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SHORT COMMUNICATION

The first fossil false click beetle larva preserved in amber

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Abstract

We report a new and unusual beetle larva preserved in ca. 100 million-year-old Kachin amber. Larvae of many modern lineages of beetles are associated with wood, breaking it into smaller pieces or directly digesting it. With such a lifestyle, beetle larvae are important for carbon cycling. We can assume that this is not only the case in modern ecosystems, but was similar in the past. Yet, wood-associated beetle larvae seem so far rare in Kachin amber despite its otherwise rich record of many different ecotypes. Only recently, solid-wood-boring larvae and those living in decaying wood have been reported from this amber deposit. Larvae of the group Eucnemidae, false click beetles, which are also wood-associated, have so far been only known from sedimentary rock deposits. Here we report the first larva of a false click beetle preserved in amber. The fossil larva combines features of different modern lineages of Eucnemidae in a unique morphology that is not known in the modern fauna. The fossil adds to the growing number of wood-associated holometabolan larvae in Kachin amber and with this contributes to a more complete view on this now extinct community and ecosystem.

Keywords Cretaceous · Burmese amber · Eucnemidae · Carbon cycling · Wood borers · Larvae

Introduction

Coleoptera (beetles) has been interpreted as the most successful group of animals (e.g. McKenna et al. 2019). Although this statement is logically not fully correct (see discussion in Haug et al. 2016 for a similar statement on Insecta), beetles are indeed dominating terrestrial ecosystems concerning species numbers, number of individuals, and ultimately biomass. A key feature of the group Holometabola, of which Coleoptera is an ingroup, is the ecological differentiation between the early post-embryonic stages, also known as larvae (see discussion in Haug 2020) and the usually very different-appearing adult (Truman and Riddiford 2019). This effect should also have positively influenced the diversification of beetles. Indeed, beetle adults tend to be easily identified as beetles due to their rather stereotypic appearance, while beetle larvae are not as easily identified as such. Beetle larvae show a wide variation of morphologies and with this also ecological functions (Böving and Craighead 1931; Peterson 1957; Klausnitzer 1978).

Most larvae of the coleopteran group Eucnemidae, false click beetles, are associated with wood (Muona 2010). Many of them apparently feed on fungi within decaying wood. Some of the larvae are also able to bore into solid wood, and some of these larvae (Muona and Teräväinen 2020) resemble at least distantly those of the more commonly known jewel beetles (Németh and Otto 2016: p. 138), better known as roundheaded wood borers (cf. Eucnemidae: Böving and Craighead 1931: plate 81M; Peterson 1957: Fig. C17A, F, I; Klausnitzer 1978: p. 160, Fig. 22/7; Muona 2010: p. 66, Fig. 4.5.4E; Otto and Gruber 2016: p. 8, Fig. 1; Muona and Teräväinen 2020: p. 8, Fig. 6A; vs. Buprestidae: Volkovitsh and Bílý 2015: p. 177, Fig. 1, p. 183, Fig. 10, p. 189, Figs. 20–27; Wei et al. 2020: p. 150, Fig. 1B, C). Yet, those larvae of false click beetles that resemble jewel beetle larvae to a certain degree are easily recognisable as false click beetles by their outward curved mandibles (Muona and Teräväinen 2020: p. 8, Fig. 6B), not found in jewel beetles.

Other larvae of Eucnemidae are more vermiform in overall appearance (e.g. Muona 2010: p. 66, Fig. 4.5.4A–D; Otto

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2012a: p. 221, Fig. 1; Otto 2012b: p. 287, Fig. 1; Otto 2014: p. 332, Fig. 1; Otto 2015: p. 30, Fig. 1, p. 31, Fig. 20, p. 32, Fig. 25, p. 36, Fig. 38, p. 38, Fig. 43, p. 41, Fig. 52, p. 43, Fig. 61, p. 45, Fig. 66; Otto 2017: p. 8, Figs. 1, 2, p. 9, Fig. 6). Some larvae of Eucnemidae also have unusual heads with jagged anterior and lateral rims ('lateral teeth') (e.g. Muona 2010: p. 68, Fig. 4.5.6A, C; Otto 2012a: p. 221, Fig. 2; Otto 2014: p. 333, Fig. 2; Otto 2015: p. 30, Fig. 16, p. 31, Fig. 21, p. 33, Fig. 26, p. 37, Fig. 39, p. 39, Fig. 44, p. 41, Fig. 53, p. 44, Fig. 62, p. 46, Fig. 67; Muona and Teräväinen 2020: p. 4, Fig. 2A–E, p. 5, Fig. 3A–C, p. 6, Fig. 4A, p. 7, Fig. 5, p. 10, Fig. 7A–C, E). These heads are used to wedge into the already rotting wood until it gives way to access the fungi as food source. Also other body shapes are known, including, for example, fusiform larvae (Németh and Otto 2016: p. 143, Fig. 12).

False click beetles are known in the fossil record from various sedimentary deposits (Li et al. 2020) and from amber. Fossils within sedimentary deposits yielded eight species (Muona et al. 2020; Li et al. 2021). Different ambers include a single species from Miocene Dominican amber (Poinar 2013) and 22 species from Cretaceous Kachin amber, Myanmar (Otto 2019; Li et al. 2020; Muona 2020). Muona (1993) mentions no less than 38 species from Baltic amber (p. 15); additional fossils may represent even more species (Muona 1993). It is noteworthy that almost all fossils of false click beetles are adults. Only a single fossil larva preserved in a sedimentary rock deposit has been reported so far (Chang et al. 2016).

One might suggest that animals living inside wood instead of on it are less likely to be preserved in amber. Yet, some finds have clearly demonstrated that such larvae may also be preserved in amber, for example, a larva of the group Micromalthidae preserved in Cretaceous Lebanese amber (Kirejtshuk and Azar 2008). Just recently, wood-borer-type larvae of jewel beetles (Buprestidae) and possible long-horn beetles (Cerambycidae) have been reported in ca. 100 million-year-old Kachin amber, Myanmar (Haug et al. 2021). Likewise, wood-decomposing larvae of the group Scraptiidae have already been known from younger ambers (Haug and Haug 2019) and have now also been found in Kachin amber (Zippel et al. 2022). These finds demonstrated the possibility to have wood-associated larvae and potentially those of false click beetles preserved in amber. We here report a first larva of the group Eucnemidae from Kachin amber.

Materials and methods

Material

The single specimen from Cretaceous Kachin amber in the centre of this study comes from the collection of one of the authors (PM) and has the repository number BUB 3710. It originates from the Hukawng Valley, Myanmar and is about 100 million years old (possibly 99 million years; Cruickshank and Ko 2003; Shi et al. 2012; Yu et al. 2019).

Documentation method

The single specimen was documented on a Keyence VHX-6000 digital microscope. It was equipped with a ZST 20×–2000× objective. The specimen was documented in front of different backgrounds (white, black) as well as different illuminations (cross-polarized co-axial light, low-angle ring light) (Haug et al. 2013, 2018). Of these four combinations, the resulting images with the highest contrast were used for presentation.

Each of these images was recorded as a composite image, i.e. as a stack of shifting focus and subsequent fusion, and with several adjacent image details and stitching to a panorama image (Haug et al. 2011). Additionally, the images were recorded as HDR (cf. Haug et al. 2013). Subsequent processing of images and colour markings were performed with Adobe Photoshop CS2.

Description of the specimen

General

Elongate vermiform larva; total length approximately 5.3 mm, accessible in dorsal and ventral view (Fig. 1a–c). Differentiated into a head (Fig. 1d) and a trunk. Trunk composed of anterior region with three segments (thorax) and a posterior region (abdomen) (Fig. 1a–c) ending in a terminal end with paired protrusions (urogomphi?) (Fig. 1e).

Head

Head relatively small in comparison to the rest of the body, roughly square-shaped, about 0.27 mm long and wide (Fig. 1d). Appears strongly sclerotised and serrated, with four projections on each side. Antennae discernible, but minute, no details accessible (Fig. 1d). No mouthparts clearly discernible but presumed. Each lateral edge of head capsule with at least two setae.

Trunk (thorax + abdomen)

Trunk with twelve distinctive units, thorax with three (pro-, meso- and metathorax) and abdomen with nine. Prothorax and mesothorax very prominent, widest segments of the trunk. Prothorax almost semicircular in dorsal view; anteriorly as wide as head (0.27 mm), posteriorly wider than head, about 2× (0.55 mm), and longer than head,

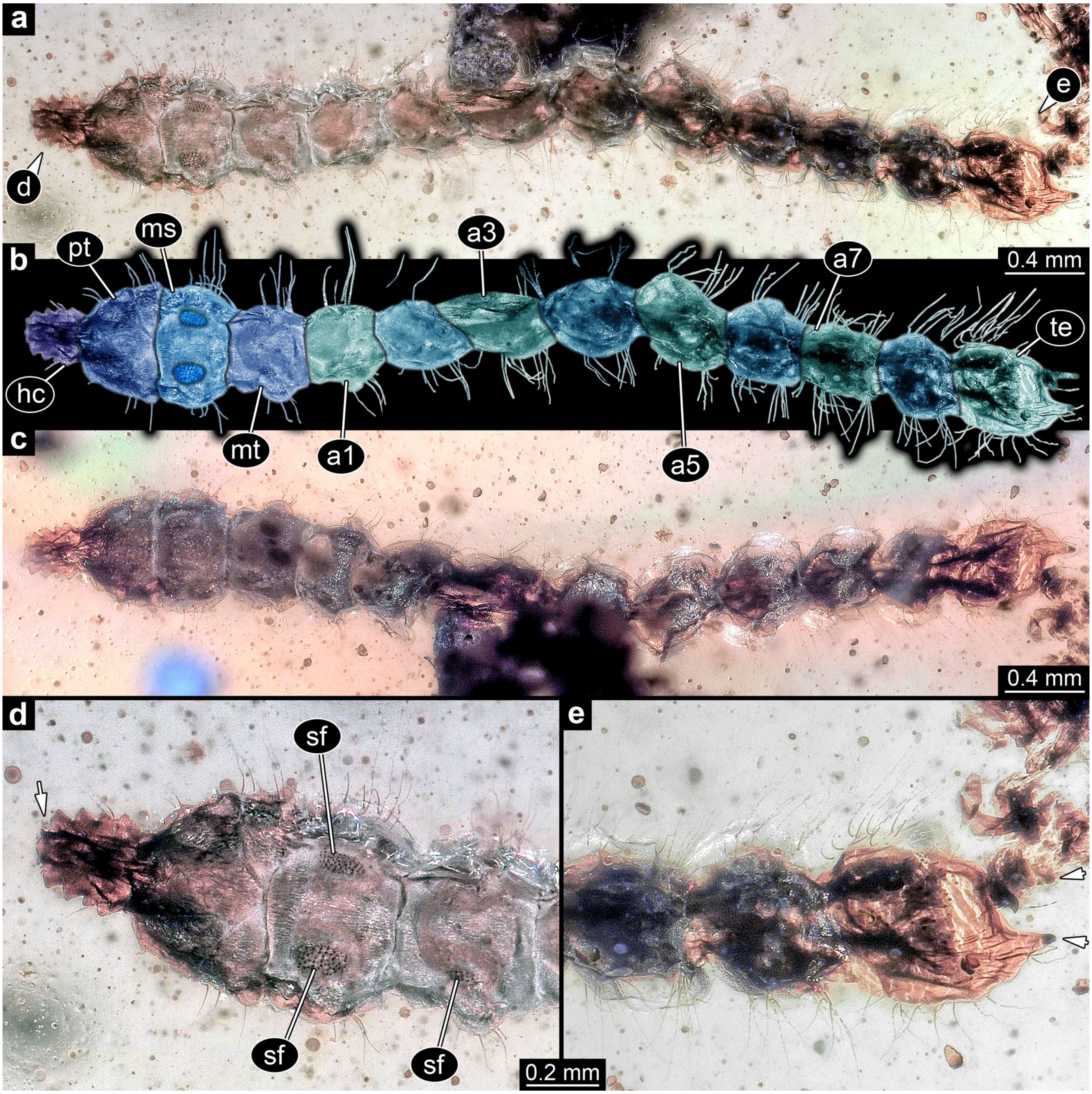

Fig. 1 Specimen BUB 3710, false click beetle larva. **a** Habitus in ventral view **b** Colour-marked version of (**a**). **c** Habitus in dorsal view. **d** Details of anterior body in ventral view; arrow marks supposed antenna. **e** Details of trunk end in ventral view, arrows mark processes. *a1–a7* abdomen segments 1–7, *hc* head capsule, *ms* mesothorax, *mt* metathorax, *pt* prothorax, *te* trunk end, *sf* setal fields

about 1.5× (0.4 mm). No locomotory appendages (legs) discernible. Each lateral edge with at least six setae.

Mesothorax ovoidal in shape, anteriorly same width as prothorax (0.55 mm), posteriorly narrower, about 70% (0.38 mm), slightly shorter than prothorax (0.38 mm). With a pair of oval fields ventrally, with numerous small setae (Fig. 1d). No locomotory appendages (legs) discernible. Each lateral edge with at least six setae; setae longer than the ones on prothorax.

Next nine units (metathorax and abdomen units 1–8) true segments, sub-similar. All roughly the same length (about 0.38 mm), widest in the middle (about 0.4 mm), but narrower anteriorly and posteriorly (about 0.25 mm). Maximum width (0.44 mm) narrower than prothorax, about 1.25×.

Metathorax and abdomen segments without locomotory appendages (legs) discernible; differentiable from other segments by the presence of two small oval fields with smaller setae, comparable to the fields on mesothorax, but smaller (Fig. 1d). All nine units of abdomen with numerous setae on the lateral edges; exact numbers difficult to discern due to preservation, up to twelve setae on each side per segment; setae as long as setae on mesothorax.

Terminal unit, abdomen end, most likely compound structure including several non-differentiated segments. Terminal end sub-similar to segments of the posterior trunk, but longer (0.48 mm) and wider (0.46 mm), terminally drawn out into paired processes (urogomphi?) (Fig. 1e). Each lateral edge with at least twelve setae; setae as long as setae on mesothorax.

Discussion

Identity of the specimen

The overall body shape of the here reported specimen is already highly reminiscent of false click beetle larvae. Still some details need to be considered. The anterior two thorax segments are widened, giving the impression of a "buprestiform" shape (i.e. a certain similarity to jewel beetle larvae, Buprestidae; expression from Németh and Otto 2016: p. 138; Otto and Gruber 2016: pp. 2, 3; Otto 2017: pp. 3, 4), and there are no legs on the thorax segments. The abdomen is not as narrow as in jewel beetle larvae and much longer. Such a shape is well known in larvae of Eucnemidae (e.g. Böving and Craighead 1931: pl. 81 M; Peterson 1957: Fig. C17A, F, I; Klausnitzer 1978: p. 160, Fig. 22/7; Becker 1991: p. 420, Fig. 34.453a; Muona 2010: p. 66, Fig. 4.5.4E; Otto and Gruber 2016: p. 8, Fig. 1). In addition, the prominent clypeus-labrum complex present in jewel beetle larvae is not apparent in the fossil here, further supporting an interpretation as a false click beetle larva. Probably the most indicative characteristic of the new fossil larva is the head with its jagged lateral rim, which is well known in many modern larvae of Eucnemidae (e.g. Muona 2010: p. 68, Fig. 4.5.6A, C; Otto 2012a: p. 221, Fig. 2; Otto 2014: p. 333, Fig. 2; Otto 2015: p. 30, Fig. 16, p. 31, Fig. 21, p. 33, Fig. 26, p. 37, Fig. 39, p. 39, Fig. 44, p. 41, Fig. 53, p. 44, Fig. 62, p. 46, Fig. 67; Muona and Teräväinen 2020: p. 4, Fig. 2A–E, p. 5, Fig. 3A–C, p. 6, Fig. 4A, p. 7, Fig. 5, p. 10, Fig. 7A–C, E).

Modern larvae of Eucnemidae (the larvae of Eucneminae and Melasinae with the larvae of the ingroups Melasini and Hylocharini) with a stronger resemblance to jewel beetle larvae seem not to possess the jagged heads. Such heads appear to be coupled to a more vermiform body organization, but as pointed out, there are also other forms of larvae within Eucnemidae. The fossil larva nevertheless shows some aspects of a buprestiform body with the presence of a jagged head.

Furthermore, the specimen has paired fields with short setae or trichomes ("microtrichial patches"; Muona and Teräväinen 2008) ventrally on two thorax segments (most likely for locomotion). In modern vermiform larvae, such fields seem to be unpaired (Otto 2015: p. 33, Fig. 28, p. 37, Fig. 41, p. 44, Fig. 64, p. 46, Fig. 69), but they are paired in "buprestiform" larvae (e.g. Otto and Gruber 2016: p. 8, Fig. 4). In this aspect, the fossil larva is more similar to modern click beetle larvae that resemble jewel beetle larvae. However, Muona and Teräväinen (2008) mention that there are variations within the ingroups of Eucnemidae, even among the different stages of the same species. As it seems, such structures are poorly developed in larvae that are completely immobile or have a sessile prepupal stage.

Another feature of the new specimen that is prominent but not immediately connected to Eucnemidae is the terminal end of the fossil with prominent bifid structures. In most modern larvae, the abdomen end is rounded (Muona 2010: p. 66, Fig. 4.5.4E; Otto 2012a: p. 221, Fig. 5; Otto 2012b: p. 287, Fig. 5; Otto 2014: p. 333, Fig. 5; Otto 2015: p. 31, Fig. 24, p. 33, Fig. 29, p. 37, Fig. 42, p. 41, Fig. 56, p. 44, Fig. 65; Otto 2017: p. 8, Fig. 5; Németh and Otto 2016: p. 143, Figs. 12, 13). There are few examples of terminal ends with paired protrusions (Muona 2010: p. 66, Fig. 4.5.4A–D), but only in species of *Perothops* (Muona 2010) and a mature larva of *Schizophilus subrufus* they are as prominent as in the fossil specimen (Otto and Young 1998: p. 307, Fig. 1).

Based on all these features we interpret the fossil as a larva of false click beetles. It combines characters today only known from different lineages of Eucnemidae: characters known today from vermiform larvae (overall body shape, jagged head) and characters known today from buprestiform larvae (wider anterior thorax segments, paired setal field). It cannot be excluded that the fossil larva is a representative of *Schizophilus* or closely related to it, and that characters known from buprestiform larvae have evolved convergently. It is also well possible that the larva is conspecific with one of the already known species of false click beetles. Without a preserved pupa stage, it will remain problematic to make an educated guess about the species identity of the larva. Yet, to avoid describing a potential junior synonym, we refrain from erecting a new species for the larva.

Mix of characters

The new larva is not the first example of a larva in Kachin amber possessing a "mix of characters". Already for different larvae of the group Neuroptera (lacewings) and Diptera (flies) comparable observations of features have been reported, which in the modern fauna characterize separate distinct lineages of the groups (Haug et al. 2019a; Baranov et al. 2020).

In contrast to that, the already known fossil larva of Eucnemidae strongly resembles modern-day larvae (Chang et al. 2016). Therefore, the group Eucnemidae emphasizes again how the large diversity of larvae in the Cretaceous fauna is structured: already very modern appearing morphologies (Chang et al. 2016; Wang et al. 2016; Haug et al. 2018) co-occur with now extinct morphologies (Badano et al. 2018; Haug et al. 2020a, b; Zippel et al. 2021); the latter ones include also animals with distinct mixes of features. Such "chimera"-type morphologies are likely "experimental" morphologies of an early phase of diversification of a lineage (Haug et al. 2019a, b; Baranov et al. 2020).

Wood-associated beetle larvae

Many beetle larvae, also those of Eucnemidae, play an important role in wood decomposition. Among such beetle larvae, solid-wood borers, i.e. larvae of Buprestidae, Cerambycidae and some of the larvae of Eucnemidae, are today often recognized as pests. Nevertheless, many other larvae, among them vermiform larvae of Eucnemidae, Micromalthidae or Scraptiidae are important in decomposition of dead trees, in other words, in carbon cycling.

We can assume that in the Cretaceous amber forests many animals must have also contributed to carbon cycling, quite similar to modern-day animals. Still, the direct record of wood-associated coleopteran larvae in Cretaceous amber forests has so far been scarce. Kirejtshuk and Azar (2008) reported a single larva of Micromalthidae, of which their modern counterparts live in rotting wood and take part in wood decomposition. Only recently, solid-wood borers, larvae of the group Buprestidae and possible larvae of the group Cerambycidae (Haug et al. 2021), as well as the dead-wood-decomposing larvae of Scraptiidae (Zippel et al. 2022) have been reported from Myanmar amber. The here reported larva is therefore a further addition to this ecologically important group of organisms.

Also in other groups of Holometabola, for example, flies, wood-associated larvae are known. Some fly larvae possibly exhibiting such ecologies have also just recently been identified (Baranov et al. 2020).

Especially for a wider-scale reconstruction of the Cretaceous ecosystems, the inclusion of many different ecosystem functions is important. Wood decomposition and carbon cycling may not be as exciting as predator-prey (Hörnig et al. 2020) or parasite-host interactions (Haug et al. 2018), but represents a crucial ecosystem function. For getting a wider view, ultimately leading to a glimpse at the food web in the Cretaceous amber forests, it is necessary and beneficial to recognize even more larvae like the one presented here.

While we can securely assume a wood-associated lifestyle for the newly described larvae, its exact lifestyle remains partly obscure. It combines features of solid-wood-boring larvae, such as the buprestiform appearance and the arrangement of the seta fields, with those of larvae living in rotten wood, such as the jagged head. It may be simpler to assume a lifestyle associated to softer wood since specializations for boring into solid wood, such as the prominent mandibles, can not be recognized. Yet as there is no such counterpart in the modern fauna, this aspect remains speculative.

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Availability of data and materials All data is provided in the text and the figure.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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