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SISTEMÁTICA FILOGENÉTICA DEL GÉNERO *STENOCHRUS* CHAMBERLIN, 1922 (SCHIZOMIDA: HUBBARDIIDAE)

TESIS

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PRESENTA:

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Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas, Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 26 de agosto de 2019, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **MONJARAZ RUEDAS RODRIGO** con número de cuenta **305068338** con la tesis titulada: **"SISTEMÁTICA FILOGENÉTICA DEL GÉNERO *STENOCHRUS* CHAMBERLIN, 1922 (SCHIZOMIDA:HUBBARDIIDAE)"**, realizada bajo la dirección del **DR. OSCAR FEDERICO FRANCKE BALLVÉ:**

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
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ÍNDICE

RESUMEN.

El género *Stenochrus* estaba conformado por 22 especies descritas, distribuidas mayoritariamente en México y Centroamérica, las cuales habitaban principalmente en cuevas, y selvas tropicales, aunque también pueden ser encontradas en selvas bajas y bosques templados. Adicionalmente, la morfología encontrada dentro del grupo era muy variable con respecto a otros géneros del orden Schizomida, debido a esta variabilidad, la caracterización morfológica del género *Stenochrus* es compleja.

La única característica diagnóstica del género *Stenochrus* era la presencia de dos pares de lóbulos en la espermateca, en las cuales, los lóbulos laterales se encuentran reducidos; adicionalmente, el flagelo de los machos presenta un relieve dorsal liso, sin ninguna modificación. Por consiguiente, el género *Stenochrus* se convirtió en un género “basurero” en el cual ubicaban a todas las especies que carecían de estructuras modificadas o que no podían encajar con la descripción de algún otro género. Lo anterior conllevo a que cerca de ocho especies fueran ubicadas dentro de *Stenochrus* en los últimos años, en las cuales se ha hecho énfasis de la ubicación de esas especies dentro de *Stenochrus* debido a que su ubicación dentro de algún otro género era conflictiva.

De esta manera se describen 10 especies nuevas, las cuales difieren de las actuales especies descritas, en su morfología y distribución geográfica (Capítulos III y IV). La mayoría de las diferencias morfológicas que pueden ser observadas en las especies de *Stenochrus* varían en las diferentes combinaciones de caracteres en el flagelo de los machos, la armadura y forma de los pedipalpos, así como la forma general de las espermatecas.

Adicionalmente se reporta por primera vez dentro del género *Stenochrus* la presencia de dimorfismo en los pedipalpos de los machos adultos, el cual había sido reportado anteriormente en los géneros *Rowlandius* y *Mayazomus* (Capítulo III). De esta forma, el dimorfismo sexual podría ayudar a la caracterización y delimitación de las especies del género *Stenochrus,* sin embargo las implicaciones biológicas o evolutivas de esta condición aún son desconocidas.

Por último se presentan los resultados filogenéticos realizados con evidencia morfológica y molecular, los cuales dieron como resultado que el género *Stenochrus* era un grupo parafilético. Tras la exhaustiva examinación de la morfología del grupo y con base en los análisis filogenéticos se propone una nueva clasificación natural, la cual refleja la historia evolutiva del grupo, describiendo seis géneros nuevos, re-diagnosticando el género *Stenochrus* y finalmente revalidando el género *Heteroschizomus* (Capítulos IV y V).

ABSTRACT.

The genus *Stenochrus* included 22 described species, mostly distributed in Mexico and Central America, which inhabited mainly in caves and tropical forests, but could also be found in dry forests and pine/oak forest. Additionally, the morphology present within the group was very variable with respect to other genera of the order Schizomida, and due to this variability, the morphological characterization of the genus *Stenochrus* was complicated.

The only diagnostic feature for *Stenochrus* was the presence of two pairs of lobes in the spermathecae, with lateral lobes reduced; additionally, the male flagellum presents a smooth dorsal relief, without any modification. Therefore, the genus *Stenochrus* became a "junkyard" genus in which they located all the species that lacked modified structures or that could not fit with the description of some other genus. This led to the fact that in the last years, about eight new species were located within *Stenochrus*, in which emphasis had been placed on the location of these species within *Stenochrus* because their location in another genus was conflictive.

Thus, we described 10 new species, which differ from the formerly described species, in their morphology and geographical distribution (Chapters III and IV). Most of the morphological differences that can be observed in *Stenochrus* species vary in the different combinations of characters in the flagellum of the males, the armature and shape of the pedipalps, as well as the general shape of the spermathecae.

Additionally, the presence of dimorphism in pedipalps of adult males was reported for the first time within the genus *Stenochrus*, which had previously been reported in the genera *Rowlandius* and *Mayazomus* (Chapter III). Therefore, the sexual dimorphism could help in the characterization and delimitation of the species of the genus *Stenochrus*; however, the biological or evolutionary implications of this dimorphic condition in males are still unknown.

Finally, the phylogenetic results of the morphological and molecular data are presented, which recovered *Stenochrus* as a paraphyletic group. The exhaustive examination of the morphology of the group and based on the phylogenetic analysis, a new and natural classification is here proposed, which reflects the evolutionary history of the group, describing six new genera, re-diagnosing the genus *Stenochrus* and revalidating the genus *Heteroschizomus* (Chapters IV and V).

INTRODUCCIÓN GENERAL.

El orden Schizomida es un grupo de arácnidos considerado como uno de los grupos menores dentro de la clase Arachnida debido a su diversidad (Harvey, 2003). Está compuesto por dos familias: Protoschizomidae Rowland, 1975 con tres géneros y 17 especies, endémica a Norteamérica y la familia Hubbardiidae Cook, 1899 con 59 géneros y 339 especies distribuidas alrededor del mundo (Harvey, 2003, 2013; Monjaraz-Ruedas et al., 2017). En el continente Americano se distribuyen aproximadamente 29 géneros de Hubbardiidae, de los cuales 14 géneros son monotípicos, seis géneros incluyen solo dos especies y solo nueve de ellos contienen más de dos especies, siendo los géneros *Rowlandius* Reddell y Cokendolpher, 1995 (56 spp.), *Stenochrus* Chamberlin, 1922 (22 spp.) y *Surazomus* Reddell y Cokendolpher, 1995 (22 spp.) los más diversos (Harvey, 2003, 2013; Monjaraz-Ruedas y Francke, 2015). En México, actualmente se distribuyen seis géneros pertenecientes a las dos familias: los géneros *Protoschizomus* Rowland, 1975 (6 spp.) y *Agastoschizomus* Rowland, 1971 (8 spp.) dentro de Protoschizomidae; y los géneros *Mayazomus* Reddell y Cokendolpher, 1995 (9 spp.), *Pacal* Reddell y Cokendolpher, 1995 (3 spp.), *Stenochrus* (22 spp.), y *Sotanostenochrus* Reddell y Cokendolpher, 1991 (2 spp.) dentro de Hubbardiidae (Harvey, 2003, 2013; Monjaraz-Ruedas y Francke, 2015).

El género *Stenochrus* está distribuido en Estados Unidos, Guatemala, Honduras, Nicaragua y México, siendo este último el país con la mayor diversidad con 22 especies (Harvey, 2003; 2013) (Tabla 1). Sin embargo, la presencia de la especie cosmopolita *Stenochrus portoricensis* Chamberlin, 1922, amplia el rango de distribución del género hacia Belice, Bermuda, Brasil, Colombia, Cuba, Dominica, Ecuador, Eslovaquia, España, Estados Unidos, Guatemala, Honduras, Inglaterra, Islas Vírgenes, Jamaica, México, Nicaragua, Panamá, Puerto Rico, República Checa y República Dominicana (Christophoryová et al., 2013; Harvey, 2013; Korenko et al., 2009).

Actualmente, las especies incluidas dentro del género *Stenochrus* presentan una amplia diversidad morfológica que puede ser observada en las diferentes formas en el flagelo de los machos (el carácter más importante en la delimitación de especies), en la diversidad de tamaños corporales, diferentes coloraciones, diferentes patrones sedales e inclusive la presencia de dimorfismo sexual en algunas especies, el cual se ve enteramente reflejado en la modificación de los pedipalpos de los machos. Esta gran diversidad morfológica puede deberse a que las especies actualmente incluidas en el género *Stenochrus* se distribuyen en una gran cantidad de hábitats diferentes, que van desde cuevas, selvas bajas, selvas altas, bosques de pino y matorrales (Rowland y Reddell, 1980). Otro factor que muy probablemente afecta la diversidad morfológica del género es la probable existencia de una mezcla de dos componentes biogeográficos diferentes, siendo que las especies distribuidas en Estados Unidos y el Norte de México tienen mayor similitud morfológica con especies del género *Hubbardia* Cook, 1899 (California, EU), mientras que las especies distribuidas en el Sur de México y Centro América, presentan una mayor afinidad morfológica a las especies de géneros Sudamericanos como *Belicenochrus* Armas y Viquez, 2010, *Rowlandius* Reddell y Cokendolpher, 1995 y *Surazomus*. Por lo cual, el género podría estar conformado por fauna Neártica y Neotropical, ampliando de esta forma la variabilidad morfológica, tal como fue reportado por Rowland (1975) y Reddell y Cokendolpher (1995). Sin embargo, la diversidad morfológica también podría estar dada por la mezcla de más de un grupo natural (diferentes géneros) en lo que actualmente está definido como *Stenochrus* (Reddell y Cokendolpher, 1995).

Historia Taxonómica

El género *Stenochrus* fue originalmente descrito por Chamberlin (1922) para ubicar a la especie *Stenochrus portoricensis*, basándose en la ausencia de mesopeltidio y la presencia de lóbulos laterales reducidos en las espermatecas de las hembras (Reddell y Cokendolpher, 1991). Más tarde Rowland (1973) sinonimizó el género *Stenochrus* con el género *Schizomus* Cook, 1899 argumentando que la presencia de mesopeltidio es una característica presente en todos los miembros del orden Schizomida (Reddell y Cokendolpher, 1991). De esta forma Rowland y Reddell (1980,1981) describen 16 especies de Guatemala, México y Estados Unidos dentro del género *Schizomus*, las cuales ubicaron en los grupos *"mexicanus"*, *"pecki"* y *"goodnightorum"*. Sin embargo, más tarde Reddell y Cokendolpher (1991) deciden resucitar el género *Stenochrus* basándose únicamente en los lóbulos laterales de las espermatecas de las hembras y ubicar en el a las 16 especies incluidas en los grupos *"mexicanus"*, *"pecki"* y *"goodnightorum"*, quedando incluida dentro del género una gran diversidad morfológica.

Los únicos trabajos filogenéticos realizados con esquizómidos del Nuevo Mundo fueron realizados con miembros de la familia Protoschizomidae. Cokendolpher y Reddell (1992) pusieron a prueba la monofília de la familia utilizando miembros del orden Thelyphonida y dos representantes de la familia Hubbardiidae como grupos externos; encontrando que la familia se recuperaba como un grupo monofiletico con dos géneros: *Agastoschizomus* Rowland, 1971 y *Protoschizomus* Rowland, 1975. Recientemente, Monjaraz-Ruedas et al. (2017) encontraron que la familia Protoschizomidae en realidad está conformada por tres géneros (incluyendo uno conocido solo de un fósil del Mioceno, de Arizona, EE. UU.) y que la posición de *Protoschizomus* en relación con *Agastoschizomus* es conflictiva.

El único trabajo referente a la familia Hubbardiidae es el de Rowland (1975) con su tesis doctoral, donde realizó la revisión de las especies del Nuevo Mundo ubicadas en el género *Schizomus* y propuso siete grupos de especies para acomodar y diferenciar a las diferentes especies. El análisis cladístico realizado por Rowland (1975) y basado en solamente 12 caracteres morfológicos, recuperó a siete grupos de especies monofiléticos, siendo el grupo *"briggsi"* el grupo hermano de los seis grupos restantes, los cuales a su vez, se agrupaban en dos grandes clados *"mexicanus"*+*"pecki"* +*"goodnightorum"* y *"brasilensis"*+*"dumitrescoae"*+*"simonis"*. Posteriormente, Rowland y Reddell (1979a, 1979b, 1980 y 1981) erigen formalmente los grupos *"brasilensis", "briggsi", "dumitrescoae", "mexicanus", "pecki", "goodnightorum" y "simonis".*

Más tarde Reddell y Cokendolpher (1991) retomaron el estudio de los esquizómidos del Nuevo Mundo y decidieron reubicar a todas las especies de los grupos *"mexicanus", "pecki"* y *"goodnightorum"* dentro del género *Stenochrus* independientemente de las características morfológicas que presentaba cada grupo de especies, ignorando el análisis cladistico de Rowland (1975), y basándose únicamente en los lóbulos laterales reducidos en las espermatecas. Finalmente realizaron la rediagnosis del género *Stenochrus*, con lo cual quedo conformado el género con 22 especies válidas.

Por otro lado, durante la revisión del género *Mayazomus* por Monjaraz-Ruedas y Francke (2016), en el cual se puso a prueba la monofília del género *Mayazomus* utilizando como grupo externo a diferentes géneros norte, centro y sudamericanos (*Hubbardia, Rowlandius, Hansenochrus y Stenochrus*), y además se incluyeron representantes de cada grupo de especies recuperado por Rowland (1975) (*"mexicanus", "pecki", "goodnightorum", "brasilensis", "dumitrescoae", "simonis"*) en una matriz morfológica con 130 caracteres, encontraron que el género *Stenochrus* se recuperaba como un grupo parafilético cercanamente relacionado a géneros centroamericanos (Fig. 2). Sin embargo, otro análisis realizado por Monjaraz-Ruedas y Francke (2017) (Capítulo II – Artículo requisito) con diferentes taxones demostró que bajo esa hipótesis, el género *Stenochrus* se recuperaba como un grupo monofilético hermano del género *Belicenochrus* (Fig. 3). Dichos resultados conflictivos, ambos basados en una muestra pequeña de la diversidad del género indicaron posibles conflictos en la verdadera naturaleza del género *Stenochrus*.

Por consiguiente, un análisis exhaustivo haciendo uso de evidencia morfología y molecular, además de adicionar las nuevas especies encontradas y ubicadas momentáneamente dentro de *Stenochrus*, era necesario, para establecer una hipótesis de las relaciones internas del género, así como de la naturaleza (monofiletico o no) del género *Stenochrus.*

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Research paper

Annuli and setal patterns in the flagellum of female micro-whipscorpions (Arachnida: Schizomida): Hypotheses of homology across an order

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ABSTRACT

Schizomid female flagellum, including the number of "flagellomeres" and the setae, are among the most important taxonomic characters within the order. It is widely used to diagnose genera within both extant families. Despite the traditional use in schizomid taxonomy, the phylogenetic signal of these characters has been only once tested in the systematics of Protoschizomidae. However, our understanding of the pseudosegmentation of the flagellum, along with different terminologies of the relative position of certain setae, creates conflict in terms of homology assessments. In the present contribution, homology hypotheses and the phylogenetic importance of these characters across the only two extant families Protoschizomidae and Hubbardiidae were established and tested. The analyses were based on 44 morphological characters of 22 schizomid exemplar species, and two thelyphonid species as outgroup. Parsimony, Bayesian inference analyses, and the ancestral state reconstruction of the "annuli" characters were conducted. The resulting topology revealed Hubbardiidae as monophyletic with the two subfamilies currently recognized (Hubbardiinae + Megaschizominae). However, Protoschizomidae was not recovered as monophyletic. The ancestral state reconstruction of the number of annuli in the common ancestor of Schizomida suggested gain and loss of the different annuli at different hierarchical levels. Finally, the flagellum contains robust taxonomic characters, but caution needs to be taken when used to diagnose genera.

1. Introduction

Body segmentation or metamerism is considered as repetition of a unit comprising characters that involve the whole body along the anterior-posterior axis (Willmer, 1990; Davis and Patel, 1999). Arthropod segmentation and tagmosis still represent a dogma in multiple discussions in a wide range of contexts such as EvoDevo, phylogeny and taxonomy (Fusco and Minelli, 2013). Accordingly to Minelli and Fusco, (2004) tagmosis in arthropods can be invariable in the number of segments of the body (e.g. decapod crustaceans) or variable (e.g. spirostrepid millipedes). In arthropod appendages the tagmosis is evident in antennae or legs, suggesting the metamerism has evolved multiple times in many contexts (Davis and Patel, 1999).

Within Arachnida, tagmosis is evident in the body, like the tergites in the opisthosoma, with subsequent losses in most of the spiders (apomorphic condition), except in Mesothelae which conserves the plesiomorphic condition (Garrison et al., 2016); and appendages, like tarsomeres of legs in Amblypygi and Opiliones (Harvey, 2003; Shultz and Pinto-da-Rocha, 2007), or in the flagellum in Thelyphonida and Palpigradi (Harvey, 2003; Giribet et al., 2014).

One of the most important characters supporting the Uropygi clade (Thelyphonida + Schizomida) is the presence of a distinctive flagellum (post anal appendage). Particularly in schizomids, the female flagellum (Fig. 1) bears different and important taxonomic characters such as "segments" (Fig. 2), and distinctive setal patterns (e.g., Harvey, 1992a; Cokendolpher and Reddell, 1992; Moreno-Gonzaílez et al., 2014; Monjaraz-Ruedas and Francke, 2015).

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Fig. 1. Habitus of *Agastoschizomus lucifer* (♀); arrow showing flagellum.

The current terminology of the setae on the flagellum in Schizomida is conflictive in terms of homology statements for phylogenetic analyses, due to the confusion of the relative position of certain setae with respect to each other in the two extant families: Protoschizomidae and Hubbardiidae. Both families were recovered as monophyletic in previous works (i.e. Cokendolpher and Reddell, 1992). The main reason for this confusion is the lack of understanding of the underlying pseudosegmentation in the flagellum. Furthermore, the terminology proposed by Cokendolpher and Reddell (1992) is unsatisfactory. In the present contribution, considering that both families (Hubbardiidae and Protoschizomidae) were recovered monophyletic in the previously mentioned work, we conducted a phylogenetic analysis using a taxon sampling, which represents the diversity of the order Schizomida. Our analyses are based on twenty two schizomid species and two thelyphonid species as outgroup, and 44 morphological characters, to establish homology hypotheses and test the phylogenetic signal of the setal patterns and annuli in female's flagellum across both schizomid families.

2. Methods

2.1. Taxa

Material examined (Supplementary file 1) is deposited in the following collections: American Museum of Natural History, New York (AMNH); Colección Nacional de Aracnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNAN); and Natural History Museum, London (NHM).

Observations were made using a Nikon SMZ-800 and a SMZ-1500 stereomicroscope, and a Nikon Eclipse E100 microscope. Terminology follows Cokendolpher and Reddell (1992), except for cheliceral (Lawrence, 1969), and flagellum setae terminology (see below).

Drawings were obtained from digital images taken under visible light with a Nikon Coolpix S10 VR camera attached to a Nikon SMZ-800. Images were edited with Adobe Photoshop CS6, and drawings were edited with Adobe Illustrator CS6.

SEM photographs for four species of the two schizomids families (*Agastoschizomus lucifer*, *Hubbardia pentapeltis*, *Stenochrus portoricensis* and *Mayazomus aluxe*); and two thelyphonid species

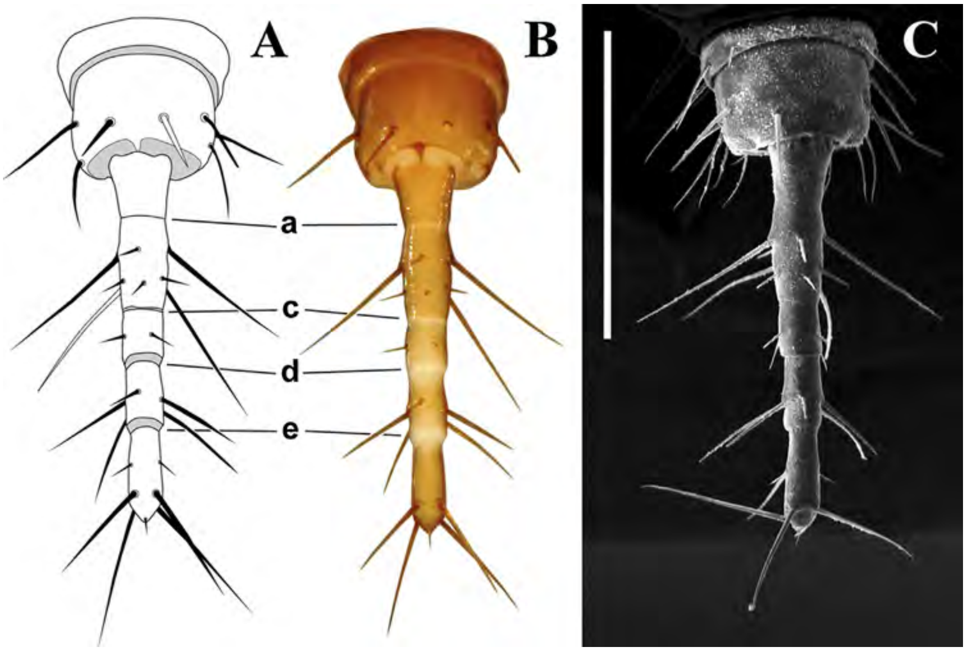

Fig. 2. *Agastoschizomus lucifer*. Showing the annuli of the female flagellum under different types of microscope. (A) Schema of the dorsal view, (B) photo of dorsal view under stereoscopic microscope. (C) SEM photograph of dorsal view.

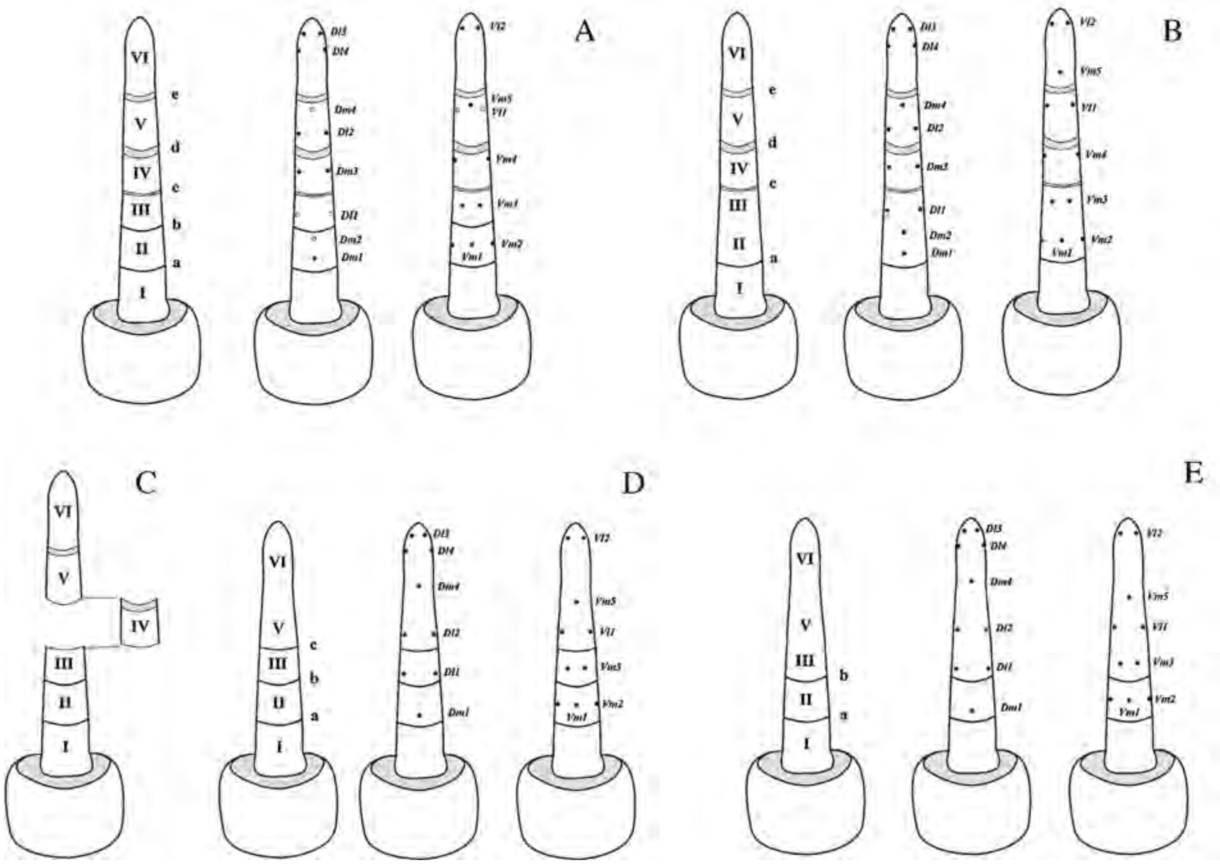

Fig. 3. Scheme representing the loss/gain of annuli and flagellomere; and the relative position of the setae in dorsal and ventral views, black dots represent the setae present whereas open circles represent absence. (A) Megaschizominae; (B) Protoschizomidae (C) scheme representing the loss of the flagellomere IV and annulus ‘d’, that produced the reduced length of the flagellum of Hubbardiinae; (D) flagellum with three annuli which can be found on genera as *Rowlandius, Piaroa, Hubbardia, Mayazomus*, etc. (E) flagellum with two annuli which can be found on genera as *Stenochrus, Surazomus, Pacal, Draculoides*, etc.

(*Mastigoproctus giganteus* and *Mastigoproctus* sp.) were taken using a Hitachi S-2460N Scanning Electronic Microscope, at the Instituto de Biología, UNAM, Mexico. Preparation of the samples follows Acosta et al. (2007).

2.2. Annuli terminology

We labelled the annuli from basalmost to distalmost with lower-case letters (a–e), based on *Megaschizomus* (genus with the highest number of annuli: five); and the flagellomeres, following Cokendolpher and Reddell (1992) with roman numerals (I–VI) (Figs. 2 and 3).

2.3. Data matrix

We examined 48 species, including all extant species in Protoschizomidae, and 33 species of 14 genera in Hubbardiidae: 31 species of 13 genera in Hubbardiinae and 2 species of genus *Megaschizomus* of Megaschizominae (including *Me. mossambicus* and one unpublished record not listed in the Supplementary file 1). Given that the number of setae and annuli in Hubbardiidae was conservative (based on our observations and the recent illustrated spieces descriptions), we only scored four representative species of Protoschizomidae, 17 Hubbardiinae species (10 species with two annuli representing 26% of the genera with two annuli; and seven species with three annuli representing 37% of the genera with three annuli) and one Megaschizominae species. From the 17 species of Hubbardinae, we examined seven and scored 10 from the literature (e.g., all species of *Apozomus*).

Forty-four qualitative characters of adult morphology (Supplementary file 2) were scored (Supplementary file 3) for 24 terminal taxa in the analysis using museum material and 13 species from the literature: *Etienneus africanus* (Hentschel, 1899)(coded from Huff and Prendini, 2009); *Apozomus watsoni*, Harvey (1992); *A. pellew*, Harvey (1992); *A. rupina* Harvey (1992); *A. sauteri* (Kraepelin, 1911)(all *Apozomus*species were coded from Harvey, 1992a); *Attenuizomus mainae* (Harvey, 1992a); *Bamazomus madagassus* (Lawrence, 1969); *Antillostenochrus cokendolpheri* Armas and Teruel (2002); *Afrozomus machadoi* (Lawrence, 1958)(coded from Reddell and Cockendolpher, 1995); *Draculoides vinei*, (Harvey, 1988)(coded from Harvey et al., 2008); *Piaroa virichaj*, Villarreal et al. (2008); *Schizomus crassicaudatus*, (O.P.-Cambridge, 1872)and *Trithyreus grassi* (Thorell, 1889)(both coded from Reddell and Cockendolpher, 1995). Fourteen characters were modified from Cokendolpher and Reddell (1992) and two characters were taken from Shultz (2007). Thirty-eight characters were binary and six multistate. Seventeen characters were scored only for females, and seven were scored only for males. Fifteen characters were scored from setal patterns and annuli in the flagellum. Five characters were uninformative.

2.4. Parsimony phylogenetic analyses

A driven search of the 39 informative characters was conducted in TNT (Goloboff et al., 2003a,b, 2008) combining three of the new technology algorithms (Nixon, 1999; Goloboff, 1999) executed using a script file modified from Dimitrov et al. (2013) and Santibáñez-López et al. (2014): *hold 100,000; rseed1; xm: noverb*

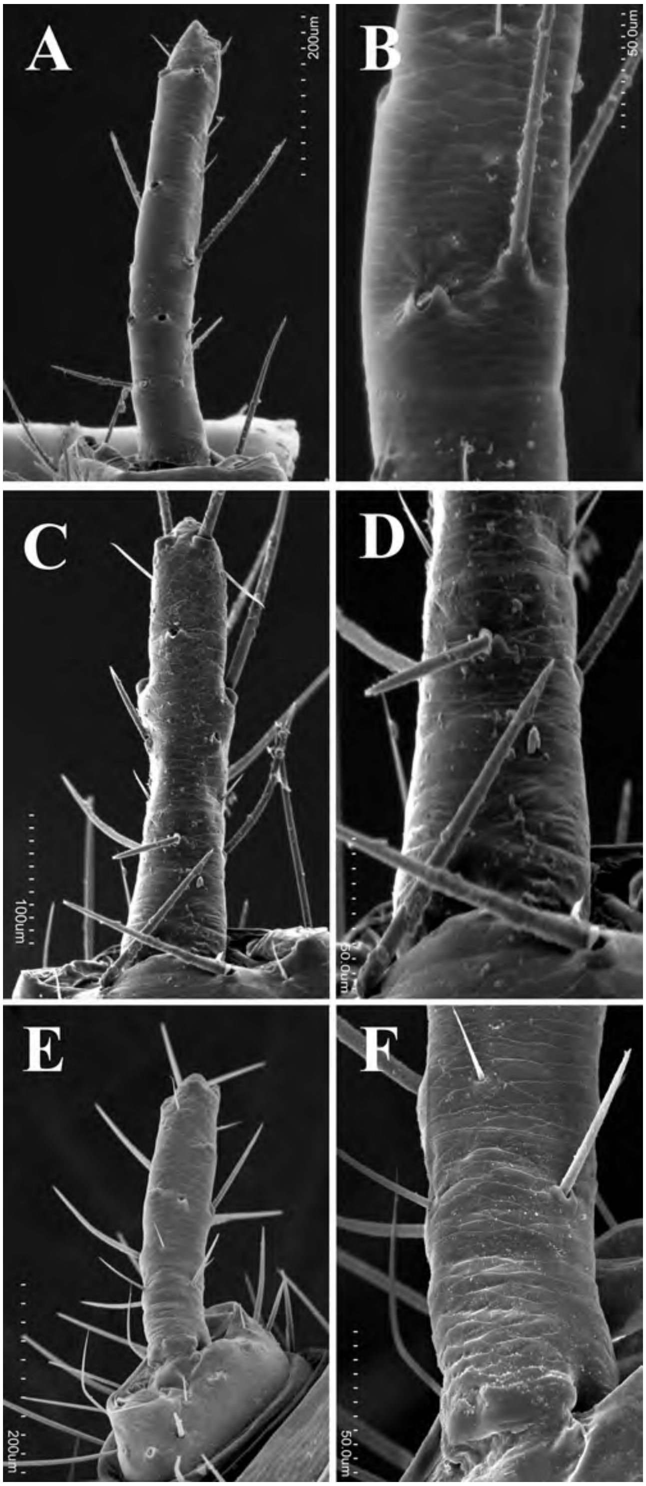

Fig. 4. SEM photographs of different members of Hubbardiinae. (A and B) *Hubbardia pentapeltis*, with three annuli. (C and D) *Stenochrus portoricensis*, with two annuli. (E and F) *Mayazomus aluxe*, with three annuli.

nokeep; rat: it 0 up 4 down 4 au 0 num 36 give 99 equa; dri: it 10 fit 1.00 rfi 0.20 aut 0 num 36 give 99 xfa 3.00 equa; sec: mins 45 maxs 45 self 43 incr 75 minf 10 god 75 drift 6 glob 5 dglob 10 rou 3 xss 10 – 14 + 2 noxev noeq; tf: rou 5 minf 3 best ke nochoo swap; xm: level 10 nochk rep 50 fuse 3 dri 10 rss css noxss mult nodump conse 5 conf 75 nogive notarg upda autoc 3 xmix; xm; xmult;. Analyses were conducted with equal weighting and implied weighting, using three values of the concavity constant (k = 1, 3, 10), to assess the homoplasious characters under the effect of weighting them (Santibáñez-López et al., 2014). The relative support for each node on the preferred hypothesis was calculated with Bremer support (Bremer, 1994) and jackknife resampling (Farris et al., 1996).

Bremer support was calculated in TNT by searching for suboptimal Trees 10 steps longer, and holding 1000 trees per replication. Jackknife support was estimated with exact searches of 1000 pseudoreplicates, using the commands resample *jak repl 1000*. Characters were optimized unambiguously on cladograms with WinClada (Nixon, 2002) and were edited with Adobe Illustrator C6.

We removed seven characters related to the annuli, to observe if these characters were contributing to the support or grouping of taxa, and conducted the same analyses mentioned above.

2.5. Bayesian inference analysis

Ever since Lewis (2001) proposed the model to analyze morphological data under model-based inference, some problems on the use of parsimony to analyze this kind of data have been argued (i.e Ronquist, 2004). However, the role of morphology in the reconstruction of the evolutionary history of organisms under the model-based approach remains subjective to the combined use with molecular data (e.g., Leaché and Reeder, 2002; Wiens, 2004; Glenner et al., 2004; Nylander et al., 2004; Rawlings et al., 2008), and only to a few studies analyzing fossil terminals (Snively et al., 2004; Friedman, 2007; Prieto-Márquez, 2010; Lee and Worthy, 2011).

Rindall and Brower (2011) presented arguments on the broad similarity between the topologies recovered by model-based inference analyses and those from parsimony; and recently, Spencer and Wilbert (2013) criticized the efficiency and the convenience of those model-based analyses versus parsimony. It is not our intention to compare the efficiency of both approaches with our dataset here, but to contrast slightly the way these approaches treat character evolution.

The matrix was analyzed (complete and without the annuli characters) under the Bayesian inference using MrBayes ver. 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The model used was set using the command *prset symdirihyperpr = fixed (infinity)*. All characters were considered unordered using the command *ctype unordered:all*. Since all characters were informative, they were coded as informative using the command *lset coding = informative*. The analysis comprised two iterations of four Markov chain Monte Carlo models, performed for 50 million generations. Trees were sampled every 1000 generations, those sampled before stationary discarded using the *burnin* command. The majority 50% rule consensus tree was obtained using the command *sumt*. It was visualized in the FigTree software and edited in Adobe Illustrator C6.

2.6. Ancestral states reconstruction

We reconstructed the ancestral states of characters 37–42 (female flagellum annuli characters). Analyses were conducted using SIMMAP (Bollback, 2006) employing Bayesian inference, and with BayesTraits ver 2.0 (Pagel and Meade, 2004, 2006) employing the Maximum Likelihood approach. For these analyses we used the topology recovered by the Bayesian analysis of the matrix without the annuli characters (chars 37–42). The SIMMAP analysis consisted in 1000 iterations under the following parameters: characters 37–41, were treated with a Beta distribution prior (as default settings), and a gamma distribution prior with k value of 90; while character 42 (multistate) was treated with an Equal (1/k) prior and same gamma distribution. The BayesTraits analyses con-

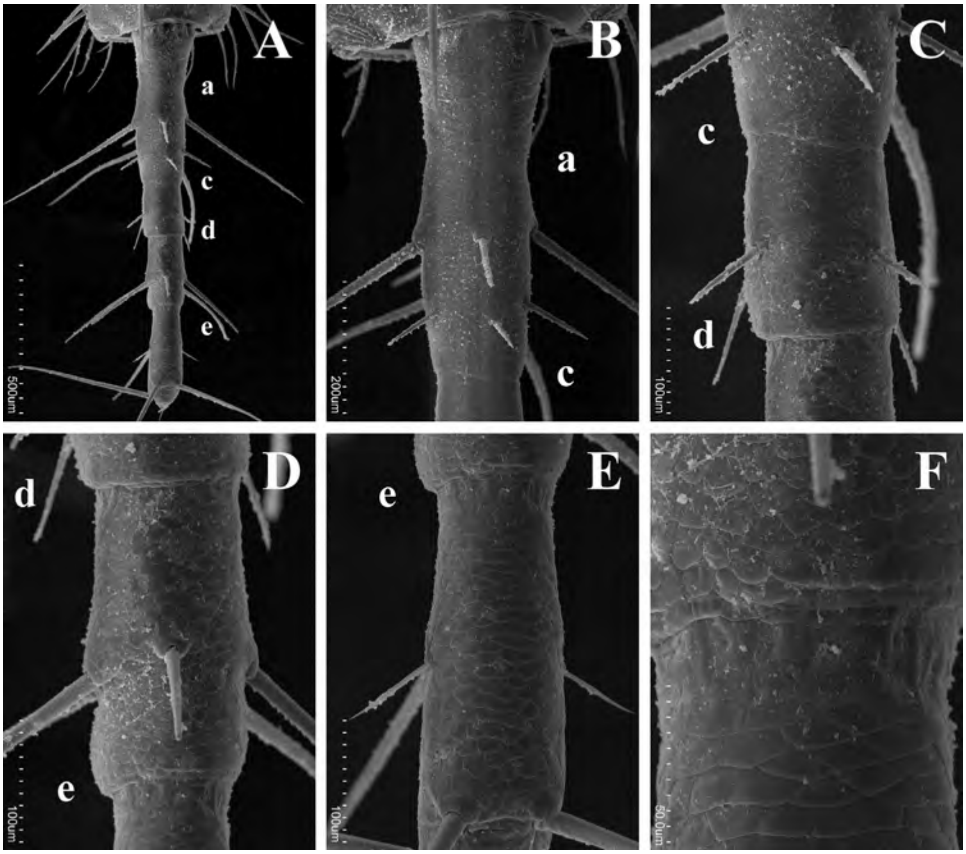

Fig. 5. *Agastoschizomus lucifer*. Female flagellum, dorsal view. Showing different close-ups of the different annuli. (A) General view. (B) Annulus ‘a’. (C) Annuli ‘c’ and ‘d’. (D) Annuli ‘d’ and ‘e’. (E) Ventral view of annulus ‘e’. (F) Close-up of annulus ‘e’.

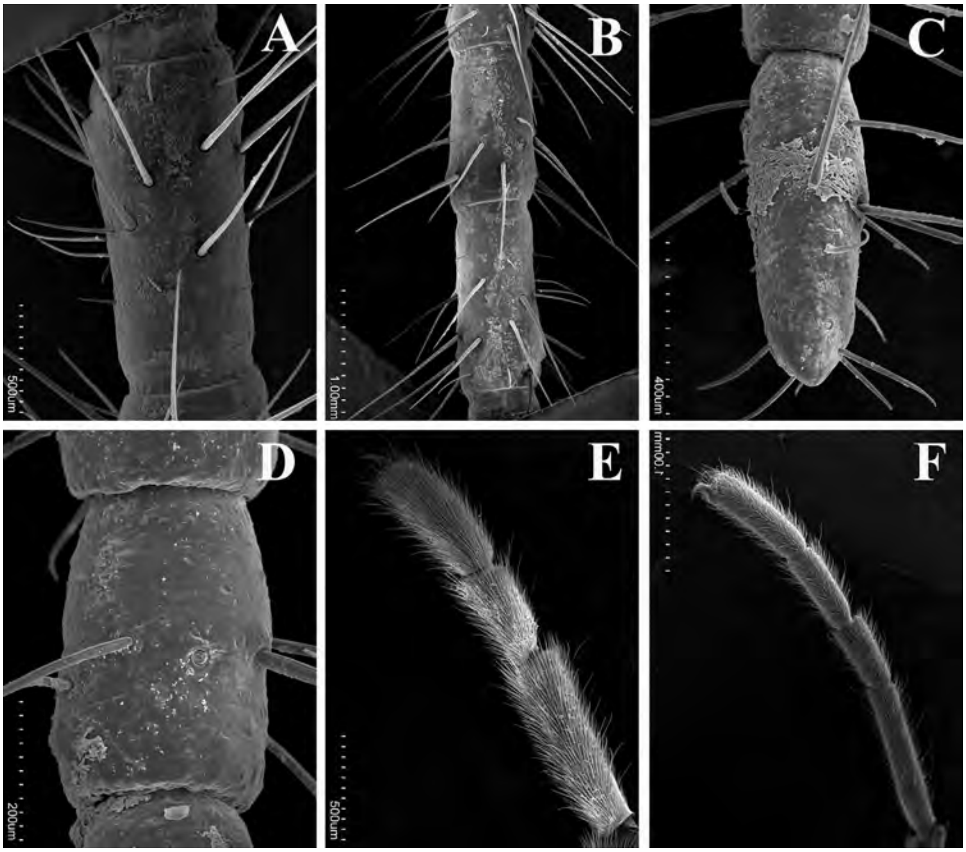

Fig. 6. SEM photos showing true segments: (A–D) flagellum of *Mastigoproctus giganteus*. (A and B) Basal segments. (C and D) Distal segments. (E and F) Legs of *Paramitraceras* sp. (Opiliones) (E) Leg I. (F) Leg II.

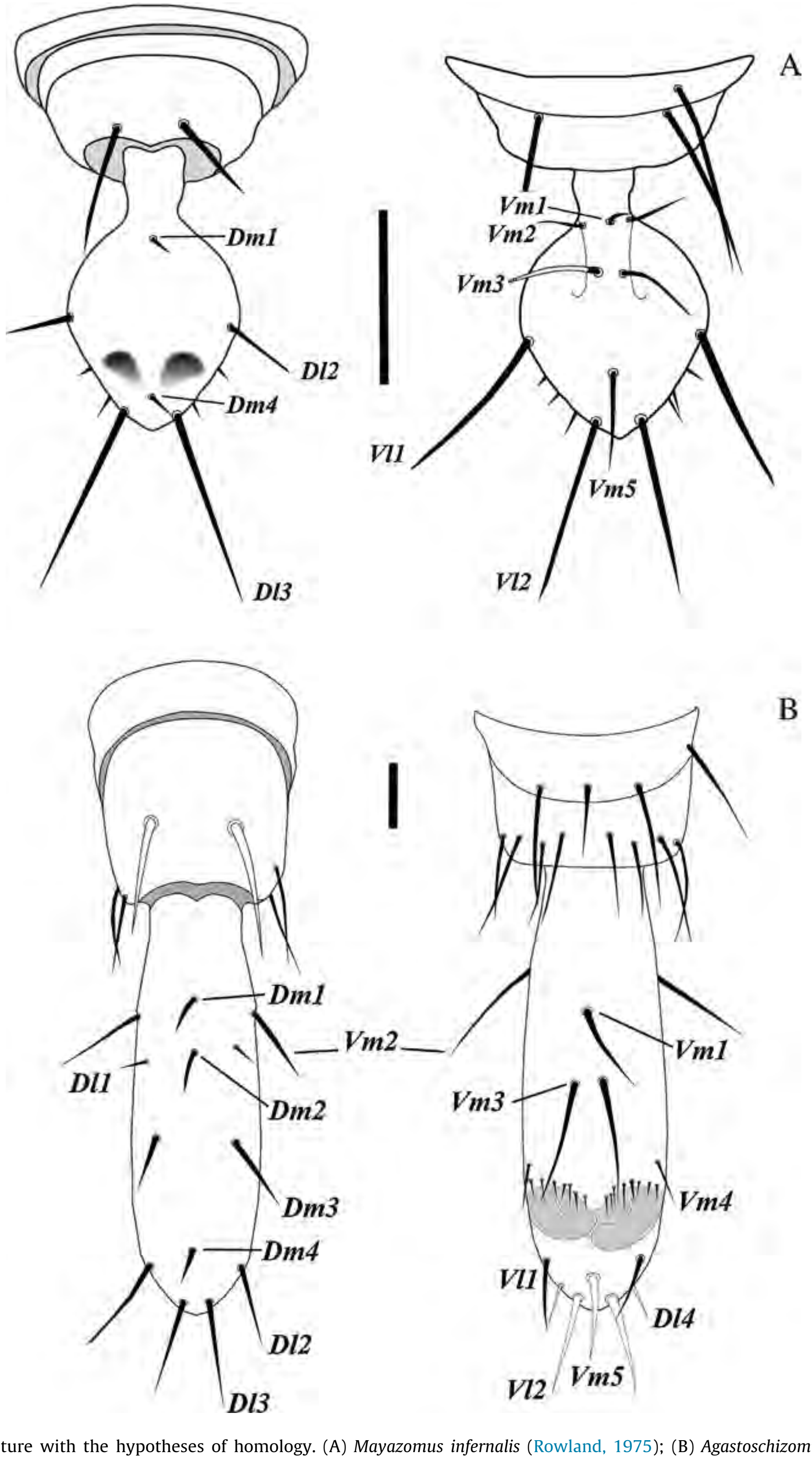

Fig. 7. Male flagellum nomenclature with the hypotheses of homology. (A) *Mayazomus infernalis* (Rowland, 1975); (B) *Agastoschizomus lucifer* Rowland (1971). Scale bars = 1 mm.

sisted in 1000 bootstrap iterations using only the clades of interest (i.e. Hubbardiidae and Hubbardiinae).

3. Results and discussion

3.1. Segments, annuli or articles?

The female flagellum of schizomids, when observed under an optical microscope, shows circular light-colored or “thinner” areas of the cuticle, each one termed “annulus” (plural = annuli) for their ring-like appearance, and whose definition and number have been used in systematics for many years. Millot (1949) in a general work about the order (Uropygi: Schizopeltida) refers to the sections of the flagellum between annuli as “articles”, even though there is not a flexible articulation between them. Lawrence (1958) indicated that the female of *Afrozomus machadoi* (Lawrence, 1958) has “no true joint, but three rather indistinct, fine ‘pseudoarticulations’ dividing the appendage into four segments”; whereas in the origi-

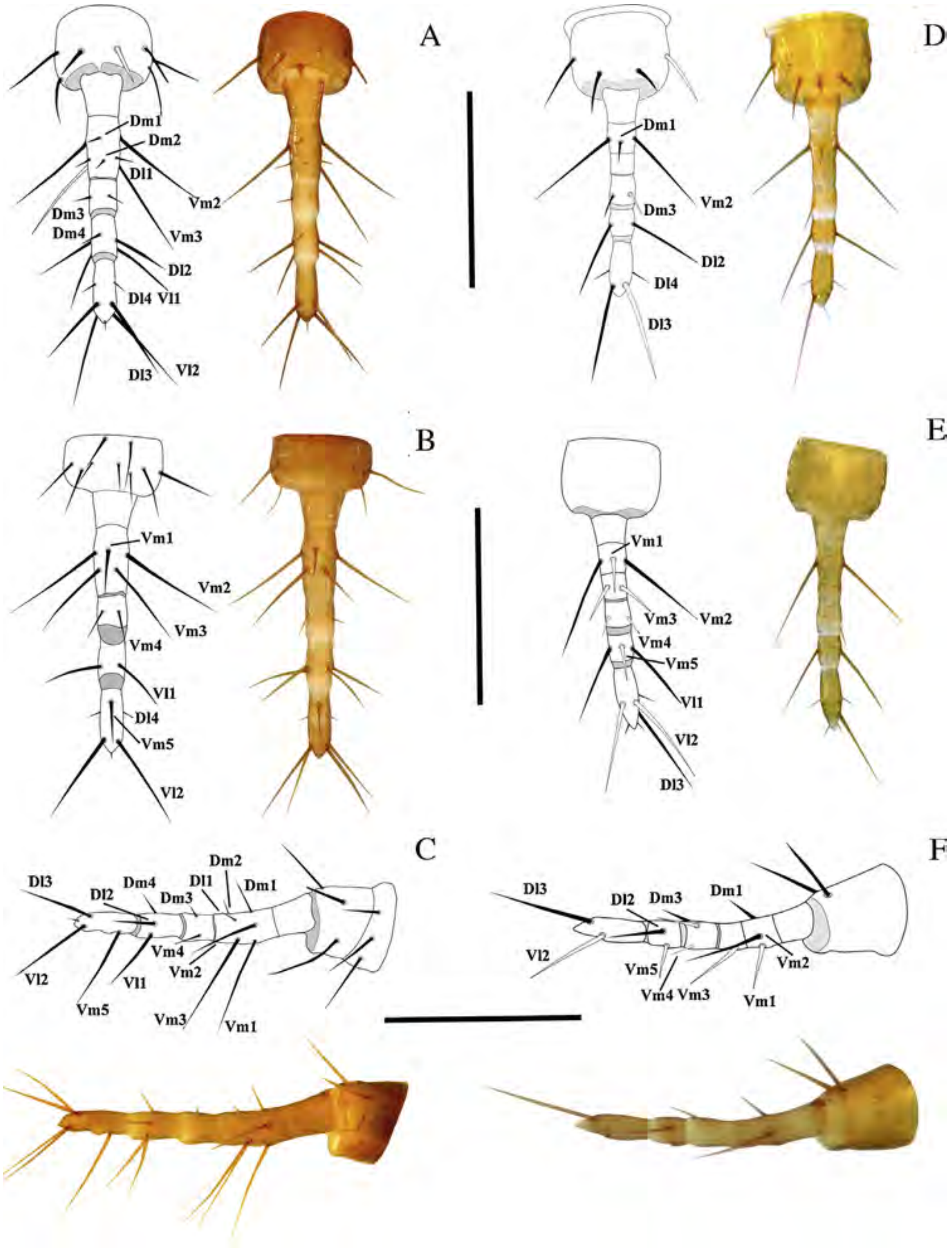

Fig. 8. Schema of the dorsal (A and D), ventral (B and E) and lateral views (C and F) of the female flagellum of Protoschizomidae and Megaschizominae. (A–C) *Agastoschizomus lucifer*. (D–F) *Megaschizomus mossambicus*. Scale bars = 1 mm.

nal description of *Me. mossambicus* (Lawrence, 1958) he described the female flagellum as "consisting of three distinct segments, a long basal and two much shorter ones, the apical one slender and distinctly pointed; the long basal segment with three fine but distinct transverse sutures dividing it into four 'pseudosegments' but quite different from the complete divisions separating the true segments."

Later, Rowland and Reddell (1979: 165) indicated that:

> "The articles of the female flagellum are joined either by segmentation and annulation or by annulation alone. The term segmentation does not suggest that the articles are derived from metameres, but only that they are separated from each other by a slight membranous region. Annulations, on the other hand, appear to represent lines of incomplete fusion of two flagellar articles."

Unfortunately, these authors left the term "article" undefined, and the distinction between "segmentation" and "annulation" in many specimens is not clear. Subsequently, working with Australian schizomids, Harvey (1992a) used the term "segments" to refer to the portions between annuli. In their revision of of Protoschizomidae, Cokendolpher and Reddell (1992: 33) indicated that:

> "There are five positions on the female flagellum of schizomids where annuli can occur. These areas may be evident as thinning of the cuticle (sometimes only on ventral surface) or as clean breaks in the cuticle. . . The distinction between segments and articles is not entirely clear. When examined under 100X the divisions between segments appear as breaks in the cuticle. The lines are generally thin and sometimes difficult to see. No musculature is evident and it is unlikely that these segments can be moved. Attempts to bend the flagellum at a segmental junction in a preserved specimen results in a clean break at

> the border. Subdivisions of the segments are evident by areas of thinned cuticle. These zones are sometimes quite wide and appear lighter in color than the surrounding cuticle. Segments do not appear to break at these subdivision zones and in preserved specimens this zone will withstand some bending. When the flagellum is divided by breaks in the cuticle we refer to the resulting subdivisions as segments. When a segment or entire flagellum is divided by only thinnings in the cuticle we refer to the resulting units as articles. Annuli are also present in juveniles but not in the flagellum of mature males."

Subsequently, the same authors (Reddell and Cokendolpher, 1995:14) in their comprehensive work on the order indicated that:

> "The female flagellum may be segmented or be segmented and contain thin areas (articles) of the cuticle that allow bending of the flagellum. . .. The Protoschizomidae and Megaschizominae have both segments and articles, whereas the Hubbardiinae possess only segments."

Based on SEM images of protoschizomids and Hubbardiinae (Figs. 4 and 5) and some of the observations of Cokendolpher and Reddell (1992), there is no evident segmentation of the flagellum of female and juvenile schizomids, since there are no divisions, breaks or muscles associated to the annuli on the cuticle, in contrast to true segmentation in the flagellum of *Mastigoproctus* (Thelyphonida; Fig. 6A–D) or in the leg tarsomeres in *Paramitraceras* (Opiliones; Fig. 6E–F). SEM images (Figs. 4 and 5) show the female's flagellum as a smooth cylinder, without any divisions (except for a tiny discontinuity in the surface of the flagellum where the annuli is observed); those that exist are only visible with transmitted light.

The apparent segments of the cuticle in the flagellum of Thelyphonida perhaps allows the observed flexibility in the longer flagellum of those arachnids (Fig. 6A-D), and for those reasons it does not break, as suggested by Cokendolpher and Reddell (1992). Thus, the annuli in schizomids are just thinning on the cuticle, of variable width and depth, which can be observed through transmitted light (Fig. 2). It is incorrect to refer as "true" segmentation or articles (given the above definition) in the female's flagellum. Furthermore, it is evident that "segments", "pseudosegments" and "articles" in the female and juvenile flagellum are homologous, as demonstrated below. Therefore, we propose the use of the term flagellomere to refer to the areas between annuli, since a flagellomere represents a part of a complete flagellum and does not involve any kind of muscles or cuticular breaks at each annulus.

3.2. *Annuli configuration in Protoschizomidae and Hubbardiidae*

The positions of setae are good indicators or "place-holders" that allow us to homologize the loss of annuli in the members of Protoschizomidae and Hubbardiinae with respect to Megaschizominae species examined (Fig. 3A). In Megaschizominae, flagellomere II bears one dorsal (*Dm1*) and three ventral (*Vm1* and *Vm2* paired); flagellomere III has one pair of dorsal (*Dl1*) and one pair of ventral (*Vm3*) setae; flagellomere IV has one pair of dorsal (*Dm3*) and one pair ventrally (*Vm4*); flagellomere V has one pair dorsal (*Dl2*) and one ventral (*Vm5*); and finally, flagellomere VI has three distal-most setae, two dorsal (*Dl3* and *Dl4*) and one ventral (*Vl2*) (Fig. 3, Table 1).

The general pattern in Protoschizomidae (Fig. 3B), where females normally have four annuli and five flagellomeres (or excep-

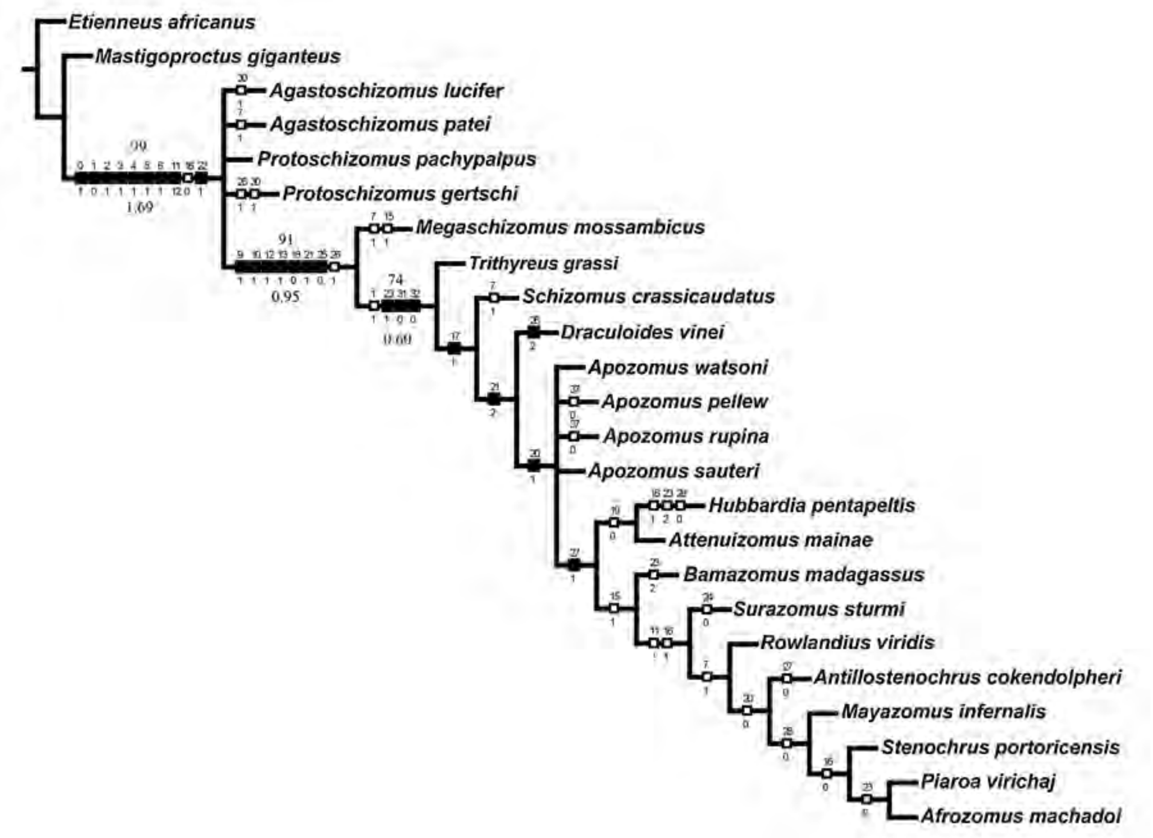

Fig. 9. Strict consensus of the five most parsimonious trees (L = 65, CI = 0.600, RI = 0.819, Fit = 27.025, adjusted homoplasy = 4.975) obtained from the analysis of 37 morphological characters (annuli characters deactived) coded for 22 schizomid species and 2 thelyphonid species with implied weighting with k value = 3. Unambiguous synapomorphies optimized on branches: black squares indicate uniquely derived apomorphic states, white squares indicate parallel derivations of apomorphic states; numbers above squares indicate characters, numbers below indicate states. Jackknife values greater than 70% indicated above branches, Bremer support values below branches.

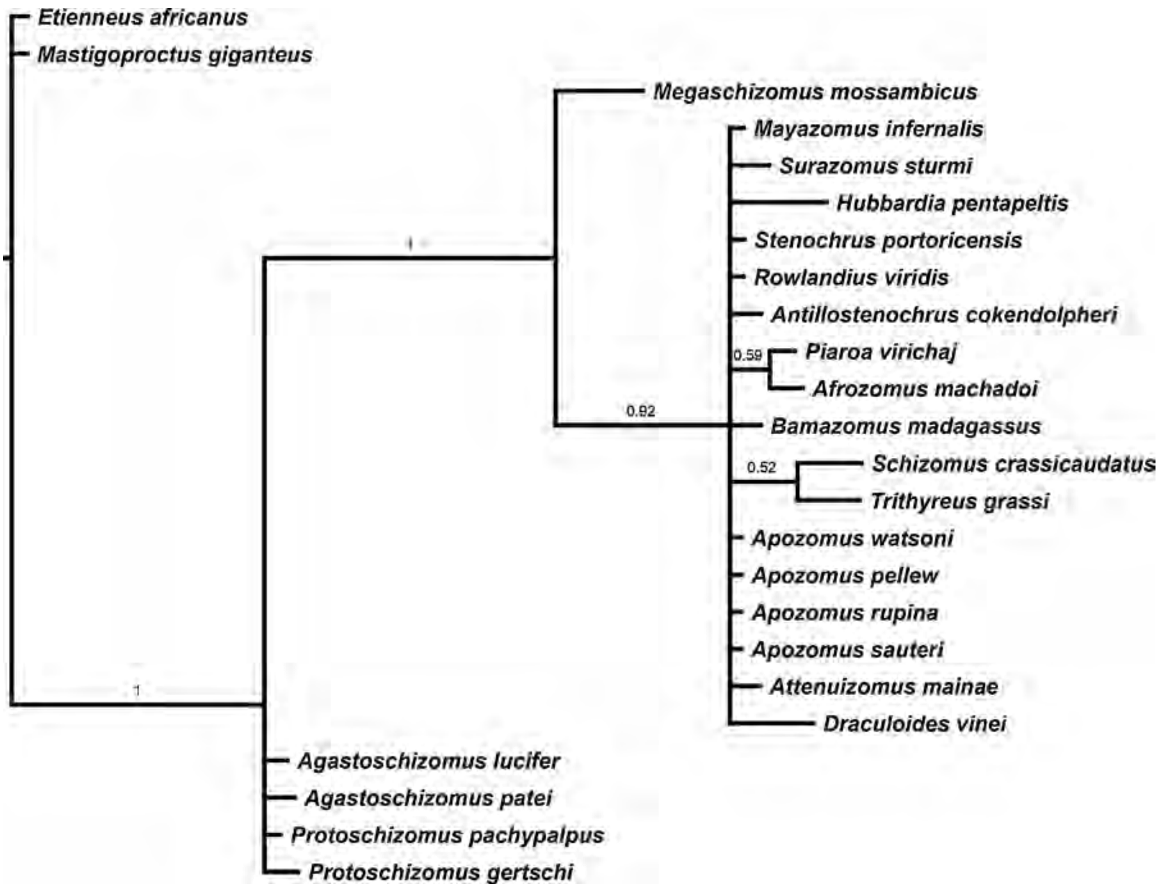

Fig. 10. Phylogram obtained by Bayesian analysis of 44 morphological characters coded for 22 schizomid species and 2 thelyphonid species. Posterior probabilities indicated on branches.

tionally less), is that annulus ‘b’ is absent, and flagellomeres II and III are thus completely fused: the fused flagellomere II + III bears setae *Dm1*, *Vm1* and *Vl2* (paired), which are homologous to those in Megaschizominae flagellomere II; and *Dl1* and *Vm3* (both paired), also homologous to those in Megaschizominae flagellomere III. In addition, protoschizomids have *Dm2*, which is absent in Hubbardiidae. Protoschizomid flagellomere IV has one pair of dorsal setae (*Dm3*) and *Vm4* (paired) homologous to those in Megaschizominae. Flagellomere V has *Dl2* (paired), which are homologus to those in Megaschizomiae; but also, presents a single *Dm4* and a pair of *Vl1* (absent in Megaschizominae, but present in Hubbardiinae). Finally, flagellomere VI bears three distal-most setae, two dorsal (*Dl3* and *Dl4*) and one ventral (*Vl2*) as in megaschizomines (Fig. 3A, Table 1).

Some genera of Hubbardiinae have three annuli (e.g. *Afrozomus*, *Attenuizomus*, *Hubbardia*, *Notozomus*, *Rowlandius*) whereas others have only two (e.g. *Apozomus*, *Bamazomus*, *Draculoides*, *Stenochrus*, *Surazomus*). There is a report of one species, *Burmezomus cavernícola* (Gravely, 1912), by Bastawade (2004) indicating that this species has no annulus; however, in his illustration (Fig. 49; page 219) the female flagellum shows what appears to be the presence of “annuli”. We could not study this species, but if indeed it does not bear annuli, it would represent a subsequent loss in the Hubbardiinae. While annulus ‘a’ is missing in two species of *Apozomus* (*A. pellew* and *A. rupina*), annulus ‘b’ is present in all Hubbardinae genera.

Annuli ‘d’ and ‘e’ are lost in all hubbardiine genera, and additionally annulus ‘c’ is lost only in those genera with two annuli. Also, the terminal flagellomere represents the fusion of flagellomeres V and VI. However, in Hubbardiinae not only are the annuli lost, and the last flagellomere is fused; but also flagellomere IV and the corresponding setae *Dm3* and *Vm4* are lost (therefore, these setae are absent in all species of the subfamily). In addition, those genera with two annuli only also have the last flagellomere as a fusion of flagellomeres III, V and VI. The loss of flagellomere IV is probably one of the reasons why the length of the female flagellum with respect to body size is shorter in Hubbardiinae than in Megaschizominae and Protoschizomidae.

Table 1
Female flagellum annuli and flagelomeres, indicating relative positions of the setae in relation to each flagellomere for species with five, four, three and two annuli (Megaschizominae, Protoschizomidae and Hubbardiinae respectively). Dotted lines indicate fusion of flagellomeres.

	I	II	III	IV	V	VI
Megaschizominae	No setae	Dm1, Dm2, Vm1, Vm2	Vm3, Dl1	Vm4, Dm3	Dm4, Dl2, Vl1, Vm5	Dl3, Dl4, Vl2
Protoschizomidae	No setae	Dm1, Dm2, Dl1, Vm1, Vm2, Vm3	–	Vm4, Dm3	Dm4, Dl2, Vl1	Dl3, Dl4, Vm5, Vl2
Hubbardiinae (3 annuli)	No setae	Dm1, Vm1, Vm2	–	–	Dl1, Vm3	Dm4, Dl2, Dl3, Dl4, Vm5, Vl1, Vl2
Hubbardiinae (2 annuli)	No setae	Dm1, Vm1, Vm2	–	–	–	Dm4, Dl1, Dl2, Dl3, Dl4, Vm3, Vm5, Vl1, Vl2
Apozomus rupina	–	Dm1, Vm1, Vm2	–	–	Dl1, Vm3	Dm4, Dl2, Dl3, Dl4, Vm5, Vl1, Vl2
Apozomus pellew	–	Dm1, Vm1, Vm2	–	–	–	Dm4, Dl1, Dl2, Dl3, Dl4, Vm3, Vm5, Vl1, Vl2

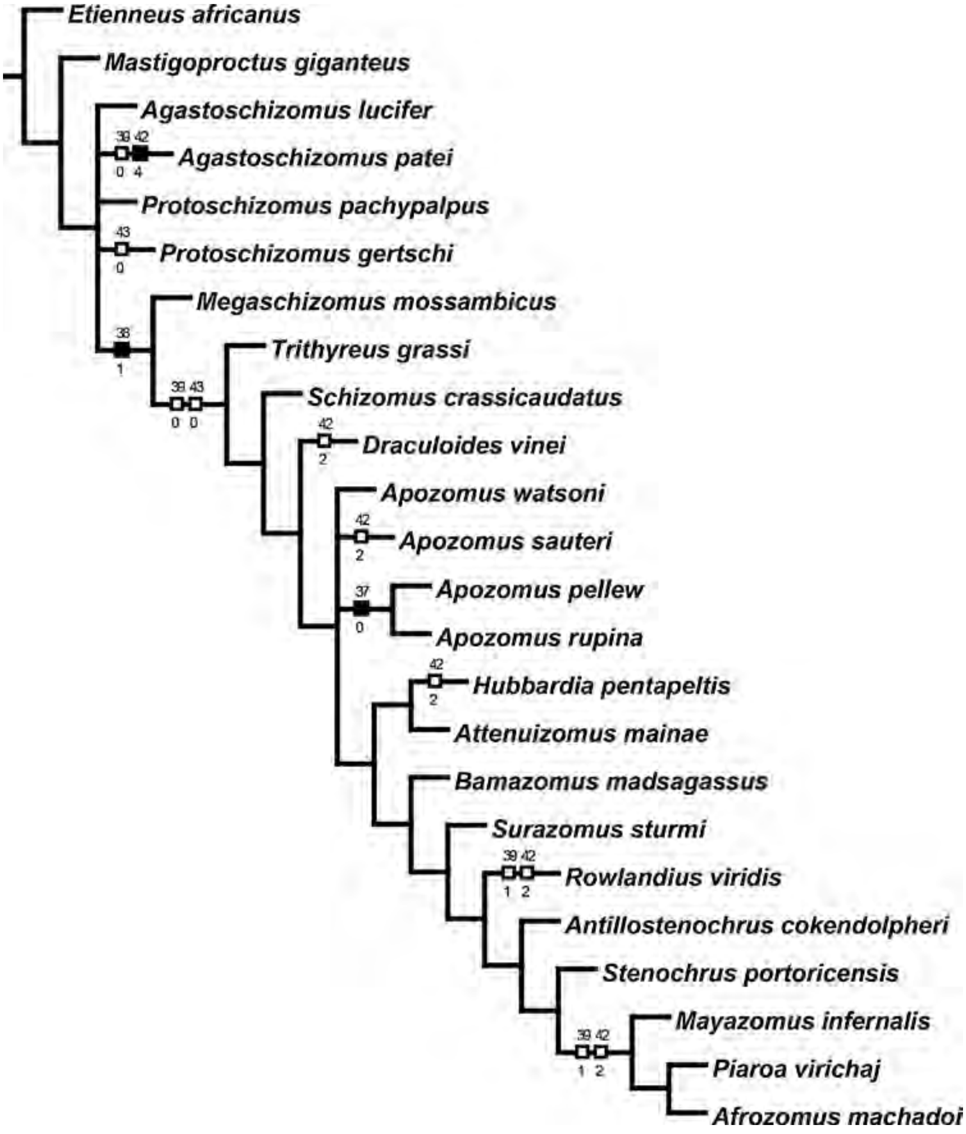

Fig. 11. Strict consensus of the 15 most parsimonious trees (L = 92, CI = 0.533, RI = 0.749, Fit = 31.64, Adjusted Homoplasy = 7.360) obtained from the analysis of 44 morphological characters coded for 22 schizomid species and 2 thelyphonid species with implied weighting with k value = 3. Only annuli characters mapped. Unambiguous synapomorphies optimized on branches: black squares indicate uniquely derived apomorphic states, white squares indicate parallel derivations of apomorphic states; numbers above squares indicate characters, numbers below indicate states.

The flagellomere I lacks setae in all members of Schizomida and Thelyphonida. *Apozomus pellew* and *A. rupina* are considered as the only two species with setae on flagellomere I. However, based on the original description of both species (Harvey, 1992a), it seems that they have flagellomeres I and II fused; and it is reflected in the length of their first flagellomere, which is unusual longer than the flagellomere I from the eight other *Apozomus* species described in the same publication. This would suggest these two species lost annuli ‘a’ as well.

Additionally, setae Dm1, Vm1 and Vm2 in these two species (*A. pellew* and *A. rupina*) are placed posteriorly near annuli ‘b’, suggesting these setae are homologous to the setae present in flagellomere II in the rest of hubbardiids (see below). In Hubbardiinae flagellomere II has a single dorsal seta (*Dm1*) and three ventral setae (*Vm1* and *Vm2* paired). Flagellomere III, present in some genera and absent in others, has *Dl2* and *Vm3* (both paired). These setae are found basally in the fused flagellomere III + V + VI in the two-annuli hubbardiines (Fig. 3C–E). The last flagellomere also has *Dl2*, *Dm4*, *Dl3*, *Dl4* and *Vl1* (absent in megaschizomines), *Vm5* and *Vl2* (homologous to protoschizomids).

3.3. *Flagellum setae and the primary hypotheses of homology between Hubbardiidae and Protoschizomidae*

Based on the relative position of the setae used recently in descriptions of hubbardiids (Harvey et al., 2008; Moreno-Gonzaílez et al., 2014; Villarreal et al., 2014) and more detailed observations in flagellar setation of protoschizomids and *Me. mossambicus* (Lawrence, 1958), here we re-evaluated the flagellar setation terminology as currently used. Setae *Dm1*, *Dm4*, *Dl1*, *Dl2*, *Dl3*, *Dl4*, *Vm1*, *Vm2*, *Vm3*, *Vl1* and *Vl2* are present in Hubbardiinae (Fig. 7A, 8, Table 2), with Megaschizominae having additionally *Dm2*, *Dm3*, and *Vm4*; whereas setae *Dm1*, *Dm2*, *Dm3*, *Dm4*, *Dl1*, *Dl2*, *Dl3*, *Dl4*, *Vm1*, *Vm2*, *Vm3*, *Vm4*, *Vm5*, *Vl1*, and *Vl2* are present in Protoschizomidae (Fig. 7B, Table 2). Moreno-Gonzaílez et al. (2014) mentioned that seta *Dm3* (a microseta) is present in hubbardiids between *Dm1* and *Dl1*; however, our observations suggest that the *Dm3* mentioned by these authors is not homologous to the *Dm3* in protoschozomids (Fig. 8).

Species of Protoschizomidae present the same microsetae at the same position as indicated by Moreno-Gonzaílez et al. (2014),

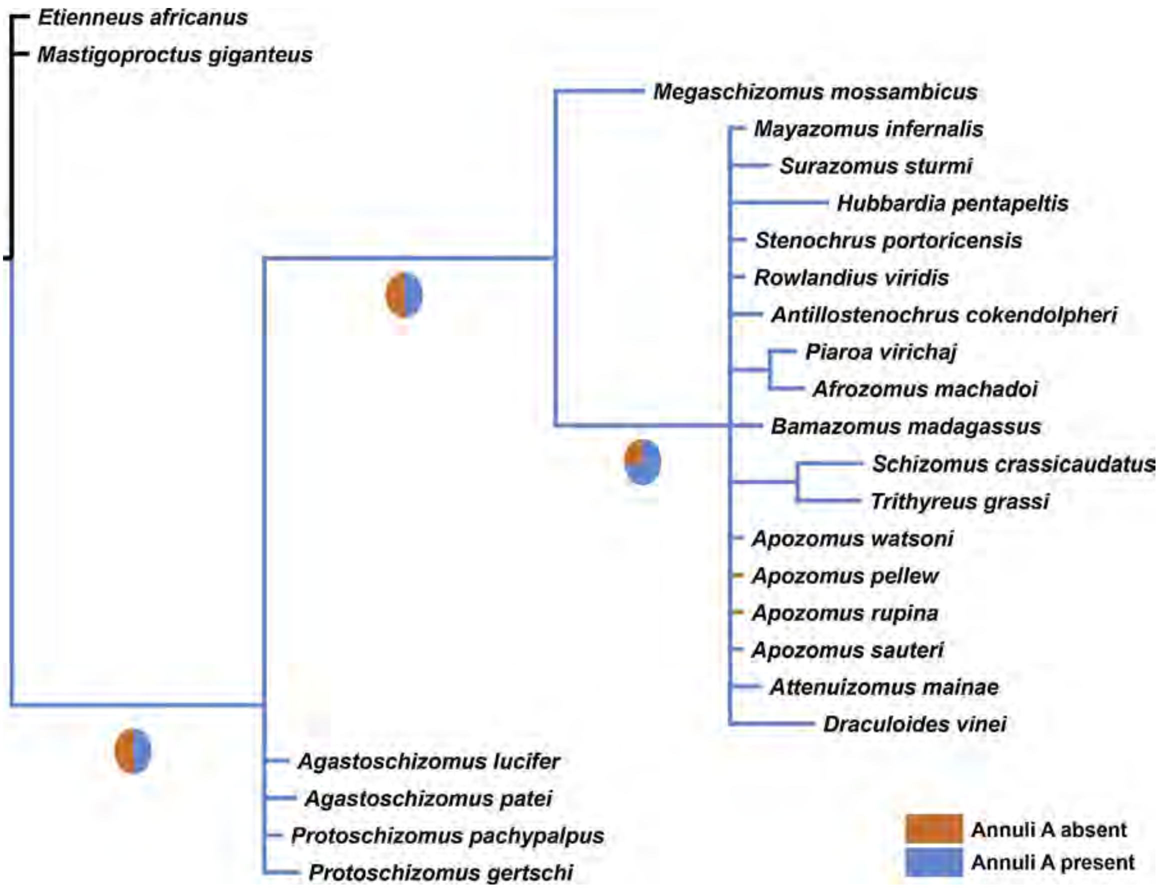

Fig. 12. Ancestral state reconstruction of character 37.

Table 2
Flagellum setae nomenclature with the new proposals for Hubbardiidae and Protoschizomidae. + = presence, – = absence, () = nomenclature used by Cokendolpher and Reddell (1992) and Harvey (1992a).

Setae	Flagellum setae			
	Male		Female	
	Protoschizomidae	Hubbardiinae	Protoschizomidae	Hubbardiinae
Dm1	+	+	+	+
Dm2	+/–	–	+/–	–
Dm3	+	–	+/+ microsetae	–
Dm4	+	+	+/–	+
Dl1	+	–	+ microsetae	+ microsetae
Dl2	+	+ (*Dl1*)	+	+ (*Dl1*)
Dl3	+	+	+	+
Dl4	+ microsetae	–	+ microsetae	+ microsetae
Vl1	+	+	+	+
Vl2	+	+	+	+
Vm1	+	+	+	+
Vm2	+	+	+	+
Vm3	+	+(*Vm4*)	+	+ (*Vm4*)
Vm4	+/–	–	+	–
Vm5	+/–	+	+	+

although some species of *Protoschizomus* present an extra pair of microsetae between *Dm3* and *Dl4* (e.g. *P. franckei* and *P. occidentalis*); for these reasons, in which some species of protoschizomids present two or three pairs of microsetae, it is difficult to homologize the microsetae of Hubbardiidae with those of protoschizomids. Also, *Agastoschizomus huitzmolotitlensis* presents an extra pair of antero-dorsal macro-setae. Females of genus *Draculoides* Harvey, 1992 present an extra pair of microsetae on the distal flagellomere, between *Dl3* and *Vl2*, which varies in its relative position, and thus it is difficult to homologize them as well. Therefore, we hypothesize that hubbardiines lost *Dm3* and *Vm4*, concurrent with the loss of flagellomere IV of megaschizomines.

Based on the relative position of the setae in Hubbardinae, Megaschizominae and Protoschizominae, we observed that setae *Dl1* and *Vm4* of Hubbardiidae are at the same position as setae *Dl2* and *Vm3* in protoschizomids (Table 1); therefore they are homologous, and *Dl1* in hubbardiids is a microseta and *Dm3* and *Vm4* are lost in hubbardiids. Harvey et al. (2008) was the first to report microsetae on the female flagellum of the Australian genus *Draculoides*; however, some illustrations on previous works (e.g. Rowland and Reddell, 1980; Reddell and Cokendolpher, 1995) shown the presence of one or two pairs of microsetae (although they never named them) in the last flagellomere. Based on our observations (Table 1; and Mark Harvey, pers. Com.) the microsetae *Dl1* and *Dl4* are present in all members of Schizomida. Males of Hubbardiidae present a pair of microsetae patches on the distal portion of the flagellum (between setae *Dl2* and *Dl3*), which are homologous to those microsetae patches in males of Protoschizomidae near the ventral lobes of the flagellum (Fig. 7). Finally, setae *Vm3* and *Vm4* of protoschizomids and megaschizomines are absent in Hubbardiinae (Table 2).

The relative positions of setae indicate that these setae are changing their position in relation with other setae. This effect can be seen in many other arachnids, such as in some opilionids (Kury and Villarreal, 2015); scorpions (Prendini et al., 2010) and pseudoscorpions (Mahnert, 1981; Harvey, 1992b). Kury and Villarreal (2015) proposed the first homology hypothesis in macrosetae on ventral plate in penis. These authors considered the presence of five setal groups on penis, which may be in different arrangements and positions (e.g. E and C setae groups in Stygnidae vs Stygnop-

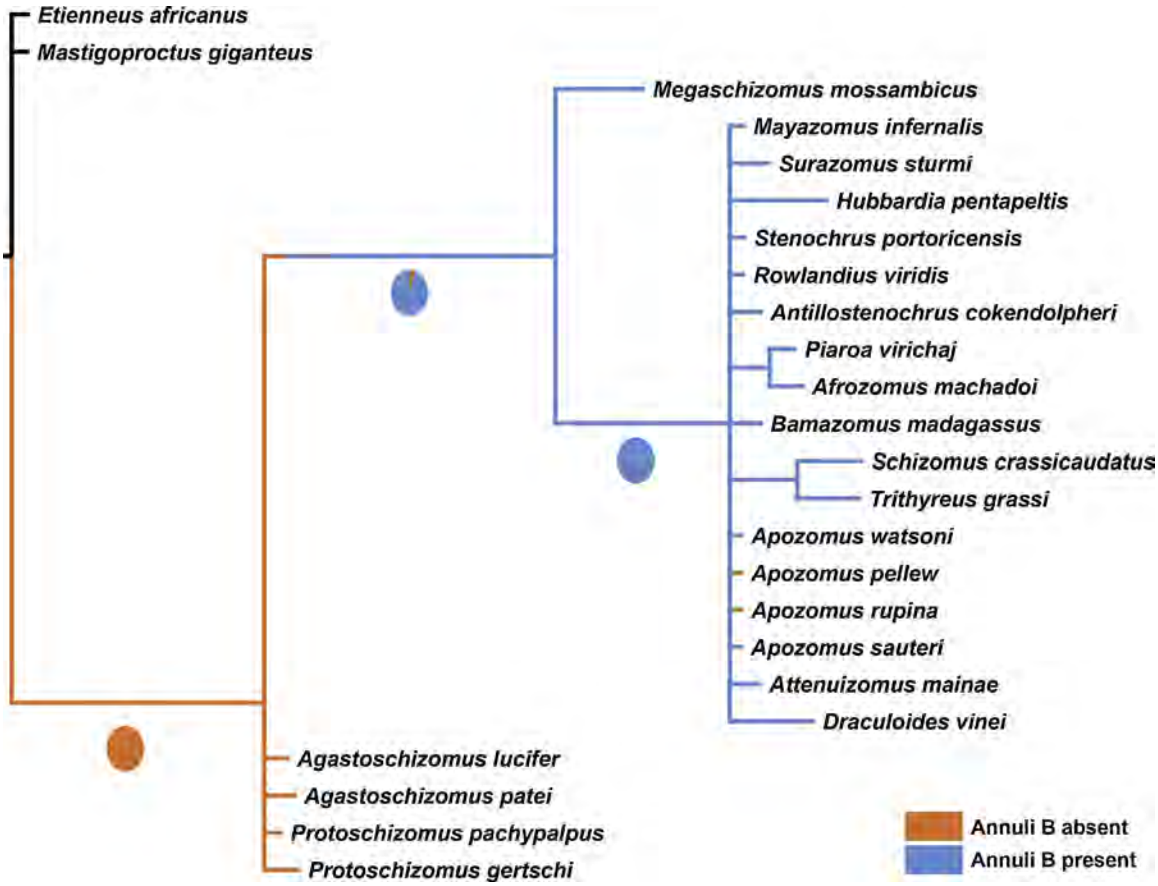

Fig. 13. Ancestral state reconstruction of character 38.

sidae, Kury and Villarreal, 2015: Figs. 1 D–F, 4 A–C). Thus it leads to confusion when considering these setae as homologous, as the principle of position is violated.

However if we follow the principle of congruence in homology, two different structures cannot be present in the same position or cannot take two positions at the same time, so it would be important to clear up if the setae (named by Cokendolpher and Reddell, 1992) are homologous. On the other hand, these homoplastic problems in position and congruence in homologous structures has been poorly explored. Homologous characters have been considered generally by topological equivalences; however, sometimes several correspondences among homologous characters can be expressed in many ways, which can be expressed in multiple explanations of homology (Ramírez, 2007).

3.4. Phylogenetic analyses

All analyses (complete matrix vs matrix without the annuli characters; equal weighting vs implied weighting, parsimony vs Bayesian inference) recovered the monophyly of Hubbardiidae, subsequently divided into Megaschizominae and Hubbardinae as currently stated by Cokendolpher and Reddell (1992), but it also recovered Protoschizomidae paraphyletic. The percentage of the support values (Jackknife in parsimony and the posterior probabilities in the Bayesian inference) for Hubbardiidae (and Hubbardinae) changed accordingly to each analysis (e.g. the analysis with the matrix without the annuli characters had higher support values in parsimony, see Table 3; and the Bayesian inference).

Our preferred topology of the parsimony analyses was the strict consensus of the five most parsimonious trees obtained from the analysis of the matrix without the annuli characters and implied weighting with *k* value = 3 given its tree statistics (shown in Fig. 9; Table 3). In this topology Hubbardiidae was supported by seven synapomorphies and one homoplasious character, and it was supported by 91% of Jackknife value (see Fig. 9 and Supplementary file 2). It was subsequently divided into the two currently established Hubbardinae and Megaschizominae (represented in our analysis by *Me. mozambicus*; Fig. 9). Subfamily Hubbardinae was supported by three synapomorphies and one homoplasious character, but with low Jackknife support value (74%); and with no internal resolution (Fig. 9). The lack of resolution of the internal relationships within Hubbardinae reflects that current morphological characters used to diagnose genera are highly homoplasious. Therefore, we recommend the use of molecular markers to resolve the relationships of Hubbardinae.

However, the monophyly of Protoschizomidae was not recovered with our dataset. All protoschizomid species came out at the base of the tree during the analyses. One hypothesis for this situation might be the plesiomorphic states of several characters in protoschizomids (e.g. the absence of a cheliceral brush, the number of dorsoventral muscles, and the male flagellum without distinct stalk) and that currently recognized "synapomorphies" for the family are indeed plesiomorphies. The status of Protoschizomidae (including the description of new characters) is revised elsewhere (manuscript in prep.).

The topology recovered with the Bayesian inference analysis was consistent with the one obtained from the parsimony analyses (Fig. 10). Unlike other studies (i.e. Friedman, 2007), our results can not be used as an extra branch support given that the values were similar. Our results suggest that analyzing our dataset with a model-based inference was unnecessary, for the same reasons Spencer and Wilbert (2013) already mentioned; however, it was

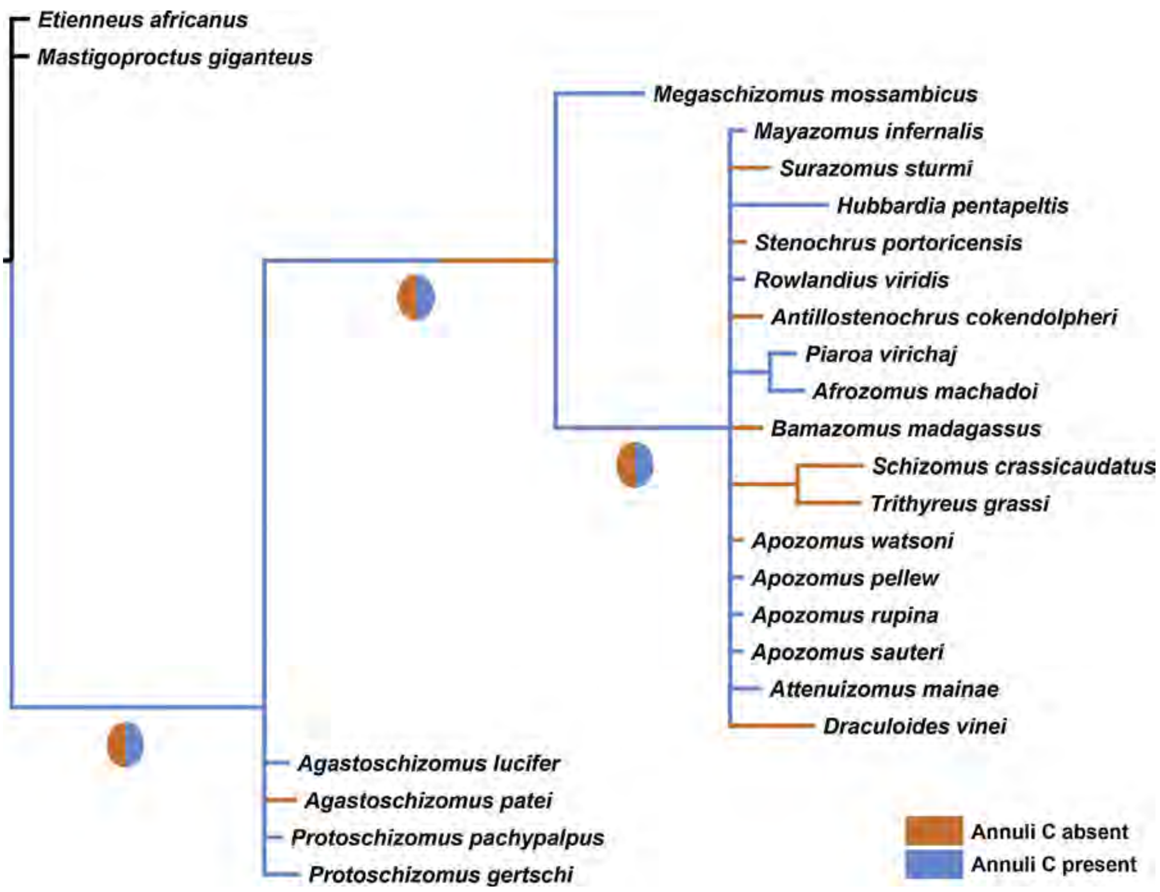

Fig. 14. Ancestral state reconstruction of character 39.

necessary to reconstruct the ancestral states to include the phylogenetic uncertainty (Ronquist, 2004). Also, this study is among the first attempts to analyze extant taxa with these approaches. Models of morphological character evolution are still in early stages of development and more research on them is necessary.

3.5. *Ancestral states reconstruction of characters 37–42: the plesiomorphic condition vs the percentage of uncertainty*

Ancestral reconstruction under Parsimony criteria consists only of mapping each character (optimization) as an observation, underestimates the possible total number of changes of character selected (Maddison, 1990). Mapping characters under Parsimony is reasonable when the rates of evolution are low, with fewest changes in the topologies generated, which it is not the case in the data matrix examined here (Huelsenbeck et al., 2003). On the contrary, the software SIMMAP and BayesTraits considered a model character, unlike Parsimony, therefore all possible character histories are considered, with probability and uncertainty (Pagel, 1999; Huelsenbeck et al., 2003). These two methods exposed these probabilities across the branches and on the most recent ancestor, respectively. We used unambiguous optimization to map the changes on the topology obtained with the analysis of the complete matrix and implied weighting with *k* value = 3 (Fig. 11; but see also Table 3), and comparing this optimization against the percentage of

Table 3
Tree statistics of most parsimonious trees (MPTs) obtained from the parsimony analyses of 22 schizomid species and two thelyphonid species as outgroup with equal weighting (Ew) or implied weighting (Iw) with three k values. Length (L), consistency index (CI), retention index (RI), Fit and adjusted homoplasy (AH). *Statistics for the consensus tree.

Matrix complete								Jackknife support values	
		MP	L	CI	RI	FIT	AH	Hubbardidae	Hubbardinae
Ew		9*	90	0.544	0.76	31.33	–	86%	75%
Iw	k = 10	15*	92	0.533	0.749	35.73	3.270	86%	81%
Iw	k = 3	15*	92	0.533	0.749	31.64	7.360	84%	82%
Iw	k = 1	5*	93	0.527	0.743	27.48	11.52	90%	85%
Matrix without annuli characters								Jackknife support values	
		MP	L	CI	RI	FIT	AH	Hubbardidae	Hubbardinae
Ew		380*	98	0.398	0.590	24.253	–	91%	63%
Iw	k = 10	5*	65	0.600	0.819	30.068	2.097	90%	69%
Iw	k = 3	5*	65	0.600	0.819	27.025	4.975	91%	74%
Iw	k = 1	20*	80	0.487	0.715	23.559	8.440	92%	78%

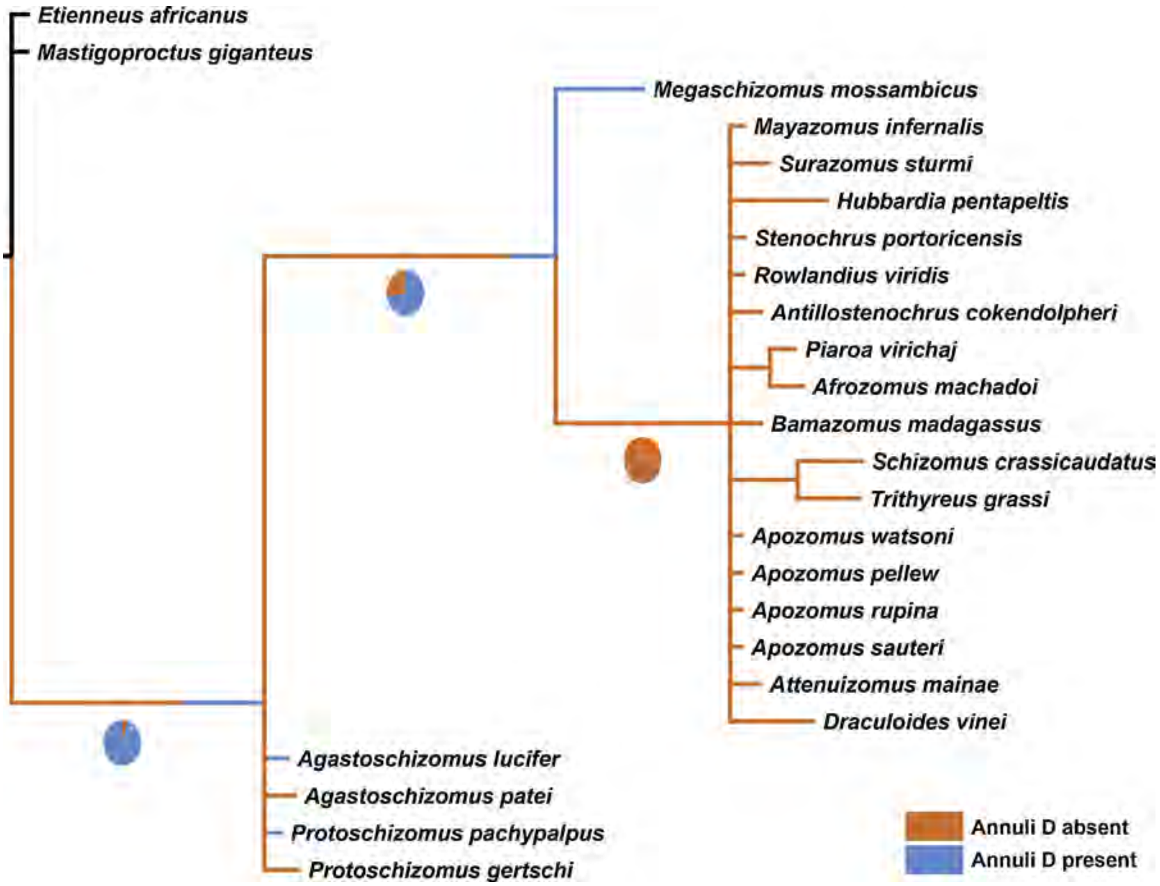

Fig. 15. Ancestral state reconstruction of character 40.

uncertainty from the ancestral state reconstruction using SIMMAP and BayesTraits.

Character 37 (annulus ‘a’), state 0 (absence) was recovered as a potential synapomorphy (Fig. 11) for two species of *Apozomus* (*A. pellew* and *A. rupina*). The rest of the terminals were recovered with state 1 (presence). The analysis with SIMMAP suggested that the absence of this annulus is a subsequent lost in these two species, because state 1 was recovered as the ancestral state for Schizomida (100%). However, the analysis with BayesTraits suggested that the presence of this annulus had an equal probability to be the ancestral state for Schizomida (49–51%: Fig. 12).

Character 38 (annulus ‘b’), state 1 (presence) was recovered as a synapomorphy for Hubbardiidae (Fig. 11). Both analyses, with BayesTraits and SIMMAP, recovered the state of presence of the annulus ‘b’ as the ancestral state in Hubbardiidae (with 95% and 96% values respectively; Fig. 13). Our observations in other protoschizomids suggest that the presence of annulus ‘b’ is an apomorphic condition for Hubbardiidae.

Character 39 (annulus ‘c’) state 0 (absence) was recovered as homoplastic character (shared by some hubbardiids and *Ag. patei* which lost annulus ‘c’, Fig. 11). The analysis with BayesTraits considered either state (presence or absence) as the ancestral state for Schizomida, Hubbardiidae and Hubbardinae, because eight terminals were coded 0. However, the analysis with SIMMAP considered the state 1 with higher probability (presence, 99%) as the ancestral state for Schizomidae and Hubbardinae (Fig. 14). In this case, it is more likely that the plesiomorphic condition (state 1) remained in the common ancestor of Hubbardiidae (which is present in several genera, e.g. *Afrozomus*, *Attenuizomus*, *Hubbardia*, *Notozomus*, *Rowlandius*) and subsequent losses occurred in other genera (e.g. *Antillostenochrus*, *Bamazomus*, *Draculoides*, *Pacal*, *Stenochrus*, *Surazomus*, etc.).

Characters 40–41 (annuli ‘d’ and ‘e’) were recovered as homoplasious characters in the current parsimony analyses (not shown in Fig. 11). Based on our observations above on setal patterns, annuli ‘d’ and ‘e’ are missing in the Hubbardiinae and in two protoschizomid species (*Ag. patei* and *P. gertschi*). The analyses with BayesTraits (Figs. 15, 16) considered the presence of these annuli as the ancestral condition for Schizomida with high probability (97%); however, the presence of these annuli got lower percentage (71%) supporting the ancestral condition for Hubbardiidae (*Me. mossambicus* has both annuli); and finally the absence of both annuli had the highest probability (100%) as the ancestral state for Hubbardinae. The analysis with SIMMAP (Figs. 15 and 16) considered the absence of annuli ‘d’ and ‘e’ as the ancestral state for Schizomida (with low probabilities, 66%); and the percentage increased for the absence of these annuli as the ancestral state for Hubbardiidae (82%) and Hubbardinae (100%). Interestingly, these two methods considered the phylogenetic uncertainty differently, as BayesTraits suggest presence while SIMMAP considered absence (Fig. 17).

Character 42 (multistate, number of annuli) was also recovered as a homoplastic character in the parsimony analyses. Given the lack of resolution for Protoschizomidae, it is hard to explain the gain or loss of annuli from a parsimony perspective. State 0 (all annuli, not mapped on the topology; Fig. 11) represents an autapomorphy for *Me. mossambicus*. State 1 (four annuli); state 2 (three annuli) and state 3 (two annuli) were recovered as homoplasious characters. Finally, state 4 (0 annulus) is autapomorphic for *Ag. patei*.

The analysis with BayesTraits considered state 0 (with 29%) as the ancestral state for Hubbardiidae; state 1 (with 81%) as the ancestral state for Schizomida; state 2 (with 43%) as the ancestral

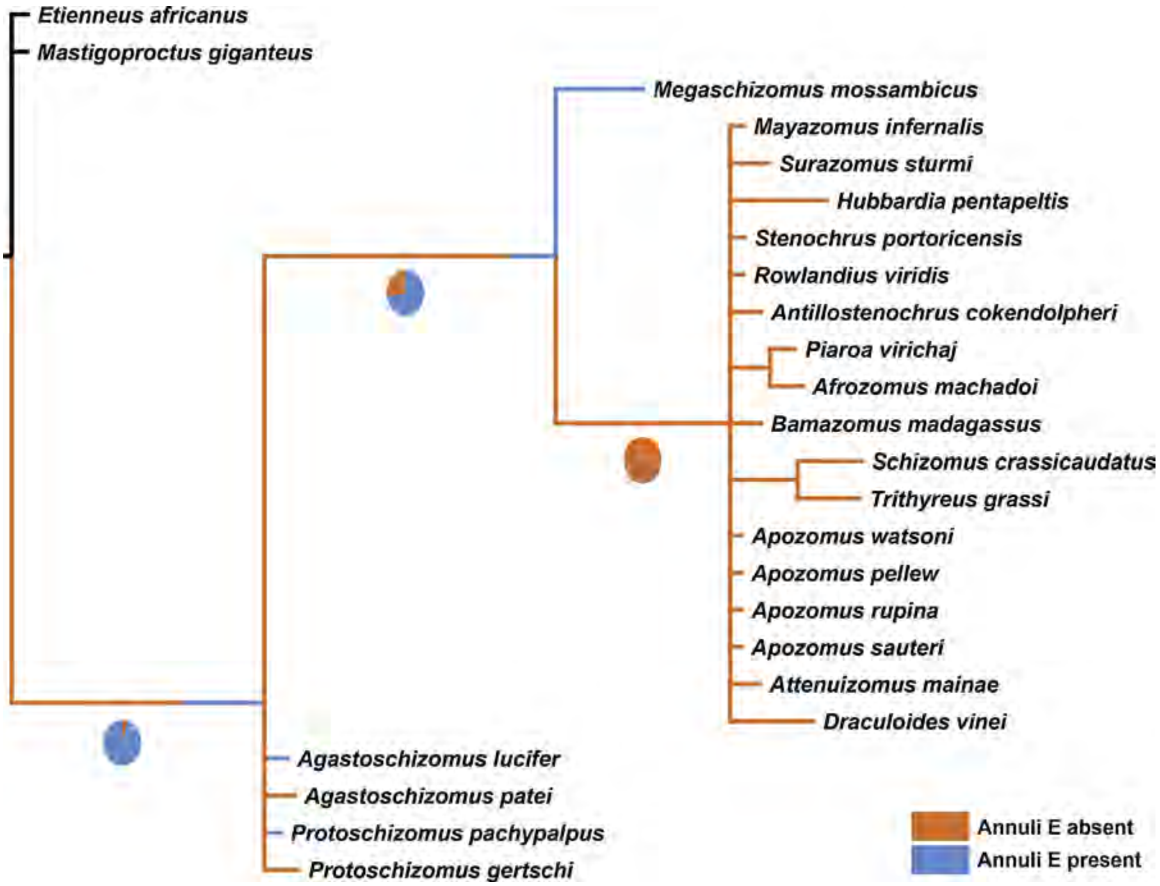

Fig. 16. Ancestral state reconstruction of character 41.

state for Hubbardinae; but also state 3 (with 57%). These results suggest 29% of probability that five annuli were the ancestral condition to Hubbardiidae, with no loss or gain in Megaschizominae, and subsequent losses (two or three annuli) in Hubbardinae. However, the analysis with SIMMAP suggests differently. It considered only state 3 (two annuli) as the ancestral state for Schizomida (97%); Hubbardiidae (80%) and Hubbardinae (100%). These results would suggest multiple gains of annuli in different taxa, and only the loss of all annuli in *Ag. patei*.

4. Conclusions

Our results indicate that the number of annuli in the female and juvenile flagellum in schizomids is a character that can be helpful to diagnose genera. However, this character fails to group genera into higher categories due to the multiple losses of different annuli in different groups. For these reasons, the hypothesis of grouping genera with three annuli, or genera with two annuli into well-supported clades failed [as previously suggested by Rowland, 1975]. This situation also was observed also in the 20th century Opiliones systematics, when the number of the leg tarsomeres was considered an important character to separate and recognize supraspecific taxa (Peírez-Gonzaílez, 2006). However, nowadays there is sufficient evidence to assume that the number of tarsomeres is a highly variable character, homoplastic and phylogenetically uninformative, because the gain (or loss) of segments occurred many times, suggesting ecological adaptations to similar habitats (Sharma and Giribet, 2009).

On the other hand, the loss of the annuli does not involve any kind of specific evolutionary process or specific structures (i. e., muscles or segments), and as it was shown before (in Protoschizomidae) the annuli are present in some members or absent in others (such as *Ag. patei*).

Our observations among subfamilies and the two families represented in character 34 (annuli shape) show that widened annuli could be found in the distal portion of the flagellum (annuli ‘c’, ‘d’ and ‘e’) corroborating the hypothesis that the wider annuli provide flexibility to the flagellum, as also present in the flagellum of Thelyphonida.

Finally, the relative positions of the flagellar setae, homologized here across families and subfamilies, are good characters to diagnose the different genera. However, we recommend cautious use of seal pattern for taxonomic decisions as the discovery of new species and genera might bring new characters (i. e., more setae on the flagellum of both, males and females) into play.

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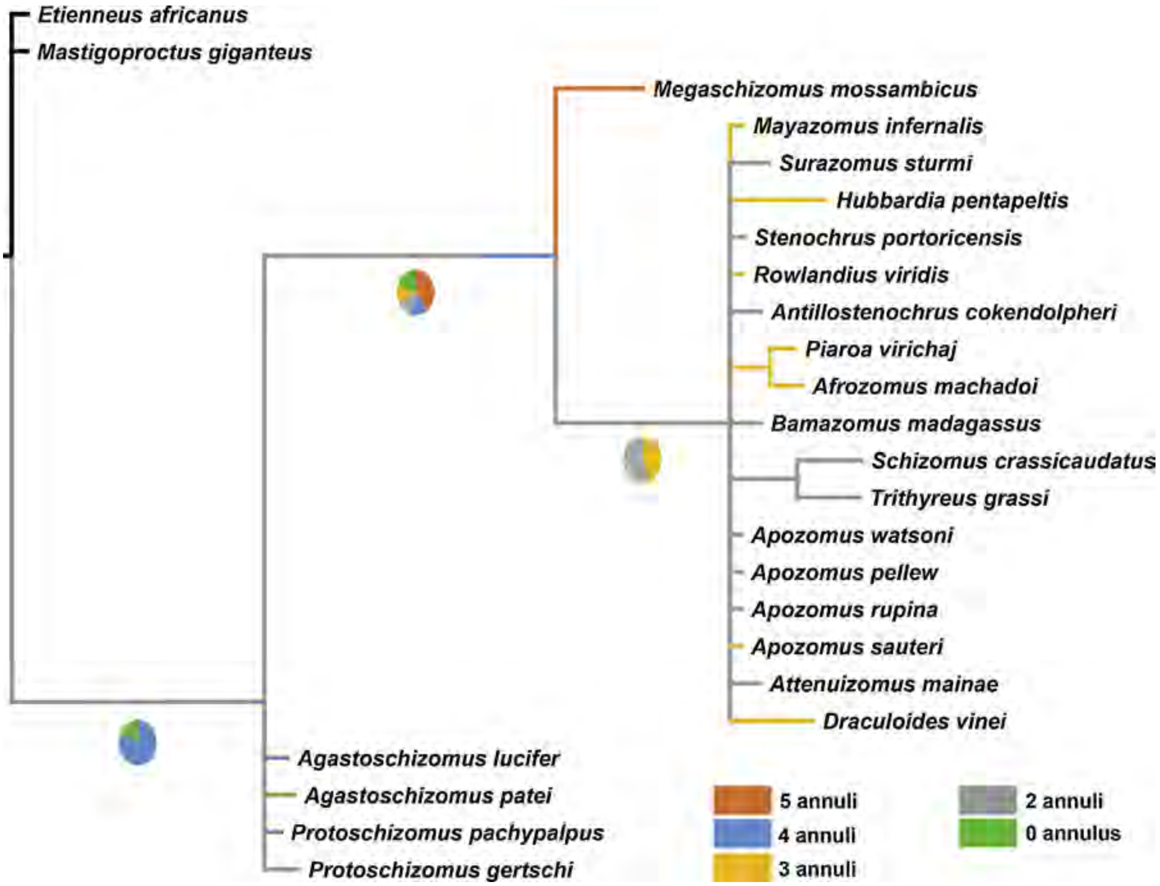

Fig. 17. Ancestral state reconstruction of character 42.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jcz.2016.05.003.

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Research Article

A new genus of schizomids (Arachnida: Schizomida: Hubbardiidae) from Mexico, with notes on its systematics

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During the systematic revision of *Mayazomus*, the third most diverse genus of micro whip-scorpions in North America, we found three species with peculiar morphological variation, which are different from those diagnostic characters for *Mayazomus*. These species share with *Mayazomus* the large body size and the unusual development of the male pedipalps; however, these three species share the shape of the female spermathecae with *Stenochrus* rather than with *Mayazomus.* Therefore, their phylogenetic placements create a dilemma. Here we perform analyses with morphological evidence, using two different methodologies (Parsimony and Bayesian inference) in order to hypothesize the phylogenetic relationships of the three species mentioned with each other and with respect to other North American and/or Central American genera. The results confirm our initial hypothesis that the species belong to a different genus, *Olmeca* gen. nov., which is recovered as the sister group of all hubbardiine genera included in these analyses, except for the genus *Hubbardia*. The results also indicate that despite sharing some morphological similarities, it is distantly related with *Mayazomus*. Three species are described herein: *Olmeca brujo* sp. nov., *Olmeca cruzlopezi* sp. nov., and *Olmeca santibanezi* sp. nov. Additionally, we provide a hypothesis of the relationships and biogeography of *Olmeca* gen. nov. with other genera.

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Key words: Bayesian inference, morphology, new-species, *Olmeca* gen. nov., parsimony, phylogenetics

Introduction

The family Hubbardiidae is represented in Mexico by four genera: *Mayazomus* Reddell and Cokendolpher, 1995 (seven species), *Pacal* Reddell & Cokendolpher, 1995 (three species), *Sotanostenochrus* Reddell and Cokendolpher, 1991 (two species), and *Stenochrus* Chamberlin, 1922, as the genus with the highest diversity (16 species) (Monjaraz-Ruedas & Francke, 2015; Reddell & Cokendolpher, 1995). These differences in the number of species are due, probably, to poor collecting efforts, and the lack of taxonomic studies with the group, as there are very few experts working with the schizomid fauna of Mexico and Central America.

Currently, the correct generic assignment of newly collected specimens in Mexico is problematic, mainly because of the lack of taxonomic publications on the group. For example, the genus *Stenochrus*, despite its high diversity and the problematic widespread species *S. portoricensis* (Christophoryová, Šestáková, Krumpál, & Fenđa, 2013; Harvey, 2013; Korenko, Pekár, & Harvey, 2009), has not been revised. On the other hand, most recent works have focused on the genus *Mayazomus*, which was recovered as a monophyletic group (Monjaraz-Ruedas & Francke, 2015, 2016). Monjaraz-Ruedas and Francke (2016) found that the most representative characteristics of *Mayazomus* are the size and shape of the male pedipalps, and the presence of spines and apophyses on the pedipalps, that diagnose this genus. Also, they demonstrated that the setae patterns of the pedipalps provide important information for the systematics of schizomids, helping us to diagnose other genera within the order Schizomida.

Traditionally, the description of new taxa in higher levels, such as family or genus, was based mainly on the morphological differences that a taxonomist recognized, and their suggestions to differentiate groups, which in

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schizomids were based upon characteristics of the male flagellum and female spermathecae (Armas, 2002, 2014; Harvey, 2001; Reddell & Cokendolpher, 1995). However, descriptions of new taxa within the Schizomida lack a phylogenetic context; this has led to a potential over- or under-estimation of diversity at various higher taxonomic levels; this is particularly reflected in the number of monotypic genera recently described (Armas, 2002; Armas & Colmenares-Garcia, 2006; Armas & Delgado-Santa, 2012; Armas & Teruel, 2002; Moreno-González & Villarreal, 2012; Teruel & Armas, 2002; Villarreal, Giupponi, & Tourinho, 2008).

Currently, only four works on schizomids have used phylogenetic systematics as a base to describe new taxa: the phylogeny of Protoschizomidae Rowland, 1973 by Cokendolpher and Reddell (1992); the description and revision of the genera *Draculoides* Harvey, 1992 and *Paradraculoides* Harvey, Berry, Edward, & Humphreys, 2008 based on molecular and morphological evidence by Harvey et al. (2008); and the revision of the genus *Mayazomus* with the description of five new species based on morphological evidence (Monjaraz-Ruedas & Francke, 2015, 2016). However, in future works with schizomids, it is necessary to make taxonomic decisions based on rigorous phylogenetic analyses, especially in the descriptions of new higher taxa such as genera.

As a result of the examination of the material studied in the revision of the genus *Mayazomus*, we found specimens with a combination of characters, which could not be assigned to any current genus. For this reason, we include those specimens in a phylogenetic analysis, comparing them with other Mexican species and other representative species of New World schizomid genera, with which they share certain traits, as evidenced by the analyses of Monjaraz-Ruedas and Francke (2016).

Materials and methods

Material examined

Specimens were deposited in the following collections: American Museum of Natural History, New York (AMNH), and Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNAN). Specimens were collected by hand and/or using an aspirator, and preserved in 80 and 96% ethanol. Observations were made using Nikon SMZ-800 stereomicroscopes, and a Nikon Eclipse E100 optical microscope. Measurements (mm) follow Reddell and Cokendolpher (1995), and were obtained with an ocular micrometre calibrated at 20×. Morphological terminology for legs and pedipalps follows Reddell and Cokendolpher (1995), cheliceral setae nomenclature follows Lawrence (1969), flagellar setae terminology after Monjaraz-Ruedas, Francke, Cruz-López, and Santibañez-López (2016), pedipalp setae terminology follows Monjaraz-Ruedas & Francke, 2016, and finally spermathecae nomenclature follows Moreno-González, Delgado-Santa, and Armas (2014).

Male chelicerae were dissected and prepared for scanning electron microscopy (SEM) according to Acosta, Pérez-González, and Tourinho (2007), with a modification to the cleaning process which consisted of a series of three cycles of washes, alternating distilled water and biological detergent, followed by 1 minute in the ultrasonic cleaner. Microphotographs were taken using a Hitachi SU1510 SEM. Female spermathecae were dissected in 80% ethanol and cleared in lactophenol for 10 min (Krantz & Walter, 2009), after which they were fixed in Hoyer's liquid and mounted in a permanent preparation. Photographs were taken under visible light with a Nikon Coolpix S10 VR camera attached to a Nikon SMZ-800 microscope. Photographs were edited with Adobe Photoshop CS6.

Taxa

We included 20 specimens, collected in Mexico, which represent three new species (described below). To test their phylogenetic position, we included in our analysis the following 17 species of the subfamily Hubbardiinae (Hubbardiidae): six species distributed in Mexico and the USA representing the North American fauna (two *Hubbardia*, two *Stenochrus* and two *Pacal*); nine species distributed in the Caribbean region and Central America (five *Mayazomus*, one *Belicenochrus*, two *Rowlandius* and one *Hansenochrus*); and finally two species distributed in South America (two *Surazomus*) with a total of 21 terminal taxa; those species were included based on the results of Monjaraz-Ruedas and Francke (2016) showing that *Mayazomus* (morphologically the most similar genus to *Olmeca*) is closely related with Central and South American genera. To root the tree, we used a member of the family Protoschizomidae: *Protoschizomus franckei* Monjaraz-Ruedas, 2013 (Appendix 1, see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2016.1271057). With this, we intended to gain an understanding of the phylogenetic affinities of the new genus.

Data matrix

One hundred and eleven qualitative characters (Appendix 2, see supplemental material online) taken from the matrix used by Monjaraz-Ruedas and Francke (2016) were scored (Appendix 3, see supplemental material online) for the 21 terminal taxa in the analyses (Appendix 1, see supplemental material online). Thirty-four characters were multistate and 76 binary, 12 characters were uninformative and deactivated in all parsimony analyses (Appendix 2, see supplemental material online).

Parsimony phylogenetic analyses

The analyses were conducted in TNT (Goloboff, Carpenter, Arias, & Miranda-Esquivel, 2008) combining three of the new technology algorithms (Goloboff, 1999; Nixon, 1999) using a script file modified from Dimitrov, Astrin, and Huber (2013) and Santibañez-López, Francke, and Prendini (2014) as implemented in Monjaraz-Ruedas and Francke (2016) for a smaller data matrix: hold 1000; rseed1; xm: noverb nokeep; rat: it 0 up 4 down 4 au 0 num 36 give 99 equa; dri: it 10 fit 1.00 rfi 0.20 aut 0 num 36 give 99 xfa 3.00 equa; sec: mins 45 maxs 45 self 43 incr 75 minf 10 god 75 drift 6 glob 5 dglob 10 rou 3 xss 10- 14 + 2 noxev noeq; tf: rou 5 minf 3 best ke nochoo swap; xm: level 10 nochk rep 50 fuse 3 dri 10 rss css noxss mult nodump conse 5 conf 75 nogive notarg upda autoc 3 xmix; xm; xmult:;. Uninformative characters were deactivated using the command xinact;. Analyses were carried out with equal weighting (EW) and implied weighting (IW) using three values of the concavity constant ($k = 1$, 3, and 10). The analyses with implied weighting were conducted as a sensitivity analysis to assess the nodal stability (Giribet, 2003) and evaluate the robustness of the clades with different parameters, in this case the different values of k in the IW analyses (Goloboff et al., 2003; Goloboff, Farris, & Nixon, 2008; Prendini, 2000; Wheeler, 1995). The relative support for each node on the preferred hypothesis was calculated with Bremer support (Bremer, 1994) and jackknife resampling (Farris, Albert, Kallersjo, Lipscomb, & Kluge, 1996). Bremer support was calculated in TNT by expanding the memory and holding suboptimal trees up to 10 steps and without collapsing nodes. Jackknife support was estimated with heuristic searches of 1000 pseudoreplicates, with a removal probability of 36%. Cladograms were generated with WinClada (Nixon, 2002) and edited with Adobe Illustrator C6.

Bayesian analyses

The analysis with Bayesian inference was performed in order to compare the results with the different topologies recovered with Parsimony analyses, because high levels of homoplasy introduce noise in the results and could lead us to an erroneous hypothesis. Moreover, studies have shown that the use of Bayesian methods with morphological data diminish resolution in the topology but generate better results (O'Reilly et al., 2016). The model implemented in the Bayesian inference for morphological data (Lewis, 2001) allows the inclusion of categorical data, which is treated without rate variation, allowing us to statistically test the importance of synapomorphies present in our hypotheses. In addition, with the branch lengths calculated with the Bayesian analysis, we can recover clades based on different parameters which allows us to recover topologies that consider the presence of one character in a branch, but also considers the probability of the absence of that character in the rest of the tree.

The Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist et al., 2012), implementing the Mkv model for categorical data, in this case morphology (Lewis, 2001). Two independent runs were conducted with four chains each (one cold and three heated) for 2 million generations, with a heat parameter of 0.2, and a sampling frequency every 1000 generations. We checked for stationarity of the chains plotting the log-likelihood of the trees against generation using TRACER 1.5 (Rambaut, Suchard, Xie, & Drummond, 2014). Twenty-five per cent of the trees were discarded as burn-in and the remaining were used to calculate the posterior probabilities. Consensus trees were plotted and edited in FigTree 1.4.2 (Rambaut, 2014).

Results

The analysis with equal weighting recovers two most parsimonious trees (MPT) (Consensus: length (L) = 310, consistency index (CI) = 0.432, retention index (RI) = 0.611)), with a polytomy on the relationships amongst *Pacal*, *Mayazomus*, and the rest of the hubbardiid schizomids, excluding *Olmeca* gen. nov. and *Hubbardia* (Fig. 1). The analysis with IW $k = 10$ recovered the same topology as one of the trees obtained with EW; but with slightly different tree statistics (Table 1). The analyses obtained with implied weighting with values of $k = 1$ and 3 recovered a different topology than the one obtained with EW, in which there are changes in the relationships

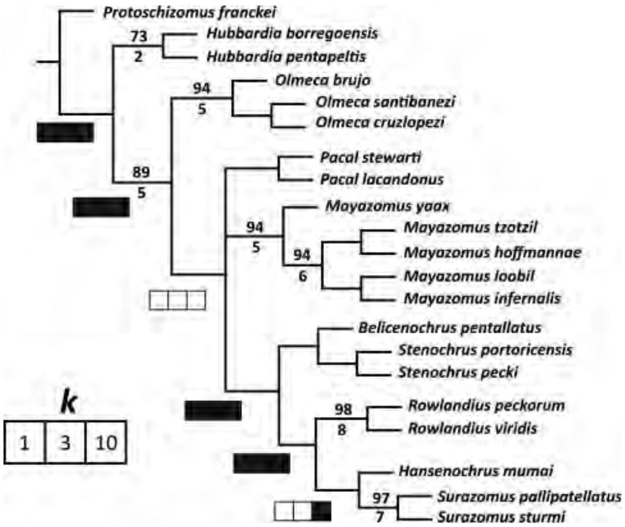


Fig. 1. Consensus of the two most parsimonious trees obtained under equal weights (L = 310, CI = 0.432, RI = 0.611). Clade support is indicated above (Jackknife values) and below (Bremer support) the branches. Sensitivity plots ('Navajo rugs') indicate the recovery of the nodes in the different analysis under implied weights with different values of '*k*' (black squares indicate clades recovered; white squares indicate clades not recovered).

Table 1. Tree statistics of the most parsimonious trees (MPTs) obtained from the parsimony analyses with equal weighting (EW) and different implied weighting (IW) under different values of the concavity constant (*k*). Length (L), consistency index (CI), retention index (RI), Fit and adjusted homoplasy (AH).

		MP	L	CI	RI	FIT	AH
EW	Consensus	2	310	0.43	0.61	46.97	—
IW	k = 10	1	307	0.44	0.62	85.31	13.69
IW	k = 3	1	309	0.43	0.61	67.77	31.23
IW	k = 1	1	309	0.43	0.61	48.23	50.77

between *Rowlandius* and *Hansenochrus* (Fig. 1). In all the analyses performed, the genus *Olmeca* is recovered as a monophyletic group, located basally in the topology, as the sister group to all the other hubbardiine genera included, except *Hubbardia* (Figs 1, 2).

Our preferred parsimony topology was the one obtained using IW under $k = 10$. Our choice was based on the index values obtained with IW (Table 1) where the most preferable topology is the one with the highest values of Fit instead of number of steps (Goloboff et al., 2008). Additionally the topology with $k = 10$ is congruent with one of the MPT and the phylogenetic affinities of the genera included are consistent with their geographic distribution and the findings of Monjaraz-Ruedas and Francke (2016).

The Bayesian Inference recovers the genus *Olmeca* gen. nov. as a monophyletic group in the consensus tree, with a posterior probability (PP) of 0.91 (Fig. 3). However *Olmeca* gen. nov. is placed in an unresolved polytomy with all the hubbardiine genera used in this analysis, and this lower resolution is a phenomenon previously mentioned by O'Reilly et al. (2016); except for *Hubbardia*, which is recovered as monophyletic (as in the Parsimony analyses), with a Posterior Probability of 0.88 (Fig. 3).

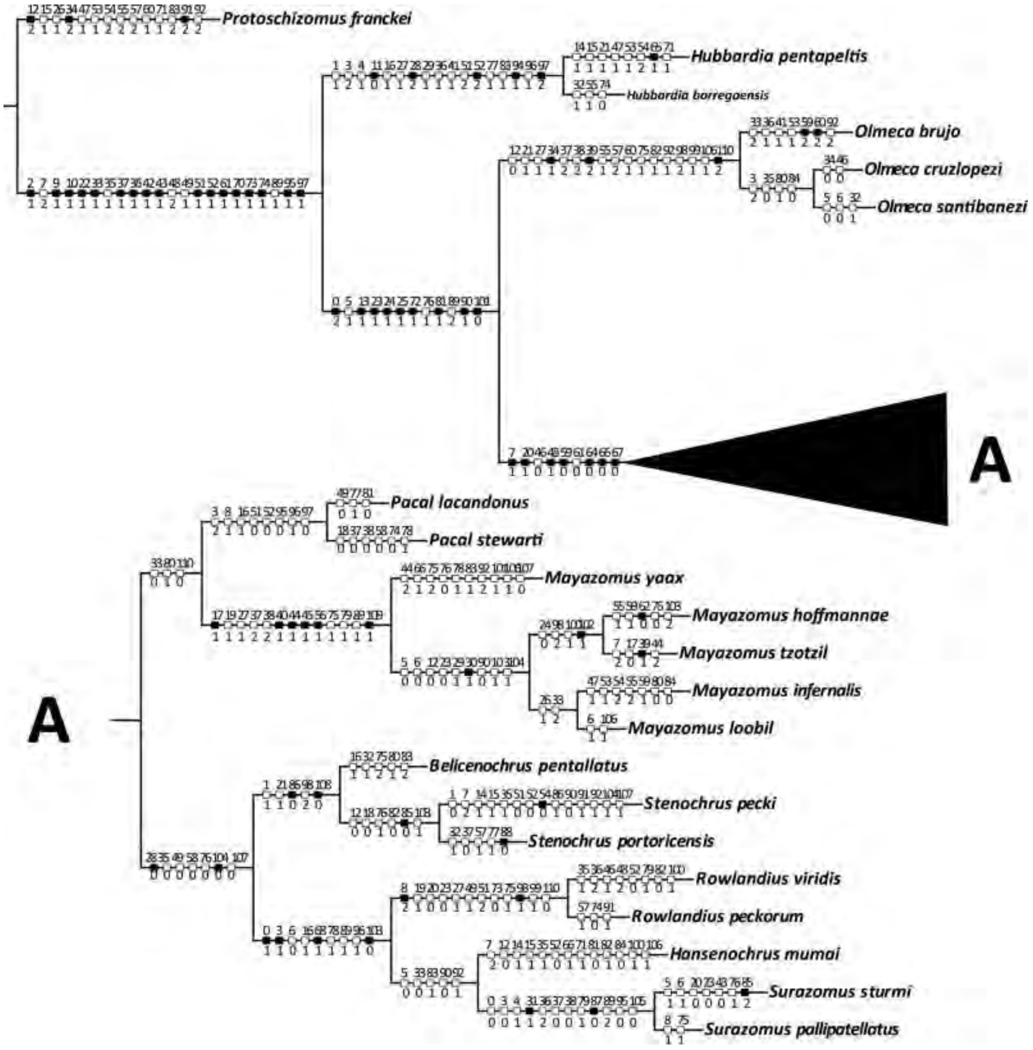


Fig. 2. Preferred single tree resulted from the analysis under implied weights with concavity constant $k = 10$. Apomorphies are plotted on branches. Black squares indicate synapomorphies; white squares indicate homoplastic character states (parallelisms or reversals) according to the character sampling. Numbers above branches indicate character number, and numbers below branches indicate character state.

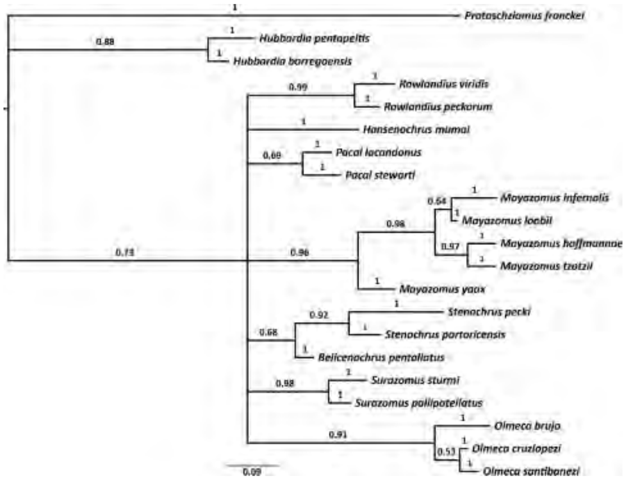
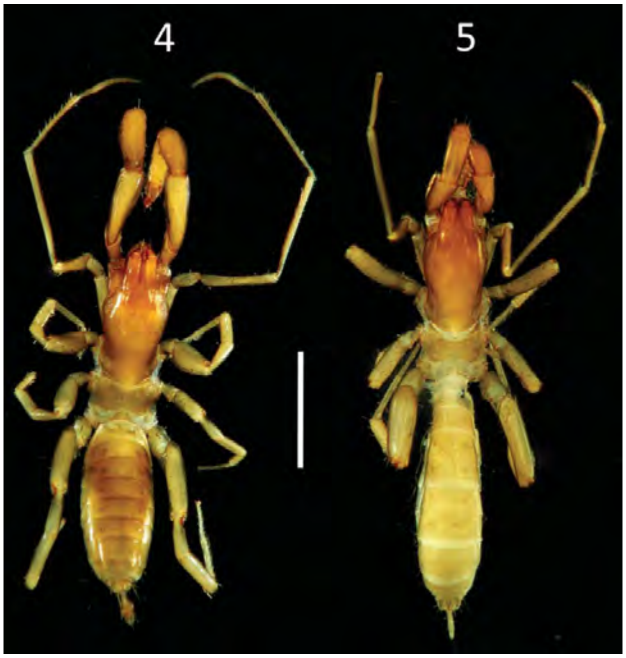


Fig. 3. Optimal tree obtained under Bayesian inference, implementing the Mkv model; posterior probability values indicated above branches.



Figs. 4–5. *Olmeca cruzlopezi*. Male holotype. Habitus: 4. Dorsal view. Female paratype. Habitus: 5. Dorsal view. Scale bar = 2 mm.

Systematics

Family **Hubbardiidae Cook, 1899**
Subfamily **Hubbardiinae Cook, 1899**

Olmeca gen. nov.

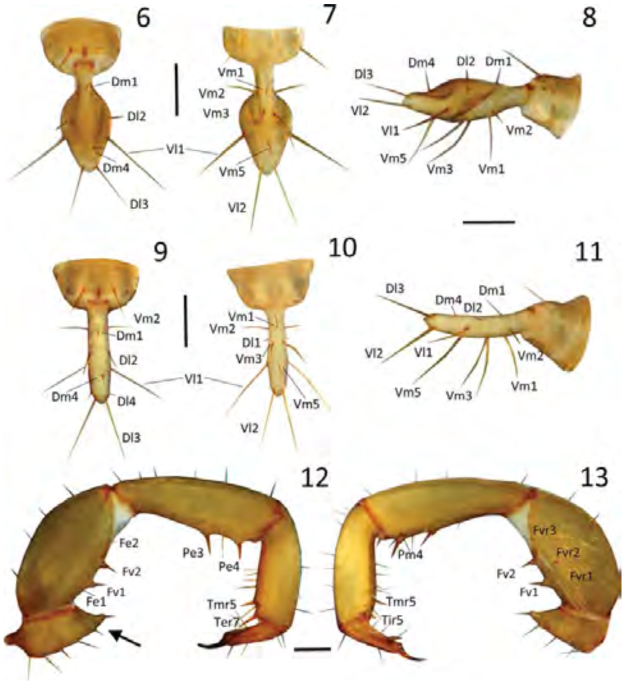
Figs 1–46; Tables 2–4 (see supplementary material online)

Type species. *Olmeca cruzlopezi* sp. nov.

Distribution. *Olmeca* is distributed throughout Southeastern México in the states of Chiapas and Veracruz.

Etymology. The generic name is a noun in apposition that honours the prehispanic Mexican tribe of the Olmecas, which was one of the oldest Mexican civilizations; they lived in the region of Veracruz, Tabasco and Chiapas before the emergence of the Mayan culture. It is masculine in gender.

Diagnosis. Anterior process of propeltidium with two anterior setae (one behind the other) and two pairs of dorsosubmedian setae; corneate eyes absent, with one pair of eyespots; metapeltidium entire; body without clavate setae. Tergite II with one pair of dorso-submedian setae; segments IX–XII not elongated. Movable cheliceral finger without accessory tooth; with a single guard tooth at end of serrula, setal group G3 with setae G3–4 basally. Pedipalps sexually dimorphic; trochanter with mesal spur and a projected rounded Apical Process (Figs 12, 13); femur with setae *Fe2* spiniform (character 34, state 1) and with setae *Fv1* and *Fv2* as well-developed spiniform setiferous tubercles, both located ventrally (character 40, state 1); tibia with seta 7 of the external row (*Ter*) and setae 5 of the internal row (*Tir*) spiniform and strongly sclerotized (Figs 12, 13). Femur IV with anterodorsal margin produced at about 90° angle. Male: without posterodorsal abdominal



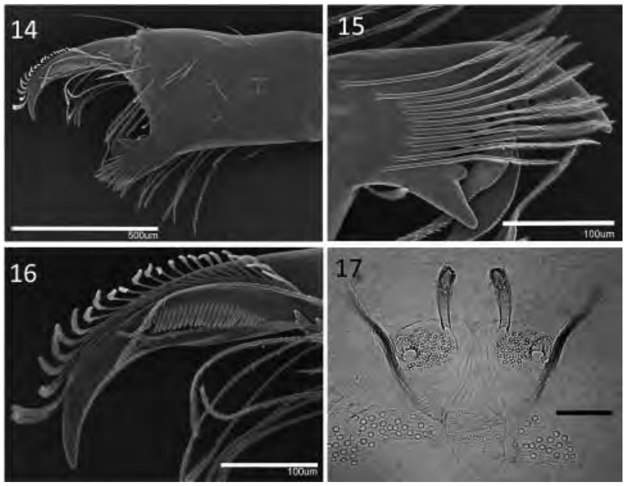
Figs. 6–13. *Olmeca cruzlopezi*. Male holotype. Flagellum (6–8): 6, dorsal view. 7, ventral view. 8, lateral view. Female. Flagellum (9–11): 9, dorsal view. 10, ventral view. 11, lateral view. Male pedipalp (G, H): 12, ectal view. 13. mesal view. Arrow indicates the anterior process. Scale bars = 0.2 mm.

process on segment XII; flagellum dorsoventrally flattened, elliptical or ovate, with one pair of dorso-submedian depressions (Figs 6–8). Female: flagellum with two annuli; spermathecae with two pairs of lobes, lateral lobes wider and smaller than medial lobes (about 1/3 or 1/2 the length of medial lobes); lateral lobes usually drop-shaped, median lobes straight to slightly curved; without bulbs; chitinized arch 'U' shaped, without anterior branch; lateral tip lobed or not sclerotized; gonopod long.

The genus *Olmeca* resembles the genus *Stenochrus* in having female spermathecae with lateral lobes reduced and with two annuli on the female flagellum; however, the spermathecae of *Olmeca* has lateral lobes smaller than those known in the species of *Stenochrus*; in addition, the median lobes in *Olmeca* are straight whereas in *Stenochrus* they are predominantly 'J' shaped. *Olmeca* also resembles *Mayazomus* in large body size, having long pedipalps, and sharing spiniform setiferous tubercles on pedipalp femur; however males of *Olmeca* do not present femoral or tibial apophyses, but instead they present spiniform setae on tibia and setae *Fv1* and *Fv2* as tubercles located ventrally, whereas in *Mayazomus* those setiferous tubercles are located ventrally (*Fv1*) or distally (*Fv2*); also *Mayazomus* presents both femoral and tibial apophyses, whereas *Olmeca* does not present any apophysis. *Olmeca* presents one pair of setae on tergite II and *Mayazomus* presents two pairs. Finally, the flagellum of females of *Mayazomus* presents three annuli, whereas in *Olmeca* it presents only two annuli.

Included taxa. *Olmeca brujo* sp. nov, *Olmeca cruzlopezi* sp. nov. and *Olmeca santibanezi* sp. nov.

Remarks. This genus shares some diagnostic characters with *Stenochrus* and *Mayazomus* such as: the reduced lateral lobes in the female spermathecae (shared with *Stenochrus*) and the setae *Fv1* and *Fv2* as spiniform setiferous tubercles (shared with *Mayazomus*). However the phylogenetic analyses show that it is completely separated from the last genus (see trees above).



Figs. 14–17. *Olmeca cruzlopezi*. Male. Chelicera (14–17): 14, mesal view. 15, fixed finger. 16, movable finger. Female. Spermathecae: 17, dorsal view. Scale bar (Fig. 17) = 0.05 mm.

Identification key to the species of *Olmeca*, gen. nov.

1a Male flagellum ovate shaped, with a pair of dorso-median depressions not connected posteriorly (Fig. 34); pedipalp femur with setae *Fe1* spiniform and strongly sclerotized; pedipalp patella with setae *Pe* 1–4 and *Pm* 1–4 spiniform (Figs 40, 41). Females and males with the same opisthosomal setation; spermathecae with lateral lobes 1/2 length of median lobes (Fig. 45) ……………………………………………..***Olmeca brujo*** sp. nov.

1b Male flagellum elliptical/lanceolate shaped, with a pair of dorso-submedian depression connected posteriorly (Figs 6, 20); pedipalp femur with setae *Fe1* acuminate, not sclerotized; pedipalp patella with setae *Pe* 2–3 and *Pm* 2–3 spiniform. Females and males with different opisthosomal setation; spermathecae with lateral lobes 1/3 length of median lobes (Figs 17, 31) ………………………… 2

2a Male flagellum lanceolate shaped (Fig. 6); pedipalp femur with seta *Fe5* acuminate; pedipalp trochanter with a triangular (<45°) apical process, with dorsal margin straight; with an acuminate seta on mesal surface near mesal spur (Figs 12, 13). Female spermathecae with lateral lobes drop shaped; chitinized arch 'V' shaped (Fig. 17) ………………………… ***Olmeca cruzlopezi*** sp. nov.

2b Male flagellum elliptical shaped (Fig. 20); pedipalp femur with setae *Fe5* spiniform; pedipalp trochanter with a triangular (45°) apical process with a dorsal margin curved; with a spiniform seta hardly projected on mesal surface near mesal spur (Figs 26, 27). Female spermathecae with lateral lobes tubular shaped; chitinized arch 'U' shaped (Fig. 31) … .***Olmeca santibanezi*** sp. nov.

Olmeca cruzlopezi sp. nov.

Figs 4–17, 13, 46; Tables 2–4 (see supplementary material online)

Type material. MEXICO: *Chiapas*: male holotype (CNAN-T1078) [20 June 2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibáñez, A. Valdez, K. Zarate], from El Rastrejón, Guadalupe Victoria (16.63049°N, 93.3451°W, 925m), Municipio Ocozocuautla. Paratypes: 1 male and 1 female (CNAN-T1079), same data as holotype. 1 male and 1 female (CNAN-T1080) [15 June 2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibáñez, A. Valdez, K. Zarate], from outside cave of Paso Burro (16.82883°N, 93.2628°W, 767 m), Municipio Berriozabal.

Habitat and distribution. Known from the Municipalities of Berriozabal, Cintalapa and Ocozocuautla in the western region of Chiapas, Mexico (Fig. 46). The specimens were collected in a very dry zone in Ocozocuautla, and in moist areas of a rain forest in Cintalapa and Berriozabal; they were collected sympatric with *Mayazomus* and *Pacal.*

Etymology. This species is named honouring our colleague Jesus A. Cruz-López for his help collecting the type material and also for his great contributions to the systematics of arachnids, specifically Opiliones in México.

Diagnosis. Males can be distinguished by trochanter with a triangular apical process (arrow in Fig. 12), less than 45° ending in a rounded tip (Fig. 12); pedipalp femur with setae *Fe1* and *Fe2* acuminate, tibia with setae *Ter5* spiniform and *Ter6* feathered (slightly sclerotized). Male flagellum lanceolate shaped with one pair of dorso submedian depressions connected distally (Figs 6–8). Females can be distinguished by the spermathecae (Fig. 17) with median lobes curved inward, lateral lobes drop shaped. *Olmeca cruzlopezi* resembles *Olmeca santibanezi* sp. nov. in the shape of the apical process of the trochanter and the *Fv1* and *Fv2* setae of the pedipalp femur; however, *O. santibanezi* has a more projected apical process than *O. cruzlopezi*; the male flagellum of *O. santibanezi* presents an elliptical shape, whereas the male flagellum in *O. cruzlopezi* is lanceolate in shape. The female spermathecae of *O. cruzlopezi* has lateral lobes drop shaped, whereas *O. santibanezi* presents lateral lobes tubular shaped.

Description. Male (holotype): Brownish (Fig. 4). Prosoma: propeltidium with two setae on anterior process (one behind the other) and two pairs of dorsal setae; ocular spots asymmetrical, slightly visible. Metapeltidium 0.53 long, 0.88 wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs 14–16): Movable finger: Serrula with 22 teeth, guard tooth present. Fixed finger with 4 smaller teeth between 2 primary teeth. Setation: Setal group formula: 1:3, 2:6, 3:4, 4:2, 5:11, 6:1. G1 with three spatulate setae, covered with few spinose and small spicules starting from the middle of the shaft; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, feathered apically and smooth basally; G4 consisting of two setae, smooth, short and thick, elongated at the tip; G5 with 11 similar sized setae, feathered apically and shorter than fixed finger; G6 with one smooth setae about 1/2 of movable finger length.

Pedipalps (Figs 12, 13): long; 2.88 times longer than propeltidium length. Trochanter with apical process triangular shaped <45° with a projected rounded tip (arrow in Fig. 12); with a row of very short setae on ventral margin plus one row of five microsetae on ectal face; mesal surface with a row of three setae near ventral margin, plus two setae near dorsal margin; with a small, distal mesal spur. Femur, 2.0 times longer than high, distal margin curved, ventral margin curved; ventral margin on ectal surface with spiniform setiferous tubercles *Fv1* and *Fv2* well developed and near each other; mesal surface with a row of three ventral setae (*Fvr* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella, setae *Pe4*, *Pe3*, and *Pm4* spiniform; without setae *Pme1* or special armature, seta *Pmm3* feathered. Setae formula on tibia 4:3:6 (external row (Ter): medial row (Tmr): internal row (Tir)), setae *Ter7*, *Tmr5*, and *Tir5* spiniform and hardly sclerotized, seta *Ter6* slightly sclerotized, seta *Tm1* feathered, setae *Tm2* acuminate. Tarsus long, 3.56 times longer than high. Claw about 1.2 times as long as dorsal length of tarsus; spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 27: 5: 6: 6: 6: 7: 15. Femur IV 2.4 times longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus one pair of macrosetae; tergite II with three pairs of microsetae anteriorly plus one pair of macrosetae; tergites III–VII with one pair dorsal setae each; tergites VIII, IX with one pair dorsal and one pair lateral setae each; segments X, XI telescoped with one pair lateral setae and six ventral setae; segment XII with one dorsal, two lateral and two ventral pairs of setae, without posterodorsal process. Sternites, with two irregular rows of setae each; genital aperture with two rows of microsetae.

Flagellum (Figs 6–8): dorsoventrally flattened, lanceolate in shape; 2.2 times longer than wide, 3.0 times longer than pedicel length; with a pair of dorso-submedian depressions fused posteriorly. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* at same level as *Vm2*; *Vm*5 posterior to *Vl1*. With one pair of antero-dorsal microsetae between *Dm1* and *Dl2*, nearest to *Dl2*; one pair of antero-lateral microsetae on flagellar pedicel; and with two pairs of microsetae between *Vl1* and *Vl2*.

Female (paratype) (Fig. 5): Pedipalps shorter and without development as on male, 1.9 times longer than propeltidium length. Abdominal setation: tergite I and segments X–IX as on male, tergites II–VIII with one pair of dorsal macroseta, plus two rows of microsetae near anterior and posterior margin of each tergite, each row with six to eight microsetae. Flagellum with two annuli (Figs 9–11). Setation: seta *Dl2* reduced and anterior to *Vl1*; *Dl3* at same level as *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present.

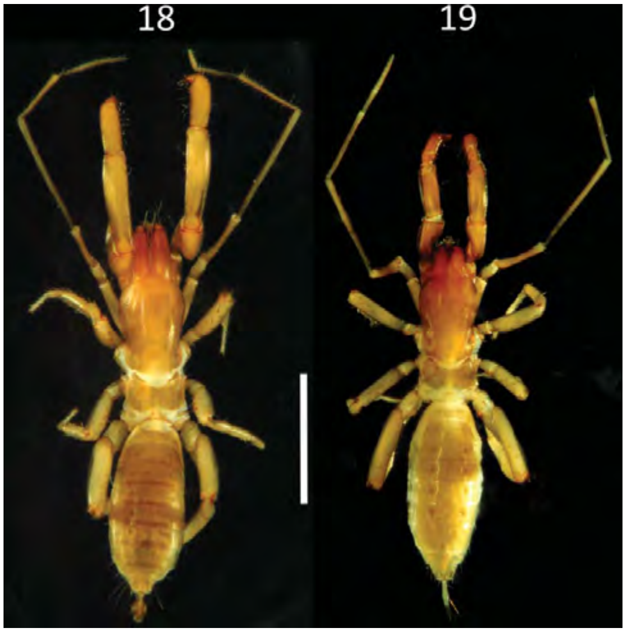
Spermathecae (Fig. 17) with two pairs of lobes; median pair slightly curved inwards, longer than lateral pair, with apical duct openings ending in a blunt margin; lateral pair shorter, about 1/3 of the median lobes, drop shaped, without duct openings. Chitinized arch U-shaped, extending laterally to almost the same size as median lobes; lateral tip not sclerotized. Gonopod long, wide. Chelicera: serrula with 20 teeth. Setal group formula 1:3, 2:8, 3:4, 4:2, 5:11, 6:1. Fixed finger with 3 teeth between two primary teeth.

Remarks. Males of *Olmeca cruzlopezi* differ in the size of the pedipalps, having males with the same setation on pedipalps and the same armature, but with evidently smaller pedipalps 3.1 vs 2.8 times longer than propeltidium length. Also the apical process of the pedipalp trochanter differs in some males, in which this process is shorter and less pronounced. The females differ considerably in the number of dorsal setae of the tergites, from eight setae to three or four setae in each tergite.

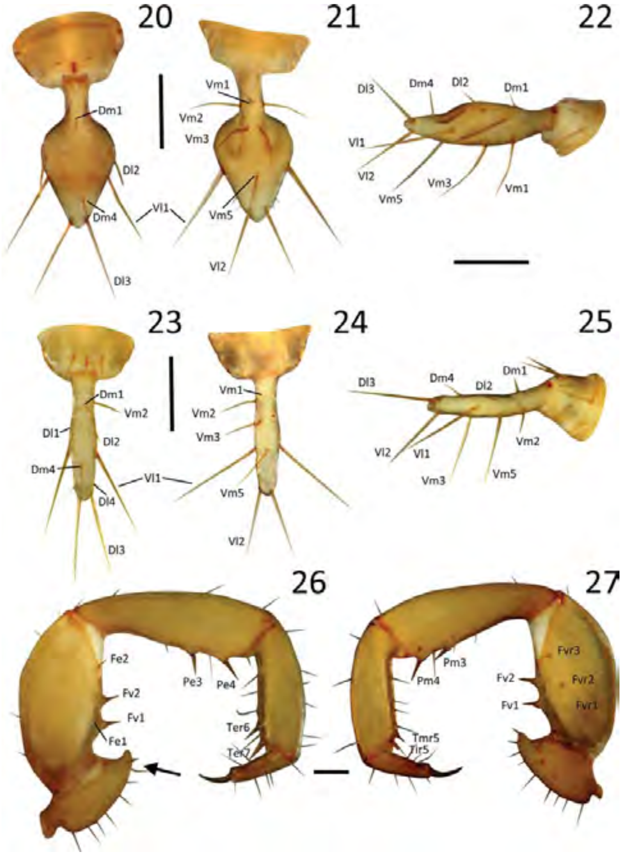
Olmeca santibanezi sp. nov.

Figs 18–31, 46; Tables 2–4 (see supplementary material online)

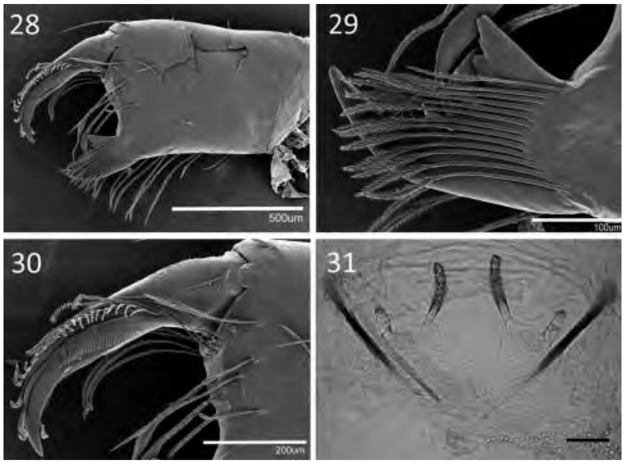
Type material. MEXICO: *Chiapas*: male holotype (CNAN-T1081) [28 July 2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibáñez, A. Valdez, K. Zarate], from



Figs. 18–19. *Olmeca santibanezi*. Male holotype. Habitus: 18. Dorsal view. Female paratype. Habitus: 19. Dorsal view. Scale bar = 2 mm.



Figs. 20–27. *Olmeca santibanezi*. Male holotype. Flagellum (20–22): 20, dorsal view. 21, ventral view. 22, lateral view. Female. Flagellum (23–25): 23, dorsal view. 24, ventral view. 25, lateral view. Male pedipalp (26, 27): 26, ectal view. 27. mesal view. Arrow indicating the anterior process. Scale bars = 0.2 mm.



Figs. 28–31. *Olmeca santibanezi*. Male. Chelicera (28–31): 28, mesal view. 29, fixed finger. 30, movable finger. Female. Spermathecae: 31, dorsal view. Scale bar (Fig. 31) = 0.05 mm.

El Aserradero (16.78533°N, 91.0382°W, 205 m), Municipio Ocosingo. Paratypes: 2 males and 1 female (CNAN-T1082), same data as holotype. 1 male (CNAN-T1083) [28 July 2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibáñez, A. Valdez, K. Zarate], from El Encaño, Sierra de la Cojolita (16.81133°N, 91.0774°W, 165 m), Municipio Ocosingo. 1 female and 2 juveniles (CNAN-T1084) [28 July 2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibáñez, A. Valdez, K. Zarate], from Arroyo Nayté, Sierra de la Cojolita (16.79406°N, 91.0423°W, 194 m), Municipio Ocosingo.

Habitat and distribution. Known from the Selva Lacandona and the Sierra de la Cojolita in the Municipio of Ocosingo, in the eastern region of Chiapas, Mexico (Fig. 46). The specimens were collected sympatric with *Mayazomus aluxe*, and *Stenochrus portoricensis*; however, the specimens of *S. portoricensis* were collected under scrap pieces of wood (many with bark attached) in the middle of the jungle, where a large tree was cut into planks, and there was a thick layer of moist sawdust underneath; whereas the *Mayazomus* and *Olmeca* were found under rocks, near small streams and rivers, in very moist microhabitats.

Etymology. The specific name is dedicated to our colleague Carlos E. Santibañez-López for his help collecting the type material, his contributions to the systematics of scorpions and for all the advice and help in past research on schizomid systematics.

Diagnosis. Males can be distinguished by trochanter with a long apical process projected distally (arrow in Fig. 26), slightly curved on the dorsal margin, ending in a pointed tip (with a setae) (Fig. 26); by the presence of a very long and sclerotized seta on mesal surface of the trochanter, near mesal spur; pedipalp femur with seta *Fe1* acuminate and seta *Fe2* spiniform; tibia with setae *Ter6* and *Ter7* spiniform strongly sclerotized. Male flagellum elliptical shaped with one pair of deep dorso sub-median depressions connected distally (Figs 20–22). Females can be distinguished by the spermathecae (Fig. 31) with median lobes curved outward, and lateral lobes tubular shaped. *Olmeca santibanezi* resembles *Olmeca cruzlopezi* in the shape of the apical process of the trochanter and the setae *Fv1* and *Fv2* of the pedipalp femur both located ventrally, however, *O. santibanezi* has a more projected apical process and curved along the dorsal margin, and *O. cruzlopezi* has a triangular apical process; also the mesal surface of the pedipalp trochanter presents a spiniform seta near mesal spur, whereas *O. cruzlopezi* has an acuminate seta. The male flagellum in *O. santibanezi* presents an elliptical shape, elongated on the posterior part, whereas in *O. cruzlopezi* it is lanceolate and rounded on the posterior region. The female spermathecae of *O. cruzlopezi* has lateral lobes drop shaped whereas *O. santibanezi* presents lateral lobes tubular shaped; in addition, the chitinized arch in *O. santibanezi* is completely 'V' shaped, whereas in *O. cruzlopezi* it is curved near the gonopod.

Description. Male (holotype): Brownish (Fig. 18). Prosoma: propeltidium with two setae on anterior process (one behind the other) and two pairs of dorsal setae; ocular spots irregular and asymmetrical, clearly visible. Metapeltidium 0.45 long, 0.85 wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs 28–30): Movable finger: Serrula with 26 teeth, guard tooth present. Fixed finger with 4 smaller teeth between 2 primary teeth. Setation: Setal group formula: 1:3, 2:6, 3:4, 4:2, 5:13, 6:1. G1 with three spatulate setae, covered with spinose spicules starting from the base of the shaft; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, two feathered apically and smooth basally with a blunt tip, and two feathered along their length and with a pointed tip; G4 consisting of two setae, smooth, short and thick, spine shaped; G5 with 13 similar sized setae, feathered apically and shorter than fixed finger; G6 with one smooth setae about 1/3 of movable finger length.

Pedipalps (Figs 26, 27): long; 3.02 times longer than propeltidium length. Trochanter with apical process triangular shaped about 45°, curved in the dorsal margin and expanded distally in the posterior part with a pointed tip (arrow in Fig. 26); with a row of long setae on ventral margin plus one row of five microsetae and one spiniform setae on ectal face; mesal surface with a row of four setae near ventral margin, the third seta spiniform, longer than the mesal spur and with an expansion of the cuticle, plus two setae near dorsal margin; with a small, medial mesal spur. Femur 2.25 times longer than high, distal margin curved, ventral margin curved; ventral margin on ectal surface with spiniform setiferous tubercles *Fv1* and *Fv2* well developed and near each other; mesal surface with a row of three ventral spiniform setae (*Fvr* 1–3) plus two dorsal spiniform setae (*Fmd2*, *Fmd3*). Patella, setae *Pe4*, *Pe3*, *Pm3*, and *Pm4* spiniform; without setae *Pme1* or special armature, seta *Pmm3* feathered. Setae formula on tibia 4:4:5 (external row (Ter): medial row (Tmr): internal row (Tir)), setae *Ter7*, *Ter6*, *Tmr5*, and *Tir5* spiniform and strongly sclerotized; setae *Tm1* and *Tm2* acuminate. Tarsus long, 3.33 times longer than high. Claw about 1.2 times as long as dorsal length of tarsus; spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 28: 5: 6: 6: 7: 7: 15. Femur IV 2.4 times longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus one pair of macrosetae; tergite II with three pairs of microsetae anteriorly plus one pair of macrosetae;

tergites III–VII with one pair dorsal setae each; tergites VIII, IX with one pair dorsal and one pair lateral setae each; segments X, XI telescoped with one pair lateral setae and five ventral setae; segment XII with one dorsal, two lateral and four ventral pairs of setae, without postero-dorsal process. Sternites, with two irregular rows of setae each; genital aperture with three rows of microsetae, one anterior and two posterior.

Flagellum (Figs 20–22): dorsoventrally flattened, ovate in shape; 2.18 times longer than wide, 2.5 times longer than pedicel length; with a pair of deep dorso-submedian depressions fused posteriorly. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* at same level as *Vm2*; *Vm*5 slightly posterior to *Vl1*. Without antero-dorsal microsetae; with one pair of antero-lateral microsetae on flagellar pedicel; and with three pairs of microsetae between *Vl1* and *Vl2*.

Female (paratype) (Fig. 19): Pedipalps shorter and without development as on male, with a short and triangular apical process, 2.09 times longer than propeltidium length. Setation: tergite I, IX and segments X–XII as on male, tergites II–VIII with two irregular rows of setae near anterior and posterior margin of each tergite, each row with a principal dorsal pair of macrosetae and with six to eight setae. Flagellum with two annuli (Figs 23–25). Setation: seta *Dl2* reduced and anterior to *Vl1*; *Dl3* posterior to *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 31) with two pairs of lobes; median pair slightly curved outwards, longer than lateral pair, with apical duct openings starting about 1/3 of the base, ending in a blunt margin; lateral pair shorter, about 1/2 length of the median lobes, tubular shaped, with apical duct openings ending in a blunt tip. Chitinized arch V-shaped, almost same size as median lobes; lateral tip lobed. Gonopod long. Chelicera: serrula with 26 teeth. Setal group formula 1:3, 2:6, 3:4, 4:2, 5:12, 6:1; G4 with smooth setae ending in a long tip. Fixed finger with 4 teeth between 2 primary teeth.

Remarks. As in *Olmeca cruzlopezi*, males of *Olmeca santibanezi* also vary in the size of the pedipalps, from 3.09 to 2.10 times longer than propeltidium length; the size and thickness of the setae in the mesal surface of the pedipalp trochanter varies amongst males, some males present more developed and sclerotized setae (similar to the mesal spur) in the three of them, whereas other males only present that sclerotization in the two distal setae. The spermathecae varies in the size of the lateral lobes, having lateral lobes wider than others or even longer, with variation in size from 1/3 to 1/2 the length of median lobes. Also the females differ in the number of dorsal setae on the tergites, having females with 9 setae per row in each tergite and other females with only 5 setae.

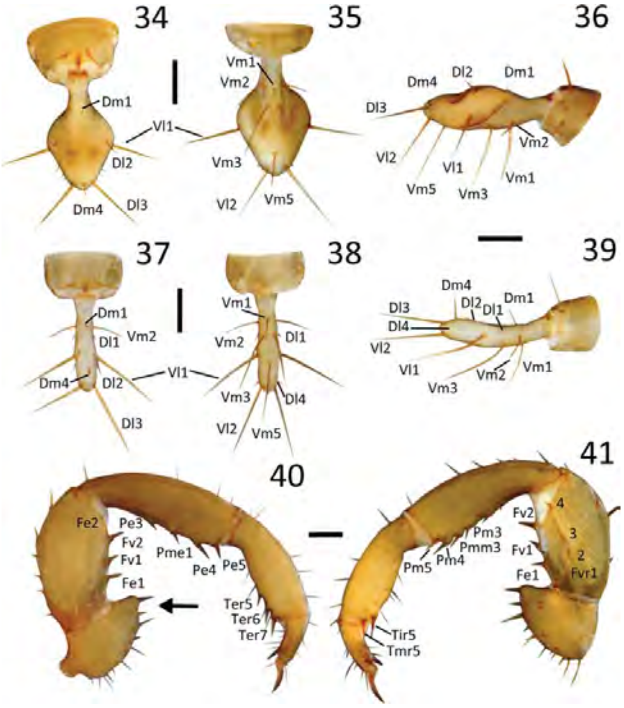
Figs. 32–33. *Olmeca brujo*. Male holotype. Habitus: 32. Dorsal view. Female paratype. Habitus: 33. Dorsal view. Scale bar = 2 mm.

Olmeca brujo sp. nov.

Figs 32–45, 46; Tables 2–4 (see supplementary material online)

Type material. MEXICO: *Veracruz*: male holotype (CNAN-T1085) [11 January 2012, J. Cruz, O. Francke, R. Monjaraz, G. Montiel.], from Estación Biológica 'Los Tuxtlas' (18.58482°N, 95.0749°W, 173 m), Municipio San Andrés Tuxtla. Paratypes: 1 male and 2 female (CNAN-T1086), same data as holotype. 1 male (CNAN-T1087) [10 November 2012, J. Cruz, O. Francke, R. Monjaraz, G. Montiel, A. Valdez], same locality as holotype. 1 female (CNAN-T1088) [11 November 2012, J. Cruz, O. Francke, R. Monjaraz, G. Montiel, A. Valdez], from 1.5 km East from Ejido la Perla de San Martín (18.55550°N, 95.12110°W, 749 m), Municipio Catemaco. 1 male (CNAN-T1089) [28 March 2013, G. Contreras.], from Río Zapota, San Martín (18.30147°N, 94.7290°W, 950 m), Municipio Pajapan.

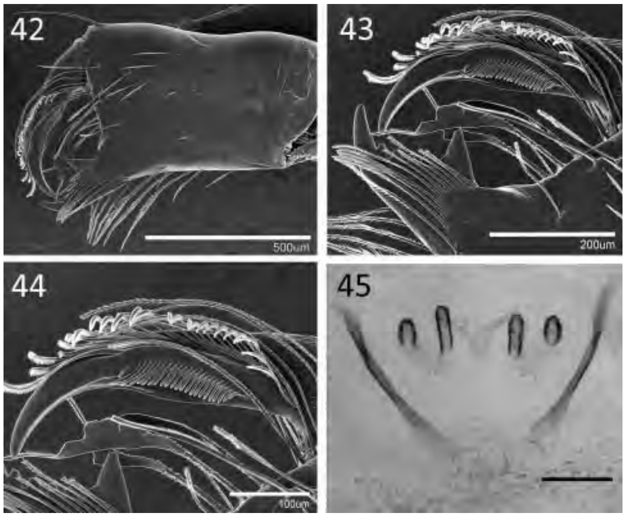
Habitat and distribution. Known from the South-east region of Veracruz known as Los Tuxtlas, that includes the UNAM Biological Station, Catemaco, San Andres Tuxtla, and Pajapan; it is also known from the foothills of Volcan San Martín and surroundings (Fig. 46). The specimens were collected under rocks in a well conserved rain forest, living sympatrically with undescribed species of *Stenochrus* and *Pacal*.



Figs. 34–41. *Olmeca brujo*. Male holotype. Flagellum (34–36): 34, dorsal view. 35, ventral view. 36, lateral view. Female. Flagellum (37–39): 37, dorsal view. 38, ventral view. 39, lateral view. Male pedipalp (40, 41): 40, ectal view. 41. mesal view. Arrow indicating the anterior process. Scale bars = 0.2 mm.

Etymology. The specific name is a noun in apposition that means wizard or shaman in Spanish, referring to the witchcraft ceremonies performed in the region of Catemaco and the Tuxtlas.

Diagnosis. Males can be distinguished by trochanter with a small triangular (more than 45°) apical process, ending in a pointed tip (arrow Fig. 40); by all rows of setae *Pe* and *Pm* on pedipalp patella with spiniform setae; pedipalp femur with setae *Fv1*, *Fv2*, *Fe1*, and *Fe2* spiniform, setae *Fvr4* present and spiniform; tibial external row (*Ter*) with spiniform strongly sclerotized setae. Male flagellum, bulbous ovate shaped, with one pair of dorso sub-median depressions not fused distally (Figs 34–36). Females can be distinguished by the spermathecae (Fig. 45) having median lobes slightly longer than lateral lobes, ending at the same level as the lateral lobes, appearing to be of the same length. *Olmeca brujo* resembles *Olmeca cruzlopezi* and *Olmeca santibanezi* having setae *Fv1* and *Fv2* as spiniform setiferous tubercles and located ventrally, but differs considerably from the last two in having a more bulbous flagellum, and pedipalp femur and patella with spiniform setae; also, the mesal row of setae on pedipalp femur presents an extra seta (*Fvr4*) absent in both *O. cruzlopezi* and *O. santibanezi*. The spermathecae of *O. cruzlopezi* and *O. santibanezi* present median lobes noticeably longer than lateral lobes, whereas *O. brujo* present lobes apparently of the same length. Finally the dorsal setation in females of *O. brujo* is the same as in males, whereas in *O. cruzlopezi* and *O. santibanezi* the females present a more complex dorsal setation than the males.



Figs. 42–45. *Olmeca brujo*. Male. Chelicera (42–45): 42, mesal view. 43, fixed finger. 44, movable finger. Female. Spermathecae: 45, dorsal view. Scale bar (Fig. 45) = 0.05 mm.

Description. Male (holotype): Brownish (Fig. 32). Prosoma: propeltidium with two setae on anterior process (one behind the other) and two pairs of dorsal setae; ocular spots irregular and asymmetrical, clearly visible. Metapeltidium 0.38 long, 0.77 wide. Anterior sternum with 10 setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs 42–44): Movable finger: Serrula with 22 teeth, guard tooth present. Fixed finger with 4 smaller teeth between 2 primary teeth. Setation: Setal group formula: 1:3, 2:8, 3:4, 4:2, 5:10, 6:1. G1 with three spatulate setae, covered with spinose spicules starting from the middle of the shaft; G2 composed of eight feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, two feathered apically and smooth basally with a blunt tip, and two feathered along their length and with a pointed tip; G4 consisting of two setae, smooth, short and thick, elongated at the tip; G5 with 10 similar sized setae, feathered apically and shorter than fixed finger; G6 with one smooth setae about 1/2 of movable finger length.

Pedipalps (Figs 40, 41): 2.4 times longer than propeltidium length. Trochanter with a small apical process triangular shaped >45°, ending in a pointed tip (with a seta) (arrow in Fig. 40); with a row of long setae on ventral margin plus two distal spiniform setae and one row of six spiniform setae on ectal face; mesal surface with a row of four spiniform setae near ventral margin, plus two spiniform setae near dorsal margin; with a small, distal mesal

Fig. 46. Distribution map of the known species of genus *Olmeca.*

spur. Femur 2.04 times longer than high, distal margin curved, ventral margin curved; ventral margin on ectal surface with spiniform setiferous tubercles *Fv1*, *Fv2*, *Fe1*, and *Fe2* well developed and strongly sclerotized; mesal surface with a row of four ventral spiniform setae (*Fvr*1–4) plus two dorsal spiniform setae (*Fmd2*, *Fmd3*). Patella with setae *Pe5–3*, *Pm5–3* spiniform, with setae *Pme1* and *Pmm3* spiniform. Setae formula on tibia 4:3:5 (external row (Ter): medial row (Tmr): internal row (Tir)), setae row *Ter*7–4 spiniform, setae *Tmr5* and *Tir5* spiniform and strongly sclerotized; seta *Tm1* acuminate, seta *Tm2* feathered. Tarsus 2.30 times longer than high. Claw about 1.7 times as long as dorsal length of tarsus; spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 22: 5: 5: 4: 5: 6: 14. Femur IV 2.5 times longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus one pair of macrosetae; tergite II with three pairs of microsetae anteriorly plus one pair of macrosetae; tergites III–VII with one pair dorsal setae each; tergites VIII, IX with one pair dorsal and one pair lateral setae each; segments X, XI telescoped with one pair lateral setae and five ventral setae; segment XII with one dorsal, two lateral and four ventral pairs of setae, without postero-dorsal process. Sternites, with two irregular rows of setae each; genital aperture with one posterior row of setae.

Flagellum (Figs 34–36): dorsoventrally flattened, ovate in shape and bulbous; 1.55 times longer than wide, 3.3 times longer than pedicel length; with a pair of dorso-submedian depressions not fused posteriorly. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally, at the same level as *Dl3*, *Dl2* at same level as *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* posteriorly to *Vm2*; *Vm*5 posterior to *Vl1*. With one pair of antero-dorsal microsetae; one pair of antero-lateral microsetae on flagellar pedicel; and four pairs of microsetae between *Vl1* and *Vl2*.

Female (paratype) (Fig. 33): Pedipalps shorter than male, 2.02 times longer than propeltidium length, but with the same setation pattern, apical process with same shape as on male but shorter. Setation as on male except for the anterior sternum with nine setae instead of 10. Flagellum with two annuli (Figs 37–39). Setation: seta *Dl2* reduced and anterior to *Vl1*; *Dl3* posterior to *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 45) with two pairs of lobes; median pair straight, longer than lateral pair, with duct openings along its length; lateral pair shorter, about 1/2 length of the median lobes, drop shaped, with duct openings along their length; base of the lobes starting posteriorly than median pair. Chitinized arch V-shaped, longer than median lobes; lateral tip irregular and projected; posterior branch slightly visible at the median portion between median lobes. Gonopod long and wide. Chelicera: serrula with 18 teeth. Setal group formula 1:3, 2:6, 3:4, 4:2, 5:8, 6:1. Fixed finger with 4 teeth between 2 primary teeth.

Remarks. Males vary in body and pedipalp size from 2.1 to 2.7 times longer than propeltidium length; however the setae patterns of the pedipalps are constant amongst males, varying only in the size of setae. Females present less development of the pedipalps that is noticeable in the size of the apical process of the pedipalp trochanter and the size of the spiniform setae of the pedipalp. The dorsal setation in *O. brujo* is constant amongst females. The number of setae on group 5 (G5) of the chelicerae varies from 8 to 10, and the number of teeth on serrula varies from 18 to 22 teeth.

Discussion

Phylogenetics of *Olmeca*

The three new species described here were consistently recovered as a different clade from the genus *Mayazomus*, with which they are more similar in male morphology. Therefore, our results justify the creation of a new genus (described below): *Olmeca* gen. nov.

Genus *Olmeca* gen. nov. was recovered as a monophyletic group with a Jackknife branch support of 94, Bremer support of 5 and by three synapomorphies: (a) setae *Fe2* spiniform (character 34, state 1), with a reversion on *O. cruzlopezi*; (b) setae *Fv1* and *Fv2* as well-developed spiniform setiferous tubercles, both located ventrally (character 39, state 2); and (c) chitinized arch of the female spermathecae with wide lateral tip (character 110, state 2); plus 14 homoplasious characters (Figs 1, 2). The species *Olmeca brujo* sp. nov. is placed as the sister species of the group including the other two species (*Olmeca santibanezi* sp. nov.+ *Olmeca cruzlopezi* sp. nov.); however, this last clade had low branch supports of 37 Jackknife and 1 Bremer, with a combination of homoplastic characters. In the case of the peculiar spiniform setae of the patella (*Pe4*, *5* and *Pm4*, *5*) present in *Olmeca* gen. nov., those setae are recovered as homoplastic characters (character 46 state 1, 48 state 2, and 50 state 1), because *Rowlandius* also presents this type of spiniform setae on the patella (Figs 1, 2).

The placement of *Olmeca brujo* sp. nov. in the topology as the sister group of the other two species of *Olmeca* gen. nov. is concordant with the geographic distribution of the species, since it is distributed in the southern region of Veracruz but north of the Isthmus of Tehuantepec, whereas *O. santibanezi* sp. nov. and *O. cruzlopezi* sp. nov. are both distributed south of the Isthmus in Chiapas: *O. cruzlopezi* sp. nov. (Ocozocuautla) separated from *O. santibanezi* sp. nov. (Ocosingo) by the Sierra of Chiapas (Fig. 46).

Additionally, *Olmeca* gen. nov. is recovered as the sister group of all hubbardiine genera included in these analyses, except for *Hubbardia*, indicating that despite sharing some morphological similarities, it is distantly related with *Mayazomus* and/or *Stenochrus* (see morphological differences below). The basal placement of *Olmeca* gen. nov. is congruent with morphology, since the presence of spiniform setae and macrosetae on pedipalps are very common characters in members of Protoschizomidae, but also in members of *Hubbardia* which are placed as the most basal genus of Hubbardiidae in our results, suggesting that the presence of spiniform setae as well as the larger body size, are plesiomorphic characters shared by *Olmeca* gen. nov., *Hubbardia*, and *Mayazomus*.

Out-group relationships

Based on the results of these analyses, the relationships of the rest of the genera studied in this work and Monjaraz-Ruedas and Francke (2016), recover *Hubbardia* as sister group to the rest of the genera of the subfamily used in our study. This hypothesis is supported also by its more northern distribution and morphology, because species of *Hubbardia* share many characters with members of Protoschizomidae, like the shape and number of setae on the pedipalp (Monjaraz-Ruedas & Francke, 2015). Our preferred tree groups of the rest of the genera studied here with support of 89% with Jackknife- and 5 with Bremer, and by nine synapomorphies (see Appendix 2, see supplemental material online; Figs 1, 2), tentatively separating *Hubbardia* from the rest of the New World schizomids sampled.

Monjaraz-Ruedas and Francke (2016) found that *Mayazomus* was closely related to *Rowlandius*; however, in our current hypothesis that relationship changed when *Belicenochrus* and *Surazomus* were added to the analyses. *Mayazomus* now appears as a sister group of *Pacal*, and this clade in turn appears as sister to the clade ((*Belicenochrus*+*Stenochrus*) + (*Rowlandius*+*Hansenochrus*+*Surazomus*)) (Fig. 2) which is concordant with the distribution of the genera. However, the inclusion of more species and the use of molecular data may give us a better understanding of the relationship of these groups.

Bayesian inference

As with the Parsimony analysis, the Bayesian inference found that the relationships amongst genera of the New World schizomids used here are not well supported, retrieving an unresolved tree with a polytomy holding two main clades (the same clades as in Parsimony), the clade of *Hubbardia*, and the clade formed by the rest of the genera (Fig. 3). As in the Parsimony, we found that the Bayesian approach recovered as the best supported clades the genus *Mayazomus* (PP = 0.99), *Olmeca* gen. nov. (PP = 0.91), *Rowlandius* (PP = 0.99) and *Surazomus* (PP = 0.99) (Fig. 3), indicating that the relationships of New World genera are still far from being resolved and an analysis including the majority if not all of the New World genera is needed.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental data for this article can be accessed here http://dx.doi.org/10.1080/14772000.2016.1271057.

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Five new species of *Stenochrus* (Schizomida: Hubbardiidae) from Oaxaca, Mexico

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Abstract

The North American genus *Stenochrus* is represented by 22 species distributed mainly in Mexico, Central America and the U.S.A.; the genus was erected originally to place the species *Stenochrus portoricensis* and was characterized by the presence of lateral lobes reduced on female spermathecae, male flagellum without important dorsal relief, pedipalps without distinctive armature and without posterodorsal process on segment XII. Here we describe five new species from the Mexican state of Oaxaca; we discuss the presence of dimorphic males in the genus. With this contribution the genus *Stenochrus* reaches 27 species, becoming the second most diverse genus of schizomids in the New World.

Key words: Taxonomy, Diversity, Short-tailed whipscorpions, Schizomids, Nearctic, Neotropical

Introduction

The genus *Stenochrus* Chamberlin, 1922 is the richest genus in North America and the second most diverse in the New World, preceded by the genus *Rowlandius* Reddell and Cokendolpher, 1995 (63 species) (Chamberlin, 1922; Reddell and Cokendolpher, 1995; Harvey, 2013; Villarreal, et al., 2016). The genus was erected to receive the new species *Stenochrus portoricensis* Chamberlin, 1922 based on the absence of mesopeltidia. Rowland (1973), however, synonymized the genus *Stenochrus* under *Schizomus* Cook, 1899, arguing that the mesopeltidia are present in all members of the order. Rowland and Reddell (1979) recognized seven New World species groups within the genus *Schizomus*, based largely on an unpublished phylogenetic analysis by Rowland (1975). Later Reddell and Cokendolpher (1991) resurrected the genus *Stenochrus* and transferred into it 18 species from *Schizomus*, representing three of Rowland's species groups (*"mexicanus," "pecki"* and *"goodnightorum"*). Subsequently, Armas (1995) described a new species of *Stenochrus* from Nicaragua: *Stenochrus leon* Armas, 1995 and since then, only three more species were described in the genus: *Stenochrus tepezcuintle* Armas and Cruz-Lopez, 2009, from Mexico; *Stenochrus meambar* Armas and Víquez, 2010, from Honduras, and *Stenochrus valdezi* Monjaraz-Ruedas, 2012 also from Mexico (Armas and Cruz-López, 2009; Armas and Víquez, 2010; Monjaraz-Ruedas, 2012).

Currently, the genus *Stenochrus* comprises 22 species distributed from southern Texas, U. S. A., throughout Mexico, and into northern Central America and the Greater Antilles; however, the type species, *S. portoricensis* has been presumably introduced to many areas, expanding the distribution of the genus to North, Central and South America and four countries in Europe (Barranco et al., 2014; Blick et al., 2006; Christophoryová et al., 2013; Korenko et al., 2009; Tourinho and Kury, 1999; Zawierucha et al., 2013).

In Mexico, the genus *Stenochrus* is distributed from northern Tamaulipas through the Sierra Madre Oriental mountain range south to Oaxaca and across the Isthmus of Tehuantepec to Chiapas and the Yucatan Peninsula. However, *S. portoricensis* has been reported from the states of Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz and Yucatan (Rowland and Reddell, 1977; Reddell and Cokendolpher, 1995). Some species in

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the genus are apparently restricted to cave environments, but there are also several epigean species such as *Stenochrus goodnightorum* (Rowland, 1973), *S. portoricensis, S. sbordonii* (Brignoli, 1973) and *S. tepezcuintle*.

Despite the numerous additional taxonomic characters proposed recently for the order (Moreno-González, et al., 2014; Villarreal et al., 2016; Monjaraz-Ruedas et al., 2016), currently the only diagnostic character for *Stenochrus* is the reduced lateral lobes of the female spermathecae, which was the character chosen by Reddell and Cokendolpher (1991) to move the three species groups from *Schizomus* to *Stenochrus*. However, the simple dorsal relief of the male flagellum is a common condition in some members of *Stenochrus*, accompanied by the presence of sub-ovate to sub-rhomboidal shaped flagella. Additionally, the male pedipalps lack distinctive ornamentations (spines or apophyses), except for *Stenochrus mexicanus* (Rowland, 1971). Finally, sexual dimorphism has been observed in one species of the genus, *S. mexicanus*; however only males with elongated pedipalps are known and the presence of homeomorphic males has not been reported or observed by us (n=6). The lack of synapomorphies for the genus results in a taxonomic headache and the correct placement of new species in the genus *Stenochrus* has become a habit, resulting in a ”catch-all” genus where species that do not fit in any other genus are lumped within *Stenochrus*. Furthermore, the fact that three of the seven species groups of Rowland were transferred from *Schizomus* into *Stenochrus* raises doubts about its monophyly. Phylogenetic analyses (currently in progress) are needed to test the monophyly of the genus and to get an overview of the relationships within *Stenochrus*.

Despite the fact that the highest diversity of arachnids in Mexico has been reported from the state of Oaxaca (Santibañez-López et al. 2016), there are only four species of schizomids reported from that state: *Pacal stewarti* (Rowland, 1973) from Cueva del Guayabo at Valle Nacional, *Stenochrus moisii* (Rowland, 1973) from Grutas de Monteflor also at Valle Nacional; *S. portoricensis* from Acatlán and Tomellín, and finally *S. tepezcuintle* from San Miguel Soyaltepec, The last three species occur in the northern mountain range of Oaxaca (Rowland & Reddell, 1977; Rowland & Reddell, 1979, 1980; Armas & Cruz-López, 2009). Additionally, Reddell and Cokendolpher (1995) tentatively report females of *Stenochrus firstmani* (Rowland, 1973) from Cueva Despareciendo, Cueva de la Finca, and Cueva del Nacimiento del Río San Antonio from near Acatlán, Oaxaca. However, the type locality of *S. firstmani* is Grutas de Atoyac, Veracruz; therefore, these records could represent *Stenochrus magico* sp. nov., since the male flagellum is very similar in these two species. Finally, as far as we have been able to determine, *S. firstmani* is restricted only to Grutas de Atoyac.

In this contribution we describe five new species of *Stenochrus* from Oaxaca, showing that the diversity of schizomids is higher in that state than previously known, and that *Stenochrus* is currently the most diverse genus in North America with 27 species. Three of the new species are known only from caves, and two are epigean. Also, the presence of dimorphic male pedipalps is discussed.

Material and methods

Specimens are deposited in the Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNAN). Specimens were collected by hand and/or using an aspirator, and preserved in 80 and 96% ethanol. Observations were made using a Nikon SMZ-800 stereomicroscope, and a Nikon Eclipse E100 optical microscope. Measurements (mm) of particular structures are as described by Reddell and Cokendolpher (1995), and were obtained with an ocular micrometer calibrated at 20X. Morphological terminology for legs and pedipalps follows Reddell and Cokendolpher (1995), cheliceral setae nomenclature follows Lawrence (1969) as modified by Villarreal et al. (2016), flagellar setae terminology after Cokendolpher and Reddell (1992) as modified by Harvey (1992) and Monjaraz-Ruedas et al. (2016); pedipalp setae terminology follows Monjaraz-Ruedas et al. (2017), spermathecae nomenclature follows Moreno-González et al. (2014); finally, opisthosomal setae nomenclature follows Villarreal et al. (2016).

Male chelicerae were dissected and prepared for scanning electron microscopy (SEM) according to Acosta et al. (2007), with a modification to the cleaning process which consisted of a series of three cycles of washes, alternating distilled water and biological detergent, followed by one minute in the ultrasonic cleaner. Microphotographs were taken using a Hitachi SU1510 SEM. Female spermathecae were dissected in 80% ethanol and cleared in lactophenol for 10 min (Krantz & Walter, 2009), after which they were preserved in Hoyer’s medium and mounted on semipermanent microscope slides. Photographs were taken under visible light with a Leica DFC490 camera adapted to a Leica Z16 APOA stereomicroscope; photographs were taken and assembled in the software LAS (Leica Application Suite) v. 4.3.0, and edited with Adobe Photoshop CS6.

Results

Taxonomy

Family Hubbardiidae Cook, 1899

Subfamily Hubbardiinae Cook, 1899

Genus *Stenochrus* Chamberlin, 1922

Type species: *Stenochrus portoricensis* Chamberlin, 1922, by original designation.

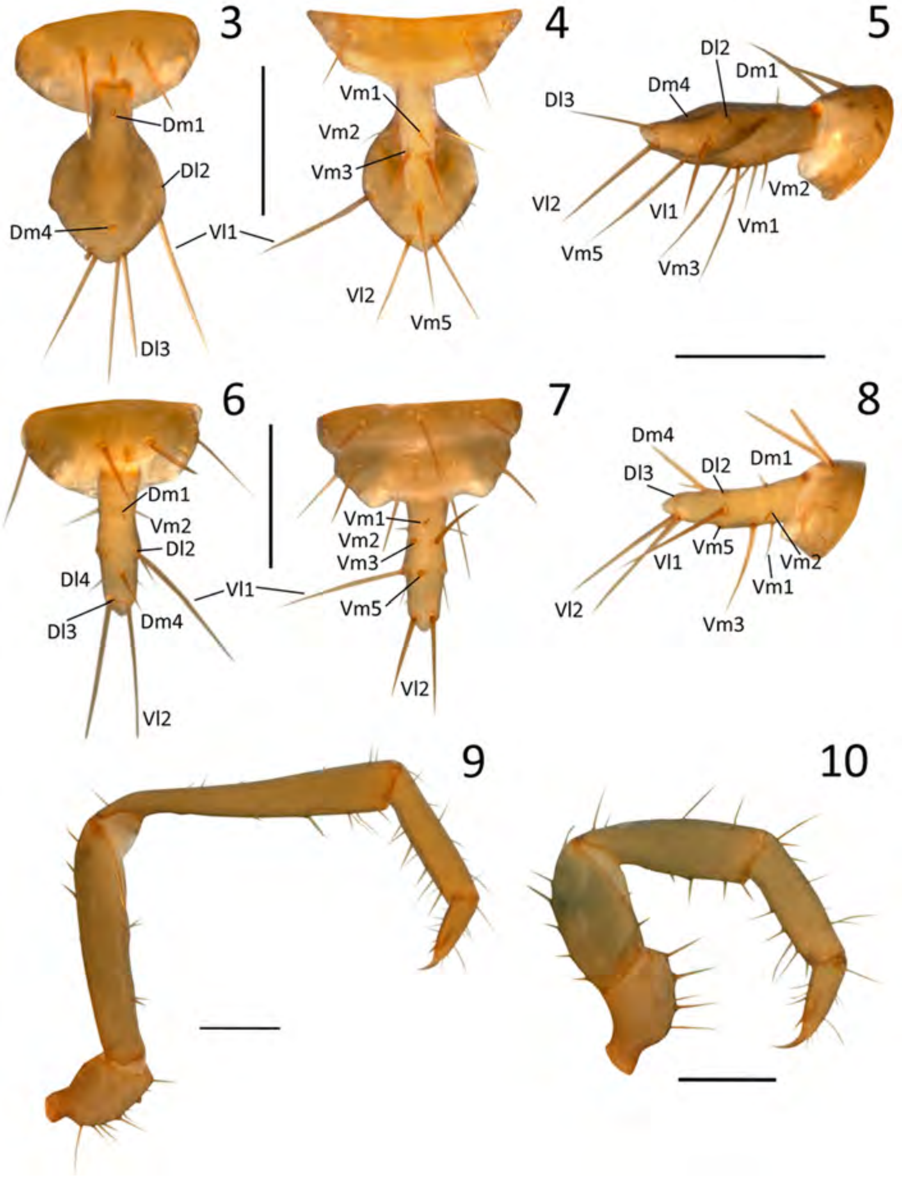
Stenochrus chimalapas, sp. nov.

Figs. 1–14, 71 Table 1.

Type material. MEXICO: *Oaxaca*: male holotype (CNAN-T1152), [25 October 2016, E. Briones, A. Juárez, A. Valdez, J. Valerdi], from Cueva de Escolapa, (16.85057ºN, 94.7481ºW, 219m), Municipio Santa María Chimalapas. Paratypes: 1 male and 2 females (CNAN-T1153) same data as holotype. 2 males (CNAN-T1154), [28 March 2010, J. Cruz, O. Francke, C. Santibañez, A. Valdez] same locality as holotype.

Distribution. This species is known only from the type locality (Fig 71).

FIGURES 1, 2. *Stenochrus chimalapas* **sp. nov**. Male holotype. Habitus: 1. Dorsal view. Female paratype. Habitus: 2. Dorsal view.

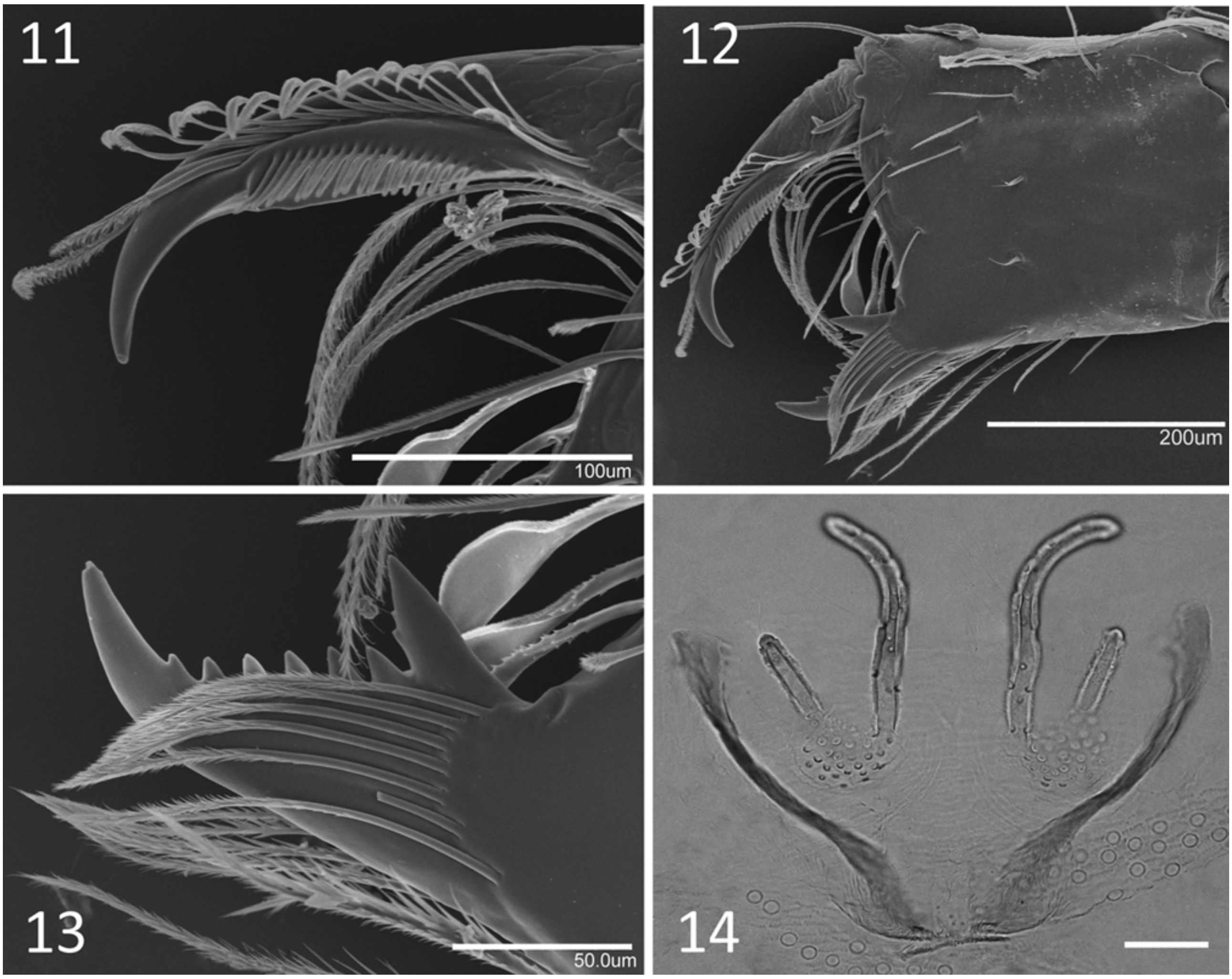


FIGURES 3–10. *Stenochrus chimalapas* **sp. nov**. Male holotype. Flagellum (3–5): 3, dorsal view. 4, ventral view. 5, lateral view. Female. Flagellum (6–8): 6, dorsal view. 7, ventral view. 8, lateral view. Pedipalps ectal view (9, 10): 9, Heteromorphic male. 10, Homeomorphic male. Scale bars = 0.2 mm.

Habitat. Collected inside the cave, which is about 50 to 60m long; specimens were collected in the deepest area in complete darkness, and were moving on the ground and the walls, between bat guano and moist organic material that had washed into the cave.

Etymology. The specific name is a noun in apposition taken from the type locality.

Diagnosis. Males can be distinguished by having an elliptical shaped flagellum with one pair of dorsosubmedian pits (Figs. 3–5); pedipalps with femur, patella and tibia elongated (Fig. 9). Females can be distinguished by the spermathecae (Fig. 14) with median lobes inverse “J” shaped, lateral lobes straight. *Stenochrus chimalapas* **sp. nov.** resembles *S. moisii*, both species with small body size and dark body coloration, and in both species the male flagellum with a pair of dorsosubmedian pits, however male flagellum in *S. moisii* has a pair of small submedian protuberances. Additionally, males of *S. chimalapas* **sp. nov.** have elongated pedipalps with respect to females, i. e., there is evident sexual dimorphism, whereas males of *S. moisii* with pedipalps very similar to the females. Females of *S. chimalapas* **sp. nov.** resemble *S. valdezi* in the shape of the spermathecae, having inverse “J” shaped median lobes; however, *S. valdezi* has lateral lobes with pointed tips, whereas the lateral pair is blunt in *S. chimalapas* **sp. nov.**, and significantly, the chitinized arch of the spermathecae of *S. chimalapas* **sp. nov.** lacks the anterior branches.



FIGURES 11–14. *Stenochrus chimalapas* **sp. nov**. Male. Chelicera (11–13): 11, movable finger. 12, mesal view. 13, fixed finger. Female. Spermathecae: 14, dorsal view. Scale bar (Fig. 14) = 0.05 mm.

Description. *Male (holotype)*: Greenish (Fig. 1). Prosoma: propeltidium with two setae on anterior process (one behind the other) and two pairs of dorsal setae; ocular spots distinct, asymmetrical. Metapeltidium 0.30 long, 0.45 wide. Anterior sternum with eleven setae, including two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs. 11–13): Movable finger: Serrula with 18 teeth, guard tooth present. Fixed finger with six smaller teeth between two primary teeth. Setation: Setal group formula: 3-6-4-2-7-5-1-5. G1 with three spatulate setae, apically covered with few small spinose spicules; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae, subequal in length, feathered apically and smooth basally; G4 consisting of two small setae, smooth, basally thick, elongated at the tip; G5A with seven similar sized setae, feathered apically and longer than fixed finger; G5B with five feathered setae, three apical ones longer than basal two; G6 with one smooth seta, about 1/2 of movable finger length; G7 with five slender, feathered setae, subequal in size.

Pedipalp (Figs. 9, 10): elongated; 1.95 times longer than propeltidium length. Trochanter without apical process, mesal surface with three setae near ventral margin, plus two setae near dorsal margin; with a long distal mesal spur. Femur, 2.4 times longer than high; ventral margin on ectal surface with setae *Fe1, Fe5*, *Fev1* and *Fev2* acuminate; mesal surface with a row of three ventral setae (*Fmv* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella with three acuminate *Pe* setae and three feathered *Pm* setae; without distinctive armature. Setae formula on tibia 3:3:4 (external row (*Ter*): medial row (*Tmr*): internal row (*Tir*)), all setae on tibia acuminate. Tarsal spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 15: 4: 3: 3: 4: 4: 10. Femur IV 2.32 times longer than high.

TABLE 1. Measurements (mm) of *Stenochrus chimalapas* **sp. nov.**

	Male CNAN-T1152	Male CNAN-T1153	Female CNAN-T1153	Female CNAN-T1153	Male CNAN-T1154	Male CNAN-T1154
Total Length	3.04	2.84	3.88	2.80	3.76	0.60
Propeltidium						
Length	0.91	0.88	0.98	0.93	0.99	0.75
Width	0.45	0.64	0.61	0.48	0.54	0.71
Flagellum						
Length	0.26	0.26	0.27	0.27	0.24	0.91
Width	0.16	0.16	0.18	0.18	0.06	2.20
Height	0.11	0.11	0.10	0.10	0.06	1.20
Leg I						
Coxa	0.42	0.43	0.40	0.34	0.43	0.62
Trochanter	0.26	0.26	0.24	0.26	0.30	0.67
Femur	0.88	0.94	0.94	0.96	0.90	0.86
Patella	0.98	1.07	1.12	1.01	0.99	0.81
Tibia	0.69	0.67	0.75	0.62	0.72	0.69
Basitarsus	0.24	–	0.27	0.30	0.29	0.84
Telotarsus	0.45	–	0.46	1.73	0.43	0.43
Total	3.90	3.38	4.19	5.22	4.06	4.14
Leg IV						
Trochanter	0.27	0.24	0.22	0.22	0.26	0.70
Femur	0.93	0.96	0.99	0.91	0.98	0.75
Patella	0.37	0.38	0.40	0.37	0.42	0.71
Tibia	0.62	0.56	0.64	0.59	0.66	0.72
Basitarsus	0.51	0.04	0.58	0.54	0.56	0.78
Telotarsus	0.38	0.38	0.38	0.38	0.37	0.83
Total	3.09	2.57	3.22	3.02	3.23	4.49
Pedipalp						
Trochanter	0.29	0.35	0.37	0.32	0.35	0.73
Femur	0.42	0.83	0.70	0.34	0.40	0.67
Patella	0.51	0.96	0.90	0.42	0.46	0.72
Tibia	0.35	0.50	0.46	0.30	0.35	0.69
Tarsus	0.21	0.22	0.24	0.18	0.19	0.73
Total	1.78	2.86	2.67	1.55	1.76	3.54

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair *Dm*; tergite II with three pairs of microsetae anteriorly, plus *Dm* pair; tergites III–VII with one pair of *Dm* setae each; tergite VIII with *Dm* and *Dl2*; tergite IX with pairs *Dl1*, *Dl2* and without *Dm*. Segments X, XI telescoped, with setal pairs *Dl2*, *Vm2*, *Vl1* and *Vl2,* plus single *Vm1* seta; segment XII with *Dm*, *Dl1*, *Dl2*, *Vm1*, *Vm2*, *Vl1* and *Vl2* setae, without posterodorsal process. Sternites with two irregular rows of setae each; genital plate with many scattered microsetae.

Flagellum (Figs. 3–5): dorsoventrally flattened, elliptical in shape; 1.6 times longer than wide; with a pair of dorsosubmedian shallow pits. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* at same level as *Vm2*; *Vm*5 distal to *Vl1*. One pair of anterodorsal microsetae between *Dm1* and *Dl2*, one pair of anterolateral microsetae on flagellar pedicel, and two patches of microsetae between *Vl1* and *Vl2* (*msp*).

Female (*paratype*) (Fig. 2): Pedipalps shorter and without enlargement as on male, 1.8 times longer than propeltidium length. Setation as on male. Flagellum with three flagellomeres (Figs. 6–8). Setation: seta *Dl2* reduced and at same level as *Vl1*; *Dl3* at same level as *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 14) with two pairs of lobes; median pair inverse "J" shaped outwards, longer than lateral pair, with few disperse duct openings ending in a blunt margin; lateral pair shorter, about 1/2 of the median lobes, with apical duct openings; median lobes bases starting anterior to those of lateral lobes. Chitinized arch U-shaped; with wide lateral tip and without anterior branch. Gonopod 2.1 times wider than long, sub rectangular-shaped, sides parallel. Chelicera: serrula with 19 teeth. Setal group formula 3-6-4-2-6-6-1-5. Fixed finger with six teeth between two primary teeth.

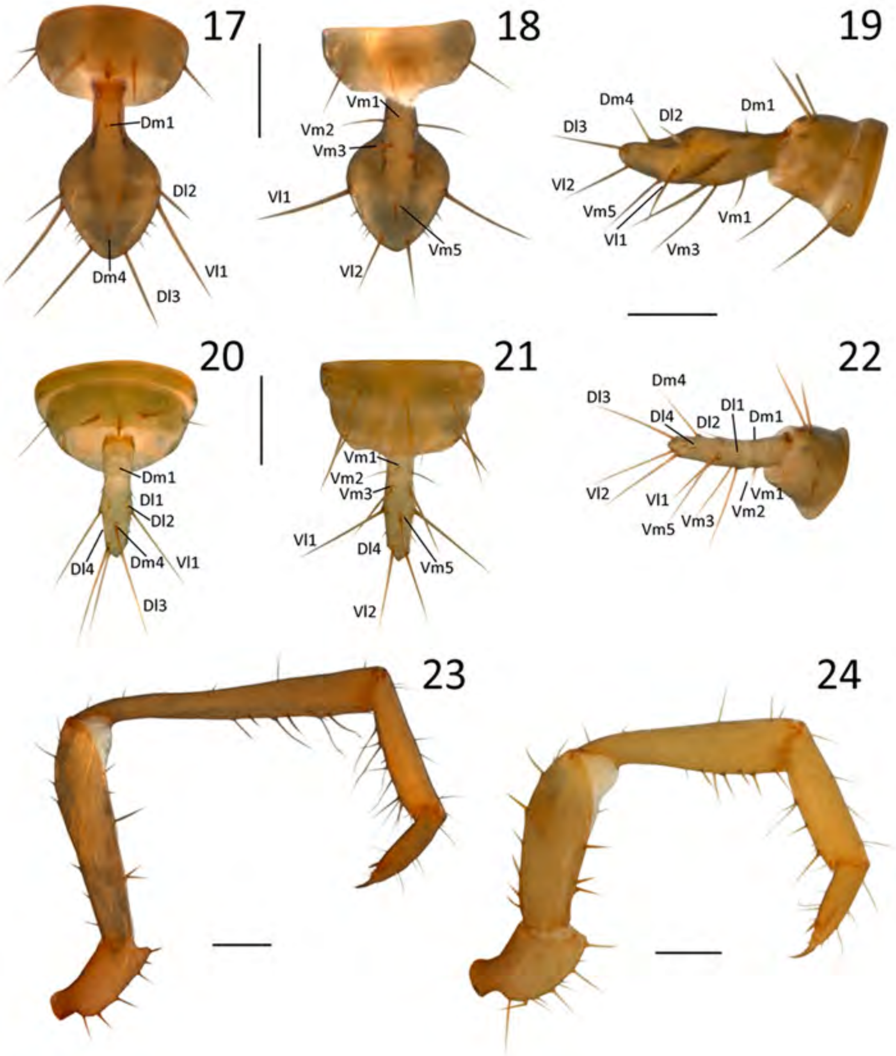
Remarks. There are dimorphic males in this species, having particularly an enlargement in the femur, patella and tibia of the pedipalps; the dimorphic male (heteromorphic) with the longest pedipalps having a ratio of 3.2 times longer than propeltidium length; whereas the homeomorphic male, with the shorter pedipalps having a ratio of only 1.7 times longer than propeltidium length: There are two intermediate (mesomorphic) males (including the male holotype) that have a ratio of pedipalp length of 2.3 and 2.7 times longer than propeltidium length. Noteworthy is the dark greenish coloration of the species, which is an uncommon feature in cave dwelling species of *Stenochrus.*

***Stenochrus gruta*, sp. nov.**

Figs. 15–28, 71, Table 2.

Type material. MEXICO: *Oaxaca*: male holotype (CNAN-T1155), [1 July 2013, G. Contreras, J. Cruz, J. Mendoza, C. Santibáñez, A. Valdez], from Gruta de San Sebastián, (16.03049ºN, 96.9692ºW, 1715m), San Sebastián de las Grutas, Municipio Sola de Vega. Paratypes: 2 males and 2 females (CNAN-T1156), same data as holotype.

FIGURES 15, 16. *Stenochrus gruta* **sp. nov**. Male holotype. Habitus: 15. Dorsal view. Female paratype. Habitus: 15. Dorsal view.



FIGURES 17–24. *Stenochrus gruta* **sp. nov**. Male holotype. Flagellum (17–19): 17, dorsal view. 18, ventral view. 19, lateral view. Female. Flagellum (20–22): 20, dorsal view. 21, ventral view. 22, lateral view. Pedipalps ectal view (23, 24): 23, Heteromorphic male. 24, Homeomorphic male. Scale bars = 0.2 mm.

Additional material examined. MEXICO: *Oaxaca*: 6 females (CNAN-Sz0193), [20 June 2006, O. Francke, H. Montaño, C. Santibáñez, A. Valdez, G. Villegas], from Gruta de San Sebastián, (16.03049ºN, 96.9692ºW, 1715m), San Sebastián de las Grutas, Municipio Sola de Vega.

Distribution. This species is known only from the type locality (Fig 71).

Habitat. The cave is a horizontal tunnel about 800m long, open at both ends. Specimens were collected inside the cave in moist, dark areas associated with bat guano, about 300 m into the long passage. The cave is promoted and used as an ecotouristic attraction; however, it is conserved in very good conditions, so we suspect that there are few visitors because it is located some distance away from the main roads.

Etymology. The specific name is a noun in apposition referring to the name of the type locality.

Diagnosis. Males can be distinguished by having a rhomboidal shaped flagellum with one pair of dorsomedian pits (Figs. 17–19); pedipalps noticeably elongated (Fig. 23). Females can be distinguished by the spermathecae (Fig. 28) having median lobes curved along their length, about 1/3 longer than lateral lobes; lateral lobes straight, their base distal to that of median lobes, with an extremely wide gonopod. *Stenochrus gruta* **sp. nov.** resembles *S. moisii* in the rhomboidal shape of the male flagellum; however, males of *S. gruta* **sp. nov.** have pedipalps elongated, and larger body size; whereas males of *S. moisii* have homeomorphic pedipalps and small body size. *Stenochrus gruta* **sp. nov,** also resembles *S. mexicanus* in both having elongated pedipalps; however, males of *S. mexicanus* have a tibial apophysis on mesal surface, absent in the new species. Female spermathecae of *S. gruta* **sp.**

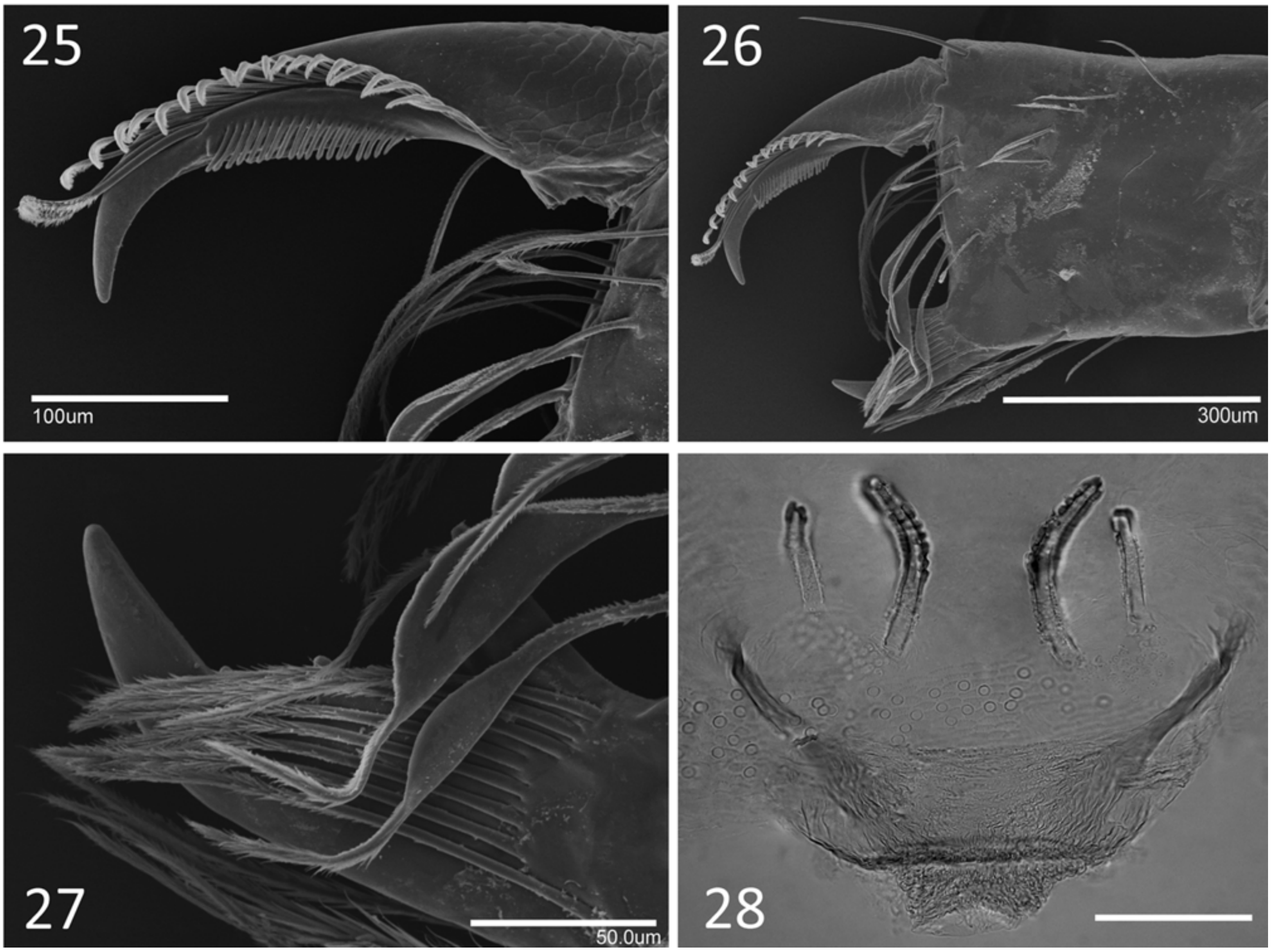
nov. resemble those of *S. portoricensis*, both having curved median lobes with apical openings, but *S. gruta* **sp. nov.** differs from *S. portoricensis* in the length and width of the lateral lobes.

Description. *Male (holotype)*: Brownish (Fig. 15). Prosoma: propeltidium with two setae on anterior process (one behind the other) and two pairs of dorsal setae; ocular spots distinct, oval shaped. Metapeltidium 0.44 long, 0.72 wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs. 25–27): Movable finger: serrula with 20 teeth, guard tooth present. Fixed finger with six smaller teeth between two primary teeth. Setation: Setal group formula: 3-6-4-2-8-3-1-6. G1 with three spatulate setae, covered with small spinose spicules starting from base of shaft; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, feathered apically and smooth basally; G4 consisting of two small setae, smooth, thick basally, elongated at the tip; G5A with eight similar sized setae, feathered apically and longer than fixed finger; G5B with three setae, two apical ones longer, smooth basally and feathered distally, and basal seta short and smooth; G6 with one smooth seta about 1/2 of movable finger length; G7 with seven apically feathered setae, subequal in size.

Pedipalps (Figs. 23, 24): elongated, 3.4 times longer than propeltidium length. Trochanter without apical process, mesal surface with three setae near ventral margin, plus two setae near dorsal margin; with a tiny, distal mesal spur. Femur, 5.6 times longer than high; ventral margin on ectal surface with setae *Fe1, Fe5*, *Fev1* and *Fev2* acuminate; mesal surface with a row of three ventral setae (*Fmv* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella with five *Pe* acuminate setae and three *Pm* feathered setae; without distinctive armature. Setae formula on tibia 3:3:4, *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 27: 4: 5: 4: 4: 5: 13. Femur IV 2.6 times longer than high.



FIGURES 25–28. *Stenochrus gruta* **sp. nov**. Male. Chelicera (25–27): 25, movable finger. 26, mesal view. 27, fixed finger. Female. Spermathecae: 28, dorsal view. Scale bar (Fig. 28) = 0.05 mm.

TABLE 2. Measurements (mm) of *Stenochrus gruta* **sp. nov.**

	Male CNAN-T1155	Male CNAN-T1156	Male CNAN-T1156	Female CNAN-T1156	Female CNAN-T1156
Total Length	3.92	3.76	4.08	4.00	4.48
Propeltidium					
Length	1.32	1.20	1.20	1.22	1.20
Width	0.70	0.62	0.66	0.67	0.80
Flagellum					
Length	0.42	0.40	0.30	0.40	0.29
Width	0.24	0.22	0.08	0.24	0.08
Height	0.14	0.14	0.08	0.14	0.08
Leg I	0.64	0.59	0.56	0.61	0.58
Coxa	0.37	0.35	0.34	0.38	0.35
Trochanter	1.42	1.39	1.22	1.36	1.20
Femur	1.64	1.60	1.31	1.58	1.36
Patella	1.20	1.10	0.91	1.14	0.96
Tibia	0.43	0.46	0.35	0.40	0.34
Basitarsus	0.06	0.06	0.06	0.06	0.06
Telotarsus	0.56	0.58	0.56	0.59	0.54
Total	6.26	6.08	5.25	6.06	5.33
Leg IV					
Trochanter	0.30	0.26	0.32	0.34	0.45
Femur	1.39	1.31	1.28	1.28	1.23
Patella	0.54	0.58	0.51	0.50	0.51
Tibia	0.96	0.90	0.58	0.90	0.85
Basitarsus	0.93	0.08	0.82	0.86	0.75
Telotarsus	0.50	0.53	0.48	0.54	0.50
Total	4.62	3.65	3.98	4.42	4.29
Pedipalp					
Trochanter	0.54	0.37	0.43	0.43	0.40
Femur	1.25	0.62	0.54	0.50	0.50
Patella	1.46	0.75	0.59	0.75	0.51
Tibia	0.80	0.53	0.48	0.54	0.46
Tarsus	0.40	0.24	0.24	0.32	0.26
Total	4.45	2.51	2.29	2.54	2.13

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair *Dm*; tergite II with three pair microsetae anteriorly plus pair *Dm*; tergites III–VII with setae pair *Dm* each; tergite VIII with *Dm* and *Dl2*; tergite IX with pairs *Dl1*, *Dl2* and without *Dm*. Segments X, XI telescoped, with setal pairs *Dl2*, *Vm2*, *Vl1* and *Vl2,* plus single *Vm1* seta; segment XII with *Dm*, *Dl1*, *Dl2*, *Vm1*, *Vm2*, *Vl1* and *Vl2* setae, without posterodorsal process. Sternites with two irregular rows of setae each; genital plate with many scattered microsetae.

Flagellum (Figs. 17–19): dorsoventrally flattened, rhomboidal in shape; 1.7 times longer than wide; with a pair of dorsomedian pits. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* at same level as *Vm2*; *Vm5* posterior to *Vl1*. With one pair of anterodorsal microsetae between *Dm1* and *Dl2*, one pair of anterolateral microsetae on flagellar pedicel, and two patches of microsetae (*msp*) between *Vl1* and *Vl2*.

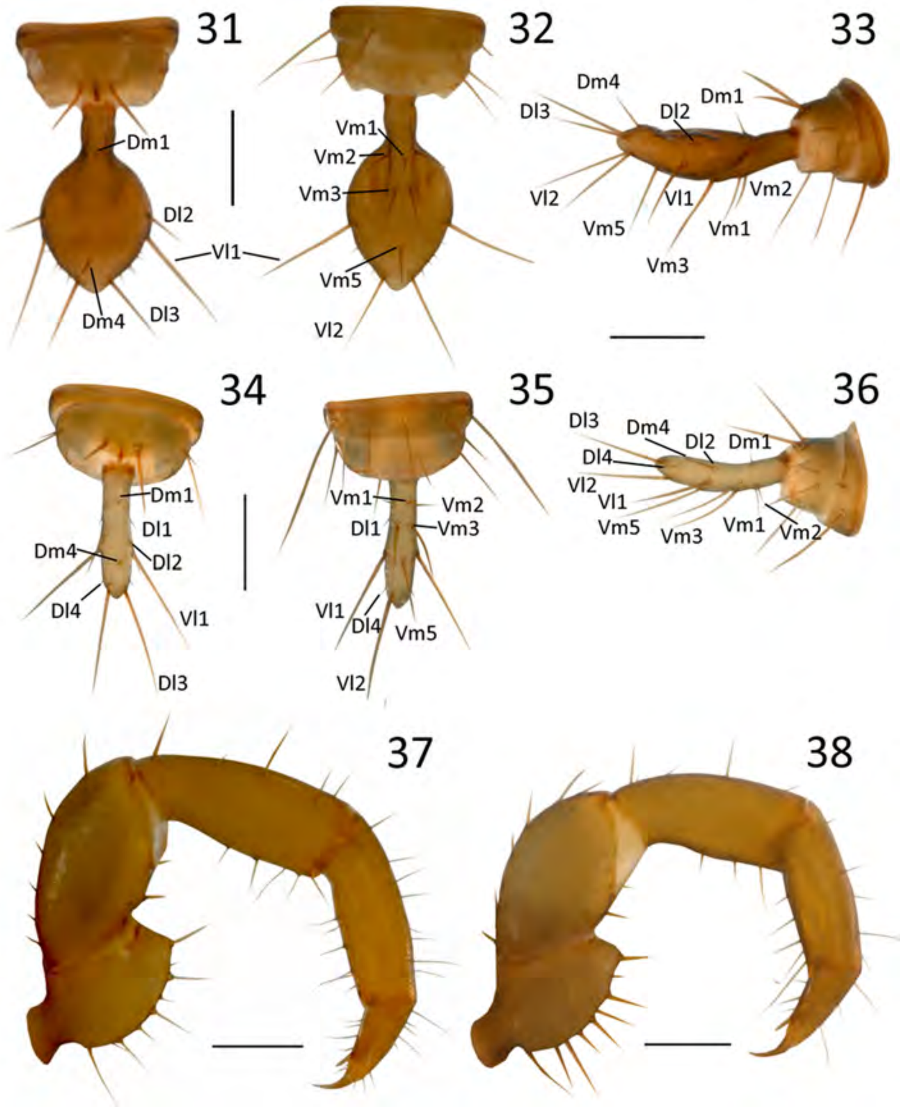
Female (*paratype*) (Fig. 16): Pedipalps shorter and without enlargement as on male, 1.9 times longer than propeltidium length. Setation as on male. Flagellum with three flagellomeres (Figs. 20–22). Setation: seta *Dl2* reduced and at same level as *Vl1*; *Dl3* at same level as *Vl2*; *Vm2* present and not reduced; seta *Vm1* anterior to *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 28) with two pairs of lobes; median pair curved outwards along their length, longer than lateral pair, with apical duct openings ending in a blunt tip; lateral pair straight, slightly shorter and narrower than median pair, without duct openings; median lobes bases starting basal to lateral lobes bases. Chitinized arch U-shaped; lateral tip not sclerotized and without anterior branch. Gonopod 4.2 times wider than long, conical-shaped. Chelicera: serrula with 21 teeth. Setal group formula 3-6-4-2-7-5-1-6. Fixed finger with six teeth between two primary teeth.

Remarks. Males of *S. gruta* **sp. nov.** have a very remarkable dimorphism in the length of the pedipalps; in this species we observed two types of males (heteromorphic and homeomorphic), where one male (heteromorphic) with the longest pedipalps presents a ratio of 3.4 times longer than propeltidium length, and the homeomorphic male with shortest pedipalps presenting a ratio of only 2.1 times longer than propeltidium length.

***Stenochrus caballero*, sp. nov.**

Figs. 29–42, 71, Table 3.

FIGURES 29, 30. *Stenochrus caballero* **sp. nov**. Male holotype. Habitus: 29. Dorsal view. Female paratype. Habitus: 30. Dorsal view.



FIGURES 31–38. *Stenochrus caballero* **sp. nov**. Male holotype. Flagellum (31–33): 31, dorsal view. 32, ventral view. 33, lateral view. Female. Flagellum (34–36): 34, dorsal view. 35, ventral view. 36, lateral view. Pedipalps ectal view (37, 38): 37, Homeomorphic male. 38, female. Scale bars = 0.2 mm.

Type material. MEXICO: *Oaxaca*: male holotype (CNAN-T1157), [10 April 2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke, J. Mendoza], from Cerro Caballero, (18.14230ºN, 96.71597ºW, 938m), San José Tenango. Paratypes: 1 male and 1 female (CNAN-T1158), [28 August 2008, J. Cruz] same locality data as holotype. 1 male and 1 female (CNAN-T1159), [11 April 2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke, J. Mendoza] from 0.6 km N of Pozo de Águilas, (18.19772ºN, 96.67682ºW, 327m), San José Tenango.

Distribution. This species is known from the foothills of the Sierra Mazateca in the northern region of Oaxaca (Fig 71).

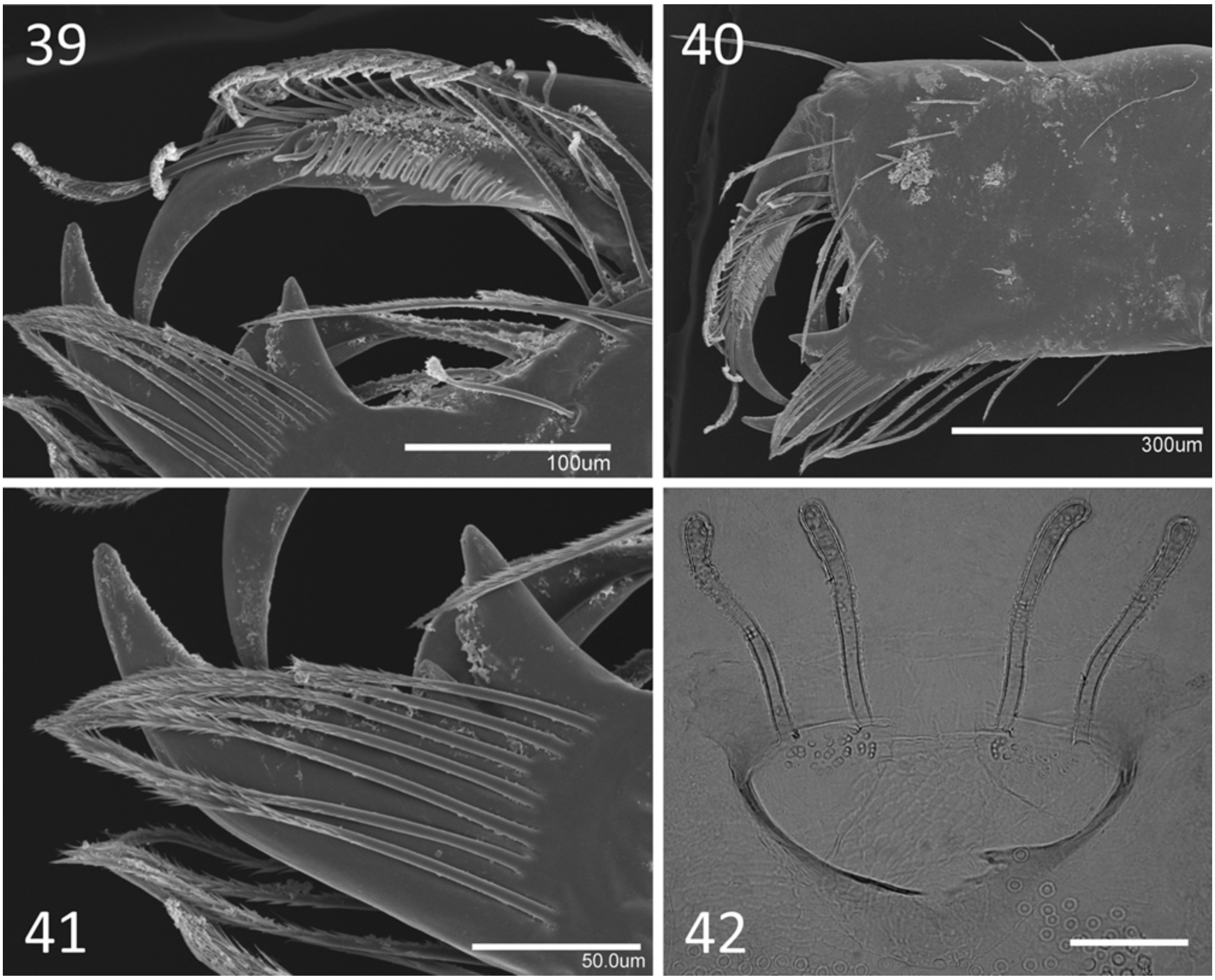
Habitat. Specimens were collected in tropical dry forest under big rocks in both conserved and disturbed habitats.

Etymology. The specific name is a noun in apposition taken from the name of the type locality.

Diagnosis. Relatively larger and darker than most congeners. Males can be distinguished by having an oval shaped flagellum with one pair of dorsosubmedian depressions (Figs. 31–33); pedipalps not elongated (=homeomorphic), trochanter without apical process (Fig. 37). Females can be distinguished by the spermathecae (Fig. 42) having median and lateral lobes of the same length and width, with their insertions at the same level. Chelicerae with a remarkable accessory tooth on movable finger (Fig. 39). *Stenochrus caballero* resembles *Stenochrus pallidus* (Rowland, 1975) in the oval shape of the male flagellum; however, males of *S. pallidus* present a pair of deep dorsosubmedian pits, whereas males of *S. caballero* present a pair of shallow dorsosubmedian depressions. Females of *S. caballero* differ from *S. pallidus* in having the median and lateral lobes of the spermathecae of the same length, whereas female spermathecae in *S. pallidus* with lateral lobes shorter than the median lobes.

Description. *Male (holotype)*: Dark brownish (Fig. 29). Prosoma: propeltidium with two setae on anterior process (one behind the other) and three pairs of dorsal setae; ocular spots distinct, irregular. Metapeltidium 0.37 long, 0.66 wide. Anterior sternum with 11 setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs. 39–41): Movable finger: Serrula with 21 teeth, guard tooth present, with a prominent accessory tooth at the middle of the movable finger. Fixed finger with four smaller teeth between two primary teeth. Setation: Setal group formula: 3-6-4-2-7-6-1-7. G1 with three spatulate setae, covered with spicules starting from the middle of the shaft; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae, subequal in length, feathered apically and smooth basally; G4 consisting of two small setae, smooth, basally thick, distally elongated; G5A with seven similar sized setae, feathered apically and longer than fixed finger; G5B with six setae, two short and smooth proximally and four long and feathered distally; G6 with one smooth setae about 1/2 of movable finger length; G7 with seven smooth setae, slightly decreasing in size distally.



FIGURES 39–42. *Stenochrus caballero* **sp. nov**. Male. Chelicera (39–41): 39, movable finger. 40, mesal view. 41, fixed finger. Female. Spermathecae: 42, dorsal view. Scale bar (Fig. 42) = 0.05 mm.

Pedipalps (Fig. 37): homeomorphic; 1.7 times longer than propeltidium length. Trochanter without apical process, mesal surface with three setae near ventral margin, plus two setae near dorsal margin; with a small, distal mesal spur. Femur, 1.9 times longer than high; ventral margin on ectal surface with setae *Fe1, Fe5*, *Fev1* and *Fev2* acuminate; mesal surface with a row of three ventral setae (*Fmv* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella with three acuminate *Pe* setae and four feathered *Pm* setae; without distinctive ornamentations. Setae formula on tibia 4:3:5, *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetrical.

TABLE 3. Measurements (mm) of *Stenochrus caballero* **sp. nov.**

	Male CNAN-T1157	Male CNAN-T1158	Female CNAN-T1158	Male CNAN-T1159	Female CNAN-T1159
Total Length	4.32	4.24	4.32	3.92	4.44
Propeltidium					
Length	1.30	1.38	1.36	1.25	1.31
Width	0.70	0.80	0.75	0.69	0.74
Flagellum					
Length	0.48	0.45	0.37	0.42	0.32
Width	0.26	0.26	0.08	0.26	0.08
Height	0.13	0.13	0.08	0.14	0.08
Leg I					
Coxa	0.64	0.77	0.62	0.66	0.56
Trochanter	0.46	0.53	0.37	0.46	0.40
Femur	1.47	1.62	1.18	1.39	1.15
Patella	1.84	2.11	1.39	1.41	1.39
Tibia	1.38	1.57	1.04	1.09	1.04
Basitarsus	0.46	0.50	0.34	0.42	0.32
Telotarsus	0.62	0.62	0.59	0.56	0.50
Total	6.88	7.71	5.54	5.98	5.36
Leg IV					
Trochanter	0.35	0.42	0.35	0.26	0.35
Femur	1.23	1.38	1.10	1.23	1.14
Patella	0.54	0.58	0.53	0.53	0.50
Tibia	0.88	0.99	0.77	0.83	0.82
Basitarsus	0.80	0.88	0.74	0.80	0.69
Telotarsus	0.53	0.58	0.48	0.53	0.45
Total	4.34	4.82	3.97	4.18	3.94
Pedipalp					
Trochanter	0.45	0.51	0.46	0.43	0.43
Femur	0.53	0.54	0.51	0.53	0.51
Patella	0.51	0.58	0.51	0.51	0.48
Tibia	0.46	0.54	0.46	0.46	0.45
Tarsus	0.26	0.26	0.24	0.24	0.24
Total	2.21	2.43	2.19	2.18	2.11

Legs: Leg I, basitarsal-telotarsal proportions: 29: 4: 5: 5: 6: 5: 14. Femur IV 2.41 times longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair *Dm*; tergite II with three pairs of microsetae anteriorly plus pair *Dm*; tergites III–VIII with setae pair *Dm* each; tergite IX with pairs *Dl1*, *Dl2* and without *Dm*. Segments X, XI telescoped, with setal pairs *Dl2*, *Vm2*, *Vl1* and *Vl2,* plus single *Vm1* seta; segment XII with *Dm*, *Dl1*, *Dl2*, *Vm1*, *Vm2*, *Vl1* and *Vl2* setae, without posterodorsal process. Sternites with two irregular rows of setae each; genital plate with scattered setae.

Flagellum (Figs. 31–33): dorsoventrally flattened, ovoid in shape; 1.9 times longer than wide; with a pair of dorsosubmedian depressions. Setation: *Dm1* situated over the bulb base; *Dm4* situated distally; *Dl2* at same level as *Vl1*; *Dl3* posterior to *Vl2*; pair *Vm2* present; seta *Vm1* posterior to *Vm2*; *Vm*5 posterior to *Vl1*. With one pair of anterodorsal microsetae between *Dm1* and *Dl2*, one pair of anterolateral microsetae on flagellar pedicel and with two patches of microsetae between *Vl1* and *Vl2* (*msp*).

Female (*paratype*) (Fig. 30): Pedipalps similar to male (Fig. 38), 1.6 times longer than propeltidium length. Setation as on male. Flagellum with three flagellomeres (Figs. 34–36). Setation: seta *Dl2* reduced and anterior to *Vl1*; *Dl3* at same level as *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 42) with two pairs of lobes; both median and lateral lobes of the same length and width, median pair straight, ending in a blunt tip; lateral pair slightly curved inwards, ending in a blunt tip; median and lateral lobes bases at the same level. Chitinized arch U-shaped; with wide lateral tip, and a straight and incomplete anterior branch. Gonopod 2.4 times wider than long, lobe-shaped. Chelicera: movable finger with a prominent accessory tooth; serrula with 22 teeth. Setal group formula 3-6-4-2-7-4-1-7. Fixed finger with four teeth between two primary teeth.

Remarks. The large size (4.4–4.6 mm) of the specimens in this species and *S. alcalai* **sp. nov.** is an uncommon characteristic in members of the genus *Stenochrus* which has in general species with small body size (2.5 to 3.8). There is no evidence of dimorphism on male pedipalps among the three known specimens, but we can’t rule out their existence. There are two important characteristics present in this species which render difficult the correct placement of this species in *Stenochrus*: The lateral lobes of female spermathecae of the same length as the median lobes, and the presence of an accessory tooth on movable finger of the chelicerae. However, there are other characters, as are the shape and relief of the male flagellum, and the general shape of the pedipalps, that permit us to group this species with members of *Stenochrus*. We tentatively place this species in *Stenochrus* due to the lack of evidence on the morphological limits of *Stenochrus*, and because there is no other described genus with the combination of characters mentioned above; its correct taxonomic placement should be resolved in the phylogenetic analyses in progress.

***Stenochrus alcalai*, sp. nov.**

Figs. 43–56, 71, Table 4.

Type material. MEXICO: *Oaxaca*: male holotype (CNAN-T1160), [23 August 2015, D. Barrales, J. Cruz, O. Francke, R. Monjaraz, J. Sánchez], from La Laguna, (17.72716ºN, 97.10172°W, 2402m), San Pedro Jocotipac. Paratypes: 1 female (CNAN-T1161), same data as holotype. 2 males 1 female (CNAN-T1162), [22 August 2016, D. Barrales, J. Cruz, O. Francke, R. Monjaraz, J. Sánchez], from El Tanque (17.74294ºN, 97.10562°W, 2402m), San Pedro Jocotipac.

Distribution. This species is known only from the type locality and a second locality fairly close by and in the same forest (Fig 71).

Habitat. Specimens were collected in a very well conserved and hyper-humid oak forest, the trees festooned with mosses and lichens, above 2,400 m elevation; individuals were found under rocks and rotten logs.

Etymology. The specific name is a noun in apposition dedicated to Diego Barrales Alcalá for his help during field trips and for his contributions to Mexican arachnology.

Diagnosis. Males can be distinguished by having an ovate shaped flagellum with one pair of deep dorsosubmedian pits (Figs. 45–47); with homeomorphic pedipalps. Females can be distinguished by the spermathecae (Fig. 56) with median lobes inverse “J” shaped, with duct openings along the entire lobe; lateral lobes straight, slender and shorter than median lobes; the bases of the lobes very close to each other and at the same level. *Stenochrus alcalai* resembles *Stenochrus pecki* (Rowland, 1973) in the ovate shape of the flagellum in males; however, the flagellum in *S. alcalai* presents a pair of deep dorsosubmedian pits, whereas in *S. pecki* it presents a single shallow posteromedian depression. In addition, male pedipalps in *S. pecki* are robust and with spiniform setae on patella and tibia; whereas on *S. alcalai* the pedipalps are normal and bear acuminate setae. Females of *S. alcalai* resemble *S. chimalapas* in the general shape of the spermathecae; however, females of *S. chimalapas* present wide lateral tips on the chitinized arch, and few duct openings; whereas females of *S. alcalai* present duct openings along the entire lobes, and with slender lateral tips; also, the bases of the lobes are fused in *S. alcalai*, whereas in *S. chimalapas* are separated and independent; finally, females of *S. alcalai* present a large, conical gonopod, whereas females of *S. chimalapas* have a short and wide gonopod.

FIGURES 43, 44. *Stenochrus alcalai* **sp. nov**. Male holotype. Habitus: 43. Dorsal view. Female paratype. Habitus: 44. Dorsal view.

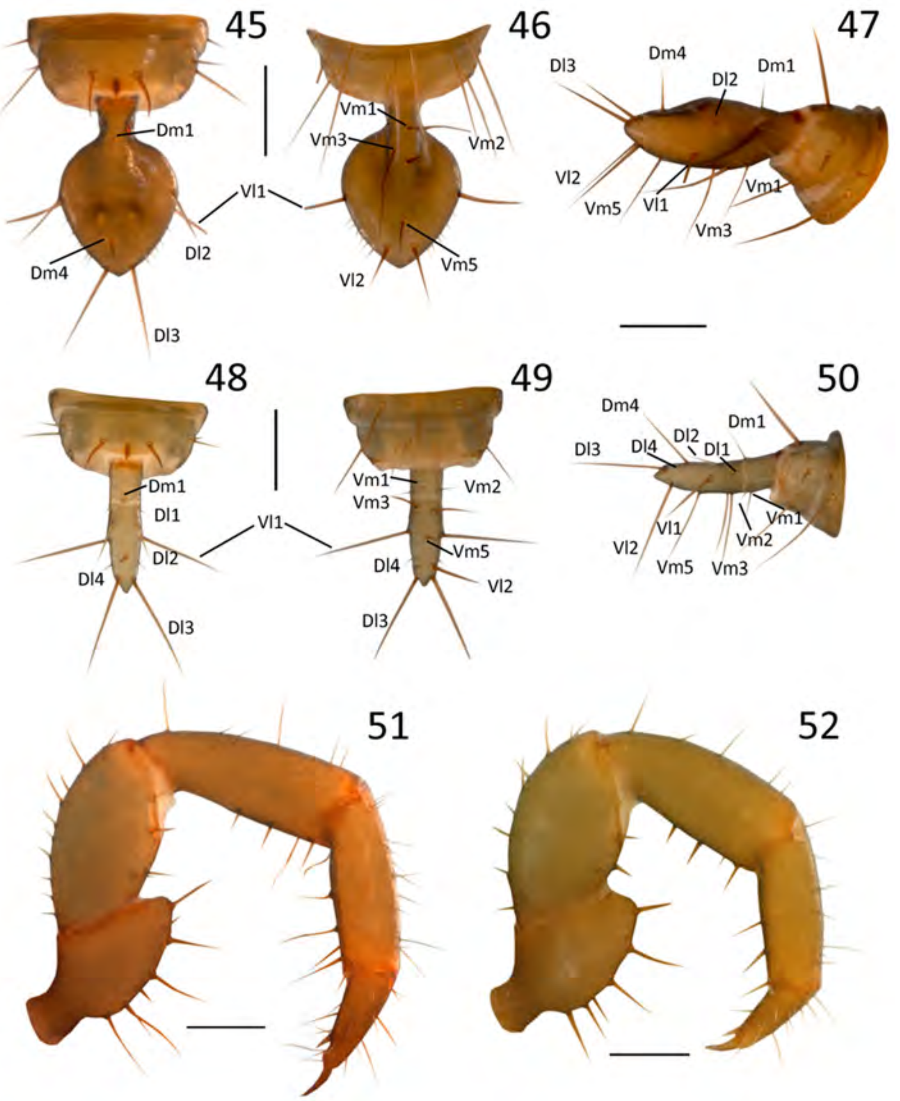
Description. *Male (holotype)*: Brownish (Fig. 43). Prosoma: propeltidium with two setae on anterior process (one behind the other) and three pairs of dorsal setae; ocular spots distinct, asymmetrical. Metapeltidium 0.42 long, 0.72 wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae (Figs. 53–55): Movable finger: serrula with 12 teeth, guard tooth present. Fixed finger with five smaller teeth between two primary teeth. Setation: setal group formula: 3-6-4-2-6-5-1-5. G1 with three spatulate setae, with few apical spicules; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, feathered apically and smooth basally; G4 consisting of two small setae, smooth, thick basally, elongated at the tip; G5A with six similar sized setae, feathered apically and longer than fixed finger; G5B with five feathered setae, increasing in size distally; G6 with one smooth setae, about 1/2 of movable finger length; G7 with five smooth, slender setae, decreasing in length distally.

Pedipalps (Figs. 51): homeomorphic; 1.7 times longer than propeltidium length. Trochanter without apical process, mesal surface with three setae near ventral margin, plus two setae near dorsal margin; with a small, medial mesal spur. Femur 2 times longer than high; ventral margin on ectal surface with setae *Fe1, Fe5*, *Fev1* and *Fev2* acuminate; mesal surface with a row of three ventral setae (*Fmv* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella with three acuminate *Pe* setae and four feathered *Pm* setae; without distinctive ornamentations. Setae formula on tibia 3:3:5 *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 31: 4: 5: 4: 6: 5: 12. Femur IV 3.4 times longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair *Dm*; tergite II with three pair microsetae anteriorly plus pair *Dm*; tergites III–VII with one pair of *Dm* setae each; tergite VIII with *Dm* and *Dl2*; tergite IX with pairs *Dl1*, *Dl2* and without *Dm*. Segments X, XI telescoped, with setal pairs *Dl2*, *Vm2*, *Vl1* and *Vl2,* plus *Vm1* seta; segment XII with *Dm*, *Dl1*, *Dl2*, *Vm1*, *Vm2*, *Vl1* and *Vl2* setae, without posterodorsal process. Sternites with two irregular rows of setae each; genital plate with scattered microsetae.

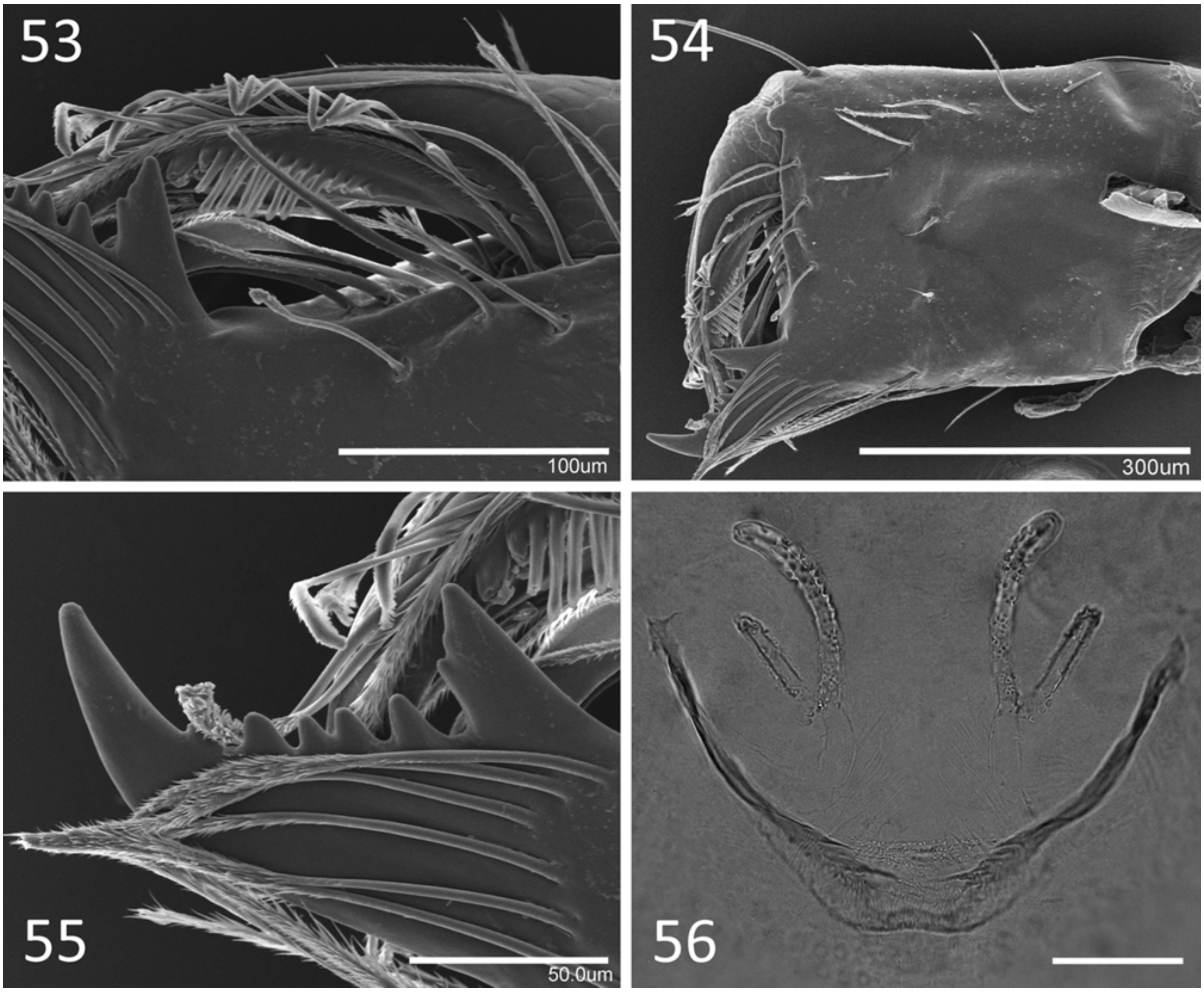


FIGURES 45–52. *Stenochrus alcalai* **sp. nov**. Male holotype. Flagellum (45–47): 45, dorsal view. 46, ventral view. 47, lateral view. Female. Flagellum (48–50): 48, dorsal view. 49, ventral view. 50, lateral view. Pedipalps ectal view (51, 52): 51, Homeomorphic male. 52, female. Scale bars = 0.2 mm.

Flagellum (Figs. 45–47): dorsoventrally flattened, ovate in shape; 1.7 times longer than wide; with a pair of deep dorsosubmedian pits. Setation: *Dm1* situated over the bulb base; *Dm4* situated medially; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* at same level as *Vm2*; *Vm*5 posterior to *Vl1*. With one pair of anterodorsal microsetae between *Dm1* and *Dl2*, one pair of anterolateral microsetae on flagellar pedicel, and two patches of microsetae between *Vl1* and *Vl2* (*msp*).

Female (*paratype*) (Fig. 44): Pedipalps slightly shorter than on male (Fig. 52), 1.6 times longer than propeltidium length. Setation as on male except for anterior sternum with 10 setae. Flagellum with three flagellomeres (Figs. 48–50). Setation: seta *Dl2* reduced and anterior to *Vl1*; *Dl3* posterior to *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 56) with two pairs of lobes, with bases fused and at the same level; median pair inverse "J" shaped outwards, longer than lateral pair, with duct openings along the entire length, ending in a blunt tip; lateral pair slender and shorter, about 1/2 length of median lobes, without duct openings, ending in a blunt tip. Chitinized arch U- shaped; with a wide lateral tip and without anterior branch. Gonopod 3.6 times wider than long, sub rectangular-shaped. Chelicera: serrula with 13 teeth. Setal group formula 3-6-4-2-7-6-1-5. Fixed finger with four teeth between two primary teeth.

Remarks. The altitudinal distribution of this species (2402m) is rare in schizomids, with *S. alcalai* representing the highest record thus far of the genus *Stenochrus*. Without evidence of dimorphic males (n=3).



FIGURES 53–56. *Stenochrus alcalai* **sp. nov**. Male. Chelicera (53–55): 53, movable finger. 54, mesal view. 55, fixed finger. Female. Spermathecae: 56, dorsal view. Scale bar (Fig. 56) = 0.05 mm.

TABLE 4. Measurements (mm) of *Stenochrus alcalai* **sp. nov.**

	Male CNAN-T1160	Female CNAN-T1161	Male CNAN-T1162	Male CNAN-T1162	Female CNAN-T1162
Total Length	4.64	4.16	4.56	4.48	4.24
Propeltidium					
Length	1.49	1.52	1.36	1.44	1.41
Width	0.78	0.80	0.80	0.74	0.72
Flagellum					
Length	0.46	0.48	0.34	0.48	–
Width	0.27	0.29	0.10	0.29	–
Height	0.19	0.18	0.10	0.18	–
Leg I					
Coxa	0.64	0.70	0.51	0.64	0.59
Trochanter	0.46	0.48	0.40	0.46	0.40

......*continued on the next page*

TABLE 4. (Continued)

	Male CNAN-T1160	Female CNAN-T1161	Male CNAN-T1162	Male CNAN-T1162	Female CNAN-T1162
Femur	1.60	1.96	1.18	1.66	1.26
Patella	1.90	2.29	1.31	2.08	1.41
Tibia	1.50	1.72	1.02	1.46	1.04
Basitarsus	0.50	0.53	0.37	0.48	0.43
Telotarsus	0.58	0.56	0.53	0.66	0.53
Total	7.18	8.25	5.33	7.44	5.66
Leg IV					
Trochanter	0.35	0.40	0.35	0.32	0.37
Femur	1.57	1.72	1.26	1.60	–
Patella	0.75	0.75	0.53	0.69	–
Tibia	1.20	1.41	0.93	1.18	–
Basitarsus	0.86	0.96	0.75	0.93	–
Telotarsus	0.56	0.56	0.51	0.59	–
Total	5.30	5.80	4.34	5.31	–
Pedipalp					
Trochanter	0.50	0.48	0.45	0.54	0.48
Femur	0.58	0.64	0.51	0.59	0.53
Patella	0.62	0.62	0.53	0.56	0.53
Tibia	0.56	0.61	0.48	0.53	0.46
Tarsus	0.30	0.30	0.24	0.27	0.27
Total	2.56	2.66	2.21	2.50	2.27

***Stenochrus magico*, sp. nov.**

Figs. 57–71, Table 5.

Type material. MEXICO: *Oaxaca*: male holotype (CNAN-T1163), [26 March 1981, A. Grubbs, S. Zeman], from Millipede Cave, Río Iglesia Dolina (18.1175ºN, 96.79983ºW, 1610m), Huautla de Jiménez. Paratypes: 1 male (CNAN-T1164), [12 April 2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke, J. Mendoza], from Cueva Li-Nita, (18.14767ºN, 96.7984ºW, 1919m), Huautla de Jiménez. 1 female (CNAN-T1165), [11 September 2010, D. Barrales, J. Cruz, O. Francke, A. Valdez], from Cueva 100m S of Puente de Fierro, (18.15085ºN, 96.85336ºW, 1197m), Huautla de Jiménez. 1 female (CNAN-T1166), [12 April 2015, G. Contreras, O. Francke, J. Mendoza, M. Minton, R. Monjaraz], from Cueva Cangrejo, San Miguel Cuahutepec, (18.10717ºN, 96.79845ºW, 1540m), Huautla de Jiménez.

Distribution. This species is known only from caves in the Sierra Mazateca in the vicinity of Huautla de Jiménez (Fig 71).

Etymology. The specific name is a noun in apposition of the Spanish word magic, in reference to the magic mushrooms (genus *Psilocybe*) which occur in the region of Huautla de Jimenez, and were popularized during the hippie years in the 1970s and 80s.

Diagnosis. Males can be distinguished by the bulbous flagellum, subquadrate in shape, without dorsal relief (Figs. 59–61); pedipalp trochanter with a small protuberance as apical process. Females can be distinguished by the spermathecae (Fig. 70) with median lobes inverse "J" shaped, without duct openings, lateral lobes curved outwards; the bases of the lobes clearly separated. *Stenochrus magico* resembles *Stenochrus firstmani* (Rowland, 1973) in the shape of the male flagellum; however, males of *S. magico* have a subquadrate-shaped flagellum, whereas males of *S. firstmani* present a sub-triangular-shaped flagellum. In addition, males of *S. firstmani* present a dorsomedian protuberance on flagellum, whereas the flagellum of males of *S. magico* lack dorsal relief. Females of

S. magico resemble *S. alcalai* in the shape of the spermathecae, having median lobes inverse "J" shaped; however, females of *S. magico* have the lateral lobes curved outwards and about 1/3 length of median lobes, whereas females of *S. alcalai* have lateral lobes straight and about 1/4 length of median lobes. Additionally, females of *S. magico* have a wide and short, subrectangular gonopod with sides parallel, while females of *S. alcalai* have a trapezoidal gonopod with oblique sides.

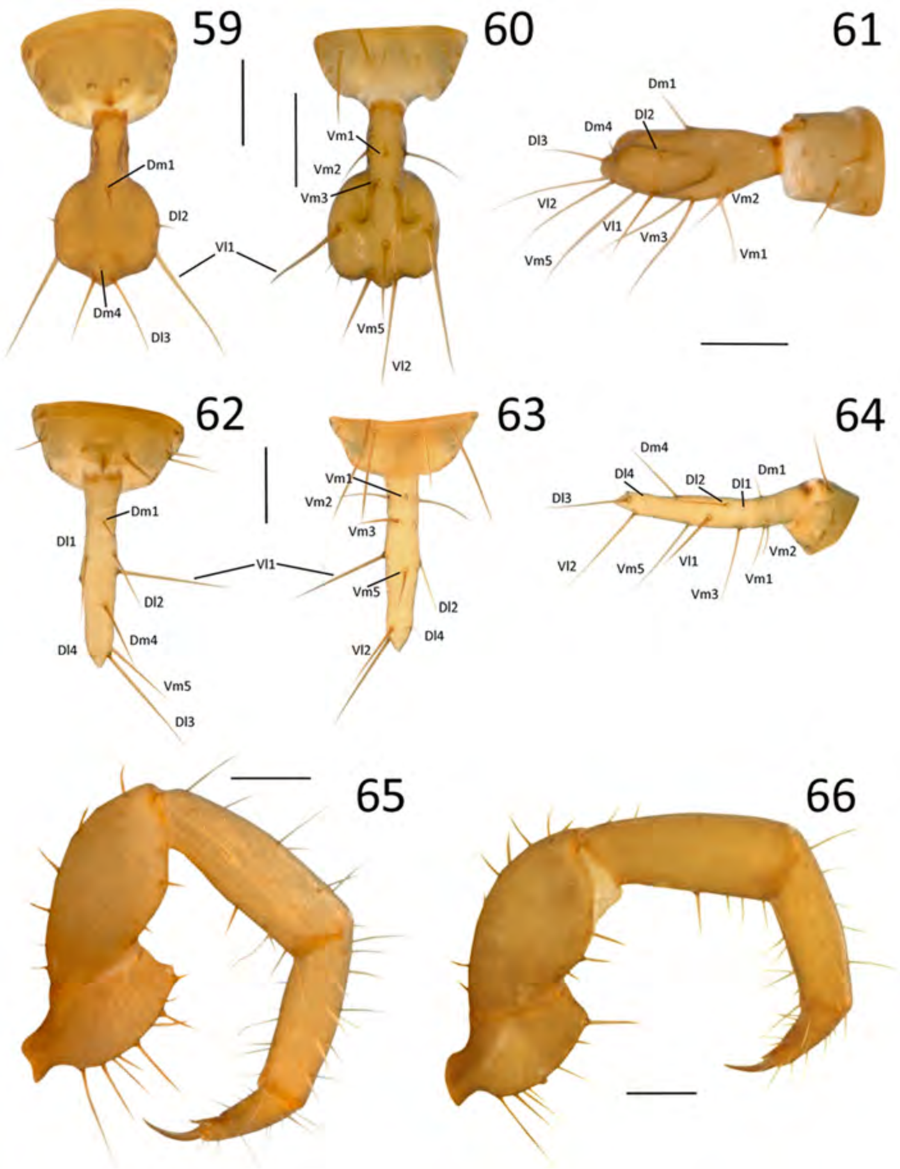
FIGURES 57, 58. *Stenochrus magico* **sp. nov**. Male holotype. Habitus: 57. Dorsal view. Female paratype. Habitus: 58. Dorsal view.

Chelicerae (Figs. 67–69): Movable finger: serrula with 22 teeth, guard tooth present. Fixed finger with five smaller teeth between two primary teeth. Setation: Setal group formula: 3-6-4-2-13-6-1-6. G1 with three spatulate setae, covered with spinose spicules from the middle of the shaft to the tip; G2 composed of six feathered setae, subequal in length, and shorter than movable finger length; G3 with four setae subequal in length, feathered apically and smooth basally; G4 consisting of two small setae, smooth, thick basally, elongated at the tip; G5A with thirteen similar sized setae, feathered apically and longer than fixed finger; G5B with six , basal three short and smooth, distal three longer and feathered; G6 with one smooth setae about 1/2 of movable finger length; G7 with six smooth and slender setae subequal in length.

Pedipalps (Figs. 65): homeomorphic; 2.1 times longer than propeltidium length. Trochanter with a small protuberance on apical process, mesal surface with three setae near ventral margin, plus two setae near dorsal margin; with a long, medial mesal spur. Femur, 2 times longer than high; ventral margin on ectal surface with setae *Fe1, Fe5*, *Fev1* and *Fev2* acuminate; mesal surface with a row of three ventral setae (*Fmv* 1–3) plus two dorsal setae (*Fmd2*, *Fmd3*). Patella with four *Pe* acuminate setae and four *Pm* feathered setae; without distinctive ornamentations. Setae formula on tibia 5:6:6 *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetrical.

Legs: Leg I, basitarsal-telotarsal proportions: 27: 3: 4: 4: 5: 5: 11. Femur IV 3.0 times longer than high.

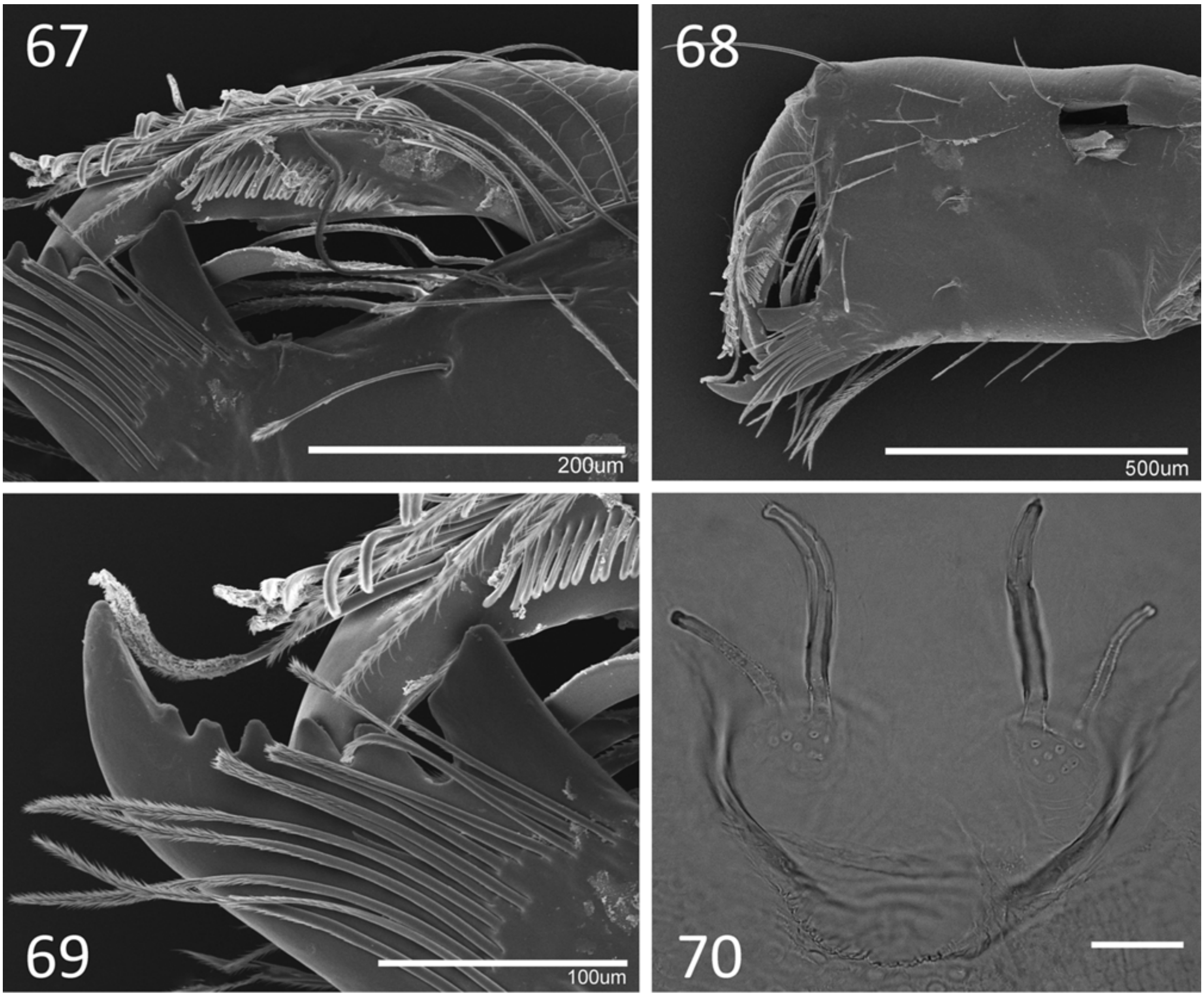
Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair *Dm*; tergite II with three pairs of microsetae anteriorly plus pair *Dm*; tergites III–VII with one pair of *Dm* setae each; tergite VIII with *Dm* and *Dl2*; tergite IX with pairs *Dl1*, *Dl2* and without *Dm*. Segments X, XI telescoped, with setal pairs *Dl2*, *Vm2*, *Vl1* and *Vl2,* plus single *Vm1* seta; segment XII with *Dm*, *Dl1*, *Dl2*, *Vm1*, *Vm2*, *Vl1* and *Vl2* setae, without posterodorsal process. Sternites with two well defined rows of setae each; genital plate with scattered setae.



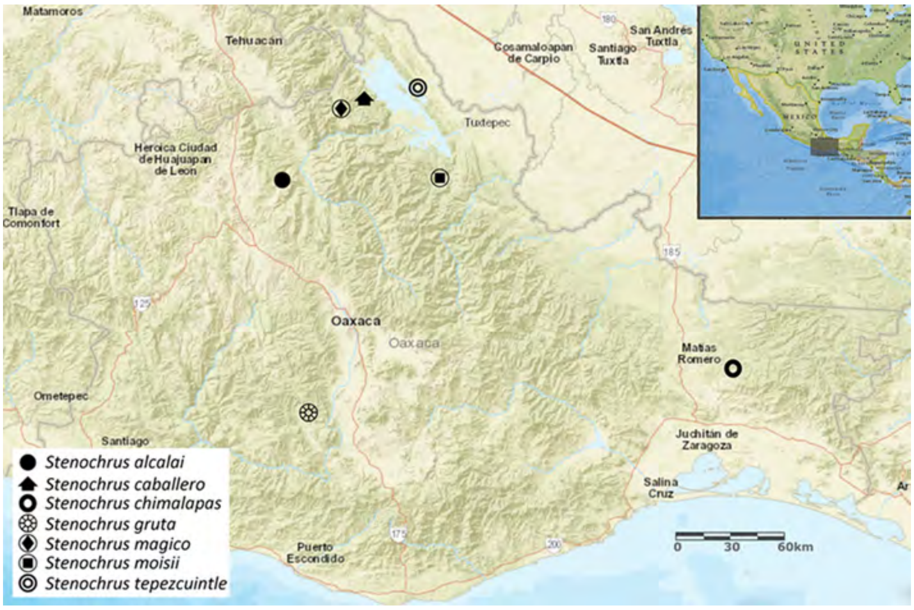
FIGURES 59–66. *Stenochrus magico* **sp. nov**. Male holotype. Flagellum (59–61): 59, dorsal view. 60, ventral view. 61, lateral view. Female. Flagellum (62–64): 62, dorsal view. 63, ventral view. 64, lateral view. Pedipalps ectal view (65, 66): 65, Homeomorphic male. 66, female. Scale bars = 0.2 mm.

Flagellum (Figs. 59–61): bulbous, subquadrate-shaped; 1.7 times longer than wide; without dorsal relief. Setation: *Dm1* situated outside of the bulb base; *Dm4* situated distally; *Dl2* anterior to *Vl1*; *Dl3* at same level as *Vl2*; pair *Vm2* present; seta *Vm1* posterior to *Vm2*; *Vm*5 posterior to *Vl1*. With one pair of anterodorsal microsetae between *Dm1* and *Dl2*, one pair of anterolateral microsetae on flagellar pedicel, and two patches of microsetae between *Vl1* and *Vl2* (*msp*).

Female (*paratype*) (Fig. 58): Pedipalps as on male (Fig. 66), 1.9 times longer than propeltidium length. Setation as on male. Flagellum with three flagellomeres (Figs. 62–64). Setation: seta *Dl2* not reduced and anterior to *Vl1*; *Dl3* posterior to *Vl2*; *Vm2* present and not reduced; seta *Vm1* at same level as *Vm2*; microsetae *Dl1* and *Dl4* present. Spermathecae (Fig. 70) with two pairs of lobes; median pair inverse "J" shaped outwards, without duct openings, ending in a blunt margin; lateral pair slender and slightly shorter, about 2/3 length of median lobes, curved outwards, with many pores along the entire length; lateral and median lobes bases at the same level. Chitinized arch U-shaped; with diffuse lateral tips and without anterior branch. Gonopod 3 times wider than long, roughly curved-shaped. Chelicera: serrula with 23 teeth. Setal group formula 3-8-4-2-11-6-1-6. Fixed finger with five teeth between two primary teeth.



FIGURES 67–70. *Stenochrus magico* **sp. nov**. Male. Chelicera (67–69): 67, movable finger. 68, mesal view. 69, fixed finger. Female. Spermathecae: 70, dorsal view. Scale bar (Fig. 70) = 0.05 mm.



FIGURES 71. Distribution map of the *Stenochrus* species know for the state of Oaxaca.

Remarks. Specimens of *Stenochrus magico* are distributed only inside the caves of the Sierra Mazateca, primarily in the Sistema Huautla. There is no evidence of dimorphic males in this species, but additional sampling is needed to verify this (n=2). There are other schizomid species outside the caves that should not be confused with *Stenochrus magico*, and the evidence suggests that *S. magico* is a troglophile without any apparent troglomorphic trait.

TABLE 5. Measurements (mm) of *Stenochrus magico* **sp. nov.**

	Male CNAN-T1163	Male CNAN-T1164	Female CNAN-T1165	Female CNAN-T1166
Total Length	3.80	4.24	5.76	5.68
Propeltidium				
Length	1.15	1.33	1.64	1.60
Width	0.64	0.69	0.92	0.90
Flagellum				
Length	0.46	0.46	–	0.59
Width	0.27	0.27	–	0.08
Height	0.21	0.21	–	0.08
Leg I				
Coxa	0.62	0.64	0.75	0.74
Trochanter	0.40	0.40	0.51	0.51
Femur	1.82	1.84	1.76	1.57
Patella	2.13	2.13	2.11	1.86
Tibia	1.47	1.57	1.50	1.38
Basitarsus	0.54	0.50	0.53	0.50
Telotarsus	0.64	0.66	0.69	0.58
Total	7.63	7.74	7.85	7.13
Leg IV				
Trochanter	0.35	–	0.58	0.40
Femur	1.68	–	1.72	1.64
Patella	0.64	–	0.80	0.70
Tibia	1.14	–	1.18	1.12
Basitarsus	1.04	–	1.10	1.04
Telotarsus	0.61	–	0.90	0.62
Total	5.46	–	6.28	5.52
Pedipalp				
Trochanter	0.43	0.50	0.72	0.64
Femur	0.62	0.77	0.80	0.69
Patella	0.61	0.69	0.77	0.72
Tibia	0.54	0.56	0.62	0.54
Tarsus	0.27	0.29	0.32	0.30
Total	2.48	2.80	3.23	2.90

Discussion

Currently, *Stenochrus* encompasses a wide range of morphological variation due to the combination of three different species groups described originally by Rowland (1975). These morphological groups were the first attempt to differentiate and recognize monophyletic groups within Schizomida and the all-encompassing old genus *Schizomus*. Later Reddell and Cokendolpher (1995) elevated several of those groups to genus level (e.g., part of the *"brasilensis"* group became *Surazomus*, *"dumitrescoae"* group became *Rowlandius*). However, in the case of the *"mexicanus"*, *"pecki"* and *"goodnightorum"* groups they were lumped in to one genus that was formed primarily by all North American schizomids; excluding the *"briggsi"* group, currently the genus *Hubbardia*, which is considerably different to the rest of New World schizomids.

Recently and as was discussed in Giupponi et al. (2016), species groups are a good approach to recognize, organize and to better understand the relationships within New World schizomids, because aside from the Protoschizomidae, the fact that the family Hubbardiidae groups all the other species in the world is a reflection of the lack of phylogenetic reconstruction and classification in the order.

However, recent developments such the new taxonomic findings in schizomids as well as the implementation of new characters, coupled with the description of new species, has created some problems in recognizing only three discrete species groups in the Mexican fauna. For example, the *"mexicanus"* group includes species from throughout the country, including *S. moisi*, *S. pallidus* and *S. portoricensis* which are species distributed principally in the south of Mexico, and are more similar among them than with members of the group which includes *S. mexicanus, S. davisi*, and *S. reddelli*, which are northern species, i. e., probably the *"mexicanus"* group might not be a monophyletic group. The species described here could be included within those southern species groups, and they are very similar in their morphology to *S. moisii* and *S. pallidus* with a probable Neotropical origin sharing some characters as is the presence of a pair of dorsal pits on the male flagellum and the predominantly dark coloration.

Regarding the dimorphic pedipalps on males, which is a characteristic fairly common in schizomids that was first reported by Armas (1989) and later analyzed by Santos et al. (2013), is a condition that has been reported for several genera, such as *Antillostenochrus*, *Sotanostenochrus*, *Rowlandius*, etc. However, the presence of two different states (homeomorphic and heteromorphic) and including a third state (mesomorphic) in one population is a condition reported only in species of *Rowlandius* and *Mayazomus* (Monjaraz-Ruedas and Francke, 2015; Santos et al., 2013). Despite the fact that *S. mexicanus* was reported as a species with sexually dimorphic males (compared with the female) there is no evidence of other intra-sexually dimorphic states in that species or the genus *Stenochrus.* Therefore, in this work we include the first report of heteromorphic, mesomorphic and homeomorphic males in two of the new species (*S. chimalapas* and *S. gruta*) of *Stenochrus*, and we have noted that this condition is apparently more common in cave dwelling species than in epigean ones.

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SYSTEMATICS OF THE SHORT-TAILED WHIPSCORPION GENUS *STENOCHRUS* CHAMBERLIN, 1922 (SCHIZOMIDA: HUBBARDIIDAE), WITH DESCRIPTIONS OF SIX NEW GENERA AND FIVE NEW SPECIES

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CONTENTS

ABSTRACT

The short-tailed whipscorpion genus, *Stenochrus* Chamberlin, 1922 (Schizomida: Hubbardiidae Cook, 1899), occurring in North and Central America, is redefined and revised based on simultaneous phylogenetic analysis of 61 morphological characters and 2968 aligned DNA nucleotides from two markers in the nuclear genome, the internal transcribed spacer (ITS) and 28S rDNA, and two markers in the mitochondrial genome, cytochome *c* oxidase subunit I (COI) and 12S rDNA, for a comprehensive taxon sample. Six new genera are described: *Ambulantactus*, gen. nov.; *Baalrog*, gen. nov.; *Harveyus*, gen. nov.; *Nahual*, gen. nov.; *Schizophyxia*, gen. nov.; *Troglostenochrus*, gen. nov. *Heteroschizomus* Rowland, 1973, stat. rev., is revalidated and its type species, *Heteroschizomus goodnightorum* Rowland, 1973, reinstated. Six new species are described: *Ambulantactus aquismon*, sp. nov.; *Ambulantactus montielae*, sp. nov.; *Baalrog yacato*, sp. nov.; *Harveyus contrerasi*, sp. nov.; *Heteroschizomus kekchi*, sp. nov.; *Nahual bokmai*, sp. nov. Eighteen new combinations are created by transferring species, previously accommodated in *Stenochrus*, to other genera: *Ambulantactus davisi* (Gertsch, 1940), comb. nov.; *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov.; *Baalrog sbordonii* (Brignoli, 1973), comb. nov.; *Harveyus mexicanus* (Rowland, 1971a), comb. nov.; *Harveyus mulaiki* (Gertsch, 1940), comb. nov.; *Harveyus reddelli* (Rowland, 1971a), comb. nov.; *Heteroschizomus meambar* (Armas and Víquez, 2010), comb. nov.; *Heteroschizomus orthoplax* (Rowland, 1973a), comb. nov.; *Heteroschizomus silvino* (Rowland and Reddell, 1977), comb. nov.; *Nahual caballero* (Monjaraz-Ruedas and Francke, 2018), comb. nov.; *Nahual lanceolatus* (Rowland, 1975), comb. nov.; *Nahual pallidus* (Rowland, 1975), comb. nov.; *Pacal moisii* (Rowland, 1973), comb. nov.; *Pacal tepezcuintle* (Armas and Cruz-López, 2009), comb. nov.; *Schizophyxia bartolo* (Rowland, 1973), comb. nov.; *Schizophyxia lukensi* (Rowland, 1973), comb. nov.; *Troglostenochrus palaciosi* (Reddell and Cokendolpher, 1986), comb. nov.; *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov. The male of *B. sbordonii* is determined to be heterospecific with the holotype female and described as *B. yacato*. The females of *H. goodnightorum* and *N. lanceolatus* are described for the first time. Following these revisions, seven species remain within *Stenochrus*: *Stenochrus alcalai* Monjaraz-Ruedas and Francke, 2018; *Stenochrus chimalapas* Monjaraz-Ruedas and Francke, 2018; *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018; *Stenochrus guatemalensis* (Chamberlin, 1922); *Stenochrus leon* Armas, 1995; *Stenochrus pecki* (Rowland, 1973); *Stenochrus portoricensis* Chamberlin, 1922. *Olmecazomus*, nom. nov., is proposed as a replacement name for the junior homonym, *Olmeca* Monjaraz-Ruedas and Francke, 2017, creating three new combinations: *Olmecazomus brujo* (Monjaraz-Ruedas and Francke, 2017), comb. nov.; *Olmecazomus cruzlopezi* (Monjaraz-Ruedas and Francke, 2017), comb. nov.; *Olmecazomus santibanezi* (Monjaraz-Ruedas and Francke, 2017), comb. nov. A key to identification of the hubbardiid genera of North America is provided and the utility of various character systems for the diagnosis of schizomid genera discussed. The integration of morphological and molecular data not only increased knowledge of the schizomid diversity in the New World but disentangled what was once considered a homoplastic and variable morphology in a large "catch-all" genus into discrete units each diagnosable by unique character combinations.

INTRODUCTION

The order Schizomida Petrunkevitch, 1945, commonly known as the short-tailed whipscorpions, schizomids, or tartarids, is among the less diverse, or minor, arachnid orders (Harvey, 2003). It currently comprises only two families, Protoschizomidae Rowland, 1975, endemic to North America, with two extant and one fossil genera and 16 species, and Hubbardiidae Cook, 1899, with 59 extant genera and 339 species worldwide (Harvey, 2003, 2013; Monjaraz-Ruedas and Francke, 2015). Within the New World, Hubbardiidae contains 27 genera, including *Stenochrus* Chamberlin, 1922, the most speciose schizomid genus in North America and the third most speciose in the New World (Reddell and Cokendolpher, 1995; Harvey, 2013).

When first described, *Stenochrus* was monotypic, including only the type species, *Stenochrus* *portoricensis* Chamberlin, 1922. Chamberlin (1922) erroneously diagnosed the genus by the absence of mesopeltidia, justifying its later synonymy with *Schizomus* Cook, 1899, by Rowland (1973a) who also created *Heteroschizomus* Rowland, 1973, to accommodate a rare new species from the Yucatán with a peculiarly enlarged opisthosoma and a lanceolate male pygidial flagellum. Rowland (1973a) mistakenly associated a heterospecific female with the holotype male of the type species of *Heteroschizomus*, leading to the erroneous conclusion that the female spermathecae of *Heteroschizomus* resembled those of *Schizomus*. *Heteroschizomus* was subsequently synonymized with *Schizomus* by Rowland and Reddell (1977), based in part on the discovery of other species with an enlarged opisthosoma.

Stenochrus remained in synonymy with *Schizomus* until it was revalidated, and *Heteroschizomus* newly synonymized with it by Reddell and Cokendolpher (1991), based in part on decisions originating from Rowland (1975b). Rowland (1975b) presented the first phylogeny of schizomids, an analysis of 12 morphological characters for the six groups of New World species in the genus *Schizomus*, which was never published. Based on the analysis, Rowland (1975b) proposed seven species groups of *Schizomus*, i.e., the *brasiliensis*, *briggsi*, *dumitrescoae*, *goodnightorum*, *mexicanus*, *pecki*, and *simonis* groups. The *briggsi* group was placed sister to a monophyletic group comprising two reciprocally monophyletic subgroups, one comprising the *brasiliensis*, *dumitrescoae*, and *simonis* groups, the other comprising the *goodnightorum*, *mexicanus*, and *pecki* groups in Rowland's (1975b) unpublished phylogeny. The seven species groups were formally diagnosed and published by Rowland and Reddell (1979a, 1979b, 1980, 1981). Rowland and Reddell (1980, 1981) placed 16 species of *Schizomus* from the United States, Mexico, and Guatemala into the *goodnightorum*, *mexicanus*, and *pecki* groups. However, further studies by Reddell and Cokendolpher (1991, 1995) demonstrated that *Schizomus* and another schizomid genus, *Trithyreus* Kraepelin, 1899, do not occur in the New World, leading Reddell and Cokendolpher (1991) to revalidate *Stenochrus* and synonymize *Heteroschizomus* with it. The genus *Sotanostenochrus* Reddell and Cokendolpher, 1991, was created for two species in the *mexicanus* group. According to Reddell and Cokendolpher (1991) all species of *Stenochrus* shared the absence of pedipalp armature and a posterodorsal process on opisthosomal segment XII, the male pygidial flagellum sloping sharply posteriorly, the female pygidial flagellum comprising three flagellomeres, and the female spermathecae with two pairs of lobes, the lateral pair reduced in size; and all except *Stenochrus mexicanus* Rowland, 1971, shared the presence of homeomorphic pedipalps. Supposedly, the "discovery" of the female of *Stenochrus goodnightorum* Rowland, 1973, with reduced lateral lobes of the spermathecae, reinforced the synonymy of *Heteroschizomus* within *Stenochrus* (Rowland and Reddell, 1980).

Having established that *Schizomus* is not a New World genus, Reddell and Cokendolpher (1995) assigned Rowland's (1975b) species groups to other existing genera and created new genera to accommodate the rest. Species of the *simonis* group were transferred to *Hansenochrus* Reddell and Cokendolpher, 1995, the *briggsi* group to *Hubbardia* Cook, 1899, and the *goodnightorum*, *mexicanus*, and *pecki* groups to *Stenochrus*. *Pacal* Reddell and Cokendolpher, 1995, and *Surazomus* Reddell and Cokendolpher, 1995, were created to accommodate species of the *brasiliensis* group, and *Rowlandius* Reddell and Cokendolpher, 1995, to accommodate the *dumitrescoae* group. Reddell and Cokendolpher (1995) transferred *Schizomus alejandroi* Armas, 1989, described from Holguín, Cuba, to *Stenochrus*, creating the new combination, *Stenochrus alejandroi* (Armas, 1989a).

Armas and Teruel (1998) created the *brevipatellatus* group of *Stenochrus*, to accommodate *Stenochrus alejandroi*, *Stenochrus brevipatellatus* (Rowland and Reddell, 1979), *Stenochrus cerdoso* (Camilo and Cokendolpher, 1988), and *Stenochrus subcerdoso* (Armas and Abud-Antun, 1990), all of which share a reduced pedipalp patella and the presence of four and six setae on opisthosomal segment II. Armas and Teruel (2002) created *Antillo-*

stenochrus Armas and Teruel, 2002, to accommodate the species of the *brevipatellatus* group, where they have remained since.

Another seven species of *Stenochrus* were subsequently described from Mexico and one from Honduras (Armas and Cruz-López, 2009; Armas and Víquez, 2010; Monjaraz-Ruedas, 2012; Monjaraz-Ruedas and Francke, 2018). A fossil species, *Stenochrus velteni* Krüger and Dunlop, 2010, was described from the Dominican Republic but subsequently tranferred to *Rowlandius* by Armas and Teruel (2011), based on the shape of the male pygidial flagellum and the apparent diversity of that genus on Hispaniola.

When the present study commenced, *Stenochrus* contained 27 species, distributed mostly in the Nearctic region, from the southern United States, through Mexico to Central America (table 1, figs. 1–5). One cosmopolitan species, *Stenochrus portoricensis* Chamberlin, 1922, was reported from North, Central, and South America and the Caribbean, as well as several countries in Europe (Korenko et al., 2009; Christophoryová et al., 2013; Harvey, 2013). The morphological disparity among species of *Stenochrus*, reflected by variation in body size, male flagellar shape, setal patterns and sexual dimorphism, including homeomorphic and heteromorphic pedipalps, and their diverse habitats, including caves, rainforest, tropical dry forest, and pine and oak forest above 2000 m, raised the question as to whether the genus is monophyletic. Given the paucity of phylogenetic analyses on schizomids, it is unsurprising that the monophyly and phylogenetic relationships of *Stenochrus* have never been tested, beyond the unpublished analysis of Rowland (1975b), which was based on 12 morphological characters, and the inclusion of several exemplar species of *Stenochrus* in recent analyses of schizomid phylogeny based on morphology (Monjaraz-Ruedas and Francke, 2016, 2017) and DNA sequences (Clouse et al., 2017). In an analysis of *Mayazomus* Reddell and Cokendolpher, 1995, phylogeny by Monjaraz-Ruedas and Francke (2016), based on 130 morphological characters, which included exemplar species of *Stenochrus* as outgroups, along with outgroup exemplars of *Hansenochrus*, *Hubbardia*, and *Rowlandius* from North, Central, and South America, that were members of the original species groups of Rowland and Reddell (1979a, 1979b, 1980, 1981), *Stenochrus* was paraphyletic. The genus was also paraphyletic in the molecular phylogenetic analysis of Clouse et al. (2017), based on two nuclear and two mitochondrial gene markers for 240 samples, which included several samples of *Stenochrus portoricensis*, one sample of *Stenochrus sbordonii* Brignoli, 1973, and several unidentified specimens from Mexico; *Hubbardia* grouped as sister to all other Hubbardiidae samples (n = 238) and *S. sbordonii* sister to the remaining taxa (n = 237). On the other hand, *Stenochrus* was monophyletic in an analysis of *Olmeca* Monjaraz-Ruedas and Francke, 2017, phylogeny, using different exemplar species of *Stenochrus*, i.e., *Stenochrus pecki* Rowland, 1973, and *S. portoricensis*, from the *Mayazomus* analysis (Monjaraz-Ruedas and Francke, 2017).

In the present contribution, the genus *Stenochrus* is redefined and revised based on simultaneous phylogenetic analysis of 61 morphological characters and 2968 aligned DNA nucleotides from two markers in the nuclear genome, the internal transcribed spacer (ITS) and 28S rDNA, and two markers in the mitochondrial genome, cytochome *c* oxidase subunit I (COI) and 12S rDNA, for a comprehensive taxon sample (fig. 6; Monjaraz-Ruedas et al., in prep.). Six new genera and six new species are described. *Heteroschizomus* is revalidated and its type species reinstated. Eighteen new combinations are created by transferring species, previously accommodated in *Stenochrus*, to other genera. The male of *Baalrog sbordonii* (Brignoli, 1973), comb. nov., is determined to be heterospecific with the holotype female and described as a new species. The females of *Heteroschizomus goodnightorum* Rowland, 1973, and *Nahual lanceolatus* (Rowland, 1975), comb. nov., are described for the first time. Following these revisions, seven species remain within *Stenochrus*. *Olmecazomus*, nom. nov., is proposed as a replacement name for the junior homonym, *Olmeca*, creating three new combinations. Another two new combinations are created by the transfer of two species to *Pacal*. A key

TABLE 1

Diversity and distribution of North American short-tailed whipscorpion taxa associated with *Stenochrus* Chamberlin, 1922 (Schizomida: Hubbardiidae Cook, 1899)

Taxon	**Distribution**
Ambulantactus, gen. nov.	
A. aquismon, sp. nov.	Mexico: San Luis Potosí: Aquismon
A. davisi (Gertsch, 1940), comb. nov.	Mexico: Tamaulipas: San Fernando
A. montielae, sp. nov.	Mexico: Morelos: Quilamula
Baalrog, gen. nov.	
B. firstmani (Rowland, 1973), comb. nov.	Mexico: Veracruz: Atoyac
B. magico (Monjaraz-Ruedas and Francke, 2018), comb. nov.	Mexico: Oaxaca: Huautla
B. sbordonii (Brignoli, 1973), comb. nov.	Mexico: Veracruz: Amatlán de los Reyes
B. yacato, sp. nov.	Mexico: Veracruz: Atoyac
Harveyus, gen. nov.	
H. contrerasi, sp. nov.	Mexico: San Luis Potosí: Xilitla
H. mexicanus (Rowland, 1971), comb. nov.	Mexico: San Luis Potosí: Ciudad Valles
H. mulaiki (Gertsch, 1940), comb. nov.	U.S.A.: Texas: Starr County: Rio Grande City
H. reddelli (Rowland, 1971), comb. nov.	Mexico: Tamaulipas: Ocampo
Heteroschizomus Rowland, 1973, stat. rev.	
H. goodnightorum Rowland, 1973	Mexico: Yucatan: Chichen-Itza
H. kekchi, sp. nov.	Guatemala: Izabal: Livingston
H. meambar (Armas and Víquez, 2010), comb. nov.	Honduras: Comayagua: La Guama
H. orthoplax (Rowland, 1973), comb. nov.	Mexico: Chiapas: Tapachula
H. silvino (Rowland and Reddell, 1977), comb. nov.	Guatemala: Izabal: Puerto Barrios
Nahual, gen. nov.	
N. bokmai, sp. nov.	Mexico: Veracruz: Xalapa
N. caballero (Monjaraz-Ruedas and Francke, 2017), comb. nov.	Mexico: Oaxaca: San José Tenango
N. lanceolatus (Rowland, 1975), comb. nov.	Mexico: Veracruz: Ciudad Mendoza
N. pallidus (Rowland, 1975), comb. nov.	Mexico: Veracruz: Tlilapan
Olmecazomus, nom. nov.	
O. brujo (Monjaraz-Ruedas and Francke, 2017), comb. nov.	Mexico: Veracruz: Los Tuxtlas
O. cruzlopezi (Monjaraz-Ruedas and Francke, 2017), comb. nov.	Mexico: Chiapas: Tuxtla Gutierrez
O. santibanezi (Monjaraz-Ruedas and Francke, 2017), comb. nov.	Mexico: Chiapas: Ocosingo
Pacal Reddel and Cokendolpher, 1995	
P. lacandonus (Rowland, 1975)	Mexico: Chiapas: Palenque
P. moisii (Rowland, 1973), comb. nov.	Mexico: Oaxaca: Valle Nacional
P. stewarti (Rowland, 1973)	Mexico: Oaxaca: Valle Nacional
P. tepezcuintle (Armas and Cruz López, 2009), comb. nov.	Mexico: Oaxaca: San Miguel Soyaltepec
P. trilobatus (Rowland, 1975)	Mexico: Tabasco: Teapa

Taxon	**Distribution**
Schizophyxia, gen. nov.	
S. bartolo (Rowland, 1973), comb. nov.	Mexico: Nuevo Leon: Santa Catarina
S. lukensi (Rowland, 1973), comb. nov.	Mexico: Tamaulipas: Gomez Farias
Stenochrus Chamberlin, 1922	
S. alcalai Monjaraz-Ruedas and Francke, 2018	Mexico: Oaxaca: San Pedro Jocotipac
S. chimalapas Monjaraz-Ruedas and Francke, 2018	Mexico: Oaxaca: Santa Maria Chimalapas
S. gruta Monjaraz-Ruedas and Francke, 2018	Mexico: Oaxaca: Sola de Vega
S. guatemalensis (Chamberlin, 1922)	Guatemala: San Rafael?
S. leon Armas, 1995	Nicaragua: León: Telica
S. pecki (Rowland, 1973)	Mexico: Tabasco: Teapa
S. portoricensis Chamberlin, 1922	Europe, North, Central and South America
Troglostenochrus, gen. nov.	
T. palaciosi (Reddell and Cokendolpher, 1986), comb. nov.	Mexico: Guerrero: Taxco
T. valdezi (Monjaraz-Ruedas, 2012), comb. nov.	Mexico: Chiapas: San Fernando

to identification of the hubbardiid genera of North America is provided and the utility of various character systems for the diagnosis of schizomid genera discussed.

MATERIALS AND METHODS

Taxon Sampling: Specimens were collected by hand and/or using an aspirator and preserved in 80% ethanol for morphological study. One or two additional specimens were preserved in 96% ethanol for DNA isolation. Material examined is deposited in the American Museum of Natural History (AMNH), New York, including the Ambrose Monell Cryocollection (AMCC); the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), Mexico City; and the Texas Memorial Museum (TMM), University of Texas, Austin. Specimens were observed using a Nikon SMZ 625 stereomicroscope with an ocular micrometer calibrated at 20×. Male chelicerae were dissected and prepared for scanning electron microscopy (SEM) following the protocol of Acosta et al. (2007), with a modified cleaning process which involved three cycles of washing alternately in distilled water and biological detergent, followed by 30 seconds in an E/MC 250 Ultrasonic Cleaner (EMC Global Technologies, Quakertown, PA). Structures were mounted on stubs using adhesive copper aluminium tape, and subsequently coated with a layer of gold-palladium in a Q150R ES Sputter Coater (Quorum Technologies, Lewes, East Sussex, UK). Prepared stubs were imaged with a Hitachi SU1510 SEM (Chiyoda City, Tokyo, Japan) at the Laboratorio Nacional de Biodiversidad (LANABIO), IBUNAM. Female spermathecae were dissected in 80% ethanol and cleared in lactophenol for 10 minutes (Krantz and Walter, 2009), preserved thereafter in Hoyer's medium, and mounted on semipermanent microscope slides. Digital photomicrographs were taken under visible light with a Leica DFC490 camera adapted to a Leica Z16 APOA stereomicroscope, assembled with LAS (Leica Application Suite) v. 4.3.0, and edited with Adobe Photoshop CS6.

Morphological Nomenclature: Morphological terminology for legs and pedipalps follows Reddell and Cokendolpher (1995), cheliceral setal nomenclature follows Lawrence (1969) as modified by Villarreal et al. (2016), pedipalp setal terminology follows Monjaraz-Ruedas et al. (2017), opisthosomal setal nomenclature follows Villarreal et al. (2016), pygidial flagellar setal terminology follows Cokendolpher and Reddell (1992) as modified by Harvey (1992) and Monjaraz-Ruedas

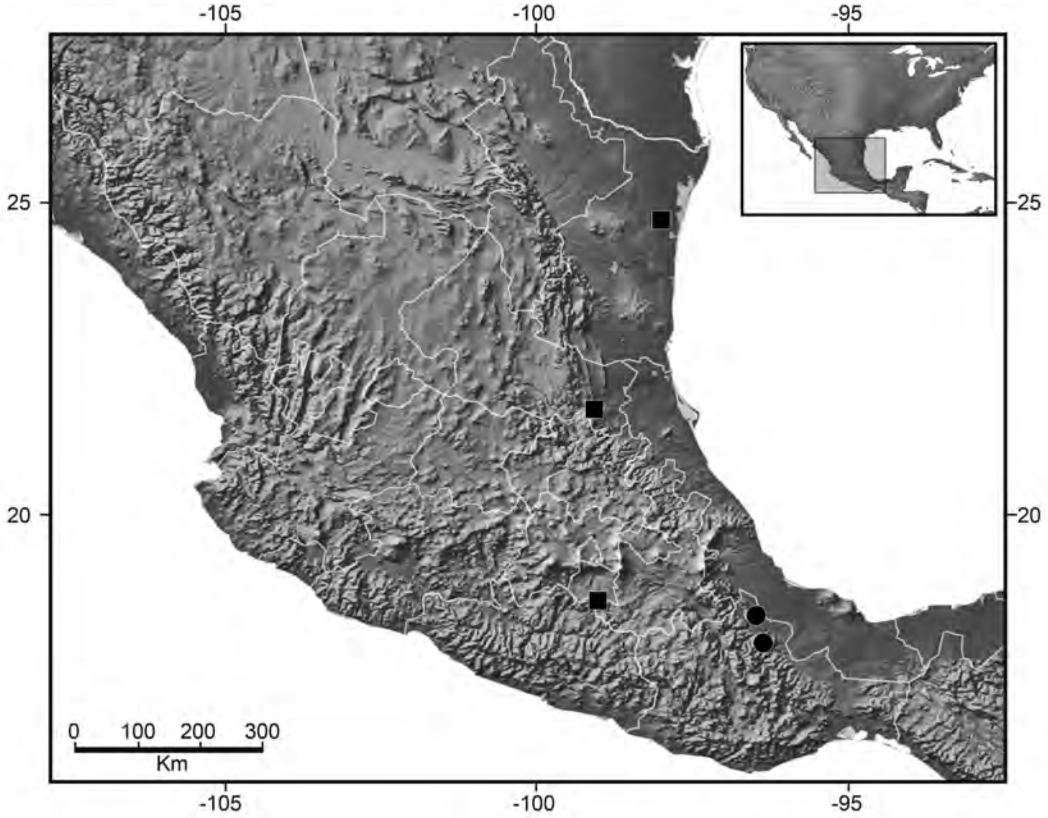

FIG. 1. Map of central Mexico, plotting known locality records for the short-tailed whipscorpion genus *Ambulantactus*, gen. nov. (squares), and the species recently tranferred to *Pacal* Reddell and Cokendolpher, 1995 (circles) (Schizomida: Hubbardiidae Cook, 1899), based on data from museum collections and the literature.

et al. (2016), and spermathecal nomenclature follows Moreno-González et al. (2014).

In order to express hypotheses of homology across morphological structures and for ease of comparison, new terminology was applied to several structures, specifically the apical process on pedipalp trochanter, the shape and ornamentation of the male pygidial flagellum, and the chitinized arch and median and lateral lobes of the female spermathecae.

Pedipalp Trochanter Apical Process: The shape of the anterior margin of the pedipalp trochanter apical process, and whether the margin projects beyond the margin of the femur, were considered. The absence of the apical process may also be interpreted as a rounded margin, i.e., not projected. The terms applied to the states of this character follow botanical terminology for leaf tips: "acute" is the most common shape observed in North American schizomids (fig. 7E, C); "acuminate" is the alternate form of the state with the margin extremely projected (fig. 7F, I); "obtuse triangle" has the margin not projected with a wide internal angle (fig. 7D); "bump" or "tubercle" is observed mainly among heteromorphic males (fig. 7H); digitiform is common in *Surazomus* and some species of *Rowlandius*.

Male Pygidial Flagellum Shape: The shape of the male pygidial flagellum in dorsal view varies depending on its size and the relief of its dorsal surface. Ten states were identified, the terms used for their description based on botanical leaf shapes: "lanceolate"; "cordate," which may also be interpreted as spade shaped; "spatulate" refers to

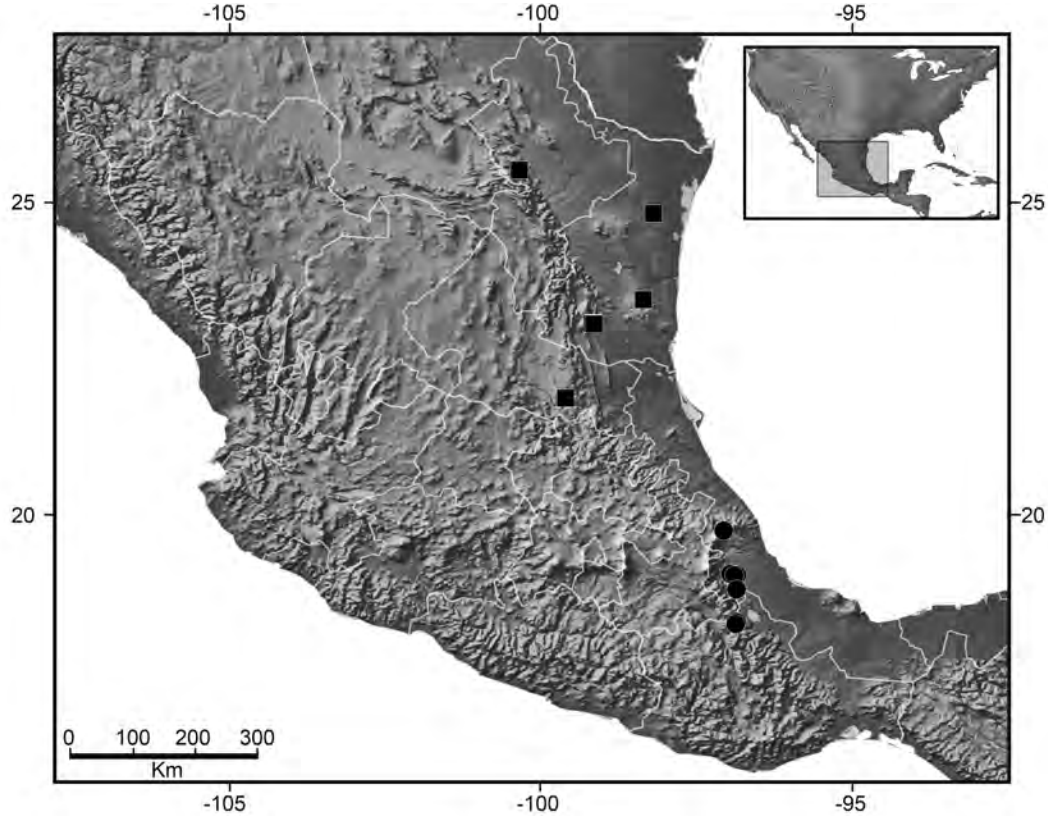

FIG. 2. Map of central Mexico, plotting known locality records for the short-tailed whipscorpion genera *Baalrog*, gen. nov. (circles), and *Schizophyxia*, gen. nov. (squares) (Schizomida: Hubbardiidae Cook, 1899), based on data from museum collections and the literature.

the flagellum observed in *Heteroschizomus*, stat. rev., and some species of *Piaroa* Villarreal et al., 2008, which comprises an anterior bulb and a posterior lobe; "subrhomboidal"; "shovel shaped"; "elliptical" may also be ovate or oval; "trilobed"; "bulbous/clavate" refers to the flagellum observed in *Baalrog*, gen. nov and some other species, e.g., *Schizophyxia bartolo* (Rowland, 1973), comb. nov., and *Harveyus mulaiki* (Gertsch, 1940), comb. nov., previously referred to as "club" (Rowland, 1975b); "spear shaped"; or "deltoid."

Male Pygidial Flagellum Ornamentation: Two distinct types of ornamentation were observed in the male pygidial flagellum, i.e., depressions and projections. Three states were observed among the former: circular depressions, appearing as dots or holes in the dorsal surface, previously termed "pits" by some authors (Rowland, 1975b; Rowland and Reddell, 1979b, 1980, 1981, Monjaraz-Ruedas and Francke, 2015, Moreno-González et. al., 2014); slump, a shallow depression without defined shape; and a combination of the two previous states, i.e., pits within a slump, a diagnostic character for *Stenochrus*. Two states were observed among projections, i.e., swellings and protuberances, which are larger, wider, and usually projected, as in *Pacal* and *Troglostenochrus*, gen. nov.

Female Spermathecae Chitinized Arch: The chitinized arch of the female spermathecae comprises several structures, i.e., the anterior branch, the posterior branch, the gonopod (atrium), and the lateral tips (Moreno-González et al., 2014). Taken together, the shapes and relative positions of these structures create a variety of unique states for the shape of the

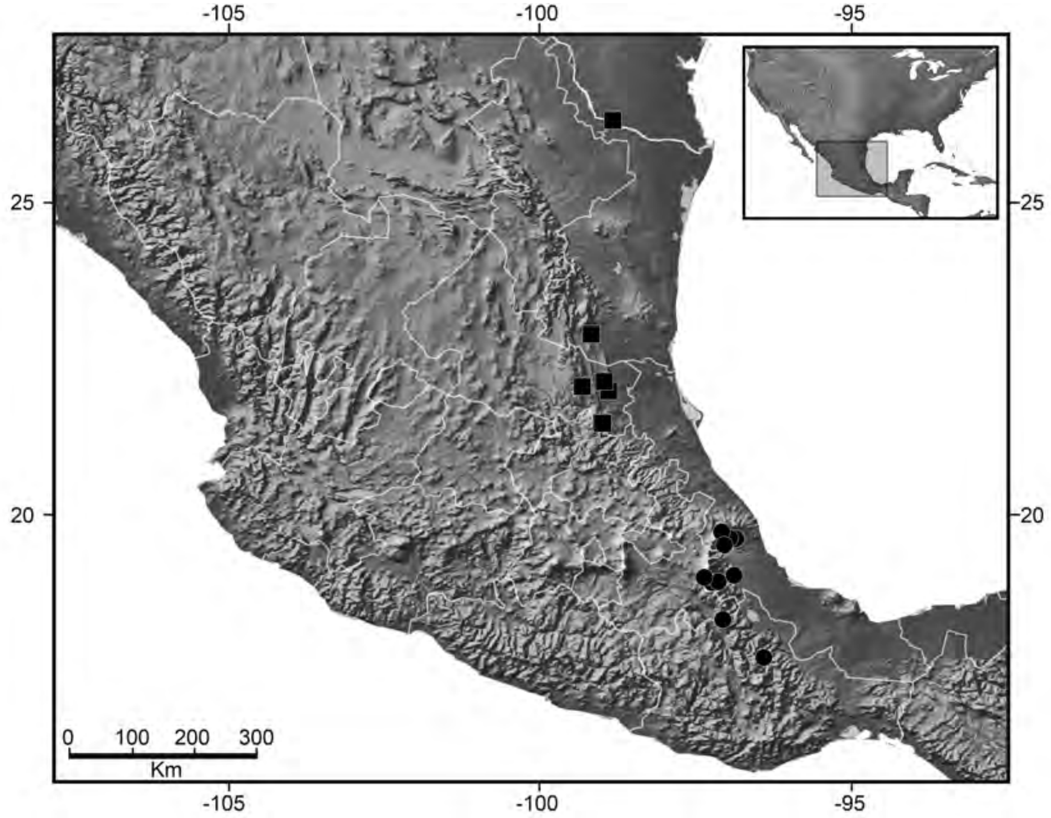

FIG. 3. Map of central Mexico, plotting known locality records for the short-tailed whipscorpion genera *Harveyus*, gen. nov. (squares), and *Nahual*, gen. nov. (circles) (Schizomida: Hubbardiidae Cook, 1899), based on data from museum collections and the literature.

chitinized arch, to which the following descriptive terms were applied: "arrow shaped" is a common condition in *Nahual*, gen. nov. (figs. 9A, B); "mug shaped" is common among species of *Heteroschizomus* (fig. 8E, F); "V-shaped" occurs in several schizomid genera, e.g., *Harveyus*, gen. nov., *Piaroa*, and *Rowlandius* (fig. 8D); "hastate" refers to spermathecae with long and wide lateral tips, as observed in *Baalrog* (fig. 8B); "bowl shaped" refers to the condition in *Stenochrus*, an inverse arch-shaped chitinized arch in which the presence of an anterior branch and a widened atrium and gonopod give the appearance of a Chinese rice bowl (fig. 9E); "inverse arch shaped" may also be interpreted as a very wide U-shaped chitinized arch (fig. 8A, C); "obtuse triangle" may also be interpreted as a wide V-shaped chitinized arch (fig. 9D); and "U-shaped," which is among the most common shapes of the chitinized arch observed in schizomids (fig. 9C).

Female Spermathecae Median and Lateral Lobes: The shape of the lobes of the female spermathecae is highly variable and may be affected by the method of fixation and slide mounting, as these lobes can move inward or outward. Despite these considerations, the general shape of the entire lobe can be reliably assessed and compared, leading to the identification of three distinct shapes: linear (I-shaped) (fig. 8A, E); inverse J-shaped (figs. 8C, 9F); curved along its length (parenthesis-shaped) (fig. 9C, E). Lobes usually bear various structures, e.g., sclerotizations, bulbs, or duct openings (figs. 8C, 9A, 9D). Sclerotizations are common among species

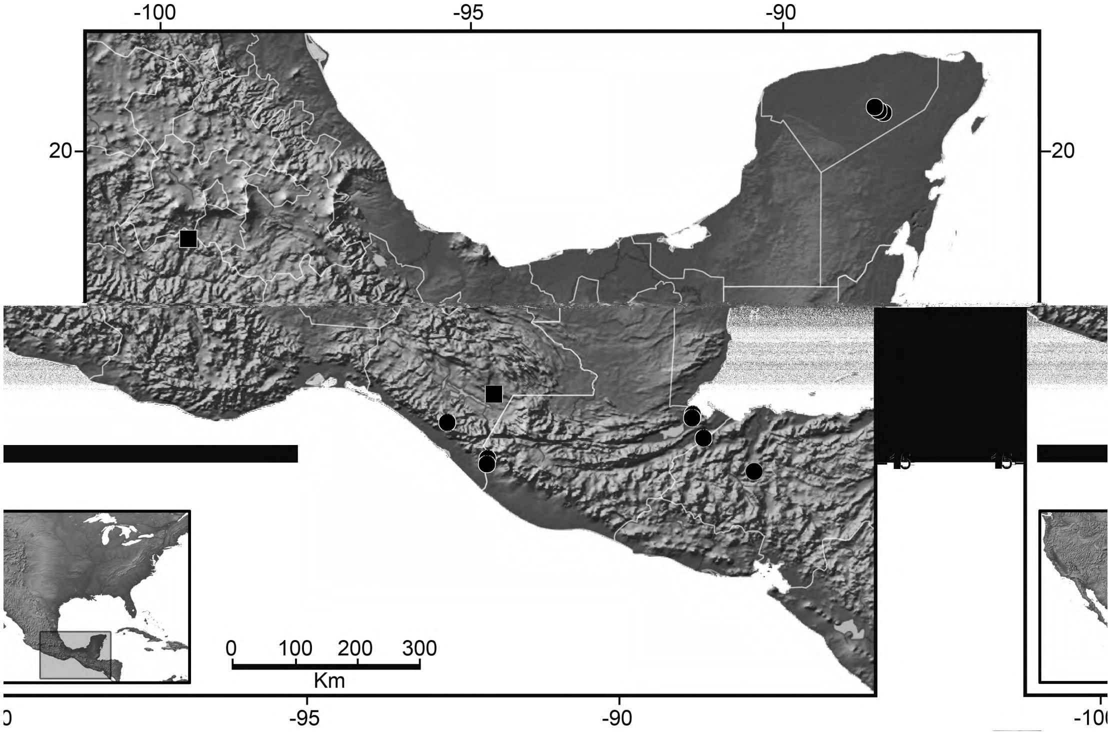

FIG. 4. Map of southern Mexico, plotting known locality records for the short-tailed whipscorpion genera *Heteroschizomus* Rowland, 1973, stat. rev. (circles), and *Troglostenochrus*, gen. nov. (squares) (Schizomida: Hubbardiidae Cook, 1899), based on data from museum collections and the literature.

of *Nahual* and *Stenochrus* (figs. 9A, B, E, 10C) whereas bulbs are observed in *Harveyus*, gen. nov., and *Pacal* (fig. 8C, D). Bulbs may vary in size: large bulbs, usually more than 4× the width of the lobe, are common in *Pacal* and some species of *Rowlandius*, whereas small bulbs, 3× or less the width of the lobes, are common among species of *Harveyus* and *Surazomus*.

PHYLOGENETIC ANALYSES: A morphological data matrix, comprising 61 morphological characters (appendix 1) scored for 41 terminal taxa, was prepared using Mesquite ver. 3.0.4 (Maddison and Maddison, 2018), and deposited in Morphobank (https://morphobank.org) with accession number P3464. Forty-three multistate and 18 binary characters were modified from Monjaraz-Ruedas and Francke (2016, 2017) and treated as nonadditive (Fitch, 1971) to avoid a priori character state transformations.

Two markers in the nuclear genome, the internal transcribed spacer (ITS) and 28S rDNA (28S), and two markers in the mitochondrial genome, cytochome *c* oxidase subunit I (COI) and 12S rDNA (12S), were Sanger-dideoxy sequenced using an ABI Prism 3730 XL DNA Sequencer (Perkin-Elmer, Melville, NY) at the AMNH Sackler Institute of Comparative Genomics and a 3500 XL Genetic Analyzer (Life Technologies, Foster City, CA) at the LANABIO Molecular Laboratory. Double-stranded sequences were edited and contiged into consensus sequences using Sequencher ver. 5.4.6 (Gene Codes Corporation, Ann Arbor, MI), and deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank) (appendix 2). Sequences of the 28S marker were length invariant, comprising 501 base pairs (bp) in all terminals whereas sequences of the ITS marker varied from 637–837 bp with an average of 806 bp, and of the 12S fragment from 319–387 bp with an

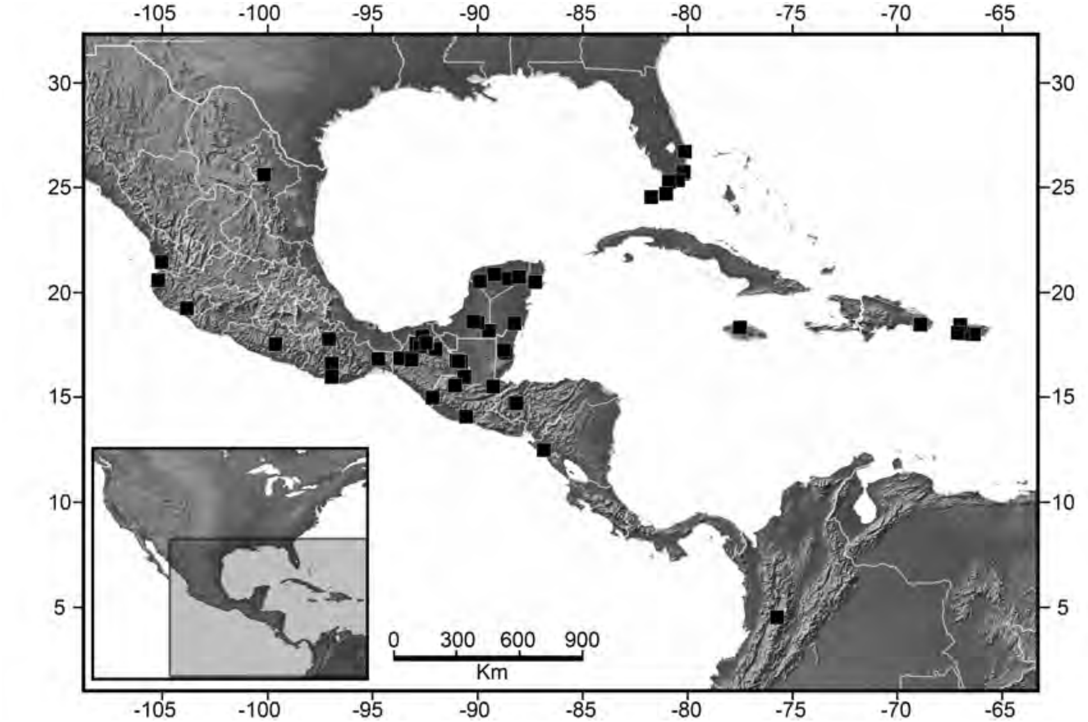

FIG. 5. Map of the Caribbean, Central America and Mexico, plotting known locality records for a cosmopolitan genus of short-tailed whipscorpions, *Stenochrus* Chamberlin, 1922 (Schizomida: Hubbardiidae Cook, 1899), based on data from museum collections.

average of 360 bp. Partial COI sequences varied from 659–1077 bp with an average of 995 bp.

The 28S, ITS, 12S, and COI sequences were aligned using MAFFT 6 (Katoh, 2013). Among the aligned loci, 74%, 49%, and 48% of the sites were variable, and 65%, 35%, and 41% parsimony informative, in the 12S, ITS, and COI, respectively, whereas 9% were variable and 5% parsimony informative in the 28S. As expected, for a protein-coding gene, the third codon position of the COI was the most informative, with 96% of the sites variable and 91% parsimony informative, followed by the first codon position, with 34% of the sites variable and 25% parsimony informative.

The aligned ITS, 12S, and COI sequences were concatenated together with the 28S sequences to produce a matrix of 2968 aligned DNA nucleotides. In the concatenated alignment 45% of the sites were variable and 36% parsimony informative. Seven data partitions were identified using PartitionFinder ver. 2 (Lanfear et al., 2016): morphology; ITS; 28S; 12S; and COI first, second, and third positions. jModelTest ver. 2.1.6 (Darriba et al., 2012) was used to select the most appropriate evolutionary model for each molecular partition.

The morphological and molecular data were analyzed separately and simultaneously using Maximum Likelihood with RAxML-HPC2 ver. 8.2.10 on XSEDE (Stamatakis, 2014) via the CIPRES Science Gateway ver. 3.3 online portal (Miller et al., 2010). Optimal trees were computed with 1000 bootstrap replicates and 500 hits for the fast bootstrap replicates, using the GTRCAT model for molecular data and the GTRGAMMA --asc-corr=Lewis for morphological data (Lewis, 2001). Characters were optimized on the preferred phylogenetic hypothesis (fig. 6) with accelerated transformation (ACCTRAN) or delayed transformation (DELTRAN) (Farris, 1970; Swofford

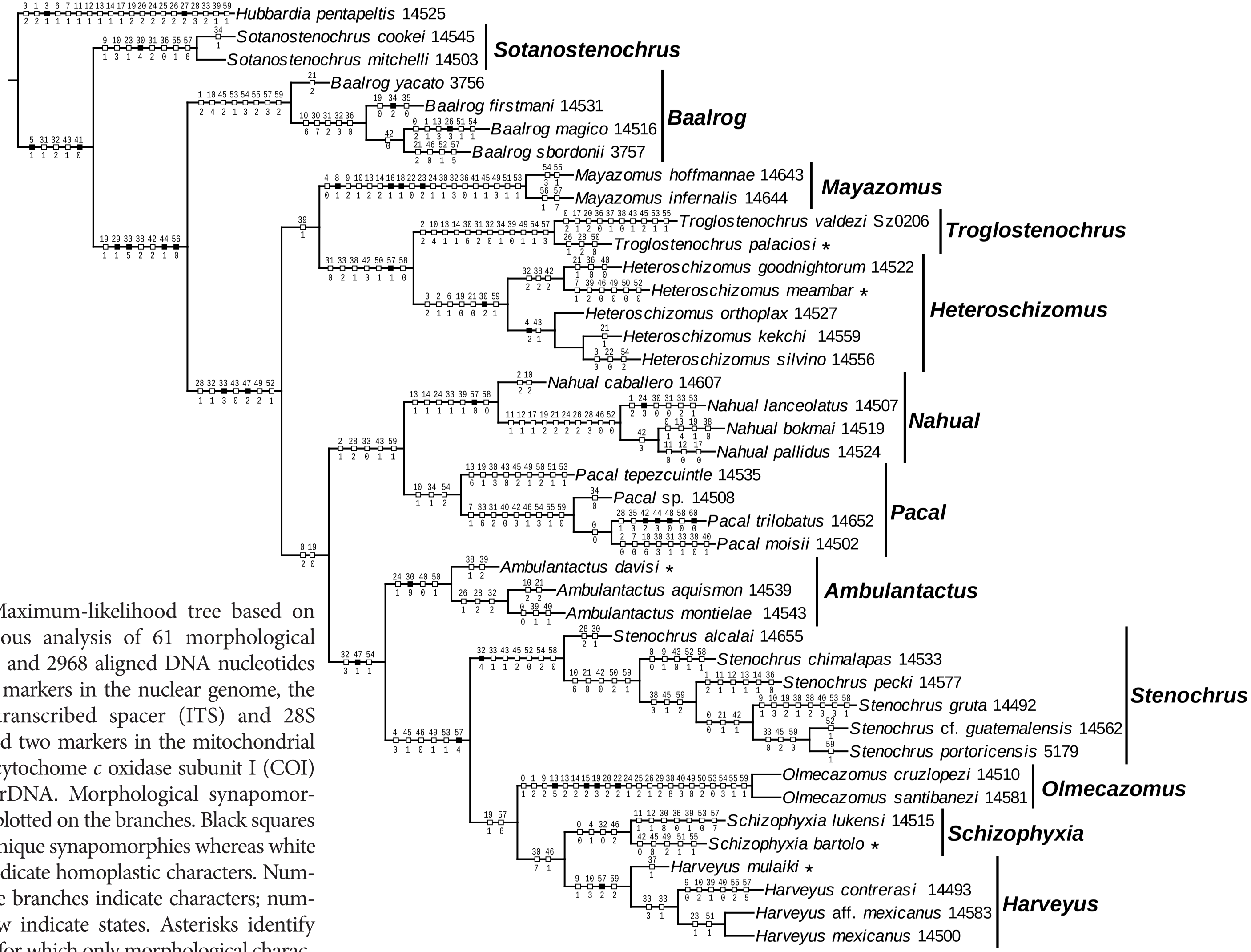

FIG. 6. Maximum-likelihood tree based on simultaneous analysis of 61 morphological characters and 2968 aligned DNA nucleotides from two markers in the nuclear genome, the internal transcribed spacer (ITS) and 28S rDNA, and two markers in the mitochondrial genome, cytochome *c* oxidase subunit I (COI) and 12S rDNA. Morphological synapomorphies are plotted on the branches. Black squares indicate unique synapomorphies whereas white squares indicate homoplastic characters. Numbers above branches indicate characters; numbers below indicate states. Asterisks identify terminals for which only morphological character data were available.

and Maddison, 1987), as appropriate (appendix 1). A more detailed explanation of the molecular and combined phylogenetic analyses will be presented elsewhere (Monjaraz-Ruedas et al., in prep.)

SYSTEMATICS

Key to Identification of the North American Genera of Hubbardiidae (Schizomida)

1. Cheliceral fixed finger with two teeth between two primary teeth, serrula composed of blunt teeth; pedipalp trochanter without prolateral spur; tarsal spurs symmetric; pygidial flagellum cylindrical, not dorsoventrally compressed (♂), with five flagellomeres (♀); spermathecae (♀) with one pair of lobes and without chitinized arch……. ……………Protoschizomidae Rowland, 1975

– Cheliceral fixed finger with three or more teeth between two primary teeth, serrula composed of several hyaline teeth (fig. 12); pedipalp trochanter with prolateral spur; tarsal spurs asymmetric; pygidial flagellum dorsoventrally compressed or globose (♂), with three or four flagellomeres (♀); spermathecae (♀) with two or more pairs of lobes and chitinized arch (figs. 8, 9)…………. ………………2 (Hubbardiidae Cook, 1899)

2. Pedipalp femur, prolateral surface with four setae (*Fvr*); opisthosomal segment XII (♂) with conspicuous posterodorsal process; spermathecae (♀) with more than three pairs of extremely short, broad, and rounded lobes, clustered in groups…………. ……………………………*Hubbardia* Cook, 1899

– Pedipalp femur, prolateral surface with three setae (*Fvr*); opisthosomal segment XII (♂) with or without inconspicuous posterodorsal process; spermathecae (♀) usually with two or four pairs of long, filiform lobes, not clustered in groups (figs. 8–10)………………3

3. Opisthosomal segment II with four setae; pedipalp femur (♂), setae Fv_1 and Fv_2 forming spiniform setiferous tubercles; prolateral tarsal spur (♂) present; pygidial flagellum (♀) with four flagellomeres……………. *Mayazomus* Reddell and Cokendolpher, 1995

– Opisthosomal segment II with two setae; pedipalp femur (♂), setae Fv_1 and Fv_2 acuminate, setiform or spiniform; prolateral tarsal spur (♂) absent; pygidial flagellum (♀) with three flagellomeres………………4

4. Cheliceral movable finger with lamella or teeth (fig. 12B, C)……………………………………5

– Cheliceral movable finger smooth (fig. 12A)…….8

5. Opisthosomal segment XII with small, inconspicuous posterodorsal process (♂); pygidial flagellum (♂) usually globose; spermathecae (♀), lateral lobes greatly reduced (usually absent) compared to median lobes, and usually with apical bulbs…………………………………………… *Pacal* Reddell and Cokendolpher, 1995

– Opisthosomal segment XII without posterodorsal process (♂); pygidial flagellum (♂) dorsoventrally compressed; spermathecae (♀), lateral and median lobes subequal, without apical bulbs…………………………6

6. Opisthosomal segments VIII–XI (♂) elongated (fig. 18C); pygidial flagellum (♂) elongated with posterior constriction in dorsal view (fig. 19D–F); spermathecae (♀), chitinized arch mug shaped (fig. 8E, F)………. *Heteroschizomus* Rowland, 1973, stat. rev.

– Opisthosomal segments VIII–XI (♂) not elongated (fig. 15); pygidial flagellum (♂) elliptical or trilobed (figs. 19G–I, 23G–I); spermathecae (♀), chitinized arch wih lateral tips projected and acute (fig. 9A, B, F)………….7

7. Cheliceral movable finger with lamella (fig. 12C); pedipalp patella with five *Pm* setae, tibia setal formula 5-5-6 (fig. 14C); pygidial flagellum (♂) with pair of dorsosubmedian circular depressions, without projections (fig. 19G–I); spermathecae (♀), lateral and median lobes equal, with several apical sclerotizations in both pairs of lobes, creating appearence of leafy tree (fig. 9A, B) ………………………………….*Nahual*, gen. nov.

– Cheliceral movable finger serrate, comprising several small teeth (fig. 13I); pedipalp patella with four *Pm* setae, tibia setal formula 3-3-4 (fig. 14D); pygidial flagellum (♂) without depressions and with pair of dorsosubmedian projections (fig. 23G–I); spermathecae (♀), lateral lobes reduced to approximately 3/4 the length of median lobes, without apical sclerotizations in both pairs of lobes (fig. 9F)..*Troglostenochrus*, gen. nov.

8. Propeltidium with three pairs of dorsal setae (fig. 11A)..9

– Propeltidium with two pairs of dorsal setae (fig. 11B)..11

9. Pedipalp tibia with prominent lateral spur; spermathecae (♀) with four asymmetric pairs of hand-shaped lobes; pygidial flagellum (♂) globose, with medial depression.................................*Sotanostenochrus* Reddell and Cokendolpher, 1991

– Pedipalp tibia without lateral spur; pygidial flagellum (♂) deltoid/spear shaped (figs. 16D–F, 19A–C), with paired submedian depressions; spermathecae (♀) with two pairs of filiform lobes.........................10

10. Pedipalp tibia, setal formula 3-3-5 (fig. 14B); pygidial flagellum (♂) bulbous/spear shaped, with paired submedian depressions not fused posteriorly (fig. 19A–C); spermathecae (♀), median lobes parenthesis shaped, apex laterally directed, median and lateral lobe bases aligned, chitinized arch U-shaped (fig. 9C)...*Schizophyxia*, gen. nov.

– Pedipalp tibia, setal formula 4-3-5 (fig. 14A); pygidial flagellum (♂) deltoid (fig. 16A–F), with paired posterior depressions fused posteriorly; spermathecae (♀), median lobes straight, apex vertically directed, median lobe bases posterior to lateral lobe bases, chitinized arch inverse arch shaped (fig. 8A)..............*Ambulantactus*, gen. nov.

11. Pedipalps (♂) robust; pedipalp femur (♂), setae Fv_1 and Fv_2 forming spiniform setiferous tubercles, Fe_1, Fe_5, Ter_7 and Tir_5 spiniform; pygidial flagellum (♂) elliptical to lanceolate, with pair of dorsosubmedian depressions fused posteriorly; spermathecae (♀), lateral lobes swollen, drop shaped..................................*Olmecazomus*, nom. nov.

– Pedipalps (♂) homeomorphic; pedipalp femur (♂), setae Fe_1, Fe_5, Fv_1, Fv_2, Ter_7 and Tir_5 acuminate, setiform; pygidial flagellum (♂) ovate, subrhomboidal, or bulbous (figs. 16G–I, 23D–F), with pair of dorsosubmedian pits or depressions not fused posteriorly; spermathecae (♀), lateral lobes slender, filiform (figs. 8B, D).......................12

12. Pedipalp trochanter, apical process with bump (fig. 7C, H); pygidial flagellum (♂) subrhomboidal, and acuminate or lanceolate posteriorly (fig. 19A–C), with pair of shallow dorsosubmedian pits; spermathecae (♀), lateral lobes at least 2/3 the length of, or longer than, median lobes, and with apical bulbs (fig. 8C, D)..*Harveyus*, gen. nov.

– Pedipalp trochanter, apical process acute or absent (fig. 7B); pygidial flagellum (♂) elliptical, cordate or bulbose, and not acuminate or lanceolate posteriorly (fig. 23D–F), with pair of deep dorsosubmedian pits or without dorsal depressions; spermathecae (♀), lateral lobes at most half the length of median lobes, and without apical bulbs (figs. 8B, 9E)....................................13

13. Pygidial flagellum (♂) ovate or cordate, with pair of dorsosubmedian pits embedded in dorsomedian depression (fig. 20B); spermathecae (♀), median lobes similar width to lateral lobes (fig. 10C), curved laterally (J-shaped or parenthesis shaped) and sclerotized apically, median lobe bases posterior to lateral lobe bases (figs. 9E, 10C)..............................*Stenochrus* Chamberlin, 1922

– Pygidial flagellum (♂) bulbous, without dorsal depressions or pits (fig. 16G–I); spermathecae (♀), median lobes broader than lateral lobes, slightly curved laterally and apically, and unsclerotized apically (fig. 8B), median and lateral lobe bases aligned (fig. 10A) ....*Baalrog*, gen. nov.

Family Hubbardiidae Cook, 1899

Subfamily Hubbardiinae Cook, 1899

Ambulantactus, gen. nov.

Figures 1, 6, 7A, B, 8A, 10D, 12C, 13A, B, 14C, 15A–C, 16A–F, 17A–C; tables 1, 2, 5

Type Species: *Ambulantactus montielae*, sp. nov., type species, here designated.

Diagnosis: *Ambulantactus*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae (fig. 11A); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Cheliceral movable finger smooth; single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (fig. 13A, B). Pedipalps homeomorphic; trochanter with mesal spur, apical process small and acute (fig. 7A, B); femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with three acuminate *Pe* setae and five feathered *Pm* setae; tibia setal formula 4-3-5 (*Ter-Tmr-Tir*) (fig. 14A). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, deltoid, with pair of posterodorsal depressions, fused posteriorly (fig. 16A–F); flagellum (♀) with two annuli (fig. 17A–C). Spermathecae (♀) with two pairs of lobes; lateral lobes slightly smaller than (ca. 3/4 the length) but similar in width to median lobes; both pairs of lobes linear, with apex directed vertically, unsclerotized apically (figs. 8A, 10D), and without bulbs; median lobe bases posterior to lateral lobe bases (fig. 10D), with duct openings; chitinized arch inverse arch shaped, without anterior branch, with lateral tips tapering; gonopod wide and short.

Comparisons: Species of *Ambulantactus*, gen. nov., are most similar morphologically to species of *Schizophyxia*, gen. nov. Both genera possess a pair of posterodorsal depressions on the male pygidial flagellum, and the lobes of female spermathecae are of similar length. The two genera differ in the shape of the male flagellum, which is deltoid in *Ambulantactus*, but spear shaped in *Schizophyxia*. Additionally, the chitinized arch of the female spermathecae is inverse arch shaped in *Ambulantactus*, but U-shaped in *Schizophyxia*. Finally, the pedipalp tibia setal formula is 4-3-5 in *Ambulantactus* and 3-3-4 in *Schizophyxia*.

Species of *Ambulantactus* resemble species of *Heteroschizomus*, stat. rev., and *Nahual*, gen. nov., in the linear median and lateral lobes of the female spermathecae. However, the lobes are considerably larger in *Ambulantactus* than in the other genera. Furthermore, the lobes are smooth in *Ambulantactus* but apically sclerotized in *Nahual*, and cylindrical in *Ambulantactus* but conical in *Heteroschizomus*.

Species of *Ambulantactus* also resemble species of *Olmecazomus*, nom. nov., especially *Olmecazomus brujo*, comb. nov., in the shape of the female spermathecae, and the posterior depressions of the male flagellum. However, *Ambulantactus* are considerably smaller than *Olmecazomus* and pedipalp setae Fv_1 and Fv_2 are acuminate setiform in *Ambulantactus*, but form spiniform setiferous tubercles in *Olmecazomus*.

Etymology: The genus name is a compound word derived from the Latin words *ambulans*, meaning "walking," and *tactus*, meaning "touch," and refers to the distinctive walking gait of schizomids. It is neuter in gender.

Included Species: *Ambulantactus aquismon*, sp. nov.; *Ambulantactus davisi* (Gertsch, 1940), comb. nov.; *Ambulantactus montielae*, sp. nov.

Distribution: The known species of *Ambulantactus*, gen. nov., are endemic to Mexico, where they display a disjunct distribution across three states (fig. 1). *Ambulantactus montielae*, sp. nov., occurs in Morelos, *A. aquismon*, sp. nov., in San Luis Potosí, and *A. davisi*, comb. nov., in Tamaulipas. This distribution resembles the distributions of some taxa in family Protoschizomidae, with species occurring in the north and south of Mexico, on either side of the Mexican Transvolcanic Belt. *Ambulantactus* is probably distributed along the entire length of the Sierra Madre Oriental.

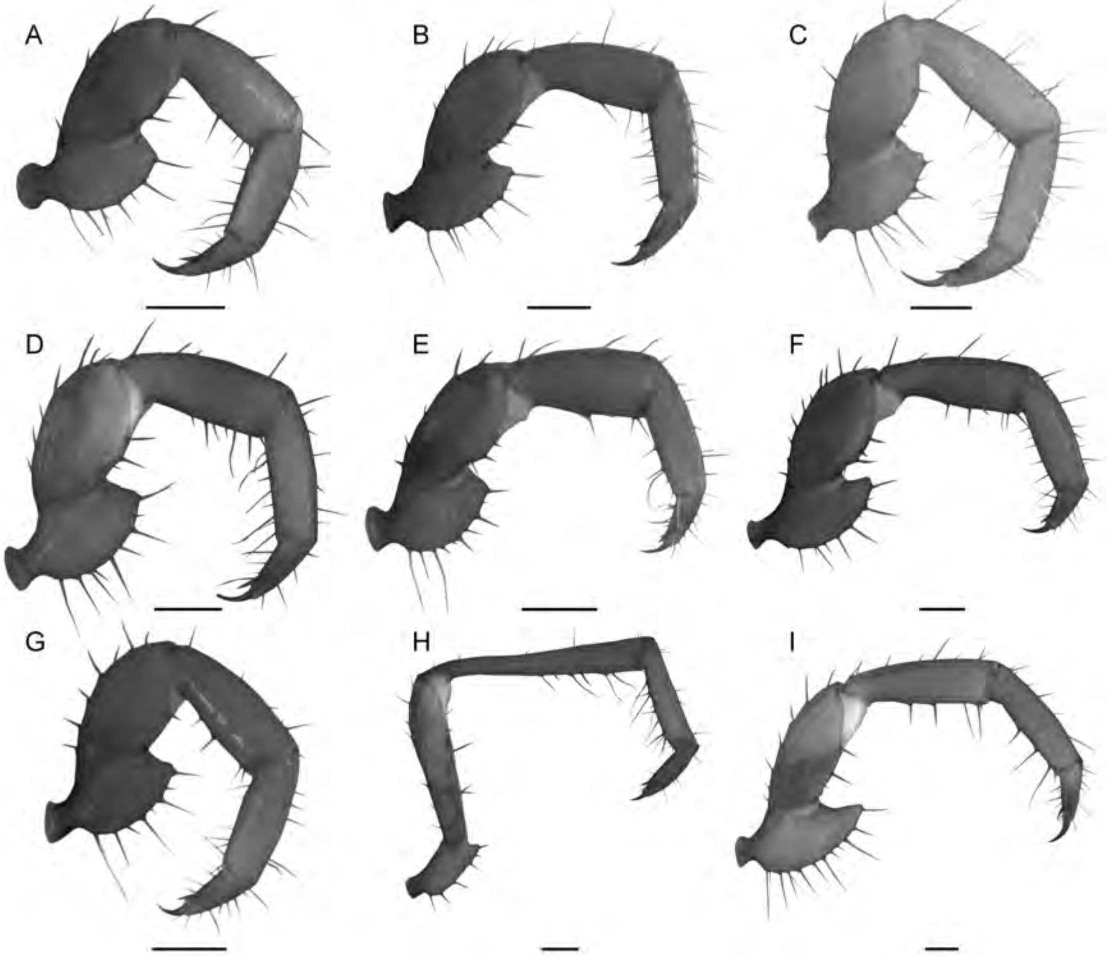

FIG. 7. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pedipalps, retrolateral view. **A.** *Ambulantactus aquismon*, sp. nov., ♂ (CNAN T1294). **B.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291). **C.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163). **D.** *Harveyus contrerasi*, sp. nov., ♂ (CNAN T1276). **E.** *Heteroschizomus kekchi*, sp. nov., ♂ (CNAN T1280). **F.** *Nahual bokmai*, sp. nov., ♂ (CNAN T1282). **G.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♂ (CNAN Sz25). **H.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018, ♂ (CNAN T1155). **I.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov., ♂ (CNAN T698). Scale bars = 0.2 mm.

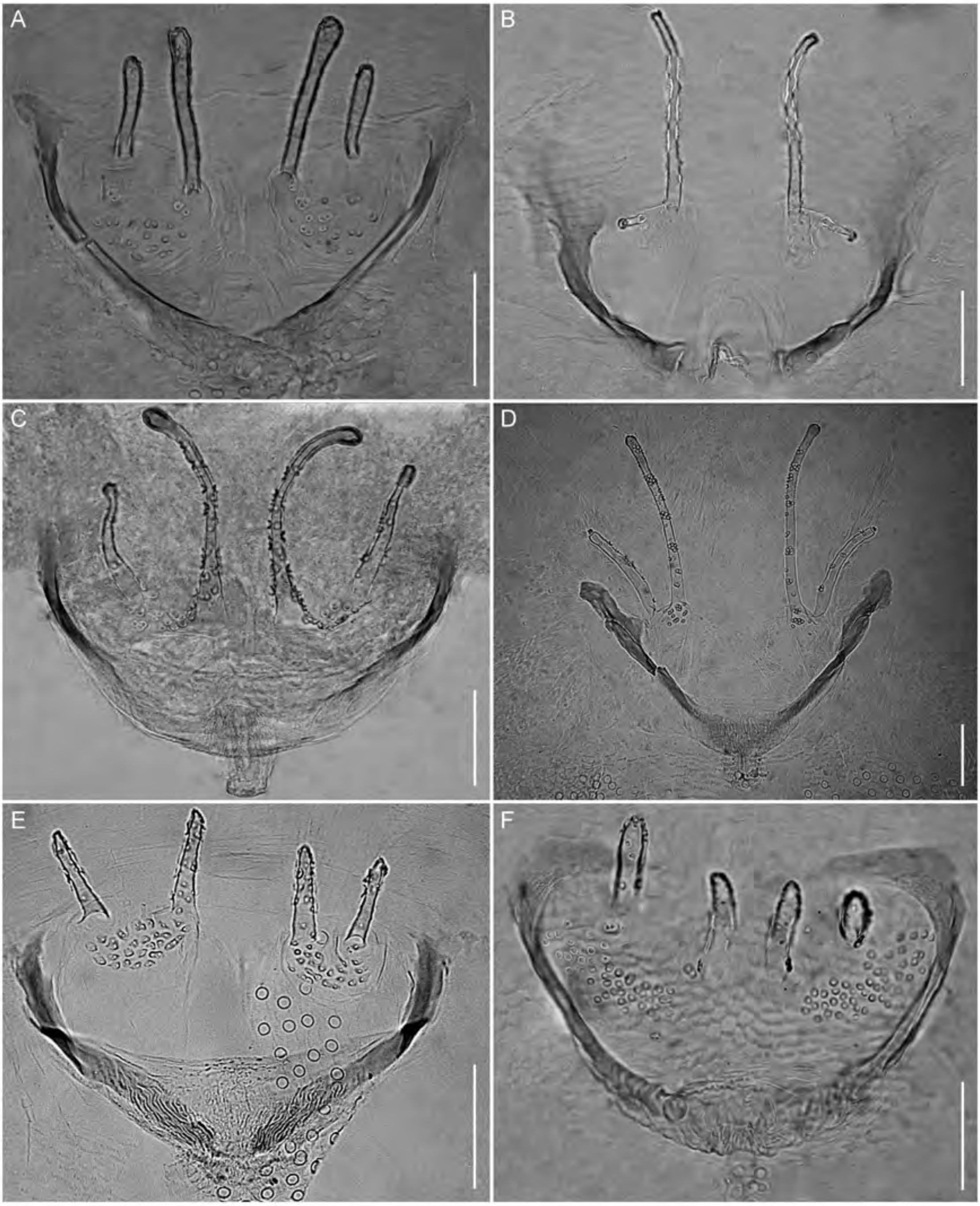

FIG. 8. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), female spermathecae, dorsal view. **A.** *Ambulantactus montielae*, sp. nov., ♀ (CNAN T1292). **B.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♀ (CNAN T1165). **C.** *Harveyus contrerasi*, sp. nov., ♂ (CNAN T1278). **D.** *Harveyus mexicanus* (Rowland, 1971), comb. nov., ♀ (CNAN Sz131). **E.** *Heteroschizomus goodnightorum* Rowland, 1973, ♀ (CNAN Sz171). **F.** *Heteroschizomus kekchi*, sp. nov., ♀ (CNAN T1281). Scale bars = 0.05 mm.

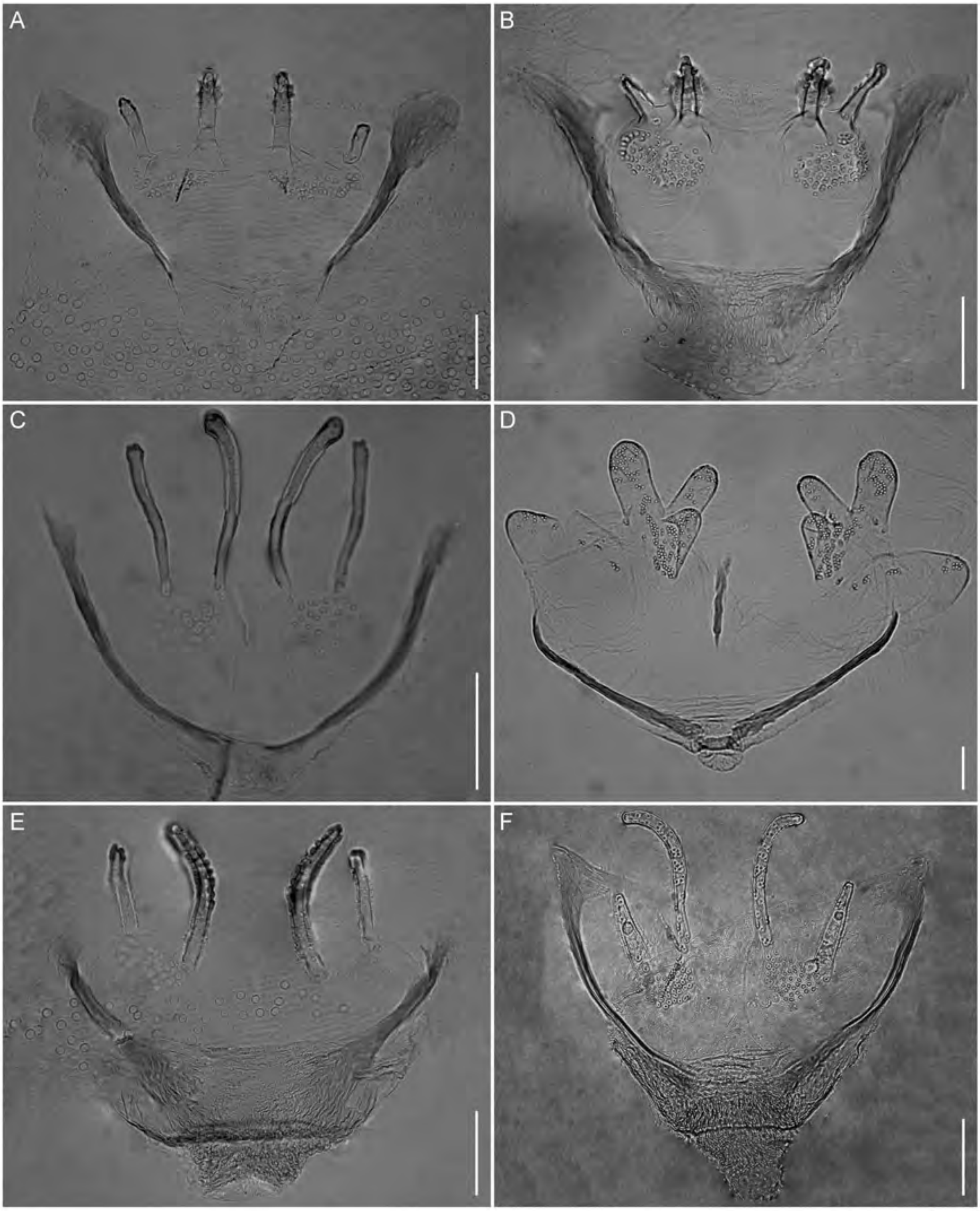

FIG. 9. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), female spermathecae, dorsal view. **A.** *Nahual bokmai*, sp. nov., ♀ (CNAN T1283). **B.** *Nahual lanceolatus* (Rowland, 1975), comb. nov., ♀ (CNAN Sz130). **C.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♀ (CNAN Sz25). **D.** *Sotanostenochrus mitchelli* (Rowland, 1971), ♀ (CNAN Sz143). **E.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018, ♀ (CNAN T1156). **F.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov., ♀ (CNAN T699). Scale bars = 0.05 mm.

Natural History: The species of *Ambulantactus*, gen. nov., are epigean, occurring under rocks in rainforest and tropical dry forest.

Remarks: Species of *Ambulantactus*, gen. nov., closely resemble some species of *Schizophyxia*, gen. nov., in the general shape of the female spermathecae. *Ambulantactus montielae*, sp. nov., was designated as the type species of the genus because it is the only species in which the female is known. Despite the absence of females of *A. aquismon*, sp. nov., and *A. davisi*, comb. nov., and the absence of molecular data for *A. davisi*, the two species grouped with *A. montielae* in the simultaneous analysis (fig. 6).

Ambulantactus aquismon, sp. nov.

Figures 1, 6, 7B, 13A, 15A, 16A–C; tables 1, 5

Type Material: **MEXICO:** *San Luis Potosí*: Municipio de Aquismón: outside Cueva del Espiritu Santo Mantetzulel, 21°37′36″N 99°03′42″W, 461 m, 13.ii.2010, G. Contreras, J. Cruz, O. Francke, C. Santibañez, and A. Valdez, holotype ♂ (CNAN T1294).

Diagnosis: *Ambulantactus aquismon*, sp. nov., may be distinguished from other species of the genus by the male pygidial flagellum, which is deltoid with an acute posterior margin, and a pair of posterodorsal depressions fused posteriorly into a triangular shape. *Ambulantactus aquismon* is closely related and morphologically similar to *A. montielae*, sp. nov., but the male pygidial flagellum is more elongated and less bulbous than in *A. montielae*. Additionally, *A. aquismon* is smaller (3.6 mm) than *A. montielae* (4.7 mm); the apical process of the male pedipalp trochanter is obtuse in *A. aquismon* but acute in *A. montielae*; and the pedipalp patella bears four *Pe* setae in *A. aquismon* and five in *A. montielae.*

Etymology: The specific name is a noun in apposition taken from the name of the municipality in which the type locality is situated.

Description: The following description is based on the holotype male (fig. 15A).

Color: Pale brownish.

Prosoma: Propeltidium with two setae on anterior process; three pairs of dorsal setae; ocular spots distinct. Metapeltidium 0.40 mm long, 0.59 mm wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae: Movable finger serrula with 19 teeth, guard tooth present (fig. 13A). Fixed finger with three smaller teeth between two primary teeth; setal group formula, 3-6-4-2-7-10-1-6; G1 with three spatulate setae, covered with small blunt spicules; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally; G4 consisting of two small, smooth, thick setae, elongated apically; G5A with seven setae, subequal, feathered apically and longer than fixed finger; G5B with eight feathered setae increasing in size apically; G6 with one smooth seta, ca. half the length of movable finger; G7 with six slender, feathered setae, subequal.

Pedipalps: Pedipalps homeomorphic (fig. 7A); 1.77× longer than propeltidium. Trochanter without apical process; prolateral surface with small apical spur. Femur 1.93× longer than high; retroventral margin with Fe_1, Fe_5, Fev_1, and Fev_2 setae acuminate; prolateral surface with row of three ventral acuminate setae (Fmv_{1-3}) and two dorsal acuminate setae (Fmd_2, Fmd_3). Patella with three acuminate *Pe* setae and four feathered *Pm* setae; without distinctive armature. Tibia setal formula, 4:3:5; *Ter* setae acuminate, *Tmr* and *Tir* setae feathered. Tarsal spurs asymmetric.

Legs: Leg I basitarsal/telotarsal proportions, 25:5:6:5:-:-:- (broken); IV, femur (missing).

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair of *Dm* setae; II with three pairs of microsetae anteriorly plus pair of *Dm* setae; III–VII each with pair of *Dm* setae; VIII with pairs of *Dm* and Dl_2 setae; IX with pairs of Dl_1 and Dl_2 setae and without pair of *Dm* setae. Segments X and XI telescoped, slightly elongated, with pairs of Dl_2,

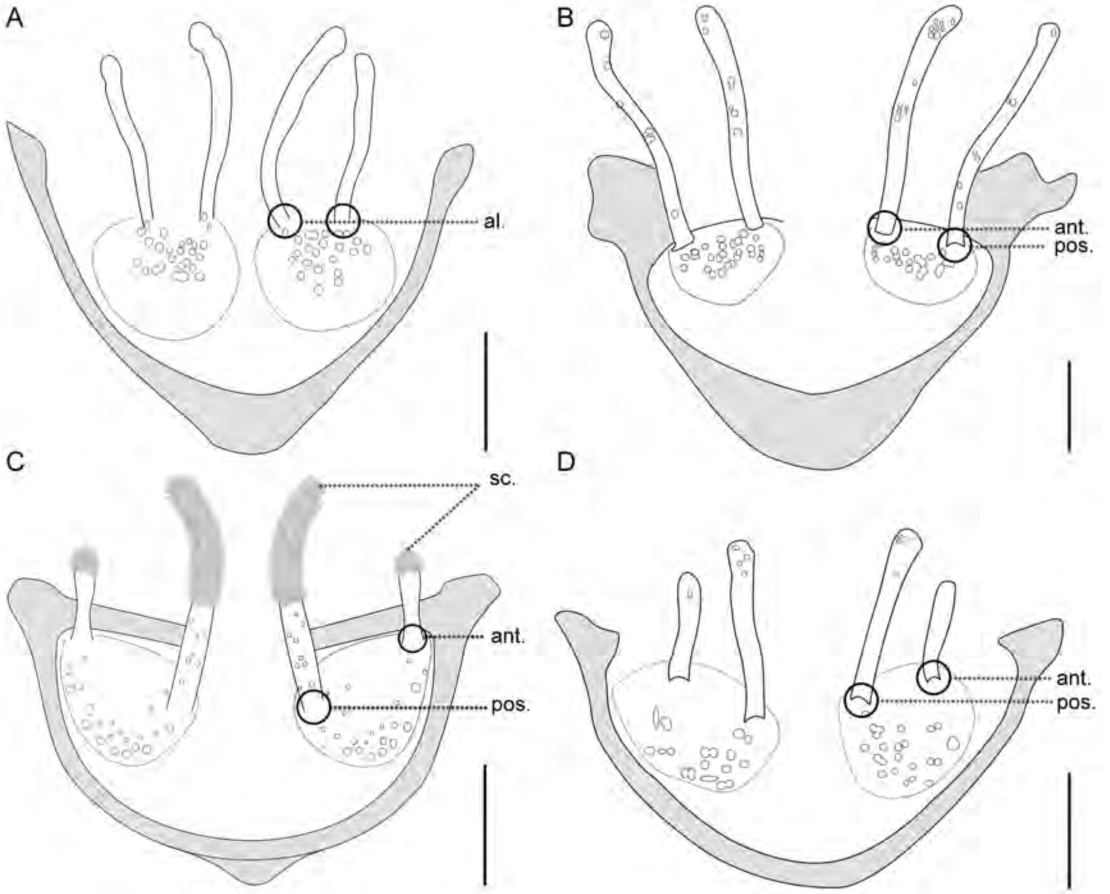

FIG. 10. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), female spermathecae, schematic illustration of lobe base positions. **A.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♀ (CNAN Sz25), aligned. **B.** *Nahual caballero* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♀ (CNAN T1158), anteromedian to lateral. **C.** *Stenochrus portoricensis* Chamberlin, 1922, ♀ (CNAN Sz93), posteromedian to lateral. **D.** *Ambulantactus montielae*, sp. nov., ♀ (CNAN T1292), posteromedian to lateral. Abbreviations: **al.,** aligned; **ant.,** anterior; **pos.,** posterior; **sc.,** sclerotizations. Scale bars = 0.05 mm.

Vm_2, Vl_1, and Vl_2 setae plus single Vm_1 seta; XII with pairs of Dm, Dl_1, Dl_2, Vm_1, Vm_2, Vl_1, and Vl_2 setae, without posterodorsal process. Sternites II–VII each with two irregular rows of setae; genital plate with scattered microsetae.

Pygidial flagellum: Flagellum dorsoventrally compressed, deltoid (fig. 16A–C), with posterior part acute; 1.77× longer than wide; pair of posterodorsal depressions fused posteriorly; seta Dm_1 situated over bulb base, Dm_4 situated posteriorly over depression, Dl_2 situated anterior to Vl_1, Dl_3 aligned with Vl_2, pair of Vm_2 setae present, Vm_1 seta aligned with Vm_2, pair of anterodorsal microsetae between Dm_1 and Dl_2, pair of anterolateral microsetae on flagellar pedicel, two patches of microsetae between Vl_1 and Vl_2 (*msp*).

DISTRIBUTION: *Ambulantactus aquismon*, sp. nov., is known only from the type locality in the state of San Luis Potosí, Mexico (fig. 1). It is codistributed in San Luis Potosí with species of

Harveyus, gen. nov., which are primarily cavernicolous. The few epigean species of *Harveyus* differ markedly from *A. aquismon* in the shape of the male flagellum (the spermathecae are unknown in this species).

Natural History: This epigean species was found under rocks in a primary rainforest near Cueva de Mantetzulel in Aquismón.

Additional Material Examined: **MEXICO:** *San Luis Potosí*: Municipio de Aquismón: Cueva del Espiritu Santo Mantetzulel, outside, 21°37′36″N 99°03′42″W, 461 m, 13.ii.2010, G. Contreras, J. Cruz, O. Francke, C. Santibañez, and A. Valdez, 1 imm. (AMCC [LP 14539]).

Ambulantactus davisi **(Gertsch, 1940)**, comb. nov.

Schizomus davisi Gertsch, 1940: 1–4, figs. 1–6; Takashima, 1951: 102; Rémy, 1961: 406; Rowland, 1971a: 117; 1973a: 21; 1973c: 135; Brignoli, 1974: 147, 149; Rowland, 1975b: 32, 166–169, 176–178, 181, 214–215, 218–219, 224–225, 228–229, 366–369, 394, map 5, figs. 157, 177, 211, 292; Rowland and Reddell, 1977: 83; 1979a: 162; 1980: 1, 2, 4, 5, 7–10, 13, 15, 20, figs. 1, 4, 24, 58; Reddell and Cokendolpher, 1995: 2, 4, 105.

Stenochrus davisi: Reddell and Cokendolpher, 1991: 18; 1995: 4, 18, 102, 105, 106; Vázquez-Rojas, 1995: 34; 1996: 65; Ruíz and Coronado, 2002: 67; Harvey, 2003: 123; Zawierucha et al., 2013: 359; Moreno-González et al., 2014: 21; Palacios-Vargas et al., 2015: 45; Monjaraz-Ruedas and Francke, 2018: 212.

Type Material: *Schizomus davisi*: **MEXICO:** *Tamaulipas*: Municipio de San Fernando, 28.iii.1937, L. Irby Davis, holotype ♂ (AMNH).

Remarks: The precise location of the type locality of *A. davisi*, comb. nov., is unclear and it is unknown whether the species is epigean or associated with a cave or riparian area like *Harveyus mulaiki* (Gertsch, 1940), comb. nov. Fresh material could not be collected for the present study.

Ambulantactus montielae, sp. nov.

Figures 1, 6, 7B, 8A, 10D, 12A, 13B, 14A, 15B, C, 16D–F, 17A–C; tables 1, 5

Type Material: **MEXICO:** *Morelos*: Municipio de Tepalcingo: REBIOSH, El Limón de Cuachichinola, 18°32′33″N 98°56′19″W, 1290 m, 30.vi.2014, M. Mendez-Acuña, E. Tinoco, and N. Ángel, holotype ♂ (CNAN T1291), 2.vi.2013, M. Mendez and M. Salas-Rod, paratype ♀ (CNAN T1292). Municipio de Tlalquiltenango: Quilamula, 18°29′38″N 99°00′14″W, 1229 m, 30.viii.2015, M. Mendez-Acuña and M. Salas, paratype ♂ (CNAN T1293).

Diagnosis: *Ambulantactus montielae*, sp. nov., may be distinguished from other species of the genus by the small, projected and acute apical process of the male pedipalp trochanter; the male pygidial flagellum, which is bulbous/deltoid with a pair of posterodorsal depressions fused posteriorly into a triangular shape; and the female spermathecae, in which both pairs of lobes are linear, the lateral pair slightly shorter than the median lobes (ca. 3/4), and the chitinized arch inverse arch shaped. *Ambulantactus montielae* differs from *A. aquismon*, sp. nov., in the larger size (4.7 mm vs. 3.6 mm); the projected apical process of the pedipalp trochanter; and the wider, more bulbous pygidial flagellum of the male, in which the posterior margin is short and obtuse.

Etymology: The specific epithet is a patronym, honoring Griselda Montiel Parra, Assistant Curator of CNAN, who collected the first samples of this species and encouraged her students to continue searching until adult males and females were collected.

Description: The following description is based on the holotype male and paratype female (fig. 15B, C).

Color: Pale brownish.

Prosoma: Propeltidium with two setae on anterior process; three pairs of dorsal setae; ocular spots indistinct. Metapeltidium 0.40 mm long, 0.70 mm wide. Anterior sternum with 11 setae, plus two sternophysial setae; posterior sternum with six setae.

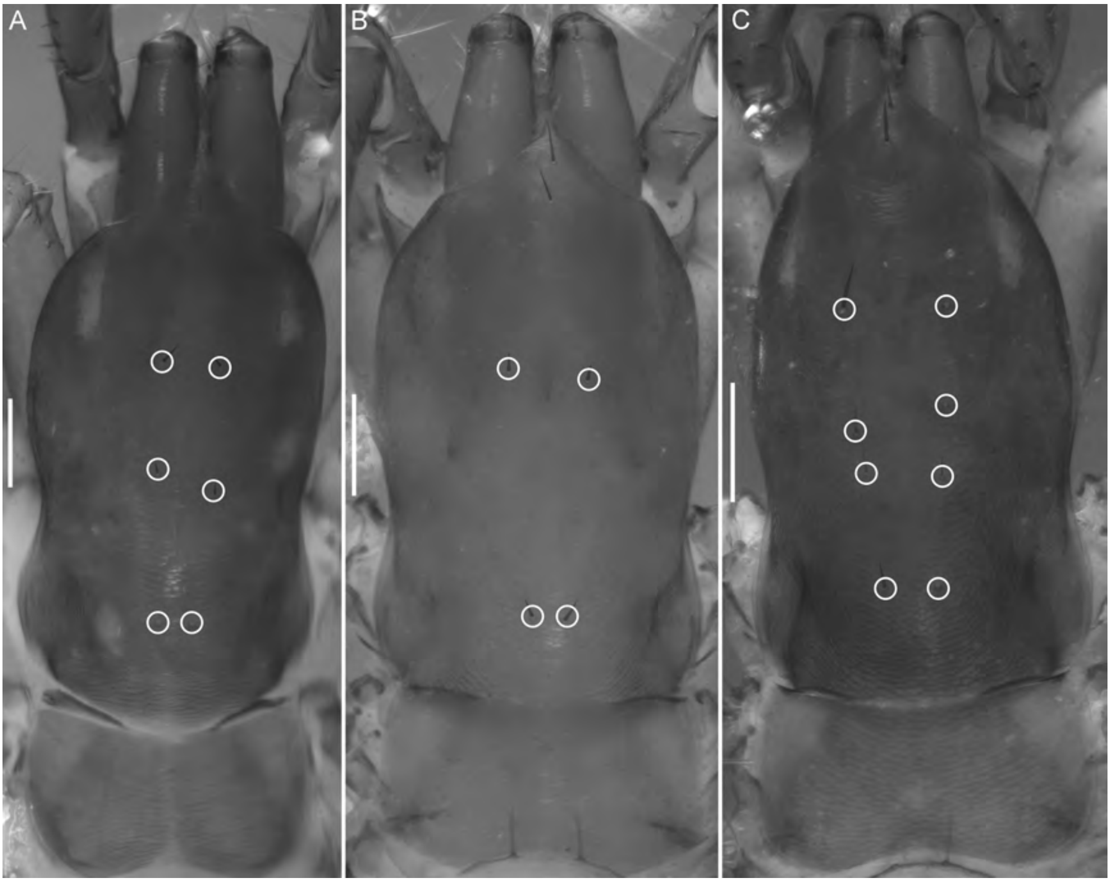

FIG. 11. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), propeltidia, dorsal view, illustrating dorsal setae. **A.** *Nahual bokmai*, sp. nov., ♂ (CNAN T1282). **B.** *Harveyus contrerasi*, sp. nov., ♂ (CNAN T1276). **C.** *Heteroschizomus kekchi*, sp. nov., ♂ (CNAN T1280). Scale bars = 0.2 mm.

Chelicerae: Movable finger serrula with 14 (♀) or 26 (♂) teeth, guard tooth present (fig. 13B). Fixed finger with three (♀) or four (♂) smaller teeth between two primary teeth; setal group formula, 3-6-4-2-10-8-1-6 (♂) or 3-6-4-2-7-10-1-6 (♀); G1 with three spatulate setae, covered with few small spicules; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally; G4 comprising two small, smooth, thick setae, elongated apically; G5A with 10 setae, subequal, feathered apically and longer than fixed finger; G5B with eight feathered setae increasing in size apically; G6 with one smooth seta, ca. 1/2 the length of movable finger; G7 with six slender, feathered setae, subequal.

Pedipalps: Pedipalps homeomorphic (figs. 7B, 15B); 1.62× (♂) or 1.52× (♀) longer than propeltidium. Trochanter apical process with small protuberance; prolateral surface with small medial spur. Femur 1.94× longer than high; retroventral margin with Fe_1, Fe_5, Fev_1, and Fev_2 setae acuminate; prolateral surface with row of three ventral acuminate setae ($Fmv_{1–3}$) and two dorsal acuminate setae (Fmd_2, Fmd_3). Patella with three acuminate *Pe* setae and five feathered *Pm* setae; without distinctive armature. Tibia setal formula, 4:3:5; *Ter* setae acuminate, *Tmr* and *Tir* setae feathered. Tarsal spurs asymmetric.

Legs: Leg I, basitarsal-telotarsal proportions, 30:4:5:5:6:7:13; IV, femur 4.4× longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair of *Dm* setae; tergite II with three pairs of microsetae anteriorly plus pair of *Dm* setae; III–VII each with one pair of *Dm* setae; VIII with pairs of *Dm* and Dl_2 setae; IX with pairs of Dl_1 and Dl_2 setae and without pair of *Dm* setae. Segments X and XI telescoped, slightly elongated, with pairs of Dl_2, Vm_2, Vl_1, and Vl_2 setae plus single Vm_1 seta; XII with pairs of *Dm*, Dl_1, Dl_2, Vm_1, Vm_2, Vl_1, and Vl_2 setae, without posterodorsal process. Sternites II–VII each with two irregular rows of setae; genital plate with scattered microsetae.

Pygidial flagellum: Flagellum (♂) dorsoventrally compressed, deltoid (fig. 16D–F); 1.75× longer than wide; pair of posterodorsal depressions fused posteriorly; seta Dm_1 situated over bulb base, Dm_4 situated posteriorly over depression, Dl_2 situated anterior to Vl_1, Dl_3 aligned with Vl_2, pair of Vm_2 setae present, Vm_1 situated posterior to Vm_2, pair of anterodorsal microsetae between Dm_1 and Dl_2, pair of anterolateral microsetae on flagellar pedicel, two patches of microsetae between Vl_1 and Vl_2 (*msp*). Flagellum (♀) with three flagellomeres (fig. 17A–C); seta Dl_2 not reduced, situated anterior to Vl_1, Dl_3 situated posterior to Vl_2, Vm_2 present, reduced, Vm_1 aligned with Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 8A); median and lateral lobes linear, similar in width, with few apical duct openings; lateral lobes shorter than median lobes (ca. 3/4); median lobe bases posterior to lateral lobe bases. Chitinized arch cup shaped; anterior branch absent; lateral tip lobed. Gonopod small, conical; length ca. 2× width.

Distribution: *Ambulantactus montielae*, sp. nov., is known only from the Reserva de la Biosfera Sierra Huautla, in the state of Morelos, Mexico (fig. 1).

Natural History: This species inhabits tropical dry forest in the Sierra Huautla, where it is often associated with small rivers. It has also been collected under rocks in the shadow of *Bursera* Jacq. ex L., 1762, plants.

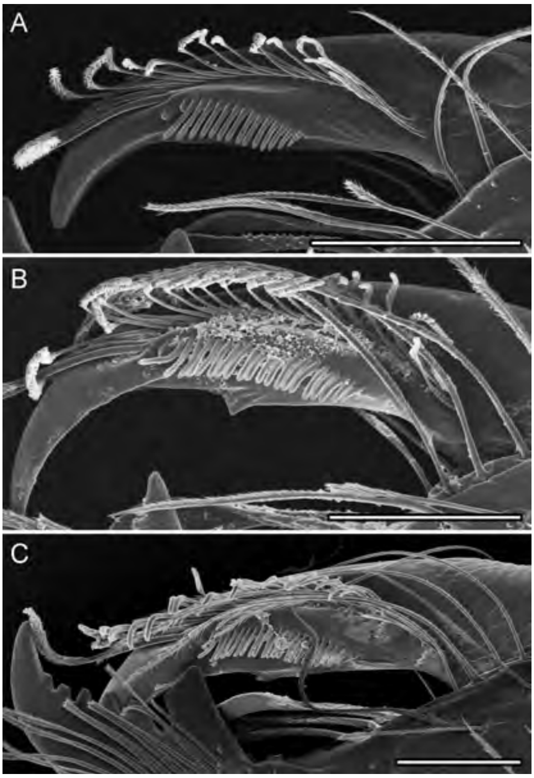

FIG. 12. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), cheliceral movable fingers, prolateral view, illustrating proventral ornamentation: **A.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291), smooth. **B.** *Nahual caballero* (Monjaraz-Ruedas and Francke, 2018) comb. nov., ♂ (CNAN T1157), one tooth. **C.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163), lamella. Scale bars = 100 µm.

Additional Material Examined: **MEXICO:** *Morelos*: Municipio de Tlalquiltenango: Quilamula, 18°29′38″N 99°00′14″W, 1229 m, 29.viii.2015, M. Mendez-Acuña, 1 imm. (CNAN Sz193), 30.viii.2015, M. Mendez-Acuña and M. Salas, 2 imm. (CNAN Sz194), 10.ix.2016, F. Pilo-Garcia, M. Mendez-Acuña, D. Rebollo-Salinas, and V. Garcia-Marquez, 2 subad. ♀, 4 imm. (CNAN Sz195), 3 imm. (AMCC [LP 14543]), 18.ix.2016, F. Pilo-Garcia, M. Mendez-Acuña, D. Rebollo-Salinas, and V. Garcia-Marquez, 10 imm. (CNAN Sz196).

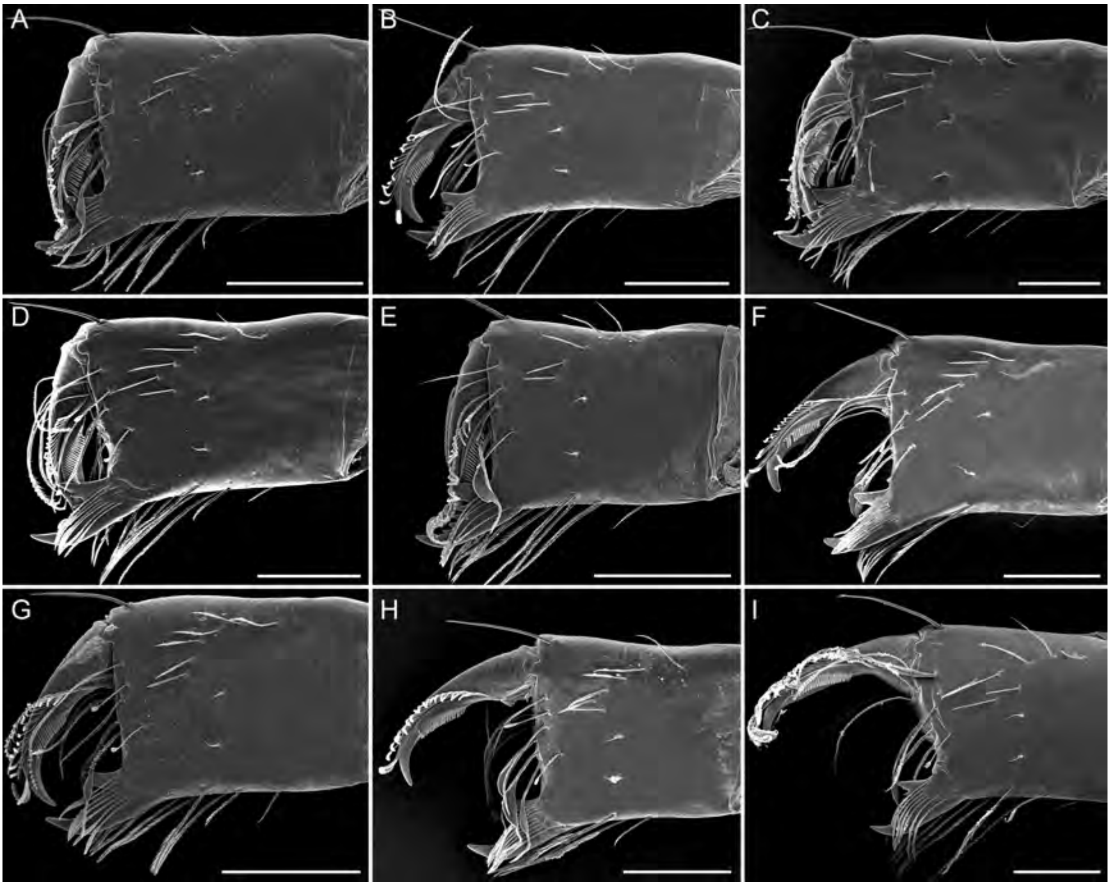

FIG. 13. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), chelicerae, prolateral view: **A.** *Ambulantactus aquismon*, sp. nov., ♂ (CNAN T1294). **B.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291). **C.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163). **D.** *Harveyus contrerasi*, sp. nov., ♂ (CNAN T1276). **E.** *Heteroschizomus kekchi*, sp. nov., ♂ (CNAN T1280). **F.** *Nahual bokmai*, sp. nov., ♂ (CNAN T1282). **G.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♂ (CNAN Sz25). **H.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018, ♂ (CNAN T1155). **I.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov., ♂ (CNAN T698). Scale bars = 200 µm.

Baalrog, gen. nov.

Figures 2, 6, 7C, 8B, 12C, 13C, 14B, 15D, E, 16G–I, 17D–F; tables 1, 2

Stenochrus (part): Reddell and Cokendolpher, 1991: 1, 3.

Schizomus pecki group (part): Rowland 1975b: 37, 39, 135, 137, 167, 168, 188, 209, 232, 233, 236, 238, 241, 246, 248, 250, 252, 255, 320, 321, 348–350, 376, 390, 396, 397; Rowland and Reddell, 1979a: 165, 171; 1979b: 90, 107; 1980: 1, 3, 22–26, 28, 29, 31; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20; Cokendolpher and Reddell, 1984b: 242; Reddell and Cokendolpher, 1986: 34, 37; Camilo and Cokendolpher, 1988: 53; Reddell and Cokendolpher, 1991: 1, 3; 1995: 101–103; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781, 783; 2018: 189, 212.

Type Species: *Schizomus firstmani* Rowland, 1973 [= *Baalrog firstmani* (Rowland, 1973), comb. nov.], type species, here designated.

Diagnosis: *Baalrog*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger smooth (fig. 12A); single guard tooth at end of serrula; setal group G3 with G3-4 setae situated posteriorly (except in *B. magico*, comb. nov.) (fig. 13C). Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae (fig. 11A); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with mesal spur, without apical process (fig. 7C); femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with four acuminate *Pe* setae and four or five feathered *Pm* setae; tibial setal formula 3-3-5 (*Ter-Tmr-Tir*) (fig. 14B). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) bulbose, without dorsal depressions (fig. 16G–I); flagellum (♀) with two annuli (fig. 17D–F). Spermathecae (♀) with two pairs of lobes; lateral lobes linear, smaller than (ca. 1/4 to 1/3 the length) and considerably narrower than median lobes, mostly unsclerotized apically; median lobes slightly curved apically (ca. 60° to 70° angle), with apex directed laterally, inverse J-shaped, unsclerotized apically (fig. 8B) and without bulbs; median lobe bases anterior to lateral lobe bases (fig. 10B), with duct openings; chitinized arch hastate, without anterior branch, with lateral tips long and diffuse; gonopod wide and short.

Comparisons: Species of *Baalrog*, gen. nov., resemble species of *Stenochrus* in the general shape of the female spermathecae. However, the lateral lobes of the spermathecae are narrower than the median lobes, the median lobes are curved apically and unsclerotized, and the median lobe bases situated anterior to the lateral lobe bases in *Baalrog*, whereas the lateral lobes are the same width as the median lobes, the median lobes curved along their entire length and apically sclerotized, and the median lobe bases situated posterior to the lateral lobe bases in *Stenochrus*. Additionally, the male pygidial flagellum is bulbous in *Baalrog*, but dorsoventrally compressed and cordate to elliptical in *Stenochrus*. Finally, the pedipalp patella and tibia are more setose, with 5 *Pm*, 4 *Pe*, and 5 *Tir* setae, in *Baalrog*, than in *Stenochrus*, with 3 *Pm*, 3 *Pe*, and 4 *Tir* setae.

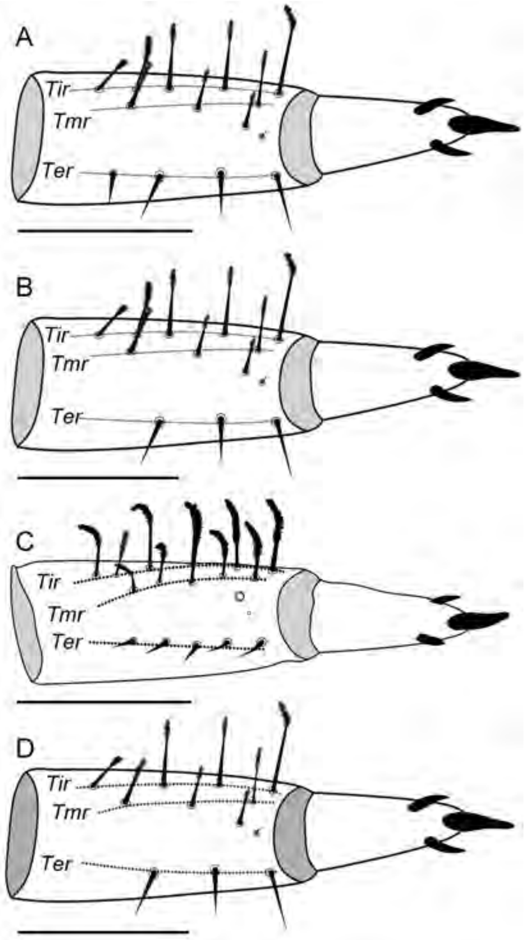

FIG. 14. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pedipalp tibiae, ventral view, illustrating setal patterns: **A.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291), 4-3-5. **B.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163), 3-3-5. **C.** *Nahual lanceolatus* (Rowland, 1975), comb. nov. ♂ (CNAN Sz130), 5-5-6. **D.** *Stenochrus pecki* (Rowland, 1973), ♂ (CNAN Sz40), 3-3-4. Scale bars = 0.2 mm.

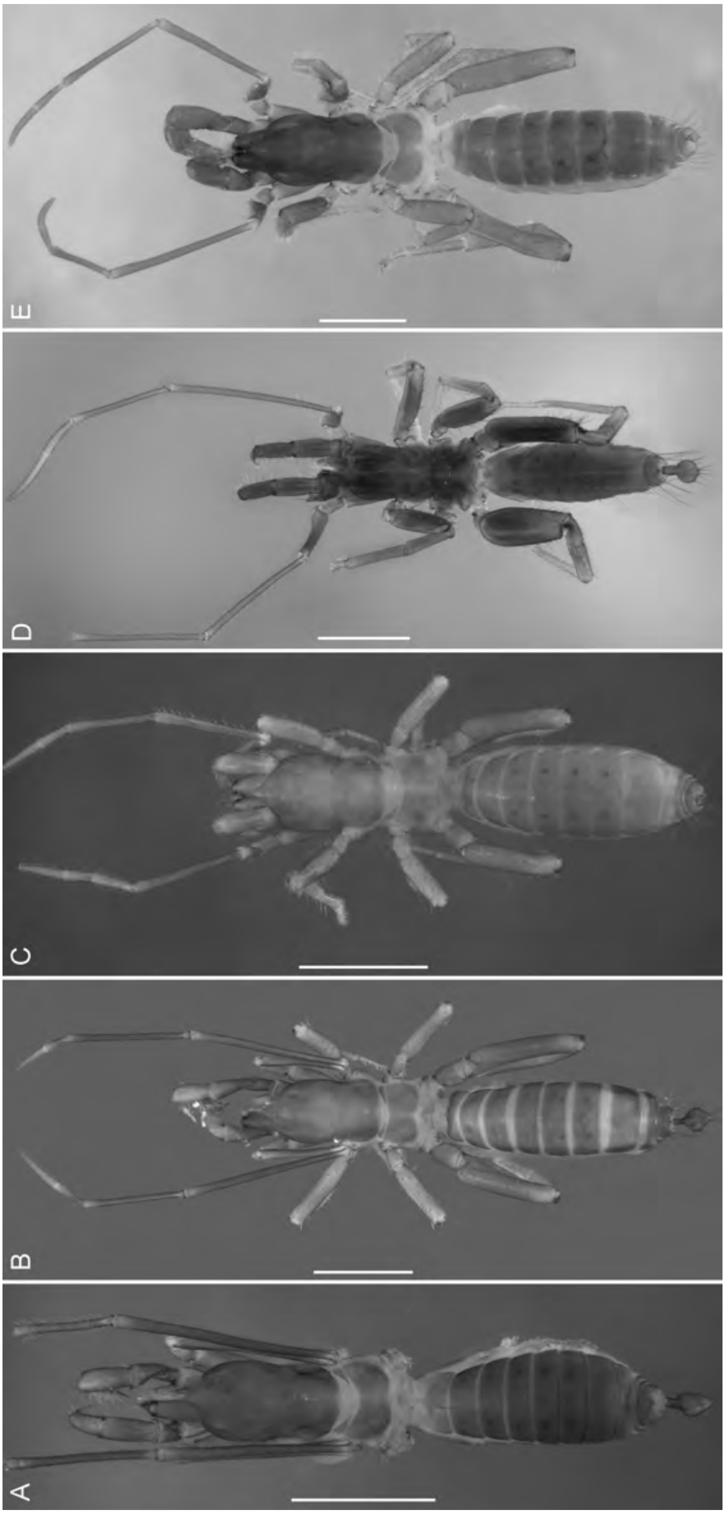

FIG. 15. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), habitus, dorsal view. **A.** *Ambulantactus aquismon*, sp. nov., ♂ (CNAN T1294). **B, C.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291) (**B**), ♀ (CNAN T1292) (**C**). **D, E.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163) (**D**), ♀ paratype (CNAN T1165) (**E**). Scale bars = 1 mm.

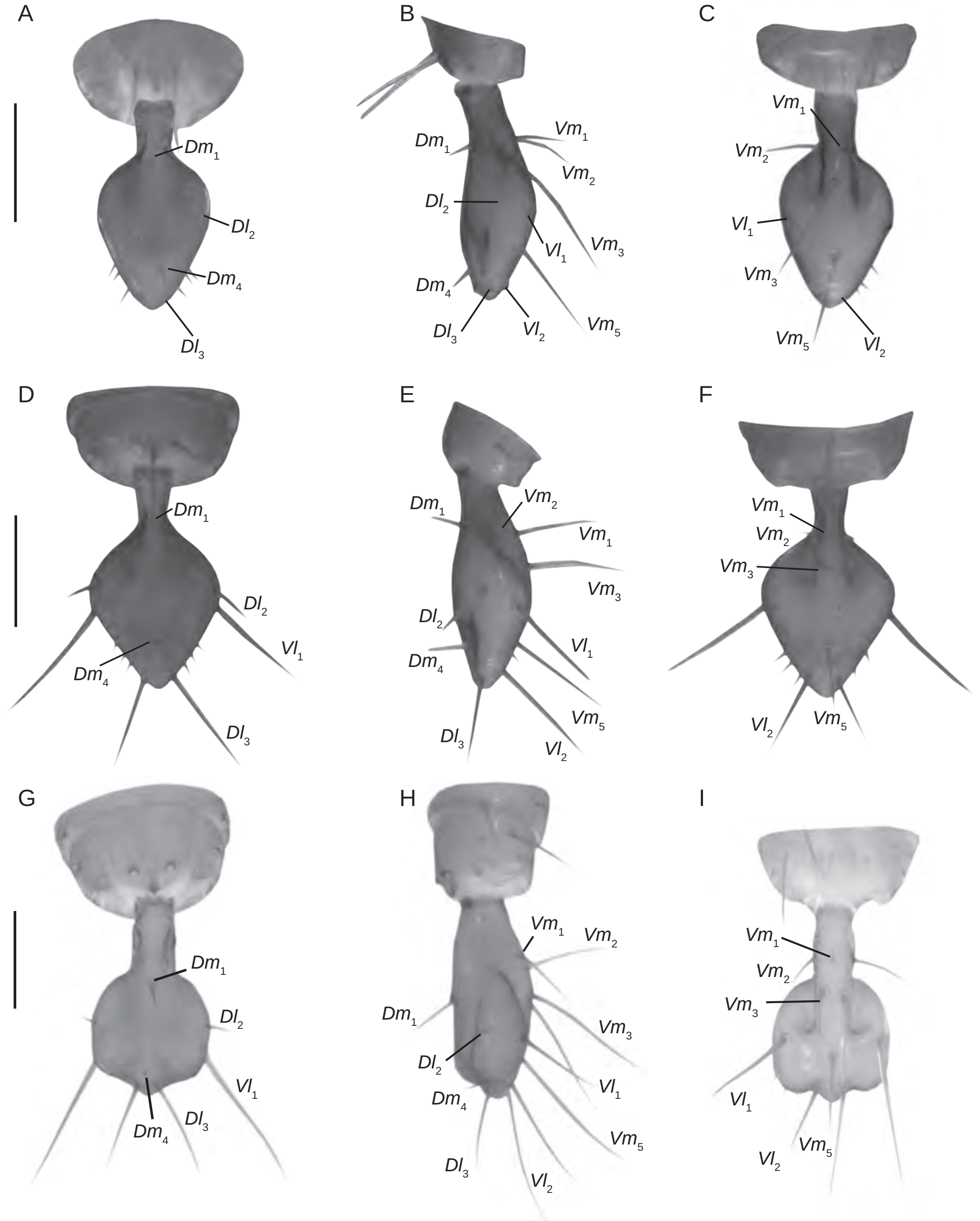

FIG. 16. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G**), lateral (**B, E, H**) and ventral (**C, F, I**) views. **A–C.** *Ambulantactus aquismon*, sp. nov., ♂ (CNAN T1294). **D–F.** *Ambulantactus montielae*, sp. nov., ♂ (CNAN T1291). **G–I.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♂ (CNAN T1163). Scale bars = 0.2 mm.

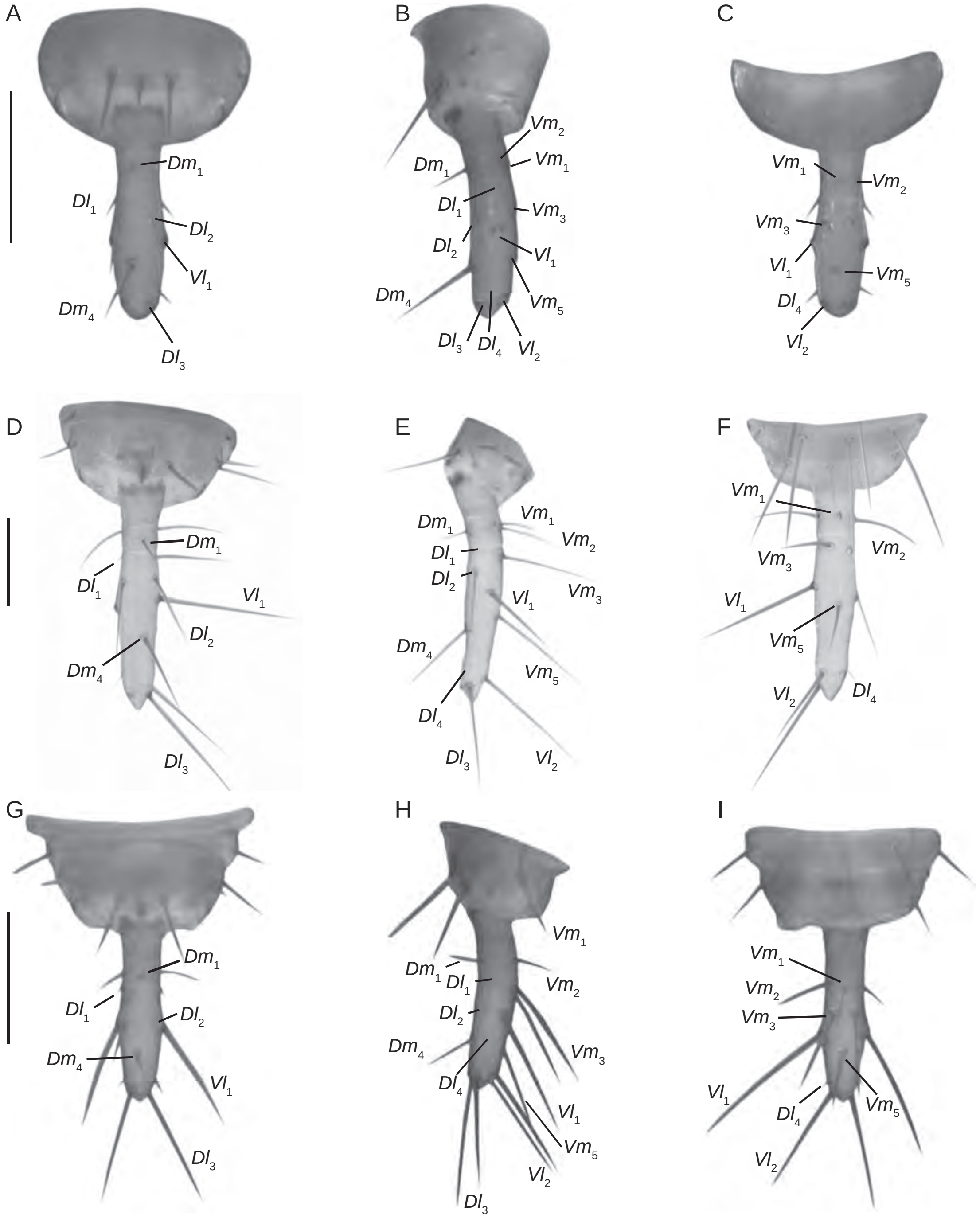

FIG. 17. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G**), lateral (**B, E, H**) and ventral (**C, F, I**) views. **A–C.** *Ambulantactus montielae*, sp. nov., ♀ (CNAN T1292). **D–F.** *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov., ♀ (CNAN T1165). **G–I.** *Harveyus contrerasi*, sp. nov., ♀ (CNAN T1278). Scale bars = 0.2 mm.

Etymology: The genus name is a compound word derived from two different words. *Baal* is a Mayan word for "devil." "Balrogs" are fictitious demons from the "Legendarium" and "The Lord of the Rings" by J.R.R. Tolkien. It is masculine in gender.

Included Species: *Baalrog firstmani* (Rowland, 1973), comb. nov.; *Baalrog magico* (Monjaraz-Ruedas and Francke, 2018), comb. nov.; *Baalrog sbordonii* (Brignoli, 1973), comb. nov.

Distribution: Species of *Baalrog*, gen. nov., are endemic to Mexico, inhabiting the caves of central Veracruz, in the Sierra de Zongolica and the foothills of Pico de Orizaba, and extending southward to Huautla de Jimenez, part of the Sierra Madre Oriental, in northern Oaxaca.

Natural History: *Baalrog*, gen. nov., is a strictly cavernicolous genus, some of its species occurring at great depths, e.g., *B. magico*, comb. nov., from the Sistema Huautla, one of the deepest cave systems in the world (Steele and Smith, 2012). Although exhibiting a similar distribution in central Veracruz, species of *Nahual*, gen. nov., are epigean, unlike species of *Baalrog*.

Remarks: Rowland and Reddell (1980) created the *pecki* group of *Schizomus* to accommodate *S. firstmani* and *S. sbordonii*, based on their larger body size and distinct pedipalp morphology. Additionally, the lateral lobes of the female spermathecae, mistakenly reported as absent by Rowland and Reddell (1980), are extremely reduced (fig. 8B). The discovery of *S. magico* revealed the unique bulbous pygidial flagellum of the male. The lateral lobes of the spermathecae are unusually variable in size in this species (Monjaraz-Ruedas and Francke, 2018: 210, fig. 70). These characters are diagnostic for *Baalrog*, gen. nov.

Cokendolpher and Reddell (1984b) described the male of *S. sbordonii* based on specimens collected in Grutas de Atoyac, Veracruz, although the holotype female was collected in Cueva de Ojo de Agua Grande in Paraje Nuevo, Veracruz. After detailed examination of the specimens, which revealed new morphological differences, and a comparison of DNA sequences, it was determined that material from Atoyac is not conspecific with material from the type locality. The population at Atoyac is described below as *Baalrog yacato*, sp. nov. Although the bulbose pygidial flagellum of the male of *B. yacato* differs markedly from the elliptical flagellum of the male of other species of *Baalrog*, it is placed in the genus based on the phylogenetic analyses (fig. 6). Discovery of the female and/or closely related new species may confirm or refute the placement of this peculiar species, which occurs in sympatry with its congener, *B. firstmani*, comb. nov.

***Baalrog firstmani* (Rowland, 1973), comb. nov.**

Schizomus firstmani Rowland, 1973a: 6, 7, 15–19, figs. 14–16; 1973c: 136; 1975b: 34, 167, 168, 232, 234, 235–240, 243, 246–249, 252, 253, map 4, figs. 217, 219, 220, 226–227; Dumitresco, 1977: 157; Rowland and Reddell, 1977: 80, 84, 98, 99, fig. 2; 1979a: 163; 1980: 1, 23–30, figs. 63, 65, 67, 68, 74, 75; Reddell, 1981: 16, 42, 45, 126, 128, 320, 321, 324, fig. 23; Palacios-Vargas, 1983: 43 (part); Cokendolpher and Reddell, 1984b: 242; Reddell and Cokendolpher, 1986: 34, 36; 1995: 5, 106.

Stenochrus firstmani: Reddell and Cokendolpher, 1991: 18; 1995: 5, 12, 18, 101, 103, 106; Vázquez-Rojas, 1995: 33; 1996: 65; Harvey, 2003: 123; Armas and Cruz-López, 2009: 20; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32; Monjaraz-Ruedas and Francke, 2018: 190, 207.

Type Material: *Schizomus firstmani*: **MEXICO:** *Veracruz*: Municipio de Atoyac: Grutas de Atoyac, 2 km E of Atoyac, 24.xii.1971, D. McKenzie, holotype ♂ (AMNH), 6.viii.1969, S. and J. Peck, 2 ♀, 3 imm. paratypes (AMNH).

Additional Material Examined: **MEXICO:** *Veracruz*: Municipio de Atoyac: Grutas de Atoyac, C. Bolivar, and Pieltain, 2 ♀ (AMNH), 13.xi.1941, C. Bolivar, Pieltain, and F. Bonet, 1 ♀, 1 imm. (AMNH); Grutas de Atoyac, 18°54′41″N

TABLE 2

Diagnostic morphological characters among four North American genera of short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899): *Ambulantactus*, gen. nov.; *Baalrog*, gen. nov.; *Harveyus*, gen. nov.; *Heteroschizomus* Rowland, 1973, stat. rev.

	Ambulantactus	***Baalrog***	***Harveyus***	***Heteroschizomus***
1. Propeltidial setae	three	three	two	four
2. Opisthosomal enlargement	absent	absent	absent	present
3. Cheliceral movable finger	smooth	smooth	smooth	lamella
4. Macrosetal group G3	G3-3 anterior	G3-4 posterior	G3-3 anterior	G3-3 anterior
5. Pedipalps sexual dimorphism	absent	absent	present	absent
6. Pedipalp apical process	acute	absent	bump	acute
7. Pedipalp macroseta	setiform, acuminate	setiform, acuminate	setiform, acuminate	setiform, acuminate
8. Tibia formula	4-3-5	3-3-5	3-3-4	3-3-4
9. Flagellum shape (♂)	deltoid	bulb	subrhomboidal	spatulate
10. Flagellum dorsal surface relief (♂)	pair of posterior fused depressions	absent	pair of shallow pits	pair of median pits or central depression
11. Spermatheca lateral lobes length	lateral reduced (3/4)	lateral reduced (1/4, 1/3)	lateral reduced (3/4)	equal to median pair
12. Spermatheca lateral apex orientation	upright	outward	outward	upright
13. Spermatheca median apex orientation	upright	outward	outward	upright
14. Spermatheca median lobes shape	straight	curved at tip	parenthesis shaped	straight
15. Spermatheca bulbs	absent	absent	small	absent
16. Spermatheca sclerotization	absent	absent	absent	absent
17. Spermatheca lobes base position	median posterior	median anterior	same level	variable
18. Spermatheca chitinized arch shape	inverse arch shaped	hastate	V- or U-shaped	mug shaped

96°46′42″W, 500 m, 6.xii.1981, V. Granados, 1 ♀ (CNAN Sz44), 19.ix.2015, J. Arreguin, D. Barrales, O. Francke, D. Guerrero, and R. Monjaraz, 1 ♂, 3 ♀ (CNAN Sz170), 16.i.2017, D. Barrales, G. Contreras, and R. Monjaraz, 2 ♂, 3 ♀ (CNAN DNA-Sz231), 1 ♀ (AMCC [LP 14531]).

***Baalrog magico* (Monjaraz-Ruedas and Francke, 2018)**, comb. nov.

Stenochrus magico Monjaraz-Ruedas and Francke, 2018: 190, 207–211, figs. 57–66.

Type Material: *Stenochrus magico*: **MEXICO:** *Oaxaca*: Municipio de Huautla de Jiménez: Millipede Cave, Río Iglesia Dolina, 18°07′03″N 96°47′59″W, 1610 m, 26.iii.1981, A. Grubbs and S. Zeman, holotype ♂ (CNAN T1163); Cueva Li-Nita, 18°08′51″N 96°47′54″W, 1919 m, 12.iv.2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke, and J. Mendoza, paratype ♂ (CNAN T1164); Cueva, 100 m S of Puente de Fierro, 18°09′03″N 96°51′12″W, 1197 m, 11.ix.2010, D. Barrales, J. Cruz, O. Francke, and A. Valdez, paratype ♀ (CNAN T1165). Municipio de San Miguel Cuahutepec: Cueva Cangrejo, 12.iv.2015, G. Contreras, O. Francke, J. Mendoza, M. Minton, and R. Monjaraz, 18°06′26″N 96°47′54″W, 1540 m, paratype ♀ (CNAN T1166).

TABLE 3

Diagnostic morphological characters among four North American genera of short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899): *Mayazomus* Cokendolpher and Reddell, 1995; *Nahual*, gen. nov.; *Olmecazomus*, nom. nov.; *Pacal* Reddell and Cokendolpher, 1995

	Mayazomus	***Nahual***	***Olmecazomus***	***Pacal***
1. Propeltidial setae	two	three	two	three
2. Opisthosomal enlargement	absent	absent	absent	absent
3. Cheliceral movable finger	smooth	lamella/ one tooth	smooth	lamella
4. Macrosetal group G3	G3-3 posterior	G3-3 anterior	G3-2,4 posterior	G3-4 posterior
5. Pedipalps sexual dimorphism	present	absent	absent	absent
6. Pedipalp apical process	acuminate	fan	digitiform	acuminate
7. Pedipalp macroseta	spiniform setiferous tubercle	spiniform	spiniform setiferous tubercle	setiform, acuminate
8. Tibia formula	4-3-4	5-5-6	4-4-4	3-3-4(5)
9. Flagellum shape (♂)	cordate	elliptical	elliptical	trilobate/ rhomboidal
10. Flagellum dorsal surface relief (♂)	pair of submedian depressions	pair of submedian pits/ slumps	pair of submedian depressions	pair of median pits with pair of swellings
11. Spermatheca lateral lobes length	lateral reduced (3/4)	equal to median pair	lateral reduced (1/4)	absent/ reduced (1/4)
12. Spermatheca lateral apex orientation	upright	outward	upright	upright
13. Spermatheca median apex orientation	outward	upright	upright	upright
14. Spermatheca median lobes shape	J-shaped	straight	parenthesis shaped	straight
15. Spermatheca bulbs	absent	absent	absent	present
16. Spermatheca sclerotization	present	present	present	absent
17. Spermatheca lobes base position	same level	median posterior	same level	same level
18. Spermatheca chitinized arch shape	U-shaped	arrow shaped	V-shaped	inverse arc shaped

ADDITIONAL MATERIAL EXAMINED: **MEXICO:** *Oaxaca*: Municipio de Plan Carlota: Church Cave, 18°07′58″N 96°46′35″W, 1500 m, 1.iv.2016, D. Barrales, G. Contreras, J. Cruz, J. Mendoza, and R. Monjaraz, 2 imm. (AMCC [LP 14516]).

Baalrog sbordonii **(Brignoli, 1973)**, comb. nov.

Schizomus sbordonii Brignoli, 1973: 7–9, fig. 4; Rowland, 1973c: 135, 136; Brignoli, 1974: 143, 146–149, 151, figs. 1e, 2c–d; Rowland, 1975b: 34, 189, 234, 236, 239; Rowland and Reddell, 1977: 80, 86, 89, 98, fig. 3; 1979a: 163; 1980: 24, 27, 29; Reddell, 1981: 45, 126, 127, fig. 22; Palacios-Vargas, 1983: 43 (part); Cokendolpher and Reddell, 1984b: 241–243, figs. 1–4; Reddell and Cokendolpher, 1984: 5; 1986: 36; 1995: 6, 115.

Schizomus cf. *sbordonii:* Rowland, 1975b: 167, 168, 232, 238–240, 248, 249, 252, 253, map

TABLE 4

Diagnostic morphological characters among four North American genera of short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899): *Schizophyxia*, gen. nov.; *Sotanostenochrus* Reddell and Cokendolpher, 1991; *Stenochrus* Chamberlin, 1922; *Troglostenochrus*, gen. nov.

	Schizophyxia	*Sotanostenochrus*	*Stenochrus*	*Troglostenochrus*
1. Propeltidial setae	three	three	two	two
2. Opisthosomal enlargement	absent	absent	absent	absent
3. Cheliceral movable finger	smooth	smooth	smooth	sawed
4. Macrosetal group G3	G3-3 anterior	G3-4 posterior	G3-4 posterior	G3-3 anterior
5. Pedipalps sexual dimorphism	absent	present	present	absent
6. Pedipalp apical process	acute	bump	absent	fan
7. Pedipalp macroseta	setiform, acuminate	setiform, acuminate	setiform, acuminate	spiniform
8. Tibia formula	3-3-4	3-3-5	3-3-4	3-3-4
9. Flagellum shape (♂)	spear-shaped	shovel	cordate/elliptical	trilobate
10. Flagellum dorsal surface relief (♂)	pair of submedian depressions	single central depression with pair of swellings	pair of pits associated with central depression	two submedian projections
11. Spermatheca lateral lobes length	lateral reduced (3/4)	subequal	lateral reduced (1/3)	lateral reduced (3/4)
12. Spermatheca lateral apex orientation	upright	upright	outward	outward
13. Spermatheca median apex orientation	outward	upright	outward	upright
14. Spermatheca median lobes shape	straight/ slightly curved	hand shaped	parenthesis/ J-shaped	J-shaped/ straight
15. Spermatheca bulbs	absent	absent	absent	absent
16. Spermatheca sclerotization	absent	absent	present	absent
17. Spermatheca lobes base position	same level	same level	median posterior	median anterior
18. Spermatheca chitinized arch shape	U-shaped	V-shaped	bowl shaped	hastate

4, fig. 225; Rowland and Reddell, 1980: 1, 23–25, 27–30, figs. 63, 73.

Stenochrus sbordonii: Reddell and Cokendolpher, 1991:18; 1995: 6, 12, 18, 101, 103, 115; Vázquez Rojas, 1995: 34; 1996: 65; Ruíz and Coronado, 2002: 62, 113; Harvey, 2003: 126; Palacios-Vargas and Reddell, 2013: 52; Moreno-González et al., 2014: 21; Palacios-Vargas et al., 2015: 32; Clouse et al., 2017: 5, 11, figs. 2–4; Wheeler et al., 2017: 582, fig. 2; Monjaraz-Ruedas and Francke, 2018: 190.

REMARKS: *Baalrog sbordonii*, comb. nov., is assigned to *Baalrog*, gen. nov., with reservation, based on the reduced size of the lateral lobes, as well as the slightly curved median lobes of the female spermathecae. Despite repeated searches at the type locality (Cueva de Ojo de Agua Grande, Municipio de Paraje Nuevo, Veracruz,

TABLE 5

Measurements (mm) of the short-tailed whipscorpions, *Ambulantactus aquismon*, sp. nov., and *Ambulantactus montielae*, sp. nov. (Schizomida: Hubbardiidae Cook, 1899)
Material deposited in the National Collection of Arachnida (CNAN) at the National Autonomous University of Mexico.

		A. aquismon	*A. montielae*		
Sex		♂	♂		♀
Collection		CNAN	CNAN		
Number		T1294	T1291	T1293	T1292
Total length		3.6	4.4	4.7	4.9
Propeltidium	Length	1.2	1.4	1.5	1.3
	Width	0.6	0.7	0.8	0.8
Flagellum	Length	0.4	0.5	0.5	0.3
	Width	0.2	0.3	0.3	0.1
	Height	0.1	0.2	0.2	0.1
Pedipalp	Trochanter length	0.4	0.5	0.6	0.4
	Femur length	0.5	0.5	0.7	0.5
	Patella length	0.5	0.5	0.7	0.4
	Tibia length	0.4	0.5	0.6	0.5
	Tarsus length	0.2	0.2	0.2	0.2
	Total length	2.0	2.3	2.9	2.0
Leg I	Coxa length	0.6	0.8	1.0	0.6
	Trochanter length	0.4	0.5	0.7	0.4
	Femur length	1.3	1.5	2.0	1.2
	Patella length	1.7	1.9	2.8	1.4
	Tibia length	1.3	1.4	2.0	1.1
	Basitarsus length	0.4	0.5	0.6	0.3
	Telotarsus length	0.3	0.6	0.8	0.6
	Total length	6.0	7.2	9.8	5.5
Leg IV	Trochanter length	-	0.4	0.5	-
	Femur length	-	1.3	1.8	-
	Patella length	-	0.6	0.8	-
	Tibia length	-	1.0	1.4	-
	Basitarsus length	-	0.8	1.2	-
	Telotarsus length	-	0.6	0.7	-
	Total length	-	4.7	6.5	-

Mexico), the male of this species remains unknown.

Material Examined: **MEXICO:** *Veracruz*: Municipio de de Paraje Nuevo: Ojo de Agua de Paraje Nuevo (Ojo de Agua Grande), 18°55′35″N 96°52′33″W, 22.ix.2004, O. Francke A. Gluesenkamp, E. González, C. Savvas, and P. Sprouse, 2 ♀ (AMNH), 18°55′32″N 96°52′58″W, 601 m, 20.ix.2015, J. Arreguin, D. Barrales, O. Francke, D. Guerrero, and R. Monjaraz. Municipio de Tepetlaxco: Cueva del Cabrito, 19°02′24″N 96°49′52″W, 1644 m, 19.ix.2015, O. Francke, D. Barrales, R. Monjaraz, D. Guerrero, and J. Arreguin, 3 imm. (AMCC [LP 14511]). Municipio Tezonapa: Presidio, 18°40′30″N 96°47′0.2″W, 351 m, 21.ix.2016, D. Barrales, A. Cruz, J. Mendoza, and R. Monjaraz, 6 ♀ (AMCC [LP 14542]).

Baalrog yacato, sp. nov.

Schizomus sbordonii male: Cokendolpher and Reddell 1984a: 5, figs. 1–4; 1984b: 241–243; Reddell and Cokendolpher, 1986: 36 [misidentification].

Stenochrus sbordonii male: Reddell and Cokendolpher, 1991: 18; 1995: 6, 12, 18, 101, 103, 115. Monjaraz-Ruedas and Francke, 2018: 190 [misidentification].

Type Material: **MEXICO:** *Veracruz*: Municipio de Atoyac: Grutas de Atoyac, 18°55′17″N 96°45′55″W, 22.ix.2004, A. Gluesenkamp, C. Savvas, P. Sprouse, E. González, and O. Francke, holotype ♂ (AMCC [LP 3756]).

Diagnosis: *Baalrog yacato*, sp. nov., resembles other species of the genus in possessing robust pedipalps with spiniform setae but may be distinguished from them by the fan-shaped apical process on the pedipalp trochanter of the male, and the ovate pygidial flagellum, with a single, circular posterodorsal depression, of the male. *Baalrog yacato* also resembles species of *Nahual*, gen. nov., in the ovate male pygidial flagellum but may be separated from the latter by the presence of a single depression, rather than a pair of depressions in the dorsal surface of the flagellum.

Etymology: The specific epithet is an anagram derived from the type locality and used as a noun in apposition.

Remarks: Based on the morphology of the male pygidial flagellum, as well as DNA sequence data, the male holotype of *B. yacato*, sp. nov., is not conspecific with *B. sbordonii*, comb. nov., as mistakenly assumed by previous authors (Cokendolpher and Reddell, 1984a, 1984b; Reddell and Cokendolpher, 1986, 1991; Monjaraz-Ruedas and Francke, 2018). The type locality of *B. sbordonii*, Cueva de Ojo de Agua, is a considerable distance from the type locality of *B. yacato*, Grutas de Atoyac, and part of a different cave system. Further collecting is needed to obtain the male of *B. sbordonii* and the female of *B. yacato*.

Additional Material Examined: **MEXICO:** *Veracruz*: Cueva de Atoyac, 2 km E Atoyac, C. Bolívar Pieltain, 1 ♂ (AMNH).

Harveyus, gen. nov.

Figures 3, 6, 7D, 8C, D, 11B, 13D, 17G–I, 18A, B, 19A–C; tables 1, 2

Stenochrus (part): Reddell and Cokendolpher, 1991: 1, 3.

Schizomus mexicanus group (part): Rowland 1975b: 37, 39, 164, 165, 167, 168, 173, 185, 209, 214, 216, 218, 220, 222, 224, 228, 255, 280, 301, 303, 320, 321, 348–350, 365, 366, 368, 369, 376, 387, 390, 391–393, 395; Rowland and Reddell, 1979a: 165, 171; 1979b: 90, 107; 1980: 1–8, 10, 11, 15–20; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20, 41; Reddell and Cokendolpher, 1986: 32, 34; Camilo and Cokendolpher, 1988: 53, 57; Armas, 1989a: 7; Armas and Abud-Antun, 1990: 14, 18; Reddell and Cokendolpher, 1991: 1, 3; 1995: 82, 99, 101–104; Krüger and Dunlop, 2010: 52; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781–783, 804; 2018: 189, 212.

Type Species: *Schizomus mexicanus* Rowland, 1971 [= *Harveyus mexicanus* (Rowland, 1971), comb. nov.], type species, here designated.

Diagnosis: *Harveyus*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger without accessory teeth or lamella; single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (fig. 13D). Propeltidium anterior process with two anterior setae (one posterior to the other) and two pairs of dorsosubmedian setae (fig. 11B); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps heteromorphic, elongated (e.g., *H. mexicanus*, comb. nov.) or homeomorphic (e.g., in *Harveyus contrerasi*, sp. nov.); trochanter with mesal spur, with small rounded or bump-shaped apical process (fig. 7D); femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with four acuminate *Pe* setae and four feathered *Pm* setae; tibial setal formula 3-3-4 (*Ter-Tmr-Tir*) (fig. 14D). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, subrhomboidal, acute posteriorly (except in *H. mulaiki*, comb. nov., which is bulb shaped), with pair of shallow, dorsosubmedian pits (fig. 19A–C); flagellum (♀) with two annuli (fig. 17G–I). Spermathecae (♀) with two pairs of lobes of similar width; lateral lobes shorter than (ca. 3/4 the length) median lobes, with the apex directed laterally; median lobes parenthesis shaped, with small apical bulbs; lobes unsclerotized apically (fig. 8C, D); median and lateral lobe bases aligned (fig. 10A), with duct openings along entire length; chitinized arch V- or arch shaped, without anterior branch, lateral tips diffuse; gonopod long and slender.

Comparisons: Species of *Harveyus*, gen. nov., resemble species of *Stenochrus* in the number of dorsal setae on the propeltidium, the pedipalp setae formula, and the general shape of the female spermathecae. However, the male pygidial flagellum is bulbous or subrhomboidal with the posterior part acuminate in *Harveyus* but cordate or elliptical in *Stenochrus*; the apical process on the pedipalp trochanter is present and bump shaped in *Harveyus*, but absent in *Stenochrus*; and the lateral lobes of the female spermathecae are ca. 3/4 the length of the median lobes, unsclerotized apically and with small apical bulbs in *Harveyus*, but ca. 1/3 the length of the median lobes, sclerotized apically and without apical bulbs in *Stenochrus*.

Etymology: This genus is named after Mark S. Harvey of the Western Australian Museum, in recognition of his many contributions to the world schizomid fauna. It is masculine in gender.

Included Species: *Harveyus contrerasi*, sp. nov.; *Harveyus mexicanus* (Rowland, 1971a), comb. nov.; *Harveyus mulaiki* (Gertsch, 1940), comb. nov.; and *Harveyus reddelli* (Rowland, 1971a), comb. nov.

Distribution: *Harveyus*, gen. nov., is distributed from Ciudad Valles in the state of San Luis Potosí, Mexico, to Edinburg and Rio Grande City in Texas, United States. Most records of this genus are from caves in the Mexican states of San Luis Potosí and Tamaulipas.

Natural History: Species of *Harveyus*, gen. nov., are mostly cavernicolous. However, *H. contrerasi*, sp. nov., and *H. mulaiki*, comb. nov., are epigean.

Remarks: The placement of *H. reddelli*, comb. nov., is problematic because, although the male morphology is consistent with the diagnosis of *Harveyus*, gen. nov., the shape of the female spermathecae more closely resembles the species of *Schizophyxia*, gen. nov. DNA sequence data are needed to test the generic placement of this species.

Harveyus contrerasi, sp. nov.

Figures 3, 6, 7D, 8C, 11B, 13D, 17G–I, 18A, B, 19A–C; tables 1, 6

Type Material: **MEXICO:** *San Luis Potosí*: Municipio de Xilitla: Tlamaya, 1 km E, 21°25′10″N 99°00′11″W, 777 m, 10.v.2012, G. Contreras, J. Cruz, J. Mendoza, and R. Monjaraz, holotype ♂ (CNAN T1276), paratype ♂ (CNAN T1277); Camino del Jobo a las pozas, 21°24′09″N 98°58′54″W, 610 m, 25.x.2013, J. Cruz, O. Francke, A. Guzman, and C. Santibañez, paratype ♂, paratype ♀ (CNAN T1278); El Nacimiento, between Xilitla and Huehuetlan, 21°27′33″N 98°58′36″W, 120 m, 11.ii.2011, G. Contreras, J. Cruz, O. Francke, C. Santibañez, and A. Valdez, paratype ♀ (CNAN T1279).

Diagnosis: *Harveyus contrerasi*, sp. nov., may be distinguished from other species of the genus by the male pygidial flagellum, which is subrhomboidal with a pair of separate, shallow pits dorsosubmedially, and the female spermathecae, which exhibit curved median lobes, with small apical bulbs and a wide U-shaped chitinized arch. *Harveyus contrerasi* is most closely related to *Harveyus mexicanus*, comb. nov. However, the male pedipalps are heteromorphic, with a prominent mesal spur on the tibia in *H. mexicanus*, but homeomorphic and without tibial spurs in *H. contrerasi*. Although the female spermathecae of the two species are similar in general shape, the median lobes are curved, the apical bulb well developed, and the chitinized arch wide and U-shaped in *H. contrerasi*, whereas the median lobes are very slightly curved, almost linear, the apical bulbs inconspicuous, and the chitinized arch V-shaped in *H. mexicanus*.

Etymology: This specific epithet is a patronym for Gerardo Contreras, in appreciation of his assistance during multiple schizomid collecting trips as well as his contributions to Mexican arachnology.

Description: The following description is based on the holotype male and paratype female (fig. 18A, B).

Color: Pale brownish.

Prosoma: Propeltidium with two setae on anterior process; two pairs of dorsal setae; ocular spots indistinct, irregular. Metapeltidium 0.38 mm long, 0.67 mm wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae: Movable finger serrula with 22 (♂) or 24 (♀) teeth, guard tooth present (fig. 13D). Fixed finger with four (♂) or five (♀) smaller teeth between two primary teeth; setal group formula, 3-6-4-2-6-8-1-7 (♂) or 3-6-4-2-7-10-1-7 (♀); G1 with three spatulate setae, covered with small spinose spicules; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally; G4 consisting of two small smooth, thick setae; G5A with six setae, subequal, feathered apically and longer than fixed finger; G5B with eight feathered setae, subequal; G6 with one smooth seta, ca. 1/2 the length of movable finger; G7 with seven slender, feathered setae, subequal.

Pedipalps: Pedipalps homeomorphic (fig. 7D); 1.73× (♂) or 1.59× (♀) longer than propeltidium. Trochanter with small rounded apical process; prolateral surface with small apical spur. Femur 1.94× longer than high; retroventral margin with setae Fe_1, Fe_5, Fev_1, and Fev_2 acuminate; prolateral surface with row of three ventral acuminate setae (Fmv_{1-3}) and two dorsal acuminate setae (Fmd_2, Fmd_3). Patella with five acuminate *Pe* setae and four feathered *Pm* setae; without distinctive armature. Tibia setal formula, 3:3:4; *Ter* setae acuminate, *Tmr* and *Tir* setae feathered. Tarsal spurs asymmetric.

Legs: Leg I, basitarsal-telotarsal proportions, 28:4:5:5:5:6:14; IV, femur 4.9× longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair of *Dm* setae; II with three pairs of microsetae anteriorly plus pair of *Dm* setae; III–VII each with one pair of *Dm* setae; VIII with pairs of *Dm* and Dl_2 setae; IX with pairs of Dl_1 and Dl_2 setae and without pair of *Dm* setae. Segments X and XI telescoped, slightly elongated, with pairs Dl_2, Vm_2, Vl_1, and Vl_2 setae plus single Vm_1 seta; XII with pairs of Dm, Dl_1, Dl_2, Vm_1, Vm_2, Vl_1, and Vl_2 setae, without posterodorsal process. Sternites II–VII each with two irregular rows of setae; genital plate with many scattered microsetae.

Pygidial flagellum: Flagellum (♂) dorsoventrally compressed, subrhomboidal (fig. 19A–C); 2.07× longer than wide; pair of shallow dorsosubmedian pits present; seta Dm_1 situated over bulb base, Dm_4 situated posteriorly, Dl_2 situated anterior to Vl_1, Dl_3 situated posterior to Vl_2; pair of Vm_2 setae present, Vm_1 situated posterior to Vm_2; pair of anterodorsal microsetae between Dm_1 and Dl_2, pair of anterolateral microsetae on flagellar pedicel, two patches of microsetae between Vl_1 and Vl_2 (*msp*). Flagellum (♀) with three flagellomeres (fig. 17G–I); seta Dl_2 reduced, aligned with Vl_1, Dl_3 aligned with Vl_2, Vm_2 present, reduced, Vm_1 aligned with Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 8C); median lobes curved J-shaped with small apical bulb, and duct openings along entire length; lateral lobes linear, shorter than median lobes, wider basally, with few duct openings; median lobe bases aligned with lateral lobe bases. Chitinized arch wide U-shaped; anterior branch absent; lateral tip wide and diffuse. Gonopod slender, cylindrical; length ca. 3× width.

DISTRIBUTION: This species is widely distributed in the vicinity of Huichihuayan and Xilitla in the southern part of San Luis Potosí state, Mexico (fig. 3).

NATURAL HISTORY: Although some specimens of *H. contrerasi*, sp. nov., were collected in a glen ca. 30 m deep, the glen has a wide entrance and multiple light entrances, hence the species is essentially epigean. Other new species may occur in the caves of the Sierra de Xilitla.

REMARKS: *Harveyus contrerasi*, sp. nov., is closely related to *H. mexicanus*, comb. nov., a species restricted to caves in the state of San Luis Potosí. Although differences in the male pygidial flagella of the two species are very subtle, their pedipalps are markedly different. The pedipalp dimorphism (enlargement) that occurs in *H. mexicanus* was not observed among males of *H. contrerasi*.

ADDITIONAL MATERIAL EXAMINED: **MEXICO:** *San Luis Potosí*: Municipio de Xilitla: Camino del Jobo a las pozas, 21°24′09″N 98°58′54″W, 610 m, 25.x.2013, J. Cruz, O. Francke, A. Guzman, and C. Santibañez, 1 ♀ (AMCC [LP 14493]).

***Harveyus mexicanus* (Rowland, 1971),** comb. nov.

Schizomus mexicanus Rowland, 1971a: 117–119, 124, 125, figs. 1–3, 16 (part, all records except Cueva de los Vampiros); Reddell and Mitchell, 1971a: 145; Brignoli, 1973: 6; Reddell, 1973: 38; Reddell and Elliott, 1973: 183; Rowland, 1973a: 10, 21, 22, figs. 20, 22; 1973b: 200, 201, fig. 1; 1973c: 135, 137; Brignoli, 1974: 143, 146–147, 149, 151, fig. l(e); Vomero, 1974: 345; Rowland, 1975a: 14, 15, 19, 20; 1975b: 10, 11, 33, 166–169, 177, 179, 180–184, 211, 213–215, 218, 219–221, 224, 225, 228, 230, 366–369, 394, 395, map 5, figs. 2 (below), 155, 156, 171, 172, 185–187,207–210, 292; Rowland and Reddell, 1977: 80, 83, 85–87, 96, fig. 3; 1979a: 163; 1980: 1, 2, 4, 5, 7, 9, 10, 12–13, 15, 17, 20, 21, figs. 1–3, 18–19, 32–34, 54–57; Reddell, 1981: 36, 38, 68, 126, 127, 129, 130, fig. 22; 1982: 263; Reddell and Cokendolpher, 1986: 32; 1995: 5, 107, 109, 115.

Stenochrus mexicanus: Reddell and Cokendolpher, 1991: 18; 1995: 5, 12, 18, 101, 102, 107, 145, fig. 6; Vázquez-Rojas, 1995: 34; 1996: 65; Armas and Teruel, 1998: 47; Harvey, 2003: 124; Zawierucha et al., 2013: 359; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32. Monjaraz-Ruedas and Francke, 2016: 783, 784, 788, 804; Villarreal et al., 2016: 4, 23; Monjaraz-Ruedas and Francke, 2018: 190, 196, 212.

TYPE MATERIAL: *Schizomus mexicanus*: **MEXICO:** *San Luis Potosí*: Municipio de Ciudad

Valles: Sótano de la Tinaja, 10 km NNE Ciudad Valles, 18.ii.1970, J.A.L. Cooke, holotype ♂, 1 ♂, 2 ♀ paratypes (AMNH).

REMARKS: Multiple records of *H. mexicanus*, comb. nov., from the Sierra El Abra in San Luis Potosí, reported by Rowland and Reddell (1980), may be different species or the complex cave system within the mountain range may have enabled this species to disperse underground and colonize the entire range. More detailed analyses, including multiple populations from this mountain range, should be undertaken to assess whether *H. mexicanus* is one species or many.

ADDITIONAL MATERIAL EXAMINED: **MEXICO:** *San Luis Potosí*: Municipio de Ciudad Valles: Cueva de los Sabinos, 20.i.1944, 1 ♂, 2 ♀, 3 imm. (AMNH); Cueva de los Sabinos, 22°05′31″N 98°57′25″W, 3.ix.2015, G. Montiel and G. Contreras 1 ♀ (CNAN DNA-Sz95); Sótano del Arroyo, 10 km NE of Ciudad Valles, 1 ♀, 1 imm. (AMNH); Cueva Grande, 14 km SE of Ciudad Valles, 1 ♀ (AMNH); Sótano de la Tinaja, 10 km NNE Ciudad Valles, 16.iii.1972, J.A.L. Cooke, 3 ♂, 2 ♀, 5 imm. (AMNH), 11.i.1980, B. and V. Roth, 1 ♂, 1 ♀, 1 imm. (AMNH); Sótano de la Tinaja, 22°04′33″N 98°58′40″W, 2338 m, 19.v.2011, D. Candia, R. Monjaraz, R. Paredes, and A. Reyna, 6 ♂, 8 ♀ (CNAN Sz131), 2 imm. (AMCC [LP 14500]). Municipio de Taninul: Cueva del Tigre, Hotel Taninul, 21°56′12″N 98°53′18″W, 39 m, 12.ii.2011, G. Contreras, J. Cruz, O. Francke, C. Santibañez, and A. Valdez, 4 ♂, 1 ♀ (CNAN Sz151), 11.v.2012, J. Cruz, J. Mendoza, G. Contreras, and R. Monjaraz, 1 ♀, 1 imm. (AMCC [LP 14537]), 2.ix.2015, G. Contreras, J. Cruz, O. Francke, C. Santibañez, and A. Valdez, 4 ♀ (CNAN Sz187).

Harveyus mulaiki **(Gertsch, 1940)**, comb. nov.

Schizomus mulaiki Gertsch, 1940: 1, 3–4, figs. 7–10; Takashima, 1951: 102; Rémy, 1961: 407; Rowland, 1971b: 304; 1975a: 32, 166–169, 172, 173, 177, 214, 215, 218, 219, 228, 229, 366, 367, 368, 369, 394, map 5, figs. 162, 178, 292; Rowland and Reddell, 1976: 3, 20, 21; 1977: 79, 83; 1979a: 162; 1980: 1, 2, 4–10, 15, figs. 1, 8, 25; Coddington et al., 1990: 12, 13; Reddell and Cokendolpher, 1995: 2, 4, 108.

Stenochrus mulaiki: Reddell and Cokendolpher, 1991: l8; Cokendolpher and Reddell, 1992: 72; Reddell and Cokendolpher, 1995: 4, 12, 18, 102, 108; Vázquez-Rojas, 1995: 34; 1996: 65; Ruíz and Coronado, 2002: 67; Harvey, 2003: 124; Zawierucha et al., 2013: 359.

TYPE MATERIAL: *Schizomus mulaiki*: **U.S.A.:** *Texas*: Starr County: Rio Grande City, 21.vi.1939, S. Mulaik, holotype ♂ (AMNH). Hidalgo County: Edinburg, 2.vi.1935, S. Mulaik, paratype ♂ (AMNH).

NATURAL HISTORY: Although *H. mulaiki* inhabits very dry areas in southern Texas, the type specimens were found in a humid microhabitat, under large concrete slabs near the Rio Grande River. This species may aestivate underground in the dry season, as several attempts to collect it were unsuccessful.

REMARKS: The discovery of the female of *H. mulaiki*, comb. nov., will permit a detailed description of its spermathecae.

Harveyus reddelli **(Rowland, 1971)**, comb. nov.

Schizomus reddelli Rowland, 1971a: 123, 124, 126, figs. 13–15; Reddell and Mitchell, 1971b: 185; Reddell, 1973: 38; Rowland, 1973a: 21; 1973c: 135; Brignoli, 1974: 147, 149; Rowland, 1975b: 34, 166–169, 177–179, 181, 214, 215, 218–221, 228–230, 366–369, 394, map 5, figs. 159, 175, 189, 190, 292; Rowland and Reddell, 1977: 80, 84, 85, fig. 2; 1979a: 163; 1980: 1, 2, 4, 5, 7, 10, 12, 13, 15, 17, figs. 1, 10, 22, 36, 37; Reddell, 1981: 16, 37, 128–130, 321, 324, fig. 23; Reddell and Cokendolpher, 1986: 32.

Schizomus mexicanus Rowland, 1971a: 117, 118, 119, 124, figs. 1–3, 16 [misidentification; part, Cueva de los Vampiros record only];

FIG. 18. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), habitus, dorsal view. **A, B.** *Harveyus contrerasi*, sp. nov.: **A.** ♂ (CNAN T1276); **B.** ♀ (CNAN T1278). **C, D.** *Heteroschizomus kekchi*, sp. nov.: **C.** ♂ (CNAN T1280); **D.** ♀ paratype (CNAN T1281). Scale bars = 1 mm.

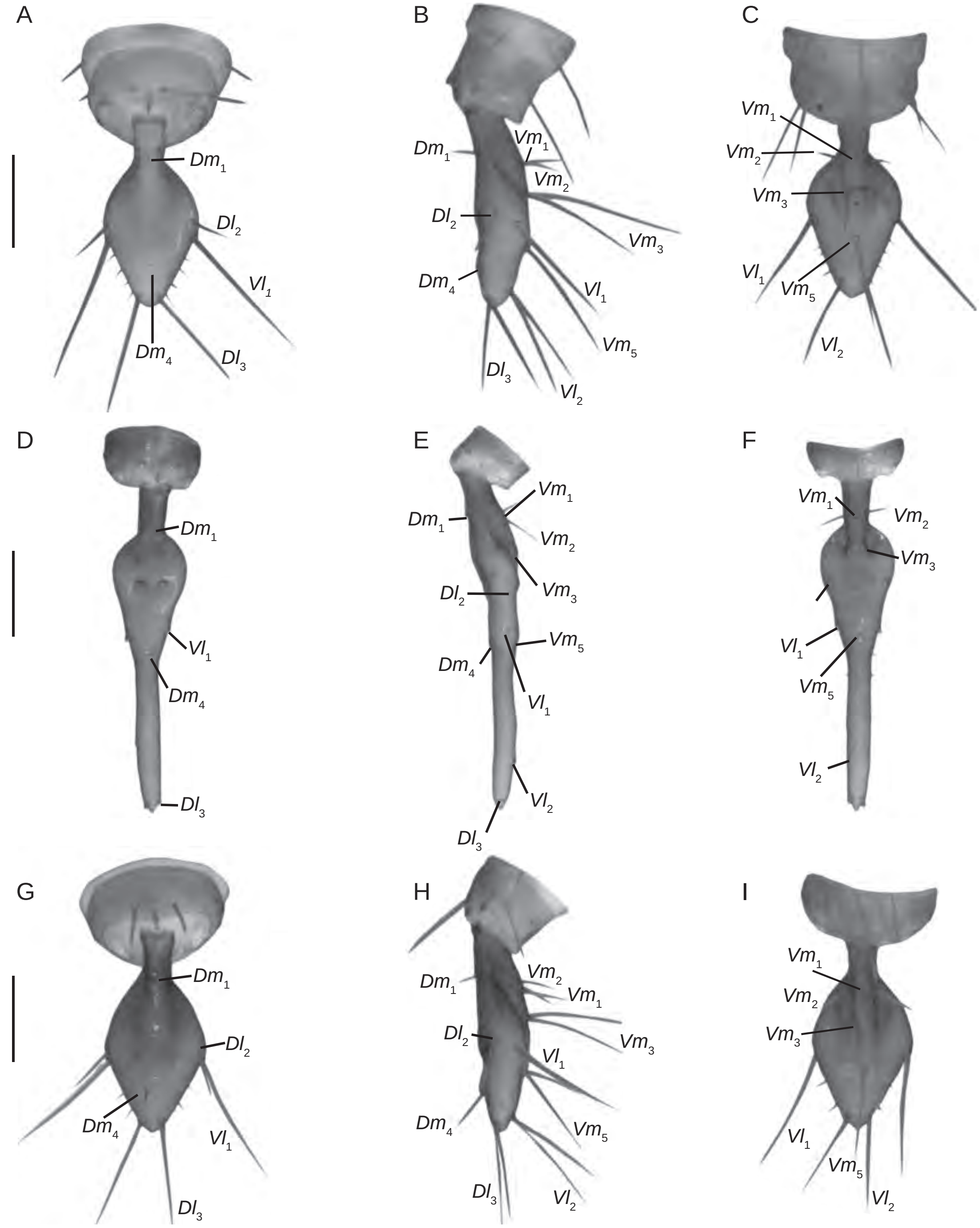

FIG. 19. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G**), lateral (**B, E, H**) and ventral (**C, F, I**) views. **A–C.** *Harveyus contrerasi*, sp. nov., ♂ (CNAN T1276). **D–F.** *Heteroschizomus kekchi*, sp. nov., ♂ (CNAN T1280). **G–I.** *Nahual bokmai*, sp. nov., ♂ (CNAN T1282). Scale bars = 0.2 mm.

Reddell and Mitchell, 1971b: 185 [misidentification]; Vomero, 1974: 341 [misidentification]; Reddell and Cokendolpher, 1995: 5, 115.

Schizomus reddeli: Dumitresco, 1977: 157 (lapsus calami).

Stenochrus reddelli: Reddell and Cokendolpher, 1991: 18; 1995: 5, 12, 18, 102, 108, 115; Vázquez-Rojas, 1995: 34; 1996: 65; Ruíz and Coronado, 2002: 67; Harvey, 2003: 125; Zawierucha et al., 2013: 359; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32; Monjaraz-Ruedas and Francke, 2018: 212.

Type Material: *Schizomus reddelli*: **MEXICO:** *Tamaulipas*: Municipio de Ocampo: Cueva de Tres Manantiales, 8 km NNE Chamal, 27.v.1968, J. Reddell, holotype ♂ (AMNH).

Remarks: Rowland and Reddell's (1980) description of the lateral lobes of the female spermathecae of *H. reddelli*, comb. nov., as "absent" is erroneous. The lateral lobes of this species are filiform, linear, and considerably narrower than the median lobes.

Additional Material Examined: **MEXICO:** *Tamaulipas*: Municipio de Gómes Farías: Cueva del Ojital, 23.xi.2005, P. Sprouse, 2 ♀ (AMCC [LP 14500]), 1 ♀ (CNAN-Sz25).

***Heteroschizomus* Rowland, 1973**, stat. rev.

Figures 4, 6, 7E, 8E, F, 11C, 13E, 18C, D, 19D–F, 21A–F; tables 1, 2, 7

Heteroschizomus Rowland, 1973a: 1, 2, 4; 1973b: 197; Rowland and Reddell, 1977: 83; Martín and Oromí, 1984: 266; Reddell and Cokendolpher, 1991: 3, 5, 18.

Stenochrus (part): Reddell and Cokendolpher, 1991: 1, 3.

Schizomus goodnightorum group: Rowland 1975b: 37, 39, 167, 168, 255, 256, 258, 259, 263, 265, 267, 320, 321, 325, 348–350, 376, 390, 397; Rowland and Reddell, 1979a: 165, 171; 1979b: 90; 1980: 3; Reddell, 1981: 126; Rowland and Reddell, 1981: 19–21, 23–25, 27; Reddell and Cokendolpher, 1991: 1, 3; 1995: 101, 102; Villarreal et al., 2008: 64, 67; Moreno-González and Villarreal, 2012: 73; Villarreal and García, 2012: 5; Villarreal et al., 2014: 371; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781, 783; 2018: 189, 212.

Type Species: *Heteroschizomus goodnightorum* Rowland, 1973, by original designation.

Diagnosis: *Heteroschizomus*, stat rev., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger with lamella (fig. 12C); single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (except in *Heteroschizomus silvino* (Rowland and Reddell, 1977), comb. nov.) (fig. 13E). Propeltidium anterior process with two anterior setae (one posterior to the other) and three or four pairs of dorsosubmedian setae (fig. 11C); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with small prolateral spur, apical process acute and not projected (fig. 7E); femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with three acuminate *Pe* setae and three or four feathered *Pm* setae; tibial setal formula 3-3-4 (*Ter-Tmr-Tir*) (fig. 14D). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII (♂) elongated (fig. 18C); XII (♂) without posterodorsal abdominal process. Pygidial flagellum (♂) dorsoventrally flattened, spatulate, with well-defined anterior bulb and posterior constriction in dorsal view, and with pair of anterodorsal pits (except *H. goodnightorum* and *Heteroschizomus meambar* (Armas and Víquez, 2010), comb. nov., with single median depression) (fig. 19D–F); flagellum (♀) with two annuli (fig. 21A–F). Spermathecae (♀) with two pairs of lobes, similar in length and width; both pairs of lobes linear with apex directed vertically, unsclerotized (fig. 8E, F); lobes without bulbs; median lobe bases variably situated with respect to lateral lobe bases, without duct openings; chitinized arch mug shaped, with wide, sclerotized base (fig. 8E, F); anterior branch curved, unfused medially, with lateral tips wide, curved, and lobed; gonopod wide and short.

COMPARISONS: Species of *Heteroschizomus*, stat. rev., resemble species of *Piaroa* in many aspects of the male morphology and, without females, it is almost impossible to differentiate between them. However, a combination of subtle characters concerning the cheliceral movable finger, the apical process of the pedipalp trochanter, and the number of dorsal setae on the propeltidium enable the males of these genera to be differentiated. The number of dorsal setae on the propeltidium is the most obvious difference between the males of *Heteroschizomus* and *Piaroa*. Although the original description of *Piaroa* mentioned three pairs of dorsal setae (Villarreal et al., 2008), this count included the anterior pair. The correct count for *Piaroa* is two pairs, as observed in all its component species, except *Piaroa youngi* Armas and Víquez, 2010, which exhibits three. In contrast, the male of *Heteroschizomus* bears more than three pairs. Additionally, the cheliceral movable finger of the male bears a small lamella in *Heteroschizomus* but is smooth or bears teeth or a lamella in *Piaroa*. The pedipalp trochanter apical process is acute but not projected or forms a small protuberance in the male of *Heteroschizomus*, but triangular or conical, and projected in the male of *Piaroa* (except for *Piaroa escalerette* Moreno-Gonzalez et al., 2014). Despite the similarity between males of *Heteroschizomus* and *Piaroa*, the females of both genera are markedly different. Correct assignment to genus is therefore best achieved with specimens of both sexes. The female pygidial flagellum possesses two annuli in *Heteroschizomus*, but three annuli in *Piaroa*; and the female spermathecae possess two pairs of lobes, a mug-shaped chitinized arch, and gonopods in *Heteroschizomus*, whereas only one pair of lobes and a mask-shaped chitinized arch are present, and gonopods absent in *Piaroa*.

INCLUDED SPECIES: *Heteroschizomus goodnightorum* Rowland, 1973; *Heteroschizomus kekchi*, sp. nov.; *Heteroschizomus meambar* (Armas and Víquez, 2010), comb. nov.; *Heteroschizomus orthoplax* (Rowland, 1973a), comb. nov.; *Heteroschizomus silvino* (Rowland and Reddell, 1977), comb. nov.

DISTRIBUTION: The distribution of *Heteroschizomus*, stat. rev., extends from the state of Chiapas in southern Mexico southward to Honduras. The southernmost record of the genus is *H. meambar*, comb. nov. There are no records of *Heteroschizomus* in Costa Rica and Nicaragua, but the northernmost record of *Piaroa*, i.e., *Piaroa bijagua* Armas and Víquez, 2009, is from Costa Rica, suggesting the two genera converge and possibly overlap in Nicaragua. More sampling efforts are needed to clarify the distributions of Central American schizomids (fig. 4).

NATURAL HISTORY: Species of *Heteroschizomus*, stat. rev., are primarily epigean, except for *H. silvino*, comb. nov., a cavernicolous species. Specimens of *H. goodnightorum* have been found near, but not inside, caves in the Yucatán Peninsula. Species of *Heteroschizomus* exhibit a unique way of walking that is faster than has been observed in other Mexican schizomids, with the elongated opisthosoma flipped over above the prosoma, like ants of the genus *Crematogaster* Lund, 1831. This has not been reported in other schizomid genera with an elongated opisthosoma, i.e., *Colombiazomus* Armas and Delgado-Santa, 2012, *Hansenochrus*, and *Piaroa*.

REMARKS: The revalidation of *Heteroschizomus*, stat. rev., is based in part on the discovery of the female of *H. goodnightorum*. Rowland and Reddell (1981) misidentified a female of *Stenochrus portoricensis*, which occurs in sympatry in the Yucatán Peninsula, as the female of *H. goodnightorum*. The female spermathecae are similar in *H. goodnightorum* and *H. silvino*, comb. nov., and although the female of *H. orthoplax*, comb. nov., remains unknown, the description of *H. kekchi*, sp. nov., confirms the diagnostic morphology of the spermathecae of

TABLE 6

Measurements (mm) of the short-tailed whipscorpion, *Harveyus contrerasi*, sp. nov. (Schizomida: Hubbardiidae Cook, 1899)

Material deposited in the National Collection of Arachnida (CNAN) at the National Autonomous University of Mexico.

		H. contrerasi					
Sex		♂				♀	
Collection		CNAN				CNAN	
Number		T1276	T1277	T1278	T1279	T1278	T1279
Total length		3.9	3.8	3.6	3.9	3.9	3.4
Propeltidium	Length	1.3	1.4	1.4	1.3	1.2	1.6
	Width	0.7	0.8	0.7	0.7	0.7	0.9
Flagellum	Length	0.5	0.5	0.5	0.5	0.3	-
	Width	0.2	0.2	0.2	0.2	0.1	-
	Height	0.1	0.1	0.1	0.1	0.1	-
Pedipalp	Trochanter length	0.5	0.5	0.5	0.4	0.4	0.5
	Femur length	0.5	0.6	0.6	0.6	0.5	0.5
	Patella length	0.5	0.6	0.6	0.6	0.5	0.5
	Tibia length	0.5	0.5	0.6	0.5	0.4	0.5
	Tarsus length	0.3	0.3	0.3	0.3	0.2	0.2
	Total length	2.3	2.5	2.6	2.3	1.9	2.3
Leg I	Coxa length	0.7	0.7	0.7	0.7	0.5	0.5
	Trochanter length	0.4	0.5	0.5	0.4	0.3	0.4
	Femur length	1.6	1.9	2.0	1.7	1.0	1.3
	Patella length	2.0	2.5	2.7	2.1	1.1	1.5
	Tibia length	1.4	1.8	1.9	1.5	0.8	1.1
	Basitarsus length	0.5	0.5	0.5	0.4	0.3	0.3
	Telotarsus length	0.6	0.7	0.8	0.7	0.5	0.6
	Total length	7.2	8.6	9.1	7.4	4.4	5.7
Leg IV	Trochanter length	0.4	0.5	0.5	0.4	0.3	0.4
	Femur length	2.4	1.6	1.7	1.5	1.0	1.2
	Patella length	0.9	0.6	0.7	0.6	0.4	0.5
	Tibia length	1.6	1.2	1.3	1.1	0.7	0.9
	Basitarsus length	0.9	1.0	1.0	0.9	0.6	0.8
	Telotarsus length	0.6	0.5	0.7	0.6	0.5	0.5
	Total length	6.7	5.4	5.8	5.0	3.6	4.3

this genus. In addition, the discovery of a lamella on the movable finger of the chelicera, not reported by Rowland and Reddell (1981), and the constriction of the posterior part of the the male pygidial flagellum, present in all known species of *Heteroschizomus* (and some species of *Piaroa*), confirms the monophyly of the genus and justifies its revalidation. The elongated opisthosoma observed in *Heteroschizomus* appears to have evolved convergently in other schizomid genera, e.g., *Hansenochrus*, *Hubbardia*, and *Piaroa*.

Stenochrus meambar Armas and Víquez, 2010 was assigned to *Heteroschizomus* based on the presence of a lamella on the cheliceral movable finger and a lanceolate pygidial flagellum, with a medial constriction and a dorsomedian depression, in the male (Armas and Víquez, 2010). The unnamed genus from Honduras described in the same publication (Armas and Víquez, 2010: 18) is probably also a female of *Heteroschizomus*, because the spermathecae are very similar, with a mug-shaped chitinized arch, and the two pairs of short lobes, similar in length.

***Heteroschizomus goodnightorum* Rowland, 1973**

Figures 4, 6, 8E, 21A–C; table 7

Heteroschizomus goodnightorum Rowland, 1973a: 2–6; 1973b: 202; 1973c: 136; 1975b: 31; Rowland and Reddell, 1977: 83; Reddell and Cokendolpher, 1991: 18; 1995: 3, 5, 101, 106.

Schizomus goodnightorum: Rowland 1975a: 34, 167, 168, 194, 257–269, 325, 397; Rowland and Reddell, 1977: 90, 99, 100; 1979a: 163, 164; 1981: 19, 21–27; Reddell and Cokendolpher, 1995: 3, 106.

Stenochrus goodnightorum: Reddell and Cokendolpher, 1991: 18; 1995: 5, 8, 18, 102, 106; Villarreal et al., 2008: 64; Villarreal and García, 2012: 5; Monjaraz-Ruedas and Francke, 2016: 783, 784, 797, 804; 2018: 190.

Type Material: **MEXICO:** *Yucatan*: Chichén Itzá, vi.1948, C. Goodnight, holotype ♂, paratype ♂ (AMNH).

Supplementary Description: The following description of the female is based on the additional material examined.

Prosoma: Propeltidium with two apical setae; three pairs of dorsal setae.

Chelicerae: Movable finger with very small lamella; serrula with 13 teeth, guard tooth present. Fixed finger with five small teeth between two primary teeth; setal group formula, 3-6-4-2-7-8-1-6.

Pedipalps: Pedipalps homeomorphic; 1.59× longer than propeltidium. Trochanter with small rounded apical process, not projected; prolateral surface with small apical spur. Femur 1.73× longer than high; retroventral margin with setae Fe_1, Fe_5, Fev_1, and Fev_2 acuminate; prolateral surface with row of three ventral setae (Fmv_{1-3}) and two dorsal setae (Fmd_2, Fmd_3). Patella with three acuminate *Pe* setae and four feathered *Pm* setae; without distinctive armature. Tibia setal formula, 3:3:4; *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetric.

Opisthosoma: Segments X–XII not elongated.

Pygidial flagellum: Flagellum (♀) with three flagellomeres (fig. 21A–C); seta Dl_2 reduced, situated posterior to Vl_1, Dl_3 situated posterior to Vl_2, Vm_2 present, Vm_1 aligned with Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 8E); median and lateral lobes conical, subequal in length and width; median lobes linear, lateral lobes sublinear, apex slightly curved laterally, unsclerotized apically, with few duct openings; median lobe bases aligned with lateral lobe bases. Chitinized arch mug shaped; anterior branch not sclerotized. Gonopod wide; width ca. 2×length.

Remarks: Rowland and Reddell (1977) synonymized *Heteroschizomus*, stat. rev., and transferred *H. goodnightorum* to *Schizomus*, based on the discovery of other species with an elongated opisthosoma. Reddell and Cokendolpher (1991) transferred *Schizomus goodnightorum* to *Stenochrus* based on the morphology of the female spermathecae described by Rowland and Reddell (1981). The discovery and correct identification of the female of *H. goodnightorum* confirmed the validity of *Heteroschizomus* and the correct placement of *H. goodnightorum* and related species, discoveries that were independently supported by the DNA sequence data.

Additional Material Examined: **MEXICO:** *Yucatán*: Municipio de Chichén Itzá: Chichen Itzá, vi.1948, C. Goodnight, 1 ♀ (AMNH); Fuera de la Cueva de Kanthon, 20°38′08″N 88°29′42″W, 23 m, 2.viii.2014, J. Mendoza and R. Monjaraz, 4 ♂ (AMCC [LP 14522]), 2 ♂, 1 ♀ (CNAN Sz171). Municipio de Kaua: Fuera de la Cueva de Kaua, 20°37′04″N 88°25′26″W, 24 m, 5.x.2014, G. Contreras and G. Montiel, 1 ♂, 2 ♀ (CNAN Sz163). *Quintana Roo*: Municipio de Cancun: Km 234 Highway Mérida–Cancun, 20°53′57″N 87°28′25″W, 19 m, 20.vii.2010, D. Barrales, G. Contreras, J. Cruz, O. Francke, G. Montiel, M. Paradiz, C. Santibañez, and A. Valdez, 1 ♂ (CNAN Sz8).

Heteroschizomus kekchi, sp. nov.

Figures 4, 6, 7E, 8F, 11C, 13E, 18C, D, 19D–F, 21D–F; table 7

Type Material: **GUATEMALA:** *Izabal Department*: Municipio de Livingston: Biotopo Chocon Machacas, Estación USAC, 15°47′15″N 88°50′34″W, 15 m, 18.viii.2017, D. Barrales and R. Monjaraz, holotype ♂ (CNAN T1280), paratype ♀ (AMCC [LP 14559]).

Diagnosis: *Heteroschizomus kekchi*, sp. nov., may be separated from other species of *Heteroschizomus*, stat. rev., by the following characters: the pedipalp trochanter of the male bears a small, acute apical process that is not projected; the male pygidial flagellum comprises a slender anterior bulb and a medial constriction with acuminate margins, terminating in a long, slender posterior lobe (fig. 19D–F); and the median and lateral lobes of the female spermathecae are slender and cylindrical, with the lateral lobes longer than the median lobes.

Comparisons: *Heteroschizomus kekchi*, sp. nov., resembles *H. silvino*, comb. nov., in the shape of the male pygidial flagellum and the female spermathecae. However, the anterior lobe of the flagellum is elliptical and much narrower in *H. kekchi* than in *H. silvino*, in which the anterior bulb is ovate; the posterior lobe of the flagellum is longer and narrower in *H. kekchi* than in *H. silvino*; and the margin of the medial constriction is acuminate in *H. kekchi* but curved in *H. silvino*. The lateral lobes of the spermathecae are longer than the median lobes and cylindrical in *H. kekchi* but shorter than the median lobes, wide and teardrop shaped in *H. silvino*.

Etymology: The specific epithet is a noun in apposition, honoring the Kekchi people, who inhabit parts of Alta Verapaz and Izabal in Guatemala.

Description: The following description is based on the holotype male and paratype female (fig. 18C, D).

Color: Olive greenish.

Prosoma: Propeltidium with two setae on anterior process; three pairs of dorsal setae; ocular spots distinct, ovate. Metapeltidium 0.37 mm long, 0.58 mm wide. Anterior sternum with nine setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae: Movable finger serrula with 17 teeth, guard tooth present, with lamella (fig. 13E). Fixed finger with five smaller teeth between two primary teeth; setal group formula, 3-6-4-2-7-5-1-5; G1 with three spatulate setae, covered with few small spinose spicules apically; G2 composed of six feathered setae, subequal, and longer than movable finger; G3 with four setae, subequal, feathered apically and smooth basally; G4 consisting of two small setae, smooth, thickened basally, elongated apically; G5A with seven setae, subequal, feathered apically and longer than fixed finger; G5B with five feathered setae, subequal; G6 with one smooth seta, ca. 1/2 the length of movable finger; G7 with five slender, feathered setae, subequal.

Pedipalps: Pedipalps homeomorphic (fig. 7E); 1.66× (♂) or 1.69× (♀) longer than propeltidium. Trochanter with small acute apical process; prolateral surface with small medial spur. Femur 1.8× longer than high; retroventral margin with setae Fe_1, Fe_5, Fev_1, and Fev_2 acuminate; prolateral surface with row of three ventral setae (Fmv_{1-3}) and two dorsal setae (Fmd_2, Fmd_3). Patella with three acuminate *Pe* setae and four feathered *Pm* setae and without distinctive armature. Tibia setal formula, 3:3:4; *Ter* setae acuminate, *Tmr* and *Tir* setae feathered. Tarsal spurs asymmetric.

Legs: Leg I, basitarsal-telotarsal proportions, 23:4:4:3:3:4:8; IV, femur 2.53× longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair of *Dm* setae; II with three pairs of microsetae anteriorly plus pair of *Dm* setae; III–VII each with one pair of *Dm* setae; VIII with pairs of *Dm* and Dl_2 setae; IX with pairs of Dl_1 and Dl_2 setae and without pair of *Dm* setae. Segments X and XI telescoped, slightly elongated, with pairs of Dl_2, Vm_2, Vl_1, and Vl_2 setae plus single Vm_1 seta; XII with pairs of *Dm*, Dl_1, Dl_2, Vm_1, Vm_2, Vl_1, and Vl_2 setae, without posterodorsal process. Sternites II–VII each with two irregular rows of setae; genital plate with many scattered microsetae.

Pygidial flagellum: Flagellum (♂) dorsoventrally compressed, acuminate (fig. 19D–F); 4.75× longer than wide; pair of anterodorsal pits present; seta Dm_1 situated over bulb base, Dm_4 situated anteriorly, Dl_2 situated posterior to Vl_1, Dl_3 situated posterior to Vl_2, pair of Vm_2 setae present, Vm_1 situated posterior to Vm_2; pair of anterodorsal microsetae between Dm_1 and Dl_2, pair of anterolateral microsetae on flagellar pedicel, two patches of microsetae between Vl_1 and Vl_2 (*msp*). Flagellum (♀) with three flagellomeres (fig. 21D–F); seta Dl_2 not reduced, aligned with Vl_1, Dl_3 situated posterior to Vl_2, Vm_2 present, reduced, Vm_1 situated posterior to Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 8F); median and lateral lobes linear, similar in width, with apical duct openings; median lobes shorter than lateral lobes (ca. 3/4); median lobe bases posterior to lateral lobe bases. Chitinized arch mug shaped; anterior branch unfused. Gonopod slender, cylindrical; length ca. 2× width.

DISTRIBUTION: This species is known only from the type locality in the vicinity of Lake Izabal, in the Izabal Department of Guatemala (fig. 4).

NATURAL HISTORY: The type specimens were collected under rocks and inside rotten logs in a unique area of mangrove swamp and flooded rainforest, which is almost entirely encroached by agriculture.

REMARKS: Despite the geographical proximity of *H. kekchi*, sp. nov., and *H. silvino*, comb. nov., the two species are markedly different morphologically and *H. kekchi* is epigean, inhabiting tropical rainforest, whereas *H. silvino* appears to be restricted to a cave.

***Heteroschizomus orthoplax* (Rowland, 1973), comb. nov.**

Schizomus orthoplax Rowland, 1973a: 6, 10–13, figs. 8–10; 1973c: 135; 1975a: 34, 167–168, 257, 258, 260–269, map 4, figs. 236, 240, 244; 1975b: 16; Rowland and Reddell, 1977: 99, 100; 1979a: 163; 1981: 19, 21–27, figs. 1, 3, 7, 11; Reddell and Cokendolpher, 1995: 5, 108.

Schizomus ortoplax: Dumitresco, 1977: 157 (lapsus calami).

Stenochrus orthoplax: Reddell and Cokendolpher, 1991: 18; 1995: 5, 18, 102, 108, 109; Vázquez-Rojas, 1995: 33; 1996: 65; Harvey, 2003: 124; Armas, 2004: 51; Villarreal et al., 2008: 64.

TYPE MATERIAL: *Schizomus orthoplax*: **MEXICO:** *Chiapas*: Municipio de Tapachula: Finca Cuauhtemoc, 8.v. 1950, C. and M. Goodnight, holotype ♂ (AMNH).

ADDITIONAL MATERIAL EXAMINED: **MEXICO:** *Chiapas*: Municipio de Cacahuatan: Cacahuatan, 15°03′37″N 92°08′45″W, 941 m, 7.iii.2017, G. Contreras, J. Cruz, J. Mendoza, and L. Olguín, 2 ♂, 2 imm. (CNAN DNA-Sz225).

TABLE 7

Measurements (mm) of the short-tailed whipscorpions, *Heteroschizomus goodnightorum* Rowland, 1973, stat. nov., and *Heteroschizomus kekchi*, sp. nov. (Schizomida: Hubbardiidae Cook, 1899)
Material deposited in the National Collection of Arachnida (CNAN) at the National Autonomous University of Mexico and the American Museum of Natural History (AMNH).

		H. goodnightorum		***H. kekchi***	
Sex		♀		♂	♀
Collection		CNAN	CNAN	CNAN	AMNH
Number		Sz0171	Sz0163	T1280	
Total length		3.6	3.0	3.8	3.1
Propeltidium	Length	1.0	0.9	1.1	1.0
	Width	0.6	0.5	0.6	0.6
Flagellum	Length	-	0.2	0.9	0.3
	Width	-	0.1	0.2	0.1
	Height	-	0.1	0.1	0.1
Pedipalp	Trochanter length	0.3	0.3	0.3	0.4
	Femur length	0.4	0.4	0.4	0.4
	Patella length	0.4	0.4	0.4	0.4
	Tibia length	0.4	0.3	0.4	0.4
	Tarsus length	0.4	0.2	0.2	0.2
	Total length	1.9	1.5	1.8	1.8
Leg I	Coxa length	0.4	0.4	0.6	0.5
	Trochanter length	0.3	0.3	0.3	0.3
	Femur length	0.9	0.8	1.3	1.0
	Patella length	1.0	0.9	1.6	1.2
	Tibia length	0.8	0.7	1.1	0.9
	Basitarsus length	0.3	0.2	0.4	0.3
	Telotarsus length	0.7	0.2	0.4	0.4
	Total length	4.3	3.6	5.7	4.6
Leg IV	Trochanter length	-	0.3	0.2	-
	Femur length	-	0.9	1.2	-
	Patella length	-	0.4	0.5	-
	Tibia length	-	0.6	0.8	-
	Basitarsus length	-	0.5	0.7	-
	Telotarsus length	-	0.4	0.4	-
	Total length	-	3.0	3.8	-

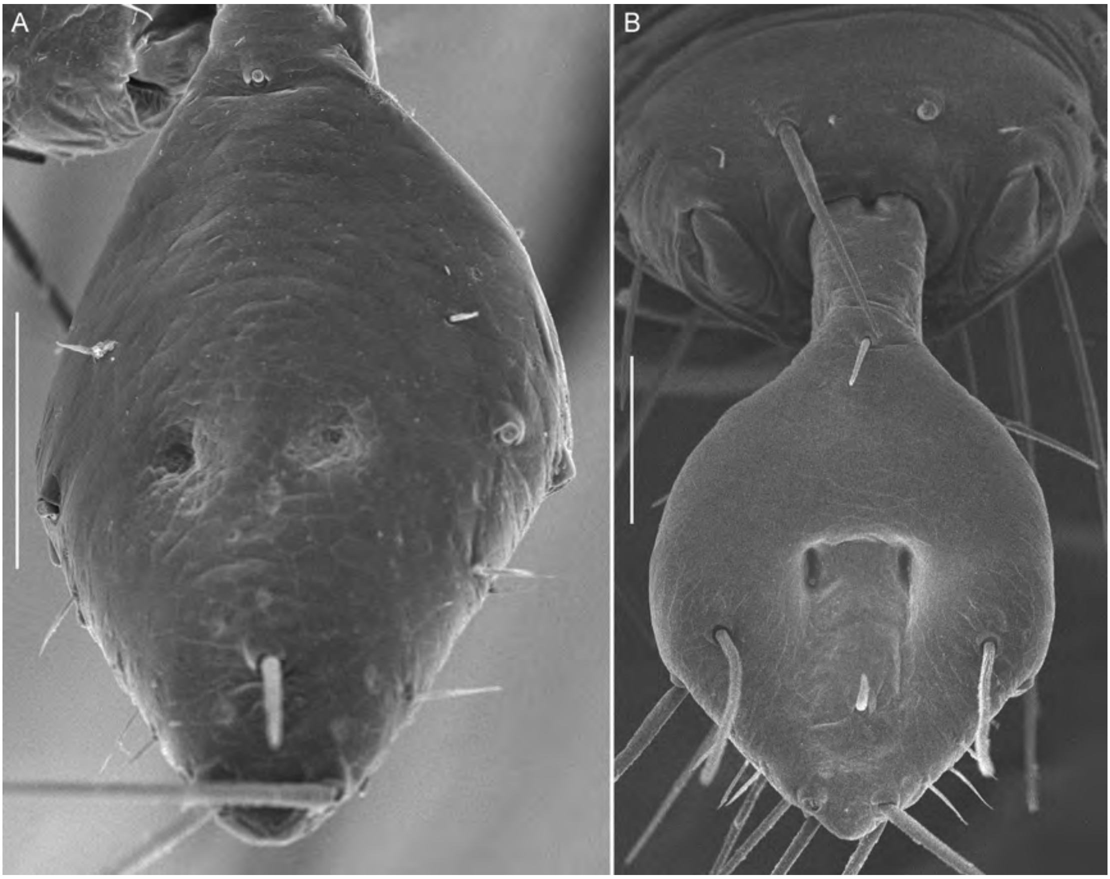

FIG. 20. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal view, illustrating two types of depressions. **A.** *Nahual bokmai*, sp. nov., ♂ (CNAN Sz197), pair of dorsosubmedian pits. **B.** *Stenochrus portoricensis* Chamberlin, 1922, ♂ (CNAN Sz93), submedian depression with two pits embedded in depression. Scale bars = 100 µm.

Municipio de Tapachula: San José Tacaná, 15°04′07″N 92°05′26″W, 1298 m, 7.iii.2017, G. Contreras, J. Cruz, J. Mendoza, and L. Olguín, 1 ♂ (CNAN DNA-Sz250).

***Heteroschizomus silvino* (Rowland and Reddell, 1977)**, comb. nov.

Schizomus silvino Rowland and Reddell, 1977: 80, 81, 86, 89, 96, 97, 99, 100, figs. 3, 19–21; Rowland, 1975b: 35, 167, 168, 188, 257–259, 261–269, map 4, figs. 237, 245, 246; Rowland and Reddell, 1979a: 163; Reddell, 1981: 54, 126; Rowland and Reddell, 1981: 19, 21–25, figs. 1, 4, 12, 13; Reddell and Cokendolpher, 1995: 6, 115.

Stenochrus silvino: Reddell and Cokendolpher, 1991: 18; 1995: 6, 12, 19, 102, 115; Harvey, 2003: 126; Armas, 2004: 52; Villarreal et al., 2008: 64.

TYPE MATERIAL: *Schizomus silvino*: **GUATEMALA:** *Izabal Departament*: Gruta de Silvino, 34 km W of Puerto Barrios, 20–22.viii.1969, S. and J. Peck, holotype ♂, 3 ♂, 7 ♀ paratypes (AMNH).

Natural History: *Heteroschizomus silvino*, comb. nov., is endemic to Grutas de Silvino, a small cave in which specimens were collected near the entrance and in the main gallery, walking on the walls in the penumbra area.

Additional Material Examined: **GUATEMALA:** *Izabal Departament*: Cayuga, Grutas de Silvino, 15°32′49″N 88°42′01″W, 64 m, D. Barrales and R. Monjaraz 17.viii.2017, 3 ♂, 1 ♀ (AMCC [LP 14556]), 3 ♂, 1 ♀ (CNAN DNA-Sz267).

Nahual, gen. nov.

Figures 3, 6, 7F, 9A, B, 10B, 11A, 12B, 13F, 14C, 19G–I, 20A, 21G–L, 22A, B; tables 1, 3, 8

Stenochrus (part): Reddell and Cokendolpher, 1991: 1, 3.

Schizomus mexicanus group (part): Rowland 1975b: 37, 39, 164, 165, 167, 168, 173, 185, 209, 214, 216, 218, 220, 222, 224, 228, 255, 280, 301, 303, 320, 321, 348–350, 365, 366, 368, 369, 376, 387, 390–393, 395; Rowland and Reddell, 1979a: 165, 171; 1979b: 90, 107; 1980: 1–10, 11, 15–20; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20, 41; Reddell and Cokendolpher, 1986: 32, 34; Camilo and Cokendolpher, 1988: 53, 57; Armas, 1989a: 7; Armas and Abud-Antun, 1990: 14, 18; Reddell and Cokendolpher, 1991: 1, 3; 1995: 82, 99, 101–104; Krüger and Dunlop, 2010: 52; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781–783, 804; 2018: 189, 212.

Type Species: *Schizomus pallidus* Rowland, 1975 [= *Nahual pallidus* (Rowland, 1975), comb. nov.], type species, here designated.

Diagnosis: *Nahual*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger with lamella or single tooth (in *Nahual caballero* (Monjaraz-Ruedas and Francke, 2018), comb. nov.) (fig. 12B, C); single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (except in *N. bokmai*, sp. nov.) (fig. 13F). Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae (fig. 11A); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with mesal spur and projected, fan-shaped apical process (fig. 7F); femur Fv_1 and Fv_2 setae spiniform, Fvr_{1-3} setae present (seta Fvr_4 present in *N. lanceolatus*, comb. nov., polymorphic in *N. bokmai* and *N. pallidus*, comb. nov.); patella with four or five acuminate *Pe* setae and five feathered *Pm* setae; tibial setal formula 5(6)-5-6 (*Ter-Tmr-Tir*) (fig. 14C). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, elliptical (lanceolate in *N. lanceolatus*), with pair of dorsosubmedian circular depressions separated from each other (pits), or circular slumps (in *N. caballero*) (figs. 19G–I, 20A); flagellum (♀) with two annuli (fig. 21G–L). Spermathecae (♀) with two pairs of lobes, of similar width and length; median lobes with apex directed vertically, sclerotized along entire length, sclerotizations increasing in size, creating appearance of leafy tree (fig. 9A, B); lateral lobes with apex directed laterally, unsclerotized; lobes without bulbs; median lobe bases posterior to lateral lobe bases (fig. 10C, D), without duct openings; chitinized arch arrow shaped, with anterior branch linear, lateral tips lobed, wide, and projected; gonopod extremely wide and long, together with chitinized arch, creating appearance of an arrow.

Comparisons: Species of *Nahual*, gen. nov., resemble species of *Stenochrus* in the presence of a pair of dorsosubmedian pits in the male pygidial flagellum. However, the flagellum of *Nahual* possesses only one pair of pits, which are well separated from each other (fig. 20A), whereas the flagellum of *Stenochrus* possesses an additional dorsal depression associated with the pits, which

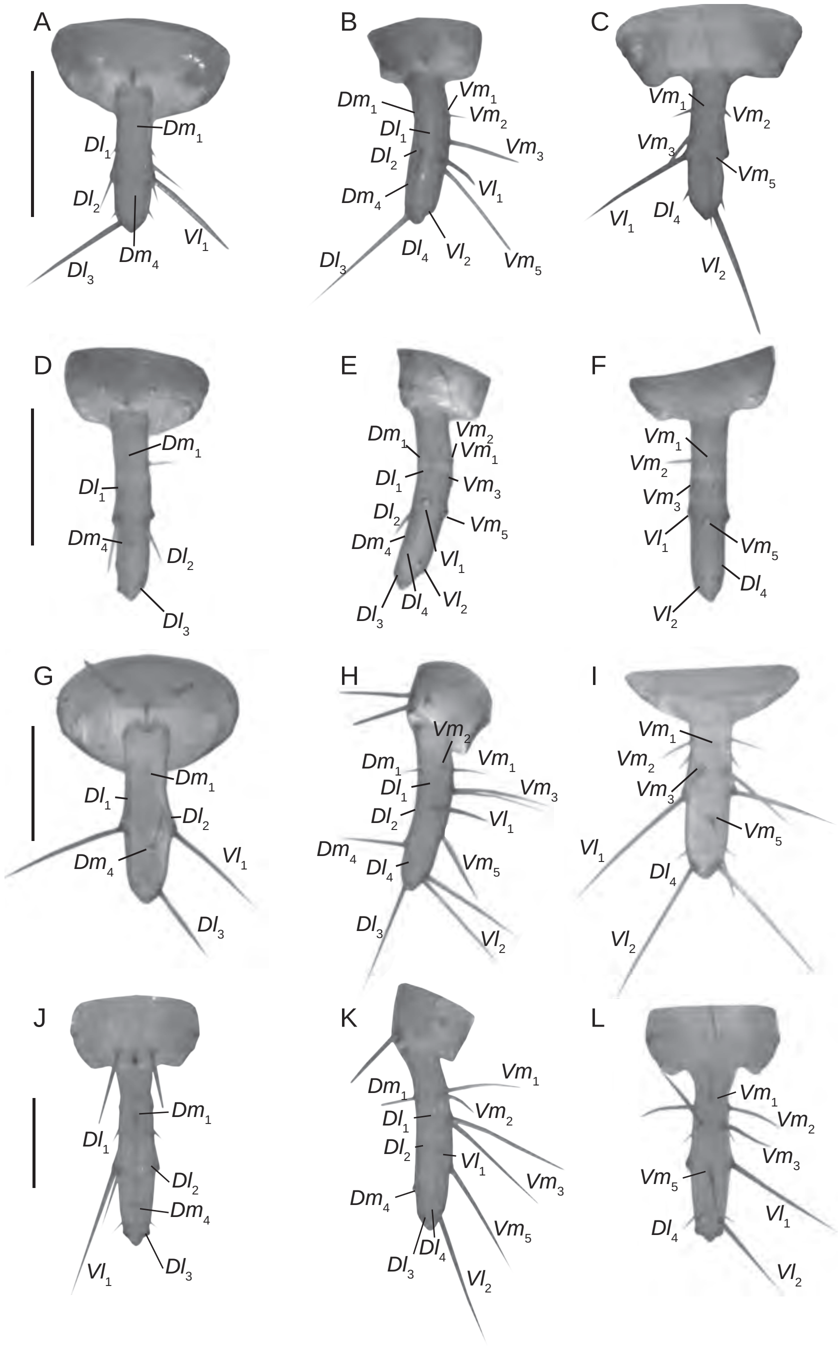

FIG. 21. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G, J**), lateral (**B, E, H, K**) and ventral (**C, F, I, L**) views. **A–C.** *Heteroschizomus goodnightorum* Rowland, 1973, stat. rev., ♀ (CNAN Sz171). **D–F.** *Heteroschizomus kekchi*, sp. nov., ♀ (CNAN T1281). **G–I.** *Nahual bokmai*, sp. nov., ♀ (CNAN T1283). **J–L.** *Nahual lanceolatus* (Rowland, 1975), comb. nov., ♀ (CNAN Sz130). Scale bars = 0.2 mm.

are situated closely adjacent to each other (fig. 20B). Additionally, the Dl_3 setae are situated posterior to the Vl_2 setae on the male pygidial flagellum in *Nahual*, whereas these setae are aligned in *Stenochrus*. Lastly, species of *Nahual* possess a lamella on the cheliceral movable finger, which is smooth in *Stenochrus*.

Species of *Nahual* also differ from species of *Baalrog*, gen. nov., and *Stenochrus* in the presence of spiniform setae Fv_1 and Fv_2 on the pedipalp femur, which are absent in the other genera. The median and lateral lobes of the female spermathecae are linear and similar in length in *Nahual*, whereas the median lobes are curved, and the lateral lobes reduced in length, in *Baalrog* and *Stenochrus*.

The female spermathecae of *Nahual* resemble those of *Heteroschizomus*, stat. rev., in possessing median and lateral lobes that are linear and similar in length. However, the lobes are sclerotized in *Nahual* and unsclerotized in *Heteroschizomus*.

Etymology: The generic name is a Nahuatl word used in several Mesoamerican cultures for wizards with the ability to transform themselves into animals. It is masculine in gender.

Included Species: *Nahual bokmai*, sp. nov.; *Nahual caballero* (Monjaraz-Ruedas and Francke, 2018), comb. nov.; *Nahual lanceolatus* (Rowland, 1975), comb. nov.; *Nahual pallidus* (Rowland, 1975), comb. nov.

Distribution: *Nahual*, gen. nov., is endemic to the Mexican states of Oaxaca and Veracruz (fig. 3). Species of *Nahual* are codistributed with species of *Baalrog*, gen. nov., in the Sierra de Zongolica of Veracruz, and extend southward to the Sierra Madre Oriental, in northern Oaxaca. However, species of *Nahual* are epigean, inhabiting tropical rainforests, and some species occur at elevations above 1800 m, whereas *Baalrog* are troglobitic, occurring mostly at elevations below 1600 m.

Natural History: Although the type localities of *N. lanceolatus*, comb. nov., and *N. pallidus*, comb. nov., are caves, the species of *Nahual*, gen. nov., are primarily epigean, occurring under rocks and inside rotten logs in tropical forests. Both *N. lanceolatus* and *N. pallidus* have been collected on the surface, suggesting they are facultatively cavernicolous. *Baalrog*, gen. nov., a strictly cavernicolous genus, is codistributed in the same area as *Nahual*.

Remarks: Rowland and Reddell (1980) assigned *Schizomus lanceolatus* Rowland, 1975, to the *goodnightorum* group, due to the lanceolate shape of the male pygidial flagellum (the female of this species was unknown), and *Schizomus pallidus* Rowland, 1975, to the *mexicanus* group, due to the shape of the male pygidial flagellum and the female spermathecae. The discovery of the female of *N. lanceolatus*, comb. nov., demonstrated a close relationship with *N. pallidus*, comb. nov., and supported their inclusion, together with the new species, in *Nahual*, gen. nov., based on their similar female spermathecae and male pygidial flagella (e.g., with a pair of dorsal pits), as well as DNA sequence data (fig. 6). The enlarged pygidial flagellum of the male of *N. lanceolatus* appears to be autapomorphic and differs from the enlarged flagella observed in species of *Heteroschizomus*, stat. rev., by the absence of a posterior constriction.

Nahual bokmai, sp. nov.

Figures 3, 6, 7F, 9A, 11A, 13F, 19G–I, 20A, 21G–I, 22A, B; table 1, 8

Type Material: **MEXICO:** *Veracruz*: Municipio de Xalapa: Cañadas de Rancho Nuevo (under the bridge), 19°30′17″N 96°47′35″W, 867 m, 19.vi.2013, A. Cruz, J. Cruz, J. Bokma, O. Francke, R. Monjaraz, and J. Sanchez, holotype ♂ (CNAN T1282), 6.ix.2015, J. Bokma, G. Contreras, O. Francke, J. Mendoza, and R. Monjaraz, 2 ♂, 2 ♀ paratypes (CNAN T1283).

Diagnosis: *Nahual bokmai*, sp. nov., may be separated from other species of *Nahual*, gen. nov., by the following characters: the pedipalp trochanter of the male bears a long, broad, and triangular apical process (fig. 7F); the male pygidial flagellum is elliptical with the posterior half acuminate (fig. 19G–I); the lateral tips of the chitinized arch of the female spermathecae (fig. 9A) are extremely widened; and the median and lateral lobes of the spermathecae are linear, with the lateral lobes slightly shorter than the median lobes.

COMPARISONS: *Nahual bokmai*, sp. nov., is most closely related to *N. pallidus*, comb. nov., but differs from the latter as follows: adults of *N. bokmai* are larger (4.7 mm) than adults of *N. pallidus* (3.4 mm); the apical process on the pedipalp trochanter of the male is broad, triangular and projected in *N. bokmai* but small, narrow and triangular in *N. pallidus*; the posterior half of the male pygidial flagellum is acuminate in *N. bokmai* but rounded in *N. pallidus*; and the median and lateral lobes of the female spermathecae are linear, with the lateral lobes slightly shorter than the median lobes, in *N. bokmai*, whereas the median lobes are curved along their entire length, and the median and lateral lobes are similar in length, in *N. pallidus*.

ETYMOLOGY: The specific name is a patronym, honoring John Bokma, a naturalist and amateur arachnologist, who has discovered many new species of arachnids in the surroundings of Xalapa, and guided the authors to the type locality of this species.

DESCRIPTION: The following description is based on the holotype male and paratype female (fig. 22A, B).

Color: Olive greenish.

Prosoma: Propeltidium with two setae on anterior process; three pairs of dorsal setae; ocular spots distinct, asymmetric. Metapeltidium 0.48 mm long, 0.74 mm wide. Anterior sternum with 10 setae, plus two sternophysial setae; posterior sternum with six setae.

Chelicerae: Movable finger with small blunt tooth; serrula with 18 (♂) or 19 (♀) teeth, guard tooth present (fig. 13F). Fixed finger with four small teeth between two primary teeth; setal group formula, 3-6-4-2-9-7-1-7 (♂) or 3-6-4-2-8-7-1-7 (♀); G1 with three spatulate setae, covered with spinose spicules; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally; G4 consisting of two setae, smooth, thickened basally, elongated apically; G5A with nine subequal setae, feathered apically and longer than fixed finger; G5B with seven feathered setae, subequal; G6 with one smooth seta, ca. 1/2 the length of movable finger; G7 with seven feathered setae, subequal.

Pedipalps: Pedipalps homeomorphic (fig. 7F); 2.16× (♂) or 1.7× (♀) longer than propeltidium. Trochanter with broad triangular apical process; prolateral surface with long medial spur. Femur 2.1× longer than high; retroventral margin with setae Fe_1 and Fe_5 acuminate, Fev_1 and Fev_2 spiniform; prolateral surface with row of three ventral spiniform setae (Fmv_{1-3}) and two dorsal spiniform setae (Fmd_2, Fmd_3). Patella with four acuminate *Pe* setae and five feathered *Pm* setae; without distinctive armature. Tibia setal formula, 5:5:6; *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetric.

Legs: Leg I, basitarsal-telotarsal proportions, 33:5:6:6:6:6:14; IV, femur 3.28× longer than high.

Opisthosoma: Tergite I with two pairs of microsetae anteriorly plus pair of *Dm* setae; II with three pairs of microsetae anteriorly plus pair of *Dm* setae; III–VII each with one pair of *Dm* setae; VIII with pairs of *Dm* and Dl_2 setae; IX with pairs of Dl_1 and Dl_2 setae and without pair of *Dm* setae. Segments X and XI telescoped, with pairs of Dl_2, Vm_2, Vl_1, and Vl_2 setae plus single Vm_1 seta; XII with pairs of *Dm*, Dl_1, Dl_2, Vm_1, Vm_2, Vl_1, and Vl_2 setae, without posterodorsal process. Sternites II–VII each with two irregular rows of setae; genital plate with many scattered microsetae.

Pygidial flagellum: Flagellum (♂) dorsoventrally compressed, elliptical (figs. 19G–I, 20A); 1.9× longer than wide; pair of dorsosubmedian pits present; seta Dm_1 situated over bulb base, Dm_4 situated posteriorly, Dl_2 aligned with Vl_1, Dl_3 situated posterior to Vl_2, pair of Vm_2 setae present, Vm_1 situated posterior to Vm_2; pair of anterodorsal microsetae between Dm_1 and Dl_2, pair of anterolateral microsetae on flagellar pedicel, two patches of microsetae between Vl_1 and Vl_2 (*msp*). Flagellum (♀) with three flagellomeres (fig. 21G–I); seta Dl_2 reduced, aligned with Vl_1, Dl_3 situated posterior to Vl_2, Vm_2 present, not reduced, Vm_1 aligned with Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 9A); median and lateral lobes linear, similar in width; lateral lobes slightly shorter than median lobes (ca. 3/4); median lobes sclerotized apically; median lobe bases anterior to lateral lobe bases. Chitinized arch U-shaped; anterior branch slightly visible, linear; lateral tip very wide, lobate. Gonopod long and wide, subtriangular.

Distribution: This species is known only from the type locality in the Municipio de Xalapa of the state of Veracruz, Mexico (fig. 3).

Natural History: All material was collected under rocks in a primary tropical rainforest along the banks of the Actopan River, near Xalapa. The locality is situated at the bottom of a deep, narrow glen, which maintains a high humidity.

Additional Material Examined: **MEXICO:** *Veracruz*: Municipio de Xalapa: Cañadas de Rancho Nuevo (under the bridge), 19°30′17″N 96°47′35″W, 867 m, 19.vi.2013, J. Bokma, G. Contreras, O. Francke, J. Mendoza, and R. Monjaraz, 3 ♂, 7 ♀ (CNAN Sz197), 6.ix.2015, J. Bokma, A. Cruz, J. Cruz, O. Francke, R. Monjaraz, and J. Sanchez, 3 ♂ (AMCC [LP 14519]), 2 ♀ (CNAN Sz198).

Nahual caballero (Monjaraz-Ruedas and Francke, 2018), comb. nov.

Stenochrus caballero Monjaraz-Ruedas and Francke, 2018: 199–202, figs. 29–42, 71.

Type Material: *Stenochrus caballero*: **MEXICO:** *Oaxaca*: Municipio de San José Tenango: Cerro Caballero, 18°08′32″N 96°42′57″W, 938 m, 10.iv.2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke and J. Mendoza, holotype ♂ (CNAN T1157), 28.viii.2008, J. Cruz, 1 ♂, 1 ♀ paratypes (CNAN T1158); Pozo de Águilas, 0.6 km N, 18°11′52″N 96°40′37″W, 327 m, 11.iv.2014, G. Contreras, J. Cruz, S. Davlantes, O. Francke, and J. Mendoza, 1 ♂, 1 ♀ paratypes (CNAN T1159).

Remarks: *Nahual caballero*, comb. nov., differs markedly from other species of the genus in several respects, e.g., the presence of a tooth instead of a lamella on the cheliceral movable finger, three *Pe* setae and four *Pm* setae on the pedipalp patella, a tibial setal formula of 4-3-5, and unsclerotized lobes of the female spermathecae. Despite these differences, however, the placement of this species within *Nahual*, gen. nov., was strongly supported by the phylogenetic analyses (fig. 6) based on the shape of the male pygidial flagellum and the female spermathecae, with lobes of similar length, a chitinized arch with lateral tips projected, and a wide and extremely long gonopod.

Additional Material Examined: **MEXICO:** *Oaxaca*: Municipio de San José Tenango: Cerro Caballero, 18°08′32″N 96°42′57″W, 938 m, 12.iv.2016, D. Barrales, G. Contreras, J. Cruz, J. Mendoza, and R. Monjaraz, 1 ♀ (AMCC [LP 14514]).

Nahual lanceolatus (Rowland, 1975), comb. nov.

Figures 3, 6, 9B, 14C, 21J–L; table 8

Schizomus lanceolatus Rowland, 1975a: 6, 7, 15–17, fig. 7; 1975b: 34, 167, 168, 257, 258, 261–268, map 4, figs. 235, 243; Rowland and Reddell, 1977: 80, 86, 99, l00, fig. 3; 1979a: 163; Reddell, 1981: 46, 126, 127, fig. 22; Rowland and Reddell, 1981: 19, 21, 23–27, figs. 1, 2, 10; Zacharda and Elliott, 1985: 477; Reddell and Cokendolpher, 1995: 6, 107.

Stenochrus lanceolatus: Reddell and Cokendolpher, 1991: 18; 1995: 6, 12, 18, 102, 107; Vázquez-Rojas, 1995: 34; 1996: 65; Harvey, 2003: 124; Villarreal et al., 2008: 64, 64; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32.

Type Material: *Schizomus lanceolatus*: **MEXICO:** *Veracruz*: Municipio de Ciudad Mendoza: Cueva del Diablo, 7.iii.1973, J. Reddell, holotype ♂ (AMNH).

SUPPLEMENTARY DESCRIPTION: The following description of the female is based on the Additional Material Examined.

Prosoma: Propeltidium with two apical setae; three pairs of dorsal setae.

Chelicerae: Movable finger with small lamella; serrula with 26 teeth, guard tooth present. Fixed finger with three small teeth between two primary teeth; setal group formula, 3-6-4-2-10-6-1-6.

Pedipalps: Pedipalps homeomorphic; 1.89× longer than propeltidium. Trochanter with small triangular apical process; prolateral surface with small medial spur. Femur 1.7× longer than high; retroventral margin with setae Fe_1, Fe_5, Fev_1, and Fev_2 spiniform; prolateral surface with row of four ventral spiniform setae (Fmv_{1-4}) and two dorsal spiniform setae (Fmd_2, Fmd_3). Patella with four acuminate *Pe* setae and five feathered *Pm* setae; without distinctive armature. Tibia setal formula, 5:5:6; *Ter* acuminate, *Tmr* and *Tir* feathered. Tarsal spurs asymmetric.

Opisthosoma: Segments X–XII not elongated.

Pygidial flagellum: Flagellum (♀) with three flagellomeres (fig. 21J–L); seta Dl_2 not reduced, situated anterior to Vl_1, Dl_3 situated posterior to Vl_2, Vm_2 present, not reduced, Vm_1 aligned with Vm_2; Dl_1 and Dl_4 microsetae present.

Female spermathecae: Two pairs of lobes (fig. 9B); median and lateral lobes similar in length and width; median lobes linear, lateral lobes sublinear, apex slightly curved laterally; median lobes sclerotized along entire length, lateral lobes sclerotized apically; median lobe bases posterior to lateral lobe bases. Chitinized arch rectangular; anterior branch linear; lateral tips elongated. Gonopod subtriangular; length ca. 2× width.

NATURAL HISTORY: Although the type locality of *N. lanceolatus*, comb. nov., Cueva del Diablo, is a large cave with a dark zone, adults of both sexes were also found on the surface in the foothills of Pico de Orizaba, Veracruz, indicating that this species is facultatively and not obligatorily cavernicolous.

REMARKS: Rowland and Reddell (1980) placed this species in the *goodnightorum* group of *Schizomus* because of the lanceolate shape of the male pygidial flagellum. The recent discovery of the female, as well as the comparison of DNA sequence data, has demonstrated that it is more closely related to the species accommodated in *Nahual*, gen. nov., however. The male flagellum lacks the posterior constriction observed in all species of *Heteroschizomus*, stat. rev., and shares with other species of *Nahual* a pair of pits separated from each other. The well-developed apical process of the pedipalp trochanter and the spiniform setae on the pedipalp trochanter, tibia, and patella further support the placement of this species.

ADDITIONAL MATERIAL EXAMINED: **MEXICO:** *Puebla*: Municipio de La Esperanza: La Calera (path to Pico de Orizaba), 18°52′04″N 97°18′51″W, 2729 m, 24.ii.2012, D. Barrales, J. Mendoza, A. Ortega, C. Santibañez, and A. Valdez, 2 ♂, 1 imm. (CNAN Sz130), 21.ix.2015, J. Arreguin, D. Barrales, O. Francke, D. Guerrero, and R. Monjaraz, 2 ♀ (CNAN DNA-Sz241), 1 ♀ (AMCC [LP 14538]). *Veracruz*: Municipio de Ciudad Mendoza: Cueva del Diablo, 18°47′00″N 97°11′27″W, 1385 m, 20.ix.2015, J. Arreguin, D. Barrales, O. Francke, D. Guerrero, and R. Monjaraz, 2 ♂, 2 ♀ (CNAN Sz169).

***Nahual pallidus* (Rowland, 1975)**, comb. nov.

Schizomus pallidus Rowland, 1975a: 6, 7, 13–15, 17, fig. 6; 1975b: 34, 166–169, 184–186, 188, 216–219, 222, 223, 228, 230, 280, 366–369, 396, map 5, figs. 166, 179, 196, 292; Rowland and Reddell, 1977: 80, 84, 87–89, fig. 2; 1979a: 163; 1980: 1, 2, 4, 5, 10, 11, 13, 15, 16, 19, figs. 1, 13, 26, 43; Reddell, 1981:17, 45, 46, 128, 129, 321, 324, fig. 23; Camilo and Cokendolpher, 1988: 57; Reddell and Cokendolpher, 1995: 6, 109.

Stenochrus pallidus: Reddell and Cokendolpher, 1991: 18; 1995: 6, 12, 18, 102, 103, 109; Vázquez-Rojas, 1995: 34; 1996: 65; Harvey, 2003: 125; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32; Monjaraz-Ruedas and Francke, 2018: 200, 201, 212.

Type Material: *Schizomus pallidus*: **MEXICO:** *Veracruz*: Municipio de Tlilapan: Cueva Macinga, 5.iii.1973, J. Reddell, holotype ♂, paratype ♀ (AMNH).

Natural History: Cueva Macinga, the type locality of *N. pallidus*, comb. nov., is a small, shallow cave without penumbra or dark zone. Specimens of *N. pallidus* were also collected in epigean habitats in the surroundings of Cueva Macinga and at another locality, Rancho San Fermín, indicating that this species is facultatively cavernicolous.

Additional Material Examined: **MEXICO:** *Veracruz*: Municipio de Atoyac: Rancho San Fermín, 18°54′30″N 96°49′19″W, 542 m, 16.i.2017, D. Barrales, G. Contreras, and R. Monjaraz, 3 ♂, 1 ♀ (CNAN DNA-Sz220), 1 ♂, 1 imm. (AMCC [LP 14524]). Municipio Amatlán de los Reyes: Cañada Blanca, 18°57′10″N 96°51′19″W, 788 m, 19.viii.2017, D. Barrales, A. Cruz, J. Mendoza, and R. Monjaraz, 1 ♀ (AMCC [LP 14557]).

Olmecazomus, nom. nov.

Figure 6; tables 1, 3

Olmeca Monjaraz-Ruedas and Francke, 2017: 399–413 (junior homonym of *Olmeca* Lamothe-Argumedo and Pineda-López, 1990).

Type Species: *Olmeca cruzlopezi* Monjaraz-Ruedas and Francke, 2017 [= *Olmecazomus cruzlopezi* (Monjaraz-Ruedas and Francke, 2017), comb. nov.], type species, by original designation.

Diagnosis: *Olmecazomus*, nom. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger without accessory tooth; single guard tooth at end of serrula; setal group G3 with setae G3-4 situated basally. Propeltidium anterior process with two anterior setae (one posterior to the other) and two pairs of dorsosubmedian setae; corneate eyes absent, one pair of eyespots present. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with prolateral spur and projected, digitiform apical process; femur Fe_2 setae spiniform, Fv_1 and Fv_2 setae forming well-developed spiniform setiferous tubercles, located retroventrally; tibia with Ter_7 and Tir_5 setae spiniform, strongly sclerotized. Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, elliptical or ovate, with pair of dorsosubmedian slumps fused posteriorly; flagellum (♀) with two annuli. Spermathecae (♀) with two pairs of lobes, lateral lobes wider and smaller than medial lobes (ca. 1/3 the length of median lobes); lateral lobes swollen, drop shaped; median lobes parenthesis shaped, with apex directed laterally, and without bulbs; lateral and median lobes apically sclerotized; chitinized arch V-shaped, without anterior branch; lateral tips lobed; gonopod wide and long.

Comparisons: Species of *Olmecazomus* resemble species of *Heteroschizomus* in the shape of the female spermathecae, with the lateral lobes approximately 1/4 the length of median lobes. However, the chitinized arch is V-shaped in *Olmecazomus* and mug shaped in *Heteroschizomus*. Males of *Olmecazomus* also resemble males of *Mayazomus* in the robust pedipalps and the presence of spiniform setiferous tubercles on the pedipalp femur. However, pedipalp tibial setae Ter_7 and Tir_5 are spiniform and prolateral tarsal spurs are absent in males of *Olmecazomus*, whereas Ter_7 and Tir_5 are acuminate, and large prolateral tarsal spurs are present in males of *Mayazomus*.

Etymology: The generic name is a compound word, derived from the word *Olmeca*, honoring the Olmecs, a prehispanic Mexican tribe, and *zomus*, a suffix commonly used for schizomid genera. It is masculine in gender.

Included Species: *Olmecazomus brujo* (Monjaraz-Ruedas and Francke, 2017), comb. nov.; *Olmecazomus cruzlopezi* (Monjaraz-Ruedas and Francke, 2017), comb. nov.; *Olmecazomus santibanezi* (Monjaraz-Ruedas and Francke, 2017), comb. nov.

REMARKS: The name *Olmeca* was first used for a trematode worm, *Olmeca* Lamothe-Argumedo and Pineda-López, 1990. A search in Neave's *Nomenclator Zoologicus* (2005) did not capture this name, which is valid and has nomenclatural priority according to the ICZN (2000). *Olmecazomus*, nom. nov., is therefore designated as a replacement name for members of the junior homonym, *Olmeca* Monjaraz-Ruedas and Francke, 2017.

Pacal Reddell and Cokendolpher, 1995

Figures 1, 6; tables 1, 3

Pacal Reddell and Cokendolpher, 1995: 1, 10, 13–15, 87, 88, 117, 140–142; Harvey, 2003: 114; Villarreal et al., 2008: 65; Montaño-Moreno and Francke, 2009: 33; Monjaraz-Ruedas, 2012: 63; Moreno-González and Villarreal, 2012: 73, 75; Monjaraz-Ruedas and Francke, 2015: 452, 454, 461, 464, 475; 2016: 782–784, 787, 790, 804; Monjaraz-Ruedas et al., 2016: 120, 131; Monjaraz-Ruedas and Francke, 2017: 399–401, 405, 408, 411.

Schizomus brasilensis group (part): Rowland 1975b: 37–39, 127–132, 134, 151, 152, 154, 156, 158, 160, 241, 305, 320, 321, 324, 335, 348–350, 360, 361, 363, 376, 384–388, 390, 393; Rowland and Reddell, 1979a: 165, 171; 1979b: 89, 90, 103, 105–112, 114, 116, 118; 1980: 1, 3; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20; Reddell and Cokendolpher, 1984: 172, 176, 177; 1986: 32; 1991: 3.

TYPE SPECIES: *Schizomus lacandonus* Rowland, 1975 [= *Pacal lacandonus* (Rowland, 1975)], type species, by original designation.

DIAGNOSIS: *Pacal* may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger with lamella; single guard tooth at end of serrula; setal group G3 with G3-4 setae situated posteriorly. Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae; corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with small prolateral spur and acuminate apical process; femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with three acuminate *Pe* setae and four feathered *Pm* setae; tibial setal formula 3-3-5(4) (*Ter-Tmr-Tir*). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) with small, inconspicuous posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, trilobed or rhomboid, with pair of dorsomedian circular depressions (pits) and pair of dorsosubmedian swellings; flagellum (♀) with two annuli. Spermathecae (♀) with one pair of lobes (two pairs in *Pacal moisii* (Rowland, 1973), comb. nov., and *Pacal tepezcuintle* (Armas and Cruz-López, 2009), comb. nov.), apex directed vertically, unsclerotized; lobes with large and prominent terminal bulbs and several duct openings; chitinized arch inverse arch shaped, with anterior branch curved and complete, lateral tips tapering; gonopod short and small.

COMPARISONS: Species of *Pacal* may be separated from other hubbardiid genera by the presence of only one pair of spermathecal lobes in the female, and large bulbs on the lobes, which are absent in the spermatheca of other North American genera. In addition, males possess a lamella on the cheliceral movable finger and a small, inconspicuous posterodorsal process on opisthosomal segment XII, unique among North American schizomid genera, except *Hubbardia*, which exhibits a large, well-developed posterodorsal process on segment XII.

INCLUDED SPECIES: *Pacal lacandonus* (Rowland, 1975); *Pacal moisii* (Rowland, 1973), comb. nov.; *Pacal stewarti* (Rowland, 1973); *Pacal tepezcuintle* (Armas and Cruz-López, 2009), comb. nov.; *Pacal trilobatus* (Rowland, 1975).

REMARKS: As redefined above, *Pacal* comprises three species previously assigned to the genus and two species newly transferred from *Stenochrus*. Although *P. moisii*, comb. nov., and

TABLE 8

Measurements (mm) of the short-tailed whipscorpions, *Nahual bokmai*, sp. nov., and *Nahual lanceolatus* (Rowland, 1975), comb. nov. (Schizomida: Hubbardiidae Cook, 1899)
Material deposited in the National Collection of Arachnida (CNAN) at the National Autonomous University of Mexico.

		N. bokmai					*N. lanceolatus*
Sex		♂			♀		♀
Collection		CNAN			CNAN		CNAN
Number		T1282			T1283		Sz0169
Total length		4.7	4.1	4.1	4.2	3.9	5.1
Propeltidium	Length	1.4	1.4	1.4	1.3	1.3	1.7
	Width	0.8	0.7	0.7	0.7	0.8	0.9
Flagellum	Length	0.5	0.5	0.5	0.3	0.4	0.5
	Width	0.3	0.3	0.2	0.1	0.1	0.1
	Height	0.2	0.1	0.1	0.1	0.1	0.1
Pedipalp	Trochanter length	0.7	0.6	0.5	0.5	0.5	0.7
	Femur length	0.7	0.6	0.6	0.5	0.6	0.7
	Patella length	0.7	0.6	0.6	0.5	0.6	0.7
	Tibia length	0.6	0.5	0.6	0.5	0.5	0.6
	Tarsus length	0.3	0.2	0.3	0.3	0.2	0.3
	Total length	3.0	2.6	2.6	2.3	2.4	3.1
Leg I	Coxa length	0.8	0.8	0.7	0.6	0.6	0.8
	Trochanter length	0.5	0.5	0.5	0.4	0.4	0.5
	Femur length	2.1	1.9	1.9	1.2	1.3	1.6
	Patella length	2.6	2.4	2.2	1.5	1.6	1.9
	Tibia length	1.8	1.7	1.3	1.1	1.2	1.4
	Basitarsus length	0.5	0.5	0.5	0.4	0.4	0.5
	Telotarsus length	0.7	0.7	0.7	0.5	0.5	0.5
	Total length	9.0	8.3	7.7	5.6	6.1	7.1
Leg IV	Trochanter length	0.4	0.3	0.4	0.4	0.4	-
	Femur length	1.7	1.6	1.6	1.2	1.4	-
	Patella length	0.7	0.6	0.7	0.5	0.6	-
	Tibia length	1.2	1.2	1.1	0.9	0.9	-
	Basitarsus length	0.6	1.0	1.0	0.8	0.9	-
	Telotarsus length	0.4	0.6	0.6	0.5	0.6	-
	Total length	5.1	5.4	5.5	4.3	4.8	-

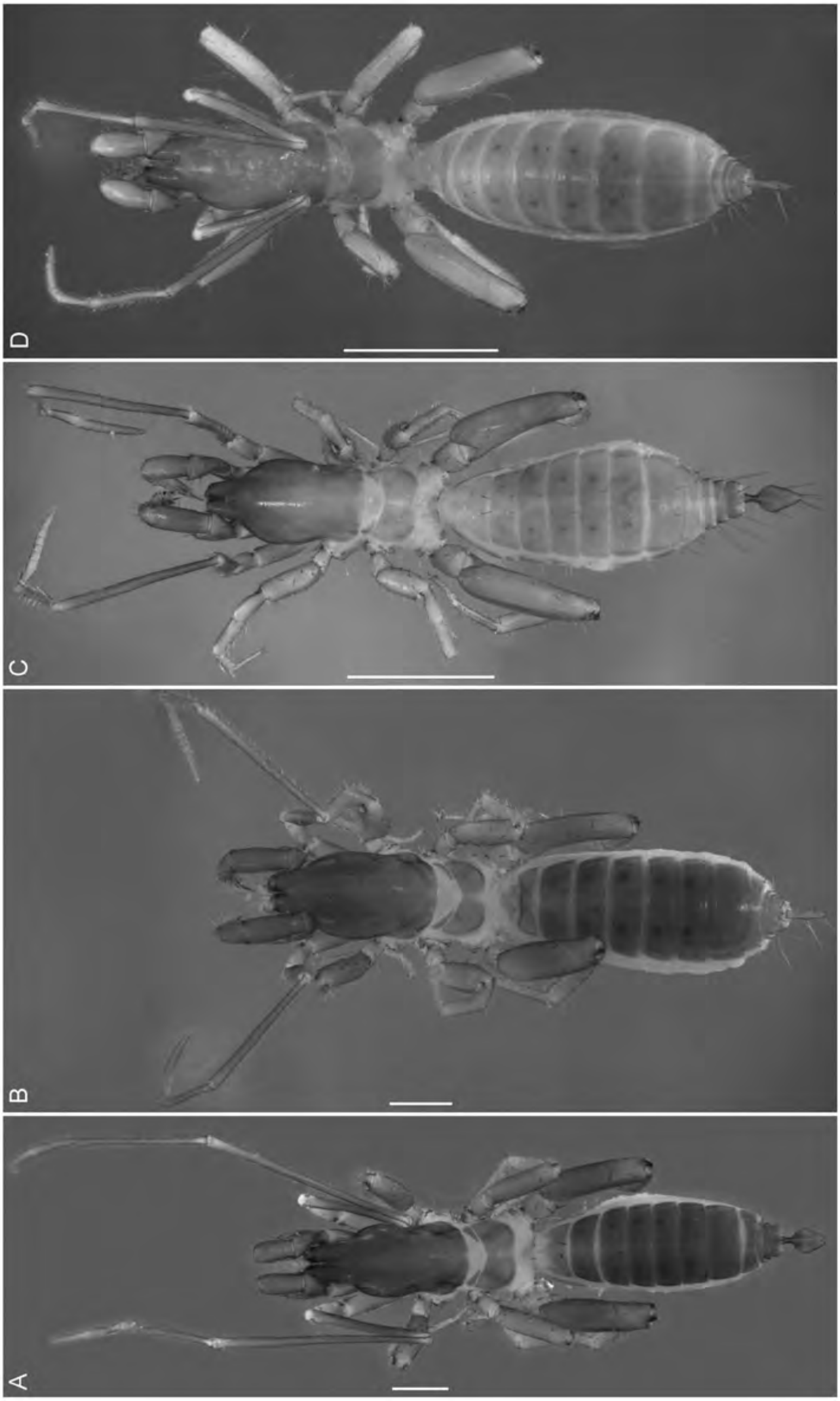

FIG. 22. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), habitus, dorsal view. **A, B.** *Nahual bokmai*, sp. nov.: **A.** ♂ (CNAN T1282); **B.** ♀ paratype (CNAN T1283). **C, D.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov.: **C.** ♂ (CNAN Sz25); **D.** ♀ (CNAN Sz25). Scale bars = 1 mm.

P. tepezcuintle, comb. nov., are morphologically similar and differ markedly from other members of *Pacal*, the two species grouped unequivocally with other species of the genus based on the molecular data (fig. 6). The description of other new species awaits a more detailed revision of the genus.

Schizophyxia, gen. nov.

Figures 2, 6, 7G, 9C, 10A, 13G, 22C, D, 23A–C, 24A–C; tables 1, 4

Schizomus mexicanus group (part): Rowland, 1975b: 37, 39, 164, 165, 167–168, 173, 185, 209, 214, 216, 218, 220, 222, 224, 228, 255, 280, 301, 303, 320, 321, 348–350, 365, 366, 368, 369, 376, 387, 390, 391–393, 395; Rowland and Reddell, 1979a: 165, 171; 1979b: 90, 107; 1980: 1–8, 10, 11, 15–20; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20, 41; Reddell and Cokendolpher, 1986: 32, 34; Camilo and Cokendolpher, 1988: 53, 57; Armas, 1989a: 7; Armas and Abud-Antun, 1990: 14, 18; Reddell and Cokendolpher, 1991: 1, 3; 1995: 82, 99, 101–104; Krüger and Dunlop, 2010: 52; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781–783, 804; 2018: 189, 212.

Type Species: *Schizomus lukensi* Rowland, 1973 [= *Schizophyxia lukensi* (Rowland, 1973), comb. nov.], type species, here designated.

Diagnosis: *Schizophyxia*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger smooth; single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (fig. 13G). Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae (fig. 11A); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with mesal spur, apical process acute, not projected (fig. 7G); femur Fv_1 and Fv_2 setae acuminate, Fvr_{1-3} setae present; patella with four acuminate *Pe* setae and four feathered *Pm* setae; tibial setal formula 3-3-4 (*Ter-Tmr-Tir*) (fig. 14D). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, spear shaped, with pair of shallow dorsosubmedian depressions (slightly visible in *S. lukensi*) not fused posteriorly (fig. 23A–C); flagellum (♀) with two annuli (fig. 24A–C). Spermathecae (♀) with two pairs of lobes; lateral lobes ca. 3/4 the length of median lobes, with apex directed laterally; median lobes linear or slightly curved laterally (parenthesis shaped); lobes unsclerotized apically and without bulbs; lobe bases aligned, with duct openings along entire length (figs. 9C, 10A); chitinized arch U-shaped, without anterior branch, lateral tips rounded; gonopod wide and short.

Comparisons: Species of *Schizophyxia*, gen. nov., resemble species of *Harveyus*, gen. nov., in the shape of the male pygidial flagellum and the female spermathecae. However, the male pygidial flagellum possesses a pair of submedian depressions and bulbs are absent from the median lobes of the female spermathecae in *Schizophyxia*, whereas the male pygidial flagellum possesses a pair of shallow pits and small bulbs are present on the median lobes of the female spermathecae in *Harveyus*. Additionally, species of *Schizophyxia* bear three pairs of dorsal setae on the propeltdium, whereas species of *Harveyus* bear only two. Although not observed in *Schizophyxia*, dimorphic males have been recorded in two species of *Harveyus*, i.e., *H. mexicanus*, comb. nov., and *H. mulaiki*, comb. nov.

Etymology: The generic name is a compound word, combining *schizo-*, referring to the order Schizomida, which means "split" in Greek, and *phyxia*, referring to fictional antlike soldiers in "De-Loused in the Comatorium," a short story by Cedric Bixler-Zavala and Jeremy Michael Ward of the progressive rock band, the Mars Volta. It is neuter in gender.

Included Species: *Schizophyxia bartolo* (Rowland, 1973), comb. nov.; *Schizophyxia lukensi* (Rowland, 1973), comb. nov.

Distribution: *Schizophyxia*, gen. nov., is distributed in the states of Nuevo León and Tamaulipas, northern Mexico (fig. 2), an area also inhabited by some species of *Harveyus*, gen. nov.

Natural History: The species of *Schizophyxia*, gen. nov., occur in seasonally dry habitats, inhabiting deciduous forest and caves, where the humidity is more optimal.

Remarks: Although the species of *Schizophyxia*, gen. nov., and *Harveyus*, gen. nov., are very similar morphologically, the two genera may be consistently separated by several characters of the male pygidial flagellum and the female spermathecae. The acquisition of DNA sequence data for *H. mulaiki*, comb. nov., and *H. reddelli*, comb. nov., are needed to test the generic placements of these species.

***Schizophyxia bartolo* (Rowland, 1973), comb. nov.**

Schizomus bartolo Rowland, 1973a: 6, 7, 13–16, 18, 19, figs. 11–13; 1973c: 135, 137; 1975b: 34, 166–169, 173, 174, 176, 177, 214, 215, 218, 219, 222, 223, 228, 229, 366–369, 394, map 5, figs. 158, 174, 193, 292; Dumitresco, 1977: 157; Rowland and Reddell, 1977: 80, 83, 84, fig. 2; 1979a: 163; 1980: 1, 2, 4–10, 15, 19, figs. 1, 5, 21, 40; Reddell, 1981: 16, 27, 126, 127, 128, 319, 324, fig. 23; Humphreys et al., 1989: 193; Reddell and Cokendolpher, 1995: 5, 105.

Stenochrus bartolo: Reddell and Cokendolpher, 1991: 18; 1995: 5, 12, 18, 102, 103, 105; Vázquez-Rojas, 1995: 33; 1996: 65; Ruíz and Coronado, 2002: 67; Harvey, 2003: 123; Armas and Víquez, 2010: 10; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32.

Type Material: *Schizomus bartolo*: **MEXICO:** *Nuevo León*: Municipio de Santa Catarina: Gruta de San Bartolo, 10 mi. SW Monterrey, 21.vi.1969, S. and J. Peck, holotype ♂, paratype ♀ (AMNH).

Additional Material Examined: **MEXICO:** *Nuevo León*: Municipio de Santa Catarina: Gruta de San Bartolo, 10 mi. SW Monterrey, ix.1971, T. Raines, 2 ♀, 2 imm. (AMNH), 29.iii.2018, M. de Luna-González, 1 subad. ♀, 1 imm. (CNAN DNA-Sz268).

***Schizophyxia lukensi* (Rowland, 1973), comb. nov.**

Schizomus lukensi Rowland, 1973c: 136–138, figs. 1, 4; 1975a: 34, 166–169, 174–177, 214, 215, 218, 219, 222, 223, 228, 229, 366–369, 394, map 5, figs. 160, 173, 191, 192, 292 (part, all records except Cueva de los Cuarteles); 1975a: 19, 20; Dumitresco, 1977: 157; Rowland and Reddell, 1977: 80, 83–85, 98, fig. 2; 1979a: 163; 1980: 1, 2, 4, 5, 7–10, 15, 19, figs. 1, 7, 20, 38; Reddell, 1981: 16, 39, 128, 129, 321, 324, fig. 23; Reddell and Cokendolpher, 1995: 5, 104, 107.

Stenochrus lukensi: Reddell and Cokendolpher, 1991: 18; 1995: 5, 12, 18, 101, 102, 107; Vázquez-Rojas, 1995: 34; 1996: 65; Ruíz and Coronado, 2002: 67; Harvey, 2003: 124; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32.

Type Material: *Schizomus lukensi*: **MEXICO:** *Tamaulipas*: Municipio de Gomez Farias: Cueva del Agua, 30 mi. SW Soto la Marina, 31.x.1970, W. Russell, G. and J. Ediger, holotype ♂, 2 ♂, 2 ♀ paratypes (AMNH).

Additional Material Examined: **MEXICO:** *Tamaulipas*: Municipio de Gomez Farias: Cueva de los Alvarez, 23°02′43″N 99°09′32″W, 335 m, 20.iv.2016, Q. Arreguin, G. Contreras, J. Cruz, D. Guerrero, R. Monjaraz, and G. Montiel, 5 ♂, 5 ♀ (CNAN DNA-Sz116), 1 imm. (AMCC [LP 14513]); Afuera de la Cueva de Ojo de Agua, 23°02′15″N 99°07′45″W, 129 m, 23.iv.2016, Q. Arreguin, G. Contreras, J. Cruz, D. Guerrero, R. Monjaraz, and G. Montiel, 3 ♂, 5 ♀ (CNAN DNA-Sz118), 1 ♂, 1 imm. (AMCC [LP 14515]); Sótano del Ojital, 23°03′11″N 117°07′49″W, 252 m, 23.xi.2005, P. Sprouse, 1 ♂, 1 ♀ (CNAN Sz25).

Stenochrus Chamberlin, 1922

Figures 5, 6, 7H, 9E, 10C, 13H, 14D, 20B, 23D–F, 24D–F, 25A, B; tables 1, 4

Stenochrus: Chamberlin, 1922: 11; Mello-Leitão, 1931: 19; Giltay, 1935: 6, 8; Werner, 1935: 334, 468, 469, 479, 480; Gertsch, 1940: 1; Takashima, 1941: 93; Petrunkevitch, 1945: 322; Takashima, 1947: 33; 1948: 99; Millot, 1948: 154; 1949: 559; Pierce, 1950: 102; 1951: 40; Cloudsley-Thompson, 1958: 122, 214; Savory, 1964: 155; Cloudsley-Thompson, 1968: 152; Levi and Levi, 1968: 122, 469; Shimojana, 1972: 100; Aoki, 1973: 197; Rowland, 1973b: 197, 200; Brignoli, 1974: 145; Rowland, 1975b: 25; Rowland and Reddell, 1977: 83; Savory, 1977: 140; Ribera, 1986: 106; Reddell and Cokendolpher, 1991: 18-19; Cokendolpher and Reddell, 1992: 39; Harvey, 1992: 78; Armas, 1995: 11; Reddell and Cokendolpher, 1995: 101; Vázquez-Rojas, 1996: 63, 65; Armas and Teruel, 1998: 47; Tourinho and Kury, 1999: 2, 5; Armas and Cokendolpher, 2001: 3, 4; Armas, 2002: 3, 6; Armas and Abud-Antun, 2002: 11; Armas and Teruel, 2002: 45; Teruel and Armas, 2002: 91, 92; Harvey, 2003: 123; Teruel, 2003: 40, 42, 66; Armas, 2004: 20; Armas and Colmenares-García, 2006: 27; Cutler and McCutchen, 2006: 263; Shultz, 2007: 224, 228, 245, 247, 249, 251; Teruel, 2007: 51; Villarreal et al., 2008: 67; Armas and Cruz-López, 2009: 20, 21; Armas and Teruel, 2009: 449; Korenko et al., 2009: 1; Montaño-Moreno and Francke, 2009: 33; Armas, 2010a: 55; 2010b: 205, 209, 211, 220; Armas and Víquez, 2010: 9, 10, 12, 18, 20; Krüger and Dunlop, 2010: 47, 49, 52; Armas, 2011: 18; Armas and Teruel, 2011: 335; Armas and Delgado-Santa, 2012: 139, 142; Monjaraz-Ruedas, 2012: 63, 64; Moreno-González and Villarreal, 2012: 73-76; Reddell, 2012: 788; Villarreal and García, 2012: 1, 5; Delgado-Santa and Armas, 2013: 37, 44; Moreno-González et al., 2014: 2, 21, 22; Palacios-Vargas et al., 2015: 8, 32; Villarreal et al., 2014: 371; Monjaraz-Ruedas and Francke, 2015: 452, 454; Souza and Lira, 2015: 766; Monjaraz-Ruedas and Francke, 2016: 782, 783, 789–791, 797; Monjaraz-Ruedas et al., 2016: 120, 126, 131; Villarreal et al., 2016: 24; Beron, 2017: 49; Clouse et al., 2017: 11; Monjaraz-Ruedas and Francke, 2017: 1, 2, 6, 10, 13; Moreno-González and Villarreal, 2017: 2; Teruel, 2017a: 46; Monjaraz-Ruedas and Francke, 2018: 189–191, 195, 203, 205, 210–212.

Schizomus pecki group (part): Rowland 1975b: 37, 39, 135, 137, 167, 168, 188, 209, 232, 233, 236, 238, 241, 246, 248, 250, 252, 255, 320, 321, 348–350, 376, 390, 396, 397; Rowland and Reddell, 1979a: 165, 171; 1979b: 90, 107; 1980: 1, 3, 22–26, 28, 29, 31; Reddell, 1981: 126; Rowland and Reddell, 1981: 19, 20; Cokendolpher and Reddell 1984b: 242; Reddell and Cokendolpher, 1986: 34, 37; Camilo and Cokendolpher, 1988: 53; Reddell and Cokendolpher, 1991: 1, 3; 1995: 101–103; Monjaraz-Ruedas and Francke, 2015: 452; 2016: 781, 783; 2018: 189, 212.

Type Species: *Stenochrus portoricensis* Chamberlin, 1922, by original designation.

Diagnosis: The species of *Stenochrus* are very conservative morphologically and some are troglomorphic. As in most genera of the order, *Stenochrus* may be separated from other hubbardiid genera by a combination of characters, as follows. Cheliceral movable finger smooth (fig. 12A); single guard tooth at end of serrula; setal group G3 with G3-4 setae situated posteriorly, except in *Stenochrus alcalai* Monjaraz-Ruedas and Francke, 2018, and *Stenochrus pecki* (Rowland, 1973) (fig. 13H). Propeltidium anterior process with two anterior setae (one posterior to the other) and two pairs of dorsosubmedian setae (fig. 11B); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps heteromorphic (as in *Stenochrus chimalapas* Monjaraz-Ruedas and Francke, 2018, and *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018), with femur, patella and tibia elongated; trochanter with small mesal spur and without apical process (except in *S. alcalai* and *S. gruta*) with an acute apical process and a bump, respectively) (fig. 7H); femur *Fv1* and Fv_2 setae acuminate (except in *S. pecki*, with spiniform setae), Fvr_{1-3} setae present; patella with three acuminate *Pe* setae and three or four feathered *Pm* setae; tibial setal formula 3-3-4 (*Ter-Tmr-Tir*) (except *S. alcalai* with 3-3-5) (fig. 14D). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) dorsoventrally compressed, cordate or elliptical, with dorsosubmedian medial depression, always associated with pair of closely adjacenr pits (figs. 20B, 23D–F); flagellum (♀) with two annuli (fig. 24D–F). Spermathecae (♀) with two pairs of lobes; lateral lobes smaller than (ca. half the length) and same width as median lobes, with apex directed laterally (figs. 9E, 10C); median lobes curved along entire length (parenthesis shaped) or curved apically (inverse J-shaped), with apex directed laterally, usually sclerotized medially to apically (fig. 10C); lobes without bulbs; median lobe bases posterior to lateral lobe bases (figs. 9E, 10C), with duct openings in both pairs of lobes; chitinized arch bowl-shaped, base widened, with slightly visible anterior branch, curved and not fused medially, lateral tips wide and sclerotized; gonopod wide and short.

Comparisons: Species of *Stenochrus* resemble species of *Nahual*, gen. nov., in the elliptical shape of the male pygidial flagellum and the presence of pits on its dorsal surface. However, a medial depression is present in the male flagellum and a small lamella absent on the cheliceral movable finger in *Stenochrus* (fig. 20), which are absent and present, respectively, in *Nahual*. Additionally, the pedipalp setae are acuminate setiform in *Stenochrus*, but spiniform in *Nahual*.

Stenochrus resembles *Baalrog*, gen. nov., in the shape of the female spermathecae, in which the lateral lobes are reduced. However, the lateral lobes are the same width and the median lobes markedly curved in *Stenochrus*, whereas the lateral lobes are narrower than the median lobes, which are only slightly curved apically, in *Baalrog*.

Included Species: *Stenochrus alcalai* Monjaraz-Ruedas and Francke, 2018; *Stenochrus chimalapas* Monjaraz-Ruedas and Francke, 2018; *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018; *Stenochrus guatemalensis* (Chamberlin, 1922); *Stenochrus leon* Armas, 1995; *Stenochrus pecki* (Rowland, 1973a); *Stenochrus portoricensis* Chamberlin, 1922.

Distribution: Species of *Stenochrus* inhabit tropical Central America and the Caribbean islands. All records reported for *S. portoricensis* are applicable to the genus, however, expanding its distribution to Europe (Clouse et al., 2017). Ongoing research on this widely distributed species, including phylogenetic analyses in preparation, suggests that the genus is endemic to the Caribbean and Central America, with multiple introductions into Europe from different sources (fig. 5).

Natural History: Although species of *Stenochrus* are primarily cavernicolous, some, notably *S. portoricensis*, are epigean and cavernicoulus, and usually found under large rocks. Some populations of *S. portoricensis* occur in dry, disturbed, or unnatural habitats, e.g., in greenhouses or associated with human waste, suggesting this species may be tolerant of desiccation and perturbation. Physiological tolerance together with parthenogenesis may explain its ability to successfully colonize new habitats over a large area.

Remarks: The presence of elongated pedipalps is dimorphic among conspecific males of some

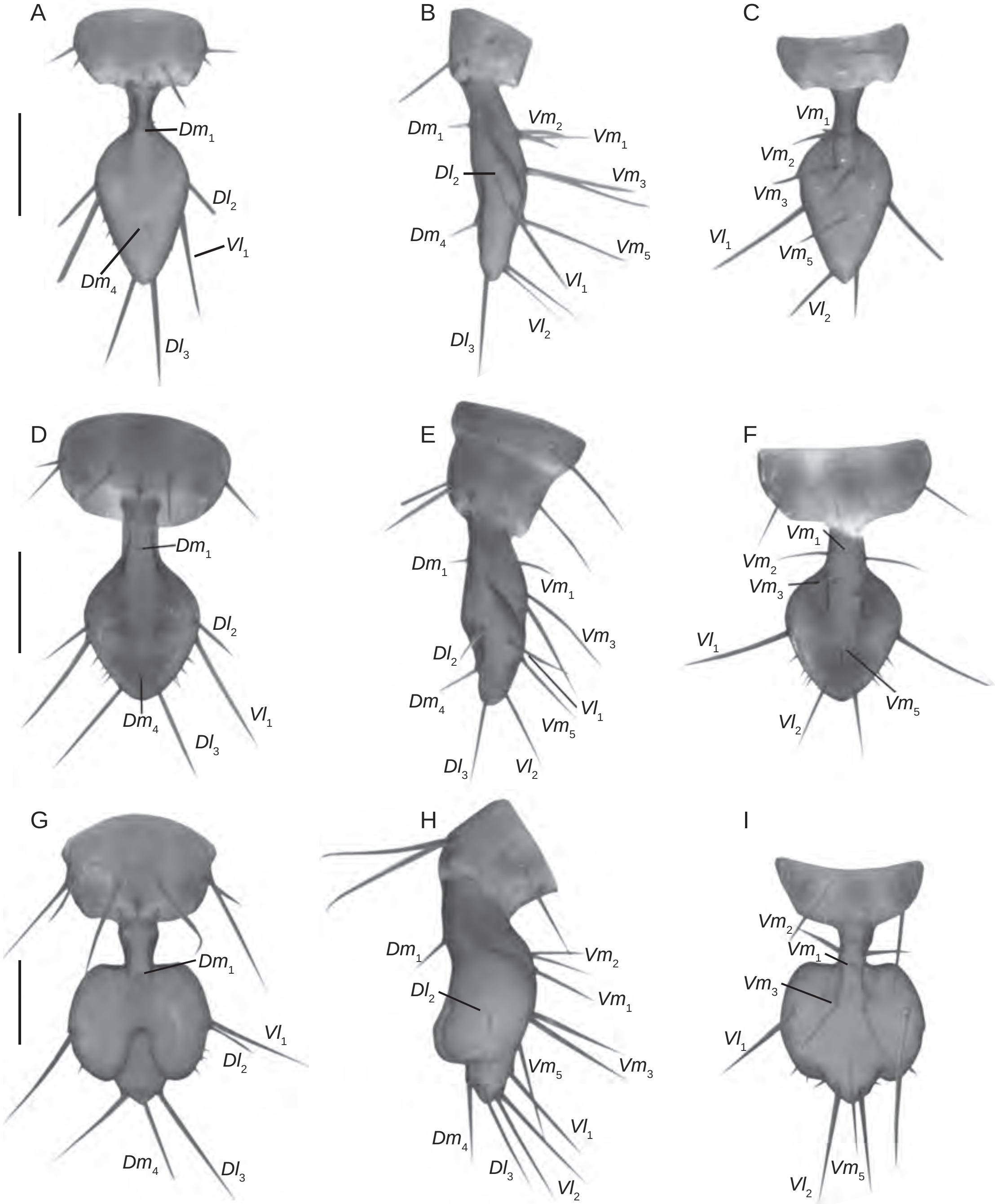

FIG. 23. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G**), lateral (**B, E, H**) and ventral (**C, F, I**) views. **A–C.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♂ (CNAN Sz25). **D–F.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018, ♂ (CNAN T1155). **G–I.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov., ♂ (CNAN T698). Scale bars = 0.2 mm.

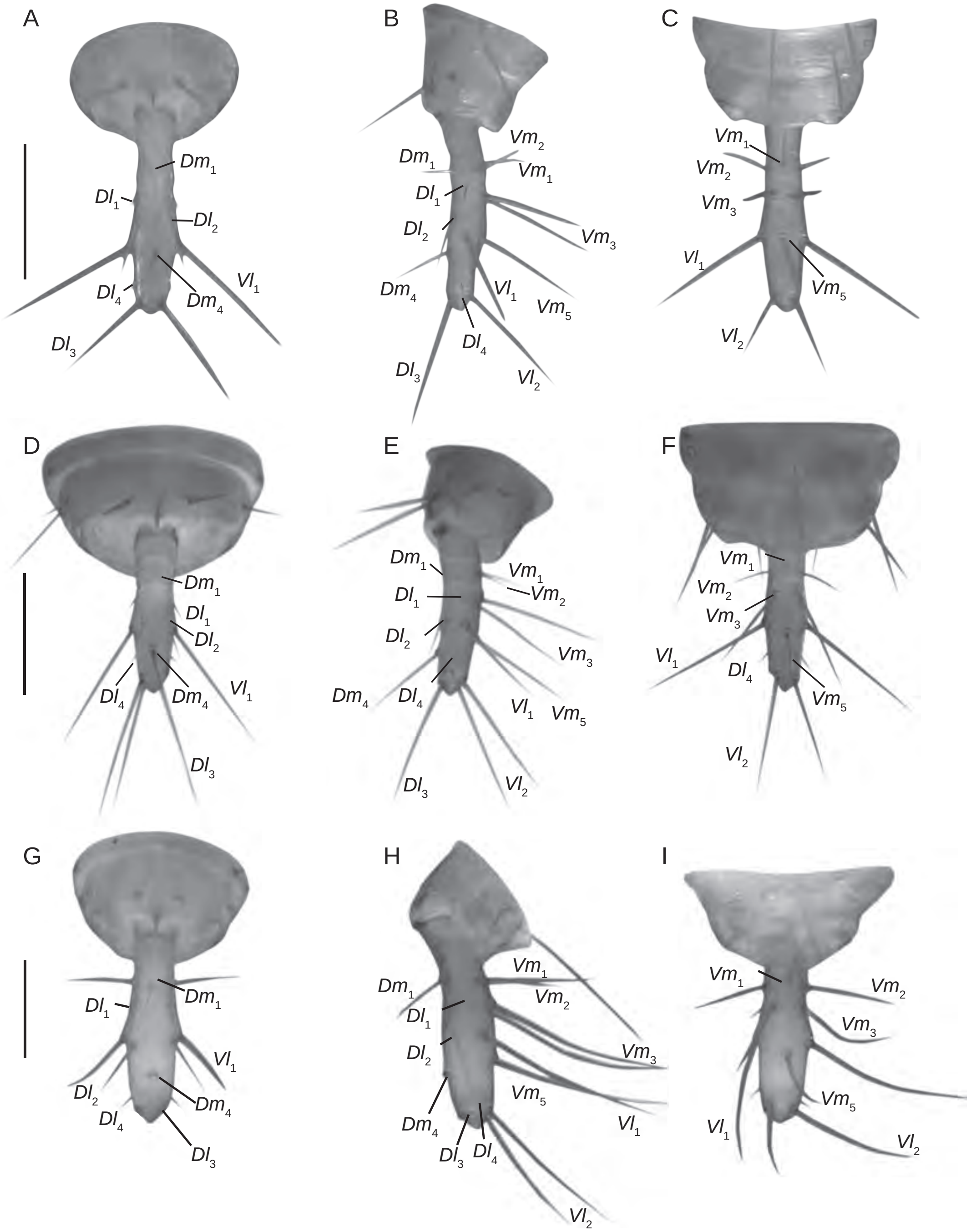

FIG. 24. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), pygidial flagellum, dorsal (**A, D, G**), lateral (**B, E, H**) and ventral (**C, F, I**) views. **A–C.** *Schizophyxia lukensi* (Rowland, 1973), comb. nov., ♀ (CNAN Sz25). **D–F.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018, ♀ (CNAN T1156). **G–I.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov., ♀ (CNAN T699). Scale bars = 0.2mm.

Stenochrus species. Pedipalp elongation results in modification of the apical process of the trochanter, as observed in *S. gruta* and *S. pecki.*

Stenochrus guatemalensis was assigned to the genus based on two pairs of dorsal setae on the propeltidium and female spermathecae with the lateral lobes reduced and the medial lobes apically sclerotized. Unfortunately, the precise type locality for *S. guatemalensis* is unknown and several attempts to collect it in Guatemala were unsuccessful.

The types and only known specimens of *S. leon*, deposited in Cuba, were not examined in the present study and the brief and poorly illustrated original description does not provide the level of detail required to accurately place it within the genera recognized herein. The species may belong to another genus because the lateral lobes of the female spermathecae are slightly shorter (i.e., less than 1/3 the length of the median lobes) than those of other species of *Stenochrus*. A detailed examination of the chelicerae and female spermathecae and/or DNA sequence data are needed to verify its generic placement. The species is retained within *Stenochrus* until additional evidence proves otherwise.

Monjaraz-Ruedas and Francke (2018) stated that *S. alcalai* bears three pairs of dorsal setae on the propeltidium, but after thorough reexamination the species was observed to bear only two pairs, consistent with the diagnosis of *Stenochrus.*

Stenochrus alcalai Monjaraz-Ruedas and Francke, 2018

Stenochrus alcalai Monjaraz-Ruedas and Francke, 2018: 203–206, 208, figs. 43–56, 71.

Type Material: **MEXICO:** *Oaxaca*: Municipio de San Pedro Jocotipac: La Laguna, 17°43′38″N 97°06′06″W, 2402 m, 23.viii.2015, D. Barrales, J. Cruz, O. Francke, R. Monjaraz, and J. Sánchez, holotype ♂ (CNAN T1160), paratype ♀ (CNAN T1161); El Tanque, 17°44′35″N 97°06′20″W, 2402 m, 22.viii.2016, D. Barrales, J. Cruz, O. Francke, R. Monjaraz, and J. Sánchez, 2 ♂, 1 ♀ paratypes (CNAN T1162).

Stenochrus chimalapas Monjaraz-Ruedas and Francke, 2018

Stenochrus chimalapas Monjaraz-Ruedas and Francke, 2018: 191–194, 203, 212, figs. 1–14, 71.

Type Material: **MEXICO:** *Oaxaca*: Municipio de Santa María Chimalapas: Cueva de Escolapa, 16°51′02″N 94°44′53″W, 219 m, 25.x.2016, E. Briones, A. Juárez, A. Valdez, and J. Valerdi, holotype ♂ (CNAN T1152), 1 ♂, 2 ♀ paratypes (CNAN T1153).

Additional Material Examined: **MEXICO:** *Oaxaca*: Municipio de Santa María Chimalapas: Cueva de Escolapa, 16°51′02″N 94°44′53″W, 219 m, 28.iii.2010, J. Cruz, O. Francke, C. Santibañez and A. Valdez, 2 ♂ (CNAN T1154), 25.x.2016, E. Briones, A. Juárez, A. Valdez, and J. Valerdi, 2 imm. (AMCC [LP 14533]).

Stenochrus gruta Monjaraz-Ruedas and Francke, 2018

Stenochrus gruta Monjaraz-Ruedas and Francke, 2018: 190, 195–198, 2012, figs. 15–28, 71.

Type Material: **MEXICO**: *Oaxaca*: Municipio de Sola de Vega: San Sebastián de las Grutas, Gruta de San Sebastián, 16°37′09″N 96°58′49″W, 1623 m, 1.vii.2013, G. Contreras, J. Cruz, J. Mendoza, C. Santibáñez, and A. Valdez, holotype ♂ (CNAN T1155), 2 ♂, 2 ♀ paratypes (CNAN T1156).

Additional Material Examined: **MEXICO**: *Oaxaca*: Municipio de Sola de Vega: San Sebastián de las Grutas, Gruta de San Sebastián, 16°37′09″N 96°58′49″W, 1623 m, 20.vii.2006, O. Francke, H. Montaño, C. Santibañez, A. Valdez, and G. Villegas, 10 ♀ (CNAN Sz199), 1.vii.2013, G. Contreras, J. Cruz, J. Mendoza, C. Santibáñez, and A. Valdez, 1 ♀, 1 imm. (AMCC [LP 14492]).

Stenochrus pecki (Rowland, 1973)

Schizomus pecki Rowland, 1973a: 6, 7, 16, 19–23, figs. 17–19; 1973c: 136; 1975a: 34, 135, 167, 168, 188, 209, 232, 234, 240–244, 246, 247, 250–253, map 4, figs. 216, 218, 221, 231; Dumitresco, 1977: 157; Rowland and Reddell, 1977: 80, 83, 84, 88, 96, 98, 99, fig. 2; 1979a: 163; 1979b: 104; 1980: 1, 16, 23–26, 29–32, figs. 63, 64, 66, 69, 79; Reddell, 1981: 16, 51, 126, 128, 129, 320, 324, fig. 23; Cokendolpher and Reddell, 1984b: 242; Reddell and Cokendolpher, 1986: 36; Camilo and Cokendolpher, 1988: 53; Reddell and Cokendolpher, 1995: 5, 109.

Stenochrus pecki: Reddell and Cokendolpher, 1991: 18; 1995: 5, 9, 12, 18, 102, 103, 109; Vázquez-Rojas, 1995: 34; 1996: 65; Harvey, 2003: 125; Armas, 2004: 51; Armas and Cruz-López, 2009: 23; Zawierucha et al., 2013: 359; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32; Monjaraz-Ruedas and Francke, 2016: 783, 784, 804, fig. 2C, D; Monjaraz-Ruedas et al., 2017: 102, 103, figs. 3C, D, 4G, H; Monjaraz-Ruedas and Francke, 2018: 203.

Type Material: *Schizomus pecki*: **MEXICO:** *Tabasco*: Municipio de Teapa: Grutas de Cocona, 2 mi. NE Teapa, 1.viii.1948, C. Goodnight, holotype ♂ (AMNH), 29 November 1971, O. McKenzie, paratype ♀ (AMNH).

Additional Material Examined: **MEXICO:** *Tabasco*: Municipio de Teapa: Grutas de Cocona, 2 mi. NE Teapa, 17°33′49″N 92°55′44″W, 27 m, 20.xii.2011, G. Contreras, E. Goyer, E. Hijmensen, and J. Mendoza, 1 ♂, 1 ♀ (CNAN Sz35).

Stenochrus portoricensis Chamberlin, 1922

Stenochrus portoricensis Chamberlin, 1922: 11, 12; Mello-Leitão, 1931: 19; Giltay, 1935: 8; Werner, 1935: 469; Takashima, 1941: 93; Bücherl, 1971: 382; Rowland, 1973b: 195, 197, 200; Brignoli, 1974: 145; Rowland, 1975b: 31, 186; Rowland and Reddell, 1977: 83; 1980: 14; Martín and Oromí, 1984: 267; Camilo and Cokendolpher, 1988: 55; Reddell and Cokendolpher, 1991: 3, 18; Muchmore, 1993: 33; 1993: 33; Humphreys, 1995: 178, fig. 4a, b; Baert et al., 1996: 16, fig. 8, map 5; Reddell and Cokendolpher, 1995: 2, 4–8, 10–12, 18, 19, 50, 92, 98, 99, 101–103, 110, 111, 156, fig. 79; Vázquez Rojas, 1995: 33; 1996: 65; Tourinho and Kury, 1999: 1, 3–5, figs. 1–4; Cokendolpher and Reddell, 2000: 187; Giribet and Ribera, 2000: 207; Armas, 2001: 53, 58, fig. 4A–D; Armas and Cokendolpher, 2001: 3, 4; Armas, 2002: 3, 5, 8; Armas and Abdun-Antun, 2002: 14; Giribet et al., 2002: 14, 62; Ruíz and Coronado, 2002: 67; Harvey, 2003: 125; Teruel, 2003: 39, 46, 47, 59, 66–68, fig. 49; Armas, 2004: 3, 4, 7, 10, 11, 16, 17, 20, 51, fig. 21A–C; Pérez and Teruel, 2004: 168, 172, 175, 176, figs. 9, 13; Teruel, 2004: 36, 40, 41, fig. 19; Wallberg et al., 2004: 571; Zonstein, 2004: fig. 12; Armas, 2005: 3; Teruel and Armas, 2005: 129, 132, fig. 5; Armas, 2006: 240; Harvey, 2006: 173; Spanga and Gillespie, 2006: 559; Klompen et al., 2007: 940; Harvey et al., 2008: 168; Pérez-Gelabert, 2008: 68; Santos et al., 2008: 1, 2, 5–7, figs. 7–9; Armas and Cruz-López, 2009: 20; Korenko et al., 2009: 1, 2, figs. 1–4; Santos and Pinto-da-Rocha, 2009: 42; Teruel and Infante, 2009: 386, 388–390, fig. 4; Armas, 2010b: 211, 218, 219; Armas and Víquez, 2010: 9, 18, 20; Armas et al., 2010: 499, 500; Dabert et al., 2010: 227; Krüger and Dunlop, 2010: 49; Kury et al., 2010: 568; Pepato et al., 2010: 5; Regier et al., 2010: 1080, fig. 1; Armas and Teruel, 2011: 335; Nedvěd et al., 2011: 539, 544, 546; Ortuño and Martínez-Pérez, 2011: 244; Armas and Delgado-Santa, 2012: 183, 185, fig. 2; Monjaraz-Ruedas, 2012: 64; Moreno-González and Villarreal, 2012: 62, 73; Teruel, 2012: 39, 40; Teruel et al., 2012: 97, 102, 104, 107, 110, 111, fig. 16; Villarreal and García, 2012: 1, 4; Armas, 2013: 93, 93; Christophoryová et al., 2013: 25, 27, 28, figs. 2A, B, 3A–E, 4A–E; Delgado-Santa and Armas, 2013: 37; He et al., 2013: 10; Santos et al., 2013: 1; Zawierucha et al., 2013: 357–360, fig. 1–3; Alegre Barroso and Barba Díaz, 2014: 54; Armas, 2014: 37; Barranco et al., 2014: 295, 296, 298, 300, fig. 3; Moreno-González et al., 2014: 22; Armas and Melic, 2015: 4, 5, fig. 15A–G; Armas and Rehfeldt, 2015: 55, 59, 60, fig. 16; Gallão et al., 2015: 1, 2, fig. 1, 3A–C; Guzmán et al., 2015: 478; Huber et al., 2015: 52; Monjaraz-Ruedas and Francke, 2015: 456, 461, 475; Palacios-Vargas et al., 2015: 32; Souza and Lira, 2015: 766, 767, fig. 1; Cabezas-Cruz et al., 2016: 307; Giupponi et al., 2016: 31; Monjaraz-Ruedas and Francke, 2016: 801; Monjaraz-Ruedas et al., 2016: 119, fig. 4E, F; Talanda, 2016: 281; Armas et al., 2017: 542; Beron, 2017: 37, 47, 49; Clouse et al., 2017: 5, 11, figs. 2–4; Delfín-González et al., 2017: 283, 284; Monjaraz-Ruedas and Francke, 2017: 399, 407; Ruiz and Valente, 2017: 89, 91; Šestáková et al., 2017: 19; Teruel, 2017a: 41, 45; 2017b: 81; Armas, 2018: 81, 87; Giupponi et al., 2018: 200–203, fig. 20A; Monjaraz-Ruedas and Francke, 2018: 189–191, 197, 212.

Schizomus antilus Hilton, 1933: 91, 92; Giltay, 1935: 6; Takashima, 1941: 94; Rowland, 1975b: 32, 186; Rowland and Reddell, 1977: 87; 1979a: 162; 1980: 2, 14; Armas and Alayón García, 1984: 9, 10; Camilo and Cokendolpher, 1988: 55; Armas, 1989a: 1, 23; Reddell and Cokendolpher, 1995: 98.

Schizomus cavernicolens Chamberlin and Ivie, 1938: 102, 103, figs. 4–7; Gertsch, 1940: 4; Takashima, 1941: 94; Pearse, 1945: 153; Cárdenas-Figueroa, 1950: 154; Rémy, 1961: 406; Nicholas, 1962: 181; Vandel, 1964: 116; 1965: 93; Reddell, 1971: 28; Rowland, 1971a: 117; 1973c: 135; Brignoli, 1974: 149; Rowland, 1975b: 186; Reddell, 1977: 230; Rowland and Reddell, 1977: 87; 1980: 14; Camilo and Cokendolpher, 1988: 55; Reddell and Cokendolpher, 1995: 110.

Schizomus portarricensis: Bolívar and Pieltain, 1944: 301 (lapsus calami).

Schizomus latipes: Cloudsley-Thompson, 1949: 261 [misidentification]; 1958: 123 (misidentification); Rémy, 1961: 407 (part, Cambridgeshire record only); Cloudsley-Thompson, 1968: 153, 154 (misidentification); Rowland and Reddell, 1977: 87 [misidentification].

Schizomus floridanus Muma, 1967: 18–20, unnumbered map, figs. 13–15; Rowland, 1971b: 304; 1973c: 135; 1975b: 186, 187; Brach, 1976: 97–99, figs. 1–3; Rowland and Reddell, 1977: 87; Gertsch, 1979: 21; Rowland and Reddell, 1980: 14; Borror et al., 1981: 123; Levi, 1982: pl. 94; Camilo and Cokendolpher, 1988: 55; Vine et al., 1988: 29; Borror et al., 1989: 107; Humphreys et al., 1989: 185, 189; Reddell and Cokendolpher, 1995: 5, 99, 110, 111.

Schizomus longimanus Rowland, 1971a: 119, 120, 124, 125, figs. 4–6, 17; Brignoli, 1973: 6–9, figs. 1, 2; Reddell, 1973: 38; Rowland, 1973a: 13, 16, 22, fig. 21; 1973c: 135, 137; Brignoli, 1974: 143, 144, 146, 147, 151, fig. 1b; Sbordoni et al., 1974: 19; Rowland, 1975b: 186; 1975b: 14, 15, 17, 19, 20; Dumitresco, 1977: 157; Rowland and Reddell, 1977: 87; 1980: 14; Camilo and Cokendolpher, 1988: 55; Armas, 1989a: 23; Reddell and Cokendolpher, 1995: 5, 99, 110, 111.

Schizomus portoricensis: Rowland, 1973b: 197; Peck, 1974: 19; 1975: 307; Rowland, 1975b: 18, 25, 32, 76, 137, 166–169, 185–206, 214–219, 224, 225, 366–369, 376, 377, 379, 383, 396, 397, map 5, figs. 161, 167–170, 181, 199–206, 292; Beck et al., 1976: 8; Reddell, 1977: 230; Rowland and Reddell, 1977: 79, 80, 81, 87–97, figs. 4–18; 1979a: 162, 165, 194; 1979b: 107; 1980: 1, 2, 4, 5, 7, 11, 13,

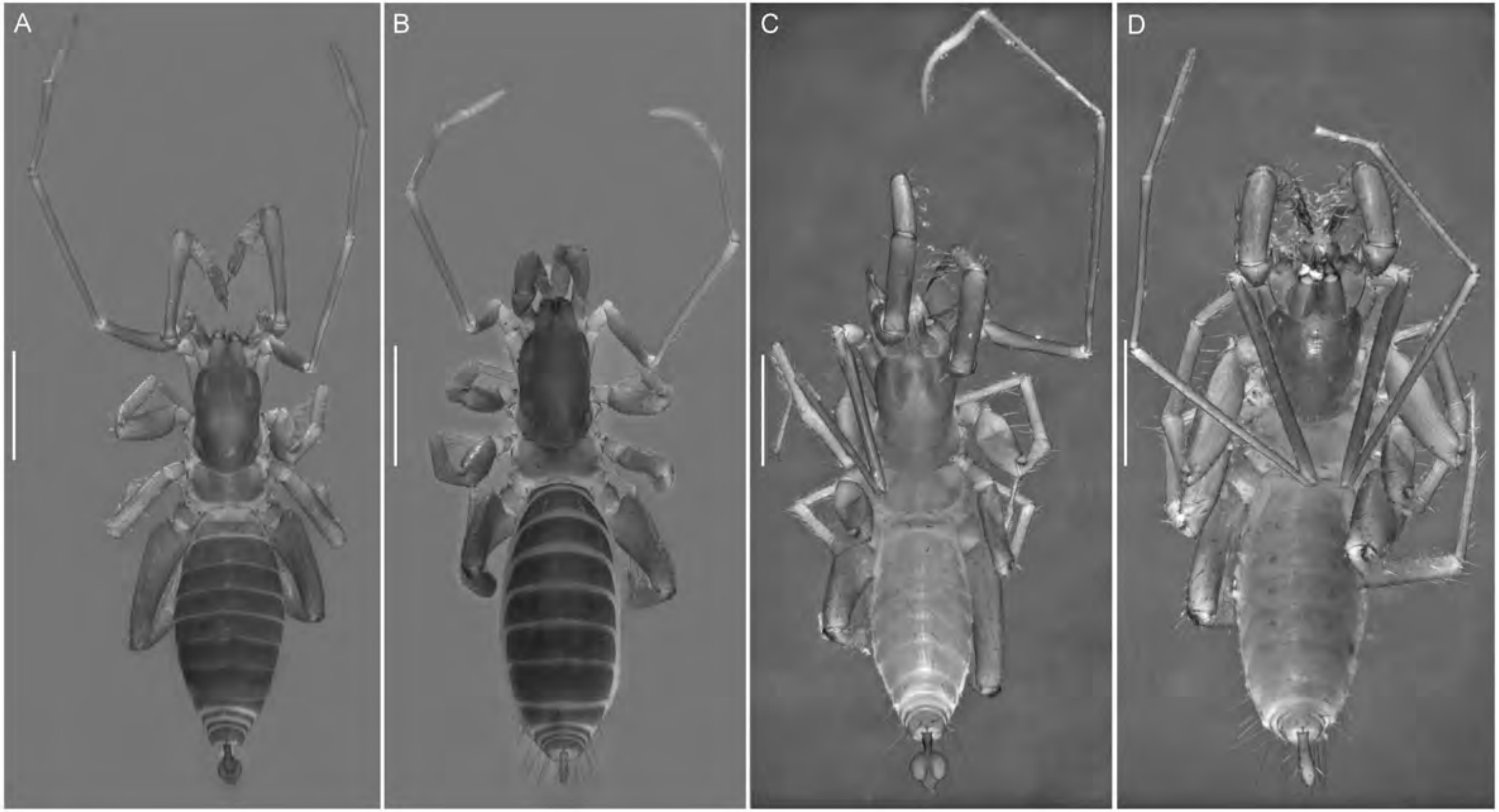

FIG. 25. Short-tailed whipscorpions (Schizomida: Hubbardiidae Cook, 1899), habitus, dorsal view. **A, B.** *Stenochrus gruta* Monjaraz-Ruedas and Francke, 2018: **A.** ♂ (CNAN T1155); **B.** ♀ paratype (CNAN T1156). **C, D.** *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov.: **C.** ♂ (CNAN T698); **D.** ♀ (CNAN T699). Scale bars = 1 mm.

14–16, 20, figs. 1, 6, 14–17, 28, 46–53; Sket and Iliffe, 1980: 873; Peck, 1981: 72; Reddell, 1981: 42, 50, 55–59, 68, 126, 127, fig. 22; Martín and Oromí, 1984: 265–270, fig. 2; Reddell and Cokendolpher, 1984: 173, 175; Martín et al., 1985: 40, 41, 43–45; Peck and Kukalova-Peck, 1986: 165; Reddell and Cokendolpher, 1986: 31–33; Ribera, 1986: 106, fig. 66; Camilo and Cokendolpher, 1988: 52–58, figs. 1, 6, 7; Armas, 1989a: 1, 2, 9, 23, 24, 34; 1989b: 3; Armas and Abud-Antun, 1990: 1, 5, 14–16, 19, figs. 7, 9; Peck, 1990: 368, 369; Oromi and Martín, 1992: 536; Peck, 1993: 42; Baert and Mahnert, 2015: 3, 15–17, 70–73, map 5, fig. 3.

Schizomus loreto Armas, 1977: 5–8, figs. 3, 4; 1984: 9; 1989a: l, 23; Reddell and Cokendolpher, 1995: 110.

Type Material Examined: *Schizomus floridanus*: **U.S.A.:** *Florida*: Dade County: Ross and Castellow Hammock, 1 ♀ holotype (AMNH). *Schizomus longimanus*: **MEXICO:** *Chiapas*: Municipio de Tuxtla Gutierrez: Cueva Cerro Hueco, 3 km SE Tuxtla Guitierrez, 18.viii.1967, J. Reddell, J. Fish, and M. Tandy, holotype ♂ (AMNH), paratype ♂ (AMNH), 2 ♀ paratypes (AMNH).

Material Examined: **BELIZE:** *Cayo District*: Belmopan, 2 ♀ (AMNH); Blue Hole National Park, 17° 08′49″N 88°40′29″W, 170 m, 6.xi.2013, R. Monjaraz and C. Santibañez, 1 ♀ (CNAN DNA-Sz197); Caves Branch, Buck's Bypass Cave, 1 ♀ (AMNH); Hummingbird Highway, 1 ♀ (AMNH). **COLOMBIA:** *Quindío Department*: Montenegro, Finca Hotel Bosque Nativo, 04°33′10″N 75°45′32″W, 1250 m, 10.xii.2011, A. Valdez 1 ♀ (CNAN Sz40). **DOMINICAN REPUBLIC:** *La Altagracia Province*: near Alto de Chavon, 18°29′27″N 68°55′04″W, 65.5 m, 15.vii.2004, J. Huff and E.S. Volschenk forested road cutting in cane fields, 1 imm. (AMCC [LP 3750]). **GUATEMALA:** Alta Verapaz, Coban, Reserva Natural Chahunpek, 16°00′35″N 90°38′56″W, 230 m, 20.viii.2017, D. Barrales and R. Monjaraz 1 ♀ (AMCC [LP 14554]); Santa Rosa, El Papayo, 14°08′17″N 90°33′52″W, 296 m, 3–4 July 2006, C. Avila, R. Estrada, J. Huff, D. Ortíz, and C. Víquez, 2 ♀ (AMCC [LP 6014]); Izabal, Río Sauce, 15 km E of El Estor, picnic area on river, 15°33′37″N 89°17′06″W, 13 m, 7.vii.2006, J. Huff, D. Ortíz, and C. Víquez, 2 ♀ (AMCC [LP 6016]). **HONDURAS:** *Santa Barbara Departament*: Municipio de Santa Barbara: San Antonio, 1 km NE Río Grande de Otoro, 14°46′28″N 88°10′15″W, 355 m, 28.ix.2008, M. Branstetter and C. Víquez, 1 ♀ (AMCC [LP 9475]). Municipio de Santa Rita: Desvio a Santa Rita, 3.4 km SW San Francisco de Ojuera, side of road, 14°44′08″N 88°13′16″W, 490 m, 28.ix.2008, M. Branstetter and C. Víquez, 1 ♀ (AMCC [LP 9473]). *Lempira Departament*: Municipio de La Iguala: La Telegrafía, side of road going to Gracias, before reaching Santa Rita, 14°45′58″N 88°14′31″W, 466 m, 28.ix.2008, M. Branstetter and C. Víquez, 2 ♀ (AMCC [LP 9474]). **JAMAICA:** *St. Ann Parish*: Falling Cave, Douglas Castle, 1 ♀ (AMNH). *Trelawny Parish*: Ulster Spring, ca. 1 km N, 18°20′39″N 77°30′47″W, 420 m, 18.vi.2005, S. Huber, 1 ♀ (AMCC [LP 5179]). **MEXICO:** *Campeche*: Municipio de Calakmul: Reserva Ejidal Ley de Fomento Agropecuario, 3.5 km from Cristobal Colon, 17°59′13″N 89°24′54″W, 243 m, 14.x.2011, D. Barrales, D. Candia, O. Francke, G. Montiel, and A. Valdez, 10 ♀ (CNAN Sz50); outside Cueva de Balam-kú (Volcán de los Murciélagos), 18°31′15″N 89°49′31″W, 191 m, 12.x.2011, D. Barrales, D. Candia, O. Francke, G. Montiel, and A. Valdez, 5 ♀ (CNAN Sz51). *Chiapas*: Municipio de Cacahuatan: Bridge Faja de Oro, 15°02′20″N 92°10′17″W, 658 m, 6.xii.2015, G. Contreras, H. Montaño, and L. Olguin, 1 ♀ (CNAN DNA-Sz125), 7.iii.2017, J. Cruz, G. Contreras, J. Mendoza, and L. Olguín, 2 ♀ (AMCC [LP 14546]). Municipio de Marquez de Comillas: Playón de la Gloria, trail Rockera, 16°09′01″N 90°50′47″W, 150 m, 13.xii.2014, G. Contreras and L. Olguín, 1 ♀

(CNAN Sz159). Municipio de Ocosingo: Arroyo Nayte, Sierra la Cojolita, 16°47′39″N 91°02′32″W, 194 m, 18.x.2006, J. Ballesteros, O. Francke, H. Montaño, and A. Valdez. 1 ♂, 3 ♀ (CNAN Sz10), 28.vii.2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 4 ♂, 4 ♀ (CNAN Sz93); El Aserradero 16°47′07″N 91°02′17″W, 205 m, 18.x. 2006, J. Ballesteros, O. Francke, H. Montaño, and A. Valdez, 37 ♀ (CNAN Sz11), 28.vii.2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 35 ♀ (CNAN Sz108); El Carton, 5 km W Frontera Corozal, 16°47′11″N 90°55′41″W, 153 m, 6.ix. 2005, M. Cordoba, O. Francke, A. Jaimes, H. Montaño, and A. Valdez, 30 ♀ (CNAN Sz15); Cueva Grande, reserva Chan-Kin, 16°41′29″N 90°49′26″W, 144 m, 19.x.2006, C. Ballesteros, O. Francke, H. Montaño and A. Valdez, 3 ♀ (CNAN Sz16); Frontera Benemerito, 10 km from junction, 16°43′21″N 90°55′29″W, 162 m, 20.x. 2006, C. Ballesteros, O. Francke, H. Montaño, and A. Valdez, 2 ♀ (CNAN Sz19). Municipio de Ocozocuautla: Cueva de los Bordos, 16°49′46″N 93°31′32″W, 615 m, 14.iv.2014, O. Sanchez and K. Zárate, 1 ♂ (CNAN DNA-Sz24). Municipio de San Fernando: Cueva de la Cañada, Ejido Benito Juárez, 16°53′50″N 93°07′59″W, 926 m, 3.vii.2014, K. Zárate, 1 ♂ (CNAN Sz158); Cueva del Guano, 16°48′50″N 93°10′19″W, 840 m, 2.iv.2014, G. Contreras and G. Montiel, 2 ♀ (CNAN Sz185); Cueva de la Mano, Ejido Miguel Hidalgo, 16°51′52″N 93°14′52″W, 1043 m, 18.vi.2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 6 ♂, 6 ♀ (CNAN Sz2); Cueva de Las Abejas, 16°50′55″N 93°14′36″W, 1190 m, 19.vi.2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 1 ♂, 5 ♀ (CNAN Sz3). Municipio de Tuxtla Gutierrez: Tuxtla Gutierrez, 16°46′27″N 93°08′02″W, 652 m, 4.viii.2006, PBN, 1 ♂ (CNAN Sz89). *Colima*: Municipio de Villa de Alvarez: Manantial Agua Fria, 19°16′23″N 103°52′40″W, 458 m, 23. vi.2014, G. Contreras and G. Montiel, 1 ♀ (CNAN DNA-Sz63). *Guerrero*: Municipio de Chilpancingo: Cueva del Borrego, Omiltemi, 17°33′19″N 99°39′17″W, 1997 m, 21 September 2012, G. Contreras, J. Cruz, J. Mendoza, and D. Ortíz, 1 imm. (CNAN Sz94), 1 ♀ (AMCC [LP 14498]). *Jalisco*: Municipio de Puerto Vallarta: Calle Olas Altas, 20°35′56″N 105°14′14″W, 32 m, 21.ii. 2015, G. Contreras, 3 ♀ (AMCC [LP 14505]). *Nayarit*: Municipio de San Blas: Cueva del Naranjo, 21°28′46″N 105°04′39″W, 580 m, 17.vi. 2015, G. Contreras and G. Montiel, 4 ♀ (CNAN Sz177). *Tabasco*: Municipio de Macuspana: outside Cueva de Agua Blanca, 17°37′12″N 92°28′12″W, 193 m, 30.ix.2014, G. Contreras and G. Montiel, 2 ♀ (CNAN Sz180). *Quintana Roo*: Municipio de Bacalar: Bacalar Lake, 18°38′51″N 88°24′46″W, 3 m, 13.vii.2014, G. Contreras, H. Montaño, G. Montiel, R. Paredes, and A. Valdez, 3 ♂, 3 ♀ (CNAN Sz174). *Yucatan*: Municipio de Chichén Itzá: Actún Xkyc (Xkyc Cave), Calcehtok, 1 ♀ (AMNH); Cenote Seco (Dry Cenote), 1 ♂, 1 ♀ (AMNH); Ruinas de Chichenitza, 20°40′49″N 88°34′10″W, 32 m, 1.viii.2014, J. Mendoza and R. Monjaraz, 2 ♂, 2 ♀ (CNAN Sz168), 3 ♀ (AMCC [LP 14506]). Municipio de Merida: Km 172 highway Merida–Cancun, 20°45′49″N 88°03′25″W, 36 m, 20.vii.2010, D. Barrales, G. Contreras, J. Cruz, O. Francke, G. Montiel, M. Paradiz, and C. Santibañez, 4 ♀ (CNAN Sz23). Municipio de Tecax: Cueva Chocantes, 20°13′28″N 89°17′58″W, 91 m, 2.x.2014, G. Contreras and G. Montiel, 1 ♂, 1 ♀ (CNAN Sz165). Municipio de Tecoh: Grutas de Tzabna, 20°43′49″N 89°28′29″W, 23 m, 3.x.2014, G. Contreras and G. Montiel, 3 ♀ (CNAN Sz164). **U.S.A:** *Florida*: Dade County: Everglades National Park, 4 imm. (AMNH); Florida City, 3.2–8 km S, 14 ♀ (AMNH); Homestead, W Mowry St., 1 ♀ (AMNH); Matheson Hammock, 22 ♀ (AMNH); Miami, 1 ♀ (AMNH); Miami Brickell Hammock, 1 ♀ (AMNH); Royal Palm State Park, 1 ♀ (AMNH). Monroe County: Marathon, 2 ♀ (AMNH); Stock Island, 1 ♀ (AMNH). *Puerto Rico*: Bosque Estatal Susua, old campsite, trail leading into forest, 18°04′03″N 66°53′50″W, 181 m, 19–20.x.2009, J. Huff and L. Prendini 1 ♀ (AMCC [LP 10149]); Cueva de los Alferos, Barrio Moza, near Isabela, 2 ♀ (AMNH); Cueva Tuna, 3.5 km S of Cabo Rojo, 1 ♂, 3 ♀, 1 imm. (AMNH).

Troglostenochrus, gen. nov.

Figures 4, 6, 7I, 9F, 13I, 23G–I, 24G–I, 25C, D; tables 1, 4

Stenochrus (part): Monjaraz-Ruedas, 2012: 63, 64; Monjaraz-Ruedas and Francke, 2018: 189, 192.

Type Species: *Stenochrus valdezi* Monjaraz-Ruedas, 2012 [= *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov.], type species, here designated.

Diagnosis: *Troglostenochrus*, gen. nov., may be separated from other hubbardiid genera by the following combination of characters. Cheliceral movable finger serrate, with multiple teeth; single guard tooth at end of serrula; setal group G3 with G3-3 setae situated anteriorly (fig. 13I). Propeltidium anterior process with two anterior setae (one posterior to the other) and three pairs of dorsosubmedian setae (fig. 11A); corneate eyes absent. Metapeltidium entire. Tegument without clavate setae. Pedipalps homeomorphic; trochanter with mesal spur, apical process long, projected and fan-shaped (fig. 7I); femur Fv_1 and Fv_2 setae spiniform, Fvr_{1-4} setae present (Fvr_{1-3} setae in *Troglostenochrus palaciosi* (Reddell and Cokendolpher, 1986), comb. nov.); patella with four acuminate *Pe* setae and four feathered *Pm* setae; tibia setal formula 3-3-4 (*Ter-Tmr-Tir*) (fig. 14D). Leg IV femur anterodorsal margin produced at ca. 90° angle. Opisthosomal tergite II with one pair of setae (*Dm*). Opisthosomal segments IX–XII not elongated; XII (♂) without posterodorsal process. Pygidial flagellum (♂) bulbous, trilobed, without dorsal depressions (fig. 23G–I), with pair of dorsosubmedian, rounded projections; flagellum (♀) with two annuli (fig. 24G–I). Spermathecae (♀) with two pairs of lobes; lateral lobes ca. 3/4 the length of median lobes, linear, with apex directed laterally; median lobes inverse J-shaped with apex directed laterally; lobes unsclerotized apically and without bulbs; median lobe bases anterior to lateral lobe bases, with duct openings along entire length (fig. 9F); chitinized arch hastate, with curved anterior branch, and lateral tips extremely projected and tapering; gonopod long and narrow.

Comparisons: Species of *Troglostenochrus*, gen. nov., resemble species of *Cokendolpherius* Armas, 2002 in the trilobed pygidial flagellum and robust pedipalps, with a projected, conical apical process of the pedipalp trochanter, of the male, and the three pygidial flagellomeres and horizontal bracket shape of the chitinized arch of the spermathecae, of the female. However, *Troglostenochrus* bears three pairs of dorsal setae on the propeltidium, whereas *Cokendolpherius* bears two pairs, and females of *Troglostenochrus* possess both Vm_2 and Dl_4 setal pairs on the pygidial flagellum, which are absent in *Cokendolpherius*, and the spermathecal lobes are considerably longer in *Troglostenochrus* than in *Cokendolpherius*.

Species of *Troglostenochrus* resemble species of *Baalrog*, gen. nov., in the shape of the female spermathecae, in which the lateral lobes are reduced, and the lateral tips projected. However, the lateral lobes are considerably longer and wider in *Troglostenochrus* than in *Baalrog*, and the anterior branches of the chitinized arch are present and curved in *Troglostenochrus*, but absent in *Baalrog*.

Etymology: The generic name is a compound word derived from *troglo* (Greek, “hole”), referring to the troglomorphic species included in the genus, and “*Stenochrus*,” the genus in which its two species were formerly accommodated. It is masculine in gender.

Included Species: *Troglostenochrus palaciosi* (Reddell and Cokendolpher, 1986), comb. nov.; *Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012), comb. nov.

Distribution: *Troglostenochrus*, gen. nov., is known from only two disjunct localities in the states of Guerrero and Chiapas, southern Mexico. Presumably, the genus extends across the entire Sierra Madre del Sur in Oaxaca and the Sierra Chiapas, although extensive searching in the caves of Chiapas have thus far failed to collect additional species (fig. 4).

Natural History: The known species of *Troglostenochrus*, gen. nov., are strictly cavernicolous, inhabiting the dark zone of caves, and have not been collected on the surface. *Mayazomus loobil* Monjaraz-Ruedas and Francke, 2015, was collected outside the cave inhabited by *T. valdezi*, comb. nov.

Remarks: Species of *Troglostenochrus*, gen. nov., closely resemble species of *Cokendolpherius*, endemic to Cuba. Unfortunately, no samples of *Cokendolpherius* were available for DNA isolation and attempts to collect fresh material of *T. palaciosi*, comb. nov., were unsuccessful (the cave was never found). Nevertheless, the morphological characters and simultaneous phylogenetic analyses (fig. 6) unequivocally support the placement of *T. palaciosi* within *Troglostenochrus*. The acquisition and analysis of DNA sequence data from *Cokendolpherius* are needed to test its relationship to *Troglostenochrus*.

***Troglostenochrus palaciosi* (Reddell and Cokendolpher, 1986)**, comb. nov.

Schizomus mexicanus: Palacios-Vargas, 1981: 64 [misidentification]; Alberti and Palacios-Vargas, 1987: 2 [misidentification].

Schizomus sp. nov.: Hoffmann et al., 1986: 151, 208, 238.

Schizomus palaciosi Reddell and Cokendolpher, 1986: 31, 35–37, figs. 1–5, 11; Alberti and Palacios-Vargas, 1987: 1–14, figs. 1–30; Alberti, 1990: 29; Ludwig and Alberti, 1990: 255–257, figs. 1, 10; Palacios-Vargas, 1990: 5; Reddell and Cokendolpher, 1995: 6, 109; Alberti, 2000: 313, figs. 3d, 7b; Giribet et al., 2002: 49.

Stenochrus palaciosi: Reddell and Cokendolpher, 1991: 18; 1995: 6, 8, 12, 18, 103, 108, 109; Vázquez-Rojas, 1995: 33; 1996: 65; Harvey, 2003: 124; Moreno-González and Villarreal, 2012: 73; Monjaraz-Ruedas, 2012: 65; Palacios-Vargas and Reddell, 2013: 52; Zawierucha et al., 2013: 359; Palacios-Vargas et al., 2015: 32.

Type Material: *Schizomus palaciosi*: **MEXICO:** *Guerrero*: Municipio de Taxco de Alarcón: Gruta de Acuitlapan, 12 km NE of Taxco, 26.v.1978, J. Palacios, holotype ♂ (CNAN T120), 23.v.1980, J. Palacios, paratype ♀ (CNAN T119).

***Troglostenochrus valdezi* (Monjaraz-Ruedas, 2012)**, comb. nov.

Stenochrus valdezi Monjaraz-Ruedas, 2012: 63–68, figs. 1–9; Moreno-González and Villarreal, 2012: 73; Palacios-Vargas and Reddell, 2013: 52; Palacios-Vargas et al., 2015: 32; Monjaraz-Ruedas and Francke, 2018: 189, 192.

Type Material: *Stenochrus valdezi*: **MEXICO:** *Chiapas*: Municipio de La Trinitaria: Cueva de San Francisco, 16°05′59″N 92°02′49″W, 1546 m, 18.vi.2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, holotype ♂ (CNAN T698), 4 ♀ paratypes (CNAN T699).

Additional Material Examined: **MEXICO:** *Chiapas*: Municipio de La Trinitaria: Cueva de San Francisco, 16°05′59″N 92°02′49″W, 1546 m, 18.vi.2011, G. Contreras, J. Cruz, O. Francke, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 3 ♀ (CNAN Sz160), 1 ♀, 1 imm. (AMCC [LP 14532]), O. Francke, J. Mendoza, R. Monjaraz, C. Santibañez, A. Valdez, and K. Zárate, 26.vi. 2013, 1 ♂, 3 ♀ (CNAN Sz92).

DISCUSSION

Until quite recently, the systematics of Schizomida focused principally on the description of new genera and species, using a limited set of morphological character systems (Rowland, 1975b; Reddell and Cokendolpher, 1995; Harvey, 2003; Monjaraz-Ruedas and Francke, 2015, 2016, 2017). The shapes of the male pygidial flagellum and the female spermathecae were emphasized for the diagnosis and delimitation of schizomid species. Although these character systems are very informative at the species level, because they are sexually selected, they are often unreliable for the diagnosis and delimitation of supraspecific taxa within the order, for the same reason (Reddell and Cokendolpher, 1995; Monjaraz-Ruedas and Francke, 2016; Villarreal et al., 2008). The relief of the dorsal surface of the flagellum and the relative positions of its setae are more informative phylogenetically than flagellar shape per se (Cokendolpher and Reddell, 1992; Harvey, 1992; Monjaraz-Ruedas et al., 2016); however, there is considerable homoplasy in these characters as well (Monjaraz-Ruedas et al., 2016).

Although a few genera, e.g., *Mayazomus*, *Surazomus*, and *Tayos* Reddell and Cokendolpher, 1995, are diagnosed by autapomorphies, the diagnosis of most schizomid genera currently requires a combination of homoplastic characters, 20 of which were listed by Reddell and Cokendolpher (1995): coronate ocelli; tegument clavate setae; cheliceral movable finger accessory teeth and/or lamella; movable finger serrula guard teeth; pedipalps sexual dimorphism (heteromorphic or homeomorphic) and male dimorphism (or polymorphism); pedipalp armature; pedipalp trochanter mesal spur development; trochanter anterior process setation; leg IV femur, anterodorsal margin development; metapeltidium divided or entire; opisthosomal elongation; opisthosomal segment II setation; opisthosomal segment XII, posterodorsal process; male pygidial flagellum dorsoventrally or laterally compressed; flagellum dorsal surface pits; female pygidial flagellum, number of flagellomeres or annuli; gonopod structure; female spermathecae, number of lobes; spermathecal lobes nodular or without nodules.

Recent investigations of other character systems, such as the counts and relative positions of setae on the chelicerae and pedipalps and a more detailed and precise description of the diverse structures comprising the female spermathecae, offered new potential for schizomid systematics at the species level and above (Moreno-González et al., 2014; Monjaraz-Ruedas et al., 2016, 2017; Villarreal et al., 2016). However, only the annuli on the female flagellum have thus far been tested in a phylogenetic framework (Monjaraz-Ruedas et al., 2016). The phylogenetic information content of other character systems, and their utility for schizomid systematics above the species level, were untested prior to the analyses of Monjaraz et al. (in prep.). Based on those results, a brief assessment is provided below.

Propeltidial Setae: The number of pairs of setae on the dorsal surface of the propeltidium was introduced as a character by Rowland (1975b), who hypothesized that reduction in the number was synapomorphic in Hubbardiidae because four or more pairs are observed in Protoschizomidae. Rowland (1975b) noted this character was highly variable within the species groups subsequently described by Rowland and Reddell (1979a, 1979b, 1980, 1981) and that three pairs was the most common condition among New World hubbardiids. However, among Mexican schizomids, two, three, or four pairs of propeltidial setae, combined with characters of the chelicerae movable finger, the male pygidial flagellum, and the female spermathecae, proved effective for generic diagnosis in the present study. The number of pairs of propeltidial setae was constant among congeners, e.g., *Harveyus*, gen. nov., and *Stenochrus* each bear two pairs of setae, *Nahual*, gen. nov., and *Schyzophyxia*, gen. nov., each bear three, and *Heteroschizomus*, stat. rev., bears four. Furthermore, the number of pairs of propeltidial setae (and the relief of the cheliceral movable finger) are independent of sex and stage, permitting immatures of both sexes to be reliably identified to genus. Based on these observations, the utility of the propeltidial setae for the generic diagnosis of schizomids appears to have been underestimated.

Pedipalp Tibial Setae: Monjaraz-Ruedas and Francke (2016) proposed the use of pedipalp setae for species delimitation and subsequently homologized the pedipalp setae of Hubbardiidae with those of Protoschizomidae (Monjaraz-Ruedas et al., 2017), demonstrating that the number and shape of these setae are informative for the diagnosis of schizomid families. Although all hubbardiids possess a similar setal configuration, especially on the pedipalp femur and patella, variation in setal patterns on the pedipalp tibia is informative at the generic level. The tibia bears three rows of setae, the retrolateral (*Ter*), median (*Tmr*), and prolateral (*Tir*) rows, which may be transformed into a formula by counting the number of setae in each (*Ter-Tmr-Tir*). In the present study, the formula of tibial setae was usually constant among congeners. For example, formulae of 5-5-6 and 3-3-4 occur in *Nahual* and *Stenochrus*, respectively, providing a diagnostic difference between them. Furthermore, as with the number of propeltidial setae, this character is independent of sex and stage, permitting immatures of both sexes to be reliably identified to genus. When used in combination, these characters reliably diagnose genera in which one is constant. For example, although *Stenochrus* and *Schizophyxia* share the tibial setae formula 3-3-4, *Schizophyxia* bears three pairs of propeltidial setae whereas *Stenochrus* bears two.

Male Pygidial Flagellum: The shape of the male pygidial flagellum was traditionally considered the most important character for species delimitation in schizomids (Reddell and Cokendolpher, 1995). However, the character is problematic for generic diagnosis for the same reason it is useful for species delimitation: sexual selection on flagellar shape has created considerable variation at the species level (Reddell and Cokendolpher, 1995; Villarreal et al., 2008), which obfuscates homology assessment and hinders the definition of character states. The coding and definition of the states of male flagellar shape could be improved by avoiding subjective assessments and quantitatively comparing homologous components of the flagellum using ratios or shape analysis with geometric morphometrics, which can then be analyzed phylogenetically as continuous characters (De Bivort et al., 2009; Magalhães and Santos, 2012), as recently applied to *Mayazomus* (Monjaraz-Ruedas and Francke, 2016). A more objective, quantitative characterization of flagellar shape may assist with generic diagnosis across the order and provide phylogenetically informative data as, e.g., in *Heteroschizomus*, which possess a distinctly elongated flagellum. This approach may also reveal homoplasy or mistaken homology assessment as, e.g., with the elongated pygidial flagellum of *Nahual lanceolatus*, comb. nov., and *Heteroschizomus*, a character that led Rowland and Reddell (1981) to assign these taxa to the same species group.

Although there are problems with using male flagellar shape as a character for generic diagnosis in schizomids, other characters of the male flagellum offer potential for the purpose. The relief of the dorsal surface of the flagellum, despite also exhibiting considerable variation, is constant or nearly so among some congeners, e.g., all known species of *Nahual*, which possess a pair of dorsosubmedian pits, and most species of *Rowlandius*, which exhibit a pair of submedian projections. The relative positions of the flagellar setae also appear to provide reliable characters for species delimitation in some genera, e.g., *Piaroa*, but exhibit considerable interspecific variation, limiting their utility for generic diagnosis beyond specific cases, e.g., in differentiating *Calima* Moreno-Gonzalez and Villarreal, 2012, and *Piaroa* from other South American genera.

Female Spermathecae: Brignoli (1973) introduced female spermathecal shape as a character for species delimitation, but Rowland and Reddell (1979a, 1979b, 1980, 1981) noted it could not be used in isolation, due to the conserved morphology of the spermatheca, suggesting these authors were aware that the character is often constant among congeners. Despite these concerns, spermathecal shape continues to be used for species delimitation and as an aid to identify females in the absence of males. This practice probably leads to erroneous delimitation and identification, especially among the many species complexes and parthenogenetic populations of schizomids. For this reason, characters of the female spermathecae should be used with caution and species descriptions should be based on their component structures, rather than solely on the general shape. In the present study, subdivision of the spermatheca into its components facilitated the identification of several characters (i.e., shape and size of the chitinized arch, relative lengths and widths of the median and lateral lobes, relative positions of the medial and lateral lobe bases, orientation of the lobe apex, and apical sclerotization or bulbs on the lobes), the combination of which was constant among congeners, permitting reliable diagnosis of genera. Some of these characters also vary interspecifically, providing information at the species level.

Phylogenetic hypotheses of DNA sequences, analysed separately and simultaneously with the morphological characters, greatly assisted the identification of monophyletic groups, defined as genera in the present contribution, and the morphological characters for their diagnosis, by optimization on the preferred phylogenetic hypothesis. Based on this assessment, characters of the female spermathecae presented herein were found to be reasonably reliable for generic recognition.

In conclusion, the integration of morphological and molecular data not only increased knowledge of the schizomid diversity in the New World but disentangled what was once considered a homoplastic and variable morphology in a large "catch-all" genus (i.e., *Stenochrus*) into discrete units each diagnosable by unique character combinations.

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APPENDIX 1

MORPHOLOGICAL CHARACTERS USED IN PHYLOGENETIC ANALYSIS OF THE SHORT-TAILED WHIPSCORPION GENUS *STENOCHRUS* CHAMBERLIN, 1922, AND RELATED GENERA (SCHIZOMIDA: HUBBARDIIDAE)

Characters optimized with ACCTRAN, except where indicated otherwise.

Chelicerae

0. Fixed finger, prolateral surface, G3 setae position: seta G3-4 posterior (0); setae G3-2 and G3-4 posterior (1); seta G3-3 anterior (2). [DELTRAN]
1. Fixed finger, prolateral surface, number of G5 setae: ≤ 8 (1); ≥ 9 (2).
2. Movable finger, mesal surface, margin: smooth (0); lamella (1); dentate (2). [DELTRAN]

Prosomal propeltidium

3. Anterior process setation: 1+1 (0); 2+1 (1).
4. Dorsal pairs of setae, number: 2 (0); 3 (1); 4 (2).

Prosomal metapeltidium

5. Metapeltidium: divided (0); entire (1).

Opisthosoma

6. Segments X–XII (♂): not elongate (0); elongate (1).
7. Segment XII, posterodorsal process (♂): absent (0); present (1).
8. Tergite II, number of setae: 2 (0); > 2 (1).

Pedipalps

9. Pedipalps, development (♂): homeomorphic (0); elongated (1); robust (2).

Pedipalp trochanter

10. Apical process: acute (0); acuminate (1); obtuse (2); bump (3); fan-shaped (4); digitiform (5); rounded (6).

Pedipalp femur

11. Retrolateral surface, seta Fe_1, type: acuminate (0); spiniform (1); macrosetae (2).
12. Retrolateral surface, seta Fe_5, type: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
13. Retrolateral surface, seta Fv_1, type: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
14. Retrolateral surface, seta Fv_2, type: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
15. Retrolateral surface, spiniform setiferous tubercles, position: Fv_1 and Fv_2 distal (0); Fv_1 ventral, Fv_2 distal (1); Fv_1 and Fv_2 ventral (2). [DELTRAN]
16. Prolateral surface, anterior margin, apophysis: absent (0); present (1).
17. Prolateral surface, ventral row of setae (Fmv_{1-4}), number: 3 (0); 4 (1).

Pedipalp patella

18. Curvature: slight (0); marked (1); none (2).
19. Retrolateral row of setae (*Pe*), count: 3 (0); 4 (1); 5 (2); 2 (3).
20. Retrolateral row of setae (*Pe*), type: acuminate (0); feathered (1); spiniform (2); macrosetae (3).
21. Prolateral row of setae (*Pm*), count: 3 (0); 4 (1); 5 (2); 6 (3).
22. Prolateral row of setae (*Pm*), type: acuminate (0); feathered (1); spiniform (2); macrosetae (3).

Pedipalp tibia

23. Spurs: absent (0); ventral (1); proventral (2).
24. Retrolateral row of setae (*Ter*), count: 3 (0); 4 (1); 5 (2); 6 (3).

25. Retrolateral row of setae (*Ter*), type: (0) acuminate (0); feathered (1); spiniform (2); macrosetae (3).
26. Medial row of setae (*Tmr*), count: 3 (0); 4 (1); 5 (2); 6 (3).
27. Medial row of setae (*Tmr*), type: acuminate (0); feathered (1); spiniform (2); macrosetae (3).
28. Prolateral row of setae (*Tir*), count: 3 (0); 4 (1); 5 (2); 6 (3).
29. Prolateral row of setae (*Tir*), type: acuminate (0); feathered (1); spiniform (2); macrosetae (3).

Male flagellum

30. Shape, dorsal view: lanceolate (0); cordate (1); spatulate (2); subrhomboidal (3); shovel shaped (4); elliptical (5); trilobed (6); bulbous or clavate (7); spear shaped (8); deltoid (9). [DELTRAN]
31. Shape, lateral view: slender (flat) (0); elliptical (1); bulbous (2).
32. Dorsal depressions: absent (0); pair of pits (1); single depression (2); pair of depressions (3); depression and pits (4).
33. Dorsal depressions, position: medial (0); submedial (1); anterior (2); posterior (3).
34. Dorsal projections: flat (0); pair of projections (1); single projection (2).
35. Dorsal projections, position: medial (0); submedial (1). [DELTRAN]
36. Seta Dm_1, position with respect to anterior margin: posterior (0); aligned with margin (1).
37. Seta Dm_4, position with respect to seta Dl_3: anterior to (0); aligned with (1).
38. Setae Dl_1, position with respect to setae Vl_1: aligned with (0); posterior to (1); anterior to (2).
39. Setae Dl_3, position with respect to setae Vl_2: aligned with (0); posterior to (1); anterior to (2).
40. Seta Vm_1, position with respect to setae Vm_2: aligned with (0); posterior to (1); anterior to (2).

Female flagellum

41. Flagellomeres, count: 3 (0); 4 (1).
42. Setae Dl_1, position with respect to setae Vl_1: aligned with (0); posterior to (1); anterior to (2).
43. Setae Dl_3, position with respect to setae Vl_2: aligned with (0); posterior to (1); anterior to (2).

Spermathecae

44. Lobes, number of pairs: 1 (0); 2 (1); 3 or more (2).
45. Median lobes, shape: linear (0); arch shaped (1); inverse J-shaped (2).
46. Median lobes, ornamentation: sclerotized (0); bulbs (1); smooth (2).
47. Median lobes, sclerotization: apically (0); half of lobe (1); entire lobe (3).
48. Median lobes, bulbs size: large (0); small (1).
49. Median lobes, apex orientation: ental (0); ectal (1); vertical (2).
50. Median lobes, base position relative to bases of lateral lobes: aligned with (0); anterior to (1); posterior to (2).
51. Lateral lobes, shape: linear (0); arch shaped (1).
52. Lateral lobes, ornamentation: sclerotized (0); smooth (1).
53. Lateral lobes, apex orientation: ental (0); ectal (1); vertical (2).
54. Lateral lobes, length compared with median lobes: equal (0); 3/4 (1); 1/2 (2); 1/4 (3).
55. Lobes, relative widths: equal (0); lateral lobes wider than median lobes (1); median lobes wider than lateral lobes (2).
56. Lobes, symmetry: symmetric (0); asymmetric (1).
57. Chitinized arch, shape: arrow shaped (0); mug shaped (1); V-shaped (2); hastate (3); bowl shaped (4); inverse arc (5); obtuse triangle (6); U-shaped (7).
58. Chitinized arch, anterior branch: present (0); absent (1).
59. Chitinized arch, lateral tip shape: pointed (0); lobed (1); widened (2).
60. Gonopod: absent (0); present (1)

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Integrative systematics untangles evolutionary history of *Stenochrus* (Schizomida, Hubbardiidae), a neglected junkyard genus of North American short-tailed whipscorpions

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Phylogenetics of the genus *Stenochrus*

Abstract

The Nearctic short-tailed whipscorpion genus, *Stenochrus* Chamberlin, 1922 includes 27 species distributed principally in Mexico, the U.S.A, and Central America. Morphological disparity among its species, associated with their adaptation to diverse habitats, raised the question as to whether *Stenochrus* is monophyletic. The phylogenetic relationships among short-tailed whipscorpions have only recently begun to be explored, and the monophyly of *Stenochrus* has never been tested. The present contribution provides the first phylogeny of *Stenochrus*, based on 61 morphological characters and 2968 aligned DNA nucleotides from two nuclear and two mitochondrial gene markers, for 80 terminal taxa. Separate and simultaneous analyses of the morphological and molecular data sets were conducted with Bayesian Inference, Maximum Likelihood, and parsimony with equal and implied weighting. Terminals represented only by morphological data (“orphans”) were included in some analyses for evaluation of their phylogenetic positions. *Stenochrus* was consistently polyphyletic and comprised eight monophyletic clades, justifying its reclassification into eight genera including *Heteroschizomus* Rowland, 1973, revalidated from synonymy with *Stenochrus*, by Monjaraz-Ruedas *et al*., 2019. Rowland & Reddell’s (1980) *mexicanus* and *pecki* species groups were consistently paraphyletic. Orphan taxa grouped with the most morphologically similar taxa.

Biodiversity – Phylogenetics – Uropygi

Introduction

The order Schizomida Petrunkevitch, 1945, commonly known as the short-tailed whipscorpions, schizomids or tartarids, is among the less diverse, or minor, arachnid orders (Harvey, 2003). It currently includes two families, Protoschizomidae Rowland, 1975, endemic to North America, and comprising two extant and one fossil genera with 16 species, and Hubbardiidae Cook, 1899, with 65 extant genera and 345 species worldwide (Harvey, 2003, 2013; Monjaraz-Ruedas *et al.*, 2019). Hubbardiidae comprises 33 genera (Reddell & Cokendolpher, 1995; Harvey, 2013; Monjaraz-Ruedas *et al.*, 2019) in the New World.

Until quite recently, the systematics of short-tailed whipscorpions focused principally on the description of new genera and species, using a limited set of morphological character systems (Reddell & Cokendolpher, 1995; Harvey, 2003; Monjaraz-Ruedas & Francke, 2015; Monjaraz-Ruedas *et al.*, 2016; Monjaraz-Ruedas *et al.*, 2017). The morphological characters used in schizomid taxonomy have undergone many changes in the past decade, with the relevance of phylogenetically informative characters increasingly recognized (Monjaraz-Ruedas & Francke, 2016; Monjaraz-Ruedas *et al.*, 2016; Villarreal *et al.*, 2016). However, few phylogenetic analyses of the relationships among schizomids have been conducted to date, and few genera have been tested for monophyly. Five phylogenetic analyses were based solely on morphological characters (Rowland, 1975; Cokendolpher & Reddell, 1992; Monjaraz-Ruedas & Francke, 2016, 2017; Monjaraz-Ruedas *et al.*, 2017), whereas four were based mostly or entirely on DNA sequences (Harvey *et al.*, 2008; Clouse *et al.*, 2017; Harms *et al.* 2018; Abrams *et al.*, 2019).

Rowland (1975) presented the first phylogenetic analysis of schizomids, based on twelve morphological characters scored for all New World species, most of which were assigned to *Schizomus* Cook, 1899 at the time. Based on Rowland's (1975) unpublished analysis, Rowland & Reddell (1979a, 1979b, 1980, 1981) proposed seven species groups of *Schizomus* in the New World, i.e., the *brasiliensis*, *briggsi*, *dumitrescoae*, *goodnightorum*, *mexicanus*, *pecki* and *simonis* groups. The *briggsi* group was placed sister to a monophyletic group comprising two reciprocally monophyletic subgroups, one comprising the *brasiliensis*, *dumitrescoae* and *simonis* groups, the other comprising the *goodnightorum*, *mexicanus* and *pecki* groups. Rowland & Reddell (1980, 1981) placed sixteen species of *Schizomus* from the U.S.A, Mexico and Guatemala into the *goodnightorum*, *mexicanus*, and *pecki* groups. However, further studies by Reddell & Cokendolpher (1991, 1995) demonstrated that *Schizomus* and another schizomid genus, *Trithyreus* Kraepelin, 1899, are actually restricted to the Old World, leading Reddell & Cokendolpher (1991) to revalidate *Stenochrus* Chamberlin, 1922 and synonymize *Heteroschizomus* Rowland, 1973 with it.

After establishing that *Schizomus* does not occur in the New World, Reddell & Cokendolpher (1991, 1995) assigned Rowland's (1975) species groups to other existing genera and created new genera to accommodate the rest. Species of the *simonis* group were transferred to *Hansenochrus* Reddell & Cokendolpher, 1995, the *briggsi* group to *Hubbardia* Cook, 1899, and the *goodnightorum*, *mexicanus* and *pecki* groups to *Stenochrus*, with two species of the *mexicanus* group accommodated in *Sotanostenochrus* Reddell & Cokendolpher, 1991. *Pacal* Reddell & Cokendolpher, 1995 and *Surazomus* Reddell & Cokendolpher, 1995 were created to accommodate species of the *brasiliensis* group, and *Rowlandius* Reddell & Cokendolpher, 1995, to accommodate the *dumitrescoae* group.

When the present study commenced, *Stenochrus* was the most speciose schizomid genus in North America and the third most speciose in the New World (Reddell & Cokendolpher, 1995; Harvey, 2013), containing 27 species, distributed mostly in the Nearctic region, from the southern U.S.A., through Mexico to Central America (Fig. 1). One cosmopolitan species, *Stenochrus portoricensis* Chamberlin, 1922, was reported from North, Central and South America and the Caribbean, as well as several countries in Europe (Korenko *et al*., 2009; Christophoryová *et al*., 2013; Harvey, 2013; Šestáková *et al*., 2017) (Fig. 1A). Ever since *Stenochrus* was redescribed by Reddell & Cokendolpher (1991), new species from Mexico and Central America have been placed within the genus, based on a single diagnostic character (the lateral pair of lobes reduced in the female spermathecae), while ignoring many other differences. Over time, *Stenochrus* became the "junkyard" for North American schizomids, comprising a plethora of morphologically disparate species, differing in body size, male flagellar shape, setal patterns, and sexual dimorphism, including homeomorphic and heteromorphic pedipalps. This disparity among *Stenochrus* species, along with their diverse habitats, including caves, rainforest, tropical dry forest, and pine and oak forest above 2000 m, raised the question as to whether the genus is monophyletic.

Given the paucity of phylogenetic analyses on schizomids, it is unsurprising that the monophyly and phylogenetic relationships of *Stenochrus* had never been tested, beyond the unpublished analysis of Rowland (1975), and the inclusion of exemplar species in recent analyses of schizomid phylogeny based on morphology (Monjaraz-Ruedas & Francke, 2016, 2017) or DNA sequences (Clouse *et al*., 2017). *Stenochrus* was paraphyletic in a phylogenetic analysis of *Mayazomus* Reddell & Cokendolpher, 1995 based on 130 morphological characters (Monjaraz-Ruedas & Francke, 2016), which included exemplar species of *Stenochrus* as outgroups, along with outgroup exemplars of *Hansenochrus*, *Hubbardia* and *Rowlandius* from North, Central and South America, once included in the *Schizomus* species groups of Rowland & Reddell (1979a, b, 1980, 1981). *Stenochrus* was also paraphyletic in the molecular analysis of Clouse *et al.* (2017), based on two nuclear and two mitochondrial gene markers for 240 samples, which included several individuals of *Stenochrus portoricensis*, one *Stenochrus sbordonii* (Brignoli, 1973), and several unidentified schizomids from Mexico; *Hubbardia* grouped sister to all other hubbardiid taxa and *S. sbordonii* sister to the remainder. On the other hand, *Stenochrus* was monophyletic in a phylogenetic analysis of *Olmecazomus* Monjaraz-Ruedas *et al.*, 2019, which included different exemplar species of *Stenochrus* from the *Mayazomus* analysis (Monjaraz-Ruedas & Francke, 2017), i.e., *Stenochrus pecki* Rowland, 1973 and *S. portoricensis*.

The present contribution provides the first phylogeny of *Stenochrus*, based on 61 morphological characters and 2968 aligned DNA nucleotides from two markers in the nuclear genome, the internal transcribed spacer (ITS) and 28S rDNA, and two markers in the mitochondrial genome, Cytochome *c* Oxidase Subunit I (COI) and 12S rDNA, for a comprehensive sample of 80 taxa. Separate and simultaneous analyses of the morphological and molecular data sets were conducted with different optimality criteria and analytical parameters: Bayesian Inference, Maximum Likelihood and parsimony with equal and implied weighting. Terminals represented only by morphological data (termed “orphans”) were included in some analyses to evaluate their phylogenetic positions. *Stenochrus* was consistently polyphyletic, and comprised eight monophyletic groups, justifying its reclassification into eight genera (Fig. 1B), including *Heteroschizomus*, revalidated from synonymy with *Stenochrus*, by Monjaraz-Ruedas *et al.* (2019).

Materials and methods

Taxon sampling and material examined

Taxonomic classification follows Monjaraz-Ruedas *et al*. (2019). The ingroup comprised 59 terminal taxa representing 26 (96%) of the 27 species formerly assigned to *Stenochrus* (Supporting Information Appendices 1, 2). Tissue samples could not be obtained for five species for which DNA sequence data were therefore unavailable: *Ambulantactus davisi* (Gertsch, 1940); *Heteroschizomus meambar* Armas & Víquez, 2010; *Stenochrus guatemalensis* Chamberlin, 1922; *Stenochrus leon* Armas, 1995; *Troglostenochrus palaciosi* (Reddell & Cokendolpher, 1986). *Ambulantactus davisi* is known only from the type specimens from a single locality in northern Tamaulipas, Mexico, to which access was problematic due to insecurity. Attempts to collect fresh material of *S. guatemalensis* and *T. palaciosi*, were unsuccessful. The type locality of *S. guatemalensis* could not be unambiguously identified (there are at least three places with the same name), but the sole female described by Chamberlin (1922) resembles *S. portoricensis*, suggesting it may be just another record of this species, which is already reported from Guatemala. Some specimens collected in Guatemala, with similar female spermathecae, were included in the analysis as *Stenochrus* cf. *guatemalensis*. The type locality of *T. palaciosi* was never located. The original collector could not locate the cave either, during a previous attempt. Finally, it was impossible to collect *H. meambar* and *S. leon*. Despite the absence of molecular data, all except one of the orphan taxa were included in the simultaneous analyses of the morphological and molecular data, to test their phylogenetic positions based solely on morphology. Type specimens of all species were examined, except for *H. meambar* and *S. leon*. *Stenochrus leon* was omitted from the morphological matrix due to the absence of specimens for examination and the limited information available from the inadequate original description (Supporting Information Appendices 3, 4).

The outgroup comprised 14 terminal taxa representing 5 (15%) of the New World genera of schizomids. Outgroup selection was intended to test the monophyly of *Stenochrus*, and guided by previous phylogenetic studies of schizomids by Rowland (1975), Monjaraz-Ruedas & Francke (2016) and Clouse *et al*. (2017), as well as by morphological similarity and geographical proximity to *Stenochrus* (Supporting Information Appendices 1, 2). The analyses were rooted on *Hubbardia* , as it was placed sister to all other New World schizomid exemplars in the phylogenies of Rowland (1975), Monjaraz-Ruedas & Francke (2016) and Clouse *et al.* (2017). The inclusion of *Mayazomus* and *Olmecazomus* was guided by the analysis of Monjaraz-Ruedas & Francke (2016, 2017), which placed *Stenochrus mexicanus* (Rowland, 1971) sister to a clade comprising *Mayazomus* and *Rowlandius*. The inclusion of *Olmecazomus* and *Sotanostenochrus* was based on their morphological similarity to *Stenochrus*. The shapes of the male pygidial flagella and female spermathecae of *Olmecazomus* resemble those of *Stenochrus*, whereas species of *Sotanostenochrus* resemble *Stenochrus mexicanus*, both obligate cavernicoles which are codistributed. *Pacal* was included based on similarities with some members of *Stenochrus*, its Neotropical distribution, and the presence of epigean and hypogean species.

Specimens were collected by hand or using an aspirator, and preserved in 80% ethanol for morphological study, with one or two preserved in 96% ethanol for DNA isolation. Material examined is deposited in the American Museum of Natural History (AMNH), New York, including the Ambrose Monell Cryocollection (AMCC); the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), Mexico City; and the Texas Memorial Museum (TMM), University of Texas, Austin.

Morphological data

A morphological data matrix, comprising 61 morphological characters scored for 80 terminal taxa (Supporting Information Appendix 4), was prepared using Mesquite ver. 3.0.4 (Maddison & Maddison, 2018), and deposited in Morphobank (https://morphobank.org) with accession number P3464 (Supporting Information Appendices 3, 4). Forty-three multistate and 18 binary characters were modified from Monjaraz-Ruedas & Francke (2016, 2017) and treated as non-additive (Fitch, 1971) to avoid *a priori* character state transformations. The matrix included character systems considered important for species recognition, e.g., chelicerae, propeltidium, pygidial flagellum shape, pedipalp setation, pedipalp dimorphism, enlargement of the opisthosoma, and female spermathecae. However, several characters from previous matrices (e.g., Monjaraz-Ruedas *et al*. 2016, 2017) were excluded, specifically those which were constant (e.g., setation of the chelicerae and opisthosoma), variable only at the family level, or highly variable at the species level (e.g., number of teeth on the cheliceral movable finger).

Morphological terminology for legs and pedipalps follows Reddell & Cokendolpher (1995); cheliceral setal nomenclature follows Lawrence (1969), as modified by Villarreal *et al*. (2016); pedipalp setal terminology follows Monjaraz-Ruedas *et al*. (2017); opisthosomal setal nomenclature follows Villarreal *et al*. (2016); pygidial flagellar setal terminology follows Cokendolpher & Reddell (1992), as modified by Harvey (1992) and Monjaraz-Ruedas *et al*. (2016); and spermathecal nomenclature follows Monjaraz-Ruedas *et al*. (2019).

Selection of gene markers

Seven gene markers which evolve at different rates, and would thus be expected to provide phylogenetic resolution at different taxonomic levels (Prendini *et al*., 2003), were initially identified as suitable candidates for the study, i.e., 18S rDNA, the D3 region of the 28S rDNA (28S), Histone H3, and the Internal Transcribed Spacer (ITS) from the nuclear genome, and 12S rDNA (12S), 16S rDNA (16S), and Cytochrome *c* Oxidase Subunit I (COI) from the mitochondrial genome. As 16S was impossible to amplify consistently with the primers available, only six of these markers were assessed for phylogenetic informativeness (López-Giráldez *et al.*, 2013), on which basis , four, i.e., the nuclear ITS and 28S, and the mitochondrial 12S and COI, were selected to reconstruct the relationships of *Stenochrus* (Fig. 2, Supporting Information Table S1).

DNA sequencing

DNA was insolated using the DNeasy Tissue kit (Qiagen, Valencia, CA). Extractions were prepared from the entire specimen when several individuals were available whereas leg pairs II–IV were used when only a singleton was available. When the extraction from leg pairs II–IV failed, the entire prosoma was used, leaving the opisthosoma, along with the flagellum and spermathecae (if applicable) intact for voucher identification.

Polymerase chain reaction (PCR) amplification was performed using standard procedures (Nishiguchi *et al.*, 2002; Prendini *et al.*, 2002, 2005), with Illustra Hot Start Mix RTG beads (GE Healthcare, Little Chalfont, Buckinghamshire) in a 25 µl reaction comprising 21 µl de-ionized water, 1 µl forward and reverse primers (Supporting Information Table S1), and 2 µl DNA. The PCR program involved an initial denaturing step at 94°C for 5 min, 35 amplification cycles (94°C for 30 s, a variable annealing temperature for 35 s, 72°C for 30 s), and a final step of 72°C for 7 min, in a GeneAmp PCR System 9700 thermocycler. The annealing temperature was 54ºC for 28S and ITS, 46ºC for COI and 42–40ºC for 12S. PCR products were purified using an AMPure Magnetic Beads Purification System (Agencourt Bioscience, La Jolla, CA) and resuspended in 40 µl de-ionized water.

PCR products were Sanger-dideoxy sequenced using an ABI Prism 3730 XL DNA Sequencer (Perkin-Elmer, Melville, NY) at the AMNH Sackler Institute of Comparative Genomics and a 3500 XL Genetic Analyzer (Life Technologies, Foster City, CA) at the Laboratorio Nacional de Biodiversidad (LANABIO), IBUNAM.

Double-stranded sequences were edited and contiged into consensus sequences using Sequencher ver. 5.4.6 (Gene Codes Corporation, Ann Arbor, MI). A total of 301 sequences were generated from 80 samples for the study (Supporting Information Appendix 1). The data matrix representativeness was of 94%: sequences of 12S were absent for 11 samples, of ITS for four samples, of 28S for three samples, and of COI for one sample (Supporting Information Appendix 1).

Sequence alignment

Edited consensus sequences of the four gene markers were aligned using MAFFT 6 (http://mafft.cbrc.jp/alignment/server/; Katoh *et al*. 2002, 2005, 2009). The L-INS-i strategy was applied for the 28S and COI markers and the G-INS-i strategy for the ITS and 12S markers, due to the trivial variation in sequence length and short gap openings (Katoh *et al.*, 2005; Swain, 2018). The COI alignment was translated into amino acids to assess its quality by identifying stop codons in Mesquite ver. 3.0.4 (Maddison & Maddison, 2018).

Alignments obtained with MAFFT were analyzed using MEGA ver. 7.0 (Kumar *et al*., 2016) to calculate matrix statistics as percentage of variable sites, conserved sites, parsimony-informative sites, A, C, G, T content and transition/transversion ratios. Calculations were conducted using the maximum composite likelihood test (mcl), applying the Tamura *et al*. (2004) substitution model (Table 1).

Phylogenetic analysis

Seven data partitions (morphology, 28S, ITS, 12S, and COI first, second and third codon positions) were identified with PartitionFinder ver. 2 (Lanfear *et al*., 2012) using the CIPRES Science Gateway ver. 3.3 online portal (Miller *et al*., 2010). jModelTest ver. 2.1.6 (Darriba *et al*., 2012) was used to select the evolutionary model for each molecular partition, by comparing the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) for each partition, and the GTR+I+G model chosen for each data partition.

Phylogenetic analyses were performed using three optimality criteria, parsimony, Bayesian Inference

(BI), and Maximum Likelihood (ML). Analyses were performed on four datasets, morphology and molecules analyzed separately, and two datasets in which morphology and molecules were analyzed simultaneously, one comprising 80 terminals (16 outgroup and 64 ingroup), the other comprising 86 terminals (16 outgroup and 70 ingroup), including terminals represented only by morphological data (i.e., orphans) (see Supporting Information Appendices 1, 2).

Parsimony analyses for each data matrix were conducted with equal weighting (EW) and implied weighting (IW), with eight values of the concavity constant (*k*) = 1, 5, 10, 15, 20, 30, 60 and 100 (Table 2), using TNT ver. 1.1 (Goloboff *et al*., 2008). Gaps were treated as missing data. Tree search was conducted using new technology algorithms (Nixon *et al*., 1999; Goloboff *et al*., 2003); the command string for each search was **piwe = x; hold 1200 xmult = level 10;** where **piwe** activates the implied weighting option, **x** indicates the *k* value for the search, and **xmult = level 10** specifies the most stringent heuristic search strategy. Nodal support values for EW analyses were calculated using 1000 bootstrap pseudoreplicates with a removal probability of 36%, using an **xmult = level 6** search strategy. Symmetric resampling, presented as group supported/contradicted, was conducted with the post search command string **nelsen*; scores; fit*; length; save/; resample replications 1000 sym;** for each *k* value, using 1000 pseudoreplicates with removal probability of 33%. IW tree selection was based on the values of Fit, adjusted homoplasy (AH) and average clade support (ACS; Table 2), where the tree with the best combination of values was preferred and used for comparisons with all other analyses (Table 2; Figs. 3–6).

BI analyses were conducted using Mr. Bayes v. 3.2.6 with XSEDE (Huelsenbeck & Ronquist, 2001) on the CIPRES Science Gateway. Each analysis comprised four simultaneous runs, with four chains default for 20,000,000 generations and a heat parameter of 0.10, sampling every 1,000 trees. The initial 25% of sampled trees were discarded as burn-in. Effective sample size (EES > 200) for each parameter was checked in TRACER v. 1.6 (Rambaut *et al.*, 2018).

ML analyses were conducted using RAxML-HPC2 v. 8.2.10 with XSEDE (Stamatakis, 2014) on the CIPRES Science Gateway. Optimal trees were computed with the **-f a** command for rapid bootstrap analysis and search for the best scoring tree in one run, computing 1000 bootstrapping replicates, using the GTRCAT model for molecular partitions, and the MkV model, with Lewis correction for morphological data, implemented with the command **asccorr=lewis**.

Clade robustness was evaluated according to two criteria (Giribet, 2003): node or branch support, reflected as bootstrap, symmetric resampling, and posterior probability values, and clade stability or sensitivity, reflected as the recovery of clades across different optimality criteria (e.g., ML, BI and parsimony) and analytical parameters (e.g., EW and IW).

The following datasets were analyzed to further evaluate clades with conflicting placements, e.g., genera *Baalrog* Monjaraz-Ruedas *et al.*, 2019 and *Schizophyxia* Monjaraz-Ruedas *et al.*, 2019: the morphological character matrix; each of the four molecular datasets (28S, ITS, 12S and COI); the nuclear dataset (28S + ITS); and the mitochondrial dataset (12S + COI). Additionally, the morphological and molecular data were analyzed simultaneously, first, excluding terminals with long branches; second, removing *Baalrog* and *Schizophyxia*; and third, excluding some terminals of *Baalrog* and *Schizophyxia* with missing sequence data.

The morphological characters were optimized on tree topologies obtained by simultaneous analysis of the morphological and molecular data with BI, ML and parsimony, using Mesquite ver. 3.0.4 (Maddison & Maddison, 2018), to calculate the consistency indices (CI), retention indices (RI) and length (L) of each topology, as well as the values for each character and their distribution on the topology (Fig. 7, Supporting Information Table S2), statistics which assisted with evaluating morphological congruence across the different topologies. Characters were optimized with accelerated transformation (ACCTRAN) (Farris, 1970; Swofford & Maddison, 1987), except where indicated otherwise (Supporting Information Appendix 3).

Results

Sequence data

Sequences of the ribosomal 28S marker were length invariant, comprising 501 nucleotide base-pairs (bp) in all terminals. The ITS sequences varied from 637–837 bp in length, with an average of 806 bp, excluding gaps. The 12S sequences varied from 319–387 bp, with an average of 360 bp. The COI sequences, amplified in two fragments, were either 658 bp (one fragment) or 1078 bp (both fragments) (Table 1).

Among the aligned loci, 74%, 49%, and 48% of the sites were variable, and 65%, 35%, and 41% parsimony-informative, in the 12S, ITS, and COI, respectively, whereas 9% were variable and 5% parsimony-informative in the 28S (Table 1). As expected for a protein-coding gene, the third codon position of the COI was the most informative, with 96% of the sites variable and 91% parsimony-informative, followed by the first codon position, with 34% of the sites variable and 25% parsimony-informative (Table 1). According to the analysis of per site informativeness, the 12S and ITS were the most informative markers (Fig. 2B).

The aligned ITS, 12S, and COI sequences were concatenated together with the 28S sequences, to produce a matrix of 2968 aligned DNA nucleotides, including gaps, in which 45% of the sites were variable and 36% parsimony-informative (Table 1).

As reported in other arthropod taxa (DeSalle *et al.*, 1987; Prendini *et al.*, 2003; González-Santillán & Prendini, 2015) the methylation process for mitochondrial markers was evident in the schizomid sequences which demonstrated an AT-bias of 79% and 68% in the nucleotide composition of the 12S and COI, respectively, whereas the nucleotide composition of the nuclear markers was more uniformly distributed with a slightly greater GC content of 58% and 56% in the ITS and 28S, respectively (Table 1).

The transition/transversion ratio (ti/tv) is usually greater than 2, as transitions are expected to occur more frequently than transversions (there are two kinds of transitions vs. four kinds of transversions). For example, if the value decreases to 0.5, indicating that the number of transversions is greater than expected, there is a higher probability of non-synonymous mutations, reflecting saturation of the data (DeSalle *et al.*, 1987; Wang *et al.*, 2015). The ti and tv proportions, as well as the ti/tv ratio (Table 1), confirmed a greater proportion of transitions in the 28S, ITS and COI markers, but a more equal proportion in the 12S (ti/tv ratio: 0.67), suggesting greater saturation in the 12S marker, also reflected in the higher percentage of variable sites in the alignment (74%) and the per site informativeness graph (Fig. 2B). This is also true for the concatenated alignment, for which the ti/tv ratio was 0.83 (Table 1). The ti/tv ratio for the different codon positions of COI was as expected, i.e., the first and third codon positions possessed a higher proportion of transitions, with values of 4.2 and 2.04, respectively, whereas the proportion was lower for the second codon position, with a value of 0.8 (Table 1). These genomic statistics are well reflected in the data partition scheme and justify the use of different models for each data partition, as indicated by Partition Finder and jModelTest.

Separate morphological analyses

Separate analyses of the morphological matrix recovered several different topologies with low support for the internal and terminal nodes. Parsimony analysis with EW retrieved 72 most parsimonious trees (MPTs), the strict consensus of which (length: 320, CI: 0.356, RI: 0.802) had the highest ACS (Table 2). Parsimony analysis with IW recovered three MPTs for all k values (except $k = 1$ with two MPTs), although the best scores for Fit, AH and ACS were obtained with $k = 100$. The tree obtained with BI of the morphological matrix was achieved in only three million generations and received higher nodal support values than the trees obtained by the analyses with ML or parsimony.

All separate morphological analyses recovered six genera monophyletic, three with high support, i.e., *Heteroschizomus* (BI/ML/parsimony = 0.99/96/70), *Schizophyxia* (0.92/98/93), and *Troglostenochrus* (1/100/99), and three with lower support values, i.e., *Ambulantactus* Monjaraz-Ruedas *et al*., 2019 (0.98/71/78), *Harveyus* Monjaraz-Ruedas *et al*., 2019 (0.83/59/37), and *Stenochrus s. str*., as redefined by Monjaraz-Ruedas *et al*. (2019) (0.97/67/14) (Table 3). *Baalrog* and *Nahual* Monjaraz-Ruedas *et al*., 2019 where not monophyletic in the separate morphological analyses (Table 3). *Nahual* was consistently polyphyletic, perhaps due to morphological variation within this genus, and the absence of males for two of the terminals.

A clade comprising *Harveyus*, *Mayazomus*, *Olmecazomus* and *Schizophyxia* was consistently recovered, perhaps due to the similarity of the male pygidial flagellum among most species of these genera. A clade comprising *Stenochrus gruta* Monjaraz-Ruedas & Francke, 2018, *S.* cf. *guatemalensis*, *S. pecki*, *S. portoricensis*, and *Stenochrus* sp. (Clade 1), was monophyletic with high support by BI, but low support by ML and parsimony with EW (Table 3). This clade was also monophyletic when *Stenochrus alcalai* Monjaraz-Ruedas & Francke, 2018 and *Stenochrus chimalapas* Monjaraz-Ruedas & Francke, 2018 (Clade 4) were included in the analyses with BI, ML, and parsimony with EW (Table 3).

Separate molecular analyses

The separate molecular analyses retrieved all except two genera monophyletic with high support (Table 3, Figs. 2, 6). *Stenochrus s. str.* (Clade 4), was paraphyletic, due to the placements of *S. alcalai* and *S. chimalapas*, which were weakly supported, reflecting their unstable positions (Fig. 6A–C, Table 3). Relationships within *Stenochrus* are summarized in Table 3 (Clades 1, 2, 3 and 4). Clade 1 was monophyletic with low support by BI, but high support by ML and parsimony with EW (0.68/98/100; Table 3). Clade 2 (Clade 1 + *S. chimalapas*) was not monophyletic, whereas Clade 3 (Clade 1 + *S. alcalai*) was monophyletic with low support by ML and parsimony with IW.

Baalrog was rendered paraphyletic in all parsimony analyses by *Schizophyxia*, which was monophyletic and strongly supported (symmetric resampling value and bootstrap percentage of 100) in the EW analyses (Fig. 6C). *Baalrog* and *Schizophyxia* were monophyletic in the analyses with BI and ML, receiving high support values of 1 and 98, respectively (Table 3). Although *Schizophyxia* was well supported in all analyses (Table 3), its placement with respect to the other genera was weakly supported, consistent with its unstable position. *Schizophyxia* was nested within *S. chimalapas* in the BI analysis, with a posterior probability of 0.7, whereas it was placed sister to *Harveyus*, with a bootstrap percentage of 37, in the ML analysis (Fig 6A, B).

Most internal nodes recovered by the separate analyses of the molecular dataset were weakly supported (Fig. 6A–C, Table 3). A clade comprising *Nahual* and *Pacal* was recovered with high support in all analyses, however. Although a clade comprising *Heteroschizomus*, *Mayazomus* and *Troglostenochrus* was not recovered in the parsimony analyses, *Troglostenochrus* consistently grouped sister to all other North American hubbardiids, and *Mayazomus* grouped sister to the clade comprising *Baalrog* and *Schizophyxia*, albeit with low support (Fig. 6A–C).

Simultaneous analyses

Simultaneous analysis of the morphological and molecular data sets recovered similar tree topologies (Figs. 3, 4), those obtained by the analyses with parsimony being the most different. All genera were monophyletic with high support in the BI and ML analyses, except for *Stenochrus*, which received a posterior probability of 0.91 in the BI analysis and a bootstrap percentage of 66 in the ML analysis (Fig. 3, Table 3). The tree topologies obtained by BI and ML were similar, except for the placement of *Ambulantactus* sister to the clade comprising *Harveyus*, *Olmecazomus*, *Schizophyxia* and *Stenochrus*, and one node which collapsed at the base of BI tree, unlike the ML tree, in which *Ambulantactus* was placed sister to *Olmecazomus* (Figs. 3, 4B). *Pacal* was monophyletic, and consistently placed sister to *Nahual* with high support. *Baalrog* was monophyletic with high support (1/99/–) in the BI and ML analyses but rendered paraphyletic by *Schizophyxia* in the parsimony analyses (Fig. 4A). All other genera and outgroup taxa were monophyletic with high support (Table 3, Fig. 3). Unlike the topologies obtained with ML and BI, however, in which *Stenochrus* was placed sister to a clade comprising *Harveyus* and *Schizophyxia*, or to a clade comprising *Harveyus*, *Schizophyxia* and *Olmecazomus*, respectively, the topology obtained by parsimony with EW and IW placed *Stenochrus* sister to *Harveyus*, and was also incongruent with the ML and BI topologies concerning the positions of *Heteroschizomus*, *Mayazomus*, *Sotanostenochrus*, *Troglostenochrus*, and the clade comprising *Nahual* and *Pacal* (Fig. 4).

Stenochrus was consistently monophyletic, albeit weakly supported, in the tree topologies obtained from the various analyses, due to the unstable positions of *S. alcalai* and *S. chimalapas.* As in the separate molecular analyses, Clade 1 was strongly supported (Table 3), with similar or higher values than in the separate molecular analyses (Table 3). Clades 2 and 3 were less well supported or not recovered with the addition of *S. alcalai* (–/–/30) and *S. chimalapas* (0.96/73/–). However, support values for Clade 4, not recovered in the separate molecular analyses, were similar or higher than those in the separate morphological analyses, suggesting strong morphological support for *Stenochrus* (Table 3).

Schizophyxia was monophyletic and placed sister to *Harveyus* with high support (0.93/70) in the BI and ML analyses (Fig. 4B, C), but sister to *Baalrog magico* Monjaraz-Ruedas & Francke, 2018 and *Baalrog sbordoni* (Brignoli, 1973), with low support (< 50), in the parsimony analyses (Fig. 4). The clades comprising *Harveyus* and *Stenochrus*, as well as *Ambulantactus* and *Olmecazomus*, were weakly supported (< 50) in the parsimony analyses, compared with the ML (46/0.76) and BI (62/0.87) analyses, in which *Schizophyxia* was included in these clades (Table 3, Fig. 3, 4).

Orphans

Simultaneous analyses of the orphan taxa, i.e., *Ambulantactus davisi*, *Harveyus mulaiki* (Gertsch, 1940), *Harveyus reddelli* (Rowland, 1971), *Heteroschizomus meambar*, *Troglostenochrus palaciosi*, and *Schizophyxia bartolo* (Rowland, 1973) were largely congruent with the analyses from which they were excluded (Fig. 5). The tree topology obtained with ML and orphans included was otherwise identical to the topology obtained with ML and orphans excluded (Fig. 4B, 5C). All genera were monophyletic with high support for *Baalrog*, *Heteroschizomus*, *Nahual*, *Pacal*, and *Troglostenochrus* but low support for *Ambulantactus*, *Harveyus Schizophyxia*, and *Stenochrus* in the tree with orphans included (Fig. 5C).

Analyses with BI or parsimony with EW and orphans included recovered similar tree topologies, differing from the topology obtained with ML (Fig. 5), in the placement of *Troglostenochrus* sister to all other schizomid taxa, rather than *Sotanostenochrus*, as in the ML analysis with orphans included. Except for *Schizophyxia*, rendered paraphyletic by the placement of *Schizophyxia bartolo* in a polytomy with *Ambulantactus*, *Harveyus*, *Nahual*, *Olmecazomus*, *Pacal*, and *Stenochrus* (Fig. 5B), all genera were monophyletic, mostly with high support, in the BI analysis; *Ambulantactus* and *Stenochrus* received posterior probabilities of 0.67 and 0.63, respectively. As in other separate and simultaneous analyses with parsimony, *Schizophyxia* was monophyletic, but nested within *Baalrog*, rendering the latter paraphyletic (Fig. 5A). Additionally, *Ambulantactus* was rendered paraphyletic by placement of the orphan, *A. davisi*, in a polytomy comprising the other two species of *Ambulantactus* and *Olmecazomus* (Fig. 5A). Parsimony analysis with IW (k = 60) and orphans included retrieved the same topology as parsimony with EW (Fig. 5A).

Most clades received low support values in the parsimony analyses with EW and IW, due to instability introduced by missing data in the orphans. Despite low support, however, the tree topology recovered by the simultaneous analysis with orphans included was identical to that with orphans excluded, except for the paraphyly of *Ambulantactus*. *Stenochrus* Clades 1 and 4 were consistently recovered in all analyses with orphans included, although Clade 4 received low support. Clade 2, a monophyletic group comprising Clade 1 and *S. chimalapas*, was recovered by the BI analyses with posterior probability of 1; whereas only Clade 3 was recovered, with low support, in the parsimony analyses (Table 3).

Stability and support

The terminal groups were largely congruent and well supported among the tree topologies obtained by analyses with different optimality criteria, analytical parameters and data combinations, whereas the internal relationships were largely incongruent, poorly resolved and/or weakly supported (Fig. 4, 5).

Separate analyses of the morphological data recovered six of the eight clades obtained by simultaneous analysis of the morphological and molecular data, regardless of the optimality criterion or analytical parameters (Fig. 3), reflecting stability despite weak support. Two exceptions, which received high support, could be explained by the distinctive morphology of *Heteroschizomus* and the presence of only one of the two species of *Troglostenochrus*. Lack of resolution among the terminal branches of the tree suggests the morphological characters were insufficiently informative to resolve schizomid phylogeny at the generic level.

Clade recovery (stability) and support were similar in the separate analyses of the molecular data and the simultaneous analysis of the morphological and molecular data. Only two genera were unstable, *Baalrog*, consistently paraphyletic in the parsimony analyses, and *Stenochrus s. str.*, paraphyletic in the separate molecular analyses with ML, BI and parsimony.

The simultaneous analyses with orphans included recovered similar topologies, but with lower support, than the simultaneous analyses with orphans excluded, largely due to the missing data. The morphological characters were nevertheless sufficiently informative to place orphans with the most morphologically similar taxa.

Phylogenetic instability was prevalent among the deeper internal nodes, especially regarding generic relationships, in all phylogenetic analyses. The tree topologies obtained using parsimony were the least congruent with those obtained using other optimality criteria. For example, parsimony with EW failed to recover the monophyly of *Schizophyxia*, perhaps due to saturation of the 12S marker, reflected in the long branches of some terminals of *Baalrog* and *Schizophyxia*, which appear to have grouped together as a consequence of long branch attraction (Felsenstein, 1978; Huelsenbeck & Hillis, 1993; Bergsten, 2005; Fig. 6). Despite this saturation, 12S was phylogenetically informative for other genera, especially *Stenochrus s. str.*, in the simultaneous analysis, mitigating against its removal from the analyses (Fig. 6H). Variation in the alignment length of the 12S and ITS markers had no apparent effect on topologies obtained by the separate or simultaneous analyses when different parameters, such as gap opening costs, were applied.

Phylogenetic tree choice

Parsimony recovered the least congruent topology along the three optimality criteria applied in the analyses, specifically regarding the positions of *Baalrog* and *Schizophyxia*, which were monophyletic with high support in the BI and ML analyses and some parsimony analyses with IW (k = 5 and 10; Fig. 6D). When different sets of terminal taxa with long branches were removed from the parsimony analyses (Fig. 6E–H), however, the position of *Schizophyxia* altered with respect to the tree topology obtained with simultaneous analysis (Fig. 6E–H) whereas the position of *Baalrog* remained unchanged (Fig. 6E).

The morphological data also contradicted the hypotheses obtained by the parsimony analyses. When the morphological characters where optimized on the topologies obtained by the simultaneous analyses with three optimality criteria, the length (number of steps) of the ML tree (372) was similar to that of the most parsimonious trees (372) and shorter than that of the BI tree (374). The nodal support values were higher for the ML tree than for the trees obtained with parsimony, even when weighting against homoplasy (IW).

The CIs and RIs of only 29 of the 61 morphological characters optimized differed among the tree topologies obtained by the simultaneous analyses with three different optimality criteria. The indices of thirteen characters were higher in the topology recovered with parsimony than those recovered with BI or ML; nine were higher in the topology recovered with ML than those recovered with BI or parsimony; and three were higher in the topology recovered with BI than those recovered with ML or parsimony (Fig. 7, Supporting Information Table S2). Five of the nine characters with higher indices in the ML topology and all three characters with higher indices in the BI topology supported the clade comprising *Harveyus* and *Schizophyxia* (Fig. 7, “stars”) whereas only three of the thirteen characters with higher indices in the parsimony topology supported the clade comprising *Baalrog* and *Schizophyxia* (Fig. 7, “circles”).

The remaining ten characters in the parsimony topology supported the placement of *Troglostenochrus* sister to all other schizomid taxa (Fig. 7, “squares”). *Troglostenochrus* shares several morphological characters, e.g., pedipalp setal configuration, with *Hubbardia pentapeltis* Cook, 1899, resulting in a more parsimonious optimization (one less reversal) with higher indices than in the BI or ML topologies.

These results suggest that the topology obtained with ML is the optimal and, hence, preferred hypothesis. Through implementation of an evolutionary model, the probabilistic method avoided erroneous results caused by saturation in the data (Table 1), which appear to have adversely affected the parsimony analyses.

Although the ML tree is the preferred hypothesis that best explains schizomid evolution based on this particular dataset, parsimony recovered a similar topology when the long branches were removed, suggesting the relationships recovered with parsimony and probabilistic methods are broadly concordant (Fig. 5D–H). This in turn leads to the conclusion that clade stability is generally high, which supports the revised classification of Monjaraz-Ruedas *et al.* (2019) based on the phylogeny presented here.

Discussion

Dataset informativeness

All datasets were informative, with complex phylogenetic structure recovered by each data partition. The inclusion of morphological data in a simultaneous analysis increased nodal support for all genera and facilitated the placement of orphan taxa for which molecular data were unavailable.

Unlike some arachnid taxa, in which, for example, the D3 region of the nuclear 28S rDNA gene is more conserved (Whiting *et al*., 1997; Prendini *et al*., 2003), this marker appears to be sufficiently variable and informative among schizomids to recover tree topologies resembling those obtained by simultaneous analyses of the morphological and molecular data.

As expected, the mitochondrial data were more informative than the nuclear data. However, the topology obtained by separate analysis of the mitochondrial data obtained a polytomy at the base of the tree, suggesting the phylogenetic signal of the mitochondrial markers was insufficient to resolve the deeper relationships of schizomids, unlike other arachnid taxa as theraphosid spiders or harvestmen (Cruz-López & Francke, 2017; Mendoza & Francke, 2017), in which COI sequences alone resolve relationships at the genus level. This may be due to saturation of the 12S and the second codon position of the COI (Table 1). It may also explain the very different topologies obtained by separate analysis of the 12S compared to the other markers (Fig. 6).

Optimization of the morphological characters used for generic diagnoses on the various phylogenetic hypotheses (Fig. 7) assisted identification of a preferred hypothesis. Based on this assessment, characters of the female spermathecae, as well as the unique character combinations recently proposed by Monjaraz-Ruedas *et al*. (2019), were found to be reasonably reliable for generic recognition.

Stenochrus *polyphyly*

Stenochrus, as originally defined by Reddell & Cokendolpher (1991, 1995), was rendered polyphyletic in all analyses with different optimality criteria, analytical parameters and datasets (Figs. 3–6), by the outgroup genera *Mayazomus*, *Olmecazomus*, *Pacal*, and *Sotanostenochrus*. This finding reflects the considerable disparity among North American schizomid lineages and justifies the revised classification of Monjaraz-Ruedas *et al*. (2019). The species groups proposed by Rowland & Reddell (1980, 1981) were largely unsupported by the preferred hypothesis presented here, according to which only the previously synonymized genus, *Heteroschizomus* (i.e., the former *goodnightorum* group) was monophyletic (Figs. 3–6). The *mexicanus* and *pecki* groups were paraphyletic, as the *mexicanus* group comprises four clades, corresponding to *Harveyus*, *Nahual*, *Schizophyxia*, and *S. portoricensis*, and the *pecki* group comprises three clades, corresponding to *Baalrog*, the remaining species of *Stenochrus*, i.e., *S. gruta*, *S. guatemalensis*, and *S. pecki*, and *Stenochrus valdezi* Monjaraz-Ruedas, 2012, the former transferred to *Troglostenochrus* by Monjaraz-Ruedas *et al*. (2019). The remaining species of the *mexicanus* group, i.e., *Stenochrus moisii* (Rowland, 1973) and *Stenochrus tepezcuintle* Armas & Cruz-López, 2009, which differ morphologically from other species of *Stenochrus*, appear to be more closely related to *Pacal* (Figs. 3–6), in which they were tentatively placed by Monjaraz-Ruedas *et al*. (2019).

As redefined by Monjaraz-Ruedas *et al*. (2019), *Stenochrus* is a Neotropical genus, distributed from southern Mexico (Oaxaca, Chiapas and the Yucatán Peninsula) to Guatemala, Honduras and Nicaragua, with most species occurring in the Mexican state of Oaxaca. All Caribbean representatives of the genus form part of the *S. portoricensis* complex.

As *S. portoricensis* is the type species of *Stenochrus*, comprehensive sampling of populations occurring in the Caribbean, North, Central, and South America, is needed to clarify its relationships with other genera, as well as its distribution, e.g., whether *S. portoricensis* actually occurs in North America, or even in continental America, or is restricted to the Caribbean. Furthermore, the different populations of *S. portoricensis* will need to be further investigated, as preliminary results indicate deep genetic divergences among populations of this species from Mexico, Central America and the Caribbean. Some of the sequences identified as *S. portoricensis* in the present study appear to be more closely related to other species of the genus, e.g., *S. gruta* and *S. pecki*, than to populations from the vicinity of the type locality, Puerto Rico, suggesting they may even be different species with a conserved or homoplastic morphology.

Outgroup relationships

The present study addressed relationships within the genus *Stenochrus* and focused on molecular markers considered phylogenetically informative for the terminal relationships, with predictably low support for the deeper internal nodes (Fig. 2). A robust, well-supported phylogeny of the North American schizomid genera would require additional molecular markers with a slower mutation rate, such as 18S rDNA, additional, more conservative fragments of 28S rDNA or nuclear protein-coding markers like EF 1 α and Polymerase II.

Despite the low support and instability of the deeper relationships, some general patterns were observed. *Baalrog*, *Sotanostenochrus*, and *Troglostenochrus* were consistently placed sister to all other genera. *Mayazomus* appears to be more closely related to *Heteroschizomus* and *Troglostenochrus* than to *Pacal*, contradicting a previous morphological hypothesis (Monjaraz-Ruedas & Francke, 2017). *Olmecazomus* was placed sister to *Ambulantactus*, together with *Harveyus* and *Stenochrus*, by several analyses, also incongruent with the morphological hypothesis of Monjaraz-Ruedas & Francke (2017), according to which *Olmecazomus* was sister to all other Neotropical schizomids.

A monophyletic group comprising *Nahual* and *Pacal* was among the more robust clades recovered by the simultaneous analyses and the separate analyses of the molecular data. This clade is concordant with the morphology and distributions of these genera, which appear to be part of the Neotropical fauna, are mostly hypogean, and share the presence of a cheliceral lamella. The two genera did not form a monophyletic group in the separate morphological analyses, however, probably because of extensive variation in body size, coloration and setal patterns within each genus.

Baalrog is restricted to caves in the Neotropical region of central and southern Mexico (Oaxaca and Veracruz). Its species exhibit several troglomorphies, morphological adaptations to life in caves, consistent with their placement close to other cavernicolous lineages, e.g., *Sotanostenochrus* and *Troglostenochrus*, in the BI and ML analyses.

Troglostenochrus was consistently monophyletic with high support. This may be due to the inclusion of only two conspecific samples in the analyses. However, the genus remained monophyletic in the simultaneous analyses with three different optimality criteria when the orphan, *T. palaciosi*, was included. *Troglostenochrus* possesses a distinctive, trident-shaped pygidial flagellum in the male and several troglomorphies, including large body size and several spiniform setae on the pedipalps and prosoma, suggesting it is restricted to cavernicolous habitats. The phylogenetic placement of *Troglostenochrus* was weakly supported; however, the CIs and RIs of the morphological characters optimized on the tree topologies obtained with different optimality criteria (Fig. 7), were higher in the parsimony topology, suggesting the position of *Troglostenochrus* in the topology obtained with parsimony, is a better fit for the morphological data.

Harveyus was also consistently monophyletic. This genus comprises most of the species occurring in northern Mexico and the southern United States. The occurrence of several morphologically variable populations, mostly from caves along the Sierra del Abra in the Mexican state of San Luis Potosí (Rowland, 1980), suggests the existence of a species complex. Populations of *Harveyus mexicanus* (Rowland, 1971) in the Mexican state of Tamaulipas, as well as the rare *H. reddelli*, differ markedly from populations of *H. mexicanus* in the state of San Luis Potosí. *Harveyus mulaiki* and *H. reddelli* were monophyletic with other species of the genus in the simultaneous analyses with orphans included, suggesting that, despite variation in the male pygidial flagellum, the spermathecal and setal characters are informative for the diagnosis of this genus. Furthermore, some species of *Harveyus* from northern Mexico and the southern United States may need to be transferred to *Schizophyxia*, which appears to be closely related and inhabits caves across a similar distribution. However, due to the unstable position of *Schizophyxia* in the analyses presented here, the hypothesis that these genera are sister taxa awaits further testing.

Ambulantactus is also represented in Tamaulipas, but the species of this genus differ markedly in morphology from the species of *Harveyus* and *Schizophyxia*. According to the phylogenetic hypothesis presented here, *Ambulantactus* is a distinct lineage, more closely related to *Olmecazomus*. It was also recovered sister to a monophyletic group comprising *Harveyus*, *Olmecazomus*, *Schizophyxia*, and *Stenochrus*. The phylogenetic position of *Ambulantactus*, together with the disjunct distributions of its component species, suggest this could be an ancient lineage of schizomids.

Nahual was consistently monophyletic in the simultaneous analyses and in the separate analyses of the molecular data. Its species consistently formed two clades, supported by morphological variation in the spermathecal lobes, as well as by their distributions, with one of the clades restricted to the northern Sierra in the Mexican state of Oaxaca and the other to the Sierra de Zongolica in the state of Veracruz.

Conclusions

The study presented here applied different optimality criteria, analytical parameters and data sets to investigate a complex phylogenetic question, the relationships among a neglected junkyard genus of North American short-tailed whipscorpions, *Stenochrus*. The effects of data removal and terminal taxa with missing data were explored, along with the utility of morphological characters traditionally used for schizomid systematics.

Based on the analyses presented here, the genus *Stenochrus*, as originally defined (Reddell & Cokendolpher, 1991, 1995) comprises eight monophyletic groups supported by both morphological and molecular data, despite similar, often convergent morphology. A combination of informative characters permitted the diagnosis and reclassification of those clades into eight genera by Monjaraz-Ruedas *et al.* (2019). Some former species groups proposed by Rowland (1975) and Rowland & Reddell (1980, 1981) were recovered as monophyletic by the analyses, e.g., the former *goodnightorum* group, leading to the revalidation of *Heteroschizomus*, whereas others, e.g., the *mexicanus* and *pecki* groups, were not.

Despite its redefinition by Monjaraz-Ruedas *et al.* (2019), the limits of *Stenochrus* remain uncertain. The genus comprises at least two distinct lineages, in addition to the typical forms, and the wide distribution of the type species, *S. portoricensis*, and uncertain status of several of its populations merit additional data and analysis.

Further assessment, incorporating additional data, is also needed to corroborate genus *Schizophyxia*, recognized by Monjaraz-Ruedas *et al.* (2019) based on a monophyletic group recovered by the simultaneous analyses with BI and ML. Indeed, as the present study makes clear, the systematics of the entire order is in dire need of more extensive and rigorous analysis.

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Figure legends

Figure 1. Map of the Caribbean, Central America and Mexico, plotting known locality records of the short-tailed whipscorpion (Schizomida: Hubbardiidae), based on data from museum collections and the literature. (**A**). Distribution of *Stenochrus* Chamberlin, 1922, as redefined by Monjaraz-Ruedas et al. (2019). (**B**). Distributions of *Ambulantactus* Monjaraz-Ruedas et al., 2019, *Baalrog* Monjaraz-Ruedas et al., 2019, *Harveyus* Monjaraz-Ruedas et al., 2019, *Heteroschizomus* Rowland, 1973, *Nahual* Monjaraz-Ruedas et al., 2019, *Schizophyxia* Monjaraz-Ruedas et al., 2019, and *Troglostenochrus* Monjaraz-Ruedas et al., 2019.

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Figure 5. Phylogeny of the short-tailed whipscorpion genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae), obtained by simultaneous analysis of the morphological and molecular data including "orphans" (i.e., terminals represented only by morphological data indicated by

stars) with parsimony (**A**), Bayesian Inference (**B**), and Maximum Likelihood (**C**). Nodal support values, i.e., bootstrap (parsimony, Maximum Likelihood) and posterior probability (Bayesian Inference) indicated above branches.

Figure 6. Phylogeny of the short-tailed whipscorpion genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae), obtained with different datasets, optimality criteria and analysis parameters. (**A–C**). Separate analysis of the molecular data with Maximum Likelihood (**A**), Bayesian Inference (**B**), and parsimony with equal weights (**C**). (**D–H**). Simultaneous analysis of morphological and molecular data using parsimony with implied weighting and *k* = 5 (**D**); equal weighting and excluding *Schizophyxia* Monjaraz-Ruedas *et al*., 2019 (**E**); equal weighting and excluding *Baalrog* Monjaraz-Ruedas *et al*., 2019 (**F**); equal weighting and excluding *Schizophyxia* and *Stenochrus chimalapas* Monjaraz-Ruedas & Francke, 2018 (**G**); equal weighting and excluding the 12S rDNA sequence data (**H**). Arrows indicate the variable positions of two species of *Stenochrus*: *S. chimalapas* and *Stenochrus alcalai* Monjaraz-Ruedas & Francke, 2018.

Figure 7. Consistency indices (CI), retention indices (RI) and length (L) of selected morphological characters optimized on phylogeny of the short-tailed whipscorpion genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae), obtained by simultaneous analysis of the morphological and molecular data with Maximum Likelihood (ML), Bayesian Inference (BI) and parsimony with equal weighting (P). Symbols indicate clades with stronger indices for a specific topology: circles = (*Baalrog* Monjaraz-Ruedas *et al*., 2019 + *Schizophyxia* Monjaraz-Ruedas *et al*., 2019); stars = (*Harveyus* Monjaraz-Ruedas *et al*., 2019 + *Schizophyxia*); squares = (*Troglostenochrus* Monjaraz-Ruedas *et al*., 2019 + other taxa).

Table 1. Genomic data statistics for aligned DNA sequences of two nuclear gene markers, 28S rDNA (28S) and internal transcribed spacer (ITS), and two mitochondrial gene markers, 12S rDNA (12S) and Cytochrome *c* Oxidase Subunit I (COI) used for phylogenetic analysis of the short-tailed whipscorpions genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae): aligned length in nucleotide base-pairs (bp); number and percentage of variable positions; number and percentage of conserved (invariant) positions; number and percentage of Parsimony-informative (PI) positions, including gaps; percentage nucleotide composition; percentage of transitions (ti) and transversions (tv) for each nucleotide combination and overall; transition/transversion ratio (ti:tv).

		28S	ITS	12S	COI	1st	2nd	3rd	Total
length (bp)		511	959	420	1078	359	359	359	2968
variable (%)		45 (9)	469 (49)	312 (74)	519 (48)	122 (34)	54 (15)	343 (96)	1345 (45)
conserved (%)		466 (91)	444 (46)	96 (23)	558 (52)	237 (66)	305 (85)	16 (4)	1564 (53)
PI (%)		24 (5)	333 (35)	274 (65)	438 (41)	88 (25)	23 (6)	327 (91)	1069 (36)
A		24.73	20.66	36.89	31.94	32.85	10.21	50.26	31.03
T		18.63	20.49	42.19	36.98	26.68	45.14	39.51	37.2
C		24.88	27.17	4.75	17.25	17.45	29.09	9.45	13.07
G		31.75	31.69	16.17	13.84	23.02	15.56	0.79	18.7
ti	A↔G	33.44	21.24	32.03	22.2	11.31	12.56	32.37	6.95
	C↔T	49.79	32.89	16.83	41.42	71.15	23.53	51.36	39.27
tv	A↔C	4.16	10.97	10.64	8.95	4.41	12.56	4.86	13.37
	A↔T	3.63	9.44	20.22	12.54	5.22	17.69	7.31	18.34
	C↔G	4.75	13.5	5.34	5.66	3.55	14.27	0.83	8.54
	G↔T	4.22	11.97	14.92	9.25	4.36	19.4	3.28	13.51
ti : tv		4.83	1.13	0.67	1.55	4.2	0.8	2.04	0.83
A-T bias		43.36	41.15	79.08	68.92	59.53	55.35	89.77	68.23
C-G composition		56.63	58.86	20.92	31.09	40.47	44.65	10.24	31.77

Table 2. Tree statistics for phylogenetic analyses of the short-tailed whipscorpions genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae), using parsimony with equal weighting (EW) and implied weighting (IW): values of the concavity constant (*k*), length (L), consistency index (CI), retention index (RI), Fit, adjusted homoplasy (AH) and average clade support (ACS) of most parsimonious trees (MPTs). Optimal tree topologies, indicated in boldface, with highest Fit, AH and ACS values. "Orphans" refers to simultaneous analyses including terminal taxa represented only by morphology.

	k	**MPTs**	**L**	**CI**	**RI**	**Fit**	**AH**	**ACS**		***k***	**MPTs**	**L**	**CI**	**RI**	**Fit**	**AH**	**ACS**
Morphology									**Simultaneous**								
EW		72	320	0.356	0.802	31.0	–	33.6	EW		1	8512	0.240	0.617	516.3	–	76.6
IW	1	2	375	0.315	0.753	22.0	4.9	27.9	IW	1	1	8923	0.264	0.610	320.1	806.8	58.2
	5	3	311	0.379	0.814	37.5	19.4	33.9		5	1	8838	0.266	0.616	626.8	500.1	66.1
	10	3	306	0.386	0.819	44.3	2.6	35.1		10	1	8835	0.266	0.616	774.6	352.3	68.7
	15	3	302	0.377	0.819	47.6	9.4	35.3		15	1	8821	0.267	0.617	852.7	274.2	68.6
	20	3	302	0.377	0.819	49.5	7.5	35.6		20	1	8821	0.267	0.617	901.8	225.1	68.8
	30	3	302	0.377	0.819	51.6	5.3	35.7		30	1	8819	0.267	0.617	960.7	166.7	69.5
	60	3	302	0.377	0.819	54.1	2.9	35.9		60	1	8819	0.267	0.617	1033.4	93.5	70.1
	100	**3**	**302**	**0.377**	**0.819**	**55.2**	**1.7**	**35.9**		**100**	**1**	**8819**	**0.267**	**0.617**	**1067.7**	**59.2**	**70.1**
Molecules									**Orphans**								
EW		2	8153	0.237	0.607	487.4	–	76.6	EW		5	8897	0.265	0.614	512.4	–	58.8
IW	1	2	8543	0.262	0.601	302.9	767	54.7	IW	1	1	9025	0.261	0.607	319.1	807.8	54.2
	5	1	8498	0.263	0.604	593.2	476.7	63.5		5	3	8913	0.264	0.613	623.6	503.3	59.0
	10	1	8451	0.264	0.607	733.5	336.4	65.0		10	3	8912	0.264	0.613	772.0	353.4	61.9
	15	1	8444	0.265	0.608	807.8	262.1	65.7		15	5	8904	0.265	0.614	850.3	276.6	62.1
	20	1	8444	0.265	0.608	854.6	215.3	66.7		20	5	8902	0.265	0.614	899.7	227.2	62.5
	30	1	8442	0.265	0.608	910.8	159.1	67.3		30	7	8897	0.265	0.614	959.0	167.9	62.6
	60	**1**	**8442**	**0.265**	**0.608**	**980.3**	**89.6**	**67.6**		**60**	**6**	**8897**	**0.265**	**0.614**	**1032.4**	**94.5**	**62.5**
	100	1	8441	0.265	0.608	1013.2	56.7	67.4		100	6	8897	0.265	0.614	1067.1	59.8	62.3

Table 3. Nodal stability for four clades and eight genera of short-tailed whipscorpions (Schizomida: Hubbardiidae) in phylogenetic analyses using parsimony with equal weighting (EW), the optimal parameter set with implied weighting (*k* value), Bayesian inference (BI) and Maximum likelihood (ML). Nodal support values, i.e., bootstrap (EW, ML), symmetric resampling (IW) and posterior probability (BI), indicated as follows: black (> 90); dark grey (≥ 50); light grey (< 50). ‘Orphans’ refers to simultaneous analyses including taxa represented only by morphology. Clade 1: (*Stenochrus gruta* + *S. guatemalensis* + *S. pecki* + *S. portoricensis*); Clade 2: (Clade 1 + *S. chimalapas*); Clade 3: (Clade 1 + *S. alcalai*); Clade 4: (Clade 2 + *S. alcalai*) = *Stenochrus* as redefined by Monjaraz-Ruedas *et al*., 2019. *Ambu.* = *Ambulantactus*; *Baal.* = *Baalrog*; *Harv.* = *Harveyus*; *Hete.* = *Heteroschizomus*; *Nahu.* = *Nahual*; *Schi.* = *Schizophyxia*; *Sten.* = *Stenochrus*; *Trog.* = *Troglostenochrus*.

		Clade 1	**Clade 2**	**Clade 3**	**Clade 4**	***Ambu.***	***Baal.***	***Harv.***	***Hete.***	***Nahu.***	***Schi.***	***Sten.***	***Trog.***
Morphology	EW	14			14	32		37	70		93	14	99
	k = 100	0			0	45		48	80		96	21	100
	BI	0.97			0.97	0.98		0.83	0.99		0.92	0.97	1
	ML	67			11	71		59	96		98	67	100
Molecules	EW	100				52		99	99	97	100		100
	k = 60	89		0		37		83	90	70	100		100
	BI	0.68				0.99	1	0.99	1	1	1		1
	ML	98		13		98	98	88	99	99	100		100
Simultaneous	EW	100		30	3	84		99	100	100	100	3	100
	k = 100	98		10	1	63		96	99	92	100	1	100
	BI	0.98	0.96		0.91	1	1	1	1	1	1	0.91	1
	ML	100	73		66	100	99	96	100	100	100	66	100
Orphans	EW	90		0	1			26	72	66	17	0	54
	k = 60	96		1	14			37	83	85	27	1	66
	BI	1	1		0.63	0.67	1	1	1	1		0.63	1
	ML	99	69		61	67	90	62	95	98	78	61	97

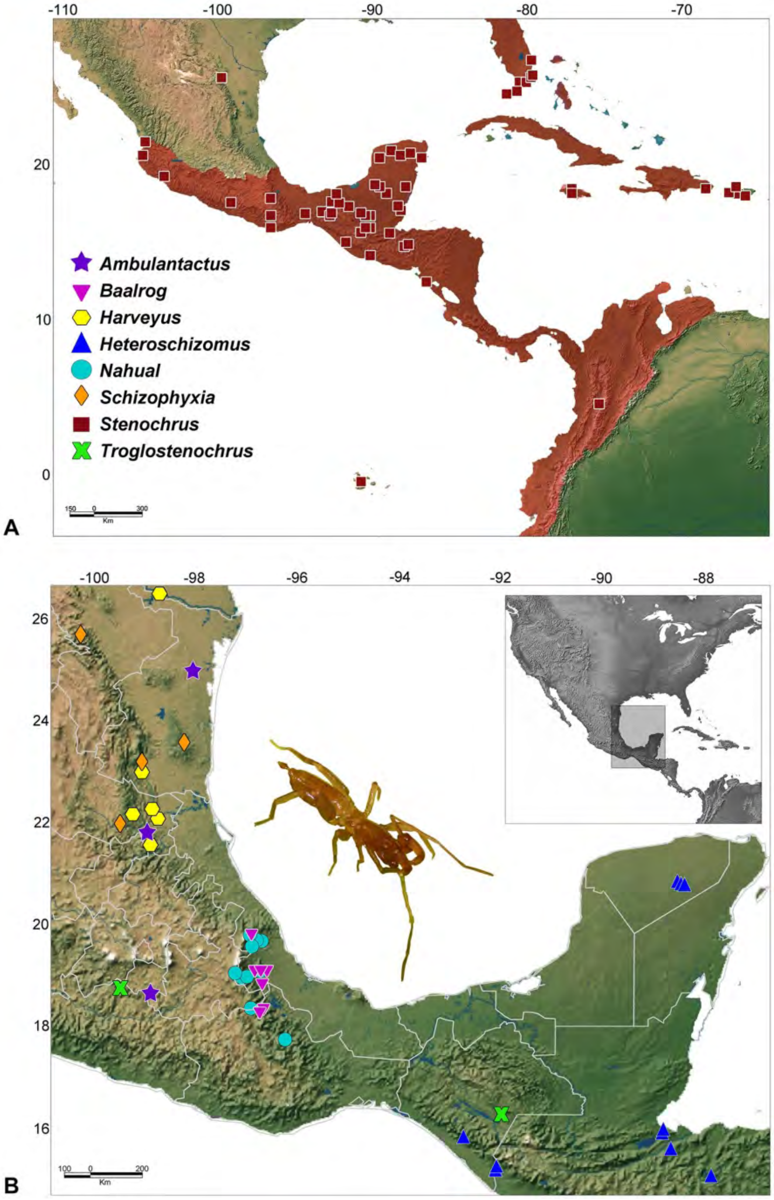

Figure 1. Map of the Caribbean, Central America and Mexico, plotting known locality records of the short-tailed whipscorpion (Schizomida: Hubbardiidae), based on data from museum collections and the literature. (A). Distribution of *Stenochrus* Chamberlin, 1922, as redefined by Monjaraz-Ruedas et al. (2019). (B). Distributions of *Ambulantactus* Monjaraz-Ruedas et al., 2019, *Baalrog* Monjaraz-Ruedas *et al*., 2019, *Harveyus* Monjaraz-Ruedas et al., 2019, *Heteroschizomus* Rowland, 1973, *Nahual* Monjaraz-Ruedas et al., 2019, *Schizophyxia* Monjaraz-Ruedas et al., 2019, and *Troglostenochrus* Monjaraz-Ruedas et al., 2019.

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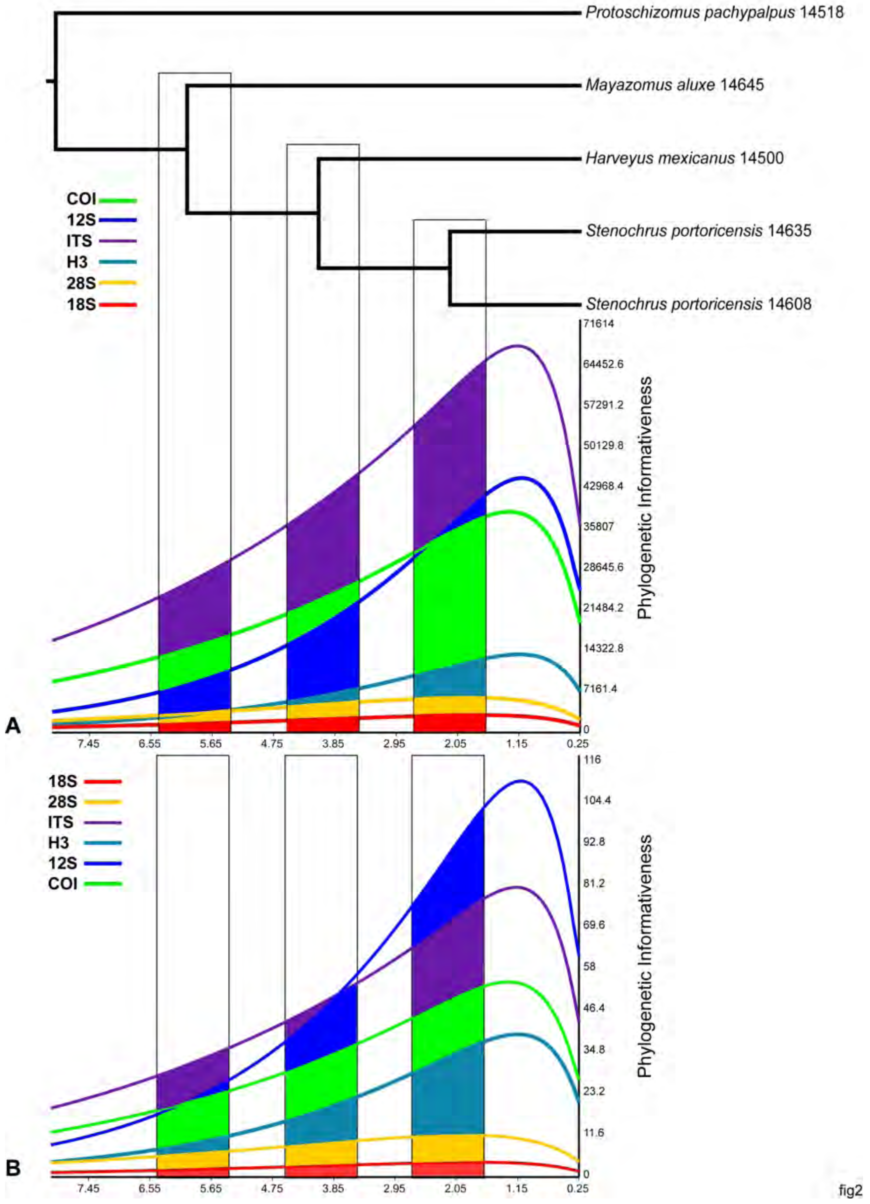

Figure 2. Phylogenetic informativeness profiles of exemplar dataset for short-tailed whipscorpion genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae). (A). Profile obtained for net rates (entire alignment). (B). Profile obtained for site rates in each gene marker. Colored areas represent the integration of the area below the curve with the highest probability of exhibiting mutations at particular levels (populations, species or genera) in the phylogeny.

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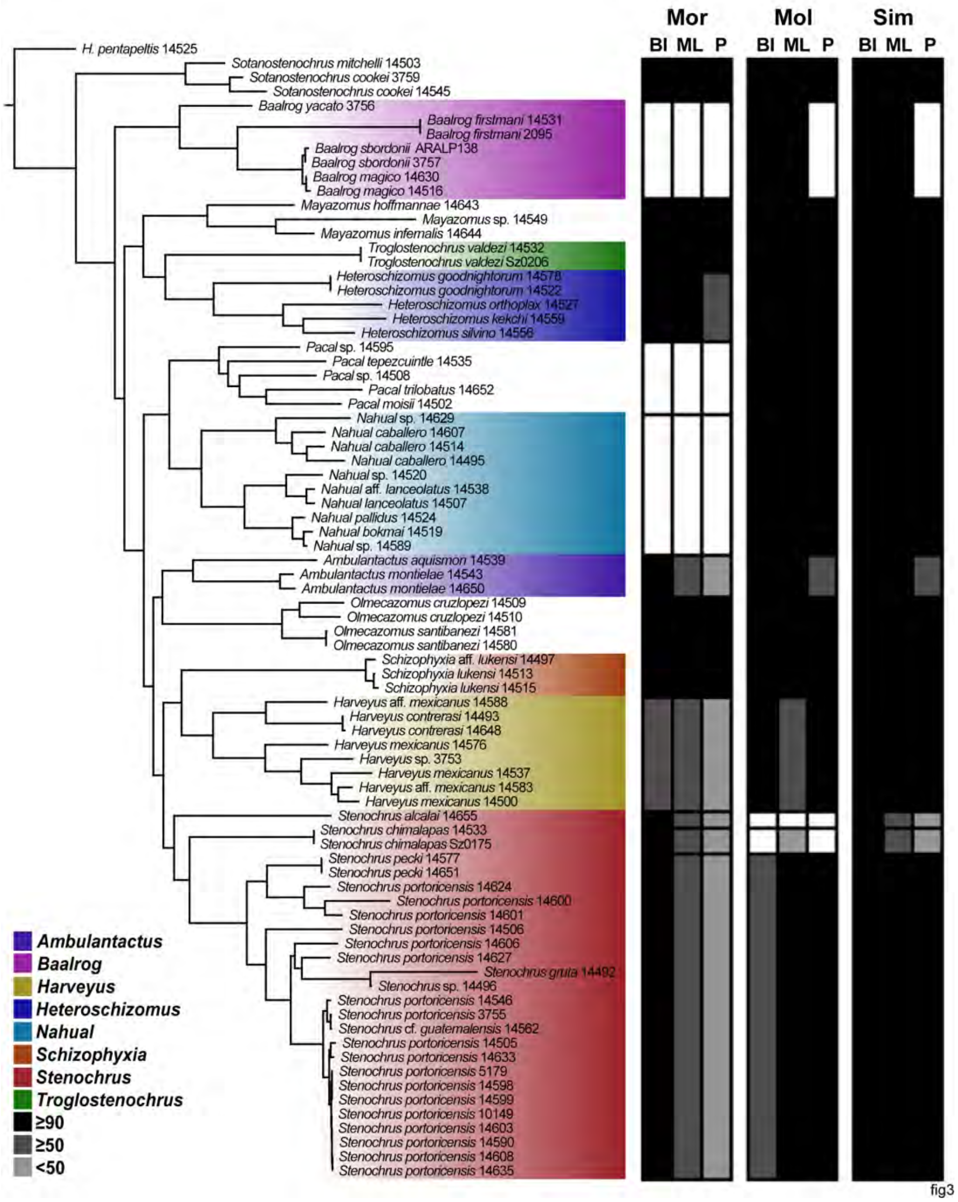

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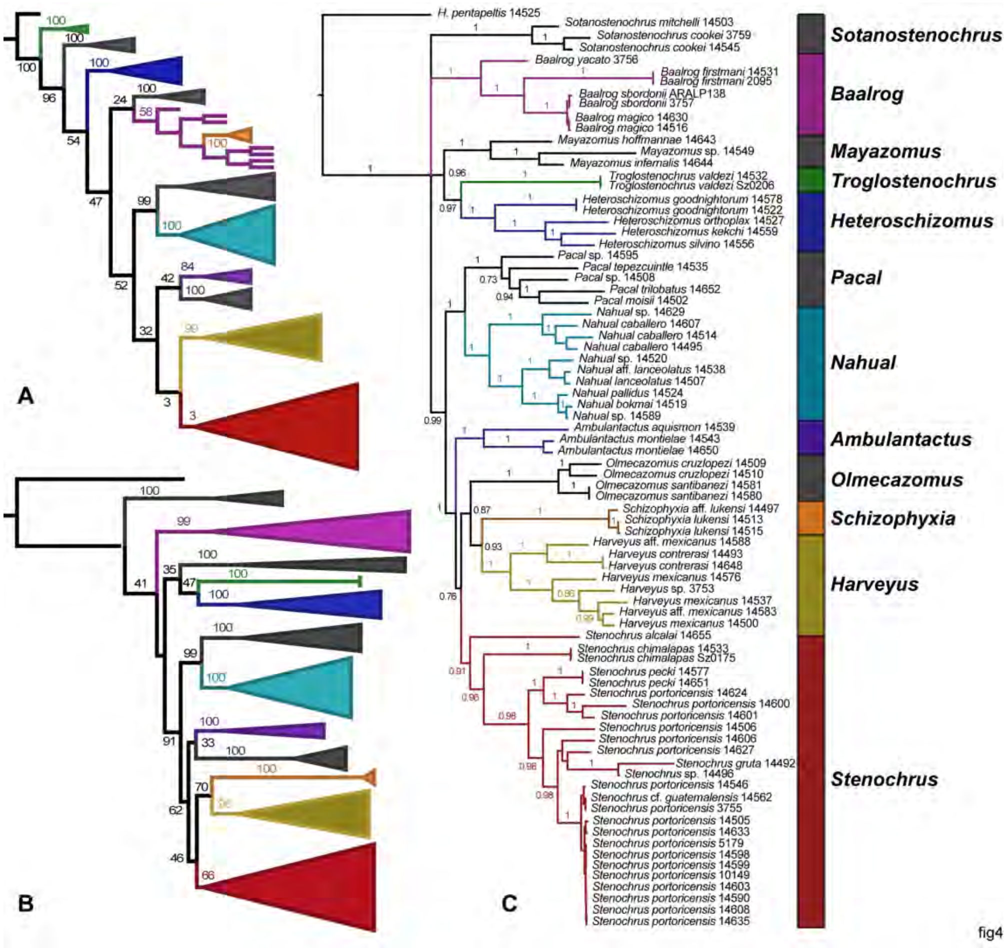

Figure 4. Phylogeny of the short-tailed whipscorpion genus *Stenochrus* Chamberlin, 1922, and related genera (Schizomida: Hubbardiidae), obtained by simultaneous analysis of the morphological and molecular data excluding "orphans" (i.e., terminals represented only by morphological data) with parsimony (A), Maximum Likelihood (B), and Bayesian Inference (C). Nodal support values, i.e., bootstrap (parsimony, Maximum Likelihood) and posterior probability (Bayesian Inference) indicated above branches.

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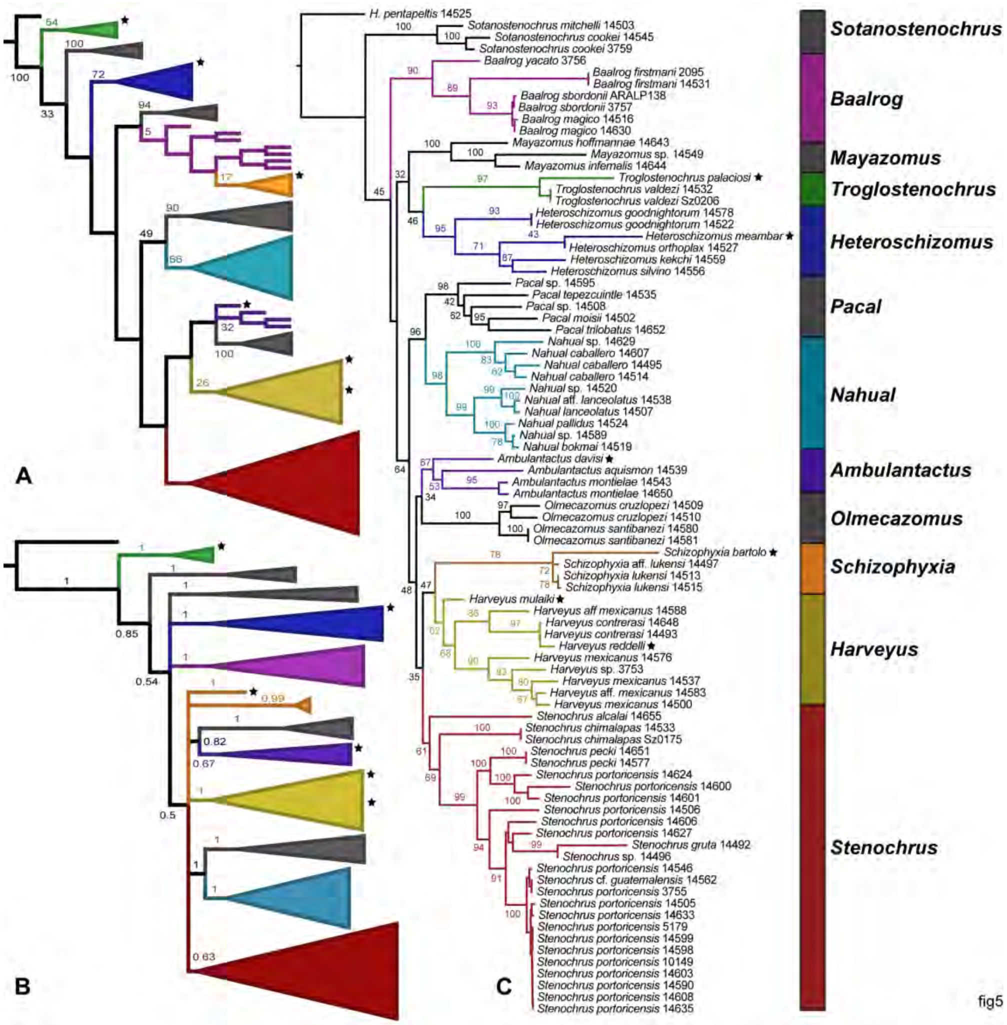

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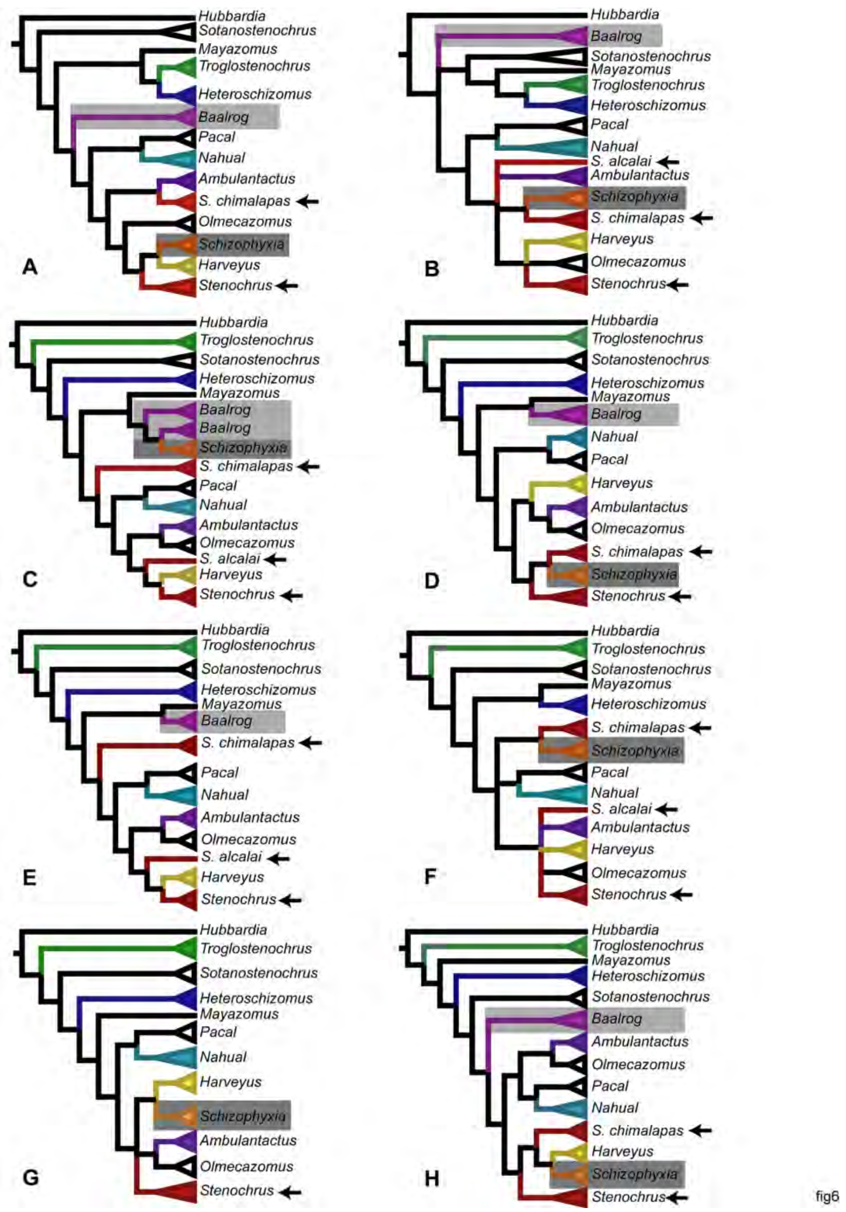

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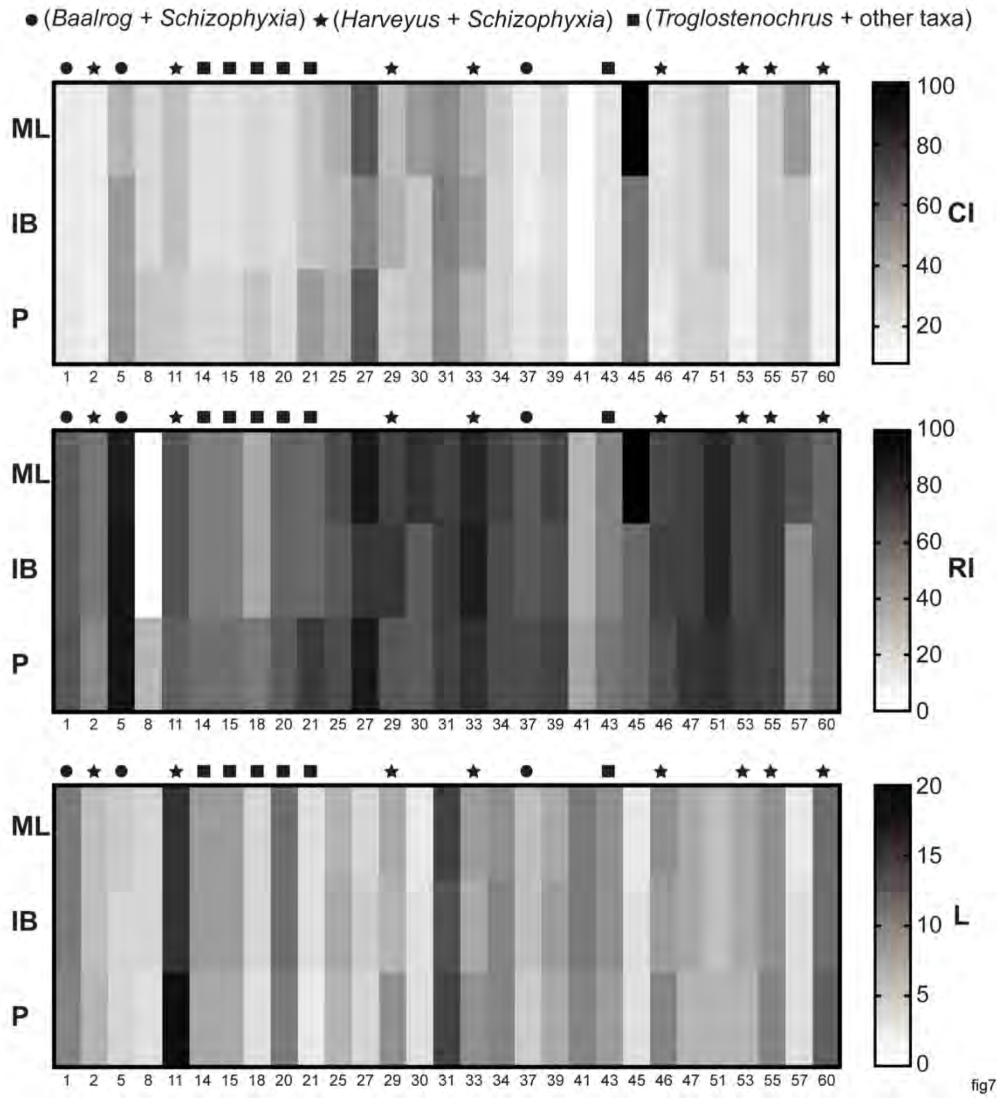

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180x197mm (300 x 300 DPI)

CONCLUSIONES GENERALES.

Se evaluó la importancia de ciertos caracteres morfológicos tradicionalmente usados en la taxonomía y diagnosis de especies tales como el flagelo de los machos y las hembras, así como las sedas del pedipalpo. El número de segmentos presentes en el flagelo de las hembras se consideraba un carácter de agrupamiento a nivel genérico, sin embargo, tras la evaluación de dicho carácter y su reconstrucción ancestral en un contexto filogenético, se descubrió que: 1) la terminología utilizada era inconsistente, ya que se consideraba que el flagelo estaba dividido por segmentos. Tras la examinación minuciosa con fotografías de barrido se encontró que los miembros de la familia Protoschizomidae presentan verdaderos segmentos, mientras que en la familia Hubbardiidae son anillos en la cutícula que no involucran ninguna musculatura; por consiguiente se propuso utilizar el término anillo para referirse a la constricción y flagelómero para referirse a la porción entre dos anillos. 2) la evolución del flagelo sugiere una pérdida o reducción en su tamaño en comparación al grupo hermano de los esquizómidos, los cuales presentan un flagelo multi-segmentado de gran tamaño en comparación a los miembros del orden Schizomida con un flagelo de tamaño reducido con segmentos en Protoschizomidae y sin segmentos en Hubbardiidae. 3) el número de anillos y flagelómeros carece de importancia filogenética ya que es un carácter que aparentemente ha evolucionado múltiples veces en la historia evolutiva del grupo; sin embargo, la reducción de tamaño y simplicidad parece ser la condición derivada.

El examen de los ejemplares, incluyendo holotipos y paratipos, nos permitió elaborar una matriz de datos con 111 caracteres morfológicos la cual fue analizada filogenéticamente de forma independiente y nos permitió reconocer y posteriormente describir un género nuevo, el cual estaba conformado por individuos con una mezcla de caracteres de dos grupos distintos: *Mayazomus* y *Stenochrus*. Esta filogenia fue la base metodológica para la selección de grupos externos utilizados para evaluar las relaciones filogenéticas de *Stenochrus*.

A su vez, tras el examen del material correspondiente al orden Schizomida en la Colección Nacional de Arácnidos (CNAN-IBUNAM), se encontró material disponible y en buen estado de 10 especies nuevas pertenecientes al género *Stenochrus*, las cuales fueron descritas en dos artículos, el primero enfocado en la descripción de cinco especies nuevas del estado de Oaxaca, en el cual se reportó por primera vez la presencia de machos dimórficos para el género *Stenochrus*. También se enfatizó sobre el reconocimiento de grupos de especies dentro del género producto de la variabilidad morfológica, lo cual fue un segundo paso en el entendimiento de la variación morfológica dentro del género y su relación con patrones geográficos.

Los análisis filogenéticos realizados con evidencia morfológica y molecular demostraron que el género *Stenochrus* se trataba de un complejo de ocho géneros distintos, los cuales fueron caracterizados de a cuerdo a su morfología y a la evidencia filogenética encontrada. Seis de los ocho géneros que conformaban al género *Stenochrus* fueron descritos por primera vez, proporcionando su correcta diagnosis morfológica, así como claves de identificación. El género *Stenochrus* fue rediagnosticado con base en la evidencia recientemente encontrada. El género *Heteroschizomus* fue revalidado con base en los hallazgos y nuevas descripciones de las espermatecas de las hembras y la evidencia filogenética. Se describieron otras seis especies nuevas, las cuales fueron asignadas a los géneros *Ambulantactus, Baalrog, Nahual, Harveyus* y *Heteroschizomus.* Los grupos de especies propuestos por Rowland y Reddell, 1980 *“mexicanus”* y *“pecki”* no se recuperaron monofiléticos con ninguno de los análisis realizados, así como con ningún set de datos analizado.

El mapeo de caracteres morfológicos como la espermateca de las hembras nos permitió evaluar su importancia en el reconocimiento, diferenciación y delimitación de géneros en lugar del uso tradicional para diferenciación entre especies, de esta forma pudimos observar que la forma general puede ser utilizada para reconocer géneros, mientras que los caracteres específicos dentro de esta estructura como son el grosor, tamaño y posición relativa de los lóbulos pueden ayudarnos a la diferenciación específica. También observamos que el uso de caracteres homoplásticos como el número de sedas en el propeltídio, la fórmula de sedas del tarso pedipalpal y del quelícero, en combinación con otros caracteres como la espermateca y el flagelo de los machos, son considerablemente informativos en el reconocimiento y diagnosis genéricos. El flagelo de los machos está sujeto a selección sexual, por tales motivos es considerablemente variable y por consiguiente debe ser utilizado en el reconocimiento de especies y no como carácter de agrupamiento a nivel genérico; dada la variabilidad de este carácter, resulta necesaria una codificación alternativa que demuestre y exprese las partes homólogas entre lo flagelos, par que esta pueda ser utilizada en la reconstrucción filogenética.

El análisis de diferentes sets de datos (morfológico, molecular y combinado) nos permitió evaluar la importancia de la morfología en la reconstrucción evolutiva, demostrando que al menos con esquizómidos, su inclusión es de vital importancia, ya que fue de ayuda tanto en la resolución como en el aumento de valores de soporte en los árboles en los que se incorporó. La evidencia molecular por otro lado debería de ser incorporada en futuros trabajos taxonómicos que involucren taxa supra específicos, ya que a pesar de que la morfología fue de vital importancia, por sí sola no es capaz de resolver relaciones filogenéticas por encima de nivel específico. Finalmente, la incorporación de un mayor número de marcadores moleculares, o inclusive el uso de transcriptomas o genomas completos, serán de ayuda para poder resolver las relaciones filogenéticas por encima de nivel genérico con miembros del orden Schizomida, ya que la poca resolución encontrada en nodos profundos, no sólo en nuestro trabajo, si no en los más recientes con el grupo (Clouse et al., 2017), demuestran esa falta de resolución obtenida con pocos marcadores moleculares. Sin embargo su uso como aproximación o inclusive como forma de proponer clasificaciones naturales es invaluable y debería ser utilizado en futuros trabajos, ya que la ausencia de filogenias en el grupo ha llevado a la actual clasificación confusa y a la sobrevaloración o infravaloración de caracteres morfológicos.

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