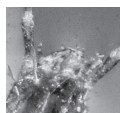# A 100 million-year-old snake-fly larva with an unusually large antenna

Joachim T. Haug, Patrick Müller & Carolin Haug

Snakeflies is the vernacular name of the representatives of the group Raphidioptera, an ingroup of Holometabola. The group Raphidioptera is rather species-poor, with only slightly more than 200 species. Snake-fly larvae are rather uniform in appearance and possess an elongate body; the trunk has similar appearing segments and lacks specialisations such as protruding structures. Such larvae are also known from the fossil record, namely from fossils preserved in amber that largely resemble extant forms. Here we report a new fossil snake-fly larva from Burmese amber. The specimen is very unusual in the morphology of the antennae. In extant snake-fly larvae, the antenna is quite short and thin, often inconspicuous at first sight on normal habitus photographs. In the new fossil, the antenna is much longer than the head and also appears very robust, comparable to the thoracic appendages. Together with another snake-fly larva previously described from Burmese amber, this find demonstrates that there were larval morphologies of snake-fly larvae back in the Cretaceous that are absent in the modern fauna. • Key words: Neuropterida, Raphidioptera, Cretaceous, Burmese amber, morphological diversity.

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Representatives of the insectan ingroup Holometabola are the dominating form of animal life on this planet. At least in terrestrial ecosystems they are unparalleled concerning biomass, species richness and individual richness. Most famous among the group Holometabola are the four 'hyperdiverse' ingroups: Hymenoptera (wasps, bees, ants), Coleoptera (beetles), Lepidoptera (moths and other butterflies) and Diptera (mosquitoes, midges and flies). Still, many other distinct groups within Holometabola also reach considerable species richness, such as Neuroptera, the group of lacewings, antlions and their kin, which count about 6,000 species (Tauber *et al.* 2003). Closely related to Neuroptera is the group Raphidioptera; together with Megaloptera, the three groups form Neuropterida (Aspöck & Aspöck 1999, 2007). Raphidioptera only counts at least 225 species in the modern fauna (Aspöck 2002, Aspöck & Aspöck 2009), but have been interpreted to have been much more diverse in the past (Aspöck & Aspöck 2009, Pérez-de la Fuente *et al.* 2012a).

Representatives of Raphidioptera, snake-flies, are quite easily identified as such. In their adult phase, the first trunk segment behind the head, the prothorax, is elongate, providing them with the appearance of an elongate "neck" (the German name 'Kamelhalsfliege', literally "camel-neck fly" is based on this morphology). Already the larvae possess this elongate prothorax. The mouth parts of the larvae are facing forward (prognathous; Gepp 1984). Also, the other trunk segments of the larvae are in general relatively long, resulting in a very elongate, slender and flexible appearance (the English name 'snake-fly' may well also refer to this aspect, yet mostly to the adult morphology). The snake-like appearance is further enhanced by the fact that the antennae are rather short and thin among extant larvae. On many backgrounds, the antennae are not easy to recognise at all, hence almost disappear (*e.g.* Aspöck & Aspöck 2009, their figs 7–9). Overall, most larvae of different snake-fly species appear quite similar concerning their morphology.

As has been pointed out previously, fossil snake flies appear to have been more diverse than modern forms (Aspöck & Aspöck 2009, Pérez-de la Fuente *et al.* 2012a). Given these data from adults we should also expect to see more morphological diversity among the larval forms. Here we report a snake-fly larva from Cretaceous Burmese amber with a rather unusual morphological feature, *i.e.* a very prominent, leg-sized antenna. We discuss the implications of this find for our understanding of the early evolution and diversification of snake flies.

Material and Methods

Material. – The single piece of amber investigated in this study comes from the *ca*. 99-million-year-old Burmese deposits, Hukawng Valley, Kachin State, Myanmar (Cruickshank & Ko 2003). It was bought by one of the authors (PM) and is currently part of his private collection under the repository number BUB 3069.

The original amber piece was first cut with a Dremel 3000. Afterwards, it was polished with wet sandpaper, first grade 200 and then subsequently grades 600, 1000 and 5000. Final polishing was performed with Sidol metal polish (Haug *et al.* 2018, 2019a).

Documentation methods. – The specimen was documented with composite imaging on a Keyence VHX-6000 microscope equipped with a 20–2000× objective under ring light and coaxial cross-polarised illumination (Haug *et al.* 2013a, 2018). Some images were recorded with different exposure times (high dynamic range, HDR; Haug *et al.* 2013b, 2018, 2019a).

Each image detail was documented as a stack, with the single images of the stack (frames) being recorded in different focal levels in the z-axis to overcome limitations in depth of field. The frames of each stack were fused to achieve an entirely sharp image detail (*e.g.* Haug *et al.* 2008, 2011; Kerp & Bomfleur 2011). This was done with the built-in software of the VHX-6000. Several adjacent stacks were recorded in x-y axis to overcome limitations in the field of view. All image details were stitched to a final panorama image with the help of the built-in software of the VHX-6000.

Drawings of the specimen and of comparative material were prepared in Adobe Illustrator CS2. Colour markings of specific structures was performed in Adobe Photoshop CS2.

Measurements. – Some aspects of the specimen were measured: the length of the antenna, the width of the head capsule, and the length of the head capsule. Also several specimens depicted in the literature were measured in this way. As not always a scale bar was provided we had to restrict comparisons to relative lengths. Ratios calculated were antenna length divided by head length and head width divided by head length. All ratios are listed in Tab. 1. The ratios were plotted against each other to visualise the exceptional morphology of the new fossil (*cf.* Haug *et al.* 2019b, c).

Description. – The description style follows the general approach laid out by Haug *et al.* (2012). Yet, for convenience of the reader the description is not presented as a table, but as running text. Insectan special terminology is provided together with a more general euarthropodan terminology to also provide non-expert readers access to the information and to facilitate future larger-scaled comparisons.

Results

Description of the specimen

General aspects. – The amber piece has only one inclusion (specimen) described below. The specimen is accessible from its latero-dorsal (Fig. 1A, B) and ventral side (Fig. 1C, D). Body elongate, organised distinctly into head and trunk (Figs 1A–D, 2A).

Anterior body, head. – Head forming enclosed, well sclerotised capsule. Head capsule dorso-ventrally flattened, rectangular in ventral view, with slightly bulging lateral sides. Longer than wide, more than 2x. With a distinct median moulting suture.

On the ocular segment antero-laterally on the head, a faint impression of sessile stemmata is present (Fig. 2D, E). Labrum anteriorly directed, triangular to trapezoidal in dorsal view (Fig. 2D, E).

Antennae (appendages of post-ocular segment 1; antennula in more neutral terminology) arising anteriorly from the head capsule (Fig. 2B–E). Insertion of antennae shortly behind the insertion of the mouth parts. Antenna very prominent, longer than head capsule. Consisting of five distinct elements (Fig. 2B, C). Proximal element short, exact proximal margin unclear. Slightly tapering distally, about as long as proximal width. Element 2 about twice as long as proximal element, slightly more slender. Element 3 slightly shorter than element 2, about as wide. Element 4 slightly longer than element 2, also slightly wider. Element 5 longer than element 4, proximally very narrow, widening to about the same diameter as element 4, gently tapering distally. No structures of post-ocular segment 2 (intercalary segment) externally visible.

All mouth parts strongly prognathous. Mandibles (appendages of post-ocular segment 3) largely covered by other mouth parts, slightly longer than labrum (Fig. 2D, E). Maxillae (appendages of post-ocular segment 4; maxillula in neutral terminology) only recognisable by their distal parts, forming a palp (endopod in neutral terminology). Palp slightly longer than mandibles; exact subdivision difficult to evaluate, most likely with 3 elements. Labium (conjoined appendages of post-ocular segment 5, maxillae in neutral terminology) only recognisable by more distal parts (palps). Labial palps slightly shorter than maxillary palps.

Several setae arising from the head capsule. Exact arrangement (chaetotaxy) difficult to discern, at least three setae in the more posterior region on each side, arranged in a row.

Figure 1. New fossil snake-fly larva from Burmese amber. All composite images under co-axial cross-polarised light illumination (A, C) and under unpolarised ring light illumination (B, D). A, B – latero-dorsal view; C, D – ventral view.

Posterior body/trunk, thorax and abdomen. – Anterior trunk (thorax) with three distinct segments (Figs 1, 2A). Thorax segment 1 (prothorax; post-ocular segment 6) dorsally strongly sclerotised (tergite, pronotum); slightly longer than head capsule, about as wide as head capsule. Dorso-laterally with few prominent setae. Postero-dorsally with a row of about 16 short setae.

Ventrally with a large prominent sclerite (sternite). Shorter than tergite, also significantly narrower. Few setae arising latero-ventrally in the posterior half of the segment, about four on each side. Ventro-laterally on each side with a jointed appendage (thoracic appendage, "leg").

Each appendage organised into five major elements. Most proximal element (coxa) cone-shaped. Proximal edge twice as wide as distal edge, proximal-distal dimension (length) about as long as distal edge wide. Element 2 (trochanter) tube-shaped, about as long as coxa, about as long as wide. Element 3 (femur) also roughly tube-shaped, about 3× as long as trochanter. Proximally slightly narrower than trochanter, further distally tapering until

Table 1. Measured ratios of the new fossil and other extinct and extant snake-fly larvae.

Specimen from	source	origin	figured in this contribution	head capsule width/head capsule length	antenna length/ head capsule length
new fossil	–	Burmese amber	1, 2, 3A	0.73	2.30
Engel 2002	fig. 4	Burmese amber	4A	0.42	1.45
Perrichot & Engel 2007	fig. 1	French amber	4D	0.96	0.50
Perrichot & Engel 2007	fig. 2	French amber	4B	0.87	0.58
Perrichot & Engel 2007	fig. 7	Lebanese amber	4E	0.71	0.76
Perrichot & Engel 2007	fig. 5	Burmese amber	4C	1.03	0.63
Grimaldi & Nascimbene 2010	fig. 8e	New Jersey amber	–	0.74	0.70
Gepp 1984	fig. 4a	extant	–	0.91	0.79
Gepp 1984	fig. 4b	extant	–	1.18	0.76
Gepp 1984	fig. 5a	extant	–	0.97	0.78
Nicoli Aldini *et al.* 2012	fig. 10	extant	–	0.86	0.59
Harmer & Shipley 1895	fig. 292	extant	–	0.92	0.99
Monserrat & Papenberg 2015	fig. 19	extant	–	0.93	0.54
Monserrat & Papenberg 2015	fig. 21	extant	–	0.79	0.51
Woglum & McGregor 1958	fig. 1	extant	–	0.92	0.82
Woglum & McGregor 1958	fig. 4	extant	–	0.96	0.88

about the middle along the proximal-distal axis, widening further distally. Distally also slightly narrower than trochanter. Element 4 (tibia) slightly longer than femur; proximally slightly narrower than femur, tapering distally. Element 5 (tarsus) shorter, about 50% of the length of the tibia. Proximally narrower than tibia, about 50%, widening distally. Distally carrying two hook-shaped pretarsal claws, about as long as tarsus wide. At least elements 3–5 carrying numerous prominent setae, exact chaetotaxy cannot be determined with certainty.

Thorax segment 2 (mesothorax; post-ocular segment 7) dorsally with a prominent sclerite (tergite, mesonotum); appears less strongly sclerotised than pronotum, indicated by lighter colour. Mesonotum shorter than pronotum, slightly longer than wide. With numerous prominent setae. Anteriorly with a row of longer setae, estimated about ten setae. Posteriorly also with a row of about ten setae but these are rather short, about half as long as those on the anterior row. Lateral edges each with about three longer setae. Ventrally with a sclerite (sternite), about as long as tergite, slightly narrower. Lateral side of body with slightly laterally bulging membrane, also visible dorsally and, more so, posteriorly. Few setae arising latero-ventrally, about nine on each side. Ventro-laterally on each side with an appendage. Appendage sub-similar to that of preceding appendage (Fig. 2F).

Thorax segment 3 (metathorax; post-ocular segment 8) dorsally with a prominent sclerite (tergite, metanotum);

sclerotisation similar to mesonotum, about as wide, but shorter than mesonotum. Similar to mesonotum with a row of anterior setae. Posteriorly also with a row of setae, but with fewer setae than on mesonotum, setae slightly longer than the anterior ones. Along the lateral side apparently only two setae on each side. Lateral side of body with slightly laterally bulging membrane, also visible dorsally, different from that of mesothorax along the entire length. Few setae arising latero-ventrally in the posterior half of the segment, about four on each side. Ventro-laterally on each side with an appendage. Appendage sub-similar to that of preceding appendage.

Posterior trunk, abdomen (not corresponding to abdomen in other representatives of Crustacea sensu lato) with ten visible units. Anterior nine units corresponding to abdominal segments 1–9 (post-ocular segments 9–17). Abdominal segment 1 shorter than preceding segment, about 50%, about as wide as preceding segment. Dorsally with a prominent sclerite (tergite), about as wide as that of the preceding segment. Anterior row of about ten long setae, posterior row of fewer (six?), but longer setae. Few setae arising latero-ventrally, about three on each side. Ventrally with a large sclerite (sternite), sub-similar in shape to tergite. Laterally with strongly bulging membranous area.

Abdominal segments 2–8 sub-similar in overall morphology, mainly differing in dimensions. Abdominal segments 2–4 consecutively longer, abdominal segment 4
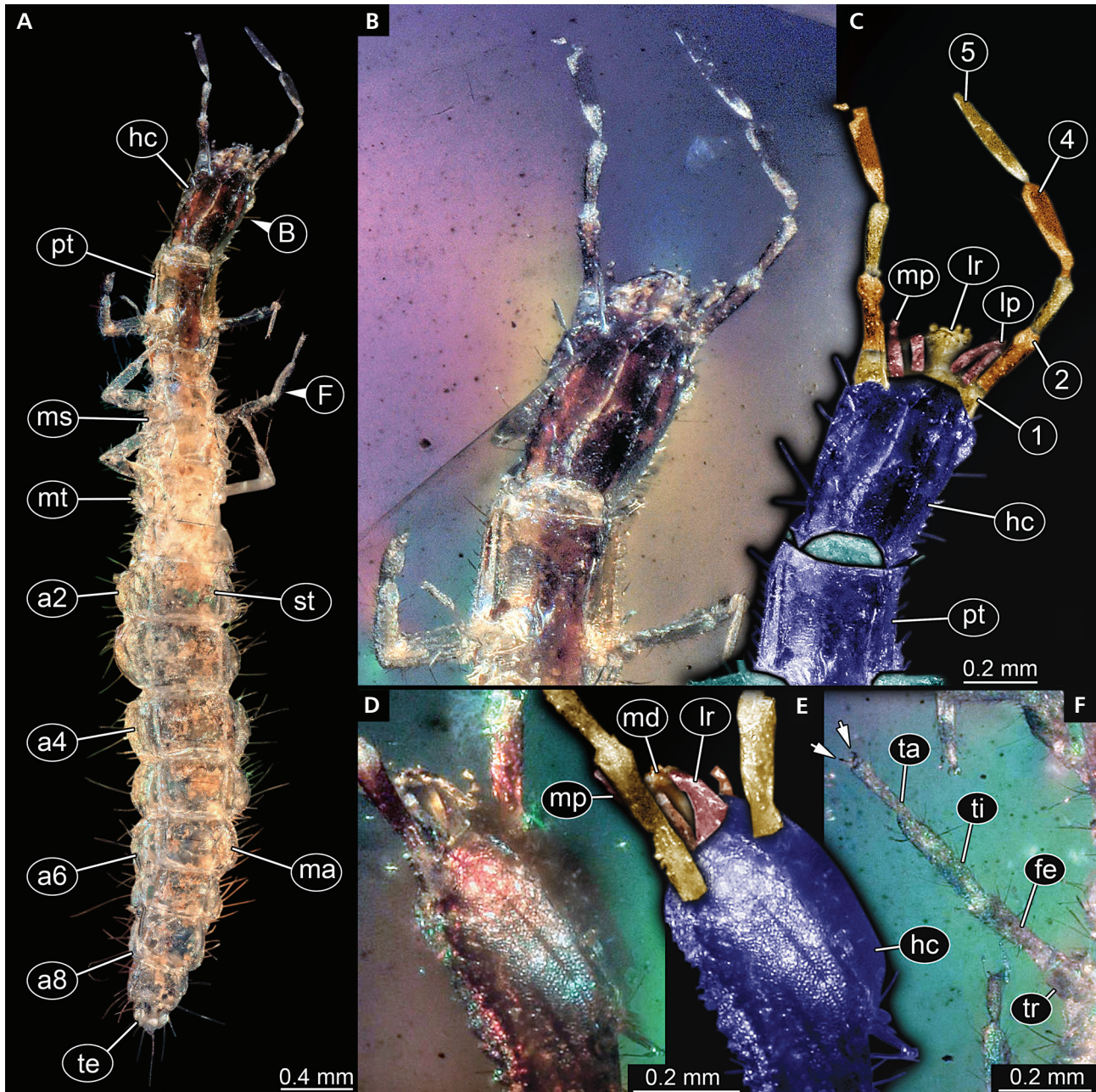
Figure 2. New fossil snake-fly larva from Burmese amber, continued; A – same view as in 1C, amber matrix digitally removed; B–F – close-ups under co-axial cross-polarised light illumination; B–E – head, B – ventral view, C – colour-marked version of B, D – latero-dorsal view, E – colour-marked version of D, F – thoracic appendage. Abbreviations: 1–5 – antenna elements 1–5; a2–a8 – abdominal segments 2–8; fe – femur; hc – head capsule; lp – labial palp; lr – labrum; ma – membranous area; md – mandible; mp – maxillary palp; ms – mesothorax; mt – metathorax; pt – prothorax; st – sternite; ta – tarsus; te – trunk end; ti – tibia; tr – trochanter.

slightly more than 2× longer and about 1.6× wider than abdominal segment 1. Most of the width difference is due to a wider membranous area, as sclerites remain more or less constant in width. Chaetotaxy appears sub-similar between all abdominal segments. Abdominal segments consecutively shorter and narrower, the latter mostly due to a narrower membranous area. Abdominal segment 8 about 0.6× of the length of abdominal segment 4, about

0.75× of the width. Abdominal segment 9 also sub-similar to preceding segment but without prominent bulging membranous area, about as wide as sclerite of preceding segment.

Trunk end (most likely conjoined abdominal segments 10 and 11, post-ocular segments 18 and 19) shorter than abdominal segment 9, also narrower, with an anterior row of long setae, and about four longer setae posteriorly.
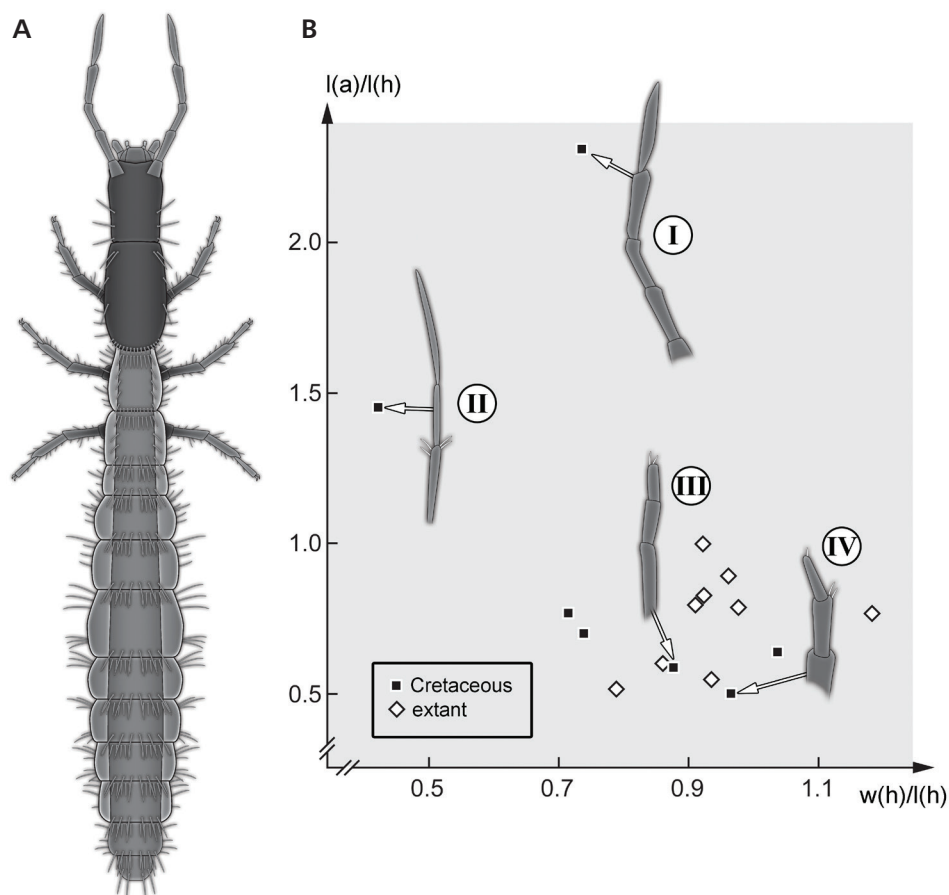
Figure 3. Comparison of new fossil with other snake-fly larvae. A – simplified restoration of the new snake-fly larva in dorsal view; B – scatter plot; l(a) = length of antenna; l(h) = length of head capsule; w(h) = width of head capsule. I–IV – antennae of fossil snake-fly larvae; I – Burmese larva described herein; II – specimen from Engel (2002); III, IV – specimens from Perrichot & Engel (2007), III – their fig. 2 (also in our Fig. 4B), IV – their fig. 1 (also in our Fig. 4D).

Description of the scatter plot

The scatter plot (Fig. 3B) depicts the principle shape of the head along the x-axis (width divided by length of head capsule) and the relative length of the antenna along the y-axis (length of antenna divided by length of head capsule). Extant larval specimens of Raphidioptera plot relative close together. Head shape varies between a width/length ratio of about 0.8 up to about 1.2. The relative antenna length of the extant forms varies from about 0.5 to 1.0. Many of the Cretaceous fossil specimens show comparable values (*cf.* Fig. 4B–F).

Yet, two fossil specimens plot in a very eccentric position. One is a specimen depicted in Engel (2002; see also Fig. 4A), preserved in Burmese amber. The specimen has a very narrow head, the ratio is 0.42, much more slender than in any extant specimen. Also the antenna is unusually long with a ratio of 1.45.

Also the here described new fossil larva is unusual (Fig. 3A). With a head shape ratio of 0.73 the head is only slightly narrower than in extant forms and much more "normal" in this aspect than the specimen reported by Engel (2002). Yet, the relative length of the antenna, a ratio of 2.3, is extreme and unparalleled.

Discussion

Systematic interpretation of the new larva

The specimen can easily be identified as a larval (see Haug 2020 for challenges of the term) representative of Raphidioptera (*cf.* Gepp 1984), based on numerous characters. The body is very elongate. The mouth parts are strictly prognathous, directed anteriorly, yet do not form prominent stylets as in larvae of Neuroptera (*e.g.* Gepp 1984; Aspöck *et al.* 2001, 2012a; Beutel *et al.* 2010). Head and prothorax are elongate and are well sclerotised. Further posterior trunk segments are less well sclerotised, but with distinct rectangular sclerites surrounded by softer membranous, bulging areas laterally. There are no abdominal appendages or leglets.

It is unfortunately not possible to further identify the specimen. To differentiate between the two major ingroups of Raphidioptera, Inocelliidae and Raphidiidae, it is necessary to either have information about the stemmata or about colour patterns of the trunk (*e.g.* Gepp 1984). Both aspects cannot be evaluated in the fossil specimen. The eyes are not accessible in a way to allow a reliable count of the number of stemmata, and colour patterns on the trunk

seem not to be preserved. Furthermore, we cannot exclude that the larva is a representative of a now extinct ingroup of Raphidioptera such as Mesoraphidiidae (*e.g.* Pérez-de la Fuente *et al.* 2012a). Identifying fossil holometabolan larvae as representatives of a species or even higher systematic group is often challenging, as many of the characters of these groups are based on the adults. Linking holometabolan larvae to their corresponding adults, hence identifying the species of a larva, is only rarely possible in fossils, even if well preserved in amber (discussion in Baranov *et al.* 2019). Ideally, this requires a direct preservation of adult and offspring together (*cf.* Wichard *et al.* 2009 for Nevrorthidae), for example in brood-caring

species, or specimens in the act of moulting with access to larval and pupal or pupal and adult morphology. Still, narrowing down the relationships of the new larva will require further finding.

It appears currently accepted to erect new species based on fossil immature specimens, especially in Neuropterida (*e.g.* MacLeod 1970; Badano *et al.* 2018; Pérez-de la Fuente *et al.* 2018, 2019) but also in other ingroups of Insecta (*e.g.* Grimaldi 1997, 2003; Grimaldi & Ross 2004; Aristov *et al.* 2006; Vršanský 2009; Delclòs *et al.*2016). It is in our view well founded to erect new species based on larvae if it is possible to provide an applicable differential diagnosis. Yet, under certain circumstances there is always
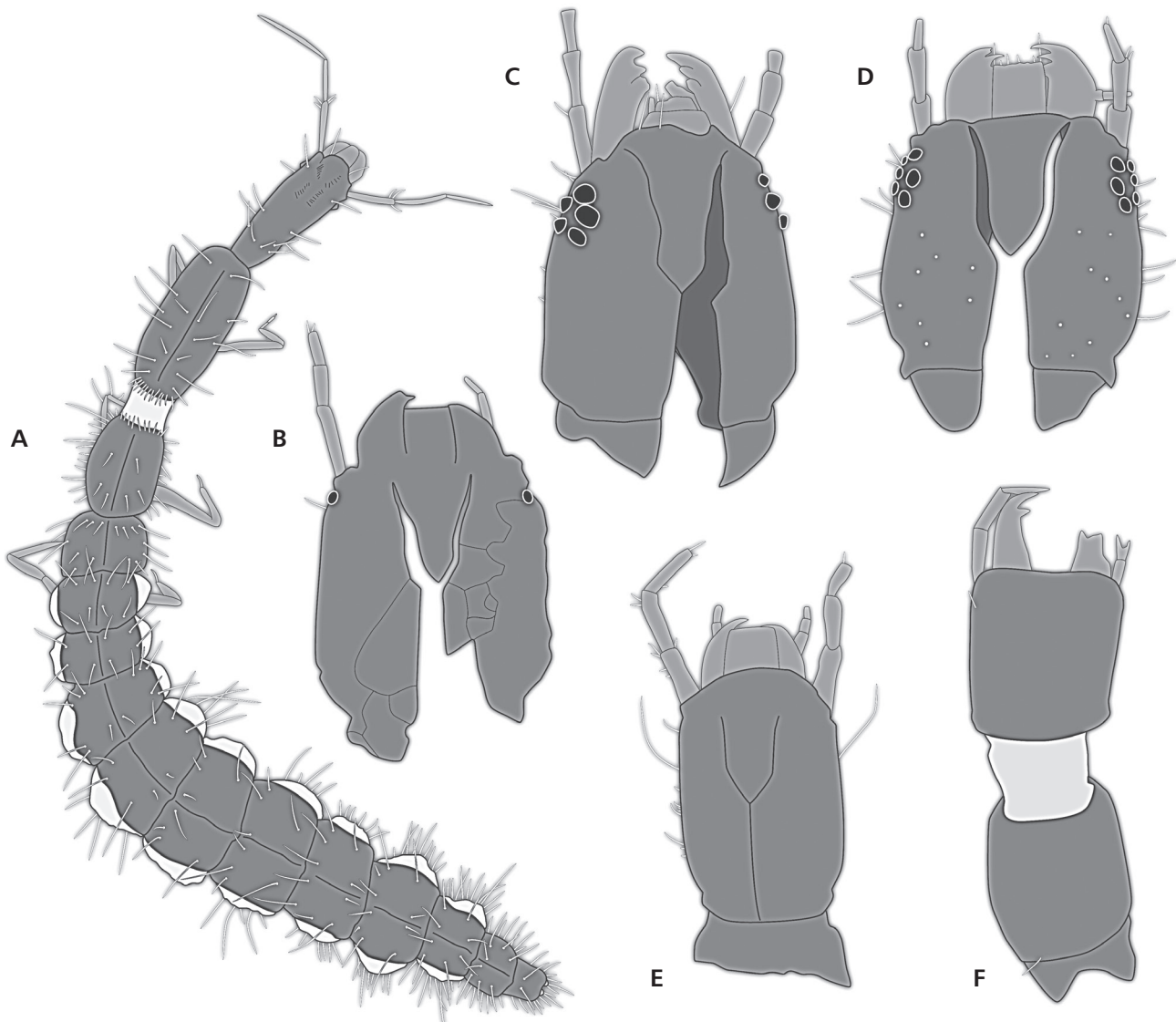

Figure 4. Simplified drawings of Cretaceous snake-fly larvae based on literature; A – from Engel (2002); B–E – from Perrichot & Engel (2007), B – their fig. 2, C – their fig. 5, D – their fig. 1, E – their fig. 7, F – their fig. 6.

the danger of creating synonyms. There have been quite some species described from Burmese amber based on adults (*e.g.* Engel 2002, Liu *et al.* 2016), hence there is the realistic chance that the adult corresponding to the here reported larva is already known and has been formally described. We therefore prefer not to erect a new species for the new larva.

Why the new specimen is unusual

Despite the systematic uncertainties, the new fossil is quite informative concerning the morphological diversity of snake flies. Snake-fly larvae are well known as fossils preserved in amber (*e.g.* Hagen 1854; Weidner 1958; Weitschat & Wichard 1998, 2002). Also in Cretaceous ambers such larvae have been reported, for example from French amber, as well as from amber from New Jersey, Myanmar and Lebanon (Engel 2002, Perrichot & Engel 2007, Grimaldi & Nascimbene 2010; see also Fig. 4). Yet, most of these larvae appear very similar to modern-day snake-fly larvae in overall habitus, also recognisable by the plotted ratios (Fig. 3B).

The new larva is significantly different from modern larvae at least in one aspect: the antennae in all extant and most fossil specimens are very small and thin (*cf.* Harmer & Shipley 1895, Woglum & McGregor 1958, Gepp 1984, Aspöck & Aspöck 2007, Beutel & Ge 2008, Nicoli Aldini *et al.* 2012, Monserrat & Papenberg 2015), almost indistinct (*cf.* Aspöck & Aspöck 2009, Aspöck *et al.* 2012b). This is the case for most fossil specimens (Fig. 4B–E). In the new fossil larva, however, the antennae are very prominent.

The ratio length of the antennae/head length, l(a)/l(h), is more than twice in the fossil than in extant and most other fossil specimens (Perrichot & Engel 2007, Grimaldi & Nascimbene 2010; see also Fig. 4B–F). An exception is a fossil larva from Burmese amber described by Engel (2002; see also Fig. 4A). In this specimen, the antennae are distinctly larger than in extant specimens (and most fossils), but far from the condition in the new fossil. Additionally, the antennae in the new larva are more robust, *i.e.* larger in diameter than in modern forms and most fossils, including the one described in Engel (2002). In the new larva, the antenna has a diameter similar to that of the thoracic appendages.

Is such a morphology part of the ground pattern of Raphidioptera?

As the new larva is of Cretaceous age, one could get the impression that the large-sized antennae is an old feature that might be interpreted as plesiomorphic, *i.e.*

an ancestral feature. Yet, this is unlikely to be the case. Other Cretaceous snake-fly larvae possess antennae very similar to those of modern day snake-fly larvae (Perrichot & Engel 2007, Grimaldi & Nascimbene 2010).

We can furthermore consider outgroups. In many larvae of Neuroptera (*e.g.* Gurney 1947; Riek 1970; Henry 1976; Mansell 1983; Gepp 1984; New 1989, 1992; Hoffman & Brushwein 1992; Tauber *et al.* 2003; Grebennikov 2004; Stürzer & Gepp 2004) and Megaloptera (*e.g.* Gepp 1984, Wachmann & Saure 1997, Contreras-Ramos & Harris 1998, New 2004, Beutel & Friedrich 2008, Clavier *et al.* 2010, Monserrat 2014) the antennae are also quite small, at least many are short and also thin (*cf.* Haug *et al.* 2019b: fig. 4). The morphology of the antenna in the ground pattern of Neuropterida is therefore more comparable to the condition in modern snake-fly larvae than to that in the new larva.

In many larval forms of Coleoptera, which are phylogenetically close to Neuropterida, the antennae are not as thin as in modern larvae of Raphidioptera, yet also many coleopteran larvae antennae are rather short and not significantly longer than the head. Even if so, the antennae are distinctly thinner than the thoracic appendages (legs). The condition of the antennae in the Cretaceous snake-fly larva described in Engel (2002) as well as in the new specimen seems most likely to represent an apomorphic, derived condition. This could also indicate a closer relationship between the two. What the specialised antenna could have been used for remains entirely unclear, as there are no counterparts among extant snake-fly larvae.

Diversity

Two Cretaceous fossils, the one reported by Engel (2002) and, particularly, the new larva described herein, clearly demonstrate that 100 million years ago there were snake-fly larvae that distinctly differed in morphology from modern day forms, but co-occurring with larvae resembling modern forms. Modern day snake-fly larvae and many fossil forms appear very uniform.

The diversity of snake flies has been suggested to have been larger in the past, considering adults. The new larva reinforces the notion that larval raphidiopterans were more diverse 100 million years ago (Aspöck & Aspöck 2009, Pérez-de la Fuente *et al.* 2012a).

Yet, the now extinct forms fall into two different categories: 1) Forms retaining numerous plesiomorphies (Badano *et al.* 2018, Hörnig *et al.* 2018). Such forms are immediately to be expected. 2) Apomorphic, *i.e.* highly specialised forms (Pérez-de la Fuente *et al.* 2012b, 2016, 2018, 2019; Liu *et al.* 2018; Haug *et al.* 2019a–c). Category 1 morphologies can be easily expected based on knowledge of modern forms, but not those of category 2.

Conclusion

While in some cases it may be easy to recognise the morphology of a new fossil as something unusual or special, this may not always be immediately the case. Taking simple measurements as performed here is a reliable tool to make morphological patterns evident (see also Haug *et al.* 2019b, c). More generally, recognising diversity of larval forms will require the consideration of morphology, using quantitative methodology as well.

Acknowledgements

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