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The strange holometabolan beak larva from about 100 million years old Kachin amber was physogastric and possibly wood-associated

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Abstract

The group Neuropteriformia (beetles, lacewings, *etc.*) is today very species-rich, but also has a good fossil record in the Mesozoic. Amber provides not only adults, but also fossil larvae; some of these fossil neuropteriformian larvae have very unusual morphologies not seen in the modern fauna. We here report an unusual new fossil neuropteriformian larva. The mouthparts form a beak. Fossil larvae with similar mouthparts are known, and it seems that this new larva is a representative of the species ?*Partisaniferus edjarzembowskii*. The new larva, unlike the already known ones, has a large and inflated trunk. Based on comparison with extant larvae, such an inflated trunk should be considered physogastric. The new larva is only the second case of physogastry in fossil holometabolan larvae. Also early larvae of this species are known. The strong difference between the different larval stages give reason to interpret the ontogeny hypermetamorphic. Also this phenomenon is in fact very rare in the fossil record; most earlier candidates remain assumptions without further substantiation. Physogastry in larvae is often coupled to a mode of life in confined spaces, for a fossil preserved in amber this may mean living inside wood. Feeding mode might have been predatory, but could also have been feeding on fungi.

Keywords: Neuropteriformia, *Partisaniferus*, Myanmar amber, Burmese amber, convergent evolution

Introduction

Neuropteriformia is a very species-rich ingroup of Pterygota (the "flying insects"), including beetles, lacewings, snakeflies and some more. Neuropteriformia has been suggested to have been part of the large diversification process in the Mesozoic (Aspöck & Aspöck, 1999, 2007; Grimaldi & Engel, 2005). Beetles are still a dominating group in modern ecosystems, while many other ingroups of Neuropteriformia have declined over time. This observation is based on Mesozoic fossils of the latter group and show morphologies that are not known from the modern fauna (*e.g.*, Yang *et al.*, 2014; Labandeira *et al.*, 2016; Chang *et al.*, 2018; Lu *et al.*, 2021).

Such morphologies unknown today do not only occur in adult forms, but also in larval forms. As many neuropteriformians in fact spend more of their life time in the larval phase, their larger ecological impact (in the sense of interaction with other components of the ecosystem) lies in this life phase (*e.g.*, Yang, 2001). Therefore, the larvae of different groups that had other morphologies in the past likely performed ecological functions nowadays no longer performed by these groups.

Especially amber has preserved spectacularly preserved fossils of unusual neuropteriformian larvae from the Mesozoic. These finds include numerous lacewing larvae (Pérez-de la Fuente *et al.*, 2012, 2016; Liu *et al.*, 2016, 2018; Badano *et al.*, 2018, 2021a; Haug *et al.*, 2019a, b, 2020a, 2021a, 2022a; Luo *et al.*, 2022), but also snakefly larvae (Haug *et al.*, 2020b, 2022b).

There is one group of very unusual larvae that have been given the nickname "beak larvae" (Haug *et al.*, 2020c, 2022c; Haug & Haug, 2022a). As the name suggests, the mouthparts of these larvae form a distinct forward-projecting beak. The morphology of these fossils, three specimens so far, does not provide good clues for systematic interpretation. An ingroup position within Neuropteriformia seems very likely. Yet, the fossils show certain features that would hint towards

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a coleopteran (beetle) relationship, others towards a neuropteran (lacewing) relationship (Haug *et al*., 2020c). This uncertainty has not decreased by finding new specimens (Haug *et al*., 2022c; Haug & Haug, 2022a). Two distinct species could be differentiated; of one species two developmental stages are known, but these are not consecutive (Haug & Haug, 2022a).

The high degree of uncertainty concerning the relationships of the beak larvae makes an interpretation of their general biology very challenging. We here report a new specimen of the beak larva type (specimen number 4) that shows new and so far unexpected details. These provide some new hints about the biology of these larvae.

Material and methods

Material

A single specimen is in the centre of this study. The specimen comes from about 100 million years old Kachin amber, Myanmar (*e.g*., Cruickshank & Ko, 2003; Shi *et al*., 2012; Yu *et al*., 2019). The specimen was legally purchased on the website ebay.com from the trader burmite-miner. The specimen is now part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany under the repository number PED 2320.

For a functional comparison, an incomplete millipede of the group Siphonophorida (PED 2611) was documented. It originated from the same source, both concerning the amber deposit and the trader.

An extant larva of a wood-boring beetle was used for ecological comparison. It was directly collected from the rubber plantation area, Dawei Tanintharyi Region, Myanmar (14.04° N, 98.13° E). The larva was found in a dead rubber tree (*Hevea brasiliensis*).

Methods

The specimens in amber were documented on a Keyence VHX-6000. They were tested on different backgrounds (black; white) and with different illuminations (unpolarised ring illumination; cross-polarised coaxial illumination). The specimens were documented from both sides. Each recorded image is a composite image. Image stacking and fusion was used to overcome limitations in depth of field, panorama imaging and merging was used to overcome limitations of field of view, HDR was used to avoid over- or underexposed areas (see, *e.g*., Haug *et al*., 2020d and references therein).

Glycerol in combination with a cover slip was placed on the amber to counteract irregularities of the surface. Yet, from one side the specimen was so close to the oblique rim that it could not be fully documented from this side (but from the other one). The amber piece is also full of particles (dirt?) concealing many details. Also other methods (*e.g*., fluorescence) did not provide better results.

The specimen of the beak larva was restored as a schematic vector graphic in Adobe Illustrator CS2. Comparative drawings were either used from our earlier studies or were drawn based on images from the literature.

For the description, we use entomological terms alongside general euarthropodan terms, the latter put in squared brackets. In this way, comparability with representatives of Euarthropoda outside Insecta is provided as we have already done in earlier studies.

Result

Description of specimen PED 2320

Small larva, about 3.5 mm (Fig. 1A, B). Body organised in head and trunk; presumably 20 body segments, ocular segment plus 19 post-ocular segments. Head small, triangular in dorsal and ventral view, presumably six segments, ocular segment plus five post-ocular segments (not directly visible, but inferred from the general body organisation of Insecta). No indications of eye structures apparent. Appendages of post-ocular segment 1, antennae [antennulae], short, with at least three antennomeres (Fig. 1B, C). Proximal antennomere not fully apparent, broad appearing. Antennomere 2 more slender, proximally narrow, distally widening. Bearing a small square-shaped jointed process disto-laterally. Antennomere 3 arising medio-distally, slightly larger than process, distally with small setae. No clear indications for further posterior structures of the head (appendages of post-ocular segments 3–5; mandibles, maxillae [maxillulae], labium [maxillae]), possibly contributing to elongate forward-projecting beak, longer than head capsule (Fig. 1D). A further pair of forward projecting structures may represent palps; as it is only one pair, it is unclear if it is part of the maxillae or the labium (see also Haug & Haug, 2022a).

Thorax and abdomen, together forming the trunk, very large (Fig. 1A, B), broader and much longer than head. Thorax segment 1 (post-ocular segment 6) slightly longer than head capsule, significantly wider, 2×. Thorax segment 2 (post-ocular segment 7) slightly longer than preceding segment, about as wide. Thorax segment 3 (post-ocular segment 8) even longer than preceding segment, about as wide. Thorax segments 1–3 differentiated from further posterior segments by having a pair of ventral short and stout legs each (Fig. 1A, B), details not accessible. Further posterior segments (forming abdomen) not well differentiated, eight units more or less well apparent, seven segments and a trunk end (likely compound of several segments). Abdomen much longer than thorax, at least

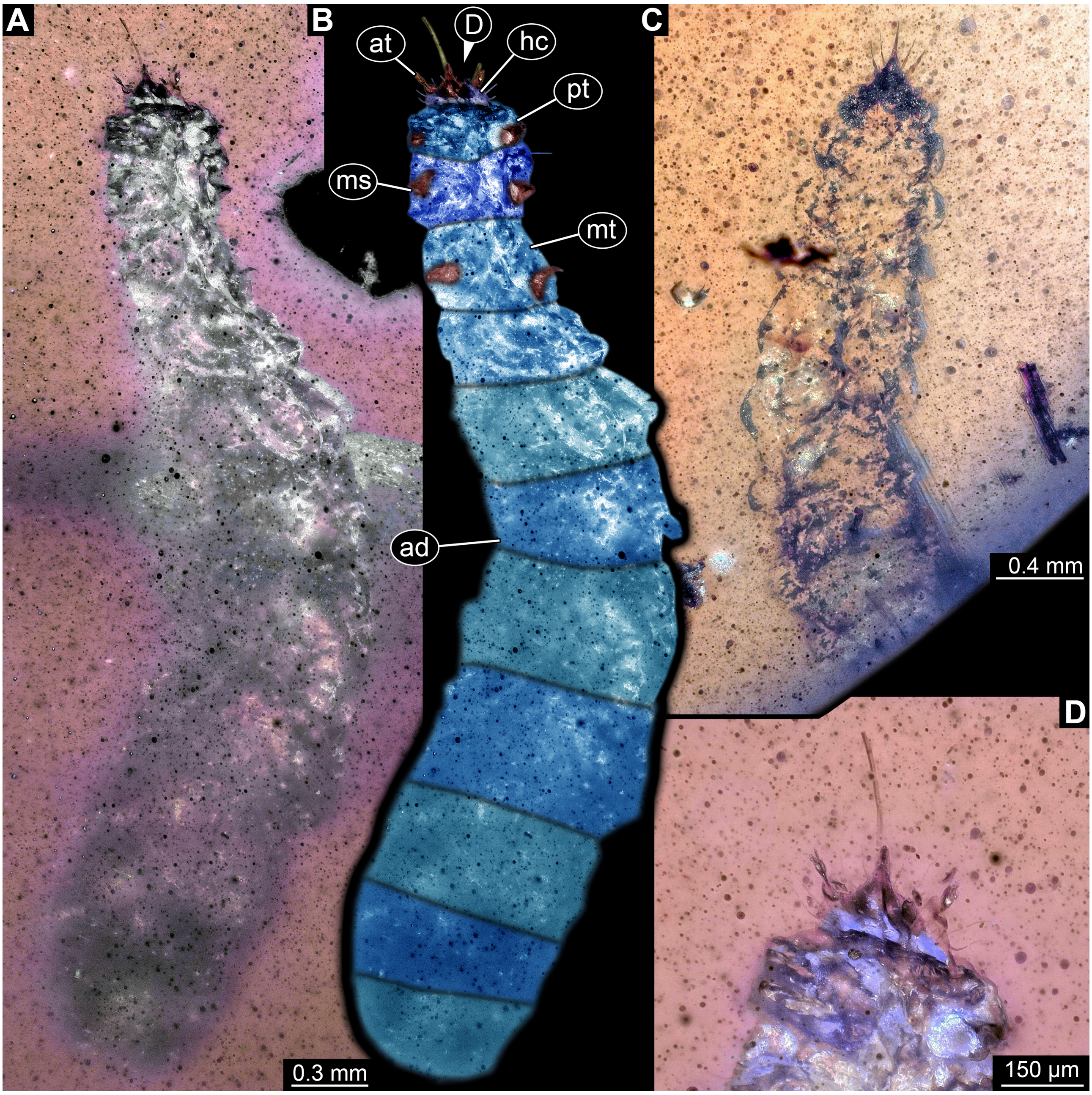

FIGURE 1. Beak larva, PED 2320, Cretaceous Kachin amber, Myanmar. **A**, Ventral view. **B**, Colour-coded version of A. **C**, Dorsal view. **D**, Close-up on anterior end in ventral view. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax.

3.5×. Also wider, at the widest point about 2×. Thorax and abdomen soft-appearing, no sclerites apparent.

Discussion

Species identity of specimen PED 2320

The head morphology of the new specimen with the long forward-projecting beak-like mouthparts and the short antennae immediately reveals that this is a beak larva, known so far from three other specimens (Haug *et al.*, 2020c, 2022c; Haug & Haug, 2022a). While these larvae can relatively easily be identified as larval stages of the group Holometabola, further reaching interpretations about their relationships remain challenging (Haug *et al.*, 2020c). It seems likely that the larvae are representatives of Neuropteriformia, yet other aspects give conflicting signal, on the one hand in the direction of Coleoptera, but on the other hand also in the direction of Neuroptera (Haug *et al.*, 2020c, 2022c; Haug & Haug, 2022a).

Two species of beak larvae have so far been recognised: *Partisaniferus atrickmuelleri* and ?*Partisaniferus edjarzembowskii*. *Partisaniferus atrickmuelleri* is characterised by distinct processes on the abdomen (Haug *et al.*, 2020c), which are absent in ?*P. edjarzembowskii* (Haug & Haug, 2022a) and the new specimen. This observation makes it more likely that the new specimen is a representative of ?*P. edjarzembowskii.* The new specimen differs from the already known specimens by size and the strongly inflated trunk.

Specimen SNHM-6013, the holotype of ?*P. edjarzembowskii*, is much smaller than the new specimen and has a rather normal, non-inflated trunk (Fig. 2C; Haug & Haug, 2022a: fig. 1). These differences may well be explained by ontogeny. In other neuropteriformian larvae with inflated and oversized trunks, these are restricted to the later developmental stages; hatchlings have a normal-sized trunk (Fig. 2; Gurney, 1947; Malicky, 1984; Redborg & MacLeod, 1985; Haug *et al*., 2019a, 2021b; Badano *et al*., 2021b; Haug & Haug, 2022b). Hence, the holotype of ?*P. edjarzembowskii* (SNHM-6013; Haug & Haug, 2022a) may represent a hatching stage, while the new specimen PED 2320 (Fig. 2B) represents a later stage, therefore being larger and having the inflated trunk.

Specimen PED 0596, which has also been interpreted as a representative of ?*P. edjarzembowskii* (Haug *et al*., 2022c), is larger than the other two specimens (Fig. 2A). It was reconstructed with a much less inflated trunk (Haug *et al*., 2022c), but the posterior abdomen is in fact not preserved. It seems therefore most likely that the original reconstruction of specimen PED 0596 was too conservative and that it also had a large inflated trunk. Hence, these differences can also be well explained as differences of an ontogenetic sequence.

We can therefore not identify differences for distinguishing the three specimens as separate species. It can still not be fully excluded that they in fact represent larvae of closely related species, yet formally they can be considered conspecific.

Unfortunately, the new specimen does not provide more details on one of the most crucial aspects of the larvae, the mouthparts. For better understanding the possible relationships of the larvae, these structures have the most potential, but will demand for finding further specimens. Still, the new specimen offers some insight into the ontogeny and morphological changes connected to it.

Reconstructing the ontogenetic sequence of ?P. edjarzembowskii

It remains unclear whether the three specimens of ?*Partisaniferus edjarzembowskii* can represent three successive stages (instars). If we compare the size gain between hatching stage and the first stage with an inflated trunk in some modern neuropteriformians with the difference between the smallest and the second smallest specimen of ?*P. edjarzembowskii*, we can recognise that the difference is larger than in the extant counterpart. Also the size difference from the second largest to the (third) largest specimen seems larger than in extant counterparts. It seems therefore unlikely that the three fossils represent successive stages; Haug & Haug (2022a) suggested that, based on the smallest and the largest specimen, it should include at least four stages. Based on the new specimen, demonstrating the enormous inflated trunk, it seems more likely that the original sequence included possibly five stages. As pointed out by Haug & Haug (2022a), this does not immediately exclude that ?*P. edjarzembowskii* is a representative of Neuroptera, most of which have only three larval stages, as there are some exceptions (see discussion in Haug *et al*., 2020e), and ?*P. edjarzembowskii* may also represent one. Hence, also this aspect does not resolve the conflict between interpreting the two species either as neuropterans or coleopterans.

Physogastry

A strongly inflated trunk, as in the new fossil, is often referred to as physogastric, the phenomenon as such as physogastry (see discussion in Haug & Haug, 2022b). In larvae, such inflated trunks are well known in lacewings (Fig. 2; Mantispidae, Berothidae, Dilardiae), but also in other neuropteriformians namely beetles and also in mecopteriformians such as flies (Wasmann, 1897; Prell, 1911; Arndt, 1993).

A soft trunk that is large is also known in larvae of other groups of Pterygota, but here usually the term physogastry has not been applied. This accounts for caterpillars (see discussion in Haug & Haug, 2022b; different larvae of the groups Lepidoptera, Mecoptera, Hymenoptera). It also accounts for grubs, larvae of certain other beetle ingroups (*e.g*. Scarabaeidae, Curculionidae, Cerambycidae; *e.g*., Vitner & Král, 2009: fig. 1, p. 52; Šípek & Král, 2012: fig. 1, p. 3; Švácha & Lawrence, 2014: fig. 2.4.20, p. 112; Muafor *et al*., 2015: fig. 2, p. 4; Viswam *et al*., 2018: fig. 2, p. 3) and other lacewing groups (Ithonidae: Tillyard, 1922; Grebennikov, 2004; some larvae of Chrysopidae: Tauber & Winterton, 2014: fig. 2, p. 97). In principle, many of these larvae could also be considered physogastric (see also Fig. 3A–C for a beetle larva with large and soft trunk collected from a modern-day tree in Myanmar).

As often with terminology, it is simply not consistently applied. The literature has many examples, *e.g*., campodeiform larvae being termed grubs (*e.g*., Beerendra *et al*., 2022: pl. 2, p. 2112). It seems unlikely that we will be able to get to a point of consistent terminology, and that may even not be important; more important are the characters behind the terms. Concerning the characters, it appears that the later larvae of ?*P. edjarzembowskii* have a soft-appearing, very large, inflated trunk and can be considered physogastric.

We still lack a second specimen for *P. atrickmuelleri*. Yet, also the small holotype, presumably representing a stage 1 larva, shows certain specialisations that are well compatible with the later stages being physogastric (Haug *et al*., 2020c): Tergites and sclerites of the

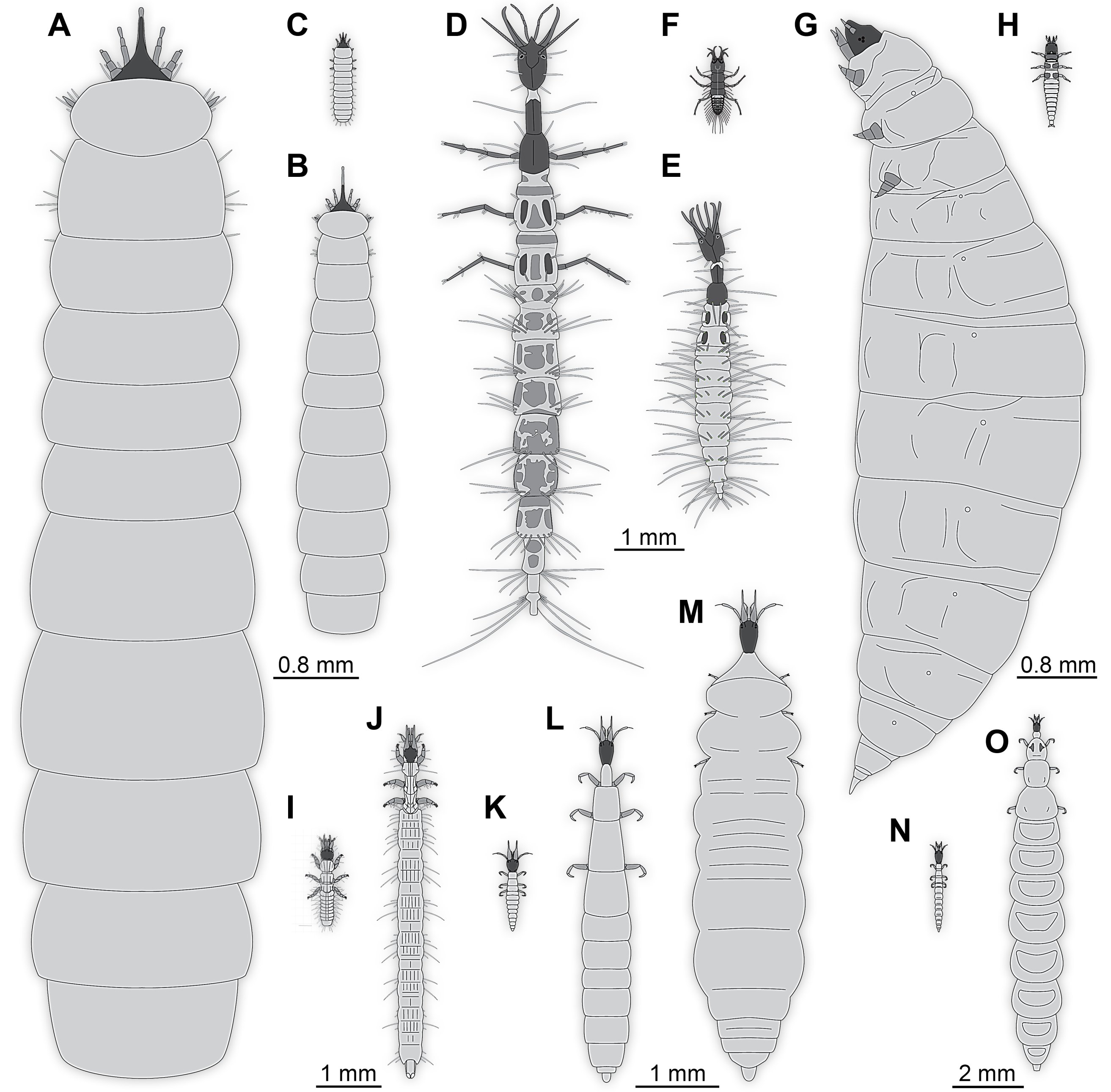

FIGURE 2. Larvae with inflated (late stages) and normal-sized trunks (early stages) for comparison with the new specimen. **A–C**, Beak larvae type 2, ?*Partisaniferus edjarzembowskii*. **A**, Possible representative of ?*P. edjarzembowskii*, PED 0596 (Haug & Haug, 2022a; Haug *et al*., 2022c). **B**, New specimen, possible representative of ?*P. edjarzembowskii*, PED 2320. **C**, Holotype, SNHM-6013 (Haug & Haug, 2022a). **D–F**, Nevrorthidae. **D**, *Nevrorthus* sp. (Gepp, 1984). **E**, *Nevrorthus fallax* (Malicky, 1984). **F**, *Rophalis relicta* (Haug *et al*., 2019a). **G**, **H**, Mantispidae, *Mantispa uhleri* (Redborg & MacLeod, 1985). **I**, **J**, Dilaridae, *Dilar duelli* (Badano *et al*., 2021b). **K–O**, Berothidae. **K**, CJW F 3198 (Haug *et al*., 2021b). **L**, CJW F 3197 (Haug *et al*., 2021b). **M**, PED 1794 (Haug & Haug, 2022b). **N**, *Lomamyia* sp. (Gurney, 1947). **O**, *Lomamyia* sp. (Gurney, 1947).

abdomen segments are not continuous, but "dissolved" into numerous smaller sclerites. Such an arrangement could indeed allow for an expansion of the trunk in later stages.

Physogastry and hypermetamorphosis

Hypermetamorphosis describes a specific post-embryonic developmental pattern within Holometabola, in which the larval phase is further differentiated into two subphases, which differ in morphology and ecology. It may be possible to find strict criteria when to apply this term in a quantitative frame (Haug, 2019; Haug *et al*., 2023), yet for the moment we can only consider the literature about when, where and how such terms are generally applied.

Within Coleoptera, hypermetamorphosis is generally accepted for the groups Meloidae, Ripiphoridae,

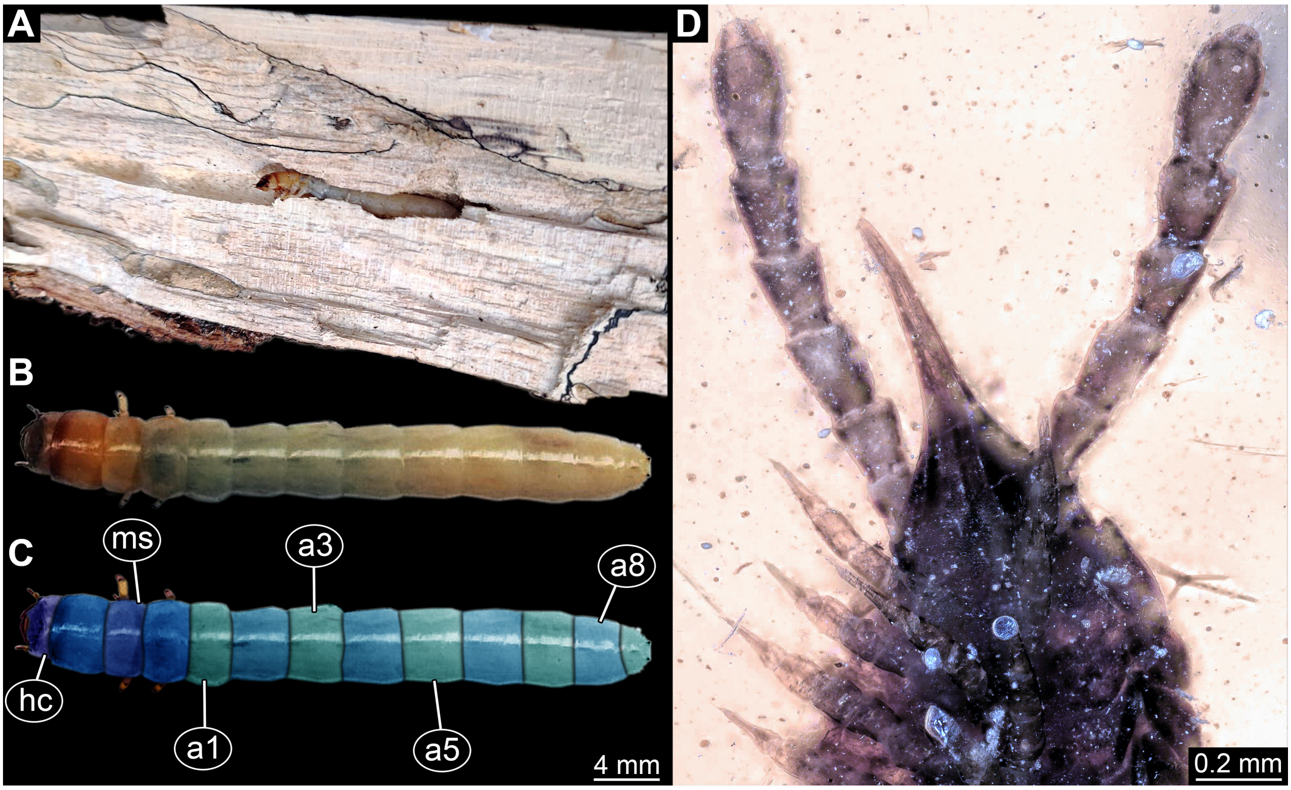

FIGURE 3. Specimens for comparison. **A–C**, Modern beetle larva from a tree in Myanmar. **A**, Piece of wood of a dead rubber tree (*Hevea brasiliensis*) with gallery and larva inside. **B**, Close-up of larva in dorsal view; note the large and soft trunk. **C**, Colour-marked version of **B**. **D**, Ventral view on anterior end of fossil siphonophoridan millipede (PED 2611) in Kachin amber; note the beak-like mouth parts. Abbreviations: a1–a8 = abdomen segments 1–8; hc = head capsule; ms = mesothorax.

Rhipiceridae and Eucnemidae (*e.g.*, Burakowski, 1989; Pinto *et al.*, 1996; Di Giulio *et al.*, 2003; Muona, 2010; Bologna & Di Giulio, 2011; Lawrence *et al.*, 2011; Lawrence, 2016; Németh & Otto, 2016; Otto, 2017; Scholtz *et al.*, 2018; Muona & Teräväinen, 2020). The first larval stages of these groups are highly mobile, often termed triungulin stages. For the first three groups, these larvae are campodeiform, first stage larvae of Eucnemidae are much more elongated and may best be considered elateriform. Later stages of Meloidae, Ripiphoridae and Rhipiceridae are grub-like and parasitic (Švácha, 1994; Lawrence *et al.*, 2011; Lawrence, 2016; Scholtz *et al.*, 2018; Bahmer & Lückmann, 2021). Later stages of Eucnemidae are legless vermiform or buprestiform (Muona, 2010; Németh & Otto, 2016; Otto, 2017; Muona & Teräväinen, 2020).

Individuals of other groups with soft-appearing larvae with prominent trunks, such as Scarabaeidae or Cerambycidae, appear grub-like already when hatching (*e.g.*, Huerta *et al.*, 2010; Švácha & Lawrence, 2014). Consistently, the term hypermetamorphosis has not been applied here.

The term hypermetamorphosis has been attributed to two groups of lacewings, Mantispidae and Berothidae (Aspöck & Aspöck, 2008; Beutel *et al.*, 2010). Also here, first stage larvae are highly mobile campodeiform (*e.g.*, Redborg & MacLeod, 1985; Minter, 1990; Möller *et al.*, 2006; Jandausch *et al.*, 2018). Later stage larvae are physogastric and live in protected spaces (see discussion in Haug & Haug, 2022b). Although a similar pattern of development seems to be present in Dilaridae (*e.g.*, Monserrat, 2005; Badano *et al.*, 2021a, b; Haug & Haug, 2022b), the term hypermetamorphosis is usually not applied here (*e.g.*, Badano *et al.*, 2021b).

Strepsipteran larvae include also a highly mobile first stage (triungulin; Brues, 1905) and less differentiated parasitic later stages (Kathirithamby, 1989, 2009; Chaudhuri & Mazumdar, 2000; Manfredini *et al.*, 2007). Also this pattern is generally considered hypermetamorphic (*e.g.*, Kathirithamby, 1989, 2009; Pohl, 2002).

In some parasitoid hymenopterans, first stage larvae are more differentiated than later ones (*e.g.*, the head is set off more pronouncedly; Gumovsky, 2006). These seem generally considered to develop in a hypermetamorphic pattern (*e.g.*, Heraty & Darling, 1984; Darling & Miller, 1991). Yet, early and late larvae appear much less differentiated than larvae of other groups. The condition in dipterans considered to be hypermetamorphic is comparable to that in hypermetamorphic hymenopterans (*e.g.*, Capelle, 1966).

As pointed out, many lepidopteran larvae may also be considered physogastric. The term hypermetamorphosis has been applied here to cases in which the ecology strongly changes (Fitzgerald & Simeone, 1971a, b; Fitzgerald, 1973; Guillén & Heraty, 2004; Davis & De Prins, 2011; Davis & Wagner, 2011; Jordan *et al*., 2016; Moreira *et al*., 2018; Vargas-Ortiz *et al*., 2019; Davis *et al*., 2020), as in the leaf-mining larvae of Gracillariidae (which do not really appear physogastric; Brito *et al*., 2013; Body *et al*., 2015).

Overall, the term hypermetamorphosis seems to be applied to quite different ontogenetic patterns. In some cases it is related to a stronger restructuring of certain aspects of the morphology. These can also be recognised quantitatively as in mantis lacewings, but in the closely related beaded lacewings this is not the case, although they are also considered hypermetamorphic. In many cases the term hypermetamorphic is coupled to a parasitic lifestyle of the later stages, yet that is not always the case. Therefore, there seems to be no real uniting character for the term. At least for neuropteriformians it appears that species generally regarded as hypermetamorphic have a mobile, campodeiform first larval stage and physogastric later larval stages. As this aspect seems also to be present in ?*P. edjarzembowskii*, we can interpret its developmental pattern as hypermetamorphic for this specific criterion.

Fossil record of grubs, physogastric larvae and hypermetamorphosis

Grubs in the strict sense, *i.e*. truly scarabaeiform larvae, have not been reported from Cretaceous ambers so far, but are known from Miocene amber (Grimaldi & Engel, 2005: fig. 10.31, p. 378). Larvae (as well as adults) of the group Cerambycidae are known from Eocene ambers, and some possible representatives have been identified in Cretaceous amber. Yet, these larvae appear less extreme than in the modern (and Eocene) larvae. The legs are proportionally still larger, and the body appears less inflated (see discussion in Haug *et al*., 2021c; Zippel *et al*., 2022a).

Strictly physogastric larvae in Cretaceous amber have so far only been reported for two specimens of beaded lacewing larvae (Berothidae; Haug & Haug, 2022b). The new specimen here is therefore only the second case of physogastry in holometabolan larvae preserved in Cretaceous amber.

Cases of hypermetamorphosis have so far been rarely suggested to be present in the fossil record. A stage 1 larva of a mantis lacewing from Eocene amber has been interpreted in this way (Ohl, 2011). Yet, without a clear indication for the morphology of the corresponding stage 2 or 3 larvae, this in fact remains unclear (Haug *et al*., 2018). Caterpillars from Cretaceous amber were also suggested to indicate the presence of hypermetamorphosis (Fischer, 2021). Yet, also here only one type of larval morphology (here the later one) is represented as fossils. Also the interpretation is strongly influenced by the assumed relationships of these larvae, which is partly challenging (Gauweiler *et al*., 2022).

There is a partially preserved ontogeny for a ripiphoridan beetle from Cretaceous amber (Batelka *et al*., 2021). Yet, only one part of that larval phase is available, making it possible that the species developed through hypermetamorphosis, but lacking a substantiation for this assumption. Also, a later stage larva of the beetle group Eucnemidae is known from the Cretaceous (Zippel *et al*., 2023). As here the early stages are unknown, it can again not be further concluded whether these beetles were already hypermetamorphic.

Overall, grub-like larvae or even physogastric ones and indications for hypermetamorphosis seem still rather rare in the fossil record and in the Myanmar amber forest 100 Ma ago. The larvae of ?*P. edjarzembowskii* seem to represent only the second clear case of this phenomenon, larvae of Berothidae being the first one (Haug & Haug, 2022b). The seeming rareness of all three aspects appears to be quite different in the modern fauna, where such larvae are quite common. It seems likely that such larvae and also the developmental pattern evolved convergently in several lineages and became more abundant either later in the Cretaceous or even after the Cretaceous.

Lifestyle of ?P. edjarzembowskii

The mouthparts of ?*P. edjarzembowskii* form a distinct unpaired beak, that of the new specimen appears even slightly longer than in the already known specimens. Such unpaired beaks are rare among holometabolan larvae (Haug *et al*., 2020c), a functional similarity to certain paired mouthparts in larvae of dustywings seems possible (Haug & Haug, 2022a). Such a larva has been recently reported from Kachin amber (Haug & Haug, 2023).

An aspect so far not discussed concerning the mouthparts of ?*P. edjarzembowskii* is the similarity to the mouthparts, in the overall morphology, to a number of different representatives of Euarthropoda. While beak-like mouthparts are well known in hemipterans, these are usually not forward-projecting and are often less tightly connected to the head, providing them a certain movability (especially in heteropterans) and may only serve for a rather distant comparison. The rather short length of the beak and the more continuous connection to the head resembles the beak-like mouthparts of palaeodictyopteroideans (immatures and adults; Prokop *et al*., 2019). Unfortunately, we do not know a lot of the feeding habits of these Paleozoic, long extinct animals.

Yet, certain siphonophoridan millipedes also possess forward-projecting beak-like mouthparts (Read & Enghoff, 2009: fig. 3, p. 549; Jiang *et al*., 2019: fig. 5B; Moritz *et al*., 2022: fig. 1F, p. 2, fig. 2C, p. 3), a condition also known from representatives in Kachin amber (Fig. 3D; Jiang *et al*., 2019: fig. 2B). These millipedes have been demonstrated to have a sucking mechanism very similar to different representatives of Insecta, hence a similarity is not surprising. Yet, unfortunately the exact food source for siphonophoridan millipedes is not known with certainty. It has been suggested that they may feed on fungi or rotten wood (see discussion in Moritz *et al*., 2022). Such a function for the beak of the beak larvae was already discussed based on the comparison with some extant beetle larvae with beak-forming mouthparts (see discussion in Haug *et al*., 2020c), yet in these the beak is not projecting forwards, differing in this aspect from the beak larvae. The mouthparts of siphonophoridan millipedes demonstrate that also forward-projecting beaks may be used in this way.

The newly reconstructed ontogenetic pattern of the beak larvae is also informative for reconstructing aspects of their life habits. The physogastric trunk in the later larval stages of modern larvae seems often to be coupled to confined spaces. Physogastric larvae of mantis lacewings (Mantispidae) live inside egg cocoons of spiders (Redborg & MacLeod, 1985; Redborg, 1998) or in nests of eusocial insects (Maia-Silva *et al*., 2013; Ardila-Camacho *et al*., 2021; Snyman & Binoy, 2022). The latter is also true for physogastric larvae of beaded lacewings (Berothidae), which live in termite nests (Wedmann *et al*., 2013; Komatsu, 2014), as do physogastric larvae of different beetles and flies (Mergelsberg, 1934; Komárek, 2003). Physogastric larvae of Dilaridae live in soil or rotting wood (Badano *et al*., 2021b). Also other grubs for which the term physogastry is usually not applied, such as larvae of moth lacewings (Ithonidae) or dung beetles (Scarabaeidae), live in confined surroundings, mostly soil (Grebennikov, 2004; Scholtz & Grebennikov, 2011). Even the slender late stage larvae of Nevrorthidae, which show no widening of the trunk, but still a remarkable elongation of the trunk (Fig. 2D), live in more confined spaces, between pebbles in fast running waters (Haug *et al*., 2020e).

It therefore seems very possible to also assume a lifestyle in confined spaces for ?*P. edjarzembowskii*. Given that the larvae were preserved in amber, living inside wood (as the confined space) seems a likely interpretation, possibly in galleries of wood-boring larvae in hard or soft wood, hunting these larvae. Indeed, hard- and soft-wood-boring immatures of different lineages are well known in Myanmar amber (beetles: Haug *et al*., 2021c; Zippel *et al*., 2022b, 2023; flies: Baranov *et al*., 2020; termites: Engel *et al*., 2016; Zhao *et al*., 2021). Alternatively, the lifestyle of ?*P. edjarzembowskii* may include living in rotting wood, feeding on fluids from the wood or fungi within the wood.

Forward-projecting piercing mouthparts in combination with a physogastric trunk occur in larvae of Mantispidae, Berothidae and Dilaridae (Haug *et al*., 2021b; Haug & Haug, 2022b and references therein). These larvae hunt for prey in confined spaces (besides mantis lacewing larvae within egg cocoons, as eggs do not run away). Assuming a comparable lifestyle for ?*P. edjarzembowskii* seems therefore a possible interpretation. Likewise, the mouthparts seem well suited to feed on fungi as suggested for siphonophoridan millipedes. We can so far not exclude either of the two feeding modes, it remains unclear whether the beak larvae were predatory, fungivorous or even feeding on other liquids.

Conclusion

A new specimen of the enigmatic beak larva type, more precisely of the species ?*P. edjarzembowskii* indicates the following new details of its ecology:

—the first larval stage is functionally comparable to a triungulin (being campodeiform);

—the later larval stages (at least from stage 3 on) have a physogastric trunk;

—the post-embryonic ontogeny is hypermetamorphic (in transitioning from campodeiform to physogastric);

—a wood-associated lifestyle seems likely;

—a predatory or a fungus-feeding lifestyle seem equally likely.

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