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Redefining the Mexican genus *Diguetinus* Roewer, 1912 (Opiliones, Phalangioidea, Globipedidae) based on morphology and molecular phylogenetic data, with the redescription of *Diguetinus spinulatus* (Banks, 1898) stat. restit.

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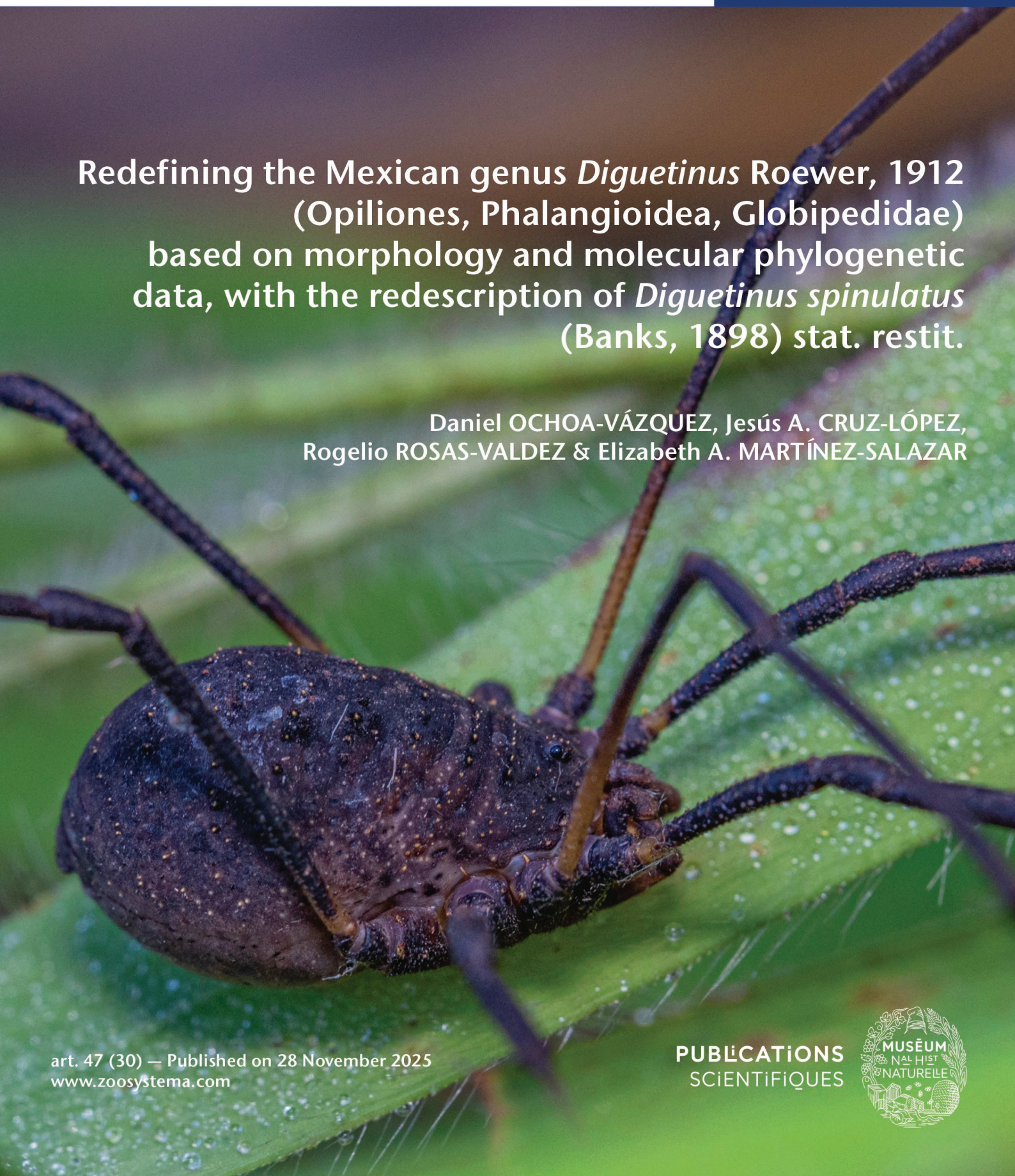

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Living female of *Diguetinus raptator* Roewer, 1912.

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ABSTRACT
The genus *Diguetinus* Roewer, 1912 (Opiliones, Globipedidae) is a monotypic genus that includes the widespread species *Diguetinus raptator* Roewer, 1912 from Mexico. Some studies have suggested that additional species could be included within the genus, particularly *Metopilio spinulatus* (Banks, 1898). This species has a brief but complicated taxonomic history, being originally described in *Leptobunus* Banks, 1893, considered in *Hadrobunus* Banks, 1900, later transferred to *Diguetinus* and currently in *Metopilio* Roewer, 1911, all changes without a solid justification. The aim of this study was to conduct a morphological revision of *D. raptator* and *M. spinulatus* using specimens from their respective type localities. In addition, a phylogenetic hypothesis that includes *D. raptator* and *M. spinulatus*, was inferred based on partial sequences of the mitochondrial gene cytochrome c oxidase subunit I (COI) gene. Our results indicate that *D. raptator* and *M. spinulatus* are related in a clade that leads to the phylogenetic redefinition of *Diguetinus*. Accordingly, the following taxonomic changes are proposed: a) a new diagnosis of *Diguetinus*; and b) the redescription of *Diguetinus spinulatus* stat. restit. (♂, ♀). Also, comparative detailed illustrations of the male and female genitalia of these species are provided, including taxonomic comments on the use of previous characters for the diagnosis of *Diguetinus* and *Metopilio*. Finally, we provide evidence of intrasexual dimorphism in males of *D. raptator*.

KEY WORDS
Emended diagnosis, Harvestmen, alpha male, *Diguetinus raptator*, COI barcoding.

RÉSUMÉ
Redéfinition du genre mexicain Diguetinus *Roewer, 1912 (Opiliones, Phalangioidea, Globipedidae) à partir de la morphologie et de données phylogénétiques moléculaires, avec redéfinition de* Diguetinus spinulatus *(Banks, 1898) stat. restit.*
Le genre *Diguetinus* Roewer, 1912 (Opiliones, Globipedidae) est un genre monotypique qui comprend l'espèce *Diguetinus raptator* Roewer, 1912, largement répandue au Mexique. Cependant, certaines études ont suggéré que d'autres espèces pourraient être incluses dans le genre, en particulier *Metopilio spinulatus* (Banks, 1898). Cette espèce a une histoire taxonomique brève mais compliquée : elle a été décrite dans *Leptobunus* Banks, 1893, puis considérée comme faisant partie de *Hadrobunus* Banks, 1900, avant d'être transférée dans *Diguetinus* et actuellement dans *Metopilio* Roewer, 1911, tous ces changements sans justification solide. L'objectif de cette étude était d'effectuer une révision morphologique de *D. raptator* et de *M. spinulatus* à l'aide de spécimens provenant de leurs localités types respectives. En outre, une hypothèse phylogénétique incluant *D. raptator* et *M. spinulatus* a été inférée à partir de séquences partielles du gène mitochondrial cytochrome c oxydase subunit I (COI). Nos résultats indiquent que *D. raptator* et *M. spinulatus* sont apparentés dans un clade qui conduit à la redéfinition phylogénétique de *Diguetinus*. En fonction des résultats, les changements taxonomiques suivants sont proposés: a) une nouvelle diagnose du genre *Diguetinus*; et b) la redescription de *Diguetinus spinulatus* stat. restit. (♂, ♀). Des illustrations détaillées et comparatives des genitalia mâles et femelles de ces espèces sont également fournies, accompagnées de commentaires taxonomiques sur l'utilisation des caractères précédemment utilisés pour la diagnose du genre *Diguetinus* et *Metopilio*. Enfin, nous apportons la preuve d'un dimorphisme intrasexuel chez les mâles de *D. raptator*.

MOTS CLÉS
Diagnose amendée, opilions, mâle alpha, *Diguetinus raptator*, code-barres COI.

INTRODUCTION

The order Opiliones Sundevall, 1833 remains understudied in certain geographic regions despite its status as one of the most species-rich groups of arachnids (Kury *et al.* 2021). Hedin *et al.* (2012) highlighted the taxonomic uncertainty in certain Mexican groups, due to the limited knowledge of the diversity of Opiliones in Mexico and the scarcity of taxonomic literature, sometimes complicated by inadequate original descriptions and a lack of study of genitalia (Kury & Cokendolpher 2000; Hedin *et al.* 2012).

One of these groups is the recently erected family Globipedidae Kury & Cokendolpher, 2020, previously referred to as the *Metopilio*-group (Giribet *et al.* 2002, 2010; Hedin *et al.* 2012). This family currently comprises 33 species, classified in six genera: *Dalquestia* Cokendolpher, 1984; *Diguetinus* Roewer, 1912; *Eurybunus* Banks, 1893; *Globipes* Banks, 1893; *Lanthanopilio* Cokendolpher and Cokendolpher, 1984; and *Metopilio* Roewer, 1911(Kury *et al.* 2021). The geographical distribution of globipedids includes Mexico, Central America, and the southwestern United States, extending as far south as Chiriqui in Panama (Kury & Cokendolpher 2020). The taxonomic history of this group is intricate, early authors considered it either as an undescribed subfamily in Sclerosomatidae Simon, 1879, as part of the dissolved Leptobunidae Banks, 1901, or and undescribed sub- or family assemblage (Gruber 1969; Cokendolpher 1984a; Cokendolpher & Cokendolpher 1984; Crawford 1992). Subsequent phylogenetic research has recovered this group either as mono- or polyphyletic group within Phalangioidea Latreille, 1802 (Giribet *et al.* 2002; 2010; Hedin *et al.* 2012). Hedin *et al.* (2012) recovered the *Metopilio*-group as monophyletic including three species: *Dalquestia grasshoffi* Cokendolpher, 1984, *Eurybunus brunneus* Banks, 1893 and *Globipes simplex* (Schenkel, 1951), being either sister to Neopilionidae Lawrence, 1931 or Phalangiidae Latreille, 1802, both hypotheses with weak support. Recently, Derkarabetian *et al.* (2023) included *Metopilio* sp. in a phylogenomic analysis, and retrieved Globipedidae as the sister group of Phalangiidae. So far, there have been no published molecular data for the remaining Globipedidae genera, such as *Lanthanopilio* or *Diguetinus*.

The genus *Diguetinus* currently includes only the species *Diguetinus raptator* Roewer, 1912, which has a widespread distribution in central Mexico. In the recent revision of the genus, Cokendolpher *et al.* (2021) mentioned that there is the possibility that members of other genera (e.g., *Metopilio*) could be included within *Diguetinus*. One of these species is the enigmatic *Metopilio spinulatus* (Banks, 1898), which originally was described in *Leptobunus* Banks, 1893, considered in *Hadrobunus* Banks, 1900 (Roewer 1910, 1923), transferred to *Diguetinus* by Goodnight & Goodnight (1942b), and assigned to *Metopilio* by Cokendolpher (1984b). These consecutive taxonomic changes occurred because *M. spinulatus* and *D. raptator* share a large body size and male genitalia pattern, nevertheless some features are different, such as the tuberculation, spination, and the lack of a prominent modification on leg I in *M. spinulatus*. Additionally, Cokendolpher *et al.* (2021) proposed that there are still other undescribed species of *Diguetinus*, and that *D. raptator* could be a species complex due to the variability of coloration and body proportions. These authors also made a redescription of *D. raptator* based on topotype specimens, illustrating the male genitalia for the first time and presented information about natural history.

The aim of the present study is to provide morphological and molecular phylogenetic evidence for the reincorporation of *M. spinulatus* into the genus *Diguetinus*. Additionally, a new diagnosis of the genera is proposed differentiating *Diguetinus* and *Metopilio*, and male dimorphism in *D. raptator* is presented with its taxonomic implications.

MATERIAL AND METHODS

Specimens and figures

The specimens examined are deposited in CNAN and CRLSM-Op collections. A total of 27 individuals (10 ♀, six ♂ of *D. raptator*; 10 ♀, one ♂ of *D. spinulatus* stat. restit.) from their respective type localities, Guadalajara, Jalisco, Mexico (GDL-JAL) and Tepic, Nayarit, Mexico (TEP-NAY) respectively (Fig. 1). We examined images of the female holotype of *Leptobunus spinulatus* (MCZ-IZ-14818) provided by the Museum of Comparative Zoology, Harvard University (MCZ). External morphological characteristics were observed under a LABOMED CZM6 stereo microscope. As a comparative reference, we took dorsal, ventral and lateral habitus photographs of the individuals of both *D. raptator* and *D. spinulatus* stat. restit. using a Sony Alpha 6400 digital camera, with a Laowa 100mm f/2.8 2:1 f/2.8 lens, and external illumination. Subsequently, the images were post-processed in Photoshop© version 22.0.0, and in some cases, photographs were stacked in Helicon Focus version 8.1.0 to obtain images with greater depth of field. For the extraction of genitalia, dissections and preparations were performed following Acosta *et al.* (2007), photographs of the genitalia were obtained using the same configuration employed for the habitus (+ Raynox DCR-250 lens).

Terminology, measurements and abbreviations

For the description of the morphological structures, the terminology described in Cokendolpher *et al.* (2021), Kury & Cokendolpher (2020), Rodriguez *et al.* (2014) and Wijnhoven (2013) were used. To obtain measurements of *D. spinulatus* stat. restit., one male and ten females were measured, following suggestions of Acosta *et al.* (2007) and Cokendolpher *et al.* (2021). All measurements were taken in millimetres, through a HY-900B digital camera adapted to the stereoscope, using Hayear Version ×64 software.

Morphology measurements

BH	body height, taken in lateral view;
CL	cephalothorax width;
DL	dorsum length, taken in lateral view;
DW	dorsum width, taken at the widest portion;
GoL	genital operculum length;
GoWb	width of genital operculum at base;
GoWn	width of genital operculum at neck;
OcH	ocularium height;
OcL	ocularium length;
OcW	ocularium width.

Repository

CNAN	Colección Nacional de Arácnidos, UNAM, Mexico.
CRLSM-Op	Colección de Referencia del Laboratorio de Sistemática Molecular, UACB, UAZ, Mexico. (Op: Opiliones section);
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge.

Molecular methods

Genomic DNA was extracted from locomotor leg tissues of five and four individuals from TEP-NAY and GDL-JAL respectively, as described in Cruz-López *et al.* (2016) and Derkarabetian *et al.* (2019), using a column extraction kit (DNeasy® Blood & Tissue Kit, Qiagen Inc., Valencia, California) according to the manufacturer's instructions. The mitochondrial protein-encoding cytochrome c oxidase subunit I (COI) was amplified using the primers LCO1490 (5'-GGTCAACAAATCAT-AAAGATATTG-3') (Folmer *et al.* 1994) and HCOoutout (5'-GTAAATATATGRTGDGCTC-3') (Prendini *et al.* 2005), following laboratory protocols outlined by Boyer *et al.* (2005) and Sharma & Giribet (2009). The following amplification conditions were used: an initial denaturation step at 95°C for 5 minutes, followed by 40 cycles of 95°C for 30 seconds, annealing at 46°C for 40 seconds, and extension at 72°C for 45 seconds; followed by a final extension at 72°C for 7 minutes. The Taq DNA Polymerase Amplification Kit (Vivantis Technologies PL1202) was used, following the manufacturer's recommended volumes and concentrations of reagents. The final volume of each reaction was 25 µL, consisting of 1 µL DNA (30 ng/µL), 0.2 µL Taq DNA Polymerase (5 u/µL), 0.5 dNTPs (10 mM), 1 µL of each oligonucleotide (10 µM), 2.5 µL 10× buffer, 1 µL MgCl2 (25 mM), and 17.9 µL H2O. The amplified products were sent to Macrogen Inc. (South Korea) for Sanger sequencing.

Phylogenetic reconstruction and genetic distances

Forward and reverse chromatograms were automatically ensembled with CodonCode Aligner version 7.1.2 and AliView programs. Sequence identity was confirmed by searches in BLAST (Basic Local Alignment Search Tool) from NCBI (National Center for Biotechnology Information). The final COI alignment included four *D. raptator* sequences and five *D. spinulatus* stat. restit. sequences. Additionally, we incorporated a segment of a sequence of *Metopilio* sp. from Oaxaca, Mexico (SAMN35540793, MCZ-IZ-95161), based on sequence capture of ultraconserved elements (UCEs) from Derkarabetian *et al.* (2023). We included a sequence of *Dalquestia formosa* (Banks, 1910) generated by Giribet *et al.* (2001). As proposed by Hedin *et al.* (2012) and Derkarabetian *et al.* (2023), the most closely related family to Globipedidae is Phalangiidae. Therefore, available sequences of Phalangiidae were used as outgroups in the phylogenetic analysis, including *Phalangium opilio* Linnaeus, 1758 (Masta & Boore 2008), *Odiellus lendii* (Sørensen, 1894), *Opilio canestrinii* (Thorell, 1876), *Mitopus morio* (Fabricius, 1779) (Astrin *et al.* 2016) and *Lophopilio palpinalis* (Herbst, 1799). Additionally, we include sequences

of Sclerosomatidae from Dewaard *et al.* (2019) as outgroups (GenBank accession numbers in Fig. 8). The COI matrix was subjected to a maximum likelihood (ML) phylogenetic inference analysis. The most appropriate evolutionary model was estimated from the jModelTest software version 2.1.10 (Darriba *et al.* 2012) based on the Akaike information criteria (AICc) and Bayesian approaches (BIC) according to Posada & Buckley (2004). The General Time Reversible (GTR) model with Gamma variation rate and parameters for invariant sites (GTR+G+I) was identified as the most appropriate evolutionary model. ML analyses were conducted using the MEGA X program (Kumar *et al.* 2018). To evaluate the reliability of the branches, a bootstrap analysis was conducted with 10 000 replicates. The resulting topologies were exported from the Dendroscope version 3 software (Huson *et al.* 2007), and figures were subsequently processed in the Illustrator© version 22.0.0 program. Average genetic distances were calculated between all nucleotide sequences obtained, as well as between the clades identified in the phylogenetic analysis. These values were estimated using the MEGA X program (Kumar *et al.* 2018).

RESULTS

Order OPILIONES Sundevall, 1833
Suborder EUPNOI Hansen & Sørensen, 1904
Superfamily PHALANGIOIDEA Latreille, 1802
Family GLOBIPEDIDAE Kury & Cokendolpher, 2020

Genus *Diguetinus* Roewer, 1912

Diguetinus Roewer, 1912: 271, pl. 1 fig. 25; 1923: 863, fig. 1030; 1956: 252. — Bronn 1932: 7, fig. 9b. — Di Caporiacco 1938: 280. — Goodnight & Goodnight 1942a: 15. — Weidner 1959: 121. — Gruber 1969: 273. — Cokendolpher 1984a: 27-28; 1984b: 377. — Cokendolpher & Cokendolpher 1984: 168. — Cokendolpher & Lee 1993: 16. — Crawford 1992: 17. — Kury & Cokendolpher 2000: 150; 2020: 52. — Cokendolpher *et al.* 2021: 119, fig. 1-9.

TYPE SPECIES. — *Diguetinus raptator* Roewer, 1912.

INCLUDED SPECIES. — *Diguetinus raptator* Roewer, 1912 and *Diguetinus spinulatus* (Banks, 1898) stat. restit.

EMENDED DIAGNOSIS. — *Diguetinus* can be recognized from others members of Globipedidae by the following combination of characters: a) large bodied (adult individuals dorsum length from 10 to 12.5 mm); b) dorsum with transverse rows of spines running across each opisthosomal tergite, from a single row configuration to a randomly ordered arrangement of at least two rows of spines; c) tergite spines yellowish-white and black tipped, usually with at least one chaetal sensilla present near the base of each spine, none spine extended to a height greater than the ocularium; d) stylus of the penis coiled in a complete circle.

Diguetinus raptator Roewer, 1912
(Figs 1A, B, E; 2A, B; 3A, B; 6A-F; 7A-C; 8-9)

Diguetinus raptator Roewer, 1912: 271, pl. 1 fig. 25; 1923: 863, fig. 1030; 1956: 252. — Bronn 1932: 7, fig. 9b. — Di Caporiacco 1938: 280. — Goodnight & Goodnight 1942a: 15. — Weidner 1959: 121. — Cokendolpher & Lee 1993: 16. — Crawford 1992: 17. — Kury & Cokendolpher 2000: 150; 2020: 52. — Cokendolpher *et al.* 2021: 119, fig. 1-9.

TYPE DATA. — See Cokendolpher *et al.* (2021).

MATERIAL EXAMINED. — **Mexico** • 6 ♂, 10 ♀; Jalisco: Guadalajara: Bosque El Centinela; 20°45'44.4"N, 103°22'51.1"W; 1584 m a.s.l.; 26.X.2023; D. Ochoa-Vázquez, O. I. Ochoa-Vázquez leg.; GenBank accession numbers: PV430733-36; CRLSM-OP_01; CNAN-OP2021.

EMENDED DIAGNOSIS. — *Diguetinus raptator* can be distinguished from *Diguetinus spinulatus* stat. restit. by the combination of the following characters: a) dorsum with transverse rows of spines running across each tergite of the opisthosoma, not in a single row (as in *Diguetinus spinulatus* stat. restit.) but rather with random to at least two rows of spines per tergite; b) leg femur predominantly dark brown; c) glans length less than length of alae section, about 1/2 the length of alae; d) alae section proportion approximately 1/6 of the total length of the penis; e) alae section internal texture with a reticulate pattern, dark in colour, present over the entire alae surface.

Diguetinus spinulatus (Banks, 1898) stat. restit.
(Figs 1C-E; 2C-D; 3C-D; 4-5; 6G-L; 7D-F)

Leptobunus spinulatus Banks, 1898: 182.

Hadrobunus spinulatus – Roewer 1910: 254, 257; 1923: 920.

Diguetinus spinulatus – Goodnight & Goodnight 1942b: 11.

Metopilio spinulatus – Cokendolpher 1984b: 376.

TYPE DATA. — **Holotype** (examined by photographs). **Mexico** • ♀; Nayarit: Tepic; 21°30'34.2"N, 104°53'44.5"W (error radius: 8832 m); Banks leg.; MCZ:IZ:14818.

MATERIAL EXAMINED. — **Mexico** • 1 ♂, 10 ♀; Nayarit: Tepic: Cerro de la Cruz; 21°32'4.5"N, 104°53'5.3"W; 1091 m a.s.l.; 28.X.2023; D. Ochoa-Vázquez, O. I. Ochoa-Vázquez leg.; GenBank accession numbers: PV430728-32; CRLSM-OP_02; CNAN-OP2022.

DIAGNOSIS. — *Diguetinus spinulatus* stat. restit. can be distinguished from *D. raptator* by the combination of the following characters: a) leg femur bicolored, first 1/4 of all femurs light yellow-brown, more evident in femur II; b) transverse rows of spines across each tergite of the opisthosoma, with one linear row configuration per tergite; c) alae and glans penis sections similar in length (*c.* 1 mm), each proportion 1/8 of the total length of the penis; d) alae section internal texture with a reticulate pattern, dark in colour, present only on apical margin.

REDESCRIPTION

Body leathery in texture, with a tuberculate-microgranulate cuticle morphology (with rounded or pointed protuberances surrounded by small obtuse to acute granules). Dorsum length 10.33 mm (male) and an average length of 11.59 mm ± 0.61 (females: ranging from 10.68 to 12.3 mm). Male dorsum light yellow-brown tone (alcohol preserved), dorsally with black patches on the cephalothorax across each opisthosomal tergite (Fig. 2C), female dorsum coloration dark-brown tone (Fig. 1C; 3C). Leg coloration with a gradual transition from light yellow-brown at the base of femurs to brown (male) and dark-brown (female) at patella and tibia, with tarsi and meta-

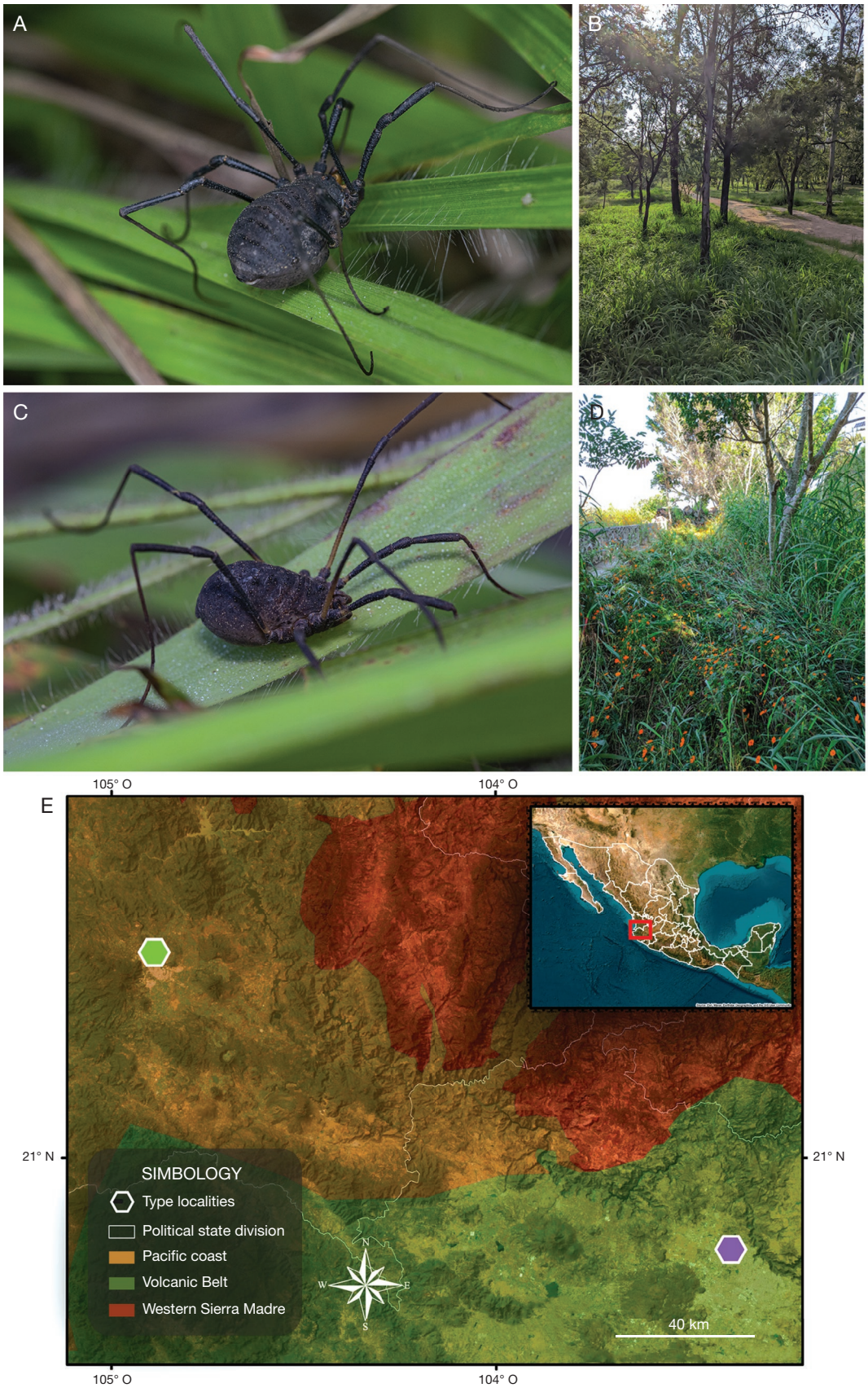

Fig. 1. — Living females and type locality habitats of *Diguetinus raptator* Roewer, 1912 (**A**, **B**) and *Diguetinus spinulatus* (Banks, 1898) stat. restit. (**C**, **D**); **E**, geographical location of the type localities of *D. spinulatus* stat. restit. (Tepic, Nayarit: TEP-NAY; **green hexagon**) and *D. raptator* (Guadalajara, Jalisco: GDL-JAL; **purple hexagon**). Biogeographic regionalization following Arriaga *et al.* (1997). Photos: A-D, DOV.

Fig. 2. — Comparison of males of *Diguetinus raptator* Roewer, 1912 and *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Guadalajara, Jalisco, Mexico and Tepic, Nayarit Mexico, respectively: **A**, **B**, *D. raptator* dorsal (**A**) and ventral (**B**) habitus; **C**, **D**, *D. spinulatus* stat. restit. dorsal (**C**) and ventral (**D**) habitus. Scale bars: 1 mm.

Fig. 3. — Comparison of females of *Diguetinus raptator* Roewer, 1912 and *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Guadalajara, Jalisco, Mexico and Tepic, Nayarit Mexico, respectively: **A**, **B**, *D. raptator* dorsal (**A**) and ventral (**B**) habitus; **C**, **D**, *D. spinulatus* stat. restit. dorsal (**C**) and ventral (**D**) habitus. Scale bars: 1 mm.

TABLE 1. — Leg and pedipalp measurements (in mm) of *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Tepic, Nayarit, Mexico. Abbreviations: **L**, length; **W**, width. Females values: minimum-maximum ranges (mean values in **bold**).

Appendage	Segment	Measure	♂ (n=1)	♀ (n=10)
Leg I	Femur	L	5.52	4.73 - 6.04 (**5.41**)
		W	0.9	0.71 - 0.78 (**0.74**)
	Tibia	L	5.2	4.17 - 4.81 (**4.48**)
		W	1.05	0.7 - 0.86 (**0.74**)
Leg II	Femur	L	9.35	8.75 - 11.57 (**10.75**)
		W	0.51	0.45 - 0.54 (**0.49**)
	Tibia	L	7.99	7.1 - 8.83 (**8.28**)
		W	0.55	0.47 - 0.59 (**0.53**)
Leg III	Femur	L	5.54	5.05 - 5.98 (**5.64**)
		W	0.87	0.61 - 0.78 (**0.70**)
	Tibia	L	4.88	3.72 - 4.74 (**4.11**)
		W	0.94	0.66 - 0.79 (**0.71**)
Leg IV	Femur	L	8.48	8.37 - 9.79 (**9.25**)
		W	0.66	0.52 - 0.75 (**0.65**)
	Tibia	L	5.31	4.17 - 5.77 (**5.30**)
		W	0.74	0.63 - 0.77 (**0.67**)
Pedipalp	Femur	L	1.88	1.52 - 1.98 (**1.68**)
		W	0.62	0.51 - 0.56 (**0.53**)
	Patella	L	0.69	0.7 - 0.88 (**0.80**)
		W	0.59	0.46 - 0.63 (**0.53**)
	Tibia	L	1.36	1.18 - 1.37 (**1.26**)
		W	0.72	0.5 - 0.61 (**0.56**)
	Tarsus	L	2.24	1.91 - 2.38 (**2.14**)
		W	0.3	0.24 - 0.39 (**0.34**)

tarsus predominantly yellow-brown tones and last metatarsus a gradual dark-brown hue; leg femur distinctively bicolored, at least the first 1/4 portion of all femurs light yellow-brown in color, more evident in femur II. These colorations paler in living organisms (Fig. 1C). Body cuticle granular, with small spines present on the anterior propeltidium, mesopeltidium, metalpentidium, and dorsal scutum. Spines yellowish-white tipped with black, with at least one chaetal sensilla present near the base of each spine, none of which extended to a height greater than ocularium.

Cephalothorax (Fig. 2C; 3C; 4) smaller in size relative to the abdomen, particularly in females. Anterior propeltidium with a transverse multiple spined ovoid-shaped area (APH: anterior propeltidium hump). APH gradually raised, wider than long and occupying approximately one-third of the anterior edge of the propeltidium, covered with small black tipped yellowish-white spines, none extended to a height greater than the ocularium (Fig. 4). Marked cuticular depression on either side of the APH area, running to the posterior part of ozopore. In dorsal view, ocularium round in shape, with a diameter of *c.* 0. 62 mm (male), *c.* 0.60 mm (female), about half that distance in height, and approximately its length from the anterior margin of cephalothorax. A light-yellow longitudinal line running through the middle part of the ocularium, dorsally with four to six black tipped yellowish-white spines over each eye. Ozopores elongate across the edge of the cephalothorax, close proximity to the bases of leg I, clearly visible in dorsal view. With small yellowish black-tipped spines (one near the anterior margin of the ozopore and one near the posterior margin). Cheliceral lamellae short and smooth, slightly visible in dorsal view, contiguous with anterior propeltidium edge. Mesopeltidium (posterior to the ocularium) and metapeltidium (final segment of the cephalothotax) each with a single row of a small black-tipped yellowish-white spines; one group of mesopeltidium spines situated within a triangle-shaped area (delineated by a darker colour), where a row of seven to eight spines forms the base of the area when observed in dorsal view (Fig. 4).

Chelicerae light yellow-brown and black tips chelal fingers. Second segment of each chelicera bearing loose cluster of sensilla chaetica near the base of the fixed digits and an arrangement of five-six slit sensilla, located just before the moveable finger. Basal segment ventrally with a short, smooth bulge.

Pedipalps clamp-like, with a smooth palpal claw that bears a small pointed conical basal denticle. Sexual dimorphism evident in the palpal tarsus, which in males bears a belt of denticles that is absent in females and juveniles. Dorsal surface of each pedipalp patella, with two pale yellow longitudinal lines running from the anterior to the posterior edges, with small dark pointed spines. These particularly noticeable in females, due to the darker coloration of their patellae in comparison with the male revised (Fig. 2C; 3C).

Leg coxae with evenly distributed sensilla chaetica and small rounded and pointed tubercles facing proxo-ventrally; a distinct row of tubercles present on the distal margin of all coxae, and dark-pointed spines present at least on the posterior-distal margin (Fig. 2D, 3D). Endites irregularly positioned setae, being more abundant towards the central margin. Neither femur exceeding the total length of the body. Tibiae II with two pseudosegments on each side. Sexual dimorphism in legs I and III; in males, legs I and III stouter than legs II and IV, primarily tibiae, with rows of spines; the metatarsus I and III ventrally with a row of dark-pointed spines, from 18 (metatarsus I) to 10 (metatarsus III) (Fig. 5A, B); these characters not present in females. Tibiae round in cross-section, with two accessory spiracles, one near the proximal and one near the apical end.

Abdomen (opisthosoma) arched, especially in females. Each tergite of the opisthosoma with a single transverse row of small spines per tergite (spines similar to those in the anterior propeltidium, mesopeltidium and metapeltidium), none of which are larger than the height of the ocularium (Figs 2C; 3C; 5A).

Male genital apparatus tubular, sclerotized penis and a basal, membranous hematodocha, accompanied by a dorsoventral pair of prominent stiffening rods. Penis (Fig. 6G-L) truncus sclerotized, long and slender, with a section of a subterminal lateral alae curved ventrally, this section approximately 1/8 of the total length of the penis. Alae internal texture with a reticulate pattern, dark in colour, present only at apical section, limited to the midpoint of the structure (Fig. 6J). Glans slightly inclined relative to the axis of the truncus, length similar to alae section (0.90 mm glans and 1.07 mm alae section), proportion approximately 1/8 of the total length of the penis. Stylus (Fig. 6H, J, L) mobile, broad medially, and thickened at the base, inserted dorso-apically on the glans. Surface predominantly dark brown, no evident rugose (wrinkled)

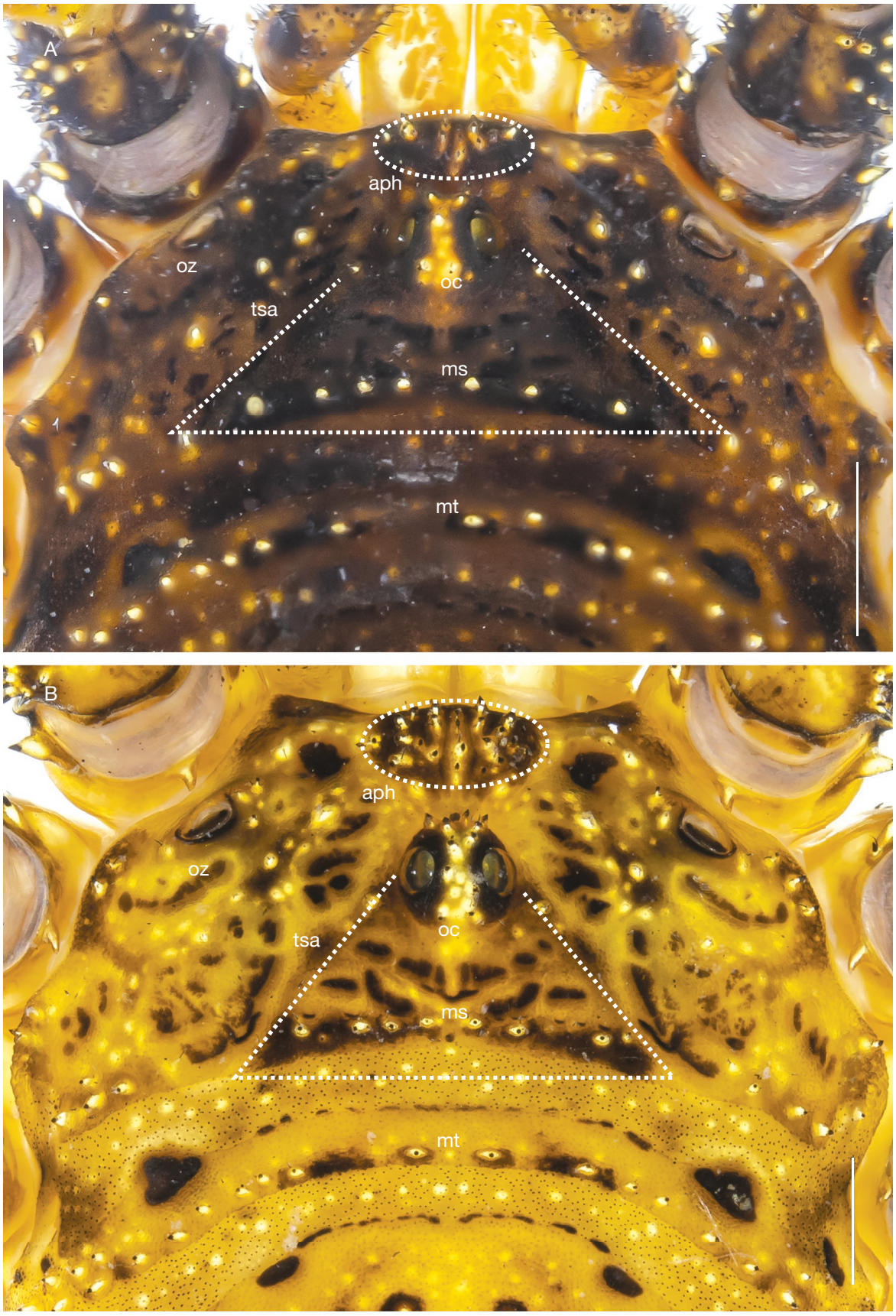

Fig. 4. — Dorsal view of cephalothorax of *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Tepic, Nayarit, Mexico: **A**, female; **B**, male. Abbreviations: **aph**, anterior propeltidium hump; **oz**, ozopore; **tsa**, triangle-shaped area; **oc**, ocularium; **ms**, mesopeltidium; **mt**, metapeltidium. Scale bars: 1 mm.

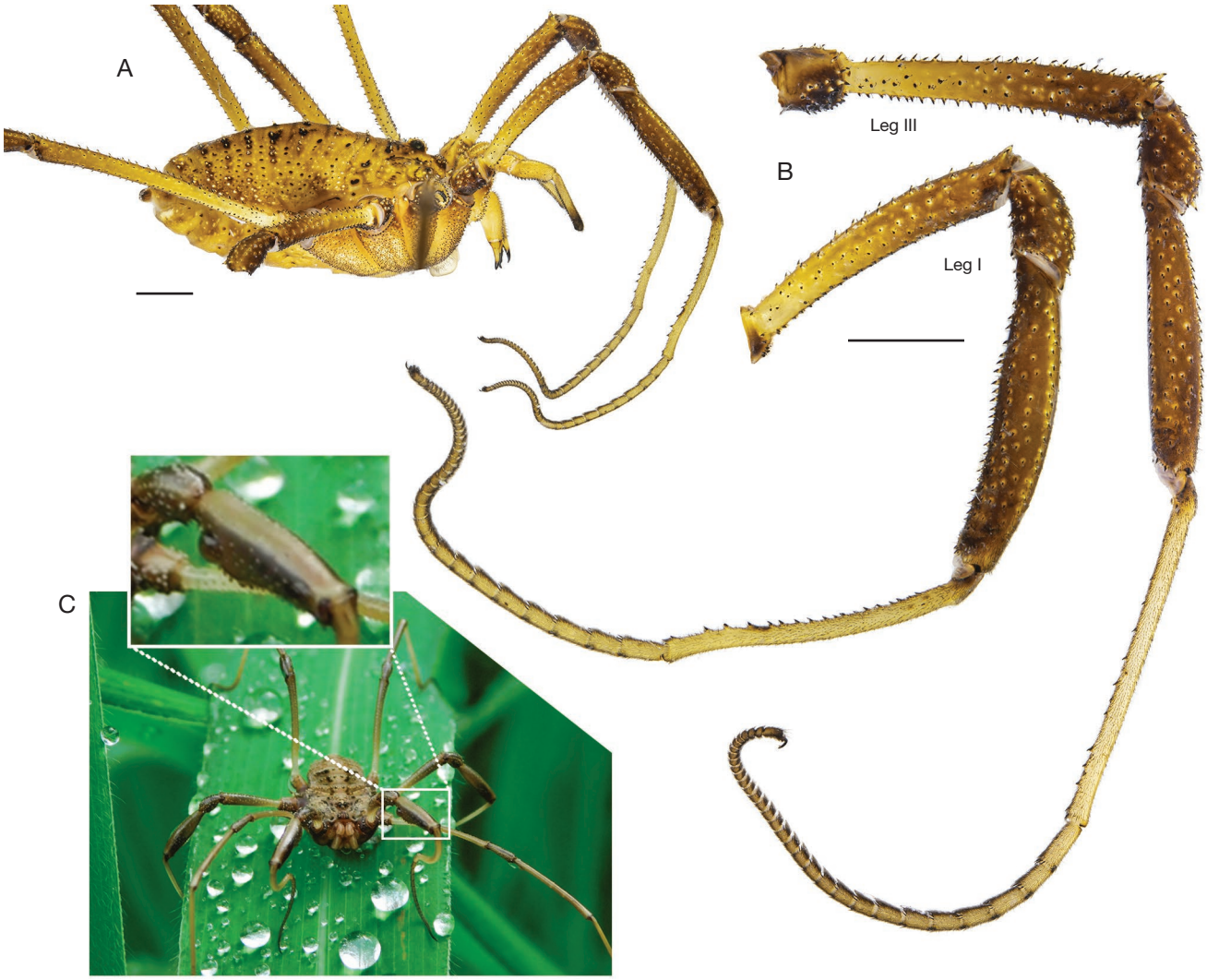

FIG. 5. — *Diguetinus spinulatus* (Banks, 1898) stat. restit. males from Tepic, Nayarit, Mexico: **A**, lateral view; **B**, retrolateral view of leg I and III. Scale bars: 2 mm; **C**, citizen science observation of a possible alpha male of *D. spinulatus* stat. restit., arrow showing tibia I ventrally with a strong tuberculate tooth; iNaturalist observations/180852338, Cerro de la Cruz, Tepic, Nayarit, Mexico. 2002, 12:00 AM MST, © guaponuel.

appearance, with a thin distal end, a coiled loop extending a full circumference in a helicoidal form. Total length of the penis, including the stylus length, 8.4 mm.

Ovipositor (Fig. 7D-F) dorsoventrally flattened cylinder, comprising more than 20 segments. Distal portion of the ovipositor constituted by a bifurcate three-segmented furca (Fig. 8E). At the base of the furca, the vagina marking the distal end of the uterus internus. On the distal segment, a rounded projection with a sensory termination inserted distolaterally on either side, with a tuft of sensory setae. Each side of segment II of the furca with a row of five sensilla chaetica, and three to four slit-sensilla. Paired seminal receptacles with a single conduct on each side, located at the level of segments 1-3 after the base of the furca (Fig. 8F).

Measurements

Male: DL=10.33, DW=5.23, BH=5.16, CL=2.93, CW=5.29, OcL=0.63, OcW=0.65, OcH=0.35, GoL=2.61, GoWn=1.07, GoWb=1.76; Female: data presented minimum-maximum values (average value), DL=10.68 – 12.3 (11.59), DW=6.68 – 7.88 (7.21), BH=6.32 – 7.43 (6.92), CL=2.63 – 3.3 (3.0), CW=4.96 – 5.46 (5.23), OcL=0.59-0.69 (0.61), OcW=0.52-0.71 (0.62), OcH=0.3-0.37 (0.32), GoL=2.33 – 2.65 (2.53), GoWn=1.04 – 1.33 (1.18), GoWb=1.87 – 2.5 (2.10). Legs and palps measurements see Table 1.

TAXONOMIC NOTES

The taxonomic classification of *Diguetinus spinulatus* stat. restit. has undergone several changes over time. Originally described in *Leptubunus spinulatus* by Banks (1898). Later, Roewer (1910, 1923) considered *L. spinulatus* part of the genus *Hadrobunus*, without having reviewed the type material, only following the taxonomic changes of *Leptobunus* species to *Hadrobunus* by Banks (1900) and the observation that *L. spinulatus* is similar to *Leptobunus grande* Say, 1821 (now *Hadrobunus grandis* (Say, 1821), type species of

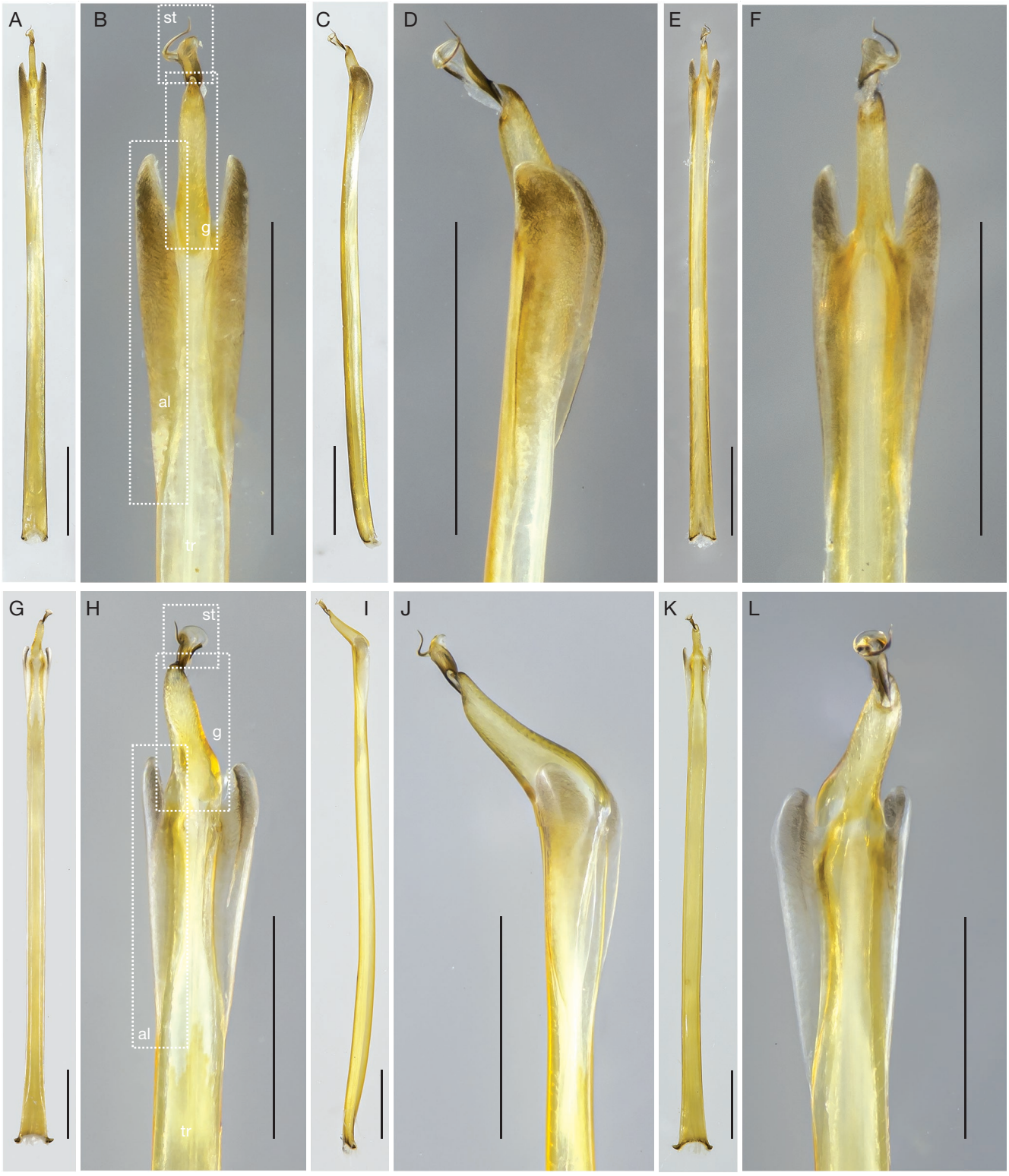

FIG. 6. — Comparison of penes of *Diguetinus raptator* Roewer, 1912 and *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Guadalajara, Jalisco, Mexico and Tepic, Nayarit Mexico, respectively. **A**-**F**, *D. raptator*; **G**-**L**, *D. spinulatus* stat. restit. Entire penis (**A**, **C**, **E**, **G**, **I**, **L**), enlargement of terminal end of penis (**B**, **D**, **F**, **H**, **J**, **L**). Ventral (**A**, **B**, **G**, **H**), lateral (**C**, **D**, **I**, **J**), dorsal (**E**, **F**, **K**, **L**). Abbreviations: **al**, alae section; **g**, glans; **st**, stylus; **tr**, truncus. Scale bars: 1 mm.

Hadrobunus). Goodnight & Goodnight (1942b) examined the type material of *Leptobunus spinulatus* Banks, 1898 and concluded that this species does not belong to *Leptobunus* or *Hadrobunus*, but rather is a member of the genus *Diguetinus* and identical to *D. raptator*. In subsequent publications the authors referred to this species as *Diguetinus spinulatus* (Banks)

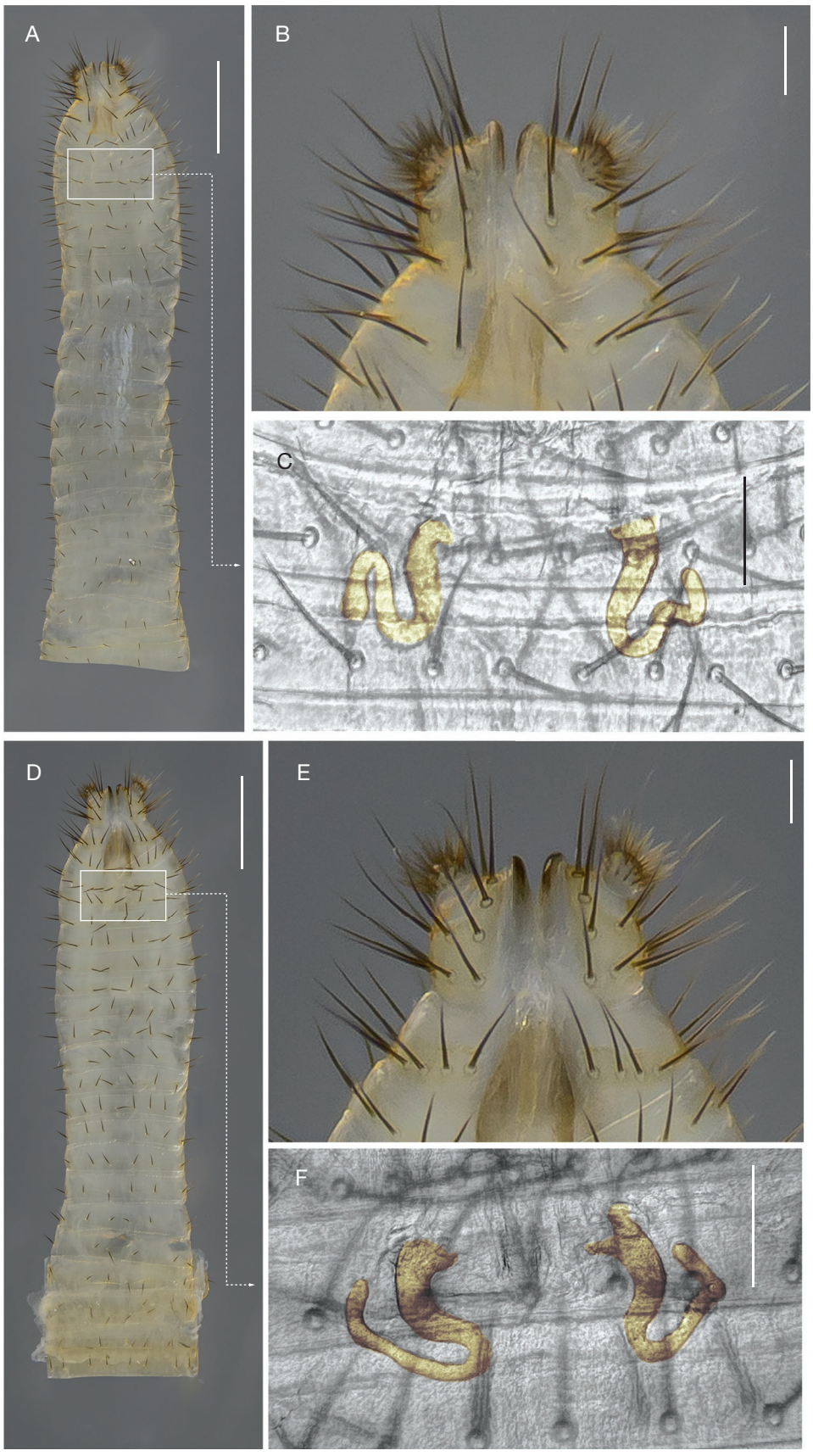

FIG. 7. — Comparison of ovipositors of *Diguetinus raptator* Roewer, 1912 and *Diguetinus spinulatus* (Banks, 1898) stat. restit. from Guadalajara, Jalisco, Mexico and Tepic, Nayarit Mexico, respectively: **A**-**C**, *D. raptator*; **D**-**F**, *D. spinulatus* stat. restit. Entire ovipositor (**A**, **D**), enlargement of distal end 3-segmented furca (**B**, **E**), paired seminal receptacles (**C**, **F**) at the level of the furca segments 1-3 from the base, digitally highlighted. Scale bars: A, D, 1 mm; B, C, E-F, 0.1 mm.

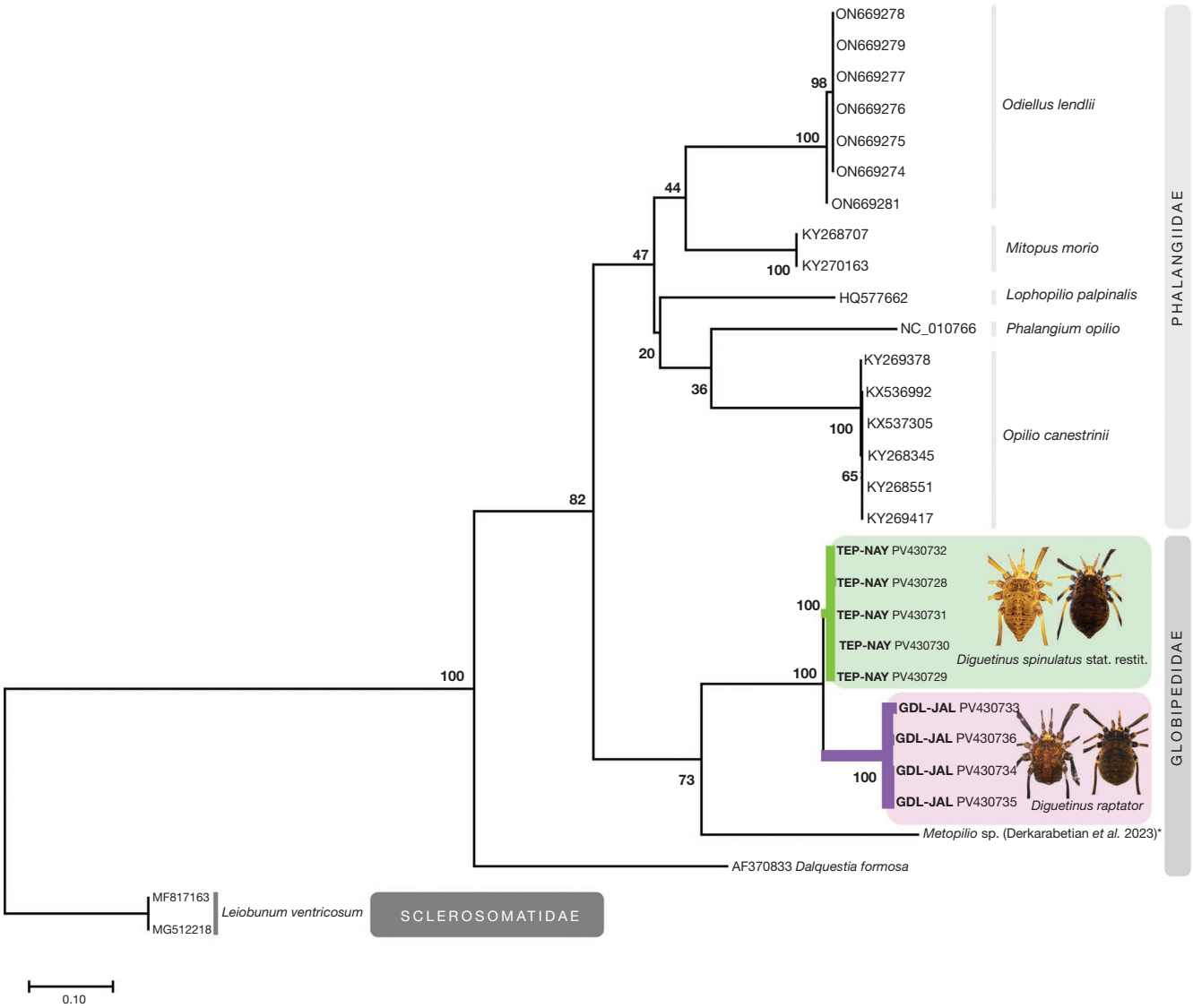

Fig. 8. — Phylogenetic relationships obtained by Maximum Likelihood analysis of the mitochondrial gene cytochrome c oxidase subunit I (COI), showing relationships between *Diguetinus sensu lato* clade (green + purple subclades), *Metopilio* sp. (MCZ-IZ-95161), *Dalquestia formosa* (Banks, 1910) (AF370833) and outgroups (Phalangiidae and Sclerosomatidae). Within the *Diguetinus sensu lato* clade are *Diguetinus spinulatus* (Banks, 1898) stat. restit. (**green subclade**) and *Diguetinus raptator* Roewer, 1912 (**purple subclade**). Numbers on nodes correspond to branch support (**bootstrap values**). * COI fragment from a UCEs sequence (SAMN35540793: Derkarabetian *et al.* 2023).

(Goodnight & Goodnight 1945, 1947). Later, Cokendolpher (1984b) undertook a reexamination of the female holotype of *L. spinulatus* from Tepic, Nayarit, Mexico, and conducted a comparison with the paratypes of *D. raptator* from Guadalajara, Jalisco, Mexico, and concluded that these individuals are not conspecific and proposed that *L. spinulatus* should be classified within the genus *Metopilio*. Cokendolpher *et al.* (2021) mentioned that the penis morphology of *M. spinulatus* is similar to that of *Diguetinus*, and that they differ only in tuberculation, spination, and the less severely modified leg I. However, none of the aforementioned publications provide a detailed description of the morphology of the examined specimens and no illustrations have been provided of morphological characters in support of the taxonomic changes. Furthermore, the male of *L. spinulatus* was unknown and the original description of the species did not take into account characters of the genitalia.

Phylogenetic analysis and genetic distances

The phylogenetic hypothesis based on the mitochondrial COI region is shown in Figure 8. ML inference indicated that all samples generated (sequences from GDL-JAL and TEP-NAY) constituted a monophyletic group with a high bootstrap value of 100%, corresponding to the *Diguetinus sensu lato* clade. As the most closely related sequence recovered the sequence of *Metopilio* sp. from Derkarabetian *et al.* (2023). This was followed by the sequences corresponding to the outgroups of the family Phalangiidae and Sclerosomatidae.

TABLE 2. — Pairwise genetic distance (expressed as percentage) between clades identified in the phylogenetic hypothesis (Fig. 8). Mean values in bold, followed by minimum-maximum ranges, **OG**, outgroup (see Fig. 8).

	D. raptator	***D. spinulatus***	***Metopilio* sp.**	***Dalquestia formosa***	**OG: Phalangiidae**
D. raptator	–	–	–	–	–
D. spinulatus	**6.3**				
	6.1-6.9	–	–	–	–
Metopilio sp.	**20.2**	**21.3**			
	20.1-20.3	21.3-21.5	–	–	–
Dalquestia formosa	30.1	**27.1**	28.1	–	–
		26.9- 27.4			
OG: Phalangiidae	**23.7**	**21.6**	**24.4**	**26.8**	
	22.4-27	20.3-24.7	24.2-25.6	26.4-29.2	–
OG: Sclerosomatidae	**34.8**	**31.9**	**34.6**	**32.7**	**32.4**
	34.4-35	31.5-32.3	34.4-34.8	32.6-32.7	31.2-36

The sequence of *Dalquestia formosa* was recovered paraphyletic with respect to the Globipedidae (only *Diguetinus* + *Metopilio*) and Phalangiidae clades. A total of two main subclades were recovered within the *Diguetinus s.l.* clade, both exhibited a bootstrap value of 100%. The purple subclade grouped the sequences from GDL-JAL (the type locality of *D. raptator*), while the green clade includes sequences from TEP-NAY (the type locality of *D. spinulatus*) (Fig. 8).

The genetic differences expressed as pairwise distance between the clades identified in the phylogenetic hypothesis described above (Table 2) showed that the highest divergence values were observed between the outgroup sequences (Sclerosomatidae and Phalangiidae) and the remaining groups (ranging from mean 31.9 to 34.6% and 21.6 to 26.8%, respectively), as well as *Dalquestia formosa* sequence and the remaining groups (from 26.8 to 32.7), then the *Metopilio* sp. lineage and the remaining groups (from 20.2 to 34.6% of mean distance). The mean divergence between subclades within the *Diguetinus s.l.* clade was 6.3% (between the *D. spinulatus* and *D. raptator* clades, with percentages ranging from 6.1 to 6.9%). Intraspecific divergence observed in *D. raptator* were from identical sequences to 0.2%, and within *D. spinulatus* from identical sequences to 0.04%.

DISCUSSION

DIGUETINUS VS *METOPILIO*

Some authors have proposed that the genus *Diguetinus* is similar to *Metopilio*, implying that they may eventually be considered synonyms, the main distinction being in the number of tubercles found in the transverse rows of the dorsum tergites and in the curved morphology of the stylus (Gruber 1969; Cokendolpher 1984a; Cokendolpher & Cokendolpher 1984; Cokendolpher & Stockwell 1986; Cokendolpher & Sissom 2000; Cokendolpher *et al.* 2021). However, in the taxonomic work by Roewer (1911, 1912, 1923), *Metopilio* is distinguished from *Diguetinus* by the presence of two median spines on each tergite of the dorsum, described as follows: "the last cephalothorax and abdominal segments with more or less clear transverse rows of pointed tubercles, the two medians of which are reinforced like thorns, so that two parallel longitudinal rows of such arise" (translated from the German from Roewer 1912: 262-263). These original definitions do not establish the number of tubercle rows per tergite as a diagnostic character, as subsequently suggested by several authors (Cokendolpher 1984a; Cokendolpher & Cokendolpher 1984; Cokendolpher & Stockwell 1986; Cokendolpher & Sissom 2000; Kury & Cokendolpher 2020; Cokendolpher *et al.* 2021). Nevertheless, Roewer (1911, 1912, 1923) stated the features that define *Diguetinus*, i.e., rough tuberculated dorsal segments, but without large spines, coarsely granulated coxae; and sexual dimorphism, in males, legs I and III strongly clubbed, tibia I ventrally with a strong tuberculate tooth and articulated against the S-shape metatarsus I, ventrally toothed, thus forming a grasping hook. Furthermore, Cokendolpher *et al.* (2021) pointed out that, in *Diguetinus*, the opisthosomal spines are not arranged in a single transverse row per tergite, but rather randomly with at least two rows of tubercles per tergite.

The specimens from *D. raptator* and *D. spinulatus* stat. restit analysed in the present study (Figs 1-4; 6-7) exhibited the diagnostic characters described by Cokendolpher *et al.* (2021) (in part) and Roewer (1912), with a notable absence of a pair of long spines on each dorsal tergite, with only one row of spines per tergite (*D. spinulatus* stat. restit.) and notably more than two rows of spines per tergite (*D. raptator*).We suggest that the dichotomy for the separation of these genera by one row of spines or irregular rows of spines on each tergite, is a misinterpretation of the original descriptions.

Otherwise, the situation in *Metopilio*, the most specious genus in the family with 18 described species, is a result of the absence of data, because the penial morphology has not been fully documented, and the genus in general requires taxonomic revision to clarify the definitions of the species (Cokendolpher & Cokendolpher 1984). Currently, only the penis morphologies of *Metopilio australis* (Banks, 1909) (Gruber 1969), *Metopilio ornatipes* (Banks, 1909), and *Metopilio niger* Goodnight & Goodnight, 1942 (Rodriguez *et al.* 2014) are known. Furthermore, an examination of various species within the genus revealed a diverse range of penis morphologies, including examples with a markedly pronounced alate region, as observed in *M. australis* (Gruber, 1969, figs 1, 4, 5), and those lacking an alate region (undescribed *Metopilio* species from

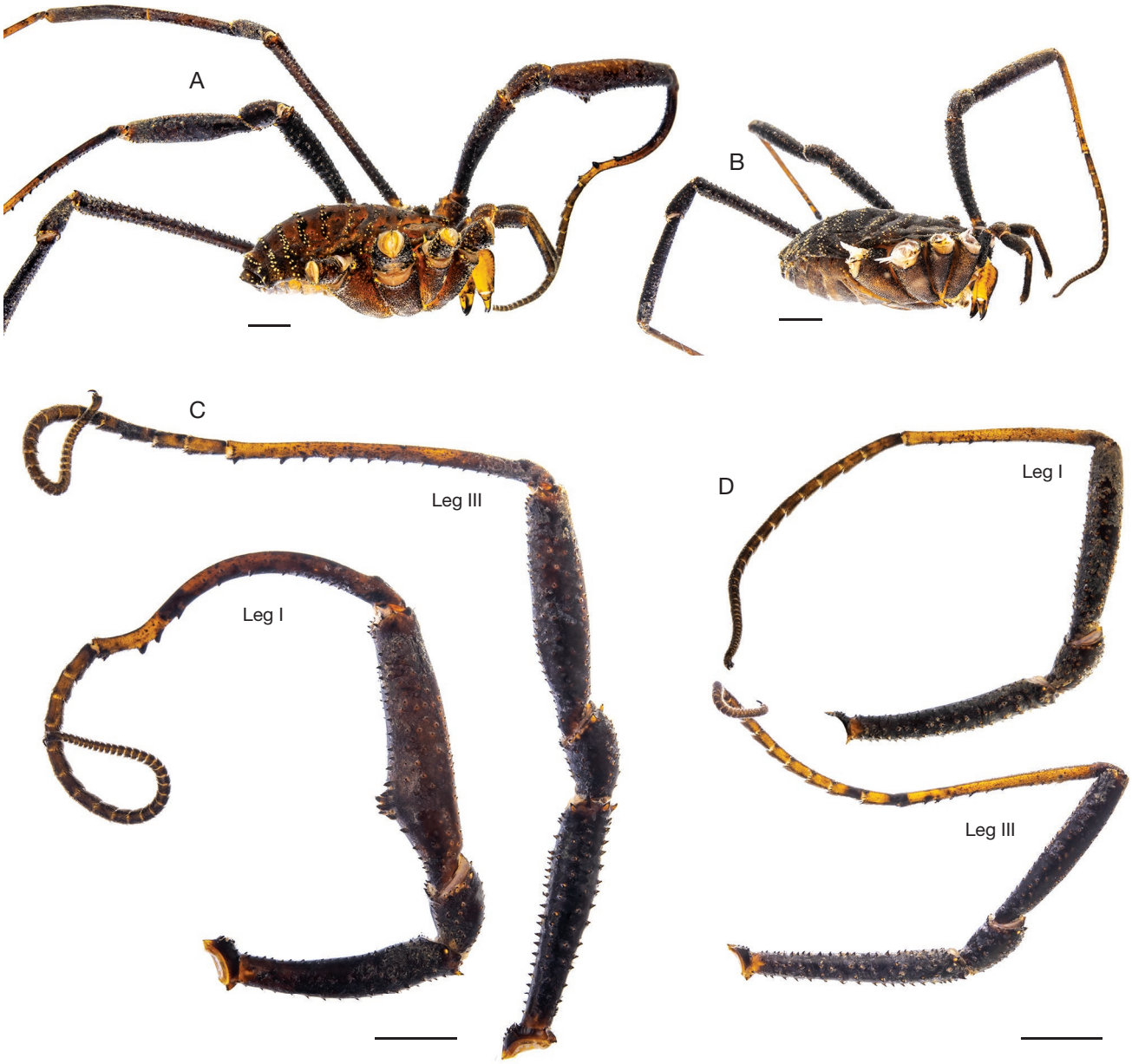

Fig. 9. — Intrasexual dimorphism of *Diguetinus raptator* Roewer, 1912 from Guadalajara, Jalisco, Mexico: **A**, **C**, alpha male; **B**, **D**, beta male. Lateral view (**A**, **B**), prolateral view of legs I and III (**C**, **D**). Scale bars: 2 mm.

Mexico; Cruz-López, personal observations). Moreover, it is notable that none of the above-mentioned specimens exhibit the distinctive stylus morphology described in *Diguetinus* (Kury & Cokendolpher 2020; Cokendolpher *et al.* 2021; this study), which is characterized by a coiled structure that forms a complete ring (Fig. 6). This observation indicates that the stylus morphology is an important taxonomic character for delineating the boundaries of *Diguetinus* and *Metopilio*.

Diguetinus systematics and geographical distribution

Our phylogenetic results, morphological description, and geographic distribution provide evidence supporting the separation of *D. spinulatus* stat. restit. and *D. raptator* as distinct species. The average genetic distance between the two clades was 6.3%, with percentages ranging from 6.1 to 6.9%. To date, no information on genetic variation within the family Globipedidae has been reported. Hedin & Thomas (2010) reported COI genetic distances between species within the family Phalangodidae to range from 12 to 30%. As an example, within Opiliones species, intraspecific variation within *Fumontana deprehendor* Shear, 1977 (Laniatores, Triaenonychoidea, Buemarinoidae) was observed to range from identical sequences to 6%. In a study conducted as part of the Barcode of Life project in Germany, Astrin *et al.* (2016) analysed the sequences of approximately 200 Opiliones species from the region, showing that the range of percent divergence between closely related species is 7 to 21.8%. Considering all evidence

presented here, the comparable genetic divergence among other harvestman and between *D. spinulatus* stat. restit. and *D. raptator*, the phylogenetic hypothesis, morphology of the stylus and other features, and the disjunct geographic distribution, we conclude that they represent distinct evolutionary lineages.

Cokendolpher *et al.* (2021) presented a distribution map of the genus *Diguetinus* based on historical records in literature, original records, and records of citizen science observations (iNaturalist platform). They noted that the distribution of the "species" of the genus aligns with the boundaries of two biogeographic provinces defined by Arriaga *et al.* (1997): the southern Mexican Plateau and the western and central Transmexican Volcanic Belt. The type localities of *D. spinulatus* stat. restit. and *D. raptator* are found in the Pacific Coast and Volcanic Belt provinces, respectively (Fig. 1E). This information demonstrates that the genus *Diguetinus* is distributed along the Mexican Pacific coast and, probably, even more widespread than previously documented. Consequently, further research under an integrative taxonomic approach will facilitate a comprehensive understanding of the phylogenetic relationships, evolutionary history, and biogeography of the potential species present in the central Mexican territory (Cokendolpher *et al.* 2021).

Finally, our phylogenetic results included a sequence of *Dalquestia formosa* (AF370833) (Giribet *et al.* 2001), which resulted in a paraphyletic relationship with respect to the Phalangiidae and Globipedidae clades. This could be due to the lack of taxa terminals sequenced in Globipedidae. It is crucial that future efforts to resolve the phylogenetic relationships of the family take this into account. In addition, there are two globipedid COI sequences, *Dalquestia grasshoffti* (JQ437182) and *Eurybunus brunneus* (JQ437181), generated by Hedin *et al.* (2012). However, these were excluded in the present study since they correspond to a different COI fragment analysed here and are therefore not alignable.

Sexual dimorphism in *Diguetinus*

Roewer (1910, 1912, 1923) used the sexually dimorphic character of legs I and III to recognize *Diguetinus* among relatives. However, in the analysed material of *D. raptator* from GDL-JAL, three adult males were observed with the described morphology and three without this morphology (legs I and III not modified) (Fig. 9). In Opiliones, several authors have employed the terms "alpha/beta" or "major/minor" to describe the dimorphic condition observed in males. This condition presents larger and more strongly armed males (classified as alpha or major) and smaller males similar to females with reduced or absent armor (beta or minor) (Kury 2008; Ferreira & Kury 2010; Zatz *et al.* 2011; Kury & Ferreira 2012; Buzatto & Machado 2014; Cruz-López *et al.* 2016; Townsend Jr. & Enzmann III 2018; Powell *et al.* 2020; Machado & Burns 2024). This morphological differentiation has been documented from males in the suborders Eupnoi and Laniatores, particularly in the families Neopilionidae Lawrence, 1931 (Taylor & Hunt 2009; Powell *et al.* 2020), Protolophidae Banks, 1893 (Tsurusaki & Cokendolpher 1990), Cosmetidae Koch, 1839 (Pérez-González & Vasconcelos 2003; Kury & Ferreira 2012), Triaenonychidae Sørensen, 1886 (Forster 1954), and Gonyleptidae Sundevall, 1833 (Pinto-Da-Rocha & Bragagnolo 2010), among others [see Buzatto & Machado (2014) table 1]. Buzatto & Machado (2014) described the Alternative Reproductive Tactics (ARTs) in Opiliones as a strategy to avoid complete exclusion from the mating pool. These tactics manifest as morphological dimorphisms in males, which promote sexual interactions such as competition and monopolization of territories, sperm competition, exclusive access to gametes, access to non-fertilized eggs, and competition for unfertilized eggs (see Buzatto & Machado (2014)).

The observations made in this study represent the first documentation of intrasexual dimorphism within the family Globipedidae. We show that males of *D. raptator* exhibit dimorphism manifested in the presence or absence of armature and swelling of the legs I and III (Fig. 9) and may indicate the potential existence of ARTs in *Diguetinus*. However, currently, there is a lack of comprehensive data on sexual behavior within the genus. Field observations of *Diguetinus* sp. revealed a scarcity of males, with only one male observed among at least 50 females, or in extreme cases, the absence of males for more than 70 females (Ochoa-Vázquez, obs. pers.). In our sampled locality of *D. raptator*, more than 20 female individuals were observed, along with three alpha males and three beta males.

In contrast, the male specimen of *D. spinulatus* stat. restit. exhibits a beta male morphology. Finding a single male individual provides the possibility that there are alpha forms in nature, as well as the close phylogenetic relationship with *D. raptator* and the observation by citizen scientists in the type locality, wich possibly represents the alpha form of the species, as evidenced by the armor of legs I and III (Fig. 5C).

In light of these observations, future studies aimed at elucidating the role of alpha/beta males in populations and the overall reproductive behaviour of these species are needed, focusing on behaviour in general and particularly sexual behaviour within the genus *Diguetinus*. Finally, considering the intrasexual dimorphism reported here, we suggest that sexual dimorphism as diagnostic taxonomic character is insufficient to define the genus *Diguetinus*, so its use should be taken with caution and not lead to misidentifications.

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REFERENCES

ACOSTA L. E., GONZÁLEZ A. P. & LÚCIA TOURINHO A. 2007. — Methods for taxonomic study, *in* PINTO-DA-ROCHA R., MACHADO G. & GIRIBET G. (eds), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, Massachusetts and London, England: 493-510.

ARRIAGA L., AGUILAR C., ESPINOSA D. & JIMÉNEZ R. 1997. — *Regionalización ecológica y biogeográfica de México*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D. F., 98 p.

ASTRIN J. J., HÖFER H., SPELDA J., HOLSTEIN J., BAYER S., HENDRICH L., HUBER B. A., KIELHORN K. H., KRAMMER H. J., LEMKE M., MONJE J. C., MORINIÈRE J., RULIK B., PETERSEN M., JANSSEN H. & MUSTER C. 2016. — Towards a DNA Barcode Reference Database for Spiders and Harvestmen of Germany. *PLoS One* 11 (9): 1-24. https://doi.org/10.1371/journal.pone.0162624

BANKS N. 1898. — Some Mexican Phalangida. *Journal of the New York Entomological Society* 6 (3): 181-182. https://www.biodiversitylibrary.org/part/84099

BANKS N. 1900. — New genera and species of American Phalangida. *Journal of the New York Entomological Society* 8 (3): 199-201. https://www.biodiversitylibrary.org/part/5559

BOYER S. L., KARAMAN I. & GIRIBET G. 2005. — The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. *Molecular Phylogenetics and Evolution* 36 (3): 554-567. https://doi.org/10.1016/j.ympev.2005.04.004

BRONN H. G. 1932. — *Dr. H.G. Bronn's Klassen und Ordnungen des Thier-Reichs: Wissenschaftlich dargestellt in Wort und Bild. Allgemeine Ubersicht der Klasse Arachnoidea (Spinnentiere)*. C. F. Winter, Leipzig und Heidelberg, 723 p. https://www.biodiversitylibrary.org/page/10455754

BUZATTO B. A. & MACHADO G. 2014. — Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behavioural Processes* 109 (Part A): 2-13. https://doi.org/10.1016/j.beproc.2014.06.008

COKENDOLPHER J. C. 1984a. — A new genus of North American harvestmen (Arachnida: Opiliones: Palpatores). *Festschrift for Walter W. Dalquest in Honor of His Sixty-sixth Birthday. Midwestern State University, Wichita Falls* xx+ (163): 27-43.

COKENDOLPHER J. C. 1984b. — Revision of the harvestman genus *Leptobunus* and dismantlement of the Leptobunidae (Arachnida: Opiliones: Palpatores). *Journal of the New York Entomological Society*: 371-402.

COKENDOLPHER J. C. & COKENDOLPHER J. E. 1984. — A new genus of harvestmen from Costa Rica with comments on the status of the Neotropical Phalangiinae (Opiliones, Phalangiidae). *Bulletin of the British Arachnological Society* 6 (4): 167-172. https://britishspiders.org.uk/system/files/library/060404.pdf

COKENDOLPHER J. C. & LEE V. 1993. — *Catalogue of the Cyphopalpatores and Bibliography of the Harvestmen (Arachnida, Opiliones) of Greenland, Canada, U.S.A., and Mexico*. James C. Cokendopher, Lubbock, Texas, 87 p.,

COKENDOLPHER J. C. & SISSOM W. 2000. — Further contributions to the study of *Dalquestia* (Opiliones: Sclerosomatidae). *Entomological News* 111 (4): 243-249. https://archive.org/details/biostor-3440

COKENDOLPHER J. C. & STOCKWELL S. A. 1986. — A new species of harvestman from Arizona (Arachnida: Opiliones: Palpatores: *Dalquestia*). *The Southwestern Naturalist* 31 (1): 49-53. https://doi.org/10.2307/3670959

COKENDOLPHER J. C., LUCIO-PALACIO C. R. & STAREGA W. 2021. — Redescription and Natural History of the Mexican harvestman *Diguetinus raptator* Roewer, 1912 (Opiliones: Globipedidae), type species of the genus. *Zootaxa* 4984 (1): 119-133. https://doi.org/10.11646/zootaxa.4984.1.12

CRAWFORD R. L. 1992. — Catalogue of the Genera and type species of the harvestman superfamily Phalangioidea (Arachnida). *Burke Museum Contributions in Antrhopology and Natural History* 8: 1-59.

CRUZ-LÓPEZ J. A., PROUD D. N. & PÉREZ-GONZÁLEZ A. 2016. — When troglomorphism dupes taxonomists: morphology and molecules reveal the first pyramidopid harvestman (Arachnida, Opiliones, Pyramidopidae) from the New World. *Zoological Journal of the Linnean Society* 177 (3): 602-620. https://doi.org/10.1111/zoj.12382

DARRIBA D., TABOADA G. L., DOALLO R. & POSADA D. 2012. — jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9 (8): 772-772. https://doi.org/10.1038/nmeth.2109

DERKARABETIAN S., BENAVIDES L. R. & GIRIBET G. 2019. — Sequence capture phylogenomics of historical ethanol-preserved museum specimens: Unlocking the rest of the vault. *Molecular ecology resources* 19 (6): 1531-1544. https://doi.org/10.1111/1755-0998.13072

DERKARABETIAN S., LORD A., ANGIER K., FRIGYIK E. & GIRIBET G. 2023. — An Opiliones-specific ultraconserved element probe set with a near-complete family-level phylogeny. *Molecular Phylogenetics and Evolution* 187 (107887): 1-13. https://doi.org/10.1016/j.ympev.2023.107887

DEWAARD J. R., RATNASINGHAM S., ZAKHAROV E. V., BORISENKO A. V., STEINKE D., TELFER A. C., PEREZ K. H. J., SONES J. E., YOUNG M. R., LEVESQUE-BEAUDIN V., SOBEL C. N., ABRAHAMYAN A., BESSONOV K., BLAGOEV G., DEWAARD S. L., HO C., IVANOVA N. V., LAYTON K. K. S., LU L., MANJUNATH R., MCKEOWN J. T. A., MILTON M. A., MISKIE R., MONKHOUSE N., NAIK S., NIKOLOVA N., PENTINSAARI M., PROSSER S. W. J., RADULOVICI A. E., STEINKE C., WARNE C. P. & HEBERT P. D. N. 2019. — A reference library for Canadian invertebrates with 1.5 million barcodes, voucher specimens, and DNA samples. *Scientific Data* 6 (1): https://doi.org/10.1038/s41597-019-0320-2

DI CAPORIACCO L. 1938. — Aracnidi del Messico, di Guatemala e Honduras britannico. *Istituto di Zoologia della R. Università di Firenze* 77 (3): 251-282.

FERREIRA C. P. & KURY A. B. 2010. — A review of *Roquettea*, with description of three new Brazilian species and notes on *Gryne* (Opiliones, Cosmetidae, Discosomaticinae). *Zoological Science* 27 (8): 697-708. https://doi.org/10.2108/zsj.27.697

FOLMER O., BLACK M., HOEH W., LUTZ R. & VRIJENHOEK R. 1994. — DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 5 (3): 294-299. https://pubmed.ncbi.nlm.nih.gov/7881515/

FORSTER R. R. 1954. — *The New Zealand harvestmen (sub-order Laniatores)*. Christchurch, New Zeland, Canterbury Museum bulletin, v. 2, 329 p., https://archive.org/details/dli.ernet.108525

GIRIBET G., EDGECOMBE G. D. & WHEELER W. C. 2001. — Arthro-

pod phylogeny based on eight molecular loci and morphology. *Nature* 413 (6852): 157-161. https://doi.org/10.1038/35093097

Giribet G., Edgecombe G. D., Wheeler W. C. & Babbitt C. 2002. — Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18 (1): 5-70. https://doi.org/10.1111/j.1096-0031.2002.tb00140.x

Giribet G., Vogt L., González A. P., Sharma P. & Kury A. B. 2010. — A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* 26 (4): 408-437. https://doi.org/10.1111/j.1096-0031.2009.00296.x

Goodnight C. J. & Goodnight M. L. 1942a. — New and little known Phalangida from Mexico. *American Museum novitates* (1163): 1-16. http://hdl.handle.net/2246/4796

Goodnight C. J. & Goodnight M. L. 1942b. — Phalangida from Mexico. *American Museum novitates* (1211): 1-18. https://www.biodiversitylibrary.org/bibliography/212220

Goodnight C. J. & Goodnight M. L. 1945. — Additional Phalangida from Mexico. *American Museum novitates* (1281): 18. http://hdl.handle.net/2246/3762

Goodnight C. J. & Goodnight M. L. 1947. — Phalangida from Tropical America. *Fieldiana: Zoology* 32 (1), https://www.biodiversitylibrary.org/part/30455

Gruber J. 1969. — Bemerkungen zur Genitalmorphologie und systematischen Stellung von *Metopilio australis* (Banks) (Phalangiidae: Opiliones, Arachnida). *Annalen des Naturhistorischen Museums in Wien* 73: 271-274. http://www.jstor.org/stable/41781736

Hedin M. & Thomas S. M. 2010. — Molecular systematics of eastern North American Phalangodidae (Arachnida: Opiliones: Laniatores), demonstrating convergent morphological evolution in caves. *Molecular Phylogenetics and Evolution* 54 (1): 107-121. https://doi.org/10.1016/j.ympev.2009.08.020

Hedin M., Tsurusaki N., Macías-Ordóñez R. & Shultz J. W. 2012. — Molecular systematics of sclerosomatid harvestmen (Opiliones, Phalangioidea, Sclerosomatidae): geography is better than taxonomy in predicting phylogeny. *Molecular Phylogenetics and Evolution* 62 (1): 224-236. https://doi.org/10.1016/j.ympev.2011.09.017

Huson D. H., Richter D. C., Rausch C., Dezulian T., Franz M. & Rupp R. 2007. — Dendroscope: An interactive viewer for large phylogenetic trees. *BMC bioinformatics* 8 (460): 1-6. https://doi.org/10.1186/1471-2105-8-460

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. — MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Molecular Biology and Evolution* 35 (6): 1547-1549. https://doi.org/10.1093/molbev/msy096

Kury A. B. 2008. — A review of *Soaresia* H. Soares, 1945, with the description of a new species from Serra da Mantiqueira, Brazil (Opiliones, Gonyleptidae, Pachylinae). *Zootaxa* 1687: 51-59. https://doi.org/10.5281/zenodo.180563

Kury A. B. & Cokendolpher J. C. 2000. — Opiliones, *in* Llorente-Bousquets J., González-Soriano E. & Papavero N. (eds), *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento*. Vol. 2. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO): 137-157.

Kury A. B. & Ferreira C. P. 2012. — Two new species of *Roquettea* Mello-Leitão, 1931 from northern Brazil (Opiliones: Laniatores: Cosmetidae). *Zootaxa* 3328: 35-46. https://doi.org/10.11646/zootaxa.3328.1.3

Kury A. B. & Cokendolpher J. C. 2020. — A new family from the New World (Eupnoi: Phalangioidea), *in* Kury A. B., Mendes A. C., Cardoso L., Kury M. S. & Granado A. d. A. (eds), *WCO-Lite: online world catalogue of harvestmen (Arachnida, Opiliones): Version 1.0—checklist of all valid nomina in Opiliones with authors and dates of publication up to 2018*. do autor, Rio de Janeiro: 52-53. https://doi.org/10.5281/zenodo.4025287.

Kury A. B., Mendes A. C., Cardoso L., Kury M. S., Granado A. A., Yoder M. J. & Kury I. S. 2021. — WCO-Lite version 1.1: an online nomenclatural catalogue of harvestmen of the world (Arachnida, Opiliones) curated in TaxonWorks. *Zootaxa* 4908 (3): 447-450. https://doi.org/10.11646/zootaxa.4908.3.10

Machado G. & Burns M. 2024. — Reproductive biology of harvestmen (Arachnida: Opiliones): a review of a rapidly evolving research field. *Current Zoology* 70 (1): 115-135. https://doi.org/10.1093/cz/zoac102

Masta S. E. & Boore J. L. 2008. — Parallel Evolution of Truncated Transfer RNA Genes in Arachnid Mitochondrial Genomes. *Molecular Biology and Evolution* 25 (5): 949-959. https://doi.org/10.1093/molbev/msn051

Pérez-González A. & Vasconcelos E. 2003. — A new species of *Arucillus* Silhavy, 1971 from the Dominican Republic (Opiliones: Laniatores: Cosmetidae). *Revista Ibérica de Aracnología* (7): 135-140. http://sea-entomologia.org/PDF/RIA_7/R07-017-135.pdf

Pinto-Da-Rocha R. & Bragagnolo C. 2010. — Review of the Brazilian Atlantic Rainforest harvestman *Longiperna* (Opiliones: Gonyleptidae: Mitobatinae). *Zoologia* 27 (6): 993-1007. https://doi.org/10.1590/s1984-46702010000600023

Posada D. & Buckley T. R. 2004. — Model Selection and Model Averaging in Phylogenetics: Advantages of Akaike Information Criterion and Bayesian Approaches Over Likelihood Ratio Tests. *Systematic Biology* 53 (5): 793-808. https://doi.org/10.1080/10635150490522304

Powell E. C., Painting C. J., Hickey A. J. & Holwell G. I. 2020. — Defining an intrasexual male weapon polymorphism in a New Zealand harvestman (Opiliones: Neopilionidae) using traditional and geometric morphometrics. *Biological Journal of the Linnean Society* 130 (2): 395-409. https://doi.org/10.1093/biolinnean/blaa040

Prendini L., Weygoldt P. & Wheeler W. C. 2005. — Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): Evidence from behaviour, morphology and DNA. *Organisms Diversity & Evolution* 5 (3): 203-236. https://doi.org/https://doi.org/10.1016/j.ode.2004.12.004

Rodriguez A. L., Townsend V. R., Jr. & Proud D. N. 2014. — Comparative Study of the Microanatomy of Four Species of Harvestmen (Opiliones, Eupnoi). *Annals of the Entomological Society of America* 107 (2): 496-509. https://doi.org/10.1603/an13109

Roewer C.-F. 1910. — Revision der Opiliones Plagiostethi (= Opiliones Palpatores). I. Teil: Familie der Phalangiidae. (Subfamilien: Gagrellini, Liobunini, Leptobunini.). *Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein in Hamburg* 19 (4): 1-294.

Roewer C.-F. 1911. — Übersicht der Genera der Subfamilie der Phalangiini der Opiliones Palpatores nebst Beschreibung einiger neuer Gattungen und Arten. *Archiv für Naturgeschichte* 77: 1-106. https://www.biodiversitylibrary.org/part/118943

Roewer C.-F. 1912. — Revision der Opiliones Palpatores (= Opiliones Plagiostethi). II. Teil: Familie der Phalangiidae. (Subfamilien: Sclerosomini, Oligolophini, Phalangiini). *Abhandlungen aus dem Gebiete der Naturwissenschaften, herausgegeben vom Naturwissenschaftlichen Verein in Hamburg* 20 (1): 1-295.

Roewer C.-F. 1923. — *Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones*. Gustav Fischer, Jena.

Roewer C.-F. 1956. — Uber Phalangiinae (Phalangiidae, Opiliones Palpatores).(Weitere Weberknechte XIX). *Senckenbergiana biol.* 37: 247-318.

Sharma P. & Giribet G. 2009. — Sandokanid phylogeny based on eight molecular markers—the evolution of a southeast Asian endemic family of Laniatores (Arachnida, Opiliones). *Molecular Phylogenetics and Evolution* 52 (2): 432-447. https://doi.org/10.1016/j.ympev.2009.03.013

Taylor C. K. & Hunt G. S. 2009. — New genus of Megalopsalidinae (Arachnida: Opiliones: Monoscutidae) from north-eastern Australia. *Zootaxa* 2130 (1): 41-59. https://doi.org/10.11646/zootaxa.2130.1.4

TOWNSEND JR. V. R. & ENZMANN III B. P. 2018. — Ontogenetic variation in the sensory structures on the pedipalps of cosmetid harvestmen (Arachnida, Opiliones, Laniatores). *Journal of Morphology* 279 (1): 109-131. https://doi.org/https://doi.org/10.1002/jmor.20758

TSURUSAKI N. & COKENDOLPHER J. C. 1990. — Chromosomes of sixteen species of harvestmen (Arachnida, Opiliones, Caddidae and Phalangiidae). *Journal of Arachnology*: 151-166.

WEIDNER H. V. 1959. — Die entomologischen Sammlungen des Zoologischen Staatsinstituts und Zoologischen Museums Hamburg, I. Pararthropoda und Chelicerata, I. *Mitteilungen Hamburger Zoologischen Museums und Instituts* 57: 89-142.

WIJNHOVEN H. 2013. — Sensory structures and sexual dimorphism in the harvestman *Dicranopalpus ramosus* (Arachnida: Opiliones). *Arachnologische Mitteilungen* 46: 27-46. https://doi.org/10.5431/aramit4605

ZATZ C., WERNECK R. M., MACÍAS-ORDÓÑEZ R. & MACHADO G. 2011. — Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). *Behavioral Ecology and Sociobiology* 65: 995-1005. https://doi.org/10.1007/s00265-010-1103-0

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