


Research article

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genus *Guaranita* (Araneae, Pholcidae)**Bernhard A. HUBER ^{1,*}, Guanliang MENG², Jiří KRÁL³,
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Abstract. The southern South American genus *Guaranita* includes tiny spiders (body length ~1 mm) that lead reclusive lives under ground-objects and run rapidly when disturbed. As a result, they have been poorly collected and studied. Here we report on a recent collection of *Guaranita* spiders from Argentina, describing one new species (*G. auadae* Huber sp. nov.) and the previously unknown female of *G. doobby* Torres *et al.*, 2016. In addition, we provide *COI* barcodes for all (now five) known species, first SEM data, and first chromosome data for the genus. The diploid number of *Guaranita goloboffi* Huber, 2000 ($2n\sigma = 11$) is among the lowest in araneomorph spiders with monocentric chromosome structure.

Keywords. Argentina, chromosome, *COI* barcode, sexual dimorphism, taxonomy.

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Introduction

Among Pholcidae C.L. Koch, 1850, commonly known as daddy-longlegs-spiders, Ninetinae Simon, 1890 are distinct at first sight in having relatively short legs. This morphological trait is probably related to the fact that most Ninetinae are fast runners, well prepared to avoid predators and generalist collectors. In addition, most representatives of Ninetinae are tiny, with body lengths usually ranging between one and two millimeters (Huber 2000). They lead reclusive lives under rocks and stones and are largely restricted to arid regions that are generally poorly sampled (Huber & Brescovit 2003; Huber *et al.* 2023a). All this combines to make Ninetinae the worst sampled and most poorly known subfamily of Pholcidae. Ninetinae is also the smallest subfamily in terms of described species numbers (Huber *et al.* 2018; currently 42 species versus 116 to ~1080 species in other subfamilies), but it remains unclear whether this is an artefact of inadequate collecting or not.

The present paper is one in an ongoing series of contributions to our knowledge about these poorly known spiders. The South American genus *Guaranita* Huber, 2000 was originally established for three species from Argentina and southern Brazil (Huber 2000); a fourth species was added recently, also from Argentina (Torres *et al.* 2016). *Guaranita* spiders are tiny (body length ~1 mm), short-legged, fast-running, and hidden under objects on the ground, but unlike most other Ninetinae, they are also found in relatively humid environments.

Previous publications reported a total of 58 adult specimens; molecular sequence data have been available for only one species; nothing has been known about characters that require SEM (spinnerets; epiandrous spigots; tarsal organ). Here we report on recent collections of over 250 adult specimens (including one new species and the previously unknown female of *G. dooby* Torres *et al.*, 2016), provide *COI* barcodes for all known species, and provide first SEM and chromosome data for the genus. A comprehensive evaluation and interpretation of these results must be delayed until the putatively closest relatives (*Galapa* Huber, 2000; *Pemona* Huber, 2019; *Kambiwa* Huber, 2000; according to analyses of ultraconserved elements; G. Meng, B.A. Huber, L. Podsiadlowski, unpubl. data) get revised in a comparable fashion (in preparation).

Material and methods

Taxonomy and morphology

The taxonomic part of this study is based on the examination of 255 adult specimens deposited in the following collections:

IRSNB	=	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
LABRE	=	Laboratorio de Biología Reproductiva y Evolución, Córdoba, Argentina
MACN	=	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
ZFMK	=	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

The taxonomic description follows the style of recent publications on Ninetinae (e.g., Huber *et al.* 2023a, 2023b; based on Huber 2000). Measurements were done on a dissecting microscope with an ocular grid and are in mm unless otherwise noted; eye measurements are $\pm 5 \mu\text{m}$. Photos were made with a Nikon Coolpix 995 digital camera (2048 \times 1536 pixels) mounted on a Nikon SMZ 18 stereo microscope or 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 later improved under a dissecting 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; two decimals: within ~1 km; one decimal: within ~10 km. Distribution maps were generated with ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA). For scanning electron microscope (SEM) photos, specimens were dried in hexamethyldisilazane (HMDS) (Brown 1993), and photographed with a Zeiss Sigma 300 VP scanning electron microscope. Abbreviations used in figures are explained in the figure legends.

Abbreviations used in the text:

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)

Karyology

Chromosome slides were obtained from the whole abdomens of three specimens of *G. goloboffi* Huber, 2000, one male from near Cabra Corral, and two males from Chumbicha (locality details in Material examined section). The slides were obtained by the plate spreading technique of Ávila Herrera *et al.* (2021) and were analyzed with an Olympus BX 50 microscope equipped with a DP 71 CCD camera. Two mitotic plates were used to determine relative chromosome length (RCL) and chromosome morphology. Relative chromosome length was estimated as the percentage of the total chromosome length (TCL) of the haploid set including the X chromosome. Chromosome morphology was based on the ratio of the longer and shorter chromosome arms (Levan *et al.* 1964). The sex chromosome system of araneomorph spiders is complex. Besides one to several non-homologous sex chromosomes, it probably contains one pair of largely undifferentiated sex chromosomes X and Y [so-called cryptic sex chromosome pair (CSCP); Král 2007; Sember *et al.* 2020]. In *Guaranita*, it was impossible to distinguish the CSCP from autosomes. Therefore, the CSCP and autosomes are collectively referred to as chromosome pairs.

Following the analysis with a light microscope, and after the removal of immersion oil and Giemsa stain, the preparation of the male from Cabra Corral was used for the visualization of nucleolus organizer regions (NORs) with a biotin-labelled 18S rDNA probe from the synspermiate spider *Dysdera erythrina* (Walckenaer, 1802) using a variant of the fluorescence in situ hybridization (FISH) described in detail by Forman *et al.* (2013); the probe is specified in Ávila Herrera *et al.* (2021). The probe was visualized by streptavidin-Cy3, with amplification of the signal (biotinylated antistreptavidin, streptavidin-Cy3). The chromosomes were counterstained by DAPI. The slides were analyzed with an Olympus IX81 microscope equipped with an ORCA-AG CCD camera (Hamamatsu). Images were pseudocolored (red for Cy3, blue for DAPI) and superimposed with Cell[^]R software (Olympus Soft Imaging Solutions).

Molecular data and analyses

Taxon sampling

We newly sequenced *COI* barcodes from seven specimens representing five species of *Guaranita* (Table 1) and added to these the single barcode previously available for the genus (from Eberle *et al.* 2018; S347: MG268616) and two outgroup species representing the Ninetinae genus *Ibotyporanga* Mello-Leitão, 1944, also from Eberle *et al.* (2018) (S443: MG268742 and JA123: DQ667852; Fig. 1).

Table 1. Geographic origins and *COI* accession numbers of newly sequenced specimens, sorted by code.

Code	Species	Vial	Country	Admin.	Locality	Lat	Long	<i>COI</i>
N002	<i>G. munda</i>	Arg126	Argentina	Córdoba	~1.5 km E of Nono	-31.7980	-64.9877	OQ453155
N027	<i>G. yaculica</i>	Arg175	Argentina	Jujuy	Calilegua National Park, ~1 km NW of headquarters	-23.7540	-64.8537	OQ453156
N029	<i>G. auadae</i>	Arg179	Argentina	Jujuy	between San Salvador and Purmamarca, 'site 2'	-23.8849	-65.4613	OQ453157
N031	<i>G. doobby</i>	Arg187	Argentina	Salta	~55 km NW of Campo Quijano	-24.4716	-65.9272	OQ453158
N032	<i>G. goloboffi</i>	Arg190	Argentina	Salta	Cabra Corral, 'site 1', ~5 km E of Coronel Moldes	-25.2870	-65.4238	OQ453159
N037	<i>G. goloboffi</i>	Arg203	Argentina	Salta	~1 km SW of Alemania	-25.6300	-65.6180	OQ453160
N046	<i>G. goloboffi</i>	Arg220	Argentina	Catamarca	~5 km NW of Chumbichica, near Balneario El Caolín, 'site 1'	-28.8152	-66.2478	OQ453161

DNA extraction, amplification and sequencing

Three or four legs of specimens stored in non-denatured pure ethanol (~99%) at -20°C were used for DNA extraction. Extracted genomic DNA is deposited at and available from the LIB Biobank, Museum Koenig, Bonn. DNA was extracted using the HotSHOT method (Truett *et al.* 2018). *COI* primers used were LCO1490-JJ and HCO2198-JJ (Astrin & Stüben 2008), with versions JJ2 (Astrin *et al.* 2016) as backup. A different tag sequence (from Srivathsan *et al.* 2021) of 13 bp length was added to the 5'-ends of forward and reverse primers, respectively. The 20 µl reaction volume consisted of 5 µl H₂O, 1 µl DNA template, 2 µl Q-Solution, 10 µl Qiagen Multiplex-Mix, 1 µl forward primer, and 1 µl reverse primer. The PCR procedure was: (1) 95°C for 15 minutes; (2) denaturation at 94°C for 35 seconds; (3) annealing at 55°C (or 40°C) for 90 seconds; (4) elongation at 72°C for 90 seconds; (5) final elongation at 72°C for 10 minutes, followed by cooling at 10°C. Steps 2–4 were repeated for 15 cycles (or 25 cycles). The PCR products were then pooled and sequenced with the Oxford Nanopore Technologies (ONT) GridION platform.

COI barcode assembly and contamination check

The *COI* sequences characterized by ONT sequencing were assembled using the ONTbarcoder (Srivathsan *et al.* 2021) pipeline (ver. 0.1.8). Taxonomic assignments of the assembled sequences were checked by: (1) blasting the assembled sequences against a local NT database; (2) the identification engine of the Barcode of Life Data System (BOLD) (<http://www.boldsystems.org/index.php>) (Ratnasingham & Hebert 2007; Yang *et al.* 2020).

Multiple sequence alignment (MSA) and Neighbor-Joining (NJ) tree construction

Nucleotide sequences of the *COI* were translated into protein sequences using BioPython (ver. 1.78) (Cock *et al.* 2009) with invertebrate mitochondrial genetic code. Next, protein-MSAs were constructed using the mafft-linsi algorithm of MAFFT (ver. 7.487) (Katoh & Standley 2013), which then assisted the construction of nucleotide level MSAs with pal2nal.pl (Suyama *et al.* 2006). This helps avoid the introduction of biologically meaningless frameshifts to the alignments (Suyama *et al.* 2006). The genetic distances between different specimens were calculated based on the Kimura 2-parameter (K2P) model (Kimura 1980) using MEGA11 (Tamura *et al.* 2021), in which ambiguous positions for each sequence pair were deleted. A NJ-tree was also constructed based on the derived genetic distances, and 500 bootstrap replicates were used to estimate the robustness of the tree (Felsenstein 1985). Tree visualizations were finished with the Newick utilities (ver. 1.6) (Junier & Zdobnov 2010) and iTOL (Letunic & Bork 2021).

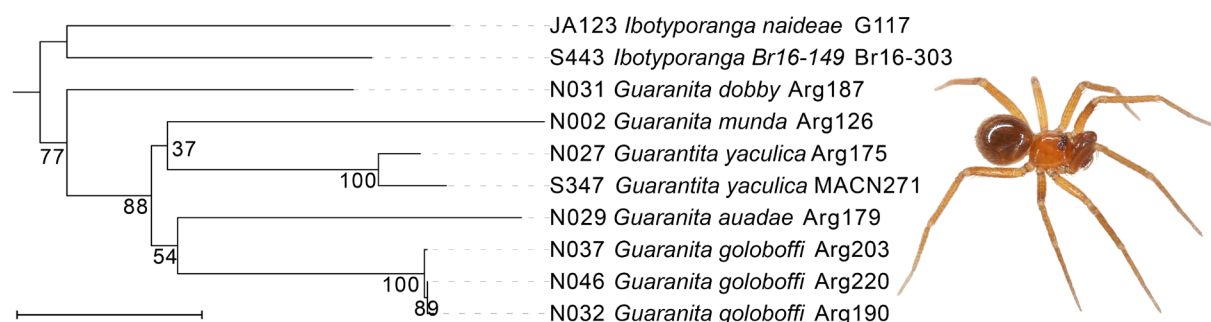


Fig. 1. NJ tree of *COI* barcodes using MEGA11. We applied the Kimura 2-parameter model (Kimura 1980) and the strategy of pairwise deletion of ambiguous positions to calculate the genetic distances between different specimens, from which the NJ-tree was constructed (500 bootstrap replicates). Tree scale = 0.05.

Results

Taxonomy

Class Arachnida Lamarck, 1801
 Order Araneae Clerck, 1757
 Family Pholcidae C.L. Koch, 1850

 Genus *Guaranita* Huber, 2000

Guaranita Huber, 2000: 96.

Type species

Guaranita goloboffi Huber, 2000.

Diagnosis

Small (body length ~1mm) short-legged pholcids with globular abdomen (Fig. 2), distinguished from most other genera of Ninetinae by dorsal flap on procurus (e.g., Figs 4F, 9F, 12D); from *Galapa*, which shares a dorsal process on the procurus (cf. Huber 2000: figs 383, 387), by pair of prominent apophyses on male chelicerae (e.g., Figs 4A–C, 11A–B; absent in *Galapa*) and by unmodified fangs of male chelicerae (with processes in *Galapa*).

Description

Male

MEASUREMENTS. Total body length 0.9–1.1, carapace width 0.4–0.5. Legs relatively short, tibia 1 0.5–0.6; tibia 1 L/d 7–9; leg formula 4-1-2-3; metatarsus 1 shorter than tibia 1 or same length (metatarsus 1/tibia 1 : 0.95–1.00); tibia 2 much shorter than tibia 4 (tibia 2/tibia 4: 0.65–0.75).

COLOUR. Live specimens reddish brown (Fig. 2); abdomen without or with very indistinct marks; legs without dark or light bands. Color in ethanol similar but paler, ochre-yellow.

BODY. Ocular area barely raised, eight eyes (Figs 6A, 11A–D, 17A, 27A), AME relatively large (diameter: 25–30 μm , i.e., 50–60% of PME diameter). Carapace without thoracic groove (Figs 6A, 11A–D, 17A, 27A). Clypeus usually unmodified, only in *G. doobby* with distinct median process (Torres *et al.* 2016: fig. 9). Sternum slightly wider than long, with pair of rounded anterior processes near leg coxae 1, processes apparently without pores. Abdomen globular; four (rarely five) epiandrous spigots arranged in two pairs (Figs 11E–F, 17F, 27F); ALS with seven spigots each (as in female, cf. Figs 6C, 11H, 17B–D, 27C–E): one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (one of which is unusually large); PMS with two short, pointed spigots (as in female, cf. Figs 6D, 27D); PLS without spigots (Figs 17B, 27C–D).

CHELICERAE. With pair of long frontal apophyses (e.g., Figs 4A–C, 11A–B); with stridulatory files on relatively small lateral patches (Figs 12A, 18A–B, 27G), with ~15–25 stridulatory ridges each.

PALPS. Coxa unmodified; trochanter without or with very indistinct ventral projection; femur cylindrical, slightly widened distally, proximally without or with very low retrolateral hump, with prolateral stridulatory pick (modified hair; Fig. 27H); patella short; tibia oval to globular, with two trichobothria; palpal tarsal organ raised, capsulate (Figs 13A, 28A–B), with small opening (diameter of opening ~1.1–1.5 μm); procurus with distinctive dorsal flap, large semi-transparent ventral membrane, and complex tip bent towards dorsal (e.g., Figs 4D–F, 12C–F); genital bulb with simple proximal sclerite, distinct distal (main) sclerite, and variably complex ‘embolar division’ consisting of membranous and sclerotized elements (Figs 4G–I, 29).

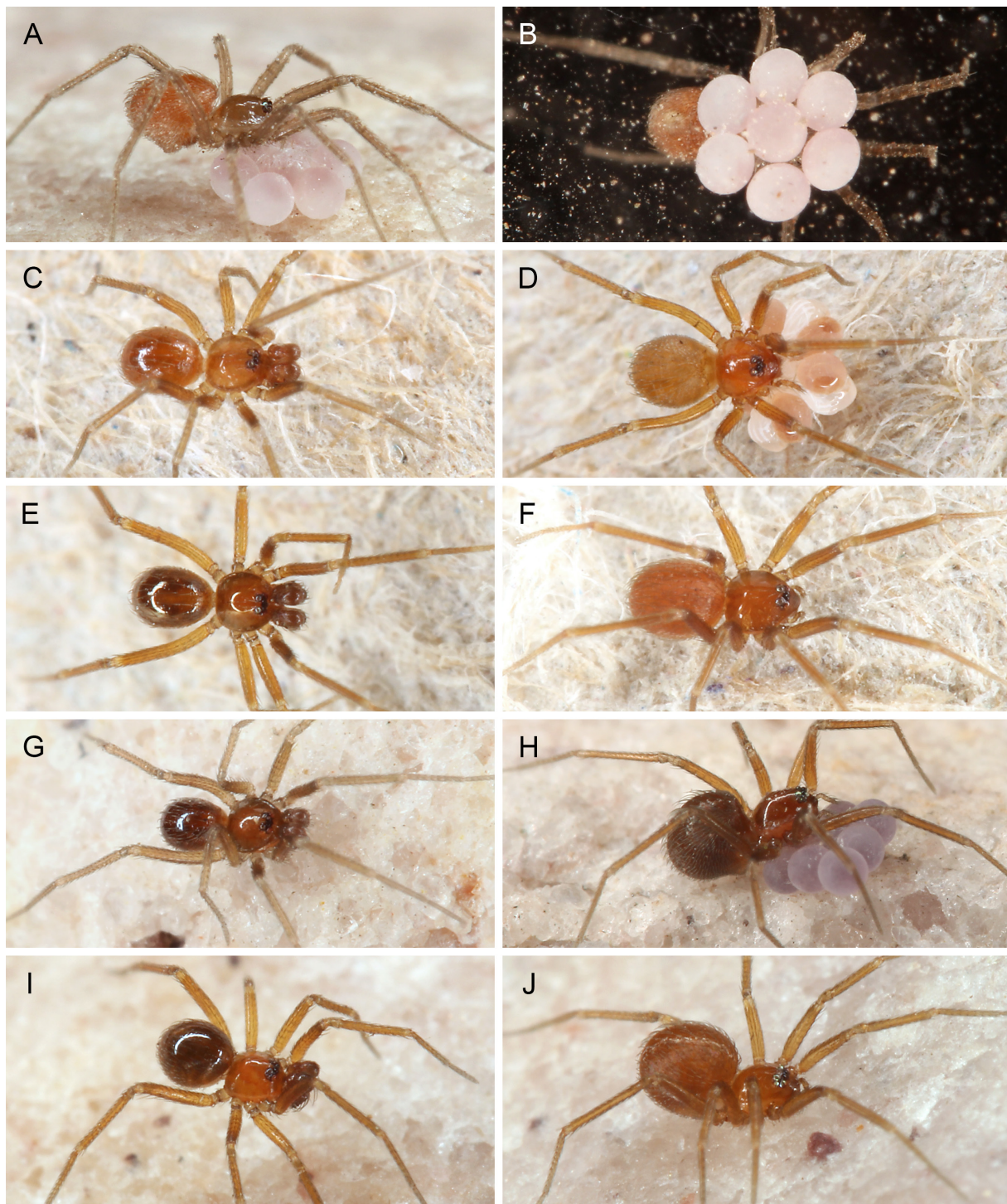


Fig. 2. *Guaranita* Huber, 2000, live specimens. **A–B.** *G. doobby* Torres *et al.*, 2016; females with egg-sacs from NW of Campo Quijano. **C–D.** *G. munda* (Gertsch, 1982); male and female with egg-sac from E of Nono. **E–F.** *G. yaculica* Huber, 2000; male and female from Calilegua National Park. **G–H.** *G. auadae* Huber sp. nov.; male and female with egg-sac from between San Salvador and Purmamarca. **I–J.** *G. goloboffi* Huber, 2000; male and female from NW of Chumbicha.

LEGS. Without spines and curved hairs; with ‘short vertical hairs’ in 1–2 rows on tibia 1 (Figs 13D, 19A–C, 30A–B; length of hairs ~10–15 μm). Trichobothria in usual arrangement: three on each tibia (except tibia 1: prolateral trichobothrium absent), one on each metatarsus, slightly feathered (as in female, cf. Fig. 28E–F); length of trichobothria ~60 μm ; retrolateral trichobothrium of tibia 1 in very distal position (at ~55–65% of tibia length). Tibiae and metatarsi with tiny pores with cuticular rim (diameter of opening ~0.6 μm ; as in female, cf. Figs 6E–F, 19F, 31A). Metatarsi 3 and 4 with ~1–5 slender hairs ventrally (Figs 13E, 19G–H, 31C), with bases as in regular hairs but shafts reminding of trichobothria (i.e., feathered and small proximal diameter: ~2 μm ; regular leg hair proximal diameter: 3–4 μm). Tarsus 1 with 5–6 pseudosegments, poorly visible in dissecting microscope; tarsus 4 distally with one comb-hair on prolateral side (as in female, cf. Fig. 31D); leg tarsal organs very small, not raised, capsulate (Fig. 13C), with small opening (diameter of opening ~0.8–1.0 μm); three claws, superior claws with 8–11 tines (as in female, cf. Figs 7F, 13F–G, 20D–H, 31D–F).

Female

In general, similar to male but chelicerae without stridulatory files (Figs 12B, 18C), sternum without pair of anterior humps, palpal tarsal organ only weakly raised (Figs 19E, 28C–D), and tibia 1 with usual low number of short vertical hairs; legs either slightly shorter than in males or of same length [only *G. goloboffi* Huber, 2000, *G. munda* (Gertsch, 1982), and *G. yaculica* Huber, 2000 with reasonable sample sizes: male/female tibia 1 length: 1.00–1.08]. Spinnerets, leg pores, leg tarsal organs, and comb-hairs as in male. Main (anterior) epigynal plate usually trapezoidal, only in *G. doobby* Torres *et al.*, 2016 rather triangular, weakly protruding (e.g., Figs 5A, 10A, 16A); posterior plate simple, short but wide. Internal genitalia very simple, usually with distinct median structure (poorly developed in *G. doobby*), sometimes with membranous median sac (receptacle?) (e.g., Figs 5C–D, 10C–D, 32); apparently with very small pore plates (arrows in Fig. 32). The ‘‘pair of receptacles’’ mentioned and illustrated in Torres *et al.* (2016: 10, fig. 14) is a misinterpretation either of the book lungs or of a pair of silk glands.

Relationships

The molecular analysis of Eberle *et al.* (2018) included only a single species of *Guaranita* (*G. yaculica*), which was placed (with moderate support) as sister to the South American Ninetinae genera *Pemona* and *Kambiwa*. Preliminary analyses of molecular (UCE) data (G. Meng, B.A. Huber, L. Podsiadlowski, unpubl. data) support the close relationship among these three genera and add *Galapa* to this clade, a genus not included in Eberle *et al.* (2018). Our new SEM data confirm the position of *Guaranita* among Ninetinae (in particular the small opening of the tarsal organs; cf. character 57 in Huber 2000). Within *Guaranita*, our *COI* data suggest that the morphologically distinct *G. doobby* is sister to the other species, a topology that is also supported by preliminary analyses of UCE data.

Natural history

While *Guaranita auadae* Huber sp. nov., *G. doobby*, and *G. goloboffi* were found in relatively arid environments with cacti and low bushes (Fig. 34A, D–F), *G. munda* and *G. yaculica* were collected in dry to humid forests (Fig. 33B–C). In arid environments, the specimens were collected by turning stones and rocks; in more humid environments by shaking dead bromeliads lying on the ground and by sifting leaf litter. *Guaranita munda* was collected by turning stones of a loosely built wall situated in a low forest (Fig. 33B). When disturbed by turning a rock, the spiders ran rapidly a few centimeters over the rock surface but seemed reluctant to drop to the ground. Webs were not seen in the field but the spiders quickly built flimsy webs in small glass vials. We never found more than one species of *Guaranita* at one locality. Other pholcid spiders sharing the microhabitats of *Guaranita* were *Gertschiola macrostyla* (Mello-Leitão, 1941) and *Nerudia* spp. (Ninetinae), and several small undescribed representatives of Modisiminae Simon, 1893. Eggs sacs were carried under the prosoma and contained 5–8 eggs arranged in a single layer (Fig. 2A–B, D, H); they are thus among the smallest egg-sacs known in pholcids (Huber & Eberle 2021).

Table 2. *COI* K2P genetic distances between sequenced specimens. Bold numbers are intraspecific distances (0.2–3.0%, mean 0.9%); interspecific distances within *Guaranita* Huber, 2000: 13.6–21.7% (mean 17.1%); intergeneric distances: 18.1–24.9% (mean 21.2%).

	N002	S347	N027	N029	N031	N032	N037	N046	S443
N002 <i>Guaranita munda</i> Arg126									
S347 <i>Guaranita yaculica</i> MACN271	0.1729								
N027 <i>Guaranita yaculica</i> Arg175	0.1752	0.0297							
N029 <i>Guaranita auadae</i> Arg179	0.2043	0.1858	0.166						
N031 <i>Guaranita doobby</i> Arg187	0.2174	0.1826	0.1805	0.195					
N032 <i>Guaranita goloboffi</i> Arg190	0.1919	0.1544	0.1394	0.1636	0.1671				
N037 <i>Guaranita goloboffi</i> Arg203	0.1919	0.1506	0.1356	0.1595	0.1651	0.0031			
N046 <i>Guaranita goloboffi</i> Arg220	0.1898	0.1525	0.1375	0.1615	0.1651	0.0015	0.0015		
S443 <i>Ibotporanga</i> Br16-149 Br16-303	0.2028	0.2007	0.2026	0.2348	0.1814	0.1932	0.1911	0.1911	
JA123 <i>Ibotporanga naideae</i> G117	0.2348	0.2143	0.2207	0.2494	0.1889	0.2285	0.2285	0.2251	0.1863

Distribution

Guaranita is widespread in northern Argentina and reaches into Paraguay and southern Brazil (and probably southern Bolivia and Uruguay) (Fig. 33). It does not seem to cross the Andes into Chile.

Composition

The genus now includes five described species, all of which are treated below. Our limited genetic data support the species limits (Table 2): intraspecific K2P distances (N = 4) range from 0.2–3.0% (mean 0.9%); interspecific distances within *Guaranita* (N = 24) range from 13.6–21.7% (mean 17.1%).

***Guaranita doobby* Torres *et al.*, 2016**
Figs 2A–B, 3–7, 32A

Guaranita doobby Torres *et al.*, 2016: 9, figs 6–12 (♂).

Diagnosis (amendments; see Torres *et al.* 2016)

Distinguished from known congeners by median process on male clypeus (cf. Torres *et al.* 2016: fig. 9; unmodified in congeners), by male cheliceral apophyses (Fig. 4A–C; short and diverging in distal view), by very small (compared with congeners) dorsal flap on procurus (Fig. 4F), and by roughly triangular (rather than trapezoidal as in congeners) anterior epigynal plate (Fig. 5A); also by relatively slender male palpal tibia (Fig. 3C; width/length 0.75; other species 0.85–1.00) and by female internal genitalia (Figs 5C–D, 32A; median structure poorly developed compared with congeners); from *G. auadae* sp. nov. and *G. goloboffi* also by narrow distal bulbal sclerite (Fig. 4G).

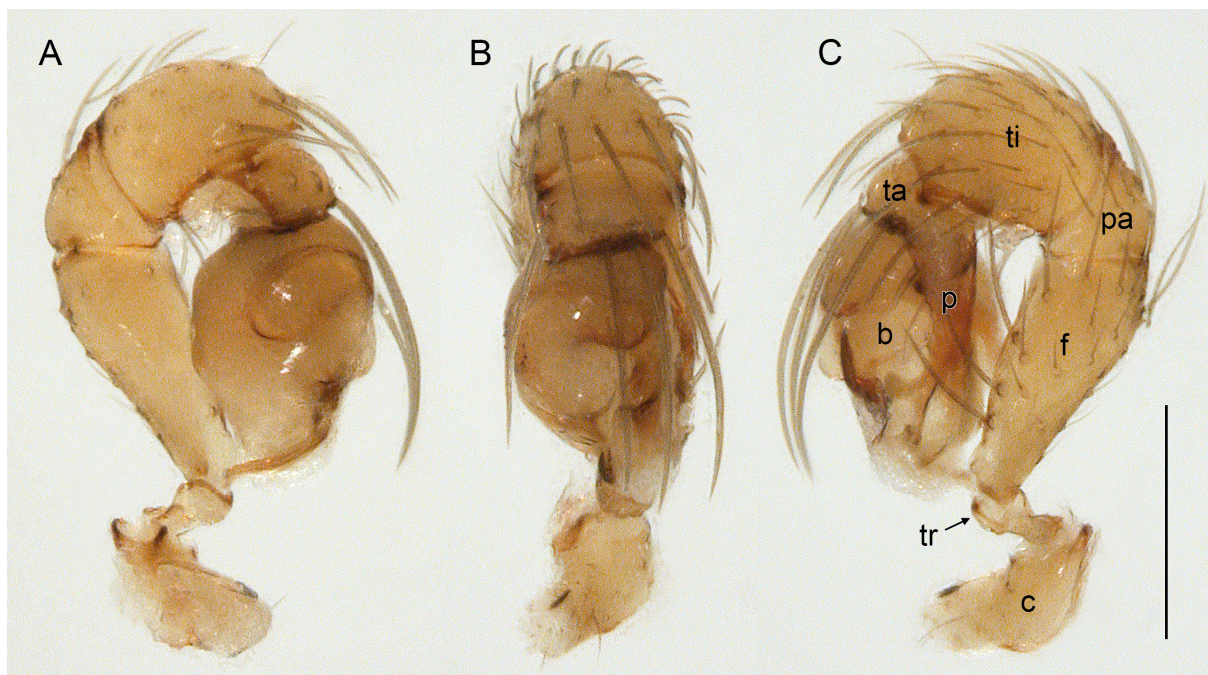


Fig. 3. *Guaranita doobby* Torres *et al.*, 2016; male from NW of Campo Quijano (ZFMK Ar 24121). Left pedipalp, prolateral (A), dorsal (B), and retrolateral (C) views. Abbreviations: b = genital bulb; c = coxa; f = femur; p = procurus; pa = patella; ta = tarsus; ti = tibia; tr = trochanter. Scale bar = 0.2 mm.

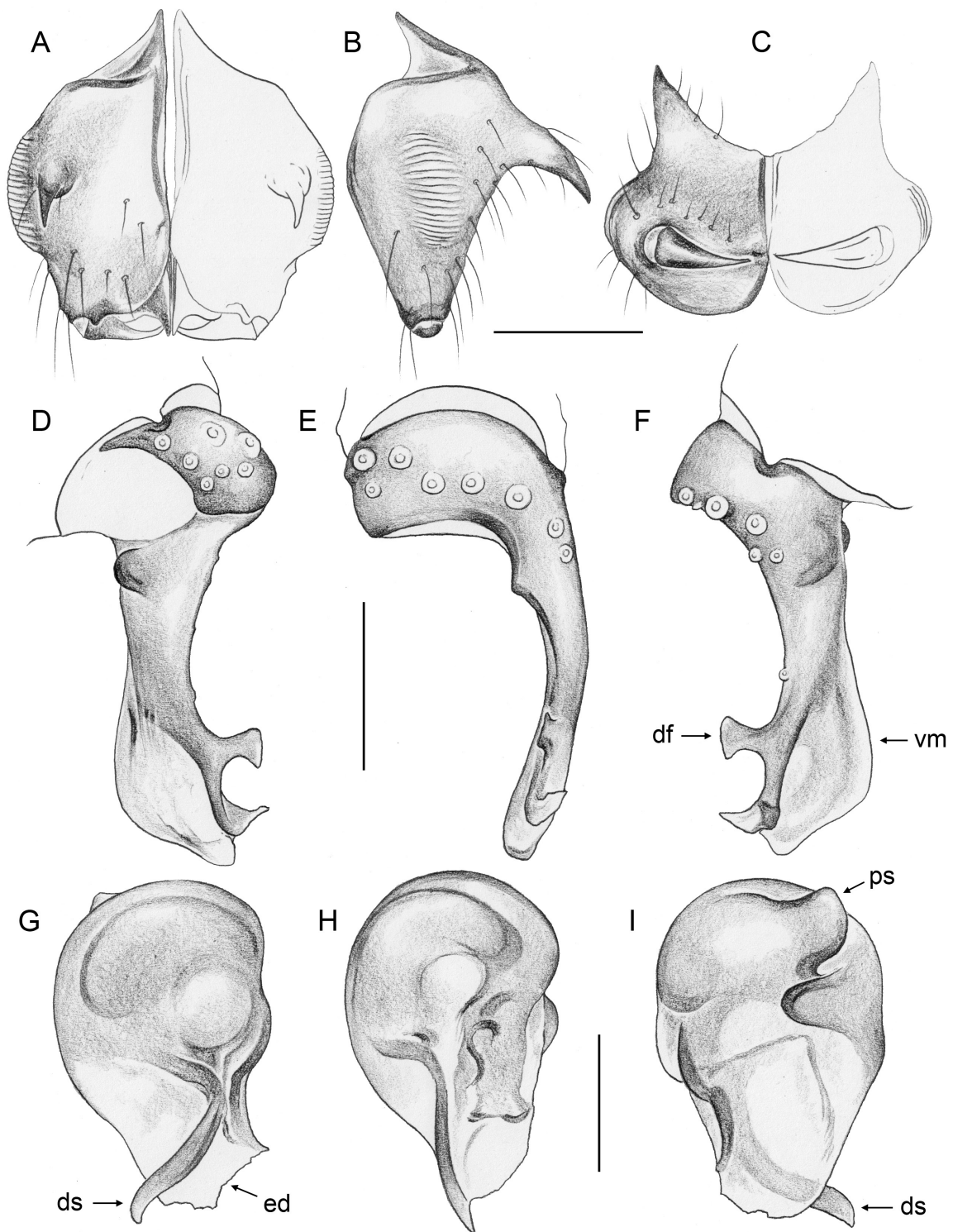


Fig. 4. *Guaranita doobby* Torres *et al.*, 2016; male from NW of Campo Quijano (ZFMK Ar 24121). **A–C.** Chelicerae, frontal, lateral, and ventral views. **D–F.** Left procurus, prolateral, dorsal, and retrolateral views. **G–I.** Left genital bulb, prolateral, dorsal, and retrolateral views. Abbreviations: df = dorsal flap; ds = distal bulbal sclerite; ed = embolar division; ps = proximal bulbal sclerite; vm = ventral membrane. Scale bars = 0.1 mm.

Material examined (new record)

ARGENTINA – **Salta** • 2 ♂♂, 3 ♀♀; ~55 km NW of Campo Quijano; 24.4716° S, 65.9272° W; 3040 m a.s.l.; 19 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24121 • 11 ♀♀ in pure ethanol (four prosomata used for molecular work; one female and one female abdomen used for SEM); same collection data as for preceding; ZFMK Arg187 • 2 ♀♀; same collection data as for preceding; LABRE-Ar 876 • 1 ♀, in pure ethanol; same collection data as for preceding; LABRE-Ar 865.

Redescription of male (amendments; see Torres *et al.* 2016)

Measurements of male from 55 km NW of Campo Quijano: total body length 1.1 (1.2 with clypeus process), carapace width 0.48; distance PME–PME 45 μ m; diameter PME 40 μ m; distance PME–ALE 20 μ m; distance AME–AME 20 μ m; diameter AME 25 μ m. Leg 1: 2.33 (0.66+0.16+0.62+0.55+0.34), tibia 2: 0.54, tibia 3: 0.48, tibia 4: 0.72; tibia 1 L/d: 9; diameters of leg femora 0.10–0.11, of leg tibiae: 0.065. Tibia 1 of second newly collected male: 0.58. Tip of clypeus process straight but at tip with hairs pointing upwards and backwards. Sternum slightly wider than long (0.34/0.30). Chelicerae as in Fig. 4A–C. Pedipalp as in Fig. 3A–C; tibia with two trichobothria; procurus as in Fig. 4D–F, with large transparent ventral membrane, distinctive dorsal flap, and tip bent towards dorsal; genital bulb as in Fig. 4G–I, with simple proximal sclerite and band-like distal sclerite (same width over most of its length). Legs without spines and curved hairs; vertical hairs not seen; retrolateral trichobothrium of tibia 1 at 60%; prolateral trichobothrium absent on tibia 1, present on other leg tibiae; tarsus 1 with 5 pseudosegments, poorly visible in dissecting microscope.

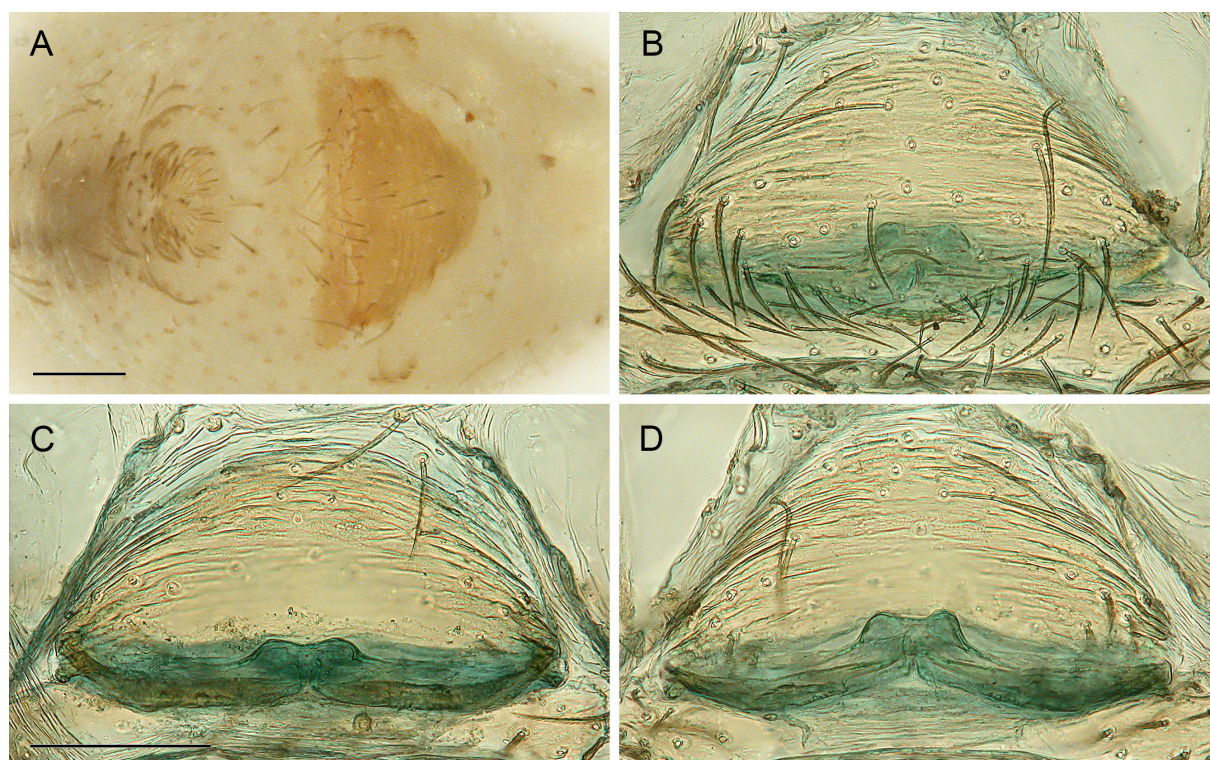


Fig. 5. *Guaranita dobbys* Torres *et al.*, 2016; females from NW of Campo Quijano (ZFMK Ar 24121). **A.** Abdomen, ventral view. **B.** Cleared epigynum, ventral view. **C–D.** Cleared epigyna of two specimens, dorsal views. Scale bars = 0.1 mm (B–D at same scale).

Description of female

In general similar to male (Fig. 2A–B) but clypeus without process, sternum without pair of anterior humps, and chelicerae without stridulatory files. Tibia 1 in seven females: 0.58–0.64 (mean 0.62). Epigynum (Figs 5A, 6B) with simple triangular anterior plate weakly bulging; posterior plate short and simple. Internal genitalia (Figs 5C–D, 32A) very simple, with median sclerotized structure (receptacle?), apparently with small pore plates. Each ALS with one strongly widened spigot, one long pointed spigot,

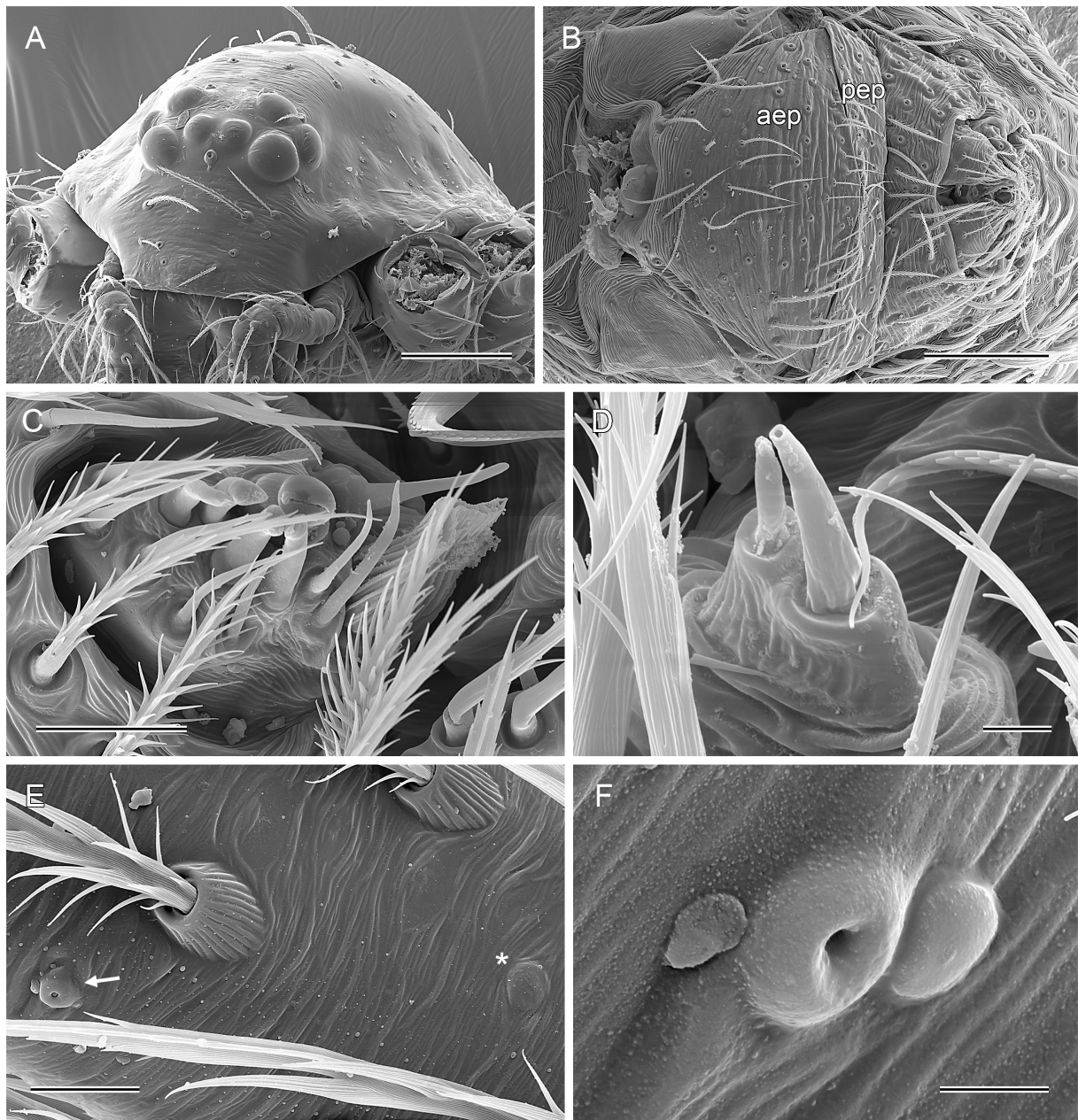


Fig. 6. *Guaranita doobby* Torres *et al.*, 2016; female from NW of Campo Quijano (ZFMK Arg187). **A.** Prosoma, oblique frontal view. **B.** Abdomen, ventral view. **C.** ALS spigots. **D.** PMS spigots. **E.** Pore (arrow) and cuticular plate (asterisk) among regular hairs on right metatarsus 3. **F.** Pore on left tibia 4. Abbreviations: aep = anterior (main) epigynal plate; pep = posterior epigynal plate. Scale bars: A–B = 100 μ m; C, E = 10 μ m; D, F = 2 μ m.

and five cylindrical spigots (of which one is much wider than the others; Fig. 6C); each PMS with two conical spigots (Fig. 6D); PLS without spigots. Leg tibiae and metatarsi with tiny pores with cuticular rim (pore diameter 0.6 μm ; Fig. 6E–F) and with small round cuticular ‘plates’ (diameter 4–5 μm ; Fig. 6E). Tarsal organs with very small openings (diameters of openings 0.8–0.9 μm ; Fig. 7D–E). Metatarsi 3 and 4 with one long slender hair each on retrolateral side (Fig. 7C).

Remarks (notes on type locality)

This species was previously known from two specimens supposedly from two localities in Salta province: the holotype locality, 9 km E of Cabra Corral dam; and a second locality, 1 km N of “Charrillos” (should be Chorrillos). Our newly collected specimens of *G. doobby* are from close to the second locality, in the same river valley, ~37 km NW of Chorrillos. However, we failed to find *G. doobby* at the holotype locality

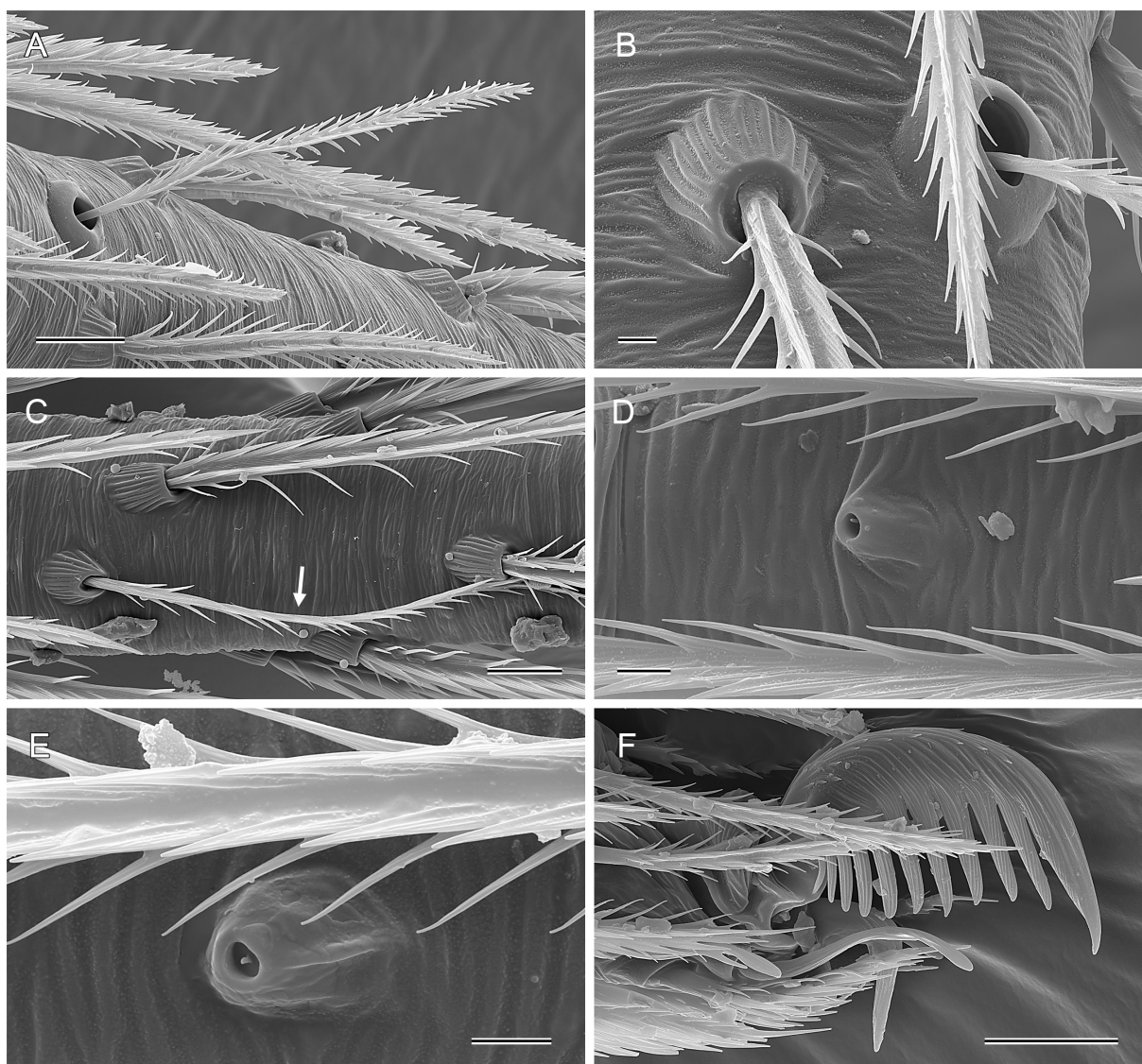


Fig. 7. *Guaranita doobby* Torres *et al.*, 2016; female from NW of Campo Quijano (ZFMK Arg187). **A.** Trichobothrium on left metatarsus 1. **B.** Bases of regular hair and of trichobothrium on left metatarsus 1. **C.** Slender hair (arrow) among regular hairs on right metatarsus 4. **D.** Tarsal organ on right tarsus 3. **E.** Tarsal organ on right tarsus 2. **F.** Tip of right tarsus 1. Scale bars: A, C, F = 10 μm ; B, D–E = 2 μm .

and at several nearby sites E of Cabra Corral dam we visited. Instead, we found *G. goloboffi* at two sites in that area. Previous collectors also found numerous specimens of *G. goloboffi* E of Cabra Corral dam (Torres *et al.* 2015). This sheds doubt on the origin of the *G. dooby* holotype. We suspect that the holotype specimen is mislabeled but according to José Corronca (pers. com. Jan. 2022) this is unlikely to be the case.

Natural history

The newly collected specimens were found under rocks in a very arid environment (Fig. 34A). Egg sacs (N = 4) contained 6–8 eggs and were carried in a single layer under the prosoma (Fig. 2B); egg diameter: 0.46–0.48.

Distribution

Known from three localities in Argentina, Salta Province (Fig. 33A); but see Notes on type locality above.

Guaranita munda (Gertsch, 1982)

Figs 2C–D, 8–13, 32B

Pholcophora munda Gertsch, 1982: 104, figs 31–33, 42–44 (♂♀).

Guaranita munda – Huber 2000: 100, figs 379–380; 2014: 140. — Avalos *et al.* 2006: 193. — Torres *et al.* 2016: 11, figs 16–18.

Diagnosis (amendments; see Huber 2000)

Distinguished from known congeners by size and shape of dorsal flap on procurus (Fig. 9F; larger than in congeners; distally widened) and by female internal genitalia (Fig. 10C–D; large membranous median sac; lateral elements medially curved, creating median posterior indentation also sometimes visible

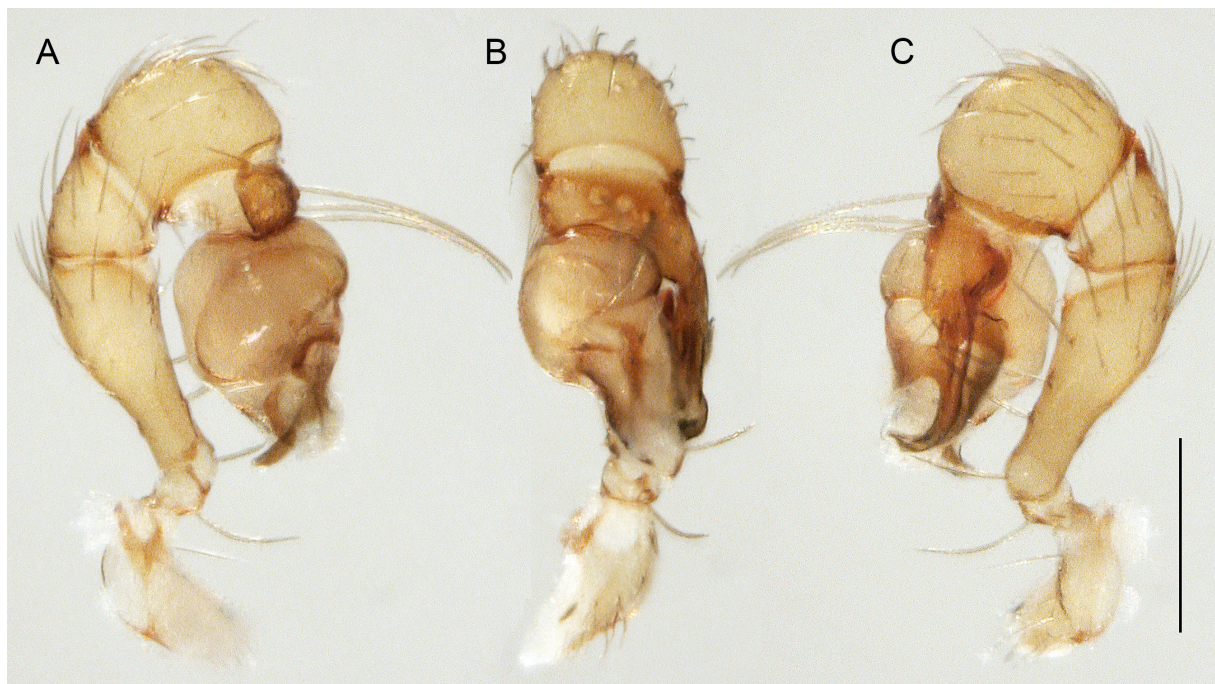


Fig. 8. *Guaranita munda* (Gertsch, 1982); male from E of Nono (ZFMK Ar 24122). Left pedipalp, prolateral (A), dorsal (B), and retrolateral (C) views. Scale bar = 0.2 mm.

in uncleared epigyna); from *G. auadae* sp. nov. and *G. goloboffi* also by narrow distal bulbal sclerite (Fig. 9G); from most congeners (except *G. dooby*) also by relatively long male palpal femur (Fig. 8C; length/width 2.50–2.55, most other species 1.85–2.25, *G. dooby* 2.50).

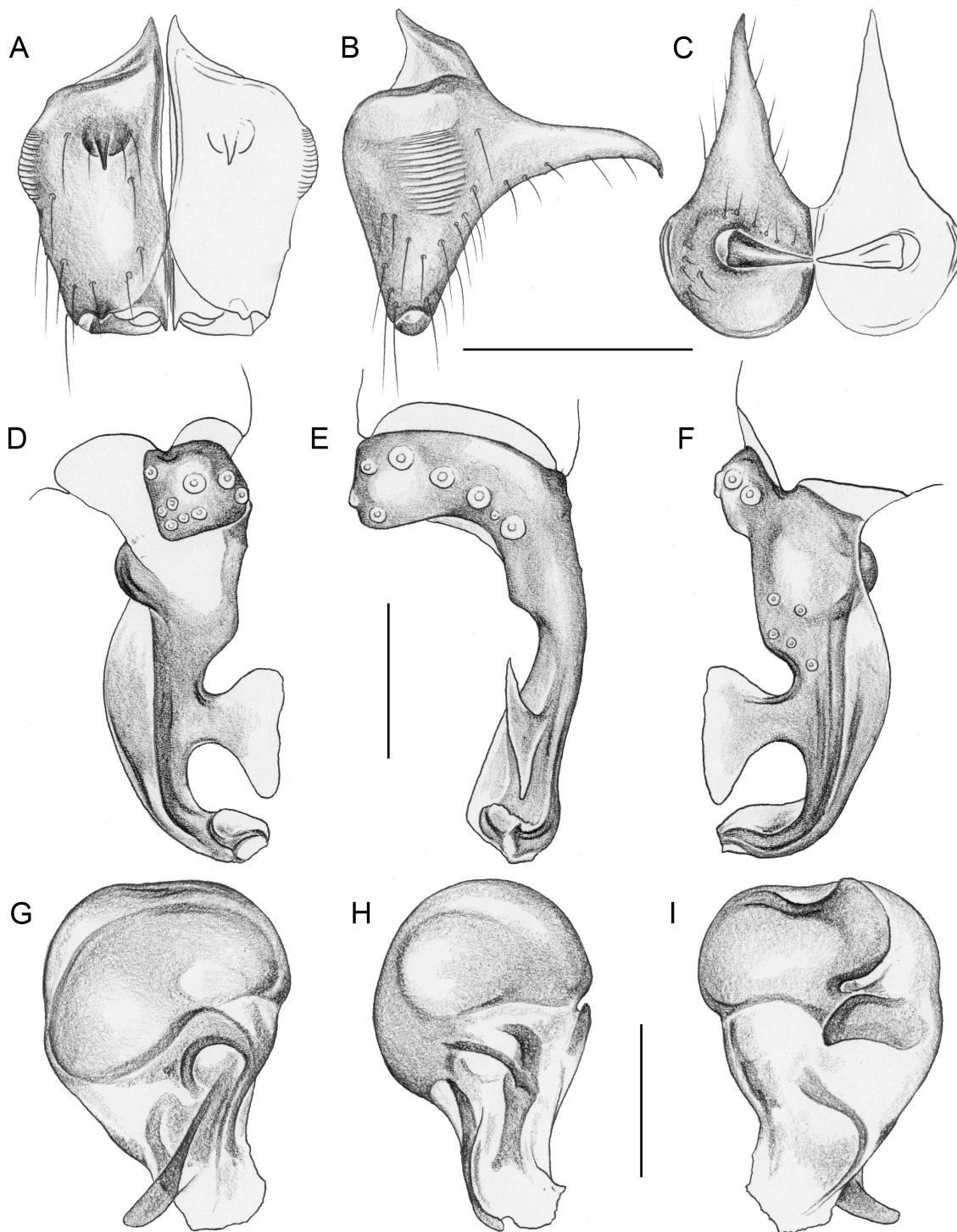


Fig. 9. *Guaranita munda* (Gertsch, 1982); male from E of Nono (ZFMK Ar 24122). A–C. Chelicerae, frontal, lateral, and ventral views. D–F. Left procurus, prolateral, dorsal, and retrolateral views. G–I. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

Material examined (new records)

ARGENTINA – **Córdoba** • 6 ♂♂, 5 ♀♀ (one male and one female used for SEM); ~2.5 km E of Nono; 31.8025° S, 64.9762° W; 915 m a.s.l.; 2 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24122 • 7 ♀♀, in pure ethanol (three prosomata used for molecular work; one female used for SEM); same collection data as for preceding; ZFMK Arg127 • 3 ♂♂, 2 ♀♀; same collection data as for preceding; LABRE-Ar 877 • 3 ♂♂; same collection data as for preceding; LABRE-Ar 878 • 3 ♀♀, in pure ethanol; same collection data as for preceding; LABRE-Ar 882, 883, 856 • 1 ♀, in pure ethanol; ~1.5 km E of Nono; 31.7980° S, 64.9877° W; 895 m a.s.l.; 2 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Arg126 • 2 ♂♂, 1 ♀, 2 juvs; Villa La Merced; 31.8397° S, 64.5249° W; 765 m a.s.l.; 17 Dec. 2019; Izquierdo and Palen Pietri leg.; litter and bark of *Eucalyptus* plantation; LABRE-Ar 873 • 1 ♂; Villa La Merced; 31.8419° S, 64.5240° W; 775 m a.s.l.; 27 Jan. 2020; Izquierdo, Abregú, and Palen Pietri leg.; LABRE-Ar 874 • 4 ♀♀, some juvs; same collection data as for preceding; LABRE-Ar 626. – **Entre Ríos** • 5 ♂♂, 3 ♀♀, 2 juvs (one male used for SEM); Dept. Colón, Parque Nacional El Palmar; 31.8653° S, 58.2375° W; 20 m a.s.l.; 6–8 Aug. 2011; M.J. Ramírez *et al.* leg.; MACN Ar 32745 • 2 ♂♂, 4 ♀♀, 2 juvs; same collection data as for preceding; MACN Ar 32741 • 1 ♂, 1 ♀; same collection data as for preceding; MACN Ar 32744 • 1 ♂; same collection data as for preceding, with label “muestra de tejido prep. CJG-3350”; MACN Ar 32743 • 1 ♀; Dept. Colón, Parque Nacional El Palmar, Arroyo El

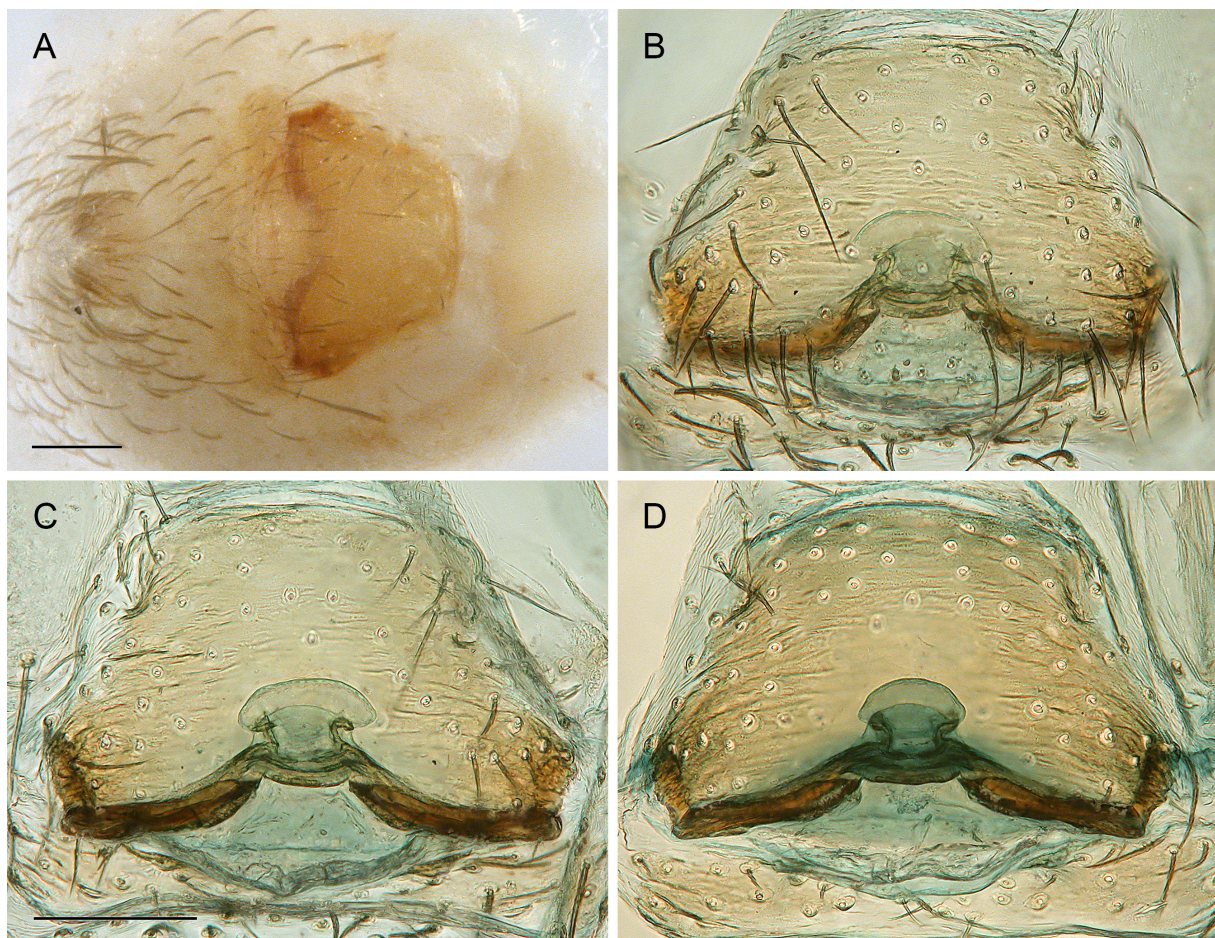


Fig. 10. *Guaranita munda* (Gertsch, 1982); females from E of Nono (ZFMK Ar 24122). **A.** Abdomen, ventral view. **B.** Cleared epigynum, ventral view. **C–D.** Cleared epigyna of two specimens, dorsal views. Scale bars: 0.1 mm (B–D at same scale).

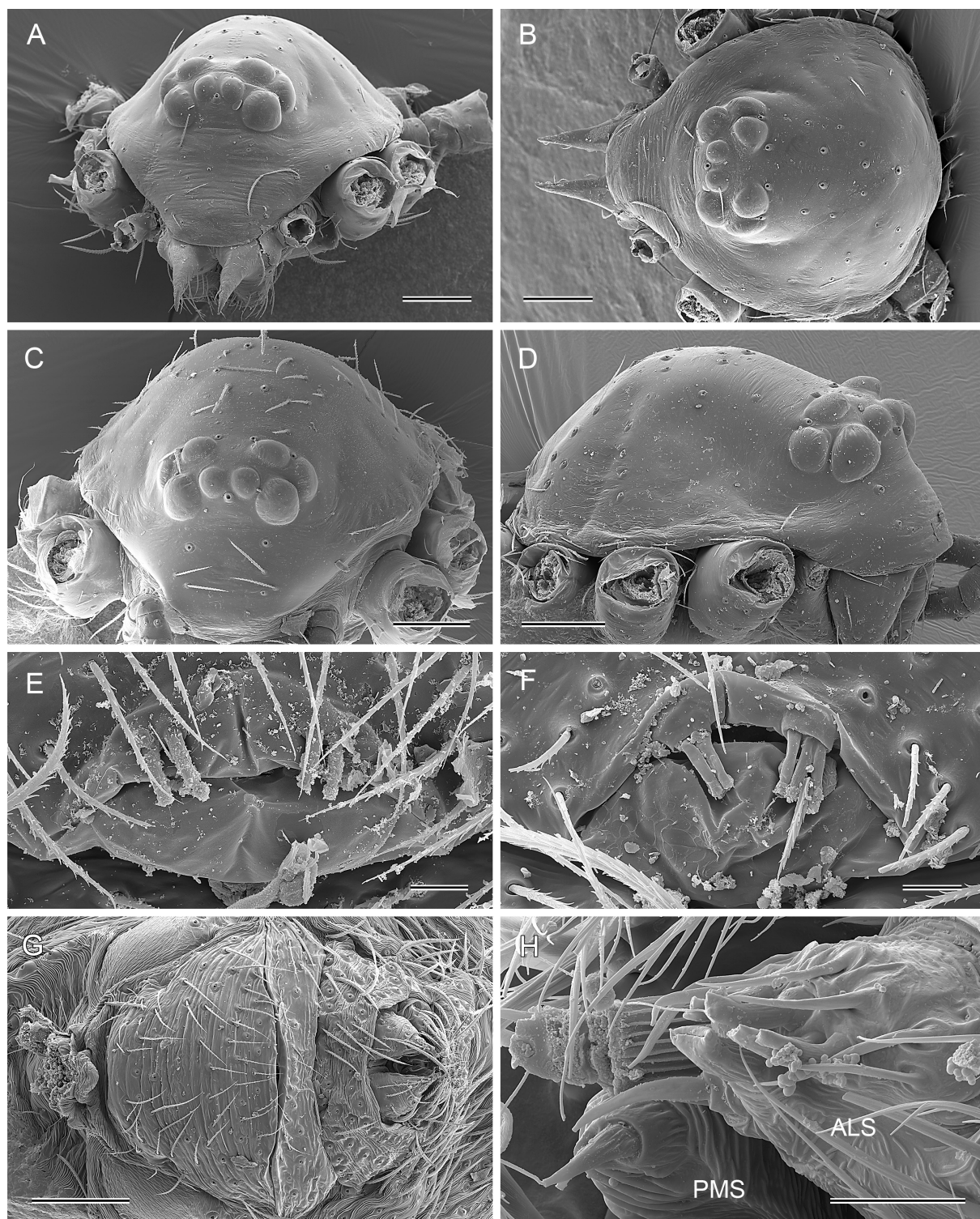


Fig. 11. *Guaranita munda* (Gertsch, 1982); from E of Nono (A–E, G; ZFMK Ar 24122) and Parque Nacional El Palmar (F; MACN Ar 32745). **A–B.** Male prosoma, oblique frontal and dorsal views. **C–D.** Female prosomata, oblique frontal and lateral views. **E–F.** Male gonopores and epiandrous spigots. **G.** Female abdomen, ventral view. **H.** Female ALS and PMS. Scale bars: A–D, G = 100 µm; E–F, H = 10 µm.

Palmar; 31.8931° S, 58.2385° W; 10 m a.s.l.; 7 Aug. 2011; M.J. Ramírez *et al.* leg.; MACN Ar 32742 • 1 ♂; Dept. Colón, Parque Nacional El Palmar, Sector Sur; 31.8877° S, 58.3119° W; 30 m a.s.l.; 7 Aug. 2011; M.J. Ramírez *et al.* leg.; MACN Ar 32740 • 1 ♀; Parque Nacional El Palmar (no precise locality information); 22–23 Nov. 2003; C. Grismado, A. Ojanguren and F. Labarque leg.; MACN Ar 25453 • 1 ♀; Villa Urquiza; ~31.65° S, 60.38° W (no precise locality information); 17 Feb. 1988; P. Goloboff and C. Szumik leg.; MACN Ar 20030.

Redescription (amendments; see Huber 2000)

Measurements of male from E of Nono: total body length 1.06, carapace width 0.42; distance PME–PME 40 µm; diameter PME 50 µm; distance PME–ALE 15 µm; distance AME–AME 15 µm; diameter

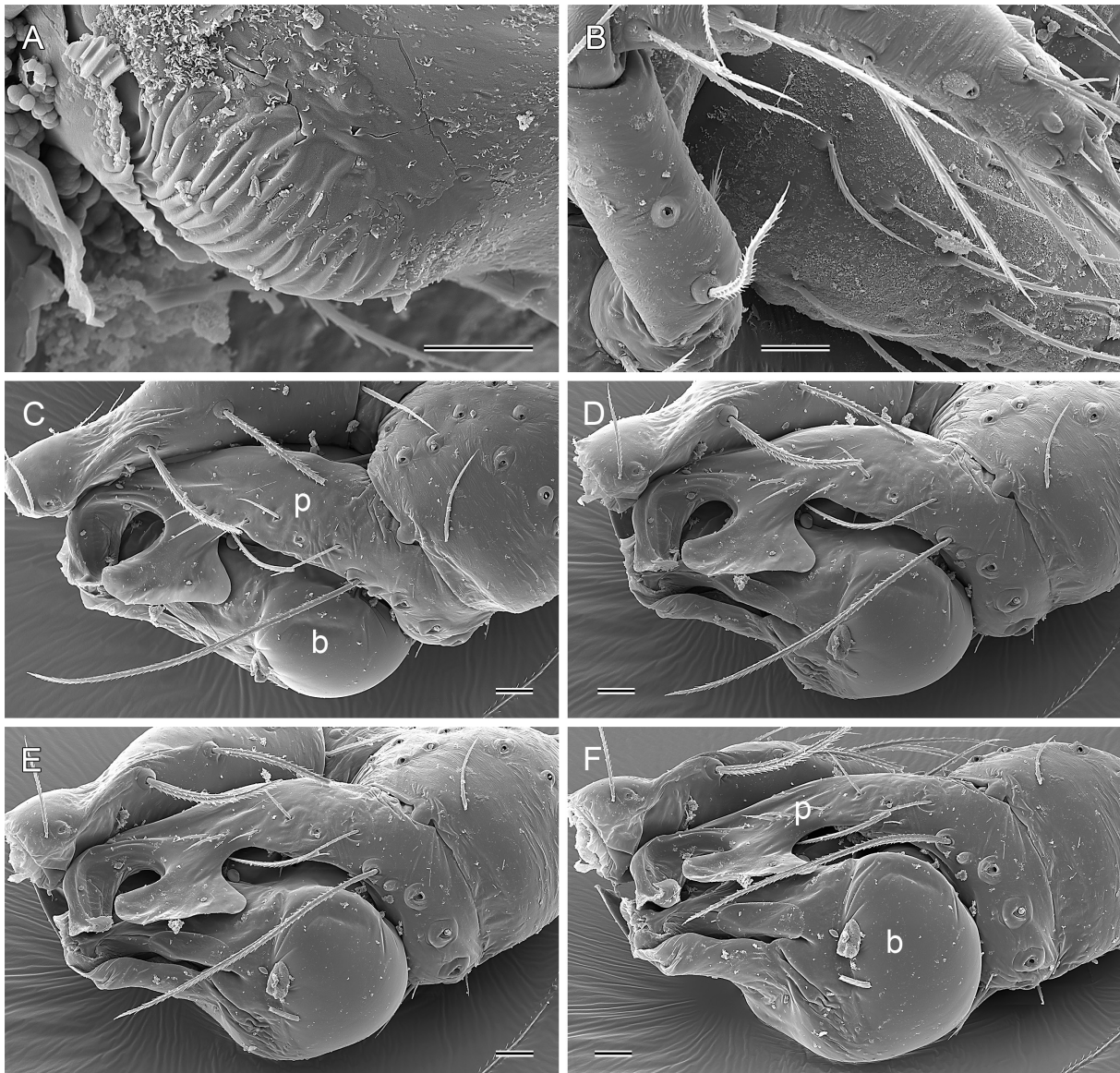


Fig. 12. *Guaranita munda* (Gertsch, 1982); from E of Nono (A–B; ZFMK Ar 24122) and Parque Nacional El Palmar (C–F; MACN Ar 32745). **A.** Stridulatory file on male chelicera. **B.** Right female palp and chelicera (note absence of stridulatory file). **C–F.** Right male pedipalp in retrolateral, retrolateral-dorsal, and dorsal views. Abbreviations: b = genital bulb; p = procurus. Scale bars: A = 10 µm; B–F = 20 µm.

AME 30 μm . Leg 1: 1.98 (0.52+0.14+0.50+0.50+0.32), tibia 2: 0.42, tibia 3: 0.38, tibia 4: 0.60; tibia 1 L/d: 8; diameters of leg femora 0.09; of leg tibiae: 0.06. Tibia 1 in 25 males (incl. holotype): 0.49–0.58 (mean 0.53). Sternum slightly wider than long (0.33/0.29). Chelicerae as in Fig. 9A–C; stridulatory files (Fig. 12A) with ~15–17 ridges each; distances between ridges proximally ~1.0 μm , distally ~2.1 μm . Pedipalp as in Fig. 8A–C; tibia with two trichobothria; palpal tarsal organ capsulate (Fig. 13A) with small opening (diameter of opening 1.15 μm); procurrus as in Fig. 9D–F, with large transparent ventral membrane, distinctive dorsal flap, and tip bent towards dorsal; genital bulb as in Fig. 9G–I, with simple proximal sclerite, distal sclerite short and simple, not widened in mid-section. Legs without spines and curved hairs; vertical hairs not seen in dissecting microscope but present on tibia 1 (Fig. 13D), apparently only one row; prolateral trichobothrium absent on tibia 1, present on other leg tibiae; metatarsi 3 and 4

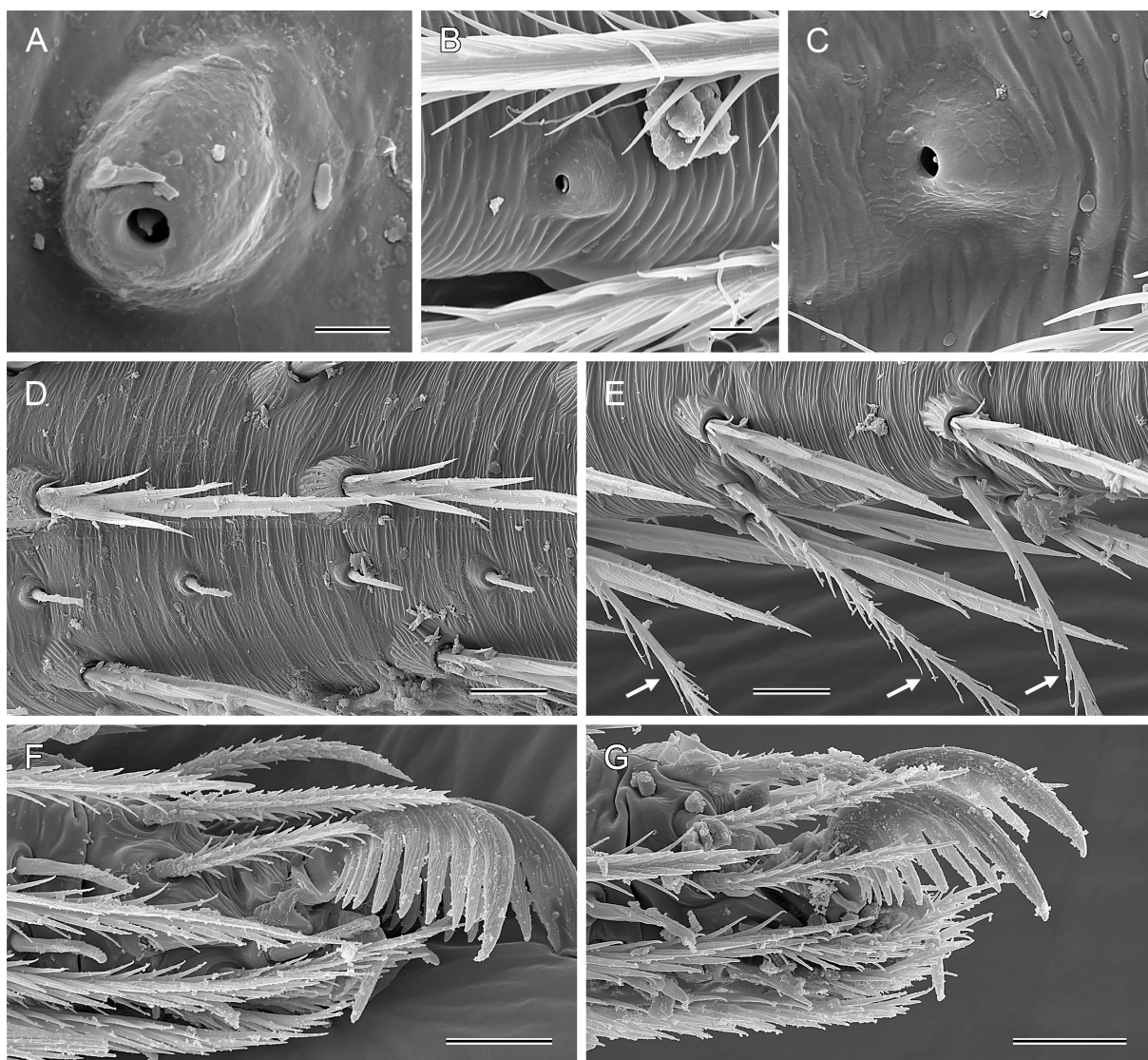


Fig. 13. *Guaranita munda* (Gertsch, 1982); from Parque Nacional El Palmar (A, C, D; ZFMK Ar 24122) and E Nono (B, E–G; MACN Ar 32745). **A.** Male palpal tarsal organ. **B.** Tarsal organ on female right tarsus 2. **C.** Tarsal organ on male right tarsus 1. **D.** Short vertical hairs (and regular hairs) on male tibia 1. **E.** Slender hairs (arrows) on male metatarsus 4. **F.** Tip of female right tarsus 1. **G.** Tip of male left tarsus 3. Scale bars: A–B = 2 μm ; C = 1 μm ; D–G = 10 μm .

with few (3–5) slender hairs proximally on retrolateral-ventral side (Fig. 13E). Gonopore with 4–5 epiandrous spigots (Fig. 11E–F); spinnerets as in female (see below).

Tibia 1 in 22 females: 0.48–0.58 (mean 0.54). Female chelicerae without stridulatory ridges (Fig. 12B). Female internal genitalia with strong median structure and membranous sac (receptacle?) (Fig. 10C–D); apparently with small pore plates (Fig. 32B). Each ALS (Fig. 11H) with one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (of which one is much wider than the others); each PMS with two conical spigots; PLS without spigots. Leg tarsal organs with very small openings (diameters of openings 0.8–0.9 μm ; Fig. 13B). Metatarsi 3 and 4 with long slender hairs as in male; tarsus 4 with single prolateral comb-hair as in male.

Remarks (notes on type locality)

The type locality of this species has been confused twice. Gertsch (1982) interpreted the label information as referring to Cerro Colorado in Nuevo León, Mexico. Later, Huber (2000), read the handwritten label as “Cerro Colorado, Cta., 14.X-61, Col: O. de Ferrariis”, and suggested that this referred to Cerro Colorado in the province of Catamarca (“Cta.”), Argentina, i.e. $\sim 28.46^\circ$ S, 65.85° W. Another interpretation for a label accompanying a specimen of the linyphiid *Scolecurea propinqua* Millidge, 1991 collected by O. de Ferrariis on the same day, was offered by Miller (2007): Cerro Colorado in the province of Córdoba, i.e. $\sim 30.10^\circ$ S, 63.93° W. A new look at both labels confirms Miller’s (2007) interpretation: the label in the type vial of *Guaranita munda* quite clearly reads “Cba.” rather than “Cta.”, and the machine-written label accompanying the *Scolecurea propinqua* specimen explicitly says “Prov. Cordoba”.

Natural history

Near Nono, the spiders were collected by turning the uppermost rocks of a stone wall in a low forest (Fig. 34B). The spiders started to run rapidly but did not drop from the rocks. A label accompanying specimens from Parque Nacional El Palmar suggests a very similar habitat: “pedras palmeras con pastizal y bosque bajo”. Two egg-sacs contained 6 and 7 eggs, respectively, and were carried under the prosoma; egg diameter: 0.44.

Distribution

Widely distributed in north-eastern Argentina, reaching Rio Grande do Sul (Brazil) (Fig. 33A). Presumably also present in Uruguay and southern Paraguay. The single record from Jujuy (Torres *et al.* 2016) appears dubious (misidentified *G. yaculica*?).

Guaranita yaculica Huber, 2000 Figs 2E–F, 14–20, 32C

Guaranita yaculica Huber, 2000: 97, fig. 378 (σ).

Guaranita yaculica – Huber 2014: 140. — Torres *et al.* 2015: 2, fig. 2a–b (σ); 2016: 10, figs 6, 13–15 (φ).

Guaranita yaculica? – Eberle *et al.* 2018 (molecular data). — Huber *et al.* 2018: 55.

Diagnosis (amendments; see Huber 2000; Torres *et al.* 2016)

Distinguished from known congeners by size and shape of dorsal flap on procurus (Fig. 15F; rounded, larger than in the similar *G. goloboffi*) and by female internal genitalia (Fig. 16C–D; membranous median sac, similar to *G. munda* but smaller; lateral elements straight, not curved as in *G. munda*); from *G. auadae* sp. nov. and *G. goloboffi* also by narrower distal bulbal sclerite (Fig. 15G).

Material examined (new records)

ARGENTINA – **Jujuy** • 2 ♂♂, 2 ♀♀, 1 juv.; Calilegua National Park, Guaraní trail, near camping area; 23.7612° S, 64.8517° W; 620 m a.s.l.; 15 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24123 • 2 ♀♀, in pure ethanol; same collection data as for preceding; LABRE-Ar 515 • 6 ♂♂, 3 ♀♀ (one male used for SEM); Calilegua National Park, ~1 km NW of headquarters; 23.7540° S, 64.8537° W; 710 m a.s.l.; 15 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24124 • 14 ♀♀, in pure ethanol (four prosomata used for molecular work; two females used for SEM); same collection data as for preceding; ZFMK Arg175 • 4 ♂♂, 7 ♀♀, 1 juv.; same collection data as for preceding; LABRE-Ar 514 • 7 ♀♀, 1 juv.; same collection data as for preceding; LABRE-Ar 520 • 1 ♂, 2 ♀♀; Calilegua National Park, Seccional Aguas Negras; 23.7619° S, 64.8514° W; 605 m a.s.l.; 6–11 Dec. 2008; C. Grismado *et al.* leg.; MACN Ar 22134 • 1 ♀, in pure ethanol; same collection data as for preceding; MACN Ar 34688 • 1 ♂, 1 ♀; Calilegua National Park, entrance area; ~23.76° S, 64.85° W; ~620 m a.s.l.; 23–24 Sep. 1995; M. Ramírez, P. Goloboff and C. Szumik leg.; MACN Ar 19977 • 1 ♂, 2 juvs; Calilegua National Park, no precise locality information; 22 Dec. 1994; C. Grismado leg.; MACN Ar 19976 • 3 ♀♀; Calilegua National Park, Aguas Negras at ~1100 m, no precise locality information; 5–7 Aug. 1997; M. Ramírez and L. Compagnucci leg.; MACN Ar 19978, 19981.

PARAGUAY – **Boquerón** • 1 ♂; Enciso, “T88.09.0 r1”; 21.2061° S, 61.6575° W; 255 m a.s.l.; 3 Nov. 2001; M. Leponce leg.; IRSNB • 1 ♂ prosoma; Enciso, “T90.09.0 r1”; 21.1998° S, 61.6608° W; 255 m a.s.l.; 4 Nov. 2001; M. Leponce leg.; IRSNB • 2 ♂♂; same collection data as for preceding, “T90.14.0 r1”; IRSNB • 1 ♀; same collection data as for preceding, “T90.12.0 r1”; IRSNB.

Redescription (amendments; see Huber 2000, Torres *et al.* 2016)

Measurements of male from Calilegua National Park: total body length 0.98, carapace width 0.45; distance PME–PME 45 µm; diameter PME 45 µm; distance PME–ALE 20 µm; distance AME–AME 20 µm; diameter AME 25 µm. Leg 1: 2.20 (0.62+0.14+0.56+0.54+0.34), tibia 2: 0.46, tibia 3: 0.40,

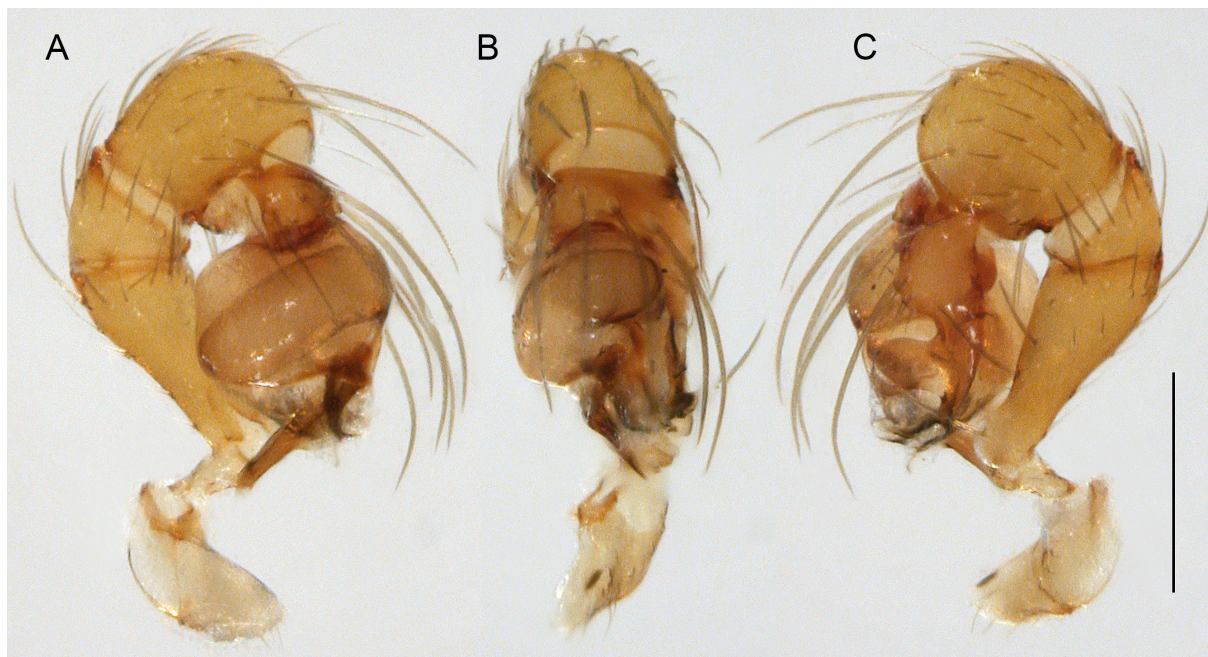


Fig. 14. *Guaranita yaculica* Huber, 2000; male from Calilegua National Park (ZFMK Ar 24124). Left pedipalp, prolateral (A), dorsal (B), and retrolateral (C) views. Scale bar = 0.2 mm.

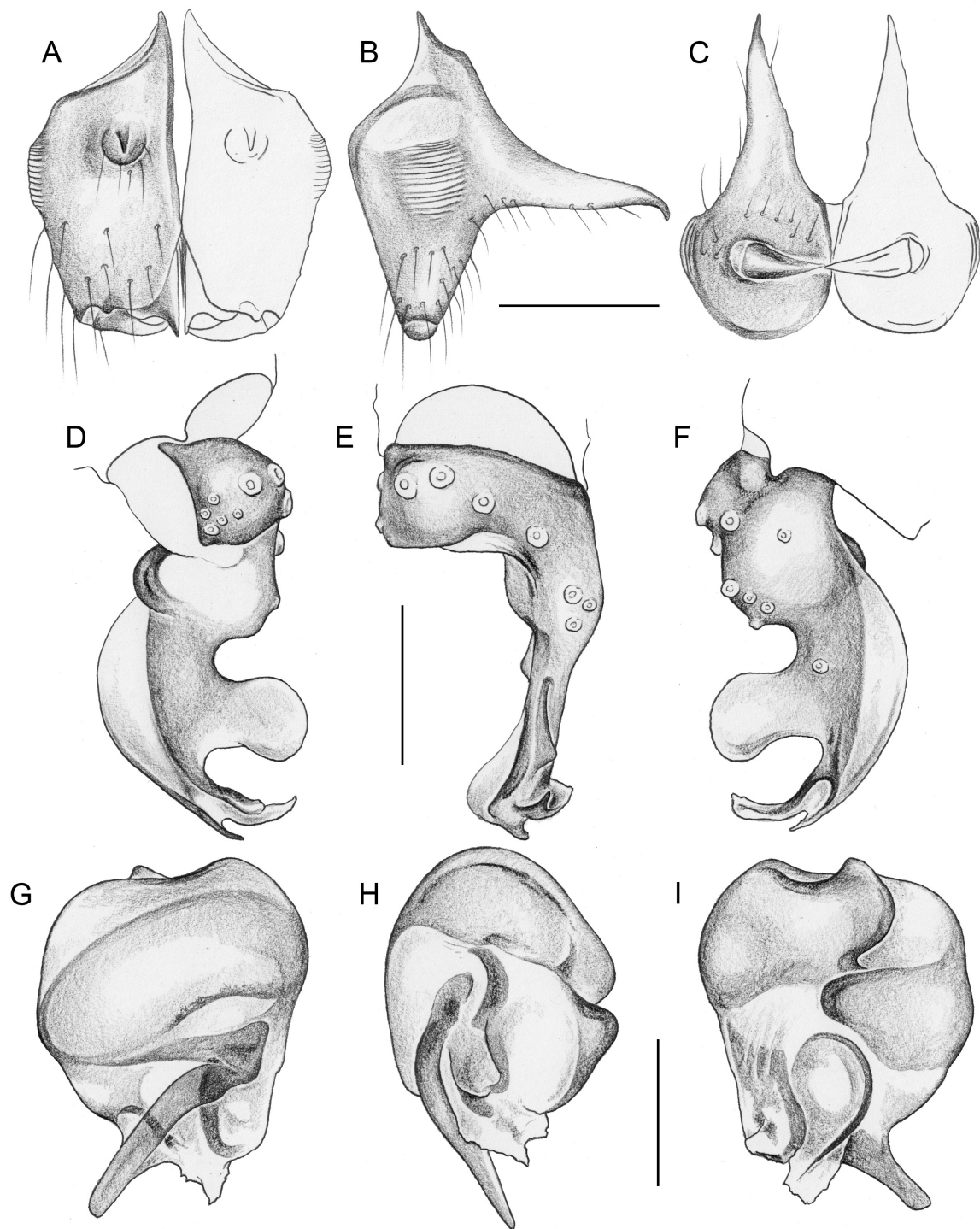


Fig. 15. *Guaranita yaculica* Huber, 2000; male from Calilegua National Park (ZFMK Ar 24124). A–C. Chelicerae, frontal, lateral, and ventral views. D–F. Left procursus, prolateral, dorsal, and retrolateral views. G–I. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

tibia 4: 0.68; tibia 1 L/d: 9; diameters of leg femora 0.10; of leg tibiae: 0.06. Tibia 1 in 16 males (incl. holotype): 0.50–0.62 (mean 0.57). Sternum slightly wider than long (0.33/0.31). Chelicerae as in Fig. 15A–C, 18A; stridulatory files with ~17–23 ridges; distances between ridges proximally ~0.6 μm , distally ~2.3 μm (Fig. 18B). Pedipalp as in Fig. 14A–C; tibia with two trichobothria; palpal tarsal organ capsulate, with small opening; procurus as in Fig. 15D–F and 18D–F, with large transparent ventral membrane, distinctive dorsal flap, and tip bent towards dorsal; genital bulb as in Figs 15G–I and 18D–F, with simple proximal sclerite, distal sclerite not widened in mid-section. Legs without spines and curved hairs; vertical hairs not seen in dissecting microscope but present on tibia 1 (Fig. 19A–C), apparently in two rows (one prolateral and one retrolateral); prolateral trichobothrium absent on tibia 1, present on other leg tibiae; metatarsi 3 and 4 with few (1–3) slender hairs proximally on retrolateral-ventral side (Fig. 19H). Gonopore with four epiandrous spigots (Fig. 17F); spinnerets as in female (Fig. 17D; see below).

Tibia 1 in 33 females: 0.48–0.64 (mean 0.55). Female chelicerae without stridulatory ridges (Fig. 18C). Female internal genitalia with median membranous sac (receptacle?) (Fig. 16C–D); apparently with small pore plates (Fig. 32C). Each ALS (Fig. 17B–C) with one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (of which one is much wider than the others); each PMS with two conical spigots; PLS without spigots. Palpal tarsal organ capsulate with small opening (diameter

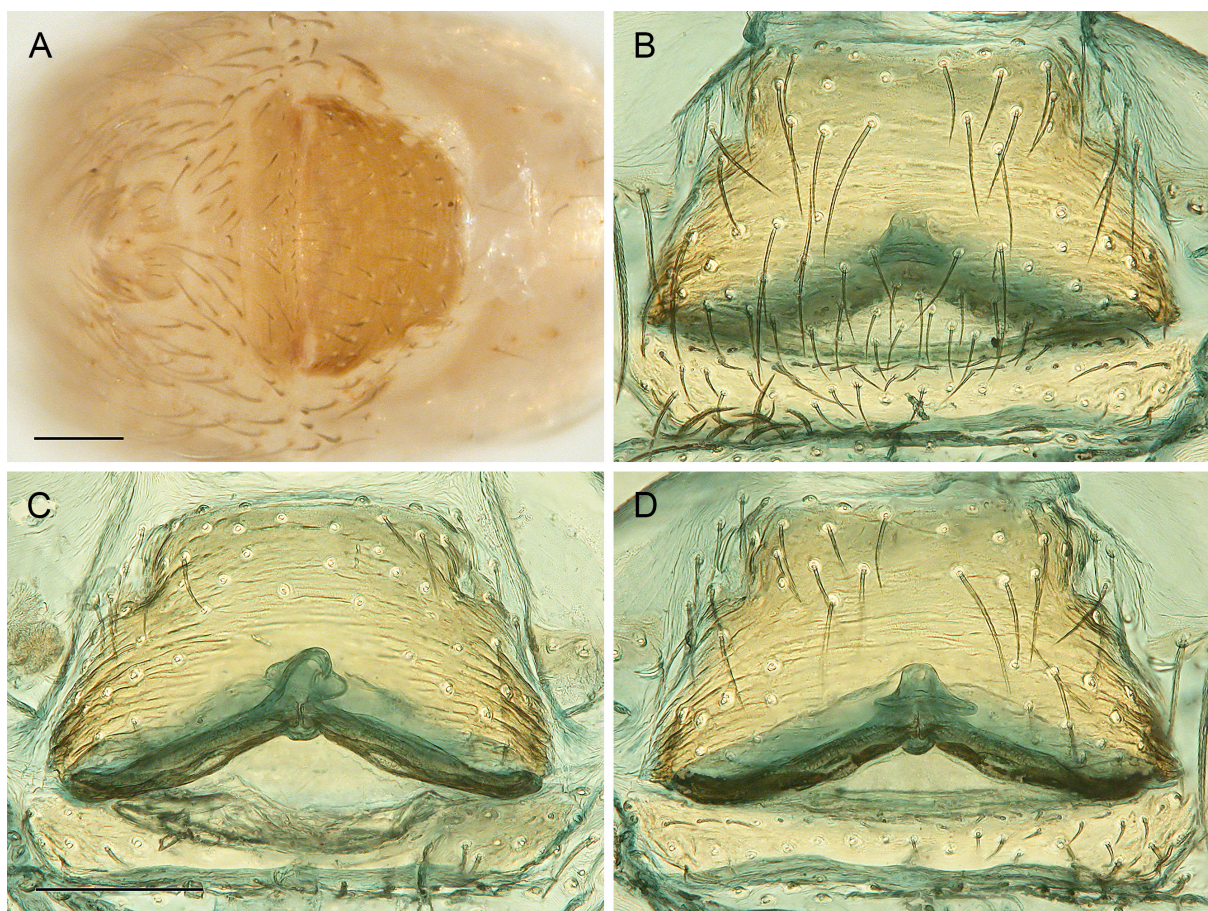


Fig. 16. *Guaranita yaculica* Huber, 2000; females from Calilegua National Park (ZFMK Ar 24124). **A.** Abdomen, ventral view. **B.** Cleared epigynum, ventral view. **C–D.** Cleared epigyna of two specimens, dorsal views. Scale bars = 0.1 mm (B–D at same scale).

of opening 1.1 μm); leg tarsal organs with very small openings (diameters 0.7–0.9 μm ; Fig. 20A–C). Metatarsi 3 and 4 with long slender hairs as in male (Fig. 19G).

Natural history

At Calilegua National Park, the spiders were collected in forest leaf litter (Fig. 34C). Two egg-sacs contained five and six eggs, respectively.

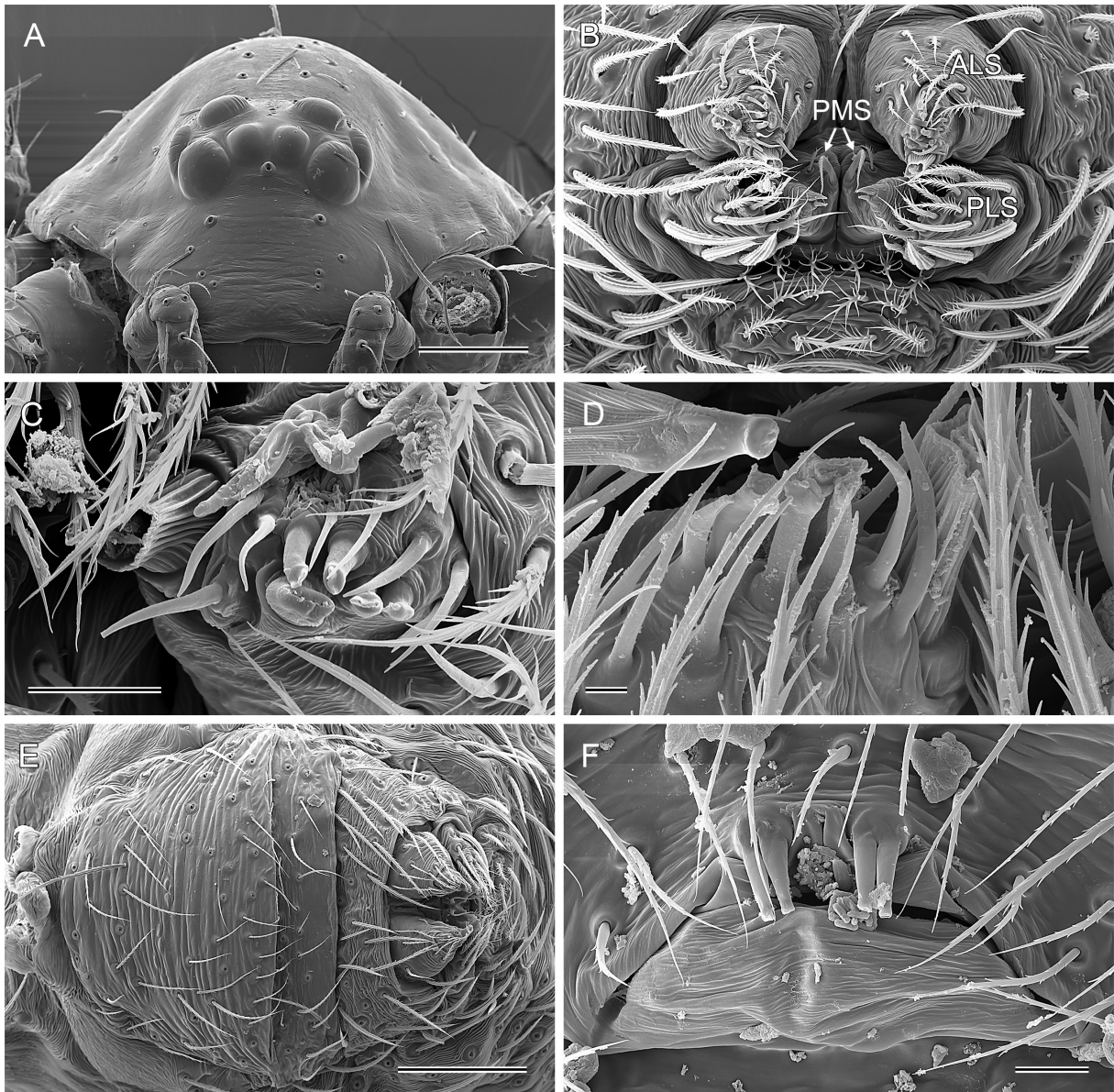


Fig. 17. *Guaranita yaculica* Huber, 2000; from Calilegua National Park (ZFMK Ar 24124, Arg175). **A.** Female prosoma, frontal view. **B.** Female spinnerets and anal cone. **C.** Female ALS. **D.** Male ALS. **E.** Female abdomen, ventral view. **F.** Male gonopore and epiandrous spigots. Scale bars: A, E = 100 μm ; B–C, F = 10 μm ; D = 2 μm .

Distribution

Most known records are from northern Argentina and north-eastern Paraguay (Fig. 33B). The single record from Corrientes in Torres *et al.* (2015) is dubious (misidentified *G. munda?*).

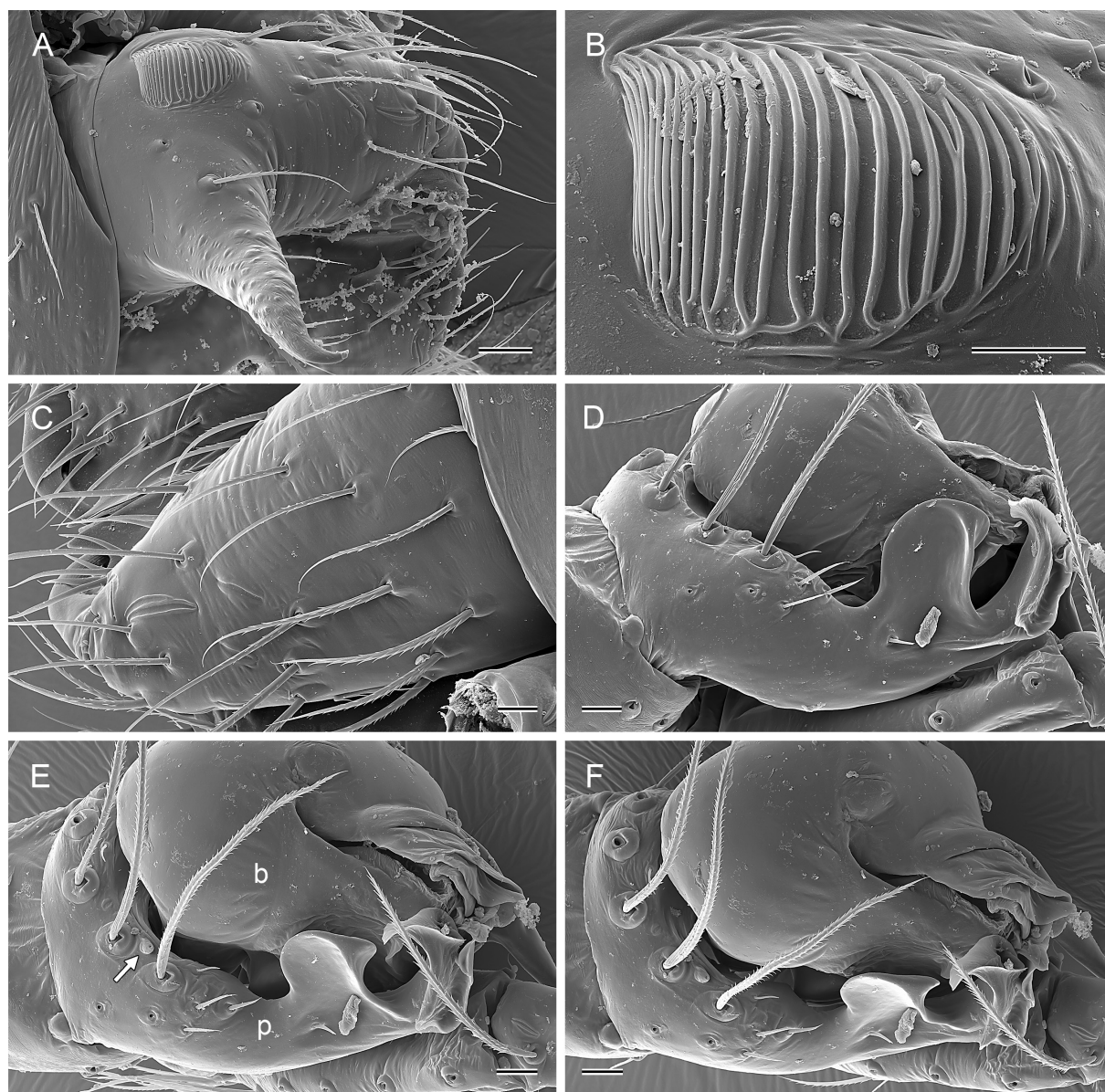


Fig. 18. *Guaranita yaculica* Huber, 2000; from Calilegua National Park (ZFMK Ar 24124). **A.** Left male chelicera. **B.** Stridulatory file on male chelicera. **C.** Left female chelicera, showing absence of stridulatory file. **D–F.** Right male palp, retrolateral, retrolateral-dorsal, and dorsal views; arrow: tarsal organ. Abbreviations: b, genital bulb; p, procursus. Scale bars: A, D–F = 20 μ m; B–C = 10 μ m.

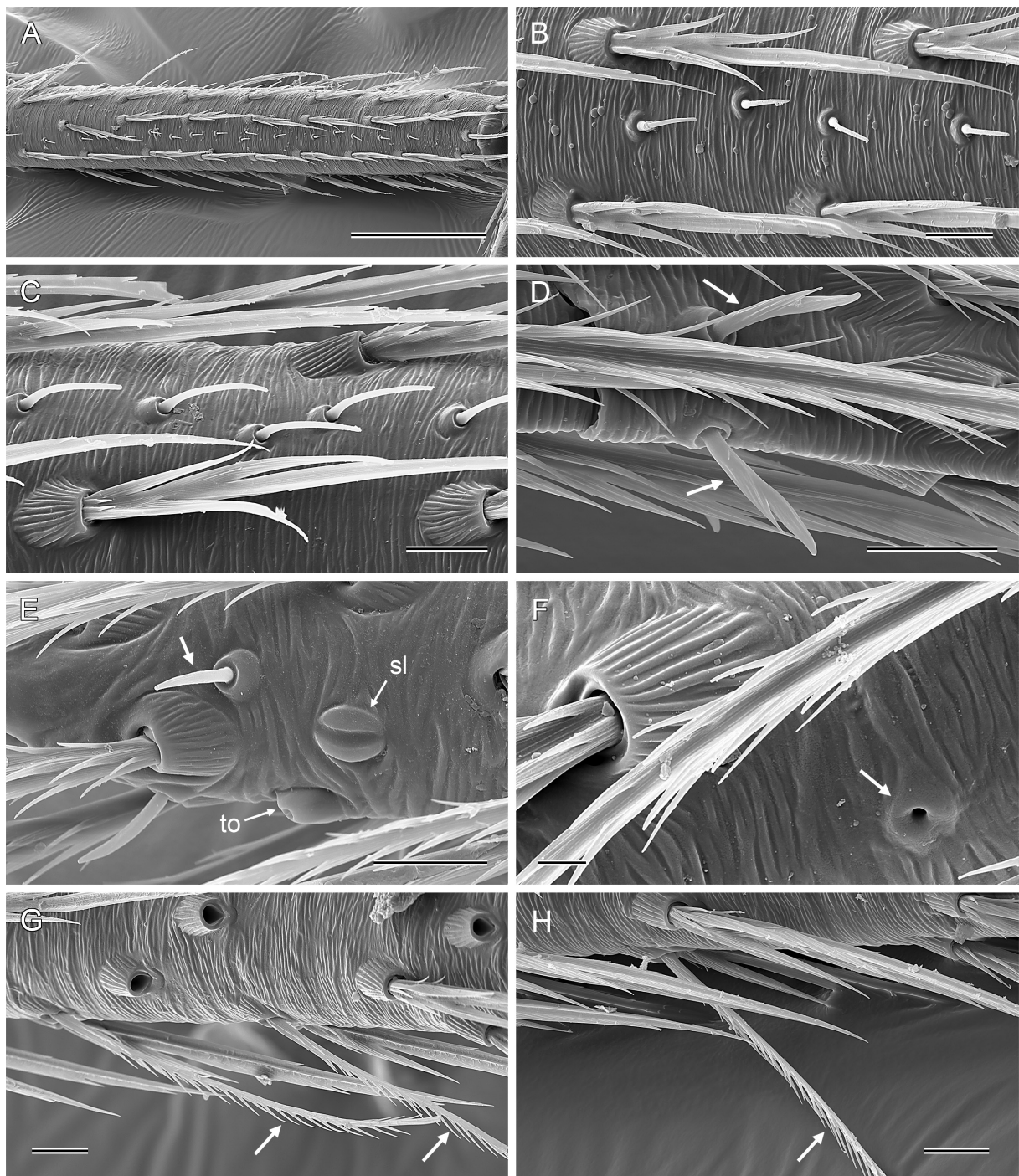


Fig. 19. *Guaranita yaculica* Huber, 2000; from Calilegua National Park (ZFMK Ar 24124, Arg175). **A.** Male right tibia 1, retrolateral view. **B.** Detail of previous figure, showing short vertical hairs (among regular hairs). **C.** Short vertical hairs on male left tibia 1, prolateral-ventral view. **D.** Chemoreceptive hairs (arrows) on female left tarsus 3. **E.** Sensory organs on left female palpal tarsus (arrow: short vertical hair). **F.** Pore with cuticular rim (arrow) on right female metatarsus 1. **G.** Slender hairs (arrows) on female metatarsus 4. **H.** Slender hair (arrow) on male left metatarsus 4. Abbreviations: sl = slit sense organ; to = tarsal organ. Scale bars: A = 100 μm ; B–E, G–H = 10 μm ; F = 2 μm .

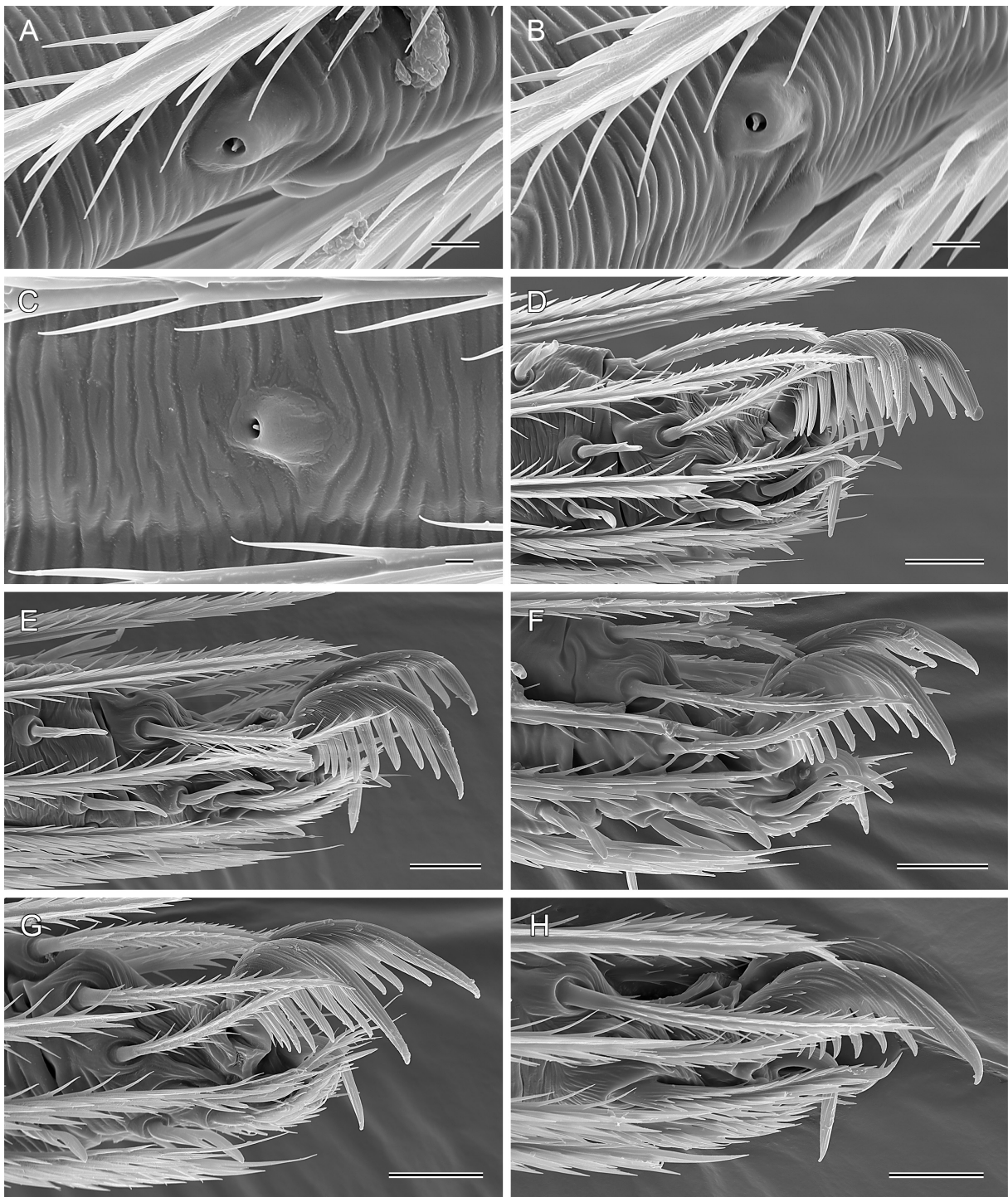


Fig. 20. *Guaranita yaculica* Huber, 2000; from Calilegua National Park (ZFMK Ar 24124, Arg175). **A.** Tarsal organ on female tarsus 2. **B.** Tarsal organ on female tarsus 3. **C.** Tarsal organ on female tarsus 4. **D.** Tip of female left tarsus 2, prolateral view. **E.** Tip of female left tarsus 1, prolateral view. **F.** Tip of male right tarsus 2, retrolateral view. **G.** Tip of female left tarsus 3, prolateral view. **H.** Tip of female right tarsus 4, retrolateral view. Scale bars: A–B = 2 μ m; C = 1 μ m; D–H = 10 μ m.

Guaranita auadae Huber sp. nov.

[urn:lsid:zoobank.org:act:8409459A-BDA1-4650-9765-44EA30ABDECF](https://urn.lsid:zoobank.org:act:8409459A-BDA1-4650-9765-44EA30ABDECF)

Figs 2G–H, 21–23, 32D

Diagnosis

Distinguished from known congeners by shape of dorsal flap on procurus (Fig. 22F; distally narrow and curved); also by wider distal bulbal sclerite (Fig. 22G; similar only in *G. goloboffi*), by relatively short male palpal femur (Fig. 21C; length/width 1.9; other species 2.1–2.6) and by female internal genitalia (Fig. 23C–D; median structure rectangular, similar to *G. goloboffi* but smaller).

Etymology

The species name honors Ángela Auad (1945–1977), an Argentine social activist who worked with the Mothers of the Plaza de Mayo until she was kidnapped, tortured and murdered.

Type material

Holotype

ARGENTINA – Jujuy • ♂; between San Salvador and Purmamarca, ‘site 2’; 23.8849° S, 65.4613° W; 2150 m a.s.l.; 16–17 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; LABRE-Ar 1016.

Paratypes

ARGENTINA • 1 ♂, 2 ♀♀; same collection data as for holotype; ZFMK Ar 24125 • 2 ♂♂, 7 ♀♀ (together with 11 juvs); same collection data as for holotype; LABRE-Ar 880.

Other material examined

ARGENTINA – Jujuy • 6 ♀♀, 1 juv., in pure ethanol (two female prosomata used for molecular work, two cleared female genitalia transferred to ZFMK Ar 24125); same collection data as for holotype; ZFMK Arg179 • 3 ♀♀, in pure ethanol; same collection data as for holotype; LABRE-Ar 867 • 1 ♀, with 6 eggs, in pure ethanol; same collection data as for holotype; LABRE-Ar 866.

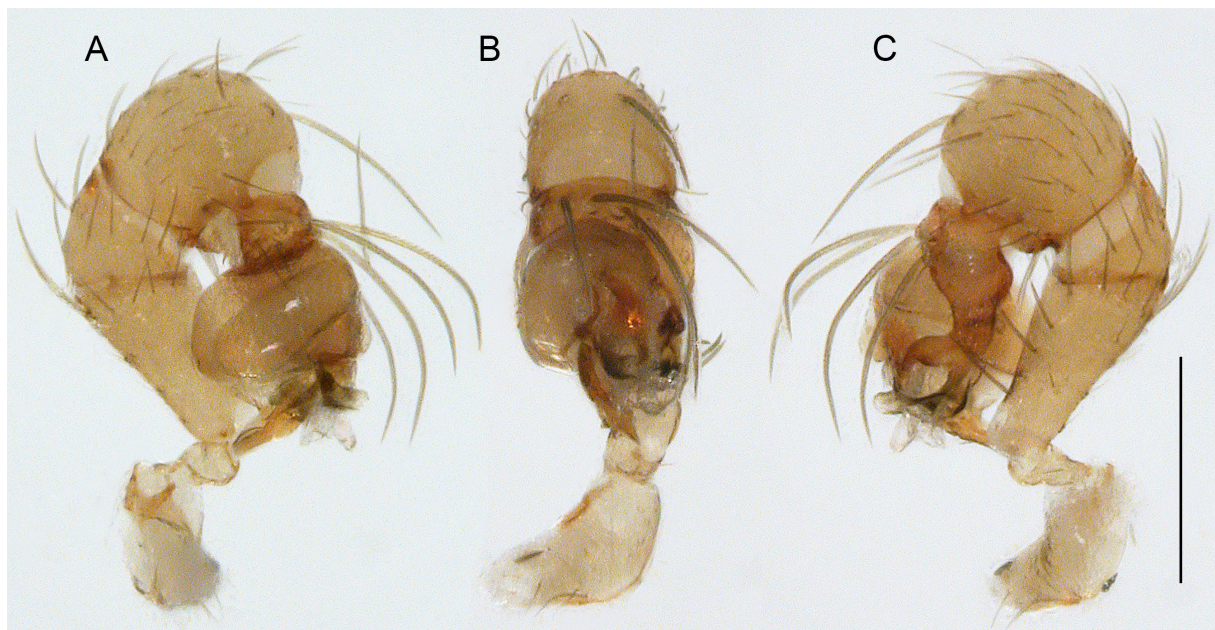


Fig. 21. *Guaranita auadae* Huber sp. nov.; male from between San Salvador and Purmamarca (ZFMK Ar 24125). Left pedipalp, prolateral (A), dorsal (B), and retrolateral (C) views. Scale bar = 0.2 mm.

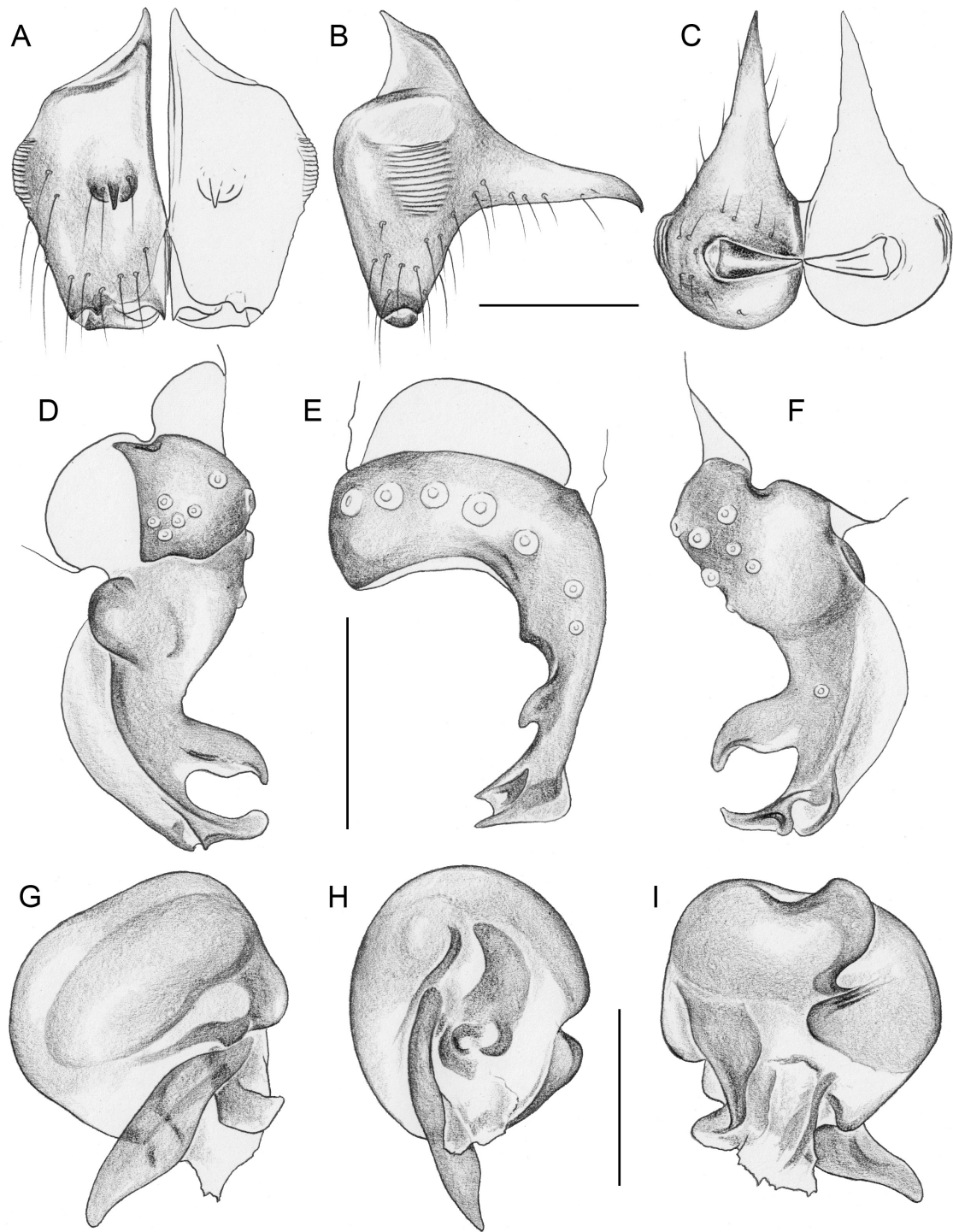


Fig. 22. *Guaranita auadae* Huber sp. nov.; male from between San Salvador and Purmamarca (ZFMK Ar 24125). **A–C.** Chelicerae, frontal, lateral, and ventral views. **D–F.** Left procurus, prolateral, dorsal, and retrolateral views. **G–I.** Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

Description

Male (holotype)

MEASUREMENTS. Total body length 0.97, carapace width 0.42. Distance PME–PME 40 μm ; diameter PME 40 μm ; distance PME–ALE 20 μm ; distance AME–AME 25 μm ; diameter AME 25 μm . Leg 1: 2.02 (0.58+0.14+0.50+0.48+0.32), tibia 2: 0.40, tibia 3: 0.36, tibia 4: 0.60; tibia 1 L/d: 7; diameters of leg femora 0.095, of leg tibiae: 0.07.

COLOUR (in ethanol). Prosoma and legs ochre-yellow, legs without darker rings; abdomen ochre-grey with indistinct internal marks.

BODY (Fig. 2G). Ocular area barely raised. Carapace without thoracic groove. Clypeus unmodified. Sternum slightly wider than long (0.34/0.31), with pair of rounded anterior processes near coxae 1. Abdomen globular.

CHELICERAE (Fig. 22A–C). With pair of long frontal apophyses; with stridulatory files poorly visible in dissecting microscope.

PALPS (Fig. 21A–C). Coxa unmodified; trochanter without process; femur proximally with prolateral stridulatory pick, distally widened but simple; femur-patella joints slightly shifted towards prolateral side; tibia globular, with two trichobothria; tibia-tarsus joints not shifted to one side; procurus as in Fig. 22D–F,

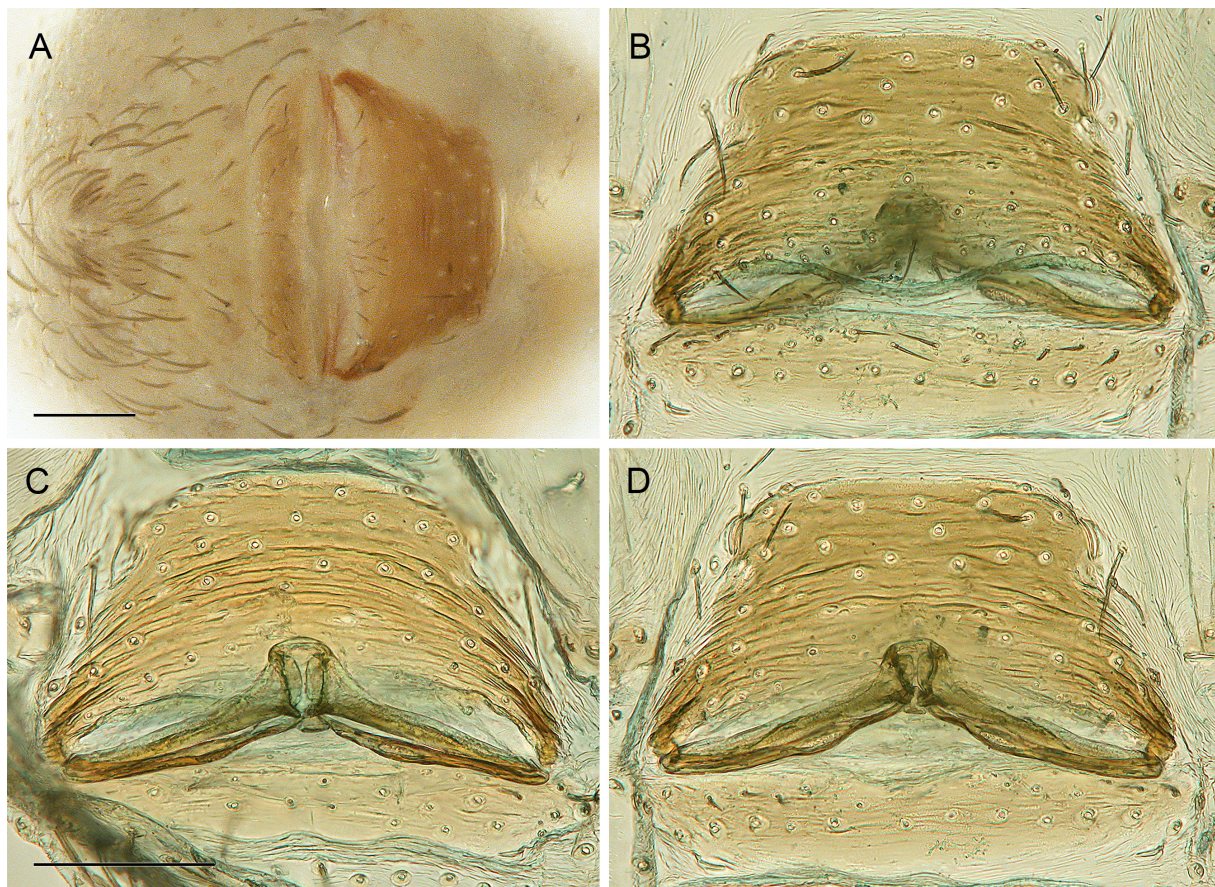


Fig. 23. *Guaranita auadae* Huber sp. nov.; females from between San Salvador and Purmamarca (ZFMK Ar 24125). **A.** Abdomen, ventral view. **B.** Cleared epigynum, ventral view. **C–D.** Cleared epigyna of two specimens, dorsal views. Scale bars = 0.1 mm (B–D at same scale).

with dorsal flap curved towards distal, large transparent ventral membrane, tip of procurus bent towards dorsal; genital bulb as in Fig. 22G–I, with simple proximal sclerite, distal sclerite wide, narrowing distally.

LEGS. Without spines and curved hairs; vertical hairs not seen; trichobothria of tibia 1 not seen; tarsus 1 with 5–6 pseudosegments, poorly visible in dissecting microscope.

VARIATION (male). Tibia 1 in three other males: 0.51, 0.52, 0.55.

Female

In general similar to male (Fig. 2H) but sternum without pair of anterior humps, and chelicerae apparently without stridulatory files. Tibia 1 in 16 females: 0.50–0.60 (mean 0.56). Epigynum (Fig. 23A) with simple trapezoidal anterior plate; posterior plate short and simple. Internal genitalia (Fig. 23C–D) very simple, with median sclerotized structure (receptacle?), apparently with small pore plates (Fig. 32D).

Natural history

The spiders were found under rocks on an arid slope (Fig. 34D). The habitat was shared with another species of Ninetinae, *Nerudia colina* Huber, 2023. Two egg-sacs contained six and eight eggs, respectively; egg diameter: 0.36.

Distribution

Known from type locality only, in Argentina, Jujuy (Fig. 33B).

***Guaranita goloboffi* Huber, 2000**
Figs 2I–J, 24–31, 32E

Guaranita goloboffi Huber, 2000: 97, figs 367–377 (♂♀)

Guaranita goloboffi – Huber 2014: 140. — Torres *et al.* 2015: 4, fig. 2c–d. — Dederichs *et al.* 2022: 18 (sperm morphology).

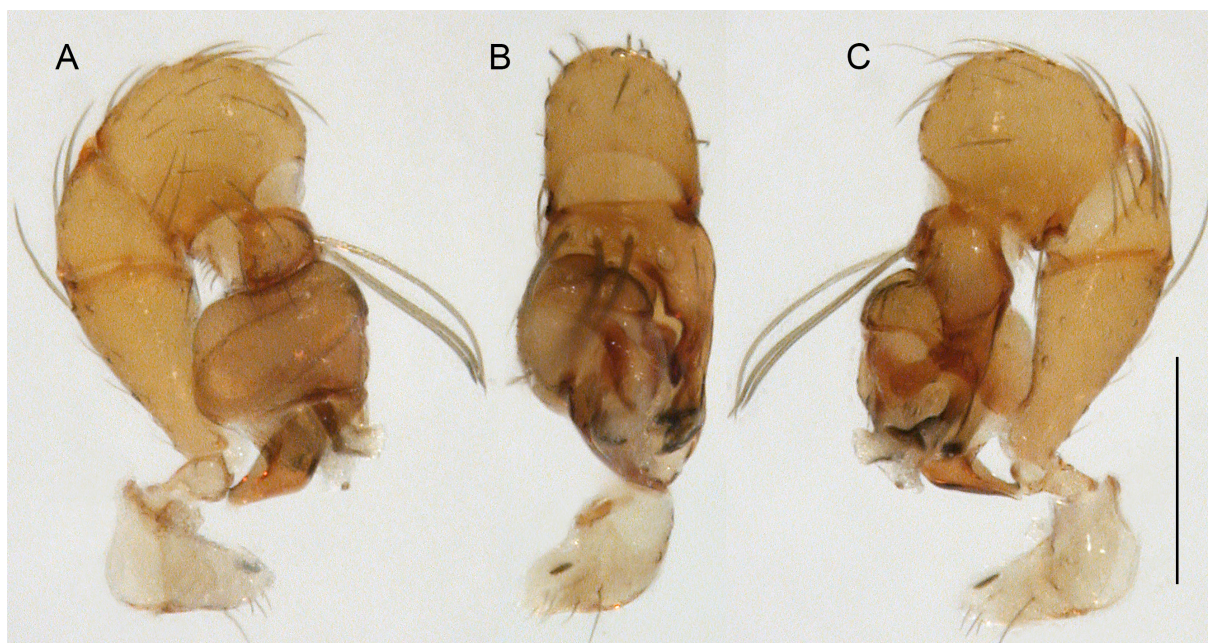


Fig. 24. *Guaranita goloboffi* Huber, 2000; male from Cabra Corral (ZFMK Ar 24129). Left pedipalp, prolateral (A), dorsal (B), and retrolateral (C) views. Scale bar = 0.2 mm.

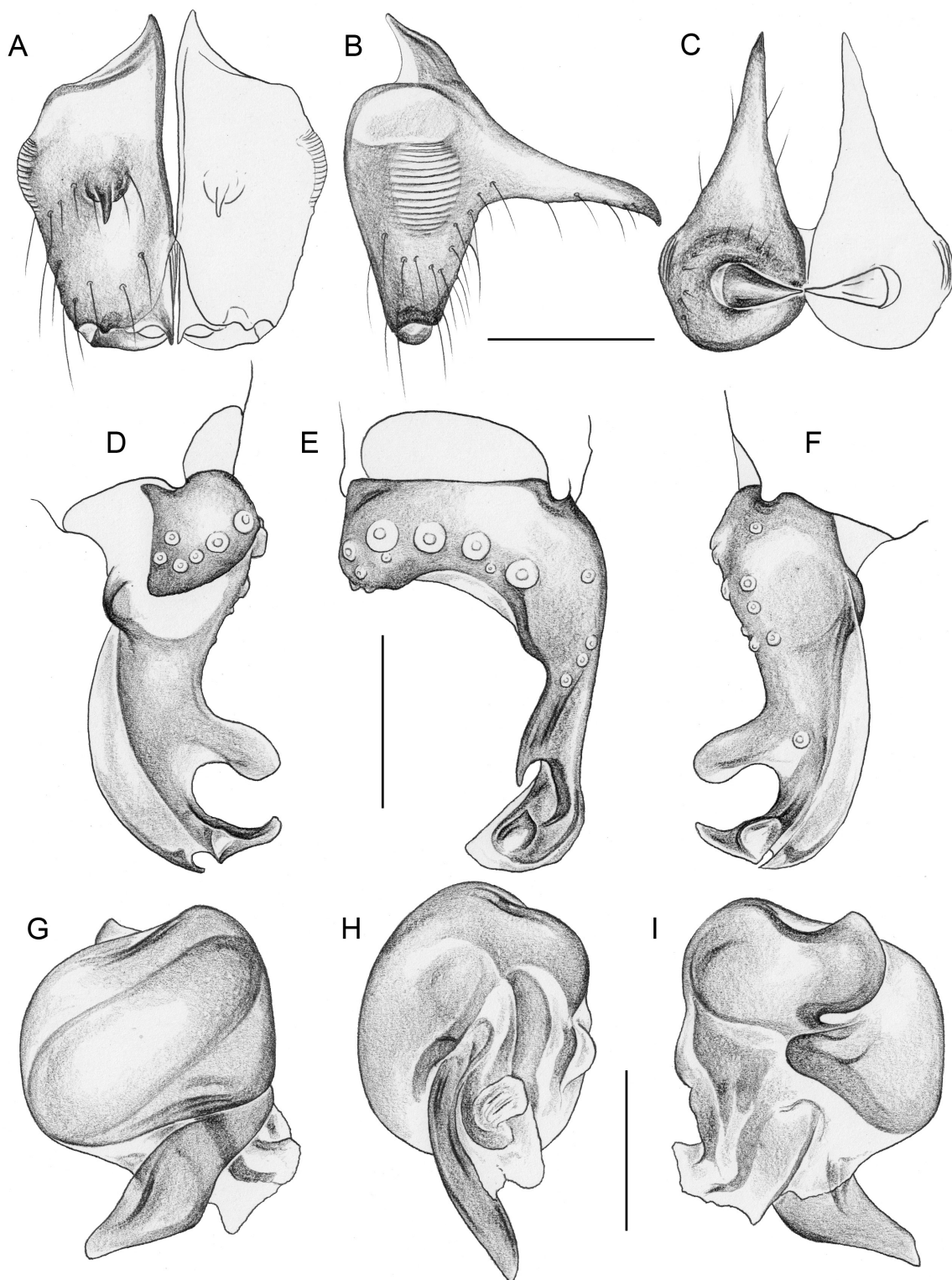


Fig. 25. *Guaranita goloboffi* Huber, 2000; males from Cabra Corral (A–C, G–I; ZFMK Ar 24129) and from NW of Chumbicha (D–F; ZFMK Ar 24130). **A–C.** Chelicerae, frontal, lateral, and ventral views. **D–F.** Left procurus, prolateral, dorsal, and retrolateral views. **G–I.** Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

Diagnosis (amendments; see Huber 2000)

Distinguished from known congeners by shape of dorsal flap on procurus (Fig. 25F; rounded, smaller than in the similar *G. yaculica*); also by wide distal bulbal sclerite (Fig. 25G; similar only in *G. auadae* sp. nov.), by relatively wide male palpal tibia (Fig. 24C; width/length 1.00; other species 0.85–0.95; tibia width/femur width: 1.75–1.80; other species 1.40–1.70) and by female internal genitalia (Fig. 26C–D; median structure rectangular, similar to *G. auadae* but larger).

Material examined (new records)

ARGENTINA – **Salta** • 1 ♂, 1 ♀; ~1 km SW of Alemania; 25.6300° S, 65.6180° W; 1210 m a.s.l.; 23 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24126 • 1 ♀, 3 juvs, in pure ethanol; same collection data as for preceding; ZFMK Arg203 • 4 ♀♀, 4 juvs, in pure ethanol; same collection data as for preceding; LABRE-Ar 860 • 1 ♀; same collection data as for preceding; LABRE-Ar 861 • 1 ♀; ~5 km W of Cafayate, ‘site 1’; 26.0641° S, 66.0294° W; 2060 m a.s.l.; 24 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24127 • 2 ♀♀, in pure ethanol; same collection data as for preceding; LABRE-Ar 857 • 1 ♀, in pure ethanol; same collection data as for preceding; LABRE-Ar 858 • 1 ♀, 1 juv.; 6 km NW of Cafayate, Chuscha; ~26.04° S, 66.02° W; ~1980 m a.s.l.; 17 Jul. 1995; M. Ramírez and P. Goloboff leg; MACN Ar 20094 • 1 ♂, 2 ♀♀; Cabra Corral, ‘site 1’, ~5 km E of Coronel Moldes; 25.2870° S, 65.4238° W; 1080 m a.s.l.; 20 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24128 • 2 ♀♀, 3 juvs, in pure ethanol; same collection data as for preceding; ZFMK Arg190 • 1 ♀, same

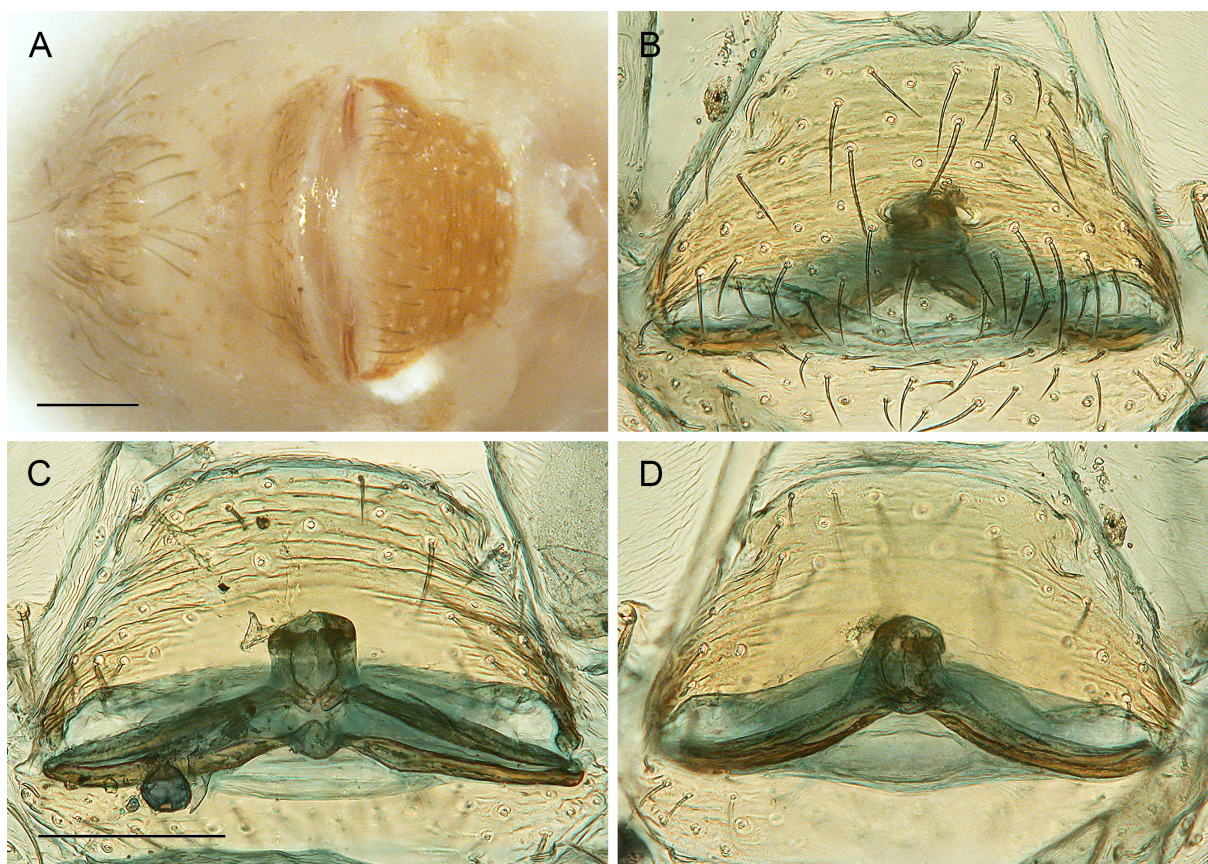


Fig. 26. *Guaranita goloboffi* Huber, 2000; females from Cabra Corral (A; ZFMK Ar 24129) and from NW of Chumbicha (B–D; ZFMK Ar 24130). **A.** Abdomen, ventral view. **B.** Cleared epigynum, ventral view. **C–D.** Cleared epigyna of two specimens, dorsal views. Scale bars = 0.1 mm (B–D at same scale).

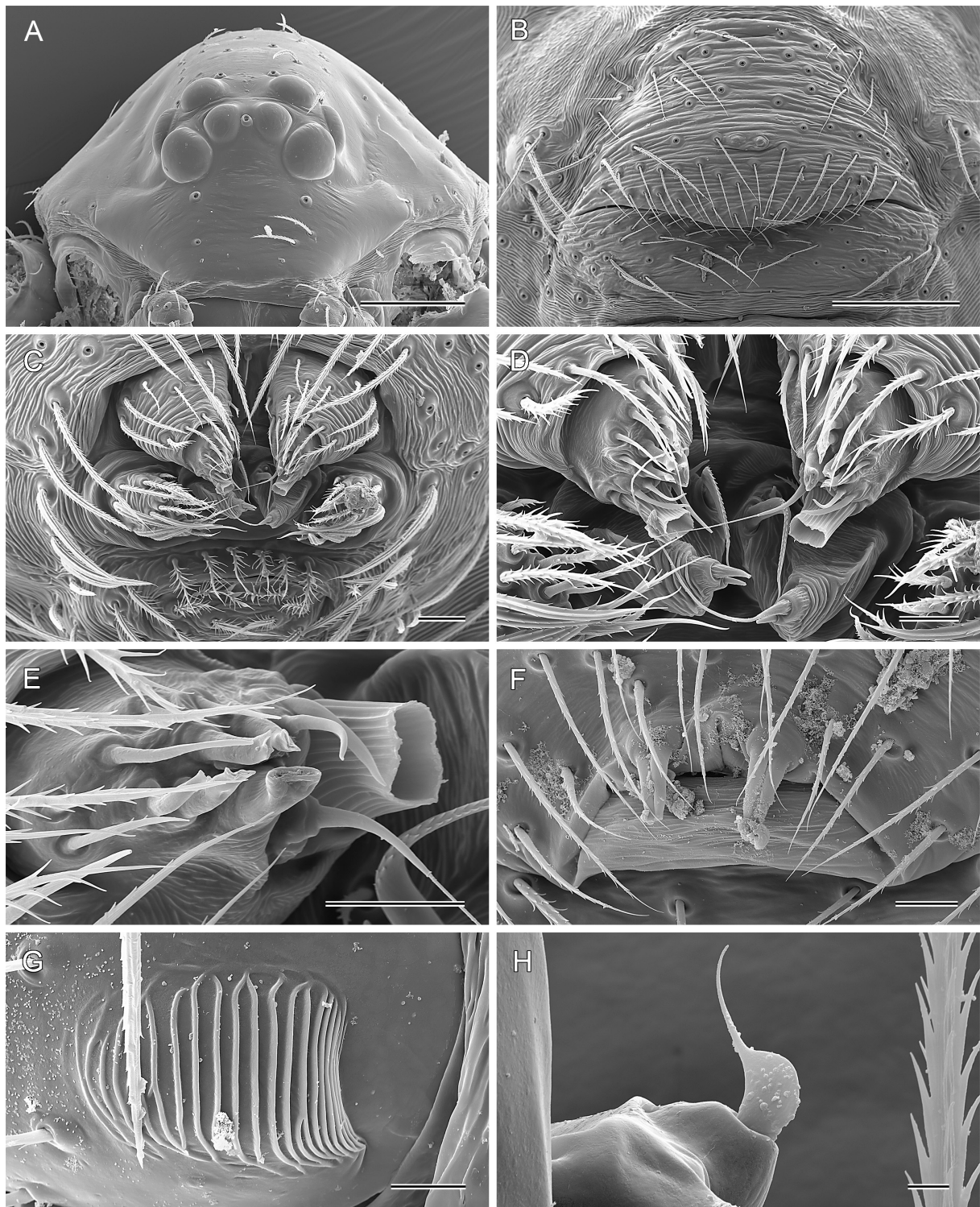


Fig. 27. *Guaranita goloboffi* Huber, 2000; from NW of Chumbicha (ZFMK Ar 24130, Arg220). **A.** Female prosoma, frontal view. **B.** Epigynum, ventral view. **C.** Female spinnerets and anal cone. **D.** Female ALS and PMS. **E.** Female ALS. **F.** Male gonopore with epiandrous spigots. **G.** Stridulatory file on left male chelicera. **H.** Stridulatory pick of male palpal femur. Scale bars: A–B = 100 μm ; C = 20 μm ; D–G = 10 μm ; H = 2 μm .

collection data as for preceding; LABRE-Ar 881 • 6 ♀♀, 1 juv., in pure ethanol; same collection data as for preceding; LABRE-Ar 864 • 5 ♂♂, 3 ♀♀ (one male and two females used for μ -CT study; one male used for karyotype study); Cabra Corral, 'site 3', ~3.5 km SE of dam; 25.2907° S, 65.3057° W; 1000 m a.s.l.; 21 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24129 • 4 ♀♀, 15 juvs, in pure ethanol; same collection data as for preceding; ZFMK Arg196 • 1 ♂, 1 ♀; same collection data as for preceding; LABRE-Ar 855 • 3 ♀♀, 4 juvs, in pure ethanol; same collection data as for preceding; LABRE-Ar 863. – **Catamarca** • 8 ♂♂, 4 ♀♀ (two males and two females used for μ -CT study; two males used for karyotype study, one male used for SEM); ~5 km NW of Chumbicha, near Balneario El Caolín, 'site 1'; 28.8152° S, 66.2478° W; 610 m a.s.l.; 28–29 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; ZFMK Ar 24130 • 1 ♂, 17 ♀♀, 5 juvs, in pure ethanol (two females used for SEM); same collection

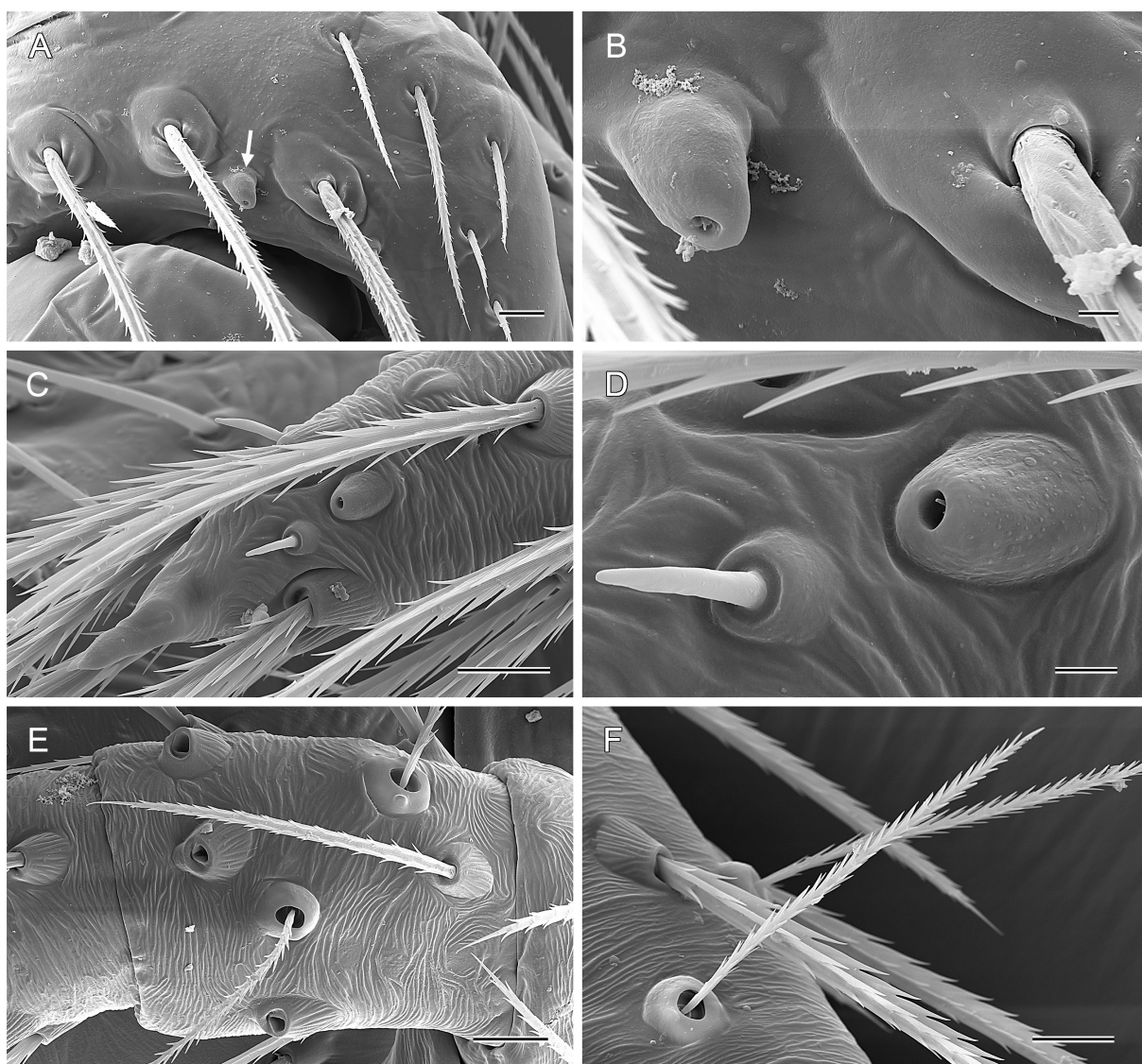


Fig. 28. *Guaranita goloboffi* Huber, 2000; from NW of Chumbicha (ZFMK Ar 24130, Arg220). **A.** Male left palpal tarsus, showing position of tarsal organ (arrow). **B.** Male palpal tarsal organ (detail of previous figure). **C.** Tip of left female palp, dorsal view. **D.** Female palpal tarsal organ (and short vertical hair). **E.** Female left palpal tibia, showing two trichobothria. **F.** Prolateral trichobothrium (and dorsal trichobothrium in the back) on female left tibia 2. Scale bars: A, C, E–F = 10 μ m; B, D = 2 μ m.

data as for preceding; ZFMK Arg220 • 8 ♂♂, 2 juvs; same collection data as for preceding; LABRE-Ar 875 • 11 ♀♀, 18 juvs, in pure ethanol; same collection data as for preceding; LABRE Ar 859.

Assigned tentatively (no males available)

ARGENTINA – **Tucumán** • 2 ♀♀, 1 juv., in pure ethanol; San Miguel de Tucumán, Parque 9 de Julio; 26.828° S, 65.186° W; 430 m a.s.l.; 1 Apr. 2015; A. Porta leg.; MACN Ar 34678. – **Salta** • 3 ♀♀; between Alemania and Cafayate; 25.7023° S, 65.7022° W; 1340 m a.s.l.; 23 Mar. 2019; B.A. Huber and M.A. Izquierdo leg.; LABRE-Ar 862.

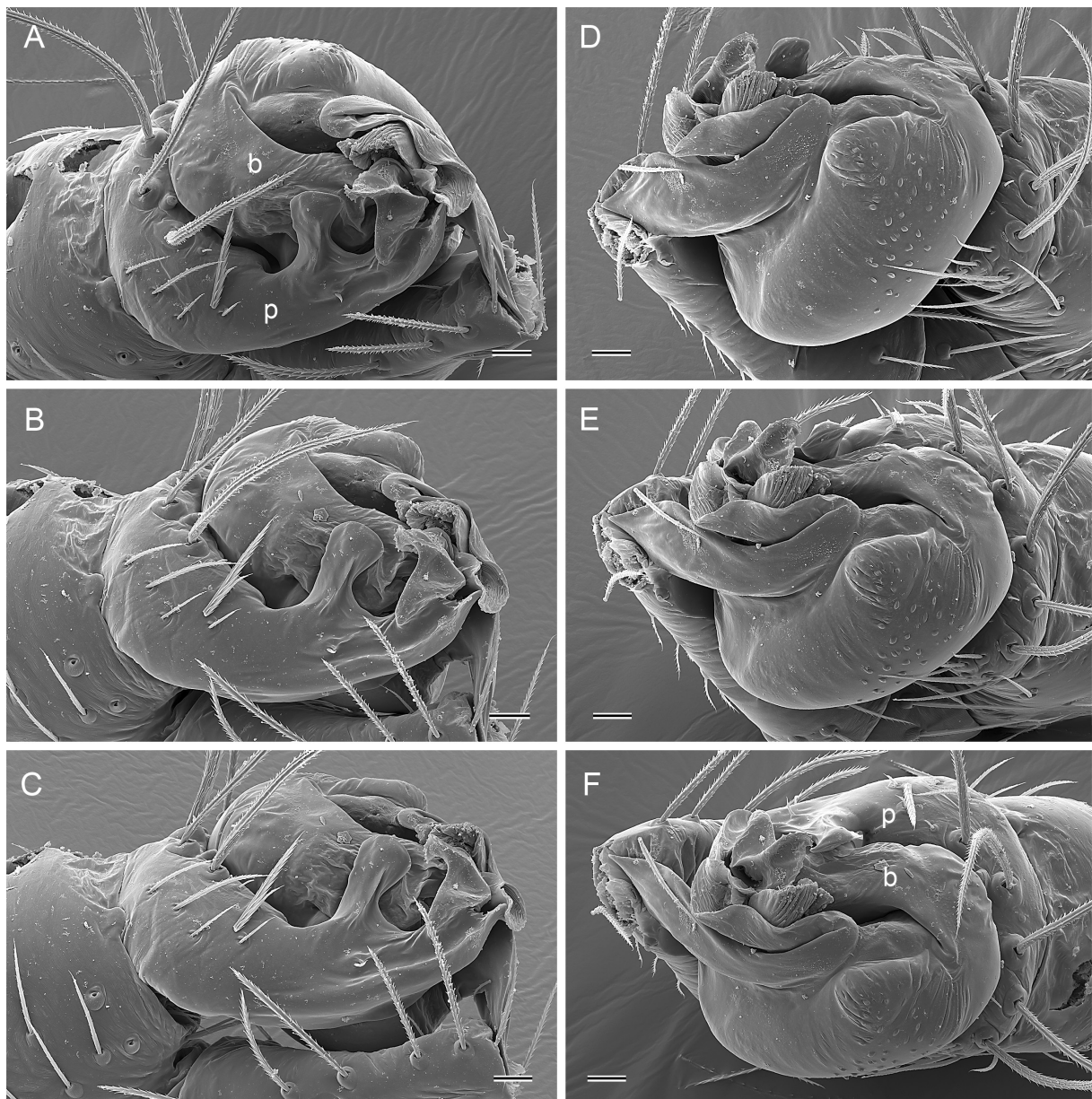


Fig. 29. *Guaranita goloboffi* Huber, 2000; male from NW of Chumbicha (ZFMK Ar 24130, Arg220). A–C. Right tarsus, procurus, and bulb, in retrolateral-dorsal, retrolateral, and retrolateral-ventral views. D–F. Right genital bulb (and neighboring elements of male palp), in prolateral, prolateral-dorsal, and dorsal views. Abbreviations: b = genital bulb; p = procurus. Scale bars = 20 μ m.

Redescription (amendments; see Huber 2000)

Measurements of male from Cabra Corral, ‘site 3’: total body length 1.08, carapace width 0.40; distance PME–PME 40 μm ; diameter PME 45 μm ; distance PME–ALE 20 μm ; distance AME–AME 20 μm ; diameter AME 25 μm . Leg 1: 2.02 (0.56+0.14+0.50+0.48+0.34), tibia 2: 0.42, tibia 3: 0.38, tibia 4: 0.63; tibia 1 L/d: 8; diameters of leg femora 0.090–0.095; of leg tibiae: 0.060. Tibia 1 in 19 males (incl. males in Huber 2000): 0.49–0.59 (mean 0.53). Sternum slightly wider than long (0.32/0.30). Chelicerae as in Fig. 25A–C; stridulatory files (Fig. 27G) with ~17–19 ridges each; distances between ridges proximally ~0.6 μm , distally ~2.7 μm . Pedipalp as in Fig. 24A–C; tibia with two trichobothria;

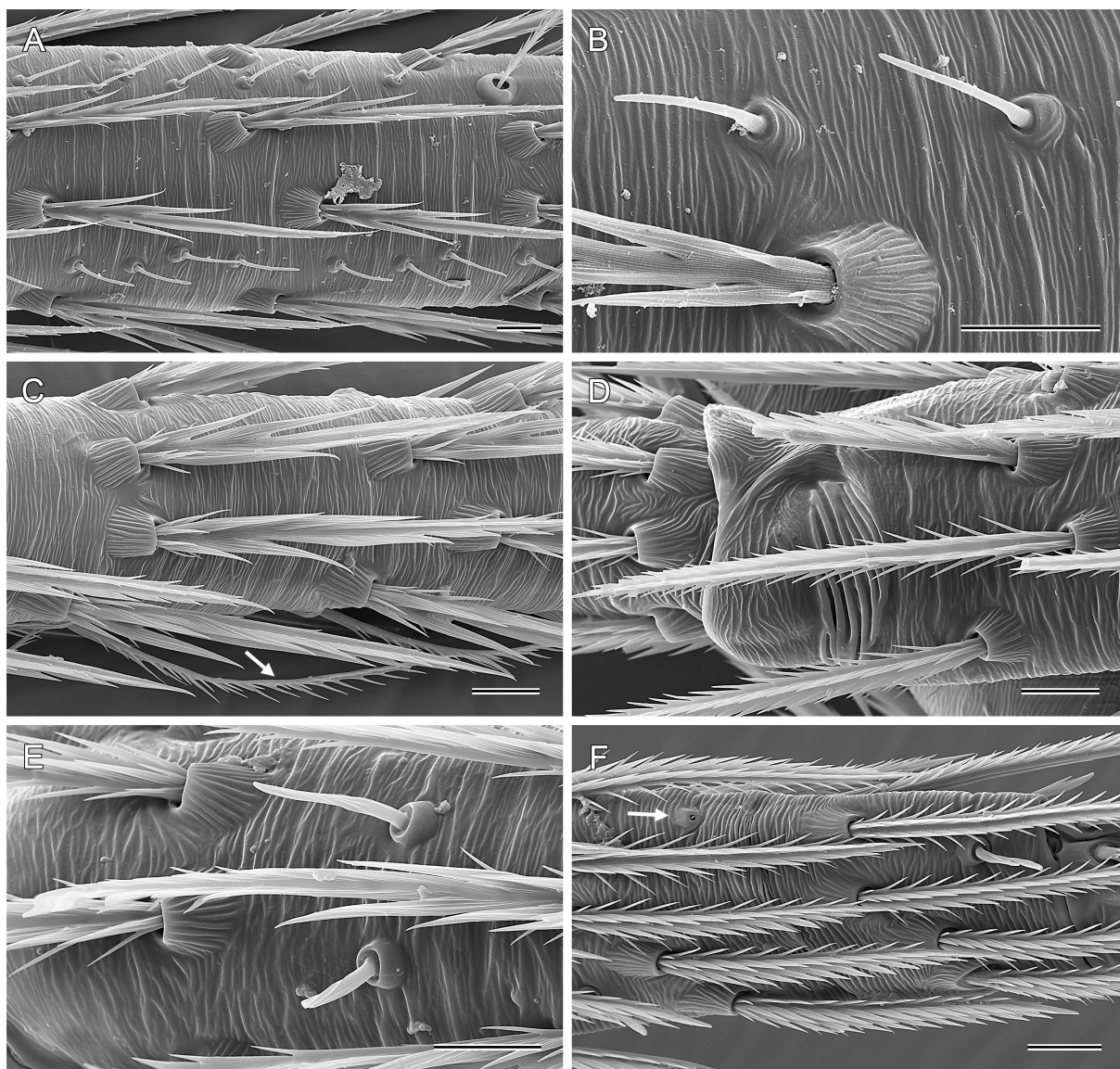


Fig. 30. *Guaranita goloboffi* Huber, 2000; from NW of Chumbicha (ZFMK Ar 24130, Arg220). **A.** Male right tibia 1, retrolateral view, showing two rows of short vertical hairs. **B.** Two short vertical hairs (and basis of regular hair) on male right tibia 1. **C.** Female metatarsus 4, showing slender hair (arrow) among regular hairs. **D.** Dorsal lyriform organ distally on female metatarsus 1. **E.** Chemoreceptive hairs distally on female left metatarsus 2. **F.** Female tarsus 4; note tarsal organ (arrow) and chemoreceptive hair (upper right). Scale bars = 10 μm .

palpal tarsal organ capsulate (Fig. 28A–B), raised, with small opening (diameter of opening $1.45\ \mu\text{m}$); procurus as in Figs 25D–F and 29A–C, with large transparent ventral membrane, distinctive dorsal flap, and tip bent towards dorsal; genital bulb as in Figs 25G–I and 29A–F, with simple proximal sclerite, distal sclerite widened in mid-section. Legs without spines and curved hairs; vertical hairs not seen in dissecting microscope but present in two retrolateral rows on tibia 1 (Fig. 30A–B); prolateral trichobothrium absent on tibia 1, present on other leg tibiae; metatarsus 4 with a few slender hairs on retrolateral-ventral side (as in female, cf. Fig. 30C); tarsus 4 with single prolateral comb-hair (as in female, cf. Fig. 31D). Gonopore with four epiandrous spigots (Fig. 27F).

Tibia 1 in 55 newly collected females 0.48–0.58 (mean 0.52). Female internal genitalia (Fig. 26C–D) with strong median structure; apparently with small pore plates (Fig. 32E). Each ALS (Fig. 27C–E) with

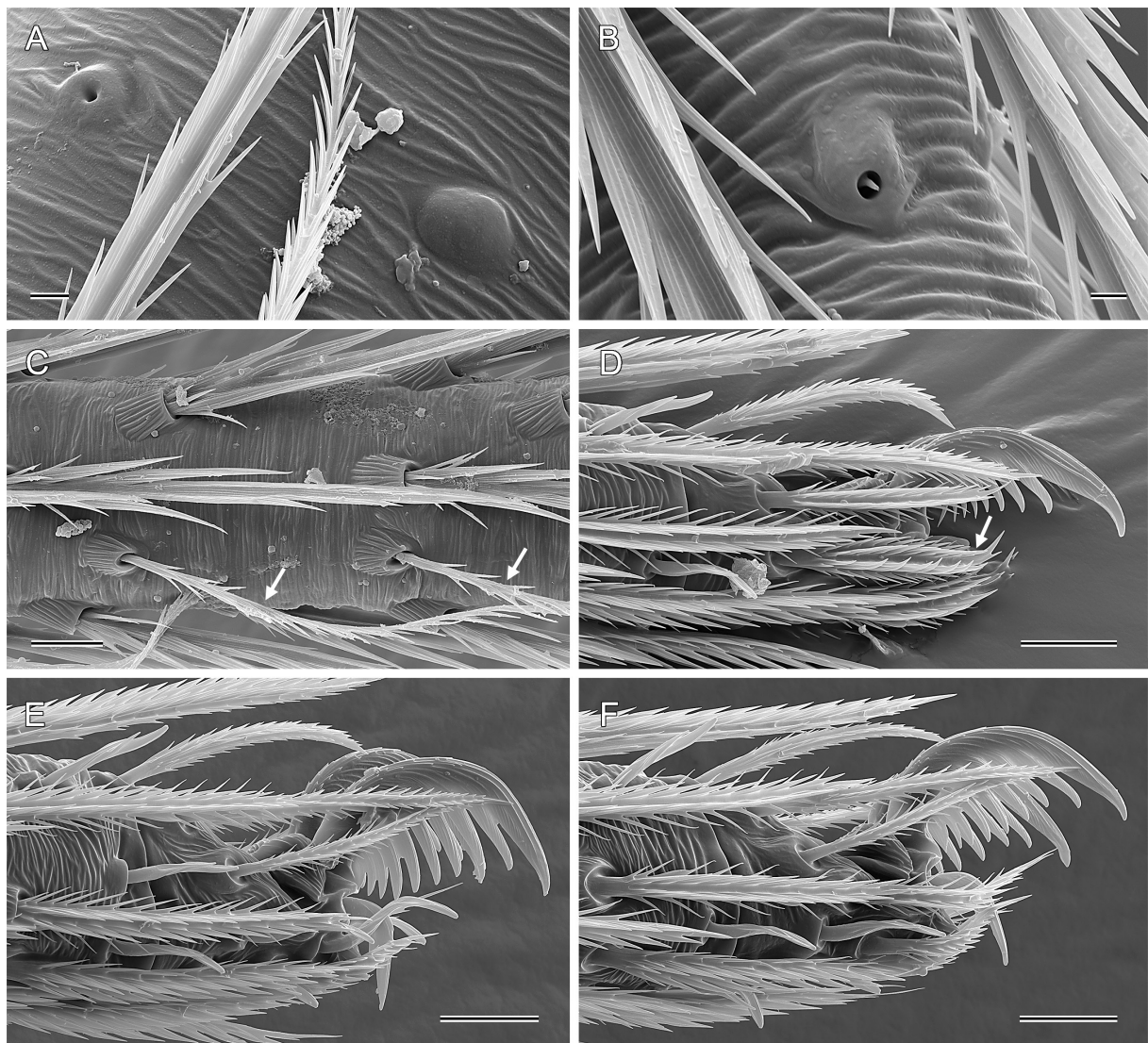


Fig. 31. *Guaranita goloboffi* Huber, 2000; from NW of Chumbicha (ZFMK Ar 24130, Arg220). **A.** Pore and cuticular plate on female right tibia 2. **B.** Tarsal organ on female right tarsus 4. **C.** Male right metatarsus 4, showing two slender hairs (arrows) and regular hairs. **D.** Tip of female tarsus 4, prolateral view, showing claws and comb-hair (arrow). **E.** Claws on female right tarsus 1, retrolateral view. **F.** Claws of female left tarsus 3, prolateral view. Scale bars: A = $2\ \mu\text{m}$; B = $1\ \mu\text{m}$; C–F = $10\ \mu\text{m}$.

one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (of which one is much wider than the others); each PMS with two conical spigots (Fig. 27D); PLS without spigots. Leg tibiae and metatarsi with tiny pores with cuticular rim (pore diameter 0.5 μ m; Fig. 31A) and with small round cuticular ‘plates’ (diameter 4–5 μ m; Fig. 31A). Tarsal organs with very small openings (palp: 1.2 μ m;

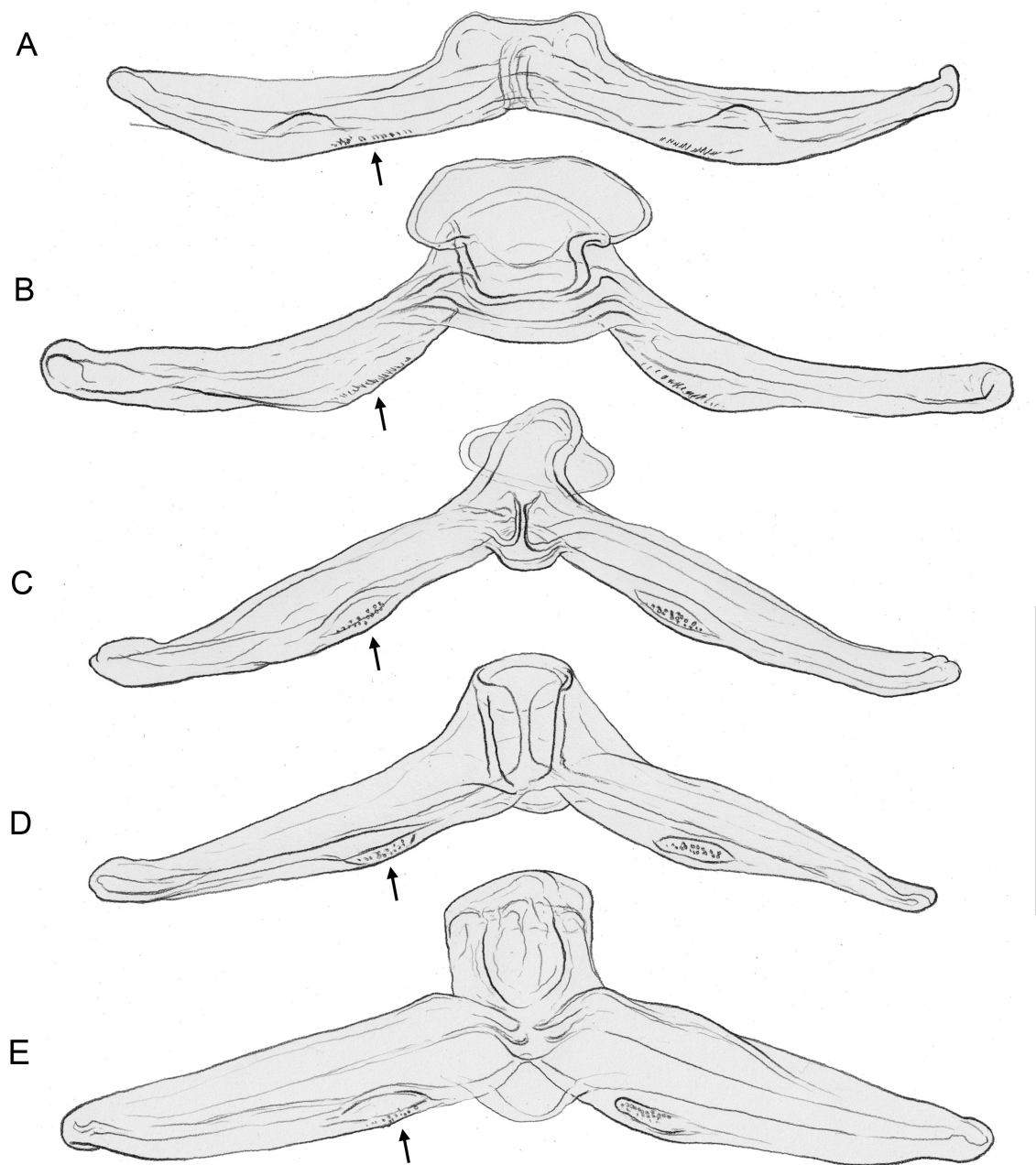


Fig. 32. *Guaranita* Huber, 2000, female internal genitalia; arrows point at possible pore plates. **A.** *G. doobby* Torres *et al.*, 2016; from NW of Campo Quijano. **B.** *G. munda* (Gertsch, 1982); from E of Nono. **C.** *G. yaculica* Huber, 2000; from Calilegua National Park. **D.** *G. auadae* Huber sp. nov., from between San Salvador and Purmamarca. **E.** *G. goloboffi* Huber, 2000; from NW of Chumbicha. Scale bar = 0.1 mm (all at same scale).

legs: $\sim 0.8 \mu\text{m}$; Figs 28C–D, 31B). Metatarsi 3 and 4 with long slender hairs as in male (Fig. 30C); tarsus 4 with single prolateral comb-hair as in male (Fig. 31D).

Natural history

The newly collected specimens were found in relatively arid environments (Fig. 34E–F), under rocks, in leaf litter, and in the dry leaves of dead bromeliads lying on the ground. Three egg-sacs contained 6–7 eggs, respectively, and were carried under the prosoma.

Distribution

Known from several localities in Salta, Tucumán, and Catamarca provinces, Argentina (Fig. 33B).

Karyology

While the preparation of the *G. goloboffi* specimen from Cabra Corral contained rare mitoses, prophases and metaphases I, preparations of the males from Chumbicha contained only a few premeiotic interphases and prophases of the second meiotic division. The male karyotype of the *G. goloboffi* specimen from Cabra Corral consisted of 11 exclusively metacentric chromosomes, namely five chromosome pairs that decreased gradually in length and a single large X chromosome (Fig. 35E). Chromosome pairs decreased gradually in length, except for the prominent first pair. The X chromosome was twice as long as the chromosomes of the first pair. Fused sister prophases II of specimens from Chumbicha also comprised 11 chromosomes (Fig. 35C), which confirms the diploid number and sex chromosome system. For the specimen from Cabra Corral we also obtained data on the NOR pattern. Two bivalents included a terminal NOR. Another NOR was possibly placed in the middle of an X chromosome arm. However, this was visible in only one of three metaphase I plates suitable for the detection of NORs.

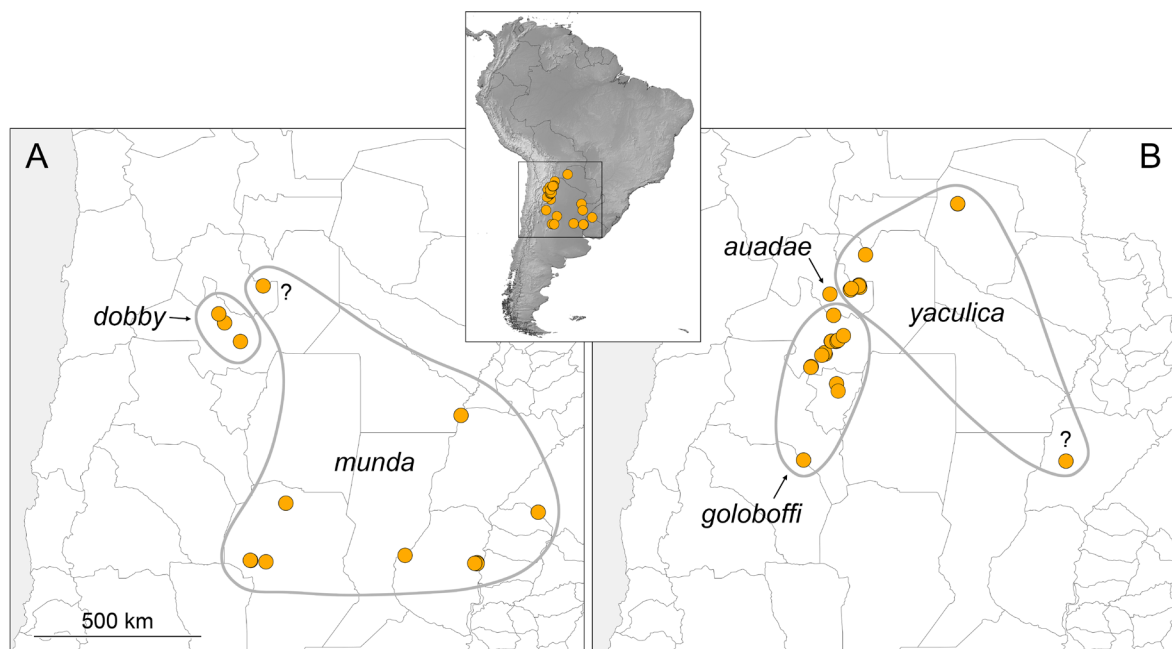


Fig. 33. Known distribution of *Guaranita* Huber, 2000. Inset: map of South America, showing all known records. **A–B.** Known distributions of individual species. Question marks denote dubious outliers (Torres *et al.* 2015, 2016; not restudied) that need confirmation.

The sex chromosome did not differ in its intensity of condensation and staining from the other chromosomes at the mitotic prophase and metaphase (Fig. 35E). The male prophase of the first meiotic division included a diffuse stage (Fig. 35B). The X chromosome was positively heteropycnotic (i.e., more intensively stained than the other chromosomes) during the premeiotic interphase (Fig. 35A) and the diffuse stage (Fig. 35B). During the prophase of the second meiotic division (Fig. 35C), however, it exhibited the same behavior and intensity of staining as the other chromosomes.



Fig. 34. Typical habitats of species of *Guaranita* Huber, 2000 in Argentina. **A.** NW of Campo Quijano (Salta), *G. doobby* Torres *et al.*, 2016. **B.** E of Nono (Córdoba), *G. munda* (Gertsch, 1982). **C.** Calilegua National Park (Jujuy), *G. yaculica* Huber, 2000. **D.** Between San Salvador and Purmamarca (Jujuy), type locality of *G. auadae* Huber sp. nov. **E.** SW of Alemania (Salta), *G. goloboffi* Huber, 2000. **F.** W of Cafayate (Salta), *G. goloboffi*.

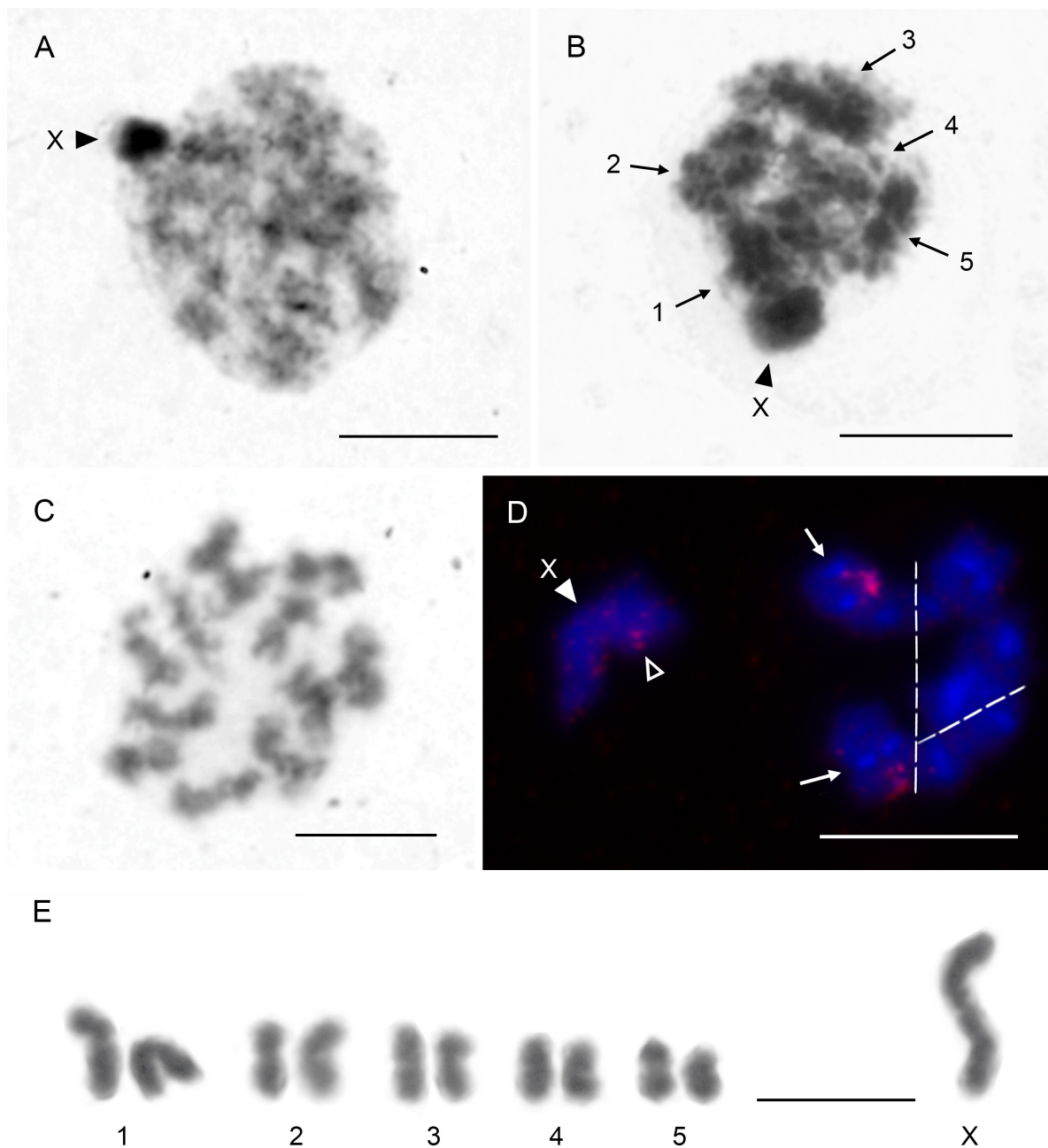


Fig. 35. Karyology of *Guaranita goloboffi* Huber, 2000; males from Chumbicha (A, C) and Cabra Corral (B, D–E). **A.** Premeiotic interphase. Note positively heteropycnotic X chromosome on the periphery of the nucleus. **B.** Late diffuse stage. Plate consists of five bivalents and peripheral X univalent, which exhibits positive heteropycnosis. **C.** Two fused sister prophase of the second meiotic division ($2n = 11$). X chromosome does not differ by condensation pattern or behavior from the other chromosomes. **D.** Metaphase I composed of five bivalents and X chromosome univalent, detection of NORs by FISH. Particular bivalents separated by dashed line. Centromeric regions of chromosomes forming bivalents exhibit a bright fluorescence. Note two NOR-bearing bivalents (shafted arrows). Another NOR is possibly placed in the middle of an X chromosome arm (empty arrowhead). **E.** Karyotype, based on mitotic metaphase. Note five metacentric chromosome pairs and a large metacentric X chromosome. Scale bars = 10 μm .

Discussion

Notes on relationships

Relationships are beyond the focus of this paper, for two reasons: first, our present molecular data set is limited to *COI*, while relationships based on an adequate molecular (UCE) dataset will be available soon (G. Meng, B.A. Huber, L. Podsiadlowski, unpubl. data); second, the putatively closest relatives of *Guaranita* (as suggested by the UCE data: *Galapa*, *Kambiwa*, *Pemona*) have not yet been revised, so our new data (especially SEM) are difficult to evaluate in a phylogenetic context. Bearing these limitations in mind, we point out two observations. First, the dorsal flap on the procurus of *Guaranita* has been thought to be a synapomorphy of the genus (Huber 2000). However, if *Galapa* is indeed closely related, then the dorsal process of the procurus of *Galapa* may be homologous to the dorsal flap in *Guaranita*, joining these two genera. Second, the ‘relationships’ suggested in our NJ *COI* tree appear supported by morphological similarities: *G. munda* and *G. yaculica* share a membranous median sac in the female internal genitalia (Fig. 32B–C), while *G. auadae* sp. nov. and *G. goloboffi* share a sclerotized rectangular median structure (Fig. 32D–E) and a widened distal bulbal sclerite (Figs 22G, 25G). The four species together share the very long male cheliceral apophyses (much shorter in *G. dooby*).

Notes on morphology

The peculiar ‘slender hairs’ on the metatarsi 3 and 4 in males and females have not been reported for Pholcidae before. Superficially, they combine the basis of a regular tactile hair with the shaft of a trichobothrium (Figs 7C, 13E, 31C). Preliminary SEM studies of *Galapa bella* (Gertsch & Peck, 1992) suggest that such hairs do not occur in that species (B.A. Huber, unpubl. data). Other potential close relatives (*Kambiwa*, *Pemona*) have not yet been studied with respect to this detail. The possible function of these hairs is unknown.

A recent review of sexual dimorphisms in Pholcidae (Huber 2021) estimated more than 120 independent origins. Of the five sexual dimorphisms reported herein for *Guaranita*, one was not included in the review, and three need to be updated; the fifth is listed here for the sake of completeness. (1) A raised tarsal organ on the male palp was not included in Huber (2021) but has also been reported for *Nerudia* Huber, 2000 (Huber *et al.* 2023a) and *Pholcophora* Banks, 1896 and *Tolteca* Huber, 2000 (Huber *et al.* 2023b). It also occurs in *Galapa bella* (B.A. Huber unpubl. data). It may thus be a general Ninetinae character. (2) The clypeus modification of *G. dooby* is shared with *Pinoquio barauna* (Huber & Carvalho, 2019) (case 13 in Huber 2021). The modifications are in fact very similar in the two species, but according to our UCE data, *P. barauna* belongs in a different group of Ninetinae (together with the Old World *Ninetis* Simon, 1890). The clypeus modifications may thus have originated independently. (3) Sexually dimorphic cheliceral stridulation (present in males, absent in females) was thought to occur in *Pinoquio barauna* but in no other Ninetinae (case 7 in Huber 2021). In the meantime, such a dimorphism was also found in *Nerudia* (Huber *et al.* 2023a), *Pholcophora* (Huber *et al.* 2023b), *Guaranita* (herein), and *Galapa bella* (B.A. Huber unpubl. data). It may thus be a common dimorphism in Ninetinae. (4) Short “vertical hairs” on one or several legs in males are much more common in Ninetinae than previously thought (case 96 in Huber 2021; see also discussion of this character in Huber *et al.* 2023b), supporting the idea that they originated only once in Ninetinae (Huber 2021). (5) Finally, a pair of humps on the male sternum has been reported for most Ninetinae (case 55 in Huber 2021), suggesting a single origin in the subfamily.

Pholcidae occupy a range of different microhabitats (Eberle *et al.* 2018) and vary accordingly with respect to body shape, size, and coloration. Some of this variation is trivial, as for example small size and short legs in leaf litter and ground dwelling species such as Ninetinae. A less obvious difference that distinguishes ground-dwelling species from those in other microhabitats refers to relative leg length: ground dwelling species tend to have long legs 4 (leg formula 1-4-2-3 or even 4-1-2-3 as in *Guaranita*), while species in other microhabitats have legs 1 longest (usually 1-2-4-3) (e.g., Huber 2005; Huber &

Carvalho 2019; Huber & Villarreal 2020). In the present study we hypothesized that the tips of the tarsi (in particular the claws) will also differ between ground-dwelling, fast-running species such as *Guaranita* and long-legged web-hanging pholcids. To our surprise, we found no such difference, neither in the present study nor in recent and ongoing studies on other Ninetinae genera (Huber *et al.* 2023a on *Nerudia*; Huber *et al.* 2023b on *Pholcophora* and *Tolteca*; B.A. Huber, unpubl. data on *Galapa*). As far as can be seen on SEM images, the tarsal pseudosegments, claws, and distal tarsal hairs in Ninetinae do not differ in any obvious way from those in other Pholcidae studied.

Notes on karyology

Diploid numbers within the subfamily Ninetinae range from 11 (*Guaranita goloboffi*; this study) to 29 [*Pholcophora americana* Banks, 1896 and *Kambiwa neotropica* (Kraus, 1957); Ávila Herrera *et al.* 2021]. The karyotype of *G. goloboffi* is formed by metacentric chromosomes. The male prophase of the first meiotic division contains a specific period, the so-called diffuse stage (this study), which is characterized by a considerable decondensation of chromosome pairs. By contrast, the sex chromosome shows a considerable condensation (cf. Benavente & Wettstein 1980). Biarmed (i.e., metacentric and submetacentric) chromosomes as well as the male diffuse stage are probably ancestral for haplogyne spiders, i.e., for a clade formed by Synspermiata Michalik & Ramírez, 2014 and two cribellate families, Filistatidae Ausserer, 1867 and Hypochilidae Marx, 1888 (Ávila Herrera *et al.* 2021). The karyotype of *G. goloboffi* contains two NOR bearing chromosome pairs, which is probably the ancestral pattern of Ninetinae (Ávila Herrera *et al.* 2021). Furthermore, this species possibly has a sex chromosome-linked NOR. Nucleolus organizer regions have frequently spread to sex chromosomes during the evolution of haplogynes, including pholcids (Král *et al.* 2006; Ávila Herrera *et al.* 2021; Huber *et al.* 2023a, 2023b).

Like in many other spider groups (e.g., Suzuki 1954; Kořínková & Král 2013; Král *et al.* 2013), the number of chromosome pairs has decreased during the evolution of all analyzed pholcid lineages (Ávila Herrera *et al.* 2021) including Ninetinae (Ávila Herrera *et al.* 2021; Huber *et al.* 2023a, 2023b). In *Tolteca oaxaca* Huber, 2023 ($2n♂ = 13$) (Huber *et al.* 2023b) and *Guaranita goloboffi* ($2n♂ = 11$) (this study), the number of chromosome pairs has been reduced considerably, namely to five. There are only a few other araneomorph spiders with a standard chromosome structure that exhibit lower numbers of chromosomes than *Guaranita*, namely pholcids of the genus *Micropholcus* Deeleman-Reinhold & Prinsen, 1987 (Pholcinae) ($2n♂ = 9$) (Lomazi *et al.* 2018; Ávila Herrera *et al.* 2021) and the uloborid *Uloborus danolius* Tikader, 1969 ($2n♂ = 10$) (Parida & Sharma 1987).

The Ninetinae *Guaranita* and *Tolteca* thus have a very low and similar number of chromosome pairs (five in *Guaranita*; five to six in *Tolteca*). However, according to preliminary analyses of molecular (UCE) data (G. Meng, B.A. Huber, L. Podsiadlowski, unpubl. data) this similarity is unlikely to reflect a sister-group relationship. Each genus appears more closely related to a geographically close neighbor with a higher number of chromosome pairs than to each other: *Guaranita* to *Kambiwa* ($2n♂ = 29$, $X_1X_2X_3X_4Y$; 12 chromosome pairs) and *Tolteca* to *Pholcophora* ($2n♂ = 29$, X_1X_2Y ; 13 chromosome pairs). A close relationship of *Guaranita* and *Kambiwa* suggests that the X0 system of *Guaranita* may have originated from a complex system, either from a $X_1X_2X_3X_4Y$ system as found in *Kambiwa* or from a $X_1X_2X_3Y$ system, which is probably the ancestral sex chromosome system of the clade formed by *Gertschiola* Brignoli, 1981, *Kambiwa* Huber, 2000, and *Nerudia* Huber, 2000 (Huber *et al.* 2023a). Within Pholcidae, the X0 system has originated at least six times independently, including *Guaranita* (Ávila Herrera *et al.* 2021; this study). Another similarity shared by *Guaranita* and *Tolteca* is the presence of a sex chromosome-linked NOR (admitting that we are not entirely sure about its presence in *Guaranita*). However, we have detected this character also in other Ninetinae genera (*Gertschiola*, *Kambiwa*, *Nerudia*) (Ávila Herrera *et al.* 2021; Huber *et al.* 2023a). This suggests that a sex chromosome-linked NOR might be an ancestral character in Ninetinae.

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Author contributions

BAH: initiation of the project, collecting, taxonomic descriptions, writing.

GM: analysis of molecular data, writing.

IMAH: preparation of chromosome slides, evaluation of karyological data, writing.

JK: preparation of chromosome slides, evaluation of karyological data, writing.

MAI: permits, collecting, writing.

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