PalZ (2024) 98:245–262
https://doi.org/10.1007/s12542-023-00682-6

RESEARCH PAPER

Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber

Ana Zippel[1] · **Carolin Haug**[1,2] · **Patrick Müller**[3] · **Joachim T. Haug**[1,2]

Received: 21 November 2022 / Accepted: 20 December 2023 / Published online: 1 May 2024

Abstract

Beetle larvae show high diversity in forms and ecological roles. Beetle larvae are often roughly categorised into certain larval types, for example: campodeiform, denisciform, scarabeiform, or elateriform. Larvae of the latter type are virtually absent from the fossil record. Here, we report three amber pieces from Cretaceous Kachin amber, Myanmar (about 100 million years old) that together include nine elateriform beetle larvae. One of the amber pieces has a single specimen included. The specimen is interpreted as a larva of Elateridae, the group of click beetles, possibly of the ingroup Elaterinae; yet accessible details are limited. Eight specimens within the other two amber pieces show certain similarities with larvae of Elateridae, but show significant differences in the trunk end, which bears two lobes armed with hooks in these fossils. This very specific structure is well known in modern larvae of Ptilodactylidae (toed-winged beetles). Therefore, the fossils are interpreted as larvae of Ptilodactylidae. Both types of here reported elateriform larvae represent the first fossil record of larvae of their respective groups. It is well known that larval morphology does not evolve in concert with adult morphology, and a modern-type morphology of the one may precede that of the other. Hence, the new fossils are important indicators of the appearance of the modern larval morphologies of their respective lineages. We also briefly discuss the fossil record of larvae of Elateriformia (of which Elateridae and Ptilodactylidae are ingroups) in general.

Keywords Elateridae · Click beetles · Ptilodactylidae · Toed-winged beetles · Burmese amber · Cretaceous

Introduction

Coleoptera is one of the most species-rich group of animals with more than 380,000 formally described species (e.g., McKenna et al. 2019). Despite the enormous species richness of beetles, people are usually able to recognise most beetles as such, at least adult beetles. Many beetles have an easily recognisable morphology as adults, with strongly sclerotised exoskeleton and elytra (Beutel and Lawrence 2016), providing a straight line on the back, instead of an oblique one (however, some ingroups do show strong modifications of elytra; e.g., Ferreira et al. 2022; Goczał 2023). In the immatures, there is not one specific morphological character uniting most of the larvae of beetles, and the larvae can have astonishingly different morphologies. To cope with the enormous form diversity of the larvae, they are often grouped into specific types: there are, for example, campodeiform larvae (Jałoszyński and Kilian 2016), onisciform ones (Jałoszyński and Beutel 2012; Jałoszyński 2018), or grubs, also known as scarabeiform larvae, typical for a specific ingroup of beetles, Scarabeidae (dung beetles). A comparable case is that of elateriform larvae, a special type of larvae that occurs in certain species of click beetles (Elateridae; especially in Elaterini, Ampedini, or Cebrionini; Hyslop 1917; Schimmel and Tarnawski 2010 fig. 98 p. 469; Costa et al. 2010; Casari and Biffi 2012).

Such larvae of Elateridae are elongate and slender, with all trunk segments basically tube-shaped. The cuticle is more or less uniformly sclerotised. The head (often) bears sickle-shaped mandibles. The locomotory appendages (legs) are well developed, but are still short in comparison to the

Handling Editor: Ulrich Kotthoff.

✉ Ana Zippel
ana.zippel@palaeo-evo-devo.info

[1] Ludwig-Maximilians-Universität München, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[2] GeoBio-Center at LMU, Richard-Wagner-Str. 10, 80333 Munich, Germany

[3] Kreuzbergstr. 90, 66482 Zweibrücken, Germany

elongate body. The trunk end has no posterior processes in the form of urogomphi (Costa et al. 2010).

Elateriform larvae occur in few other lineages, for example, in other lineages of beetles, such as false click beetles (Eucnemidae; e.g., Otto 2017 p. 3, fig. 1 p. 8), darkling beetles (Tenebrionidae; e.g., Costa and Vanin 2010 fig. 14 left p. 8), riffle beetles (Elmidae; e.g., Barr et al. 2015 fig. 22 p. 543; González-Córdoba et al. 2020 fig. 3B p. 535; Shepard et al. 2020 fig. 2 p. 4), or toed-winged beetles (Ptilodactylidae; e.g., Stribling 1986 fig. 33 p. 227; Lawrence and Stribling 1992 fig. 12), but also in non-coleopteran lineages, such as butterflies and moths (Lepidoptera; Hoare et al. 2006 fig. 25 p. 578) or some scorpionflies (Mecoptera: Nannochoristidae; Pilgrim 1972 figs. 1–3 p. 153). Yet, most common elateriform larvae seem to be representatives of click beetles.

Click beetle larvae can fulfil numerous ecological roles. Some are, for example, ferocious predators that can also subdue much larger prey, such as the likewise predatory larvae of antlions (Devetak and Arnett 2010). Others are saprophagous or phytophagous. With these ecological roles, they are important, and also not rare, components in many habitats.

Click beetles have a quite astonishing fossil record with more than 250 formally described species (recently summarised in Kundrata et al. 2021a tab. A1 pp. 82–88). Of these, 23 species appear to be based on exceptionally preserved specimens in different types of ambers from various ages, including Miocene (Becker 1963; Zaragoza Caballero 1990), Eocene (Iablokoff-Khnzorian 1961; Schimmel 2005; Kirejtshuk and Kovalev 2015; Kundrata et al. 2020), and also Cretaceous ambers (Cockerell 1917; Otto 2019; Zhao et al. 2023). So far, all of these fossils seem to be adult individuals. Also general books providing overviews over amber from different deposits did not include any elateriform larva (Penney 2010; Gröhn 2015).

Toed-winged beetles, on the contrary, have so far quite a scarce fossil record and appear overall understudied (Kundrata et al. 2021b p. 1). Kundrata et al. (2021b) listed five fossil species (their tab. A1 pp. 11–12), each represented by very few specimens (Motschulsky 1856; Chatzimanolis et al. 2012; Alekseev and Jäch 2016; Kirejtshuk et al. 2019). Similarly to the fossil record of click beetles, the fossil record of toed-winged beetles so far includes only adult specimens.

The seeming absence of elateriform larvae is quite remarkable, given the fact that amber in general, and specifically Cretaceous amber has provided numerous types of holometabolan larvae. This includes, for example, larvae of hymenopterans (Lohrmann and Engel 2017), dipterans (Baranov et al. 2020; Liu et al. 2020), lepidopterans (Haug and Haug 2021; Gauweiler et al. 2022), lacewings (Badano et al. 2021; Haug et al. 2021b, c, d, e, 2022a; Hörnig et al. 2022; Zippel et al. 2021; Liu et al. 2022; Luo et al. 2022), and their closer relatives (Haug et al. 2022b; Baranov et al. 2022), but especially also beetles (Haug et al. 2021a, 2023b; Zippel et al. 2022a, 2023). Given the fact that in the modern fauna, elateriform larvae are relatively well-known components of aquatic ecosystems and that adults of Elateridae are known in Cretaceous Myanmar amber, we should expect to be able to find such larvae also in this type of amber.

We here report the first elateriform larvae from Myanmar amber. We discuss implications of this finding.

Materials and methods

Material

In total, three amber pieces are in the centre of this study: BUB 4275, PED 0369, and PED 0925. All three amber pieces originate from about 100-million-year-old Cretaceous Myanmar Kachin amber from the Hukawng Valley (Cruickshank and Ko 2003; Shi et al. 2012). BUB 4275 comes from the collection of one of the authors (PM), PED 0369 and PED 0925 are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München. The PED specimens were legally acquired via the online platform ebay.com from two different traders (globalburmiteamber, burmite-miner).

The three pieces of amber include in total nine elateriform larvae. BUB 4275 includes a single larva of interest, PED 0369 includes in total three larvae of interest, and PED 0925 includes five larvae of interest. All three amber pieces are filled with additional inclusions, such as air bubbles, detritus, or cuticle fragments.

Measuring methods

All specimens were measured separately in ImageJ (Schneider et al. 2012) based on the scales we obtained from the inbuilt software of the Keyence VHX-6000 digital microscope. Each structure of interest was measured with precision, because the most of the specimens we work with are of small size, with very small body parts. However, there are possible small deviations due to the human error, because the measuring process includes a subjective decision on the measuring starting point, and therefore, even such precise measurements are approximate.

Documentation methods

The specimens were documented on a Keyence VHX-6000 digital microscope in front of a white and black background under different illumination settings (cross-polarised, co-axial light, and low-angle ring light; Haug et al. 2018). All images were recorded as composite images (Haug et al. 2011; Kerp and Bomfleur 2011), combining several images of varying focus and several adjacent image details as well as different exposure times (HDR, cf. Haug et al. 2013). Images were further processed and colour-marked with Adobe Photoshop CS2. Comparative drawings were prepared in Adobe Illustrator CS2.

Results

Description of specimen BUB 4275

Amber piece with a single beetle larva. Total body length approximately 8.70 mm. Body elongate, cylindrical (Fig. 1a–c), differentiated into head and elongated trunk. Head prognathous, mouthparts facing forwards, slightly flattened (Fig. 1d, e), semi-ovoid in antero-lateral view, longer than wide, 1.9 × (~ 0.47 mm long). No stemmata discernible. Labrum (derivative of ocular segment), wider

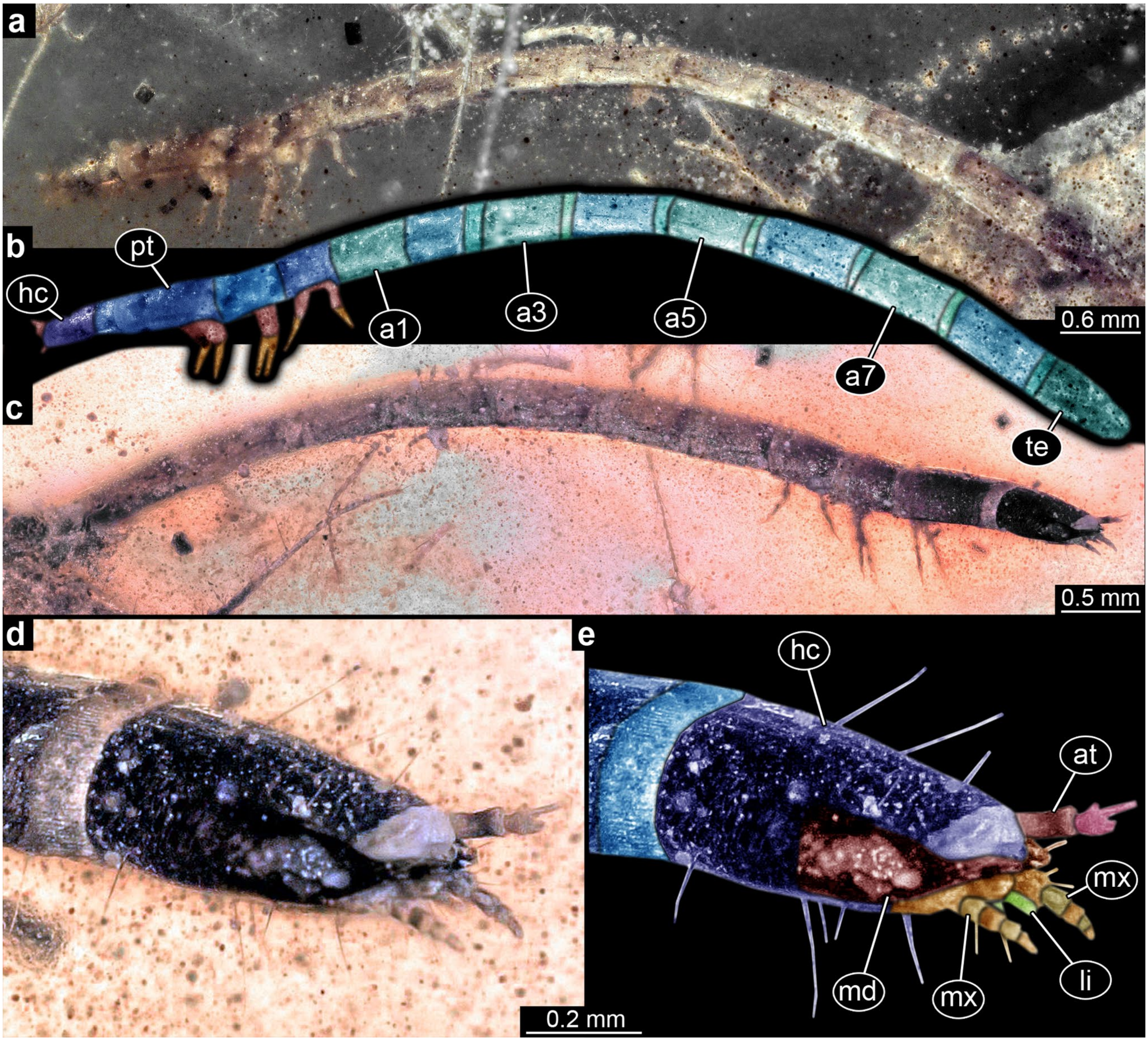

Fig. 1 Fossil specimen BUB 4275, possible larva of Elateridae: **a** habitus in lateral view; **b** colour-marked version of **a**; **c** habitus in antero-lateral view; **d** head in antero-lateral view; **e** colour-marked version of head and its mouthparts based on **d**. *a1–a7* abdomen segments 1–7, *at* antenna, *hc* head capsule, *li* labium, *md* mandible, *mx* maxilla, *pt* prothorax, *te* trunk end

than long, antero-medially drawn out into pentagonal (in antero-lateral view) projection (nasale) (Fig. 1d, e). Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna with two elements discernible, shorter than head capsule, 2.8 × (~ 0.17 mm long). Possible further distal antenna element not accessible. Preserved distal element distally wider and with a spine-like process (Fig. 1d, e). Intercalary segment (post-ocular segment 2) without externally recognisable structures.

Mandibles (appendages of post-ocular segment 3) strongly sclerotised, only partially accessible, appear sickle-shaped in antero-lateral view, right mandible ~ 0.32 mm long. A single seta discernible on left mandible (Fig. 1d, e). Maxillae (appendages of post-ocular segment 4) with two major parts discernible: rectangular proximal part, longer than wide (0.19 mm long), and distal palp, ~ 0.13 mm long. Maxillary palp with four elements (Fig. 1d, e). Labium (conjoined appendages of post-ocular segment 5) partially accessible, distal palps discernible in antero-lateral view.

Trunk further differentiated into thorax and abdomen. Thorax with three segments (pro-, meso-, and metathorax). Each thoracic segment with a pair of locomotory appendages (legs). Prothorax rectangular in lateral view, longer than wide, 2 × (~ 0.67 mm long), also longest segment of thorax. Anterior part of prothorax with a structurally differentiated, possibly more sclerotised region, probably as a ring around the body. Meso- and metathorax sub-similar. Mesothorax wider than long, 1.3 × (~ 0.42 mm long). Metathorax slightly wider than long, 1.1 × (~ 0.34 mm long) (Fig. 1a–c). Legs discernible, ~ 0.55 mm long (Fig. 1a–c).

Abdomen with nine discernible units. Abdomen segments 1–8 subsimilar, rectangular in lateral view, longer than wide (between 0.56 and 0.82 mm long and between 0.29 and 0.37 mm wide). Anterior part of abdomen units 3–9 each with a short, structurally differentiated, possibly more sclerotised region, probably as a ring around the body. Terminal end semi-ovoid in lateral view, longer than proximally wide, 2.1 × (~ 0.75 mm long) (Fig. 1a–c).

General description of larvae in amber pieces PED 0369 and PED 0925

Beetle larvae with elongate, cylindrical body. Body differentiated into head and elongated trunk. Trunk further differentiated into thorax and abdomen. Head prognathous, mouthparts facing forwards. Thorax with three segments (pro-, meso-, and metathorax). Thorax bears on each segment a pair of locomotory appendages (legs). Abdomen with ten discernible units, nine segments, and the trunk end. Segment 9 with tergite and sternite forming a single continuous sclerotic structure. Entire sclerotic structure of subtrapezoid shape in lateral view, with sternal region of approximately half the length of tergal region. Trunk end partly overhung by dorsal part of segment 9, hence functionally ventrally articulated to it. Trunk end with two postero-ventrally orientated, thin, spine-like processes and a two-lobed structure (possible pygopod) with multiple hooks (at least five hooks per lobe).

Description of specimen 1 in amber piece PED 0369 (Fig. 2a–c)

Total body length approximately 9.93 mm. Head semicircular in dorso-lateral view, wider than long, 1.3 × (~ 0.38 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible in dorso-lateral view. Antennae (appendages of post-ocular segment 1) with at least two elements discernible, longer than head, 1.3 × (~ 0.51 mm long) (Fig. 2b, c). Intercalary segment (post-ocular segment 2) without externally recognisable structures. Mandibles (appendages of post-ocular segment 3) not discernible. Proximal parts of maxillae (appendages of post-ocular segment 4) not accessible, possible distal part (palp) apparent (Fig. 2c), no details accessible. Labium (appendages of post-ocular segment 5) not accessible. Anterior and lateral rim of head with several long setae (~ 0.32 mm long).

Three thoracic segments with prominent dorsal sclerite each (tergite, notum; pro-, meso-, and metanotum). Pronotum trapezoid in dorso-lateral view, longer than wide at anterior end, 2 ×, and at posterior end, 1.4 × (~ 0.94 mm long), longest tergite of thorax. Meso- and metanotum subsimilar, rectangular in dorso-lateral view. Mesonotum wider than long, 1.2 × (~ 0.6 mm long). Metanotum wider than long, 1.3 × (~ 0.6 mm long) (Fig. 2b, c). Legs not accessible.

Abdomen segments 1–8 subsimilar, rectangular in dorso-lateral view. Segments 1 and 2 shorter than wide (~ 0.68 mm long and between 0.77 and 0.81 mm wide), segment 5 as long as wide (~ 0.77 mm long), segments 3–4 and 6–8 longer than wide (between 0.82 and 0.86 mm long and between 0.68 and 0.78 mm wide). Abdomen segment 9 sub-trapezoid in dorso-lateral view, longer than proximally wide, 2 × (~ 1.2 mm long) (Fig. 2b, c). Posterior half of segment 9 bears multiple setae (between 0.17 and 0.51 mm long). Trunk end largely concealed, partially visible lobe structure (Fig. 2c).

Description of specimen 2 in amber piece PED 0369 (Figs. 2a, 3a)

Total body length unknown due to the inaccessibility of anterior parts of the specimen (Fig. 3a). Head unaccessible. Thorax and its appendages unaccessible. Abdomen segments 2–9 discernible with total length of ~ 5.95 mm. Segments 2–8 subsimilar, rectangular in dorsal view, between 0.51 and 0.79 mm long and between 0.59 and 0.67 mm wide. Abdomen segment 9 subtriangular in dorsal view, longer than proximally wide, 1.4 × (~ 0.58 mm long) (Fig. 3a). Trunk end not accessible.

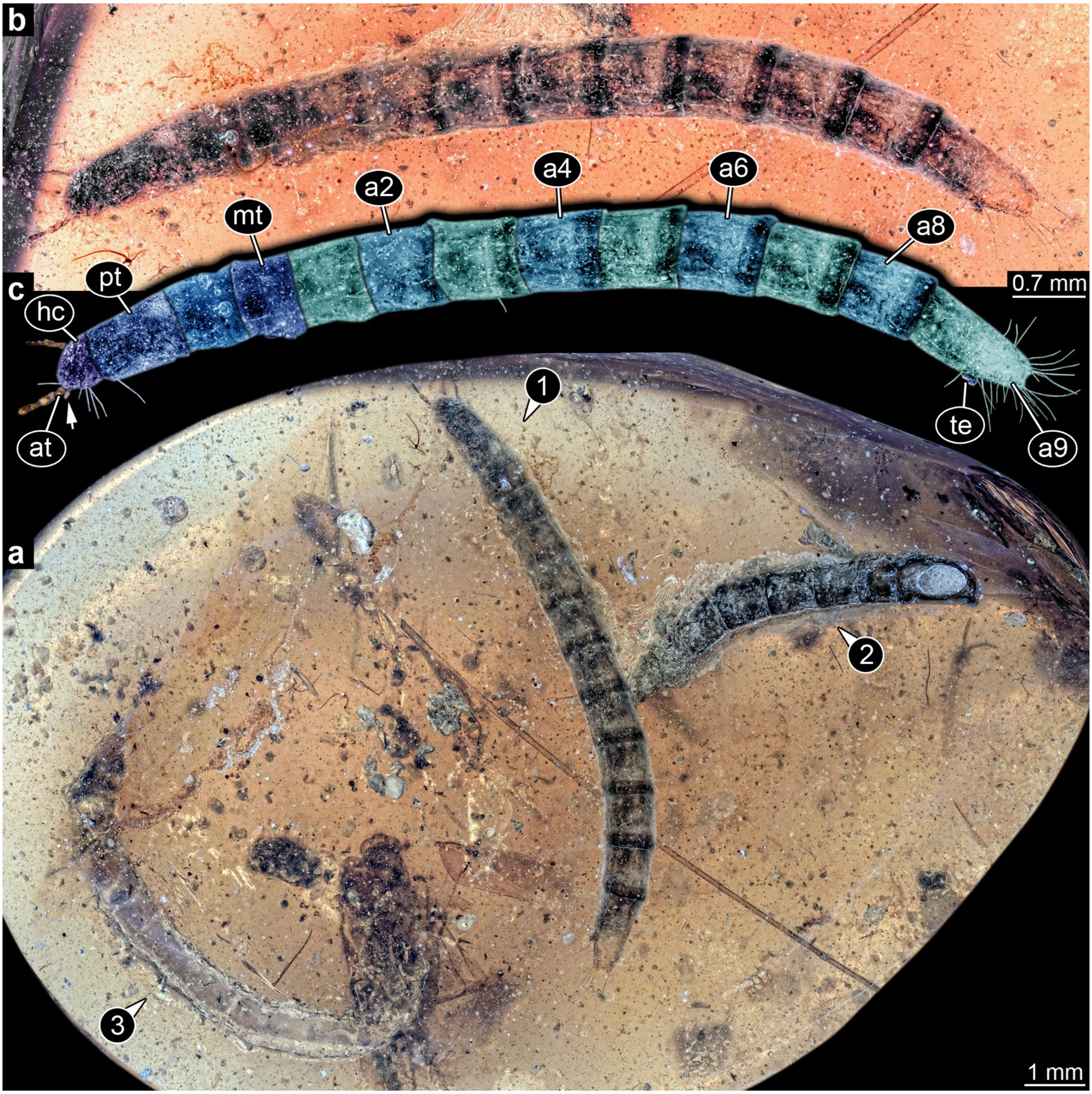

Fig. 2 Amber piece PED 0369 with close-up on specimen 1; **a** amber piece with various inclusions, three specimens of larvae of Ptilodactylidae are numbered 1–3; **b** habitus of specimen 1 in dorso-lateral view; **c** colour-marked version of **b**, palp of maxilla discernible (white arrow). *a2–a9* abdomen segments 2–9, *at* antenna, *mt* metathorax, *pt* prothorax, *te* trunk end

Posterior half of segment 9 bears multiple setae (between 0.01 and 0.21 mm long).

Description of specimen 3 in amber piece PED 0369 (Figs. 2a, 3b–d)

Specimen is damaged in the posterior part of abdomen (Fig. 3b). Total body length only estimated to approximately 9.14 mm. Head pentagonal in dorso-lateral view, longer than wide, 1.7 × (~ 0.68 mm long) (Fig. 3c). No stemmata discernible. Labrum (derivative of ocular segment) strongly sclerotised, pentagonal in dorso-lateral view, posteriorly wider than long, 1.2 × (~ 0.43 mm long) (Fig. 3d). Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna with at least two elements discernible, accessible part shorter than

Fig. 3 Specimens 2 and 3 of amber piece PED 0369; **a** habitus of specimen 2 in dorsal view; **b** habitus of specimen 3 in dorso-lateral view, hooks of trunk end discernible (white arrow); **c** head in dorso-lateral view; **d** colour-marked version of head and its mouthparts based on **c**, palps of maxillae discernible (white arrows). *at* antenna, *hc* head capsule, *li* labium, *lr* labrum, *md* mandible, *mx* maxilla

head. Intercalary segment (post-ocular segment 2) without externally recognisable structures. Mandibles (appendages of post-ocular segment 3) strongly sclerotised, only partially accessible (Fig. 3c, d). Proximal parts of maxillae (appendages of post-ocular segment 4) only partially accessible, distal part (palp) apparent. Maxillary palp with four elements (Fig. 3d, white arrows). Labium (conjoined appendages of post-ocular segment 5) partially accessible, possible distal palps discernible in dorso-lateral view.

Thorax tube-like in lateral view, with total length of ~ 1.35 mm. Separate thoracic segments not discernible (Fig. 3b). Legs not accessible.

Abdomen tube-like in lateral view, with total length of ~ 7.12 mm. Separate abdomen segments 1–8 not clearly discernible. Abdomen segment 9 triangular in lateral view, longer than proximally wide, 2.3 × (~ 1.42 mm long) (Fig. 3b). Trunk end largely concealed, partially visible hooks on lobe structure (Fig. 3b, white arrow).

Description of specimen 1 in amber piece PED 0925 (Fig. 4a, b)

Total body length approximately 8.25 mm. Head trapezoidal in lateral view, longer than wide, 1.4 × (~ 0.37 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible in lateral view. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible, accessible part shorter than head capsule, 1.7×(~0.22 mm long). Number of elements not discernible (Fig. 4b). Intercalary segment (post-ocular segment 2) without externally recognisable structures. Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4), and labium (appendages of post-ocular segment 5) not accessible.

Prothorax tube-like in lateral view, anteriorly and posteriorly wider, longer than wide at posterior end, 2.2×(~0.78 mm long), also longest segment of thorax. Meso- and metathorax subsimilar, rectangular in lateral view. Mesothorax wider than long, 2.1×(~0.25 mm long). Metathorax wider than long, 1.2×(~0.47 mm long) (Fig. 4b). Legs discernible, ~0.6 mm long (Fig. 4b, white arrows).

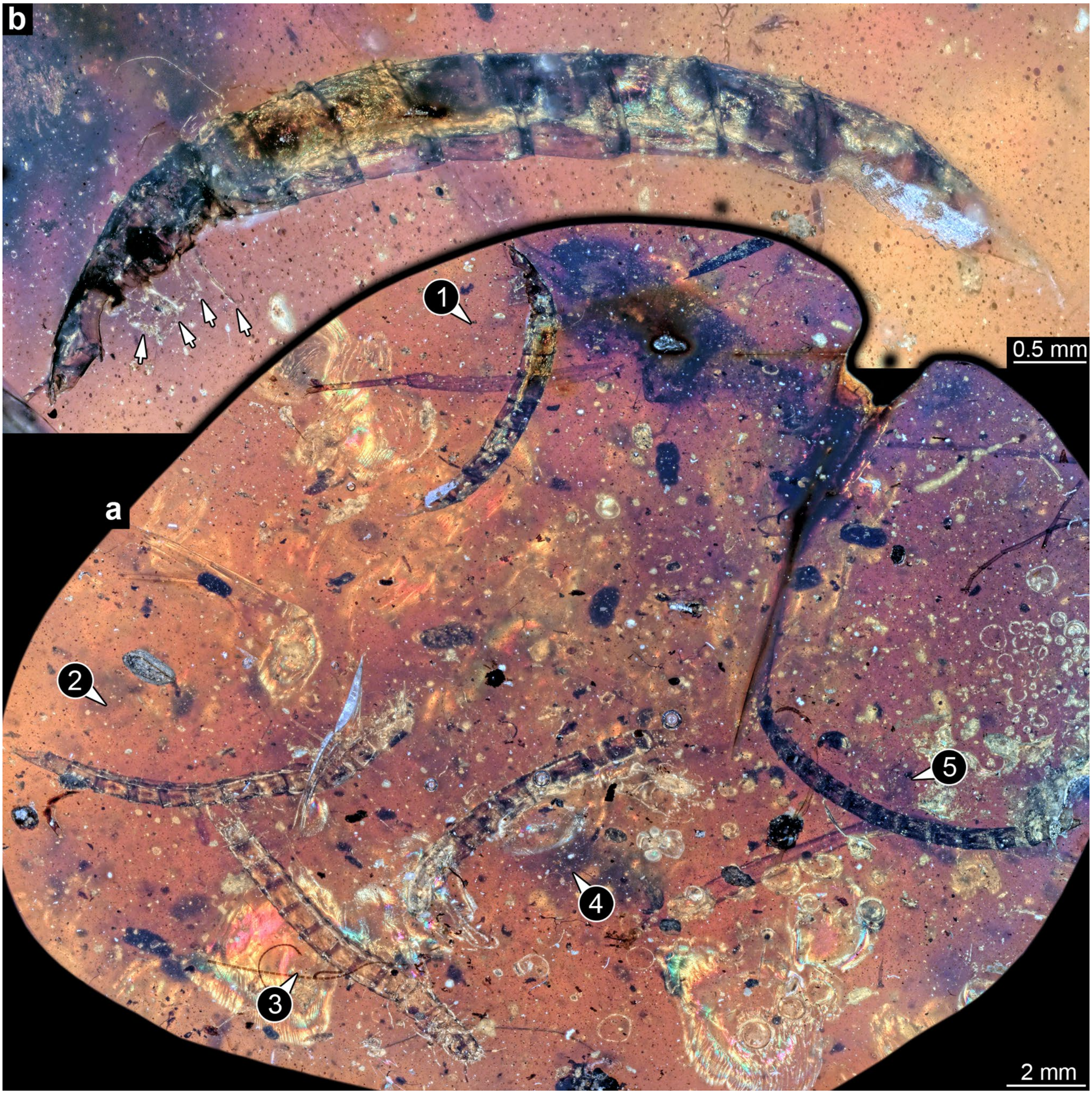

Fig. 4 Amber piece PED 0925 with close-up on specimen 1; **a** amber piece with various inclusions, five specimens of larvae of Ptilodactylidae are numbered 1–5; **b** habitus of specimen 1 in lateral view, probable legs discernible (white arrows)

Abdomen segments 1–8 subsimilar, rectangular in lateral view. Abdomen segments 1–6 wider than long (between 0.47 and 0.72 mm long and between 0.7 and 0.82 mm wide). Abdomen segments 7–8 longer than wide (between 0.8 and 0.95 mm long and 0.55 and 0.66 mm wide) (Fig. 4b). Abdomen segment 9 triangular in lateral view, longer than wide at proximal end, 2.5 × (~ 1.17 mm long) (Fig. 4b). Trunk end not accessible.

Description of specimen 2 in amber piece PED 0925 (Figs. 4a, 5a, 6c, d)

Total body length approximately 10.87 mm. Head semi-ovoid in lateral view (Fig. 5a), longer than wide, 1.3 × (~ 0.51 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not accessible. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible, longer than head, 1.7 × (~ 0.86 mm long) (Fig. 5a, white arrow). Intercalary segment (post-ocular segment 2) without externally recognisable structures. Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4), and labium (appendages of post-ocular segment 5) not accessible.

Prothorax tube-like, subrectangular in lateral view, longer than wide, 1.8 × (~ 1.14 mm long), also longest segment of thorax. Meso- and metathorax subsimilar, wider than long, 1.1 × (~ 0.78 mm long) (Fig. 5a). Legs discernible, ~ 1.38 mm long (Fig. 5a).

Abdomen segments 1–8 subsimilar, rectangular in lateral view, longer than wide (between 0.75 and 0.86 mm long and between 0.51 and 0.77 mm wide). Abdomen segment 1 widest segment of abdomen. Abdomen segment 9 trapezoidal in

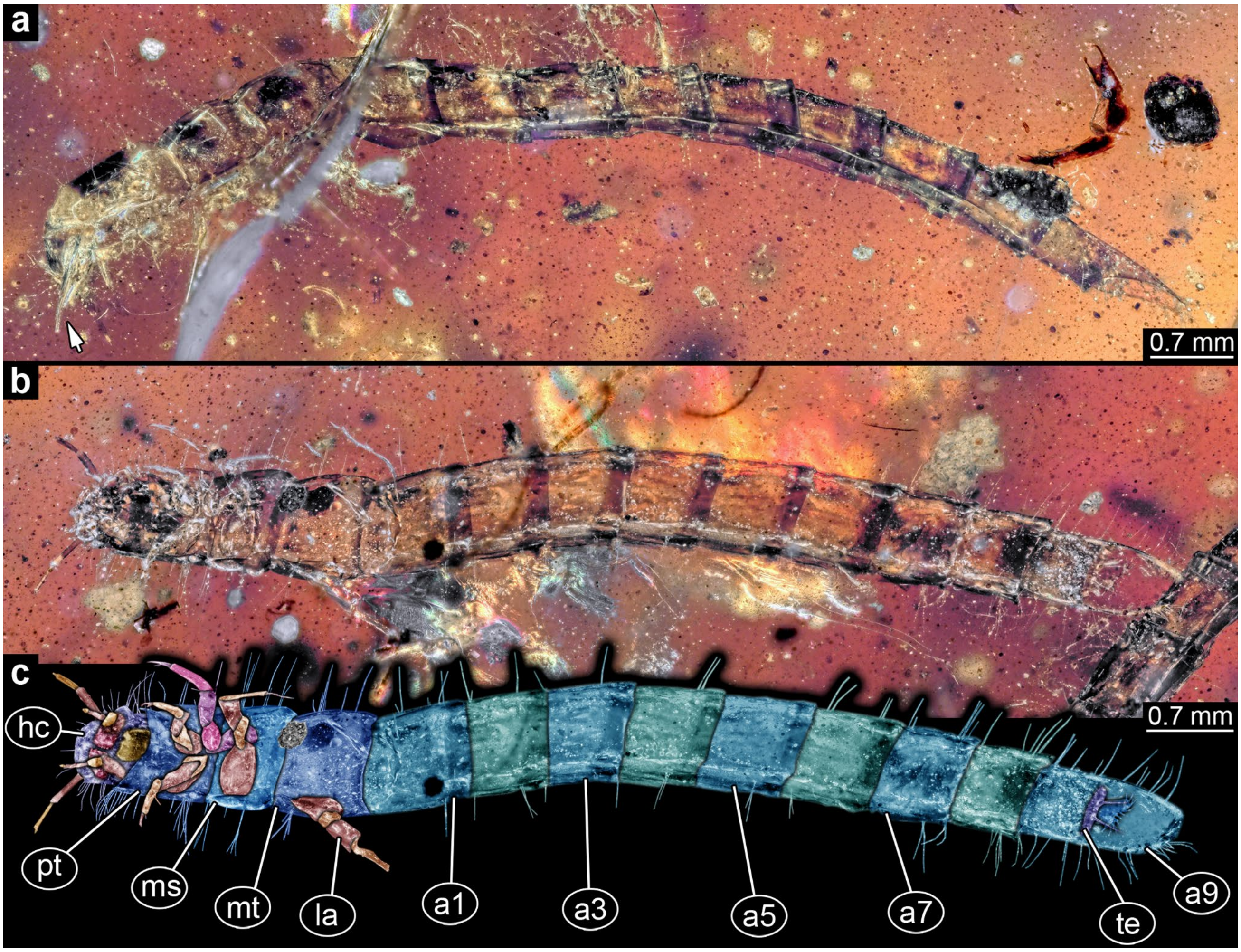

Fig. 5 Specimens 2 and 3 of amber piece PED 0925; **a** habitus of specimen 2 in lateral view, probable antenna discernible (white arrow); **b** habitus of specimen 3 in ventral view; **c** colour-version of **b**. *a1–9* abdomen segments 1–9, *hc* head capsule, *la* locomotory appendages (legs), *ms* mesothorax, *mt* metathorax, *pt* prothorax, *te* trunk end

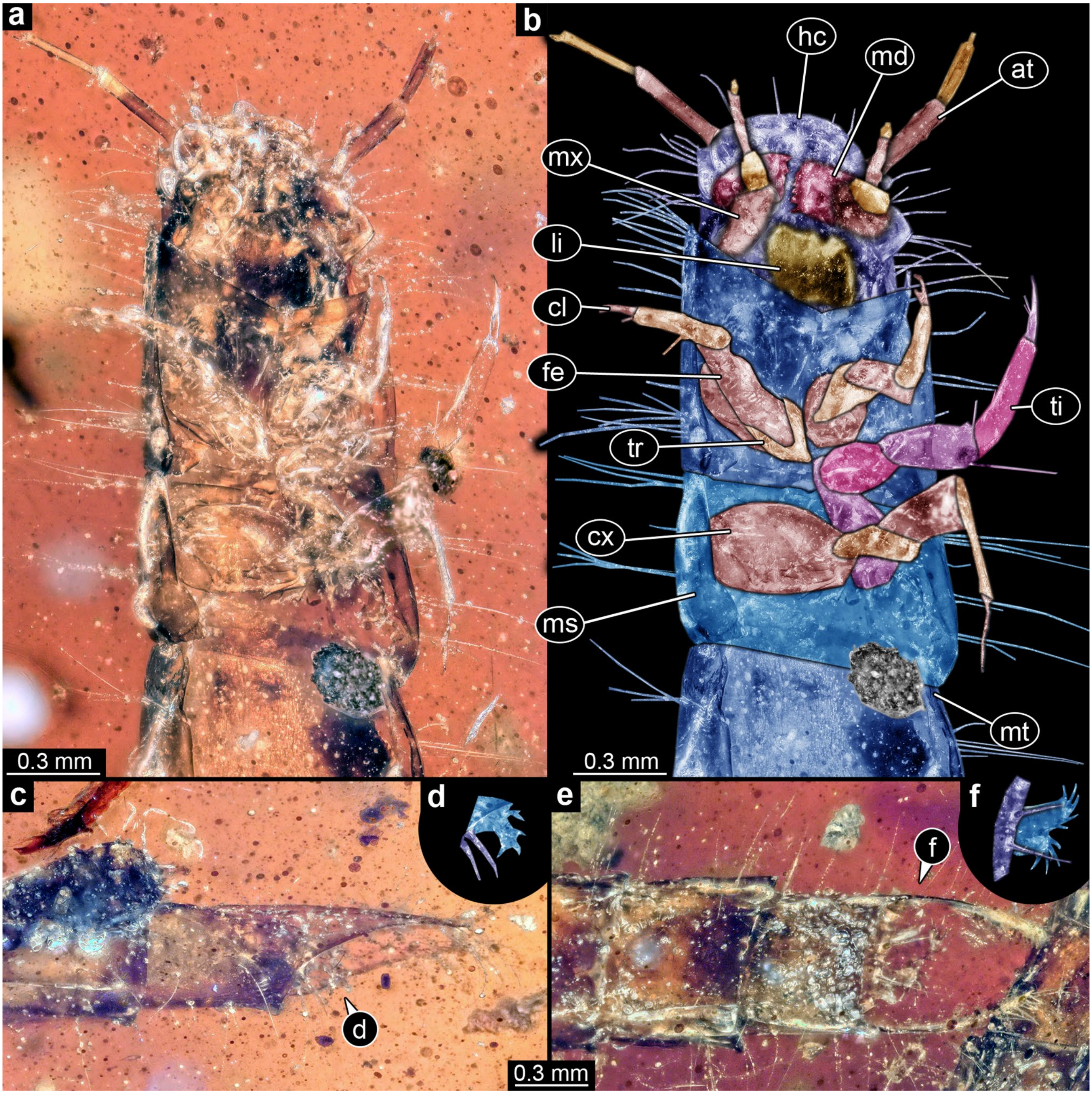

Fig. 6 Close-ups of specimens 2 and 3 of amber piece PED 0925; **a** close-up of head, pro-, and mesothorax of specimen 3 in ventral view; **b** colour-marked version of **a**; **c** close-up of abdomen segment 9 and trunk end of specimen 2; **d** colour-marked version of trunk end from **c**; **e** close-up of abdomen segments 8–9 and trunk end of specimen 3; **f** colour-marked version of trunk end from **e**. *at* antenna, *cl* claw, *cx* coxa, *fe* femur, *hc* head capsule, *li* labium, *md* mandible, *ms* mesothorax, *mt* metathorax, *mx* maxilla, *ti* tibia, *tr* trochanter

lateral view, with convex posterior lateral sides of segment, tergite longer than sternite, 2.4 × (tergite ~ 1.38 mm long) (Figs. 5a, 6c). Trunk end partially concealed, with partially visible two postero-ventrally orientated, thin, spine-like processes and lobed structure with hooks (Fig. 6c, d). Body bears setae (between 0.1 and 0.28 mm long).

Description of specimen 3 in amber piece PED 0925 (Figs. 4a, 5b, c, 6a, b, e, f)

Total body length approximately 9.55 mm. Head (Fig. 6b) semicircular in ventral view, wider than long, 1.3 × (~ 0.53 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible, but presumed. Antennae (appendages

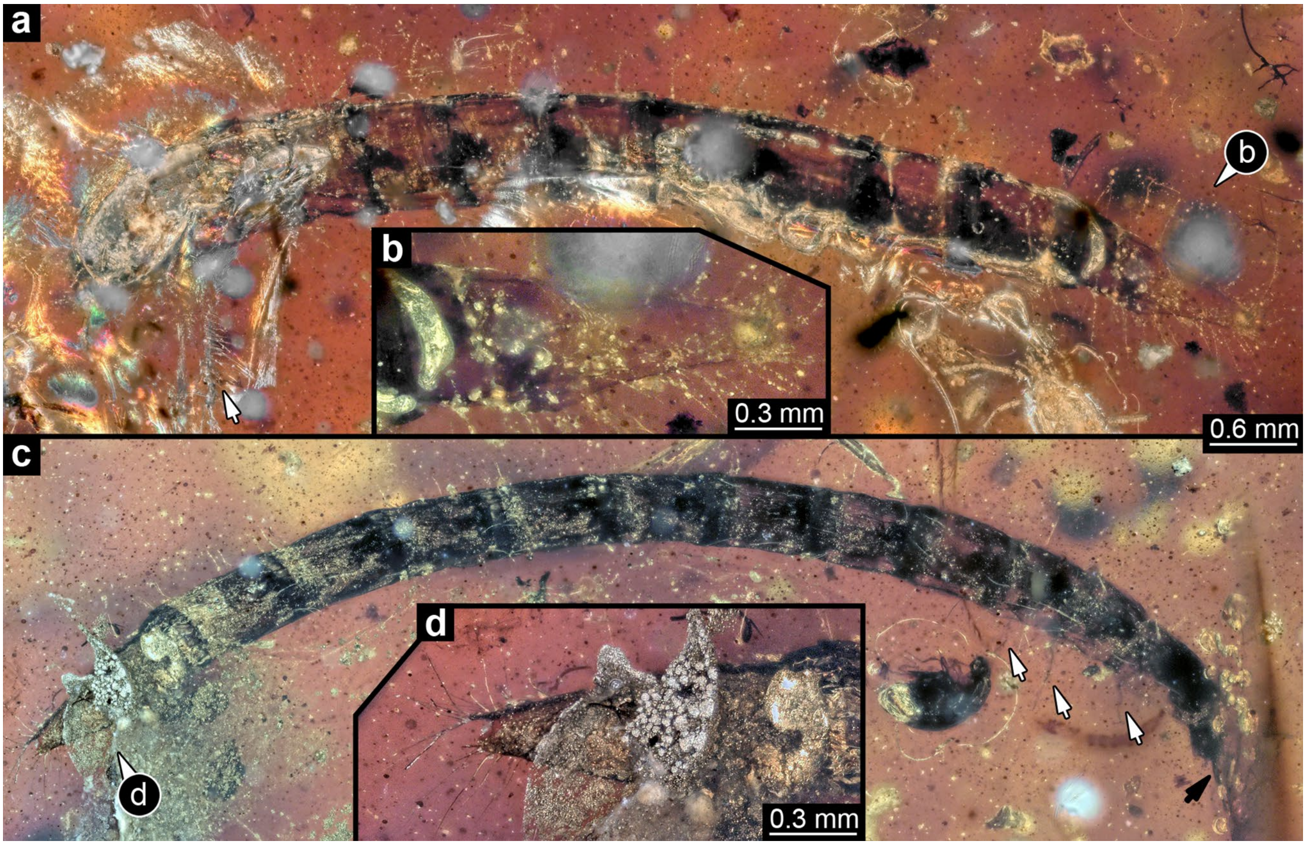

Fig. 7 Specimens 4 and 5 of amber piece PED 0925; **a** habitus of specimen 4 in dorsal view, probable leg discernible (white arrow); **b** close-up of abdomen segment 9 of specimen 4; **c** habitus of specimen 5 in dorso-lateral view, probable antenna (black arrow) and legs (white arrows) discernible; **d** close-up of abdomen segment 9 of specimen 5 in dorsal view

of post-ocular segment 1) with two elements and a short distal process discernible, longer than head, 1.2×(~0.66 mm long). Proximal element longer than distal element, 1.3×(~0.34 mm long) (Figs. 5b, c, 6a, b). Intercalary segment (post-ocular segment 2) without externally recognisable structures. Mandibles (paired appendages of post-ocular segment 3) only partially accessible, rectangular in ventral view with serrated gnathal edge, longer than wide, 1.8×(~0.31 mm long) (Fig. 6a, b). Maxillae (paired appendages of post-ocular segment 4) with three parts discernible: trapezoidal proximal part, longer than wide, 2.6×(~0.27 mm long), distal inner setous part (presumably lacinia and galea), and distal outer part (palp) (~0.36 mm long). Maxillary palp with three elements (Fig. 6a, b). Labium (conjoined appendages of post-ocular segment 5) subrectangular in ventral view, wider than long, 1.3×(~0.24 mm long), no palps discernible.

Prothorax rectangular in ventral view with convex anterior rim, as wide as long (~0.76 mm long). Meso- and metathorax subsimilar, trapezoidal in ventral view. Posterior rim of mesothorax wider than segment is long, 1.5×(~0.57 mm long). Posterior rim of metathorax slightly wider than segment is long, 1.1×(~0.76 mm long) (Fig. 5b, c). Legs discernible (one leg of metathorax presumably ripped out), with five elements (coxa, trochanter, femur, tibia, and claw), ~1.52 mm long (Figs. 5b, c, 6a, b).

Abdomen segments 1–8 subsimilar, rectangular in lateral view. Abdomen segment 1 slightly longer than wide, 1.1×(~0.95 mm long). Abdomen segments 2–8 wider than long (between 0.61 and 0.76 mm long and between 0.72 and 0.83 mm wide). Abdomen segment 9 elongate, semi-ovoid in ventral view, also longest segment of abdomen, longer than proximally wide, 2.2×(~1.27 mm long) (Fig. 6e). Trunk end rectangular in ventral view, wider than long, 4.2×(~0.11 mm long) with two postero-ventrally orientated, thin, spine-like processes (~0.25 mm long) and two-lobed structure (~0.32 mm long) with at least five hooks per lobe (Fig. 6e, f). Body bears setae (between 0.1 and 0.42 mm long).

Description of specimen 4 in amber piece PED 0925 (Figs. 4a, 7a, b)

Total body length approximately 8.71 mm. Head only partly accessible due to way of inclusion. Appendages of ocular and post-ocular segments not accessible (Fig. 7a).

Pronotum of prothorax semi-ovoid in dorsal view, with anterior rim concave, longer than wide, 1.3 × (~ 0.91 mm long). Mesonotum subrectangular in dorsal view, slightly wider than long, 1.1 × (~ 0.74 mm long). Metanotum trapezoidal in dorsal view, wider than long, 1.4 × (~ 0.54 mm long) (Fig. 7a). One leg discernible, ~ 1.4 mm long (Fig. 7a, white arrow), others not accessible.

Abdomen segments 1–8 subsimilar, rectangular in dorsal view. Abdomen segments 1, 2, and 7 slightly wider than long, 1.2 × (between 0.65 and 0.51 mm long). Abdomen segments 3–6 longer than wide (between 0.71 and 0.8 mm long and between 0.61 and 0.73 mm wide). Abdomen segment 8 as long as wide (~ 0.57 mm long). Segment 9 triangular in dorsal view, also longest segment of abdomen, longer than proximally wide, 2.7 × (~ 1.24 mm long) (Fig. 7b). Trunk end not accessible. Body bears setae (between 0.13 and 0.45 mm long).

Description of specimen 5 in amber piece PED 0925 (Figs. 4a, 7c, d)

Total body length approximately 9.42 mm. Head pentagonal in dorso-lateral view, longer than wide, 1.3 × (~ 0.29 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not accessible. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible (Fig. 7c, black arrow), longer than head, 1.3 × (~ 0.37 mm long). Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4), and labium (appendages of post-ocular segment 5) not accessible (Fig. 7c).

Prothorax trapezoid in dorso-lateral view, longer than posterior rim wide, 1.8 × (~ 0.79 mm long), pronotum strongly sclerotised. Mesothorax and metathorax subsimilar, rectangular in dorso-lateral view. Mesothorax slightly wider than long, 1.2 × (~ 0.42 mm long). Metathorax as long as wide (~ 0.52 mm long) (Fig. 7c). Legs discernible, ~ 0.62 mm long (Fig. 7c, white arrows).

Abdomen segments 1–8 subsimilar, tube-like, rectangular in dorsal view, longer than wide (between 0.7 and 0.96 mm long and between 0.48 and 0.52 mm wide) (Fig. 7c). Segment 9 trapezoidal in dorsal view, also longest segment of abdomen, longer than proximally wide, 2.7 × (~ 1.26 mm long). Posterior end of tergite 9 laterally on both sides bearing tufts of hairs (Fig. 7d). Trunk end not accessible. Body bears setae (between 0.18 and 0.38 mm long).

Discussion

Identity of specimen BUB 4275

The overall morphology of all the here reported specimens is clearly elateriform, immediately identifying these specimens as larval representatives of the group Holometabola. Still, as pointed out, larvae of this general organisation occur in several lineages of Holometabola. We therefore need to use some more details for further identifying them more precisely.

Specimen BUB 4275 is preserved in an unfortunate orientation, prohibiting access to many details. Yet, the overall arrangement of the antennae and mouthparts, although only seen in antero-lateral view, is strongly resembling that in modern larvae of Elaterinae (e.g., Casari and Biffi 2012 fig. 15 p. 69). Despite the limited access to details, we therefore see an interpretation of this larva as representatives of Elateridae and also Elaterinae as the most likely one.

As pointed out, the fossil record of Elateridae is relatively rich, at least for adults (Kundrata et al. 2021a). Many of the known fossils of adults of Elateridae are from Cretaceous deposits, including the Kachin Myanmar amber (Kundrata et al. 2021a). It should therefore not be surprising that an immature specimen of Elateridae is found in Myanmar amber as well. However, since the larvae and the adults of beetles, therefore also of Elateridae, drastically differ, it is hard to know which fossil adult and immature counterparts are of the same species. Therefore, it is likely that the new larva is an immature representative of an already-described species represented so far only by the fossil adults. We are therefore refraining from erecting a new species for the larva. The fact that we cannot further narrow down the interpretation of the larva combined with the fact that modern larvae have a variety of different roles does not allow us to further speculate about the ecological role of the fossil larva.

Identity of the other specimens

The three specimens preserved in PED 0369 do not provide many details. The accessible details, especially of abdomen segment 9, resemble those of the overall better preserved specimens in PED 0925. Very informative details are accessible especially in specimens 2 and 3, mainly of the posterior end. Abdomen segment 9 is elongated, as for example also in many larvae of Elateridae (Hyslop 1917; Costa et al. 2010; Casari and Biffi 2012). Yet, there is a significant difference between the fossils and click beetle larvae: In larvae of Elateridae, the trunk end is positioned far anteriorly on abdomen segment 9; it seems that the trunk end is functionally in contact with abdomen segment 8 and that abdomen segment 9 basically has no real ventral structure. This is different in the fossils; there is clearly a ventral part of abdomen segment 9, reaching to about half of the overall length of the dorsal side. Accordingly, the trunk end is positioned further posteriorly.

Also the trunk end in the fossils is very distinct and unlike those of the larvae of Elateridae (cf. Costa et al. 2010, fig. 4.7.12.C, D and Lawrence 2005, fig. 18.9.1.). It basically appears to form two lobes, which are armed with few hooks, giving it almost the appearance of two hands. Such an arrangement of abdomen segment 9 with a two-lobed hooked trunk end is well known in larvae of Ptilodactylidae (LeSage and Harper 1976 fig. 1 p. 234; Stribling 1986 fig. 33 p. 227, figs. 34–39 p. 228), which are also elateriform (Stribling 1986 fig. 33 p. 227). Due to the distinct similarity of this very specific structure, we interpret the new fossils as larvae of Ptilodactylidae, toed-winged beetles.

The fossil specimens in PED 0925 have many details accessible, and therefore, a comparison with known extant larval representatives of Ptilodactylidae is possible. The overall appearance of the fossils strongly resembles that of extant representatives of the group *Anchytarsus* Guérin-Méneville, 1843. The characters shared by the fossils and extant larvae of *Anchytarus*, but differing in other larvae of Ptilodactylidae, include: a relatively small prognathous head in comparison to the prothorax; moderately long antennae with multiple visible elements; an elongated and rectangular prothorax in lateral view; abdomen segment 9 being the longest one of the abdomen and with dorso-ventrally flattened posterior part; a membranous terminal end with hand-like lobes with hooks; and relatively long setae on all segments. Also, the shape and the position of the antennae (Figs. 4b, 5a, b, 7c) strongly resemble the condition in extant representatives of *Anchytarsus* (Fig. 8a; Lawrence 2005 fig. 18.9.1.C). The mandibles of the fossils appear symmetrical, broad, and stout with multiple teeth. The maxillae have distally moderately long palps with multiple elements and setous endites (lacinia and/or galea; Fig. 6b). Therefore, also these mouthparts are similar to extant larvae of *Anchytarsus* (Lawrence 2005 fig. 18.9.2.C). Based on this, we conclude that the specimens within PED 0925 are either larval representatives of *Anchytarsus* or at least closely related representatives within the group of Anchytarsinae. This find would represent the first record of the group Anchytarsinae from the Cretaceous. The larvae in PED 0369 might be conspecific, yet this must remain unclear due to fewer preserved details. Further reaching comparisons on species level are not possible due to inaccessibility of certain details of the terminal ends (Stribling 1986).

Fossil record of Ptilodactylidae

The group Ptilodactylidae was so far represented by very few specimens (Motschulsky 1856; Chatzimanolis et al. 2012; Alekseev and Jäch 2016; Kirejtshuk et al. 2019). The eight specimens reported here therefore expand the fossil record of the group from the perspective of individuals. A taxonomic interpretation of the specimens is much more challenging. As Kundrata et al. (2021b) pointed out, the group Ptilodactylidae seems in urgent need of taxonomic re-working. Also, as in many other beetle groups, it appears that extant larvae are known for relatively few species (see discussion in Haug and Haug 2019). Hence the correspondence of larval morphologies to certain taxonomic groups is not well established (see discussion in Haug and Haug 2019).

There is one formally described species of Ptilodactylidae from Kachin amber, *Aphebodactyla rhetine* Chatzimanolis et al. 2012 (Chatzimanolis et al. 2012) based on an adult male. Although the here reported larvae have strong similarities with modern larvae of the group *Anchytarsus,* it cannot be easily excluded that the larvae are those of *Aphebodactyla rhetine.* The new fossils therefore do not necessarily increase the species richness of the fossil record of Ptilodactylidae. Yet, they demonstrate that such beetles are more common than indicated by only adults. Also the presence of a specific adult morphology is not a reliable indicator of a specific larval morphology (Scholtz 2005; Haug et al. 2015). The newly reported larvae resemble a very modern type of larva of Ptilodactylidae. This find demonstrates that this morphology was already present 100 million years ago and indicates a similar ecological role of the larvae.

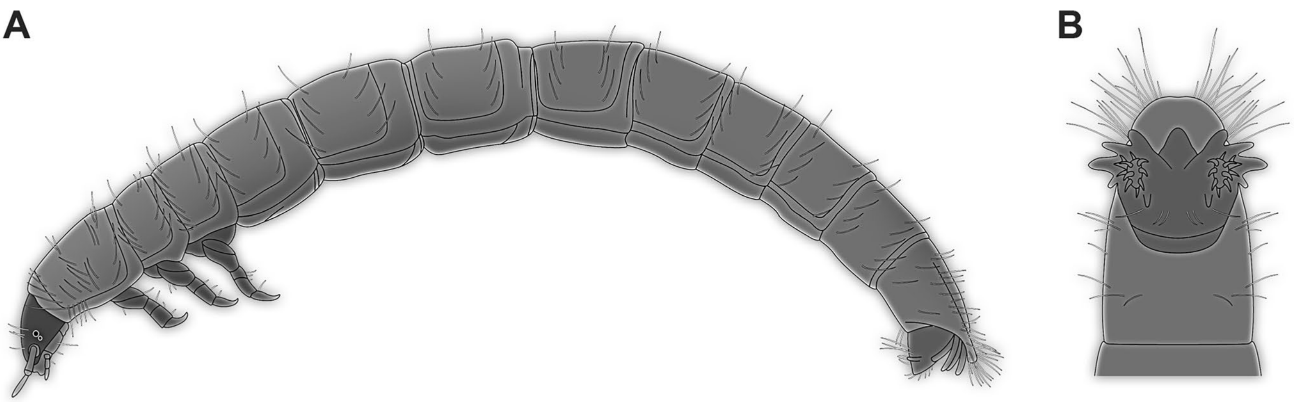

Fig. 8 Schematic representation of extant larva of Ptilodactylidae based on Stribling (1986, fig. 33); **a** habitus of larva in lateral view; **b** close-up of trunk end with lobes and hooks in ventral view

Possible ecology of larvae of Ptilodactylidae

In extant representatives of Ptilodactylidae (Byrrhoidea), the larvae live close to or in rivers (Alekseev and Jäch 2016 p. 593) and other water bodies (Kundrata et al. 2021b), in moist litter or rotten logs (Chatzimanolis et al. 2012 p. 570), and feed on decaying vegetation or rotting wood (Alekseev and Jäch 2016 p. 593) or possibly on fungi on these substrates (Chatzimanolis et al. 2012 p. 570). We can assume that the fossil larvae had also one of the mentioned life styles. The extant larvae of *Anchytarsus,* which the specimens in PED 0925 strongly resemble, live in an aquatic environment on or within submerged decaying wood, on which they also feed (LeSage and Harper 1976; Lawrence 2005). A xylophagous lifestyle is not restricted to terrestrial environments, but is also quite common among extant aquatic larvae of different insect groups (Cranston and McKie 2006). The fossil record of terrestrial beetle larvae shows that xylophagous lifestyle was already common in the Cretaceous (Haug et al. 2021a; Zippel et al. 2022a, 2023), but has so far been relatively rarely reported (Peris and Rust 2020). The modern-appearing morphology of the new fossils of Ptilodactylidae implies that larvae possibly led a similar aquatic xylophagous lifestyle as their extant counterparts. Such a life style is so far quite rare in the fossil record. A fossil larva of Elmidae (Byrrhoidea) from Eocene Baltic amber that was recently described in Zippel et al. (2022b) also possibly led a xylophagous lifestyle in aquatic environment. This may hold true as well for another larva of Elmidae from Eocene of India that was recently described by Kirejtshuk et al. (2023). It shows that this lifestyle might have been already widely present in the past. The new fossils push the time boundary of this type of lifestyle all the way back to Cretaceous.

While both general lifestyles, living in water or inside wood, may appear as not very beneficial for becoming preserved in amber, there are in fact numerous examples for both cases in Myanmar amber. Aquatic organisms include numerous larvae of various lineages of Pterygota (e.g., Sroka et al. 2018; Gustafson et al. 2020; Schädel et al. 2020; Haug et al. 2021g; Zippel et al. 2022b), but also many others (Xing et al. 2018; Salamon et al. 2019; Schädel et al. 2019, 2021a, b; Yu et al. 2019, 2021; Wang et al. 2020; Bolotov et al. 2021). Larvae known to feed on or live inside wood are also well known as amber inclusions (Baranov et al. 2020), especially various types of beetle larvae (Peris and Rust 2020; Haug et al. 2021a; Zippel et al. 2022a, 2023).

Source of variation among larvae within one amber piece

Two amber pieces that contain multiple specimens of Ptilodactylidae (PED 0369 and PED 0925) contain in total eight larvae of relatively similar sizes (total body length between 8.7 and 10.9 mm). It is possible that the larvae within one amber piece hatched from the same clutch of eggs, therefore, might be conspecific. They do show variation in habitus, but that might be due to different views in which they are accessible.

An additional source of differences might be ontogeny. LeSage and Harper (1976) noted that the species *Anchytarsus bicolor* develops through ten instars. Larval instars were differentiated based on the size of the pronotum. Indeed there is a small variation in size of the whole prothorax among newly described specimens, but the size of the pronotum as a criterion for differentiating the instars cannot be considered here as the new larvae are accessible in different views or are partially hidden by inclusions; therefore, measuring of the same two points on the pronotum was not possible. In addition to size, other characteristics, such as number of setae or hooks on the trunk end, were also changing during the development of the larvae described by LeSage and Harper (1976). Once again, this is not a clear factor we can rely on, since there is a possibility that specimens got damaged during the process of inclusion within the resin. Nevertheless, we presume that the specimens are not first instars, but later ones. Out of these reasons, we cannot clearly say where the variation of the specimens comes from, even within one amber piece.

Fossil record of larvae of Elateroidea

Within the larger group Elateroidea, Elateridae is very species-rich and has a quite good overall fossil record (Kundrata et al. 2021a). Still, there is so far only the single larva reported here. Other ingroups of Elateroidea, which are much less species-rich and with a less good fossil record, have a record of at least some fossil larvae, including possible Lycidae and Lampyridae (Ferreira et al. 2022; Haug et al. 2023b), Cantharidae (Fowler 2019), or Eucnemidae (Chang et al. 2016; Zippel et al. 2023). Especially remarkable is the fossil record of larvae of the group Brachypsectridae, which is quite species-poor in the modern fauna, but is known from larvae in amber from the Cretaceous (Zhao et al. 2020; Haug et al. 2021f), Eocene (Scheven 2004; Klausnitzer 2009; Haug et al. 2021f), and Miocene (Wu 1996; Woodruff 2002; Klausnitzer 2009; Poinar 2010; all records recently reviewed in Haug et al. 2021f). The larvae of Brachypsectridae are very prominent and rather easy to identify as such, possibly explaining why these larvae have a (seemingly) better record. We still expect that more fossil larvae of Elateridae should be present in ambers, but simply have not been reported.

Fossil record of larvae of Byrrhoidea and Elateriformia

Ptilodactylidae is recognised either as an ingroup of Dryopoidea (e.g., Kundrata et al. 2021b; Cai et al. 2022) or as an ingroup of Byrrhoidea (e.g., McKenna et al. 2019). Byrrhoidea, like Elateroidea, is a large ingroup of Elateriformia that may even be more species-rich than often anticipated, especially if one recent phylogenetic analysis is considered in which Buprestidae was resolved as an ingroup of Byrrhoidea (McKenna et al. 2019 figs. 1, 2). Even if the position of Buprestidae within Byrrhoidea will not be further supported in future work, the group of Buprestidae stays widely recognised as an ingroup of Elateriformia (e.g., Zhang et al. 2018 fig. 2 p. 3). Larvae of Buprestidae, metallic wood-boring beetles, are known from Cretaceous and Eocene ambers (Haug et al. 2021a and references therein; Haug et al. 2023a).

Different larvae of Byrrhoidea have also been reported in the fossil record, including: Elmidae (riffle beetles; Eocene amber, Zippel et al. 2022b; Eocene, Kirejtshuk et al. 2023), Heteroceridae (variegated mud-loving beetles; Miocene amber, Zippel et al. 2022c), Psephenidae (water penny beetles; Cretaceous amber, Bao et al. 2018; Eocene, Wedmann et al. 2011; Miocene, Hayashi and Kawakami 2009; Pleistocene, Hayashi et al. 2020). The findings reported here further expand this record.

Overall, it appears that many specialised larval forms are present from early on, in many cases already in the Cretaceous (see also Muona et al. 2020). Yet, many of these early larvae show at least some differences to their modern counterparts (e.g., Haug et al. 2021a, 2023a; Zippel et al. 2022b, 2023). This phenomenon has been not only recognised in beetles, but also in other lineages of Holometabola. In lacewings, for example, there are also very modern-appearing larvae known from the Cretaceous (e.g., Wang et al. 2016; Badano et al. 2018; Haug et al. 2018, 2021e; Haug and Haug 2022), but also more larvae with more plesiomorphic (≈ancestral) characters, and also highly specialised larvae not known before or afterwards (e.g., Badano et al. 2018, 2021; Haug et al. 2019a, b, 2020a). This observation emphasises that it is important to report and describe fossil larvae and not assume the presence of a certain larval morphology based on the presence of a certain adult morphology (Haug et al. 2015; Baranov et al. 2019).

The observable details in the larvae of Ptilodactylidae here appear very similar to those of their modern counterparts. At most, the antennae appear slightly longer in fossil larvae in comparison to those of the modern counterparts. Similar, or even more expressed, cases of this phenomenon are already known from other larvae preserved in Cretaceous amber (Haug et al. 2020b, 2021d). Hence, the new larvae seem to be a case of a very modern-appearing type of morphology back in the Cretaceous.

Acknowledgements Gideon T. Haug, Neuried, is thanked for his time and efforts invested into the image processing and drawings for this publication. M. Jäch, Vienna, is thanked for his expert advice regarding the specimens of Ptilodactylidae in this manuscript. J. Matthias Starck, LMU Munich, is thanked for long-time support. The authors thank all people providing low-cost, open-access, or open-source software. This is LEON publication #48.

Author contributions Conceptualization: CH, JTH, and AZ; methodology: CH, PM, JTH, and AZ; investigation: CH, PM, JTH, and AZ; writing—original draft preparation: CH, JTH, and AZ; writing—review and editing: CH, PM, JTH, and AZ; funding acquisition: JTH; resources: PM and JTH.

Funding Open Access funding enabled and organized by Projekt DEAL. The study is kindly supported by the German Research Foundation (DFG Ha 6300/6-1) and Volkswagen Foundation with a Lichtenberg Professorship to JTH.

Availability of data and materials All data are provided in the text and the figures.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest and no competing interests.

References

Alekseev, V.I., and M.A. Jäch. 2016. *Electrolichas circumbalticus* gen. et sp. nov. (Coleoptera: Byrrhoidea: Ptilodactylidae) from Baltic amber, the first anchytarsine toed-winged beetle described from Europe. *Zootaxa* 4136 (3): 593–599. https://doi.org/10.11646/zootaxa.4136.3.10.

Badano, D., M.S. Engel, A. Basso, B. Wang, and P. Cerretti. 2018. Diverse Cretaceous larvae reveal the evolutionary and behavioural history of antlions and lacewings. *Nature Communications* 9: 3257. https://doi.org/10.1038/s41467-018-05484-y.

Badano, D., M. Fratini, L. Maugeri, F. Palermo, N. Pieroni, A. Cedola, J.T. Haug, T. Weiterschan, J. Velten, M. Mei, A. Di Giulio, and P. Cerretti. 2021. X-ray microtomography and phylogenomics provide insights into the morphology and evolution of an enigmatic Mesozoic insect larva. *Systematic Entomology* 46: 672–684. https://doi.org/10.1111/syen.12482.

Bao, T., J. Rust, and B. Wang. 2018. Systematics, phylogeny and taphonomy of Cretaceous Psephenidae (Insecta: Coleoptera) from Burmese amber. *Palaeontographica Abteilung A* 310: 131–159. https://doi.org/10.1127/0375-0442/2018/0086.

Baranov, V., C. Hoffeins, H.-W. Hoffeins, and J.T. Haug. 2019. More than dead males: Reconstructing the ontogenetic series of terrestrial non-biting midges from the Eocene amber forest. *Bulletin of Geosciences* 94: 187–199.

Baranov, V.A., Y. Wang, R. Gašparič, S. Wedmann, and J.T. Haug. 2020. Eco-morphological diversity of larvae of soldier flies and their closest relatives in deep time. *PeerJ* 8: e10356. https://doi.org/10.7717/peerj.10356.

Baranov, V., C. Haug, M. Fowler, U. Kaulfuss, P. Müller, and J.T. Haug. 2022. Summary of the fossil record of megalopteran and megalopteran-like larvae, with a report of new specimens. *Bulletin of Geosciences* 97: 89–108. https://doi.org/10.3140/bull.geosci.1840.

Barr, C.B., J.R. Gibson, and P.H. Diaz. 2015. *Typhloelmis* Barr (Coleoptera: Elmidae: Elminae), a new stygobiontic riffle beetle genus with three new species from Texas, USA. *The Coleopterists Bulletin* 69: 531–558.

Becker, E.C. 1963. Three new fossil elaterids from the amber of Chiapas, Mexico, including a new genus (Coleoptera). *Journal of Paleontology* 37: 125–128.

Beutel, R. G., and J. F. Lawrence. 2016. 4. Coleoptera, morphology. In *Coleoptera, Beetles: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)* (Vol. 1), volume eds. R. G. Beutel, and R. A. B. Leschen, 35–40. In *Handbook of Zoology: Arthropoda: Insecta (2nd edition),* eds. R. G. Beutel, and N. P. Kristensen. Berlin, Boston: Walter de Gruyter. https://doi.org/10.1515/9783110373929-007.

Bolotov, I.N., O.V. Aksenova, I.V. Vikhrev, E.S. Konopleva, Y.E. Chapurina, and A.V. Kondakov. 2021. A new fossil piddock (Bivalvia: Pholadidae) may indicate estuarine to freshwater environments near Cretaceous amber-producing forests in Myanmar. *Scientific Reports* 11: 6646. https://doi.org/10.1038/s41598-021-86241-y.

Cai, C., E. Tihelka, M. Giacomelli, J.F. Lawrence, A. Ślipiński, R. Kundrata, S. Yamamoto, M.K. Thayer, A.F. Newton, R.A.B. Leschen, M.L. Gimmel, L. Lü, M.S. Engel, P. Bouchard, D. Huang, D. Pisani, and P.C. Donoghue. 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science* 9 (3): 211771.

Casari, S.A., and G. Biffi. 2012. Immatures of *Dicrepidius* Eschscholtz, 1829 and *Dipropus* Germar, 1839 (Elateridae, Elaterinae, Ampedini: Dicrepidiina). *Zootaxa* 3587 (1): 65–77.

Chang, H., J. Muona, H. Pu, L. Xu, C. Wang, M. Teräväinen, D. Ren, Q. Yang, X. Zhang, and S. Jia. 2016. Chinese Cretaceous larva exposes a southern Californian living fossil (Insecta, Coleoptera, Eucnemidae). *Cladistics* 32: 211–214. https://doi.org/10.1111/cla.12124.

Chatzimanolis, S., M.E. Cashion, M.S. Engel, and Z.H. Falin. 2012. A new genus of Ptilodactylidae (Coleoptera: Byrrhoidea) in mid-Cretaceous amber from Myanmar (Burma). *Geodiversitas* 34: 569–574. https://doi.org/10.5252/g2012n3a6.

Cockerell, T.D.A. 1917. Insects in Burmese amber. *Annals of the Entomological Society of America* 10 (4): 323–329. https://doi.org/10.1093/aesa/10.4.323.

Costa, C., and S.A. Vanin. 2010. Coleoptera larval fauna associated with termite nests (Isoptera) with emphasis on the "bioluminescent termite nests" from Central Brazil. *Psyche* 2010: 723947. https://doi.org/10.1155/2010/723947.

Costa, C., J. F. Lawrence, and S. P. Rosa. 2010. 4.7. Elateridae Leach, 1815. In *Coleoptera, Beetles: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (Vol. 2), volume eds. R. A. B. Leschen, R. G. Beutel, and J. F. Lawrence, 75–103. In *Handbook of Zoology, Arthropoda: Insecta, Teilband 39,* eds. N. P. Kristensen, and R.G. Beutel. Berlin: Walter de Gruyter. https://doi.org/10.1515/9783110911213.75.

Cranston, P. S., and B. McKie. 2006. Aquatic wood – an insect perspective. In *Insect Biodiversity and Dread Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology,* eds. S. J. Grove, and J. L. Hanula, 9–14. Asheville: United States Department of Agriculture, The Forest Service.

Cruickshank, R.D., and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* 21 (5): 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5.

Devetak, D., and A.E. Arnett. 2010. A click beetle larva (Coleoptera: Elateridae) preying upon an antlion larva (Neuroptera: Myrmeleontidae). *Entomological News* 121: 514–516. https://doi.org/10.3157/021.121.0515.

Ferreira, V.S., A. Solodovnikov, M.A. Ivie, and R. Kundrata. 2022. Dominican amber net-winged beetles suggest stable paleoenvironment as a driver for conserved morphology in a paedomorphic lineage. *Scientific Reports* 12: 5820. https://doi.org/10.1038/s41598-022-09867-6.

Fowler, M.J.F. 2019. Eocene world: Imaging fossil insects in Baltic amber. *Bulletin of the Amateur Entomologists' Society* 78: 139–146.

Gauweiler, J., C. Haug, P. Müller, and J.T. Haug. 2022. Lepidopteran caterpillars in the Cretaceous: were they a good food source for early birds? *Palaeodiversity* 15: 45–59. https://doi.org/10.18476/pale.v15.a3.

Goczał, J. 2023. Captain America without the shield: Elytra loss and the evolution of alternative defence strategies in beetles. *Zoomorphology* 142: 131–136. https://doi.org/10.1007/s00435-023-00593-9.

González-Córdoba, M., M.D.C. Zúñiga, and V. Manzo. 2020. La familia Elmidae (Insecta: Coleoptera: Byrrhoidea) en Colombia: riqueza taxonómica y distribución. *Revista De La Academia Colombiana De Ciencias Exactas, Físicas y Naturales* 44: 522–553. https://doi.org/10.18257/raccefyn.1062.

Gröhn, C. 2015. *Einschlusse im baltischen Bernstein*. Kiel: Wachholtz Verlag, Murmann Publishers.

Gustafson, G.T., M.C. Michat, and M. Balke. 2020. Burmese amber reveals a new stem lineage of whirligig beetle (Coleoptera: Gyrinidae) based on the larval stage. *Zoological Journal of the Linnean Society* 189: 1232–1248. https://doi.org/10.1093/zoolinnean/zlz161.

Haug, J.T., and C. Haug. 2019. Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). *PeerJ* 7: e7871. https://doi.org/10.7717/peerj.7871.

Haug, J.T., and C. Haug. 2021. A 100-million-year-old armoured caterpillar supports the early diversification of moths and butterflies. *Gondwana Research* 93: 101–105. https://doi.org/10.1016/j.gr.2021.01.009.

Haug, J.T., and C. Haug. 2022. 100 million-year-old straight-jawed lacewing larvae with enormously inflated trunks represent the oldest cases of extreme physogastry in insects. *Scientific Reports* 12: 12760. https://doi.org/10.1038/s41598-022-16698-y.

Haug, J.T., C. Haug, V. Kutschera, G. Mayer, A. Maas, S. Liebau, C. Castellani, U. Wolfram, E.N.K. Clarkson, and D. Waloszek. 2011. Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244: 259–272. https://doi.org/10.1111/j.1365-2818.2011.03534.x.

Haug, C., K.R. Shannon, T. Nyborg, and F.J. Vega. 2013. Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. *Bolétin de la Sociedad*

Geológica Mexicana 65: 273–284. https://doi.org/10.18268/BSGM2013v65n2a9

Haug, J.T., J.W. Martin, and C. Haug. 2015. A 150-million-year-old crab larva and its implications for the early rise of brachyuran crabs. *Nature Communications* 6: 6417. https://doi.org/10.1038/ncomms7417.

Haug, J.T., P. Müller, and C. Haug. 2018. The ride of the parasite: A 100-million-year old mantis lacewing larva captured while mounting its spider host. *Zoological Letters* 4: 31. https://doi.org/10.1186/s40851-018-0116-9.

Haug, C., A.F. Herrera-Flórez, P. Müller, and J.T. Haug. 2019a. Cretaceous chimera–an unusual 100-million-year old neuropteran larva from the "experimental phase" of insect evolution. *Palaeodiversity* 12: 1–11. https://doi.org/10.18476/pale.v12.a1.

Haug, J.T., P. Müller, and C. Haug. 2019b. A 100-million-year old predator: A fossil neuropteran larva with unusually elongated mouthparts. *Zoological Letters* 5: 29. https://doi.org/10.1186/s40851-019-0144-0.

Haug, J.T., V. Baranov, M. Schädel, P. Müller, P. Gröhn, and C. Haug. 2020a. Challenges for understanding lacewings: How to deal with the incomplete data from extant and fossil larvae of Nevrorthidae? (Neuroptera). *Fragmenta Entomologica* 52: 137–167. https://doi.org/10.13133/2284-4880/472.

Haug, J.T., P. Müller, and C. Haug. 2020b. A 100 million-year-old snake-fly larva with an unusually large antenna. *Bulletin of Geosciences* 95: 167–177. https://doi.org/10.3140/bull.geosci.1757.

Haug, C., G.T. Haug, A. Zippel, S. van der Wal, and J.T. Haug. 2021a. The earliest record of fossil solid-wood-borer larvae—Immature beetles in 99 million-year-old Myanmar amber. *Palaeoentomology* 4: 390–404. https://doi.org/10.11646/palaeoentomology.4.4.14.

Haug, G.T., V. Baranov, G. Wizen, P.G. Pazinato, P. Müller, C. Haug, and J.T. Haug. 2021b. The morphological diversity of long-necked lacewing larvae (Neuroptera: Myrmeleontiformia). *Bulletin of Geosciences* 96: 431–457. https://doi.org/10.3140/bull.geosci.1807.

Haug, G.T., C. Haug, and J.T. Haug. 2021c. The morphological diversity of spoon-winged lacewing larvae and the first possible fossils from 99 million-year-old Kachin amber, Myanmar. *Palaeodiversity* 14: 133–152. https://doi.org/10.18476/pale.v14.a6.

Haug, J.T., V. Baranov, P. Müller, and C. Haug. 2021d. New extreme morphologies as exemplified by 100 million-year-old lacewing larvae. *Scientific Reports* 11: 20432. https://doi.org/10.1038/s41598-021-99480-w.

Haug, J.T., G.T. Haug, A. Zippel, S. van der Wal, P. Müller, C. Gröhn, J. Wunderlich, C. Hoffeins, H.-W. Hoffeins, and C. Haug. 2021e. Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings and their closer relatives over 100 million years. *Insects* 12: 860. https://doi.org/10.3390/insects12100860.

Haug, J.T., A. Zippel, G.T. Haug, C. Hoffeins, H.-W. Hoffeins, J.U. Hammel, V. Baranov, and C. Haug. 2021f. Texas beetle larvae (Brachypsectridae)—The last 100 million years reviewed. *Palaeodiversity* 14: 161–183. https://doi.org/10.18476/pale.v14.a8.

Haug, J.T., P. Müller, and C. Haug. 2021g. Fossil dragonfly-type larva with lateral abdominal protrusions and implications on the early evolution of Pterygota. *iScience* 24: 103162. https://doi.org/10.1016/j.isci.2021.103162.

Haug, G.T., C. Haug, S. van der Wal, P. Müller, and J.T. Haug. 2022a. Split-footed lacewings declined over time: Indications from the morphological diversity of their antlion-like larvae. *PalZ* 96: 29–50. https://doi.org/10.1007/s12542-021-00550-1.

Haug, J.T., M.S. Engel, P. Mendes dos Santos, G.T. Haug, P. Müller, and C. Haug. 2022b. Declining morphological diversity in snakefly larvae during last 100 million years. *PalZ* 96: 749–780. https://doi.org/10.1007/s12542-022-00609-7.

Haug, C., V.A. Baranov, M.K. Hörnig, J. Gauweiler, J.U. Hammel, E.E. Perkovsky, and J.T. Haug. 2023a. 35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests. *Palaeobiodiversity and Palaeoenvironments* 103: 521–530. https://doi.org/10.1007/s12549-022-00552-0.

Haug, C., A. Zippel, P. Müller, and J. T. Haug. 2023b. Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. *PalZ* 97: 485–496. https://doi.org/10.1007/s12542-023-00648-8.

Hayashi, M., and Y. Kawakami. 2009. Fossil of the genus *Eubrianax* (Coleoptera, Psephenidae) from the Upper Miocene Ningyôtôge formation in Tottori Prefecture, Japan. *Elytra* 37: 99–103.

Hayashi, M., H. Aiba, E. Nakano, Y. Takahashi, and T. Sato. 2020. Fossilized water pennies (Coleoptera: Psephenidae) in the Middle Pleistocene lake deposits in Shiobara site, Tochigi Prefecture, Japan. *Japanese Journal of Systematic Entomology* 26: 84–86.

Hoare, R., J. Dugdale, and C. Watts. 2006. The world's thinnest caterpillar? A new genus and species of Batrachedridae (Lepidoptera) from *Sporadanthus ferrugineus* (Restionaceae), a threatened New Zealand plant. *Invertebrate Systematics* 20: 571–583. https://doi.org/10.1071/IS06009.

Hörnig, M.K., C. Haug, P. Müller, and J.T. Haug. 2022. Not quite social – possible cases of gregarious behaviour of immatures of various lineages of Insecta preserved in 100-million-year-old amber. *Bulletin of Geosciences* 97: 69–87. https://doi.org/10.3140/bull.geosci.1818.

Hyslop, J.A. 1917. The phylogeny of the Elateridae based on larval characters. *Annals Entomological Society of America* 10: 241–263.

Iablokoff-Khnzorian, S.M. 1961. Novye zhestkokrylye semeystva Elateridae iz baltiyskogo yantayra. *Paleontologicheskii Zhurnal* 1961: 84–97.

Jałoszyński, P. 2018. Morphological Diversity of Immature Scydmaeninae. In *Biology of Rove Beetles (Staphylinidae),* eds. O. Betz, U. Irmler, and J. Klimaszewski, 321–333. Cham: Springer. https://doi.org/10.1007/978-3-319-70257-5_14.

Jałoszyński, P., and R.G. Beutel. 2012. Functional morphology and evolution of specialized mouthparts of Cephenniini (Insecta, Coleoptera, Staphylinidae, Scydmaeninae). *Arthropod Structure & Development* 41: 593–607. https://doi.org/10.1016/j.asd.2012.07.002.

Jałoszyński, P., and A. Kilian. 2016. Description of the second-and third-instar larva of South African S*tenomastigus longicornis* (Boheman) (Coleoptera: Staphylinidae, Scydmaeninae). *Zootaxa* 4158 (2): 151–182. https://doi.org/10.11646/zootaxa.4158.2.

Kerp, H., and B. Bomfleur. 2011. Photography of plant fossils—new techniques, old tricks. *Review of Palaeobotany and Palynology* 166: 117–151. https://doi.org/10.1016/j.revpalbo.2011.05.001.

Kirejtshuk, A.G., and A.V. Kovalev. 2015. First fossil representative of the family Omalisidae (Coleoptera, Elateroidea sensu lato) from the Baltic amber. *Paleontological Journal* 49: 1413–1416. https://doi.org/10.1134/S0031030115130031.

Kirejtshuk, A.G., A.G. Ponomarenko, A.S. Kurochkin, A.V. Alekseev, V.G. Gratshev, A.V. Solodovnikov, F.-T. Krell, and C. Soriano. 2019. The beetle (Coleoptera) fauna of the Insect Limestone (late Eocene), Isle of Wight, southern England. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 110: 405–492. https://doi.org/10.1017/S1755691018000865.

Kirejtshuk, A.G., R. Patel, R.S. Rana, A. Prokin, A. Nel, and M.A. Jäch. 2023. Discovery of the oldest known elmid larva (Coleoptera, Elmidae) from the Lower Eocene of Rajasthan (India, Palana Formation). *Palaeoentomology* 6 (3): 235–241. https://doi.org/10.11646/palaeoentomology.6.3.5.

Klausnitzer, B. 2009. Bemerkungen zu rezenten und fossilen Larven (Bernstein) der Gattung *Brachypsectra* LeConte (Coleoptera, Brachypsectridae). *Contributions to Natural History* 12: 721–742.

Kundrata, R., A. Bukejs, A.S. Prosvirov, and J. Hoffmannova. 2020. X-ray micro-computed tomography reveals a unique morphology in a new click-beetle (Coleoptera, Elateridae) from the Eocene Baltic amber. *Scientific Reports* 10: 20158. https://doi.org/10.1038/s41598-020-76908-3.

Kundrata, R., G. Packova, A.S. Prosvirov, and J. Hoffmannova. 2021a. The fossil record of Elateridae (Coleoptera: Elateroidea): Described species, current problems and future prospects. *Insects* 12: 286. https://doi.org/10.3390/insects12040286.

Kundrata, R., G. Packova, K. Kairišs, A. Bukejs, J. Hoffmannova, and S.M. Blank. 2021b. The first *Ptilodactyla* Illiger, 1807 (Coleoptera: Dryopoidea: Ptilodactylidae) described from Eocene Baltic amber. *Biology* 10: 877. https://doi.org/10.3390/biology10090877.

Lawrence, J. F. 2005. Ptylodactylidae Laporte, 1836. In *Coleoptera, Beetles: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), Vol. 1*, volume eds. R. A. B. Leschen and R. G. Beutel, 536–542. In *Handbook of Zoology, Arthropoda: Insecta, Teilband 38,* eds. N. P. Kristensen, and R. G. Beutel. Berlin, New York: Walter de Gruyter.

Lawrence, J.F., and J.B. Stribling. 1992. A new genus of Ptilodactylidae (Coleoptera: Elateriformian) from North Queensland, with description of the presumed larva. *Australian Journal of Entomology* 31: 19–27. https://doi.org/10.1111/j.1440-6055.1992.tb00454.x.

LeSage, L., and P.P. Harper. 1976. Notes on the life history of the toed-winged beetle *Anchytarsus bicolor* (Melsheimer) (Coleoptera: Ptilodactylidae). *The Coleopterists Bulletin* 30: 233–238.

Liu, Y., M. Hakim, and D. Huang. 2020. First stratiomyomorphan larvae in the mid-Cretaceous amber from Myanmar (Diptera: Brachycera). *Cretaceous Research* 106: 104265. https://doi.org/10.1016/j.cretres.2019.104265.

Liu, H., C. Luo, E.A. Jarzembowski, and C. Xiao. 2022. *Acanthochrysa langae* gen. et sp. Nov., a new lacewing larva (Neuroptera: Chrysopoidea) from mid-Cretaceous Kachin amber. *Cretaceous Research* 133: 105146. https://doi.org/10.1016/j.cretres.2022.105146.

Lohrmann, V., and M.S. Engel. 2017. The wasp larva's last supper: 100 million years of evolutionary stasis in the larval development of rhopalosomatid wasps (Hymenoptera: Rhopalosomatidae). *Fossil Record* 20: 239–244. https://doi.org/10.5194/fr-20-239-2017.

Luo, C., H. Liu, and E.A. Jarzembowski. 2022. High morphological disparity of neuropteran larvae during the Cretaceous revealed by a new large species. *Geological Magazine* 159: 954–962. https://doi.org/10.1017/S0016756822000176.

McKenna, D.D., S. Shin, D. Ahrens, M. Balke, C. Beza-Beza, D.J. Clarke, A. Donath, H.E. Escalona, F. Friedrich, H. Letsch, S. Liu, D. Maddison, C. Mayer, B. Misof, P.J. Murin, O. Miehuis, R.S. Peters, L. Podsiadlowski, H. Pohl, E.D. Scully, E.V. Yan, X. Zhou, A. Ślipiński, and R.G. Beutel. 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences* 116: 24729–24737. https://doi.org/10.1073/pnas.1909655116.

Motschulsky, M. 1856. Voyages: Lettres de M. de Motschulsky à M. Ménétriés. No. 4. *Etudes Entomologiques* 5: 21–38.

Muona, J., H. Chang, and D. Ren. 2020. The clicking Elateroidea from Chinese Mesozoic deposits (Insecta, Coleoptera, Elateroidea). *Insects* 11: 875. https://doi.org/10.3390/insects11120875.

Otto, R.L. 2017. Eucnemid larvae of the Nearctic Region. Part VII: Description of the larvae of *Nematodes penetrans* (LeConte, 1852) (Coleoptera: Eucnemidae: Macraulacinae: Nematodini), with notes on its hypermetamorphic life cycle. *Insecta Mundi* 0545: 1–9.

Otto, R.L. 2019. Descriptions of two new elateroid beetles (Coleoptera: Eucnemidae, Elateridae) from Burmese amber. *Insecta Mundi* 702: 1–6.

Penney, D. 2010. *Biodiversity of fossils in amber from the major world deposits*. Manchester: Siri Scientific Press.

Peris, D., and J. Rust. 2020. Cretaceous beetles (Insecta: Coleoptera) in amber: The palaeoecology of this most diverse group of insects. *Zoological Journal of the Linnean Society* 189: 1085–1104. https://doi.org/10.1093/zoolinnean/zlz118.

Pilgrim, R.L.C. 1972. Aquatic larva and the pupa of *Choristella philpotti* Tillyard, 1917 (Mecoptera: Nannochoristidae). *Pacific Insects* 14 (1): 151–168.

Poinar, G., Jr. 2010. Palaeoecological perspectives in Dominican amber. *Annales De La Société Entomologique De France (n.s.)* 46 (1–2): 23–52. https://doi.org/10.1080/00379271.2010.10697637.

Salamon, M.A., J.P. Lin, P. Duda, P. Gorzelak, W.I. Ausich, and T. Oji. 2019. Paleoenvironmental and biostratigraphic implications of echinoderm ossicles trapped within Burmese amber. *Palaios* 34: 652–656. https://doi.org/10.2110/palo.2019.084.

Schädel, M., V. Perrichot, and J.T. Haug. 2019. Exceptionally preserved cryptoniscium larvae—Morphological details of rare isopod crustaceans from French Cretaceous Vendean amber. *Palaeontologia Electronica* 22: 71. https://doi.org/10.26879/977.

Schädel, M., P. Müller, and J.T. Haug. 2020. Two remarkable fossil insect larvae from Burmese amber suggest the presence of a terminal filum in the direct stem lineage of dragonflies and damselflies (Odonata). *Rivista Italiana di Paleontologia e Stratigrafia* 126: 13–35. https://doi.org/10.13130/2039-4942/12720.

Schädel, M., M.K. Hörnig, M. Hyžný, and J.T. Haug. 2021a. Mass occurrence of small isopodan crustaceans in 100-million-year-old amber: An extraordinary view on behaviour of extinct organisms. *PalZ* 95: 429–445. https://doi.org/10.1007/s12542-021-00564-9.

Schädel, M., M. Hyžný, and J.T. Haug. 2021b. Ontogenetic development captured in amber – the first record of aquatic representatives of Isopoda in Cretaceous amber from Myanmar. *Nauplius* 29: e2021003. https://doi.org/10.1590/2358-2936e2021003.

Scheven, J. 2004. *Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut.* Hofheim a. T.: Kuratorium Lebendige Vorwelt.

Schimmel, R. 2005. Die Megapenthini-Arten Süd- und Südostasiens. Vierter Teil: Phylogenese, Zoogeographie und Katalog (Coleoptera: Elateridae). *Pollichia-Buch* 48: 1–411.

Schimmel, R., and D. Tarnawski. 2010. Monograph of the subtribe Elaterina (Insecta: Coleoptera: Elateridae: Elaterinae). *Genus* 21 (3): 325–487.

Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9 (7): 671–675.

Scholtz, G. 2005. Homology and ontogeny: Pattern and process in comparative developmental biology. *Theory in Biosciences* 124: 121–143. https://doi.org/10.1007/BF02814480.

Shepard, W.D., S. Clavier, and A. Cerdan. 2020. A generic key to the known larval Elmidae (Insecta: Coleoptera) of French Guiana. *Papéis Avulsos de Zoologia* 60: 1–9. https://doi.org/10.11606/1807-0205/2020.60.special-issue.15.

Shi, G., D.A. Grimaldi, G.E. Harlow, J. Wang, J. Wang, M. Yang, W. Lei, Q. Li, and X. Li. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014.

Sroka, P., A.H. Staniczek, and B.C. Kondratieff. 2018. 'Rolling' stoneflies (Insecta: Plecoptera) from mid-Cretaceous Burmese amber. *PeerJ* 6: e5354. https://doi.org/10.7717/peerj.5354.

Stribling, J.B. 1986. Revision of *Anchytarsus* (Coleoptera: Dryopoidea) and a key to the New World genera of Ptilodactylidae. *Annals of the Entomological Society of America* 79: 219–234.

Wang, B., F. Xia, M.S. Engel, V. Perrichot, G. Shi, H. Zhang, J. Chen, E.A. Jarzembowski, T. Wappler, and J. Rust. 2016. Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Science Advances* 2: e1501918. https://doi.org/10.1126/sciadv.1501918.

Wang, H., M. Schädel, B. Sames, and D.J. Horne. 2020. New record of podocopid ostracods from Cretaceous amber. *PeerJ* 8: e10134. https://doi.org/10.7717/peerj.10134.

Wedmann, S., T. Hörnschemeyer, and H. Schmied. 2011. Fossil water-penny beetles (Coleoptera: Psephenidae: Eubrianacinae) from the Eocene of Europe, with remarks on their phylogenetic position and biogeography. *Palaeontology* 54: 965–980. https://doi.org/10.1111/j.1475-4983.2011.01088.x.

Woodruff, R.E. 2002. A new species of the beetle genus Brachypsectra from the Dominican Republic, with fossil connections (Coleoptera: Brachypsectridae). *Insecta Mundi* 549: 161–170.

Wu, R.J.C. 1996. *Secrets of a Lost World: Dominican Amber and its Inclusions*. Santo Domingo: Privately published.

Xing, L., B. Sames, R.C. McKellar, D. Xi, M. Bai, and X. Wan. 2018. A gigantic marine ostracod (Crustacea: Myodocopa) trapped in mid-Cretaceous Burmese amber. *Scientific Reports* 8: 1365. https://doi.org/10.1038/s41598-018-19877-y.

Yu, T., U. Thomson, L. Mu, A. Ross, J. Kennedy, P. Broly, F. Xia, H. Zhang, B. Wang, and D. Dilcher. 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences of the United States of America* 116: 11345–11350. https://doi.org/10.1073/pnas.1821292116.

Yu, T., T.A. Neubauer, and A. Jochum. 2021. First freshwater gastropod preserved in amber suggests long-distance dispersal during the Cretaceous Period. *Geological Magazine* 158: 1327–1334. https://doi.org/10.1017/S0016756821000285.

Zaragoza Caballero, S. 1990. Descripción de una especie nueva fósil de *Glyphonyx* Candèze (Coleoptera: Elateridae, Adrastinae) del ámbar de Simojovel, Chiapas, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología* 61 (3): 147–151.

Zhang, S.Q., L.H. Che, Y. Li, D. Liang, H. Pang, A. Ślipiński, and P. Zhang. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* 9: 205. https://doi.org/10.1038/s41467-017-02644-4.

Zhao, J., C. Shih, and D. Ren. 2023. A new genus and species of click beetle (Coleoptera, Elateridae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research* 142: 105387. https://doi.org/10.1016/j.cretres.2022.105387

Zhao, X., X. Zhao, E. Jarzembowski, Y. Tian, and L. Chen. 2020. The first record of brachypsectrid larva from mid-Cretaceous Burmese amber (Coleoptera: Polyphaga). *Cretaceous Research* 113: 104493. https://doi.org/10.1016/j.cretres.2020.104493.

Zippel, A., C. Kiesmüller, G.T. Haug, P. Müller, T. Weiterschan, C. Haug, M.K. Hörnig, and J.T. Haug. 2021. Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. *Palaeoentomology* 4: 475–498. https://doi.org/10.11646/palaeoentomology.4.5.14.

Zippel, A., C. Haug, C. Hoffeins, H.-W. Hoffeins, and J.T. Haug. 2022a. Expanding the record of larvae of false flower beetles with prominent terminal ends. *Rivista Italiana di Paleontologia e Stratigrafia* 128: 81–104. https://doi.org/10.54103/2039-4942/17084.

Zippel, A., V.A. Baranov, J.U. Hammel, M.K. Hörnig, C. Haug, and J.T. Haug. 2022b. The first fossil immature of Elmidae: An unusual riffle beetle larva preserved in Baltic amber. *PeerJ* 10: e13025. https://doi.org/10.7717/peerj.13025.

Zippel, A., C. Haug, J. Gauweiler, M.K. Hörnig, G.T. Haug, and J.T. Haug. 2022c. A small beetle larva preserved in 23-million-year-old Mexican amber: possible first fossil record of an immature variegated mud-loving beetle. *Boletín de la Sociedad Geológica Mexicana* 74: A150322. https://doi.org/10.18268/BSGM2022v74n2a150322.

Zippel, A., C. Haug, P. Müller, and J.T. Haug. 2023. The first fossil false click beetle larva preserved in amber. *PalZ* 97: 209–215. https://doi.org/10.1007/s12542-022-00638-2.