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Cretaceous chimera – an unusual 100-million-year old neuropteran larva from the "experimental phase" of insect evolution

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A b s t r a c t

Neuropteran insects possess very distinct larval stages with prominent paired piercing sucking stylets and a specialised sclerite, the neck, between the head and the first thoracic segment. Some larva of Crocinae (Nemopteridae) are further specialised by possessing a very elongated neck region. The fossil record has already provided a large variety of neuropteran larvae, yet so far a truly long-necked form was missing. Here we report such a fossil larva, with an elongated neck region from 100-million-year old Burmese amber. The specimen possesses a unique combination of characters unknown in any modern or fossil neuropteran larva. Besides the elongated neck it possesses three distinct teeth in the stylets, a character mostly known in larval forms of owl flies (Ascalaphidae) and ant lions (Myrmeleontidae), and a slender trunk as known in aphid lions (larvae of the groups Chrysopidae and Hemerobiidae). We must therefore conclude that the fossil species must have evolved certain characters in convergence to other lineages of Neuroptera resulting in a chimera-like morphology. We discuss possible interpretations of character evolution of larvae within Neuroptera.

K e y w o r d s : Crocinae; Neuroptera; Myrmeleontiformia; convergent evolution; Burmese amber.

1. Introduction

Our modern terrestrial world is dominated by smaller-sized animals of the group Insecta, more precisely, of Holometabola. These animals dominate our terrestrial ecosystem, concerning number of species, number of individuals and biomass, but also ecological roles. Holometabola includes the "big four" groups: Hymenoptera (wasps, ants, bees), Coleoptera (beetles, weevils and allied) Lepidoptera (moths and other butterflies) and Diptera (mosquitoes, midges, flies), but also some other smaller groups such as Neuroptera – lacewings and their relatives.

In general, among holometabolans, but especially among neuropterans, most of the ecological impact and diversity is in fact not represented by the adult forms, but by the larvae. Holometabolan individuals spend quite some time, in many groups in fact most of their life, in their larval phase. Also, the ecology of the larvae is usually very different from that of the adults, a possible clue for understanding the evolutionary success of the Holometabola.

Most neuropteran larvae are fierce predators that are able to inject venom into their prey with their specialised mouthparts: each mandible and part of each maxilla form a sucking tube, providing the larva with a pair of injecting and sucking stylets (e.g., Aspöck et al. 2001, 2012; Beutel et al. 2010). Larvae of the different ingroups of Neuroptera have become specialised for quite different hunting strategies. Some larvae are aquatic or semi-aquatic and are presumed to hunt other aquatic insects or other small non-vertebrates (larvae of Nevrorthidae, Osmylidae; e.g., New 2004; Matsuno & Yoshitomi 2016) or parasitize freshwater sponges (Sisyridae; e.g., Aspöck et al. 2012). Most terrestrial forms are active hunters and therefore in some cases quite beneficial for humans, e.g., in terms of agriculture (e.g., McEwen et al. 2007). Important in this case are, for example, aphid lions, the larvae of species of the groups Chrysopidae and Hemerobiidae.

Myrmeleontiformia – with its five major ingroups Myrmeleontidae, Ascalaphidae, Nymphidae, Nemopteridae, Psychopsidae (see Aspöck et al. 2012 for details) – is a major subgroup of Neuroptera with rather large and sometimes aberrant-appearing larvae. The most widespread known type of larva of this group is most likely that of the antlions. Larvae of antlions (Myrmeleontidae) and their closer relatives, the owlflies (Ascalaphidae, sister group to Myrmeleontidae) and split-footed lacewings (Nymphidae, sister group to Ascalaphidae + Myrmeleontidae), are quite fierce, with rather wide bodies and large prominent stylets that are additionally armed with one to three teeth each (e.g., Gepp 1984; New 1992). Yet, the larval forms of thread-winged lacewings (Nemopteridae: Crocinae) appear even more weird. They strongly resemble the fierce antlions, but additionally are unique in possessing an astonishingly long neck region separating the head distinctly from the trunk (e.g., Pierre 1952; Monserrat 1983, 2008; recent summary of most extreme forms in Herrera-Flórez et al. in review). It has been proposed that this long neck is beneficial for their overall hunting success (Aspöck & Aspöck 2007).

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The fossil record has already provided quite a number of neuropteran larvae. Especially in recent years some quite astonishing and unexpected forms have appeared (e.g., Pérez-de la Fuente et al. 2012, 2016, 2018, early view; Wang et al. 2016; Badano et al. 2018). Even smaller larvae with rather unusual life strategies have been found as fossils (e.g., Wichard et al. 2009; Ohl 2011; Haug et al. 2018). Despite this rich and diverse fossil record of neuropteran larvae, we so far lack any long-necked form as seen in Crocinae. The only exception showing a moderately long neck was reported by Badano et al. (2018: fig. 3d). Here we report the first fossil larva with a long neck comparable to that of larvae of Crocinae, discuss its possible phylogenetic position within Neuroptera and its impact on our understanding of character evolution within Myrmeleontiformia and Neuroptera.

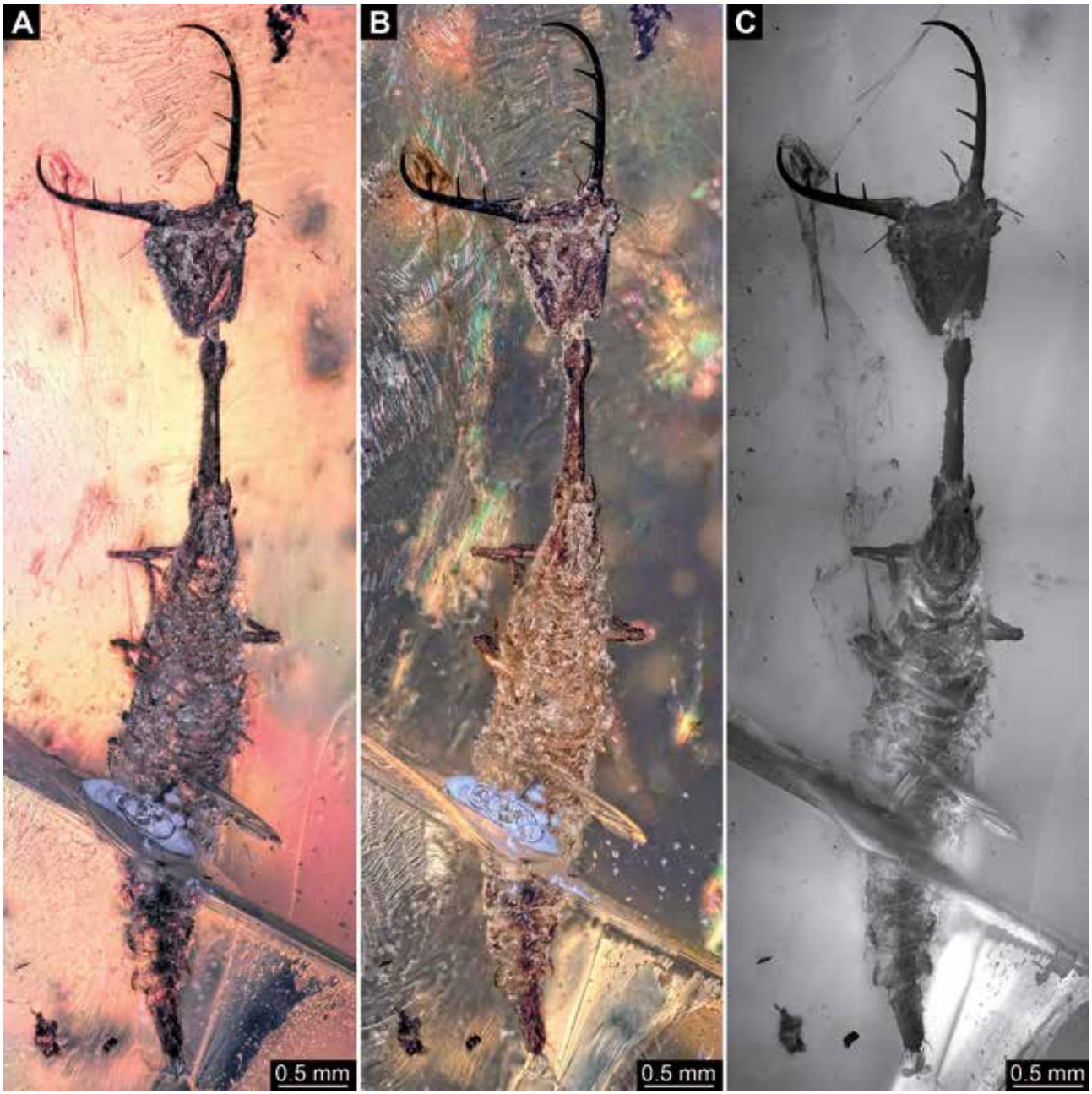


Fig. 1. Long-necked neuropteran larva, specimen SMNS BU-340 (BUB 3061), documented under different light settings; **A**, **B**: white light conditions, HDR; **A**: ring illumination; **B**: coaxial cross-polarised illumination; **C**: autofluorescence illumination.

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2. Material and methods

A single piece of amber comes from the about 100-million-year-old Burmese deposits, Hukawng Valley, Kachin State, Myanmar (Cruickshank & Ko 2003). It has been bought by one of the authors (PM), was part of his private collection under the repository number BUB 3061, and is now deposited in the Staatliches Museum für Naturkunde Stuttgart under SMNS BU-340.

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.

The specimen was documented with composite imaging under different light conditions. Images under white light conditions were recorded with a Keyence VHX-6000 microscope equipped with a 20–2000× objective, either under ring illumination (Fig. 1A) or under coaxial cross-polarised illumination (Fig. 1B). To achieve an optimal result, some images were recorded with different exposure times (high dynamic range, HDR). Images under fluorescence light were recorded on a Keyence BZ-9000 inverse microscope, with a TRITC filter cube (excitation wavelength: 543 nm; Fig. 1C) (e.g., Haug et al. 2009, 2011).

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. This was done either with the built-in software of the VHX-6000 or with the freely available software CombineZP. 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, or with Adobe Photoshop CS3 or Elements 11 (e.g., Haug et al. 2008; Kerp & Bomfleur 2011).

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.

3. Description of the specimen

3.1. General aspects

The amber piece has only one inclusion (specimen) described below. The amber piece includes bubbles of different size, mostly on the right side of the included specimen, when viewed from dorsally. The area surrounding the specimen contains some bubbles, most of them of medium size. The amber piece seems to be broken at the level of the middle part of the abdomen of the species, even though, the specimen looks complete (Fig. 1). The specimen is only accessible from the dorsal side.

3.2. Anterior body: head and neck

Body elongate, in total ca. 6.2 mm long (without stylets), organised distinctly into head and trunk (Figs. 1A–C, 2A). Head forming capsule. Base of the head capsule (close to the following structure, the neck or cervix) narrower than remaining head. Posterior part of the head capsule without pronounced temples, i.e. not having an angular appearance (Fig. 2C).

Head capsule ca. 0.9 mm long, dorso-ventrally flattened, trapezoidal in dorsal view, longer than wide, reaching maximum width far anteriorly, and gently tapering posteriorly; anterior rim more than 2x as wide as posterior rim; lateral sides more than 2x as long as posterior rim.

On the ocular segment antero-laterally on the head, groups with 5(?) sessile stemmata on each side apparent (Fig. 2C). Labrum appears continuous with clypeus; anterior clypeo-labral edge not forming a rostrum, i.e. not drawn out anteriorly.

Antennae (appendages of post-ocular segment 1) arising antero-laterally from the head capsule. Insertion of antenna situated just below the base of the forward oriented mouthparts. Antenna clearly shorter than the mouthparts, with the first element (scape?) tubular, wider than following element (exact subdivision difficult to assess, estimated between 10 and 15 antennomeres). There seems to be no terminal filament.

No structures of post-ocular segment 2 (intercalary segment) externally visible. Mandibles and maxillae (appendages of post-ocular segments 3 and 4) forming a pair of prominent stylets (Fig. 2B, C). Stylets well separated at base; complete, slender, relatively thin and strongly sclerotized; with ca. 1.23 mm length (direct distance from insertion to tip) clearly longer than head capsule; strongly inward curved (from approximately the apical 1/3 of it) tapering distally. Each mandibular part of the stylets bears three teeth, which are longer than stylet width. Stylets arising functionally anteriorly (prognath). Other aspect of the maxillae, e.g. subdivision, difficult to access, distal part of maxilla (maxillary palps) absent.

Appendages of post-ocular segment 5 conjoined to form labium. No median endites (glossa, paraglossa) developed. Distally, functionally anteriorly with a pair of palps (labial palps). The labial palps are situated just below the inner margin of the stylets (Fig. 2B, C). Each palp with three tubular elements (palpomeres). Palp slightly thicker than antenna and clearly longer than stylet width. First element (palpomere) partly concealed by head capsule and stylet. Second element elongate, about 6x as long as basal width. Third element about the same length of the second

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one; first widening until 50% of the entire length, then gradually tapering towards the apex. About 6x as long as basal width. Only the right labial palp present, thin and less than one third of the length of the stylets.

Distinct collar-like membranous area between head capsule and neck, well recognizable and clearly narrower than neck (Fig. 2C). Neck region (cervix), tubular (cylindrical), elongate, slender; with ca. 1 mm length longer than the head capsule, narrower in the posterior margin than in the anterior margin (close to the head) which has a curved shape. Neck articulating to the trunk.

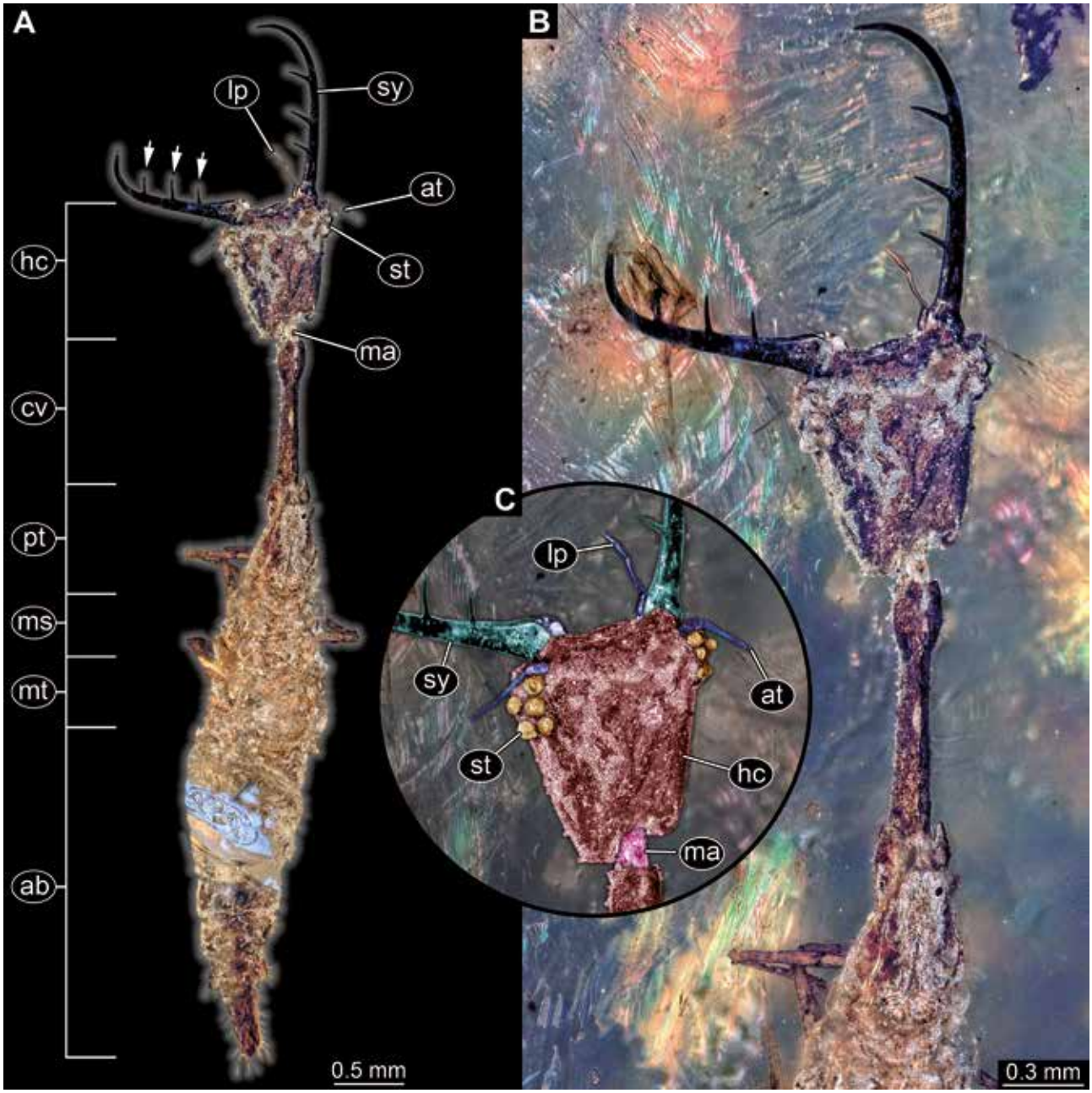


Fig. 2. Long-necked neuropteran larva, specimen SMNS BU-340 (BUB 3061) under coaxial cross-polarised illumination with HDR; **A**: interpretative image of Fig. 1B with labelling of body parts; arrows point to teeth in the stylet; **B**: close-up of head and neck area; **C**: close-up of head with colour markings of different structures. Abbreviations: ab = abdomen; at = antenna; cv = cervix; hc = head capsule; lb = labial palp; ma = membraneous area; ms = mesothorax; mt = metathorax; pt = prothorax; st = stemmata; sy = stylet.

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3.3. Posterior body/trunk: thorax and abdomen

Trunk surface with numerous smaller setae, barely visible. Exact arrangement only apparent in the further posterior region (see below). Anterior trunk (thorax) with three distinct segments.

Prothorax with two antero-lateral processes that surround the insertion of the cervix (Fig. 1C). Prothorax almost triangular in dorsal view, quite long in anterior-posterior axis. Posterior margin of prothorax more than 3x as wide as anterior margin. Maximum width of meso- and metathorax larger than that of prothorax. Exact borders of meso- and metathorax indistinct. Meso- and metathorax very uniformly shaped, in the middle region slightly broader than further anterior and posterior. Thoracic segments lacking dorsal thoracic processes. Mesothoracic spiracle sessile (i.e. not elevated; Fig. 1B). Three pairs of walking legs of similar size present and complete, yet largely obscured by the body. Exact lengths of the individual elements not measurable. Two major elements (femur and tibia) partly visible; appear elongate and slender, cylindrical and bearing numerous short setae. Pretarsi only recognisable as a pair of inconspicuous claws, yet only visible under very low angle of view.

Posterior trunk (abdomen) with indistinct borders between abdominal segments (Fig. 1). Recognition of individual segments furthermore complicated by the fact that at least the anterior segments seem to possess additional folds in their dorsal surfaces (tergites) that might be misunderstood as joints between tergites. Also, a crack in the amber conceals details of the middle abdominal segments. Hence, only approximately seven segments visible, while there are ten to be expected (the last one in fact representing two conjoined segments, 10+11). Anterior segments with the same width as the maximum thorax width.

Last two abdominal segments (most likely segment 9 and terminal end with segments 10+11 conjoined) clearly narrower than the rest. Penultimate abdominal segment (most likely 9) with two lobe-like postero-lateral extensions carrying setae (Figs. 1, 2A). At least five setae on each side; most posterior seta longest of the series. Last abdominal segment (most likely 10+11) elongated, almost rectangular shaped, with posterior margin narrower. Carrying numerous setae; exact number difficult to assess, at least nine on each side; a pair of longer setae at postero-lateral corner on each side. Terminal end of rectangular shape additionally drawn out into lobe-like extension, yet exact shape of this extension unclear as concealed under a bubble in the amber (Fig. 1). Abdomen overall lacking prominent abdominal processes.

4. Discussion

4.1. Systematic interpretation: step 1

The overall body organisation easily identifies the fossil as a representative of Insecta (Hexapoda in Anglo-American tradition). The organisation of the eyes, i.e. the indication that these are stemmata, provides a reasonable criterion for identifying the specimen as the larval stage of a holometabolan species. The prominent mouthparts apparently forming stylets, the overall arrangement of the head structures, and the distinct sclerotized neck between head and prothorax clearly identify the fossil as the larva of a neuropteran. Within Neuroptera at least 17 distinct different larval forms can be recognised that relate to traditional "family"-grouping (although some authors also distinguish more; recent simplified comparison in Haug et al. in review). Yet, fossil larval forms of neuropterans seem to often possess characters that do not easily fit into these 17 categories (e.g., Badano et al. 2018; Haug et al. in review). The same applies to the new fossil here.

4.2. Prominent characters of the fossil

Three characters are very prominent in the fossil. Astonishing, however, is not their mere presence, but the combination of all these three in a single specimen.

4.2.1. Long neck

The new larva has a long, slender neck, almost 1.5 times as long as the longest tergite, the pronotum, and about 5 times as long as wide. This is so far the relatively longest neck in a fossil neuropteran larva.

An elongated slender neck region is in modern neuropterans only known in larvae of the group Crocinae (thread-winged lacewings; see references above). In other larvae the neck region is not distinctly longer than any of the thoracic tergites and not distinctly longer than wide. In thread-winged lacewing larvae, especially in stages two and three, the neck can be several times as long as wide and also several times as long as a tergite (see Herrera-Flórez et al. in review for a recent summary). The only other neuropteran ingroups that have larvae with a quite prominent neck are *Nevrorthus* and *Austroneurorthus* (Nevrorthidae). These elongate, almost worm-like, aquatic larvae have a neck that is slightly longer than the pronotum and more than twice as long as wide (e.g., Zwick 1967; Rieck 1970; Malicky 1984; Beutel et al. 2010). Although such a neck is quite long, even the neck of first stage larvae of the group Crocinae, which have in comparison the shortest necks, can be distinctly longer in relation to the

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overall body length. The fossil described here, therefore, possesses a neck as only known from modern-day larvae of the group Crocinae.

Yet, it is in fact not only the neck that is elongated in larvae of the group Crocinae. Usually also the prothorax is elongated, slender and has the thoracic appendages inserting far posterior. The elongated neck and the elongated prothorax together form an even longer 'functional neck' (see Herrera-Flórez et al. in review). This seems to apply for the new fossil as well.

4.2.2. Prominent stylets with three teeth

The new larva has large curved mandibular-maxillary stylets, each equipped with three prominent teeth. Prominent teeth are known in extant larvae of Nymphidae (split-footed lacewings), but which possess only one tooth each, and especially of Ascalaphidae (owlflies) and Myrmeleontidae (antlions) that mostly have three prominent teeth on each stylet (see references above). Extant larvae of the other ingroups of Myrmeleontiformia, Psychopsidae (silky lacewings) and Nemopteridae (including Nemopterinae, spoon-winged lacewings, and Crocinae, thread-winged lacewings) generally seem to lack such prominent teeth (but see further below). The fossil larva therefore possesses stylets that are mainly known for modern larvae of Ascalaphidae and Myrmeleontidae.

4.2.3. Slender trunk region

The new larva has a rather slender trunk region. Most larvae of the group Myrmeleontiformia have a rather broad trunk. In extreme cases it can appear almost circular as in some larvae of the groups Nymphidae, Ascalaphidae or, when ignoring the elongated neck, Crocinae. Yet, besides these extremes, the trunk of larvae of Myrmeleontiformia in general is quite wide. Larvae of Nevrorthidae (possible sistergroup to all remaining neuropterans) are quite the opposite: they are extremely slender, elongate and almost worm-shaped (e.g., Zwick 1967; Rieck 1970; Malicky 1984). Larvae of Hemerobiiformia (or in all remaining groups, as Hemerobiiformia might not be monophyletic, see Aspöck et al. 2012) are somewhere in-between (e.g., New 1992; Tauber et al. 2003); besides the grub-like larval forms of Ithonidae, Polystoechotidae and larval stages two and three of Mantispidae (e.g., Gepp 1984; Redborg & MacLeod 1985; Grebennikov 2004). They are not elongate worm-shaped, but still rather slender in most cases. This is quite similar to the shape in the fossil. This aspect is less simple to address, compared to the first two aspects, yet we should still summarise that the trunk shape of the new larva is at best comparable to the trunk shape in extant larvae of Hemerobiiformia. Also, some fossil neuropteran larvae recently reported by Badano et al. (2018) have been resolved within Myrmeleontiformia, but possess rather slender trunks. Yet, the exact trunk shape is still quite different to that of larvae of Hemerobiidae or Chrysopidae as in the latter two the trunk tapers significantly. This tapering is also present in the new fossil.

4.3. Systematic interpretation: step 2

There is a distinct consequence of finding the combination of these three characters in the fossil larva. There are several possible systematic interpretations of the fossil, yet all require that several prominent characters have evolved in convergence. Additionally, the internal phylogeny of Neuroptera is still not very stable (Aspöck et al. 2012; Wang et al. 2017; Jandausch et al. 2018): We here use an established phylogeny with monophyletic Myrmeleontiformia, and for simplicity also monophyletic Hemerobiiformia. It is possible that the latter group is in fact non-monophyletic (see discussion in Haug et al. in review for consequences concerning group names). Yet, this does not heavily affect the character evolution, as the polarity for the characters within Myrmeleontiformia does not change significantly. Hence, despite this uncertainty the reconstruction of the character evolution is largely unaffected and reliable.

1) We could interpret the specimen as a representative of Hemerobiiformia due to the morphology of the trunk. In this case, we would need to accept that: a) stylets with three prominent teeth each have evolved convergently within Myrmeleontiformia, for example, in the lineage towards Ascalaphidae + Myrmeleontidae as well as in the new fossil larva, and that b) the long neck (meaning 'functional neck', as also the prothorax is elongated) has evolved convergently in the lineage towards Crocinae and in the new fossil larva (Fig. 3A, B).

2) We could interpret the specimen as a representative of Crocinae due to the long neck. In this case, we would need to accept that: a) the trunk morphology would have evolved convergently, either in the lineage towards Hemerobiiformia and the fossil, or in the lineage towards Verineuroptera (Neuroptera without Nevrorthidae), lost in Myrmeleontiformia and convergently re-evolved in the fossil, and that b) stylets with three prominent teeth have evolved convergently in the lineage towards Ascalaphidae + Myrmeleontidae and in the fossil (Fig. 3A, C).

3) We could interpret the specimen as a representative of the group Ascalaphidae + Myrmeleontidae, due to the presence of three teeth on each stylets. In this case, we would need to accept that: a) the trunk morphology would have evolved convergently, either in the lineage towards

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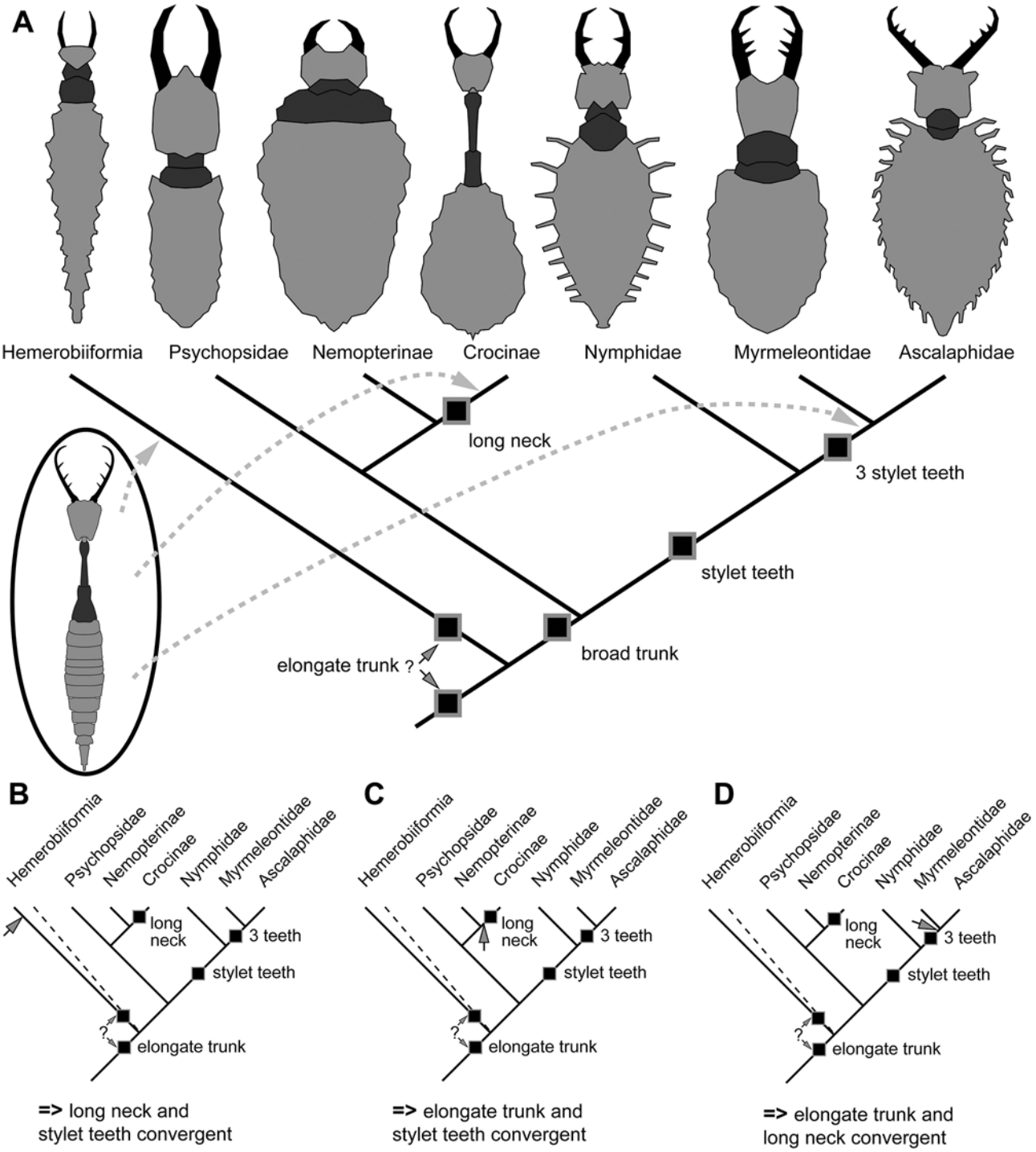


Fig. 3. Possible phylogenetic interpretation of the new neuropteran larva (grey arrows) and consequences for the character evolution resulting from the different options; **A**: summary of the discussed possible positions of the new larva; **B**: ingroup position within Hemerobiiformia; **C**: ingroup position within Crocinae; **D**: ingroup position within Ascalaphidae + Myrmeleontidae. Drawings simplified from (left to right): Tauber et al. 2014: fig. 5A; New 1989: fig. 145; Mansell 1973: fig. 1; Mansell 1981: fig. 3; Gepp 1984: pl. 9, fig. 19a; Pantaleoni et al. 2010: fig. 6A; Henry 1976: fig. 5. Functional neck (cervix+prothorax) depicted in darker grey.

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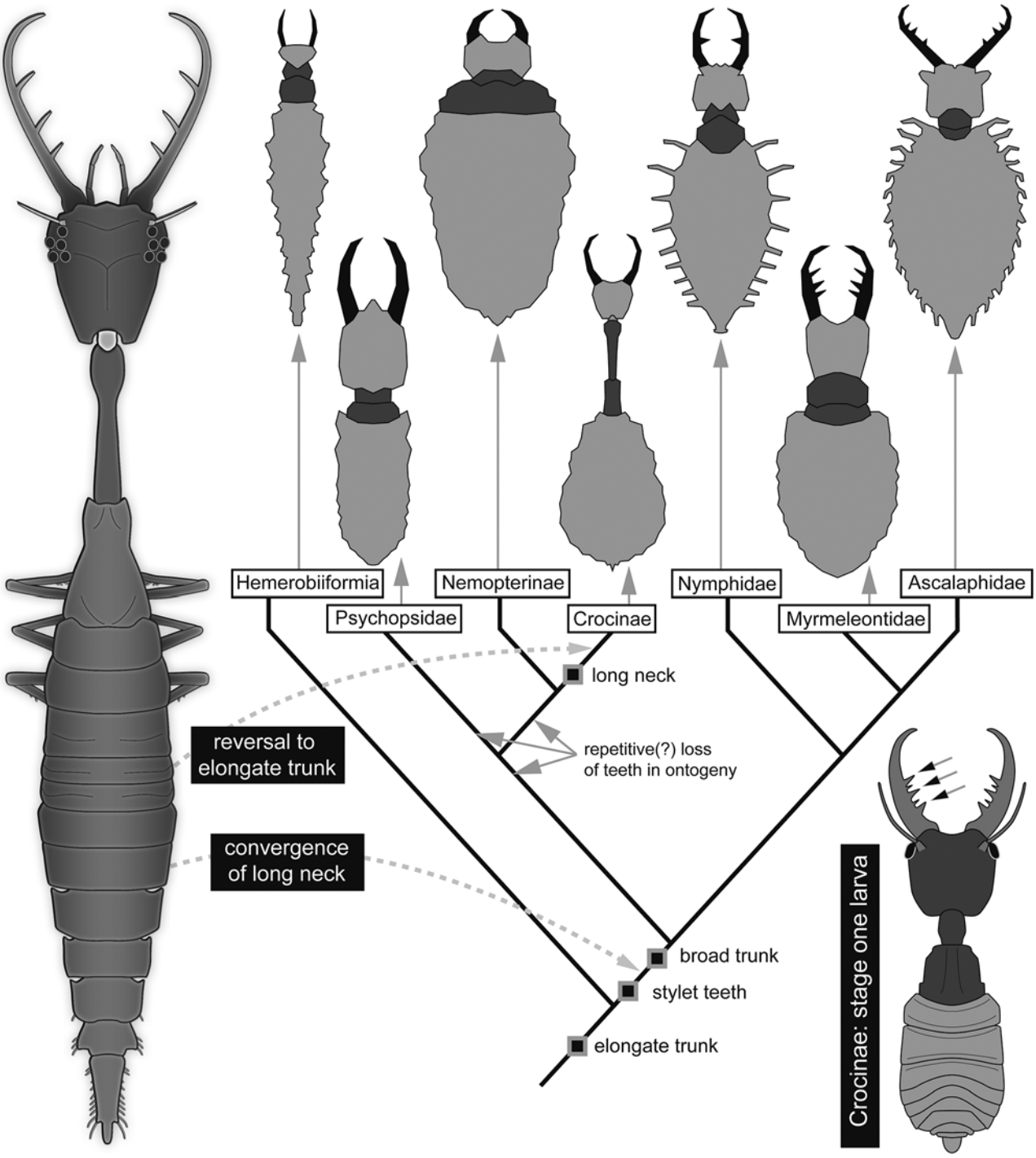


Fig. 4. Possible phylogenetic interpretation of the new neuropteran larva (grey arrows) and consequences for the character evolution resulting from the different options, continued; left: general restoration of the new chimera-like larva; note the three prominent teeth (arrows) in the stylet of a stage one larval form of Crocinae (lower right corner, simplified from Monserrat 2008: fig. 9f); drawings on top based on the same publications as in Fig. 3.

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Hemerobiiformia and the fossil, or in the lineage towards Verineuroptera, lost in Myrmeleontiformia and convergently re-evolved in the fossil, and that b) the long neck has evolved convergently in the lineage towards Crocinae and in the fossil (Fig. 3A, D).

All these three interpretations are in fact equally parsimonious and equally unsatisfying. Yet, we should also consider that some of the character reconstructions based on the extant larvae of neuropterans are more complicated than apparent after a first look, leading to further possible interpretations:

4) In modern larvae, the teeth on the stylets seem to produce a stable pattern: they seem only present in representatives of Nymphidae, which have always one each, Ascalaphidae, which have mostly three pairs, and Myrmeleontidae, which have one, two or three pairs. Yet, fossils from Cretaceous amber have already shown that possible ascalaphidans also are more variable in having two pairs of teeth on the stylets (Wang et al. 2016; Badano et al. 2018). Furthermore, if we look more closely there are in fact teeth on the stylets of Nemopterinae (e.g., Monserrat 1996: fig. 17; Monserrat 2008: fig. 6) and Crocinae (e.g., Mansell 1983: figs. 53, 54) although they do not appear as prominently as in Nymphidae, Ascalaphidae and Myrmeleontidae. Especially in the latter group, each stylet can in fact possess one or two more prominent teeth (Montserrat 1983: figs. 2, 6, 8, 12). In one case, even three seem to be present (Monserrat 2008: fig. 9f), quite comparable to the morphology in the new fossil larva (Fig. 4). Yet, the teeth seem to be most prominent only in first larval stages, which are less often taken into consideration, and are less prominent in the later stages.

Teeth are therefore not only present in larvae of the group Nymphidae + (Ascalaphidae + Myrmeleontidae), but also in larvae of Nemopteridae (= Nemopterinae + Crocinae). Hence, we would need to consider an additional convergence in these two lineages, or alternatively consider that teeth on stylets appear in the lineage towards Myrmeleontiformia and become reduced secondarily in Psychopsidae. It might be worthwhile in this aspect to investigate the early ontogeny of psychopsid species for the possible presence of teeth. If the presence of teeth on larval stylets is an autapomorphy of Myrmeleontiformia, the new fossil larva could be interpreted as an ingroup of Crocinae, due to the long neck, retaining the teeth and convergently evolving (or re-evolving) a hemerobiiformian type trunk (Fig. 4).

5) Alternatively, the fossil could (under the assumption that stylet teeth are part of the ground pattern of Myrmeleontiformia) represent the sister group to the remaining group of Myrmeleontiformia. These would be united by the possession of a new trunk morphology, while the fossil would retain plesiomorphically the morphology of the trunk as in representatives of Hemerobiiformia. This would work if Hemerobiiformia is monophyletic, but also if this is not the case. The long neck would then have to be interpreted as convergently evolved in Crocinae and the new fossil larva (Fig. 4).

4.4. Convergent evolution

As lined out above, independent of the systematic interpretation of the fossil, each interpretation demands for a certain degree of convergent evolution. It almost appears as if neuropteran larvae would have something like a basic set of attributes that can be combined to form specific mixture types of larvae, i.e. evolving chimera-like forms of combination of characters so far considered "typical" of single ingroups of Neuroptera. Especially the case of reappearing older, supposedly lost characters is interesting in this aspect.

Teeth on stylets and the trunk shape of the fossil represent such characters. Both characters may be ancestral features, lost or better suppressed during evolution, but can be "reactivated" if necessary, i.e. if specific selective pressures act in certain directions. In general, our concept of convergence is still not well-delineated, and numerous evolutionary phenomena seem to be summarised under this term.

As outlined in the present case, evolutionary reversals could be understood as cases of convergence. One could argue that reversals have at least the chance to be understood in the future from a gene-regulatory point of view. Such cases are most likely fundamentally different from the independent de novo evolution of a character ("novelty"). If this could be the basis for an argument in evolutionary reconstructions, which needs to be shown in the future, reconstruction 4 would be the more likely one, requiring only a single convergence, but via a reversal. These thoughts might still be speculative, yet we need to improve our concept of convergence, as it is a prime ad hoc explanation in evolutionary reconstructions and we clearly need to be more precise in how we understand this phenomenon.

4.5. Conclusions

– The fossil neuropteran larva described here possesses a unique combination of characters, unknown from the modern fauna.

– This emphasises that the Cretaceous fauna has seen many "experimental morphologies".

– It indicates that convergent evolution has occurred in the diversification of Neuroptera. It either demands for a convergent evolution of an elongated neck in Crocinae

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and the new fossil which could represent the sistergroup to Myrmeleontiformia, or, if the fossil is a representative of Crocinae, it would demand for a reversal to an elongated trunk.

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