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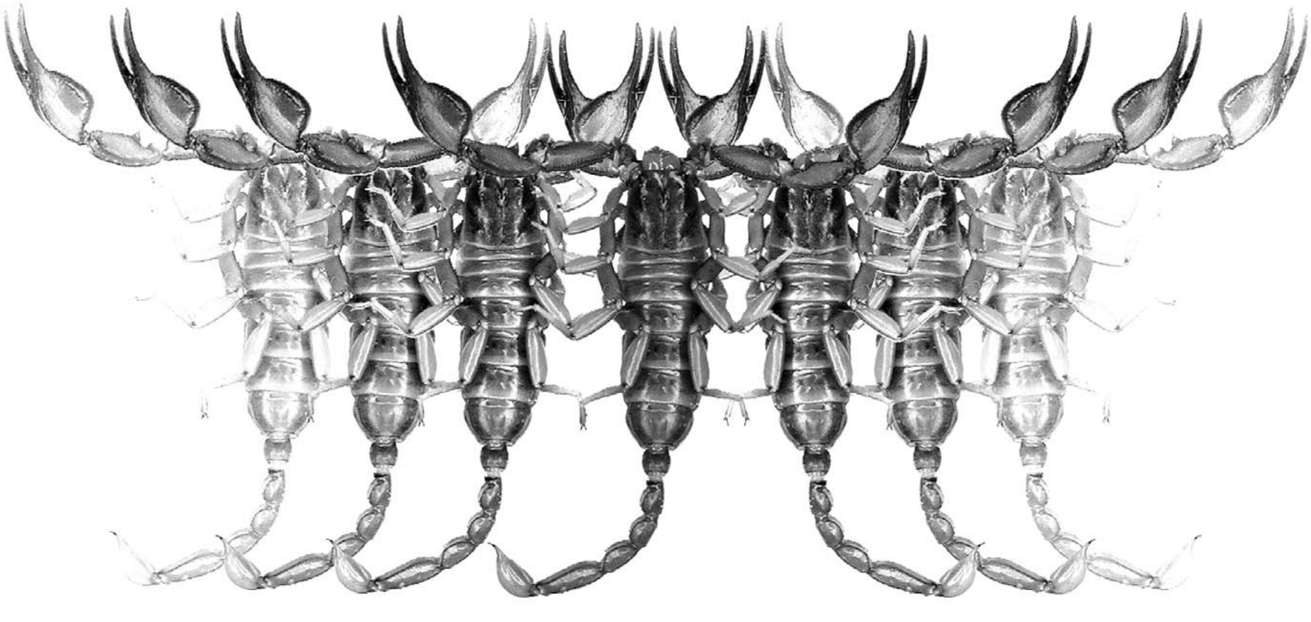

Graemeloweus, a New Scorpion Genus from Northern California, USA (Scorpiones: Vaejovidae)

Michael E. Soleglad, Victor Fet, Matthew R. Graham, and Richard F. Ayrey

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Graemeloweus, a new scorpion genus from northern California, USA (Scorpiones: Vaejovidae)

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Summary

Genus *Graemeloweus*, **gen. nov.** (Scorpiones: Vaejovidae) is described from northern California, USA. The genus is composed of three species formerly placed in *Pseudouroctonus*: *Graemeloweus iviei* (Gertsch et Soleglad, 1972), **comb. nov.** (type species), *G. glimmei* (Hjelle, 1972), **comb. nov.**, and *G. maidu* (Savary et Bryson, 2016), **comb. nov**. Major diagnostic characters of *Graemeloweus* include a non-bifurcated primary lamellar hook, the presence of a secondary lamellar hook, a complex mating plug with a two part base and an asymmetric crescent-shape barb, and the presence of a well-developed ventromedian (*V2*) carina on the pedipalp chela. Evidence is presented suggesting that *Graemeloweus* is more closely related to *Kovarikia* than *Pseudouroctonus*.

Introduction

Considerable new research on the relatively large vaejovid genus *Pseudouroctonus* has occurred in the last three years. Tate et al. (2013) named an unusual new species *P. peccatum* from Nevada, Bryson et al. (2013) presented a molecular-based study of several species currently placed in the genus *Pseudouroctonus*, Soleglad, Fet & Graham (2014) named the new genus *Kovarikia* from southern California, Ayrey & Soleglad (2015) named two new species from southern Arizona closely related to *Pseudouroctonus apacheanus*, *P. santarita* and *P. kremani*, and Savary & Bryson (2016) recently named new species *Graemeloweus maidu* from northern California (placed in *Pseudouroctonus* at the time).

Based, in part, on the results of the papers listed above combined with extensive analysis conducted by our research group, including preliminary cladistic analysis (in prep.), the overall phylogeny of this interesting group of scorpions is becoming clear. Soleglad, Fet & Graham (2014: 1) wrote: "… our ongoing revision of genera *Pseudouroctonus* and *Uroctonites*, which currently contain 22 species and probably *several additional, unrecognized genera*. …". In addition to the new genus defined in this paper, it appears that the "*apacheanus*" group, which currently includes species *P. apacheanus*, *P. santarita*, *P. kremani*, *P. rufulus*, *P. savvasi*, and *P. chicano* should probably be considered a unique genus. Similarly, species *P. minimus*, *P. thompsoni*, *P. castaneus*, and *P. andreas* also form a clade that appear to have diverged from the "*apacheanus*" group in the Palaeogene. These conclusions are also supported by a DNA-based study of Bryson et al. (2013: fig. 3). It is also clear that *Pseudouroctonus lindsayi* is only remotely related to the other species in *Pseudouroctonus* and represents another undescribed genus. Based on *P. lindsayi*'s hemispermatophore, it is more closely related to *Uroctonites*, and to some degree, the North American chactids. Species *P. peccatum* (found in Nevada, USA) and *P. cazieri* (found in central Baja California, Mexico) share a chelicerae very similar to that found in *P. reddelli* and *P. sprousei*. It remains to be determined if these two geographically isolated species are related to the troglophile species listed above. However, when this analysis is finally completed, the only legitimate species remaining in genus *Pseudouroctonus* may be its type species, *P. reddelli* and close relative *P. sprousei*!

Herein, we describe and illustrate major diagnostic characters for new genus *Graemeloweus*, including the hemispermatophore and mating plug structures, development of pedipalp chelal and patellae carinae, telson morphology, and other taxonomically relevant structures. Comparisons are made between genera *Graemeloweus* and *Kovarikia*, suggesting that they are taxonomic sister genera. A key to the three species, discussion on biogeographical considerations, and a map showing their known distribution is provided. Three Appendices provide additional information and illustrations of *Graemeloweus* hemispermatophores, hemispermatophores of other relevant genera, and complete trichobothrial patterns for the three species of *Graemeloweus*.

Methods and Material

Abbreviations

List of depositories: MES, Personal collection of Michael E. Soleglad, Winchester, California, USA; MRG, Personal collection of Matthew R. Graham, Willimantic, Connecticut, USA; RA, Personal collection of Richard F. Ayrey, Flagstaff, Arizona, USA.

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

Terminology and conventions

The systematics adhered to in this paper follows the classification as established in Fet & Soleglad (2005) and as modified by Soleglad & Fet (2008). Terminology describing trichobothria follows that described in Vachon (1974); pedipalp chelal finger dentition follows that described and illustrated in Soleglad & Sissom (2001); that of the sternum follows Soleglad & Fet (2003a); cheliceral dentition, the metasomal and pedipalp carination, and leg tarsus armature follows Soleglad & Fet (2003b); and the hemispermatophore terminology follows Soleglad & Fet (2008), Soleglad, Fet & Graham (2014), and Ayrey & Soleglad (2015).

Map generation software package

Maps were generated by Earth Explorer 6.1, with positional and altitude data compiled through Google Maps.

Material Examined

***Graemeloweus glimmei* (Hjelle, 1972):** *USA, California*: Lake Co., Cache Creek, 27 April 2016, 1 ♂, 2 ♀, leg. R.F. Ayrey (RA).

***Graemeloweus iviei* (Gertsch et Soleglad, 1972):** *USA, California*: Trinity Co., 2 mi. E. Del Loma, Little French Creek, 6 April 1960, 1 ♂, 1 ♀, leg. W.J. Gertsch, W. Ivie, R. Schrammel (MES); El Dorado Co., American River, 28 April 2016, 2 ♂, 2 ♀, leg. R.F. Ayrey (RA).

***Graemeloweus maidu* (Savary et Bryson, 2016):** *USA, California*: El Dorado Co., American River, 28 April 2016, 1 ♀, leg. R.F. Ayrey (RA).

***Kovarikia bogerti* (Gertsch et Soleglad, 1972):** *USA, California*: San Diego Co., Palomar Mountain Road, June 2013, 1 ♂, leg. M.R. Graham (MRG).

***Kovarikia williamsi* (Gertsch et Soleglad, 1972):** *USA, California*: San Diego Co., Santa Ysabel Preserve, 1 ♂, leg. USGS pitfall trap (MES).

***Pseudouroctonus andreas* (Gertsch et Soleglad, 1972):** *USA, California*: San Diego Co., Chariot Canyon, ABDSP, 30 August 1997, 1 ♂, leg. M.E. Soleglad (MES).

***Pseudouroctonus apacheanus* (Gertsch et Soleglad, 1972):** *USA, Arizona*: Cochise Co., Rucker Canyon, Chiricahua Mountains, 5 September 2008, 1 ♂, leg. R.F. Ayrey (RA).

***Pseudouroctonus castaneus* (Gertsch et Soleglad, 1972):** *USA, California*: San Diego Co., Vista, 1 ♂, (MES).

***Pseudouroctonus kremani* Ayrey et Soleglad, 2015:** *USA, Arizona*: Pima Co., Molino Basin, Santa Catalina Mountains, 19 August 2012, 1 ♂, leg. R.F. Ayrey (RA).

***Pseudouroctonus peccatum* Tate, Riddle, Soleglad & Graham, 2013:** *USA, Nevada*: Clark Co., Kyle Canyon, Spring Mountains, 22 September 2014, 1 ♀, leg. R.F. Ayrey (RA), 12 September 2015, 1 ♂, leg. R.F. Ayrey (RA).

***Pseudouroctonus reddelli* (Gertsch et Soleglad, 1972):** *USA*, *Texas*: Comal Co., Little Gem Cave, 21 May 1965, 1 ♂, leg. T. Barr & J. Reddell (MES).

***Pseudouroctonus thompsoni* (Gertsch et Soleglad, 1972):** *USA, California*: Santa Barbara Co., Santa Cruz Island, 1 ♂, leg. M.R. Graham (MRG).

***Uroctonites huachuca* (Gertsch et Soleglad, 1972):** *USA, Arizona*: Cochise Co., Miller's Canyon, Huachuca Mountains, 22–24 July 1958, 1 ♂, leg. M.E. Soleglad & D.S. Douglass (MES).

***Vaejovis carolinianus* (Beauvois, 1805):** *USA*, *Georgia*: Clarke Co., Athens, 1 ♂ (MES).

***Vaejovis jannsi* Williams, 1980:** *MEXICO*, *Baja California Sur*: Isla Socorro, 1 ♂ (MES).

***Franckeus peninsularis* (Williams, 1980):** *MEXICO*, *Baja California Sur*: San Raymundo, 1 ♂ (MES).

***Anuroctonus pococki pococki* Soleglad et Fet, 2004:** *USA, California*: San Diego Co., Santee, 1 ♂, leg. M.E. Soleglad (MES).

***Nullibrotheas alleni* (Wood, 1863):** *MEXICO*, *Baja California Sur*: Los Planes, 20 Dec 1958, 1 ♂, leg. A. Leviton (MES).

***Uroctonus mordax* Thorell, 1876:** *USA, California*: Humboldt Co., Weott, 1 ♂ (MES).

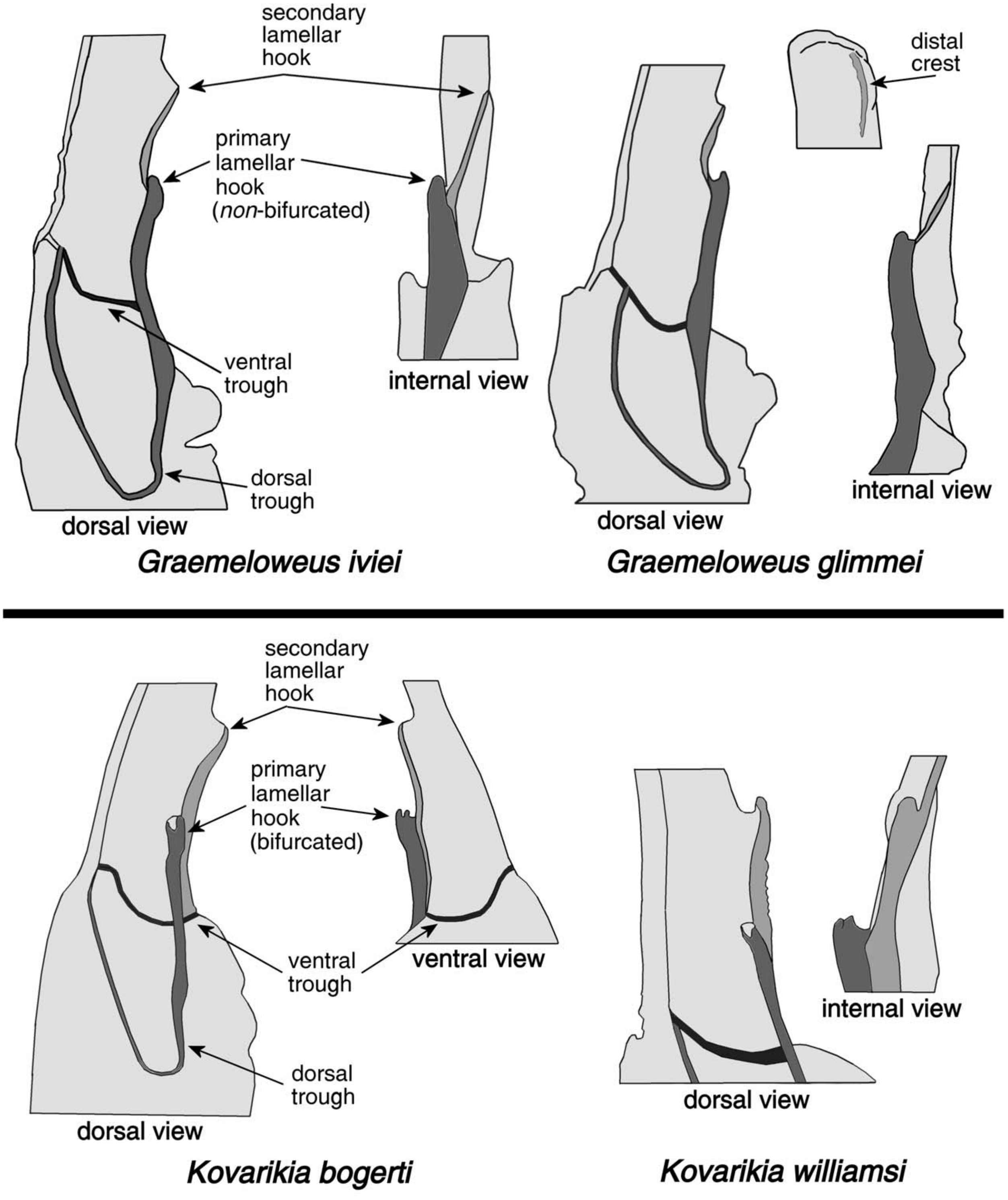


Figure 1: Diagrammatic illustrations comparing the hemispermatophore median area of genera *Graemeloweus* and *Kovarikia*. Of particular note, both genera have a well developed secondary lamellar hook, but different between the two, the primary lamellar hook in *Graemeloweus* is *not* bifurcated as it is in *Kovarikia*. *Graemeloweus* also has a distal crest on the dorsointernal aspect of the lamina termius, shown in this Figure for *G. glimmei*. *Kovarikia* lacks this crest. Note, due to the translucency of the hemispermatophore, the ventral trough is visible from the dorsal side.

Structure Analysis

Important diagnostic structures discussed in this section are the hemispermatophore and mating plug. In particular, the morphology of these structures supports the conclusion that new genus *Graemeloweus* is closely related to *Kovarikia*. The carinal structure of the pedipalp chela and the patella, in part, are compared to other related genera such as *Pseudouroctonus*, *Kovarikia*, and *Uroctonites*, as well as to the North American chactid genera. Other structures germane to *Graemeloweus*'s definition are also discussed, such as the carapace, chelicerae, telson, pectines, and the leg tarsus spination.

Hemispermatophore and mating plug

One of the most important structures in the distinction of *Graemeloweus* is the hemispermatophore and its mating plug. These structures were very important in the description of genus *Kovarikia* recently published by Soleglad, Fet & Graham (2014), shown in this paper to be related to *Graemeloweus*. This structure is becoming extremely important in the high-level analysis of scorpion systematics. For example, the hemispermatophore was a major structure in distinguishing genera of family Iuridae; see Soleglad et al. (2012: figs. 2–3) and Yagmur et al. (2013: figs. 1–7).

Published mating plug descriptions in Vaejovidae, in most cases, are limited to "barb toothed" or "barb smooth". In many other cases the mating plug is not even reported, probably due to the difficulty in properly cleansing the hemispermatophore. It is becoming clear now that the mating plug is a complex structure that needs to be studied more extensively. This requires proper cleansing in order to uncover the minute substructures of the plug. Soleglad, Fet & Graham (2014: 5–6; figs. 2–3, A-4) described/illustrated a complicated mating plug for genus *Kovarikia* (i.e., they illustrated the mating plugs for two species). Recently Ayrey & Soleglad (2015: 5–7, 27; figs. 2, 35) provided new information for the relatively simple mating plug found in the "*apacheanus*" group of *Pseudouroctonus*, where the mating plugs of three species were described and illustrated.

The following analyses of the hemispermatophore and its mating plug are augmented with numerous illustrations in Appendices A and B. This includes detailed hemispematophore and mating plug illustrations of species *Graemeloweus glimmei* and *G. iviei*, hemispermatophore illustrations of representative groups of *Pseudouroctonus*, genera *Kovarikia*, *Uroctonites*, *Anuroctonus*, and several illustrations of the lamellar hook from literature on various *Vaejovis* species groups, in particular, the Arizona "sky island" species of *Vaejovis*.

Lamellar hook development. In Figure 1 we present diagrammatic illustrations of the hemispermatophore median area of genera *Graemeloweus* and *Kovarikia* showing their lamellar hook configurations. In particular, two lamellar hooks are present, unique to these genera: the *primary lamellar hook* (PLH) found throughout the Vaejovidae, and an unique *secondary lamellar hook* (SLH) found exclusively in these two genera. The PLH is an extension of the dorsal trough which forms a concaved area at the base of the lamina. The SLH, which is situated distal to the PLH on the lamina internal edge, is an extension of the ventral trough, which forms a concaved area on the ventral surface. Though its terminus is rounded, the majority of the SLH extends along the PLH before it terminates into the ventral trough.

As stated above, the terminus of the SLH is rounded in these two genera, i.e., it is not bifurcated, as shown in Fig. 1. However, for the PLH the two genera *differ* in this substructure: the terminus of the PLH is bifurcated in *Kovarikia*, as it is in most reported vaejovine species (see exceptions below), but in *Graemeloweus*, the PLH terminus is not bifurcated, instead terminating into a single rounded point on its internal edge, which is unique within a large portion of Vaejovinae. This is a *major diagnostic character* for this new genus.

In Appendix A, Fig. A-1 shows photographs of the dorsal, dorsointernal, internal, and ventral views of the two lamellar hooks for species *G. iviei* and *G. glimmei*, definitely establishing that the PLH is not bifurcated. Appendix A, Figs. A-2 and A-3, show photographs of the hemispermatophore and mating plugs for species *Graemeloweus iviei* and *G. glimmei*. In Appendix B, Figure B-1, the hemispermatophore median area of the genus *Kovarikia* and several "groups" of *Pseudouroctonus* are shown, again emphasizing the bifurcated terminus of the primary lamellar hook. In Figure B-2, 23 species of vaejovine species (i.e., *Vaejovis* and *Franckeus*) are illustrated showing the bifurcated PLH. In particular, eight "sky island" *Vaejovis* species, found primarily in Arizona, are illustrated. This species group of *Vaejovis* is the closest geographically to new genus *Graemeloweus*.

It must be pointed out here, that the hemispermatophores of genus *Uroctonites* and *Pseudouroctonus lindsayi* (see Williams & Savary, 1991, fig. 21) are quite similar and distinct, both have lamellar hooks positioned basally that are not bifurcated, similar to that found in chactid genera *Uroctonus* (Soleglad & Fet, 2004: fig. 26) and *Anuroctonus*. See Appendix B, Fig. B-3, for the illustrations of *Uroctonites huachua* and *Anuroctonus pococki* hemispermatophores.

Distal crest. A distal crest is often found on the dorsointernal edge of the lamina terminus in species of subfamily Vaejovinae, including some *Pseudouroctonus* (see Ayrey & Soleglad, 2015: figs. 14, 34). Typically this small crest is quite weak and is only detectable if the hemispermatophore is thoroughly cleansed. A modest

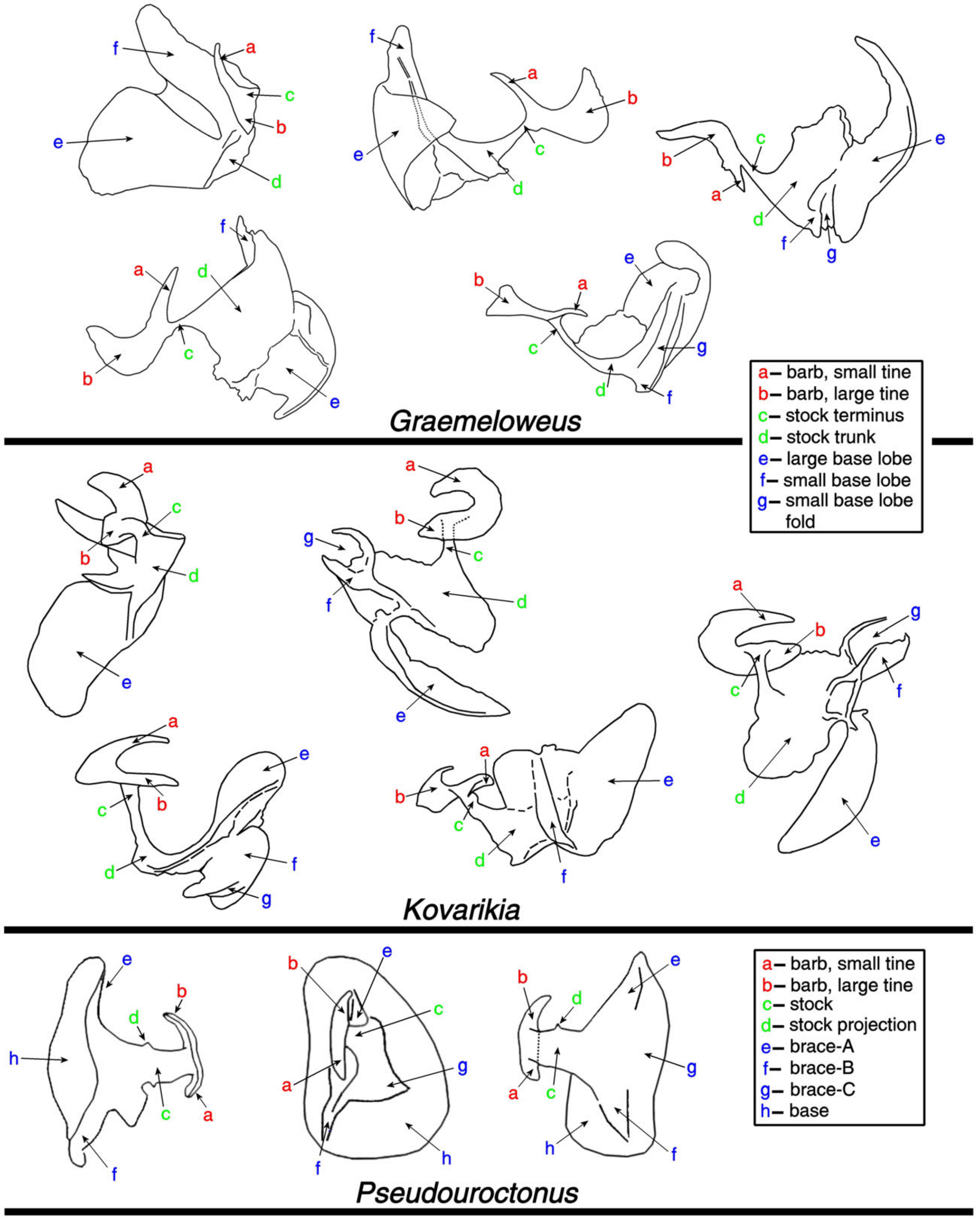


Figure 2: Diagrammatic illustrations comparing the hemispermatophore mating plug of genera *Graemeloweus*, *Kovarikia*, and *Pseudouroctonus* (i.e., the "*apacheanus*" group). It is clear from these illustrations that the mating plug structure of genera *Graemeloweus* and *Kovarikia* is essentially the same, considerably different from the relatively simple mating plug found in the *Pseudouroctonus* "*apacheanus*" group. Illustratiions based on *Graemeloweus glimmei*, *Kovarikia bogerti*, and *Pseudouroctonus kremani* (after, in part, Ayrey & Soleglad (2015: fig. 35)).

distal crest is present in genus *Graemeloweus*, depicted for two species in this paper, *G. iviei* (Fig. A-3) and *G. glimmei* (Fig. A-2).

Ayrey & Soleglad (2015: 7) provided a list of vaejovine species that have been reported with a distal crest. Since that paper, Sissom et al. (2016: figs. 16, 21) also reported and illustrated a somewhat large and well defined distal crest for two new species from Mexico, *Vaejovis sierrae* and *V. mcwesti*.

Mating plug. The mating plug of *Graemeloweus* (see Fig. 2 and Appendix A, A-2) has a complex structure, very similar to that found in genus *Kovarikia* (see Soleglad, Fet & Graham (2014: 2, A-4)). In Fig. 2 we show several diagrammatic views of the mating plug for these two genera, identifying key substructures they have in common. The base is composed of two "petal-shaped" components (labeled "e" and "f") that are roughly perpendicular to the complex stock of the mating plug. These two base substructures are not the same size, the larger base component ("e") is convex on the side furthest from the barb, and its other side is highly concaved. The smaller base component ("f") is folded with the open edge (labeled "g") pointing outward. Both base components are connected to a large vertical stock trunk (labeled "d") that tapers considerably into a small narrow stock terminus (labeled "c"). The stock terminus ("c") connects to the base of the barb (labeled "a" and "b"). The external extremities of the barb are unequal in size, together forming a rough crescent-shaped barb. There are no "teeth" on the barb, so therefore it can be classified as "smooth".

Both *Graemeloweus* and *Kovarikia* possess all the substructures described above. However, there are differences between the two: though the external extremities of the barbs are unequal in size, it is much more exaggerated in *Graemeloweus*, the small extremity ("a") is quite narrow and pointed, not curved that much. The larger extremity ("b") is much wider and highly flared (i.e., shaped like a khukuri-blade), contributing the most to the barb's crescent-like shape. In *Kovarikia*, the size difference between the two barb extremities is minor, and both extremities are shaped the same, highly curved, both contributing to the barb's crescent-like shape. In *Graemeloweus*, the stock terminus ("c") is shorter than it is in *Kovarikia*.

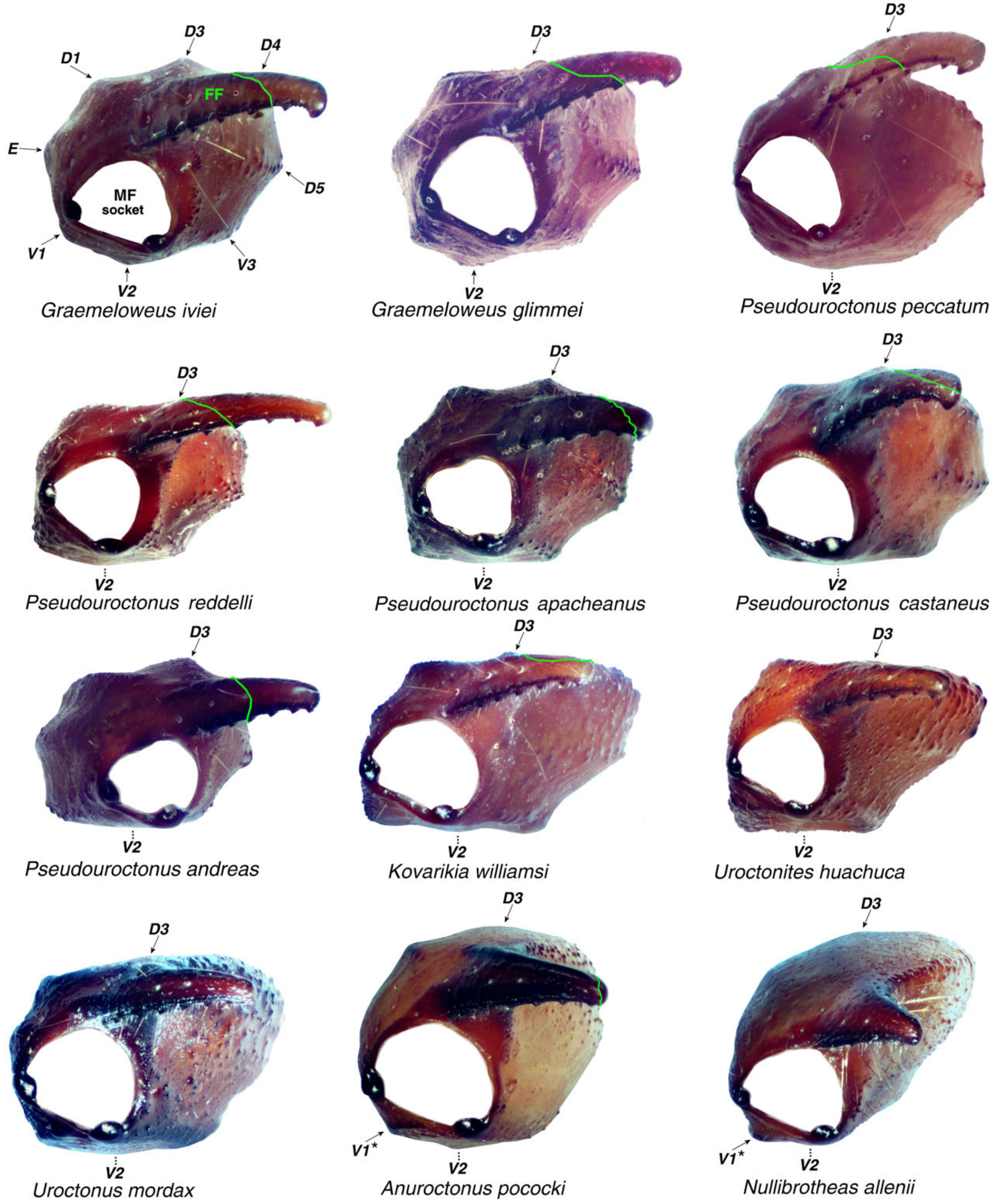
Also in Fig. 2, we show diagrammatic illustrations of the mating plug of *Pseudouroctonus kremani*. Clearly this mating plug is considerably simpler than that found in genera *Graemeloweus* and *Kovarikia*. The base (labeled "h") is a somewhat flat substructure shaped like an irregular rounded triangle. Its internal surface is slightly convexed and its external surface slightly concaved. Connected to the base is the stock (labeled "c") an irregular shaped substructure that tapers slightly as it extends towards the barb. The stock's connection to the base is reinforced by three low-profile braces (labeled "e", "f", and "g"). The stock/barb connection is much wider, more substantial, than that seen in *Graemeloweus* and *Kovarikia*, which is quite narrow and delicate. The two barb extremities (labeled "a" and "b") are similar in length and show very little curvature.

Note, we verified the mating plug structure of *Graemeloweus glimmei* from both left and right mating plugs. For *G. iviei*, only one mating plug was retrievable with most of its base missing, only its barb being discernable. Savary & Bryson (2016: 58) reported a mating plug for *G. maidu*, but no description or illustrations were provided.

***Vaejovis* "*mexicanus*" group.** Ayrey & Soleglad (2011: p. 1–2) briefly discussed the taxonomic history of the "*mexicanus*" group of *Vaejovis* suggesting: "…the "*mexicanus*" group is a much smaller assemblage …. the true scope of this group, which must be formed around *Vaejovis*'s type species, *V. mexicanus* C.L. Koch, 1836 …". Stockwell's (1989: 147–153; tab. 6; fig. 257) cladistic analysis based on 138 two-state characters hypothesized a gelatinous mating plug (i.e., char-117) as plesiomorphic for family Vaejovidae, only genus *Vaejovis* complied to this state (i.e., Stockwell had broken out other "*Vaejovis*" groups at that time into separate genera). He hypothesized the sclerotized mating plug is derived for the remaining vaejovid genera. He also hypothesized the gelatinous mating plug to be a secondary derivation (i.e., char-118) for *Uroctonites* and *Uroctonus* (note, *Uroctonus* at that time was placed in family Vaejovidae). Based, in part, on Stockwell's analysis, we suggest that species now placed in the "*mexicanus*" group of *Vaejovis* may not have a sclerotized mating plug. This conclusion is based on Stockwell (1989) as well as several recent species descriptions from Mexico where sclerotized mating plugs are not reported: *Vaejovis morelia* (López et al., 2012: fig. 14), *Vaejovis tenamaztlei* (Félix et al., 2015: figs. 12–14), *Vaejovis setosus*, *V. franckei*, *V. prendinii*, *V. zapoteca*, *V. dzahui*, and *V. darwini* (López & Francke, 2010: figs. 50–55). In these references, the authors, in most cases, specifically state that a sclerotized mating plug is not present. It should also be pointed out that hemispermatophores illustrated by these authors appear to have weak non-bifurcated primary lamellar hooks. However, the quality of these illustrations/photos is too poor to ascertain the true structure of the hooks. In either case, they do appear to be distinctly different from the hemispermatophores illustrated in this paper.

Pedipalp carinal development

Chela. Ayrey & Soleglad (2015: p. 5; fig. 2) discussed in detail the importance of the chelal carinal configuration in the definition of the genus *Pseudouroctonus*: "… the overall shape of the chelal palm is an important diagnostic character at the genus level and



Graemeloweus iviei
Graemeloweus glimmei
Pseudouroctonus peccatum
Pseudouroctonus reddelli
Pseudouroctonus apacheanus
Pseudouroctonus castaneus
Pseudouroctonus andreas
Kovarikia williamsi
Uroctonites huachuca
Uroctonus mordax
Anuroctonus pococki
Nullibrotheas allenii

Figure 3: Distal perspective of the right pedipalp chela showing the carinal configuration of two species of *Graemeloweus* in comparison to select species of *Pseudouroctonus*, *Kovarikia*, *Uroctonites*, and three North American chactids. Of particular importance is the well developed ventromedian carina (*V2*) exhibited by *Graemeloweus* in comparison to its essential absence in the other genera. Also of importance, we see the flattening of the dorsosecondary (*D3*) carina in some of the other genera, combined with the absence of *V2*, making the two planes *D1*|*D3*|*D4* and *V1*|*V2*|*V3* essentially parallel. Note, *green lines* indicate the *D3* or *D4* carina which are blocked or partially blocked from view by the fixed finger terminus. MF = movable finger, FF = fixed finger, *D1* = digital carina, *D3* = dorsosecondary carina, *D4* = dorsomarginal carina, *D5* = dorsointernal carina, *V1* = ventroexternal carina, *V2* = ventromedian carina, *V3* = ventrointernal carina, and *E* = exterosecondary carina. Note, the subdigital carina (*D2*), which is vestigial in most species, is not shown. * The distal aspect of the *V1* carina curves significantly towards the internal condyle.

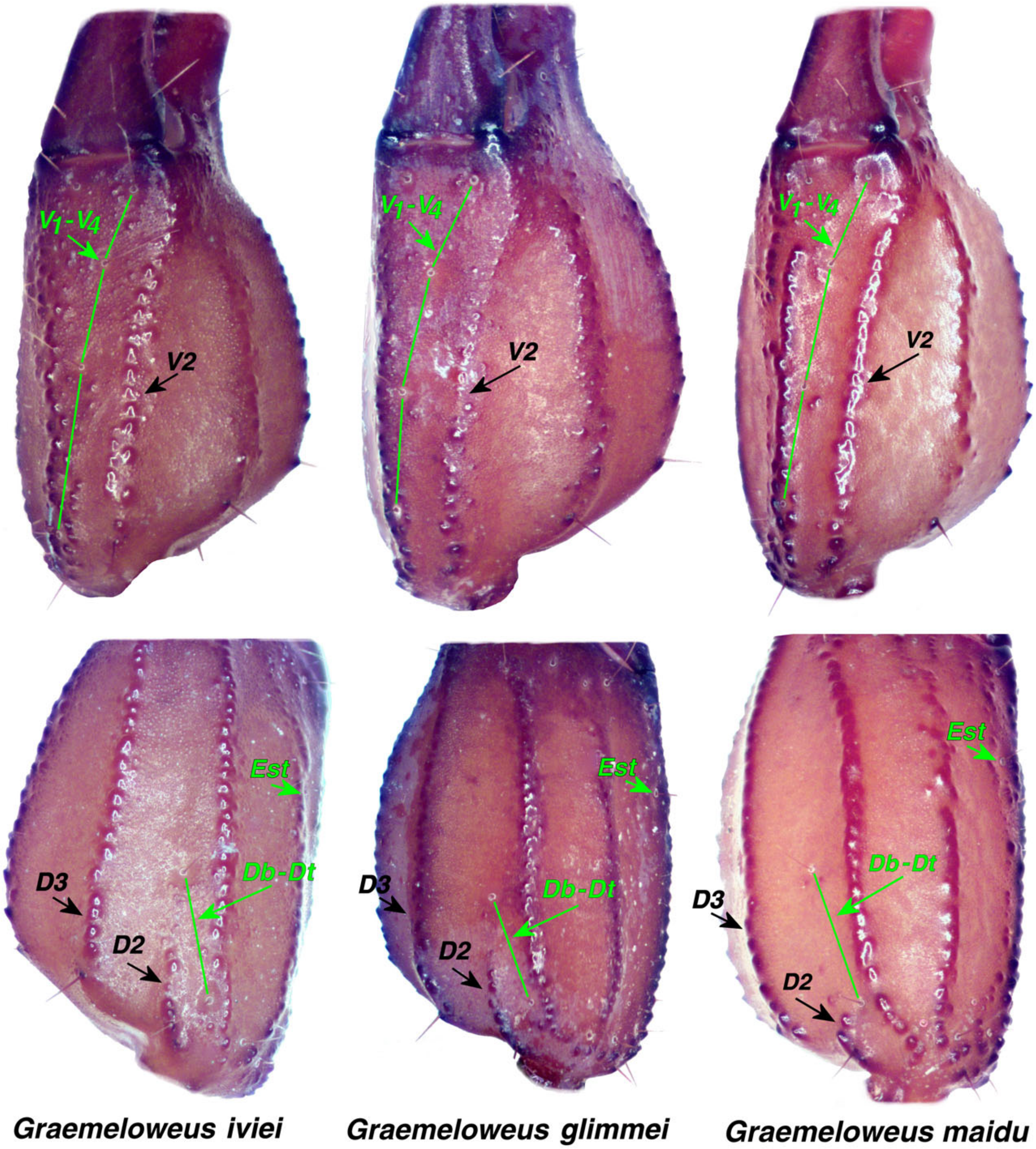
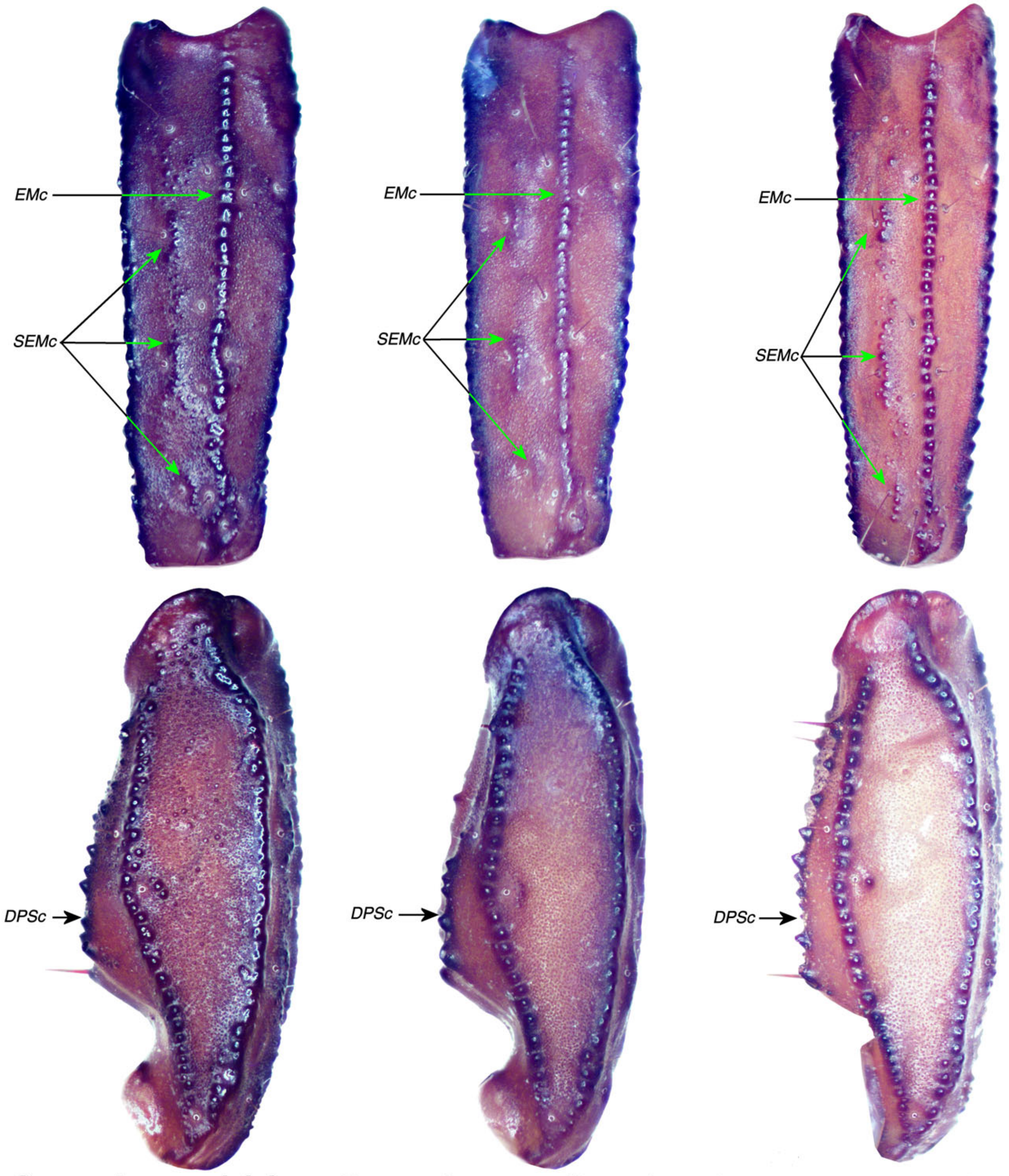


Figure 4: Right chela showing diagnostic carinae of genus *Graemeloweus*. **Left.** *Graemeloweus iviei*, male, American River, El Dorado Co., California. **Center.** *G. glimmei* (left chela reversed), female, Cache Creek, Lake Co., California. **Right.** *G. maidu* (left chela reversed), female, American River, El Dorado Co., California. Top images show a strong, well developed ventromedian (*V2*) carinae terminating at the internal condyle of the movable finger, and the bottom images show a relatively well developed subdigital (*D2*) carina with 4–7 granules. Carinae are indicated with *black arrows* and relevant trichobothrial series, V_1–V_4, *Db–Dt*, and *Est* are indicated with *green arrows*. Also see Figure 3 for another perspective of the *V2* carina.

higher. The shape is dictated by the alignment and relative development of its carinae …". In genera *Kovarikia*, *Pseudouroctonus*, and *Uroctonites* the somewhat low-profile development of the dorsosecondary (*D3*) carina combined with the absence of the ventromedian (*V2*) carina forces the overall shape of the palm to have a somewhat flat appearance when viewed from the fingers.



Graemeloweus iviei **Graemeloweus glimmei** **Graemeloweus maidu**

Figure 5: Patella of right pedipalp of *Graemeloweus* species, external (above) and dorsal (bottom) views. External view shows the external median (*EMc*) carina and a partially developed *secondary* median carina (*SEMc*) (as indicated with *arrows*). Note, the *SEMc* carina is disjoint, occurring in three separate areas on the patella, internal to trichobothria *est*, esb_1, and eb_2; also, trichobothria et_2, em_1, esb_2, and eb_3 are located between the two external carinae. Finally, note in all three species, trichobothrium eb_4 is located within a carinal depression originating from the *EMc* carina. Dorsal view shows the profile of the dorsal patellar spur carina (*DPSc*), comparing its relative development between the three species. **Left.** *Graemeloweus iviei*, female, American River, El Dorado Co., California, USA. **Center.** *Graemeloweus glimmei*, female, Cache Creek, Lake Co., California, USA. **Right.** *Graemeloweus maidu*, female, American River, El Dorado Co., California, USA.

Ayrey and Soleglad (2015: 5) also pointed out the differences found in species *Graemeloweus iviei* and *G. glimmei* with respect to this character: "… the clade *P. glimmei* + *P. iviei* does not comply to this organization of parallel planes, the chelal shape more typical of other vaejovids, carinae *D3* and *V2* well developed …". Hjelle (1972: 10, figs. 31–32) also indicated the chela ventral carination when contrasting *G. glimmei* with *Uroctonus mordax*. This distinction is quite important in the definition of new genus *Graemeloweus*. Figure 3 shows a wide sampling of relevant genera with a reduced to obsolete ventromedian (*V2*): major groups within *Pseudouroctonus*, *Kovarikia*, *Uroctonites*, and the three North American chactids, *Uroctonus*, *Anuroctonus*, and *Nullibrotheas*. This figure also shows the chelal diagram of *Graemeloweus iviei* and *G. glimmei* where it is clear that carina *V2* is well developed, in strong contrast to the other genera. Figure 4 shows two different perspectives of the chelal carinal structure for all three species of *Graemeloweus*. Not only is carina *V2* well developed, it is conspicuously granulated. The dorsosecondary (*D3*) carina is not low-profile as in *Pseudouroctonus reddelli* and genera *Kovarikia* and *Uroctonites* (see Fig 3) but instead well defined and granulate. Finally, the vestigial sub-digital carina (*D2*) is more developed in genus *Graemeloweus* comprised of four to eight granules.

Patella. Soleglad, Fet & Graham (2014: 6: fig. 4) described a well developed secondary exteromedian (*EMc*) carina on the patella of genus *Kovarikia.* These authors state further for *Kovarikia*: "…Though this carina is as strongly granulated and continuous as the primary carina, it is not as well developed, not extending the entire length of the segment. Distally it begins approximately at the et_2 trichobothrium and terminates basally at eb_3 …". Also, the primary *EMc* carina in *Kovarikia* is considerably well developed and granulated its entire length.

In genus *Graemeloweus* the primary *EMc* carina is also well developed and granulated (see Fig. 5 for all three species). However, the secondary *EMc* carina is not as well developed as in *Kovarikia* but instead curiously is segregated into three disjoint sections: each section located internal to trichobothria *est*, esb_1, and eb_2, respectively.

Savary & Bryson (2016: figs. 13–16) compared the relative development of the dorsal patellar spur (*DPSc*) carina (referred to by these authors as the "internomedial carina") of species *Graemeloweus glimmei* and *G. maidu.* This was offerred as a species level diagnostic character, separating the two species, *G. maidu* with a well developed *DPSc* in constrast to a lessor developed carina in *G. glimmei*. Note, the *DPSc* is also well developed in *G. iviei*, similar to that found *G. maidu* (see Fig 5).

Telson

The telson of genus *Graemeloweus* (see Figure 6) is formed as in most vaejovids, lacking the vesicular ridges which are diagnostic of genus *Kovarikia* (see Soleglad, Fet & Graham (2014: 6–8: fig. 5)). The subaculear setal pair is located on vesicle/aculeus juncture, not on the aculeus base as in *Kovarikia*. Also, the *vesicular linear patch* found on dorsal surface of adult *Kovarikia* males is not found on male *Graemeloweus* specimens (see Soleglad, Fet & Graham (2014: 8, fig. 5)).

Laterobasal Aculear Serrations (LAS) are absent in genus *Graemeloweus*. Fet, Soleglad & Brewer (2006: tab. 1) examined 80 species in family Vaejovidae stating whether a LAS is present and if so, the number of spines present (note, 33 of these were verified with SEM microscopy). Interestingly, most of the species in their study that *lacked* a LAS were contained in subfamily Vaejovinae (ten out of twelve), and a majority of these were in genera *Pseudouroctonus* and *Uroctonites*. Also of note, three species in *Pseudouroctonus* that exhibited a LAS were three closely related species, *P. andreas*, *P. castaneus*, and *P. thompsoni*.

Carapace

The carapace of *Graemeloweus* is typical of that found in *Pseudouroctonus* with its conspicuous narrow anterior indentation (see Fig. 6). However, this anterior indentation is not as deep in this genus, its depth when compared to the carapace length is only 0.0374 (i.e., the mean value of three adult female species), as compared to 0.0603 for *Kovarikia*, or *Uroctonites* where the indentation ratio averaged 0.0414 (after Soleglad, Fet & Graham, 2014: 9).

Soleglad & Fet (2008: 51, figs. 126–127) presented three carapace-based morphometric ratios across the family Vaejovidae and demonstrated that the clade *Pseudouroctonus* + *Uroctonites* (nine species were represented) exhibited the smallest median eye tubercle, the smallest median eyes, and the most anteriorly advanced median eyes in the family. The three *Graemeloweus* carapaces, two illustrated in this paper, do fall within the ranges of *Pseudouroctonus* as originally shown in Soleglad & Fet (2008), but towards the high range end of the histograms. The mean values for the three *Graemeloweus* species for these three ratios are: *med-eye_tub_pos / cara_L* = 0.347, *med-eye_tub_W / cara_med_W* = 0.175, and *med_eye_dia / cara_L* = 0.058.

Trichobothrial pattern

Graemeloweus trichobothrial patterns are Type C, orthobothriotaxic. This implies that chelal trichobothria

Figure 6: Telson, carapace, and closeup of lateral eyes of genus *Graemeloweus*. **Top.** Telson, lateral (left) and ventral (right) views. *Graemeloweus iviei*, female, American River, El Dorado Co., California, *G. glimmei*, female, Cache Creek, Lake Co.,California, and *G. maidu*, female, American River, El Dorado Co., California. Note, the *subaculear setal pair* (SSP) is located on the vesicle/aculeus juncture (indicated by *arrows*). **Bottom.** Carapace and closeup of lateral eyes, three in number. *Graemeloweus iviei*, female, American River, El Dorado Co., California, USA and *Graemeloweus glimmei*, female, Cache Creek, Lake Co.,California, USA.

	G. iviei		***G. glimmei***		***G. maidu***
	Female	**Male**	**Female**	**Male**	**Female**
Total length	38.35	26.95	39.75	40.75	34.50
Carapace length	4.85	3.55	4.85	4.70	4.60
Mesosoma length	13.00	8.50	14.40	12.60	9.00
Metasoma length	15.55	11.30	15.50	17.95	15.80
Segment I length/width	2.10/2.65	1.50/1.90	2.00/2.30	2.40/2.60	2.15/2.25
Segment II length/width	2.35/2.60	1.70/1.90	2.35/2.25	2.75/2.60	2.45/2.20
Segment III length/width	2.55/2.50	1.90/1.90	2.55/2.20	3.00/2.45	2.60/2.10
Segment IV length/width	3.30/2.40	2.40/1.80	3.30/2.10	3.75/2.30	3.30/2.00
Segment V length/width	5.25/2.40	3.80/1.70	5.30/2.10	6.05/2.25	5.30/2.00
Telson length	4.95	3.60	5.00	5.50	5.10
Vesicle length	3.20	2.30	3.40	3.80	3.30
width/depth	2.00/1.40	1.50/1.10	2.10/1.70	2.20/2.00	2.00/1.55
Aculeus length	1.75	1.30	1.60	1.70	1.80
Pedipalp length	15.30	10.15	15.90	17.00	16.70
Femur length/width	3.90/1.45	2.15/1.00	4.00/1.45	4.20/1.50	4.20/1.50
Patella length/width	4.20/1.60	2.95/1.15	4.45/1.60	4.60/1.70	4.70/1.75
Chela length	7.20	5.05	7.45	8.20	7.80
Palm length	3.60	2.40	3.90	4.30	3.95
width/depth	2.20/2.60	1.50/1.80	2.30/2.80	2.60/3.10	2.30/2.65
Fixed finger length	3.00	2.30	3.10	3.40	3.40
Movable finger length	4.15	3.00	3.90	4.50	4.40
Pectines					
teeth	9-9	10-10	10-10	11-11	x-10
middle lamellae	5+-6+	6+-6	6+-6+	7-7	x-5+
Sternum length/width	1.20/1.50	0.80/1.10	1.15/1.50	1.05/1.35	1.15/1.55

Table 1: Morphometrics (mm) of *Graemeloweus* species from northern California. *G. iviei*, American River, El Dorado Co., California, USA, *G. glimmei*, Cache Creek, Lake Co.,California, USA, and *G. maidu*, American River, El Dorado Co., California, USA.

Esb, Et_4, and patellar trichobothrium esb_2 are petite. In Appendix C, we present the trichobothrial patterns for all three species of *Graemeloweus.*

Important trichobothria positions consistent with *Pseudouroctonus* are as follows: chelal trichobothria *ib-it* are situated basally on the fixed finger, *ib* adjacent to the fixed finger/palm juncture. Trichobothria Et_1 and V_1 are parallel to the fixed finger juncture/condyle complex; trichobothrium V_4 is located in a depression on the ventroexternal carina (*V1*); *Db* is positioned dorsal of the digital carina (*D1*); and patellar trichobothrium v_3 is distal to et_3.

An important trichobothrial position *Graemeloweus* has in commen with genus *Kovarikia* was described by Soleglad, Fet & Graham (2014: 3, fig. 1): the relatively close proximity of trichobothria *Dt* and *Est* in relationship to the distance of *Dt* from the chelal palm's base. These authors included species *G. iviei* and *G. glimmei* (placed in *Pseudouroctonus* at the time) with their new genus *Kovarikia*. The ratio values for *Kovarikia* is 0.167–0.599 (0.350) and for *Graemeloweus* 0.444–0.686 (0.550). Other *Pseudouroctonus* species ratio values are larger, 0.700–1.071 (0.855) [10] as reported by Soleglad, Fet & Graham (2014: 3). *Kovarikia* differs from *Graemeloweus* exhibiting neobothriotaxy on the ventral surface of the chela, typically found with five ventral trichobothria.

Complete trichobothrial patterns for a large majority of species in *Kovarikia*, *Pseudouroctonus*, and *Uroctonites* can be found in Soleglad, Fet & Graham (2014:

appendix A) and Ayrey & Soleglad (2015: figs. 1, 13, 28; appendix A).

Pectinal Tooth Counts

The structure of the *Graemeloweus* pectines (see Figure 7) is complex, comprised of three anterior lamellae, multiple middle lamellae, and a fulcrum situated between the base of each tooth. Well developed sensorial areas are found on all teeth including the basal tooth.

Following are statistical data of the pectinal tooth counts of the three species of *Graemeloweus* based on small to medium sample sizes. It is clear from this data that there is little difference between the three species in their pectinal tooth counts, the mean value differences less than one tooth. And, the range within genders per species is only two teeth.

G. iviei: ♂ 10–11 (10.625) (±0.518) [8], ♀ 9–10 (9.750) (±0.463) [8]
G. glimmei: ♂ 11–12 (11.500) (±0.577) [4], ♀ 10–11 (10.500) (±0.548) [6]
G. maidu: ♂ 11–11 (11.000) (±0.000) [4], ♀ 10–11 (10.636) (±0.505) [11]

The pectinal tooth counts of *Graemeloweus*, as in other *Pseudouroctonus* species groups, are reduced in number when compared to the adult size of the individual species. The size-to-pectinal tooth count ratio was discussed in detail by Soleglad (1973: 353–360), suggesting that these ratios can be used to delineate, in part, genera and species groups. Soleglad & Fet (2008: 69–71) also discussed this ratio in detail, in their revision of family Vaejovidae, showing that the species of *Pseudouroctonus* and *Uroctonites* had a relatively reduced number of pectinal teeth as compared to the adult size of individual species. This is indicated by the larger ratio values (i.e., caused by the considerably smaller mean value of the pectinal tooth counts).

For the three species of *Graemeloweus* by gender, the "total length/PTC mean ratio" is as follows:

G. iviei: ♂ 3.012, ♀ 3.795
G. glimmei: ♂ 3.043, ♀ 3.810
G. maidu: ♂ 3.182, ♀ 3.855

Predictable here, is the larger ratio values seen in the females, which is caused by their smaller pectinal tooth counts and, in general, the female being slightly larger than the male. In Soleglad & Fet (2008: 71), which only included the adult female in their ratio analysis, the stated average for *Pseudouroctonus* is 3.459 and for *Uroctonites* 4.531. The ratio value for *Graemeloweus* females is larger than the average reported by Soleglad & Fet (2008: 71) for *Pseudouroctonus*, which was based on twelve species.

Finally, it must be emphasized here that the relatively large ratio value exhibited in *Graemeloweus* is consistent with other *Pseudouroctonus* species groups, further endorsing its close relationship with *Pseudouroctonus*, *Kovarikia*, and, to some extent, *Uroctonites*.

Other structures

Below we discuss additional structures that collectively differentiate *Graemeloweus*, but are not exclusive to the genus when considered individually. These, however, are taxonomically important structures to complete the description of genus *Graemeloweus*.

Metasoma. The metasomal carinae of genus *Graemeloweus* are in general well developed and crenulated to serrulate on all five segments (see Fig. 7).

The morphometrics of the metasomal segments are diagnostic at the species level (see Tables 1–2), in particular for species *G. iviei* which has a much heavier metasoma than that found in the other two species. Based on morphometric ratios comparing a single adult female and male per species, we find the following differences (note, male *G. maidu* data are from Savary & Bryson (2016: tab. 1)). First we must state here that *G. maidu* had the thinnest metasoma for all segments when compared to the other two species, female and male. And, *G. glimmei* was also thinner than *G. iviei*, for all segments, female and male. In Table 2 we present the percentage (%) of difference of the five metasomal segments when the length is divided by its width for both genders across all three species. From these data it is clear that both *G. glimmei* and *G. maidu* are considerably more slender than *G. iviei*: the range of percentage differences between *G. maidu* and *G. iviei* for the five metasomal segments for the female is 0.2000–0.2321 and for the male 0.2488–0.3209. These are very significant differences involving all five segments across both genders. Similarly, though not as large, differences are also seen when *G. glimmei* and *G. iviei* are compared, ranges 0.0973–0.1556 for the female and 0.1692–0.2245 for the male. Finally, when we compare *G. maidu* with *G. glimmei* the percentage differences are in general small, only one over 10 percent.

The morphometric proportions of metasomal segment V also provide a low-level diagnostic character for separating *Graemeloweus* from genus *Kovarikia*. Soleglad, Fet & Graham (2014: 9-10, fig. 7) discussed the relatively slender segment V found in *Kovarikia*, where they state: "…Only *P. reddelli* and its sister species *P. sprousei* have comparable or thinner segment V, in particular the latter where only the male is known …". Above we discussed the percentage of differences between the three species of *Graemeloweus* for all five metasomal segments, using it as a species-level diagnostic character. In *Graemeloweus*, the morphomet-

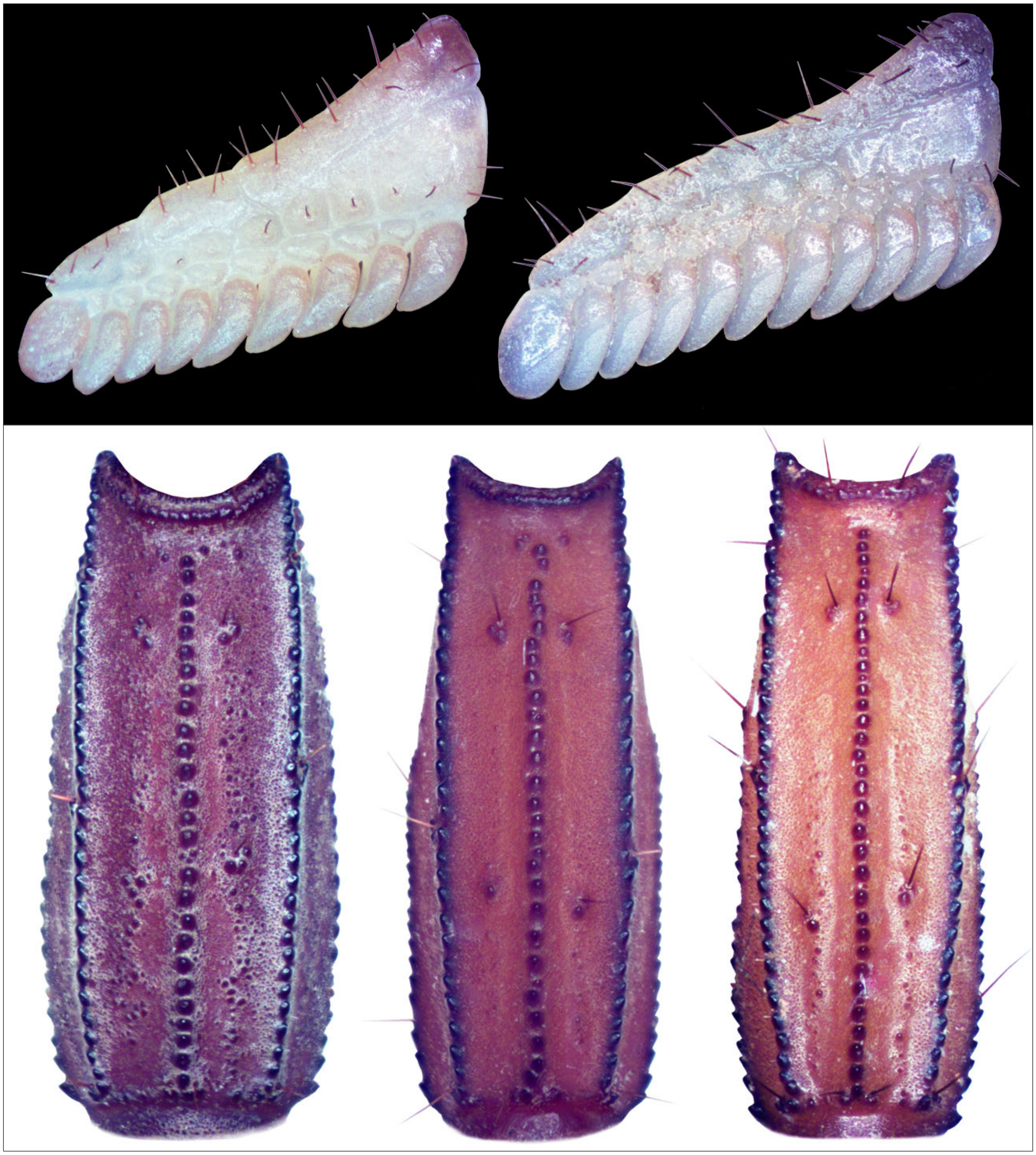


Figure 7: Right pecten and metasomal segment V, ventral view, of *Graemeloweus* species. **Pecten.** *Graemeloweus iviei*, female, American River, El Dorado Co., California, USA and *Graemeloweus glimmei*, male, Cache Creek, Lake Co.,California, USA. **Metasomal Segment V**. *Graemeloweus iviei*, female, American River, El Dorado Co., California, *G. glimmei*, female, Cache Creek, Lake Co., California, and *G. maidu*, female, American River, El Dorado Co., California.

ric ratio for segment V when the length is compared to its width is as follows (based on a single adult specimen per species and gender):

G. iviei: ♂ 2.235, ♀ 2.188
G. glimmei: ♂ 2.689, ♀ 2.524
G. maidu: ♂ 2.888, ♀ 2.650

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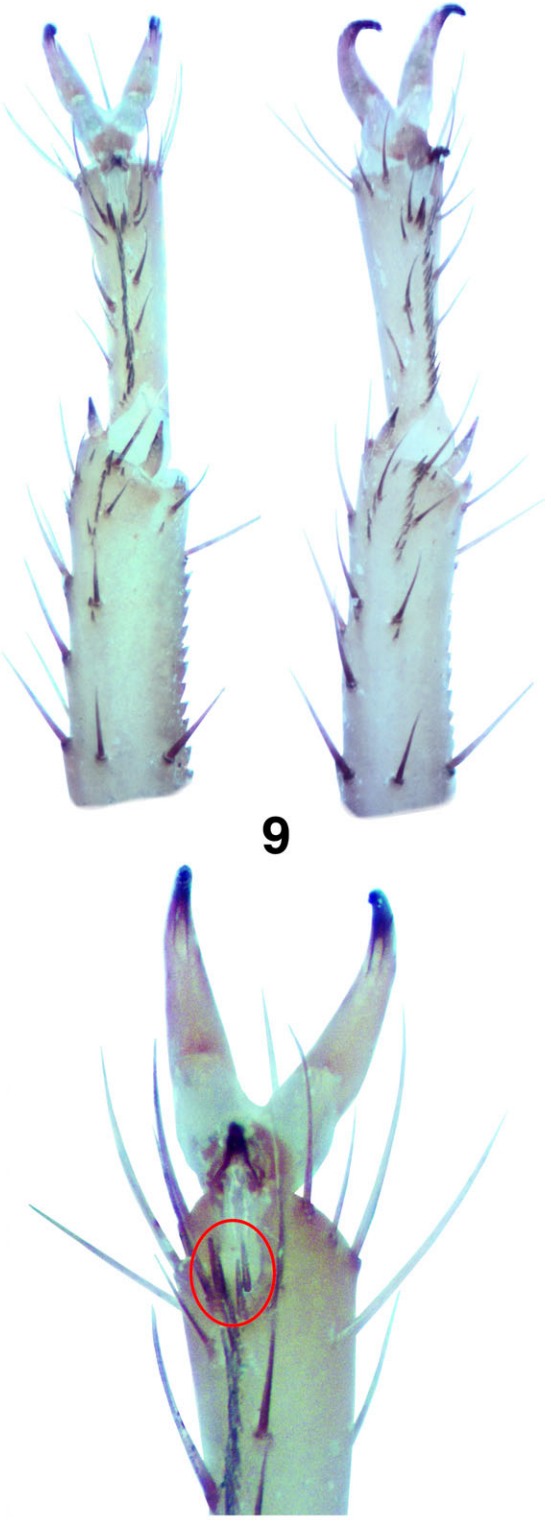

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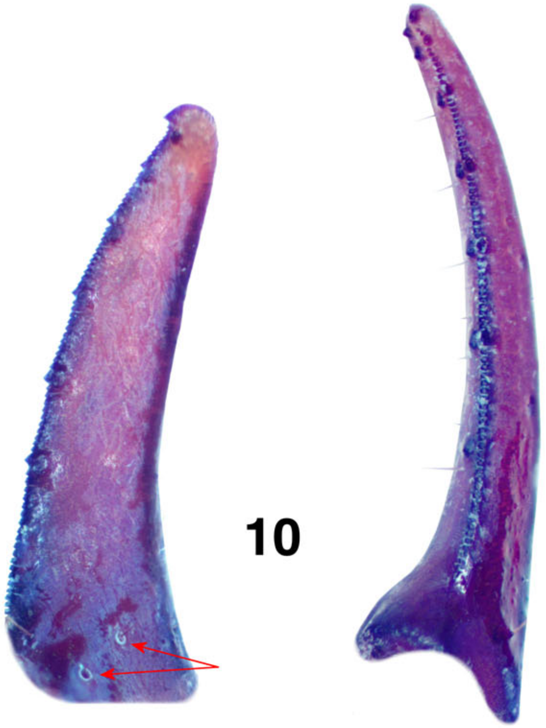

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Figures 8–10: 8. *Graemeloweus iviei*, female, American River, El Dorado Co., California. Chelicera, ventral, external, and dorsal views showing typical dentition of genus *Graemeloweus*: two subdistal (*sd*) denticles on the movable finger dorsal edge, lack of dentition and strong development of serrulae on the ventral edge, and the lack of protuberances on the fixed finger ventral surface. **9.** *G. maidu*, female, American River, El Dorado Co., California. Right leg tarsus III, ventral views showing typical spination: two pedal spurs and single median row of spinules terminating distally with *two* closely positioned spinule pairs (indicated with *red ellipse*). **10.** *G. glimmei*, female, Cache Creek, Lake Co., California. Movable and fixed fingers of the chela showing typical dentition: seven inner denticles (*ID*) and six *ID* on the movable and fixed fingers respectively. Also note the basally positioned trichobothria *ib* and *it* (indicated with *red arrows*).

Metasoma Segments (L/W)		**Female (n=1)**		**Male (n=1)**	
		G. iviei	***G. glimmei***	***G. iviei***	***G. glimmei***
Seg I	***G. maidu***	0.2058	0.0989	0.2667	0.0833
	G. glimmei	0.0973		0.1692	
Seg II	***G. maidu***	0.2321	0.0662	0.3209	0.1174
	G. glimmei	0.1556		0.1821	
Seg III	***G. maidu***	0.2138	0.0682	0.3188	0.0771
	G. glimmei	0.1364		0.2245	
Seg IV	***G. maidu***	0.2000	0.0500	0.2488	0.0212
	G. glimmei	0.1429		0.2228	
Seg V	***G. maidu***	0.2114	0.0500	0.2919	0.0739
	G. glimmei	0.1537		0.2029	

Table 2: Morphometric ratio analysis of metasomal segments I−V (length/width) for the three species of genus *Graemeloweus*. Values state the percentage (%) of difference of the five segments for both genders across all three species. The *G. iviei* columns indicate large percentage differences when compared to the other two species. In contrast, the *G. glimmei* columns show small percentages of difference when compared to *G. maidu*. Note, this data is based on only one adult sample per gender/species comparison.

Soleglad, Fet & Graham (2014: 10) reported the followinig ranges for *Kovarikia*:

K. angelena: ♂ 3.059–3.170, ♀ no data.
K. bogerti: ♂ 3.087–3.444, ♀ 3.091–3.333
K. williamsi: ♂ 3.130–3.400, ♀ 3.093–3.400

At a genus level (three species per genus) we have the following ranges:

Graemeloweus:
♂ 2.235–2.888, ♀ 2.188–2.650
Kovarikia:
♂ 3.059–3.444, ♀ 3.091–3.400

The percentage of difference between the range mid-points is 26.94% for the male and 34.17% for the female, definitely showing that *Kovarikia* has the thin-nest metasomal segment V.

Chelicerae. The chelicerae of genus *Graemeloweus* is structured the same as that found in *Kovarikia* (see Figure 8 and Soleglad, Fet & Graham (2014: fig. 8)): the dorsal edge of the movable finger is equipped with two subdistal (*sd*) denticles, its ventral edge is smooth, lacking denticles. However, this edge distally is equipped with well developed serrulae, numbering over 20 tines; the fixed finger basal (*b*) and median (*m*) denticles are formed as a bicuspid, and the ventral surface of this finger is smooth, lacking protuberances. Finally, on the movable finger, the ventral distal denticle (*vd*) extends considerably beyond that of it dorsal counterpart (*dd*).

Although many species in *Pseudouroctonus* have chelicerae structured as in *Graemeloweus*, others do not. For example, *P. reddelli*, *P. cazieri*, *P. sprousei*, and *P. peccatum* have chelicerae equipped with denticles and/or protuberances on the ventral surface of both cheliceral fingers; see Gertsch & Soleglad (1972: figs. 39, 31), Francke & Savary (2006: fig. 4), and Tate et al. (2013: fig. 10).

Leg tarsus. The legs of genus *Graemeloweus*, as in all vaejovids, are equipped with two pedal spurs and lack tibial spurs. The basitarsus lacks a "setal comb", commonly found in smeringurines, most of which are psammophiles.

The ventral surface of the leg tarsus is equipped with a single row of spinules terminating with one to two pairs of distal spinules. Curiously, *Graemeloweus iviei* has only one pair (originally reported by McWest, 2001, 34), whereas *G. maidu* (see Fig. 9) and *G. glimmei* have two pairs of distal spinules (note, Savary & Bryson (2016: 57) also reported two pairs for *G. maidu*).

Chelal finger dentition. The chelal finger dentition of genus *Graemeloweus* (see Fig. 10) is typical of most

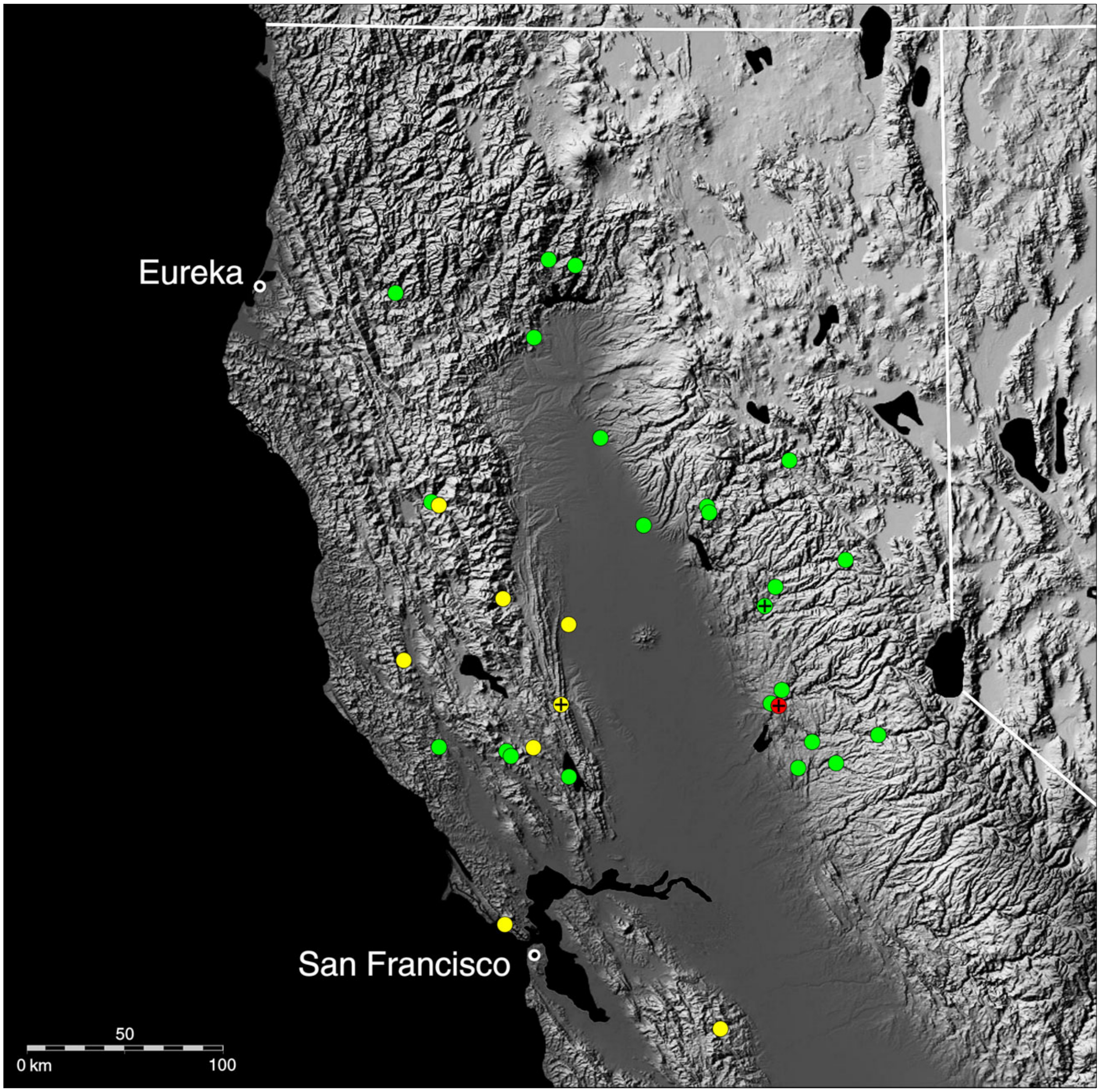

Figure 11: Distribution of genus *Graemeloweus* in northern California, USA. Individual localities based on Gertsch & Soleglad (1972: 595), Hjelle (1972: 12), and Savary & Bryson (2016: 50–52). *Graemeloweus iviei* green icons, *G. glimmei* yellow icons, and *G. maidu* red icon. Type localities indicated with a '+'.

vaejovids. Median denticle (*MD*) row groups are aligned in a straight line, six on the fixed and movable fingers; six internal (*ID*) denticles are located on the fixed finger and seven on the movable finger; five outer (*OD*) denticles are found on the fixed and movable fingers. No accessory denticles are present.

Systematics

Order **SCORPIONES** C. L. Koch, 1850
Suborder Neoscorpiones Thorell et Lindström, 1885
Infraorder Orthosterni Pocock, 1911
Parvorder Iurida Soleglad et Fet, 2003
Superfamily Chactoidea Pocock, 1893
Family Vaejovidae Thorell, 1876
Subfamily Vaejovinae Thorell, 1876

Genus *Graemeloweus* Soleglad, Fet, Graham et Ayrey gen. nov.

Figures 1–10, 12–13; Tables 1–2
http://zoobank.org/urn:lsid:zoobank.org:act:D7006B77-5CFE-4514-A27C-85DBD17DD421

Figure 12: *Graemeloweus iviei*, female and *G. maidu*, female, American River, El Dorado Co., California, USA.

Figure 13: *Graemeloweus glimmei*, female and habitat, Cache Creek, Lake Co., California, USA.

Type Species. *Graemeloweus iviei* (Gertsch et Soleglad, 1972), **comb. nov.** [= *Vejovis iviei* Gertsch et Soleglad, 1972], designated here.

Composition. This genus contains three species: *G. iviei*, **comb. nov.** [= *Vejovis iviei* Gertsch et Soleglad, 1972] (type species); *G. glimmei*, **comb. nov.** [=*Pseudouroctonus glimmei* (Hjelle, 1972)]; and *G. maidu*, **comb. nov.** [=*Pseudouroctonus maidu* (Savary et Bryson, 2016)].

Distribution. Found in northern California, USA (Butte, El Dorado, Lake, Marin, Mendocino, Napa, Nevada, Placer, Plumas, Shasta, Sierra, Sonoma, Stanislaus, Tehama, Trinity, and Yuba Counties.). See map in Figure 11.

Diagnosis. Orthobothriotaxic. Hemispermatophore median area equipped with a non-bifurcated primary lamellar hook and a secondary lamellar hook; mating plug is complex, possesses a two-part base, and a large asymmetric smooth edged barb. Chelal palm planes formed by carinae *D1|D3|D4* and *V1|V2|V3* are not subparallel, due to a well developed ventromedian (*V2*) carina. Telson vesicle lacks ventral ridges at the aculeus juncture, subaculear setal pair located on vesicle/aculeus juncture, and vesicular linear patch not presence on the dorsal surface. Cheliceral movable and fixed fingers lack dentition and/or protuberances on their ventral surfaces. Ventral surface of leg tarsus with 1–2 distal spinule pairs. See Table 1 for measurements of these species.

Etymology. This genus (masculine in gender) is named in honor of our colleague and friend Graeme Lowe (Philadelphia, Pennsylvania, USA) who has made significant contributions to scorpion systematics.

Key to Species of *Graemeloweus*

1 — Metasoma segment-V length / width in female 2.524–2.650 and in male 2.690–2.890; leg tarsus with *two* ventral distal spinule pairs ……………………….… **2**
■ — Metasoma segment-V length / width in female 2.188 and in male 2.235; leg tarsus with *one* ventral distal spinule pair ………………. …………………..… …….. ***Graemeloweus iviei*** **(Gertsch et Soleglad, 1972)**
2 — Interocular area of carapace smooth; *DPSc* of patella granulated on its basal one-third …………….. …………...…… ***Graemeloweus glimmei*** **(Hjelle, 1972)**
■ — Interocular area of carapace granulated; *DPSc* of patella granulated its entire length ……….……….. ……... ***Graemeloweus maidu*** **(Savary et Bryson, 2016)**

Discussion

Graemeloweus is clearly in the family Vaejovidae: 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, in part, on the finger, not on the palm; V_1–V_4 series extends most of the palm length and V_1–V_2–V_3 juncture is straight, not angled towards the internal condyle; patellar trichobothrium v_3 is located on the external surface; chelal finger median (*MD*) denticle row groups are aligned in a straight line; inner accessory (*IAD*) and outer accessory (*OAD*) denticles are not present (genus *Stahnkeus* is an exception with *IAD*, a derived character within the Vaejovidae); genital operculum of the female is not separated its entire length, but instead is connected at least for the anterior half; the pedipalp patellar *DPSc* carina is well developed; the terminus of the dorsolateral (*DL*) carina is flared, not coinciding with the articulation condyle. See Soleglad & Fet (2008: p. 74).

Interestingly, Gertsch & Soleglad (1972: 593) considered *G. iviei* to be different from the other new species they assigned to genus *Uroctonus*, placing *G. iviei* in *Vaejovis*. They stated: "… Small, brown, granulated scorpion with appearance of *Uroctonus* group but presenting several important differences: … lower margin of movable finger of chelicera essentially smooth … chela with inner ventral keel well developed …". Even at this time, these authors noticed the well developed chelal *V2* carina now considered a major diagnostic character for genus *Graemeloweus*.

The clade *Uroctonites* + ((Graemeloweus + *Kovarikia*) + *Pseudouroctonus*) proposed here is based on the following shared characters. The chelae are stocky with swollen palms and are somewhat flat in appearance due to the weak to obsolete development of the dorsosecondary and ventromedian carinae. (Note: we consider the well developed *V2* carina found in *Graemeloweus* to be derived from a near obsolete condition described for the clade, thus a synapomorphy.) Chelal internal trichobothria *ib–it* are located basal on the fixed finger, trichobothrium *ib* sometimes occurring on the extreme distal aspect of the palm, adjacent to the movable finger membrane. The carapace exhibits a conspicuous anterior median indentation, and the median eyes are reduced in size and located considerably anterior of the carapace midpoint. The serrula are well developed and the pectinal tooth counts as compared to the scorpion's adult size are relatively small. The hemispermatophore of the clade ((*Graemeloweus* + *Kovarikia*) + *Pseudouroctonus*) is similar to that found in other vaejovines whereas the hemispermatophore of *Uroctonites* exhibits several structural differences.

Within this clade, *Graemeloweus*'s placement with *Kovarikia* + *Pseudouroctonus* is quite straightforward (as compared to *Uroctonites*). The hemispermatophore lamina sides are sub-parallel (not tapered), the terminus is truncated (not pointed); and the lamellar hook is located distal of dorsal trough (not adjacent to). The mating plug is sclerotized (not partially gelatinous).

Figure 14: Microhabitats of *Graemeloweus iviei*, American River, El Dorado Co., California, USA and *Graemeloweus maidu*, American River, El Dorado Co., California, USA.

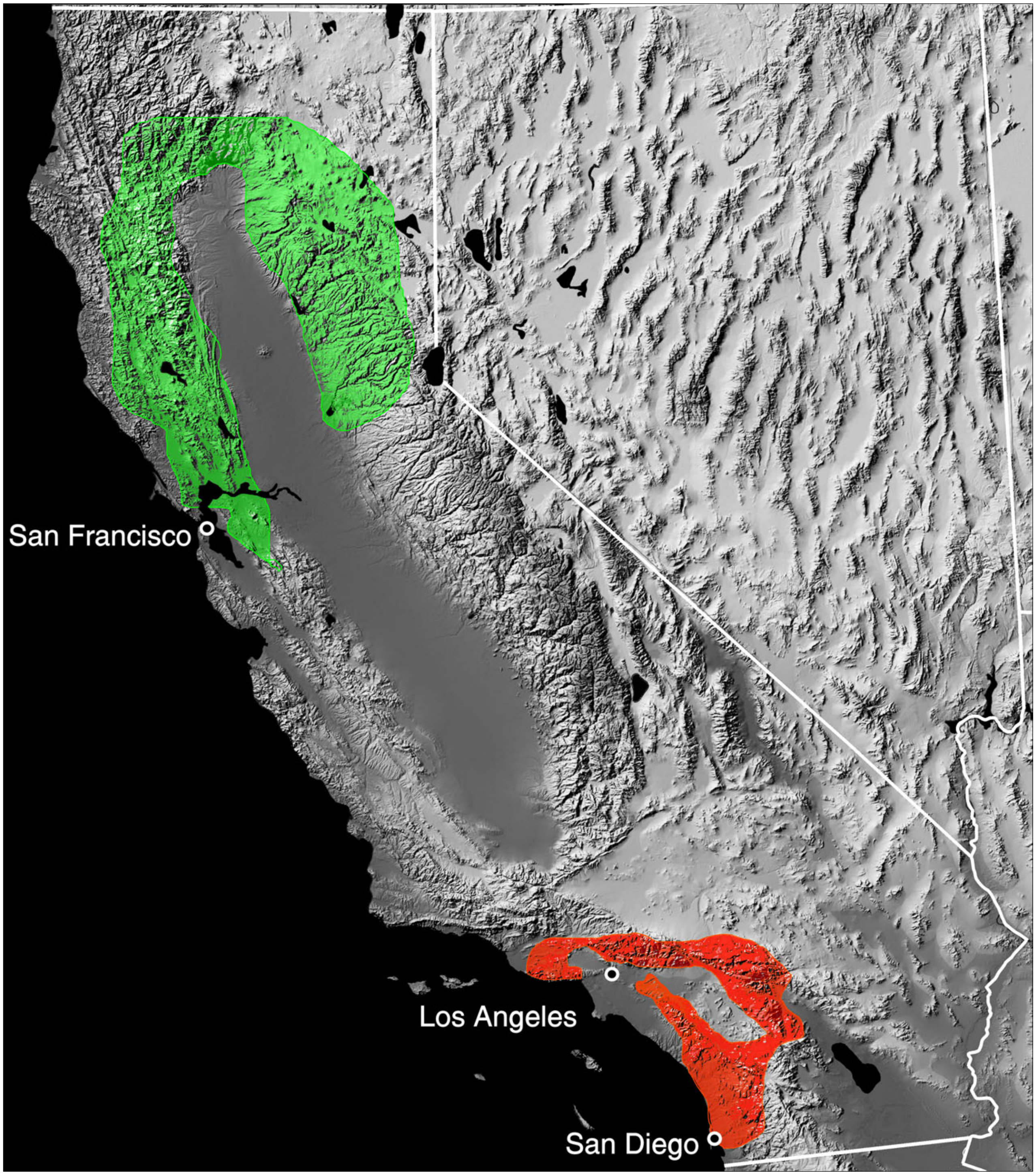

Figure 15: General distribution of genera *Graemeloweus* and *Kovarikia* in California, USA. Distributions based on Gertsch & Soleglad (1972: 595), Hjelle (1972: 12), Savary & Bryson (2016: 50–52), and Soleglad, Fet & Graham (2014: 15, fig. 11). General distribution of *Graemeloweus* indicated by the *green* area and *Kovarikia* by the *red* area.

Ventral setal pairs of the leg tarsus are irregularly positioned (not aligned); setae irregularly sized, but never stout (not the same size and stout).

Except for the newly defined *G. maidu*, the other two species comprising *Graemeloweus* are known from several locations. Their distribution is shown in the map in Figure 11. Figures 12–14 show live specimens and examples of their natural habitat for all three species.

Ecological Observations

RA collected all three species of the new genus *Graemeloweus* using a blacklight at night. Similar to *Kovarikia,* each *Graemeloweus* species was found in rocky habitats near water, from a few meters to several hundred meters above riparian areas. Some *G. maidu* were found in narrow rock crevices on steep rocky hillsides.

Biogeography

From a biogeographical perspective, our strong morphological evidence for a sister relationship between *Graemeloweus* and *Kovarikia* is curious. The distribution of *Kovarikia* throughout the Transverse and Peninsular ranges of southern California and *Graemeloweus* in the mountains of northern California forms a disjunction in central California where neither taxon has been documented yet habitat seems ideal (see map in Figure 15). Specifically, the southern Sierra Nevada and southern Coastal Range provide mountainous, rocky environments that are quite similar to those they already inhabit and seem suitable. So why are they not there?

Intriguingly, the range of the sympatric chactid genus *Uroctonus* does extend into the southern Sierra Nevada, but not south into the southern Coastal Range. A recent phylogeographic appraisal of *Uroctonus* using extensive phylogenomic data revealed two genetic groups comprising the northern and southern halves of the taxon's range (Bryson et al., 2016). The authors hypothesized that the two groups probably diverged during the Late Miocene when tectonic activity at the Mendocino Triple Junction, a region where three plates converge, accelerated uplift and drainage formation in the Coastal and Sierra Nevada ranges, sundering populations to the north and south. Such north-south genetic discontinuities have been discovered in other animal groups as well, and authors have proposed vicariance hypotheses attributed to uplift to the Transverse Ranges and inundation of the Los Angeles Basin and Central Valley (Calsbeek et al., 2003; Lapointe & Rissler, 2005; Feldman & Spicer 2006; Spinks et al., 2010; Myers et al., 2013). Perhaps some of these processes could have affected a *Graemeloweus/Kovarikia* ancestor, causing allopatric populations to diverge to the north and south and then going extinct in, or never colonizing, the southern Coastal Range.

The unusual distribution of *Graemeloweus* is remarkably similar to that of *Antrodiaetus riversi,* a dispersal-limited mygalomorph spider found in moist north-facing woodlands of the mountains surrounding the northern Central Valley (Sacramento Valley). Phylogeographic investigations of *A. riversi* uncovered eight distantly related but microendemic clades that probably represent a complex of at least eight cryptic species (Hedin et al., 2013). Microendemism is common in this region, particularly in dispersal-limited species like salamanders and arachnids, and is probably the result of periodic fragmentation of large tracts of forest during Pleistocene fluctuations (reviewed in Bryson et al., 2016). This could explain the small ranges of *G. glimmei* and *G. maidu*, the latter of which has only been discovered from one site.

Conversely, *G. iviei* is more widely distributed, forming an upside-down U-shape around the Sacramento Valley. We find this pattern intriguing. Does gene flow occur between populations along the U like in the famed ring-species *Ensatina eschscholtzii* (Moritz et al., 1992)? Or are there populations of *G. iviei* from the coastal ranges that are more closely related to populations in the in the Sierra Nevada, forming clades that span the Central Valley? Two of the *A. riversi* clades showed such "trans-valley" biogeographic patterns where haplotypes found east and west of the arid Central Valley were closely related (Starrett & Hedin, 2007; Hedin et al., 2013), a pattern also replicated in some vertebrate taxa (i.e. Wake, 1997; Matocq, 2002; Martinez-Solano et al., 2007). Finally, does *G. iviei* represent yet another complex of cryptic scorpion species?

To answer these questions, and to gain insight into their unusual disjunct distributions, we advocate that *Graemeloweus* and *Kovarikia* are ideal, and overdue, for a thorough phylogenetic and phylogeographic analysis.

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Appendix A
Hemispermatophore and Mating Plug of genus *Graemeloweus*

The hemispermatophore and mating plug for *Graemeloweus* is presented in this Appendix for the two species *G. glimmei* and *G. iviei*. Of particular note, Figure A-1 shows four views of the median area of these two species, definitely establishing that the primary lamellar hook is not bifurcated.

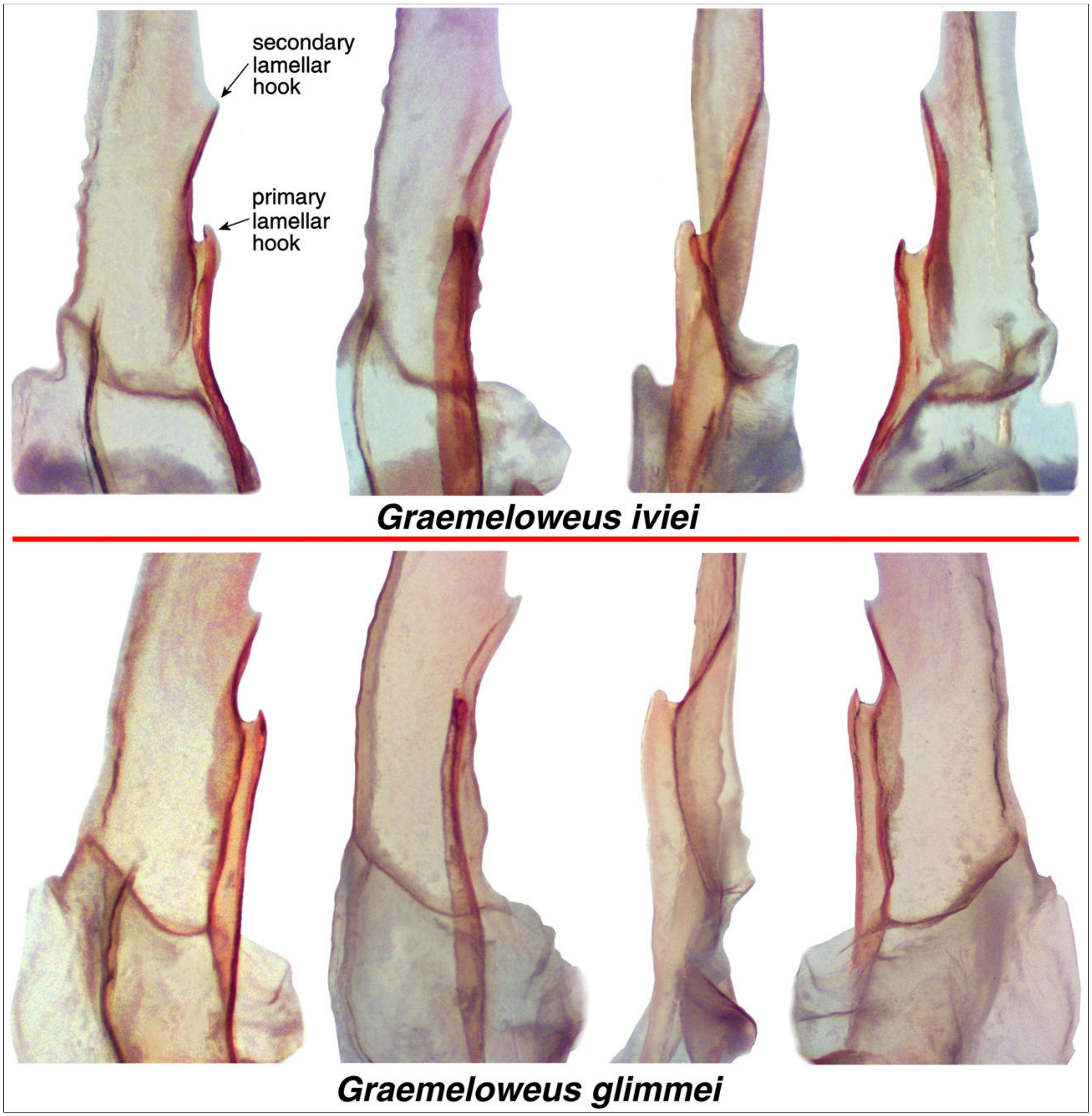


Figure A-1: Different perspectives of the primary and secondary lamellar hooks of the right hemispermatophore (photographed submerged in alcohol). Dorsal, dorsointernal, internal, and ventral views. Images demonstrate that the terminus of the primary lamellar hook in genus *Graemeloweus* is *not* bifurcated. **Top.** *Graemeloweus iviei*, American River, El Dorado Co., California, USA. **Bottom.** *G. glimmei*, Cache Creek, Lake Co., California, USA.

Figure A-2: *Graemeloweus glimmei*, type locality, Cache Creek, Lake Co., California, USA. Right hemispermatophore and mating plug (photographed submerged in alcohol). **Top.** Entire hemispermatophore, dorsal (left) and ventral (right) views, closeups of the median area, dorsal and ventral views, and closeup of the distal crest on the lamina termimus visible in the dorsal view. **Bottom.** Mating plug in various positions and angles: two *internal* views showing two asymmetric basal lobes, the barb closest to the viewing plain, four *ventral* views, and four *dorsal* views. Smooth asymmetric barb edge indicated by arrows.

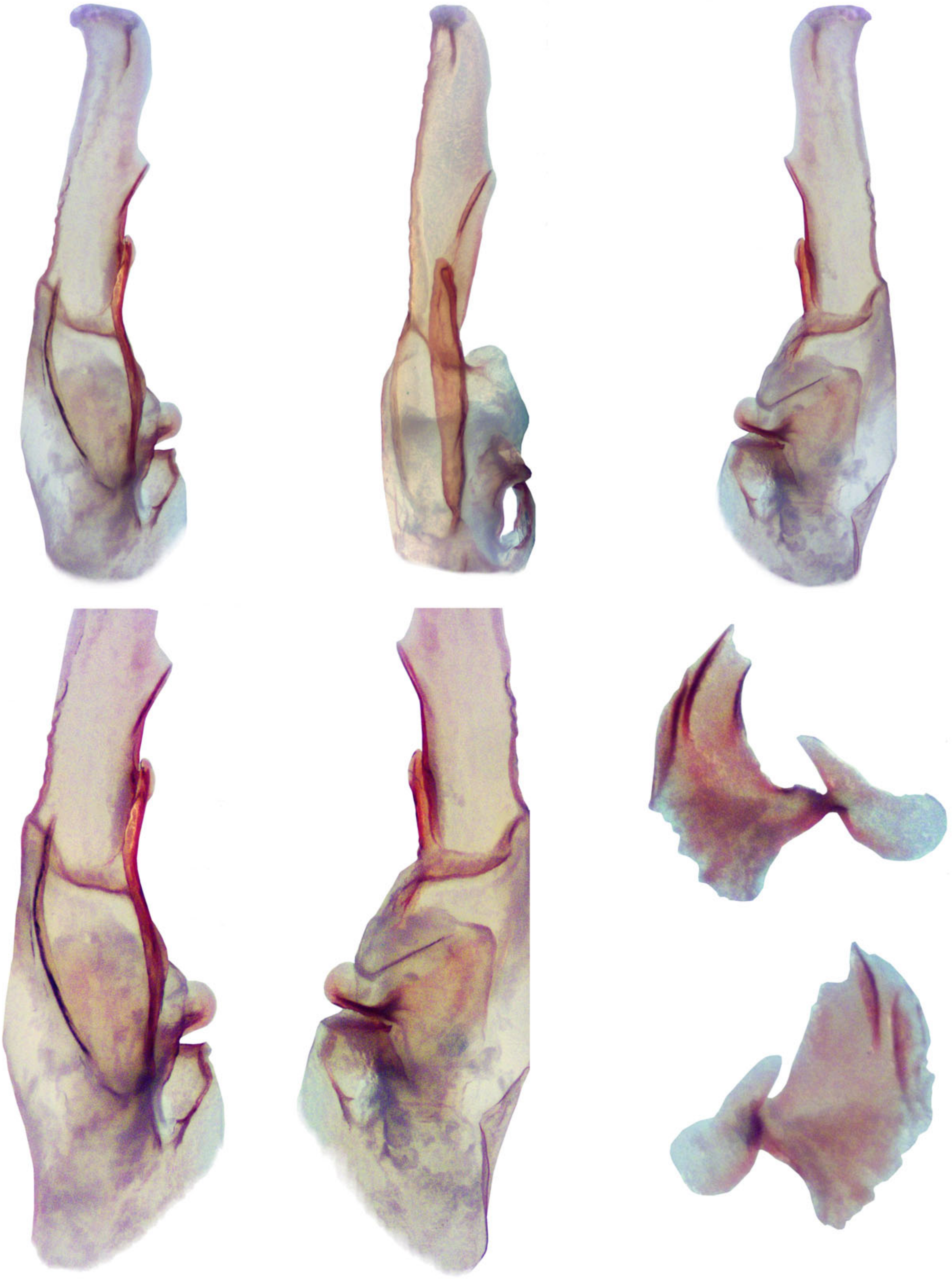


Figure A-3: *Graemeloweus iviei*, American River, El Dorado Co., California. Right hemispermatophore and left mating plug (photographed submerged in alcohol). **Top**. Hemispermatophore, dorsal, interodorsal, and ventral views. Note a distal crest is visible on the dorsal inner edge of the lamina terminus (also visible from the ventral view). Hemispermatophore trunk terminus not shown. **Bottom Left.** Closeup of lamellar hooks and median area, dorsal and ventral views. **Bottom Right.** Mating plug barb (reversed), dorsal and ventral views. Note most of the base is missing.

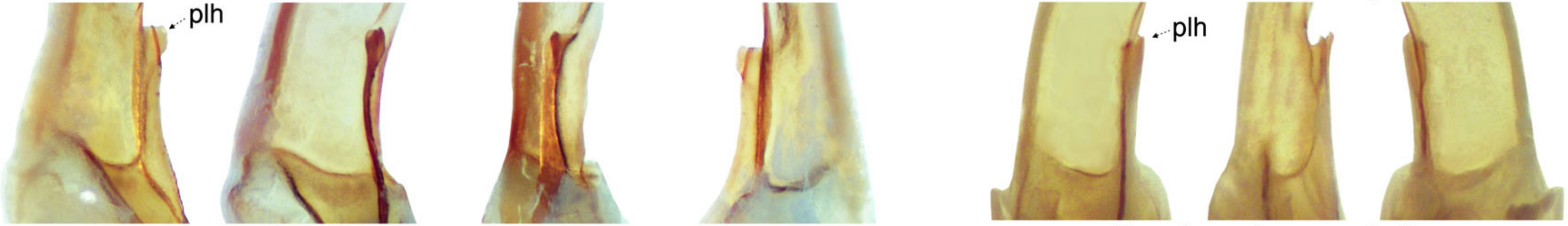
Appendix B
Hemispermatophore *Primary Lamellar Hook* (PLH) Configurations in Subfamily Vaejovinae and *Anuroctonus*

This Appendix provides many illustrations of the hemispermatophore of genera *Kovarikia*, *Pseudouroctonus*, *Uroctonites*, and the chactid genus *Anuroctonus*. As presented in the body of this paper, the hemispermatophore primary lamellar hook (PLH) of new genus *Graemeloweus* is *not* bifurcated. This is quite unusual in subfamily Vaejovinae, normally not reported for species of *Vaejovis*. To emphasize the uniqueness of a non-bifurcated PLH, we illustrate the hemispermatophore median areas of genus *Kovarikia* and key groups within *Pseudouroctonus*. This establishes the uniqueness of this character for *Graemeloweus* within its previous genus placement. We also show the hemispermatophore median areas for 23 species of "non *Pseudouroctonines*" currently placed in subfamily Vaejovinae. This includes species of *Franckeus*, members of the "*nigrescens*" group, and other *Vaejovis* species found in Mexico and the United States. Of particular importance, we show the median area of eight "sky island" *Vaejovis* species, primarily found in Arizona, the closest geographically *Vaejovis* group to *Graemeloweus.*

Kovarikia bogerti *Kovarikia williamsi*

Pseudouroctonus reddelli *Pseudouroctonus peccatum*

Pseudouroctonus castaneus *Pseudouroctonus thompsoni*



Pseudouroctonus apacheanus *Pseudouroctonus santarita*

Figure B-1: Hemispermatophore median area of *Kovarikia* and major groups currently placed in genus *Pseudouroctonus* (photographed submerged in alcohol). Views show different perspectives of the primary and/or secondary lamellar hooks illustrating the *bifurcated primary lamellar hook*. *Kovarikia bogerti*, Palomar Mountain Road, San Diego Co., California and *K. williamsi*, Santa Ysabel Preserve, San Diego Co., California (after, in part, Soleglad, Fet & Graham (2014: figs. A-4, 2)); *Pseudouroctonus reddelli*, Little Gem Cave, Comal Co., Texas, *P. peccatum*, Spring Mountains, Clark Co., Nevada (after, in part, Tate et al. (2013: fig. 17)), *P. castaneus*, Vista, San Diego Co., California, *P. thompsoni*, Santa Cruz Island, Santa Barbara Co., California, *P. apacheanus*, Rucker Canyon, Chiricahua Mountains, Cochise Co., Arizona, and *P. santarita* (after, in part, Ayrey & Soleglad (2015: figs. 34, 14)). plh = primary lamellar hook, slh = secondary lamellar hook.

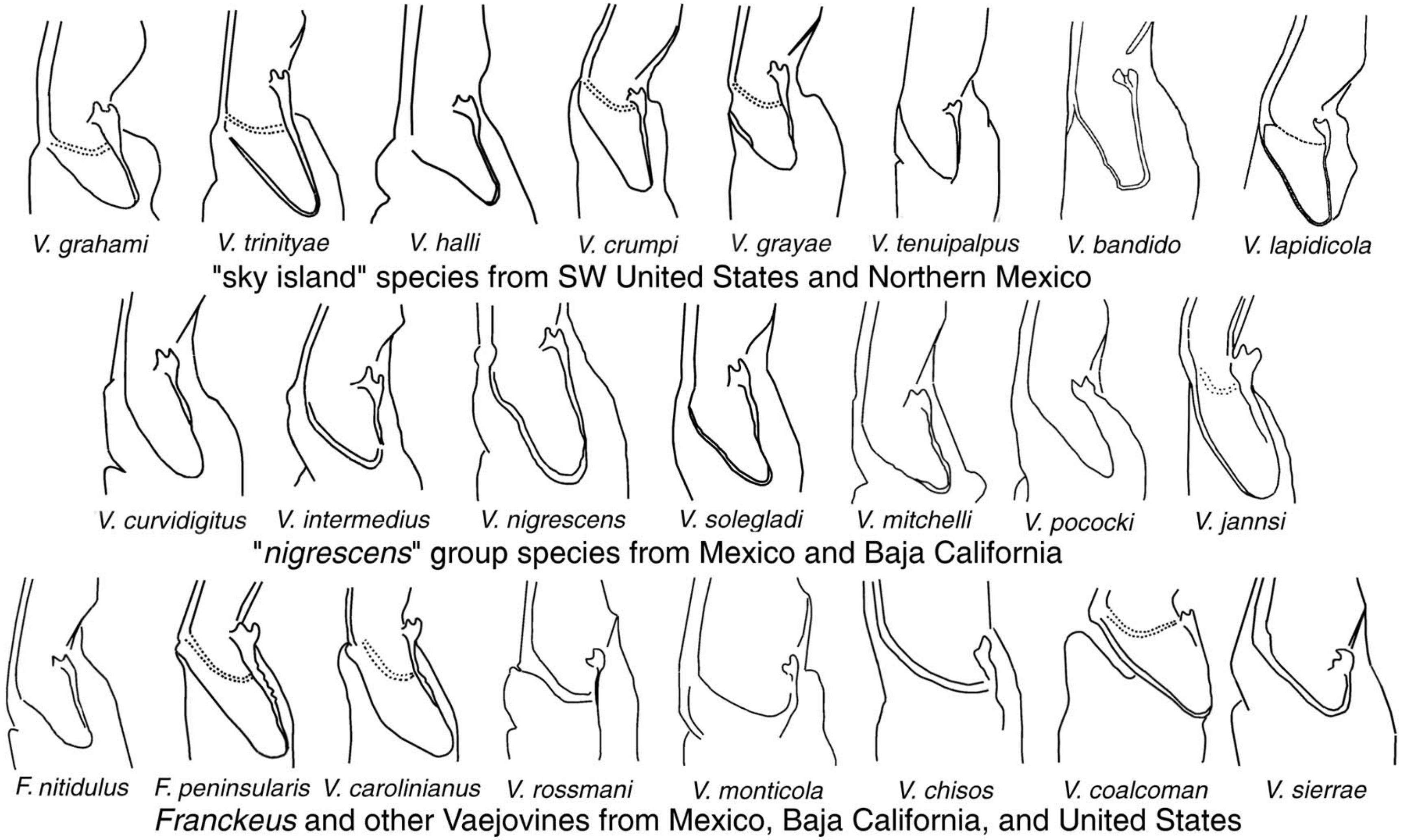


Figure B-2: Diagrammatic illustrations of the dorsal view of the right hemispermatophore showing the *bifurcation of the primary lamellar hook* for several "vaejovine" scorpion species. Illustrations taken from literature as well as specimens examined. All illustrations are of the median area showing the bifurcated lamellar hook, the dorsal trough, and the ventral trough (showing through from the ventral aspect, indicated by dotted line: note not shown in all figures). The illustrations are divided into three groups: **"sky island" species, southwestern United States and northern Mexico:** *Vaejovis grahami* (after, in part, Ayrey & Soleglad (2014: fig. 12)), *V. trinityae* (after, in part, Ayrey (2013: fig. 11)), *V. halli* (after, in part, Ayrey (2012: fig. 11)), *V. crumpi* (after, in part, Ayrey & Soleglad (2011: fig. 18)), *V. grayae* (after, in part, Ayrey (2014: fig. 10)), *V. tenuipalpus* (after, in part, Sissom (2012: fig. 5)), *V. bandido* (after, in part, Graham, Ayrey & Bryson (2012: fig. 17)), and *V. lapidicola* (after, in part, Soleglad & Fet (2008: fig. 71)). **"*nigrescens*" group species from Mexico and Baja California:** *Vaejovis curvidigitus*, *V. intermedius*, *V. nigrescens*, *V. solegladi*, *V. mitchelli*, *V. pococki* (after, in part, Sissom (1991: figs. 71, 73, 75, 77, 79, and 81)), and *V. jannsi* (Isla Socorro, Mexico). ***Franckeus* and other vaejovines from Mexico, Baja California, and United States:** *Franckeus nitidulus* (after, in part, Sissom (1991: fig. 83)), *F. peninsularis* (San Raymundo, Baja California Sur, Mexico), *Vaejovis carolinianus* (Athens, Georgia, USA), *V. rossmani*, *V. monticola* (after, in part, Sissom (1989: figs. 76, 78)), *V. chisos* (after, in part, Jarvis, Sissom & Henson (2004: fig. 1)), *V. coalcoman* (after, in part, Contreras & Francke (2014: fig. 9)), and *V. sierrae* (after, in part, Sissom et al. (2016: fig. 16)).

Figure B-3: Hemispermatophore of genera *Uroctonites* and *Anuroctonus*. **Top.** *Uroctonites huachuca*, Huachuca Mountains, Cochise Co., Arizona, USA. Left hemispermatophore (reversed, photographed submerged in alcohol). Complete structure, exterodorsal, dorsal, internal, interoventral, and ventral views. showing the construction of the *non-bifurcated* lamellar hook. **Bottom.** *Anuroctonus pococki pococki,* Santee, San Diego Co., California, USA, Right hemispermatophore (photographed submerged in alcohol). Lamina and median area, exterodorsal, dorsal, and interoventral views.

Appendix C
Trichobothrial Patterns of *Graemeloweus* Species

This Appendix presents the trichobothrial patterns of the three species of genus *Graemeloweus*, *G. iviei*, *G. glimmei*, and *G. maidu*.

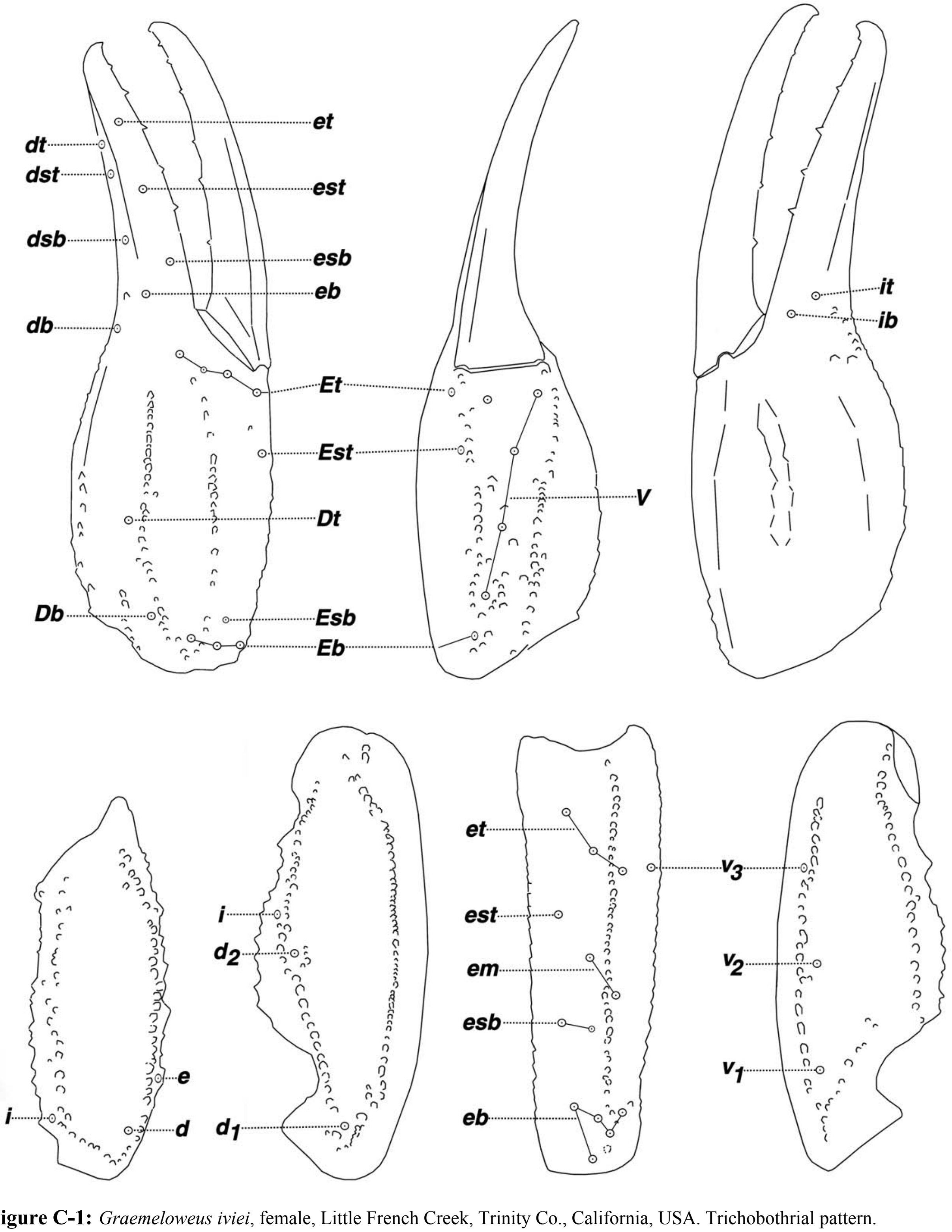


Figure C-1: *Graemeloweus iviei*, female, Little French Creek, Trinity Co., California, USA. Trichobothrial pattern.

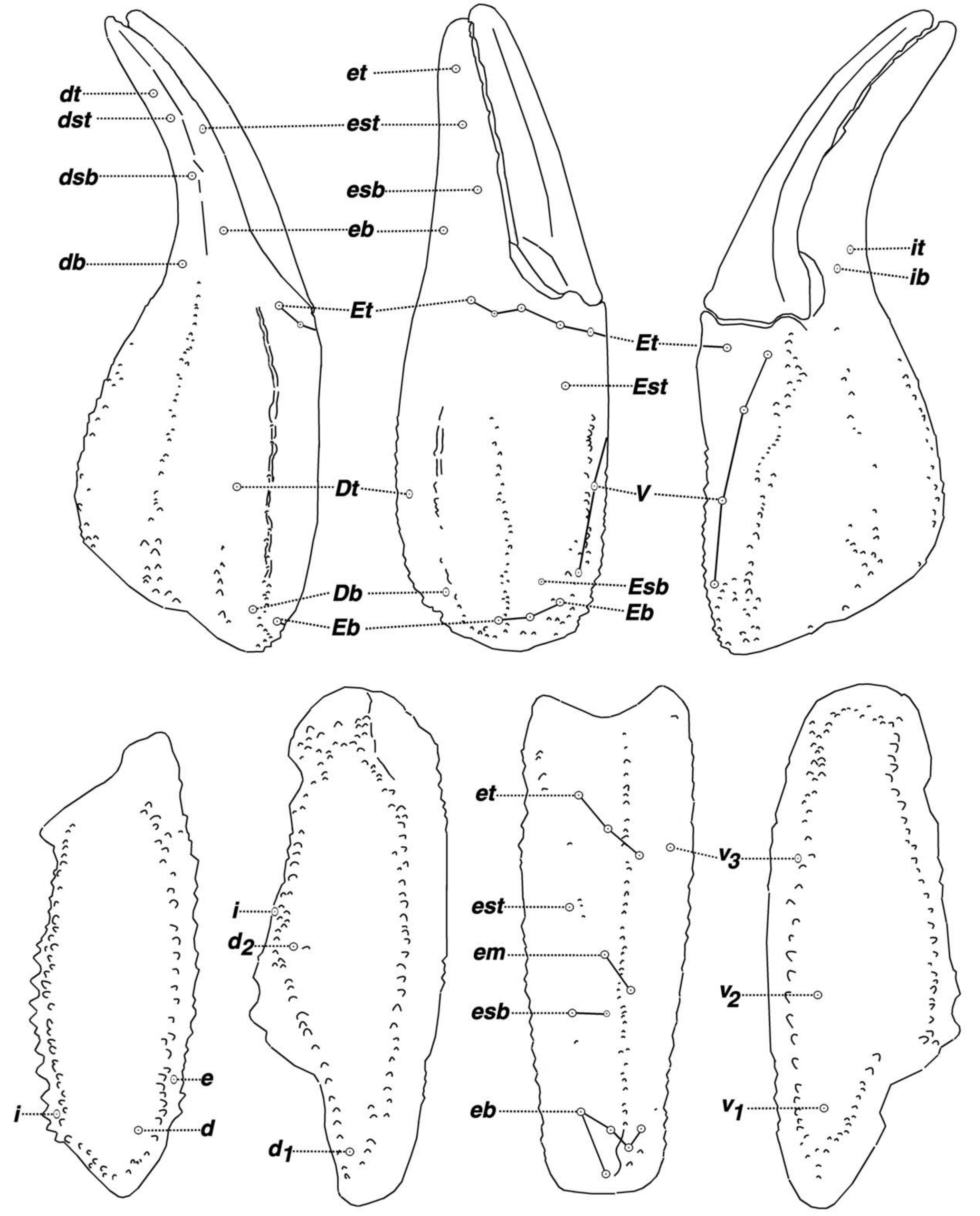


Figure C-2: *Graemeloweus glimmei*, female, Cache Creek, Lake Co., California, USA. Trichobothrial pattern. Illustration is based on a photograph courtesy of František Kovařík.

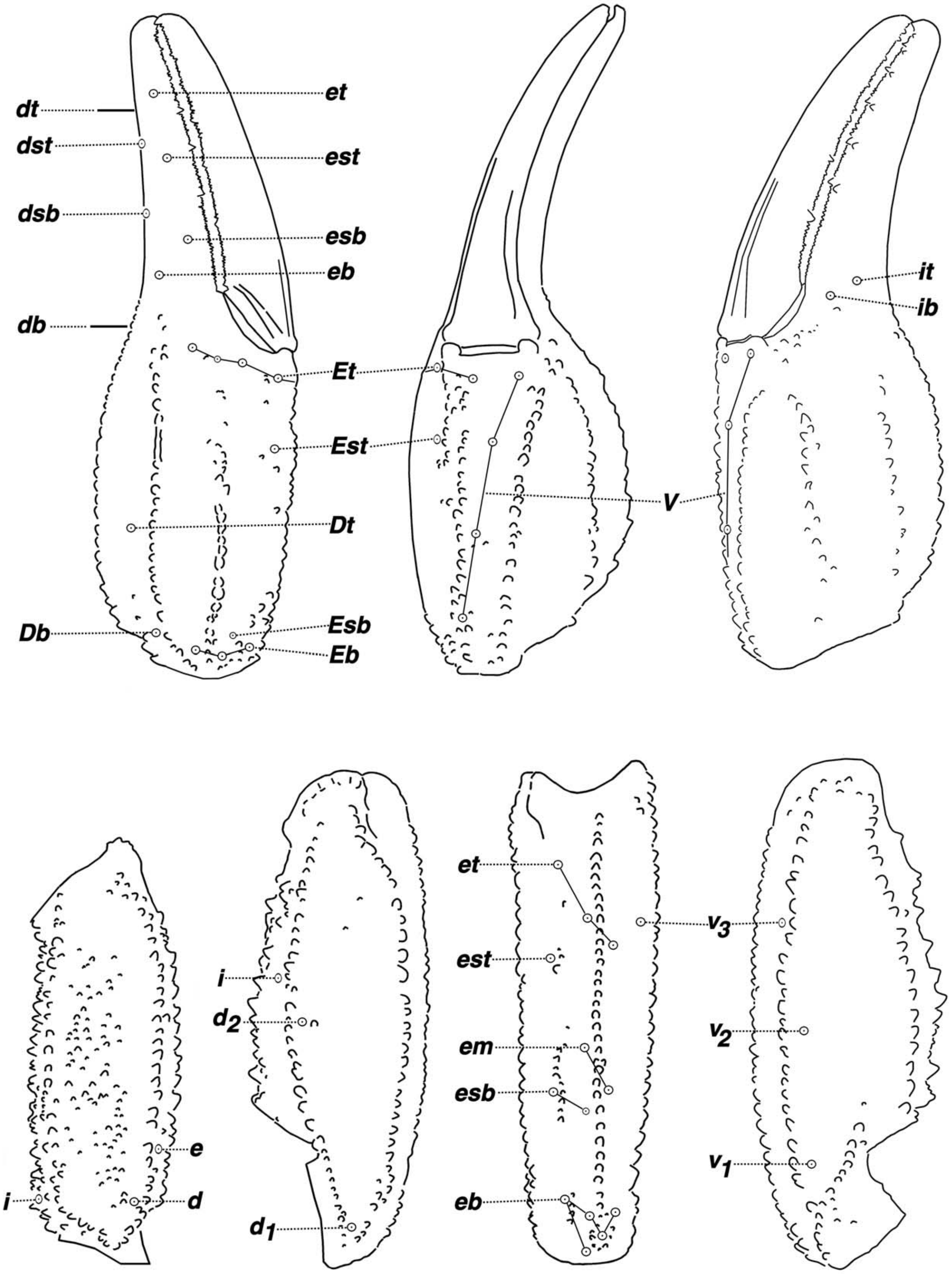


Figure C-3: *Graemeloweus maidu*, female, American River, El Dorado Co., California, USA. Trichobothrial pattern.