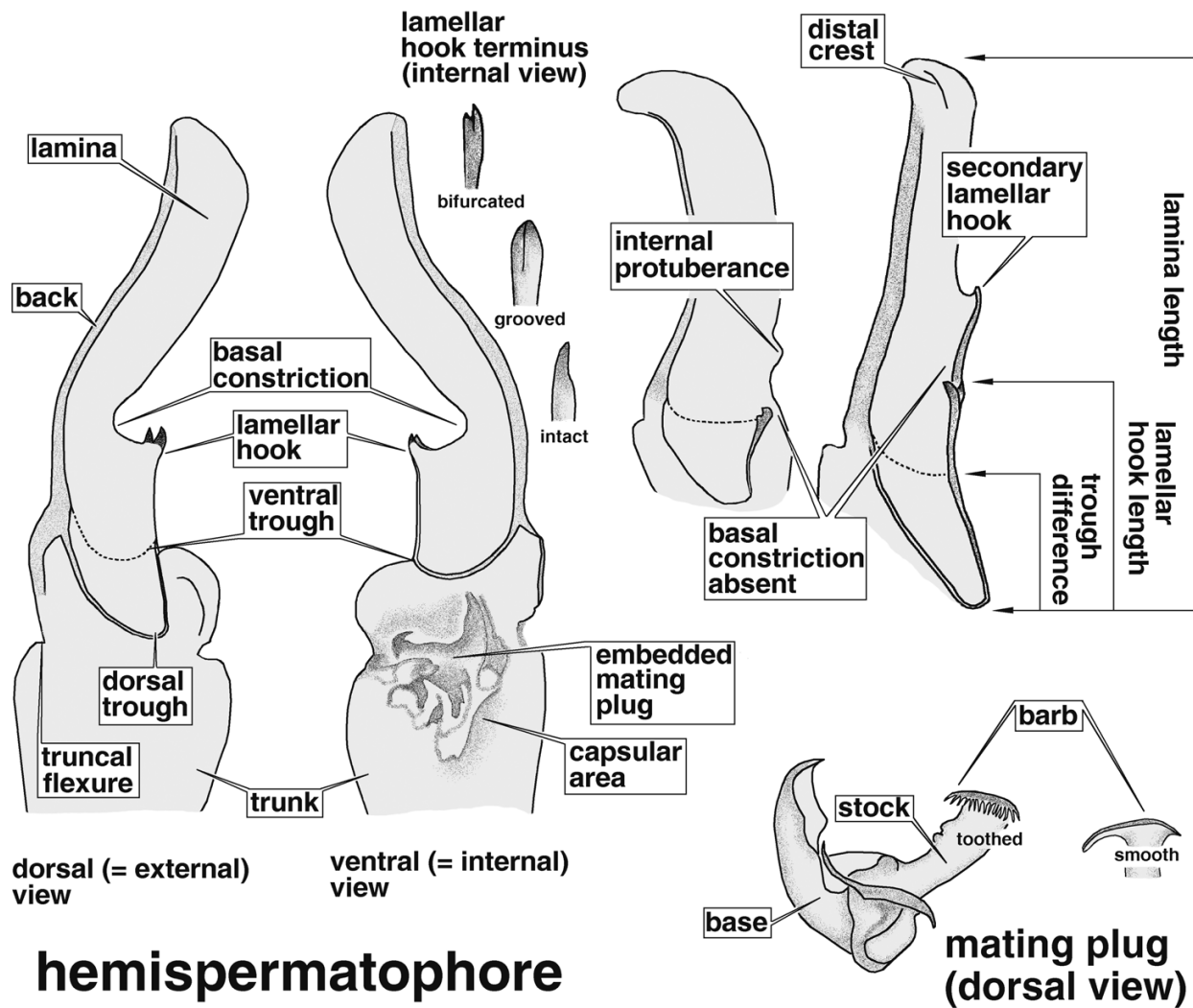
### *Hemispermatothore*

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

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

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

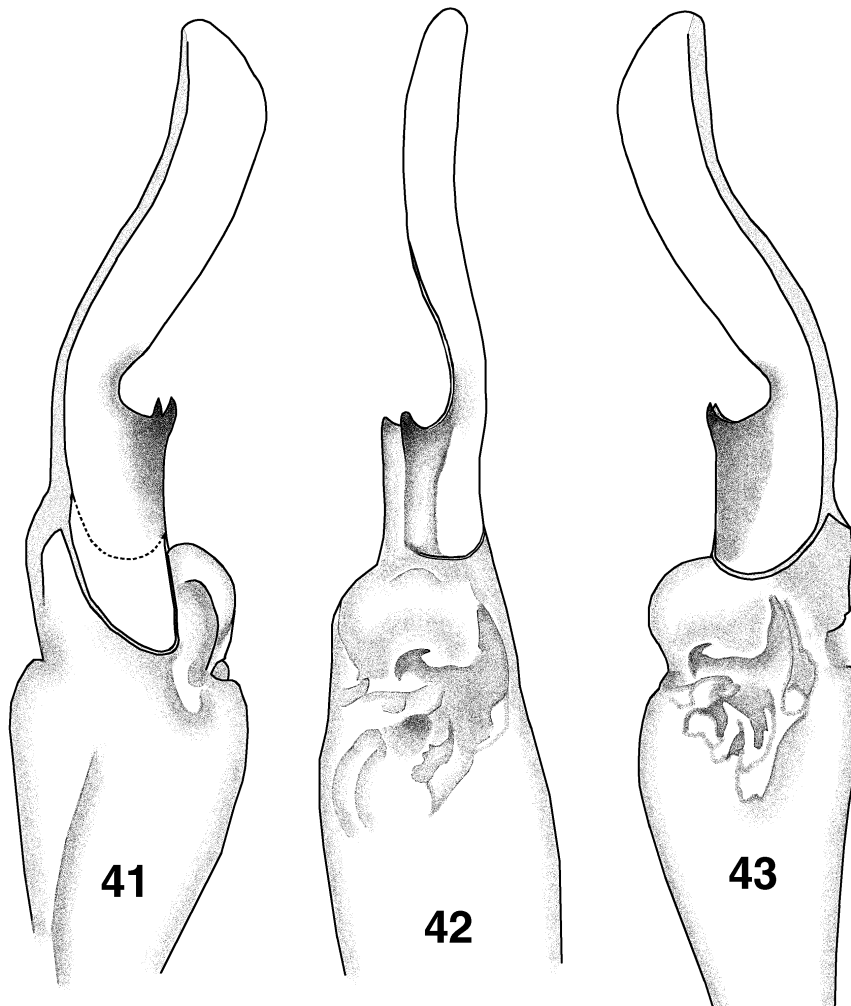
The first hemispermatothores illustrated for family Vaejovidae (lamelliform type) were by Francke & Soleglad (1981; note that all analysis and illustrations of this structure were provided by Francke), for *Paruroctonus utahensis*, *Vaejovis spinigerus*, and *Pseudouroctonus apacheanus*. Interestingly,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



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

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

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



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

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

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

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

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