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Oldest record of a dustywing-type larva in about 100-million-year-old amber

JOACHIM T. HAUG & CAROLIN HAUG

Abstract

Larvae of Neuroptera (lacewings) significantly differ in morphology and ecology from the corresponding adults. Especially the often-pronounced mouthparts shaped as stylets for catching prey are prominent in lacewing larvae. These stylets make them quite easily identifiable also as fossils, and indeed a large number of fossil lacewing larvae has been described in recent years. Larvae of Coniopterygidae (ingroup of Neuroptera, dustywings) with their rather straight stylets have to date been reported since the Eocene; one report from the Cretaceous having been reinterpreted as a larva of Berothidae (beaded lacewings). We report here a lacewing larva from about 100-million-year-old Cretaceous Kachin amber from Myanmar with strong similarities to modern larvae of Coniopterygidae. The new larva possesses characters known from different extant ingroups of dustywing larvae, but in a combination not known from any modern dustywing larva. Such unusual character combinations occur in different fossils, among them in prominent examples such as *Archaeopteryx*, often due to a mixture of apo- and plesiomorphic characters from different groups, and partly complicated by the occurrence of convergences. Despite the unusual character combination in the new larva, it can be clearly identified as a dustywing-type larva, with this extending the record of these larvae into the Cretaceous.

Key words: Coniopterygidae; beak larvae; intermediate morphologies; convergence; Cretaceous; Burmese amber.

1. Introduction

The group Neuropterida is one of the species-poorer lineages of Holometabola. The latter includes the mega-diverse lineages of Hymenoptera (wasps), Coleoptera (beetles), Diptera (flies), and Lepidoptera (moths). The group Neuropterida includes Raphidioptera (snakeflies), Megaloptera (fishflies, dobsonflies, alderflies) and Neuroptera (lacewings), the latter two being sister groups (ASPÖCK & ASPÖCK 1999, 2007).

The group Neuropterida has generally been interpreted as being less diverse in the modern fauna than it was in the Mesozoic (ASPÖCK & ASPÖCK 1999, 2007). Neuropteridans seem to have diversified during the early diversification of Holometabola, performing ecological roles that in the modern fauna are namely performed by representatives of the mega-diverse lineages (e.g., LABANDEIRA et al. 2016). As for most holometabolans, the larvae have quite different ecological roles in comparison to their adults, and therefore also the morphology of the larvae differs strongly from that of the adults (e.g., MACLEOD 1964). Most larvae of Neuropterida are active predators. Mesozoic deposits (especially ambers) have provided a wealth of fossils of larvae of neuropteridans, including Raphidioptera (HAUG et al. 2020a, 2022a), Megaloptera (BARANOV et al. 2022a), and numerous finds of Neuroptera.

Among the fossil lacewing larvae, there are many highly aberrant forms (PÉREZ-DE LA FUENTE et al. 2012, 2016; LIU et al. 2016, 2018; ZHANG 2017; BADANO et al.

2018, 2021; HAUG et al. 2019a–c, 2020b, 2021a; ZIPPEL et al. 2021; LUO et al. 2022), but also larvae with a rather modern type of appearance (WANG et al. 2016; BADANO et al. 2018; HERRERA-FLÓREZ et al. 2020; HAUG et al. 2020c, d, 2022b; HÖRNIG et al. 2020; PÉREZ-DE LA FUENTE et al. 2020), including modern-like behaviour (HAUG et al. 2018; PÉREZ-DE LA FUENTE et al. 2018, 2019a; HÖRNIG et al. 2022). Overall, most modern types of larvae can be recognised in the Cretaceous (BADANO et al. 2018; PÉREZ-DE LA FUENTE et al. 2020; HAUG et al. 2021b, 2022c), although in some cases the resemblance of Cretaceous and modern representatives is less strongly expressed than in others (HAUG et al. 2021c, d). Yet, there are some notable exceptions of lineages with distinct larval types well known in the modern fauna, but larvae with such morphologies so far being absent in the Cretaceous (HAUG et al. 2022d), namely larvae of Ithonidae, Sisyridae and Coniopterygidae. Especially the latter case is worth noting, as Coniopterygidae (dustywings) has been resolved as the sister group to all other lacewings in numerous recent phylogenetic reconstructions (ENGEL et al. 2018; WINTERTON et al. 2018; VASILIKOPOULOS et al. 2020), indicating that the lineage is a relatively old one, and adults of dustywings are known in Cretaceous ambers (ENGEL 2004, 2016; PERRICHOT et al. 2014; SZIRÁKI 2016, 2017; LIU & LU 2017; MAKARKIN & PERKOVSKY 2017, 2019; LI et al. 2019a, b; PÉREZ-DE LA FUENTE et al. 2019b; RUŽIČKOVÁ et al. 2019; LU & LIU 2021). It is still possible that a specific larval morphology evolves later in a lineage (HAUG et al. 2015a, b), and one can specu-

late that this is also the case for Coniopterygidae, of which fossil larvae with modern appearance are known from the Eocene (HAUG et al. 2022d and references therein). ENGEL (2016) had suggested that a small lacewing larva with straight mouthparts, as they are also known in dustywing larvae, preserved in a piece of Myanmar amber right next to an adult dustywing could represent a non-modern-like larva of Coniopterygidae. The specimen was later re-interpreted as a possible larva of Berothidae (beaded lacewings; PÉREZ-DE LA FUENTE et al. 2020). Some aberrant larvae from Myanmar amber have been recognised as resembling dustywing larvae in certain morphological aspects (HAUG et al. 2020e, 2022d; HAUG & HAUG 2022), but more likely represent unusual beetle larvae (HAUG & HAUG 2022).

Modern larvae of Coniopterygidae are usually quite small compared to those of other lacewings (their adults are also small), and only the later instars are known (HAUG et al. 2022d and references therein). The body is overall spindle-shaped with a rather small and short head, a broad anterior trunk region (thorax), and an often strongly tapering posterior trunk (abdomen). Mouthparts mostly include a pair of straight venom-injecting stylets, each stylet formed by a mandible and the corresponding maxilla, and the labium, of which mostly the distal palps are apparent (MACLEOD 1964; ZIMMERMANN et al. 2009, 2019). The morphology of the head furthermore allows to roughly categorise two different types of modern larvae (MACLEOD 1964; ZIMMERMANN et al. 2009): 1) Larvae of the Conwentzia-type have a very triangular-appearing head (in dorsal view), the labrum is projecting forward. The head is small and often partly retracted into the thorax. The stylets are very short, often barely projecting forward from under the labrum. 2) In larvae of the Aleuropteryx-type, the stylets are much more prominent and project significantly beyond the labrum. The stylets are at least as long as the head capsule or even longer.

We here report a new fossil lacewing larva preserved in about 100-million-year-old Cretaceous Kachin amber from Myanmar. The larva shows strong similarities to modern dustywing larvae and is interpreted as the first record of a larva with affinities to Coniopterygidae in Cretaceous amber. We discuss implications of this find.

2. Material and methods

2.1. Material

The single specimen studied herein is preserved in about 100-million-year-old Kachin amber, Myanmar. It was legally purchased on the internet platform ebay.com from the trader “burmite-miner”. The specimen is now deposited in the collection of the Palaeo-Evo-Devo (PED) Research Group, Ludwig-Maximilians-Universität München (LMU Munich), Germany, under repository number PED 1970.

2.2. Documentation methods

The specimen was documented on a Keyence VHX 6000 digital microscope under low-angle ring light or cross-polarised light (HAUG et al. 2013a). Each image is a composite of several focus layers (stacking and fusing) to overcome limitation in depth of field and several adjacent image details (merged to a panorama) to overcome limitation in field of view. To avoid over- or underexposed areas, images were recorded as HDR (cf. HAUG et al. 2013b). Images were optimised (histogram, saturation, contrast) to enhance details in Adobe Photoshop CS2.

Important structures in images were colour-marked for interpretation purposes. Restoration drawings and comparative drawings were performed in Adobe Illustrator CS2.

2.3. Terminology

Comparative biology is often limited by language traditions. Each smaller group of animals has its own special type of terminology allowing specialists to communicate without ambiguities, but often prohibiting easy access to information by non-experts. Wider reaching comparisons often become challenging as similar structures have been addressed with different names in different lineages, or vice versa, the same term addresses different structures. We therefore try to use common terms, specialist terms (in brackets), and general euarthropodan terminology [in square brackets] to facilitate access for readers with different backgrounds.

3. Description of the specimen

3.1. General habitus

Small holometabolous larva, about 3.3 mm long (Figs. 1A, 2A). Body (presumably) organised into 20 segments. Ocular and following five post-ocular segments form a distinct head with sclerotised head capsule. Trunk subdivided into two functional parts. Anterior three trunk segments (post-ocular segments 6–8; thorax) similar to each other, all bearing prominent appendages (thorax appendages); posterior segments (post-ocular segments 9–19; abdomen [not corresponding to abdomen in other crustaceans]) without appendages.

3.2. Head region

Head capsule appears triangular, yet difficult to discern as only accessible in dorso-lateral (Fig. 1A), or ventro-lateral view (Fig. 2A). Head capsule short compared to body length. Anterior edge drawn out, most likely representing clypeo-labral complex [hypostome-labrum complex]. Posterior edge of head not accessible, apparently partly retracted into the broader trunk.

Ocular segment recognisable by possible labrum, yet no clear suture apparent; also no larval eyes (stemma)

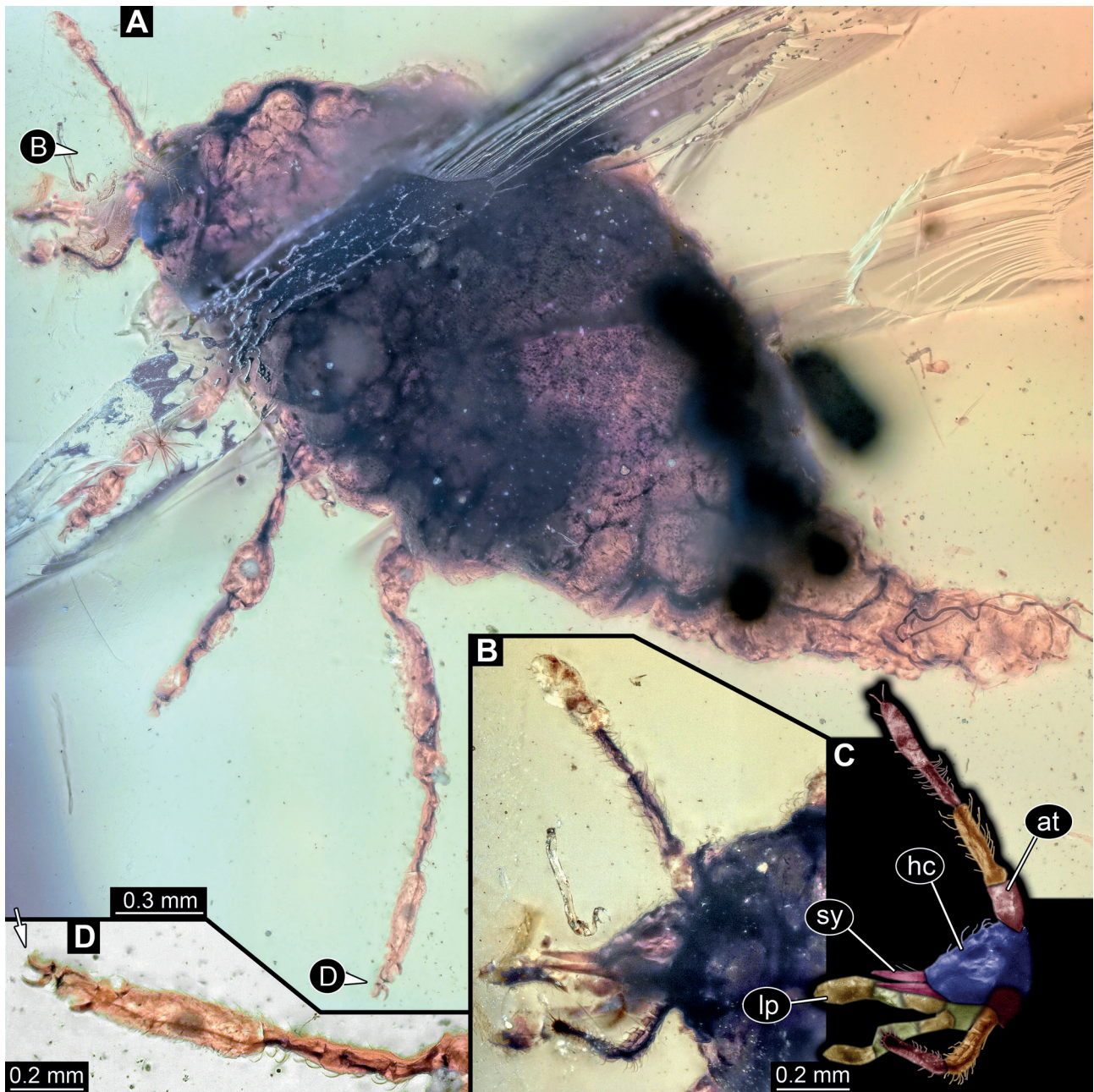


Fig. 1. Fossil dustywing-type larva from Cretaceous Kachin amber, Myanmar, PED 1970; **A:** specimen in dorso-lateral view; **B:** close-up on head; **C:** colour-marked version of **B**; **D:** close-up on thorax appendage 3. Abbreviations: at = antenna; hc = head capsule, lp = labial palp, sy = stylet.

discernible. Post-ocular segment 1 recognisable by its pair of appendages, antennae [antennulae]. Antenna arising from antero-dorsal region of head capsule (Figs. 1B, C, 2B, C). Antenna longer than head capsule, more than 2x. Antenna subdivided into three visible elements. Proximal element stout, only slightly longer than wide (diameter). Element 2 longer than preceding element, about 2x, slightly thinner in diameter, bearing numerous short setae.

Distal element of antenna even longer, about as long as element 1 and 2 combined; distally slightly expanding and rounded, overall roughly club-shaped. Also bearing numerous short setae. Post-ocular segment 2 without externally visible structures.

Pair of short stylets interpreted as compound structures of appendages of post-ocular segment 3 (mandibles) and post-ocular segment 4 (maxillae) [maxillulae]. Sty-

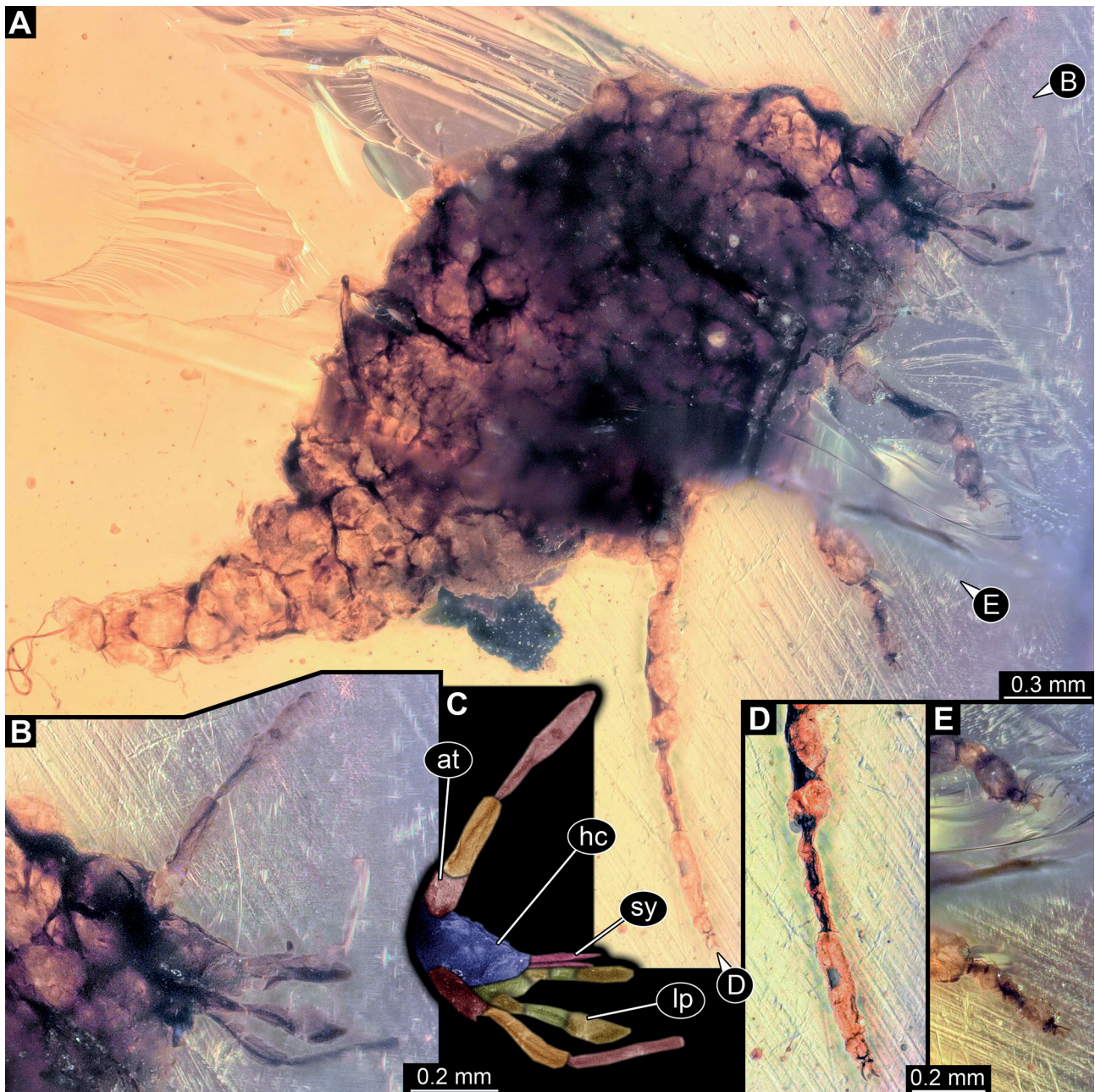


Fig. 2. Fossil dustywing-type larva from Cretaceous Kachin amber, Myanmar, PED 1970, continued; **A:** specimen in ventro-lateral view; **B:** close-up on head; **C:** colour-marked version of **B**; **D:** close-up on thorax appendage 3; **E:** close-up on thorax appendages 1 and 2. Abbreviations: at = antenna; hc = head capsule, lp = labial palp, sy = stylet.

lets short, protruding forward from under the head capsule, about as long as head capsule or only slightly shorter; exact border not apparent (Figs. 1B, C, 2B, C). Stylets with pointed tips.

Post-ocular segment 5 apparent by its appendages, medially conjoined to form the lower lip (labium) [maxillae] (Figs. 1B, C, 2B, C). Proximal part not well appar-

ent, largely concealed by head capsule. Distally with a pair of palps [endopods]. Palps shorter than antennae, with three elements each. Proximal element longer than wide, about 2x. Element 2 slightly longer than preceding element, about as wide. Distal element of the palp slightly longer and wider than preceding element, distally rounded, club-shaped.

3.3. Anterior trunk region (thorax)

Transition from head to trunk not well apparent, subdivision of trunk also not obvious. Thorax segments mainly apparent due to presence of ventral locomotory appendages (legs) [thoracopods] (Figs. 1A, 2A). Thorax segment 1 (interpreted as region close to first leg) wider than head, widening posteriorly, much wider than long, more than 3x. Thorax segment 2 even wider, widening posteriorly. Thorax segment 3 about as wide as posterior region of thorax segment 2, anterior and posterior edge about the same width.

All three thorax appendages appear sub-similar. Appendage 1 with five elements. Element 1 (coxa) [basipod] not fully accessible, appears short. Element 2 (trochanter) [endopod element 1] also short, slightly longer than wide. Element 3 (femur) [endopod element 2] longer than preceding element, about 2x. Element 4 (tibia) [endopod element 3] shorter and thinner. Element 5 (tarsus) [endopod element 4] about as long as tibia, slightly wider. Distally with a pair of pretarsal claws, no traces of an empodium (Fig. 2E). Appendage 2 similar in dimensions to appendage 1.

Appendage 3 longer than the others, with five elements. Element 1 (coxa) [basipod] short, about as long as wide. Element 2 (trochanter) [endopod element 1] similar in dimensions to coxa. Element 3 (femur) [endopod element 2] longer than preceding element, about 4x. Element 4 (tibia) [endopod element 3] shorter and thinner. Element 5 (tarsus) [endopod element 4] about as long as tibia, slightly wider. Distally with a pair of pretarsal claws, no traces of an empodium (Figs. 1D, 2D). Leg elements with numerous small setae.

3.4. Posterior trunk (abdomen)

Transition of thorax and abdomen not well discernible, individual segments of abdomen not discernible. Abdomen strongly tapering posteriorly, giving the entire body a spindle-shaped appearance (Figs. 1A, 2A).

4. Discussion

4.1. Identity of the specimen

Although the head is not ideally accessible in dorsal or ventral view; the stylets are well apparent. Together with the forward-projecting head capsule (not very well apparent), the palps and the overall body shape, the larva shows a high resemblance to modern-day larvae of Coniopterygidae. A minor point of difference on a first glance is the structure of the palps, which have three visible elements in the fossil, but in most depictions of modern-

day larvae of Coniopterygidae only two are visible (e.g., ZIMMERMANN et al. 2009, fig. 3). Yet, the ventral view (e.g., MACLEOD 1964) also reveals three elements in the modern larvae. The antenna has three elements in the fossil, but two in many extant forms (e.g., ZIMMERMANN et al. 2009 fig. 3), yet some larvae also have three elements (GEPPE 1984, pl. 3, fig. 6).

As pointed out when looking at modern larvae, we can recognise two principal types. Larvae of *Conwentzia* have very short stylets, barely projecting from under the labrum, much shorter than the palps, the antennae are usually longer than the labial palps, in some cases much longer; the palps appear bulbous (Fig. 3A). In larvae of *Aleuropteryx*, the stylets are longer, about as long or longer than the head capsule and the palps, the antennae are shorter, about the length of labial palps; the palps appear slender (Fig. 3C).

The fossil has some similarities to both types, but is also different from both (Fig. 3B). The stylets are longer than in *Conwentzia*-type larvae, but shorter and stouter than in *Aleuropteryx*-type larvae. The palps of the fossil are longer than the stylets and shorter than the antennae as in *Conwentzia*-type larvae. The palps of the fossil are distally slightly thickened, unlike in *Aleuropteryx*-type larvae, but not as bulbous as in *Conwentzia*-type larvae. The new fossil larva is therefore somehow intermediate in morphology and cannot easily be further narrowed down regarding its relationships.

The new larva is distinct from the “beak larvae” (HAUG et al. 2020e, 2022d; HAUG & HAUG 2022), although these resemble dustywing larvae to a certain degree. In the “beak larvae”, the mouthparts form a single undivided “beak” (Fig. 3D–F), while in the new larva the two separated stylets are well apparent (Fig. 3B).

4.2. Possible species identity

There are several formally described species of Coniopterygidae in Myanmar amber based on adult specimens (e.g., ENGEL 2004, 2016; LI et al. 2019a). Chances that the here reported larva could be the immature stage of one of these already named species are high. We therefore refrain from erecting a new species based on the specimen. Yet, we are also unable to provide a possible connection of the larva and an adult. Reconstructing ontogenetic sequences for fossils is challenging, but possible in cases of rather gradual ontogenetic sequence. For holometabolans, with their strongly expressed metamorphosis, this is much more challenging. In principle, such a reconstruction ideally requires an exuvia of a larva preserved together with a pupa and a second specimen where an exuvia of a pupa is preserved together with an emerged adult. Such cases are rare (see discussion in BARANOV et al. 2019, 2022b).

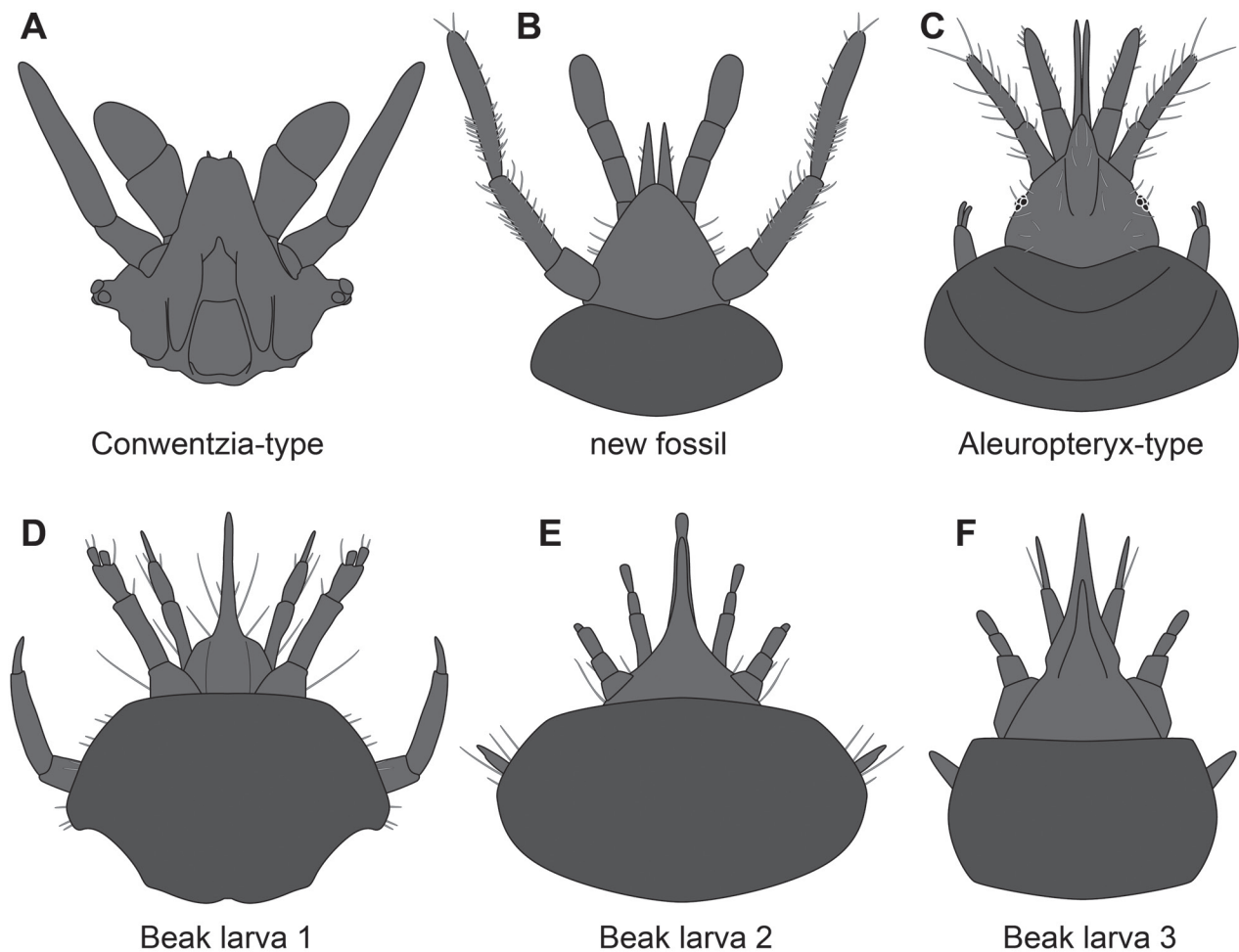


Fig. 3. Comparison of the anterior body region of the new larva with other fossil and extant larvae, modified after different literature sources; **A:** modern dustywing larva of the Conwentzia-type (MACLEOD 1964, pl. 20, fig. 62); **B:** new fossil, PED 1970; **C:** modern dustywing larva of the Aleuropteryx-type (ROUSSET 1966, figs. 47, 48); **D–F:** currently known “beak larvae”, all from Cretaceous Kachin amber, Myanmar; **D:** from HAUG et al. (2020e); **E:** from HAUG et al. (2022d); **F:** from HAUG & HAUG (2022).

Pupae of lacewings are almost absent in the fossil record, with so far only a single specimen from Cretaceous amber (HAUG et al. 2023). This situation makes it unlikely that we will be able to make a connection of the new larva to an adult in the near future.

4.3. The problem of intermediate fossils: plesiomorphies and convergences

As pointed out, the new larva is morphologically “in between” the two modern types of larvae. This statement is, of course, tricky as it relates to a purely typological type of thinking. Yet, it is a general phenomenon for fossils to show a mixture of characters known from separate modern lineages (e.g., HAUG et al. 2019a; LUQUE et al. 2019;

ZIPPEL et al. 2022, 2023). There are two major factors for this phenomenon: plesiomorphies and convergences.

Plesiomorphies play a particularly important role when assessing early representatives of a lineage, which possess only part of the apomorphies of the modern groups, but not all of them, otherwise retaining plesiomorphies. The most famous example is *Archaeopteryx*, possessing part of the apomorphies of modern birds, but otherwise retaining many plesiomorphic characters. In a typological way of thinking, *Archaeopteryx* causes interpretation problems as it is neither a bird (in the strict, classic use of the term) nor a reptile (“transitional form”). Yet, when leaving typology behind and understanding birds as derived reptiles, *Archaeopteryx* becomes much less of a problem, but an interesting piece of information for reconstructing character evolution.

Still, for taxonomic approaches (which are basically typological) such cases represent practical challenges. As an example from Euarthropoda, *Eocarcinus praecursor* was long interpreted as the earliest crab. Yet, FELDMANN & SCHWEITZER (2010) pointed out that *E. praecursor* lacks some apomorphies of crabs and removed it therefore from the group Brachyura. As a next step, the species was ascribed to the sister lineage of Brachyura, namely Anomala (“Anomura”). As pointed out already by FELDMANN & SCHWEITZER (2010), also the fit to this group was not perfect, therefore, a separate superfamily was erected within Anomala to house the single species. As SCHOLTZ (2020) pointed out, in a non-typological phylogenetic framework the species can be interpreted as an early relative of modern crabs, more precisely as a derivative of the early lineage towards modern crabs (“stem-lineage”).

It seems to be a common strategy to simply exclude fossils that do not perfectly match with the idea of a group (“Gestalt”), the latter being strongly influenced by the modern fauna. It needs to be pointed out that this type of exclusion relates to the fact that in such a case taxa are treated as logical classes with unchangeable defining properties; yet, monophyletic groups are in fact not logical classes (e.g., AX 1993). Therefore, ingroups can, and do, differ from the ground pattern state of a group. Excluding is therefore not possible, only an alternative interpretation can be suggested; yet, this does not falsify the original interpretation, it represents a competing one.

Especially within Insecta, the case is additionally complicated by the fact that we see regular convergences in closely related lineages. This phenomenon leads to even more problems in taxonomic treatments of many fossils. Such chimera-type fossils are highly challenging and, in some cases, remain in a kind of interpretive limbo. This fact is not well received in a taxonomic frame. Yet, it shows that a simple exclusion with the argument “it differs from the modern-day morphology, therefore it does not fit here” is not well founded.

For the new fossil presented here it is not easy to evaluate which characters represent plesiomorphies or convergent characters. Hence, as in other fossil larvae (e.g., HAUG et al. 2019a; ZIPPEL et al. 2022, 2023), the new larva has characters that are known from modern relatives, but not necessarily in the same combination. A more precise interpretation is not possible with the available characters.

Although the larva differs from its modern counterparts in the combination of characters, it clearly represents a dustywing-type larva. This find reduces the number of “missing” morphologies of lacewing larvae in the Cretaceous.

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