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Description of adult and larval *Loricera* from mid-Cretaceous Kachin amber (Coleoptera: Carabidae)

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Abstract

Loricera is a morphologically distinctive genus in Carabidae, exhibiting specialized feeding habits on springtails. Here we provide descriptions for both adult and larval specimens of *Loricera* from mid-Cretaceous Kachin amber. The adult specimen, named as *Loricera carsteni* Li, Tihelka & Cai **sp. nov.**, is characterized by the posteriorly unconstricted pronotal disc with produced anterior pronotal angles, wide and almost orthogonal elytral humeri, and elytral surface with no more than ten punctate striae. The validity of previously reported *Cretoloricera* is also critically reviewed.

Keywords: Carabidae, *Loricera*, taxonomy, fossil, Kachin amber, Cretaceous

Introduction

Loricera Latreille is the sole genus in the carabid subfamily Loricerinae (Erwin, 1991), with 13 extant species currently recognized (Sciaky & Facchini, 1999; Barševskis, 2006). The genus contains three subgenera: *Loricera s. str.*, *Elliptosoma* Wollaston, and *Plesioloricera* Sciaky & Facchini (Ball & Erwin, 1969; Sciaky & Facchini, 1999). The phylogenetic placement of Loricerinae within Carabidae has not been well resolved, with limited evidence suggesting that Loricerinae might be closely related to Migadopinae (Maddison *et al.*, 1999; Ribera *et al.*, 2005), and more distantly related to Broscinae, Rhysodinae, Paussinae, Scaritinae, and Harpalinae (Maddison *et al.*, 2009; López-López & Vogler, 2017).

Loricera is one of the three carabid lineages that independently evolved specialized feeding on springtails (Forsythe, 1982, 1983; Baulechner *et al.*, 2020). Adult *Loricera* has distinctive antennae, with basal antennomeres bearing long stout setae (Bauer, 1982; Altner & Hintzpeter 1984; Hintzpeter & Bauer, 1986). The antennae can quickly close medially when an individual prey moves under its head, with the setae forming a cage trapping the prey. Larval *Loricera* has elongate maxillary stipites and galeae (Bauer & Kredler, 1988; Betz & Kölsch, 2004).

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The long setae on the larval stipites could similarly trap the prey, while the galea possesses a sticky layer, which can immobilize the prey and deliver it into the range of the mandibles.

Typical-looking fossils of *Loricera* have been known from Eocene Baltic amber in both adult and larval forms (Klausnitzer, 2003; Cai *et al*., 2017). Liu *et al*. (2023) described a loricerine larva from mid-Cretaceous Kachin amber, and placed it in a new genus, *Cretoloricera* Liu *et al*. Recently Li *et al*. (2024) reported both adult and larval specimens of *Loricera* from Kachin amber, and discussed their evolutionary implications, but the formal descriptions were not provided there. Here we critically review the validity of *Cretoloricera*, and provide descriptions for both adult and larval fossils of *Loricera* from Kachin amber.

Materials and methods

The Kachin (Burmese) amber specimens (Figs 1–10) studied herein originated from amber mines near Noije Bum (26°20′ N, 96°36′ E), Hukawng Valley, Kachin State, northern Myanmar. The specimen NIGP203254 is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The specimen BA202301 is deposited in the Lingpoge Amber Museum, Shanghai, China. The specimen GPIH no. 5061 (CCGG no. 20038) is deposited in the Leibniz-Institut zur Analyse des Biodiversitätswandels—Hamburg site (LIB, partim formerly museum of the Geological-Palaeontological Institute of the University Hamburg / GPIH, later Centrum für Naturkunde / CeNak). The specimen BUB 4025 belongs to the personal collection of Patrick Müller.

For specimens NIGP203254 and BA202301, photographs under reflected light were taken with a Zeiss Discovery V20 stereo microscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon) or 561 nm (DPSS 561-10) laser excitation line (Fu *et al*., 2021). The original confocal data are available in the Zenodo repository (https://doi.org/10.5281/zenodo.10937403). Images under incident light were stacked in Helicon Focus 7.0.2. Confocal images were semi-manually stacked with Helicon Focus 7.0.2 and Adobe Photoshop CC. Images were further processed in Adobe Photoshop CC to adjust brightness and contrast.

For specimens GPIH no. 5061 and BUB 4025, photographs were obtained with a Keyence VHX-6000 digital microscope under reflected light, either cross-polarized light or low-angle non-polarized ring light. The images were recorded with HDR and stacked (see Haug *et al*., 2020 and references therein for details), which were processed with the built-in software and further optimized in Adobe Photoshop CS2.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Adephaga Schellenberg, 1806
Family Carabidae Latreille, 1802
Subfamily Loricerinae Bonelli, 1810
Genus *Loricera* Latreille, 1802

***Loricera carsteni* Li, Tihelka & Cai sp. nov.**
(Figs 1–3)

Material. Holotype, NIGP203254, adult (Li *et al*., 2024).

Etymology. The species is named after Mr. Carsten Gröhn, who kindly donated the larval specimen GPIH no. 5061 used in this study to the Leibniz-Institut zur Analyse des Biodiversitätswandels. He is honoured for his large contributions to amber research for many years.

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. Anterior pronotal angle produced (Fig. 2A, D); pronotal disc not strongly narrowed posteriorly (Fig. 2E). Elytral humerus wide and almost orthogonal (Fig. 2E); elytral surface with no more than ten punctate striae (Fig. 2E).

Description. Body elongate, about 5.0 mm long.

Head prognathous, slightly elongate, with distinct neck (Fig. 2A). Compound eyes prominent. Labrum apically rounded, with four setae on anterior margin (Fig. 2A). Antennae (Figs 2A, B, 3) 11-segmented, filiform; antennomeres 1–6 with long, stout setae (chaetotaxy almost identical to extant *Loricera*; Hintzpeter & Bauer, 1986: fig. 1); antennomeres 5–11 with denser hair-like setae. Mandibles short, strongly curved, apically unidentate (Fig. 2A, B). Lacinia falcate, with dense setae along inner edge (Fig. 2A, C); maxillary palp 4-segmented, with apical palpomere fusiform (Fig. 2C). Ventral surface of head with dense long, stout setae (Figs 2C, 3A).

Pronotal disc widest at middle, slightly narrowed posteriorly; anterior angles projected and rounded (Fig. 2D). Elytral humeri wide, almost orthogonal; elytral surface with relatively sparse striae (not exceeding ten) (Fig. 2E).

Legs long, slender (Fig. 2F–H). Tibiae with sparse stout setae; tibial spurs paired; protibia of anisochaetous type, with subapical antenna cleaner. Tarsi 5-5-5;

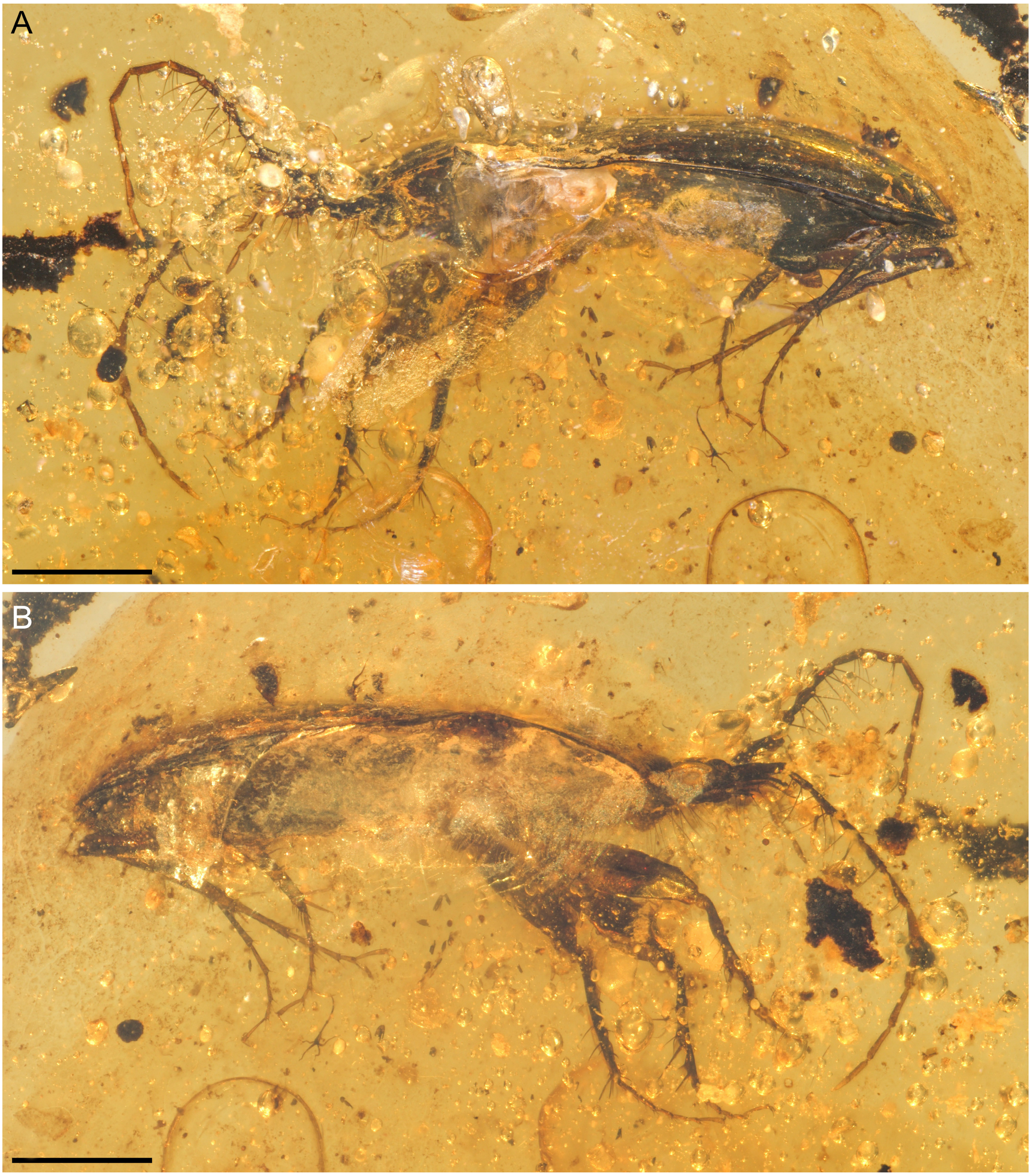

FIGURE 1. General habitus of *Loricera carsteni* Li, Tihelka & Cai **sp. nov.**, holotype, adult, NIGP203254, under incident light, lateral views of the the left (**A**) and right (**B**) sides. Scale bars: 1 mm.

tarsomeres simple, with sparse setae. Pretarsal claws simple.

Remarks. The new species differs from extant species, as well as *Loricera groehni* Cai *et al.* from Baltic amber, mainly by the shape of pronotal disc. The anterior pronotal angle is not produced in most *Loricera*. The new species shares a produced anterior pronotal angle only with *L.* (*Elliptosoma*) *wollastoni* Javet (Ball & Erwin, 1969). However, the pronotal disc of *L. wollastoni*, as well as the remaining *Loricera*, is strongly narrowed posteriorly (*e.g.*, Ball & Erwin, 1969: figs 14–22), while in the new species the pronotal disc is not strongly narrowed posteriorly, with the basal pronotal width almost equal to the combined elytral width at base. Additionally, the

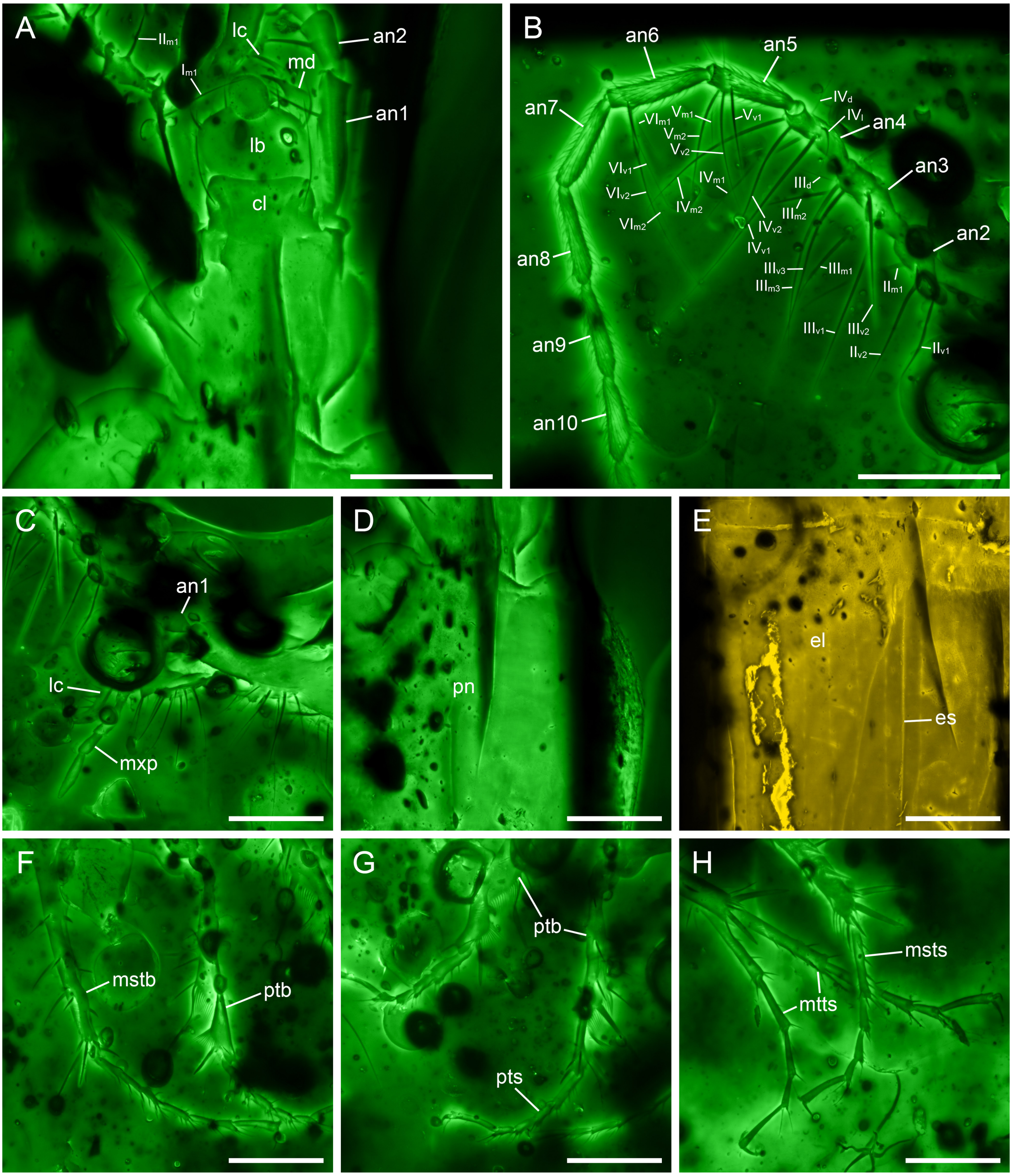

FIGURE 2. Details of *Loricera carsteni* Li, Tihelka & Cai **sp. nov.**, holotype, adult, NIGP203254, under confocal microscopy. **A**, Head, dorsal view. **B**, Left antenna. **C**, Mouthparts, lateral view. **D**, Prothorax, dorsal view. **E**, Elytral base, dorsal view. **F**–**H**, Legs. Abbreviations: an1–10, antennomeres 1–10; cl, clypeus; el, elytron; es, elytral suture; lb, labrum; lc, lacinia; md, mandible; mstb, mesotibia; msts, mesotarsus; mtts, metatarsus; mxp, maxillary palp; pn, pronotum; ptb, protibia; pts, protarsus. Scale bars: 400 µm.

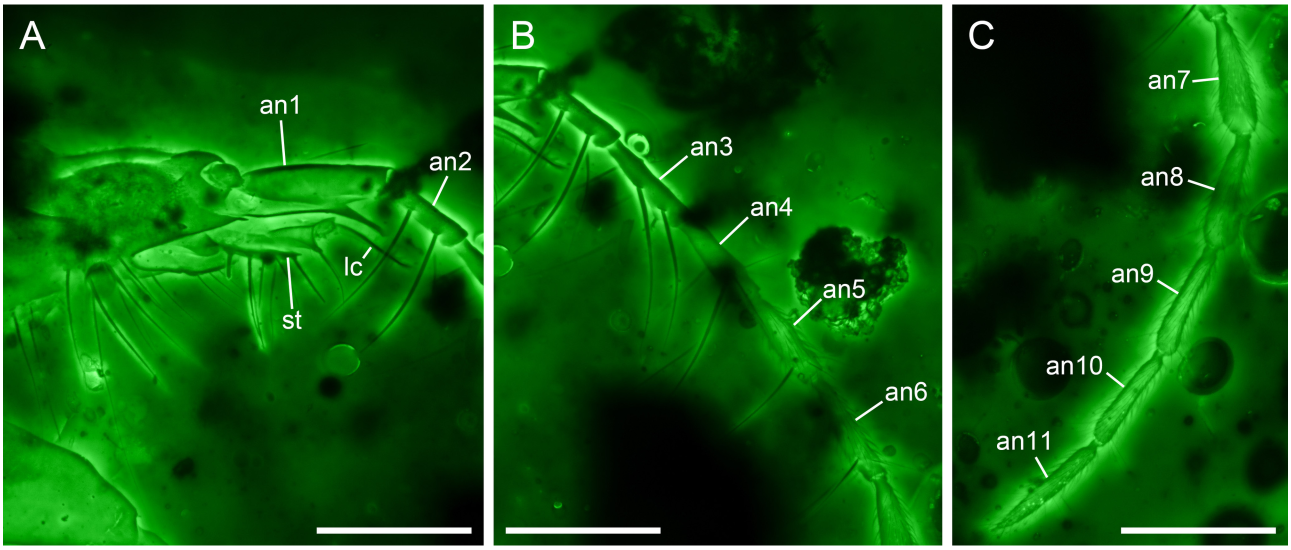

FIGURE 3. Details of *Loricera carsteni* Li, Tihelka & Cai **sp. nov.**, holotype, adult, NIGP203254, under confocal microscopy. **A**, Head, lateral view. **B**, **C**, Right antenna. Abbreviations: an1–11, antennomeres 1–11; lc, lacinia; st, stipe. Scale bars: 400 µm.

FIGURE 4. General habitus of *Loricera* larval morphotype I, BUB 4025. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

elytral humeri of the new species are wide and almost right-angled, while in other *Loricera* the humeri are more or less narrowed and rounded (*e.g.*, Ball & Erwin, 1969: figs 23–26). The elytra have 12 punctate striae in most *Loricera* except *L.* (*Plesioloricera*) *balli* Sciaky & Facchini, which has only eight (Sciaky & Facchini, 1999). Although the exact number of elytral striae cannot be confidently determined for *L. carsteni*, it seems that its elytral striae are relatively sparse (not exceeding ten), somewhat resembling *L. balli*.

Loricera larval morphotype I

(Fig. 4)

Material. BUB 4025; YU-CO-2022-002 (Liu *et al.*, 2023).

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.

Remarks. Liu *et al.* (2023) reported a loricerine larva, YU-CO-2022-002, from Kachin amber, and placed it in a new genus, *Cretoloricera*. They claimed that *Cretoloricera* could be separated from *Loricera* larvae based on the combination of following characters: "terminal galeomere bearing an extremely elongate process, hyaline exudation thinly covering 2nd galeomere, strongly elongate tarsi with an unusual chaetotaxy, seta UR9 obviously shorter than setae UR7 and UR8". However, their proposed diagnosis seems to be problematic.

The length ratio between tarsi and tibiae is variable among instars of extant *Loricera*. For example, according to the drawings of *L. pilicornis* (Fabricius) by Ball & Erwin (1969: figs 50, 53), although in the third instar the tarsi are about as long as the tibiae, in the first instar the tarsi are about twice as long as tibiae, which is close to the ratio observed in YU-CO-2022-002. Long setae are also present along the tarsi of extant *Loricera* larvae, and Liu *et al.* (2023) did not provide any explanation on how

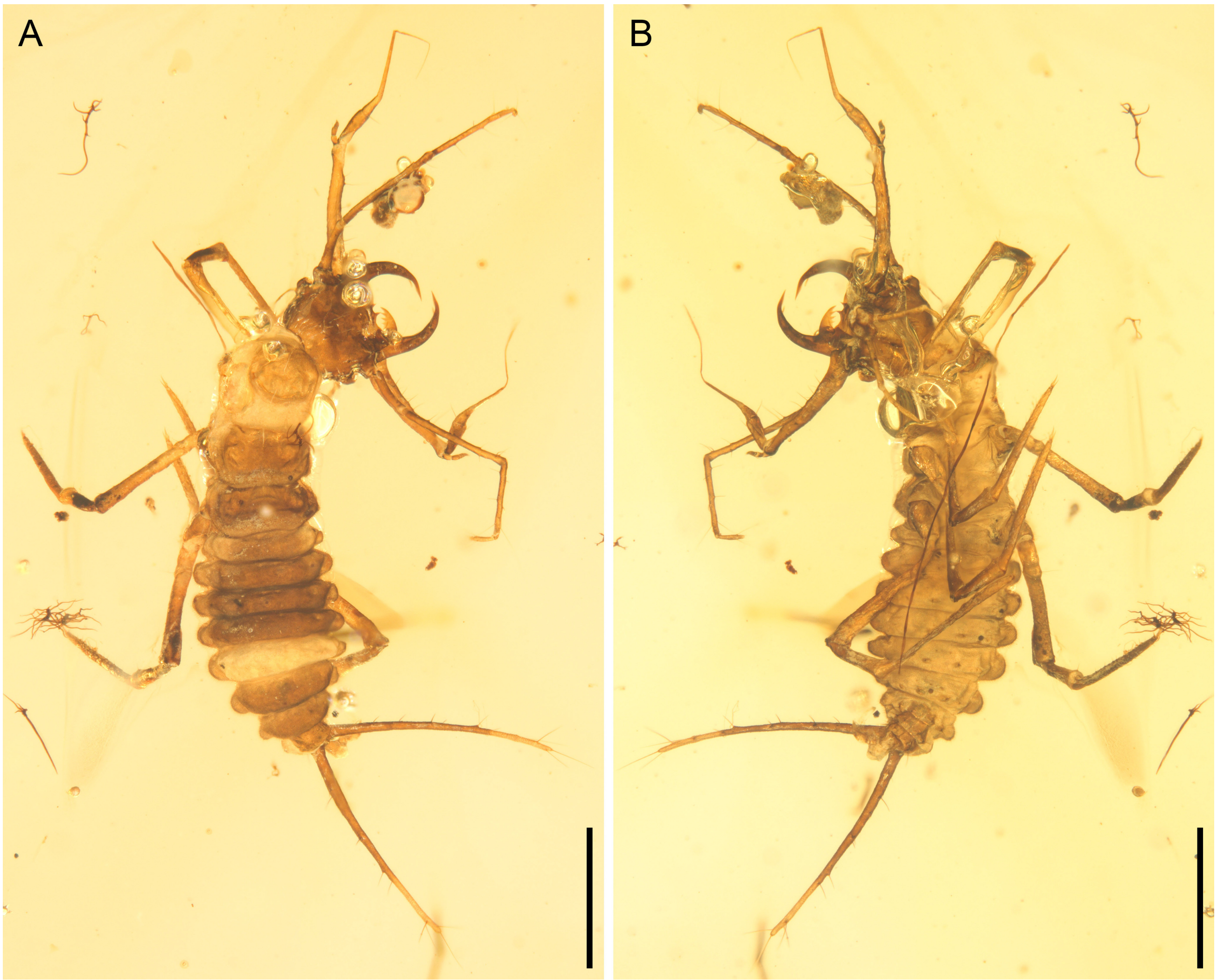

FIGURE 5. General habitus of *Loricera* larval morphotype II, BA202301, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

the tarsal chaetotaxy of their specimen differs from that in extant *Loricera*.

Although Liu *et al*. (2023) did not explicitly explain how the setae on urogomphi of *Loricera* differ from that of *Cretoloricera*, their diagnosis likely implies that they believed in extant *Loricera* the seta UR9 would be relatively long compared with UR7 and UR8. However, the chaetotaxy of urogomphi displays conspicuous variation among species and instars in extant *Loricera*. It is difficult to establish the corresponding relationship of different setae among species. Thus, it is not really clear which seta UR9 (and UR7 and UR8) would refer to in extant *Loricera*. Actually, the numbering of the setae itself is dubious in Liu *et al*. (2023). They identified ten macrosetae on the urogomphi, with UR7, UR9 and UR8 being the apical three. However, in their fig. 4D, at least

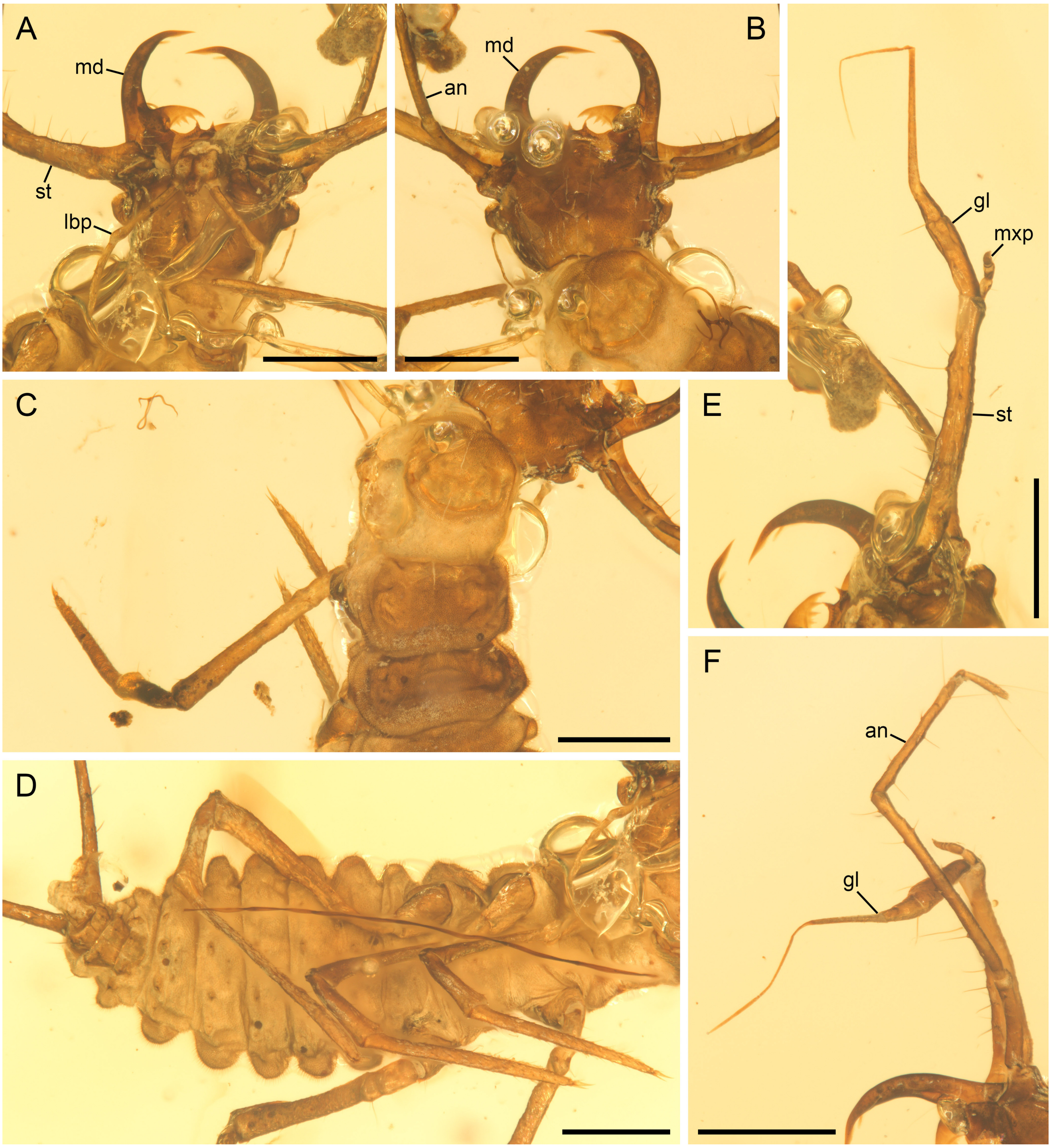

FIGURE 6. Details of *Loricera* larval morphotype II, BA202301, under incident light. **A**, Head, ventral view. **B**, Head, dorsal view. **C**, Thorax, dorsal view. **D**, Thorax and abdomen, ventral view. **E**, Left maxilla. **F**, Right antenna and maxilla. Abbreviations: an, antenna; gl, galea; md, mandible; mxp, maxillary palp; lbp, labial palp; st, stipe. Scale bars: 500 µm.

FIGURE 7. Details of *Loricera* larval morphotype II, BA202301, under incident light. **A**, Thorax and abdomen, dorsal view. **B**, Urogomphi, dorsal view. **C**, Urogomphi, ventral view. Scale bars: 500 µm.

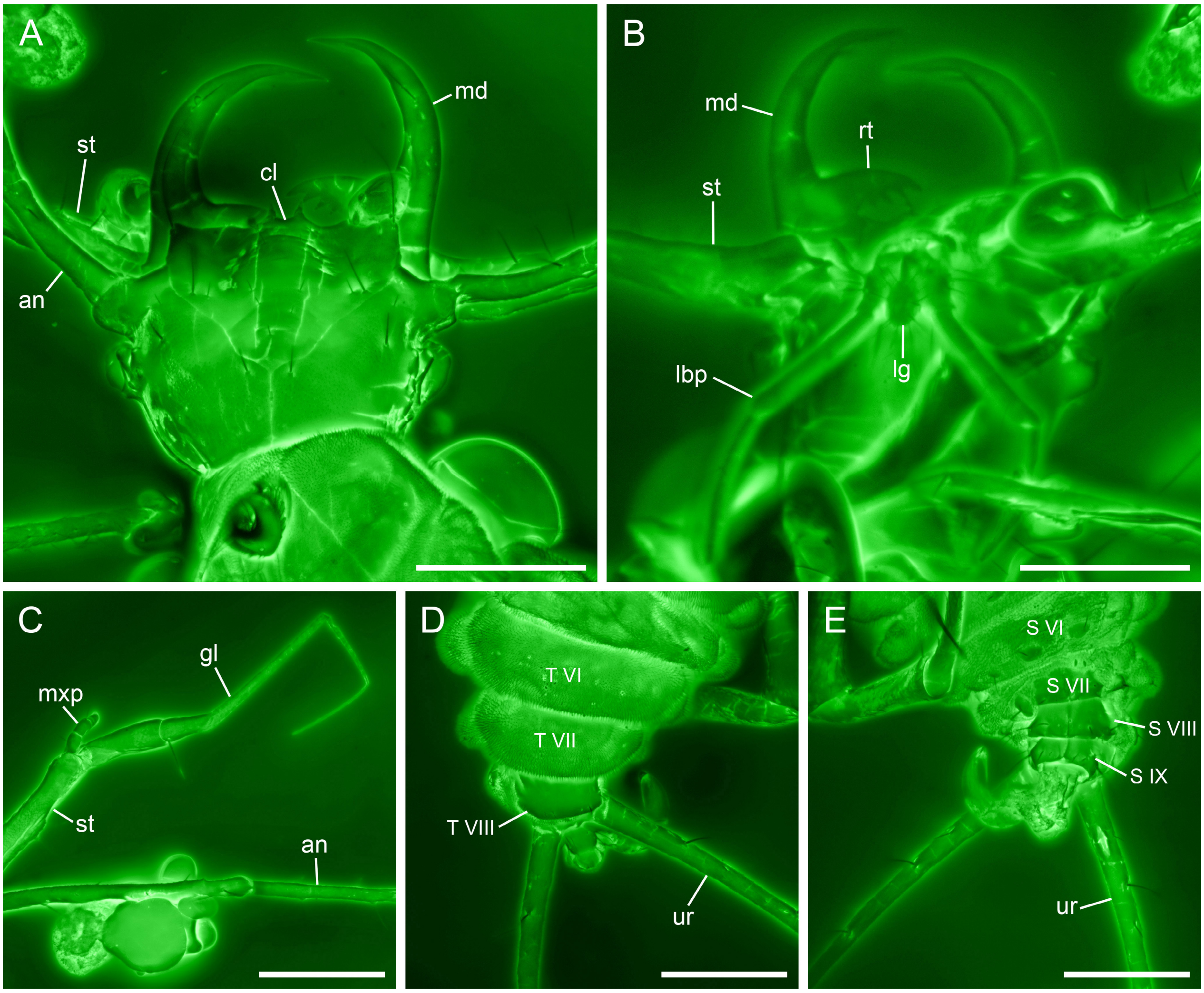

FIGURE 8. Details of *Loricera* larval morphotype II, BA202301, under confocal microscopy. **A**, Head, dorsal view. **B**, Head, ventral view. **C**, Left maxilla. **D**, Abdominal apex, dorsal view. **E**, Abdominal apex, ventral view. Abbreviations: an, antenna; cl, clypeolabrum; gl, galea; md, mandible; mxp, maxillary palp; lbp, labial palp; lg, ligula; rt, retinaculum; S VI–IX, abdominal sternum VI–IX; st, stipe; T VI–VIII, abdominal tergum VI–VIII; ur, urogomphus. Scale bars: 400 µm.

12 setae (which are all at least as stout as “UR9”) can be seen.

Liu *et al*. (2023) did not provide further explanation on why they listed “hyaline exudation thinly covering 2nd galeomere” as a diagnostic character as well. Although we believe that their fossil probably had the hyaline layer when alive, it is unlikely for this transparent layer to be preserved (in an easily visible state) during fossilization. Actually, we cannot see any trace of this hyaline layer in their photos. Even if they managed to detect some trace of the hyaline layer under microscope, it is improper to use the thickness of this layer as a diagnostic character, as it would likely be affected easily by the fossilization process.

The strongly elongate apical galeomere would then be the only possibly genuine diagnostic character left for *Cretoloricera*. However, among the 13 recognized extant species of *Loricera*, the larvae of nine species are still unknown, including the only members of the subgenera *Elliptosoma* and *Plesioloricera*. The interspecific variation of this character is therefore not fully clear. Accordingly, it is premature to establish a separate genus for YU-CO-2022-002. Here we provisionally consider *Cretoloricera* **syn. nov.** as a junior synonym of *Loricera* (and *Cretoloricera electra* Liu *et al*. recombined as *Loricera electra* (Liu *et al*.) **comb. nov.**).

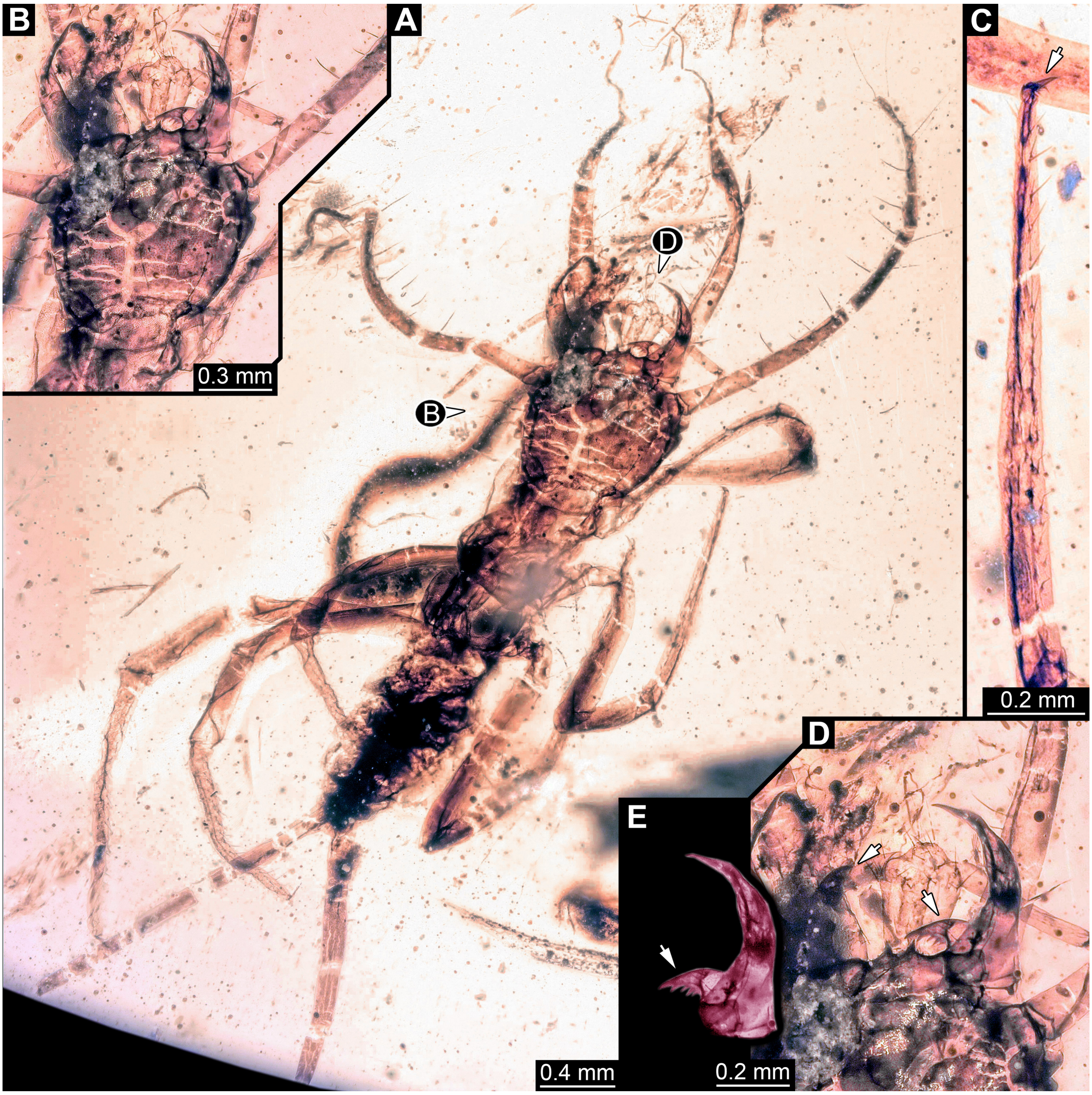

FIGURE 9. *Loricera* larval morphotype II, GPIH no. 5061. **A**, Habitus, dorsal view. **B**, Head, dorsal view. **C**, Mesotarsus, with unequal pretarsal claws (arrow). **D**, Mandibles with retinacula (arrows). **E**, Single mandible from **D** with serrate retinaculum (arrow), colour-marked.

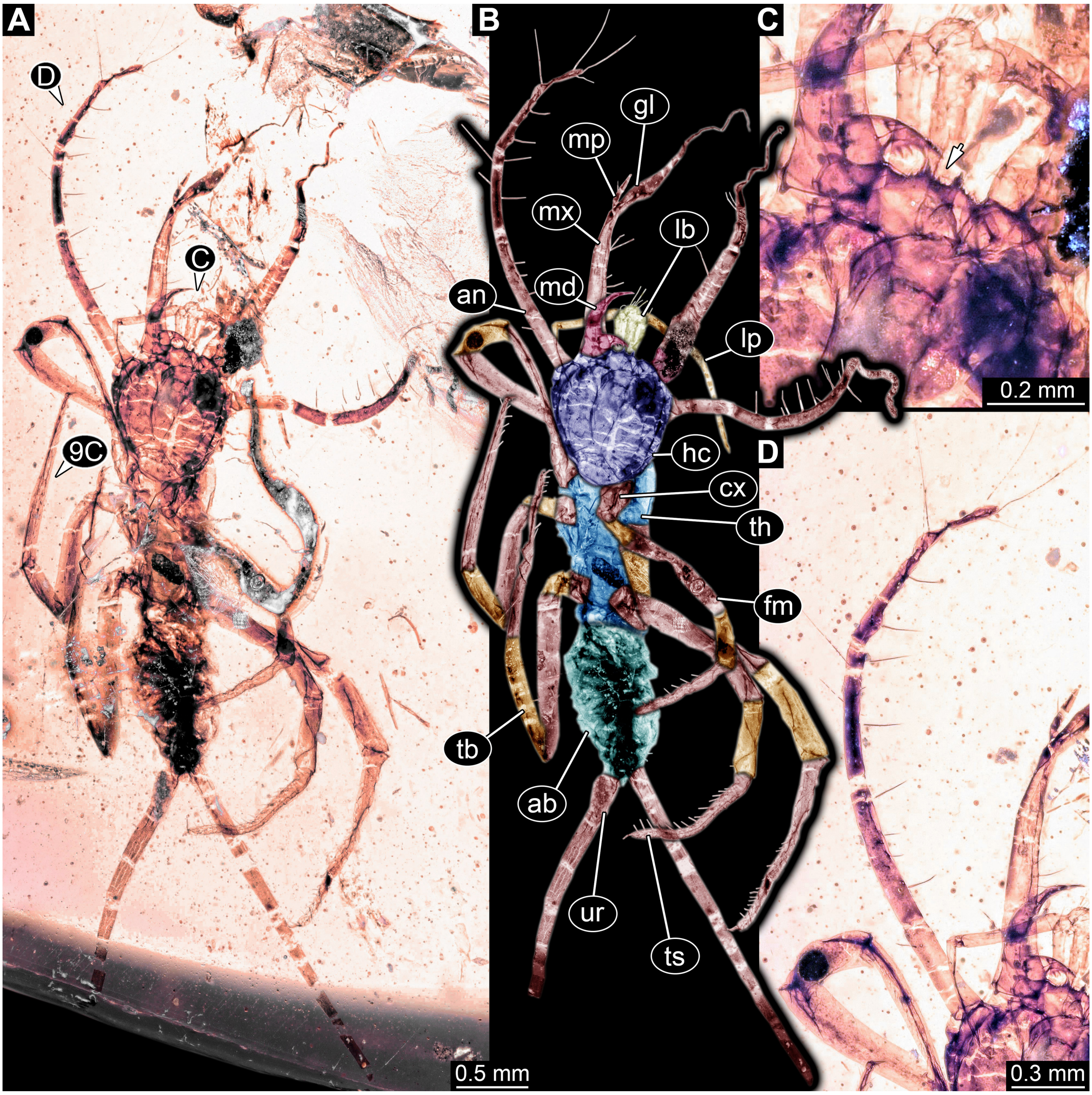

FIGURE 10. *Loricera* larval morphotype II, GPIH no. 5061, ventral view. **A**, Habitus. **B**, Colour-marked version of **A**. **C**, Anterior clypeolabral margin with two acute nasal teeth (arrow). **D**, Antenna. Abbreviations: ab, abdomen; an, antenna; cx, coxa; fm, femur; gl, galea; hc, head capsule; lb, labium; lp, labial palp; md, mandible; mp, maxillary palp; mx, maxilla; ts, tarsus; th, thorax; tb, tibia; ur, urogomphus.

***Loricera* larval morphotype II**
(Figs 5–10)

Material. BA202301 (Li *et al.*, 2024); GPIH no. 5061 (CCGG no. 20038).

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.

Description. Body campodeiform, about 3.7 mm long in BA202301, 3.0 mm long in GPIH no. 5061 (mouthparts and urogomphi not included).

Head prognathous, roughly as long as wide. Epicranial stem and frontal arms well-developed (Figs 6B, 8A). Anterior clypeolabral margin with two acute nasal teeth and a row of smaller teeth (Figs 6B, 8A, 10C). Antennae 4-segmented, with isolated setae (Figs 6F, 10D). Mandibles large, strongly curved, apically unidentate; retinaculum large, serrate along inner edge (Figs 6A, B, 8A, B, 9D, E). Stipes elongate, stout, with isolated setae; galea 2-

segmented, palpiform; basal galeomere moderately long and wide; apical galeomere extremely long, gradually narrowed distally; maxillary palp quite short (Figs 6E, F, 8C, 9D, E). Ligula with numerous long setae; labial palp elongate, 2-segmented (Fig. 8B).

Thorax (Fig. 6C, D) densely covered with short, fine setae. Prothorax about as long as wide. Mesothorax and metathorax transverse, with dorsally exposed portions 0.6× and 0.5× as long as prothorax, respectively (as measured in BA202301). Legs elongate, 6-segmented. Tarsi with short setae only. Pretarsal claws paired, unequal.

Abdominal segments I–VIII with pleural lobes; segments I–VII dorsally densely covered with short and fine setae; segment VIII dorsally almost glabrous; segments I–VI ventrally densely covered with short and fine setae; segments VII–IX ventrally subglabrous medially, except for a few moderately long setae (Figs 7, 8D, E). Paired urogomphi present on segment IX, elongate (Figs 7, 8D, E). Segment X short, visible from above.

Remarks. The larval morphotype II shares with the above mentioned morphotype I the strongly elongate apical galeomere, which differentiates them from all known extant larvae of *Loricera*, as well as *L. electrica* Klausnitzer from Baltic amber. In the morphotype I and known extant *Loricera* larvae, the thorax and abdomen have several prominent setae projecting dorsally and laterally (*e.g.*, Fig. 4; Ball & Erwin, 1969: figs 49–53), while the morphotype II completely lacks these prominent setae (Fig. 7A). The dorsal side of the thorax and abdomen is instead densely covered with much shorter and weaker setae only (Figs 7A, 8D). The morphotype II additionally differs from the morphotype I in the tarsi with short setae only (no longer than tarsal width).

In the larvae of extant *L. pilicornis*, the head is relatively large and much wider than the prothorax in the first instar, while the head is narrower than the prothorax in the third instar (Ball & Erwin, 1969). Compared to BA202301, GPIH no. 5061 has a smaller body size and a proportionally larger head. Therefore GPIH no. 5061 probably represents an earlier developmental stage, although it is difficult to determine whether or not the two specimens are conspecific.

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