

Received: 28 March 2025 • Accepted: 28 August 2025 • Published: 20 November 2025

Topic editor: Tony Robillard • Section editor: Arnaud Henrard • Desk editor: Pepe Fernández

Research article

[urn:lsid:zoobank.org:pub:2D1E72FA-7236-40F6-9D22-DED6E774317D](https://zoobank.org/pub:2D1E72FA-7236-40F6-9D22-DED6E774317D)

New species of *Metagonia* Simon with directionally asymmetric male and female genitalia (Araneae, Pholcidae)

Bernhard A. HUBER^{1,*}   & Guanliang MENG^{1,2}  

¹Zoological Research Museum Alexander Koenig, LIB, Bonn, Germany.

²Present address: Institute of Zoology, Chinese Academy of Sciences, China.

*Corresponding author: b.huber@leibniz-lib.de

²Email: guanliang.meng@ioz.ac.cn

Abstract. Genital asymmetry is a rare phenomenon in spiders, and directional asymmetry, where all specimens are same-sided, is particularly scarce. In the New World genus *Metagonia*, only *M. mariguitarensis* (González-Sponga, 1998) was previously known to be directionally asymmetric. Here we describe three further species in the genus *Metagonia* that all share directionally asymmetric male and female genitalia: *M. embera* Huber sp. nov. (Colombia and Panama), *M. uca* Huber sp. nov. (Colombia), and *M. wayuu* Huber sp. nov. (Colombia and Venezuela). *Metagonia uca* is the species with the most extreme asymmetry and also the only species where female asymmetry is not limited to internal structures but extends to the epigynal scape. Interspecific CO1 distances among these four species ranged from 15.5 to 20.9%. Intraspecific distances mostly ranged from 0.0–1.7%, but higher values were found for *M. mariguitarensis* (up to 9.1%). While the available evidence suggests that directional asymmetry in *Metagonia* arose only once (in the last common ancestor of the four species above), the origin of the more widespread asymmetry in *Metagonia* (female antisymmetry) is less clear. We briefly discuss the phylogenetic pattern of antisymmetry in *Metagonia*, concluding that further focused research is necessary to provide the basic data for such an analysis.

Keywords. Antisymmetry, Colombia, CO1 barcodes, Panama, taxonomy, Venezuela.

Huber B.A. & Meng G. 2025. New species of *Metagonia* Simon with directionally asymmetric male and female genitalia (Araneae, Pholcidae). *European Journal of Taxonomy* 1026: 199–235.
<https://doi.org/10.5852/ejt.2025.1026.3117>

Introduction

While genital asymmetry is a common and widespread phenomenon in some arthropods such as insects, it is exceedingly rare in others, such as spiders (Huber *et al.* 2007; Huber 2010; Rivera-Quiroz *et al.* 2020). As a possible explanation, it has been suggested that one-sided mating positions are an option for animals with an unpaired median intromittent organ (such as the insect aedeagus) but not for animals with paired male genitalia (such as the spider pedipalps, or palps) (Huber *et al.* 2007; Huber 2010). In such a scenario, males in many insect groups may have been under selection to switch from the plesiomorphic

and symmetric female-above position to a position that gives the male more control over copulation. In many cases, such a switch will necessarily result in an asymmetric mating position. If the mating position becomes one-sided, this may cause or allow components of the genitalia to become asymmetric too. In spiders, both palps need to be employed to transfer the full amount of sperm, and in many cases also to supply both sides of the paired female internal sperm storage organs. While asymmetric mating positions have also evolved in spiders (e.g., Helversen 1976), the need to use both palps prevented the evolution of one-sided positions, i.e., males that use asymmetric mating positions typically shift from one side to the other within a single copulation. Symmetric and two-sided mating positions in spiders have apparently disfavored the evolution of asymmetric genitalia.

Pholcidae C.L. Koch, 1850 are among the few spider families with several cases of genital asymmetry, reflecting at least four independent origins (Huber *et al.* 2023). Pholcidae typically mate in a symmetric position, and both palps are usually inserted simultaneously. It has thus been suggested that asymmetry in Pholcidae may have originated via a different route than in insects, i.e., without involving evolutionary changes of mating position. One possibility that was proposed is the ‘space constraint hypothesis’ (Huber *et al.* 2007; Huber 2010): exaggerated male genital characters may require females to develop correspondingly complex internal genitalia that are difficult to arrange symmetrically within the available space. At some point, further female exaggeration may only be possible if one side is reduced, resulting in asymmetry. As long as the sidedness of the asymmetry is not fixed, i.e., females are antisymmetric rather than directionally asymmetric, there will be no selection on males to evolve asymmetry. This idea was developed based mainly on studies of the internal female genitalia of *Metagonia* Simon, 1893 and *Mesabolivar yuruani* (Huber, 2000) (Huber 2004, 2006). It remains unclear if and to which extent it may also apply to the other Pholcidae cases (*Panjange* Deeleman-Reinhold & Deeleman, 1986 and *Mecolaesthus* Simon, 1893) and to other spider families with several independent origins of genital asymmetry such as Oonopidae Simon, 1890.

In the species-rich New World genus *Metagonia*, female internal genital asymmetry seems to be common, and in most cases it seems to fall in the category of antisymmetry: roughly half of the females are ‘right-sided’, the other half are ‘left-sided’ (Huber 1997b; Huber & Villarreal 2020). Males in those species are symmetric. The only exception previously known was *M. mariguitarensis* (González-Sponga, 1998), a leaf-dwelling species originally described from Venezuela and later recorded from neighboring South American countries. In this species, all females are same-sided, and this directional asymmetry also extends to the male palps. Right male palps are overall much bigger than left palps. Intriguingly, however, the sperm containers, i.e., the genital bulbs, show the opposite pattern, with bigger left than right bulbs. It has thus been suggested that *M. mariguitarensis* males use their palps for different purposes: a predominantly stimulating right palp and a predominantly sperm transferring left palp (Huber 2004).

Here we describe two new species that appear closely related to *M. mariguitarensis* judging by numerous specific similarities, and one new species that may be the closest known relative of this ‘*mariguitarensis*-group’, judging by molecular data (Huber *et al.* 2022). All these species seem to share directionally asymmetric male and female genitalia (sample sizes are partly small), suggesting that this group of species represents a single origin of this rare phenomenon.

Material and methods

Material examined

The taxonomic part of this study is based on the examination of 160 adult specimens (listed in the descriptions below as well as Huber 2004 and Huber & Villarreal 2020), deposited in the following collections: Museo de Entomología de la Universidad del Valle, Cali, Colombia (MUSENUV);

Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK); and Zoological Museum of the University of Copenhagen, Denmark (ZMUC).

Taxonomy and morphology

Taxonomic descriptions follow the style of recent taxonomic work on *Metagonia* (e.g., Huber & Villarreal 2020; Huber *et al.* 2022; based on Huber 2000). Measurements were done on a Nikon SMZ18 stereo microscope with an ocular grid and are in mm unless otherwise noted; eye measurements are $\pm 5 \mu\text{m}$. Genital bulb diameter is given as the mean of bulb length and bulb width (as defined in Huber 2004: fig. 17). Photos were either made with a Canon EOS 2000D digital camera mounted on a Nikon SMZ18 stereo microscope or with a Nikon Coolpix 995 digital camera mounted on a Leitz Dialux 20 compound microscope. CombineZP (<https://combinezp.software.informer.com/>) was used for stacking photos. Drawings are partly based on photos that were traced on a light table and finalized under a stereo microscope, or they were directly drawn with a Leitz Dialux 20 compound microscope using a drawing tube. Cleared epigyna were stained with chlorazol black. The number of decimals in coordinates gives a rough indication about the accuracy of the locality data: four decimals means that the collecting site is within about 10 m of the indicated spot; three decimals: within ~ 100 m. The distribution map was generated with ArcMap ver. 10.0 (Environmental Systems Research Institute, Redlands, CA). Species descriptions are sorted by similarity to *Metagonia mariguitarensis*, the only previously known species of *Metagonia* with asymmetric male genitalia.

Abbreviations

ALE	=	anterior lateral eye(s)
ALS	=	anterior lateral spinneret(s)
AME	=	anterior median eye(s)
a.s.l.	=	above sea level
L/d	=	length/diameter
PME	=	posterior median eye(s)
PMS	=	posterior median spinneret(s)

Abbreviations used in figures only are explained in the figure legends.

Molecular data and analyses

Of the eleven ingroup CO1 barcodes used in this study (Table 1), four were newly generated using Sanger sequencing as described in Huber & Meng (2024) (UH codes in Table 1), seven were taken from the literature (JA23 from Astrin *et al.* 2006, M codes and BH codes from Huber *et al.* 2022). As a root, we used *Metagonia taruma* Huber, 2000 (from Huber *et al.* 2022). DNA extraction, amplification, sequencing, barcode assembly, and alignment followed the same protocols as described in Huber *et al.* (2024). A neighbor-joining (NJ) tree (Saitou & Nei 1987) and genetic distances among specimens were calculated using the Kimura 2-parameter model (Kimura 1980) in MEGA 11 (Tamura *et al.* 2021), during which pairwise deletion of gaps in the alignment was applied. The NJ tree was assessed with 5000 bootstrap replications (Felsenstein 1985).

Table 1. Geographic origins and GenBank accession numbers of ingroup specimens. Specimens are sorted as in Fig. 23. Previously published sequences are included for the sake of completeness: BH codes and M codes from Huber *et al.* 2022; JA23 from Astrin *et al.* 2006.

Code	Genus	Species	Vial	Country	Admin	Locality	Lat	Long	COI
UH542	<i>Metagonia</i>	<i>uca</i> sp. nov.	Col238	Colombia	Quindío	Armenia, Universidad del Quindío	4.5537	-75.6608	PV788227
UH254	<i>Metagonia</i>	<i>uca</i> sp. nov.	Col237	Colombia	Quindío	N of Circasia, Bosque del Silencio	4.6411	-75.6379	PV788224
UH260	<i>Metagonia</i>	<i>embera</i> sp. nov.	Col247	Colombia	Risaralda	near Santa Cecilia	5.3458	-76.1094	PV788225
M025	<i>Metagonia</i>	<i>embera</i> sp. nov.	Car260	Colombia	Chocó	Jardín Botánico del Pacífico	6.2663	-77.3749	OL870383
UH288	<i>Metagonia</i>	<i>wayuu</i> sp. nov.	Col290	Colombia	La Guajira	Tomarrazón	11.0701	-72.9357	PV788226
M092	<i>Metagonia</i>	<i>wayuu</i> sp. nov.	Ven20-149	Venezuela	Falcón	near Santa Cruz de La Alegria	10.8795	-68.4949	OL870413
BH45	<i>Metagonia</i>	<i>mariguitarensis</i>	Ven18-163	Venezuela	Bolívar	Ciudad Guayana, Parque La Llovizna	8.3130	-62.6724	OL870335
BH118	<i>Metagonia</i>	<i>mariguitarensis</i>	Ven18-163	Venezuela	Bolívar	Ciudad Guayana, Parque La Llovizna	8.3130	-62.6724	OL870348
BH46	<i>Metagonia</i>	<i>mariguitarensis</i>	Ven02/100-43	Venezuela	Sucre	Marigüitar	10.4390	-63.9080	OL870336
BH117	<i>Metagonia</i>	<i>mariguitarensis</i>	Ven02/100-43	Venezuela	Sucre	Marigüitar	10.4390	-63.9080	OL870347
JA23	<i>Metagonia</i>	<i>mariguitarensis</i>	Ven02/100-43	Venezuela	Sucre	Marigüitar	10.4390	-63.9080	DQ667887

Results

Taxonomy

Class Arachnida Lamarck, 1801
 Order Araneae Clerck, 1757
 Family Pholcidae C.L. Koch, 1850
 Genus *Metagonia* Simon, 1893

Metagonia mariguitarensis (González-Sponga, 1998)
 Figs 1A–B, 2A–B, 3–7

Anomalaiia mariguitarensis González-Sponga, 1998: 25, figs 21–32 (fig. 28 missing).

Metagonia mariguitarensis – Huber 2000: 67, figs 256–263 (except specimens from Peru, figs 264–267, see Distribution below); 2004: 318, figs 15–28. — Carvalho *et al.* 2017: 13. — Huber & Villarreal 2020: 179, figs 640–643, 1052 (except specimens from Falcón, see Distribution below). — Huber *et al.* 2022: 678 (molecular data, except specimen M092 *Metagonia mariguitarensis* Ven20-149, see *Metagonia wayuu* sp. nov. below).

Notes

This species has been studied extensively (see synonymy) and we do not have new material. However, it is included here because two very similar species newly described below require an updated diagnosis, and because a few details were missing in previous studies. In addition, some specimens previously assigned tentatively to this species are now considered to belong to other species (see Distribution below).

Diagnosis

Leaf-dwelling, long-legged pholcid with dark pattern on carapace (Figs 1–2). Easily distinguished from most known congeners (except *M. wayuu* sp. nov. and *M. uca* sp. nov.) by strongly asymmetric male palps (Figs 3–4; including asymmetry of femur and tibia), by male chelicerae with pair of strong lateral protrusions (Fig. 5A), and by female external and internal genitalia (Figs 5C, 6–7; epigynum with posterior semicircular process, or ‘scape’; internal genitalia with complex system of pouches, ducts, and folds). Distinguished from both *M. wayuu* and *M. uca* by male chelicerae with rounded rather than pointed distal apophyses (Fig. 5A), by main branch of left procurus with distinctive ventral indentation (bold arrow in Fig. 4C), by hair-like process on right procurus (arrow in Fig. 4D), and by less pronounced palpal asymmetry, i.e., absolutely and relatively smaller right palp (e.g., right/left tibia diameter <2.5 vs >2.6; see also Fig. 22). Further distinguished from *M. uca* by different color pattern on carapace (both in males and females; Fig. 2), by smaller size and shorter legs (e.g., male tibia 1 \leq 5.0 vs \geq 6.5; female tibia 1 \leq 4.0 vs \geq 5.5), and by female external genitalia (epigynal scape without asymmetric groove; compare Fig. 6B with Fig. 16B).

Description (amendments; see Huber 2000, 2004)

Right procurus with hair-like process on retrolateral side (arrow in Fig. 4D). Prolateral trichobothrium absent on tibia 1, present on other leg tibiae. Female tibia 1 length (N = 50): 3.2–3.8 (mean 3.5). Shape of pore plates slightly variable (Fig. 7B, D).

Barcodes

We sequenced five specimens from two localities (geographic distance: 270 km) (Table 1; Fig. 23). Within localities, distances were 0.0%; between localities, distances ranged from 8.4–9.1% (Table 2). Distances to the other three species treated herein ranged from 15.5 to 20.2 %.

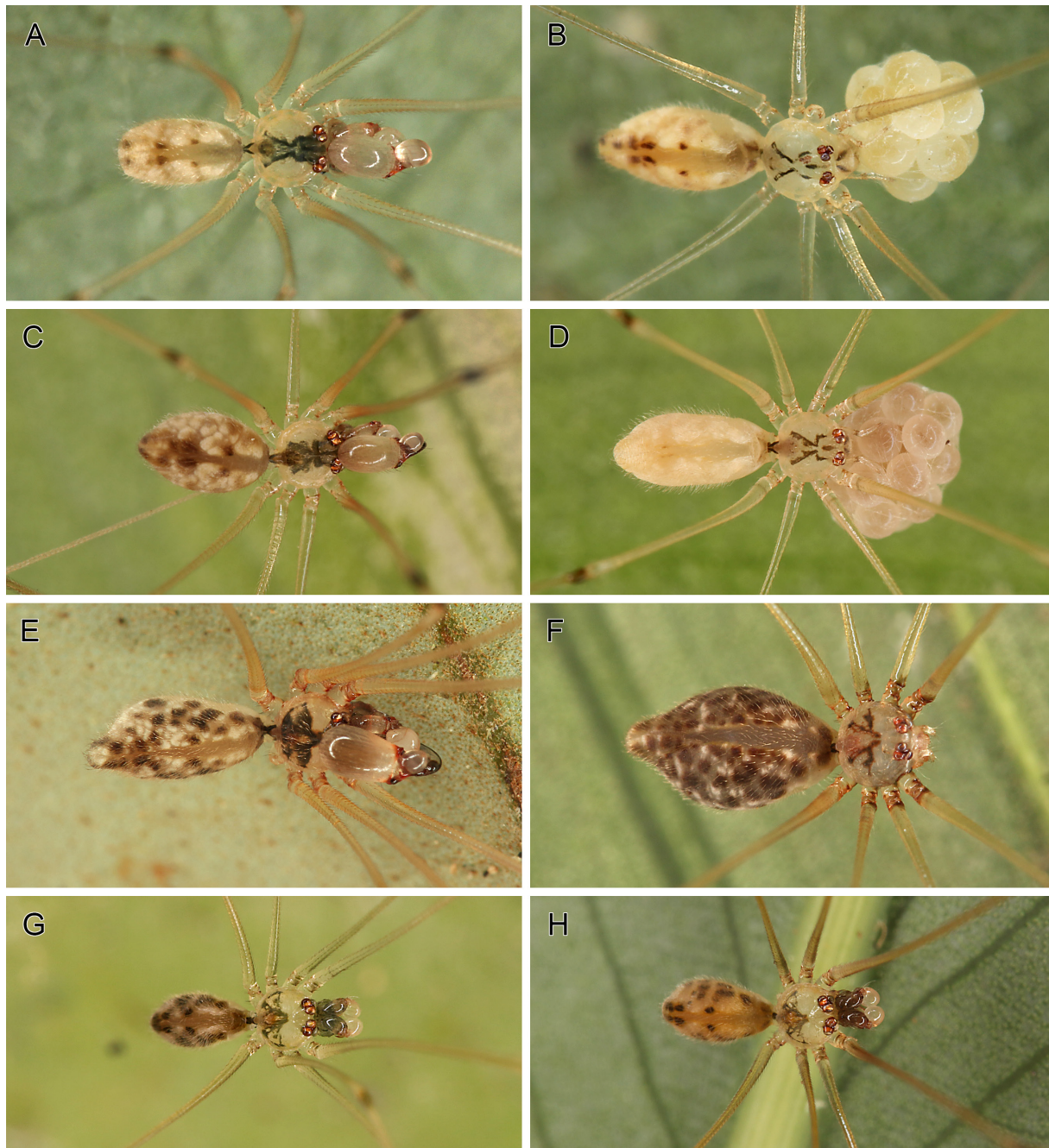


Fig. 1. Life specimens. **A–B.** *Metagonia mariguitarensis* (González-Sponga, 1998), male and female with eggsac from Venezuela, Ciudad Guayana, Parque La Llovizna. **C–D.** *Metagonia wayuu* Huber sp. nov., male and female with eggsac from Colombia, La Guajira, Tomarrazón. **E–F.** *Metagonia uca* Huber sp. nov., from Colombia, Quindío, Armenia and female from Quindío, Bosque del Silencio. **G–H.** *Metagonia embera* Huber sp. nov., males from Colombia, Risaralda, Santa Cecilia. At various scales.

Table 2. CO1 K2P genetic distances among ingroup specimens. Bold numbers are intraspecific distances (N = 13, 0.0–9.1%, mean 4.2%), interspecific distances (N = 42): 15.5–20.9% (mean 18.5%).

	UH254	UH542	M025	UH260	M092	UH288	BH45	BH118	BH46	JA23
UH254 <i>Metagonia uca</i> Col237										
UH542 <i>Metagonia uca</i> Col238	0.002									
M025 <i>Metagonia embera</i> Car260	0.205	0.209								
UH260 <i>Metagonia embera</i> Col247	0.200	0.205	0.006							
M092 <i>Metagonia wayuu</i> Ven20-149	0.192	0.195	0.173	0.172						
UH288 <i>Metagonia wayuu</i> Col290	0.200	0.203	0.169	0.167	0.017					
BH45 <i>Metagonia mariguitarensis</i> Ven18-163	0.195	0.193	0.190	0.186	0.159	0.164				
BH118 <i>Metagonia mariguitarensis</i> Ven18-163	0.195	0.193	0.190	0.186	0.159	0.164	0.000			
BH46 <i>Metagonia mariguitarensis</i> Ven02/100-43	0.188	0.191	0.188	0.188	0.155	0.164	0.084	0.084		
JA23 <i>Metagonia mariguitarensis</i> Ven02/100-43	0.197	0.202	0.194	0.194	0.176	0.189	0.091	0.091	0.000	
BH117 <i>Metagonia mariguitarensis</i> Ven02/100-43	0.188	0.191	0.188	0.188	0.155	0.164	0.084	0.084	0.000	0.000

Distribution

Known from several localities in eastern Venezuela (Sucre, Bolívar) and northwestern Brazil (Roraima) (Fig. 24). The females from Falcón listed in Huber & Villarreal (2020) are here assigned to the newly described *M. wayuu* sp. nov. (see below). Specimens from Peru listed and illustrated in Huber (2000) are considered to represent a distinct, formally undescribed species (or more than one species).

Metagonia wayuu Huber sp. nov.

[urn:lsid:zoobank.org:act:BCE082D1-FE9C-446F-BD02-AA5ACA06CBE2](https://zoobank.org/urn:lsid:zoobank.org:act:BCE082D1-FE9C-446F-BD02-AA5ACA06CBE2)

Figs 1C–D, 2C–D, 8–12

Metagonia mariguitarensis – Huber & Villarreal 2020: 179 (misidentification; specimens from Falcón only).

— Huber *et al.* 2022: 678 (molecular data, specimen M092 *Metagonia mariguitarensis* Ven20-149).

Diagnosis

Easily distinguished from most known congeners (except *M. mariguitarensis* and *M. uca* sp. nov.) by strongly asymmetric male palps (Fig. 8), by male chelicerae with pair of strong lateral protrusions

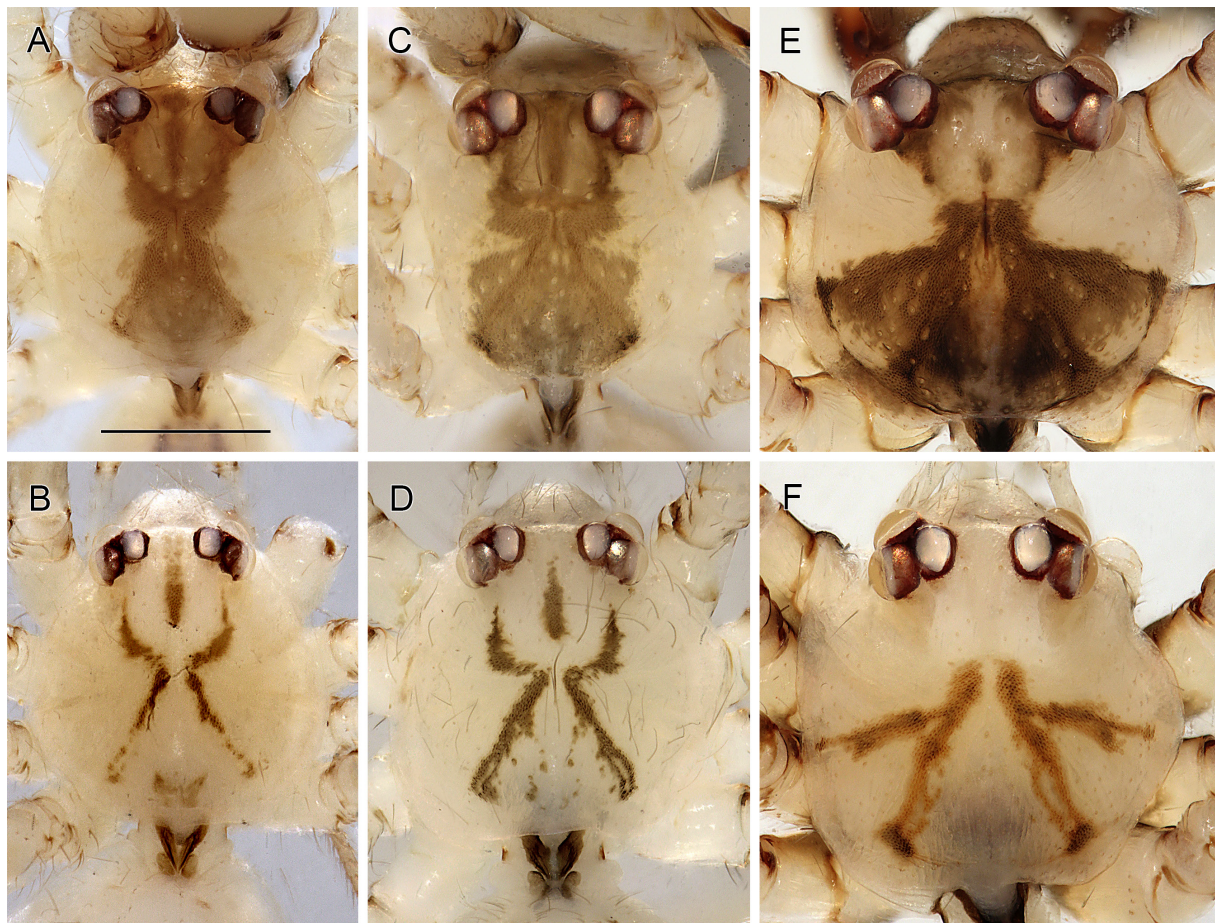


Fig. 2. Male (top) and female (bottom) prosomata, dorsal views, at same scale. **A–B.** *Metagonia mariguitarensis* (González-Sponga, 1998), from Venezuela, Sucre, Marigüitar (ZFMK Ar 22011). **C–D.** *Metagonia wayuu* Huber sp. nov., paratypes from Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). **E–F.** *Metagonia uca* Huber sp. nov., paratypes from Colombia, Quindío, Armenia (ZFMK Ar 24781, 24782). Scale line = 0.5 mm.

(Fig. 10A), and by female external and internal genitalia (Figs 11–12; epigynum with posterior semicircular process, or ‘scape’; internal genitalia with complex system of pouches, ducts, and folds). Distinguished from *M. mariguitarensis* by male chelicerae with pointed rather than rounded distal apophyses (Fig. 10A), by main branch of left procurus without distinctive ventral indentation (compare Fig. 4C with Fig. 9C), by absence of hair-like process on right procurus (compare Fig. 4D with Fig. 9D), and by stronger palpal asymmetry, i.e., absolutely and relatively bigger right palp (e.g., right/left tibia diameter >2.6 vs <2.5; see also Fig. 22). Further distinguished from *M. uca* by different color pattern on on

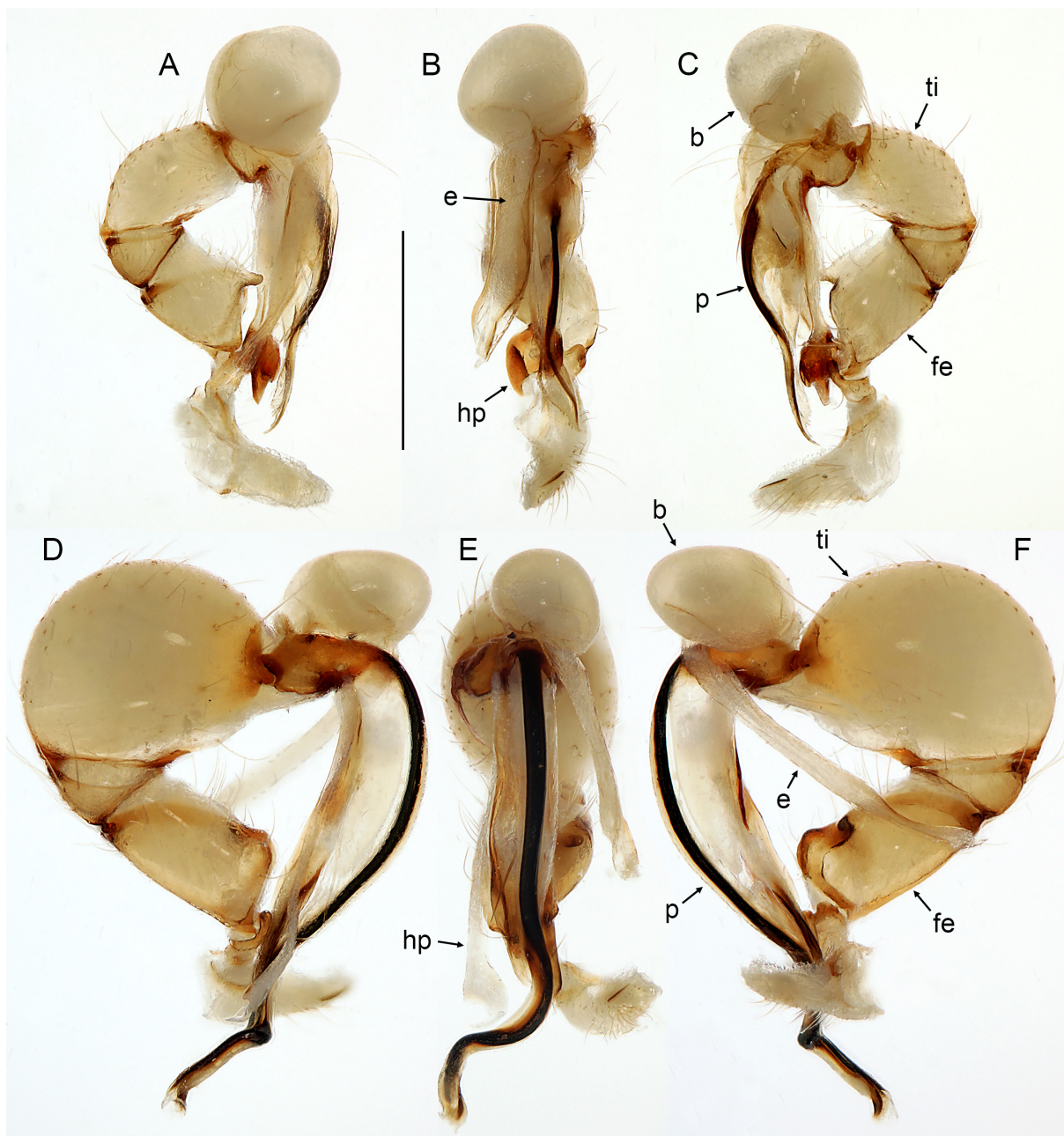


Fig. 3. *Metagonia mariguitarensis* (González-Sponga, 1998), male from Venezuela, Sucre, Marigüitar (ZFMK Ar 17867). Left and right palps at same scale. **A–C.** Left palp, prolateral, dorsal, and retrolateral views. **D–F.** Right palp, retrolateral, dorsal, and prolateral views. Abbreviations: b = genital bulb; e = embolus; fe = femur; hp = hinged process; p = procurus (main branch); ti = tibia. Scale line = 0.5 mm.

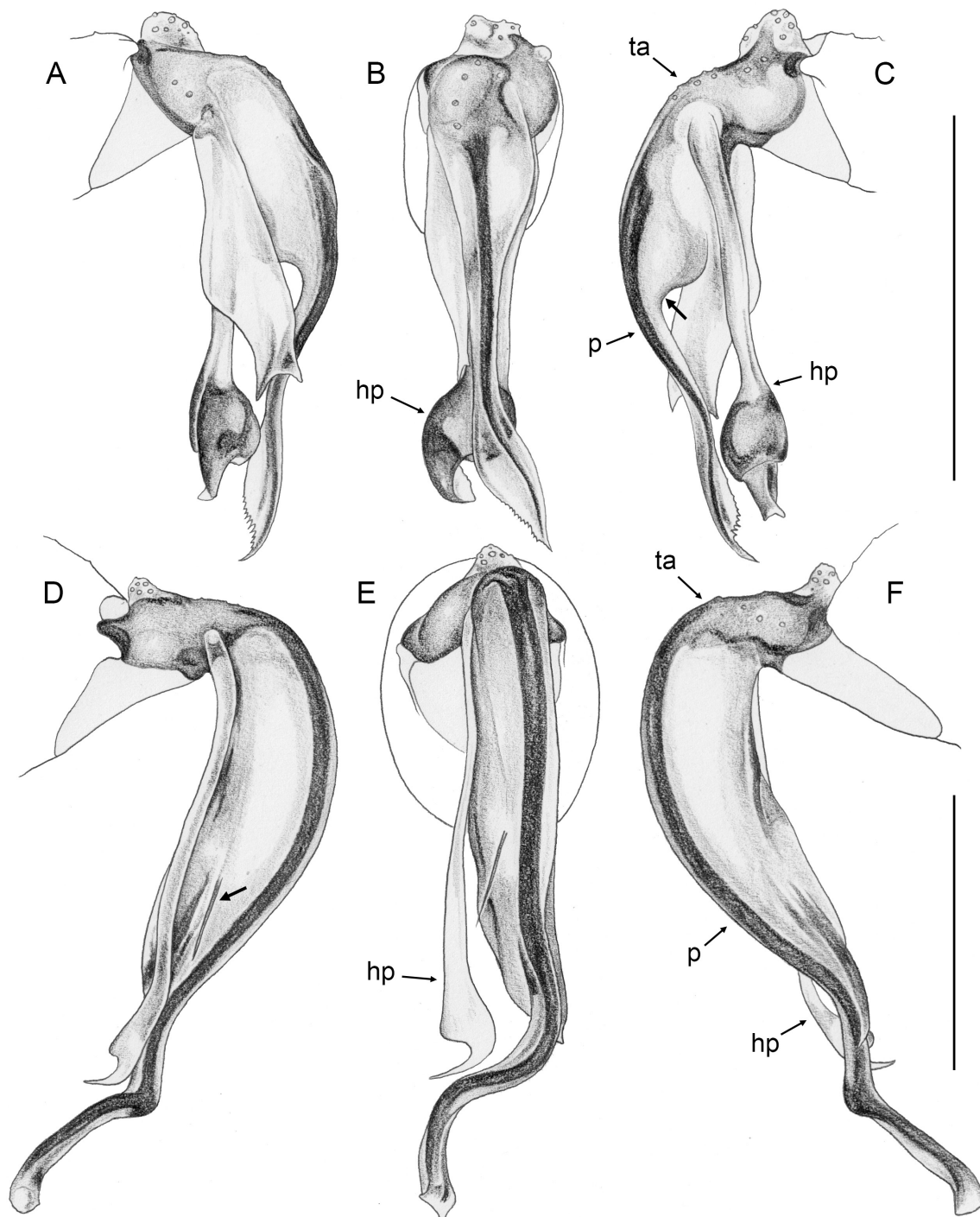


Fig. 4. *Metagonia mariguitarens* (González-Sponga, 1998), male from Venezuela, Sucre, Marigüitar (ZFMK Ar 17867). Left and right palpal tarsi and procursi at different scales. **A–C.** Left tarsus and procursus, prolateral, dorsal, and retrolateral views; bold arrow in C points at distinctive ventral indentation of main branch of procursus. **D–F.** Right tarsus and procursus, retrolateral, dorsal, and prolateral views; arrow in D points at hair-like process on main branch of procursus. Abbreviations: hp = hinged process; p = procursus (main branch); ta = tarsus. Scale lines = 0.5 mm.

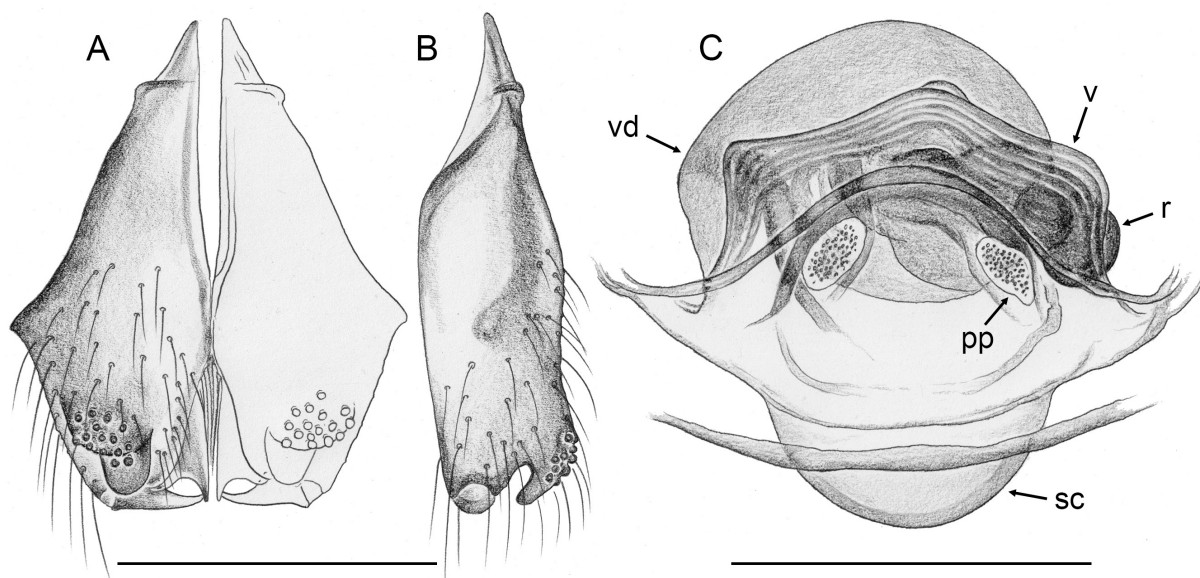


Fig. 5. *Metagonia mariguitarensis* (González-Sponga, 1998), from Venezuela, Sucre, Marigüitar. **A–B.** Male chelicerae, frontal and lateral views (ZFMK Ar 17867). **C.** Cleared female genitalia, dorsal view (ZFMK Ar 17944). Abbreviations: pp = pore plate; r = receptacle; sc = scape; v = valve; vd = “ventral duct” of Huber (2004). Scale lines = 0.3 mm.

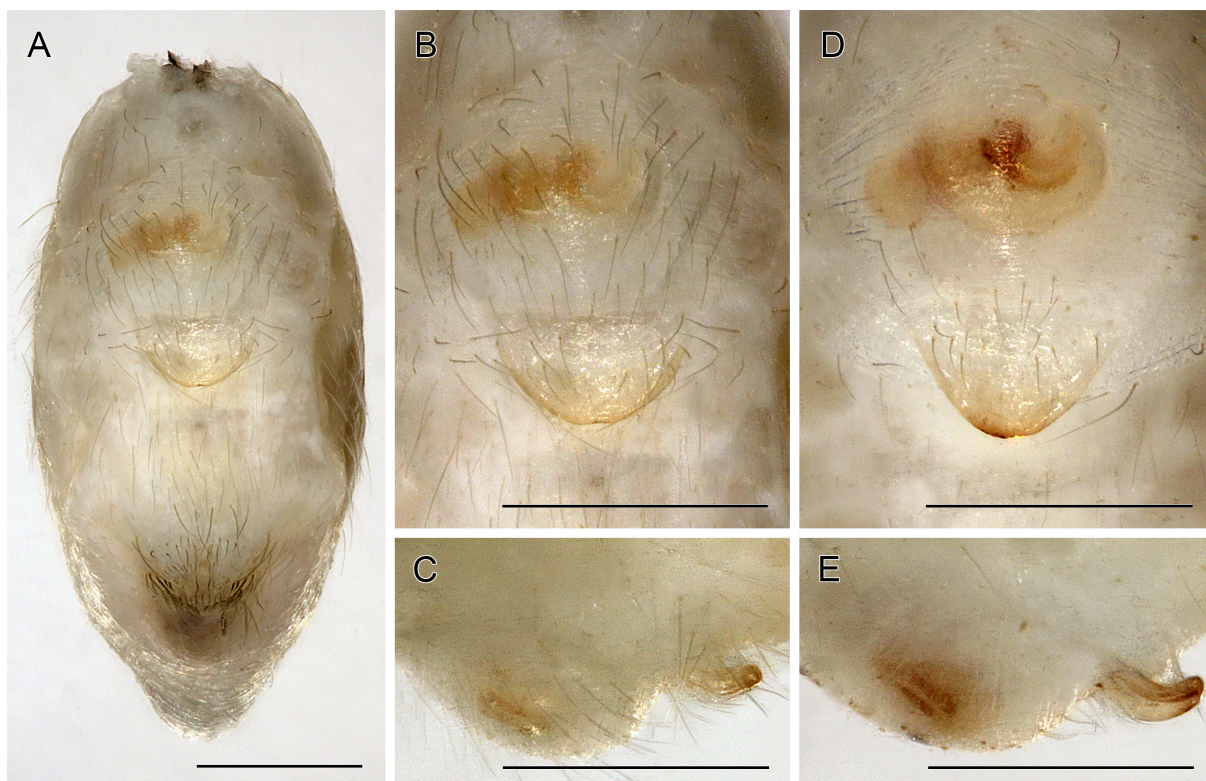


Fig. 6. *Metagonia mariguitarensis* (González-Sponga, 1998), females. **A–C.** From Venezuela, Sucre, Marigüitar (ZFMK Ar 17944). **D–E.** From Bolívar, Ciudad Guayana (ZFMK Ar 22014). **A.** Abdomen, ventral view. **B, D.** Epigyna, ventral views. **C, E.** Epigyna, lateral views. Scale lines = 0.3 mm.

carapace (both in males and females; Fig. 2), by smaller size and shorter legs (e.g., male tibia 1 \leq 5.0 vs \geq 6.5; female tibia 1 \leq 4.0 vs \geq 5.5), and by female genitalia (epigynal scape without asymmetric groove; compare Fig. 11B with Fig. 16B).

Etymology

The species name honors the Wayuu, an indigenous ethnic group of the Guajira Peninsula in northernmost Colombia and northwestern Venezuela.

Type material

Holotype

COLOMBIA – La Guajira • ♂; Tomarrazón; 11.0701° N, 72.9357° W; 310 m a.s.l.; 19 Sep. 2022; B.A. Huber leg.; degraded forest along river; MUSENUV Ar 3531.

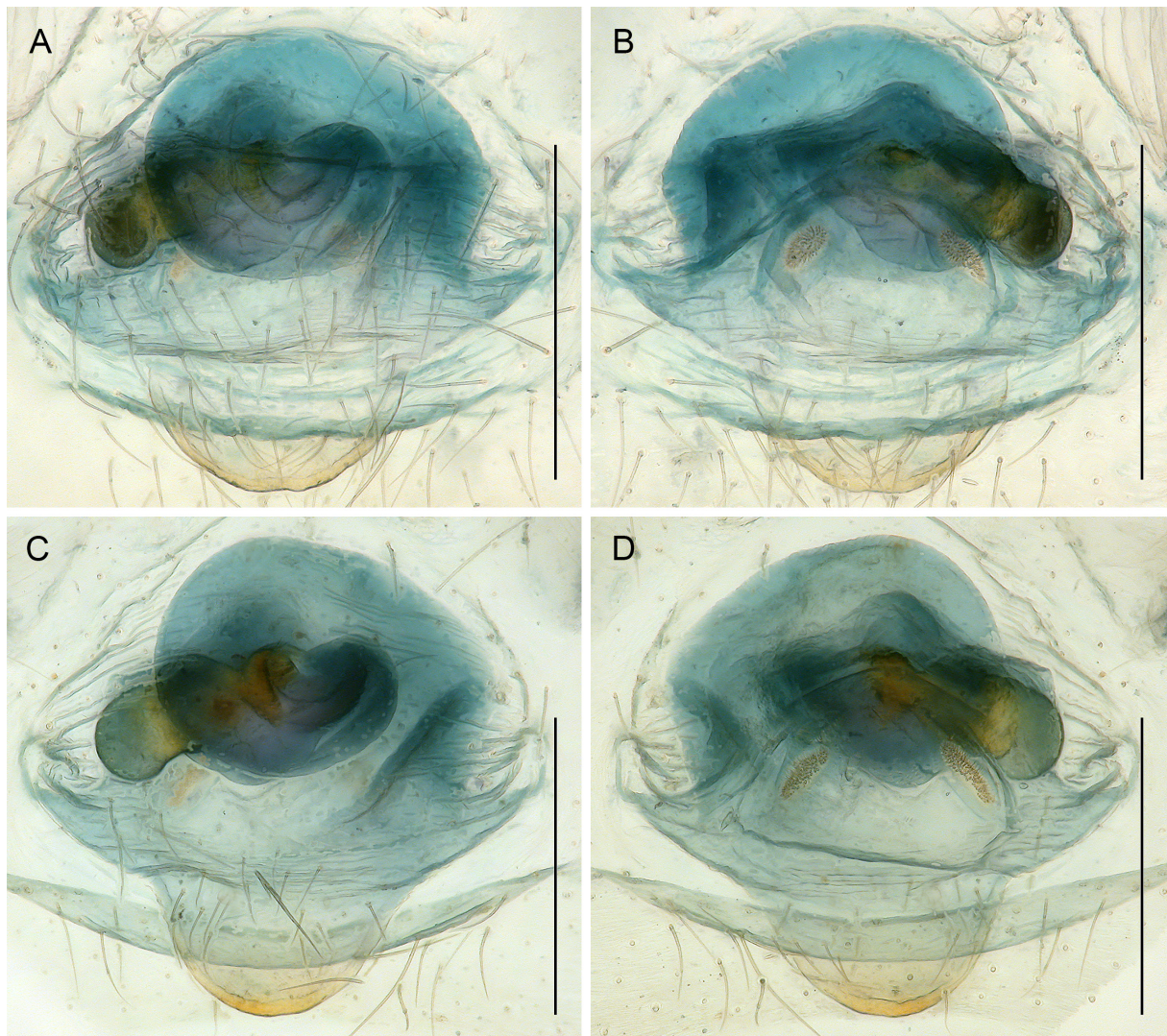


Fig. 7. Fig. 7. *Metagonia mariguitarensis* (González-Sponga, 1998), cleared female genitalia in ventral (A, C) and dorsal (B, D) views. **A–B.** From Venezuela, Sucre, Marigüitar (ZFMK Ar 17944). **C–D.** From Venezuela, Bolívar, Ciudad Guayana (ZFMK Ar 22014). Scale lines = 0.3 mm.

Paratypes

COLOMBIA – **La Guajira** • 1 ♂, 2 ♀♀; same collection data as for holotype; MUSENUV Ar 3532 • 2 ♂♂, 2 ♀♀; same collection data as for holotype; ZFMK Ar 24780.

Other material examined

COLOMBIA – **La Guajira** • 4 ♀♀, in pure ethanol; same collection data as for holotype; ZFMK Col290 (voucher of UH288; one abdomen cleared and transferred to ZFMK Ar 24780).

VENEZUELA – **Falcón** • 1 ♀; forest near Santa Cruz de La Alegria; 10.8795° N, 68.4949° W; 100 m a.s.l.; 15 Feb. 2020; B.A. Huber, O. Villarreal M. and Q. Arias C. leg.; ZFMK Ar 22013 • 4 ♀♀, in pure ethanol; same collection data as for preceding; ZFMK Ven20-149 (voucher of M092).



Fig. 8. *Metagonia wayuu* Huber sp. nov., paratype, ♂, from Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). Left and right palps at same scale. A–C. Left palp, prolateral, dorsal, and retrolateral views. D–F. Right palp, retrolateral, dorsal, and prolateral views. Scale line = 1 mm.

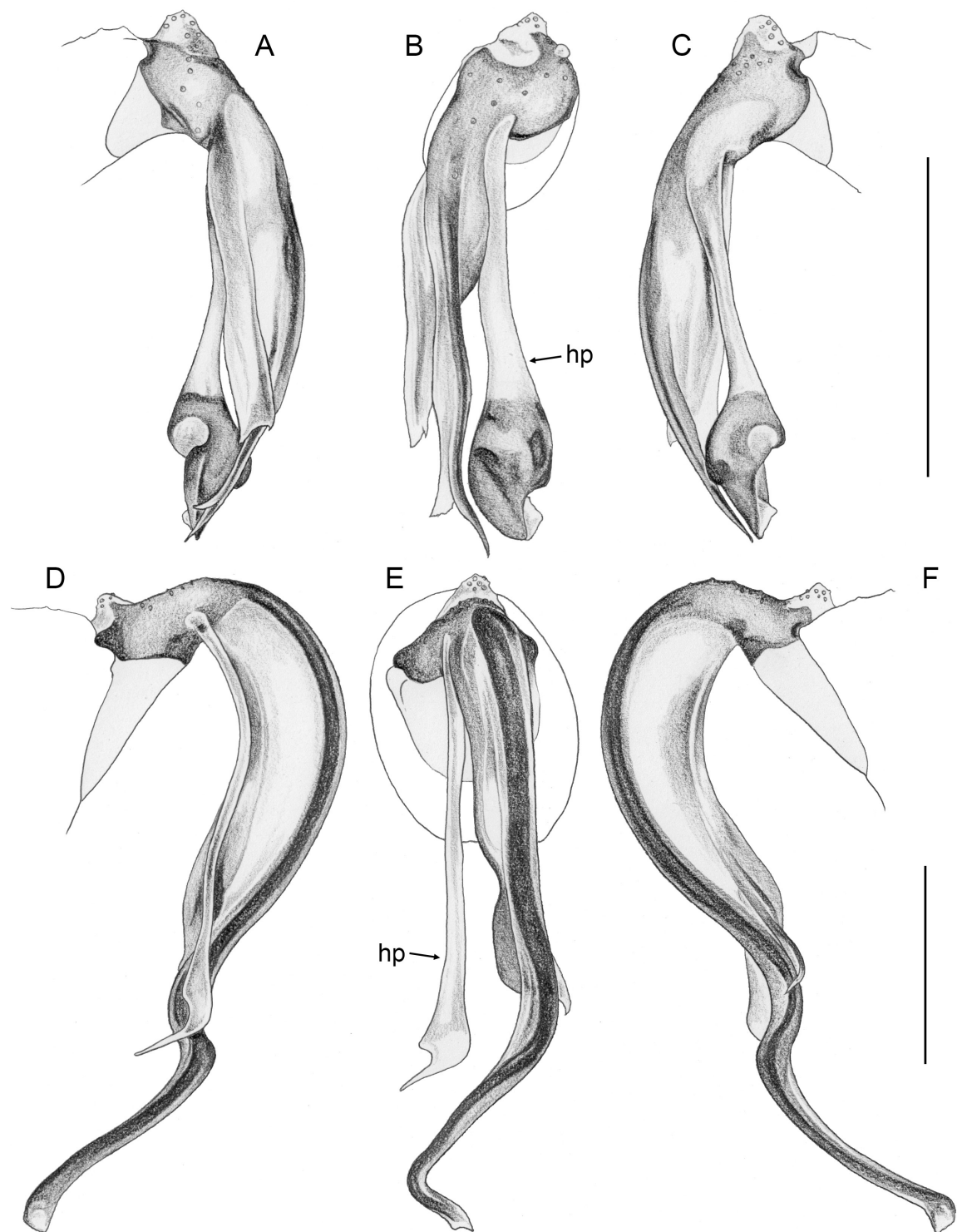


Fig. 9. *Metagonia wayuu* Huber sp. nov., paratype, ♂, from Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). Left and right palpal tarsi and procursi at different scales. **A–C.** Left tarsus and procursus, prolateral, dorsal, and retrolateral views. **D–F.** Right tarsus and procursus, retrolateral, dorsal, and prolateral views. Abbreviation: hp = hinged process. Scale lines = 0.5 mm.

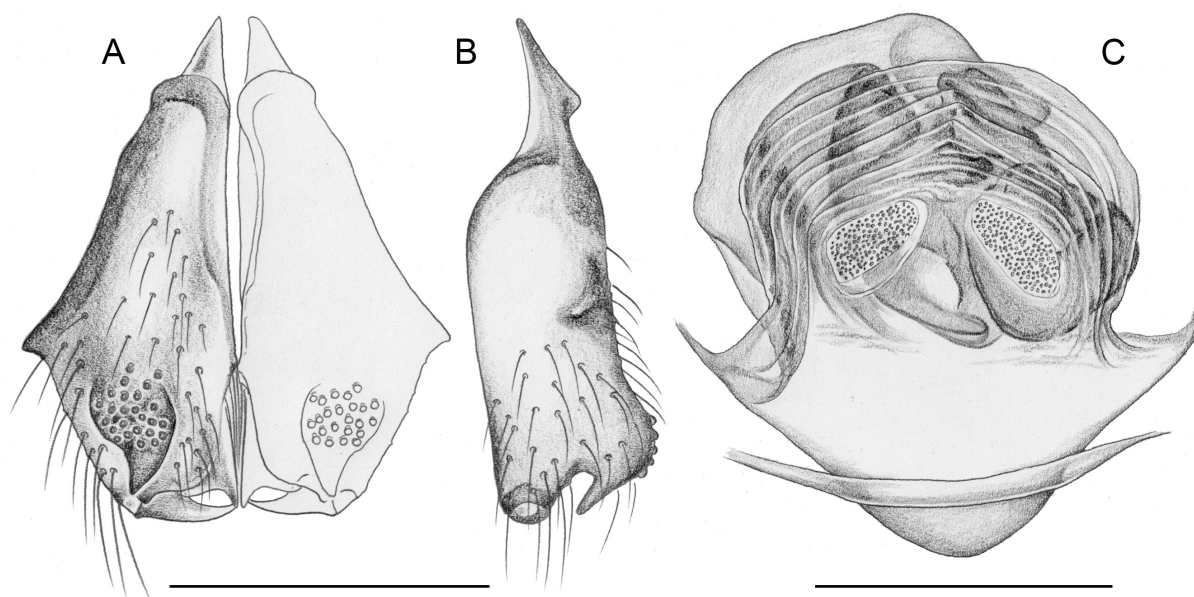


Fig. 10. *Metagonia wayuu* Huber sp. nov., paratypes from Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). **A–B.** Male chelicerae, frontal and lateral views. **C.** Cleared female genitalia, dorsal view. Scale lines = 0.3 mm.

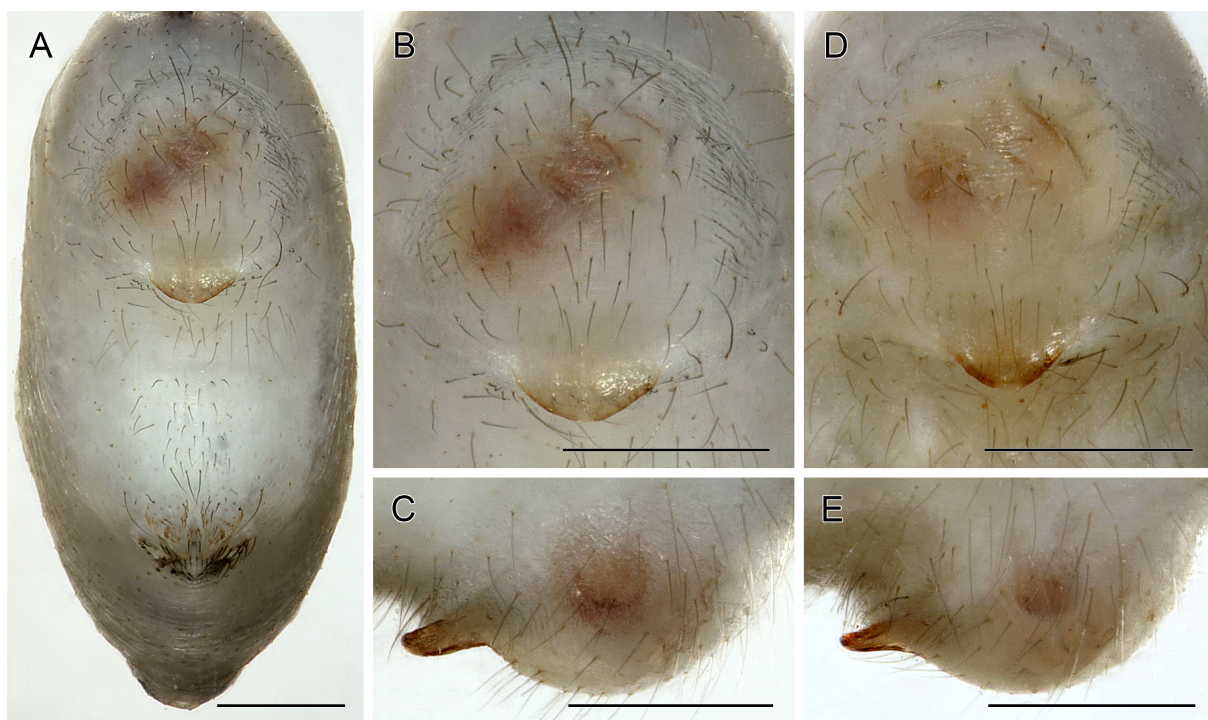


Fig. 11. *Metagonia wayuu* Huber sp. nov., females. **A–C.** From Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). **D–E.** From Venezuela, Falcón, Santa Cruz (ZFMK Ven20-149). **A.** Abdomen, ventral view. **B, D.** Epigyna, ventral views. **C, E.** Epigyna, lateral views. Scale lines = 0.3 mm.

Description

Male (holotype)

MEASUREMENTS. Total body length 2.8, carapace width 0.75. Distance PME–PME 170 μm ; diameter PME 90 \times 110 μm ; distance PME–ALE 25 μm ; AME absent. Leg 1: 18.7 (5.0+0.4+4.7+7.6+1.0), tibia 2: 2.8, tibia 3: 1.8, tibia 4: 2.8; tibia 1 L/d: 59; diameters of leg femora (at half length) 0.10; of leg tibiae 0.08.

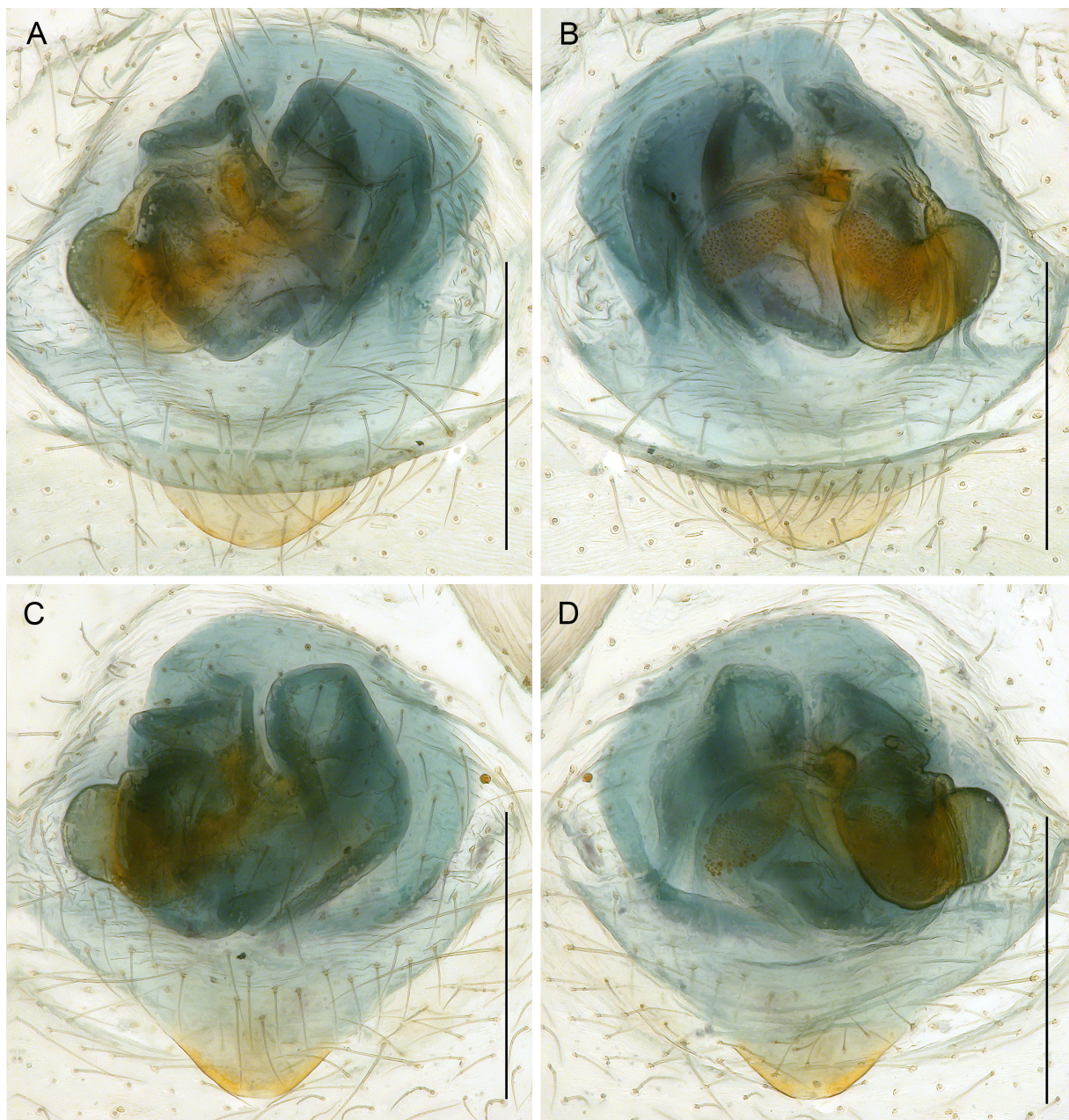


Fig. 12. *Metagonia wayuu* Huber sp. nov., cleared female genitalia in ventral (A, C) and dorsal (B, D) views. A–B. From Colombia, La Guajira, Tomarrazón (ZFMK Ar 24780). C–D. From Venezuela, Falcón, Santa Cruz (D–F) (ZFMK Ven20-149). Scale lines = 0.3 mm.

COLOR (in ethanol). Carapace pale whitish ochre, with median brown mark including ocular area (Fig. 2C), clypeus not darkened; sternum whitish; legs whitish ochre, patellae and tibia-metatarsus joints brown; abdomen whitish, dorsally with few dark marks.

BODY. Habitus as in Fig. 1C. Ocular area slightly raised. Carapace without thoracic groove. Clypeus with sclerotized rim (sclerotized rim narrower than in *M. uca* sp. nov.; cf. Fig. 15A). Sternum wider than long (0.54/0.46), unmodified. Abdomen approximately twice as long as wide, dorso-posteriorly pointed.

CHELICERAE. As in Fig. 10A–B; with pair of lateral conical processes, pair of distal frontal processes set with ~23 modified (globular) hairs each, and pair of slightly diverging apophyses in front of fang joints.

PALPS. As in Fig. 8; coxa unmodified, apparently symmetric; trochanter with short rounded ventral process, apparently symmetric; all other segments directionally asymmetric, see below; femur with distinct process on prolateral-ventral side; procurus consisting of main branch and ventral hinged process; genital bulb simple, consisting of globular part and embolus.

ASYMMETRY. Right femur rather cylindrical, with cylindrical prolateral-ventral process; left femur smaller, distally strongly widened, and with conical prolateral-ventral process. Right tibia much bigger than left tibia (maximum diameter in lateral view 0.56–0.61 vs 0.21–0.22). Right procurus consisting of strongly sclerotized main branch (distally the sclerite is partly internal, covered by weakly sclerotized semitransparent cuticle) and weakly sclerotized semitransparent ventral hinged process; left procurus much smaller, with slender main branch, with distally widened and heavily sclerotized ventral hinged process. Right genital bulb with small globular part (diameter 0.27–0.29) and long slender embolus; left genital bulb with larger globular part (diameter 0.36–0.38) and with shorter and strongly widened embolus (similar to *M. uca* sp. nov.; cf. Fig. 15B–C).

LEGS. Without spines, without curved hairs, without sexually dimorphic short vertical hairs; retrolateral trichobothrium of tibia 1 at 9%; prolateral trichobothrium absent on tibia 1; tarsus 1 with ~20 pseudosegments, very indistinct except distally.

Variation

Males

Tibia 1 in three other males: 4.2, 4.2, 4.5. Color pattern on carapace consistent but pattern on abdomen variable, entirely whitish or with black and white marks dorsally.

Females

In general very similar to male (Fig. 1D) but carapace pattern limited to black lines (Fig. 2D), clypeus unmodified, sternum color variable, in some females with brown marks near leg coxae or entire sternum speckled; abdomen color variable as in males. Tibia 1 in ten females: 3.6–3.9 (mean 3.7). Epigynum (Fig. 11) simple, mostly weakly sclerotized, posteriorly with sclerotized scape, apparently symmetric; internal asymmetric structures visible through cuticle; posterior epigynal plate short and indistinct. Internal genitalia (Figs 10C, 12) with sclerotized receptacle on right side, with complex system of pouches, ducts, and folds (apparently similar to *M. mariguitarensis*; cf. Huber 2004: figs 1–2); with pair of oval pore plates (possibly slightly asymmetric, but this might be an artifact of preparation).

Barcodes

We sequenced two specimens from two localities (geographic distance: 485 km) (Table 1; Fig. 23). The CO1 distance was 1.7% (Table 2). Distances to the other three species treated herein ranged from 15.5 to 20.3%.

Distribution

Known from northern Colombia (La Guajira) and northwestern Venezuela (Falcón) (Fig. 24).

Natural history

At the type locality, the spiders were collected from palm and *Heliconia* L. leaves in a disturbed forest remnant along a river. The locality was shared with *Mesabolivar eberhardi* Huber, 2000 and an undescribed species of *Chibchea* Huber, 2000. In Falcón, the five females were collected close to the forest margin of a well-preserved forest. They shared the locality with two further representatives of *Metagonia*, *M. latigo* Huber, 2020 and *M. guttata* Huber, 2020. The latter species seemed to share the same large dicot plant leaves with *M. wayuu* sp. nov. (Huber & Villarreal 2020).

Metagonia uca Huber sp. nov.

[urn:lsid:zoobank.org:act:FB512521-5B86-4526-8AEF-0FF99EAAA7C3](https://zoobank.org/urn:lsid:zoobank.org:act:FB512521-5B86-4526-8AEF-0FF99EAAA7C3)

Figs 1E–F, 2E–F, 13–16

Diagnosis

Easily distinguished from most known congeners (except *M. mariguitarensis* and *M. wayuu* sp. nov.) by strongly asymmetric male palps (Fig. 13), by male chelicerae with pair of strong lateral protrusions (Fig. 15D), and by female external and internal genitalia (Figs 15F, 16; epigynum with posterior semicircular process, or ‘scape’; internal genitalia with complex system of pouches, ducts, and folds). Distinguished from both *M. mariguitarensis* and *M. wayuu* by different color pattern on carapace (both in males and females; Fig. 2), by larger size and longer legs (e.g., male tibia 1 ≥ 6.5 vs ≤ 5.0 ; female tibia 1 ≥ 5.5 vs ≤ 4.0), and by female genitalia (epigynal scape with asymmetric groove; Fig. 16B). Further distinguished from *M. mariguitarensis* by male chelicerae with pointed rather than rounded distal apophyses (Fig. 15D), by main branch of left procurus without distinctive ventral indentation (compare Fig. 4C with Fig. 14C), by absence of hair-like process on right procurus (compare Fig. 4D with Fig. 14D), and by stronger palpal asymmetry, i.e., absolutely and relatively bigger right palp (e.g., right/left tibia diameter > 2.6 vs < 2.5 ; see also Fig. 22).

Etymology

The species name alludes to fiddler crabs (*Uca* and other genera), where the males have a major claw significantly larger than the minor claw.

Type material

Holotype

COLOMBIA – **Quindío** • ♂; Armenia, Universidad del Quindío; 4.5537° N, 75.6608° W; 1500 m a.s.l.; 8 Sep. 2022; B.A. Huber and G.A. Rodríguez leg.; MUSENUV Ar 3533.

Paratypes

COLOMBIA – **Quindío** • 1 ♂, 2 ♀♀; same collection data as for holotype; MUSENUV Ar 3534 • 7 ♂♂, 9 ♀♀; same collection data as for holotype; ZFMK Ar 24781, 24782.

Other material examined

COLOMBIA – **Quindío** • 3 ♀♀, 1 juv., in pure ethanol; same collection data as for holotype; ZFMK Col238 (voucher of UH542) • 1 ♀; 3 km N of Circasia, Reserva Bosque del Silencio; 4.6411° N, 75.6379° W; 1850 m a.s.l.; 7 Sep. 2022; B.A. Huber and G.A. Rodríguez leg.; ZFMK Ar 24783 • 2 ♀♀, in pure ethanol; same collection data as for preceding; ZFMK Col237 (voucher of UH254). – **Risaralda** • 1 ♀; La Celia, Vereda San Eugenio; 4.970° N, 75.006° W; 1600 m a.s.l.; 25 Feb. 2010; N. Betancour

leg.; MUSENUV 2214 • 1 ♀; same collection data as for preceding; MUSENUV 2220 • 1 ♂, 1 ♀; same collection data as for preceding; MUSENUV 2226.

Description

Male (holotype)

MEASUREMENTS. Total body length 3.2, carapace width 0.9. Distance PME–PME 250 µm; diameter PME 120 × 130 µm; distance PME–ALE 30 µm; AME absent. Leg 1: 31.5 (7.8+0.5+7.7+14.0+1.5), tibia 2: 4.9, tibia 3: 2.8, tibia 4: 4.4; tibia 1 L/d: 86; diameters of leg femora (at half length) 0.10–0.11; of leg tibiae 0.09.



Fig. 13. *Metagonia uca* Huber sp. nov., paratype, ♂, from Colombia, Universidad del Quindío (ZFMK Ar 24781). Left and right palps at same scale. **A–C.** Left palp, prolateral dorsal, and retrolateral views. **D–F.** Right palp, retrolateral, dorsal, and prolateral views; note that right bulb is artificially rotated away from resting position (cf. Fig. 8F). Scale line = 1 mm.

COLOR (in ethanol). Carapace anteriorly pale ochre-yellow, posterior half dark brown (Fig. 2E), ocular area with brown pattern, clypeus brown; sternum whitish; legs ochre-yellow, patellae and tibia-metatarsus joints dark brown; abdomen pale ochre-gray, dorsally and laterally with dark and whitish marks.

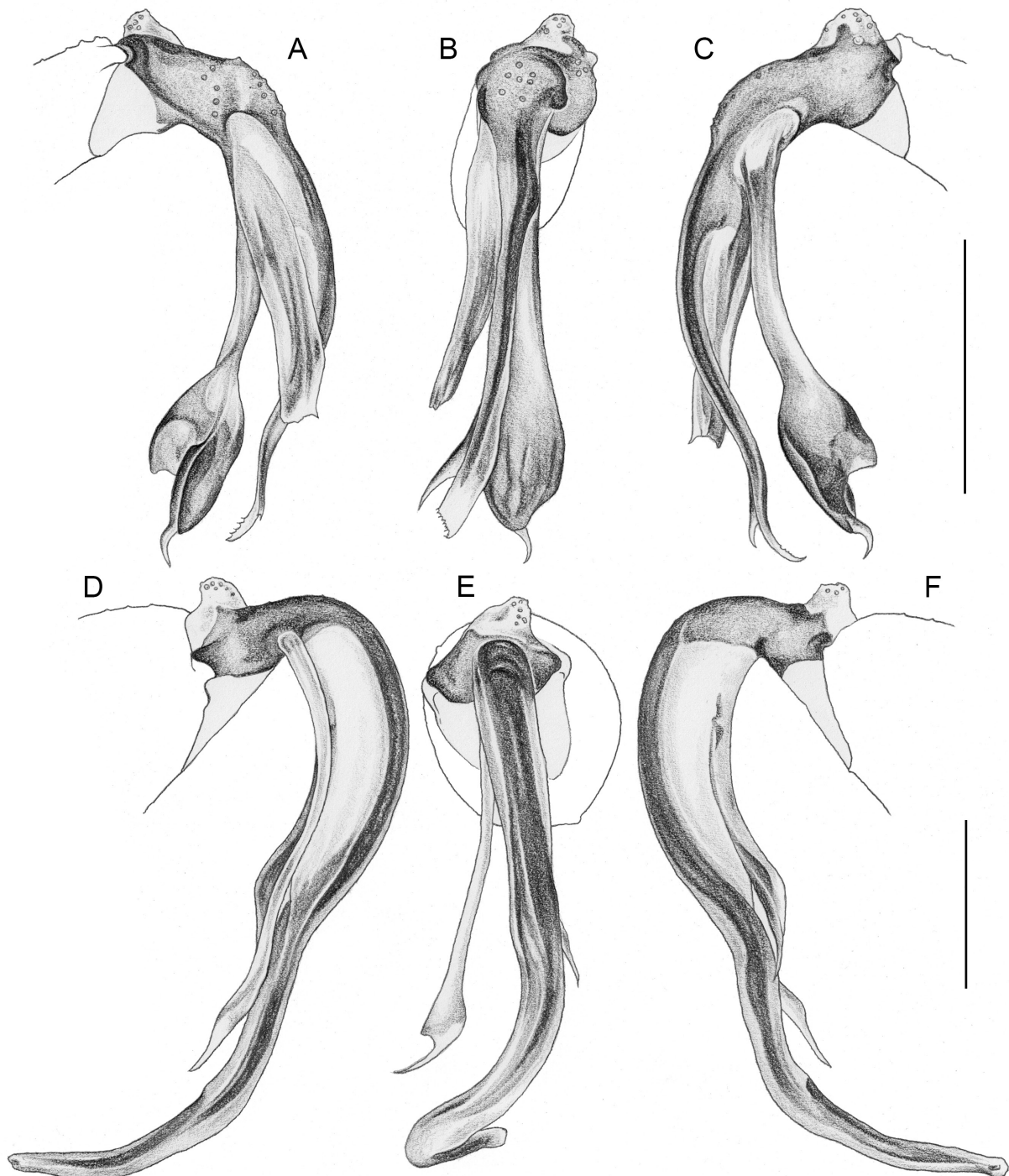


Fig. 14. *Metagonia uca* Huber sp. nov., paratype, ♂, from Colombia, Universidad del Quindío (ZFMK Ar 24781). Left and right palpal tarsi and procursi at different scales. **A–C.** Left tarsus and procursus, prolateral, dorsal, and retrolateral views. **D–F.** Right tarsus and procursus, retrolateral, dorsal, and prolateral views. Scale lines = 0.5 mm.

BODY. Habitus as in Fig. 1E. Ocular area slightly raised. Carapace without thoracic groove. Clypeus with strongly sclerotized rim (Fig. 15A). Sternum wider than long (0.68/0.56), unmodified. Abdomen approximately twice as long as wide, dorso-posteriorly pointed.

CHELICERAE. AS in Fig. 15D–E; with pair of lateral conical processes, pair of distal frontal processes set with ~12–14 modified (globular) hairs each, and pair of diverging apophyses near fang joints.

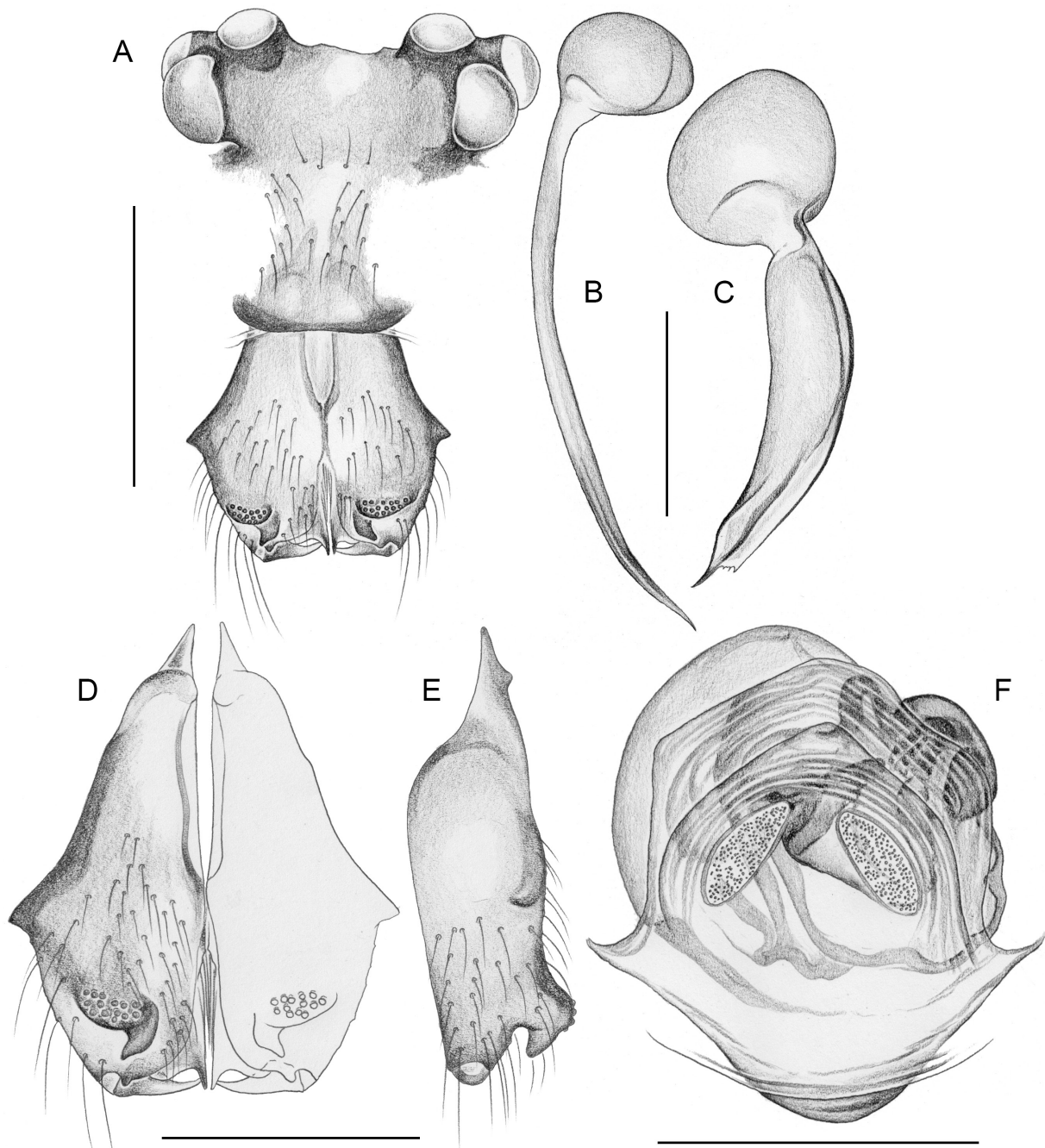


Fig. 15. *Metagonia uca* Huber sp. nov., paratypes, male and female, from Colombia, Universidad del Quindío (ZFMK Ar 24781, 24782). **A.** Male ocular area, clypeus, and chelicerae, oblique frontal view. **B–C.** Right and left genital bulbs, prolateral views, at same scale. **D–E.** Male chelicerae, frontal and lateral views. **F.** Cleared female genitalia, dorsal view. Scale lines: A–C, F = 0.5 mm; D–E = 0.3 mm.

PALPS. As in Fig. 13; coxa unmodified, apparently symmetric; all other segments directionally asymmetric, see below; trochanter with short ventral apophysis; femur with distinct process on prolateral-ventral side; procurus consisting of main branch and ventral hinged process; genital bulb simple, consisting of globular part and embolus.

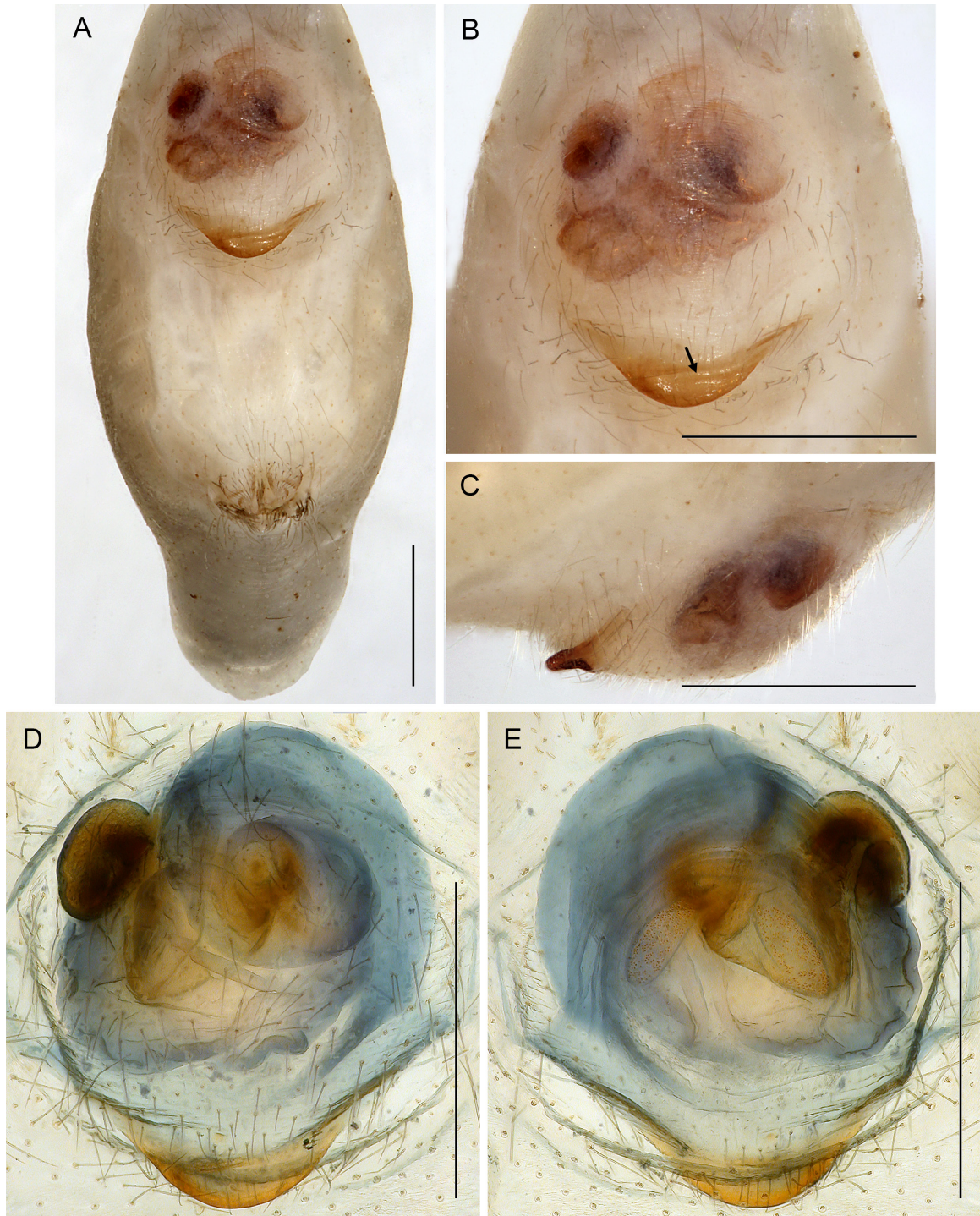


Fig. 16. *Metagonia uca* Huber sp. nov., paratype, ♀, from Colombia, Universidad del Quindío (ZFMK Ar 24782). **A.** Abdomen, ventral view. **B–C.** Epigynum, ventral and lateral views; arrow in B points at asymmetric groove. **D–E.** Cleared female genitalia, ventral and dorsal views. Scale lines = 0.5 mm.

ASYMMETRY. Right trochanter slightly larger than left trochanter. Right femur rather cylindrical, with cylindrical prolateral-ventral process; left femur smaller, distally strongly widened, and with conical prolateral-ventral process. Right tibia much bigger than left tibia (maximum diameter in lateral view: 0.70–0.77 vs 0.25–0.27). Right procurus consisting of strongly sclerotized main branch (distally the sclerite is mostly internal, covered by weakly sclerotized and semitransparent cuticle) and weakly sclerotized semitransparent ventral hinged process; left procurus much smaller, with slender main branch, with distally widened and heavily sclerotized ventral hinged process. Right genital bulb with small globular part (diameter 0.30–0.34) and long slender embolus; left genital bulb with larger globular part (diameter 0.42–0.46) and with shorter and strongly widened embolus (Fig. 15B–C).

LEGS. Without spines, without curved hairs, without sexually dimorphic short vertical hairs; retrolateral trichobothrium of tibia 1 at 8%; prolateral trichobothrium absent on tibia 1; tarsus 1 with ~25 pseudosegments, very indistinct.

Variation

Males

Tibia 1 in ten males: 6.7–7.8 (mean 7.4).

Females

In general very similar to male (Fig. 1F) but carapace posteriorly with two Y-marks (Fig. 2F), ocular area and clypeus not darkened, clypeus unmodified, sternum darker (either dark brown with small light spots or light brown and medially ochre). Tibia 1 in 18 females: 5.7–6.6 (mean 6.2). Epigynum (Fig. 16A–C) simple, mostly weakly sclerotized, posteriorly with sclerotized and slightly asymmetric scape (groove on left side; all females same-sided); internal asymmetric structures visible through cuticle; posterior epigynal plate short and indistinct. Internal genitalia (Figs 15F, 16D–E) with sclerotized receptacle on right side, with complex system of pouches, ducts, and folds (apparently similar to *M. mariguitarensis*; cf. Huber 2004: figs 1–2); with pair of elongated pore plates (possibly slightly asymmetric, but this might be an artifact of preparation). One cleared female from Vereda San Eugenio apparently identical to female from type locality.

Barcodes

We sequenced two specimens from two localities (geographic distance: 10 km) (Table 1; Fig. 23). The CO1 distance was 0.2% (Table 2). Distances to the other three species treated herein ranged from 18.8 to 20.9%.

Distribution

Known from three neighboring localities in Colombia (Fig. 24).

Natural history

In Armenia, most specimens were collected from palm leaves in the entrance area of the small secondary forest within the university campus; deeper in the forest they seemed to be very rare or absent. They shared the locality with a second (undescribed, symmetric) species of leaf-dwelling *Metagonia*. In Reserva Bosque del Silencio, the three females were collected on a single small palm tree; no further specimens were found despite focused search.

Metagonia embera Huber sp. nov.

[urn:lsid:zoobank.org:act:1E9D5F43-AB9F-4C3F-981A-341B529C64DC](https://zoobank.org/act:1E9D5F43-AB9F-4C3F-981A-341B529C64DC)

Figs 1G–H, 17–21

M025 *Metagonia* Car260 – Huber *et al.* 2022: 678 (molecular data).

Diagnosis

Easily distinguished from known congeners by male palpal asymmetry largely restricted to procurus (Figs 17–18), i.e., barely involving palp size as in other species with asymmetric males described above. Also by rounded median process on clypeus (Fig. 19A), by male chelicerae with small, modified (globular) hairs arranged in two lateral bands (Fig. 19A), by epigynum without scape (Fig. 20B), and by asymmetric structures in female internal genitalia (Figs 19B, 20D–G; sclerotized receptacle on right side and arched membranous structure on left side).

Etymology

The species name honors the Emberá, an indigenous people in the Chocó Department of western Colombia and in Panama.

Type material

Holotype

COLOMBIA – **Risaralda** • ♂; near Santa Cecilia; 5.3458° N, 76.1094° W; 450 m a.s.l.; 9 Sep. 2022; B.A. Huber and G.A. Rodríguez leg.; on leaves at forest edge; MUSENUV Ar 3535.

Paratype

COLOMBIA – **Risaralda** • 1 ♂; same collection data as for holotype; ZFMK Ar 24784.

Other material examined

COLOMBIA – **Chocó** • 1 ♂, 1 ♀, in pure ethanol; Jardín Botánico del Pacífico, “trail to Mirador after stream crossings”; 6.266° N, 77.375° W; 16 Jan. 2014; CarBio team leg.; ZFMK Car260 (voucher of M025) • 1 juv., assigned tentatively, in pure ethanol; Jardín Botánico del Pacífico, Ceiba Loop Trail; 6.266° N, 77.375° W; 13 Jan. 2014; CarBio team leg.; ZFMK Car257. – **Risaralda** • 1 ♂, in pure ethanol; same collection data as for holotype; ZFMK Col247 (voucher of UH260).

PANAMA – **Colón** • 1 ♂; San Lorenzo Protected Area; 9.267° N, 79.967–79.983° W; ~150 m a.s.l.; 13 May 2004; J. Schmidl and J. Bail leg.; fogging; ZMUC • 1 ♂; same locality as for preceding; 15 May 2004; J. Schmidl and J. Bail leg.; ZMUC • 1 ♀; same locality as for preceding; 17 Oct. 2003; J. Schmidl and A. Floren leg.; ZMUC • 1 ♂; same locality as for preceding; 17 Oct. 2003; J. Schmidl and J. Bail leg.; ZMUC • 1 ♂; same locality as for preceding; 12 May 2003; J. Schmidl and J. Bail leg.; ZMUC • 1 ♀; same locality as for preceding; 27 May 2004; J. Schmidl and J. Bail leg.; ZMUC • 1 ♂; same locality as for preceding; 8 Oct. 2004; J. Bail leg.; ZMUC • 2 ♂♂; same locality as for preceding; 15 May 2004; J. Schmidl and J. Bail leg.; ZMUC.

Description

Male (holotype)

MEASUREMENTS. Total body length 2.1, carapace width 0.7. Distance PME–PME 70 µm; diameter PME 90 × 110 µm; distance PME–ALE 30 µm; AME absent. Leg 1: 22.9 (5.7+0.3+5.4+10.3+1.2), tibia 2: 3.5, tibia 3: 2.1, tibia 4: 3.3; tibia 1 L/d: 77; diameters of leg femora (at half length) 0.09; of leg tibiae 0.07.

COLOR (in ethanol). Carapace pale ochre-yellow with distinct ochre-brown pattern on posterior half, ocular area and clypeus without dark marks (Fig. 1G–H); sternum mostly whitish, only posteriorly with small ochre mark; legs ochre-yellow, patellae and tibia-metatarsus joints dark brown; abdomen pale ochre-gray, dorsally and laterally with dark marks.

BODY. Habitus as in Fig. 1G–H. Ocular area slightly raised. Carapace without thoracic groove. Clypeus with short median process at rim (length ~30 μm). Sternum wider than long (0.56/0.44), unmodified. Abdomen approximately twice as long as wide, dorso-posteriorly pointed.

CHELICERAE. As in Fig. 19A; with series of ~16–19 modified (globular) hairs on each side and pair of distal apophyses near fang joints, without proximal lateral processes.

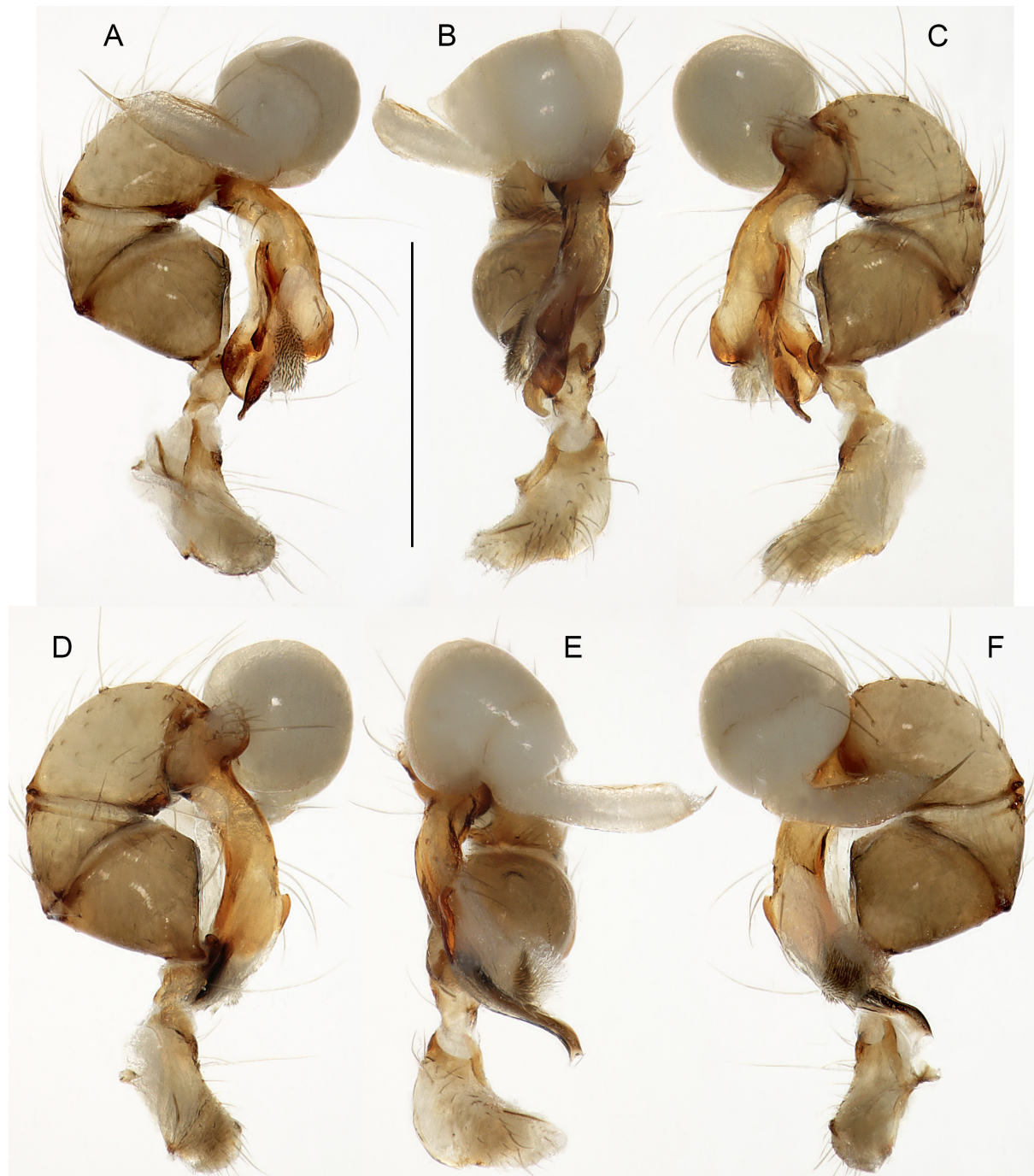


Fig. 17. *Metagonia embera* Huber sp. nov., paratype, ♂, from Colombia, Risaralda, Santa Cecilia (ZFMK Ar 24784). Left and right palps at same scale. A–C. Left palp, prolateral, dorsal, and retrolateral views. D–F. Right palp, retrolateral, dorsal, and prolateral views. Scale line = 0.5 mm.

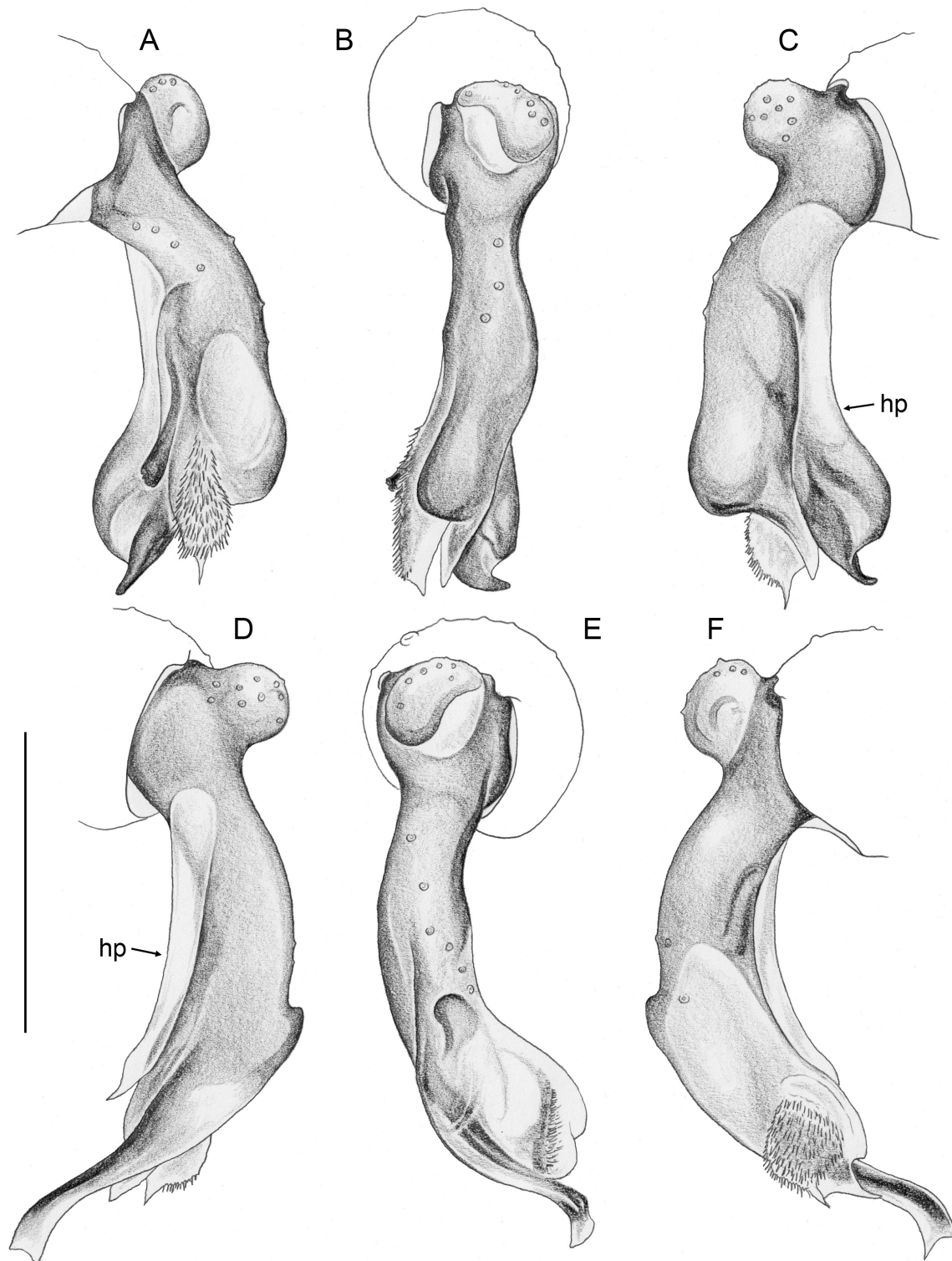


Fig. 18. *Metagonia embera* Huber sp. nov., paratype, ♂, from Colombia, Risaralda, Santa Cecilia (ZFMK Ar 24784). Left and right palpal tarsi and procursi at same scale. **A–C.** Left tarsus and procurus, prolateral, dorsal, and retrolateral views. **D–F.** Right tarsus and procurus, retrolateral, dorsal, and prolateral views. Abbreviation: hp = hinged process. Scale line = 0.3 mm.

PALPS. As in Fig. 17; coxa unmodified; trochanter with short ventral apophysis; femur short, distally strongly widened, with short conical process on prolateral side, apparently symmetric; femur-patella hinges and tibia-tarsus hinges slightly shifted toward prolateral side; tibia short, slightly asymmetric (see below), with two trichobothria in relatively distal position; procursi strongly asymmetric, see below; genital bulb simple, with small conical process on prolateral side and long weakly sclerotized embolus ending with pointed process, slightly asymmetric (see below).

ASYMMETRY. Proximal palpal segments (coxa, trochanter, femur) apparently symmetric. Right tibia slightly thicker than left tibia (maximum diameter in lateral view ~220 vs 210 μm). Procursi directionally asymmetric (Fig. 18): left procursus with strong and distally sclerotized ventral hinged process, with slender prolateral sclerotized process, prominent dorsal hump, without distal sclerite; right procursus with slender and weakly sclerotized ventral hinged process, without prolateral sclerotized process, with smaller dorsal hump, with long distal sclerite directed towards ventral and prolateral. Genital bulbs weakly asymmetric: right embolus slightly longer than left embolus (~340 vs 310 μm).

LEGS. Without spines, without curved hairs, without sexually dimorphic short vertical hairs; retrolateral trichobothrium of tibia 1 at 7%; prolateral trichobothrium absent on tibia 1; tarsus 1 with ~20 pseudosegments, very indistinct.

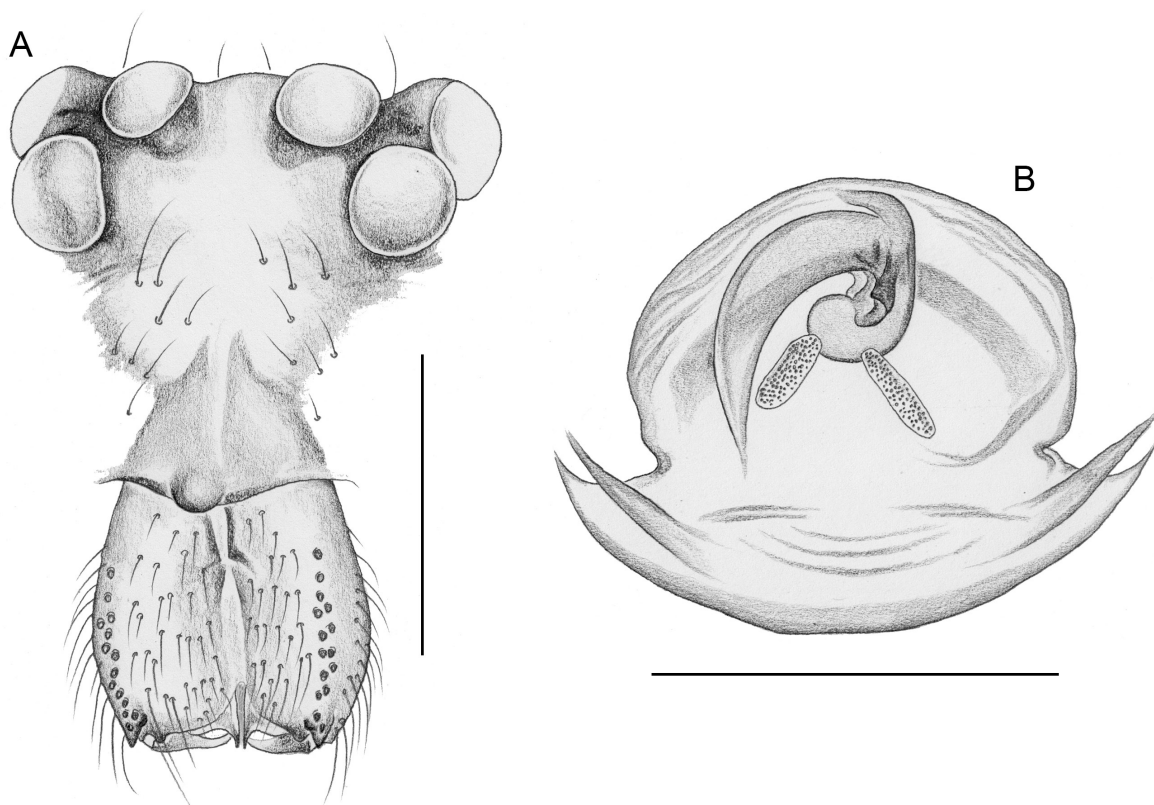


Fig. 19. *Metagonia embera* Huber sp. nov. **A.** Paratype, ♂, from Colombia, Risaralda, Santa Cecilia (ZFMK Ar 24784). Ocular area, clypeus, and chelicerae, oblique frontal view. **B.** Female from Colombia, Chocó, Jardín Botánico del Pacífico (ZFMK Car260). Cleared genitalia, dorsal view. Scale lines = 0.3 mm.

Variation

Males

Tibia 1 in eight males: 4.8–5.9 (mean 5.5). Sternum in some males with small dark marks near bases of leg coxae.

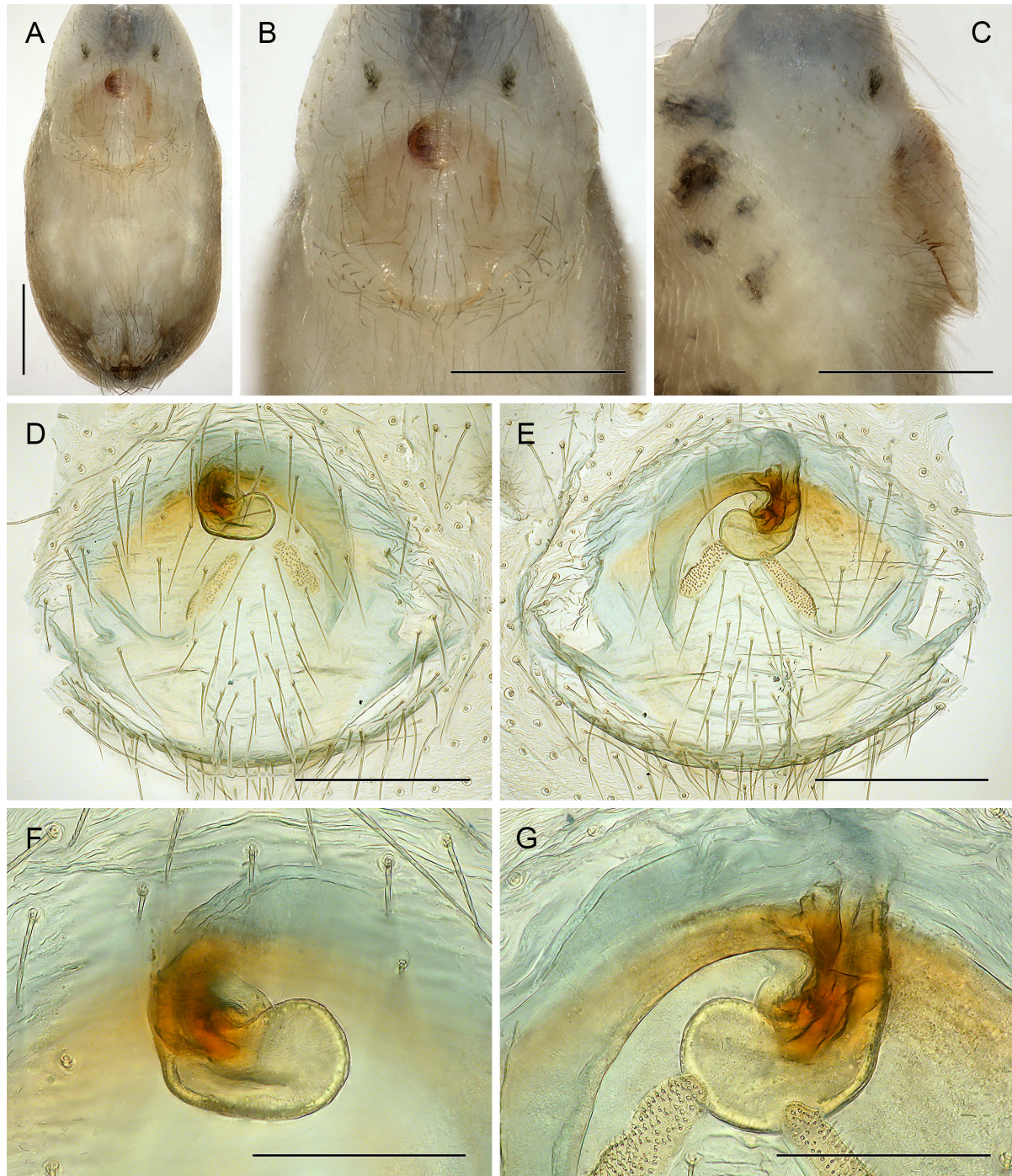


Fig. 20. *Metagonia embera* Huber sp. nov., ♀, from Colombia, Chocó, Jardín Botánico del Pacífico (ZFMK Car260). **A.** Abdomen, ventral view. **B–C.** Epigynum, ventral and lateral views. **D–E.** Cleared genitalia, ventral and dorsal views. **F–G.** Details from D and E, respectively. Scale lines: A–C = 0.3 mm; D–E = 0.2 mm; F–G = 0.1 mm.

Females

In general, very similar to male (including color pattern on carapace) but clypeus unmodified. Tibia 1 in two females: 4.5, 5.3 (missing in third female). Epigynum (Fig. 20A–C) very simple, weakly sclerotized, without scape; internal asymmetric structures visible through cuticle; posterior epigynal plate short and indistinct. Internal genitalia (Figs 19B, 20D–G) asymmetric, with sclerotized receptacle on right side connected with arched membranous structure on left side; the three examined females were same-sided; with pair of elongated pore plates (possibly slightly asymmetric, but this might be an artifact of preparation). One cleared female from Panama very similar but pore plate slightly longer (Fig. 21).

Barcodes

We sequenced two specimens from two localities (geographic distance: 173 km) (Table 1; Fig. 23). The CO1 distance was 0.6% (Table 2). Distances to the other three species treated herein ranged from 16.7 to 20.9%.

Distribution

Known from two localities in Colombia and one locality in Panama (Fig. 24).

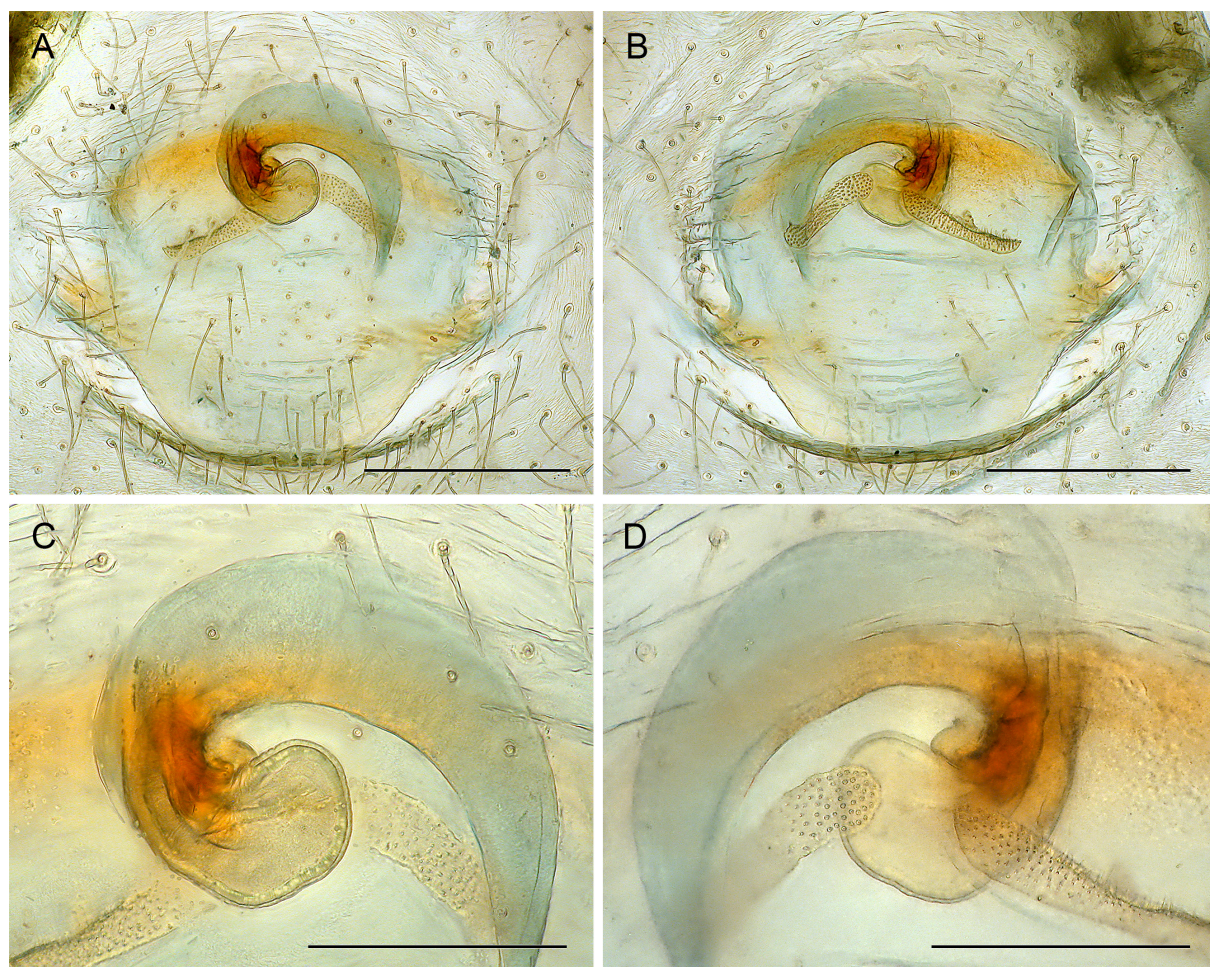


Fig. 21. *Metagonia embera* Huber sp. nov., ♀, from Panama, Colón, San Lorenzo (ZMUC). **A–B.** Cleared genitalia, ventral and dorsal views. **C–D.** Details from A and B, respectively. Scale lines: A–B = 0.2 mm; C–D = 0.1 mm.

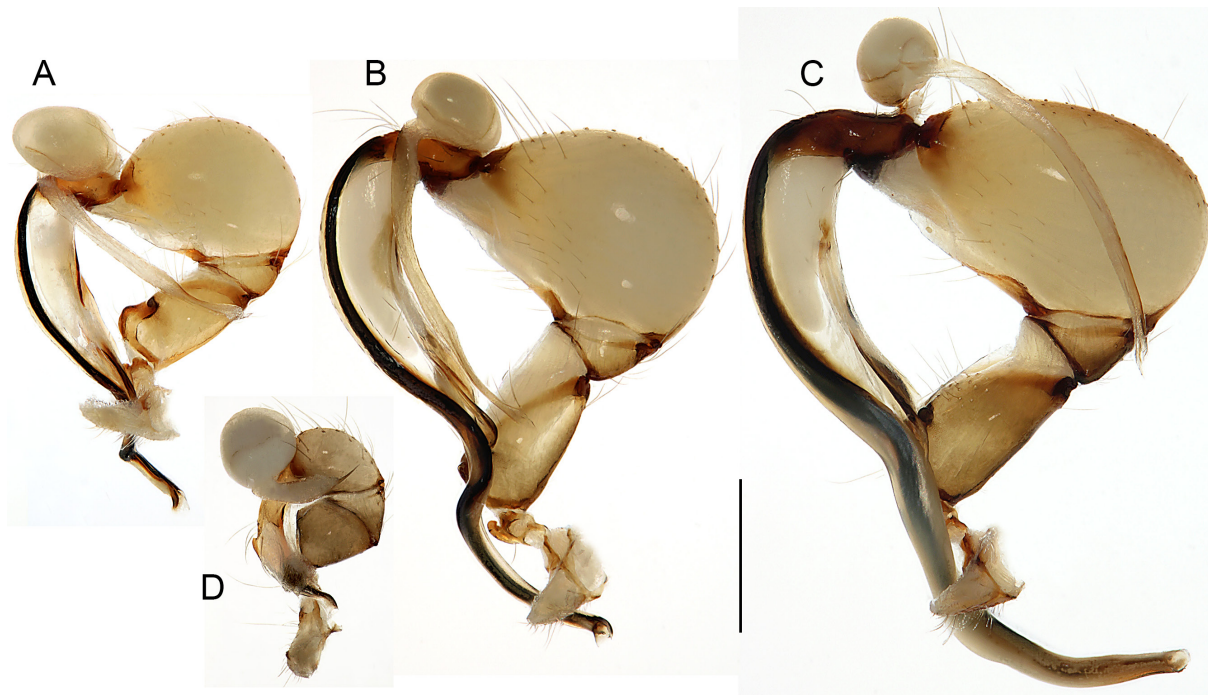


Fig. 22. Right palps at same scale, illustrating size differences among species. **A.** *Metagonia mariguitarensis* (González-Sponga, 1998) (from Fig. 3F). **B.** *M. wayuu* Huber sp. nov. (from Fig. 8F). **C.** *M. uca* Huber sp. nov. (from Fig. 13F). **D.** *M. embera* Huber sp. nov. (from Fig. 17F). Scale line = 0.5 mm.

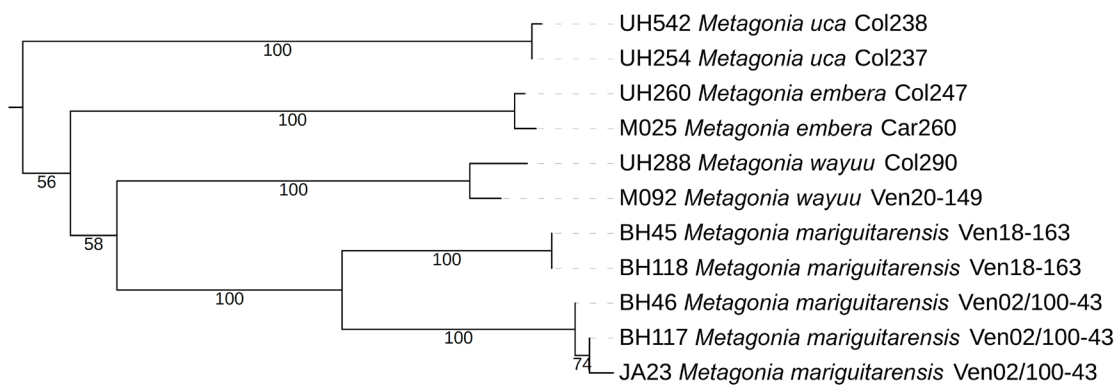


Fig. 23. Neighbor-joining tree based on all available CO1 sequences of directionally asymmetric species of *Metagonia* Simon, 1893 (outgroup *M. taruma* Huber, 2000 not shown), using the Kimura 2-parameter model; numbers on the branches are bootstrap supports from 5000 replications (%).

Discussion

The genus *Metagonia* includes both species with symmetric and species with asymmetric female genitalia (Fig. 25). The available evidence (see Appendix 1) suggests that within *Metagonia*, directional asymmetry has evolved only once, in the most recent common ancestor of the four species treated herein. The origin of female antisymmetry in the genus is much less clear. Mapping of female symmetry and asymmetry on the tree in Huber *et al.* 2022 (Appendix 1) suggests a complex picture of several gains

and/or losses. For example, both symmetric and asymmetric female genitalia occur in a clade composed of the *taruma*, *petropolis*, and *bifida* groups (Fig. A1); the same is true for the *rica* group (Fig. A2), for the *potiguar* group (Fig. A2) and for the *delicata* group (Fig. A3). We acknowledge that a convincing interpretation will need a more solid basis in several aspects. First, while the tree in Huber *et al.* (2022) offers a first comprehensive hypothesis for relationships within *Metagonia*, it is based on a limited sample of genes and species, and we expect at least minor rearrangements in future more complete phylogenies. Second, the tree in Huber *et al.* (2022) contains a large number of undescribed species whose female internal genitalia have not yet been studied (26 of the 67 species in the tree, i.e., 39%). Third, it is unclear to which extent older publications showing symmetric female genitalia can be trusted. Gertsch's (1986) otherwise very valuable revision of *Metagonia* with many new species described in the *rica* group illustrates the point: it does not mention asymmetry at all, and most drawings appear to show perfectly symmetric female internal genitalia. For example, his figure 39 shows symmetric female genitalia of *M. belize* Gertsch, 1986, while a later illustration of this species shows an asymmetric arrangement of receptacle and duct (Huber 1998: fig. 92). Future taxonomic work on *Metagonia* will not only have to pay particular attention to subtle asymmetries in newly described species, but also to sufficiently large sample sizes in order to establish the type of asymmetry (antisymmetry vs directional asymmetry) and to rule out artifacts of preparation, as well as to re-analyses of previously described species.

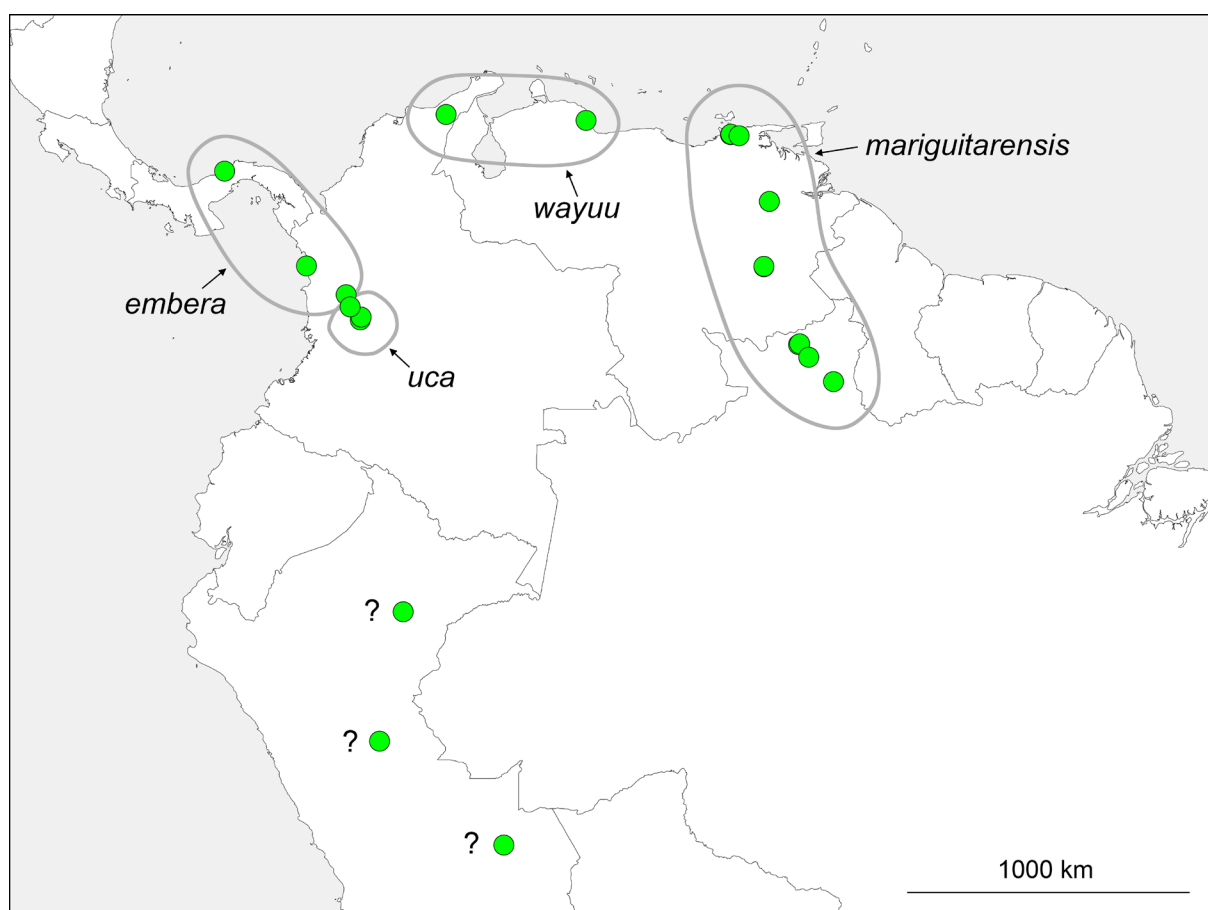


Fig. 24. Known distributions of species of *Metagonia* Simon, 1893 with directionally asymmetric male and female genitalia. Question marks denote Peruvian specimens that were tentatively assigned to *M. mariguitarensis* (González-Sponga, 1998) in Huber (2000); they probably represent one or more additional species.

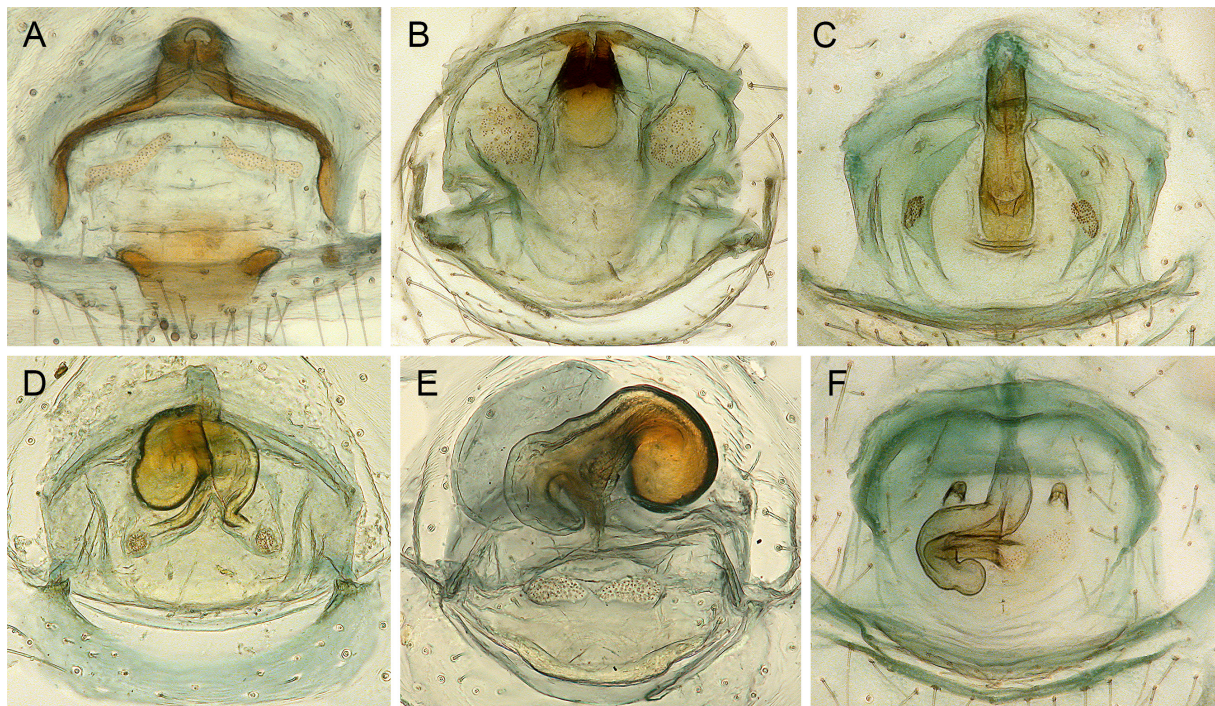


Fig. 25. Examples of symmetric (A–C) and antisymmetric (D–F) female internal genitalia in *Metagonia* Simon, 1893, from Huber & Villarreal (2020). **A.** *M. triocular* (González-Sponga, 2011). **B.** *M. guttata* Huber, 2020. **C.** *M. guianesa* Huber, 2020. **D.** *M. beni* Huber, 2000. **E.** *M. latigo* Huber, 2020. **F.** *M. conica* (Simon, 1893). At various scales.

Acknowledgements

For support with field work in Colombia, BAH thanks Jimmy Cabra García (organization and collection permit), Germán Andrés Rodríguez, William Galvis, and David Vergara Moreno (assistance in the field), and Pedro Londoño (permit to enter Bosque del Silencio). Colombian specimens were collected under permit #1070 granted by the Autoridad Nacional de Licencias Ambientales (ANLA) to the Universidad del Valle. For support with field work in Venezuela, BAH thanks the directors of the Museo del Instituto de Zoología Agrícola (Maracay), Vilma Savini and José Clavijo, for facilitating field work; Boris Striffler, Quintín Arias, and Osvaldo Villarreal for support in the field; Abel Pérez-González for his help with getting a collection permit, and the Dirección General de Fauna y Oficina Nacional de Diversidad Biológica in Caracas for issuing permit No 01-11-0966. Additional specimens from Panama and Colombia were kindly provided by Jan Pedersen (University of Copenhagen) and Ingi Agnarsson (CarBio project). We thank Laura von der Mark (ZFMK) for help with CO1 barcoding, and Abel Pérez-González and an anonymous reviewer for valuable comments on the manuscript. Trips to Venezuela and Colombia were financially supported by the German Research Foundation (DFG, projects HU 980/1-1, HU 980/13-1, HU 980/14-1).

Author contributions

BAH: initiation of project, funding acquisition, collecting, taxonomy, writing.
GM: curation and analysis of molecular data, writing.

References

- Astrin J.J., Huber B.A., Misof B. & Kluetsch C.F.C. 2006. Molecular taxonomy in pholcid spiders (Pholcidae, Araneae): Evaluation of species identification methods using CO1 and 16S rRNA. *Zoologica Scripta* 35: 441–457. <http://dx.doi.org/10.1111/j.1463-6409.2006.00239.x>
- Carvalho L.S., Dias S.C., Candiani D.F. & Bonaldo A.B. 2010. On the female of *Metagonia taruma* (Araneae: Pholcidae), ecology of the pholcid spiders in the Urucu River Basin, Amazonas, Brazil and new records from Brazilian Amazonia. *Zoologia* 27: 431–439. <https://doi.org/10.1590/S1984-46702010000300016>
- Carvalho L.S., Martins P.H., Schneider M.C. & Cabra-García J. 2017. New records of spiders (Arachnida, Araneae) from the state of Roraima, northern Brazil. *Check List* 13 (1): 2040. <https://doi.org/10.15560/13.1.2040>
- Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791. <https://doi.org/10.2307/2408678>
- Ferreira R.L., Souza M.F.V.R., Machado E.O. & Brescovit A.D. 2011. Description of a new *Eukoenenia* (Palpigradi: Eukoeneniidae) and *Metagonia* (Araneae: Pholcidae) from Brazilian caves, with notes on their ecological interactions. *Journal of Arachnology* 39: 409–419. <https://doi.org/10.1636/Ha11-03.1>
- Gertsch W.J. 1971. A report on some Mexican cave spiders. *Association of Mexican Cave Studies, Bulletin* 4: 47–111.
- Gertsch W.J. 1977. Report on cavernicole and epigeal spiders from the Yucatan Peninsula. *Association of Mexican Cave Studies, Bulletin* 6: 103–131.
- Gertsch W.J. 1986. The spider genus *Metagonia* (Araneae: Pholcidae) in North America, Central America, and the West Indies. *Texas Memorial Museum, Speleological Monographs* 1: 39–62.
- González-Sponga M.A. 1998. Arácnidos de Venezuela. Cuatro nuevos géneros y cuatro nuevas especies de la familia Pholcidae Koch, 1850 (Araneae). *Memorias de la Sociedad de Ciencias naturales La Salle* 57: 17–31.
- Helversen O. 1976. Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida: Araneae). *Entomologica Germanica* 3 (1/2): 13–28. <https://doi.org/10.1127/entom.germ/3/1976/13>
- Huber B.A. 1997a. Redescriptions of Eugène Simon's neotropical pholcids (Araneae, Pholcidae). *Zoosystema* 19 (4): 573–612. <https://doi.org/10.5962/p.268855>
- Huber B.A. 1997b. On American 'Micromerys' and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. *Zoologica Scripta* 25: 341–363. <https://doi.org/10.1111/j.1463-6409.1996.tb00170.x>
- Huber B.A. 1998. Report of some pholcid spiders collected in Guatemala and Honduras (Araneae, Pholcidae). *Revue suisse de Zoologie* 105 (1): 49–80. <https://doi.org/10.5962/bhl.part.80031>
- Huber B.A. 2000. New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. *Bulletin of the American Museum of Natural History* 254: 1–348. Available from http://www.pholcidae.de/PDFs/new_world_pholcidae_2000.pdf [accessed 27 Oct. 2025].
- Huber B.A. 2004. Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) (Pholcidae: Araneae). *Journal of Zoology* 262: 317–326. <https://doi.org/10.1017/S0952836903004709>
- Huber B.A. 2006. Cryptic female exaggeration: The asymmetric female internal genitalia of *Kaliana yuruani* (Araneae: Pholcidae). *Journal of Morphology* 276: 705–712. <https://doi.org/10.1002/jmor.10431>

- Huber B.A. 2010. Mating positions and the evolution of asymmetric insect genitalia. *Genetica* 138: 19–25. <https://doi.org/10.1007/s10709-008-9339-6>
- Huber B.A. & Meng G. 2024. Old World *Micropholcus* spiders, with first records of acrocerid parasitoids in Pholcidae (Araneae). *ZooKeys* 1213: 95–182. <https://doi.org/10.3897/zookeys.1213.133178>
- Huber B.A. & Villarreal O. 2020. On Venezuelan pholcid spiders (Araneae, Pholcidae). *European Journal of Taxonomy* 718: 1–317. <https://doi.org/10.5852/ejt.2020.718.1101>
- Huber B.A., Rheims C.A. & Brescovit A.D. 2005. Two new species of litter-dwelling *Metagonia* spiders (Araneae, Pholcidae) document both rapid and slow genital evolution. *Acta Zoologica (Stockholm)* 86: 33–40. <https://doi.org/10.1111/j.0001-7272.2005.00184.x>
- Huber B.A., Sinclair B. & Schmitt M. 2007. The evolution of asymmetric genitalia in spiders and insects. *Biological Reviews* 82: 647–698. <https://doi.org/10.1111/j.1469-185X.2007.00029.x>
- Huber B.A., Meng G., Acurio A.E., Astrin J.J., Inclán D.J., Izquierdo M. & Valdez-Mondragón A. 2022. *Metagonia* spiders of Galápagos: Blind cave-dwellers and their epigean relatives (Araneae, Pholcidae). *Invertebrate Systematics* 36 (7): 647–678. <https://doi.org/10.1071/IS21082>
- Huber B.A., Meng G., Dupérré N., Herrera M., Inclán D., Wipfler B. 2023. Humpback spiders from Ecuador: Relationships, prosoma ‘inflation’, and genital asymmetry (Araneae: Pholcidae: *Mecolaesthus*). *Invertebrate Systematics* 37 (2): 117–151. <https://doi.org/10.1071/IS22052>
- Huber B.A., Meng G., Dederichs T.M., Michalik P., Forman M. & Král J. 2024. Castaways: the Leeward Antilles endemic spider genus *Papiamenta* (Araneae: Pholcidae). *Invertebrate Systematics* 38 (2): IS23052. <https://doi.org/10.1071/IS23052>
- Kimura M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. <https://doi.org/10.1007/bf01731581>
- Rivera-Quiroz F.A., Schilthuizen M., Petcharad B. & Miller J.A. 2020. Imperfect and askew: A review of asymmetric genitalia in araneomorph spiders (Araneae: Araneomorphae). *PLoS ONE* 15 (6): e0220354. <https://doi.org/10.1371/journal.pone.0220354>
- Saitou N. & Nei M. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4: 406–425. <https://doi.org/10.1093/oxfordjournals.molbev.a040454>
- Tamura K., Stecher G. & Kumar S. 2021. MEGA 11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution* 38: 3022–3027. <https://doi.org/10.1093/molbev/msab120>

Printed versions of all papers are deposited in the libraries of three of the institutes that are members of the *EJT* consortium: Muséum national d’Histoire naturelle, Paris, France; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Appendix 1. Genital asymmetry in *Metagonia* Simon, 1893 – an overview.

Genital symmetry (blue) and asymmetry (red), mapped on the phylogeny of *Metagonia*. The tree is an exact copy of the tree published in Huber *et al.* (2022) except that two new names proposed herein are updated (in Fig. A3: M025 and M092). Light red stands for female asymmetry, which is antisymmetry in all cases where this detail has been studied. Dark red (in Fig. A3 only) stands for directional female and male asymmetry. No color means that the internal female genitalia have not yet been studied.

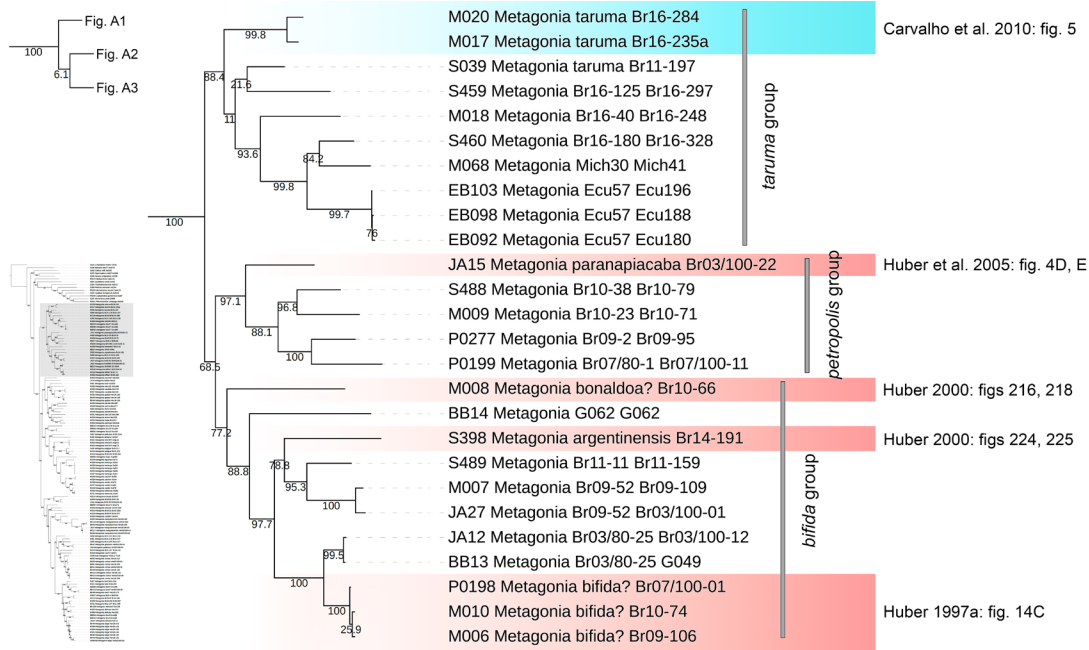


Fig. A1. The *Metagonia taruma*, *petropolis*, and *bifida* groups. Upper inset: relationships to other species groups. Lower inset: position of this clade in the complete tree.

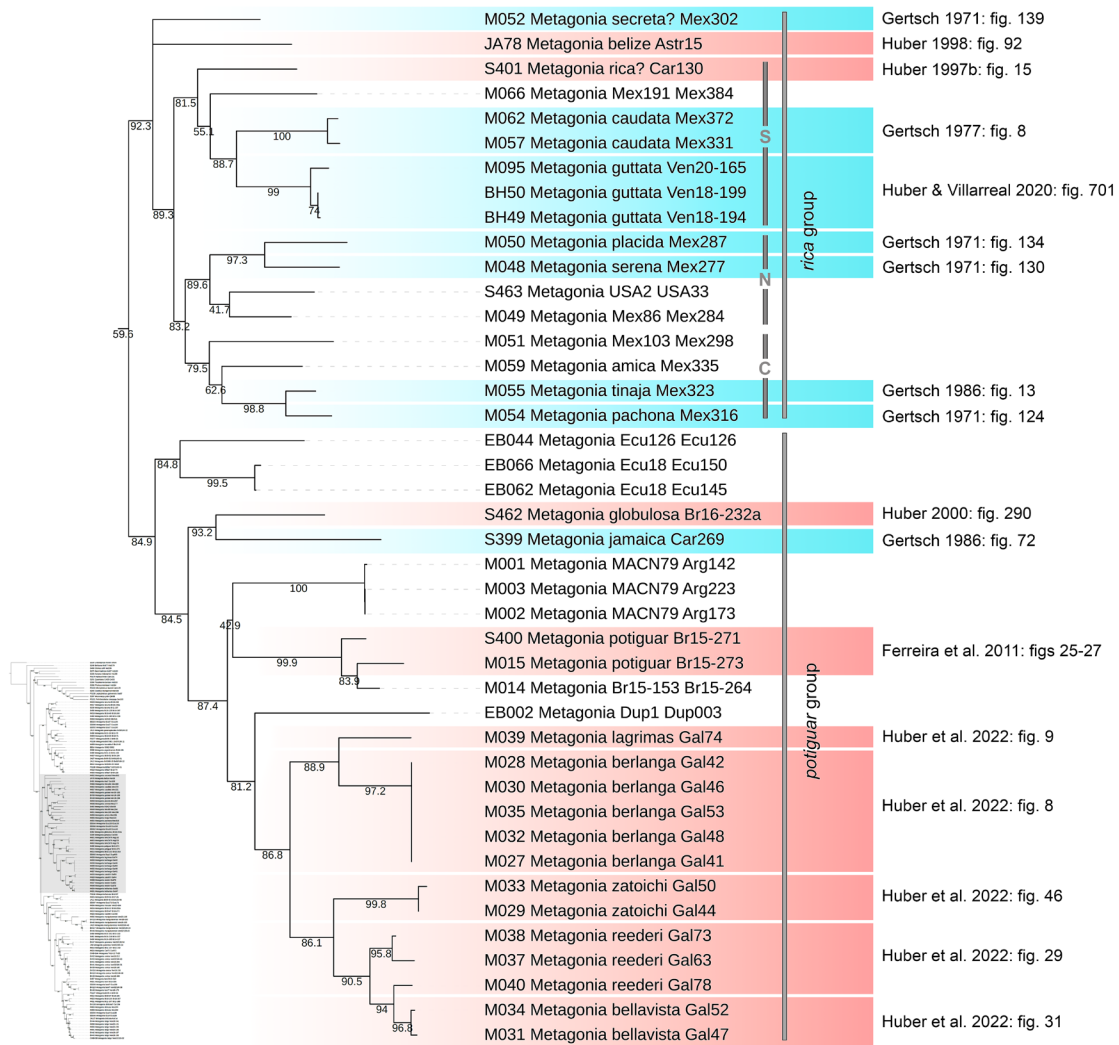


Fig. A2. The *Metagonia rica* and *potiguar* groups. Inset: position of this clade in the complete tree.

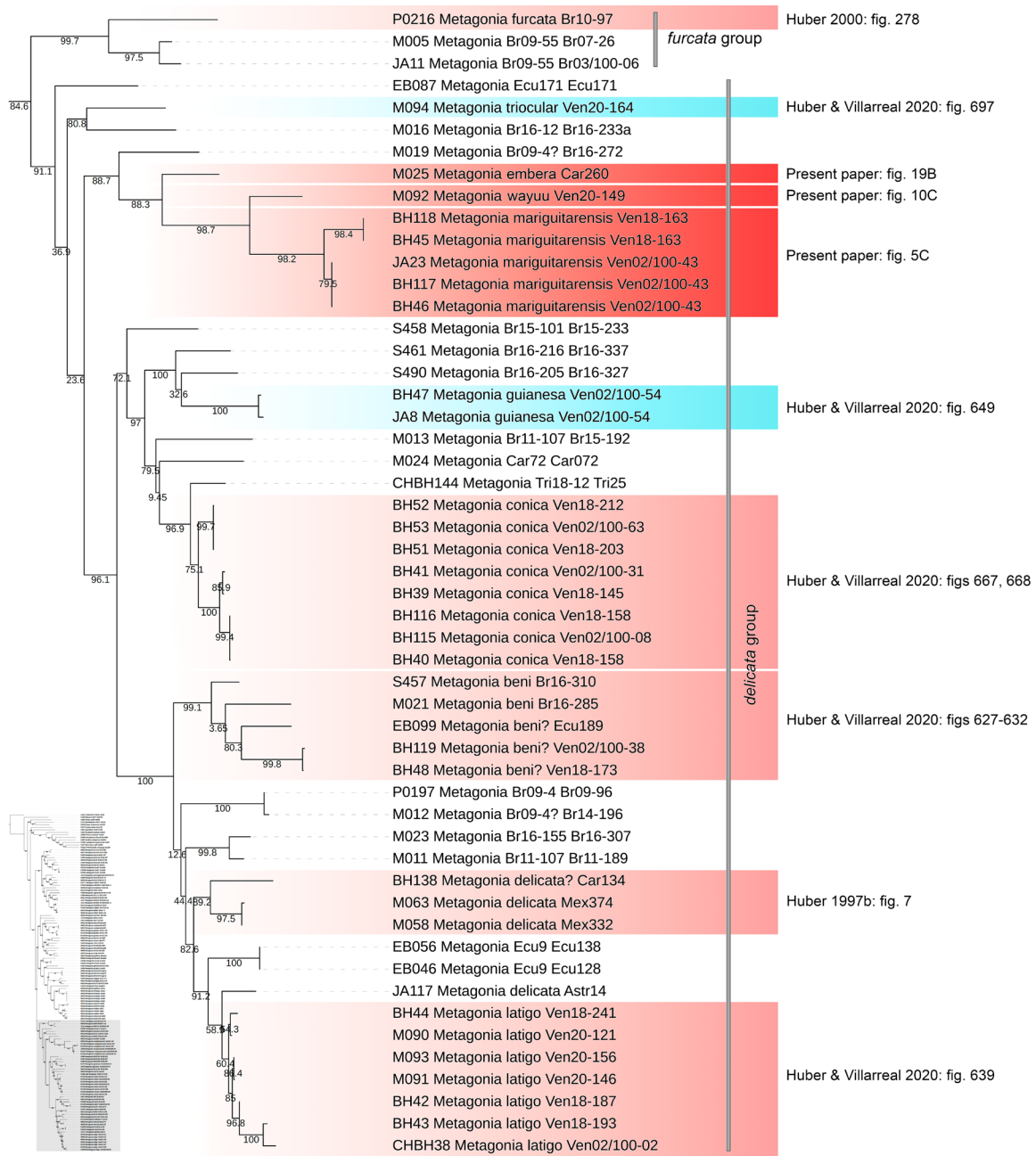


Fig. A3. The *Metagonia furcata* and *delicata* groups. Inset: position of this clade in the complete tree.