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Three new species of the extant genus *Eucinetus* from mid-Cretaceous amber of northern Myanmar (Coleoptera: Eucinetidae)

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Abstract

Three new species of plate-thigh beetles are described and figured from mid-Cretaceous Kachin amber, all representing the extant genus *Eucinetus* Germar. The species, *Eucinetus debilispinus* Li & Cai **sp. nov.**, *E. panghongae* Li & Cai **sp. nov.**, and *E. zhenhuai* Li & Cai **sp. nov.**, are distinguished from each other by the forms of the antennomeres, leg spination, and form of the spurs. The genus *Eucinetus* represents a key example of long-term evolutionary stasis with a subcortical lifestyle. This further demonstrates the role of stable cryptic microhabitats in the persistence of some lineages over vast spans of geological time.

Key words: Eucinetidae, taxonomy, fossil, Kachin amber, Cretaceous

Introduction

Eucinetidae are a small polyphagan beetle family, with 11 extant genera and less than 60 described species (Leschen 2016; Lawrence 2019; Jałoszyński & Wakimura 2023). The family is most distinctively characterized by the large and oblique metacoxal plates. Eucinetidae had long been placed in the superfamily Scirtoidea, together with Scirtidae and Clambidae (Crowson 1960; Lawrence & Newton 1995; Bouchard *et al.* 2011). But later, molecular phylogenetic studies excluded Eucinetidae and Clambidae from Scirtoidea and placed them in a newly defined Clamboidea together with Derodontidae (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2022).

Despite the family's antiquity based on molecular-dating estimates, the fossil record of Eucinetidae is quite sparse. Definitive eucinetid fossils described include only two species from mid-Cretaceous Kachin amber of northern Myanmar (Jałoszyński 2019; Du *et al.* 2020) and one species from the Eocene Insect Limestone of the Isle of Wight (England) (Kirejtshuk *et al.* 2019). Hong (1995) described the fossil genus *Huaxiacinectus* Hong with two species from the Lower Cretaceous Huanhe Formation of the Ordos Basin (China) and assigned it to Eucinetidae, but the original description and line drawings were insufficient for reliable placement, and re-examination of the type specimens is needed to further solve the problem. Kirejtshuk & Ponomarenko (2010) placed five genera from the Upper Jurassic and Lower Cretaceous of Mongolia and Russia in the exclusively fossil family Mesocinetidae, which was suggested to share characters with both Scirtidae and Eucinetidae. However, Cai *et al.* (2022) suggested that the type genus of Mesocinetidae, *Mesocinetus* Ponomarenko, may be placed directly in Eucinetidae, rather than in a separate fossil family.

The type genus of the family, *Eucinetus* Germar, is the most species-rich group, with about 21 described

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extant species (Leschen 2016; Lawrence 2019). The genus occurs in all major zoogeographic regions (Vit 1977a, 1983, 1985, 1990; Lawrence 2019; Hinson & Keller 2020). Kirejtshuk & Ponomarenko (in Kirejtshuk *et al.* 2019) placed the eucinetid fossil from the Eocene Insect Limestone in the genus *Eucinetus*, although the assignment was only tentative, as many important diagnostic characters were not preserved. The only fossil that is definitively of *Eucinetus* was reported from Kachin amber by Du *et al.* (2020). Its assignment could be justified by the structure of mouthparts and antennae, as well as the obtuse inner anterior angle of the mesepimeron.

Here we describe three new species of *Eucinetus* from Kachin amber, increasing our knowledge of the paleodiversity of this long-lasting genus and further demonstrating its considerable stasis for at least 100 million years.

Material and methods

The Kachin amber (Burmese amber) specimens studied herein (Figs 1–12) 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. Individual 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. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon) laser excitation line (Fu *et al.* 2021). Images were stacked with Helicon Focus 7.0.2, Zerene Stacker 1.04 and Adobe Photoshop CC, and were further processed in Adobe Photoshop CC to adjust brightness and contrast.

Microtomographic data were obtained with a Zeiss Xradia 520 Versa 3D X-ray microscope at the micro-CT laboratory of NIGP and analyzed in VGStudio MAX 3.0. Scanning parameters were as follows: NIGP203939 [isotropic voxel size, 2.2345 µm; power, 3 W; acceleration voltage, 40 kV; exposure time, 2 s; projections, 1401]; NIGP203940 [isotropic voxel size, 2.9369 µm; power, 3 W; acceleration voltage, 40 kV; exposure time, 4 s; projections, 2601]; NIGP203941 [isotropic voxel size, 3.5820 µm; power, 3 W; acceleration voltage, 40 kV; exposure time, 2 s; projections, 2501].

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Superfamily Clamboidea Fischer, 1821

Family Eucinetidae Lacordaire, 1857

Genus *Eucinetus* Germar, 1818

Remarks. The three new species described here have unspecialized mouthparts, distinguishing them from the genera with suctorial or semisuctorial mouthparts: *Bisayodes* Wakimura & Jałoszyński, *Eucilodes* Vit, *Cretohlezkus* Jałoszyński, *Bisaya* Reitter, *Jentozkus* Vit, *Tohlezkus* Vit and *Proeuzkus* Vit (*e.g.*, Vit 1977b, 1981, 2000; Sakai 1980; Jałoszyński 2019; Jałoszyński & Wakimura 2023). The remaining "non-suctorial" group of Eucinetidae includes *Eucinetella* Nikitsky, *Eucinetus*, *Nycteus* Latreille, *Euscaphurus* Casey and *Noteucinetus* Bullians & Leschen. These new species differ from *Eucinetella* and *Euscaphurus* by having slender and filiform antennae, with antennomeres loosely assembled (antennae claviform to subclaviform in *Eucinetella* and *Euscaphurus*: Nikitsky 1996; Vit 1996), and from *Noteucinetus* in the more elongate and less convex body (Bullians & Leschen 2004; Lawrence 2019).

Du *et al.* (2020) claimed that the antennomere 3 in *Nycteus* is distinctly shorter than the adjacent antennomeres, while in *Eucinetus* it is almost the same length as antennomere 4. However, according to Lawrence (2019), some *Eucinetus* species also have a short antennomere 3 (*e.g.*, *E. brindabellae* Lawrence and *E. similis* Lawrence). Actually, *Nycteus* could be separated from *Eucinetus* by the completely exposed antennal insertions and antennal grooves, Ushaped frontoclypeal suture and acute inner anterior angle of mesepimeron (Vit 1985: figs 2, 61; Vit 1999; Lawrence 2019). The three new species all have a frontoclypeal suture straight anteriorly with distinct anterolateral angles (Figs 3A, 7A, 11A), which is characteristic of *Eucinetus* (*e.g.*, Vit 1977a: figs 2, 4, 5; Vit 1985: fig. 60; Kim & Ahn 2008: fig. 2). Therefore, these fossils can all be assigned to the extant *Eucinetus*, demonstrating its considerable antiquity and remarkable stasis over the course of 100 million years of global biotic and abiotic change.

The four species of *Eucinetus* from Kachin amber (those described herein and the one described by Du *et al.* 2020) are known only from the holotypes. Two of the specimens are male, and the other two are female. To our knowledge, there is no notable sexual dimorphism in *Eucinetus*, except that in males one of the two mesotibial spurs is modified with a cleft apex (Lawrence 2019). Thus, it would be justified to treat these four specimens as separate species.

Key to species of *Eucinetus* from Kachin amber

1. Meso- and metatibiae with relatively dense spines along the outer edge (Fig. 11D,E). Antennomere 3 strongly elongate (Fig. 11A) . . . .***Eucinetus zhenhuai*** **Li & Cai sp. nov.**

\- Meso- and metatibiae at most with very sparse spines along the outer edge (Figs 3E, 7D,E). Antennomere 3 less elongate (Figs 3A, 7A). **2**

2. Mesotibial spurs small; the smaller one not distinctly stouter than the spines along the apical fringe of mesotibia (Fig. 3E) . . . . ***Eucinetus debilispinus*** **Li & Cai sp. nov.**

\- Mesotibial spurs larger; the smaller one distinctly stouter than the spines along the apical fringe of mesotibia (Fig. 7C,D). . . **3**

3. Metatibial spurs equal (Fig. 7F) . . . . ***Eucinetus panghongae*** **Li & Cai sp. nov.**

\- Metatibial spurs unequal. . . . . ***Eucinetus parvus*** **Du *et al.***

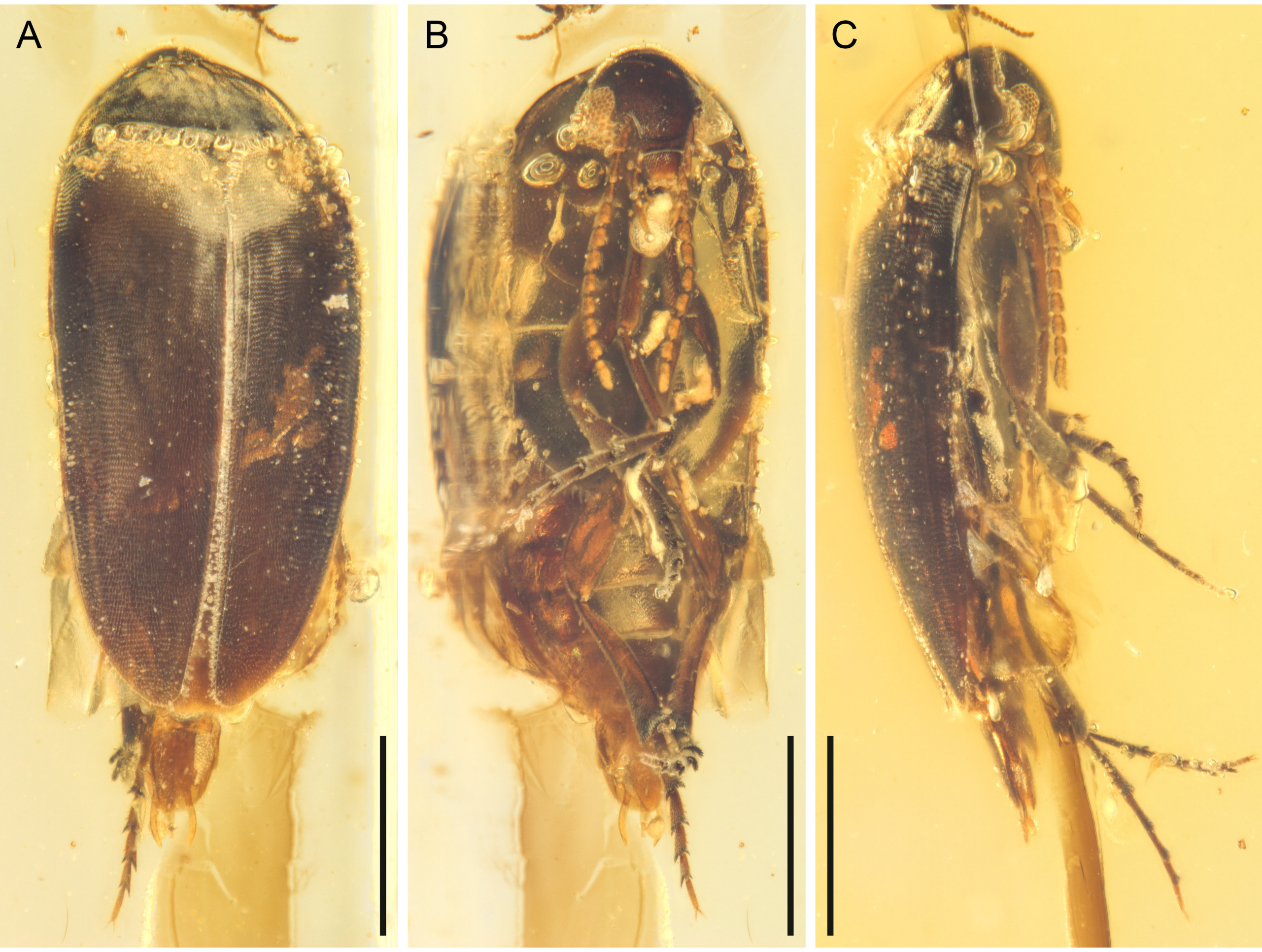

FIGURE 1. General habitus of *Eucinetus debilispinus* Li & Cai **sp. nov.**, holotype, NIGP203939, under incident light. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars: 500 µm.

FIGURE 2. General habitus of *Eucinetus debilispinus* Li & Cai **sp. nov.**, holotype, NIGP203939, under confocal microscopy. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bars: 500 µm.

Eucinetus debilispinus **Li & Cai sp. nov.**
(Figs 1–4)

Material. Holotype, NIGP203939, male.

Etymology. The specific name refers to its relatively small mesotibial spurs.

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.

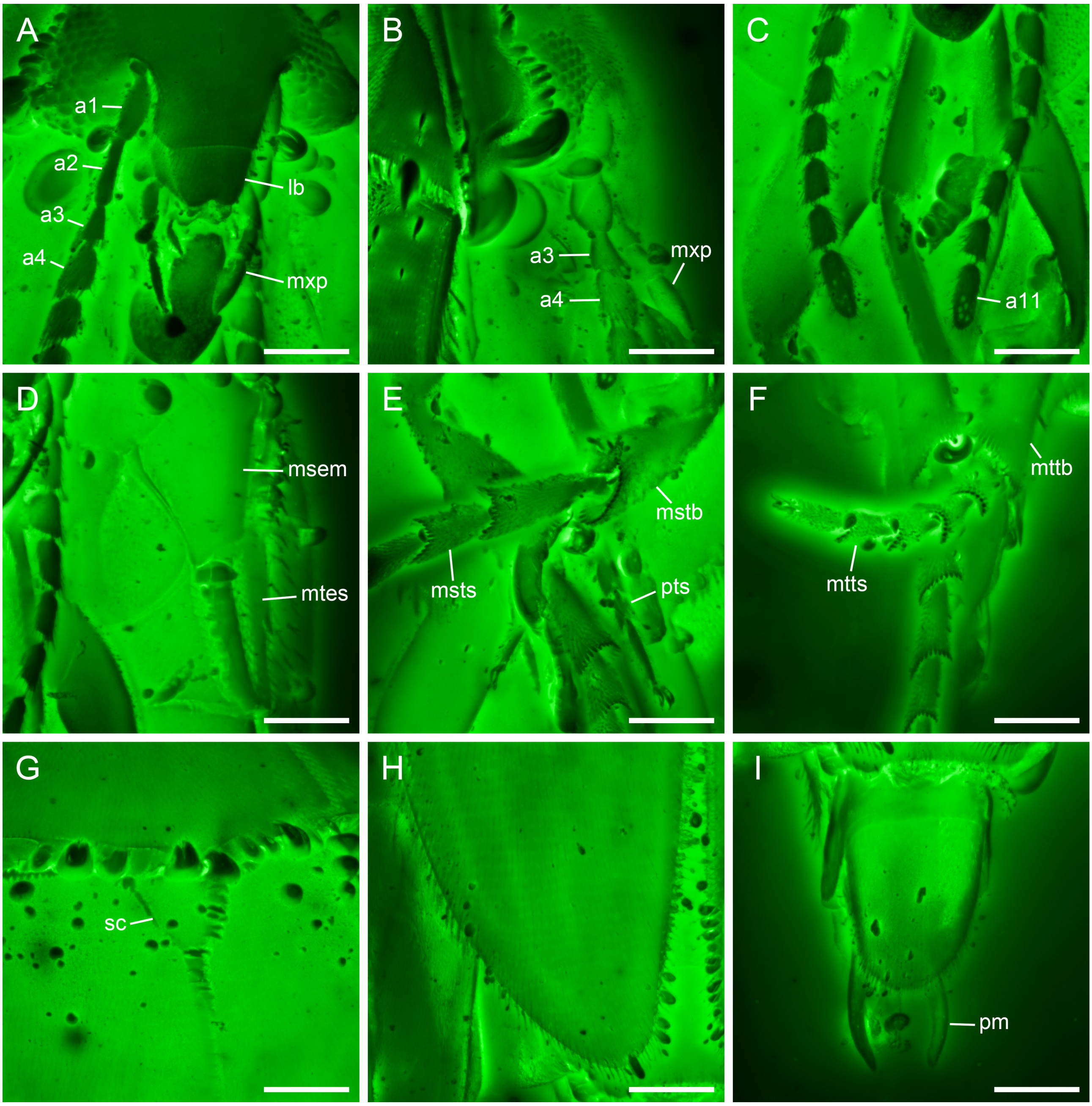

FIGURE 3. Details of *Eucinetus debilispinus* Li & Cai **sp. nov.**, holotype, NIGP203939, under confocal microscopy. **A**, Head, dorsal view. **B**, Head and prothorax, lateral view. **C**, Antennae. **D**, Meso- and metathorax, ventral view. **E**, Fore and mid legs. **F**, Hind legs. **G**, Scutellar shield, dorsal view. **H**, Elytral apex, dorsal view. **I**, Abdominal apex, dorsal view. Abbreviations: a1–11, antennomeres 1–11; lb, labrum; msem, mesepimeron; mstb, mesotibia; msts, mesotarsus; mtes, metanepisternum; mttb, metatibia; mtts, metatarsus; mxp, maxillary palp; pm, paramere; pts, protarsus; sc, scutellar shield. Scale bars: 100 µm.

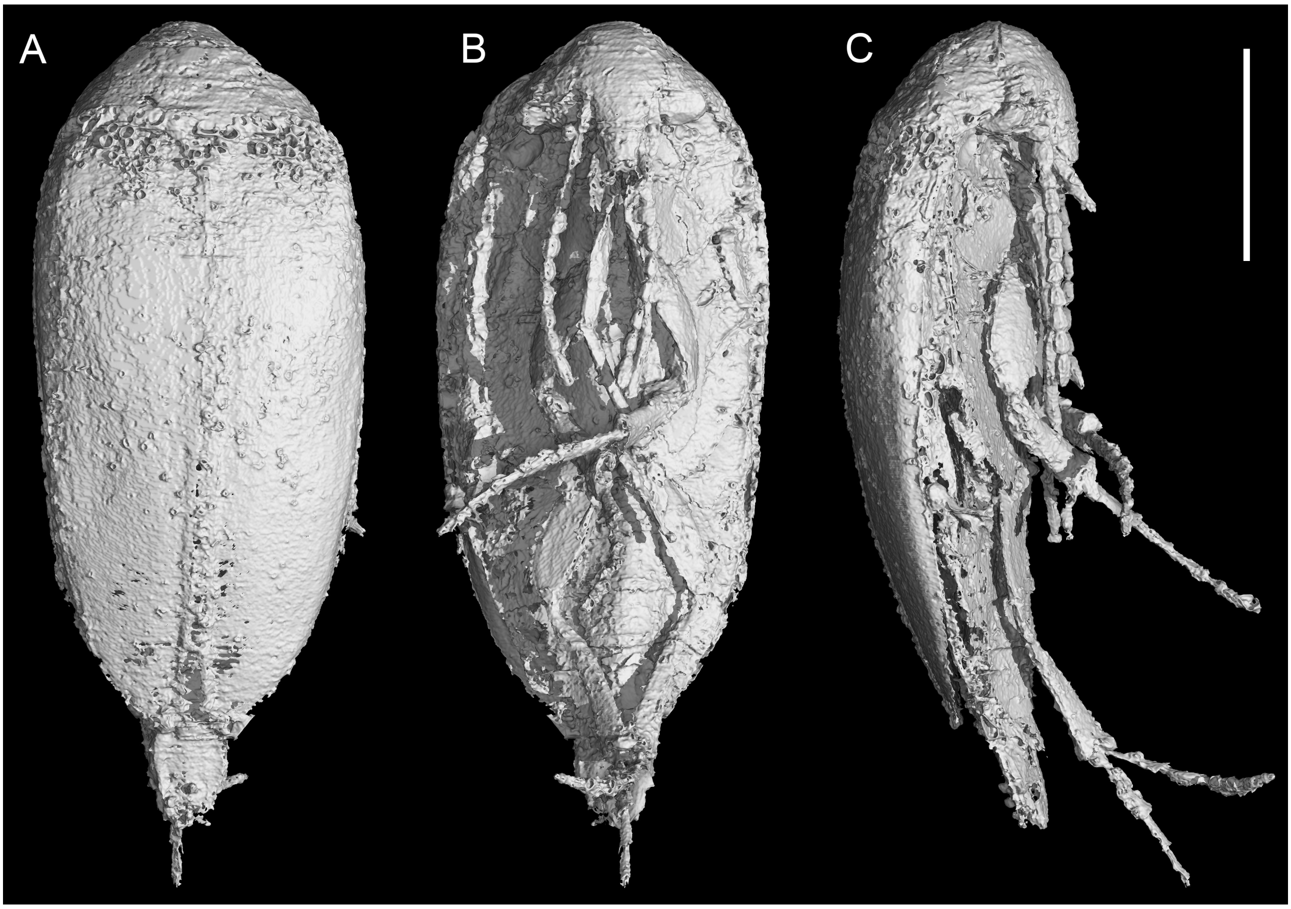

FIGURE 4. X-ray microtomographic reconstruction of *Eucinetus debilispinus* Li & Cai **sp. nov.**, holotype, NIGP203939. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bar: 500 µm.

Diagnosis. Labrum emarginate (Fig. 3A). Apical maxillary palpomere narrow and symmetrical, apically acute (Fig. 3A,B). Antennomere 3 about 0.70 times as long as 4 (Fig. 3A); antennomere 11 about 2.7 times as long as wide (Fig. 3C). Elytra about 1.8 times as long as combined width. Hind wings present. Metanepisternum at least twice as long as wide (Fig. 3D). Meso- and metatibiae at most with only one or two spines along outer edge (Figs 2B,C, 3E). Mesotibial spurs small; the smaller one not distinctly stouter than spines along apical fringe of mesotibia (Fig. 3E). Parameres distinctly bowed outwardly (Fig. 3I).

Description. Body fusiform and slender, about 1.7 mm long, 0.8 mm wide; surface with fine short setae.

Head deflexed against ventral side of prothorax; entirely concealed from above by pronotum. Compound eyes weakly emarginate anteriorly, with interfacetal setae. Antennae 11-segmented, filiform; antennomere 2 elongate; antennomeres 3–10 slightly longer than wide, somewhat submoniliform; antennomere 3 about 0.70 times as long as 4, distinctly narrower than 4; antennomere 11 about 2.7 times as long as wide, with distinct pattern of sensillae (Fig. 3C). Frontoclypeal suture straight anteriorly and with distinct anterolateral angles. Labrum weakly narrowed toward apex, apically emarginate. Mouthparts non-suctorial. Apical maxillary palpomere narrow and symmetrical, apically acute.

Prothorax widest at base. Lateral pronotal carinae complete, simple. Pronotal disc simple. Procoxae obliquely oriented, well-projecting, narrowly separated. Scutellar shield triangular, possibly with acute apex. Elytra about 1.8 times as long as combined width; transversely strigulate; sutural stria present; epipleuron narrow, incomplete. Hind wings present. Metanepisternum at least twice as long as wide. Metacoxae contiguous; metacoxal plates well-developed and greatly enlarged.

Mid and hind legs with fringe of spines at apices of tibiae and tarsomeres; fore legs without apical fringes of spines. Meso- and metatibiae at most with only one or two spines along outer edge. Mesotibial spurs small; the smaller one not distinctly stouter than spines along apical fringe of mesotibia. Tarsi 5-5-5, simple. Meso- and metapretarsal claws with accessory lobes (Fig. 3F).

Abdomen with six ventrites. Aedeagus of trilobate type; penis shorter than parameres; parameres distinctly bowed outwardly.

Eucinetus panghongae **Li & Cai sp. nov.**
(Figs 5–8)

Material. Holotype, NIGP203940, male.

Etymology. The species is named after the coleopterist Dr. Hong Pang.

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. Labrum emarginate (Fig. 7A). Apical maxillary palpomere asymmetrical, apically with aciculate tip (Fig. 7A). Antennomere 3 about 0.85 times as long as 4 (Fig. 7A); antennomere 11 about 2.5 times as long as wide (Fig. 7B). Scutellar shield rounded at apex (Fig. 7F). Elytra about 1.8 times as long as combined width. Hind wings present. Metanepisternum at least twice as long as wide. Meso- and metatibiae at most with only one or two spines along outer edge (Figs 6B, 7E). Mesotibial spurs large; both distinctly stouter than spines along apical fringe of mesotibia (Fig. 7D). Metatibial spurs equal (Fig. 7F).

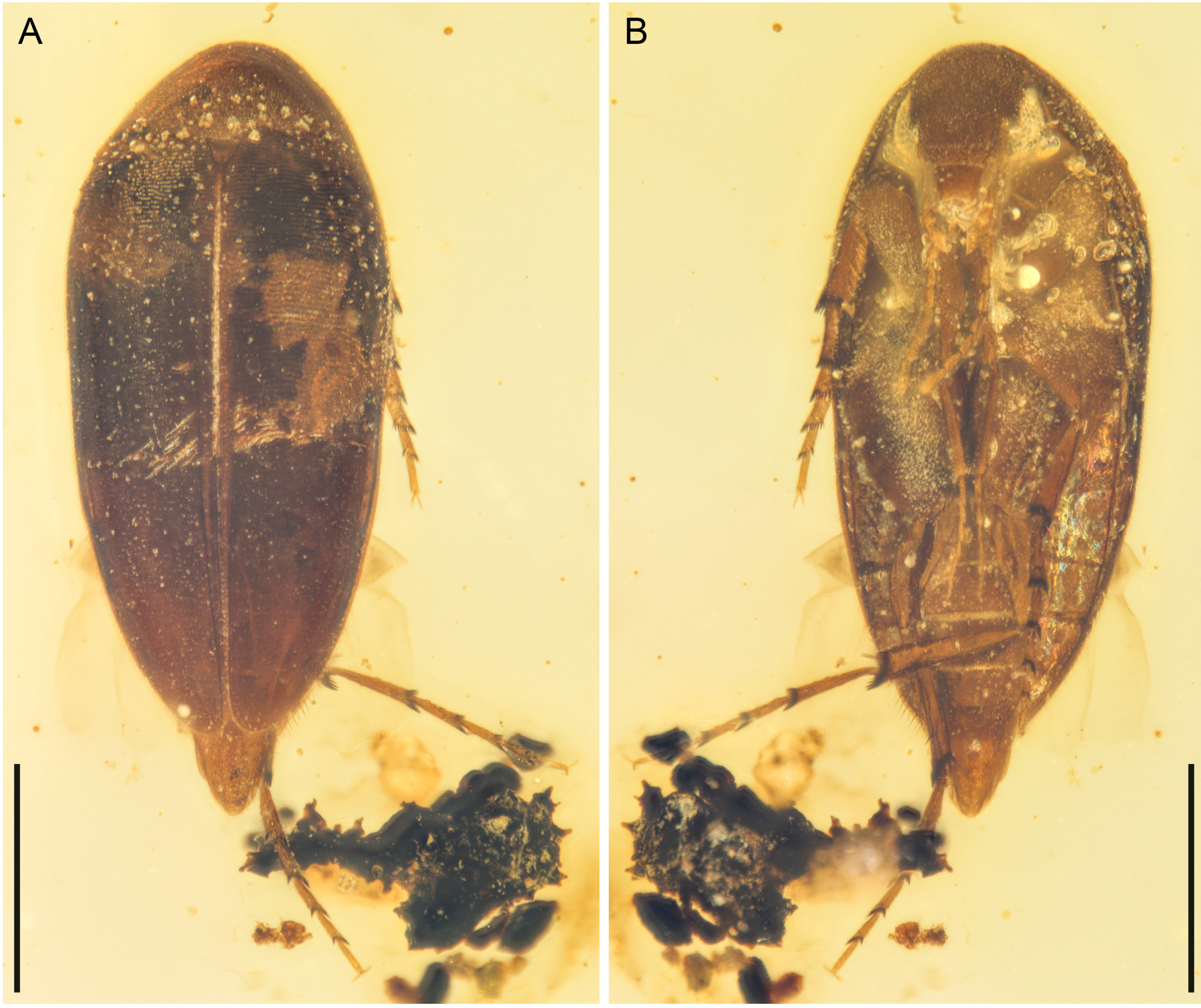

FIGURE 5. General habitus of *Eucinetus panghongae* Li & Cai **sp. nov.**, holotype, NIGP203940, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 µm.

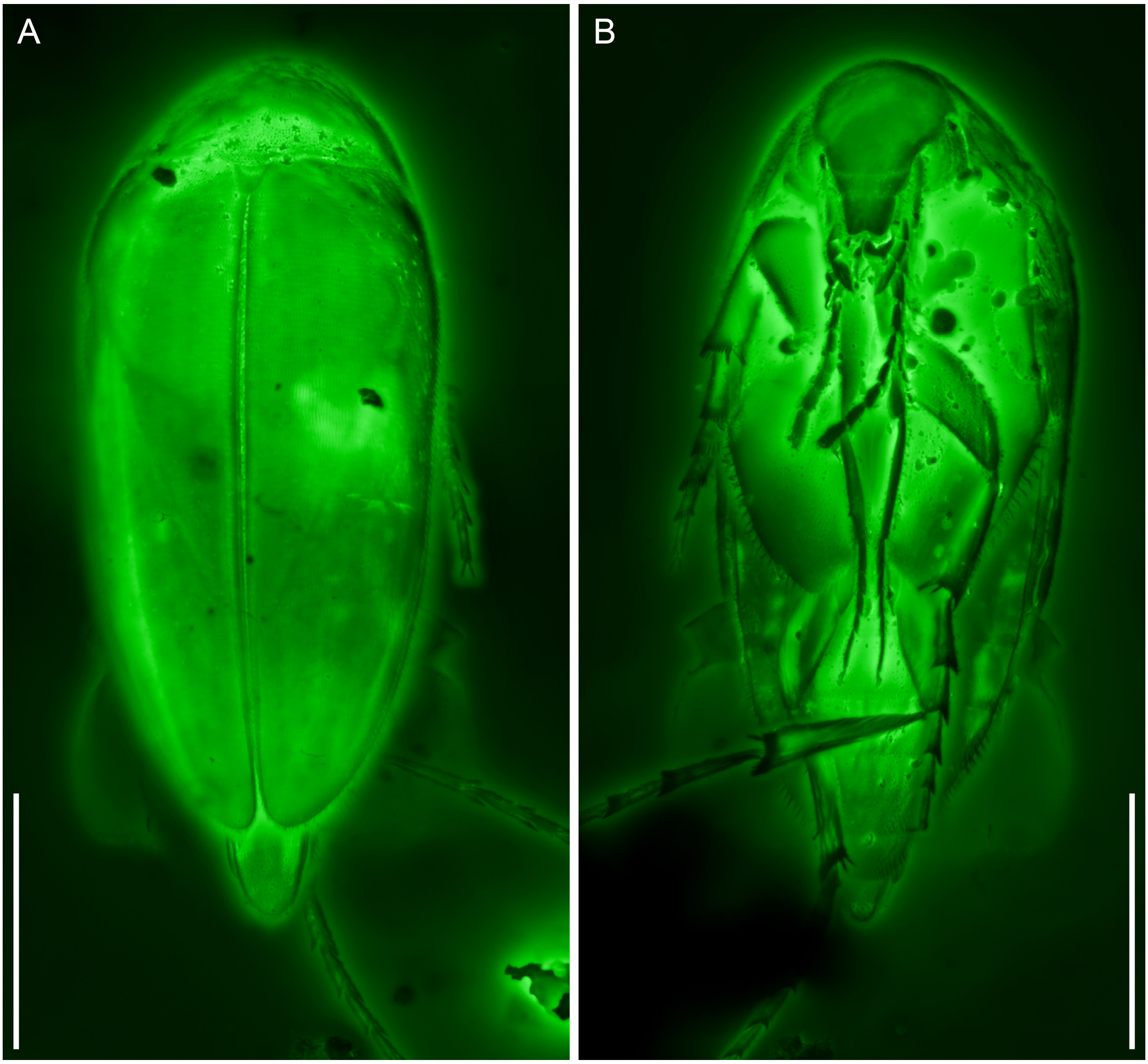

FIGURE 6. General habitus of *Eucinetus panghongae* Li & Cai **sp. nov.**, holotype, NIGP203940, under confocal microscopy. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 µm.

Description. Body fusiform and slender, about 1.6 mm long, 0.7 mm wide; surface with fine short setae.

Head deflexed against ventral side of prothorax; entirely concealed from above by pronotum. Compound eyes weakly emarginate anteriorly, with interfacetal setae. Antennae 11-segmented, filiform; antennomere 2 elongate; antennomeres 3–10 moderately longer than wide; antennomere 3 about 0.85 times as long as 4; antennomere 11 about 2.5 times as long as wide. Frontoclypeal suture straight anteriorly and with distinct anterolateral angles. Labrum weakly narrowed toward apex, apically emarginate. Mouthparts non-suctorial. Apical maxillary palpomere asymmetrical, apically with aciculate tip.

Prothorax widest at base. Lateral pronotal carinae complete, simple. Pronotal disc simple. Procoxae obliquely oriented, well-projecting, narrowly separated. Scutellar shield rounded at apex. Elytra about 1.8 times as long as combined width; transversely strigulate; sutural stria present; epipleuron narrow, incomplete. Hind wings present. Metaventral posterior process with distinct median discrimen. Metanepisternum at least twice as long as wide. Metacoxae contiguous; metacoxal plates well-developed and greatly enlarged.

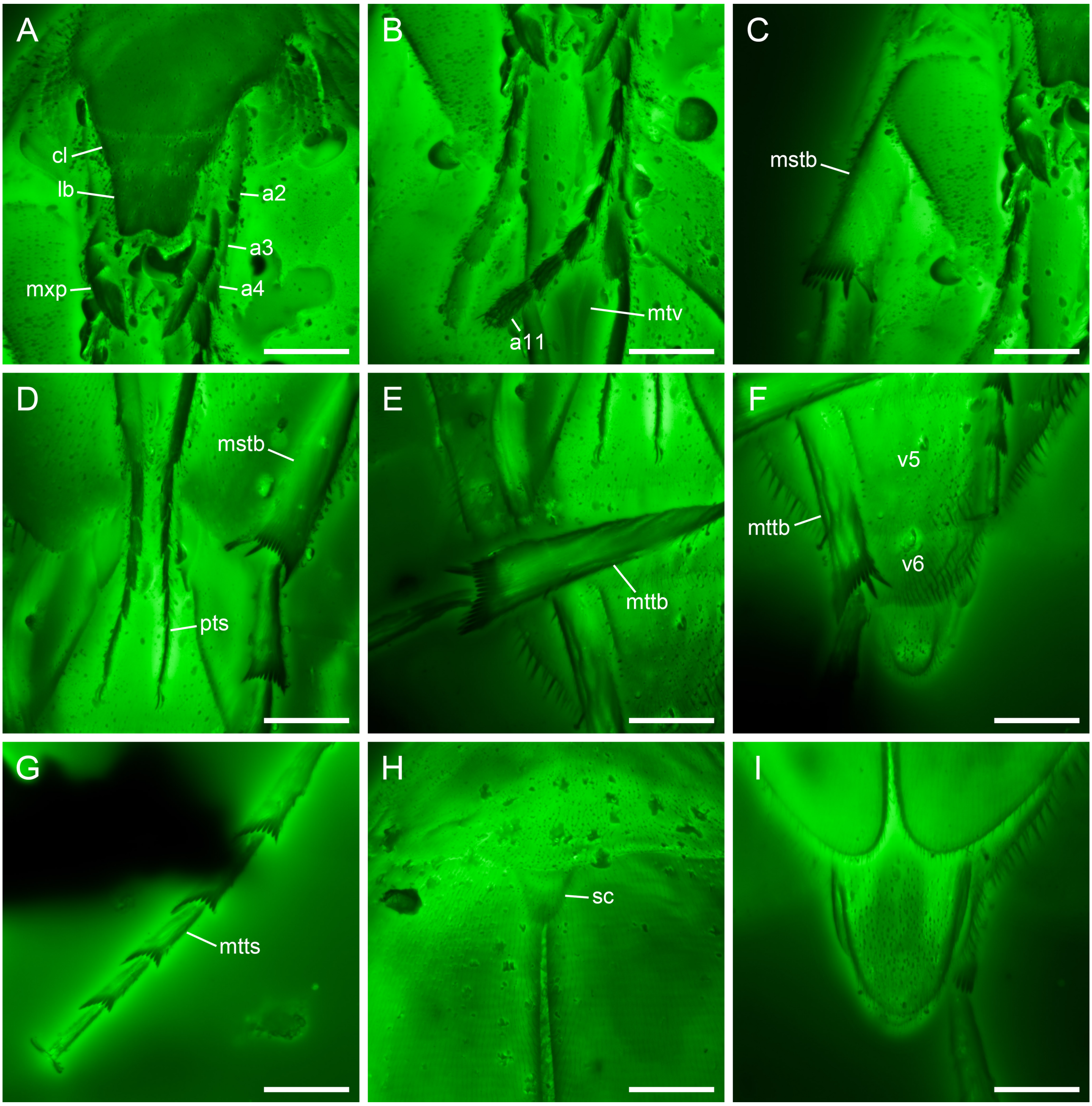

FIGURE 7. Details of *Eucinetus panghongae* Li & Cai **sp. nov.**, holotype, NIGP203940, under confocal microscopy. **A**, Head, dorsal view. **B**, Antennae. **C**, Mid leg. **D**, Fore and mid legs. **E**, Mid leg. **F**, Abdominal apex, ventral view. **G**, Hind leg. **H**, Scutellar shield, dorsal view. **I**, Abdominal apex, dorsal view. Abbreviations: a2–11, antennomeres 2–11; cl, clypeus; lb, labrum; mstb, mesotibia; mttb, metatibia; mtts, metatarsus; mtv, metaventrite; mxp, maxillary palp; pts, protarsus; sc, scutellar shield; v5–6, ventrites 5–6. Scale bars: 100 µm.

Mid and hind legs with fringe of spines at apices of tibiae and tarsomeres; fore legs without apical fringes of spines. Meso- and metatibiae at most with only one or two spines along outer edge. Mesotibial spurs large; both distinctly stouter than spines along apical fringe of mesotibia. Metatibial spurs equal. Tarsi 5-5-5, simple. Meso- and metapretarsal claws with accessory lobes (Fig. 7G).

Abdomen with six ventrites. Posterior margin of ventrite 5 subtruncate, not emarginate.

Remarks. The sternite VIII of NIGP203940 (and also NIGP203939) is densely covered with setae like the preceding ventrites (Fig. 7F). It should be normally exposed when alive, representing the sixth ventrite. In some recent comprehensive coleopteran compendia, the abdomen is described as having only five ventrites for the whole

Eucinetidae (Lawrence & Ślipiński 2013; Leschen 2016). However, the sternite VIII is actually commonly exposed in many extant members of *Eucinetus* (Vit 1977a).

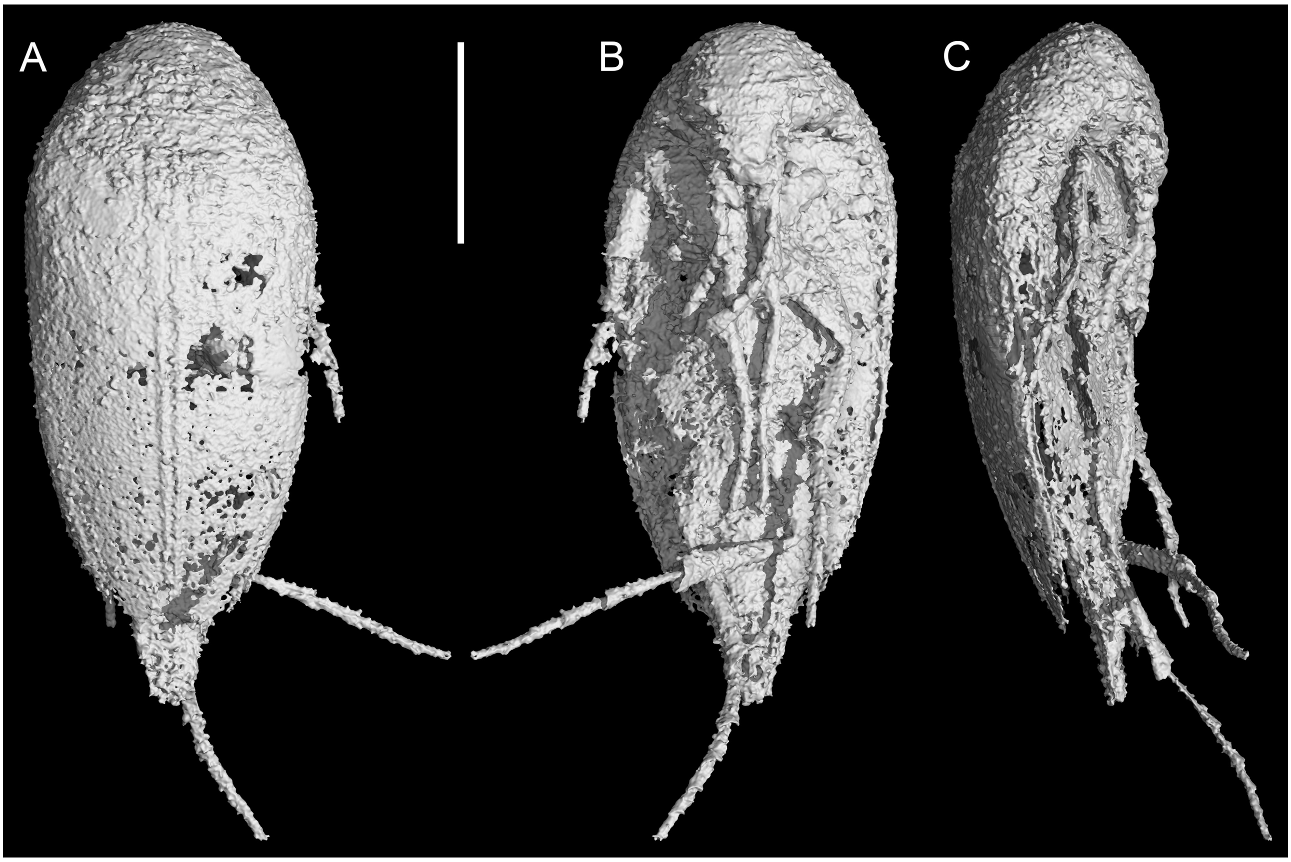

FIGURE 8. X-ray microtomographic reconstruction of *Eucinetus panghongae* Li & Cai **sp. nov.**, holotype, NIGP203940. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bar: 500 µm.

***Eucinetus zhenhuai* Li & Cai sp. nov.**
(Figs 9–12)

Material. Holotype, NIGP203941, female.

Etymology. The species is named after the coleopterist Dr. Zhenhua Liu.

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. Labrum weakly biemarginate (Fig. 11A). Apical maxillary palpomere asymmetrical (Fig. 11A). Basal antennomeres relatively elongate (especially antennomeres 3–5); antennomere 3 about 0.85 times as long as 4 (Fig. 11A); antennomere 11 about 2.1 times as long as wide (Fig. 11B). Scutellar shield acute at apex (Fig. 11GA). Elytra about 2.1 times as long as combined width. Hind wings present. Metanepisternum at least twice as long as wide. Meso- and metatibiae with relatively dense spines along outer edge (Fig. 11D,E). Mesotibial spurs large; both distinctly stouter than spines along apical fringe of mesotibia (Fig. 11D). Metatibial spurs unequal (Fig. 11D).

Description. Body fusiform and slender, about 2.5 mm long, 1.0 mm wide; surface with fine short setae.

Head deflexed against ventral side of prothorax; entirely concealed from above by pronotum. Compound eyes weakly emarginate anteriorly, with interfacetal setae. Antennae 11-segmented, filiform; basal antennomeres distinctly elongate (especially antennomeres 2–5); distal antennomeres somewhat shortened; antennomere 3 about 0.85 times as long as 4; antennomere 11 about 2.1 times as long as wide. Frontoclypeal suture straight anteriorly and with distinct anterolateral angles. Labrum transverse, apically very weakly biemarginate. Mouthparts non-suctorial. Apical maxillary palpomere asymmetrical.

FIGURE 9. General habitus of *Eucinetus zhenhuai* Li & Cai **sp. nov.**, holotype, NIGP203941, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 µm.

Prothorax widest at base. Lateral pronotal carinae complete, simple. Pronotal disc simple. Procoxae obliquely oriented, well-projecting, narrowly separated. Scutellar shield triangular, acute at apex. Elytra about 2.1 times as long as combined width; transversely strigulate; sutural stria present; epipleuron narrow, incomplete. Hind wings present. Metaventral posterior process without externally discernable discrimen. Metanepisternum at least twice as long as wide. Metacoxae contiguous; metacoxal plates well-developed and greatly enlarged.

Mid and hind legs with fringe of spines at apices of tibiae and tarsomeres; fore legs without apical fringes of spines. Meso- and metatibiae with relatively dense spines along outer edge. Mesotibial spurs large; both distinctly stouter than spines along apical fringe of mesotibia. Metatibial spurs unequal. Tarsi 5-5-5, simple. Meso- and metapretarsal claws with accessory lobes (Fig. 11F).

Abdomen with five ventrites. Ovipositor simple, with gonocoxites and gonostyli (Fig. 11H,I).

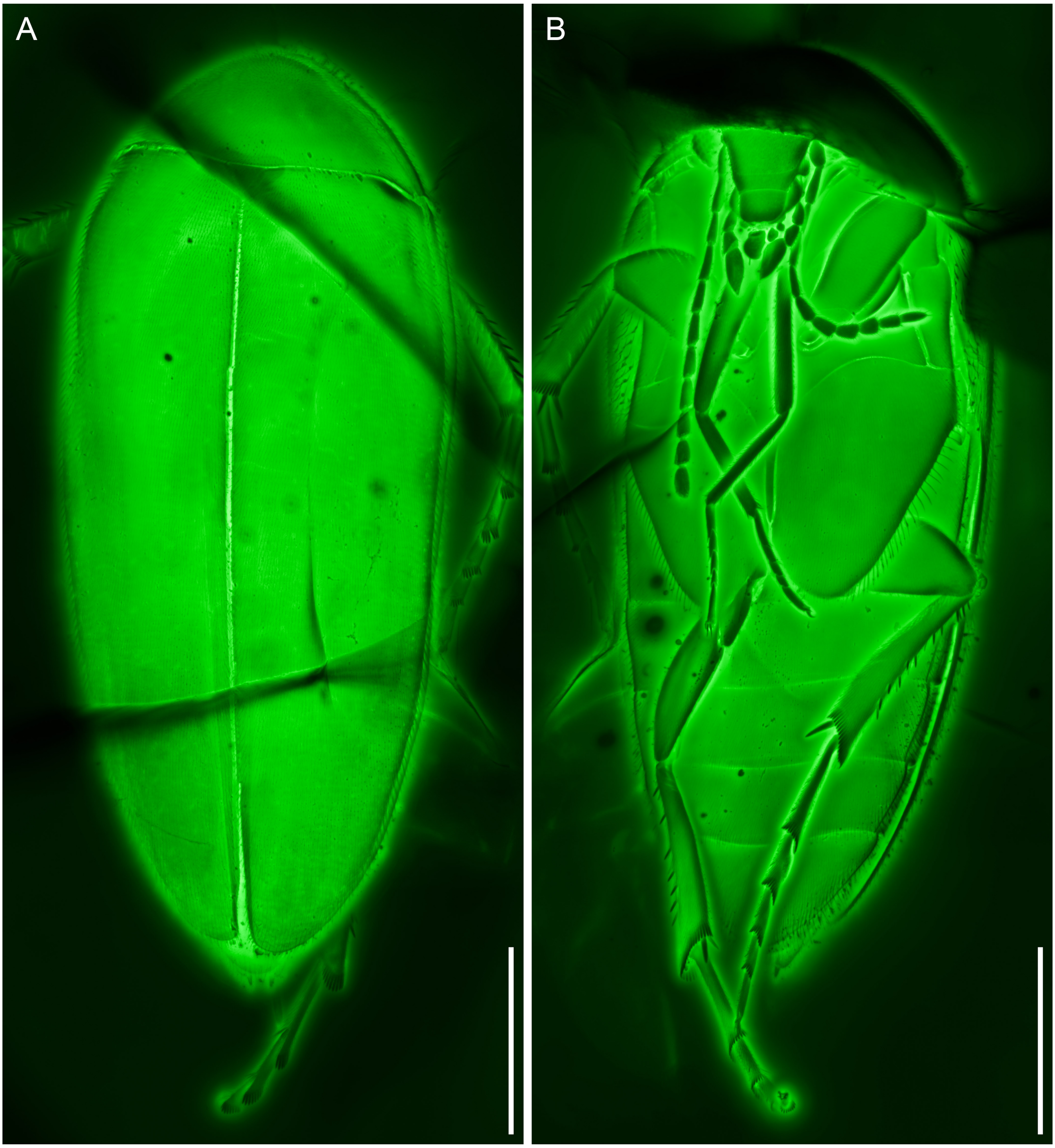

FIGURE 10. General habitus of *Eucinetus zhenhuai* Li & Cai **sp. nov.**, holotype, NIGP203941, under confocal microscopy. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 μm.

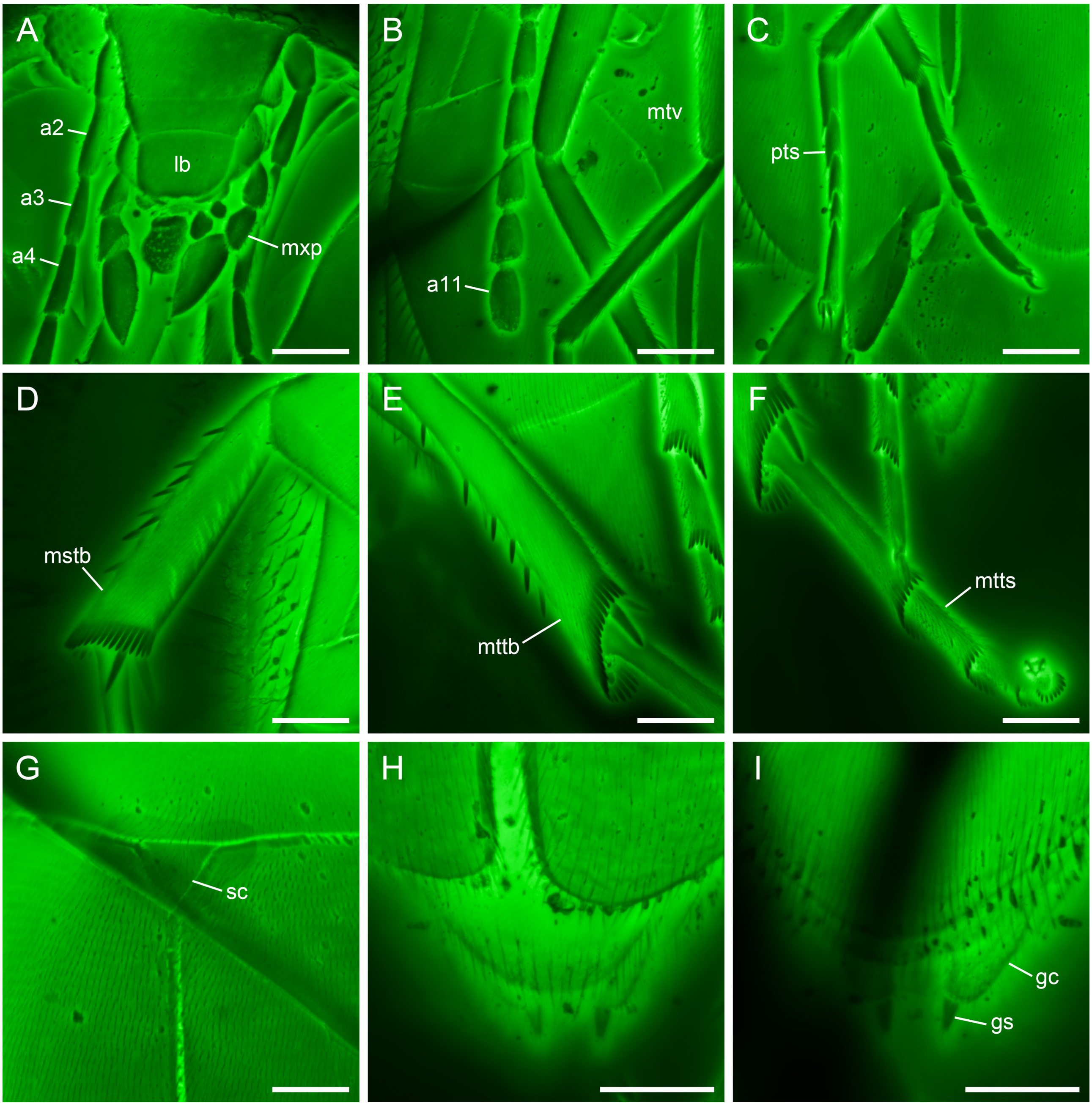

FIGURE 11. Details of *Eucinetus zhenhuai* Li & Cai **sp. nov.**, holotype, NIGP203941, under confocal microscopy. **A**, Head, dorsal view. **B**, Antenna. **C**, Fore legs. **D**, Mid leg. **E**, Hind legs. **F**, Hind legs. **G**, Scutellar shield, dorsal view. **H**, Abdominal apex, dorsal view. **I**, Abdominal apex, ventral view. Abbreviations: a2–11, antennomeres 2–11; gc, gonocoxite; gs, gonostylus; lb, labrum; mstb, mesotibia; mttb, metatibia; mtts, metatarsus; mxp, maxillary palp; pts, protarsus; sc, scutellar shield. Scale bars: 100 µm.

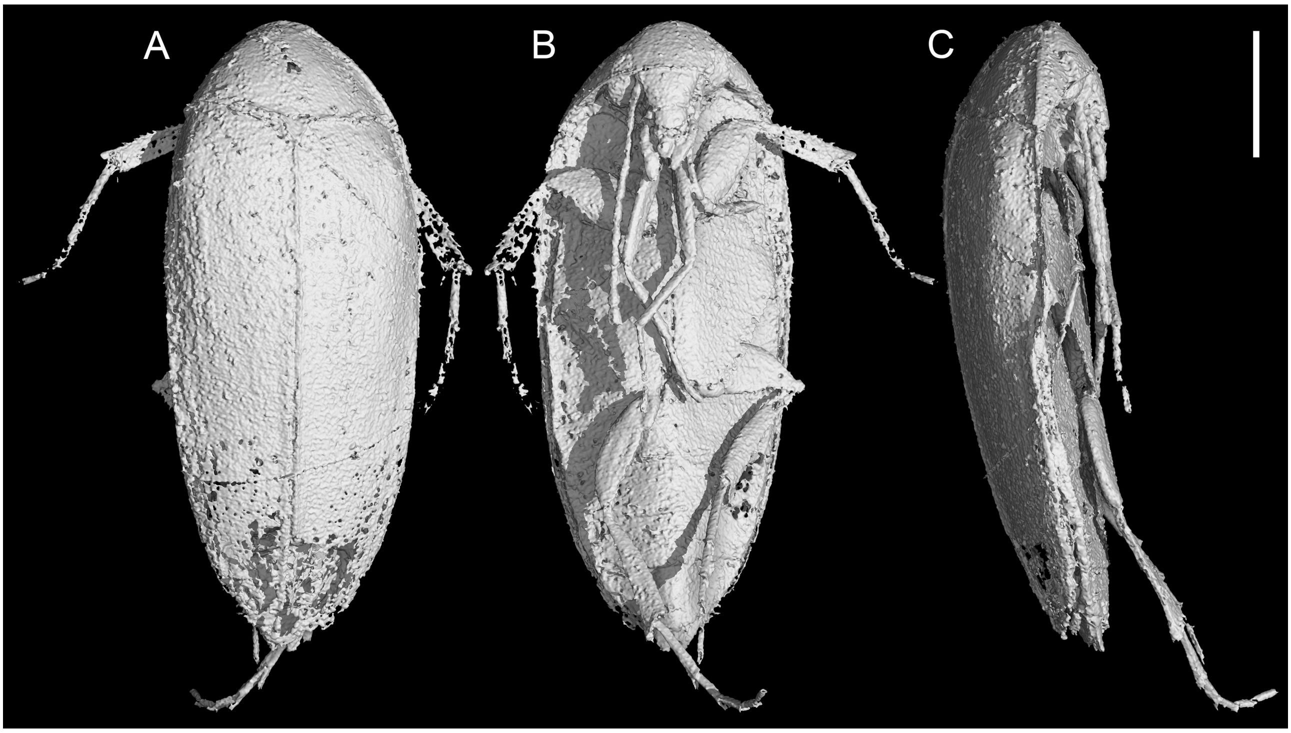

FIGURE 12. X-ray microtomographic reconstruction of *Eucinetus zhenhuai* Li & Cai **sp. nov.**, holotype, NIGP203941. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. Scale bar: 500 µm.

Discussion

The genus *Eucinetus* stands out as one of the growing examples of extant beetle genera discovered in Cretaceous Kachin amber that demonstrate considerable stasis over 100 million years. Many of them are associated with microhabitats of leaf litter or decaying wood (*e.g.*, Cai *et al.* 2018, 2019; Yu *et al.* 2019; Liu *et al.*, 2020; Li *et al.* 2021, 2024; Yamamoto 2021, 2024; Yamamoto & Newton 2023). In these examples, species live in relatively stable microenvironments and feed on a consistent suite of resources occurring in this stable habitat, such as fungi involved in wood decomposition, as is the case for *Eucinetus* (*e.g.*, Wheeler & Hoebeke 1984; Hoebeke *et al.* 1987; Stephenson *et al.* 1994). Thus, while the global environment has undergone significant changes in flora, fauna, and general climate over the millennia, these “cryptic” microhabitats have remained constant, allowing species that are specialized for these microhabitats to persist with few changes. These stand in stark contrast to other lineages, which live more exposed lives, and have experienced considerable evolutionary change and even extinction. Naturally, the confines of such microhabitats have limitations, such as the relatively ephemeral nature of the wood, which eventually becomes exhausted through decomposition and necessitates dispersal and the dangers involved. Regardless, the existence of taxa such as these species of *Eucinetus* highlights the role of specialized microhabitats in the survival of certain lineages over extended episodes of geological history.

Data availability

The original confocal and micro-CT data are available in the Zenodo repository (https://doi.org/10.5281/zenodo.11201148).

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