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## Unusual snakefly larvae in about 100 million-year-old amber and the evolution of the larva-pupa transition

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### Abstract

The evolutionary success of Insecta, more precisely of its ingroup Holometabola, has partly been explained by their ontogeny, with larvae and adults differing in their morphology and ecology. This differentiation occurs in large and well-known groups such as beetles, butterflies and bees, but also in the relatively species-poor group of snakeflies (Raphidioptera). Despite the rather small number of species, snakeflies are evolutionarily very significant as they were part of the early diversification of Holometabola and still exhibit several plesiomorphic traits retained from the ground pattern of the latter, for example, a mobile pupa. Furthermore, during development, some snakeflies show a mixture of larval and pupal, sometimes even of adult characters, a phenomenon called metathetely. We here report a 100 million-year-old fossil snakefly larva from Myanmar amber with possible characters reminiscent of metathetely. Different dimensions of the body were measured in the specimen and other snakefly larvae and pupae, and ratios were calculated and compared among the larvae. The new fossil shows similarities to extant pupae in the larger length of the prothorax, similarities to modern adults in the small width of the prothorax, but also similarities to other fossil snakefly larvae such as the undivided tarsus and the antenna being subdivided into only five elements. Such a mixture of characters from different developmental stages points to a less pronounced metamorphosis in fossil snakeflies than in extant ones. Similar ontogenetic patterns, with a more gradual development in earlier representatives evolving into a more pronounced metamorphosis in modern representatives, are also known in other groups of Euarthropoda and point to heterochronic events in the evolution of these lineages.

**Keywords:** metathetely, heterochrony, fossil, ontogenetic pattern, Cretaceous, Myanmar

### Introduction

The group Insecta has been recognised as a dominating part of the continental ecosystem (e.g., Suter & Cormier, 2015; Jankielsohn, 2018; Crespo-Pérez *et al.*, 2020; Wagner *et al.*, 2021; Wermelinger, 2021). More precisely, the dominance is represented by the group Holometabola, which includes beetles, bees, butterflies, and flies (among others). Generally, the enormous evolutionary success of holometabolans has been attributed to their specific ontogeny, with larvae (see Haug, 2020a for difficulties with the term) differing ecologically and morphologically from their corresponding adults (Truman & Riddiford, 2019).

Raphidioptera, the group of snakeflies, is rather species-poor and less ecologically dominating. Yet, snakeflies are generally understood as evolutionary important as they were part of the early diversification of Holometabola and seem to have been more diverse in the past (Aspöck & Aspöck, 2007; Haug *et al.*, 2022). Also, the ontogeny of snakeflies seems important for understanding the evolution of holometaboly.

Snakeflies represent an interesting case within the group Holometabola. Their pupae, unlike those of many other holometabolans, are quite mobile and can even walk around (e.g., Wachmann & Saure, 1997). This character has generally been interpreted as a plesiomorphic trait. Therefore, snakeflies, and especially their pupae, should be quite informative for understanding (= reconstructing) the developmental pattern of the stem species ( $\approx$  ancestor) of Holometabola (e.g., Jindra, 2019).

Snakefly development has been recognised for another

peculiar feature of its post-embryonic development. Under certain circumstances, some individuals, mostly reared under controlled laboratory conditions, show a mixture of larval and pupal characters (Aspöck *et al.*, 2018, 2019 and references therein). Occasionally, such specimens have been seen in the wild. More rarely, even mixtures including adult characters have been mentioned. This phenomenon has been termed prothetely or metathetely (see discussion in Aspöck *et al.*, 2018, 2019). Yet, in the early 20<sup>th</sup> century it was pointed out that this phenomenon (also known in some other lineages) may be well explained in the framework of developmental plasticity and that there is no necessity for a specific terminology for this phenomenon (Pruthi, 1927).

In any case, this type of variability is quite interesting in better understanding the early evolution of the pupa as a specific stage. We here report a new unusual fossil larva of a snakefly from about 100 million-year-old amber from Myanmar. We compare it with other fossil snakefly larvae and compare the ontogenetic pattern indicated by fossil larvae with those known from modern representatives of Raphidioptera in order to improve our understanding of developmental plasticity in Raphidioptera and Holometabola in general.

## Material and methods

### Material

In the focus of this study is a single specimen within Kachin amber from the Hukawng Valley, Myanmar. The amber is approximately 100 million years old (possibly 99 million years; Cruickshank & Ko, 2003; Shi *et al.*, 2012; Yu *et al.*, 2019). The specimen comes from the collection of one of the authors (PM) and is stored under the repository number BUB 4261.

### Documentation methods

The fossil specimen was documented using a Keyence VHX-6000 digital microscope in front of white and black background, using different types of illumination (cross-polarised co-axial light and low-angle ring light) (Haug *et al.*, 2013a, 2018). All images were recorded as composite images (Haug *et al.*, 2011) by combining several images of varying focus as well as several adjacent image details and images recorded with different exposure times (HDR, *cf.* Haug *et al.*, 2013b). Images of the specimens were further processed and colour-marked with Adobe Photoshop CS2.

### Measurements

We followed earlier approaches and partly re-used the data set from Haug *et al.* (2022), but expanded it by the

additional fossil specimen reported here, as well as pupae from the literature (Suppl. Table 1, Suppl. Text 1). We plotted the ratio head length / prothorax length over the ratio prothorax length / body length.

## Results

### Description of new specimen BUB 4261

*General.* Elongate, slender larva, total body length ~6.84 mm (Fig. 1A, E). Differentiated into a head and trunk, trunk further differentiated into anterior trunk (thorax) and posterior trunk (abdomen).

*Head.* Head elongate, dorso-ventrally flattened, prognathous (mouthparts orientated forwards) oval in dorsal view, ~0.87 mm long and ~0.34 mm wide at the widest point (Fig. 1C). Head capsule appears strongly sclerotised with clearly visible epicranial suture with “arms”, resulting in Y-shape; arms meet in anterior part of head capsule in dorsal view, at approximately 1/3 of length of head capsule. Lateral edge of head capsule with at least three setae (~0.09 mm long).

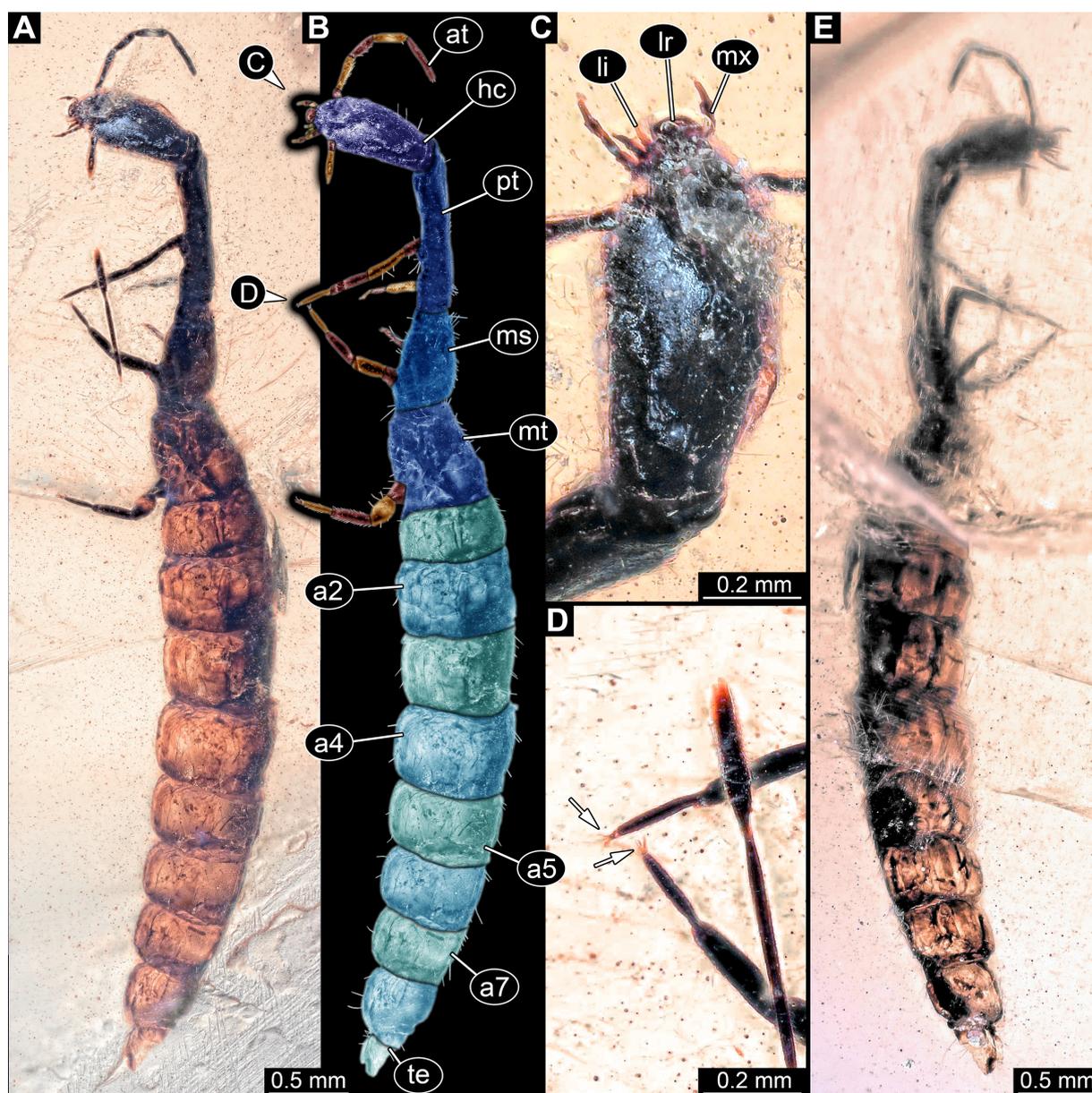
No stemmata (larval eyes) discernible. Labrum (derivative of ocular segment), wider than long, 1.5× (~0.06 mm) (Fig. 1C). Antennae (appendages of post-ocular segment 1) discernible, with five elements (Fig. 1A, B), most proximal element the shortest, ~0.07 mm, three middle elements longer than basal, at least 3×, most distal element the longest, ~0.33 mm. Intercalary segment (post-ocular segment 2) without externally visible structures. Mouthparts only partially discernible.

Mandibles (appendages of post-ocular segment 3) not accessible, probably concealed by other mouthparts.

Maxillae (appendages of post-ocular segment 4) only accessible distally, *i.e.*, maxillary palps, ~0.19 mm long, each palp with four elements of similar length (Fig. 1C).

Labium (conjoined appendages of post-ocular segment 5) only accessible distally, *i.e.*, labial palps, ~0.08 mm long (Fig. 1C).

*Trunk.* Thorax trapezoid in dorso-lateral view, with narrower anterior rim (~0.19 mm) and wider posterior rim (~0.61 mm), ~2.26 mm long, longer than head, 2.6× (Fig. 1A, B). Prothorax very elongate, almost tube-like, appears dorsally strongly sclerotised (tergite, pronotum), ~1.01 mm long, longer than wide, 5.3× (Fig. 1B). Mesothorax trapezoid in dorso-lateral view, with narrower anterior rim (~0.22 mm) and wider posterior rim (~0.35 mm), ~0.6 mm long, longer than wide at its widest point, 1.7× (Fig. 1B). Metathorax trapezoid in dorso-lateral view, with narrower anterior rim (~0.36 mm) and wider posterior rim (~0.61 mm), ~0.66 mm long, longer than wide at its widest point, 1.1× (Fig. 1B). Thorax bears multiple short setae.



**FIGURE 1.** New specimen BUB 4261, snakefly larva. **A**, Habitus of the larva with some pupa and adult characters in dorso-lateral view. **B**, Color-marked version of **A**. **C**, Close-up of head capsule with mouthparts in dorso-lateral view. **D**, Close-up of distal elements of legs (arrows mark claws). **E**, Habitus of the larva in ventro-lateral view. Abbreviations: a2–a7 = abdomen segments 2–7; at = antenna; hc = head capsule; li = labium palp; lr = labrum; ms = mesothorax; mt = metathorax; mx = maxilla; pt = prothorax; te = trunk end.

Each thorax segment ventrally with a pair of locomotory appendages (legs).

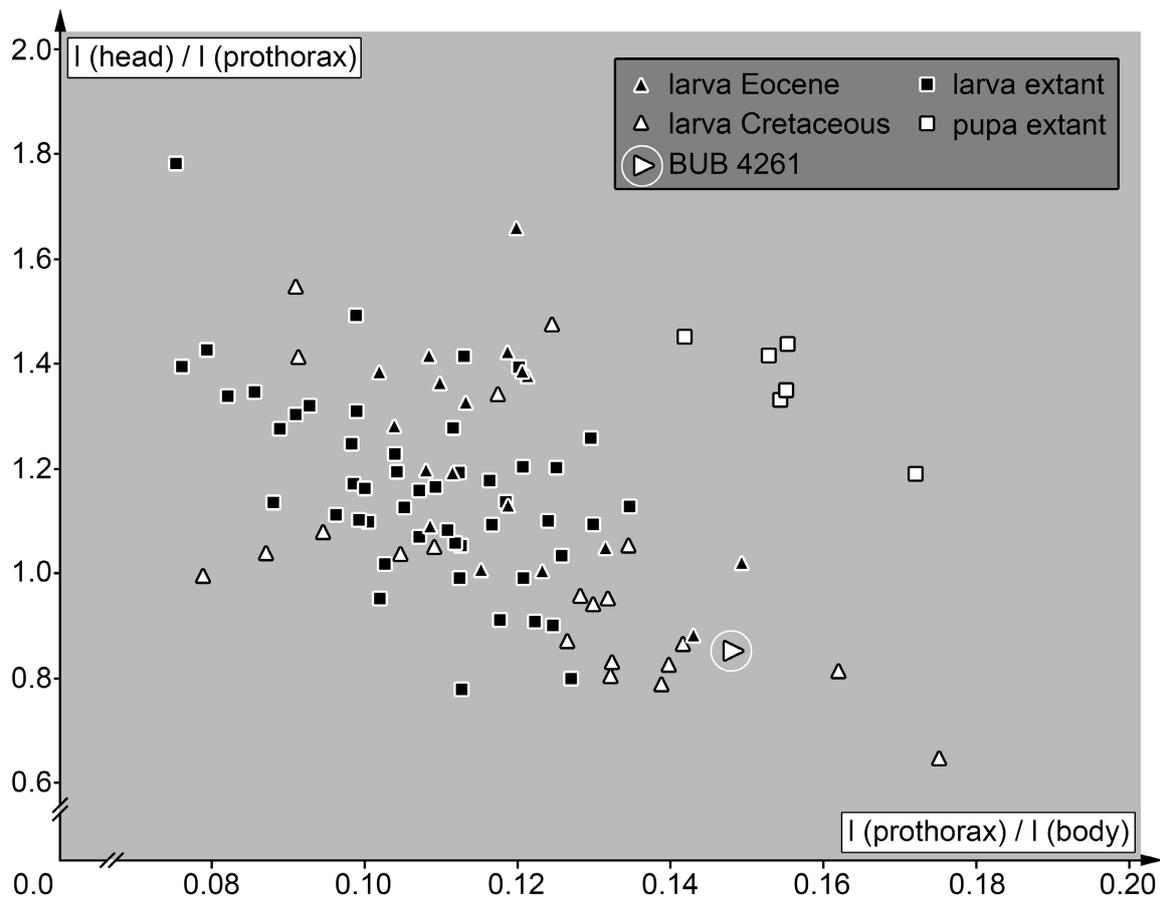
Legs elongate (~0.73 mm long), slightly longer than metathorax, 1.1× (Fig. 1B). Legs subdivided into five major elements. Elements of legs of varying lengths: coxa (~ 0.1 mm long), trochanter not clearly discernible (length not clear), femur (~ 0.21 mm long), tibia (~ 0.25 mm long), tarsus (~ 0.18 mm long). Each leg distally with three fine claws (Fig. 1D, white arrows). Femur bears multiple short setae (~0.06 mm long).

Abdomen elongate, posteriorly tapering in dorso-

lateral view, ~3.71 mm long, longer than head, 4.3× (Fig. 1A, B), maximal width of abdomen ~0.76 mm (abdomen segment 4). Trunk end much smaller than trunk segments, ~0.23 mm long and ~0.22 mm wide at the middle (Fig. 1B). Entire abdomen bears short setae (~0.07–0.13 mm long).

#### *Comparison of measurements*

In modern snakeflies, the occupied areas in the plot are clearly separated into two groups (Fig. 2): the larvae plot on the left side (=  $l(\text{prothorax})/l(\text{body}) < 0.14$ ), while pupae



**FIGURE 2.** Scatter plot of the ratio head length / prothorax length over the ratio prothorax length / body length of extant and fossil snakefly larvae and pupae (the latter not differentiated by geological period), including the new specimen BUB 4261 (in circle). For details on the measured specimen, see Supplementary Table 1.

plot on the right side ( $=l(\text{prothorax})/l(\text{body}) > 0.14$ ). Yet, among the fossil larvae, both from the Eocene and the Cretaceous, some also plot on the right side. These larvae differ from modern pupae in relatively shorter heads.

## Discussion

### *Similarities of some fossil larvae with modern pupae*

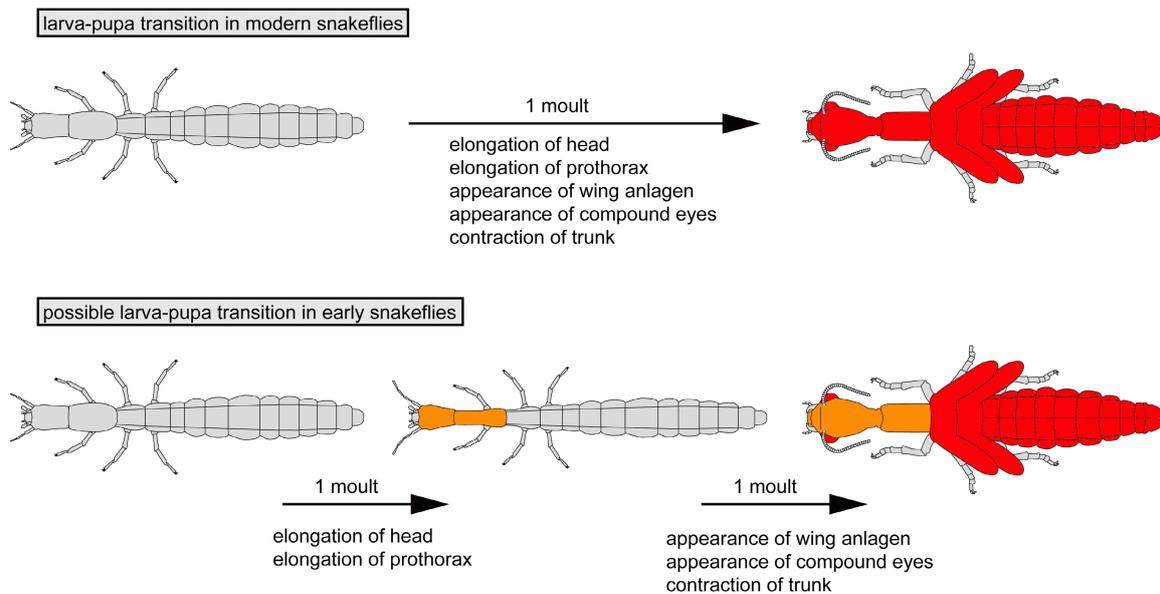
As apparent from the comparative plots, the new fossil larva, together with some already known fossils, plots in an area not occupied by modern specimens. These larvae all have a relatively long prothorax similar to modern pupae, but differ from these by having relatively shorter heads. Presumably, the new larva represents a late larval stage, but the exact instar can not be determined.

In addition, it is worth to consider some qualitative aspects. The prothorax in some of the fossils, especially in the newly reported one, is already very adult-like concerning its slender and slightly tapering appearance. In modern larvae, the prothorax is rather broad.

This leaves the impression that the prothorax

morphology of some fossil larvae is already more adult-like than in modern larvae. It has been demonstrated that in fossil snakefly larvae the morphological diversity and variation is larger than in modern forms, both in the Cretaceous as well as in the Eocene (Haug *et al.*, 2020, 2022). In general, larvae in the Cretaceous seem to provide superlatives when it comes to relative lengths of structures (Haug *et al.*, 2019a, b, 2021). The longer prothorax could therefore be seen as an example in the same frame, a hypertrophied larval structure.

Yet, the case is in fact different concerning the developmental pattern. Extreme mouthparts and trunk processes in Cretaceous lacewing larvae (Haug *et al.*, 2019a, b, 2021) are clearly larval features, which become restructured and rebuilt during metamorphosis (Zimmermann *et al.*, 2019; Zhao *et al.*, 2020). The elongation of the prothorax in snakeflies is an adult character. It is unlikely that the elongate prothorax in a Cretaceous larva will be shortened during the formation of the pupa and re-elongated in the formation of the adult. Hence, the elongate prothorax in some of the fossil larvae is indeed best understood as an early occurrence of an



**FIGURE 3.** Comparison of larva → pupa transition in extant snakeflies (top) and early snakeflies (bottom); the (presumed) morphological changes happening during each moult are listed.

adult condition. For such an interpretation we need to assume that the larvae with such elongated prothorax regions are indeed in a late stage or even last stage.

As pointed out above, comparable occurrences have been discussed in modern forms in the frame of plasticity (metathetely). For the fossils it seems unlikely that the observed morphology is just such a case of plasticity. While there are now quite some snakefly larvae known in the fossil record (recently reviewed in Haug *et al.*, 2022), the numbers are still too low to expect such a relatively high number of plastic specimens, given the fact that in the modern fauna the phenomenon seems quite rare (Aspöck *et al.*, 2018). Yet, we could also consider that plasticity was much higher back in the Cretaceous. Independent if plastic or regular, the fossils indicate that already later stage larvae of snakeflies possessed the adult-type prothorax morphology.

#### Timing in holometabolan metamorphosis

At first look, holometabolan metamorphosis seems rather simple, in the sense of a one-step transformation. However, when looking closer, it becomes apparent that it is in fact at least a two-step pattern or can be even seen as several steps (see *e.g.*, discussion in Saltin *et al.*, 2016). Having several steps in a process leaves the possibility of variation in the overall process, *i.e.*, when and in which order certain changes can occur.

The change of interest in the case of the snakefly larvae is the elongation of the prothorax. For comparison, we can look at other structures that become elongated during the last-larva → pupa → adult transition. We can, for example, consider mouthpart elongation.

Scorpionflies as well as many beetles are good examples for holometabolans with an elongated anterior head region in the adults, including the mouthparts, and lacking such an elongation in the mouthparts in larvae, hence this elongation happens somewhere in the last-larva → pupa → adult transition. Although very different structures become elongated, in general the mechanical problem of fitting an elongate structure into a non-elongated one remains the same (Saltin *et al.*, 2016). We can therefore investigate when the elongation occurs.

In the case of several beetles, we can recognise that already the pupa has strongly elongated heads and associated structures, about as elongate as in the adult (*e.g.*, Oseto & Braness, 1979; May, 1987; Sousa *et al.*, 2004; Gosik, 2006, 2009, 2010; Gosik & Sprick, 2013; Stejskal *et al.*, 2014). The elongation is therefore already occurring inside the last larval stage, and with the moult to the pupa this part of the transformation is already complete.

The situation is very different in scorpionflies of the group *Panorpa*. Here pupae have clearly longer heads than larvae, but much shorter ones than adults. The elongation apparently occurs in two steps, a partial elongation is preformed inside the last larva, the final elongation is preformed inside the pupa (Saltin *et al.*, 2016). The timing is therefore quite different to the case in beetles.

With the elongate neck in snakeflies it appears that in the fossils the adult condition is already pre-formed at least inside the penultimate larva and therefore already externally expressed in the possible last larva. So far we have no reliably reconstructed ontogenetic sequences of fossil snakeflies (see discussion in Haug *et al.*, 2022) to

further narrow down a more exact timing. Yet, already this observation is quite telling.

### *Evolving metamorphosis*

The ground pattern of Euarthropoda seems characterised by a rather gradual (see Haug, 2019 on terminology) developmental pattern (e.g., Haug *et al.*, 2010a). This gradual pattern seems to be also part of the ground pattern of Crustacea *sensu lato* (Haug *et al.*, 2010a, b; Haug & Haug, 2015) of which Insecta is an ingroup (Zhang *et al.*, 2007). Also the ground pattern of Insecta is characterised by such a pattern (Haug *et al.*, 2015, 2016). With the occurrence of wings, strong selective pressures appear to have evolved a much more metamorphic pattern (Haug *et al.*, 2016) by postponing the formation of adult-specific structures such as wings (Haug *et al.*, 2016; Haug, 2020b). Due to this strong selection, only a single transitory stage is seen in all modern holometabolans, the pupa. This condition is at least comparable to the so-called megalopa stage in decapodan crustaceans, especially in reptantians, *i.e.*, lobsters and crab-like forms (Haug, 2020b). There is also only a single megalopa stage in (most) modern reptantians. Yet, from time to time so-called early-megalopa stages occur (Haug & Haug, 2013; Haug, 2020b). These are last-stage planktic larvae (called zoea) that already have some characters of megalopae. Also this aspect is quite comparable to the cases of plasticity in modern snakefly pupae.

When we look in the fossil record of megalopa-type larvae, we can recognise a different pattern. Modern spiny and slipper lobsters have a single megalopa-type larva (puerulus, resp. nisto). Yet, in fossil representatives of both lineages the developmental pattern was still more gradual, the transition from the planktic larva to the ground-dwelling juvenile involved several moults instead of just two (Haug & Haug, 2013, 2016; Haug *et al.*, 2013c, 2019c). Hence, the modern condition with only a single transitory stage has evolved at least three times independently once in slipper lobsters, once in spiny lobsters and at least once (more likely several times) in other lobsters and crab-like forms. To also mention even more extreme cases: there are also examples in crabs that seem to skip the megalopa stage, moulting directly from the last planktic larva into the crab juvenile (Haug, 2020b and references therein).

With this comparison and the data from the fossil snakefly larvae, we should consider that the ancestral developmental pattern of snakeflies was still more gradual than it is today, with last-stage larvae possibly already possessing some adult-type characters (Fig. 3 bottom). An evolutionary shifting of such characters is well understandable in the frame of heterochrony, which is an evolutionary shift in developmental timing. The pressure to reduce the number of transitory stages is likely coupled

to the evolution of the strong niche partitioning between adults and larvae.

### *Consequences: a more gradual type of ancestral development*

If we indeed consider that early snakeflies had a more gradual developmental pattern, where does this leave us? First, we need to accept that the larva → pupa transition we are used to from the extant fauna (Fig. 3 top) was likely much less strict in the past than we think. The last-stage larvae, or potentially also more general late-stage larvae, may have ancestrally been more pupa-like or even adult-like (Fig. 3 bottom). The strong selective pressures as seen in other lineages of Euarthropoda (Haug *et al.*, 2016; Haug, 2020b) have likely led to the postponement of these characters and a more pronounced metamorphosis in modern snakeflies.

We can furthermore assume that this ancestral, more gradual type of development is not a specialisation of Raphidioptera, but ancestrally retained from the ground pattern of Holometabola, as snakeflies are generally considered to retain many plesiomorphic traits. This interpretation would in consequence require that a similar transition from a more gradual type of development to a single pronounced transitory stage must have evolved not only in Raphidioptera, but also (at least) in Hymenoptera, Coleoptera, Megaloptera+Neuroptera and Mecoptera, hence a minimum of five times. While this may not seem parsimonious at first glance, we need to consider that we see similar evolutionary patterns elsewhere (Haug *et al.*, 2016; Haug, 2020b). Further specimens and a quantitative comparative frame will be necessary to further support, or reject, these assumptions.

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Supplementary materials:

**Suppl. Table 1.** Ratios of measured body dimensions and literature sources of fossil and extant snakeflies included in this study.

**Suppl. Text 1.** References in Suppl. Table 1 not cited in main manuscript.