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Impressive cave-adapted japygids (Diplura, Japygidae) from Mediterranean and Southeast Asia caves

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Abstract. Three specimens of Dipluran Japygidae, collected from two widely separated caves – one in the western Mediterranean and the other in Southeast Asia – have revealed the existence of an impressive, distinctive and unusual cercal amour pattern, unlike that of other Japygidae, characterized by two to three pairs of subsymmetrically arranged teeth. Consequently, two taxa have been described: a new species, *Troglojapyx angelginesi* Sendra sp. nov., from l'Avenc des Pouàs in Ibiza, Balearic Islands, related to the previously monotypic genus *Troglojapyx*, known from a cave in mainland Greece; and a new genus and species, *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., from Tham Van Ngo Cave in Laos. However, the phylogenetic significance of cercal morphology appears limited, as suggested by the wide geographic distribution of soil- and cave-adapted japygids. The two new species are highly specialized cave dwellers, exhibiting clear subterranean adaptations, including elongate bodies, slender appendages, and an impressive abundance of antennal placoid sensilla, reaching up to 72 in *L. chloeae*.

Keywords. Taxonomy, *Troglojapyx*, *Laolaojapyx*, cercal morphology, basal Hexapoda.

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Introduction

Nearly half a century ago, the French entomologist Jean Pagés (1980) described an extraordinary cave-adapted japygid and established a unique genus: *Troglojapyx hauseri* Pagés, 1980. This taxon belongs to the family Japygidae Haliday, 1864, the second most diverse family within the basal hexapod order Diplura Börner, 1904 (Pagés 1959; Sendra *et al.* 2021b). Pagés' description (1980) was based on a single juvenile specimen, which nevertheless showed clear morphological differences from other genera of the family, particularly in the cerci, which bear two subsymmetrical teeth, a feature that justifies the two taxonomical proposals discussed here. The specimen was collected by Dr H. Hauser of the Natural History Museum of Geneva in a touristic cave at Paiania, near Athens (Greece). Pagés (1980) considered *T. hauseri* an "ideal troglobitic" sensu Racovitza (1907), ranking it among the most cave-adapted species of the family. Nevertheless, Japygidae remains poorly represented in subterranean ecosystems, with only 15 described cave-adapted species compared with the 328 soil-dwelling japygid species (Pagés 1964; Bareth & Pagés 1984; Sendra *et al*. 2021a). Across subsurface habitats – from soil to deep caves – japygids function as high-level predators, feeding on a broad range of small- to medium-sized invertebrates (Sendra *et al.* 2021b; Potapov *et al.* 2022).

Recently, two japygid samples from two widely separated caves, collected by different speleological teams, revealed two remarkable new taxa. The first sample, comprising two specimens from "L'Avenc des Pouàs" Cave (Fig. 1), in Sant Antoni de Portmany on Eivissa Island in the Balearic archipelago, was collected during a palaeontological excavation of Pleistocene fauna remains directed by Dr Josep A. Alcover i Tomàs. The second sample consisted of a single specimen collected during the 2023 K23 speleological expedition of the Explo-Laos Association, which explored the Tham Van Ngo Cave (Fig. 2) in Khammouane Province, Laos (Lao People's Democratic Republic). These two geographically distant cave systems yielded two extraordinary new taxa: a new species of *Troglojapyx* Pagés, 1980 from the Mediterranean region (Eivissa) and a new genus from Southeast Asia (Laos), both formally described in this study.

Material and methods

The three japygid dipluran specimens, previously mounted in semipermanent medium on slides, were studied. General visualization and photography were performed using a Leica DMS1000 phase-contrast microscope, a Leica 5000 fluorescence microscope, and a Nikon Eclipse Ni stereo microscope. For scanning electron microscopic (SEM), one antenna and the segment X – including the cerci – of the Tham Van Ngo specimen were coated with palladium-gold and examined with a Hitachi S-4900 scanning electron microscope. Final photo plates were processed and edited using Adobe Photoshop CS2 (ver. 9.0).

For the nomenclature of the rows of macrosetae (= M) on the urosternites, we followed the terminology for extant Japygidae proposed by Pagés (1953). For the setae and macrosetae of the cerci, we used the terminology of Muegge & Bernard (1990).

The following abbreviations are used in the main text and figure captions (Pagés 1953, 1984; Smith 1962; Muegge & Bernard 1990).

A, B, C = A, B, and C rows of urosternal macrosetae
D, L, V = dorsal, lateral, and ventral positions of cercal macrosetae
GS = glandular seta
I, L, M, P = rows of macrosetae on dorsal head
la = macroseta lateral anterior
lp = macroseta lateral posterior
M = macroseta with four different positions (see *la, lp. ma, mp*)
ma = macroseta medial anterior
mp = macroseta medial posterior

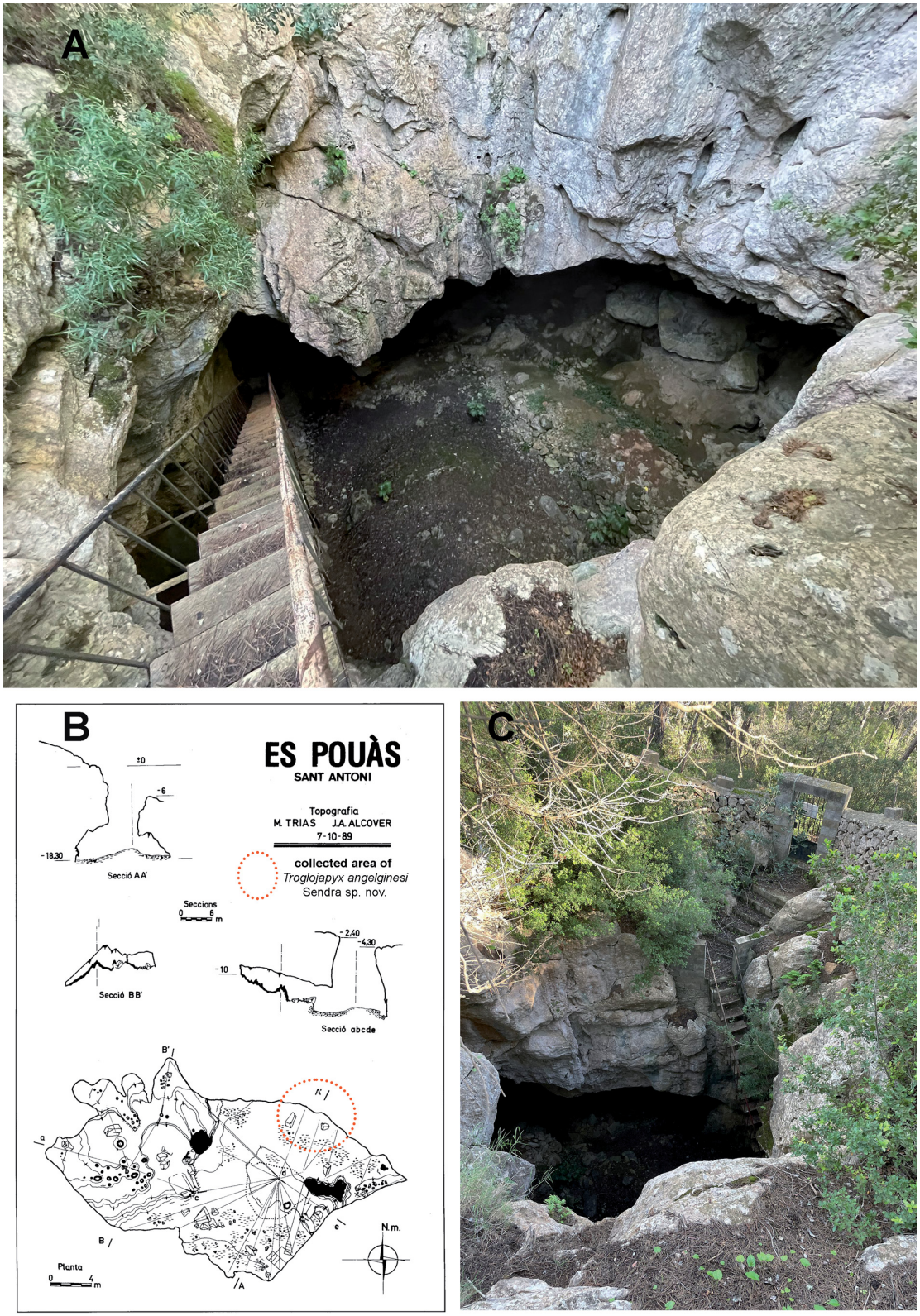


Fig. 1. "L'Avenc des Pouàs" Cave in Sant Antoni de Portmany in Eivissa, Balearic Islands. **A**. Entrance to well and staircase descending into the cave. **B**. Cave topography indicating the collecting sites of the two specimens of *Troglojapyx angelginesi* Sendra sp. nov. **C**. General view of the entrance with the gate and cave facilities. Photos: A, C: Samuel Pinya.

For urotergites:

M1–5 = 1 to 5 macrosetae on thoracic and abdominal tergites
sl = long seta
ssh = short seta
tr = trichobothrium

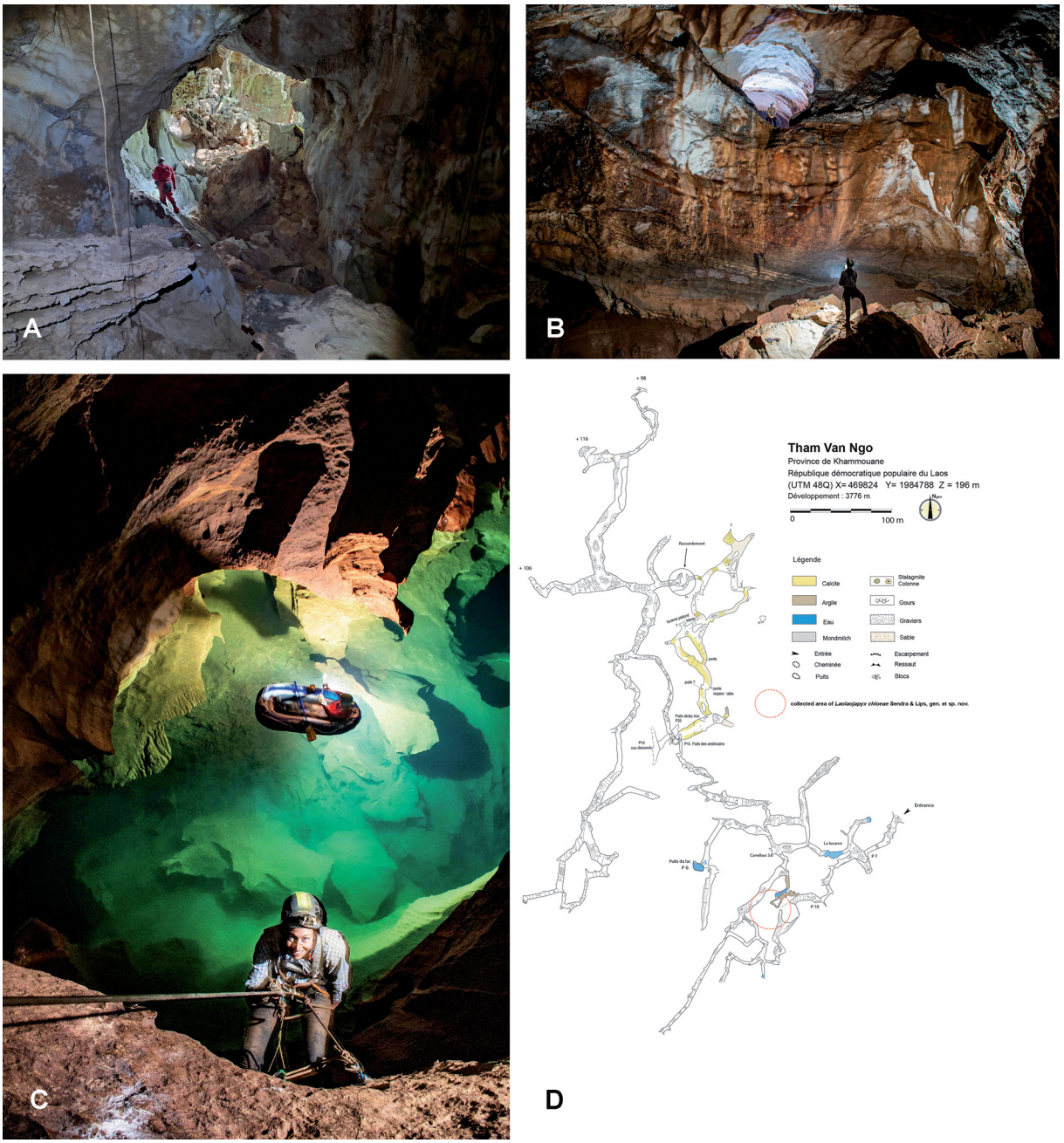


Fig. 2. Tham Van Ngo Cave, Laos. **A**. Cave entrance. **B**. First pit (P7) near the entrance, showing the large chamber at the bottom. **C**. 6-m-deep pit with the Lac (P6). **D**. Cave topography indicating the collection site of the female of *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov. in the humid gallery with clay and standing water. Photos: A–C: Jean-Michel Ostermann.

Type material was deposited at the following institutions:

IMEDEA-UIB = Institut Mediterrani d'Estudis Avançats de la Universitat de les Illes Balears
MUVHN = Museu de la Universitat de València d'Història Natural, València, Spain

Results

Class Diplura Börner, 1904
Superfamily Japygoidea Lubbock, 1873
Family Japygidae Haliday, 1864

Genus ***Laolaojapyx*** Sendra & Lips gen. nov.
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Type species

Laolaojapyx chloeae Sendra & Lips gen. et sp. nov.

Diagnosis

Body elongate; epicuticle with micropores on dorsal surface of several sclerites. Dorsal head with slightly reinforced frontal area, in addition to a few A, S, M, I, L and P macrosetae; submentum with 1+1 M in posterior position; admentum with 3+3 M; mentum at base of labial palps with 1+1 M; lacinia with five pectinate laminae. Antenna with 45 antennomeres; third antennomere with a distinct long and external macroseta on; antennal trichobothria on IV (1 dorsal / 1 ventral) and on antennomeres V–VI (3 dorsal and 2 ventral); the dorsal trichobothria of antennomere IV surpasses the whorl of the M-setae. Medial and distal antennomeres with smooth and micro-barbed surface; last antennomere with 72 placoid sensilla. Pronotum to metanotum with 5+5 M; prescutum of mesonotum and metanotum with 1+1 M. Prosternum to metasternum with 11+11–18+18 M. Legs long; pretarsus with two slightly unequal claws and sharp medial unguiculus. Scutum of urotergite I with 1+1 M5; urotergite II with 2+2 M1, 5; urotergites III–VII 5+5 M1−5 plus one additional pair of M; urotergite VIII with 2+2 M4−5; urite X with 3+3 M dorsally, 12+12 M laterally, and 15+15 M ventrally. Posterolateral angles of urotergites IV to VIII increasingly become more pronounced, from slightly protruding to a strong elongated point. Scutum of urosternite I with 25+25 M plus a narrow band of short setae anterior to the lateral subcoxal organ. Urosternite II with 23+23 M; urosternites III–VII with 24+24 M; urosternite VIII with ~12+12 M. Median glandular organ with pseudospori. Each lateral subcoxal organ with 1–2 rows of short glandular setae (GS) and one row of much longer sensory setae (SS) with large bases. Female genital papillae with the typical japygid morphology. Cerci subsymmetric, with lateral external margins subparallel and incurved, strongly narrowed in the distal third to form a hook-like apex bearing numerous campaniform sensilla. Each cercus with three subsymmetrical, submedial teeth, delimiting four marginal areas: (1) predental margin to the first, large subtriangular tooth with a row of three large denticles; (2) margin between the first and second (smaller) tooth with a row of small pointed denticles; (3) margin between the second and third tooth with small rounded denticles; and (4) distal to the third tooth, with tiny rounded denticles.

Laolaojapyx chloeae Sendra & Lips gen. et sp. nov.
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Figs 3–12

Etymology

The specific name honors French speleologist Chloé Gombault, a member of the 2023 K23 expedition of the Association Explo-Laosto (Lao People's Democratic Republic), who collected the specimen during the exploration of Tham Van Ngo Cave. Gombault is a caver who began biospeology a few years

ago. During the expedition, she mainly focused on exploring and mapping caves but, drawing on her background as a biologist, also searched for cave fauna, leading to the discovery of this remarkable new dipluran japygid.

Type material

Holotype

LAOS • ♀; Khammouane Province, Tham Van Ngo Cave; 17.9510° N, 104.7150° E; 196 m a.s.l.; 22 Feb. 2023; Chloé Gombault leg.; MUVHN ZE 10010.

Description

Body. Body elongated; total length 11 mm (holotype) plus 1.1 mm for the cerci. Maximum width 1.4 mm at urotergite II (Fig. 3A). Epicuticle mostly smooth but with micropores on the dorsal surface of the head, antennomeres I–IV and abdominal segments VI–X, particularly abundant and well defined, and broader (0.1–0.4 µm diameter) on sclerites of segments VIII–X (Fig. 10D−F). Cuticle unpigmented, with sclerotized areas restricted to the mandible tips, claws, abdominal stylus ending, cerci; and femoral, tibial, and especially cercal condyles. Body and appendages covered with normal setae (*s*), short setae (*ss*), long setae (*ls*), and microsetae (*ms*), in addition to a set of macrosetae (M) following the typical japygid pattern across the head, thoracic, and abdominal sclerites, and appendages.

Head. Dorsal side with 15+15 M: A1,3; S1,4,6; M2–3,5; I2,5, L2,4–5 and P1–2, plus 2 long M in ventral position on the oral folds (Fig. 5A). Ventral side with the submentum bearing 1+1 M in posterior position; admentum with 3+3 M; mentum at base of labial palps with 1+1 M; external lobes of the mentum bearing abundant thick setae. Labial palp 3 × as long as wide, with two apical M, three subapical M, and one medial M with several sl. Labrum is short, with numerous short, thick setae. Lacinia falciform, well sclerotized, with five pectinate laminae, the first laminae very shortly pectinate (Fig. 3B). Mandible with four distensible teeth and a tiny tooth in interior position.

Antennae. Antenna 0.5 × length of body, with 45 antennomeres; first antennomere subquadrangular, second to fifth antennomeres slightly longer (1.3) than wider with tiny, reinforced borders, of which II and III antennomeres are the bigger ones; medial and distal antennomeres as long as wide. First to fourth antennomeres have uneven M macrosetae and some sl setae, with one distinguishable distal long and external macrosetae on the third antennomere (Fig. 3C−D). Antennomere IV has 1 dorsal / 1 ventral trichobothria; antennomeres V–VI have 3 dorsal and 2 ventral trichobothria; the dorsal trichobothria of the IV antennomere overpasses the whorl of M. Medial and distal antennomeres that have two whorls of macrosetae with a smooth and micro-barbed surface, in addition to some *sl* setae either micro-barbed or not (Fig. 4G–I). The last antennomere has 72 placoid sensilla arranged in three whorls and the fourth is isolated near the apical end and covers the distal half (Fig. 4A–F).

Thorax. Thoracic segments elongated, each bearing a few ls, ss, and a typical series of M from pronotum to metanotum with 5+5 M (M1–5) on each nota, and 1+1 M on the prescutum of both mesonotum and metanotum (Fig. 5B–D). Thoracic sternites, intersternites, and presternites are well defined, each with very few *ss*, *sl*, and several M setae; the margins of the leg articulations bear *ms* functioning as proprioceptors (Fig. 6). Pro-presternites and pro-, meso- and metasternites each possess internal Y-shaped cuticular furcisternites (Barlet & Carpentier 1962). In pro-presternites, the prolongation of the posterior branch (spine) is externally visible (Denis 1949). Pro-presternum has 2+2 M; prosternum with 5+5 lateral anterior M, of which 2+2 are longer than the remainder; 1+1 medial anterior M; and 5+5 lateral posterior M. Meso-poststernum with 6+4 M. Meso-intersternum with 3+3 M. Mesosternum with 5+5 lateral anterior M (again 2+2 longest) 2+2 medial anterior, 1+1 medial intermediate, 2+2 medial posterior, and 5+5 lateral posterior M, with 2+2 longest. Meta-poststernum with 6+7 M; meta-intersternum with 3+3 M; metasternum with 5+5 lateral anterior M (2+2 longest), 2+2 medial anterior,

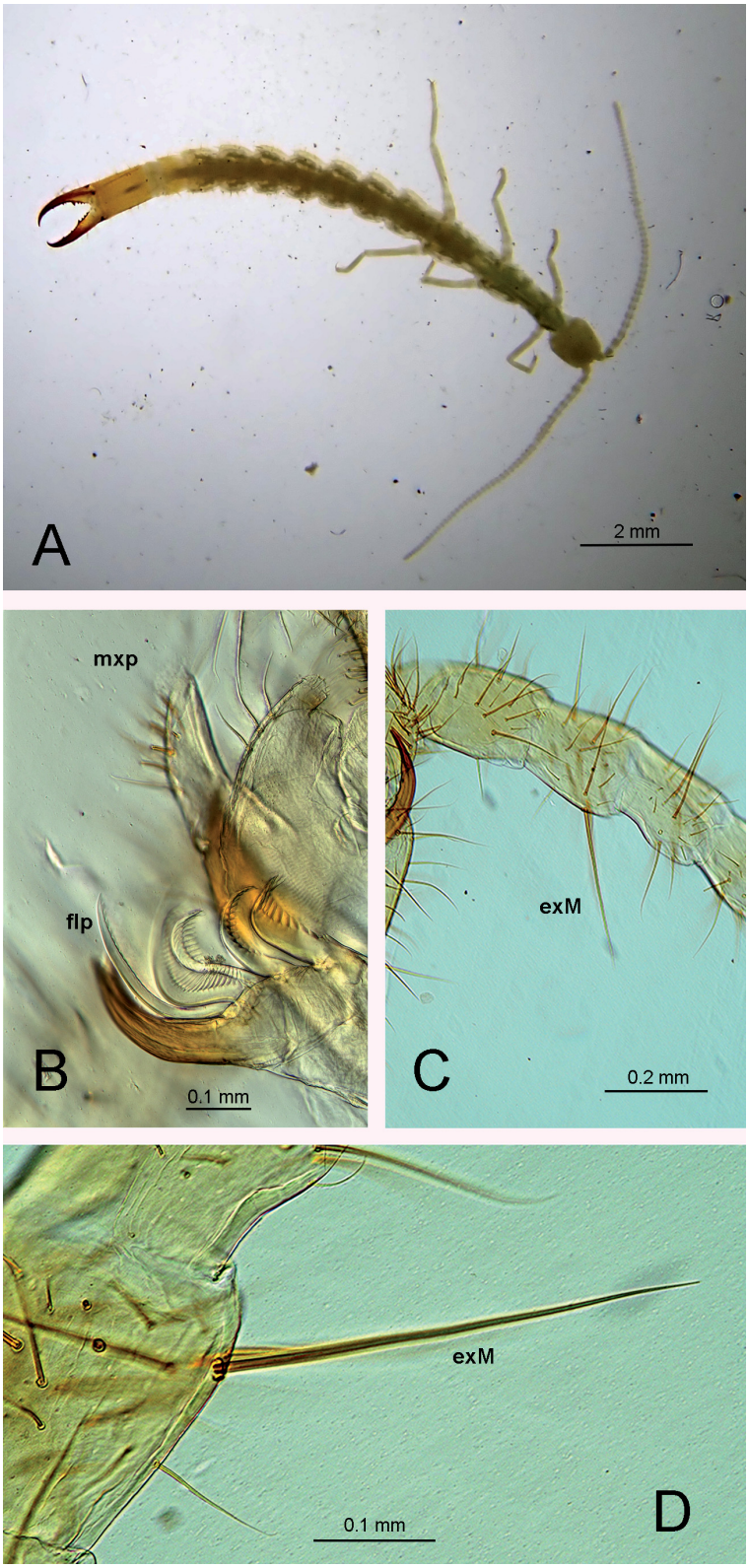


Fig. 3. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Habitus. **B**. Maxillary buccal pieces including lacinia and palp. **C**. Proximal portion of left antenna. **D**. Lateral external portion of fourth antennomere. Abbreviations: exM = lateral external macrosetae of the third antennomere; flp = first pectinated lamina; Mxp = maxillar palp.

2+2 medial intermediate, 2+2 medial posterior, and 7+7 lateral posterior M (Fig. 6). Legs long, hind leg reaching the posterior border of abdominal segment IV. Coxa with 1 dorsal M and 3 ventral M; trochanter with 2 ventral M; femur with 7 ventral and 6 dorsal M; tibia with 2 long calcars and 7 M; tarsus with 5 dorsal M and two ventral rows of 3 and 6 thick setae. Pretarsus with two slightly unequal claws (1.2 anterior to posterior claw) and a sharp medial unguiculus.

Abdomen. Prescutum of urotergite I with 1+1 M, scutum with 1+1 M5; urotergite II with 2+2 M1, 5; urotergites III–VII each with 5+5 M1−5 plus one additional pair of M (Fig. 7A). Urotergite VIII with 2+2 M4−5 (Fig. 7B). Urite IX lacks dorsal M but bears 2+2 M ventrally. Urite X (Figs 10A–D, 11A) 1.7 × as long as wide, with distinctly developed carinae; carinal margins subparallel, slightly converging posteriorly. Dorsal side with 3+3 intracarinal M (D1 and D4 and an additional submedial pair) (Fig. 10A, D). Acropygium small and suboval, preceded by a broad transverse suture (Figs 10D, 11A). Lateral

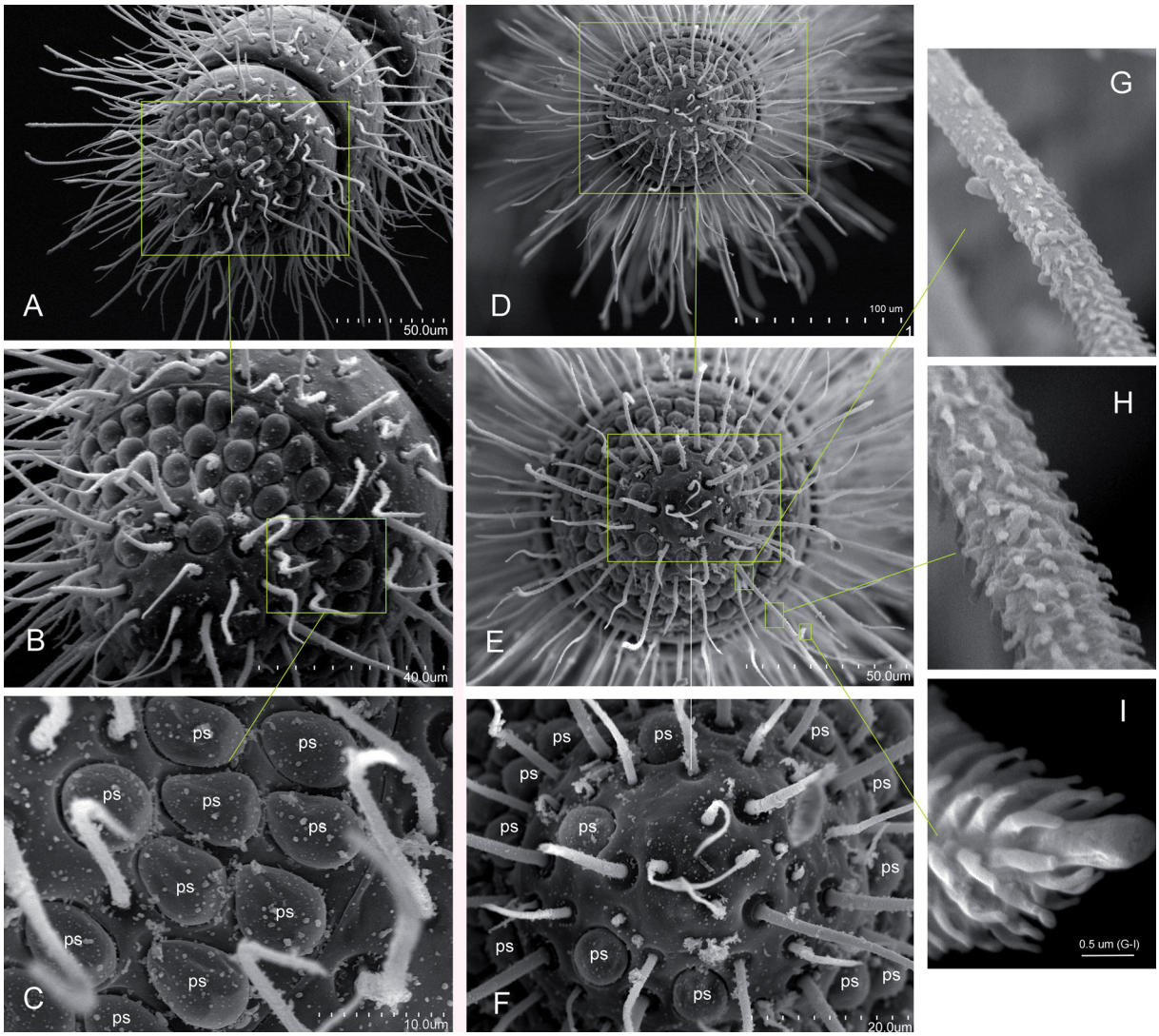


Fig. 4. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Distal portion of antenna. **B**. Apical antennomere lateral view. **C**. Detail of the distal portion of last antennomere. **D**. Apical antennomere, apical view. **E**. Apical antennomere, apical view (detail). **F**. Apical detail of apical antennomere. **G**. Proximal portion of a micro-barbed seta. **H**. Medial portion of a micro-barbed seta. **I**. Distal portion of a micro-barbed seta. Abbreviation: ps = placoid sensillum.

surface with three rows of four M (L1–4). Ventral surface with 15+15 M arranged in four uneven rows (Fig. 10C). Posterolateral angles of lateral posterior urotergites extreme I–III blunt and rounded; from urotergites IV to VIII the angles become progressively more pronounced, ranging from slightly protruding to a sharply elongated point on VIII (Fig. 9A–D). Urosternites with sparse ms and ss setae. Prescutum of urosternite I with 5+5 M; scutum with 25+25 M arranged in four uneven rows, plus a narrow band of ~20 short setae anterior to lateral subcoxal organ (Fig. 8A). Urosternite II with 23+23 M

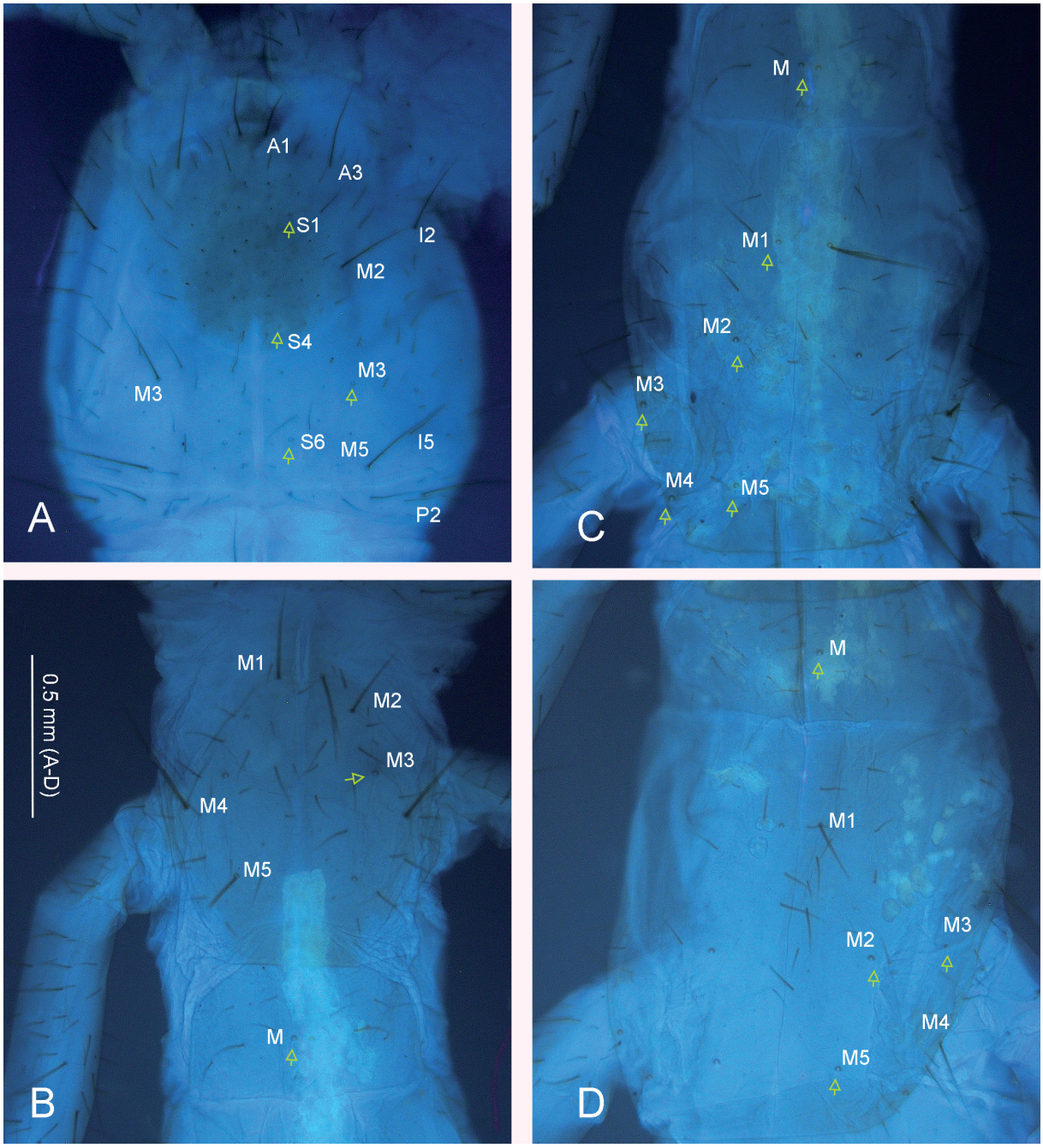


Fig. 5. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Head, dorsal view. **B**. Pronotum and prescutum of the mesonotum. **C**. Prescutum of the mesonotum, mesonotum, and prescutum of the metanotum **D**. Prescutum of the metanotum and metanotum. Abbreviations: A, S, M, I and P = macrosetae of dorsal head; M = macrosetae; M1–M5 = macrosetae 1 to 5 of the nota.

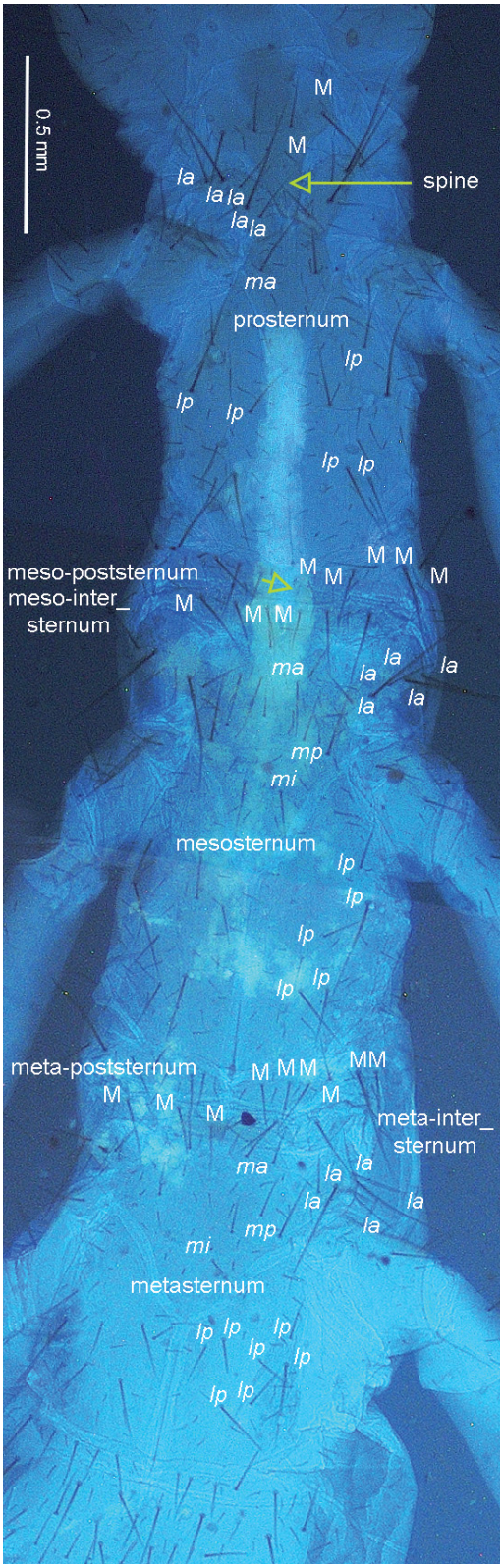


Fig. 6. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). Thoracic sternites, intersternites, and presternites. Abbreviations: la = lateral anterior; lp = lateral posterior; M = macroseta; *ma* = medial anterior; *mi* = medial intermedia; *mp* = medial posterior; *p* = posterior macrosetae.

(A1–8, B1–7, C1–8). Urosternites III–VII each with 24+24 M (A1–8, B1–8, C1–8) (Fig. 7C). Urosternite VIII with ~10+10 M between two well-defined carinae, plus 2+2 M lateral to carinae (A1–3, B1–5, C1–4) (Fig. 7D). Median glandular organ with 3+3 pseudospori, each accompanied by a microseta, shorter than in males. Lateral subcoxal organ with 1–2 rows of 26+34 short glandular setae (GS) and one row of 10+10 long sensory setae (SS) with a large bases; SS distinctly longer than GS (GS/SS = 0.40. The organ occupies 0.58× the interstylar area (GS/st1= 0.10; SS/st1= 0.37) (Fig. 8A–E). Stylus elongated; the stylus of the first abdominal segment with two short latero-internal setae, and those of abdominal segments II–VII each with one additional long external seta. Female genital papillae with the typical shape observed in Japygidae.

Cerci. Subsymmetric, 1.1 mm in length (approximately 0.1 mm shorter than body length), with lateral external margins subparallel and slightly incurved, narrowing abruptly in the distal third to form a hook-like apex. Inner margins and the apex bear regularly distributed campaniform sensilla (Fig. 11B). Cercal borders strongly sclerotized, with dorsal and ventral outer carinae arising from the dorsal and ventral acetabular articulations (Fig. 10A–C). Each cercus bears three subsymmetrical, submedial teeth, delimiting four margin areas: (1) predental margin from the cercal base to the first, large subtriangular tooth, bearing a single row of three large, strong, and protruding denticles on each cercus; (2) margin between the first and second (smaller) tooth, with a row of small pointed denticles (four on the right cercus and two on the left); (3) margin between the second and third tooth, bearing four small rounded denticles; and (4) margin distal to third tooth, with a row of tiny rounded denticles (Figs 10A–C, 11A, C–D). Right cercus with 10 D M, 24 L M and 18 V M; left cercus with 10 D M, 20 L M and 18 V M.

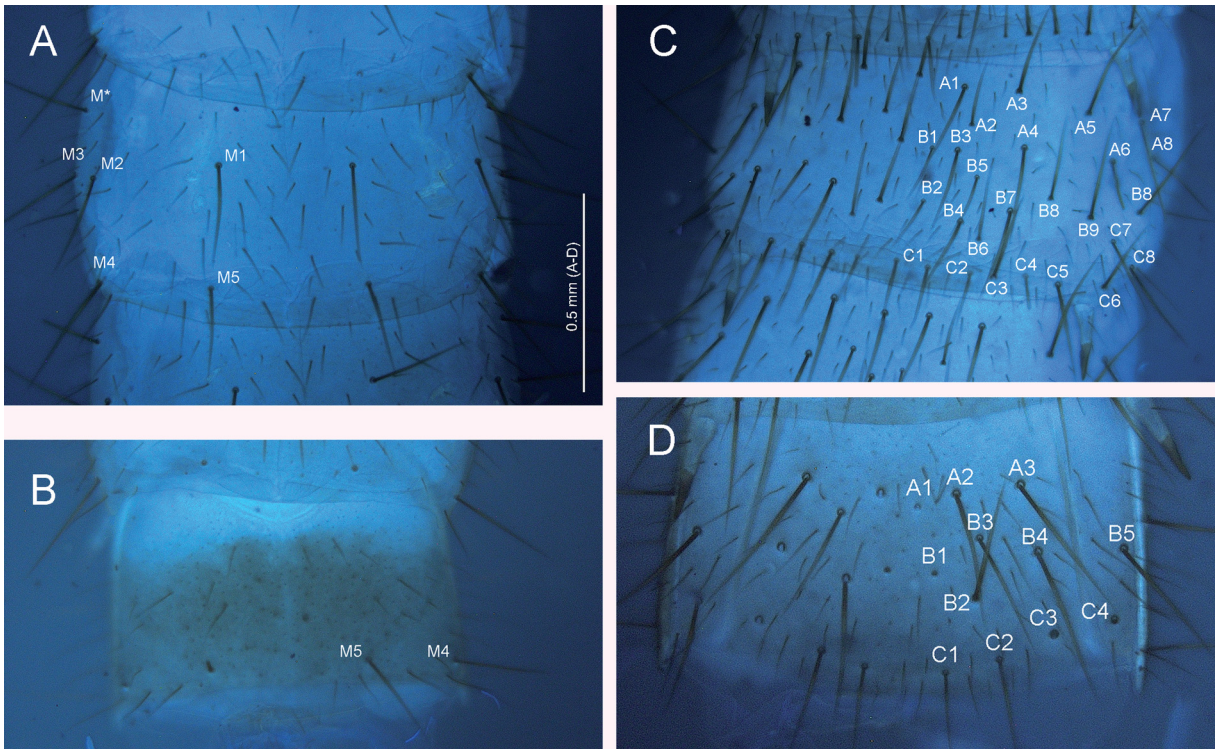


Fig. 7. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Fifth urotergite **B**. Eigth urotergite. **C**. Fifth urosternite. **D**. Eight urosternite. Abbreviations: A, B, and C = macrosetae arranged in three horizontal rows; M* = extra macrosetae; M1–5 = macrosetae 1 to 5.

Taxonomic affinities of the genus and species

The proposal of a new genus, represented by *Laolaojapyx chloeae* gen. et sp. nov., is supported by three unique features: (1) cerci bearing three subsymmetrically arranged inner teeth; (2) the lateral subcoxal organs of the first urosternite, which bears broad-based glandular setae longer than the glandular setae of the same organ; and (3) the presence of more than seventy placoid sensilla on the apical antennomere. This new genus shows similarities with *Troglojapyx*, particularly the general shape of the cerci and the presence of subsymmetrical teeth (two pairs in *Troglojapyx* vs three pairs in *Laolaojapyx* gen. nov.), as well as a high number of placoid sensilla (approximately 20 in *Troglojapyx* compared with ~70 in *Laolaojapyx*).

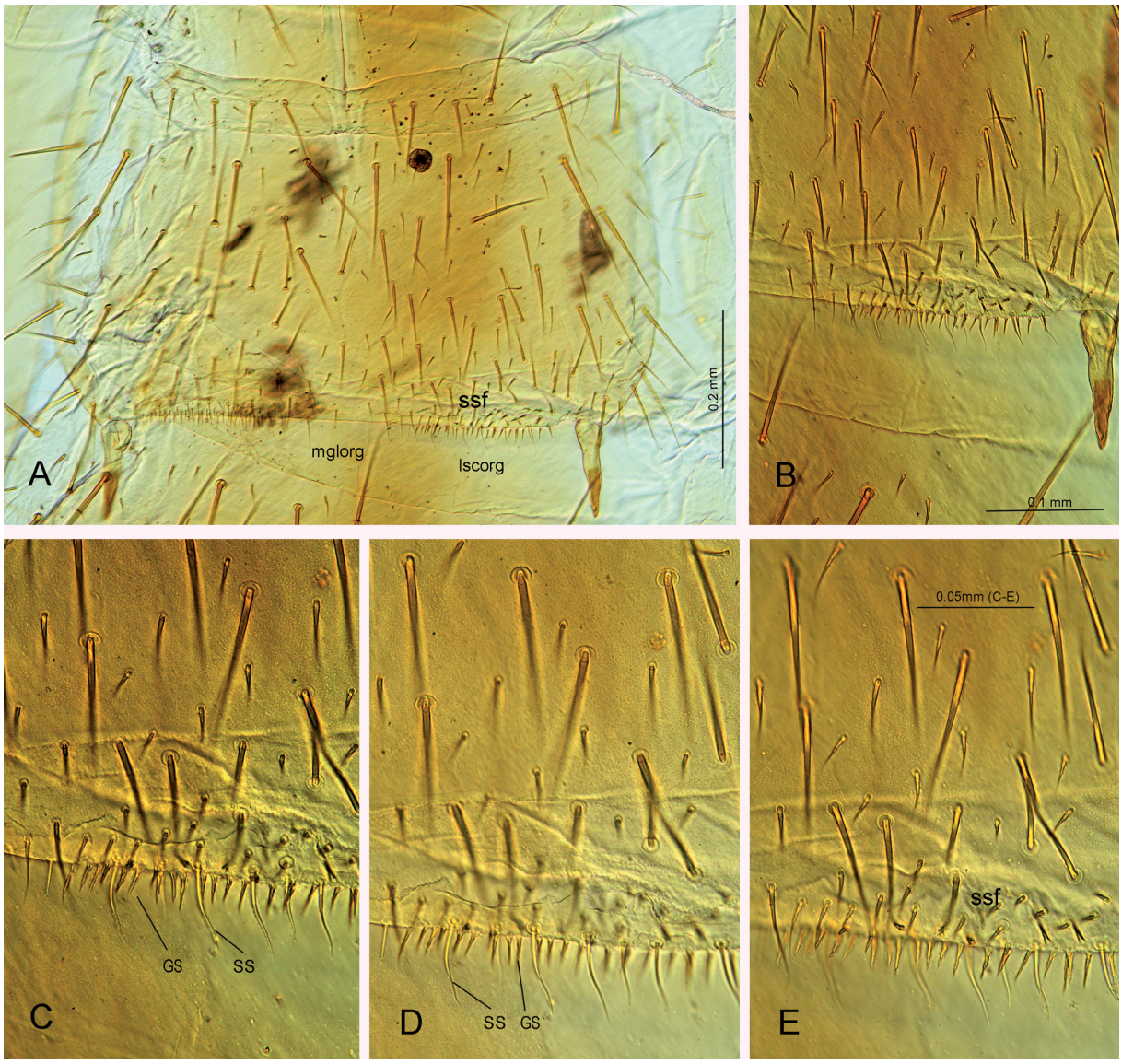


Fig. 8. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. First urosternite. **B**. Right lateral subcoxal organ of the fist urosternite. **C**. Left detail of the right lateral subcoxal organ of the first urosternite. **D**. Central detail of the right lateral subcoxal organ of the first urosternite. **E**. Right detail of the right lateral subcoxal organ of the first urosternite. Abbreviations: GS = glandular setae; lscorg = lateral subcoxal organ; mglorg = medial glandular organ; SS = sensorial setae; ssf = short sensilla field.

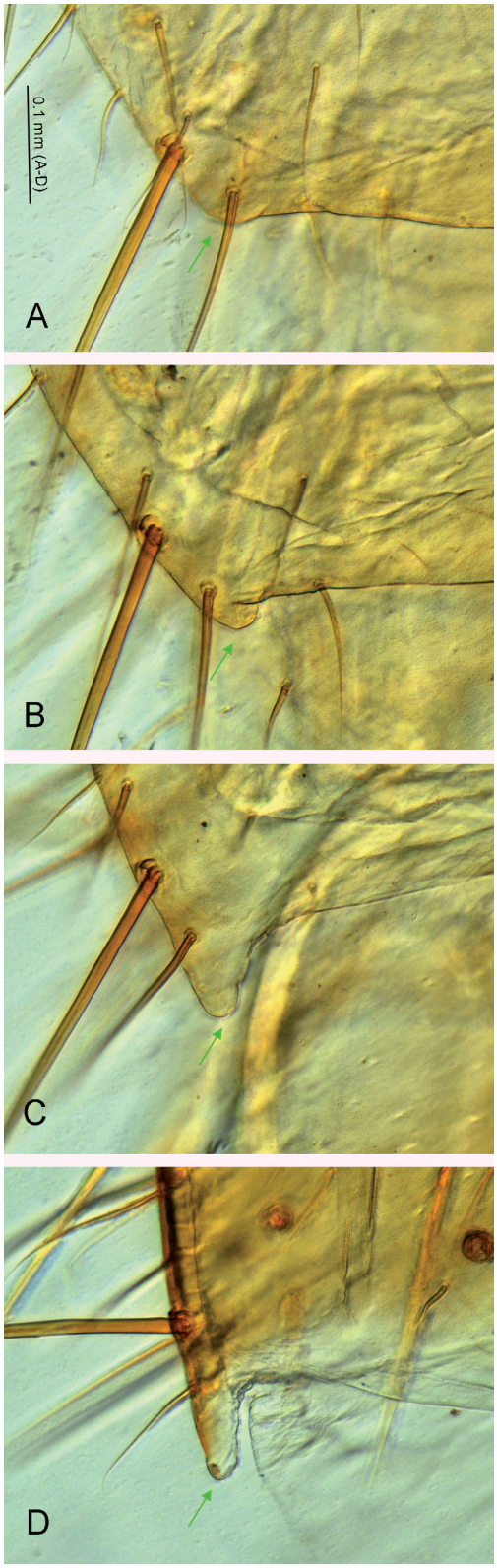


Fig. 9. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Left posterolateral extremity of the fifth urotergite. **B**. Left posterolateral extremity of the sixth urotergite. **C**. Left posterolateral extremity of the seventh urotergite. **D**. Left posterolateral extremity of the eighth urotergite. Green arrows indicate the shape of posterolateral angles.

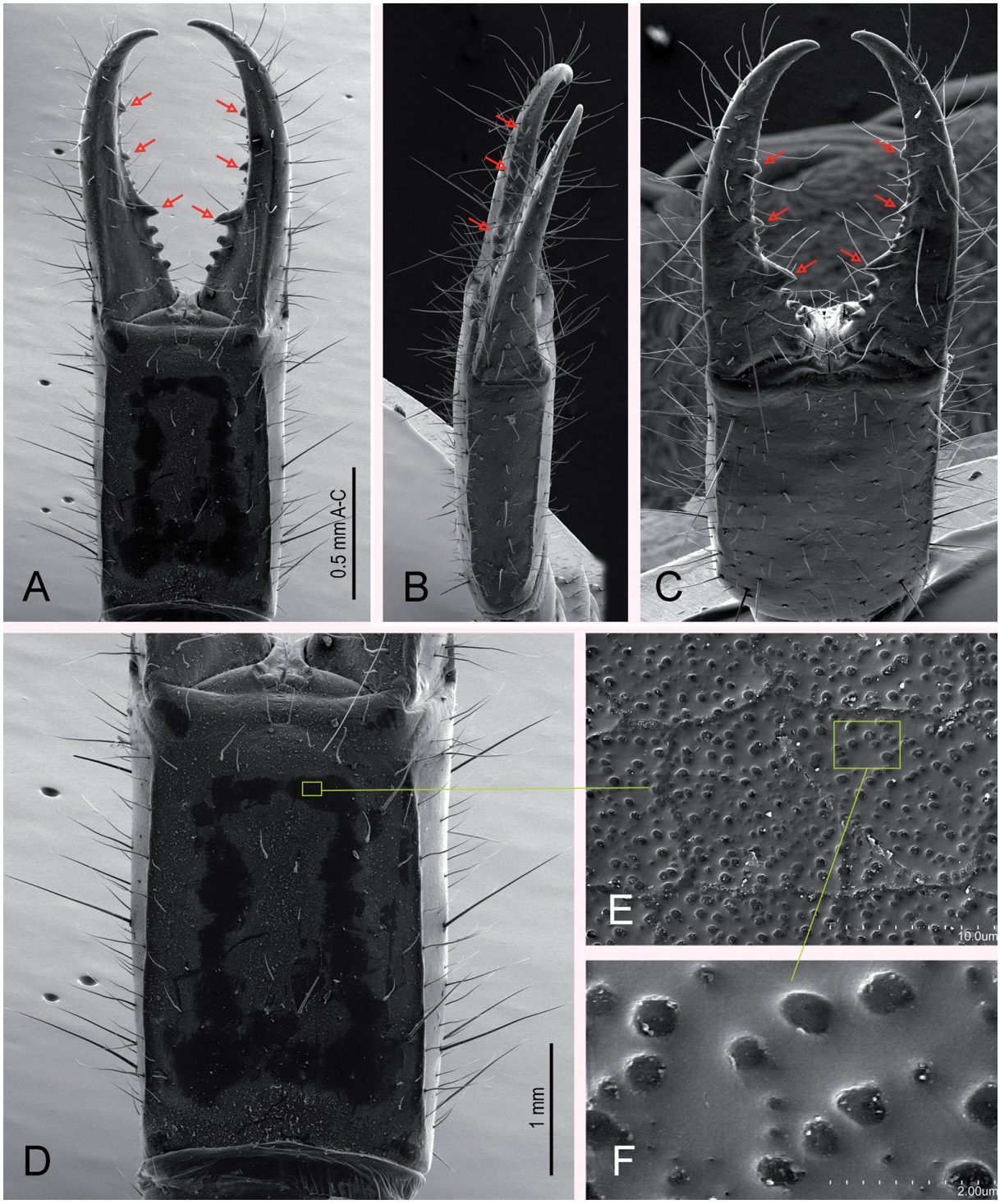


Fig. 10. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). Cerci and urite X observed under electron scanning microscope. **A**. Cerci and urite X, dorsal view. **B**. Cerci and urite X, lateral view. **C**. Cerci and urite X, ventral view. **D**. Urite X, dorsal view **E–F**. Details of the dorsal cuticle of urite X. Red arrows indicate the positions of the three pairs of teeth.

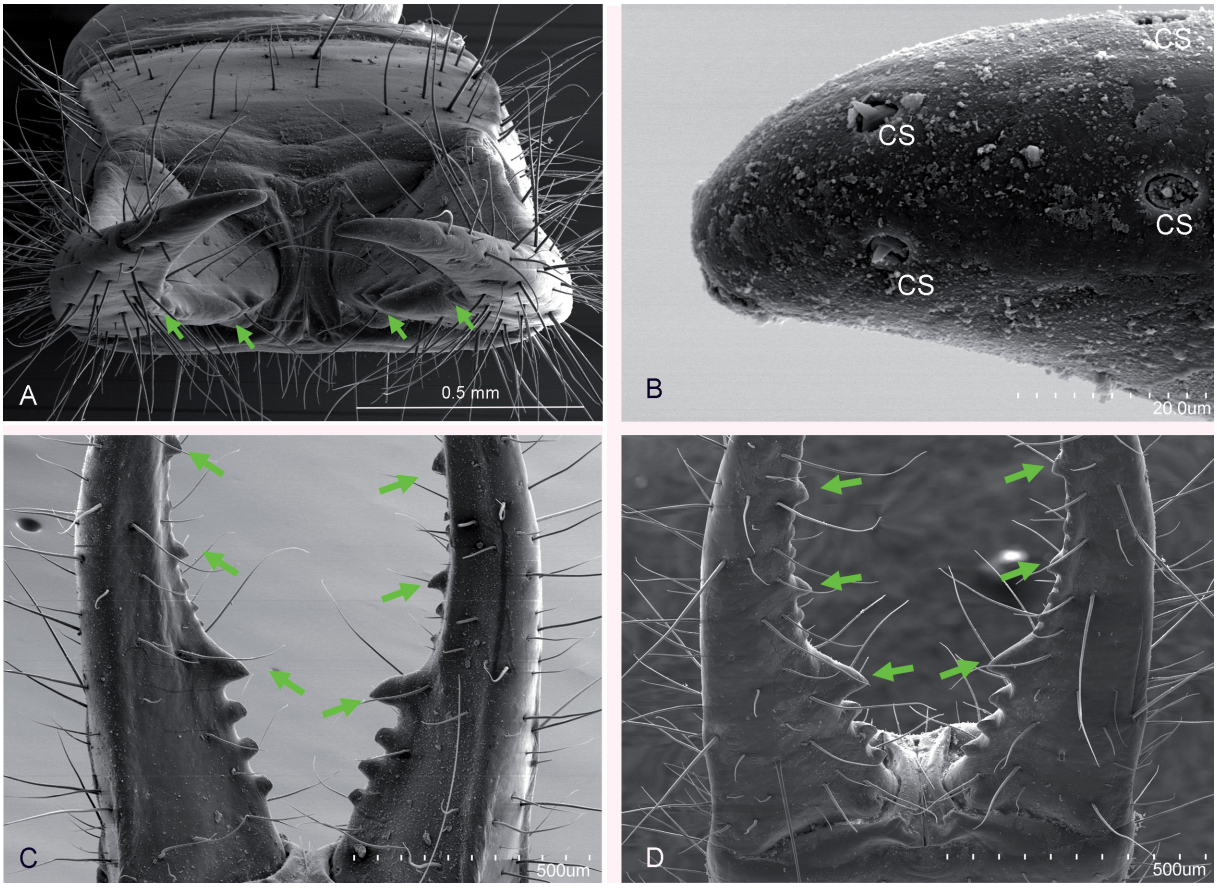


Fig. 11. *Laolaojapyx chloeae* Sendra & Lips gen. et sp. nov., holotype, ♀ (MUVHN ZE10010). **A**. Cerci and urite X, posterior frontal view. **B**. Distal extremity of the right cerci. **C**. Proximal and medial portion of the cerci, dorsal view. **D**. Proximal and medial portion of the cerci, ventral view. Green arrows indicate the positions of the three pairs of teeth.

Habitat

This new taxon was found in a deep zone of the Tham Van Ngo Cave (Fig. 2), in a humid gallery with clay and standing water. The cave entrance provides direct access to a chamber reached via a 10-metre shaft. At its base, a low, water-filled passage leads to westward into a series of labyrinthine galleries, with substantial clay infill, which become partially flooded during the monsoon season. Another gallery extends northward towards the coast at +116 m altitude and remains under exploration. This section of the cave contains substantial dry clay deposits and calcite concretions. A noticeable air draught moves through this part of the system, likely produced by an upper entrance.

Distribution

The Tham Van Ngo Cave in Laos (Southeast Asia) currently represents the only known locality of the new species and genus *Laolaojapyx chloeae* gen. et sp. nov. (Fig. 12).

Genus ***Troglojapyx*** Pagés, 1980

Type species

Troglojapyx hauseri Pagés, 1980.

Diagnosis

Elongate body, epicuticle smooth and clearly visible under optical microscope. Five laminae well pectinated. Antenna with 38 and 45 antennomeres; apical antennomere bearing 10 to 21 placoids; *a* trichobothria on antennomere IV in proximal and medial position. Thoracic segments elongated; pronotum, mesonotum and metanotum each with 5+5 M (M1–5). Legs long, with the hind leg reaching the posterior margin of abdominal segment III–V. Scutum of urotergite I lacking macrosetae, urotergite II with 1+1 *ma* (= M) setae, 1+1–2+2 M4–5; urotergites III–VII with 1+1 ma (= M), 4+4–6+6 M1–5; urotergite VIII with 3+3 M2,4–5. Urite X 1.5–1.6 × as long as wide; dorsal side with at least 2+2 intracarinal M (D1, D3); acropygium short, round to sub-rectangular. Lateral urotergites I–VI with blunt, rounded posterolateral angles; urotergite VII with distinctly protruding, spiniform angles. Prescutum of urosternite I with 3+3–4+4 M; scutum with about 13+13–20+20 M and a posterior field of 50 short, slightly thickened setae preceding each lateral subcoxal organ; urosternites II–III with 16+16–18+18 M arrange in three horizontal rows; urosternite VIII with central sclerite bearing 6+6–7+7 M, lateral with 1+1–2+2 M. Median glandular organ with pseudospori; lateral subcoxal organ with one or two rows of glandular setae (GS) and one row of sensory setae (SS). Cerci subsymmetric and robust, with lateral external borders subparallel and incurved in distal third, forming a hook-like apex; length 1.5 × the maximum width. Each cercus with two subsymmetrical, submedial, pointed medial teeth, defining three marginal areas.

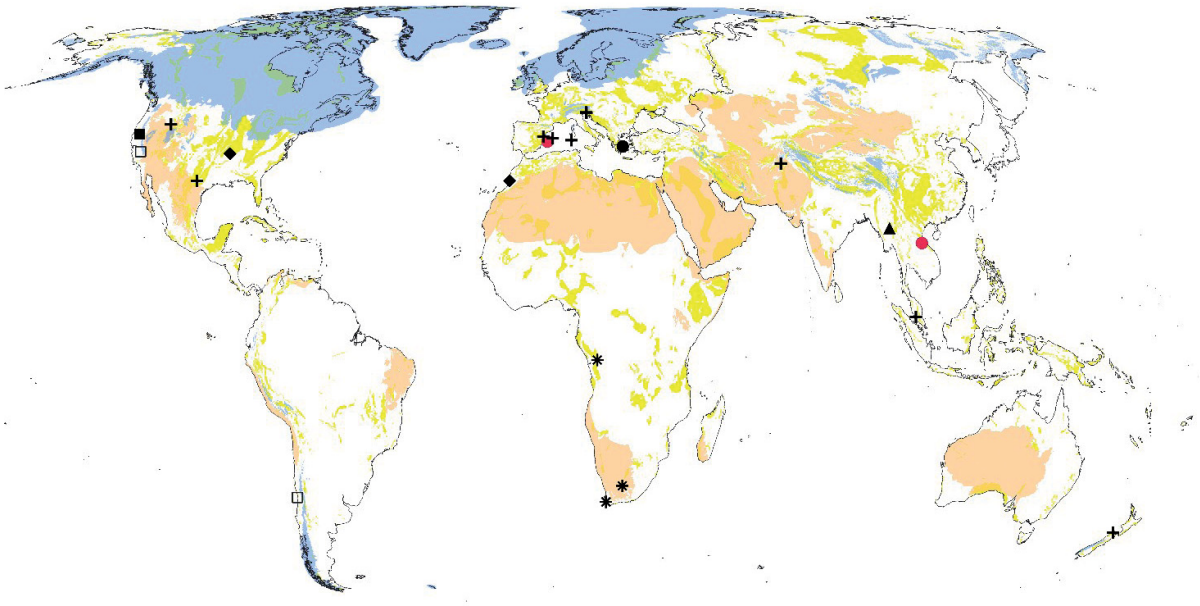


Fig. 12. Records of some japygids taxa mentioned in the text showing the global geographical distribution of the cercal morphology. In white, epigean taxa data based on Smith (1959a, 1962); in black, subterranean taxa data from Sendra *et al*. (2023, 2026); in red, subterranean taxa data from this study. Circles: two or three subsymmetrical teeth in each cercus (*Troglojapyx* Pagés, 1980 and *Laolaojapyx* Sendra & Lips gen. nov.); squares: two asymmetrical teeth in each cercus (*Chiljapyx* Smith, 1962, *Occasjapyx* Silvestri, 1948 and *Hecajapyx* Smith, 1959); diamonds: one subsymmetrical tooth in each cercus (*Quapawjapyx* Sendra, 2026 and *Imazighenjapyx* Sendra & Sánchez-García, 2023); stars: one tooth in only one cercus (*Austrjapyx* Silvestri, 1948 and *Opisthjapyx* Silvestri, 1929); crosses: one asymmetrical tooth in each cercus (*Burmjapyx* Silvestri, 1930, *Gollumjapyx* Sendra & Ortuño, 2006, *Holjapyx* Silvestri, 1948, *Kohjapyx* Pagés, 1953, *Metajapyx* Silvestri, 1933, *Teljapyx* Silvestri, 1949, *Mixojapyx* Silvestri, 1933, and *Homojapyx* Pagés, 1953); triangle: no teeth(*Mueggejapyx* Sendra & Komerički, 2021). A single point may represent several nearby localities. In yellow: karst areas (Chen *et al*. 2017). In orange: desert areas (Olson & Dinerstein 2002). In blue: ice cover during the Last Glacial Maximum (Ehlers *et al*. 2011).

Troglojapyx angelginesi Sendra sp. nov.
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Figs 13–17

Diagnosis

Elongated body, epicuticle smooth and clearly visible under optical microscope. Dorsal side of the head with 15+15 M (A, S, M, I, L, and P); submentum with 1+1 M; admentum with 3+3 M; mentum at base of labial palps with 1+1 M; lacinia falciform with five well-pectinated laminae. Antenna with 45 antennomeres; apical antennomere with at least ten placoid sensilla unevenly distributed; *a* trichobothria of antennomere IV in medial position. Thoracic segments elongated; pronotum, mesonotum, and metanotum each with 5+5 M (M1–5); prescutum of mesonotum and metanotum with 1+1 M. Propresternum with 2+2 M; prosternum with 3+3 lateral anterior M, 1+1 medial anterior M, and 4+4 posterior M; meso-poststernum with 5+5 M; meso-intersternum with 4+4 M; mesosternum with 3+3 *la* M, 1+1 medial anterior, 1+1 medial posterior M, one sagittal intermediate M and 7+7 posterior M; meta-poststernum with 5+5 M; meta-intersternum with 4+4 M; metasternum with 3+3 *la* M, 1+1 medial anterior M, 1+1 medial posterior M, one sagittal M and 7+7 posterior M. Legs long, hind leg reaching the posterior margin of abdominal segment V. Pretarsus with two unequal claws. Prescutum of urotergite I with 1+1 M, scutum without macrosetae, urotergite II with 1+1 *ma* (= M), 1+1 M5; urotergites III–VII with 1+1 ma (= M), 4+4 M2–3, 4–5; urotergite VIII 3+3 M2,4–5; urite IX without dorsal M; urotergite VIII and urite IX with abundant microsetae. Urite X 1.6× as long as wide, carinae with subparallel margins slightly converging posteriorly; dorsal side with 2+2 intracarinal M (D1, D3); acropygium short, subrectangular; lateral side with 3+3 M (L); ventral side with 16+16 M setae arranged in three rows. Lateral urotergites I–VI with blunt, rounded posterolateral angles; lateral urotergite VII a strongly protruding spiniform angle, reduced again in urotergite VIII. Prescutum of urosternite I with 4+4 M; scutum with about 20+20 M and a posterior field of 50 short, slightly thickened setae preceding each lateral subcoxal organ. Urosternites II–III with 18+18 M arranged in three horizontal rows; urosternite VIII with central sclerite bearing 7+7 M, and lateral sclerite with 1+1 M; ventral side of abdominal segment IX with 2+2 M. Median glandular organ with pseudospori; lateral subcoxal organ with one or two rows of about glandular setae (GS) and one row of sensory setae (SS). Styli of abdominal segments I–VII each bearing a long external basal seta. Cerci subsymmetrical and robust, with lateral external margins subparallel and incurved in the distal third, forming a hook-like apex. Each cercus bears two subsymmetrical, submedial, pointed medial teeth, defining three margin areas: (1) basal predental margin, slightly concave, with two rows of smooth denticles; (2) medial margin between the two teeth, with one row of smooth denticles; (3) distal postdental margin, strongly concave distally, with a row of tiny rounded denticles.

Etymology

We dedicated this species in memory of our colleague Àngel Ginés Gracia (1950–2024). Those of us fortunate enough to know him were constantly aware of his humanity, warmth, and kindness toward those around him. Within the speleological community, he will be remembered for his scientific merit – as a naturalist speleologist who became a legend in speleology of the Balearic Islands and across the world.

Type material

Holotype

SPAIN – **Eivissa, Balearic Island** • ♂; "L'Avenc des Pouàs" Cave, Santa Agnès de Corona; 39.03512° N, 1.35074° E; 2 Nov. 1990; Palmer and Pons leg.; IMEDEA-INSECTA 19251.

Paratype

SPAIN – **Eivissa, Balearic Island** • 1 ♂; same collection data as for holotype; 31 Dec. 1990; MUVHN ZE10072.

Description

Body. Elongate body, length 15 mm (holotype) and 17 mm (paratype) in adults, plus cercal length; maximum width 1.5 mm at urotergite IV (Fig. 13A). Epicuticle smooth and clearly visible under optical microscope. Cuticle unpigmented, with sclerotized areas on the mandible tips, claws, apices of the abdominal styli, lateral apodemes of abdominal segments VII–X, cerci, and the femoral, tibial, and especially cercal condyles. Body and appendages covered with very sparse short setae (ss) and a few long setae (ls); scattered microsetae (ms) visible under fluorescence microscopy and locally abundant on dorsal side of abdominal segment VIII, where they are detectable under transmitted light microscopy; in addition, the body bears they typical macrosetal (M) pattern of Japygidae and abdominal sclerites and appendages.

Head. Dorsal side about 15+15 M: A1,3; S1,4,6; M1,3,5; I2,5, L2,4–5 and P1–2, plus 2 long M on the oral folds in ventral position (Fig. 14A). Ventral side with submentum bearing 1+1 M in posterior position; admentum with 3+3 M; mentum at base of labial palps with 1+1 M; external lobes of mentum with abundant thick setae. Labial palp longer than wide (deformed during slide preparation), with two apical M, one subapical M, and several sl. Labrum short, with abundant short thick setae. Lacinia falciform, well sclerotized, with five well-pectinated laminae. Mandible with four distensible teeth and one tiny internal tooth.

Antennae. Antenna 0.53 × as long as body, with 45 antennomeres. First antennomere shorter than wide, antennomeres II–IV slightly longer than wide, with tiny reinforced margins; medial and distal antennomeres likewise slightly longer than wide. All antennomeres bear *ss*, *ls*, and a whorl of M. The last antennomere carries at least ten placoid sensilla, unevenly distributed. Trichobothria present on antennomeres IV–VI: 1 dorsal / 1 ventral on IV, 2 / 1 on V–VI. The dorsal trichobothria (*a* trichobothria of the IV antennomere) is positioned medially.

Thorax. Thoracic segments elongated, each with a few *ls*, *ss* and a typical pattern of M on scutum of pronotum, mesonotum and metanotum with 5+5 M (M1–5); prescutum of mesonotum and metanotum with 1+1 M (Fig. 14B–D). Thoracic sternites, intersternites, and presternites well defined with ss, scarce sl, and several M (Fig. 15A–D). Pro-presternites and pro-, meso-, and metasternites each possess internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); in the propresternites, only the prolongation of the posterior branch (spine) is visible (Denis 1949). Propresternum with 2+2 M; prosternum with 3+3 lateral anterior M, 1+1 medial anterior M, and 4+4 posterior M; meso-poststernum with 5+5 M; meso-intersternum with 4+4 M; mesosternum with 3+3 *la* M, 1+1 medial anterior M, 1+1 medial posterior M, one sagittal intermediate M, and 7+7 posterior M; meta-poststernum with 5+5 M; meta-intersternum with 4+4 M; metasternum with 3+3 *la* M, 1+1 medial anterior M, 1+1 medial posterior M, one sagittal M and 7+7 posterior M (Fig. 15A–D). Legs long, with the hind leg reaching the posterior margin of abdominal segment V; coxa with 1–2 sternal M; trochanter with 2 sternal M; femur with 11 M and a row of thick setae in apical position; tibia with 13 M plus poorly visible calcars; tarsus with two ventral rows of 10 thick setae. Pretarsus with two unequal claws (1.3 anterior to posterior claw) and a small, sharp medial unguiculus.

Abdomen. Abdominal tergites with scarce *ss* and *sl* setae. Prescutum of urotergite I with 1+1 M, scutum without macrosetae (Fig. 16A). Urotergite II with 1+1 *ma* (= M) setae, 1+1 M5 (Fig. 16B). Urotergites III–VII with 1+1 *ma* (= M), 4+4 M2–3, 4–5; urotergite VIII with 3+3 M2, 4–5 (Fig. 16C–D); urite IX lacking dorsal M. Urotergites VIII and urite IX with abundant microsetae. Urite X 1.6 × as long as wide, with distinctly marked carinae; carinal with subparallel margins slightly converging towards posterior border Dorsal side with 2+2 intracarinal M (D1, D3); acropygium short, subrectangular, with slightly rounded margins (Fig. 16E). Lateral side with 3+3 M (L); ventral side with 16+16 M, arranged in three rows (Fig. 16F). Lateral urotergites I–VI with blunt, rounded posterolateral angles; lateral urotergite VII

with a strongly protruding spiniform angle, reduced again in urotergite VIII. Urosternites with *ss* and a few *sl* setae. Prescutum of urosternite I with 4+4 M; scutum with ~20+20 M and a posterior field of 50 short, slightly thickened setae preceding each lateral subcoxal organ. Urosternites II–III with 18+18 M, arranged in three horizontal rows: 7+7 A1–7, 5+5 B1–5, and 6+6 C1–6 (Fig. 17B). Urosternite VIII with a central portion bearing 8+8 M; the central sclerite separated by a well-defined carina bearing 7+7 M (A1-2, B1–2, C1–3), lateral sclerites with 1+1 M (B3) (Fig. 17C); ventral side of abdominal segment IX with 2+2 M. Median glandular organ with 4+4 pseudospori, each accompanied by a microseta. Lateral subcoxal organ with one or two rows of ~70 glandular setae (GS) and one row of ~40 sensory setae (SS) (GS/SS= 2.22); the organ occupies 0.7 × of interstylar area. Setae relatively long with GS/st1 = 0.20; SS/st1= 0.10 (stylus of first urosternite) (Fig. 17A). Styli of abdominal I–VII each bearing a long external basal seta. Male

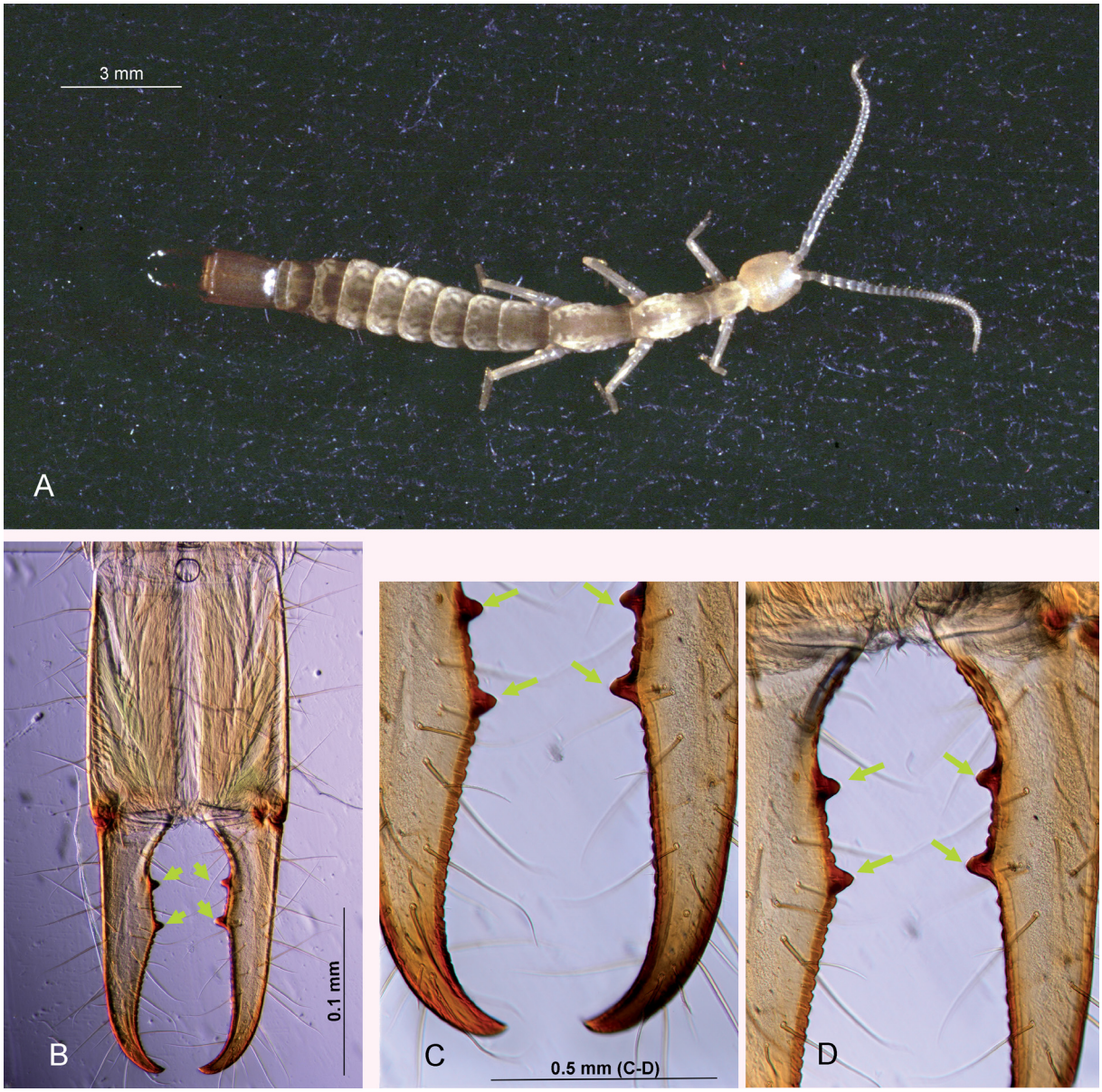


Fig. 13. *Troglojapyx angelginesi* Sendra sp. nov., holotype, ♂ (IMEDEA INSECTA 19251). **A**. Habitus (photograph by Josep Antoni Alcover Tomàs). **B**. Urite X and cerci. **C**. Medial and distal portion of cerci. **D**. Medial and proximal portion of the cerci. Arrows indicated the pairs of teeth.

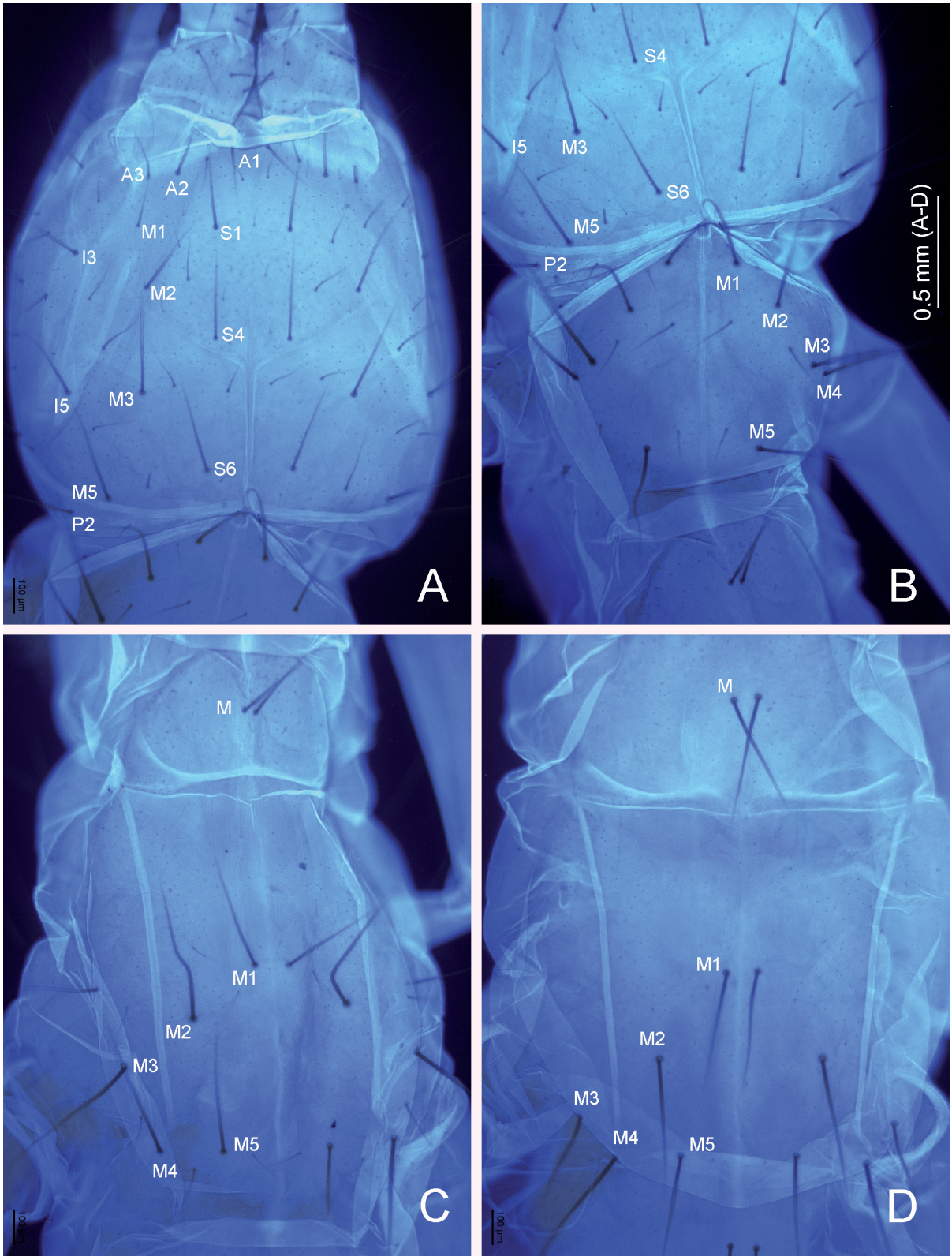


Fig. 14. *Troglojapyx angelginesi* Sendra sp. nov., holotype, ♂ (IMEDEA INSECTA 19251). **A**. Head, dorsal view. **B**. Pronotum. **C**. Prescutum of the mesonotum and mesonotum. **D**. Prescutum of the metanotum and metanotum. Abbreviations: A, S, M, I and P = macrosetae of the dorsal head; M1–5 = macrosetae 1 to 5.

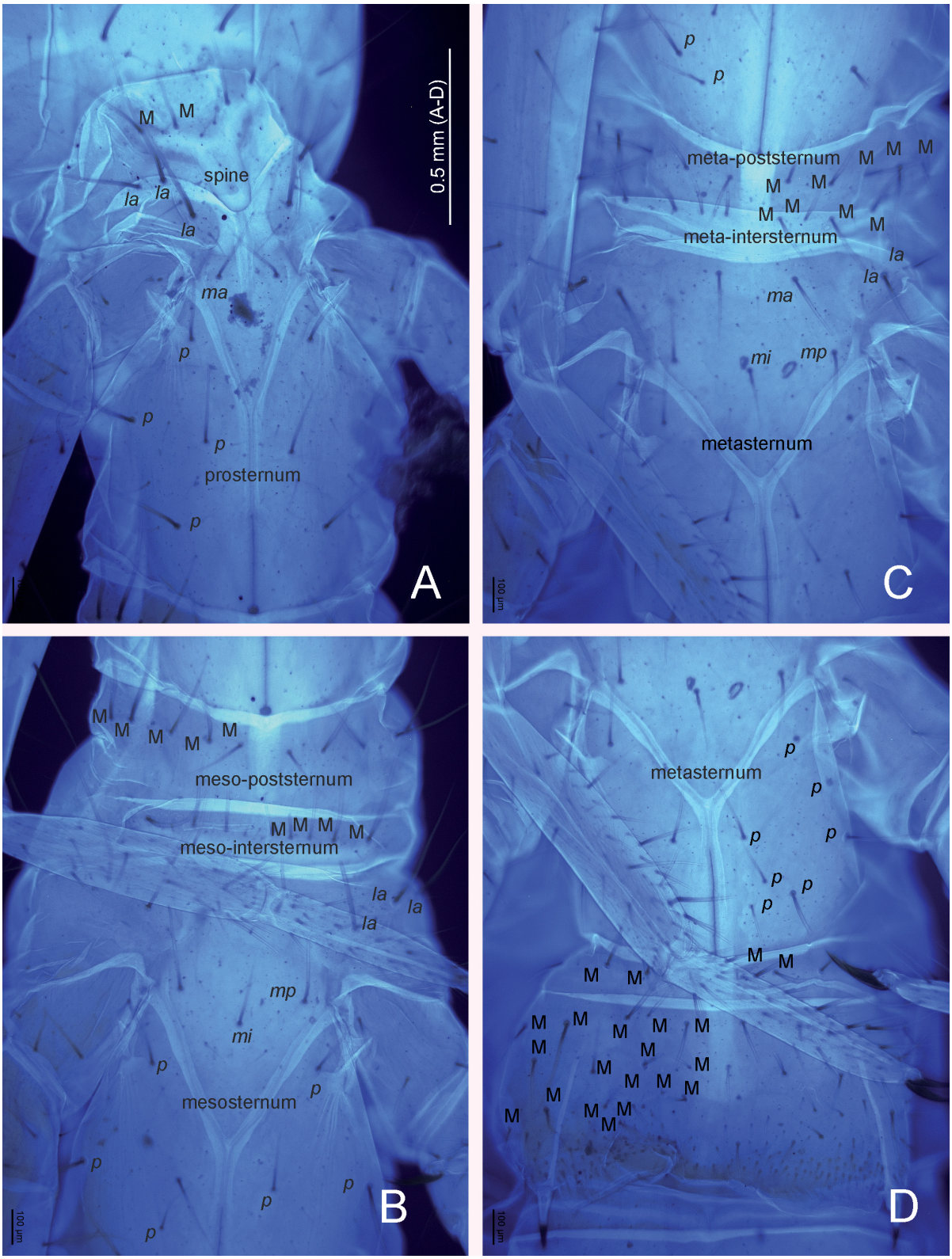


Fig. 15. *Troglojapyx angelginesi* Sendra sp. nov., holotype, ♂ (IMEDEA INSECTA 19251). Thoracic sternites, intersternites, and presternites. **A**. Prosternum. **B**. Mesosternum. **C**. Metasternum. **D**. Metasternum and first urosternite. Abbreviations: *la* = lateral anterior; M = macroseta; *ma* = medial anterior; *mi* = medial intermedia; *mp* = medial posterior; *p* = posterior macrosetae.

genital with the typical papillae of male with typical japygid form, with slightly elongated appendages, 2.2× as long as wide, bearing *ss* and numerous *sl* setae surrounding the genital opening.

Cerci. Subsymmetrical and robust, length 1.45 mm in the holotype and 1.93 mm in the paratype (0.10−0.11× body length, respectively). Lateral external borders subparallel and incurved in the distal third, forming a hook-like apex. Borders strongly sclerotized, with dorsal and ventral outer carinae arising from the corresponding acetabular articulations. Overall, cerci are 1.5× as long as wide (Fig. 13B). Each cercus bears two subsymmetrical, submedial, pointed medial teeth, defining three margin areas: (1) basal predental margin, slightly concave, with two rows of smooth denticles (holotype with 4/5 right cercus and 5/5 left cercus; paratype 7/3 and 5/6); (2) medial margin, between the two teeth, with one row of smooth denticles (holotype 4 right and 4 left cercus; paratype 3 right and 4 left cercus); (3) distal postdental margin, strongly concave distally, with a row of tiny round denticles (holotype 19 right cercus,

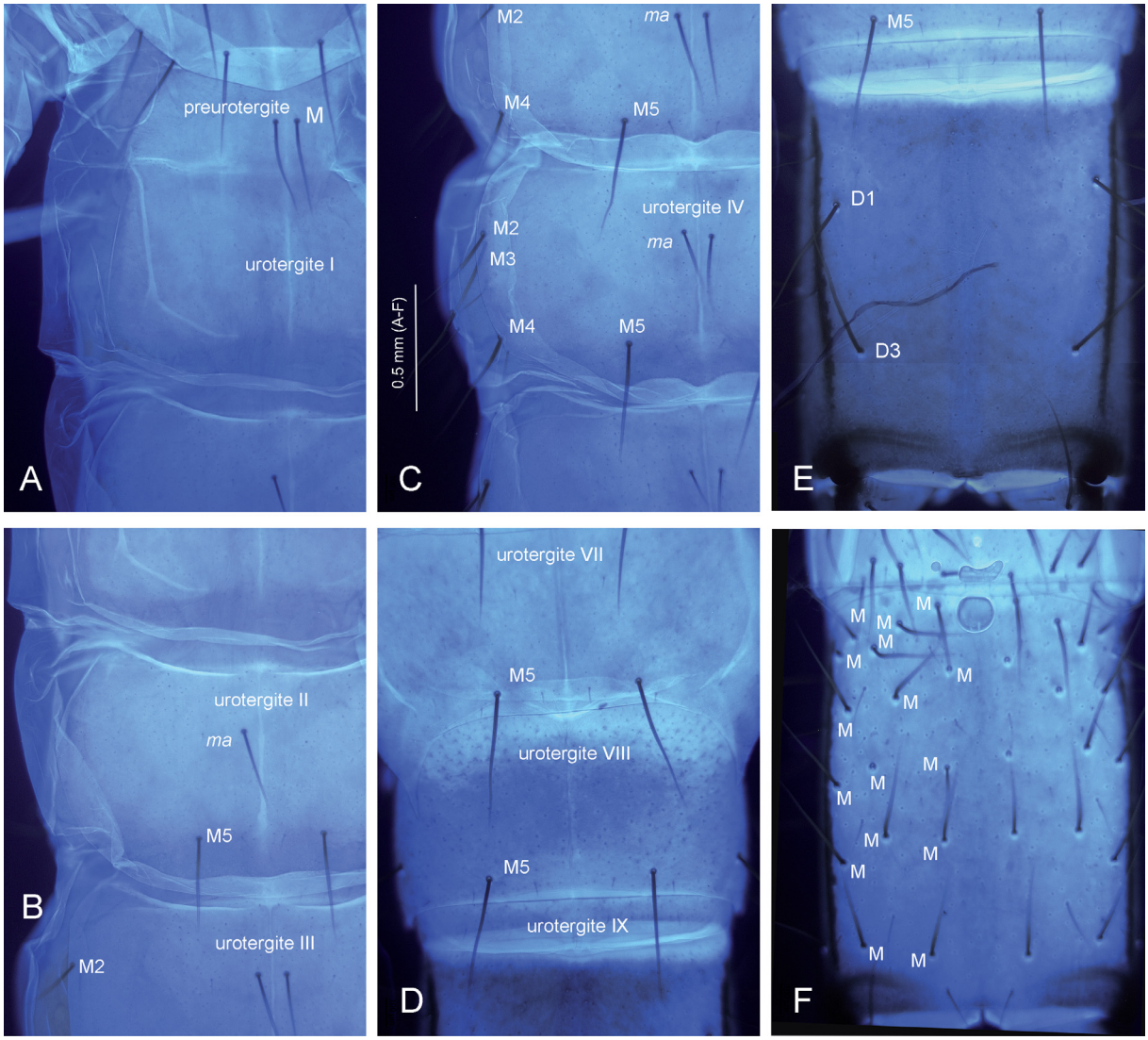


Fig. 16. *Troglojapyx angelginesi* Sendra sp. nov., holotype, ♂ (IMEDEA INSECTA 19251). **A**. First presternite and urotergite. **B**. Second and third urotergites. **C**. Third and fourth urotergites. **D**. Seventh to ninth urotergites. **E**. Tenth urite. Abbreviations: D1, D3 = macrosetae D1 and D3; M = macrosetae; M2–5 = macrosetae 2 to 5; ma = macroseta medial anterior.

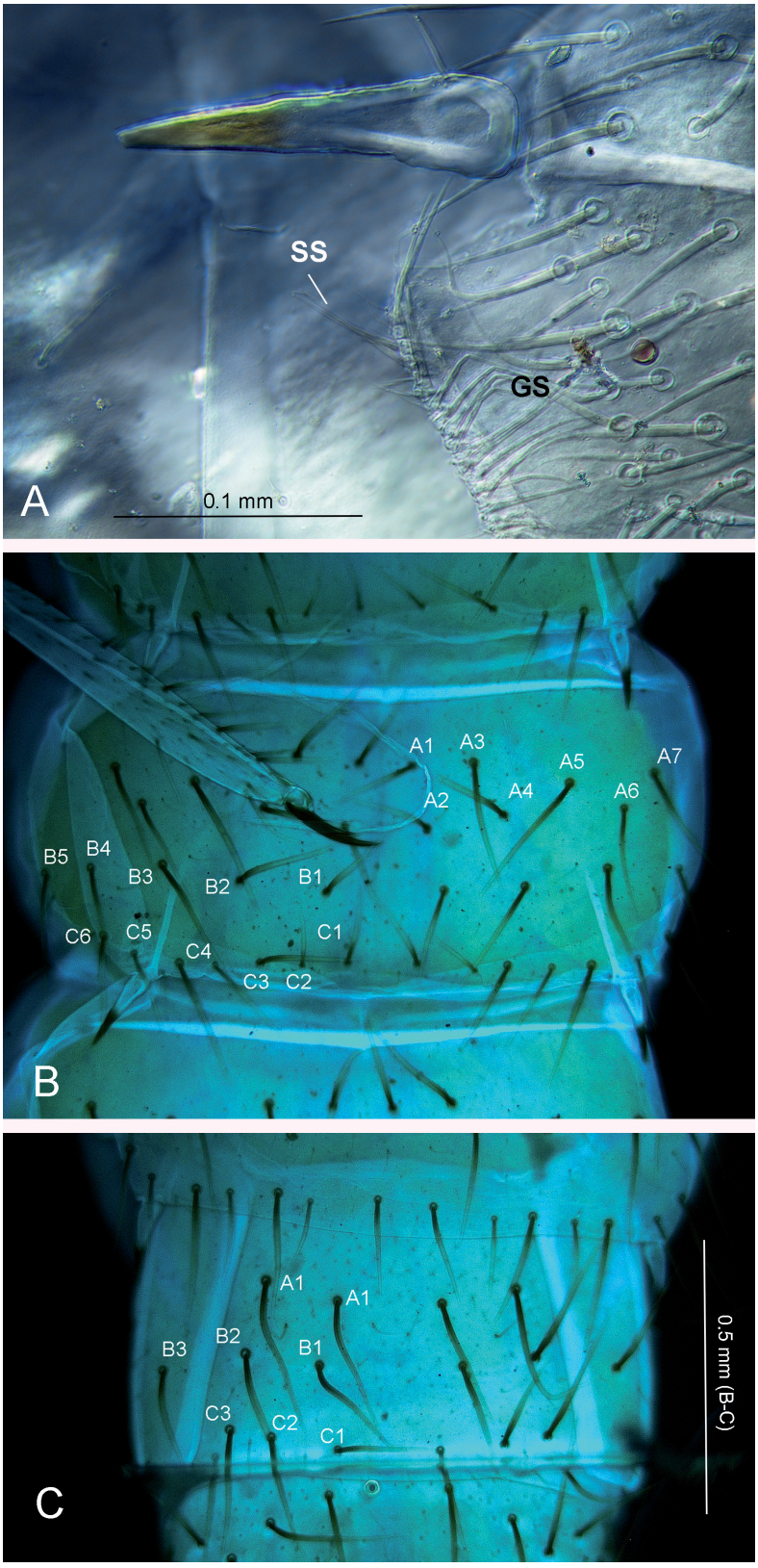


Fig. 17. *Troglojapyx angelginesi* Sendra sp. nov., holotype, ♂ (IMEDEA INSECTA 19251). **A**. Lateral posterior extreme of the first urosternite. **B**. Third urosternite. **C**. Eight urosternite. Abbreviations: A, B and C = urosternal macrosetae rows; GS = glandular setae; SS = sensory setae.

15 left cercus, paratype 25 in right and left cerci) (Fig. 13C–D). Right cercus with 8 D M, 5 L M, and 19 V M; left cercus with 12 D M, 7 L M, and 10 V M.

Taxonomic affinities

Troglojapyx angelginesi sp. nov. is closely related to the type species of the previously monotypic genus *Troglojapyx*, *T. hauseri*, based on similarities in cercal shape and internal cercal armature, both species bearing two subsymmetrical teeth, as well as on aspects of body chaetotaxy, including the shared notal macrosetal pattern (5+5 M1–5) and generally comparable abdominal sclerites. However, a plethora of taxonomic characters clearly distinguish *T. angelginesi* from *T. hauseri*. Most notably: *T. hauseri* possesses ~20 placoid sensilla, whereas *T. angelginesi*bears ~10; *a* trichobothria of the IV antennomere are proximally positioned in *T. hauseri* but medially positioned in *T. angelginesi*; antennae with 38 antennomeres in *T. hauseri* vs 45 antennomeres in *T. angelginesi*; and urotergal chaetotaxy differs, *T. hauseri* showing a complete set of 7+7 macrosetae (ma macrosetae, M1–5, plus an extra pair), whereas *T. angelginesi* bears 5+5 macrosetae (ma macrosetae and M2–5).

Habitat

The two specimens were collected in the deep interior of "L'Avenc des Pouàs" (Fig. 1), a cave that opens to the surface through a shaft about 7 m in diameter and 19 m deep, leading to a lateral chamber with a sloping floor, oriented east-west. The chamber is irregular in shape, with maximum dimensions of 32 m in length and 52 m in width. Pouàs is also notable for its archaeological and palaeontological significance, as it is the site where the earliest evidence of human presence in prehistoric Ibiza has been discovered.

Distribution

The "L'Avenc des Pouàs" Cave in Eivissa, Balearic Islands, is currently the only known locality for the new species *Troglojapyx angelginesi*, the second described species of the genus *Troglojapyx* was previously known only from a cave in continental Greece near Athens. Thus, the genus as a whole is distributed across both the western and eastern regions of the Mediterranean (Fig. 12).

Discussion

When Professor Jean Pagés (1980) described *Troglojapyx hauseri* from a single juvenile specimen (stage 3B, 5.9 mm in body length) collected in the tourist-accessible Koutouki Cave – a cave excavated in the limestone rocks of Hymette Mountain, in Peania, near Athens (Greece) – he did not hesitate to propose a new genus. The cerci, with straight outer edges along their proximal two-thirds and bearing two clearly visible subsymmetrical teeth, represent a morphology previously unknown in the family Japygidae. This cercal morphology had not been previously mentioned in the dipluran literature: either in the comprehensive monograph by Paclt (1957) or in subsequent works on japygid diversity worldwide (e.g., Pagés & Schowing 1958; Smith 1959a, 1959b, 1964; Pagés 1962, 1978a, 1978b, 1981, 1983, 1984, 1987, 1993, 1994, 1995, 2000, 2002; González & Smith 1964; Smith & Bolton 1964; Muegge & Bernard 1990; Muegge 1992, among others). The trait is also absent from more recent studies on extant japygids (Sendra *et al.* 2021c, 2023) and fossil japygids (Sánchez-García *et al.* 2023, 2024; Wang *et al.* 2023).

The study of the new taxa from two different caves in the Mediterranean and Southeast Asia confirms the existence of the unusual cercal morphology described in *T. hauseri*, now also documented in *Troglojapyx angelginesi* sp. nov., represented by two males from "L'Avenc des Pouàs" Eivissa (Balearic Island, Mediterranean Sea). In addition, a related but distinct condition occurs in the new genus and species *Laolaojapyx chloeae* gen. et sp. nov., discovered in Tham Van Ngo Cave, Laos (Southeast Asia), where the cerci bear three pairs of subsymmetric teeth.

Among japygids described to date, the most common cercal morphology consists of a single pair of teeth, usually arranged asymmetrically, as seen in genera such as *Burmjapyx* Silvestri, 1930; *Dipljapyx* Silvestri, 1948; *Gollumjapyx* Sendra & Ortuño, 2006; *Holjapyx* Silvestri, 1948; *Homojapyx* Pagés, 1953; *Kohjapyx* Pagés, 1953; *Megajapyx* Verhoeff, 1904; *Metajapyx* Silvestri, 1933; *Mixojapyx* Silvestri, 1933; and *Teljapyx* Silvestri, 1949, among others. Most of these genera include one or more cave-adapted species, with the exception of *Dipljapyx*. Less frequently, the single pair of teeth is arranged subsymmetrically, as in *Quapawjapyx* Sendra, 2026; *Imazighenjapyx* Sendra & Sánchez-García, 2023; *Indjapyx* Silvestri, 1930; *Parindjapyx* Silvestri, 1933; *Pauperojapyx* Pagés, 1995; and *Silvestrijapyx* Pagés, 1981, among others (Silvestri 1930; Pagés 1978b, 1981, 1994, 1995). Among these, cave-adapted species are known in the monotypic genera *Quapawjapyx* and *Imazighenjapyx*. Finally, cercal teeth may be entirely absent, as in the monotypic cave-adapted *Mueggejapyx* Sendra & Komerički, 2021 genus.

Nonetheless, three genera within the Japygidae exhibit two pairs of cercal teeth, but in all known species these teeth are asymmetrically arranged (Silvestri 1928a, 1948; Smith 1959a, 1962, 1964; Allen 1988). These include *Occasjapyx californicus* Silvestri, 1948; *Occasjapyx sierrensis* Smith, 1959; *Occasjapyx carltoni* Allen, 1988; *Occasjapyx kofoidi* Silvestri, 1928; *Hecajapyx vulgaris* Smith, 1959; and *Hecajapyx bucketti* Smith, 1964, all reported from several counties in California (North America). Additional species of *Occasjapyx* Silvestri, 1948 from East Asia (China and Japan) show a less pronounced double pair of cercal teeth (Silvestri 1928b; Chou & Chen 1983), as in *Occasjapyx yangi* Chou & Chen, 1983 and *Occasjapyx japonicus* (Enderlein, 1907). Finally, a third taxon with two pairs of cercal teeth occurs in the monotypic genus *Chiljapyx* Smith, 1962, *C. caltagironei* Smith, 1962, from the Valparaiso region of Chile.

Under this scenario of taxonomic relationships – assuming affinities among genera bearing two or more pairs of cercal teeth, either asymmetrically (*Occasjapyx*, *Hecajapyx* Smith, 1959, and *Chiljapyx*) or subsymmetrically (*Laolaojapyx* gen. nov. and *Troglojapyx*) – the group would exhibit an exceptionally wide distribution across four biogeographical realms: *Occasjapyx* (Nearctic and Palearctic), *Hecajapyx* (Nearctic), *Chiljapyx* (Neotropical), *Laolaojapyx* (Oriental), and *Troglojapyx* (Palearctic) (see Fig. 11). Such a pattern, however, does not seem to support the validity of cercal morphology as a reliable criterion to infer taxonomic affinities.

Regarding the distribution patterns of macrosetae and the morphology of glandular organs – including the lateral subcoxal organs and the central organ of the first urosternite –, these features are similar to those observed in other described species; an exception is the lateral subcoxal organ of *L. chloeae* gen. et sp. nov., which exhibits a peculiar morphology, with glandular setae clearly shorter than the sensory setae.

From an ecological perspective, the two new taxa described, *L. chloeae* gen. et sp. nov. and *T. angelginesi* sp. nov., inhabit deep subterranean environments, living within cavities and exhibiting clear morphological adaptations to subterranean life. Pagés (1980) likewise highlighted several troglomorphic traits in *T. hauseri*, including a slender body and appendages, metathoracic legs extending to the middle of the third abdominal segment, and the abundance of placoid sensilla on the apical antennomere. *Troglojapyx angelginesi* exhibits elongated body segments, metathoracic legs reaching the posterior margin of the fifth abdominal segment, and an apical antennomere bearing approximately ten placoid sensilla. *Laolaojapyx chloeae* gen. et sp. nov. likewise displays an elongated body, segments, and appendages, with metathoracic legs extending the fourth abdominal segment, and it exhibits the highest number of placoids sensilla recorded to date, 72 placoids on the apical antennomere.

Cave-dwelling species of japygid diplurans are particularly rare, a fact already noted by Pagés (1964), who recognized only three species with adaptations to underground life. This number has recently

increased to 15 species, representing barely 2% of the family's diversity (Sendra *et al.* 2023) and rises to 19 including two additional taxa currently in press from North American caves and the two described in this study. Cave-dwelling japygids occur in nearly all regions of the world (Fig. 12) and, like many cave-adapted taxa (Sendra *et al.* 2023), are concentrated in karstic regions, generally avoiding desert and glaciated areas (Fig. 12). These patterns indicate that cave-adapted japygids may be more widespread in subterranean habitats than previously assumed.

Author contributions

Conceptualization: AS, AJV. Data curation: AS, JL, JS, GXP, AJV. Formal analysis: AS, AJV. Investigation & Validation: AS, JL, JS. GXP, AJV. Methodology: AS, AJV. Writing – original draft: AS, AJV Writing – review and editing: AS, JL, JS, GXP, AJV.

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