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A new japygid species (Hexapoda: Diplura) from Cretaceous Kachin amber

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Abstract

A new species of Diplura, belonging to the little-known and poorly diverse hexapod family Japygidae, is described as *Metajapyx zhangi* Sendra, Sánchez-García, Peñalver & Luan **sp. nov.** The specimen, a complete and well-preserved male, was discovered in mid-Cretaceous (Cenomanian) Kachin amber from northern Myanmar. Diplurans are rare in the fossil record due to their soil and subterranean habits. The new species is assigned to the genus *Metajapyx* Silvestri, 1933, and represents its first fossil species. *Metajapyx zhangi* **sp. nov.** is compared with the extant species of the genus and with the only other japygid species described from Kachin amber. The diagnosis is based on a combination of characters, including the number of antennomeres, body chaetotaxy, and the characteristics of the abdominal sclerites and cerci. These results improve understanding of anatomical variation among *Metajapyx* species and point to remarkable morphological stasis across deep geological time. This discovery also provides new evidence on the early morphological diversification of Japygoidea and the faunal composition of Cretaceous soil-dwelling predators.

Keywords: Cenomanian, Japygoidea, Myanmar, taxonomy

Introduction

Understanding the origin and evolution of hexapods requires detailed knowledge of the basal lineages, yet this is hindered by their extremely scarce fossil record. Among these lineages, Diplura is a particularly understudied clade, whose fossil history is only recently beginning to emerge—largely thanks to discoveries in amber deposits. In this context, Cretaceous amber from northern Myanmar (Kachin State) is proving especially valuable, yielding an increasing number of well-preserved specimens that contribute to our understanding of dipluran diversity during the Mesozoic.

Extant diplurans comprise over 1,000 described species distributed across 10 families and three superfamilies, inhabiting various soil layers and cave environments: Campodeoidea, Projapygoidea, and Japygoidea (Pagés, 1959; Sendra *et al.*, 2021). These groups are primarily distinguished by the morphology of their cerci—appendages whose structure is strongly tied to their ecology. Campodeoidea, characterised by long, segmented, filiform cerci, are generally herbivorous. In contrast, both Projapygoidea and Japygoidea are predominantly predatory. Projapygoidea possess multi-segmented cerci traversed by ducts that can eject chemical secretions for defence or hunting, while Japygoidea bear unsegmented, forceps-like cerci (Condé, 1956; Pagés, 1959; Sendra *et al.*, 2021; Potapov *et al.*, 2022). Nonetheless, the phylogenetic relationships among these three groups remain unresolved. Morphological data have

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traditionally grouped Campodeoidea and Projapygoidea together due to their segmented cerci, whereas molecular analyses suggest a closer affinity between Projapygoidea and Japygoidea (Luan *et al*., 2005; Du *et al*., 2024). Hence, the discovery of transitional fossils could be pivotal in resolving these controversies.

Among the three superfamilies, the Japygoidea are particularly striking for these pincer-like cerci converging with the much more familiar Dermaptera. Within Japygoidea, five extant families are recognised: Dinjapygidae and Heterojapygidae (each with a single genus, included the largest known diplurans), Parajapygidae (four genera), Evalljapygidae (five genera) and the most diverse Japygidae (63 genera) (Paclt, 1957; Pagés, 1959, 1989; Sendra *et al*., 2021). Notably, the only fossils regarded as diplurans predating the mid-Cretaceous have been referred to Japygoidea. One is the enigmatic *Testajapyx thomasi* from the Late Carboniferous (~308 Ma) Mazon Creek deposits of Illinois, USA, discussed as a stem-group Japygoidea (Kukalová-Peck, 1987; Grimaldi, 2010). However, its attribution to Diplura has been challenged, and alternative placements within Hexapoda have been proposed (Staniczek *et al*., 2014). The other is the unequivocal japygoid *Ferrojapyx vivax* from the Early Cretaceous Crato Formation of Brazil (Wilson & Martill, 2001).

To date, the oldest amber-preserved diplurans are from Cretaceous Kachin amber and include representatives of all three superfamilies, although the reported diversity is still very low: *Electroprojapyx alchemicus* (Projapygoidea), *Cretojapyx huangi* (Japygoidea), and unstudied Campodeoidea specimens (Zhang, 2017; Sánchez-García *et al*., 2023; Wang *et al*., 2023). No other Cretaceous amber has yielded diplurans. In the Cenozoic, only a handful of occurrences are known: two Campodeoidea species from Baltic amber and two from Dominican amber, as well as three Projapygidae species (two unnamed) from Dominican amber (Silvestri, 1912; Sánchez-García *et al*., 2023, 2024). Three additional species have been reported from the Onyx marble of Arizona, but these need revision (Pierce, 1950, 1951).

In this study, we report and describe the second known fossil of a japygoid dipluran from mid-Cretaceous Kachin amber, based on a complete, well-preserved male specimen.

Material and methods

The studied specimen is present in Cenomanian (mid-Cretaceous) Kachin amber from Myanmar (Yu *et al*., 2019). The fossil was collected in 2015 in full compliance with the laws of Myanmar and China. This specimen was not involved in armed conflict or ethnic strife in Myanmar and was acquired before the Rohingya genocide in that country. We follow the considerations of Haug *et al.* (2020) regarding the controversy generated around the armed conflict and the ethics in the scientific study of the Kachin amber, as well as subsequent clarifications published in recent years, such as Peretti (2020), which address certain misinterpretations related to this issue. The fossil material is permanently deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, well-established public museum, in full compliance with the international Palaeoentomological Society Statement (Szwedo *et al*., 2020). The amber piece was trimmed and polished for optimal visualization of its bioinclusions.

General visualization and photography of the fossil specimen were carried out with a Keyence VHX-6000 digital microscope (at Guangdong Provincial Key Laboratory of Insect Development Biology and Applied Technology, Guangdong, China) and an Olympus BX53 compound microscope (at IGME, CSIC, València, Spain), under both transmitted and reflected light. Photographs were taken with the Keyence VHX-6000 digital microscope. The specimen was illustrated with the aid of an Olympus U-DA drawing tube attached to the Olympus BX53 microscope, and additionally by tracing directly over the photographs. Final photo-plates were processed and edited using Adobe Photoshop CS2 (version 9.0).

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

The following abbreviations are used in the main text and figure captions (Pagés, 1953, 1984; Smith, 1962; Muegge & Bernard, 1990): A, B, C = A, B, and C rows of urosternal macrosetae; D, L and V = dorsal, lateral and ventral positions of cercal macrosetae; GS = glandular seta; A, I, L, M = rows of macrosetae on dorsal head; M = macroseta; M1–5 = 1 to 5 macrosetae on thoracic and abdominal tergites; ma = medial anterior seta; sl = long seta; ssh = short seta.

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Systematic palaeontology

Order Diplura Börner, 1904

Superfamily Japygoidea Ewing, 1942
Family Japygidae Haliday, 1864
Genus *Metajapyx* Silvestri, 1933

Type species. *Metajapyx aemulans* (Silvestri, 1933); as proposed by Silvestri (1948b) based on the subgenus *Japyx* (*Metajapyx*).

Metajapyx zhangi **Sendra, Sánchez-García, Peñalver & Luan sp. nov.**
urn:lsid:zoobank.org:act:D9003ED0-D751-4228-B718-EEF96F53B691
(Figs 1–6)

Material. Holotype male, NIGP209792 deposited at Nanjing Institute of Geology and Palaeontology.

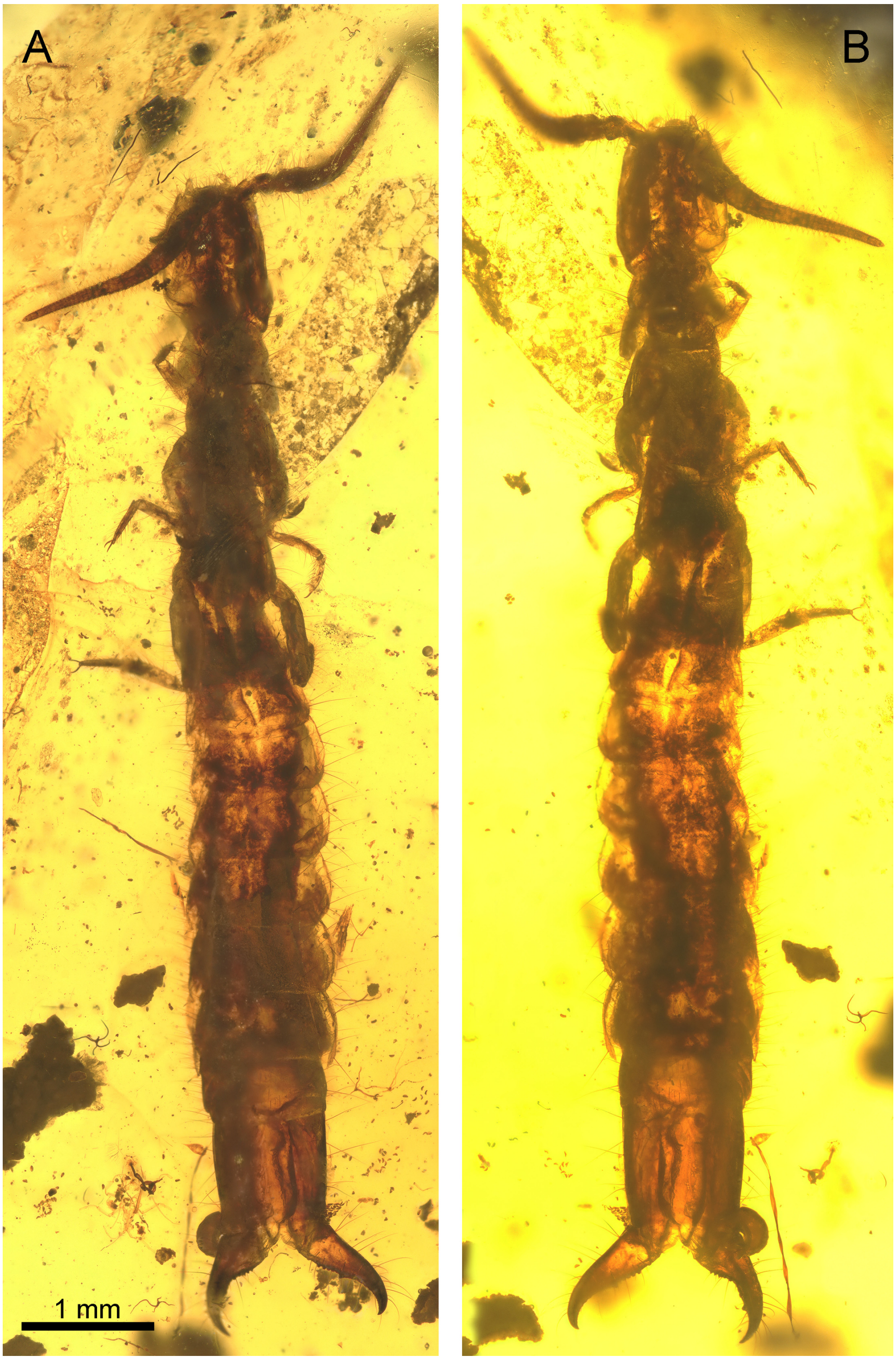

FIGURE 1. Male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Habitus in dorsal view. **B**, Habitus in ventral view. Both at same scale.

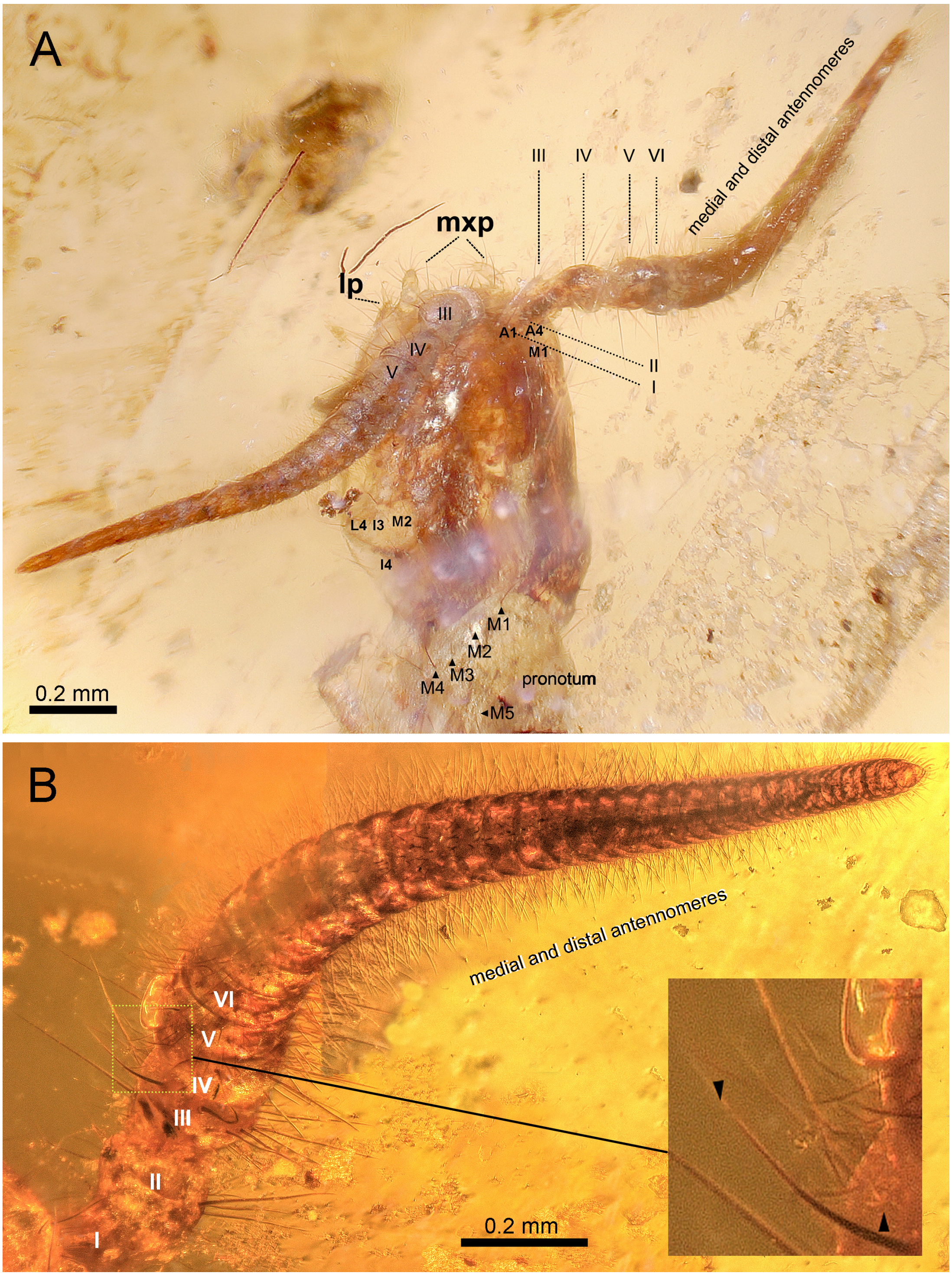

FIGURE 2. Head and pronotum features of the male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Dorsal view of head and pronotum. **B**, Dorsal view of the right antenna, and detail of latero-internal side of IV and V antennomeres (arrowheads indicate the basal and apical extremes of the dorsal trichobothrium). Abbreviations: I–VI = proximal antennomeres; A, I, L, M = dorsal head macrosetae; lp = labial palp; M1–5 = macrosetae in 1 to 5 positions; mxp = maxillar palp.

Syninclusions: the exuvium of a heteropteran insect, a mite (Fig. 4A, B), pollen grains of the form genus *Cycadopites*, some of them in clusters (Fig. 6A, C), and abundant plant trichomes of the typical form present in Burmese amber. The piece also contains soil debris.

Etymology. The specific epithet is dedicated in honour of Prof. Haichun Zhang for his seminal contributions to palaeoentomology.

Diagnosis. The new species is distinguished by a unique combination of features: Middle-sized male.

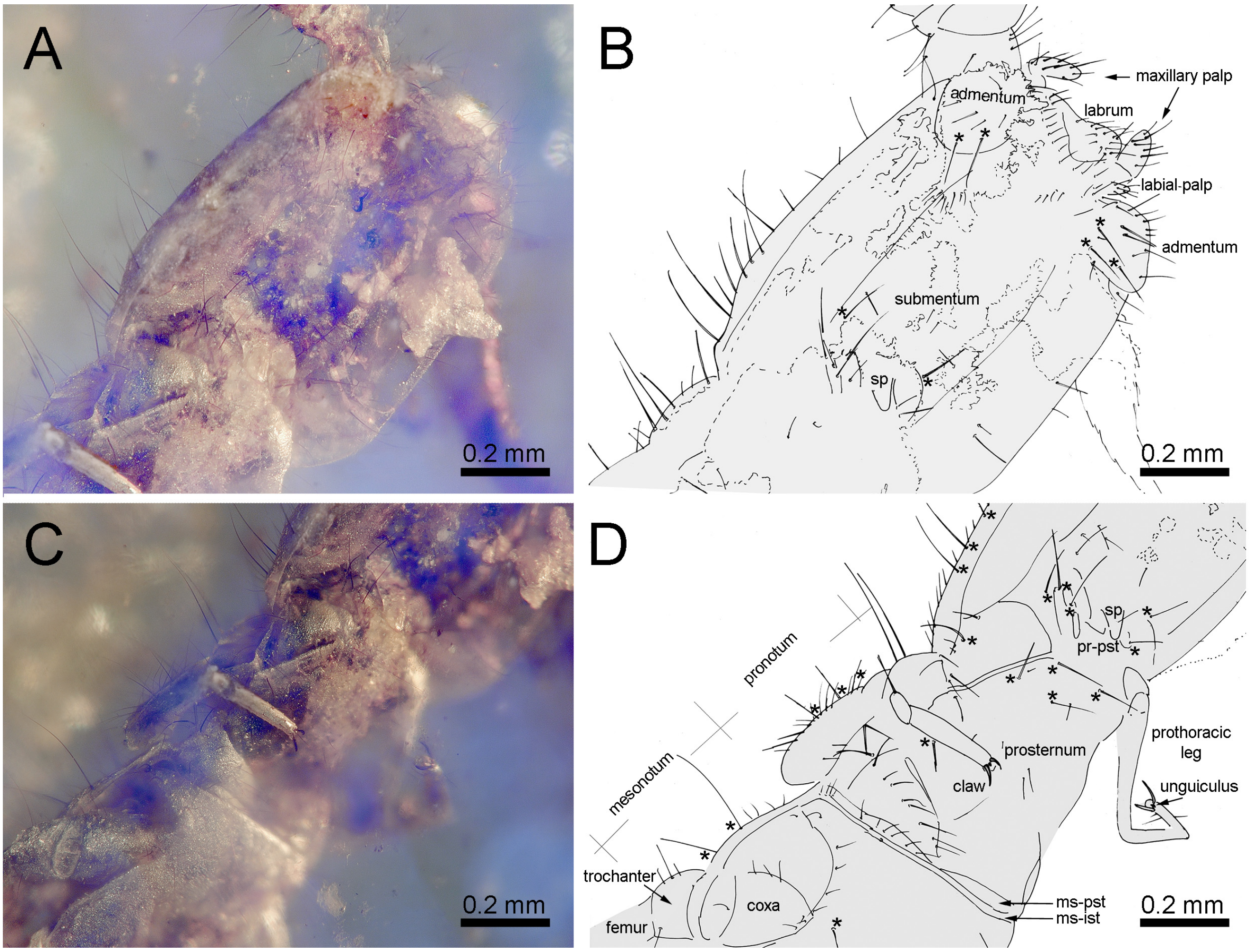

FIGURE 3. Head and prosternum-mesosternum features of the male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Ventral view of the head and anterior portion of prosternum. **B**, Interpretative drawing of **A**. **C**, Ventral view of the posterior portion of the head and anterior portion of mesosternum. **D**, Interpretative drawing of **C**. Abbreviations: ms-ist = meso-intersternum; ms-pst = meso-presternum; pr-pst = pro-presternum; sp = spine; * = position of some macrosetae.

Antennae with 39 antennomeres. Pronotum and mesonotum with 5+5 M1–5; metanotum with 4+4 M1–4. Legs short and robust, reaching the middle of abdominal segment IV. Urotergites I–VII with 1+1 *ma* and 5+5 M1–5; abdominal segments VIII–IX shorter than the rest, with segment IX the shortest; latero-posterior margins of urotergites rounded; abdominal segment X subquadrangular, with two distinctly marked dorsal carinae; urosternite I with a median glandular organ bearing tiny domes (disculis), and a lateral subcoxal organ with one row of GS; urosternites I–VIII with three irregular rows of A, B and C macrosetae. Cerci asymmetric; right cercus with a medial tooth, predental portion with a row of denticles and postdental portion crenulated; left cercus with one distal tooth, predental portion with a proximal row of sharp denticles splitting into two well-separated rows of smooth denticles forming a concavity ending in the sharp tooth, followed by a slightly crenulated postdental portion.

Locality and horizon. Kachin State, northern Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Description. Body (Fig. 1) 7.6 mm in length; maximum width 1.1 mm at abdominal segments VI and VII. Body covered with typical smooth long (sl) and short (ssh) setae and smooth macrosetae (M). Cuticle strongly sclerotised at tips of both mandible and maxillary lacinia, distal third of abdominal styli, claws, and edges of abdominal segment X and cerci.

Head 1.0 mm in length, subtrapezoidal, with oral folds; few macrosetae visible, arranged in the typical A, I, L and M rows (Fig. 2A). Labrum with several ssh and sl. Mentum with 1+1 posterior M and several ssh and sl. Admentum with 4–6 ssh and 2–3 sl. Mouthparts not visible with the exception of the lacinia apex and maxillary and labial palps; maxillary palp biarticulated, with ssh; labial palp slightly elongate, subconical, about 3× longer than wide, with few ssh and sl (Figs 2A, 3A, B).

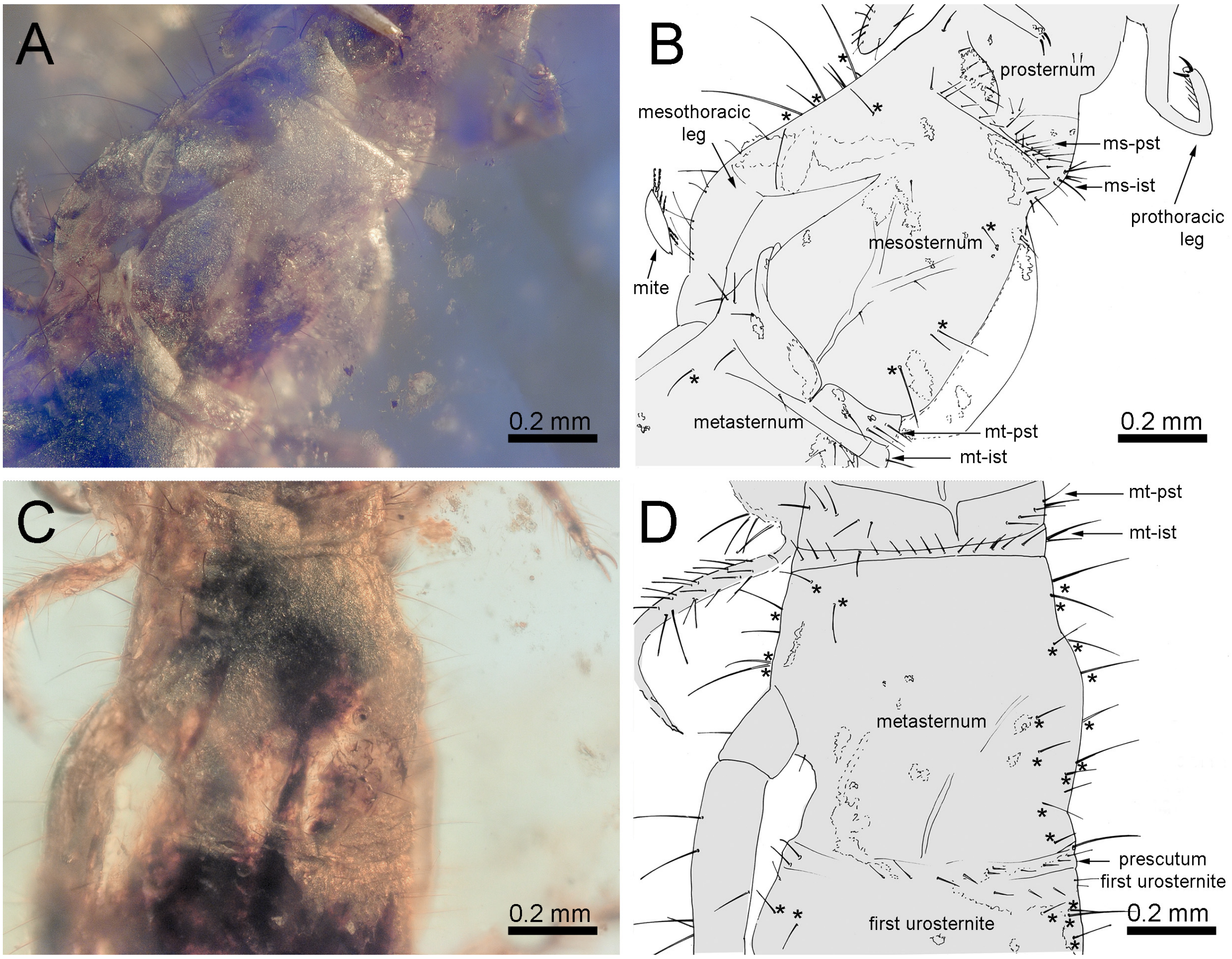

FIGURE 4. Prosternum, metasternum and first urosternite features of the male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Posterior portion of prosternum to anterior portion of metasternum. **B**, Interpretative drawing of **A**. **C**, Metasternum and anterior portion of first urosternite. **D**, Interpretative drawing of **C**. Abbreviations: ms-ist = meso-intersternum; ms-pst = meso-presternum; mt-ist = meta-intersternum; mt-pst = meta-presternum; * = position of some macrosetae.

Antenna 1.8 mm in length (measured on right antenna), with 39 antennomeres; antennomeres I and II 1.6× wider than long; III–V 1.4× longer than wide, slightly expanded on their latero-internal sides; medial and distal antennomeres telescoped up to antennomere V; apical antennomere subconical (Fig. 2A, B). All antennomeres with sl and ssh arranged in 2–3 irregular whorls, gradually shorter towards the distal antennomeres. Trichobothria present at least on antennomere IV (Fig. 2B). No placoid sensilla observed, likely due to preservation.

Thorax 2.7 mm in length. Dorsal and sternal sclerites with sl, ssh and M; pronotum and mesonotum with 5+5 M1–5 (Fig. 2A); metanotum with 4+4 M1–4. Sternites, intersternites, and poststernites well defined; pro-, meso- and metasternites with strong internal Y-shaped cuticular structures (furcisternites) , though not always visible; pro-presternum prolonged into a short posterior spine; anterior portion of prosternum with 3+1 visible M; prosternum with 5+2 M (Fig. 3C, D); meso-presternum and meso-intersternum with a row of sl; mesosternum with at least 1+3 M (Fig. 4A, B); meta-presternum and meta-intersternum with a row of sl; metasternum with 1+2 visible M (Fig. 4C, D).

Legs short and robust; hind leg 2.1 mm in length, reaching the middle of abdominal segment IV (Fig. 1). Legs with ssh, sl and M; ventral side of tarsus with thickened setae. Pretarsi with two subequal claws and a tiny, medial unguiculus (Fig. 3C, D).

Abdomen 4.2 mm in length. Urotergites, urosternites and uropleurites with ssh, sl and M. Urotergites I–VII with 1+1 ma and 5+5 M1–5; abdominal segments VIII–IX shorter than the rest, IX being the shortest, both with unclear number of M, which are only visible in lateral position. Latero-posterior margins of urotergites apparently rounded; lateral sides of abdominal segments VI–VII partially broken (Fig. 1). Abdominal segment X

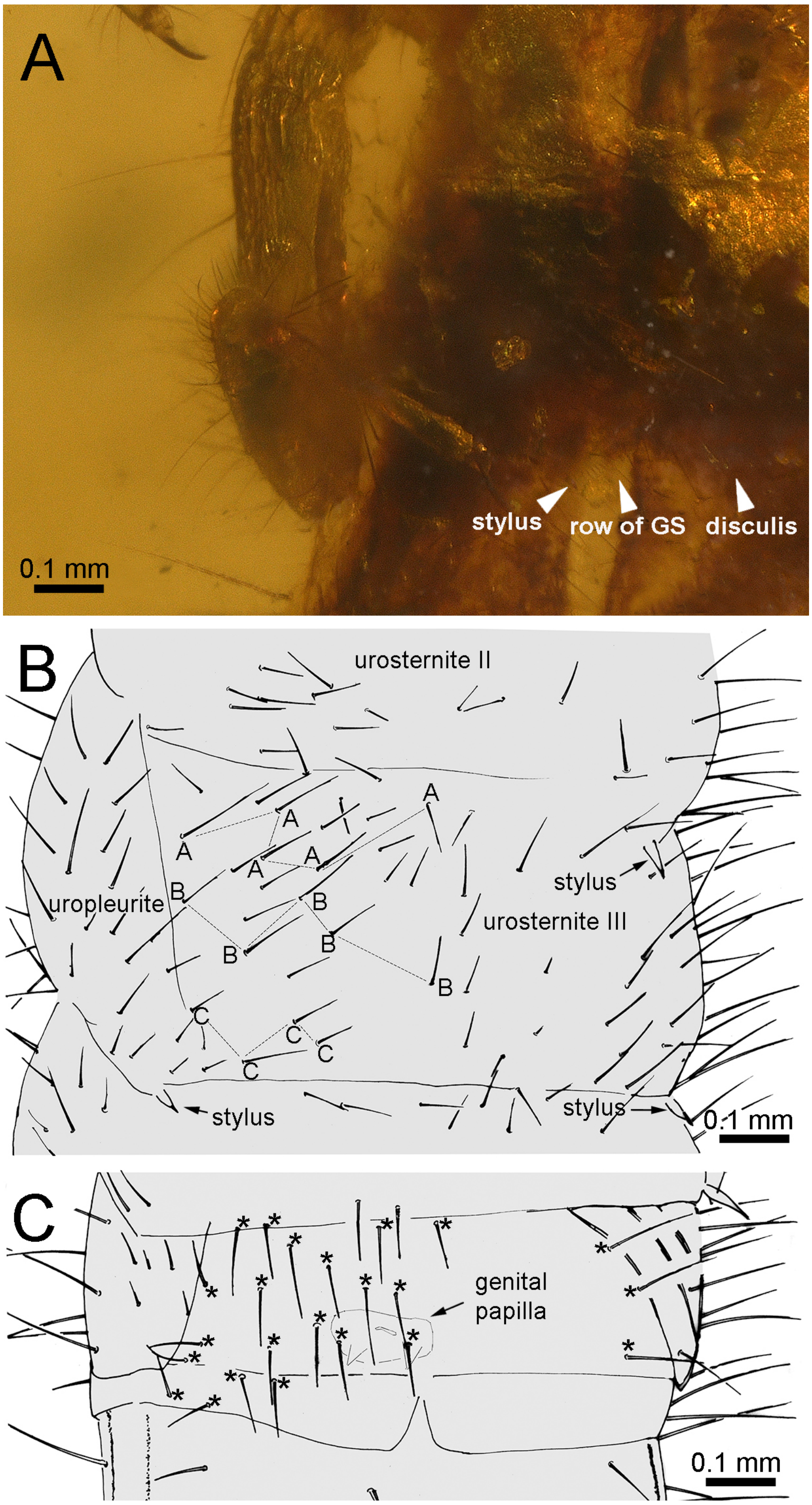

FIGURE 5. Metathorax and abdominal features of the male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Ventrolateral view of posterior portion of metathorax to anterior portion of abdominal segment II. **B**, Interpretative drawing of the ventral view of posterior portion of abdominal segment II to anterior portion of abdominal segment IV. **C**, Interpretative drawing of the ventral view of posterior portion of abdominal segment VIII to anterior portion of abdominal segment X, showing the male genital papilla. Abbreviations: A, B, C = rows of urosternal macrosetae; GS = glandular seta; * = position of some macrosetae.

0.9 mm in length, subquadrangular, with strongly marked lateral margins on both dorsal and ventral sides; dorsal side with distinct carinae, subparallel and slightly converging posteriorly; acropygium indistinct; dorsal side with up to 2+0 visible M; lateral sides with up to 10+10 M; ventral side having four rows of short M. First urosternite with median glandular organ bearing several disculis, and two lateral subcoxal organs each with a row of GS; sensorial

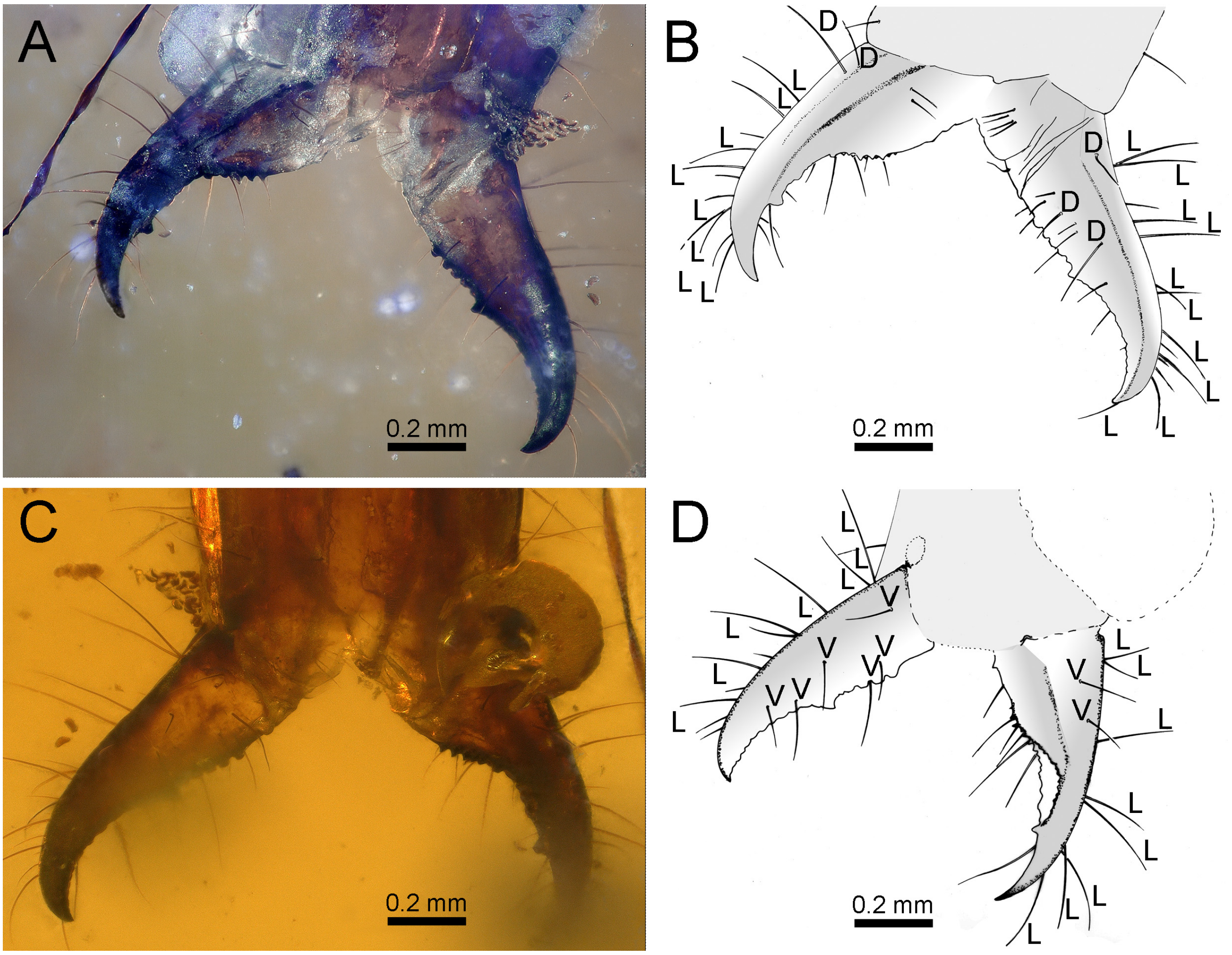

FIGURE 6. Cerci of the male holotype of *Metajapyx zhangi* **sp. nov.** (Japygidae), NIGP209792. **A**, Dorsal side. **B**, Interpretative drawing of **A**. **C**, Ventral side. **D**, Interpretative drawing of **C**. A cluster of pollen grains of the form genus *Cycadopites* is visible close to the base of the right cercus (see **A** and **C**). Abbreviations: D = dorsal cercal macrosetae; L = lateral cercal macrosetae; V = ventral cercal macrosetae.

setae not visible (Fig. 5A). Urosternites I–VII with a pair of slightly elongated styli, sclerotised at their apices. Urosternites I–VIII with three irregular rows of M (A, B and C) but only a few M are visible (Fig. 5B). Urosternite VIII with apparent male genital papilla bearing two short conical appendages partly hidden beneath posterior margin of the segment (Fig. 5C). Urosternite IX with up to four visible setae. Uropleurites with several setae; spiracles not visible.

Cerci (Fig. 6) 0.9 mm in length, asymmetric and well sclerotised, including their edges and the two pairs of condyles; dorsal condyle apparently displaced towards the centre, probably due to the fossilization process. Right cercus with a medial tooth on the inner margin; predental portion with a row of five subquadrangular denticles; postdental portion slightly crenulated. Left cercus with a distal tooth on the inner margin; predental portion with a proximal row of five sharp denticles, dividing into two well-separated rows of 4–5 smooth denticles forming a concavity ending in a sharp tooth; postdental portion slightly crenulated. Cerci covered by ssl, ls and M; right cercus with 3D, 10L and 5V macrosetae; left cercus with at least 2D, 8L and 2V macrosetae (Fig. 6B, D).

Discussion

The new fossil species can be confidently assigned to superfamily Japygoidea based on the presence of well-developed forceps-like cerci (Verhoeff, 1923; Pagés, 1959; Sendra *et al*., 2021). In addition, it shows lateral and central organs on the first urosternite, two lateral styli on urosternites I–VII, smooth macrosetae and biarticulated maxillary palps, features supporting its inclusion in the family Japygidae (Paclt, 1957; Pagés, 1959, 1989). Among japygids, the morphology of the forceps-like cerci exhibits considerable variability in terms of relative length and width, denticulation of the inner margin with 0 to 3 rows of denticles, and 0 to 2 teeth in both cercus or only in one of them, and also variability in their curvature and degree of asymmetry (Silvestri, 1948a; Sendra *et al.*, 2023). Among these features, the cerci denticulation pattern is considered one of the most reliable traits for delimiting genera and species within the family (*e.g.*, Verhoeff, 1923; Silvestri, 1948a; Paclt, 1957; Pagés, 1989; Sendra *et al.*, 2023), although additional anatomical features of other structures provide a more natural classification of japygids (*e.g.*, Pagés, 1995).

The fossil specimen (holotype) shares a combination of cerci features with extant *Burmjapyx* Silvestri, 1930, *Notojapyx* Paclt, 1957, *Metajapyx* Silvestri, 1933, and *Protjapyx* (Grassi, 1886), including asymmetrical morphology, one row of denticles on the right cercus, two rows on the left cercus, and a basal enlargement of the left cercus. Another trait shared with these genera is the distribution of notal macrosetae, with no more than 7+7 macrosetae on the pronotum (see Silvestri, 1929, 1930, 1933; Paclt, 1957). Furthermore, the new species displays a relevant morphological similarity with *Metajapyx* species in the presence of a median glandular organ on the first urosternite, having disculis. This combination of taxonomic features supports its assignment to the extant genus *Metajapyx* and the proposal of a new fossil species, *Metajapyx zhangi* **sp. nov.**, based on additional anatomical features, the most significant of which is a higher number of antennomeres (39) than in any known *Metajapyx* species (Smith & Bolton, 1964); the genus comprises 36 extant known species (Sendra *et al.*, 2021). The close morphological similarity between this fossil species and extant representatives of *Metajapyx* indicates a remarkable degree of morphological stasis. Such long-term conservatism is consistent with bradytely, a pattern observed in arthropod lineages inhabiting ecologically stable environments. Japygids are edaphic hexapods with limited dispersal and strong dependence on stable soil microhabitats, conditions that likely reduce selective pressures on external morphology and promote persistence of an established groundplan. Comparable cases of morphological stasis have been documented in other Mesozoic–Recent arthropod lineages occupying soil, litter, or subcortical habitats (*e.g.*, Engel & Grimaldi, 2002; Cognato & Grimaldi, 2008; Engel *et al.*, 2016; Sánchez-García & Engel, 2017). In this context, the presence of *Metajapyx* in mid-Cretaceous amber suggests that key aspects of its morphology and ecological niche were already established by that time, reinforcing the role of edaphic environments as long-term refugia promoting evolutionary stability.

In Burmese amber, only one species of Japygidae has been formally described to date, *Cretojapyx huangi* Wang, Huang & Cai, 2023 (Wang *et al.*, 2023), although at least three additional specimens remain undescribed (Xia *et al.*, 2015; Zhang, 2017). In comparison with *Cretojapyx*, *Metajapyx zhangi* **sp. nov.** presents several distinguishing features. Regarding abdominal segment X, *Cretojapyx* possesses strong carinae that converge distally, whereas in *Metajapyx zhangi* **sp. nov.**, the abdominal segment X is subquadrangular and bears two straight, parallel dorsal carinae without clear apical convergence. The morphology of the cerci further differentiates the two genera. The genus *Cretojapyx* shows a relatively simple configuration: the right cercus has a postmedian tooth followed by a uniseriate row of denticles, while the left cercus lacks distinct dentition. In contrast, *Metajapyx zhangi* **sp. nov.** exhibits a more complex cerci morphology: the right cercus has a medial tooth, and the left cercus bears a distal tooth flanked by a concavity formed by two well-separated rows of smooth denticles, followed distally by a crenulated postdental region. This configuration is unique among known fossils and is present in extant *Metajapyx* species, which further supports separating the new fossil from *Cretojapyx*. Moreover, the new species possesses a well-developed median glandular organ with disculis and a lateral subcoxal organ composed of a row of glandular setae on urosternite I. These last structures are not reported in *Cretojapyx*, possibly due to limitations in preservation or imaging of the amber specimen.

The poor preservation of minute anatomical features of *Ferrojapyx vivax,* a compression fossil from the Lower Cretaceous (Aptian) Crato Formation of Brazil (Wilson & Martill, 2001), which shows a habitus and some features reminiscent of the family Japygidae, prevents detailed comparison with the new Cretaceous species.

The syninclusions in the japygid amber piece do not provide much palaeobiological context. For instance, the presence of abundant gymnosperm pollen grains of *Cycadopites* very close to the japygid body is likely coincidental. However, the presence of soil particles indicate that this piece is litter amber. Furthermore, it suggests that the new species was a soil-dwelling predator, like its extant counterparts. From a taphonomic perspective, the soil and cave habitats of modern forcepstails best explain the group's scarce fossil record (Sánchez-García *et al.*, 2024). The new species certainly did not inhabit caves, as the chance of resin entrapment there would have been negligible.

Acknowledgments

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