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Life in darkness: an overview of cave-adapted japygids (Hexapoda, Diplura)

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Abstract. Few species of Japygidae (Diplura) have been discovered in cave ecosystems despite their importance as large predators. A small collection of rare specimens of this hexapod group has allowed to explore the taxonomy of japygids from caves in New Zealand, Morocco and South Africa, and to describe one new genus: *Imazighenjapyx* Sendra & Sánchez-García gen. nov., as well as four new species: *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov. and *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov. For each of the new taxa we give a comprehensive description of their habitats. These new findings resulted in a revision of the distribution and allowed to re-evaluate the morphological traits of the fifteen cave-adapted japygids species already known worldwide. The functional morphology of the remarkable abdominal pincers of Japygidae and their adaptation to predation are discussed, as well as their potential role in mating behaviour.

Keywords. Japygidae, taxonomy, phylogeny, cave-dwelling, biogeography.

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Introduction

Japygidae Haliday, 1864 is a relatively large family with more than three hundred species belonging to the small group of entognathous hexapod Diplura Börner, 1904, which comprises just over a thousand species (Sendra *et al.* 2021a). Like all diplurans, japygids are present in different soil types with a certain degree of humidity, in both epiedaphic and endogean habitats, and can sometimes be found in cave environments (Pagés 1964; Sendra *et al.* 2020). Although most diplurans feed on living roots, detritus, and fungi, japygids prefer living animals and very rarely dead animals (Pagés 1951, 1967; Gyger 1960; Potapov *et al.* 2022).

Japygids as diplurans have an insect-like hexapod body plan with three tagmata, entognatha mouthparts partially concealed by two oral folds, and an abdomen divided into 10 complete segments, some of which retain vestiges of legs represented by pairs of articulated styli and water absorbing eversible vesicles. The last abdominal segment bears the typical paired cerci, from which Diplura in general receives the common name of two-pronged bristletails or ‘double tail’. These cerci have evolved among the ten families of diplurans into a great variety of shapes and functions. Japygids possess uniarticulate pincer-like cerci supported by a well-sclerotized tenth abdominal segment, a feature shared with four other families of diplurans. All the families with pincer-like cerci are classified within the superfamily Japygoidea Ewing, 1942, and were formerly considered subfamilies of Japygidae (Pagés 1959). Although phyletic affinities among Diplura families is now well established (Pagés 1959; Koch 2009; Sendra *et al.* 2021a), our understanding of the relationships within the families remains limited, despite many decades of detailed anatomical studies and modest amounts of molecular data. This is especially true in japygids, where the few taxonomic characters used have shown little value in suggesting robust phyletic relationships between genera or species (Pagés 1978, 1995). The use of scanning electron microscopy could provide us with a new set of morphological characters that might help to clarify phylogenetic relationships in Japygidae, as we do in this study with the description of four new species.

We review the morphological characters traditionally used in the taxonomy of japygids and highlight the difficulties already pointed out by authors such as the French entomologist Jean Pagés, the most prolific expert on japygids. To this end, we studied a collection of nine cave-adapted japygids specimens from expeditions in New Zealand, South Africa, and North Africa. We also provide updated information on cave-dwelling japygids (Pagés 1964; Bareth & Pagés 1994; Sendra *et al.* 2020), with a review of their diversity, distribution limits, and cave-adapted characters. Finally, we describe in detail the most fascinating structure of japygids, their strong pincers, and we discuss its role in predatory behaviour. The pincers allow these arthropods to function as a top-level predator in their habitats, primarily in cave-ecosystems where they can be the largest predator of invertebrates (Sendra *et al.* 2006).

Material and methods

Studied areas

Specimens of the four new species described were sampled in caves in Morocco, South Africa, and New Zealand. Specific details on their habitats are provided following each species' description.

Sampling and imaging

The japygids were sampled during surveys intended to collect cave invertebrates. Invertebrates were collected along the entire caves' extension by visually searching, using tweezers and brushers, and paying special attention to microhabitats such as under rocks and organic matter deposits. All specimens collected were preserved in vials containing 70% ethanol for later examination and identification.

In the laboratory, several specimens were washed with distilled water, macerated using 10% potassium hydroxide, and mounted on a slide with glycerine. The specimens were examined under a phase-contrast optical microscope, and measurements were taken with an ocular micrometre. Photomicrography was performed with a stereo microscope (Leica M165C) with an integrated capture system image (LAS ver. 4.13) and software LCS Lite, and a compound microscope with a photographic camera K3 C/M and the software LCS Lite. We used the software Helicon Focus to combine photos of a specimen at different foci, which helped us to get a more accurate and complete illustration. Specimens for SEM photography (Hitachi S-4900) were coated with palladium-gold.

Morphological study

The morphological terminology used throughout is from Smith (1962) and Pagés (1953b, 1984): M = macrosetae (large smooth setae with robust socket); sM = sub-macrosetae (medium-sized smooth setae usually set on simple sockets); s = setae (short smooth setae set on small simple sockets); ms = microsetae or minute setae (visible only under high magnification and always set on simple sockets); the setae found on antennae of a couple of species described here have been named: mbsM = microbarbed sub-macrosetae.

Macrosetae (M) position in dorsal head: A = macrosetae in A position, B = macrosetae in B position, C = macrosetae in C position, D = macrosetae in D position, L = macrosetae in L position, V = macrosetae in V position, P = macrosetae in P position; for thoracic and abdominal tergites: macrosetae in M1 to M5 positions in addition to extra M; for abdominal sternites: A = line of macrosetae in anterior position, B = line of macrosetae in medial position, C = line of macrosetae in posterior position; for abdominal segment tenth: D = macrosetae in D position, L = macrosetae in L position; ap = acropygium; for lateral organs of the first urosternite: GS = glandular setae; SS = sensory setae; for cerci: cs = campaniform sensillum. Specific terminology for thoracic sclerites follows Barlet & Carpentier (1962) and Pagés (1989).

Institutional abbreviations

The specimens are housed in the following institutions:

AI = Museum of New Zealand Te Papa Tongarewa, New Zealand
Coll. AS = Private collection of Alberto Sendra, València, Spain
ISAM = Entomology Collection at the Iziko South African Museum, South Africa
MHNM = Museum of Natural History of Marrakesh, Morocco
MZB (MCNB) = Museu de Ciències Naturals de Barcelona, Spain

Results

Class Diplura Börner, 1904
Superfamily Japygoidea Ewing, 1942
Family Japygidae Haliday, 1864
Genus *Austrjapyx* Silvestri, 1949

Austrjapyx wynbergensis Sendra & Sánchez-García sp. nov.
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Figs 1–7

Etymology

The specific epithet "wynbergensis" refers to the cave inhabited by the species.

Type material

Holotype

SOUTH AFRICA • ♀; Cape Town, Wynberg Cave; 33°59′10.48″ S, 18°24′10.64″ E; 12 Oct. 2019; Rodrigo Lopes Ferreira leg.; labelled "♀1-holotype SAM-MNW-CO15126"; ISAM.

Paratypes

SOUTH AFRICA • 1 ♀; same collection data as for holotype; labelled "♀2-paratype-MZB (MCNB) 2023-0618"; MZB.

Other studied material

SOUTH AFRICA • 1 ♀; same collection data as for holotype; AS.

Description

Body. Elongate (Fig. 1A), length 15 mm in ♀1-holotype, 8.8 mm in ♀2-paratype. Maximum width at urotergite VII 1.7 mm in ♀1-holotype, 1.1 mm in ♀2-paratype. Epicuticle smooth under optical microscope and with numerous micropores at higher magnifications (sternites with 4–5 micropores/μm^2, diameter 0.2–0.3 µm; urite X with 3–4 micropores/μm^2, diameter 0.10–0.15 µm) (Fig. 5D). Body with s, sM, and M setae, and with few or no ms. Cuticle unpigmented, with sclerotized areas on mandible tips, femoral and tibial condyles, abdominal segments VIII–X and cerci.

Head. Antenna length 3.5 mm, 0.4× as long as body, with 31 antennomeres; antennomeres telescopate in holotype, basal antennomere short, followed by slightly longer antennomeres II and III, 1.3× as long as wide; medial antennomeres as long as wide. All antennomeres with sM, a few ms, and abundant s setae; sM apparently distributed in two whorls. Trichobothria present on antennomeres IV–VI in a 2/3/3 pattern, with *a* trichobothria in distal position. Apical antennomere with 10 placoid sensilla distributed in two irregular whorls (Fig. 2). Dorsal and ventral side of head with a few sM and several M setae; on dorsal side: A1–4, S1, 4, 6, M2–3, 5, I1–2, I5, L1–3 and P2 macrosetae (Fig. 1B); on ventral side:

submentum with large 1+1 M in posterior position, admentum with 9+9 M, mentum at base of labial palps with 1+1 M; external lobes of mentum with abundant sM; the pair of exertil vesicles of the external lobes visible in the holotype. Labial palp elongate, 9× as long as wide, with one proximal sM and five medial and distal sM. Lacinia falciform, well sclerotized, all five laminae pectinate (Fig. 3A).

Thorax. Thoracic segments elongate. Pronotum with 5+5 M1–5 (Fig. 1B); prescutum of mesonotum with 1+1 M; mesonotum with 5+5 M1–5 and a few sM (Fig. 1C); prescutum of metanotum with 1+1 M, metanotum with 5+5 M1–5 and a few sM (Fig. 1E). Thoracic sternites, intersternites, and presternites well-defined, with a few s and M setae. Pro-presternites and pro-, meso- and metasternites with strong internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); only in pro-presternites the prolongation of the posterior branch (spine) is visible on the surface (Denis 1949). Pro-presternum with 1+1 lateral anterior M; prosternum with 1+1 medial anterior M, 3+3 lateral anterior M, 1+1 medial posterior M, and 2+2 lateral posterior M; meso-poststernum with 3+3 M; meso-intersternum with 3+3 M; mesosternum with 1+1 medial anterior M, 2+2 lateral anterior M, 1+1 medial intermediate M, 1 sagittal M, 1+1 medial posterior M and 2+2 lateral posterior M; meta-poststernum with 4+4 M; meta-

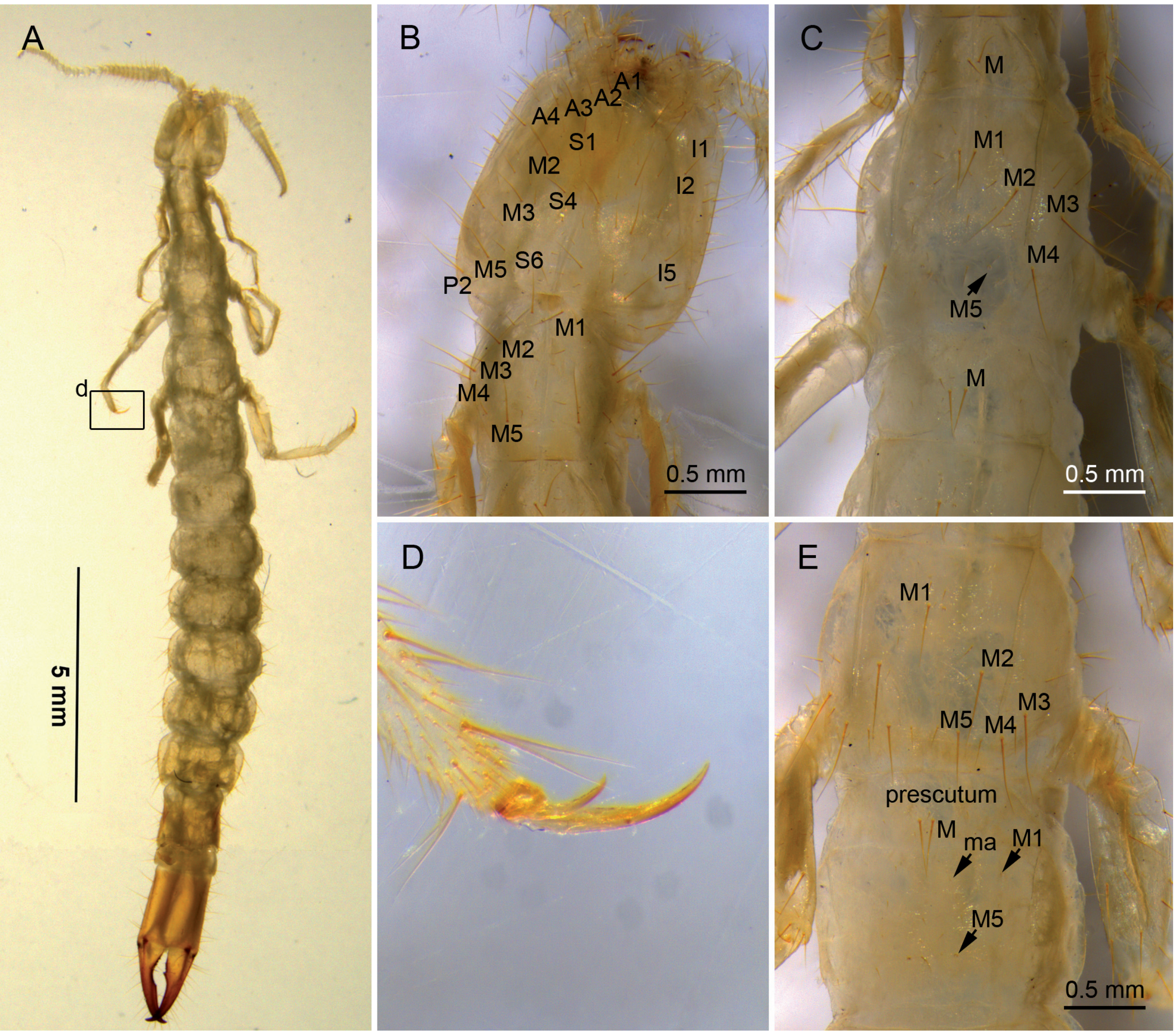

Fig. 1. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Dorsal habitus. **B**. Head and pronotum in dorsal view. **C**. Mesonotum. **D**. End of metatarsus and claws. **E**. Metanotum and first urotergite.

intersternum with 3+3 M; and metasternum with 1+1 medial anterior M, 3+3 lateral anterior M, 1+1 medial intermediate M, 1+1 sagittal M, 1+1 medial posterior and 2+2 lateral posterior M (Fig. 3D). Legs elongate, hind leg 3.6 mm long, reaching sixth abdominal segment in holotype. Femur-tibia-tarsus articulations with a row of sM setae; coxa with 1 ventral M; trochanter with 3 ventral M; femur with 8 ventral and 5 dorsal M; tibia with 4 ventral and 5 dorsal M; tarsus with 5 dorsal M and abundant sM plus two ventral rows of 4 long, thick setae. Pretarsus with two rather unequal claws and a sharp medial unguiculus; posterior claw 1.7× as long as anterior claw (Fig. 3E–F).

Abdomen. Abdominal tergites with large M, and a few sM and ms. Prescutum of urotergite I with 1+1 M, scutum with 1+1 M (ma), 1+1 M1 and 1+1 M5 (Fig. 1E); urotergites II–VII with 1+1 M (ma) and 5+5 M1–5 (Fig. 4A); urotergite VIII with 7+7 M (Fig. 4B); urite IX with 5+5 M. Urite X 1.6× as long as wide, with distinctly marked carinae; carinae with subparallel margins slightly converging towards anterior border; dorsal side with 2+2 M intracarinal D1, 3 (plus one sagittal M between D1), acropygium rounded (Fig. 6A); lateral side with 3+3 M (L1, 3, 5); ventral side with four rows of 3+3 M, 3+3 M, 2+2 M and 2+2 M (Fig. 6C). Urotergites I–VI with blunt, slightly rounded posterolateral angles; angles in tergites VII and VIII with sclerotized tip; rounded and sclerotized in tergite IX (Fig. 4). Urosternites with s and strong M. Surface of urosternite I multiperforated and with rounded protrusions (Fig. 5D); prescutum with 3+3 M; scutum with 12+12 M. Median glandular organ without setae or disculis. Lateral subcoxal organ with one row of glandular setae (GS) (19 GS in holotype; 18 GS in ♀3-paratype and 6 GS in ♀2-paratype) and one row of sensory setae (SS) (about 40 SS in holotype and ♀3-paratype); lateral

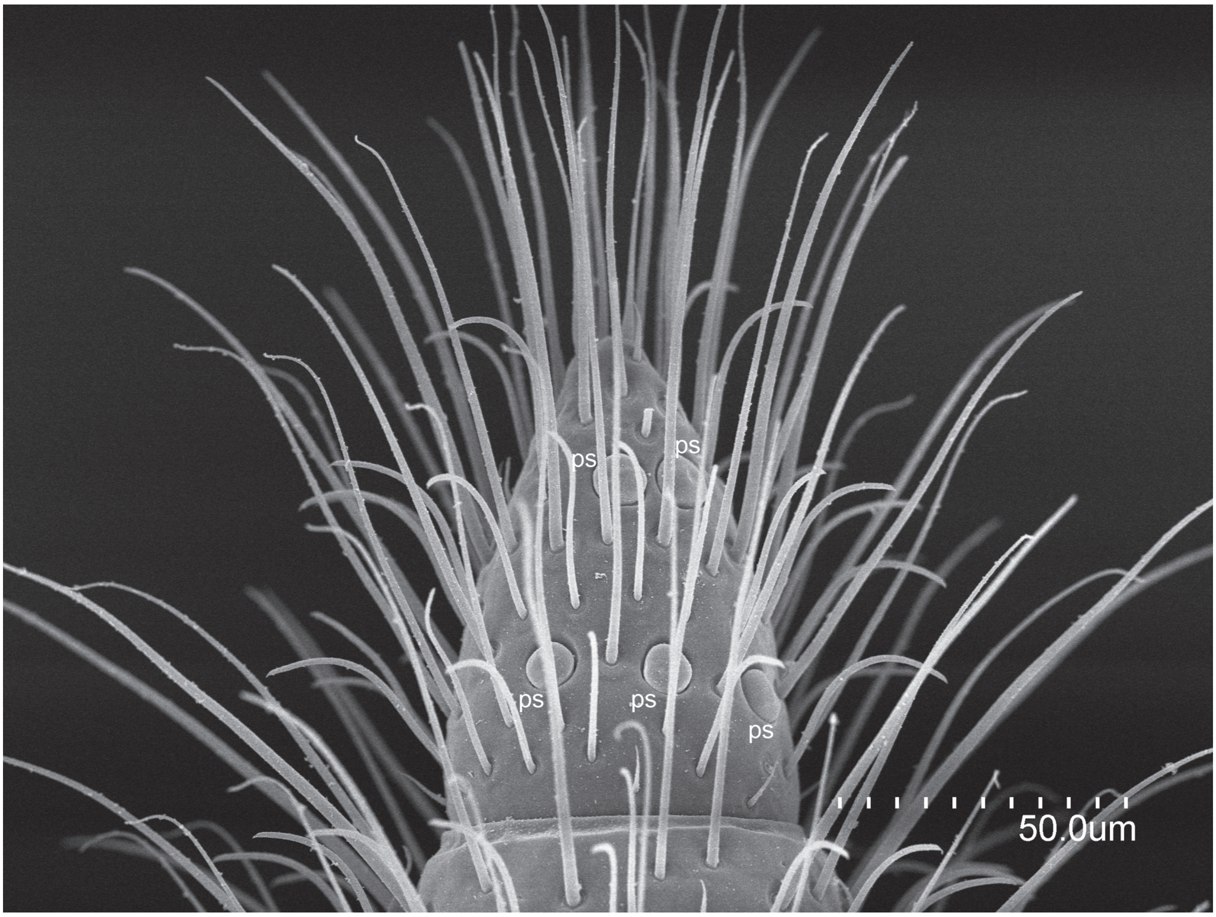

Fig. 2. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). Distal antennomere. See terminology in the text.

subcoxal organ occupying 0.2–0.3 of interstylar area; GS/st1 (stylus of first sternite) = 0.3, SS/st1= 0.15 (Fig. 5A–B, E). Urosternites II–VII with 7+7 A M, 4+4 B M, and 5+5 C M; urosternite VIII with 3+3 A M, 2+2 B M, and 3+3 C M (Fig. 5F). Cerci asymmetric, strong, well-developed, elongate, straight in the proximal half and curved in the distal half, ending in a hook (Fig. 6B, D); length ranging from

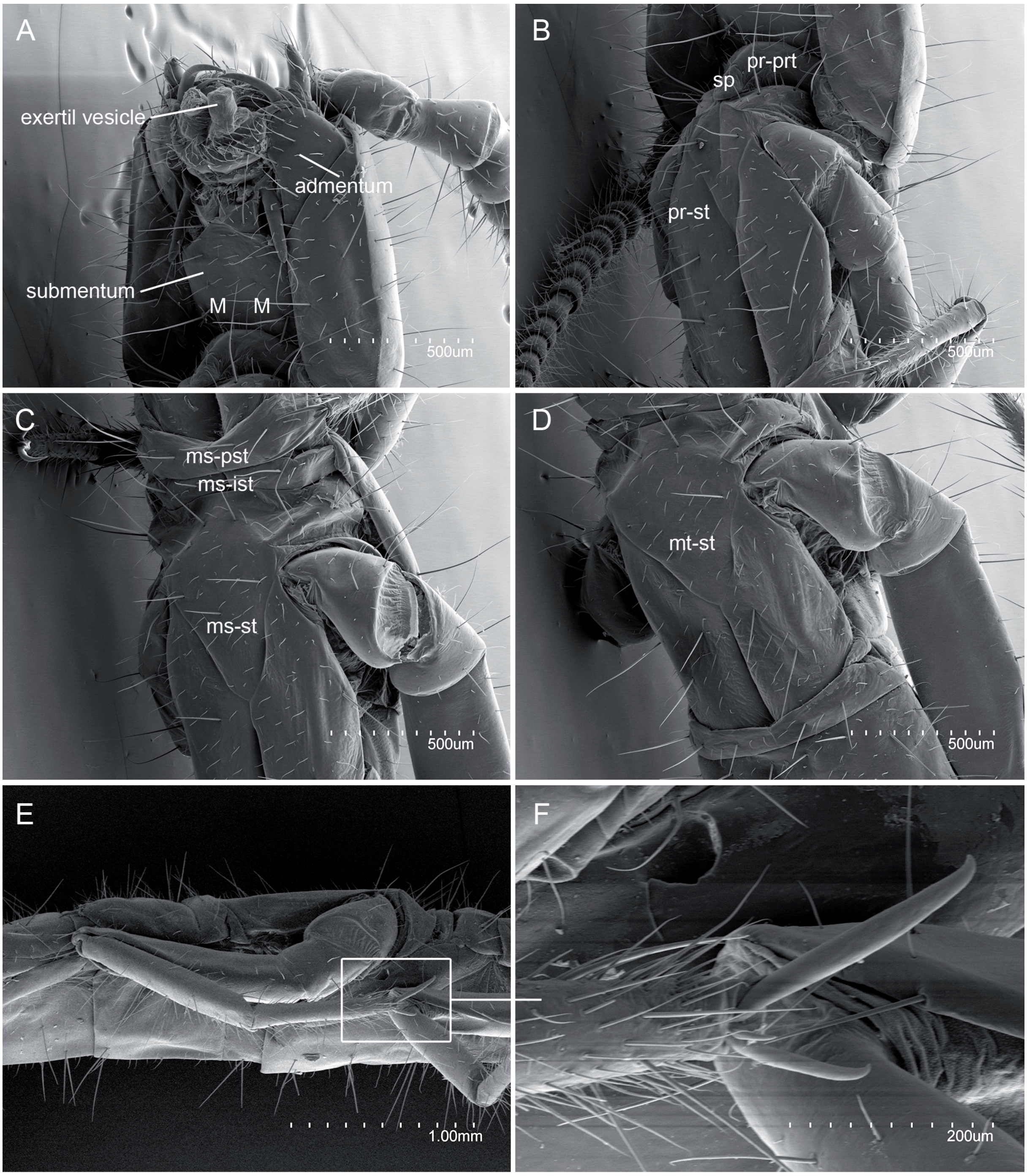

Fig. 3. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., ♀ (AS). **A**. Head in ventro-lateral view. **B**. Pro-prosternum (pr-prt) with spine (sp) and prosternum (pr-st). **C**. Meso-poststernum (ms-pst), meso-intersternum (ms-ist) and mesosternum (ms-st). **D**. Metasternum (mt-st). **E**. Lateral view of metathoracic leg. **F**. Detail of metathoracic tarsus and claws.

1.32 mm in holotype to 0.6 mm in ♀2-paratype, always slightly shorter than urite X; heavily sclerotized, with dorsal and ventral outer carinae arising from dorsal and ventral acetabular articulations; carinae extending almost to apex ventrally and halfway dorsally. Cerci dorsally concave and with the distal end slightly upward. Right cercus with postmedial tooth pointed; predental margin with a row of three round denticles; postdental margin with a row of more than 20 small denticles gradually decreasing in size until disappearing near the hook. Left cercus with two rows of denticles: superior predental row with three proximal denticles followed by 4–6 small, round denticles; inferior predental row with 12 round denticles starting with a large proximal one and ending in a very small one; the inferior row prolonged in a postdental, knife-shaped margin up to the hook, with a few tiny denticles distally. Campaniform sensilla distributed in the distal part of the cerci.

Taxonomic affinities

Austrjapyx wynbergensis sp. nov. with its premedial tooth in the right cercus and its denticles pattern, two rows in the left cercus and a single row on the right, led us to cautiously include it in the genus *Austrjapyx* following Pagés (1952) criteria. Nevertheless, a protruding knife-shaped distal margin on the left cercus of *Austrjapyx wynbergensis* separates it from the two African species of *Austrjapyx*: *Austrjapyx leleupi* Pagés, 1952 and *Japyx proditus* Silvestri, 1918, considered by Pagés (1952) as *Austrjapyx proditus* but with no formal taxonomical designation. The peculiar knife-shaped distal margin on the left cercus is not seen in the 13 species of *Austrjapyx* already described from South America where the genus is more diversified (Silvestri 1948a; Smith & Gonzalez 1964). *Autrjapyx leleupi* seems the closest species to *A. wynbergensis* sp. nov. due to seven geographical, ecological, and morphological reasons: (1) geographical proximity, both are from Africa and *A. leleupi* was collected near Mbanza-Ngungu, Democratic Republic of Congo (Central Province in the west), about three thousand kilometres to the north of the type locality of *A. wynbergensis*; (2) both inhabit cave ecosystems; (3) they exhibit an elongated body and appendages and have more than ten large and protruding placoid sensilla; (4) they

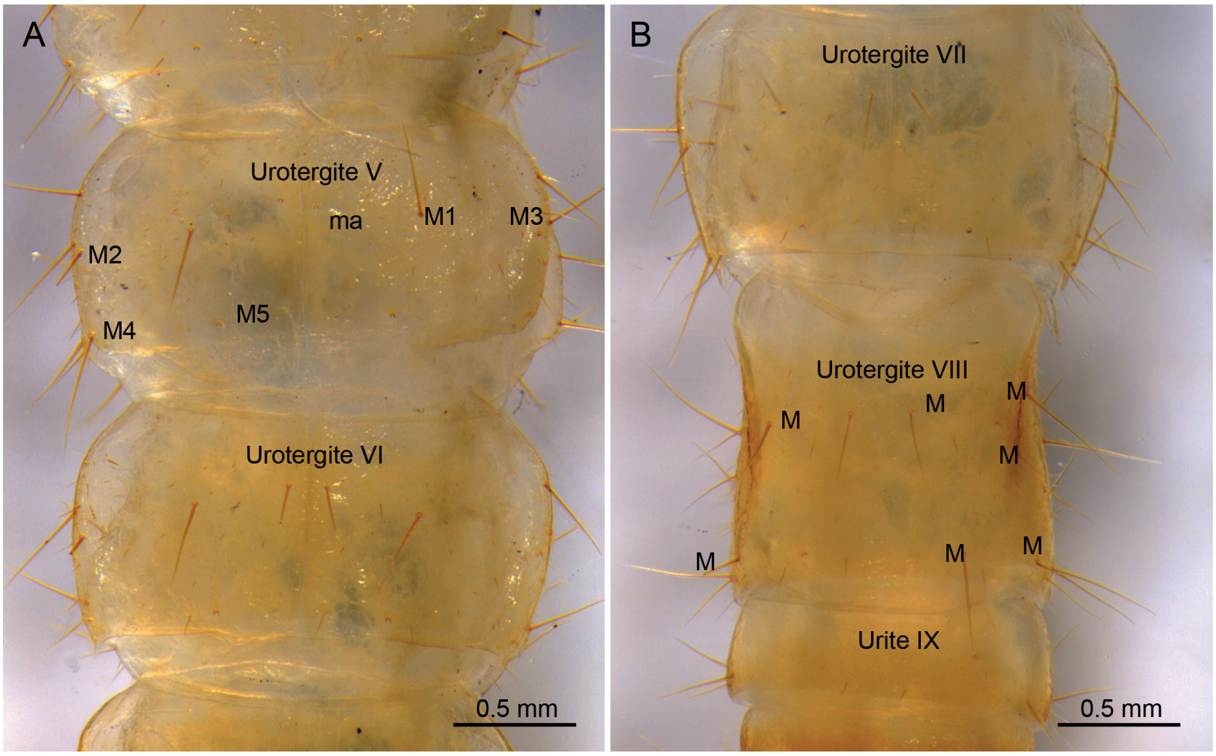

Fig. 4. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Urotergites V and VI. **B**. Urotergites VII–IX.

share the same pattern of thorax macrosetae (M); (5) there are similarities in the shape and distribution of macrosetae (M) in the abdomen; (6) their first urosternal organs, both medial and lateral, are similar; and (7) both have roundish lateral angle urotergites. Despite the similarities, *A. wynbergensis* differs from *A. leleupi* in at least five morphological features: (1) the knife-shaped distal on the left cercus' margin;

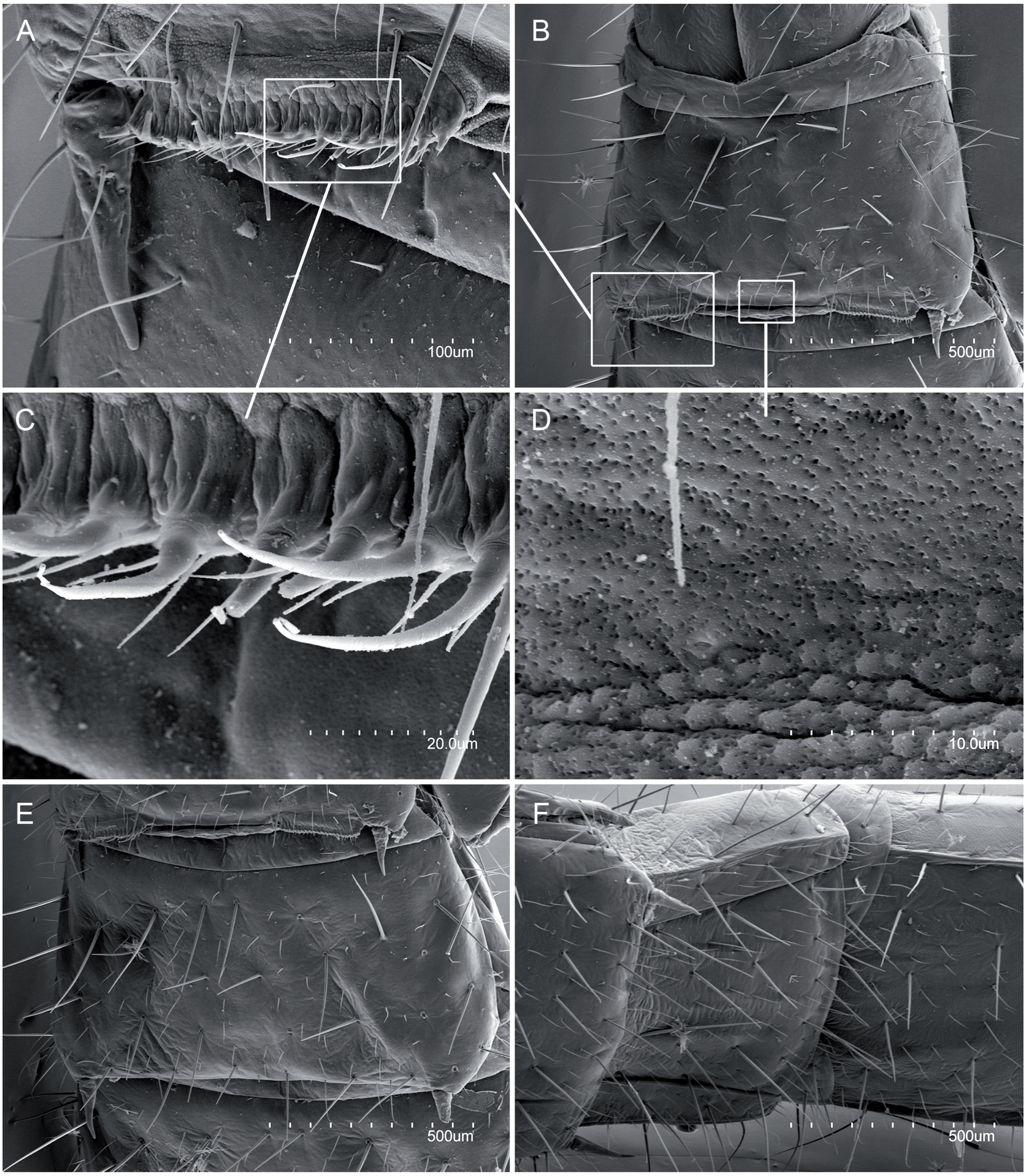

Fig. 5. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., 2-paratype, ♀ (AS). **A**. Lateral organ of urosternite I in B. **B**. Urosternite I. **C**. Detail lateral organ of the first urosternite. **D**. Micropores in posterior part of urosternite I. **E**. Urosternite II. **F**. Abdominal segments VII–X in latero-ventral view.

(2) 30 antennomeres in *A. leleupi* instead of 31 in *A. wynbergensis*; (3) scutum of urotergite I with 3+3 macrosetae (M) in *A. wynbergensis*, that are absent in *A. leleupi*; (4) no small setae or pseudospores visible in medial organ in *A. wynbergensis*, but a dozen in *A. leleupi*; and (5) 2+2 macrosetae (M) on dorsal side of utite X in *A. wynbergensis*, instead of 4+4 M in *A. leleupi*.

Habitat

The Wynberg Cave, along with other caves (such as Bats, Climbers, Giants, Hangman, Metro, and Smugglers caves), forms the largest cave system in the Cape Peninsula region (with more than 1.2 km in length), which is referred to as the Wynberg Cave System (WCS; Ferreira *et al.* 2020) (Fig. 7). The caves are associated with quartzite rocks, occurring at altitudes ranging from 450 m to 750 m a.s.l. The region presents a temperate climate, with hot and dry summers and cold and humid winters (Marker & Swart 1995). The average temperature inside the caves is around 10°C (Sharratt 1998). Most caves within the Table Mountain National Park are located at relatively high altitudes, presenting predominantly vertical passages of different sizes. The WCS presents a remarkable cave-restricted fauna, especially if we consider the endemicity and rarity of some species. Ferreira *et al.* (2020) listed 19 cave-restricted species occurring in the WCS and is one step closer to becoming a subterranean biodiversity hotspot (Ferreira *et al.* 2020).

Sharratt (1998) mentioned the presence of a troglobitic Dermaptera DeGeer, 1773 in the WCS. It is possible that the authors misidentified the specimens of *Austrjapyx wynbergensis* sp. nov. given the

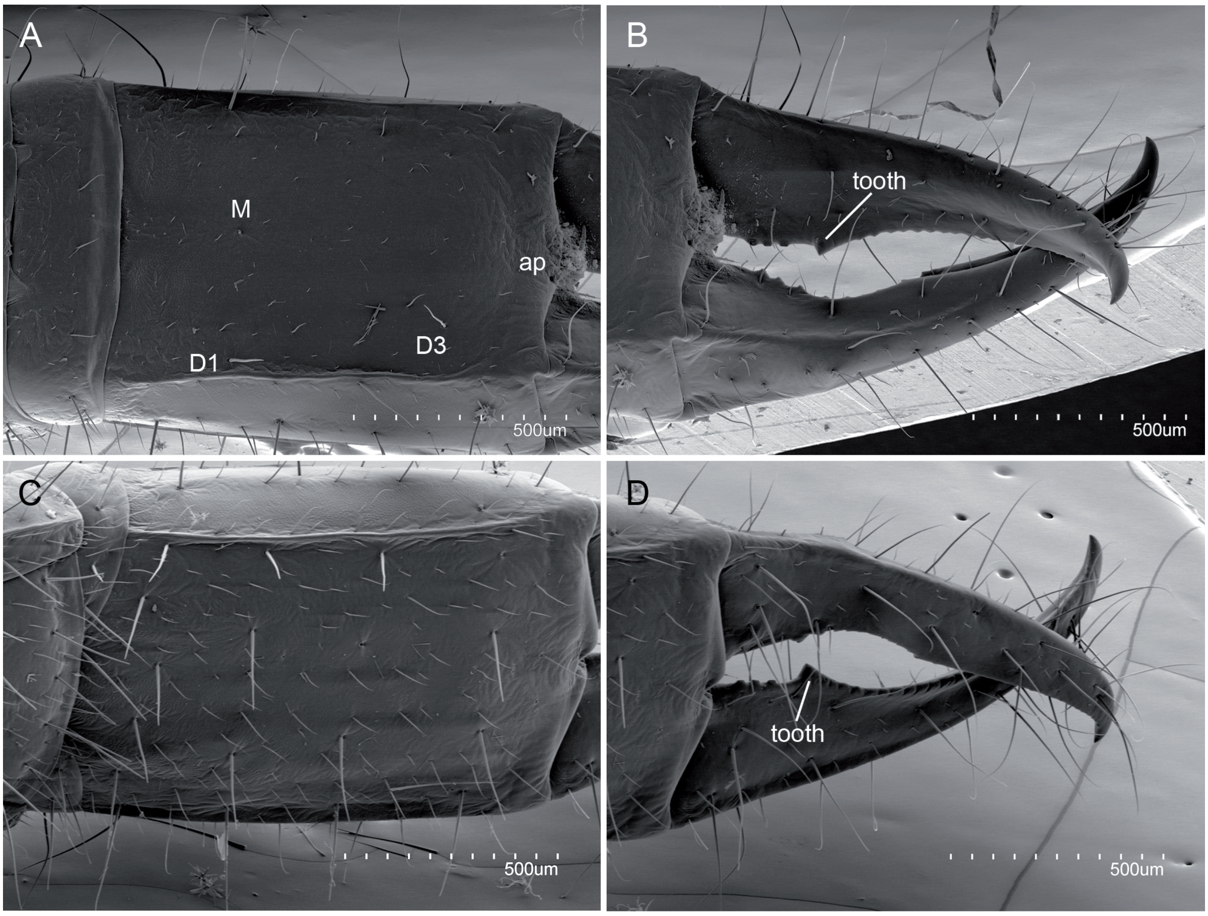

Fig. 6. *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Abdominal segments IX and X in dorsal view. **B**. Cerci, dorsal view. **C**. Abdominal segments VIII–X in latero-ventral view. **D**. Cerci, ventral view.

Fig. 7. Location and habitat of *Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov. **A**. External area at the Table Mountains in the surroundings of the Wynberg cave. **B**. Wynberg cave interior, general appearance. **C**. Living specimen of *Austrjapyx wynbergensis*.

morphological similarities with eyeless earwigs (Ferreira *et al.* 2020). Hence, the new species herein described may have been known for the last two decades.

The two specimens of *Austrjapyx wynbergensis* sp. nov. in this study were found under fallen rocky blocks in the lower level of the cave. This species is quite rare since Sharratt (1998) registered only a few specimens found in the Wynberg and Bats caves in deep cave zones (assuming that this species corresponds to the troglobitic Dermaptera mentioned by that author). Unfortunately, there are no data regarding any biological aspects for this new species despite having been registered on the WCS for a long time.

The main threat to cave species in the Table Mountain area is human visitation (Sharratt 1998; Ferreira *et al*. 2020). The uncontrolled recreational use of these caves crushes the fauna and alters the micro-habitats. Additionally, such activities can pollute terrestrial and aquatic environments with waste (including batteries containing toxic chemicals). Furthermore, these visits can disturb the bat population and alter the cave's temperature and moisture conditions. Ferreira *et al.* (2020) verified several impacts in the cave, such as graffiti on the walls and passages with intense trampling. We need to implement emergency measures to ensure the conservation of this cave from the uncontrolled human impact (Ferreira *et al.* 2020).

Genus ***Imazighenjapyx*** Sendra & Sánchez-García gen. nov.

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Type species

Imazighenjapyx marocanus Sendra & Sánchez-García gen. et sp. nov.

Diagnosis

Body large and elongate; epicuticle reticulate; abdominal segment X with micropores at high magnification. Antennae with 41 antennomeres; medial and distal antennomeres with a few ms and abundant s setae, plus two whorls of micro-barbed sM setae; apical antennomere with abundant placoid sensilla (up to 24). Pronotum, mesonotum, and metanotum with 5+5 M1−5. Prosternum with up to 72 M; meso-poststernum with up to 19 M; meso-intersternum with up to 22 M; mesosternum with up to 84 M; meta-poststernum with up to 26 M; meta-intersternum with up to 21 M; and metasternum with up to 99 M; scutum urotergite I with 1+1 M5; urotergite II with 10 M; urotergites III–VII with 12 M; urite X with 17 M, ventral side with 52 M setae; urosternite I with up to 120 M setae on scutum, plus 200 sM setae on posterior position. Median glandular organ with abundant pseudospores; each lateral subcoxal organ with one row of glandular setae and one row of sensory setae; urosternites II–III with about 140 M setae; urosternites IV–VII with about 160 M setae; urosternite VIII with about 50 M setae between two well-defined carinae; cerci asymmetric with subsymmetric teeth, rectilinear along the proximal half, and curved in the distal half. Cerci with concave top side and with distal end up; right cercus with pointed medial tooth, predental margin bearing two rows of denticles; very protruded postdental margin looking like a scraper shape with a row of denticles; left cercus predental margin with three rows, postdental margin with small round denticles ending before the hook.

Etymology

The genus name is a combination of the prefix *Imazighen* and the suffix *Japyx*. Berbers call themselves Imazighen, which means 'free men' or 'noble men'.

Imazighenjapyx marocanus Sendra & Sánchez-García gen. et sp. nov.

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Figs 8–15

Etymology

The specific name refers to the country of origin, Morocco.

Type material

Holotype

MAROC • ♀; Agadir-Ida Outanane region, Imi Ougoug Cave; 30°36′44.83″ N, 9°28′1.64″ W; 26 Feb. 2020; Rodrigo Lopes Fereira leg.; labelled "♀-holotype-MHNM-ZAD01"; MHNM.

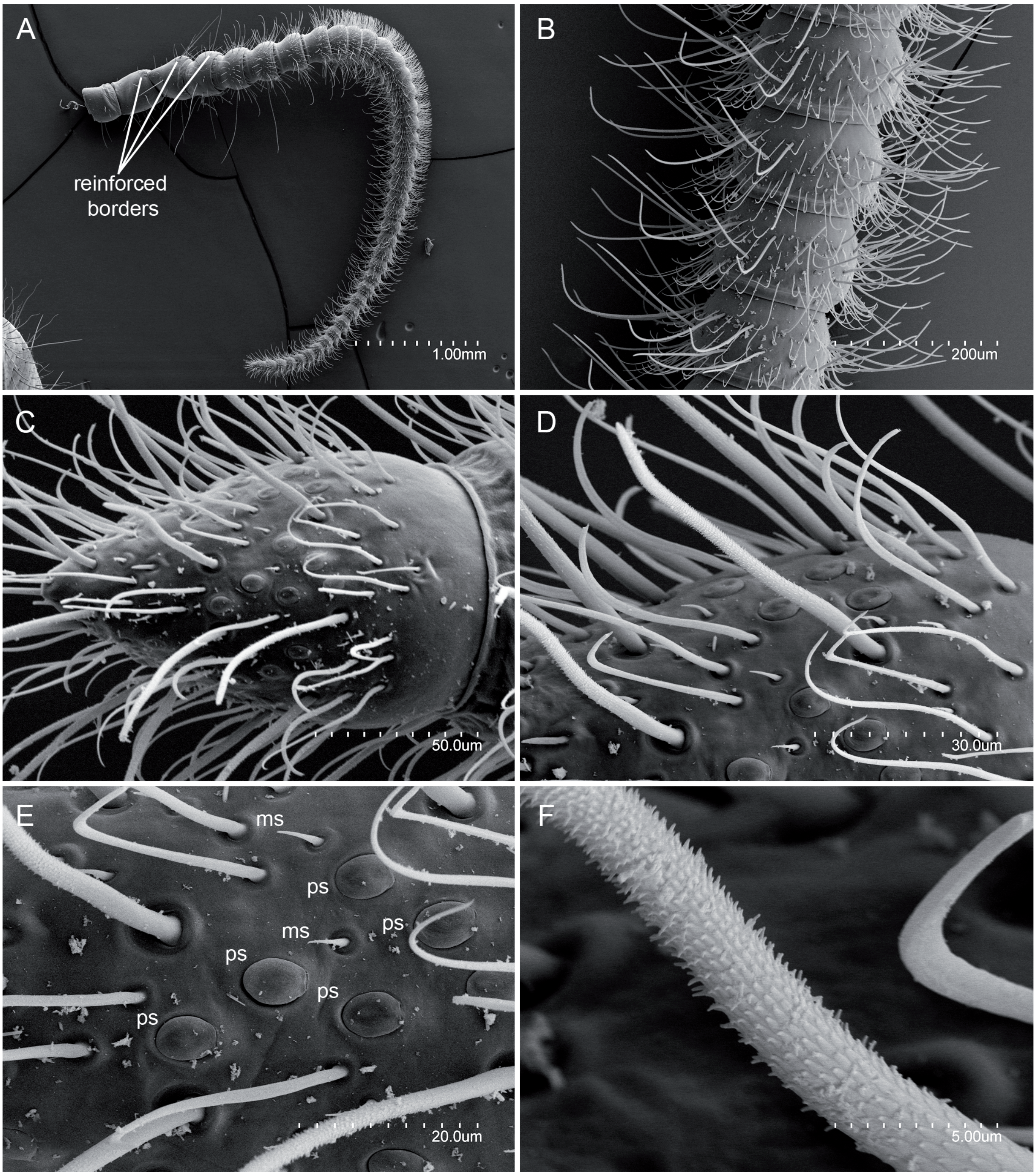

Fig. 8. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Antennae. **B**. Central antennomeres. **C**. Apical antennomere. **D**. Lateral side of the apical antennomere. **E**. Detail of apical antennomere. **F**. Detail of antennal micro-barbed sM setae.

Description

Body. Elongate (Fig. 15C–D), length 26 mm; maximum width at urotergite VII 2.6 mm. Epicuticle reticulate under optical microscope; with micropores at higher magnifications (urite X with 4 micropores/μm^2, diameter 0.10–0.14 µm (Fig. 11B). Cuticle unpigmented, with sclerotized areas on mandible tips, femoral and tibial condyles, ventral apodemes of abdominal segment VIII, distal part of styles, abdominal segment X, and cerci. Body and appendages covered with very abundant ms setae as well as s, sM, and M, in addition to abundant mbsM on antennae.

Head. Antenna length 8.6 mm, 0.33× length of body, with 41 antennomeres; basal antennomere short, followed by three slightly longer antennomeres with reinforced borders visible on ventral side; medial antennomeres as long as wide (Fig. 8A–B). Proximal antennomeres with ms, s, and a few long M; medial and distal antennomeres with a few ms and abundant s setae plus to two whorls of mbsM (Fig. 8B); apical antennomere with s and mbsM and about 24 placoid sensilla distributed in 4–5 groups (Fig. 8C–F). Trichobothria present on antennomeres IV–VI in a 2/3/3 pattern, with *a* trichobothria (dorsal one) in proximal position. Head with a few *s* setae and M and abundant ms setae; on dorsal side 14+14 M: A1,

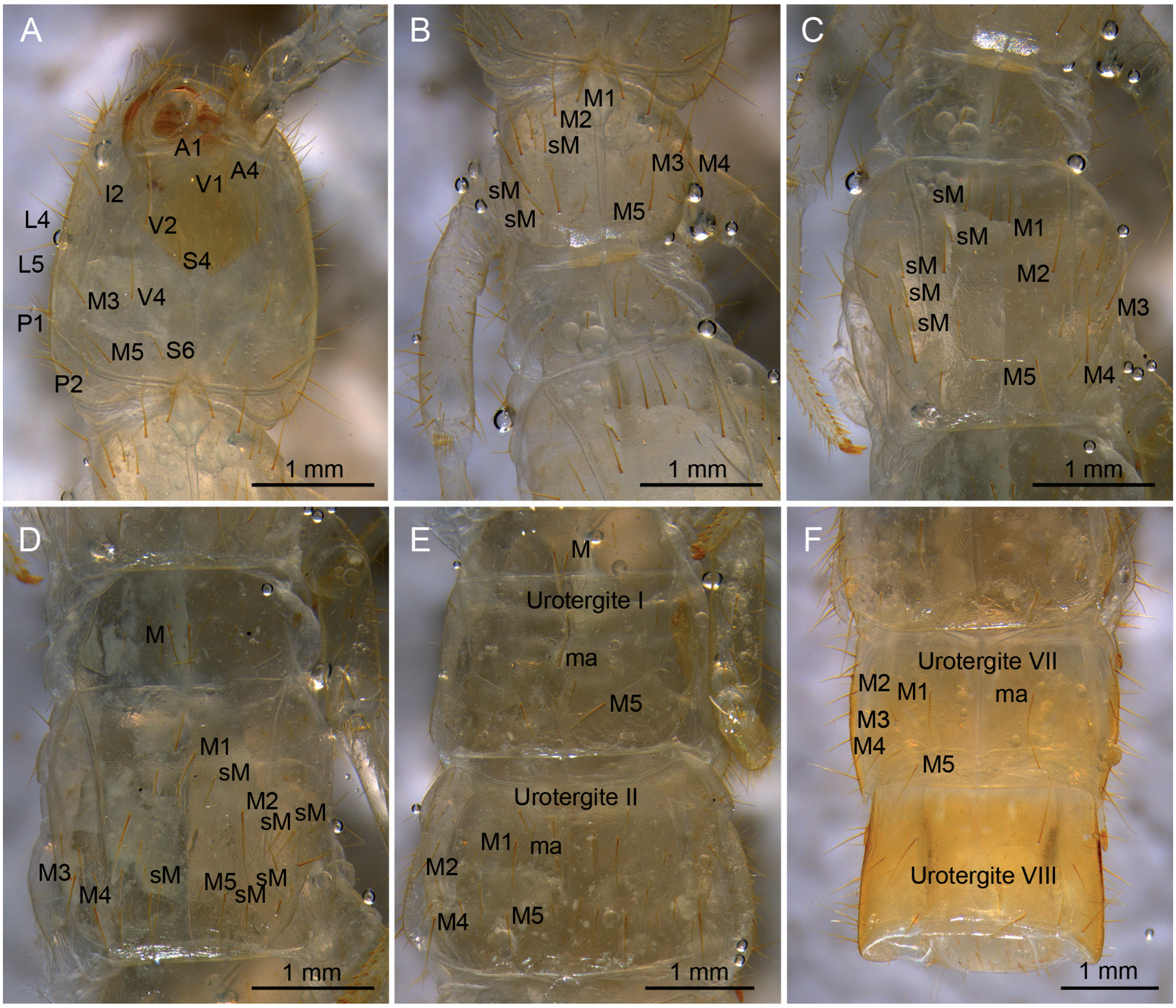

Fig. 9. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Dorsal side of head and anterior part of pronotum. **B**. Pronotum and anterior part of mesonotum. **C**. Mesonotum. **D**. Metanotum. **E**. Urotergites I and II. **F**. Urotergites VII and VIII.

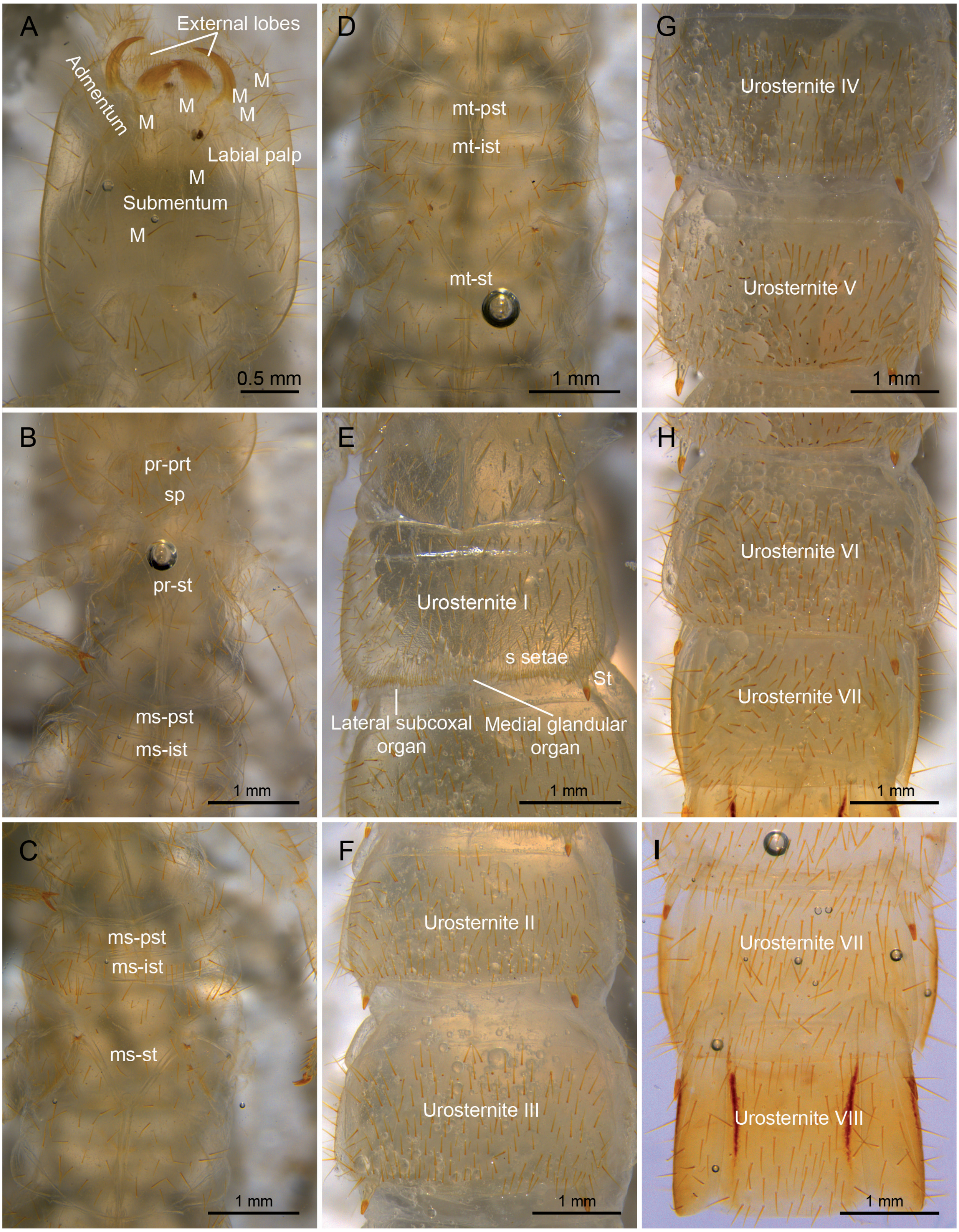

Fig. 10. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Ventral side of head. **B**. Pro-prosternum (pr-prt) with spine (sp), prosternum (pr-st), meso-poststernum (ms-pst), and meso-intersternum (ms-ist). **C**. Mesosternum (ms-st). **D**. Meta-poststernum (mt-pst), meta-intersternum (mt-ist), and metasternum (mt-st). **E**. Urosternite I. **F**. Urosternites II and III. **G**. Urosternites IV and V. **H**. Urosternites VI and VII. **I**. Urosternites VII and VIII.

4, S4, 6, V1−2, V4, M3, M5, I2, L4−5 and P1−2 (Fig. 9A); on ventral side: submentum with large 2+2 M in anterior and posterior position plus 5+5 sM, admentum with 3+3 M, mentum at base of labial palps with 2+2 M; external lobes of mentum with abundant sM; the pair of the exertil vesicles of the external lobes visible in the holotype (Fig. 10A). Labial palp 4× as long as wide, with one proximal sM and seven medial and distal sM. Lacinia falciform, well sclerotized, with the five laminae pectinate.

Thorax. Thoracic segments elongate, with a few s and abundant ms setae. Pronotum with 5+5 M1−5 and 6+6 sM; prescutum of mesonotum with 1+1 M; mesonotum with 5+5 M1−5 and 6+6 sM; prescutum of metanotum with 1+1 M and 3+3 sM; metanotum with 5+5 M1−5 and 11+11 sM (Fig. 9B–D). Thoracic sternites, intersternites, and presternites well-defined with ms, s, and M; sM difficult to distinguish from M so they have all been counted as M (Fig. 10B–D). Pro-presternites and pro-, meso- and metasternites with internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); only in pro-presternites the prolongation of the posterior branch (spine) is visible on the surface (Denis 1949). Pro-presternum with 4+5 M; prosternum with 6 medial anterior M, 7+7 lateral anterior M, and 26+26 lateral posterior M; meso-poststernum with 10+9 M; meso-intersternum with 11+11 M; mesosternum with 12 medial anterior M, 11+11 lateral anterior M, and 25+25 posterior M; meta-poststernum with 14+12 M; meta-intersternum with 11+10 M; metasternum with 19 medial anterior M, 12+14 lateral anterior M, and 20+24 posterior M (Fig. 10B–D). Legs slightly short, hind leg 4.9 mm long, reaching third abdominal segment. Femur-tibia-tarsus articulations with a row of sM; coxa and trochanter with 9 ventral M; femur with 6 ventral and 5 dorsal M; tibia with 6 ventral and 3 dorsal M; tarsus with 3 dorsal M and abundant sM plus two ventral rows of seven and six thick setae and a calcar at ventral apex thicker than other M. Pretarsus with two short, thick, unequal claws and a sharp medial unguiculus.

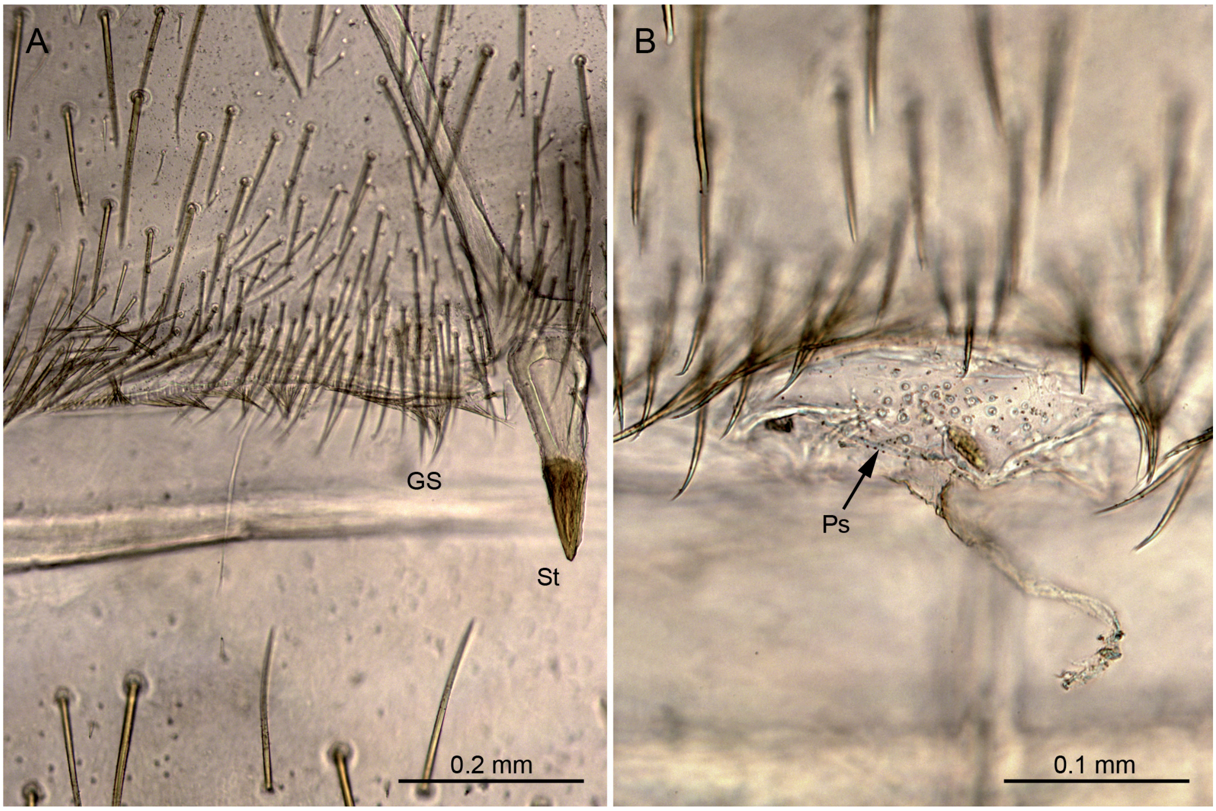

Fig. 11. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Lateral posterior part of first urosternite. **B**. Median glandular organ. Abbreviations: GS = glandular setae; Ps = pseudospores; St = stylus.

Abdomen. Abdominal tergites with scarce s and sM. Prescutum of urotergite I with 1+1, scutum with 1+1 sM (ma), 1+1 M5 and 2+1 sM; urotergite II with 1+1 sM (ma), 2+2 M1−2, and 2+2 M4−5; urotergites III–VII with 1+1 ma and 5+5 M1–5; tergite VIII with 5+5 M1−5; urite IX with 8+8 ventral M (Fig. 9E–F). Urite X (Fig. 12A–D) 1.8× as long as wide, with distinctly marked carinae; carinae with subparallel margins slightly converging towards posterior border; dorsal side with 6+6 M intracarinal (D1−6 M), 1+1 M between D2, one sagittal M between D4, 1+1 M between D6 (Fig. 12A), acropygium rounded (Fig. 12A); lateral side with 7+7−8+8 M (L), and several sM (Fig. 12C); ventral side with 52 M setae apparently arranged in 6 rows from right lateral side to left lateral side (Fig. 12D). Urosternites with scarce ms and s setae and abundant sM and short M. Prescutum of urosternite I with 12+13 M; scutum with up to 120 M plus 200 sM on posterior position (Fig. 10E). Median glandular organ with abundant pseudospores (Ps), more than 30 (Fig. 11B). Lateral subcoxal organ with one row of about 120 glandular setae (GS) and one row of 140 sensory setae (SS); lateral subcoxal organ occupying 0.38× of interstylar area; GS/st1 (stylus of first sternite) = 0.3; SS/st1= 0.08 (Fig. 11A). Urosternites II–III with about 140 M; urosternites IV–VII with about 160 M; urosternite VIII with about 50 M between two well-defined carinae plus 5+5 M on lateral side of carinae (Fig. 10F–I). Cerci asymmetric, strong, length 2.3 mm, straight in the proximal half and curved in the distal half, becoming a large hook towards apex; heavily sclerotized with dorsal and ventral outer carinae arising from dorsal and ventral acetabular articulations; carinae extending

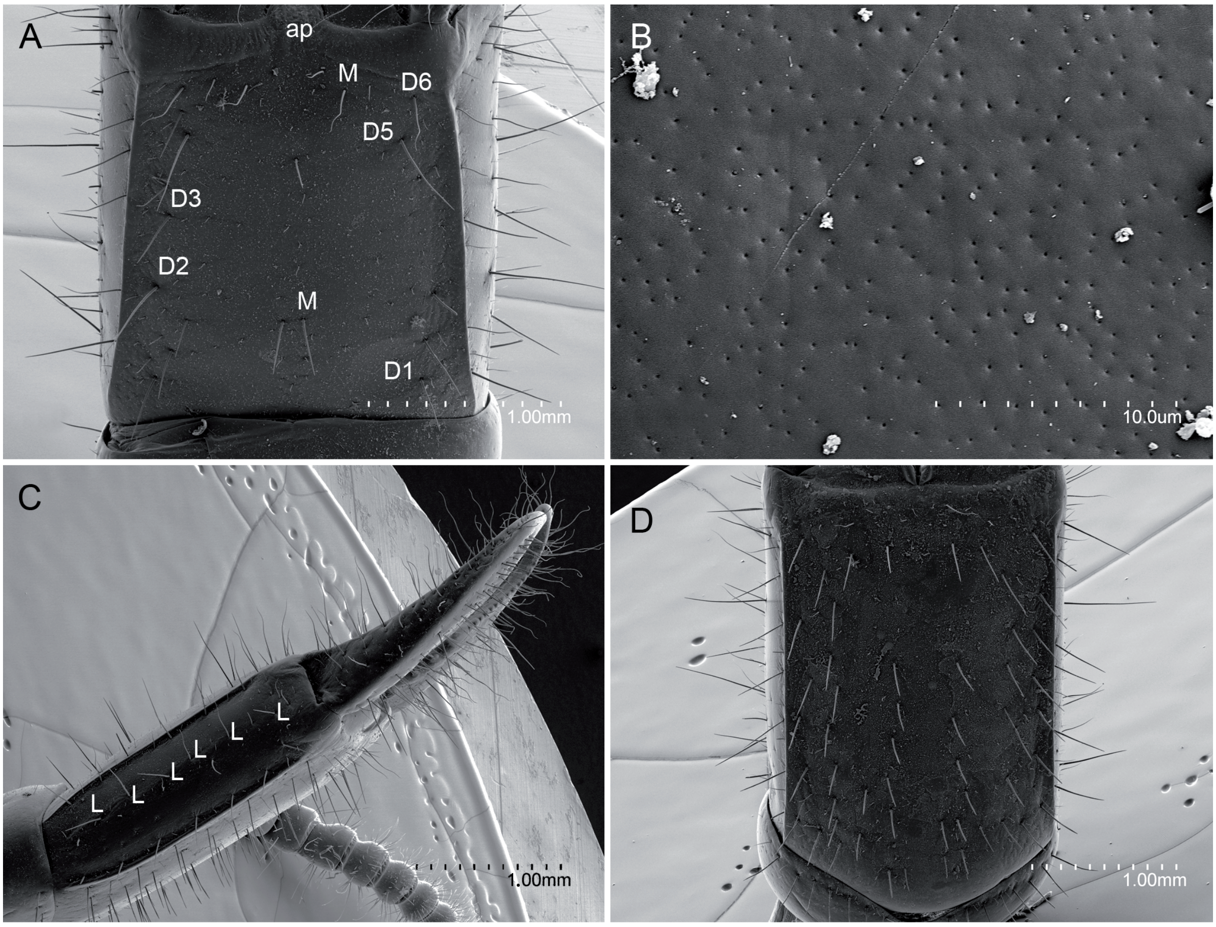

Fig. 12. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Abdominal segment X, dorsal view. **B**. Detail of abdominal segment X, dorsal view. **C**. Lateral view of abdominal segment X and cerci. **D**. Abdominal segment X, ventral view.

to apex ventrally and almost reaching the apex dorsally (Figs 13A, 14A–B). Cerci dorsally concave and with the distal ends upward (Fig. 12C). Teeth subsymmetrical. Right cercus with medial tooth pointed; predental margin with two rows of 3+3 small round denticles; postdental margin scraper-like, very protruding, with a row of 15 denticles terminating near the hook. Predental margin of left cercus with three rows of 8+5+7 denticles (superior and intermediate rows with round denticles; inferior row with pointed denticles) terminating at medial large tooth; postdental margin with 11 small round denticles terminating before the hook. Right cercus with 18, 32, 30 M (dorsal, lateral, and ventral); left cercus with 19, 30, 30 M (dorsal, lateral, and ventral). Campaniform sensilla present on hook and inner margins of cerci (Figs 13–14).

Taxonomic affinities

Following Paclt (1957a) *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov. resembles *Indjapyx* in the morphology of the cerci with two predental rows on the right and left margins, and in simple lateral subcoxal organ with pseudospores on the medial organ. The genus *Indjapyx* has 27 described species, all of which are from southern mainland Asia and islands (Pagés 1984, 1994, 2002). As pointed out by Silvestri (1930a) and Pagés (1984), a distinctive feature of *Indjapyx* is the proximal position of the *a* trichobothria (dorsal one), which is also present in *Imazighenjapyx marocanus* gen. et sp. nov. However, *I. marocanus* lacks the typical abundant ms setae on dorsal head and shows

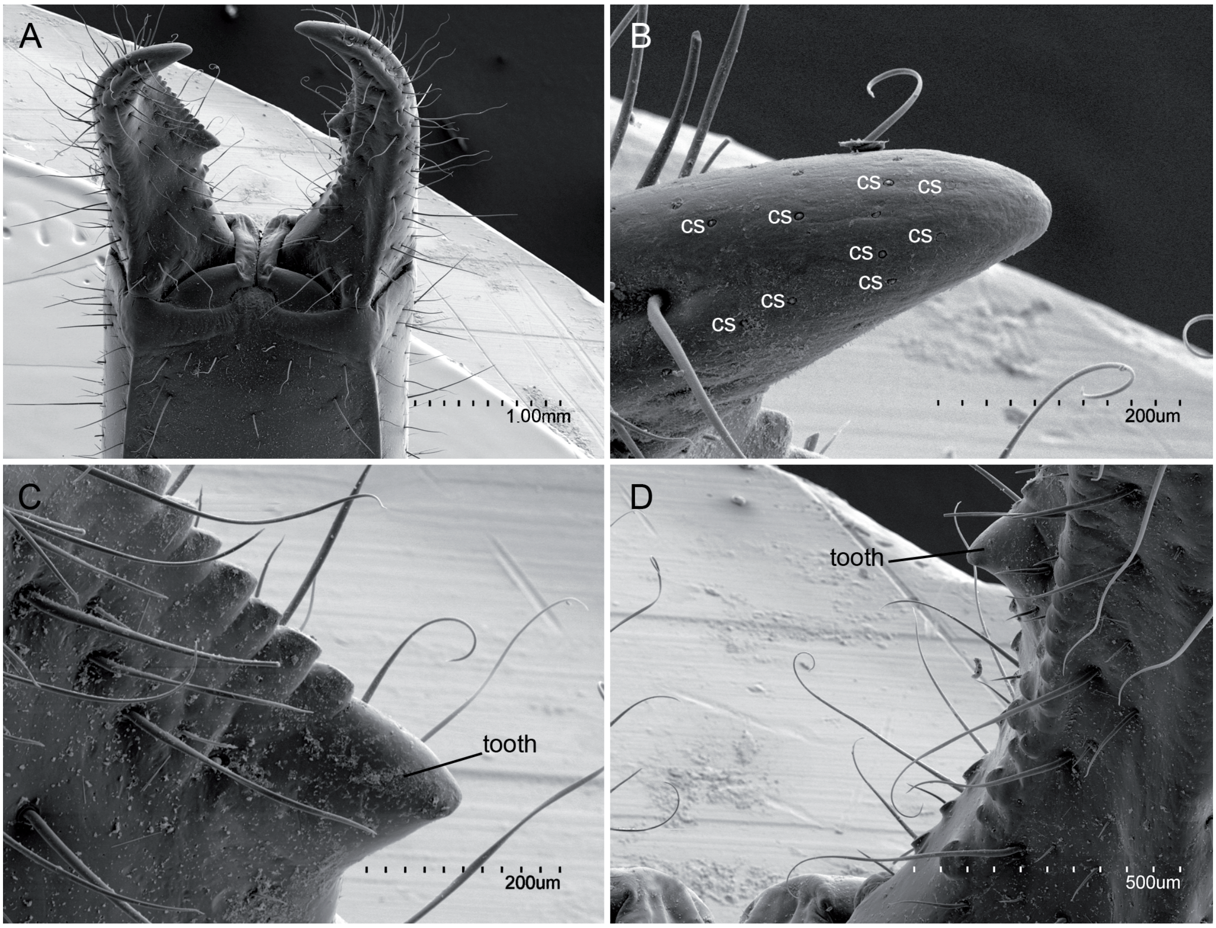

Fig. 13. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Terminal part of abdominal segment X and cerci in dorsal view. **B**. Tip of right cercus. **C**. Medial part of inner side of right cercus. **D**. Proximal to medial part of inner side of right cercus.

three characters unknown in other japygid taxa: the right cercus has a highly protruding, scraper-like postdental margin; the numerous thoracic macrosetae (prosternum with 72 M, mesosternum with 84 M and metasternum 89 M); and the singular micro-barbed sM on antennomeres.

Habitat

Imi Ougoug is a limestone cave located 43 kilometres northeast of Agadir City, at the bottom of a cliff overlooking the Talmat River. The cave is 1097 meters long. It has a low entrance leading to a narrow zig-zag passage that bifurcates after 10 meters; on the left, the largest upstream segment leads to a large chamber (32 m long and 9 m high in the middle). This part is separated into two sections that end with siphons. On the right, a sinuous path with casings and basins continues alternately and terminates 435 m from the entrance, at -65 m, on a little siphoning lake (Fig. 15).

Forty meters from the entrance, a single specimen of *Imazighenjapx marocanus* gen. et sp. nov. was discovered in the right branch. The specimen was found on the cave wall in a lateral overflow of the meander between a temporary waterfall and the first lake.

The entrance's morphology, which is completely rounded, and all other morphological elements clearly indicate a losing stream function for the downstream part (right): pebbles and a giant's kettle indicate

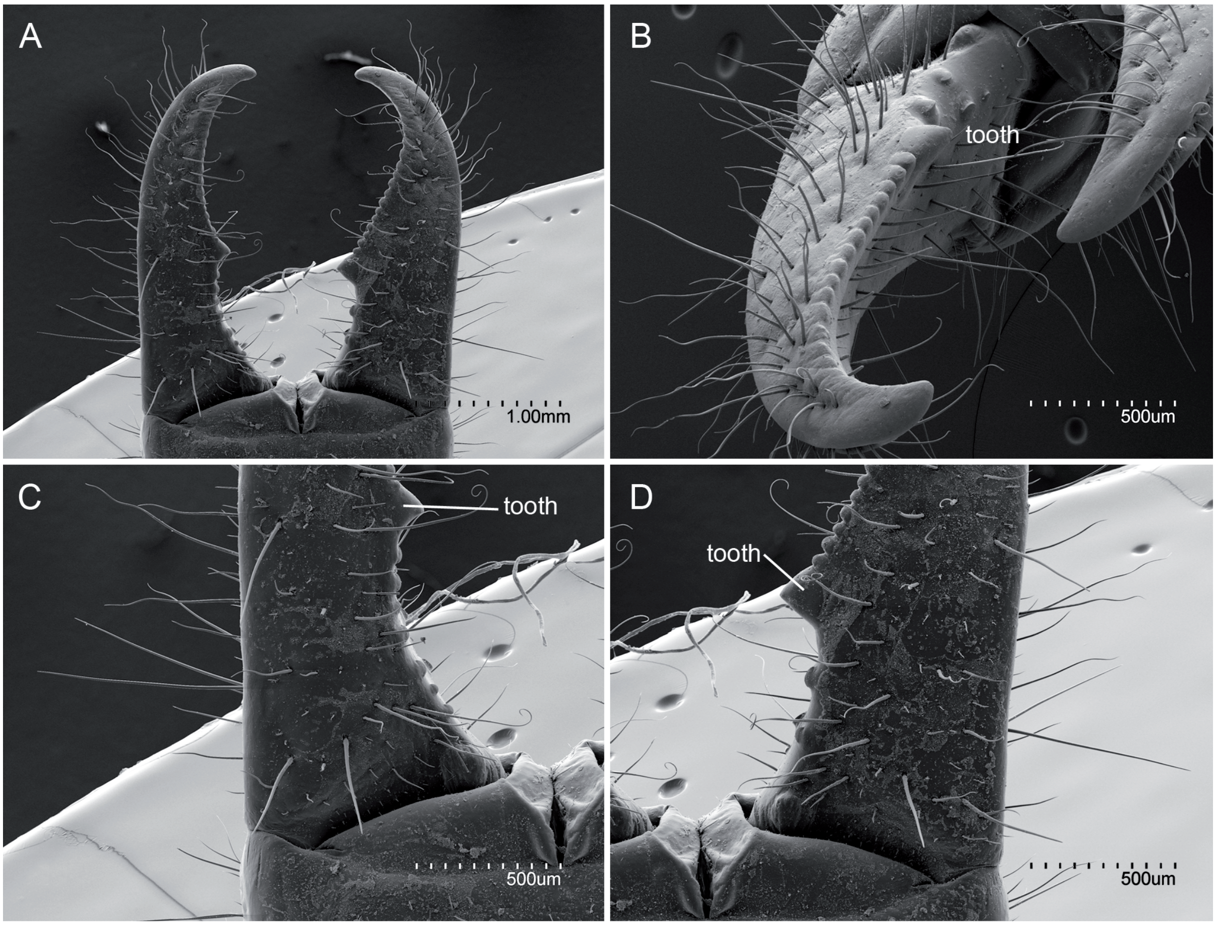

Fig. 14. *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov., holotype, ♀ (MHNM). **A**. Cerci, ventral view. **B**. Detail of right cercus in ventro-lateral view. **C**. Right cercus, ventral view. **D**. Leaft cercus, ventral view.

a free flow. Many ancient stalagmitic masses that eroded and polished with a marble appearance stand noticeably. However, it appears that in the event of a severe flood, the cavity will almost completely fill up.

Fig. 15. Location and habitat of *Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov. **A**. External area in the surroundings of the Imi Ougoug cave the arrow indicates the location of the cave entrance). **B**. Imi Ougoug cave interior general aspect. **C**–**D**. Living holotype specimen.

After “Win-Timdouine” Cave, this is the region’s second most touristic cave. It has several names: “Ifri Ouado”, a Berber term that means “the blowing cave” due to the air current that comes out of it. The other name for the cave is “grotte des araignées,” which means “cave of spiders” referring to the large quantity of opilions that can be found there behind the entrance.

Genus *Opisthjapyx* Silvestri, 1929

Opisthjapyx naledi Sendra & Sánchez-García sp. nov.
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Figs 16–23

Etymology

The epithet *naledi* refers to *Homo naledi*, an extinct hominid species discovered within the Dinaledi chamber located in the Rising Star Cave, a World Heritage Site in South Africa. The cave where the japygid was found is located on the same hill as Rising Star Cave and separated approximately 425 meters.

Type material

Holotype

SOUTH AFRICA • ♀; Gauteng Province, Maquassi Hills Municipality, Villa Louisa Cave; 26º01′25.5″ S, 27º42′43.0″ E; 9 Oct. 2019: Rodrigo Lopes Ferreira leg.; labelled “♀-holotype, SAM-ENW-C015127”; ISAM.

Description

Body. Elongate, length 27.5 mm, maximum width at urotergite VII 2.6 mm. Epicuticle smooth under optical microscope; with few micropores visible at higher magnifications (dorsal side of urite X with 1 micropore per 10 μm^2, diameter 0.6–0.7 μm) (Fig. 21B). Cuticle unpigmented with slightly sclerotized areas on dorsal frontal head, mandible tips, femoral and tibial condyles, abdominal segments VIII−X, and cerci.

Head. Antenna length 9.5 mm, 0.35× length of body, with 49 antennomeres; basal antennomere short, followed by two slightly longer antennomeres; antennomeres I−IV with reinforced borders visible on ventral side (Fig. 16C); medial antennomeres 1.1× wider than long (Fig. 16B). All antennomeres with M and a few ms setae, plus three whorls of mbsM (Fig. 16A–C). Trichobothria present on antennomeres IV–VII in a 3/4/4/4 pattern, with *a* trichobothria in central position (Fig. 16C). Apical antennomere with 16–18 placoid sensilla distributed in three irregular groups; penultimate antennomere with two placoid sensilla (Fig. 16A–B). Dorsal and ventral side of head with abundant sM and ms uniformly distributed and apparently without M (Fig. 17A); on ventral side: submentum with 2+2 M in anterior position plus 2+2 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 sM and the pair of exertil vesicles visible (Fig. 18A). Labial palp short, length 0.24 mm, 3.2× as long as wide, with one proximal sM and four medial and distal sM plus several ms. Lacinia falciform, well sclerotized, all five laminae large and pectinate.

Thorax. Thoracic segments elongate, with extra M, several sM, and abundant ms uniformly distributed. Pronotum with 5+5 M1−5 plus extra 6+5 M; prescutum of mesonotum with 1+1 M; mesonotum with 5+5 M1−5 plus extra 4+4 M; prescutum of metanotum with 1+1 M, metanotum with 5+5 M1−5 plus extra 4+4. (Fig. 17B–D). Thoracic sternites, intersternites, and presternites defined, with ms, sM and M (Fig. 18A−D). Pro-presternites and pro-, meso- and metasternites with strong internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962), only in pro-presternites the prolongation of posterior branch (spine) is visible on the surface (Denis 1949). Pro-presternum with no clearly defined limits, spine with apparently 3+3 M and some sM; prosternum with about 70 M or sM well distributed

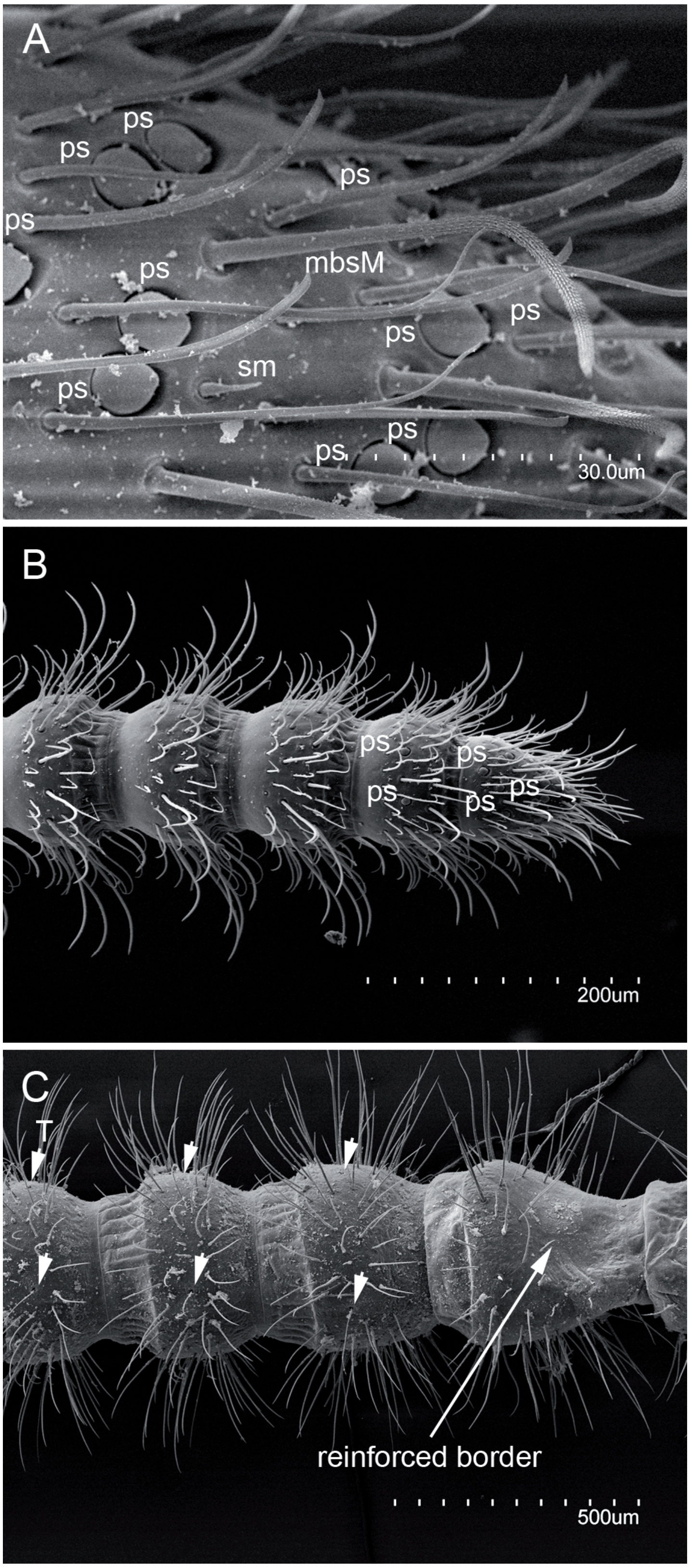

Fig. 16. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Detail of placoid sensilla on distal antennomere. **B**. Distal antennomeres. **C**. Proximal antennomeres, arrows indicate the position of some trichobothria.

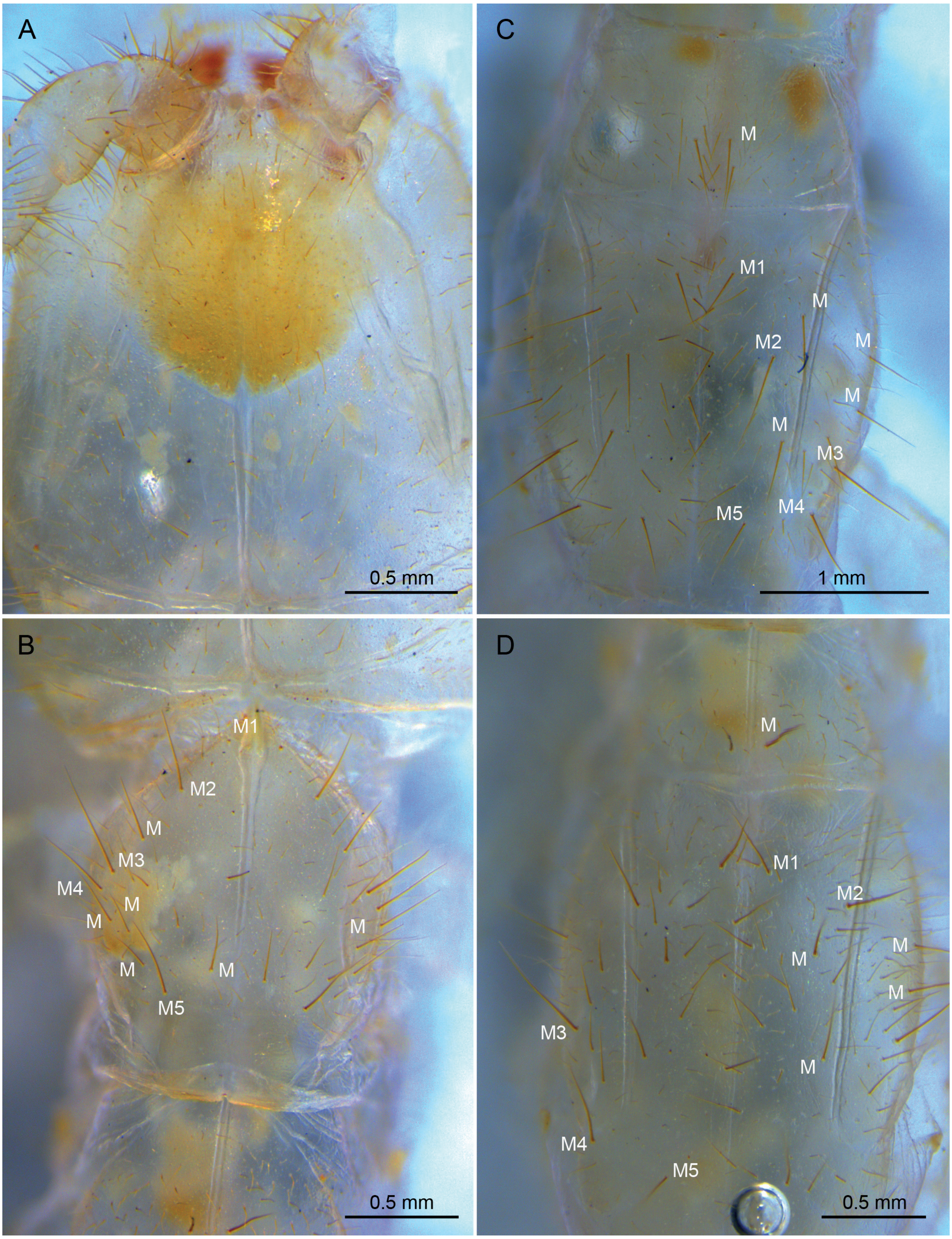

Fig. 17. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Head, dorsal side. **B**. Pronotum. **C**. Mesonotum. **D**. Metanotum.

in a variety of shapes; meso-poststernum with 10+10 M-sM; meso-intersternum with 7+7 M-sM; mesosternum with about 100 M-sM; meta-poststernum with 16+16 M-sM; meta-intersternum with 10+10 M-sM; and metasternum with about 160 M-sM. Legs slightly short, hind leg 4.6 mm long, reaching third abdominal segment. Femur-tibia-tarsus articulations with a row of sM; coxa with 14 ventral M-sM; trochanter with 10 M-sM; femur with 24 ventral M-sM and 16 dorsal M-sM; tibia with 20 M-sM; tarsus with 30 M-sM plus two ventral rows of 5 and 6 thick setae. Pretarsus with two short, thick, unequal claws, and a rounded medial unguiculus.

Abdomen. Abdominal tergites with a few ms and sM plus several M or sM. Prescutum of urotergite I with 1+1 M, scutum with 1+1 M or sM (ma), 1+1 M1, 1+1 M5 and 2+2 medial intermediate M; urotergite II with 1+1 M(ma), 2+2 M1−2, 2+2 M4−5, 1+1 medial intermediate M and 1+1 lateral intermediate M; urotergites III−VII with 1+1 M or sM (ma), 5+5 M1–5, 1+1 medial intermediate M and 1+1 lateral intermediate M; urotergite VIII with 2+2 M; urite IX with 12+12 ventral M (Fig. 19A−D). Urite X 1.5× as long as wide; with distinctly marked carinae; carinae with subparallel margins; dorsal side with 6+7 intracarinal D1−6 M plus 2+2 lateral M between D2, 1+1 medial M and 1+1 lateral M between D3, 1+1 lateral M between D3−4, and 3+3 M between D6; acropygium rounded; lateral side with 5 rows of 8−10 M; ventral side with 4+4 rows from lateral to central with 7−8 M (Fig. 21A–D). All tergites with blunt, slightly rounded posterolateral angles (Figs 19C−D, 20C–D). Urosternite I (Fig. 20A−B)

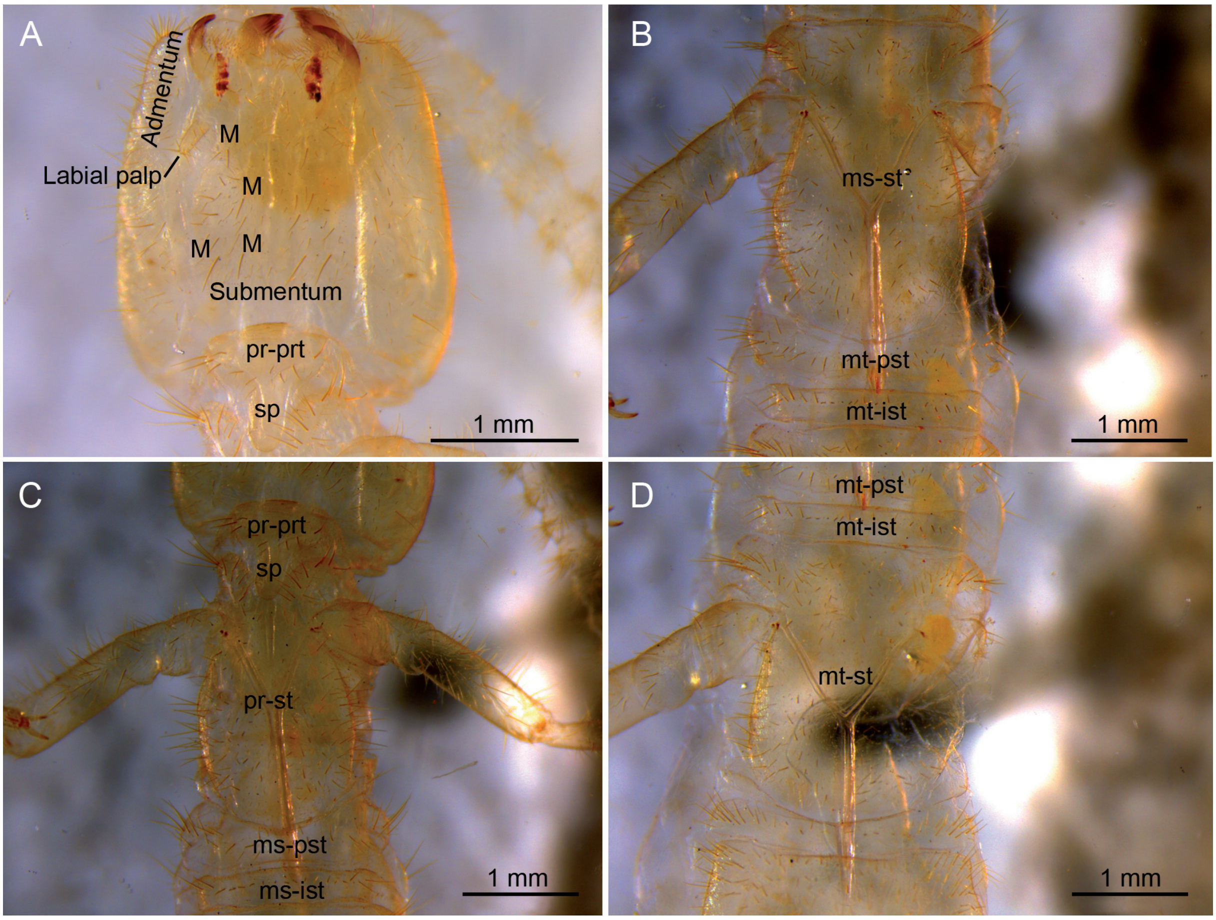

Fig. 18. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Head, ventral side and pro-prosternum (pr-prt) with spine (sp). **B**. Pro-prosternum (pr-prt) with spine (sp), prosternum (pr-st), meso-poststernum (ms-pst) and meso-intersternum (ms-ist). **C**. Mesosternum (ms-st), meta-poststernum, and meta-intersternum. **D**. Meta-poststernum, meta-intersternum, and metasternum (mt-st).

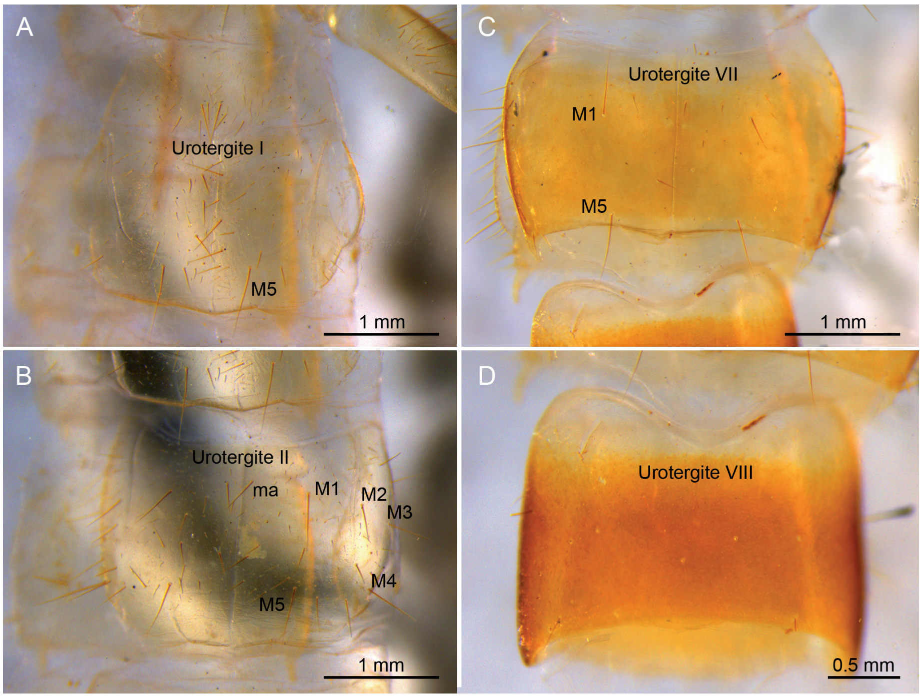

Fig. 19. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Urotergite I. **B**. Urotergite II. **C**. Urotergite VII. **D**. Urotergite VIII.

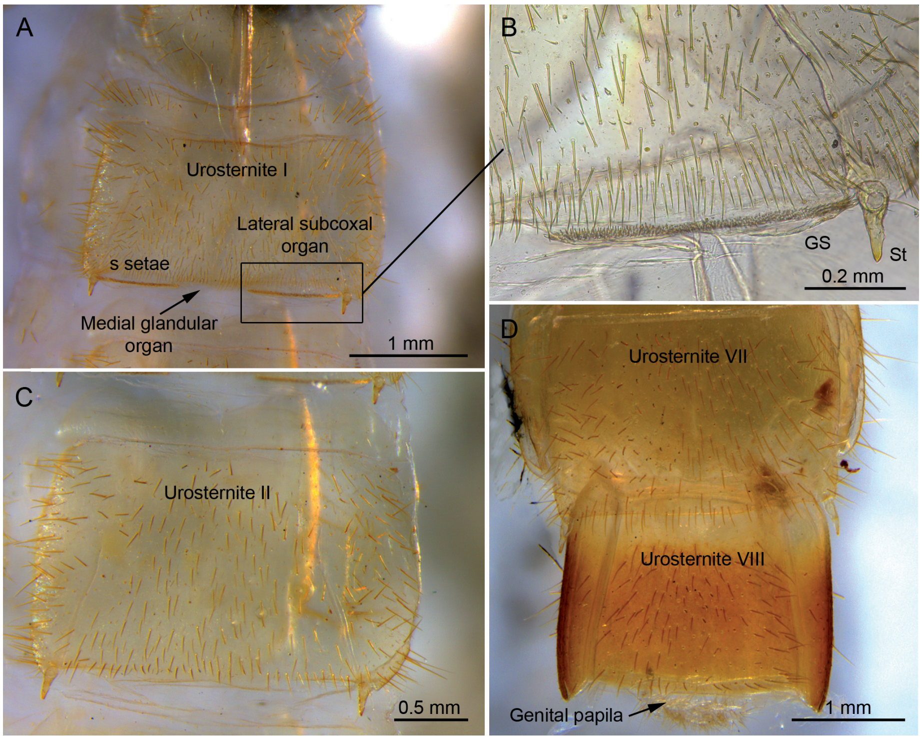

Fig. 20. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Urosternite I. **B**. Latero-posterior portion of the first urosternite. **C**. Urosternite II. **D**. Urosternites VII and VIII.

with scarce ms and abundant sM indistinct from M; sM more abundant at the narrow anterior portion of lateral subcoxal organ, with about 90 sM each. Median glandular organ with several tiny setae (Fig. 19E). Lateral subcoxal organ with three rows of short glandular setae (GS) (about 240 GS) and one posterior row of about 60 sensory setae (SS); lateral subcoxal organ occupying 0.36× of interstylar width/area; GS/st1 and SS/st1similar= 0.14 (Fig. 20A–B); urosternites II–VII with scarce ms and abundant sM undifferentiated from the thick and bunt apex shape M (Fig. 20C–D). Cerci asymmetric, strong, well-developed, length 1.4 mm, rectilinear along the proximal half and curved in the distal half, becoming a large hook towards apex; heavily sclerotized with external dorsal and ventral carinae arising from dorsal and ventral acetabular articulations; ventral carinae reaching apex and dorsal carinae before the end (Fig. 22A–D). Right cercus with proximal tooth pointed; predental margin with two rows of 3+3 round denticles; postdental margin with a row of 16 small round denticles reaching near the hook. Left cercus toothless, proximal margin with three rows of 4+3+4 denticles: superior and inferior round rows with denticles, intermediate row with tiny round denticles; medial and distal margin with 12 small round denticles ending before the hook. Right cercus with 18, 32, 30 dorsal, lateral, and ventral M; left cercus with 19, 30, 30 dorsal, lateral, and ventral M; both with a few sM and ms, plus campaniform sensilla regularly distributed on internal margins and at the hook (Fig. 22B).

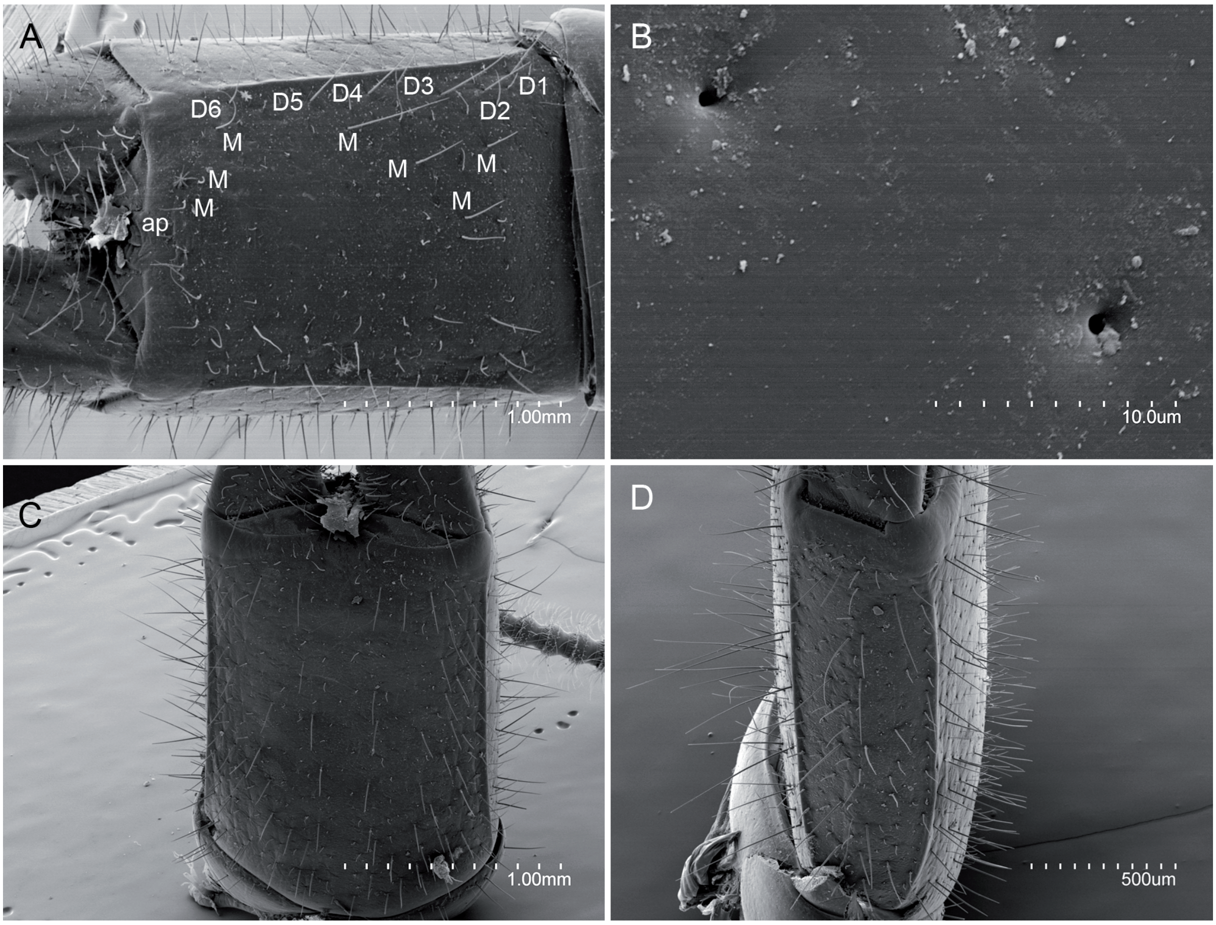

Fig. 21. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Abdominal segment X, dorsal view. **B**. Detail of porus on dorsal side of abdominal segment X. **C**. Abdominal segment X, ventral side. **D**. Abdominal segment X, lateral view.

Taxonomic affinities

In 1929, Silvestri described a new genus and species, *Opisthjapyx seurati* Silvestri, 1929, from the central Sahara at the Oued Tezzeït in the south of Algeria. This species is well-defined by its abundant macrosetae (M) along the body, with 14+14 M on the pronotum and 15+15 M on the mesonotum and metanotum. Additionally, it exhibits urosternites with abundant macrosetae and double rows of denticles in both cerci. *Opisthjapyx naledi* sp. nov., found in a South African cave, exhibits several differences from *O. seurati*. Four of these differences can be attributed to cave life: a larger body size (27.5 mm compared to 17 mm in *O. seurati*), longer antennae (0.35 ratio of body length to antenna length compared to 0.23 in *O. seurati*), 49 antennomeres (compared to 36 in *O. seurati*), and a greater number of placoid sensilla on distal antennomeres. Two other distinguishing features of *O. naledi* include the number of thoracic macrosetae (M), with 11+10 M on the pronotum and 9+9 M on the mesonotum and metanotum (compared to 14+14 and 15+5 in *O. seurati*), as well as the presence of three rows of denticles instead of two rows as seen in *O. seurati*.

Habitat

The single known specimen of *Opisthjapyx naledi* sp. nov. was found in the Villa Louisa Cave. This cave is located in the Cradle of Humankind, UNESCO World Heritage Site (Gauteng Province, South Africa). The region is highly diverse in species, as it is associated with the Rocky Highveld Grassland.

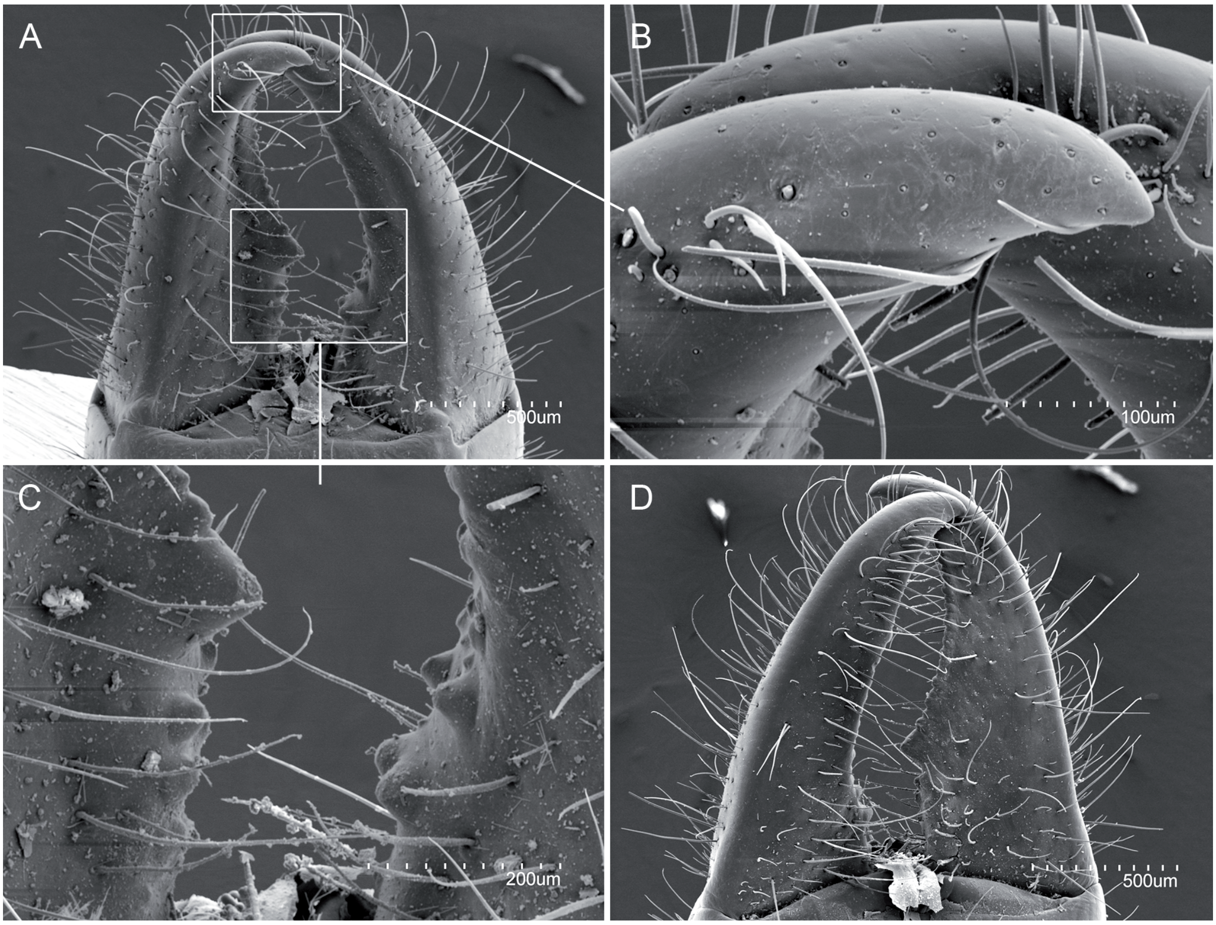

Fig. 22. *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov., holotype, ♀ (ISAM). **A**. Cerci, dorsal view. **B**. Close up of distal part of cerci. **C**. Close up of medial part of cerci from dorsal view. **D**. Cerci, ventral view.

Fig. 23. Location and habitat of *Opisthjapyx naledi* Sendra & Sánchez-García sp. nov. **A**. Villa Louise cave entrance. **B**. Villa Louise cave interior general aspect. **C**. Interior of Villa Louise cave near the entrance, showing altered floor. **D**. *Opisthjapyx naledi* inside a small shelter visible behind a removed rock that was covering it r. **E**. Live holotype of *Opisthjapyx naledi*.

The rainy period is during the hot summer months, with an annual average of 700 mm. The caves in the area are mainly developed in dolomitic bedrock, associated to the Monte Christo Formation (Malmani Subgroup, Transvaal Supergroup) (Dirks *et al.* 2015). Despite extensive search efforts for invertebrates in the cave, only one single specimen was found, thus indicating the rarity of this species. The specimen was found in a deeper, moist, and aphotic area within the cave. The specimen was found under a rock, sheltering in a small chamber, likely dug by itself (Fig. 23D). After removing the rock, the japygid remained immovable and only left the soil chamber after it was disturbed with a brush tip; it started to run in search of another shelter. However, it did not react to the light, thus not presenting any phototaxy.

The Villa Louisa Cave's external area is highly altered, especially by deforestation. Furthermore, near the cave's entrance (approximately 70 meters), there is an asphalt factory posing a pollution threat. The caves' entrance has small bush patches surrounded by grass (Fig. 23A). Its interior is highly impacted due to the removal of calcite deposits, and the conduits and floor were severely altered in part by walls that were built inside it (Fig. 23B) and tyres that were installed to serve as a staircase in the entrance chamber (Fig. 23C). The cave still receives local visitors and presents signs of religious use (candles and jars).

The risk of contaminants originating from the farms and factories near the cave certainly represents a major concern for this species' conservation. Furthermore, we need further samplings in the area to determine the actual distribution of this rare species.

Genus *Teljapyx* Silvestri, 1948

Teljapyx aotearoa Sendra & Sánchez-García sp. nov.

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Figs 24–31

Etymology

The specific name *aotearoa* refers to the Māori name for New Zealand, often translated as "land of the long white cloud".

Type material

Holotype

NEW ZEALAND • ♂; Takaka, Council Cave; 40°52′35.95″ S, 172°50′46.55″ E, 4 Dec. 2020; Rodrigo Lopes Ferreira leg.; labelled "♂1-holotype-AI.052510"; AI.

Paratypes

NEW ZEALAND • 1 ♀; same collection data as for holotype; labelled "♀1-paratype-MZB (MCNB) 2023-0619"; MZB • 1 ♂; same collection data as for holotype; labelled "♂2-paratype-AI.052511"; MZB.

Other studied material

NEW ZEALAND • 1 ♀; same collection data as for holotype; AS.

Description

Body. Elongate (Figs 24D, 25B), length 28 mm in male holotype (29 mm in ♂2-paratype and 27.5 mm in ♀1-paratype). Maximum width at urotergite VII of 3 mm in ♂2-paratype, and 2.9 mm in holotype and ♀1-paratype. Epicuticle smooth, with numerous micropores in tergites and urosternites, with about 12 micropores/µm^2, diameter 0.18–0.26 µm (Fig. 28B). Cuticle unpigmented, with slightly sclerotized areas on dorsal frontal head, mandible tips, femoral and tibial condyles, abdominal segments VIII–X, and cerci. Body and appendages covered with ms, s, sM, and M.

HEAD. Antenna with 32 antennomeres, 0.50–0.55× the length of body (14 mm long in holotype and ♀1-paratype; 16 mm in ♂2-paratype); first antennomere short, followed by three longer and wider antennomeres, the third and fourth being the largest and most elongated, twice as long as wide (Fig. 26C); medial antennomeres elongated, 1.3× as long as wide, with a large intersegmental ring between them (Fig. 26B). All antennomeres with sparse ms setae, plus three apparently whorls of long sM. Trichobothria present on antennomeres IV–VI in a 2/3/3 pattern, with *a* trichobothria in distal position (Fig. 26C). Apical antennomere with 16–18 placoid sensilla distributed in three irregular groups (Fig. 26A). Head with a few sM and ms; on dorsal side 18+18 M setae: A2−4, S2, 4, 6, M2−4, V2, 4, I1−3, I5, L5 and P1−2 (Fig. 24A); on ventral side: submentum with 1+1 large M in posterior position, admentum with

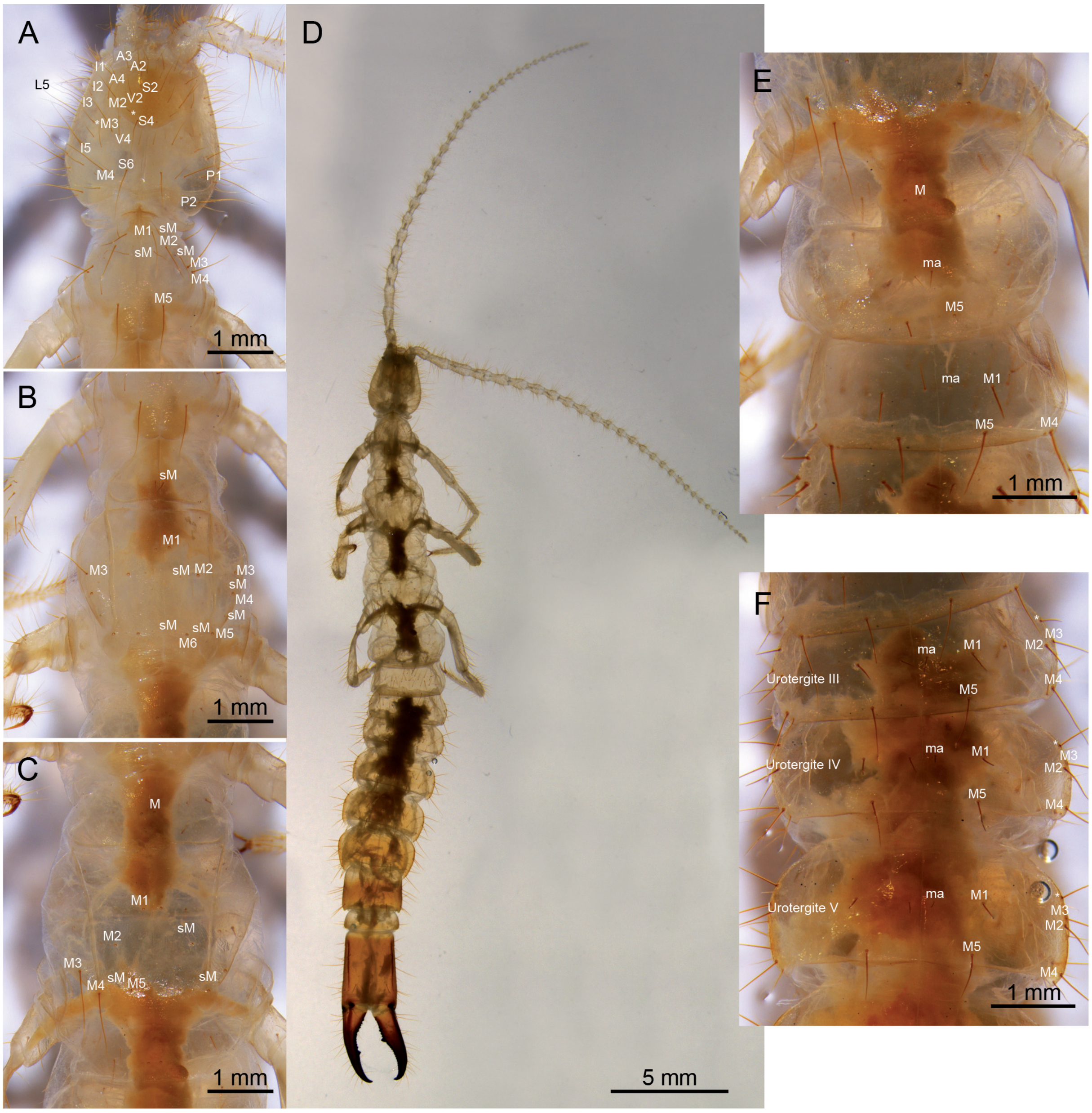

Fig. 24. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., holotype, ♂ (AI). **A**. Dorsal side of head and pronotum. **B**. Mesonotum. **C**. Metanotum. **D**. Habitus, dorsal side. **E**. Urotergites I–II. **F**. Urotergites III–V.

3+3 M, mentum with 1+1 M; external lobes of mentum with abundant sM. Pair of exertil vesicles of the external lobes visible in the holotype. Labial palp elongate, 10× as long as wide, with one proximal sM and four medial and distal sM, plus several ms. Lacinia falciform, well sclerotized, with the five laminae pectinate (Fig. 25A).

Thorax. Thoracic segments elongate (Figs 24A–C, 27A–C). Pronotum with 5+5 M1–5, 4+4 sM, and numerous ms uniformly distributed; prescutum of mesonotum with 1+1 M; mesonotum with 6+6 M1–6 and abundant ms or sM; prescutum of metanotum with 1+1 M, metanotum with 5+5 M1–5 and a few ms; both prescuta with 1+1 M and scattered sM and ms. Thoracic sternites, intersternites, and

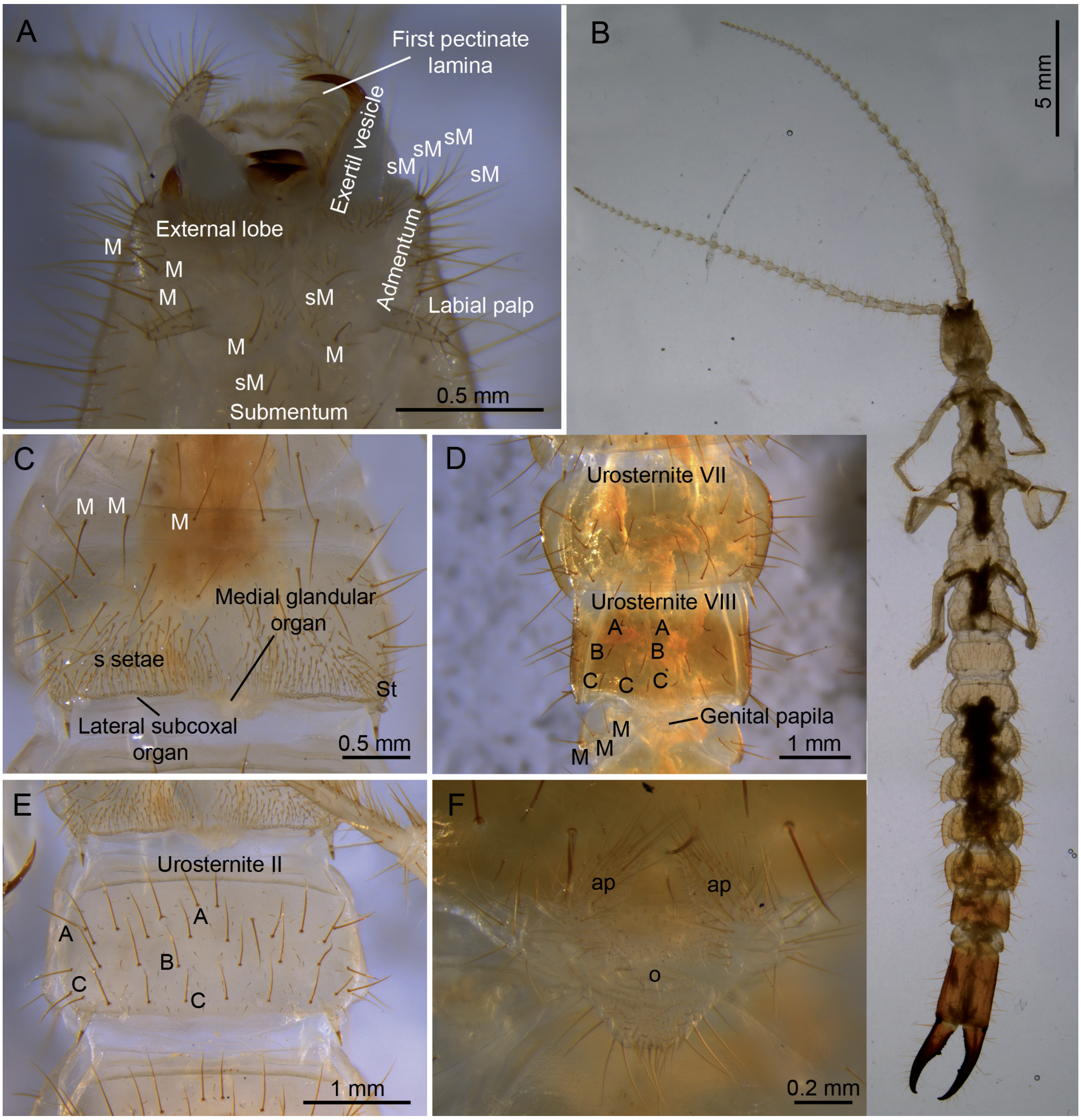

Fig. 25. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., holotype, ♂ (AI). **A**. Anterior part of head, ventral side. **B**. Habitus, ventral side. **C**. First urosternite. **D**. Urosternites VII–IX. **E**. Urosternite II. **F**. Genital papilla. Abbreviations: ap = appendages; o = opening.

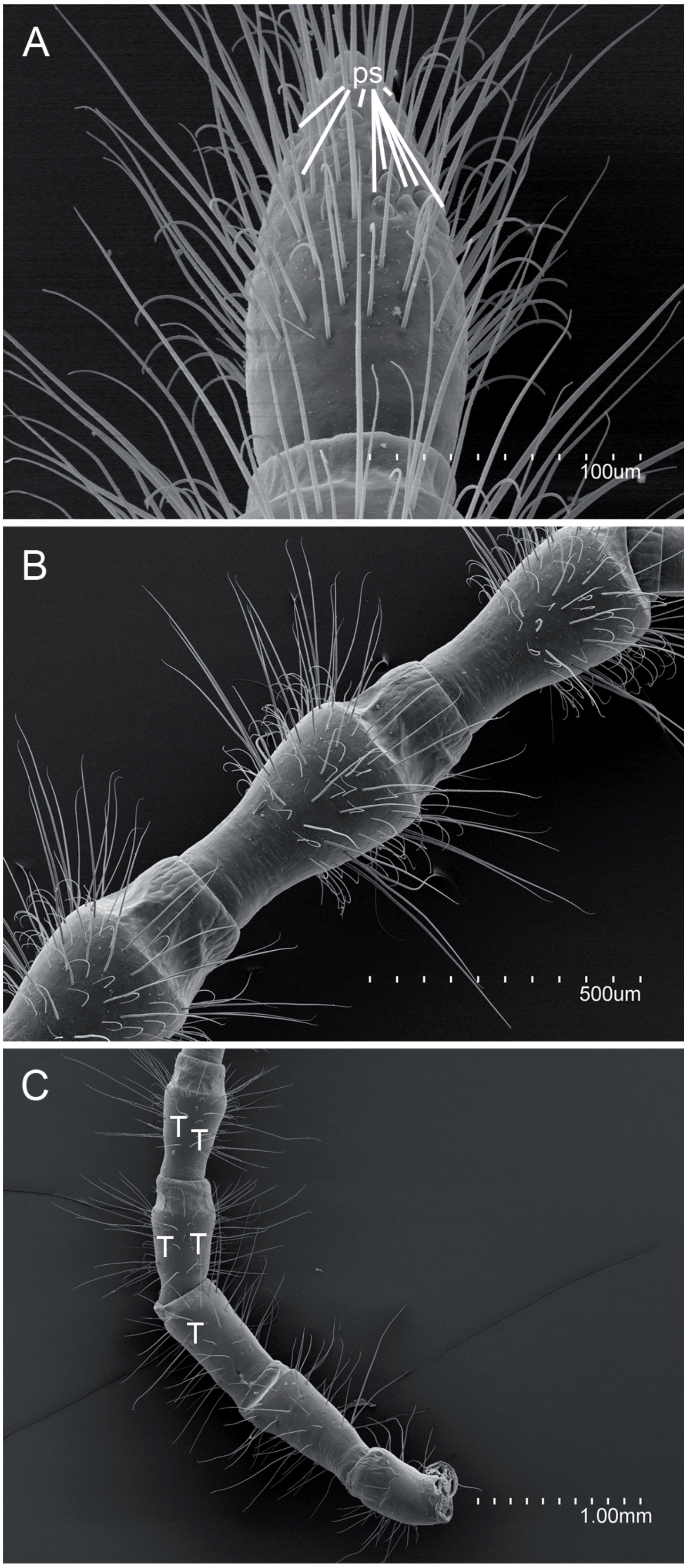

Fig. 26. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., ♀1-paratype, ♀ (MZB). **A**. Distal antennomere. **B**. Central antennomeres. **C**. Proximal antennomeres II–VI. Abbreviation: T = trichobothria.

presternites well-defined, with ms, sM, and M setae (Fig. 27A–C). Pro-presternites and pro-, meso- and metasternites with strong internal Y-shaped cuticular structures (furcisternites) (Barlet & Carpentier 1962); only in pro-presternites the prolongation of the posterior branch (spine) is visible on the surface (Denis 1949). Pro-presternum with 1+1 lateral anterior M and 1+1 nearby sM; prosternum with 1+1 medial anterior M; 3+3 lateral anterior M, 1+1 medial intermediate M and 2+2 lateral posterior M; meso-poststernum with 4+4 M; meso-intersternum with 2+2 M; mesosternum with 1+1 medial anterior M, 3+3 lateral anterior M, 1+1 medial intermediate M, 1 sagittal M, 9+10 medial posterior M and 2+2 lateral posterior M; meta-poststernum with 4+4 M; meta-intersternum with 2+2 M; metasternum with 1+1 medial anterior M, 2+2 lateral anterior M, 1+1 sagittal M, 1+1 medial intermediate M, 10+13 medial posterior M and 2+2 lateral posterior M (Fig. 27A−C). Legs elongate, hind leg reaching sixth abdominal segment, 6.8 mm long in holotype, 7.6 mm in ♀1-paratype and 8 mm in ♂2-paratype. No frictional setae between trochanter-coxa-femur articulations; femur-tibia-tarsus articulations with a row of long M or sM setae set on large sockets. Coxa with 4 distinct M; femur with 9–10 M; tibia with more than 30 M, and tarsus with almost 30 M. Calcars not distinguishable from M in shape. Pretarsus with two simple and unequal claws (the shortest ⅔ the longest), and a pointed and short medial unguiculus.

Abdomen. Abdominal tergites with a few ms, s, sM and M. Prescutum of urotergite I with 1+1 M, scutum with 1+1 M or sM (ma) and 1+1 M5 (Fig. 24E); urotergite II with 1+1 M (ma), 1+1 M1, and 2+2 M4–5; urotergites III–VII with 1+1 M (ma) and 5+5 M1–5 (Fig. 24F); urotergite VIII with 7+7 M; urite IX with 3+3 ventral M. Urite X 1.5× as long as wide, with marked carinae with subparallel margins slightly converging towards the posterior border; on dorsal side with 2+2 M intracarinal D1, 3, plus 1+1 M or 1 M between D1 (1 M in holotype); acropygium rounded (Fig. 29A); on lateral side with 3+3 M (L1, 3, 5) on carinae; on ventral side with four rows of 3+3 M, 3+3 M, 2+2 M and 2+2 M from anterior to posterior position. Lateral urotergites I–IV with blunt, slightly rounded to pointed posterolateral angles; angles on urotergites V and VII slightly more conspicuous with small point; on urotergite VIII and urite IX with round end (Fig. 24E–F). Urosternite I (Figs 25C, 28A) with ms and s setae; s setae being so abundant as to define a lateral field of up to 150 on each side of the posterior half of scutum, previous to the lateral subcoxal organs; prescutum with 3+3 M and scutum with 11+11 M. Medial glandular organ with 2+2 minute setae or no visible setae. Lateral subcoxal organ with one to three rows of glandular setae (GS) with about 140–180 in males and 60–70 in females and one row of sensory setae (SS) with about

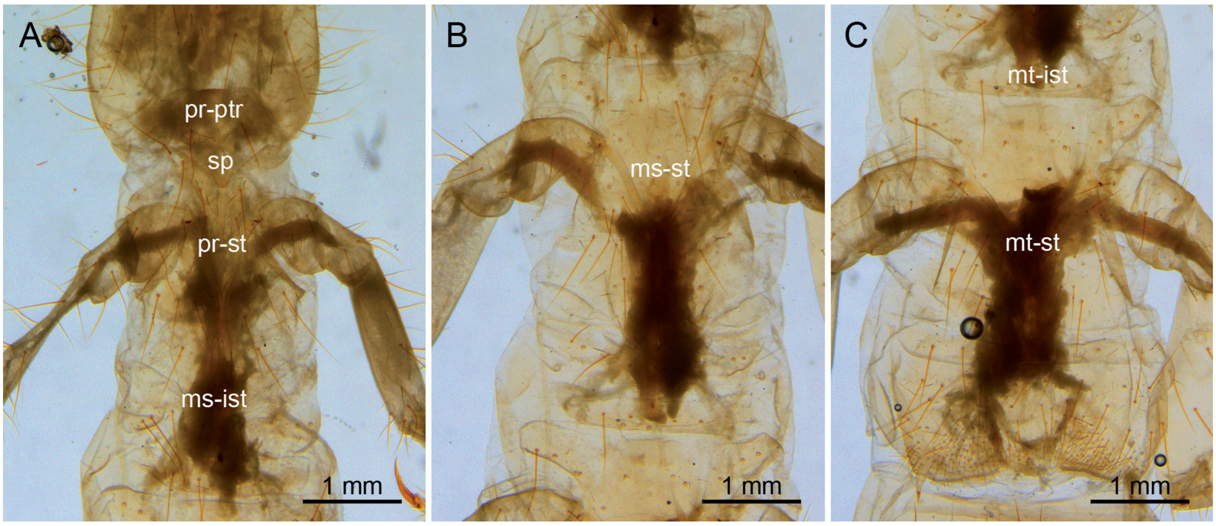

Fig. 27. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., holotype, ♂ (AI). **A**. Pro-prosternum (pr-prt) with spine (sp), prosternum (pr-st), and meso-intersternum (ms-ist). **B**. Mesosternum (ms-st). C. Meta-intersternum (mt-ist.) and metasternum (mt-st).

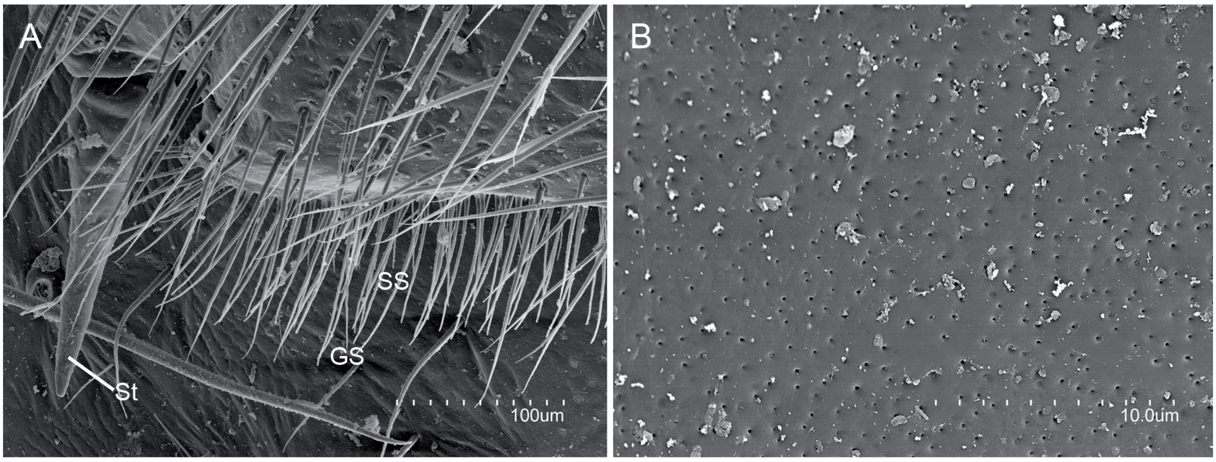

Fig. 28. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., ♀1-paratype, ♀ (MZB). **A**. Lateral posterior portion of the first urosternite. **B**. Detail of cuticle of first urosternite. Abbreviation: St = stylus.

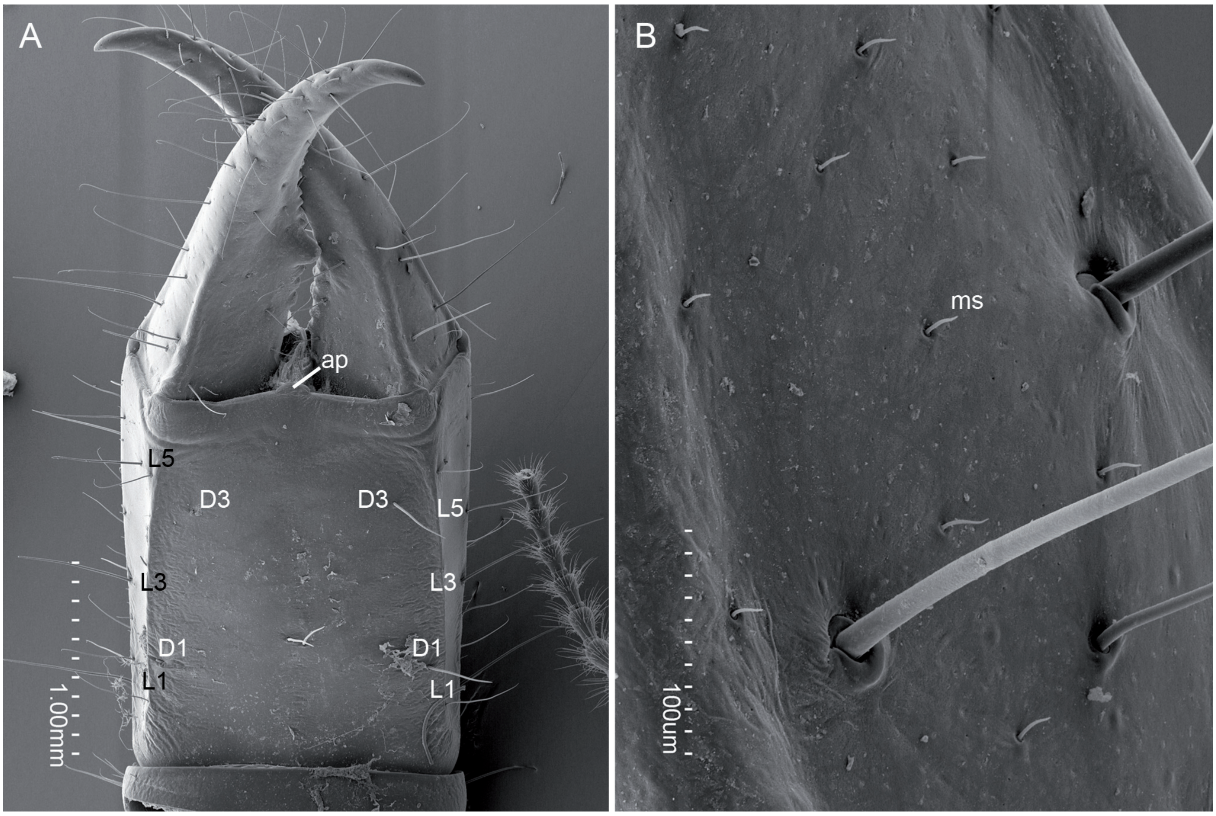

Fig. 29. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., ♀1-paratype, ♀ (MZB). **A**. Abdominal segment X and cerci, dorsal side. **B**. Cuticle detail of cerci, dorsal side.

60–90 in males and 30 in females; lateral subcoxal organ occupying 0.30× of interstylar area (in males and females); GS/st1 (stylus of first sternite) = 0.2–0.3 (males) and 0.35–0.45 (females), SS/st1= 0.12 (males) and 0.2 (females) (Fig. 28A). Urosternites II–VII with a few ms and strong M setae; urosternites II–VII with three rows of: 7+7 A M, 4+4 B M and 5+5 C M; urosternite VIII with: 2+2 A M, 2+2 B M

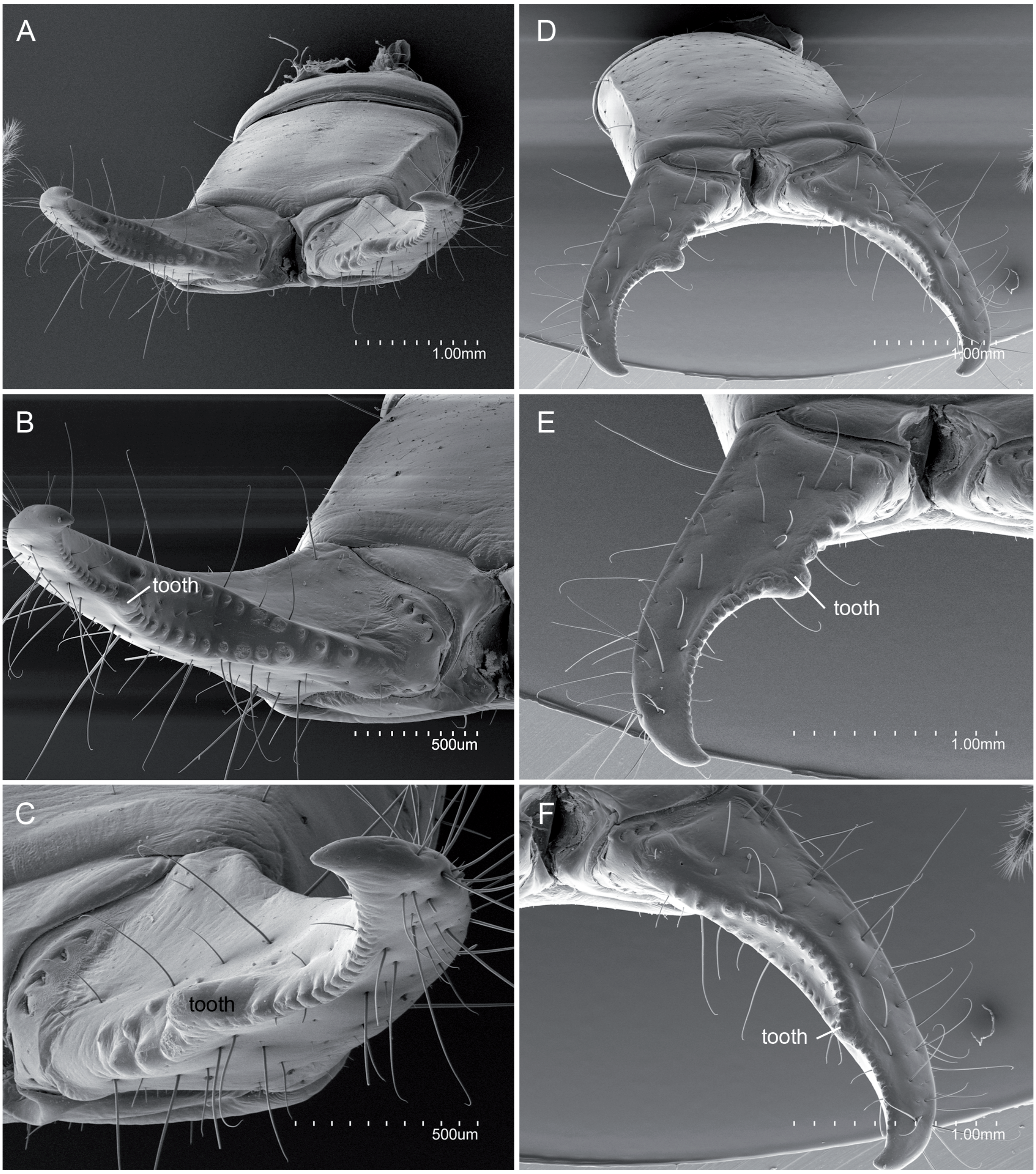

Fig. 30. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., ♀1-paratype, ♀ (MZB). **A**. Abdominal segment X and cerci, dorsal view. **B**. Left cercus, inner side in dorsal view. **C**. Right cercus, inner side in dorsal view. **D**. Abdominal segment X and cerci, ventral view. **E**. Right cercus, inner side in ventral view. **F**. Left cercus, inner side in ventral view.

and 3+3 C M (Fig. 25D). Genital papilla in male with large lateral appendages (Fig. 25F). Cerci strong, well-developed, elongate, straight along the proximal half and curved in the distal half, becoming a small hook towards apex (Figs 29–31); length ranging from 3 mm in largest specimen (♂2-paratype) to 2.9 mm in holotype and ♀-paratype, always slightly longer than urite X; cerci heavily sclerotized, with dorsal and ventral outer carinae arising from dorsal and ventral acetabular joints; carinae extending almost to apex ventrally and halfway dorsally. Cerci asymmetric with a distinct concave top side with distal end slightly upward. Right cercus with round or pointed medial tooth; predental margin with two rows of 3+3 small, round denticles; postdental margin with a row of 14–16 small denticles reaching near the hook. Predental margin of left cercus with two rows of denticles apart mostly on the middle; superior row with 14 small round denticles ending before the postmedial denticle smaller than the right cercus; inferior row with 12 small round denticles ending in the postmedial tooth; postdental margin with a row of 12 tiny denticles ending before the hook. Right/left cercus with about 12/15, 15/12, 20/25 dorsal, lateral and ventral long and short M; campaniform sensilla distributed mainly on hook and scarce on inner margins (Figs 29−31). We have included cerci morphology observations in a video production, an animated movie produced with scientific supervision by José Antonio Peñas (see Supp. file 1).

Taxonomic affinities

The taxonomical features of *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov. in cerci morphology, coxal organs of the first urosternite and pectinate maxillae match the original description of the genus *Teljapyx* Silvestri, 1949. *Teljapyx* was proposed for two species from South America (Silvestri 1949): *Teljapyx riestrai* Silvestri, 1949 and *Teljapyx megalocerus*, an already described species (Silvestri 1905). Paclt (1957a) in his monography of the group proposed to include within the genus *Teljapyx* a total of 19 species from five other genera: *Japyx* Haliday, 1864; *Catajapyx* Silvestri, 1933; *Sinjapyx* Silvestri, 1949; *Proncojapyx* Silvestri, 1949 and *Congjapyx* Pagés, 1954. Furthermore, Smith (1959) included another species but using different criteria from those presented by Silvestri (1949) and Paclt (1957a), that is, the presence of a pair of predental denticles in both cerci. *Teljapyx aotearoa* has close morphological and geographical similarities to *Teljapyx leai* (Silvestri, 1930), described from Tasmania and later found in mainland Australia (Womersley 1939). Several differences between *T. leai* and *T. aotearoa* can be observed. First, body size and appendages are larger and more elongated in *T. aotearoa* than in *T. leai*: *T. leai* with a body length of up to 13.2 mm and a cerci length of 1.2 mm vs up to 29 mm body and 3 mm cerci in *T. aotearoa*. Second, *T. leai* has 30 antennomeres vs 32 antennomeres in *T. aotearoa*; the urotergite X in *T. leai* has 3+3 D1–3 intracarinal dorsal macrosetae and *T. aotearoa* has 2+2 D1, 3 but

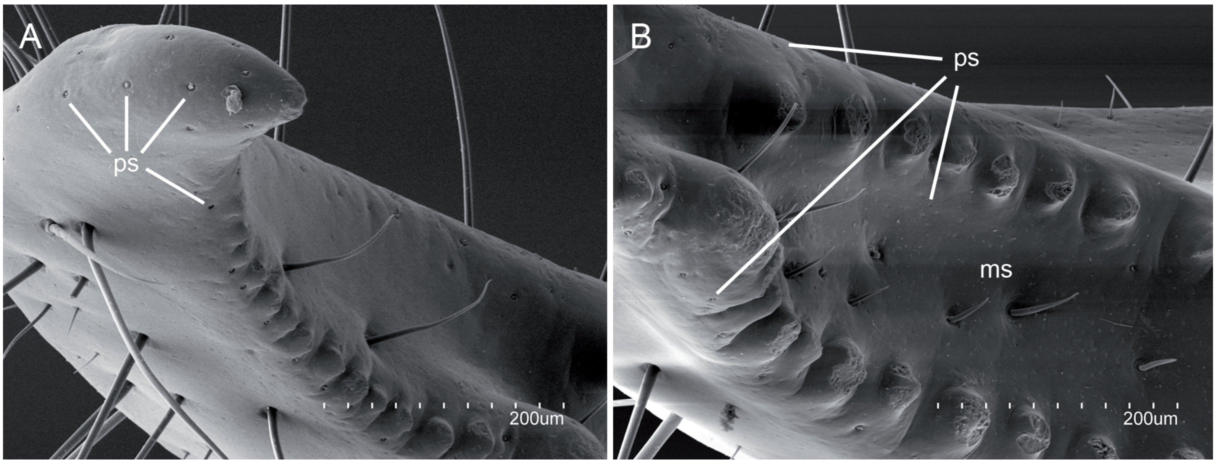

Fig. 31. *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov., ♀1-paratype, ♀ (MZB). **A**. Distal part of left cercus, latero-internal view. **B**. Central part of left cercus, latero-internal view.

Fig. 32. Location and habitat of *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov. **A**. External area in the surroundings of the Council cave. **B**. Council cave entrance. **C**. General view of the interior of the Council Cave. **D**. Living specimen of *Teljapyx aotearoa*.

1 or 2 sagittal between D1 macrosetae; and the right cercus has a predental margin with two rows of 1+3 denticles in *T. leai* vs 3+3 denticles in *T. aotearoa*.

Habitat

Council Cave is located near the Motupipi settlement in Golden Bay, on a small limestone outcrop approximately 1 km long and less than 100 m wide exposed by the uplift of the nearby Pikikiruna Fault. The Motupipi limestone is presumed to be continuous under the bed of Dry River with a larger block immediately north of Dry River. It also continues beneath overlying geologies to the west, probably for a considerable distance. Almost the entire Motupipi limestone outcrop, including the section containing Council Cave, is overlain by the Council Cave Scenic Reserve. The reserve still maintains a reasonable amount of native vegetation (Fig. 32A) although it is heavily covered by exotic species.

Council Cave is the largest known cave in the outcrop. The main entrance (Fig. 32B), at the northernmost point of the cave, is located close to a small road lying at about the level of the pasture, which extends from the western side of the limestone. The cave has a main, mostly dry, horizontal passage 170 m long that runs parallel with the edge of the limestone. This passage has suffered much damage in the past, from speleothem breakage to extensive graffiti. A second parallel conduit, which frequently holds a small stream, lies below and west of the main passage and has been explored up to at least 20 m beyond the end of the upper level. This lower conduit is often inaccessible due to water rising to roof level in many low areas.

The main conduit of Council Cave presents several speleothems (Fig. 32C), although the floor is mainly covered by sediments. Specimens of *Teljapyx aotearoa* sp. nov. were observed, especially at the deeper regions of the cave. During the samplings, specimens were observed freely walking on the cave floor, notably on areas covered by sediments (Fig. 32D). Individuals moved slowly by feeling the substrate with their long antennae. Specimens seem not to react to light, so that these organisms apparently do not show phototaxy. No specimens were observed close to each other. When disturbed (by the touch of a brush) they moved quickly, trying to hide in cracks or spaces under rocks.

It is important to note that Council Cave is one of the most important caves in New Zealand for its cave-restricted fauna, which has beetles, harvestmen, diplurans, centipedes, and spiders (Santos *et al.* 2019). Fortunately, the cave is now protected by its scenic reserve status, and visitors can only access its main cave conduit via a locked gate. The key is held at the local office of the Department of Conservation, thereby ensuring sufficient protection. In this way, the Department is aware of who enters the cave and for what reason. At present, there is no official permit system for entry, although it could be implemented in the future.

Discussion

Taxonomical traits and the unresolved phylogenetic affinities within japygids

The taxonomy of japygids, like the rest of dipluran families, was established by the Italian entomologist Filippo Silvestri, who suggested some morphological features to classify japygid into species and genera (Silvestri 1949). However, the phyletic affinities remain uncertain. Among all taxonomic traits proposed by Silvestri, the most reliable features are related to the cerci shape, which are highly variable between species, mostly on each of the cercus internal side. We can observe interspecific variation in cerci morphology in several specific characters: relative length, width, denticulation of the inner margin, and degree of curvature and asymmetry. Verhoeff (1923) recognized that the cerci morphology in adult specimens, especially the denticulation of their inner margin, was a valuable taxonomic character to identify Japygidae with certainty at species level. The French entomologist Jean Pagés (1951: 33) corroborated Verhoeff's statement and reported a high degree of interspecific variability in the configuration of the median surfaces of the cerci (size, number and shape of tubercles, teeth and denticles), stating that each species had its own combination of these characters, and that intraspecific variation was low. Nevertheless, in some species these cercal features show such an intraspecific variation that doubts about their taxonomical value arise; also, a few species show sex differences in ornamentation which makes it more difficult to use this feature in taxonomy (Gyger 1960; Pagés 1987), as discussed below.

Other taxonomical features are related to the central glandular organs which can have two types of gland outlets: one through a tiny seta and the other through open pores. Furthermore, the morphology and the abundance of glandular and sensorial setae on the lateral organs – both located on the posterior region of the first urosternite – have taxonomical importance. However, these glandular organs may represent sexual and ontogenetic variations, thus they must be interpreted with caution. The chaetotaxy on dorsal and sternal tergites is more or less uniform and shows little variation in macrosetae distribution. Thus, the most useful features are those related to cerci morphology and lateral organs. Pagés, during his long dedication to japygids taxonomy, substantially improved the taxonomical descriptions of the new taxa with accurate explanations and excellent illustrations using optical microscopy. Furthermore, Pagés (1953b, 1984) established the terminology for setae. He also recognized the importance of some other taxonomic characters such as: the number and distribution of placoid sensilla, the urosternal glands in the second and third urosternites, and the variation of genital papilla (Pagés 1952, 1954a, 1957, 1993). Sadly, he never published a complete review of the numerous genera and species that he described. The only reliable taxonomic revision was made by Paclt (1957a), but even so the phyletic affinities within japygids remained obscure. Pagés (2000), commenting upon Paclt' revison, suggested relying more on integrating taxonomical and biogeographical evidence to resolve the phyletic affinities to get some satisfactory results (Pagés 1978). Recently, Sendra *et al.* (2021b) introduced scanning electron microscopy which permits the observation and description of previously ignored morphological features, such as the cuticular microstructures visible only at high magnification

For this study, we applied the current taxonomic features together with our observations using optical stereo microscopy, microscope and SEM. Additionally, we used photography instead of drawings. These techniques allowed us to include the most accurate description of the specimens' whole body and its characters. It is hoped that the information obtained will eventually be synthesized across several genera to clear the phylogenetic affinities within japygids. Finally, we did molecular analyses with no clear results yet, but that will be surely useful in the future.

Cave-adapted japygids

Here, we synthesize the current knowledge about cave japygids around the world by contributing additional data from previous overviews (Pagés 1964; Sendra *et al.* 2020) and summarize their diversity and distribution, as well as examine their morphological adaptations to thec cave environment.

Diversity and distribution

Japygidae harbours 347 species within 63 genera, including the new taxa described in this study. It is the second most diverse Diplura family within the order after Campodeidae Meinert, 1865 (Sendra *et al.* 2021a). In Diplura, the bulk of cave-restricted species belong to Campodeidae, with cave species representing 31% (i.e., 157 species) of the family, followed by Japygidae with only 4% of are cave species: 15 species in 13 different genera (5 of them monotypic: *Gollumjapyx* Sendra & Ortuño, 2006; *Homojapyx* Pagés, 1950; *Imazighenjapyx* Sendra & Sánchez-García gen. nov.; *Mueggenjapyx* Sendra & Komerički, 2021 and *Troglojapyx* Pagés, 1950) (Table 1).

Diplurans do not live beyond the polar circles (Sendra *et al.* 2021a); japygids in particular have a more restricted distribution than campodeids, being confined within a latitude of 57º N in Eurasia (50º N in

Table 1 (continued on next page). List of all known cave-adapted japygids. [1]Number referenced in the map, Fig. 33.

Map number[1]	Species	Localities	Reference
8	*Austrjapyx leleupi* Pagés, 1952	M'Boma Cave, Thysville, Republic of the Congo	Pagés 1952
10	*Austrjapyx wynbergensis* Sendra & Sánchez-García sp. nov.	Cape Twon, Wynberg Cave, South Africa	
14	*Burmjapyx inferus* (Carpenter, 1932)	Batu Cave, Kuala Lumpur, Selangor, Malaysia	Pagés 1977
4	*Gollumjapyx smegal* Sendra & Ortuño, 2006	Cova del Mas de Gaspar, Serra d'en Galcerán, Castelló, Spain	Sendra *et al*. 2006
4	*Gollumjapyx smeagol* Sendra & Ortuño, 2006	Avenc de Canals, Ulldecona, Tarragona, Spain	Sendra *et al*. 2006
4	*Gollumjapyx smegal* Sendra & Ortuño, 2006	Avenc d'en Serenge, Cabanes, Castelló, Spain	Sendra *et al*. 2006
4	*Gollumjapyx smegal* Sendra & Ortuño, 2006	Avenc Mas de la Cova, Cabenes, Castelló, Spain	Sendra *et al*. 2006
4	*Gollumjapyx smegal* Sendra & Ortuño, 2006	Avenc Mas Nou, Coves de Vinromà, Castelló, Spain	Sendra *et al*. 2006
5	*Homojapyx espanoli* Pagés, 1950	Campanet Cave, Mallorca Island, Baleares, Spain	Pagés 1950
5	*Homojapyx espanoli* Pagés, 1950	Sa Font Cave or Moro Cave, Sa Dragonera Island, Baleares, Spain	unpublish data
3	*Imazighenjapyx marocanus* Sendra & Sánchez-García gen. et sp. nov.	Imi Ougoug Cave, Agadir-Ida Outanane region, Morocco	
12	*Kohjapyx lindbergi* Pagés, 1962	Grotte de Dahan-Ghar, Tang-Lalaudar, Afghanistan	Pagés 1962
6	*Metajapyx moroderi patrizianus* Pagés, 1953	Grotta San Giovanni, Domus novas, Sardinia Island, Italy	Pagés 1953
7	*Metajapyx peanoi* Pagés, 1980	Grotta delle Radici, 13 km NNW of Trieste, 213 m a.s.l., Duino-Aurisina, Frioul, Italy	Pagés 1993
7	*Metajapyx peanoi* Pagés, 1980	Grotta Regina del Carso, Mt S. Michele, Savogna d'Isonzo, 196 m a.s.l., Italy	Pagés 1980a
2	*Mixojapyx reddelli* Muegge, 1992	Indian Creek Cave, Uvalde County, Texas, USA	Muegge1992
2	*Mixojapyx reddelli* Muegge, 1992	Llewellyn Rose Cave, Kimble County, Texas, USA	Muegge 1992
2	*Mixojapyx reddelli* Muegge, 1992	Tooth Cave, Travis County, Texas, USA	Muegge 1992
2	*Mixojapyx reddelli* Muegge, 1992	Powell's Cave, Menard County, Texas, USA	Muegge 1992

Table 1 (continued). List of all known cave-adapted japygids. [1]Number referenced in the map, Fig. 33.

Map number[1]	Species	Localities	Reference
2	*Mixojapyx reddelli* Muegge, 1992	Robber Baron Cave, Bexar County, Texas, USA	Muegge 1992
2	*Mixojapyx reddelli* Muegge, 1992	Honey Creek Cave, Comal County, Texas, USA	Muegge 1992
13	*Mueggejapyx brehieri* Sendra & Komerički, 2021	Win Twin Cave (Kuauk Hgak Cave) Kuank Hgak Ywa Ngan, Southern Shan, Myanmar	Sendra *et al.* 2021
13	*Mueggejapyx brehieri* Sendra & Komerički, 2021	Kyauk Khaung = Stone Cave, Shan, Myanmar	Sendra *et al.* 2021
13	*Mueggejapyx brehieri* Sendra & Komerički, 2021	Parpent Cave, Shan, Myanmar	Sendra *et al.* 2021
1	*Occasjapyx kofoidi* (Silvestri, 1928)	Potter Creek Cave, Shasta County, California, USA	Silvestri 1928
11	*Opisthjapyx primihominis* Sendra & Sánchez-García sp. nov.	Vila Louisa Cave, South Africa	
15	*Teljapyx aotearoa* Sendra & Sánchez-García sp. nov.	Takaka, Council Cave, New Zealand	
9	*Troglojapyx hauseri* Pagés, 1980	Koutouki Cave, Peania, Hymette Mountain, Attique, Greece	Pagés 1980b

North America) and 44º S in Argentina (Fig. 33). As is generally the case in Diplura, the spatial diversity pattern of the family within these limits depends entirely on sampling effort, which has traditionally focused on the Holarctic region with a total of 134 japygid species reported (Sendra *et al.* 2021a) (Fig. 33). Certainly, several japygid genera show a Pangean distribution, like other families of diplurans (Sendra *et al.* 2021a).

The 15 cave-adapted species of japygid follow the same sampling-biased distributional pattern as the rest of diplurans, with eight species located in Holarctic caves (Fig. 33). The highest known latitude is 46º N, corresponding to *Metajapyx peanoi* Pagés, 1980 in northern Italian Peninsula. Three other cave-adapted species have been found in the Ethiopican and Oriental regions as well as in New Zealand. No cave-japygids are known from the Neotropical region, although R.L. Ferreira (pers. obs.) recognized one species in Gruta do Maquiné Cave, Brazil. Despite the great paucity of data, it seems that cave-adapted japygids have a narrower distribution than soil japygid species, at least in the northern hemisphere (Fig. 33).

Cave-adapted features

Typical cave-adapted traits include regressive ones related to the absence of light, such as the loss of visual organs, surface body pigments, and wings. Nevertheless, diplurans in general, especially japygids, do not have colour pigments or wings, so they can be considered a preadapted group for the subterranean life. Cave-adapted japygids (as well as other cave-adapted dipluran species) show several constructive features: increase in body and segment size and elongation and increase in the number and complexity of sensilla, all of which are related to some peculiarities of the cave ecosystem, such as the presence of large voids in the rocks or the scarcity of energy supplies (Christiansen 1962; Howarth & Moldovan 2018).

Cave-adapted japygid species have several morphological features considered constructive, which are not seen in soil-adapted species. For example, the enlargement and elongation of the body, body segments, antennae, and cerci, as well as an increase in the number of antennomeres. All these characteristics mean more numerous mechanoreceptor setae plus the evident presence of extra placoid sensilla on the antennomeres (Pagés 1964; Sendra *et al*. 2020).

In Table 2, we compile and summarize the characters of japygids affected by cave environment based on a literature review and the new data from our study; differences among soil and cave species are easily identified. An increase in body size of cave species – total body length measured from the anterior part of the head to the apical end of the cerci (Fig. 34) – is evident in genera such as *Kohjapyx*, *Mixojapyx* and *Opisthtjapyx.* In addition to this enlargement, they show an elongation of the body (increase in the ratio between length and width) that is particularly well-observed in the thoracic segments as well as in the tenth abdominal segment. Thus, the ratio between length and width of the tenth abdominal segment (urite X) is 2 in *Kohjapyx lindbergi*, while in *Kohjapyx* edaphic species the ration equals 1 (Table 2). We also observed the elongation of the tenth abdominal segment in cave dwellers in other genera such as *Metajapyx*, *Mixojapyx*, *Muggenjapyx*, *Occasjapyx* and *Teljapyx* (Table 2). The general lengthening of the appendages in cave-adapted species is also evident in the antennae, both in their elongation of antennomeres and in the increase in the number of antennomeres. Thus, we found antenna length/body length ratios of 0.59 in *Teljapyx aotearoa* compared to 0.29 in *Teljapyx* edaphic species, or ratios of 0.6 in *Mixojapyx reddelli* compared to 0.4 in edaphic species of *Mixojapyx* (Table 2). Monotypic species such as *Gollumjapyx smeagol* Sendra & Ortuño, 2006 also show a remarkable elongation of the antennae compared with other epigean japygids, with a ratio value of 0.56. In the case of cerci, their elongation has been studied by comparing the ratio between their total length and their maximum width at the line of insertion with the tenth abdominal segment (Fig. 34). Cave-adapted species consistently show higher ratios than edaphic species, as in the case of *Kohjapyx lindbergi*, with a ratio of 1.5, which is especially noteworthy; other two examples are the monotypic *Gollumjapyx smeagol* and *Muggenjapyx brehieri*. Regarding the legs, the relative length of the metathoracic pair has been assessed from its total extension, taking as reference the abdominal segment reached by the end of the pretarsal claws (Fig. 34).

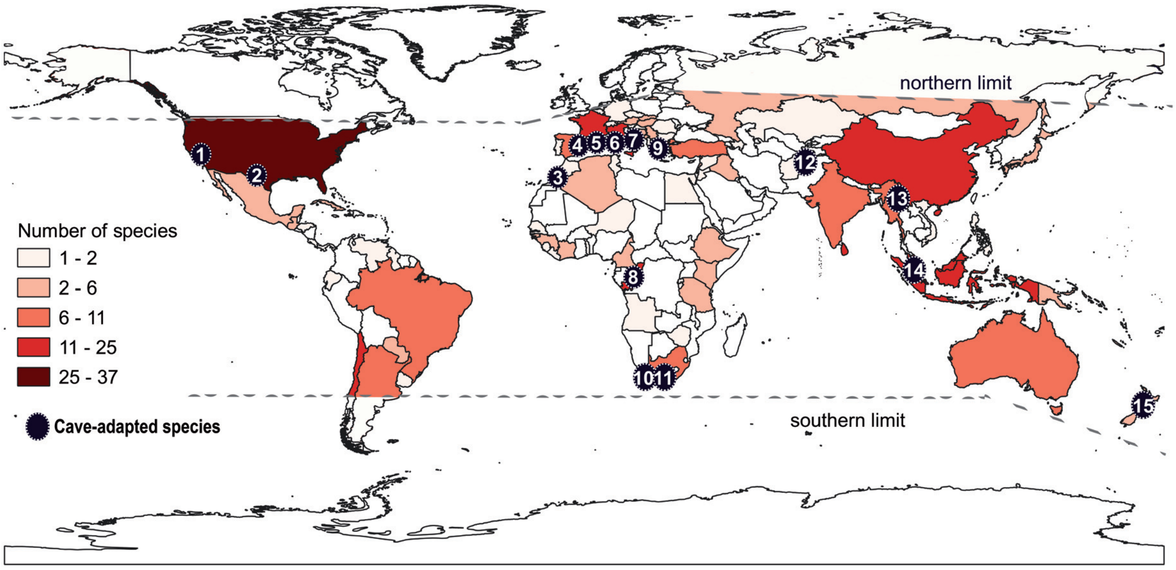

Fig. 33. Map showing the known world´s Japygidae Haliday, 1864 species richness and the location of the 15 cave-adapted species (species-number correspondence as in Table 1).

In four of the cave-adapted species, the apical claws of the methatoracic legs exceed the third or fourth segment as in all edaphic species, while they reach the fifth segment in *Muggenjapyx brehieri*, the sixth in *Teljapyx aotearoa* and *Mixojapyx reddelli*, and up to the tenth in *Gollumjapyx smeagol*.

Regarding the increase in the number of antennomers, a common cave-adapted feature in arthropods, japygids do not show conclusive results (Table 2). Thus, the number of antennomeres is greater in cave species than in soil-dwelling species: *Kohjapyx lindbergi* has up to 40 antennomeres, edaphic *Kohjapyx* species reach 34; in *Mixojapyx reddelli* it is 53, with 46 being the maximum in soil species of *Mixojapyx*; in *Opisthjapyx naledi* it is 49 compared to the 36 maximum in the non-cave-dwelling species of *Opisthjapyx*, whereas in other genera such as *Austrjapyx*, *Metajapyx* and *Occasjapyx* the number of antennomeres reaches higher figures in species dwelling in edaphic environments.

All species adapted to cave ecosystems show a clear trend towards an increase in their number of antennal placoid sensilla (Table 2). Edaphic species have 6 to 8 placoid sensilla located exclusively on the apical antennomere, but this number is always higher in cave-adapted species, reaching a maximum of 24 in *Imazighenjapyx marocanus*. There is also an extra placoid sensillum on one or more antennomeres previous to the apical one in five cave-adapted species (*Burmjapyx inferus*, *Gollumjapyx smeagol*, *Mixojapyx reddelli*, *Muggenjapyx brehieri* and *Opisthjapyx naledi*), a characteristic that has never been observed in any edaphic species.

Finally, we should mention two features apparently related to cave life that have not been cited in the literature: the presence of micro-barbed setae (Figs 10B–F, 25A) on the antennae in *Imazighenjapyx marocanus* and *Opisthjapyx naledi* with unknown function, a character also seen in the highly cave-

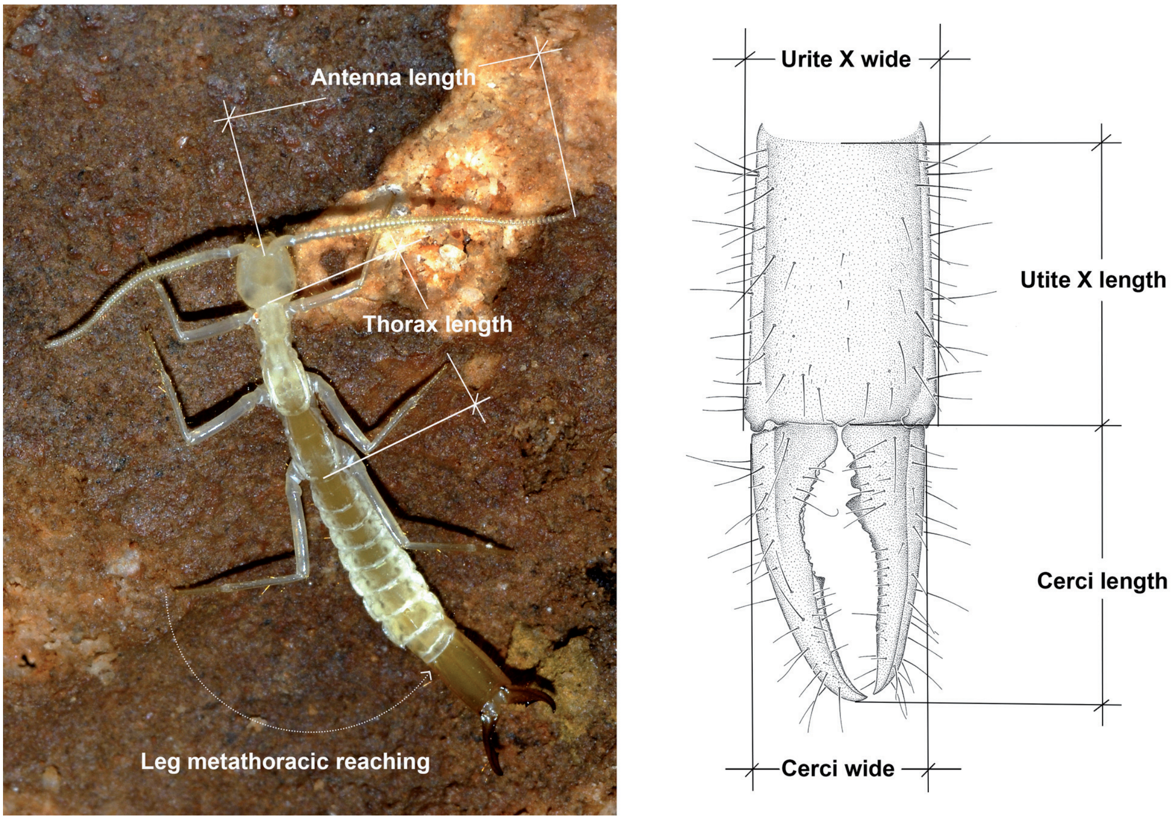

Fig. 34. *Gollumjapyx smeagol* Sendra & Ortuño, 2006, photo and drawing modified from Sendra *et al.* (2006). Measurements correspond to those listed in Table 2.

Table 2 (continued on next page). Morphological features of cave-dwelling species of Japygidae Haliday, 1864 compared to soil-dwelling species of the same genus.

Cave and non-cave species	Body shape	Body length	Antennomeres number	antennae/ body length ratio	placoid sensilla on preapical antennomere	placoid sensilla on apical antennomere	length/wide Labial palp ratio	Legs III reaching urotergite	length/wide urite 10th ratio	length/wide cerci ratio	References
Austrjapyx leleupi Pagés, 1952	elongated	6	30	(4)	without	14	2.6×	(4)	0.8	1.4	Pagés 1952
Austrjapyx wynbergensis Sendra & Sánchez-García sp. nov.	elongated	8.8–15	31	0.3 (5)	without	10	5.3×	4th	1.3	1.4	
non-cave *Austrjapyx* species	non elongated	5.2–18	28–45	0.2–0.48	without	8	2×	short legs	0.94–1.126	0.90–1	Silvestri 1948a; Smith & González 1964
Burmjapyx inferus (Carpenter, 1932)	sligtly elongated	17	32	(7)	on several	10	3×	4th	1.0	1.3	Pagés 1977a
non-cave *Burmjapyx* species	non elongated	9.5–15	28–32	3.3–4.5	without	6	(7)	4th	0.76–0.97	0.98–1.24	Chou & Chen 1983; Silvestri 1930b; Pagés 2000
Gollumjapyx smeagol Sendra & Ortuño, 2006	elongated	21	55	0.56	penultimate	14–16	5.4×	10th	1.4	1.5	Sendra *et al*. 2006
Homojapyx espanoli Pagés, 1950	elongated	15	36	(7)	without	8	2×	3rd	1.5	1.2	Pagés 1950
Imazighenjapyx marocanus Sendra & Sánchez-García gen. et sp. nov.	elongated	26	41	0.33	without	24	4×	3rd	1.1	1.1	
Kohjapyx lindbergi Pagés, 1962	elongated	24	40	(7)	without	12	3.6×	(7)	2.0	1.5	Pagés 1962
non-cave *Kohjapyx* species	non elongated	12–14	32–34	(7)	without	8	(7)	(7)	1	0.98–1.18	Pagés 1962
Metajapyx moroderi patrizianus Pagés, 1953	elongated	13	28	(7)	without	8	3×	3rd	1.5	1.3	Pagés 1953a, 1964
Metajapyx peanoi Pagés, 1980	elongated	21	37	(7)	without	8	3.25×	(7)	1.3	1.38	Pagés 1980a
non-cave *Metajapyx* species	non elongated to slightly elongated	4.5–15	28–38	0.19–0.33	without	6 to 8	2–3×	4th	0.93–1.18	1.09–1.27	Ewing & Fox 1942; Paclt 1957b; Pagés 1953b, 1954b, 1978, 1983, 1993; Silvestri 1912, 1929a, 1933a,1934, 1948b, 1948c, 1948d; Smith & Bolton 1964
Mixojapyx reddelli Muegge, 1992	elongated	48	53	0.60	Antepenultimate & penultimate	12	(3)	6th	1.2	1.3	Muegge 1992

Table 2 (continued). Morphological features of cave-dwelling species of Japygidae Haliday, 1864 compared to soil-dwelling species of the same genus.

Cave and non-cave species	Body shape	Body length	Antennomeres number	antennae/ body length ratio	placoid sensilla on preapical antennomere	placoid sensilla on apical antennomere	length/wide Labial palp ratio	Legs III reaching urotergite	length/wide urite 10th ratio	length/wide cerci ratio	References
non-cave *Mixojapyx* species	non elongated	3.6–24	28–46	0.28–0.4	without	6 to 8	2.2×	3rd to 4th	0.79–1.2	1–1.05	Ewing & Fox 1942; Muegge 1992; Pagés 1977b; Silvestri 1933b, 1948b
Muggenjapyx brehieri Sendra & Komerički, 2021	elongated	23	36	0.39	on several	16–18	3.7×	5th	1.25	1.5	Sendra *et al.* 2021
Occasjapyx kofoidi (Silvestri, 1928)	elongated	22	26	0.36	(6)	(1)	4.2×	(2)	1.3	1.3	Silvestri 1928
Non-cave *Occasjapyx* species	non-elongated	10.5–20	24–27	0.25–0.30	without	6	3×	–	0.96–1.2	1–1.2	
Opisthjapyx primihominis Sendra & Sánchez-García sp. nov.	elongated	27.5	49	0.35	penultimate	16-18	3.2×	3rd	1.20	1.08	Allen 1988; Chou 1966; Chou & Chen 1983; Silvestri 1948b; Smith 1959; Xie & Yang 1991
Non-adapted *Opisthtjapyx* species	non elongated	17	33–36	0.23	without	(6)	short	(7)	1.20	1.0	Silvestri 1929b
Teljapyx aotearoa Sendra & Sánchez-García sp. nov.	elongated	27.5–29	32	0.50–0.55	without	16-18	3.7×	5th-6th	1.42	1.32	
non-adapted *Teljapyx* species	non elongated	14–37	30–52	0.23–0.29	without	6	3×	(7)	1–1.2	1.23–1.0	Gonzalez & Smith, 1964; Silvestri, 1948a; Smith, 1962
Troglojapyx hauseri Pagés, 1980	elongated	5.9 young	38	(7)	without	21	3.6	3rd	1.2	1.4	Pagés, 1980b

(1) Elongated antennomeres, apical almost 4 times longer than wide from the original description (Silvestri 1928)

(2) "Legs relatively long" from the original description (Silvestri 1928)

(3) "Labial palpus conical, much longer than wide, …" from the original description (Muegge 1992)

(4) No data in the original description (Pagés 1952)

(5) Uncertain ratio; it has been estimated using length of their telescoping antennae

(6) Old fashioned description without such sensilla observation

(7) Didn't mentioned in the references

adapted campodeid *Hubeicampa melissa* Sendra & Lips, 2021 from China (Sendra *et al.* 2021b); and cerci with the distal part curved upward, a character present in all four new taxa described here (see later).

The morphology and function of the cerci in japygids

Preliminary remarks

The most prominent feature of the Japygidae is their pincer- or forceps- shaped appendages on the tenth abdominal segment: the cerci. Their shape varies among taxa, ranging from short and claw-like (e.g., *Allurjapyx* Silvestri, 1930, *Epijapyx* Silvestri, 1933, *Japyginus* Silvestri, 1930 and *Japygellus* Silvestri, 1930) to long and slender in some cave-adapted species (e.g., *Gollumjapyx smeagol*, *Kohjapyx lindbergi*, *Muggenjapyx brehieri*). Pincer-like cerci are also present in the Dermaptera (earwigs), constituting a classic example of convergent evolution (Haas 2007). Whereas cerci in earwigs have been extensively studied, in japygids, despite their conspicuous morphology, the role of cerci in different behavioural contexts (prey catching, defence, and potentially, mating behaviour) have hitherto been addressed by very few authors. Our accurate observations using SEM technique have raised questions worth investigating further; thus, we first summarize current knowledge of japygid behaviour involving the cerci; second, we present hypotheses on whether cerci morphology correlates a) with the nature of their prey and b) with the characteristics of their habitat; and third, we point out research perspectives.

The role of cerci in catching and steadying prey

Detailed descriptions of prey-catching behaviour in japigids were given by Kosaroff (1935), Schaller (1949), and Pagés (1951). Schaller (1949) vividly described the feeding behaviour of *Japyx solifugus* individuals from garden soil near Vienna, Austria, under laboratory conditions. The animals perpetually patrolled back and forth with waving antennae, exploring every crack in the soil. When Collembola Lubbock, 1871 were transferred to the jar, *Japyx* individuals seemed to increase their activity level, even before physical contact with the potential prey had occurred. Prey capture was only successful when *Japyx* touched a collembolan with its antennae. The prey was usually grasped with the mandibles and eaten immediately. If the collembolan wriggled about, *Japyx* would curl the abdomen up- and forward, and grab the prey with the cerci to hold it steady. In this manner, a single *Japyx* would eat 5–6 collembolans successively. In cases where *Japyx* discovered a collembolan in a crack in the soil and attempts to grasp it with the mandibles failed, it would quickly move out of the crack as a flash, turn around, stick the abdomen into the crack and pull out the prey with the cerci (Schaller 1949: 296). Schaller (l.c.) assumed that Collembola were the diplurans only prey, as – during his studies – *Japyx solifugus* never accepted either fly maggots, mites, or nematodes, which were offered as alternative choices. Moreover, he only observed enhanced unrest and search motions when collembolans were present. From these behavioural observations Schaller (l.c.) deduced that the pincers of japygids must be covered with mechano- and chemoreceptors.

Schaller (1949) was perhaps unaware of Kosaroff´s earlier study (Kosaroff 1935) stating that *Japyx solifugus* attacked also living Symphyla Ryder, 1880 and campodeids but seemed to prefer symphylans, presumably due to their thinner cuticle and lower mobility. Kosaroff (1935) also found that when *Japyx solifugus* were offered small living geophilids, they avoided attacks but accepted the cadavers that had been cut into pieces, and pulled and ate their intestines. Pagés (1951) studied the feeding behaviour of a different species, *Dipljapyx humberti*, and found that Isopoda Latreille, 1817 and Acari Leach, 1817 (Oribatidae and Gamasidae) were also consumed and in rare cases the larvae of Diptera Linnaeus, 1758 and Coleoptera Linnaeus, 1758 as well.

More recently, Christian & Bauer (2007) studied the food acquisition and processing in *Catajapyx aquilonaris* and *Metajapyx braueri*. They confirmed that the prey was always attacked using the mouthparts, and only successful attacks were followed by attempts to grab the prey with the cerci.

They also found that japygids do not rely on living prey, at least under laboratory conditions; they also accepted dead arthropods, fragments of earthworms, and even sausage, as well as detritus of plants and fungi. Based on their observations the authors assumed that japygids perceived prey upon physical contact rather than upon olfactory clues. Christian & Bauer (2007: 18) concluded that "Central European Japygidae are likely opportunistic polyphagous predators and scavengers rather than specialized hunters."

Concerning the cerci´s furnishment with sensilla, Eisenbeis & Wichard (1985) confirmed Schaller´s (1949) assumption of predation behaviour and documented various types of sensilla on the inner and outer surface, as well as the presence of numerous pores in the cuticle surface of the cerci. Pagés (1989: 524) assumed these pores, which are particularly abundant on the apex and along the inner margin of the cerci, to be orifices of cuticular sensilla (campaniform or placodea) and/or tegumental glands. In our study, we have observed the presence of such cuticular sensilla in the half distal part of all cerci in the four taxa described (see Figs 6, 13, 22, 31).

Is there a correlation between the morphology of the cerci and the nature of their prey?
As the cerci play an important role in the process of catching and steadying prey organisms, it appears logical to assume that the specific configuration of the forceps has evolved in adaptation to the specific organisms they prey upon. Insights on the functional morphology of japygid cerci may come from looking at the forceps as a mechanical tool. The mechanics of a forceps or pincers, follows the physics of the lever principle (see Davidovits 2008) which defines them as the connection of two levers sharing a joint centre of rotation. Grasping an object with a forceps requires a certain power exerted to both levers. In mechanical tools, (muscle) power transmission is enhanced when the levers are curved, and when the gripping surface is asymmetrical, the latter facilitates a better grip of the object. A similar principle is likely to apply for the cerci forceps in japygids.

It is thus conceivable that cerci morphology evolved as an adaptation to certain characteristics of the prey (e.g., overall body size, hardness of the integument, agility) and to overcome defence strategies (e.g., rapid moves, potentially toxic secretions) rather than an adaptation to specific taxa.

Interestingly, the relative length and degree of curvature of the forceps seems to be partially related to the habitat. Japygids living in soil – A and B horizons – usually display cerci which are wide at their base, short, and directed straight when in repose. In contrast, in many cave-restricted japygids we found cerci that are relatively longer, slender throughout, and curved upward in their distal portion (Figs 6–7, 14–16, 21, 29). Thus, we can only hypothesize the advantages the respective configuration may have in these environments. In the soil, prey organisms (e.g., collembolans) may be more abundant than in caves, thus enhancing the chance of random physical encounters between japygids and their prey. In cave environments where prey organisms are assumed to be less frequent, longer cerci may be advantageous as they have a larger operating range and perhaps enhance the chance of locating potential preys. Their upward curvature, in conjunction with asymmetrical gripping surface, may increase lever efficiency (see above) and improve energy economy, a strategy often observed in cave-dwelling organisms (e.g., Fiser 2019). In addition, longer cerci with larger surfaces would perhaps carry a higher number of mechano- and chemoreceptors, aiding in orientation and prey location. This hypothesis may be corroborated by the fact that elongated sensory appendages, such as antennae, are frequently observed in obligate cave arthropods.

Several observations regarding the cerci in the new taxa described in this study could enlighten the observations gather from the literature to support the mechanical use of the forceps. Firstly, all forceps from cave restrictived species have sclerotized and elongated first abdominal segment and cerci, both with two lateral large, prolonged carina that support the powerful muscles responsible for closing and opening the cerci (Figs 6, 13, 22, 29–30). Such characteristics have also been described in some soil japygid species, for instance in the genera *Congjapyx* Pagés 1954, *Protjapyx* Silvestri, 1948 or *Megajapyx* Verhoeff, 1904 (Silvestri 1948a; Pagés 1953b, 1954a). Observations from all preserved specimens pointed out the asymmetry not only in the internal shape of the left and right cerci, as it is frequent in all japygids species, but also the overlapping of the right cercus over the left one (see Supp. file 1). This closing mechanism involves presumably the activation of mechanoreceptors (macrosetae and microsetae) as well as baroreceptors (campaniform sensilla).

Another interesting observation are the differences (or variation) in the median/inner margin of both cerci, as well as the configuration of the denticles they carry and the shape of the margins. These features on the margins may point to specialized functions.

In summary, although it seems reasonable to speculate that such differences in cerci morphology could be related with the kind of prey japygids consume, without further behavioural studies, these far-fetched suggestions remain as such.

Are the cerci potentially involved in reproductive behaviour?

Although neither the direct or indirect transfer of sperm by japygid males has been observed in the field nor in the laboratory, we cannot exclude that the cerci may play a role in copulatory behaviour.

In his comprehensive study on the biology of *Dipljaypx humberti*, Pagés (1967) found that, under laboratory conditions, male-female encounters usually led to one individual being eaten by the other. Only in rare cases, he observed what he called a “parade sexuelle” (Pagés 1967: 57). In these cases, a male and a female faced each other head on and palpated each other with their antennae. In fact, the reinforced interior on the basal antennomeres observed in three cave-adapted species (*Muggenjapyx brehieri* (Sendra *et al.* 2021b), *Imazighenjapyx maraccanus* (Fig. 8A), and *Opisthjapyx naledi* (Fig. 16C)) could be an adaptation related to this behaviour. Meanwhile, their abdomina were curled upward and their cerci were brought in position as if at the beginning of an attack, but then withdrew, and assumed a waiting position. Pagés (l.c.) observed these “parades sexuelles” only in autumn and spring during the period of about one week, but several times a day, each parade lasting from a few minutes up to 2 hours and 21 minutes. The “parades” usually ended with the female devouring the male (never vice versa). Pagés (1967) assumed internal fertilization; however, he did not observe a copula nor the deposit of a spermatophore.

In his study on the postembryonic development of *Dipljapyx humberti*, Gyger (1960) assumed indirect sperm transfer in Japygidae, which he deduced from observations in *Campodea* Westwood, 1842 by Schaller (1954) and von Orelli (1956) but he could not observe or document this behaviour in his own study object. When individuals of *Dipljapyx* were introduced into a container where another individual had already established, aggressive attacks carried out with the forceps would inevitably follow the encounters. Attacks occurred both between individuals of the same or opposite sex. These encounters usually ended with the death of one of the fighting parties, which was eventually eaten by the larger and stronger individual.

Interestingly, Gyger (1960: 72) discovered a secondary sexual character in the forceps. He found that, in the 3rd larval stage and onward the forceps in juvenile *Dipljapyx* become increasingly sclerotized. The juvenile forceps already shows a distinct asymmetry in its parts. They bear a distinct tooth-like spine on the median side on the left cercus, at ca half length. This prominent tooth persists only in adult females, while it is strongly reduced in adult males. In both sexes, the right cercus also bears a distinct tooth, which is at ca ⅓ of the cercus’ length. Sexual dimorphism in cerci has also been reported in *Catajapyx confusus* by Pagés (1987). In this species, females (and juveniles) possess a single row of 6–14 apically rounded denticles, while males possess two rows of denticles (9–15 each) in the distal (postdental) portion of left cercus´ inner margin. Pagés (1987: 757) explicitly states that the presence of this secondary sexual character is unique among European Japygidae.

Gyger's (1960) and Pagés' (1987) findings suggest at least some involvement of the forceps in sexual behaviour, at least in *Dipljapyx humberti* and *Catajapyx confusus*. Then, further observational studies are necesary to understand if and how the evolution of cerci morphology was influenced by sexual selection. Previous attempts of such studies by Pagés (1957) and Gyger (1960) were impeded by the cannibalistic behaviour of their study objects, which apparently arises easily in captivity.

As adults and juveniles of japygids pinch their forceps when disturbed, it appears logical to assume that cerci first evolved as a defence against predators. It is conceivable that once the forceps "tool" was available, aggressive behaviours developed, such as prey capture (resp. steadying of prey), perhaps even competition with other conspecifics for food or, in the case of males, for females. Briceno & Eberhard (1995), in their detailed study on the functional morphology of the forceps in Dermaptera (a taxon with confirmed direct sperm transfer), hypothesized that defence behaviours were most likely plesiomorphic, while the use of the forceps to gain sexual access to females, either through male-male competition or via manipulation of the female to facilitate intromission, was assumed to be secondary, or derived.

Research perspectives

To fully understand the selective forces which are influencing the morphological configuration of the cerci, it is required to explore the full range of behaviours in which the forceps are involved. Novel digital analysis tools make it possible to study their morphology at various levels of integration in a non-invasive way (see video in Supp. file 1). We expect that many questions on the biomechanics of cerci in action can be addressed by these new methods. Results from these studies, however, need to be accompanied by observations of the living organism to unravel important facts relating to japygid biology, e.g., reproductive behaviour. So far, even basic facts pertaining to their mating system (e.g., direct or indirect sperm transfer) remain unknown. One aspect which has not been addressed by any author so far is the possibility that the hardened, movable forceps may also act as signalling devices, e.g., by tapping on the substrate. E.O. Wilson (2017) in his book *Half-Earth: Our Planet's Fight for Life* specifically mentions the Japygidae as an example of taxa which are ubiquitous yet widely unknown with respect to their biology and ecological significance.

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Supplementary material

Supp. file 1. Video of cerci movement based of the *Teljapyx aotearoa* Sendra & Sánchez-García sp. nov. morphology. An animated movie produced with scientific supervision by José Antonio Peñas. https://doi.org/10.5852/ejt.2022.894.2287.9875