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Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva

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Abstract

Lacewing larvae (Neuroptera) are known to be fierce predators which are morphologically highly specialised for a raptorial lifestyle. Mandibular-maxillary stylets are characteristic for all larvae of this group; these stylets can be extraordinarily massive. Despite these distinct sucking-piercing stylets, also other extreme features occur in some ingroups, such as an extremely elongated neck. In larvae of thread-winged lacewings (Crocinae) the neck can reach up to about one third of the body length; they are also called 'long-necked antlions'. Even though the larvae of living neuropteran species show a variety of conspicuous morphologies today, indeed 100 million years ago, in the Cretaceous, Neuroptera seems to have had an even more "experimental phase". Several larval specimens are known so far especially in Myanmar, Spanish and Lebanese amber from the Cretaceous with unique and unusual character combinations not found in any group living today. We describe here ten new fossil findings of one of these types of larvae with elongated head capsule in Myanmar amber, previously only known from a single specimen. We compared the head shapes of the new specimens with those of 190 specimens of other lacewing larvae and discuss further implications of our findings, especially making functional comparisons with long-necked antlions.

Keywords: Neuroptera, Myrmeleontiformia, Myanmar amber, *Macleodiella electrina*, Elliptic Fourier Analysis, Principal Component Analysis

Introduction

Within the group Holometabola, extreme differences between larval and adult forms with respect to their morphology, lifestyle as well as ecological role can occur. This is also the case for lacewings (Neuroptera), including about 6600 formally described living species today (Oswald, 2021) with a nearly worldwide distribution, and about 1000 formally described extinct species (Oswald, 2021). In contrast to most other holometabolan groups, the conspicuous larvae of lacewings, such as those of antlions, are more widely known than the rather delicate appearing adults they develop into.

Although most lacewings are predators as larvae and adults, the way of prey capturing and the morphology of structures involved in the preying process are extremely different between the two life phases (*e.g.*, Aspöck & Aspöck, 1999, 2007; Zimmermann *et al.*, 2019). Adult lacewings possess biting-chewing-type mouthparts; the mouthparts of the larvae are strongly specialised not only for piercing and sucking, but in many groups also for capturing and immobilisation of prey items (*e.g.*, Aspöck & Aspöck, 1999, 2007; Zimmermann *et al.*, 2019). Most lacewings (except Ithonidae, moth lacewings or giant lacewings, Tillyard, 1922, and possibly Nevrorthidae, Haug, J.T. *et al.*, 2020a) have three larval stages before reaching the pupal stage (Aspöck & Aspöck, 1999).

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The larvae of lacewings feature high morphological diversity; even the larval stages within one species can differ dramatically in morphology (*e.g.*, Gepp, 1984). Nevertheless, all are characterised especially by a pair of massive stylets. These stylets are formed by the upper jaw (mandible) and the lower jaw (maxilla) of each body side, between them with a channel not only for sucking *e.g.*, the haemolymph of the prey, but also with channels for saliva and venom injection in most groups (Aspöck & Aspöck, 1999; Zimmermann *et al*., 2019).

The shape of the larval sucking-piercing stylets is highly characteristic within neuropteran groups and of phylogenetic relevance (Aspöck and Aspöck, 2007; Zimmermann *et al*., 2019). They can be, for example, fairly straight and long such as in the often semi-aquatic larvae of Osmylidae, or curved inwards with a pincer-like shape, but rather short in relation to body size such as in Chrysopidae and Hemerobiidae (see Haug, J.T. *et al*., 2019a: fig. 4, for a more detailed overview of different lacewing stylets).

Very prominent stylets in relation to the body size can be found within the group of Myrmeleontiformia (Ascalaphidae, Myrmeleontidae, Nymphidae, Nemopteridae and Psychopsidae; Aspöck *et al*., 2001, 2012; Tauber *et al*., 2009), especially within the closely related owlflies (Ascalaphidae, unclear if monophyletic; Machado *et al*., 2019) and antlions (Myrmeleontidae, unclear if monophyletic; Machado *et al*., 2019), as well as split-footed lacewings (Nymphidae; possibly the sister group of Ascalaphidae + Myrmeleontidae; phylogeny of these groups is still under discussion, *e.g.*, Aspöck *et al*., 2001, 2012; but see Badano *et al*., 2017; Winterton *et al*., 2010, 2018 for different view). Stylets of modern-day myrmeleontiformian larvae are massive and curved inwards, with three additional teeth along the median edge in owlflies and antlions, and one additional tooth in split-footed lacewings (New, 1991; Tauber *et al*., 2009; Aspöck & Aspöck, 2007).

Fossil findings of myrmeleontiformian larvae show distinct variations in the morphology of the stylets compared to today living species, such as a variable number of additional teeth at the median edge of the stylets (Haug, J.T. *et al*., 2019b; see also Hörnig *et al*., 2020; Haug, G.T. *et al*., 2021a), which cannot be found in any modern lacewing larvae. However, it is not only the stylet morphology that highly differs in fossil findings. The combination of characters, which can be found in larvae of different neuropteran ingroups today, seems to be completely mixed in several fossil representatives of the Cretaceous (*e.g.*, Wang *et al*., 2016; Badano *et al*., 2018; Liu *et al*., 2018; Pérez-de la Fuente *et al*., 2018; Haug, C. *et al*., 2019; Haug, J.T. *et al*., 2020b). This observation of a kind of "experimental phase" of this insect group is becoming more and more evident, since quite a number of Cretaceous neuropteran larvae were described preserved in Myanmar amber (*e.g.*, Wang *et al*., 2016; Liu *et al*., 2016, 2018; Badano *et al*., 2018; Haug, C. *et al*., 2019; Haug, J.T. *et al*., 2019a, b, 2020a, b; Haug, G.T. *et al*., 2020, 2021a, b, online first), but also Spanish (Pérez-de la Fuente *et al*., 2012, 2016, 2020) and Lebanese amber (Pérez-de la Fuente *et al*., 2018, 2019).

Further findings of neuropteran larvae in Cretaceous amber indicate that there is even more variation in morphology which is still unknown and unexpected. Here, we show ten new myrmeleontiformian larvae of an already known type (*Macleodiella electrina*, Badano *et al*., 2018). The new larvae show even more subtle variation of this material and reveal additional details of this type of larva.

Material and methods

Material

Specimens for this study came from various collections: seven specimens (PED 0134, 0344, 0407, 0436, 0453, 0566, 0582) come from the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München; three specimens come from collections of the authors: two specimens come from the collection Müller (BUB 3384 and 3954), and one specimen comes from the collection Weiterschan (BuB 10).

The PED specimens were acquired legally from various traders over the online platform ebay.com (burmitefossil, burmite-miner, burmite-researcher). All the specimens described are inclusions in Kachin amber, Myanmar, from the Cretaceous. For a recent discussion on the issues around Myanmar amber see Haug, J.T. *et al*. (2020c) and on the issues around private collections see Haug, C. *et al*. (2020).

Documentation methods

Specimens were documented with a Keyence VHX-6000 digital microscope equipped with a 20–2000x objective. Images were taken under cross-polarised illumination to reduce reflections (*e.g.*, Haug, J.T. *et al*., 2013) or low-angle ring light and in part recorded in HDR-mode (high dynamic range). Black and white background was used. Several images along the z-axis were recorded and fused to a consistently sharp image to overcome limitations in depth of field. To generate high-resolution images of all details several stacked images along the x-y-axis were taken and subsequently stitched to a panorama image. Image stacking and stitching was performed with the built-in software of the Keyence VHX-6000. Post-processing of images and colour markings were performed with Adobe Photoshop CS2.

Shape analysis

For a wider ranging discussion, we compared the head shapes of the larvae reported in this paper to a diverse set of head shapes of major groups of Myrmeleontiformia. We re-use data sets already used in Haug, G.T. *et al*. (2020, 2021a, b, online first), also including some unusual fossils (Badano *et al*., 2018; Haug, J.T. *et al*., 2019b), as well as extant specimens used in Herrera-Flórez *et al*. (2020b) and additional specimens from the literature (Suppl. Tab. 1). Unfortunately, two specimens from the new larvae could not be included in the shape analysis due to the missing anterior parts of the stylets (PED 0344) or the unclear posterior rim of the head capsule (BuB 10).

The outlines were reconstructed by drawing only one half of each head capsule and one stylet at first, based on an image. Each stylet was rotated forward so that the tip was in line with the most proximal inner edge. Subsequently, the structures were mirrored to achieve a bilaterally-symmetrical shape (otherwise a possible left-right asymmetry might provide a strong signal, concealing other aspects).

All of the redrawn shapes were saved as bitmap files and further processed in the program package SHAPE (© National Agricultural Research Organization of Japan; Iwata & Ukai, 2002; *cf*. Braig *et al*., 2019; Haug, G.T. *et al*., 2020). The program enables an Elliptic Fourier Analysis followed by a Principal Component Analysis (PCA).

Results

Overall description of the specimens

The *head* is trapezoid in dorsal view and heavily sclerotised. The stemmata (ocular segment) are situated antero-laterally on the dorsal side of the head capsule; they consist of circular isolated lenses that are arranged in a circular pattern in dorsal view (not discernible in all specimens). There are anterior paired projections of the clypeo-labrum medially in between the stylets (conjoined mandibles and maxillae) and labial palps discernible; an individual projection is triangular in dorsal view and tapering distally (not visible in all specimens). Antenna (post-ocular segment 1) arises very antero-laterally and more ventral on the head capsule. It consists of at least two visible elements where discernible. It is elongated rectangular in dorsal view, in total many times longer than wide, very slender and about as long as or even longer than the head capsule. Stylets (post-ocular segments 3–4) arise antero-laterally on the head capsule and are directed anteriorly. They are elongated rectangular in dorsal view and curve distally medially; they are widest proximally and taper distally. There are median protrusions on the stylets, the teeth, tapering distally; at least three larger teeth present in all specimens. The middle tooth is slightly closer to the distal tooth than to the proximal one. The stylets are about as long as or longer than the head capsule. Of the labium (post-ocular segment 5) only the labial palps are discernible; they consist of at least two elements (number apparently varies within specimens due to preservation) which are elongated rectangular in anterior view. The labial palp is overall shorter than the antenna. Neck region membranous, rectangular in ventral view, and much wider than long where discernible. There seems to be no sclerite (cervix) present in any of the specimens.

Thorax segments (post-ocular segments 6–8) are overall rectangular in ventral view where discernible; they appear to be overall rather soft. The first thorax segment or prothorax (post-ocular segment 6) is longer than wide; there may be a subdivision of the tergite (and correspondingly on the sternite as well). Locomotory appendage 1 arises more anteriorly on the prothorax; it consists of six elements. The two most proximal elements (coxa and trochanter) are overall square-shaped or circular in posterior view and about as long as wide. The subsequent three elements (femur, tibia and tarsus) are elongated rectangular in posterior view and (mostly) much longer than wide. The most distal element (praetarsus) is preserved with one or two claws, which arise most distally on the tarsus, and the (adhesive) empodium medially in between the claws. The claws are rectangular in posterior view, curved and tapering distally, and show no lateral or median protrusions (teeth). Empodium is proximally rectangular in posterior view and very much longer than wide, and the distal part is stirrup-shaped in posterior view, smaller more proximally and widening significantly most distally ("trumpet-shaped"). Second thorax segment or mesothorax (post-ocular segment 7) is mostly longer than wide; there may also be a subdivision of the tergite and sternite as in the prothorax. Locomotory appendage 2 is similar to locomotory appendage 1, but slightly longer. Third thorax segment or metathorax (post-ocular segment 8) is mostly about as long as wide; there are no subdivisions in tergite or sternite apparent. Locomotory appendage 3 is similar to locomotory appendage 2.

Abdomen segments (post-ocular segments 9–19) are overall rectangular in ventral view where discernible; they also appear to be overall rather soft. There are at least eight abdomen segments discernible (the trunk end most likely being a compound of several segments); in most, the anterior edge is wider than the posterior edge. The abdomen is tapering posteriorly; the trunk end is mostly square-shaped in ventral view, with a rounded posterior edge.

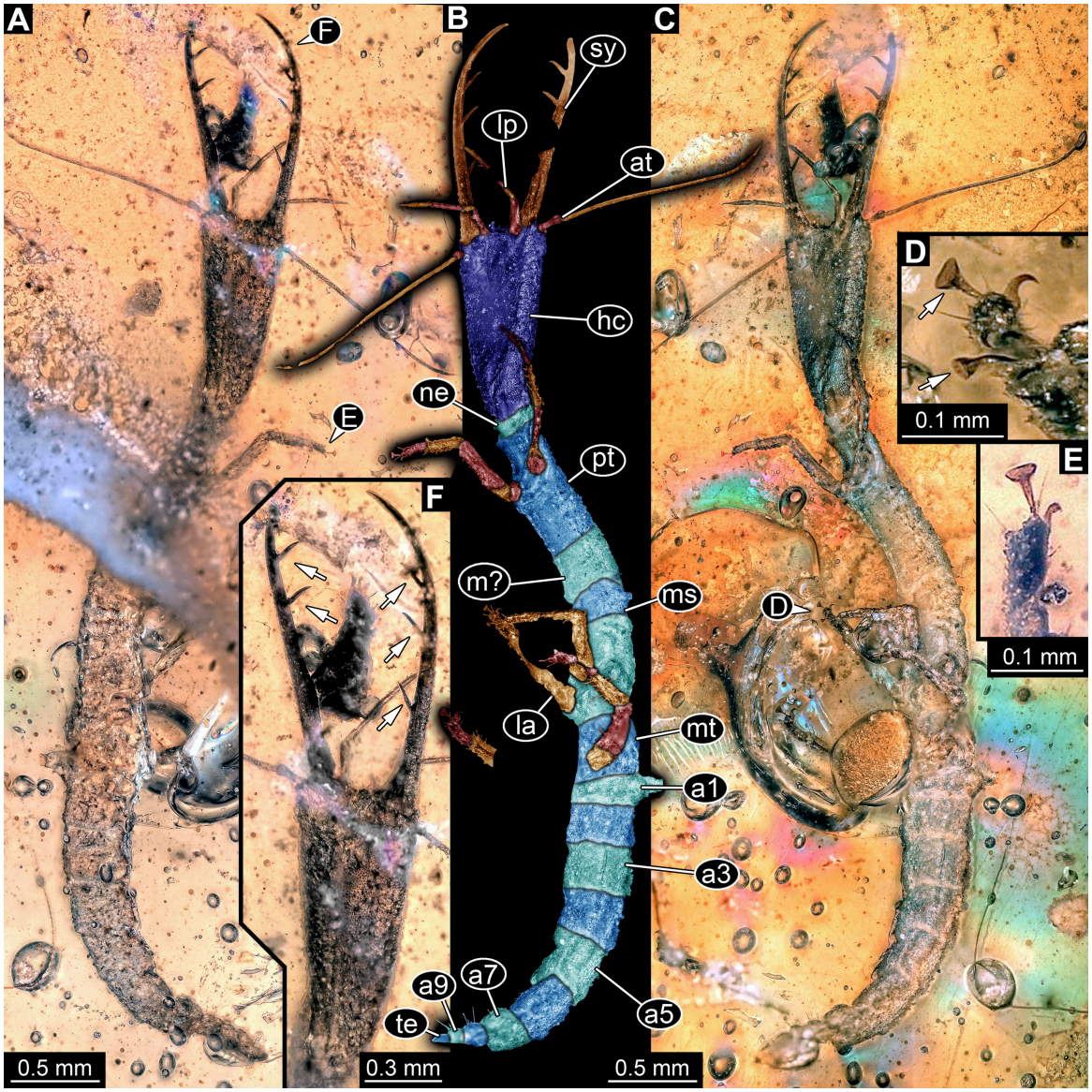

FIGURE 1. Longhead larva preserved in Myanmar amber, specimen BUB 3954; all composite images. **A**, Habitus in dorsal view, cross-polarised co-axial light on white background. **B**, Colour-marked version of **C**. **C**, Habitus in latero-ventral view, cross-polarised co-axial light on black background. **D**–**F**, Close-ups. **D**, Distal part of locomotory appendages of mesothorax, with trumpet-shaped empodia (marked by arrows). **E**, Tarsus with a claw and an empodium of right locomotory appendage of prothorax. **F**, Head capsule and stylets, teeth on stylets are marked with arrows. Abbreviations: a1–9 = abdomen segment 1–9; at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; m? = membrane; ms = mesothorax; mt = metathorax; ne = neck; pt = prothorax; sy = stylet; te = terminal end.

Specific description of the specimens

BUB 3954

Specimen entirely preserved (Fig. 1A, B, C); entire length about 5.13 mm.

Head capsule longer than wide (without appendages), two times; widest anteriorly in ventral view (length 1.03 mm, maximum width 0.5 mm). Stemmata (ocular segment) not discernible. Slight protrusion medially on the anterior edge of the head capsule discernible, but seemingly not paired; possible projection of clypeolabrum. Antenna (post-ocular segment 1) about 1.4 mm long and 0.04 mm wide at its widest point (proximal); longer than stylets. Two elements of antenna discernible; tapering distally with seta at tip. Stylets (post-ocular segment 3–4) about 1.3 mm long and 0.1 mm wide at its widest point (proximal); longer than head capsule. Three large teeth discernible (Fig. 1F). Labial palps (post-ocular segment 5) about 0.6 mm long and 0.06 mm wide at widest point; shorter than head capsule. Four elements discernible; tapering distally. Neck region membranous, wider than long, about three times.

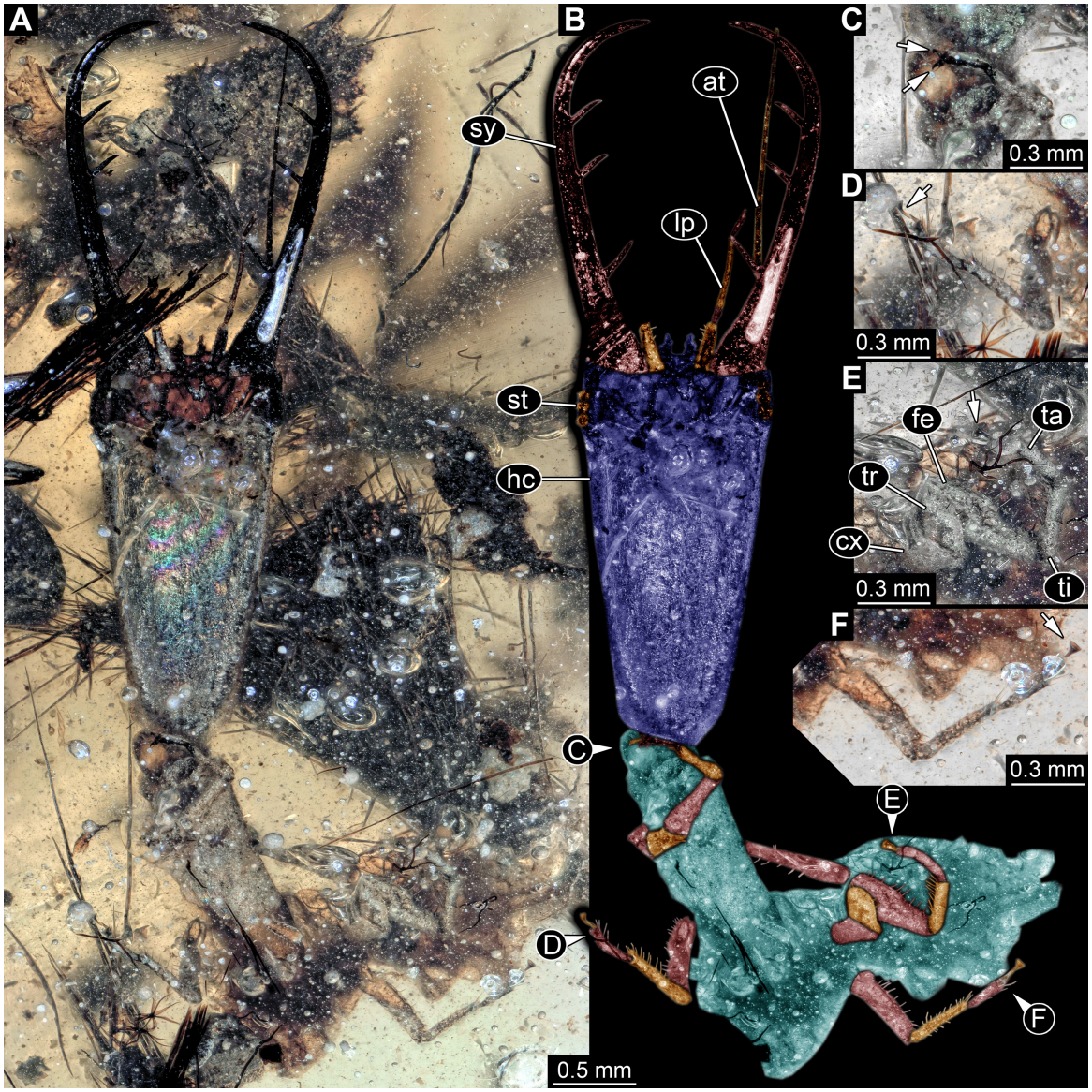

FIGURE 2. Longhead larva preserved in Myanmar amber, specimen PED 0436; all composite images. **A**, Habitus in ventral view, non-polarised ring light on white background. **B**, Colour-marked version of A. **C–F**, Close-ups. **C**, Right locomotory appendage of prothorax; claws are marked with arrows. **D**, Right locomotory appendage of mesothorax, with trumpet-shaped empodium (marked by arrow). **E**, Left locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). **F**, Right locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow) Abbreviations: at = antenna; cx = coxa; fe = femur; hc = head capsule; lp = labial palp; st = stemmata; sy = stylet; ta = tarsus; ti = tibia; tr = trochanter.

Thorax: Prothorax (post-ocular segment 6) seemingly subdivided into two units; anterior unit longer than wide, about two times at its widest point, and posterior unit about as long as wide. All elements of locomotory appendage 1 discernible. Praetarsus with at least one claw, probably two; empodium 0.05 mm long (Fig. 1E). Mesothorax (post-ocular segment 7) also seemingly subdivided into two units; anterior unit wider than long, more than 1.5 times, and posterior unit longer than wide, about 1.5 times at its widest point. All elements of locomotory appendage 2 discernible; slightly longer than locomotory appendage 1. Praetarsus with at least one claw, probably two; empodium 0.05 mm long (Fig. 1D). Metathorax (post-ocular segment 8) not seemingly subdivided; slightly wider than long at its widest point. Most proximal elements of locomotory appendage 3 not really discernible, but seemingly as long as locomotory appendage 2. Praetarsus with at least one claw, probably two; empodium 0.06 mm long.

Abdomen segment 1 (post-ocular segment 9) with latero-dorsal protrusion (tubercle?); anterior abdomen segments wider than long, more posterior abdomen segments about as long as wide. Trunk end trapezoidal in lateral view, with rounded ventro-posterior corner; longer than wide.

PED 0436

The specimen is nearly entirely preserved, but the posterior part, especially the abdomen and also parts of the thorax, is not clearly discernible (Fig. 2A, B). The entire specimen is about 7.77 mm long.

Head capsule longer than wide (without appendages), two times; widest anteriorly in dorsal view (length 2.29 mm, maximum width 1.15 mm). Stemmata (ocular segment) antero-laterally discernible; at least three lenses discernible in dorsal view. Clear anterior paired projections of the clypeo-labrum discernible between the stylets; individual one triangular in dorsal view and tapering distally. Projections about half as long as most proximal element of the labial palp. Antenna (post-ocular segment 1) at least 1.4 mm long and 0.04 mm wide at its widest point (more proximal); about as long as the stylets. Proximal part of antenna not discernible, so just one element of antenna (flagellum?) discernible. Discernible part of antenna longer than wide, 35 times; tapering slightly distally. Most distal parts probably not discernible. Stylets (post-ocular segments 3–4) about 2.4 mm long and 0.4 mm wide at its widest point (proximal); about as long as head capsule. Three large teeth discernible. Labial palps (post-ocular segment 5) about 1 mm long and 0.09 mm wide at widest point; about half as long as head capsule. Four elements discernible; tapering slightly distally. Neck region membranous, wider than long, about two times, but not entirely discernible.

Thorax: Prothorax (post-ocular segment 6) not really discernible from other parts of the thorax, but seemingly longer than wide, nearly two times. Locomotory appendage 1 and all its elements discernible. Praetarsus with two claws; empodium 0.09 mm long (Fig. 2C). Mesothorax (post-ocular segment 7) also not discernible from other parts of the thorax, but locomotory appendage 2 and distal four elements discernible. Praetarsus with at least one claw, probably two; empodium 0.13 mm long (Fig. 2D). Metathorax (post-ocular segment 8) also not discernible from other parts of the thorax, but locomotory appendage 3 and all elements discernible (Fig. 2E). Praetarsus with no claw discernible, but view obscured there on both appendages; empodium 0.11 mm long (Fig. 2F).

Abdomen segments (post-ocular segments 9–19) not discernible; abdomen seemingly tapering distally.

PED 0453

The specimen is similarly to the previous specimen nearly entirely preserved, but the posterior part, especially the abdomen and also parts of the thorax, is not clearly discernible (Fig. 3A, B, C). The entire specimen is about 2.25 mm long.

Head capsule longer than wide, widest posteriorly in dorsal view; almost square-shaped in dorsal view (length 0.56 mm, maximum width 0.49). Stemmata (ocular segment) not discernible. Projections of clypeo-labrum discernible. Antenna (post-ocular segment 1) about 0.77 mm long and 0.05 mm wide at its widest point (proximal); slightly longer than stylets. Two elements of antenna discernible; tapering slightly distally. Stylets (post-ocular segments 3–4) about 0.76 mm long and 0.09 mm wide at its widest point (proximal); longer than head capsule. Three large and two smaller teeth discernible on left stylet, the smaller spines being in between the two proximal larger teeth (Fig. 3D). Labial palps (post-ocular segment 5) about 0.15 mm long and 0.03 mm wide at widest point; about half as long as head capsule. No individual elements discernible, but distally tapering. Neck region not discernible.

Thorax: Prothorax (post-ocular segment 6) longer than wide, seemingly at least two times, but thorax segments not clearly distinguishable. Locomotory appendage 1 with only distal elements discernible. Praetarsus with at least one claw discernible, probably two; empodium 0.06 mm long (Fig. 3E). Mesothorax (post-ocular segment 7) not really discernible; locomotory appendage 2 also only distally discernible. Praetarsus with two claws; empodium 0.07 mm long (Fig. 3F). Metathorax (post-ocular segment 8) also not really discernible, but locomotory appendage 3, at least distally, discernible. Praetarsus with probably two claws; empodium 0.08 mm long (Fig. 3G).

Abdomen segments (post-ocular segments 9–19) not discernible, but seemingly wider than anterior part of thorax, but this could also be due to the preservation as the whole posterior part of the specimen is sort of 'squished together'.

PED 0566

Specimen anteriorly entirely preserved, metathorax and abdomen not preserved, but locomotory appendage 3 present (Fig. 4A, B, D); entire preserved length about 9.49 mm.

Head capsule longer than wide (without appendages), two times at its widest point; widest anteriorly in ventral view and tapering slightly posteriorly (length 2.31 mm, maximum width 1.17 mm). Stemmata (ocular segment) not discernible. No protrusion medially on the anterior edge of the head capsule discernible, but not exclude-able due to preservation either. Antenna (post-ocular segment 1) about 2.65 mm long and 0.15 mm wide at its widest point (proximal); about as long as stylets. Two elements of antenna discernible; tapering slightly distally. Stylets (post-ocular segments 3–4) about 2.88 mm long and 0.27 mm wide at widest point (proximal); slightly longer than head capsule. Three large teeth discernible. Labial palps (post-ocular segment 5) not discernible. Neck region membranous, wider than long, more than three times; not clearly discernible.

Thorax: Prothorax (post-ocular segment 6)

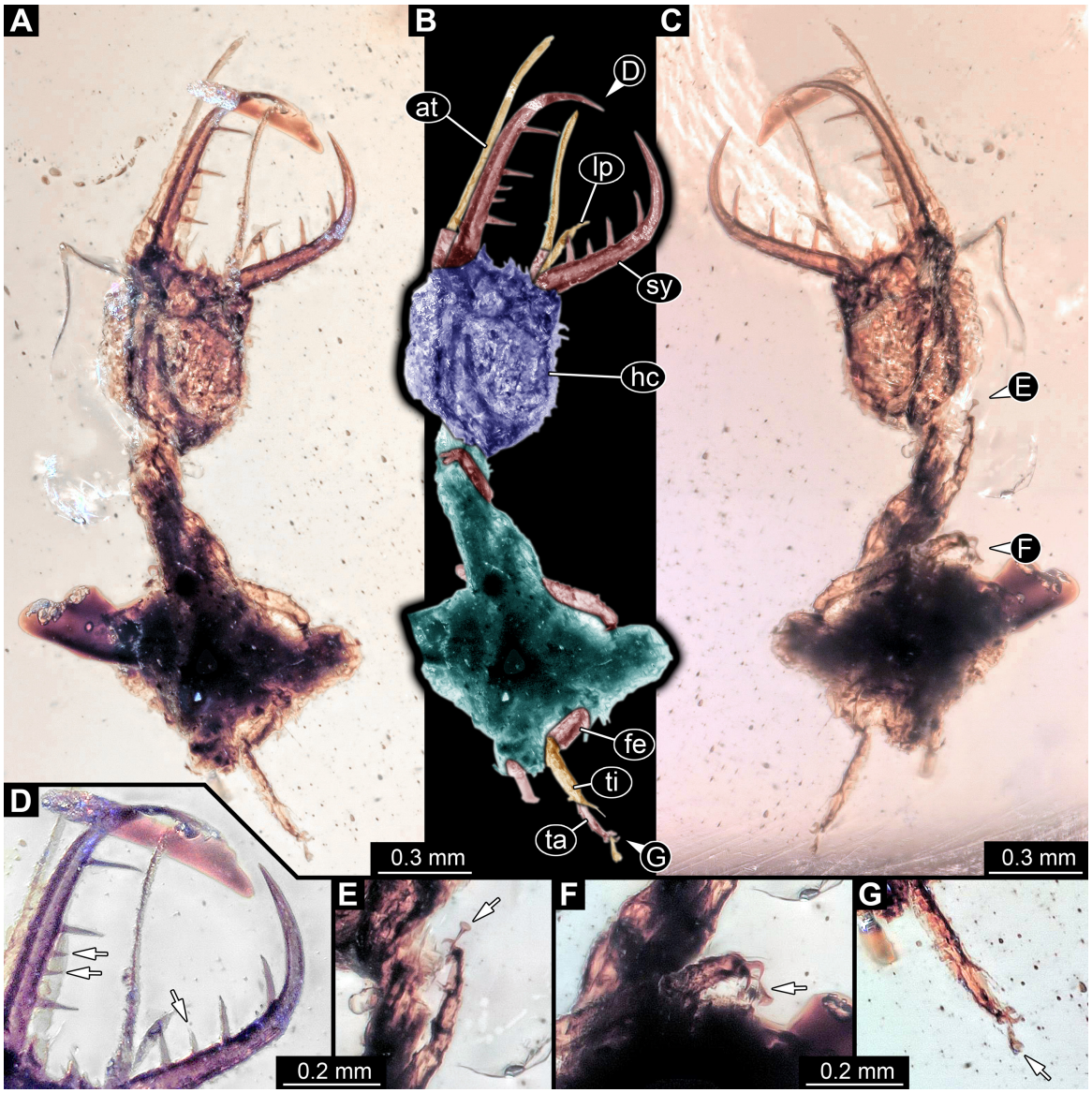

FIGURE 3. Longhead larva preserved in Myanmar amber, specimen PED 0453; all composite images. **A**, Habitus in (possible) dorsal view, non-polarised ring light on white background. **B**, Colour-marked version of A. **C**, Habitus in (possible) ventral view, non-polarised ring light on white background. **D–G**, Close-ups. **D**, Stylets with prominent teeth; small teeth are marked by arrows. **E**, Supposed left locomotory appendage of prothorax, with trumpet-shaped empodium (marked by arrow). **F**, Supposed left locomotory appendage of mesothorax, with trumpet-shaped empodium (marked by arrow). **G**, Supposed right locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). Abbreviations: at = antenna; fe = femur; hc = head capsule; lp = labial palp; sy = stylet; ta = tarsus; ti = tibia.

longer than wide, more than 2.5 times at widest point; possible subdivisions not discernible. Not all elements of locomotory appendage 1 discernible. Praetarsus with two claws; empodium about 0.22 mm long. Mesothorax (post-ocular segment 7) potentially only partly discernible; visible parts longer than wide, about 1.25 times at its widest point. Also not all elements of locomotory appendage 2 discernible. Praetarsus with two claws; empodium 0.11 mm long. Metathorax (post-ocular segment 8) not preserved, but locomotory appendage 3 distally discernible. Praetarsus with two claws; empodium 0.13 mm long (Fig. 4C, E).

Abdomen segments (post-ocular segments 9–19) not preserved.

PED 0582

Specimen entirely preserved (Fig. 5A, B); entire length about 5.44 mm.

Head capsule longer than wide (without appendages), about two times at its widest point; widest anteriorly in dorsal view and tapering slightly distally (length 0.83 mm, maximum width 0.42 mm). Stemmata (ocular segment) not really discernible. A pair of protrusions (clypeo-

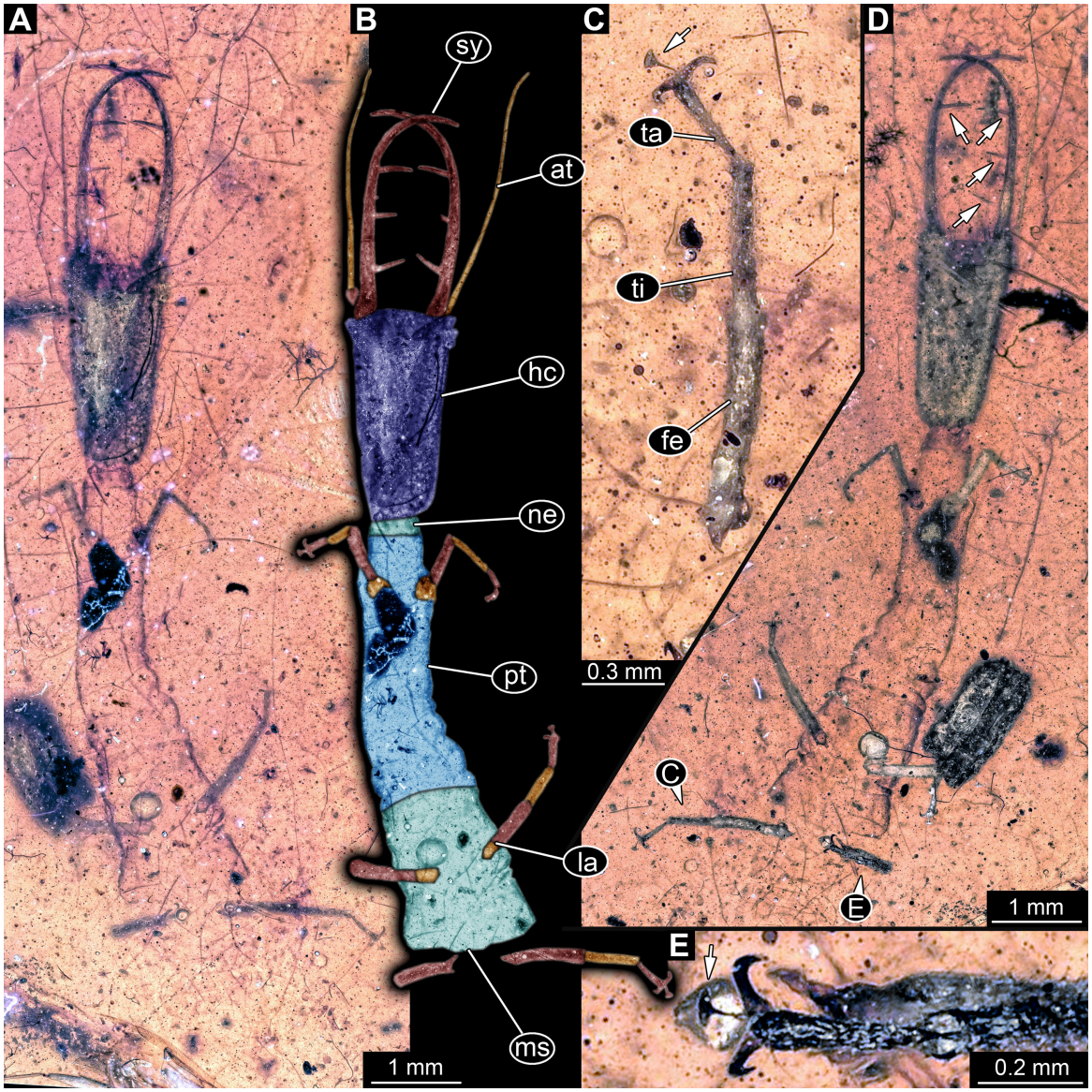

FIGURE 4. Longhead larva preserved in Myanmar amber, specimen PED 0566; all composite images. **A**, Habitus in dorsal view, non-polarised ring light on white background. **B**, Colour-marked version of **A**. **C**, Close-up; right locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). **D**, Habitus in ventral view, non-polarised ring light on white background. **E**, Close-up; distal part of left locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). Abbreviations: at = antenna; fe = femur; hc = head capsule; la = locomotory appendages; ms = mesothorax; ne = neck; pt = prothorax; sy = stylet; ta = tarsus; ti = tibia.

labrum) medially on the anterior edge of the head capsule discernible, each triangular and tapering distally in dorsal view. Antenna (post-ocular segment 1) about 1.2 mm long and 0.04 mm wide at its widest point (proximal); about as long as stylets. Three elements of antenna discernible. Flagellum distally (seemingly) subdivided; most distal portion of flagellum (at least on left antenna) separate and longer than wide, about nine times (Fig. 5 inlet).

Stylets (post-ocular segments 3–4) about 1.04 mm long and 0.09 mm wide at its widest point (proximal); longer than head capsule. Three large teeth discernible (Fig. 5C). Labial palps (post-ocular segment 5) about 0.42 mm long and 0.02 mm wide at widest point; about half as long as head capsule. Two elements discernible; tapering slightly distally. Neck region membranous, wider than long, more than 1.5 times.

Thorax: Prothorax (post-ocular segment 6) seemingly subdivided into two units; anterior unit longer than wide at its widest, about 4.25 times, and posterior unit wider than long, about 1.33 times. Distal elements of locomotory appendage 1 discernible. Praetarsus with two claws; empodium 0.07 mm long (Fig. 5E). Mesothorax (post-ocular segment 7) not seemingly subdivided; wider than long, more than 1.33 times. Not all elements of locomotory appendage 2 discernible. Praetarsus with

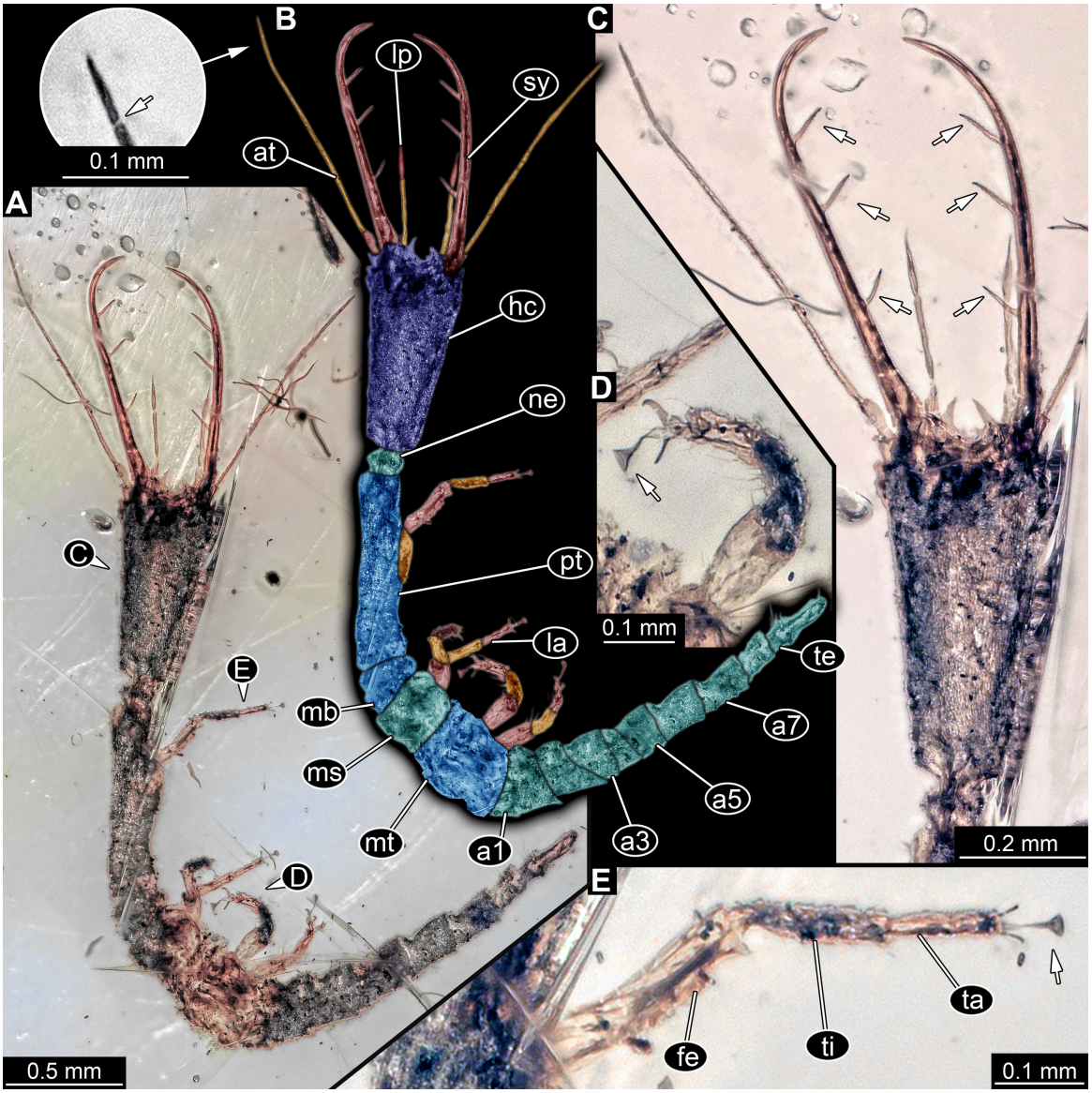

FIGURE 5. Longhead larva preserved in Myanmar amber, specimen PED 0582; all composite images. **A**, Habitus in dorso-lateral view, cross-polarised co-axial light on white background. **B**, Colour-marked version of **A**; inlet: close-up of tip of left antenna; subdivision of flagellum is marked with an arrow. **C–E**, Close-ups. **C**, Head capsule and its appendages, non-polarised ring light on white background; teeth on stylets are marked with arrows. **D**, Left locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). **E**, Right locomotory appendage of prothorax, with trumpet-shaped empodium (marked by arrow). Abbreviations: a1–7 = abdomen segment 1–7; at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; mb = membrane; ms = mesothorax; mt = metathorax; ne = neck; pt = prothorax; sy = stylet; ta = tarsus; te = terminal end; ti = tibia.

two claws; empodium about 0.07 mm long. Metathorax (post-ocular segment 8) also not seemingly subdivided; slightly longer than wide. Not all elements of locomotory appendage 2 discernible. Praetarsus with two claws; empodium 0.08 mm long (Fig. 5D).

Abdomen segments (post-ocular segments 9–17) slightly less wide than thorax segments and tapering posteriorly. Trunk end trapezoidal in lateral view, with rounded posterior corners and slightly tapering most distally; longer than wide.

BUB 3384

Specimen entirely preserved (Fig. 6A, B, C); entire length about 3.8 mm.

Head capsule longer than wide (without appendages), more than 1.33 times at its widest point; widest anteriorly in dorsal view and tapering slightly posteriorly (length 0.57 mm, maximum width 0.42 mm). Stemmata (ocular segment) antero-laterally discernible; at least five lenses discernible in dorsal view. No protrusion medially on the anterior edge of the head capsule discernible, but view obstructed here in dorsal and ventral view (Fig. 6D, E).

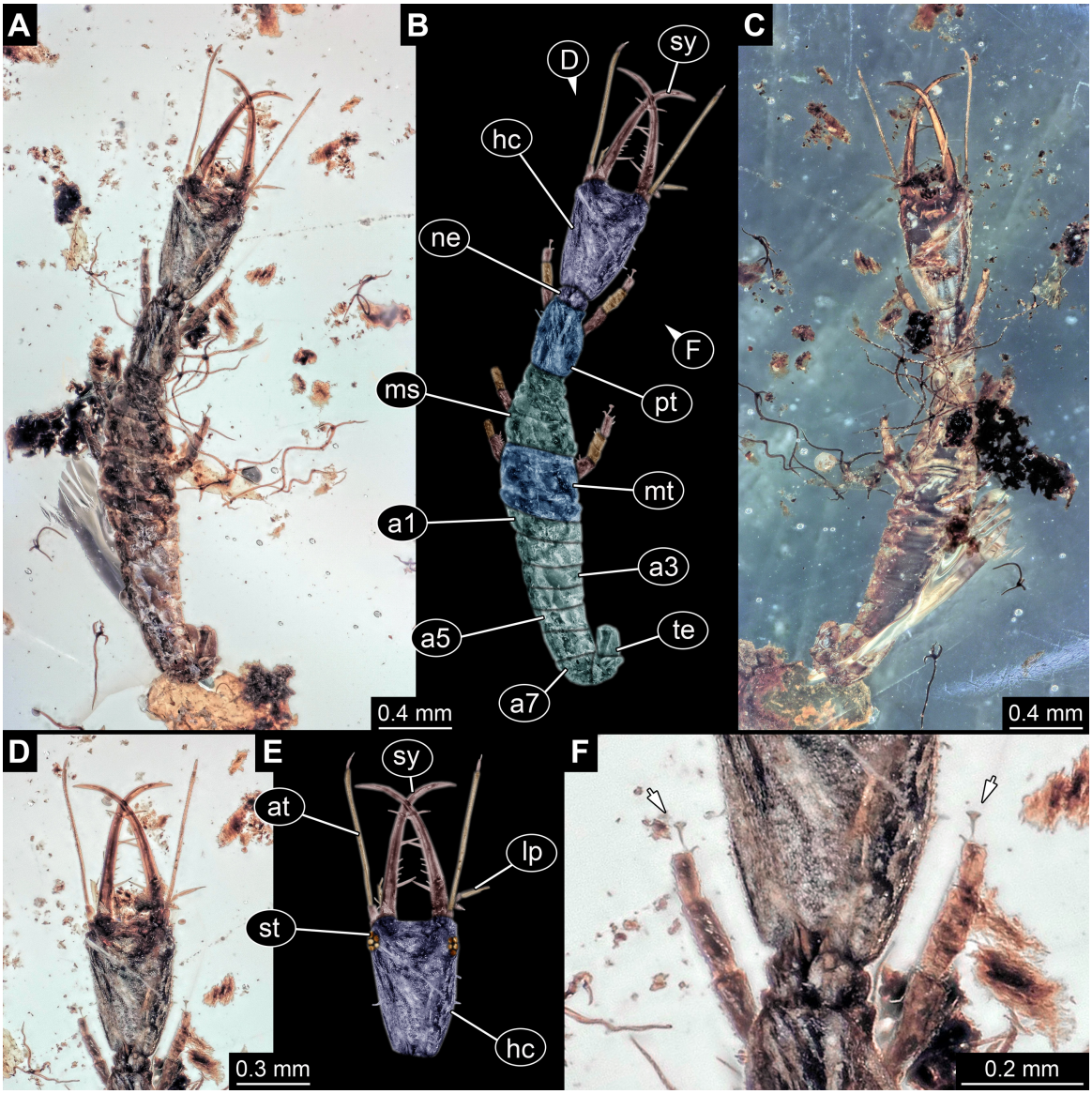

FIGURE 6. Longhead larva preserved in Myanmar amber, specimen BUB 3384; all composite images. **A**, Habitus in dorsal view, unpolarised ring light on white background. **B**, Colour-marked version of **A**. **C**, Habitus in ventral view, unpolarised ring light on black background. **D–F**, Close-ups. **D**, Head capsule and its appendages. **E**, Coloured-marked version of **D**. **F**, Locomotory appendage of prothorax, with trumpet-shaped empodia (marked by arrows). Abbreviations: a1–7 = abdomen segment 1–7; at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; ms = mesothorax; mt = metathorax; ne = neck; pt = prothorax; st = stemmata; sy = stylet; te = terminal end.

Antenna (post-ocular segment 1) about 0.8 mm long and 0.05 mm wide at its widest point (proximal); about as long as stylets. Three elements of antenna discernible; with seta at its distal tip.

Stylets (post-ocular segments 3–4) about 0.77 mm long and 0.08 mm wide at its widest point (proximal); longer than head capsule. Three large and five smaller teeth discernible, the smaller teeth being in between the two proximal larger teeth. Labial palps (post-ocular segment 5) about 0.17 mm long and 0.03 mm wide at widest point; about half as long as head capsule. Only one element seemingly discernible, but partly obscured by stylets. Neck region membranous, wider than long, more than two times.

Thorax: Prothorax (post-ocular segment 6) seemingly not subdivided into two units; wider than long, about 1.33 times. Only distal elements of locomotory appendage 1 discernible. Praetarsus with at least one claw, probably two; empodium 0.04 mm long (Fig. 6F). Mesothorax (post-ocular segment 7) also seemingly not subdivided, but dorsal surface with distinct folds; slightly longer than wide at its widest. No praetarsus discernible. Metathorax (post-ocular segment 8) also seemingly not subdivided, but dorsally at least two folds are discernible; wider than

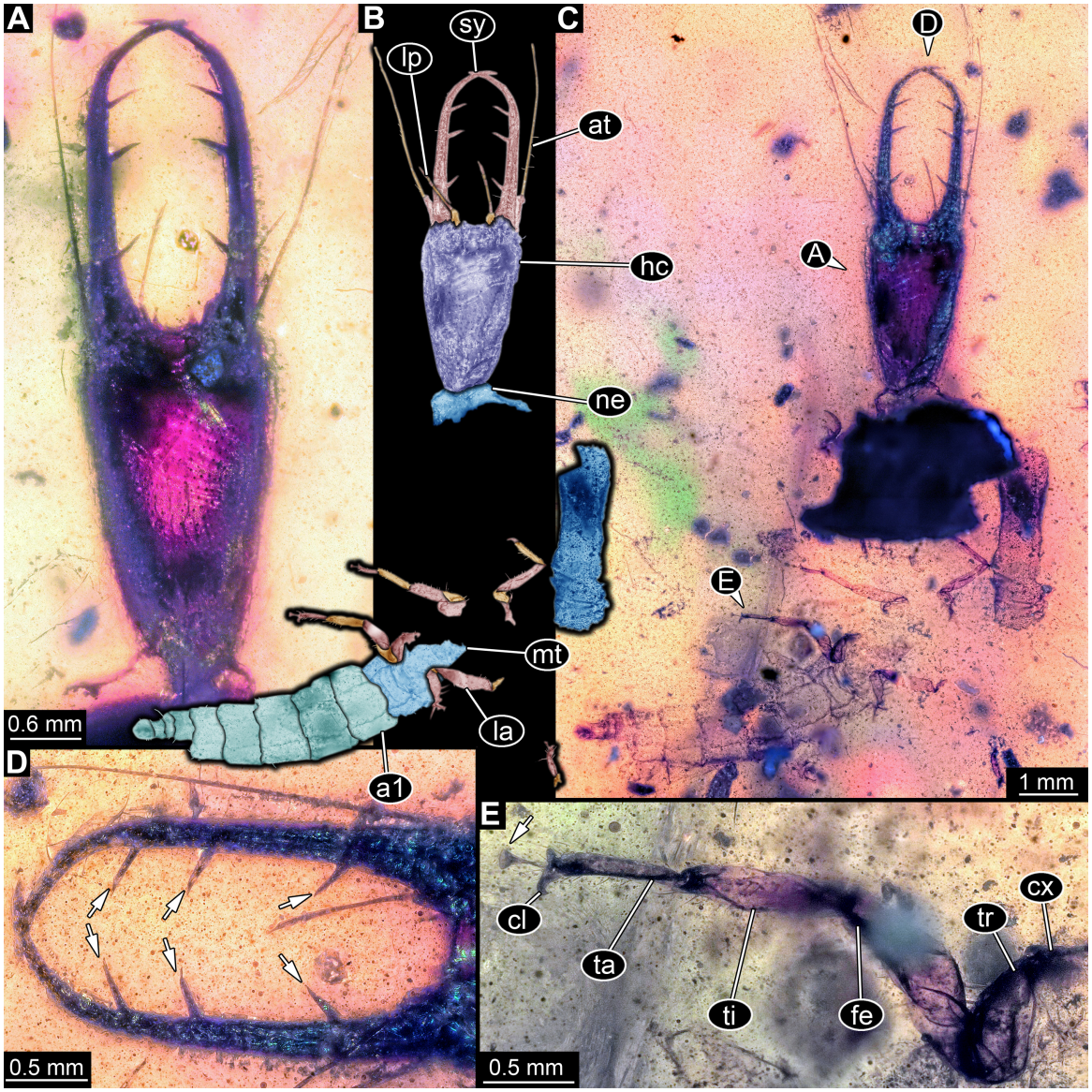

FIGURE 7. Longhead larva preserved in Myanmar amber, specimen PED 0134; all composite images. **A**, **D**, **E**, Close-ups. **A**, Head capsule and its appendages, non-polarised co-axial light on black background. **B**, Colour-marked version of **C**. **C**, Habitus in (possible) ventral view, non-polarised co-axial light on white background. **D**, Stylets with teeth (marked with arrows). **E**, Supposed right locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). Abbreviations: a1 = abdomen segment 1; at = antenna; cl = claw; cx = coxa; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; mt = metathorax; ne = neck; sy = stylet; ta = tarsus; ti = tibia; tr = trochanter.

long, more than 1.25 times. Praetarsus with at least one claw, probably two; empodium 0.06 mm long.

Abdomen segments 1–7 (post-ocular segments 9–15) wider than long. Abdomen segment 8 (post-ocular segment 16) and the trunk end flipped anteriorly, so slightly obscured. Abdomen segment 9 (post-ocular segment 17) and trunk end longer than wide.

PED 0134

Specimen entirely preserved, but thorax area incomplete (Fig. 7B, C); entire length about 15.5 mm.

Head capsule longer than wide (without appendages), more than 1.6 times at its widest point; widest anteriorly in ventral view (length 2.83 mm, maximum width 1.72 mm). Stemmata (ocular segment) not discernible. A pair of protrusions (clypeo-labrum) medially on the anterior edge of the head capsule discernible in ventral view, each triangular and tapering distally in dorsal view (Fig. 7A). Antenna (post-ocular segment 1) about 3.14 mm long and 0.11 mm wide at its widest point (proximal); about as long as stylets. Two elements of antenna discernible; proximal element (pedicellus?) longer than wide, more than 4.5 times, distal element (flagellum) longer than wide, 33 times, and tapering slightly distally. Stylets (post-ocular

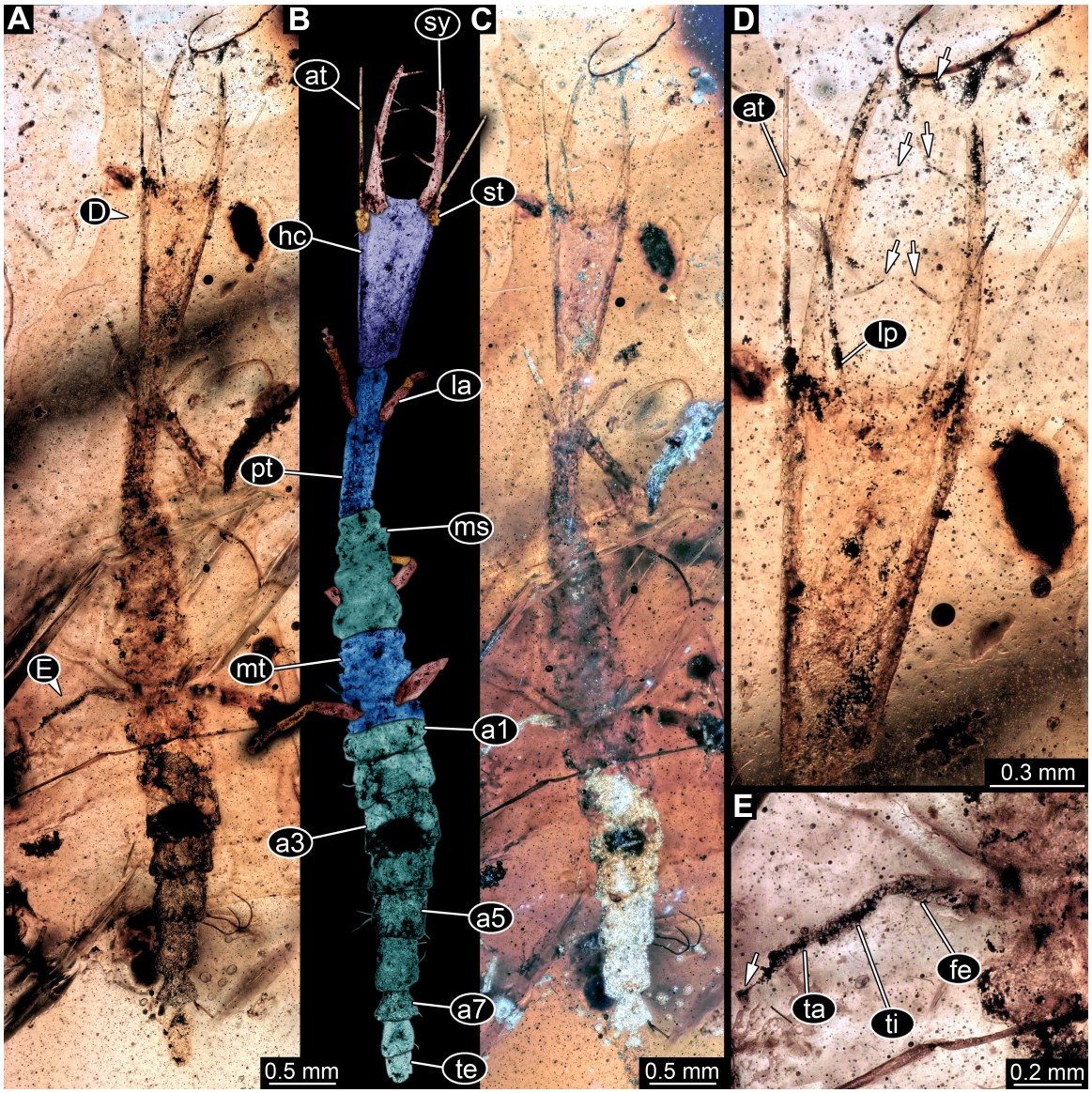

FIGURE 8. Longhead larva preserved in Myanmar amber, specimen PED 0344; all composite images. **A**, Habitus in ventral view, transmitted light. **B**, Colour-marked version of **A**. **C**, Habitus in ventral view, non-polarised ring light on white background. **D–E**, Close-ups. **D**, Head capsule and its appendages; teeth on stylets are marked with arrows. **E**, Right locomotory appendage of metathorax, with trumpet-shaped empodium (marked by arrow). Abbreviations: a1–7 = abdomen segments 1–7; at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; st = stemmata; sy = stylet; ta = tarsus; te = terminal end; ti = tibia.

segments 3–4) about 3.04 mm long and 0.31 mm wide at its widest point (proximal); about as long as head capsule. Three large teeth discernible (Fig. 7D). Labial palps (post-ocular segment 5) about 1.21 mm long and 0.13 mm wide at widest point; about half as long as head capsule. Six elements discernible; tapering distally. Neck region membranous, wider than posterior part of head capsule, but length not discernible.

Thorax: Prothorax (post-ocular segment 6) seemingly much longer than wide; locomotory appendage 1 not discernible. Mesothorax (post-ocular segment 7) not really discernible, but potentially as wide as the prothorax; yet all elements of locomotory appendage 2 are discernible. Praetarsus with at least one claw, probably two; empodium 0.13 mm long. Metathorax (post-ocular segment 8) also not entirely discernible, but longer than wide, probably more than 1.35 times. Locomotory appendage 3 and all its elements discernible. Praetarsus with two prominent claws; empodium 0.15 mm long (Fig. 7E).

Abdomen segments 1–5 (post-ocular segments 9–13) all about as wide as the metathorax and overall wider than long. Abdomen segments 6–8 (post-ocular segments 14–16) only about 2/3 the width of preceding segments, but still also wider than long. The trunk end is circular with a slight pointy end medio-posteriorly in ventral view and slightly longer than wide.

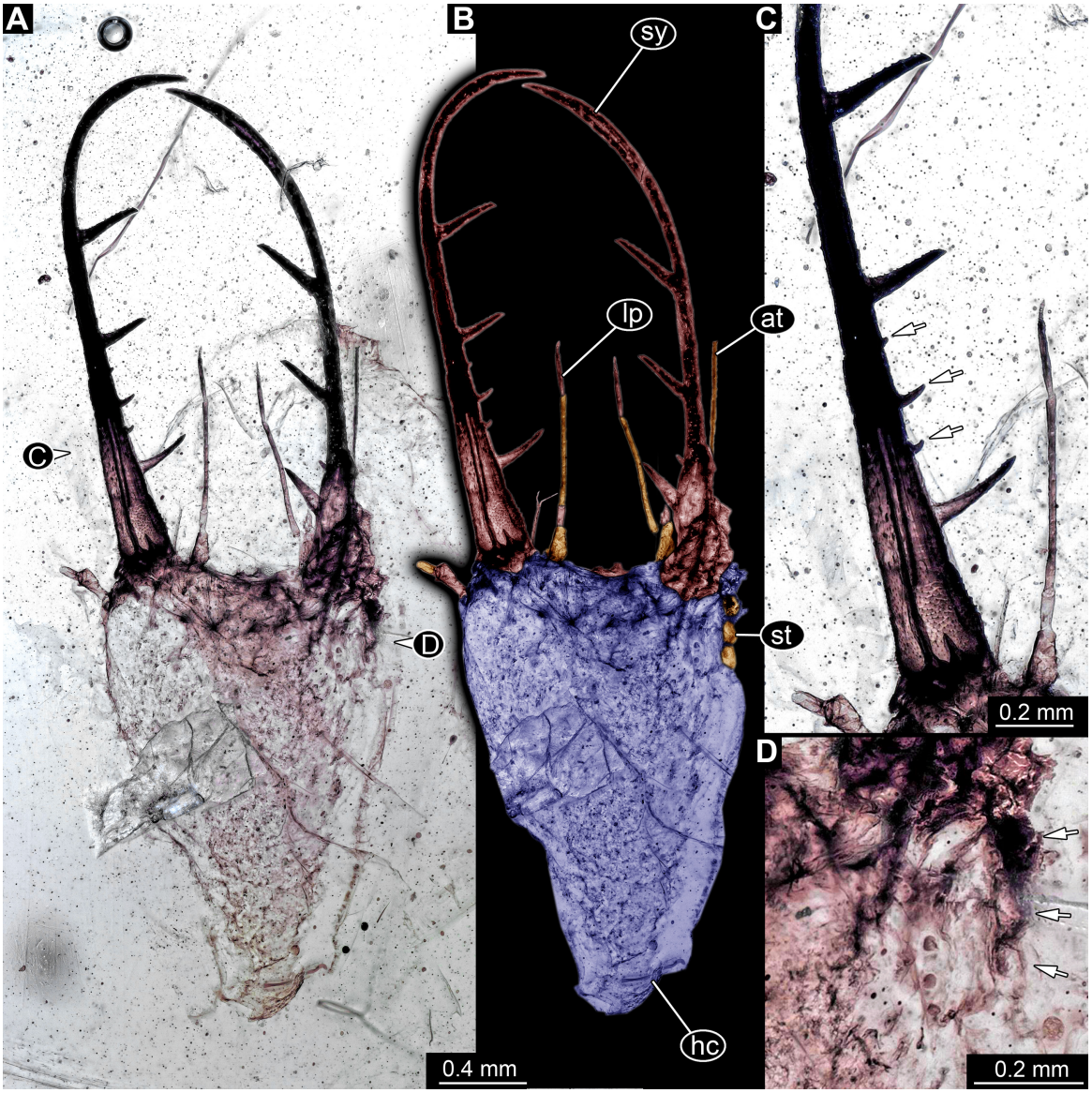

FIGURE 9. Longhead larva preserved in Myanmar amber, specimen PED 0407; all composite images. **A**, Head capsule and its appendages in dorsal view, cross-polarised co-axial light on white background. **B**, Colour-marked version of **A**. **C–D**, Close-ups. **C**, Stylets with various teeth, small teeth are marked with arrows. **D**, Stemmata are marked with arrows. Abbreviations: at = antenna; hc = head capsule; lp = labial palp; st = stemmata; sy = stylet.

PED 0344

Specimen nearly entirely preserved (Fig. 8A, B, C), stylets incomplete; entire length about 7.48 mm.

Head capsule longer than wide (without appendages), more than two times at its widest point; widest anteriorly in ventral view and tapering slightly posteriorly (length 1.24 mm, maximum width 0.55 mm). Stemmata (ocular segment) antero-laterally discernible; at least five lenses discernible in dorsal view. No protrusion medially on the anterior edge of the head capsule discernible, but not exclude-able due to preservation either. Antenna (post-ocular segment 1) only proximally discernible, distally probably broken off; discernible parts of antenna about 1.4 mm long and 0.04 mm wide at its widest point (proximal). Discernible parts as long as discernible parts of stylets. Five elements of antenna discernible. Discernible part of stylets (post-ocular segments 3–4) about 1.14 mm long and 0.17 mm wide at its widest point (proximal); discernible parts slightly shorter than head capsule, but probably slightly longer. Three large and four smaller teeth discernible, the smaller teeth being in between the two proximal larger teeth (Fig. 8D). Labial palps (post-ocular segment 5) about 0.61 mm long and 0.04 mm wide at widest point; slightly less than half as long as head capsule. Four(?) elements discernible; tapering distally. Neck region membranous, wider than long, about 3.2 times.

Thorax: Prothorax (post-ocular segment 6) seemingly

not subdivided; longer than wide, about four times. Only distal elements of locomotory appendage 1 discernible. Praetarsus with at least one claw, probably two; empodium 0.05 mm long. Mesothorax (post-ocular segment 7) also seemingly not subdivided, but in ventral view at least four units slightly discernible; entire mesothorax longer than wide, about 1.7 times (anterior two units wider than long, about three times, and posterior two units wider than long, about two times). Locomotory appendage only partly discernible; distal part not discernible. Metathorax (post-ocular segment 8) also seemingly not subdivided, but in ventral view about four units slightly discernible. Entire mesothorax longer than wide, about 1.2 times (all slightly discernible units wider than long). Only distal elements of locomotory appendage 3 discernible. Praetarsus with two claws; empodium 0.11 mm long (Fig. 8E).

Abdomen segments 1–7 (post-ocular segments 9–15) wider than long each. Abdomen segment 7 (post-ocular segment 15) more trapezoidal in ventral view than preceding segments. Abdomen segment 8 (post-ocular segment 16) as long as wide. Trunk end with rounded posterior edge and also as long as wide.

PED 0407

Only head of specimen preserved (Fig. 9A, B); entire length (head with appendages) about 4.28 mm.

Head capsule longer than wide (without appendages), about 1.6 times at its widest point; widest anteriorly in dorsal view and tapering posteriorly (length 1.98 mm, maximum width 1.22 mm). Stemmata (ocular segment) antero-laterally discernible (Fig. 9D); at least three lenses discernible in dorsal view. A pair of protrusions (clypeo-labrum) medially on the anterior edge of the head capsule discernible, each trapezoidal and tapering slightly distally in dorsal view. Antenna (post-ocular segment 1) not entirely preserved, but probably at least 1.1 mm long and 0.09 mm wide at its widest point (proximal); discernible part half as long as stylets, but probably longer than that. At least two elements discernible, but probably distally broken off. Stylets (post-ocular segments 3–4) about 2.65 mm long and 0.28 mm wide at its widest point (proximal); slightly longer than head capsule. Three large and three smaller teeth discernible, the smaller teeth being in between the two proximal larger teeth (Fig. 9C). Labial palps (post-ocular segment 5) about 1.01 mm long and 0.09 mm wide at widest point; about half as long as head capsule. Four elements discernible; distal element widening slightly at about half its length and then tapering slightly distally; longer than wide at its widest point.

BuB 10

Specimen only anteriorly with head and thorax preserved, but thorax not clearly discernible (Fig. 10A, C). The entire specimen is about 5.4 mm long.

Head capsule longer than wide, about 1.8 times (without appendages); widest anteriorly and tapering posteriorly in dorsal view (length 1.85 mm, maximum width 1.04 mm). Stemmata (ocular segment) not discernible. Slight protrusion medially on the anterior edge of the head capsule discernible, but seemingly not paired; triangular and tapering distally in ventro-lateral view. Possible projection of clypeo-labrum. Antenna (post-ocular segment 1) at least 2.75 mm long and 0.09 mm wide at its widest point (more proximal); slightly longer than stylets. At least two elements discernible and tapering distally. Stylets (post-ocular segments 3–4) about 2.4 mm long and 0.4 mm wide at its widest point (proximal); longer than head capsule. Three large teeth discernible (Fig. 10D). Labial palps (post-ocular segment 5) about 0.74 mm long and 0.04 mm wide at widest; less than half as long as head capsule. Four elements discernible and tapering distally. Neck region wider than long, about 1.8 times.

Thorax segments (post-ocular segments 6–8) not clearly discernible; at least two thorax segments discernible, anterior one (prothorax?; post-ocular segment 6?) wider than long and posterior one (mesothorax?; post-ocular segment 7?) longer than wide. One locomotory appendage (probably 1; post-ocular segment 6) distally discernible. Praetarsus with two claws; empodium about 0.13 mm long (Fig. 10B).

Shape analysis

The shape analysis resulted in five effective Principal Components (PCs; values and measures can be found in Suppl. Tab. 2 and 3 and in Suppl. Text 1).

PC1 explains 57.97% of the total variance. It is mainly influenced by the length of the posterior head capsule rim and the thickness and position of the stylets. A high value indicates a relatively long anterior-posterior axis of the head capsule with an elongated convex posterior rim. It also indicates stylets that are wider at the anterior tip, where the tips of both stylets are positioned wide apart. A low value indicates relatively short anterior-posterior axis of the head capsule with a relatively flat posterior rim. It also indicates stylets that are narrower at the anterior tip, where the tips of both stylets are closer to each other than in high values (Suppl. Fig. 1).

PC2 explains 20.73% of total variance. It is mainly influenced by the length of the stylets, length of the anterior-posterior axis of the head capsule and the shape of the posterior rim of the head capsule. A high value indicates a relatively short head capsule with a concave posterior rim. It also indicates relatively long stylets, often being longer than the head capsule. A low value indicates a relatively long head capsule with a convex posterior rim, ending with a convex angle in the middle. Stylets are shorter and stout (Suppl. Fig. 1).

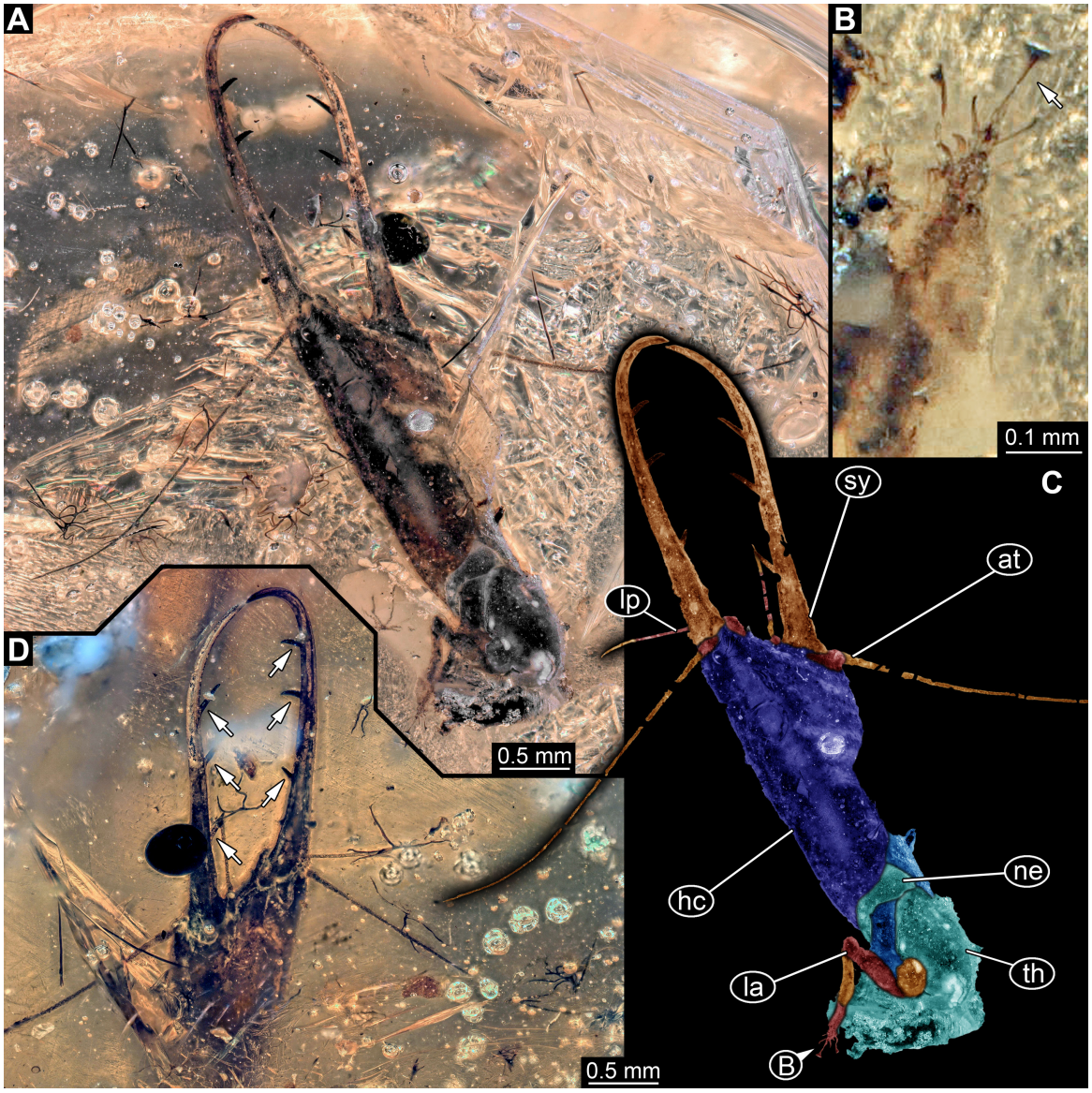

FIGURE 10. Longhead larva preserved in Myanmar amber, specimen BuB 10; all composite images. **A**, Habitus in dorsal view, non-polarised ring light on black background. **B**, Close-up; distal part of a locomotory appendage, with trumpet-shaped empodium (marked by arrow). **C**, Colour-marked version of **A**. **D**, Head capsule in ventral view, cross-polarised co-axial light on black background; teeth on stylets are marked with arrows. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; ne = neck; sy = stylet; th = thorax.

PC3 explains 8.73% of total variance. It is mainly influenced by the combined length of the anterior-posterior axis of the head capsule with stylets. It is also influenced by the anterior rim of the head capsule itself and the width of the proximal part of stylets. A high value indicates a longer combined length of the head capsule with stylets and a convex anterior rim of the head capsule with narrower proximal part of stylets. A low value indicates a shorter combined length of the head capsule with stylets and a concave anterior rim of the head capsule with wider proximal part of stylets (Suppl. Fig. 1).

PC4 explains 3.84% of total variance. It is mainly influenced by the shape of the anterior and of the posterior rim of the head capsule and the combined length of head capsule and stylets. It is also influenced by the position of the anterior tips of the stylets and the width of the proximal part of the stylets. A high value indicates a rounded concave anterior rim and convex posterior rim of the head capsule. Stylets have a wider proximal part and a wider anterior tip than in low values. The anterior tips of the stylets are closer to each other than in low values. The combined length of the head capsule and stylets is bigger than in low values. A low value indicates a relatively straight anterior and posterior rim of the head capsule. Stylets are straighter, with a narrower proximal part than in high values. Anterior parts of the tips are wider apart from each other than in high values (Suppl. Fig. 1).

PC5 explains 2.96% of total variance. It is mainly

influenced by the length and shape of the head capsule. It is also influenced by the length of stylets and the width of the stylet anterior tip. A high value indicates a concave anterior and straight posterior rim of the head capsule. Stylets are somewhat shorter and have a wider anterior tip. A low value indicates a somewhat more straight anterior and a convex rounded posterior rim of the head capsules. Stylets are somewhat longer and have a narrower anterior tip than in high values (Suppl. Fig. 1).

When plotting the first two principal components for all 200 specimens from our study, we recognise a certain sorting of known groups but with quite some overlap (Fig. 11). All the new larvae plot close to the holotype of *Macleodiella electrina*, in the lower right quadrant of the scatter plot with higher values of PC1 and lower values of PC2.

In this plot, the new specimens and the holotype of *M. electrina* form two more or less distinct subgroups. One subgroup with four new specimens is closer to the centre of the plot, overlapping with some larvae of Ascalaphidae. The other subgroup includes four new specimens and the holotype of *Macleodiella electrina*; it is close to the first subgroup, but plots further to the lower right, overlapping with some larvae of Crocinae.

When plotting head capsule width over head capsule length (Fig. 12A), also two distinct groups are recognisable. However, these are not the same two groupings as in the shape analysis, *i.e.* not the same specimens plot together.

When plotting PC1 over head capsule length (Fig. 12B) it becomes apparent that the pattern is in fact caused by four different groups. Plotting relative stylet length over head capsule length (Fig. 12C) and width (Fig. 12D) again results in two groups each.

Discussion

Uniformity of the specimens

It is apparent that all specimens discussed here share distinct morphological features with the larva that was formally described as *Macleodiella electrina* by Badano & Engel (in Badano *et al*., 2018). All share: a rather elongated head capsule; prominent stylets that are, roughly, about the same length as the head capsule; stylets that have a curvature stronger expressed towards the distal region; stylets that bear three prominent teeth, a middle tooth that is closer to the distal tooth than to the proximal one; stylets that are overall rather slender (compared to those of many modern antlion and owlfly larvae); when preserved, trunk appendages with a prominent trumpet-shaped empodium; a trunk that is, where known, rather slender. Despite these similarities there is quite some variation among the specimens, not least concerning the size. We therefore need to consider these differences in more detail in the following.

Possible sources of variation: ontogeny

When simply plotting head capsule width versus head length of all specimens of "longheads" + *Macleodiella*

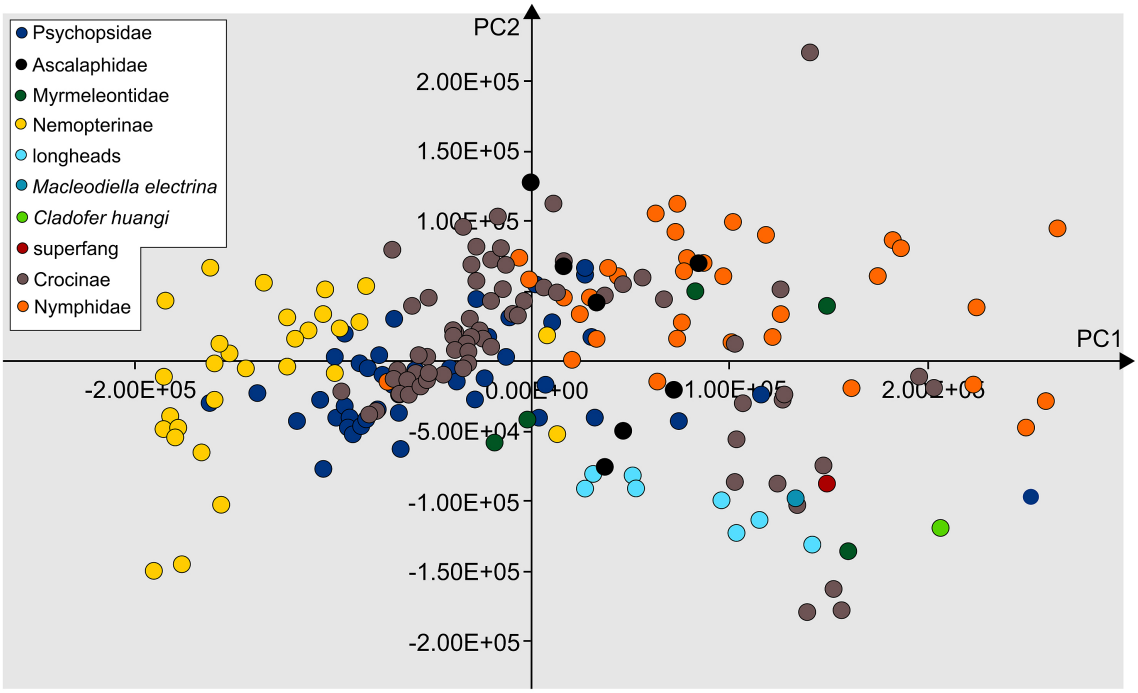

FIGURE 11. Scatterplot of PC2 over PC1, representing the shapes of head capsules and stylets of different larvae of Myrmeleontiformia. The group "longheads" includes the new larvae described in this study and the holotype of *Macleodiella electrina* (see discussion).

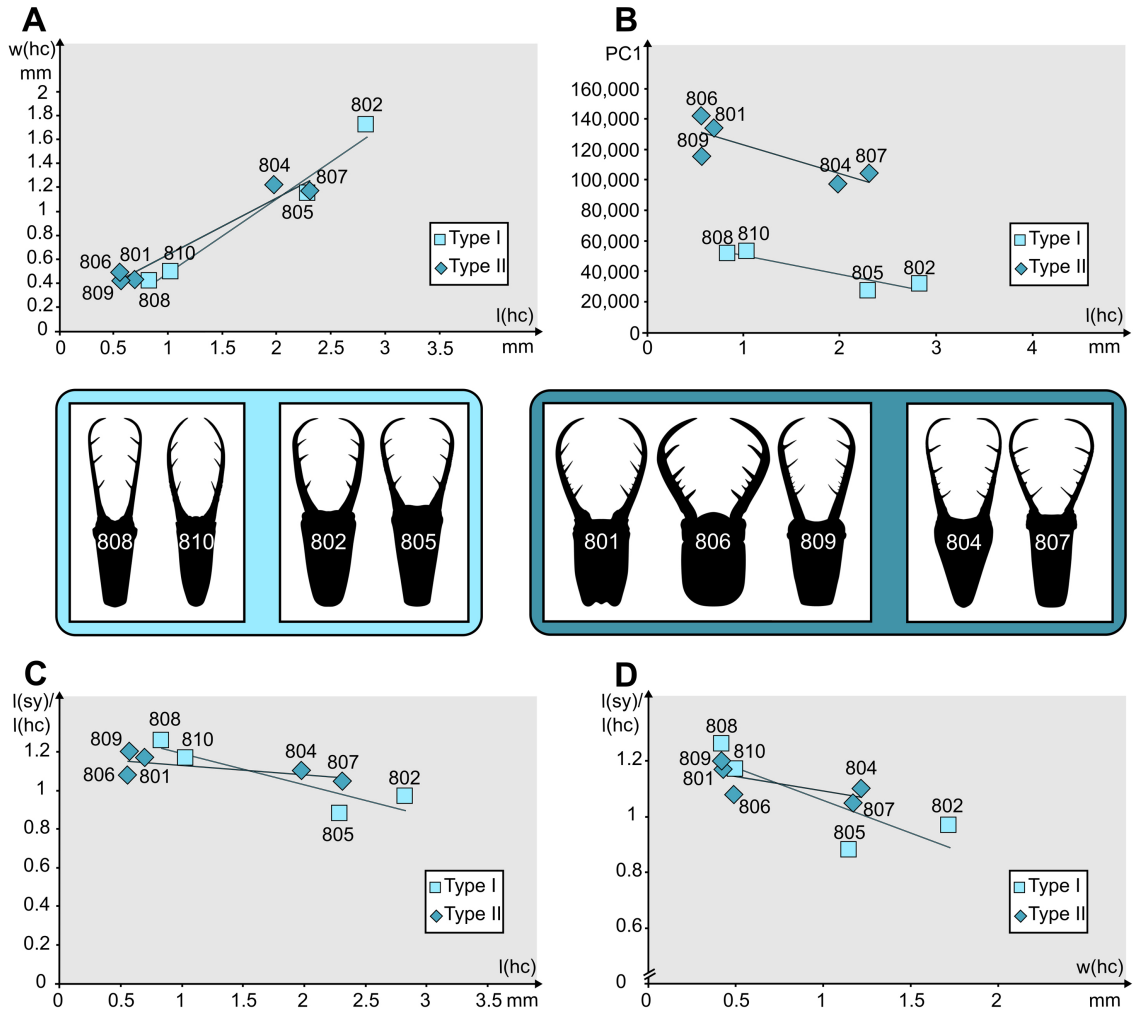

FIGURE 12. Additional quantitative aspects of longhead larvae with outlines of head capsules and stylets that were used in shape analysis. **A**, Scatterplot of head capsule width over head capsule length. **B**, Scatterplot of PC1 (shape of stylets and head capsule) over head capsule length. **C**, Scatterplot of relative stylet length over head capsule length. **D**, Scatterplot of relative stylet length over head capsule width.

electrina, one could get the impression that the specimens separate into two or maybe three distinct groups on a first glimpse (Fig. 12A). However, the smallest supposed group would show quite a wide range of size variation in head length (0.56–1.24 mm) which is almost as large (0.68 mm) as the distance between the smallest specimen of a supposed group 2 and the single specimen of a supposed group 3 (1.98–2.83 mm, *i.e.*, 0.85 mm). This variation immediately casts some doubt on the interpretation as three distinct groups.

When plotting the overall shape (≈ PC1) versus head length (Fig. 12B), we can recognise four more or less distinct groups: an upper group with shorter heads, an upper group with longer heads, a lower group with shorter heads, and a lower group with longer heads. It appears that a major shape difference between the upper and the lower groups is the presence of smaller teeth in between the three large teeth on the mandible in the specimens in the upper groups. The specimens in the lower groups have only the three large teeth.

We know that in other ingroups of Neuroptera, teeth can be lost or gained over ontogeny (see Haug, C. *et al*., 2019 for a longer discussion; Haug, G.T. *et al*., 2021a). Some stage 1 larvae of Crocinae bear three large teeth and some smaller ones on the mandibles (Monserrat, 2008: fig. 9f), a comparable condition to that of the larvae of the upper groups, while later stage larvae of the same species have smooth mandibles without teeth (*e.g.*, *Josandreva sazi* Monserrat, 1983b). It would therefore not have been surprising if the additional, smaller teeth had been present in smaller specimens, but would have become reduced throughout ontogeny and would hence have been absent in the larger specimens. Yet, this is not the case.

It therefore seems that there are larvae with smaller

teeth in between the larger ones and these are represented by two different stages (instars). In addition, there are also larvae without smaller teeth in between the larger ones, and also this morphotype is represented by two stages.

Other possible sources of variation

Ontogeny can apparently only explain the size variation within the sample, but the noticeable variation concerning the teeth in the mandibles can not be explained this way. A closer comparison of the upper and lower groups in the shape *vs*. length plot (Fig. 12B) also reveals that the heads in the lower groups are additionally slightly slenderer.

Finally, another subtle difference can be recognised in the relative length of the stylets in comparison to the head capsule. Firstly, it appears to decrease over ontogeny in both, the morphotype without the additional teeth and the one with additional teeth. For both morphotypes the smaller specimens have relatively longer stylets (Fig. 12C, D). While this is similar in both morphotypes, it is more apparent in the morphotype without teeth: smaller specimens have longer stylets than the smaller specimens of the morphotype with additional teeth, while in the larger specimens this is reversed. This would mean that the relative loss of stylet length is stronger expressed in the morphotype without additional teeth.

These subtle differences all support that there are, at least, two distinguishable morphotypes among the specimens discussed here. Still, it leaves the question, what are these two morphotypes? Are these separate species? This interpretation is quite possible, but it seems premature to erect a new species as these differences could be explained by other factors as well.

While not common, in larvae a simple dimorphism could always be indicative of two different sexes of a single species. Also, different ecotypes of a single species could explain the observed variation. Such ecotypes could be caused by various factors, most simply, the one type could be first generation larvae ("spring larvae") and the other type second generation larvae ("summer larvae").

Also given the low sample size of the specimens, the seeming distinct separation into two morphotypes might be an artefact or sampling bias masking a much more gradual type of variation. While indeed the observed differences speak for a two morphotype separation within these types, there is still variation within these types. For the smaller-sized specimens of the morphotype with additional teeth, there is specimen PED 0453 which differs from the others in the quite massive size of teeth and also in overall head shape. Unfortunately, the specimen appears to be an exuvia, which is additionally slightly twisted, concealing further structures for comparison.

In conclusion, it remains unclear whether all specimens discussed here are conspecific with *Macleodiella electrina*. There are at least two different types, each apparently represented by two stages, still we can not corroborate whether these represent distinct species. If yes, these would most probably be very closely related to each other (see comparable case in Badano *et al*., 2021). We therefore suggest to either refer to the entirety of these larvae either as *Macleodiella*-type larvae or to use a similar nickname as for other larvae (see *e.g*., Haug, J.T. *et al*., 2019a; see also discussion in Haug, C. *et al*., 2016), namely "longhead larvae".

What makes longhead larvae special?

Longhead larvae are quite unique in several aspects. First, they plot outside the area occupied by other lacewing larvae, although only slightly. That means already from a quantitative point of view longhead larvae expand the morphological diversity of lacewing larvae in general, and especially of larvae in the Cretaceous.

Concerning qualitative characters, longhead larvae differ from many modern larval forms of Myrmeleontiformia already by the quite slender body shape, yet this has already been pointed out also for some other myrmeleontiformian larvae from the Cretaceous (Haug, C. *et al*., 2019; Haug, J.T. *et al*., 2019b; Haug, G.T. *et al*., 2021a). However, the combination of the presence of prominent teeth on the stylets and the presence of empodia on the trunk appendages is so far unique. In modern myrmeleontiformian larvae, teeth are present in larvae of antlions (Myrmeleontidae), owlflies (or better owl lacewings; Ascalaphidae), split-footed lacewings (Nymphidae) and some larvae of spoon-winged and thread-winged lacewings (Nemopteridae), but all these lack empodia. Long-nosed antlions (larvae of silky lacewings; Psychopsidae) have prominent empodia but lack teeth in their mandibles (recent review in Haug, G.T. *et al*., 2020).

Among unusual fossil myrmeleontiformians (which can not be immediately identified as representatives of the five major modern lineages), chimera-type and decadent-type larvae (possible representatives of Crocinae) have teeth and lack empodia (Haug, G.T. *et al*., 2021a). Also, the forms represented by single specimens each, such as *Cladofer huangi*, *Electrocaptivus xui* (Badano *et al*., 2018) or the superfang larva (Haug, J.T. *et al*., 2019b), have prominent teeth and seem to lack empodia. Since the trunk appendages are not always fully accessible, it is at least possible that these might have born empodia, but this remains unclear.

The unusual combination of empodia and teeth is likely a plesiomorphic condition retained from the ground pattern of Myrmeleontiformia (Badano *et al*., 2018). It appears that teeth have been secondarily lost within some lineages (*e.g*., Psychopsidae). Reduction over ontogeny, as observed in some long-necked antlions (larvae of thread-winged lacewings, Crocinae), offers a simple mechanism

explaining how this could have occurred. The loss of the empodium might represent an autapomorphy of an ingroup of Myrmeleontiformia (*e.g.*, Beutel *et al*., 2010; Jandausch *et al*., 2018, 2019). Hence longhead larvae are special in this aspect by retaining a plesiomorphic (≈ ancestral) condition.

Longhead larvae are, of course, additionally special in possessing a long head, as the name suggests. This condition can be clearly identified as an apomorphic condition for these larvae. Hence longhead larvae are special in retaining a quite ancestral state on the one hand in combination with a very special new condition on the other hand.

Possible function of the elongated head

The long head of longhead larvae begs for the question: what is it good for? In one aspect, it is reminiscent of the long-necked antlions: The mouth parts are further anterior, further separated from the trunk appendages. In long-necked antlions (larvae of the group Crocinae) this is achieved most prominently by the elongate sclerotised cervix, which in some forms can only be described as astonishingly long (see recent summary in Herrera-Flórez *et al*., 2020a). However, it is in fact not only the cervix that contributes to the length in some larvae, but also the prothorax (see discussion for the problem of neck versus prothorax in Haug, J.T. *et al*., 2020a). For example, in larvae of *Necrophylus*, the insertions of appendages of the prothorax are far posterior on the segment. The anterior part of the segment is narrowed down to form a slender cone-like region. With this arrangement the cone-like region adds to the functional neck by further increasing the distance between the mouth parts and the trunk appendages (Herrera-Flórez *et al*., 2020a). In addition, we can recognise based on the shape analysis (Fig. 11) that the head capsules of at least some of the very long-necked forms are also slenderer and more elongated, hence contributing further to adding distance.

The exact advantages of the large distance are not fully clear. It is also not found in all long-necked antlions to the extreme (*cf*. recent review in Haug, G.T. *et al*., 2021a). Yet it appears that the elongation protects the trunk of the larvae and its appendages when catching prey, prohibiting that a still struggling prey item injures them (see discussion in Haug, G.T. *et al*., 2021a). In addition to this protective aspect, the elongated head may provide an advantage in reaching hidden prey and maybe even allow, in combination with the elongated body, a more subterranean mode of hunting. Thus, the larvae could possibly occupy an ecological niche different to most other myrmeleontiformian larvae (see also discussion in Haug, J.T. *et al*., 2019b).

The elongated head in longhead larvae may therefore have had a similar function. Unfortunately, we do not have field observations of the earlier stage long-necked antlions that still possess three prominent teeth, as this condition is even more comparable to that of longhead larvae.

Although the head elongation lets longhead larvae stand out, there is at least a tendency in this direction also in other Cretaceous larvae. Also, the heads of some decadent-type and chimera-type larvae, which both have long necks, are elongated (Haug, C. *et al*., 2019; Haug, G.T. *et al*., 2021a), as is the head of the superfang larva (Haug, J.T. *et al*., 2019b). Nevertheless, in all cases the elongation is clearly less strongly expressed than in longhead larvae.

Overall, it appears that the elongation of the head in longhead larvae is a functional convergence to long-necked antlions for optimising the prey-catching process, but stronger affecting a different body region. This again emphasises that in the Cretaceous the lineage of Neuroptera has seen quite some "experimental forms" (*e.g.*, Wang *et al*., 2016; Badano *et al*., 2018; Liu *et al*., 2018; Pérez-de la Fuente *et al*., 2018; Haug, C. *et al*., 2019; Haug, J.T. *et al*., 2020b). It also again emphasises that this has led to cases of convergent evolution (Badano *et al*., 2018, pp. 11, 12) using the same features in different combinations in different lineages.

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Supplementary materials:

All Supplementary materials are available at:
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Suppl. Tab 1. Information on sources of all the specimens used in the shape analysis. Explanation of specimen numbers: 00xx = Psychopsidae; 02xx = Nymphidae; 04xx = Crocinae; 06xx = Nemopterinae; 08xx = Weirdos; 1xxx = Myrmeleontidae; 2xxx = Ascalaphidae. Explanation of time code: 1 = Cretaceous; 2 = Eocene; 3 = Miocene; 4 = extant.

Suppl. Tab 2. Measurements and PC1 and 2 of specimens from this study plus additional specimen from the literature. Abbreviations (sorted by first occurrence in the table): l(hc) = maximum length of head capsule, w(hc) = maximum width of head capsule, l(sy) = maximum length of stylets, PC = principal component.

Suppl. Tab 3. Values of PC1–PC5 of all specimens used in the shape analysis. Explanation of specimen numbers: 00xx = Psychopsidae; 02xx = Nymphidae; 04xx = Crocinae; 06xx = Nemopterinae; 08xx = Weirdos; 1xxx = Myrmeleontidae; 2xxx = Ascalaphidae.

Suppl. Text 1. General outcome of the shape analysis.

Suppl. Fig 1. Factor loadings of the shape analysis.