A split-footed lacewing larva from about 100-million-year-old amber indicates a now extinct hunting strategy for neuropterans

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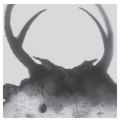

In larvae of lacewings (Neuroptera), each mandible is conjoined with its corresponding maxilla (upper and lower jaws) forming a stylet. Stylets are specialized for piercing, liquefying and sucking the tissues of their prey. The shape, length and thickness of the stylets can differ immensely among larvae of different in-groups of Neuroptera. In addition, the stylets may possess a single tooth or multiple teeth of various sizes and positions, or may totally lack teeth. The larvae of split-footed lacewings (Nymphidae) are often characterized by a single tooth on each stylet and a relatively wide head capsule. The tooth in known larvae is arranged in the plane of movement of the stylet itself, as also often seen in other lacewing larvae. Here we describe and analyse a new type of fossil representatives of Nymphidae from about 100-million-year-old Kachin Myanmar amber. The new fossil type has a special morphology with prominent lateral processes on the head capsule and a single prominent tooth per stylet. The fossil type differs from all the other known larvae of Nymphidae by the arrangement of the tooth: it extends outside of the plane of movement of the stylets. Similar arrangements of teeth or spines outside of the plane of movement also occur in some raptorial appendages of other representatives of Euarthropoda, where they form a grasping basket. We discuss the implications of this unusual fossil type, concerning its functional morphology and ecology. • Key words: Nymphidae, Kachin amber, Myanmar, Cretaceous, quantitative morphology, raptorial appendages.

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Lacewing larvae (Neuroptera) are, mostly, fierce predators, as prominently demonstrated by the widely known larvae of antlions. A key feature of lacewing larvae is the structure of their mouthparts: each upper jaw forms a distinct stylet with its corresponding lower jaw; hence each lacewing larvae bears a pair of stylets, which are far anterior on the head (prognathous). The stylets allow to pierce the prey, to inject neurotoxic venom followed by saliva, and finally the liquefied tissues can be sucked through the stylets (*e.g.* MacLeod 1964, Aspöck & Aspöck 2007, Zimmermann *et al.* 2019).

Mostly the stylets are elongate and curved to allow a counteraction for penetrating the prey easier. In some larvae, the stylets are straight or even outward curved (*e.g.* MacLeod 1964). One larger ingroup of Neuroptera, Myrmeleontiformia, the group of antlion-like lacewings, is characterised by an additional specialisation of the stylets, namely teeth. Such teeth can be lost in some lineages; in some cases this is apparent during ontogeny (see discussion in Haug *et al.* 2019a). Among modern representatives, smaller teeth are known in some larvae of thread-winged lacewings (Crocinae; see discussion in Haug *et al.* 2021a) and spoon-winged lacewings (Nemopterinae; Monserrat 1996: p. 104, Haug *et al.* 2021b). Prominent teeth occur in larvae of the group Myrmeleontidae + Ascalaphidae (Badano 2012, Badano & Pantaleoni 2014a, b; monophyly of ingroups currently unclear, *e.g.* Machado *et al.* 2019, Badano *et al.* 2021) and also in larvae of split-footed lacewings (Nymphidae; *e.g.* MacLeod 1964, Haug *et al.* 2022a). Among the modern groups, there is a certain variation in the number of teeth, but three is rather common (MacLeod 1970: p. 165), besides in split-footed lacewings which usually have a single one (*e.g.* New 1982, 1983; New & Lambkin 1989; Haug *et al.* 2022a).

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Among fossil myrmeleontiformian larvae, the arrangement of teeth appears to be even more variable. Some of them have a much higher number, up to ten teeth (Badano *et al.* 2018; Haug *et al.* 2019b, 2021a, b; Luo *et al.* 2022) or have teeth with more than one cusp (Badano *et al.* 2018: fig. 3d, Haug *et al.* 2021c: fig. 3d).

It appears that the teeth play a role in immobilising the prey. The stylets are functionally raptorial appendages. Also in raptorial appendages of other representatives of Insecta, protruding structures have evolved, here mostly named spines or setae (see discussion of some of these terms, *e.g.* in Pérez-de la Fuente & Peñalver 2019). In lacewing larvae, the teeth are arranged in the plane of movement. In raptorial appendages of other representatives of Insecta, the protrusions may also be arranged in this plane, but also above or below the plane of movement.

Here we report a new fossil type of lacewing larvae preserved in about 100-million-year-old Kachin amber from Myanmar. The new type of larva has a single tooth on each stylet, similar to split-footed lacewing larvae. Yet, the tooth is very long and is projecting below the plane of movement of the stylets. We discuss the implications of this unusual fossil type concerning its functional morphology and ecology.

Material and methods

Material. – Two specimens are in the centre of this study. Both are preserved in about 100-million-year-old Kachin amber, Myanmar (Cruickshank & Ko 2003, Shi *et al.* 2012, Yu *et al.* 2019). The specimens were legally purchased on ebay.com from the traders "cretaceous-burmite" and "burmite-miner". The specimens are now deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München, Germany (LMU Munich), Germany, under repository numbers PED 1795 and PED 2040.

Documentation methods. – The amber pieces were prepared with a drop of glycerine and a cover-slip, fixed with modelling clay to provide an even surface and to get the best possible angle on the posterior and anterior sides of the specimen. A Keyence VHX 6000 digital microscope was used for documentation under white light. The specimens were photographed from both sides using various combinations of illumination: unpolarized low-angle ring light, either in front of white or black background or in combination with transmitted light on a transparent background; cross-polarised co-axial light in front of white or black background or in combination with transmitted light on a transparent background; or transmitted light on a transparent background. All the images were recorded as composite images and processed using the built-in software of the Keyence VHX 6000 digital microscope. Images were recorded as regular versions and additionally with HDR. Images with the best contrast of details were used for the presentation (Haug *et al.* 2019c).

In addition, the heads of the specimens were documented on a Keyence BZ 9000 fluorescence microscope. The specimens were illuminated with transmitted light, and stacks of images were recorded. The stacks of images were processed following Haug *et al.* (2009, 2012).

The images were further optimised (histogram, sharpness, saturation) with Adobe Photoshop CS2. The distinguishable structures were colour-marked to provide the reader with an interpretation of the observed details.

Shape analysis. – For the shape analysis, the head capsule and stylet of PED 1795 were redrawn with Inkscape and Adobe Illustrator CS2. PED 2040 is preserved in a too oblique position for a reliable shape drawing. Elliptic Fourier Analysis followed by a Principal Component Analysis (PCA) was performed using SHAPE (© National Agricultural Research Organization of Japan); we re-used parts of the data set from Haug *et al.* (2022a) and added the new specimen PED 1795. The procedure follows Iwata & Ukai (2002) and Braig *et al.* (2019). SHAPE transforms an ellipse step-by-step to approximate the drawn outlines and turns them into a vectorized shape (chain code). This shape is represented by numeric values, which can be transformed into normalized Elliptic Fourier Descriptors (EFDs) and then be analysed with PCA. The results were visualized with OpenOffice and redrawn in Adobe Illustrator CS2. The two most important dimensions (principal components) PC1 and PC2 were plotted against each other.

Results

Description of the specimen PED 1795

Specimen PED 1795 is partly obscured by other inclusions and impurities in the amber piece (Fig. 1). It is accessible from the dorsal and ventral side.

The total body length is approximately 6.61 mm. The body is differentiated into anterior head with short neck region (cervix) and posterior trunk (Fig. 1A–C). The head is prognathous, mouthparts facing forwards. The head capsule is oval to rectangular in ventral view with concave posterior rim left and right of medial line; it is wider than long, × 1.75 (~ 1.27 mm long) (Fig. 2A, D). The lateral rims of the head capsule possess triangular protrusions, in ventral view (Fig. 2D). The left rim shows five protrusions; the right rim shows four protrusions, the fifth one (the most posterior one) possibly being damaged. The most anterior protrusion is the largest of the series (~ 0.34 mm long, ~ 0.28 mm wide proximally at its widest point),

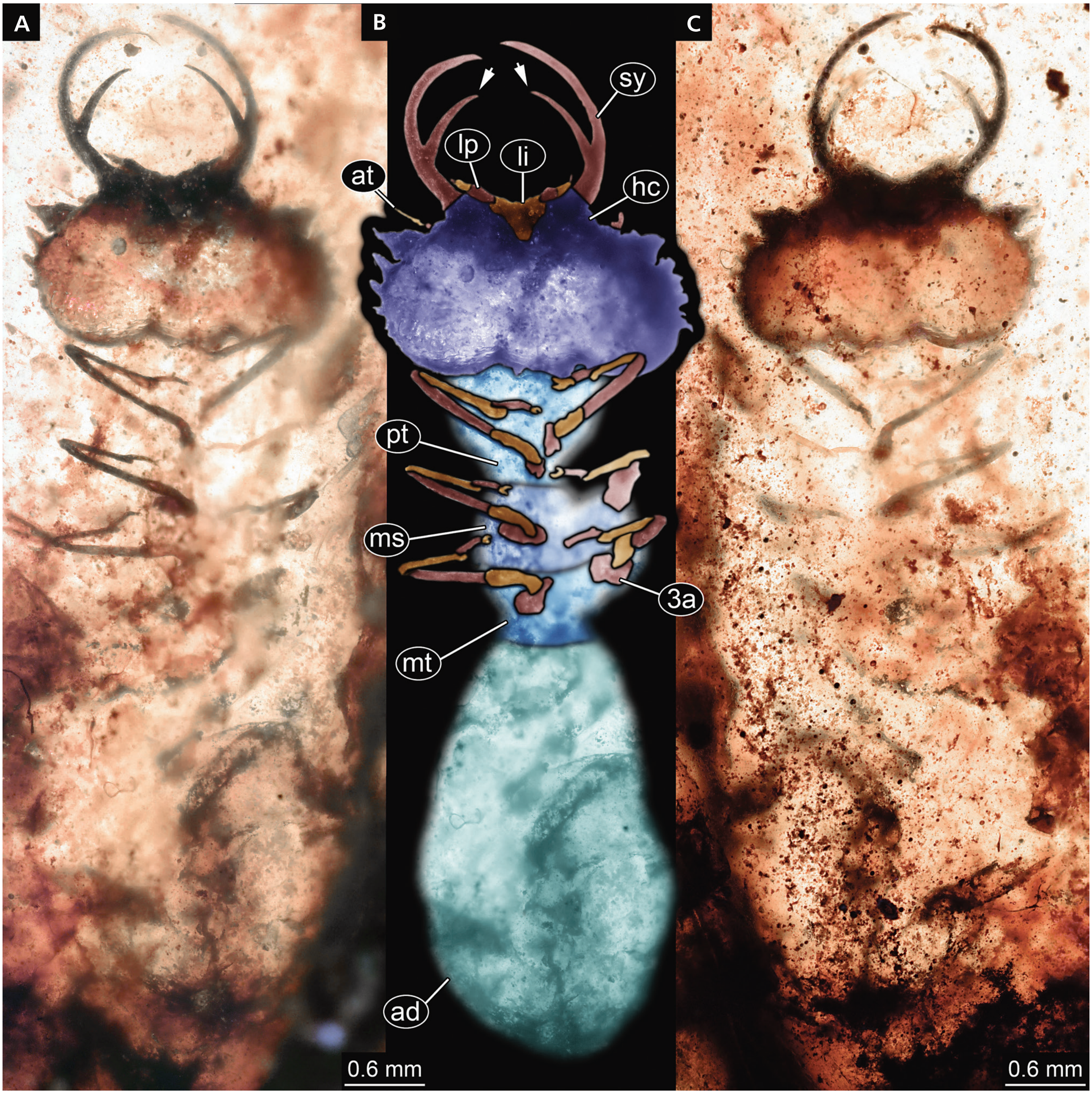

Figure 1. Overview of the new larval type, PED 1795. A – overview in ventral view with transmitted light and ring light. B – colour-marked version of A. C – overview in dorsal view with transmitted light and ring light. Abbreviations: ad – abdomen; at – antenna; hc – head capsule; li – labium; lp – labial palp; ms – mesothorax; mt – metathorax; pt – prothorax; sy – stylets; 3a – (locomotory) appendage 3.

the following ones are progressively shorter, the middle anterior protrusion is ~ 55% of the anterior protrusion (~ 0.19 mm long), the middle protrusion is ~ 40% of the anterior protrusion (~ 0.13 mm long), the middle posterior protrusion is ~ 30% of the anterior protrusion (~ 0.1 mm long), the posterior protrusion is not accessible well enough for measuring (Figs 1C, 2A).

Stemmata (larval eyes) or labrum (structures of ocular segment) are not discernible. The antennae ('antennulae', appendages of post-ocular segment 1) are partly accessible, with at least two elements, the distal element being accessible, elongate, tapering towards the tip, ~ 20% of head capsule length (~ 0.28 mm long). The intercalary segment (post-ocular segment 2) has no externally recognizable structures.

Mandibles (appendages of post-ocular segment 3) and maxillae ('maxillulae', appendages of post-ocular segment 4) are conjoined into stylets. The stylets are strongly sclerotized, sickle-shaped in ventral view, longer than the head capsule, × 1.3 (~ 1.68 mm long), each with a prominent

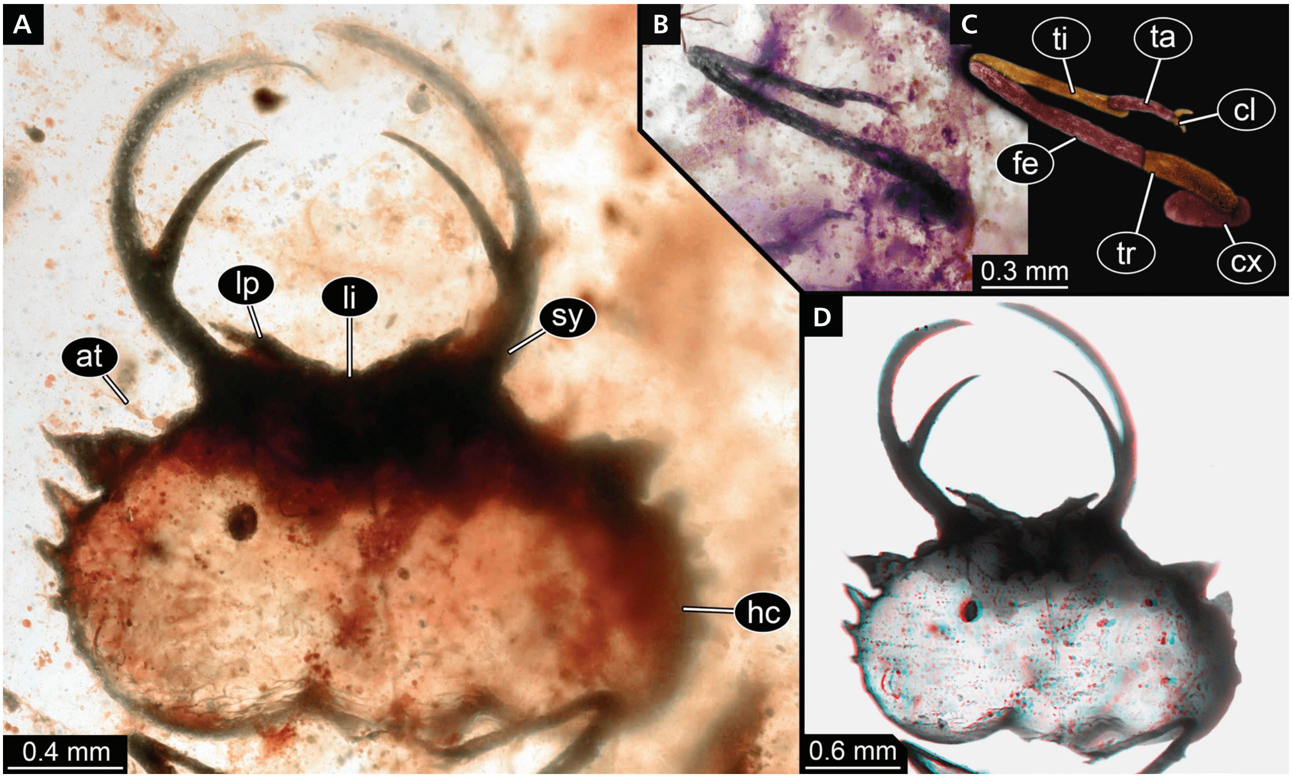

Figure 2. Details of the new larval type, PED 1795. A – head capsule with lateral protrusions in ventral view (close-up from Fig. 1A). B – locomotory appendage (leg) (close-up from Fig 1A). C – colour-marked version of B. D – stereo anaglyph of the head capsule. Abbreviations: at –antenna; cl – claw; cx – coxa; fe – femur; hc – head capsule; li – labium; lp – labial palp; sy – stylets; ta – tarsus; ti –tibia; tr – trochanter.

single tooth (~ 0.67 mm long); each tooth is slightly forward-inward curved and pronounced ventrally curved (Fig. 2).

The labium (‘maxillae’, conjoined appendages of post-ocular segment 5) is longer than wide, × 1.6 (~ 0.34 mm long), the proximal part is deeply embedded in the head capsule sclerites; the distal parts, palps, are composed of three elements (~ 0.44 mm long) (Fig. 2D). The neck region is short, wider than long, × 3.3 (~ 0.3 mm long).

The trunk is further differentiated into an anterior region, the thorax, and a posterior region, the abdomen. The thorax is elongated, longer than wide (~ 1.97 mm long), with three segments (pro-, meso-, and metathorax). The prothorax is trapezoid in ventral view and has a concave anterior rim (~ 0.76 mm long, ~ 1.21 mm wide at its widest point); it is also the longest and widest segment of the thorax. One side of the posterior part is possibly ripped out. Meso- and metathorax are partially torn apart. Each thorax segment possesses ventrally a pair of locomotory appendages (legs).

The legs are about 2.36 mm long (Fig. 1A–C), each with five major elements, coxa (‘basipod’, ~ 0.32 mm long) and four distal elements (‘endopod’): trochanter (~ 0.16 mm long), femur (~ 1.07 mm long), tibia (~ 0.56 mm long), tarsus (~ 0.19 mm long); tarsus distally with a pair of claws (~ 0.06 mm long; Fig. 2B, C).

The abdomen is only vaguely discernible; it is longer than wide (~ 3.53 mm long), widest in the middle, wider than the thorax, tapering posteriorly.

Second specimen PED 2040

Specimen PED 2040 represents an isolated head and part of a prothorax (Fig. 3). It closely resembles specimen PED 1795 and is therefore not described in detail here.

Shape analysis of the head capsule and stylet

The analysis of the head capsule and stylet resulted in six effective principal components (PCs; Suppl. Text 1, Suppl. Files 1–5). Principal component 1 (PC1) explains 58.87% of the overall variation. It is dominated by the relative position of the stylets on the head capsule, but also by the position of the tooth on the stylet. Low values indicate a far lateral insertion of the stylet and a rather proximal position of the tooth. High values indicate a further median insertion of the stylet and a further distal position of the tooth (Suppl. Fig. 1).

Principal component 2 (PC2) explains 10.24% of the overall variation. It is dominated by the relative length of

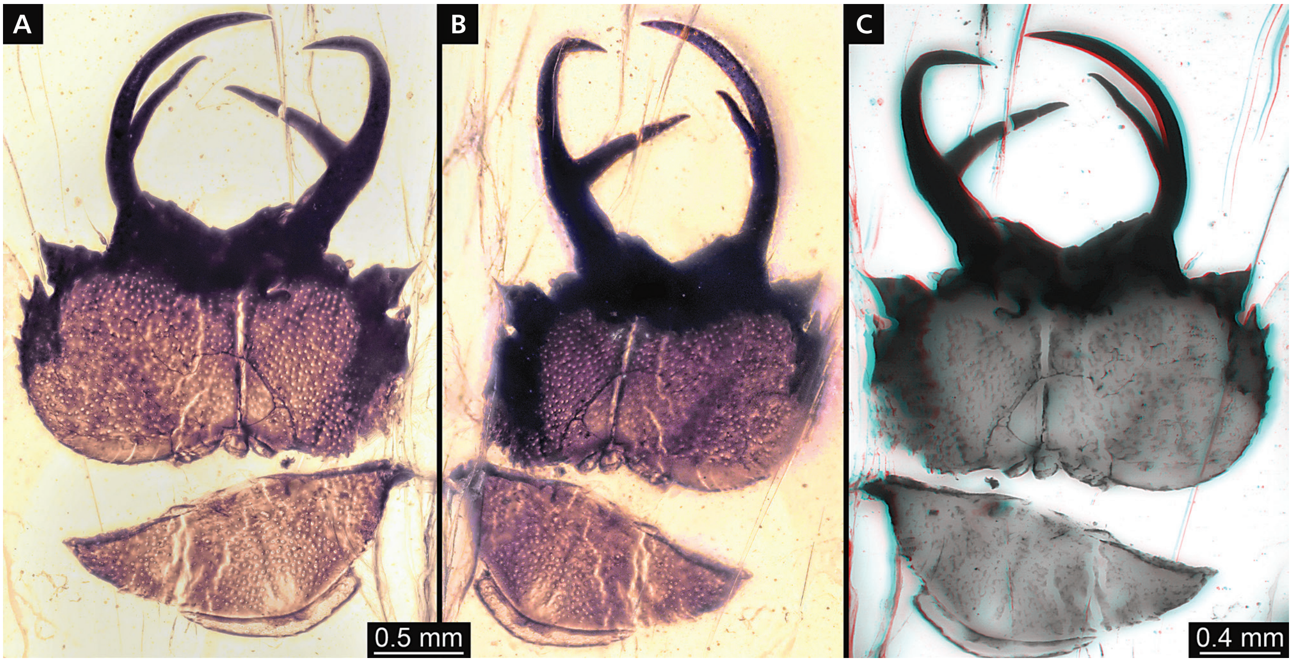

Figure 3. Details of the new larval type, PED 2040, head capsule and part of prothorax. A – ventral view. B – dorsal view. C – stereo anaglyph in dorsal view.

the head capsule, but also by the thickness of the distal tip of the stylet. Low values indicate a relatively shorter head capsule and a thin distal tip of the stylet. High values indicate a relatively longer head capsule and a thicker distal tip of the stylet (Suppl. Fig. 1).

Principal component 3 (PC3) explains 8.54% of the overall variation. It is dominated by the curvature of the stylet. Low values indicate a more curved stylet. High values indicate a less curved stylet (Suppl. Fig. 1).

Principal component 4 (PC4) explains 6.04% of the overall variation. It is dominated by the thickness of the distal part of the stylet and of the tooth. Low values indicate a thinner distal part and tooth. High values indicate a thicker distal part and tooth (Suppl. Fig. 1).

Principal component 5 (PC5) explains 4.93% of the overall variation. It is dominated by the position of the tooth. Low values indicate a further proximal position of the tooth. High values indicate a further distal position of the tooth (Suppl. Fig. 1).

Principal component 6 (PC6) explains 2.80% of the overall variation. It is dominated by the relative size of the tooth. Low values indicate a more prominent tooth. High values indicate a less prominent tooth (Suppl. Fig. 1).

Shape analysis of the stylet

The analysis of the stylet resulted in six effective principal components (PCs; Suppl. Text 2, Suppl. Files 6–10). Principal component 1 (PC1) explains 49.19% of the overall variation. It is dominated by the position of the tooth. Low values indicate a far distal position of the tooth. High values indicate a far proximal position of the tooth (Suppl. Fig. 2).

Principal component 2 (PC2) explains 21.88% of the overall variation. It is dominated by the prominence of the tooth in relation to the entire stylet. Low values indicate a rather indistinct tooth. High values indicate a very prominent tooth (Suppl. Fig. 2).

Principal component 3 (PC3) explains 13.22% of the overall variation. It is dominated by the thickness of the distal part of the stylet. Low values indicate a far distal position of the tooth. High values indicate a far proximal position of the tooth (Suppl. Fig. 2).

Principal component 4 (PC4) explains 7.03% of the overall variation. It is dominated by the prominence of the tooth in relation to the entire stylet and the thickness of the distal part. Low values indicate a not very prominent tooth and a thick distal part. High values indicate a prominent tooth and a thin distal part (Suppl. Fig. 2).

Principal component 5 (PC5) explains 2.25% of the overall variation. It is dominated by the curvature of the entire stylet. Low values indicate a straighter proximal part of the stylets. High values indicate a gently curved stylet (Suppl. Fig. 2).

Principal component 6 (PC6) explains 1.78% of the overall variation. It is dominated by the shape of the tooth. Low values indicate a broad tooth. High values indicate a slimmer tooth (Suppl. Fig. 2).

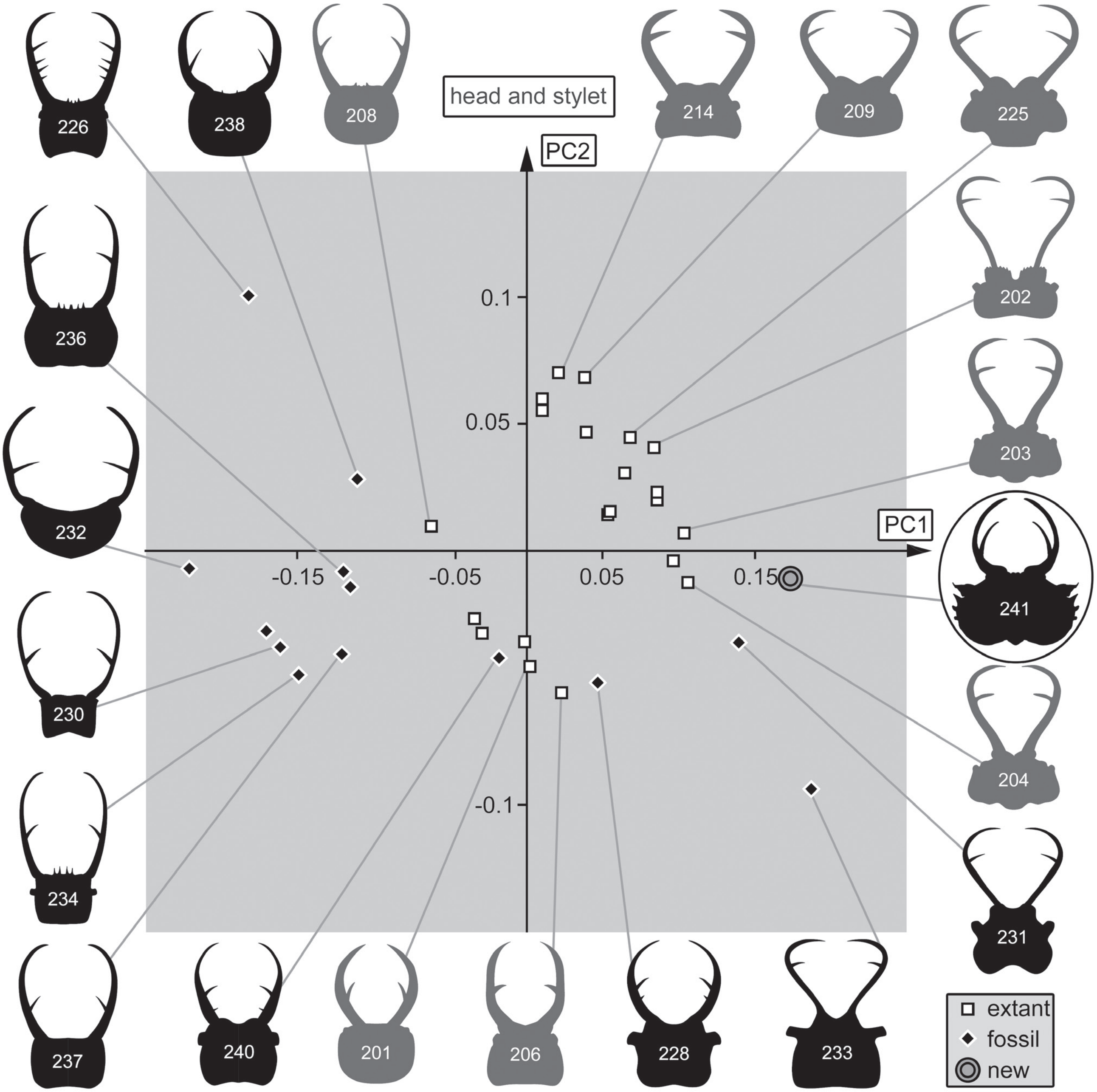

Figure 4. Scatterplot of principal components PC2 *vs*. PC1 values of head and stylet shapes of fossil and extant larvae of split-footed lacewings including the new specimen PED 1795.

Discussion

Identity of the new larval type

A very prominent structure of the new larval type is the large pair of forward-projecting mouthparts, the stylets. Other apparent mouthparts are only the rather inconspicuous labial palps. This combination safely identifies the specimens as larvae of the group Neuroptera.

The single prominent tooth is especially known in larvae of split-footed lacewings (Nymphidae).

MacLeod (1970: p. 165) mentions that also larvae of Nymphidae may have more teeth (especially in fossil forms) and also larvae of other groups may have only one tooth. Still, the overall morphology of the larvae, for example, the rather wide head capsule, is well compatible with an interpretation of the larvae as representatives of Nymphidae.

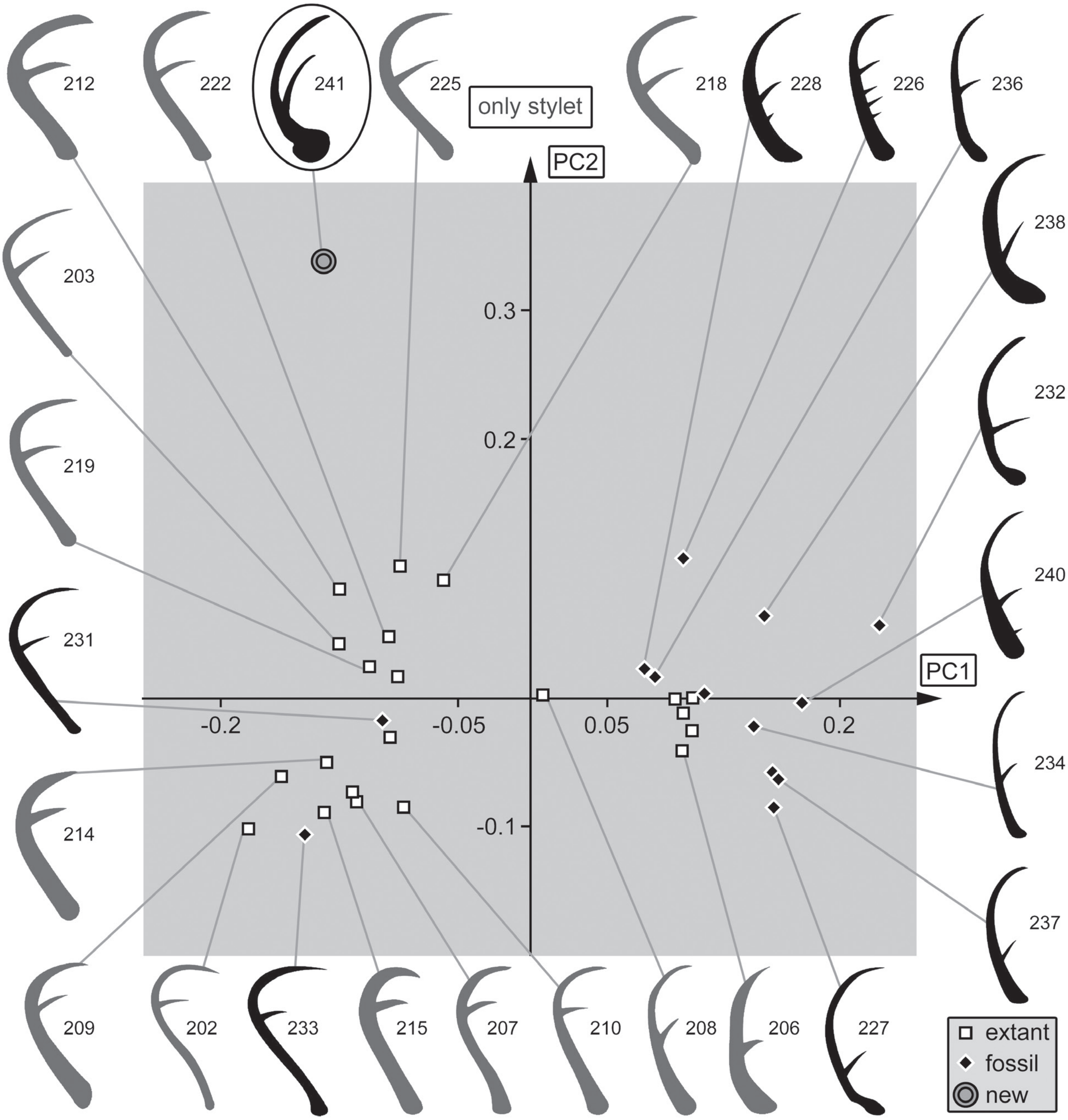

Figure 5. Scatterplot of principal components PC2 *vs*. PC1 values of stylet shapes of fossil and extant larvae of split-footed lacewings including the new specimen PED 1795.

The unusual arrangement of the tooth on the stylets

Despite the fact that the new larval type has large overall similarities with known fossil and extant larvae of split-footed lacewings, it also differs from the known ones. This becomes apparent in the shape analysis. In the analysis of head and stylet shape, the new specimen PED 1795 plots not far away from known fossil ones (Fig. 4), but further right (higher PC1 values) than any of the known fossil ones. The head capsule is very broad in the new fossil type, broader than in other fossil larvae, in this aspect more similar to some extant ones (*e.g.* Badano *et al.* 2017: fig. 1e, Haug *et al.* 2022a: fig. 1.25). Another factor contributing to this dimension is the relative position of the stylets on the head capsule. High values, as in the new fossil type, indicate a rather median insertion. The relative insertion of the stylets is, of course, coupled to the overall width of the head capsule: the wider the head capsule is, the further median the insertion of the stylets can appear in relation to the lateral rim. The width of the head capsule of the new fossil type is additionally influenced by the unusual prominent lateral protrusions not seen in other larvae, giving it an even wider appearance. The position of the new larval type in this plot is therefore well understandable.

Yet, the real difference appears to be the morphology of the stylets. In the analysis of the stylets, the new specimen PED 1795 plots far apart from all other larvae in PC2 (Fig. 5). This dimension is dominated by the prominence of the tooth in relation to the entire stylet, and the new larva is special in having a tooth that is very prominent. Therefore, also this position in the plot is well comprehensible and emphasises the special condition of the stylet of the new larval type.

Besides these quantitative aspects, it is a qualitative aspect of this tooth of the stylet that is very unusual. In other toothed stylets, the teeth are arranged in the plane of movement, which means that in lateral view the teeth are not visible. This is well demonstrated, for example, for the larvae of the group Myrmeleontidae + Ascalaphidae by the excellent documentation of Badano and co-workers (Panteleoni & Badano 2012; Badano *et al.* 2017, 2018). This arrangement with the teeth in the plane of movement is also present in other extant lineages, but also in fossils with toothed stylets (Badano *et al.* 2018: fig. 3c, p. 5).

In the new fossil type, this is different, which becomes already obvious in the non-stereo images (Figs 1A, B; 2A; 3A, B). As the amber is not as clear as in other cases, it is well possible to see that the tip of the stylet and the tip of the tooth are not in the same plane.

It becomes even clearer when looking at the stereo anaglyphs (Figs 2D, 3C). The tooth curves not only forward-inward, but additionally ventrally. The joints of the stylets are rather inflexible concerning the plane of movement; hence this arrangement cannot be explained by a dislocation or similar reason.

Also the tooth itself is not straight, but gently curved. This curvature appears to be the same on both sides, indicating that this unusual arrangement is indeed original morphology.

Comparison to other raptorial appendages

In other raptorial appendages, protrusions (spines, setae) can be arranged like the protrusions (teeth) in most myrmeleontiformian stylets, *i.e.* with the protrusions in the plane of movement.

In the distal part of the sub-chelate major raptorial claws of spearer-type mantis shrimps (Stomatopoda: Verunipeltata), this is the case (Ahyong 2001). Here the protrusions pierce the prey; an effective penetration is only possible when the protrusions are indeed arranged in the plane of movement; otherwise, the generated forces would be oblique to the prey and lead to pushing away the prey instead of penetrating it. In a comparable way, the tips of stylets are facing in the plane of movement in lacewing larvae. In other marine crustaceans, fossil and extant, similar claws to those of mantis shrimps are known (Pazinato *et al.* 2021).

In the proximal region of sub-chelate claws, the protrusions need to be slightly shifted off the plane of movement in order to allow the distal part to have space for folding in. Hence, here the protrusions are slightly off the plane, but parallel to it. This arrangement is well observable also in spearer-type mantis shrimps, in adult mantis lacewings (Mantispidae; *e.g.* Machado 2007:

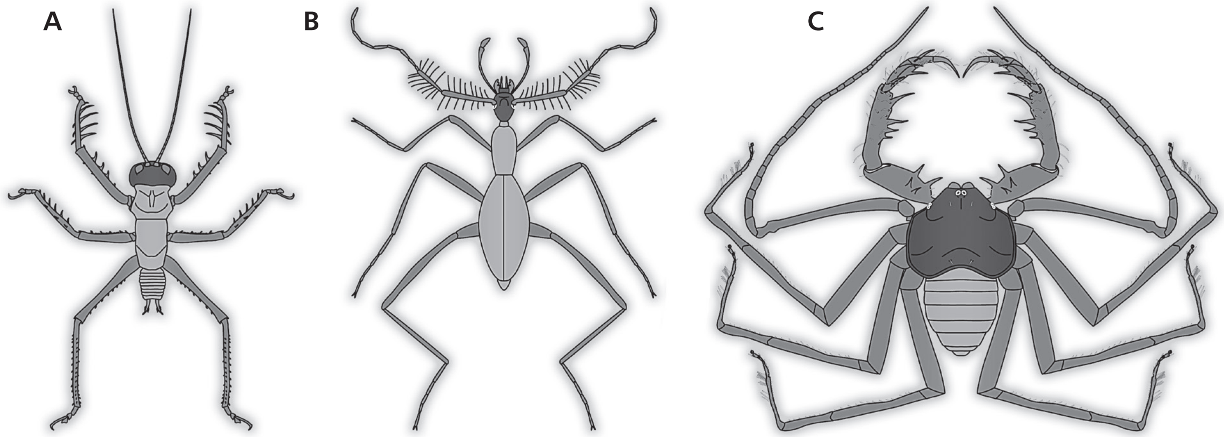

Figure 6. Comparison to other raptorial appendages in which the protrusions are not in the plane of movement; simplified representations. • A – raptorial cricket *Cerberodon viridis* (extant; modified after Fialho *et al.* 2014). • B – ant-like stone beetle *Clidicostigus arachnipes* (Cretaceous amber; modified after Jałoszyński *et al.* 2017). • C – whip spider *Paracharonopsis cambayensis* (Eocene amber; modified after Engel & Grimaldi 2014).

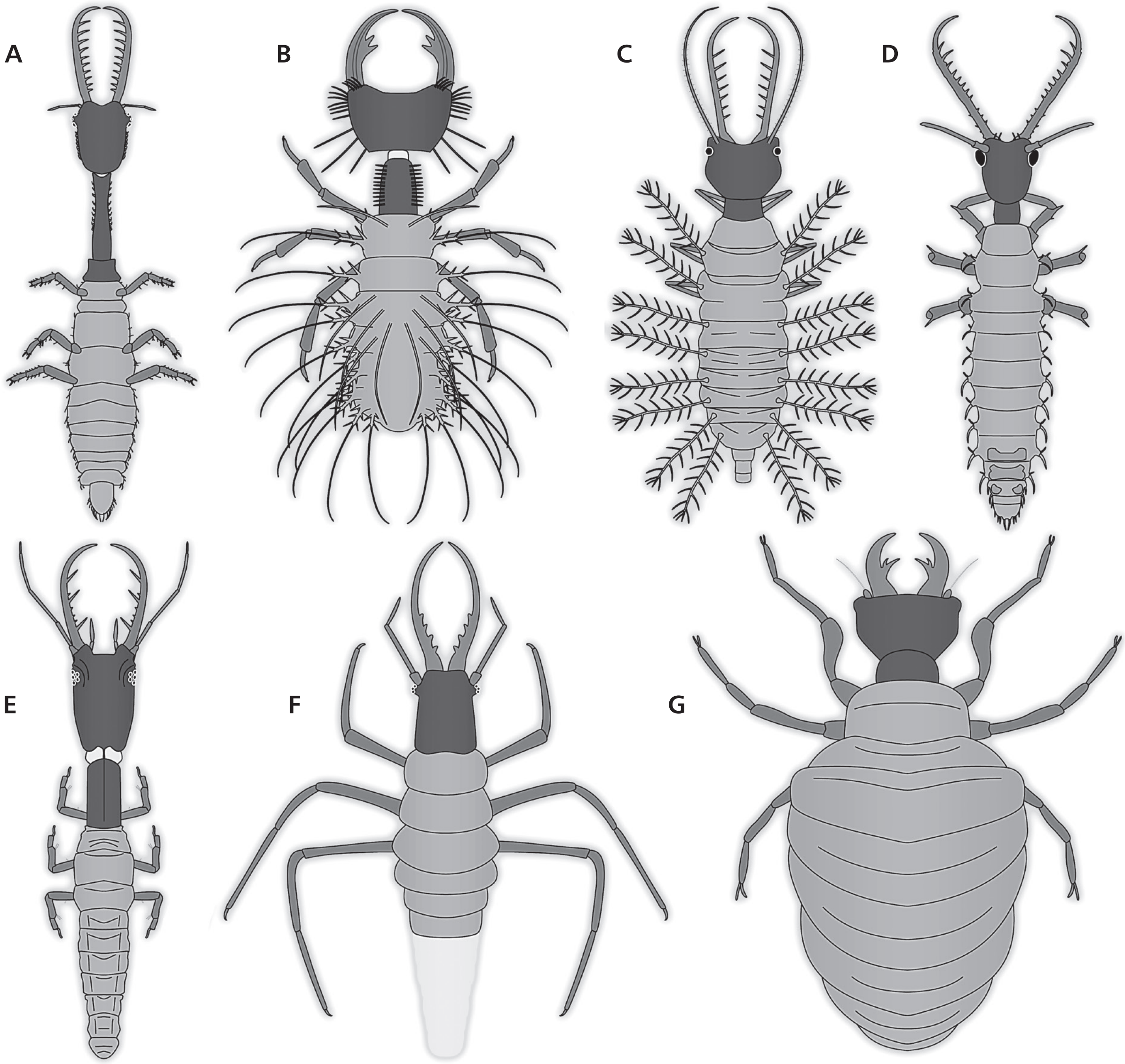

Figure 7. Comparison to other larvae with toothed stylets from Cretaceous Kachin amber, whose morphology is now extinct. • A – decadent-type larva (Haug *et al.* 2021a). • B – *Electrocaptivus xui* (modified after Badano *et al.* 2018). • C – *Cladofer huangi* (modified after Badano *et al.* 2018). • D – superfang type 1 (modified after Haug *et al.* 2019b). • E – *Macleodiella electrina* (modified after Badano *et al.* 2018). • F – *Kuafupolydentes hui* (modified after Luo *et al.* 2022). • G – possible larva of spoon-winged lacewing (modified after Haug *et al.* 2021c).

fig. 7d, p. 29, fig. 9e, p. 36, fig. 15f, p. 54; Alvim *et al.* 2019: fig. 3d, e, p. 280, fig. 5d, e, p. 283, fig. 6e, p. 284), in rock crawlers (Mantophasmatodea; Engel & Grimaldi 2004: fig. 3, p. 6) and in praying mantises (Mantodea; Wieland 2008: figs 8–10, p. 161).

In other raptorial appendages, the spines may clearly protrude not in the plane of movement, while usually having a pronounced curvature. When such an appendage is folded, the protrusions then form a kind of grasping basket. Such an arrangement has been demonstrated in fossil ant-like stone beetles, which appear to have caught springtails with their antennae (Fig. 6B; Yin *et al.* 2017, 2018).

The pedipalps of many whip spiders also have numerous protrusions, which partly protrude not in the plane of movement (Fig. 6C). Yet, most protrusions are more straight and less curved (Cokendolpher & Sissom 2001: figs 6, 7, p. 20; Armas & Arias 2008: fig. 7, p. 27; Teruel *et al.* 2009: fig. 14b, p. 208; Giupponi & Miranda 2012: fig. 5, p. 168; Armas 2014: fig. 17c, p. 50; Harms 2018: fig. 5a, p. 51). Still, the protrusions clearly form an overall basket-like structure when the pedipalps are folded. This arrangement seems to be most expressed in Carboniferous representatives (Haug & Haug 2021), in which it resembles that of the pedipalps of certain armoured harvestmen (*e.g.* Monte *et al.* 2015: fig. 6a, p. 6).

Less well known examples include raptorial crickets (Fig. 6A). In some, the curved spines are rather short, yet in others the spines are quite prominent (Hemp 2001: fig. 6, p. 125; Hemp 2006: fig. 6, p. 101; Mugleston *et al.* 2018: fig. 6d, p. 13, fig. 11, p. 17, see discussion in Haug *et al.* 2022b).

The case of the new fossil type with a curved protrusion is therefore well in line with the observed morphologies in many raptorial appendages. Still, one aspect is quite unusual: in the other examples there are always several such protrusions, while in the present case there is only a single one. In a functional sense, both stylets will have acted together, hence there would be a pair of protrusions, yet this number is still quite low in comparison to the other examples.

An extinct prey catching strategy for lacewings?

How could the new larval type have employed the teeth of its stylets? As apparent, the basket formed by the teeth is ventral to the plane of movement and may have been used to lift a possible prey item from the ground. Such an action would in principle be possible with tips and teeth that had pierced the prey; yet, this would require more force for penetrating the prey on more than one spot. The ventrally curved spines could hence allow supporting a lifting, while only the tips would have penetrated the prey. An uplift would require strong muscles for lifting the head. Uplifting of the head is well known for at least some ingroups of Neuroptera, such as Nevrorthidae (Zwick 1967: fig. 2, p. 67) and pit-building antlions (Büsse *et al.* 2021). The very broad head of the new larval type would indeed provide space for a large muscle for lifting the head and, by this, the prey. Overall, such an interpretation for the new larval type is plausible; still it remains speculative as further corroboration through direct observation of behaviour is not possible in fossils (see discussion in Hörnig *et al.* 2020, 2022).

Also numerous other lacewing larvae with teeth from Kachin amber have morphologies that are unknown today and likely employed strategies unparalleled in the modern fauna (Fig. 7). In addition, quantitative morphology has indicated that for Nymphidae the morphological diversity of the larvae and likely their ecological functions have decreased over time (Haug *et al.* 2022a). The new specimens increase the extinct morphologies from the qualitative side, but also from the quantitative one. The new fossil type therefore further emphasises the decrease of larval diversity through time in lacewings (Haug *et al.* 2020, 2021b, 2022a, c; Luo *et al.* 2022) and their closer relatives (Haug *et al.* 2022a).

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Electronic supplementary data

Suppl. Text 1. Results of the principal component analysis of the head capsules and stylets.

Suppl. Text 2. Results of the principal component analysis of the stylets.

Suppl. Figure 1. Graphical representation of the factor loadings of the principal component analysis of the head capsules and stylets.

Suppl. Figure 2. Graphical representation of the factor loadings of the principal component analysis of the stylets.

Suppl. Files 1–5. Files resulting from the shape analysis of the head capsules and stylets, including chain codes, aligned shapes, and principal component analysis.

Suppl. Files 6–10. Files resulting from the shape analysis of the stylets, including chain codes, aligned shapes, and principal component analysis.