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Another strange holometabolan larva from Kachin amber—the enigma of the beak larva (Neuropteriformia)

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Abstract

Holometabolan larvae are dominating components of modern terrestrial and freshwater ecosystems and have a significant ecological impact. Also in past ecosystems, various types of such larvae have been present, which is especially well known from ambers from all over the world. During the Cretaceous, holometabolan larvae with a very modern appearance co-occur with those of morphologies totally unknown in the ecosystems of today. One of these morphologies only known from ca. 100-million-year-old Kachin amber from Myanmar is represented by the so-called “beak larvae”, which possess an anteriorly projecting beak-like mouth cone, previously being described from two specimens. We describe here a third specimen as a new species, *?Partisaniferus edjarzembowskii* **sp. nov.** This new species differs from the previously described beak larva species *Partisaniferus atrickmuelleri* in the shape of the trunk end as well as in lacking a differentiation of the tergites into distinct sclerites and in the absence of abdomen protrusions. We discuss possible aspects of the ontogeny of the beak larvae, including the possibility that the here described specimen and one of the previously known ones are different larval stages of *?P. edjarzembowskii* **sp. nov.** Furthermore, we discuss possible relationships of beak larvae within Neuropteriformia.

Keywords: Myanmar amber, Burmese amber, Cretaceous, Holometabola, Neuropteriformia

Introduction

Insecta is the group of animals dominating most terrestrial and freshwater habitats. Looking at a less coarse level of resolution reveals that in fact most of this dominance comes from an ingroup of Insecta, namely Holometabola. Many holometabolans, such as beetles, bees, and butterflies spend a major share (if not the largest one) of

their life not in their adult winged forms, but as larvae, *i.e.*, as caterpillars, grubs, maggots and alike.

This domination, especially of the larvae, is not only present in modern-day ecosystems, but has likely been the case also quite some time in the past. The late Mesozoic, especially the Cretaceous, is generally recognised as a time in which many lineages of Holometabola diversified, some of them in co-evolution with flowering plants (Labandeira *et al.*, 2016; Liu *et al.*, 2018a; Khramov *et al.*, 2020). We can also expect that many specialised larval morphologies evolved in this time.

Different types of ambers from Canada, USA, Spain, France, Lebanon, and Myanmar have provided a unique window into the Cretaceous, facilitating a view on early specialisations of the larvae of various lineages within Holometabola such as Neuroptera (Pérez-de la Fuente *et al.*, 2012, 2016, 2018, 2019, 2020; Wang, 2016; Liu *et al.*, 2016, 2018b, 2022; Wichard, 2017; Badano *et al.*, 2018, 2021; Haug *et al.*, 2018, 2019a–c, 2020a–c, 2021a–d, 2022a; Zippel *et al.*, 2021), Raphidioptera (Perrichot & Engel, 2007, Haug *et al.*, 2020d, early view), Megaloptera (Baranov *et al.*, 2022), Coleoptera (Grimaldi *et al.*, 2002, 2005; Grimaldi & Engel, 2005; Kirejtshuk & Azar, 2008; Beutel *et al.*, 2016; Batelka *et al.*, 2019, 2021; Gustafson *et al.*, 2020; Zhao *et al.*, 2020; Haug *et al.*, 2021e, f; Zippel *et al.*, 2022a, b; see also Batelka & Engel, 2022), Strepsiptera (Pohl *et al.*, 2018), Lepidoptera (MacKay, 1970; Xia *et al.*, 2015; Ailvarez-Parra *et al.*, 2021; Fischer, 2021; Haug & Haug, 2021; Gauweiler *et al.*, 2022), and Diptera (Baranov *et al.*, 2020; Liu *et al.*, 2020). While some of these larvae are astonishingly modern in appearance, others appear highly unusual (*e.g.*, Pérez-de la Fuente *et al.*, 2012; Liu *et al.*, 2016, 2018b; Haug *et al.*, 2019b, c, 2021c). Such unusual larvae can often be more difficult to interpret in a phylogenetic context (Haug *et al.*, 2019b), but if they are sufficiently well preserved, they might offer such an opportunity (Badano *et al.*, 2018, 2021).

In many cases, holometabolan larvae may appear simpler in morphology than their corresponding adults. However, larvae may also possess highly specialised structures (see discussion in Haug *et al.*, 2021c). Yet, certain types of mouthpart arrangement clearly appear rarer in holometabolan larvae. Elongated mouthparts forming a single unpaired functional sucking mouth cone have evolved in adults in different lineages of Holometabola (*e.g.*, within Sisyridae, Nemopteridae, Antliophora, Lepidoptera). In larvae, such an arrangement seems very uncommon.

Larvae of lacewings, Neuroptera, have paired sucking mouthparts, not forming a single beak-like structure, but instead two distinct stylets (Aspöck & Aspöck, 2007). Only in few, apparently species-poor lineages of Coleoptera, beak-like posteriorly directed mouth cones have evolved in larvae in order to pierce fungi and feed on them (Ślipiński, 1991; Ślipiński & Lawrence, 2010).

A highly unusual-appearing larva from *ca.* 100-million-year-old Kachin amber from Myanmar was the first larva with an anteriorly projecting beak-like mouth cone (Haug *et al.*, 2020e), formally described as *Partisaniferus atrickmuelleri*. The larva shows certain characters of beetle larvae like the specific arrangement of sclerites on the trunk segments, but also reminds of some aspects of megalopteran larvae such as movable protrusions on the trunk. Finally, the arrangement of the head appendages also has some similarities with that in neuropteran larvae, besides the fact that the mouthparts form an unpaired beak, which is not the case in neuropteran larvae. Besides some distant similarities with mecopteran larvae, *P. atrickmuelleri* hence is likely a larva of the group Neuropteriformia (including Coleoptera, Strepsiptera, Neuroptera, Megaloptera, and Raphidioptera), but of unclear more detailed affinities.

A second larva with an anteriorly projecting beak was recently reported from the same deposit (Haug *et al.*, 2022b). This second larva is less complete and differs in certain aspects from the first one, including details of the head appendages, the sclerites, and an apparent lack of abdomen protrusions. Yet, this specimen is significantly larger than the holotype of *P. atrickmuelleri*, and it cannot easily be excluded that the differences are caused by ontogenic changes.

The two beak larvae were compared with certain lineages of Neuroptera concerning head and mouthpart shape (Haug *et al.*, 2022b). As the authors pointed out, the two beak larvae showed a high similarity to certain larvae of Coniopterygidae, the group of dustywings, when using quantitative morphology of the head as a comparative frame. However, the two larvae differ also in many aspects from dustywing larvae, not least by the fact that in larvae of dustywings the paired stylets are in close proximity, but can still be recognised as separate entities, while in

the two beak larvae the mouth parts seem to clearly form a single, unpaired structure. Still the similarity to dustywing larvae might be an indicator for the life habits of the two beak larvae, *i.e.*, potentially preying on small-sized soft representatives of Euarthropoda.

Here we report a third larva from Kachin amber with mouthparts forming a beak-like structure. We provide a comparison to the already known larvae and discuss possible relationships between these, including aspects of ontogeny.

Material and methods

Material

In the centre of this study is a single specimen preserved in Kachin amber, Myanmar, and is about 99 million years old (Cruikshank & Ko, 2003; Shi *et al.*, 2012; Yu *et al.*, 2019). The specimen was legally purchased via the online platform ebay.com from the trader burmite-miner and was originally part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München, Germany under the number PED 0740. The specimen is now deposited in the Staatliches Naturhistorisches Museum Braunschweig, Germany, under repository number SNHM-6013.

Documentation methods

The specimen was documented under reflected light on a Keyence VHX-6000 digital microscope as well as a Keyence BZ-9000 inverse fluorescence microscope, but with transmitted light. All images were recorded as compound images, combining images of shifting focus (image stacks) with each image stack representing adjacent image details. Stacks were combined to sharp image details, adjacent image details to a single panorama. Images under reflected light were additionally recorded with HDR (for details of the documentation, see Haug *et al.*, 2020e and references therein). Processing of reflected light images was performed with the built-in software, transmitted light images were processed with CombineZP and Adobe Photoshop CS3. All images were optimised in Adobe Photoshop CS2. The specimen did not provide contrast in X-ray illumination.

Terminology

Each ingroup of Insecta has its own special terminology for certain structures. As the exact relationships of the larva discussed here remain unclear, it proves difficult to choose which of these terminologies should be applied. We therefore use a neutral type of terminology, including reference to the wider comparative frame of Euarthropoda in square brackets. This approach may be

unusual in an entomological frame, but is necessary for wider comparisons.

Systematic palaeontology

Holometabola Burmeister, 1835

Neuropteriformia Ax, 2000

?*Partisaniferus* Haug, Schädel, Baranov & Haug, 2020

Type species. *Partisaniferus atrickmuelleri* Haug, Schädel, Baranov & Haug, 2020

Amended diagnosis. Larval stage with anterior part of head (and mouthparts?) drawn out into anteriorly projecting unpaired beak-like structure, leading to triangular head shape in dorsal view. Antennae short with few elements. A single pair of palps (unclear if maxillary or labial), with few elements. Prothorax large, broader than head, further posterior trunk segments similar in width, only very posterior ones narrower.

?*Partisaniferus edjarzembowskii* sp. nov.

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Holotype. SNHM-6013 (formerly PED 0740)

Additional material. PED 0596

Etymology. The species is named in honour of Edmund Jarzembowski and his work on fossil insects. When written as ?*P. edjarzembowskii*, the name reads basically as “PED jarzembowskii” in honour of his contributions, especially also on immatures of fossil insects and their study, as a part of PED = Palaeo-Evo-Devo.

Diagnosis. Trunk segments with continuous tergites without subdivision in several sclerites. No apparent protrusions on abdomen segments. Trunk end broad, only slightly narrower than preceding trunk, posteriorly rounded.

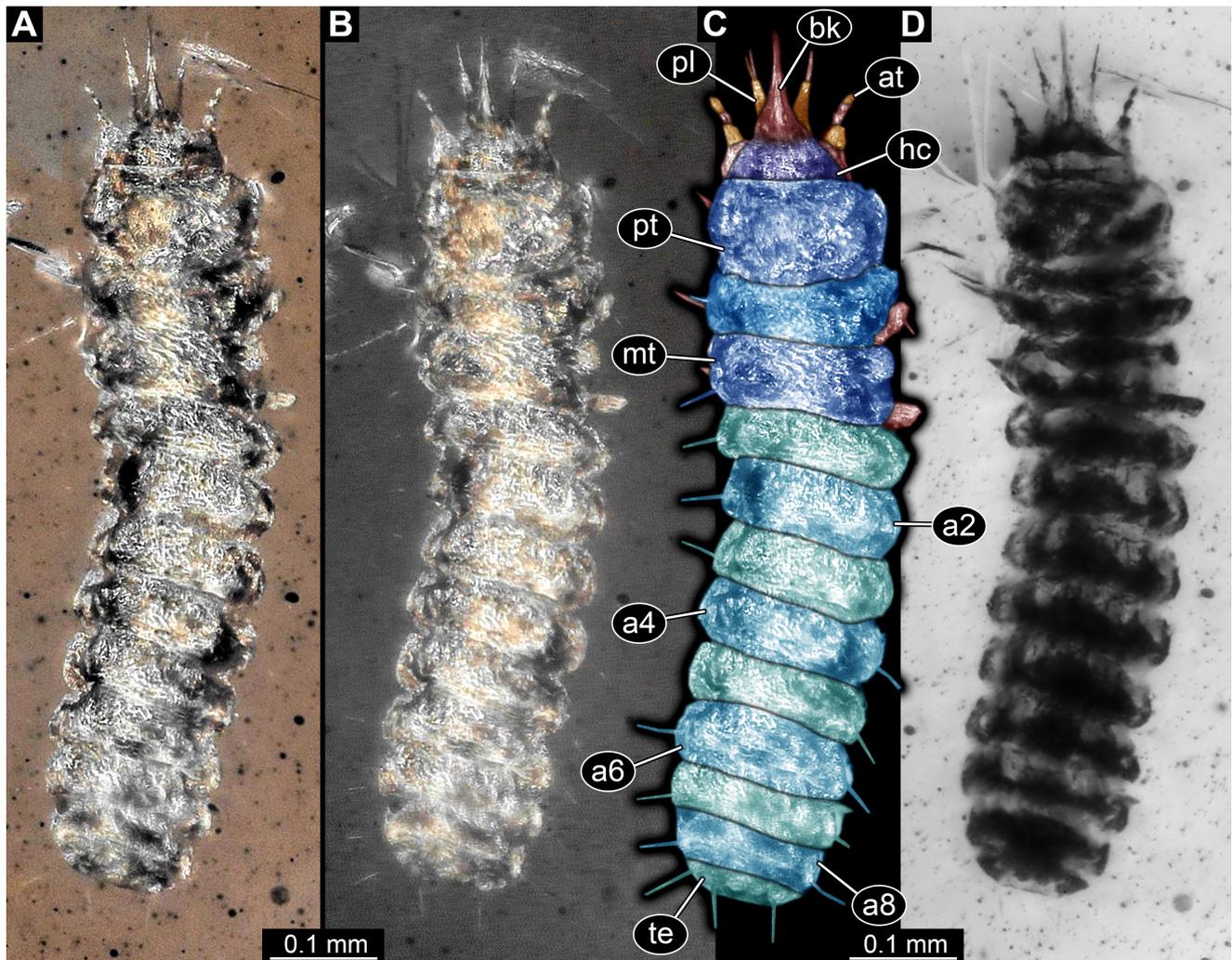


FIGURE 1. ?*Partisaniferus edjarzembowskii* sp. nov., beak larva, SNHM-6013, Kachin amber, Myanmar, in dorsal view under different light settings. **A**, Under unpolarised ring light with black background. **B**, Under cross-polarised light with black background. **C**, Colour-marked version of **B**. **D**, Under transmitted light. Abbreviations: a2–a8 = abdomen segments 2–8; at = antenna; bk = beak; hc = head capsule; mt = metathorax; pl = palp; pt = prothorax; te = trunk end.

Differential diagnosis. Differs from *Partisaniferus atrickmuelleri* in lacking any differentiation into distinct sclerites and abdomen protrusions, and in the shape of the trunk end, which is narrow trapezoid in dorsal view.

Locality and horizon. Kachin, Myanmar, earliest Cenomanian.

Description. *General.* Very small holometabolan larva (Figs 1A–D, 2A). Body organised into head and trunk. Head composed of six segments (inferred, see discussion). Anterior trunk (thorax) with three longer segments (pro-, meso-, metathorax), ventrally each carrying a pair of locomotory appendages (legs). Posterior trunk (abdomen) with nine units, anterior eight representing true segments, last unit, trunk end, likely a compound structure of several segments. All trunk units with prominent dorsal sclerites (tergites). Each trunk segment with convex lateral rims, with a pair of setae one on each side, trunk end with two pairs of setae.

Head. Triangular in dorsal view. Anteriorly drawn out into beak-like protrusion (Fig. 1C), most likely formed by some components of mouthparts, but unclear by which ones. No clear structures of ocular segment visible, no eye structures apparent, clypeo-labrum complex (possible appendage derivative) possibly contributing to beak; faint V-shaped line on beak, possibly as edge of clypeo-labrum.

Antennae [antennulae] inserting far lateral on head, with four visible elements (Fig. 1C, D). Proximal element proximally very wide, strongly tapering distally to about 50% of proximal width; length about as long as distal width. Element 2 of similar length, also tapering distally to about 50% of the proximal width. Element 3 tubular, slightly narrower than distal width of element two, slightly longer than wide. Element 4 slightly shorter, but about as wide as element 3, distally rounded.

A single pair of palps apparent (Fig. 1C, D), unclear if maxillary [maxillulary] or labial [maxillary] palps, with two elements. Proximal element conical, nearly twice as long as proximal width. Distal width only half of proximal width. Distal part narrow, elongate, spine-like.

Anterior trunk (thorax). Trunk segment 1 (prothorax) largest, slightly wider than posterior width of head, nearly twice as long as head capsule without beak (Fig. 1A, C). Ventrally with a pair of locomotory appendages (legs), no details discernible.

Trunk segment 2 (mesothorax) slightly shorter than prothorax, similar in width (Fig. 1A, C). Ventrally with a pair of locomotory appendages (legs), no details discernible.

Trunk segment 3 (metathorax) similar in size to mesothorax (Fig. 1A, C). Ventrally with a pair of locomotory appendages (legs), no details discernible.

Posterior trunk (abdomen). Trunk segment 4 (abdomen segment 1) slightly shorter than metathorax,

similar in width. Trunk segments 5–10 (abdomen segments 2–7) similar to trunk segment 4. Trunk segment 11 (abdomen segment 8) about as long, but slightly narrower than preceding segments. Trunk end anteriorly narrower than trunk segments and slightly shorter, posteriorly rounded (Fig. 1A–D).

Remarks.

Size differences and number of moults

Holometabolan larvae can grow drastically from moult to moult, especially when compared to other closer related moulting animals. While the number of moults can be very high in some holometabolans, in many cases only few larval stages (instars) have evolved. There appears to be a general selective pressure towards a lower number of moults (Haug, 2020a). In most neuropterans, the post-embryonic ontogeny includes only three larval stages (problem of terminology in this aspect discussed in Haug, 2020b), more rarely possibly five (Tillyard, 1922). In some lineages, the exact number of stages is still a matter of debate, but the size gain in these lineages indicates more than three (Haug *et al.*, 2020b). The size difference between specimen 2 and 3 would also require to assume more than two moults if they are stages of a single ontogenetic sequence (compare size difference between first and last stage of Nevrothidae, Fig. 2F, G, and Psychopsidae, Fig. 2H, I). If specimen 3 represents a stage 1 larva (“first instar”), then specimen 2 would at least represent a stage 4 larva when estimating a size gain of 100% per moult (see discussion in Haug *et al.*, 2020b); when assuming less size gain, even more moults would be necessary.

One could now argue that these differences make it unlikely that the two larvae are conspecific, but that argumentation would require to assume that they are indeed lacewings and that all lacewings always have three larval stages. Yet, it remains unclear whether the larvae are lacewings, and as pointed out, there might be exceptions to the three-stages-rule.

One might also argue that the possible higher number of larval stages indicates a position outside Neuroptera. Yet, also in this aspect there are too many uncertainties. As pointed out, most similarities of the beak larvae with lacewings can be seen with dustywings. Our knowledge on dustywing larvae is unfortunately incomplete; early instars have not been described in detail so far, and the number of moults in this group is in fact a matter of debate (see Haug *et al.*, 2022b and references therein).

Are beak larvae lacewings?

As laid out, the ontogeny does not provide a clear signal against or for an interpretation of the beak larvae as lacewings, but we can also consider other aspects. The trunk of specimen 1 was very unusual (Haug *et al.*,

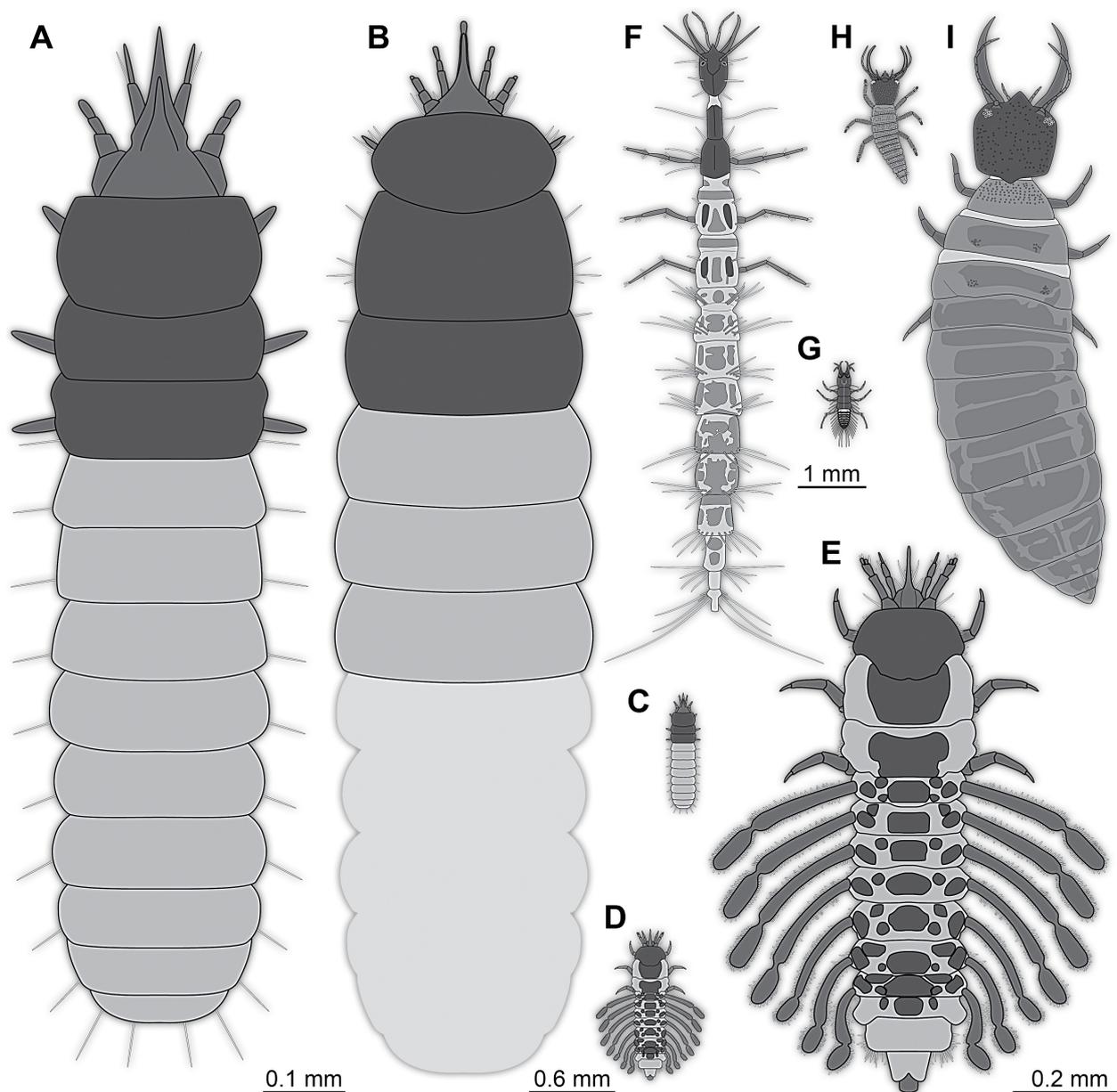


FIGURE 2. Comparison of drawings of the different beak larvae and other larvae to illustrate possible ontogenetic changes. **A**, *?Partisaniferus edjarzembowskii* **sp. nov.**, beak larva 3, SNHM-6013; scale bar on the lower right. **B–D**, All known beak larvae at the same scale; note that the larva in **B** has a much larger body size than those in **C** and **D**; scale bar between **B** and **D** applies to **B–D**. **B**, Possible second specimen of *?Partisaniferus edjarzembowskii* **sp. nov.**, beak larva 2, based on Haug *et al.* (2022b). **C**, *?Partisaniferus edjarzembowskii* **sp. nov.**, beak larva 3, based on this study. **D**, *Partisaniferus atrickmuelleri*, beak larva 1, based on Haug *et al.* (2020e). **E**, Enlarged version of **D**; scale bar on the lower right. **F** and **G**, Comparison of first and last larval stage of a representative of Nevrothidae at the same scale; scale bar under **G** applies to **F** and **G**. **F**, Last larval stage of *Nevrothus* sp. based on Gepp (1984). **G**, First larval stage based on Haug *et al.* (2019b). **H** and **I**, Comparison of first and last larval stage of a representative of Psychopsidae (*Psychopsis elegans*) at the same scale based on Tillyard (1918); size provided by magnification factor, hence no scale bar provided. **H**, Last larval stage. **I**, First larval stage.

2020e), that of specimen 2 was rather incompletely known (Haug *et al.*, 2022b). Specimen 3 offers some additional insights here. The trunk segments are very similar in size (the trunk is “parallel sided”). Many lacewing larvae have spindle-shaped trunks tapering posteriorly, at least in the very posterior region. Only in some the trunk end is more rounded, yet in such forms (*e.g.*, in aphid lions, ant lions)

the trunk appears inflated, widening in the middle region. While this character may not be very strong for excluding the possibility that specimen 3 is a lacewing larva, it makes it at least less likely. Given that we can assume a close relationship among the beak larvae, it seems more comprehensible to assume a position of those outside Neuroptera.

A more definite interpretation of the beak larvae will require more material, ideally a larva in conjunction with a pupa. Still, the new find allows us to increase the species number of these forms.

Discussion

The new specimen: a beak larva

Similar to the already known two specimens, the new larva possesses a beak-like, anteriorly projecting mouth cone (giving the head an overall triangular shape in dorsal view), as well as a pair of robust antennae with few elements, and a single pair of palps. As it is only one pair, it remains unclear whether these are maxillary or labial palps. The new specimen is, therefore, considered a third find of a beak larva.

It seems likely that this highly specialised morphology of a larva evolved only once and does not represent a case of convergence (although it cannot be entirely ruled out), further supported by the fact that we do not have any modern counterpart with such a morphology. We can therefore assume that the three larvae were at least closely related. Still, the question remains whether at least two of them, or even all three, were conspecific.

Ontogeny

As already pointed out for the first two beak larvae (Haug *et al.*, 2022b), the differences in morphology between them may well be caused by ontogenetic changes. In this aspect, the new larva provides a new piece to the puzzle. The holotype of *P. atrickmuelleri*, *i.e.*, specimen 1 is rather small, specimen 2 is rather large (*cf.* Fig. 2B *vs.* 2D). The new specimen 3 is also quite small, in fact even smaller than specimen 1 (*cf.* Fig. 2C *vs.* 2D). While there are only small differences in size, there are expressed differences in morphology between specimens 1 and 3. To highlight only the major ones (Fig. 2A, D): specimen 3 lacks the distinct sclerites and protrusions on the trunk segment present in specimen 1; specimen 3 has a simple rounded trunk end, while specimen 1 has a distinct narrowing trunk end; specimen 3 has a larger head in relation to the prothorax than specimen 1.

Given the rather small difference in size in combination with the differences in morphology, it is highly unlikely that specimens 1 and 3 are conspecific and only differing as they represent different instars. Hence it appears consequent to consider specimen 3 as the larva of a different species of Neuropteriformia, but closely related to *P. atrickmuelleri*.

Specimen 2 is much larger than specimens 1 and 3. Hence, in this case all differences to the other two may indeed be explained by changes during ontogeny. Yet,

given the fact that it shares more similarities with specimen 3 (*e.g.*, absence of distinct sclerites and protrusions on trunk segments), makes it easier to interpret it as a later stage of specimen 3 than specimen 1. An aspect more similar between specimen 1 and 2 is the ratio of head and prothorax size, yet this ratio is well known to change during larval growth (compare Fig. 2H and Fig. 2I) and hence even makes an interpretation of specimen 2 as an older stage of specimen 3 in fact more comprehensible. While it cannot be ruled out that specimen 2 represents yet another species, we vote here for a more conservative view suggesting conspecificity between specimen 2 and 3.

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