



<https://doi.org/10.11646/palaeoentomology.3.4.12>

<https://zoobank.org/urn:lsid:zoobank.org:pub:128BF355-04DF-4E04-ABF1-55811A3E78E8>

Muonabuntor gen. nov., a new genus of false click beetles from mid-Cretaceous Burmese amber (Coleoptera: Elateroidea: Eucnemidae)

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Abstract

Eucnemidae is a relatively large beetle family belonging to the polyphagan superfamily Elateroidea. Numerous fossil eucnemids have been reported from Cenozoic deposits, but the Mesozoic record of Eucnemidae is much sparser. Here we describe and figure a new eucnemid beetle, *Muonabuntor grandinotalis* gen. et sp. nov., discovered from mid-Cretaceous Burmese amber (ca. 99 Ma). The new genus resembles extant *Jenibuntor* and *Euryptychus* in having simple hypomera and tubular antennomeres 9–11, but differs from the latter genera by its comparatively longer pronotum, weakly striate elytra, and large metacoxal plates. The fossil record and classification system of Eucnemidae are also reviewed.

Keywords: Eucnemidae, *Muonabuntor*, Burmese amber, phylogeny, fossil

Introduction

The family Eucnemidae, or false click beetles, is a large group of widespread beetles belonging to the polyphagan superfamily Elateroidea (Muona, 2010). False click beetles are represented in the Recent fauna by nearly 200 described genera and about 1,500 species, and much of their biodiversity in tropical regions remains undocumented (Muona, 2010). Most eucnemids are lignicolous, and adults can be found on trunks and stumps (Muona, 1993a, 2010). As their name suggests, these beetles resemble true click beetles (Elateridae) in their

body shape, and most of them are also capable of clicking in the elaterid manner (Muona, 1993a, 2010). Eucnemids are characterized by their concealed labrum, pedicels inserted apicolaterally into scapes, and connate ventrites (Muona, 1993; Oberprieler *et al.*, 2016).

Eucnemidae has been suggested to be closely related to the elateroid families Cerophytidae and Throscidae (Lawrence *et al.*, 2011; Kundrata *et al.*, 2014; Kusy *et al.*, 2018; McKenna *et al.*, 2019). Eight subfamilies were recognized within Eucnemidae by Muona (1993a). Subfamily Anischiinae, which had been placed in Elateridae for a long time, was also moved to Eucnemidae later based on larval and molecular evidence (Lawrence *et al.*, 2007). Though Muona & Teräväinen (2020) claimed that Muona's subfamily-level classification was supported by the molecular phylogeny of Kundrata *et al.* (2014), most sequences used in Kundrata *et al.* (2014) had unclear generic affinity, and therefore their results cannot be viewed as a strong evidence for the monophyly of the subfamilies. Results of a more recent molecular phylogenetic study were considerably discordant with Muona's classification for Eucnemidae, although only three genes were sampled (Seung, 2017; see also Discussion). Further molecular studies making use of more genes and more extensive taxon sampling are needed to establish a more natural classification system for Eucnemidae.

Various eucnemid fossils have been reported from Baltic amber (*e.g.*, Muona, 1993b), Dominican amber (Poinar, 2013), and other Cenozoic deposits (Muona, 1993b). The Mesozoic fossil record of Eucnemidae is

much sparser. Oberprieler *et al.* (2016) discovered several possible eucnemids from the Upper Jurassic Talbragar Fish Bed in Australia. A well-preserved eucnemid larva similar to extant *Palaeoxenus* Horn was reported from the Lower Cretaceous Yixian Formation in northeastern China (Chang *et al.*, 2016). Recently, Otto (2019) described a new genus, *Cenomana* Otto, from mid-Cretaceous Burmese amber. Here, we report the second false click beetle from Burmese amber, which enriches our knowledge on the early diversity of the family. We furthermore review the fossil record of the family and discuss its classification in light of recent molecular phylogenetic studies.

Material and methods

The Burmese amber specimen studied here is derived from amber mines near the Noiye Bum Hill (26°20' N, 96°36' E), Hukawng Valley, Kachin State, northern Myanmar. The specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP), Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery papers of different grain 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. Images were stacked in Helicon Focus 7.0.2 to increase the depth of field, and further processed in Adobe Photoshop CC to enhance contrast.

The phylogenetic trees presented in discussion were drawn with the online tool iTOL 5.5.1 (Letunic & Bork, 2019).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Elateroidea Latreille, 1804
Family Eucnemidae Eschscholtz, 1829

Genus *Muonabuntor* Li, Tihelka & Cai gen. nov.

Type species. *Muonabuntor grandinotalis* sp. nov.

Etymology. The generic name is composed of the last name of the Finnish entomologist Jyrki Muona, in recognition of his contributions to the study of extant and fossil Eucnemidae, and the last six letters of the generic name “*Jenibuntor*”, in reference to its general similarity to *Jenibuntor*. The name is masculine in gender.

Diagnosis. Antennomeres 9–11 elongate and tubular. Pronotal disc large. Hypomera simple, without antennal grooves. Metacoxal plates large. Protibiae with only one prominent spur. Tarsomeres 4 simple. Elytra weakly striate.

Remarks. The new genus is similar to extant *Jenibuntor* Muona (Fig. 3A–C) and *Euryptychus* LeConte (Fig. 3D–F; fig. 1 in Seung *et al.*, 2017). However, it can be easily differentiated from *Jenibuntor* and *Euryptychus* primarily based on its relatively large pronotal disc. In *Jenibuntor* and *Euryptychus* the length of pronotum along the middle is shorter than one third of the elytral length, while in *Muonabuntor* the length of pronotum along the middle is distinctly longer than one third of the elytral length. The metacoxal plates of *Muonabuntor* also appear to be larger than that of *Jenibuntor*.

***Muonabuntor grandinotalis* Li, Tihelka & Cai sp. nov.**
(Figs 1, 2)

Material. Holotype, NIGP173376, sex unknown.

Etymology. The specific name refers to its relatively large pronotal disc.

Diagnosis. As for the genus.

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

Description. Body oblong, 6.0 mm long and 2.2 mm wide, covered with short hairs.

Head transverse; frons without median carina. Eyes large, without interfacetal setae. Antennae with 11 antennomeres; antennomere 1 (scape) elongate and stout; antennomere 2 shorter, inserted apicolaterally into scape; antennomere 3 elongate and slender; antennomeres 4–5 subequal, shorter than antennomere 3; antennomeres 6–8 subequal, shorter than antennomere 5; antennomere 9–11 elongate and tubular, approximately symmetrical, forming a distinct club; antennomere 9 about 3.4 times as long as wide; antennomere 10 about 0.75 times as long as antennomere 9; apical antennomere fusiform, about 1.5 times as long as antennomere 10.

Pronotal disc large, about 1.6 times as wide as long along the middle, without distinct depressions; sides converging anteriorly; posterior angles strongly acute and produced posteriorly. Elytra about 1.8 times as long as wide combined, about 2.7 times as long as pronotal disc along the middle, subparallel-sided, gradually narrowed in the posterior half; elytral striae inconspicuous, without visible punctures.

Prosternum subtrapezoidal, with curved sides, and slightly widened anteriorly; prosternal process narrow, tapered posteriorly, apically acute, fitting into mesoventral cavity. Hypomera simple, without notosternal or lateral



FIGURE 1. General habitus of *Muonabuntor grandinotalis* **gen. et sp. nov.**, holotype, NIGP173376, under incident light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

antennal grooves; sides unparallel, converging anteriorly. Metaventricle without discrimen; mesotarsal grooves absent. Metacoxal plates large, triangular, gradually expanded medially. Protibiae with only one prominent spur. Tarsomeres 4 simple, not bilobed.

Abdomen with five connate ventrites. Ventrite 1 clearly longest, 1.3 times as long as the following segment, lacking metatarsal grooves. Ventrites 2–4 gradually narrowed apically. Ventrite 5 simply rounded at apex.

Discussion

Comparison between Muonabuntor gen. nov. and similar genera

Among all extant Eucnemidae, some of the species in *Phlegon* Laporte, *Euryphlegon* Otto, *Jenibuntor* and *Euryptychus* are known to possess simple hypomera and tubular antennomeres 9–11 (Muona, 1993a; Otto, 2017). The Neotropical genera *Phlegon* and *Euryphlegon* have bilobed tarsomere 4 (Otto, 2017), which distinctly differs

from *Muonabuntor* **gen. nov.** *Phlegon* also have two protibial spurs (Muona, 1993a), while only one prominent protibial spur can be seen in *Muonabuntor*. A lateral spine on the scape is present in *Euryphlegon* (Otto, 2017), while such structure is absent in *Muonabuntor*. The new genus is more similar to the Australian genus *Jenibuntor* (Fig. 3A–C) and the cosmopolitan genus *Euryptychus* (Fig. 3D–F; fig. 1 in Seung *et al.*, 2017). Both *Jenibuntor* and *Euryptychus* have simple tarsomere 4 and protibia with one apical spur (Muona, 1993a). In fact, *Jenibuntor* and *Euryptychus* are very alike in morphology. The perhaps only major difference between the two genera is the shape of male genitalia: *Jenibuntor* has dorsal basal struts on median lobe, while such struts are absent in *Euryptychus* (Muona, 1993). Unfortunately, the reproductive organ of our fossil specimen is not visible. Therefore, a more meaningful comparison between genitalia of *Muonabuntor* and extant species would be currently impossible.

Muonabuntor can be easily differentiated from the only eucnemid reported from Burmese amber (*Cenomana clavata* Otto) based on its general body shape and antennal morphology. While the body of *Cenomana* is more or less parallel-sided, the pronotum and elytra of the present

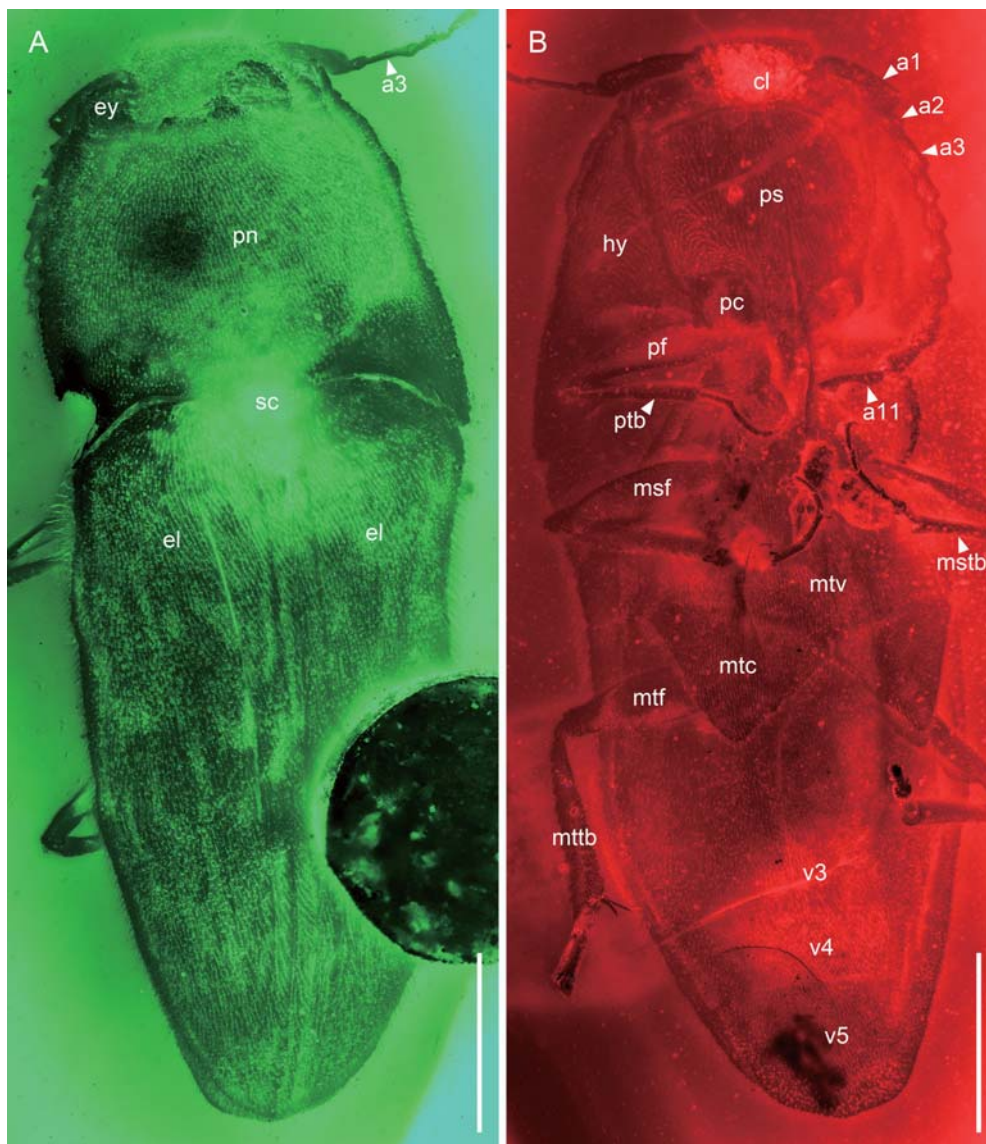


FIGURE 2. General habitus of *Muonabuntor grandinotalis* gen. et sp. nov., holotype, NIGP173376, under widefield fluorescence. **A**, Dorsal view. **B**, Ventral view. Abbreviations: a1–3,11, antennomeres 1–3,11; cl, clypeus; hy, hypomeron; msf, mesofemur; mstb, mesotibia; mtc, metacoxa; mtf, metafemur; mttb, metatibia; mtv, metaventrite; pc, procoxa; pf, profemur; pn, pronotal disc; ps, prosternum; ptb, protibia; sc, scutellum; v3–5, ventrites 3–5. Scale bars: 1 mm.

fossil are widest basally and narrow distally. *Muonabuntor* moreover differs from *Cenomana* in being larger (the body length of *C. clavata* is 3 mm), antennomeres 9–11 not distinctly asymmetrical, median pronotal groove absent, and elytra only weakly striate (strongly striate in *C. clavata*).

Notes on the classification of false click beetles

Muona (1993a) performed a cladistic analysis of extant Eucnemidae based on 52 morphological characters (Fig. 4A). He rejected, however, numerous branches of the cladogram without providing reasonable explanations, and manually redrew a tree of Eucnemidae (Fig.

4B). The subfamily- and tribe-level classification for Eucnemidae in Muona (1993a) was completely based on such a manually drawn tree, which was not resulted from a valid phylogenetic analysis at all. For example, the “monophyletic” Melasinae and Macraulacinae in the tree were both paraphyletic, or even polyphyletic in his cladistic analysis. Euryptychini occupied a relatively basal position in the parsimonious tree, while it was placed as a more derived branch within Macraulacinae in the manually drawn tree.

Even more unfortunately, neither the morphological parsimonious tree nor the tree manually drawn by Muona (1993a) was supported by recent molecular phylogenetic analyses (Seung, 2017). Even though only few genes

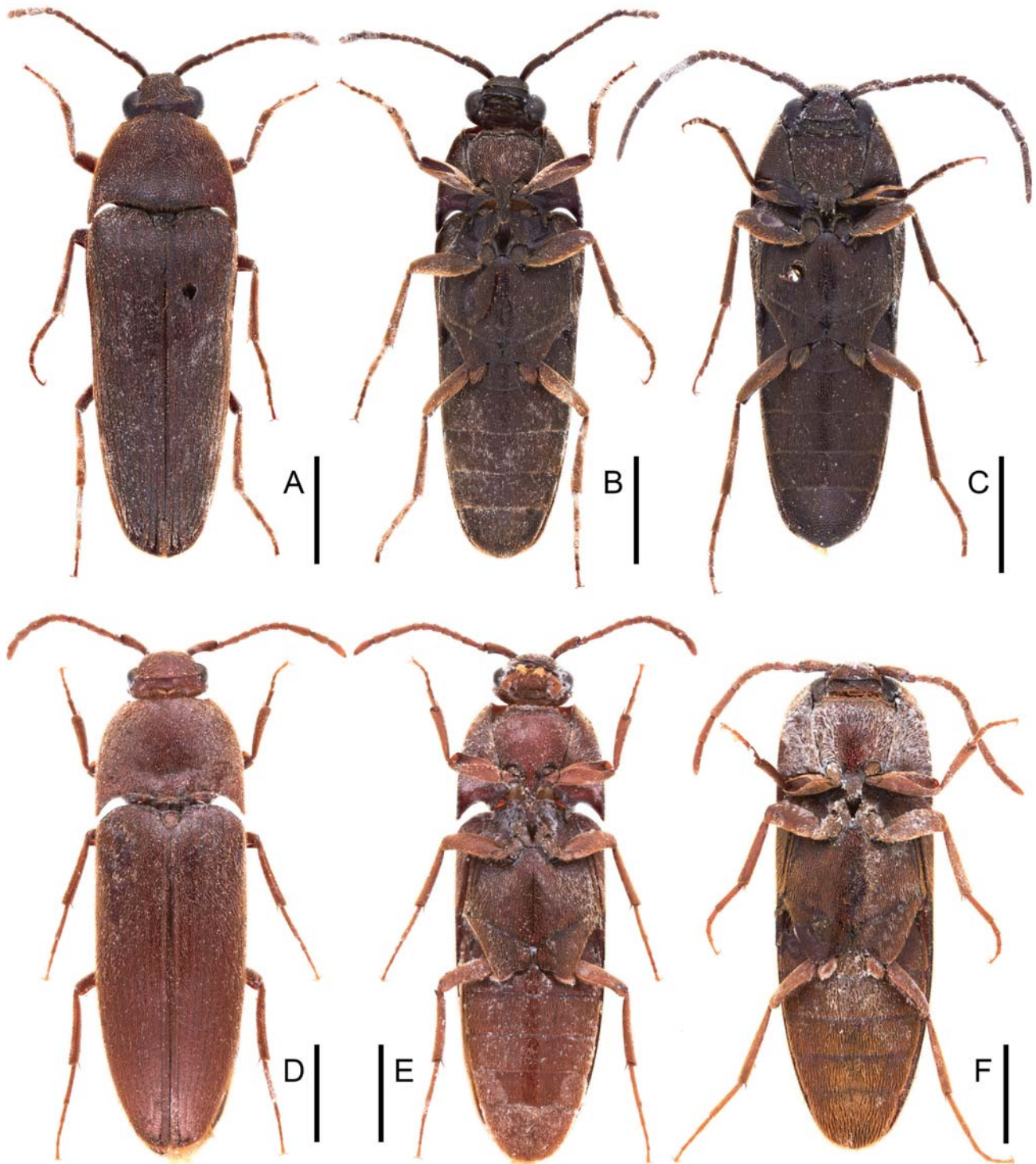


FIGURE 3. Extant *Jenibuntor* and *Euryptychus* preserved in Australian National Insect Collection. **A–C**, *Jenibuntor tabang*. **A**, Female, dorsal view. **B**, Female, ventral view. **C**, Male, ventral view. **D–F**, *Euryptychus concolor*. **D**, Female, dorsal view. **E**, Female, ventral view. **F**, Male, ventral view. Scale bars: 3 mm in **A–C**, 2 mm in **D–F**.

and taxa were sampled in the molecular analyses, the results nevertheless provided important insights for the true phylogeny of Eucnemidae (Fig. 4C). Melasinae and Macraulacinae defined by Muona (1993a) were both proved to be paraphyletic. Dirhagini was closely

related to Macraulacinae, rather than other tribes in Melasinae. Euryptychini was separated from other clades in Macraulacinae, and appeared to be closely related to Epiphanini. Therefore the current higher level classification system of Eucnemidae primarily based on Muona (1993a)

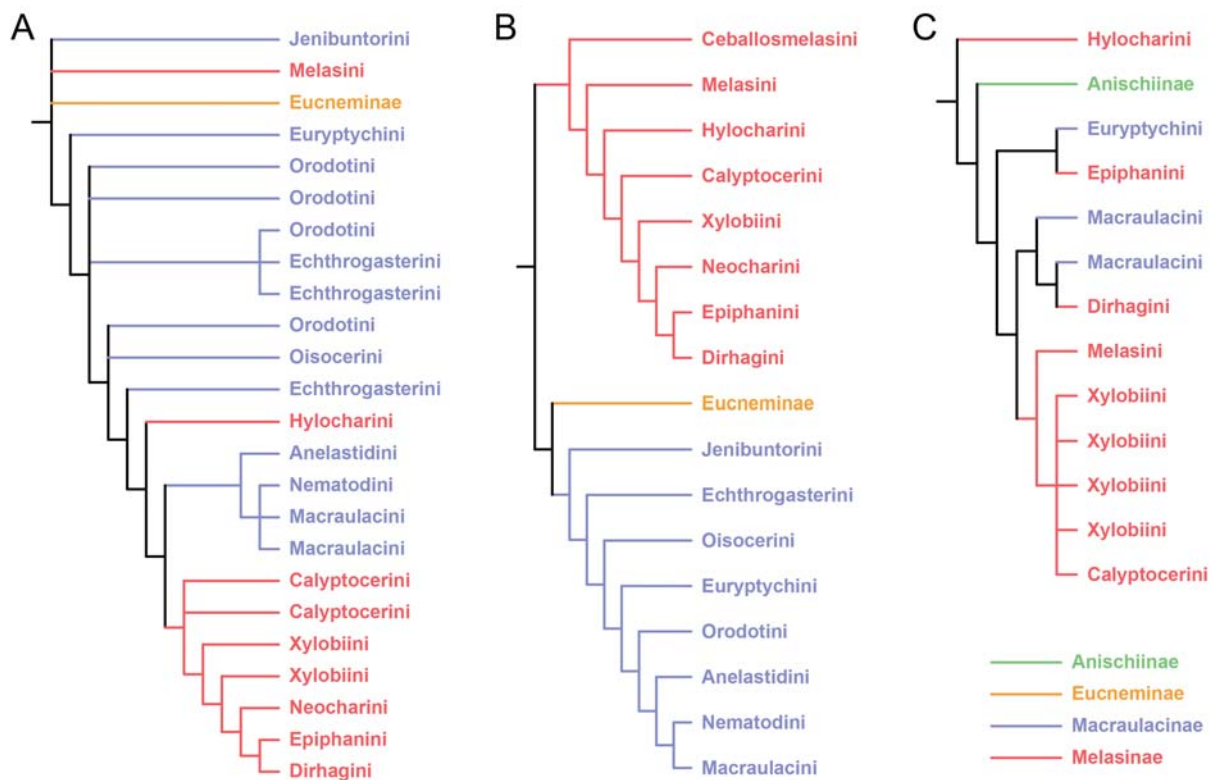


FIGURE 4. Comparison between morphological and molecular phylogeny of Melasinae and Macraulacinae (Eucnemidae), with circumscription of subfamilies and tribes following Muona (1993a), except for Anischiinae, which was not treated there. **A**, Morphological parsimonious tree by Muona (redrawn based on fig. 281 in Muona, 1993a). **B**, Manually drawn tree by Muona (redrawn based on fig. 282 in Muona, 1993a). **C**, Molecular Bayesian tree by Seung, with incomplete taxon sampling (redrawn based on fig. 10A in Seung, 2017).

is quite problematic. On the other hand, it has to be pointed out that Seung's phylogeny was based on only three gene fragments analysed with a site-homogeneous model, which has been shown to be prone to long-branch attraction artefacts (Lartillot *et al.*, 2007; Pisani *et al.*, 2015; Cai *et al.*, 2020). More extensive molecular studies sampling a wider range of taxa and genes will be necessary to elucidate the internal relationships within Eucnemidae. It would be impossible to properly discuss the systematic position of the fossil without a correct phylogenetic basis for the family. Thus here we decide not to place our new fossil genus *Muonabuntor* into any subfamily or tribe.

The fossil record of Eucnemidae

The oldest fossil record of false click beetle comes from the Upper Jurassic Talbragar Fish Bed in New South Wales, Australia (*ca.* 152 Ma; Oberprieler *et al.*, 2016). *Beattieellus jurassicus* Oberprieler *et al.* cannot be placed into any eucnemid subfamily with certainty due to its incomplete preservation. At least three other possible eucnemids were also mentioned from that deposit, but

these have not been formally described due to their poor state of preservation.

Chang *et al.* (2016) described *Palaeoxenus sinensis* Chang *et al.* based on an exquisitely preserved larval specimen from the Lower Cretaceous Yixian Formation in China. The fossil larva resembles the extant genus *Palaeoxenus* belonging to the monogeneric subfamily Palaeoxeninae which is today restricted to the mountain ranges of southern California. Chang *et al.* (2010) further reported several fossil elaterids from Yixian Formation in China, and placed them in a fossil tribe Desmatini erected by Dolin (1975). However, we think that at least some of these fossils may not belong to Elateridae at all. Indeed, the status of Desmatini itself is quite dubious. Fossils in Desmatini are characterized by highly developed metacoxal plates (Dolin, 1975; Chang *et al.*, 2010), a critical character not found in all extant Elateridae but common in eucnemids. Some extant and fossil eucnemids, including *Muonabuntor*, have enlarged club-forming antennomeres 9–11. The antennomeres 9–11 of *Apoclion antennatus* Chang *et al.* are also enlarged and form a distinct club. Such a characteristic antennal morphology and the body shape are very similar to females of extant

Jenibuntor. Additionally, based on the recently published time tree of beetles (McKenna *et al.*, 2019), Eucnemidae appears to have a much longer history than Elateridae. It is more appropriate to expect eucnemids, rather than elaterids to be found in the Lower Cretaceous Yixian Formation. The poorly preserved *Cretopoena gratshevi* Alexeev from the Lower Cretaceous Shar-Tolgoy locality in Mongolia originally described as a member of Eucnemidae (Alexeev, 2008), is another fossil that is difficult to place, since it lacks antennae and much of the fine morphological detail necessary to separate Eucnemidae from similar families such as Elateridae. It is thus formally excluded from the family and treated as Elateriformia *incertae sedis*.

The fossil record of Eucnemidae in Cretaceous ambers is sparse. Burmese amber has to date yielded two eucnemids, *C. clavata* (Otto, 2019) and *M. grandinotalis* (this study). Two undescribed Burmese amber eucnemids have been mentioned from the collections of the Natural History Museum in London by Rasnitsyn & Ross (2000). Grimaldi & Engel (2005) illustrated a group of putative eucnemids from Cretaceous New Jersey amber, which actually belong to the related family Cerophytidae (Chang *et al.*, 2016).

The Cenozoic fossil record of Eucnemidae is considerably richer than the Cretaceous. The Lower Eocene *Potergites senectus* Britton from London Clay is most likely an eucnemid, but its systematic position within the family is uncertain (Muona, 1993b). The largest number of species is known from Eocene Baltic and Oligocene Bitterfeld ambers; this fauna has been reviewed in detail by Muona (1993b). “*Eucnemis*” *antiquatus* Wickham, “*Microrhagus*” *fossilis* (Wickham), and “*Microrhagus*” *miocenicus* Wickham from the Priabonian Florissant lakebeds in Colorado, USA lack diagnostic features of Eucnemidae (Muona, 1993b) and should be treated as Elateriformia *incertae sedis*. “*Fornax*” *relictus* Wickham and “*Microrhagus*” *vulcanicus* Wickham from the same deposit appear to be eucnemids, although their exact position within the family and generic affiliation remain obscure (Muona, 1993b). Scudder (1876) reported a fossil from the Green River Formation in the western United States, and placed it in the now eucnemid genus *Epiphaniis* Eschscholtz. However, the illustration of this fossil lacks detail (plate 5, figs 113, 114 in Scudder, 1890), making it hard to confirm its affiliation with the family. Miocene Dominican amber also yielded a single extinct eucnemid genus (*Lissantauga* Poinar, 2013).

Undescribed putative eucnemids are known from the Eocene limnic sediments of the Eckfeld Maar in Germany, late Eocene Bembridge Marls of the Isle of Wight, Late Oligocene Enspel Lagerstätte in Germany, as well as the uppermost Oligocene of Aix-en-Provence in southern France (Wappler, 2003; Wedmann *et al.*,

2010; Kirejtshuk *et al.*, 2019). Subfossil eucnemids have also been recovered from Quaternary sediments (*e.g.*, Whitehouse, 2006).

Acknowledgements

We are grateful to Qi-Chao Su for help in translating the Russian literature. Financial support was provided by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDB18000000), the National Natural Science Foundation of China (41672011, 41688103), and the Second Tibetan Plateau Scientific Expedition and Research project (2019QZKK0706).

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