

A comparative study of the male genitalia of the Cacodemoniini (Pseudoscorpiones: Withiidae)

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Abstract. Propositions of homology are fundamental in systematics, since they provide the basis for supporting clades. Consequently, such phylogenetic propositions rely on correct character and character state definitions. Although male genital morphology is a key source of information for understanding the phylogeny and classification of the Withiidae (Pseudoscorpiones), they have only been subjected to examination in six of the 170 species of the family. The suprageneric classification of the Withiidae is unstable, as subfamilies and tribes are not well supported by morphological characters, and only the unranked group of genera Cacodemoniini is currently accepted. The aim of the present work is to characterize the male genital armature of the Cacodemoniini and propose homology statements for these structures based upon their morphological correspondence. Through direct examination and literature review of 12 of the 13 genera of the Cacodemoniini, we provide the first structural correspondence statements and descriptions of variation for the dorsal apodemes, the ejaculatory canal, the lateral apodemes, and the lateral rods; we also conclude that unlike other pseudoscorpions, the Cacodemoniini have paired, independent lateral rods and a long ejaculatory canal formed not by the dorsal apodemes exclusively, but by a fusion of the dorsal and the lateral apodemes. The proposed interpretations lay the groundwork for phylogenetic testing of homologies and may allow a better understanding of the formation of the spermatophore, given that it is molded by the genital armature.

Keywords: Chelonethi, male genital armature, homology.

<https://doi.org/10.1636/JoA-S-19-068>

In the phylogenomic era, large datasets of molecular information are being used to solve systematic problems. However, phylogenies need morphological data, since they serve as independent sources of information for testing hypotheses (Pyron 2015; Reeder et al. 2015; Wipfler et al. 2016) and improving estimations of topology and branch lengths (Donoghue et al. 1989; Wright & Hillis 2014; Pyron 2015), as well as allowing the inclusion of fossil taxa (Wiens et al. 2010; Wright & Hillis 2014). Additionally, when the phylogeny is used in historical reconstructions of the phenotype, ecology, physiology and behavior of the taxa under study, morphology becomes crucial (Giribet 2015).

Since homology propositions are fundamental to phylogenetic systematics and provide the basis for supporting clades in an evolutionary framework (Patterson 1982; De Pinna 1991; Nixon & Carpenter 2012), authors have focused on the importance of correct character and character state definitions (Serenó 2007; Vogt et al. 2010) standardizing terminology to facilitate understandability, character statement construction and information exchange (Vogt et al. 2013).

Pseudoscorpiones is a meso-diverse arachnid group with about 3600 valid species (Harvey 2002, 2013). They are small animals (less than 1.2 cm long) with cryptic habits, and are present in all terrestrial biogeographical regions except for the polar regions (Weygoldt 1969; Harvey 2013). The reproductive behavior of pseudoscorpions show a wide array of patterns from simple deposition of the spermatophore without direct interaction between the sexes, to complex courtship dances where the male takes the female by the chelae and moves her to the place where he has deposited the spermatophore (Weygoldt 1969). These complex patterns are especially seen in the superfamily Cheliferoidea (e.g., Weygoldt 1969; Harvey 1992; Andrade & Gnaspini 2003), which in turn is the sister-group to (Sternophoroidea + Cheiridioidea) (Harvey 1992; Benavides et al. 2019).

Withiidae is one of the four cheliferoid families, with about 171 species which are arranged into two subfamilies: Paragoniocheretinae, with five genera and 11 species, restricted to southern Africa, and Withiinae, with four tribes (Cacodemoniini, Juxtacheliferini, Protowithiini and Withiini), 32 genera and 159 species distributed worldwide (Harvey 2015). Thirteen of the 37 genera of the family are monotypic and nine include only two species. *Withius* Kew, 1911 is an exceptionally large genus with 50 species. The Withiidae are cosmopolitan but their highest diversity occurs in tropical and subtropical regions (Harvey 2015).

Although the Withiidae appears to be a monophyletic group (Harvey 1992; Muriene et al. 2008; Harvey et al. 2016; Benavides et al. 2019) and is morphologically characterized by the presence of patches of glandular setae in the abdomen (absent in *Juxtachelifer* Hoff, 1956, *Termitowithius* Muchmore, 1990, and *Protowithius* Beier, 1955) (Fig. 1) and by the perpendicular division of the femur and patella of leg I (Weygoldt 1970; Harvey 2015), the classification of its subfamilies and tribes was questioned by Harvey (2015), who stated that there are no synapomorphies for most of these taxa.

The Cacodemoniini is the only group of Withiidae that can be morphologically characterized: the long lateral apodemes in their male genital armature are developed into an extended triangle. Although this feature is not found in other pseudoscorpions, its monophyletic status has not been tested phylogenetically (Harvey 2015). The name was proposed by Chamberlin (1931a) based on the Neotropical genus *Cacodemonius* Chamberlin, 1931, and defined by several somatic character states. However, Harvey (2015) broadened the definition to include those withiids with the long, triangular lateral apodemes, and included 12 additional genera from the Americas, Australasia and Africa: *Balanowithius* Beier, 1959, *Cystowithius* Harvey, 2004, *Dolichowithius* Chamberlin, 1931, *Metawithius* Chamberlin, 1931, *Microwithius* Redikorzev, 1938, *Parawithius* Chamberlin, 1931, *Pycnowithius* Beier,

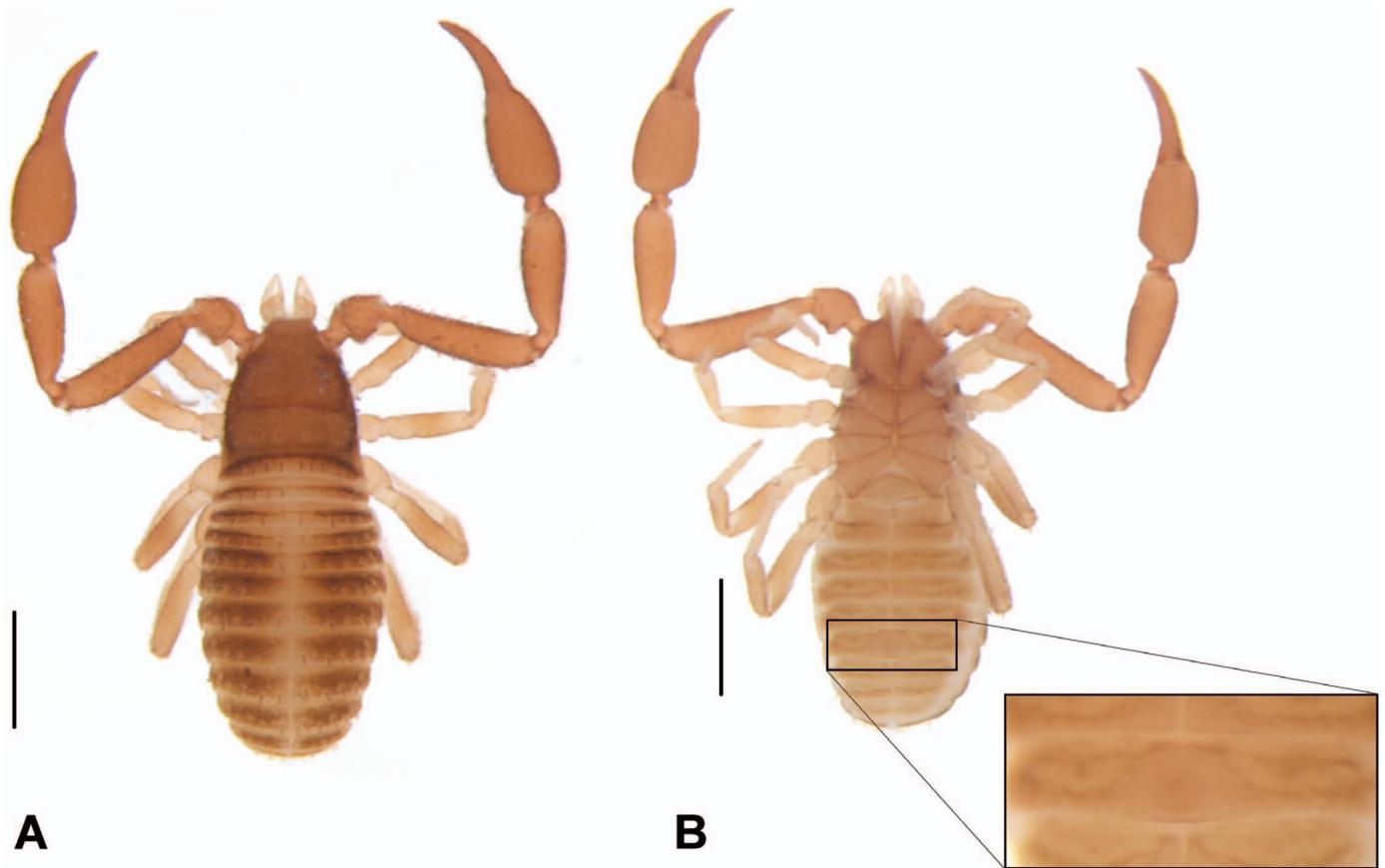


Figure 1.—Habitus of a male pseudoscorpion of the family Withiidae (nr. *Victorwithius*): (A) Dorsal; (B) Ventral. Inset shows the patches of glandular setae, one of the diagnostic characters of the family. Scale lines = 500 μm .

1979, *Rexwithius* Heurtault, 1994, *Rugowithius* Harvey, 2015, *Thaumatowithius* Beier, 1940, *Trichotowithius* Beier, 1944, and *Victorwithius* Feio, 1944.

The morphology of the male reproductive system has been described for a variety of pseudoscorpions (e.g., Vachon 1938; Legg 1971, 1974a, b, c, 1975a, b, c), and the most detailed comparative study was presented by Klausen (2005) for the family Atemnidae. For the Withiidae, Mahnert (1975) and Dashdamirov (1992) suggested that a thorough examination of the male and female genitalia will be important for understanding the classification within the family. Nevertheless, only 13 of the 170 species belonging to six genera, have been subjected to detailed studies (Heurtault 1971; Harvey 1988, 2004, 2015; Mahnert 1988; Dashdamirov 1992), perhaps because it is difficult to examine the reproductive system *in situ* (Klausen 2005) and its extraction entails destruction of other traditionally used characters.

Legg (1974c) provided a generalized account of the male genitalia and associated glands for pseudoscorpions and established the correspondence between the terminologies employed by different authors such as Schtschelkanovzeff (1910), Kästner (1927), Chamberlin (1931b), Vachon (1938), and Weygoldt (1966, 1969). Legg (1974c) noted that the genitalia consist of the genital atrium, the genital armature, the accessory glands, and the genital sacs. The genital atrium is constituted of a series of apodemes which serve as muscle attachments and support the diverticula and the ejaculatory canal; the atrium also

receives the products of the testis and accessory glands. Although the genitalia of Withiidae fits this description in general terms, their complexity and poor sclerotization make a proper understanding of its organization difficult.

In view of the above, the aims of this study are to (1) characterize the morphology of the male genital armature in several genera of the Cacodemoniini, and (2) propose homology statements for these structures based on morphological correspondence.

METHODS

We studied 19 cacodemoniine specimens, representing all six Neotropical genera and thus about half of the global genera of Cacodemoniini (Table 1). This included: two specimens of *Balanowithius egregius* Beier, 1959; for *Cacodemonius* Chamberlin, 1931 and *Cystowithius* Harvey, 2004 two clearly differentiated specimens from different localities of each genus were included. For *Dolichowithius* Chamberlin, 1931, four specimens belonging to three clearly differentiated morphospecies (msp) were examined. For *Parawithius* Chamberlin, 1931, a single specimen was studied. For *Victorwithius* Feio, 1944 seven specimens belonging to five clearly differentiated morphospecies (msp) were examined. However, two of these morphospecies (msp. 4 and 5) exhibit significant differences in somatic and genital morphology and thus are treated separately from that genus and named as *nr. Victorwithius* (see below).

Table 1.—Material examined for the study of the male genitalia in Cacodemoniini. All specimens were collected in Colombia (South America). Morphospecies codes are shown as ‘msp’.

Species	Department	Municipality	Locality	Collection number	No. of specimens
<i>Balanowithius egregius</i>	Nariño	Barbacoas	Vereda Altaquer, Reserva Natural Río Ñambí	ICN-APs-473	2
<i>Cacodemonius</i> msp1	Cundinamarca	Cachipay	—	ICN-APs-091	1
<i>Cacodemonius</i> msp2	Atlántico	Usiacurí	Reserva La Montaña	ICN-APs-614	1
<i>Cystowithius</i> msp1	Tolima	Juntas	Reserva Natural Ibanasca	ICN-APs-077	1
<i>Cystowithius</i> msp2	Cundinamarca	San Antonio del Tequendama	Parque Nacional Natural Chicaque	ICN-APs-298	1
<i>Dolichowithius</i> msp1	Cundinamarca	Cachipay	—	ICN-APs-027	2
<i>Dolichowithius</i> msp2	Sucre	San Marcos	La Florida	ICN-APs-145	1
<i>Dolichowithius</i> msp3	Santander	Suaita	San Jose de Suaita. Fundación San Cipriano	ICN-APs-413	1
<i>Parawithius</i> msp1	Cundinamarca	Cogua	Embalse del Neusa Teusa. Llano Grande	ICN-APs-082	1
<i>Victorwithius</i> msp1	Arauca	Arauca	Sede Universidad Nacional	ICN-APs-384	1
<i>Victorwithius</i> msp2	Meta	Vista Hermosa	Vereda La Reforma. Finca. Los Moriches	ICN-APs-405	2
<i>Victorwithius</i> msp3	Caquetá	Florencia	CIMAZ Macagual. Río Sarabando	ICN-APs-573	1
<i>nr. Victorwithius</i> msp1	Meta	San Martín	Vereda San Francisco. Hacienda La María	ICN-APs-076	1
<i>nr. Victorwithius</i> msp2	Cesar	Valledupar	Ecoparque Los Besotes. Campamento base	ICN-APs-597	1

The specimens were identified based on published descriptions (e.g., Chamberlin 1931a; Feio 1944; Beier 1959; Harvey 2004), comparison with specimens lodged in the Western Australian Museum, and the advice of Dr. Mark Harvey (Western Australian Museum). We also reviewed the available descriptions and illustrations of six of the seven genera of non-Neotropical Cacodemoniini (e.g., Harvey 1988, 2015; Mahnert 1988; Dashdamirov 1992; Heurtault 1994; Johnson et al. 2019). We had no access to specimens of *Thaumatoewithius* Beier, 1940 and no descriptions are available for the male genitalia for either of the two described species. Thus, we had data for 12 of the 13 cacodemoniine genera.

The Neotropical specimens came from the arachnological collection of the Instituto de Ciencias Naturales-Universidad Nacional de Colombia (ICN-APs) and were preserved in 75% or 100% ethanol.

We cleared and dissected males using the following protocol: (1) immerse the specimen in KOH 10% at room temperature for 4 hours or until the soft tissues disappeared; two lateral incisions in the abdomen of the individual were cut beforehand to facilitate the penetration of the KOH; (2) rinse in distilled water for 3 minutes; (3) transfer to 5% acetic acid for three minutes to neutralize the KOH; (4) rinse in distilled water for 1 minute; (5) the genitalia were extracted as follows: with the specimen upside down, forceps were used to create a

gentle push over the proximal and distal regions of the genital opercula and simultaneously, a minuten pin was used to pull the opercula anteriorly such that the genital armature popped out; once out, the minuten pin was used to sever the connections between the opercula and the armature; (6) after examination in glycerin, the genitalia is stored in a PCR tube in glycerin that was placed inside the vial with the body in ethanol. We took multifocal photographs of the genitalia with a Leica MC-170 HD digital camera attached to a Leica M205A stereomicroscope, which were processed with Leica Application Suite version 4.6.0.

Morphological nomenclature mainly follows Legg (1974c). We followed Klausen (2005) in using the terms “anterior” for the region of the genital armature that faces the prosoma, and “posterior” for the region that faces the opisthosoma. However, we use “ventral” to refer to the region attached to the genital opercula, and “dorsal” for the opposite region (Fig. 2). As suggested by Mahnert (1975), we concentrated on the chitinized parts of the genitalia, because the shape and location of soft tissue such as the diverticula could vary according to the method of preparation. Structural equivalence between genitalia components of different genera was based on their relative position, without further considerations on the history of the character which would require a thorough phylogenetic study.

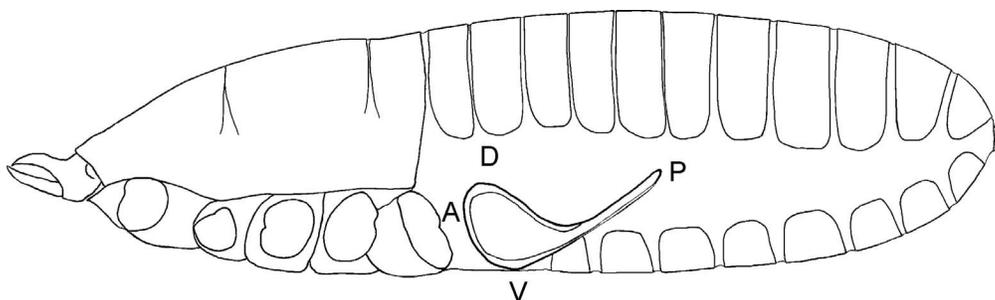


Figure 2.—Schematic representation in lateral view showing the orientation of the male genitalia of Cacodemoniini. Abbreviations: A= Anterior, P= Posterior, D= Dorsal, V= Ventral face.

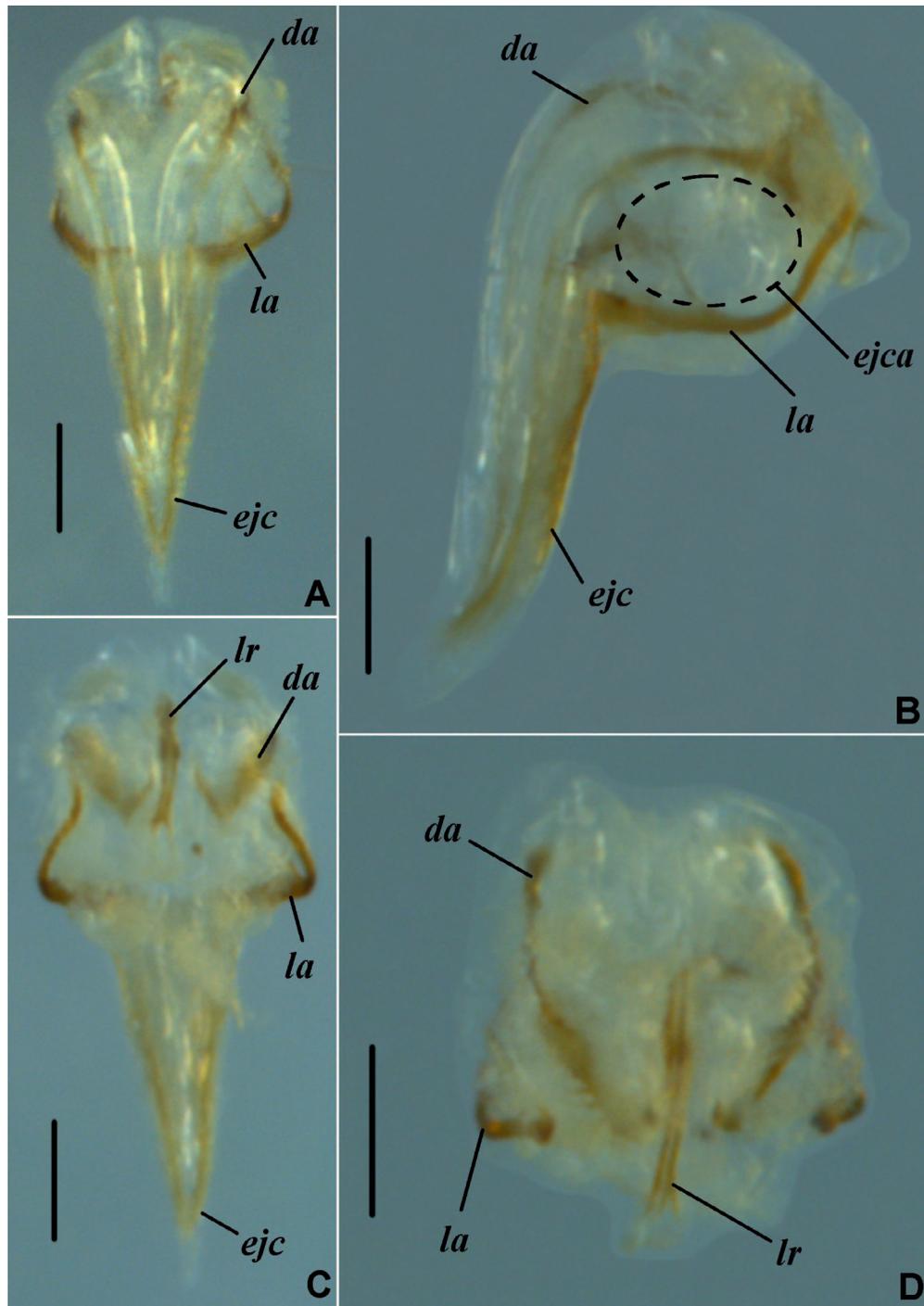


Figure 3.—Male genitalia of Cacodemoniini with indication of the main structures. (A) Ventral; (B) Lateral; (C) Dorsal; (D) Anterior views. Abbreviations: *da*: dorsal apodemes, *la*: lateral apodemes, *ejc*: ejaculatory canal, *lr*: lateral rods. Scale lines = 100 μm.

Abbreviations used: *da*—dorsal apodemes, *ejc*—ejaculatory canal, *ejca*—ejaculatory canal atrium, *la*—lateral apodemes, *lr*—lateral rods.

RESULTS AND DISCUSSION

As mentioned above, we identified two morphospecies that are morphologically similar to *Victorwithius*. They share important characters such as the presence of a patch of

glandular setae only on sternite VIII of the male, and the presence of an inconspicuous tactile seta on leg IV. However, they differ in other characteristics including the shape of the patch of glandular setae, which is circular in *Victorwithius* but oblong to elongated in the other taxa, and in the location of the patch, which lies in the pleural membrane in *Victorwithius* but lies within the sternite in the others. To signify these differences, which are likely to be of generic significance, we

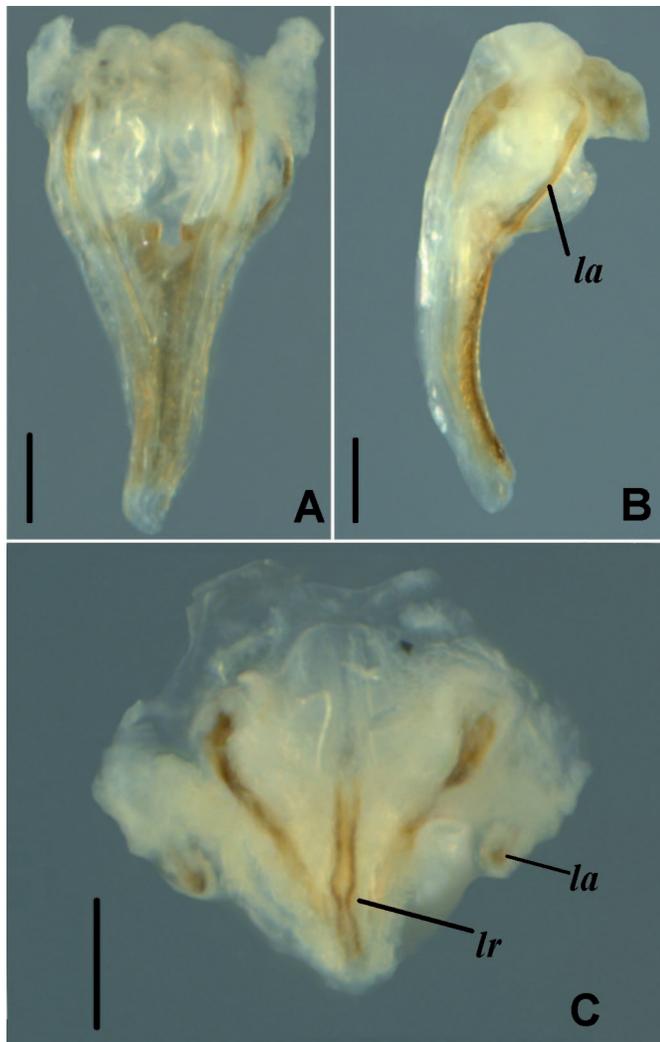


Figure 4.—Male genitalia of *Balanowithius egregius* Beier, 1959. (A) Ventral; (B) Lateral; (C) Anterior views. Scale lines = 100 μ m.

refer these two species as *nr. Victorwithius*. Further phylogenetic analysis is needed to test their status and relationships.

Structural correspondence and variation.—Overall, the male genital armature of Cacodemoniini comprises the dorsal apodemes (*da*) that extend posteriorly to form the ejaculatory canal (*ejc*), which is elongated, giving a triangular shape to the genitalia, and the lateral apodemes (*la*) which enclose the ejaculatory canal atrium (*ejca*), which is supported in its anterior region by the lateral rods (*lr*) (Fig. 3).

Dorsal apodemes (*da*): For Atemnidae, the closest family to the Withiidae (Benavides et al. 2019), Klausen (2005) defines the dorsal apodemes as an elongated fusion of the lateral rods. In contrast, cacodemoniines, they are not fused and appear as structures separate from the lateral rods (Figs. 3C, D). The genital atrium and the ejaculatory canal are formed by the dorsal and the lateral apodemes. In the genital atrium, the dorsal and lateral apodemes are separated surrounding it, while in the ejaculatory canal, the apodemes are fused (Fig. 3).

The degree and extent of sclerotization and the shape of the dorsal apodemes vary between genera. Sclerotization is very

marked in *Cacodemonius* (Figs. 5A, D) and *nr. Victorwithius* (Figs. 12A, D), while it is moderate in the genera *Balanowithius* (Fig. 4A), *Cystowithius* (Figs. 6A, D), *Dolichowithius* (Figs. 7A, D), and *Victorwithius* (Figs. 10A, D, G), and weak in *Parawithius* (Fig. 9A). The sclerotization covers the entire genital atrium in *Cacodemonius* (Figs. 5B, E), *Dolichowithius* (Figs. 7C, F), *Victorwithius* (Figs. 10C, F), and *nr. Victorwithius* (Figs. 12B, C, E, F), while in the genera *Balanowithius*, *Cystowithius* and *Parawithius* it covers less than half of the genital atrium (Figs. 4A, 6A, 9A). The first half of the *da* are sinuous in *Dolichowithius* (Fig. 7D) and straight in the other taxa. The *da* are wider in the proximal third in *Cystowithius* (Fig. 6A), while they are uniform in the other genera.

The dorsal apodemes in *Metawithius* and *Rugowithius* were labeled by Harvey (2015) and Johnson et al. (2019) as median diverticula; however, these structures appear in the corresponding position of the dorsal apodemes of the Neotropical Cacodemoniini. In addition, their illustrations suggest that these are sclerotized structures, whereas the diverticula are not sclerotized. The dorsal apodemes of *Metawithius* are short and straight while these are long and straight in *Rugowithius* (Harvey 2015) and *Trichotowithius* (Dashdamirov 1992). The illustration of the latter did not name this structure. In *Microwithius*, the dorsal apodemes cannot be seen due to a wide lateral apodeme covering the structures (Harvey 1988). Finally, in *Pycnowithius* and *Rexwithius*, these structures are not visible in the published illustrations [Mahnert (1988) and Heurtault (1994) respectively].

Ejaculatory canal (*ejc*): Unlike that of other pseudoscorpions (see e.g., Vachon 1938; Legg 1974c; Klausen 2005), the ejaculatory canal of cacodemoniines extends posteriorly as an inverted triangle seen in either dorsal or ventral view. The ejaculatory canal is formed by the elongation of the dorsal and lateral apodemes. This is the diagnostic character for the Cacodemoniini (Harvey 2015), and Klausen (2005) proposed that this is a functional extension of the ejaculatory canal atrium. This ejaculatory canal atrium (*ejca*) is a capsule surrounded by both the lateral apodemes and the dorsal apodemes (Fig. 3); as stated by Legg (1974c), it receives products of the testis and the accessory glands.

We found differences for this structure in its length, shape, sclerotization of the posterior tip, and its direction in lateral view. The *ejc* is shorter than the width of the ejaculatory canal atrium in *Cystowithius* (Fig. 6) and *Parawithius* (Fig. 9), while it is longer in the other genera. The posterior end of the *ejc* is acute in *nr. Victorwithius* (Figs. 12A, D), wide or even lanceolate in *Dolichowithius* (Fig. 7D) and rounded in the other Neotropical taxa. The posterior tip of the *ejc* is sclerotized in *Cystowithius* (Fig. 6A) and *nr. Victorwithius* (Fig. 12A) while it is not in the other genera (e.g. Figs. 7A, D, G, 10A). The *ejc* is straight in *Cacodemonius* (Figs. 5C, F), *Victorwithius* (Figs. 10E, H), and some species of *Dolichowithius* (Fig. 7E), while it is curved ventrally in *Balanowithius* (Fig. 4B), *Cystowithius* (Figs. 6B, E), and *Parawithius* (Fig. 9B), and curved dorsally in *nr. Victorwithius* (Figs. 12B, E) and some species of *Dolichowithius* (Figs. 7B, H).

The *ejc* is longer than the ejaculatory canal atrium in *Trichotowithius* and *Metawithius* (Dashdamirov 1992; Harvey 2015) and is either as long as or shorter than the ejaculatory canal atrium in *Pycnowithius* and *Rugowithius* respectively

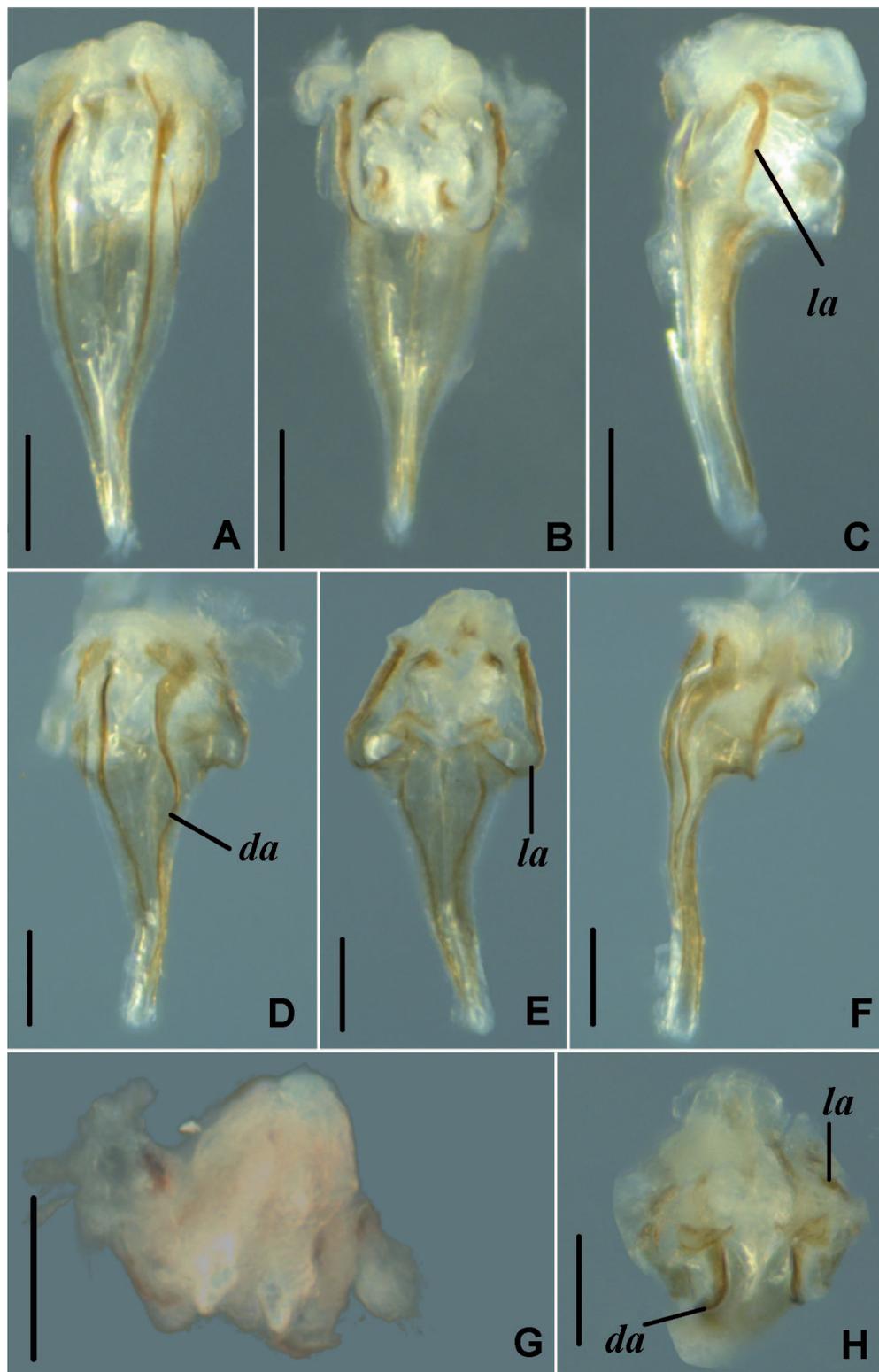


Figure 5.—Male genitalia of *Cacodemonius* msp. 1 (A–C, G) and *Cacodemonius* msp. 2 (D–F, H). A & D, Ventral; B & E, Dorsal; C & F, Lateral; G & H, Anterior views. Scale lines = 100 μ m.

(Mahnert 1988; Harvey 2015). It is straight in ventral view in all non-Neotropical genera, but the illustrations and descriptions do not indicate whether it is directed dorsally or ventrally in lateral view. The posterior end is clearly obtuse in

Trichotowithius (Dashdamirov 1992), but no information is available for the other genera. For *Microwithius* and *Rexwithius*, the *ejc* is not visible in the illustrations (Harvey 1988; Heurtault 1994). In *Rugowithius* the *ejc* is labeled as *ejca*

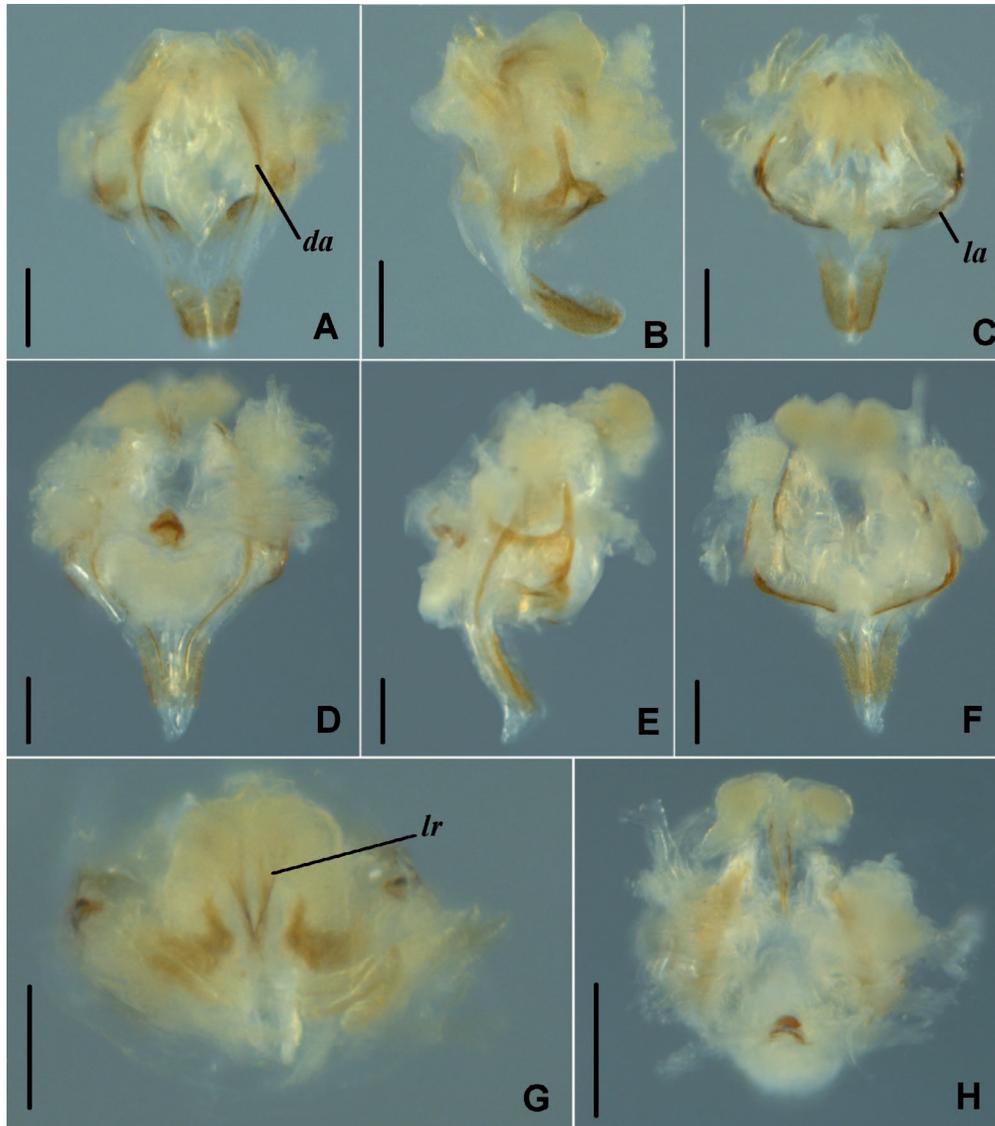


Figure 6.—Male genitalia of *Cystowithius* msp. 1 (A–C, G) and *Cystowithius* msp. 2 (D–F, H). A & D, Ventral; B & E, Lateral, C & F, Dorsal; G & H, Anterior views. Scale lines = 100 μ m.

(Harvey 2015) but the structure does not correspond to our definition.

Lateral apodemes (la): According to Klausen (2005) the lateral apodemes are formed by the anterolateral sides of the two dorsal and medial diverticula. Legg (1974b, c) described that the lateral apodemes support the dorsal and medial diverticula and serve as attachment sites for the sterno-coxal and coxal muscles, specifically the segmental dorso-ventral muscles, the longitudinal-ventral muscles, the appendicular muscles, and the transverse muscle. We could not observe whether Neotropical specimens follow Klausen's and Legg's interpretation as we did not study the diverticula due to the clearing process.

We observed that, in the Neotropical *Cacodemoniini*, the lateral apodemes (*la*) are paired and together with the dorsal apodeme form a bowl that protects the ejaculatory canal atrium. In lateral view, the apodemes exhibit different levels of curvature, and in ventral view they seem to merge with the

bifid dorsal apodeme. Together with the dorsal apodeme they extend posteriorly to form the ejaculatory canal. This general description of the lateral apodemes applies to the non-Neotropical *Cacodemoniini*.

The *la* vary between genera in their extension, shape of the basal region, and orientation of the concavity in lateral view. The *la* cover almost the whole genital atrium in *Balanowithius* (Fig. 4B), *Cacodemonius* (Figs. 5C, F), *Victorwithius*, and *nr. Victorwithius* (Figs. 10B, E, H, 12B, E), but they do not go beyond half of the genital atrium in *Cystowithius* (Fig. 6B, E), *Dolichowithius* (Figs. 7B, E, H), and *Parawithius* (Figs. 9A, B). The shape of the basal region is clearly angled in *Cacodemonius* (Figs. 5D, E), *Dolichowithius* (Figs. 7A, D, G), and *nr. Victorwithius* (Figs. 12A, D), but it is rounded in the other genera. The curvature is more pronounced anteriorly in *Balanowithius* (Fig. 4B) and *Cacodemonius* (Figs. 5C, F), but it is more pronounced dorsally in the other genera.

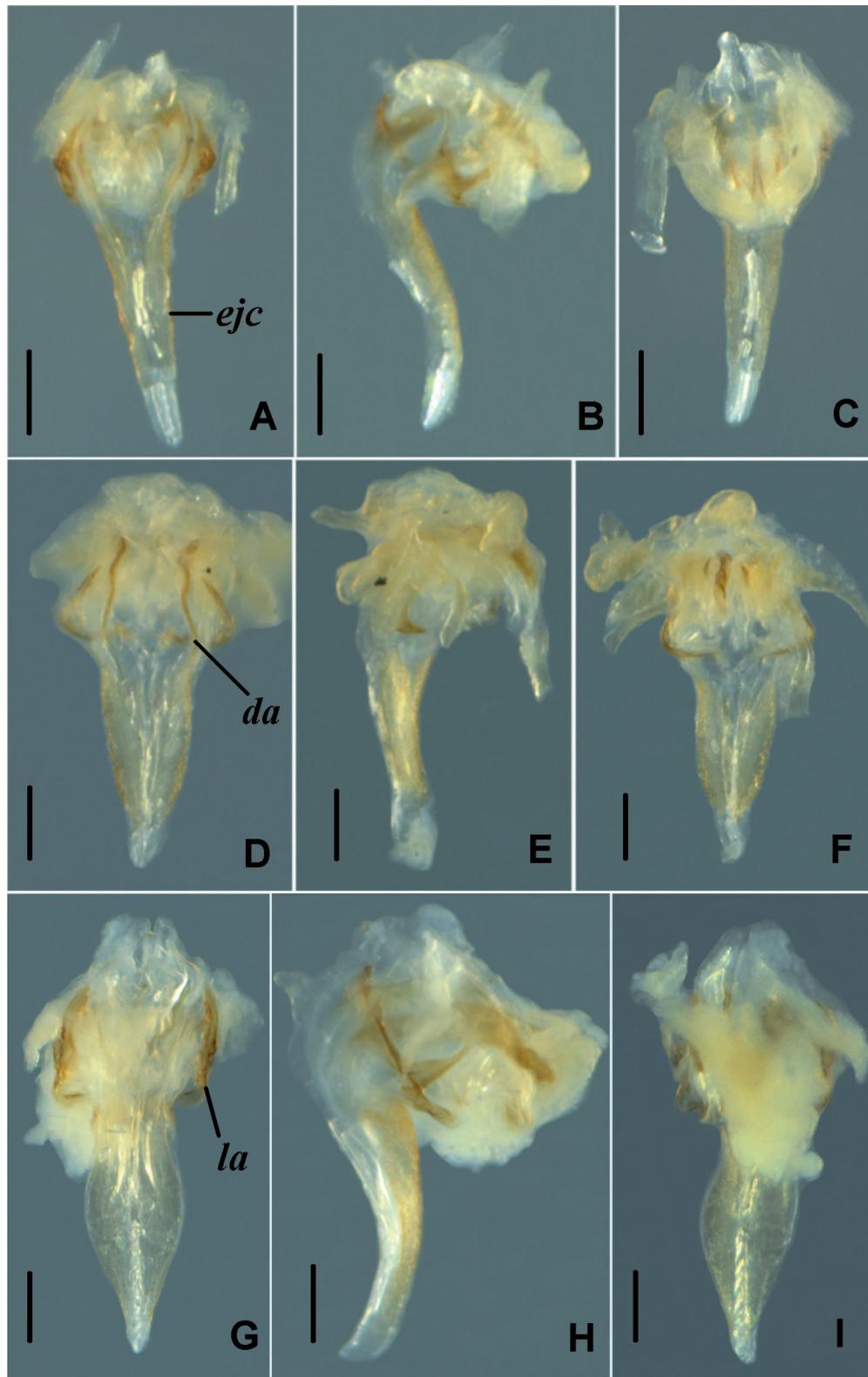


Figure 7.—Male genitalia of *Dolichowithius* msp. 1 (A–C), *Dolichowithius* msp. 2 (D–F) and *Dolichowithius* msp. 3 (G–I). A, D & G, Ventral; B, E & H, Lateral; C, F & I, Dorsal views. Scale lines = 100 μ m.

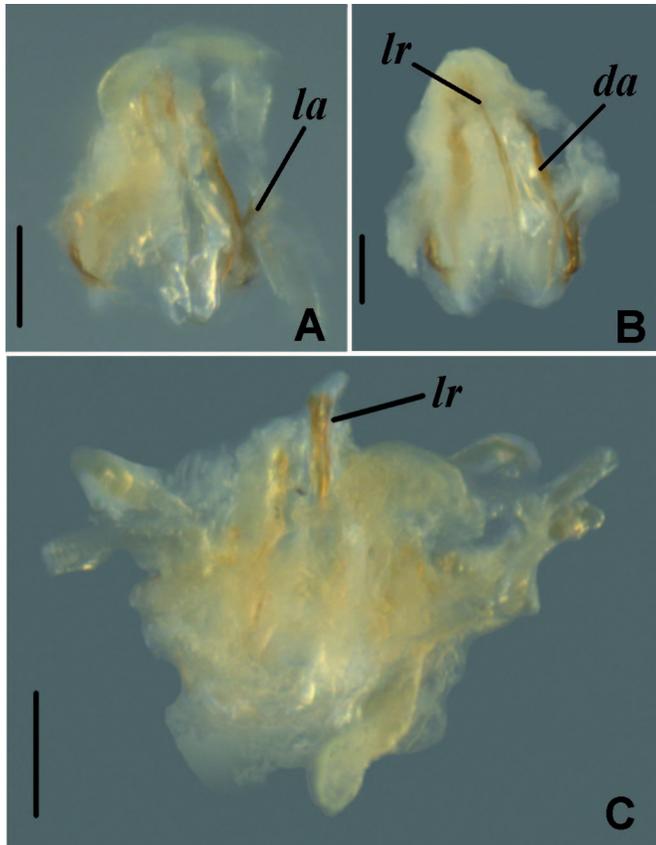


Figure 8.—Male genitalia of *Dolichowithius* spp., anterior view: (A) *Dolichowithius* msp. 1; (B) *Dolichowithius* msp. 3; (C) *Dolichowithius* msp. 2. Scale lines = 100 µm.

Heurtault (1971) named the lateral apodemes “arc chitinisé” for *Withius hispanus* (L. Koch, 1873), *W. faunus* (Simon, 1879) and *W. neglectus* (Simon, 1878). Using the English version, “chitinized arch”, Harvey (2015) and Johnson et al. (2019) follow this nomenclature for *Metawithius*. Since the chitinized arch corresponds to the lateral apodemes of Legg (1974c), we follow this original nomenclature. The *la* are wide in *Microwithius*, *Pycnowithius* and *Rugowithius* (Harvey 1988, 2015; Mahnert 1988), while they are thin in *Metawithius* and *Trichotowithius* (Dashdamirov 1992; Harvey 2015; Johnson et al. 2019). The only figure available for *Rexwithius* (Heurtault 1994) does not allow us to locate the *la*.

Lateral rods (*lr*): The lateral rods are only visible in anterior view. In the Cacodemoniini, they are placed between the anterior ends of the dorsal and lateral apodemes, and vary in shape, alignment and length. They are sinuous only in *Balanowithius* (Fig. 4C). They diverge dorsally in *Cystowithius* (Figs. 6G, H) and *Parawithius* (Fig. 9D), while they are parallel in the other genera. The lateral rods do not extend beyond the lateral apodemes in *Balanowithius* (Fig. 4C), whereas they are longer in the other genera. In many of the studied specimens, they were not visible due to the high amount of tissue around this area.

Concerning the non-Neotropical genera, the lateral rods are only visible in the illustrations of *Metawithius* and *Microwithius* provided by Johnson et al. (2019) and Harvey (1988),

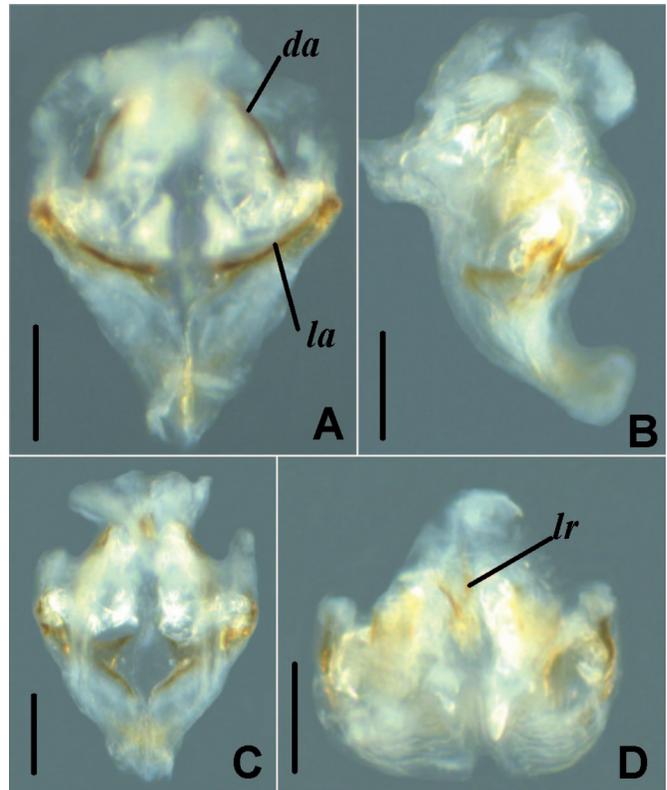


Figure 9.—Male genitalia of *Parawithius* msp. 1: (A) Ventral; (B) Lateral; (C) Dorsal; (D) Anterior views. Scale lines = 100 µm.

respectively. In *Metawithius*, they are sinuous and parallel, while in *Microwithius* they are divergent dorsally. In *Trichotowithius*, Dashdamirov (1992) labels as lateral rods two longitudinal projections located together with the ejaculatory canal; however, this location does not fit our observations in other Cacodemoniini and we were unable to establish their correspondence to known structures. Since lateral rods are present in all the other cheliferoid families (e.g., Legg 1974c; Klausen 2005), it is likely that these structures are present in all Cacodemoniini.

Taxonomic characterization of the male genital armature for each genus.—A description of the genital armature of each of the Neotropical genera of Cacodemoniini is provided below.

Balanowithius (Fig. 4)

Dorsal apodemes with sclerotization moderate to almost absent, stronger in the first half of its length; straight and of uniform width throughout its length; (Fig. 4A). **Lateral apodemes** covering most of the ejaculatory canal atrium; rounded basally; projecting anteriorly in lateral view (Fig. 4B). **Ejaculatory canal** long, two thirds length of genital armature; tip rounded, not sclerotized posteriorly; curved ventrally in lateral view (Fig. 4A). **Lateral rods** sinuous; parallel; not extending beyond lateral apodemes in dorsal view (Figs. 4B–C). This characterization is based on two specimens of *Balanowithius egregius*.

Cacodemonius (Fig. 5)

Dorsal apodemes intensely and entirely sclerotized; straight and of uniform width throughout its length; (Figs. 5A, D).

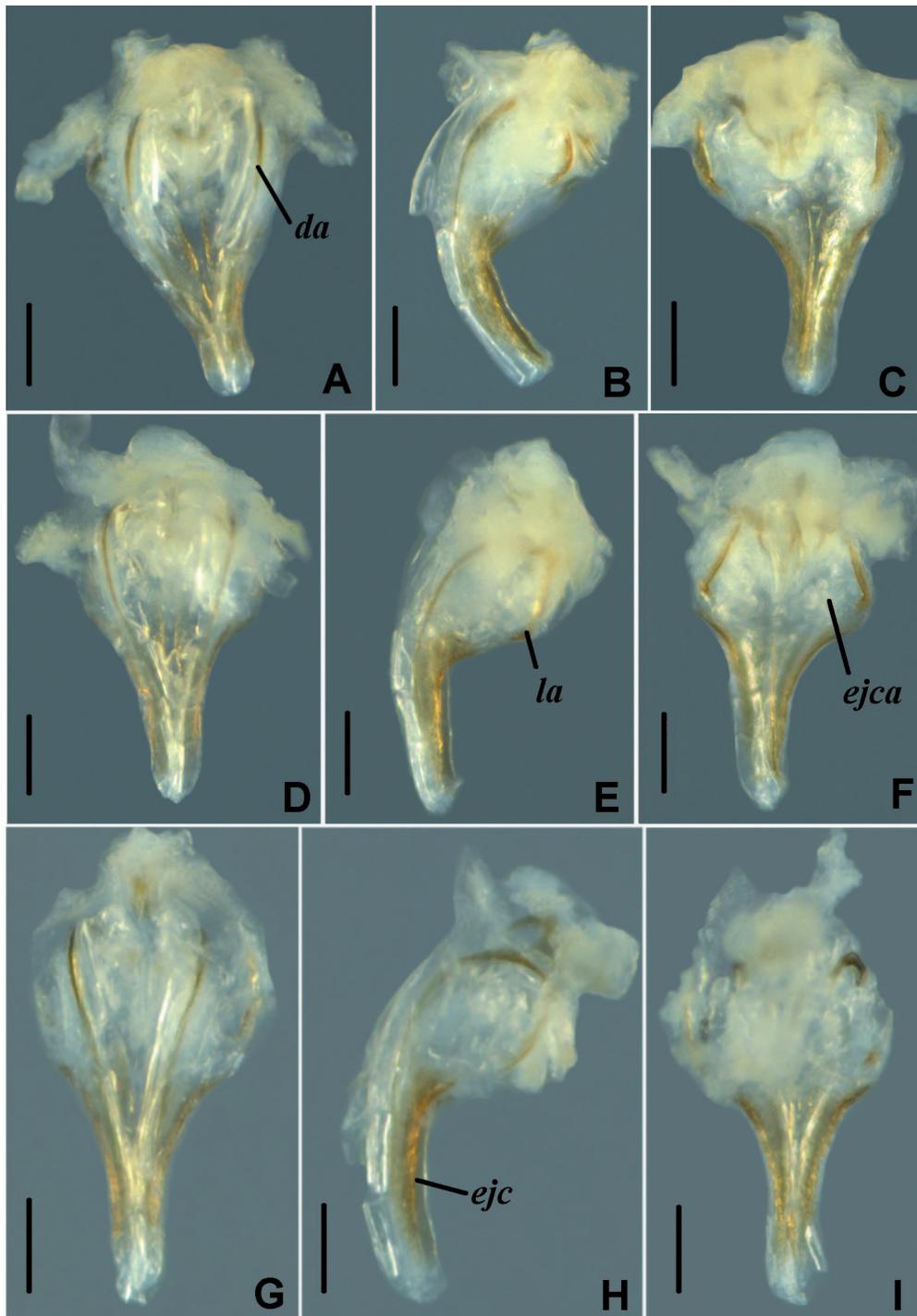


Figure 10.—Male genitalia of *Victorwithius* spp. *Victorwithius* msp. 1 (A–C), *Victorwithius* msp. 2 (D–F), and *Victorwithius* msp. 3 (G–I). A, D & G, Ventral; B, E & H, Lateral; C, F & I, Dorsal views. Scale lines = 100 μm .

Lateral apodemes extending over most of ejaculatory canal atrium; angular basally; projecting anteriorly in lateral view (Figs. 5A, C, D). *Ejaculatory canal* long, two thirds length of genital armature; tip rounded, not sclerotized posteriorly; straight in lateral view (Figs. 5A, C, D, F). *Lateral rods* extending beyond lateral apodemes in dorsal view (Figs. 5G, H). This characterization is based on two specimens of two morphospecies of the genus *Cacodemonius*.

Cystowithius (Fig. 6)

Dorsal apodemes with sclerotization moderate to almost absent, reaching half or less of its length; straight throughout its length; the sclerotization of its border is wider at the ejaculatory canal atrium (Figs. 6A, D). *Lateral apodemes* at most half length of the ejaculatory canal atrium; rounded basally; projecting dorsally (Figs. 6B, C, E, F). *Ejaculatory*

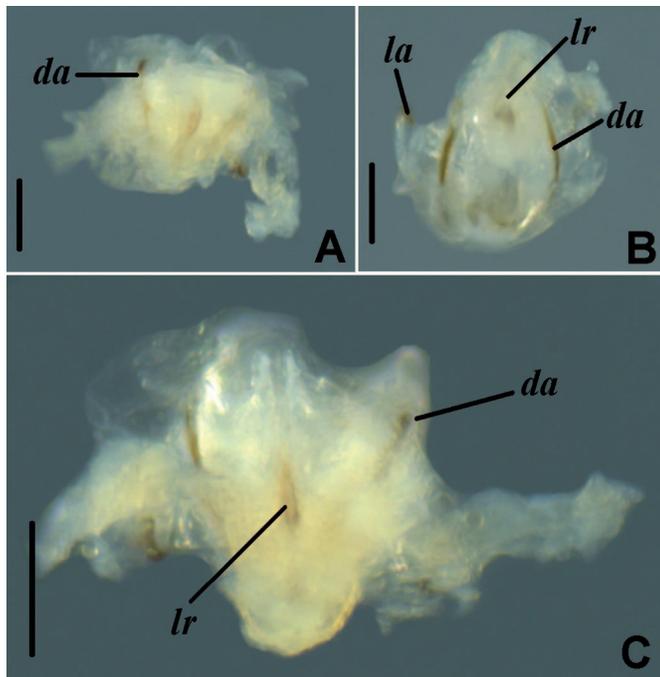


Figure 11.—Male genitalia of *Victorwithius* spp., anterior view: (A) *Victorwithius* msp. 2; (B) *Victorwithius* msp. 3; (C) *Victorwithius* msp. 1. Scale lines = 100 μ m.

canal short, one third of genital armature length; tip rounded, sclerotized posteriorly; curved dorsally in lateral view (Figs. 6A, B, D, E). *Lateral rods* straight; divergent dorsally; extending beyond lateral apodemes in dorsal view (Figs. 6F,G). This characterization is based on two specimens of two morphospecies of the genus *Cystowithius*.

Dolichowithius (Figs. 7, 8)

Dorsal apodemes with sclerotization moderate to almost absent, extending over half or less of its length; sinuous in proximal third and straight distally; of uniform width throughout (Figs. 7A, D, G). *Lateral apodemes* extending over at most half of ejaculatory canal atrium; angular basally; projecting dorsally (Fig. 7). *Ejaculatory canal* long, two thirds of genital armature length; tip acute; not sclerotized posteriorly; straight in lateral view, sometimes curved ventrally (Figs. 7A, B, D, E, G, H). *Lateral rods* straight; parallel; extending beyond lateral apodemes in dorsal view (Fig. 8). This characterization is based on four specimens belonging to three morphospecies of the genus *Dolichowithius*.

Parawithius (Fig. 9)

Dorsal apodemes with sclerotization moderate to almost absent, extending over half or less of its length; straight throughout its length; of uniform width throughout (Fig. 9C). *Lateral apodemes* extending over at most half of ejaculatory canal atrium; rounded basally, projecting dorsally (Figs. 9A–C). *Ejaculatory canal* short, one third of genital armature length; tip rounded, not sclerotized posteriorly; curved dorsally in lateral view (Figs. 9B, C). *Lateral rods* straight; divergent dorsally; extending beyond lateral apodemes in

dorsal view (Fig. 9D). This characterization is based on one specimen of the genus *Parawithius*.

Victorwithius (Figs. 10, 11)

Dorsal apodemes entirely sclerotized but the sclerotization is moderate to weak; straight and of uniform width throughout its length (Figs. 10A, D, G). *Lateral apodemes* extending over most of ejaculatory canal atrium; rounded basally; projecting dorsally (Fig. 10). *Ejaculatory canal* long, two thirds of genital armature length; tip rounded, not sclerotized posteriorly; straight in lateral view (Figs. 10A, B, D, E, G, H). *Lateral rods* straight, parallel; extending beyond lateral apodemes in dorsal view (Fig. 11). This characterization is based on five specimens belonging to three morphospecies of the genus *Victorwithius*.

nr. Victorwithius (Fig. 12)

Dorsal apodemes intensely sclerotized; extending over its entire length; straight and of uniform width throughout its length (Figs. 12A, D). *Lateral apodemes* extending over most of ejaculatory canal atrium; angular basally; projecting dorsally (Figs. 12A–F). *Ejaculatory canal* long, two thirds of the genital armature length; tip acute, sclerotized posteriorly; curved dorsally in lateral view (Figs. 12A, B, D, E). *Lateral rods* straight, parallel; extending beyond lateral apodemes in dorsal view (Figs. 12G, H). This characterization is based on two specimens belonging to two morphospecies of this undescribed taxon.

Final remarks.—Our analysis explored, for the first time, the male genitalia of the Cacodemoniini using a comparative approach and provides hypotheses of structural correspondences, covering six of the 13 cacodemoniine genera by direct examination of specimens, and six genera using published descriptions and illustrations (Harvey 1988, 2015; Mahnert 1988; Dashdamirov 1992; Heurtault 1994; Johnson et al. 2019).

Structural correspondence conclusions: In agreement with Harvey (2015), our analyses allow us to characterize the Cacodemoniini genitalia as follows: The dorsal apodemes and the lateral apodemes are separated in the most anterior region and surround the ejaculatory canal atrium. Posteriorly, they are fused and extend to form the ejaculatory canal. The lateral rods are separated from the apodemes. Variation on the genitalia is found in the shape of the lateral apodemes, the length of the ejaculatory canal and its projection in lateral view.

Regarding the triangular projection of the ejaculatory canal, we disagree with Harvey (2015) who attributes this projection to the lateral apodemes. Whenever we could inspect the genitalia in sufficient detail, through direct examination or drawings, we observed that such elongation includes the fusion of the dorsal apodemes with the lateral apodemes.

Taxonomic implications: Although we have not observed every species of Neotropical Cacodemoniini, our data suggest that the differences in the male genital armature of each genus follow the current classification of the group, agreeing with the proposition of Mahnert (1975) that this is a helpful structure for taxonomy at this taxonomic rank. This result contrast with the findings of Klausen (2005) for the genera of Atemnidae where there is little taxonomic correspondence.

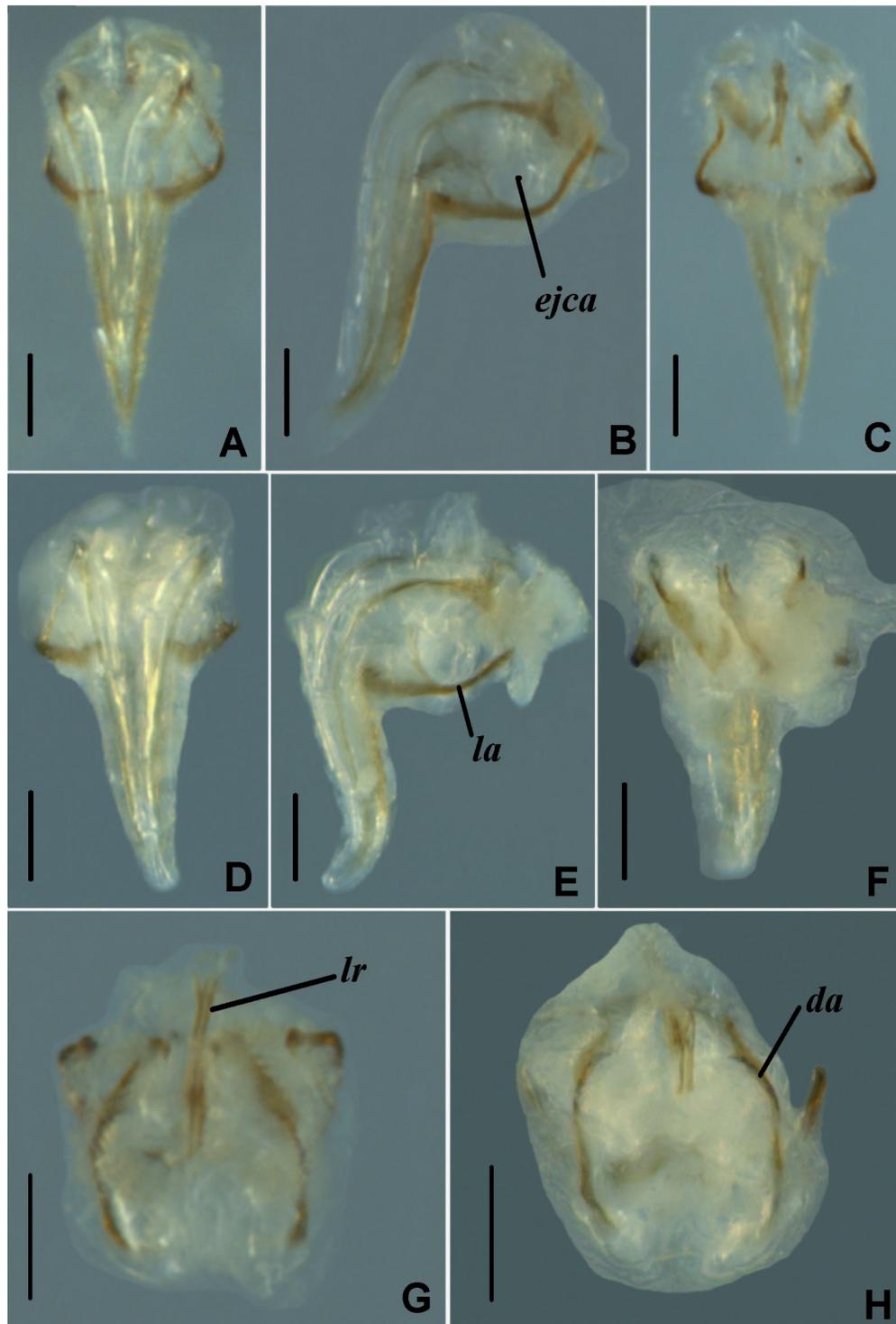


Figure 12.—Male genitalia of *nr. Victorwithius* msp. 1 (A–C, G); *nr. Victorwithius* msp. 2 (D–F, H). A & D, Ventral; B & E, Lateral; C & F, Dorsal; G & H, Anterior views. Scale lines = 100 μm.

Phylogenetic connotations: The taxonomic distribution of the characters of the male genital armature across the Cacodemoniini genera makes it difficult to even speculate on their relationships using this character system. For example, the dorsal apodeme sclerotization is moderate and straight throughout its length in *Balanowithius* and *Victorwithius*, while

the lateral apodemes are projected anteriorly in *Balanowithius* as opposed to dorsally in *Cystowithius* and *Victorwithius*. Another example is the presence of a short ejaculatory canal in *Cystowithius* and *Parawithius*, while *Cystowithius* and *nr. Victorwithius* share a sclerotized tip of the ejaculatory canal which is absent in *Parawithius*.

Examining some species of *Withius*, Klausen (2005) found that, like in Atemnidae, the lateral rods are neither merged proximally nor directed anteriorly and concluded that both families could be closely related. Our more extensive sampling of the Withiidae concur with his observation on *Withius* and with the phylogenetic hypothesis of Benavides et al. (2019), who found strong molecular evidence to support a sister-group relationship between Atemnidae and Withiidae.

Despite the impressive advances using molecular data for phylogenetic and biodiversity studies, morphological analyses, such as the one provided here, are still required to understand the history of the phenotypes as the substrate of evolution. A thorough understanding of the genitalia in pseudoscorpions may shed further light into the diversity and history of their courtship strategies.

ACKNOWLEDGMENTS

We are very grateful to Dr. Gerald Legg and Dr. Finn Klausen for their contributions to our knowledge of the pseudoscorpion genitalia and their help answering our questions and giving us helpful comments on the development of this study. Also, we thank Andrea Carvajal for her time and willingness to check the descriptions, as well as Dr. Mark Harvey and two anonymous reviewers who made several comments that greatly improved our manuscript. We acknowledge the Universidad Nacional de Colombia and Colciencias for support to CRO with the scholarship Doctorados Nacionales: 727-2015.

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Manuscript received 14 November 2019, revised 28 September 2020.