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First false darkling beetle from mid-Cretaceous Burmese amber (Coleoptera: Melandryidae)

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The false darkling beetles (Melandryidae) are a small but morphologically diverse and taxonomically problematic family belonging to the polyphagan superfamily Tenebrionoidea. The Mesozoic record of Melandryidae is sparse, with only three described species. A new genus and species, *Longicrusa jaracimmani* gen. et sp. nov., is described here from the mid-Cretaceous Burmese amber (ca 99 Ma), representing the oldest false darkling beetle described to date. The modified maxillary palpi of *L. jaracimmani* gen. et sp. nov. suggest that the species probably fed on fungi, and its prominent pectinate spurs indicate that the ability to jump had already developed in false darkling beetles by the mid-Cretaceous. A checklist of fossil melandryid beetles is provided.

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Key words: Tenebrionoidea, Melandryidae, Mesozoic, fossil, palaeoecology, Myanmar.

WITH OVER 420 extant species, the Melandryidae represent a small and poorly known beetle family belonging to the diverse polyphagan superfamily Tenebrionoidea (Nikitsky & Pollock 2010). The false darkling beetles, as they are often referred to, have a global distribution but are most diverse in the tropics (Pollock 2002). Melandryids are thought to be mycetophagous, with the larvae occurring under the bark of dead trees or in fungal fruiting bodies (Hinson 2016). The adults are typically collected on mature and rotting trees, under bark and in wood. Imagoes of extant representatives have also been collected on flowering plants (Konvička 2016), indicating that they may feed on nectar. Some species that attack healthy trees are regarded as pests (Camilli *et al.* 2012). At least some false darkling beetles are able to escape danger by jumping (Pollock 2002).

Melandryids have traditionally been a loosely defined and problematic group that served as a 'waste bin' for unusual tenebrionid species. Historically, various members of the families Pythidae, Pyrochroidae, Scraphiidae, Stenotrachelidae, Synchronidae, and Tetratomidae were placed among the false darkling beetles (Crowson 1955, 1966, Arnett 1968, Lawrence 1991). At present, Melandryidae includes two subfamilies, Melandryinae and Osphyinae, with the

former comprised of eight tribes and the latter containing just two genera (Nikitsky & Pollock 2010). Pollock (2002) concluded that the classification of the family is in disarray, especially at the tribe level, and in need of urgent revision. Indeed, molecular studies carried out over the past ten years have consistently failed to recover Melandryidae as a monophyletic group (Levkaničová 2009, Gunter *et al.* 2014, Zhang *et al.* 2018).

The enigmatic status of the family is not helped by the sparsity of the melandryid fossil record (Table 1). It has been estimated that the Melandryidae originated in the Early Cretaceous, at approximately 130–140 Ma (Zhang *et al.* 2018), although only three Mesozoic representatives of the family have been described to date (Batelka *et al.* 2018). *Archaeoxylita zherichini* Nikitsky, 1977 is known from amber of the Upper Cretaceous Kheta Formation, Russia, whereas *Archaeserropalpus cretaceus* Nikitsky, 2002 and *Pseudocuphosis tristis* Nikitsky, 2002 were described from the Upper Cretaceous New Jersey amber. A possible melandryid beetle from the Lower Cretaceous Purbeck Limestone of Dorset, England, was mentioned by Ponomarenko *et al.* (2000) but not formally described, and some undescribed specimens are known from the Lower Cretaceous Yixian Formation of China (Kirejtshuk *et al.* 2010). All other fossil false darkling beetles have been reported from Paleogene deposits.

Table 1. Overview of fossil false darkling beetles described to date (Melandryidae).

Taxon	Deposit	Age
CRETACEOUS		
<i>Longicrusa jaracimrmani</i> Tihelka, Huang & Cai gen. et sp. nov.	Burmese amber, Myanmar	Albian–Cenomanian
<i>Archaeoserropalpus cretaceus</i> Nikitsky, 2002	New Jersey amber, New Jersey, USA	Turonian
<i>Pseudocuphosis tristis</i> Nikitsky, 2002	New Jersey amber, New Jersey, USA	Turonian
<i>Archaeoxylita zherichini</i> Nikitsky, 1977	Kheta Formation amber, Russia	Santonian
EOCENE		
<i>Cicindelopsis eophilus</i> Cockerell, 1921	Green River Formation, Colorado, USA	Ypresian
<i>Abderina helmii</i> Seidlitz, 1898	Baltic amber, Poland	Priabonian
<i>Melandrya colorata</i> Scudder, 1900	Florissant Formation, Colorado, USA	Priabonian
<i>Orchesia rasnitsyni</i> Nikitsky, 2011	Rovno amber, Ukraine	Priabonian
<i>Abdera hoffeinsorum</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Abdera rikojotensis</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Electroabdera marisbaltici</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Serropalpus ingemmescus</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Serropalpus ryzhkovianus</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Serropalpus vivax</i> Alekseev, 2014	Baltic amber, Baltic Sea coast	Priabonian
<i>Orchesia turkini</i> Alekseev & Bukejs, 2012	Baltic amber, Russia	Priabonian
<i>Orchesia canaliculata</i> Alekseev & Bukejs, 2015	Baltic amber, Russia	Priabonian
<i>Quasianisoxya curonensis</i> Alekseev, 2015	Baltic amber, Russia	Priabonian
<i>Microscapha andrzeji</i> Bukejs & Alekseev, 2015	Baltic amber, Poland	Priabonian

Beetles of the family Melandryidae have not been described previously from the Burmese amber (Ross 2019), although Rasnitsyn & Ross (2000) listed two undescribed specimens in the collections of the Natural History Museum in London. Here we describe the first false darkling beetle from Burmese amber. The new species represents the earliest false darkling beetle described to date.

Geological background

Burmese amber contains what is thought to be the world's most diverse Cretaceous entomofauna, and thus offers a unique window into the ecology of Mesozoic insects (Cai *et al.* 2018, 2019, Yin *et al.* 2018). The amber specimen described here was obtained from a mine site at the summit of Noiye Bum (26°20'N, 96°36'E) in the Hukawng Valley, Kachin State, northern Myanmar (Cruickshank & Ko 2003). The resin was most likely secreted by Araucariaceae or Pinaceae trees in a humid tropical rainforest (Poinar *et al.* 2007, Dutta *et al.* 2011). The precise age of the Burmese amber remains a hotly debated topic. Cockerell (1917) was the first to work extensively on Burmese amber insects and insightfully proposed a Cretaceous age. Renewed interest in, and new palaeontological investigations into, the Burmese amber at the start of the 21st century narrowed the interpreted age range down to the mid-Cretaceous (Grimaldi *et al.* 2002, Ross *et al.* 2010). The amber-bearing horizon was radiometrically dated to approximately 99 Ma (Shi *et al.* 2012), but this should be taken as a minimum age (Mao *et al.* 2018). A recent discovery of an ammonite in the amber indicates that the resin was secreted no earlier than the late Albian (Yu *et al.* 2019). The presence of bivalve borings (Smith & Ross 2018) suggests that the fossil resin was secondarily redeposited.

Material and method

The amber piece was prepared using a handheld cutter, different grades of sandpaper, and rare-earth powder (Cai & Huang 2014a). Habitus images of the specimen were taken using a Canon EOS 5 D Mark III digital camera equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and attached Canon MT-24EX twin flash. The images were processed in Adobe Photoshop. The holotype is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS), Nanjing, China. The publication LSID is: urn:lsid:zoobank.org:pub:1A6D7681-969B-4B18-B2D8-F8902790D9B6.

Systematic palaeontology

Order COLEOPTERA Linnaeus, 1758
 Superfamily TENEBRIONIDEA Latreille, 1802
 Family MELANDRYIDAE Leach, 1815
 Subfamily MELANDRYINAE Leach, 1815
 Tribe SERROPALPINI Latreille & Tome, 1829

Longicrusa gen. nov.

Diagnosis. Head entirely concealed from above by pronotum; apical maxillary palpomere enlarged, with a sensory structure; apical antennomere with a row of setate spines; mesotibia, metatibia, three basal mesotarsi, and all metatarsi with transverse rows of spines; abdominal ventrites bilobed apically, shortest medially.

Type species. *Longicrusa jaracimrmani* sp. nov.

Etymology. From the Latin words 'longus', for long, and 'crus', for leg, in reference to the elongated legs of the type species.

***Longicrusa jaracimrmani* sp. nov. (Figs 1–3)**

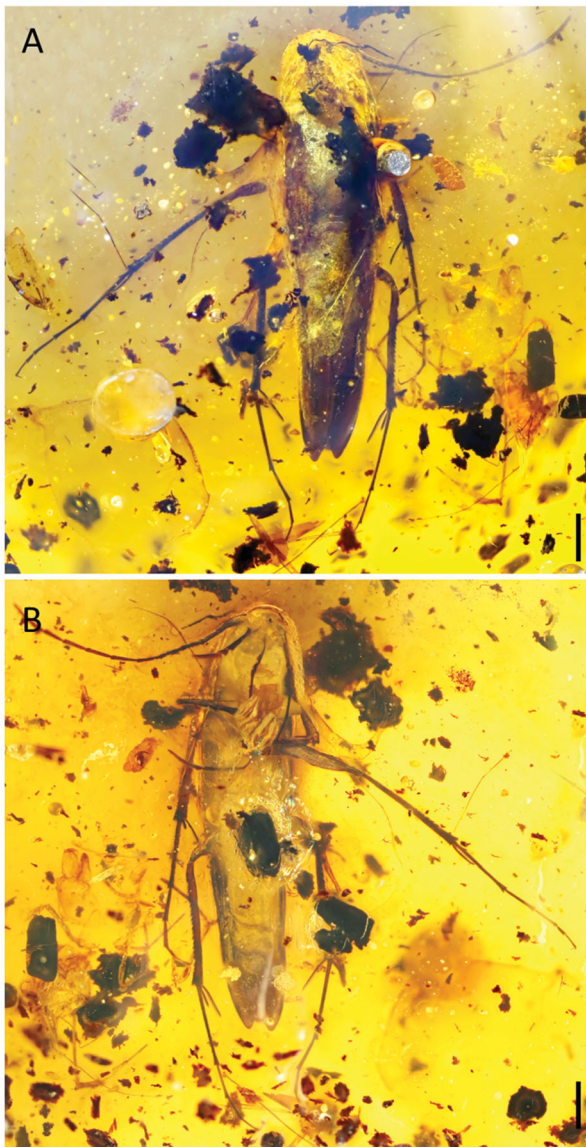


Fig. 1. Habitus photographs of *Longicrusa jaracimrmani* sp. nov. (holotype, NIGP170802): **A**, Dorsal view; **B**, Ventral view. Scale bars = 1 mm.

Diagnosis. As for genus, with additional characters: body length 9.26 mm, filiform maxillary palpi with apical segment almost parallel sided in its basal two thirds and narrowing gradually in apical third.

Description. Body elongate, subcylindrical, somewhat narrowed posteriorly (Fig. 1). Body length 9.26 mm, width across elytral base 2.13 mm. Body surface apparently more or less glabrous; short, sparse hairs visible on elytral margin.

Head not visible from above, concealed under pronotum and entirely covered in white foam (Fig. 2A). Maxillary palpi elongated, four segmented, filiform. Maxillary palpomere 1 slender, partially obscured by foam; maxillary palpomere 2 elongate and slightly widening apically, 3.0 times longer than following segment; maxillary palpomere 3 short, apical

end uneven with single row of setae; maxillary palpomere 4 enlarged and more-or-less parallel sided in basal two thirds but narrowing gradually in apical third, 3.4 times longer than preceding segment, covered on one side with dense translucent sensory structures with dense setae (Fig. 2B). Antennae 11-segmented, filiform, extending to over half of the elytral length. Antennomere 1 (scape) elongate, as wide as following segment; antennomere 2 (pedicel) representing 0.4 times length of following segment; antennomeres 3 and 4 subequal and each 1.9 times longer than pedicel; antennomeres 5–8 each 1.1 times longer than antennomere 4; antennomere 9 constituting 0.9 times length of preceding segment; antennomere 10 1.1 times longer than preceding segment; antennomere 11 twice as long as preceding segment, with single row of unequally spaced lateral triangular spines, each spine ending with one seta (Fig. 2C). Number of spines on apical antennomere unequal on the two antennae, with one segment terminating with a single curved apical protrusion (Fig. 2C), and the other broadly rounded.

Pronotum, mesothorax, scutellum, and basal abdomen obscured by cloudy foam. Pronotum approximately 1.3 times longer than wide, broadest basally. Elytra 3.3 times as long as the combined width, broadest basally and tapering apically, exposing just the tip of apical ventrite, lacking rows of punctures or stria, apparently glabrous with only sparse short pubescence on elytral margin. Elytral apices rounded, separated by distinct gap.

Legs long, mesothoracic leg measuring 8.14 mm in length, or 0.88 times body length. Femora wide and flattened, broadest medially. Meso- and metatibia with rows of spines and strong bristles (Fig. 2D). Tibia as thick as femora at apex, ending with pair of elongate spurs and comb of large setae or spines. Mesotibia 1.6 times longer than mesotarsomere 1, metatibia 1.5 times longer than metatarsomere 1. Tibial spurs pectinate, unequally long with shorter spur half as long as longer spur; the longer of two meso- and metatibial spurs representing 0.4–0.5 times length of tarsomere 1 (Fig. 2E). Tarsal formula 5-5-4. Mesotarsomeres 1–3 and metatarsomeres 1–4 with rows of spines (Fig. 3A: tas). Mesotarsomere 1 2.0 times longer than following segment; mesotarsomere 2 1.3 times longer than following segment; mesotarsomere 3 2.8 times longer than following segment; mesotarsomere 4 shortened, constituting 0.6 times length of apical tarsomere; mesotarsomere 5 constituting 0.25 of basal mesotarsomere. Metatarsomere 1 elongate, 2.4 times longer than following segment; metatarsomere 3 constituting 0.9 times of preceding segment length; metatarsomere 4 constituting 0.9 times of previous segment length. Tarsal base always thinner than apex of preceding tarsomere with tarsi widening apically, tarsal apices bearing single comb of spines or large setae. Claws simple, without teeth or membranous lobes.

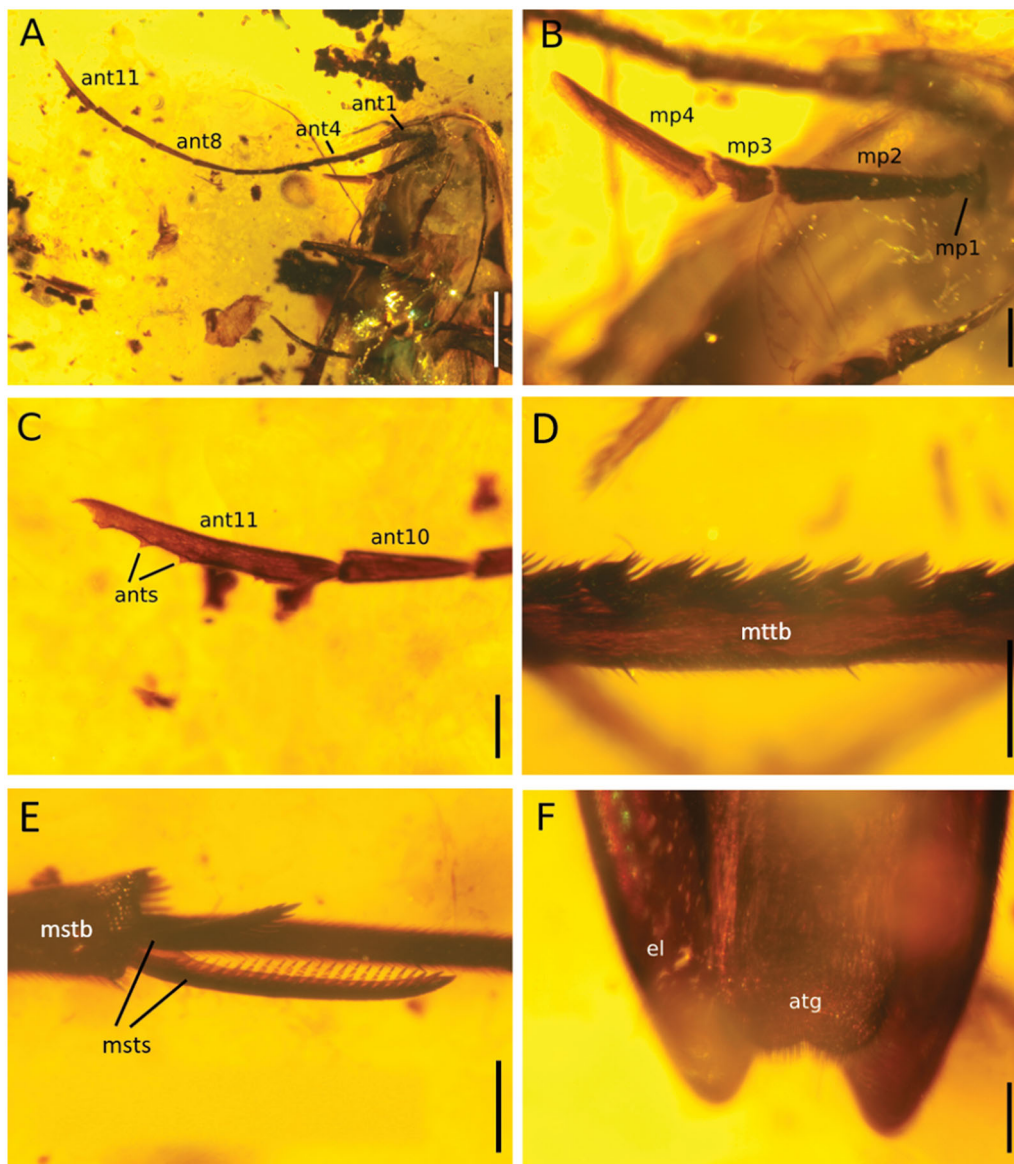


Fig. 2. Morphological details of *Longicrusa jaracimrmani* sp. nov. (holotype, NIGP170802): **A**, Head and mesothorax in ventral view, scale bar = 1 mm; **B**, Maxillary palpi, scale bar = 200 μ m; **C**, Apical antennomere, scale bar = 200 μ m; **D**, Metatibial surface, scale bar = 200 μ m; **E**, Mesotibial spurs, scale bar = 200 μ m; **F**, Apical tergite, scale bar = 200 μ m. Abbreviations: ant1–11, antennomere 1–11; ants, antennal spines; atg, apical tergite; el, elytra; mp1–4, maxillary palpomere 1–4; mstb, mesotibia; msts, mesotibial spurs; mttb, metatibia.

Abdomen apparently five segmented, widest basally and clearly narrower than elytra. Ventrites subequal, overlapping, shortening apically, and bilobed, being longest laterally and shortest medially (Fig. 1B). Apical ventrite at base approximately half the width of the basal ventrite. Apical tergite bilobed, entirely covered with long and dense pubescence (Fig. 2F).

Etymology. The species is named in honour of Jára Cimrman, a Czech theatre hero.

Holotype. NIGP170802. Male, as indicated by the broad, bilobed apical tergite entirely covered with long dense pubescence (Konvička 2014).

Type locality and age. Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian–Cenomanian.

Discussion

Systematic position

Longicrusa jaracimrmani gen. et sp. nov. can be placed into the family Melandryidae on the basis of its 5-5-4 tarsal formula, filiform antennae consisting of 11 antennomeres, well-developed and distinctly modified maxillary palpi, well-developed elytra, large, unequal and pectinate tibial spurs, simple tarsi without teeth or membranous lobes, five ventrites with the penultimate segment not significantly shortened and the apical segment not extended into a spine (Nikitsky 2002, Lawrence & Ślipiński 2013). Further, it can be placed into the tribe Serropalpini based on its elongate body shape, modified maxillary palpi, and large tibial spurs (Pollock 2002). The new species differs from all hitherto known members of the tribe Serropalpini in the

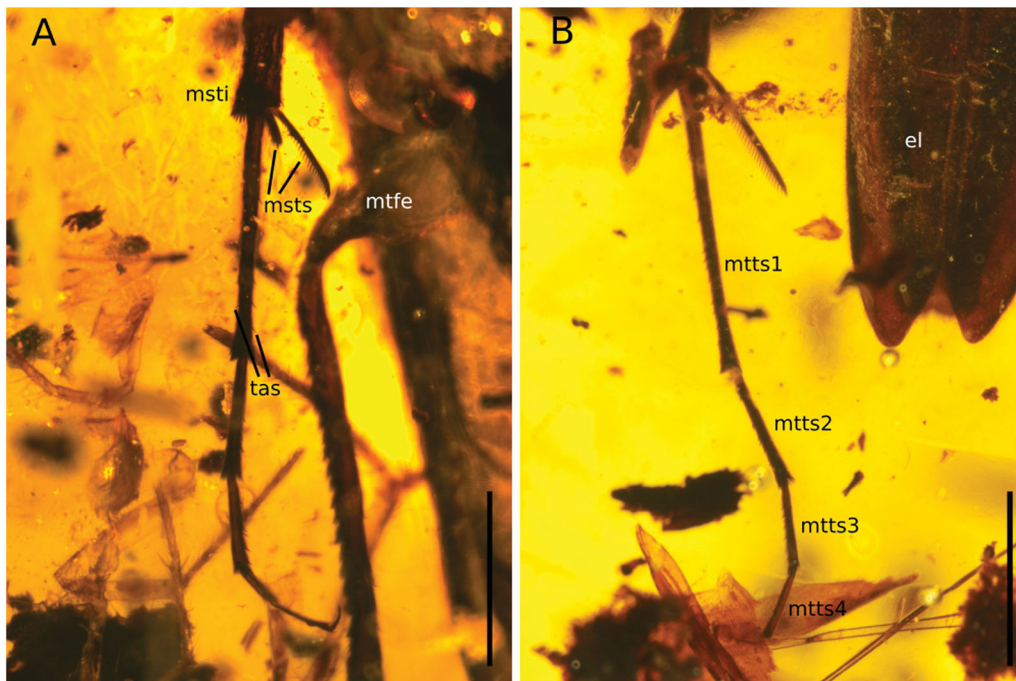


Fig. 3. Morphological details of *Longicrusa jaracimrmani* sp. nov. (holotype, NIGP170802): **A**, Mesothoracic leg; **B**, Metathoracic leg. Scale bars = 1 mm. Abbreviations: el, elytra; msti, mesotibia; msts, mesotibial spurs; mtfe, metafemur; mmts 1–4, metatarsi 1–4; tas, rows of tarsal spines.

combination of head not visible from above, toothed apical antennomeres, modified apical maxillary palpi, bilobed ventrites, and rows of spines located on the mesotibia, metatibia, basal three mesotarsi, and basal four metatarsi. Although transverse rows of spines or large bristles are present on the mesotibial edge of many serropalpines (Nikitsky & Pollock 2010), their location in *L. jaracimrmani* gen. et sp. nov. is unique.

Palaeoecology

Our knowledge of Serropalpini biology is scant and comes mostly from studying modern representatives of the cosmopolitan genus *Serropalpus* Hellenius, 1786 (Mank 1939, Moore 2015). The larvae tunnel in xylem, with an apparent habitat preference for conifers infested with wood rot (Lawrence 1991). The short-lived adults are crepuscular to nocturnal, actively running on tree trunks on warm evenings (Bletchly 1955, Hoebeke & McCabe 1977).

Large, pectinate, and sometimes unequally long tibial spurs (Fig. 2E) are present in a range of serropalpines, including the new species. It is possible that this interesting feature is responsible for the melandryid beetles' well-known jumping ability (Sasaji 1995, Pollock 2002). Melandryids lack the metafemoral spring present in other jumping beetles, but can jump by depressing their hind legs strongly against the substrate with the aid of their metatibial spurs and then quickly releasing (Furth & Suzuki 1992, Richards & Davies 1997).

Enlarged apical palpi with sensory organs are found in some extant coleopterans including oxyporine rove beetles and erotyid beetles (Hanley & Goodrich 1995, Cai & Huang 2014b, Cai *et al.* 2017). These taxa are fungivorous and probably use their modified palpi for recognizing and evaluating the quality of fungi (Hanley & Goodrich 1995). It is probable that the unusual palpi and apical antennomeres with short setate spines of *Longicrusa jaracimrmani* gen. et sp. nov. (Fig. 2B, C) fulfilled a similar sensory function.

Taphonomy and fossilization

Despite their high levels of activity on coniferous trees, false darkling beetles are rare in the fossil record and only infrequently encountered in amber. It is probably due to their large size and good flight abilities that these beetles are able to escape resin flow and consequently become entombed only rarely. The specimen studied herein is surrounded by wood and arthropod body fragments in the amber matrix, suggesting that it may have been removed from a tree hollow by a predator. A greater part of the beetle is also covered by a foamy white film. This is not an uncommon phenomenon in amber beetles small and large; some other melandryid inclusions are also cloaked in a similar white film (e.g., Alekseev & Bukejs 2015). This white film, commonly referred to as 'Verlumpung' (Penney & Jepson 2014), is particularly prevalent in some amber deposits, such as the Baltic amber, and probably consists of gases produced during the decomposition of the cadaver. Since the bodies of larger

insects have a higher water content, these specimens are more likely to undergo complete or partial decay in resin, as appears to have been the case in the present specimen.

Conclusions

The first false darkling beetle from mid-Cretaceous Burmese amber is described. *Longicrusa jaracimrmani* gen. et sp. nov. probably inhabited conifers in the Burmese amber rainforest and fed on fungi, as suggested by the modified apical maxillary palpi. Just like many modern melandryids, it may have possessed the ability to escape danger by jumping. At present, *L. jaracimrmani* gen. et sp. nov. represents the world's earliest fully described false darkling beetle.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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