

YET ANOTHER UNUSUAL NEW TYPE OF LACEWING LARVA PRESERVED IN 100-MILLION-YEAR OLD AMBER FROM MYANMAR

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Abstract. Lacewing larvae are mostly predatory, highly mobile larval forms of Insecta. The modern fauna yields several morphotypes of lacewing larvae, each closely associated with a distinct evolutionary lineage within the group of lacewings, Neuroptera. Back in the Cretaceous, about 100 million years ago, many of these larval forms had already evolved. Additionally, many larval forms seem to have been present that are now extinct. We report here a new form, which appears to be extinct now. This new larva has a prominent forward projecting labrum like larval forms of Nevrorthidae and Psychopsidae. It furthermore has (again similar to the latter two) curved venom-injecting stylets formed by mandibles and maxillae. We used quantitative outline analysis to compare the new larva to those of Nevrorthidae and Psychopsidae. The results of this analysis demonstrate that the new larva differs in all aspects of head capsule shape from all known larvae of Nevrorthidae. Its head shape is more similar to that of many larvae of Psychopsidae, yet also here the new larva differs recognisably in one principal component. Also qualitative differences clearly differentiate the new larva from already known ones. Hence, the new larva represents a new, so far unknown morphotype of lacewing larva. This finding adds to the growing 'zoo' of unusual lacewing larvae back in the Cretaceous, indicating that form diversity and ecological diversity of lacewings were much higher 100 million years ago.

INTRODUCTION

Neuroptera, the group of lacewings, is one of the smaller ingroups of Holometabola (Aspöck & Aspöck 1999, 2007; Aspöck et al. 2001, 2012; Winterton et al. 2010, 2018). While considered species-poor, especially the larval forms of lacewings show an astonishing degree of morphological differentiation (MacLeod 1964; Aspöck & Aspöck 2007). Lacewings are already quite unusual among

larval forms of Holometabola in not possessing plesiomorphic (ancestral) types of cutting-grinding mouth parts, but a pair of highly specialised piercing-venom-injecting-sucking mouth parts (MacLeod 1964; Aspöck & Aspöck 2007). These are formed by one upper jaw and a part of the lower jaw on each side. Hence all lacewing larvae have a pair of stylets, which may be differentiated in various ways (MacLeod 1964). In many groups the stylets are inward curved, the tips are facing each other. In this way, the stylets provide the counterforce necessary for indeed penetrating prey. This is the case in aphid lions, the larvae of Chrysopidae (green lacewings)

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and also Hemerobiidae (brown lacewings). It is also present in many larvae of Myrmeleontiformia (ant lion-like lacewings), yet here the stylets of many ingroups additionally bear prominent teeth (MacLeod 1964; Badano 2013; Badano et al. 2017, 2018).

In larvae of Nevrothidae there are also proximally straight, but distally curved stylets (Zwick 1967; Malicky 1984). In larvae of Osmylidae (lance lacewings) the stylets are slightly outward-curved (Gepp 1984, 2003; Aspöck 2002; Matsuno & Yoshitomi 2016). Larvae of Sisyridae (spongilla “flies”) have rather long, thin and straight stylets (Gepp 1984; Weißmair 1999). The stylets are shorter but broader and still prominent in larvae of Dilaridae (pleasing lacewings; Gurney 1947; Gepp 1984), Berothidae (beaded lacewings; Gepp 1984; Möller et al. 2006; Monserrat 2006) and Mantispidae (mantis lacewings; MacLeod 1964; Hoffman & Brushwein 1992; Dorey & Merritt 2017; Jandausch et al. 2018; yet also slightly curved stylets occur in some species, MacLeod 1964).

Other mouth parts are small in most groups, at least in comparison to the often impressive stylets. The upper lip is only apparent as such in few groups, but there it can represent a distinct nose-like protrusion, such as in larvae of Nevrothidae (Zwick 1967; Malicky 1984), Dilaridae (Gurney 1947; Gepp 1984) or Psychopsidae (silky lacewings; ingroup of Myrmeleontiformia; Froggatt 1907; Tillyard 1918).

Also the body form appears highly variable. Larvae of Nevrothidae are very elongate and almost worm-like (Malicky 1984). Aphid lions have a more conical, but rather slender body (Tauber et al. 2003, 2014; Tauber 2014). Most of the larvae of ant lion-like lacewings have a rather broad trunk (Badano 2013; Badano et al. 2017; Haug et al. 2019a). Many bodies are rather simple, yet some have very prominent processes for carrying camouflaging objects, as in larvae of Ascalaphidae (owl flies; Badano 2013; Badano et al. 2017) and also in many aphid lions (Toschi 1965; Tauber et al. 2014). Also grub-like bodies occur in later larvae of Mantispidae (Redborg & MacLeod 1985) and in larvae of Ithonidae (moth lacewings; Grebennikov 2004).

Hence, the diversity of morphologies of lacewing larvae is quite astonishing in the modern fauna. Back in the Cretaceous many larvae have been found strongly resembling modern ones

(e.g., Wang et al. 2016; Badano et al. 2018; Haug et al. 2018; Herrera-Flórez et al. 2020; Pérez-de la Fuente et al. 2020). Yet, in addition, there is a number of highly specialised lacewing larvae preserved in Cretaceous ambers which are quite unique and unexpected in their appearance. This includes aphid lion-like forms with very long and prominent camouflaging structures (Pérez-de la Fuente et al. 2012, 2016, 2018, 2019; Wang et al. 2016), aphid lion-like forms with very unusual autecologies (Liu et al. 2016, 2018; Zhang 2017), unusually slender ant lion-like forms (Badano et al. 2018; Haug et al. 2019c), ant lion-like larvae with unusual character combinations (Xia et al. 2015; Zhang 2017; Haug et al. 2019a), larvae that are so unusual that their relationship remains currently unclear (Haug et al. 2019b) and even larvae of which we can guess that they might be lacewings, but it remains unclear (Haug et al. 2020a).

The fact that we find rather many modern appearing lacewing larvae together with numerous types of now extinct larval types back in the Cretaceous indicates that the morphological diversity of lacewing larvae was considerably higher 100 million years ago. Here we report another unusual type of lacewing larvae found in 100-million-year old amber from Myanmar. We use qualitative and quantitative methods for demonstrating the uniqueness of the new larva type. We mostly employ a phenetic frame to evaluate whether the larva indeed represents an unknown morphotype as many characters that would be crucial for phylogenetic analyses are not available in this specimen. The specimen has a prominent nose-like labrum and is therefore compared in detail to larvae of Nevrothidae and Psychopsidae. With this study, we further increase the Cretaceous ‘zoo’ of unusual lacewing larvae, even though preservation of the specimen is not perfect.

MATERIAL AND METHODS

Material

The focus of this study is a single specimen of a lacewing larva preserved in amber from Myanmar, often termed Burmese amber. The age of this type of amber is supposed to be about 100 million years. The specimen was originally purchased on ebay.com from the trader burmite-miner. It is now deposited in the collection of the Palaeo-Evo-Devo (PED) Research Group, Ludwig-Maximilians-University of Munich, Germany, under repository number PED 0284.

Comparative material was based on literature. Data sets were compiled originally by two earlier studies: 1) Haug et al. (2020b), including Froggatt (1907), Tillyard (1918), Withycombe (1925), Ma-

cLeod (1970), New (1989, 1991), Weitschat & Wichard (1998), Aspöck & Aspöck (1999), Perrichot (2003), Scheven (2004), Engel & Grimaldi (2008), Gröhn (2015), Zhang (2017), Badano et al. (2017, 2018), Bakkes et al. (2018), and Makarkin (2018); and 2) Haug et al. (in review), including Takahashi (1942), Zwick (1967), Riek (1970), Gepp (1984), Malicky (1984), Grimaldi & Engel (2005), Aspöck & Aspöck (2010), and Markovič et al. (2016). Additional data are from Beutel et al. (2010).

Documentation methods

Documentation was performed on a Keyence VHX 6000 microscope. We photographed the specimen from both sides, once illuminated by coaxial cross-polarised light (Haug et al. 2013a) and once by unpolarised ring light. Under both illuminations, a white and a black background were used. The images providing the best contrast were used. Each image was documented as a composite (Haug et al. 2008, 2011), which means that each image detail was documented by a stack of images of varying focus; several adjacent images details were recorded covering the entire specimen. Each image was documented under several exposure times (Haug et al. 2013b).

Shape analysis

A comparative statistical analysis of the morphology of the specimens was conducted by visualization of a Principal Component Analysis (PCA) from the results of an Elliptic Fourier analysis. All accessible heads, in total 57, were redrawn by hand in Adobe Illustrator CS2 (Suppl. Fig. 1). Hereby, the better-preserved head half was drawn and mirrored. The resulting image was checked against the original to reduce possible artefacts. Dorsal and ventral view were used. Although there are slight differences between the two views, the important criterion was a well accessible posterior rim of the head capsule.

Re-drawn images were analysed in SHAPE (Iwata & Ukai 2002), a free software providing the tools to perform Elliptic Fourier and PCA analyses. The software transforms the outlines of the head reconstruction drawings into a vectorized object, also called chain code. The vectorized shapes (chain codes) are represented by numeric values, which are then transformed into normalized Elliptic Fourier Descriptors (EFDs). The program uses a vector-based step-by-step approximation of ellipses to the outline of the head, approximating the geometric information of the chain codes as simpler functions, composed of harmonics. This method represents a variation of the well-known Fourier transformation, practically applied on shapes of natural objects. For the Fourier transformation in this analysis we used 20 harmonics. The 57 EFDs were finally analysed with a PCA that resulted in the most important characters for morphological diversity in the data set (Suppl. Tab. 1). The entire procedure including the PCA was applied following Iwata & Ukai (2002); see also Braig et al. (2019). The results of the PCA were visualized using OpenOffice. The most important dimensions (Principal Components) were plotted.

RESULTS

Description of specimen

Body differentiated distinctly into head and trunk (Figs. 1A, B, 2A). Head well preserved, rounded to drop-shaped in dorsal view (Fig. 2B). Anteriorly drawn out into prominent labrum (appendage derivative of ocular segment). Tip of labrum with

short, straight edge. Indications of three stemmata on each side of the head (Fig. 2B). Post-ocular segment 1 recognisable by its pair of appendages, antennae ('antennulae' in more neutral terms for Euarthropoda). Antenna elongate, about as long as head capsule; about as wide (diameter) as width of anterior edge of labrum; no subdivision apparent (Fig. 1B).

Post-ocular segment 2 not recognisable from external structures. Post-ocular segments 3 and 4 recognisable by their pairs of appendages, mandibles and maxillae ('maxillulae' in more neutral terms for Euarthropoda). Mandible and maxilla on each side forming a compound structure, a stylet (Figs. 1B, 2B). Stylet shorter than head capsule, gently curved, tapering distally, overall sickle-shaped in appearance. Proximally wider than antenna, about 2.5x. No indications of to be expected structures of post-ocular segment 5 (labial palps). Unclear if true primary absence or lack due to preservation.

Trunk less well preserved, overall crumpled in appearance, concealing borders of individual sclerites (Figs. 1A, B, 2A). Trunk longer than head, about 7x. Maximum width about as wide as head width. Trunk with three pairs of locomotory appendages, indicating post-ocular segments 6–8. Locomotory appendage 1 (foreleg) arising at about 15% along the trunk length. Locomotory appendage 2 (mid-leg) arising at about 30% along the trunk length. Locomotory appendage 3 (hind leg) arising at about 40% along the trunk. All locomotory appendages appear sub-similar. With five more or less well differentiated elements (corresponding to basipod and four endopod elements in more neutral terms for Euarthropoda) (Fig. 2C). Proximal element, coxa, elongate, slightly wider than stylet in the proximal region; longer than wide, about 3x. Element 2, trochanter, not well set off from next distal one, possibly due to preservational influences. More slender than element 1, also shorter, less than 30%. Element 3, femur, longer than element 1, about 1.3x; more slender than coxa, about 60%. Longer than wide, about 5.3x. Median with indications of serrations. Element 4, tibia, about as wide as element 3, but shorter, about 60%. Longer than wide, about 3.3x. Element 5, tarsus, slightly shorter than element 4, about 80%, also more slender than element 4, about 65%; longer than wide, about 4.1x. Distally with at least one claw and long empodium, longer than claw, about 2x.

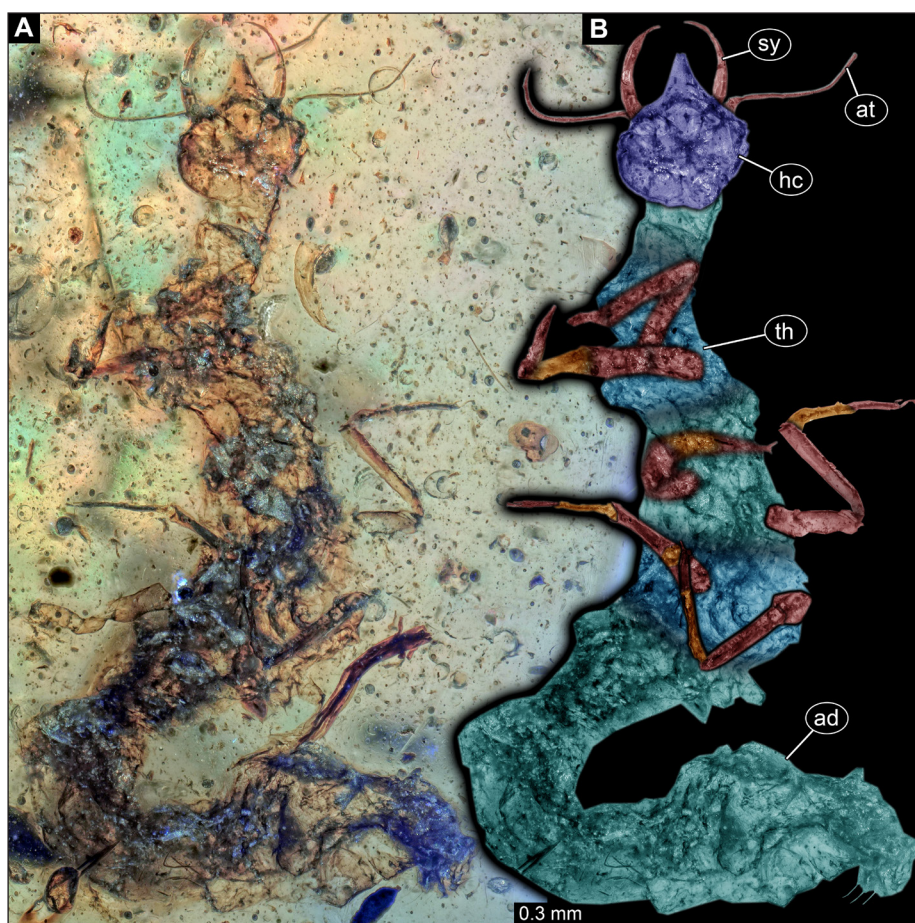


Fig. 1 - Overview of the new type of lacewing larva, PED 0284. A) Composite-micrograph under cross-polarised light, ventral view. B) Colour-marked version of A, background virtually removed. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; sy = stylet; th = thorax.

Further posterior trunk not well preserved, appears overall elongate. Indications of setae, yet setae arrangement not accessible.

Shape analysis

Overall, the principal components (PCs) have rather low explanation values. Also, each PC seems to be dominated by several shape aspects (Suppl. Fig. 2).

PC1 explains about 46% of the overall shape variation. It appears to be influenced by the roundness of the head and the slenderness of the labrum. A low value indicates a rather rectangular head and a rather broad proximal region of the labrum; a high value indicates a more rounded head and a labrum with a rather slender proximal region.

PC2 explains about 21% of the overall shape variation. It appears to be influenced by the position of the maximum width on the head and again the slenderness of the labrum. A low value indicates that the maximum width of the head is far posterior and that the proximal region of the labrum is rather slender; a high value indicates that the maximum width of the head is far anterior and that the proximal region of the labrum is rather broad.

PC3 explains about 10% of the overall shape variation. It appears to be influenced by width of the anterior region of the head and the massiveness of the labrum. A low value indicates that the anterior width of the head is relatively small and that the labrum is rather massive; a high value indicates that the anterior width of the head is relatively large and that the labrum is less massive.

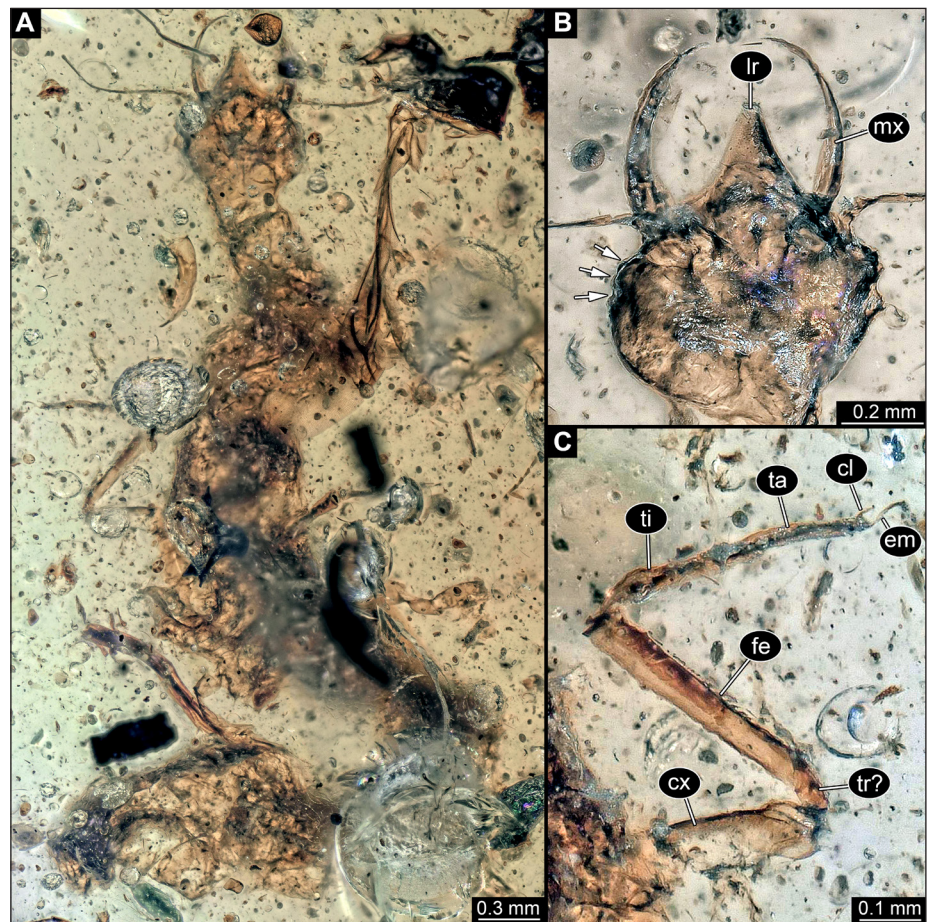
PC4 explains about 8% of the overall shape variation. It appears to be influenced by the shape of the posterior edge of the head capsule. A low value indicates a protruding posterior edge; a high value indicates a straight posterior edge.

PC1–4 sum up to about 85% explanation of shape. All other PCs are below 4% and are not further considered here.

When plotting PC1 against PC2, all data points representing Nevrothidae plot within a smaller area, which is part of a larger area in which the data points representing Psychopsidae plot. The data point representing the new specimen PED 0284 plots outside this area (Fig. 3A).

Looking at the individual principal components reveals that the new specimen differs in all

Fig. 2 - Overview and details of the new type of lacewing larva, PED 0284. A) Overview in dorsal view. B) Close-up on head in ventral view; arrows point to three stemmata. C) Close-up on left second walking appendage (mid-leg). Abbreviations: cl = claw; cx = coxa; em = empodium; fe = femur; lr = labrum; mx = maxilla; ta = tarsus; ti = tibia; tr? = possible trochanter.



aspects from Nevrothidae, i.e. the range of values of Nevrothidae does not include the values of the new larva; it is always larger or smaller (Fig. 3B). The range of values of Psychopsidae is much larger, always including the range of values of Nevrothidae. In most cases also the value of the new specimen lies within this range. Only for PC2, the value of the new specimen lies outside the range of Psychopsidae (Fig. 3B).

DISCUSSION

Preservation

The new specimen appears overall complete, yet especially the trunk region is definitely not well preserved. The surface appears strongly crumpled, the body is not straight, but positioned more or less S-shaped. The combination of these two aspects conceals most of the subdivision of the trunk. The locomotory appendages (walking legs) indicate the position of the three anterior trunk segments (thorax). At least one locomotory appendage is rather well preserved (Fig. 2C), still a clear identification of

element 2 (trochanter) is challenging. The armature of the appendages is also not well preserved, but there are at least indications of serration along the median edge of element 3 (femur).

The best preserved region seems to be the head (Fig. 2B). It appears less crumpled, the overall symmetry indicates that the head capsule shape is in its original condition. The prominent labrum does not appear deformed. Also stylets appear well preserved, as both resemble each other. The antennae are attached, both have the same length, making it likely that they are complete. A clear subdivision is not apparent.

The specimen could represent an exuvium. This would explain the strongly crumpled trunk surface. In most holometabolan larvae the moulting suture will lead to rather deformed head capsules in fossil (see e.g., Perrichot & Engel 2007 for fossil snake fly larvae). However, it seems that in lacewing larvae the head capsule retains a rather natural shape even in the exuvium (see e.g., Monserrat 2008, his fig. 10g). This makes the head capsule a reliable structure for drawing information. Also the preserved appendages, mostly stylets and locomo-

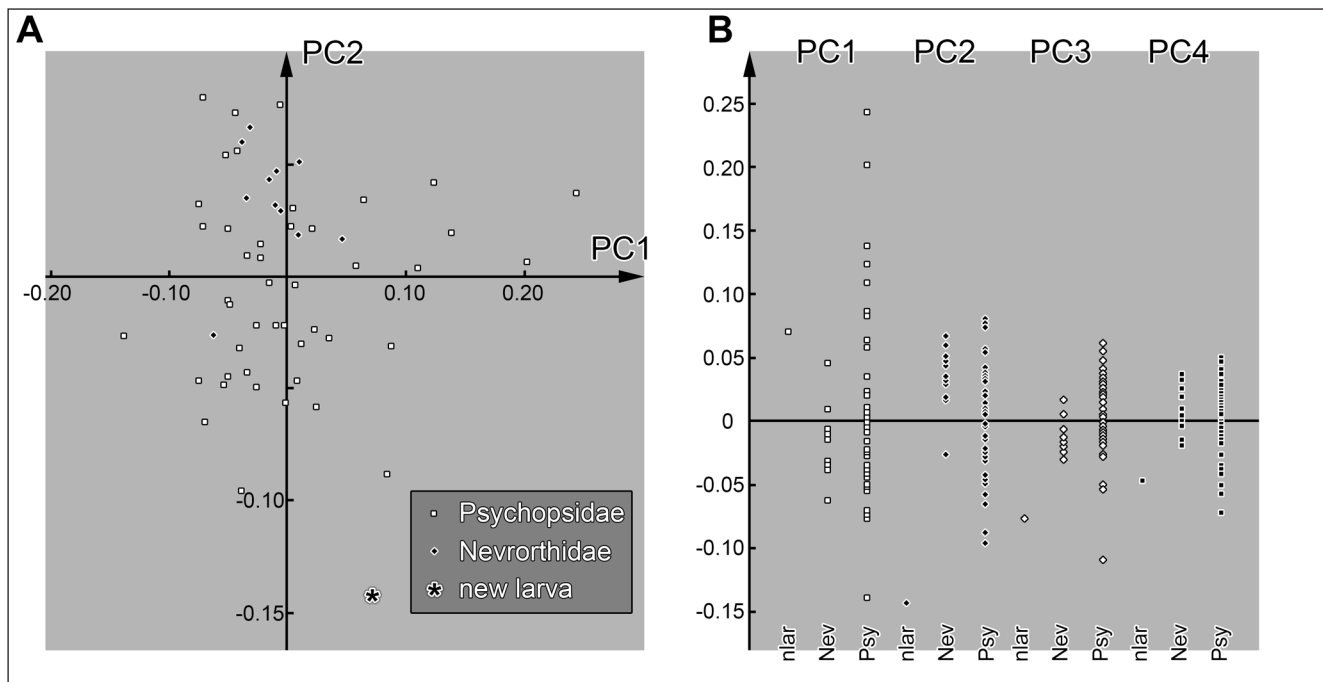


Fig. 3 - Graphical plots of the principal components describing the shape of the head capsules. A) Scatter plot of PC2 over PC1, demonstrating the position of the new larva far outside the range of larvae of Nevrorthidae and Psychopsidae. B) Range of larvae of Nevrorthidae and Psychopsidae concerning PC1 to PC4 and the corresponding PC values of the new larva in comparison; the new larva lies outside the range of the larvae of Nevrorthidae, but within the range of the larvae of Psychopsidae, except for PC2.

tory appendages, can be considered. The trunk is less easy to interpret. It clearly appears significantly longer than the head; it is clearly much longer than wide, hence rather elongate. Yet, it remains difficult to estimate the exact ratios. We can therefore not use a ratio-based identification approach (see e.g., Herrera-Flórez et al. 2020).

Systematic interpretation: the coarser frame

Despite the partly problematic preservation, the available morphological details at least already allow us to identify lineages of Neuroptera in which the morphology of the larvae differs from that of the new fossil. The larva does not possess a grub-like morphology as in larvae of Ithonidae (Grebennikov 2004) or in stage 3 larvae of Mantispidae (Hoffman & Brushwein 1992). It does also not possess the very long and thin mouthparts of larvae of spongilla flies (Sisyridae; Weißmair 1999; Jandausch et al. 2019). Also, it does not possess the very long and outward-curved mouthparts of larvae of lance lacewings (Osmylidae; Gepp 2003). Therefore, it is unlikely that the new specimen is closely related to these groups.

For further discussion, especially the head capsule and mouth parts are quite informative. The new larva has a prominent anterior projection most likely representing the labrum. Comparably prominent labra are known in larvae of only few lineages of Neuroptera, including Nevrorthidae (although here the labrum is usually addressed to as ‘rostrum’; see discussion in Beutel et al. 2010), Psychopsidae (silky lacewings; e.g., Froggat 1907; MacLeod 1964; New 1989, 1991; Bakkes et al. 2018), Coniopterygidae (dusty lacewings; MacLeod 1964; Monserrat et al. 1990), Dilaridae (pleasing lacewings; MacLeod 1964; Monserrat 2005), Berothidae (beaded lacewings; MacLeod 1964) and very few representatives of Myrmeleontidae (e.g., *Acanthaclisis occitanica*; Badano 2013). To a certain degree also the stage 2 and 3 larvae of Mantispidae (mantis lacewings) have a drawn out labrum, but less prominent than in the other groups (MacLeod 1964).

Among these groups, the larvae of Coniopterygidae, Dilaridae, and Berothidae are characterised by straight stylets (Gurney 1947; MacLeod 1964; Gepp 1984; Monserrat et al. 1990; Möller et al. 2006; Monserrat 2006), differing strongly from the gently curved stylets in the new larva. Larvae

of Mantispidae with a recognisable labrum have likewise straight stylets (Hoffman & Brushwein 1992; Dorey & Merritt 2017). Larvae of Mantispidae with curved stylets lack a forward projecting labrum (MacLeod 1964). All larvae of Myrmeleontidae, including the few with a projecting labrum, have prominent teeth in their stylets unlike the new larva. This comparison therefore leaves mostly larvae of Psychopsidae and Nevrorthisidae for closer consideration.

Systematic interpretation: quantitative head shape

Comparing the principal components, which describe the shape of the head, we can see clear differences between two groups of larvae, those of Psychopsidae and Nevrorthisidae, and the new specimen (Fig. 3B). First, Psychopsidae occupy a larger range in each dimension (principal component, PC) than Nevrorthisidae. Yet, this difference is not very telling as the sample size of Nevrorthisidae is significantly smaller than that of Psychopsidae. This difference could therefore represent a simple sample-size artefact.

More telling than the size of the occupied range of one dimension is the relative position within each dimension. The new specimen always plots outside the range occupied by larvae of Nevrorthisidae. The head shape provides therefore no indication that the new specimen is closely related to Nevrorthisidae.

In most dimensions the new specimen lies within the shape range of larvae of Psychopsidae. Yet, in principal component 2 the new specimen lies clearly outside the (quite large) range of Psychopsidae. Hence, while the head shape of the new larva is clearly more similar to that of larvae of Psychopsidae than of Nevrorthisidae, it is still recognisably different. Therefore, there is also no clear indication that the new specimen is closely related to Psychopsidae.

Further differences to Psychopsidae

Besides the quantitative aspects of the head shape there are also quite some qualitative differences between the new larva and the larvae of Psychopsidae. The stylets of the new larva are, in relation to the length of the head capsule, shorter than in larvae of Psychopsidae (Fig. 4A). In the latter, the stylets are more prominent (Fig. 4C).

Another ratio aspect, although more difficult to exactly grasp, is the shape of the trunk. Though the trunk of the new larva is not well preserved, its overall impression is that it is rather slender (Fig. 4A), not as strongly expressed as in Nevrorthisidae (Fig. 4B), but clearly more elongate than in the slenderest larva of Psychopsidae (Fig. 4C). Interestingly, the latter originates also from the amber of Myanmar.

The new larva also lacks some of the smaller details characterising larval forms of Psychopsidae, such as the tubercles on the head capsule or a spine-like seta on the tip of the antenna (e.g., Makarkin 2018). The absence of the tubercles cannot be easily explained by preservational factors. Preservation may explain the absence of a spine-like seta at the tip of the antenna.

Another morphological detail: the empodium

Despite the rather imperfect preservation of the trunk region of the larva, it preserves one interesting detail: the new larva possesses prominent trumpet-shaped empodia on its walking appendages (Fig. 2C). This attachment structure is present in larvae of many ingroups of Neuroptera: Chrysopidae, Hemerobiidae, Berthidae, Rhachiberthidae, Dilaridae, Mantispidae, and Psychopsidae, but absent in other lineages of Neuroptera (Beutel et al. 2010). Given this distribution, an empodium appears to have been lost secondarily within several groups, for example, in Myrmeleontiformia, here only retained in Psychopsidae. Hence, the presence of an empodium in the new larva is not very informative concerning its relationships.

Taxonomic interpretation

Despite the similarity in many shape aspects to larvae of Psychopsidae, it seems unlikely that the new larva is closely related to Psychopsidae. The new larva basically lacks the characterising features of Myrmeleontiformia. The prominent labrum might have evolved repetitively independently within Neuroptera. This leaves the new larva without any real indication where it could be closer related to.

It remains therefore largely unclear whether a possible adult has already been formally described, which is always the danger when formally describing a new species based on a larval specimen. Even if the possible corresponding adult has not already

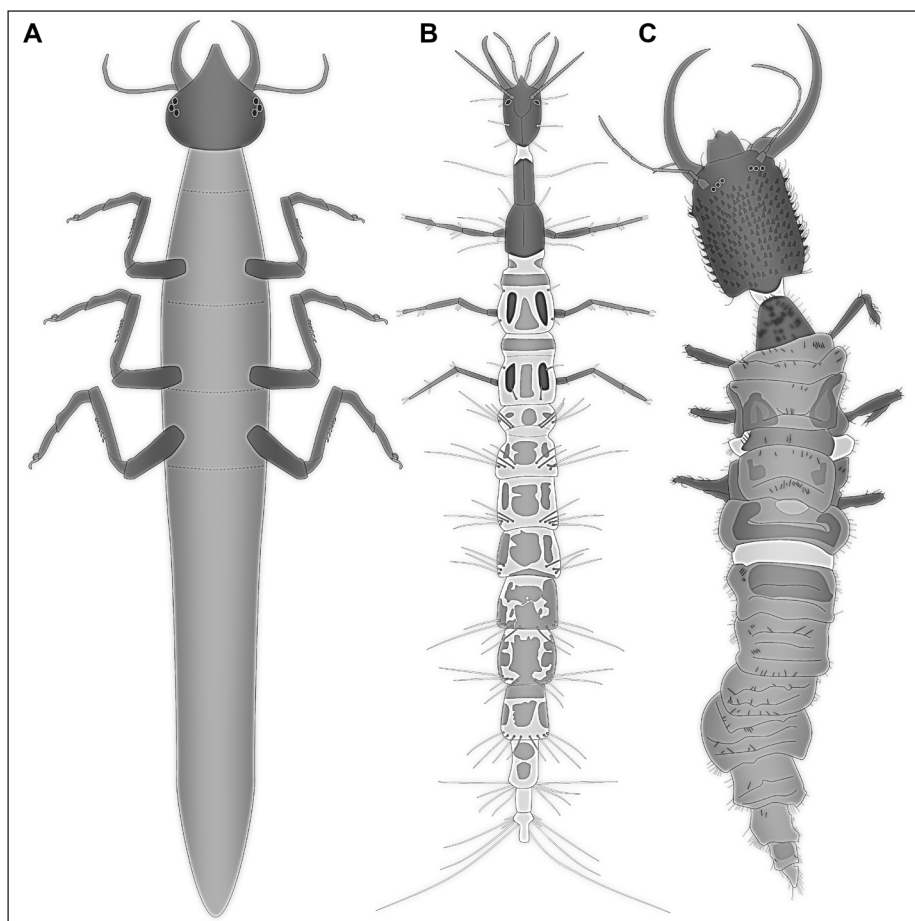


Fig. 4 - Tentative restoration of the new type of lacewing larva and specimens for comparison. A) New larva, PED 0284, ventral view. B) Larva of an extant representative of *Nevrothus* sp. (Nevrothidae; from Gepp 1984, his fig. 12a), dorsal view. C) Larva of a fossil representative of Psychopsidae from Cretaceous Burmese amber (from Makarkin 2018, his fig. 5B), dorsal view. Not to scale.

been formally described, the future formal description of a possible adult will complicate the situation.

It is possible by careful differential diagnosis to recognise a new larval form as a representative of a new species. This is especially well possible if a finer graded evolutionary framework is available, as performed for some lacewing larvae (Badano et al. 2018). Even a coarser phylogenetic consideration might already be well suited (Pérez-de la Fuente et al. 2018, 2019 for lacewings; Haug et al. 2015a, b; Hyžný et al. 2016; Schädel et al. 2019a, b, 2020 for other groups of Euarthropoda) for providing a reliable frame. Yet, in many cases the phylogenetic frame remains too unclear, even after careful consideration (Hörnig et al. 2014, 2016, 2019; Haug et al. 2015c, d, 2019a, b; Serrano-Sánchez et al. 2016), or the available comparison is so scarce that no proper differential diagnosis can be provided (Haug & Haug 2019). In such a case, it is in our view not appropriate to formally erect a new species. As the phylogenetic position of the new specimen is so uncertain, we refrain from formally describing a new species based on it. It appears to be generally assumed that species names would provide an

easier communication. We agree that a ‘name tag’ indeed makes communication easier, but follow the approach of using a nickname for doing so (Haug et al. 2016, 2019a, b, c). The new larva possesses a prominent labrum that is especially large in relation to the head capsule. We therefore suggest the nickname ‘supernose’ to refer to the prominent nose-like labrum in the new larva.

Impact of the new larva

This is not the first case of such an unusual larva that cannot be easily interpreted in a phylogenetic framework. In fact, mostly the work of Badano et al. (2018) managed to identify some unusual larvae as being related to specific modern lineages, mostly within Myrmeleontiformia. For most of the other lacewing larvae from the Cretaceous only coarser phylogenetic interpretations are possible so far. For example, many of them have been interpreted as being closely related to Chrysopidae (Pérez-de la Fuente et al. 2012, 2018, 2019; Liu et al. 2016, 2018), yet without a more precise phylogenetic consideration. Other larvae show mixtures of morphological features, which as isolated features

characterise certain modern lineages, but are not known from modern representatives in these specific combinations. Hence, such forms currently remain in an unresolved position within Myrmeleontiformia (Haug et al. 2019a, c). Other larvae cannot even be narrowed down that far (Haug et al. 2019b) and basically remain Neuroptera incertae sedis. The new larva seems to fall into this last category as well.

The new fossil represents a distinct morphotype of a lacewing larva characterised by a prominent nose-like labrum leading to a distinct derived shape of the head capsule that differs from other larvae with such a nose-like labrum (Psychopsidae and Nevrorthidae). Otherwise, many plesiomorphic characters are retained, such as simple-curved toothless mandibles, presence of empodia and an elongate, slender trunk.

The new larva, hence, does currently not provide a deeper insight into the phylogenetic relationships of Neuroptera (but may potentially do so if, for example, further specimens are found providing additional morphological details). Yet, it again adds a new larval morphotype to the Cretaceous ‘zoo’ of lacewing larvae. The indications keep growing that back in the Cretaceous the morphological diversity and most likely also the ecological diversity of lacewings, and especially of lacewing larvae, was much higher than in the modern fauna.

This appears to be true within recognisable ingroups, such as Myrmeleontiformia (Badano et al. 2018), and even further ingroups of it, such as Psychopsidae (Haug et al. 2020b). It furthermore also applies to the large group of Neuroptera as a whole. It remains still partly unclear when exactly the large loss of neuropteran larval diversity occurred. Currently, we have a very massive fossil record of larval lacewings in the Cretaceous. In younger ambers we find quite fewer specimens, about more than a dozen in Eocene ambers and only about half a dozen in Miocene ambers (Pérez-de la Fuente et al. 2020). Quantitative comparisons of larval silky lacewings indicate that the loss might have occurred after the Cretaceous-Palaeogene mass extinction.

For a reliable quantitative analysis for estimating changes of the larval diversity of the entire group of Neuroptera we need to increase the data set, especially for the younger ambers. Yet, also for the Cretaceous, new specimens adding new morphologies (qualitatively and quantitatively) as the

here reported specimen, are an important add-on for a future larger-scale analysis.

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