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A contribution to the taxonomy of Eucnemidae from mid-Cretaceous Kachin amber (Coleoptera: Elateroidea)

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Abstract

Two new genera and species of false click beetles are described and illustrated from mid-Cretaceous Kachin amber. *Yallmoleia arriagavarelai* **gen. et sp. nov.** differs from similar species that have basally closed lateral antennal grooves on the hypomeron primarily by the absence of elytral striae and the morphology of antennae and legs. *Xanrofeurya tomaszewskae* **gen. et sp. nov.** is distinctive among Eucnemidae from Kachin amber in having basally open lateral antennal grooves on the hypomeron, and differs from extant species with this feature by its antennal morphology. *Muonabuntor grandinotalis* Li *et al.* and *Jenibuntor pusillus* Muona, previously described from Kachin amber, are transferred into *Euryptychus* LeConte as *Euryptychus grandinotalis* **comb. nov.** and *Euryptychus pusillus* **comb. nov.** *Sieglindea antiqua* Muona, which was claimed to originate from Kachin amber, is instead suggested to be from Eocene Baltic amber.

Keywords: Eucnemidae, Kachin amber, Cretaceous, fossil, taxonomy

Introduction

Eucnemidae is a hard-bodied elateroid family commonly known as false click beetles. They are closely related to Cerophytidae and Throscidae, but more distantly related to the true click beetles of the Elateridae (McKenna *et al.*, 2019; Cai *et al.*, 2022).

The current classification system for Eucnemidae is largely based on a monograph by Muona (1993a), in which he proposed a comprehensive classification framework at the tribe level. However, as noted by Li *et al.* (2020), although Muona (1993a) conducted a morphology-based cladistic analysis, his classification system was not directly derived from this analysis and did not adhere to generally accepted phylogenetic principles. The subfamilies Melasinae and Macraulacinae, as defined by Muona (1993a), were not supported as monophyletic in his own analysis (summarized in Li *et al.*, 2020: fig. 4) or in subsequent analyses by Lawrence *et al.* (2007).

Little information has been provided for the internal relationships of Eucnemidae from molecular data. Kundrata *et al.* (2014) analysed the phylogeny of Elateroidea based on four gene fragments, and found the following relationship for Eucnemidae: (Anischiinae, (Melasinae, (Eucneminae, Macraulacinae))). However, most sequenced eucnemid specimens in Kundrata *et al.* (2014) were not identified beyond the family level, making the study insufficient to support the monophyly of the subfamilies. Seung (2017) analysed the phylogeny of Eucnemidae with three gene fragments, mostly based on Korean specimens and again found that both Melasinae and Macraulacinae were non-monophyletic. Further molecular investigations encompassing more extensive taxonomic and genetic sampling will be necessary to clarify the relationships within Eucnemidae.

The fossil record of Eucnemidae has been recently reviewed by Li *et al.* (2020) and Otto (2023). Particularly, regarding Eucnemidae from mid-Cretaceous Kachin amber, Otto (2019), Li *et al.* (2020) and Hsiao & Otto (2024) each described a single species, while Han *et al.* (2024) described two new species. Muona (2020) described 20 new species, claimed to be from Kachin amber (see Discussion). However, most of the fossils described by Muona were poorly illustrated, making

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it difficult for others to reassess their morphology and systematic placements. Zippel *et al*. (2023) additionally reported a larva from Kachin amber, which was believed to belong to Eucnemidae. In the present study, two new genera and species of Eucnemidae are further described from Kachin amber.

Material and methods

The Kachin (Burmese) amber specimens studied herein (Figs 1–7) originated from amber mines near Noije Bum (26°20’ N, 96°36’ E), Hukawng Valley, Kachin State, northern Myanmar. The amber specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber pieces containing the new species were trimmed with a saw mounted on a handheld rotary tool, 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) 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.14996960). 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.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Superfamily Elateroidea Leach, 1815
Family Eucnemidae Eschscholtz, 1829
Subfamily Eucneminae Eschscholtz, 1829

Genus *Yallmoleia* gen. nov.

Type species. *Yallmoleia arriagavarelai* **sp. nov.**

Etymology. The generic name is an arbitrary combination of letters, inspired by the name *Myall* Muona. The name is feminine in gender.

Diagnosis. Clypeus apically denticulate (Fig. 3A). Antennomeres 4–8 submoniliform; antennomeres 9–11 weakly enlarged, forming club (Fig. 3C). Mandibles elongate (Fig. 3A). Hypomeron with basally closed lateral antennal grooves (Fig. 3C). Prosternal process with V-shaped groove running along sides (Fig. 3B). Elytra without striae (except for the posteriorly hooked subsutural stria); punctures irregularly distributed (Fig. 3H, I). Metaventrite without mesotarsal grooves, with a pair of weak postcoxal lines (Fig. 3E).

Remarks. According to Muona (1993a), all eucnemids with basally closed lateral antennal grooves on the hypomeron are classified in the subfamily Eucneminae. Among extant Eucneminae, only Phaenocerini and Proutianini may have both antennal grooves and enlarged antennomeres 9–11. Both tribes differ from *Yallmoleia* in having sharply defined striae on the elytra (Muona, 1993a).

Among eucnemids from Kachin amber, the following genera have basally closed lateral antennal grooves on the hypomeron: *Cylus* Muona, *Falsothambus* Muona, *Myall* Muona, *Pseudomyall* Muona, *Paleoeucnemis* Muona and *Protovitellius* Muona (Muona, 2020). *Falsothambus*, *Myall*, *Pseudomyall* and *Paleoeucnemis* further share with *Yallmoleia* the 3-segmented antennal club. *Yallmoleia* could be distinguished from *Cylus*, *Falsothambus*, *Myall* and *Pseudomyall* by the absence of elytral striae (except for the subsutural one), and further from *Cylus* by the presence of antennal club (antennomeres 2–10 subequal in *Cylus*), from *Myall* by the absence of any trace of metaventral tarsal grooves (vestigial tarsal grooves present in *Myall*), and from *Pseudomyall* by the shorter antennal club (antennomeres 9–11 about as long as antennomeres 1–8 combined in *Pseudomyall*). *Protovitellius* shares with *Yallmoleia* the absence of elytral striae, but differs in antennomeres 4–10 elongate and meso- and metatarsi with tarsomere 2 longer than 3–5 combined. Based on the photos provided (Muona, 2020: figs 47–50), *Paleoeucnemis* appears to be most similar to *Yallmoleia* (particularly in antennal shape). However, according to the description by Muona (2020), *Paleoeucnemis* has meso- and metatarsi in which tarsomere 1 is longer than the remaining tarsomeres combined, whereas in *Yallmoleia*, mesotarsomere 1 is clearly shorter than mesotarsomeres 2–5 combined.

As noted by Li *et al*. (2020), the current classification system of Eucnemidae is likely largely unnatural. A thorough molecular study is needed to clarify the composition of subfamilies and tribes. Therefore, we refrain from assigning *Yallmoleia* to any tribe at this time.

Yallmoleia arriagavarelai sp. nov.

(Figs 1–3)

Material. Holotype, NIGP204232.

Etymology. The species is named after the coleopterist Dr. Emmanuel Arriaga-Varela.

Diagnosis. As for the genus.

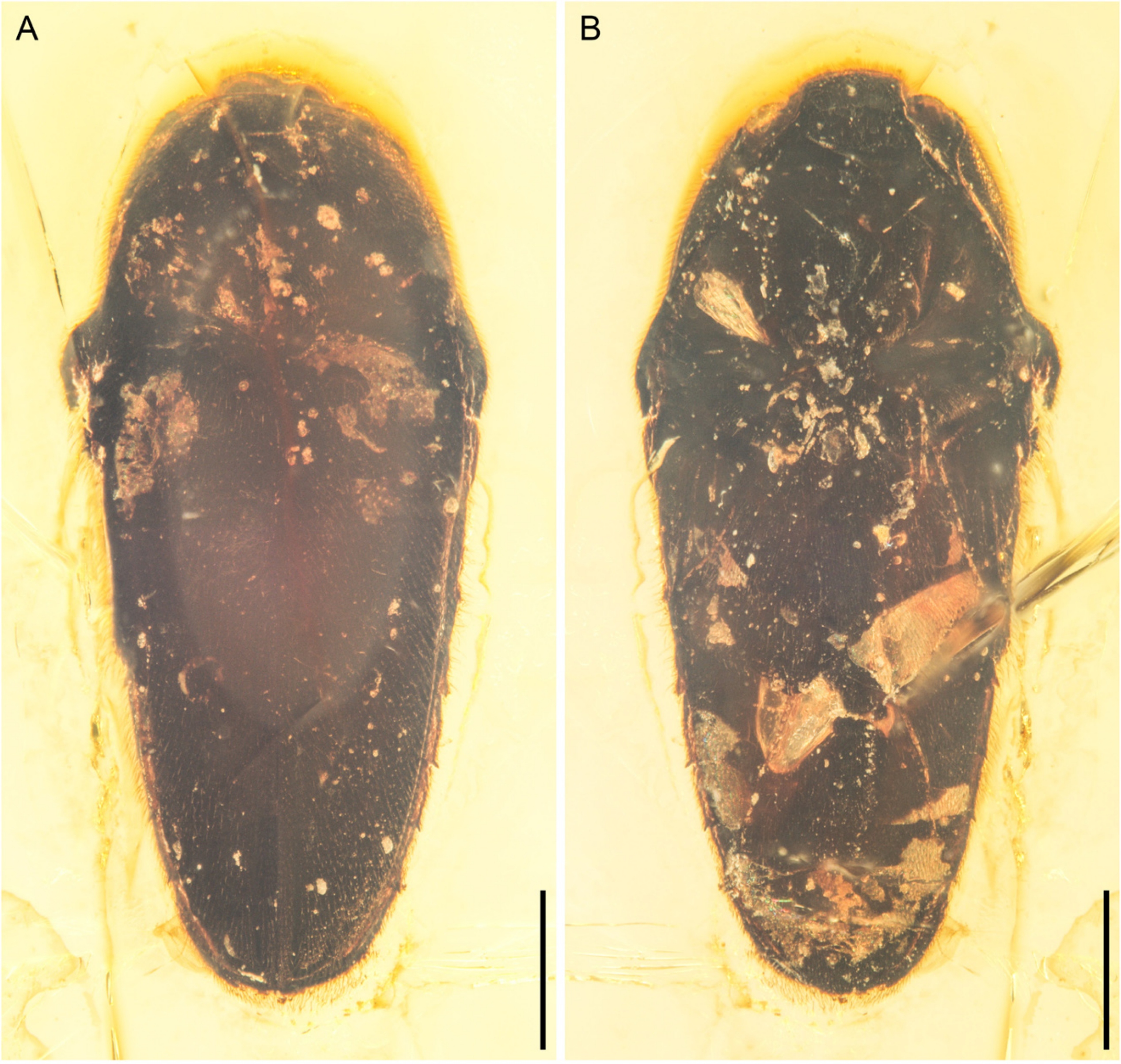

FIGURE 1. General habitus of *Yallmoleia arriagavarelai* **gen. et sp. nov.**, holotype, NIGP204232, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 µm.

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 oblong, about 2.9 mm long and 1.3 mm wide, covered with decumbent, posteriorly orientated hairs.

Head hypognathous, transverse, deeply inserted into prothorax. Frons without median carina. Eyes large, without interfacetal setae. Frontoclypeal region between antennal insertions only slightly constricted. Clypeus apically broadly rounded, denticulate. Antennae 11-segmented; antennomere 1 strongly elongate, seemingly not distinctly wider than following antennomeres; antennomere 2 slightly longer than wide; antennomere 3 moderately elongate, about 2.5× as long as wide; antennomeres 4–8 slightly longer than wide to slightly wider than long; antennomeres 9–11 weakly enlarged, forming compact club. Mandibles elongate.

Pronotum wider than long, widest posteriorly; anterior edge simple; posterior angles acute and produced. Lateral pronotal carinae entire, anteriorly visible only ventrally. Hypomeron with basally closed lateral antennal grooves; posterior surface of hypomeron with crural impression for reception of profemora. Notosternal suture complete. Prosternum in front of coxae well developed, smooth; prosternal process well developed, with sides gradually converging apically, acute at apex, fitting into mesoventral cavity; surface with V-shaped groove running along sides of prosternal process. Procoxae globular.

FIGURE 2. General habitus of *Yallmoleia arriagavarelai* **gen. et sp. nov.**, holotype, NIGP204232, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 500 µm.

Scutellar shield seemingly subtrapezoidal. Elytra about 1.7× as long as width combined, tapering posteriorly; subsutural stria present, apically developed as hooked specialized pore (*cf.* Muona *et al.*, 2020: fig. 1); other striae absent; punctation irregular. Mesocoxae separated by about longitudinal coxal diameter. Meso-metaventral junction externally straight. Metaventrite transverse, without discrimen, with a pair of weak postcoxal lines (grooves) beginning at posteromesal edge of cavity and extending posterolaterally; mesotarsal grooves absent. Metacoxae contiguous, extending laterally to meet epipleura; coxal plates well developed and complete but narrowed laterally.

Legs slender. Tibiae likely rounded in cross section; lateral surface of meso- and metatibiae with isolated spines. Tarsi 5-5-5, simple; tarsomere 1 longest, in mid and hind legs distinctly longer than any other tarsomeres, but shorter than tarsomeres 2–5 combined; tarsomeres 2–4 each shorter than previous segment; tarsomere 5 longer than 4 but shorter than 3 and 4 combined. Pretarsal claws simple.

Abdomen with five ventrites; metatarsal grooves absent.

Subfamily Macraulacinae Fleutiaux, 1922

Genus *Xanrofeurya* gen. nov.

Type species. *Xanrofeurya tomaszewskae* **sp. nov.**

Etymology. The generic name is an arbitrary

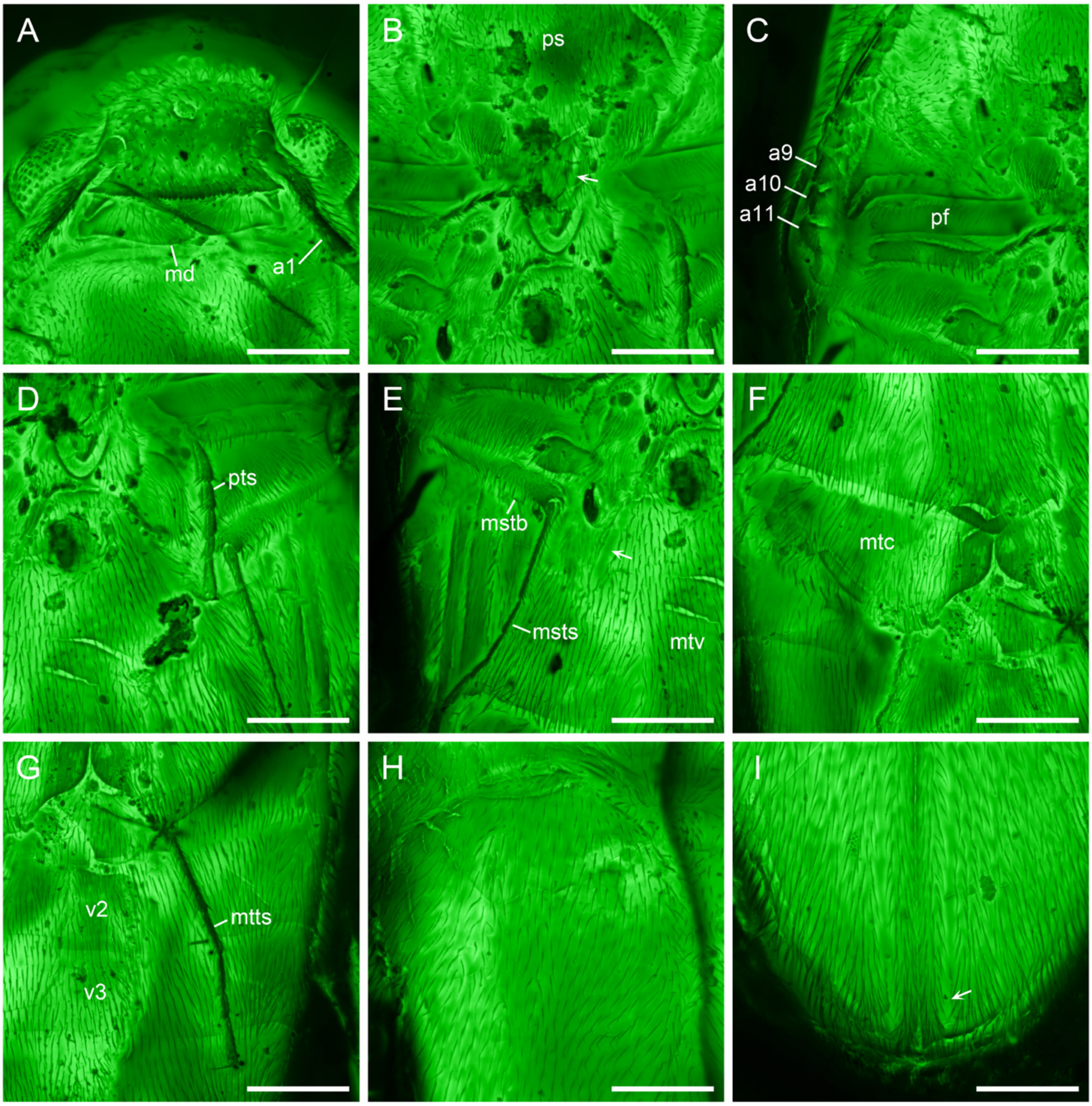

FIGURE 3. Details of *Yallmoleia arriagavarelai* **gen. et sp. nov.**, holotype, NIGP204232, under confocal microscopy. **A**, Head, ventral view. **B**, Pro- and mesothorax, ventral view, with arrow indicating groove on prosternal process. **C**, Hypomeron and antenna, ventral view. **D**, Meso- and metathorax, ventral view. **E**, Metathorax, ventral view, with arrow indicating postcoxal groove. **F**, Metacoxae, ventral view. **G**, Abdomen, ventral view. **H**, Elytral base, dorsal view. **I**, Elytral apex, dorsal view, with arrow indicating hooked specialized pore. Abbreviations: a1–11, antennomeres 1–11; md, mandible; mstb, mesotibia; msts, mesotarsus; mtc, metacoxa; mtts, metatarsus; mtv, metaventrite; pf, profemur; ps, prosternum; pts, protarsus. Scale bars: 200 µm.

combination of letters, inspired by the name *Fornax* Laporte. The name is feminine in gender.

Diagnosis. Mandibles elongate (Fig. 6A). Antennomeres 4 and 6 short; antennomere 5 elongate (Fig. 6D). Hypomeron with basally open lateral antennal grooves (Fig. 6E, F). Elytra with weak striae (except for the more distinct subsutural stria); punctures irregularly distributed. Metaventrite with tarsal grooves (Fig. 6G).

Remarks. According to Muona (1993a), only Macraulacini has basally open lateral antennal grooves on the hypomeron. In the presumably closely related Nematodini (Muona, 1993a), the antennal grooves are generally strongly reduced or obliterated (Muona, 2000). *Graciliforma* Otto also has well-developed basally open lateral antennal grooves, which was, however, assigned to Nematodini by Otto (2016). Nevertheless,

FIGURE 4. General habitus of *Xanrofeurya tomaszewskae* **gen. et sp. nov.**, holotype, NIGP204233, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

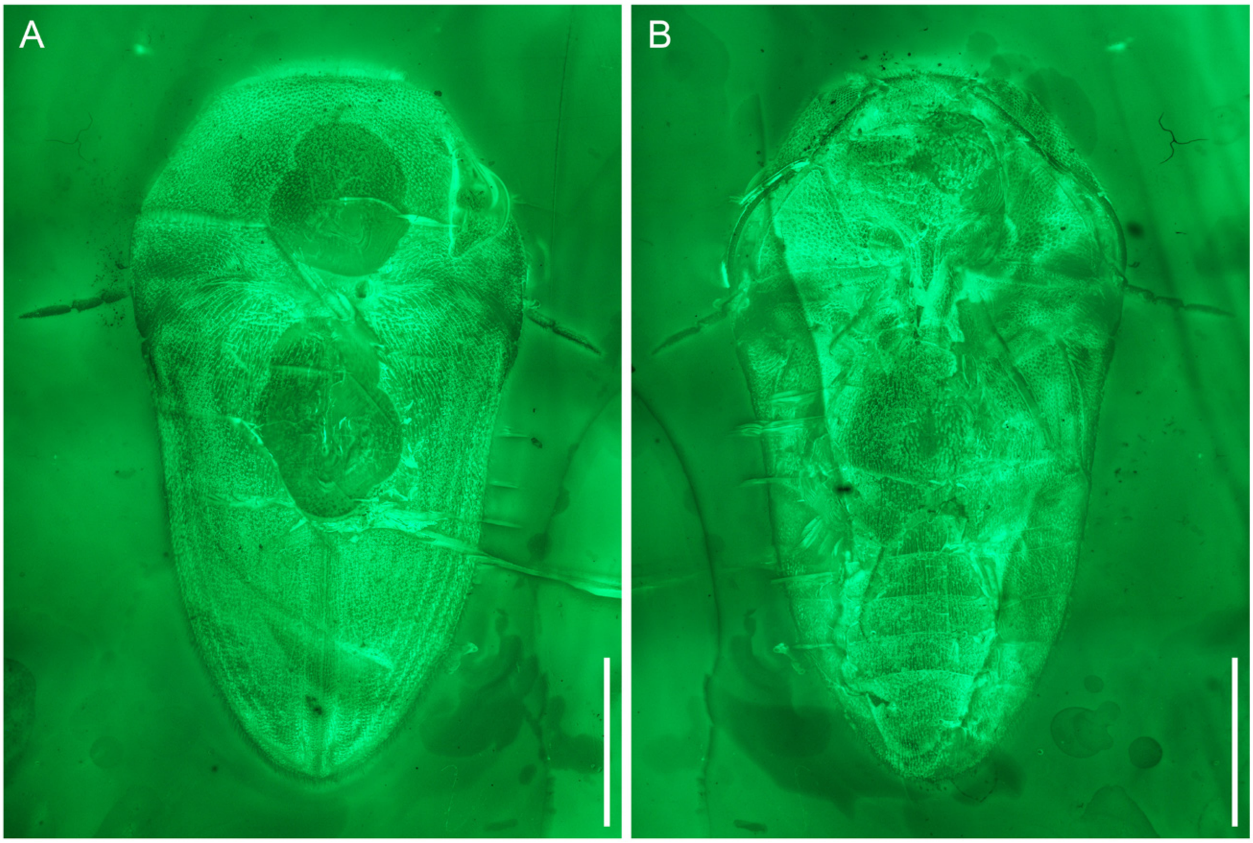

FIGURE 5. General habitus of *Xanrofeurya tomaszewskae* **gen. et sp. nov.**, holotype, NIGP204233, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

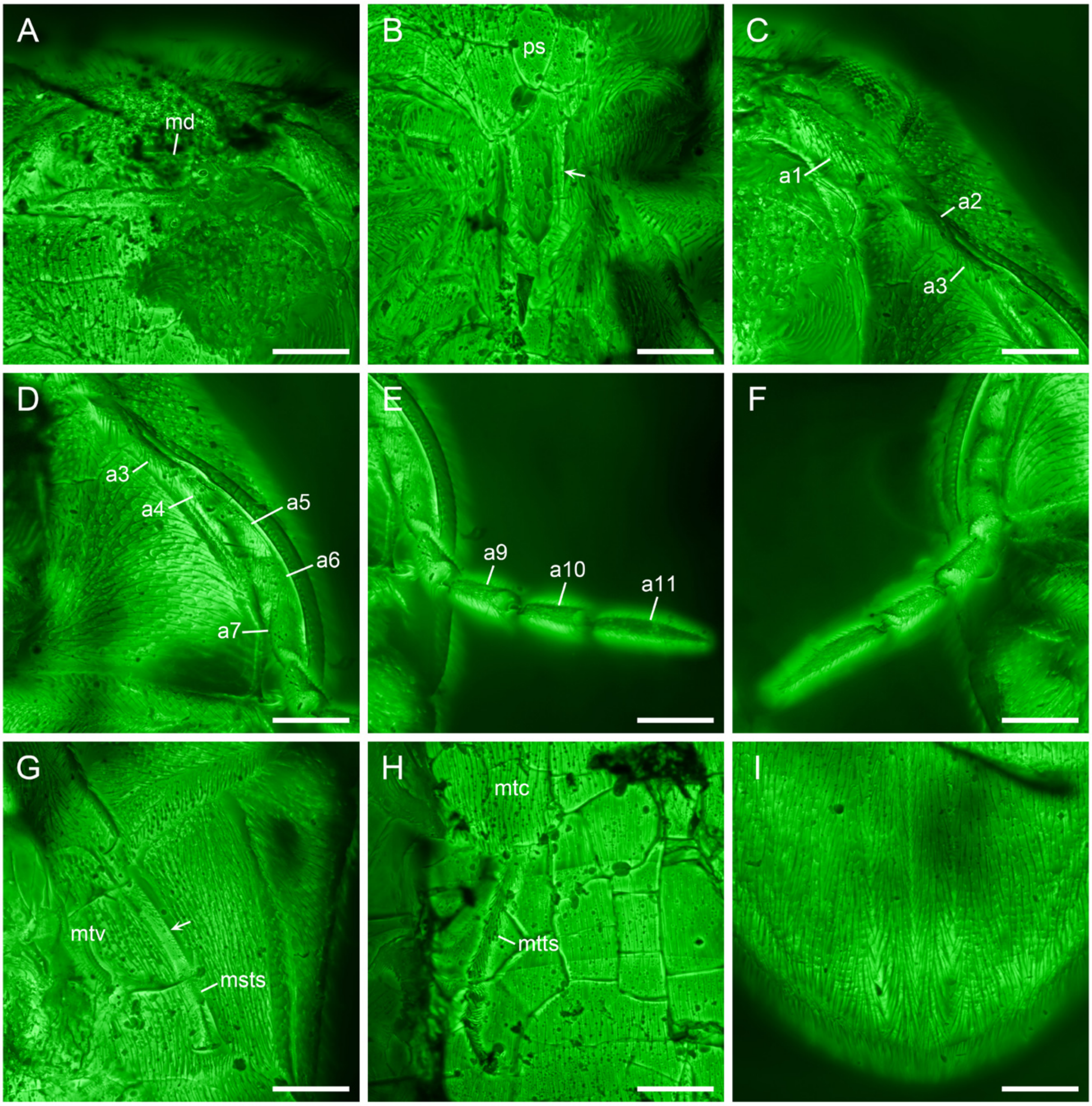

FIGURE 6. Details of *Xanrofeurya tomaszewskae* **gen. et sp. nov.**, holotype, NIGP204233, under confocal microscopy. **A**, Head, ventral view. **B**, Pro- and mesothorax, ventral view, with arrow indicating groove on prosternal process. **C**, Antennal base. **D**, Hypomeron and antenna, ventral view. **E**, **F**, Antennal apex. **G**, Metathorax, ventral view, with arrow indicating mesotarsal groove. **H**, Abdomen, ventral view. **I**, Elytral apex, dorsal view. Abbreviations: a1–11, antennomeres 1–11; md, mandible; msts, mesotarsus; mtc, metacoxa; mtts, metatarsus; mtv, metaventrite; ps, prosternum. Scale bars: 200 μm.

Xanrofeurya can be distinguished from previously known Macraulacini and Nematodini by its antennal morphology. Macraulacini has antennomeres 4–10 (sub)equal, and Nematodini has antennomeres 6–11 (or rarely 8–11) more or less elongated (Muona, 1993a; Otto, 2016). In *Xanrofeurya*, antennomeres 7–10 are moderately elongate, antennomeres 4 and 6 are shorter, and antennomere 5 is more elongate.

No fossils of Macraulacini or Nematodini have been reported from Kachin amber previously. Muona (2021) even suggested that "the tribe Macraulacini is possibly not at all present in Late Cretaceous". The discovery of *Xanrofeurya* from Kachin amber demonstrates that this lineage originated no later than the mid-Cretaceous. Nevertheless, specimens with affinity to Macraulacini (with basally open lateral antennal grooves) are indeed very rare in our eucnemid collection from Kachin amber, implying a low diversity of this group at that time.

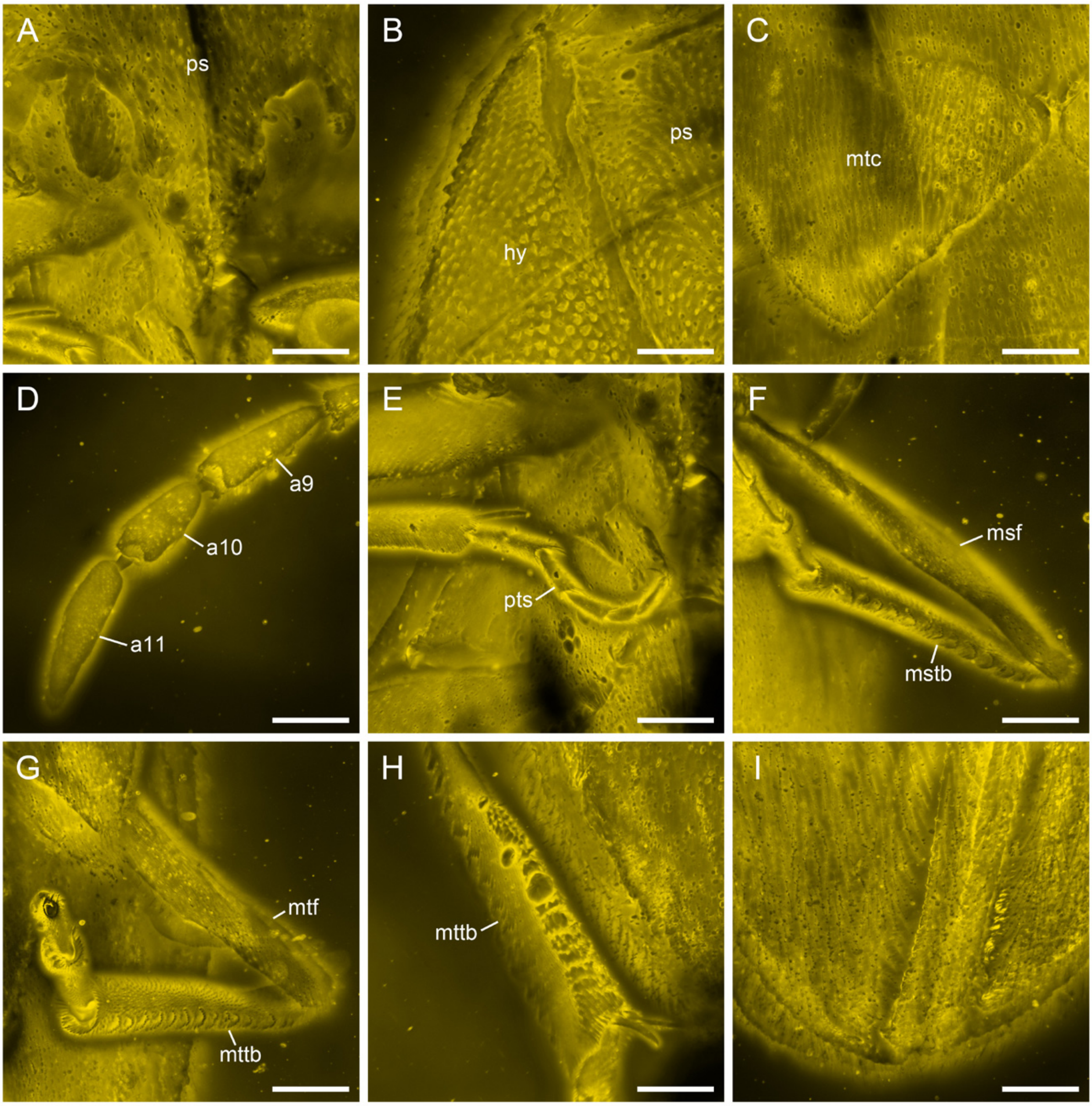

FIGURE 7. Details of *Euryptychus grandinotalis* **comb. nov.**, holotype, NIGP173376, under confocal microscopy. **A**, Prosternal process, ventral view. **B**, Hypomeron, ventral view. **C**, Metacoxae, ventral view. **D**, Antenna. **E**, Fore leg. **F**, Mid leg. **G**, **H**, Hind legs. **I**, Elytral apex, dorsal view. Abbreviations: a9–11, antennomeres 9–11; hy, hypomeron; msf, mesofemur; mstb, mesotibia; mtc, metacoxa; mtf, metafemur; mttb, metatibia; ps, prosternum; pts, protarsus. Scale bars: 200 µm.

Xanrofeurya tomaszewskae sp. nov.

(Figs 4–6)

Material. Holotype, NIGP204233.

Etymology. The species is named after the coleopterist Dr Wioletta Tomaszewska.

Diagnosis. As for the genus.

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 oblong, relatively broad, about 4.3 mm long and 2.4 mm wide, covered with decumbent, posteriorly orientated hairs.

Head hypognathous, transverse, deeply inserted into prothorax. Frons without median carina. Eyes large, without interfacetal setae. Frontoclypeal region between antennal insertions only slightly constricted. Clypeus apically smooth. Antennae 11-segmented; antennomere 1 elongate; antennomeres 2, 4 and 6 relatively short; antennomere 3 moderately elongate; antennomere 5 elongate; antennomeres 7–10 moderately elongate, antennomere 11 strongly elongate. Mandibles elongate.

Pronotum wider than long, widest near posterior 1/4; anterior edge simple; posterior angles acute and produced. Lateral pronotal carinae probably entire, anteriorly visible only ventrally. Hypomeron with basally open lateral antennal grooves; posterior surface of hypomeron with crural impression for reception of profemora. Notosternal suture complete. Prosternum in front of coxae well developed, smooth; prosternal process well developed, with sides parallel in middle, acute at apex, fitting into mesoventral cavity; surface with possibly posteriorly open grooves running along sides of prosternal process. Procoxae globular.

Scutellar shield seemingly subtrapezoidal, with lateral sides converging posteriorly. Elytra about 1.3× as long as width combined, tapering posteriorly; subsutural stria more distinctly developed, apically developed as hooked specialized pore (*cf.* Muona *et al.*, 2020: fig. 1); other striae weakly developed; punctation irregular. Mesocoxae separated by distance slightly less than longitudinal coxal diameter. Meso-metaventral junction externally straight. Metaventrite transverse, without discrimen; mesotarsal grooves distinctly developed. Metacoxae contiguous, extending laterally to meet epipleura; coxal plates well developed and complete but narrowed laterally.

Legs slender. Tibiae likely rounded in cross section; lateral surface of meso- and metatibiae with isolated spines. Tarsi 5-5-5, simple. Pretarsal claws simple.

Abdomen with five ventrites; metatarsal grooves absent.

Discussion

Provenance of Sieglindea antiqua

Sieglindea Muona was originally described from Eocene Baltic amber, with two species, *S. siegfriedi* Muona and *S. hundingi* Muona (Muona, 1993b). Muona (2020) later claimed that he discovered the oldest species of *Sieglindea* from mid-Cretaceous Kachin amber, *S. antiqua* Muona. The dorsal surface of its holotype is covered with white opaque cloud (Muona, 2020: fig. 64), which has been variously referred to as “cotton-like cloud”, “frothy coating”, “milky substance”, or “whitish emulsion” by different authors.

This white cloud is commonly associated with arthropods in Baltic amber (*e.g.*, Bukejs & Háva, 2018; Shavrin & Yamamoto, 2019; Alekseev *et al.*, 2020, 2021; Kundrata *et al.*, 2020; Yamamoto, 2024) and the closely related Rovno amber (*e.g.*, Alekseev & Bukejs, 2022; Legalov *et al.*, 2023; Lyubarsky *et al.*, 2023). It is therefore also known as “Baltic mould” (Dierick *et al.*, 2007). It is now thought to result from the diffusion of body fluids into the surrounding resin (as summarized by Judson, 2003 and Kypke & Solodovnikov, 2020). This phenomenon is predominantly observed in ambers belonging to the Baltic amber group (Kypke & Solodovnikov, 2020), and is, to our knowledge, unknown in Kachin amber. Thus, we suggest that *S. antiqua* is unlikely to have originated from Kachin amber, and is probably from Baltic amber as its congeners.

Other specimens reported by Muona (2020) may also suffer from the same provenance issue, especially if some of them were obtained from the same amber dealer. Further spectroscopic analyses would be helpful to confirm the source of these specimens (*e.g.*, Shi *et al.*, 2023).

Placement of Muonabuntor grandinotalis and Jenibuntor pusillus

Li *et al*. (2020) suggested that *Muonabuntor grandinotalis* is most similar to *Euryptychus* (Euryptychini) and *Jenibuntor* (Jenibuntorini), based on the tubular antennomeres 9–11, simple hypomera and simple tarsomere 4. Li *et al*. (2020) did not place *Muonabuntor* into any tribe (contrary to the claim by Muona, 2020). As noted by Muona (2020), the shape of mandibles would be a character differentiating *Euryptychus* and *Jenibuntor*. However, the mandibles are covered by bubbles and not visible in the holotype of *M. grandinotalis*.

Another important difference between *Euryptychus* and *Jenibuntor* is the pattern of spines on the meso- and metatibiae: *Euryptychus* has transverse rows of spines (spine combs), while *Jenibuntor* has only isolated spines (Muona, 1993a). Our re-examination of *M. grandinotalis* reveals the presence of transverse rows of spines on its meso- and metatibiae (Fig. 7F–H). Therefore, *M. grandinotalis* likely belongs to Euryptychini as suggested by Muona (2020). Li *et al.* (2020) originally differentiated *Muonabuntor* from *Euryptychus* by the proportionally longer pronotum, but Muona (2020) pointed out that many *Euryptychus* species have even shorter elytra than *M. grandinotalis*. Thus, we propose to synonymize *Muonabuntor* **syn. nov.** with *Euryptychus*, and recombine *M. grandinotalis* as *Euryptychus grandinotalis* **comb. nov.**

Similarly, *Jenibuntor pusillus* Muona also has strong spine combs on meso- and metatibiae (Muona, 2020: fig. 74). Although Muona (2020) suggested that its expanded head is characteristic of *Jenibuntor*, the head of *Euryptychus* could also be somewhat expanded (*e.g.*, Li *et al*., 2020: fig. 3; see Muona in Otto, 2023 for generic identification). Thus, *J. pusillus* is also here transferred to *Euryptychus*, as *Euryptychus pusillus* **comb. nov.**

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