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Short-legged daddy-long-leg spiders in North America: the genera *Pholcophora* and *Tolteca* (Araneae, Pholcidae)

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Abstract. The North American-Caribbean genera *Pholcophora* Banks, 1896 and *Tolteca* Huber, 2000 are representatives of Ninetinae, a group of small, cryptic, and thus poorly known pholcid spiders. We present the first comprehensive revisions of the two genera, including extensive SEM data and descriptions of seven new species from Mexico (*Pholcophora mazatlan* Huber sp. nov., *P. papanoa* Huber sp. nov., *P. tehuacan* Huber sp. nov., *Tolteca huahua* Huber sp. nov., *T. manzanillo* Huber sp. nov., *T. oaxaca* Huber sp. nov., and *T. sinnombre* Huber sp. nov.). We add new CO1 sequences of nine species to previously published molecular data and use these for a preliminary analysis of relationships. We recover a North American-Caribbean clade including 'true' (mainland) *Pholcophora*, *Tolteca* (Mexico), and a Caribbean clade consisting of the genus *Papiamenta* Huber, 2000 (Curaçao) and Caribbean '*Pholcophora*'. First karyotype data for *Tolteca* ($2n♂ = 13$, X_1X_2Y and 15, X_1X_2Y, respectively) reveal a strong reduction of the number of chromosome pairs within the North American-Caribbean clade, and considerable karyotype differentiation among congeners. This agrees with considerable CO1 divergence among species of *Tolteca* but contrasts with very inconspicuous morphological divergence. Environmental niche analyses show that the widespread *P. americana* Banks, 1896 (western USA, SW Canada) occupies a very different niche than its Mexican congeners and other close relatives. Caribbean

taxa also have a low niche overlap with 'true' *Pholcophora* and *Tolteca*, supporting the idea that Caribbean '*Pholcophora*' are taxonomically misplaced.

Keywords. Ninetinae, Mexico, barcodes, karyotype, environmental niche.

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Table of contents

Introduction

Pholcid spiders are commonly known as daddy-long-leg spiders, and in fact the large majority of known species are characterized by long and thin legs, reminding of harvestmen, or daddy-long-legs. However, just like harvestmen, Pholcidae C.L. Koch, 1850 includes some short-legged species as well. When Eugène Simon, the founder of modern spider systematics, discovered the first such species in Yemen, he created a separate subfamily for it, the "Ninetidinae" (now Ninetinae) (Simon 1890, 1893). Since then, a few further species have been described, mainly from the New World (Mello-Leitão 1944; Brignoli 1981; Gertsch 1982; Huber 2000; Huber & Carvalho 2019; Huber & Villarreal 2020), but with currently ~50 nominal species, the subfamily continues to be the smallest in terms of species numbers among the five pholcid subfamilies. In part, this is certainly due to their small size and cryptic lifestyle. With body lengths of ~1 mm, many species are among the smallest known Pholcidae (Huber & Eberle 2021), and most species live hidden under rocks and stones. Other aspects that probably contribute to our poor knowledge of the subfamily are the geographic restriction of most species to arid (and thus relatively poorly sampled) regions (Huber & Brescovit 2003; Huber & Carvalho 2019); their phylogenetically conserved environmental niche; and the apparent ability of representatives of certain genera to avoid pitfall traps (Huber *et al.* 2023).

In the New World, almost any tiny pholcid was originally assigned to *Pholcophora* Banks, 1896, a genus created for a species of Ninetinae from the western USA (Banks 1896). The majority of species originally described in *Pholcophora* have since been moved to other genera, partly to newly established genera of Ninetinae (*Galapa* Huber, 2000; *Tolteca* Huber, 2000; *Papiamenta* Huber, 2000; *Guaranita* Huber, 2000), partly to other subfamilies (*Anopsicus* Chamberlin & Ivie, 1938: Modisiminae Simon, 1893; *Chisosa* Huber, 2000: Arteminae Simon, 1893) (Gertsch 1982; Huber 2000; Huber *et al.* 2018). As a result, *Pholcophora* ended up including only three Dominican amber fossil species and five extant species, restricted geographically to North America and the Caribbean. The genus exemplifies well our poor general knowledge of Ninetinae: of the eight nominal species, five have been known from only a single specimen each. The situation is similar with the only other North American genus of Ninetinae: *Tolteca* Huber, 2000. This genus was created for two species originally described in *Pholcophora*; one of them has been known from a single specimen only.

Our knowledge about the phylogenetic relationships among these North American pholcids has also been rudimentary. The most comprehensive phylogeny of Pholcidae (Eberle *et al.* 2018) recognized a "North and Central American and Caribbean" clade of Ninetinae, but the species sample was small (four species, of which two could not confidently be assigned to a genus) and lacked the genus *Tolteca*. A recent comparative study of pholcid sperm ultrastructure (Dederichs *et al.* 2022) found that *Pholcophora* and *Tolteca* share cleistospermia while all other studied Ninetinae have synspermia; since synspermia are thought to be plesiomorphic for Pholcidae, this was a first indication that *Pholcophora* and *Tolteca* might be closely related.

The purpose of this study is a comprehensive revision of North American Ninetinae (*Pholcophora* and *Tolteca*). We provide taxonomic descriptions of several new species and redescriptions of most previously described species, including numerous new records and first extensive SEM data for both genera as a basis for future cladistic analyses of morphological data; we provide first molecular data and first karyotype data for the genus *Tolteca*; and we provide an analysis of niche overlap and of altitudinal ranges in North American ninetines.

Material and methods

Material examined

This study is based on the examination of ~400 adult specimens deposited in the following collections:

AMNH = American Museum of Natural History, New York, USA
LATLAX = Laboratory of Arachnology, Institute of Biology, UNAM-Tlaxcala, Mexico
USNM = National Museum of Natural History, Washington D.C., USA
ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

Further material deposited in the AMNH was examined by the first author in 1999 but not re-examined for the present study.

Taxonomy and morphology

Taxonomic descriptions follow the style of recent publications on Pholcidae (e.g., Huber *et al.* 2023; 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 ± 5 µm. Photos were made with a Nikon Coolpix 995 digital camera (2048 × 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 ver. 10.0. For SEM photos, specimens were dried in hexamethyldisilazane (HMDS) (Brown 1993), and photographed with a Zeiss Sigma 300 VP scanning electron microscope. SEM data are presented within the descriptions but are usually not based on the specific specimen described.

Abbreviations used in figures only 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)

Molecular data and analyses

Taxon sampling

Three Arteminae outgroup taxa, two specimens of *Pholcophora americana* Banks, 1896, and seven further species of Ninetinae were taken from Eberle *et al.* (2018). To this, we added three further specimens of *P. americana*, four other species of *Pholcophora*, five species of *Tolteca*, and a second specimen of *Papiamenta levii* Huber, 2000. Table 1 lists the newly sequenced specimens. For details on previously sequenced specimens, see Eberle *et al.* (2018).

Gene sampling

For the taxa taken from Eberle *et al.* (2018) we used all available sequences (CO1 barcode, 12S, 16S, 18S, 28S, and H3). The CO1 barcode of one specimen of *Papiamenta levii* was combined with "S011 *Papiamenta MRAC639* MRAC640" from Eberle *et al.* (2018), since they actually came from the same specimen. For all newly added taxa, we sequenced the CO1 barcode only. In total, there were 69 sequences and 27 specimens.

Table 1. Geographic origins of newly sequenced specimens, sorted by code.

Code	Genus	Species	Vial	Country	Admin.	Locality	Lat.	Long.	CO1
N051	*Pholcophora*	*americana*	G090	USA	Idaho	Custer Co., Salmon-Challis Nat. Forest	44.2775	-114.4078	ON970474
N052	*Pholcophora*	*americana*	G091	USA	Oregon	Josephine Co., Siskiyou Nat. Forest	42.3370	-123.6095	ON970475
N057	*Pholcophora*	*mazatlan*	Mex209	Mexico	Guerrero	~2 km N of Mazatlán	17.4567	-99.4740	ON970476
N059	*Tolteca*	*huahua*	Mex229	Mexico	Michoacán	~4 km W of Huahua	18.1972	-103.0449	ON970481
N061	*Tolteca*	*manzanillo*	Mex232	Mexico	Colima	~17 km E of Manzanillo	19.0115	-104.1382	ON970482
N063	*Tolteca*	*jalisco*	Mex241	Mexico	Jalisco	N of La Quemada, 'site 2'	21.1922	-104.0975	ON970483
N064	*Tolteca*	*hesperia*	Mex253	Mexico	Sinaloa	~3 km S of Rosario	22.9584	-105.8490	ON970484
N065	*Pholcophora*	*texana*	Mex341	Mexico	Hidalgo	~2.5 km SW of Jacala	20.9948	-99.2138	ON970477
N066	*Pholcophora*	*tehuacan*	Mex353	Mexico	Puebla	SE of Tehuacan, N of Calapa bridge	18.1652	-97.2605	ON970478
N067	*Pholcophora*	*Mex354*	Mex354	Mexico	Puebla	SE of Tehuacan, N of Calapa bridge	18.1652	-97.2605	ON970479
N068	*Tolteca*	*oaxaca*	Mex362	Mexico	Oaxaca	~3 km N of San Pedro Totolapa	16.6976	-96.3180	ON970485
N069	*Tolteca*	*oaxaca*	Mex368	Mexico	Oaxaca	~17 km NW of Tehuantepec	16.3919	-95.3865	ON970486
N070	*Papiamenta*	*levii*	MRAC639	Curaçao		near San Juan, Manzalina beach	12.2450	-69.1050	ON970473
N071	*Papiamenta*	*levii*	MRAC640	Curaçao		near San Juan, Manzalina beach	12.2450	-69.1050	ON970487
N085	*Pholcophora*	*americana*	USA16	USA	Colorado	Lookout Mountain near Golden	39.7300	-105.2400	ON970480

DNA extraction, amplification and sequencing

One to 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.* 2000). CO1 primers used were LCO1490-JJ and HCO2198-JJ (Astrin *et al.* 2016; primer versions JJ2 served as backup), but with a different tag sequence (from Srivathsan *et al.* 2021) of 13 bp length at the 5'-ends of forward and reverse primers, respectively. The 20 µl reaction volume consisted of 5 µl H_2O, 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) GridON platform.

DNA sequence alignment and editing

The newly sequenced CO1 barcodes were then assembled using the ONTbarcoder (Srivathsan *et al.* 2021) pipeline. Taxonomic assignments of the assembled sequences were checked by: (1) blasting 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)

For the protein-coding genes CO1 and H3, DNA sequences were translated into protein sequences using BioPython (ver. 1.78) (Cock *et al.* 2009) with invertebrate mitochondrial genetic code and standard genetic code, respectively. 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 alignments of rRNA genes (12S, 16S, 18S, and 28S) were constructed based on secondary structure information using the mafft-xinsi algorithm in MAFFT (ver. 7.487) (Katoh & Standley 2013) and MXSCARNA (Tabei *et al.* 2008). Poorly aligned regions in the MSAs were then trimmed with Gblocks (ver. 0.91b) (Talavera & Castresana 2007) (-b5 = h), TrimAl (ver. 1.4.rev15) (Capella-Gutiérrez *et al.* 2009) (-automated 1) and ClipKIT (ver. 1.1.3) (Steenwyk *et al.* 2020), respectively. In the ClipKIT program, we used different trimming strategies (-modes gappy, kpi, kpic, kpic-gappy, kpic-smart-gap, kpi-gappy, kpi-smart-gap, smart-gap).

Phylogenetic inference

Maximum-likelihood trees were constructed based on concatenated alignments using IQ-TREE (ver. 2.1.3) (Minh *et al.* 2020). We did both an unpartitioned analysis (i.e., the whole concatenated MSA shares one evolutionary model) and a partitioned (by locus) analysis on each concatenated MSA. To overcome local optima during heuristics, we performed 10 independent IQ-TREE runs (-runs 10), with a smaller perturbation strength (-pers 0.2) and larger number of stop iterations (-nstop 500). Branch supports were evaluated with 2000 ultrafast bootstrap (UFBoot) (Minh *et al.* 2013) with the risk of potential model violations considered (-B 2000 -bnni). SH-aLRT branch test (Guindon *et al.* 2010) was performed using 2000 bootstrap replicates (-alrt 2000). Best-fitting substitution models were automatically determined by the ModelFinder algorithm (Kalyaanamoorthy *et al.* 2017) in IQ-TREE. Tree visualizations were finished with iTOL (Letunic & Bork 2021).

Preparation of chromosome slides and their evaluation

Three adult males of *Tolteca hesperia* (Gertsch, 1982) from Rosario (Mexico, Sinaloa), three adult males of *T. oaxaca* Huber sp. nov. from San Pedro Totolapa (Mexico, Oaxaca), and two adult males

of *T. oaxaca* from Tehuantepec (Mexico, Oaxaca) were used for the preparation of chromosomes (see Material examined sections of the respective species for detailed collection data). Voucher specimens are deposited at the Zoological Research Museum Alexander Koenig (Bonn, Germany). Chromosome preparations were obtained from testes. These organs contained meiotic cells except for a few mitotic cells and premeiotic interphases in *T. oaxaca* sp. nov.

Chromosome slides were produced by the spreading technique described in Ávila Herrera *et al.* (2021). Slides were analysed with an Olympus BX 50 microscope equipped with a DP 71 CCD camera. Several metaphases II were used to determine the relative chromosome length (RCL) and chromosome morphology. In *T. hesperia*, plates containing both sister metaphases II were available for evaluation. In *T. oaxaca* sp. nov., only single metaphase II cells were found. Relative chromosome length was estimated as the percentage of the total chromosome length (TCL) of the haploid set. This set also included the sex chromosomes X_1, X_2, and Y. Chromosome morphology was based on the position of the centromere (Levan *et al.* 1964), which was calculated as the ratio of the longer and shorter chromosome arms.

Following the analysis with a light microscope, and after the removal of immersion oil and Giemsa stain, preparations were used for the detection of nucleolus organizer regions (NORs) with a biotin labelled 18S rDNA probe from the haplogyne spider *Dysdera erythrina* (Walckenaer, 1802) using fluorescence in situ hybridization (FISH). The technique used is described in detail in Forman *et al.* (2013); the probe is specified in Ávila Herrera *et al.* (2021). The probe was detected by streptavidin-Cy3, with amplification of the signal (biotinylated antistreptavidin, streptavidin-Cy3). Chromosomes were counterstained by DAPI. Selected chromosome plates were photographed with an Olympus IX81 microscope equipped with an ORCA-AG CCD camera (Hamamatsu). Images were pseudocoloured (red for Cy3, blue for DAPI) and superimposed with Cell^R software (Olympus Soft Imaging Solutions).

Environmental niche similarity and equivalency

The results of the phylogenetic analyses allowed the proposition of biogeographic hypotheses concerning the environmental niches occupied by representatives of the North American-Caribbean clade. We aimed to describe and compare the environmental niches occupied by six different clades or groups of species: (1) *Pholcophora americana* only; (2) Caribbean clade (i.e., *Papiamenta* and Caribbean species of '*Pholcophora*'); (3) Mexican *Pholcophora* (includes species known mainly from Mexico, with one species ranging into southern Texas); (4) Non-Caribbean ('true') *Pholcophora* (i.e., groups 1 + 3); (5) *Papiamenta*; and (6) *Tolteca*. The analyses were based on the null expectation of a high similarity and equivalency among them, corroborating the niche conservatism previously shown for Ninetinae in general (Huber *et al.* 2023). We performed tests for niche overlap (Schoener's overlap 'D' metric; Schoener 1970), similarity, and equivalency (both described in detail in Warren *et al.* 2008) by making pairwise comparisons among the groups. These analyses were implemented using functions available in the R package 'ecospat' (Di Cola *et al.* 2017). The analyses did not consider using Caribbean '*Pholcophora*' as an independent group, as the used functions require a minimum of five sites where the taxa occur (only four are known in this group). Three pairwise comparisons (Caribbean clade vs *Papiamenta*; non-Caribbean *Pholcophora* vs Mexican *Pholcophora*; non-Caribbean *Pholcophora* vs *P. americana*) include several duplicate occurrences (i.e., same occurrence used in both compared groups). In these comparisons, a high niche overlap is expected, and, if observed, potentially artificial. However, the use of pairwise comparisons seems to be the only way to allow the assessment of niche variation within the Caribbean (owing to the low number of occurrences in this region) and between the Caribbean taxa and other compared groups.

To run these analyses, we defined a background area as a 500 km radius buffer around the sampling points of each of the six analysed groups. This buffer is subjective, but compared to other studies, it seems neither too conservative (cf. 800 km in Cuervo *et al.* 2021) nor exaggerated (cf. 33 km in

Herrando-Moraira *et al.* 2019; 111 km in Silva *et al.* 2016). The buffer was filled by a 0.5 side-by-side degree hexagon grid, and further clipped to country borders. At each hexagon, up to ten random points were created, with a distance of at least 1 km from each other. This procedure aimed to provide a more homogeneous distribution of random points through the area to estimate the available environmental niche for each group of taxa. For each of these points, we extracted the values for 21 predictive variables, including the 19 climatic layers of the WorldClim 2 database (Fick & Hijmans 2017), the mean tree density (Crowther *et al.* 2015) and the mean canopy height (Simard *et al.* 2011), the latter two at a 1 km^2 scale.

The 21 predictive variables were used in a principal component analysis calibrated on the entire environmental space of the study area, including species occurrences. This analysis, the so-called PCA-env (as described by Broennimann *et al.* 2012), was carried out to provide a kernel density of the environmental niche occupied by each taxon, based on their sites of occurrences. Then, the niche overlap, equivalency, and similarity tests were performed, each with 100 replicates. The D metric for niche overlap ranges from 0 (no overlap) to 1 (complete overlap) (Broennimann *et al.* 2012). Equivalency and similarity analyses compare the observed environmental niche overlap against null models simulated by randomly reallocating the occurrence records between distribution ranges (for the equivalency tests); or by randomly shifting the niches within the available conditions of the study area (for the similarity tests) (Broennimann *et al.* 2012; Di Cola *et al.* 2017; Hazzi & Hormiga 2021). As we aimed to test for niche conservatism between sister taxa, the parameter 'overlap.alternative' was set to 'higher' (i.e., the niche overlap is more equivalent/similar than random), and 'rand.type' was set to '1' (i.e., there is no assumption about a reference niche, and the niches of both groups can be simultaneously shifted), following recommendations from Di Cola *et al.* (2017).

Building on the results of the previous analyses, we further explored the microhabitat occupied by each taxon by comparing the altitudes of the records of *P. americana*, Mexican *Pholcophora*, *Tolteca*, and the Caribbean clade. The altitude was not used as a predictor in the previous approaches as it would result in a tautological variable, owing to its direct effect on temperature and precipitation (see Hof *et al.* 2012), detailed in the climatic variables taken from WorldClim. To compare the altitude occupied by each taxon, we performed a generalized linear model with quasi-poisson distribution of errors, using base R functions. This analysis was preferred over a poisson distribution owing to overdispersion issues, checked using the function 'rdiagnostic' from the R package 'RT4Bio' (Reis *et al.* 2015). Post hoc contrast analyses (see Crawley 2012) were performed using the 'coms' function from the R package 'RT4Bio' (Reis *et al.* 2015). The elevation data was taken from the WorldClim 2 database (Fick & Hijmans 2017) and the values were extracted using the R package 'raster' (Hijmans 2022).

Results

Molecular data

All unpartitioned analyses using the ClipKIT trimming strategies consistently recovered a clade consisting of 'true' (North American) *Pholcophora*, *Tolteca*, two undescribed Caribbean species tentatively assigned to *Pholcophora*, and the Caribbean (Curaçao) genus *Papiamenta* (Fig. 1; Supp. file 1: Fig. S76). The support for this clade varied widely (SH-aLRT supports: 25–90). Since this clade is also strongly supported by preliminary analyses of UCE data (G. Meng, L. Podsiadlowski, B.A. Huber, unpubl. data), we chose a ClipKIT tree for Figure 1 and did not further consider the TrimAI and Gblocks trees (in which this clade was not recovered). For the same reason we also rejected the trees resulting from partitioned analyses: in all of them (except when using untrimmed sequences), this North American-Caribbean clade was not recovered. In addition, unpartitioned analyses recovered the same interspecific relationships within *Tolteca* as the analysis of UCE data (see below) while the partitioned analysis did not. A summary tree showing these alternative topologies is shown in Supporting Information (Supp. file 1: Fig. S77).

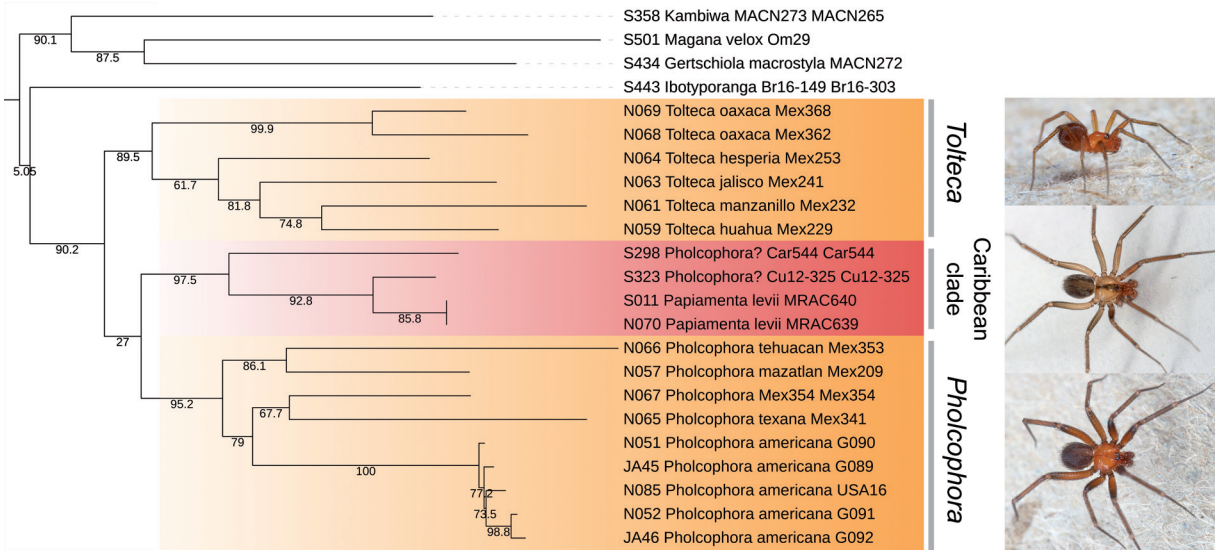

Fig. 1. Relationships of *Pholcophora* Banks, 1896 and *Tolteca* Huber, 2000 derived from analysis of molecular data using IQ-Tree and the ClipKIT gappy trimming strategy. Newly generated CO1 sequences (codes starting with N) were combined with data from Eberle *et al.* (2018) (all other codes). Numbers on the branches are SH-aLRT supports (%). The tree shows only the ingroups and the Ninetinae outgroups. Clade colours are as in Figs 2 and 35. For the complete tree, and for clade support using different alignment strategies, see Supp. file 1: Fig. S76. Photos on the right from top to bottom: *Tolteca manzanillo* Huber sp. nov.; *Papiamenta savonet* Huber, 2000; *Pholcophora papanoa* Huber sp. nov.

Within this North American-Caribbean clade, there was consistently reasonable to high support for *Tolteca* (unpartitioned analysis: 84–90; partitioned analysis: 78–81), for 'true' *Pholcophora* (unpartitioned analysis: 91–95; partitioned analysis: 76–81), and for a Caribbean clade consisting of *Papiamenta* and Caribbean '*Pholcophora*' (unpartitioned analysis: 97–98; partitioned analysis: 90–92). All analyses recovered a sister group relationship between 'true' *Pholcophora* and the Caribbean clade, but partly with low support (unpartitioned analysis: 27–80; partitioned analysis: 86–90). For further details, see Relationships sections in the genus descriptions below.

Taxonomy

Class Arachnida Cuvier, 1812
Order Araneae Clerck, 1757
Family Pholcidae C.L. Koch, 1850
Subfamily Ninetinae Simon, 1890

Genus ***Pholcophora*** Banks, 1896

Pholcophora Banks, 1896: 57. Type species: *P. americana* Banks, 1896.

Pholcophora – Gertsch 1971: 76; 1977: 112; 1982: 96. — Huber 2000: 113.

Diagnosis

Easily distinguished from only other North American Ninetinae genus *Tolteca* by strong male cheliceral apophyses originating proximally (Figs 5A–B, 10A–B; in *Tolteca* small and originating distally); also by presence of stridulatory ridges on male chelicerae; most species (except *P. tehuacan* Huber sp. nov.) also

by larger size (body length ~1.7–3.1; in *Tolteca* ~1.1–1.4) and longer legs (tibia 1 > 1.0, in *Tolteca* < 0.7); from most species of *Tolteca* also by absence of knob-shaped structure between epigynum and pedicel (also absent in *Tolteca sinnombre* Huber sp. nov.). From other geographically close genera (*Papiamenta*, *Galapa*) also by simple rod-shaped procursus (Figs 5C–E, 10C–E; much shorter in *Papiamenta*; with dorsal process in *Galapa*); by presence of humps on male sternum (absent in *Papiamenta*); and by unmodified male cheliceral fangs (with processes in *Galapa*).

Description

Male

Measurements. Total body length 1.2–3.1, carapace width 0.55–1.40. Legs relatively short, tibia 1: 0.65–1.85, i.e., 1.2–2.0 × carapace width; tibia 1 L/d 8–16; tibia 2 much shorter than tibia 4 (tibia 2 / tibia 4: 0.75–0.85).

Colour. Live specimens (Fig. 3) ochre to brown, prosoma sometimes reddish (which is lost in ethanol); carapace monochromous, sometimes with indistinct darker median Y-mark; abdomen colour slightly variable, usually monochromous, sometimes with indistinct dorsal marks (bluish in ethanol); legs without dark or light bands, femora sometimes distally darkened.

Body. Ocular area barely raised (cf. Fig. 8A), eight eyes, AME relatively large, diameter 20–60 μm, 45–75% of PME diameter; carapace with low and indistinct thoracic groove (cf. Figs 8A, 13A). Clypeus unmodified but sometimes slightly more protruding than in female. Sternum wider than long, with pair of distinct anterior processes near leg coxae 1. Abdomen globular; gonopore with four epiandrous spigots arranged in two pairs (Fig. 29C; examined: *P. americana* Banks, 1896; *P. tehuacan* sp. nov.); ALS with seven spigots each (cf. Figs 8C, 29G): one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (one of which is unusually large); PMS with two short, pointed spigots; PLS without spigots.

Chelicerae. With one pair of large frontal apophyses (Figs 5A–B, 10A–B); with stridulatory files (Fig. 29A), distances between ridges ~2.0–3.8 μm, distances proximally often smaller than distally.

Palps. Coxa unmodified; trochanter barely modified (with indistinct or without ventral projection); femur proximally with retrolateral-ventral process and prolateral stridulatory pick (modified hair), distally widened but simple, slightly curved towards dorsal, in *P. texana* Gertsch, 1935 with distinctive brush of feathered hairs ventrally (Fig. 19A, C); femur-patella joints slightly shifted toward prolateral side; tibia globular, with two trichobothria; tibia-tarsus joints not shifted to one side; palpal tarsal organ raised, capsulate with small opening (Fig. 29E; diameter of opening ~1.5 μm – measured in *P. tehuacan* sp. nov. only); procursus simple and straight, without dorsal flap, not strongly elongated, often with semi-transparent distal element; genital bulb distally cone-shaped, with species-specific sclerotized and membranous elements.

Legs. Without spines and curved hairs; in some species with very short vertical hairs in higher than usual density on tibiae (only anterior tibiae or all tibiae) (length of hairs ~30 μm). Trichobothria in usual arrangement: three on each tibia (except tibia 1: prolateral trichobothrium absent), one on each metatarsus; slightly feathered (Figs 18F, 24E); length of dorsal trichobothrium on tibia 1: ~90 μm; retrolateral trichobothrium of tibia 1 in very distal position (at 50–65% of tibia length). Tarsus 1 with 5–8 pseudosegments, sometimes only distally fairly distinct; tarsus 4 distally with one comb-hair on prolateral side (cf. Figs 13H, 24H); leg tarsal organs very small, capsulate with small opening (cf. Fig. 8F–H; diameter of opening ~1.3–1.8 μm); three claws (cf. Figs 13G, 24G, 29H).

Female

In general (size, colour) similar to male but sternum without pair of anterior humps, leg tibia 1 with usual low number of short vertical hairs, and chelicerae without stridulatory ridges; legs either slightly shorter than in males or of same length (only *P. americana* with reasonable sample size: male/female tibia 1 length: 1.12). Spinnerets, comb-hairs, and leg tarsal organs as in male; palpal tarsal organ slightly less strongly raised (Figs 18E, 23H). Epigynum main (anterior) plate large, rectangular to oval, sometimes posteriorly excavated, weakly protruding in lateral view; posterior plate also large, short but wide, median part sometimes separated from lateral parts by whitish band. Without knob-shaped structure between epigynum and pedicel. Internal genitalia variable: either without sacs (Fig. 33A–H; *P. americana* Banks, 1896; *P. mazatlan* Huber sp. nov.; *P. papanoa* Huber sp. nov.; *P.* "Mex354") or with pair of distinct membranous sacs (Fig. 33I–L; *P. texana* Gertsch, 1935; *P. tehuacan* sp. nov.); in Caribbean '*Pholcophora*' with single median tube-like sac (Fig. 33M–N; *P. bahama* Gertsch, 1982; *P.* "Car544"; *P.* "Cu12-325"); with pair of distinct transversal sclerites; apparently without pore plates (possibly with very indistinct pair of pore plates near median line, indicated in Fig. 33E–F, J–L).

Relationships

In the molecular analysis of Eberle *et al.* (2018), the type species *Pholcophora americana* was part of a North American-Caribbean clade of Ninetinae, together with "*Pholcophora*? Car544", an unidentified Cuban species ("Gen. Cu12-325"; treated below as "*Pholcophora*? Cu12-325"), and the genus *Papiamenta*. The genus *Tolteca* was not included.

Our new molecular analyses mostly support this North American-Caribbean clade (Fig. 1; see also general results of molecular analyses above), and they also support the idea that Caribbean '*Pholcophora*' are not true *Pholcophora* but more closely related with the Caribbean genus *Papiamenta*. Our analyses suggest a sister group relationship between true *Pholcophora* and the Caribbean clade (*Papiamenta* + Caribbean '*Pholcophora*'). By contrast, preliminary analyses of UCE data (G. Meng, L. Podsiadlowski, B.A. Huber, unpubl. data) suggest a sister-group relationship between true *Pholcophora* and *Tolteca*. Since we consider these UCE results more reliable, we will not further discuss relationships here, except for two species not yet included in any molecular dataset: *Pholcophora maria* Gertsch, 1977 from Yucatán, and *Pholcophora bahama* Gertsch, 1982 from the Bahamas. Judging from the female internal genitalia (compare Huber 2000: fig. 1357 with Fig. 28B), we hypothesize that *Pholcophora maria* is closely related with the newly described *P. tehuacan* sp. nov. It is thus probably a true *Pholcophora*. *Pholcophora bahama* resembles "*Pholcophora*? Car544" in having a median tube-like sac in the female internal genitalia (compare Huber 2000: fig. 1356 with Fig. 31G). It is thus probably not a true *Pholcophora* but part of the Caribbean clade.

Distribution

The genus appears limited to North America (Fig. 2); Caribbean species (including Dominican amber fossils) currently placed in *Pholcophora* are probably misplaced (see Relationships above). Of the seven North American named species, six are largely or entirely restricted to Mexico.

Natural history

Gertsch (1982) briefly characterized *Pholcophora* spiders as living "reclusive lives under ground objects, in leaf and plant detritus, and in soil openings and caves", and mentioned that they "spin web tangles in dark spaces and remain there in close contact with such webs as permanent residents, often in informal colonies". Our newly collected species and specimens fit this description. Most were collected by turning rocks or sifting litter in shady spots of low and dry forests (Fig. 34). They usually shared the microhabitat with one or more other pholcids. In only one case we found two species of *Pholcophora* at a single locality; we never found *Pholcophora* to share a locality with *Tolteca*. Females carried their

flattened egg-sacs slightly under the prosoma (Fig. 3); eggs sacs contained ~6–30 eggs, each with a diameter of ~0.40–0.60 mm (Huber & Eberle 2021). Some females had a genital plug (cf. Fig. 16C).

Composition

The genus now includes 11 nominal species. Of these, seven occur in North America and are here considered to represent 'true' *Pholcophora*: *Pholcophora americana* Banks, 1896; *P. maria* Gertsch, 1977; *P. mazatlan* sp. nov.; *P. mexcala* Gertsch, 1982; *P. papanoa* sp. nov.; *P. tehuacan* sp. nov.; *P. texana* Gertsch, 1935. The Caribbean *P. bahama* Gertsch, 1982 is here considered to be misplaced (see Relationships above). All extant species are treated below except *P. bahama* and *P. mexcala* for which we have no new data [in 2019 we searched at four localities close to Mezcala (= "Mexcala") but could not find *P. mexcala*].

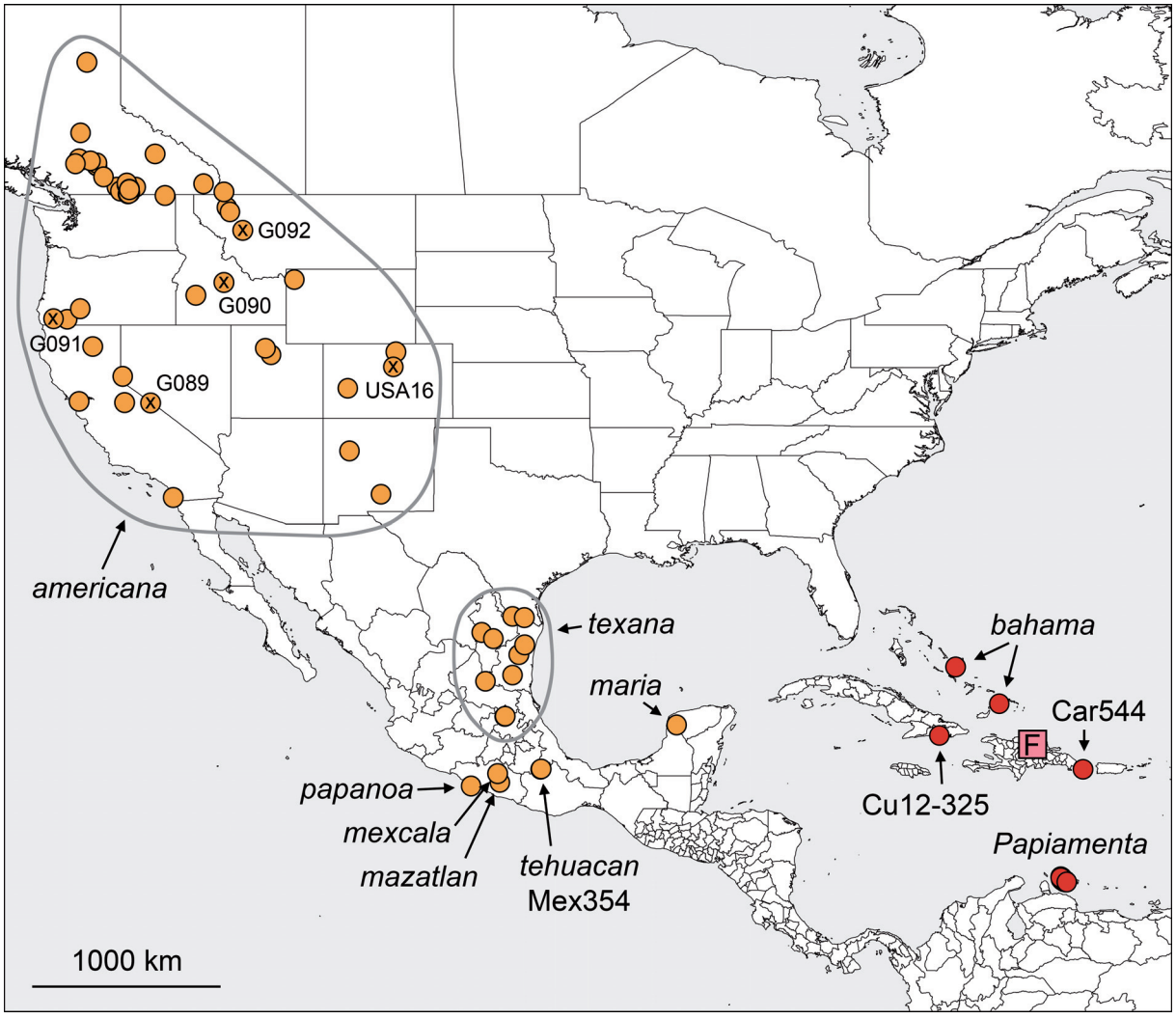

Fig. 2. Known distributions of 'true' *Pholcophora* Banks, 1896 (orange marks) and of presumably misplaced Caribbean '*Pholcophora*' and of *Papiamenta* Huber, 2000 (red marks). Dominican amber species currently placed in *Pholcophora* are represented by an "F" in a pink square. Our molecular data suggest that Caribbean '*Pholcophora*' are more closely related with the genus *Papiamenta* than with true *Pholcophora*. Barcoded specimens of *Pholcophora americana* Banks, 1896 are marked with an "x" and accompanied by the vial code (see Table 1 for details).

Three nominal species are only known from amber fossils originating from Hispaniola (Wunderlich 1988): *P. brevipes* Wunderlich, 1988; *P. gracilis* Wunderlich, 1988; and *P. longicornis* Wunderlich, 1988. We did not re-examine the amber specimens but judging from their geographic origin we speculate that the three species are part of the clade including Caribbean '*Pholcophora*' and *Papiamenta*. However, the three amber species fit the diagnosis above with respect to the strong male cheliceral apophyses originating proximally and the simple rod-shaped procursus. They are unusually small (but in this respect similar to the exceptionally small extant *P. tehuacan* sp. nov. and *P. maria*), and the original

Fig. 3. *Pholcophora* Banks, 1896, live specimens. **A**. *P. americana* Banks, 1896, male from USA, Colorado, near Golden. **B–E**. *P. mazatlan* Huber sp. nov., males and females with egg-sacs from Mexico, Guerrero, N of Mazatlán. **F–G**. *P. papanoa* Huber sp. nov., male and female from Mexico, Guerrero, S of Papanoa. **H–I**. *P. texana* Gertsch, 1935, male and female with egg-sac from Mexico, Hidalgo, SW of Jacala. **J–K**. *P. tehuacan* Huber sp. nov., male and female with egg-sac from Mexico, Puebla, SE of Tehuacan. **L**. *P.* "Mex354", female with egg-sac from Mexico, Puebla, SE of Tehuacan.

descriptions remain silent about male cheliceral stridulation and male sternal humps. The females of the three fossil species remain unknown.

Pholcophora americana Banks, 1896
Figs 3A, 4–8, 33A–B

Remark

For synonymy, type material, and redescription, see Huber (2000).

Diagnosis

Easily distinguished geographically by being the only representative of *Pholcophora* (and of Ninetinae) in the western USA and Canada (Fig. 2); morphologically distinguished from similar congeners (*P. mexcala*; *P. mazatlan* sp. nov.; *P. papanoa* sp. nov.) by shape of male cheliceral apophyses (Fig. 5A–B; directed towards frontal rather than upwards, without proximal humps, relatively short), by tip of procursus (Fig. 5C–E; semi-transparent process widening distally), and by epigynum (main epigynal plate posteriorly strongly indented, Fig. 6A, C).

Material examined (new records)

USA – **Colorado** • 3 ♀♀, in pure ethanol; Lookout Mountain near Golden, 'sites 1 & 2'; 39.73° N, 105.24° W; 2220–2230 m a.s.l.; 6 Jul. 2016; B.A. Huber leg.; one female used for SEM, two prosomata used for molecular work; ZFMK USA16 • 2 ♂♂, in pure ethanol; same collection data as for preceding; vouchers of Ávila Herrera *et al.* (2021); ZFMK Kra55–56. – **California** • 2 ♂♂, 5 ♀♀, 1 juv., in pure ethanol; Mono County, Inyo Nat. Forest; 37.80° N, 118.38° W; 15 Jun. 2003; P. Paquin and N. Dupérré leg.; under wood debris in pine forest; ZFMK G089 • 1 ♂, 1 ♀; Plumas County, Lassen National Forest, Warner Creek Campground; 40.3625° N, 121.3081° W; 1540 m a.s.l.; 18 May 2015; K. Schneider leg.; beaten from fallen pine cones; ZFMK Ar 23944. – **Idaho** • 1 ♀, in pure ethanol; Custer County,

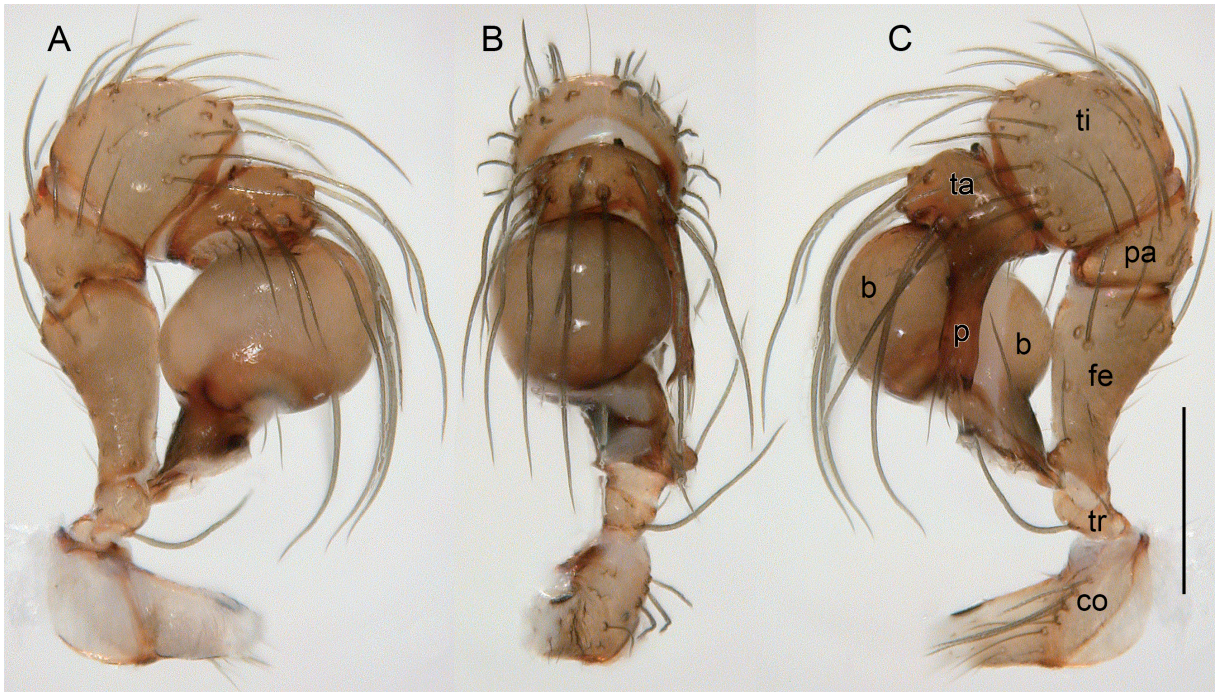

Fig. 4. *Pholcophora americana* Banks, 1896, male from USA, Colorado, near Golden (ZFMK Kra55). Left palp, prolateral, dorsal, and retrolateral views. Abbreviations: b = genital bulb; co = coxa; fe = femur; p = procursus; pa = patella; ta = tarsus; ti = tibia; tr = trochanter. Scale bar = 0.3 mm.

Salmon-Challis Nat. Forest, Kinnikinic Creek Road; 44.278° N, 114.408° W; 19 Sep. 2003; P. Paquin and D. Wytrykush leg.; scree under *Picea glauca* forest; ZFMK G090. – **Montana** • 1 ♂, 2 ♀♀, 1 juv., in pure ethanol; Missoula County, Lolo Nat. Forest, near Salmon Lake; 47.072° N, 113.384° W; 18 Sep. 2003; P. Paquin and D. Wytrykush leg.; under rocks, scree; ZFMK G092. – **Oregon** • 2 ♂♂, 2 ♀♀, 1 juv., in pure ethanol; Josephine County, Siskiyou Nat. Forest, Briggs Valley Road; 42.337° N, 123.610° W; 23 Sep. 2003; P. Paquin and D. Wytrykush leg.; ZFMK G091.

Description (amendments; see Huber 2000)

Male

Measurements of a male from Hat Creek, California: carapace width 0.95; tibia 1 length: 1.75; distance PME-PME 75 µm; diameter PME 80 µm; distance PME-ALE 30 µm; distance AME-AME 20 µm; diameter AME 60 µm; diameters of leg femora 0.20–0.23, of leg tibiae 0.11–0.12. Clypeus unmodified, clypeus rim to ALE 0.30. Chelicerae as in Fig. 5A–B; distances between cheliceral stridulatory ridges 2.5–2.7 µm. Procursus as in Fig. 5C–E, with distinctive transparent element distally; genital bulb as in

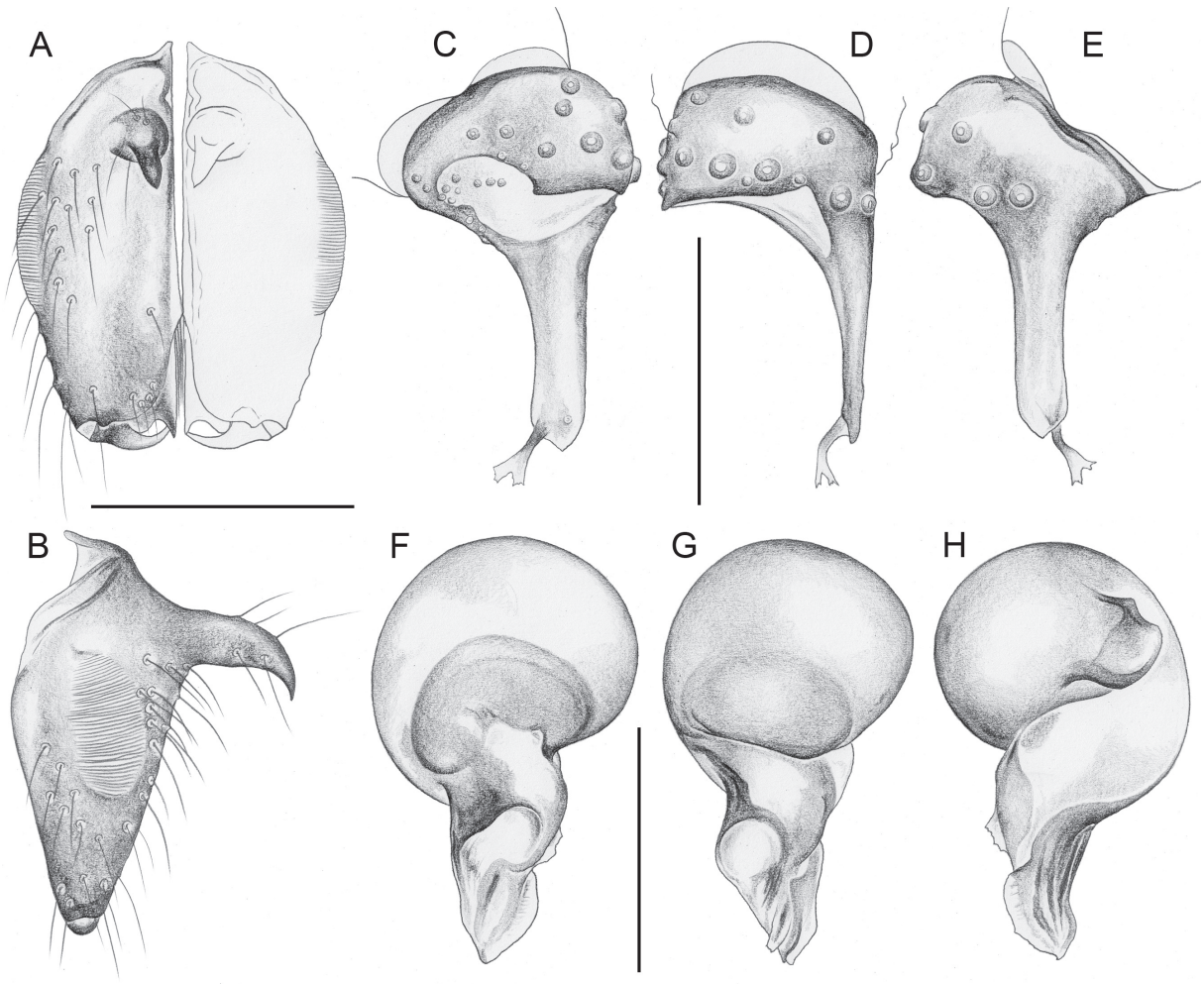

Fig. 5. *Pholcophora americana* Banks, 1896, males. **A–E**. From USA, Montana, Lolo Nat. Forest (ZFMK G092). **F–H**. From California, Inyo Nat. Forest (ZFMK G089). **A–B**. Chelicerae, frontal and lateral views. **C–E**. Left palpal tarsus and procursus, prolateral, dorsal, and retrolateral views. **F–H**. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.3 mm.

Fig. 5F–H. Legs with few vertical hairs; prolateral trichobothrium absent on tibia 1. Tibia 1 length in 14 males (incl. specimens measured in Huber 2000): 1.50–1.75 (mean 1.62).

Female

In general similar to male but sternum without pair of anterior humps, and chelicerae without stridulatory files. Tibia 1 in 15 females (incl. specimens measured in Huber 2000): 1.25–1.70 (mean 1.48). Epigynum and internal female genitalia as in Figs 6–7, apparently without median receptacle, without or with very small pore plates.

Distribution

Widely distributed in the western USA, ranging into SW Canada (British Columbia) (Fig. 2). The map in Fig. 2 includes many records from British Columbia that were first shown in a map in Bennett (2014: fig. 5). A list of locality names was later published online in the Checklist of the Spiders (Araneae)

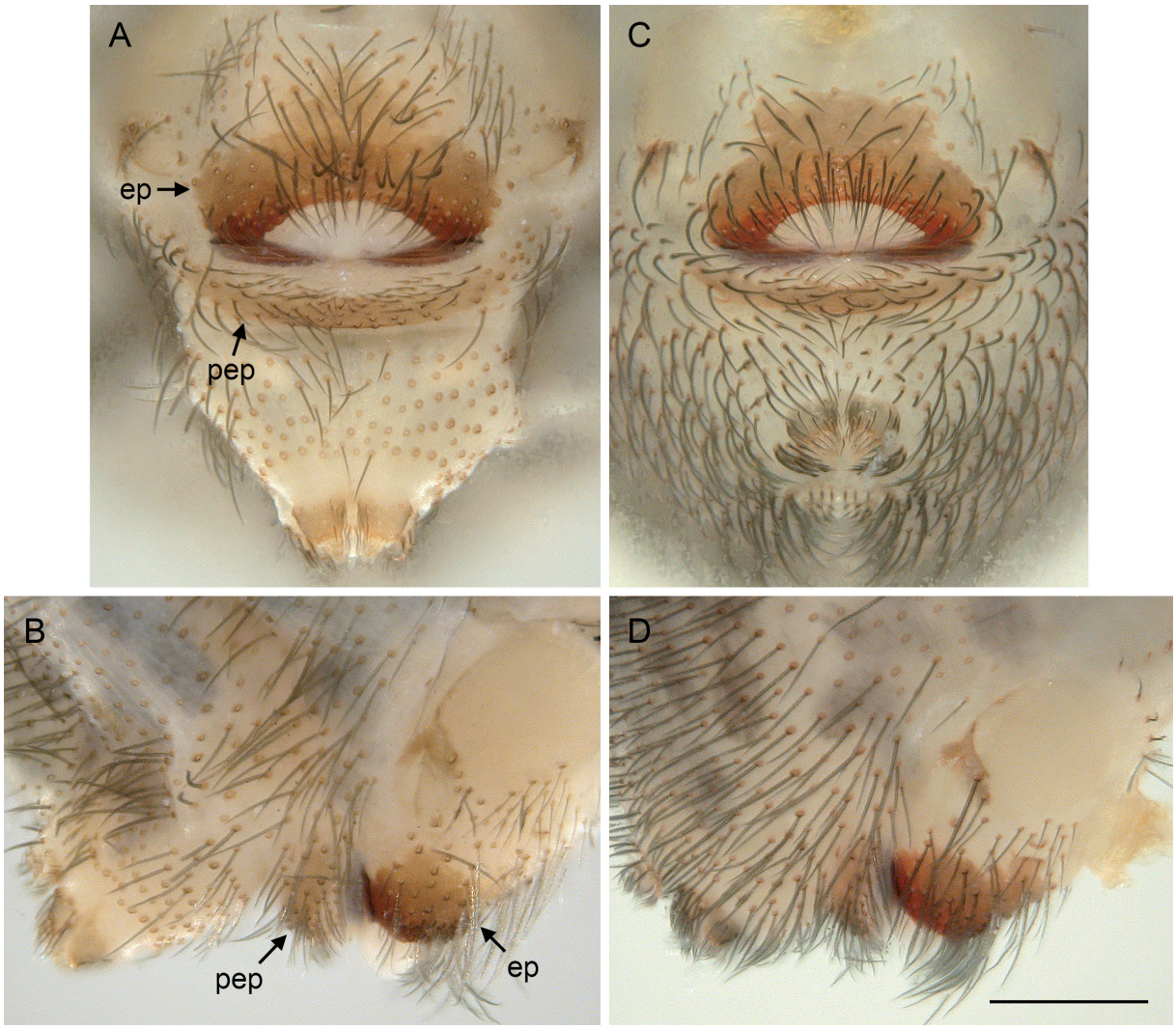

Fig. 6. *Pholcophora americana* Banks, 1896, females. **A–B**. From USA, California, Inyo Nat. Forest (ZFMK G089). **C–D**. From Colorado, near Golden (ZFMK USA16). Epigyna, ventral and lateral views. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bar = 0.3 mm (all at same scale).

of British Columbia (http://staff.royalbcmuseum.bc.ca/). The Canadian dots in Fig. 2 are based on coordinates of specimens digitized at the Royal British Columbia Museum that were kindly provided by C. Copley (pers. com. Feb. 2017).

Natural history

Surprisingly, nothing is known about the biology of this widespread spider beyond some basic habitat data taken from labels. It has usually been found under rocks, wood debris, and other objects on the ground, often in pine forests. The most northern records (British Columbia) suggest that this species tolerates very cold winters, with occasional temperatures below -10°C.

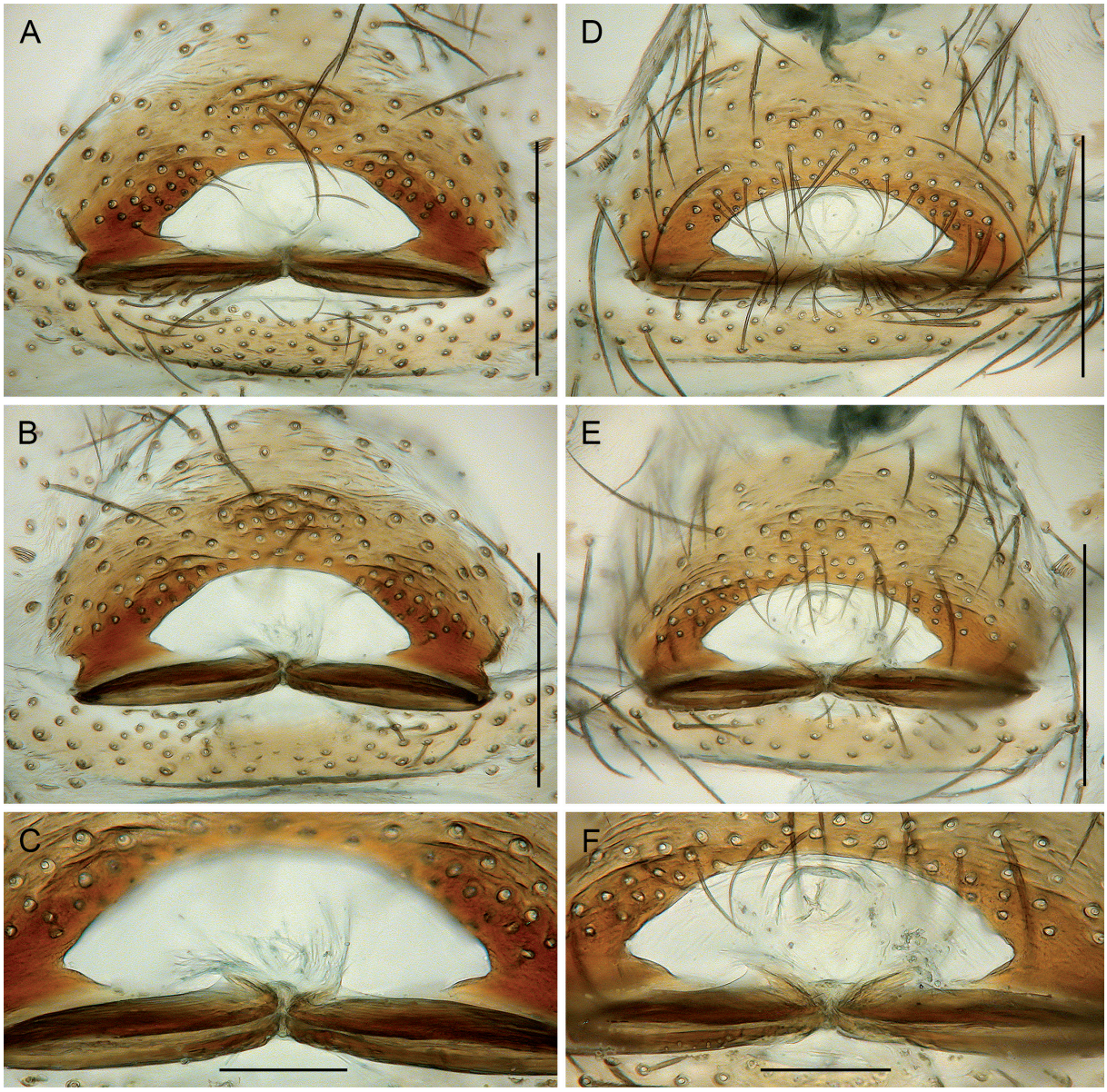

Fig. 7. *Pholcophora americana* Banks, 1896, cleared female genitalia. **A–C**. From USA, California, Inyo Nat. Forest (ZFMK G089). **D–F**. From Colorado, near Golden (ZFMK USA16). **A, D**. Ventral views. **B, E**. Dorsal views. **C, F**. Detail of median internal structures. Scale bars: A–B, D–E = 0.3 mm; C, F = 0.1 mm.

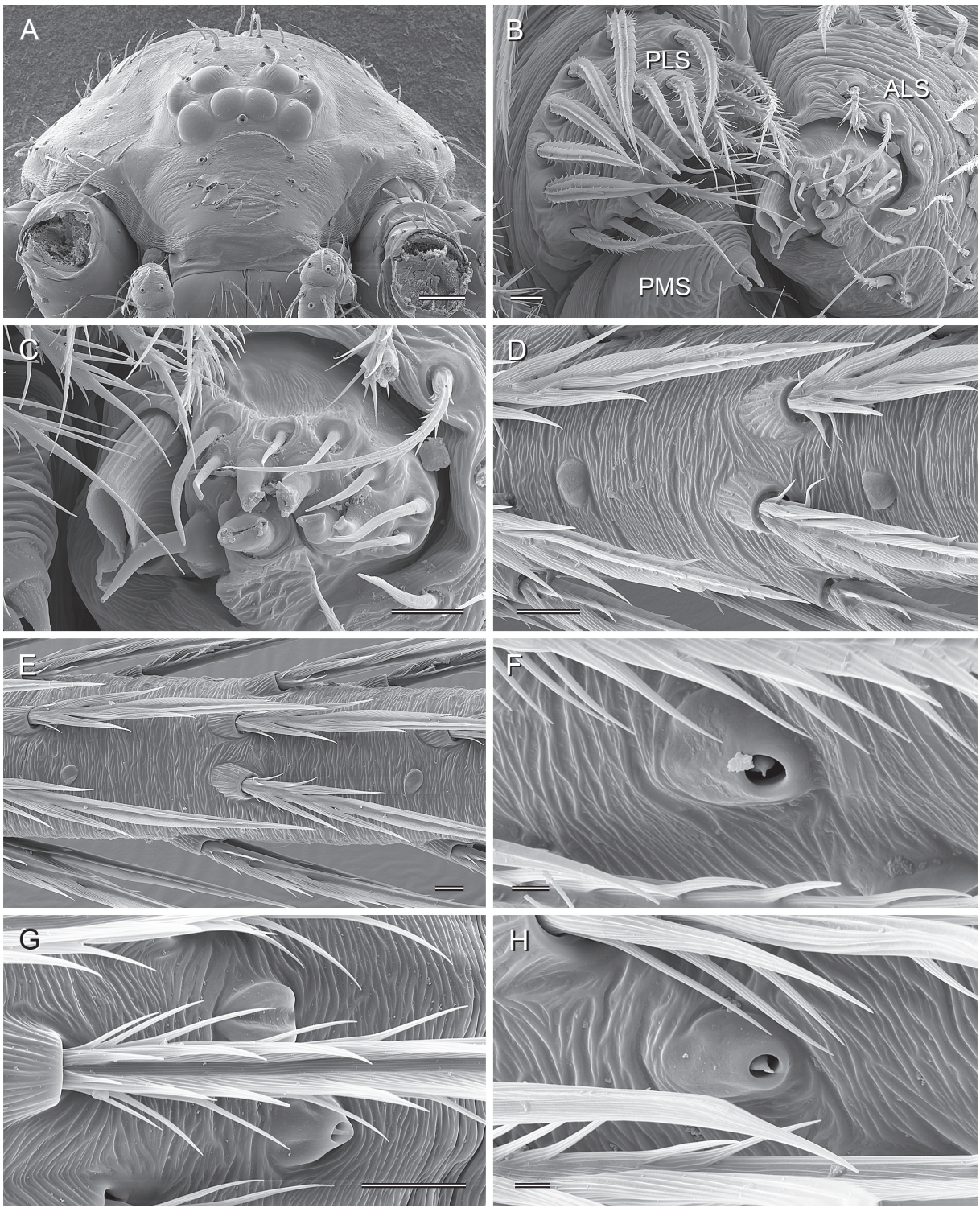

Fig. 8. *Pholcophora americana* Banks, 1896, female from USA, Colorado, near Golden (ZFMK USA16). **A**. Prosoma, frontal view. **B**. Right spinnerets. **C**. Anterior lateral spinneret. **D**. Detail of tibia 1. **E**. Detail of metatarsus 4. **F**. Tarsal organ on tarsus 1. **G**. Tarsal organ and slit sensillum on tarsus 3. **H**. Tarsal organ on tarsus 4. Scale bars: A = 100 µm; B–E, G = 10 µm; F, H = 2 µm.

Pholcophora mazatlan Huber sp. nov.
urn:lsid:zoobank.org:act:C787210E-FE17-42BD-AF00-7C5364558495
Figs 3B–E, 9–13, 33C–D

Diagnosis

Distinguished from similar congeners (*P. papanoa* sp. nov., *P. mexcala*, *P. americana*) by shape of male cheliceral apophyses (Fig. 10A–B; very long, directed upwards, without proximal humps) and by shape of male bulbal process (Fig. 10F–H; small dorsal process in very distal position; distinctive semi-transparent ventral flap). From very similar *P. papanoa* also by main element of procursus more gradually narrowing distally (Fig. 10E), by male cheliceral apophyses more strongly directed upwards, and by thinner male leg femora (0.18–0.20 vs 0.28–0.30). From *P. americana* also by tip of procursus (semi-transparent process not widening distally) and by shape of epigynum (Fig. 11A, C; main epigynal plate posteriorly straight).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Guerrero** • ♂; ~2 km N of Mazatlán; 17.4567° N, 99.4740° W; 1300 m a.s.l.; 3 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Paratypes

MEXICO – **Guerrero** • 1 ♀; same collection data as for holotype; ZFMK Ar 23943 • 1 ♂, 11 ♀♀; same collection data as for holotype; LATLAX.

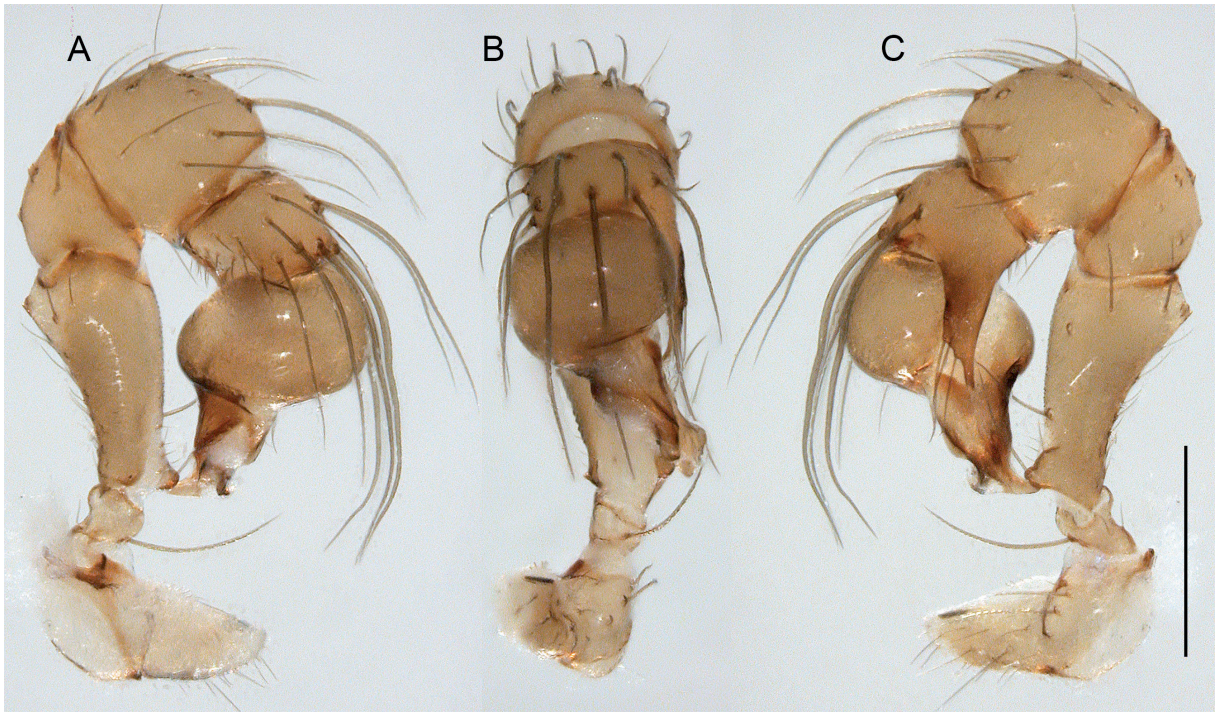

Fig. 9. *Pholcophora mazatlan* Huber sp. nov., male holotype from Mexico, Guerrero, N of Mazatlán (LATLAX). Left palp, prolateral, dorsal, and retrolateral views. Scale bar = 0.3 mm.

Other material examined

MEXICO – **Guerrero** • 3 ♀♀, in pure ethanol; same collection data as for holotype; one female used for SEM; ZFMK Mex209 • 3 ♀♀ abdomens, together with female paratype; same collection data as for holotype; prosomata used for molecular work; ZFMK Ar 23943.

Description

Male (holotype)

Measurements. Total body length 1.90, carapace width 0.80. Distance PME-PME 70 µm; diameter PME 60 µm; distance PME-ALE 30 µm; distance AME-AME 20 µm; diameter AME 30 µm. Leg 1: 4.55 (1.30 + 0.30 + 1.15 + 1.30 + 0.50), tibia 2: 1.00, tibia 3: 0.85, tibia 4: 1.25; tibia 1 L/d: 12; diameters of leg femora 0.18–0.20, of leg tibiae 0.10.

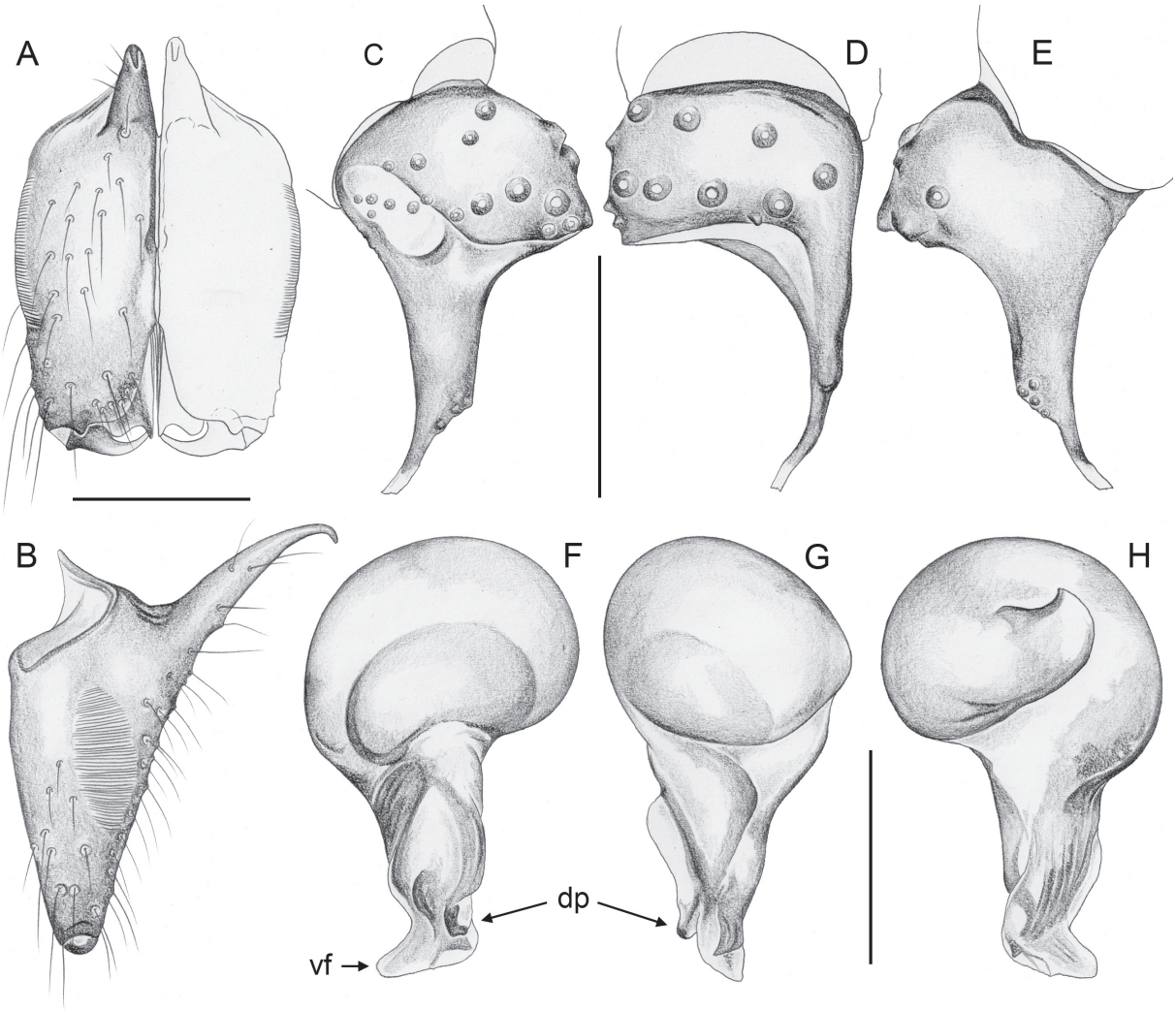

Fig. 10. *Pholcophora mazatlan* Huber sp. nov.; male holotype from Mexico, Guerrero, N of Mazatlán (LATLAX). **A–B**. Chelicerae, frontal and lateral views. **C–E**. Left palpal tarsus and procursus, prolateral, dorsal, and retrolateral views. **F–H**. Left genital bulb, prolateral, dorsal, and retrolateral views. Abbreviations: dp = dorsal process; vf = ventral flap. Scale bars = 0.2 mm.

Colour (in ethanol). Prosoma and legs ochre-yellow, carapace with indistinct Y-mark, legs without darker rings; abdomen grey with dark bluish internal marks; ventrally with ochre plate in front of gonopore.

Body (Fig. 3B–C). Ocular area barely raised. Carapace with distinct but shallow thoracic groove (cf. Fig. 13A). Clypeus unmodified, very short (clypeus rim to ALE: 0.22). Sternum slightly wider than long (0.56/0.46), oval (not narrow posteriorly), with pair of distinct anterior processes (~0.1 long) near coxae 1. Abdomen globular.

Chelicerae (Fig. 10A–B). With pair of long frontal apophyses; stridulatory files very fine, poorly visible in dissecting microscope; distances between cheliceral stridulatory ridges proximally 2.4 μm, distally 3.5 μm.

Palps (Fig. 9). Coxa unmodified; trochanter without process; femur proximally with retrolateral-ventral process and prolateral stridulatory pick, distally widened but simple, slightly curved towards dorsal; femur-patella joints slightly shifted toward prolateral side; tibia globular, with two trichobothria; tibia-

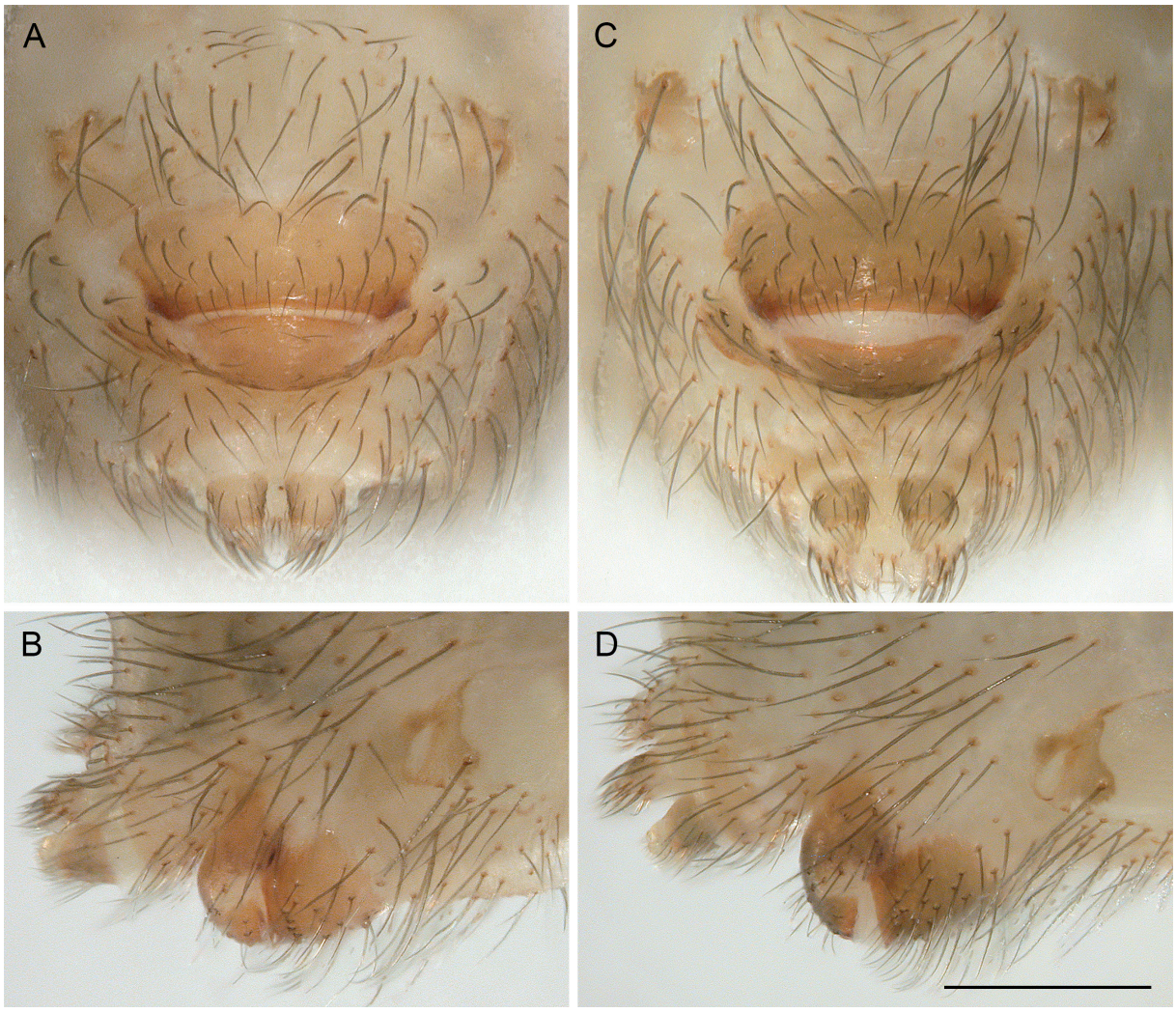

Fig. 11. *Pholcophora mazatlan* Huber sp. nov., females from Mexico, Guerrero, N of Mazatlán (ZFMK Ar 23943). Epigyna, ventral and lateral views. Scale bar = 0.3 mm (all at same scale).

tarsus joints not shifted to one side; procursus very simple (Fig. 10C–E), narrow distal part slightly bent towards prolateral, with semi-transparent tip; genital bulb with small dorsal process in very distal position, distally with distinctive semi-transparent ventral flap (Fig. 10F–H).

Legs. Without spines and curved hairs; with vertical hairs in two narrow dorsal bands proximally on tibiae 1 and 2 (length ~30 µm; length of dorsal trichobothrium on tibia 1: ~90 µm); retrolateral trichobothrium of tibia 1 at 64%; prolateral trichobothrium absent on tibia 1; tarsus 1 with ~7 pseudosegments, only distally 2–3 distinct.

Variation (male)
Tibia 1 in second male: 1.30.

Female
In general, similar to male (Fig. 3D–E) but sternum without pair of anterior humps, tibiae without higher than usual density of short vertical hairs, and chelicerae without stridulatory files. Tibia 1 in

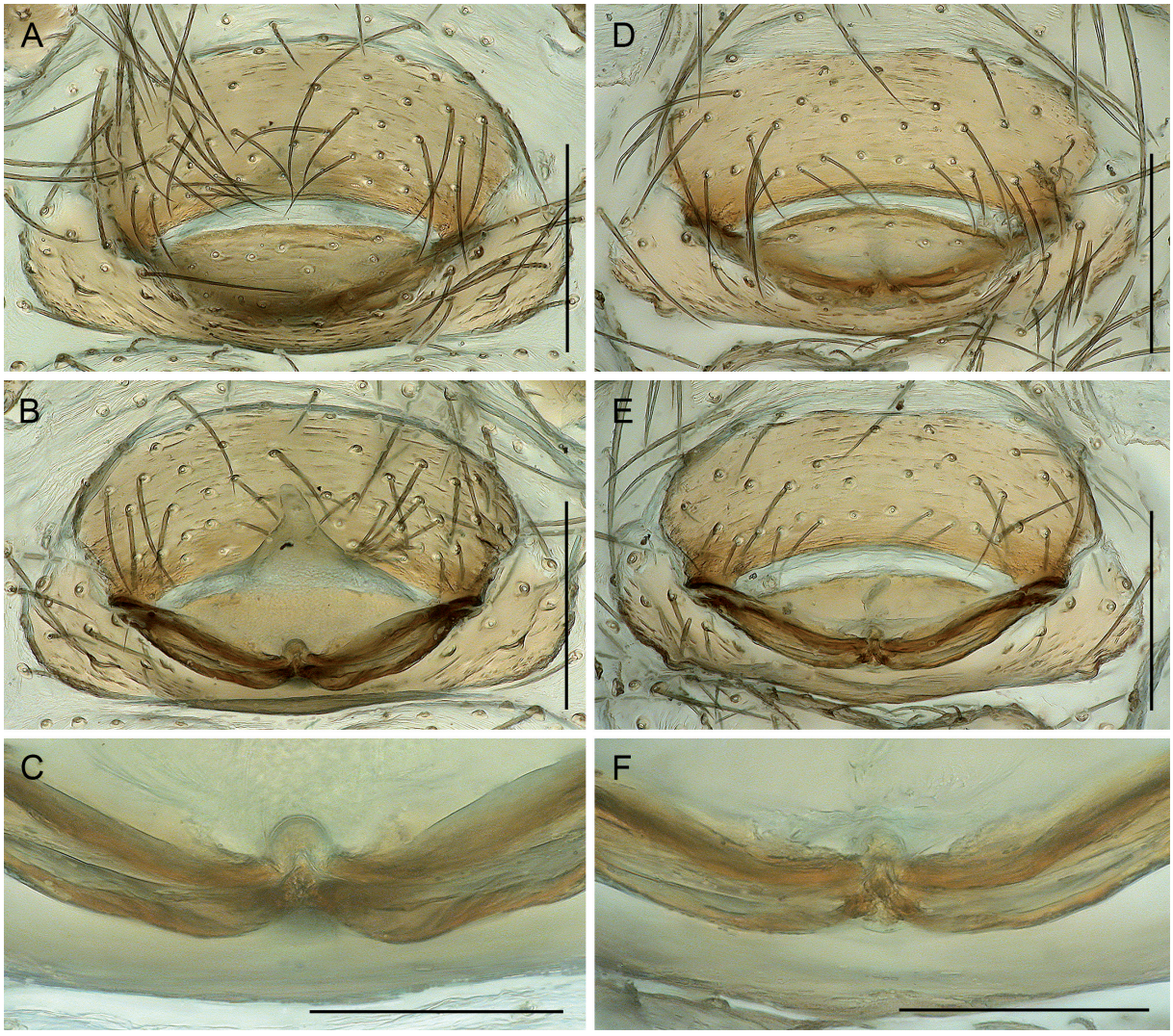

Fig. 12. *Pholcophora mazatlan* Huber sp. nov., females from Mexico, Guerrero, N of Mazatlán (ZFMK Ar 23943), cleared female genitalia. **A, D**. Ventral views. **B, E**. Dorsal views. **C, F**. Detail of median internal structures. Scale bars: A–B, D–E = 0.2 mm; C, F = 0.1 mm.

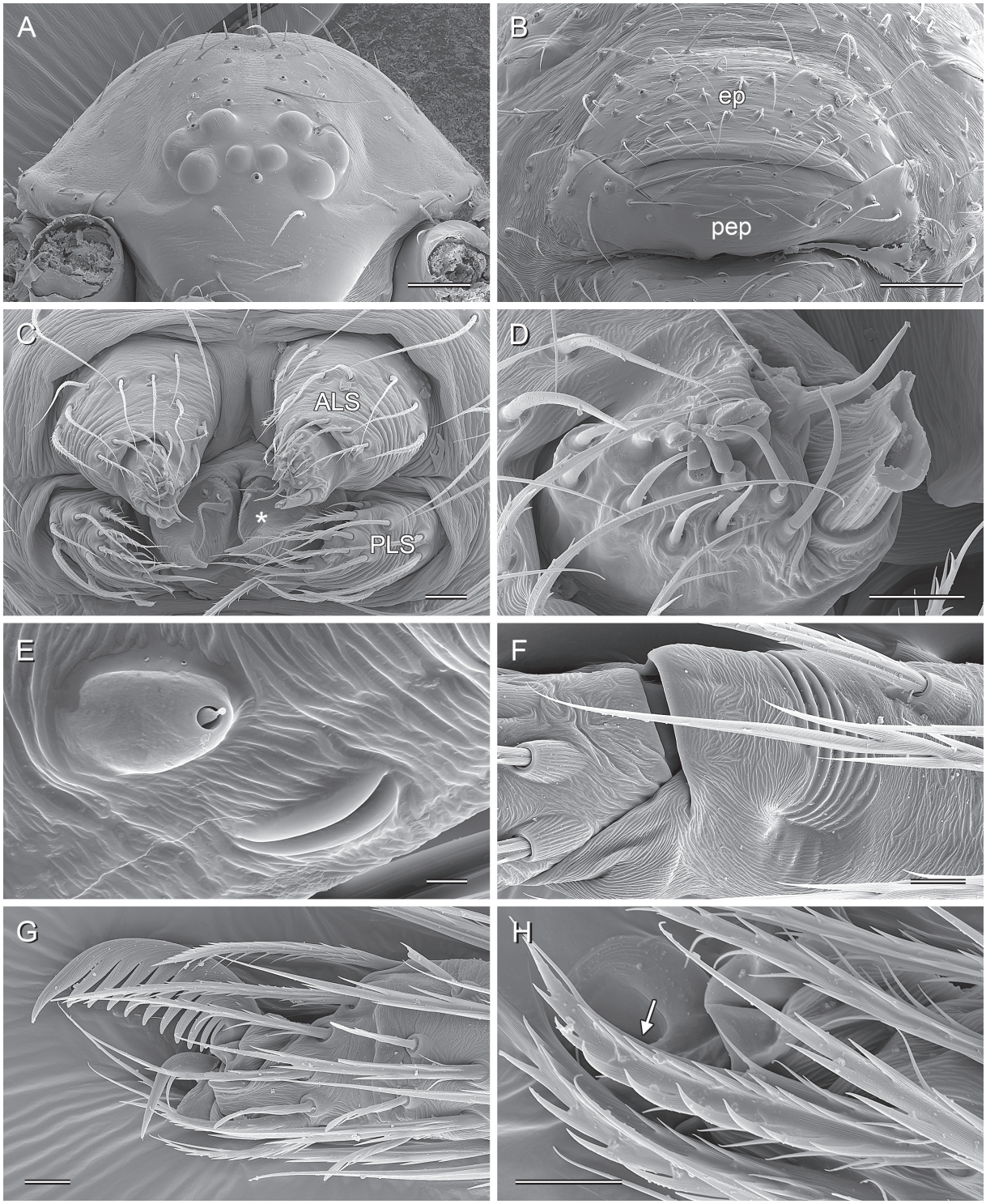

Fig. 13. *Pholcophora mazatlan* Huber sp. nov., female from Mexico, Guerrero, 2 km N of Mazatlán (ZFMK Mex209). **A**. Prosoma, frontal view. **B**. Epigynum, ventral view. **C**. Spinnerets; asterisk: PMS. **D**. Anterior lateral spinneret. **E**. Tarsal organ and slit sensillum on tarsus 3. **F**. Metatarsus-tarsus 1 joint with lyriform organ, dorsal view. **G**. Tip of right tarsus 3, prolateral view. **H**. Comb hair (arrow) on tarsus 4, prolateral view. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A–B = 100 μm; C = 20 μm; D, F–H = 10 μm; E = 2 μm.

11 females: 1.00–1.20 (mean 1.08). Epigynum (Figs 11, 13B) with simple anterior plate protruding in lateral view; posterior plate wide, median part separated anteriorly from lateral parts by pair of whitish areas. Internal genitalia (Fig. 12) very simple, apparently without or with small and indistinct median receptacle, without or with very small pore plates.

Distribution

Known from type locality only, in Mexico, Guerrero (Fig. 2).

Natural history

The spiders were found by turning rocks in a forested valley (Fig. 34A). They shared the microhabitat with at least four further species of Pholcidae (Modisiminae): two representatives of *Modisimus* Simon, 1893, one *Psilochorus* Simon, 1893, and one species of uncertain generic position.

Pholcophora papanoa Huber sp. nov.
urn:lsid:zoobank.org:act:C2E5858B-2822-4630-BCEC-D34864087C0A
Figs 3F–G, 14–18, 33E–F

Diagnosis

Distinguished from similar congeners (*P. mazatlan* sp. nov., *P. mexcala*, *P. americana*) by shape of male bulbal process (Fig. 15F–H; distinctive dorsal process, without ventral flap) and by shape of male cheliceral apophyses (Fig. 15A–B; long, directed upwards, without or with barely visible proximal humps); from very similar *P. mazatlan* also by main element of procursus more truncated (Fig. 15E), by male cheliceral apophyses less strongly directed upwards, and by thicker male leg femora (0.28–0.30 vs 0.18–0.20). From *P. americana* also by tip of procursus (semi-transparent process not widening distally) and by shape of epigynum (Fig. 16; main epigynal plate posteriorly straight).

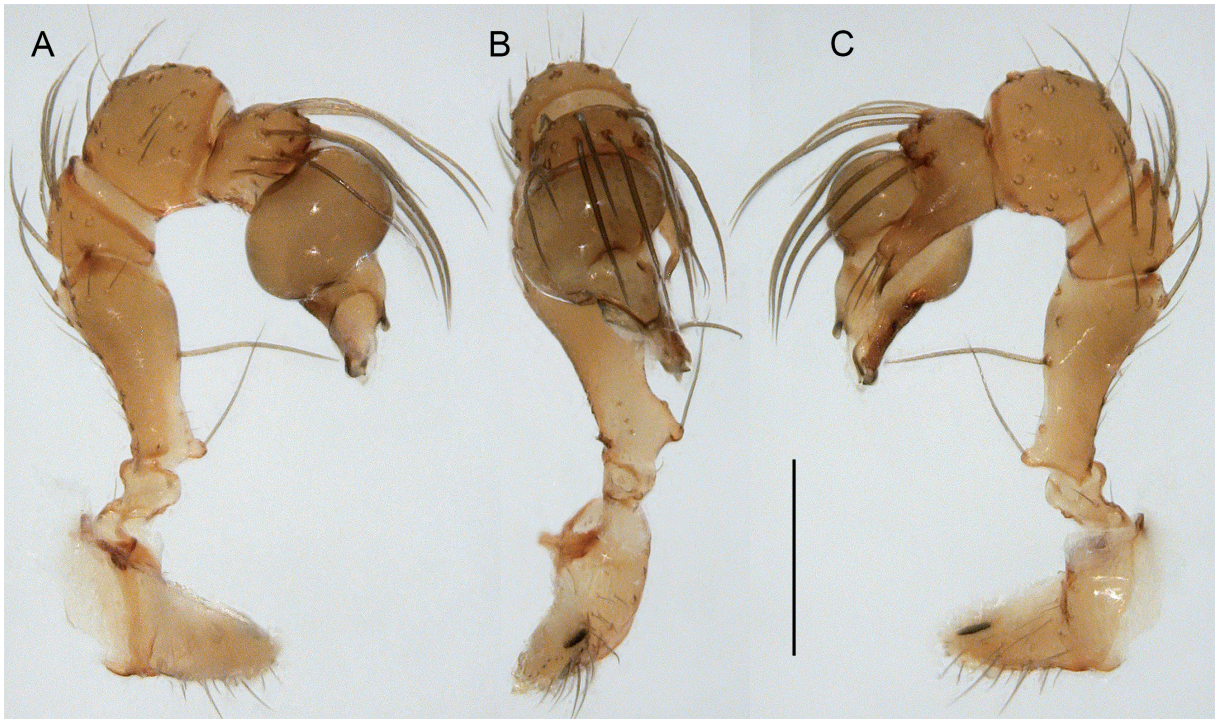

Fig. 14. *Pholcophora papanoa* Huber sp. nov., male paratype from Mexico, Guerrero, S of Papanoa (ZFMK Ar 23945). Left palp, prolateral, dorsal, and retrolateral views. Scale bar = 0.3 mm.

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Guerrero** • ♂; ~5 km S of Papanoa; 17.2711° N, 101.0328° W; 75 m a.s.l.; 4 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; low forest, leaf litter; LATLAX.

Paratypes

MEXICO – **Guerrero** • 1 ♂, 1 ♀; same collection data as for holotype; ZFMK Ar 23945.

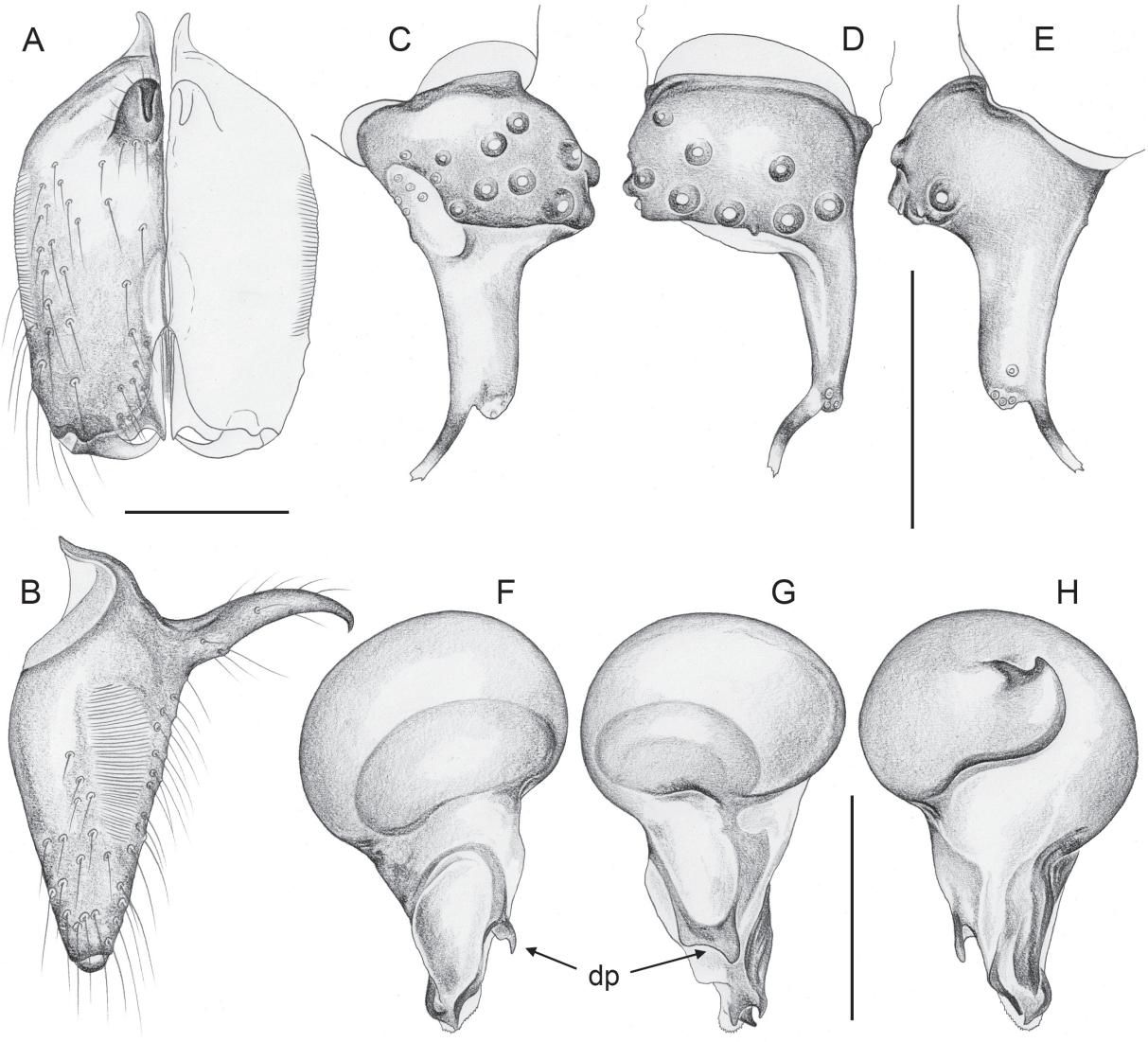

Fig. 15. *Pholcophora papanoa* Huber sp. nov., male paratype from Mexico, Guerrero, S of Papanoa (ZFMK Ar 23945). **A–B**. Chelicerae, frontal and lateral views. **C–E**. Left palpal tarsus and procursus, prolateral, dorsal, and retrolateral views. **F–H**. Left genital bulb, prolateral, dorsal, and retrolateral views. Abbreviation: dp, dorsal process. Scale bars = 0.2 mm.

Other material examined

MEXICO – **Guerrero** • 3 ♀♀, 1 juv., in pure ethanol (one female used for SEM); same collection data as for holotype; ZFMK Mex216 • 3 ♀♀ abdomens, together with paratypes (prosomata used for molecular work); same collection data as for holotype; ZFMK Ar 23945 • 2 ♂♂ (partly used for µ-CT study); same collection data as for holotype; ZFMK Ar 23947 • 1 ♂ (partly used for karyotype analysis); same collection data as for holotype; ZFMK Ar 23948.

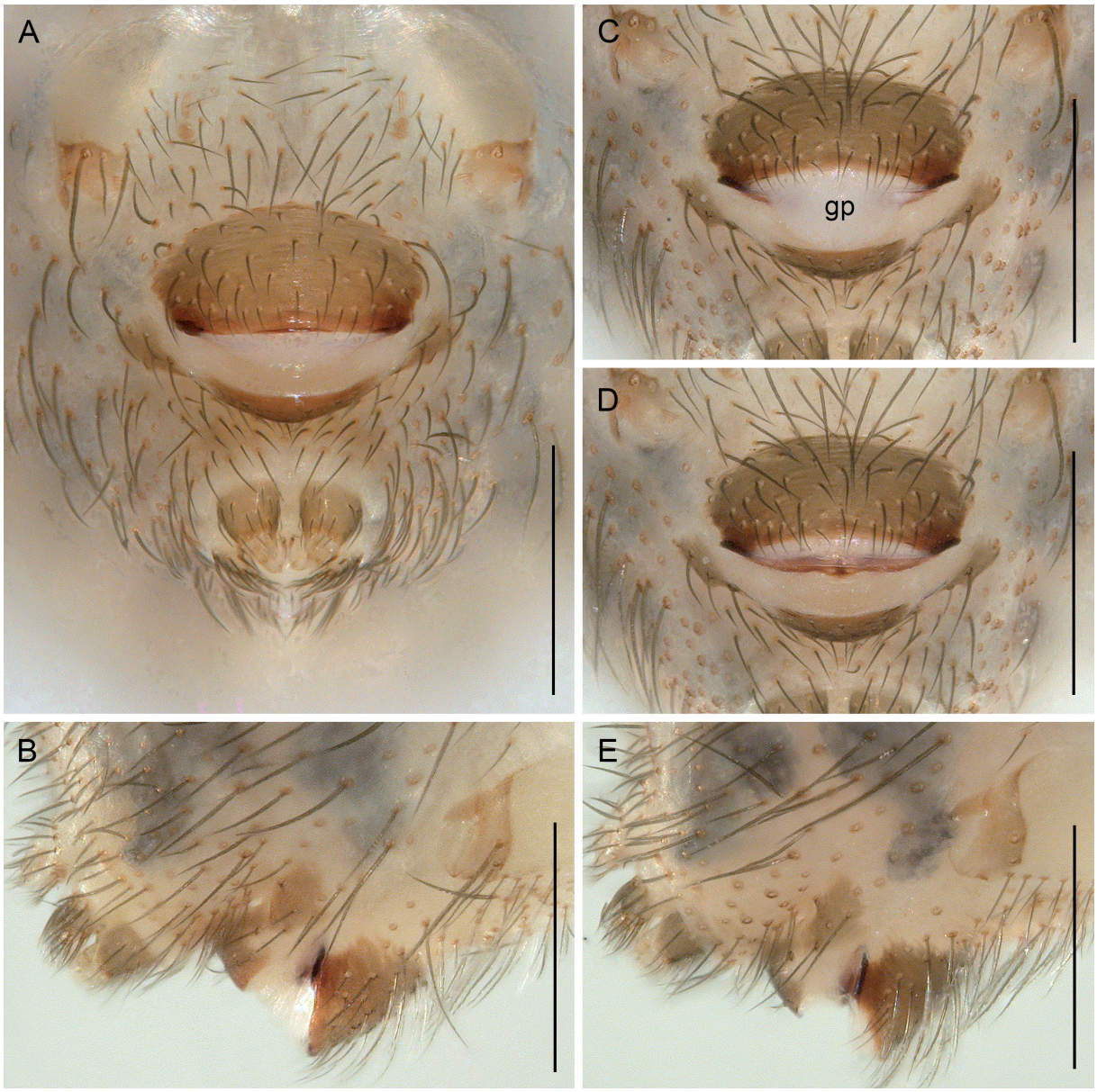

Fig. 16. *Pholcophora papanoa* Huber sp. nov., females from Mexico, Guerrero, S of Papanoa (ZFMK Ar 23945), epigyna. **A, C–D**. Ventral views. **B, E**. Lateral views. Figs C and D show the same specimen, with genital plug (gp) and without plug. Scale bars = 0.3 mm.

Description

Male (holotype)

Measurements. Total body length 2.4, carapace width 1.05. Distance PME-PME 60 µm; diameter PME 70 µm; distance PME-ALE 30 µm; distance AME-AME 20 µm; diameter AME 40 µm. Leg 1: 5.30 (1.50 + 0.40 + 1.30 + 1.55 + 0.55), tibia 2: 1.15, tibia 3: 1.05, tibia 4: 1.50; tibia 1 L/d: 9; diameters of leg femora 0.28–0.30, of leg tibiae 0.14–0.15.

Colour (in ethanol). Prosoma and legs ochre-orange, no dark marks on carapace, leg femora distally darkened; abdomen grey with dark bluish internal marks; ventrally with light brown plate in front of gonopore.

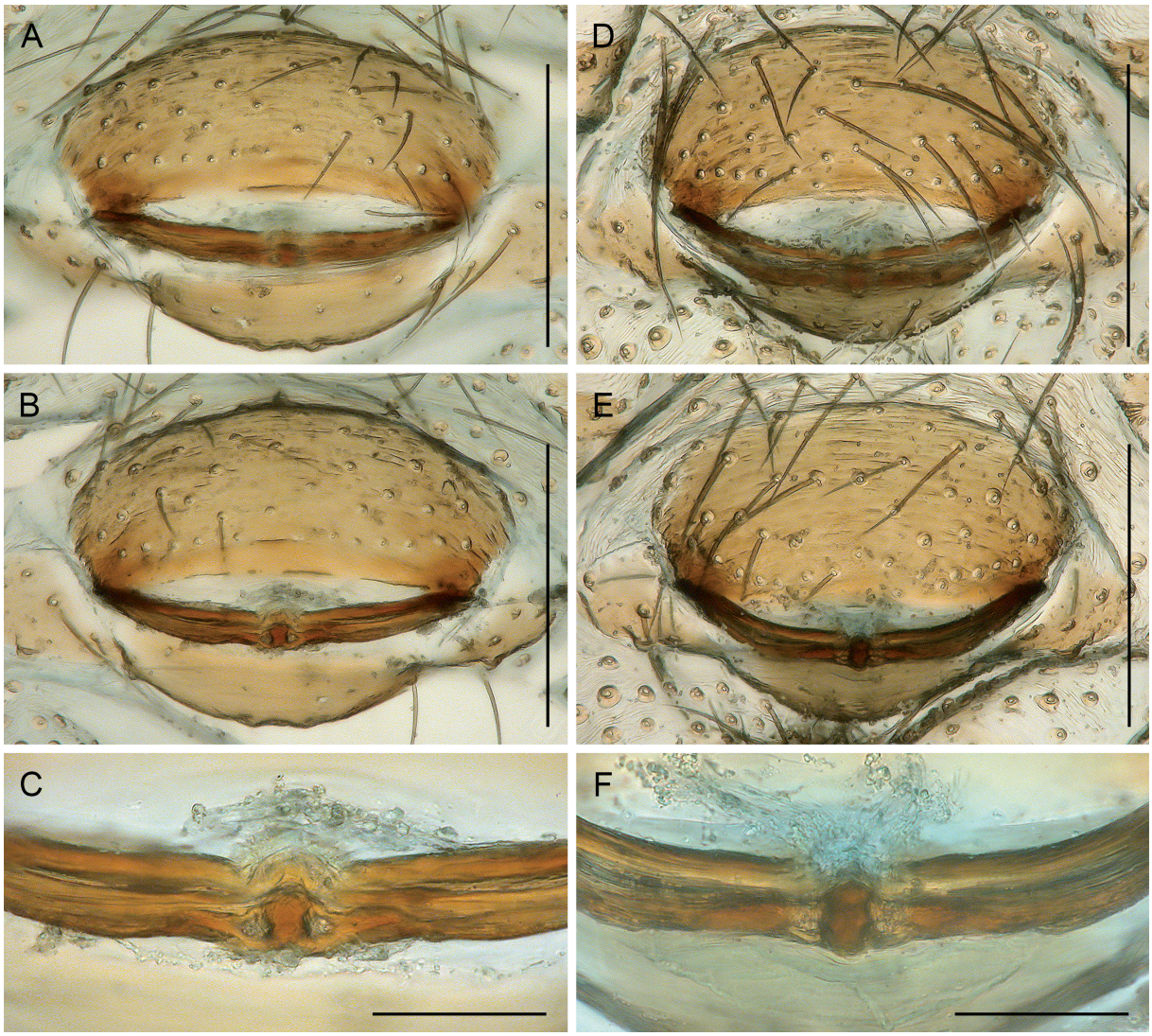

Fig. 17. *Pholcophora papanoa* Huber sp. nov., females from Mexico, Guerrero, S of Papanoa (ZFMK Ar 23945), cleared female genitalia. **A, D**. Ventral views. **B, E**. Dorsal views. **C, F**. Detail of median internal structures. Scale bars: A–B, D–E = 0.2 mm; C, F = 0.05 mm.

Body (Fig. 3F). Ocular area barely raised. Carapace with distinct but shallow thoracic groove. Clypeus unmodified, very short (clypeus rim to ALE: 0.24). Sternum slightly wider than long (0.68/0.58), heart-shaped (i.e., narrow posteriorly), with pair of distinct anterior processes near coxae 1. Abdomen globular.

Chelicerae (Fig. 15A–B). With pair of long frontal apophyses; stridulatory files fine but clearly visible in dissecting microscope; distances between cheliceral stridulatory ridges proximally 3.0 μm, distally 3.8 μm.

Palps (Fig. 14). Coxa unmodified; trochanter without process; femur proximally with retrolateral-ventral process and prolateral stridulatory pick, distally widened but simple, slightly curved towards

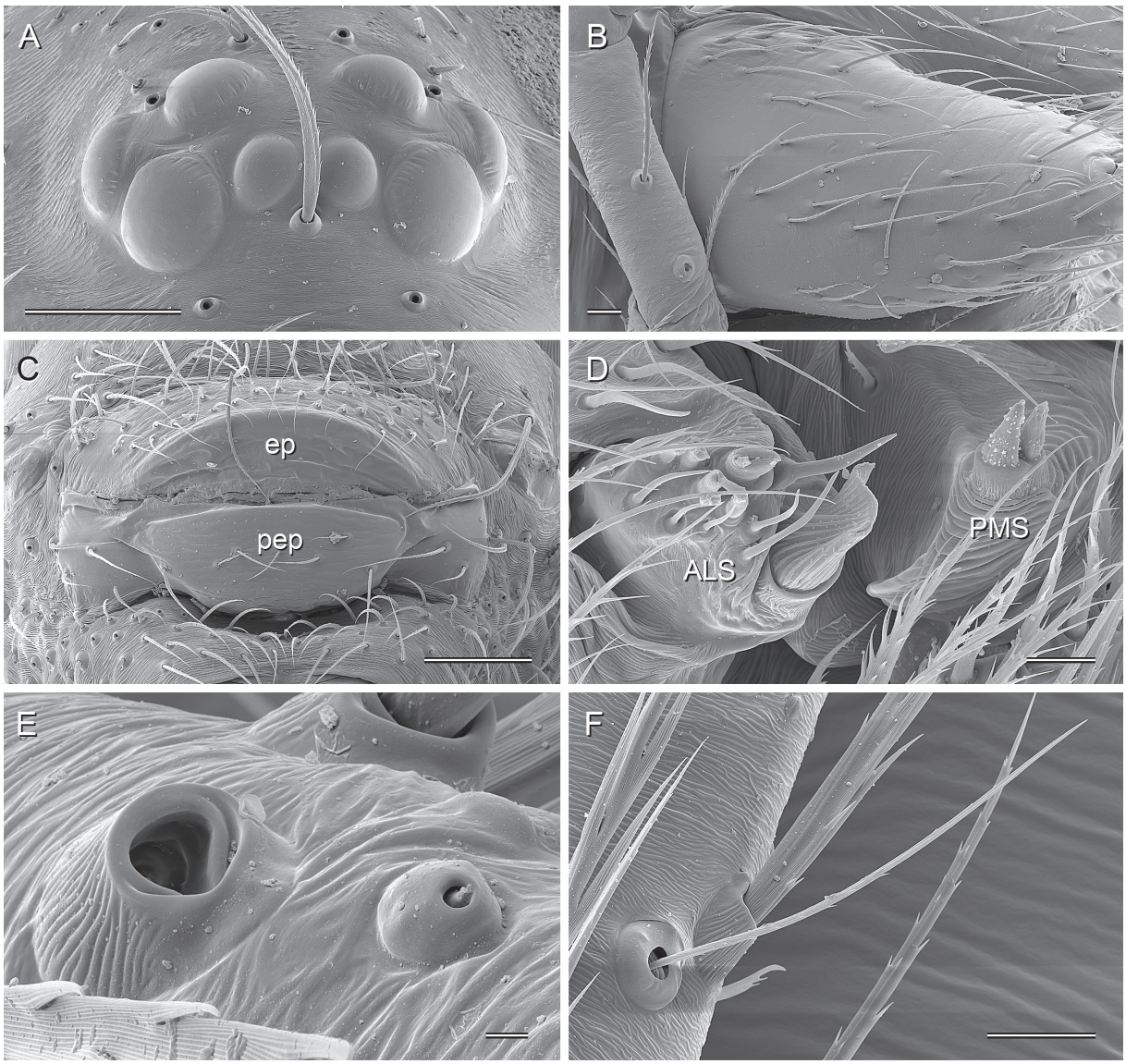

Fig. 18. *Pholcophora papanoa* Huber sp. nov., female from Mexico, Guerrero, S of Papanoa (ZFMK Mex216). **A**. Ocular area, frontal view. **B**. Right chelicera, lateral view, showing absence of stridulatory file. **C**. Epigynum, posterior view. **D**. Spinnerets. **E**. Palpal tarsal organ (and base of 'regular' hair). **F**. Prolateral trichobothrium on tibia 2. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A, C = 100 μm; B, F = 20 μm; D = 10 μm; E = 2 μm.

dorsal; femur-patella joints slightly shifted toward prolateral side; tibia globular, with two trichobothria; procursus very simple (Fig. 15C–E), narrow distal part directed towards prolateral, with semi-transparent tip; genital bulb with distinctive dorsal process and sclerotized and membranous distal elements (Fig. 15F–H).

Legs. Without spines and curved hairs; with vertical hairs in two narrow dorsal bands on all tibiae (length ~20 μm); length of dorsal trichobothrium on tibia 1: ~100 μm; retrolateral trichobothrium of tibia 1 at 57%; prolateral trichobothrium absent on tibia 1; tarsus 1 with ~7 pseudosegments, only distally 2–3 distinct.

Variation (male)
Tibia 1 in other male: 1.35.

Female
In general, similar to male (Fig. 3G) but sternum without pair of anterior humps, tibiae without higher than usual density of short vertical hairs, and chelicerae without stridulatory files. Tibia 1 in four females: 0.90, 0.90, 1.00, 1.05. Epigynum (Figs 16, 18C) with simple anterior plate protruding posteriorly; posterior plate wide, median part separated anteriorly from lateral parts by pair of whitish areas. Internal genitalia (Fig. 17) very simple, apparently without or with small and indistinct median receptacle, without or with very small pore plates.

Distribution

Known from type locality only, in Mexico, Guerrero (Fig. 2).

Natural history

The spiders were found in dry leaf litter in a low hillside forest (Fig. 34C). They shared the microhabitat with at least three further species of Pholcidae (Modisiminae): one representative of *Modisimus* Simon, 1893, one *Anopsicus* Chamberlin & Ivie, 1938, and one species of uncertain generic position.

Pholcophora texana Gertsch, 1935
Figs 3H–I, 19–24, 33I–J

Remark

For synonymy, type material, and redescription, see Huber (2000).

Diagnosis

Easily distinguished from known congeners by unique brush of modified hairs on male palpal femur (Fig. 19A, C) and by pair of round sacs in female internal genitalia (Fig. 22B–D); also by shape of procursus (Fig. 20C–E; tip in lateral view with wide transparent flap), by shape of distal bulbal process (Fig. 20F–H), and by indistinct plate in front of main epigynal plate (Fig. 21A, C).

Material examined (new record)

MEXICO – **Hidalgo** • 1 ♂, 1 ♀, 3 female abdomens; ~2.5 km SW of Jacala; 20.9948° N, 99.2138° W; 1430 m a.s.l.; 21 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; ZFMK Ar 23952 • 7 ♀♀, 2 juvs, in pure ethanol (three female prosomata used for molecular work, abdomens transferred to ZFMK Ar 23952); same collection data as for preceding; ZFMK Mex341 • 6 ♀♀, 2 juvs (subadult ♂♂); same collection data as for preceding; LATLAX.

Description (amendments; see Huber 2000)

Male

Measurements of male from SW of Jacala, Hidalgo (ZFMK Ar 23952): body length 1.75, carapace width 0.70; tibia 1 length 1.25, metatarsus 1 length 1.30, tibia 2 length 0.95, tibia 4 length 1.25. Distance PME-PME 70 µm; diameter PME 50 µm; distance PME-ALE 25 µm; distance AME-AME 15 µm; diameter AME 30 µm. Diameters of leg femora 0.14–0.16, of leg tibiae 0.08–0.09. Clypeus unmodified, but slightly more protruding than in female; clypeus rim to ALE 0.21. Distances between cheliceral stridulatory ridges proximally 2.0 µm, distally 3.2 µm. Sternum humps very distinct, ~0.08 long. Procursus as in Fig. 20C–E, with distinctive transparent element distally (barely visible in dissecting microscope); genital bulb as in Fig. 20F–H. Leg tibiae with slightly higher number of vertical hairs than in female (proximally on tibiae 1 and 2); prolateral trichobothrium absent on tibia 1. Tibia 1 in previously measured specimens: 0.72 (Gertsch 1982); 0.96, 0.97, 1.39 (Huber 2000).

Female

In general, similar to male but sternum without pair of anterior humps, and chelicerae without stridulatory files. Tibia 1 in 11 females from SW of Jacala: 0.90–1.18 (mean 1.03). Epigynum and internal female genitalia as in Figs 21, 22, 23C, with pair of receptacles (shape varies slightly with angle of view), without (or with very small?) pore plates.

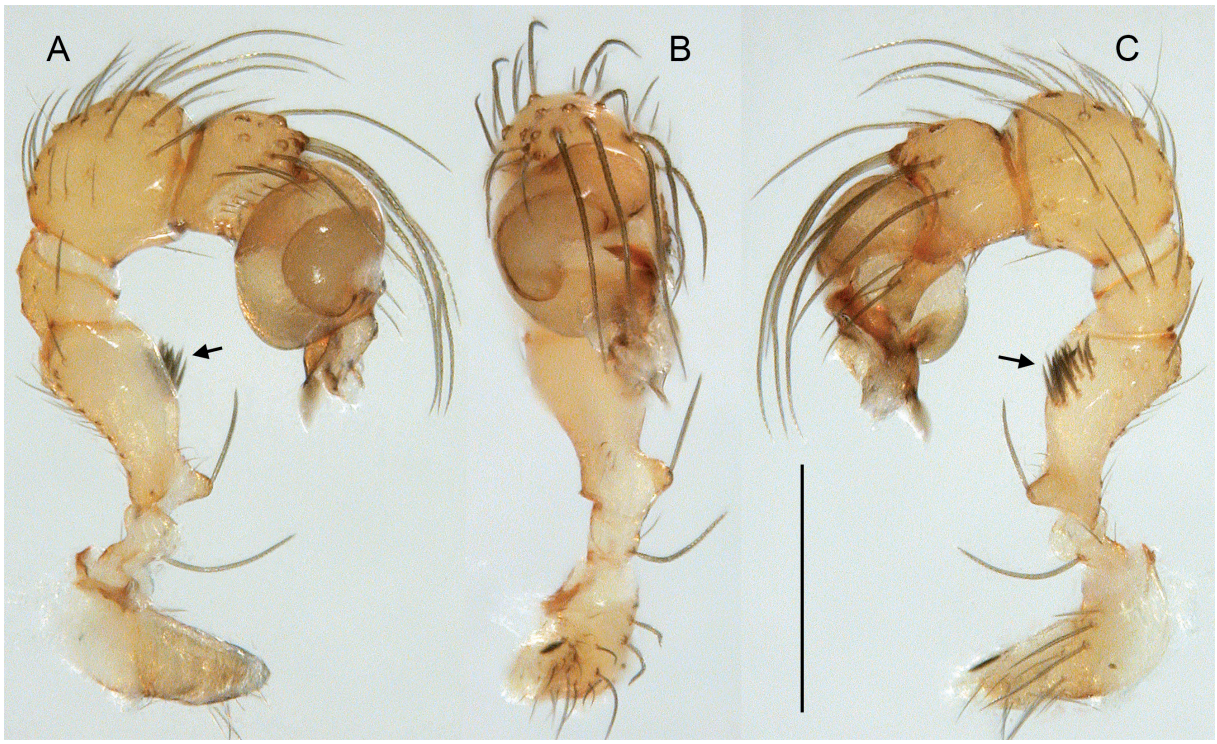

Fig. 19. *Pholcophora texana* Gertsch, 1935, male from Mexico, Hidalgo, SW of Jacala (ZFMK Ar 23952). Left palp, prolateral, dorsal, and retrolateral views; arrows point at unique brush of modified hairs. Scale bar = 0.3 mm.

Distribution

Apparently widely distributed in north-eastern Mexico, ranging into southern Texas (Fig. 2). However, the map in Fig. 2 includes four records that are based exclusively on females, i.e., the identifications should be verified (e.g., by collecting males or by sequencing specimens from these localities).

Natural history

The newly collected specimens were found under rocks on an arid hillside set with low thorn scrub (Fig. 34B).

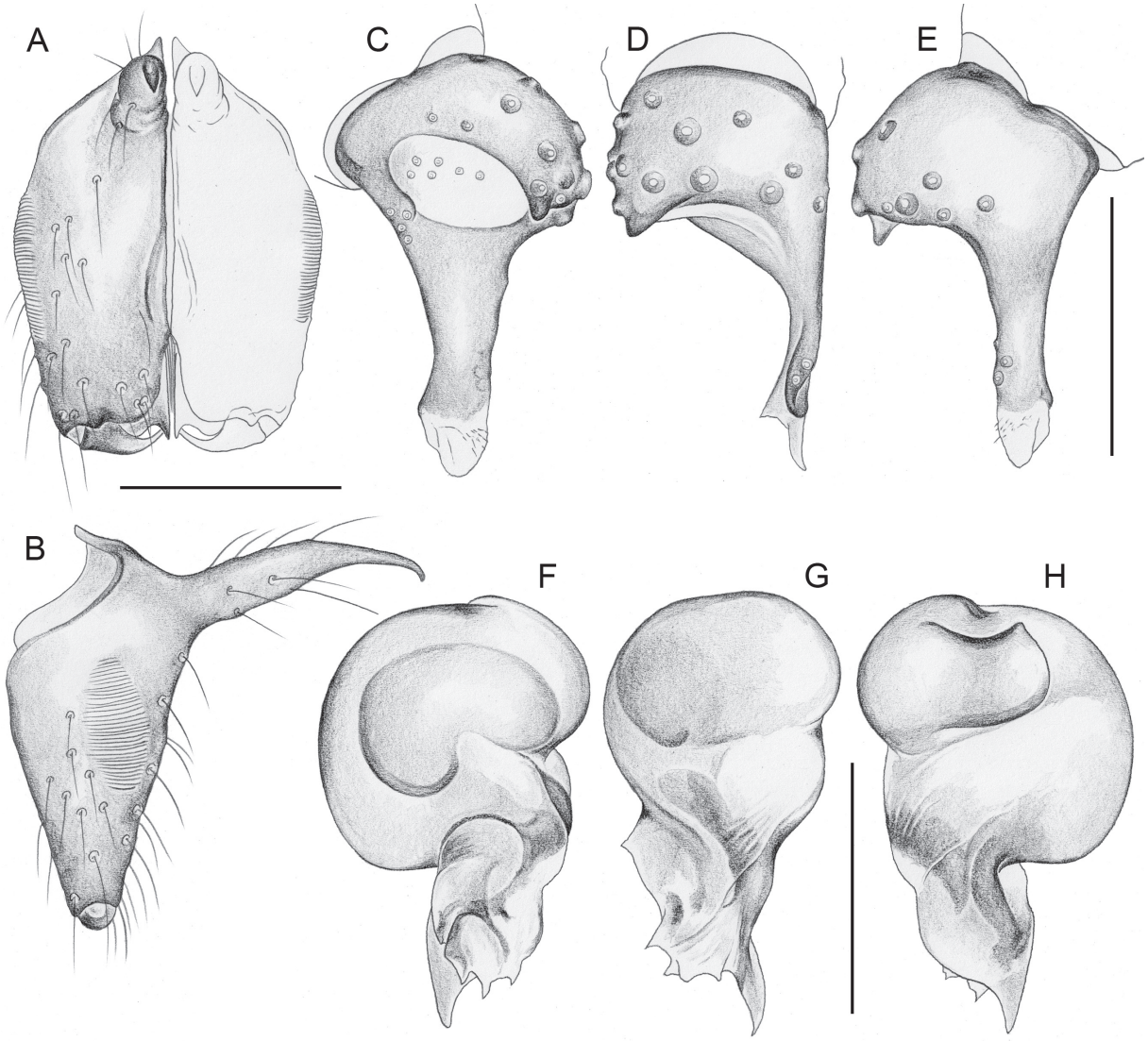

Fig. 20. *Pholcophora texana* Gertsch, 1935, male from Mexico, Hidalgo, SW of Jacala (ZFMK Ar 23952). **A–B**. Chelicerae, frontal and lateral views. **C–E**. Left palpal tarsus and procursus, prolateral, dorsal, and retrolateral views. **F–H**. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.2 mm.

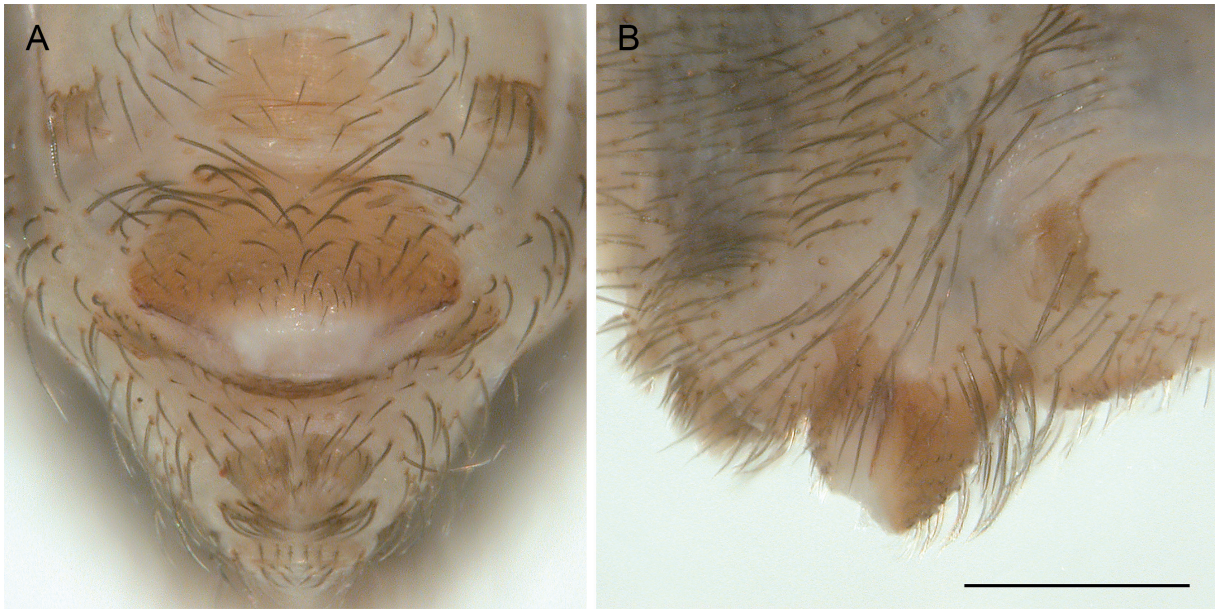

Fig. 21. *Pholcophora texana* Gertsch, 1935, female from Mexico, Hidalgo, SW of Jacala (ZFMK Ar 23952), epigynum. **A**. Ventral view. **B**. Lateral view. Scale bar = 0.3 mm (both at same scale).

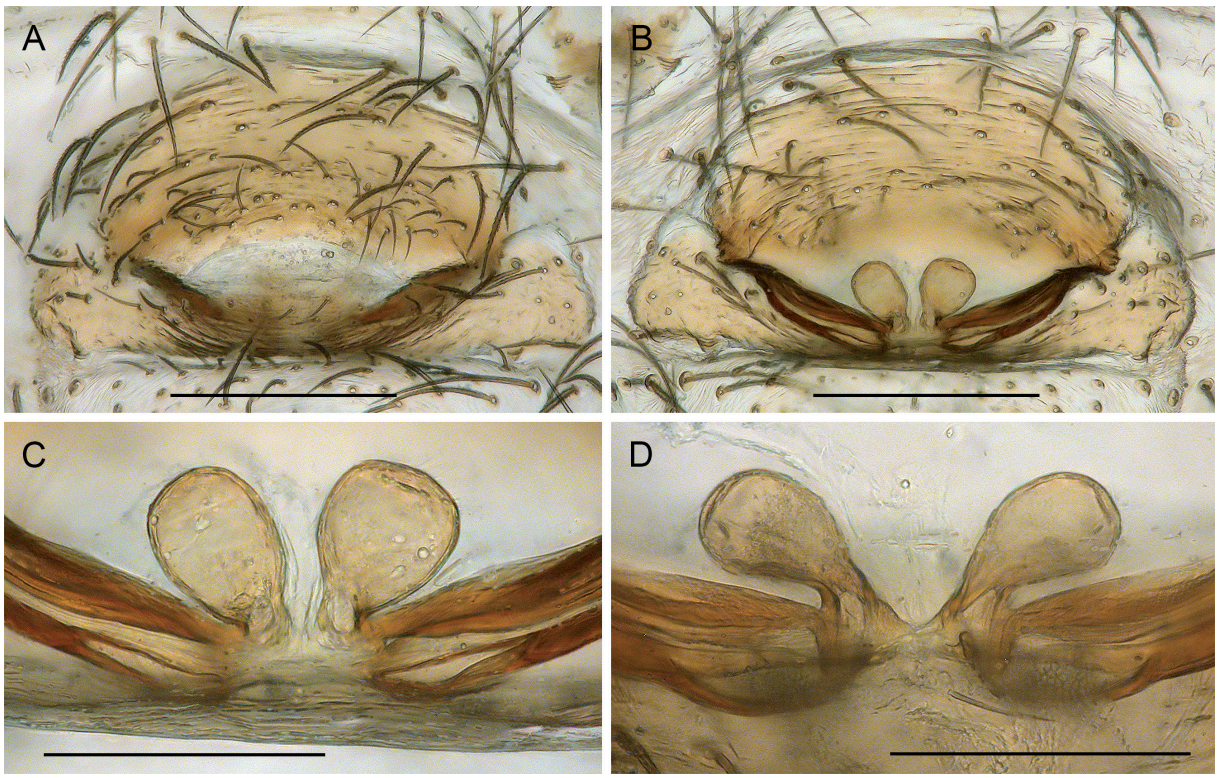

Fig. 22. *Pholcophora texana* Gertsch, 1935, females from Mexico, Hidalgo, SW of Jacala (ZFMK Ar 23952). **A–B**. Cleared female genitalia, ventral and dorsal views. **C–D**. Detail of median internal structures in two different specimens (slightly different angles of view). Scale bars: A–B = 0.2 mm; C–D = 0.1 mm.

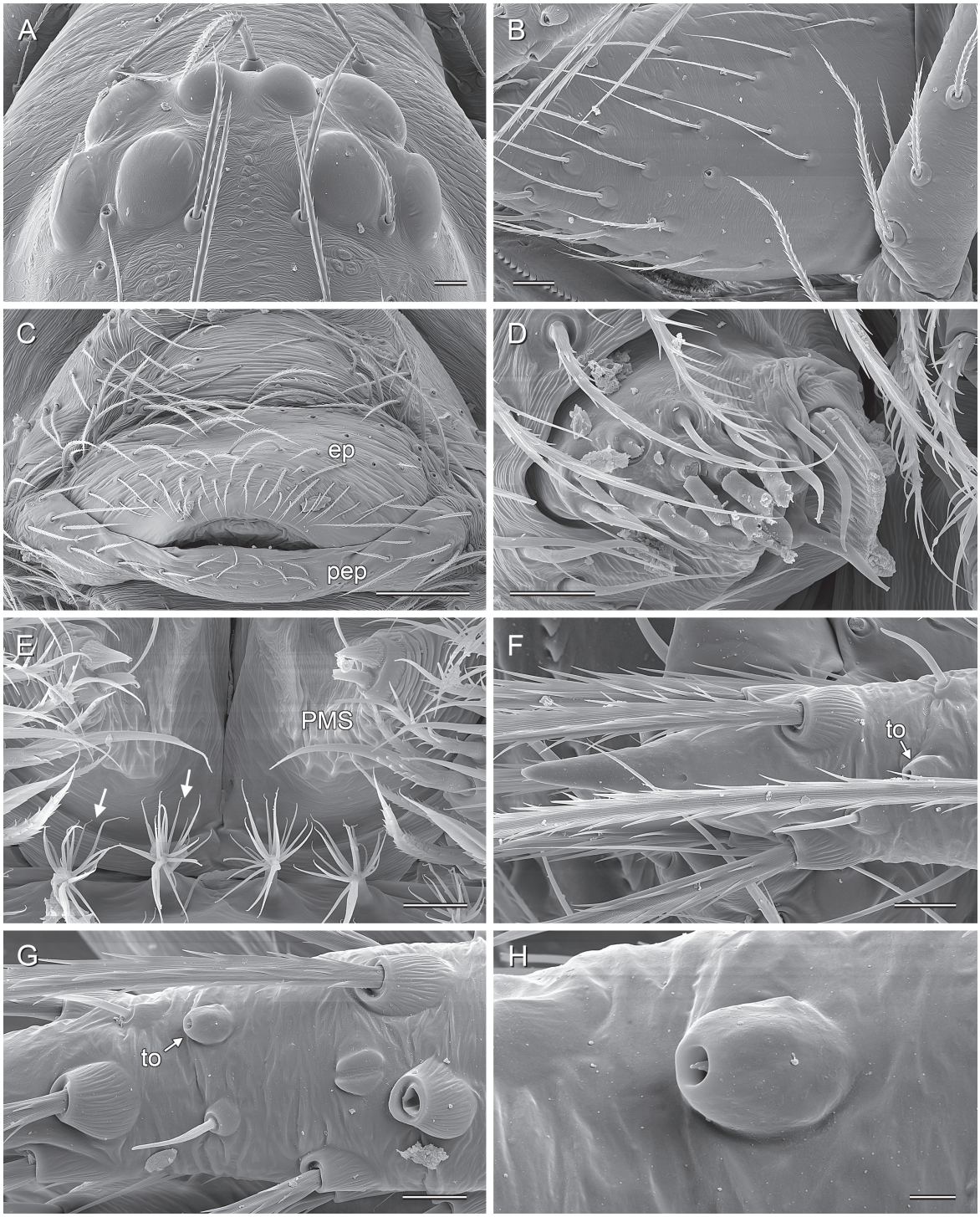

Fig. 23. *Pholcophora texana* Gertsch, 1935, female from Mexico, Hidalgo, 2.5 km SW of Jacala (ZFMK Mex341). **A**. Ocular area, dorsal view. **B**. Lateral face of chelicera, showing absence of stridulatory file. **C**. Epigynum, ventral (slightly posterior) view. **D**. ALS. **E**. PMS and anal hairs (arrows). **F**. Tip of left palpal tarsus, dorsal view. **G**. Detail of right palpal tarsus, dorsal view. **H**. Palpal tarsal organ. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate; to = tarsal organ. Scale bars: A–B = 20 μm; C = 100 μm; D–G = 10 μm; H = 2 μm.

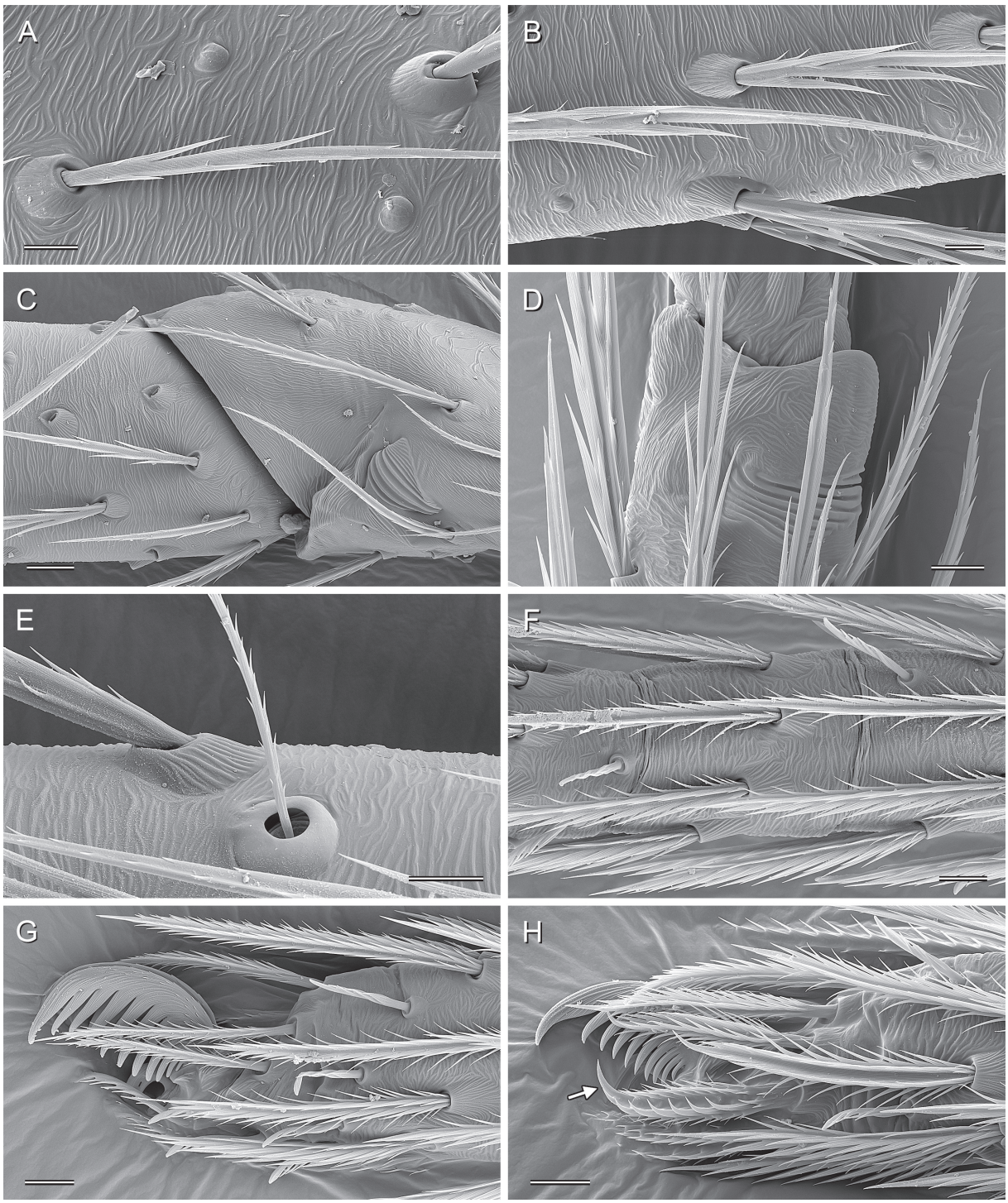

Fig. 24. *Pholcophora texana* Gertsch, 1935, female from Mexico, Hidalgo, 2.5 km SW of Jacala (ZFMK Mex341). **A**. Detail of femur 2, retrolateral view. **B**. Detail of tibia 4, retrolateral view. **C**. Patella-tibia 1 joint, retrolateral view. **D**. Metatarsus-tarsus 2 joint, retrolateral view. **E**. Retrolateral trichobothrium of tibia 1. **F**. Detail of tarsus 1, showing pseudosegmentation. **G**. Tip of tarsus 2, retrolateral view. **H**. Tip of tarsus 4, prolateral view, showing comb-hair (arrow). Scale bars: A–B, D–H = 10 µm; C = 20 µm.

Pholcophora tehuacan Huber sp. nov.
urn:lsid:zoobank.org:act:D7F69EC5-F4AB-4425-AABF-3257B146EA8A
Figs 3J–K, 25–29, 33K–L

Diagnosis

Easily distinguished from most known congeners (except *P. maria* Gertsch, 1977) by small size (carapace width < 0.70; tibia 1 length < 1.0) and by pair of tube-like sacs in female internal genitalia (Fig. 28B). From *P. maria* by shorter female internal sacs (60 µm vs 110 µm), smaller body (total body length 1.2 vs 1.65; carapace width 0.55 vs 0.65) and shorter legs (female tibia 1: 0.60–0.65 vs 0.93). Male of *P. maria* unknown.

Remark

Judging from the female internal genitalia (compare Fig. 28B with Huber 2000: fig. 1357), this species may be closely related to *P. maria* Gertsch, 1977 which is known from a single female specimen originating from Yucatan, Cueva (Gruta, Actún) Xpukil (20.551° N, 89.912° W, 80 m a.s.l.). This implies that *P. maria* is probably correctly placed in *Pholcophora* (it was considered incertae sedis in Huber 2000).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Puebla** • ♂; ~35 km SE of Tehuacan, Calapa bridge, N side; 18.1652° N, 97.2605° W; 1020 m a.s.l.; 24 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Paratypes

MEXICO – **Puebla** • 2 ♂♂, 1 ♀, and 1 female abdomen; same collection data as for holotype; ZFMK Ar 23949 • 4 ♂♂, 22 ♀♀; same collection data as for holotype; LATLAX • 1 ♂, 1 ♀; same collection

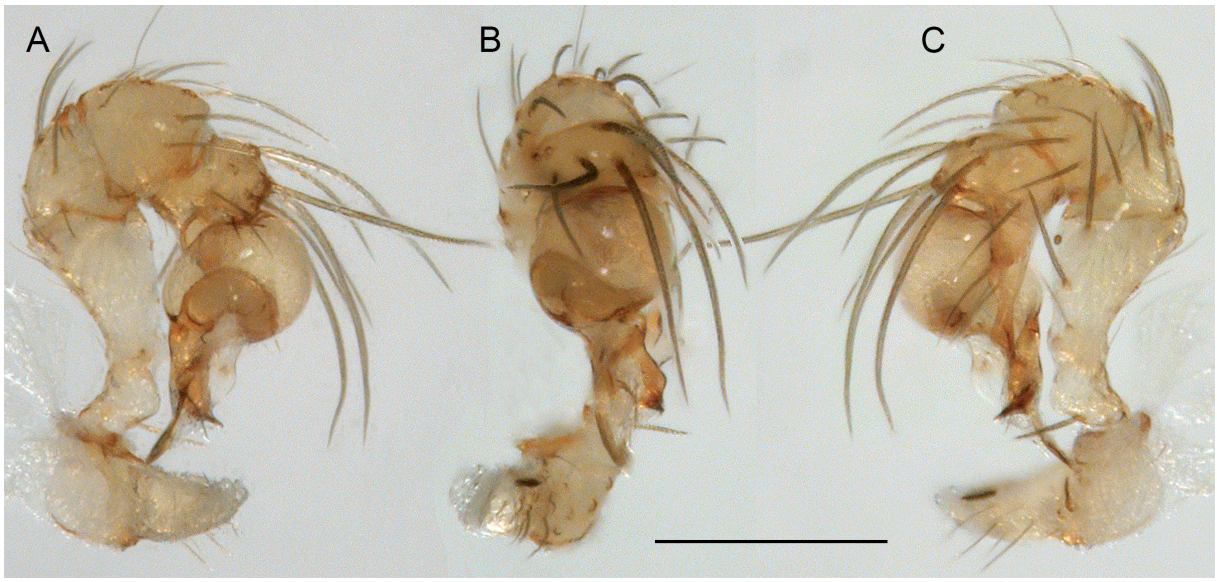

Fig. 25. *Pholcophora tehuacan* Huber sp. nov., male paratype from Mexico, Puebla, SE of Tehuacan (ZFMK Ar 23949). Left palp, prolateral, dorsal, and retrolateral views. Scale bar = 0.2 mm.

data as for holotype but W side of Calapa bridge; 18.1619° N, 97.2647° W; 1010 m a.s.l.; 23 Oct. 2019; ZFMK Ar 23950.

Other material examined

MEXICO – **Puebla** • 2 ♂♂, 6 ♀♀, 5 juvs, in pure ethanol; same collection data as for holotype; four female prosomata used for molecular work, 1 ♂ 1 ♀ used for SEM, 1 female abdomen transferred to ZFMK Ar 23949; ZFMK Mex353 • 1 ♂, 1 ♀; same collection data as for holotype; partly used for µ-CT study; ZFMK • 1 ♂; same collection data as for holotype; partly used for karyotype analysis; ZFMK 23951 • 1 juv., in pure ethanol; same collection data as for holotype but W side of Calapa bridge; ZFMK Mex350.

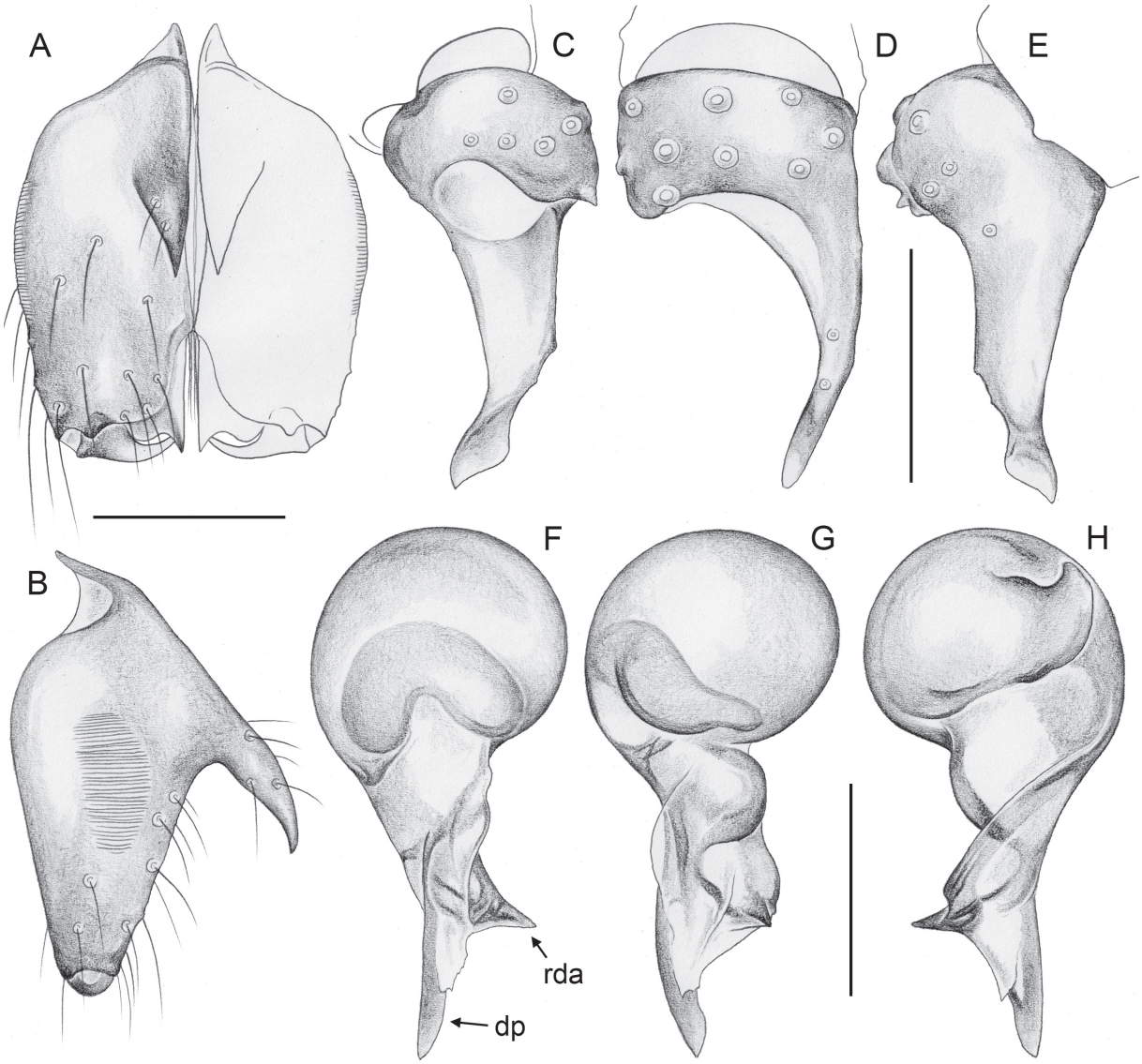

Fig. 26. *Pholcophora tehuacan* Huber sp. nov., male paratype from Mexico, Puebla, SE of Tehuacan (ZFMK Ar 23949). **A–B**. Chelicerae, frontal and lateral views. **C–E**. Left palpal tarsus and procursus, prolateral, dorsal, and retrolateral views. **F–G**. Left genital bulb, prolateral, dorsal, and retrolateral views. Abbreviations: dp = distal process; rda = retrolateral-dorsal apophysis. Scale bars = 0.1 mm.

Description

Male (holotype)

Measurements. Total body length 1.20, carapace width 0.55. Distance PME-PME 40 µm; diameter PME 45 µm; distance PME-ALE 20 µm; distance AME-AME 15 µm; diameter AME 20 µm. Leg 1: 2.55 (0.75 + 0.20 + 0.65 + 0.60 + 0.35), tibia 2: 0.55, tibia 3: 0.50, tibia 4: 0.75; tibia 1 L/d: 8; diameters of leg femora 0.11–0.12, of leg tibiae 0.08.

Colour (in ethanol). Prosoma and legs monochromous pale ochre-yellow; abdomen slightly darker, also monochromous.

Body. Habitus as in Fig. 3J. Ocular area barely raised. Carapace with low thoracic groove. Clypeus unmodified, very short (clypeus rim to ALE 0.12). Sternum slightly wider than long (0.34/0.32), almost round (i.e., not heart-shaped), with pair of small but distinct anterior processes (~30 µm long) near coxae 1. Abdomen globular; gonopore with four epiandrous spigots (Fig. 29C); ALS with seven spigots, PMS with two spigots (Fig. 29G).

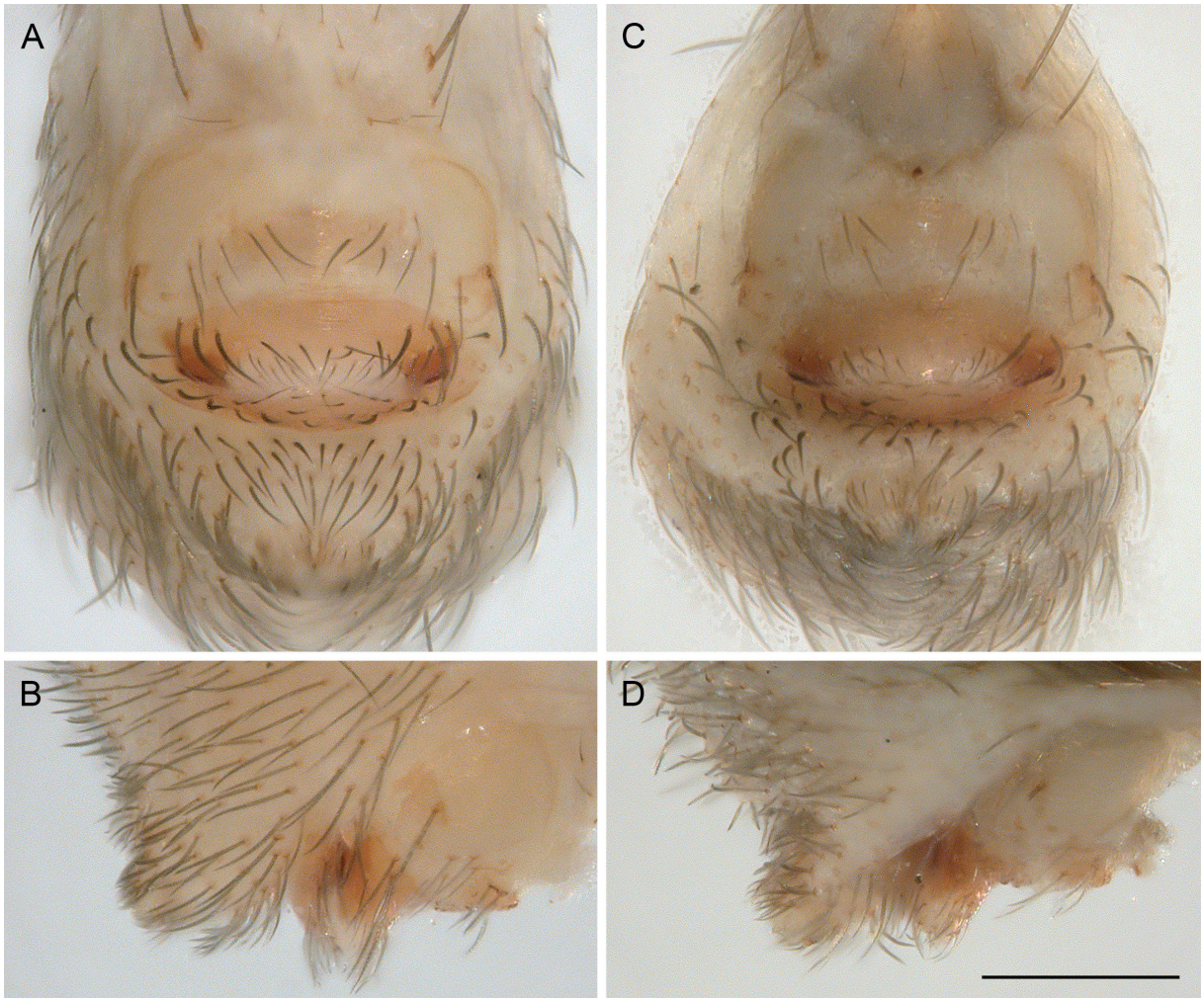

Fig. 27. *Pholcophora tehuacan* Huber sp. nov., females from Mexico, Puebla, SE of Tehuacan (ZFMK Ar 23949), epigyna. **A, C**. Ventral views. **B, D**. Lateral views. Scale bar = 0.2 mm (all at same scale).

Chelicerae (Fig. 26A–B). With pair of frontal apophyses directed downwards; stridulatory ridges very fine (Fig. 29A; distances between ridges 2.0–2.2 µm), not visible in dissecting microscope.

Palps (Fig. 25). Coxa unmodified; trochanter without process; femur proximally with retrolateral-ventral process and prolateral stridulatory pick, distally widened but simple, slightly curved towards dorsal; femur-patella joints slightly shifted toward prolateral side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; tarsal organ raised, with small opening (Fig. 29E); procursus very simple (Fig. 26C–E), with subdistal constriction and semi-transparent tip; genital bulb complex (Fig. 26F–H), with distinctive retrolateral-dorsal apophysis and long distal process.

Legs. Without spines and curved hairs; with usual low number of short vertical hairs; retrolateral trichobothrium of tibia 1 at 60%; prolateral trichobothrium absent on tibia 1; tarsus 1 with 6 pseudosegments, all fairly distinct.

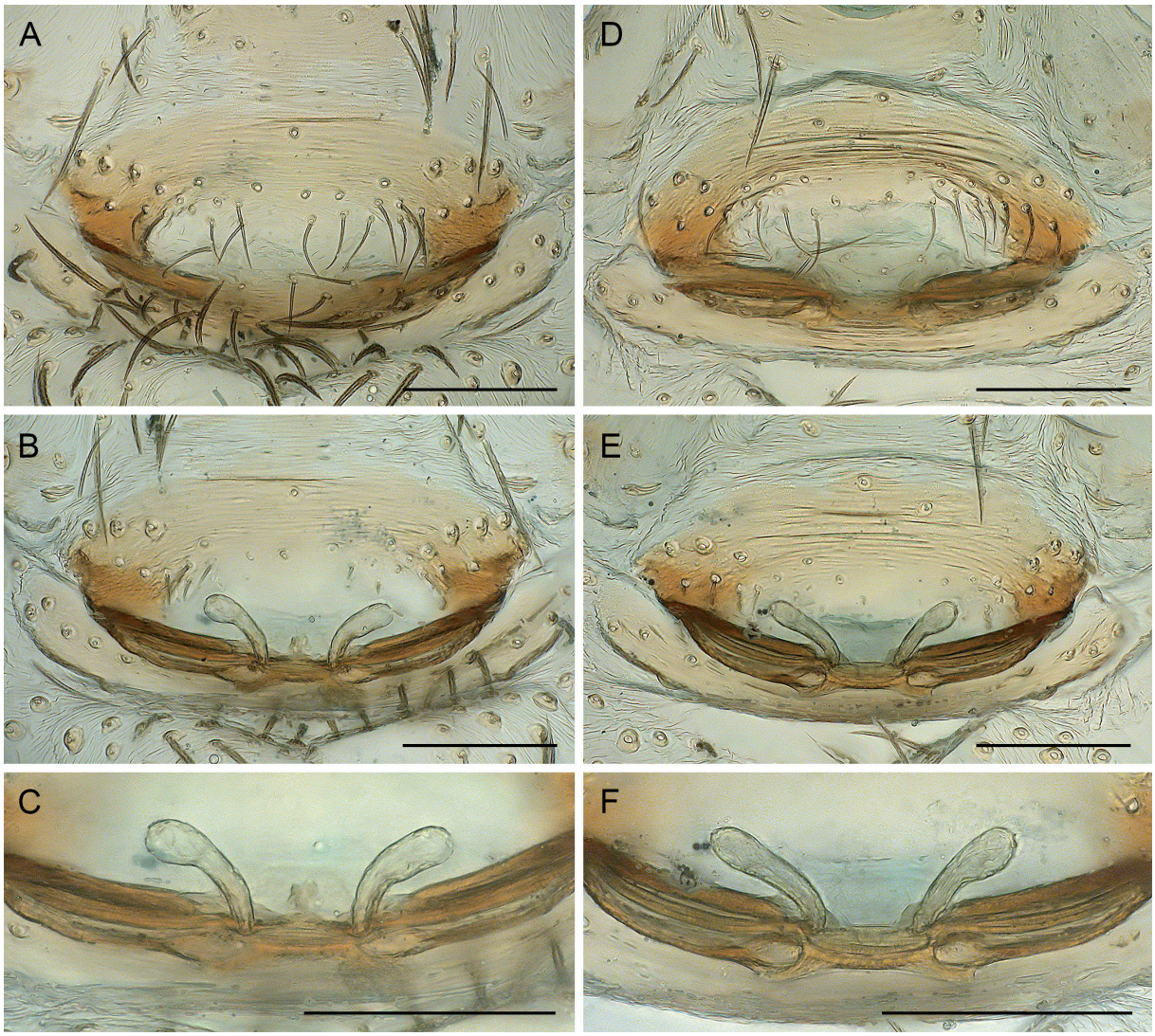

Fig. 28. *Pholcophora tehuacan* Huber sp. nov., females from Mexico, Puebla, SE of Tehuacan (ZFMK Ar 23949), cleared female genitalia. **A, D**. Ventral views. **B, E**. Dorsal views. **C, F**. Detail of median internal structures. Scale bars = 0.1 mm.

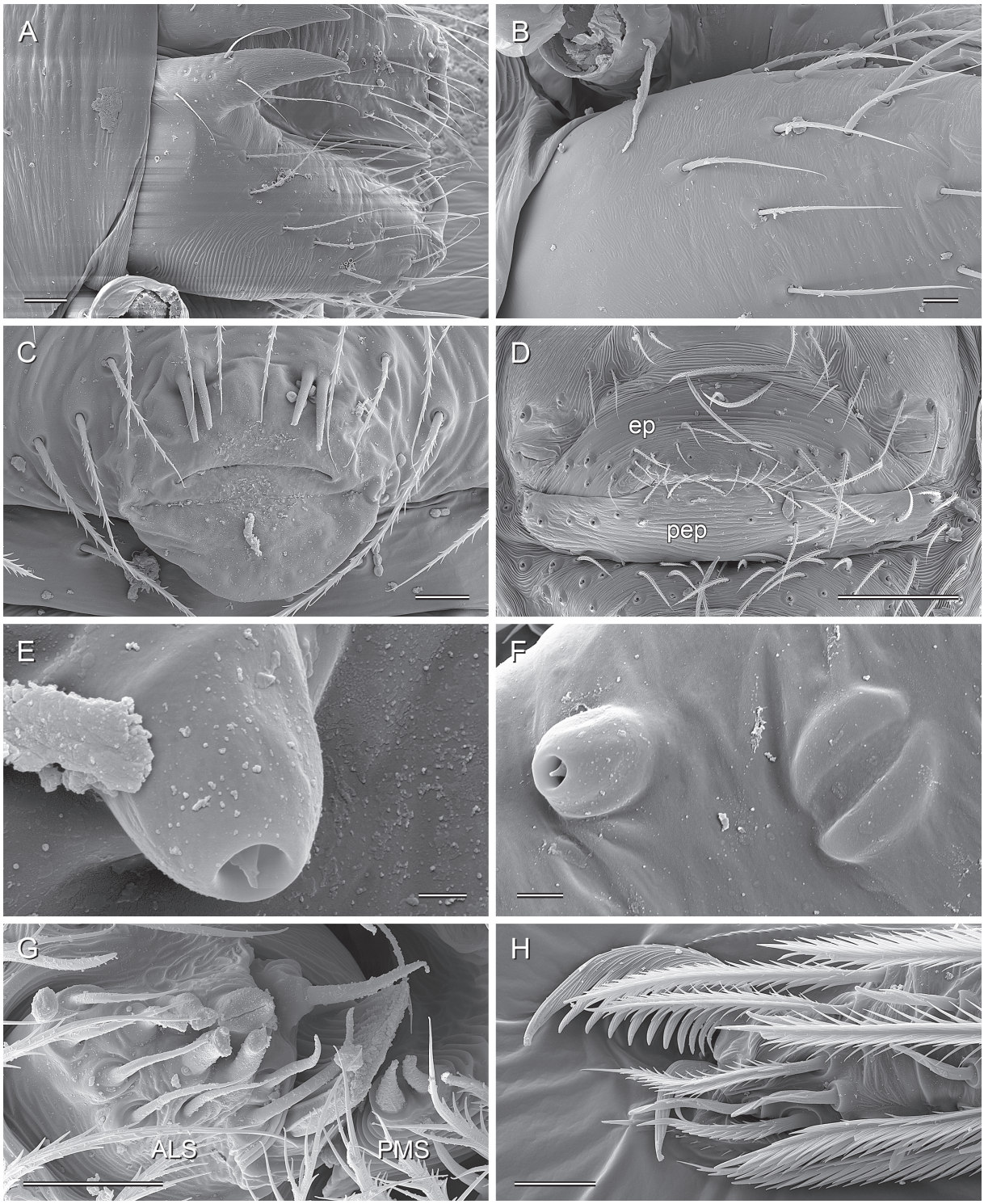

Fig. 29. *Pholcophora tehuacan* Huber sp. nov., male and female from Mexico, Puebla, 35 km SE of Tehuacan (ZFMK Mex353). **A**. Male chelicerae, oblique frontal view. **B**. Lateral face of female chelicera, showing absence of stridulatory file. **C**. Male gonopore with epiandrous spigots. **D**. Epigynum, ventral view. **E**. Male palpal tarsal organ. **F**. Female palpal tarsal organ and slit sensillum. **G**. Male ALS and PMS. **H**. Tip of right male tarsus 2, prolateral view. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A = 20 μm; B–C, G–H = 10 μm; D = 100 μm; E = 1 μm; F = 2 μm.

Variation (male)
Tibia 1 in ten males (incl. holotype): 0.60–0.65 (mean 0.62).

Female
In general, similar to male (Fig. 3K) but sternum without pair of anterior humps, and chelicerae without stridulatory files (Fig. 29B). Total body length ~1.20–1.40; tibia 1 in 14 females 0.60–0.65 (mean 0.62). Epigynum (Fig. 27) with short and simple anterior plate slightly protruding in lateral view; posterior plate wide, median part not separated from lateral parts by pair of whitish anterior areas. Internal genitalia (Fig. 28) with pair of distinct sacs (receptacles?) 60 μm long, without (or with very small?) pore plates.

Distribution

Known from type locality only, in Mexico, Puebla (Fig. 2).

Natural history

The spiders were found by turning rocks in a very dry area (Fig. 34D). They shared the microhabitat and sometimes the individual rock with a small undescribed species of *Physocyclus* Simon, 1893, and were difficult to distinguish from juveniles of that species. At disturbance they started to run rapidly and dropped from the rock to the ground (where they could no longer be found). The area was shared by a second representative of *Pholcophora* ("Mex354", see below), which also shared the microhabitat but was never found on the same rock as *Pholcophora tehuacan* sp. nov.

Putative further species

Pholcophora "Mex354"
Figs 3L, 30, 33G–H

This species is not formally described because no male is available. The morphology of the epigynum (Fig. 30A–B) reminds of geographically close congeners (*P. mazatlan* sp. nov.; *P. papanoa* sp. nov.) but the main epigynal plate is not straight posteriorly but has a pair of lateral indentations, and the legs tend to be longer (tibia 1 in 10 females 1.12–1.40, mean 1.28). The female of *P. mexcala* is unknown, but *P. mexcala* seems to be a much bigger species (male tibia 1 length > 4.0). The specimens were collected in a dry area, together with a second representative of *Pholcophora* (*P. tehuacan* sp. nov.), and five further species of Pholcidae (*Physocyclus modestus* Gertsch, 1971; *Physocyclus* sp.; *Modisimus* sp.; *Psilochorus* spp.). The spiders were usually found on the undersides of rocks, apparently in tiny webs; they did not run unless the web was damaged by turning the rock.

Material examined

MEXICO – **Puebla** • 5 ♀♀, in pure ethanol; ~35 km SE of Tehuacan, N of Calapa bridge; 18.1652° N, 97.2605° W; 1020 m a.s.l.; 24 Oct. 2019; B.A. Huber and Valdez-Mondragón leg.; thorn scrub, under rocks; two prosomata used for molecular work; ZFMK Mex354 • 8 ♀♀; same collection data as for preceding; LATLAX.

Pholcophora? "Car544"
Figs 31, 33M

S298 *Pholcophora*? *Car544* Car544 – Eberle *et al.* 2018 (molecular data). — Huber *et al.* 2018: 55.

Remarks

The two adult females available of this species resemble *P. bahama* Gertsch, 1982 that is known from a single adult female specimen (from Bahamas, West Caicos Island). The two species are distinguished by the strong rectangular sclerite between pedicel and epigynum in the present species (Fig. 31C). Habitus

and size of the two species appear identical, and the female internal genitalia share a median tube-like sac (compare Fig. 31G with Huber 2000: fig. 1356). The distinctive pair of internal posterior structures appears more widely separated in the present species (only one female cleared). Our molecular data

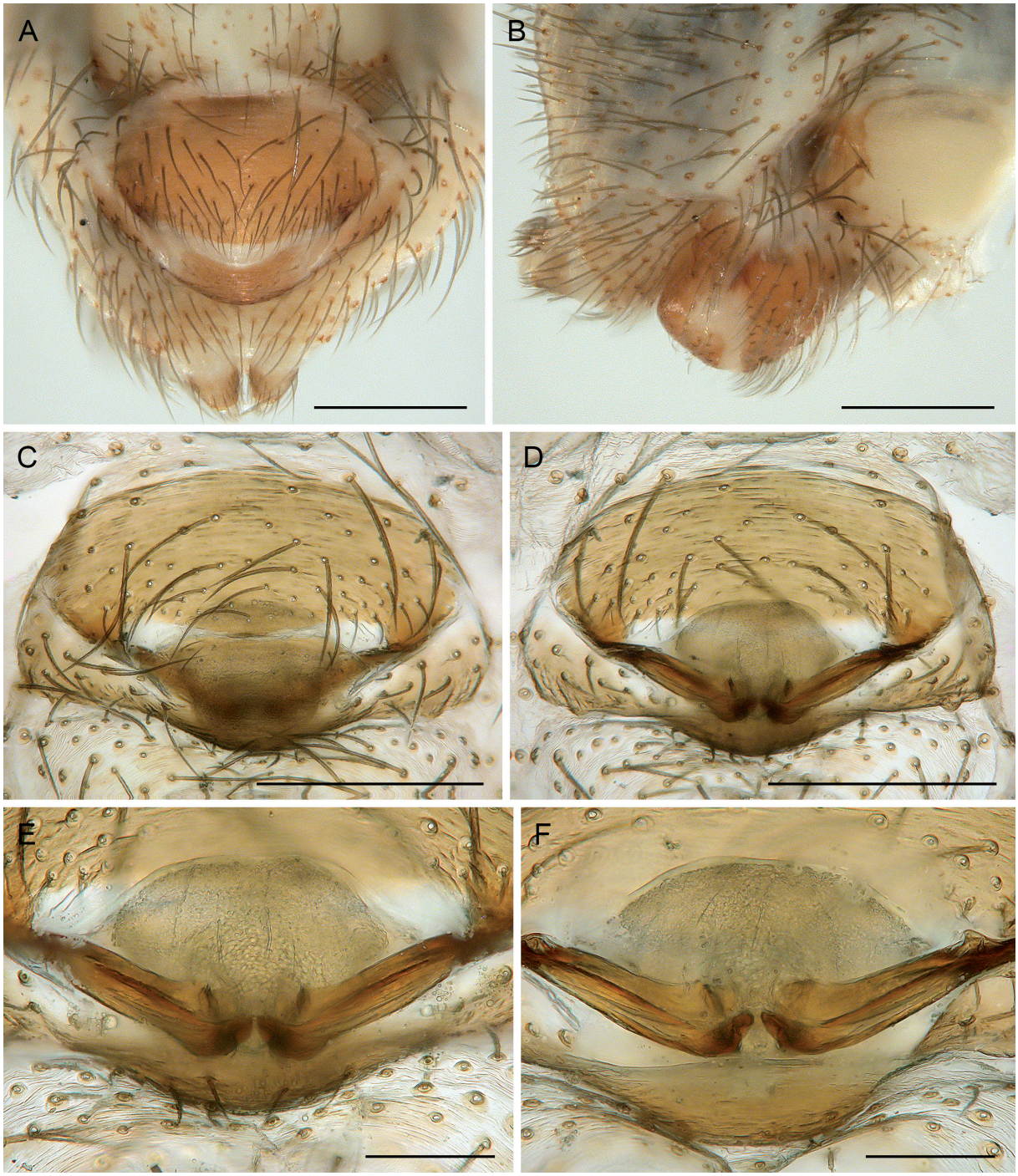

Fig. 30. *Pholcophora* "Mex354", females from Mexico, Puebla, SE of Tehuacan (ZFMK Mex354). **A–B**. Epigynum, ventral and lateral views. **C–D**. Cleared female genitalia, ventral and dorsal views. **E–F**. Detail of median internal structures in two different specimens. Scale bars: A–D = 0.3 mm; E–F = 0.1 mm.

suggest that the present species (together with *Pholcophora bahama* if the similarity above indeed reflects close relationship) is more closely related with an undescribed Cuban species (see below) and

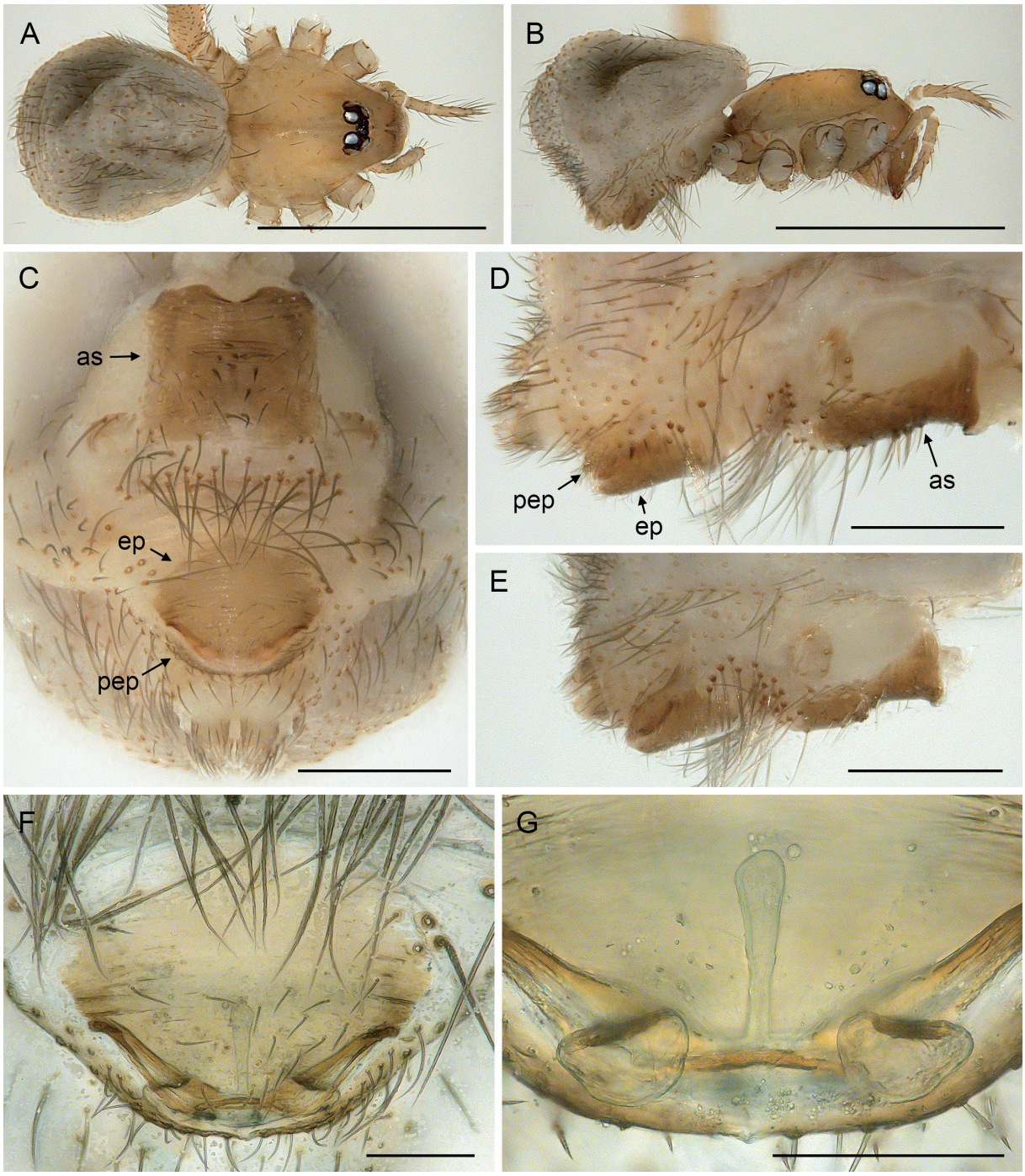

Fig. 31. *Pholcophora*? "Car544", females from Puerto Rico, Isla Mono (USNM ENT 783464, 783466). **A–B**. Habitus, dorsal and lateral views. **C**. Abdomen, ventral view. **D–E**. Abdomens of two specimens, lateral views (at same scale). **F**. Cleared female genitalia, ventral view. **G**. Detail of median internal structures, dorsal view. Abbreviations: as = anterior sclerite; ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A–B = 1 mm; C–E = 0.3 mm; F–G =0.1 mm.

with the Caribbean (Curaçao) genus *Papiamenta* Huber, 2000 than with true *Pholcophora*. Our UCE dataset (G. Meng, L. Podsiadlowski, B.A. Huber, unpubl. data) does not include the present species.

Material examined

PUERTO RICO – **Isla Monito** • 2 ♀♀, 1 juv., in pure ethanol; precise locality not specified; 18.16° N, 67.95° W; 14 Aug. 2012; I. Agnarsson *et al.* leg.; USNM ENT 783463, 783464, 783466.

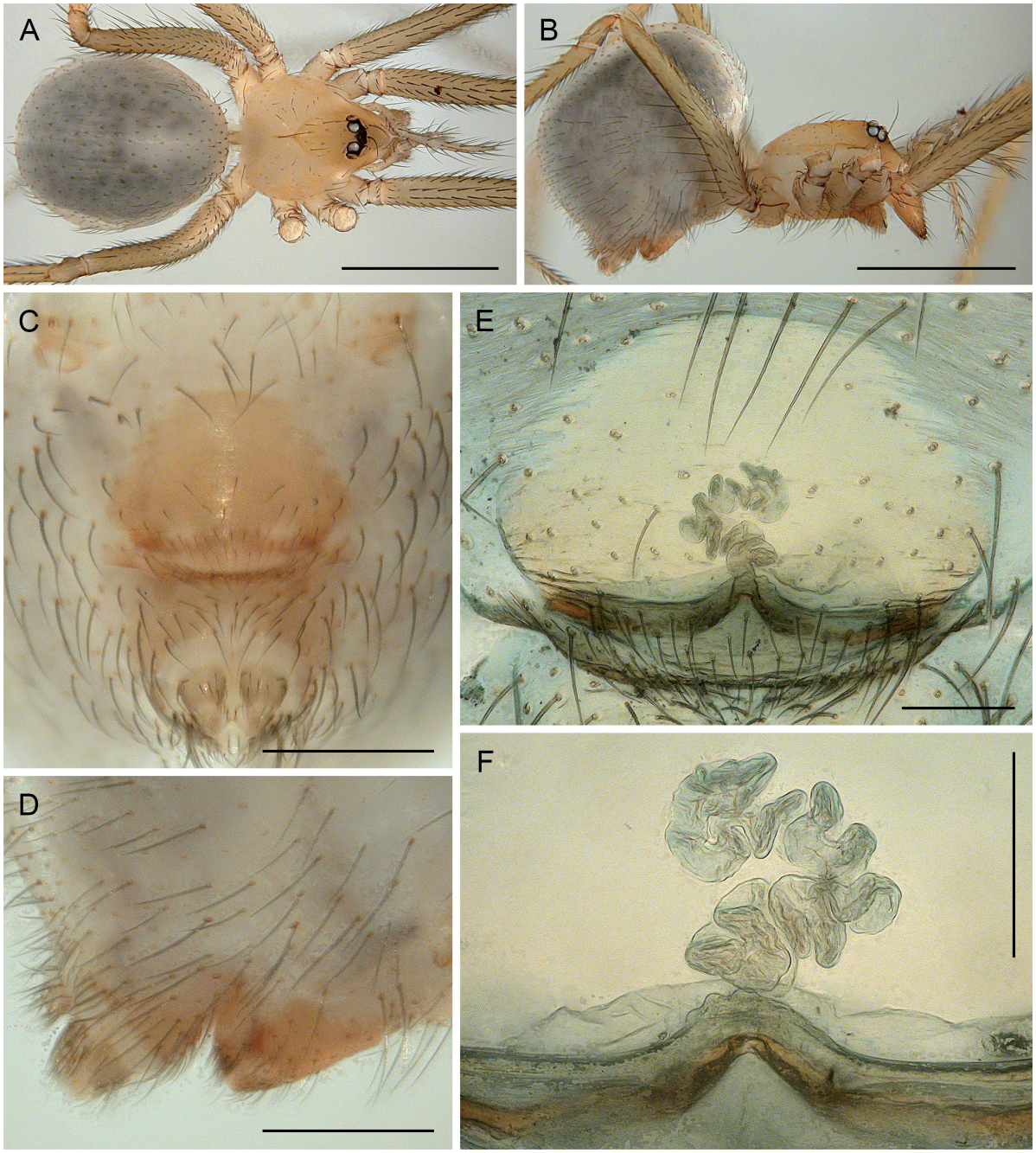

Fig. 32. *Pholcophora*? "Cu12-325", female from Cuba, Santiago de Cuba, Siboney (ZFMK Cu12-325). **A–B**. Habitus, dorsal and lateral views. **C–D**. Abdomen, ventral and lateral views. **E**. Cleared female genitalia, ventral view. **F**. Detail of median internal structures, dorsal view. Scale bars: A–B = 1 mm; C–D = 0.3 mm; E–F = 0.1 mm.

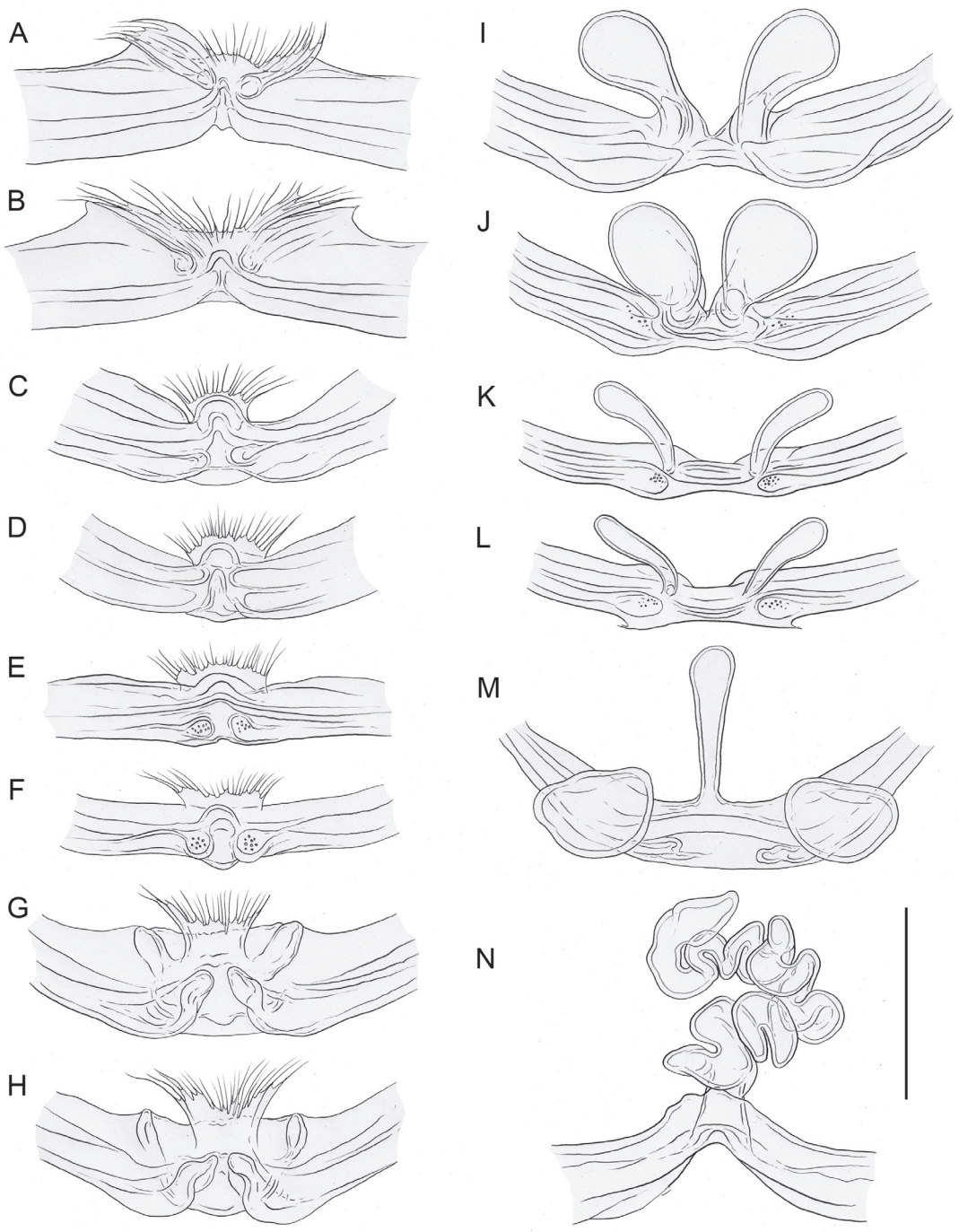

Fig. 33. *Pholcophora* internal female genitalia, median sections of main transversal internal sclerite. **A–B**. *P. americana* Banks, 1896, females from USA, California, Inyo Nat. Forest (ZFMK G089) and Colorado, near Golden (ZFMK USA16). **C–D**. *P. mazatlan* Huber sp. nov., females from Mexico, Guerrero, N of Mazatlán (ZFMK Ar 23943). **E–F**. *P. papanoa* Huber sp. nov., females from Mexico, Guerrero, S of Papanoa (ZFMK Ar 23945). **G–H**. *P.* "Mex354", females from Mexico, Puebla, SE of Tehuacan (ZFMK Mex354). **I–J**. *P. texana* Gertsch, 1935, females from Mexico, Hidalgo, SW of Jacala (ZFMK Ar 23952). **K–L**. *P. tehuacan* Huber sp. nov., females from Mexico, Puebla, SE of Tehuacan (ZFMK Ar 23949). **M**. *Pholcophora*? "Car544", female from Puerto Rico, Isla Mono (USNM ENT 783464). **N**. *Pholcophora*? "Cu12-325", female from Cuba, Santiago de Cuba, Siboney (ZFMK Cu12-325). Scale bar = 0.1 mm.

***Pholcophora*? "Cu12-325"**
Figs 32, 33N

S323 Gen. *Cu12-325* Cu12-325 – Eberle *et al.* 2018 (molecular data). — Huber *et al.* 2018: 55.

Remarks

The two adult females available of this species resemble other large representatives of the genus (Fig. 32A–B); body length 2.4; tibia 1 length 1.28, 1.36. Epigynum (Fig. 32C–D) consisting of trapezoidal anterior plate and short but wide posterior plate; internal genitalia (Fig. 32E–F) with distinctive median tube, curled up and ~600 µm long (reminding of the putatively distantly related *Gertschiola neuquena* Huber, 2000; see Huber 2000: fig. 354).

Our molecular data suggest that the present species is more closely related with other Caribbean taxa (*Pholcophora bahama*, the undescribed *Pholcophora*? "Car544", and the genus *Papiamenta*) than with true *Pholcophora*.

Material examined

CUBA – **Santiago de Cuba** • 2 ♀♀, in pure ethanol; Siboney, Cueva de los Majases; 19.9623° N, 75.7171° W; ~90 m a.s.l.; Apr. 2012; F. Cala Riquelme leg.; ZFMK Cu12-325.

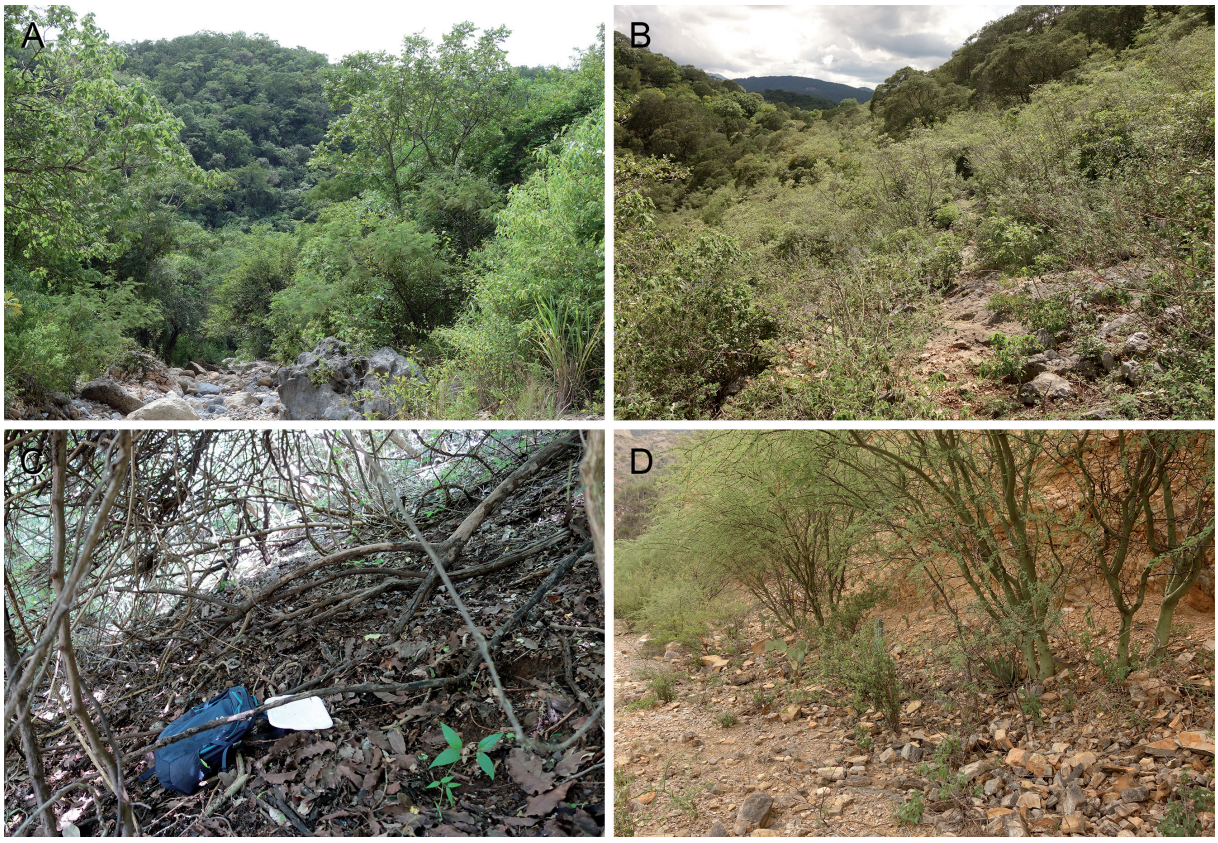

Fig. 34. Representative sample of habitats of *Pholcophora* Banks, 1896 in Mexico. **A**. Guerrero, 2 km N of Mazatlán (type locality of *P. mazatlan* Huber sp. nov.). **B**. Hidalgo, 2.5 km SW of Jacala (*P. texana* Gertsch, 1935). **C**. Guerrero, 5 km S of Papanoa (type locality of *P. papanoa* Huber sp. nov.; with collecting tray). **D**. Puebla, 35 km SE of Tehuacan (type locality of *P. tehuacan* Huber sp. nov.).

Genus ***Tolteca*** Huber, 2000

Tolteca Huber, 2000: 117. Type species: *Pholcophora hesperia* Gertsch, 1982.

Diagnosis

Easily distinguished from only other North American Ninetinae genus *Pholcophora* by small male cheliceral apophyses originating distally (Figs 38A–B, 44; in *Pholcophora* large and originating proximally); also by absence of stridulatory ridges on male chelicerae (Figs 41A, 46F); most species (except *T. sinnombre* sp. nov.) also by knob-shaped structure between epigynum and pedicel (Figs 43A, 45A, 49A); from most species (except *P. tehuacan* sp. nov.) also by smaller size (body length ~1.1–1.4; in *Pholcophora* ~1.7–3.1) and shorter legs (tibia 1 < 0.7, in *Pholcophora* > 1.0). From other geographically close genera (*Papiamenta*, *Galapa*) also by simple rod-shaped procursus (Figs 38C, 51C; much shorter in *Papiamenta*; with dorsal process in *Galapa*), by presence of humps on male sternum (absent in *Papiamenta*), and by unmodified male cheliceral fangs (with processes in *Galapa*).

Description

Male

Measurements. Total body length 1.1–1.4, carapace width 0.45–0.55. Legs very short, tibia 1 ~0.45–0.60; tibia 1 ~1.0–1.1 x carapace width; tibia 1 L/d 7–9; tibia 2 much shorter than tibia 4 (tibia 2 / tibia 4: 0.6–0.7).

Colour. Live specimens reddish brown (Fig. 36); carapace usually monochromous, sometimes with very indistinct darker median line widening anteriorly behind ocular area; abdomen colour slightly variable, usually monochromous, sometimes with indistinct dorsal marks; legs without dark or light bands. Colour in ethanol similar but paler, rather yellowish.

Body. Ocular area barely raised, eight eyes, AME relatively large, diameter ~25–30 µm, ~60–80% of PME diameter; Carapace without thoracic groove or with very indistinct low median indentation (visible in frontal view only). Clypeus unmodified or with rim slightly more sclerotized than in female. Sternum wider than long, with pair of distinct anterior processes near leg coxae 1. Abdomen globular; presence of epiandrous spigots unclear (reported as present in Huber 2000: fig. 126; not seen in two newly examined males of *T. hesperia* and *T. manzanillo* Huber sp. nov.; Fig. 46G); ALS with seven spigots each (Fig. 54C): one strongly widened spigot, one long pointed spigot, and five cylindrical spigots (one of which is unusually large); PMS with two short, pointed spigots (Fig. 54C); PLS without spigots.

Chelicerae. With one pair of simple frontal apophyses (Figs 38A–B, 41A–B); without stridulatory files (Figs 41A, 46F).

Palps. Coxa unmodified; trochanter barely modified (indistinct ventral projection); femur cylindrical, slightly widened distally, proximally without retrolateral hump; patella short; tibia globular, with two trichobothria; palpal tarsal organ raised, capsulate with small opening (Figs 41E–F, 46C–D; diameter of opening ~1.1–1.3 µm); procursus simple and straight (Figs 38C, 46A–B), without dorsal flap, not strongly elongated; genital bulb large (compared to palp size), with complex distal system of sclerites and folds, partly only visible in SEM (Figs 41C–D, 46A–B).

Legs. Without spines and curved hairs; with very short vertical hairs in higher density on tibia 1 (Fig. 42A–B; length of hairs ~20 µm). Trichobothria in usual arrangement: three on each tibia (except tibia 1: prolateral trichobothrium absent), one on each metatarsus; slightly feathered (Fig. 54D); length of dorsal trichobothrium on tibia 1: ~100 µm; retrolateral trichobothrium of tibia 1 in very distal

position (at 59–65%). Tarsus 1 with 4–6 distinct pseudosegments; tarsus 4 distally with one comb-hair on prolateral side (cf. Fig. 54H); leg tarsal organs very small, capsulate with small opening (Fig. 46E; diameter of opening ~1.0–1.4 µm); three claws (Fig. 42H).

Female

In general (size, colour) similar to male (Fig. 36) but sternum without pair of anterior humps, palpal tarsal organ less strongly raised (Figs 41G, 54E), and leg tibia 1 with usual low number of short vertical hairs; legs either slightly shorter than in males or of same length (only *T. oaxaca* sp. nov. with reasonable sample size: male/female tibia 1 length: 1.06). Spinnerets and comb-hairs as in male. Epigynum main (anterior) plate transversal band-shaped to crescent-shaped, weakly protruding in lateral view; posterior plate often indistinct, short but wide, usually with median anterior projection. Usually with distinct knob-shaped structure between epigynum and pedicel (Figs 43A, 45A, 49A, 54A–B; absent in *T. sinnombre* sp. nov.). Internal genitalia very simple, with pair of distinct transversal sclerites and pair of membranous sacs originating medially (Fig. 55), sacs very short in *T. oaxaca* (9–13 µm) and in *T. jalisco* (Gertsch, 1982) (18 µm), very long in *T. sinnombre* (85 µm); in other species ~42–48 µm; apparently without pore plates (possibly with very indistinct tiny groups of pores near median line).

Relationships

The genus *Tolteca* was not included in the molecular analysis of Eberle *et al.* (2018). Our new molecular data mostly suggest that *Tolteca* is sister to a clade consisting of true *Pholcophora* and a Caribbean clade (*Papiamenta* Huber, 2000 + Caribbean '*Pholcophora*'). This supports a monophyletic North American-Caribbean clade of Ninetinae (Fig. 1; see also general results of molecular analyses above). The latter clade is also strongly supported in our preliminary analyses of UCE data (G. Meng, L. Podsiadlowski, B.A. Huber, unpubl. data), but in that case with *Papiamenta* as sister to *Tolteca* + true *Pholcophora* (no Caribbean '*Pholcophora*' is included in the UCE dataset).

Within *Tolteca*, our unpartitioned analysis suggests that the most southern species (*T. oaxaca* sp. nov.) is sister to all other species; among those, *T. hesperia* is sister to *T. jalisco* + (*T. manzanillo* sp. nov. + *T. huahua* Huber sp. nov.). Our unpublished UCE dataset does not include *T. huahua* but otherwise it supports the same intrageneric relationships.

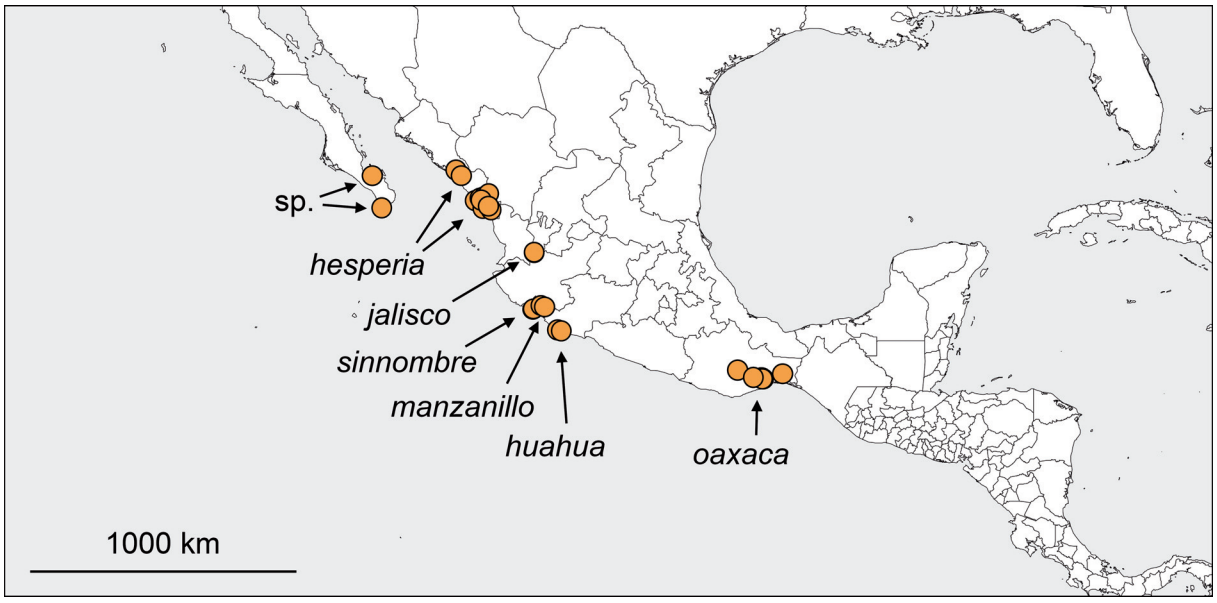

Fig. 35. Known distribution of *Tolteca* Huber, 2000.

Distribution

The genus appears restricted to the Pacific Lowlands and Baja Californian biogeographic provinces of Mexico, as delimited in Morrone *et al.* (2017) (Fig. 35). The female specimens originating from San Luis Potosí and Puebla provinces tentatively identified as *Tolteca* and briefly mentioned in Huber (2000: 120) are possibly not *Tolteca*.

Natural history

Most newly collected specimens were found in low, relatively dry forests (Fig. 56). Here they occupied the thin layers of leaf litter and sometimes the spaces under small stones and pebbles. They often shared

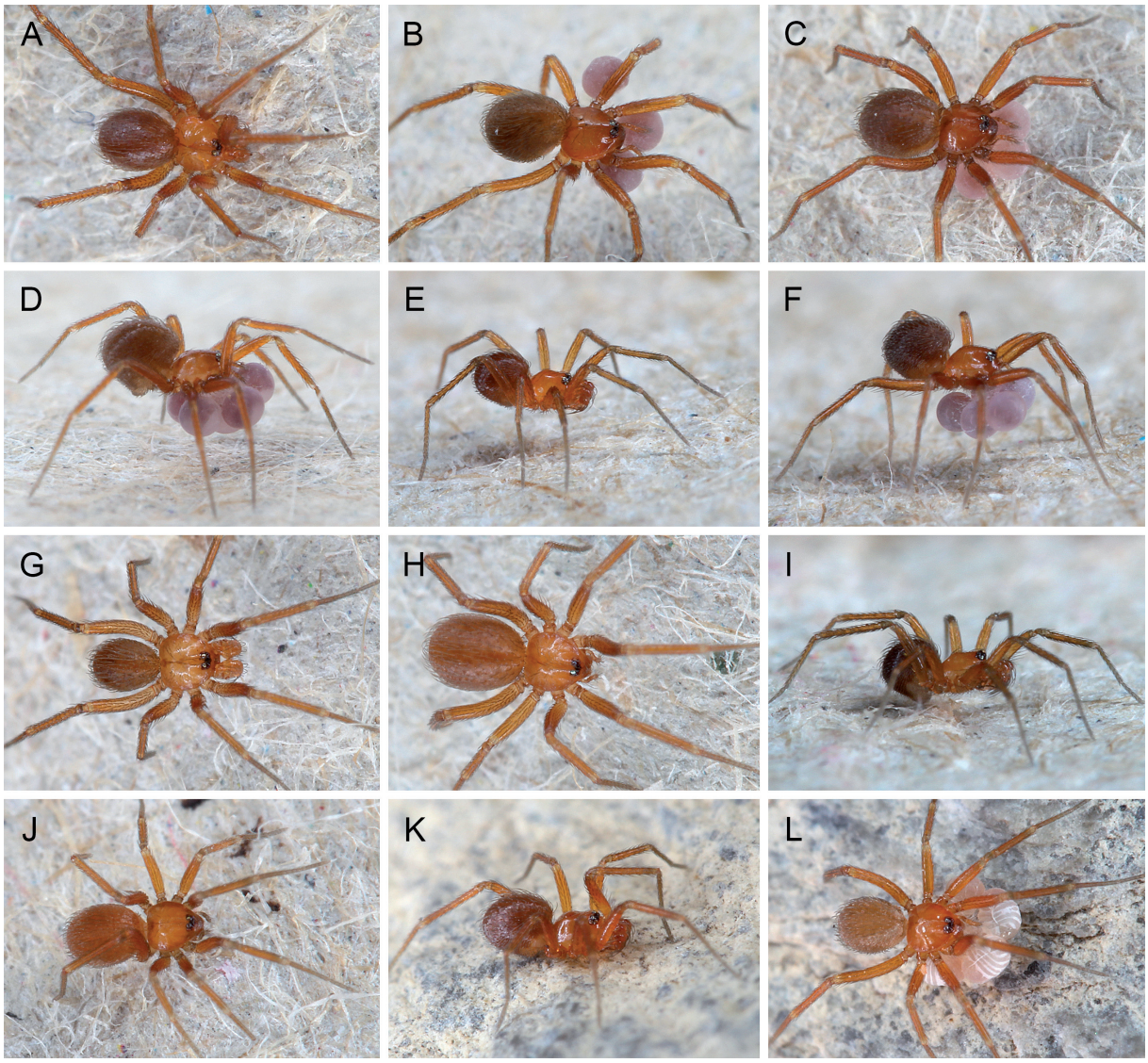

Fig. 36. *Tolteca* Huber, 2000 live specimens. **A–B**. *T. hesperia* (Gertsch, 1982), male and female with egg-sac from Mexico, Sinaloa, S of Rosario. **C–D**. *T. jalisco* (Gertsch, 1982), females with egg-sacs from Mexico, Jalisco, N of La Quemada. **E–F**. *T. manzanillo* Huber sp. nov., male and female with egg-sac from Mexico, Colima, E of Manzanillo. **G–H**. *T. sinnombre* Huber sp. nov., male and female from Mexico, Colima, S of Coquimatlán. **I–J**. *T. huahua* Huber sp. nov., male and female from Mexico, Michoacán, W of Huahua. **K–L**. *T. oaxaca* Huber sp. nov., male and female with egg-sac from Mexico, Oaxaca, NW of Tehuantepec.

the microhabitat with other species of Pholcidae, but *Tolteca* appeared largely restricted to the dryer areas while other genera (mostly *Modisimus*) seemed to prefer slightly more humid leaf litter. No webs were observed in the field, but the spiders built tiny silk mats in the glass vials. When disturbed, they ran rapidly and barely slowed down for several minutes. Females carried their disc-shaped egg-sacs under the prosoma (Fig. 36); egg-sacs usually contained 5 or 6 eggs, each with a diameter of ~0.35–0.45 mm (Huber & Eberle 2021). Some females had a genital plug (cf. Fig. 49A–B).

Composition

The genus now includes six nominal species, all of which are treated below.

Tolteca hesperia (Gertsch, 1982)
Figs 36A–B, 37–42

Pholcophora hesperia Gertsch, 1982: 102 (part; see Remarks below), figs 34–36, 45–47 (♂♀).

Tolteca hesperia – Huber 2000: 118 (part, see Remarks below), fig. 454 (other figures refer to *T. oaxaca* sp. nov.; see Remarks below).

Remarks

Gertsch (1982) designated a male specimen from Sinaloa as holotype, and in the text description he explicitly refers to that specimen. However, it is not clear if the figures of the male (Gertsch 1982: figs 34–36) are from the holotype or not. The procursus (narrowing gradually) and chelicerae (apophyses weakly protruding) suggest he drew another specimen of what is now considered a different species (maybe *T. huahua* sp. nov. or *T. manzanillo* sp. nov.). Gertsch's (1982) figures from the female (Gertsch

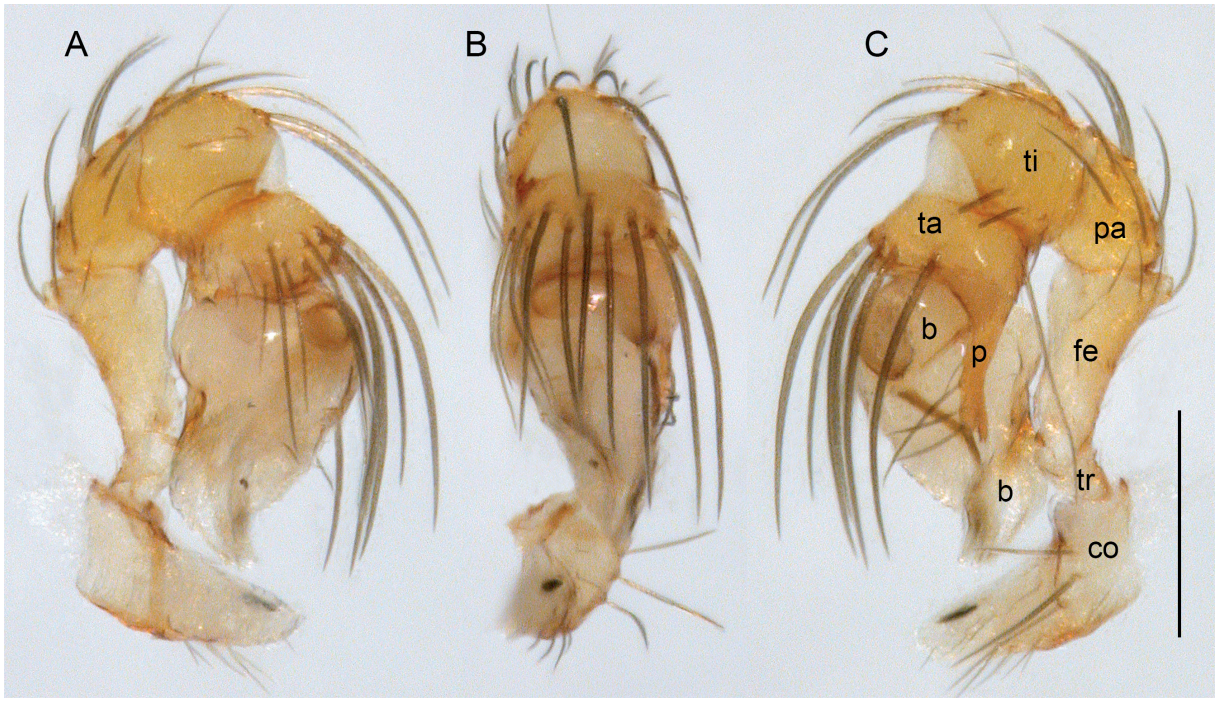

Fig. 37. *Tolteca hesperia* (Gertsch, 1982), male from Mexico, Sinaloa, S of Rosario (ZFMK Ar 23953). Left palp, prolateral, dorsal, and retrolateral views. Abbreviations: b = genital bulb; co = coxa; fe = femur; p = procursus; pa = patella; ta = tarsus; ti = tibia; tr = trochanter. Scale bar = 0.2 mm.

1982: figs 45–47) are certainly not from a topotypical female as no such female was available to him. It is not possible to tell from Gertsch's figures which species he illustrated.

The redescription of *T. hesperia* in Huber (2000) is mainly based on specimens from Oaxaca (2 mi SE of Niltepec) that are here considered a different species (*T. oaxaca* sp. nov.). Only the illustration of the procursus (Huber 2000: fig. 454) is from the holotype.

We have not restudied Gertsch's (1982) *T. hesperia* specimens but consider all specimens except for those from Sinaloa to represent other species. Judging from the geographic closeness to newly collected specimens, Gertsch's specimens from Colima probably represent *T. sinnombre* sp. nov. (10 mi S of Colima) and *T. manzanillo* sp. nov. (12 mi E of Manzanillo); those from Oaxaca probably represent *T. oaxaca* sp. nov. We cannot comment on the specimens from Baja California Sur listed in Gertsch (1982) and Huber (2000).

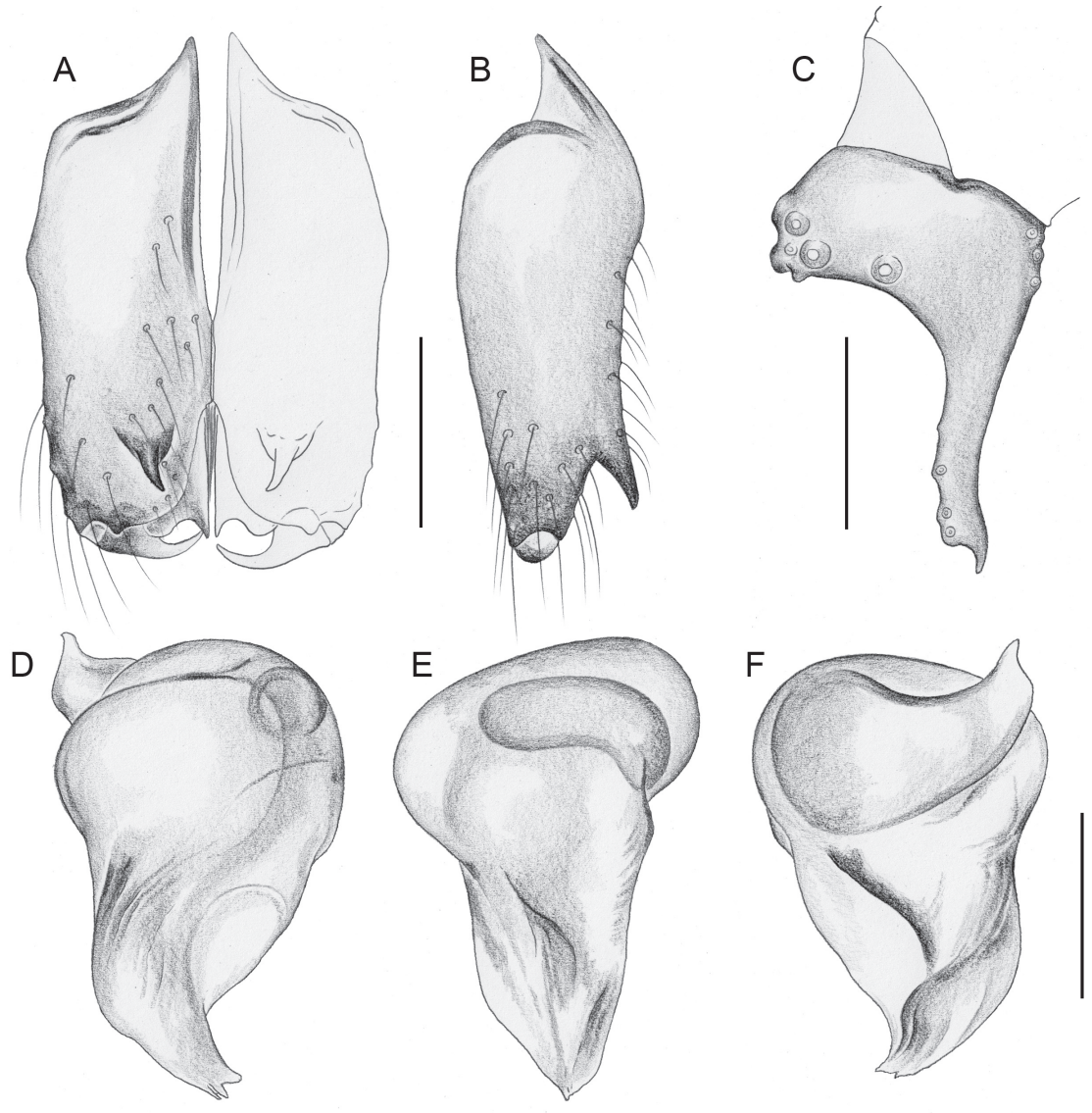

Fig. 38. *Tolteca hesperia* (Gertsch, 1982), male from Mexico, Sinaloa, S of Rosario (ZFMK Ar 23953). **A–B**. Chelicerae, frontal and lateral views. **C**. Left palpal tarsus and procursus, retrolateral view. **D–F**. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

Diagnosis

Distinguished from known congeners by the combination of: male genital bulb without dorsal ridge (Fig. 38F; unlike *T. jalisco*); procursus tip abruptly narrowing (Fig. 38C; similar to *T. sinnombre* sp. nov., unlike other species); male cheliceral apophyses in lateral view with large angle against distal-frontal face of chelicera (Fig. 38B; ~60° versus 25–35° in other species; not checked in *T. jalisco*); main epigynal plate band-like (Fig. 39A, C; rather than crescent-shaped as in *T. manzanillo* sp. nov., *T. huahua* sp. nov., and *T. oaxaca* sp. nov.); sacs in female internal genitalia ~40–50 µm long (Fig. 40C, F; i.e., longer than in *T. jalisco* and *T. oaxaca*, shorter than in *T. sinnombre*).

Material examined

Holotype

MEXICO – **Sinaloa** • ♂; 5 mi S of Mazatlán; ~23.20° N, 106.36° W; ~10–20 m a.s.l.; 23 Jul. 1954; W.J. Gertsch leg.; AMNH; examined (Huber 2000).

New record

MEXICO – **Sinaloa** • 4 ♂♂, 1 ♀, and 2 cleared epigyna; ~3 km S of Rosario; 22.9584° N, 105.8490° W; 65 m a.s.l.; 9 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; one male used for SEM; ZFMK Ar 23953 • 12 ♀♀, 5 juvs, in pure ethanol; same collection data as for preceding; one female used for SEM,

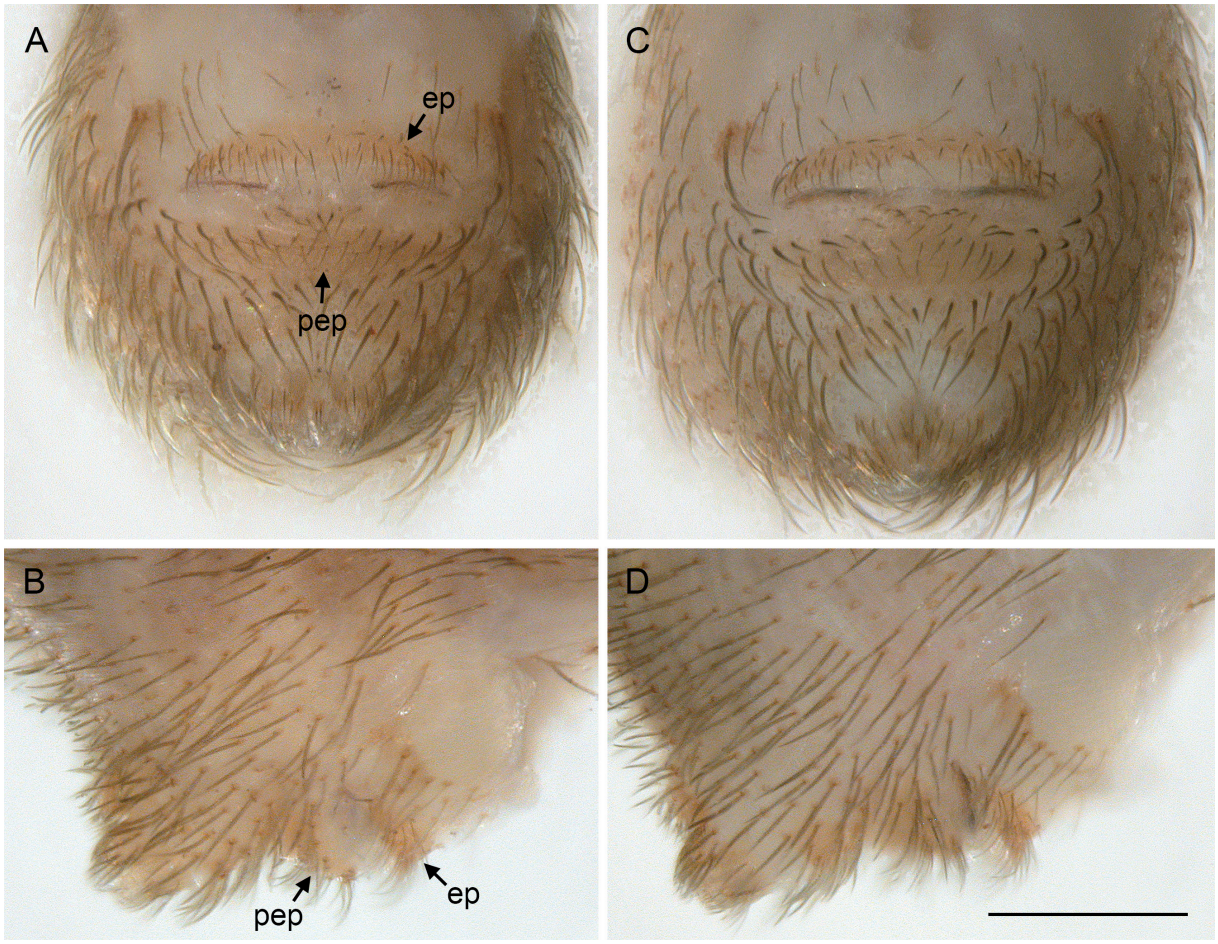

Fig. 39. *Tolteca hesperia* (Gertsch, 1982), females from Mexico, Sinaloa, S of Rosario (ZFMK Mex253), epigyna. **A, C**. Ventral views. **B, D**. Lateral views. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bar = 0.2 mm (all at same scale).

four female prosomata used for molecular work, two abdomens cleared and transferred to ZFMK Ar 23953; ZFMK Mex253 • 2 ♂♂; same collection data as for preceding; partly used for karyotype analyses; ZFMK Ar 23954 • 3 ♂♂, 2 ♀♀; same collection data as for preceding; partly used for µ-CT study; ZFMK Ar 23955 • 1 ♂, 4 ♀♀, 1 juv. (subadult male); same collection data as for preceding; LATLAX.

Description (amendments; see Gertsch 1982; Huber 2000)

Male (ZFMK Ar 23953)

Measurements. Total body length 1.40, carapace width 0.52. Distance PME-PME 40 µm; diameter PME 40 µm; distance PME-ALE 15 µm; distance AME-AME 10 µm; diameter AME 30 µm. Leg 1: 2.32 (0.65 + 0.17 + 0.57 + 0.60 + 0.33), tibia 2: 0.47, tibia 3: 0.43, tibia 4: 0.73; tibia 1 L/d: 7; diameters of leg femora 0.135, of leg tibiae 0.08.

Colour (in ethanol). Prosoma and legs monochromous ochre-yellow; abdomen ochre-grey, also monochromous.

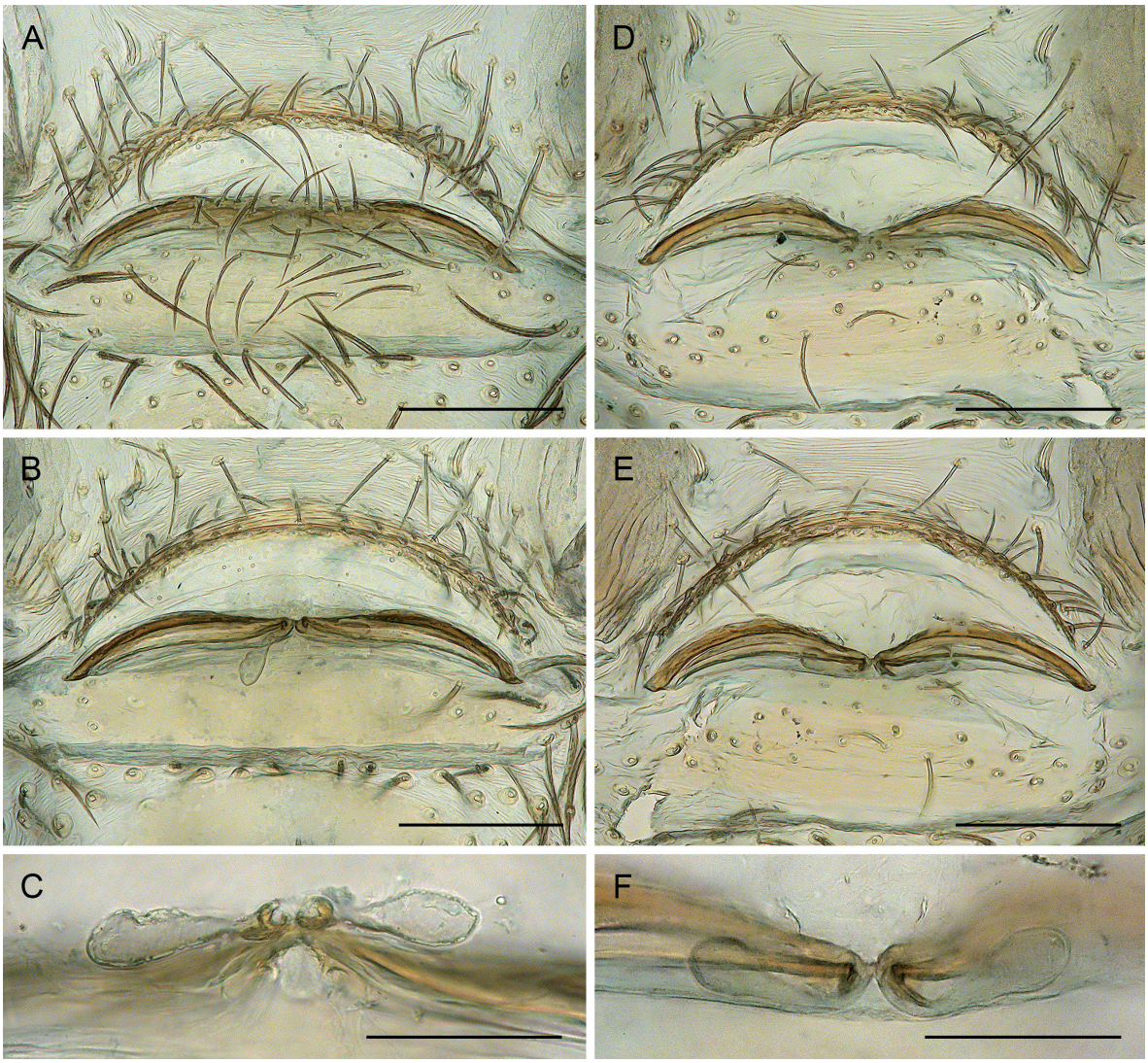

Fig. 40. *Tolteca hesperia* (Gertsch, 1982), females from Mexico, Sinaloa, S of Rosario (ZFMK Ar 23953), cleared female genitalia, **A, D**. Ventral views. **B, E**. Dorsal views. **C, F**. Detail of median internal structures. Scale bars: A–B, D–E = 0.1 mm; C, F = 0.05 mm.

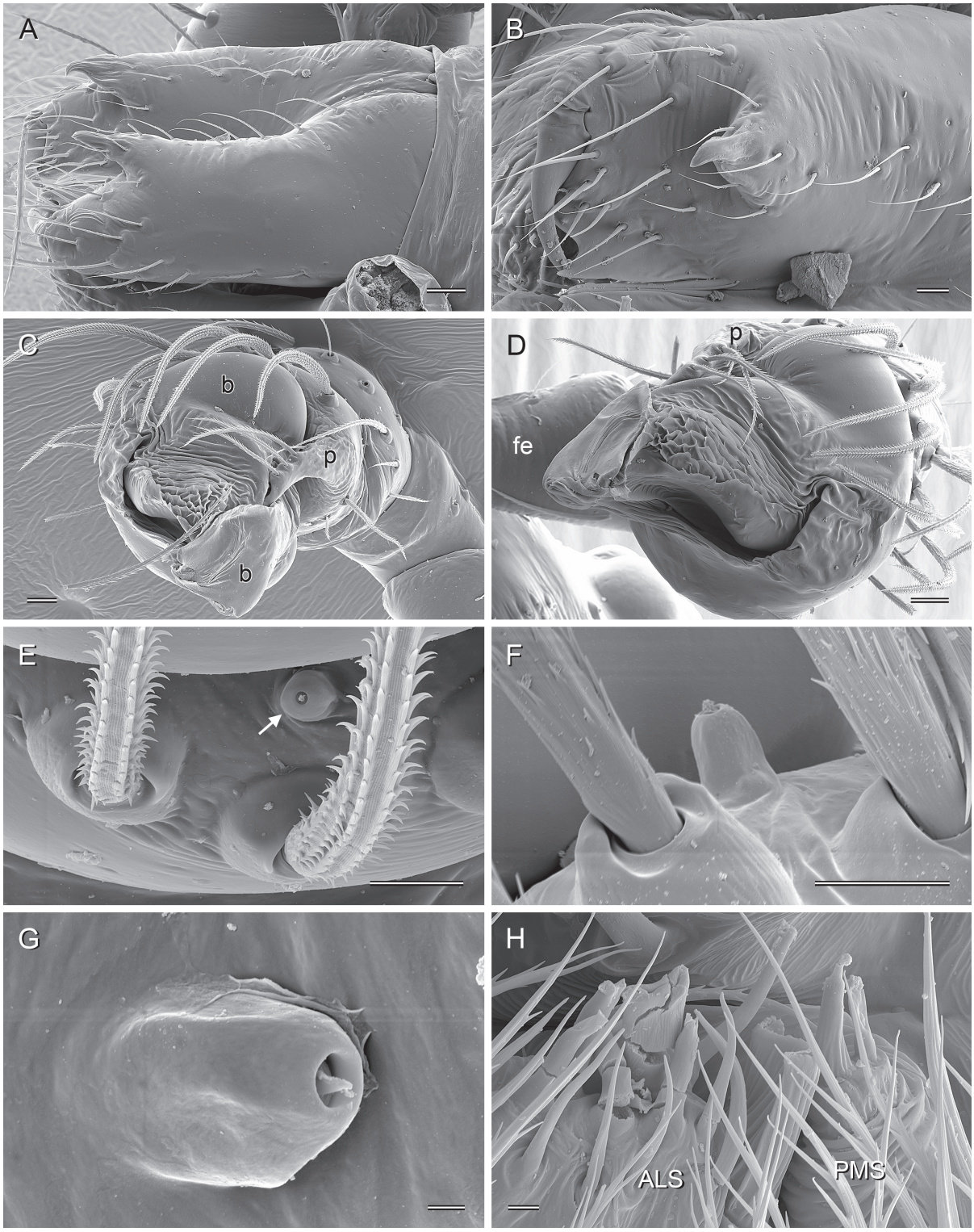

Fig. 41. *Tolteca hesperia* (Gertsch, 1982), male and female from Mexico, Sinaloa, 3 km S of Rosario (ZFMK Ar23953 and Mex253). **A**. Male chelicerae, lateral view. **B**. Male right chelicera, frontal view. **C**. Left male palp, distal view. **D**. Right genital bulb (and procursus), dorso-distal view. **E**. Detail of male palpal tarsus showing position of tarsal organ (arrow). **F**. Male palpal tarsal organ. **G**. Female palpal tarsal organ. **H**. Male ALS and PMS. Abbreviations: b = genital bulb; fe = femur; p = procursus. Scale bars: A, C–D = 20 μm; B, E–F = 10 μm; G = 1 μm; H = 2 μm.

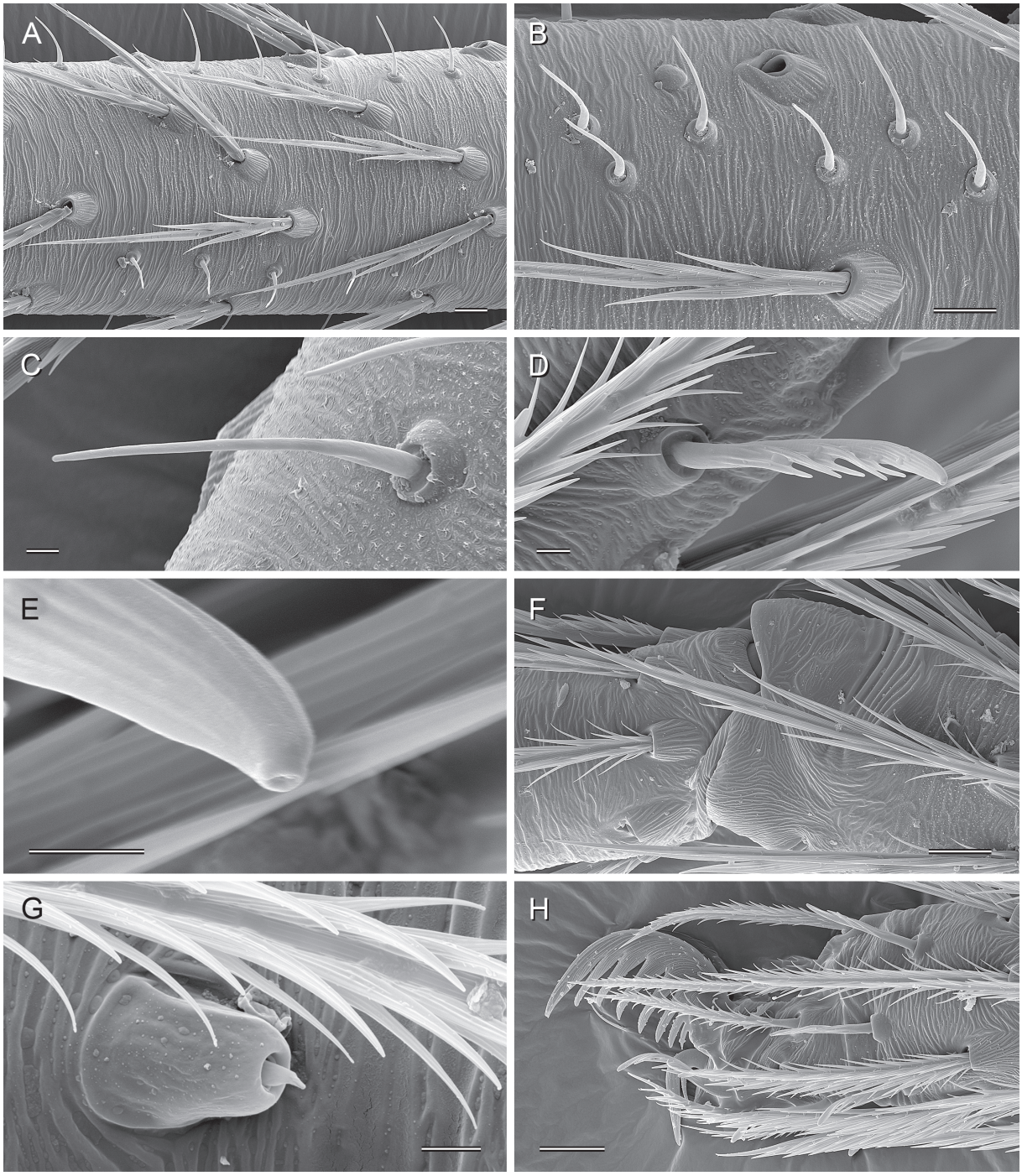

Fig. 42. *Tolteca hesperia* (Gertsch, 1982), male and female from Mexico, Sinaloa, 3 km S of Rosario (ZFMK Ar23953 and Mex253). **A**. Male tibia 1, prolateral view. **B**. Male tibia 1, retrolateral view. **C**. Sexually dimorphic short vertical hair on male tibia 1. **D**. 'Regular' short vertical hair on male metatarsus 1. **E**. Tip of 'regular' short vertical hair, detail of preceding image. **F**. Male metatarsus-tarsus 1 joint, retrolateral-dorsal view. **G**. Tarsal organ on female tarsus 1. **H**. Tip of left male tarsus 2, retrolateral view. Scale bars: A–B, F, H = 10 μm; C–D, G = 2 μm; E = 1 μm.

Body (Fig. 36A). Ocular area barely raised. Carapace without thoracic groove. Clypeus unmodified, only rim slightly more sclerotized, short (clypeus rim to ALE: 160 µm). Sternum wider than long (0.40/0.37), with pair of small but distinct anterior processes (~60 µm diameter at basis, ~60 µm long) near coxae 1. Abdomen globular.

Chelicerae (Figs 38A–B, 41A–B). With pair of frontal apophyses pointing downwards, distance between tips of apophyses: 60 µm; without stridulatory files.

Palps (Fig. 37). Coxa unmodified; trochanter without process; femur proximally without process, distally widened but simple, slightly curved towards dorsal; femur-patella joints minimally shifted toward prolateral side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; procursus very simple (Figs 38C, 41C), with distal ventral process; genital bulb (Figs 38D–F, 41C–D) large, complex, possibly indistinguishable from congeners.

Legs. Without spines and curved hairs; with slightly increased density of short vertical hairs on tibia 1 (Fig. 42A–C; barely visible in dissecting microscope); retrolateral trichobothrium of tibia 1 at 64%; prolateral trichobothrium absent on tibia 1; tarsus 1 with five pseudosegments, all fairly distinct.

Variation (male)

Tibia 1 in three other newly collected males: 0.55, 0.57, 0.60.

Female

In general, similar to male (Fig. 36B) but sternum without pair of anterior humps and tibia 1 without increased density of short vertical hairs. Total body length: ~1.20–1.40; tibia 1 in 12 newly collected females: 0.47–0.62 (mean 0.52). Epigynum (Fig. 39) very short band-shaped anterior plate slightly protruding in lateral view; posterior plate wide, median part slightly protruding anteriorly. With distinct knob between epigynum and pedicel (accidentally missing in specimens shown in Figs 39 and 40 – the knob sometimes stays attached to the prosoma when the abdomen is detached from it). Internal genitalia (Fig. 40) with pair of strong transversal sclerites, pair of distinct sacs (receptacles?), without (or with very small?) pore plates.

Distribution

Apparently widely distributed in southern and central Sinaloa, Mexico (Fig. 35). All specimens from outside of Sinaloa listed in Gertsch (1982) and Huber (2000) are here either considered to represent different (new) species (specimens from Colima and Oaxaca) or dubious (specimens from Baja California Sur – not re-examined).

Natural history

The newly collected spiders were found in the thin leaf litter layer and under stones in a low and quite dry roadside forest (Fig. 56A). They shared the locality with up to four unidentified species of *Modisimus*, one of them apparently in much the same microhabitat.

Tolteca jalisco (Gertsch, 1982)
Figs 36C–D, 43, 55C

Pholcophora jalisco Gertsch, 1982: 102, figs 40–41 (♂).

Tolteca jalisco – Huber 2000: 120, figs 458–459 (♂).

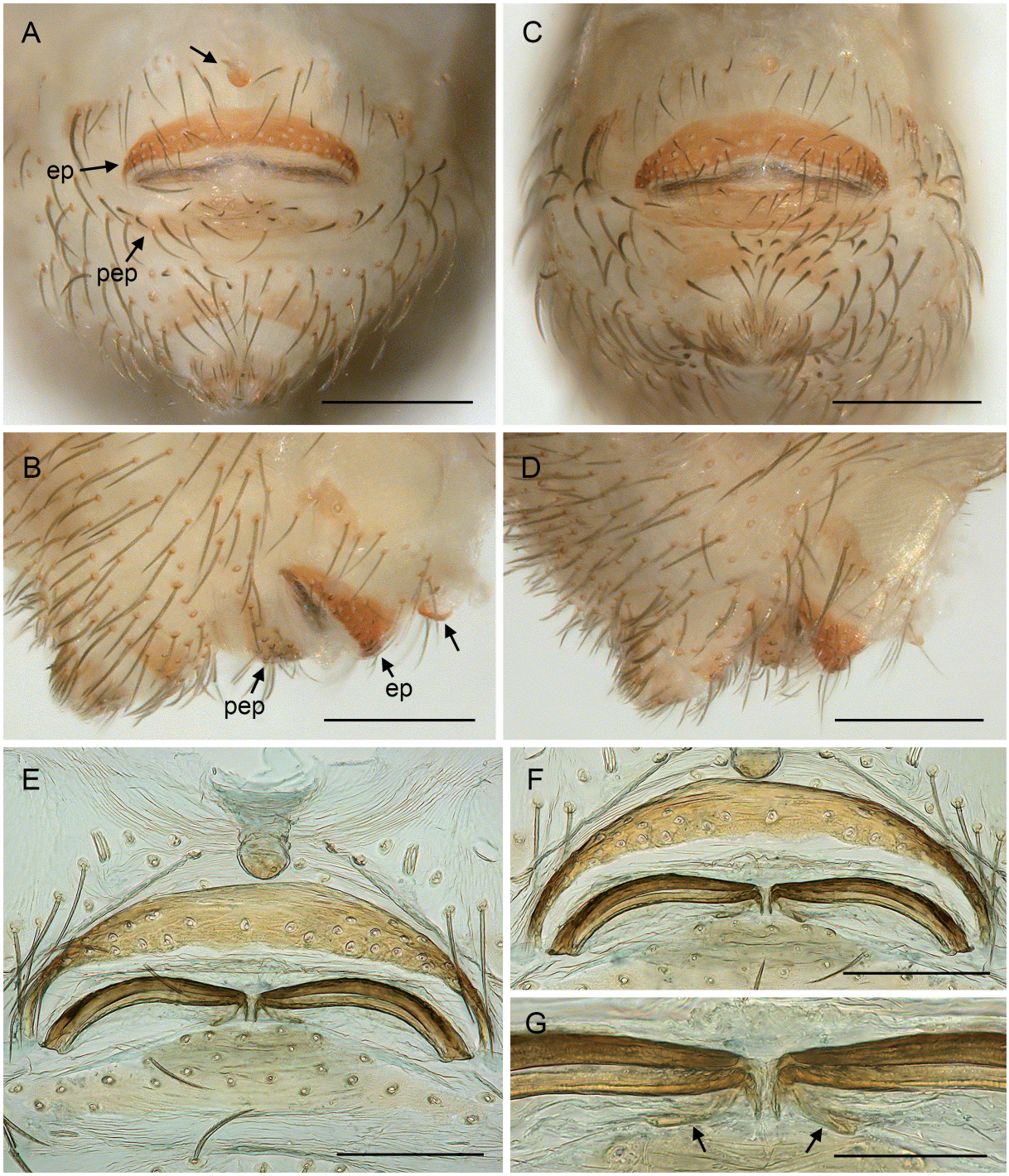

Fig. 43. *Tolteca jalisco* (Gertsch, 1982), females from Mexico, Jalisco, N of La Quemada (ZFMK Ar 23956). **A–D**. Epigyna, ventral (A, C) and lateral (B, D) views; arrows point at anterior knob-shaped structure. **E–G**. Cleared female genitalia, ventral (E) and dorsal (F) views, and detail of median internal structures (G); arrows point at membranous sacs (cf. Fig. 55C). Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A–D = 0.2 mm; E–F = 0.1 mm; G = 0.05 mm.

Diagnosis

Distinguished from known congeners by dorsal ridge on male genital bulb (Gertsch 1982: fig. 40; Huber 2000: fig. 458); also by the combination of: procursus tip gradually narrowing (Gertsch 1982: fig. 40; Huber 2000: fig. 459; unlike *T. hesperia* and *T. sinnombre* sp. nov.); main epigynal plate band-like (Fig. 43A, C; rather than crescent-shaped as in *T. manzanillo* sp. nov., *T. huahua* sp. nov., and *T. oaxaca* sp. nov.); sacs in female internal genitalia ~18–25 µm long (Fig. 55C; i.e., longer than in *T. oaxaca*, shorter than in all other species).

Material examined

Holotype

MEXICO – **Jalisco** • ♂; 20 mi N of La Quemada; ~21.18° N, 104.085° W; 28 Jul. 1954; W.J. Gertsch leg.; AMNH; examined (Huber 2000).

Remark

The information on the label accompanying the holotype deviates slightly from the data published by Gertsch (1982). This affects not only the date (28 or 24 Jul. 1954) but also the exact type locality, which is either 20 mi N of La Quemada (i.e., ~21.18° N, 104.085° W) or 29 mi N of La Quemada (i.e., ~21.23° N, 104.06° W).

New record

MEXICO – **Jalisco** • 2 ♀♀ abdomens; N of La Quemada, 'site 2'; 21.1922° N, 104.0975° W; 630 m a.s.l.; 7 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; ZFMK Ar 23956 • 6 ♀♀ in pure ethanol; same collection data as for preceding; two abdomens transferred to ZFMK Ar 23956, three prosomata used for molecular work; ZFMK Mex241.

Description

Female

In general, very similar to congeners (Fig. 36C–D); total body length 1.25; tibia 1 in three females: 0.50, 0.50, 0.53. Epigynum (Fig. 43A–D) very distinct short band-shaped anterior plate slightly protruding in lateral view; posterior plate wide, median part slightly protruding anteriorly. With distinct knob between epigynum and pedicel. Internal genitalia (Fig. 43E–G) with pair of strong transversal sclerites, pair of very small sacs (receptacles?), without (or with very small?) pore plates.

Distribution

Known from type locality and one neighbouring site only, in Mexico, Jalisco (Fig. 35). The exact coordinates of the type locality are unknown, but the type locality is either within ~2 km from the new locality or ~6 km NE of the new locality (see Remark above).

Natural history

The newly collected specimens were found in a small forest remnant at the roadside. Few specimens were found despite of intensive search (>2 hrs); no other pholcid species shared the leaf litter with *Tolteca*. The locality was shared with *Physocyclus brevicornus* Valdez-Mondragón, 2010.

Tolteca manzanillo Huber sp. nov.
urn:lsid:zoobank.org:act:97805AAF-C4EE-4A3E-A1F7-4B980E70005E
Figs 36E–F, 44A–C, 45–46, 55E

Pholcophora hesperia Gertsch, 1982: 102 (only specimens from 12 mi E of Manzanillo; see Remarks under *T. hesperia*).

Diagnosis

Distinguished from known congeners by the combination of: male genital bulb without dorsal ridge (unlike *T. jalisco*); procursus tip gradually narrowing (Fig. 44C; unlike *T. hesperia* and *T. sinnombre* sp. nov.); male cheliceral apophyses wide apart (Fig. 44A; distance between tips ~65 µm, i.e., much wider apart than in *T. huahua* sp. nov. and *T. oaxaca* sp. nov.), in lateral view with small angle against distal-frontal face of chelicera (Fig. 44B; unlike *T. hesperia*; not checked in *T. jalisco*); main epigynal plate crescent-shaped (Fig. 45A, C; rather than band-like as in *T. hesperia* and *T. jalisco*); sacs in female internal genitalia ~40–50 µm long (Fig. 55E; i.e., longer than in *T. jalisco* and *T. oaxaca*, shorter than in *T. sinnombre*).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Colima** • ♂; ~17 km E of Manzanillo; 19.0115° N, 104.1382° W; 35 m a.s.l.; 6 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Paratypes

MEXICO – **Colima** • 7 ♂♂; same collection data as for holotype; one male used for SEM; ZFMK Ar 23958 • 4 ♂♂, 8 ♀♀, 4 juvs; same collection data as for holotype; LATLAX.

Other material examined

MEXICO – **Colima** • 4 ♀♀, 9 juvs, in pure ethanol; same collection data as for holotype; two prosomata used for molecular work, two abdomens transferred to ZFMK Ar 23958; ZFMK Mex232 • 1 ♂; same collection data as for holotype; partly used for karyotype analyses; ZFMK 23959.

Description

Male (holotype)

Measurements. Total body length 1.10, carapace width 0.45. Distance PME-PME 40 µm; diameter PME 30 µm; distance PME-ALE 20 µm; distance AME-AME 10 µm; diameter AME 25 µm. Leg 1: 2.01 (0.55 + 0.15 + 0.50 + 0.48 + 0.33), tibia 2: 0.40, tibia 3: 0.37, tibia 4: 0.60; tibia 1 L/d: 7; diameters of leg femora 0.10, of leg tibiae 0.07.

Colour (in ethanol). Prosoma and legs monochromous ochre-yellow; abdomen slightly darker ochre-grey, also monochromous.

Body (Fig. 36E). Ocular area barely raised. Carapace without thoracic groove. Clypeus unmodified, short (clypeus rim to ALE: 120 µm). Sternum wider than long (0.36/0.30), almost round (i.e., not heart-shaped), with pair of small but distinct anterior processes (~40 µm diameter at basis, ~40 µm long) near coxae 1. Abdomen globular; gonopore apparently without epiandrous spigots (Fig. 46G); ALS with seven spigots each (Fig. 46H).

Chelicerae (Fig. 44A–B). With pair of frontal apophyses pointing downwards; distance between tips of apophyses 65 µm; without stridulatory files (Fig. 46F).

Palps. In general possibly indistinguishable from congeners (cf. Figs 37, 50); coxa unmodified; trochanter without process; femur proximally without process, distally widened but simple, slightly curved towards dorsal; femur-patella joints not shifted to one side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; procursus very simple (Figs 44C, 46A–B), with distal ventral process;

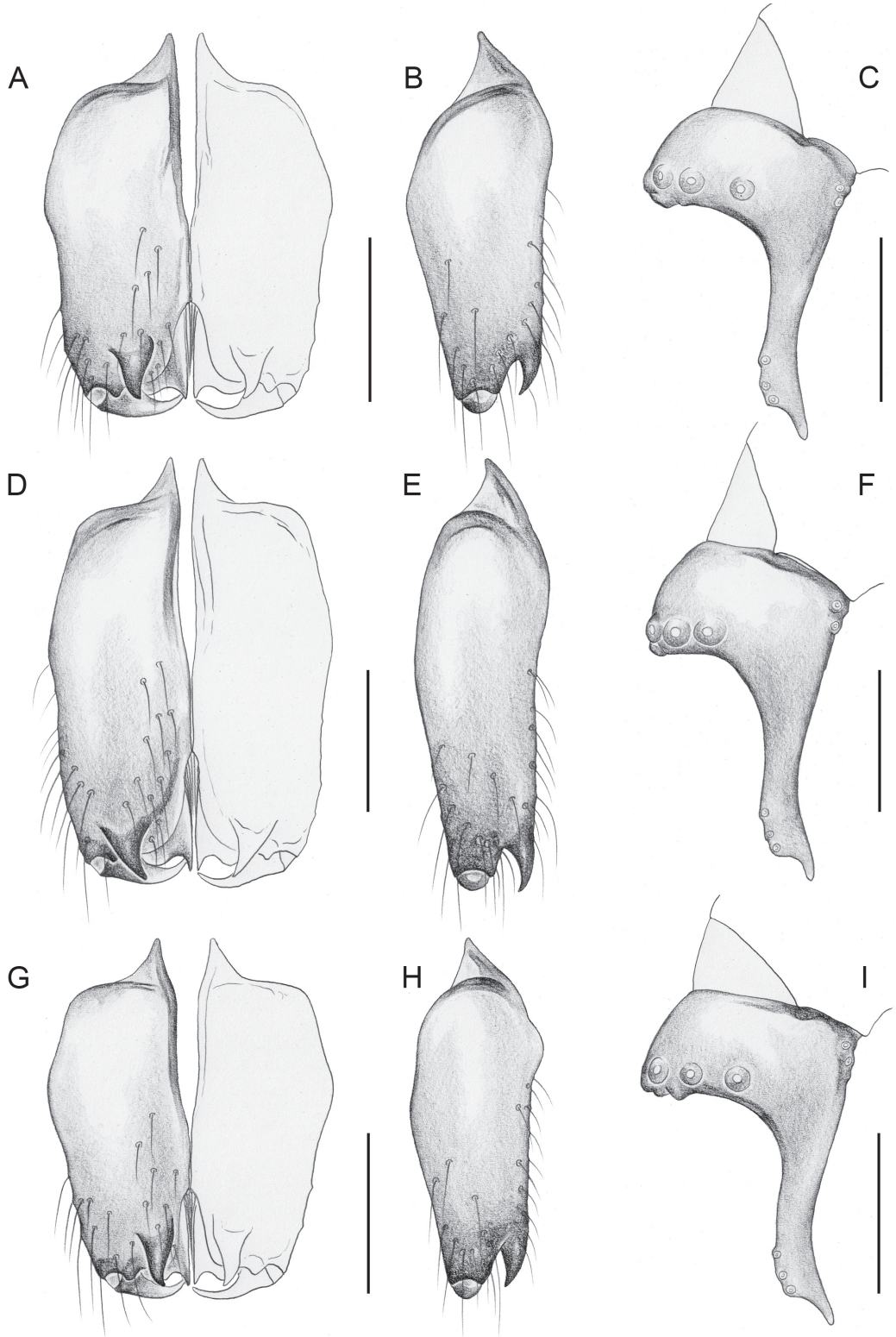

Fig. 44. *Tolteca* spp., male chelicerae, frontal and lateral views, and left male palpal tarsi and procursi, retrolateral views. **A–C**. *T. manzanillo* Huber sp. nov., paratype from Mexico, Colima, E of Manzanillo (ZFMK Ar 23958). **D–F**. *T. sinnombre* Huber sp. nov., holotype from Mexico, Colima, S of Coquimatlán (LATLAX). **G–I**. *T. huahua* Huber sp. nov., paratype from Mexico, Michoacán, W of Huahua (ZFMK Ar 23957). Scale bars = 0.1 mm.

genital bulb large, complex (Fig. 46A–B), in light microscope possibly indistinguishable from congeners (cf. Figs 38D–F, 51D–F).

Legs. Without spines and curved hairs; with slightly increased density of short vertical hairs on tibia 1 (barely visible in dissecting microscope); retrolateral trichobothrium of tibia 1 at 61%; prolateral trichobothrium absent on tibia 1; tarsus 1 with four pseudosegments, all fairly distinct.

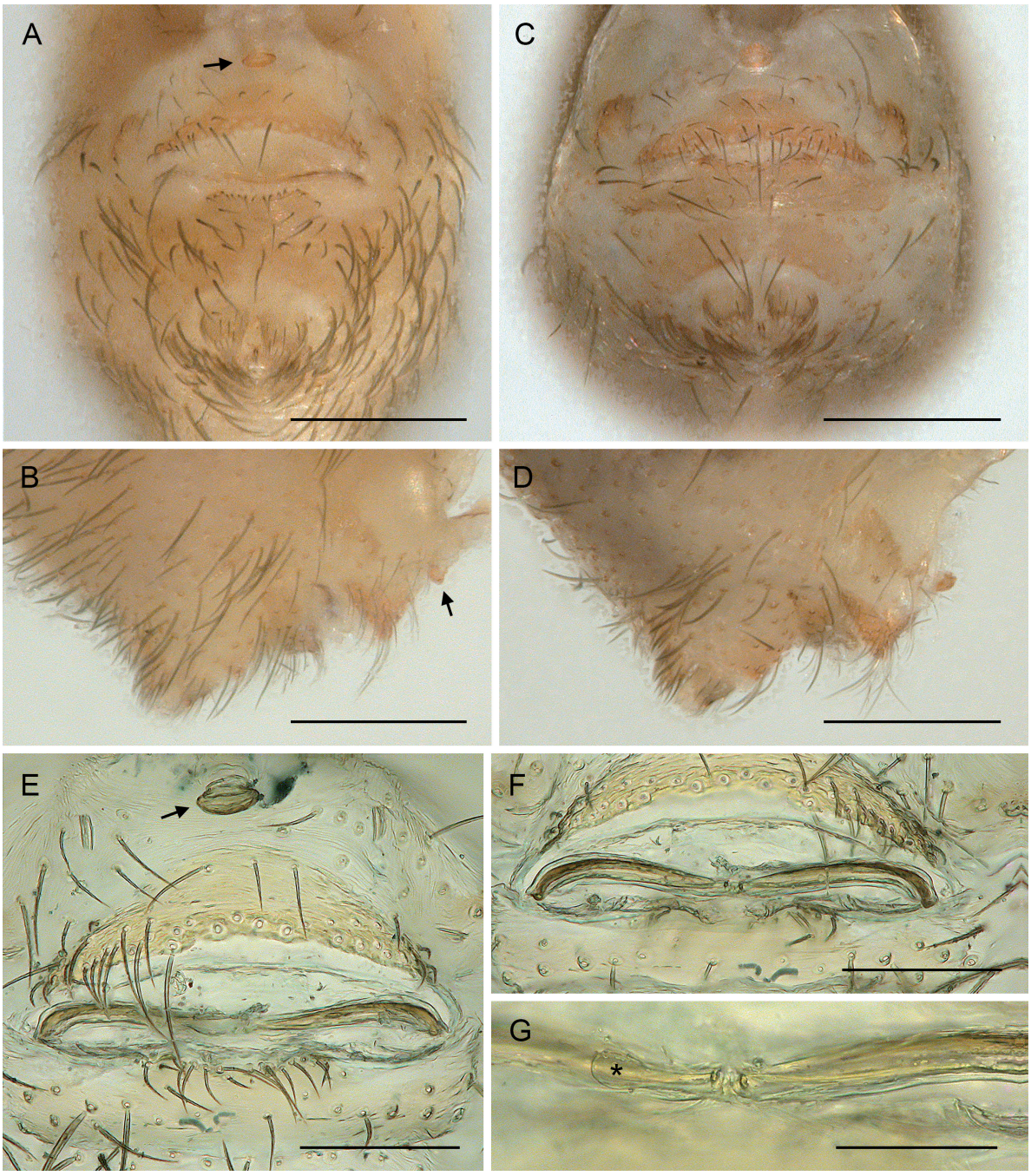

Fig. 45. *Tolteca manzanillo* Huber sp. nov., females from Mexico, Colima, E of Manzanillo (ZFMK Ar 23958). **A–D**. Epigyna, ventral (A, C) and lateral (B, D) views. **E–G**. Cleared female genitalia, ventral (E) and dorsal (F) views, and detail of median internal structures (G). Arrows point at anterior epigynal knob. Asterisk: membranous sac (cf. Fig. 55E). Scale bars: A–D = 0.2 mm; E, F = 0.1 mm; G = 0.05 mm.

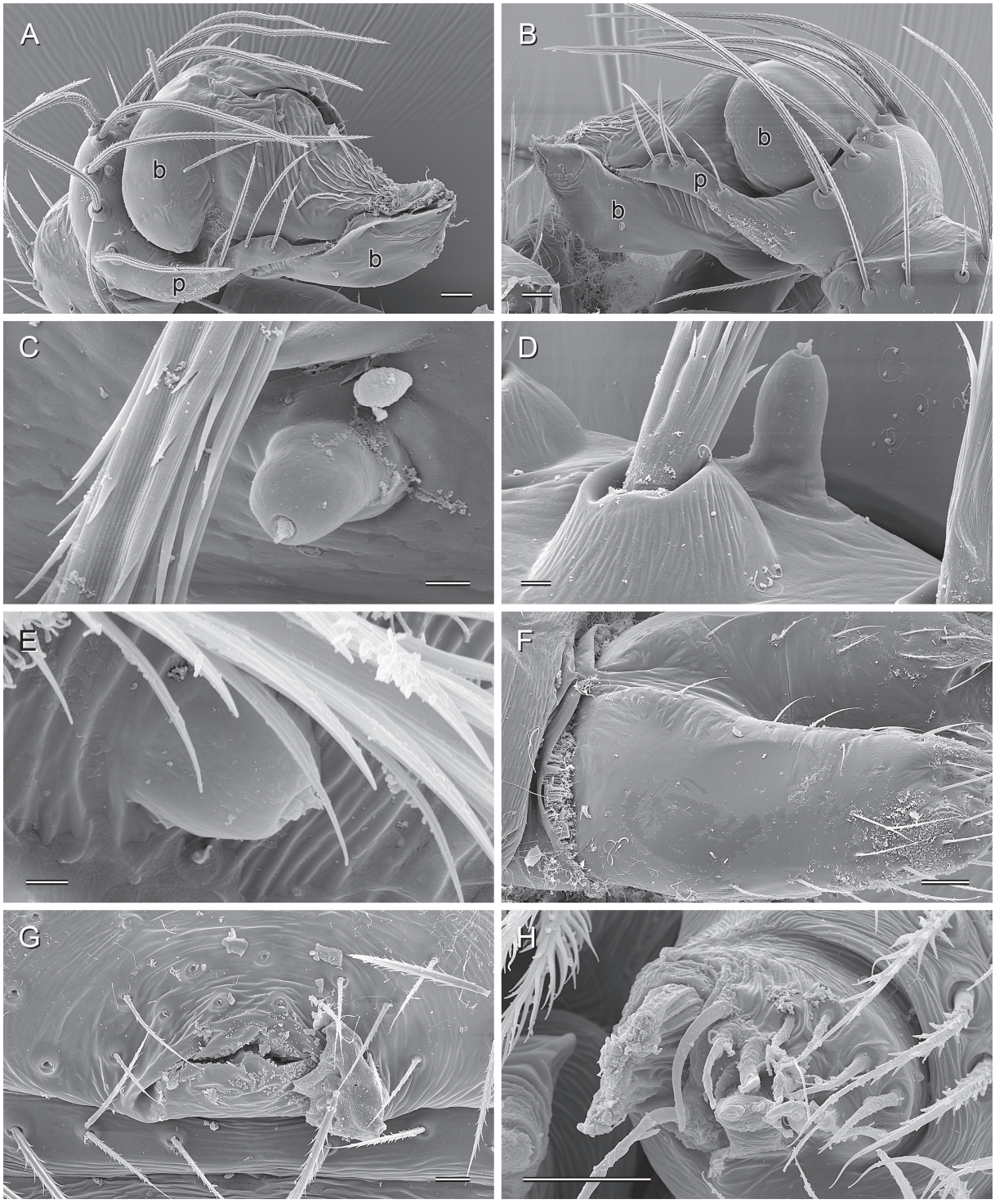

Fig. 46. *Tolteca manzanillo* Huber sp. nov.; male from Mexico, Colima, 17 km E of Manzanillo (ZFMK Ar 23958). **A**. Right palp, retrolateral-distal view. **B**. Left palp, retrolateral-dorsal view. **C–D**. Palpal tarsal organ. **E**. Tarsal organ on tarsus 2. **F**. Lateral face of right chelicera, showing absence of stridulatory file. **G**. Gonopore. **H**. ALS. Abbreviations: b = genital bulb; p = procursus. Scale bars: A–B, F = 20 μm; C–D = 2 μm; E = 1 μm; G–H = 10 μm.

Variation (male)
Tibia 1 in six males (incl. holotype): 0.45–0.52 (mean 0.48).

Female
In general, similar to male (Fig. 36F) but sternum without pair of anterior humps. Total body length: ~1.20–1.30; tibia 1 in eight females: 0.43–0.47 (mean 0.45). Epigynum (Fig. 45A–D) short crescent-shaped anterior plate slightly protruding in lateral view; posterior plate wide, median part slightly protruding anteriorly. With distinct knob between epigynum and pedicel. Internal genitalia (Fig. 45E–G) with pair of strong transversal sclerites, pair of distinct sacs (receptacles?), without (or with very small?) pore plates.

Distribution

Known from type locality and one poorly specified neighbouring locality in Mexico, Colima (Fig. 35). We do not have exact coordinates for Gertsch's (1982) specimens from "12 mi. E Manzanillo", but that locality is probably within a few km from the type locality.

Natural history

The spiders were very abundant in the dry leaf litter of a low thorn forest covering a hill near the Laguna of Cuyutlán (Fig. 56B).

Tolteca sinnombre Huber sp. nov.
urn:lsid:zoobank.org:act:51577DD3-55BD-4916-B9C2-E8A52181090C
Figs 36G–H, 44D–F, 47–48

Pholcophora hesperia Gertsch, 1982: 102 (only specimens from 10 mi S of Colima; see Remarks under *T. hesperia*).

Diagnosis

Distinguished from known congeners by the combination of: male genital bulb without dorsal ridge (unlike *T. jalisco*); procursus tip abruptly narrowing (Fig. 44F; similar to *T. hesperia*, unlike other species); male cheliceral apophyses wide apart (distance between tips ~75 µm, i.e., much wider apart than in *T. huahua* sp. nov. and *T. oaxaca* sp. nov.), in lateral view with small angle against distal-frontal face of chelicera (Fig. 44E; unlike *T. hesperia*; not checked in *T. jalisco*); main epigynal plate very short, band-shaped, densely set with short hairs (Fig. 48A–B); without knob between epigynum and pedicel (Fig 47A, C); female internal genitalia with pair of very long sacs (85 µm) (Figs 48D, 55F).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype
MEXICO – **Colima** • ♂; ~6 km S of Coquimatlán, near 'Cueva sin Nombre'; 19.1521° N, 103.8350° W; 280 m a.s.l., 6 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Other material examined

MEXICO – **Colima** • 2 ♀♀ abdomens; same collection data as for holotype; ZFMK Ar 23960 • 2 ♀♀ and 2 female prosomata (abdomens transferred to ZFMK Ar 23960), in pure ethanol; same collection data as for holotype; ZFMK Mex237.

Description

Male (holotype)
Measurements. Total body length 1.25, carapace width 0.56. Distance PME-PME 45 µm; diameter PME 45 µm; distance PME-ALE 20 µm; distance AME-AME 15 µm; diameter AME 30 µm. Leg 1:

2.26 (0.63 + 0.17 + 0.58 + 0.55 + 0.33), tibia 2: 0.47, tibia 3: 0.43, tibia 4: 0.72; tibia 1 L/d: 7; diameters of leg femora 0.130–0.135, of leg tibiae 0.08.

Colour (in ethanol). Prosoma and legs monochromous ochre-yellow, only carapace with slightly darker median line widening anteriorly; abdomen slightly darker ochre-grey, with some indistinct darker marks dorsally.

Body (Fig. 36G). Ocular area barely raised. Carapace without thoracic groove. Clypeus unmodified but with sclerotized rim, short (clypeus rim to ALE: 170 µm). Sternum wider than long (0.40/0.36), almost round (i.e., not heart-shaped), with pair of small but distinct anterior processes (~80 µm diameter at basis, ~80 µm long) near coxae 1. Abdomen globular.

Chelicerae (Fig. 44D–E). With pair of frontal apophyses pointing downwards; distance between tips of apophyses 75 µm; without stridulatory files.

Palps. In general possibly indistinguishable from congeners (cf. Figs 37, 50) but patella ventrally apparently longer than in other species; coxa unmodified; trochanter without process; femur proximally without process, distally widened but simple, slightly curved towards dorsal; femur-patella joints very

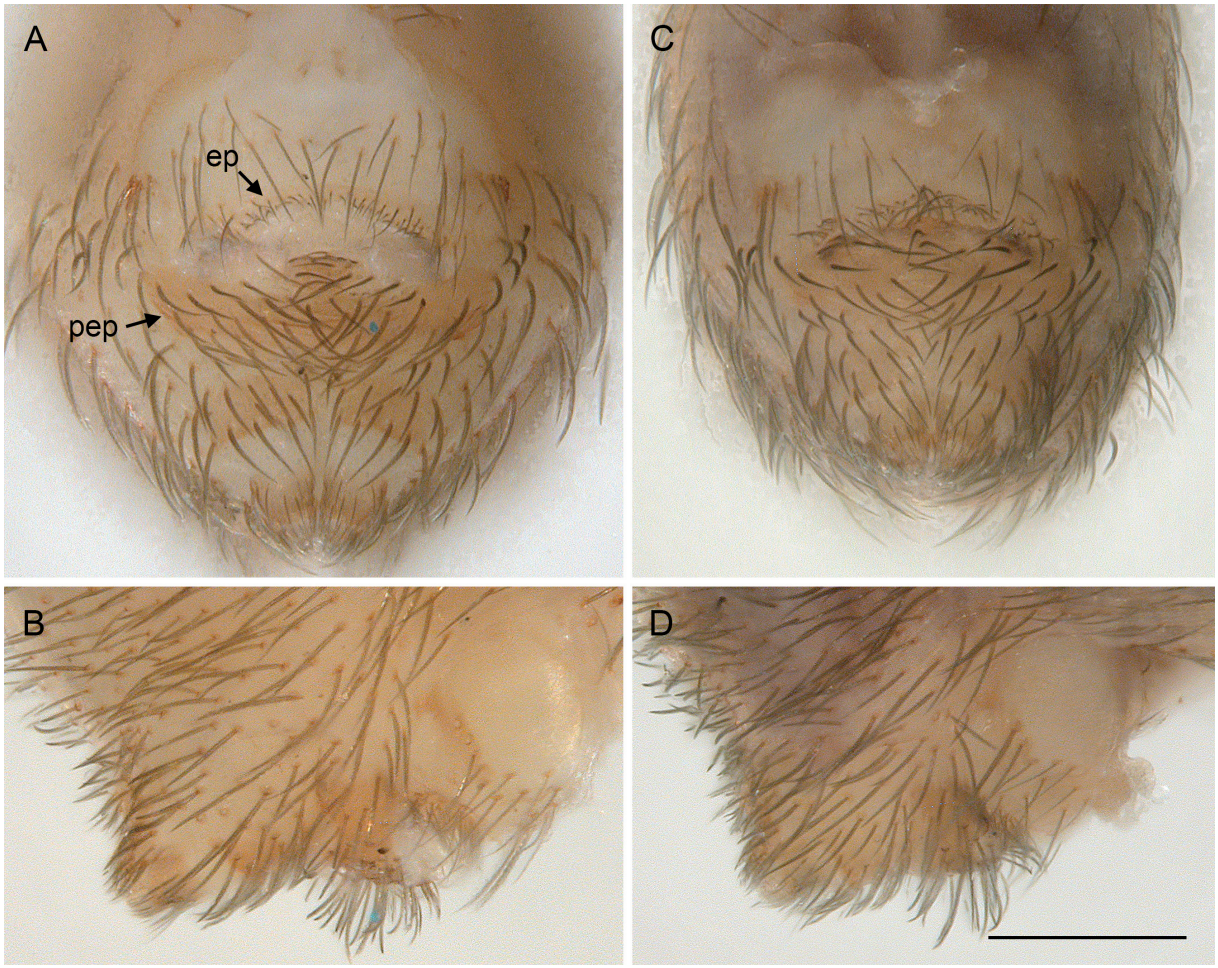

Fig. 47. *Tolteca sinnombre* Huber sp. nov., females from Mexico, Colima, S of Coquimatlán (ZFMK Ar 23940), epigyna. **A, C**. Ventral views. **B, D**. Lateral views. Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bar = 0.2 mm (all at same scale).

slightly shifted toward prolateral side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; procursus very simple (Fig. 44F), with distal ventral process; genital bulb large, complex, in light microscope possibly indistinguishable from congeners (cf. Figs 38D–F, 51D–F).

Legs. Without spines and curved hairs; with slightly increased density of short vertical hairs on tibia 1 (barely visible in dissecting microscope); retrolateral trichobothrium of tibia 1 at 63%; prolateral trichobothrium absent on tibia 1; tarsus 1 with five pseudosegments, all fairly distinct.

Female

In general, similar to male (Fig. 36H) but sternum without pair of anterior humps. Total body length: ~1.20–1.30; tibia 1 in four females: 0.48, 0.50, 0.53, 0.58. Epigynum (Fig. 47) with very short band-shaped anterior plate densely set with short hairs; posterior plate wide, median part distinctly protruding anteriorly. Without knob between epigynum and pedicel. Internal genitalia (Fig. 48) with pair of strong transversal sclerites, pair of distinct sacs (receptacles?), without (or with very small?) pore plates.

Distribution

Known from type locality and one poorly specified neighbouring locality in Mexico, Colima (Fig. 35). We do not have exact coordinates for Gertsch's (1982) specimens from "10 mi. S Colima", but that locality is probably within 10 km from the type locality.

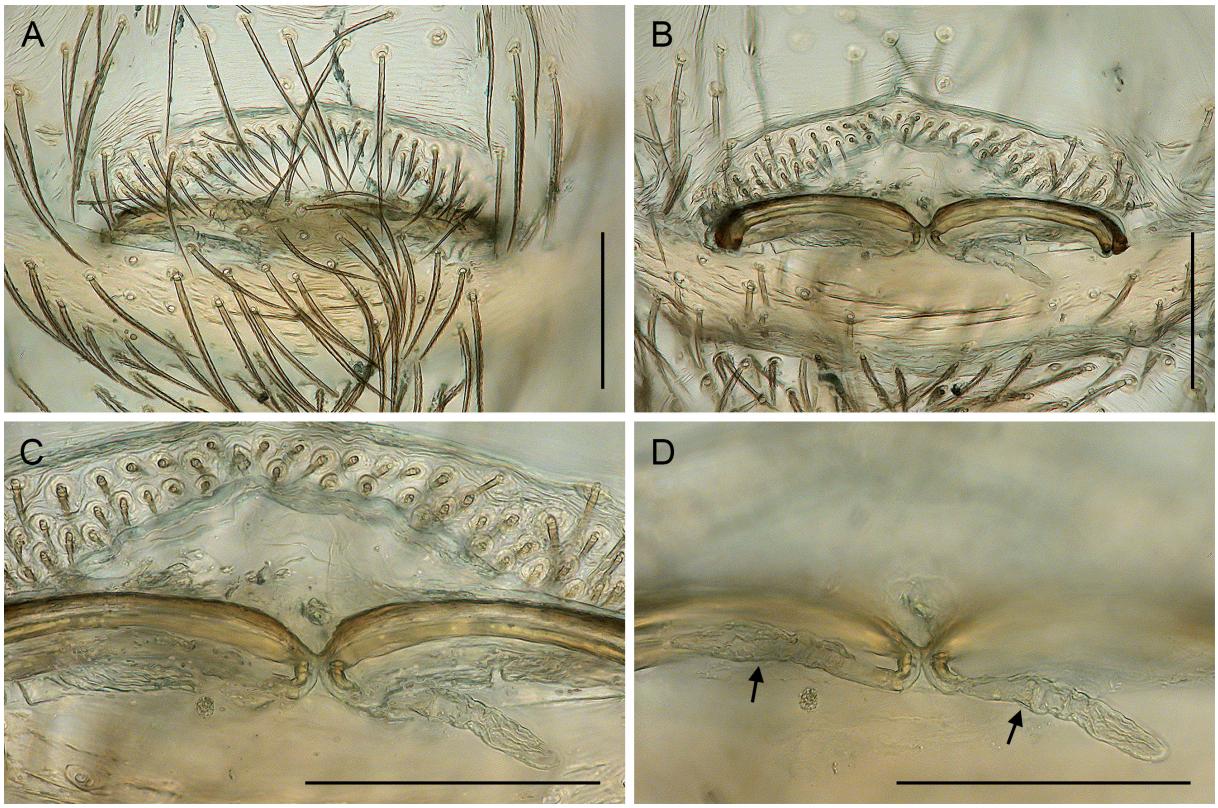

Fig. 48. *Tolteca sinnombre* Huber sp. nov., female from Mexico, Colima, S of Coquimatlán (ZFMK Ar 23960), cleared female genitalia. **A**. Ventral view. **B**. Dorsal view. **C–D**. Detail of median internal structures. Arrows point at membranous sacs (cf. Fig. 55F). Scale bars = 0.1 mm.

Natural history

The specimens were collected in a low forest in a sink below the 'Cueva sin Nombre' cave. The leaf litter was partly humid and was shared with two other small pholcids (*Anopsicus* sp., *Modisimus* sp.).

Tolteca huahua Huber sp. nov.
urn:lsid:zoobank.org:act:DE7A2222-3EA8-49E2-8BA1-FEBC61571376
Figs 36I–J, 44G–I, 49, 55D

Diagnosis

Distinguished from known congeners by the combination of: male genital bulb without dorsal ridge (unlike *T. jalisco*); procursus tip gradually narrowing (Fig. 44I; unlike *T. hesperia* and *T. sinnombre* sp. nov.); male cheliceral apophyses close together (Fig. 44G; distance between tips ~40 μm, similar to *T. oaxaca* sp. nov.), in lateral view with small angle against distal-frontal face of chelicera (Fig. 44H; unlike *T. hesperia*; not checked in *T. jalisco*); main epigynal plate crescent-shaped (Fig. 49A, C; rather than band-like as in *T. hesperia* and *T. jalisco*); sacs in female internal genitalia ~40–50 μm long (Figs 49G, 55D; i.e., longer than in *T. jalisco* and *T. oaxaca*, shorter than in *T. sinnombre*).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Michoacán** • ♂; ~20 km W of Huahua; 18.2346° N, 103.2020°W; 205 m a.s.l.; 5 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Paratypes

MEXICO – **Michoacán** • 1 ♂; same collection data as for holotype; ZFMK Ar 23957 • 3 ♂♂, 9 ♀♀, 2 juvs; same collection data as for holotype; LATLAX.

Other material examined

MEXICO – **Michoacán** • 3 ♀♀, 2 ♀♀ prosomata (abdomens transferred to ZFMK Ar 23957), 5 juvs, in pure ethanol; same collection data as for holotype; ZFMK Mex231 • 1 ♀, 2 juvs, in pure ethanol; ~4 km W of Huahua; 18.1972° N, 103.0449° W; 40 m a.s.l.; 5 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; ZFMK Mex229.

Description

Male (holotype)

Measurements. Total body length 1.10, carapace width 0.46. Distance PME-PME 40 μm; diameter PME 40 μm; distance PME-ALE 20 μm; distance AME-AME 10 μm; diameter AME 25 μm. Leg 1: 1.89 (0.50 + 0.17 + 0.47 + 0.47 + 0.28), tibia 2: 0.37, tibia 3: 0.35, tibia 4: 0.60; tibia 1 L/d: 7; diameters of leg femora 0.10, of leg tibiae 0.07.

Colour (in ethanol). Prosoma and legs monochromous ochre-yellow; abdomen slightly darker ochre-grey, with very indistinct large dorsal marks.

Body (Fig. 36I). Ocular area barely raised. Carapace without thoracic groove (very low indentation visible in frontal view only). Clypeus unmodified, short (clypeus rim to ALE 150 μm). Sternum wider than long (0.34/0.26), with pair of small but distinct anterior processes (~50 μm diameter at basis, ~50 μm long) near coxae 1. Abdomen globular.

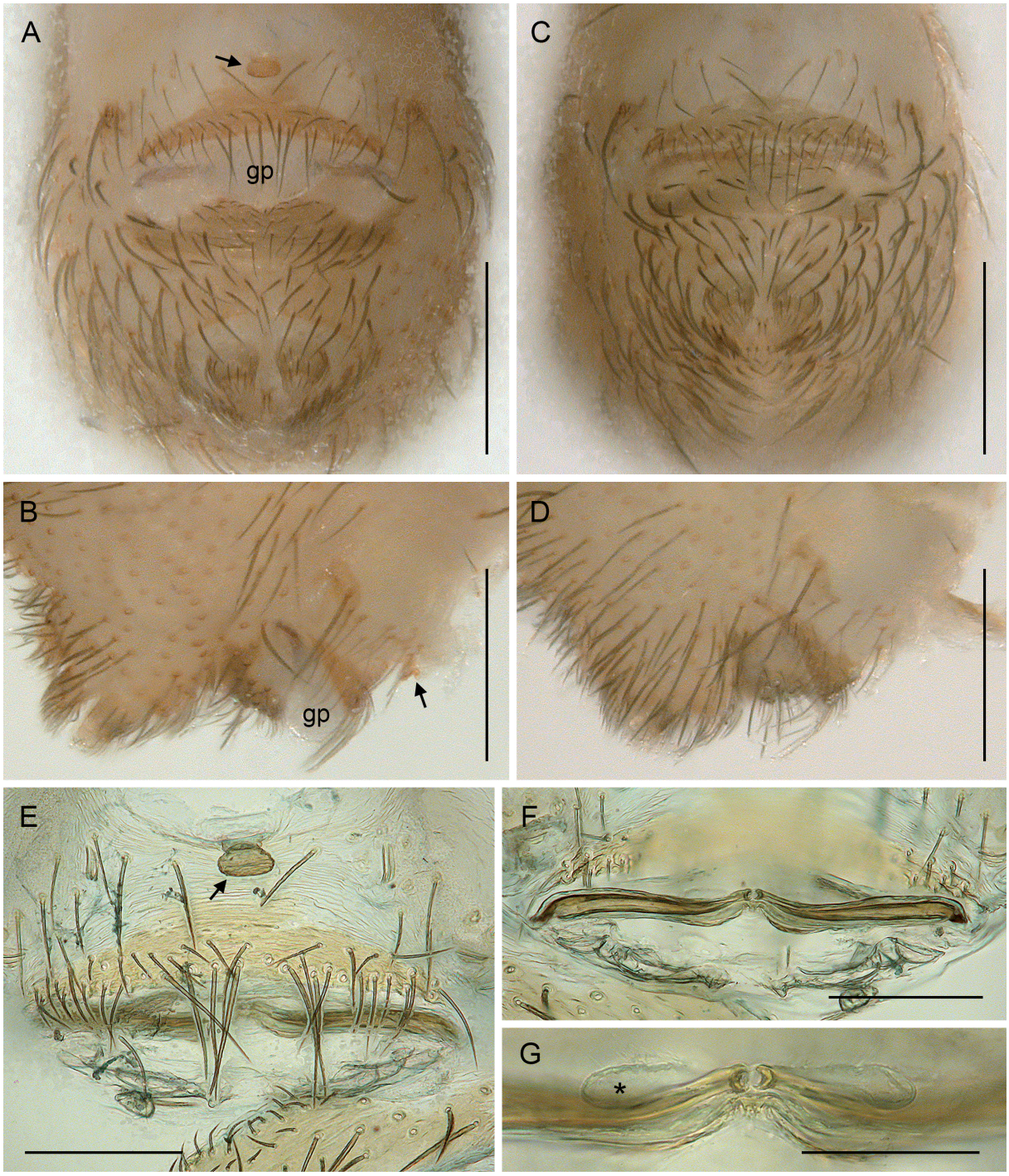

Fig. 49. *Tolteca huahua* Huber sp. nov., females from Mexico, Michoacán, W of Huahua (ZFMK Ar 23957). **A–D**. Epigyna, ventral (A, C) and lateral (B, D) views. **E–G**. Cleared female genitalia, ventral (E) and dorsal (F) views, and detail of median internal structures (G). Arrows point at knob-shaped structure. Asterisk: membranous sac (cf. Fig. 55D). Abbreviation: gp = genital plug. Scale bars: A–D = 0.2 mm; E–F = 0.1 mm; G = 0.05 mm.

Chelicerae (Fig. 44G–H). With pair of frontal apophyses pointing downwards, distance between tips: 50 μm; without stridulatory files.

Palps. In general possibly indistinguishable from congeners (cf. Figs 37, 50); coxa unmodified; trochanter without process; femur proximally without process, distally widened but simple, slightly curved towards dorsal; femur-patella joints very slightly shifted toward prolateral side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; procursus very simple (Fig. 44I), with distal ventral process; genital bulb large, complex, in light microscope possibly indistinguishable from congeners (cf. Figs 38D–F, 51D–F).

Legs. Without spines and curved hairs; with slightly increased density of short vertical hairs on tibia 1 (barely visible in dissecting microscope); retrolateral trichobothrium of tibia 1 at 63%; prolateral trichobothrium absent on tibia 1; tarsus 1 with four pseudosegments, all fairly distinct.

Variation (male)

Tibia 1 in five males (incl. holotype): 0.47–0.55 (mean 0.50).

Female

In general, similar to male (Fig. 36J) but sternum without pair of anterior humps; tibia 1 not with increased density of short vertical hairs. Total body length: ~1.20; tibia 1 in 12 females: 0.43–0.51 (mean 0.47). Epigynum (Fig. 49A–D) with short crescent-shaped anterior plate slightly protruding in lateral view; posterior plate wide, median part slightly protruding anteriorly. With distinct knob between epigynum and pedicel. Internal genitalia (Fig. 49E–G) with pair of strong transversal sclerites, pair of distinct sacs (receptacles?), without (or with very small?) pore plates.

Distribution

Known from two neighbouring localities in Mexico, Michoacán (Fig. 35).

Natural history

At the type locality, a low roadside forest, *Tolteca* was only found in rather dry leaf litter, while more humid litter contained different species of Pholcidae (*Modisimus* sp.; *Anopsicus* sp.; *Physocyclus lautus* Gertsch, 1971). At the second locality, *Tolteca* was only found in the dry leaf litter of a sun-exposed part of the forest. In the leaf litter of the neighbouring, more humid part of the forest, four other species of Pholcidae were found (*Anopsicus* sp.; *Modisimus* spp.).

Tolteca oaxaca Huber sp. nov.
urn:lsid:zoobank.org:act:85F8D1C1-9EC5-407C-A507-90D0270F18A9
Figs 36K–L, 50–54, 55G–H

Pholcophora hesperia Gertsch, 1982: 102 (specimens from Oaxaca only; see Remarks under *T. hesperia*).

Tolteca hesperia – Huber 2000: 118 (part; see Remarks under *T. hesperia*), figs 75, 126, 448–453, 455–457 (not fig. 454).

Diagnosis

Distinguished from known congeners by the combination of: male genital bulb without dorsal ridge (unlike *T. jalisco*); procursus tip gradually narrowing (Fig. 51C; unlike *T. hesperia* and *T. sinnombre* sp. nov.); male cheliceral apophyses close together (Fig. 51A; distance between tips ~40 μm, i.e., closer together than in *T. manzanillo* sp. nov. and *T. sinnombre*), in lateral view very small and with small angle against distal-frontal face of chelicera (Fig. 51B; unlike *T. hesperia*; not checked in *T. jalisco*); main

epigynal plate crescent-shaped (Fig. 52A, C; rather than band-like as in *T. hesperia* and *T. jalisco*); sacs in female internal genitalia tiny, only ~9–13 µm long (Fig. 55G–H; smaller than in all known congeners).

Etymology

The species name is derived from the type locality; noun in apposition.

Type material

Holotype

MEXICO – **Oaxaca** • ♂; ~3 km N of San Pedro Totolapa; 16.6976° N, 96.3180° W; 1100 m a.s.l.; 26 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; LATLAX.

Paratypes

MEXICO – **Oaxaca** • 4 ♂♂; same collection data as for holotype; ZFMK Ar 23961.

Other material examined

MEXICO – **Oaxaca** • 19 ♀♀, in pure ethanol; same collection data as for holotype; four prosomata used for molecular work, two females used for SEM, two cleared abdomens transferred to ZFMK Ar 23961; ZFMK Mex362 • 3 ♂♂; same collection data as for holotype; partly used for karyotype analyses; ZFMK 23962 • 3 ♂♂, 3 ♀♀; same collection data as for holotype; partly used for µ-CT study; ZFMK 23963 • 2 ♂♂, 2 ♀♀ abdomens; ~17 km NW of Tehuantepec; 16.3919° N, 95.3865° W; 165 m a.s.l.; 27 Oct. 2019; B.A. Huber and A. Valdez-Mondragón leg.; ZFMK Ar 23964 • 4 ♀♀, 4 juvs, in pure ethanol; same collection data as for preceding; two female abdomens transferred to ZFMK Ar 23964; ZFMK Mex368 • 2 ♂♂; same collection data as for preceding; partly used for karyotype analyses; ZFMK 23965 • 2 ♂♂, 3 ♀♀; same collection data as for preceding; partly used for µ-CT study; ZFMK 23966 • 2 ♂♂, 11 ♀♀, 2 juvs (subadult males); same collection data as for preceding; LATLAX.

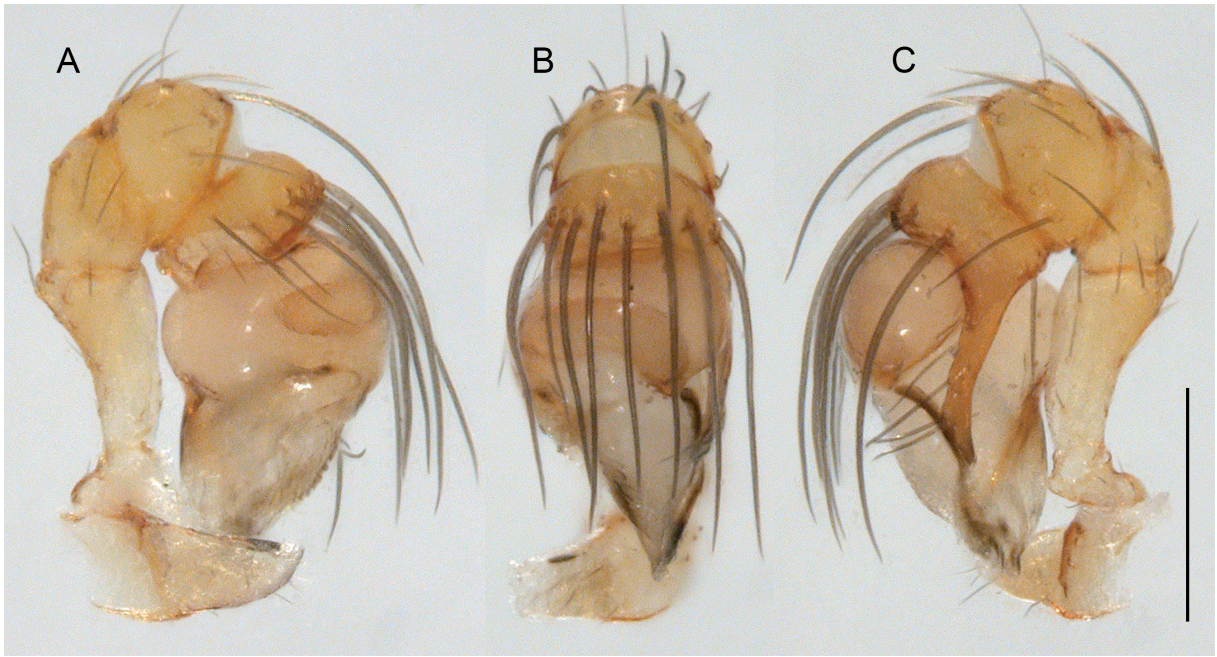

Fig. 50. *Tolteca oaxaca* Huber sp. nov., male paratype from Mexico, Oaxaca, N of San Pedro Totolapa (ZFMK Ar 23961). Left palp, prolateral, dorsal, and retrolateral views. Scale bar = 0.2 mm.

Description

Male (holotype)

Measurements. Total body length 1.13, carapace width 0.47. Distance PME-PME 45 µm; diameter PME 45 µm; distance PME-ALE 15 µm; distance AME-AME 10 µm; diameter AME 30 µm. Leg 1: 2.07 (0.55 + 0.17 + 0.52 + 0.53 + 0.30), tibia 2: 0.42, tibia 3: 0.38, tibia 4: 0.65; tibia 1 L/d: 9; diameters of leg femora 0.11, of leg tibiae 0.06.

Colour (in ethanol). Prosoma and legs monochromous ochre-yellow; abdomen slightly darker ochre-grey, also monochromous.

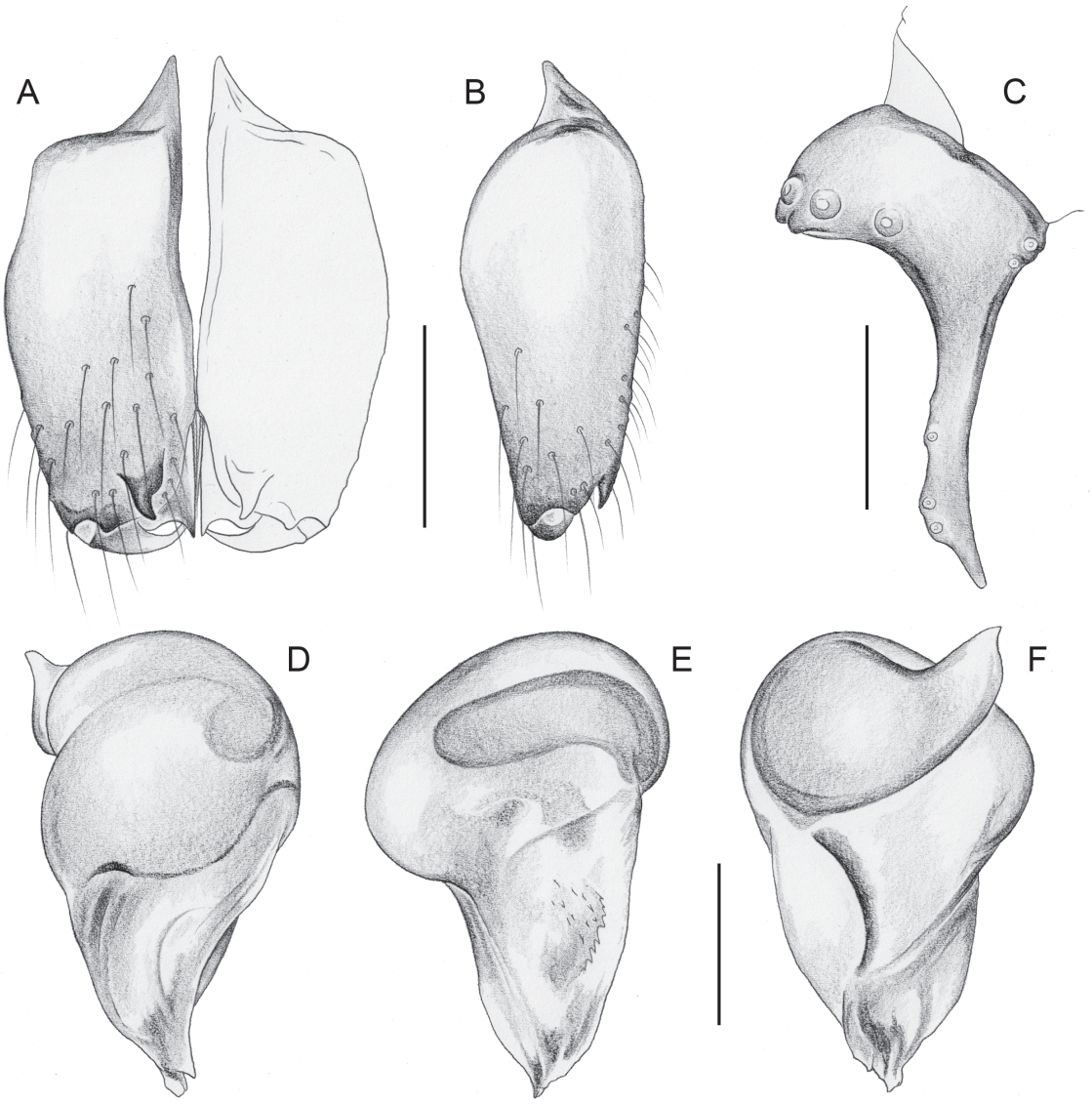

Fig. 51. *Tolteca oaxaca* Huber sp. nov., male paratype from Mexico, Oaxaca, N of San Pedro Totolapa (ZFMK Ar 23961). **A–B**. Chelicerae, frontal and lateral views. **C**. Left palpal tarsus and procursus, retrolateral view. **D–F**. Left genital bulb, prolateral, dorsal, and retrolateral views. Scale bars = 0.1 mm.

Body (Fig. 36K). Ocular area barely raised. Carapace without thoracic groove. Clypeus unmodified, short (clypeus rim to ALE: 130 µm). Sternum wider than long (0.35/0.30), almost round (i.e., not heart-shaped), with pair of small but distinct anterior processes (~50 µm diameter at basis, ~50 µm long) near coxae 1. Abdomen globular.

Chelicerae (Fig. 51A–B). With pair of frontal apophyses pointing downwards, distance between tips of apophyses: 50 µm; without stridulatory files.

Palps (Fig. 50). Coxa unmodified; trochanter without process; femur proximally without process, distally widened but simple, slightly curved towards dorsal; femur-patella joints not (or barely) shifted to one side; tibia very short, with two trichobothria; tibia-tarsus joints not shifted to one side; procursus very simple (Fig. 51C), with distal ventral process; genital bulb as in Fig. 51D–F, in light microscope possibly indistinguishable from congeners.

Legs. Without spines and curved hairs; with slightly increased density of short vertical hairs on tibia 1 (barely visible in dissecting microscope); retrolateral trichobothrium of tibia 1 at 59%; prolateral trichobothrium absent on tibia 1; tarsus 1 with six pseudosegments, all fairly distinct.

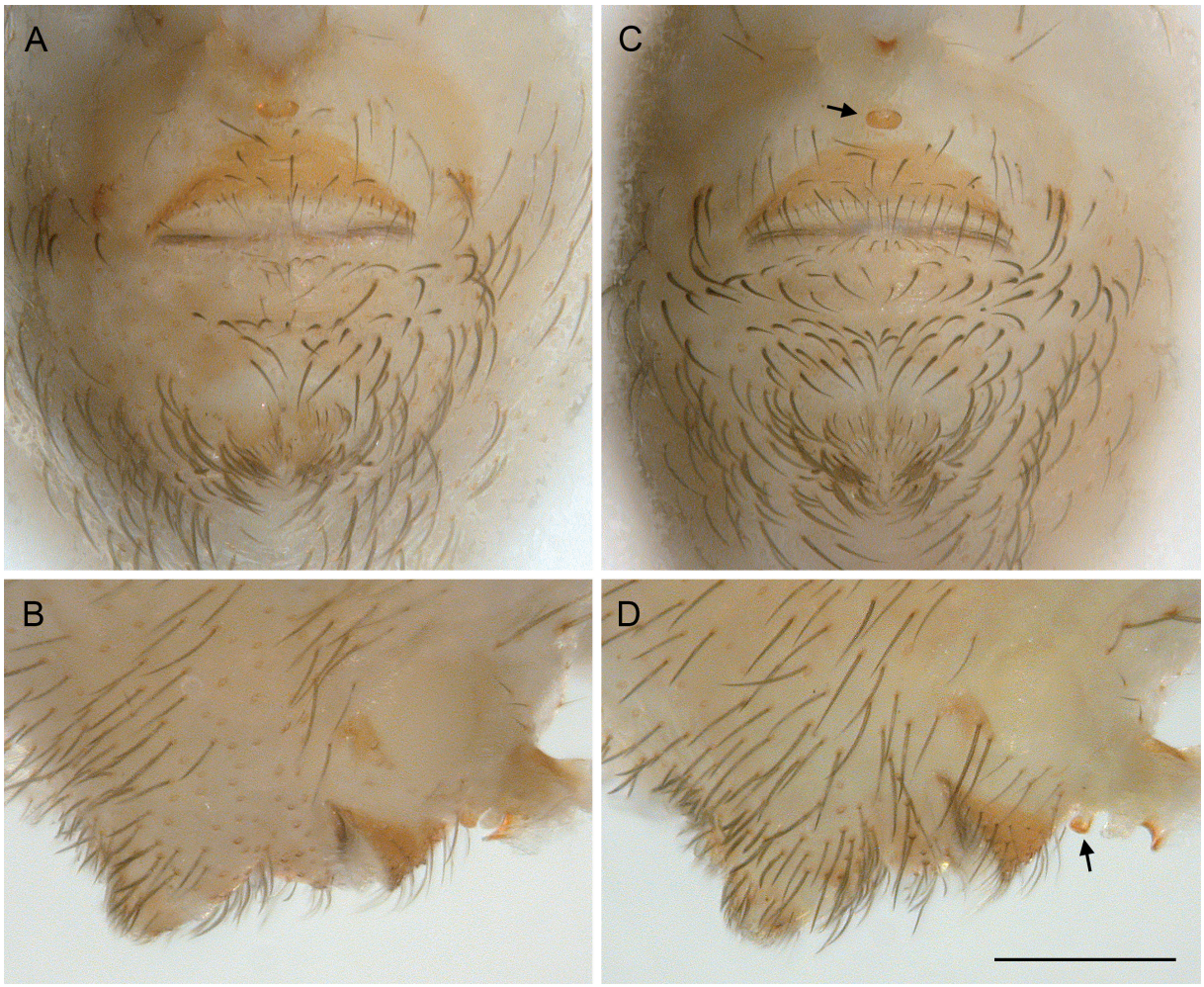

Fig. 52. *Tolteca oaxaca* Huber sp. nov., females from Mexico, Oaxaca, N of San Pedro Totolapa (ZFMK Ar 23961), epigyna. **A, C**. Ventral views. **B, D**. Lateral views. Arrows: knob-shaped structure. Scale bar = 0.2 mm (all at same scale).

Variation (male)
Tibia 1 in seven newly collected males (incl. holotype): 0.48–0.58 (mean 0.53).

Female
In general, similar to male (Fig. 36L) but sternum without pair of anterior humps, tibia 1 without increased density of short vertical hairs. Total body length: ~1.20; tibia 1 in 21 newly collected females: 0.47–0.56 (mean 0.51). Epigynum (Figs 52, 54A) short crescent-shaped anterior plate slightly protruding in lateral view; posterior plate short and wide, very indistinct, barely visible. With distinct knob between epigynum and pedicel (Fig. 54B). Internal genitalia (Fig. 53) with pair of strong transversal sclerites, with very short sacs (Fig. 55G–H), without (or with very small?) pore plates.

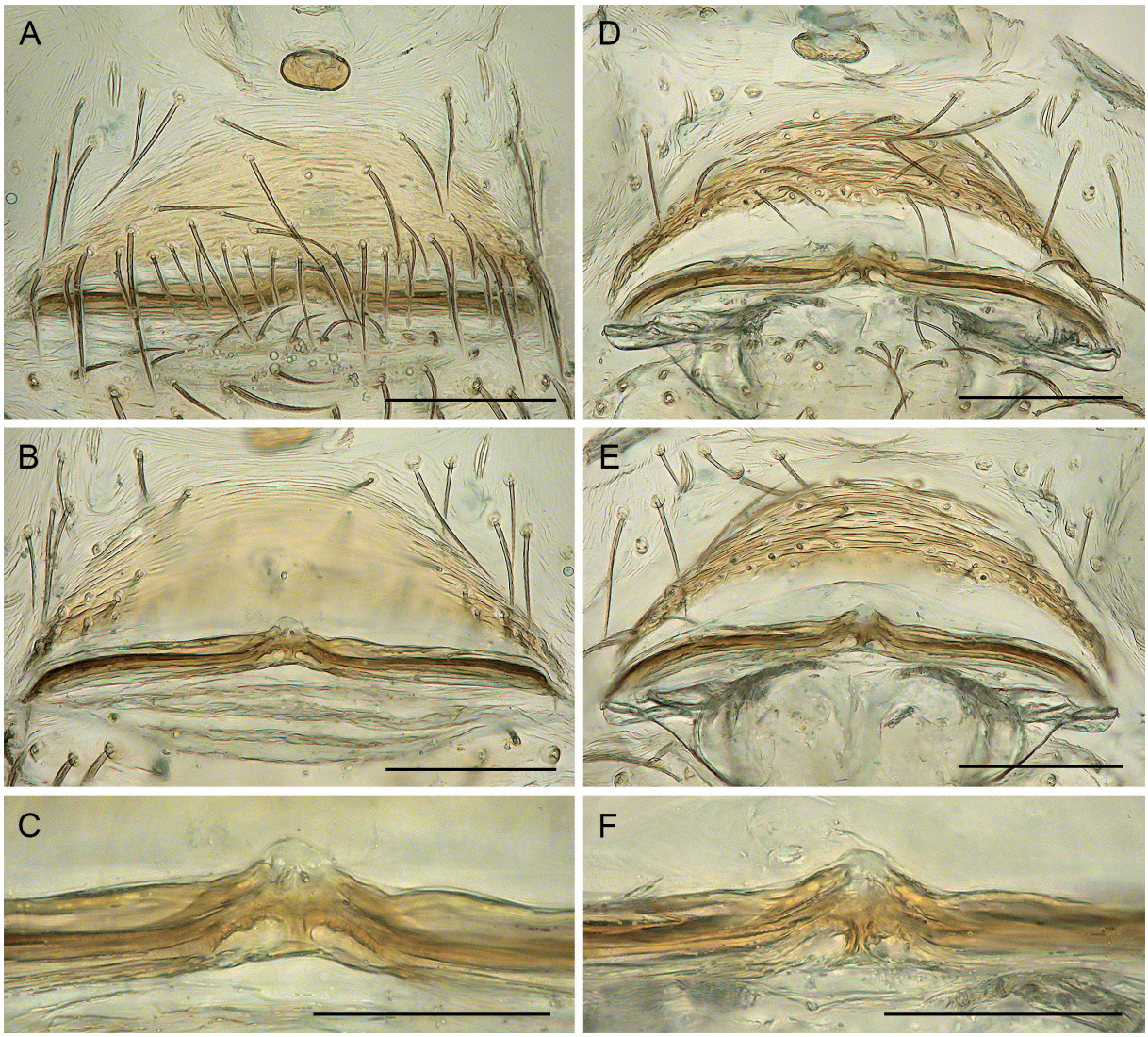

Fig. 53. *Tolteca oaxaca* Huber sp. nov., females from Mexico, Oaxaca, N of San Pedro Totolapa (ZFMK Ar 23961). **A–B, D–E**. Cleared female genitalia, ventral (A, D) and dorsal (B, E) views. **C, F**. Detail of median internal structures. Scale bars: A–B, D–E = 0.1 mm; C, F = 0.05 mm.

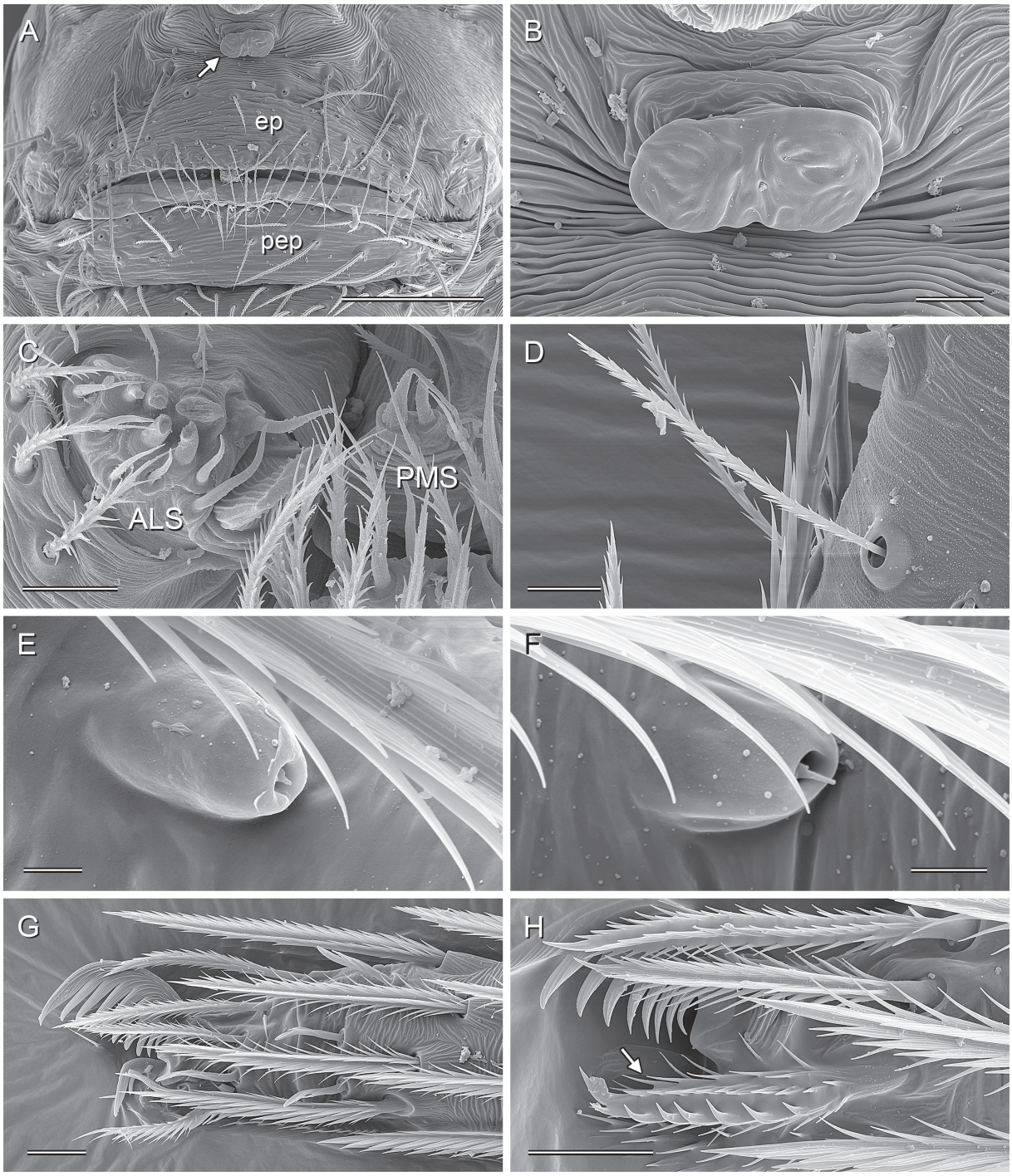

Fig. 54. *Tolteca oaxaca* Huber sp. nov., female from Mexico, Oaxaca, 3 km N of San Pedro Totolapa (ZFMK Mex362). **A**. Epigynum, ventral view (arrow: knob-shaped structure). **B**. Knob-shaped structure between epigynum and pedicel. **C**. ALS and PMS. **D**. Prolateral trichobothrium on tibia 3. **E**. Palpal tarsal organ. **F**. Tarsal organ on tarsus 2. **G**. Tip of left tarsus 2, retrolateral view. **H**. Tip of right tarsus 4, prolateral view, showing comb hair (arrow). Abbreviations: ep = epigynum (main epigynal plate); pep = posterior epigynal plate. Scale bars: A = 100 µm; B–D, G–H = 10 µm; E–F = 2 µm.

Distribution

Apparently widely distributed in the state of Oaxaca, Mexico (Fig. 35). We have not restudied Gertsch's (1982) and Huber's (2000) specimens but consider all their records of *Pholcophora/Tolteca hesperia* from Oaxaca to represent this species.

Natural history

At the type locality, a dry hill with a sparse and low tree cover (Fig. 56C), the spiders were found in high densities in the thin layer of leaf litter and among small pebbles on the ground (Fig. 56D). Within ~1.5 h, ~30 individuals were seen within an area of ~4 m^2. In slightly more humid (shaded) areas on the same hill, two other species of Pholcidae were found (*Modisimus* sp.; *Physocyclus paredesi* Valdez-Mondragón, 2010). At the second locality, a slightly higher and denser roadside forest, *Tolteca* was also collected at a rather dry spot with a thin layer of leaf litter, while more humid areas contained other Pholcidae genera (*Modisimus* sp.; *Physocyclus paredesi*; *Anopsicus* sp.; *Psilochorus* sp.).

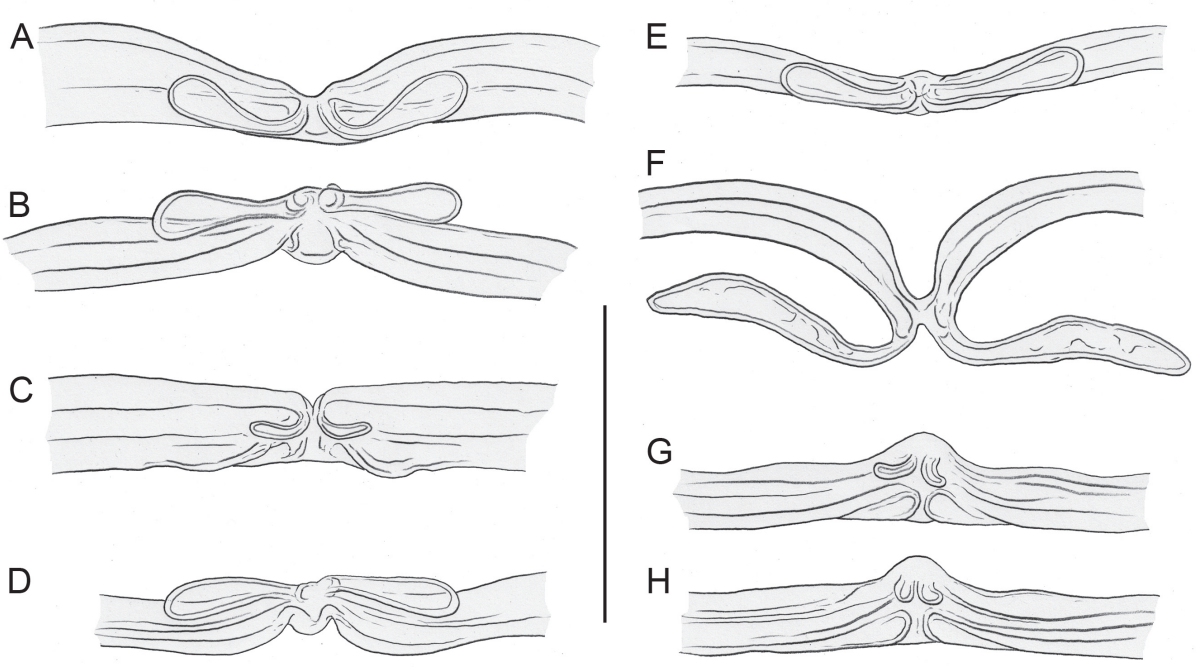

Fig. 55. *Tolteca* Huber, 2000 internal female genitalia, median section of main transversal internal sclerite. **A–B**. *T. hesperia* (Gertsch, 1982); females from Mexico, Sinaloa, S of Rosario (ZFMK Ar 23953). **C**. *T. jalisco* (Gertsch, 1982), female from Mexico, Jalisco, N of La Quemada (ZFMK Ar 23956). **D**. *T. huahua* Huber sp. nov., female from Mexico, Michoacán, W of Huahua (ZFMK Ar 23957). **E**. *T. manzanillo* Huber sp. nov., female from Mexico, Colima, E of Manzanillo (ZFMK Ar 23958). **F**. *T. sinnombre* Huber sp. nov., female from Mexico, Colima, S of Coquimatlán (ZFMK Ar 23960). **G–H**. *T. oaxaca* Huber sp. nov., females from Mexico, Oaxaca, N of San Pedro Totolapa (ZFMK Ar 23961). Scale bar = 0.1 mm.

Fig. 56. Representative sample of habitats of *Tolteca* Huber, 2000 in Mexico. **A**. Sinaloa, 3 km S of Rosario (*T. hesperia* (Gertsch, 1982)). **B**. Colima, 17 km E of Manzanillo (type locality of *T. manzanillo* Huber sp. nov.; showing collection method). **C–D**. Oaxaca, 3 km N of San Pedro Totolapa (type locality of *P. oaxaca* Huber sp. nov.; overview and spot with high abundance of specimens).

Karyology

The male karyotype of *T. hesperia* consisted of 15 chromosomes including a X_1X_2Y system. Chromosome pairs were metacentric. The last two chromosome pairs were much shorter than the first four pairs. X chromosomes were probably metacentric. The Y chromosome was a tiny element (3.35% of TCL); its morphology was not resolved (Fig. 57A). The male set of *T. oaxaca* sp. nov. comprised five chromosome pairs and a X_1X_2Y system, i.e., 13 chromosomes. The haploid karyotype consisted of five chromosomes (each representing a particular chromosome pair), which decreased gradually in size, and the sex chromosomes X_1, X_2, and Y. All chromosomes were metacentric except for the chromosome representing the third pair, which was submetacentric. The Y chromosome was a tiny element (4.33% of TCL) (Fig. 57B). Three chromosome pairs contained a NOR (Fig. 58). In some plates, the sex chromosome body also included a signal, which suggests the presence of a sex chromosome-linked NOR (Fig. 58B). However, we were not able to determine which sex chromosome carried a NOR.

Sex chromosomes did not differ by behaviour or intensity of staining from the other chromosomes at spermatogonial prometaphase (Fig. 57C). They formed an overcondensed body on the periphery of the premeiotic nucleus, which exhibited positive heteropycnosis (i.e., more intensive staining than the other chromosomes) (Fig. 57D). Bivalents were considerably decondensed during the diffuse stage.

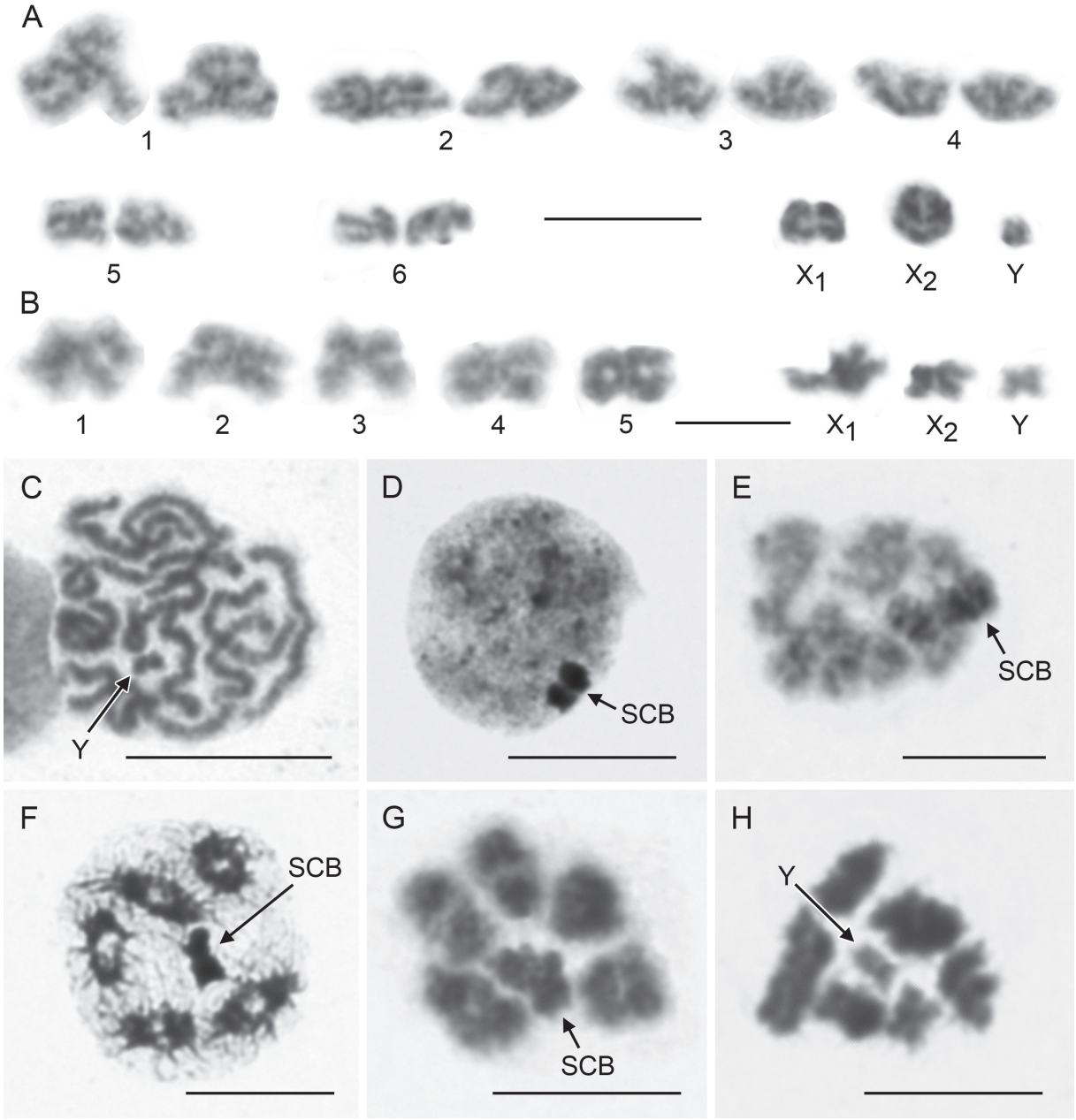

Fig. 57. *Tolteca* Huber, 2000, karyotypes and sex chromosome behaviour in male germline; stained by Giemsa. **A**. *T. hesperia* (Gertsch, 1982), diploid karyotype (2n♂ = 15, X_1X_2Y), based on two fused sister prometaphases II. X chromosomes are probably metacentric, morphology of Y chromosome is unresolved. Note positive heteropycnosis of X chromosomes. **B–G**. *T. oaxaca* Huber sp. nov. **B**. Haploid karyotype (n♂ = 8, X_1X_2Y), based on metaphase II. Note positive heteropycnosis of X chromosomes. **C**. Spermatogonial prometaphase. Note metacentric morphology of tiny Y chromosome. **D**. Premeiotic interphase. Sex chromosomes form an overcondensed body on the periphery of the nucleus. **E**. Late diffuse stage. Sex chromosomes are positively heteropycnotic; bivalents are considerably decondensed. **F**. Diplotene. Note five bivalents and sex chromosome body exhibiting a positive heteropycnosis. **G**. Metaphase I containing five bivalents and sex chromosome body. **H**. *T. hesperia*, metaphase II consisting of seven chromosomes. Note tiny Y chromosome. Abbreviations: SCB = sex chromosome body; X_1 = X_1 chromosome; X_2 = X_2 chromosome; Y = Y chromosome. Scale bars= 10 µm.

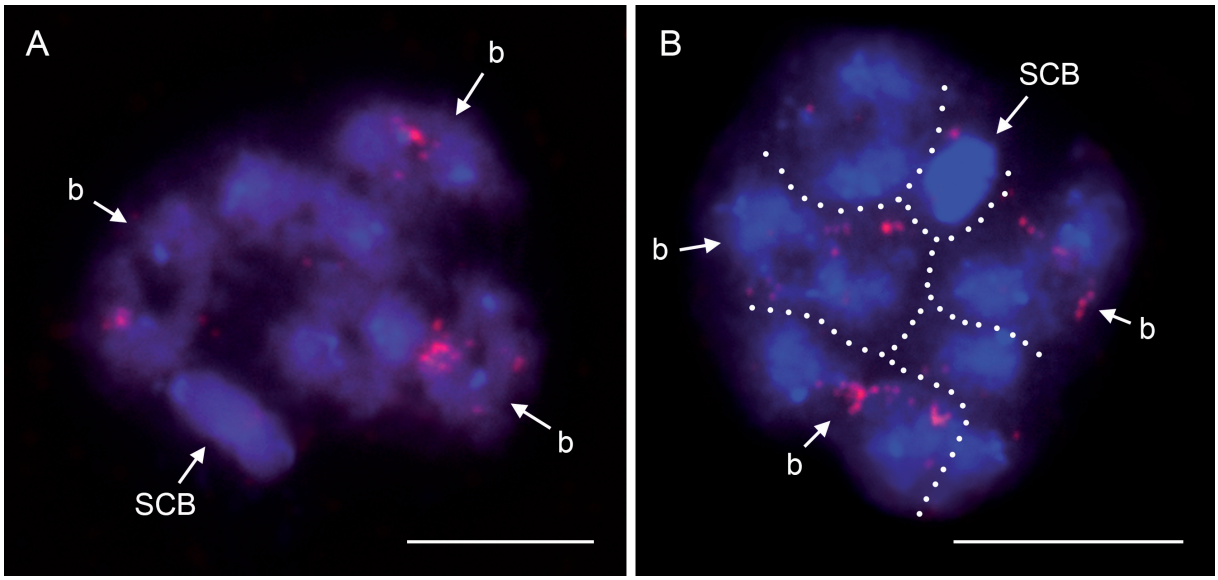

Fig. 58. *Tolteca oaxaca* Huber sp. nov., male meiosis, detection of NORs (FISH). Metaphase I comprising five bivalents and sex chromosome body; three bivalents contain NORs. **A**. Sex chromosome body without visible signal. **B**. Sex chromosome body includes signal. Individual elements separated by dashed line. Abbreviations: b = NOR bearing bivalent; SCB = sex chromosome body. Scale bars = 10 µm.

In contrast to this, sex chromosomes formed a highly condensed body during this stage (Fig. 57E). This body persisted until metaphase I (Fig. 57G), which impeded the determination of the mode of sex chromosome pairing during late prophase I (i.e., diplotene and diakinesis) and metaphase I. Bivalents contained a single chiasma only (Fig. 57F). X chromosomes were associated at metaphase II being positively heteropycnotic (Fig. 57A–B).

Biogeography

The environmental niche occupied by non-Caribbean ('true') *Pholcophora* is more similar to the niche occupied by *Tolteca* than to randomly generated niches (p = 0.010; Table 2; Fig. 59A; Supp. file 1: Fig. S54), and vice-versa (p = 0.010; Table 2; Supp. file 1: Fig. S69). The equivalency tests between the niches occupied by non-Caribbean *Pholcophora* and *Tolteca* revealed that their niche overlap is constant when randomly reallocating the occurrences of both groups between their ranges (p = 0.015; Table 2; Fig. 59B). These groups also exhibited a relatively high niche overlap (D = 0.40; Table 2; Fig. 59D).

The niche similarity tests were also significant between non-Caribbean *Pholcophora* and (1) the Caribbean clade (p = 0.010; Table 2; Supp. file 1: Figs S51, S63), (2) Mexican *Pholcophora* (p = 0.049; Table 2; Supp. file 1: Figs S52, S67), and (3) *Papiamenta* (p = 0.010; Table 2; Supp. file 1: Figs S53, S63). Besides, the niches occupied by the Caribbean clade and *Papiamenta* were significantly more similar than expected by chance (p = 0.010; Table 2; Supp. file 1: Figs S46, S61).

The niche overlap between *Pholcophora americana* and any other group was extremely low (Table 2), even when compared with congeneric but disjunct taxa, such as "Mexican *Pholcophora*" (i.e., Mexican species of *Pholcophora* incl. *P. texana*; D = 0.00). As expected (see Material and methods), the niche of the Caribbean clade (i.e., *Papiamenta* spp. and Caribbean '*Pholcophora*') showed a large overlap with the niche of *Papiamenta* (D = 0.59; Supp. file 1: Fig. S16). The niche overlap between the Caribbean

clade and both the non-Caribbean *Pholcophora* (D = 0.21; Supp. file 1: Fig. S21) and Mexican *Pholcophora* (D = 0.11; Supp. file 1: Fig. S18) is higher than the overlap between the Caribbean clade and *P. americana* (D = 0.00; Supp. file 1: Fig. S25) and *Tolteca* (D = 0.06; Supp. file 1: Fig. S17).

The altitudinal range differed among the compared groups (d.f. = 131, resid. def. = 46268, p = 0.000; Fig. 61). Taxa from the Caribbean clade were recorded from sea level up to ~70 m a.s.l., presenting the lowest altitudinal range (mean 25 m a.s.l.). They were followed by *Tolteca* (sea level to 1540 m a.s.l.; mean 286 m a.s.l.). The highest altitudinal range was observed for *Pholcophora* (30 to >3000 m a.s.l.; mean 970 m a.s.l.), without statistically significant differences between *P. americana* and Mexican *Pholcophora* (Fig. 61).

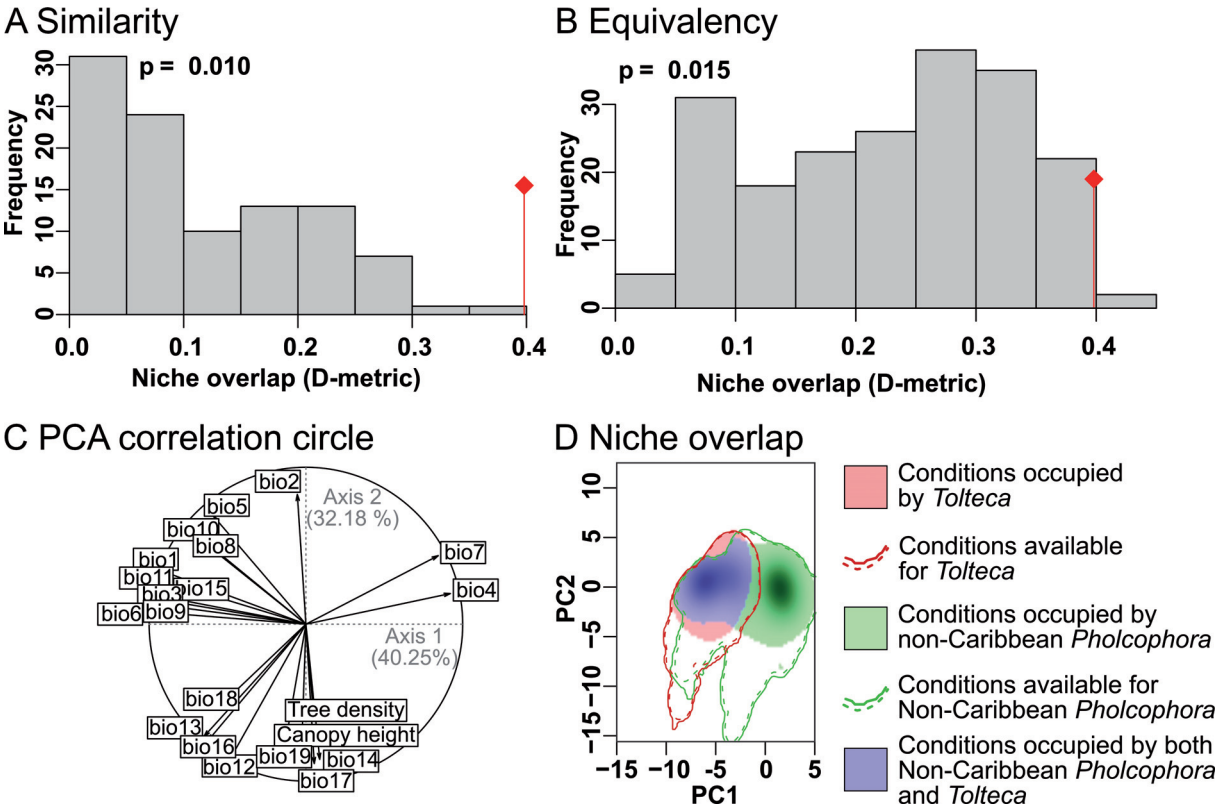

Fig. 59. Environmental niche comparisons between non-Caribbean ('true') *Pholcophora* Banks, 1896 and *Tolteca* Huber, 2000. Red lines in similarity and equivalency graphs indicate the observed niche overlap (D-metric), while grey bars show the distribution of the D-metric for 100 simulated comparisons. Note that the similarity and equivalency of the environmental niche between non-Caribbean *Pholcophora* and *Tolteca* was higher than randomly expected. The distribution of *Pholcophora* includes areas with high temperature annual range (bio7 in C) and seasonality (bio4 in C) not occupied by *Tolteca*. The two taxa exhibit a relatively high niche overlap (D = 0.40; bluish area in D). Climatic variables in the PCA: bio1 = annual mean temperature; bio2 = mean diurnal range; bio3 = isothermality; bio4 = temperature seasonality; bio5 = max temperature of warmest month; bio6 = min temperature of coldest month; bio7 = temperature annual range; bio8 = mean temperature of wettest quarter; bio9 = mean temperature of driest quarter; bio10 = mean temperature of warmest quarter; bio11 = mean temperature of coldest quarter; bio12 = annual precipitation; bio13 = precipitation of wettest month; bio14 = precipitation of driest month; bio15 = precipitation seasonality; bio16 = precipitation of wettest quarter; bio17 = precipitation of driest quarter; bio18 = precipitation of warmest quarter; bio19 = precipitation of coldest quarter.

Discussion

Morphology

Both in *Pholcophora* and in *Tolteca*, males but not females have short vertical hairs in higher than usual density on some or all of their leg tibiae (e.g., Fig. 42A–B). Our SEM data show that these hairs are structurally very different from the 'usual' short vertical hairs found on the legs (mainly the distal segments) of males and females of all pholcid spiders: they are simple without branches and apparently without an opening at the tip (Fig. 42C), while the 'usual' short vertical hairs have several short side branches and an opening at the tip (Fig. 42D–E). These latter hairs are very likely chemoreceptors (Foelix & Chu-Wang 1973). In the recent taxonomic literature on Pholcidae, numerous descriptions refer to "short vertical hairs" without discriminating between the 'usual' hairs found in males and females and the sexually dimorphic hairs found in males only (e.g., Lee *et al.* 2021; Yao *et al.* 2021; Zhu & Li 2021). In at least some of the treated taxa (e.g., *Pholcus* Walckenaer, 1805) sexually dimorphic vertical hairs are not known to exist, and the descriptions thus probably refer to the trivial presence of the ubiquitous chemoreceptors.

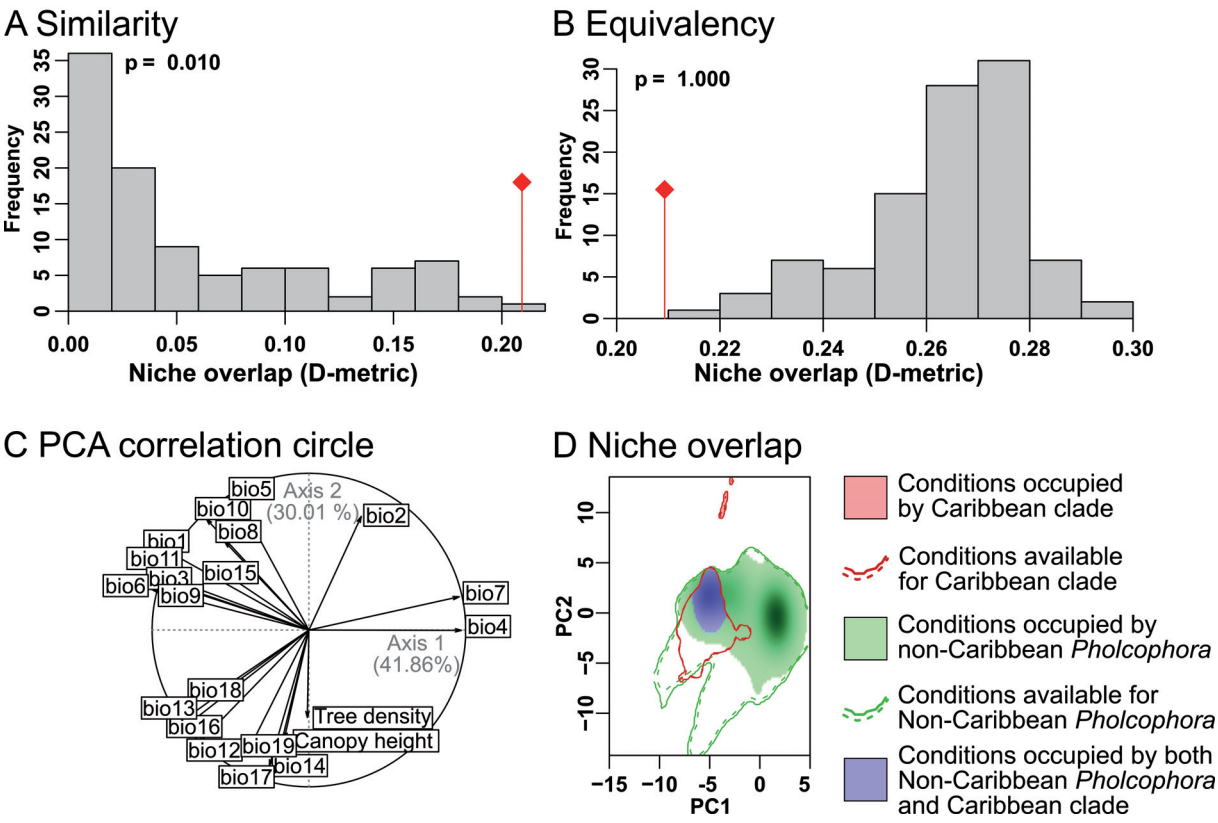

Fig. 60. Environmental niche comparisons between non-Caribbean ('true') *Pholcophora* Banks, 1896 and the Caribbean clade. Red lines in equivalency and similarity graphs indicate the observed niche overlap (D-metric), while grey bars show the distribution of the D-metric for 100 simulated comparisons. Note that the similarity of the environmental niche between non-Caribbean *Pholcophora* and the Caribbean clade was higher than randomly expected, while the equivalency was not (i.e., the niche is similar, but not identical). The distribution of the Caribbean clade is related to warmer conditions (bio5, bio8, and bio10 in C), while the distribution of non-Caribbean *Pholcophora* is more related to temperature annual range (bio7 in C) and seasonality (bio4 in C). A relatively low niche overlap is observed (D = 0.209; bluish area in D). Climatic variables in the PCA as in Fig. 59.

The function of the sexually dimorphic hairs remains a mystery. In Pholcidae, such hairs have apparently evolved several times convergently, in at least three subfamilies (Huber 2021). In Ninetinae, they have been reported for *Ibotyporanga* Mello-Leitão, 1944; *Papiamenta* Huber, 2000; and *Nerudia* Huber, 2000 (Huber 2000; Huber & Villarreal 2020; Huber *et al.* 2023), and they also occur in *Guaranita* Huber, 2000 and in *Galapa* Huber, 2000 (B.A. Huber unpubl. data). In other Ninetinae genera they may have been overlooked due to their size (~2 µm diameter at the basis, ~20–30 µm long).

Relationships

Our molecular data support the idea that a northern clade of Ninetinae (North America and Caribbean taxa) is nested within South American Ninetinae (cf. Huber *et al.* 2018). The monophyly of this northern clade suggests that cleistospermia have evolved at least twice in Pholcidae: once in the ancestor of *Pholcophora* and *Tolteca* (Dederichs *et al.* 2022), and once in all Pholcidae except Ninetinae. The sperm transfer form of *Papiamenta* is unknown but our results generate the prediction that *Papiamenta* males also transfer cleistospermia.

Within the northern clade, we found high support for the Mexican genus *Tolteca*, for a core-group of non-Caribbean (true) *Pholcophora*, and for a Caribbean clade consisting of *Papiamenta*, '*Pholcophora*' *bahama*, and some undescribed species tentatively placed in *Pholcophora*. All these extant Caribbean '*Pholcophora*' are known from females only. We thus prefer to keep them as "*Pholcophora*?" until males become available. We expect that the study of males will facilitate a decision as to whether they should be (1) described in one or more new genera, (2) assigned to *Papiamenta*, or (3) if *Papiamenta* should be synonymized with *Pholcophora*. In this context, the three Dominican amber fossil species currently placed in *Pholcophora* should also be restudied. They are known from males only, and the original drawings suggest that they partly resemble *Pholcophora* (long procursus), and partly *Papiamenta* (genital

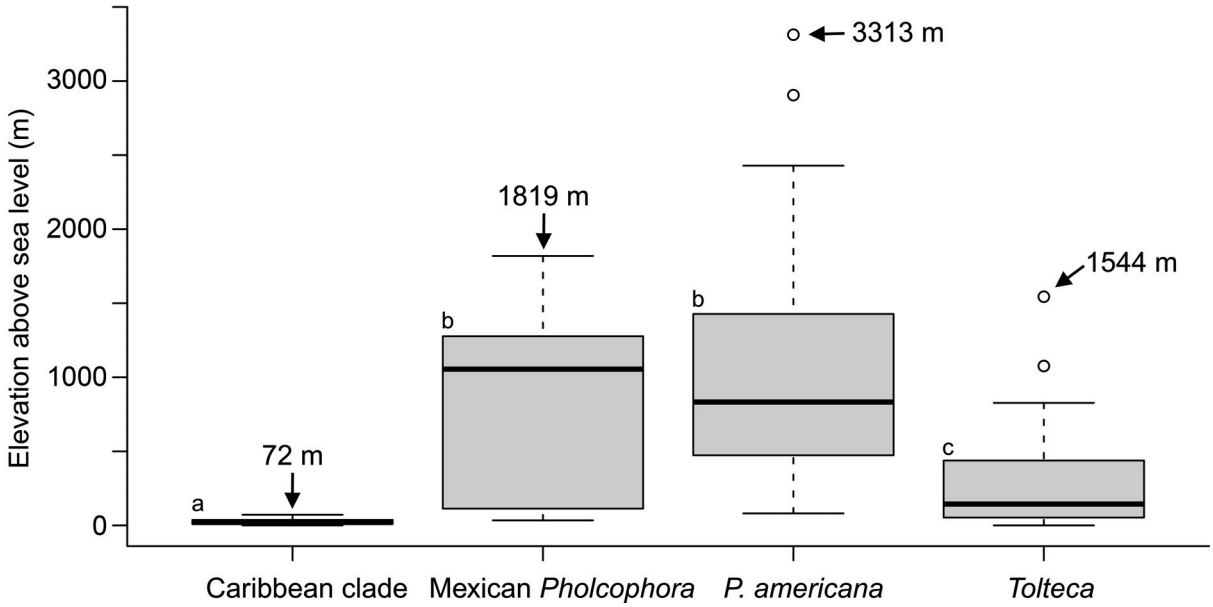

Fig. 61. Known altitudinal variation for records of the Caribbean clade, Mexican *Pholcophora* Banks, 1896, *P. americana* Banks, 1896, and *Tolteca* Huber, 2000. Highest altitudinal record for each group is detailed. Letters indicate statistically significant groups (p = 0.000). Note that the altitudinal range is significantly lower for the Caribbean clade, intermediate for *Tolteca*, and higher for both *Pholcophora* groups. Note that the two outliers for *P. americana* result from rough estimates of the coordinates; the actual collecting sites may have been lower.

bulb with distinct sclerite). We predict that extant Caribbean (Greater Antilles, Bahamas) '*Pholcophora*' males will most closely resemble these Dominican amber fossil species.

Karyology

The karyotypes of *Pholcophora* (Avila-Herrera *et al.* 2021) and *Tolteca* (this study) are formed by biarmed (i.e., metacentric and submetacentric) chromosomes. The prophase of the first meiotic division of males contains the so-called diffuse division, which is characterized by considerable decondensation of chromosome pairs (Ávila Herrera *et al.* 2021; this study). These features 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 behaviour of sex chromosomes during male meiosis is similar to other pholcids examined except for the persistence of the sex chromosome body until metaphase I in *Tolteca*. In other pholcids studied, this behaviour was found only in the distantly related *Cantikus sabah* (Huber, 2011) (Ávila Herrera *et al.* 2021). The number of NOR bearing chromosome pairs in *T. oaxaca* sp. nov. (three) is close to the supposed ancestral pattern of ninetines (two NOR bearing chromosome pairs) (Ávila Herrera *et al.* 2021). Furthermore, this species probably displays a sex chromosome-linked NOR. Nucleolus organizer regions often spread to sex chromosomes during the evolution of haplogynes, including pholcids (Král *et al.* 2006; Ávila Herrera *et al.* 2021).

The karyotype of *Pholcophora americana* ($2n♂ = 29$, X_1X_2Y) is close to the supposed ancestral karyotype of pholcid spiders (Ávila Herrera *et al.* 2021). Like in many other spider groups (e.g., Suzuki 1954; Kořínková & Král 2013; Král *et al.* 2013), the number of chromosome pairs decreased during the evolution of many pholcid lineages (Ávila Herrera *et al.* 2021) including ninetines (Huber *et al.* 2023; this study). In *Tolteca*, the number of chromosome pairs has been reduced considerably, namely to six (*T. hesperia*) or even five (*T. oaxaca* sp. nov.) (this study). There are only a few other araneomorph spiders with standard chromosome structure that exhibit lower numbers of chromosome pairs than *T. oaxaca*, namely representatives of the genus *Micropholcus* Deeleman-Reinhold & Prinsen, 1987 (Pholcinae) (Lomazi *et al.* 2018; Ávila Herrera *et al.* 2021) and *Uloborus danolius* Tikader, 1969 (Uloboridae) (Parida & Sharma 1987).

Closely related genera of pholcids do usually not differ considerably in the number of chromosome pairs. A notable exception is a clade in Pholcinae including the genera *Cantikus* Huber, 2018; *Leptopholcus* Simon, 1893; *Micropholcus* Deeleman-Reinhold & Prinsen, 1987; *Pehrforsskalia* Deeleman-Reinhold & van Harten, 2001; and *Pholcus* Walckenaer, 1805; in this clade, the number of pairs decreased from eleven (*Pholcus*) to four (*Micropholcus*) (Ávila Herrera *et al.* 2021). The clade formed by the genera *Pholcophora* (13) and *Tolteca* (5–6) seems to be another case of considerable reduction of the number of chromosome pairs among closely related pholcids. Despite the molecular support for the close relationship between *Pholcophora* and *Tolteca*, the considerable difference in the number of chromosome pairs in the two genera motivates us to speculate about a possible alternative. Such an alternative phylogenetic placement of *Tolteca* is suggested by the presence of a sex chromosome-linked NOR in *Tolteca* but not in *Pholcophora*. Among ninetines, this marker was also found in the genera *Gertschiola* Brignoli, 1981, *Kambiwa* Huber, 2000, and *Nerudia* Huber, 2000, which may form a separate clade being characterised by complex sex chromosome systems ($X_1X_2X_3Y$ and $X_1X_2X_3X_4Y$) and sex chromosome-linked NOR (Huber *et al.* 2023). These systems arose from X_1X_2Y, which is most probably the ancestral sex chromosome system of haplogynes (Paula-Neto *et al.* 2017; Ávila Herrera *et al.* 2021). Provided that the sex chromosome-linked NOR has originated already in the X_1X_2Y system of ninetines, *Tolteca* could be a basal member of the clade containing *Gertschiola*, *Kambiwa*, and *Nerudia.*

The two analysed species of *Tolteca* differ in several karyotype features, which indicates a considerable karyotype differentiation within the genus despite very little morphological differentiation. First, the karyotype of *T. hesperia* contains one chromosome pair more than the karyotype of *T. oaxaca* sp. nov., which suggests a reduction of the number of chromosome pairs by fusion in the latter species. While the chromosome pairs of *T. oaxaca* decrease gradually in length, the last two pairs of *T. hesperia* are much smaller than the other pairs. Moreover, one pair of *T. oaxaca* has a submetacentric morphology. These differences suggest operation of additional rearrangements, namely inversions and translocations. Such changes frequently took part in the karyotype evolution of pholcids (Ávila Herrera *et al.* 2021; Král *et al.* 2022). They might be involved in the formation of interspecific reproductive barriers (e.g., Rieseberg 2001; Ayala & Coluzzi 2005).

Biogeographic analyses

The niche overlap, similarity, and equivalence used in the present study are frequently applied to describe these parameters for native and invaded localities of introduced species (e.g., Broennimann *et al.* 2007). For spiders, these analyses were recently used to show that the non-native American populations of the orb-weaver spider *Cyrtophora citricola* (Forsskål, 1775) occupy climatic conditions with a higher similarity to those in southern Africa than to those in the Mediterranean (Segura-Hernández *et al.* 2022). These analyses thus favoured the hypothesis of an African origin of the American populations of *C. citricola* (Segura-Hernández *et al.* 2022). To date, there is no evidence for human-mediated dispersal in any species of *Pholcophora*, *Tolteca*, and *Papiamenta*. However, the wide geographic distribution of *P. americana*, covering much of the western USA and ranging into Canada (Fig. 2), raises questions about the dispersal strategies of this species. *Pholcophora americana* is likely to be the most widespread Ninetinae species in the World (Huber *et al.* 2023: Table S4). The results shown in the present study suggest that *P. americana* occupies a very distinct environmental niche compared to related taxa (see Table 2 and Supp. file 1). Further studies should address the phylogeography and genetic diversity of *P. americana* to provide further details on its population structure and the colonization history of such a different niche.

The environmental niche analyses carried out in the present study were first used to compare the niches between closely related taxa by Broennimann *et al.* (2014). These authors showed that the niche overlap between polymorphic local populations of two European snake species was higher than that of polymorphic and monomorphic populations of each species individually. This conclusion allowed the authors to suggest that polymorphism may enable the exploitation of different resources (Broennimann *et al.* 2014). Similar analyses showed that two phylogenetically related wandering spiders (*Phoneutria* Perty, 1833) exhibited a higher-than-expected niche conservatism and equivalency, corroborating the hypothesis of allopatric speciation for these species (Hazzi & Hormiga 2021).

The highest niche overlap we found in this study was between the Caribbean clade and *Papiamenta*. However, this is a somewhat tautological result, owing to the low number of Caribbean species currently assigned to *Pholcophora*, yielding a background dominated by the occurrence records of *Papiamenta*. Upon the discovery of further records of '*Pholcophora*' taxa in the Caribbean region, these analyses should be carried out independently between the Caribbean '*Pholcophora*' and *Papiamenta* species. No major niche overlap (i.e., $D > 0.5$) was observed for any other pairwise comparisons (see Table 2). It is important to highlight that, apart from the tautological comparison above, the D-metric for niche overlap was not higher than 0.21 for any other comparison with the Caribbean clade (Table 2). This suggests that the Caribbean taxa occupy a very distinct environmental niche compared to other taxa in the North American-Caribbean clade of Ninetinae.

Some Mexican species of *Pholcophora* and *Tolteca* are known from relatively close localities (ca 250 km straight-line), but never in sympatry. The niche overlap among these taxa is relatively

Table 2. Niche overlap metrics (Schoener's D-index), equivalency and similarity tests in environmental space among six compared groups. The 'Caribbean clade' includes *Papiamenta* and Caribbean '*Pholcophora*'. 'Mexican *Pholcophora*' refers to all Mexican species of *Pholcophora* including *P. texana*. Bold underlined values are significant p-values. Similarity is shown by the two-way (1 vs 2 / 2 vs 1) comparison between groups. Graphs corresponding to all pairwise comparisons are shown in Supp. file 1: Figs S1–75.

Group 1	Group 2	Schoener's D-index	Equivalency p-value	Similarity (1 vs 2) p-value	Similarity (2 vs 1) p-value
Caribbean clade	*Papiamenta*	0.592	0.198	**0.010**	**0.020**
Caribbean clade	*Tolteca*	0.065	0.980	0.119	0.129
Mexican *Pholcophora*	Caribbean clade	0.114	1.000	0.198	0.188
Mexican *Pholcophora*	*Papiamenta*	0.109	1.000	0.188	0.188
Mexican *Pholcophora*	*Tolteca*	0.187	0.762	0.267	0.307
Non-Caribbean *Pholcophora*	Caribbean clade	0.209	1.000	**0.010**	**0.020**
Non-Caribbean *Pholcophora*	Mexican *Pholcophora*	0.239	1.000	**0.049**	**0.049**
Non-Caribbean *Pholcophora*	*Papiamenta*	0.183	1.000	**0.010**	**0.030**
Non-Caribbean *Pholcophora*	*Tolteca*	0.398	**0.015**	**0.009**	**0.020**
P. americana	Caribbean clade	0.000	1.000	1.000	1.000
P. americana	Mexican *Pholcophora*	0.002	1.000	0.574	0.554
P. americana	Non-Caribbean *Pholcophora*	0.096	1.000	0.277	0.267
P. americana	*Papiamenta*	0.000	1.000	1.000	1.000
P. americana	*Tolteca*	0.004	1.000	0.525	0.564
Papiamenta	*Tolteca*	0.054	0.980	0.099	0.099

low (D = 0.19; see Table 2). However, upon comparing the niche overlap between *Tolteca* and 'true' (non-Caribbean) *Pholcophora*, a significantly higher index was observed (D = 0.40). This pair also included taxa with similar and identical niches (hence the significant equivalency test; see Warren *et al.* 2008) (Table 2). This result might be biased by methodological constraints, as the background for both groups encompasses most of Mexico and the southwestern USA, which includes a huge variation in environmental conditions. Additionally, the significantly different altitudinal ranges occupied by *Tolteca* and non-Caribbean *Pholcophora* species suggests that additional environmental variables not used in the present study constrain the geographic distribution of these taxa.

The low number of statistically significant similarity and equivalency tests, associated with the low niche overlap, corroborates the environmental niche conservatism reported for ninetines in general (Huber *et al.* 2023). The niche in ninetines has been shown to evolve following the expectations of Brownian motion evolution (Huber *et al.* 2023), i.e., this trait changes randomly and continuously through time (Revell 2021). As such, the compared groups occupy environments that are as similar and equivalent as expected, not identical. The decrease in biodiversity shortfalls (see Hortal *et al.* 2015) related to ninetines (e.g., Huber & Villarreal 2020; Huber *et al.* 2023) has revealed taxa with island and continental representatives, which suggests that the diversification of these spiders is likely to be as complex as observed for other arachnids (e.g., McHugh *et al.* 2014; Chamberland *et al.* 2018; Esposito & Prendini 2019; Cala-Riquelme *et al.* 2022). Therefore, upon availability of a comprehensive phylogeny of Ninetinae, the effects of dispersal, vicariance, and allopatric speciation processes should be re-evaluated under a niche conservatism scenario for the diversification of these pholcids.

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Author contributions

BAH: initiation of project, collecting, taxonomy, writing
GM: analysis of molecular data, writing
AVM: permits, collecting, writing
IMAH and JK: karyology, writing
LSC: biogeography, writing

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Supplementary material

Supp. file 1. Supplementary figures. https://doi.org/10.5852/ejt.2023.880.2173.9287

Figs S1–S15. Equivalency among the compared groups.
Figs S16–S30. Niche overlap among the compared groups.
Figs S31–S45. PCA correlation circles for the compared groups.
Figs S46–S75. Similarity among the compared groups.
Fig. S76. Summary tree of all trees using unpartitioned analysis.
Fig. S77. Summary tree of all trees using partitioned analysis.