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Research article

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Two new cave-adapted *Juxtlacampa* species from Central America (Diplura: Campodeidae) with new data to disavow the tachycampoid monophyletic line

Alberto SENDRA [1,*], J. Judson WYNNE [2], Alba SÁNCHEZ-GARCÍA [3], Alberto JIMÉNEZ-VALVERDE [4], Jesús SELFA [5], José G. PALACIOS-VARGAS [6], Raquel DAZA BRUNET [7] & Rodrigo LOPES FERREIRA [8]

[1] Colecciones Entomológicas Torres-Sala, Servei de Patrimoni Històric,
Ajuntament de València, València, Spain.
[2] Department of Biological Sciences and Center for Adaptable Western Landscapes,
Northern Arizona University, Flagstaff, Arizona, USA.
[3] Departament de Botànica i Geologia, Facultat de Ciències Biològiques,
Universitat de València, Burjassot, Spain.
[4] Department of Biogeography and Global Change, Museo Nacional de
Ciencias Naturales (MNCN-CSIC), Madrid, Spain.
[5] Laboratori d'Investigació d'Entomologia, Departament de Zoologia,
Universitat de València, Burjassot, València, Spain.
[6] Laboratorio de Ecología y Sistemática de Microartrópodos, Departamento de
Ecología y Recursos Naturales, Facultad de Ciencias,
Universidad Nacional Autónoma de México, Ciudad de México, México.
[7] Deceased [24 May 2025]. Former address: Carbonate and Karst laboratory, Institute of Geology,
Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México.
[8] Centro de Estudos em Biologia Subterrânea, Departamento de Ecologia e Conservação,
Universidade Federal de Lavras, Lavras, Brazil.

[*] Corresponding author: alberto.sendra@uv.es
[2] Email: Jut.Wynne@nau.edu
[3] Email: alba.sanchez@uv.es
[4] Email: alberto.jimenez@mncn.csic.es
[5] Email: jesus.selfa@uv.es
[6] Email: troglolaphysa@hotmail.com
[8] Email: drops@dbi.ufla.br

Abstract. The short-range distributions of cave-dwelling Campodeidae species, together with their ancient origin, make them a key taxonomic group from a paleogeographical perspective. Nevertheless, the systematic validity of several campodeid lineages remains unresolved. In this paper, we examine the tachycampoid group (sensu Bareth & Condé 1981) by reassessing its principal taxonomic traits in comparison with Campodeinae and Plusiocampinae. We suggest that the monophyly of the entire tachycampoid lineage (sensu Bareth & Condé 1981) should be rejected based on new morphological, and ecological data for several species of *Juxtlacampa*, *Tachycampa*, and *Paratachycampa*. Furthermore, we provide a comprehensive revision of the entire genus *Juxtlacampa* and describe two new cave-adapted species: *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov. and *Juxtlacampa xkiq* Sendra & Wynne sp. nov.

Keywords. Biogeography, morphology, phylogeny, taxonomy, troglobiomorphism.

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We would like to pay tribute to our dear co-author, colleague and friend Dr. Raquel Daza Brunet, who devoted her life to geological studies of caves, mainly in volcanic areas of Mexico, Portugal and Spain. Dr. Daza passed away on May 24th 2025 in a tragic speleological accident while she was carrying out one of her dearest scientific activities.

Introduction

Diplura Börner, 1904 are basal hexapods considered to be the sister group of insects (Beutel *et al.* 2017) and one of the first animals to colonize land, probably through caves (Sendra *et al.* 2021b). This group is particularly relevant for evolutionary and biogeographical studies. They comprise over a thousand extant species across ten families (Pagés 1959; Sendra *et al.* 2021b) with almost half of the known species (496 spp.) belonging to the Campodeidae Lubbock, 1873 family. Diplurans include more than 10% cave-adapted species (170 spp.), inhabiting continental karstic and volcanic regions globally (Sendra *et al.* 2020b). When compared to their epigean confamilials, cave-adapted campodeids exhibit remarkable troglomorphic features such as body and appendage elongation, and an increase in the number, size, and complexity of chemoreceptors (Condé 1956; Bareth & Juberthie-Jupeau 1984; Sendra *et al.* 2020b).

The short-range distributions of these endemic species, together with their relictual origin, make Campodeidae a key taxonomic group from a paleogeographical perspective. Nevertheless, the systematic validity of several Campodeidae lineages remains unresolved. Most cave-dwelling campodeids with cave-adapted features belong to three subfamilies: Plusiocampinae Paclt, 1957 (almost all species are cave-dwelling), Campodeinae Paclt, 1957 and Lepidocampinae Condé, 1956 (Condé 1956, 1989; Sendra *et al.* 2020b). Bareth & Condé (1981) proposed a Tachycampoid lineage, with an unclear subfamily position, that includes five genera from caves on both sides of the Atlantic Ocean (Sendra *et al.* 2016). Importantly, doubts concerning the validity of this group were recently raised by Sendra *et al.* (2020a).

In this paper, we discuss the validity of the Tachycampoid group (Bareth & Condé 1981) by revising its main taxonomical characters, compared with Campodeinae and Plusiocampinae, and using new morphological and ecological data. We revise the entire genus *Juxtlacampa* Wygodzinsky, 1944 and include morphological evidence from two new species. Optical and scanning electron microscopy were used to redress the diagnosis of *Juxtlacampa* and illustrate previously undescribed morphological features.

Material and methods

Study areas

Study area descriptions are provided together with habitat and management implications as Suppl. File 1.

Sampling methods

Diplurans were sampled by direct intuitive searches using an aspirator or paintbrushes in the deep zones of the caves. Researchers examined flood detritus, bat guano concentrations, animal carcasses, as well as other allochthonous organic materials on mud floors and within and along the edges of pools (Wynne *et al.* 2019). Specimens were placed in vials containing ~70% ethanol. Type material were deposited at the following institutions:

Institutional abbreviations

MCNB (MZB)	=	Museu de Ciències Naturals de Barcelona (Museu de Zoologia de Barcelona)
ASPC	=	Alberto Sendra Personal Collection, Museu de Ciències Naturals de València
NAUAC	=	Northern Arizona University Arthropod Collection, Flagstaff, USA

Morphological study

Specimens were washed with distilled water, mounted on slides with Marc André II solution, and examined using a Leica DMLS phase-contrast optical microscope. This method allowed the observations of stomach content of cuticle remains and minerals. Illustrations were made with a drawing tube, and measurements were taken with an ocular micrometer. To determine body length, specimens were mounted in toto and measured from the base of the distal macrosetae on the frontal process to the end of the supra-anal abdominal valve. For scanning electron microscopic (SEM) photography and sensilla measurements, nine specimens were coated with palladium-gold and examined using a Hitachi S-4900 scanning electron microscope. Morphological descriptions and abbreviations follow Condé (1956). The term 'gouge sensilla' refers to the concavo-convex shaped sensilla on the antennae (Bareth & Condé 1981) while the term 'rosette-like' refers to the epicuticle gland formation. To designate the position of macrosetae, we employed the abbreviations of Condé (1956).

Morphological abbreviations

ma	=	medial-anterior
la	=	lateral-anterior
lp	=	lateral-posterior
mp	=	medial-posterior
post	=	posterior
rs	=	rosette-like gland
sla	=	lateral-anterior submacrosetae

Results

Class Diplura Börner, 1904
Superfamily Campodeoidea Lubbock, 1873
Subfamily Campodeinae Plact, 1957
Genus ***Juxtlacampa*** Wygodzinsky, 1944

Emended diagnosis

Epicuticle reticulated with conspicuous microdenticles in the form of thorns or with a rounded tip. Body with short clothing setae and short macrosetae covered with short barbs (except for *Juxtlacampa fernandodebueni* Sendra & García, 2016, which has long clothing setae and macrosetae). Pronotum with 3+3 (*ma*, *la*, *lp*) or 2+2 (*ma*, *lp*) macrosetae; mesonotum with 3+3 (*ma*, *la*, *lp*) to 1+1 (*ma*) macrosetae; metanotum with 1+1 (*ma*) macrosetae or without macrosetae. Femur without dorsal macrosetae. Eighth urosternite with 2+2 or 3+3 macrosetae. Elbow-like subequal claws with well-developed crests. The lateral process of the pretarsus is highly variable: from setiform and smooth to laminar with either short or long barbs.

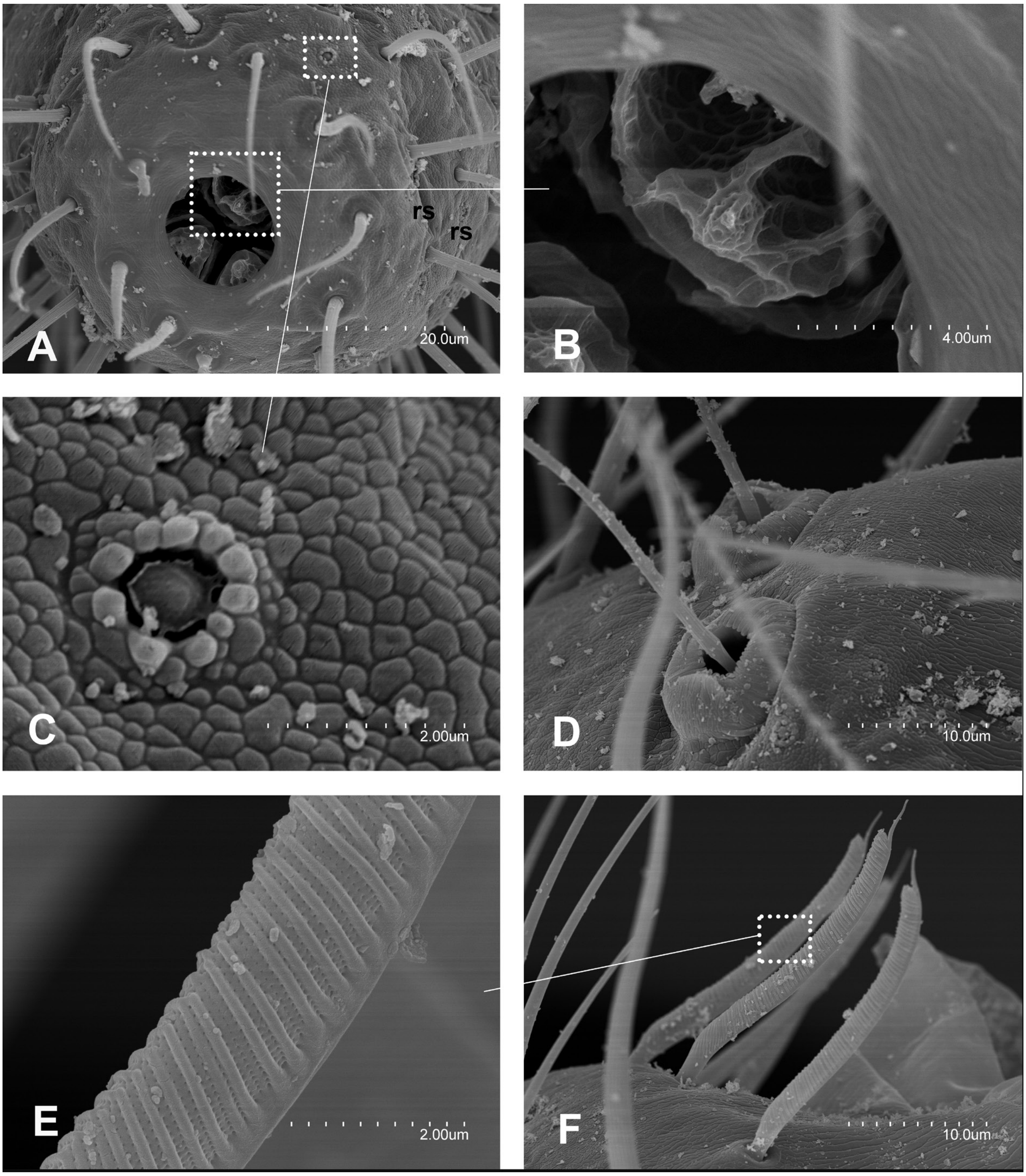

Fig. 1. *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., ♂ (ASPC). **A**. Apical view of the last antennomere. **B**. Detail of sensillum of the cupuliform organ. **C**. Detail of 'rosette-like' gland on the surface of antennomeres. **D**. Trichobothria on antennomere. **E**. Detail of 'gouge' sensillum. **F**. 'Gouge' sensilla of the distal whorl of antennomeres. Abbreviations: see Material and methods.

Juxtlacampa gabrielleae Sendra & Ferreira sp. nov.

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Figs 1–6

Diagnosis

Epicuticle reticulated with blunt tip spines. Antennae shorter than the body length with 24 antennomeres. Third antennomere with bacilliform sensillum between c and d macrosetae; trichobothria with large, protruding base, showing typical distribution pattern. Cupuliform organ with about ten complex olfactory chemoreceptors; each with two complete folds surrounding central cylinder. Few 'rosette-like' cuticular gland formations on antennomeres. Frontal process slightly protruding, plain, with non-tubercular setae. Pronotum with 1+1 *ma* and 1+1 lp_3 macrosetae; mesonotum with 1+1 *ma*; notal macrosetae relatively short and covered by thin distal barbs; marginal setae slightly longer and thicker than clothing setae and covered throughout with short barbs. Pretarsus of metathoracic legs reaching end of abdomen. Tibiae I–III without macrosetae. Claws subequal, emerging from ending of abrupt tarsus; both claws elbow at basal portion with slightly backward overhang; lateral crests well-developed on dorsal, with ventral side almost smooth. Pretarsal lateral process with basal portion in laminar shape narrowing almost abruptly in distal portion in thin prolongation overpassing end of the claws. 1+1 *lp* macrosetae on urotergite VIII, 4+4 $lp_{1–4}$ on urotergite IX, and 3+3 *mp* on abdominal segment X. Urosternite I with 8+1+8 macrosetae; II–VII with 4+4 and VIII with 2+2 macrosetae. Apical stylar seta divided into two to three branches from

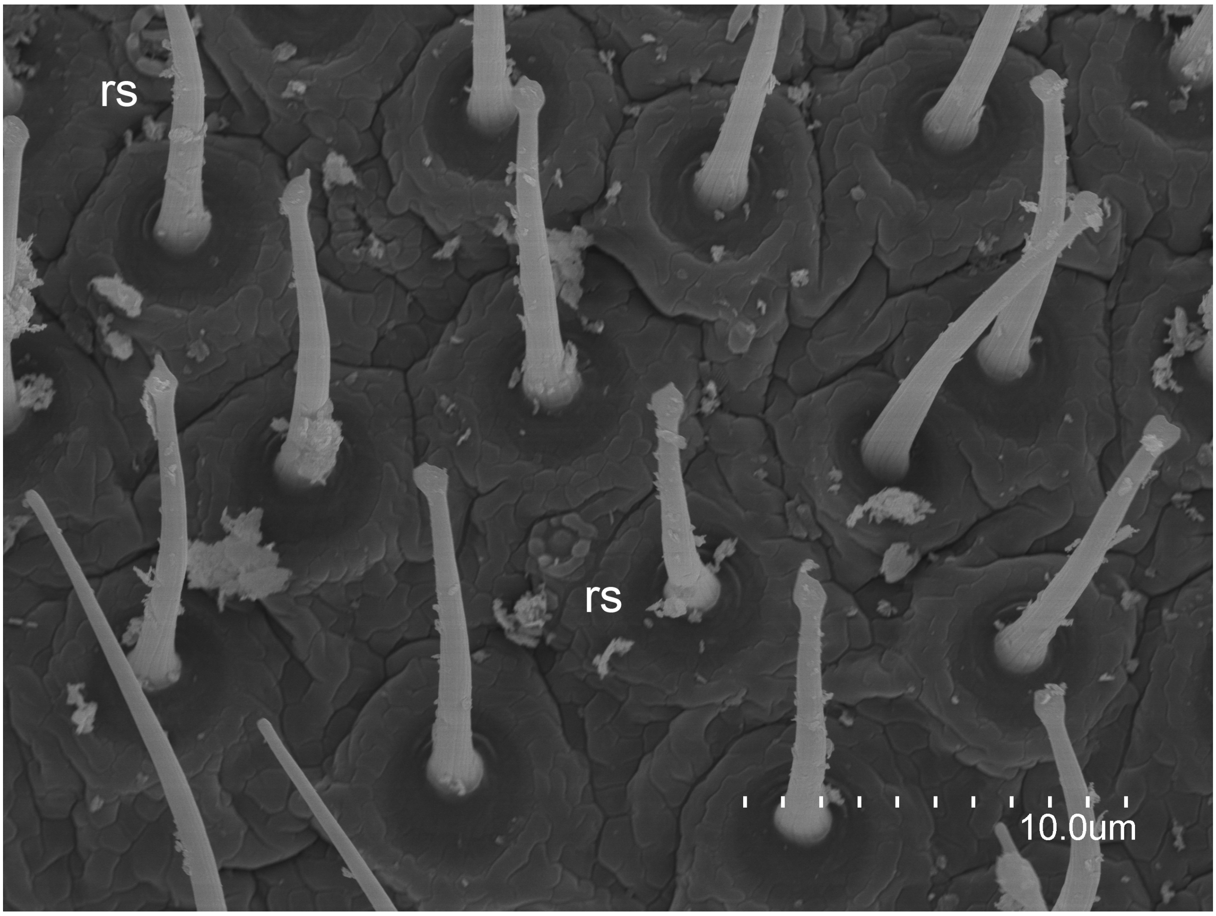

Fig. 2. Glandular setae of the labial palp of *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., ♂ (ASPC). Abbreviations: see Material and methods.

its base with strong short barbs; subapical stylar seta with strong short barbs; and ventromedial stylar seta with few thin short barbs. Cerci up to 3 times longer than body length with up to 64 primary articles. Male urosternite I with slightly enlarged short subcylindrical appendages each with glandular a_1 and g_1 glandular setae. Female appendages similar to male with glandular a_1 setae.

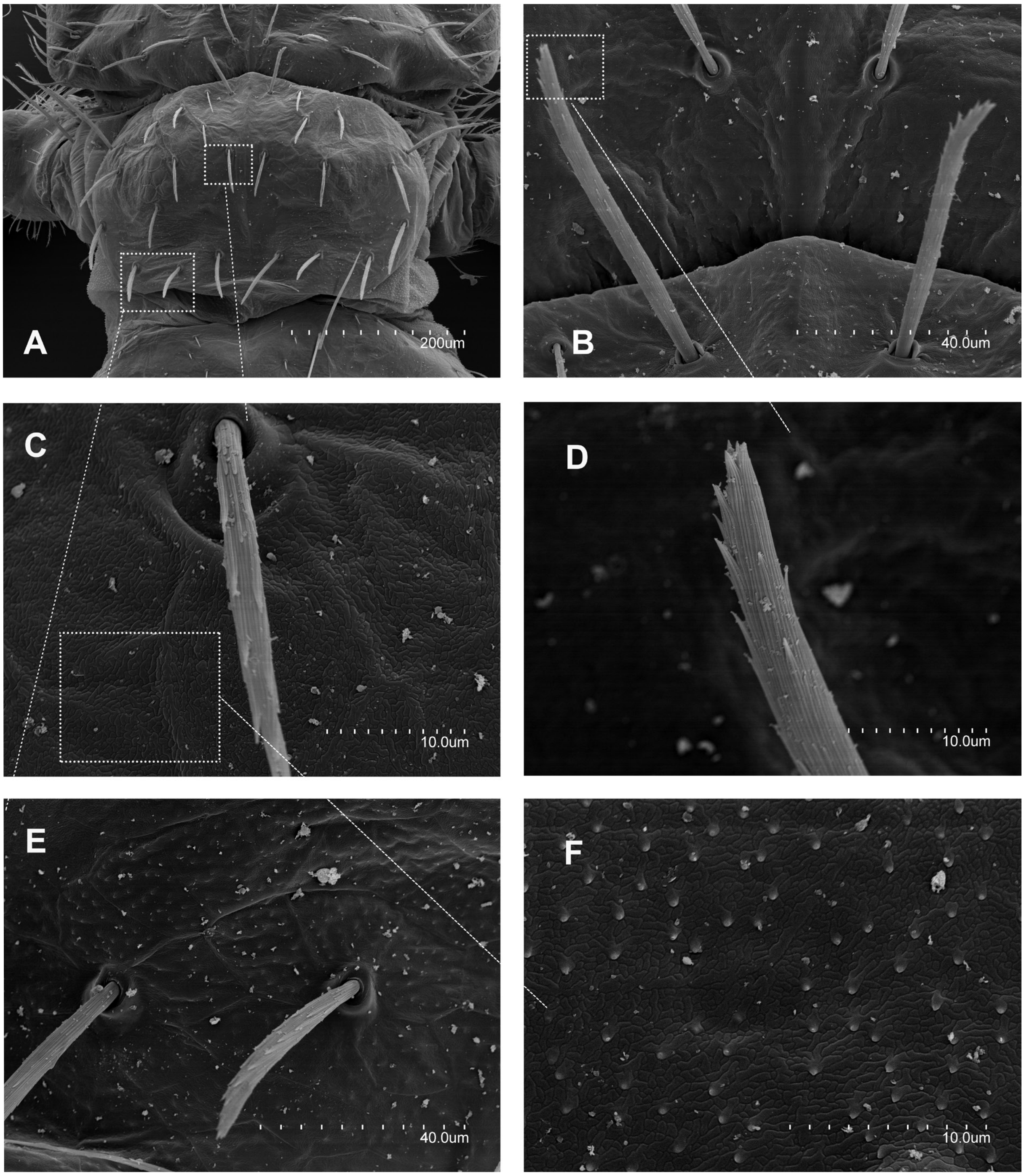

Fig. 3. *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., ♂ (ASPC). **A**. Pronotum. **B**. Medial anterior macrosetae of pronotum. **C**. Medial portion of pronotum. **D**. Detail of apical part of medial anterior macrosetae of pronotum. **E**. Marginal setae of pronotum. **F**. Detail of epicuticle of pronotum.

Etymology

The specific epithet is in honour of the cave biologist Gabrielle Soares Muniz Pacheco for her valuable contributions to the knowledge of cave fauna in Guatemala.

Type material

Holotype

GUATEMALA • 1 ♀; Raxruhá, Alto Verapaz, Cueva Blanca cave; 15.866313° N, -90.095303° W; elev. 306 m; 27 Jun. 2017; G. Pacheco leg.; MZB 2024-3911.

Paratypes

GUATEMALA • 1 ♀, 1 ♂; same data as for holotype; ♀ MZB 2024-3912, ♂ MZB 2024-3913 • 4 ♀♀, 1 ♂, 1 juvenile; same data as for holotype; 15.865118° N, 90.095068° W; elev. 208 m; 27 Jun. 2017; G. Pacheco leg.; ♀♀ MZB 2024-3914 – MZB 2024-3917, ♂ MZB 2024-3918, juvenile MZB 2024-3919.

Other material examined

GUATEMALA • 1 ♂; Flores, Peñón, Actun Kan cave; 16.902757° N, -89.895371° W; elev. 174 m; 30 Jun. 2017; G. Pacheco leg.; ASPC.

BELIZE – **Cayo District** • 1 ♂; San Ignacio, Actun Tunichil Muknal cave; 17.113361° N, -88.862745° W; 2 Jul. 2017; G. Pacheco leg.; ASPC.

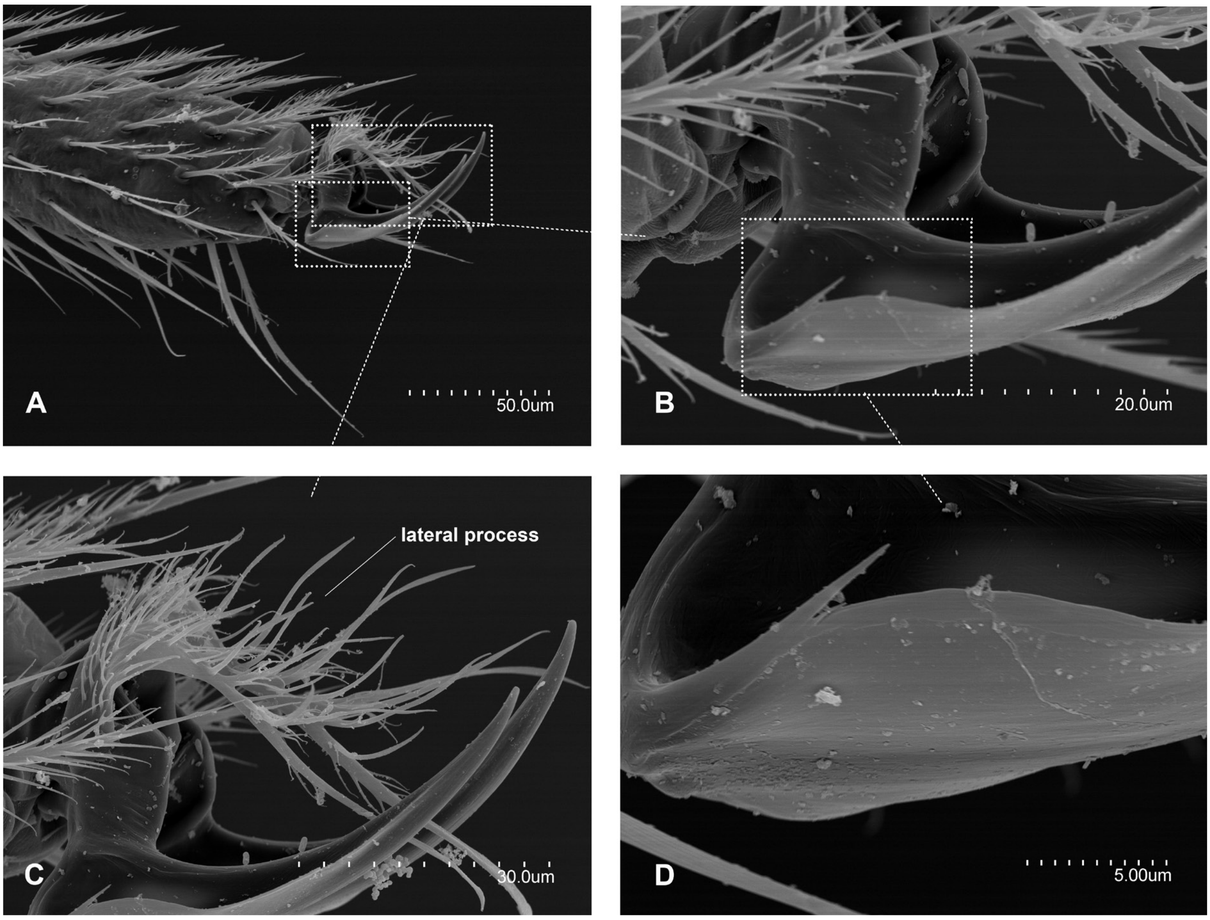

Fig. 4. *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., ♂ (ASPC). **A**. Distal part of tarsus with the pretarsus. **B**. Detail of claws. **C**. Detail of lateral processes. **D**. Detail of lateral crest of the claws.

Description

Body. Length 3.3–5.1 mm in females, 2.6–2.7 mm in males. Epicuticle reticulated with blunt tip spines (Fig. 3E–F); body covered with short, barbed setae (Fig. 3C).

Head. Antennae 0.6–0.7 × as long as body (length measured on four intact antennae), with 24 antennomeres. Third antennomere with bacilliform sensillum located in ventral position between *c* and *d* macrosetae; trichobothria with large, protruding base, showing typical distribution pattern (Fig. 1D). Central antennomeres 2.3 × as long as wide, apical antennomere 2.9 × as long as wide. Cupuliform organ occupying ⅛ of total length of apical antennomere, with about ten complex olfactory chemoreceptors; each olfactory chemoreceptor with two complete folds surrounding central cylinder in three entirely reticulated and perforated radial expansions (Fig. 1A–B). Few 'rosette-like' cuticular gland formations on antennomeres, including an apical one (Fig. 1C). 'Gouge' sensilla 18–21 µm long, in single distal whorl of 18–21 sensilla on each medial and distal antennomere, and with one to three pores between cross-grooves (Fig. 1E–F). Frontal process slightly protruding, plain, with non-tubercular setae; macrosetae along the insertion line of antennomere: a/i/p with relative lengths of 28/30/26 in holotype, X setae indistinguishable from the thin clothing setae; dorsal occipital side covered by up to 12+12 short, thin setae with thin barbs throughout. For specimens from both Actun Kan cave and Actun Tunich Muknal

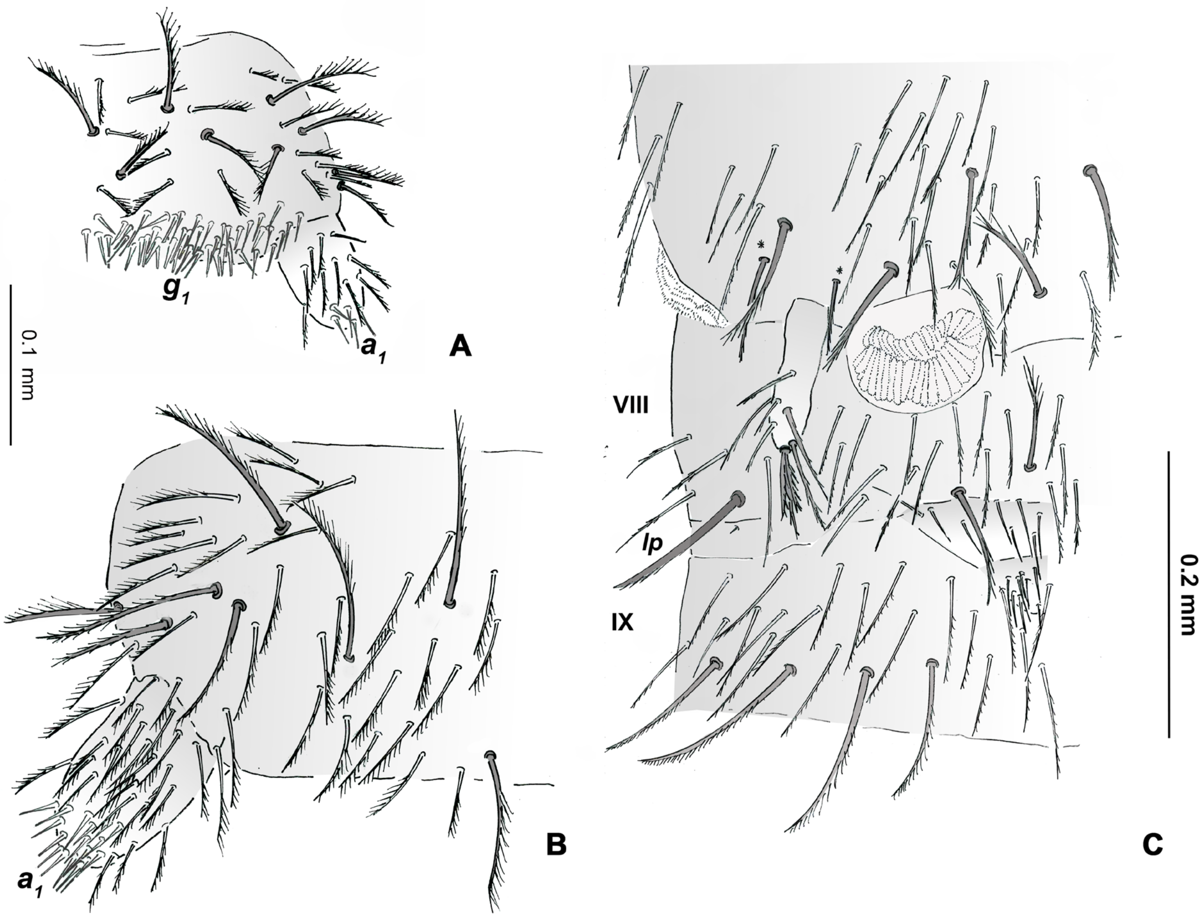

Fig. 5. *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov. **A**. First urosternite of the male, left side (paratype, MZB (MCNB) 20243118). **B**. First urosternite of the female, right side (holotype, MZB (MCNB) 2024-3911). **C**. Seventh to ninth urosternites of female (holotype, MZB (MCNB) 2024-3911), right side. Abbreviations: g_1 = posterior glands g_1 of first urosternite, a_1 = apical a_1 glands of first urosternite appendages.

cave, thicker dorsal head setae. Labial palps large, suboval, with large bacilliform latero-external sensillum, two external guard setae, up to 15 setae on anterior border and up to 130 neuroglandular setae in holotype (Fig. 2).

Thorax. Thoracic macrosetae distribution (Fig. 3A): pronotum with 1+1 *ma* and 1+1 lp_3; mesonotum with 1+1 *ma*; notal macrosetae relatively short and covered by thin distal barbs (Fig. 3A–D); marginal setae slightly longer and thicker than clothing setae and covered throughout with short barbs (Fig. 3A, E). Legs elongate, pretarsus of metathoracic legs slightly reaching or extending beyond end of abdomen; lengths in mm of articles of metathoracic legs (coxa/trochanter/femur/tibia/tarsus plus pretarsus/complete leg): 0.22/0.21/0.68/0.81/0.58/2.50 mm in holotype, 0.21/0.20/0.74/0.85/0.68/2.68 mm in ♀ paratype MZB2024-3912, and 0.15/0.12/0.43/0.50/0.41/1.61mm in ♂ paratype. Femora I–III with one barbed ventral macroseta. Tibiae I–III without macrosetae; calcars with 2–3 rows of 4–5 long barbs on one side. Tarsi with two rows of thick ventral setae with numerous thin barbs along middle portion; three dorsal subapical tarsal setae: two smooth and one well-barbed. Claws subequal, emerging from ending of abrupt tarsus; both claws elbow at basal portion with slightly backward overhang; lateral crests well-developed on dorsal, with ventral side almost smooth. Pretarsal lateral process with basal portion in laminar shape narrowing almost abruptly in distal portion in thin prolongation overpassing end of the claws. Very long barbs with hook ending on ventral side of pretarsal lateral process (Fig. 4A–D).

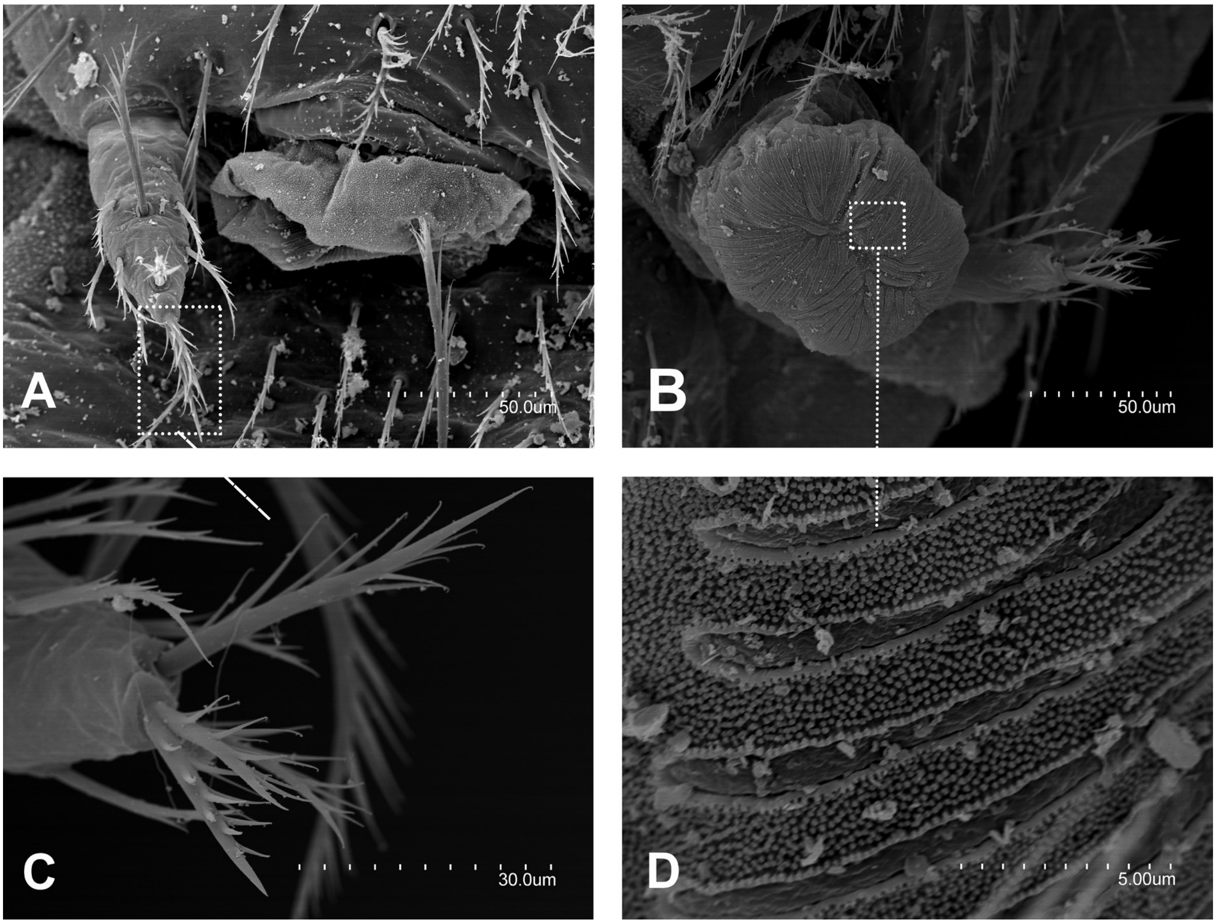

Fig. 6. *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., ♂ (ASPC). **A**. Lateral posterior side of fifth urosternite. **B**. Exertil vesicle fourth urosternite. **C**. Distal portion stylus fifth urosternite. **D**. Detail surface of exertil vesicle.

Abdomen. Distribution of abdominal macrosetae on tergites: 1+1 *lp* on urotergite VIII, 4+4 lp_{1-4} on urotergite IX, and 3+3 posterior macrosetae on abdominal segment X (Fig. 5C); all post urotergal macrosetae are long and covered with thin barbs along distal four-fifths. Urosternite I with 8+1+8 macrosetae (Fig. 5A–B); urosternites II–VII with 4+4 macrosetae plus 2+2 parastylar setae; urosternite VIII with 2+2 macrosetae (Fig. 5C); all urosternal macrosetae large and covered by long barbs along distal third to four-fifths. Apical stylar seta divided into two to three branches from its base with strong short barbs; subapical stylar seta with strong short barbs; and ventromedial stylar seta with few thin short barbs (Figs 5C, 6A, C). Large eversible vesicles with two absorbing zones: one proximal with uniform protruding surface, other distal with more evident protruding surface with regular concentric circles around external vesicle area (Figs 5C, 6B, D).

Cerci. Extremely long; a complete cercus in holotype measures 16.2 mm, 3.44 × as long as the body length. Basal article covered by barbed setae with three distinguishable rows of shorter setae: two on dorsal and one on internal side; 64 primary articles with two or three constrictions, each bearing three whorls of large and long setae intercalated with shorter thinner setae, in addition to whorl of short setae in apical position.

Secondary sex characters. Male urosternite I (Fig. 5A) with slightly enlarged short subcylindrical appendages each bearing up to 7 glandular a_1 setae in addition to field of about 160 g_1 glandular setae arranged in 3–5 transversal rows. Female appendages similar to male appendages, with up to 20 glandular a_1 setae (Fig. 5B).

Stomach content observations

All specimens from Cueva Blanca contained arthropod remains, and some contents that appeared to be appendages of mites. Specimens from Cueva del Rostro contained mineral elements and arthropod eggshells.

Juxtlacampa hauseri Condé, 1975

Figs 7–10

Material examined

GUATEMALA • 13 ♀♀; Alta Verapaz, Gruta de Lanquín cave; 15.580415° N -89.990575° W; elev. 299 m; 23 Jun. 2017; G. Pacheco leg.; ASPC.

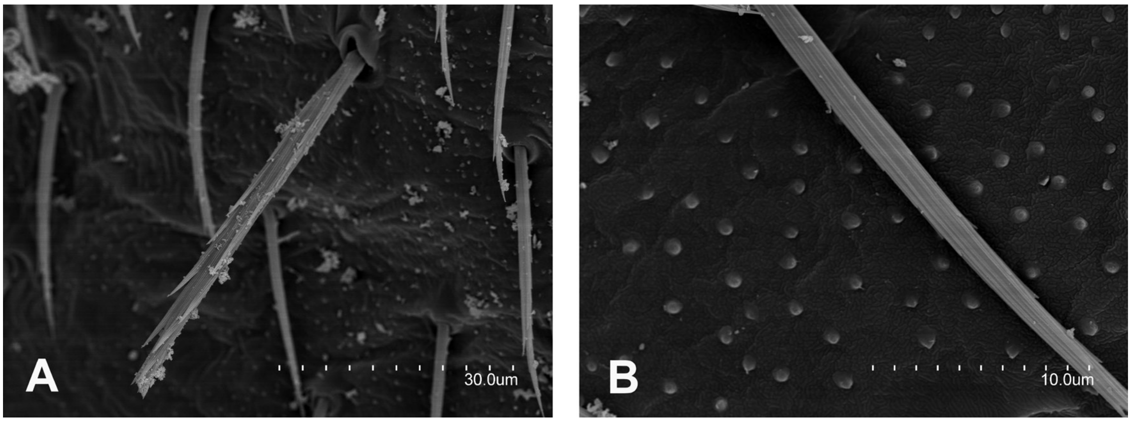

Fig. 7. *Juxtlacampa hauseri* Condé, 1975, ♀ (ASPC). **A**. Mesonotal macrosetae and epicuticle surface. **B**. Detail of epicuticle.

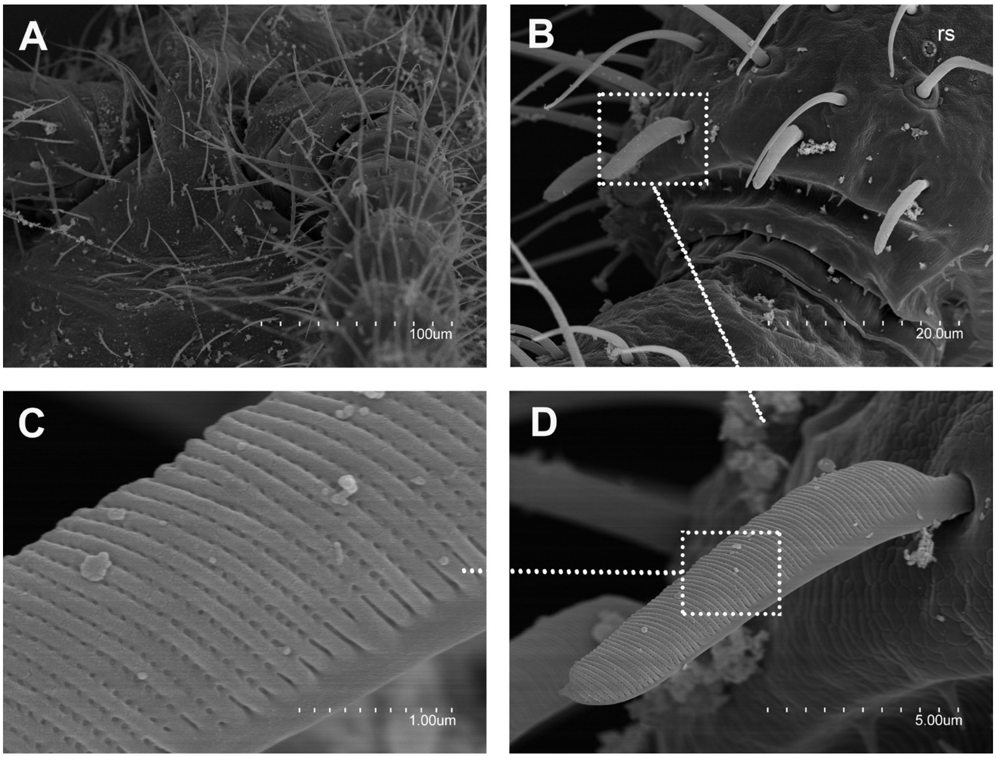

Fig. 8. *Juxtlacampa hauseri* Condé, 1975, ♀ (ASPC). **A**. Dorso-lateral frontal part of the head. **B**. Distal portion of the fourteenth antennomere. **C**. Detail of a 'gouge' sensillum. **D**. 'Gouge' sensillum. Abbreviations: see Material and methods.

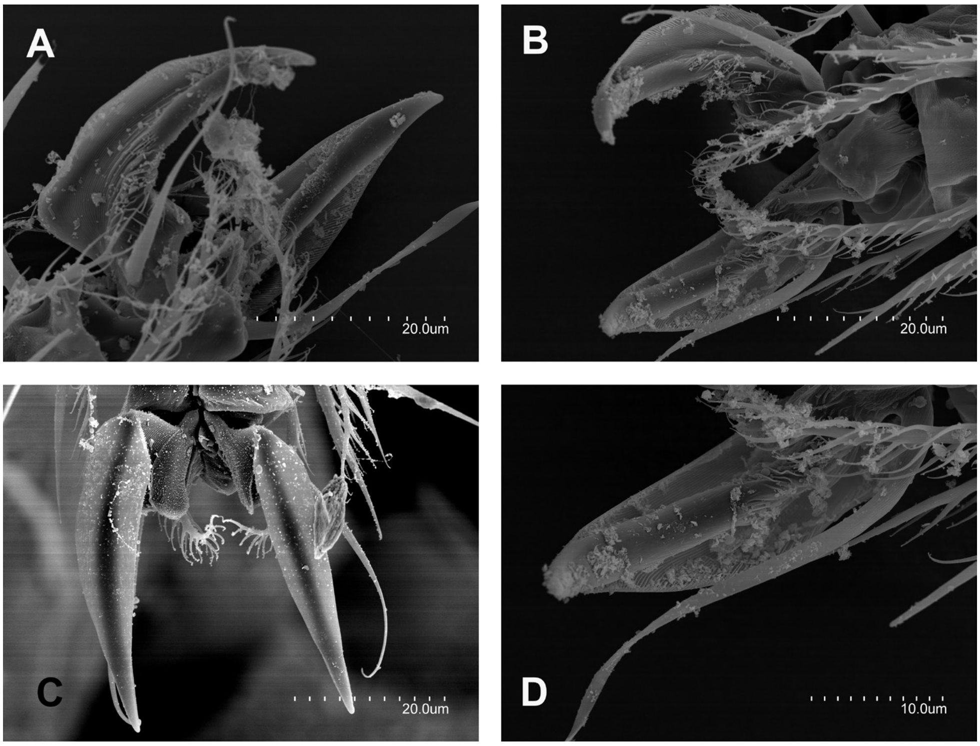

Fig. 9. Pretarsus of a metathoracic leg of *Juxtlacampa hauseri* Condé, 1975, ♀ (ASPC). **A**. Lateral view. **B**. Ventral view. **C**. Dorsal view of a metathoracic leg. **D**. Detail of a claw in ventral view.

Remarks

All examined specimens display taxonomic features similar to those of a young female specimen from Chirrepeck Cave in Alta Verapaz (Guatemala) which was initially described by Condé (1975) and considered a cave-adapted species. The use of SEM enabled a more thorough examination of some characters including: epicuticle reticulated with tiny blunt tip spines (Fig. 7A–B); clothing setae with a few thin distal barbs, appearing smooth under optical microscopy (Fig. 7B); thick 'gouge' sensilla in a distal whorl on each medial antennomere (Fig. 8B–D); frontal process with a marked anterior ridge bearing three distinguishable macrosetae and several barbed clothing setae in a posterior position (Fig. 8A); pretarsus with subequal elbow claws with basal barbs below bearing large dorsal crests (Fig. 9A–D); each stylus of urosternites with apical seta bearing a long basal barb, plus subapical seta and submedial seta with a few long barbs (Fig. 10A); big eversible vesicles with three absorbing zones (Fig. 10A–B); and urosternal macrosetae with long barbs (Fig. 10C–D).

Juxtlacampa xkiq Sendra & Wynne sp. nov.

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Figs 11–12

Diagnosis

Epicuticle reticulated with tiny spines uniformly distributed. Body with short and slightly thick clothing setae covered with few short barbs along tiny crests. Third antennomere with bacilliform, long sensillum between c and d macrosetae. Short thick 'gouge' sensilla. Frontal process slightly protruding, plain, with non-tubercular setae. Pronotum with 1+1 *ma* and 1+1 lp_3 macrosetae, and 1+1 sla_3 submacrosetae;

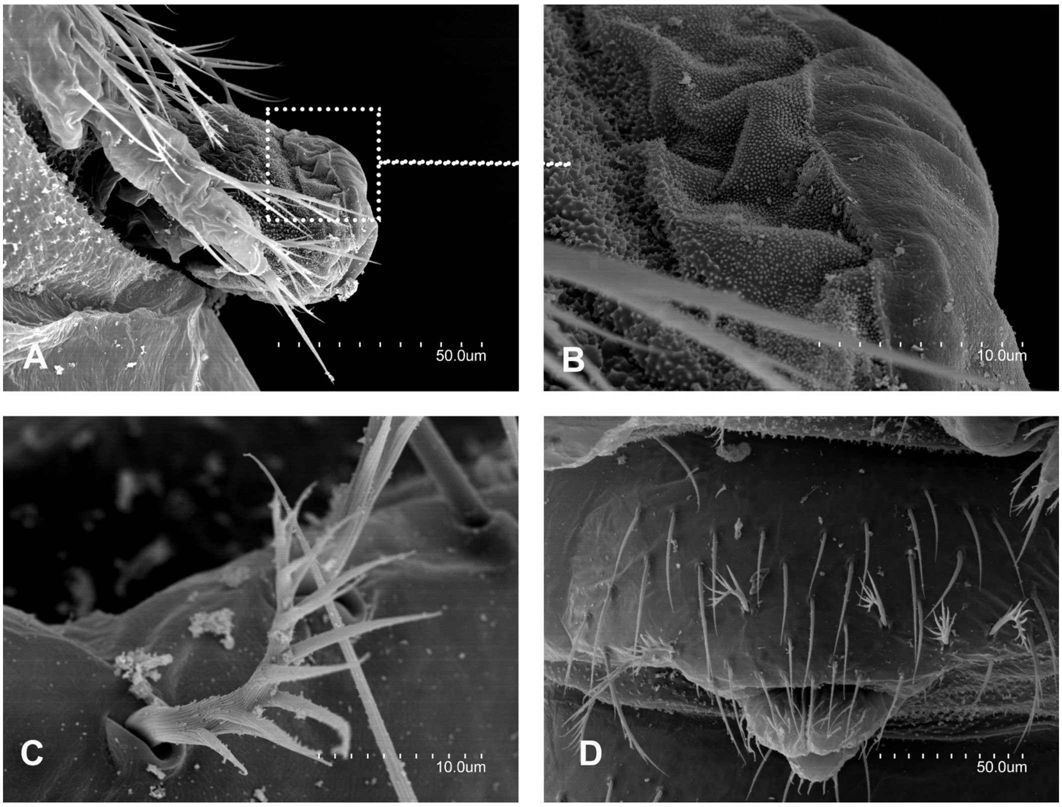

Fig. 10. *Juxtlacampa hauseri* Condé, 1975, ♀ (ASPC). **A**. Left stylus and eversible vesicle of the seventh urosternite. **B**. Detail of the surface of the eversible vesicle. **C**. Urosternal macroseta. **D**. Eighth urosternite of female.

mesonotum with 1+1 *ma*; notal macrosetae thick, relatively long, with thick barbs throughout giving crested appearance; marginal setae more than twice as long and thicker than clothing setae, both with crested appearance. Metathoracic legs reaching abdominal segment X. Tibiae without macrosetae. Claws subequal, emerging from the ending of abrupt tarsus; with large base elbowed and prolonged into narrower claw with small dorsal lateral crests; large base with long transversal barbs. Pretarsal process starting in laminar shape becoming prolonged in narrow axis curved overpassing end of claws and divided with long thin expansions; longer claws with hook ending in multiple fringes either simple or subdivided with hook ending. Without, 0+1 or 1+1 la macrosetae on urotergite VII, 4+4 $lp_{1–4}$ on urotergite VIII, and 6+6 posterior macrosetae on abdominal segment IX. Urosternite I with 6+6 macrosetae; urosternites II–VII with 4+4 macrosetae; urosternite VIII with 2+2 macrosetae. Cerci up to 3.6 × as long as body length. Female conical appendages with truncated end in narrower apical area, and small area with glandular a_1 setae.

Etymology

The species name, in the K'iche' Maya language is used as a noun in apposition to honor the Maya culture of Belize. Xkiq (pronounced 'sh-kek') is a goddess of Xibalba (the Maya underworld); Her name translates to English as 'blood'. She is known as the 'Blood Moon Goddess' or 'Blood Maiden', and is the virgin mother of the Hero Twins, Hunahpú and Xbalanqué, who are all prominently featured in the Maya Book of Creation, the Popul Vuh (Tedlock 1996).

Type material

Holotype

BELIZE – **Belize District** • 1 ♀; Runaway Creek Nature Reserve, Crocodile Cave 1; 17.310731° N, -88.445867° W; 23 Jun. 2019; J.J. Wynne leg.; NAUAC BECA-001.

Paratypes

BELIZE – **Belize District** • 1 ♀; same data as for holotype; NAUAC BECA-002 • 3 ♀, 1 juvenile; same data as for holotype; J.J. Wynne leg.; ♀ MZB 2024-3920, ♀ MZB (MCNB) 3921, juvenile MZB (MCNB) 2024-3922.

Other material examined

BELIZE – **Belize District** • 1 ♀; same data as for holotype; J.J. Wynne leg.; ASPC.

Description

Body. Length 3.4–4.6 mm in females, 2.7 mm in the juvenile. Epicuticle reticulated with tiny spines uniformly distributed (Fig. 11D); body with short and slightly thick clothing setae covered with few short barbs along tiny crests.

Head. Antennae incomplete; regenerated in MZB (MCNB) 2024-3920. Third antennomere with bacilliform, long sensillum located in ventral position between *c* and *d* macrosetae. Central antennomeres 1.7 × as long as wide, with three distinguishable whorls of barbed macrosetae and setae among them. Short thick 'gouge' sensilla present in all antennomeres except apical and proximal ones, arranged in single distal whorl of 14–16 units; 'gouge' sensilla 12–16 µm long, 2 µm in diameter, with tiny transversal grooves; pores arranged in two to five among them (Fig. 12A–B). Frontal process slightly protruding, plain, with non-tubercular setae; macrosetae along insertion line of antennomere: a/i/p/x with relative lengths of 20/23/28/21 in paratype MZB (MCNB) 2024-3920, indistinguishable from other dorsal occipital setae of head characterized by thick morphology and covered by tiny barbs all around; central area behind Y sutural branches with 14+14 thick setae. Labial palps large, suboval, with large bacilliform latero-external sensillum, two external guard setae, up to 11 setae on anterior border, and up to 180 neuroglandular setae in holotype.

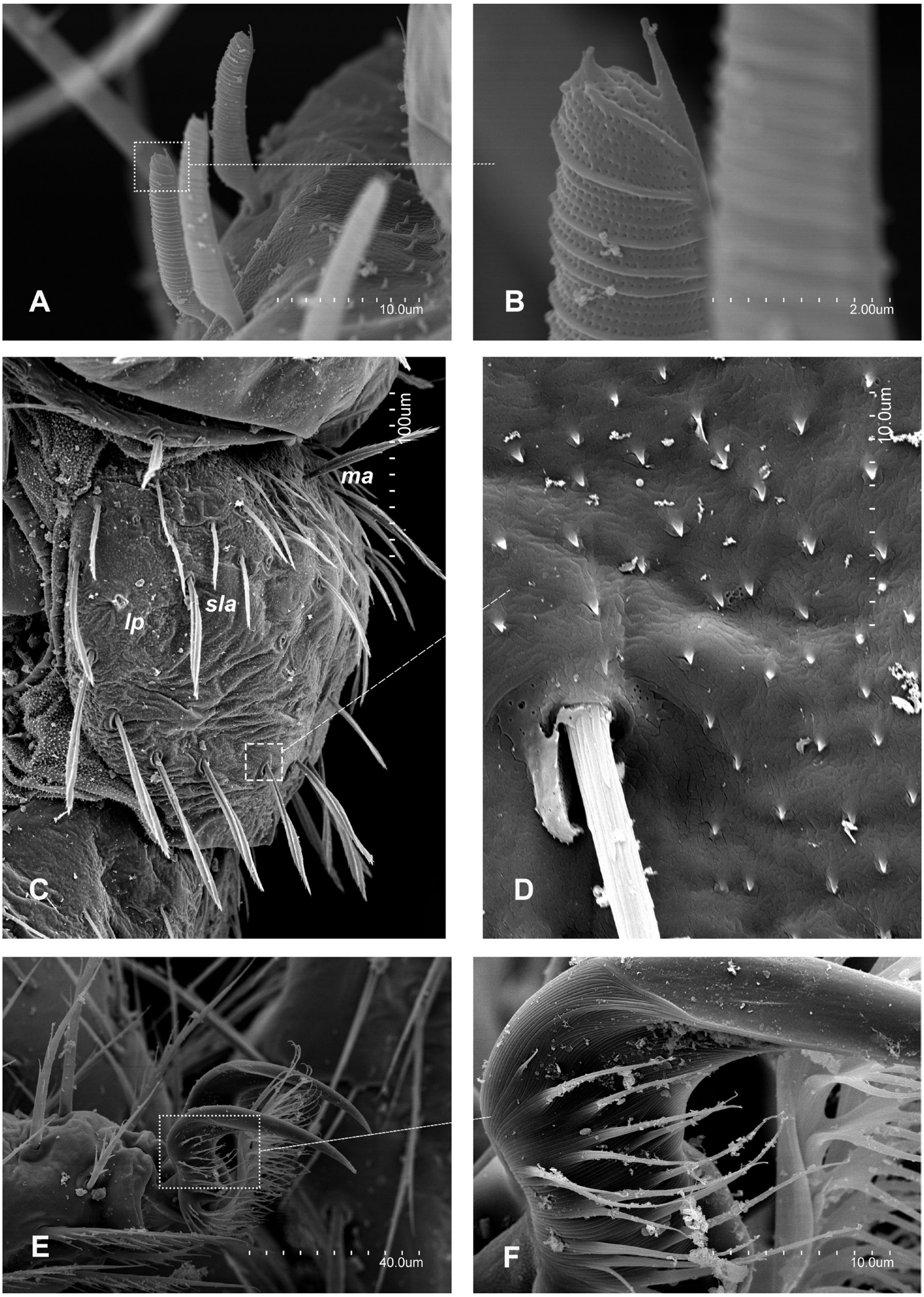

Fig. 11. *Juxtlacampa xkiq* Sendra & Wynne sp. nov., ♀ (ASPC). **A**. 'Gouge' sensilla of the distal whorl of medial antennomeres. **B**. Detail of 'gouge' sensilla. **C**. Lateral view of pronotum, left side. **D**. Detail of epicuticle of the pronotum. **E**. Apical part of tarsus with the pretarsus. **F**. Detail of claws. Abbreviations: see Material and methods.

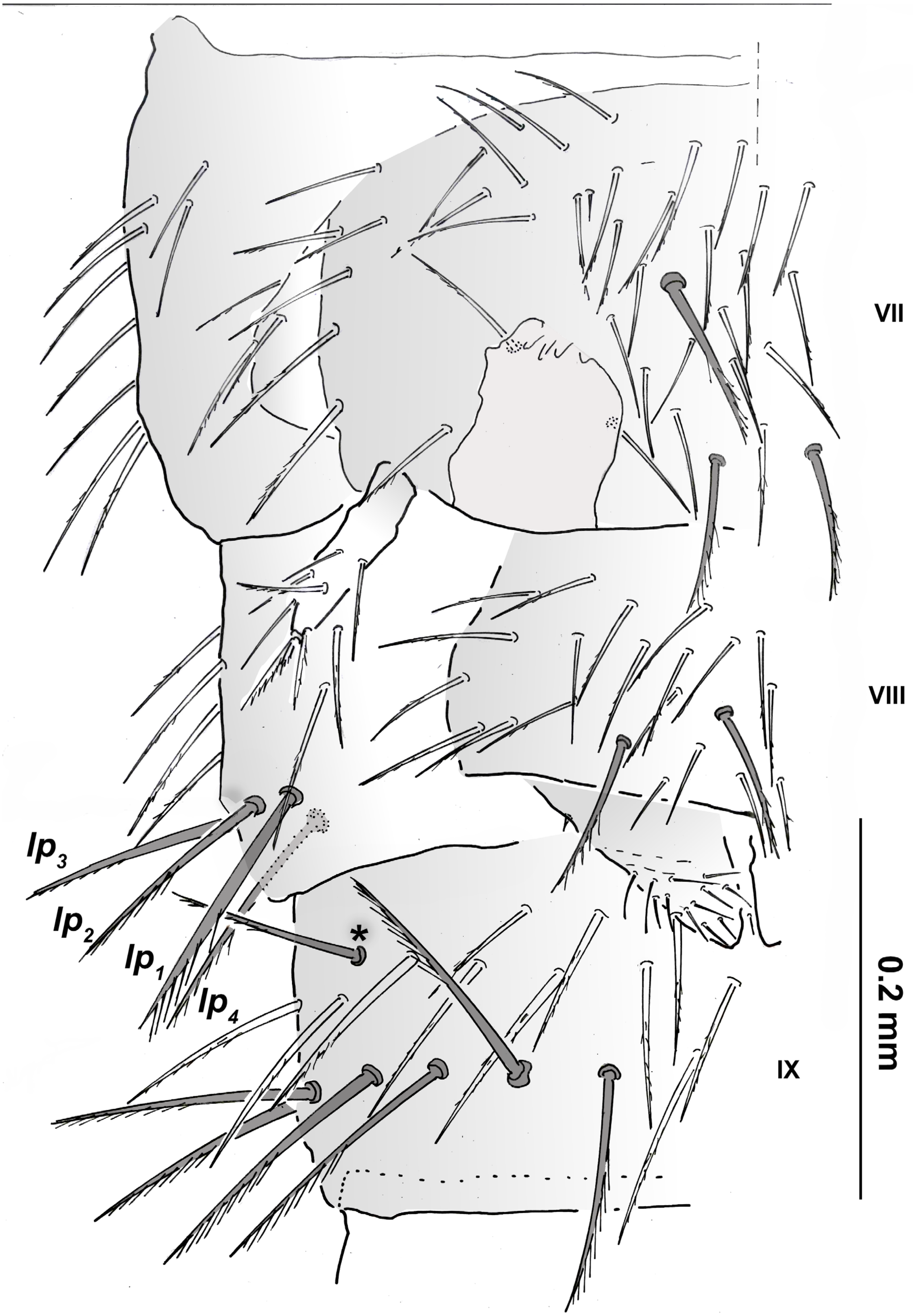

Fig. 12. *Juxtlacampa xkiq* Sendra & Wynne sp. nov., holotype, ♀ (NAUAC BECA-001). Urosternites VII–IX of the female, right side. *aberrant macrosetae. Abbreviations: see Material and methods.

Thorax. Thoracic macrosetae distribution: pronotum with 1+1 *ma* and 1+1 lp_3 macrosetae, and 1+1 sla_3 submacrosetae, all distinguishable from clothing setae by size (twice as large) and clear crest from base to tip with tiny barbs; mesonotum with 1+1 *ma*; notal macrosetae thick, relatively long, with thick barbs throughout giving crested appearance (Fig. 11C); marginal setae more than twice as long and thicker than clothing setae, both with crested appearance (Fig. 11C). Legs elongate, pretarsus of metathoracic legs reaching abdominal segment X; lengths in mm of articles of metathoracic legs (coxa/trochanter/femur/tibia/tarsus plus pretarsus/complete leg): 0.25/0.14/0.60/0.73/0.53/2.25 mm in holotype; 0.22/0.19/0.55/0.66/0.46/2.08 mm in paratype ♀ MZB (MCNB) 2024-39320 and 0.23/0.14/0.46/0.55/0.45/1.83 mm in paratype ♀ MZB (MCNB) 2024-3931. Femora I–III with one middle-size 0.10–0.12 mm thick barbed ventral macroseta in distal position. Tibiae without macrosetae; calcars with 2–3 rows of short barbs on one side. Tarsi with two rows of thick ventral setae with numerous thin barbs along the middle portion; three dorsal subapical tarsal setae with few barbs all along. Claws subequal, emerging from the ending of abrupt tarsus; with large base elbowed and prolonged into narrower claw with small dorsal lateral crests; large base with long transversal barbs. Pretarsal process starting in laminar shape becoming prolonged in narrow axis curved overpassing end of claws and divided with long thin expansions; longer claws with hook ending in multiple fringes either simple or subdivided with hook ending (Fig. 12E–F).

Abdomen. Distribution of abdominal macrosetae on tergites (Fig. 12): 0, 0+1 or 1+1 *la* on urotergite VII, 4+4 $lp_{1–4}$ on urotergite VIII, and 6+6 posterior macrosetae on abdominal segment IX; in two specimens, including the holotype, 1+0 extra *la* macrosetae; all post urotergal macrosetae long and covered with thin barbs along distal half to four-fifths. Urosternite I with 6+6 macrosetae; urosternites II–VII with 4+4 macrosetae; urosternite VIII with 2+2 macrosetae (Fig. 12); all urosternal macrosetae large and covered by barbs along distal half to one-third. Apical stylar seta bearing 3–5 barbs with long basal tooth containing 2–3 barbs; subapical and ventromedial stylar setae with few thin short barbs (Fig. 12). Large eversible vesicles with two absorbing zones: one proximal with uniform protruding surface, other distal with more evident protruding surface drawing regular circles around external vesicle area. Cerci not preserved in the collected specimens, but photographs taken of live individuals in cave showed cerci up to 3.6 × as long as body length.

Secondary sex characters. No males were collected. Female conical appendages with truncated end in narrower apical area, and small area with up to six glandular a_1 setae.

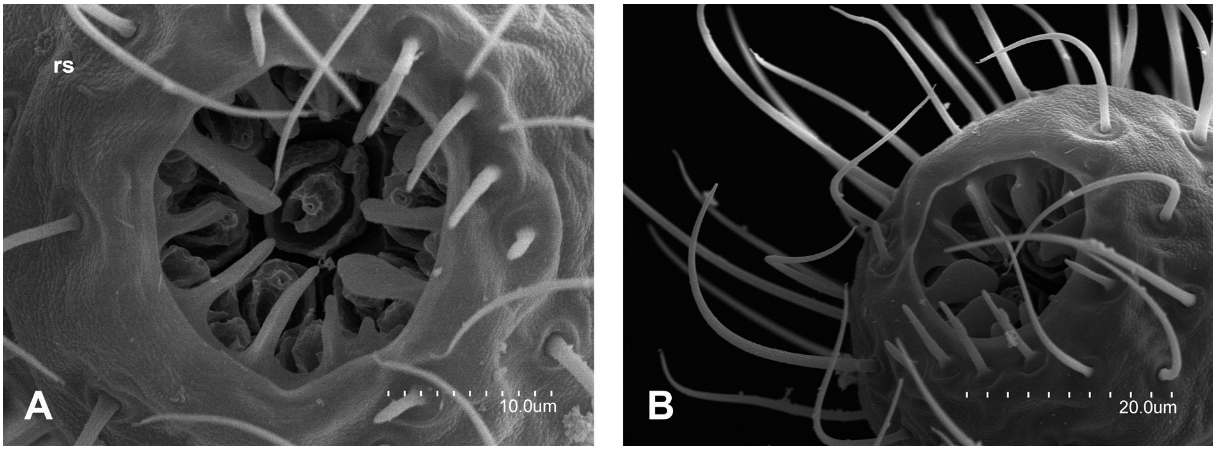

Fig. 13. Cupuliform organ of *Juxtlacampa juxtlahuacensis* Wygodzinsky, 1944, ♂ (ASPC). **A**. Apical view. **B**. Latero-apical view. Abbreviations: see Material and methods.

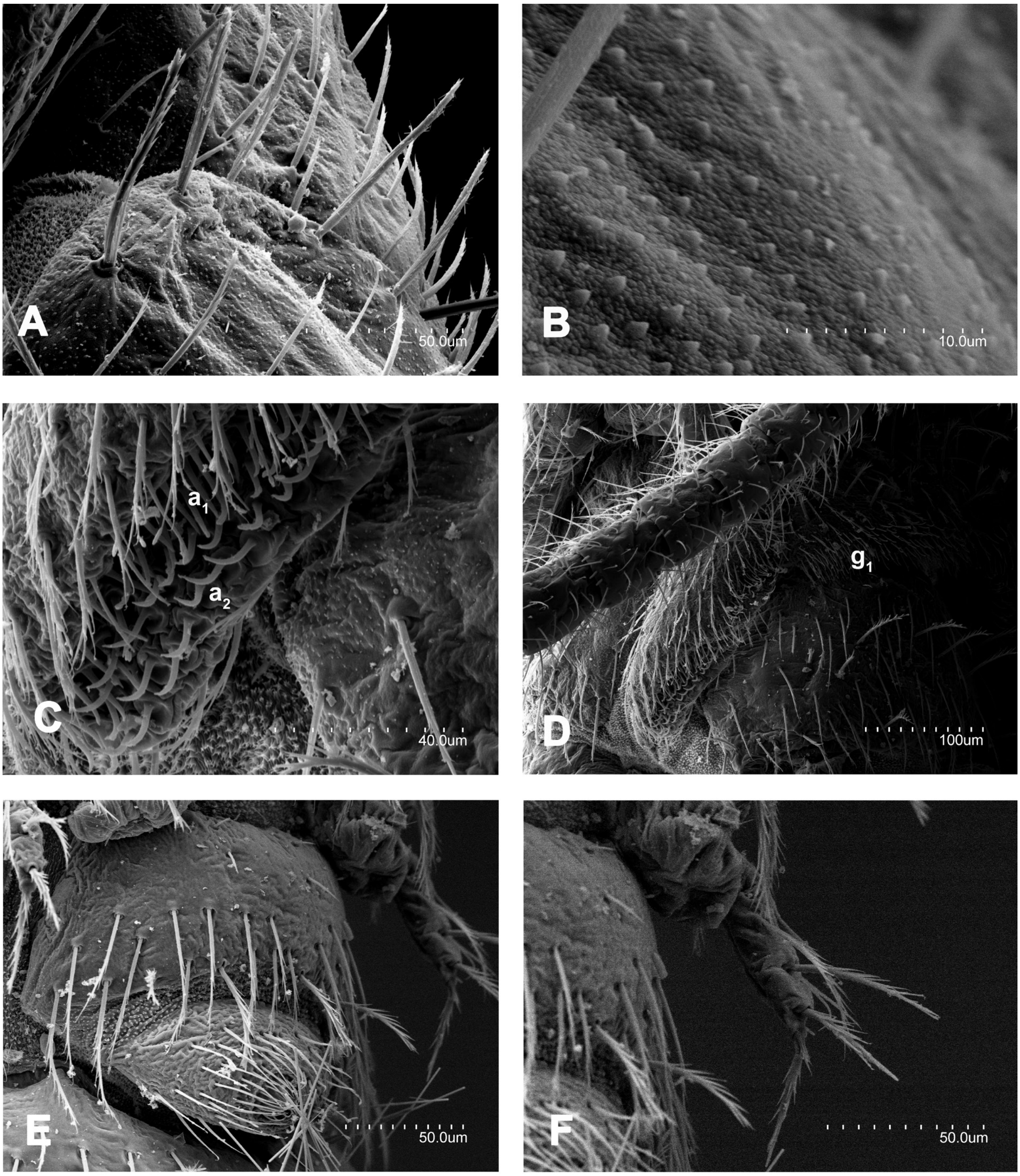

Fig. 14. *Juxtlacampa juxtlahuacensis* Wygodzinsky, 1944, ♂ (ASPC). **A**. Latero-posterior side of the mesonotum with clothing and marginal setae. **B**. Detail of epicuticle of mesonotum. **C**. Appendages of the first urosternite of male. **D**. Lateral side of first abdominal segment. **E**. Eighth urosternite of male. **F**. Stylus and eversible vesicle of seventh abdominal segment. Abbreviations: g_1 = posterior glands g_1 of first urosternite, a_1 = apical a_1 glands of first urosternite appendages, a_2 = distal a_2 glands of first urosternite appendages.

Juxtlacampa juxtlahuacensis Wygodzinsky, 1944

Figs 13–14

Material examined

MEXICO – **Guerrero** • 1 ♂; Xotlametzi limestone hill at Quechultnango, Grutas de Juxtlacampa cave; 17.439392° N -99.159540° W; 8 Nov. 2014; O. Moldovan leg.; ASPC.

Remarks

The species under examination is a well-described cave-adapted species (Wydodzinsky 1944; Sendra *et al*. 2016). However, further investigation using SEM imagery revealed unique features such as a cupuliform organ with large folds that start below the upper border of the organ and extend inward without reaching the center (Fig. 13A–B) and 'rosette-like' glands on the surface of the last antennomere, (Fig. 13A). Additional observations include the notal epicuticle with a reticulated surface and blunt-tipped spines (Fig. 14A–B), the glandular setae of the first urosternite of males (Fig. 14C–D), stylar setae with abundant long barbs along the length (Fig. 14E), and numerous long barbs on urosternal macrosetae (Fig. 14F). These findings contribute to a more comprehensive description of the species, which is currently only known from its type locality, Grutas Juxtlahuaca. No cerci were observed in the collected specimens, but photographs taken in the cave showed cerci up to 3.8 times the length of the body.

Juxtlacampa carlosjuarezi (Palacios-Vargas & Sendra, 2016)

Figs 15–16

Material examined

MEXICO – **Moleros** • 2 specs; Tepozlán, Suchiooc Volcano, Cueva San Juan Tepozlán lava tube; 13 Jan. 2014; I. Ramirez leg.; ASPC.

Remarks

Unfortunately, the two specimens of this cave-adapted species examined were in poor condition, which made it impossible to determine the sex under the SEM. However, microcopy observations revealed several important features, including relatively short sensilla in 'gouge' (Fig. 15A–B); a large base of the trichobothria (Fig. 15C); dorsal head with clear apodeme marks parallel to the posterior border; frontal process with a marked anterior ridge having three distinguishable macrosetae and several clothing barbed setae in a posterior position (Fig. 15D–F); a reticulated epicuticle with thorny microdenticles, and a few 'rosette-like' gland formations (Fig. 16A–B); and claws with well-developed lateral crests and lacking backward prolongation, with thin ridges on the ventral side (Fig. 16C–D). These described characters provide additional information concerning this species morphology, which were not discussed in Sendra *et al.* (2016).

Discussion

Phyletic affinities and distribution of the tachycampoid "phyletic line"

Morphological features of the five *Juxtlacampa* species were compared with existing literature information. We examined the relationships among *Juxtlacampa* species, and between this genus and other tachycampoid genera.

To date, *Juxtlacampa* comprises six known species inhabiting caves in Latin America: *J. juxtlahuacensis* Wygodzinsky, 1944, *J. fernandodebueni* and *J. carlosjuarezi* (Palacios-Vargas & Sendra, 2016) from Mexico; *J. hauseri* Condé, 1975 from Guatemala; *J. gabrielleae* sp. nov. from Guatemala and Belize, and *J. xkiq* sp. nov. from Belize. These species are considered troglobites according to the ecological classification for cave animals (Racovitza 1907). In this study, new observations were provided for all taxa except *J. fernandodebueni*. The genus has a relatively small distributional range between Guerrero and Morelos, Mexico, extending approximately 1000 km south into the karst areas of Belize and Guatemala (Fig. 17). This comparatively small range is similar to that observed in other cave-dwelling diplura genera (Sendra et al. 2020a).

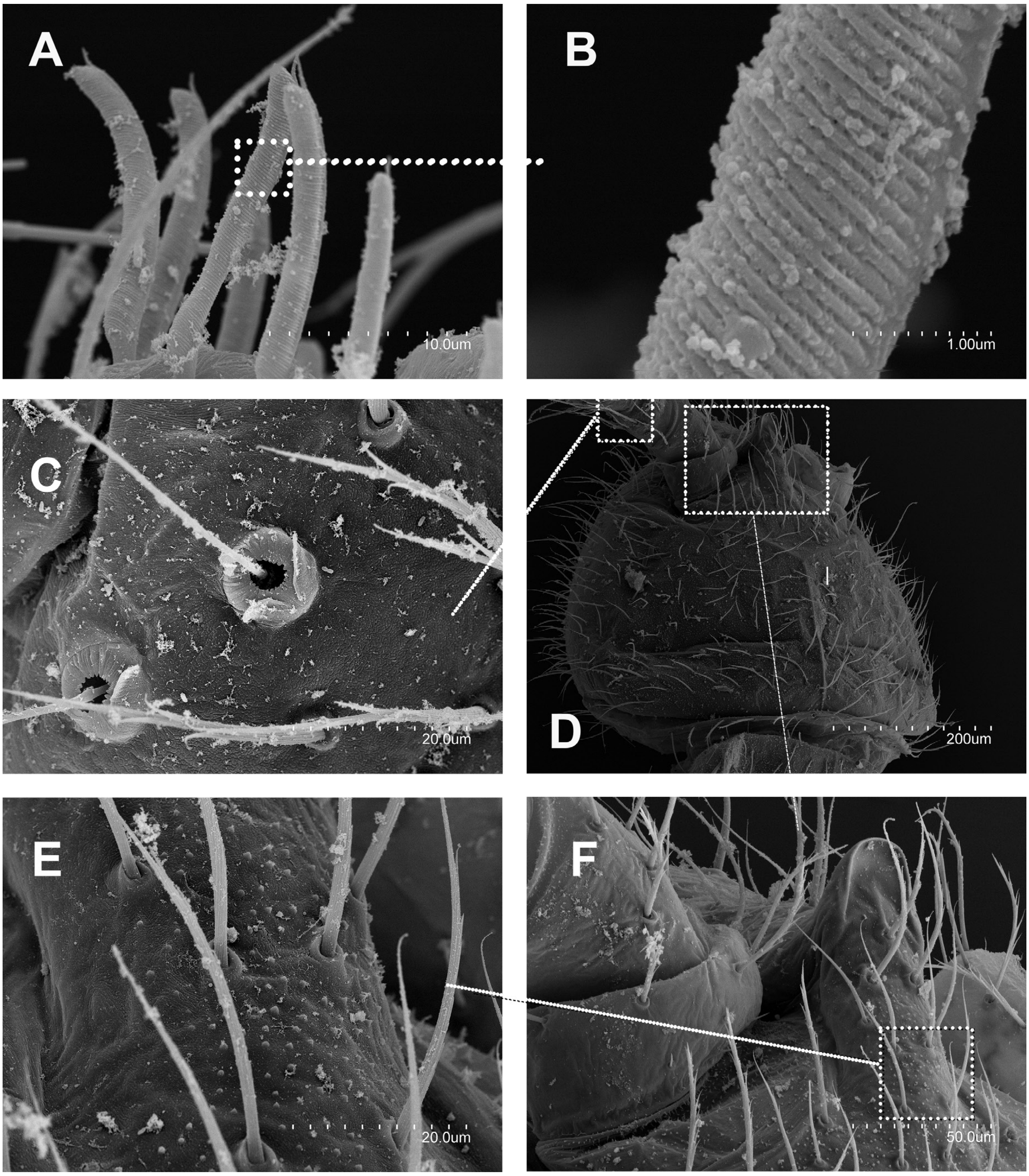

Fig. 15. *Juxtlacampa carlosjuarezi* (Palacios-Vargas & Sendra, 2016) (adult specimen, ASPC). **A**. Distal whorl of 'gouge' sensilla. **B**. Detail of 'gouge' sensillum. **C**. Trichobothria sensilla. **D**. Dorsal side of the head. **E**. Posterior portion frontal process. **F**. Frontal process.

Wygodzinsky (1944) established the genus *Juxtlacampa* and its type species *J. juxtlahuacensis*, based on three remarkable features: the particular distribution of macrosetae on the thorax and abdomen, the shape of the pretarsus, and the presence of large appendages on the first urosternite in males. These characters (see diagnosis of the genus) also occur in some species of Campodeinae and Plusiocampinae subfamilies. For example, some subgenera of *Campodea* Westwood, 1842 have a similar number and distribution of macrosetae, and most Plusiocampinae species exhibit elbow-like claws with lateral crests, as well as 2+2 macrosetae on the eighth urosternite. Furthermore, several Plusiocampinae species have urosternites with extra macrosetae, completely barbed stylar macrosetae, big eversible vesicle with complex surfaces, and large appendages in males.

Some species of *Juxtlacampa* exhibit additional morphological features similar to those of Campodeinae. These include the presence of 'rosette-like' epidermal glands on the cuticle (Fig. 2C) observed in *J. juxtlahuacensis*, *J. gabrielleae* sp. nov. and *J. carlosjuarezi*, as well as the presence of short and thick to moderate short 'gouge' sensilla in *J. carlosjuarezi*, *J. juxtlahuacensis*, *J. gabrielleae*, *J. hauseri*, and *J. xkiq* sp. nov. (Figs 2E–F, 10B–D, 13A–B). Additionally, a unique feature in all Campodeidae is represented by peculiar folds opening in the cupuliform organ on the last antennomere of *J. juxtlahuacensis* (Fig. 16A–B).

Despite the similarities among *Juxtlacampa* species, there are important differences that might justify splitting the genus into three distinct genera. One notable difference exists in the presence of extra

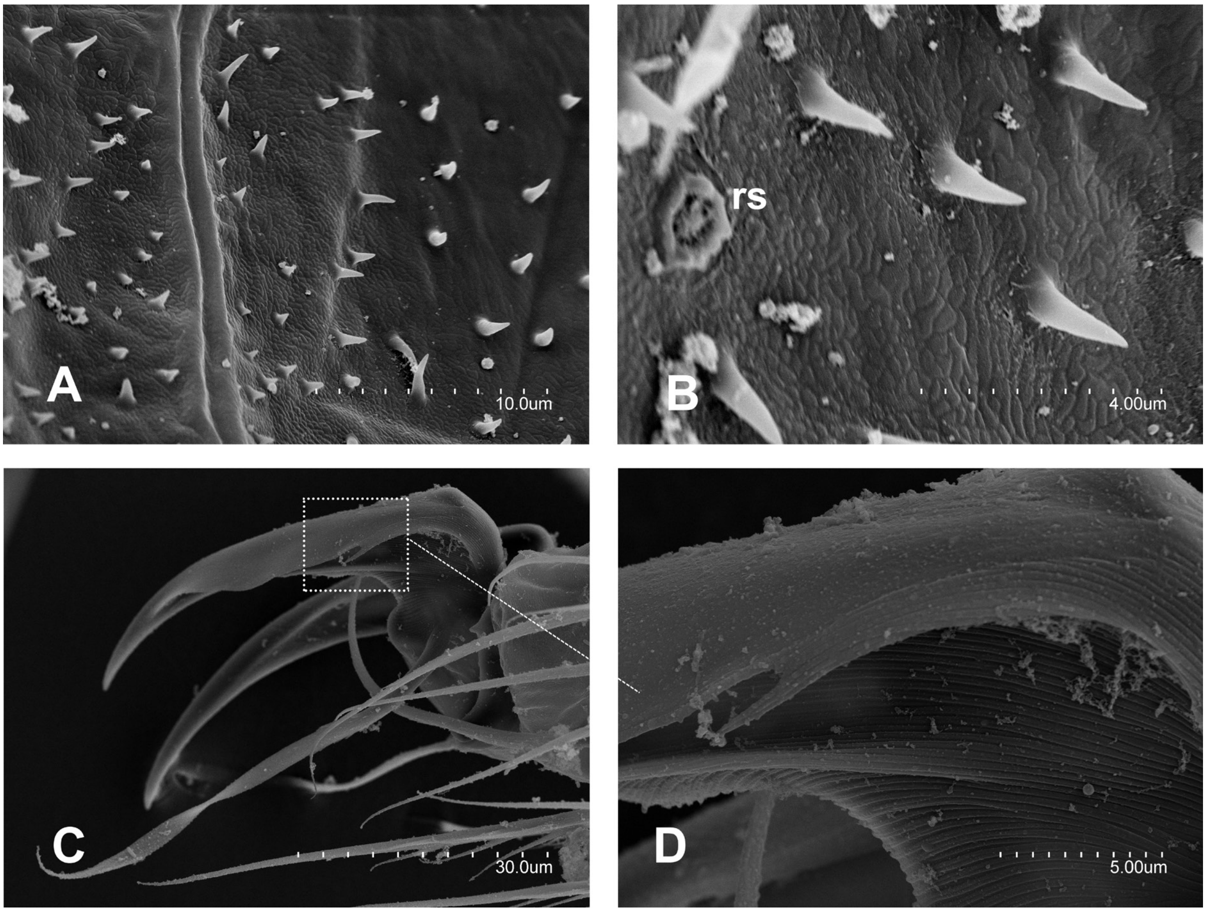

Fig. 16. *Juxtlacampa carlosjuarezi* (Palacios-Vargas & Sendra, 2016) (adult specimen, ASPC). **A**. Detail medial portion of mesonotum. **B**. Epicuticle microdenticles and 'rosette-like' gland. **C**. Pretarsus with its claws. **D**. Detail lateral crest of a claw. Abbreviations: see Material and methods.

macrosetae (more than 44 macrosetae in total) on the first urosternite in *J. juxtlahuacensis*, *J. hauseri*, and *J. fernandodebueni*, whereas the usual number is less than 18 macrosetae as described in *J. gabrielleae* sp. nov. and *J. xkiq* sp. nov. However, the most substantial differences are observed in the shape of pretarsus lateral processes, which are setiform and smooth in *J. hauseri*, *J. carlosjuarezi*, and *J. fernandodebueni* (Fig. 16A–D); laminar with short pubescent in *J. juxtlahuacensis*; laminar on the basal portion and narrow at the distal portion with long barbs throughout in *J. gabrielleae* and *J. xkiq* (Figs 4A–C, 12E–F); and claws with a large base and long transversal barbs in *J. xkiq* (Fig. 12E–F).

Several of the features shared with the genus *Podocampa* Silvestri, 1932 are well distributed on both sides of the Atlantic Ocean (including Mexico and Cuba, but also the Riff and Atlas Mountains in Morocco, Iberian Peninsula, and Occitanic region of France). The genus is closely related to *Parallocampa* Silvestri, 1933, which is presently known only from Mexico and may in fact be invalid. Note the only morphological difference between *Podocampa* and *Parallocampa* is the shape of the pretarsus lateral process, but Condé (1959) already identified the lateral process as an unreliable feature that can change during molting in a single specimen (i.e., being different in the former cuticle and the post-molting one). High variability in the shape of the lateral process was also reported by Condé & Geeraert (1962) and Sendra et al. (1986) after observing several specimens across different *Podocampa* species from North America and the Iberian Peninsula. This variability raises questions about whether similar variation

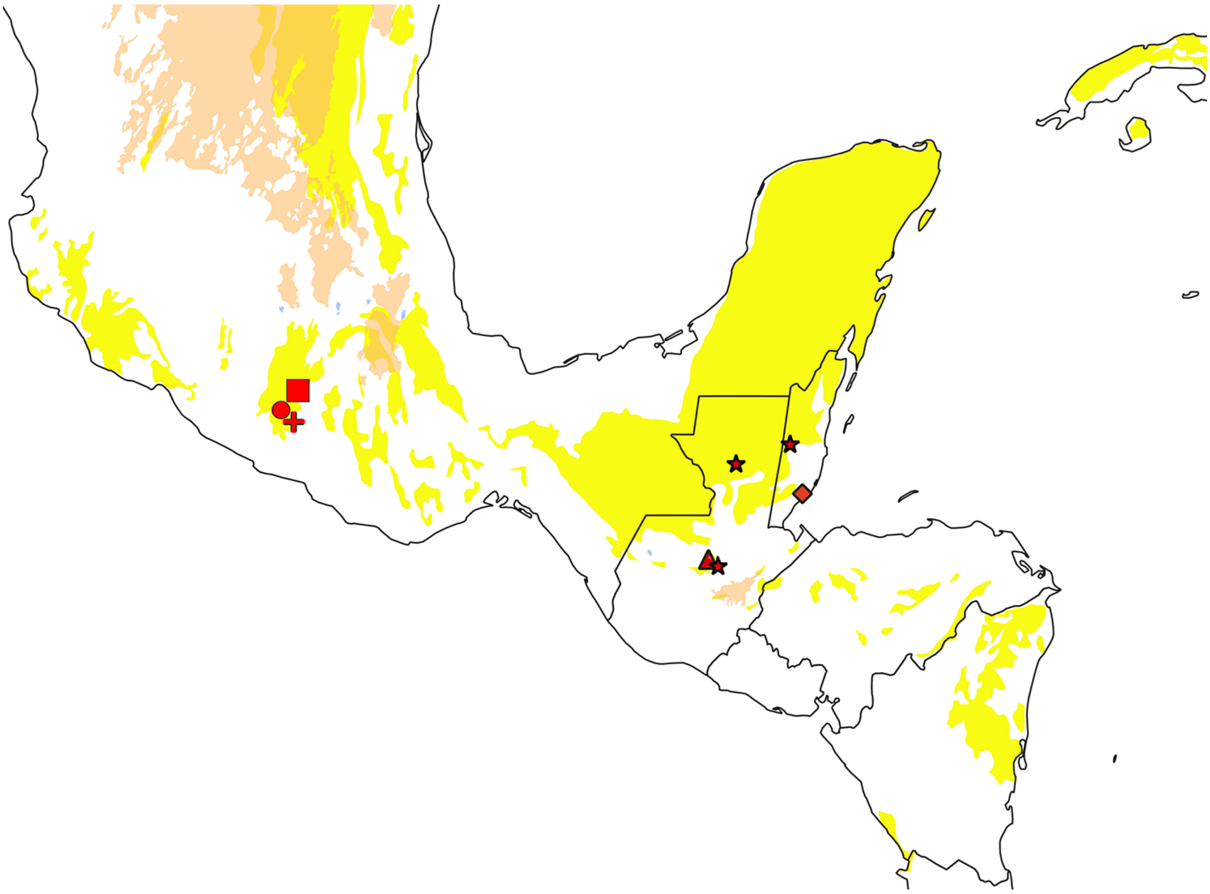

Fig. 17. Distribution of *Juxtlacampa* Wygodzinsky, 1944 species: *J. juxtlahuacensis* Wygodzinsky, 1944 (circle); *J. fernandodebueni* Sendra & García, 2016 (cross); *J. carlosjuarezi* (Palacios-Vargas & Sendra, 2016) (square); *J. hauseri* Condé, 1975 (triangle); *J. gabrielleae* sp. nov. (stars); and *J. xkiq* sp. nov. (diamond). Karst areas are shown as yellow polygons (Chen *et al*. 2017), while deserts are depicted in brown (Olson & Dinerstein 2002).

exists in *Juxtlacampa* species. While a definitive answer is currently unavailable, our observations and previous studies do not support establishing new genera solely based on such variation. Nevertheless, *Juxtlacampa* and *Podocampa* are clearly distinct based on overwhelming morphological differences, including macrosetae number and distribution, epicuticle formations and sensorial equipment.

Former tachycampoid phyletic line

The tachycampoid phyletic line was proposed by Bareth & Condé (1981) to comprise seven cave-adapted species across four genera: *Tachycampa lepineyi* Silvestri, 1936 from the Middle Atlas, Morocco; *Jeannlelicampa stygia* Condé, 1952 from Oran, Algeria; three species of *Paratachycampa* Wygodzinsky, 1944 including *P. boneti* Wygodzinsky, 1944 from Nuevo León, México; *P. hispanica* Bareth & Condé, 1981 and *P. penyoensis* Bareth & Condé, 1981, both from east of the Iberian Peninsula (Catalano Mountains and the eastern of the Iberic Mountains System); and two species of *Juxtlacampa*, *J. juxtlahuacensis* from Guerrero, México and *J. hauseri* from Alta Verapaz, Guatemala.

The delineation of the tachycampoid lineage was based on the macrosetae number, and reduction of nota and urotergites (Bareth & Condé 1981). The authors identified definitive features as the number and distribution of the notal macrosetae to be 3+3 (*ma*, *la*, *lp*) on the pronotum, 2+2 (*ma*, *la*) on the mesonotum and 1+1 (*ma*) on the metanotum, as well as the absence of macrosetae on the urotergites I to VII. Nevertheless, Bareth & Condé (1981) made an exception for the extra number of macrosetae in the pronotum (4+4 *ma*, $la_{1,2}$, *lp*) and the presence of up to 4+3 *post* macrosetae on the urotergites VI−VII in the two *Paratachycampa* from the Iberian Peninsula. However, these extra macrosetae (lp_1 macrosetae on pronotum and abundant *post* macrosetae on the urotergites) resulted in *Paratachycampa* being closer to the Plusiocampina phyletic line.

Later, Condé (1982) proposed including the genus *Oncinocampa* Condé, 1982 in the tachycampoid line. This genus harbored only one species, *Oncinocampa falcifer* Condé, 1982, a cave-adapted species from Cueva de la Marniosa in the Sobra Valley of Cantabria, Spain. Additionally, Condé (1982) identified another tachycampodea with a probable relationship with *Podocampa* and *Litocampa* (*Litocampa*) Silvestri, 1933. Since then, five additional *Oncinocampa* species have been described: two species from the Cantabrian Mountains, north of the Iberian Peninsula, with cave-adapted features (*Oncinocampa asonensis* Sendra & Condé, 1988 from near Ason, Cantabria and *Oncinocampa genuitei* Bareth, 1989 from the Trave System, Picos de Europa, Asturias); one soil-dwelling species from Sardinia (*Oncinocampa placti* (Condé, 1981)); one cave-dwelling species (probably an edaphic species) found in a two caves in Ribera Valley, São Paulo State, Brazil, showing no troglomorphic characters (*Oncinocampa trajanoae* Condé, 1997), and one cave-adapted species from Cueva Galicia cave, Ixtaczoquitlán, Veracruz, México (*Oncinocampa bolivarurrutiai* Sendra & García, 2016. All *Oncinocampa* species were characterized by the number and distribution of macrosetae on nota (3+3 *ma*, *la*, *lp* pronotum; 2+2 *ma*, *la* mesonotum; 1+1 *ma* metanotum) and the presence of elbow-like claws, which had a very small lateral crest and similar (*O. placti* and *O. trajanoae*) or unequal claws (as with other *Oncinocampa* species).

Additionally, two *Tachycampa* species were recently described from México (Sendra *et al.* 2016). These include *T. bolivarpieltaini* Sendra & García, 2016 from Sótano Los Hernández Cave, San Joaquín, Querétaro and *T. clemenciae* Sendra & García, 2016 from Grutas Karmidas, Puebla Massif. The genus *Tachycampa* is characterized by the same notal macrosetae distribution as most tachycampoid species (3+3 *ma*, *la*, *lp*; 2+2 *ma*, *la*; 1+1 *ma* macrosetae), as well as a distinguished pretarsus with elbow-like claws, which has a large lateral crest but lacks backwards extensions.

Thus, the key morphological features described above (macrosetae and sensilla distribution; see further details below) provide ample evidence to withdraw the tachycampoid lineage as monophyletic. Subsequently, tachycampoids should no longer be considered as such.

Further revisions to Campodeidae

The following revisions to Campodeidae are proposed: *Paratachycampa* should be moved into the Plusiocampinae subfamily, and *Tachycampa*, *Oncinocampa*, *Jeannelicampa* Condé, 1952 and *Juxtlacampa* into the Campodeinae subfamily. The presence of 3+3 macrosetae on the pronotum in *Paratachycampa* species has been considered a synapomorphic feature in Plusiocampinae (Sendra & Deharveng 2020), as well as the presence of more than 2+2 posterior macrosetae on urotergites VI–VII and the presence of 2+2 – 3+3 macrosetae on urosternite VIII. Two additional non-setae features further support the inclusion of *Paratachycampa* in Plusiocampinae: (1) the absence of microdenticles on the non-reticulated epicuticle, which is a common characteristic for many Plusiocampinae species (Sendra *et al.* 2021a, 2021c) and (2) the presence of elbow-like claws with well-developed lateral crests overpassing backwards the end of the tarsus in cave-adapted species.

The following morphological characteristics support the assignment of *Tachycampa*, *Jeannelicampa*, *Oncinocampa* and *Juxtlacampa* to the subfamily Campodeinae. First, the absence of extra macrosetae in the nota, with up to 3+3 *ma*, *la*, *lp* on the pronotum 2+2 *ma*, *la* on the mesonotum, and 1+1 *ma* on the metanotum occur in all species across the four genera. Secondly, the presence of microdenticles on the epicuticle, which has a reticulated surface (as observed in our SEM imagery). Finally, the number and distribution of abdominal macrosetae including the presence of only 1+1 macrosetae on urosternite VIII – barring some *Juxtlacampa* species that have 2+2 or 3+3.

Although the results disavow the monophyly of tachycampoids, additional morphological evidence and further molecular analysis will be required to resolve the detailed relationships across campodeid taxa.

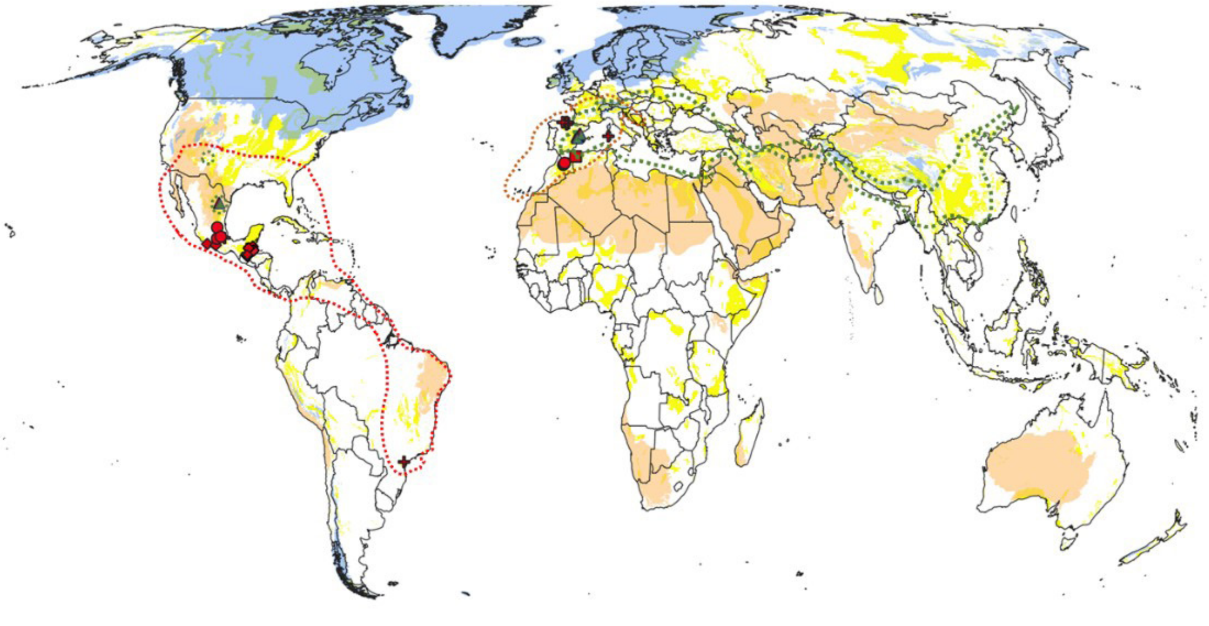

Fig. 18. Distribution of former tachycampoid genera including areas occupied by Plusiocampinae Paclt, 1957 species (dashed green line) and *Podocampa* Silvestri, 1932 and *Litocampa* Silvestri, 1933 species (dashed red line in the western hemisphere and dashed orange line in Europe). Locations of additional genera including *Paratachycampa* Wygodzinsky, 1944 (green triangles), *Tachycampa* Silvestri, 1936 (red circles), *Jeannelicampa* Condé, 1952 (red square), *Oncinocampa* Condé, 1982 (red crosses) are also provided. Yellow represents karst areas (Chen *et al.* 2017), brown are deserts (Olson & Dinerstein 2002), and blue is the extent of glaciation during the Quaternary period (Ehlers *et al.* 2011).

Biogeographical implications

This proposal to remove the tachycampoid lineage has significant biogeographical implications. Firstly, the Plusiocampinae subfamily, now including *Paratachycampa*, has a well-defined Euro-Asiatic distribution that extends from Russia and China to the Mediterranean region (Fig. 18). Although most of these species were described from karst areas in the Mediterranean basin, recent evidence provides strong support of an east Asian origin for this subfamily (Silvestri 1931; Condé 1993; Sendra & Deharveng, 2020; Sendra *et al.* 2021c). In this scenario, the Anatolian Peninsula (which encompasses most of modern Turkey) arose as a land bridge facilitating the dispersal of Plusiocampinae into Europe (Sendra *et al*. 2022). In North America, Plusiocampinae was represented by a single species, *Condeicampa langei* Ferguson, 1996, an endemic cave-adapted species from Whipple Cave, Lincoln County, Nevada. After the reassignment of *Paratachycampa*, there would be a second species of Plusiocampinae on the American continent: *P. boneti*, occurring 2000 km south in Gruta de Garcia caves, Nuevo León, México. It is hypothesized that Plusiocampinae arrived from Asia as the Atlantic Ocean formed towards the end of the Cenozoic era (Sendra *et al.* 2020a), although further research is needed to fully understand the dispersal of this family to North America. The four genera *Jeannelicampa*, *Juxtlacampa*, *Oncinocampa*, and *Tachycampa* (now part of the Campodeinae subfamily) were probably most closely related to *Litocampa* and *Podocampa* – as they share a similar distribution (Fig. 18). These genera occupy a large area on both sides of the Atlantic Ocean including the western part of the Mediterranean region, the Caribbean Sea including Cuba, and portions of southern North America, Central America, and South America (Condé 1956; Paclt 1957; Sendra *et al.* 2020a, 2021b). Sendra *et al*. (2020a) suggested this distributional pattern was likely caused by an ancient occupation of Pangaea prior to the opening of the Atlantic Ocean.

Habitat and species persistence

The rapid acceleration of global biodiversity loss also affects subterranean ecosystems (Mammola *et al.* 2019; Wynne *et al.* 2021; Ferreira *et al.* 2022). Questions including how the impacts of recreational activities affect subterranean environments and the optimal integration of education, research, and management interventions to protect subterranean biodiversity are central to conservation biology (Mammola *et al.* 2022). Presently, only *J. gabrielleae* sp. nov. and *J. xkiq* sp. nov. occur within protected areas; for the other three endemic species, which occur in unregulated tourism caves, the greatest proximal impact may be human visitation – both from tourism and researchers. If tourism continues unregulated, these activities may challenge the persistence of these populations (Moulds 2005; Pacheco *et al.* 2021). Losing these short-range endemic species would hamper our efforts to unravel the complex evolutionary relationships among diplurans. Despite the significant results presented in this study, phylogenetic analyses using molecular techniques and morphological investigations using SEM imagery will be required to robustly characterize this group of great paleogeographical importance.

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Authors' contributions

All authors worked on illustrations, descriptions, and the first draft of the manuscript; JW, JP-V and RL collected the specimens; AS and AS-G identified the first specimens found. All authors contributed to the revision of the manuscript, approved the final manuscript, and consent to publication.

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Supplementary files.

Suppl. File 1. Study area descriptions of the research and habitat and management implications of *Juxtlacampa gabrielleae* Sendra & Ferreira sp. nov., *Juxtlacampa hauseri* Condé, 1975, *Juxtlacampa xkiqi* Sendra & Wynne sp. nov., *Juxtlacampa juxtlahuacensis* Wygodzinsky, 1944 and *Juxtlacampa carlosjuarezi* (Palacios-Vargas & Sendra, 2016). https://doi.org/10.5852/ejt.2026.1048.3237.14337