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Looks are deceiving: a cladistic analysis, three new species, and a new diagnosis of *Paravima* Caporiacco, 1951 (Opiliones: Agoristenidae)

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Abstract

A morphological cladistic analysis, consisting of 45 terminals and 58 characters was performed to evaluate the monophyly of the genus *Paravima* Caporiacco, 1951, and its relationship to other Leiosteninae. The analysis resulted in two most parsimonious trees, all recovering *Paravima* as monophyletic with the inclusion of two species formerly described in *Avima* Roewer, 1949, therefore, the following nomenclatural acts are herein proposed: *Paravima plana* (Goodnight & Goodnight, 1949) **comb. nov.**, and *Paravima quirozi* (González-Sponga, 1981) **comb. nov.**, *Avima vigirima* (Villarreal-M & Rodríguez-Manzanilla, 2003) is here considered as a junior subjective synonym of *P. quirozi* (González-Sponga, 1981) **comb. nov.**, *Paravima acanthoconus* Villarreal-Manzanilla & DoNascimiento, 2005 is here considered as a junior subjective synonym of *Paravima propespelunca* González-Sponga, 1987, and *Paravima flumencaurimarensis* González-Sponga, 1987 is here considered as a junior subjective synonym of *Paravima goodnightorum* Caporiacco, 1951. Additionally, three new species are described: *P. lokura* **sp. nov.** (Tamá National Natural Park, Norte de Santander department) and *P. magistri* **sp. nov.** (Los Tunos Natural Reserve, Cundinamarca department), both from Colombia; and *P. totoro* **sp. nov.** (Henri Pittier National Park, Aragua state) from Venezuela. Finally, an emended generic diagnosis, a key for all the species, and a distributional map are presented.

Keywords

Colombia, Cordillera de la Costa, harvestmen, monophyly, phylogeny, Venezuela

1. Introduction

The Neotropical family Agoristenidae Šilhavý, 1973, is an uncommon albeit diverse taxon (26 gen., 80 spp.), as is reflected for the small number of specimens deposited in natural collections, divided into three subfamilies, the most diverse being Leiosteninae Šilhavý, 1973, from northern South America (13 gen., 62 spp.) (Villarreal & García 2021). This group is distributed mainly in the Andes, Amazon, and Caribbean regions, spread across Brazil, Colombia, French Guiana, Guyana, Peru, Suriname, Trinidad and Tobago, and Venezuela (Porto & Colmena-

res 2014; García & Villarreal 2020: fig. 9). Except for *Avima* Roewer, 1949, most of the genera of Agoristenidae are not very diverse, many of them being monotypic (14 gen.), and the phylogenetic relationships between them are poorly understood. Only three phylogenetic analyzes have been conducted with this objective (Kury 1997, Pinto-da-Rocha & Hara 2009, Villarreal & García 2021), however, the monophyly of its genera has not been tested. In this work, a cladistic analysis of *Paravima* Caporiacco, 1951 is performed, to test its monophyly and evaluate its systematic position within the subfamily.

Paravima, as currently diagnosed, is a small group of six species associated with forests in the central region of the Cordillera de la Costa in Venezuela. The genus was described by Caporiacco (1951) to accommodate the single species *Paravima goodnightorum* Caporiacco, 1951, from El Junquito, Venezuela. González-Sponga (1987) in his most comprehensive work on Leiosteninae, described the remaining species of the genus: *Paravima flumencaurimarensis* González-Sponga, 1987, *P. locumida* González-Sponga, 1987, *P. morritomacairensis* González-Sponga, 1987, and *P. propespelunca* González-Sponga, 1987, except *P. acanthoconus* Villarreal-Manzanilla & DoNascimiento, 2005, which was described 18 years later (Villarreal-M. and DoNascimiento 2005).

On the other hand, *Avima* is the most diverse genus of Leiosteninae, however, it is most likely an amalgam of unrelated lineages as partially suggested by Villarreal and García (2021), Garcia et al. (2022a, b), and the present analysis. The lack of ornamentation in area III has been referred to as the main generic diagnostic character of *Avima* (see García et al 2022a), ignoring a significant amount of hidden information in the morphological heterogeneity of the group. Some species currently located in *Avima* exhibit some aspects of external morphology (e.g. DS shape or eyes position) and genital morphology (e.g. stylus and lamina parva shape) that caught our attention, making us question its generic position. In addition, when compared to the generic nucleus recently defined by García et al (2022a) for *Avima*, it raises suspicions about a possible relationship between these species and those currently found in *Paravima* instead of being related to the *Avima* core. *Avima plana* (Goodnight & Goodnight, 1949) was described from the Cordillera de la Costa (Venezuela), and later erroneously recorded to Cueva de Benito (Mérida state), in the Venezuelan Andes, by Rambla (1978) (González-Sponga 1987; Kury 2003). González-Sponga (1981) described *Avima quirozi* González-Sponga, 1981 from Yaracuy state (Venezuela), and Villarreal-M. and Rodríguez-Manzanilla (2003) described *Avima vigirima* Villarreal-M. & Rodríguez-Manzanilla, 2003 from Carabobo state (Venezuela), and commented about the possible relationship between these three species.

In the present work, a phylogenetic analysis based on morphological characters was carried out. The monophyly of *Paravima* was tested and the relationship between the three previously mentioned *Avima* species and the genus *Paravima* was evaluated. So, after two new combinations, three synonyms, and the description of three new species, the genus *Paravima* passes from six to nine species, all of them included in an identification key and an updated geographical distribution map.

2. Material and Methods

Individuals of the species were imaged from varied sources. We mostly used a Nikon 5200, a Canon PowerShot S3IS, and a Sony Cybershot DSC-V1 camera attached to a stereomicroscope. Multiple images of each selected specimen at different focal planes were combined with Zerene Stacker of CombineZP (Hadley 2015). The holotype of *Paravima magistri* **sp. nov.** was photographed with a Leica M205C stereoscope attached to a Leica DFC450 digital camera, and combined with Leica Application Suite (LAS) software version 4.6.2. All resultant photographs were posteriorly edited in Photoshop CC 2014 software. All measurements are in mm unless otherwise noted.

The male genitalia illustrated with Scanning Electron Microscopy (SEM) was dehydrated with Critical Point Drying (CPD), sputter-coated with gold-palladium, and examined with a JEOL JSM-6390LV Scanning Electron Microscope at the Center for Scanning Electron Microscopy of Museu Nacional de Rio de Janeiro (MNRJ), with an accelerating voltage of 10 kV. Drawings were made using a stereomicroscope with camera lucida, and digitized with Inkscape 0.91 software. Some penis drawings have no scale. Color descriptions use the standard names of the 267 Color Centroids of the NBS/IBCC Color System as named in Centore (2016) and color description refers to specimens preserved in ethyl alcohol.

The distribution map was made with Quantum GIS 2.18.19 software (QGIS team 2020). The references to biogeographic provinces in the text and map follow the biogeographic regionalization proposed by Morrone et al. (2022). Geographic coordinates have been transcribed verbatim from the labels and are in different formats. When no original coordinates were available, those were estimated using Google Maps and placed between square brackets.

Patterns of description follow Villarreal and García (2021). Terminology for the integumentary ornamentation follows DaSilva and Gnaspini (2010). Chaetotaxy of penis lamina parva and truncus follows Kury and Villarreal (2015). Dorsal scutum outline types follow Kury and Medrano (2016), with the modifications explained in Villarreal and García (2021). The complementary descriptions of the species do not repeat the generic characteristics.

Remark: The material marked with an asterisk (*) was destroyed in the fire at the National Museum / Federal University of Rio de Janeiro, Brazil (September 2018). There is no formal impediment per ICZN rules to describe a species whose holotype was lost before the publication of the description (Krell and Marshall 2017).

2.1. Abbreviations

AL = Abdomen length, **AW** = Abdomen width, **BaCh** = basichelicerite, **Ch** = chelicera, **CL** = Carapace length, **ctr** = character, **CW** = Carapace width, **DP** = Dorsal process, **DS** = Dorsal scutum, **Fe** = Femur, **G-S** = González-Sponga, **LP** = Lamina parva, **MS** = Macrosetae of penis, **Pa** = Patella, **St** = Stylus, **Ta** = Tarsus, **Ti** = Tibia, **Tr** = Trochanter.

Repositories: Brazil • **MNRJ** = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro. • Colombia • **ICN** = Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogota; **MUSENUV** = Museo de Entomología de la Universidad del Valle, Cali. • Venezuela • **MAGS** = Manuel Ángel González Sponga collection (donated to MIZA collection); **MBUCV** = Museo de Biología, Universidad Central de Venezuela, Caracas; **MCNC** = Fundación Museo de Ciencias Naturales de Caracas, Caracas); **MIZA** = Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez", Maracay.

2.2. Character sampling

The phylogenetic analysis was performed using 39 somatic and 19 genital characters. All the logical descriptions of the characters were written according to the recommendations by Sereno (2007). Characters were mainly based on Villarreal and García (2021), with the addition of 11 characters and some adjustments according to the newly included taxa.

The matrix, including 45 terminal taxa (25 ingroup and 20 outgroup) (Table S1), is a modified version of that given by Villarreal and García (2021), and was built in Mesquite v. 3.2 (Maddison and Maddison 2017). The following species were included in the present work because (1) they are species currently in the genus *Avima*, but morphologically similar to the ingroup studied here (2) they are species of *Paravima*, so they are part of the ingroup (3) they have recently been described under *Avima*, not necessarily morphologically similar to our ingroup, but described under standards that allow their inclusion in the analysis: *Avima albiornata* (Goodnight & Goodnight, 1947), *Avima plana*, *Avima quirozi*, *Avima tuttifrutti* García & Pastrana, 2021, *Avima vigirima*, *Avima wayuunaiki* García, González & Gutiérrez, 2022, *Paravima acanthoconus*, *P. flumencaurimarensis*, *P. locumida*, *P. lokura* **sp. nov.**, *P. magistri* **sp. nov.**, *P. morritomacairensis*, and *P. totoro* **sp. nov.**

2.3. Phylogenetic analyses

Parsimony analyses were performed in TNT v.1.5 (Goloboff and Catalano 2016), using heuristic methods ("traditional search") under implied weights (Goloboff et al. 2008) and equal weights. Tree bisection-reconnection (TBR) and the following setting for starting trees (mult = tbr replic 1000 hold 1000) were used. Branches with no possible support were collapsed (collapsing "strict (= nelsen)") during and after the tree search. All characters were unordered and the multistate characters were treated as non-additive (Fitch 1971). The searches under implied weighting (IW) were run with the concavity constant (K) set to 1–500 (piwe = 1; mult = tbr replic 1000 hold 1000). Implied weighting in TNT weights the characters according to a concave function of homoplasy (K) that is set by the user and negatively correlates with how strongly homoplastic characters are down-weighted (Goloboff 1993). In this study, we used a TNT script (setk.run) written by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucumán, Argentina) to calculate the value for the concavity constant K, which best matches our data (for details see Goloboff et al. 2008), and additionally, four searches were conducted with TNT using IW with K concavity values of 1, 2, 4 and 8. In parallel, an analysis was conducted using equal weights (EW) and the results between both are compared. The characters were studied and optimized, and trees were edited in WinClada 10.00.08 (Nixon 2002). All discussion of the cladistic analyses was made under ACCTRAN optimization as a way to preserve the primary homology (de Pinna 1991). To establish group support, bremer support (Bremer 1994), relative bremer support (Goloboff & Farris 2001), and bootstrap values were calculated using TNT.

3. Results

3.1. Character list

The data matrix (Table S1) consists of 45 taxa and 58 characters. The numbers in parentheses refer to the character numbering in Villarreal & García (2021). DS = Dorsal scutum; LP = Lamina parva; MS = Macrosetae.

1. DS, outline shape: **(0)** Zeta (Kury and Medrano 2016: figs 2e–i); **(1)** Epsilon (Kury and Medrano 2016: figs 2b–d); **(2)** Eta (Kury and Medrano 2016: figs 2j–n); **(3)** Beta (Kury and Medrano 2016: figs 1i–k); **(4)** Gamma (Kury and Medrano 2016: figs 1p–s); **(5)** Iota (Kury and Medrano 2016: figs 2s–t).
2. DS, outline shape, Epsilon type, kind: **(0)** Epsilon type 1 (Kury and Medrano 2016: figs 2b); **(1)** Epsilon type 2 (Kury and Medrano 2016: figs 2c); **(2)** Epsilon type 3 (Fig. 1A); **(3)** Epsilon type 4 (Villarreal & García 2021: fig. 4A).
3. DS, posterior margin: **(0)** almost same width as anterior margin (García and Kury 2020: fig. 3A); **(1)** posterior border distinctly wider than anterior (Fig. 2A, B).
4. DS, scutal lateral margins, texture (3): **(0)** smooth or finely granular (Pinto-da-Rocha and Hara 2009: fig. 1A); **(1)** intensely wrinkled (García and Villarreal, 2020: fig. 1b).

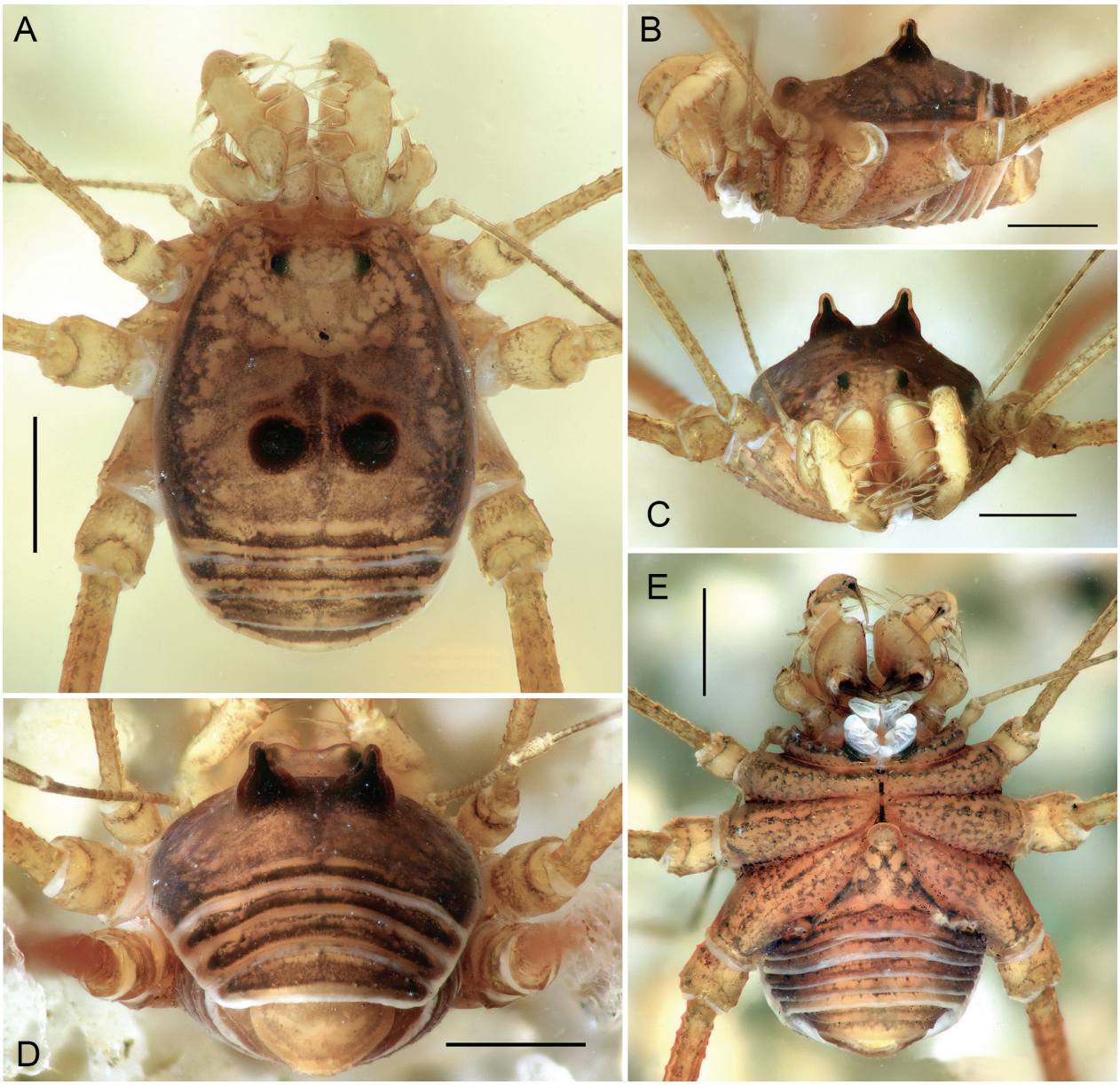

Figure 1. *Paravima flumencaurimarensis* González-Sponga, 1987 (MAGS 1115, MIZA 0105921) female. Habitus: **A** Dorsal view; **B** lateral view; **C** anterior view; **D** posterior view; **E** ventral view. Scale bars: 1 mm.

5. DS, tegument, texture (4): **(0)** finely granular (Figs 1A, 2B); **(1)** densely covered with large granules (Villarreal & García 2021: figs 4A, 5A).

6. DS, posterior margin, armature (5): **(0)** unarmed (Fig. 3A–D); **(1)** with a pair of spines (Villarreal & García 2021: figs 4A); **(2)** one tubercle (Cruz-López and Francke 2017: figs 9, 13).

7. DS, carapace, ocularium, interocular distance, proportion to carapace width: **(0)** 1/3 of carapace width (Šilhavý 1973: fig. 1); **(1)** 1/4 of carapace width (García et al 2022b: fig. 1B); **(2)** 1/2 of carapace width (Fig. 4A); **(3)** greater than 60 % of carapace width (Pinto-da-Rocha 1997: fig. 1).

8. DS, carapace, placement of the eyes (6): **(0)** directly on the ocularium (Fig. 5A, B, D, E); **(1)** on a separate protuberance (Pinto-da-Rocha 1997: fig. 1).

9. DS, carapace, ocularium, shape (7): **(0)** with median depression (saddle-shaped) (Fig. 2E); **(1)** domed (González-Sponga 1987: figs 539, 540); **(2)** in form of a forward oblique very high protuberance (Kury 2012: fig. 5).

10. DS, carapace, ocularium, armature (8): **(0)** unarmed (Fig. 6A, B); **(1)** with a pair of spines (Villarreal & García 2021: figs 5B, C); **(2)** with single spine (Yamaguti and Pinto-da-Rocha 2009: fig. 24); **(3)** with granules (Pinto-da-Rocha and Hara 2009: figs 1A, C).

11. DS, carapace, ocularium, placement (9): **(0)** middle of carapace (Villarreal & García 2021: fig. 4A); **(1)** located in the anterior half of the carapace (Fig. 6A, B).

12. DS, carapace length (10): **(0)** shorter than opisthosoma (at least 1/2 times) (Figs 1A, 7B, C, 8A, B); **(1)** equal to opisthosoma (Kury 2012: figs 4, 5).

13. DS, lateral margins, yellow-greenish spots (11): **(0)** absent (Figs 1A–D, 7A–C, E); **(1)** present (García and Villarreal, 2020: fig. 2b).

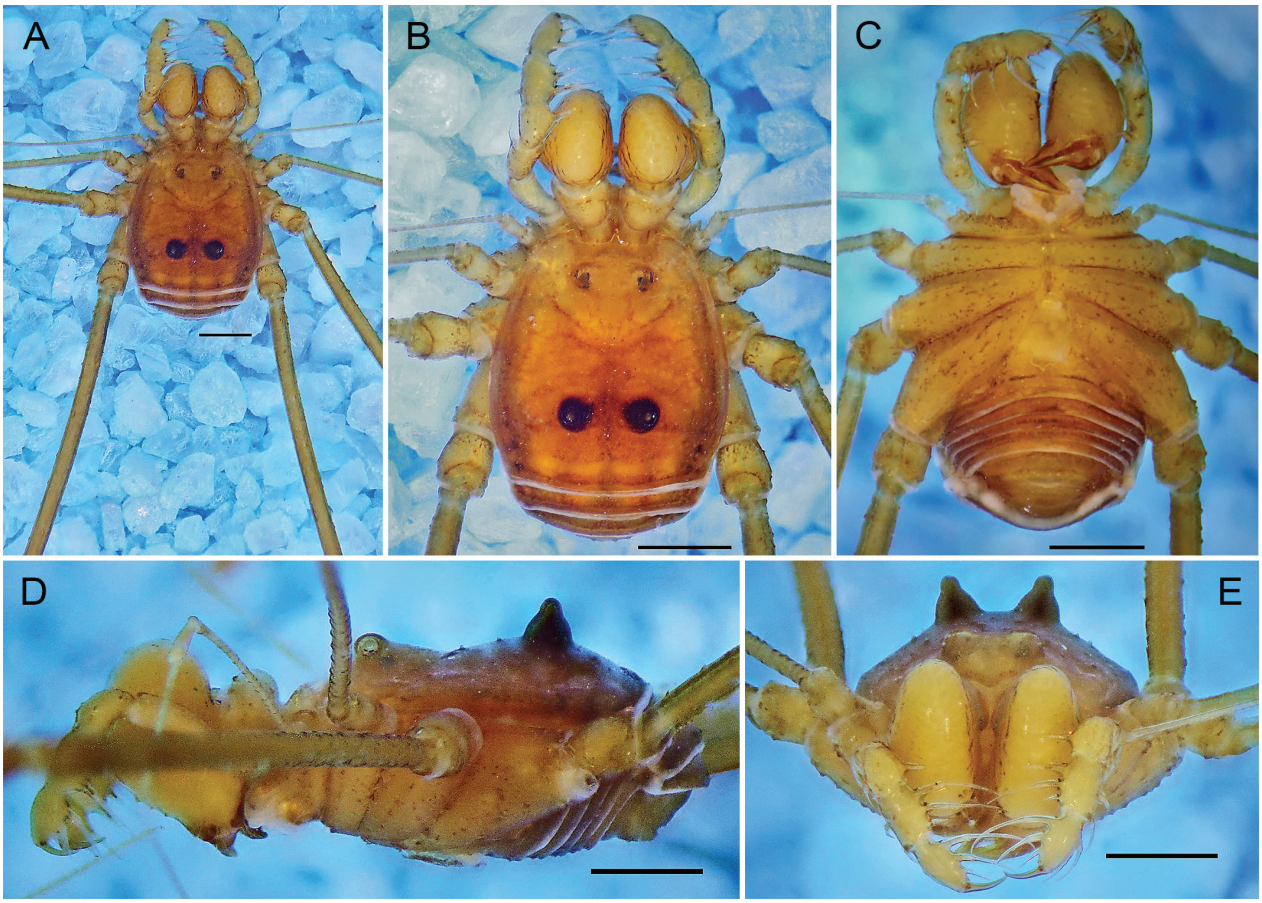

Figure 2. *Paravima goodnightorum* Caporiacco, 1951 (MNRJ 18301*) male. Habitus: **A** Panoramic view; **B** dorsal view; **C** ventral view; **D** lateral view; **E** anterior view. Scale bars: 1 mm.

14. DS, scutal areas, brilliant yellowish spots (12): **(0)** absent (Figs 1A–D, 7A–C, E); **(1)** present (García and Villarreal, 2020: fig. 3b).

15. DS, mesotergum, scutal area I (13): **(0)** divided by median longitudinal groove (Fig. 8A); **(1)** undivided (Kury 2012: fig. 4).

16. DS, mesotergum, scutal area II, paired spines (14): **(0)** absent (Figs 6A, B, 7B, C, 9A–C); **(1)** present (González-Sponga 1987: figs 573, 574).

17. DS, mesotergum, scutal area III, armature (15): **(0)** absent (Fig. 10A–D); **(1)** present (Figs 5A, B, D, E, 7C, E, 11A–C, 12).

18. DS, mesotergum, scutal area IV, armature (16): **(0)** unarmed (Figs 11A, D, 13 A, E); **(1)** armed with a pair of spines (Šilhavý 1973: fig. 1); **(2)** with a dorsal rounded prominence (García and Pastrana-M 2021: fig. 2B).

19. DS, light longitudinal medial stripe (17): **(0)** absent (Fig. 1A); **(1)** present (Šilhavý 1973: fig. 43).

20. DS, mesotergum, area II invading area I (18): **(0)** absent (Fig. 1A); **(1)** present (Villarreal et al. 2021: fig. 9).

21. DS, mesotergum, scutal area III, spines, shape; **(0)** slender, acute spines (García and Villarreal, 2020: figs 3b, d); **(1)** dome (Šilhavý 1973: fig. 14; Figs 14C, E, 15A, B); **(2)** conical wide tubercles (Fig. 5D, E); **(3)** mammilliform (Fig. 2D, E); **(4)** conical high tubercles (García and Villarreal 2020: fig. 1d).

22. DS, mesotergum, scutal area III, variation between base and tip of the mammilliform tubercles: **(0)** gradual (Fig. 9B, C); **(1)** abrupt (Fig. 1B, C).

23. DS, mesotergum, scutal area III, spines (15): **(0)** separated (Fig. 7E); **(1)** together or fused (García and Villarreal 2020: figs 1d, 2d, e).

24. Opisthosoma, free tergite II (19): **(0)** unarmed (Fig. 6A); **(1)** two large tubercles (Šilhavý 1973: fig. 18); **(2)** with three large tubercles (Villarreal & García 2021: fig. 4A).

25. Opisthosoma, free tergite III (20): **(0)** unarmed (Fig. 6A); **(1)** two large tubercles (Šilhavý 1973: fig. 18); **(2)** with three large tubercles (Villarreal & García 2021: fig. 4A).

26. Chelicera, hand, dimorphism (21): **(0)** sexually dimorphic, swollen in male (García and Kury 2017: figs 2d, e); **(1)** dimorphism attenuate (García and Villarreal 2020: figs 1, 7); **(2)** monomorphic, chelicerae similar in both sexes (Šilhavý 1973: fig. 2).

27. Pedipalps, articles (tibia and tarsus), constitution (22): **(0)** stout (Villarreal & García 2021: fig. 6E, F); **(1)** slender (Figs 8E, 10B).

28. Pedipalps, femur, distal inner spine (23); **(0)** present (García and Villarreal 2020: fig. 4c); **(1)** absent (Pinto-da-Rocha and Hara 2009: figs 2E, G).

29. Pedipalps, femur, spines in ventral row, size (24): **(0)** short (Pinto-da-Rocha and Hara 2009: figs 1D, E); **(1)** long (García and Kury 2020: fig. 3E).

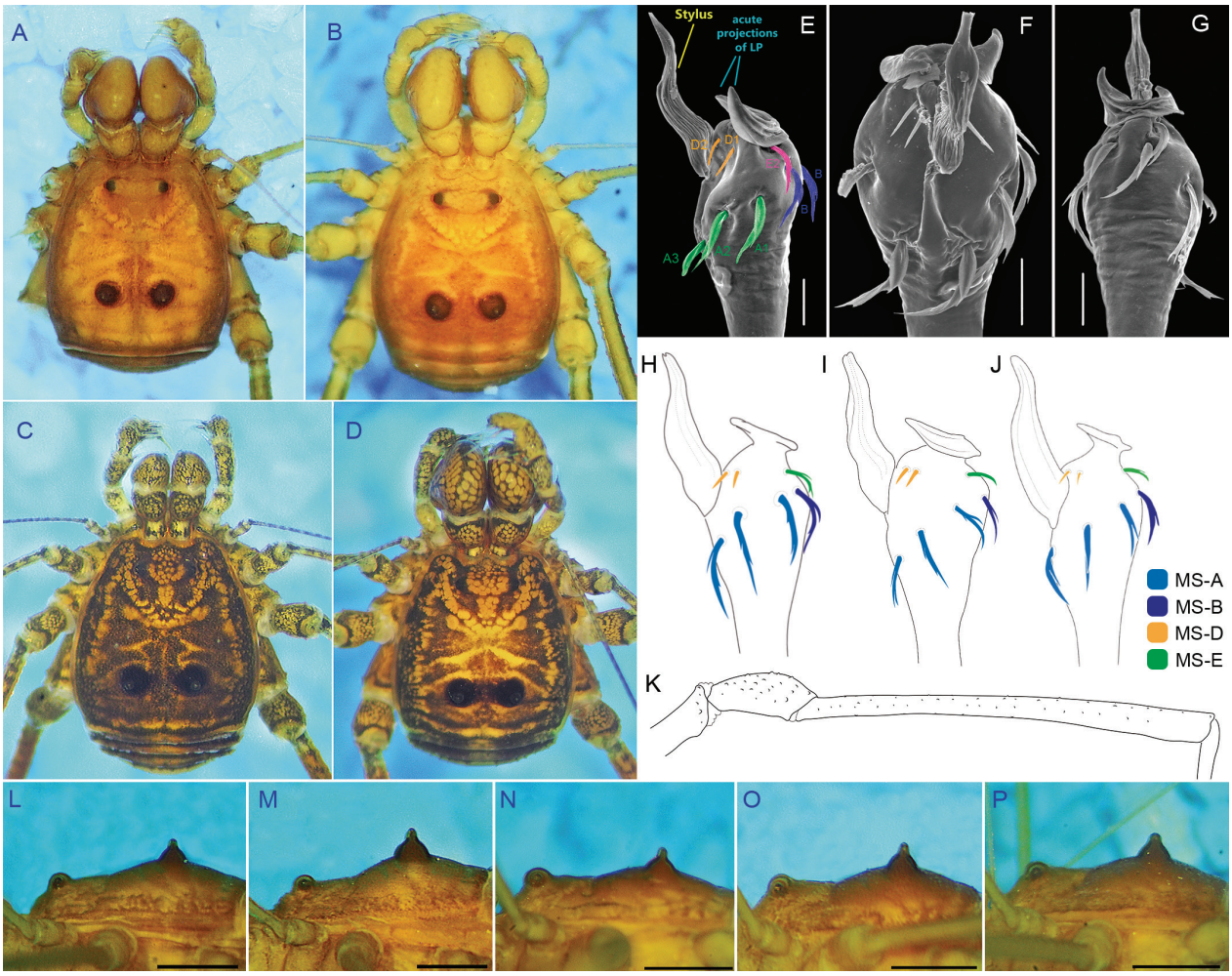

Figure 3. Habitus, male genitalia and leg of *Paravima goodnightorum* Caporiacco, 1951. Males, dorsal view: **A** From Caurimare river, Caracas (MIZA 0105918, paratype of *P. flumencaurimarensis*); **B** from Colonia Tovar, Aragua state (MIZA 0105920, paratype); **C** from Cerro El Volcán, south of Caracas, Miranda state (MIZA 0105904); **D** from El Limón, near Colonia Tovar, La Guaira state (MIZA 0105911). Apical portion of the penis under SEM (MNRJ 18301*): **E** Lateral view; **F** dorsal view; **G** ventral view. Drawings of the apical part of the penis under optical microscopy: **H** From El Volcán (MIZA 0105904); **I** paratype of *P. flumencaurimarensis* (MIZA 0105918); **J** paratype from Colonia Tovar, Aragua state (MIZA 0105920); **K** leg IV, patella and tibia, retrolateral view (MIZA 0105918); **L–P** variation of the paramedian tubercles of area III, in lateral view: males (L, M) and females (N–P) (MAGS 237). Macrosetae A–E follows the Kury and Villarreal (2015) system. Abbreviations: LP = Lamina Parva, MS = Macrosetae. Scale bars: E–G = 50 µm; A–D, H–K = not scaled. SEM photos courtesy of Adriano B. Kury.

30. Pedipalps, patella, median spine (25): **(0)** present (Fig. 8E); **(1)** absent (Kury and Villarreal 2015: fig. 18c, d).

31. Leg I, thickness (26): **(0)** normal thickness (slightly slender than the other legs) (Villarreal et al 2019: fig. 2a); **(1)** filiform (extremely slender) (Fig. 2A–C).

32. Leg I, coxa, anterior ventral apophysis (27): **(0)** absent (Šilhavý 1973: fig. 41); **(1)** present (Fig. 6C; González-Sponga 1987: figs 568, 595).

33. Leg I, metatarsus, row of modified setae (28): **(0)** absent (González-Sponga 1987: fig. 7); **(1)** present-character used in Kury and Villarreal 2015 and Villarreal and García 2021 analyses, but never illustrated[1].

34. Leg I, tarsus, basitarsus (29): **(0)** swollen, never illustrated[2]; **(1)** not swollen, same thickness as the others (Villarreal et al. 2019: fig. 4k, l).

35. Legs I, tarsus, distitarsus (30): **(0)** with three joints (Kury 2014: fig. 23E); **(1)** with two joints (Kury 2004: figs 6–7).

36. Legs II–IV, femora and tibiae, longitudinal rows of conspicuous tubercles (31): **(0)** absent (Figs 7A, 10A); **(1)** present (Villarreal and García 2021: figs 3A, 4D–G).

1 The modified metatarsal setae found in Nomoclastidae are a synapomorphy to this family. Their variation and morphology are currently being studied by the second author and other colleagues. As there are no existing illustrations or photographs in the literature, we have refrained from presenting any new information prior to publication.

2 This character is autapomorphic to Ahotta, which is part of the outgroup and not the main focus of our study. Despite the lack of illustrations in the literature, it has been previously used. However, due to unavailability of some specimens in the collections we studied, we were unable to examine them. Nevertheless, we have decided to follow the published matrix proposed by previous authors for this character, as it is self-explanatory.

37. Leg IV, tarsal process (32): **(0)** absent (García and Kury 2020: fig. 3H); **(1)** present (Villarreal et al. 2019: figs 6a, c).
38. Leg IV, ratio femur length / DS length: (0) short (about 1) (Kury 2012: fig. 4); (1) between 1.6 and 3.2 (Villarreal and García 2021: fig. 3A); (2) more than 3.7 (Fig. 12A).
39. Penis, truncus, LP, shape (33): **(0)** as a plate (Kury and Villarreal 2015: fig. 8); **(1)** as two-horned (Fig. 15E–G).
40. Penis, LP, corners, shape (34): **(0)** rounded (García et al 2022b: fig. 3); **(1)** not curved, not differentiated sharp tips (Fig. 6G); **(2)** curved differentiated tips (Šilhavý 1973: fig. 6).
41. Penis, stylus, shape (35); **(0)** straight (Kury and Villarreal 2015: fig. 2E); **(1)** sinuous (Fig. 3E).
42. Penis, stylus, longitudinal dorsal keel (36): **(0)** absent (Figs 3A, 6G); **(1)** present (García and Villarreal 2020: figs 5a, b, f).
43. Penis, stylus, dorsal process (37): **(0)** absent (Fig. 6G); **(1)** present (González-Sponga 1987: fig. 577).
44. Penis, stylus, distal region, ventral process (38): **(0)** absent (Fig. 3H–J); **(1)** present (Kury 2019: fig. 1).
45. Penis, stylus, stylar caps (39): **(0)** absent (Kury and Villarreal 2015: fig. 2); **(1)** present (Villarreal et al. 2015: figs 12C–E).
46. Penis, stylus, tip: **(0)** in the same direction of the stylus (Fig. 3E); **(1)** angled dorsally (González-Sponga 1987: fig. 577); **(2)** dorsally curved (García et al 2022b: figs 3C, E).
47. Penis, LP, base: **(0)** enlarged (Kury and Villarreal 2015: fig. 2F); **(1)** short (Fig. 6F, G).
48. Penis, LP, subdistal depression in lateral view: **(0)** absent (Kury and Villarreal 2015: figs 2B, 2E); **(1)** present (Figs 6G, 8H).
49. Penis, MS-A/ MS-B, size (40): **(0)** erect (Kury and Villarreal 2015: figs 11 A–C); **(1)** bowed (Fig. 3E–G).
50. Penis, MS-A, quantity: **(0)** three pairs (Fig. 6); **(1)** two pairs (Kury and Villarreal 2015: fig. 2).
51. Penis, size of MS-A/B branches (42): **(0)** minute (almost inconspicuous) (Villarreal and García 2021: fig. 8A); **(1)** short (García and Villarreal 2020: figs 5a, b); **(2)** at least one very long (Kury and Villarreal 2015: figs 2A–C).
52. Penis, MS-A/MS-B, structure (41): **(0)** uniramous (Kury and Villarreal 2015: fig. 3); **(1)** branched (Kury and Villarreal 2015: figs 2A–C).
53. Penis, MS-C (43): **(0)** present (Kury and Villarreal 2015: fig. 3); **(1)** absent (Figs 3E, H–J, 6G).
54. Penis, gap between MS-C/MS-A (44): **(0)** absent (Fig. 5E); **(1)** present (Kury and Villarreal 2015: figs 9D–E).
55. Penis, MS-E2, structure (45): **(0)** uniramous (Kury and Villarreal 2015: figs 2B, C); **(1)** branched (Figs 3E, 6F, G).
56. Penis, size of MS-E2 branches (46): **(0)** minute, almost inconspicuous (Villarreal and García 2021: figs 8A–D); **(1)** conspicuous (Fig. 6F).
57. Penis, MS-D, alignment in lateral view (47): **(0)** vertical (Kury and Villarreal 2015: fig. 2B); **(1)** oblique (Fig. 8H).
58. Penis, MS-E1: (0) present (Villarreal and García 2021: figs 8C, D); absent (1) (Fig. 3H–J).

3.2. Cladistic analysis

We obtained two parsimonious trees, using a value of K = 6.4844 whose strict consensus is presented in the figure 16 (L=189, CI=43, RI=73). *Paravima* was recovered as monophyletic, grouping all the previously described Venezuelan species, plus the species *Avima plana* and *A. quirozi*, together with the species described here, *Paravima lokura* **sp. nov.**, *P. magistri* **sp. nov.**, and *P. totoro* **sp. nov.** A sister group relationship between *Avima venezuelica* and *Paravima* was found under the following values of K: 2, 4, 6,4844 and 8 (Figs 16, 17A). When performing an analysis using equal weights, 138 equally parsimonious trees were obtained but, the hypothesis of internal relations within *Paravima* does not change in relation to another K values analyzed. However, the hypothesis of relationships with other Leiosteninae were modified, forming a large polytomy with several of the outgroup genera included (Fig. 17A). Some issues that could be influencing these results are discussed (see discussion for details).

3.3. Taxonomy

3.3.1. *Paravima* Caporiacco, 1951

https:zoobank.org/E26B7BC1-DAD7-4B7D-AFD1-4DAB9AA38A71

Figs 1–19

Paravima Caporiacco 1951: 11; Soares & Avram 1981: 76; González-Sponga 1987: 469; Kury 1997: 344; Kury 2003: 31.
Paraavima (incorrect subsequent spelling): Soares & Avram 1981: 76.

Type species. *Paravima goodnightorum* Caporiacco, 1951, by monotypy.

Placement.. Originally in Tricommatinae. Transferred to Leiosteninae by Soares & Avram (1981).

Diagnosis. The genus can be diagnosed within Leiosteninae by the placement of the ocularium, located close to the anterior half margin of the carapace and the absence of a longitudinal dorsal keel in the stylus of the penis, and additionally by the combination of characters presented in the description.

Description. DS outline Epsilon type 3, with posterior border distinctly wider than anterior border, giving an

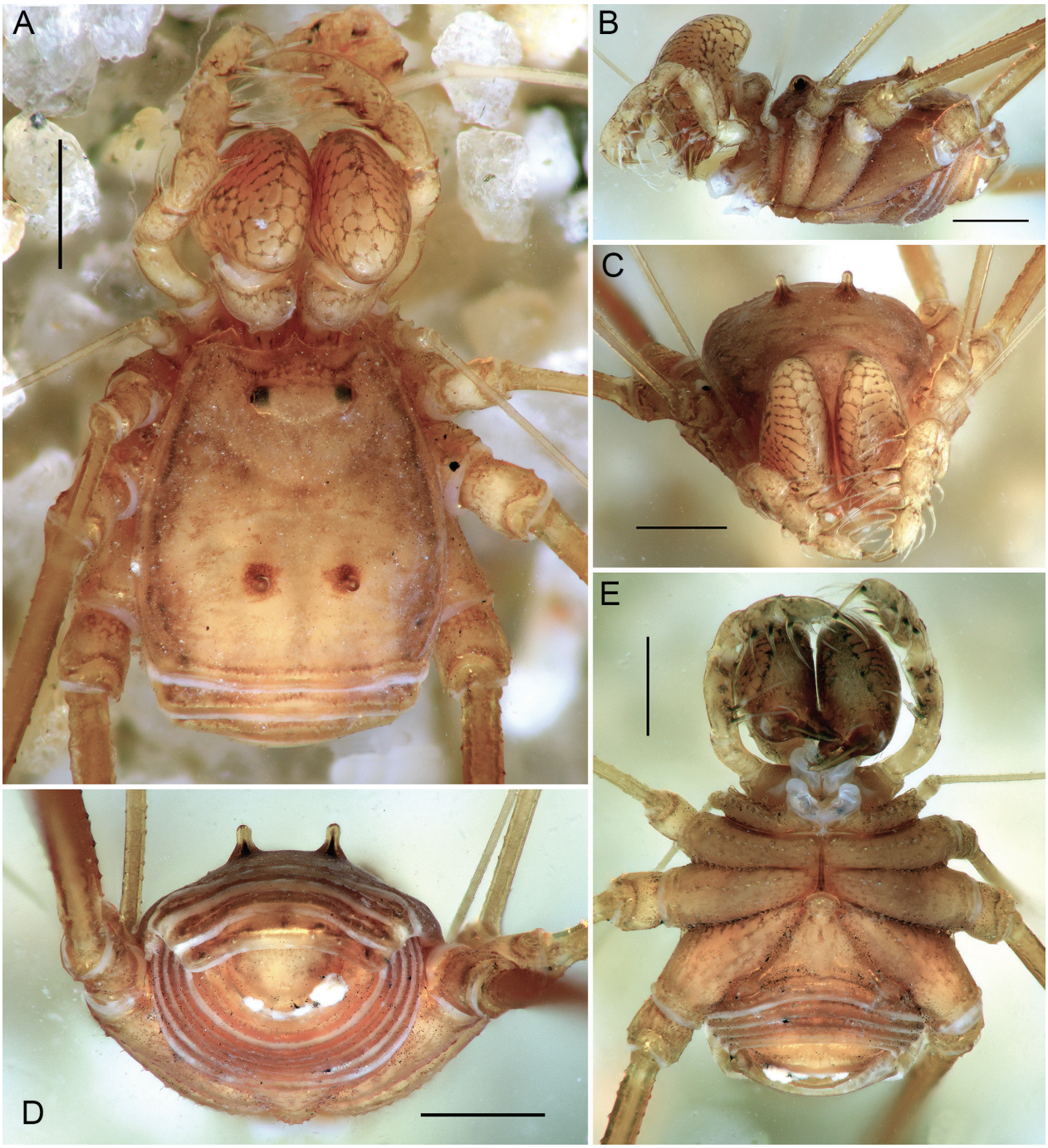

Figure 4. *Paravima locumida* González-Sponga, 1987 (MAGS 324) male. Habitus: **A** Dorsal view; **B** lateral view; **C** anterior view; **D** posterior view; **E** ventral view. Scale bars: 1 mm.

ovoid appearance. Ocularium low, very close to the anterior margin of DS, smooth (granulate in *P. lokura* **sp. nov.**), and with median concavity. Interocular distance half of carapace width (except in *P. magistri* **sp. nov.** that is one third). Mesotergum concolor with the rest of the DS (except in *P. magistri* **sp. nov.,** *P. plana* **comb. nov.**, and *P. quirozi* **comb. nov.**, with a dark spot). Mesotergal area III with paramedian ornamentation (except in *P. plana* **comb. nov.** and *P. quirozi* **comb. nov.**, smooth). Long legs (FeIV length at least 3.7 times DS length). Penis with tips of LP sharp, not differentiated and not curved; subdistal depression between MS-E2 and horned LP; malleus with three pairs of branched MS-A (except in *P. magistri* **sp. nov.** where it has two pairs); MS-C and MS-E1 absent; stylus sinuous (except in *P. magistri* **sp. nov.,** *P. plana* **comb. nov.**, *P. quirozi* **comb. nov.**, and *P. totoro* **sp. nov.**, where it is straight), and without dorsal keel or process.

Derivatio nominis. From Greek παρά (beside) and the pre-existing genus *Vima*. Gender: feminine.

Distribution. Venezuela: Cordillera de la Costa mountain range (Distrito Capital, Aragua, Carabobo, Miranda, Guárico and Yaracuy states); Colombia: P.N.N Tamá (Norte de Santander department) and San Antonio del Tequendama (Cundinamarca department).

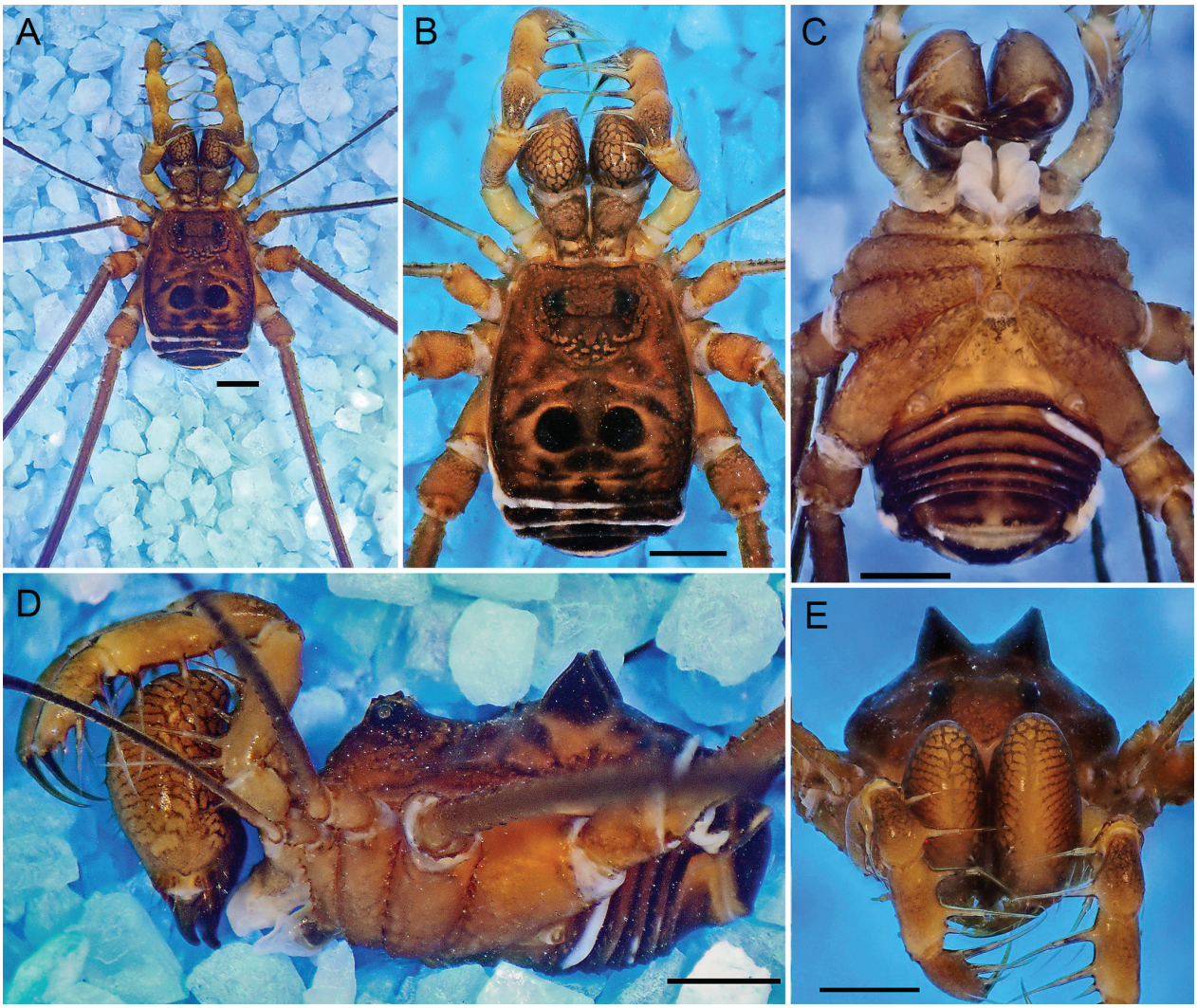

Figure 5. *Paravima lokura* **sp. nov.** (ICN-Ao-1490*) male holotype. Habitus: **A** Panoramic view; **B** dorsal view; **C** ventral view; **D** lateral view; **E** anterior view. Scale bars: 1 mm.

Included species. *Paravima goodnightorum* Caporiacco, 1951; *Paravima locumida* González-Sponga, 1987; *Paravima lokura* **sp. nov.**; *Paravima magistri* **sp. nov.**; *Paravima morritomacairensis* González-Sponga, 1987; *Paravima plana* (Goodnight & Goodnight, 1949) **comb. nov.**; *Paravima propespelunca* González-Sponga, 1987; *Paravima quirozi* (González-Sponga, 1981) **comb. nov.,** and *Paravima totoro* **sp. nov.**

Key to the species of *Paravima* (males)

1a Mesotergal area III unarmed or with small paired granules (Figs 10C, 13D) **2**
1b Mesotergal area III with paired large tubercles (Figs 2D, 4C, 5E, 7E, 9B) **3**
2a Mesotergal areas with a dorsal dark spot (Fig. 13A) ..... ***P. quirozi* comb. nov.**
2b. Mesotergal areas reticulated, irregularly spotted, without a dorsal dark spot (Fig. 11A, B)..... ***P. plana* comb. nov.**

3a Paired tubercles on the mesotergal area III dome-shaped or conical (Fig. 13C, E)..... **4**
3b Paired tubercles on the mesotergal area III mammilliform or spiniform (Figs 4C, D, 7C, E, 8B)..... **6**
4a Paired tubercles on the mesotergal area III dome-shaped (Fig. 14C, E)..... ***P. totoro* sp. nov.**
4b Paired tubercles on the mesotergal area III conical (Fig. 5D, E) **5**
5a Conical tubercles large, close to each other (separated by less the diameter of a cone) (Fig. 5B, E), ocularium tuberculated (Fig. 6A) ..... ***P. lokura* sp. nov.**
5b Conical tubercles small, far from each other (separated by the diameter of a cone) (Fig. 11 C, D), ocularium unarmed..... ***P. propespelunca***
6a Tubercles of the area III mammilliform (with the base wider than the tip) (Fig. 9C, D) **7**
6b Tubercles of the area III spiniform (gradually sharpening) (Fig. 4C, D)..... **8**

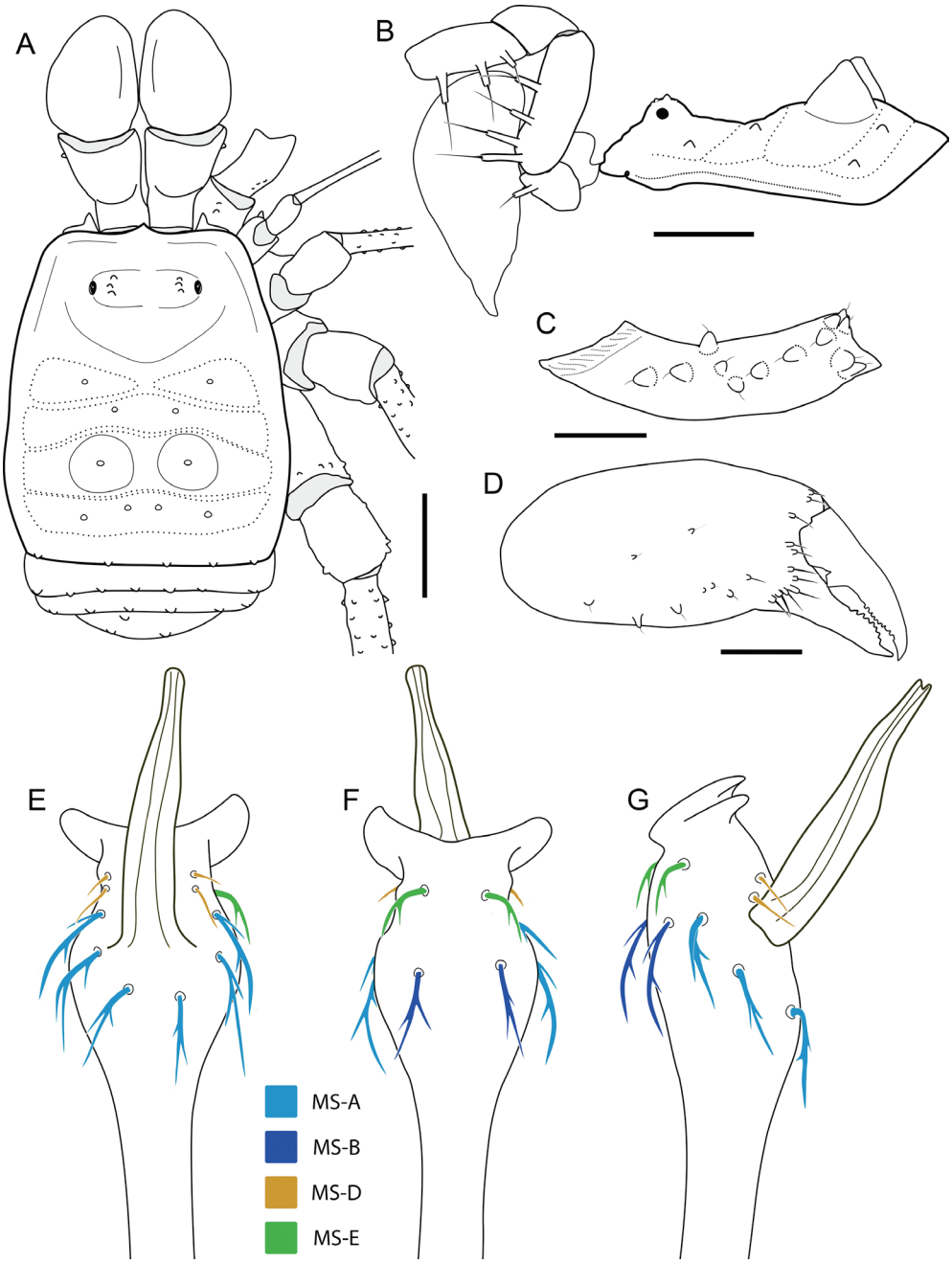

Figure 6. *Paravima lokura* **sp. nov.** (ICN-Ao-1490*) male holotype. **A** Habitus, dorsal view; **B** lateral view; **C** left coxa I, ventral view; **D** chelicera, anterior view. Apical part of the penis: **E** Dorsal view; **F** ventral view; **G** lateral view. Scale bars: 1 mm (penis with not scaled figures). Abbreviation: Macrosetae (MS).

7a Tip of the mammilliform tubercles acute and slightly higher than the base (Fig. 4C, D) ..... ***P. locumida***
7b Tip of the mammilliform tubercles blunt and shorter than the base (Figs 1B, C, 2D)..... ***P. goodnightorum***
8a Mesotergum darker than the rest of the dorsal scutum (Fig. 7B)..... ***P. magistri* sp. nov.**
8b Mesotergum with the same coloration as the rest of the dorsal scutum (Fig. 9A)..... ***P. morritomacairensis***

Paravima goodnightorum Caporiacco, 1951

Figs 1, 2, 3, 18, 19C–F

Paravima goodnightorum Caporiacco, 1951: 11, figs 5a–b; González-Sponga, 1987: 475, figs 606–611; Kury, 2003: 31.

= *Paravima flumencaurimarensis* González-Sponga 1987: 470, figs 600–605; Kury 2003: 31. **syn. nov.**

Diagnosis. Paired tubercles on the mesotergal area III mammilliform, with blunt tip shorter than the base (in *P. locumida* the tip is acute and slightly higher than the base; in the remaining species, the mesotergal area III is unornamented or exhibits conical or domed tubercles).

Description. See González-Sponga (1987). Here we offer a complementary description based on MNRJ 18301

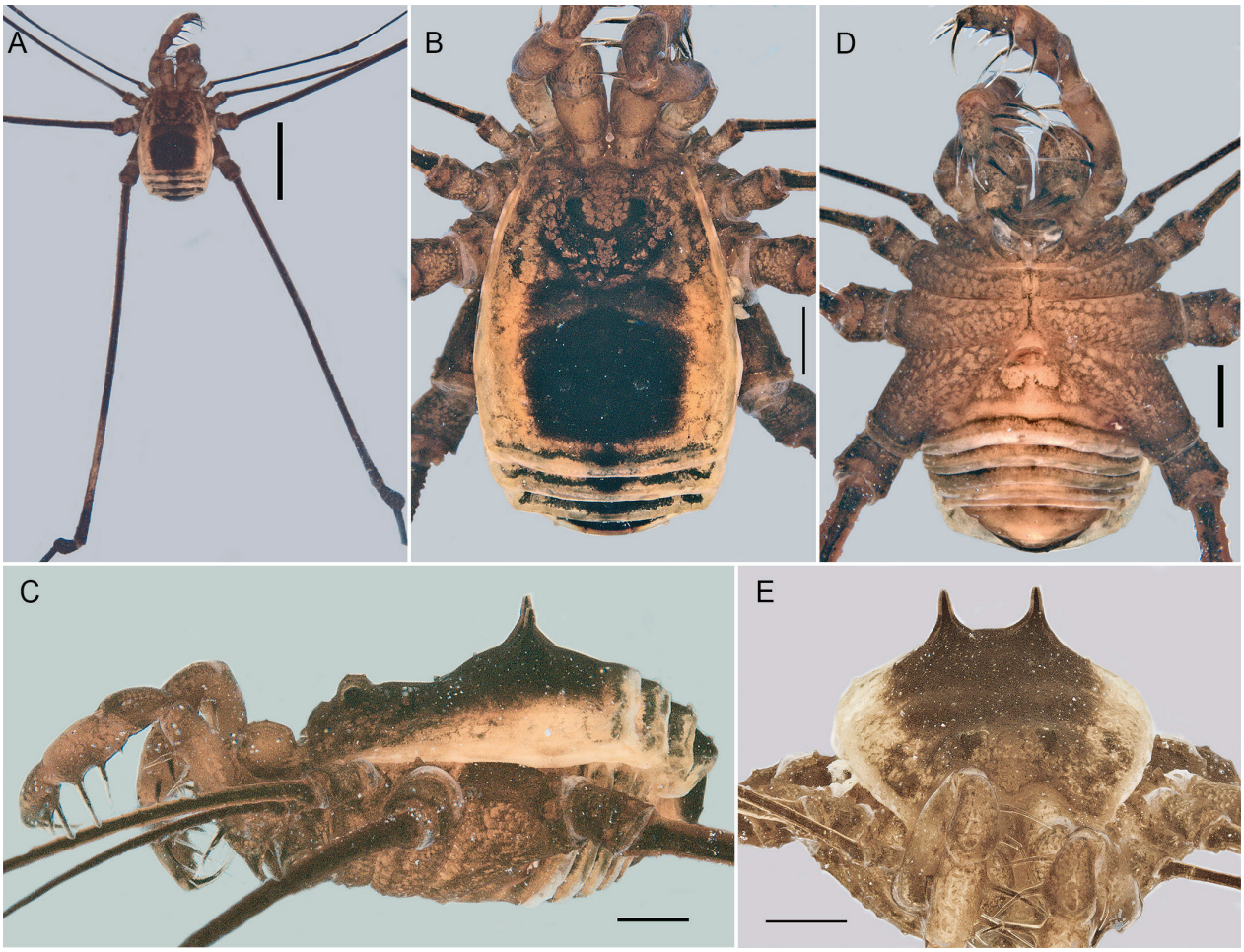

Figure 7. *Paravima magistri* **sp. nov.** (ICN-Ao-1671.1) male holotype. Habitus: **A** Panoramic view; **B** dorsal view; **C** lateral view; **D** ventral view; **E** anterior view. Scale bars: 1 mm.

and MIZA 0105921: Anterior and lateral margins of DS smooth, sometimes variegated. (Figs 2A, B, 3A–D). Mesotergum ill delimited, divided into four areas: area I divided into two halves, areas II–IV undivided; areas I, II, and IV with a pair of granules, area III with a pair of paramedian mammilliform tubercles darker than the rest of the mesotergum and higher than the ocularium (Figs 1A–D, 2B, D, E, 3A–D). Posterior margin of DS substraight, smooth (sometimes with some granules). Free tergites I–III with granules (Fig. 2B). Anterior margin of coxa I with two rows of median irregular tubercles (Figs 1E, 2C). Cheliceral hand swollen. Legs increasing in thickness from leg I to leg IV; Fe IV three times DS length (Fig. 2A); Pa IV with some granules (Fig. 3K); Ti IV thickened distally (Fig. 3K). Penis with small LP (height shorter than width), apex with anterolateral crescent-shaped corners (Fig. 3E–J). Hammer (malleus) with three pairs of branched MS-A (see Remarks); one pair of branched MS-B (Fig. 3A, G–J); two pairs of MS-D (Fig. 3E, F, H–J); one pair of MS-E2 large and branched, MS-E1 absent (Fig. 3E, G–J). Stylus elongated, sigmoidal, surpassing the lamina parva (Fig. 3E–J).

Distribution. Known from Distrito Capital, Aragua, La Guaira and Miranda states, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** *Paravima goodnightorum*: Syntype ♀, VENEZUELA, Distrito Federal, El Junquito | v.1949 | Marcuzzi leg. (MBUCV, lost); 2 ♂ syntypes, Rancho Grande | 31.xii.1949 | Monk leg. (MBUCV, lost); 1 ♂ neotype (designated by González-Sponga, 1987), El Junquito | [10.460146°, –67.074705°] | A.R. Delgado de González, J.A. González Delgado, and M.A. González-Sponga leg. (MBUCV 1195, not examined).–*Paravima flumencaurimarensis*: 1 ♂ holotype, VENEZUELA, Miranda, Sucre, Urbanización La Urbina Norte, Caurimare river | [10.49355° –66.80486°] | 850 m | 3.vi.1979, M. von Dangel [Miguel von Dangel], J.A. González Delgado, and M.A. González-Sponga leg. (MCNC 963).–Paratypes 1 ♀, same data as holotype (MCNC 964); 7 ♂ 9 ♀, same data as for preceding, 26.i.1985 (MAGS, not examined). — ***Other material*:** VENEZUELA: 1 ♂ 5 ♀ 1 imm., La Guaira (not Aragua, as originally stated in the label), Colonia Tovar, [near Villa Bahareque], [10.4273°, –67.235°], xii. 2002, A. Pérez, A. Giupponi leg. (MNRJ 18301*) (New Record); 2 ♂, El Limón, 10.4774º, –67.2819º, forest along stream, 1235 m, 21.ii.2020, O. Villarreal, B.A. Huber leg. (MIZA 0105911) (New Record); 76 ex., a 4 km de la Colonia Tovar y en la desviación hacía la Hacienda El Limón, Aragua y Distrito Capital (now La Guaira), 2200 m, 10.i.1981, 27.iii.1981 and 4.iv.1981, A.R. Delgado, M.A. González S. leg. (MAGS 237 (MIZA 0105931)); 1 ♂, same data as previous, dissected (MIZA 0105920); 11 ex., Picacho de Galipán, [10.5639°, –66.9112°], [1850 m a.s.l.], 23.ix.1982, M. von Dangel leg. (MAGS 545 (MIZA 0105929)).–2 ♀, Miranda, San Antonio de los Altos, [10.3885°, –66.9517°], 1250 m, 13.vii.1974, J.M. Ayala leg. (MAGS 5 (MIZA 0105928)) (New Record); 1 ♂ 4 ♀, cerro

El Volcán, El Topito, 10.4144º, –66.8474°, 1300 m, 6.iv.2022, O. Villarreal, Q. Arias leg. (MIZA 0105904) (New Record); 2 ♂ 3 ♀, Jardines Topotepuy, bosque nublado, 10.4180º, –66.8530º, 1460 m, 12.xi.2019, O. Villarreal, J. Rodríguez leg. (MIZA 0105905) (New Record); 3 ♀ 2 ♂, Jardines Topotepuy, bosque nublado, 10.4187º, –66.8533º, 1470 m, 12.xi.2019, O. Villarreal, J. Rodríguez leg. (MNRJ 60618) (New Record); 6 ♀ 2 ♂, Cerro El Volcán, Jardines Topotepuy, 10.4182 N, 66.8534 W, 1440 m, 07.iv.2022, Villarreal O., Arias C. leg. (MIZA 0105871); 1 ♀, Parque Vinicio Adames, [10.39643°, –66.89329°], 1000 m, 11.vii.1979, ARDG [Angela Rosa Delgado de González], JAGD [José Antonio González Delgado] and MAGS [Manuel Ángel González Sponga] leg. (MAGS 230) (MIZA 0105930); 1 ♀, Distrito Federal, Parque Nacional El Ávila, Los Venados, 1500 m, 9.x.1989, E. González S., M. A. González-Sponga leg. (MAGS 1115 (MIZA 0105921)); 1 ♂, Río Curimare, Distrito Sucre, 1000 m, 3.vi.1979, M. von Dangel, J.A. González Delgado, M.A. González-Sponga leg.(MIZA 0105918); 6 ♂ 13 ♀, same data as previous (MAGS 208 (MIZA 0105919)).

Remarks. The female specimen MAGS 1115 (MIZA 0105921), identified by González-Sponga as *P. flumencaurimarensis*, seems to correspond to one of the female paratypes of *P. flumencaurimarensis* cited as type data above as MAGS, without number. The penis drawing (González-Sponga 1987: 473, fig. 604) shows one pair of MS-D and two pairs of MS-A, but after studying males from four localities (including paratypes of *P. flumencaurimarensis* and *P. goodnightorum*) (Fig. 3A–D, H–J), all exhibited two pairs of MS-D, and three pairs of MS-A. Likewise, we have found a subtle unnoticed variation in the color patterns of the dorsal shield (Fig. 3A–D) and in the shape of the mammilliform tubercles of the mesotergal area III (Fig. 3L–P). The right lateral SEM image (Fig. 3E) of the penis shows three MS-A, but the dorsal view (Fig. 3F) shows two pairs of MS-A on the left side. We consider the common in the genus is three pairs of MS-A, as seen in all other species of *Paravima*. The LP is slightly collapsed (Fig. 3E), this collapse could be an artifact of the preparation of the genitals, which can be reflected into slight variations in the drawings (Fig. 3H–J).

Paravima locumida González-Sponga, 1987

Figs 4, 18

Paravima locumida González-Sponga, 1987: 479, figs 612–617; Kury, 2003: 31.

Diagnosis. Paired tubercles on the mesotergal area III mammilliform, with acute tip and narrow base, the only other species with paired mammilliform tubercles is *P. goodnightorum* (see details in the diagnosis of that species).

Description. See González-Sponga (1987). Here we offer a complementary description based on González-Sponga 1987: figs 616, 617: Anterior and lateral margins of DS smooth, posterior margin with some granules (Fig. 4A–D). Mesotergum ill delimited, divided into four areas: area I divided into two halves; areas II–IV undivided; area III with a pair of paramedian mammilliform spines (higher than ocularium) slightly darker than the rest of the mesotergum (Fig. 4A–C). Anterior margin of coxa I with a high proximal conical tubercle (Fig. 6E). Fe IV four times DS length. Malleus of penis with one pair of branched MS-B; two pairs of MS-D; one pair of MS-E2 large and branched. Stylus elongated, surpassing the lamina parva.

Distribution. Known from Miranda state, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** Holotype ♂, VENEZUELA, Miranda, Acevedo, Parque Nacional Guatopo | [10.217055° –66.45721°] | 1200 m | 3.x.1980, A.R. Delgado de González, J.A. González Delgado, and M.A. González-Sponga leg. (MCNC 965).–Paratypes 1 ♀, same data as holotype (MCNC 966); 5 ♂ 5 ♀ 3 imm., same data as holotype (MAGS, not examined). — ***Other material*:** VENEZUELA: 5 ♂ 5 ♀, Miranda, Acevedo, Parque Nacional Guatopo, 320 m, 3.x.1980, ARDG [Angela Rosa Delgado de González], JAGD [José Antonio González Delgado] and MAGS [Manuel Ángel González Sponga] leg. (MAGS 324); 1 ♂ 3 ♀, Acevedo, Boca de Curia, [10.2°, –66.3°], 14.xi.1987, A.R. Delgado and M.A. González S. leg. (MAGS 1033 (MIZA 0105925)).

Remarks. One male from MAGS 324 was photographed in 2017 (Fig. 4). However, in a recent revision in 2022, we found the material totally deteriorated and that all the specimens are useless for taxonomic purposes (a lot of fungus on it). We suspect that MAGS 324 corresponds to one of the male paratypes cited as MAGS in type data, without number. Of all the drawings of *Paravima* genitalia made by G-S, those of *P. locumida* (González-Sponga 1987: figs 616, 617) are the only ones that show all the MS known for the genus.

Paravima lokura sp. nov.

https://zoobank.org/4F6A4D10-9436-4F98-AD28-5B7E3D0B-1B4A

Figs 5, 6, 18

Diagnosis. Ocularium tuberculate. Mesotergal area III with large conical paramedian tubercles, close to each other (Figs 5D, E) (in *P. propespelunca*, *P. flumencaurimarensis*, *P. goodnightorum*, *P. locumida*, and *P. morritomacairensis* ocularium unarmed and mesotergal area III with separated conical/mammilliform tubercles).

Description. ***Holotype*** **(**ICN-Ao-1490*). — Measurements: CL: 1.2, AL: 1.8, CW: 2.0, AW: 2.6, BaCh: 0.4, IOD: 0.9; Leg I (Tr: 0.3, Fe: 4.0, Pa: 0.9, Ti: 3.0, Mt: 4.3, Ta: 1.7); Leg II (Tr: 0.4, Fe: 9.5, Pa: 1.1, Ti: 8.0, Mt: 10.1, Ta: 3.5); Leg III (Tr: 0.7, Fe: 8.0, Pa: 1.6, Ti: 5.0, Mt: 9.0, Ta: 1.9); Leg IV (Tr: 0.9, Fe: 10.1, Pa: 1.3, Ti: 7.0, Mt: 10.3, Ta: 2.8). — *Dorsum*: Anterior and lateral margins of DS smooth. Ocularium with granules (Figs 5B, D, 6A). Mesotergum delimited, divided into four areas,

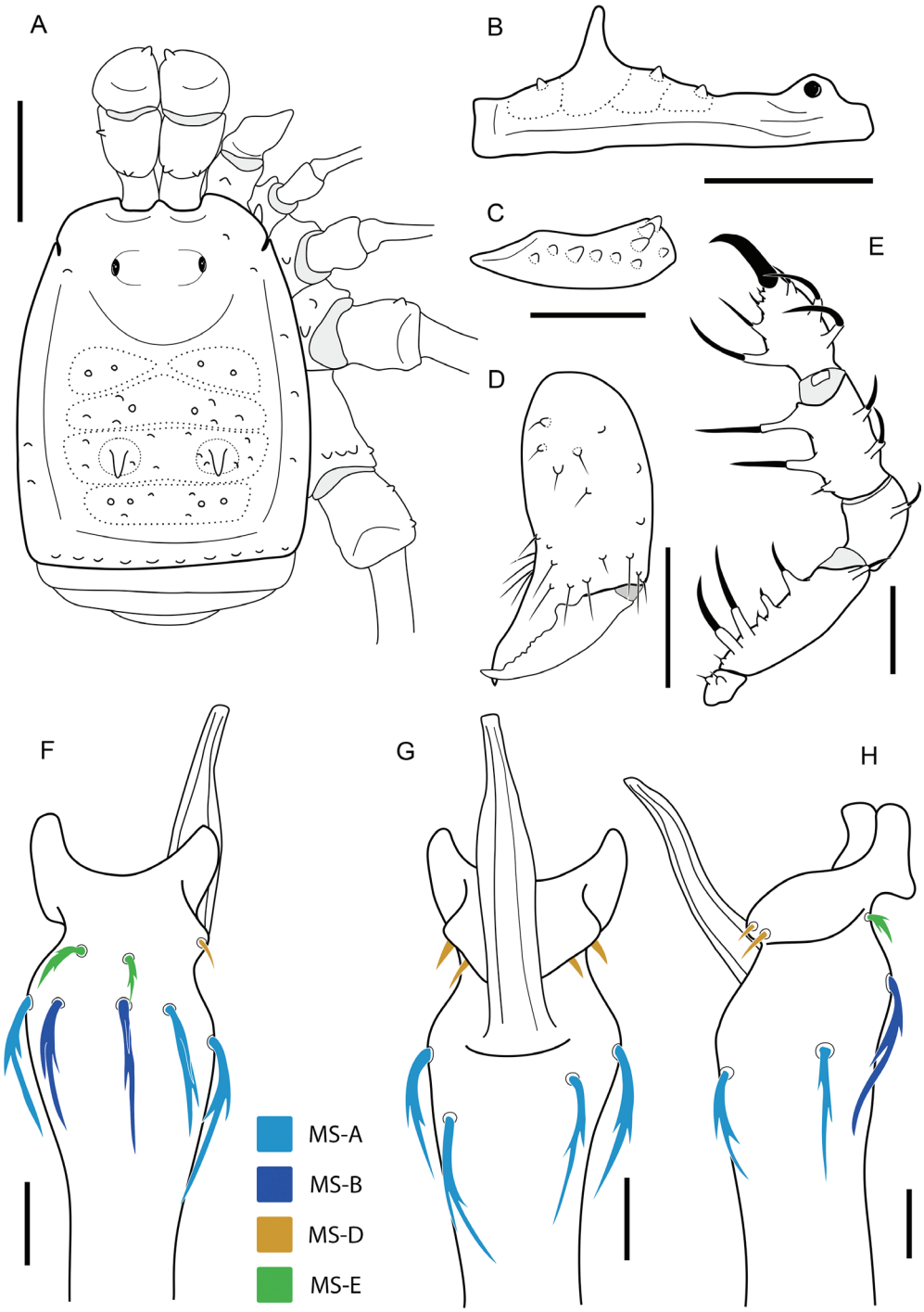

Figure 8. *Paravima magistri* **sp. nov.** (ICN-Ao-1671.1) male holotype. **A** Habitus, dorsal view; **B** lateral view; **C** left coxa I, ventral view; **D** chelicera, anterior view; **E** Pedipalp, mesal view. Apical part of the penis: **F** Dorsal view; **G** ventral view; **H** lateral view. Scale bars: A, B = 1 mm; C–E = 0.5 mm; F–H = 0.05 mm. Abbreviation: Macrosetae (MS).

mostly smooth. Area I divided into two halves, each one with one small tubercle; area II–IV undivided; II with a pair of medium-sized tubercles close to the medial axis of the body (Fig. 6A, B); III with a pair of conical wide tubercles close to each other (Figs 5D, E, 6B); IV with four small tubercles. Posterior border of scutum straight, with some tubercles. Free tergites I–II and anal operculum with some tubercles (Fig. 6A). — *Venter*: Coxae I–IV with some granules (Fig. 5C). Coxa I with one medial tubercle on the anterior margin, a longitudinal row of tubercles at the medial region, a group of three tubercles on the anterodistal margin, and two tubercles close to the posterodistal margin (Fig. 6C); coxa II longer than coxa I; coxa III longer than I and II; coxa IV backward projected (Fig. 5C). Sternites with a row of small tubercles each. Stigmatic area smooth. Stigmata large, oval and transverse (Fig. 5C). — *Chelicerae*: Segment I rectangular, with well-marked bulla (Figs 5B, 6A), one ectal subdistal tubercle, and two tubercles on the proximal border (Fig. 4B). Chelicera swollen (Figs 5B, E, 6B). Hand with some sparse setiferous tubercles of different sizes in the fronto mesal portion, and a frontal row of small setifer-

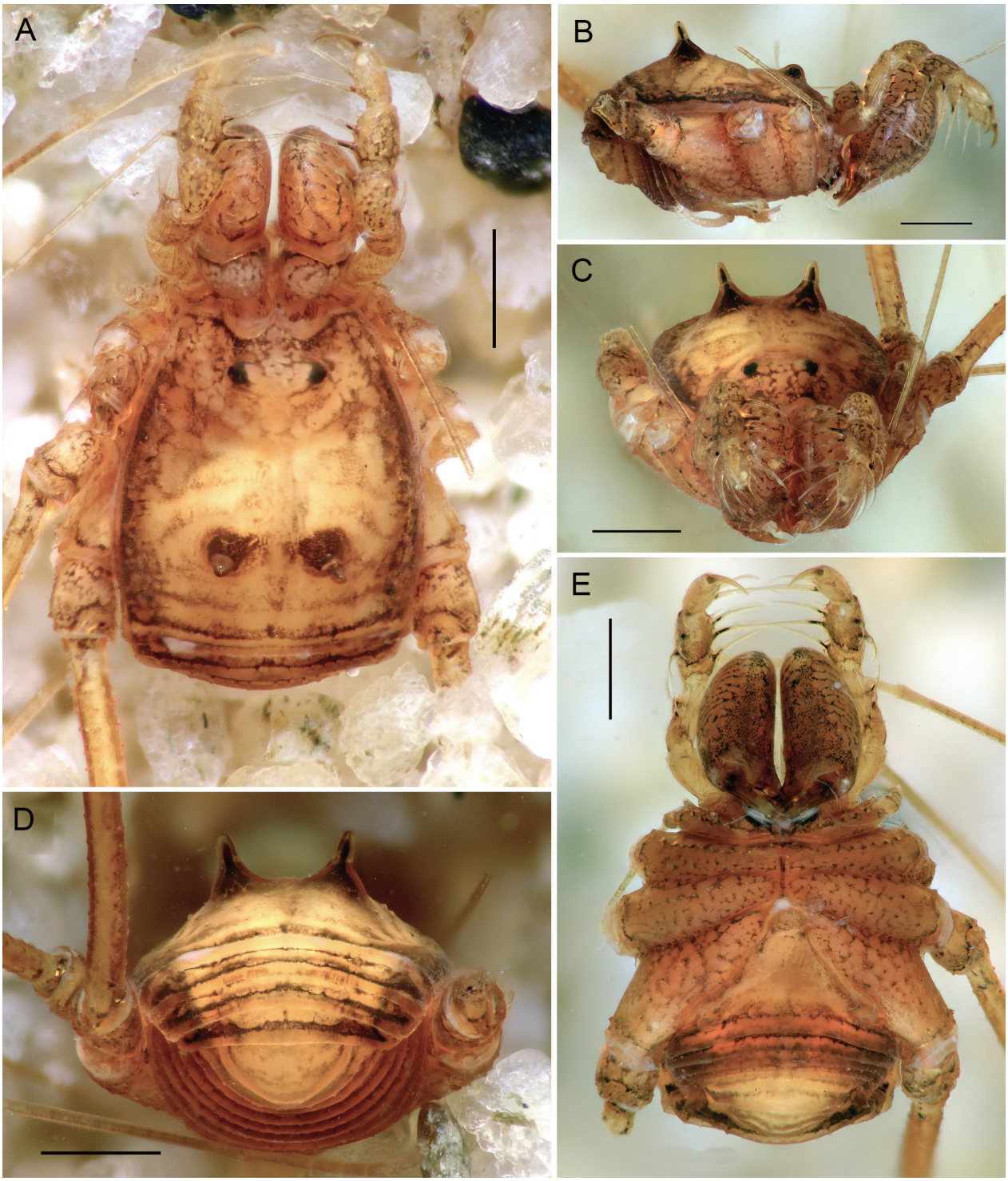

Figure 9. *Paravima morritomacairensis* González-Sponga, 1987 (MAGS 504, MIZA 0105923) male. Habitus: **A** Dorsal view; **B** lateral view; **C** anterior view; **D** posterior view; **E** ventral view. Scale bars: 1 mm.

ous tubercles extending from the mesal to the ectal face of the chelicera close to the base of the fingers (Fig. 6D). Fixed finger with the inner surface irregularly dentated. Movable finger with one trapezoid, sub-basal tooth and with the inner surface dentate (Fig. 6D). — *Pedipalps*: Longer than DS length, smooth. Tr ventrally with one subapical setiferous tubercle. Fe with a ventromesal row of five setiferous tubercles (the third shorter than the others), and one large ventroectal setiferous tubercle in the distal portion (Fig. 5C). Pa with one large mesal setiferous tubercle. Ti ectal iII, mesal IIi. Ta ectal IIi, mesal IIi (Figs 5, 6B). — *Legs*: Leg I smooth, legs II–IV with minute granules. Leg I filiform, the rest, getting steadily thicker from leg II to IV (Fig. 5A). Fe IV three times DS length. Tarsal formula: 9(3)–9(3)/20(3)–20(3)/8–9/8–8. — *Penis*: LP short and depressed, half-moon shaped, with anterolateral sharp corners dorsally pointed (Fig. 6E–G). Malleus carrying the branched MS-A-B (three pairs of MS-A and one pair of MS-B); MS-B at the same level of MS-A1 (Fig. 6G). MS-D1-2 long, located in a

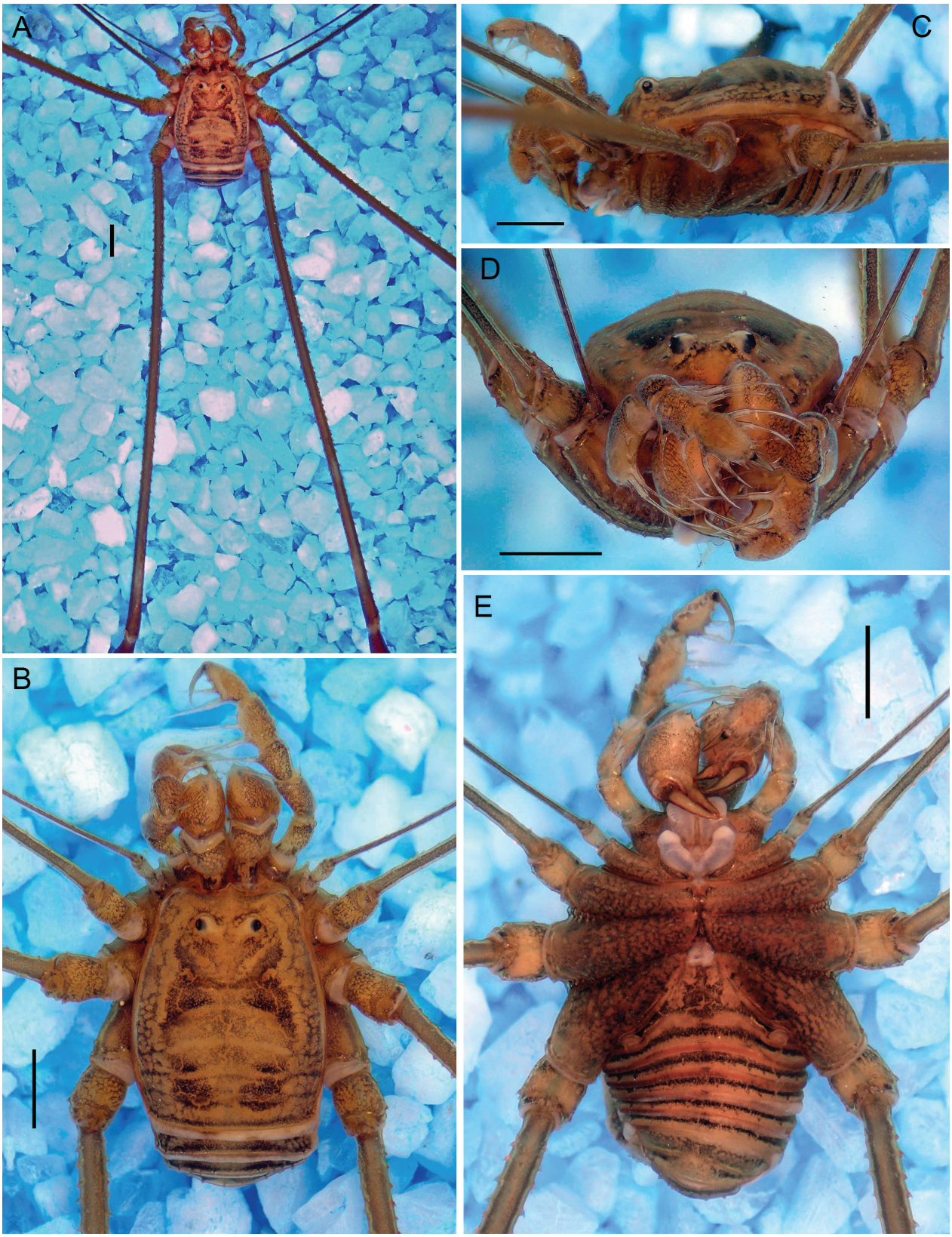

Figure 10. *Paravima plana* (Goodnight & Goodnight, 1949) **comb. nov.** (MNRJ 9328*) male. Habitus: **A** Panoramic view; **B** dorsal view; **C** lateral view; **D** anterior view; **E** ventral view. Scale bars: 1 mm.

vertical line on a keel between the LP and the base of the stylus (Fig. 6G). MS-E2 large and branched (Fig. 6F). Stylus sinuous, surpassing the lamina parva, narrower at distal region, tip irregular (Fig. 6G). — *Color* (in ethanol): Carapace and mesotergum reticulated Deep Brown (56) on Brownish Orange (54). Area III tubercles Brownish Black (65). Pedipalps and chelicerae Strong Orange Yellow (68). Posterior border and free tergites Dark Brown (59). Legs I–IV Deep Orange Yellow (69). — *Female*: Unknown.

Derivatio nominis. In the Tunebo language, spoken by the indigenous people that inhabit the region where the species was collected, *lokura* means spider. Noun in apposition.

Distribution. Known just from the type locality, PNN Tamá, Norte de Santander department, in the Páramo biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** Holotype ♂, COLOMBIA, Norte de Santander, Parque Nacional Natural Tamá | [7.26214° –72.25064°] | 2170 m | 25.vi.1999, V.R. Mayusa leg. (ICN-Ao-1490*).

Paravima magistri sp. nov.

https:zoobank.org/0025ECB0-E624-4B11-8F35-A1DD-3AF16012

Figs 7, 8, 18, 19G

Diagnosis. Mesotergal area III with large paramedian spines (the remaining species of *Paravima*, except *P. morritomacairensis*, without ornamentation or with conical, mammilliform or domed tubercles). Can be distinguished from that species by the coloration of mesotergal areas I–IV darker than the rest of the DS (concolorous in *P. morritomacairensis*).

Description. ***Holotype*** (ICN-Ao-1671.1). Measurements: CL: 0.8, AL: 1.6, CW: 1.6, AW: 2.1, BaCh: 0.3, IOD: 0.5; Pedipalp: Tr: 0.4, Fe: 0.5, Pa: 0.5, Ti: 0.5, Ta: 0.5, Claw: 0.4; Leg I (Tr: 0.3, Fe: 3.8, Pa: 0.6, Ti: 2.5, Mt: 4.7, Ta: 1.5); Leg II (Tr: 0.4, Fe: 8.7, Pa: 0.9, Ti: 7.0, Mt: 8.7, Ta: 3.3); Leg III (Tr: 0.5, Fe: 6.8, Pa: 1.0, Ti: 3.6, Mt: 7.4, Ta: 1.7); Leg IV (Tr: 0.7, Fe: 9.7, Pa: 1.1, Ti: 5.0, Mt: 10.8, Ta: 2.6). — *Dorsum*: Anterior and lateral margins of DS smooth. Ocularium smooth (Figs 7B, 8A). Mesotergum delimited, darker than the rest of the DS, divided into four areas, with some granules. Area I divided into two halves, each one with a pair of tubercles; area II–IV undivided; II with a pair of medium-sized tubercles close to the medial axis of the body (Figs 7B, C, 8A); III with a pair of high paramedian spines (Figs 7C, E, 8A, B); IV with four small tubercles. Posterior border of scutum substraight, with a row of tubercles. Free tergites I–II and anal operculum with a few tubercles (Fig. 8A). — *Venter*: Coxae I–IV with some granules (Fig. 7D). Coxa I with a longitudinal row of tubercles at the medial region, being the third larger than the others, three large tubercles reaching the anterodistal region, and one small tubercle close to the posterodistal margin (Fig. 8C); coxa II longer than coxa I; coxa III longer than I and II; coxa IV backward projected (Fig. 7D). Sternites and anal operculum with a few small tubercles. Stigmatic area smooth. Stigmata large, oval and transverse (Fig. 7D). — *Chelicerae*: Segment I rectangular, with well-marked bulla (Fig. 7B, C), two small ectal subdistal tubercles, and two separated tubercles on the proximal border (Fig. 7B). Chelicera not swollen, monomorphic (Figs 7C, E, 8A). Hand with some sparse setiferous tubercles of different sizes on the frontomesal region, a group of setae on the mesal face of the fixed finger, and some setiferous tubercles close to the base of the fixed finger (Fig. 8D). Fixed finger with the inner surface irregularly dentated. Movable finger with one trapezoid, sub-basal tooth and with the inner surface dentate (Fig. 8D). — *Pedipalps*: Longer than DS length, smooth. Tr ventrally with two subapical tubercles. Fe with a ventromesal row of six setiferous tubercles (the second and the third larger than the others), and one large ventroectal setiferous tubercle in the distal portion (Figs 7C, 8E). Pa with one large mesal setiferous tubercle. Ti ectal II, mesal iII. Ta ectal IIi, mesal IIii (Fig. 8E). — *Legs*: Legs I–IV smooth. Leg I filiform, the rest, getting steadily thicker from leg II to IV. Fe IV four times DS length (Fig. 7A). Tarsal counts: 7(3)–8(3)/18(3)–18(3)/7–7/7–7. — *Penis*: LP short and depressed, half-moon shaped, with anterolateral blunt corners apically pointed (Figs 8F–H). Malleus carrying the branched MS-A-B (two pairs of MS-A and one pair of MS-B in a diagonal alignment) (Fig. 8H). MS-D1-2 short, located in an oblique line on a keel between the LP and the base of the stylus (Fig. 8G, H). MS-E2 medium-sized and branched (Fig. 8F). Stylus straight, surpassing the lamina parva, tip truncate (Fig. 8H). — *Color* (in ethanol): Carapace reticulated dark brown (59) on light orange yellow (70). Mesotergum dark brown (59). Pedipalps and chelicerae deep yellowish brown (75). Posterior border and free tergites Dark Olive (108). Legs I–IV dark yellowish brown (78).

Remarks. The coloration in vivo (Fig. 19G) is quite different, with carapace, chelicerae, pedipalps, coxae and trochanters strong reddish brown (40); laterals of DS vivid orange yellow (66); mesotergum and medial region of free tergites brownish black (65); free tergites vivid yellow green (115); and the rest of the legs brownish black (65). — *Female*: Chelicerae of the same size as male (monomorphic). Femora slightly thinner than in male.

Derivatio nominis. The species name honors professor Eduardo Flórez, curator of the ICN Arachnological collection. Professor, in Latin magister, (magistri in genitive case), in recognition of his excellent work in the teaching and development of arachnology in Colombia and his interest in the divulgation of scientific knowledge about the arthropods in the country.

Distribution. Known just from the type locality, RN Los Tunos, Cundinamarca department, in the Magdalena biogeographic province (Fig. 18).

Material examined. ***Type material:*** Holotype ♂, COLOMBIA, Cundinamarca, San Antonio del Tequendama, Reserva Natural Los Tunos, colecta manual diurna | [4,56071° –74,31366°] | 2300 m |, 28.v.2012, D. Martínez leg. (ICN-Ao-1671.1). – Paratypes 2 ♀ 2 ♂, same data as holotype, (ICN-Ao-1671); 4 ♂, same data as holotype, (ICN-Ao-1980); 2 ♀ 2 ♂, same data as preceding, 28–29.vii.2021, S. Galvis and A.F. García leg. (MNRJ 1179); 1 ♂ 1 ♀, same data as previous, (MUSENUV-Ar 2112).

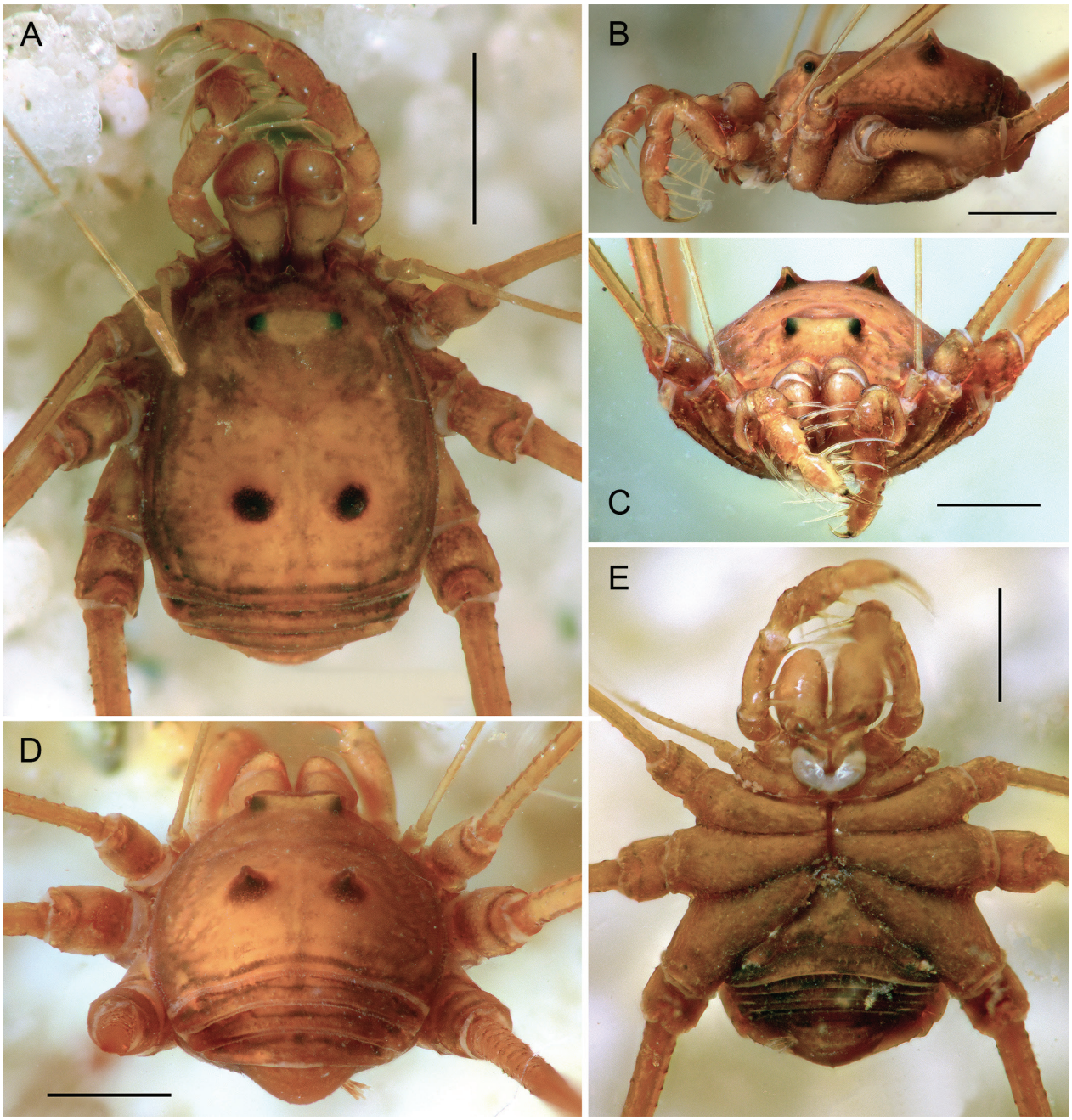

Figure 11. *Paravima propespelunca* González-Sponga, 1987 (MAGS 103) male. Habitus: **A** Dorsal view; **B** lateral view; **C** anterior view; **D** posterior view; **E** ventral view. Scale bars: 1 mm.

Paravima morritomacairensis González-Sponga, 1987

Figs 9, 18

Paravima morritomacairensis González-Sponga, 1987: 482, figs 618–623; Kury, 2003: 31.

Diagnosis. Paired tubercles on the mesotergal area III spiniform, gradually sharpening (shared with *P. magistri* **sp. nov.**, from which it can be distinguished by the absence of a dark spot in the mesotergal areas). The remaining *Paravima* species lack ornamentation or have conical, mammilliform or domed tubercles).

Description. See González-Sponga (1987). Here we offer a complementary description (based on MIZA 0105923 and González-Sponga 1987: figs 622, 623): Margins of DS, chelicerae, and pedipalps variegated (Fig. 9A). Anterior and lateral margins of DS smooth, posterior margin with some granules (Fig. 9A, B, D). Area III with a pair of paramedian mammilliform tubercles (higher than ocularium) darker than the rest of the mesotergum (Fig. 9A–C). Anterior margin of coxa I with a high proximal conical tubercle (Fig. 9E). Fe IV is three and a half times DS length. Malleus of penis with one pair of branched MS-B; MS-D absent (see Remark); one pair of MS-E2 large and branched. Stylus elongated, surpassing the lamina parva.

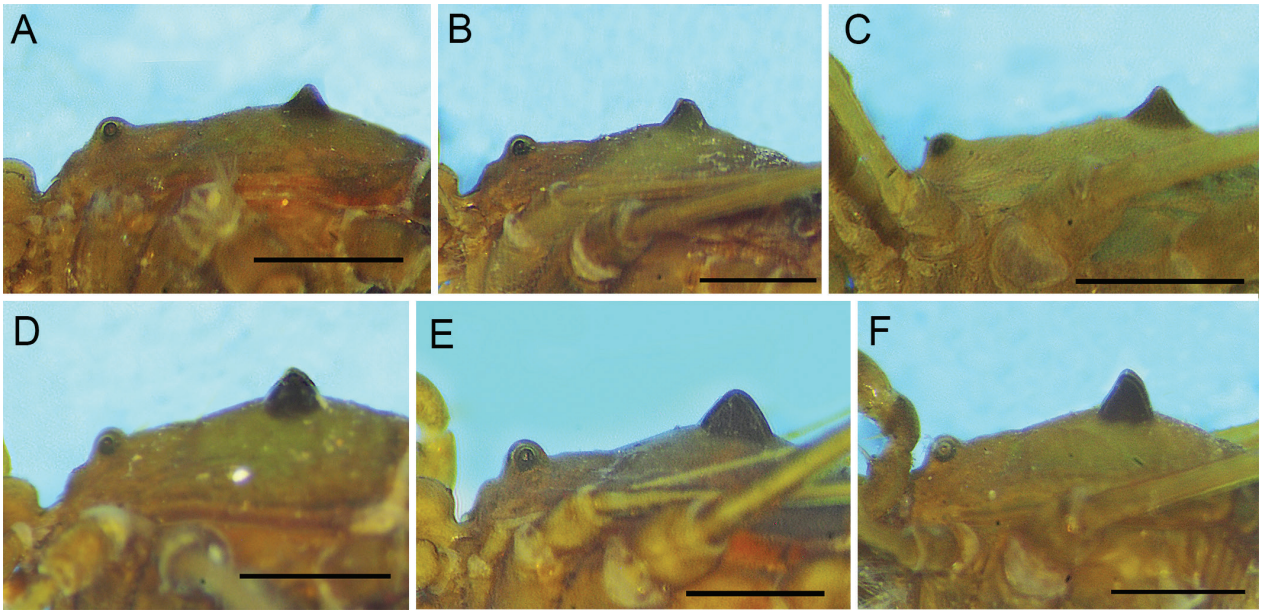

Figure 12. *Paravima propespelunca*, variation of the paramedian tubercles of area III, in lateral view. **A–D, F**: From Quebrada Cambural, Birongo (MAGS 103); **E** from 8 Km N of Guatire (MAGS 109). Males: A, B, E; Females: C, D, F. Scale bars = 1 mm.

Distribution. Known from Guárico state, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** Holotype ♂, VENEZUELA, Guárico, Monagas, El Morrito, road Altagracia de Orituco-San Francisco de Maicara [Macaira] | [9.89933° –66.30614°] | 850 m | 10.iv.1982, Reyes Torrealba leg. (MCNC 967, not examined).–Paratypes 1 ♀, same data as holotype, (MCNC 968, not examined); 1 ♂ 10 ♀, same data as holotype, (MAGS, not examined). — ***Other material*:** VENEZUELA: 2 ♂ 8 ♀, Guárico, Monagas, El Morrito de San Francisco de Macaira, 10.iv.1982, Reyes Torrealba leg. (MAGS 504 (MIZA 0105923)); 1 ♂, same data as previous (dissected), (MIZA 0105924).

Remarks. One of the males of MIZA 0105923 was dissected but the genital was not together with the male; another male was without genital operculum nor penis. MCNC material seems to be lost (not found in MAGS collection). We suspect that MAGS 504 corresponds to the material cited as MAGS, without number. The figures of the penis by González-Sponga (1987: figs 622, 623) does not show MS-D, but this is probably an omission (*Paravima* typically has two pairs of MS-D). Specimens of this species are extremely similar to *P. locumida* and a detailed review of the genitalia and variability of both taxa would be useful to determine their identity.

Paravima plana (Goodnight & Goodnight, 1949) comb. nov.

Figs 10, 18

Vima plana Goodnight & Goodnight, 1949: 21, figs 1–2; Rambla, 1978: 12, figs 4–6, 16 [misidentification]; González-Sponga, 1987: 525, figs 678–683.

Trinella plana: Pinto-da-Rocha, 1996: 319; Kury, 2003: 33.

Avima plana: Villarreal-M. & Kury, 2009: 67.

Ayachuco (incorrect subsequent spelling) *scabrifemur* Caporiacco 1951: 9, fig. 4a–b. Synonymy established by González-Sponga (1997).

Trinella scabriferum, (incorrect subsequent spelling): Soares & Avram, 1981: 95; Soares & Avram, 1982: 19, figs 32–35.

Diagnosis. Mesotergal area III unarmed (shared with *P. quirozi* **comb. nov.**). The remaining *Paravima* species have paired conical, mammilliform, spiniform or domed tubercles. Mesotergal areas reticulated, with irregular spots on laterals of areas I and III.

Description. See González-Sponga (1987). Here we offer a complementary description based on (MNRJ 9328* and MIZA 0105868): Anterior and lateral margins of DS smooth, posterior margin with some granules. Margins of DS variegated; posterior region of carapace, areas I and IV, the laterals of areas II–III, and the anterior region of area V with a dark spot (Fig. 10A–D). Mesotergum delimited, divided into four areas: area I divided into two halves; areas II–IV undivided; areas I–IV with a pair of paramedian low tubercles, those of area III domed (Fig. 10B, D). Cheliceral hand swollen. Pedipalpal segments slender (Fig. 10A–D). Legs increasing in thickness from leg I to leg IV. Leg I filiform. Legs III and IV with granules (Fig. 10A, B). Coxa I with one proximal conical tubercle at the anterior margin and a longitudinal row of tubercles at the medial portion (Fig. 10E). Fe IV four times DS length (Fig. 10A).

Distribution. Known from Aragua state, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** Holotype ♂, VENEZUELA, Aragua, Girardot, Parque Nacional Henri Pittier | [10.3494° –67.6840°] | ([Department of Tropical Research, New York Zoological Society], not

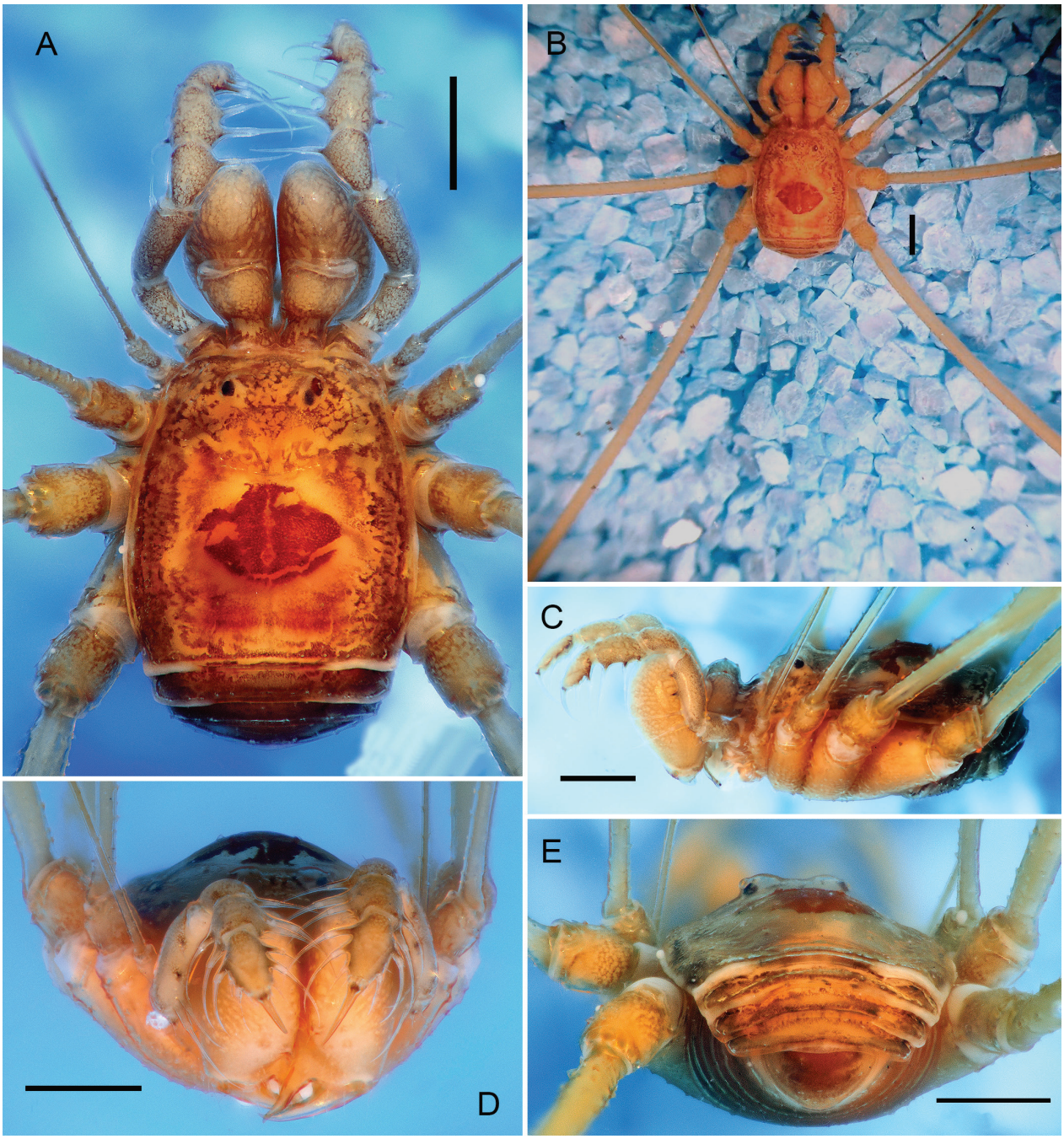

Figure 13. *Paravima quirozi* (González-Sponga, 1981) **comb. nov.** (MCNC 757) male holotype. Habitus: **A** Dorsal view: **B** panoramic view; **C** lateral view; **D** anterior view; **E** posterior view. Scale bars: 1 mm.

examined). — ***Other material*:** VENEZUELA: 1 ♀, Aragua, [Girardot], Parque Nacional Henri Pittier, Pico Periquito | [10.33909° –67.70320°] | 1100 m | 6.x.2008, O. Villarreal leg. (MNRJ 9327*); 1 ♂ 2 ♀, same locality as previous, Estación Biológica Rancho Grande, sendero Andrew Field, [10.34969°, –67.68471°], 6.x.2008, R. Batista and O. Villarreal leg. (MNRJ 9328*); 3 ♀ 2 ♂, same locality as previous, Hacienda La Trilla [vertiente norte], [10.38889°, –67.74611°], [128 m], x.2008, R. Batista, O. Villarreal, J. Valeria, C. Rodríguez, and Q. Arias leg. (MIZA 0105868, new Record); 5 ♂ 1 ♀, Cumboto, Hacienda Santa María, [10.3603º, –67.8218º], 650 m, 30.viii.2003, C. Rodríguez leg. (MIZA 0105906).

Paravima propespelunca González-Sponga, 1987

Figs 11, 12, 18

Paravima propespelunca González-Sponga, 1987: 486, figs 624–629; Kury, 2003: 31.

Paravima acanthoconus Villarreal-Manzanilla & DoNascimento, 2005: 102, figs 1–5. syn. nov.

Diagnosis. Paired tubercles on the mesotergal area III small and conical (in *P. lokura* **sp. nov.** large), the remaining *Paravima* lack ornamentation or have mammilliform, domed tubercles or spines).

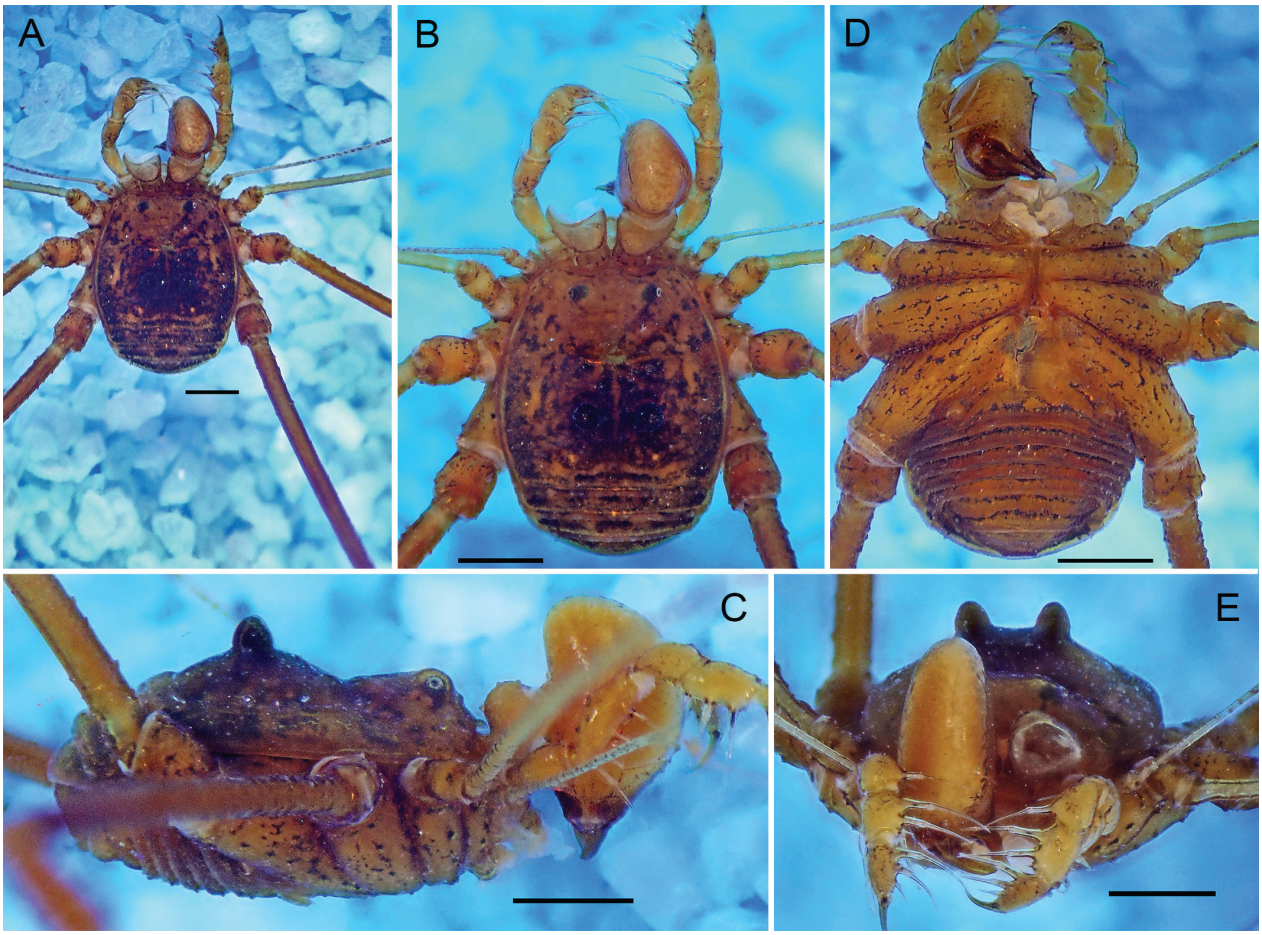

Figure 14. *Paravima totoro* **sp. nov.** (MNRJ 9255*) male holotype. Habitus: **A** Panoramic view; **B** dorsal view; **C** lateral view; **D** ventral view; **E** anterior view. Scale bars: 1 mm.

Description. See González-Sponga (1987). Here we offer a complementary description (based on MAGS 103, González-Sponga 1987: figs 624–629, and Villarreal-Manzanilla & DoNascimiento 2005: fig. 4): Margins of DS variegated. Anterior and lateral margins of DS smooth, posterior margin with some granules (Fig. 11A, B, D). Mesotergum ill delimited, divided into four areas: area I divided into two halves; areas II–IV undivided; area II with a pair of low tubercles centrally located; area III with a pair of paramedian conical tubercles (higher than ocularium) darker than the rest of the mesotergum (Fig. 11A–C). Anterior margin of coxa I with a high proximal conical tubercle (Fig. 11E). Fe IV four times DS length. Malleus of penis with one pair of branched MS-B; three pairs of branched MS-A; two pairs of medium-sized MS-D; one pair of MS-E2 large and branched. Stylus elongated and sinuous, surpassing the lamina parva (fig. 4).

Distribution. Known from Parque Nacional El Ávila and Birongo, Miranda state, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** *Paravima propespelunca*: Holotype ♂, VENEZUELA, Miranda, Acevedo, 4 km NW Birongo, near Cueva Alfredo Jahn | [10.48523° –66.24280°] | 210 m | 7.vii.1980, A.R. Delgado de González, J.A. González Delgado, and M.A. González-Sponga leg. (MCNC 969).–Paratypes 1 ♀, same data as preceding, 22.x.1983 (MCNC 970); 2 ♂ 6 ♀ 1 imm., same data as preceding, 9.iii.1985 (MAGS, not examined).–*Paravima acanthoconus*: Holotype ♂, VENEZUELA, Miranda, Parque Nacional El Ávila, [Guatire], Quebrada del Norte [Río del norte; | [10.51°, –66.52°] | [600 m] | 25.vi.2002, Villarreal O., Hernández L. leg. (MHNLS-IV-001).–Paratypes 1 ♀, same data as for preceding, 20.vi.2002, Villarreal O. leg. (MHNLS-IV-0002); 1 ♂ 2 ♀, same data as holotype (MHNLS-IV-0003, not examined). — ***Other material*:** VENEZUELA: 3 ♂♂ 6 ♀♀ 1 imm., Miranda, Dtto. [Distrito] Brión, Birongo, Quebrada Cambural, 7.viii.1980, 22.x.1983 and 9.iii.1985, RDG [Rosa Delgado de González], JAGD [José Antonio González Delgado], and MAGS [Manuel Ángel González Sponga] leg. (MAGS 103 (MIZA 0105926); material partially destroyed, very damaged; two males without genitals); 1 ♂ 2 imm., Salmerón, Distrito Zamora, [10.4666°, –66.3833°], [329 m.], 31.viii.1986 and 12.iii.1987, A.R. Delgado de González, Hernán Biord, and MAGS [Manuel Ángel González Sponga] leg. (MAGS 921 (MIZA 0105927)); 1 ♂, Zamora, Hacienda Santa Rosa, 8 km N from Guatire, [10.52741°, –66.52856°], 1125 m, 5.vii.1980, M. von D. [Miguel von Dangel], ARDG [Angela Rosa Delgado de González], JAGD [José Antonio González Delgado], and MAGS [Manuel Ángel González Sponga] leg. (MAGS 109 (MIZA 0105922)).

Remarks. We suspect that MAGS 103 corresponds to one of the male paratypes cited in type data as MAGS, without number. The synonym of *P. acanthoconus* with

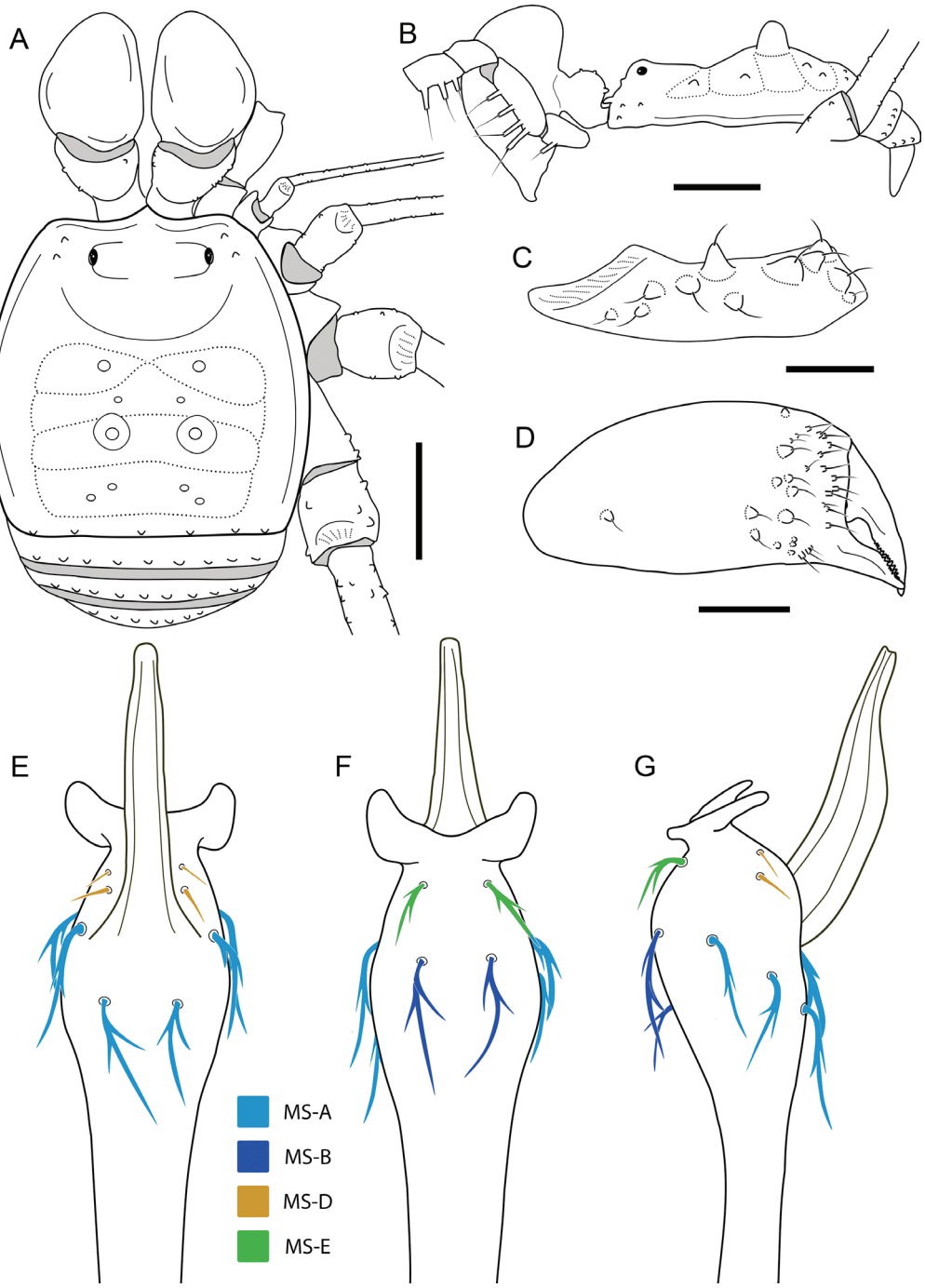

Figure 15. *Paravima totoro* **sp. nov.** (MNRJ 9255*) male holotype. **A** Habitus, dorsal view; **B** habitus, lateral view; **C** left coxa I, ventral view; **D** left chelicera, frontal view. Apical part of the penis in **E** dorsal view, **F** ventral view, and **G** lateral view. Scale bars: A, B = 1 mm; C, D = 0,5 mm (penis with not scaled figures). Abbreviation: Macrosetae (MS).

P. propespelunca is based in: (1) The drawing in the original description (González-Sponga, 1987: fig. 625) presents tubercles on area III with a slightly mammilliform shape which do not fully correspond to what is observed in the studied material (Fig. 11B–D). However, some unnoticed variations of the shape of these tubercles between different specimens were found (Fig. 12); (2) The schematic drawing of the genital morphology (figs 628, 629) shows a supposed reduction in the number of MS-A, absence of MS-D1-2, and a short and erected style, barely exceeding the height of the LP. Nevertheless, after examination of the male genitalia of *P. propespelunca*, we noted that this matches perfectly with that of *P. acanthoconus*; (3) Villarreal-Manzanilla & DoNascimiento (2005: fig. 3b) show that the pedipalpal femur of *P. acanthoconus* bears four spiniform tubercles (against five in *P. propespelunca*, very similar in its external morphology), but, after revision of new material, we noted that this is a variable character even in the same population or when comparing right and left pedipalp of the same individual, so, it is not a reliable character to differentiate species.

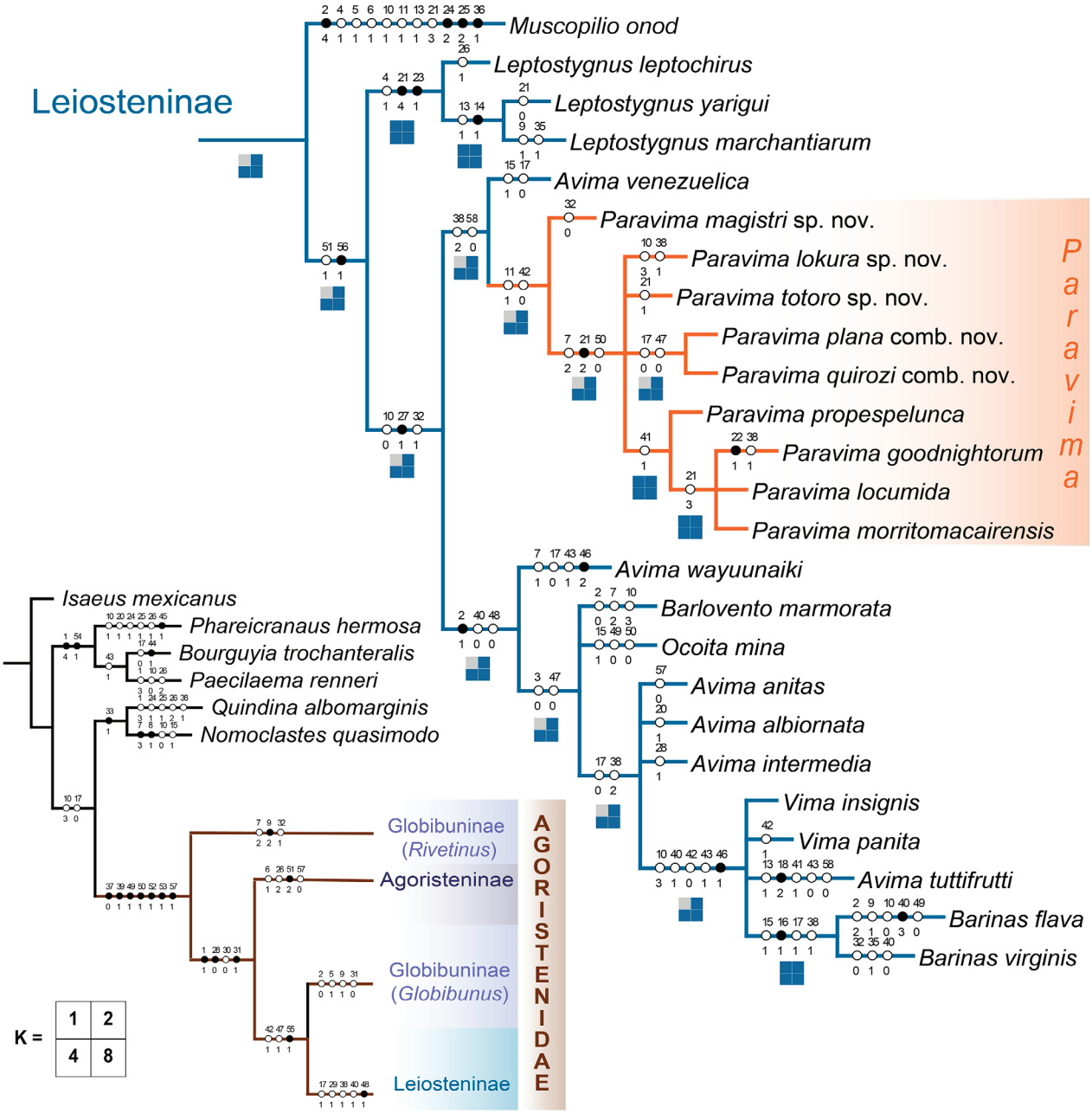

Figure 16. Phylogenetic relationship of Leiosteninae based on cladistic analyses using morphological data (in the left tree the terminals of Globibuninae and Agoristeninae are not shown; Globibuninae (*Rivetinus*) and Agoristeninae branches are condensed; the right tree is a continuation of the left tree). Sensitivity plots ('Navajo rugs') indicate the recovery of the nodes in the analyses under implied weights with K values of 1, 2, 4 and 8. Clear circles represent homoplastic synapomorphies and filled circles represent non-homoplastic synapomorphies.

Paravima quirozi (González-Sponga, 1981) comb. nov.

Figs 13, 19

Vima quirozi González-Sponga, 1981: 33, figs 1–4, 13; González-Sponga, 1987: 533, figs 690–695 (types MCNC 757, ♂ holotype; MCNC 758, 1 ♀ paratype; MAGS 294a–c, ♂ paratypes).

Trinella quirozi: Pinto-da-Rocha, 1996: 320; Kury 2003: 33.

Avima quirozi: Villarreal-M. & Kury, 2009: 67.

Trinella vigirima Villarreal-M. & Rodríguez-M., 2003: 178, figs 1–5. Syn. nov.

Avima vigirima: Villarreal-M. & Kury, 2009: 67.

Diagnosis. Mesotergal area III unarmed (shared with *P. quirozi* **comb. nov.**). The remining *Paravima* species have paired conical, mammilliform, spiniform or domed tubercles. Mesotergal areas with a semicircular or elliptical dark spot on the areas II and III.

Description. See González-Sponga (1981, 1987). Here we offer a complementary description (based on MCNC 757, MAGS 294, MIZA 0105916, and Villarreal-M & Rodriguez-Manzanilla, 2003: figs 1, 5): Anterior and lateral margins of DS smooth, posterior margin with some granules. DS variegated, mesotergum with an irregular dark spot covering the center of area I, all area II, and

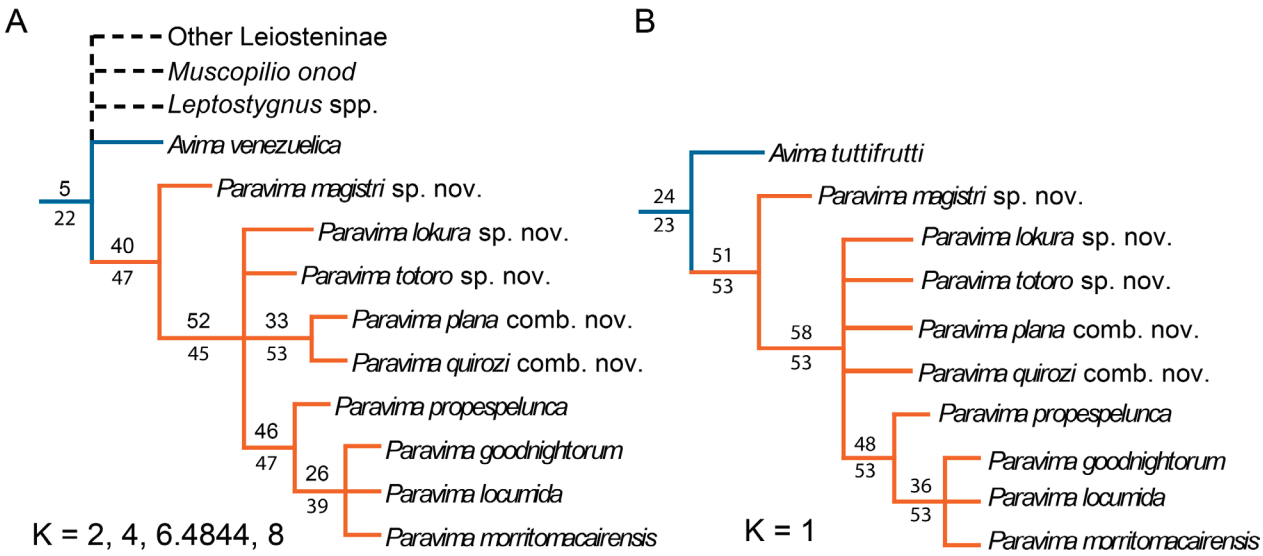

Figure 17. Simplified phylogenetic trees showing the relationships of *Paravima* Caporiacco, 1951 based on cladistic analyses using morphological data. **A** Consensus tree of the analysis using equal weights and implied weights with K values of 2, 4, 8 and 6.4844 (the dashed lines represent the unresolved relationships of other Leiosteninae under equal weights). **B** Analysis using implied weights with K = 1. The numbers in the nodes represent the bootstrap (above) and bremer relative (under) supports.

two-thirds of area III (Fig. 13A–E; figs 1a, b). Mesotergum delimited, divided into four areas: area I divided into two halves; areas II–IV undivided; areas I–IV with a pair of paramedian low tubercles, those of area III domed; areas II–IV with a wide hump (Fig. 13B–E; figs 1a, b). Pedipalpal segments slender (Fig. 13C; fig. 3). Legs increasing in thickness from leg I to leg IV. Leg I filiform. Legs III and IV with granules (Fig. 13C–E; fig. 4). Patella IV with some conspicuous distal tubercles (fig. 4). Tibia III–IV distally thickened. Fe IV is four and a half times DS length. Penis with small LP (height shorter than width), apex with anterolateral crescent-shaped corners (fig. 5). Hammer (malleus) with three pairs of branched MS-A; one pair of branched MS-B; two pairs of MS-D (fig. 5b); one pair of MS-E2 large and branched, MS-E1 absent (fig. 5). Stylus elongated, sigmoidal, surpassing the lamina parva (fig. 5).

Distribution. Known from Carabobo and Yaracuy states, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** *Vima quirozi*: Holotype ♂, VENEZUELA, Yaracuy, Urachiche, Maimire | [10.1550° –69.0102°] | 1200 m | 29.ix.1979, Neryz Quiroz and Tito Quiroz leg. (MCNC 757). — Paratypes 1 ♀, same data as holotype, (MCNC 758); 1 ♂, same data as holotype, (MAGS 294a, 294b and 294c). Remark: The original description of *P. quirozi* strangely lists one male paratype under codes MAGS 294a, 294b and 294c. However, only one lot MAGS 294 (MIZA 0105917) was found, containing 11 ♂, 8 ♀ and 2 imm. So, we believe that the male paratype cited by G-S is part of these male specimens. Besides that, we extracted and dissected one male from MIZA 0105917 (MIZA 0105916).–*Trinella vigirima*: Holotype ♂, VENEZUELA, Carabobo, Quebrada El Corozo, Parque Nacional San Esteban, sector Vigirima | lat 10º 21'N, long 67º 54'W [10.34276° –67.87613°] | 650 m | 14.vi.2003, L. Ovalles, L. Hernández, C. Rodríguez, O. Villarreal leg. (MHNLS IV-0126).–Paratypes 1 ♀, same data as holotype, (MHNLS IV-0127); 2 ♂ 2 ♀, same data as holotype, (MIZA 0025, not examined). — ***Other material*:** VENEZUELA: 2 ♂ 4 ♀, Yaracuy, La Guáquira, 10.2807° –68.6530°, 150 m, forest along stream, 17.ii.2020, B.A. Huber, O. Villarreal M., and Q. Arias C. leg. (MIZA 0105827, new Record); 1 ♂ 1 ♀, same data as previous, (MNRJ 60621).

Remarks. The differences in shape and size of the dark spot in the mesotergal areas of *P. quirozi* seems to be populational: specimens from Maimire (Yaracuy) have more rounded spots, individuals from La Guáquira (Yaracuy) exhibit wider and shorter spots (Fig. 19A, B) and specimens from Carabobo have an intermediate state. On the other hand, after revision of the male genitalia of paratypes of *P. quirozi*, we observe the presence of two pairs of MS-D and three pairs of MS-A, contrary to the original drawings of G-S that lacks MS-D and show just two pairs of MS-A (González-Sponga, 1981: fig. 13). Besides that, one of the male paratypes of *P. quirozi* from Yaracuy (MAGS 294) exhibits a gap between MS-A1 (most dorsal MS-A) and MS-A2/MS-A3 (located more basally). Not finding genital differences between the males studied, we prefer to synonymize both species and understand spot shape differences as intraspecific variations. Villarreal-M & Rodriguez-Manzanilla (2003: 181) suggested a morphological similarity between *Avima vigirima* syn. nov. *Paravima plana* **comb. nov.** and *Paravima quirozi* **comb. nov.**, which appears reflected in our analyzes (Figs 16, 17).

Paravima totoro sp. nov.

https://zoobank.org/06A646EB-4735-4078-B3A5-3A36A3ED964C

Figs 14, 15, 18

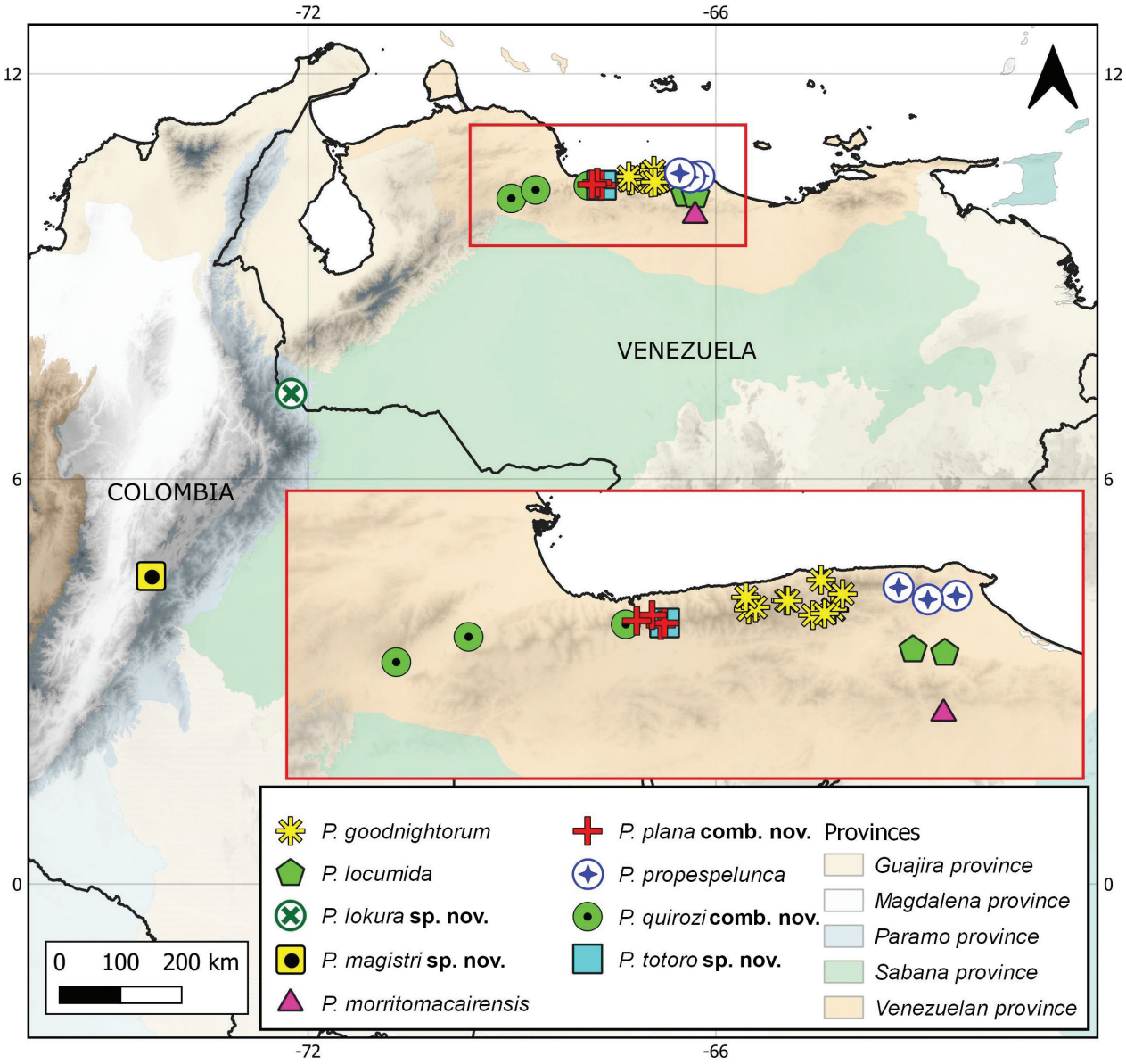

Figure 18. Map showing the geographic distribution of *Paravima* in Northern South America. The background colored shapes refer to the biogeographic provinces of Morrone et al. (2022).

Diagnosis. Mesotergal area III with paired dome-shaped tubercles (the remaining *Paravima* varies between acute spines, conical/mammilliform tubercles, or lack of tubercles). DS variegated, with mesotergal areas II–III darker in the center and gradually fading towards the laterals (in *P. magistri* **sp. nov.** variegated in the anterior region of DS; in the other *Paravima* species uniformly variegated).

Description. ***Holotype*** (MNRJ 9255*). Measurements: CL: 1.1, AL: 1.5, CW: 2.0, AW: 2.3, BaCh: 0.3, IOD: 0.9; Leg I (Tr: 0.3, Fe: 3.2, Pa: 0.3, Ti: 2.0, Mt: 4.5, Ta: 1.6); Leg II (Tr: 0.3, Fe: 8.2, Pa: 0.7, Ti: 6.0, Mt: 10.1, Ta: 3.4); Leg III (Tr: 0.5, Fe: 6.7, Pa: 1.0, Ti: 3.1, Mt: 7.0, Ta: 1.7); Leg IV (Tr: 0.6, Fe: 10.8, Pa: 1.1, Ti: 5.0, Mt: 10.0, Ta: 2.7). — *Dorsum*: Anterior and lateral margins of DS smooth. Ocularium smooth (Figs 14C, E, 15A). Mesotergum delimited, divided into four areas. Area I divided into two halves, each one with one tubercle; area II–IV undivided; II invading I, and with a pair of small tubercles close to the medial axis of the body (Fig. 15A); III with a pair of high paramedian domed tubercles (Figs 14C, E, 15B); IV with four small tubercles. Posterior border of scutum straight, with a row of small tubercles. Free tergites and anal operculum with some tubercles (Figs 14D, 15A). — *Venter*: Coxae I–IV with some granules (Fig. 14D). Coxa I with one medial tubercle on the anterior margin, a group of five tubercles on the proximal region, three large tubercles reaching the anterodistal margin, and two tubercles close to the posterodistal region (Fig. 15C); coxa II longer than coxa I; coxa III longer than I and II; coxa IV backward projected (Fig. 14D). Sternites and anal operculum with a few small tubercles. Stigmatic area smooth. Stigmata large, oval and transverse (Fig. 14D). — *Chelicerae*: Segment I rectangular, with well-marked bulla (Fig. 15A, B), one small ectal subdistal tubercle, and two tubercles on the proximal border (Fig. 14B). Chelicera swollen (Figs 14C, E, 15B). Hand with one tubercle at the mesal subapical

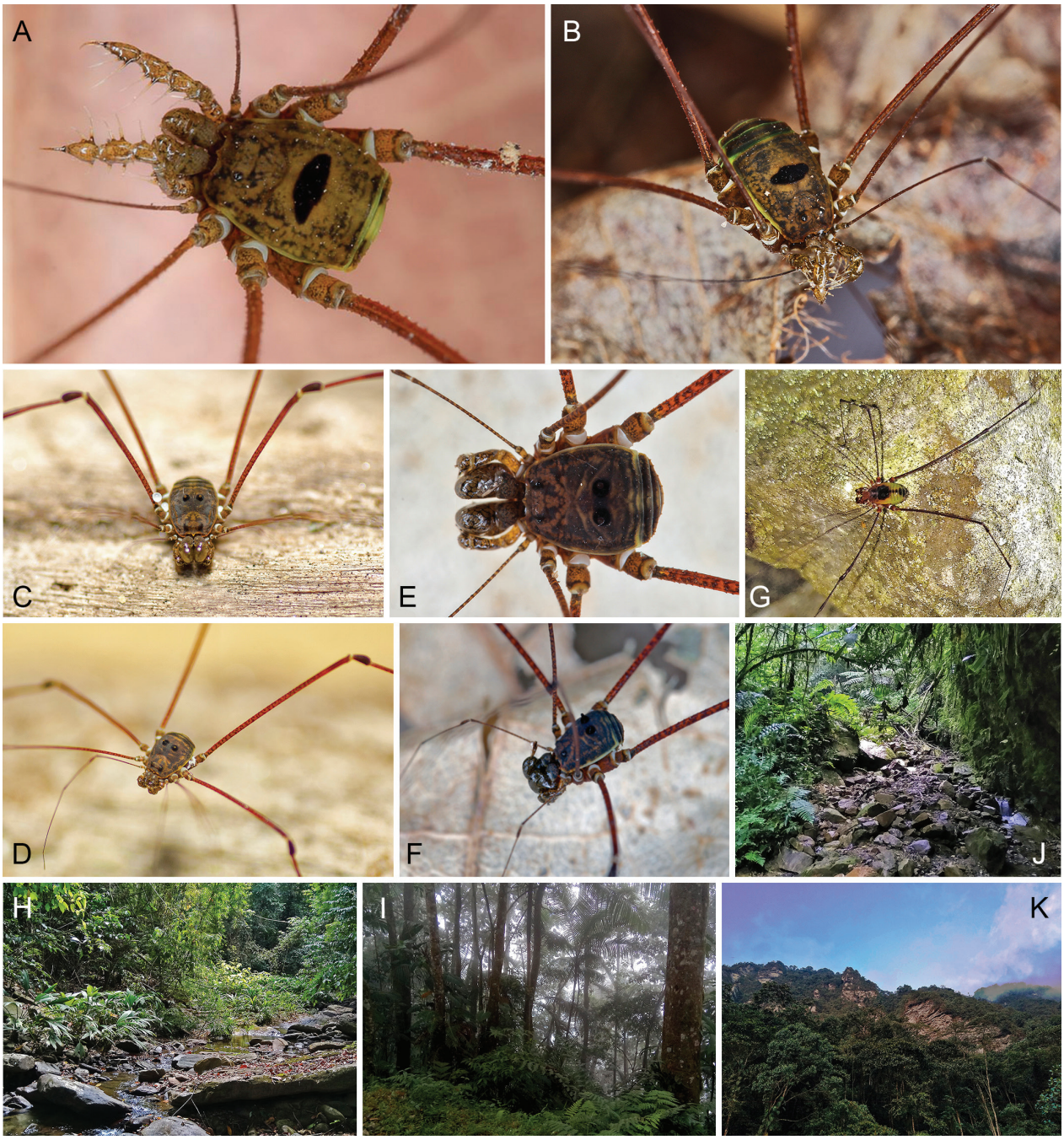

Figure 19. Living specimens and habitats of some *Paravima* spp. **A**, **B** *P. quirozi* from Yaracuy, Venezuela; **C**, **D** *P. goodnightorum,* from Cerro El Volcán, Miranda, Venezuela (MIZA 0105871); **E**, **F** *P. goodnightorum*, from La Guaira, Venezuela; **G** *P. magistri* **sp. nov.**, from San Antonio del Tequendama, Cundinamarca, Colombia; **H** La Guáquira, Yaracuy, habitat of *P. quirozi*; **I** Henri Pittier National Park, Aragua, Venezuela, habitat of *P. totoro* **sp. nov.**; **J**, **K** Los Tunos Natural Reserve, Cundinamarca, Colombia, habitat of *P. magistri* **sp. nov.**

region, a group of nine transversal tubercles going from ectal to mesal region, and a group of setiferous tubercles close to the base of the fingers (Fig. 15D). Fixed finger with some teeth on the inner surface. Movable finger with one trapezoid, sub-basal tooth and with the inner surface dentate (Fig. 16D). — *Pedipalps*: Longer than DS length, smooth. Tr ventrally with one subapical setiferous tubercle. Fe with a ventromesal row of five setiferous tubercles (the basalmost larger than the distalmost), and one large ventroectal setiferous tubercle in the distal portion (Fig. 14C, D). Pa with one large mesal setiferous tubercle. Ti ectal iII, mesal IIi. Ta ectal IIi, mesal IIi (Figs 14B, D). — *Legs*: Legs I–IV smooth. Leg I filiform, the rest, getting steadily thicker from leg II to IV (Fig. 14A). Fe IV four times DS length. Tarsal counts: 6(3)–6(3)/?–14(3)/7–7/7–7. — *Penis*: LP short and depressed, half-moon shaped, with anterolateral corners dorsally pointed (Fig. 15E–G). Malleus carrying three pairs of branched MS-A and one pair of branched MS-B (Fig. 15G). MS-D1-2 long, located in a vertical line on a keel between the LP and the base of the stylus (Fig. 15E, G). MS-E2 large and branched (Fig. 15F, G). Stylus sinuous, surpassing the lamina par-

va, narrower at distal region, tip irregular (Figs 15E–G). — *Color* (in ethanol): Carapace reticulated Dark Brown (59) on Deep Orange Yellow (51). Mesotergum, posterior border and free tergites Dark Brown (59). Pedipalps, chelicerae and legs Vivid Orange Yellow (66). — *Female*: Unknown.

Derivatio nominis. Totoro is a character in the Japanese animated fantasy film My Neighbor Totoro (directed by Hayao Miyazaki and animated by Studio Ghibli), being a friendly wood spirit in post-war rural Japan. For us, the paramedian armature of the new species resembles the ears of the charismatic Totoro. We take advantage of exalting the excellent work of Studio Ghibli with this tribute. Noun in apposition.

Distribution. Known just from the type locality, PN Henri Pittier, Aragua state, in the Venezuelan biogeographic province (Morrone et al. 2022) (Fig. 18).

Material examined. ***Type material*:** Holotype ♂, VENEZUELA, Aragua, Parque Nacional Henri Pittier, Rancho Grande | [10,34947° –67,6843°] | 1200 m | 31.iii.1983, C. Bordón leg. (MNRJ 9255*).

4. Discussion

The monophyly of *Paravima* has not been previously tested in a phylogenetic context, with former analyzes including a single species of the genus (Kury 1997, Pinto-da-Rocha & Hara 2009, Villarreal & García 2021). In the most recent hypothesis of generic relationship within Agoristenidae (Villarreal & García 2021), *Paravima* was positioned in a polytomy with two major clades within Leiosteninae, defined by one synapomorphy: (S1) stylus shape sinuous [ctr 41(1)] and three homoplastic synapomorphic characters: (HS1) DS outline shape Epsilon type 3 [ctr 2(2)]; (HS2) the ocularium placed close to the anterior margin of carapace [ctr 11(1)], and (HS3) absence of longitudinal dorsal keel of the stylus [ctr 42(0)].

In the present analysis, we found that character (S1) defines a derived group within *Paravima*, and occurs homoplastically in *Avima tuttifrutti*. Additionally, (HS1) was reinterpreted as the generalized condition in Agoristenidae, except for some cases (e.g. *Globibunus* Roewer, 1912, *Muscopilio* Villarreal & García, 2021, *Barlovento* González-Sponga, 1987, *Leptostygnus* Mello-Leitão, 1940, *Vima* Hirst, 1912, and some species of *Avima*). We obtained a monophyletic *Paravima* in all cases, defined by (a) ocularium placed close to the anterior margin of the carapace [ctr 11(1)], and (b) absence of longitudinal dorsal keel on the stylus [ctr 42(0)], both homoplastic synapomorphies (Fig. 16).

However, the internal relationships within *Paravima* have not been fully resolved (Figs 16, 17), mainly due to the limitation of not being able to study the genitalia of some species and the low degree of detail of previous descriptions. This led us to focus our analysis on the generic relationships of *Paravima* with other Leiosteninae and the generic rediagnosis.

Paravima magistri appears as sister group to the rest of the species, supported by (a) the proportion of interocular distance vs width of carapace; (b) the unmodified shape of the spines of area III and (c) MS-A quantity (only two pairs vs three pairs). The remaining taxa are clustered in a polytomy formed by two groups of species and two isolated species. The more specious group gathers most of the species with area III armed, from sectors further east of Cordillera de la Costa in Venezuela (except *P. totoro*). *P. plana* and *P. quirozi*, the unarmed species, are clustered for sharing, in addition to the absence of ornamentation on mesotergal area III [17(0)], the elongation of the base of the LP [47(0)] (Fig. 16).

Due to the unarmed mesotergal area III, these species were historically related to *Avima.* However, our study confirms the degree of homoplasy of this character. Other morphological similarities, which are now known to be shared with *Paravima*, were first detected by Villarreal-M & Rodríguez-Manzanilla (2003), but not tested in a phylogenetic analysis. Our results strongly support the monophyly of *Paravima*, but the internal relationships within the genus are not stable enough to propose any infrageneric or supraspecific taxonomic organization at this time.

The interpretation of some states of character in some species was difficult, due to the unavailability of genitalia specimens for study (e.g. *P. morritomacairensis*, *P. locumida*) which necessitated reliance on schematic drawings from the literature, e.g. MS D and MS E, being hard to discern between if these drawings are incomplete or if certain genital structures truly do not exist. Additionally, limited information on morphological variability (Fig. 12) has led to the description of species that we have now synonymized. The case of *Avima venezuelica* Soares & Avram, 1981, is particularly noteworthy. Some genital and external characters, such as the shape of DS or the LP of the penis, seem to indicate a possible relationship of this species with *Paravima*. However, its genitalia is only known from a simplified schematic drawing that is not fully informative. The phylogenetic position of *A. venezuelica* remains uncertain until the genitalia can be studied. A taxonomic decision regarding this species will require expanding the generic diagnosis to include it or creating a monotypic genus, as it does not conform to the *Avima* core diagnosis as defined by García et al. (2022a).

A parallel analysis under equal weights offers interesting results (Fig. 17A), recovering the monophyly of the genus and even get the same internal relations. The phylogenetic relationship with other genera is perhaps the main point of discrepancy between both analyzes (Fig. 17A). This inconsistency in the trees, as well as the degree of polytomy, suggest that our understanding of the relationships in Leiosteninae is still far from optimal, however, our approach allowed for improved diagnosis of the genus, the identification of monophyletic groups with biogeographic congruence, and provides direction for future studies to refine the hypotheses of relationships.

4.1. About the geographic distribution and habitats of *Paravima*

Little is known about the natural history of the *Paravima* species, with limited information available on the biomes and microhabitats they occupy. From a biogeographical approach, most species are restricted to the biogeographic Venezuelan province in the Cordillera de la Costa in Venezuela. However, two new species have been recorded in the Magdalena province in Colombia (Fig. 18), expanding the known distribution of the genus by approximately 500 km southwest and across other biogeographical provinces. Some groups of Neotropical Opiliones have a restricted geographic distribution, and they are associated with few or even a single biogeographical region (e.g. the cosmetids of the genus *Neocynorta* Roewer, 1915, in the Venezuelan Andes), however, this extreme degree of endemism may also be related with the lack of sampling to cover these false gaps, what is known as the Wallacean shortfall (Whittaker et al. 2005, Bini et al. 2006).

Paravima species occupy a wide range of altitudes and diverse biomes. Many of the species have been recorded from Montane Cloud Forests at altitudes between ~1200–1945 m a.s.l. (*P. totoro*, *P. plana*, *P. goodnightorum*) (Fig. 19F) or even higher (*P. lokura* and *P. magistri* in Andean Montane Forests, between 2170–2300 m a.s.l.) (Fig. 19H, I). *Paravima quirozi* is known from Subhumid tropophilous forest at 1200 m a.s.l., while *P. goodnightorum* is known from riparian forests at 160–900 m a.s.l. (Fig. 19C), in areas with high impact from human activities such as urban sprawl, agriculture, slash and burn (González-Sponga 1997, Villarreal-M & Rodríguez-Manzanilla 2003). *Paravima morritomacairensis* was described from semi-deciduous forests at ~850 m a.s.l. grown on a calcareous formation composed of three massifs, with numerous caves crossed by watercourses. *Paravima propespelunca* has been collected in transitional evergreen forests with marine influence (González-Sponga 1997).

Two major problems have affected the taxonomy of *Paravima*: (1) the use of the Roewerian taxonomic system and, (2) the incomplete original descriptions/drawings. The armature of the scutal area III was used for the creation of artificial groups, i.e. all the agoristenid without any armature on area III were classified as *Avima*, ignoring other characters, as the genital morphology (see García et al. 2022a). Following that criteria, a lot of unrelated species were grouped, including three that after a phylogenetic analysis have been transferred here to *Paravima*. Morphological homoplasy in some groups can make appearances deceiving. Additionally, the deficient/incomplete species descriptions have hindered the interpretation of characters and limited the degree of resolution in morphological analyses. Our analysis provides an important step in the diagnosis and redefinition of the genus; however, as new descriptions of the genitalia of the species are made, more robust relationship hypotheses with better resolution can be obtained and taxonomic decisions can be made more simply.

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Supplementary Material 1

Table S1

Authors: Garcia AF, Villarreal O (2023)
Data type: .docx
Explanation note: Matrix used in the phylogenetic analysis. Characters and character states are explained in Results.

Link: https://doi.org/10.3897/asp.81.e85571.suppl1