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FOSSIL SNAKEFLY PUPAE FROM ABOUT 100 MILLION YEARS OLD AMBER REVEAL AN UNUSUAL MORPHOLOGY OF THE ANTENNAE

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Abstract: A key aspect of the holometabolan evolutionary success is their metamorphosis. It allows larvae and adults to exploit quite different resources and reduce competition between the two. The often strongly differing morphology of larvae and adults is mediated by the specific intermediate stage, the pupa. Fossil pupae provide valuable information for the reconstruction of the evolutionary history of this so important developmental stage. However, pupae are relatively rarely found in the fossil record, and they seem even less often depicted in the literature. Here, we report two new fossil pupae preserved in about 100 million years old Kachin amber, Myanmar. These represent the first fossil pupae of the group of snakeflies, Raphidioptera. The two specimens resemble modern snakefly pupae in overall morphology and especially in the morphology of the ovipositor. However, they also differ in certain aspects, indicating differences in developmental timing. One specimen is particularly notable for its long, curled antennae. Extant snakeflies have rather short antennae in all life stages. Yet, in the Cretaceous few species have long antennae as adults, and also some larvae are known with rather long antennae. The other pupa has shorter antennae and is preserved in the same amber specimen as another snakefly, a larva with rather long antennae. The new snakefly pupa with its extraordinarily long antennae underpins the exceptional evolutionary radiations in the Cretaceous.

INTRODUCTION

Holometabola, the group including bees, beetles and butterflies, represents a major share of the diversity, biomass and ecological function in terrestrial and freshwater ecosystems (Hynes 1970; Benefer et al. 2010; Hershey et al. 2010; Schowalter et al. 2018; Dangles & Casas 2019; Morimoto 2020). The key innovation of the group is a distinct ecological and morphological differentiation of the early post-embryonic stages, the larvae (see Haug 2020a for challenges of the term), and the later adults (Whiting 2003; Grimaldi & Engel 2005; Hammer & Moran 2019). The transition between these often strongly differing stages is mediated by a specific stage, the pupa. Although other related

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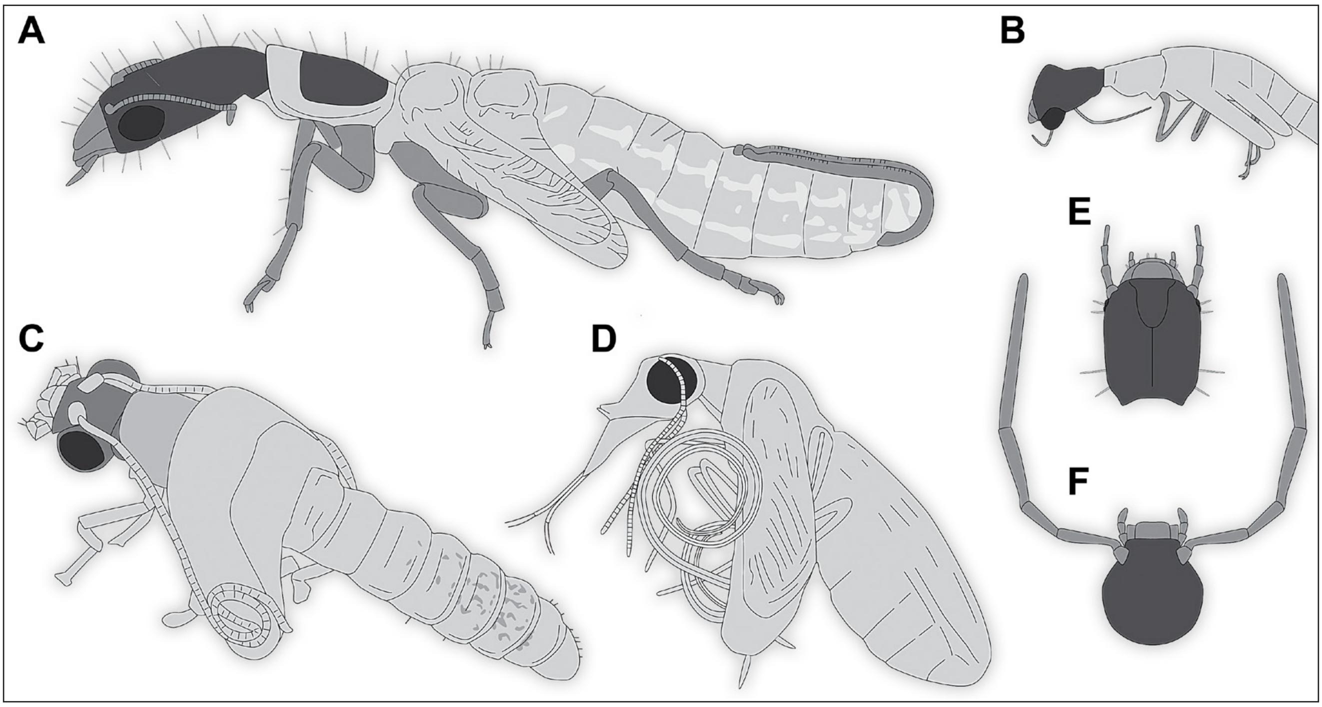

Fig. 1 - Different pupae and larvae of snakeflies and relatives, re-interpreted from various sources. A) Extant female snakefly pupa (due to ovipositor) in mobile phase (from Wachmann & Saure 1997). B) Fossil snakefly pupa preserved in Kachin amber (from Zhang 2017). C) Extant pupa of green lacewing; note the curled antennae (from bugguide #874428 John Rosenfeld 2013). D) Extant pupa of thread-winged lacewing; note the curled hindwings (from Pierre 1952). E) Head of extant snakefly larva; note the short antennae (from Haug et al. 2022). F) Head of fossil snakefly larvae from Kachin amber; note the large antenna (from Haug et al. 2022).

lineages have functionally comparable stages (Haug 2020b), the pupa is often considered as something rather special. Therefore, it is quite surprising that the pupa stage appears to be the least depicted stage in holometabolans, far less than the larvae and significantly less than the adults (Saltin et al. 2016).

This effect is even more pronounced in the fossil record (Haug et al. 2023a). Due to the rareness of extant pupae in literature, interpreting the few fossil pupae is often challenging (e.g. Haug et al. 2017 vs. Baranov et al. 2019). Still, fossil pupae are important for reconstructing aspects of the evolution of ontogeny for holometabolans.

The group of snakeflies, Raphidioptera, is generally understood as having representatives with plesiomorphic traits from the ground pattern of Holometabola, such as the long ovipositor or the mouthpart morphology (e.g. Aspöck & Aspöck 1999, 2007). This fact also applies to their pupae. Snakefly pupae demonstrate that the idea of the pupa as a principal quiescent (≈ resting) stage is incorrect, as especially later-stage snakefly pupae can walk quite well. This mobility possibly caused at least some depictions of extant snakefly pupae (Fig. 1A; Woglum & McGregor 1958 fig. 14 p. 134, fig. 17 p. 135; Wachmann & Saure 1997 p. 23 bottom; Aspöck & Aspöck 2007 fig. 6 p. 457; Aspöck et al. 2012 fig. 4 p. 567; Monserrat & Papenberg 2015 fig. 23 p. 9; Aspöck et al. 2019 fig. 5 p. 80; Jindra 2019 fig. 1b p. 3; Haug et al. 2022 fig. 3 p. 752; Schmitt 2022 fig. 9.59d p. 270).

On the other hand, the fossil record of snakefly pupae is so far scarce. A single specimen was depicted in Zhang (2017, lower image p. 415, see Fig. 1B) and identified as a snakefly "incerta sedis". The specimen was not fully depicted (the trunk end is outside the image), yet the prominent wing anlagen clearly indicate that this specimen is a pupa. A supposed snakefly pupa from Cretaceous French amber (Soriano et al. 2010) is more likely a lacewing pupa (Haug et al. 2023a). The scarceness of snakefly pupae in amber is partly surprising given the fact that snakefly larvae are not uncommon in amber (Fig. 1F; Grimaldi 2000; Engel 2002; Weitschat & Wichard 2002; Scheven 2004; Grimaldi & Engel 2005; Perrichot & Engel 2007; Gröhn 2015; Xia et al. 2015; Zhang 2017; Haug et al. 2020, 2022).

Here, two well-preserved snakefly pupae embedded in about 100 million years old Kachin amber, Myanmar, are reported. These are compared to the few known extant specimens, and the evolutionary implications are discussed.

MATERIAL AND METHODS

Material

Two amber specimens are in the centre of this study, both from the collection of one of the authors (PM; BUB 4719; BUB 4838). A further amber specimen originated from the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München (PED 3600). It was purchased on the trading platform ebay.com (trader: burmite-miner). All amber specimens have been legally acquired. The amber is from Kachin, Myanmar (ca. 100 Ma, possibly 99 Ma; Cruickshank & Ko 2003; Shi et al. 2012; Yu et al. 2019).

Documentation

The specimens were photographed with a Keyence VHX-6000 digital microscope with built-in 20-2000x objective. The images were taken under cross-polarised illumination or low-angle ring light, as well as low-angle ring and coaxial light. All images were recorded in high dynamic range (HDR) mode. Black and white backgrounds were tested; images with best contrast were used for further processing. Image stacking (fusing of images with differing focus levels) and stitching (merging of adjacent image details) was performed by the built-in software of the microscope. All post-processing of the images (optimisation of contrast, sharpness, saturation, colour markings) was performed with Adobe Photoshop CS2 (9.0, Adobe Inc., San José, CA, USA).

Terminology

We use entomological terminology for the descriptions of the specimens. To improve understandability also for non-entomologists, we additionally provide more general terminology for Euarthropoda in squared brackets.

RESULTS

Description of BUB 4719

Body ca. 3.6 mm long (excluding appendages), organised in head and trunk (Fig. 2A, B). Head segments forming capsule (presumably ocular segment and five post-ocular segments), ca. 0.43 mm long. Head capsule appears elongate, yet oblique angle of view makes it difficult to estimate width. Ocular segment with prominent compound eyes, number of ommatidia cannot be estimated. Post-ocular segment 1with prominent feeler-type antennae [antennulae]. Exact number of antennomeres [elements] can only be estimated, more than 100; each antennomere bearing numerous setae. Antennae curled up (Fig. 2C). Further posterior segments with mouthparts, most details obscured. Prominent palps [endopods] apparent, but unclear from which mouthparts.

Trunk further differentiated into anterior thorax and posterior abdomen. Specimen preserves pro-, meso-, and metathorax. Prothorax [trunk segment 1; post-ocular segment 6] elongate, about as long as head (Fig. 2A, B). Ventrally with a pair of legs [trunk appendages; locomotory appendages] arising from the segment far posteriorly. Proximal region of leg (coxa, trochanter) [basipod, endopod element 1] not well accessible. Distal part with three elements (femur, tibia, tarsus) [endopod elements]. All partly distorted, hence lengths difficult to discern. Femur elongate, longer than wide, at least 5×. Tibia shorter than femur, only about 20% of the length. Distally with at least two prominent setae. Tarsus slightly longer than tibia, distally with two prominent setae and two prominent claws.

Mesothorax medially (mesonotum) shorter than prothorax, about 0.5× the length (Fig. 2A, B). Latero-dorsally with a developing wing (wing “sheath”), ca. 1.3 mm. Wing about as wide as mesonotum long, projecting about 45° backwards, longer than wide, about 5×. Surface with few prominent setae. Wing of pupa transparent, revealing the developing cuticle of the adult. Surface of adult wing with numerous shorter setae, not yet folded (indicating an earlier developmental state). Ventrally with a pair of legs [trunk appendages; locomotory appendages], arising from the segment far posteriorly. Sub-similar to leg of prothorax. Tibia appears longer, distally with more setae. Tarsus with indications of subdivision of three regions, yet without distinctly formed joints. Subdivision indications by medially drawn-out leaf-like structures (possible future attachment structures). Metathorax, including its structures, largely resembling mesothorax.

Abdomen slightly longer than head and thorax together, subdivision largely obscured; few long

Fig. 2 - BUB 4719. A) Latero-ventral view, overview. B) Latero-dorsal view, overview. C) Close-up on long, curled-up antenna. D) Close-up on ovipositor.

setae (at least four per segment) indicate at least eight individual units. Posterior region carries a tube-shaped structure ventrally (ovipositor; Fig. 2D), projecting posteriorly, but curving around the trunk end and dorsally forward to about half the length of the abdomen.

Description of BUB 4838

The amber specimen has two main inclusions (Fig. 3A). One (BUB 4838a) is sub-similar in many aspects to the specimen described above, about 9.4 mm long (excluding appendages), with a head length of ca. 1.5 mm (Fig. 3E). This similarity concerns especially overall body organisation, head shape and developing wings. Yet, the specimen is less well preserved, not allowing to compare many of the aspects in detail. Therefore, it remains for example unclear whether a structure at the trunk end also represents an (in this case deformed) ovipositor.

Some aspects are visible, like the mandibles, which are not apparent in the otherwise better-preserved specimen BUB 4719. These are well preserved and prominent (Fig. 3F). A major difference is the morphology of the antenna, which is in this specimen much shorter and thinner (Fig. 3G).

The second inclusion is a larva (BUB 4383b; Fig. 3B). Body ca. 5.7 mm long, organised in head and trunk. Head segments forming capsule (presumably ocular segment and five post-ocular segments), ca. 0.56 mm long. Head capsule appears elongate, longer than wide, about 2×. Ocular segment with prominent labrum projecting forward. Post-ocular segment 1with prominent feeler-type antennae [antennulae] with four major elements. Antennae longer than head capsule, about 2×. Further posterior segments with mouthparts, most details obscured. Prominent palps [endopods] apparent (Fig. 3C) but unclear from which mouthparts.

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments, pro-, meso-, and metathorax. Prothorax [trunk segment 1; post-ocular segment 6] elongate, about as long as head. Ventrally with a pair of legs [trunk appendages; locomotory appendages] (Fig. 3D). Proximal region of leg (coxa, trochanter) [basipod, endopod element 1] not well accessible. Distal part with three elements (femur, tibia, tarsus) [endopod elements], all elongate. Femur elongate, longer than wide, at least 5×. Tibia slightly longer than femur, but narrower. Tarsus slightly shorter than tibia, with two prominent claws.

Mesothorax medially (mesonotum) slightly shorter than prothorax. Ventrally with a pair of legs [trunk appendages; locomotory appendages], arising from the segment far posteriorly. Sub-similar to leg of prothorax. Metathorax largely resembling mesothorax, including its structures.

Abdomen slightly longer than thorax, about 2×. Subdivision into ten individual units indicated by bulging lateral rims. Abdomen tapering posteriorly (Fig. 3B).

Short description of PED 3600

Adult female snakefly, body length ca. 4.6 mm (excluding appendages), head length ca. 0.7 mm. No entire description is envisaged as it is not in the focus of this study, it only serves as a basis for comparison with the pupae. Antenna long, at least as long as the main body (Fig. 4A). Wings well developed, ca. 4.0 mm long. Legs with differentiated tarsus, subdivided into several elements (Fig. 4B, C). Ovipositor long, about as long as head and thorax together, ca. 2.25 mm.

Discussion

Identity of BUB 4719

The new specimen strongly resembles modern snakefly pupae (Fig. 1A; cf. Woglum & McGregor 1958 fig. 14 p. 134, fig. 17 p. 135; Wachmann & Saure 1997 p. 23 bottom; Aspöck & Aspöck 2007 fig. 6 p. 457; Aspöck et al. 2012 fig. 4 p. 567; Monserrat & Papenberg 2015 fig. 23 p. 9; Aspöck et al. 2019 fig. 5 p. 80; Jindra 2019 fig. 1b p. 3; Schmitt 2022 fig. 9.59d p. 270; Haug et al. 2022 fig. 3 p. 752). The long head and prothorax are not visible directly dorsally, but appear to match the length known in modern pupae and already give a strong indication of the identity of the specimen. The most striking similarity is the shape of the ovipositor (cf. Wachmann & Saure 1997 p. 23 bottom, see Fig. 1A; Aspöck & Aspöck 1999 fig. 59 p. 22; Monserrat & Papenberg 2015 fig. 23 p. 9). This character furthermore indicates that the specimen is a female, as the structure exactly matches the ovipositor in modern female snakefly pupae.

It has been suggested that snakefly pupae are least derived in comparison to the ground pattern of Holometabola (Beutel et al. 2014 p. 399). One could therefore argue that the new fossil could also be a representative of an earlier branch within Holometabola, but the elongation of head and prothorax clearly supports an interpretation of a position within Raphidioptera.

Identity of BUB 4838a and BUB 4383b

As BUB 4838a strongly resembles BUB 4719, it likewise represents the pupa of a snakefly, although less well preserved. It stronger resembles modern-day snakefly pupae, especially in the shorter antennae. It is therefore unlikely that the two fossil pupae are conspecific.

The other inclusion in this amber specimen, BUB 4383b, is clearly the larva of a snakefly, strongly resembling earlier reported larvae (Haug et al. 2022 fig. 15c p. 764). Whether larva and pupa could be conspecific will be discussed further below.

Unusual feature of BUB 4719: the antennae

While many of the characters of BUB 4719 are clearly shared with modern-day snakefly pupae, there is one feature in the fossil that is quite different from all modern forms: the strongly curled, very

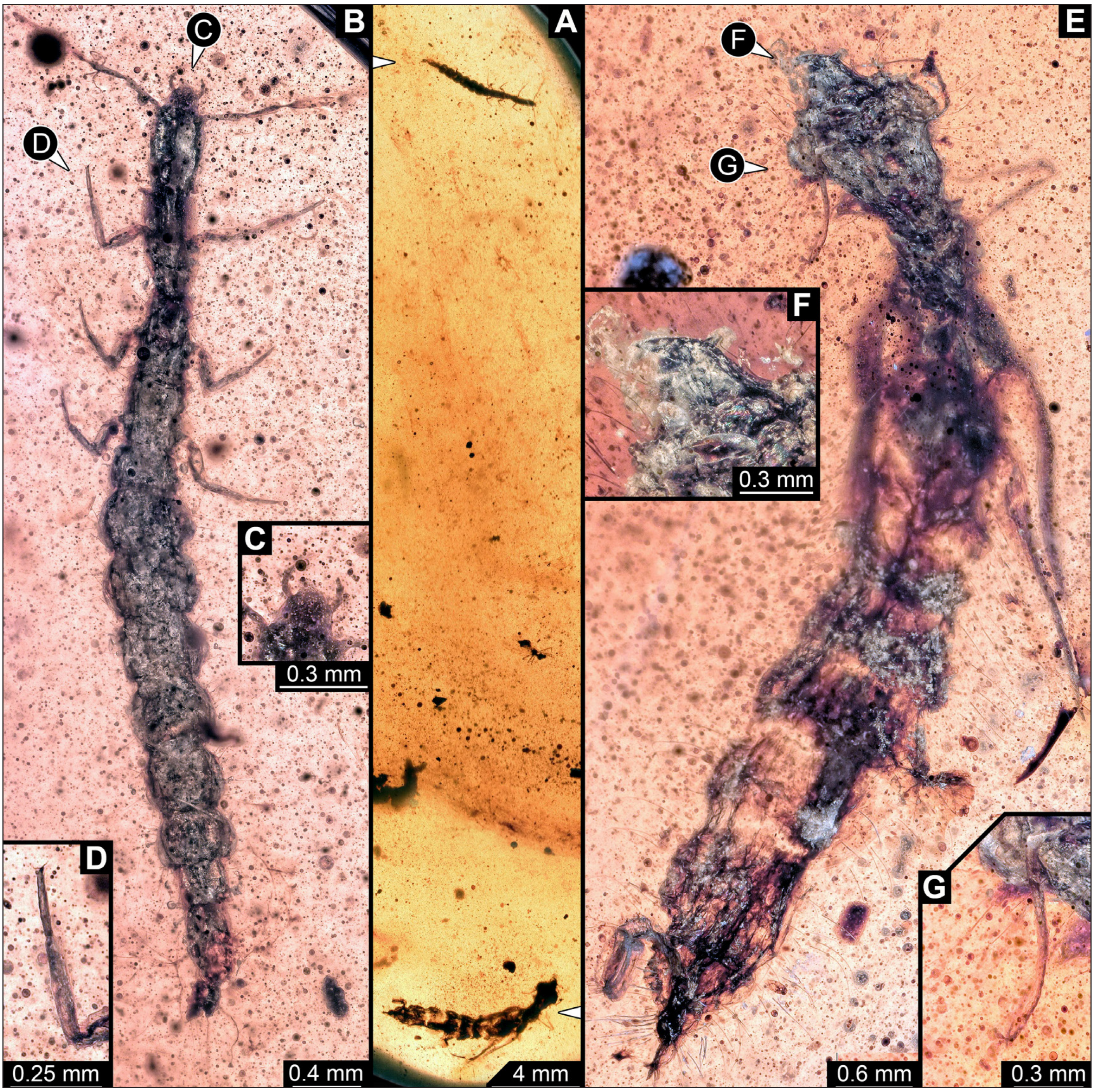

Fig. 3 - Amber specimen BUB 4383. A) Overview. B–D) BUB 4383b, larva. B. Overview. C. Close-up on mouthparts. D. Close-up on leg. E–G) BUB 4383a, pupa. E. Overview. F. Close-up on mandibles. G. Close-up on antenna.

long antennae. The curled appearance may appear bewildering at first, yet as both antennae show it, it seems unlikely to be caused by preservation. Such a morphology is not present in any modern snakefly pupa. However, we can find comparable morphologies in close relatives.

There is one pupa of a green lacewing (*Chrysoperla*) that also has a curled antenna (on the repository bugguide #874428 John Rosenfeld 2013; see Fig. 1C). Although not as obvious, such a curling can also be seen in other green lacewing pupae (Zhao et al. 2020 fig. 2 day 6 p. 9; fig. 3 day 11 p. 10; fig. 14C p. 24). The curling appears to be a simple space-saving strategy, as curling up allows to securely store a very long antenna without damaging it. Such a mechanical solution can also be seen in other structures. In another group of lacewings, thread-winged lacewings (Crocinae), the hindwings are long and thin. They are likewise curled up in the pupa (Fig. 1D; Pierre 1952 figs. 27, 28; Aspöck

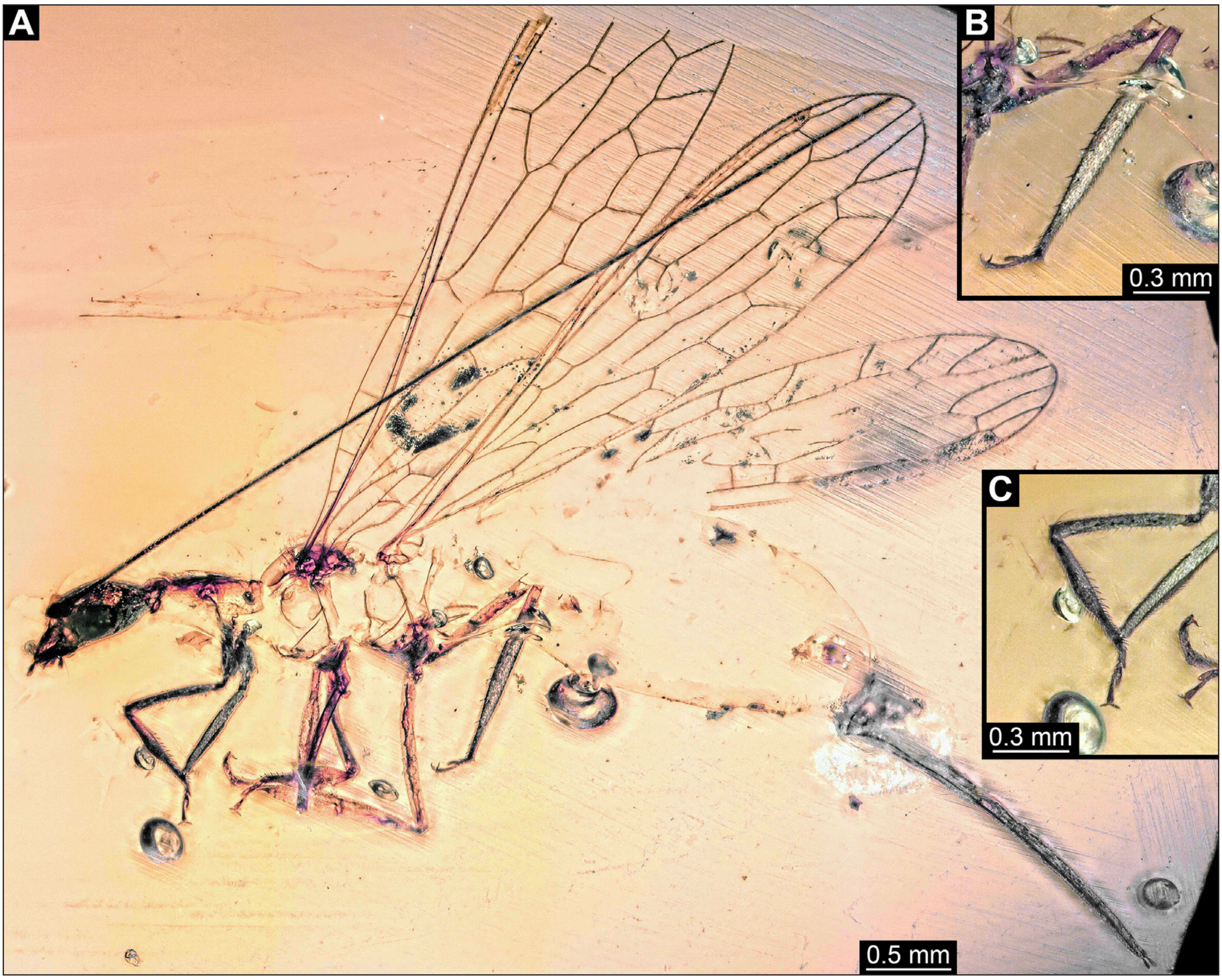

Fig. 4 - PED 3600, adult female snakefly. A) Overview, note the long antenna and the long ovipositor. B, C) Close-ups on legs.

& Aspöck 1999 fig. 63 p. 23; re-fig. in Aspöck & Aspöck 2007 fig. 45).

Modern-day snakeflies do not have excessively long antennae as adults. The new pupa indicates therefore that the corresponding adult snakefly may have possessed rather long antennae. Long antennae seem to be rare but present in Kachin amber as demonstrated by PED 3600 (Fig. 4), but here the antenna is incomplete. Even longer antennae have been reported for *Dolichoraphidia aspoecki* (Liu et al. 2016 p. 304 fig. 1A) and *D. engeli* (Liu et al. 2016 p. 307 fig. 3A). Both, PED 3600 and BUB 4719, may well be representatives of the group *Dolichoraphidia*.

Quite long antennae are known in larvae of snakeflies from the Cretaceous, not only in BUB 4383b, but also in other specimens (Haug et al. 2020, 2022). Such long antennae in larvae are unparalleled in the modern fauna (see Fig. 1E, F). It is therefore well possible that also other larvae with long antennae are either conspecific or closely related to *Dolichoraphidia*. The finding of such a larva close to a pupa, which has no indication of long antennae, complicated the find. Although it seems consistent to have already a long antenna in the larva and then also in the pupa and adult, this is not a strict necessity in holometabolans. Furthermore, the co-occurrence of two organisms in the same amber specimen is not strictly indicative of conspecifity. Only a pupa with a larval exuvia will be able to further support or reject such a possibility.

More differences in comparison to modern snakeflies

While the antennae of BUB 4719 are truly exceptional, there are also other differences to modern snakefly pupae recognisable (unfortunately these aspects are not accessible in BUB 4383a). The legs are elongate, especially femur and tibia make the legs extend beyond the head when stretched forward. In modern pupae, the legs do not reach the anterior rim of the head (cf. Woglum & McGregor 1958 fig. 14 p. 134, fig. 17 p. 135; Wachmann & Saure 1997 p. 23 bottom; Aspöck & Aspöck 2007 fig. 6 p. 457; Aspöck et al. 2012 fig. 4 p. 567; Monserrat & Papenberg 2015 fig. 23 p. 9; Aspöck et al. 2019 fig. 5 p. 80; Jindra 2019 fig. 1b p. 3; Schmitt 2022 fig. 9.59d p. 270; Haug et al. 2022 fig. 3 p. 752). The tarsus is quite different from that of their modern counterparts as well. The protruding structures on the proximal part of the tarsus seem to correspond to attachment structures in modern snakefly pupae (e.g. Haug et al. 2022 fig. 3 p. 752). Yet, in the latter these are much less prominent than in the here described fossil. Also, the distal region of the tarsus, distally to the protrusions, is significantly more elongate in the fossil than in modern pupae. This stronger elongation of legs and leg structures is in correspondence with the elongation of the antennae. A comparable phenomenon has been observed in Cretaceous larvae of lacewings, some of which also have elongated mouthparts and elongated antennae and legs (e.g. Haug et al. 2021).

Overall stronger elongated structures are often interpreted as “further developed” structures, i.e. peramorphic or adultising events of heterochrony (Webster & Zelditch 2005; Haug et al. 2023b). On the contrary, another aspect in the legs of the fossil pupa appears more immature (i.e. paedomorphic) than in modern pupae, namely the lack of clear subdivisions of the tarsus. In modern pupae the tarsus seems well subdivided into usually three tarsomeres (e.g. Haug et al. 2022 fig. 3 p. 752).

Changes in developmental timing (heterochrony)

It should not be surprising that some aspects of the fossil pupa BUB 4719 indicate a less developed state of ontogeny on one hand, and a further developed state on the other hand. Already other fossils have indicated that the developmental sequence in fossil snakeflies differs from that of modern representatives (Haug et al. 2024a). The fossil is also clearly not a moult remain, as the next cuticle layer, i.e. that of the developing adult, is apparent in the wings. However, this well preserved inner cuticle does not show signs of folding, which is surprising, because the fossil already shows the posture of an active state. Modern snakefly pupae develop through two phases: in the early phase they are largely immobile and attain an “embryonic” posture (e.g. Woglum & McGregor 1958 fig. 14 p. 134; Monserrat & Papenberg 2015 fig. 23 p. 9), while in the later phase they are mobile and accordingly have an “active” posture (Wachmann & Saure 1997 p. 23 lower; Aspöck et al. 2018). In the active phase, modern snakefly pupae show some folding of the wings. It is hard to see in most extant snakefly pupae as the pupa cuticle appears largely non-transparent. However, there are indications of folding in some available images (Wachmann & Saure 1997 p. 23 lower). The active posture of the fossil combined with non-folded visible wing cuticles leave us with the conclusion that the specimen is unusual concerning the developmental states of different structures.

Extreme morphologies in the Cretaceous

Excessively long morphological structures have been reported for Cretaceous lacewing larvae (Haug et al. 2019a, b, 2021; Zippel et al. 2021) and lacewing adults (Makarkin 2016, 2017), for other representatives of Pterygota such as plant hoppers (Szwedo 2009; Emeljanov & Shcherbakov 2018; Amaral et al. 2024) and earwigs (Haug et al. 2023c), but even for other representatives of Euarthropoda (Haug et al. 2024b). It appears that the Cretaceous was a time of experimental morphologies (Haug et al. 2019c), leading to many morphologies that are rather extreme compared to their modern counterparts. The new snakefly pupa with an extraordinarily long antenna is therefore an amendment to this phenomenon, underpinning the exceptional evolutionary radiations at this time.

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