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New species of *Vetuprostomis* from mid-Cretaceous amber of northern Myanmar (Coleoptera: Tenebrionoidea: Prostomidae)

YAN-DA LI[1,5], YUN HSIAO[2,3,6], DI-YING HUANG[1,7] & CHEN-YANG CAI[1,4*]

[1]*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Centre for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China*
[2]*Australian National Insect Collection, CSIRO, GPO Box 1700, Canberra ACT 2601, Australia*
[3]*Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia*
[4]*School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK*
[5] *ydli@pku.edu.cn; https://orcid.org/0000-0002-9439-202X*
[6] *yunhsiao@outlook.com; https://orcid.org/0000-0003-2619-3296*
[7] *dyhuang@nigpas.ac.cn; https://orcid.org/0000-0002-5637-4867*
[*]*Corresponding author. cycai@nigpas.ac.cn; https://orcid.org/0000-0002-9283-8323*

Abstract

Two new species of the prostomid genus *Vetuprostomis* Engel & Grimaldi (Coleoptera: Tenebrionoidea: Prostomidae), *V. angularis* Li & Cai **sp. nov.** and *V. gaoi* Li & Cai **sp. nov.**, are described from the mid-Cretaceous Burmese amber. *Vetuprostomis* is suggested to be more closely related to extant *Dryocora* Pascoe distributed in Australia and New Zealand, rather than the widespread genus *Prostomis* Latreille. A key to prostomid genera, as well as species in genus *Vetuprostomis*, is provided.

Key words: Prostomidae, fossil, Burmese amber, Cretaceous, paleobiogeography

Introduction

The family Prostomidae, a small family in the superfamily Tenebrionoidea, comprises only two extant genera, *Dryocora* Pascoe (Fig. 1) and *Prostomis* Latreille. *Dryocora* occurs only in Australia (including Tasmania) and New Zealand (e.g., Waterhouse, 1877; Broun 1880; Lea 1904; Ewers & Didham 2004; Lawrence & Ślipiński 2013), with three uncontested species (*D. cephalotes* (Waterhouse), *D. howitti* Pascoe, and *D. walkeri* Lea). *Prostomis* has almost worldwide distribution, occurring on all major continents except South America and Antarctica (Schawaller 2019), with about 37 species recognized (as listed in Baena *et al*. 2021). The adults of Prostomidae are distinctly characterized in Tenebrionoidea by the 4-4-4 tarsal formula and the presence of a pair of jugular processes on the ventral side of head. The shape of jugular processes is very important for differentiating species of *Prostomis* (e.g., Schawaller 1991, 1992, 1993). The shape of the mandibles, the shape of the aedeagus, and the body length could serve as additional diagnostic character for species (Ito & Yoshitomi 2016, 2017a, 2017b). Both adults and larvae of Prostomidae are associated with decomposing wood (e.g., Schawaller 1993; Baena *et al*. 2021).

The accurate phylogenetic position of Prostomidae is not yet settled. Schunger *et al*. (2003) suggested an affinity between Prostomidae and Boridae, Mycteridae or Pyrochroidae based on the comparison of larval morphology. The morphology-based phylogeny of Lawrence *et al*. (2011) recovered Prostomidae nested within a paraphyletic Salpingidae, which was supported by the molecular phylogeny by Bocak *et al*. (2014). The molecular phylogeny by Gunter *et al*. (2014) focusing on Tenebrionoidea, however, suggested a position of Prostomidae within a branch of Melandryidae (Melandryidae2 *sensu* McKenna *et al*. 2019). McKenna *et al*. (2015), instead, suggested a sister relationship between Prostomidae and Oedemeridae based on the analysis of eight nuclear genes.

The fossil record of Prostomidae is quite sparse. Undescribed fossils of genus *Prostomis* have been reported from the Eocene Baltic amber (Schawaller 2003). Engel & Grimaldi (2008) described the earliest prostomid fossil, *Vetuprostomis consimilis* Engel & Grimaldi, from the mid-Cretaceous Burmese amber. In the present study, we further describe and illustrate two new species of *Vetuprostomis* from Burmese amber.

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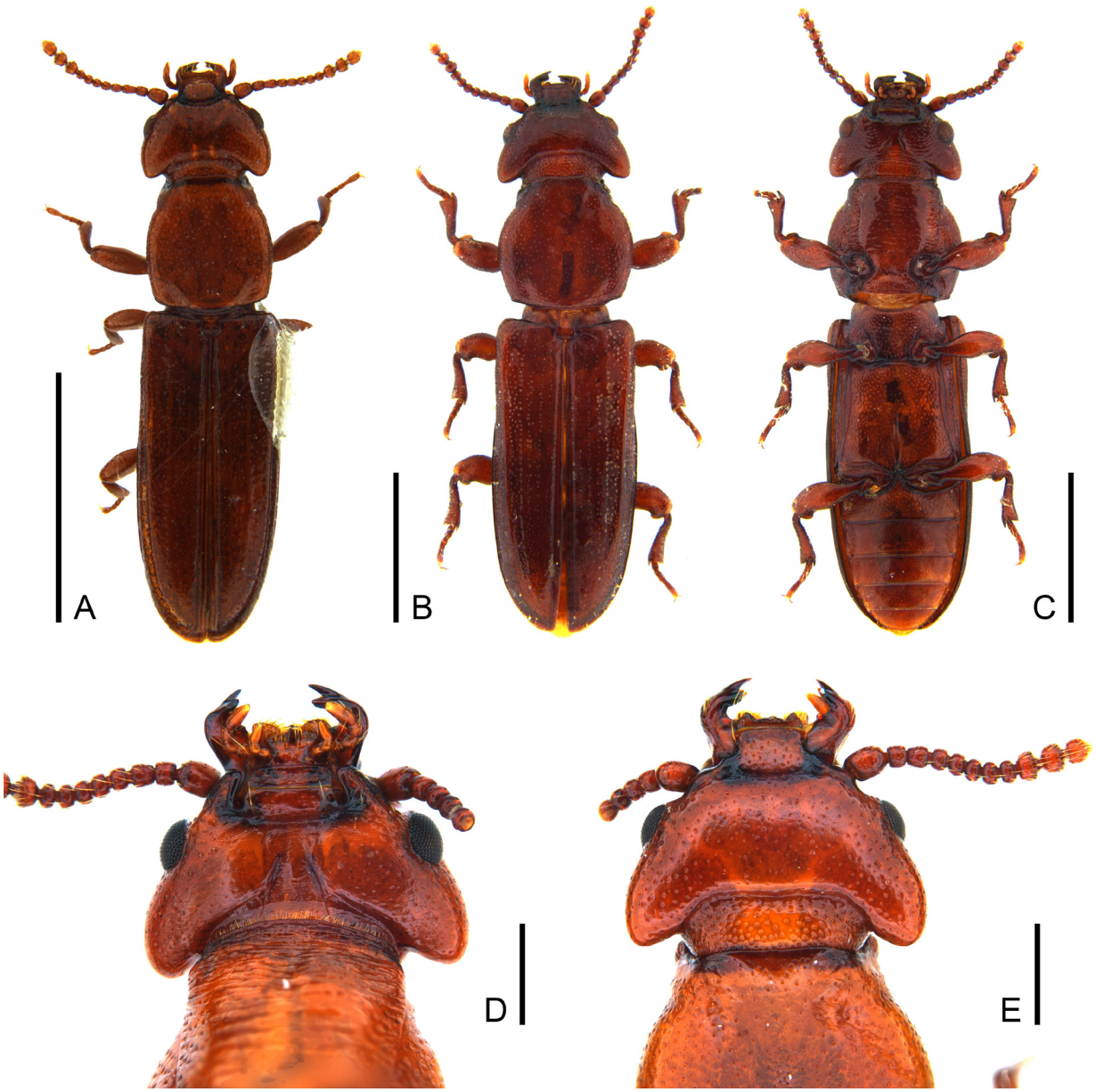

FIGURE 1. Extant *Dryocora* spp., deposited in Australian National Insect Collection. **A**, *Dryocora walkeri*, dorsal view. **B–E**, *Dryocora howitti*. **B**, Habitus, dorsal view. **C**, Habitus, ventral view. **D**, Head, ventral view. **E**, Head, dorsal view. Scale bars: 2 mm in **A–C**, 500 μm in **D–E**.

Materials and methods

The Burmese amber specimens of *Vetuprostomis* studied herein (Figs 2–7) originated from amber mines near Noije Bum (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber pieces were trimmed with a small table saw, ground with emery paper of different grit sizes, and finally polished with polishing powder.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Widefield fluorescence images were captured with a Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon; for *V. angularis*) or 561 nm (DPSS 561-10; for *V. gaoi*) laser excitation lines (Fu *et al*. 2021). Images under incident light and widefield fluorescence were stacked in Helicon Focus 7.0.2 or Zerene Stacker 1.04. Con-

focal images were stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Tenebrionoidea Latreille, 1802

Family Prostomidae Thomson, 1859

Key to extant and extinct genera of Prostomidae

1. Temples not prominent; neck region indistinct (e.g., fig. 1 in Ito & Yoshitomi 2017a). Mandibles elongate; incisor edge with many teeth (fig. 32 in Schawaller 1991). Jugular processes (anteriorly produced genae) elongate, usually as long as mandibles (fig. 2 in Ito & Yoshitomi 2017a) . . . . . ***Prostomis*** **Latreille**

- Temples distinctly projected posterolaterally; neck region distinct (Figs 1D,E, 3A,B, 7B). Mandibles short; incisor edge with 1–2 teeth (Figs 1E, 3D, 7H). Jugular processes shorter (Figs 1D, 3B, 7A) **2**

2. Temporal projections large, broadly rounded (Fig. 1D,E). Pronotum with sides gradually converging anteriorly in anterior half (Fig. 1A,B) . . . . . ***Dryocora*** **Pascoe**

- Temporal projections weaker and sharper (Figs 3A,B, 7B). Pronotum with sides subparallel or weakly converging posteriorly (Figs 2, 5) . . . . . ***Vetuprostomis*** **Engel & Grimaldi**

Genus *Vetuprostomis* Engel & Grimaldi, 2008

Remarks. Although Engel & Grimaldi (2008) mentioned that Prostomidae consist of two extant genera, *Prostomis* and *Dryocora*, it seems that they did not compare their fossil with members of *Dryocora* at all. Their differential diagnosis was proposed based on comparison with *Prostomis* solely. Engel & Grimaldi (2008) claimed that *Vetuprostomis* differs from modern prostomids in the shorter jugular processes, and the wider (about as wide as head) and the anteriorly constricted pronotum. However, extant *Dryocora* also has short jugular processes and anteriorly constricted pronotum. The pronotum can even be wider than head at least in some of *Dryocora* species. Indeed, *Vetuprostomis* is more similar to *Dryocora* than *Prostomis*. In addition to the characters mentioned above, *Vetuprostomis* and *Dryocora* share the shorter and more simple mandibles and the posterolaterally projected temples compared to the nominal genus.

Extant prostomids have mandibles with three apical teeth. In Engel & Grimaldi (2008), *Vetuprostomis* was described as having apically bidentate mandibles. This difference is merely due to a different terminology. The first apicomarginal tooth *sensu* Engel & Grimaldi (2008) is identical to the dorsal apical tooth in extant prostomids. In the present paper we follow the terminology used for the extant Prostomidae (e.g., Lawrence & Ślipiński 2013).

Key to species of *Vetuprostomis*

1. Lateral sides of clypeus anteriorly converging (fig. 2A in Engel & Grimaldi 2008). Penultimate maxillary palpomere wider than long, shorter than half length of apical one (?) (fig. 2C in Engel & Grimaldi 2008). Jugal processes symmetrical, without lateral teeth or knobs (fig. 2C in Engel & Grimaldi 2008). Median groove of pronotum well developed, (almost) as long as pronotal length (fig. 1 in Engel & Grimaldi 2008) . . . . . ***V. consimilis*** **Engel & Grimaldi**

- Lateral sides of clypeus subparallel (or weakly diverging) in anterior portion (Figs 4D, 7H). Penultimate maxillary palpomere longer than wide, distinctly longer than half length of apical one (Figs 4A,D, 7A,H). Jugal processes asymmetrical; right process longer; inner sides with a tooth (Figs 4A, 7A). Median groove of pronotum absent or weakly developed, shorter than half length of pronotum (Fig. 4E) **2**

2. Jugal processes longer (e.g., right process: portion above tooth more than twice as long as portion below tooth) (Fig. 4A). Teeth on incisor edge of left mandible moderately separated (Figs 3A, 4D). Anterior angles of pronotum pointed (Figs 2, 4E) . . . . .

. . . . . ***V. angularis* Li & Cai sp. nov.**

- Jugal processes shorter (e.g., right process: portion above tooth less than twice as long as portion below tooth) (Fig. 7A). Teeth on incisor edge of left mandible more narrowly separated and strongly jointed basally; interspace only very weakly notched (Fig. 7H). Anterior angles of pronotum not pointed (Fig. 5) . . . . . ***V. gaoi* Li & Cai sp. nov.**

Vetuprostomis consimilis Engel & Grimaldi, 2008

Remarks. The original description and illustrations of this species by Engel & Grimaldi (2008) are not sufficient, which makes it difficult to provide a detailed comparison between *V. consimilis* and the two new species described here. In one of their line drawings (fig. 2C in Engel & Grimaldi 2008), the penultimate palpomere of both maxillary palps seems to be distinctly shortened, which if true, could serve as a distinctive character separating *V. consimilis* from *V. angularis* and *V. gaoi*. However, in another line drawing (fig. 2A in Engel & Grimaldi 2008), the penultimate palpomere of left maxillary palp appears to have a longer length. Thus, the effectiveness of this character should be treated carefully.

Vetuprostomis angularis Li & Cai sp. nov.

(Figs 2–4)

FIGURE 2. General habitus of *Vetuprostomis angularis* Li & Cai **sp. nov.**, holotype, NIGP177907, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1.5 mm.

Material. Holotype, NIGP177907.

Etymology. The specific name refers to its projected anterior pronotal angles.

Locality and horizon. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

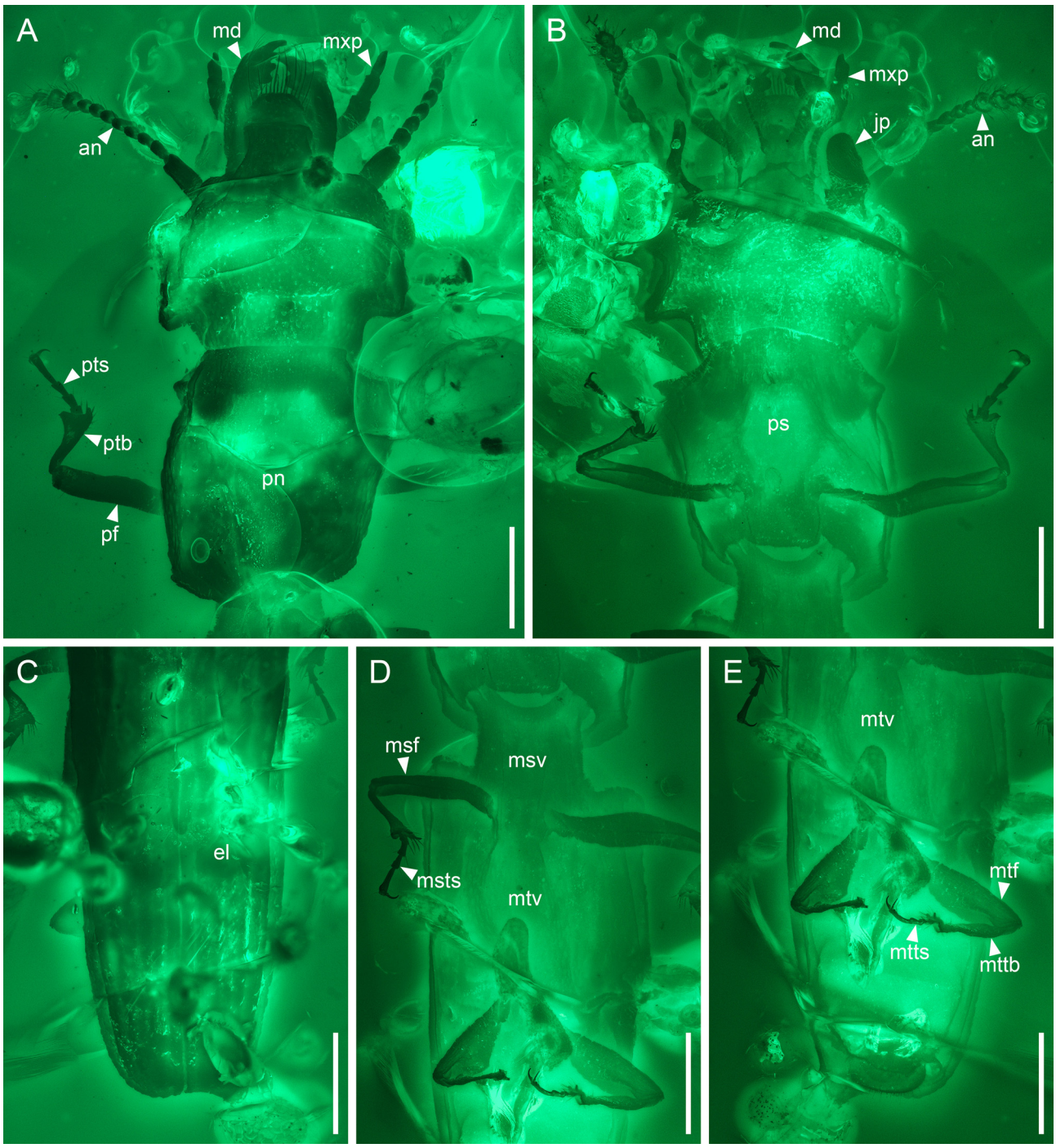

FIGURE 3. *Vetuprostomis angularis* Li & Cai **sp. nov.**, holotype, NIGP177907, under widefield fluorescence. **A**, Head and prothorax, dorsal view. **B**, Head and prothorax, ventral view. **C**, Elytral apex, dorsal view. **D**, Pterothorax, ventral view. **E**, Abdomen, ventral view. Abbreviations: an, antenna; el, elytron; jp, jugular process; md, mandible; msf, mesofemur; msts, mesotarsus; msv, mesoventrite; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus. Scale bars: 500 μm.

Diagnosis. Lateral sides of clypeus subparallel in anterior half (Fig. 4D). Left mandible with three apical teeth and two moderately separated teeth on incisor edge (Fig. 4D). Penultimate maxillary palpomere about as long as

apical one (Fig. 4A,D). Jugal processes asymmetrical, comparatively long; right process longer than left one; inner sides with a tooth (Fig. 4A). Median groove of pronotum probably absent (Fig. 4E). Anterior angles of pronotum pointed (Fig. 4E).

Description. Body elongate and flattened, about 5.2 mm long, 1.3 mm wide.

Head (Fig. 3A,B) prognathous, constricted posteriorly, with distinct neck region. Temples distinctly projected posterolaterally. Eyes small, round and finely facetted, without interfacetal setae. Antennal insertions slightly concealed from above; subantennal grooves absent. Frontoclypeal suture not clearly discerned. Clypeus (Fig. 4D) with lateral sides subparallel (or weakly diverging) in anterior portion; anterior margin truncate. Labrum (Fig. 4D) narrowed anteriorly, apically truncate, with numerous elongate setae. Antennae 11-segmented, moniliform, with weak, 3-segmented club. Mandibles (Fig. 4D) tridentate apically; left mandible with two moderately separated teeth on incisor edge; right mandible with one blunt tooth on incisor edge. Maxillary palps (Fig. 4A) probably 4-segmented; palpomere 1 short; palpomere 2 elongate; palpomere 3 longer than wide, distinctly longer than half length of apical one. Mentum strongly transverse. Jugal processes (Fig. 4A) asymmetrical; inner sides with a tooth; right process longer than left one, strongly constricted above tooth; left process weakly constricted above tooth.

Pronotal disc (Fig. 4E) longer than wide; anterior angles pointed laterally; median groove not clearly discerned. Prosternal process (Fig. 4B) wide, expanding beyond procoxae and meeting broad postcoxal projections, apically truncate. Procoxal cavities (Fig. 4B) circular, widely separated. Elytra (Fig. 3C) about 2.2 times as long as width combined; surface with longitudinal carinae. Mesoventrite (Fig. 4C) relatively narrow. Mesocoxal cavities (Fig. 4C) moderately separated.

Legs (Fig. 4F) short. Femora distally with groove on inner side. Tibiae shorter than femora, widened apically with spinose outer apical angle; spurs large and stout, paired on all legs. Tarsi 4-4-4; tarsomeres simple, without ventral lobes. Pretarsal claws simple.

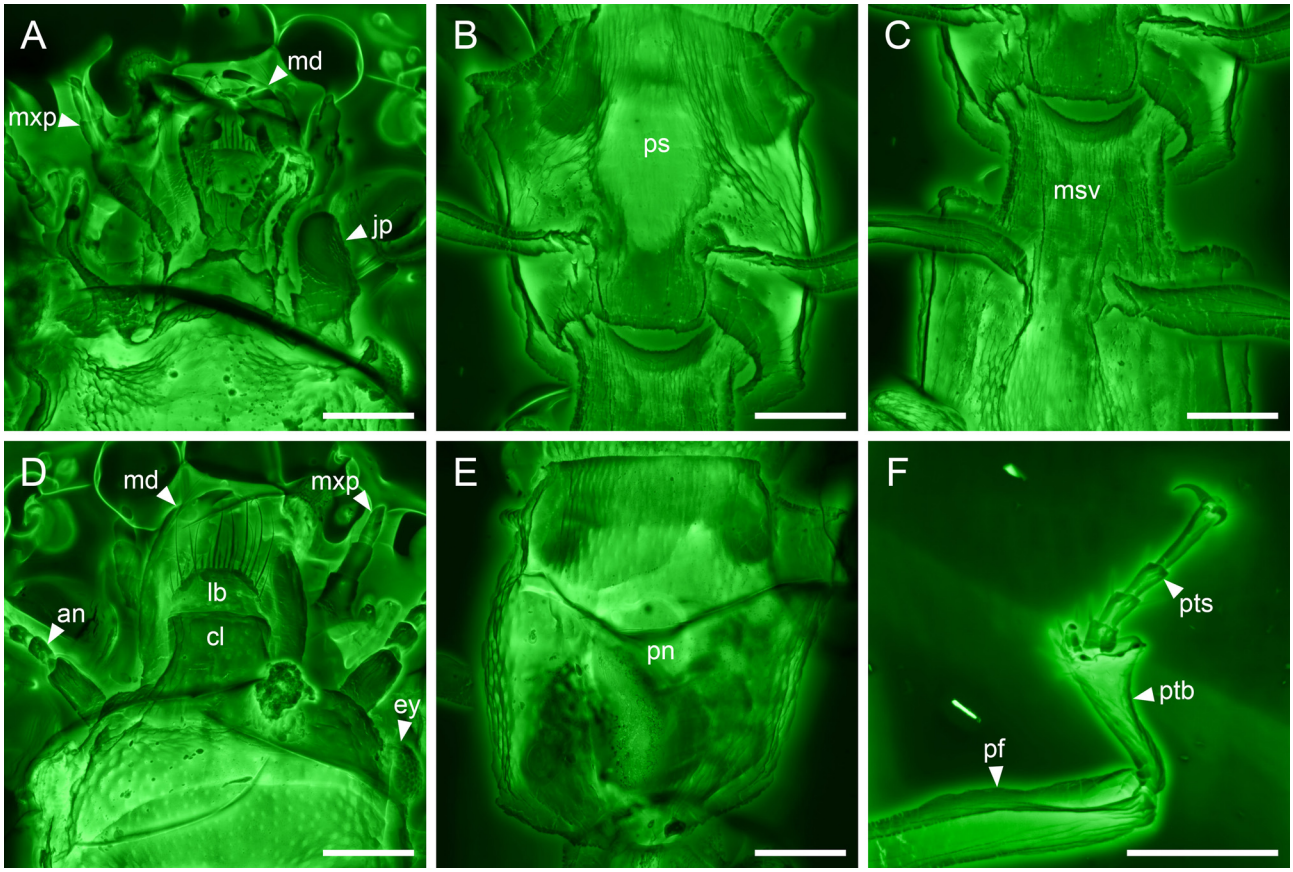

FIGURE 4. *Vetuprostomis angularis* Li & Cai **sp. nov.**, holotype, NIGP177907, under confocal microscopy. **A**, Mouthparts, ventral view. **B**, Prothorax, ventral view. **C**, Mesothorax, ventral view. **D**, Mouthparts, dorsal view. **E**, Prothorax, dorsal view. **F**, Fore leg. Abbreviations: an, antenna; cl, clypeus; ey, compound eye; jp, jugular process; lb, labrum; md, mandible; msv, mesoventrite; mxp, maxillary palp; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus. Scale bars: 300 μm.

***Vetuprostomis gaoi* Li & Cai sp. nov.**
(Figs 5–7)

Material. Holotype, NIGP177908.

Etymology. The species is named after Mr. Yu-He Gao, who kindly donated many fossils for our research.

Locality and horizon. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Diagnosis. Lateral sides of clypeus subparallel in anterior half (Fig. 7H). Left mandible with three apical teeth and two narrowly separated and basally strongly jointed teeth on incisor edge (Fig. 7H). Penultimate maxillary palpomere about as long as apical one (Fig. 7A). Jugal processes asymmetrical, comparatively short; right process longer than left one; inner sides with a tooth (Fig. 7A). Median groove of pronotum weakly developed, shorter than half length of pronotum (Fig. 5). Anterior angles of pronotum not pointed (Fig. 5).

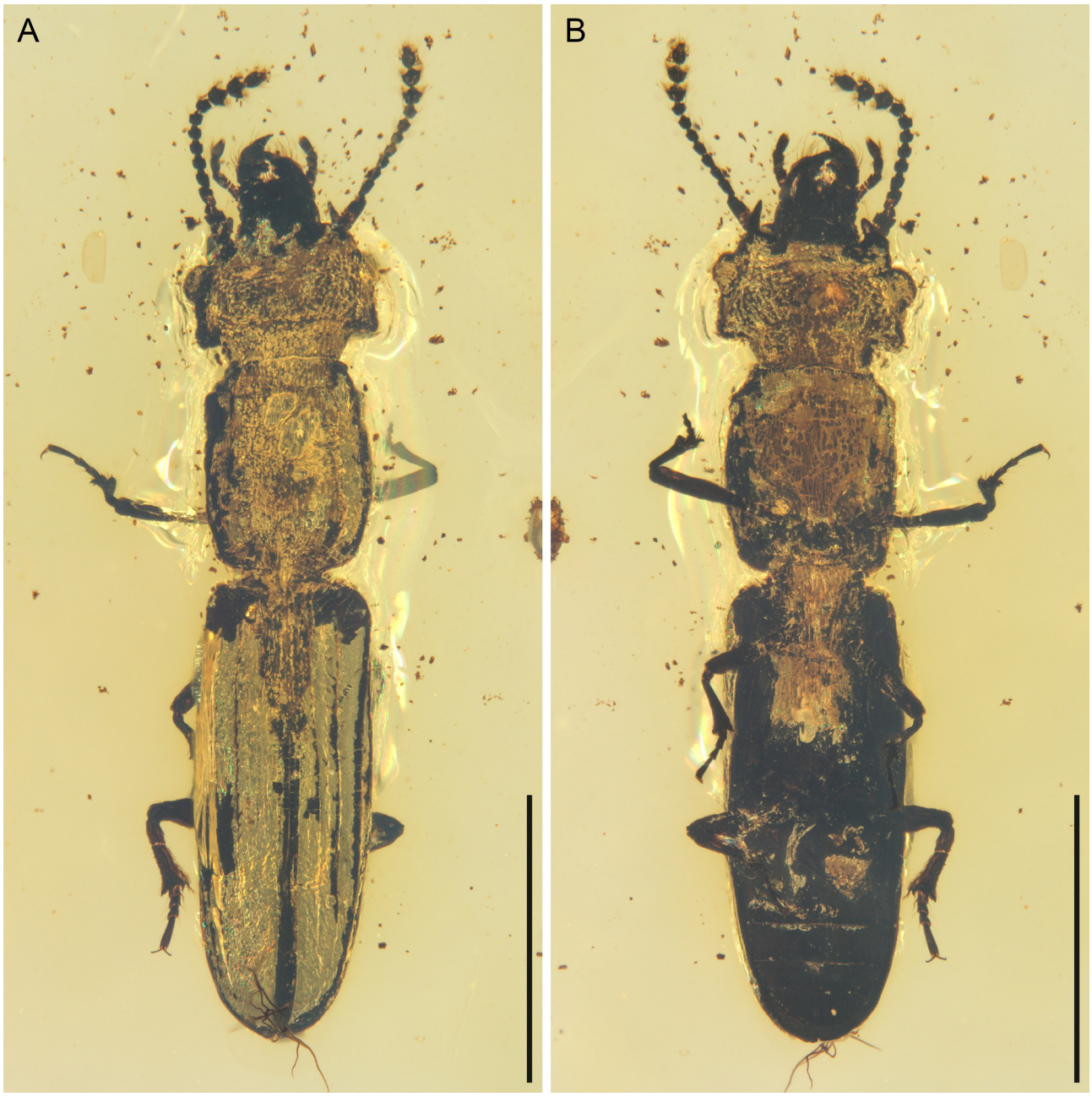

FIGURE 5. General habitus of *Vetuprostomis gaoi* Li & Cai **sp. nov.**, holotype, NIGP177908, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1.5 mm.

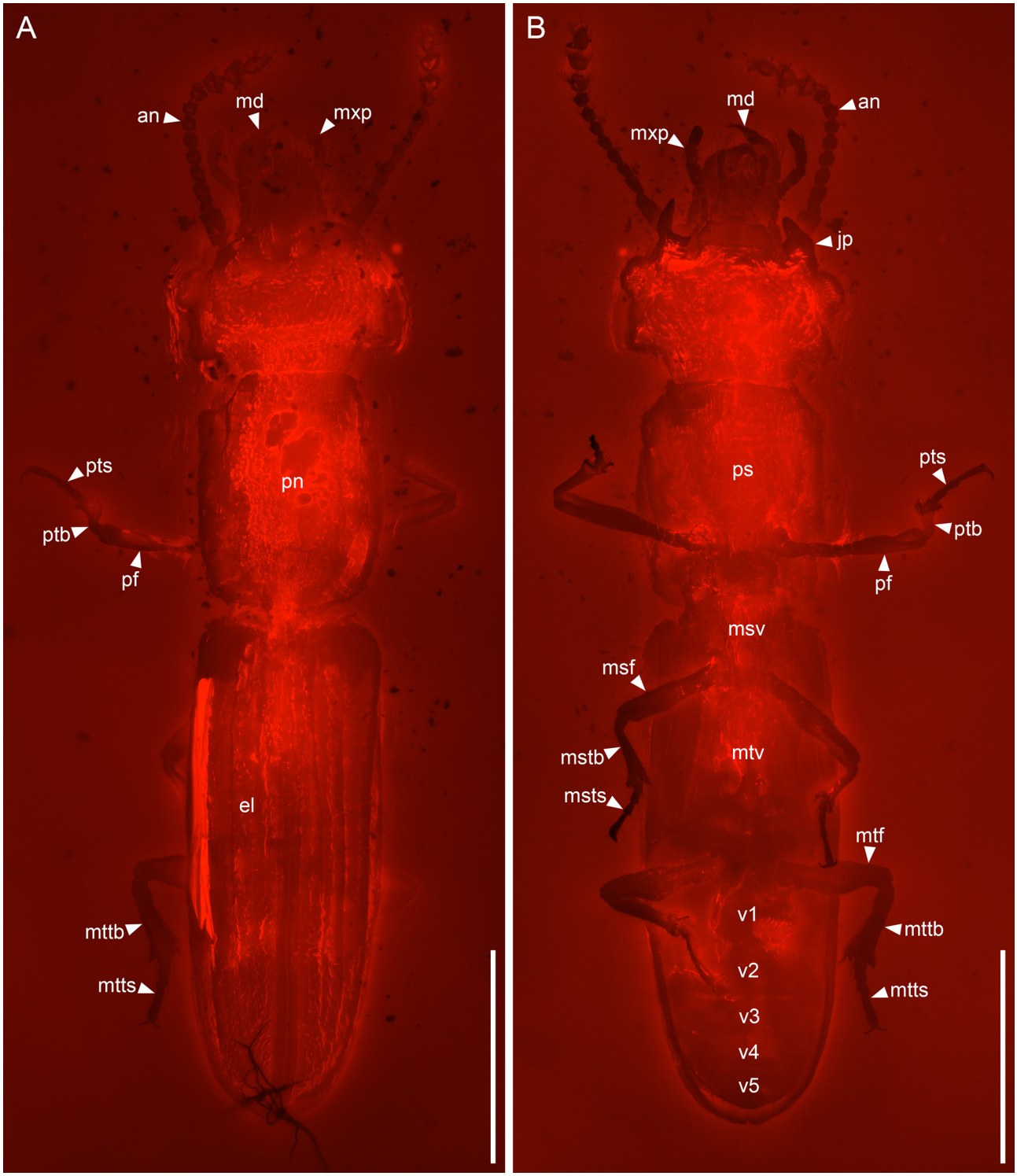

FIGURE 6. *Vetuprostomis gaoi* Li & Cai **sp. nov.**, holotype, NIGP177908, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Abbreviations: an, antenna; el, elytron; jp, jugular process; md, mandible; msf, mesofemur; mstb, mesotibia; msts, mesotarsus; msv, mesoventrite; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pf, profemur; pn, pronotum; ps, prosternum; ptb, protibia; pts, protarsus; v1–5, ventrites 1–5. Scale bars: 1 mm.

Description. Body elongate and flattened, about 4.7 mm long, 1.0 mm wide (maximum width across head).

Head prognathous, constricted posteriorly, with distinct neck region. Temples (Fig. 7B) distinctly projected posterolaterally. Eyes small, round and finely facetted, without interfacetal setae. Antennal insertions slightly concealed from above; subantennal grooves absent. Frontoclypeal suture not clearly discerned. Clypeus (Fig. 7H) with

lateral sides subparallel (or weakly diverging) in anterior portion; anterior margin truncate. Labrum (Fig. 7H) narrowed anteriorly, apically truncate, with numerous elongate setae. Antennae 11-segmented, moniliform, with weak, 3-segmented club. Mandibles (Fig. 7H) tridentate apically; left mandible with two narrowly separated and basally strongly jointed teeth on incisor edge; right mandible with one blunt tooth on incisor edge. Maxillary palps (Fig. 7A) probably 4-segmented; palpomere 1 short; palpomere 2 elongate; palpomere 3 longer than wide, distinctly longer than half length of apical one. Labial palps 3-segmented; palpomere 1 short; palpomeres 2 and 3 elongate. Ligula (Fig. 7A) biemarginate apically. Mentum strongly transverse. Jugal processes (Fig. 7A) asymmetrical; inner sides with a tooth; right process longer than left one, strongly constricted above tooth; left process weakly constricted above tooth.

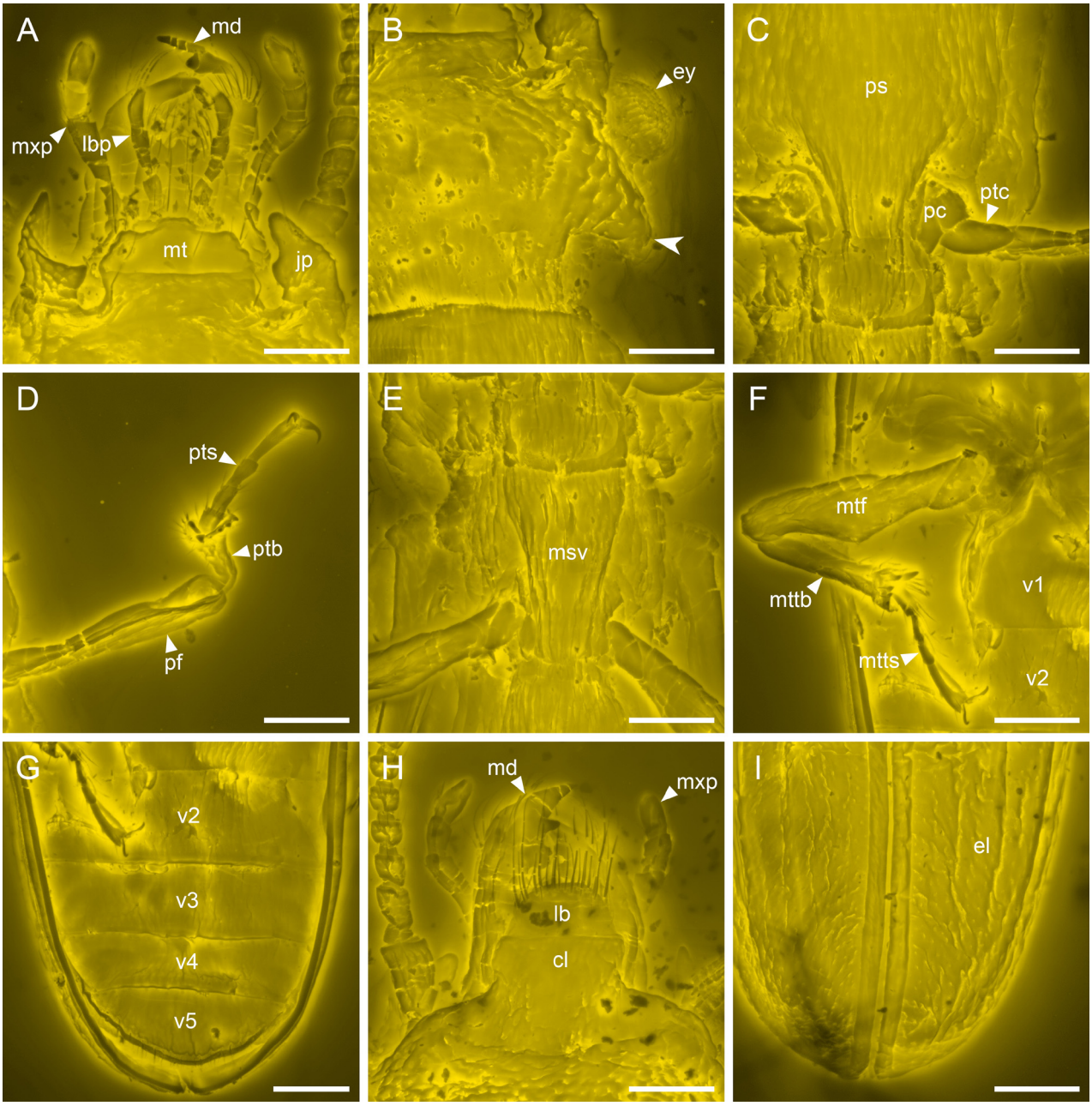

FIGURE 7. *Vetuprostomis gaoi* Li & Cai **sp. nov.**, holotype, NIGP177908, under confocal microscopy. **A**, Mouthparts, ventral view. **B**, Temporal projection (arrowhead), ventral view. **C**, Prothorax, ventral view. **D**, Fore leg. **E**, Mesothorax, dorsal view. **F**, Hind leg. **G**, Abdomen, ventral view. **E**, Mouthparts, dorsal view. **F**, Elytral apex, dorsal view. Abbreviations: cl, clypeus; el, elytron; ey, compound eye; jp, jugular process; lb, labrum; lbp, labial palp; md, mandible; msv, mesoventrite; mt, mentum; mtf, metafemur; mttb, metatibia; mtts, metatarsus; mxp, maxillary palp; pc, procoxa; pf, profemur; ps, prosternum; ptb, protibia; ptc, protrochanter; pts, protarsus; v1–5, ventrites 1–5. Scale bars: 200 μm.

Pronotal disc longer than wide; anterior angles not pointed; lateral sides subparallel; median groove not clearly discerned. Prosternal process (Fig. 7C) wide, expanding beyond procoxae and meeting broad postcoxal projections, apically truncate. Procoxal cavities (Fig. 7C) circular, widely separated. Elytra about 2.6 times as long as width combined; surface with longitudinal carinae. Mesoventrite (Fig. 7E) relatively narrow. Mesocoxal cavities (Fig. 7E) moderately separated. Exposed portion of metanepisternum elongate and narrow. Metaventral discrimen (Fig. 7F) short, only visible near the posterior end. Metacoxae (Fig. 7F) not meeting elytra laterally.

Legs (Fig. 7D,F) short. Femora distally with groove on inner side. Tibiae shorter than femora, widened apically with spinose outer apical angle; spurs large and stout, paired on all legs. Tarsi 4-4-4; tarsomeres simple, without ventral lobes. Pretarsal claws simple.

Abdomen (Fig. 7G) with five ventrites. Ratio of ventrite lengths along middle: 2.4 : 1.8 : 1.4 : 1.0 : 1.4. Ventrite 5 apically broadly rounded.

Discussion

Vetuprostomis appears to be most closely related to the genus *Dryocora*, which is distributed in Australia and New Zealand today. A similar distribution mode (fossils in Burmese amber with closest relatives in present day Southern Hemisphere) can be found in many other beetle taxa, including Clambidae (Cai *et al*. 2019), Cantharidae (Hsiao *et al*. 2021), Boganiidae (Cai *et al*. 2018), Monotomidae (Liu *et al*. 2020), and Cyclaxyridae (Gimmel *et al*. 2019). This distribution is accordant with a Gondwanan origin of the Burma Terrane (Poinar 2019). Thus, the *Vetuprostomis* + *Dryocora* lineage might originate in Gondwana continent before the separation of Burma Terrane from Gondwana. However, the possibility of a much wider historical distribution with subsequent extinction in other continent can not be ruled out (like the case of *Omma* Newman; Escalona *et al*. 2020).

Data availability

The original confocal data are available in Zenodo repository (https://doi.org/10.5281/zenodo.6333634).

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