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New predatory beetle larvae from about 100 million years ago and possible niche differentiation effects in the Kachin amber forest

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Abstract

Beetle larvae are common occurrences in modern terrestrial and freshwater fauna. We can assume that this was the case in the past as well, yet fossil beetle larvae are still reported relatively rarely. Here we report fossil larval specimens of the group of click beetles, Elateridae, from Kachin amber. The specific ecological role of the larvae can be gleaned from the specimens, they are predators, most likely wood-associated. The larvae seem differentiated from other common types of predatory larvae, the most common being lacewing larvae, based on a quantitative morphological comparison of head and mandible shape. We emphasise the use of fossil beetle larvae for functional ecological comparisons, even if the exact taxonomic relationships are unclear, because they can still provide important information for palaeoecological questions.

Keywords Burmese amber, Coleoptera, Elateridae, Myanmar amber, Palaeoecology, Quantitative morphology

Introduction

The more than 380,000 species of the group Coleoptera, also known as beetles, dominate modern ecosystems (Boudinot et al., 2023; McKenna et al., 2015, 2019; Zhang, 2011, 2013). Interestingly, larval stages represent the larger share of the biomass in Coleoptera. The heaviest individual beetle is not an adult, but a larval stage of the Goliath beetle (Sverdrup-Thygeson, 2020). Most people can identify an adult beetle as such, yet beetle larvae differ in appearance and ecology from their adult counterparts (Belles, 2011; Beutel & Lawrence, 2005; Böving & Craighead, 1931; Lawrence et al., 2011). Ignoring larvae therefore gives us an incomplete image of an ecosystem, modern or past.

The ecological differentiation between beetle life-stages, where larvae utilize different resources from adults, has been interpreted as part of their success, and is likely to have triggered the early diversification of the group (Béthoux, 2009; Nicholson et al., 2014; Schachat et al., 2018). Despite their importance, larvae are considered and depicted in the scientific literature far less often than their adult counterparts, both in the extant and fossil record (Haug et al., 2019a; Peris & Rust, 2020; Zippel et al., 2022a). This skewed view towards adults is likely heavily influenced by the adult paradigm (Minelli et al., 2006) that is coupled to biodiversity measurements based on numbers of species in a specific fauna or community: it is simply easier to recognise new species based on adults.

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Using quantifiable morphological traits as measures of diversity can circumvent the challenges of incomplete taxonomic information (Haug et al., 2023a, 2024a) and ambiguity due to convergent evolution. While convergence, also among larvae, may lead to diverging taxonomic interpretations, the functional ecological interpretations are often not affected (Grimaldi et al., 2005 vs. Beutel et al., 2016; Zippel et al., 2022b vs. Rasnitsyn & Müller 2023).

The use of quantitative morphological measures instead of taxonomic ones also compensates for differences in sample size (Haug et al., 2020a, 2023a), reducing the Lagerstätten effect, which causes biases or potential overinterpretations of palaeodiversity (De Celis et al., 2021; Flannery Sutherland et al., 2019). Lagerstätten are extremely important in the study of fossil beetle larvae. One of the most productive Lagerstätten concerning holometabolan larvae is Kachin amber from Myanmar. So far, just over 100 larval beetle specimens have been figured from Kachin amber (Grimaldi et al., 2002; Poinar & Brown, 2014; Xia et al., 2015; Beutel et al., 2016; Poinar & Poinar 2016; Zhang, 2017; Bao et al. 2018; Zhao et al., 2019, 2020; Batelka et al., 2019, 2021; Gustafson et al., 2020; Haug et al., 2021a, b, 2022a, 2023b; Háva, 2022; Kiesmüller et al., 2022; Zippel et al., 2022a, 2022a; Kolibáč et al., 2023; Linhart et al., 2023). While this number is larger than that for larvae of scorpionflies (Mecoptera; one specimen; Haug et al. 2024b), wasps (Hymenoptera; about five specimens; Haug et al. 2024b), or moths (Lepidoptera; seven specimens; Gauweiler et al., 2022; Haug & Haug, 2021), it is lower than the number of fly larvae (Diptera; almost 150 specimens; Amaral et al., 2023; Baranov et al., 2020) and, most surprisingly, lower than the number of larvae of lacewings and their close relatives (Neuropterida; more than 400 specimens; Badano et al., 2018, 2021; Braig et al., 2023a; Engel, 2016; Engel & Grimaldi, 2008; Hassenbach et al., 2023; Haug & Haug, 2023; Haug et al., 2018, 2019a). Given that Coleoptera is an unusually large and species-diverse group, it is crucial that more beetle larvae fossils are reported from Kachin amber, especially for use in quantitative methods.

Elateridae, the group of click beetles, has more than 10,000 species in the modern fauna (Costa et al., 2010 p. 75) and a fossil record with more than 250 formally described species (recently summarised in Kundrata et al. 2021a, Table A1, pp. 82–88). However, only four fossil click beetle larvae have been yet reported, all from Kachin amber, representing three types: one elateriform (Zippel et al., 2024), one with very stout appendages, which has no extant counterpart (Haug et al., 2025), as well as one less-elongate form with prominent posterior projections (urogomphi; Kundrata et al., 2025). Here, we report new specimens of the third type of beetle larva from Kachin amber, increasing the fossil record of larval specimens of click beetles. We also compare the morpho-ecological aspects of the new specimens with other predatory larvae from Kachin amber to draw conclusions about their potential ecological functions.

Material and methods

Material

In the centre of this study are several specimens preserved in Kachin amber, Myanmar. Specimens came from two collections. Specimens SNHMB.G 8519, SNHMB.G 8520, SNHMB.G 8521, and SNHMB.G 8522 are from the collection of one of the authors (PM) and have been donated to the public collection of the Staatliches Naturhistorisches Museum Braunschweig, Germany. The other specimens are from the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München (PED 0347, PED 0436a, b, c, PED 0498, PED 1816, PED 1978, PED 2457, PED 2879, PED 3006, PED 3206, PED 3550).

The amber pieces used in this study were purchased legally on ebay.com from the trader "burmite-miner." Half of them were exported before February 2021 with certainty: the SNHMB specimens were exported on 20/09/2016; the PED specimens were purchased between 09/2019 and 17/2023 (02/09/2019; 23/10/2019; 23/11/2019; 27/02/2022; 20/05/2022; 20/09/2022; 19/03/2023; 19/04/2023; 27/06/2023; 07/10/2023). For the PED specimens, export dates are not available.

In light of the military conflict in Myanmar, studying Kachin amber has sparked a discussion among scientists that has left some uncertainty (Dunne et al., 2022; Haug et al., 2020d, 2023c; Peretti, 2021; Poinar & Ellenberger, 2020; Rayfield et al., 2020). It has resulted in a push to provide export papers for fossil specimens from Myanmar (Theodor et al., 2021). However, according to trader information and personal experience, amber pieces, often sold for a few dollars, generally do not receive separate export papers. In our publications, we are providing all information available to us about the provenance of the specimens for maximum transparency (Haug et al., 2023c).

For a general introduction to the morphology of Elateridae larvae, an extant larva from the collections of the Leibniz-Institut zur Analyse des Biodiversitätswandels (LIB), formerly the Centrum für Naturkunde (CeNak), Hamburg (ZMH) is also presented. The specimen is stored under repository number ZMH 62853 and was labelled *Campylus linearis* Elateridae: Dendrometrinae, which is now *Denticollis linearis*.

The Kachin amber forest is dated to the Lower Cenomanian (Cretaceous, ca. 99 mya; Shi et al., 2012). The material is from the Hukawng valley mines of Kachin state, the geology of the area is described in detail by Cruickshank and Ko (2003). Briefly, the amber-bearing horizon of the valley consists of folded sedimentary and volcanic rock, dated to the Upper Albian to Lower Cenomanian. Maps of the area are provided by Grimaldi et al. (2002) and Yu et al. (2019), however, the exact locality of the specimens in this study is unknown.

Documentation methods

The 17 newly reported beetle larvae from amber were documented on a Keyence VHX-6000 digital microscope equipped with a 20–2000 × magnification objective. The images were recorded under cross-polarised light or low-angle ring light, as well as low-angle ring and coaxial light, using the High Dynamic Range-mode (HDR) of the VHX-6000. Black and white backgrounds were tested for all specimens, the background providing larger contrast was then chosen for further processing. Stacking (fusing of images with differing focus levels) and stitching (merging of adjacent image details) of images were performed by the built-in software of the Keyence VHX-6000 (VHX). Finally, processing of the images was performed with Adobe Photoshop CS2 to adjust colour coding, saturation, and contrast, and to label images (Braig et al., 2023a).

Shape analysis

From the documented images, we created outlines of the head capsules and stylets. Tracing of the stylets based on the images was performed in Inkscape or Adobe Illustrator CS2. The outlines were drawn symmetrically with the stylets oriented forward, lining up the tip with the inner joint of the stylet. To create a comparative frame for the fossil beetle larvae, we used a large dataset of predatory lacewing larvae (Neuropterida). This data set included lacewing larvae that, like the predatory larvae of Elateridae, have at least one tooth on their mandibles. The mandibles are part of compound structures often forming long stylets in many Cretaceous lacewing larvae. In total, we considered 413 larvae, ten of which are fossil beetle larvae, and the rest of which are lacewing larvae (fossil and extant), including:

- specimens of thread-winged and spoon-winged lacewings (Nemopteridae; Ghosh, 1910; Imms, 1911; Mansell, 1981a, 1981b, 1983; Monserrat, 1983a, 1983b; Navás, 1919; Pierre, 1952; Satar et al., 2007; Withycombe, 1923);
- specimens of owllions (see discussion in Haug et al., 2022b for name; these animals have been generally considered as the groups "Ascalaphidae" and "Myrmeleontidae"; described in Ábrahám & Papp, 1990; Acevedo et al., 2013; Aspöck & Aspöck, 1964; Badano, 2012; Beutel et al., 2010; Brauer, 1854; Gupta & Badano, 2021; Henry, 1976; Hévin et al., 2023; Kamiya & Ando 1985; Lehnert et al., 2022; Lin et al., 2021; Matsuno, 2017; McClendon, 1902; Miller & Stange, 2016; Nicoli Aldini, 2007; Pantaleoni et al., 2010; Peterson, 1957; Principi, 1943; Ramos & Monserrat, 2022; Riek, 1970; Satar et al., 2006, 2014a, 2014b; Stitz, 1931; Townsend, 1939; Van der Weele, 1908; Withycombe, 1925;);
- split-footed lacewings (Nymphidae; Froggatt, 1907; Gepp, 1984; New, 1982, 1983; New & Lambkin, 1989; Tillyard, 1926);
- fossils that are not within modern ingroups of Myrmeleontiformia (e.g. Badano et al., 2018).

Myrmeleontiformian larvae that lack teeth, such as larvae of the group of silky lacewings (long-nosed antlions; Psychopsidae), most larvae of thread-winged and spoon-winged lacewings (Nemopteridae), as well as the two species of the group *Ankyloleon* were not considered.

We analysed the combined data set of predatory lacewing larvae and click beetle larvae in the R-statistics environment (ver. 4.1.039; Braig et al., 2023b; R Core Team, 2021). The shapes of the head capsules with stylets including teeth were reconstructed to a standardized size (600 pixel height canvas) to resolve issues of scales (and lack thereof) in the source material. The shapes were then quantified with an elliptic Fourier analysis (EFA) using the R-package Momocs (ver. 1.3.2; Bonhomme et al., 2014). EFA applies the principle of the Fourier transformation to translate the two-dimensional outline into a mathematical object (Bonhomme et al., 2014; Braig et al., 2023b; Haug et al., 2023b). The shape is decomposed into a harmonic sum of trigonometric functions, weighted with harmonic coefficients (Bonhomme et al., 2014; Braig et al., 2023b). We first aligned the shapes along the anterior–posterior axis of the head, which corresponds to the first fitted ellipse. We then centred the shapes in the coordinate space. These two steps allowed us to normalize the harmonic coefficients extracted from the shapes. We then tested the data to find an appropriate number of harmonics to describe the shapes, in this case 14 harmonics. The extracted harmonic coefficients, which can be considered as quantitative variables, are analysed with a principal component analysis (PCA; Bonhomme et al., 2014). We chose to retain the first 27 PCs, because they amounted to more than 99% of variation in the data set. The matrix of principal components (PCs) was then used to create the morphospace, by plotting PCs against each other in scatterplots.

Results

Description of the specimens

Table 1

Description of the general morphotype

The new fossil specimens presented herein share a general morphology. The body can be differentiated into a functional head (head capsule) and a trunk. The trunk is further differentiated into three segments forming the anterior part of the trunk (thorax) with locomotory appendages (legs) and nine following units forming the posterior part of the trunk (abdomen). The head capsule and the segments of the trunk bear long setae (Figs. 1A, 2A, B, 3A, 4A, 5A, B, E, G, 6A, 7A, E, 8A, 9A, D, E, 10A, E, I, 11A). In dorsal view, a moulting suture on the head capsule, which is leaf- or tongue-shaped posteriorly, is present (Figs. 1A, 3B, 4A, 6E, 7C, D, 8B, 8C, 9E, 10C, H, J, 10K). Stemmata are barely recognisable (due to preservation). The antenna has a length of about one third the length of the head capsule, consists of three (Figs. 1D, 2C, 5C) to four elements (Figs. 3B, 4D, 6E, 7D, 8B, D, 11A), and often bears a sensorial structure on the second-most distal element (Figs. 2C, 3B, C, 4D, 5C, G, 6A, 7D, 8D, 9E, 10C, H, J, 11A). The mandibles are curved inward and bear a single tooth on the inside (Figs. 1D, E, 2C, 3B, 4E, 6B, E, 7C, 8E, 9B, E). The maxillae and the labium constitute a maxillo-labial complex. The overall complex is rounded, tapering posteriorly. The palps of the maxillae project forward and consist of four elements. The labium is narrower than the maxilla, slightly triangular, and narrows posteriorly (Figs. 1F, 1G, 2D, 3C, 3D, 4B, 4C, 5B, 5C, 5F, 5G, 6B, 8G, 8F, 9B, 9C, 9F, 9G, 10D, 10H). The palps of the labium are shorter than the palps of the maxillae, project forward, and consist of two (Figs. 4C, 5F, 7C, 8G, 9C) or three (Fig. 2D) elements.

The following three segments bear locomotory appendages (legs). The locomotory appendages have a relatively long tarsungulum (Figs. 5H, 6D, 6F, 9A, 10A, F, I, 11B). It appears from curved to more straightened, and is sometimes as long as the tibia (Figs. 5H, 9A, 10E, 10I). The posterior trunk (abdomen) consists of nine units, of which the anterior eight are true segments (Figs. 1A, 2B, 5A, E, 6E, 7E, 9A, D, E, 10B, F, I, 11A). The trunk end (amalgam of several segments) bears two projections postero-dorsally (urogomphi; Figs. 1A, 2E, 5D, 5E, 6C, 7E, 9A, D, E, 10A, E, I, 11A). Ventrally, the anal membrane is differentiated as a pygopod (i.e., a specialised structure of the anal opening; Figs. 1B, 2E, 5D, E, 6C, 7A, 10B, E, 11C).

Shape analysis

The PCA resulted in 27 PCs explaining over 99% of variation in the data set. PC1–PC4 were plotted to visualize the morphospace, as they represent the largest amount of variation (PC1 = 35.6%; PC2 = 24.1%; PC3 = 10.5%; PC4 = 6.4%; scree plot available in Suppl. 1). The results of the PCA are available in Suppl. 2.

PC1 is mostly explained by the thickness of the tip of the stylet and the head capsule shape. Negative values represent head capsules with antero-lateral protrusions and thin stylet tips, while positive values represent slim head capsules with thick stylet tips. PC2 is mostly explained by the attachment site of the stylet and the width of the head capsule. Negative values represent slim head capsules with laterally attaching stylets, while positive values represent wide head capsules with medially attaching stylets. PC3 is mostly explained by the overall width of the head. Negative values represent wide head capsules with thick proximal stylets, while positive values represent slim head capsules with thin proximal stylets. PC4 is mostly explained by the curvature and dentation of stylets. Negative values represent strongly curved stylets with distally inserting teeth, while positive values represent straight stylets with proximally inserting teeth. Graphical component loadings for all 27 PCs are depicted in Suppl. 3.

Investigation of the morphospace of PC1 and PC2 showed a pattern similar to that found in earlier studies of differences between fossil and extant predatory lacewing larvae (e.g., Braig et al., 2023a; Fig. 12). The extant predatory lacewing larvae form a more or less circle-shaped cluster around the centre of the morphospace, showing a range of morphologies from straight slim head capsules with equally straight stylets to head capsules with strongly curved stylets. They show some exclusivity on the left side of the morphospace, where no fossil larvae plot. The fossil predatory lacewing larvae mostly cover the same area within the morphospace, but extend further to the bottom, right, and top, showing also forms with far laterally attaching stylets, or prominent teeth. The beetle larvae plot above the centre of the morphospace in a tight cluster, indicating relatively shorter stylets.

Investigation of the morphospace of PC3 and PC4 showed a clear separation of beetle larvae and predatory lacewing larvae without overlap (Fig. 13). The beetle larvae formed, again, a tight cluster in the top left corner of the morphospace, indicating relatively shorter stylets with wider head capsules. The fossil and extant predatory lacewing larvae strongly overlap, plotting in a widespread cluster in the centre of the morphospace, extending to the top right and bottom left of the morphospace. The fossil larvae showed more slim and elongated head

Table 1 Description table for the newly described specimens in this study. Contains relevant morphological features for taxonomic interpretation.

Specimen	Figure	Preserved in 70% Ethanol	Preserved in Kachin amber	Dorsal view	Ventral view	Dorsal view head	Ventral view head	Fronto-clypeus (or nasale)
(1) ZMH 62853	Figure 1	x	–	x	x	x	x	x
(2) PED 0498	Figure 2	–	x	–	x	x	x	0
(3) PED 0347	Figure 3	–	x	x	–	x	x	x
(4) PED 0436a	Figure 4	–	x	–	–	x	x	x
(5) PED 0436b	Figure 5A–D	–	x	–	x	–	x	0
(6) PED 0436c	Figure 5E–H	–	x	–	x	–	x	0
(7) PED 1816	Figure 6	–	x	x	x	x	x	x
(8) PED 1978	Figure 7A–D	–	x	x	x	x	x	x
(9) PED 3206	Figure 7E	–	x	x	–	x	–	0
(10) PED 2879	Figure 8	–	x	–	–	x	x	x
(11) PED 3006	Figure 9A–C	–	x	–	x	–	x	0
(12) PED 2457	Figure 9D	–	x	–	x	–	x	0
(13) PED 3550	Figure 9E–G	–	x	x	–	x	x	0
(14) SNHMB.G 8522	Figure 10A–D	–	x	x	x	x	x	x
(15) SNHMB.G 8521	Figure 10E–H	–	x	x	x	x	x	x
(16) SNHMB.G 8520	Figure 10I-K	–	x	x	–	x	–	x
(17) SNHMB.G 8519	Figure 11	–	x	–	x	–	–	0

Specimen	Figure	Maxillo-labial complex	Triangular shaped labium	Forward projecting mouthparts	Sensorial structures on antenna and mouthparts	Projections on the posterior end	Prominent anal opening	Narrow tarsus
(1) ZMH 62853	Figure 1	x	x	x	–	x	x	–
(2) PED 0498	Figure 2	x	x	x	x	x	x	0
(3) PED 0347	Figure 3	x	x	x	0	0	0	0
(4) PED 0436a	Figure 4	x	x	x	x	0	0	0
(5) PED 0436b	Figure 5A–D	x	x	x	x	x	x	x
(6) PED 0436c	Figure 5E–H	x	x	x	x	x	0	x
(7) PED 1816	Figure 6	0	0	0	0	x	x	x
(8) PED 1978	Figure 7A–D	0	0	x	x	x	x	0
(9) PED 3206	Figure 7E	0	0	0	0	x	0	0
(10) PED 2879	Figure 8	x	x	0	x	0	0	0
(11) PED 3006	Figure 9A–C	x	x	x	x	x	0	x
(12) PED 2457	Figure 9D	0	0	0	0	x	0	0
(13) PED 3550	Figure 9E–G	0	0	0	0	x	0	0
(14) SNHMB.G 8522	Figure 10A–D	0	0	x	0	x	0	x
(15) SNHMB.G 8521	Figure 10E–H	0	0	x	0	x	x	x
(16) SNHMB.G 8520	Figure 10I–K	0	0	x	0	0	0	x
(17) SNHMB.G 8519	Figure 11	x	0	x	0	x	x	x

x applies, – does not apply, 0 not recognizable

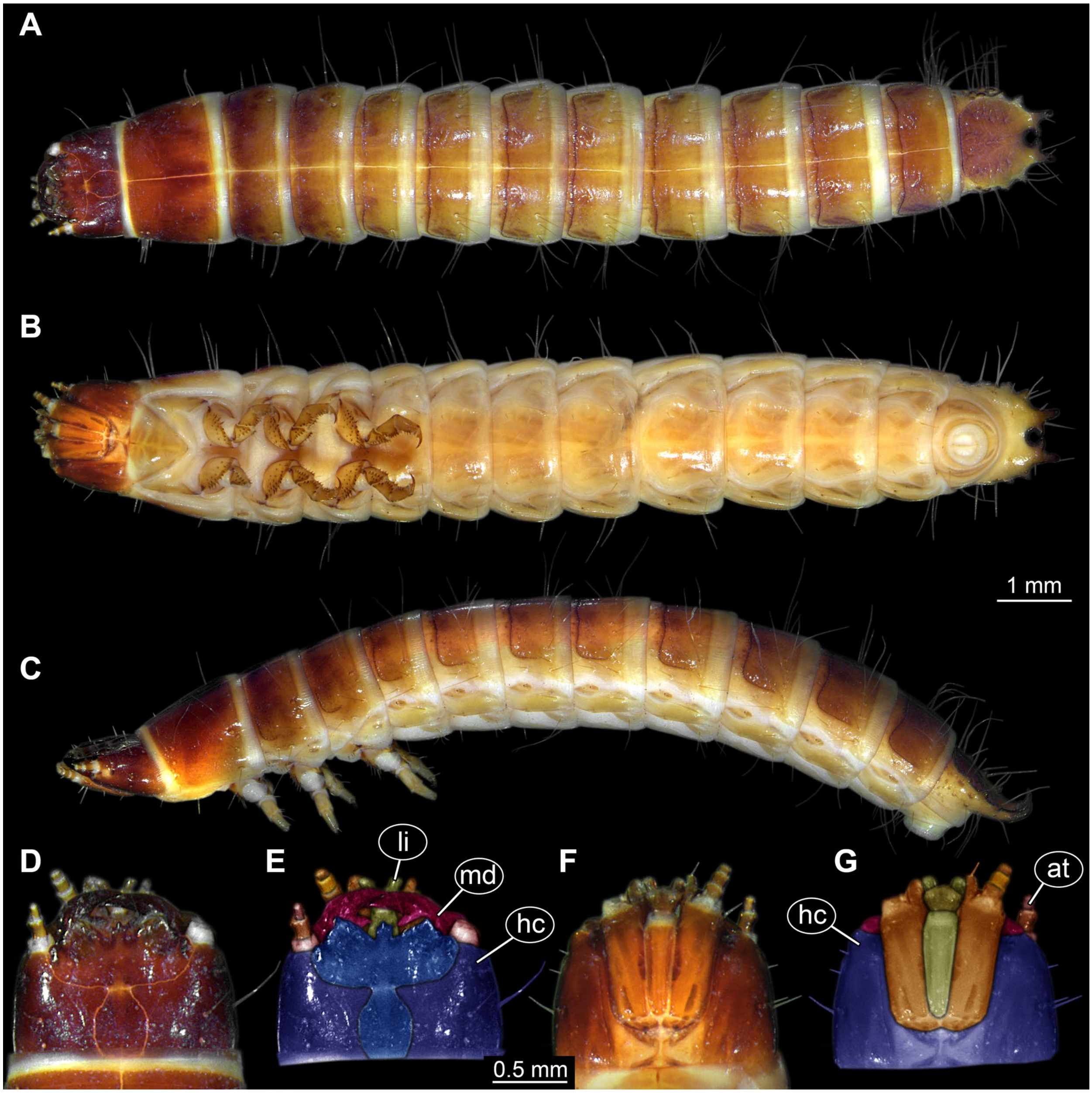

Fig. 1 Extant larva of Elateridae, *Denticollis linearis* (formerly *Campylus linearis*), ZMH 62853. **A**–**C** Overviews. **A** Dorsal view. **B** Ventral view. **C** Lateral view. **D**–**G** Close-ups on head. **D** Dorsal view. **E** Colour-marked version of **D**. **F** Ventral view. **G** Colour-marked version of **F**. *at* antenna, *hc* head capsule, *li* labium, *md* mandible

capsules towards the top right, the extant specimens showed more curved stylets towards the bottom left of the morphospace.

Discussion

Identity of the newly reported fossil specimens

In many of the better-preserved new specimens, several important morphological features are well apparent: (1) The head capsule has a distinct moulting suture that sets off an anterior region (fronto-clypeus or nasale). This region has a distinct posterior extension that is leaf- or tongue-shaped. (2) The maxillo-labial complex is gently rounded posteriorly, but the labium is strongly narrow and triangular, endites and palps project forward, often well visible before the head capsule (in two specimens this part is missing (PED 1816 and 2879), but the shape of the complex is still shown). (3) The trunk end has distinct posterior projections; the prominent anal opening

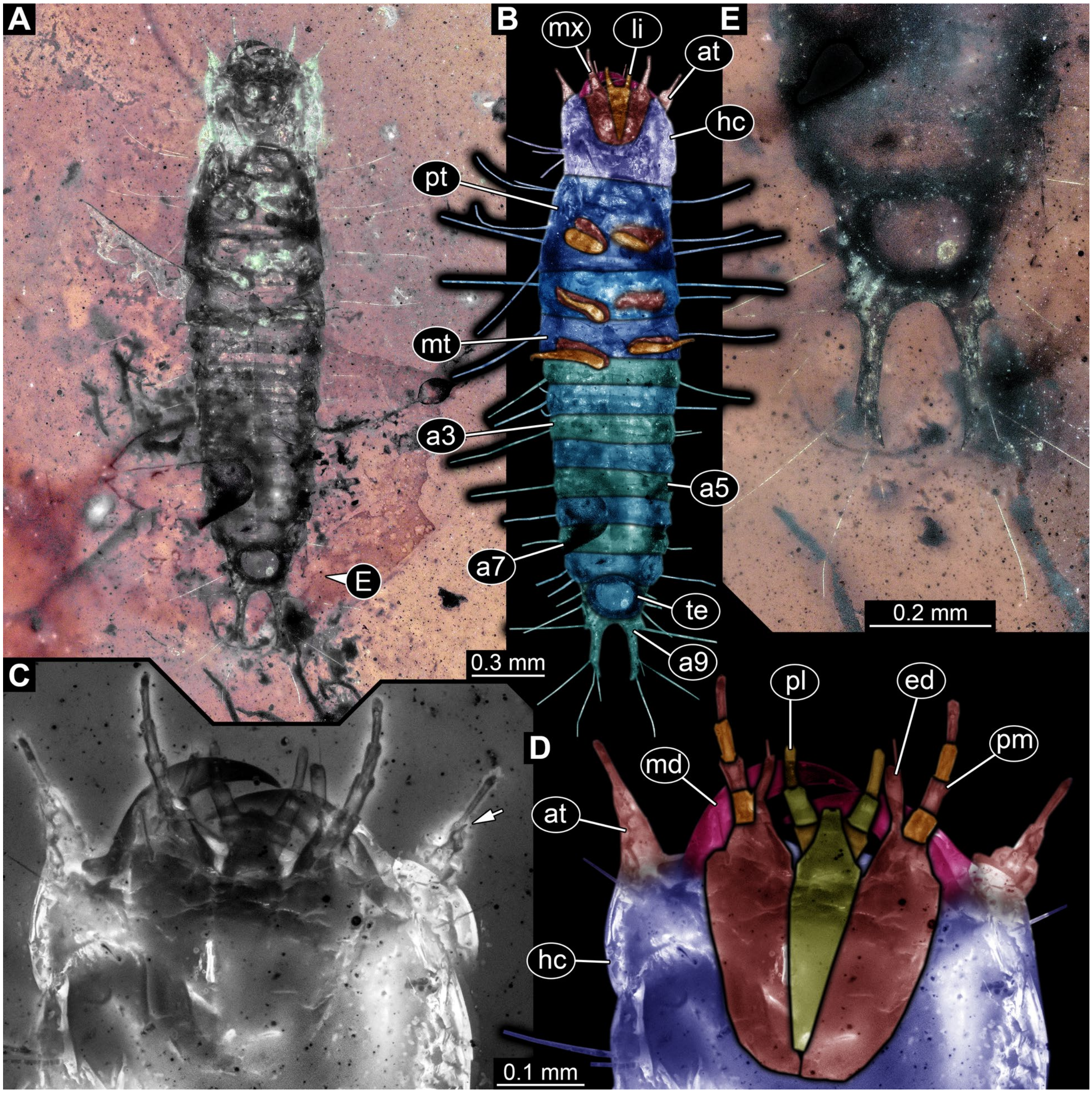

Fig. 2 Fossil larva, PED 0498. **A** Overview in ventral view. **B** Colour-marked version of **A**. **C** Close-up on head, ventral view, autofluorescence, arrow marks sensorial structure. **D** Colour-marked version of **C**. **E** Close-up on posterior trunk region; note ventrally-directed trunk end. *a3–9* abdomen segment 3–9, *at* antenna, *ed* endite (possible galea), *hc* head capsule, *li* labium, *md* mandible, *mt* metathorax, *mx* maxilla, *pl* palp of labium, *pm* palp of maxilla, *pt* prothorax, *te* trunk end

is directed ventrally. Many of these aspects are known in larvae of the group Elateridae, e.g., Dendrometrinae (Fig. 1), Pedillidae (Young, 1991, fig. 34.726 p. 545), or Carabidae (Lawrence et al., 2011, fig. 64H).

Kundrata et al. (2025) reported two larvae in Kachin amber that strongly resemble the ones reported here and likely represent either the same species, or closely related species. Kundrata et al. (2025) pointed out similarities of the larvae to those of Dendrometrinae and Agrypninae, but concluded that their larvae are representatives of Pityobiinae. Due to the high similarities, we also assume this interpretation for the newly reported specimens here.

The variation among the new specimens likely exceeds ontogenetic variation. The specimens with longer heads (most extreme in PED 0436a; Fig. 4) are unlikely to be conspecific with the other specimens. We expect that

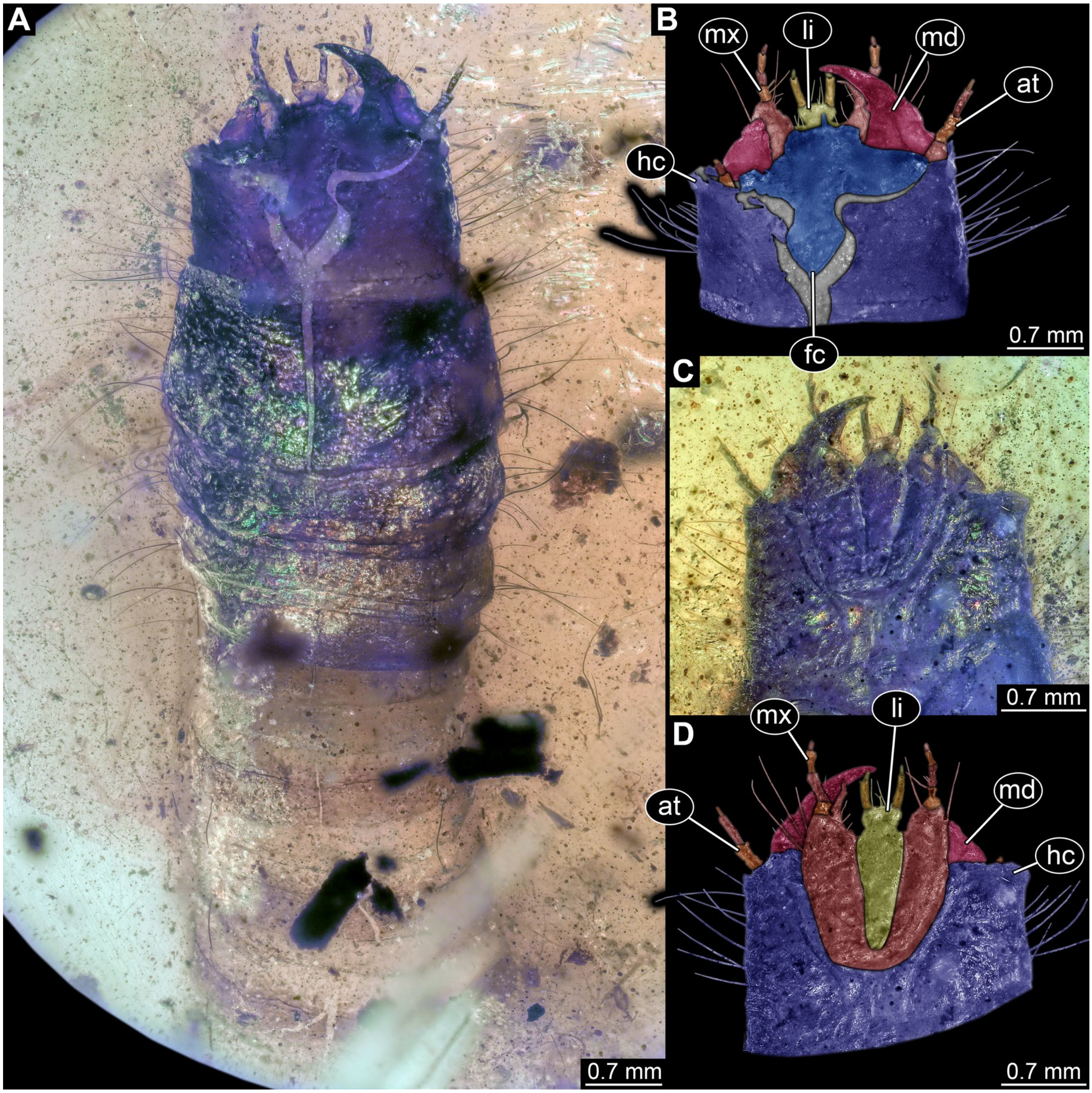

Fig. 3 Fossil larva, PED 0347. **A** Overview in dorsal view. **B** Colour-marked version of head region of **A**. **C** Ventral view of head region. **D** Colour-marked version of **C**. *at* antenna, *fc* fronto-clypeus (or nasale), *hc* head capsule, *li* labium, *md* mandible, *mx* maxilla

among the relatively large specimens, those with longer heads (Fig. 4) and those with shorter heads (Fig. 3), belong to different species. More material could provide a basis to establish possible growth trajectories in the future.

Ecology

Few details are known about the ecology of extant larvae of Pityobiinae, except that they have been found under the bark of dead trees (e.g. bugguide.net #50504). The morphologically similar larvae of Agrypninae often live in association with wood and prey on wood-feeding animals (mostly beetle larvae and termites; Casari, 2002; Costa et al., 2010; Craighead, 1950). Some modern larvae of Agrypninae are not directly associated with wood, feeding within termite mounds. But representatives of early termite lineages from the Cretaceous were strictly wood-feeding (Engel, 2019; Zhao et al., 2021). It is possible that

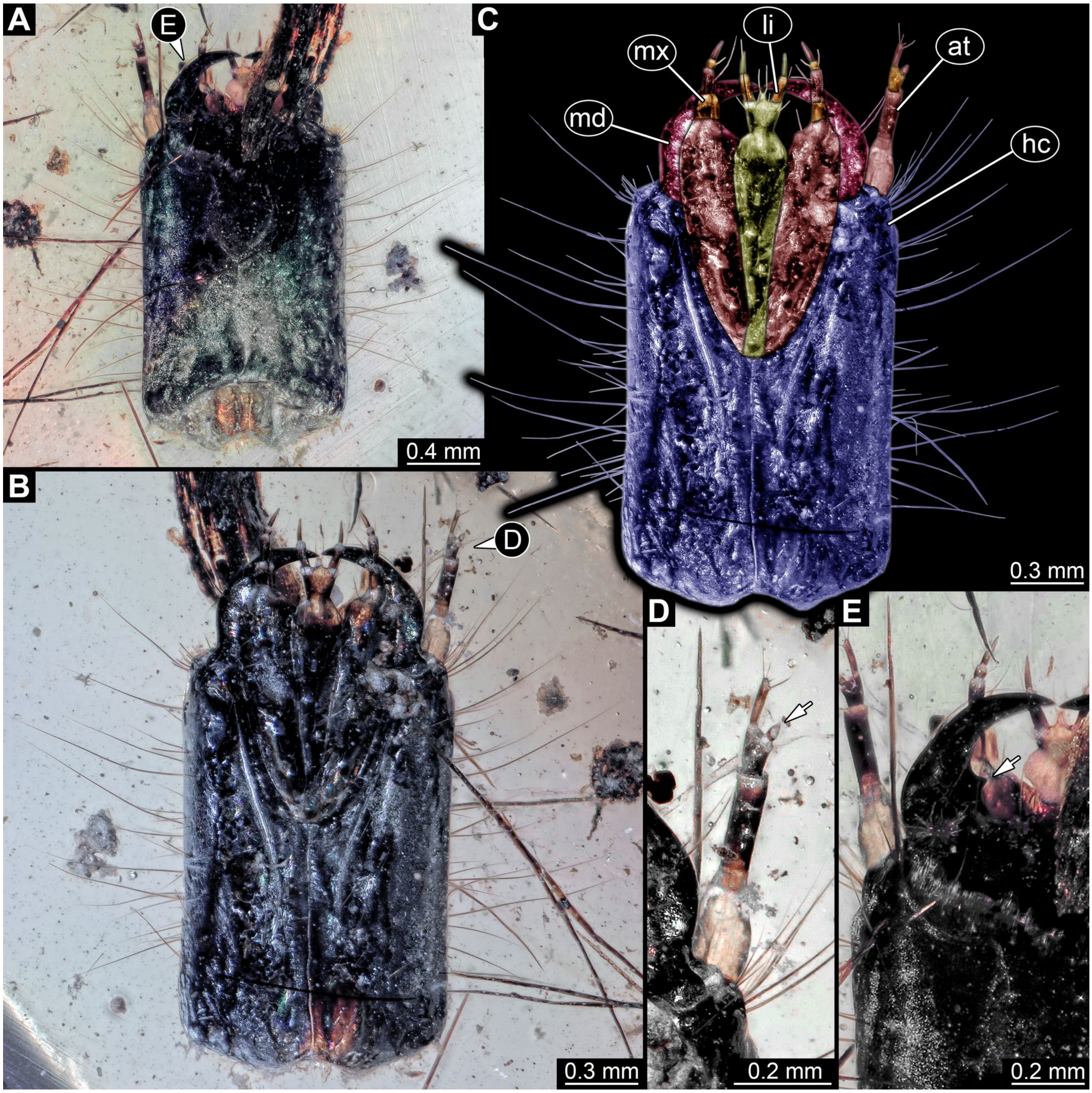

Fig. 4 Fossil larva, PED 0436a. **A** Overview in dorsal view. **B** Overview in ventral view. **C** Colour-marked version of **B**. **D** Close-up on antenna; arrow marks sensorial structure. **E** Close-up on mandible; arrow marks tooth. *at* antenna, *hc* head capsule, *li* labium, *md* mandible, *mx* maxilla

all newly reported larvae had a similar wood-associated lifestyle, preying on wood-associated beetle larvae or termites. As wood-associated animals have a higher chance of being preserved in amber, the common occurrence of the larvae in amber further supports this lifestyle (Azar, 2007). The shape of the mandibles is also compatible with a wood-associated predator lifestyle, as plant-feeding larvae of Elateridae have differently shaped mandibles (Emden, 1942; Furlan et al., 2021).

The larvae of lacewings and allies vs. the larvae of beetles: abundance

Early studies in fossil neuropteridan larvae from Kachin amber largely focused on reporting single specimens (Haug et al., 2018, 2019a; Luo et al., 2022) or a few special specimens (Badano et al., 2018, 2021; Baranov et al., 2022; Engel & Grimaldi, 2004; Makarkin, 2018; Perrichot & Engel, 2007; Wang et al., 2016; Wichard, 2017; Xia et al., 2015; Zhang, 2017). Larger-scaled quantitative

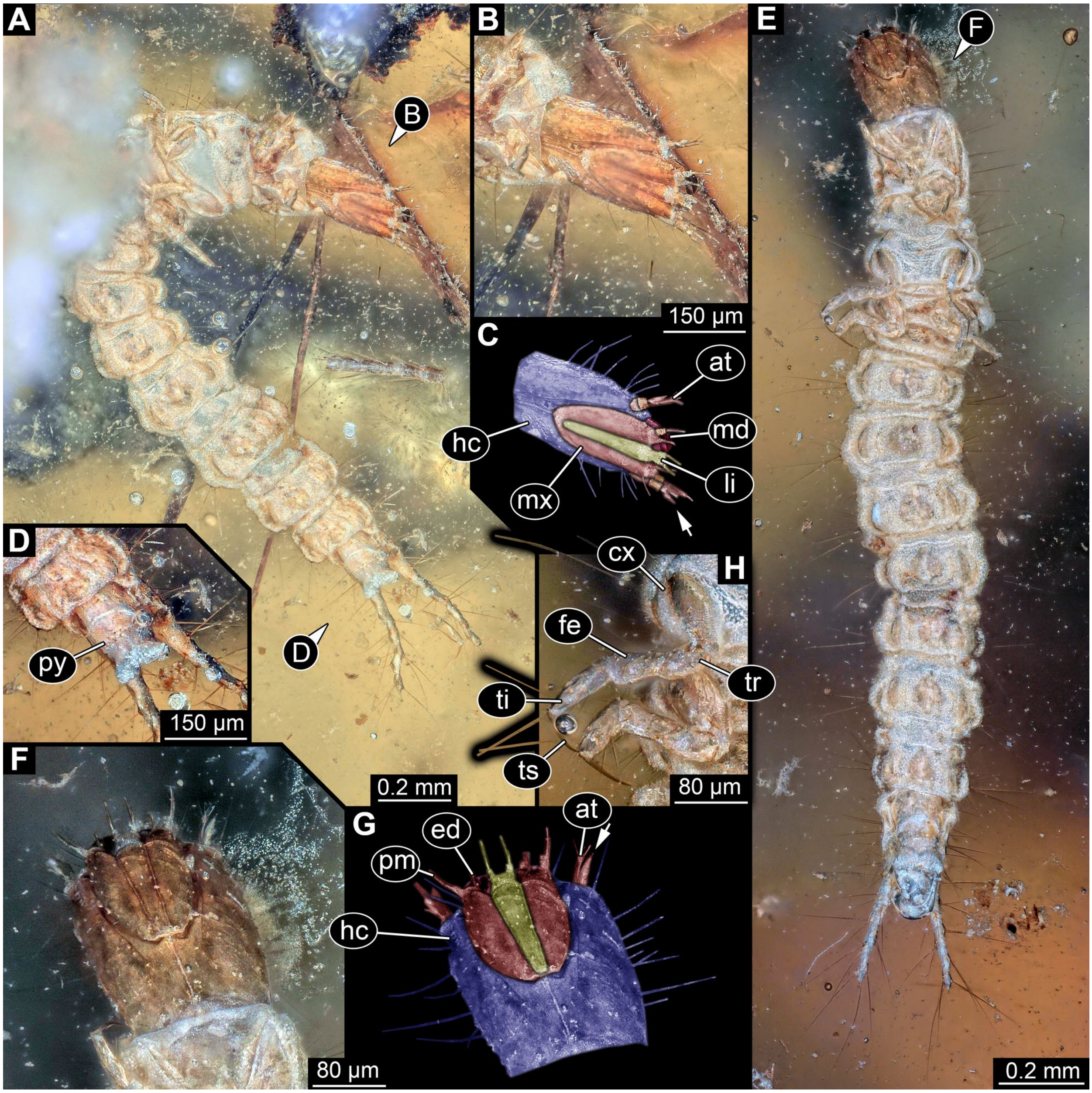

Fig. 5 Fossil larvae. **A**–**D** PED 0436b. **A** Overview in oblique ventral view. **B** Close-up on head in oblique ventral view. **C** Colour-marked version of **B**; arrow marks sensorial structure. **D** Close-up on trunk region. **E**–**H** PED 0436c. **E** Overview in ventral view. **F** Close-up on head region in ventral view. **G** Colour-marked version of **F**; arrow marks sensorial structure. **H** Close-up on locomotory appendages (legs). *at* antenna, *cx* coxa, *ed* endite (possible galea), *fe* femur, *hc* head capsule, *li* labium, *md* mandible, *mx* maxilla, *pm* palp of maxilla, *py* possible pygopod, *ti* tibia, *tr* trochanter, *ts* tarsungulum

studies only became possible after a certain database had been built up (Haug et al., 2020a, 2021c, d, f, 2022b, 2023a; Braig et al., 2023a; Hassenbach et al., 2023; Mengel et al., 2023).

From Kachin amber, beetle larvae are usually reported in single specimens (Haug et al., 2021b, 2023b, 2024b; Liu et al., 2023a; Rosová et al., 2023; Zippel et al., 2022a, 2022b), with some exceptions of syninclusions of multiple larvae (Batelka et al., 2021; Linhart et al., 2023; Zippel et al., 2024; but see Haug et al., 2021a). Screening of material has shown that beetle larvae appear in higher specimen counts than

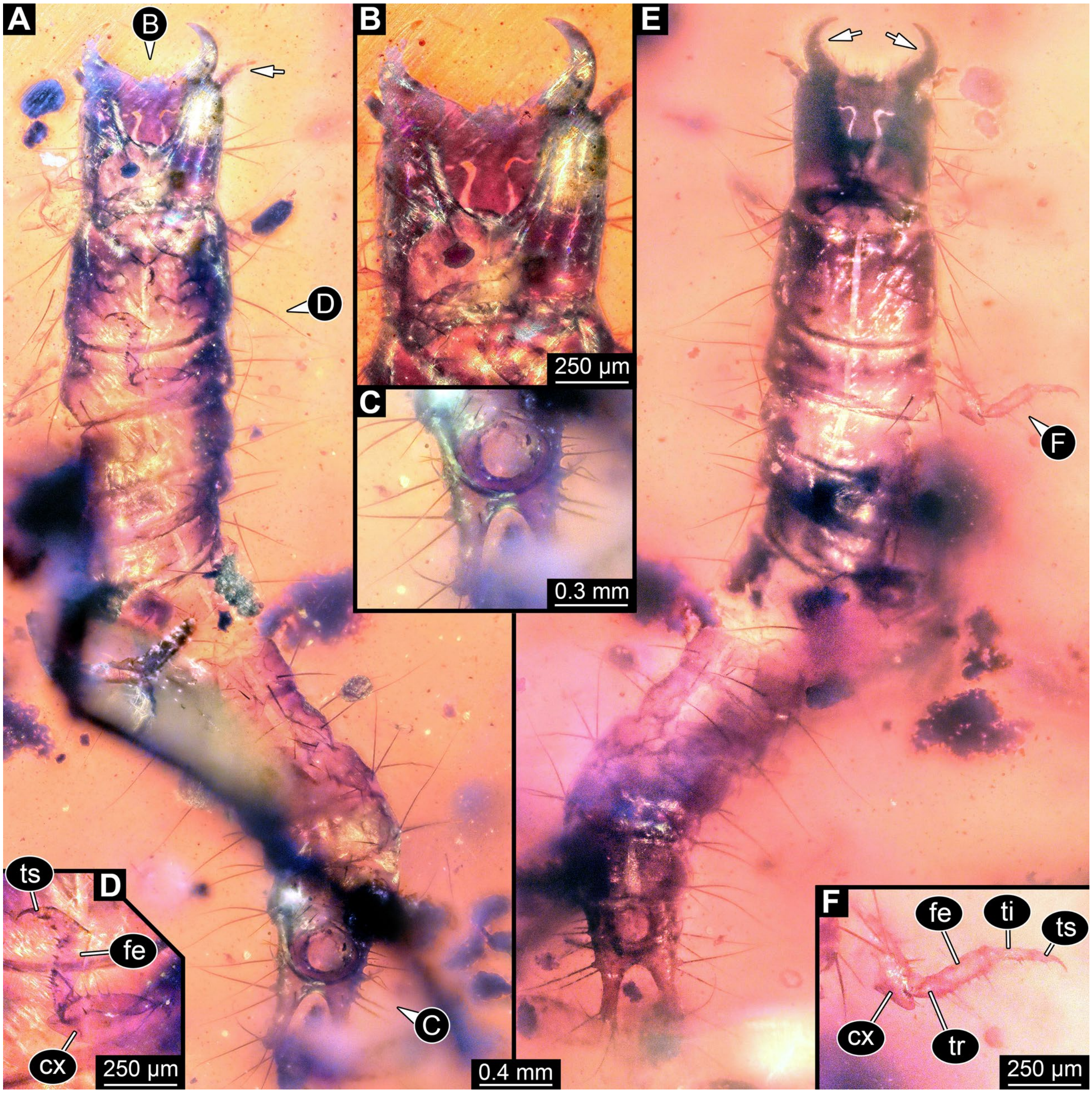

Fig. 6 Fossil larva, PED 1816. **A** Overview in ventral view; arrow marks sensorial structure. **B** Close-up on head region; note the missing maxillo-labial complex. **C** Close-up on posterior trunk region; note ventrally-directed trunk end. **D** Close-up on locomotory appendage (leg). **E** Overview in dorsal view; arrows mark teeth on mandibles. **F** Close-up on locomotory appendage (leg). *cx* coxa, *fe* femur, *ti* tibia, *tr* trochanter, *ts* tarsungulum

larvae of lacewings and their closer relatives. Hence, there is a discrepancy between available and published material, and we present this study as a first step toward correcting this aspect. This observed higher abundance of beetle larvae also indicates an important ecological role of beetles in the Cretaceous amber forests of Kachin.

The larvae of lacewings and allies vs. the larvae of beetles: ecological functions

Lacewing larvae are numerous in Kachin amber, indicating a wood-associated lifestyle. Furthermore, one amber piece described in this study also contained a larva of a lacewing (*Macleodiella* co-occurring with PED 0436a–c; Zippel et al., 2021, p. 479, fig. 2). Such syninclusions

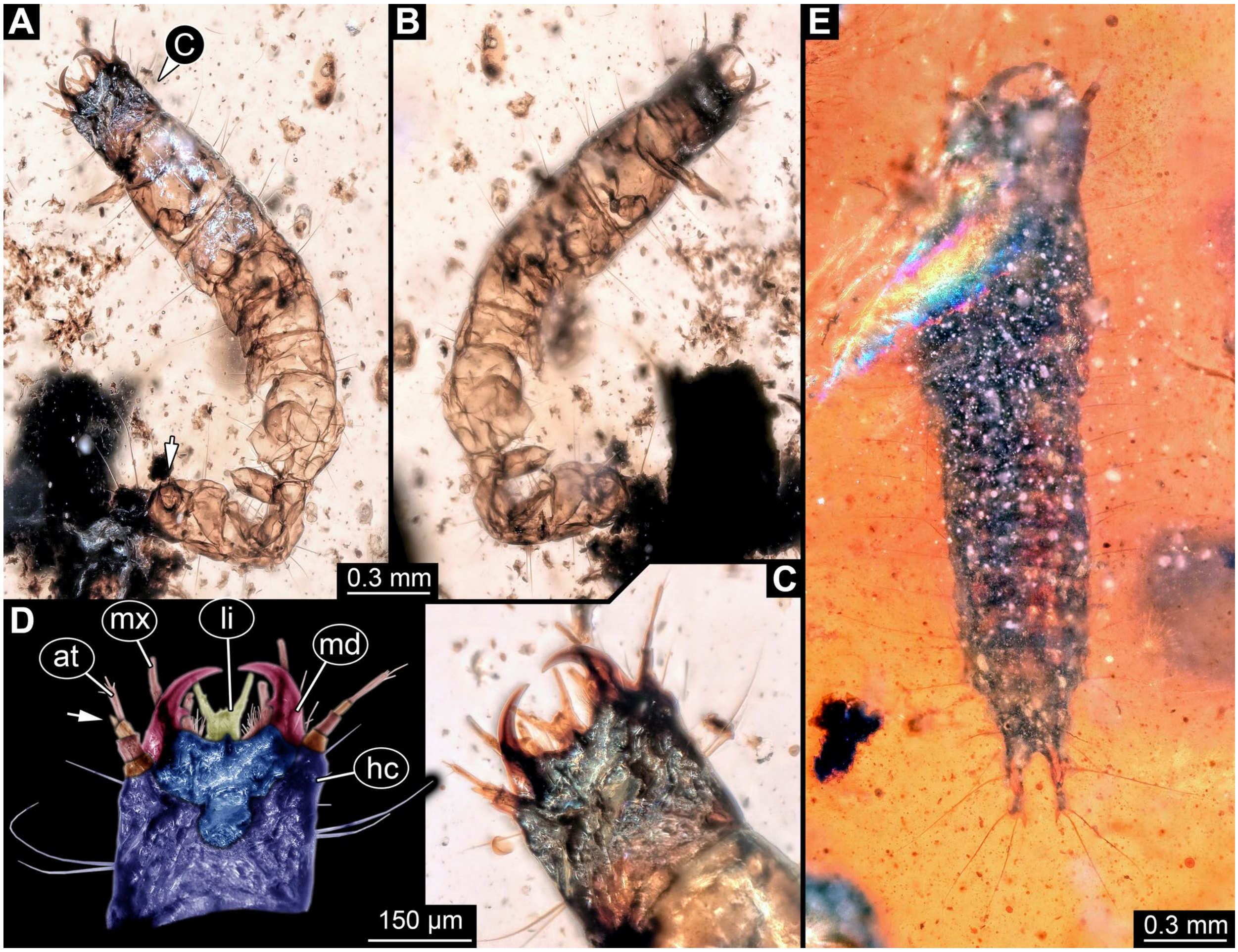

Fig. 7 Fossil larvae. **A**–**D** PED 1978. **A** Overview; anterior region in dorsal view, posterior region in ventral view, arrow marks sensorial structure. **B** Overview; anterior region in ventral view, posterior region in dorsal view. **C** Close-up on head region in dorsal view. **D** Colour-marked version of **C**; arrow marks sensorial structure. **E** PED 3206, overview in presumed dorsal view. *At* antenna, *hc* head capsule, *li* labium, *md* mandible, *mx* maxilla

usually indicate a shared habitat, especially due to the poor dispersal capabilities of these larvae (Solórzano-Kraemer et al. 2015, 2018). Together with the similar size and common predatory nature in both groups, these findings warrant an ecological comparison between larvae of lacewings and larvae of beetles.

The relative length of the mouthparts and the width of the head capsule have a direct influence on the power transmission from the predator onto the prey (Fig. 14). A shorter mouthpart means a shorter lever, which means that the power can be transferred more effectively. A relatively broader head leaves more space within the head capsule for muscles, and the levering angle acting on the mandibles is more effective (Gorb & Beutel, 2000; Hörnschemeyer et al., 2013; Lawrence, 1991). We can therefore assume a relatively powerful biteforce in the beetle larvae presented here, compared to the larvae of lacewings (Fig. 13). As many of the Cretaceous lacewing larvae had longer stylets, i.e. compound structures including the mandibles, and seemingly rather weak force transmission (Haug et al., 2019b, 2023c; Fig. 13), a possible balance to make lacewing larvae capable predators may have been the injection of venom.

The larvae of the closely related groups Raphidioptera (e.g., Aspöck et al., 1975; Woglum & McGregor, 1958, 1959) and Megaloptera (e.g., Beutel & Friedrich, 2008; Bowles & Contreras-Ramos, 2016; Bowles & Sites, 2015) have shorter mandibles and do not inject venom, reinforcing this assumption. Some beetle larvae do inject venom into their prey despite having short mandibles, such as larvae of Texas beetles that feed on other small representatives of Euarthropoda (Brachypsectridae;

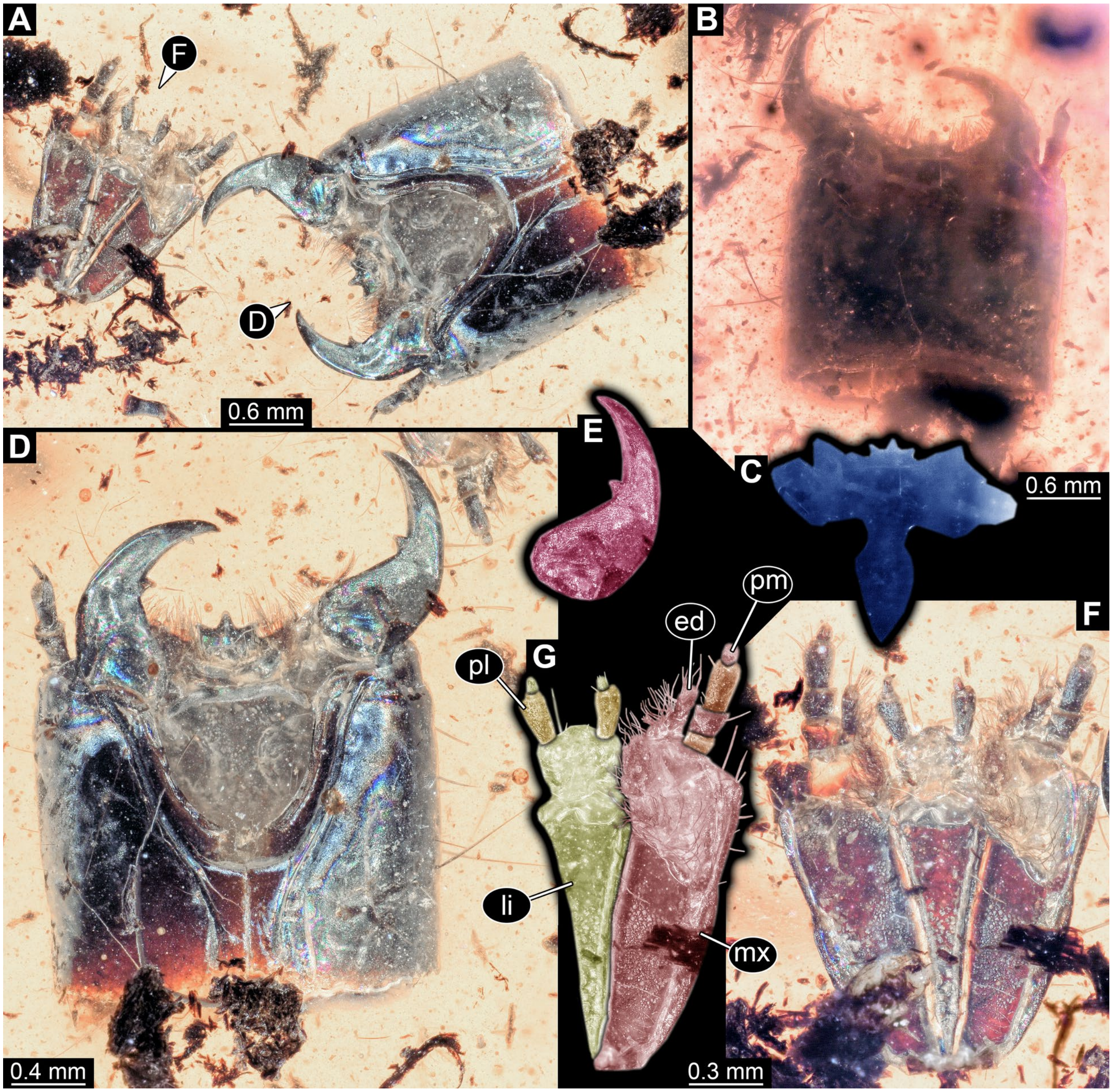

Fig. 8 Fossil larva, PED 2879. **A** Overview of head and isolated maxillo-labial complex. **B** Head in dorsal view. **C** Colour-marked fronto-clypeus (or nasale) of **B**. **D** Head in ventral view, note missing maxillo-labial complex. **E** Colour-marked mandible of **D**. **F** Maxillo-labial complex. **G** Colour-marked left maxilla and labium of **F**. *ed* endite (possible galae), *li* labium, *mx* maxilla, *pl* palp of labium, *pm* palp of maxilla

Costa et al., 2006; Haug et al., 2021b; Lawrence et al., 2011) or some larvae of click beetles, namely of the group Drilini, that predate on terrestrial snails (Bocak et al., 2005, fig. 4.9.4.C). Exceptions include some venomous predatory larvae of diving beetles (Dytiscidae) that have relatively long mandibles (e.g., Michat, 2006, figs. 16–18 p. 836; Michat, 2010, fig. 2 p. 379; Yee, 2014 fig. 1.4 p. 6), most strongly expressed in cases where the labrum is elongated and forms a special three-finger grasping structure (e.g., Michat & Torres, 2011; Spangler, 1963, 1966; Wise, 1961).

It seems possible that lacewings and beetles fulfilled different ecological functions, specialising on different prey items and hunting strategies: beetles on biteforce, lacewings on reach and potentially venom injection. Predators like the larvae of Myrmeleontiformia

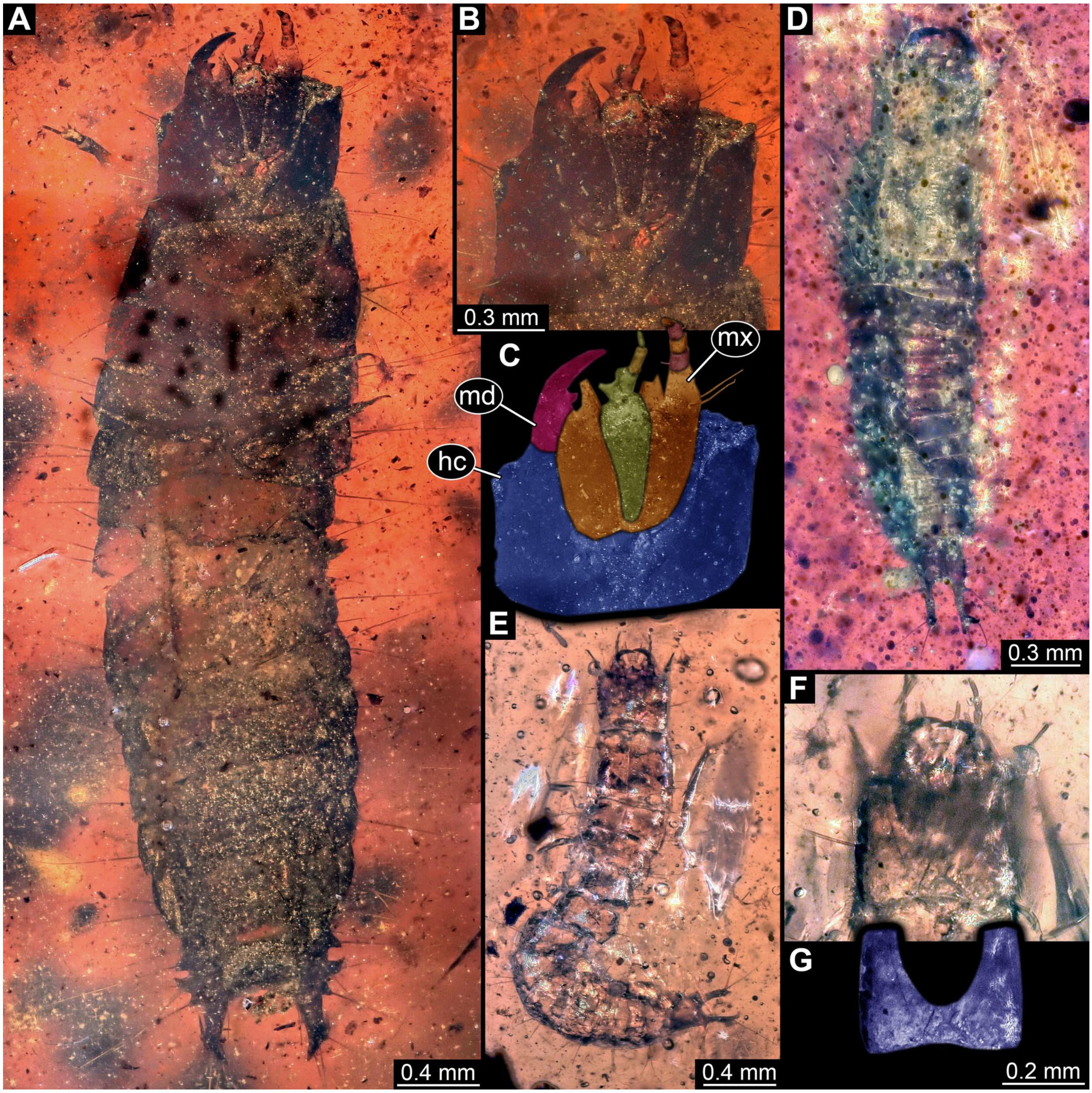

Fig. 9 Fossil larvae. **A**–**C** PED 3006. Overview in ventral view. **B** Close-up on head in ventral view. **C** Colour-marked version of **B**. **D** PED 2457; overview in possible ventral view. **E**–**G** PED 3550. **E** Overview in dorsal view. **F** Close-up on head in ventral view. **G** Colour-marked head capsule of **F**; note the large U-shaped indentation for the maxillo-labial complex. *hc* head capsule, *md* mandible, *mx* maxilla

(including the famous antlions) and aphidlions (Chrysopidae), for example, are specialised in grabbing and piercing (larger) prey like ants or aphids. Their stylets are curved, and some can open their stylets up to 180°. Straight stylets like the ones of Mantispidae are specialised in piercing. They are used for feeding on eggs from spider egg sacks (Aspöck & Aspöck, 2007). Niche differentiation is a well-known phenomenon in co-occurring organisms, reducing exploitation competition (e.g., Peterson & Holt, 2003; Zuppinger-Dingley et al., 2014). As more than just these two groups of predators are known in the Kachin amber forest, there must have been consecutively more differentiation of ecological functions between these predators, even

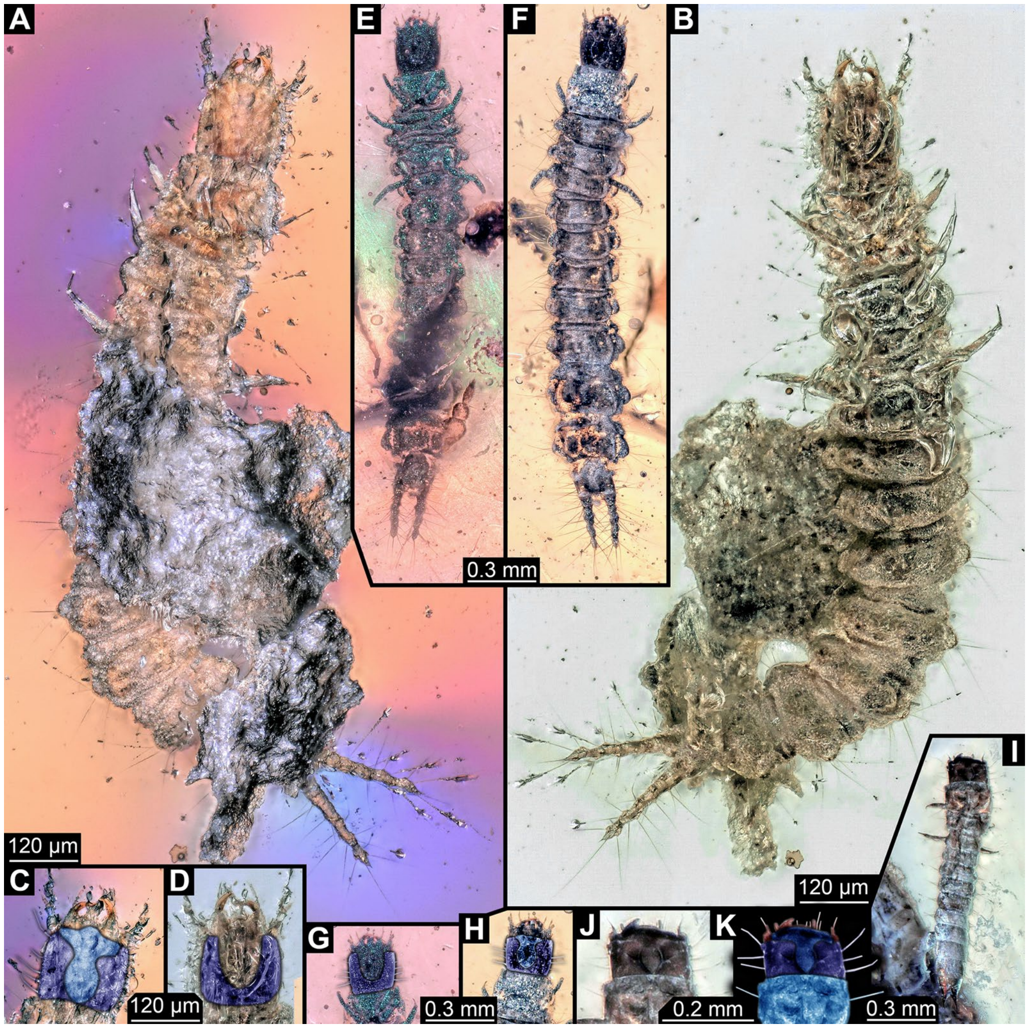

Fig. 10 Fossil larvae. **A**–**D**. SNHMB.G 8522. **A** Overview in dorsal view. **B** Overview in ventral view. **C** Colour-marked head capsule and fronto-clypeus (or nasale) of **A**. **D** Colour-marked head capsule of **B**; note the large U-shaped indentation for the maxillo-labial complex. **E**–**H**. SNHMB.G 8521. **E** Overview in ventral view. **F** Overview in dorsal view. **G** Colour-marked head capsule of **E**; note the large U-shaped indentation for the maxillo-labial complex. **H** Colour-marked head capsule and fronto-clypeus (or nasale) of **F**. **I**–**K**. SNHMB.G 8520. **I** Overview in dorsal view. **J** Close-up on head in dorsal view. **K** Colour-marked head capsule and fronto-clypeus (or nasale) of **J**

when restricting the view to the terrestrial realm. While the larvae reported here seem likely to have hunted for prey on or in wood, the few known ground beetle larvae from Kachin amber (Li et al., 2024; Liu et al., 2023a, 2023b; Rosová et al., 2023) are likely surface-runner types hunting on the ground, further demonstrating that predatory beetle larvae and lacewing larvae showed signs of niche differentiation.

Predatory beetle larvae at other time slices

The reported material of beetle larvae likely reflects a fraction of the available material, hampering large-scale comparisons, but constructs certain patterns. In the Palaeozoic record, there are no predatory larvae of beetles (Kirejtshuk, 2020; Shcherbakov & Ponomarenko, 2023). In the Triassic, larvae of ground beetle relatives seem to be the earliest predatory forms in the terrestrial realm (Prokin et al., 2013), though aquatic predatory beetle larvae are also shown to be present in both the Triassic (Ghosh et al., 2007) and the Jurassic (Wang et al., 2009; Wooton 1988). In Cretaceous ambers, click beetle larvae seem to be among the most common predatory beetle larvae, but also other forms are known (Gustafson et al., 2020; Liu et al., 2023a; Rosová et al., 2023; Zhao et al., 2019). In the Eocene, common

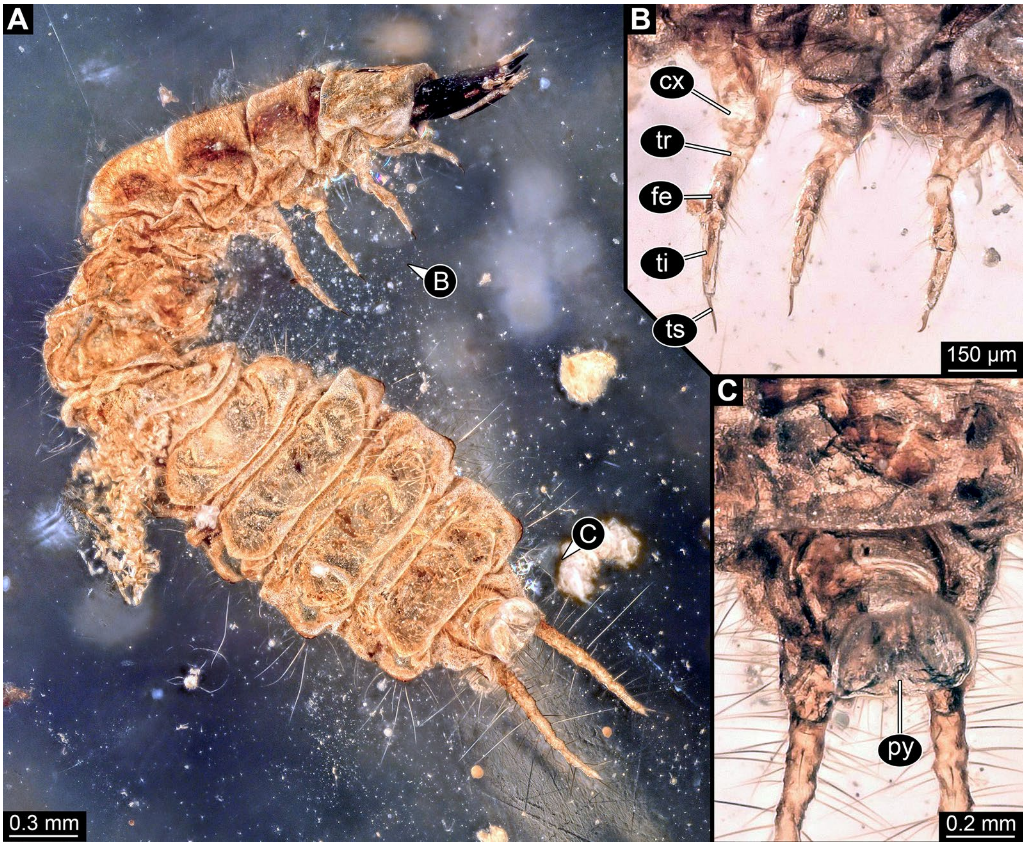

Fig. 11 Fossil larva SNHMB.G 8519. **A** Overview. **B** Close-up on locomotory appendages (legs). **C** Close-up on posterior trunk region. *cx* coxa, *fe* femur, *py* pygopod, *ti* tibia, *tr* trochanter, *ts* tarsungulum

predatory larvae are those of checker beetle relatives (Gröhn, 2015; Lawrence et al., 2008; Weitschat, 2009; Weitschat & Wichard, 2002).

This incomplete specimen data suggests a series of substitutions in the terrestrial fauna, first larvae of ground beetles, then click beetles, then checker beetles. However, molecular reconstructions suggest a Triassic origin for all three groups, with a first diversification in the Jurassic (McKenna et al., 2019). The difference between Kachin amber and the younger ambers still demands further investigation.

Conclusion

The herein newly described specimens are click beetle larvae of the Cretaceous from Kachin. They most likely are representatives of the group Elateridae: Pityobiinae. Their morphology indicates a predatory lifestyle associated to wood-dwelling. They show functional differences and also can be quantitatively differentiated from other predatory holometabolan larvae that shared the same habitat, indicating different ecological functions in the amber forests of Kachin. The discrepancy between beetle larvae available in amber and published specimens is high and needs to be addressed to further our understanding of ancient ecosystems.

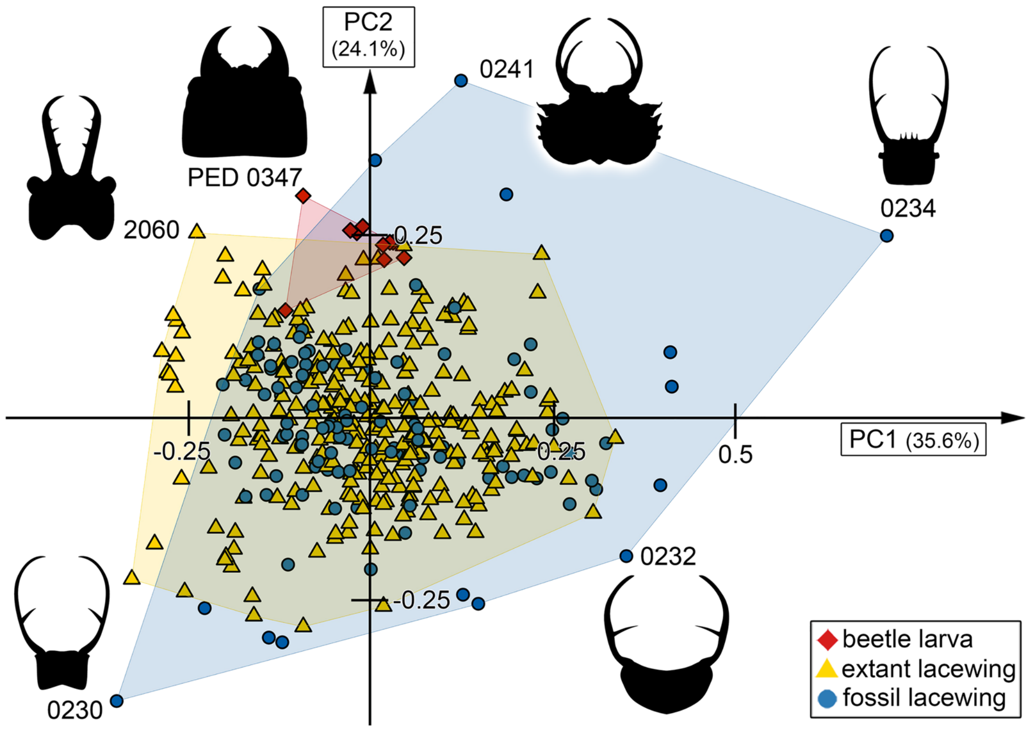

Fig. 12 Morphospace represented by scatter plot of the principal components (PCs) 1 and 2 of the head capsule with mouthparts of fossil beetle larvae and extant and fossil lacewing larvae; numbers represent either collection numbers (PED) or numbers in the dataset

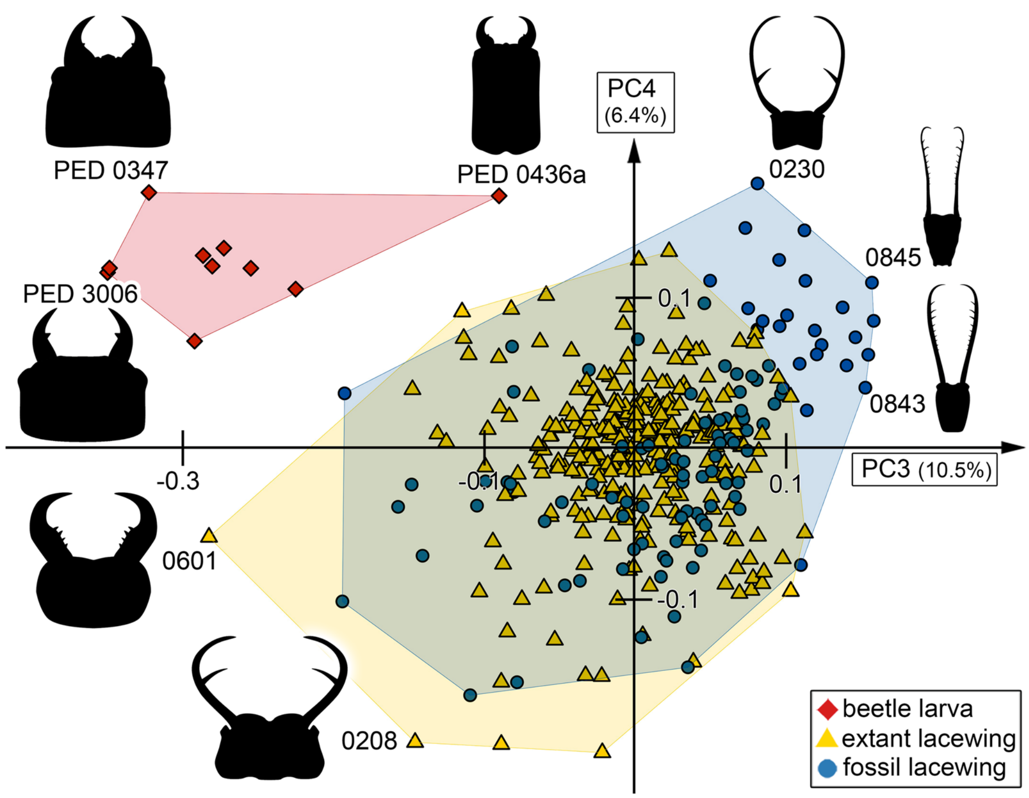

Fig. 13 Morphospace represented by scatter plot of the principal components (PCs) 3 and 4 of the head capsule with mouthparts of fossil beetle larvae and extant and fossil lacewing larvae; numbers represent either collection numbers (PED) or numbers in the dataset

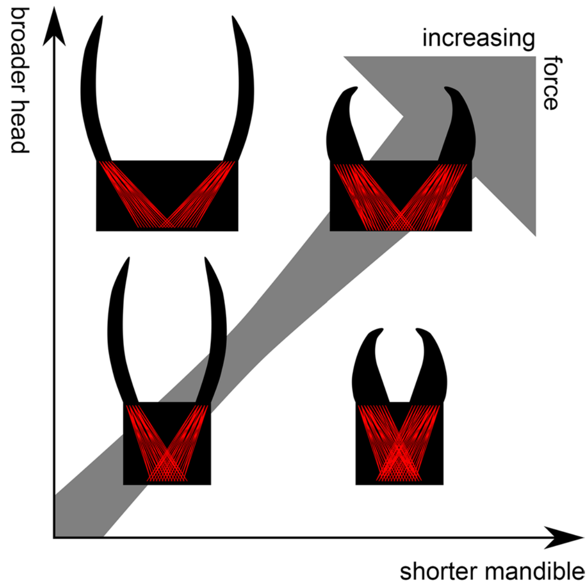

Fig. 14 Scheme on the influence of head width and mandible length on the biting force

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-025-00393-2.

Supplementary file 1. Scree plot of the component loadings from the PCA on the head capsule shape with stylets. Depicted are the respective proportions of variation in the data explained by the first 27 principal components amounting together to over 99% of variation in the data as grey bar plots. Labels represent percentage values.

Supplementary file 2. Table including specimen identifier, sorting variable and scores for the first 27 principal components of the PCA on the head capsule shape with stylets, used for the morphospace analysis.

Supplementary file 3. Graphical component loadings of the PCA on the head capsule shape with stylets. Depicted are the mean shape, and +/- 0.5, 1, 2 standard deviations of the mean shape into one or the other direction for every of the 27 principal components.

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Author contributions
Conceptualization, SL, AZ, CH, JTH and FB; funding acquisition, JTH; investigation, SL, AZ, CH, JTH and FB; methodology, SL, AZ, GTH, CH, JTH and FB; resources, PM, CH and JTH; writing—original draft preparation, SL, AZ, JTH and FB; writing—review and editing, SL, AZ, GTH, PM, CH, JTH and FB; visualization, SL, GTH, CH, JTH and FB. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials
All data generated or analysed during this study are included in this published article, its figures and its supplementary files. The reconstructed shapes, a reference table detailing source material and meta data of reconstructed specimens, and custom scripts for the R-statistics environment can be downloaded at doi.org/https://doi.org/10.5281/zenodo.15464090 or from the corresponding author upon request (florian.braig@palaeo-evo-devo.info).

Declarations

Ethics approval and consent to participate
The current hard moratorium by the Society of Vertebrate Palaeontology (SVP) suggests February 2021 as a cut-off date for acquired amber material from Myanmar (Theodor et al., 2021). The amber pieces of this study were exported mostly before February 2021, but export dates are not available for all specimens. Another contemporary concern is that of involving local people in research in order to avoid so-called "parachute science" (e.g., Haug et al., 2023c; Stefanoudis et al., 2021; Zin-Maung-Maung-Thein & Zaw 2021). We have successfully established a collaboration with biologists from the University of Yangon, Myanmar, to improve this aspect and recently published the first papers resulting from this collaboration (Haug et al., 2023d, 2023e).

Competing interests
The authors declare no competing interests.

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