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First species of *Surazomus* (Schizomida: Hubbardiidae) from North America illuminate biogeography of short-tailed whipscorpions in the New World

Rodrigo Monjaraz-Ruedas*[,1,2], Lorenzo Prendini[3] & Oscar F. Francke[2]

[1] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Av. Universidad 3000, C.P. 04510, Coyoacán, Mexico City, Mexico; Rodrigo Monjaraz-Ruedas * [roy_monrue@hotmail.com] — [2] Colección Nacional de Arácnidos, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, 3er. Circuito exterior s/n, Apartado Postal 70-153, C.P. 04510, Ciudad Universitaria, Coyoacán, Mexico City, Mexico; Oscar F. Francke [offb@ib.unam.mx] — [3] Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, U.S.A.; Lorenzo Prendini [lorenzo@amnh.org] — * Corresponding author

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Abstract. Three new species of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher (Hubbardiidae Cook, 1899) are described from Mexico: *Surazomus chiapasensis* sp.n., from Chiapas, *Surazomus escondido* sp.n., and *Surazomus peregrinus* sp.n., both from Oaxaca. *Surazomus* was previously known primarily from South America, its northernmost record reported from Costa Rica. The placement of the new species within *Surazomus* is tested and verified with a phylogenetic analysis, integrating morphology and DNA sequence data for a representative sample of ingroup and outgroup taxa. Biogeographical implications are discussed.

Key words. South America, Biodiversity, Uropygi, Amazonia.

1. Introduction

The discovery of new arachnid taxa well beyond their previously known geographical distributions is not uncommon (Harvey 2002; Sharma & Giribet 2012; Mendoza-Marroquín 2014). In recent years, several arachnid taxa, previously thought restricted to South America, were reported from the Mexican tropics for the first time. For example, a new member of the mygalomorph spider family Paratropididae Simon, 1889, otherwise restricted to South America, was recently discovered in the state of Veracruz (Valdez-Mondragón et al. 2014), and a Miocene amber fossil of the buthid scorpion genus *Tityus* C.L. Koch, 1836, without extant species recorded north of Costa Rica, was discovered in Chiapas (Riquelme et al. 2015).

These surprising and unexpected discoveries often raise important biogeographical questions, such as whether these range extensions represent anthropogenic introductions, long-distance dispersal events, the remnants of ancient, more widespread distributions drastically reduced by subsequent extinction (Weygoldt et al. 2010; Sharma & Giribet 2012; Vicente et al. 2017) or merely reflect the poor collecting efforts and attention given to arachnids in many parts of the World.

The arachnid order Schizomida Petrunkevitch, 1945, also known as the short-tailed whipscorpions or micro-whipscorpions, are a mesodiverse group of arachnids distributed principally in the Neotropics. The genus *Surazomus* Reddell & Cokendolpher, 1995 (family Hubbardiidae Cook, 1899), presently comprising 25 species (Harvey 2013; Villarreal et al. 2016; Ruiz & Valente 2017), is among of the most diverse schizomid genera in South America. The genus reaches its greatest diversity in Brazil, specifically Amazonia. Its northernmost record was previously reported from Costa Rica (Fig. 1),

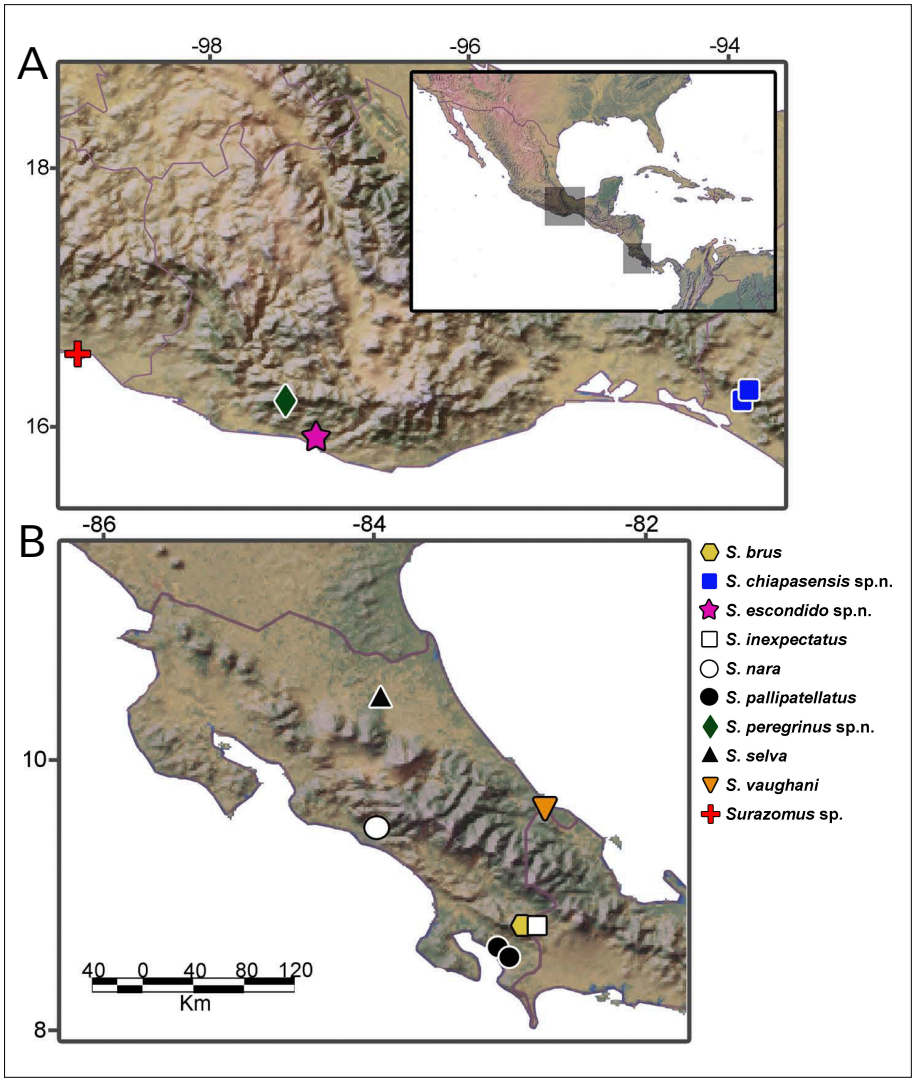


Fig. 1. Maps of southern Mexico (**A**) and Costa Rica (**B**), plotting northern records of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), based on museum collections.

its southernmost record from Peru, and its westernmost record from the state of Pará, Brazil (Pinto-da-Rocha 1996; Armas et al. 2010; Villarreal et al. 2016; Ruiz & Valente 2017).

The present contribution describes three new species of *Surazomus* from Mexico, extending the distribution of the genus into North America, and raising questions concerning the monophyly and historical biogeography of the genus. The phylogeny of *Surazomus* was first addressed with a morphological phylogenetic analysis (Rowland 1975), which included all members of the former *brasiliensis* species group of *Schizomus* Cook, 1899, and later with multilocus DNA sequence data, which included only four identified species of *Surazomus* (Clouse et al. 2017). Both analyses confirmed the monophyly of *Surazomus*, but included a limited sample of its component species, insufficient to rigorously evaluate its internal phylogenetic relationships. Despite the absence of a comprehensive phylogeny for *Surazomus*, two species groups have been proposed within the genus. Armas et al. (2010) diagnosed the *pallipatellatus* group on the basis of whitish coloration of the patella of the first leg, and the presence of "membranous" areas on the dorsal surface of the male pygidial flagellum (Villarreal et al. 2016). Ruiz & Valente (2019) diagnosed the *arboreus* group according to the peculiar trapezoidal shape, setal pattern and dorsal relief of the male pygidial flagellum. The monophyly of these groups has not been tested, however, and many species of *Surazomus* have not been assigned to either.

In the present contribution, the monophyly of *Surazomus*, and placement of the new species within it, are tested and confirmed with a phylogenetic analysis, integrating morphology and DNA sequence data, for a representative sample of ingroup and outgroup taxa. Two alternative biogeographical hypotheses may be considered in light of the range extension and phylogenetic reconstruction.

2. Material and methods

2.1. Taxon sampling

Twenty-five terminal taxa, representing 20 species of *Surazomus*, were included as ingroup taxa (Table 1, Table 4, Electronic Supplement 1, 2), to test the phylogenet-

Table 1. GenBank accession codes for DNA sequences from the 28S rDNA (28S), and Cytochrome *c* Oxidase Subunit I (COI) gene loci used for phylogenetic analysis of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899). Newly generated sequences in boldface. Tissue samples deposited in the Ambrose Monell Cryocollection (AMCC) of the American Museum of Natural History (AMNH), New York, U.S.A., the Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A., and the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México, México City.

Species	Sample	Country	28S	COI
Hubbardiidae indet.	MCZ IZ 80075	Costa Rica	KY573767	KY573170
Hubbardiidae indet.	MCZ IZ 125060	Nicaragua	KY573854	KY573332
Hubbardiidae indet.	MCZ IZ 132979	Colombia	KY573765	KY573168
Hubbardiidae indet.	MCZ IZ 132987	Ecuador	KY573768	KY573171
Hubbardiidae indet.	MCZ IZ 132981	Colombia	KY573764	KY573167
Hubbardiidae indet.	MCZ IZ 136549	Brazil	KY573742	KY573155
Hubbardiidae indet.	MCZ IZ 136512	Brazil	KY573741	KY573154
Hubbardiidae indet.	MCZ IZ 132977	Colombia	KY573766	KY573169
Hubbardiidae indet.	MCZ IZ 129081	Brazil	KY573739	KY573152
Harveyus mexicanus	AMCC [LP 14576]	Mexico	MK849702	MK801844
Heteroschizomus goodnightorum	AMCC [LP 14522]	Mexico	MK849704	MK801846
Heteroschizomus silvino	AMCC [LP 14556]	Guatemala	MK849707	MK801849
Hubbardia pentapeltis	AMCC [LP 14525]	USA	MK849708	MK801850
Pacal moisii	AMCC [LP 14502]	Mexico	MK849716	MK801858
Pacal tepezcuintle	AMCC [LP 14535]	Mexico	MK849718	MK801860
Pacal trilobatus	AMCC [LP 14652]	Mexico	MK849719	MK801861
Rowlandius linsduarteae	**CNAN DNA Sz31**	**Brazil**	**MN999737**	**MN996833**
Sotanostenochrus cookei	AMCC [LP 14545]	Mexico	MK849713	MK801855
Sotanostenochrus mitchelli	AMCC [LP 14503]	Mexico	MK849715	MK801857
Stenochrus pecki	AMCC [LP 14577]	Mexico	MK849724	MK801866
Stenochrus portoricensis	AMCC [LP 10149]	Puerto Rico	MK849725	MK801867
Surazomus brasiliensis	979.2.1	Brazil	KY573744	KY573157
Surazomus brasiliensis	981	Brazil	KY573745	KY573159
Surazomus brasiliensis	982	Brazil	KY573746	KY573160
Surazomus escondido	**AMCC [LP 14504]**	**Mexico**	**MN999732**	**MN996828**
Surazomus manaus	979.1	Brazil	KY573743	KY573156
Surazomus aff. *cuenca*	MCZ IZ 132978	Colombia	KY573762	KY573165
Surazomus aff. *sturmi*	MCZ IZ 132980	Colombia	KY573763	KY573166
Surazomus aff. *manaus*	984	Brazil	KY573747	KY573161
Surazomus aff. *manaus*	992.1.1	Brazil	KY573748	KY573162
Surazomus aff. *manaus*	992.1.2	Brazil	KY573749	KY573163
Surazomus aff. *manaus*	992.1.3	Brazil	KY573750	KY573164

ic positions of the three new Mexican species described herein: *Surazomus chiapasensis* sp.n., *Surazomus escondido* sp.n., and *Surazomus peregrinus* sp.n., each represented by a single terminal taxon. Seventeen terminals represented twelve species assigned to *Surazomus* by Clouse et al. (2017) (Table 1). Another five terminals, each representing a different species, were included to represent the geographical distribution and morphological variation of the genus, including the *arboreus* and *pallipatellatus* species groups: *Surazomus arboreus* Cokendolpher & Reddell, 2000, *Surazomus brus* Armas et al., 2010, *Surazomus cumbalensis* (Kraus, 1957), *Surazomus nara* Armas & Víquez, 2011 and *Surazomus uarini* Santos & Pinto-da-Rocha, 2009. Morphological characters for the latter five species were scored from the literature (Santos & Pinto-da-Rocha 2009; Cokendolpher & Reddell 2000; Armas et al. 2010; Armas & Víquez 2011; Villarreal et al. 2016)

The outgroup taxon sample included 14 species representing eight genera, selected on the basis of previous phylogenetic hypotheses (Clouse et al. 2017; Monjaraz-Ruedas et al. 2019), as well as morphological similarities with *Surazomus* (Table 1, Electronic Supplement 1). Two unidentified samples from Costa Rica and Nicaragua (MCZ IZ 80075 and MCZ IZ 125060) were included as outgroup taxa on the basis of their distribution, and close association with species of *Surazomus* in the analyses of Clouse et al. (2017).

Nine of the terminal taxa taken from Clouse et al. (2017) lack species-level identifications, and some are identified only to family level. The imprecise identifications of these specimens prevented the scoring of morphological data for these terminals (Table 1). DNA sequence data were missing from seven species of *Surazomus*, including two of the three new species described herein (Table 4).

2.2. Materials, microscopy and imaging

Specimens were collected by hand and/or using an aspirator and preserved in 80% and 96% ethanol. Material examined is deposited in the American Museum of Natural History (AMNH), New York, including the Ambrose Monell Cryocollection (AMCC) and the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), Mexico City.

The distribution map, based on locality records from museum collections and the literature, was prepared with gvSIG, ver. 1.11-RC1 (Valencia, Spain), and edited with Adobe Photoshop CS5.

Specimens were observed using a Nikon SMZ 725 stereomicroscope with an ocular micrometer calibrated at 20X. Chelicerae and female spermathecae were dissected in 80% ethanol, mounted for observation in a Nikon Eclipse E100 microscope and photographed with a Nikon Coolpix S10 VR camera. Female spermathecae were cleared in lactophenol for 10 minutes (Krantz & Walter 2009), preserved thereafter in Hoyer's medium, and mounted on semi-permanent microscope slides. Digital photomicrographs were taken with a Leica DFC490 camera fitted to a Leica Z16 APOA stereomicroscope, assembled with Leica Application Suite v. 4.3.0 (Wetzlar, Germany), and edited with Adobe Photoshop CS5.

2.3. Morphology

Morphological terminology for the pedipalps and legs 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).

A morphological data matrix, comprising 25 characters scored for 33 terminal taxa (Appendix 1, Table 4, Electronic Supplement 2), was prepared using Mesquite ver. 3.0.4 (Maddison & Maddison 2018). Twelve binary and thirteen multistate characters were modified from Monjaraz-Ruedas et al. (2019) and treated as non-additive (Fitch 1971) to avoid *a priori* character state transformations. The matrix included character systems considered important for species recognition in the genus *Surazomus*, such as the shape of the posterodorsal process on opisthosomal segment XII, the presence and shape of the ventral apophysis on the pedipalp femur, and the shape of the male pygidial flagellum (Villarreal et al. 2016).

2.4. DNA sequencing

Two markers, the D3 region of the nuclear 28S rDNA (28S) gene, and the mitochondrial Cytochrome *c* Oxidase Subunit I (COI) gene, were used to reconstruct the phylogeny and test the position of the three new Mexican *Surazomus* species.

Sixty-four sequences were used in the analyses (Table 1), sixty of which were published in previous studies (Clouse et al. 2017; Monjaraz-Ruedas et al. 2019), and four newly generated for the study following standard procedures for DNA extraction, amplification and sequencing, described in more detail by Monjaraz-Ruedas et al. (2019). PCR amplifications 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) Molecular Laboratory at IBUNAM. 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).

2.5. Phylogenetic analyses

The 28S and COI sequences were aligned using MAFFT ver. 6 (Katoh & Standley 2013) with the L-INS-i strategy. The aligned 28S sequences (512 bp) were concatenated with the COI sequences (664 bp) to produce a matrix of 1176 aligned DNA nucleotides. Five data partitions and their evolutionary models were identified using PartitionFinder ver. 2 (Lanfear et al. 2012): morphology; 28S; COI first, second and third positions.

The morphological and molecular data were analyzed simultaneously using Maximum Likelihood (ML) 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 using the **-f a** command for rapid bootstrap analysis and search for the best scoring ML tree in one run, computing 1000 bootstrapping replicates, using the GTRCAT model for each molecular partition, and the MkV model, with Lewis correction for morphological data, implemented with the command **asccorr=lewis**.

The morphological and molecular data were also analyzed simultaneously using parsimony with equal weighting (EW) and implied weighting (IW) (Goloboff et al. 2008a), applying seven values of the concavity constant (k = 1, 3, 5, 10, 30, 60 and 100) (Table 2). Gaps were treated as missing data. Tree search was conducted using new technology algorithms (Nixon 1999; Goloboff et al. 2003) in TNT ver. 1.1 (Goloboff et al. 2008b), using the following command string for each search: *piwe = x; hold 80000 xmult = level 10;*. Nodal support values for EW analyses were calculated using 1000 bootstrap pseudoreplicates with a removal probability of 36%. Symmetric resampling for each k value was conducted using 1000 pseudoreplicates with removal probability of 33%.

Table 2. Tree statistics for phylogenetic analyses of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995, and related genera (Schizomida: Hubbardiidae Cook, 1899). 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) using parsimony with equal weighting (EW) and implied weighting (IW) in simultaneous analyses of the morphological and molecular data. Optimal tree topology, indicated in boldface, with highest Fit, AH and ACS values.

Weighting	*k*	MPTs	L	Ci	Ri	Fit	AH	ACS
EW	—	2	1509	0.368	0.534	170.61	—	30.0
IW	1	4	1547	0.359	0.516	110.51	195.48	33.6
IW	3	6	1526	0.364	0.526	171.00	134.98	35.0
IW	5	5	1526	0.364	0.526	202.08	103.91	35.7
IW	**10**	**2**	**1516**	**0.366**	**0.531**	**239.53**	**66.46**	**35.4**
IW	30	1	1504	0.369	0.537	278.54	27.45	35.0
IW	60	1	1502	0.370	0.538	291.32	14.67	34.7
IW	100	1	1502	0.370	0.538	296.94	9.05	34.2

3. Results

Simultaneous analyses of the morphological and molecular data with ML and parsimony consistently recovered the monophyly of *Surazomus* with high support, except for parsimony with EW which recovered low support values (Fig. 2, Electronic Supplement 2). Three major clades were obtained within *Surazomus*, the first comprising *S. chiapasensis* sp.n. and some members of the *pallipatellatus* group, the second comprising *Surazomus escondido* sp.n., *Surazomus peregrinus* sp.n., and members of the *arboreus* group, and the third comprising *S. brasiliensis* (Kraus & Beck, 1967) and the four unidentified *Surazomus* from Clouse et al. (2017) (MCZ IZ – 132987, 132981, 136549 and 136512) from Brazil, Colombia and Ecuador. The topologies obtained by analyses with parsimony were congruent with that obtained by analysis with ML in recovering the *pallipatellatus* and *arboreus* clades, but incongruent in the positions of the Mexican species of *Surazomus*. *Surazomus escondido* sp.n. grouped with the *S. brasiliensis* clade; whereas *S. peregrinus* sp.n. and *S. chiapasensis* sp.n. were basal to the *pallipatellatus* and *brasiliensis* clades in the parsimony analyses.

Most clades of *Surazomus* received low bootstrap support, presumably because of the missing data added by the terminal taxa represented only by morphology.

Simultaneous analyses of the morphological and molecular data with parsimony and implied weighting, applying different *k* values, recovered several different topologies. One clade comprising representatives of the *arboreus* group and another comprising *S. chiapasensis* sp.n. and representatives of the *pallipatellatus* group were recovered in all IW analyses (Table 2, Fig. 2, Electronic Supplement 2). The topology with highest fit, adjusted homoplasy and average clade recovery was obtained by IW with $k = 10$ (Table 2). This topology recovered clades comprising members of the *arboreus* group and the clade comprising *S. chiapasensis* sp.n. and members of the *pallipatellatus* group, but the positions of *S. brasiliensis*, *S. escondido* sp.n., *S. peregrinus* sp.n., and the undetermined *Surazomus* were unresolved.

The three new Mexican species of *Surazomus* were consistently placed within *Surazomus* by the analyses (Fig. 2). The ML analysis placed *S. escondido* sp.n. and *S. peregrinus* sp.n. in a clade with an unidentified specimen from Colombia (MCZ IZ 132977), sister to the *arboreous* clade, but placed *S. chiapasensis* sp.n. sister to the *pallipatellatus* clade (Fig. 2). Parsimony analyses with IW placed the Mexican species in a similar position: *S. chiapasensis* sp.n. was placed with the Costa Rican and Colombian terminals, and *S. escondido* sp.n. sister to MCZ IZ 132977 from Colombia, but the position of *S. peregrinus* sp.n. was unresolved. *Surazomus chiapasensis* sp.n. and *S. peregrinus* sp.n. formed a grade, basal to a clade comprising the Costa Rican and Colombian terminals, *S. brasiliensis* and *S. escondido* sp.n., in the parsimony analysis with EW.

Outgroup relationships were congruent with the analysis of Monjaraz-Ruedas et al. (2019), recovering the monophyly of each genus with high support, except for *Pacal* (Fig. 2). Two unidentified samples from Costa Rica (MCZ IZ 80075) and Nicaragua (MCZ IZ 125060) grouped with *Rowlandius lindsduarteae* Santos et al., 2008, suggesting they might be congeneric.

4. Discussion

Phylogenetic analyses of the molecular and morphological data with ML and parsimony consistently recovered the monophyly of *Surazomus*, as in previous phylogenetic analyses (Rowland 1975; Clouse et al. 2017). Despite the inclusion of species of *Pacal* Reddell & Cokendolpher, 1995, and *Rowlandius* Reddell & Cokendolpher, 1995, which share several morphological characters with *Surazomus*, and other taxa with similar distributions in Mexico and South America, the three new Mexican species were placed within *Surazomus*.

Although the sampling of *Surazomus* species was incomplete, comprising only 12 of the 25 currently described species, the monophyly of the genus was stable and well supported under a range of different analytical

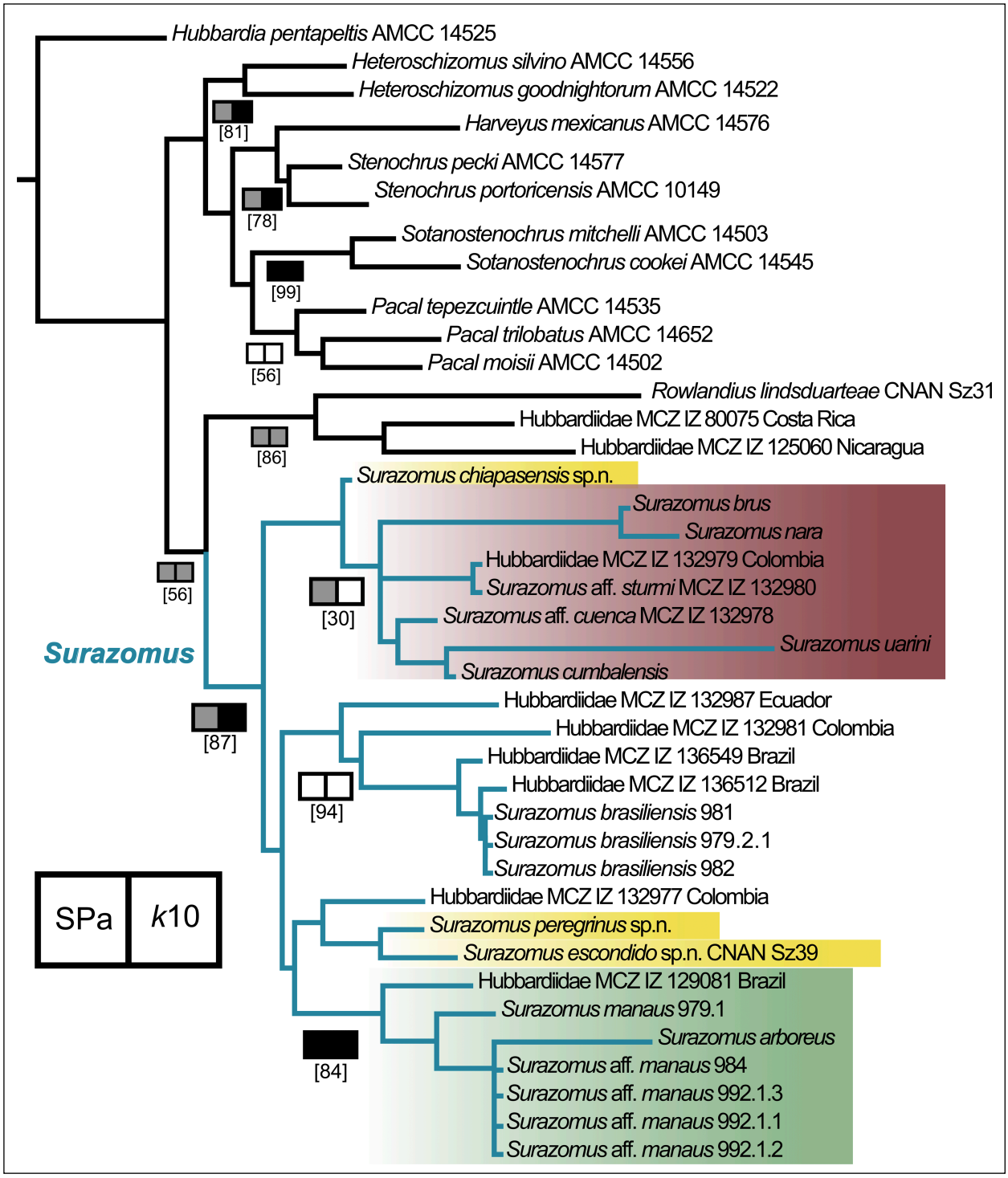
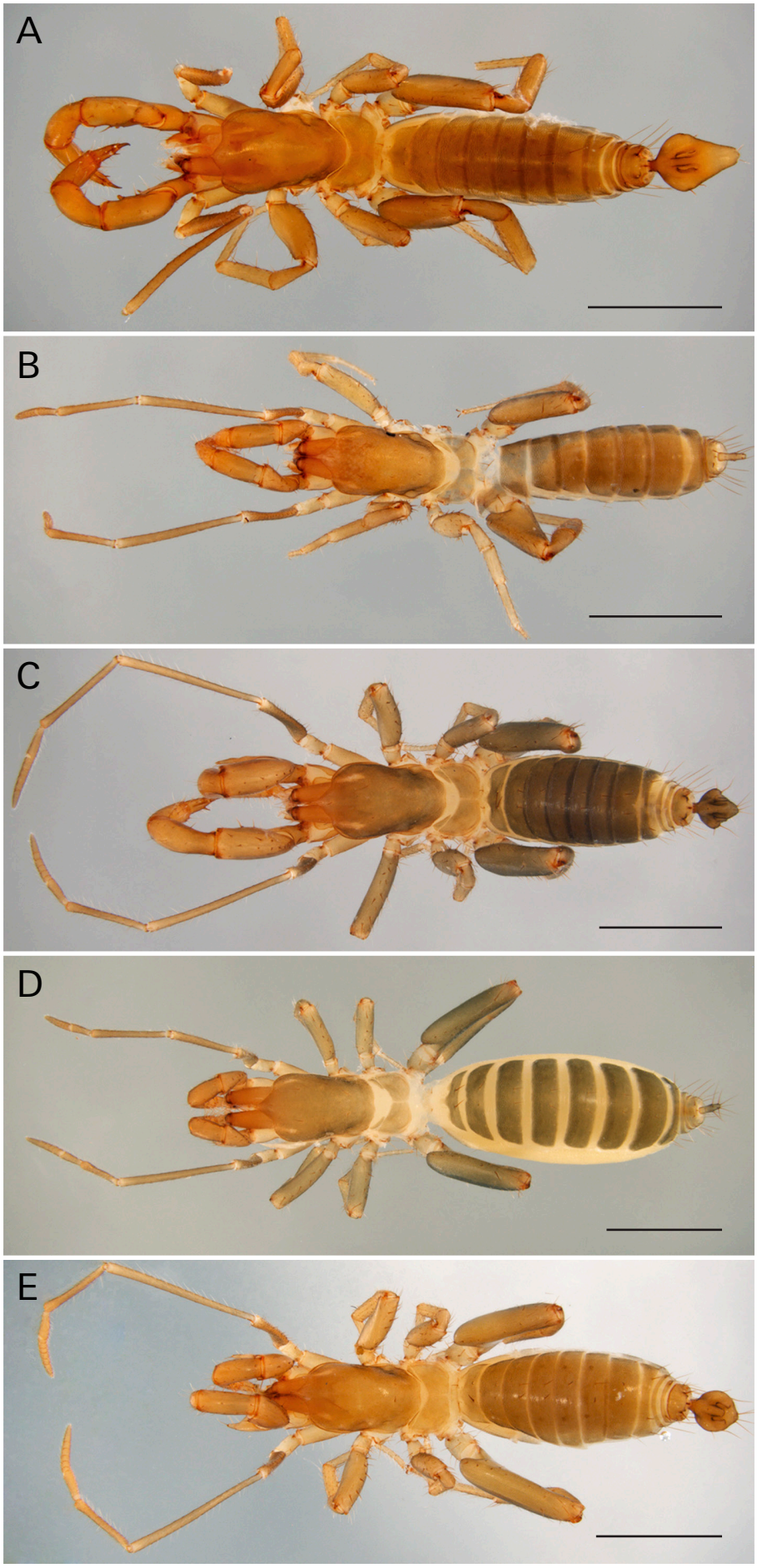


Fig. 2. Maximum likelihood tree for the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 and related genera (Schizomida: Hubbardiidae Cook, 1899) based on simultaneous analysis of 25 morphological characters (see Appendix 1 and Table 4) and 1176 aligned DNA nucleotides from the nuclear 28S rDNA and mitochondrial Cytochome *c* Oxidase Subunit I gene loci. Mexican species of *Surazomus* colored yellow, the *pallipatellatus* group, red, and the *arboreus* group, green. Bootstrap values in brackets. Box diagrams indicate clade recovery for different data sets and optimality criteria, colored in accordance with bootstrap values, as follows: black, > 50%; grey, < 50%; white, not recovered. *Abbreviations*: SPa, molecular and morphological data analysed simultaneously with parsimony; *k*10 = molecular and morphological data analysed simultaneously with parsimony and implied weighting ($k = 10$).

→ **Fig. 3.** Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), habitus, dorsal aspect. **A**,**B**: *Surazomus chiapasensis* sp.n. ♂ (CNAN T01371) (**A**), paratype ♀ (CNAN T01373) (**B**). **C**,**D**: *Surazomus escondido* sp.n. ♂ (CNAN T01374) (**C**), ♀ (CNAN T01375) (**D**). **E**: *Surazomus peregrinus* sp.n. ♂ (CNAN T01376). Scale bars = 1 mm.


A
B
C
D
E

parameters (Fig. 2), suggesting it will not be falsified by addition of the remaining species.

4.1. Species groups

Although the sampling for this contribution was insufficient for testing the monophyly of the species groups of *Surazomus*, some phylogenetic patterns were congruent with previous hypotheses based on morphology. For example, Armas et al. (2010) proposed that white coloration on the patella of the first leg (Character 12, Appendix 1) could be synapomorphic for the *pallipatellatus* group. Villarreal et al. (2016) later suggested that some members of the *pallipatellatus* group possess white membranous areas on the dorsal surface of the male pygidial flagellum (Character 16, Appendix 1). The species possessing these characters were monophyletic in the analyses (Fig. 2). However, *S. chiapasensis* sp.n., which lacks the membranous areas of the male flagellum and the discoloration of the patella on the first leg, was placed sister to this clade, suggesting the diagnosis for this group will need to be revised if *S. chiapasensis* is assigned to it.

The second species group of *Surazomus* was first mentioned by Villarreal et al. (2016) and later formalized by Ruiz & Valente (2019) as the *arboreus* group, diagnosed by the trapezoidal shape, position of the setae, and dorsal surface macrosculpture of the male pygidial flagellum (Characters 13 and 14, Appendix 1). A clade comprising *S. arboreus* and *S. manaus* Cokendolpher & Reddell, 2000, recovered in the analyses presented here, represents part of the *arboreus* group (Fig. 2).

Surazomus escondido sp.n. and *S. peregrinus* sp.n., the other Mexican species described below, formed a sister clade to the *arboreus* group in the analyses presented here (Fig. 2), suggesting these new species do not belong to either the *arboreus* group or the *pallipatellatus* group, the only two groups formally recognized at present. Those two species did not form a monophyletic group with *S. brasiliensis* either, despite their morphological resemblance to the latter.

The clade comprising specimens of *S. brasiliensis*, unidentified samples MCZ IZ 136549 and 136512 from Reserva Ducke, Manaus, Brazil, and two other specimens from Ecuador and Colombia, may represent a third species group. Other *brasiliensis*-like species inhabiting Reserva Ducke, such as *Surazomus mirim* Cokendolpher & Reddell, 2000 and *Surazomus rodriguesi* Cokendolpher & Reddell, 2000, along with *Surazomus rafaeli* Salvatierra, 2018, may belong to the same group. However, parsimony analyses failed to recover this clade, probably due to the absence of morphological synapomorphies.

4.2. Historical biogeography

According to Clouse et al. (2017), schizomids may have originated in what is presently North America ca. 270 mya, a predictable hypothesis considering that the basal schizomid family Protoschizomidae Rowland, 1975 is restricted to Mexico and the southern U.S.A. (Monjaraz-Ruedas et al. 2016, 2017). In addition, the fossil record for schizomids is primarily distributed in North America and Europe, suggesting a Laurasian distribution of the stem group of Schizomida, also supported by the climatic conditions of Laurasia (Clouse et al. 2017). After originating in North America, schizomids could have subsequently colonized South America (Clouse et al. 2017), supported by the placement of the South American clades in the analyses of Clouse et al. (2017) and Monjaraz-Ruedas et al. (2019), in which North American representatives (e.g. family Protoschizomidae and genus *Hubbardia* Cook, 1899) are placed basally. Rowland (1975), in an unpublished morphological phylogenetic analysis, postulated that the former *brasiliensis* group of *Schizomus*, currently accommodated in *Surazomus*, originated in Central America and Mexico.

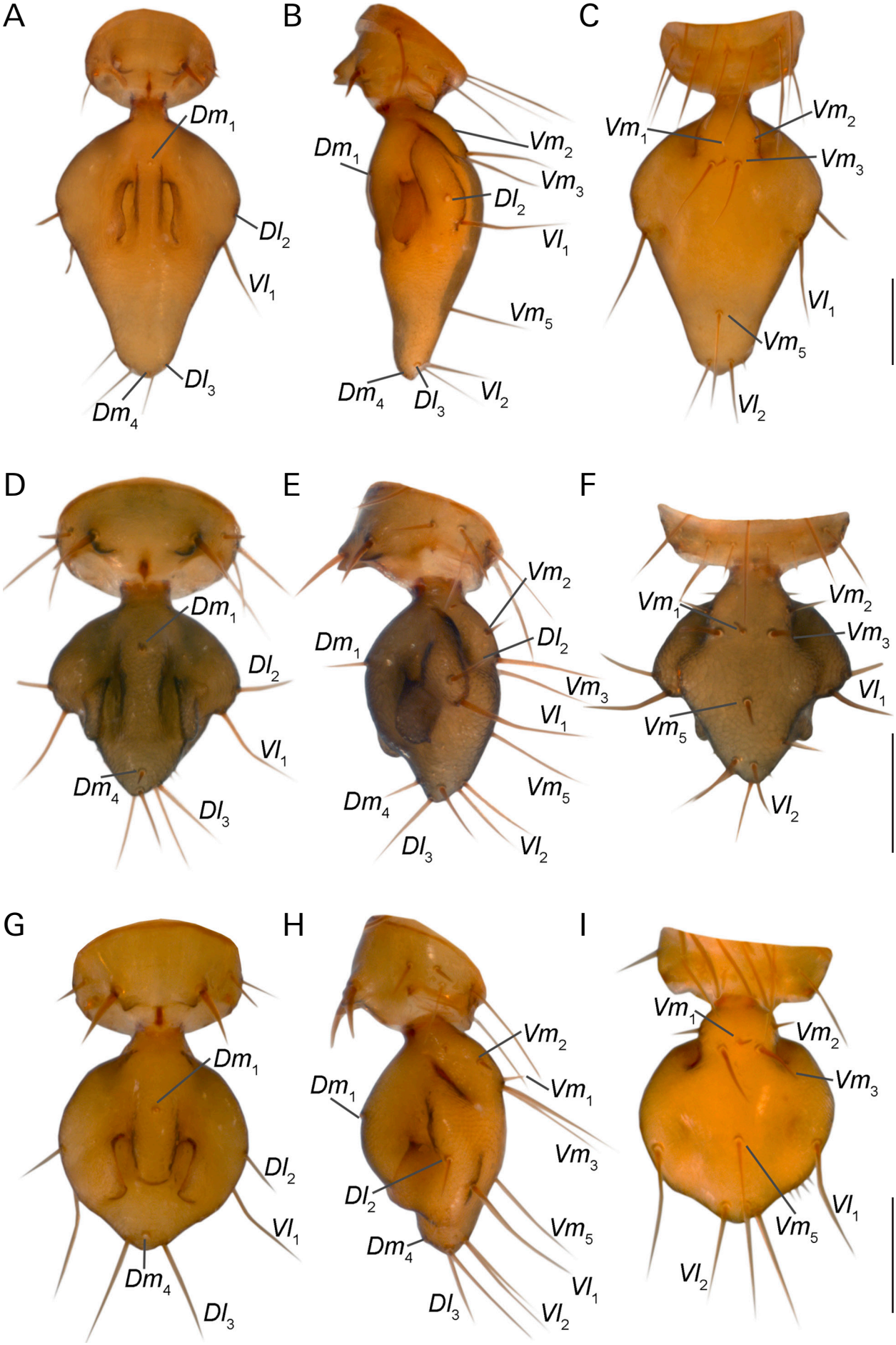
Until recently, *Surazomus* was thought to be an almost exclusively South American genus; its northernmost record was reported from Costa Rica. The discovery of three new Mexican species, one from Chiapas and two from Oaxaca, west of the Isthmus of Tehuantepec, as well as the female of an undescribed congener (based on the female spermathecae) from the Mexican state of Guerrero (Fig. 1) extends the distribution of *Surazomus* to North America. Two alternative biogeographical hypotheses may be considered in light of the range extension and phylogenetic reconstruction presented here.

1) The North American distribution of *Surazomus* may represent additional evidence for the hypothesis that schizomids originated in North America, dispersed southwards, via Central America and the Isthmus of Panama, into South America, and subsequently radiated in Amazonia.

2) Alternatively, *Surazomus* may have originated and diversified in Amazonia and dispersed northward out of South America, into Mesoamerica and eventually North America. The second hypothesis is supported by the phylogenetic placements of the North American *Surazomus* within an otherwise exclusively South American clade.

Additional data, including molecular data from more North and Central American species of *Surazomus*, along with a dated phylogeny, are needed to elucidate the origin and evolutionary history of this genus.

→ **Fig. 4.** Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), male pygidial flagellum, dorsal (**A**,**D**,**G**), lateral (**B**,**E**,**H**) and ventral (**C**,**F**,**I**) aspects. **A–C**: *Surazomus chiapasensis* sp.n., holotype ♂ (CNAN T01371). **D–F**: *Surazomus escondido* sp.n., holotype ♂ (CNAN T01374). **G–I**: *Surazomus peregrinus* sp.n., holotype ♂ (CNAN T01376). Scale bars = 0.2 mm.


A
Dm1
Dl2
Vl1
Dl3
Dm4
B
Dm1
Vm2
Vm3
Dl2
Vl1
Vm5
Dm4
Dl3
Vl2
C
Vm1
Vm2
Vm3
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Vm5
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Dm1
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Dl2
Vm5
Dm4
Vl1
Dl3
Vl2
I
Vm1
Vm2
Vm3
Vl1
Vm5
Vl2

5. Systematics

Family **HUBBARDIIDAE** Cook, 1899

Subfamily **HUBBARDIINAE** Cook, 1899

Genus ***Surazomus*** Reddell & Cokendolpher, 1995

5.1. *Surazomus chiapasensis* sp.n.

Figs. 1–3A,B, 4A–C, 5A–C, 6A, 7A,B, 8A, Table 3

Diagnosis. *Surazomus chiapasensis* sp.n. resembles the other two Mexican species of *Surazomus* in the shape of the posterodorsal process of opisthosomal segment XII, which bears two prominent, acuminate projections, with the *Dm* setal pair located medially (Fig. 4B). This species may be distinguished from the other two species based on the morphology of the adult male. The apical process of the pedipalp trochanter is long, digitiform, and projects outwards at an angle of 90º from the base, and the retroventral apophysis of the pedipalp femur is digitiform, blunt and slightly curved in *S. chiapasensis* sp.n. (Fig. 7A,B), whereas the apical process is slender and projects outwards at an angle of 120º and the retroventral apophysis is not curved in *S. escondido* sp.n., and the apical process is short and conical, and the retroventral apophysis pointed in *S. peregrinus* sp.n. The pygidial flagellum is globose and spear-shaped with a pair of longitudinal dorsomedian depressions in *S. chiapasensis* sp.n., bordered by a pair of small lateral projections (Fig. 4A–C), whereas the flagellum is deltoid in *S. escondido* sp.n. and orbicular in *S. peregrinus* sp.n.

Surazomus chiapasensis sp.n. resembles *Surazomus cumbalensis* from Ecuador in the spear-shaped pygidial flagellum of the male but differs in the shape and position of the dorsal depressions. Whereas *S. chiapasensis* sp.n. possesses one pair of longitudinal and median depressions, the posterior depression is divided by a median prominence in *S. cumbalensis*. Additionally, the metapeltidium is entire and the posterodorsal processes of opisthosomal segment XII prominent and well-developed in *S. chiapasensis* sp.n. whereas the metapeltidium is divided and the posterodorsal processes reduced to two short projections in *S. cumbalensis*. The pedipalp femur of the male bears only one ventral apophysis in *S. chiapasensis* sp.n. and the patella of the first leg is the same color as the soma unlike *S. cumbalensis*, in which the femur bears two apophyses and the patella of the first leg is paler (whitish) than the soma.

Description. The following description is based on the holotype male (Fig. 3A) and paratype female (Fig. 3B). ***Color***: Pale brownish. Leg I same color as pedipalps. ***Prosoma***: Propeltidium with two setae on anterior process, one posterior to the other; three pairs of dorsal setae; ocular spots distinct, asymmetric. Metapeltidium 0.34 mm long, 0.64 mm wide, undivided. Anterior sternum with ten setae, plus two sternophysial setae; posterior sternum with six setae. ***Chelicerae***: Movable finger serrula with 14 teeth, guard tooth present (Figs. 6A), ventral margin with small lamella. Fixed finger with four smaller teeth between two primary teeth; setal group formula, 1:3, 2:6, 3:4, 4:3, 5A:6, 5B:9, 6:1, 7:6; G1 with three spatulate setae, covered with large, spinose spicules apically; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally, G3-3 seta anterior; G4 comprising three small, thick, apically elongated setae; G5A with six equal setae, feathered apically and longer than fixed finger; G5B with nine feathered setae, increasing in size apically; G6 with one smooth seta, ca. half the length of movable finger; G7 with five feathered setae, subequal. ***Pedipalps***: Pedipalps robust (Fig. 7A,B); 2.45 × longer than propeltidium. Trochanter subrectangular; apical process well-developed, digitiform, with blunt apex and terminal seta; prolateral surface with small medial spur, two setae near dorsal margin and three setae near ventral margin. Femur 1.68 × longer than high; prolateral surface with three dorsal setae (Fmd_{1-3}) and row of three ventral setae (Fmv_{1-3}); retroventral margin with Fe_1, Fe_5, Fev_1 and Fev_2 setae acuminate; ventral margin with digitiform apophysis, blunt apically. Patella straight, without distinctive armature; with four acuminate *Pe* setae and three feathered *Pm* setae. Tibial setal formula (retrolateral row, *Ter* : medial row, *Tmr* : prolateral row, *Tir*), 3:3:4; all tibial setae acuminate. Tarsal spurs asymmetric. ***Legs***: Leg I, basitarsal-telotarsal proportions (female): 18: 3: 4: 3: 4: 5: 11; IV, femur 2.71 × 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, without pair of *Dm* setae. Segments X and XI telescoped, each 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 and well-developed posterodorsal process, comprising two long, pointed tubercles, *Dm* setal pair situated apically on tubercle. Sternites each with two irregular rows of setae; genital plate with many scattered microsetae. ***Pygidial flagellum***: Flagellum globose, spear-shaped (Fig. 4A–C); 1.53 × longer than wide; pair of dorsomedian longitudinal depressions, bordered by pair of small, rounded, lateral projections; whitish membranous areas absent; Dm_1 seta situated over bulb; Dm_4 situated posteriorly; Dl_2 anterior to Vl_1; Dl_3 aligned with Vl_2; pair of Vm_2 setae present; Vm_1 seta situated posterior to Vm_2, aligned with Vm_3; Vm_5 posterior to Vl_1; 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*). ***Female***: Differing from male as follows. Pedipalps shorter, 1.79 × longer than propeltidium; trochanter without apical process; femur without apophysis. Opisthosomal segment XII without posterodorsal process. Pygidial flagellum with two annuli (Fig. 5A–C); seta Dl_2 reduced and anterior

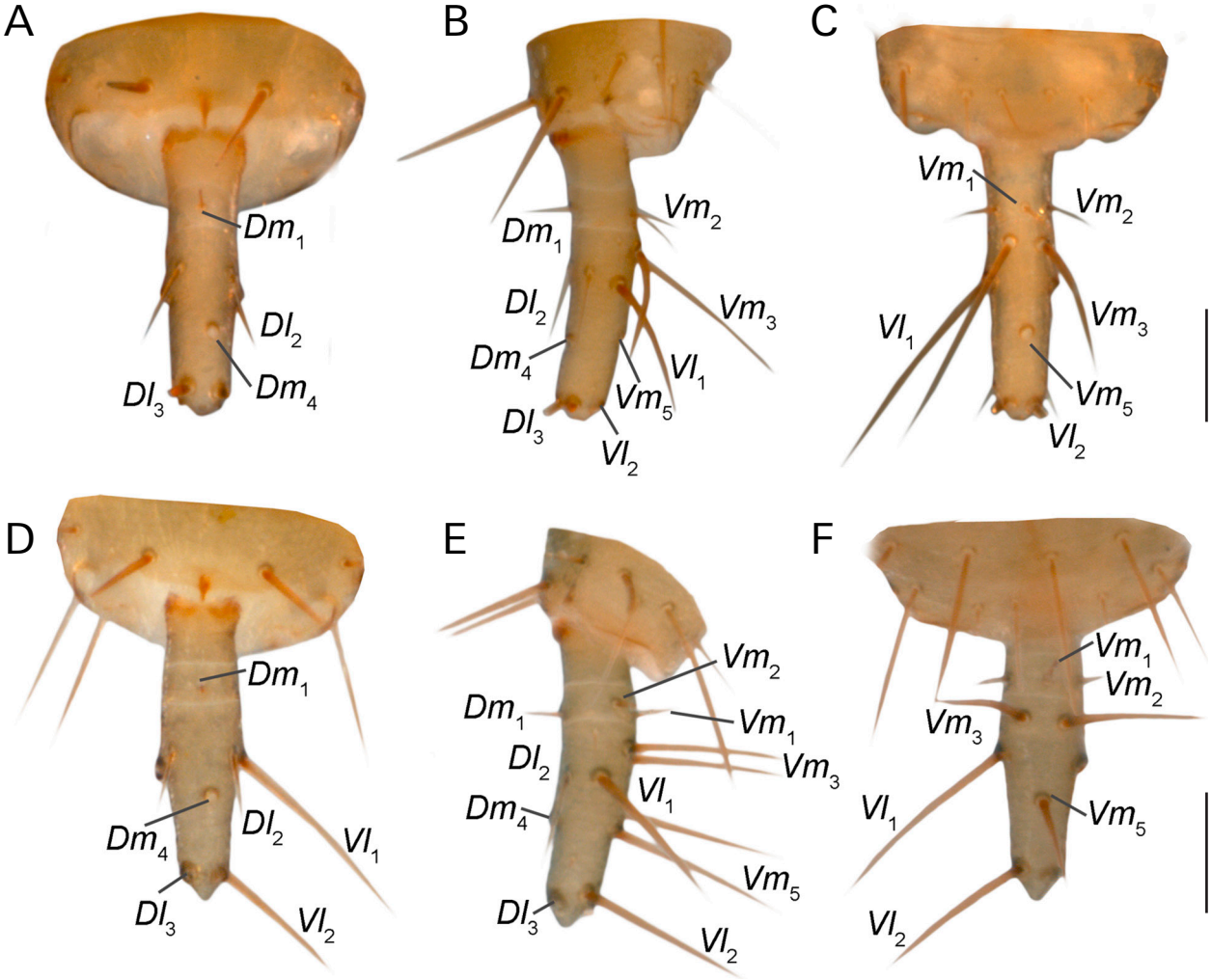

Fig. 5. Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), female pygidal flagellum, dorsal (**A**,**D**), lateral (**B**,**E**) and ventral (**C**,**F**) aspects. **A–C**: *Surazomus chiapasensis* sp.n., paratype ♀ (CNAN T01373). **D–F**: *Surazomus escondido* sp.n., paratype ♀ (CNAN T01375). Scale bars = 0.1 mm.

to Vl_1; Dl_3 aligned with Vl_2; seta Vm_2 present, reduced; Vm_1 aligned with Vm_2; microsetae Dl_1 and Dl_4 present. Spermathecae with two pairs of lobes (Fig. 8A); median and lateral lobes slightly curved, similar in length and width, with few duct openings along entire lobe; each pair with slightly distinguishable, spatulate bulb; lobe bases aligned; chitinized arch and gonopod absent.

Derivatio nominis. The specific epithet refers to the state of Chiapas, Mexico, where the type material was collected.

Life history. Specimens of *S. chiapasensis* sp.n. were collected under rocks and rotten logs in a mixed pine-oak forest.

Distribution. In the moist mountains around Arriaga, in the Mexican state of Chiapas (Fig. 1).

Material examined. ***Type material***: MEXICO: *Chiapas*: Municipio Arriaga: Santa Isabel, 4 km S on Highway 190, 16°20′35″N 93°51′50″W, 805 m, 1.ix.2005, M. Cordoba, O. Francke, A. Jaimes, H. Montaño and A. Valdez, holotype ♂ (CNAN T01371), 1 subad. ♀ paratype (CNAN T01372); Arriaga, 4 km NE, 16°15′41″N 93°51′58″W, 163 m, 1.ix.2005, M. Cordoba, O. Francke, A. Jaimes, H. Montaño and A. Valdez, 3 ♀ paratypes (CNAN T01373).

5.2. *Surazomus escondido* sp.n.

Figs. 1–3C,D, 4D–F, 5D–F, 6B, 7C,D, 8B, Table 4

Diagnosis. *Surazomus escondido* sp.n. resembles the other two Mexican species of *Surazomus* in the shape of the posterodorsal process of opisthosomal segment XII, which bears two prominent, acuminate projections, with the *Dm* setal pair located medially (Fig. 4E). This species may be distinguished from the other two species based on the morphology of the adult male. The apical process of the pedipalp trochanter is long, slender, digitiform, and projects outwards at an angle of 120º from the base, the retroventral apophysis of the pedipalp femur is blunt, and the pedipalp patella is curved in *S. escondido* sp.n. (Fig. 7C,D), whereas the apical process is wider and projects outwards at an angle of 90º, and the retroventral

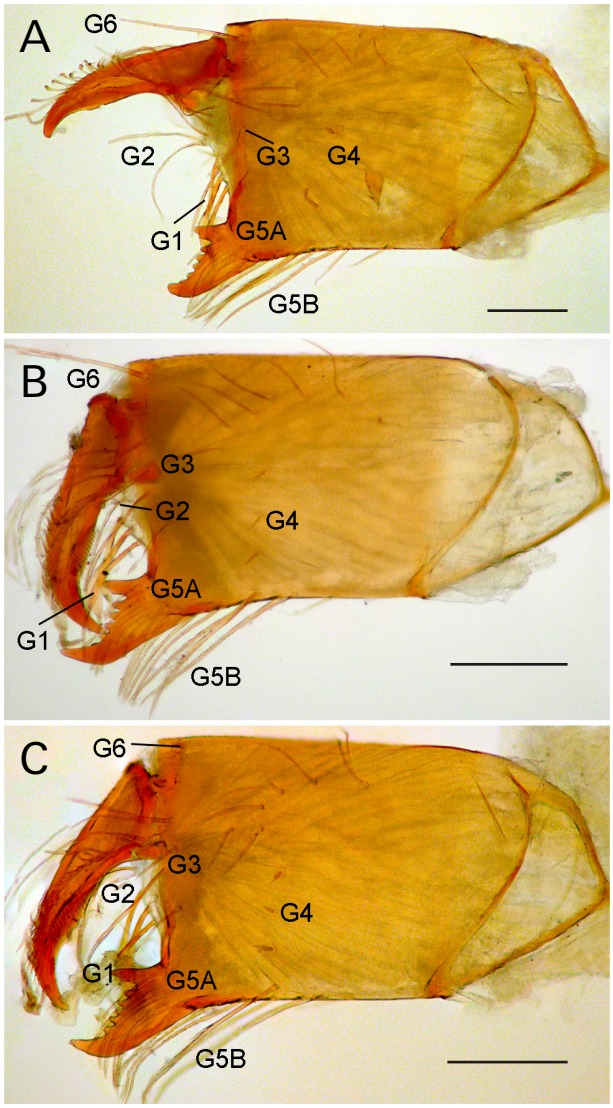

Fig. 6. Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), chelicerae, prolateral aspect. **A**: *Surazomus chiapasensis* sp.n., paratype ♀ (CNAN T01372). **B**: *Surazomus escondido* sp.n., paratype ♂ (CNAN T01375). **C**: *Surazomus peregrinus* sp.n., holotype ♂ (CNAN T01376). Scale bars = 0.2 mm.

apophysis is slightly curved in *S. chiapasensis* sp.n., and the apical process is short and conical, and the retroventral apophysis pointed in *S. peregrinus* sp.n. The pygidial flagellum is deltoid and trilobed, with two dorsosubmedian depressions and one pair of lateral projections, in *S. escondido* sp.n. (Fig. 4D–F) whereas the flagellum is spear-shaped in *S. chiapasensis* sp.n. and orbicular in *S. peregrinus* sp.n.

Surazomus escondido sp.n. resembles *S. brasiliensis* in the shape of the male pedipalps and pygidial flagellum. However, the flagellum of *S. escondido* sp.n. is more elongated and triangular than that of *S. brasiliensis*. Additionally, the apical process on the pedipalp trochanter is long and prominent in *S. escondido* sp.n., whereas it is shorter in *S. brasiliensis*, and the posterodorsal process of opisthosomal segment XII bears two projections in *S. escondido* sp.n., whereas the posterodorsal process bears only one rounded and reduced projection in *S. brasiliensis*.

Description. The following description is based on the holotype male (Fig. 3C) and paratype female (Fig. 3D). ***Color***: Greenish, with chelicerae, pedipalps and leg I pale brown. ***Prosoma***: Propeltidium with two setae on anterior process, one posterior to the other; three pairs of dorsal setae; ocular spots distinct, asymmetric. Metapeltidium 0.34 mm long, 0.69 wide mm, divided by faint suture. Anterior sternum with eleven setae, plus two sternophysial setae; posterior sternum with six setae. ***Chelicerae***: Movable finger serrula with 13 teeth, guard tooth present (Fig. 6B), ventral margin with small lamella. Fixed finger with four smaller teeth between two primary teeth; setal group formula: 1:3, 2:6, 3:4, 4:3, 5A:7, 5B:8, 6:1, 7:6; G1 with three spatulate setae, covered with small, spinose spicules apically; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally, G3-3 seta anterior; G4 comprising three small, thick, apically elongated setae; G5A with seven equal setae, 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 five feathered setae, subequal. ***Pedipalps***: Pedipalps robust (Fig. 7C,D); 2.74 × longer than propeltidium. Trochanter subtrapezoidal; apical process long, slender and digitiform, with pointed apex and terminal setae; prolateral surface with small distal spur, two setae near dorsal margin and three setae near ventral margin. Femur 2.16 × longer than high; prolateral surface with three dorsal setae (Fmd_{1-3}) and row of three ventral setae (Fmv_{1-3}); retroventral margin with Fe_1, Fe_5, Fev_1 and Fev_2 setae acuminate; ventral margin with small, blunt apophysis. Patella curved, without distinctive armature; with three acuminate *Pe* setae and three feathered *Pm* setae. Tibial setal formula (retrolateral row, *Ter* : medial row, *Tmr* : prolateral row, *Tir*), 3:3:4; all tibial setae acuminate. Tarsal spurs asymmetric. ***Legs***: Leg I, basitarsal-telotarsal proportions: 19: 3: 4: 4: 4: 5: 10; IV, femur 2.34 × 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, without pair of *Dm* setae. Segments X and XI telescoped, each 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 and well-developed posterodorsal process, comprising two long, conical tubercles, *Dm* setal pair located medially on tubercle. Sternites each with two scattered, irregular rows of setae; genital plate with many scattered microsetae. ***Pygidial flagellum***: Flagellum globose, trilobed and deltoid in shape (Fig. 4D–F); 1.13 × longer than wide; pair of dorsosubmedian depressions, surrounded by pair of rounded, lateral prominences; whitish membranous areas absent; Dm_1 seta situated over bulb; Dm_4 situated posteriorly; Dl_2 anterior to Vl_1; Dl_3 aligned with Vl_2; pair

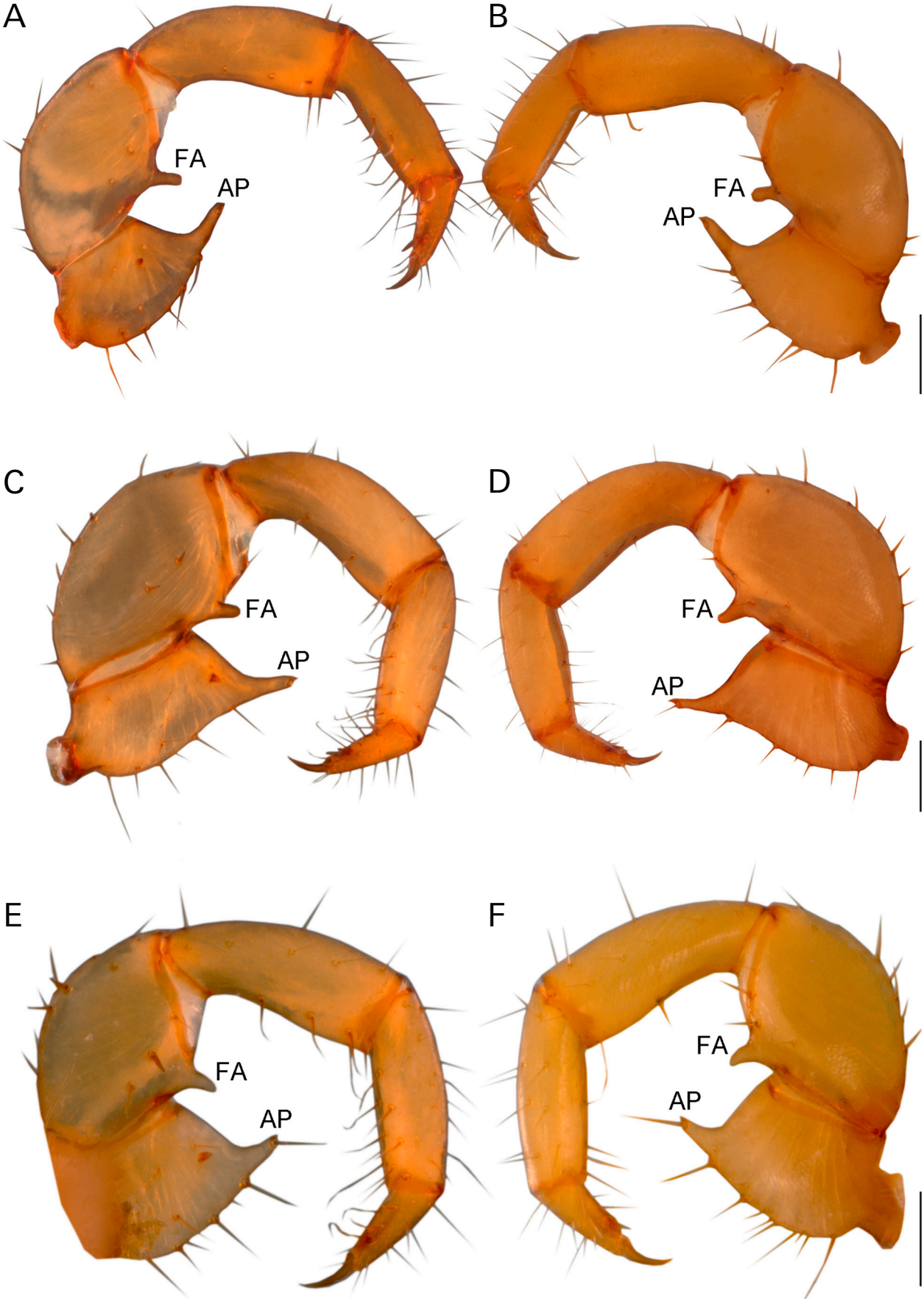

Fig. 7. Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), pedipalps, prolateral (**A**,**C**,**E**) and retrolateral (**B**,**D**,**F**) aspects. **A**,**B**: *Surazomus chiapasensis* sp.n., holotype ♂ (CNAN T01371). **C**,**D**: *Surazomus escondido* sp.n., holotype ♂ (CNAN T01374). **E**,**F**: *Surazomus peregrinus* sp.n., holotype ♂ (CNAN T01376). — ***Abbreviations***: AP – apical process; FA – femoral apophysis. Scale bars = 0.2 mm.

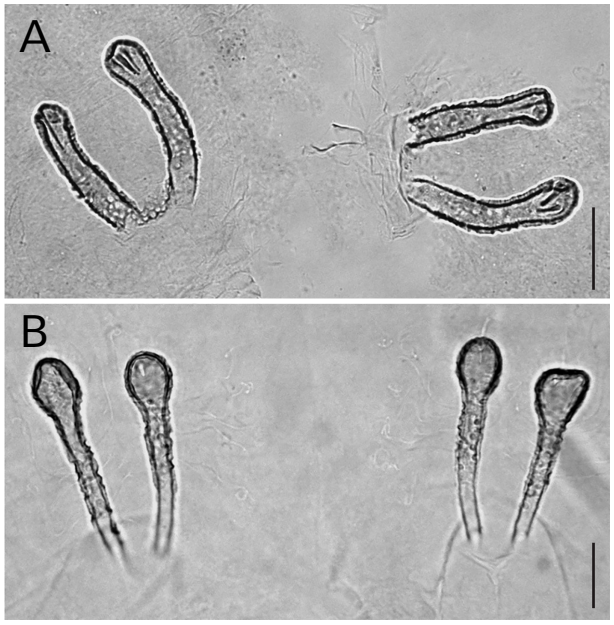

Fig. 8. Short-tailed whipscorpions of the genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), female spermathecae, dorsal aspect. **A**: *Surazomus chiapasensis* sp.n., paratype ♀ (CNAN T01373). **B**: *Surazomus escondido* sp.n., paratype ♀ (CNAN T01375). Scale bars = 0.05 mm.

of Vm_2 setae present; Vm_1 seta situated posterior to Vm_2, aligned with Vm_3; Vm_5 aligned with Vl_1; additional setae between pairs of Vl_1 and Vl_2 setae; 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*). ***Female***: Differing from male as follows. Pedipalps shorter, 1.67 × longer than propeltidium; trochanter without apical process; femur without apophysis. Opisthosomal segment XII without posterodorsal process. Pygidial flagellum with two annuli (Figs. 6–8); seta Dl_2 reduced and aligned with Vl_1; Dl_3 aligned with Vl_2; seta Vm_2 present, not reduced; Vm_1 aligned with Vm_2; microsetae Dl_1 and Dl_4 present. Spermathecae with two pairs of lobes (Fig. 8B); median and lateral lobes linear, similar in length and width, with few apical duct openings; each pair with small terminal, spatulate bulb; lobe bases aligned; chitinized arch and gonopod absent.

Derivatio nominis. The specific epithet is a noun in apposition taken from the type locality, and is also a Spanish word meaning "hide", applicable to the cryptic diversity of the genus *Surazomus* in North America.

Remarks. The presence of an extra seta between the Vl_1 and Vl_2 pairs of the male pygidial flagellum is uncommon among schizomids. However, this seta is present only in the holotype male of *S. escondido* sp.n., and absent in the two paratype males, suggesting it may be an abnormality. As noted by Ruiz & Valente (2019), the setal patterns of *Surazomus* must be carefully assessed as this genus differs markedly from other genera in the subfamily. Additionally, one of the males is dimorphic in both the pedipalp and pygidial flagellar morphology. Its pedipalps are shorter than the pedipalps of the other two males, as first reported for *Surazomus* by Armas & Víquez (2014), and its flagellum considerably smaller and less sculptured, but with the same general shape, similar to that reported for *Surazomus sturmi* (Kraus, 1957).

Life history. Specimens were collected under rocks in a disturbed tropical rainforest along the sides of the highway.

Distribution. Known only from the type locality in the Mexican state of Oaxaca (Fig. 1).

Material examined. ***Type material***: MEXICO: *Oaxaca*: Municipio Puerto Escondido: Km 232 Highway Oaxaca–Puerto Escondido, 15°55′57″N 97°04′50″W, 142 m, 8.vi.2015, G. Contreras, D. Guerrero, R. Monjaraz, G. Montiel & C. Santibañez, holotype ♂ (CNAN T01374), 1 ♂, 1 ♀ paratypes (AMNH), 1 ♂, 1 ♀ paratypes (CNAN T01375).

5.3. *Surazomus peregrinus* sp.n.

Figs. 1–3E, 4G–I, 6C, 7E,F, Table 4

Diagnosis. *Surazomus peregrinus* sp.n. resembles the other two Mexican species of *Surazomus* in the shape of the posterodorsal process of opisthosomal segment XII, which bears two prominent and acuminate projections, with the *Dm* setal pair located medially (Fig. 4H). This species can be distinguished from the other two species based on the morphology of the adult male. The apical process of the pedipalp trochanter is short, conical, and projects outwards at an angle of 90º from the base, the retroventral apophysis of the pedipalp femur is small, curved, and pointed, and the pedipalp patella is not curved in *S. peregrinus* sp.n. (Fig. 7E,F), whereas the apical process is digitiform and the tip of the retroventral apophysis blunt in the other species. The pygidial flagellum is globose and orbicular with a pair of deep dorsosubmedian depressions surrounded by a wider pair of prolaterally curved projections, with a prominent medial swelling between them, in *S. peregrinus* sp.n. (Fig. 4G–I), whereas the flagellum is spear-shaped in *S. chiapasensis* sp.n. and deltoid in *S. escondido* sp.n.

Surazomus peregrinus sp.n. resembles *Surazomus macarenensis* (Kraus, 1957) from Colombia and *Surazomus uarini* Santos & Pinto-da-Rocha, 2009 from Brazil, in the rounded shape of the male pygidial flagellum. However, the flagellum of *S. peregrinus* sp.n. possesses lateral projections which are absent in *S. macarenensis*, as well as an anterior swelling and separate (unfused) median depressions, unlike in *S. uarini*, the flagellum of which possesses a posterior swelling and medially fused depressions. Additionally, the anterior process of the pedipalp trochanter projects only from the base in *S. peregrinus* sp.n., whereas it projects all along the anterior margin in *S. macarenensis* and *S. uarini*. The ventral apophysis of the pedipalp femur is small and conical in *S. peregrinus* sp.n., whereas it is prominent and claw-shaped in *S. macarenensis*. The apophysis is also conical in *S. uarini* but wider and not curved

Table 3. Measurements (mm) of type material of the short-tailed whipscorpions, *Surazomus chiapasensis* sp.n., *Surazomus escondido* sp.n., and *Surazomus peregrinus* sp.n. (Schizomida: Hubbardiidae Cook, 1899), deposited in the American Museum of Natural History (AMNH), New York, U.S.A., and the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México, México City.

		S. chiapasensis					***S. escondido***					***S. peregrinus***
Sex		♂	♀	♀	♀	♀	♂	♂	♂	♀	♀	♂
Collection		CNAN	CNAN	CNAN	CNAN	CNAN	CNAN	CNAN	AMNH	CNAN	AMNH	CNAN
Number		T01371	T01372	T01373	T01373	T01373	T01374	T01375		T01375		T01376
Total length		3.60	2.76	3.46	3.76	3.44	3.32	3.32	4.48	4.32	4.48	3.60
Propeltidium	Length	1.17	1.10	1.14	1.12	1.06	1.22	1.14	1.17	1.17	1.17	1.15
	Width	0.70	0.67	0.62	0.64	0.59	0.69	0.64	0.64	0.64	0.64	0.67
Flagellum	Length	0.74	0.29	0.29	0.29	0.26	0.42	0.42	0.30	0.26	0.30	0.45
	Width	0.48	0.08	0.06	0.06	0.11	0.37	0.35	0.24	0.06	0.24	0.37
	Height	0.30	0.08	0.06	0.06	0.10	0.24	0.24	0.19	0.06	0.19	0.27
Pedipalp	Trochanter length	0.72	0.42	0.48	0.45	0.40	0.77	0.80	0.58	0.37	0.58	0.56
	Femur length	0.67	0.48	0.46	0.48	0.43	0.86	0.82	0.61	0.50	0.61	0.61
	Patella length	0.66	0.45	0.45	0.45	0.42	0.80	0.75	0.54	0.48	0.54	0.54
	Tibia length	0.54	0.34	0.37	0.40	0.35	0.59	0.56	0.43	0.38	0.43	0.46
	Tarsus length	0.27	0.22	0.26	0.22	0.18	0.30	0.26	0.26	0.22	0.26	0.24
	Total length	2.86	1.90	2.02	2.00	1.78	3.33	3.18	2.42	1.95	2.42	2.42
Leg I	Coxa length	0.61	0.42	0.51	0.48	0.45	0.58	0.56	0.53	0.45	0.53	0.56
	Trochanter length	0.34	0.27	0.27	0.24	0.29	0.34	0.30	0.35	0.29	0.35	0.29
	Femur length	1.49	0.86	0.96	0.96	0.90	1.18	1.17	1.01	0.96	1.01	1.17
	Patella length	1.78	1.07	1.09	1.06	1.04	1.57	1.38	1.23	1.15	1.23	1.31
	Tibia length	–	0.77	0.80	0.78	0.75	1.01	0.98	1.07	0.83	1.07	0.99
	Basitarsus length	–	0.24	0.27	0.29	0.26	0.30	0.32	0.29	0.29	0.29	0.35
	Telotarsus length	–	0.50	0.42	0.48	0.50	0.48	0.50	0.48	0.46	0.48	0.51
	Total length	4.21	4.13	4.32	4.29	4.18	5.46	5.20	4.96	4.43	4.96	5.18
Leg IV	Trochanter length	0.32	0.27	0.34	0.29	0.32	0.29	0.29	0.29	0.29	0.29	0.27
	Femur length	1.22	0.94	1.02	0.96	0.99	1.20	1.17	1.06	1.09	1.06	1.17
	Patella length	0.43	0.40	0.43	0.42	0.35	0.48	0.48	0.5	0.43	0.50	0.48
	Tibia length	0.82	0.64	0.69	0.70	0.62	0.75	0.75	0.7	0.69	0.70	0.78
	Basitarsus length	0.72	0.62	0.59	0.59	0.56	0.72	0.64	0.59	0.61	0.59	0.70
	Telotarsus length	0.51	0.40	0.40	0.40	0.35	0.45	0.29	0.43	0.37	0.43	0.46
	Total length	4.02	3.28	3.47	3.36	3.20	3.89	3.62	3.57	3.47	3.57	3.87

like the apophysis of *S. peregrinus* sp.n. Finally, the posterodorsal process of opisthosomal segment XII is well developed and bears two conical projections in *S. peregrinus* sp.n., unlike *S. macarenensis*, in which the posterodorsal process bears one rounded prominence, and *S. uarini*, in which it is very small and rectangular.

Surazomus peregrinus sp.n. resembles *S. brasiliensis* in the presence of lateral swellings surrounding the dorsosubmedian depressions of the male pygidial flagellum. However, the flagellum is rounded in *S. peregrinus* sp.n. and trilobed in *S. brasiliensis*.

Description. The following description is based on the holotype male (Fig. 3E). ***Color***: Pale brownish. Leg I same color as pedipalps. ***Prosoma***: Propeltidium with two setae on anterior process, one posterior to the other; three pairs of dorsal setae; ocular spots distinct, asymmetric. Metapeltidium 0.35 mm long, 0.62 mm wide, undivided but with small suture in posterior part. Anterior sternum with ten setae, plus two sternophysial setae; posterior sternum with six setae. ***Chelicerae***: Movable finger serrula with 15 teeth, guard tooth present (Fig. 6C), ventral margin with prominent lamella. Fixed finger with five smaller teeth between two primary teeth; setal group formula: 1:3, 2:6, 3:4, 4:3, 5A:7, 5B:7, 6:1, 7:6; G1 with three spatulate setae, covered with few small, spinose spicules apically; G2 composed of six feathered setae, subequal, shorter than movable finger; G3 with four setae, subequal, feathered apically and smooth basally, G3-3 seta anterior; G4 comprising three thick, small, apically elongated setae; G5A with seven equal setae, feathered apically and longer than fixed finger; G5B with seven feathered setae, increasing in size apically; G6 with one smooth seta; G7 with five slender, feathered setae, subequal. ***Pedipalps***: Pedipalps robust (Fig. 7E,F); 2.10 × longer than propeltidium. Trochanter trapezoidal; apical process conical, projecting, with acute apex and terminal setae; prolateral surface with medial spur, two setae near dorsal margin and three setae near ventral margin. Femur 1.65 × longer than high; prolateral surface with three dorsal spiniform setae (Fmd_{1-3}) and row of three ventral spiniform setae (Fmv_{1-3}); retroventral margin with Fe_1 and Fe_5 setae acuminate, Fev_1 and Fev_2 spiniform; ventral margin with digitiform apophysis, curved ventrally and blunt apically. Patella straight, without distinctive armature; with three acuminate *Pe* setae and four

Table 4. Distribution of 25 morphological characters among ingroup and outgroup taxa used in phylogenetic analysis of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899). Character descriptions in Appendix 1.

Character:	**0 0 0 0 0 0 0 0 0 1**	**1 1 1 1 1 1 1 1 1 2**	**2 2 2 2 2**
Taxon:	**1 2 3 4 5 6 7 8 9 0**	**1 2 3 4 5 6 7 8 9 0**	**1 2 3 4 5**
Harveyus mexicanus AMCC [LP 14576]	0 1 1 0 – – 2 0 – 0	2 1 1 1 3 1 0 1 1 0	1 0 0 0 1
Heteroschizomus goodnightorum AMCC [LP 14522]	1 1 1 0 ? ? 3 0 ? 0	2 1 3 0 3 1 0 1 0 ?	1 2 0 0 1
Heteroschizomus silvino AMCC [LP 14556]	1 2 1 0 – – 3 0 – 0	2 1 3 1 3 1 0 1 0 –	1 2 0 0 1
Hubbardia pentapeltis AMCC [LP 14525]	0 1 0 1 – 1 1 0 – 0	2 1 3 1 3 1 0 0 0 –	2 2 0 0 1
Pacal moisii AMCC [LP 14502]	1 1 1 1 – 1 3 0 – 0	2 1 1 1 1 1 0 1 1 0	1 0 0 0 1
Pacal tepezcuintle AMCC [LP 14535]	1 1 1 0 – – 3 0 – 0	2 1 1 1 1 1 0 1 0 –	1 2 0 0 1
Pacal trilobatus AMCC [LP 14652]	1 1 1 1 – 1 3 0 – 0	2 1 2 1 1 1 1 1 1 1	0 1 0 0 1
Rowlandius lindsduarteae CNAN Sz31	2 0 1 1 ? 1 2 0 ? 0	2 1 1 3 1 1 0 0 1 1	1 0 1 0 1
Sotanostenochrus cookei AMCC [LP 14545]	0 1 1 0 – – 3 0 – 0	– 1 1 0 1 1 0 1 0 –	2 2 0 0 1
Sotanostenochrus mitchelli AMCC [LP 14503]	0 1 1 0 – – 3 0 – 0	– 1 1 0 1 1 0 1 0 –	2 2 0 0 1
Stenochrus pecki AMCC [LP 14577]	0 0 1 0 – – 3 0 – 0	2 1 1 1 3 1 0 1 0 –	1 2 0 0 1
Stenochrus portoricensis AMCC [LP 10149]	0 0 1 0 – – 3 0 – 0	2 1 1 1 3 1 0 1 0 –	1 2 0 0 1
Surazomus arboreus	0 1 0 1 – 0 0 1 1 1	2 1 0 2 0 1 0 1 0 –	1 2 1 1 0
Surazomus brasiliensis 979.2.1	0 1 0 1 – 1 2 1 1 0	0 1 2 1 1 1 1 1 1 1	1 1 0 0 0
Surazomus brasiliensis 981	0 1 0 1 – 1 2 1 1 0	0 1 2 1 1 1 1 1 1 1	1 1 0 0 0
Surazomus brasiliensis 982	0 1 0 1 – 1 2 1 1 0	0 1 2 1 1 1 1 1 1 1	1 1 0 0 0
Surazomus brus	1 2 0 2 0 – 1 1 0 0	2 0 2 1 1 0 2 1 1 0	1 0 0 0 0
Surazomus aff. *cuenca* MCZ IZ 132978	0 1 0 2 1 ? 0 1 1 0	1 1 2 0 1 1 2 1 1 1	1 1 0 0 0
Surazomus aff. *manaus* 984	0 1 1 1 – 0 0 1 2 0	0 1 0 2 0 1 0 1 0 –	1 0 1 1 0
Surazomus aff. *manaus* 992.1.1	0 1 1 1 – 0 0 1 2 0	0 1 0 2 0 1 0 1 0 –	1 0 1 1 0
Surazomus aff. *manaus* 992.1.2	0 1 1 1 – 0 0 1 2 0	0 1 0 2 0 1 0 1 0 –	1 0 1 1 0
Surazomus aff. *manaus* 992.1.3	0 1 1 1 – 0 0 1 2 0	0 1 0 2 0 1 0 1 0 –	1 0 1 1 0
Surazomus aff. *sturmi* MCZ IZ 132980	0 1 0 1 – 2 2 1 1 0	2 1 2 1 0 1 1 1 1 0	1 0 0 0 0
Surazomus chiapasensis sp.n.	0 1 1 2 1 – 0 1 1 0	2 1 2 1 1 1 1 1 1 0	1 0 0 0 0
Surazomus cumbalensis	0 1 0 2 1 – 0 1 1 0	1 0 2 1 1 1 0 1 1 0	1 0 0 0 0
Surazomus escondido sp.n. AMCC [LP 14504]	0 1 0 2 1 ? 0 1 1 0	0 1 2 1 2 1 1 1 1 0	1 0 0 0 0
Surazomus manaus 979.1	0 1 1 1 – 0 0 1 2 0	0 1 0 2 0 1 0 1 0 –	1 0 1 1 0
Surazomus nara	1 1 1 2 0 – 1 1 0 1	2 0 2 1 1 0 2 1 1 0	1 0 0 0 0
Surazomus peregrinus sp.n.	0 1 1 2 1 – 0 1 1 0	0 1 1 1 2 1 0 ? ? ?	? ? ? ? ?
Surazomus uarini	0 1 0 1 – 1 1 1 0 0	1 0 1 0 0 1 0 1 1 1	1 1 0 0 0

feathered *Pm* setae. Tibial setal formula (retrolateral row, *Ter* : medial row, *Tmr* : prolateral row, *Tir*), 3:3:4; *Tmr* and *Tir* setae feathered. Tarsal spurs asymmetric. ***Legs***: Leg I, basitarsal-telotarsal proportions: 22: 3: 4: 4: 5: 5: 11; IV, femur 2.52 × 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, without pair of *Dm* setae. Segments X and XI telescoped, each 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 and well-developed posterodorsal process, comprising two pointed tubercles, *Dm* setal pair located medially, resembling bifid tubercle. Sternites each with two irregular rows of setae; genital plate with many scattered microsetae. ***Pygidial flagellum***: Flagellum globose, orbicular in shape (Fig. 4G–I); 1.22 × longer than wide; pairs of deep dorsosubmedian depressions and small lateral projections separated by prominent anteromedian swelling; whitish membranous areas absent; Dm_1 seta situated over bulb; Dm_4 situated posteriorly; Dl_2 anterior to Vl_1; Dl_3 posterior to Vl_2; pair of Vm_2 setae present; Vm_1 seta situated posterior to Vm_2 and anterior to Vm_3; Vm_5 aligned with Vl_1; 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*). ***Female***: Unknown.

Derivatio nominis. The specific name, a noun in apposition, is the Latin word for pilgrim, and refers to the pilgrims who visit the virgin of Santa Catarina Juquila annually, an event which is among the most famous in the state of Oaxaca.

Life history. The specimen was collected in very disturbed tropical rainforest, in which most of the vegetation was already cleared for cattle pastures.

Distribution. Known only from the type locality in the Mexican state of Oaxaca (Fig. 1).

Material examined. ***Type material***: MEXICO: *Oaxaca*: Municipio Santa Catarina Juquila: Juquila, 5 km NW on road to Panixtlahuaca, 16°15′04″N 97°18′48″W, 1447 m, 27.vi.2006, O. Francke, H. Montaño, C. Santibañez, A. Valdez and G. Villegas, holotype ♂ (CNAN T01376).

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Appendix 1

List of 25 morphological characters and states scored for phylogenetic analysis of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899). Character sampling and matrix was modified from Monjaraz-Ruedas et al. (2019).

Chelicerae

1. Movable finger, mesal surface, margin: smooth (0); with lamella (1); dentate (2).

Prosomal propeltidium

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

Prosomal metapeltidium

3. Metapeltidium: divided longitudinally (0); entire (1).

Opisthosoma

4. Segment XII, posterodorsal process (♂): absent (0); single (1); pair (2).
5. Segment XII, posterodorsal process, paired projections, shape (♂): conical (0); digitiform (1). — Not applicable to taxa with state (0) or (1) in character 4.
6. Segment XII, posterodorsal process, single projection, shape (♂): digitiform (0); small, rounded (1); rounded, projected (2). — Not applicable to taxa with states (0) and (2) in character 4.

Pedipalps

7. Trochanter, apical process: digitiform (0); obtuse (1); small knob (2); rounded along entire margin (3).
8. Femur, prolateral surface, anterior margin, apophysis: absent (0); present (1).
9. Femur, prolateral surface, anterior margin, apophysis, shape: claw-like (0); digitiform (1); small knob-like (2). — Not applicable to taxa with state (0) in character 8.
10. Patella, prolateral surface, anterior margin, apophysis: absent (0); present (1).
11. Patella, curvature: slight (0); marked (1); none (2).

Legs

12. Leg I, patella, anterior margin, white coloration: present (0); absent (1).

Male flagellum

13. Shape, dorsal aspect: trapezoidal (0); cordate (1); trilobed (2); lanceolate (3).
14. Dorsal depressions: single medial depression (0); pair of depressions, situated side by side (1); two depressions, situated one behind the other (2); none (3).
15. Dorsal projections: single (0); pair, submedian (1); pair submedian plus single median (2); absent (3).
16. Dorsal surface, membranous areas: present (0); absent (1).
17. Anterolateral projections, dorsal view: absent (0); small (1); well developed (2).

Female flagellum

18. Flagellomeres, count: 4 (0); 3 (1).

Spermathecae

19. Lobes, bulbs: absent (0); present (1).
20. Lobes, bulbs size: small (0); large (1). — Not applicable to taxa with state (0) in character 19.

21. Lobes, number of pairs: 1 (0); 2 (1); 3 or more (2).
22. Lobes, shape: spoon (0); club (1); digitiform (2).
23. Median lobes, apex shape: rounded (0); pointed (1).
24. Lateral lobes, apex shape: rounded (0); pointed (1).
25. Chitinized arch: absent (0); present (1).

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ASP_78-2_Monjaraz_Electronic_Supplements.zip

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File 1: monjarazruedas&al-surazomussystematics-asp2020-electronicsupplement-1.doc. — Material examined for phylogenetic analysis of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899), deposited in the Ambrose Monell Cryocollection (AMCC) and the Collections of Arachnida and Myriapoda at the American Museum of Natural History (AMNH), New York, U.S.A., and the Colección Nacional de Arácnidos (CNAN) at the Instituto de Biología, Universidad Nacional Autónoma de México, México City.

File 2: monjarazruedas&al-surazomussystematics-asp2020-electronicsupplement-2.nex. — Nexus file for phylogenetic analysis of the short-tailed whipscorpion genus *Surazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae Cook, 1899) containing alignments for 28S rDNA gene, the mitochondrial Cytochrome *c* Oxidase Subunit I (COI) gene, and themorphological matrix, along with the trees resulting from analyses of each data matrix with Maximum Likelihood and parsimony with equal and implied weighting.

Zoobank registrations

at http://zoobank.org

Present article: http://zoobank.org/urn:lsid:zoobank.org:pub:508F6E02-7981-4883-8530-5CC47E0D5CCB

***Surazomus chiapasensis* Monjaraz-Ruedas, Prendini & Francke, 2020:** http://zoobank.org/urn:lsid:zoobank.org:act:985AA558-940B-43E8-9A0D-576128BCF6D3;

***Surazomus escondido* Monjaraz-Ruedas, Prendini & Francke, 2020:** http://zoobank.org/urn:lsid:zoobank.org:act:68E4DBF4-CBFD-4577-84E5-4C9C8FFC2519;

***Surazomus peregrinus* Monjaraz-Ruedas, Prendini & Francke, 2020:** http://zoobank.org/urn:lsid:zoobank.org:act:B4127D5C-D301-439A-8E84-332442FF7127

Authors' contributions

RMR conducted the molecular work, analyses and taxonomy. RMR, OFF and LP conceived the project and wrote the manuscript.