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New cave japygids (Diplura: Japygidae) from North America

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Abstract. We studied a significant collection of Japygidae (Diplura) deposited in the Texas A&M University Insect Collection, sampled from several caves in North America, mostly in the early 21st century by a group of American speleologists. Among this biological material, a new genus and species, *Quapawjapyx osage* Sendra gen. et sp. nov., is described from four caves in Arkansas, and a new species, *Holjapyx nimiipuu* Sendra sp. nov., from five caves in Idaho; both are named in honor of native American tribes. *Quapawjapyx osage* can be distinguished from *Indjapyx*, *Paurojapyx*, and *Parindjapyx* – which share symmetrical cerci – by the combination of the shape and disposition of the glandular and sensory setae on the first urosternite, together with differences in cercal ornamentation. *Holjapyx nimiipuu* is characterized by the presence of two conspicuously large predental denticles on the right cercus. Both new taxa of cavernicolous japygids show slight cave-adaptation features, such as large body size, slight elongated appendages, and a small increase in the placoid sensilla of last antennomere. These two new taxa double the number of known cave-adapted japygids in North America, a seemingly low figure that is nonetheless comparable to other karst regions worldwide.

Keywords. Japygoidea, cave-adapted fauna, Nearctic region, taxonomy.

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Introduction

Diplura Börner, 1904 have been considered, since Racovitza´s (1907) seminal biological contribution to the study of subterranean ecosystems, as one of the best cave-adapted arthropod groups. In fact, diplurans are among the most represented animal groups in caves, accounting for 16% of the total diversity, with around 1050 known species (Plact 1957; Sendra *et al.* 2020; Deharveng & Bedos 2018). This prominence in subterranean ecosystems is especially notable in the most diverse family, Campodeidae Lubbock, 1873, which includes 154 described species (Condé 1956; Sendra *et al.* 2021a, 2021b, 2021c, 2021d, 2022). In contrast, the other diverse family, Japygidae Haliday, 1864, include only 13 described cave-adapted species. While campodeid species are detritivores, japygid species occupy a higher trophic level, preying on a wide range of small- to medium-sized invertebrates (Sendra *et al.* 2021a; Potapov *et al.* 2022).

Japygids have been present at least since the end of the Mesozoic Era, as evidenced by two fossil species: *Ferrojapyx vivax* Wilson & Martill, 2001, from the Early Cretaceous Crato Formation of Brazil, and *Cretojapyx huangi* Wang, Huang & Cai, 2023, found in Cretaceous Kachin amber (Wilson & Martill 2001; Wang *et al.* 2023). The continuous speciation and dispersal of japygid species have extended across almost all terrestrial habitats on all continents, primarily in tropical and temperate climates, where they are best represented. Currently, 349 species have been described across a broad range, with the remarkable exception of vast frozen soils and deserts (Condé 1956; Sendra *et al.* 2023). Nevertheless, japygids have managed to colonize subterranean habitats in tropical and temperate regions, showing a preference for deep soil layers and cave environments.

We focus our study on the poorly known North American cave-dwelling japygids of the Nearctic region thanks to a small collection of well-preserved specimens mounted on slides in a semi-permanent medium, housed at the Texas A&M University Insect Collection (TAMUIC). In our study, we would like to dedicate the newly described Japygidae taxa as a small gesture in honor of Native American tribes. We believe it is important not to remain silent in the face of the injustices these communities have endured, and to recognize and help preserve their cultural richness and enduring legacy.

Material and methods

A small collection of 22 specimens of dipluran Japygidae already prepared with semipermanent medium in slides were studied. General visualization and photography of and examined and photograph were carried out with a microscope Leica DMS1000 phase-contrast optical, a fluorescence microscope Leica 5000 and a stereo microscope Nikon Eclipse Ni. For scanning electron microscopic (SEM), one specimen was coated with palladium-gold and observed using 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) in the urosternites, we followed the terminology for extant Japygidae proposed by Pagés (1953), and for the setae and macrosetae of the cerci, the terminology of Muegge & Bernard (1990).

Abbreviations for morphological terms

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

A, B, C = A, B, and C rows of urosternal macrosetae
D, L, V = dorsal, lateral, ventral positions of cercal macrosetae
GS = glandular seta
I, L, M, P = rows of macrosetae on dorsal head

la = lateral anterior macrosetae
lp = lateral posterior macrosetae
M = macroseta with four different position (*ma*, *la*, *lp*, *mi, mp*)
M1–5 = 1 to 5 macrosetae on thoracic and abdominal tergites
ma = medial anterior macrosetae (for uroterguites: *ma* = medial anterior seta)
mi = medial intermedia macrosetae
mp = medial posterior macrosetae
ms = microsetae considered as proprioceptors when they are nearby articulations of the body
ms-ist = meso-intersternum
ms-pst = meso-poststernum
ms-st = mesosternum
mt-ist = meta-intersternum
mt-pst = meta-poststernum
mt-st = metasternum
pr-prt = pro-presternum
sl = long seta
sp = spine
pr-prt = pro-presternum
pr-st = prosternum
ps = pseudoespori
sagM = macroseta in sagittal position
SS = sensorial setae
ss = short seta
tr = trichobothrium

Institutional abbreviations

ASPC = Alberto Sendra personal collection
MUVHN = Museu Universitat de València d'Història Natural, València, Spain
TAMUIC = Texas A&M University Insect Collection, USA

Results

Taxonomy

Class Diplura Börner, 1904
Superfamily Japygoidea Ewing, 1942
Family Japygidae Haliday, 1864

Genus ***Quapawjapyx*** Sendra gen. nov.
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Type species

Quapawjapyx osage Sendra gen. et sp. nov.

Diagnosis

Slightly elongate and large body, over 20 mm in large adults. Epicuticle smooth visible under optical microscope. Set of macrosetae (M) in a resemble as the typical pattern in head, thorax and abdomen sclerites and appendages in Japygidae – dorsal head A, S, M, I, L and P macrosetae; 1+1 macrosetae on submentum; 5+5, 6+6 and 5+5 macrosetae on pronotum, mesonotum and metanotum; 7+7, 8+8, 8+8-9+9 macrosetae on pro. meso. and metathoracic sternum; 1+1 *ma* setae and 5+5 macrosetae on most urotergites; 2+2 macrosetae D on urite X; 13+13-15+14 macrosetae on first urosternites with three horizontal rows up to 16+16 macrosetae. Dorsal side of head and antennomeres with micropores on the surface. Lacinia falciform, well sclerotized, with the five laminae pectinate. Antennae with 26 antennomeres. Trichobothria with 2 dorsal / 1 ventral on IV and VI antennomeres, dorsal trichobothria (a) of IV on medial position. Prosternum and interstermun well defined in thorax. Pretarsus with two unequal claws and a sharp medial unguiculus. Lateral urotergites angles V–VIII angles more and more conspicuous with small point on VIII urotergites. Urite X with distinctly marked carinae with subparallel margins slightly converging towards posterior border; acropygium sub-quadrangular with borders slightly rounded. Lateral organ occupying half interstylar area; females with one row of GS, males with 2–3 GS rows, both setae shorter than stylus length. Median glandular organ with a few pseudospori with a microsetae. Median glandular organ with a few pseudospori (microsetae). Male and female genital papillae have typical shape as in Japygidae; male papillae show large and short lateral appendages. Cerci symmetric with two main teeth, Cerci symmetric, with one proximal tooth in cercus *r* (predental/postdental length) 0,5–0,7; right and left cercus with predental margin with two rows of denticles.

Etymology

The generic name is in honor of the Quapaw Nation of Native Americans, who thrived along the lowlands of the Arkansas river five hundred years ago. Today, they live alongside much later European settlers from other nations.

Quapawjapyx osage Sendra gen. et sp. nov.

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Figs 1–9, 19

Diagnosis

Slightly elongate and large body; over 20 mm in larger adults. Dorsal side of the head with abundant micropores mostly between two Y branches; a set of 14+14 M (A1, 3; S2, 4, 6; M2, 3, 5; I1–3, 5; L3 and P1–2). Labial palp 3 × as long as wide; lacinia falciform with five laminae pectinate. Antenna 0.32–0.35 × as long as body, with 26, 28 antennomeres; first and second antennomeres shorter than wide, third and fourth antennomeres slightly longer than wide with tiny reinforced borders; medial and distal antennomeres slight longer than wide. Proximal antennomeres with abundant micropores that disappear in medial and distal antennomeres; apical antennomere with about 8 placoid sensilla uneven distributed. Trichobothria with 2 dorsal/ 1 ventral on IV and VI antennomeres, dorsal trichobothria of IV antennomere overpassing whorl of M. Thoracic segments slightly elongated, pronotum with 1+1 *ma*, 1+1 *la*, 3+3 *lp*1-3; prescutum of mesonotum with 1+1 M; mesonotum with 1+1 *ma*, 1+1 *la*, 1+1 *mp*, 3+3 *lp*1-3; prescutum of metanotum with 1+1 M, scutum of the metanotum with 1+1 *ma*, 1+1 *la*, 1+1 *mp*, 3+3 *lp*1–3. Propresternum with 1+1 M; prosternum with 3+3 *la*, 2+2 *ma* and *mp* and 2+2 *lp*; meso-poststernum with 4+4 M; meso-intersternum with 2+2 M; mesosternum with 3+3 *la*, 3+3 *ma*, *mi* and *mp* plus one sagM intermediate and 2+2 *lp*; metapoststernum with 3+3 M; meta-intersternum with 2+2 M; metasternum with 4+4–3+3 *la*, 3+3 *ma*, *mi* and *mp* and one single sagM, and 2+2 *lp*. Legs slightly long, hind leg reaching posterior border of third abdominal segment. Pretarsus with two unequal claws (1.2–1.3 anterior to posterior claw) and sharp medial unguiculus. Urotergite I with 1+1 M, scutum with 1+1 M5; urotergite II–VII with 1+1 *ma* setae, 5+5 M1–5 and two additional M; urotergite VIII with 3+3 M2,4–5 and one additional M; urite IX without M on dorsal position 8+8; urite X 1.1–1.3 × as long as wide, with distinctly marked carinae slightly converging towards posterior border; dorsal side with 2+2 D1 and D4 intracarinal; acropygium sub-quadrangular with borders slightly rounded; lateral side with 3–4+3–4 L; ventral side with 10+10 M setae arranged in 3+3 rows from right lateral side to left lateral side. Lateral urotergites I–IV with blunt, slightly rounded posterolateral angles; from urotergites V–VIII angles more and more conspicuous with small point on VIII urotergites. Prescutum of urosternite I with 3+3 M; scutum with 13+13–14+15 M and posterior field of short slightly thicker setae preceding each lateral subcoxal organ. Urosternites II–III with 15–16+15–16 M arrange in three horizontal rows A–C; urosternite VIII with about 7+7 M between two well-defined carinae plus 3+3 M on lateral side of carinae; ventral side of abdominal segment IX with 3+3–4 M. Median glandular organ with 4–9 pseudospori with microsetae. Lateral subcoxal organ, with one row of 52–54 GS and one row of 35–38 SS, organ occupying 0.58 × of interstylar area; GS/st1 (stylus of first urosternite) = 0.33; SS/st1 = 0.22, each organ with 2–3 rows of 124 GS and one row of 26 SS, organ occupying 0.58 × of interstylar area; GS/st1 (stylus of first urosternite) = 0.25; SS/st1= 0.15. In addition to these glandular organs, only males showing impair of central glandular organ located in anterior position of third urosternite constituted by open narrow channel surrounding by long barbed setae. Male and female genital papillae with typical shape as in Japygidae. Cerci symmetric, 0.08–0.1 × as long as body, with one proximal tooth in cercus r (predental length/postdental length) = 0,5–0,7. Right cercus with proximal pointed tooth; predental margin with two rows of 6+5 round denticles, postdental crenelated margin by one row of 25–30 round denticles. Left cercus with proximal tooth; predental margin with two rows of 5+5 round denticles; postdental margin with two crenelated rows of tiny scale shape denticles.

Etymology

The specific epithet is in honor of the Osage Nation of Native Americans, who now reside in Osage County, Oklahoma. They arrived and thrived a few hundred years ago in the northern mountains of Arkansas.

Type material

Holotype

USA – **Arkansas** • ♀; Marion County, Dogman Cave; 26 Jul. 2002; M.E. Slay leg.; TAMUIC, TAMU-ENTO X1831147.

Paratypes

USA – **Arkansas** • 1 ♂; Newton County, Filton cave; 13 Dec. 2004; M.E. Slay, C. Bitting, G.O. Groening and D. Fenolio leg.; TAMUIC, TAMU-ENTO X1832015 • 1 ♂; Newton County, Pretty Clean cave; 7 Jul. 2001; M.E. Slay and C. Bitting leg.; MUVHN, MUVHN-ZE8000 • 1 ♂; Newton County, Toney Bend Mine#2; 27 May 2004; M.E. Slay and C. Bitting leg.; ASPC.

Description

Body. Slightly elongate and large body; length 13–22 mm in adults; maximum width at urotergite II 2.2 mm (Fig. 1A). Epicuticle smooth visible under optical microscope. Cuticle unpigmented, with sclerotized areas on mandible tips, claws, abdominal stylus ending, lateral apodemes of abdominal segments VII–X and cerci; and femoral, tibial and mostly cercal condyles. Body and appendages covered with normal setae (s), short setae (ss), long setae (ls) and microsetae (ms) mostly acting as proprioceptors in some body parts articulations, in addition to set of macrosetae (M) with typical pattern in head, thoracic and abdominal sclerites and appendages in Japygidae. Dorsal side of head and antennomeres with micropores on surface (Fig. 1D).

Head. Dorsal side with slightly sclerotized area between two branches of Y ecdysial line: few ms; with abundant micropores mostly between two Y branches; and 14+14 M: A1, 3; S2, 4, 6; M2, 3, 5; I1–3, 5; L3 and P1–2 (♂, paratype TAMU-ENTO X1832015) (Fig. 2A). On ventral side submentum with 1+1 M in posterior position; admentum with 3+3 M; mentum at base of labial palps with 4+4 M; external lobes of mentum with abundant thick setae. Labial palp 3 × as long as wide, with two apical M, one subapical M, one medial M and one proximal M and several sl. Labrum short with abundant short thick setae.

Lacinia falciform, well sclerotized, with five laminae pectinate (Fig. 1C). Mandible with four distensible teeth and one tiny tooth in interior position (Fig. 1C).

Antennae. Antenna 0.32–0.35 × as long as body, with 26 antennomeres and 28 antennomeres of left antennae in ♀ holotype; first and second antennomeres shorter than wide, third and fourth antennomeres slightly longer than wide with tiny reinforced borders; medial and distal antennomeres slight longer than wide. Proximal antennomeres with abundant micropores mostly on dorsal side (Fig. 1D), in addition to ms, ss, ls and one whorl of M; micropores disappear in medial and distal antennomeres; apical antennomere including additional whorl of M and about 8 placoid sensilla uneven distributed (Fig. 1B). Trichobothria with 2 dorsal / 1 ventral on IV and VI antennomeres, dorsal trichobothria of IV antennomere overpassing whorl of M.

Thorax. Thoracic segments slightly elongated, with few ls, ss and typical pattern of M: pronotum with 5+5 M (1+1 *ma*, 1+1 *la*, 3+3 lp_{1-3}) (Fig. 2B); prescutum of mesonotum with 1+1 M; mesonotum with 6+6 M (1+1 *ma*, 1+1 *la*, 1+1 *mp*, 3+3 lp_{1-3}) (Fig. 2C); prescutum of metanotum with 1+1 M, scutum of the metanotum with 5+5 M (1+1 *ma*, 1+1 *la*, 1+1 *mp*, 3+3 $lp_{1–3}$) (Fig. 3A). Thoracic sternites, intersternites, and presternites well defined with few ss, sl, and several M; border of leg articulations with ms (Fig. 2D). Pro-presternites and pro-, meso- and metasternites with internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); only in propresternites prolongation of posterior branch (spine) is visible on surface (Denis 1949); propresternum with 1+1 M; prosternum with 3+3 *la*, 2+2 *ma* and *mp* and 2+2 *lp*; meso-poststernum with 4+4 M; meso-intersternum with 2+2 M; mesosternum with 3+3 *la*, 3+3 *ma*, *mi* and *mp* and one sagM intermediate and 2+2 *la*; meta-poststernum with 3+3 M; meta-intersternum with 2+2 M; metasternum with 4+4–3+3 *la*, 3+3 *ma*, *mi* and *mi* and one single sagM, and 2+2 *lp* (Fig. 2D). Legs slightly long, hind leg reaching posterior border of third abdominal segment. Femur with 7–8 M; tibia with 4–7 M and calcars at ventral apex thicker very lightly than M; tarsus with 7–10 dorsal M and two ventral rows of 10–14 thick setae. Pretarsus with two unequal claws (1.2–1.3 anterior to posterior claw) and sharp medial unguiculus (Fig. 1E).

Abdomen. Abdominal tergites with scarce s and sM. Prescutum of urotergite I with 1+1 M, scutum with 1+1 M5 (Fig. 3B); urotergite II–VII with 1+1 *ma* setae, 5+5 M1–5 and two additional M (Fig. 3C); tergite VIII with 3+3 M2,4–5 and one additional M (Fig. 3D); urite IX without M on dorsal position 8+8. Urite X (Fig. 3E) 1.1–1.3 × as long as wide, with distinctly marked carinae; carinae with subparallel margins slightly converging towards posterior border; dorsal side with 2+2 M (D1 and D4) intracarinal (Fig. 3E), acropygium sub-quadrangular with borders slightly rounded (Fig. 3E); lateral side with 3–4+3–4 M (L) (Fig. 3E); ventral side with 10+10 M setae arranged in 3+3 rows from right lateral side to left lateral side (Fig. 5C). Lateral urotergites I–IV with blunt, slightly rounded posterolateral angles; from urotergites V–VIII angles more and more conspicuous with small point on VIII urotergites (Fig. 4A–C). Urosternites with scarce ms and ss. Prescutum of urosternite I with 3+3 M; scutum with 13+13–14+15 M and posterior field of short slightly thicker setae preceding each lateral subcoxal organ (45–90 setae each). Urosternites II–III with 15–16+15–16 M arrange in three horizontal rows A–C (Fig. 5A); urosternite VIII with about 7+7 M between two well-defined carinae plus 3+3 M on lateral side of carinae (Fig. 5B); ventral side of abdominal segment IX with 3+3–4 M. Median glandular organ with 4–9 pseudospori with microsetae, more abundant in females (Fig. 6C) than in males (Fig. 6F). Lateral subcoxal organ, in holotype each organ with one row of 52–54 GS and one row of 35–38 SS, organ occupying 0.58 × of interstylar area; GS/st1 (stylus of first urosternite) = 0.33; SS/st1 = 0.22 (Fig. 6A–B; ♂, paratype TAMU-ENTO X1832015), each organ occupying 0.58 of the interstylar area have 2–3 rows of 124 GS and one row of 26 SS; GS/st1 (stylus of first urosternite) = 0.25; SS/st1= 0.15 (Fig. 6D–E). In addition to these glandular organs, only males showing impair of central glandular organ located in anterior position of third urosternite constituted by open narrow channel surrounding by long barbed setae (Fig. 7B). Male and female genital papillae with typical shape as in Japygidae; male papillae show large and short lateral

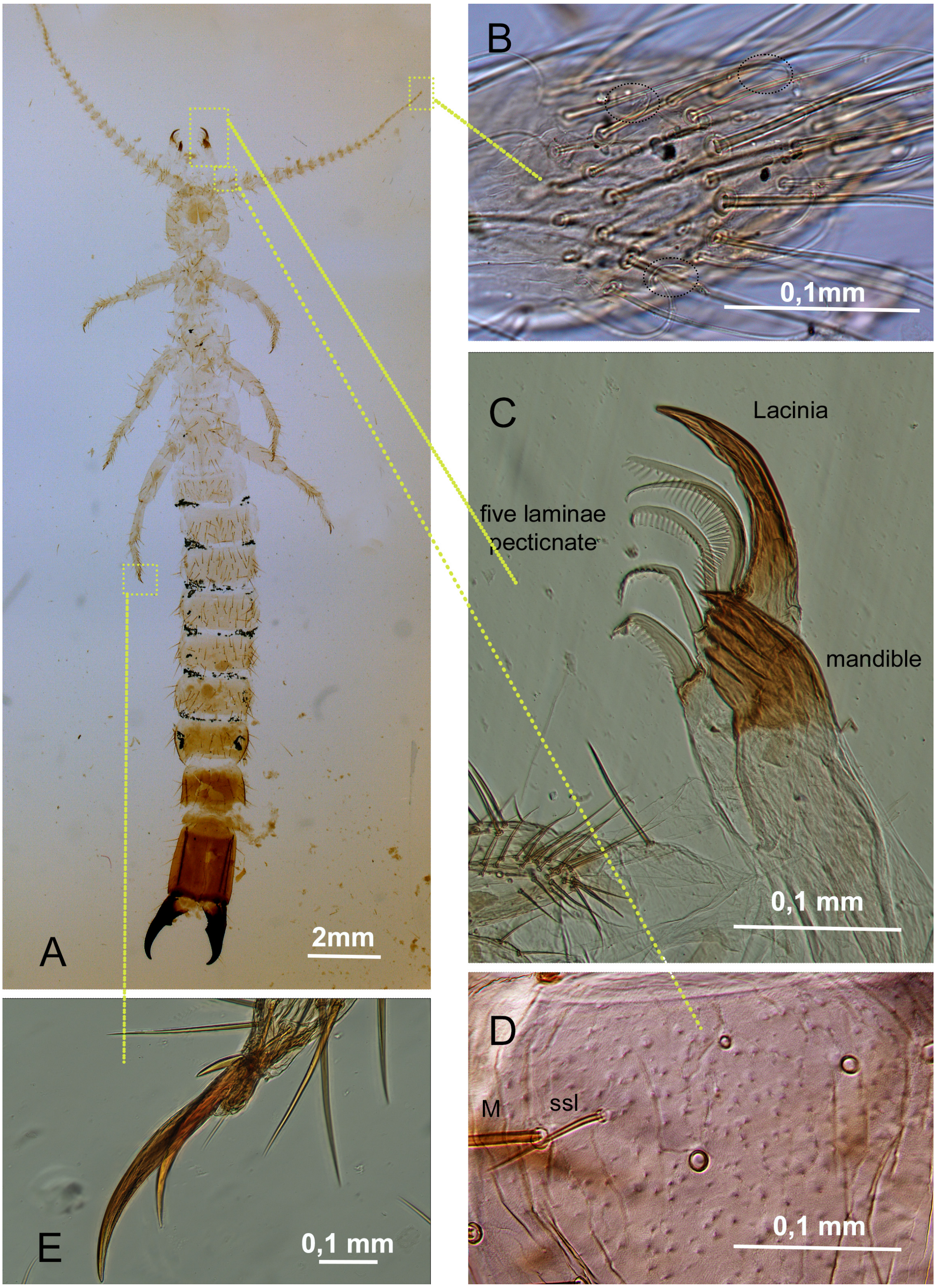

Fig. 1. *Quapawjapyx osage* Sendra gen. et sp. nov. **A**. Paratype, ♂ (TAMU-ENTO X1831026). **B, D–E**. Paratype, ♂ (TAMU-ENTO X1832015). **C**. Holotype, ♀ (TAMU-ENTO X1831147). **A**. Habitus. **B**. Last antennomere; placoid sensilla remarked by spotted line. **C**. Lacinia with interior laminae and mandible. **D**. Dorsal portion on third antennomere with pores. **E**. Metathoracic claws. Abbreviations: see Material and methods.

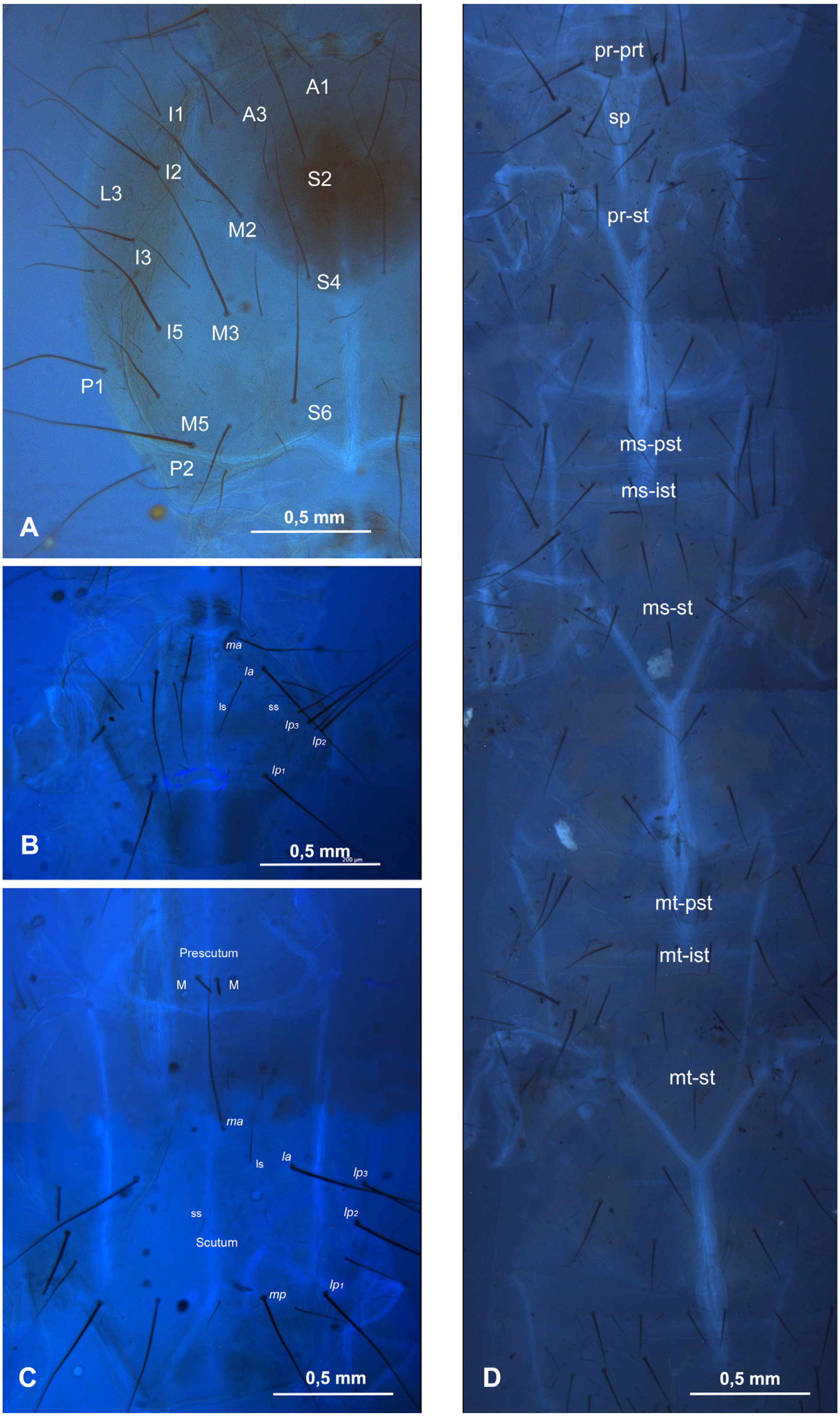

Fig. 2. *Quapawjapyx osage* Sendra gen. et sp. nov. **A**–**C**. Paratype, ♂ (TAMU-ENTO X1832015). **D**. Paratype, ♂ (MUVHN-ZE8000). **A**. Head, dorsal view. **B**. Pronotum. **C**. Mesonotum. **D**. Prothorax, mesothorax and metathorax sternites. Abbreviations: see Material and methods.

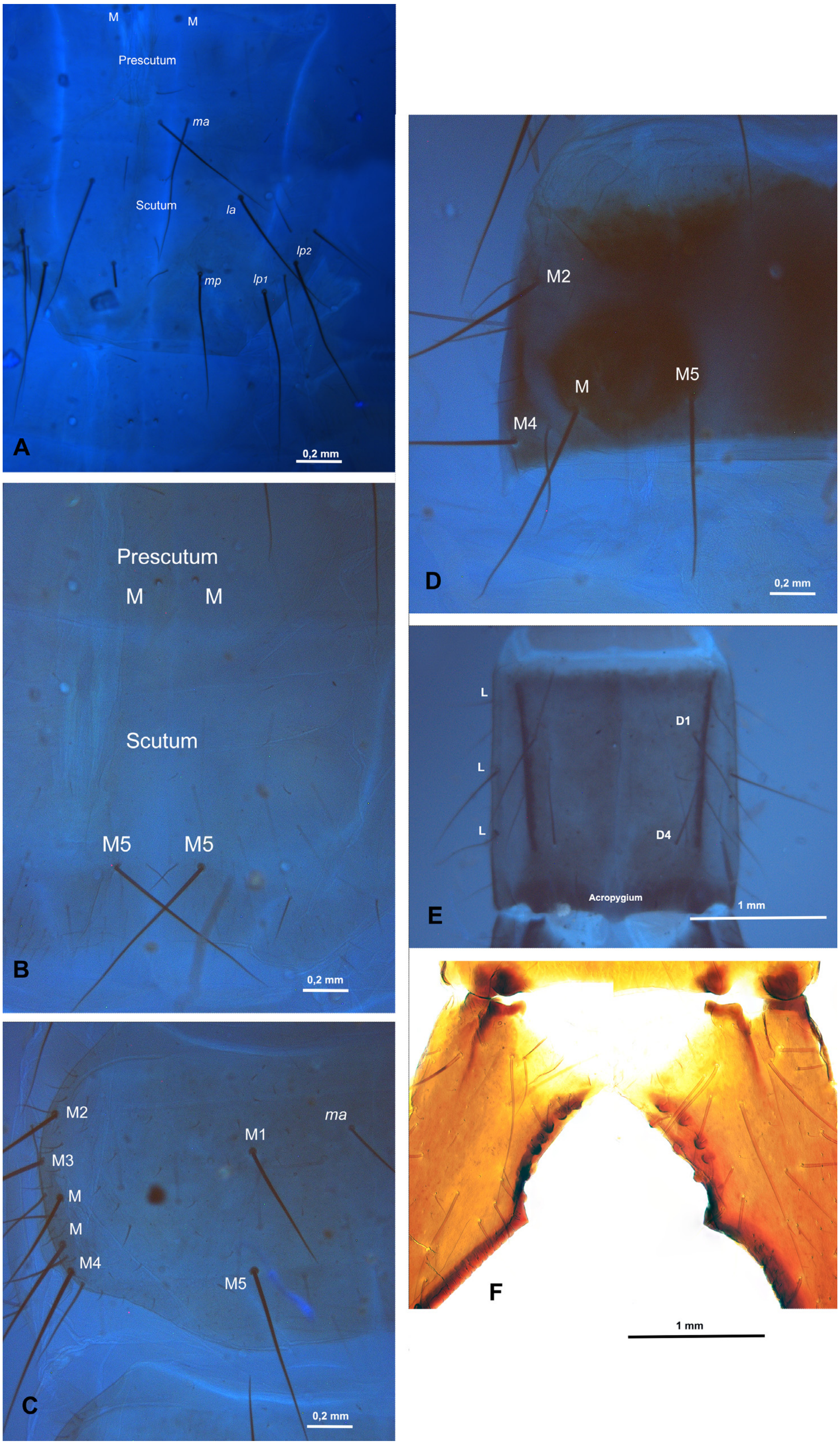

Fig. 3. *Quapawjapyx osage* Sendra gen. et sp. nov. **A–D, F**. Paratype, ♂ (TAMU-ENTO X1832015). **E**. Paratype, ♂ (MUVHN-ZE8000). **A**. Metanotum. **B**. First urotergite. **C**. Fifth urotergite. **D**. Eighth urotergite. **E**. Urite X, dorsal view. **F**. Cerci, proximal portion. Abbreviations: see Material and methods.

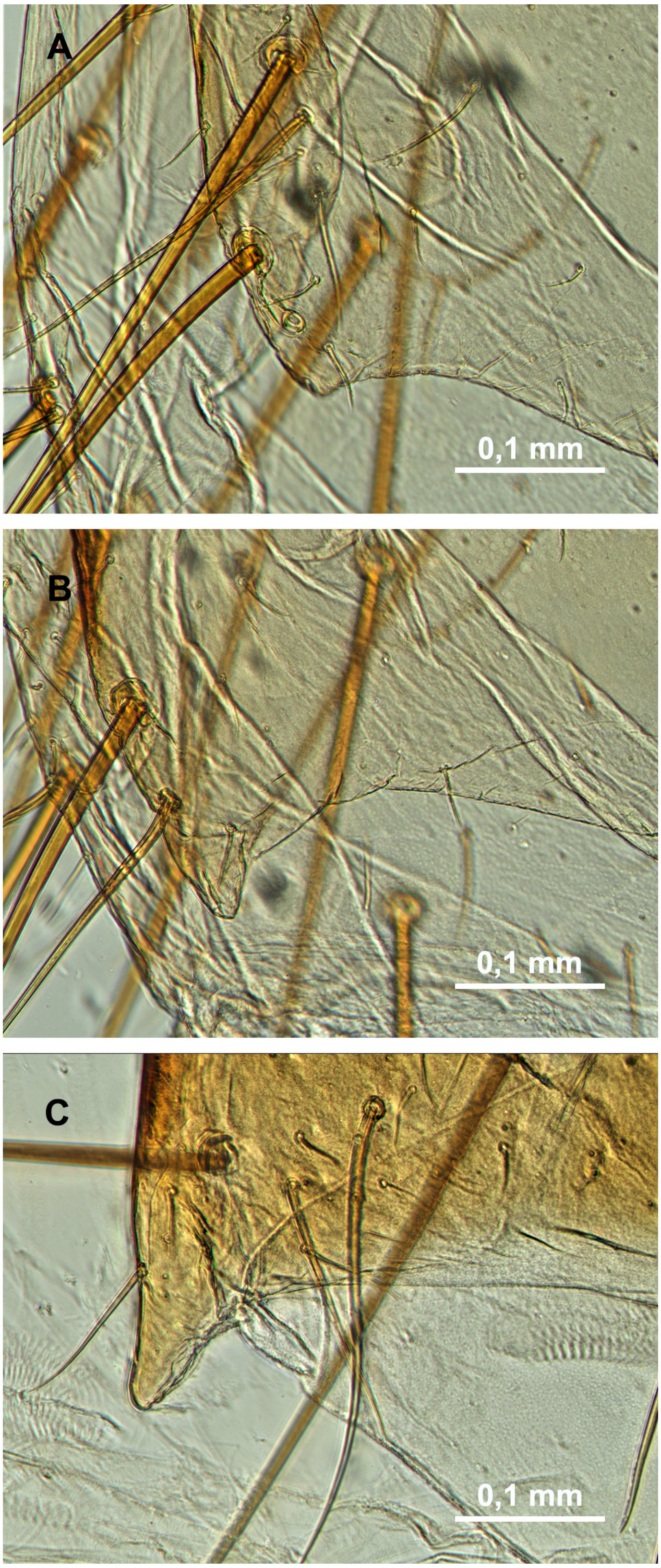

Fig. 4. *Quapawjapyx osage* Sendra gen. et sp. nov., paratype, ♂ (TAMU-ENTO X1832015). **A**. Posterolateral angle of sixth urotergite. **B**. Posterolateral angle of seventh urotergite. **C**. Posterolateral angle of eighth urotergite.

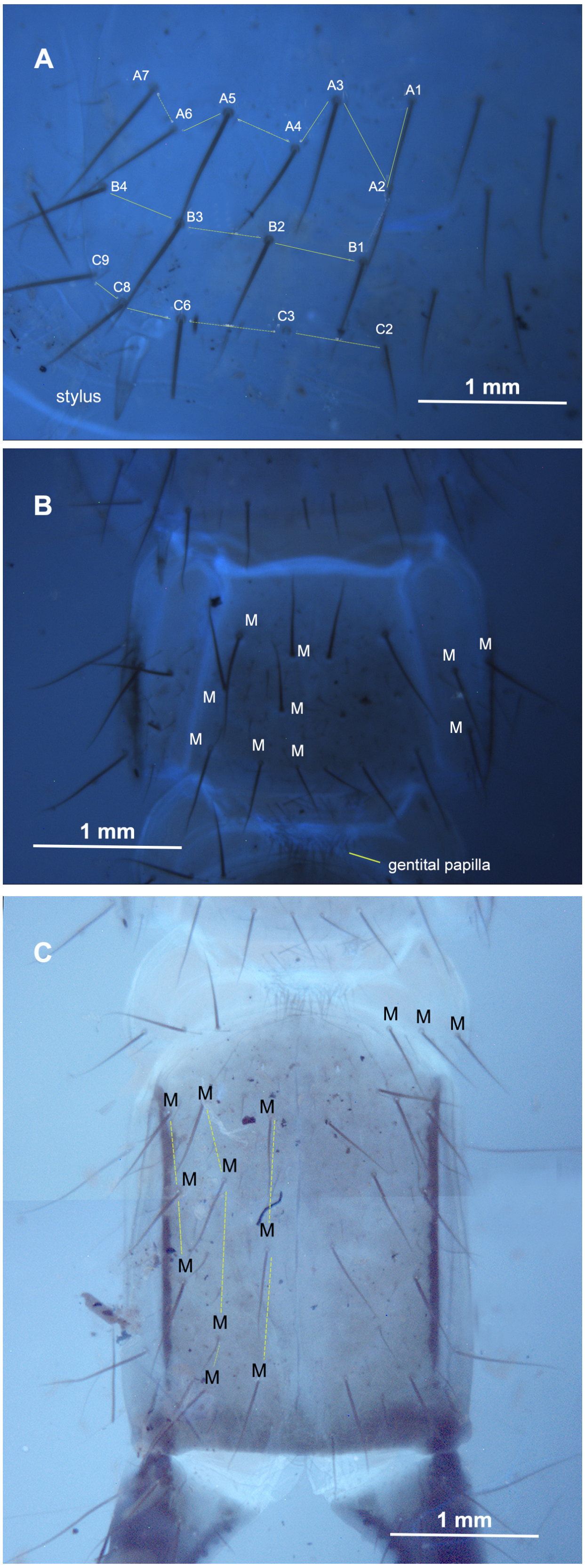

Fig. 5. *Quapawjapyx osage* Sendra gen. et sp. nov. **A**–**C**. Paratype, ♂ (MUVHN-ZE8000). **A**. Fifth urosternite. **B**. Eighth urosternite. **C**. Urite X, ventral view. Abbreviations: see Material and methods.

appendages bearing ss and numerous sl (Fig. 7A). Cerci symmetric, length 1.1–1.9 mm (0.08–0.1 × as long as body), with one proximal tooth in cercus r (predental length / postdental length) = 0,5–0,7. External shape of cerci straight in proximal half and curved in distal half, becoming hook towards apex; heavily sclerotized with dorsal and ventral outer carinae arising from dorsal and ventral acetabular articulations (Fig. 3E–F). Right cercus dorsally concave and with distal ends upward, less evident in left cercus (Fig. 8A). Teeth almost symmetrical. Right cercus with proximal pointed tooth; predental

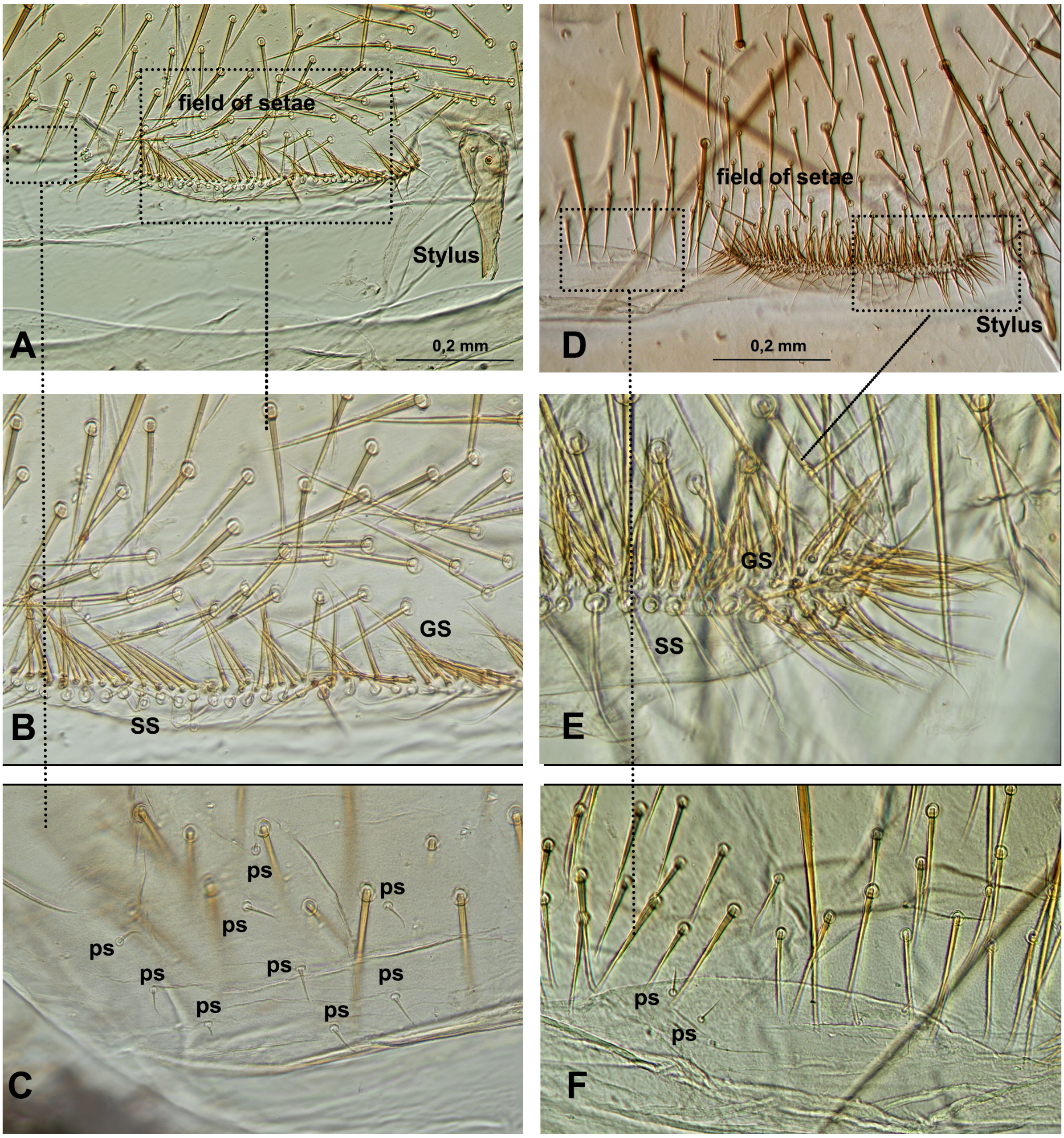

Fig 6. *Quapawjapyx osage* Sendra gen. et sp. nov. **A–C**. Holotype, ♀ (TAMU-ENTO X1831147). **D–F**. Paratype, ♂ (TAMU-ENTO X1832015). **A**. Latero-posterior border of the first urosternite. **B**. Detail of lateral organ. **C**. Central organ of the first urosternite. **D**. Latero-posterior border of the first urosternite. **E**. Detail of lateral organ. **F**. Central organ of the first urosternite. Abbreviations: see Material and methods.

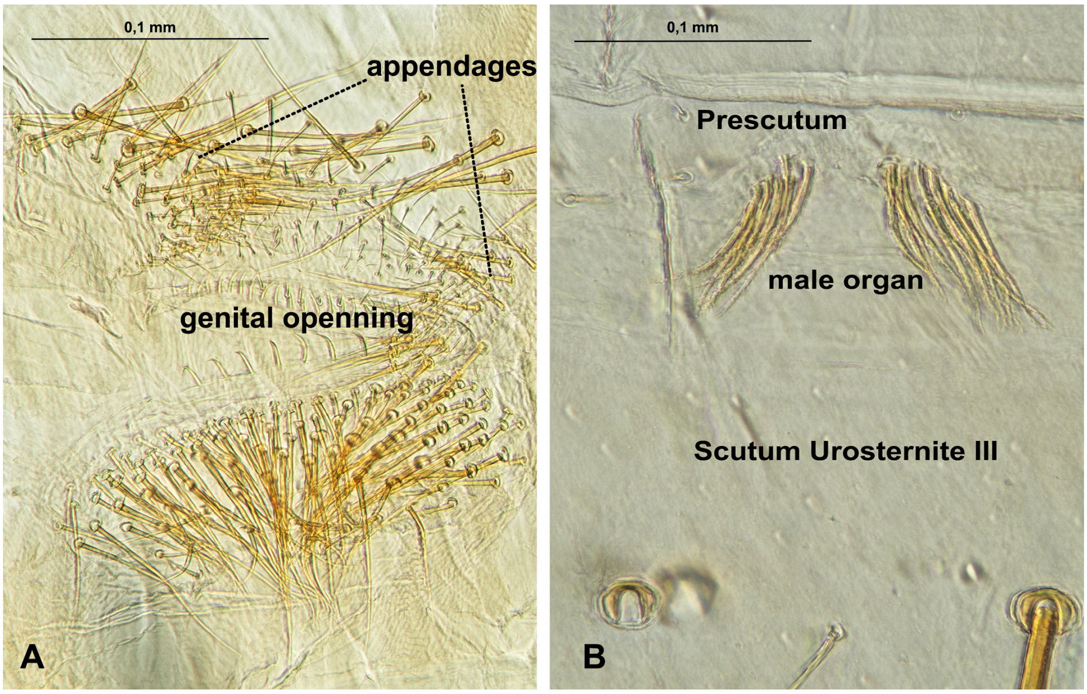

Fig 7. *Quapawjapyx osage* Sendra gen. et sp. nov., paratype, ♂ (TAMU-ENTO X1832015). **A**. Genital papillae. **B**. Central organ of third urosternite.

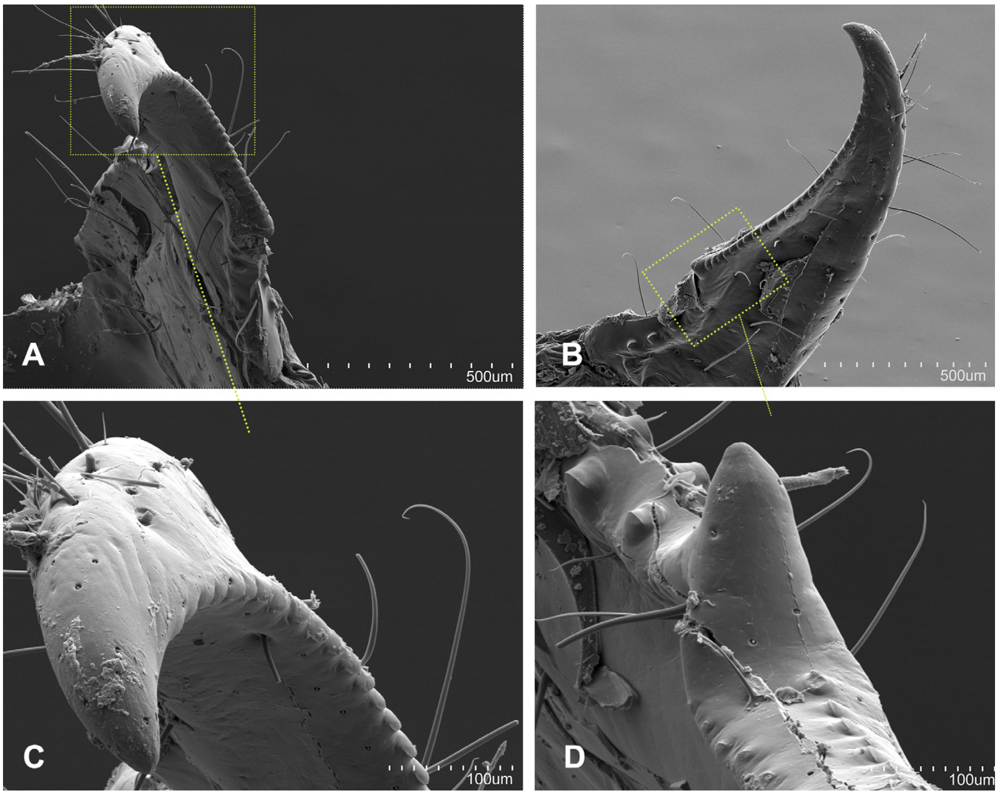

Fig. 8. *Quapawjapyx osage* Sendra gen. et sp. nov., ♀ (ASPC), cerci under electron scanning microscope. **A**. Right cercus latero-interior view. **B**. Left cercus, dorsal view. **C**. Detail distal portion of right cercus, view of postdental margin. **D**. Left cercus central portion of interior margin.

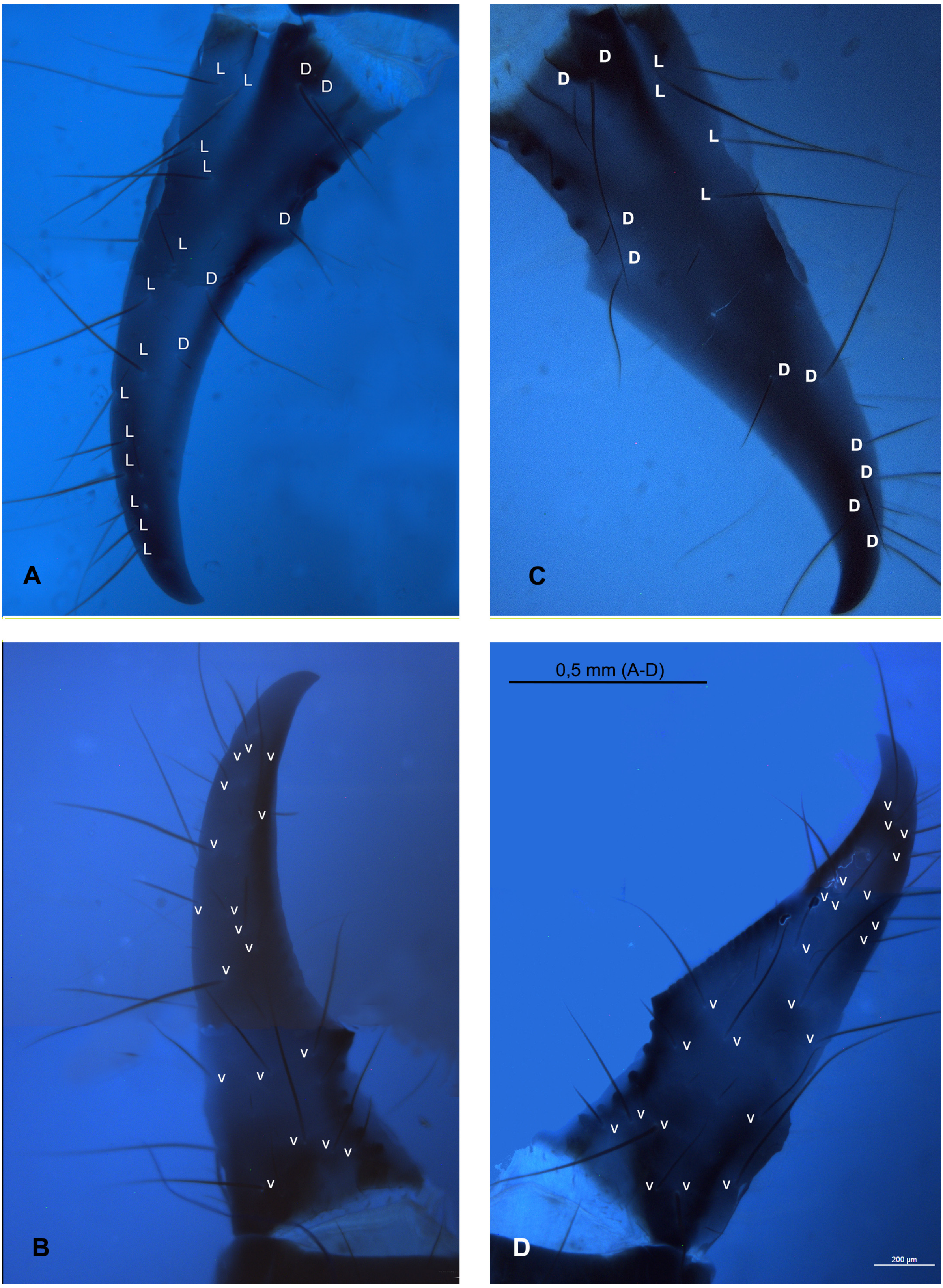

Fig. 9. *Quapawjapyx osage* Sendra gen. et sp. nov. **A**–**D**. Paratype, ♀ (TAMU-ENTO X1832015). **A**. Left cercus, dorsal view. **B**. Right cercus, dorsal view. **C**. Left cercus, ventral view. **D**. Right cercus, ventral view. Abbreviations: see Material and methods.

margin with two rows of 6+5 round denticles (Fig. 3F), postdeltal crenelated margin by one row of 25–30 round denticles (Fig. 8A, C). Left cercus with proximal tooth, less conspicuous than right one; predental margin with two rows of 5+5 round denticles; postdental margin with two crenelated rows of tiny scale shape denticles (Fig. 8B, D). Right cercus with 16 dorsal M and 14 ventral M position; left cercus with 12 dorsal M and 6 ventral M position (Fig. 9A–D). Campaniform sensilla present on hook and inner margins of cerci (Fig. 8C–D).

Taxonomic affinities of the genus and species

The species of Japygidae started to be described in the second half of the 19th century and the beginning of the 20th (Cook 1899; Grassi 1886, 1889; Haliday 1864; Péringuey 1901; Verhoeff 1904, 1923; Westwood 1842), including for North American caves (Packard 1874). Nevertheless, roughly speaking, it is not until Filipo Silvestri's contributions that the taxonomy of the family started to be worked out more comprehensively – see for instance Silvestri (1928, 1929a, 1929b, 1930a, 1934, 1948a, 1948b, 1948c, 1948d). Yet, only a few taxonomic characters have been used for the classification of genera and species within the family. These include the cercal ornamentation, the presence of lateral and central glands on the first urosternite, and the number of pectinate laminae on the lacinia, among a few others. Nonetheless, Juraj Paclt (1957) paid special attention to the morphology of the cerci as a primary criterion of classification, which led him to reduce the number of genera – most of them originally described by Silvestri (1949) – from 42 to 23. In contrast, and in later years, Jean Pagés (1995) downplayed Paclt's criteria, which he considered overly simplistic. Instead, he emphasized chaetotaxy features such as the arrangement of macrosetae, sensorial and glandular setae, and so reinstated several of the former genera, and proposed new ones (Pagés 1953, 1955, 1980, 1981, 1993, 1994, 1995, 2000).

If we followed Paclt's (1957) criterion, the specimens studied from caves in Arkansas (North America) would have led us to propose the new species within the genus *Indjapyx* Silvestri, 1930, which includes 32 species widely distributed across tropical and subtropical regions from Oriental Asia to the Pacific Islands (i.e., Silvestri 1930b, 1948d; Pagés 1995, 1978, 2002). However, we have considered additional chaetotaxy characters, such as the glandular setae of the lateral and central organs and certain ornamentation on the cerci, to propose a new taxon at the genus level: *Quapawjapyx* Sendra gen. nov.

Quapawjapyx Sendra gen. nov. shares a notable similarity in cercal morphology with *Indjapyx*: species of both genera have subsymmetrical cerci, each bearing a main tooth and two rows of predental tubercles along the inner margin (Silvestri 1930b; Pagés 1978, 1994). This general cercal structure is also shared by eighth other genera within the Japygidae: *Abjapyx* Silvestri, 1949, *Catajapyx* Silvestri, 1933, *Imazighenjapyx* Sendra & Sánchez-García, 2023, *Isojapyx* Silvestri, 1948, *Japyx* Haliday, 1864, *Monojapyx* Paclt, 1957, *Parindjapyx* Silvestri, 1933, and *Pauperojapyx* Pagés, 1995 (Silvestri 1933a; Silvestri 1948d, 1948e; Paclt 1957; Pagés 1995; Sendra *et al.* 2023). However, only four of these genera (*Imazighenjapyx*, *Indjapyx*, *Paurojapyx*, and *Parindjapyx*) share with *Quapawjapyx* two additional key taxonomic characters: a pectinate first lamina of the maxillae, and the presence of pseudosporis (glandular micro-pores, with or without microsetae) in the median glandular organ of the first urosternite. Nevertheless, each of these genera is characterized by several distinctive features that clearly differentiate them from one another.

On the one hand, *Imazighenjapapyx* is characterized by an unusual high number of macrosetae on the thoracic sternal sclerites (e.g., prosternum with 72 M, mesosternum with 84 M and metasternum 89 M) (Sendra *et al.* 2023). In contrast, *Quapawjapyx* Sendra gen. nov. presents much lower counts: prosternum with 16 M, mesosternum with 17 M and metasternum with up to18 M. On the other hand, *Indjapyx*, *Paurojapyx*, and *Parindjapyx* possess lateral organs on the first urosterntite bearing few GS setae, generally about a dozen, usually similar in size to or longer than the adjacent styli (GS/st1 about 1) (Silvestri 1930b, 1933a; Pagés 1995). This condition is markedly different in *Quapawjapyx,* which exhibits up to 3 rows with as many as 128 GS, all distinctly shorter than the nearby styli. Additionally, the cerci of *Quapawjapyx* have a very proximal tooth (r = 0,5–0,7), clearly separated from the central tooth, unlike in *Indjapyx*, *Paurojapyx*, and *Parindjapyx,* where the ratio is higher (*r* around 0.8–1.3) (Silvestri 1930b, 1933a; Pagés 1995). All these distinguishing features support the recognition of *Quapawjapyx* and characterize its sole species, *Q. osage* Sendra gen. et spec. nov.

Quapawjapyx osage Sendra gen. et spec. nov. shows moderate cave-adapted features (Pages 1964; Sendra *et al.* 2023), starting with its slender body, particularly in the thoracic segments, and a relatively large overall body size of 13–22 mm in adults. The last antennomere bears 8 placoid sensillae; the labial palp is 3 × as long as wide; and the hind leg reaches the posterior border of the third abdominal segment.

Genus *Holjapyx* Silvestri, 1948

Holjapyx nimiipuu Sendra sp. nov.

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Figs 10–19

Diagnosis

Slightly elongate body, length 18–20 mm in adults. Epicuticle smooth visible under optical microscope with cuticle unpigmented, with small sclerotized areas. Dorsal head side about 9+9 M (A1, 4; S1, 4, 6; M2, 3, 5; I2–3, 5, P2). Submentum with 1+1 M, admentum with 3+3 M; mentum with 1+1 M. Labial palp 3.3 × as long as wide. Lacinia falciform with the five laminae pectinate; besides third lamina pectinate insertion there are two thin spines. Antenna 0.37 × as long as body, with 30 antennomeres; last antennomere with more than 10 placoid sensilla unevenly distributed. Thoracic segments slightly elongated; scutum of pronotum, mesonotum and metanotum with 5+5 M; prescutum of mesonotum and metanotum with 1+1 M; propresternum with 1+1 M; prosternum with 3+3 *la*, 2+2 *ma* and *mp*, one short sagM intermediate and 3+3 *lp* M; meso-poststernum with 5+5 M; meso-intersternum with 3+3 M; mesosternum with 3+3 *la*, 2+2 *ma* and two sagM intermediate and 8+8 *lp*; meta-poststernum with 5+5 M; meta-intersternum with 3+3 M; metasternum with 3+3 *la*, 2+2 *ma* and *mp* and two sagM. Hind leg reaching the posterior border of fifth abdominal segment. Prescutum of urotergite I with 1+1 M, scutum without macrosetae; urotergites II–V with 1+1 *ma* setae, 5+5 M1–5 and one additional M; urotergites VI–VII with 1+1 *ma*, 5+5 M1–5 and two additional M; urotergite VIII with 1+1 *ma*, 4+4 M1–2,4–5. Urite X 1.6–1.7× as long as wide, with distinctly marked subparallel carinae converging towards posterior border; dorsal side with M (D1–2, 4) intracarinal, acropygium sub-quadrangular with borders slightly rounded; lateral side with 3+3 M (L); ventral side with 10+10 M setae arranged in 3+3 rows from right lateral side to left lateral side each with 5+5 M. Lateral urotergites I–VII with blunt, slightly rounded posterolateral angles; urotergites VIII with an apparent lateral angle. Prescutum of urosternite I with 4+4 M; scutum with 13+13 M arranged in three rows (A–C) and posterior field of short slightly thicker setae preceding each lateral subcoxal organ. Urosternites II–III with 16–16+17–17 M arranged in three horizontal rows; urosternite VIII with central portion with 5+1+5 M and one sagittal M, lateral sides separated by well-defined carinae, with 4+4 M (A and B); ventral side of abdominal segment IX with 3+3 M. Median glandular organ with 4–6 pseudospori with microsetae. Lateral subcoxal organ in females each organ with two rows of about 110 GS and one row of about 50 SS, organ occupying 0.60 × of interstylar area, being their setae relatively short with GS/st1; in males each organ with three rows of about 220 SG and one row of about 12 SS, organ occupying 0.64 × of interstylar area, being their setae relatively shorter than female. In males an impair of central glandular organ in the anterior position of the third and fourth urosternites. Cerci asymmetric, strong, 0.08–0.1 × as long as body; right cercus with medial pointed tooth; predental margin with two large pointed denticles, postdental margin crenelles by 9–10 tiny denticles. Left cercus with distal tooth, less conspicuous than right one; predental margin with two rows of 11 dorsal denticles and 7 ventral denticles, one of them larger than others; postdental margin smooth.

Etymology

'Nimiipuu' ('we, the people') is the name by which the Nez Perce Native American tribe refers to themselves. They have thrived in the Pacific Northwest of North-America for more than ten thousand years and today live primarily on their tribal reservation in Idaho. We dedicate this new species to the Nimiipuu people and to their enduring struggle for survival.

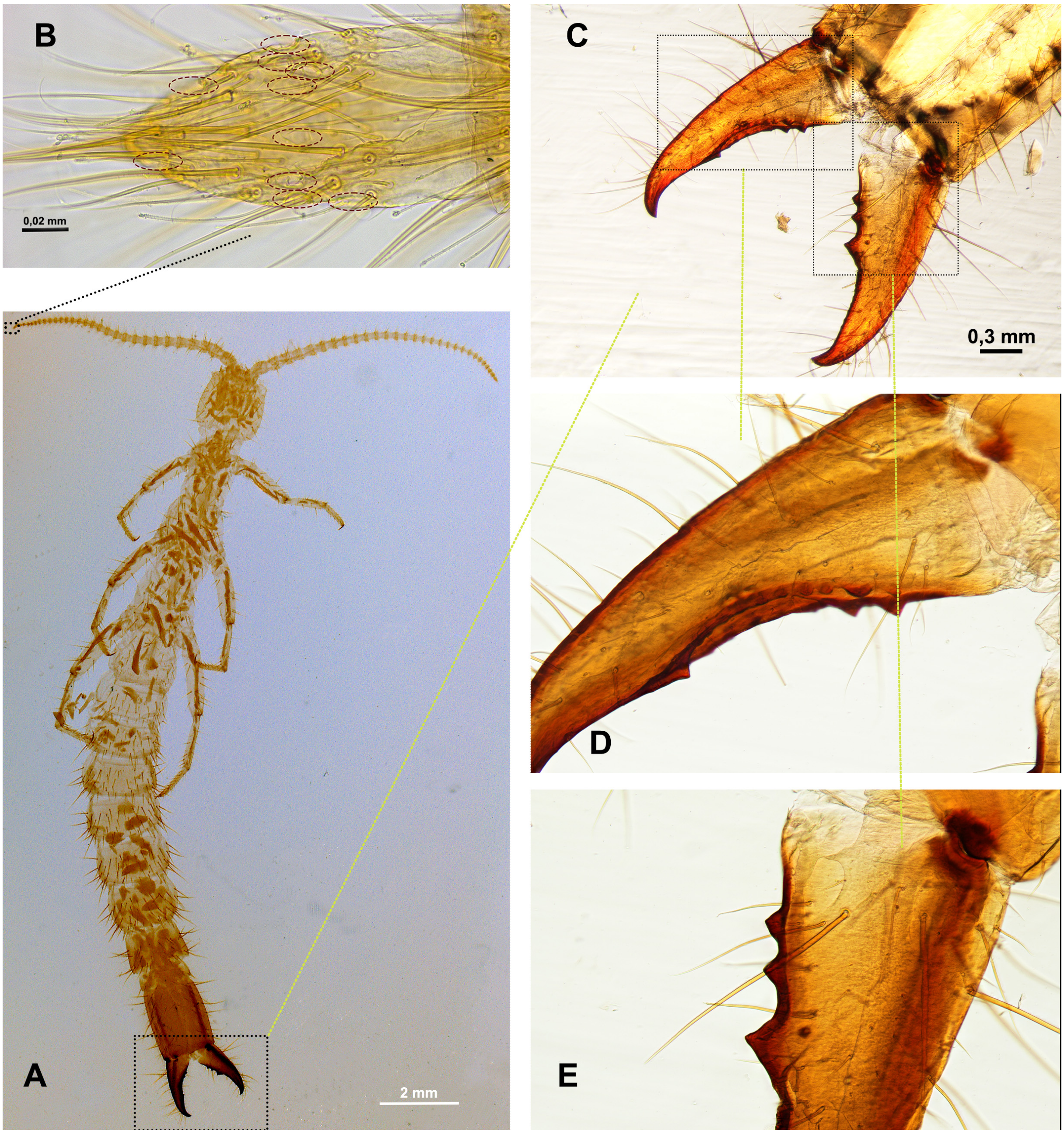

Fig. 10. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. Habitus. **B**. Last antennomere. **C**. Distal portion of urite X including cerci. **D**. Left cercus. **E**. Right cercus; placoid sensilla remarked by dash line.

Type material

Holotype

USA – **Idaho** • ♀; Lincoln County, Little Arch Cav.; 16 Jul. 1999; D. Hubbard Jr leg.; TAMUIC, TAMU-ENTO X1831140.

Paratypes

USA – **Idaho** • 1 ♀; Blaine County, Chalk Cave; 11 Jul. 2000; D. Hubbard Jr leg.; MUVHN, MUVHN-ZE8001 • 1 ♂; Blaine County, Wagon Butte Cave; 13 Jul. 2000; D. Hubbard Jr leg.; TAMUIC, TAMU-ENTO X1856622 • 2 incomplete specs; Government Cave, Blaine County; 16 Jul. 2000; D. Hubbard Jr leg.; TAMUIC, TAMU-ENTO X1856559,TAMU-ENTO X1835908.

Other material examined

USA – **Idaho** • 1 incomplete ♂; Lincoln County, Tee Cave; 12 July 2000; D. Hubbard Jr leg.; ASPC.

Description

Body. Slightly elongate body, length 18–20 mm in adults; maximum width at urotergite IV 1.8 mm (Figs 10A, 11A). Epicuticle smooth visible under optical microscope. Cuticle unpigmented, with sclerotized areas on mandible tips, claws, abdominal stylus ending, lateral apodemes of abdominal segments VII–X and cerci; and femoral, tibial and mostly cercal condyles. Body and appendages covered

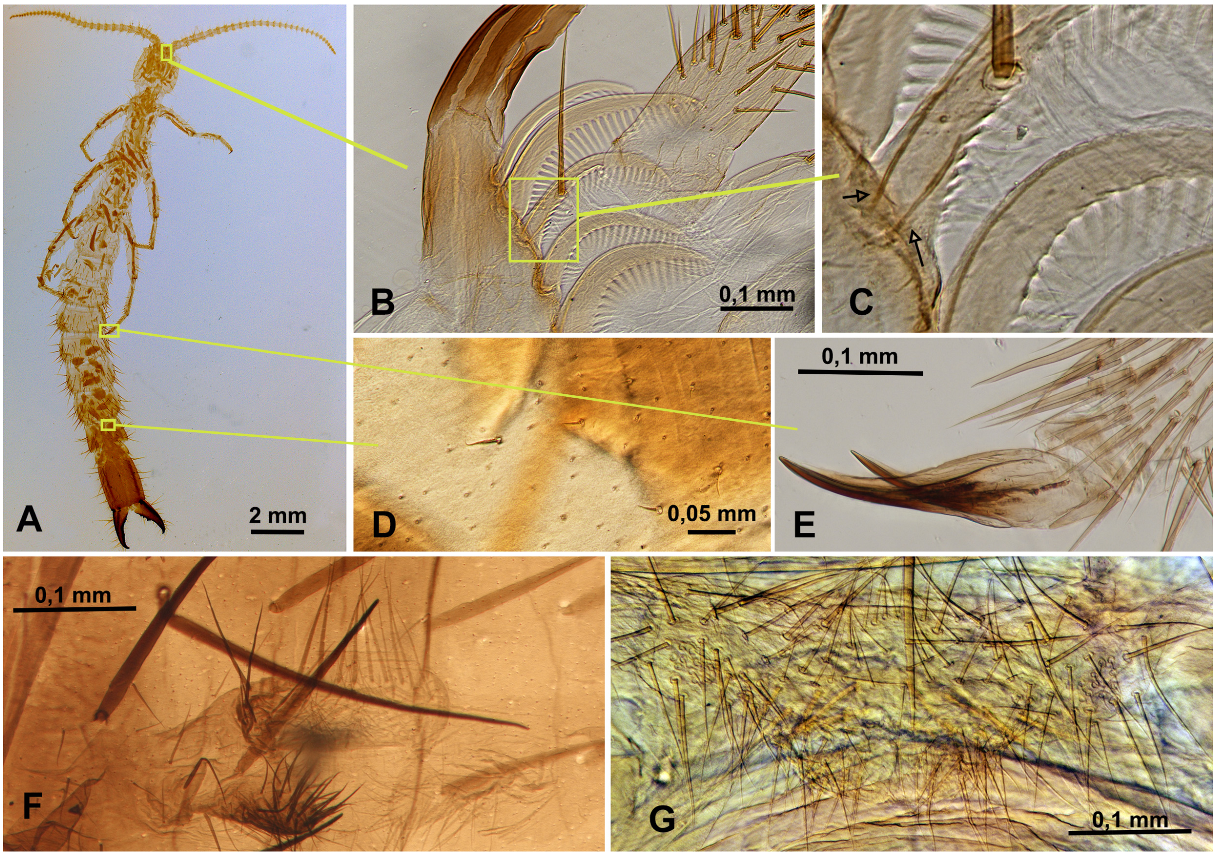

Fig. 11. *Holjapyx nimiipuu* Sendra sp. nov. **A–E, G**. Holotype, ♀ (TAMU-ENTO X1831140). **F**. Paratype, ♂ (TAMU-ENTO X185622). **A**. Habitus. **B**. Laminae pectinate. **C**. Spines (marked with arrows) besides insertion of third lamina pectinae. **D**. Detail surface urotergite VI. **E**. Claw of metathoracic leg. **F**. Genital papilla. **G**. Genital papilla.

Fig. 12. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. Pronotum. **B**. Prosternum. Abbreviations: see Material and methods.

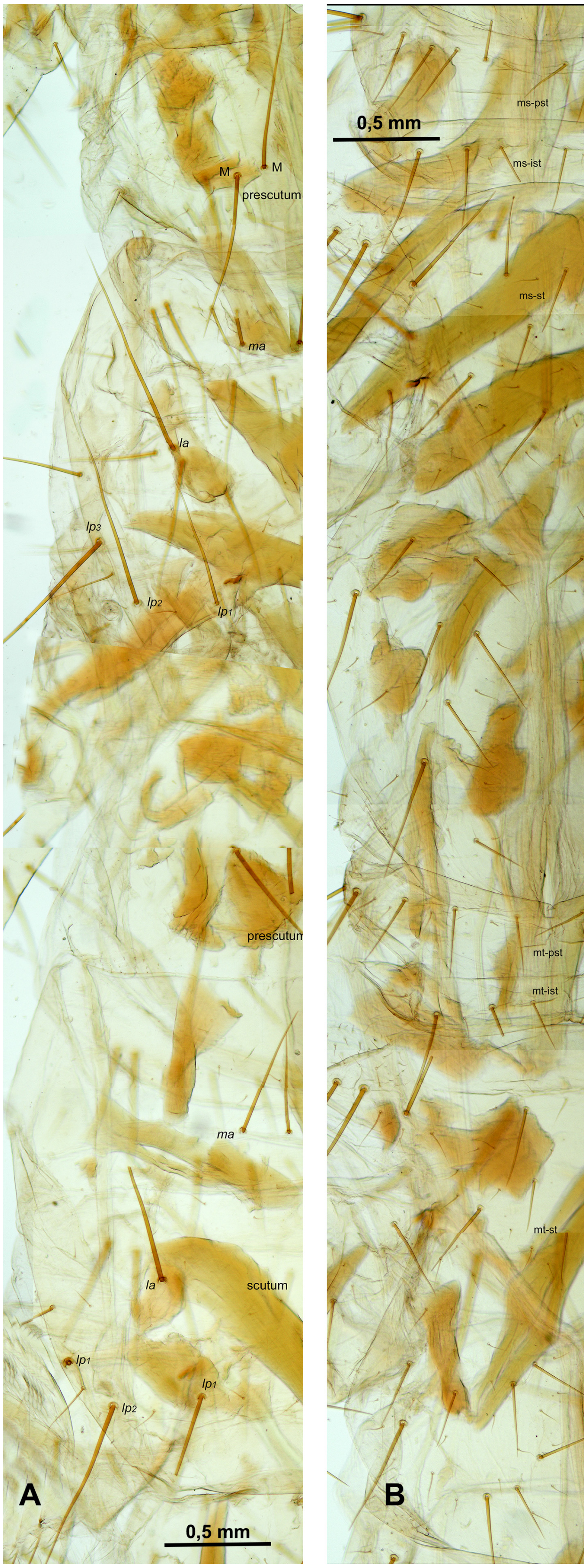

Fig. 13. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. Mesonotum and metanotum. **B**. Mesosternum and metasternum. Abbreviations: see Material and methods.

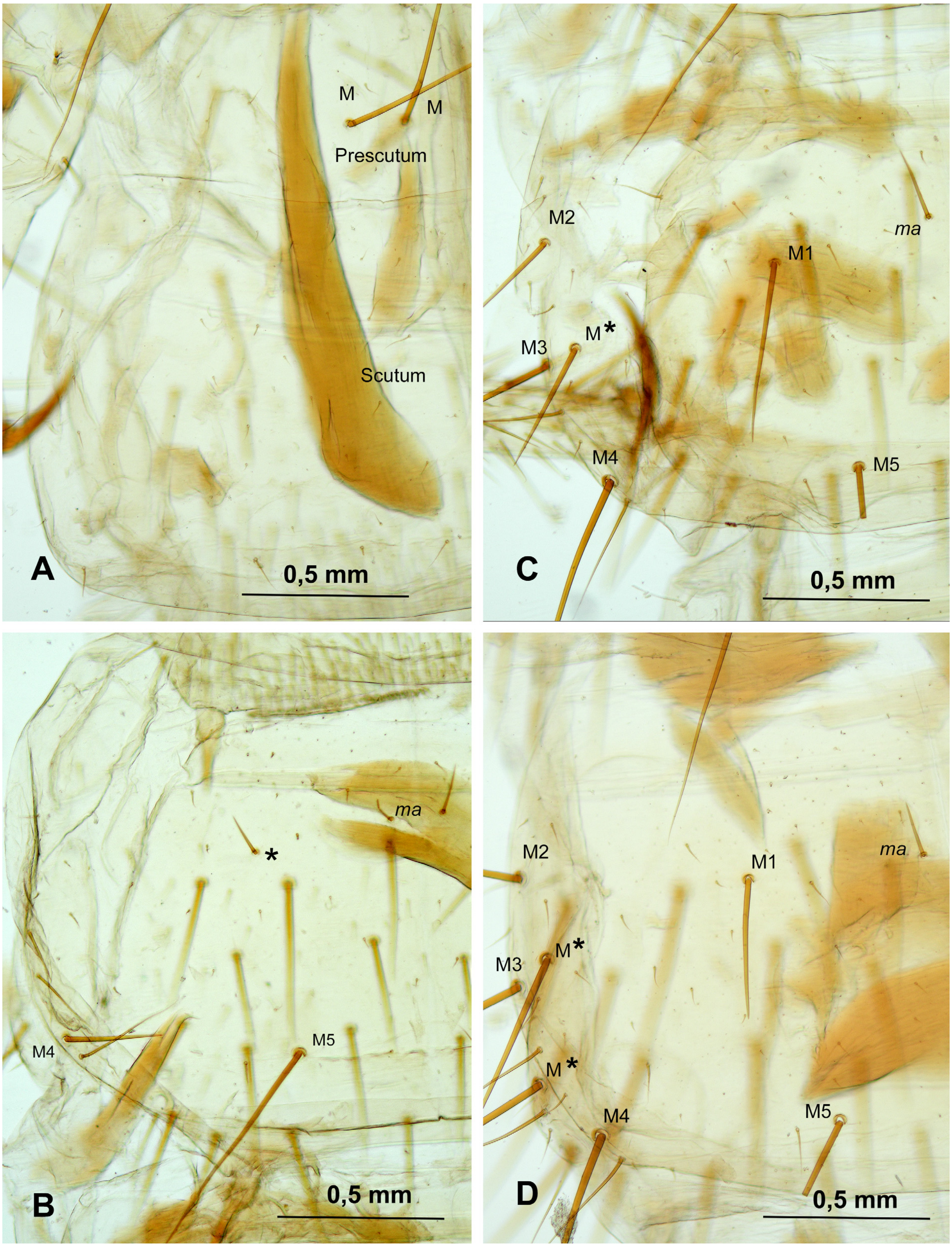

Fig. 14. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. First urotergite. **B**. Second urotergite. **C**. Third urotergite. **D**. Sixth urotergite. Abbreviations: see Material and methods; M* = supernumerary macrosetae urotergal; * = setae instead of macrosetae.

with normal short setae (ss) and few long setae (ls) and microsetae (ms) mostly acting as proprioceptors in some body parts articulations, plus the typical pattern of macrosetae (M) in thoracic and abdominal sclerites and appendages in Japygidae; sclerites of V–X abdominal segments covered by micropores and ms, also present scares on other segments (Fig. 11D).

HEAD. Dorsal side about 9+9 M: A1, 4; S1, 4, 6; M2, 3, 5; I2–3, 5 and P2 (on Idaho_1_holotype). On ventral side submentum with 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 3.3 × as long as wide, with two apical M, one subapical M and several sl. Labrum short with abundant short thick setae. Lacinia falciform, well sclerotized, with five laminae pectinate, first one modestly pectinate with distal fringe. Besides third lamina pectinate insertion there are two thin spines (Fig. 11B–C). Mandible with four distensible teeth and one tiny tooth in interior position.

ANTENNAE. Antenna 0.37× length of body, with 30 antennomeres; first antennomere short than wide, second to fourth antennomeres slightly longer than wide with tiny reinforced borders; medial and distal antennomeres slight longer than wide: all antennomeres covered with ss, ls and one whorl of M, but two whorls of M in penultimate and ultimate antennomere; this last antennomere also included more than10 placoid sensilla uneven distributed (Fig. 10B). Thirteen trichobothria present on antennomeres IV–VI: 2 dorsal / 1 ventral on IV, 3/2 on V and VI; with dorsal trichobothria (*a* trichobothria of the IV antennomere overpassing the whorl of M.

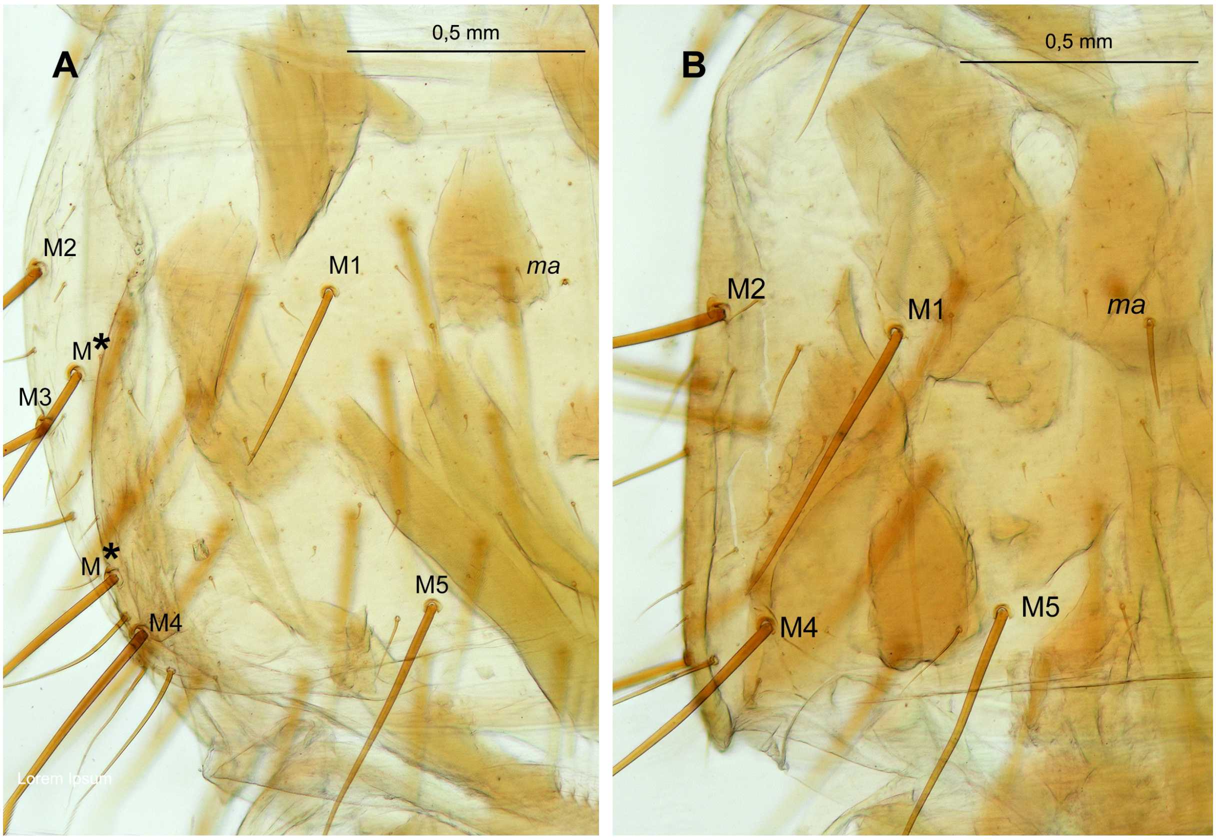

Fig. 15. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. Seventh urotergite. **B**. Eighth urotergite. Abbreviations: see Material and methods; M*= supernumerary macrosetae urotergal..

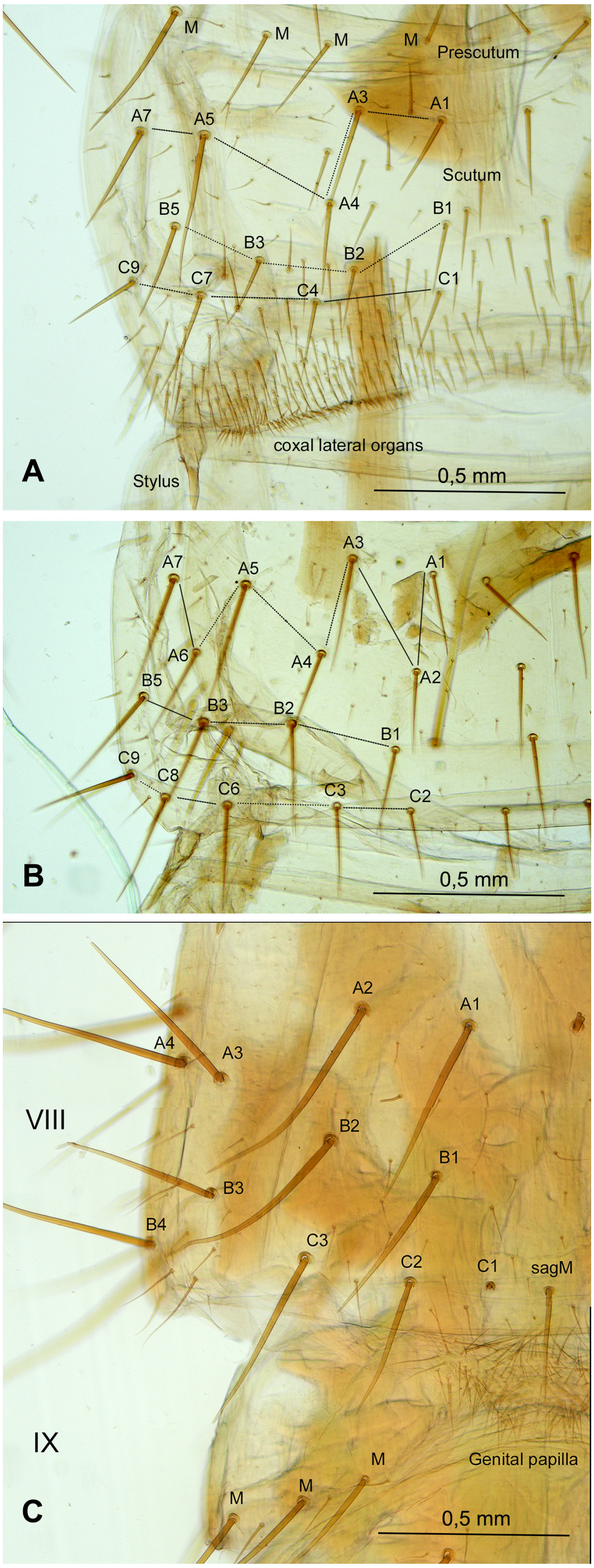

Fig. 16. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. First urosternite. **B**. Second urosternite. **C**. Eighth and ninth urosternites. Abbreviations: see Material and methods.

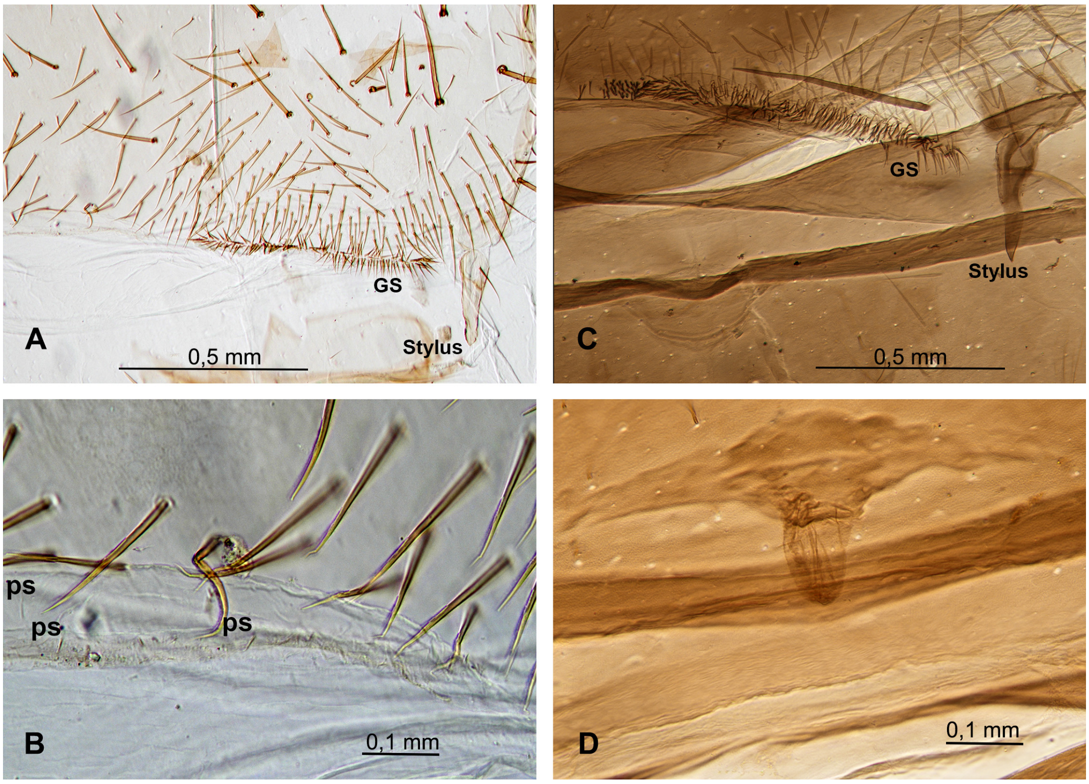

Fig. 17. *Holjapyx nimiipuu* Sendra sp. nov. **A, C**. Paratype, ♀ (MUVHN-ZE8001). **B, D**. Paratype, ♂ (TAMU-ENTO X1856622). **A–B**. First urosternite. **C**. Central organ first urosternite. **D**. Sac organ of third urosternite. Abbreviations: see Material and methods.

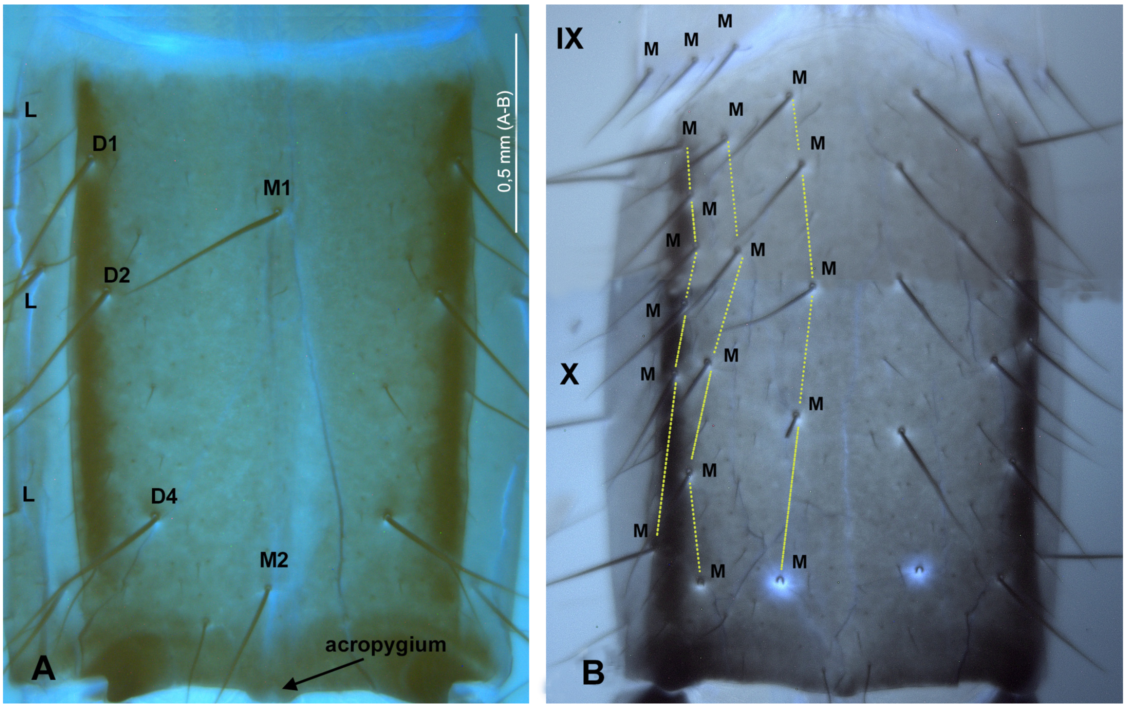

Fig. 18. *Holjapyx nimiipuu* Sendra sp. nov., holotype, ♀ (TAMU-ENTO X1831140). **A**. Urite X, dorsal view. **B**. Urite X, ventral view. Abbreviations: see Material and methods.

THORAX. Thoracic segments slightly elongated, with few ls, ss and typical pattern of M: scutum of pronotum, mesonotum and metanotum with 5+5 M (1+1 *ma*, 1+1 *la*, 3+3 *lp1-3*); prescutum of mesonotum and metanotum with 1+1 M (Fig. 12A). Thoracic sternites, intersternites, and presternites well-defined with ss, sl, and several M; border of leg articulations with fields of ms as proprioceptors (Figs 12B, 13A–B). Pro-presternites and pro-, meso- and metasternites with internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); only in propresternites prolongation of the posterior branch (spine) is visible on surface (Denis 1949). Propresternum with 1+1 M; prosternum with 3+3 *la*, 2+2 medial anterior and posterior M, one short sagittal M intermediate and 3+3 *lp*; meso-poststernum with 5+5 M; meso-intersternum with 3+3 M; mesosternum with 3+3 *la* M, 2+2 *ma* and two sagittal *mi* and 8+8 *lp*; meta-poststernum with 5+5 M; meta-intersternum with 3+3 M; metasternum with 3+3 *la*, 2+2 *ma*, *mp* and two sagM (Figs 12B, 13B). Legs slightly long, hind leg reaching the posterior border of the fifth abdominal segment. Coxa with 3 sternal M; trochanter with 4 sternal M and one interior M; femur with 10 M mostly in ventral position and row of thick setae in apical position; tibia with 4 long M on dorsal position and 5 thick M on ventral in addition to calcars; tarsus with 5 dorsal long M and two ventral rows of 12 thick setae. Pretarsus with two unequal claws (1.4–1.5 anterior to posterior claw) and sharp medial small unguiculus (Fig. 11E).

ABDOMEN. Abdominal tergites with scarce ss and sl. Prescutum of urotergite I with 1+1 M, scutum without macrosetae (Fig. 14A); urotergites II–V with 1+1 *ma* setae, 5+5 M1–5 and one additional M in lateral position (Fig. 14B–C); urotergites VI–VII with 1+1 *ma*, 5+5 M1–5 and two additional M in lateral position (Figs 14D, 15A); urotergite VIII with 1+1 *ma*, 4+4 M1–2,4–5 (Fig. 15B); urite IX without M on dorsal position. Urite X (Fig. 18A–B) 1.6–1.7× as long as wide, with distinctly marked carinae; carinae with subparallel margins slightly converging towards posterior border; dorsal side with M (D1–2, 4) intracarinal (Fig. 18A), acropygium sub-quadrangular with borders slightly rounded (Fig. 18A); lateral side with 3+3 M (L) (Fig. 18A); ventral side with 10+10 M setae arranged in 3+3 rows from right lateral side to left lateral side with each with 5+5 M (Fig. 18B). Lateral urotergites I–VII with blunt, slightly rounded posterolateral angles; urotergite VIII with apparent lateral angle conspicuous (Fig. 15B).

UROSTERNITES. With ss and few sl. Prescutum of urosternite I with 4+4 M; scutum with 13+13 M arranged in three rows (A1, 3–5, 7, B1–3,5, C1, 4, 7, 9) and posterior field of short slightly thicker setae preceding each lateral subcoxal organ (98–104 setae each) (Fig. 16A). Urosternites II–III with 16–16+17–17 M arrange in three horizontal rows (A1–7)1–9, B1–3, 5, C2–3, 6, 8–9 (Fig. 16B); urosternite VIII with central portion with 5+1+5 M (A1–2, B1–2, C1–3 and one sagittal M, lateral sides separated by well-defined carinae, with 4+4 M (A3–4, B3–4) (Fig. 16C); ventral side of abdominal segment IX with 3+3 M (Fig.16C).

MEDIAN GLANDULAR ORGAN. Of 4–6 pseudospori with a microsetae (Fig. 17B). Lateral subcoxal organ: in female (paratype MUVHN-ZE8001), each organ with two row of about 110 GS and one row of about 50 SS, organ occupying 0.60 × of interstylar area, being their setae relatively short with GS/st1 (stylus of first urosternite) = 0.19; SS/st1= 0.16 (Fig. 17A); in male (paratype TAMU-ENTO X1856622), each organ with three rows of about 220 SG and one row of about 12 SS, organ occupying 0.64 × of interstylar area, being their setae relatively shorter than female: GS/st1 (stylus of first urosternite) = 0.16; SS/st1 = 0.11 (Fig. 17C). In addition to these glandular organs, in males impair of central glandular organ located in anterior position of third and fourth urosternites constituted by open narrow channel surrounding by few long setae (Fig. 17D).

GENITAL PAPILLAE (male and female). With typical Japygidae shape; male papilla with conical appendages, 1.3 × as long as wide, bearing ss and numerous sl and long and large row of posterior setae on posterior border of genital opening (Fig. 11F–G).

Cerci. Asymmetric, strong, length 1.4–1.8 mm (0.08–0.1 × as long as body), slightly curved in proximal and medial exterior shape becoming hook towards apex; borders sclerotized with dorsal and ventral outer carinae arising from dorsal and ventral acetabular articulations (Fig. 10C). Right cercus with medial pointed tooth; predental margin with two large pointed denticles, postdental margin crenelles by 9–10 tiny denticles (Fig. 10C, E). Left cercus with distal tooth, less conspicuous than right one; predental margin with two rows of 11 dorsal denticles and 7 ventral denticles, one of them larger than others; postdental margin smooth (Fig. 10C–D). Right cercus with 8 D dorsal, 10 L and 12 V; left cercus with 6 D M, 16 L and 15 V M.

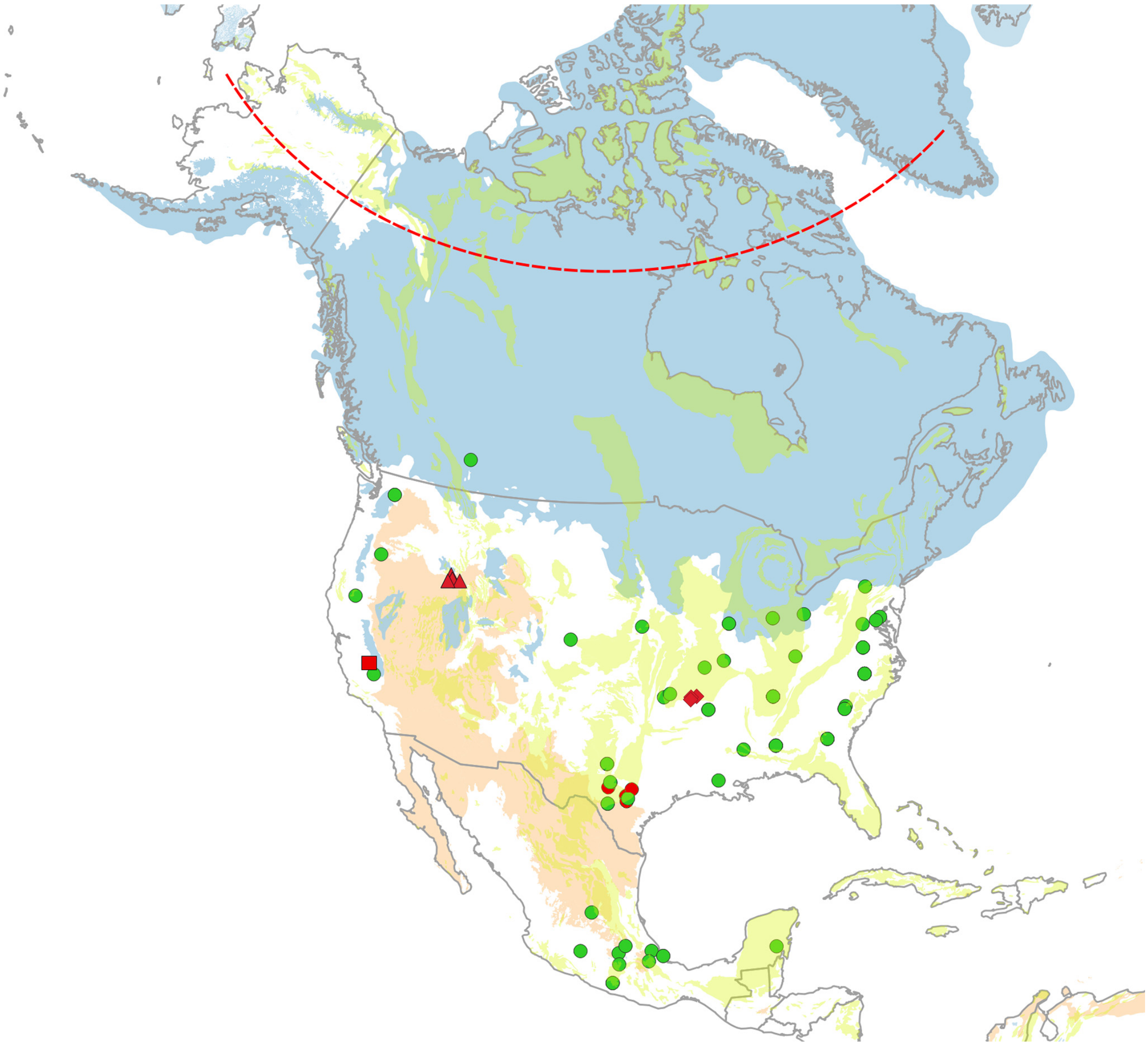

Fig. 19. Distribution of North American japygids. In yellow: karst areas (source: Chen *et al.* 2017); in orange: deserts (source: Olson & Dinerstein 2002); in blue: ice cover during the Last Glacial Maximum (source: Ehlers *et al.* 2011); green dots: known records of soil-adapted of the species of Japygidae Haliday, 1864; red colour symbols cave-adapted species of Japygidae: red triangles = *Holjapyx nimiipuu* Sendra sp. nov.; red diamonds = *Quapawjapyx osage* Sendra gen. et sp. nov.; red square = *Occasjapyx kofoidi* (Silvestri, 1928); red circles = *Mixojapyx reddelli* Muegge, 1992; red striped line: 64º N parallel, the known northern limit of Campodeidae.

Taxonomic affinities

Taking into account the simplistic taxonomic perspective adopted by Paclt (1957), the specimens studied from caves in Idaho would be assigned to *Burmjapyx* Silvestri, 1930. Paclt (1957) grouped under *Burmjapyx* eighth previously described genera: *Holjapyx* Silvestri, 1948, *Protjapyx* Silvestri, 1948, *Austrjapyx* Silvestri, 1949, *Hapljapyx* Silvestri, 1949, *Merojapyx* 1949, *Henicjapyx*, 1949, *Xenjapyx* Silvestri; 1949, and *Homojapyx* Pagés, 1953. In Paclt's redefinition, *Burmjapyx* is characterized by a medial organ lacking *disculis*, five pectinate laminae on the maxillae, and asymmetric cerci bearing two predental denticles on the left cercus and only one on the right cercus. However, following the approach of Pagés (1995), we have adopted a more detailed chaetotaxy criterion for distinguishing genera within Japygidae. Accordingly, we retain the original genera described prior to Paclt's revision and, based on these criteria, we assign the Idaho cave japygids to the genus *Holjapyx*.

Silvestri (1948a) established the genus *Holjapyx* to accommodate a previously described species, *Holjapyx diversiunguis* (Silvestri, 1911) [= *Japyx diversiunguis* Silvestri, 1911], originally found in Yosemite Park (California). In his initial description, Silvestri (1911) highlighted the unequal proportions between the two main claws and the presence of a small unguiculus in between. Later, in his diagnosis of the genus, Silvestri (1948a) emphasized several key characters, in addition to those adopted for *Burmjapyx* by Paclt (1957), such as the presence of 26 antennomers and more notable, a specialized glandular organ or sac in males, located in the anterior medial region of the third and fourth urosternites.

Four years later, Pagés (1952) described three species from New Zealand, which he tentatively assigned to *Holdajpyx*, using the provisional designation "*Holjapyx?*". He noted that males of these species lack the medial sac on any urosternite and possess a greater number of antennomeres. However, he also highlighted their similarity to *H. diversiunguis* in two features not mentioned by Silvestri (1948a): (1) the presence of fine spines in the middle of the pectinated laminae on the internal lobe of the maxilla, and; (2) the number of additional macrosetae on urosternites III–VII, which display the typical 5+5 macrosetae (M1–5) plus two extra macrosetae (Pagés 1952).

In the same decade, Leslie M. Smith (1959) made the last major contribution to the taxonomy of *Holjapyx* with the description of nine new species, all from California State. These species were distinguished based on minor morphological differences, and Smith (1959) also published a taxonomic key for the species of *Holjapyx*, excluding the species of "*Holjapyx?*" described by Pagés (1952). In the same work, Smith (1959b) redefined the genus *Holjapyx*, highlighting the diagnostic value of the position of the main tooth on the left cercus. He introduced the ratio R, defined as the distance from the base of the left cercus to the main tooth divided by the total length of the cercus (see Fig. 10D–F), and reported R values ranging from 0.371 to 0.541 for the Californian species of *Holjapyx*.

We proposed *Holjapyx nimiipuu* Sendra sp. nov., which exhibits all generic features previously described along with several exclusive characters that justify its recognition as a new species. Three of these distinguishing characters are related to cave adaptations: (1) the larger body size, reaching up to 20 mm in *H. nimiipuu*, which is more than twice the size of soil-dwelling species of *Holjapyx*; (2) the longer antennae, with 30 antennomeres instead of the usual 26; and (3) the significantly higher number of placoid sensilla, with at least ten (Fig. 10B), compared to the only three in other species of *Holjapyx*. Additionally, *H nimiipuu* is characterized by the presence of two conspicuously large predental denticles on the right cercus (Fig. 10D–F).

As previously noted regarding the antennae, *H. nimiipuu* Sendra sp. nov. shows clear cave-adapted features (Pagés 1964; Sendra *et al.* 2023), which are also evident in its slightly elongated body – particularly the thoracic segments –, its labial palp, which is 3.3 × as long as wide, the hind leg, which reaches the posterior margin of the fifth abdominal segment, and the urite X, which is 1.6–1.7 × as long as wide.

Other studied material from the Texas University Collection

Alongside these two new cave-adapted japygid species, the Texas University collection includes several non-cave-adapted japygids listed below and included in the distributional map (Fig. 19).

Genus *Hecajapyx* Smith, 1959

Hecajapyx buckeli Smith, 1964

Material examined

USA – **California** • 1 ♂; Tulare County, Lost Soldier's Cave; 21 Jul. 2003; TAMUIC, TAMUIC_JKK 54-A-5 • 1 ♀; Tulare County, Lost Soldier's Cave; 23 Jul. 2003; TAMUIC, TAMUIC_JKK 79-A-2 • 1 ♀; Tulare County, Lost Soldier's Cave; 6 Jul. 2004; TAMUIC, TAMUIC_JKK 12-D-3 • 2 ♂♂; Tulare County, Lost Soldier's Cave; 7 May 2004; TAMUIC, AMUIC_JKK 102-C-2, TAMUIC_JKK 101-C-9 • 1 ♂; Tulare County, Lost Soldier's Cave; 9 Jun. 2003; TAMUIC, TAMUIC_JKK 103-C-7.

Description

Body length: 2 ♀♀ 14–22 mm; 4 ♂♂ 15–19 mm.

Genus *Occasjapyx* Silvestri, 1948

Occasjapyx californicus Silvestri, 1948

Material examined

USA – **Oklahoma** • 1 ♀; Delaware County, McGee Cave; 31 Sep. 2001; S. Mc Ginnis and D. Fenolio leg.; TAMUIC, TAMUIC.

Occasjapyx sp.

Material examined

USA – **Oklahoma** • 1 ♀; Mayes County, Black Bone Cave; 29 Jul. 2004; G.O. Graening and M.E. Slay leg.; TAMUIC. – **Texas** • 1 spec., indeterminate sex; Uvalde County, Indian Creek Cave; Jun. 1966; Mitchell Bogert leg.; TAMUIC • 1 spec., indeterminate sex; Comal County, Honey Cr. Cave; 15 Aug. 1987; TAMUIC. – **Illinois** • 1 ♀; Monroe County, Brows Cave; 12 Nov. 1998; J. Lewis and P. Moss leg.; TAMUIC. – **Virginia** • 1 spec., indeterminate sex; Skyline Cavern; 2 Dec. 1995; Hubbard leg.; TAMUIC.

Discussion

A total of 44 North American japygid species have been described to date, mostly summarized brilliantly by Reddell (1983), including the two new species presented here. These species belong to nine different genera: *Allojapyx* Silvestri, 1948 (one species), *Catajapyx* Silvestri, 1933 (one species), *Hecajapyx* (two species), *Holjapyx* Silvestri, 1948 (11 species), *Japyx* Haliday, 1864 (five species), *Metajapyx* Silvestri, 1948 (nine species), *Mixojapyx* Silvestri, 1933 (seven species), *Occasjapyx* Silvestri, 1948 (five species), and *Quapawjapyx* gen. nov. (one species) (Silvestri 1911, 1933b, 1948a, 1948c; Smith 1959a, 1959b, 1964; Smith & Bolton 1964; Muegge & Bernard 1990; Muegge 1992; Allen 2002; this paper). The distribution of North-American japygids does not extend beyond 51° N, roughly corresponding to the southern limit of the ice during the Last Glacial Maximum, and reaching the Neotropical region in Central and South America (Sendra *et al.* 2023). In contrast, campodeids go much further north, reaching up to 64º N in Alaska (Sikes & Allen 2016; Sendra & Wagnell 2019). Japygids prefer temperate climates and tend to avoid desert regions, as illustrated in the North-American japygid distribution map (Fig. 19).

Focusing on cave-adapted North American japygids, there is a modest total of four species, including the two newly described here, each belonging to a different genus: *Occasjapyx kofoidi* (Silvestri, 1928), found in Potter Creek Cave, Shasta Co., California, *Mixojapyx reddelli* Muegge, 1992, recorded from six caves across six different counties within the Edwards Plateau karst region of central Texas, *Quapawjapyx osage* Sendra gen. et sp. nov., occurring in three caves across two counties in the Ozark Mountains of northern Arkansas, and *Holjapyx nimiipuu* Sendra sp. nov., which inhabits five caves in two counties in central Idaho (Fig. 19).

This diversity of cave-adapted japygids in the Nearctic region – four species across four different genera – may seem low, but it is relatively high compared to other regions worldwide. No cave-adapted japygids are known from the Neotropical region; only one species of the genus *Teljapyx* Silvestri, 1949 is recorded in the Australasian region; two species (of the genera *Burmjapyx* and *Mueggenjapyx* Sendra & Komerički, 2021) are found in the Indomalayan region; three species (two in *Austrjapyx* and one in *Opisthjapyx* Silvestri, 1929) in the Afrotropical region; and seven species (one species each in *Gollumjapyx* Sendra & Ortuño, 2006, *Homojapyx*, *Imazighenjapyx*, *Kohjapyx* Pagés, 1953 and *Troglojapyx* Pagés, 1980, and two in *Metajapyx*) have been described in the Palearctic, all of them in the West-Palearctic.

A total of seventeen cave-adapted japygids worldwide represents a modest number within this widely distributed family of diplurans. These subterranean animals, like other cave-adapted dipluran species, exhibit several distinctive morphological features not seen in soil-adapted relatives. Such features include enlargement and elongation of the body, body segments, antennae, and cerci, as well as an increased number of antennomeres. These characteristics result in a greater abundance of mechanoreceptor setae and a pronounced presence of extra placoid sensilla on the antennomeres (Pagés 1964; Sendra *et al.* 2023). These traits are considered adaptations to some specific cave ecosystem challenges, such as large voids in the rock substrate and limited energy availability (Sendra *et al.* 2023).

Nevertheless, when comparing the limited known distribution areas of cave-adapted japygids in North America and the other continents to the vast karstic regions containing thousands of caves, it is reasonable to assume that a considerable hidden diversity of japygids remains to be discovery. Currently, five remarkable new cave-adapted japygids from Southeast Asia and the Mediterranean regions are under study by the japygid taxonomic community.

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References

Allen R.T. 2002. A synopsis of the Diplura of North America: keys to higher taxa, systematics, distributions and descriptions of new taxa (Arthropoda: Insecta). *Transactions of the American Entomological Society (Philadelphia)* 128 (4): 403–466.

Barlet J. & Carpentier F. 1962. Le thorax des Japygides. *Bulletin et Annales de la Société royale d'Entomologie de Belgique* 8: 95–127.

Chen Z., Auler A., Bakalowicz M., Drew D., Griger F., Hartmann J., Jiang G., Moosdorf N., Richts A., Stevanovic Z., Veni G. & Goldscheider N. 2017. The World Karst Aquifer Mapping project: concept, mapping procedure and map of Europe. *Hydrogeology Journal* 25: 771–785. https://doi.org/10.1007/s10040-016-1519-3

Condé B. 1956. Matériaux pour une monographie des Diploures Campodéidés. *Mémoires du Muséum national d'Histoire naturelle Série A – Zoologie* 12: 1–202.

Cook O.F. 1899. New Dicellura. *Proceedings of the Entomological Society of Washington* 4: 222–229.

Deharveng L. & Bedos A. 2018. Diversity of terrestrial invertebrates in subterranean habitats. *In*: Moldovan O.T., Kováč L. & Halse S. (eds) *Cave ecology*: 107–172. Springer Nature Switzerland, Cham. https://doi.org/10.1007/978-3-319-98852-8_7

Denis J.R. 1949. Ordre des Diploures. *In*: Grassé P.P. (ed.) *Traité de Zoologie* IX: 160–185. Masson, Paris.

Ehlers J., Gibbard P.L. & Hughes P.D. 2011. *Quaternary Glaciations – Extent and Chronology: a Closer Look*. Elsevier, Amsterdam.

Grassi B. 1886. I progenitori degli Insetti e dei Miriapodi. *Accademia gioenia di scienze naturali in Catania* 9: 1–83.

Grassi B. 1889. Les ancêtres des Myriapodes et des Insectes. Anatomie comparée des Thysanoures et considérations générales sur l'organisation des Insectes. *Archives italiennes de Biologie* 11: 312–417.

Haliday A.H. 1864. *Iapyx*, a new genus of insects belonging to the stirps Thysanura. in the order Neuroptera. *Transactions of the Linnean Society of London* 24: 441–447. https://doi.org/10.1111/j.1096-3642.1863.tb00166.x

Muegge M.A. 1992. New species of cavernicolous japygid (Diplura: Japygidae) from Texas. *Annals of the Entomological Society of America* 85 (4): 406–412. https://doi.org/10.1093/aesa/85.4.406

Muegge M.A. & Bernard E.C. 1990. Two new species of *Metajapyx* (Diplura: Japygidae) from Tennessee. *Proceedings of the Entomological Society of Washington* 92 (4): 793–801.

Olson D. & Dinerstein E. 2002. The global 200: priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* 89: 199–224. https://doi.org/10.2307/3298564

Paclt J. 1957. Diplura. *In*: P. Wytsman (ed.) *Genera Insectorum. 212º Fasc*: 1–123.

Pagés J. 1952. Diploures Japygidés de Nouvelle-Zélande. *Records of the Canterbury Museum* 6: 149–162.

Pagés J. 1953. The 3rd Danish expedition to Central Asia. *Zoological Results* 8. Japygidae (Insecta) de l'Afganistan. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn* 115: 159–167.

Pagés J. 1955. Un Japygidae remarquable du Nyassaland. *Annals and Magazine of Natural History Series 12* 8: 321–325. https://doi.org/10.1080/00222935508655647

Pagés J. 1964. Remarques sur les Japygidae signales dans le domaine souterrain. *International Journal of Speleology* 1: 191–201. https://doi.org/10.5038/1827-806X.1.1.15

Pagés J. 1978. Japygidés du Sud-Est asiatique nº 2 – Dicellurata Genavensia VI. *Revue suisse de Zoologie* 85 (3): 597–606. https://doi.org/10.5962/bhl.part.82247

Pagés J. 1980. Dicellurata Genavensia VII. Japygidés d'Europe et du bassin méditerranéen nº 2. *Revue suisse de Zoologie* 87 (2): 637–645. https://doi.org/10.5962/bhl.part.85537

Pagés J. 1981. Japygidés du Sud-Est asiatique nº 3 – Dicellurata Genavensia IX. *Revue suisse de Zoologie* 88 (1): 239–247. https://doi.org/10.5962/bhl.part.82368

Pagés J. 1984. Dicellurata Genavensia XIII. Japygidés du Sud-Est asiatique. Nº 4. *Revue suisse de Zoologie* 91 (1–2): 329–368. https://doi.org/10.5962/bhl.part.81883

Pagés J. 1993. Japygidés d'Europe et du bassin méditerranéen, nº 7 – Dicellurata Genavensia XVII. *Revue suisse de Zoologie* 100 (1): 47–64. https://doi.org/10.5962/bhl.part.82499

Pagés J. 1994. Japygidés du Sud-Est asiatique nº 6: Malaysia (Sabah) – Dicellurata Genavensia XIX. *Revue suisse de Zoologie* 101 (2): 413–434. https://doi.org/10.5962/bhl.part.82494

Pagés J. 1995. Japygidés (Diplura) du Sud-Est asiatique nº 7: Malaysia (Sarawak), Indonésie (Java, Sumatra) et Sri Lanka – Dicellurata Genavensia XX. *Revue suisse de Zoologie* 102 (2): 277–305. https://doi.org/10.5962/bhl.part.80466

Pagés J. 2000. Japygidés du Sud-Est asiatique nº 9 – Dicellurata Genavensia XXIV. *Revue suisse Zoologie* 107 (4): 737–764. https://doi.org/10.5962/bhl.part.80146

Pagés J. 2002. Japygidés du Sud-Est asiatique nº 10 – Dicellurata Genavensia XXVI. *Revue suisse de Zoologie* 109 (3): 653–677. https://doi.org/10.5962/bhl.part.79615

Packard A.S. 1874. Occurrence of *Japyx subterraneus* in the United States. *The American Naturalist* 8: 501.

Péringuey L. 1901. Description of a new species of the genus *Japyx* (Order Thysanura) from the Cape colony. *Annals of the South African Museum* 2: 133–135.

Potapov A.M., Beaulieu F., Birkhofer K., Bluhm S.L., Degtyarev M.I., Devetter M., Goncharov A.A., Gongalsky K.B., Klarner B., Korobushkin D.I., Liebke D.F., Maraun M., Mc Donnell R.J., Pollierer M.M., Schaefer I., Shrubovych J., Semenyuk I.I., Sendra A., Tuma J., … & Scheu S. 2022. Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biological Reviews* 97 (3): 1057–1117. https://doi.org/10.1111/brv.12832

Racovitză E.G. 1907. Essai sur les problèmes biospéologiques. *Archives de Zoologie expérimentale et générale* 6: 371–488.

Reddell J.R. 1983. A checklist and bibliography of the Iapygoidea (Insecta: Diplura) of North America, Central America, and the West Indies. *The Pearce-Sellards Series. Univ. Texas* 73: 1–41.

Sendra A. & Wagnell C. 2019. The cave-dwelling dipluran (Diplura, Campodeidae) on the edge of the Last Glacial Maximum in Vancouver Island caves, North America (Canada). *Subterranean Biology* 29: 59–77. https://doi.org/10.3897/subtbiol.29.31467

Sendra A., Palero F., Jiménez-Valverde A. & Reboleira A.S.P.S. 2020. Diplura in caves: diversity, ecology, evolution and biogeography. *Zoological Journal of the Linnean Society* 192: 675–689. https://doi.org/10.1093/zoolinnean/zlaa116

Sendra A., Jiménez-Valverde A., Selfa J. & Reboleira A.S.P.S. 2021a. Diversity, ecology, distribution and biogeography of Diplura. *Insect Conservation and Diversity* 14: 415–425. https://doi.org/10.1111/icad.12480

Sendra A., Komerički A., Lips J., Luan Y., Selfa J. & Jiménez-Valverde A. 2021b. Asian cave-adapted diplurans, with the description of two new genera and four new species (Arthropoda, Hexapoda, Entognatha). *European Journal of Taxonomy* 731: 1–46. https://doi.org/10.5852/ejt.2021.731.1199

Sendra A., Palero F., Sánchez-García A., Jiménez-Valverde A., Selfa J., Maghradze E. & Barjadze S. 2021c. A new Diplura species from Georgia caves, *Plusiocampa* (*Plusiocampa*) *imereti* (Diplura, Campodeidae), with morphological and molecular data. *European Journal of Taxonomy* 778: 71–85. https://doi.org/10.5852/ejt.2021.778.1567

Sendra A., Sánchez-García A., Selfa J., Milko D.A. & Ferreira R.L. 2021d. Campodeidae (Hexapoda: Diplura) from Kyrgyzstan, Central Asia, with the description of a remarkable new genus and species. *European Journal of Taxonomy* 782: 1–20. https://doi.org/10.5852/ejt.2021.782.1585

Sendra A., Palero F., Sánchez-García A., Selfa J., Tusun S. & Satar A. 2022. New evidence for an Anatolian bridge: colonization of Euromediterranean lands by cave-adapted Plusiocampinae (Diplura, Campodeidae), with establishment of a new genus. *Zoologischer Anzeiger* 301: 205–214. https://doi.org/10.1016/j.jcz.2022.10.006

Sendra A., Sánchez-García A., Hoch H., Jiménez-Valverde A., Selfa J., Moutaouakil S., du Preez G., Millar R. & Ferreira R.L. 2023. Life in darkness: an overview of cave-adapted japygids (Hexapoda, Diplura). *European Journal of Taxonomy* 894: 1–54. https://doi.org/10.5852/ejt.2023.894.2287

Sikes D.S. & Allen R.T. 2016. First Alaskan records and a significant northern range extension for two species of Diplura (Diplura, Campodeidae). *ZooKeys* 563: 147–157. https://doi.org/10.3897/zookeys.563.6404

Silvestri F. 1911. Nuovi generi e nuove specie di Campodeidae (Thysanura) dell'America settentrionale. *Bolletino del Laboratorio di Zoologia generale e agraria in Portici* 5: 72–99.

Silvestri F. 1928. Japygidae (Thysanura) dell'Estremo Oriente. *Bolletino del Laboratorio di Zoologia generale e agraria in Portici* 22: 49–80.

Silvestri F. 1929a. Note su Tisanuri Italiani. 1. Nova specie di *Japyx*. 2. Il nido e le ova di *Japyx solifugus. Bollettino della Società entomologica Italiana* 61 (8–7): 126–130.

Silvestri F. 1929b. Contribución al conocimiento de los Japygidae (Thysan.) de España. *Eos* 5: 81–95.

Silvestri F. 1930a. Contribuzione alla conoscenza degli Japygidae (Thysanura) dell'Africa occidentale. *Bolletino del Laboratorio di Zoologia generale e agraria in Portici* 23: 149–196.

Silvestri F. 1930b. Contributions to a knowledge of the Indo-Malayan Japygidae (Thysanura). *Records of Indian Museum* 32: 439–489. https://doi.org/10.26515/rzsi/v32/i4/1930/162518

Silvestri F. 1933a. Nuovi contributi alla conoscenza della fauna delle isole Italiane dell'Egeo. *Bolletino del Laboratorio di Zoologia generale e agraria in Portici* 27: 61–111.

Silvestri F. 1933b. Nuovo contributo alla conoscenza dei Tisanuri del Messico. *Bolletino del Laboratorio di Zoologia generale e agraria in Portici* 27: 127-144.

Silvestri F. 1934. Dicellura, Japygidae (première série). *Archives de Zoologie experimentale et générale. Biospeologica* 76 (6): 385–398.

Silvestri F. 1948a. Descrizioni di alcuni Japyginae (Insecta Diplura) del Nord America. *Bolletino del Laboratorio d'Entomologia agraria in Portici* 8: 118–136.

Silvestri F. 1948b. Japyginae (Japygidae: Insecta Diplura) della fauna italiana finora note. *Bollettino del Laboratorio di Entomologia agraria di Portici* 8: 238–296.

Silvestri F. 1948c. Specie di Japygidae (Insecta, Diplura) finora raccolti nel Messico. *Bollettino del Laboratorio entomologia agraria di Portici* 8: 297–320.

Silvestri F. 1948d. Contributo alla conoscenza degli Japygidae (Insecta Diplura). *Società Italana delle Scienze detta Accademia dei XL, Serie III*, 27: 3–115.

Silvestri F. 1948e. Description of two new species of Japygidae (Insecta, Diplura) from Gold Coast (W. Africa). *Proceedings of the Zoological Society of London* 118: 416–419. https://doi.org/10.1111/j.1096-3642.1948.tb00386.x

Silvestri F. 1949. Japygidarum et Projapygidarum Catalogus. *Bollettino del Laboratorio di Entomologia Agraria di Portici* 9: 3–38.

Smith L.M. 1959a. The Japygidae (Diplura) of North America, 3. *Occasjapyx* Silvestri and *Hecajapyx* n. gen. *Annals Entomological Society America* 52: 363–368. https://doi.org/10.1093/aesa/52.4.363

Smith L.M. 1959b. Japygidae of North America 2. The Genus *Holjapyx* and descriptions of new species. *The Pan Pacific Entomologist*, 35 (4): 177–186.

Smith L.M. 1962. Japygidae of South America, 3. Japygidae of Chile. *Proceedings of the Biological Society of Washington* 75: 273–292.

Smith L.M. 1964. Japygidae of North America 11: The Genus *Hecajapyx*. *The Pan Pacific Entomologist* 40 (1): 37–39.

Smith L.M. & Bolton C.L. 1964. Japygidae of North America 9. The Genus *Metajapyx*. *Journal of Kansas Entomological Society* 37 (2): 126–138.

Verhoeff K.W. 1904. Zur vergleichenden Morphologie und Systematik der Japygiden, zugleich zweiter Aufsatz über den Thorax der Insekten. *Archiv für Naturgeschichte* 70 (1): 63–114.

Verhoeff K.W. 1923. Zur Kenntnis der Japygiden. III. *Deutsche entomologische Zeitschrift* (1923): 33–52.

Westwood J.O. 1842. Description of a new genus of apterous hexapod insects found near London. *Annals and Magazine of Natural History* 10: 71–71. https://doi.org/10.1111/j.1365-2311.1842.tb03276.x

Wilson H.M. & Martill D.M. 2001. A new japygid dipluran from the Lower Cretaceous of Brazil. *Palaeontology* 44: 1025–1031. https://doi.org/10.1111/1475-4983.00213

Wang Y.-H., Huang D-Y. & Cai C.-Y. 2023. A new genus of japygids (Diplura: Japygidae) in mid-Cretaceous amber from northern Myanmar. *Zootaxa* 5396 (1): 64–73. https://doi.org/10.11646/zootaxa.5396.1.12

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