

NEW FOSSIL LACEWING LARVAE WITH TRUMPET-SHAPED ELONGATE EMPODIA PROVIDE INSIGHT INTO THE EVOLUTION OF THIS ATTACHMENT STRUCTURE

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Abstract. The larval life phase often represents the major share of the life span of holometabolans, such as beetles or flies. Therefore, knowledge of these larvae is crucial concerning ecological functions, but also concerning the evolutionary history of the different groups. In the holometabolan group Neuroptera (lacewings), larvae have numerous specialisations, among them the venom-injecting mouthparts, the stylets. Another such very characteristic feature of many lacewing larvae is the empodium, an attachment structure at the tip of the leg, which varies in shape in the larvae of the different lacewing groups. One type of empodium is the elongate trumpet-shaped type, which is found in several lacewing groups today as well as in many fossil representatives, especially well visible due to preservation in amber. Based on the pattern of phylogenetic distribution of the elongate trumpet-shaped empodium, different reconstructions of the evolution of this structure have been put forward, some suggesting possibly convergent evolution, others repetitive losses. In this study, new lacewing larvae preserved in 100-million-year-old amber from Myanmar are presented, which expand the number of lineages with an elongate trumpet-shaped empodium. Based on these new data, the implications on the evolutionary history of the different lineages within Neuroptera are discussed. The fossils demand for an earlier evolution in some reconstructions, but especially for more and later losses of this structure.

INTRODUCTION

Holometabola, the group including beetles, bees, butterflies and their closer relatives, represents a major share of the continental animal biodiversity (e.g., Grimaldi & Engel 2005). More precisely, the larval stages represent a major part of the biomass in terrestrial and freshwater ecosystems, ful-

filling numerous ecological functions. A smaller ingroup of Holometabola is Neuroptera, the group of lacewings (Aspöck & Aspöck 2007). This group is especially interesting for understanding the early diversification of Holometabola as it is generally understood as having been part of the early radiations, but having declined since then (Aspöck & Aspöck 2007; Winterton et al. 2018).

It seems therefore important to reconstruct the evolutionary history and character evolution of this group, especially of its larvae, to improve our

understanding of processes such as radiations and declines. The group of lacewings, Neuroptera, is characterised by many apomorphies, particularly of their larval stages concerning their mouthparts that are highly modified into a pair of venom-injecting sucking tubes (stylets; MacLeod 1964; Aspöck & Aspöck 2007; Zimmermann et al. 2019). Yet, other larval structures are also unusual within the group; one of these is the empodium, an attachment structure arising distally right between the claws of the locomotory appendages or legs (New 1989; Beutel et al. 2010).

In many neuropteran ingroups, this empodium is quite prominent, trumpet-shaped and elongate, often as long as or longer than the claws (Monserrat 2008; Jandausch et al. 2018a). Yet, the structure is not present in all groups and not in all larval stages (lacewings mostly have three larval stages; see discussion in Haug et al. 2020). Reconstructions based on extant specimens have indicated the possibility of convergent evolution of this structure, but usually, a single evolution of this type of empodium with repeated losses seems to be the preferred interpretation (for details see discussion in Beutel et al. 2010 and discussion below). Furthermore, exceptionally preserved lacewing larvae found in amber have provided a clear indication that a trumpet-shaped elongate empodium was even more widespread in the past (Badano et al. 2018; Haug et al. 2021a; Zippel et al. 2021).

We report here new specimens of lacewing larvae preserved in about 100-million-years-old Kachin amber, Myanmar, that also possess trumpet-shaped elongate empodia. These findings expand the number of lineages with such an attachment structure. Based on these new findings, we explore the possible evolutionary history of this structure within Neuroptera.

MATERIAL AND METHODS

Material

Several new fossil specimens directly investigated are preserved in Kachin amber from Myanmar. Kachin amber is about 100 million years old (e.g., Cruickshank & Ko 2003; Shi et al. 2012; Yu et al. 2019). Specimens were legally purchased on the trading platform ebay.com from different traders (burmitefossil, burmite-miner, macrocretaceous). They are now stored in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-University Munich, Germany under repository numbers PED 0783, 0890, 1526, 1738, 2403, 2732. In addition, each specimen is referred to with a four-digit specimen number that links to larger-scaled data sets (e.g. Haug et al. 2023a).

Extant comparative material was provided by the entomological collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Centrum für Naturkunde (CeNak), Leibniz-Institut zur Analyse des Biodiversitätswandels (LIB), Hamburg (ZMH). From the SMNS, a single larva of the group Hemerobiidae was considered; the specimen was collected on 22.06.1988 in Trins, Austria. The species is not determined. It has the internal reference number ESMNS_016. From the ZMH, a single larva of the group Osmylidae was considered; the specimen was collected in 1930 in Rügen, Germany. The species was determined as *Osmylus fulvicephalus*. It has the (internal) reference number ZMH_Osmylus3.

Documentation methods

The fossil and extant specimens were documented on a Keyence VHX 6000 digital microscope. The specimens were documented with different illuminations: unpolarised low-angle ring light, cross-polarised co-axial light, and transmitted light (e.g., Haug et al. 2021a and references therein). The first two settings were performed with white and black backgrounds, the third setting was performed with a glass plate. The images were further processed with Adobe Photoshop CS2. A redrawing from the literature was performed in Inkscape.

RESULTS

We found several fossil larvae with prominent empodia that have an overall morphology that is unusual in combination with the presence of such empodia. We provide only brief descriptions highlighting important structures.

Description of lance-lacewing-type larva

Specimen 5878 (PED 1526) is well accessible in ventral view (Fig. 1A, B). Stylets long, overall elongate, bulbous proximally, tapering distantly, and slightly curving outwards. Head capsule shorter than stylets, about 50%. Antenna and labial palps about as long as the stylets. Trunk spindle-shaped, quite long, about 6x the length of the stylets. Anterior trunk (thorax) with prominent locomotory appendages (legs). Distally locomotory appendages each with a pair of claws. Between the claws, a well-developed, prominent and elongated trumpet-shaped empodium on each leg (Fig. 1C). The specimen has a length of about 1.8 mm.

Description of split-footed-lacewing-type larvae

1) Specimen 0243 (PED 0783) is well accessible in dorsal (Fig. 2A, B) and ventral view (Fig. 2C). The stylet is partially concealed by a distortion in the amber. Each stylet bears one slightly s-curved tooth (Fig. 2D). A narrow cervix seems to be present. Protrusions at each trunk segment are visible

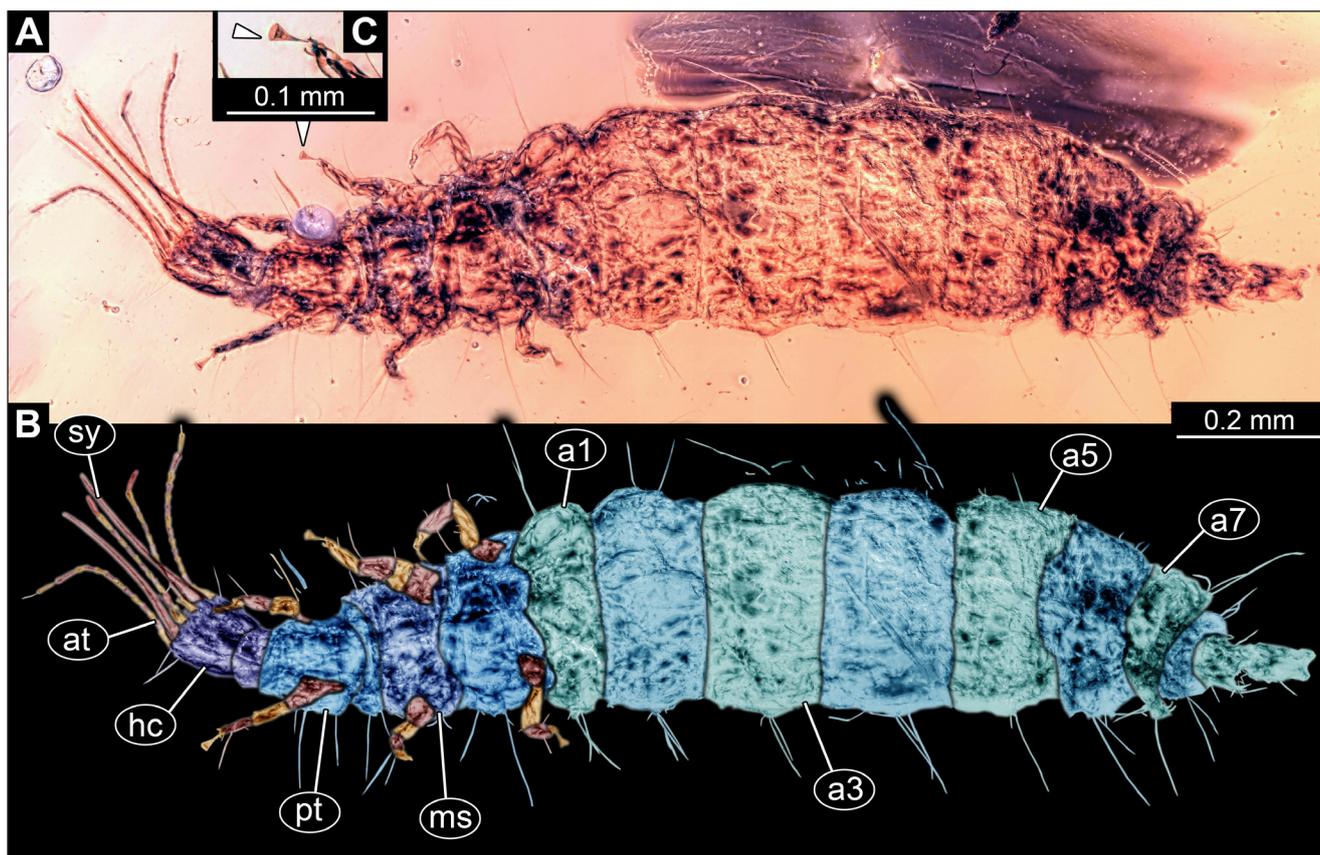


Fig. 1 - Specimen 5878 (PED 1526), Myanmar amber. A) Ventral view. B) Ventral view, colour-marked. C) Close-up of empodium (arrowhead). Abbreviations: a1–7 = abdomen segments 1–7; at = antenna; hc = head capsule; ms = mesothorax; pt = prothorax; sy = stylet.

(Fig. 2E). Trumpet-shaped empodia between the claws at the end of locomotory appendages are visible (Fig. 2F). The specimen has a length of about 3.5 mm.

2) Specimen 0245 (PED 0890) is well accessible in ventral view (Fig. 3A–C). Each stylet bears one slightly forward-inward-curved larger tooth and a smaller straight tooth (Fig. 3E). Four protrusions on the anterior rim of the head are visible (Fig. 3F). Trumpet-shaped empodia between the claws at the end of locomotory appendages are visible (Fig. 3D). The posterior trunk seems to be missing. The specimen has a length of about 1.2 mm.

3) Specimen 0248 (PED 1738) is well accessible in ventral (Fig. 4A, B) and dorsal view (Fig. 4C). Each stylet bears one forward-inward-curved larger tooth and a smaller distally pointing tooth (Fig. 4D). Four protrusions on the anterior rim of the head are visible (Fig. 4E). Eyes are very prominent on each lateral side. Trumpet-shaped empodia between the claws at the end of locomotory appendages

are visible (Fig. 4F). The specimen has a length of about 5.8 mm.

4) Specimen 0252 (PED 2403) is well accessible in dorsal (Fig. 5A, B) and ventral view (Fig. 5C). Each stylet bears one slightly forward-inward-curved tooth (Fig. 5D). Four protrusions on the anterior rim of the head are visible (Fig. 5D). A rather long, slender neck seems to be apparent. Protrusions at each trunk segment are visible (Fig. 5F). Each distal end of the walking appendages bears claws and a trumpet-shaped empodium (Fig. 5E). The specimen has a length of about 4.1 mm.

5) Specimen 0259 (PED 2732) is well accessible in ventral view (Fig. 6A, B), but partly concealed by dirt in dorsal view (Fig. 6C). Each stylet bears one slightly forward-curved larger tooth and a smaller straight tooth (Fig. 6D). Four protrusions on the anterior rim of the head are visible (Fig. 6D). Claws with trumpet-shaped empodia at the end of locomotory appendages are visible (Fig. 6E). The specimen has a length of about 3.6 mm.

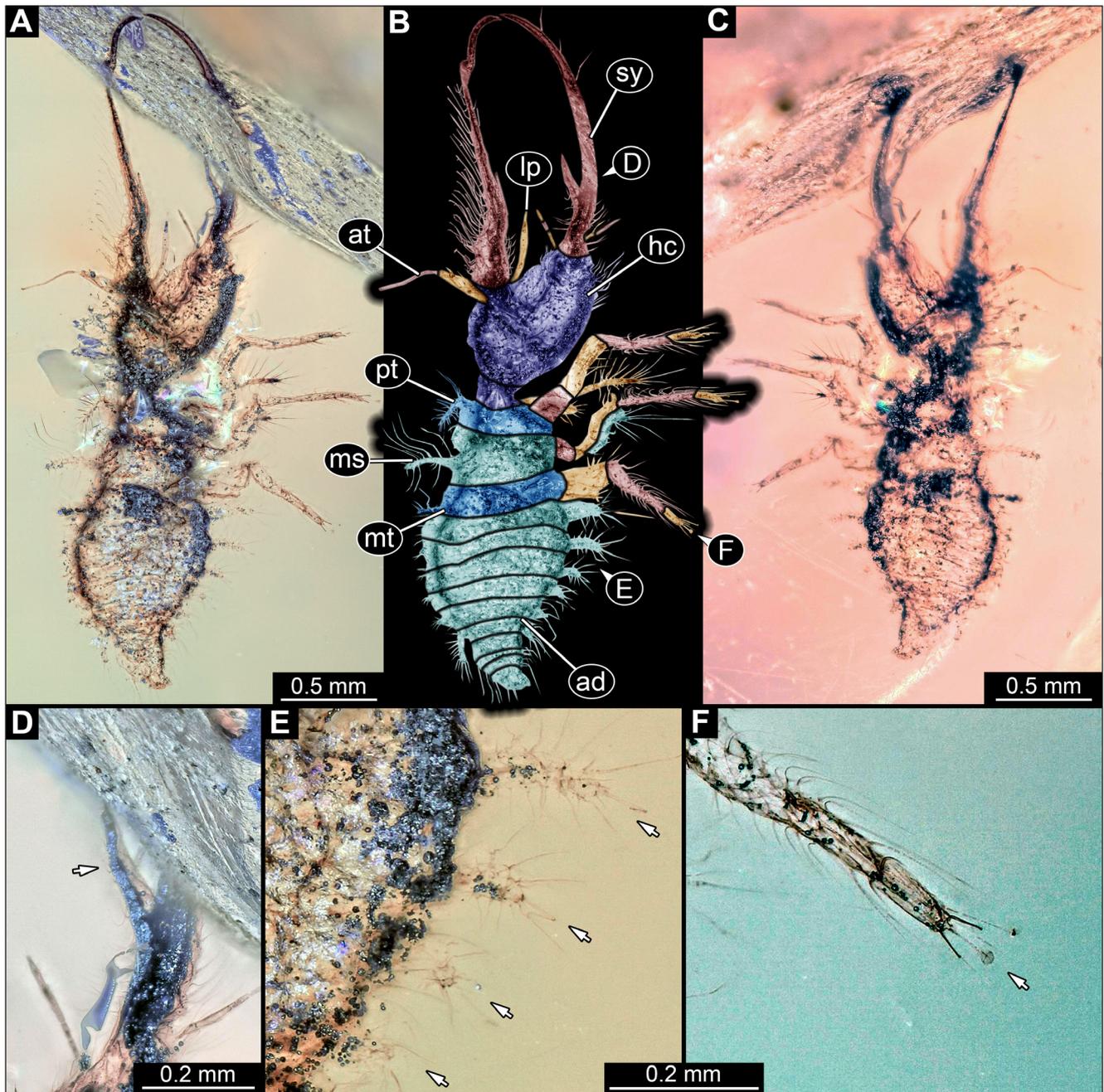


Fig. 2 - Specimen 0243 (PED 0783), Myanmar amber. A) Dorsal view. B) Dorsal view, colour-marked. C) Ventral view. D) Close-up of stylet in dorsal view, arrow marks tooth. E) Close-up of the abdomen in dorsal view, arrows mark protrusions. F) Close-up of third locomotory appendage in dorsal view, arrow marks empodium. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet.

DISCUSSION

Phylogenetic comparison

We did not attempt to include the fossils reported here into a phylogenetic analysis. It has been demonstrated that such an attempt is in principle possible (e.g. Badano et al. 2018, 2021a). Yet, in the fossils at hand, many details are not accessible. The

specimens were not selected for access of structures of phylogenetic relevance, but especially for access to the empodia. In consequence, many (other) crucial characters are simply not available.

Instead of including the specimens into a larger-scaled phylogenetic analysis, we will discuss a coarser frame of relationships for the fossils, i.e. which larger lineages they represent. Then the pos-

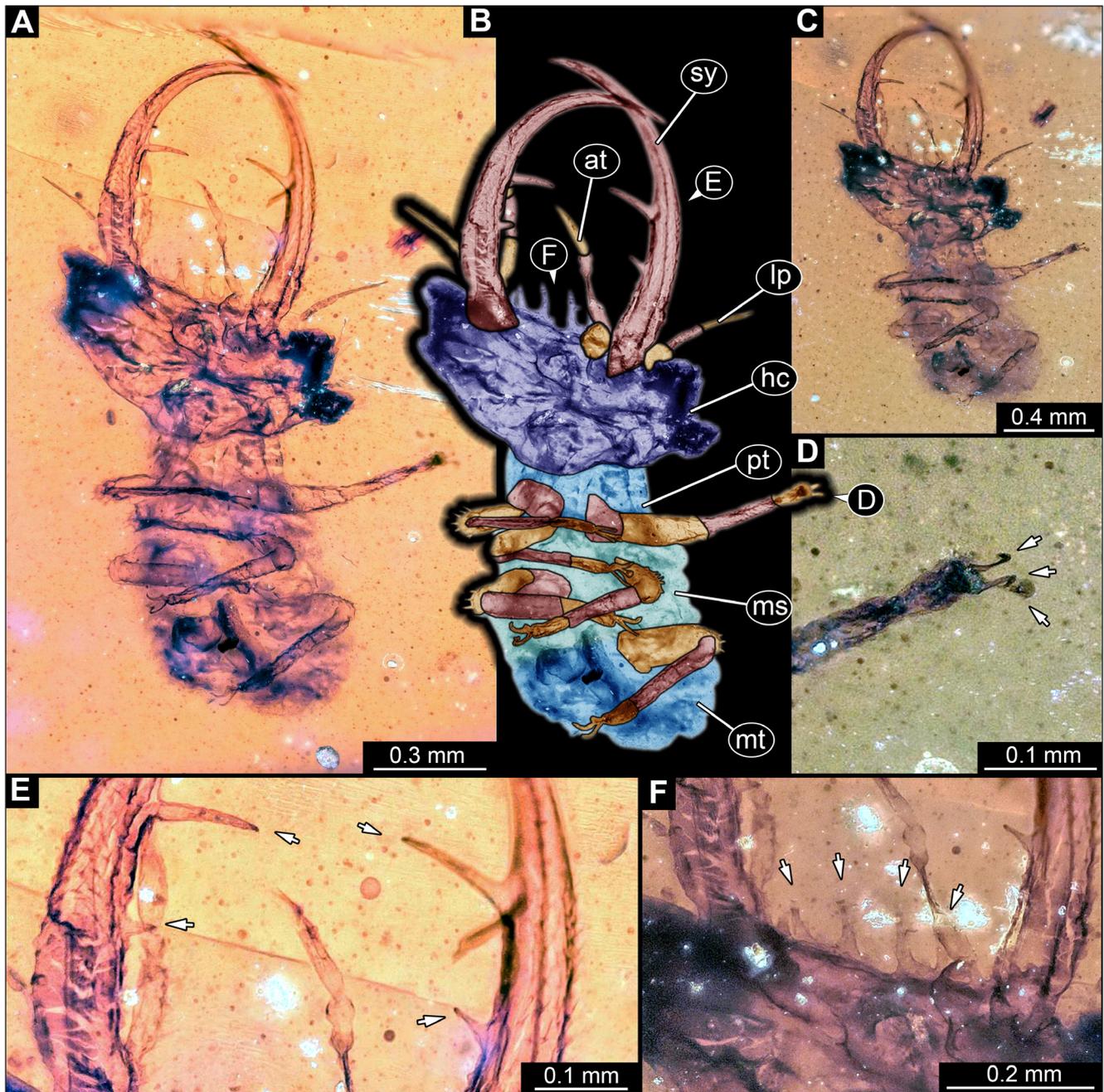


Fig. 3 - Specimen 0245 (PED 0890), Myanmar amber. A) Ventral view, cross-polarised light. B) Ventral view, colour-marked. C) Ventral view, unpolarised ring light. D) Close-up of third locomotory appendage in dorsal view, arrows mark empodium and claws. E) Close-up of stylet in ventral view, arrows mark teeth. F) Close-up of head capsule in ventral view, arrows mark protrusions. Abbreviations: at = antenna; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet.

sible consequences for character reconstruction are discussed (see also discussion in Haug et al. 2023b).

As a side note: Although many authors term the major lineages “families”, there is no uniform concept of “families” in Neuroptera. Therefore, the number of families varies drastically (Haug et al. 2023a), further emphasising that the rank of groups lacks a scientific basis (Ax 1995; Avise & Liu 2011; Zachos 2011, 2014; Lambertz & Perry 2015, 2016).

Identity of specimen PED 1526

The specimen has prominent stylets, which are at least two times the length of the head capsule; the stylets are broad proximally, strongly tapering distally, and more or less straight, but slightly outward curving. Such a morphology of the stylet is only known in larvae of Osmylidae, the group of lance lacewings.

The only unusual detail is the morphology of the empodium, which is trumpet-shaped elongate.

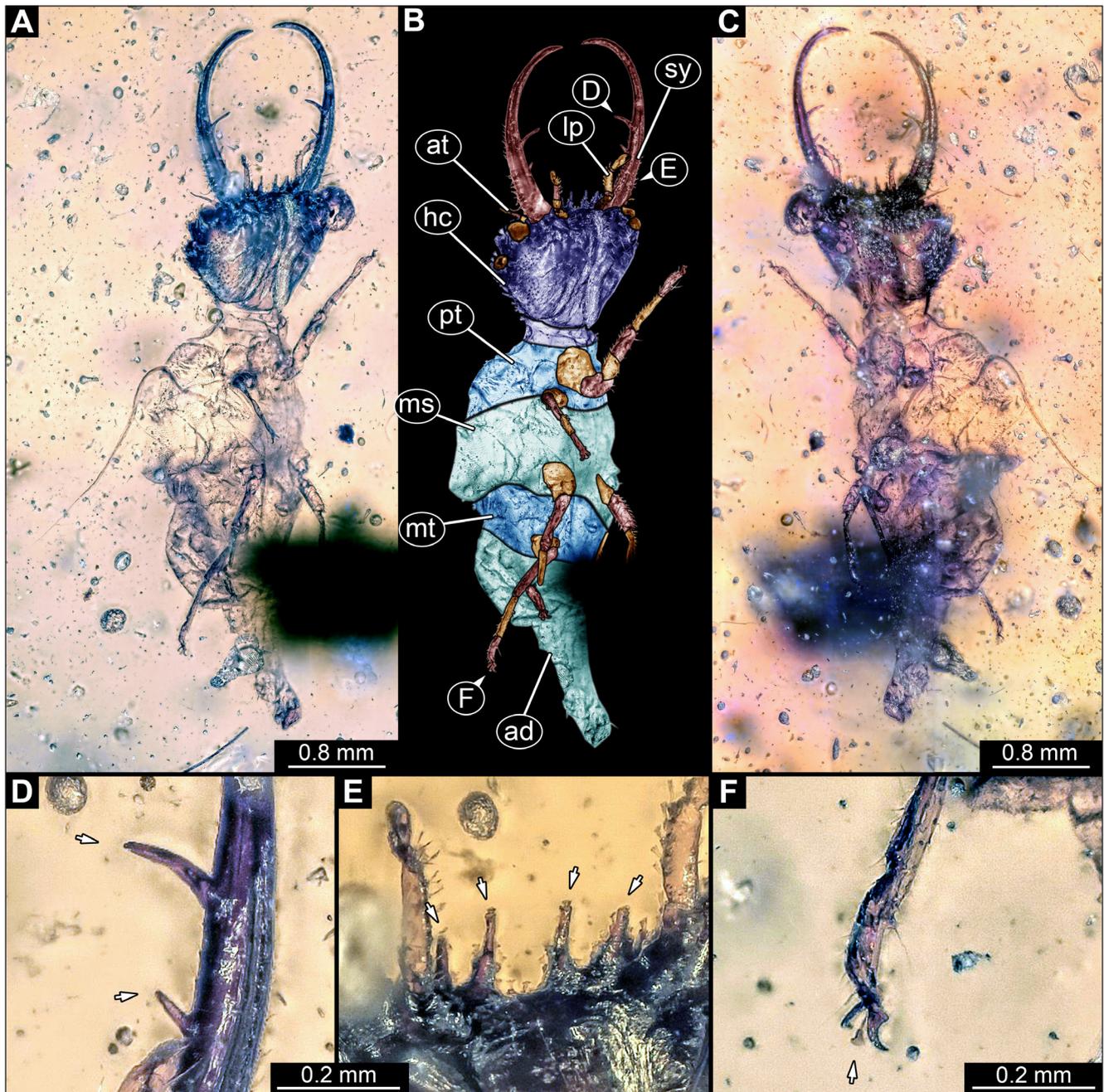


Fig. 4 - Specimen 0248 (PED 1738), Myanmar amber. A) Ventral view. B) Ventral view, colour-marked. C) Dorsal view. D) Close-up of stylet in ventral view, arrows mark teeth. E) Close-up of head capsule in ventral view, arrows mark protrusions. F) Close-up of third locomotory appendage in dorsal view, arrow marks empodium. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet.

In modern lance lacewing larvae, the empodium appears very similar to a strong seta (Fig. 7A–D; e.g., Martins et al. 2018 figs. 5a, 11e). This leaves two possible interpretations: The specimen could be the larva of a lance lacewing (or closely related ≈ “stem-lineage”) as indicated by the stylets and the overall appearance, but either has retained a trumpet-shaped elongate empodium from an earlier an-

cestor (≈ node) or evolved it convergently. Alternatively, this type of empodium could be understood as a character excluding a relationship to lance lacewings, and the special stylets evolved convergently to those in lance lacewings. Given the challenging reconstruction of the empodium, indicating either several losses or independent gains (or re-gains?), it seems more likely that the larva is indeed a lance

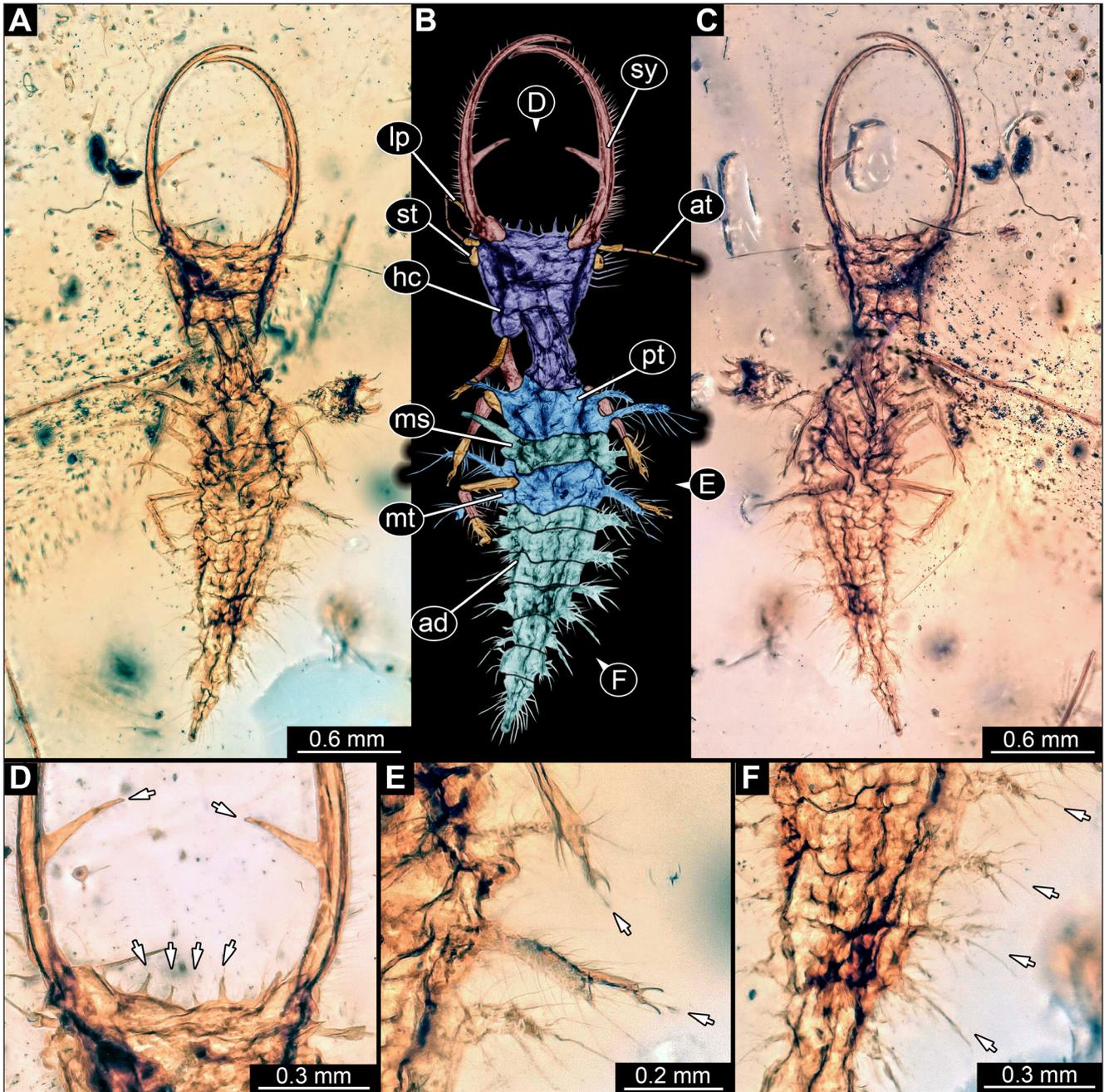


Fig. 5 - Specimen 0252 (PED 2403), Myanmar amber. A) Dorsal view. B) Dorsal view, colour-marked. C) Ventral view. D) Close-up of stylet and head capsule in dorsal view, arrows mark teeth and protrusions. E) Close-up of first and third locomotory appendages in dorsal view, arrows mark empodia. F) Close-up of abdomen in dorsal view, arrows mark protrusions. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; lp = labial palps; ms = mesothorax; mt = metathorax; pt = prothorax; st = stemmata; sy = stylet.

lacewing possessing a trumpet-shaped elongate empodium. Yet, we also need to consider that the larvae of extant lance lacewings are understudied. The details of the distal structures, such as the empodium, are often not known. We can therefore not easily exclude that the trumpet-shaped empodium was lost later within the group and the fossil may be further derived inside the group.

Identity of the other specimens

The other specimens also have trumpet-shaped elongate empodia. Their stylets are gently curved inwards and either bear a single prominent tooth (PED 0783, 2403) or one large tooth and one smaller tooth (PED 0890, 1738, 2732). Such stylets are not exclusively known in larvae of Nymphidae (split-footed lacewings), but such morphology is

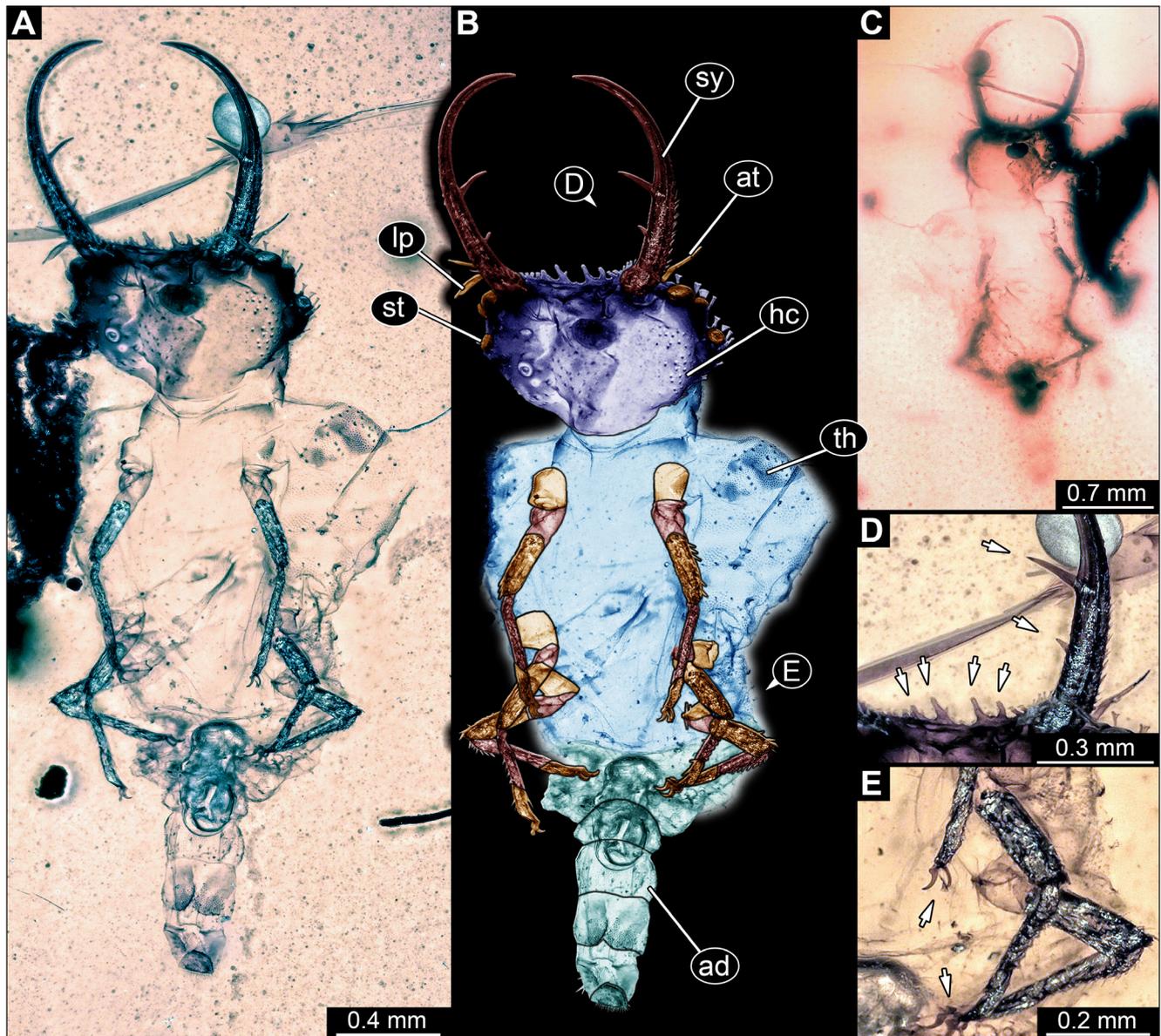


Fig. 6 - Specimen 0259 (PED 2732), Myanmar amber. A) Ventral view. B) Ventral view, colour-marked. C) Dorsal view. D) Close-up of stylet and head capsule in ventral view, arrows mark teeth and protrusions. E) Close-up of locomotory appendages in ventral view, arrows mark empodia. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; lp = labial palp; st = stemmata; sy = stylet; th = thorax.

already indicative for this group. Most specimens (PED 0890, 1738, 2403, 2732) in addition have four spines at the anterior edge of the head. In the other specimen (PED 0783), this very area is strongly deformed, but at least two such spines are discernible, indicating that in fact also this specimen had four such spines. Four such spines are known for other lacewing larvae from the Cretaceous that have been formally described as *Nymphavus progenitor* (Badano et al. 2018). Similar-appearing larvae have been addressed as Nymphavus-type larvae (Haug et al. 2022a). *Nymphavus progenitor* has been resolved as a representative of Nymphidae in phylogenetic analy-

ses (Badano et al. 2018). We, therefore, see it as the most likely interpretation that, despite the presence of a trumpet-shaped elongate empodium, all these are larvae of the group Nymphidae.

Empodia in other groups of lacewings

Other types than trumpet-shaped elongate empodia have been reported in certain lacewing groups, such as seta-like ones of extant lance lacewing larvae (Fig. 7A–D). In Nevrorthidae, the empodium is cylindrical with a terminal seta (Fig. 7G; Zwick 1967 fig. 7 right p. 72; Beutel et al. 2010 pp. 535, 557); also the empodium is shorter than the

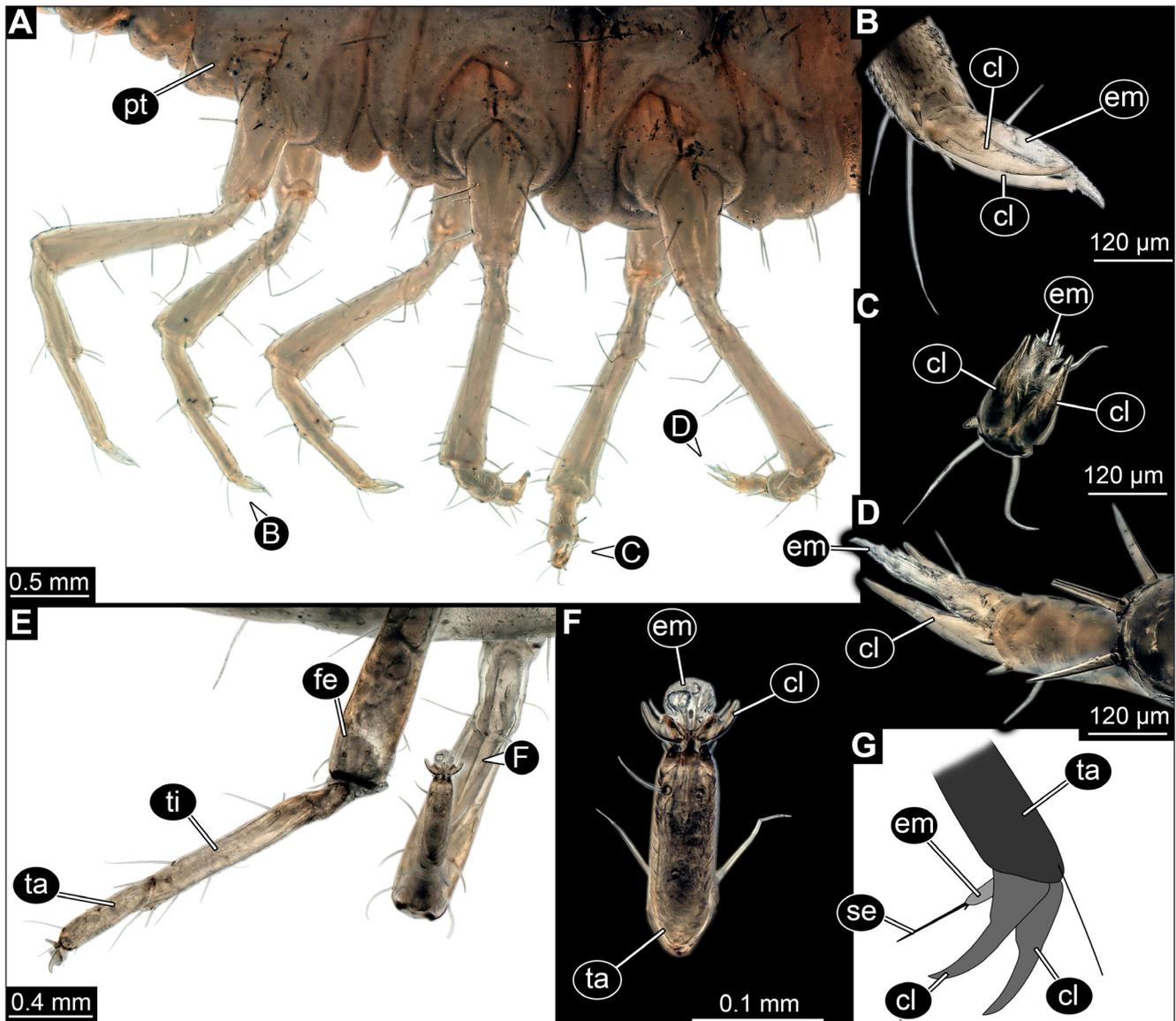


Fig. 7 - Empodia in different modern lacewing larvae. A–D) Osmylidae, specimen ZMH_Osmylus3. A - Lateral view of legs. B–D - Close-ups of empodia. E, F) Hemerobiidae, specimen ESMNS_16. E - Lateral view of legs. F - Close-up of empodium. G) Nevrothidae, close-up on empodium, based on Zwick (1967, fig. 7 right). Abbreviations: cl = claw; em = empodium; fe = femur; pt = prothorax; se = seta; ta = tarsus; ti = tibia.

claws, only half the length of the latter (Zwick 1967 fig. 7 right p. 72). Similar types of empodia have been suggested to be present also in some larvae of Osmylidae (Jandausch et al. 2018a p. 455). According to Jandausch et al. (2018a p. 455), a similar type of empodia is also present in larvae of Crocinae (thread-winged lacewings; long-necked antlions), an ingroup of Myrmeleontiformia. Nevertheless, the literature cited therein (Mansell 1976, 1983) does not specify nor describe any presence of empodia for larvae in this group. Therefore, after thorough research in the literature on the morphology of the larvae of Crocinae (recently summarised in Haug et al. 2021b), to the best of our knowledge, there are no

empodia in long-necked antlions.

The empodium appearing seta-like in at least some larvae of lance lacewings (Osmylidae) and being about as long as the claws, without a differentiated proximal cylindrical region, while in others it seems to have this type of socket may mean that within the group the exact morphology is variable. The new fossil lance lacewing larva expands this variability, now also including a trumpet-shaped elongate empodium.

A trumpet-shaped elongate empodium is present in larvae of Chrysopidae, Hemerobiidae, Mantispoidea, Dilaridae and Psychopsidae (Beutel et al. 2010 p. 551; Jandausch et al. 2018b p. 553). The

statement does not imply that the structure is present in all three larval stages (instars; see below). The trumpet-shaped elongate nature of the empodium in these groups is backed up by numerous sources (e.g., Tillyard 1918 text-fig. 2b p. 790; Killington 1936 pl. V fig. 1; Tauber et al. 2006 fig. 8 p. 223; Jandausch et al. 2018a figs. 2, 3, 5; Badano et al. 2021b fig. 4C p. 251; Badano 2022 fig. 1 p. 19). The group of silky lacewings (Psychopsidae) is the only ingroup of Myrmeleontiformia with trumpet-shaped elongate empodia in extant larvae (long-nosed antlions). In addition, several now extinct early branches within Myrmeleontiformia possessed such empodia (Badano et al. 2018 fig. 3a p. 5; Haug et al. 2021a fig. 2C p. 3; Zippel et al. 2021 various figs.).

Reconstructing the evolution of the trumpet-shaped elongate empodium: a case of convergence?

Beutel et al. (2010) resolved the presence of a trumpet-shaped elongate empodium as convergently evolved three times (once in Chrysopidae + Hemerobiidae, once in Mantispodea + Dilaridae, once in Psychopsidae). However, the authors also discussed and seemed to favour, the possibility that the trumpet-shaped elongate empodium evolved only once early within Neuroptera (in the remaining group, excluding Nevrothidae; suggested name Verineuroptera from Haug et al. 2019). In consequence, this type of empodium would have to be assumed secondarily lost several times.

The absence of an empodium seems indeed explainable via ontogenetic aspects. The larvae of the group of Hemerobiidae possess an empodium, but it differs between the larval stages. In the first larval stage, they have a trumpet-shaped empodium, but not in the second and third stages (Gurney 1947 p. 157; MacLeod 1960; Tauber 1974 p. 1134; Miller & Lambdin 1984; New 1991, 1992; Monserrat et al. 2001; MacLeod & Stange 2005). Instead, in Hemerobiidae the second and third larval stages have a pad-shaped empodium (Fig. 7E, F) that is often described as short (Tauber et al. 2003 p. 795), abbreviated (Mitchell 1962) or as a (fan-like) arolium (MacLeod 1960). Hence, the originally trumpet-shaped empodium seems to have been reduced to a pad-shaped empodium from the first to the second larval stage (Gurney 1947; Monserrat et al. 2001; Dey 2014). The example of Hemerobiidae, therefore, provides an ontogenetic explanation of how a trumpet-shaped

elongate empodium could become reduced.

Also in Berothidae, the group of beaded lacewings, the presence or absence of the trumpet-shaped elongated empodium is connected to the ontogeny. In modern beaded lacewings only larvae of stages 1 and 3 possess a trumpet-shaped elongate empodium. The second larval stage has been reported to be inactive (Tauber & Tauber 1968), C-shaped and has reduced mouthparts and legs (Minter 1990; Oswald et al. 2002; Möller et al. 2006); also the trumpet-shaped elongate empodium seems to be absent (Möller et al. 2006). However, this might not be the ancestral state for the group as there are presumed stage 2 larvae from the fossil record (Haug & Haug 2022) that seem to possess an empodium (Haug et al. 2021 fig. 12D p. 37), although they indeed appear C-shaped.

Jandausch et al. (2018b) with an updated version of the analysis of Beutel et al. (2010) likewise suggested that the trumpet-shaped elongate empodium evolved early within Neuroptera, this time in a group excluding Coniopterygidae and Osmyloidea (= Osmyliidae + Sisyridae + Nevrothidae). Also here it was assumed to have been lost secondarily several times (Jandausch et al. 2018b p. 535). For example, Jandausch et al. (2018b) suggested that the ingroups of Myrmeleontiformia, excluding Psychopsidae, could be characterised by a loss of the trumpet-shaped elongate empodium (p. 554), hence supporting a sistergroup relationship of Psychopsidae to the remaining groups. The presence of the empodium in other early representatives of the group (as reported by Badano et al. 2018) was suggested to be a further support for this interpretation (Jandausch et al. 2018b p. 554).

Reconstructing the evolution of the trumpet-shaped elongate empodium within Myrmeleontiformia

The interpretation of Jandausch et al. (2018b) was well compatible with their tree, which was also congruent with those resulting from some other analyses concerning the position of Psychopsidae (e.g. Winterton et al. 2010 fig. 7 p. 370; Badano et al. 2017; Engel et al. 2018; Cai et al. 2023). Yet, there have been also quite some other interpretations of the position of Psychopsidae within Myrmeleontiformia (Aspöck & Aspöck 2007; Aspöck et al. 2012 fig. 2 p. 124; see partial overview in Winterton et al. 2010 fig. 2 p. 352).

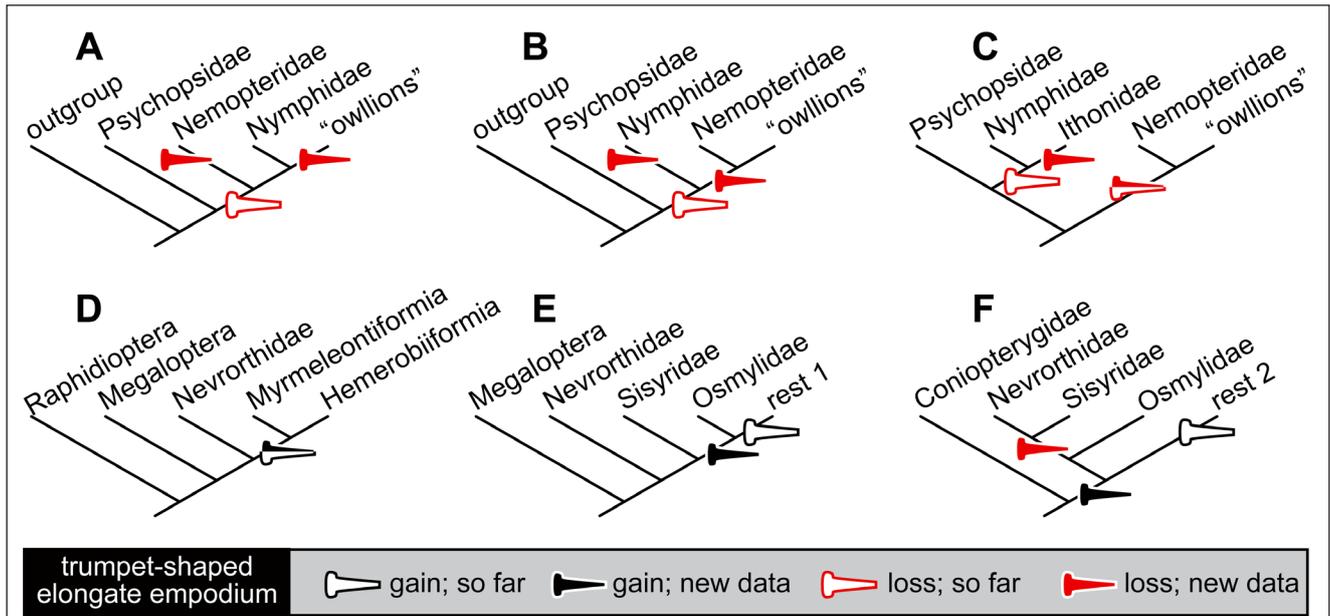


Fig. 8 - Representation of the evolution of the trumpet-shaped elongate empodium according to new data reported here. A-C) Within Myrmeleontiformia; based on phylogenetic trees by Badano et al. 2017 (A); Cai et al. 2023 (B); and Winterton et al. 2018 (C). D-F) Within Neuroptera; based on phylogenetic trees by Beutel et al. 2010 (D); Aspöck & Aspöck 2008 (E) and Jandausch et al. 2019 (F).

In many recent analyses, the picture is indeed different, but rather consistent. Nymphidae is resolved as closely related to Psychopsidae in a larger group also including some fossils; Ithonidae is even closer related to Nymphidae, i.e. Psychopsidae is the sistergroup to a larger group including Nymphidae, Ithonidae and (sometimes) some exclusively fossil groups (Winterton et al. 2018 fig. 1 p. 337; Machado et al. 2019 fig. 1; Badano et al. 2021a fig. 4 p. 679; the large-scaled analysis of Vasilikopoulos et al. 2020 did unfortunately not include Psychopsidae).

In each of the branching patterns, the new fossils give a signal that empodia were retained in Nymphidae (Fig. 8A, B, C) and were lost within the group. They must also be interpreted as lost in Ithonidae (Fig. 8B). A larger group including Nemopteridae and the group of “owllions” (a group composed of what was formerly included into Ascalaphidae and Myrmeleontidae; see discussion of the complex situation in Haug et al. 2022b) has reduced the empodium (Fig. 8B, C).

Reconstructing the evolution of the trumpet-shaped elongate empodium within Neuroptera

With the single new lance lacewing-type

fossil, it seems most likely that a trumpet-shaped elongate empodium was also present in the ground pattern of Osmylidae, but reduced or simplified within the group. Depending on where Osmylidae is resolved in the lacewing tree, the first occurrence of a trumpet-shaped elongate empodium may shift.

In trees with a monophyletic group of Hemerobiiformia, with Osmylidae as an ingroup (as e.g. in Beutel et al. 2010; Aspöck et al. 2012 fig. 2 p. 124), there is no change to the character reconstruction (Fig. 8D). Yet, Hemerobiiformia is generally considered non-monophyletic in more recent analysis (see already discussion in Aspöck et al. 2012).

In trees with Osmylidae branching off as the third lineage of Neuroptera, after Nevrothidae and Sisyridae (Haring & Aspöck 2004; Aspöck & Aspöck 2008; Aspöck et al. 2012 fig. 3 p. 125), the appearance of the trumpet-shaped elongate empodium is shifted one node further down (Fig. 8E). Comparably for most of the more recent trees, in which Osmylidae is within a group Osmyloidea (with Nevrothidae and Sisyridae; Jandausch et al. 2019), the appearance of the special type of empodium is shifted downwards, characterising a large group within Neuroptera only excluding Coniopterygidae (Fig. 8F).

CONCLUSION

The new fossils demonstrate the presence of trumpet-shaped elongate empodia in two groups, Nymphidae and Osmylidae, in which this character has not been observed before. This observation supports earlier reconstructions (e.g. Beutel et al. 2010; Jandausch et al. 2018b) in which the empodium did not evolve convergently in several lineages within Neuroptera, but evolved only once and was lost several times. The fossils also indicate that it evolved slightly earlier and was retained longer than anticipated before. The case again demonstrates that fossils provide a signal for character reconstructions also for groups with ample extant representatives by providing more plesiomorphic character states for some of these groups.

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