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New details of the enigmatic 100 million years old antlion-like larvae of *Ankyloleon* (Myrmeleontiformia, Neuroptera)

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Abstract. Lacewing larvae in the Cretaceous were more diverse in appearance than they are today, best documented by numerous fossils preserved in amber. One morphotype of an unusual larva from about 100 Ma old Kachin amber (Myanmar) was formally recognised as a distinct group called *Ankyloleon*. The original description erected a single formal species, *Ankyloleon caudatus*. Yet, it was indicated that among the five original specimens, more species were represented. We here report five new specimens. Among these is the so far largest as well as the so far smallest specimen. Based on this expanded material we can estimate certain aspects of the ontogenetic sequence and are able to recognise a second discrete species, *Ankyloleon caroluspetrus* sp. nov. We discuss aspects of the biology of *Ankyloleon* based on newly observed details such as serrations on the mandibles. Long and slender mouthparts, legs and body together with a weakly expressed outer trunk segmentation provide indications for a lifestyle hunting for prey in more confined spaces. Still many aspects of the biology of these larvae must remain unclear due to a lack of a well comparable modern counterpart, emphasising how different the fauna of the Cretaceous was.

Keywords. Myrmeleontiformia, Neuroptera, ontogeny, Cretaceous, Burmese amber.

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Introduction

Biodiversity and its protection has been recognised as an important task for humankind. The biodiversity crisis is recognised by changes of biodiversity, namely a loss in abundance, in species richness and ultimately ecological function. Also faunas of the past have undergone significant changes and losses. The group of lacewings, Neuroptera Linnaeus, 1758, is today one of the less species-rich groups compared to the hyper-diverse lineages such as Coleoptera Linnaeus, 1758 (beetles). Yet, in the past lacewings seem to have been one of the more important groups, for example, in the Cretaceous (Aspöck & Aspöck 2007).

It is assumed that in the past, lacewings fulfilled ecological roles nowadays partly taken over by moths (Lepidoptera), at least in the adult phase (Labandeira *et al.* 2016). Larvae of lacewings are, mostly, fierce predators, also in the modern fauna. Yet, in the Cretaceous many now extinct larval morphologies indicate ecological roles back then that are neither performed by modern lacewing larvae, nor by moth larvae, i.e., caterpillars, which are mostly foliage feeders (see also discussion in Gauweiler *et al.* 2022). Together with some quite modern-appearing larvae (e.g., Engel & Grimaldi 2008; Wang *et al.* 2016; Wichard 2017; Makarkin 2018; Pérez-de la Fuente *et al.* 2020), the overall diversity of lacewing larvae was larger in the Cretaceous than it is today (e.g., Badano *et al.* 2018; Haug *et al.* 2020a, 2022a).

Among the now extinct morphologies are some that at least distantly remind of some modern forms, providing a good guess what their exact ecology might have been (e.g., Pérez-de la Fuente *et al.* 2012, 2016, 2018, 2019; Wang *et al.* 2016; Haug *et al.* 2018; Hörnig *et al.* 2022). Yet, in other cases the morphology is unparalleled in the modern fauna, and the interpretation of the exact function demands for further reaching comparisons (e.g., Liu *et al.* 2016, 2018; Haug *et al.* 2022b; Luo *et al.* 2022). Some of the morphologies are also extremer versions of modern forms (e.g., Pérez-de la Fuente *et al.* 2012, 2016; Haug *et al.* 2019a, 2019b, 2021a; Zippel *et al.* 2021).

Few larvae have a quite bewildering appearance. An example for such an unusual appearance is represented by larvae of the group *Ankyloleon* Badano, Haug & Cerretti in Badano *et al.*, 2021. Originally, five specimens were reported, all preserved in about 100 Ma old amber from Myanmar (Badano *et al.* 2021). These larvae are immediately recognisable by a differentiation of the posterior trunk (abdomen) into an anterior region with rather broad segments and a posterior region with narrow segments, giving this region an overall tail-like appearance. Also the mouthparts are unusual, especially given the relationships of *Ankyloleon*. In lacewing larvae, each mandible (upper jaw) is conjoined with its corresponding maxilla (lower jaw) to form a venom-injecting-sucking stylet (MacLeod 1964; New 1992; Cover & Bogan 2015; Zimmermann *et al.* 2019). In the group Myrmeleontiformia Latreille, 1802 (the group of antlion-like lacewings), these larval stylets are usually gently curved and additionally armed with teeth, although the teeth become secondarily reduced in some lineages (e.g., Badano *et al.* 2018; Haug *et al.* 2019c). *Ankyloleon* has been resolved as an ingroup of Myrmeleontiformia, but also here the larvae lack teeth (Badano *et al.* 2021). More unusual, the stylets are proximally straight and are only curved closely to the tip. Such a stylet shape is known in larvae of dragon lacewings (Nevrorthidae; Haug *et al.* 2020b), but these are only distantly related to Myrmeleontiformia (e.g., Winterton *et al.* 2010, 2018; Engel *et al.* 2018), and this stylet shape must be the result of convergent evolution. The exact relationship of *Ankyloleon* within Myrmeleontiformia was resolved in Badano *et al.* (2021) as closely related to Ithonidae Newman, 1838 and *Ankyloleon* together with Ithonidae as closely related to Nymphidae Rambur, 1842. Originally, a single species of *Ankyloleon* was formally described, but it was already indicated that the group was more species-rich (Badano *et al.* 2021).

We here report new specimens of *Ankyloleon*. We compare these to the five already known specimens and aim at unravelling some aspects of species diversity and ontogenetic sequence of these still enigmatic animals.

Material and methods

Material

In the centre of this study are five specimens preserved in Kachin amber, Myanmar, which are about 99–100 Ma old (Cruickshank & Ko 2003; Shi *et al.* 2012; Yu *et al.* 2019). The specimens were legally purchased via the online platform ebay.com from the traders burmite-miner, burmite-researcher, jingzhax0, and xinxin1013. They are now part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München, Germany under repository numbers PED 1727, PED 1877a, PED 2038, PED 2475, and PED 2619.

For comparison, a modern larva of an owllion ("Ascalaphidae", for terminology see Haug *et al.* 2022c and Terminology paragraph further below) was documented. The specimen is part of the collection of the Leibniz-Institut zur Analyse des Biodiversitätswandels–Hamburg site (LIB, formerly Centrum für Naturkunde / CeNak / ZMH) under repository number ZMH 62877.

Documentation methods

The specimens were documented under reflected light on a Keyence VHX-6000 digital microscope, as well as a Keyence BZ-9000 inverse fluorescence microscope, but with transmitted light. All images were recorded as compound images, combining images of shifting focus (image stacks) with each image stack representing adjacent image details. Stacks were combined to sharp image details, adjacent image details to a single panorama. Images under reflected light were additionally recorded with HDR (for details of the documentation, see Haug *et al.* 2020a and references therein).

The modern specimen was documented with a Canon EOS Rebel T3i with an MP-E 65 mm macro-lens. Lighting was provided by a Yongnuo YN24EX E-TTL twin flash.

Processing of reflected light images was performed with the built-in software, transmitted light images and macro-photographic images were processed with CombineZP and Adobe Photoshop CS3. All images were optimised in Adobe Photoshop CS2.

Terminology

Each ingroup of Insecta Linnaeus, 1758 has its own special terminology for certain structures. Yet, in order to provide access for non-specialised readers and for providing a basis for a wider comparative frame, we use a neutral type of terminology, including reference to the wider comparative frame of Euarthropoda Lankester, 1904. This approach is consistent with comparable earlier publications (see discussion in Haug *et al.* 2021b).

The post-embryonic ontogeny of holometabolans includes three major phases: the larval phase, the pupa phase, and the adult phase. In (almost) all known cases, the adult and pupa each represent a single stage. The larval phase (usually) includes several stages and instars. Stages can be differentiated by different morphological aspects, instars are separated by moults. Especially in groups in which only few larval stages occur, each stage likely corresponds to a single instar. However, in fossils the process of moulting cannot be observed, only morphologically differing stages can be identified. Hence, we here refer to 'stages' when addressing different larvae. These likely correspond directly to instars, yet this remains an assumption.

A significant taxonomic uncertainty complicates discussions within the group Myrmeleontiformia. Traditionally, the two groups Ascalaphidae Rambur, 1842 (owllfies) and Myrmeleontidae Latreille, 1803 (antlions) are sistergroups. Yet, in many recent analyses different patterns emerged with the one group inside the other or vice versa (see recent discussion and references in Haug *et al.* 2022c). These results led to the problem that some authors consider Ascalaphidae as no longer valid (most of it now being included in Ascalaphinae), other authors saw the necessity of re-characterising Myrmeleontidae. We cannot contribute to this problem, but see the necessity to refer to it. We therefore refer to the larger group of what has been considered to include Ascalaphidae and Myrmeleontidae as the group of owllions (Haug *et al.* 2022c). In this way, the uncertainty is expressed, it becomes clear what should be included, and it does not create a new taxonomic name, but also emphasises the provisional nature of the term until more stable phylogeny has been resolved.

Results

Descriptions of specimens

Specimen PED 2475

General. Elongate and rather large larva, about 15 mm in total length (Fig. 1A–D). Body presumably organised into 20 segments, ocular segment and 19 post-ocular segments. Anterior six segments (ocular plus five post-ocular segments) forming capsulate head. Trunk segmentation not well apparent. Anterior three trunk segments (thorax) differentiated from further posterior ones by each bearing a pair of ventral locomotory appendages (legs). Posterior trunk (abdomen) differentiated into two distinct regions, anterior abdomen segments dorsally sub-similar to thorax segments, posterior abdomen long and slender.

Head. Head capsule more or less square-shaped in dorsal view (Fig. 1C–D); maximum height about 50% of its width, flattening anteriorly (Fig. 1B). Bearing numerous tubercles. From each tubercle a seta arises. Ocular segment recognisable by possible larval eyes, indicated by a protrusion on each anterior lateral side of the head capsule; no distinct stemmata apparent. No externally visible structures of post-ocular segments 1 or 2. Appendages of post-ocular segments 3 and 4, mandibles and maxillae (maxillulae), forming a pair of compound structures, stylets. Stylets longer than head capsule, about 1.5 ×, protruding forwards. Stylets tapering distally; proximally straight, only at the tip with a distinct inward curvature, leading to a tip that is almost curved medially (Fig. 1E). Inner edge of the curvature and also very distal inner edge of the straight region of the stylets with tiny serrations. No clear structures of post-ocular segment 5, e.g., labium (maxillae), apparent.

Prothorax. Region posterior to the head soft-appearing (neck region), narrower than head (about 50%), about as long as wide (Fig. 1F). Post-ocular segment 6 (prothorax) with a distinct dorsal sclerite, pronotum. Rectangular in dorsal view, slightly wider than neck region. Longer than wide, about 2.5 ×. With numerous setae, especially prominent ones along each lateral edge, about 15, each with a distinct small socket. Prothorax ventrally with a pair of prominent legs (Fig. 1D). Leg elements rather elongate, slender, presumed element 3 (femur) about as long as pronotum, further details not accessible due to preservation.

Anterior trunk region posterior to prothorax. Post-ocular segments 7 and 8 (mesothorax and metathorax) and anterior abdomen segments not discernible as individual segments dorsally, as no distinct sclerites are apparent (Fig. 1C–D). Region slightly wider than pronotum, slightly widening towards the middle of the body, tapering again towards the posterior. Longer than pronotum, slightly more than 3 ×. Dorsal surface appears rather soft with numerous transverse folds concealing segment borders. Mesothorax and metathorax each ventrally with a pair of prominent legs. Legs sub-similar to those of the prothorax (Fig. 1B). Laterally, this trunk region has numerous protrusions bearing setae. Protrusions more pronounced towards the posterior (Fig. 1D).

Posterior trunk. No subdivision of segments apparent. About as long as anterior trunk region posterior to prothorax, but more slender, less than 50% (Fig. 1B–D). Tapering first, then widening slightly, very posterior region paddle-shaped (Fig. 1G). Laterally with numerous prominent and rather long setae, some more than 3 × the length of setae on the anterior trunk. Many further details not accessible due to limitations of the preservation.

Specimen PED 1877a

Large piece of amber with numerous syn-inclusions. Specimen of interest is an isolated head with attached stylets, slightly more than 2.6 mm in total length (Fig. 2A). Stylets longer than head capsule, about 2 ×, protruding forwards. Stylets tapering distally; proximally straight, only at the tip with a distinct inward curvature leading to a tip that is almost curved medially. Other details of head not accessible due to preservation.

Specimen PED 2619

Isolated head with attached stylets, more than 5 mm in total length (Fig. 2B). Stylets longer than head capsule, slightly less than 2 ×, protruding forwards. Stylets tapering distally; proximally straight, only at the

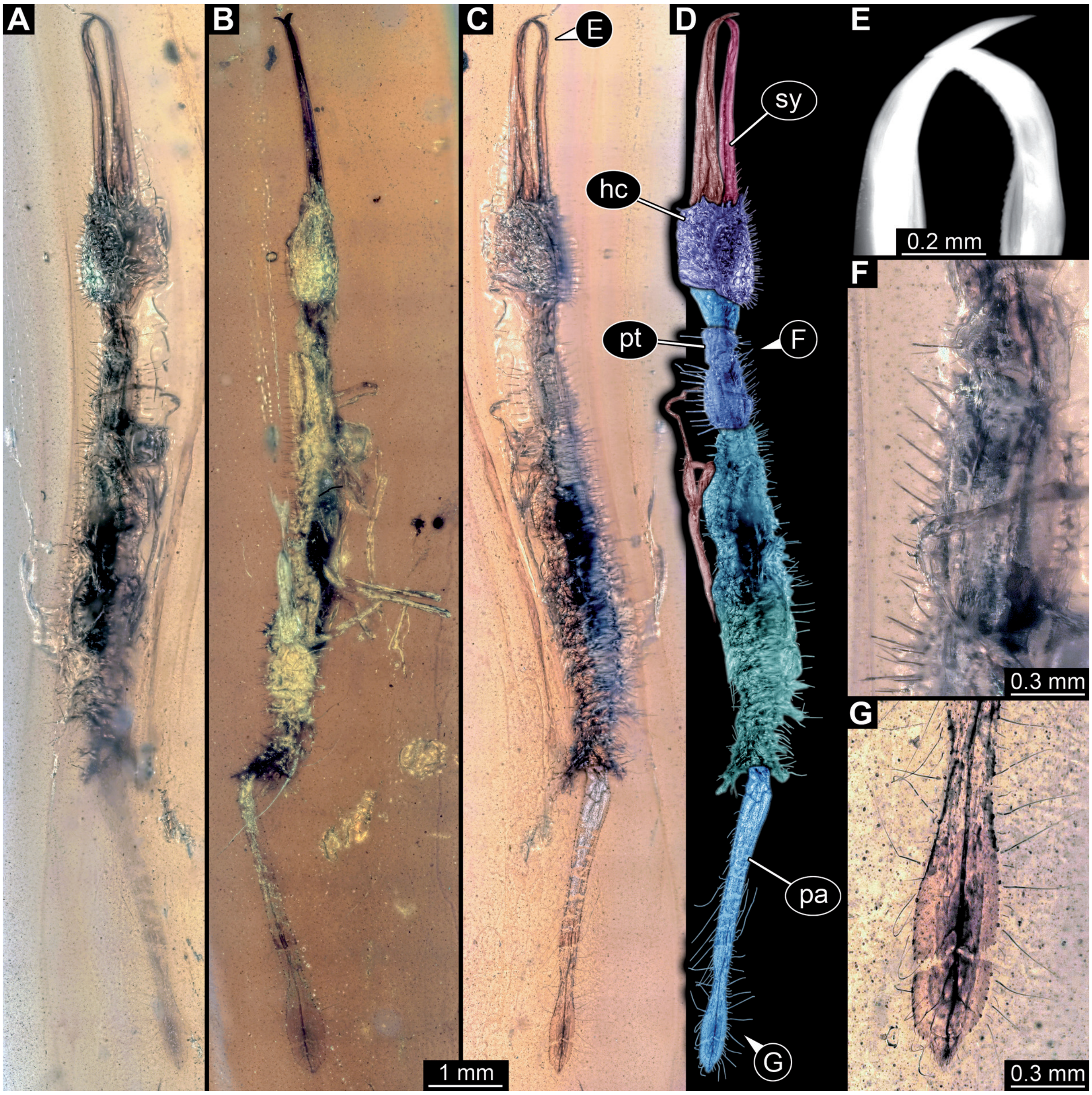

Fig. 1. Late stage larva of *Ankyloleon caudatus* Badano, Haug & Cerretti, 2021, PED 2475. **A**. Ventral view. **B**. Lateral right view. **C**. Dorsal view. **E**. Colour-marked version of a combined image of A and C. **E**. Close-up on tip of stylets, showing serrations. **F**. Close-op of pronotum with prominent setae. **G**. Close-up on paddle-shaped trunk end. E is an inverted image under transmitted light; all other images under reflected light. Abbreviations: hc = head capsule; pa = posterior abdomen; pt = prothorax; sy = stylet.

tip with a distinct inward curvature leading to a tip that is almost curved medially. Inner edge of the straight region of the stylets with tiny serrations (Fig. 2C). Head capsule more or less rectangular in dorsal view. Bearing numerous tubercles. From each tubercle a seta arises; tubercles (= sockets) short. Setae simple.

Specimen PED 1727

General. Rather small larva, about 2.45 mm in total length (Fig. 3A–C). Body presumably organised into 20 segments, ocular segment and 19 post-ocular segments. Anterior six segments (ocular plus five post-ocular segments) forming capsulate head. Trunk segmentation not well apparent. Anterior three trunk segments (thorax) differentiated from further posterior ones by each bearing a pair of ventral locomotory

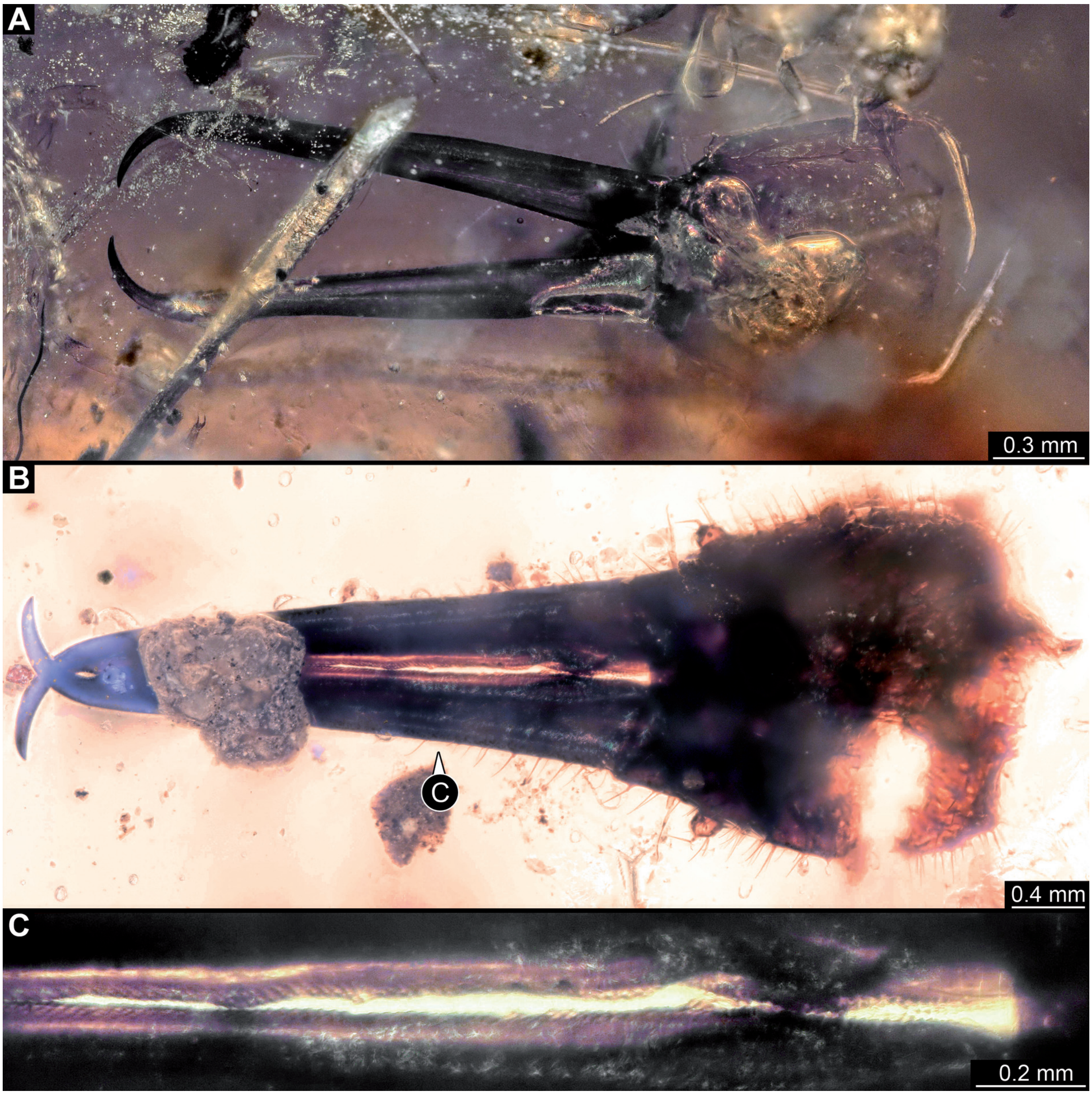

Fig. 2. Larvae of *Ankyloleon* Badano, Haug & Cerretti, 2021, isolated heads with stylets. **A**. PED 1877a, species unclear. **B**–**C**. PED 2619, *Ankyloleon caudatus* Badano, Haug & Cerretti, 2021. **B**. Overview. **C**. Close-up on inner edges of stylets with serrations.

appendages (legs). Posterior trunk (abdomen) differentiated into two distinct regions, anterior abdomen segments dorsally sub-similar to thorax segments, posterior abdomen elongate.

Head. Head capsule more or less rectangular in dorsal view, sightly wider than long (Fig. 3C). Ocular segment recognisable by possible larval eyes, indicated by a protrusion of each anterior lateral side of the head capsule; no distinct stemmata apparent. No externally visible structures of post-ocular segments 1 or 2. Appendages of post-ocular segments 3 and 4, mandibles and maxillae (maxillulae), forming a pair of compound structures, stylets. Stylets longer than head capsule, less than 1.5 ×, protruding forwards (Fig. 3A–C). Stylets tapering strongly distally; proximally straight, only at the tip with a distinct inward curvature leading to a tip that is almost curved. Distantly resembling a jai alai cesta in having the inner side concavely shaped.

Anterior trunk. In anterior trunk region (thorax and and anterior abdomen segments) no individual segments discernible dorsally, as no distinct sclerites are apparent. Dorsal surface appears rather soft with numerous transverse folds concealing segment borders. Region anteriorly narrower than head capsule, widening posteriorly to about the width of the head capsule, then strongly tapering. With numerous setae along each lateral edge. Anterior three segments (pro-, meso-, metathorax) ventrally each with a pair of prominent legs (Fig. 3A–C). Leg elements rather elongate, slender, presumed element 3 (femur) about

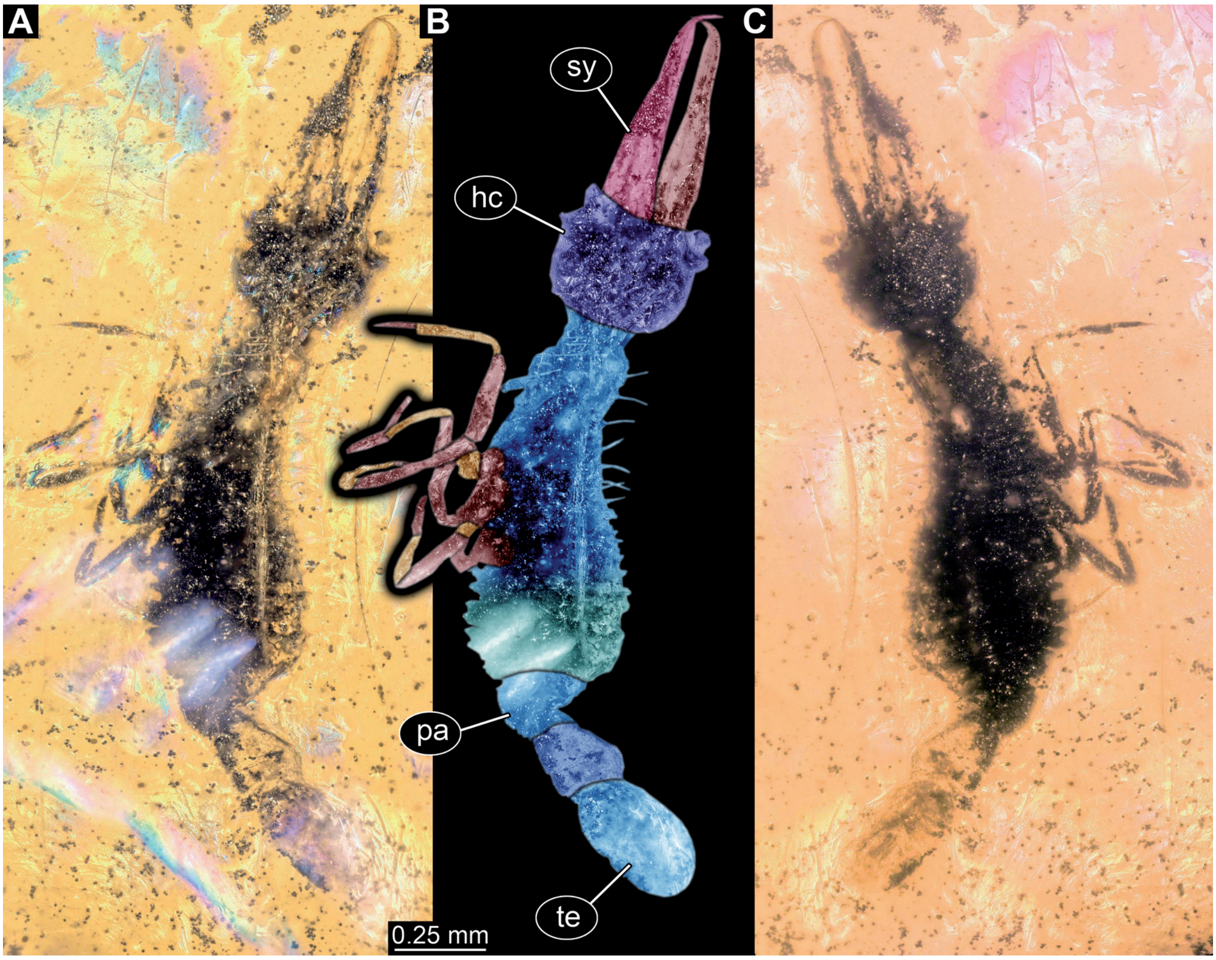

Fig. 3. Early stage larva (stage 1?) of *Ankyloleon* Badano, Haug & Cerretti, 2021, species unclear, PED 1727. **A**. Ventro-lateral view. **B**. Colour-marked version of A. **C**. Dorso-lateral view. Abbreviations: hc = head capsule; pa = posterior abdomen; sy = stylet; te = trunk end.

as long as head capsule. Distal part, element 4 and 5 (tibia and tarsus) about as long as femur. Further details not accessible due to preservation.

Posterior trunk. Posterior trunk slightly shorter than anterior trunk, more slender, about 50% of the width. Three units apparent, anterior two supposedly true abdomen segments, last unit, trunk end most likely compound of several segments (Fig. 3A–B). Anterior two segments each about as long as wide. Trunk end slightly longer, posteriorly round, overall paddle-shaped.

Specimen PED 2038

General. Larger larva, about 8.3 mm in total length (Fig. 4A–C). Body presumably organised into 20 segments, ocular segment and 19 post-ocular segments. Anterior six segments (ocular plus five post-ocular segments) forming capsulate head. Trunk segmentation not well apparent. Anterior three trunk segments (thorax) differentiated from further posterior ones by each bearing a pair of ventral locomotory appendages (legs). Posterior trunk (abdomen) differentiated into two distinct regions, anterior abdomen segments dorsally sub-similar to thorax segments, posterior abdomen long and slender.

Head. Head capsule more or less square-shaped in dorsal view (Fig. 5A). Bearing numerous tubercles. From each tubercle a seta arises; tubercles (= sockets) very long, almost as long as seta (Fig. 5D). Seta distally hammer-like, dolichaster-like. Ocular segment recognisable by possible larval eyes, indicated by a prominent protrusion of each anterior lateral side of the head capsule; no distinct stemmata apparent. Post-ocular segment 1 apparent by its possible appendage, antenna (antennula). Possible antenna rather small, indistinct, distally with a seta. No externally visible structures of post-ocular segment 2. Appendages of post-ocular segments 3 and 4, mandibles and maxillae (maxillulae), forming a pair of compound structures, stylets. Stylets longer than head capsule, about 1.5 ×, protruding forwards. Stylets tapering distally; proximally straight, only at the tip with a distinct inward curvature leading to a tip that is almost curved medially (Fig. 5B). Inner edge of the curvature and also very distal inner edge of the straight region of the stylets with tiny serrations (Fig. 5C). No clear structures of post-ocular segment 5, e.g., labium (maxillae), apparent.

Prothorax. Region posterior to the head soft-appearing (neck region), narrower than head (about 50%), about as long as wide (Fig. 4A–C). Post-ocular segment 6 (prothorax) with a distinct dorsal sclerite, pronotum. Trapezoidal in dorsal view, slightly wider than neck region anteriorly, widening posteriorly. Longer than posterior edge is wide, about 2 ×. With numerous setae, especially prominent ones along each lateral edge, about 15, resembling those of the head capsule, socketed, dolichaster-like. Prothorax ventrally with a pair of prominent legs (Fig. 6A–C). Leg elements rather elongate, slender, with five major elements. Proximal element, coxa, elongate, longer than wide, slightly less than 4 ×. Element 2 short, about 50% of coxa. Element 3, femur, longer than coxa, more than 2 ×, tapering distally, medially with a double row of short setae. Element 4, tibia, and element 5, tarsus, together about as long as femur, as wide as femur distally. Tibia longer than tarsus, about 1.3 ×. Tibia medially with a double row of short spines; medio-distally with a group of longer setae. Tarsus distally with a pair of claws.

Anterior trunk region posterior to prothorax. Post-ocular segments 7 and 8 (mesothorax and metathorax) only weakly discernible as individual segments dorsally, as no distinct sclerites are apparent (Fig. 4A–C). Slightly wider than posterior part of prothorax. With numerous setae similar to those on the prothorax. Meso- and metathorax each ventrally with a pair of prominent legs, sub-similar to those of the prothorax (Fig. 6A–C).

Posterior trunk. Posterior trunk (abdomen) differentiated into two distinct regions (Fig. 4A–C). Entire abdomen bearing numerous setae of similar length to those of the thorax. Anterior abdomen segments sub-similar to thorax segments, but wider. Further anterior segments only slightly wider than meso- and metathorax, then widening towards the middle of the body to about 2× the width of the mesothorax, tapering again towards the posterior. Region longer than pronotum, slightly more than 2×. Dorsal surface appears rather soft with numerous transverse folds concealing segment borders, yet laterally prominent protrusions bearing setae indicate the individual segments. Protrusions more pronounced towards the posterior. Posterior abdomen shorter than anterior abdomen, only about 50%, more slender, less than 50% of the maximum width. Three units apparent, anterior two supposedly true abdomen segments, last unit, trunk end, most likely compound of several segments. Anterior two segments each about as long as wide. Trunk end slightly longer and slightly narrower, posteriorly rounded.

Size and qualitative comparison to the already known specimens of Ankyloleon

The known five specimens of *Ankyloleon* (all larvae) seem all roughly in the same size range (Fig. 7C–F, I); although one of them is most likely an exuvium and partly crumpled (Badano *et al.* 2021), the head provides an impression for the relative size. All five new specimens expand the size range. Even the smaller one of the isolated heads (PED 1877a) is larger (Fig. 7G) than the heads of the known five specimens; the other one (PED 2619) is the largest of the entire series (Fig. 7A). Specimen PED 2038 has a slightly smaller head compared to the isolated specimens, but is overall significantly larger than the already known five specimens (Fig. 7J). The by far largest of the series is PED 2475 (Fig. 7B), although the larger isolated head indicates that this larva must have been even larger when complete (Fig. 7A). On the contrary, PED 1727 is by far smaller than the known specimens (Fig. 7H). The overall more stout appearance indicates that this specimen is an earlier larval stage.

PED 2475 (Fig. 7B) shares some characteristics with the holotype of *Ankyloleon caudatus* Badano, Haug & Cerretti in Badano *et al.*, 2021 (Fig. 7C), especially the very slender and rather long posterior region of the abdomen. It therefore seems likely that this is a later stage of this species. This makes it unlikely that differences to other specimens are explained by ontogenetic differences and more likely represent species differences. Although one could still argue that differences in the trunk could reflect differences in the feeding status or preservation of the larvae, the differences in head and setation cannot be explained in this way. This makes it more likely that also the differences in the trunk indeed reflect species differences. We therefore expand the taxonomic interpretation of *Ankyloleon*.

Taxonomic treatment

Insecta Linnaeus, 1758
Neuropterida Boudreaux, 1979
Neuroptera Linnaeus, 1758
Myrmeleontiformia Latreille, 1802

Ankyloleon Badano, Haug & Cerretti in Badano *et al.*, 2021

Amended diagnosis

Lacewing, larva campodeiform, elongate, head capsule well sclerotized; stemmata on distinct tubercles; antennae short; mandibular-maxillary stylets elongate, straight, curved inwards only at tip, without teeth, but with serrations; prothorax elongated, tubular; abdomen differentiated into a broader anterior region and a posterior narrower region.

Ankyloleon caudatus Badano, Haug & Cerretti in Badano *et al.*, 2021
Figs 1, 2B–C, 7A–C

Amended diagnosis

Lacewing of the group *Ankyloleon*. Posterior region of abdomen long, longer than anterior part of abdomen. Most posterior region paddle-shaped, in early stage ventrally with a paired pygopod. Later larval stages without subdivision into segments in the posterior abdomen and without pygopod.

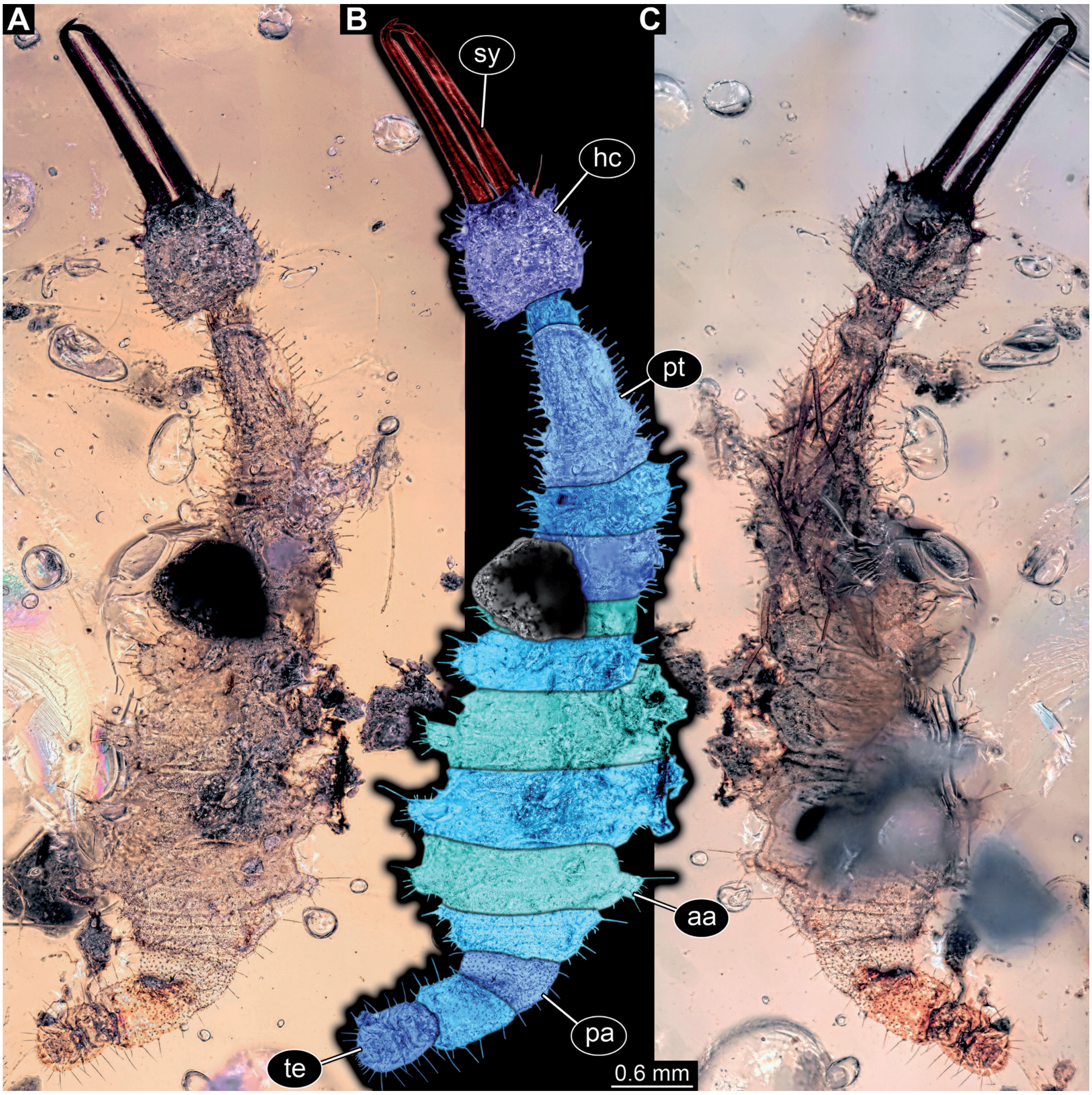

Fig. 4. Late stage larva of *Ankyloleon caroluspetrus* sp. nov., holotype, PED 2038. **A**. Dorsal view **B**. Colour-marked version of A. **C**. Ventral view. Abbreviations: aa = anterior abdomen; hc = head capsule; pa = posterior abdomen; pt = prothorax; sy = stylet; te = trunk end.

Ankyloleon caroluspetrus sp. nov.

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Figs 4–6, 7J

Diagnosis

Lacewing of the group *Ankyloleon*. Posterior region of the abdomen shorter than anterior part of abdomen. Most posterior region simply rounded. Head and prothorax with prominent socketed dolichaster-like setae.

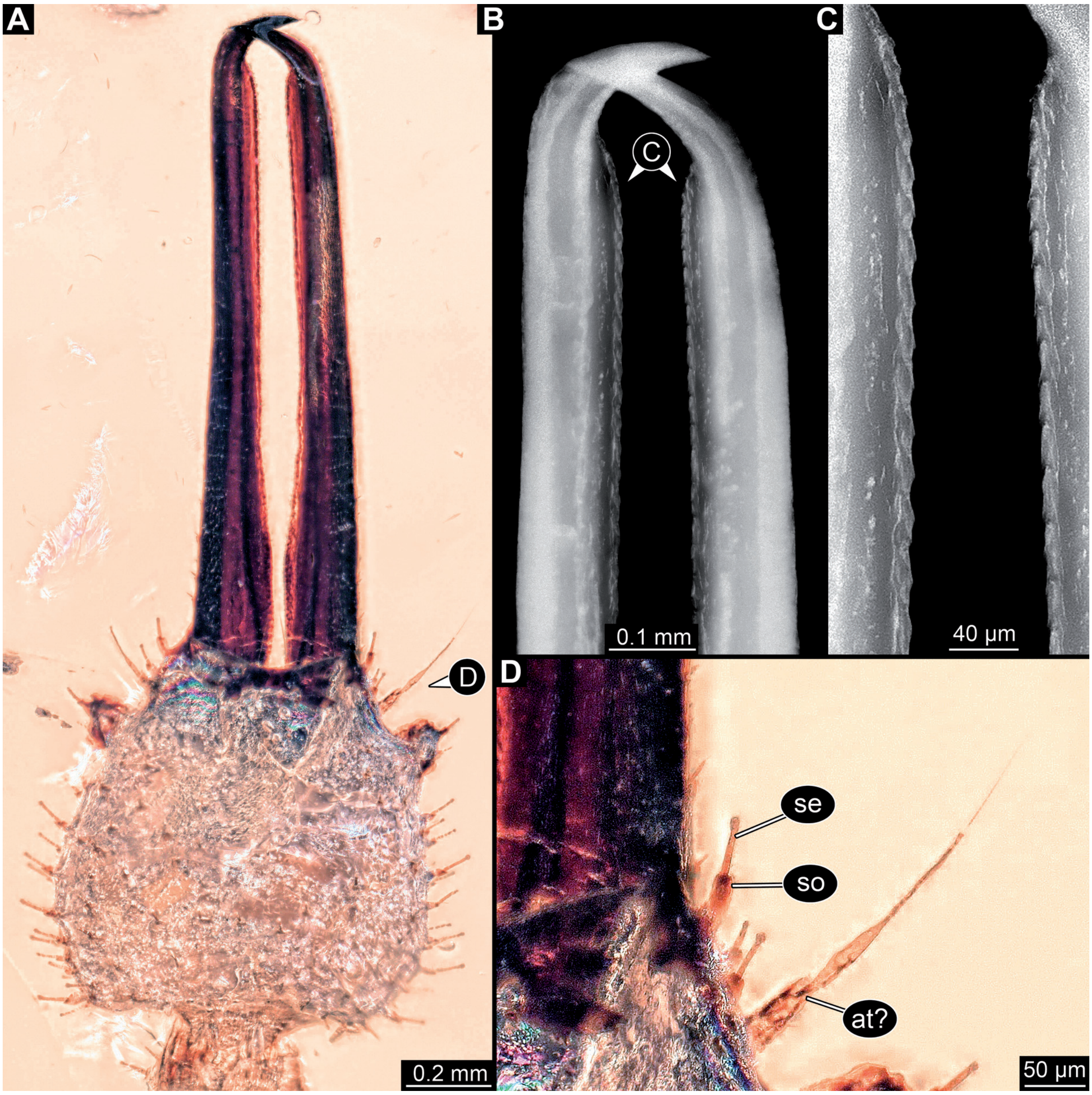

Fig. 5. Late stage larva of *Ankyloleon caroluspetrus* sp. nov., holotype, PED 2038, continued. **A**. Close-up of head. **B**. Close-up of distal part of stylets. **C**. Close-up on inner edges of stylets with serrations. **D**. Close-up on possible antenna and dolichaster-like setae with prominent sockets. Abbreviations: at? = possible antenna; se = seta; so = socket. A, D are images under reflected light; B–C are inverted images under transmitted light.

Etymology

In honour of the late Karl-Peter Haug, important supporter of our research.

Type material

Holotype

MYANMAR • PED 2038.

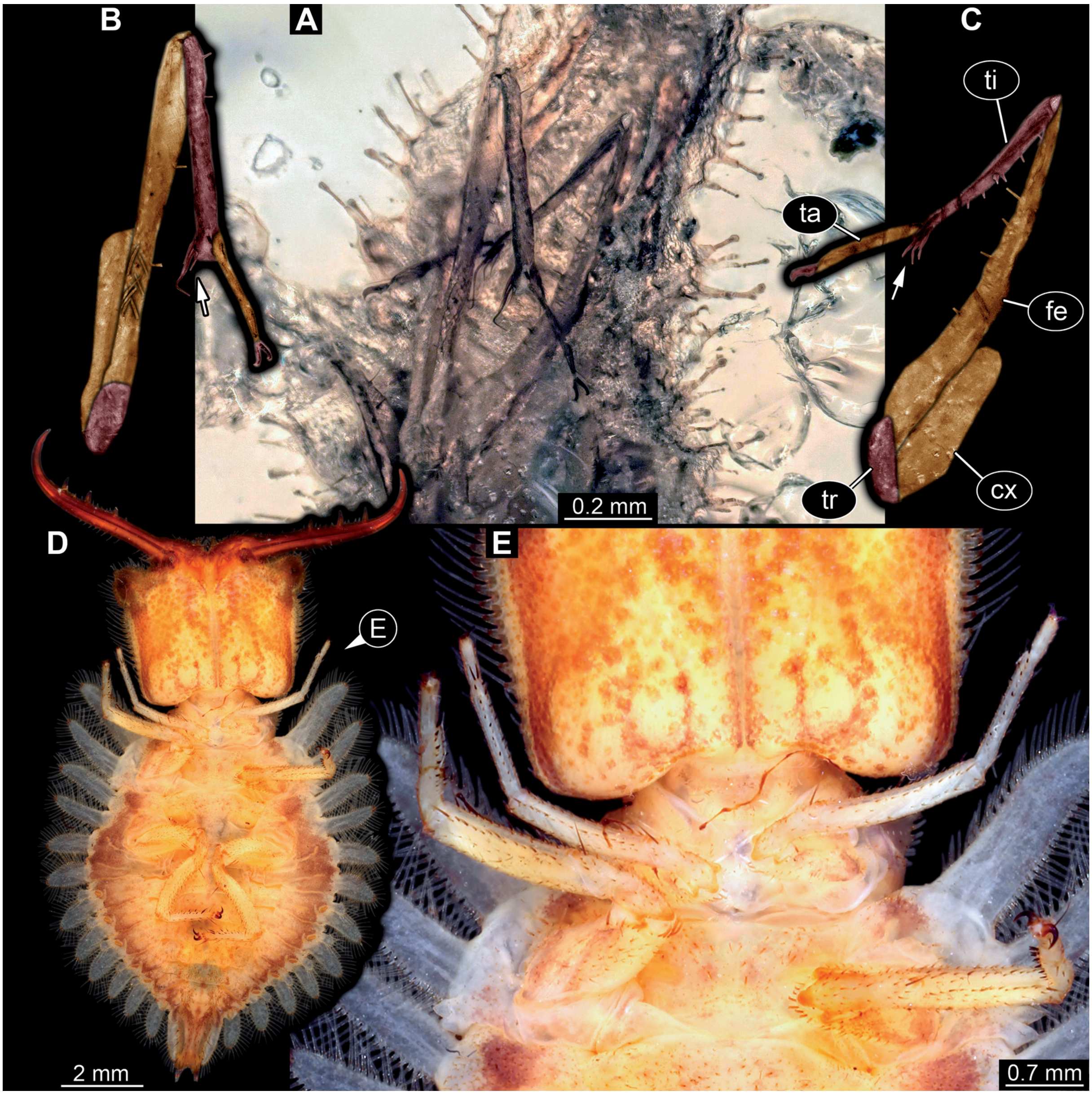

Fig. 6. Late stage larva of *Ankyloleon caroluspetrus* sp. nov., holotype, PED 2038, and modern larva for comparison. **A**–**C**. Legs of PED 2038. **A**. Close-up on first pair of walking legs. **B**. Colour-marked version of right leg of larva. **C**. Colour-marked version of left leg of larva. **D**–**E**. Modern larva of an owllion (“Ascalaphidae”; for terminology issues, see Haug *et al.* 2022c), ZMH 62877. **D**. Overview in ventral view. **E**. Close-up on legs. Abbreviations: cx = coxa; fe = femur; ta = tarsus; ti = tibia; tr = trochanter.

Locality and horizon

Northern Myanmar, Kachin region, Late Cretaceous (Cenomanian).

Differential diagnosis

The new species differs in several relative lengths from *A. caudatus*. The head of the new species is wider, as is the anterior part of the abdomen. The posterior tail-like region of the abdomen is shorter than in *A. caudatus*. Also the setation differs: the new species has strongly socketed dolichaster-like setae; the setae in *A. caudatus* also have sockets, but not reaching that far distally. Setae in *A. caudatus*

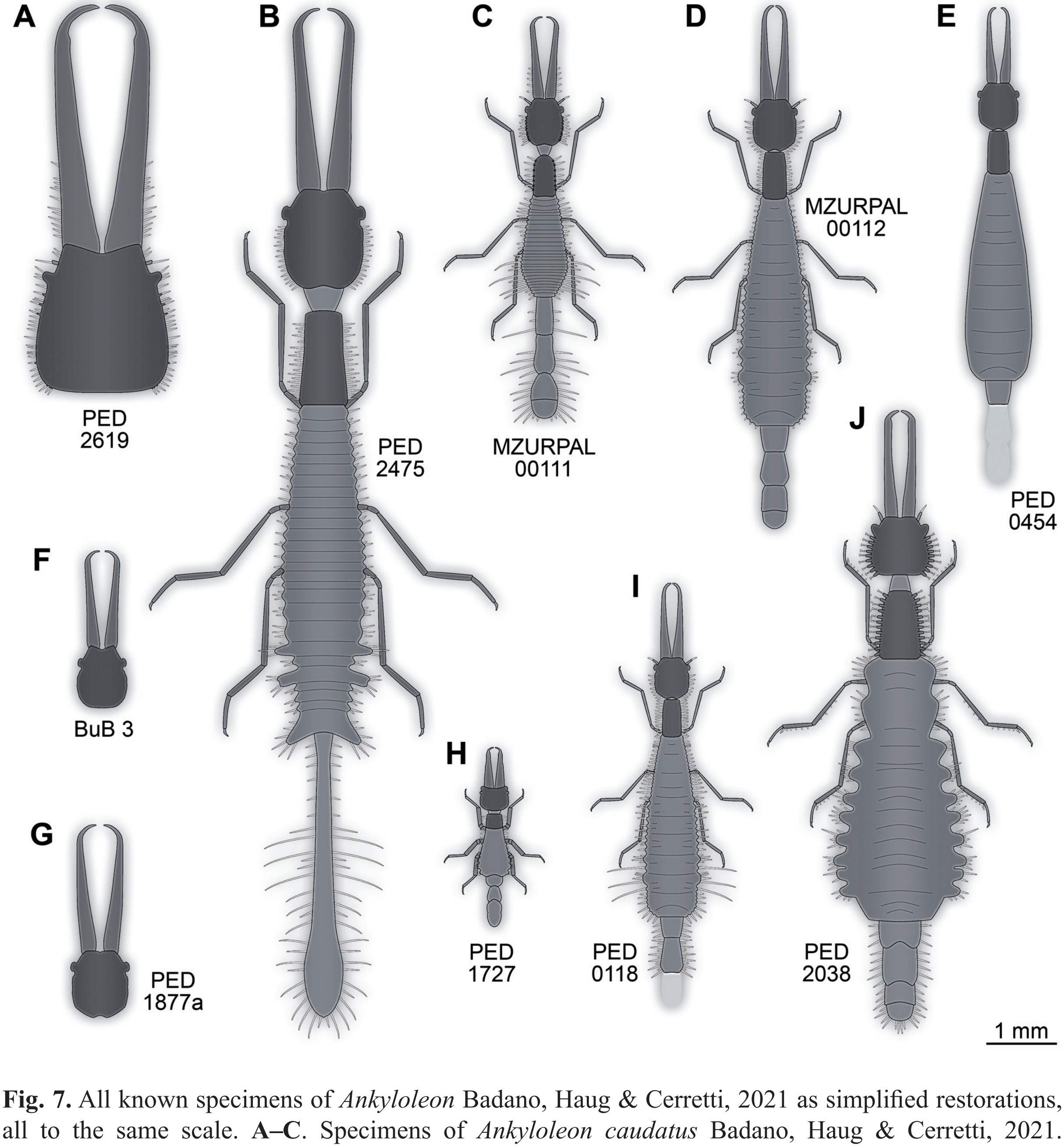

Fig. 7. All known specimens of *Ankyloleon* Badano, Haug & Cerretti, 2021 as simplified restorations, all to the same scale. **A–C**. Specimens of *Ankyloleon caudatus* Badano, Haug & Cerretti, 2021. **D–I**. Specimens of unclear species. **J**. Holotype (PED 2038) of *A. caroluspetrus* sp. nov. C–F and I based on Badano *et al.* (2021).

are prominent but simple, tapering distally, not being dolichoaster-like. At the posterior abdomen, *A. caudatus* has very long and prominent setae; the new species has rather short setae in this region.

Discussion

Ontogenetic sequence of *Ankyloleon*

The new specimens provide a wider size range for larvae of *Ankyloleon*. Based on this, we can now recognise a second species, as not all differences can be explained as ontogenetic differences.

For the species *Ankyloleon caudatus* it seems most likely that the largest complete specimen (PED 2475, Fig. 7B) is conspecific with the holotype (Fig. 7C), based on the similarities in relative body region lengths. The size difference between the two is quite significant. Still, also the large isolated head (PED 2619; Fig. 7A) is likely conspecific, as the sockets of the setae are less pronounced and the setae are simple to hammer-like. Therefore, it seems likely that these three specimens represent three different stages of *A. caudatus*.

The supposed exuvia (BuB 3; Fig. 7F) may be a slightly larger specimen in the same stage as the holotype (Fig. 7C) based on the size of the head. At least the exuvia seems to have a paddle-shaped trunk end (Badano *et al.* 2021: fig. 2c).

For the new species *Ankyloleon caroluspetrus* sp. nov., three of the specimens reported by Badano *et al.* (2021) could be conspecific (Fig. 7D–E, I); yet, many details are not accessible, and it cannot be excluded that these represent additional species. Even more problematic in this respect is the smaller isolated head (PED 1877a; Fig. 7G). Also relatively poor in characters is the small specimen (PED 1727; Fig. 7H). It might represent a stage 1 larva of *A. caroluspetrus*, but of course could also represent another species. In any case, it is likely a stage 1 larva. If it indeed is a stage 1 representative of *A. caroluspetrus*, PED 0118 (Fig. 7I) could then be interpreted as a stage 2 larva, and the holotype (PED 2038; Fig. 7J) as a stage 3 larva. Yet, in general we have only few specimens and only more material will allow a statistic comparison.

Life style

Larvae of *Ankyloleon* are rather unusual for antlion-like larvae, i.e., those of the group Myrmeleontiformia. Especially the stylet shape is very unusual. As Badano *et al.* (2021) already pointed out, the proximally straight and distally curved stylets partly resemble those of larvae of Nevrorthidae Nakahara, 1958. Yet, those in *Ankyloleon* are relatively longer. Also the new detail of serrations close to the tip, as seen in specimens of both species, have not been reported in larvae of Nevrorthidae, although imaging techniques that could resolve such structures have been employed (Beutel *et al.* 2010: 537, fig. 3, 540, fig. 6).

Notably, such small serrations in otherwise smooth-appearing regions of stylets seem known in numerous other larvae, but are rarely explicitly depicted. This observation holds true for larvae of quite different neuropteran ingroups: Mantispidae Leach, 1815 (MacLeod 1964: pl. XIV figs 42, 44; Jandausch *et al.* 2018: 535, fig. 6d), Nymphidae (New 1982: 84, fig. 8.12), Chrysopidae Schneider, 1851 (Tauber 2003: 477, fig. 5b), Myrmeleontidae (Satar *et al.* 2006: 61, fig. 16; 2014: 69, fig. 11; Lehnert *et al.* 2022: 3, fig. 2a) and Crocinae Navás, 1910 (Tusun & Satar 2016: 148, fig. 11).

The function of the serrations in *Ankyloleon* is partly puzzling. Such serrations usually either help penetrating (in a saw-like manner) or prohibit slipping out (in a barb-like manner). Yet, based on the position of the serrations it seems that the serrated part did not penetrate the prey. Therefore, it seems unlikely that the serrations could fulfil the expected function.

A further difference of *Ankyloleon* larvae and those of Nevrorthidae is that the latter have stronger upward-curved stylets (Beutel *et al.* 2010: 540, fig. 6b) and hunt their prey in water. Hence, there are few parallels left to the larvae of *Ankyloleon*.

As a consequence, mostly mechanical aspects of the stylets of larvae of *Ankyloleon* remain for further interpretation. Despite having now nine specimens at hand, none of these shows widely opened stylets as in some other fossil larval representatives of Myrmeleontiformia (Wang *et al.* 2016: fig. 3b, d, f; Badano *et al.* 2018: fig. 3g; Haug *et al.* 2020a: 28, fig. 22a–c; 2021a: 3, fig. 2b; 2022c: 7, fig. 3a–c, 14, fig. 10a–c). While not a strong signal, it is at least an indication that the stylets could not be widely opened. Together with the short curved part at the tip, which will only allow for a rather small depth of penetration, this indicates a rather small prey item size. The serrations could indicate that the prey items may have been more difficult to pierce (but see above). Yet, the rather long lever and narrow position of the stylets on the head capsule indicates that the larvae could not generate much force (see also discussion in Haug *et al.* 2023).

The legs of the larvae of *Ankyloleon* are rather slender, not unlike those of some long-necked antlions (Herrerra-Flórez *et al.* 2020; Haug *et al.* 2021c); the arrangement of the setae resembles that of other antlion-like larvae (Fig. 6D–E). Therefore, also the legs are not very indicative, besides being comparable to long-necked antlions for a strategy of keeping the prey items at distance, which also fits with the elongated neck (see also discussion in Haug *et al.* 2023).

The slenderness of the larvae also makes them appearing different from modern antlion-like larvae. Yet, this has also been observed in other Cretaceous antlion-like larvae. Still, especially the largest specimen seems so far unparalleled in antlion-like larvae, demanding again for a comparison to Nevrorthidae. Slender bodies may have enabled the animal to move in crevices and in confined spaces in general. Also the lack of distinct segmentation in the trunk may be understood in this frame, as life in confined spaces seems also to lead to such reduced expression of segmentation (see discussion in Haug & Haug 2022). Based on these indications, we can speculate that larvae of *Ankyloleon* hunted for smaller prey items in crevice-rich confined spaces. Possible confined spaces may have been rocky grounds, but also wood. A lifestyle closely associated with wood would have been beneficial for a preservation in amber.

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Author contributions

Both authors conceived and designed the study, studied, photographed and described the material, composed the figures and wrote the paper.

Data availability statement

All data are available in this paper.

Conflict of interest disclosure

The authors declare that they have no conflict of interest.

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