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The morphological diversity of spoon-winged lacewing larvae and the first possible fossils from 99 million-year-old Kachin amber, Myanmar

Gideon T. Haug, Carolin Haug & Joachim T. Haug

Abstract

Antlion-like lacewings (Myrmeleontiformia) have comparably large predatory larvae; most well-known are the larvae of antlions (Myrmeleontidae) and owlflies (Ascalaphidae). Yet, larvae of spoon-winged lacewings (Nemopterinae, also an ingroup of Myrmeleontiformia) are less well studied and differ in their overall habitus, with a broader head and stouter mouthparts. We here review the known record of spoon-winged lacewing larvae and report two new fossil larvae preserved in 99 million-year-old Kachin amber from Myanmar that have some characteristics of spoon-winged lacewing larvae. We quantitatively compare morphological aspects of all these larvae with those from other myrmeleontiformian larvae. Our analyses suggest that one fossil larva may indeed be closely related to extant spoon-winged lacewings, but retains some plesiomorphies shared with Crocinae, the sister group of Nemopterinae. The other larva shows many unique features, but also some similarities to spoon-winged lacewing larvae, hence might be a highly specialised early representative of the lineage. These two larvae are the first potential larvae of Nemopterinae in the fossil record. Therefore, they are important indicators for the structure of the early diversification of lacewings.

K e y w o r d s : ribbon-winged lacewings; Nemopterinae; Cretaceous; Burmite; quantitative morphology.

1. Introduction

There are about 6,000 known species of lacewings (Neuroptera) in the modern fauna (Winterton et al. 2010; Engel et al. 2018). As other holometabolans, lacewings spend most of their lifespan as larvae. Lacewing larvae are (mostly) highly specialised predators with mouthparts that project forward; each mandible forms a venom-injecting, sucking stylet together with its corresponding maxilla (Heckman 2017).

The most famous larvae within Neuroptera are those of antlions (Myrmeleontidae), mostly known for digging sandpits to trap their prey (although not all antlion larvae show this behaviour). Myrmeleontiformia is a larger ingroup of Neuroptera including antlions as well as some closer relatives, together known as the antlion-like lacewings. Myrmeleontiformian larvae are well represented in the fossil record, especially in 99 million-year-old Cretaceous amber from Myanmar, also known as Kachin amber, Burmese amber or Burmite (e.g., Wang et al. 2016; Badano et al. 2018; Haug et al. 2019a, 2019b, 2020; Herrera-Flórez et al. 2020; Pérez-de la Fuente et al. 2020).

It appears that larvae of most major lineages of Myrmeleontiformia are already represented in Myanmar amber, including Myrmeleontidae (antlions; Badano et al. 2018), Ascalaphidae (owlflies or at least larvae resembling them; Wang et al. 2016; Badano et al. 2018; Herrera-Flórez et al. 2020), Nymphidae (split-footed lacewings; Wang et al. 2016; Haug et al. in press) and Psychopsidae (silky lacewings; Badano et al. 2018; Makarkin 2018; Haug et al. 2020). The group Nemopteridae is more problematic. First, while it is classically ranked at the same taxonomic level as the other four lineages (exceptions Monserrat 2008; Monserrat et al. 2012), there are in fact two ingroups that differ drastically in their larvae, i.e., Crocinae and Nemopterinae. Crocinae is characterised by in part very graceful larvae with elongated necks, hence known as long-necked antlions. Certain fossils have been interpreted as possible larvae of its ingroup Crocinae (Haug et al. 2019a, accepted a). Yet, Nemopterinae seems so far not represented by any fossil larvae.

Nemopterinae, the group of spoon-winged lacewings (sometimes also ribbon-winged lacewings), includes slightly more than 100 formally described species in the modern fauna (Abraham 2014). As the name suggests, the adults are characterised by spoon- or ribbon-shaped hind wings; those of the closely related thread-winged lacewings, Crocinae, are narrower. In both groups, the mouthparts of the adults are often somewhat elongated to feed on pollen (e.g., Tjeder 1967; Mansell 1996; Monserrat et al. 2012, fig. 5c, d). Spoon-winged lacewings are native to Australia, South America, Africa, Asia, and Europe and prefer arid climates; hence, they are commonly found in desert regions (Mansell 1996; Monserrat 1996; Aspöck et al. 2006; Miller & Stange 2012). Larvae of Nemopte-

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rinae are quite the opposite to those of Crocinae (i.e., long-necked antlions) as their body appears rather stout. In general, the larvae of Nemopterinae differ from those of other myrmeleontiformians by a rather broad head and shorter, stouter stylets. These larvae dig and live underground at a depth of between 150 and 300 mm under the surface (Monserrat 1996; Miller & Stange 2012: 6). At least some larvae are blind (Miller & Stange 2012: 6), others have seven stemmata on each side of the head (Monserrat 1996: 104). Monserrat & Martinez (1995: 62) mentioned that larvae of Nemopterinae feed on ants under laboratory conditions. It is possible that these larvae enter ant nests underground (yet also other mechanisms have been suggested). Other authors suggested a more general food spectrum (e.g., Tröger 1993).

For a long time, larvae of Nemopterinae were considerably less well known than those of Crocinae (MacLeod 1964). The situation has only slightly improved; even though there are more than twice as many described species of Nemopterinae than of Crocinae, many more larvae of Crocinae are still known, i.e., more than 70 (Haug et al. accepted a), while there are only less than 30 of Nemopterinae (see Results for details). We here review the reported records of larvae of Nemopterinae and compare their morphology quantitatively with that of other myrmeleontiformian larvae, especially long-necked antlions (larvae of Crocinae). Furthermore, we report two new larvae preserved in Myanmar amber that possess some characters shared with the larvae of Nemopterinae.

2. Material and methods

2.1. Material

In this study, we report two new specimens from the collection of the Palaeo-Evo-Devo (PED) Research Group, Ludwig-Maximilians-Universität München (LMU Munich), Germany (PED 0581, PED 0929). They were legally purchased on ebay.com from different traders (burmite-researcher, burmite-miner). Both specimens are preserved in 99 million-year-old amber from Myanmar. Some extant specimens we examined originated from the collections of the Zoological State Collection Munich (ZSM). Most of the investigated specimens were redrawn from the literature (for a complete list see Suppl. Table 1).

2.2. Documentation methods

The documentation of the fossil specimens was performed on a Keyence VHX-6000 digital microscope. We photographed the specimens from two sides (if possible), once illuminated under cross-polarised light and once illuminated under unpolarised ring illumination, and with white and black background. Several adjacent details were documented, and each image detail was documented by a stack of images of varying focus. The image with the best access to details was selected for presentation (Baranov et al. 2019; Haug & Haug 2019).

2.3. Image processing

Initial images were processed automatically by the built-in software, including fusion of stacks, stitching of image details to panorama images, and HDR (e.g., Haug et al. 2013; Hörnig et al. 2016). Resulting images were optimised for levels, saturation and sharpness in Adobe Photoshop CS2.

2.4. Presentation

Visible structures of the two fossil specimens were colour marked in Adobe Photoshop CS2 to provide an interpretation. Specimens from the literature were redrawn in Adobe Illustrator CS2. The drawings were slightly simplified and idealised. Similar structures were given the same colour. Restoration drawings of the two fossils follow the same style.

2.5. Shape analysis

A comparative statistical analysis of certain aspects of the morphology of the specimens was conducted by a Principal Component Analysis (PCA) of the results of an Elliptic Fourier analysis. Two subsets of lacewing larvae were analysed: 1) the outline of the head capsule including stylets and 2) the outline of the entire body without appendages besides the stylets.

Outlines were hand-drawn in Adobe Illustrator CS2. All outlines were drawn symmetrically; stylets were oriented forward, so that the tip was in line with the inner point of the base of the stylet. In total, 118 heads were used (Suppl. Figs. 1–4, including all available heads of larvae of Nemopterinae (27), Crocinae and long-necked fossils (69, from Haug et al. accepted a), five heads of Psychopsidea (see Haug et al. 2020), five of Nymphidae (see Haug et al. in press), ten of the larger group Myrmeleontidae/Ascalaphidae (as both might be non-monophyletic, but together represent a well-accepted monophyletic group, see e.g., Aspöck et al. 2001, 2012; Winterton et al. 2010, 2018), and the two new fossils (complete list in Suppl. Table 1). In total, 85 outlines of entire bodies were used (Suppl. Figs. 5, 6), including larvae of Nemopterinae (26), Crocinae and long-necked fossils (57), and the two new fossils (complete list in Suppl. Table 1).

Redrawn images were analysed in SHAPE (© National Agricultural Research Organization of Japan; Iwata & Ukai 2002), a free software providing the tools for an Elliptic Fourier Analysis and PCA analysis (for more details, see Haug et al. 2020). The results of the PCA were visualised in OpenOffice and redrawn in Adobe Illustrator CS2.

2.6. Terminology

For describing representatives of Insecta, a very specific terminology is often used. To be more precise, in several groups of Insecta different terminologies have emerged. This makes communication and comparisons beyond specific groups often challenging. Moreover, Insecta is an ingroup of Crustacea sensu lato (sensu Stein et al. 2008; see also discussion in Haug & Haug 2015). The terminology of various crustacean ingroups differs even more (e.g., Haug 2020), which makes comparisons still more problematic. Therefore, we think it is important to provide information in a neutral terminology for the non-expert reader in order to facilitate comparisons, but also in the specialist terminology to provide the necessary information also for this

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audience. We follow the basic description scheme of 'segment by segment' (Haug et al. 2012), but present it as running text (as this seems to be preferred by most readers) and provide specialist terms (alternative terms in normal brackets) alongside with general terms (in square brackets). Although some specialists may consider this unnecessary, we think, for the given reasons, that this extra effort is in fact important.

3. Results

Some authors were able to observe the eggs of a species, but could not breed the larvae (e.g., Picker 1984, 1987).

1) Navás (1919: 50, fig. 2) provided a drawing of a larval representative of *Nemoptera bipennis* in dorsal view

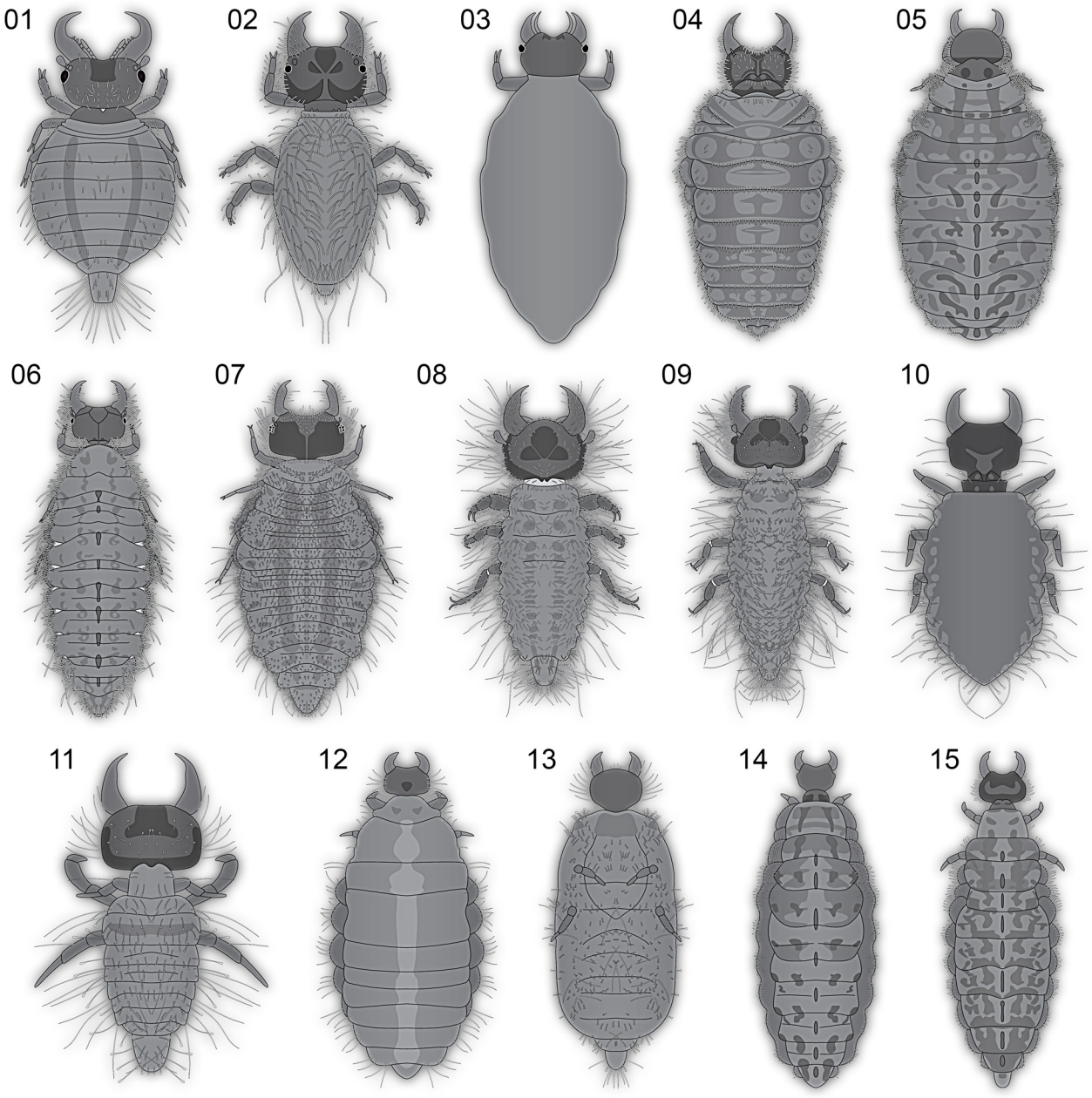

Fig. 1. Extant larvae of Nemopterinae retrieved from the literature; all drawings simplified; 01: Navás (1919); 02: Withycombe (1925); 03: Mathews (1947); 04: Mansell (1973); 05, 06: Tröger (1993); 07: Mansell (1996); 08–15: Monserrat (1996).

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(specimen 1; Fig. 1). The drawing is detailed and appears barely idealised. No indication of size was provided. Navás was apparently able to obtain a larva hatched from an egg; hence, it must be a stage 1 larva. Note: MacLeod (1964) cites this paper as 1918. The image was re-figured in Gepp (1984) and Tröger (1993). Further details were also provided by Navás (1919) as drawings (all p. 51), including mandible (fig. 3a), antenna (fig. 3b) and a seta (fig. 3c).

2) Navás (1923) seems to have re-figured specimen 1, i.e., the specimen from Navás (1919). This contribution was not directly seen by the current authors and is cited after Tröger (1993).

3) Navás (1924) seems to have re-figured specimen 1, i.e., the specimen from Navás (1919). This contribution was not directly seen by the current authors and is cited after Tröger (1993).

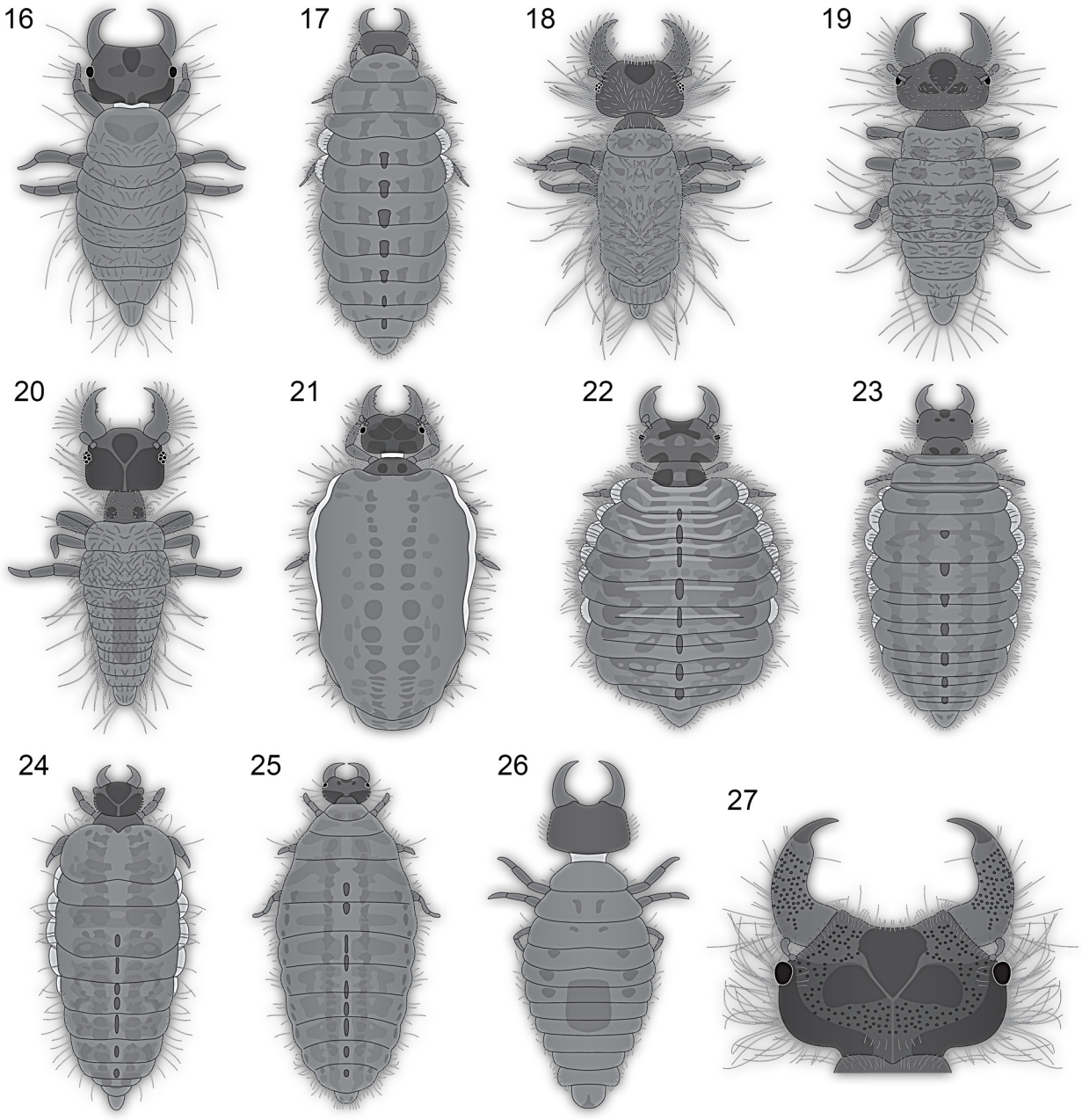

Fig. 1 continued. Extant larvae of Nemopterinae retrieved from the literature, continued; all drawings simplified; 16–25: Monserrat (2008); 26: Miller & Stange (2012); 27: Badano et al. (2017).

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4) Saz (1925) seems to have re-figured specimen 1, i.e., the specimen from Navás (1919). This contribution was not directly seen by the current authors and is cited after Tröger (1993).

5) Withycombe (1925, pl. 34, fig. 4) provided a drawing of a larval representative of *Nemoptera bipennis* in dorsal view (Note: the paper itself states 1924 as publication date, yet this accounts for the volume number, the specific issue was indeed published in February 1925). The drawing is detailed and appears barely idealised. Size was given as 2.13 mm (p. 343). It appears to be a stage 1 larva. According to the text (p. 343), the specimen is stored in the British Museum of Natural History, London, UK. MacLeod (1964: 433) stated that the specimen is a re-figure of the image from Navás (1919). However, the specimen appears very different from that figured in Navás (1919). While one could explain certain differences by damage due to storage, the head capsule and mandible shape can usually not be altered without heavy indications of breakage. There are significant differences in head capsule and mandible shape. The antennae, which appear undamaged, differ significantly as well. Therefore, we see it as highly unlikely that this is the same specimen. We therefore interpret the image by Withycombe (1925) as a distinct specimen (specimen 2; Fig. 1). Additionally, a detail is provided as a drawing, namely a part of the head capsule and mandible (his pl. 34, fig. 3). The specimen was re-figured by Tjeder (1967).

6) Mathews (1947) figured a photograph of a larva (specimen 3; Fig. 1) of *Chasmoptera hutti*. This contribution was not directly seen by the current authors and is cited after Monserrat (2008). The specimen was re-figured by Tjeder (1967) and Monserrat (2008).

7) Friedrich (1953) seems to have re-figured specimen 1, i.e., the specimen from Navás (1919). This contribution was not directly seen by the current authors and is cited after Tröger (1993).

8) Tjeder (1967: 311) re-figured several images of larvae of Nemopterinae. The first one (fig. 1962) is a drawing representing specimen 3, i.e., based on the photograph provided by Mathews (1947). The second one (fig. 1956) is a re-figure of specimen 2, i.e., the drawing from Withycombe (1925). Furthermore, several details from Navás (1919: 311, fig. 1958-60) and Withycombe (1925: 311, fig. 1957) were re-figured.

9) Mansell (1973: 134, fig. 1) provided a drawing of a larval representative of *Derhynchia vansoni* in dorsal view (specimen 4; Fig. 1). The drawing is detailed and appears barely idealised. According to the provided the scale, the specimen measured about 10 mm. It was stated to be a stage 3 larva (p. 133). Additionally, details are provided as drawings (all on p. 134), including head in ventral view (fig. 2), antenna (fig. 3), and the walking appendages (fig. 4). The specimen was re-figured by New (1989), Aspöck & Aspöck (2007) and Monserrat (2008).

10) Gepp (1984: 199, pl. 8, fig. 18c) re-figured specimen 1, i.e., the drawing from Navás (1919).

11) New (1989: 104, fig. 148A) re-figured specimen 4, i.e., the specimen from Mansell (1973). It was labelled "*Derhynchia vansoni* (Nemopterinae)".

12) Tröger (1993) provided several images of larvae of Nemopterinae. The first (p. 359, fig. 3) was a re-figure of specimen 1, i.e., the drawing from Navás (1919).

The second was a micrograph (p. 360, fig. 4) of a larva of *Nemoptera coa*, stated to be a stage 3 larva (specimen 5; Fig. 1). No indication of size was provided.

Tröger (1993) also provided a habitus drawing of a similar specimen (p. 362, fig. 5), also a stage 3 larva. The specimen does not appear to be the same specimen that was shown on the micrograph. Tröger (1993: 360) stated to have had three specimens in total. One was sacrificed in stage 2, one in stage 3; the third was allowed to pupate. It is therefore possible that two specimens in stage 3 were documented. Therefore we consider this drawing as the depiction of another specimen (specimen 6; Fig. 1). Size according to scale was 8.7 mm.

Additionally, numerous details were provided as drawings (all on p. 364), including head (fig. 6), mouthparts (fig. 7), antenna and eye (fig. 8), seta (fig. 9), spiracle (fig. 10) and parts of walking appendages (figs. 11, 12).

13) Monserrat & Martinez (1995) provided several photographic images of larvae of *Nemoptera bipennis*, all in dorsal view. There is an overlap with images in Monserrat (1996; see there), which makes a consecutive numbering of the specimens challenging. We consider Monserrat (1996) as the more complete source and use it for numbering. Therefore, the two specimens mentioned in the following are not numbered as specimens 7 and 8, but follow the numbering as they appear in Monserrat (1996) (see also explanation below).

The first larva (specimen 11; Fig. 1) is a newly hatched one (Monserrat & Martinez 1995, fig. 3). The second one (specimen 12; Fig. 1) is an eight month old larva (fig. 3), apparently still a stage 1. The third one is a stage 3 larva (fig. 4). Also a detail of the head was provided for the stage 3 larva (fig. 5). For the stage 3 larva it remains unclear whether it is also figured in Monserrat (1996), as the image is rather dark; due to this uncertainty and low quality of the image, the specimen was not included in our analysis. No indication of size was provided for all three specimens.

14) Mansell (1996: 175, fig. 3) provided a drawing of a larval representative of a species of *Semirhynchia* in dorsal view (specimen 7; Fig. 1). The drawing is detailed and appears barely idealised. According to the figure caption, the specimen measured 10 mm in total length. The speci-

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men was re-figured by Tauber et al. (2003) and Monserrat (2008).

15) Monserrat (1996) provided several photographic images and drawings of larvae of the group Nemopterinae. Some of the images appear to be re-figured from Monserrat & Martinez (1995). This paper was not cited in Monserrat (1996). It could be possible that the papers were published in "wrong order", i.e., different from the intended way. Yet, Monserrat & Martinez (1995) do also not cite Monserrat (1996; or as in press or similar). Hence we can only use the years provided and take some of the images in Monserrat (1996) as re-figured, although this has not been indicated here.

Images of a newly hatched larva (specimen 8; Fig. 1) of *Lertha sofiae* include numerous SEM micrographs of surface details (figs. 7–13), drawings in dorsal view (fig. 16) and detailed drawings of mandible (fig. 17), maxillae and labium (fig. 18) and trunk appendages (figs. 19–21). According to scale, the larva was 2.1 mm long.

Images of a newly hatched larva (specimen 9; Fig. 1) of *Nemoptera bipennis* include drawings in dorsal view (fig. 24) and detailed drawings of mandible (fig. 25), maxillae and labium (fig. 26) and a detail of the tip of a trunk appendage (fig. 27). According to scale, the larva was 2.4 mm long.

Detailed drawings of third instar larvae include mandible (fig. 28), maxillae and labial palp (fig. 29) and antenna (fig. 30) of *Lertha sofiae* and mandible (fig. 31), maxillae and labial palp (fig. 32) and antenna (fig. 33) of *Nemoptera bipennis*.

Numerous additional photographs of different larvae, most in dorsal view, were provided. All these are clearly different from the individuals shown in the drawings and are therefore considered as additional specimens. This includes a fed stage 1 larva (specimen 10; Fig. 1; Monserrat 1996, fig. 34 right), an unfed stage 1 larva (specimen 11; Fig. 1; fig. 34 left), a stage 2 larva (specimen 12; Fig. 1; fig. 35) also with a close-up on the head (fig. 36), exuvia of a stage 2 larva in ventral view (specimen 13; Fig. 1; fig. 37), all of *Nemoptera bipennis*, a stage 3 larva (specimen 14; Fig. 1) of *Lertha sofiae* in dorsal (fig. 39) and ventral view (fig. 40) and a close-up on the trunk end (fig. 41), and finally a stage 3 larva (specimen 15; Fig. 1) of *Nemoptera bipennis* in dorsal (fig. 42) and ventral view (fig. 43) and a close-up on the trunk end (fig. 44). No indication of size was provided for the specimens shown in the photographs. Specimen 14 was re-figured by Monserrat (2008), specimens 8, 9, 14 and 15 were re-figured by Monserrat et al. (2012).

16) Tauber et al. (2003) re-figured specimen 7 (fig. 5B), i.e., the specimen from Mansell (1996).

17) Aspöck & Aspöck (2007) re-figured the head of specimen 4 (fig. 101), i.e., the specimen from Mansell (1973).

18) Monserrat (2008) figured photographs of numerous larvae of *Lertha sheppardi* including a stage 1 larva (specimen 16; Fig. 1) feeding on another one (Monserrat 2008, fig. 4c, d), a stage 3 larva (specimen 17; Fig. 1) in various positions (fig. 4e–i) including a dorsal view (fig. 4j), a stage 1 larva (specimen 18; Fig. 1) in dorsal view (fig. 6a) with details of the head in dorsal (fig. 6b) and ventral view (fig. 6c).

Further photographs show a stage 1 larva (specimen 19; Fig. 1) of *Lertha sofiae* in dorsal view (Monserrat 2008, fig. 6d) with details of the head in dorsal (fig. 6e) and ventral view (fig. 6f). Further photographs show a stage 1 larva (specimen 20; Fig. 1) of *Lertha extensa* in dorsal view (fig. 6g) with details of the head in dorsal (fig. 6h) and ventral view (fig. 6i), and a stage 1 larva (specimen 21; Fig. 1) at the end of stage one in dorsal view (fig. 6j) and ventral view (fig. 6k).

Further photographs show a stage 3 larva (specimen 22; Fig. 1) of *Nemoptera bipennis* with a detail of the head (Monserrat 2008, fig. 7a), an overview in dorsal (fig. 7b) and ventral view (fig. 7c), and a detail of the trunk end (fig. 7d). Further photographs show a stage 3 larva (specimen 23; Fig. 1) of *Lertha sheppardi* with a detail of the head (fig. 7e), an overview in dorsal (fig. 7f) and ventral view (fig. 7g), and a detail of the trunk end (fig. 7h). Further photographs show a stage 1 larva (specimen 24; Fig. 1) at the end of the stage of *Lertha extensa* in dorsal (fig. 7i) and ventral view (fig. 7j), and a stage 1 larva (specimen 25; Fig. 1) at the end of the stage of *Lertha sheppardi* in dorsal (fig. 7k) and ventral view (fig. 7l). Detail drawings show the antennae of a larva of *Lertha sofiae* (fig. 7mA) and *Nemoptera bipennis* (fig. 7mB), re-figured from Monserrat (1996). For none of these specimens a clear indication of size was provided.

Monserrat (2008) also re-figured several specimens: specimen 4 (fig. 8a), i.e., the specimen from Mansell (1973), specimen 7 (fig. 8b), i.e., the specimen from Mansell (1996), specimen 3 (fig. 8c), i.e., the specimen from Mathews (1947), and specimen 14 (fig. 8d), i.e., a specimen from Monserrat (1996).

19) Miller & Stange (2012) provided numerous micrographs of a larva (specimen 26; Fig. 1) of *Stenorrhachus walkeri*. Images included overviews in dorsal (Miller & Stange 2012, fig. 20) and ventral view (fig. 21), the head in dorsal (fig. 22) and ventral view (fig. 23), details of the trunk appendages (figs. 24, 25) and the trunk end (fig. 26). According to the text, the larva was 8 mm long.

20) Monserrat et al. (2012) re-figured several specimens from Monserrat (1996). Images include a drawing of specimen 9 (fig. 2a) and specimen 8 (fig. 2b), photographs of specimen 15 (fig. 2c) and specimen 14 (fig. 2d) as well as drawings of antennae.

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21) Badano et al. (2017) figured a micrograph of the anterior region of a stage 3 larva (specimen 27; Fig. 1) of *Nemoptera bipennis* (Badano et al. 2017, fig. 6B). In addition, a stage 1 larva of the same species was shown in lateral view (fig. 7E).

22) We here report a new fossil (PED 0929) that possesses some characteristics of larvae of Nemopterinae (specimen 28; Fig. 2):

3.1. Morphological description of PED 0929 (specimen 28)

3.1.1. General habitus

Small holometabolan larva, about 1.92 mm long (Fig. 2a–c). Body (presumably) organised into 20 segments. Ocular and following five post-ocular segments

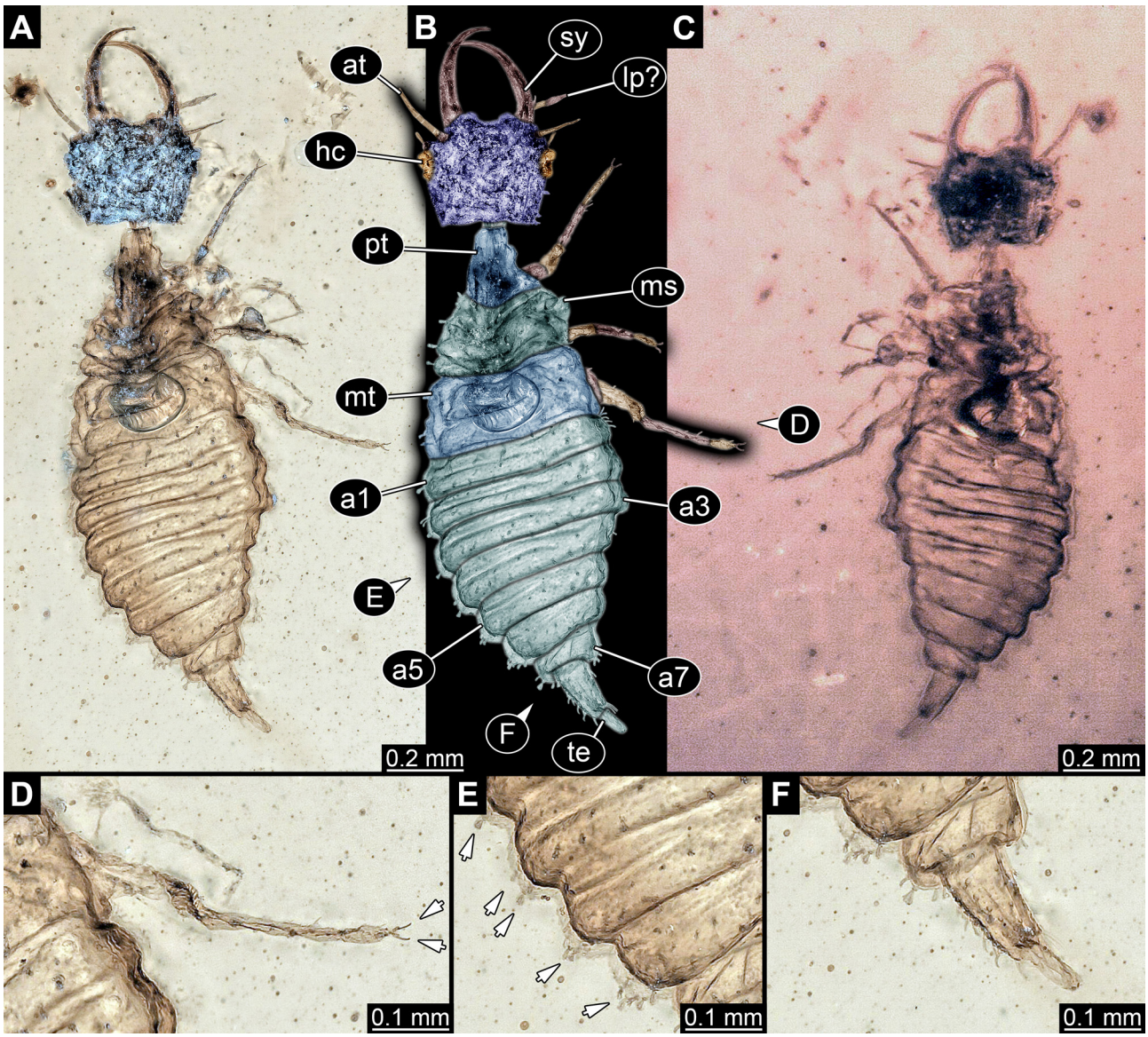

Fig. 2. PED 0929, specimen 28; **A**: dorsal view; **B**: colour-marked version of A; **C**: ventral view; **D**: detail of trunk appendage (leg), with distal claws (arrows); **E**: dolichaster-like setae on trunk (arrows); **F**: trunk end. Abbreviations: a1–a7 = abdomen segments 1–7; at = antenna; hc = head capsule; lp? = possible labial palp; ms = mesothorax; mt = metathorax; pt = prothorax te = trunk end; sy = stylet.

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form a distinct head with sclerotized head capsule. Trunk subdivided into two functional parts. Anterior three trunk segments (post-ocular segments 6–8; "thorax") similar to each other, all bearing prominent walking appendages (thorax appendages); posterior segments (post-ocular segments 9–19; "abdomen" [not corresponding to abdomen in other arthropods]) without appendages. Dorsal surface of entire trunk with fine reticulate pattern.

3.1.2. Head region

Head capsule hexagonal in dorsal (or ventral) view, dorso-ventrally flattened (Fig. 2a–c). Head capsule about 15% of entire body length. Anterior edge of head slightly curved; maximum width of head capsule about 115% of head length. Posterior edge of head almost straight, slightly wider than anterior edge. Dorsal and ventral side of head capsule covered by dirt particles, concealing most details.

Ocular segment recognisable by prominent eye protuberances at about 35% of head length; individual stemmata not discernible. Post-ocular segment 1 recognisable by its pair of appendages, the antennae [antennulae]. Antenna arising from anterior-dorsal region of head capsule (Fig. 2b). Antenna short, elongate, about 50% of head capsule length. Antenna subdivided into at least six visible articles. Proximal article about as long as wide (diameter), further distal articles slenderer, longer than wide, about two times. Post-ocular segment 2 without externally visible structures.

Post-ocular segment 3 recognisable by its pair of appendages, the mandibles. Post-ocular segment 4 recognisable by its pair of appendages, the maxillae [maxillulae]. Mandible and maxilla closely associated, forming a pair of mandible-maxilla complexes, functional stylets. Stylet gently curved, about as long as head capsule, distally tapering, proximal width slightly less than 20% of length.

Post-ocular segment 5 recognisable by possible palp [endopod] of labium [maxilla]. No details accessible.

3.1.3. Anterior trunk (thorax)

Transition of head to trunk without clearly visible prominent collar-like sclerite (cervix; Fig. 2a, b). All trunk segments with distinct dorsal or ventral surfaces, set off from anterior and posterior structures by distinct folds, but without hard-appearing sclerites (tergites, sternites), soft.

Trunk segment 1 (post-ocular segment 6, prothorax) trapezoid in dorsal (or ventral) view, slightly shorter than head capsule. Anterior edge slightly less than 30% of posterior width of head capsule. Posterior edge about as wide as the segment length. Ventrally with a pair of prominent appendages (leg, thoracopod).

Trunk segment 2 (post-ocular segment 7, mesothorax) trapezoid in dorsal (or ventral) view, slightly shorter than prothorax. Anterior edge as wide as posterior width of prothorax. Posterior edge wider, about 135%. Dorsal surface with two prominent abaxial folds; lateral side with short setae, at least four. Ventrally with a pair of prominent appendages (leg, thoracopod).

Trunk segment 3 (post-ocular segment 8, metathorax) rectangular to trapezoid in dorsal (or ventral) view, slightly shorter than mesothorax. Anterior edge as wide as posterior width of mesothorax. Posterior edge slightly wider, about 165%. Dorsal surface with single prominent abaxial fold; lateral side with short setae, at least three. Ventrally with a pair of prominent appendages (leg, thoracopod).

All three pairs of appendages appear sub-similar (Fig. 2d). Appendages with presumably five major elements, proximal region not well accessible. Possible element 2 (trochanter) incompletely accessible, appears rectangular in anterior view. Element 3 (femur) elongate, tapering distally. Element 4 (tibia) longer and slenderer than femur, tube-shaped. Element 5 (tarsus) shorter than tibia, as wide, tube-shaped; distally with a pair of claws (pretarsal claws), no traces of an empodium. Only few setae preserved, exact pattern not reconstructible.

3.1.4. Posterior trunk (abdomen)

Trunk segment 4 (post-ocular segment 9, abdomen segment 1) rectangular to trapezoid in dorsal (or ventral) view, shorter than metathorax, about 50%. Anterior edge as wide as posterior width of metathorax. Posterior edge slightly wider, about 110%. Dorsal surface with single prominent abaxial fold; lateral side with short dolichaster-like setae, at least five (Fig. 2e). Ventral surface also with single prominent abaxial fold.

Trunk segment 5 (post-ocular segment 10, abdomen segment 2) rectangular in dorsal (or ventral) view, about as long as preceding segment. As wide as preceding segment. Dorsal surface with single prominent abaxial fold; lateral side with short setae, at least three. Ventral surface also with single prominent abaxial fold.

Trunk segment 6 (post-ocular segment 11, abdomen segment 3) trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge as wide as posterior width of metathorax. Posterior edge slightly narrower, about 90%. Dorsal surface with single prominent abaxial fold; lateral side with short setae. Ventral surface also with single prominent abaxial fold.

Trunk segment 7 (post-ocular segment 12, abdomen segment 4) trapezoid in dorsal (or ventral) view, about as

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long as preceding segment. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 80%. Dorsal surface with single prominent abaxial fold; lateral side with short setae, at least two. Ventral surface also with single prominent abaxial fold.

Trunk segment 8 (post-ocular segment 13, abdomen segment 5) trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 85%. Dorsal surface with single prominent abaxial fold; lateral side with short setae, at least three. Ventral surface also with single prominent abaxial fold.

Trunk segment 9 (post-ocular segment 14, abdomen segment 6) trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 70%. Dorsal surface with single abaxial fold, weaker than in preceding segment; lateral side with short setae, at least four. Ventral surface without abaxial fold.

Trunk segment 10 (post-ocular segment 15, abdomen segment 7) trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 65%. Dorsal surface without abaxial fold; lateral side with short setae, at least four. Ventral surface without abaxial fold.

Trunk segment 11 (post-ocular segment 16, abdomen segment 8) elongate trapezoid in dorsal (or ventral) view, longer than preceding segment, about 190% (Fig. 2f). Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 45%. Dorsal surface without abaxial fold; lateral side with short setae, at least five. Ventral surface without abaxial fold.

Trunk end (possible conjoined post-ocular segments 17–19), rectangular in dorsal (or ventral) view, shorter than preceding segment, about 50% (Fig. 2f). Posterior edge convex, gently rounded.

23) We here also report another new fossil (PED 0581) that possesses some characteristics of larvae of Nemopterinae (specimen 29; Fig. 3):

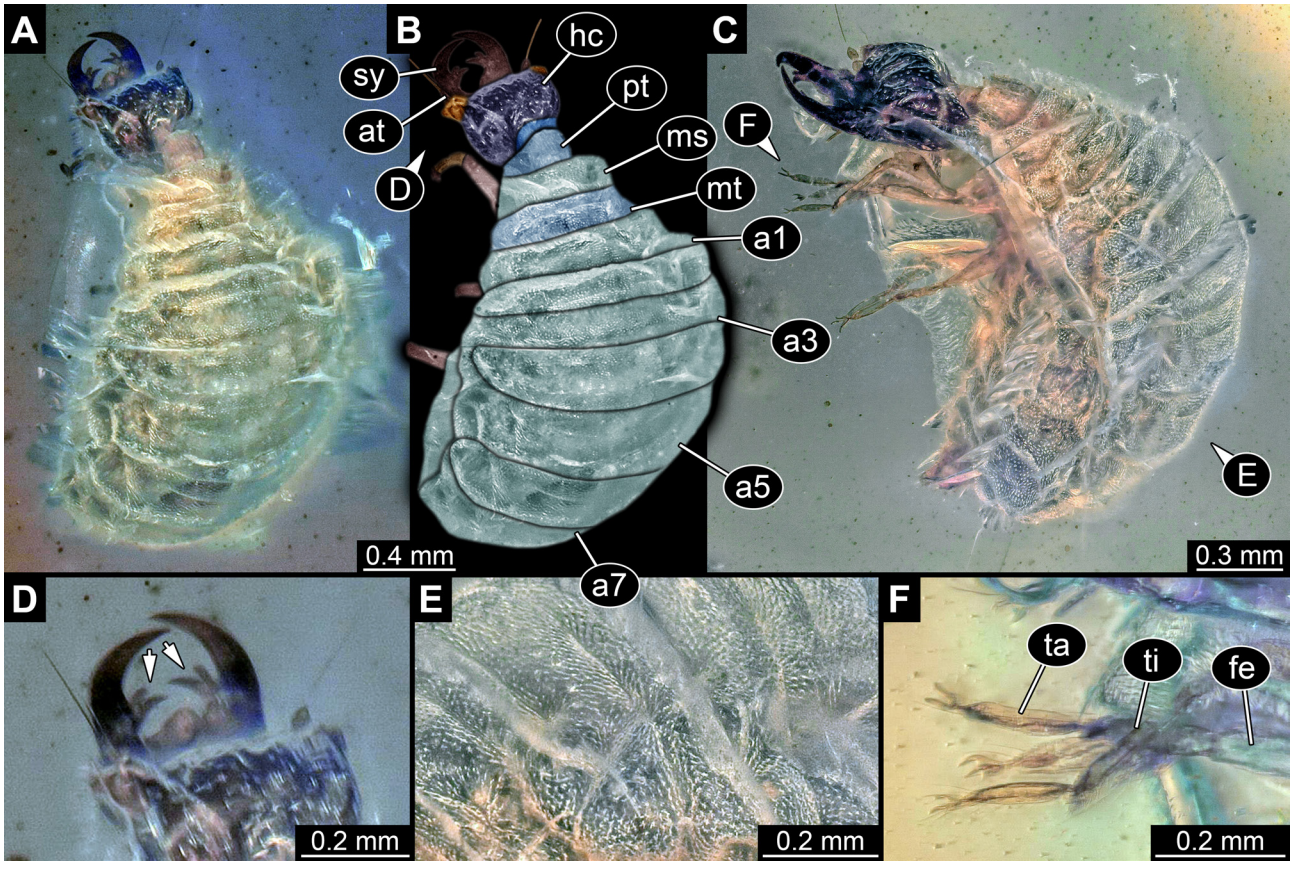

Fig. 3. PED 0581, specimen 29; **A**: dorsal view; **B**: colour-marked version of A; **C**: lateral view; **D**: detail of stylets with teeth with two cusps each (arrows); **E**: detail of surface of trunk; **F**: detail of trunk appendage (leg). Abbreviations: a1–a7 = abdomen segments 1–7; at = antenna; fe = femur; hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax; ta = tarsus; ti = tibia; sy = stylet.

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3.2. Morphological description of PED 0581 (specimen 29)

3.2.1. General habitus

Small holometabolan larva, about 2.54 mm long (Fig. 3a–c). Body (presumably) organised into 20 segments. Ocular and following five post-ocular segments form a distinct head with sclerotized head capsule. Trunk subdivided into two functional parts. Anterior three trunk segments (post-ocular segments 6–8; "thorax") similar to each other, all bearing prominent appendages (thorax appendages); posterior segments (post-ocular segments 9–19; "abdomen" [not corresponding to abdomen in other arthropods]) without appendages. Dorsal surface of parts of head and entire trunk with many small humps possibly representing sockets of small setae.

3.2.2. Head region

Head capsule rectangular to trapezoid in dorsal (or ventral) view, dorso-ventrally flattened (Fig. 3a, b, d). Head capsule about 10% of entire body length. Anterior edge of head slightly curved, about 135% of head length. Posterior edge of head almost straight, slightly narrower than anterior edge. Dorsal and ventral side of head capsule partly verlumt, concealing details.

Ocular segment recognisable by prominent eye protuberances at about 35% of head length; individual stemmata not discernible. Post-ocular segment 1 recognisable by its pair of appendages, the antennae [antennulae]. Antenna arising from anterior-dorsal region of head capsule (Fig. 3b). Antenna short, elongate, about 65% of head capsule length. Antenna subdivided into at least two visible articles. Proximal article about as long as wide (diameter), further distal article slenderer, longer than wide, about six times. Post-ocular segment 2 without externally visible structures.

Post-ocular segment 3 recognisable by its pair of appendages, the mandibles. Post-ocular segment 4 recognisable by its pair of appendages, the maxillae [maxillulae]. Mandible and maxilla closely associated, forming a pair of mandible-maxilla complexes, functional stylets. Stylet gently curved, about as long as head capsule, distally tapering, proximal width slightly less than 20% of length. Each stylet bears one prominent tooth, each with two cusps.

Post-ocular segment 5 not recognisable by visible appendages.

3.2.3. Anterior trunk (thorax)

Transition of head to trunk without collar-like sclerite (cervix; Fig. 3a, b). All trunk segments with distinct dorsal or ventral surfaces, set off from anterior and posterior structures by folds, but without hard-appearing sclerites (tergites, sternites), soft (Fig. 3d).

Trunk segment 1 (post-ocular segment 6, prothorax) trapezoid in dorsal (or ventral) view, about 50% of head capsule length. Anterior edge slightly curved; about same width of posterior width of head capsule. Posterior edge slightly wider, about 115%. Ventrally with a pair of prominent appendages (leg, thoracopod).

Trunk segment 2 (post-ocular segment 7, mesothorax) trapezoid in dorsal (or ventral) view, slightly longer than prothorax. Anterior edge wider than posterior width of prothorax, about 145%. Posterior edge wider, about 120% of anterior width. Ventrally with a pair of prominent appendages (leg, thoracopod).

Trunk segment 3 (post-ocular segment 8, metathorax) rectangular to trapezoid in dorsal (or ventral) view, slightly longer than mesothorax. Anterior edge about as wide as posterior width of mesothorax. Posterior edge slightly wider, about 130%. Ventrally with a pair of prominent appendages (leg, thoracopod).

All three pairs of appendages appear sub-similar (Fig. 3F). Appendages with presumably five major elements, proximal region not well accessible. Possible element 2 (trochanter) incompletely accessible, appears rectangular in anterior view. Element 3 (femur) elongate, tapering distally. Element 4 (tibia) longer and slenderer than femur, tube-shaped. Element 5 (tarsus) shorter than tibia, as wide, tube-shaped; distally with a pair of claws (pretarsal claws), no traces of an empodium. No setae preserved.

3.2.4. Posterior trunk (abdomen)

Trunk segment 4 (post-ocular segment 9, abdomen segment 1) rectangular to trapezoid in dorsal (or ventral) view, slightly longer than metathorax. Anterior edge as wide as posterior width of metathorax. Posterior edge slightly wider, about 140%.

Trunk segment 5 (post-ocular segment 10, abdomen segment 2) rectangular to trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge about as wide as posterior edge of preceding segment. Posterior edge wider, about 110%.

Trunk segment 6 (post-ocular segment 11, abdomen segment 3) rectangular to trapezoid in dorsal (or ventral) view, about as long as preceding segment. Anterior edge as wide as posterior width of preceding segment. Posterior edge about as broad as anterior edge.

Trunk segment 7 (post-ocular segment 12, abdomen segment 4) trapezoid in dorsal (or ventral) view, slightly longer than preceding segment, about 150%. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 90%. Dorsal sur-

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face with single prominent abaxial fold; lateral side with short setae, at least two. Ventral surface also with single prominent abaxial fold.

Trunk segment 8 (post-ocular segment 13, abdomen segment 5) trapezoid in dorsal (or ventral) view, slightly curved, longer than preceding segment, about 115%. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 115%. Dorsal surface with two possible abaxial folds.

Trunk segment 9 (post-ocular segment 14, abdomen segment 6) trapezoid in dorsal (or ventral) view, slightly curved, possibly shorter than preceding segment, about 80%. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 75%. Dorsal surface with possible single abaxial fold.

Trunk segment 10 (post-ocular segment 15, abdomen segment 7) trapezoid in dorsal (or ventral) view, slightly curved, possibly shorter than preceding segment, about 75%. Anterior edge as wide as posterior width of preceding segment. Posterior edge slightly narrower, about 65%. Dorsal surface without abaxial fold; lateral side with short setae, at least four. Ventral surface without abaxial fold.

Trunk segment 11 (post-ocular segment 16, abdomen segment 8) rectangular in lateral view, shorter than preceding segment, about 80%. Other information cannot be given, because dorsal (or ventral) view is not provided.

Trunk segment 12 (post-ocular segment 17, abdomen segment 9) rectangularly in lateral view, shorter than preceding segment, about 85%. Other information cannot be given, because dorsal (or ventral) view is not provided.

Trunk end (possible conjoined post-ocular segments 18, 19), rectangular in dorsal (or ventral) view, shorter than preceding segment, about 35%. Posterior edge convex, gently rounded.

Restoration drawings of specimens 28 and 29 are presented in Fig. 4.

3.3. Results of shape analysis

The shape analysis of the head capsule resulted in six effective principal components (PCs) (Suppl. Fig. 7; Suppl. Text 1, 2), summarizing to a total of 95.5% of overall variation in the data set. The first two principal compo-

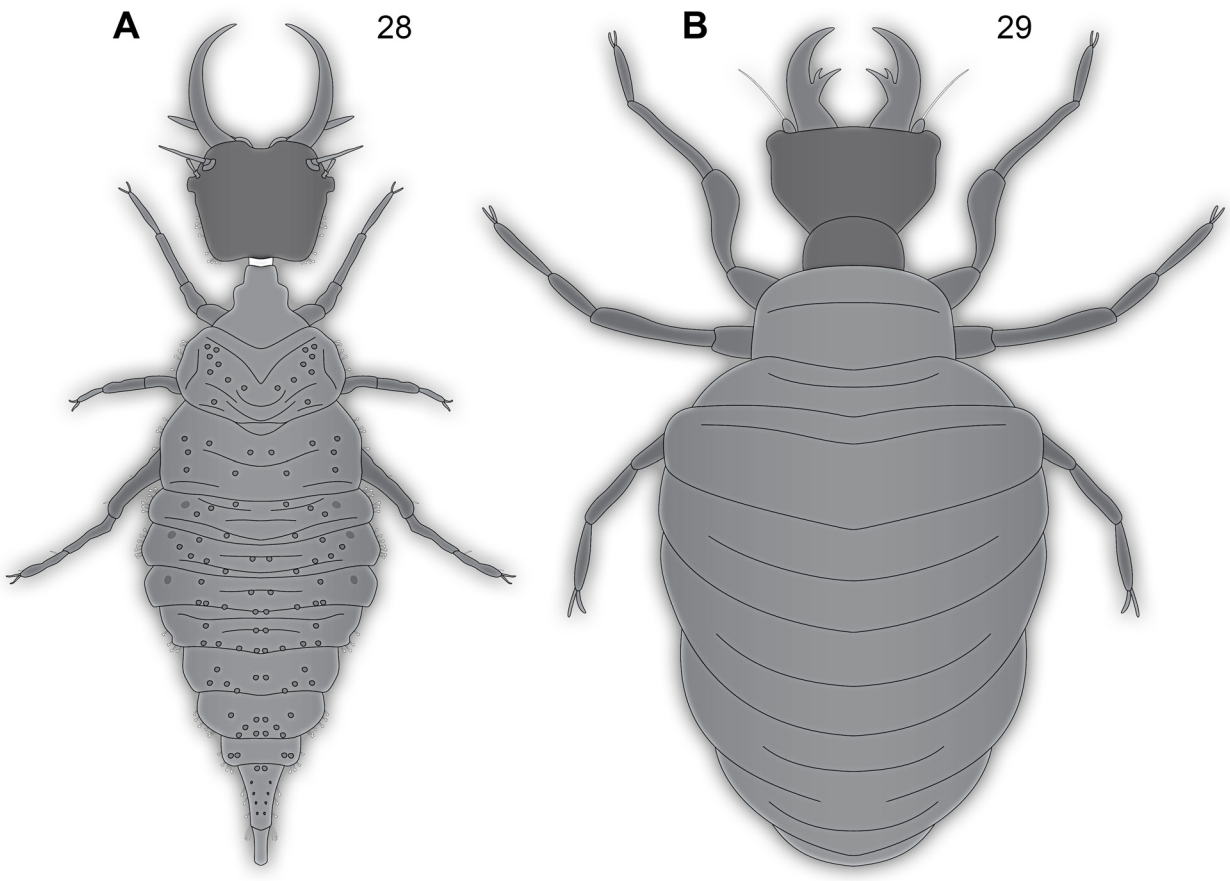

Fig. 4. Restoration drawings of the two new fossils in dorsal view; **A**: specimen 28, PED 0929; **B**: specimen 29, PED 0581.

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nents sum up to 80.0% of overall variation of the data set. PC1 explains 55.9% of overall variation and PC2 explains 24.1% of overall variation (Suppl. Text 1).

PC1 is dominated by the length of the head capsule (Suppl. Fig. 8). It describes very short to very long shapes; yet the width of the mandibles also influences this PC; low values indicate a short head with distally tapering mandibles, and high values indicate a long head with mandibles that are in the distal region as broad as in the proximal region.

PC2 is dominated by the length of the mandibles and the shape of the head; especially focussing on the posterior edge. It describes convex to concave posterior edges of the head; low values indicate a convex posterior edge of the head with short mandibles, and high values indicate a concave posterior edge of the head with long mandibles.

PC3 explains 5.5% of the overall variation. It appears to be dominated by similar phenomena as PC2. It describes convex to concave posterior edges of the head and the shape of the mandibles; low values indicate a concave posterior edge of the head with strongly curved mandible tips, and high values indicate a convex posterior edge of the head with straight mandible tips.

PC4 explains 4.7% of the overall variation and seems to be dominated by the anterior shape of the head; low values indicate a convex anterior edge of the head capsule, and high values indicate a concave anterior edge of the head capsule.

PC5 explains 3.6% of the overall variation and seems to be dominated by the width of the mandible tips; low values indicate narrow mandible tips, and high values indicate wide mandible tips.

PC6 explains 1.8% of the overall variation and seems to be dominated by the width of the head capsule; low values indicate a narrow head, and high values indicate a wide head.

The shape analysis of the entire body outline resulted in four effective principal components (Suppl. texts 3, 4), summarizing to a total of 95.4% of overall variation in the data set. The first two principal components sum up to 86.9% of overall variation of the data set. PC1 explains 73.8% of overall variation and PC2 explains 13.2% of overall variation (Suppl. Text 3).

PC1 is dominated by the length of the body in correlation to the length of the mandibles and the position of the widest part of the body (Suppl. Fig. 9). Low values indicate relatively long mandibles and often a further anteriorly located widest part of the body; high values indicate relatively short mandibles and often a further posteriorly located widest part of the body.

PC2 is dominated by the length of the mandibles. It describes very long to very short mandibles; low values indicate short mandibles, and high values indicate long mandibles.

PC3 explains 6.1% of overall variation and seems to be dominated by the shape of the main body; yet, also the shape of the mandibles seem to influence this PC; low values indicate a body with pointed posterior ends and elongate mandibles, and high values indicate a body with a stouter, truncated posterior end and curved mandibles.

PC4 explains 2.4% of overall variation and seems to be dominated by the width of the main body; low values indicate a broader posterior body region, and high values indicate a narrower posterior body region.

4. Discussion

4.1. Larvae of Nemopterinae

The number of known extant larvae of Nemopterinae depicted in the literature is rather low. Within Myrmeleontiformia, only in Psychopsidae fewer extant larvae have been depicted (Haug et al. 2020). Yet, the number of known species of Psychopsidae is only one third of that of Nemopterinae (Abraham 2014; Makarkin 2018), making Nemopterinae the relatively least known larger group concerning their larvae. Overall, the larvae of Nemopterinae appear rather uniform, especially regarding the head shape (Fig. 5; yet, we cannot exclude that this might be a bias of our still poor knowledge of larval morphology of Nemopterinae). The major differentiation within the known larvae can be recognised between early and later developmental stages, also on a quantitative level, concerning the trunk shape (Fig. 6). The trunk region is much enlarged in stage 2 and 3 larvae. The enlargement of the trunk is a rather common feature among lacewing larvae (e.g., Psychopsidae, Nymphidae). While it is not as extreme as in other ingroups of Neuroptera, such as later stages of Dilaridae (e.g., Gepp 1984: 196, pl. 5, fig. 11a) and Berothidae (Gepp 1984: 195, pl. 4, fig. 8a), the change is still quite extreme in Nemopterinae.

It has been suggested that certain features represent larval traits autapomorphic for Nemopterinae: soft body (Monserrat 1996: 65) with rather short legs (Mansell 1996: 176; Monserrat 1996: 65), short cervix region (Tröger 1993: 366; Mansell 1996: 176), shorter antennae, special setae on the legs, and digging behaviour (Badano et al. 2017: 99). Yet, most of these features are in fact far from unique; therefore, it depends on the exact phylogeny whether these are indeed autapomorphies or plesiomorphies (some aspects are discussed further below).

4.2. Nemopterinae and Crocinae

There are significantly more species known in Nemopterinae than in Crocinae, i.e., more than 100 species ver-

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sus more than 50 (Abraham 2014). It may therefore seem surprising on first glance that there are significantly more extant larvae depicted in the literature for Crocinae than for Nemopterinae, 57 vs. 27 (Haug et al. accepted a). The rareness of larvae of Nemopterinae is most likely related to the specific life habits of the larvae, as they dig relatively deep into the soil, making access to them more challenging.

The head shapes of the larvae differ significantly between the two groups. Two qualitative aspects are immediately apparent: 1) The stylets are rather short and stout in larvae of Nemopterinae, but rather slender and long in Crocinae. 2) The head is rather broad in larvae of Nemopterinae, but more squared to triangular-shaped in larvae of Crocinae.

In both aspects, larvae of Crocinae are much more similar to larvae of Ascalaphidae, Myrmeleontidae, Nym-

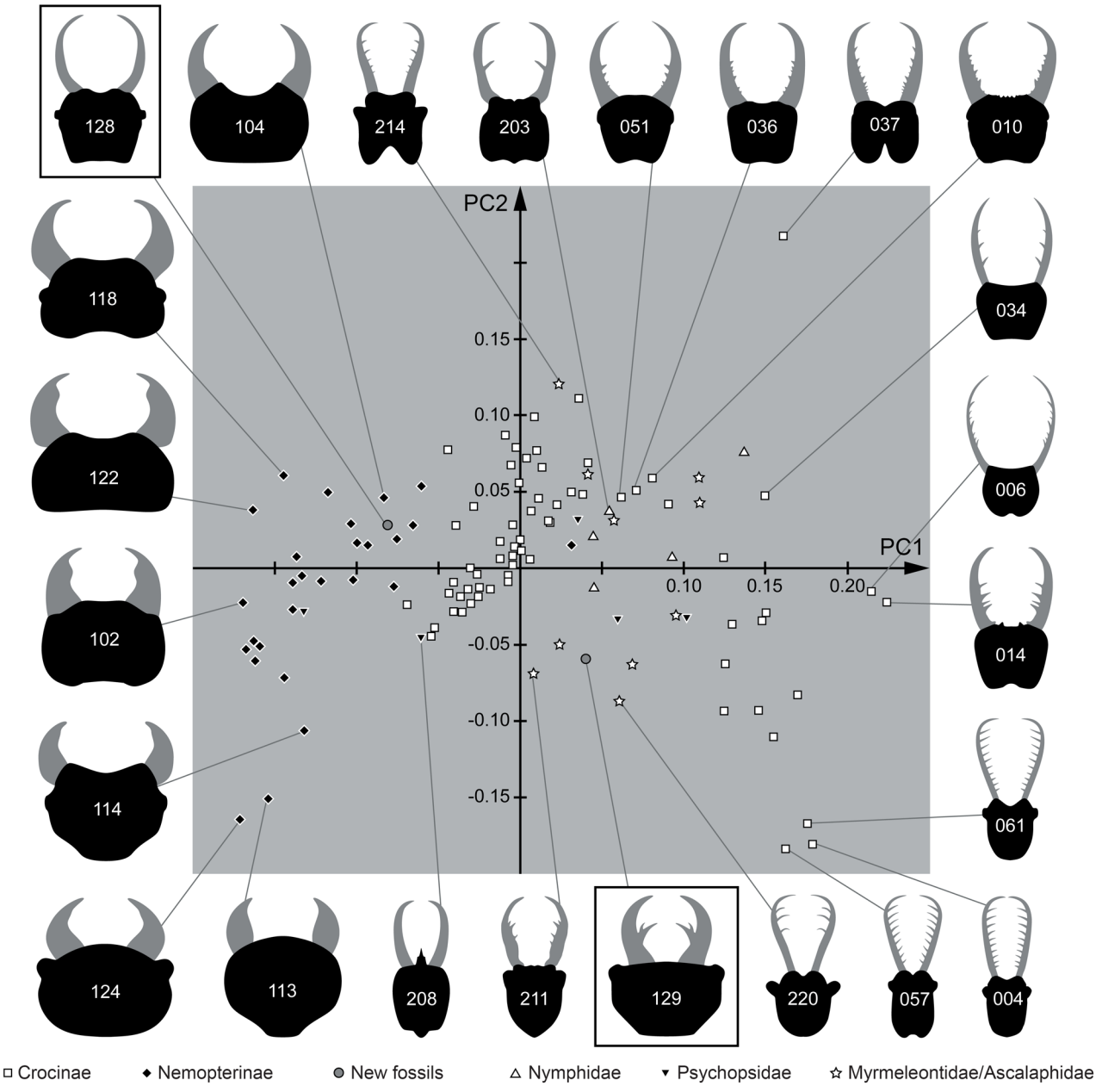

Fig. 5. Shape analysis of the heads of larval specimens of Myrmeleontiformia; examples of heads are depicted around the plot; the two new fossil specimens (specimens 28 and 29, here labelled 128 and 129 in accordance with Suppl. Tab. 1) are highlighted by rectangles.

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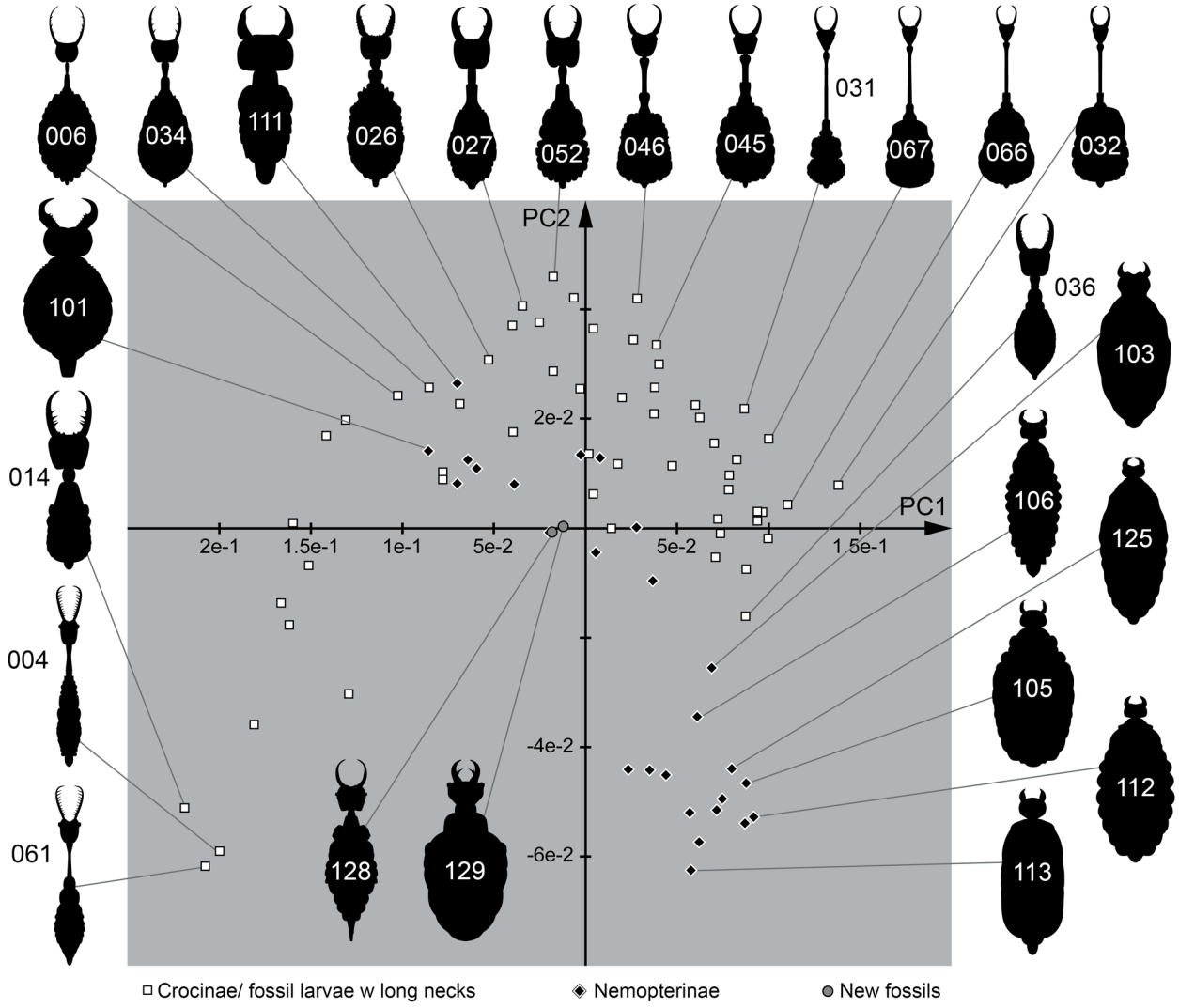

Fig. 6. Shape analysis of the body outlines of larval specimens of Nemopteridae; examples of body outlines are depicted around the plot; the two new fossil specimens are shown in the lower middle; note that stage 1 larvae of Nemopterinae (e.g., 101, 111) plot far separate from later stage larvae of Nemopterinae (103, 105, 106, 112, 113, 125).

phidae and most larvae of Psychopsidae, while larvae of Nemopterinae are clearly set apart, also in the quantitative analysis (Fig. 5). Only a single larval specimen of the group Psychopsidae is similar in head shape to some larvae of Nemopterinae (i.e., the specimen from New 1989). This distribution makes it most likely that the head shape of Crocinae is largely plesiomorphic, but that of larvae of Nemopterinae is apomorphic.

A character warranting separate discussion is the presence or absence of tooth-like protrusions ("teeth") on the stylets. Generally, such teeth have been identified as a characteristic feature of the larvae of Nymphidae, Ascalaphidae and Myrmeleontidae (Badano 2012: 10; Badano & Pantaleoni 2014a, 2014b); larvae of Crocinae and Nemopterinae are generally thought to lack teeth, at least in the larval stages 2 and 3 (Mansell 1996: 176; Beutel et al. 2010: 549; Badano 2012: 11). Yet, fossil larvae resembling larvae of Crocinae by possessing an elongated neck also possess prominent teeth (Haug et al. 2019a, accepted a). Also, there are clear cases of extant larvae of Crocinae that bear teeth on their stylets, most prominently in stage 1 larvae, indicating that absence of teeth in larvae of Crocinae may represent an apomorphic state, added as new condition later in ontogeny (see discussion in Haug et al. 2019a). This feature also leads to a clustering of such an early extant larva with some of the fossils in the quan-

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titative analysis (Fig. 6, extant larva 014, fossil larvae 004 and 061).

In addition, some larvae of Nemopterinae have tooth-like protrusions on the stylets (specimens 1, 18–21). Already Monserrat (1996: 104) described these as "macrotrichie [or macrotrichia] as teeth on the internal margin". It therefore seems very likely that in fact "tooth-bearing stylets" is an ancestral condition for Myrmeleontiformia or a large ingroup of it, and that the absence of teeth in many later-stage larvae of Crocinae and Nemopterinae is a secondarily derived character. The absence of teeth in larvae of Psychopsidae might still represent a retained original character, similar to the presence of empodia on the trunk appendages. Such an interpretation could be seen as an indication for a monophyletic group including Nemopteridae, Nymphidae, Ascalaphidae and Myrmeleontidae (as resolved in Jandausch et al. 2018: 554). This group would in this case be characterised by the presence of teeth and the absence of empodia. Yet, not all phylogenetic reconstructions support this assumption (e.g., Winterton et al. 2010, 2018).

The case becomes even more complicated when considering fossil forms. Some of these have significantly more teeth than modern forms (Haug et al. accepted a), or very unusual teeth with two cusps (Badano et al. 2018, fig. 3d). This demonstrates that the common modern pattern with 1–3 (rarely 4) teeth is only a remnant of a formerly larger diversity of teeth. The fossils further support the idea that teeth evolved already in the lineage towards Myrmeleontiformia (cf. Badano et al. 2018), making the absence of them in Psychopsidae more likely a derived character.

4.3. Systematic interpretation of the two new specimens

The two new specimens are so far unique, no second similar specimen is currently known for each of them. Some aspects, especially concerning smaller details such as seta morphology or setae arrangement, remain difficult to assess. Therefore, we did not attempt to code the specimens into the matrix of Badano et al. (2018). Instead, here we aim to discuss the available characters in a phylogenetic frame, without performing a new phylogenetic analysis.

Both new specimens lack an empodium on the thorax appendages. The absence of this feature does not appear to be an artefact caused by preservation, but original morphology. The loss of the empodium in larvae is a possible apomorphy of a large ingroup of Myrmeleontiformia (Jandausch et al. 2018: 554). Only in larvae of Psychopsidae the empodium is retained in modern representatives of Myrmeleontiformia. In addition, some fossil larvae, possible early representatives of Myrmeleontiformia, also retain the empodium (Badano et al. 2018).

The absence of an empodium in combination with the overall habitus in the new specimens is therefore indicative of an ingroup position within Myrmeleontiformia. Although most details of the setae remain difficult to assess, the setae on specimen 28 (PED 0929) appear dolichaster-like (Fig. 2E, F), which is another characteristic feature of Myrmeleontiformia (Engel et al. 2018: 543).

Another important character is the small cervix and that sclerites in this region appear to be absent. Such a short cervix is also a common feature within Myrmeleontiformia, basically only larvae of the group Crocinae retain a well sclerotized, prominent (often very prominent) cervix. This aspect is therefore similar in the two new larvae and those of Psychopsidae, Nemopterinae, Nymphidae, Ascalaphidae, and Myrmeleontidae.

Specimen 28 (PED 0929) has no teeth in the stylets. In combination with the absence of the empodium and the very short, unsclerotized cervix, it has most similarities with most larvae of Nemopterinae. When considering the head shape quantitatively, the specimen plots among modern larvae of Nemopterinae (Fig. 5). Of course, also some clear differences are apparent. While the head is rather broad in the new larva, it is not as broad as in most extant larvae of Nemopterinae. Also the stylets are comparably long and slender, not as stout as in extant forms. Also, the overall appearance of the larvae is reminiscent of the larva *Thysanocroce damarae* (Crocinae; Mansell 1996: 177, fig. 5), the major difference again being that in specimen 28 the neck is clearly much shorter and unsclerotized. Similarities to the larvae of Crocinae include the distinct abaxial folds; yet similar folds are also known in larvae of Nemopterinae (e.g., Mansell 1996: 175, fig. 3).

It is possible that the new larva is an early representative of the lineage of Nemopterinae, basically the sister group to all remaining species, while retaining quite some plesiomorphic traits, therefore resembling larvae of Crocinae in some aspects. The softness of the trunk is also compatible with such an interpretation. The overall body outline of the larva provides scarce evidence on that end. It plots close to certain larvae of Nemopterinae, but also close to some larvae of Crocinae (Fig. 6). The overall body outline may indeed be rather plesiomorphic.

In that regard, we still need to consider that the larva is quite small. Smaller larvae often appear to retain a more plesiomorphic appearance. Also here, older larvae of Nemopterinae plot further separated from larvae of Crocinae than earlier ones (Fig. 6). In summary, an interpretation of specimen 28 as a larva of Nemopterinae is reasonable.

Specimen 29 (PED 0581) is even more unusual. A single prominent tooth with two cusps on the stylet is not known in this form in modern larvae of Myrmeleontiformia. Only few fossils have such teeth, but differ other-

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wise from the new larva (e.g., Badano et al. 2018), e.g., by the orientation of the tooth and prominent processes on the trunk. The differences make a close relationship of the new larva to these already known ones not very likely. Concerning quantitative aspects of overall body shape, the larva plots extremely close to specimen 28 (Fig. 6). Concerning quantitative head shape, it plots closer to extant larvae of Myrmeleontidae and Ascalaphidae (Fig. 5). Concerning qualitative aspects, the head of the larva is rather broad, resembling larvae of Nemopterinae. Also the stylets are rather broad. Both aspects could be seen as an argument for a closer relationship to Nemopterinae as well. The even broader and softer appearing body would also well be compatible with such an interpretation, although the special tooth would then represent a specialisation. Yet, the specimen could also as well be seen as a highly specialised larva closer related to Myrmeleontidae or Ascalaphidae, but this is not supported by the analysis.

4.4. Diversity of myrmeleontiformian larvae

Both new specimens are candidates to represent larvae of Nemopterinae, although only of the early lineage. This circumstance appears to be more likely in the case of specimen 28, but less so for specimen 29. The group Crocinae seems likewise represented in Myanmar amber (see discussion in Haug et al. 2019a, accepted a), but this remains unclear. Similar to the case of larvae of Crocinae, the modern-day habitat of larvae of Nemopterinae could be an explanation why such larvae are almost absent, or at least rare. Extant larvae of Nemopterinae are relatively deep diggers. The likewise digging larvae of Myrmeleontidae are also extremely rare in Myanmar amber, as only a single specimen has so far been reported (Badano et al. 2018; it is still surprising that such larvae are comparably well represented in Miocene Dominican amber, see recent discussion in Haug et al. accepted b). The groups Psychopsidae and Nymphidae are quite well represented in Myanmar amber, and even more diverse than in the modern fauna (Haug et al. 2020, in press). Also, larvae resembling those of Ascalaphidae appear to be quite common in Myanmar amber (for details, see Wang et al. 2016; Badano et al. 2018; Herrera-Flórez et al. 2020).

Taking into account the two new larvae herein described, it seems reasonable to assume that now larvae from all six major lineages of Myrmeleontiformia were already present in the fauna of Myanmar almost 100 million years ago. This might be seen as an indication of a rather stable diversity within Myrmeleontiformia over a long time span. Yet, such interpretations on coarse taxonomic levels remain oversimplifications. In the modern fauna, Myrmeleontidae represents quite a major share of the myrmeleontiformian larval diversity. Back in the Cretaceous, especially the larvae of Psychopsidae and Nymphidae were quite more diverse and hence, also different in most cases from the extant larvae. The possible larvae of Crocinae differ significantly in morphology and likely also in ecology from their modern counterparts. This also seems to be true for the two possible specimens of Nemopterinae. Modern larvae of Nemopterinae seem less well known as they live relatively deep underground, coming rarely to the surface. Such a behaviour makes preservation in amber not very likely. The two specimens may therefore have been different in their ecology as well, making preservation in amber more likely.

Hence, in more detailed comparison the Cretaceous larval myrmeleontiformian lacewing fauna could have been quite different from the extant one, with:

1) lineages nowadays less important having had a greater form diversity in the past (indicating a greater ecological diversity) such as Psychopsidae (Haug et al. 2020) and Nymphidae (Haug et al. in press);

2) lineages with less diverse forms, but very different ones, indicating a significant difference in ecology in the past that is not represented in the modern fauna, such as Crocinae (Haug et al. accepted a) and Nemopterinae (as shown here);

3) lineages with larvae resembling modern forms being also already likewise common and performing similar tasks and behavioural aspects such as larvae of the lineage of Ascalaphidae + Myrmeleontidae which resemble modern larvae of Ascalaphidae in many aspects (Badano et al. 2018; Herrera-Flórez et al. 2020; Hörnig et al. in review);

4) lineages that were not yet diversified, but play a major role in the modern fauna, such as Myrmeleontidae (Badano et al. 2018);

5) and finally "experimental" lineages that contributed to an enormous diversity in the past, but are now entirely extinct (Badano et al. 2018; Haug et al. 2019a, 2019b).

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Suppl. Fig. 1. Head shapes of Crocinae and long-necked fossils used in the shape analysis.

Suppl. Fig. 2. Head shapes of Crocinae and long-necked fossils used in the shape analysis, continued.

Suppl. Fig. 3. Head shapes of Nemopterinae and possible fossil representatives used in the shape analysis.

Suppl. Fig. 4. Head shapes of other myrmeleontiformian ingroups used in the shape analysis.

Suppl. Fig. 5. Entire body shapes of Crocinae and long-necked fossils used in the shape analysis.

Suppl. Fig. 6. Entire body shapes of Nemopterinae and possible fossil representatives used in the shape analysis.

Suppl. Fig. 7. Range of the six effective principal components of the shape analysis of the heads of myrmeleontiformian larvae.

Suppl. Fig. 8. Graphical representation of the factor loadings of the shape analysis of the heads.

Suppl. Fig. 9. Graphical representation of the factor loadings of the shape analysis of the entire bodies.

Suppl. Table 1. List of all specimens used in this study including their source data.

Suppl. Text 1. Results of the principal component analysis of the head shapes.

Suppl. Text 2. Values of the effective principal components for the head shape of each specimen.

Suppl. Text 3. Results of the principal component analysis of the entire body shapes.

Suppl. Text 4. Values of the effective principal components for the entire body shape of each specimen.

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