

Article

The Diversity of Larvae with Multi-Toothed Stylets from About 100 Million Years Ago Illuminates the Early Diversification of Antlion-like Lacewings

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Abstract: Neuroptera, the group of lacewings, is well known to have been more diverse in the past, offering to study patterns of biodiversity loss over time. This loss of diversity has been quantitatively established by the morphological diversity of lacewing larvae. Here, we explore in more detail the diversity of lacewing larvae with tooth-bearing mouthparts. All these larvae are representatives of Myrmeleontiformia, the group of antlion-like lacewings. Today, larvae of several major ingroups bear teeth on their mouthparts: (1) owlions (formerly Ascalaphidae and Myrmeleontidae; taxonomic status is currently unclear); (2) Nymphidae; (3) Crocinae (mostly in younger larvae); and (4) Nemopterinae (only micro teeth). In addition, there are several now extinct larval types with teeth known from Cretaceous ambers (about 100 million years old). These larvae also possess several plesiomorphic characters, indicating that they were part of the early diversification of Myrmeleontiformia. We report numerous new specimens of these now extinct forms and provide a quantitative morphological comparison of head and mouthpart shapes, demonstrating that some of these Cretaceous larvae possessed morphologies not represented in the extant fauna. The resulting pattern is complex, indicating that at least some extinct morphologies have been later replaced by modern-day antlions due to convergent evolution.

Keywords: Myrmeleontiformia; Cretaceous; Kachin amber; Burmese amber; Myanmar



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1. Introduction

The loss of biodiversity, especially of Insecta, has been recognised not only among scientists but also in broader society [1–13]. But loss of biodiversity means more than just loss of species and biomass; it also means loss of ecosystem functions and services [14–16]. Naturally, most concern is put on the supposed important ingroups of Insecta, the big four [17], i.e., groups with more than 100,000 formally described species: Hymenoptera (e.g., wasps [18–20]), Coleoptera (beetles [21–23]), Lepidoptera (e.g., butterflies [24–26]), and Diptera (e.g., flies [27–29]). These four groups are all part of Holometabola. Holometabolans have been suggested to be so successful due to a differentiation of ecological functions between adults and larvae [30–33] (for challenges of the term larva, see [34]).

Yet, there are also less successful holometabolan lineages, one of them being Neuroptera, the group of lacewings, with only about 6000 formally described species in the modern-day fauna [35–42]. In contrast to the modern-day fauna, Neuroptera has been

assumed to have been more diverse in the past [36,43]. Despite this common assumption, demonstrating this loss quantitatively remained challenging [44] and could best be recognised by investigating the larval forms.

Lacewing larvae are characterised by prominent forward-projecting stylets formed by the upper jaw (mandible) and lower jaw (maxilla) [35,45–49]. These stylets are piercing-sucking mouthparts that are used to inject venom into their prey, then inject saliva, and finally suck out the dissolved tissues of the prey [50]. Studying losses of lacewing larval diversity over geological time spans is facilitated by a rich fossil record of these larvae in different types of ambers: Baltic amber [51–61], Dominican and Mexican amber [62–64], New Jersey amber [65], Myanmar amber [44,66–99], French amber [100], Spanish amber [101–103], Lebanese amber [104,105], and Chinese amber [106].

A major share of the diversity in Neuroptera is formed by the group of antlion-like lacewings, Myrmeleontiformia [41]. Traditionally, five major extant lineages (“families”) have been distinguished [36], yet newer analyses have either reduced that number to four [107] or increased it to nine [108–110], demonstrating again that ranked taxonomy cannot be used for reliable quantitative comparisons [44]. Unchallenged extant lineages include Psychopsidae (silky lacewings), Nymphidae (split-footed lacewings), and Nemopteridae (although its two major ingroups, Nemopterinae and Crocinae, are sometimes treated not as “subfamilies” but as “families”; e.g., [108]). The status of the two traditional groups Myrmeleontidae (antlions) and Ascalaphidae (owlflies) is currently unclear, as one of the two is likely an ingroup of the other [76,107,109,110], and different interpretations of the taxonomic schemes have been suggested. In some analyses [76], Ithonidae is also resolved inside Myrmeleontiformia.

In addition to the extant lineages, numerous fossils have been reported that are clearly representatives of Myrmeleontiformia but not of any of the extant lineages [41,111–113]. Larvae of such early lineages are known as well [75,76,80,85,95], although there has been no connection between adults and larvae of extinct lineages so far. Still, these fossil larvae inform us about the early diversification of the now successful lineage of Myrmeleontiformia.

We here report new larval specimens of these now extinct lineages of Myrmeleontiformia. We compare them to their modern-day counterparts in terms of their morphological diversity. With this type of analysis, we identify morphologies (and, coupled to that, ecological functions) that: (1) were only present in the past and are now extinct; (2) must have evolved only later, indicating younger diversification events; and (3) represent cases of convergent evolution in which morphologies that became extinct in one lineage evolved later in another lineage, leading to possible ecological substitutions.

2. Material and Methods

2.1. Material

In total, 54 amber pieces from Cretaceous Kachin amber, Myanmar, were directly studied; Kachin amber has been dated to the late Cretaceous [114–116]. The specimens came from three collections: 46 specimens from the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München (PED 0054, 0088, 0112, 0339, 0361, 0372, 0394, 0476, 0510, 0586, 0630, 0657, 0658, 0671, 0716, 0739, 0784, 0963, 1034, 1068, 1110, 1165, 1242, 1255, 1293, 1326, 1327, 1334, 1337, 1367, 1409, 1610, 1739, 1810, 1822, 1885, 1971, 2190, 2255, 2274, 2292, 2335, 2599, 2633, 2708, 2780); three specimens came from the collection of one of the authors (Weiterschan BuB 1, 9, 30); five specimens came from the collection of another one of the authors (Müller BUB 3067, 3371, 3381, 3392, 3998).

Specimens from the PED collection were legally purchased on the trading platform [ebay.com](https://www.ebay.com) from numerous traders (burmitefossil; burmite-miner; burmite-researcher; macrocretaceous). Recent issues have turned up concerning the study of Myanmar amber, the use of non-institutionalised collections, and parachute sciences [117]. We have considered these aspects in detail [118,119]; our strategy to deal with these issues for Kachin amber is intensifying collaboration with colleagues from Myanmar [91,120].

2.2. Imaging and Documentation

All specimens were photographed with a digital microscope VHX-6000, Keyence, Osaka, Japan with a built-in 20–2000× objective. The images were taken under cross-polarised illumination or low-angle ring light, as well as low-angle ring and coaxial light. All taken images were recorded in HDR-mode (high dynamic range). Black and white backgrounds were tested; images with the best contrast were used for further processing. Stacking (fusing of images with differing focus levels) and stitching (merging of adjacent image details) of images were performed by the built-in software of the Keyence VHX-6000. All post-processing of the images (optimisation of contrast, sharpness, saturation, and colour markings) was carried out with Adobe Photoshop CS2. Measurements were made in Adobe Acrobat Reader 11.0.10.

2.3. Shape Analysis

Different structures of the larvae were considered and analysed with the aid of an elliptic Fourier transformation. The data set was based on the directly studied specimens and larvae from the literature, partly assembled from earlier datasets [44,83,84,87–89], including all lacewing larvae that possess teeth. In total, 424 larvae were considered (for a specimen list, see table in Supplementary Materials), including:

- Few specimens of Nemopteridae (those with teeth; the presence of teeth often depends on the larval stage [121–132]);
- Numerous specimens of owallions (see discussion in [87] for this term) that were traditionally considered “Ascalaphidae” and “Myrmeleontidae” [133–163];
- Nymphidae [164–171];
- Fossils that are not part of modern ingroups of Myrmeleontiformia [75] (“stem group,” but see discussions in [172,173]).

Myrmeleontiformian larvae without teeth, i.e., larvae of Psychopsidae, most larvae of Nemopteridae, as well as *Ankyloleon*, were not considered to avoid an unnecessary polarisation of the dataset. Analysed structures included: (1) head + stylets (403 specimens); (2) stylets (424 specimens); and (3) head capsule (132 specimens). To quantitatively compare these outlines, we employed elliptic Fourier analysis (EFA) following earlier studies [44,81,99]. Hereby, the two-dimensional shield outline is decomposed into a mathematical object. This decomposition involved representing the outline as a harmonic sum of trigonometric functions, with the shape described by weighted harmonic coefficients [174,175]. We aligned, centred, and scaled the harmonic coefficients and then used a principal component analysis (PCA) to extract the dimensions of the largest variation [175–177].

The outline analysis was conducted with the R-statistics environment (ver. 4.1.0 [178]) along with the package Momocs (ver. 1.3.2 [175]) for the head capsule and mandibles and with the SHAPE software package (© National Agricultural Research Organization of Japan [179], cf. [176]) for the stylets. To determine the optimal number of harmonics, we employed calibration functions from the Momocs package, which resulted in using 11 harmonics for the head capsule and 15 harmonics for the mandibles. The SHAPE software package does not provide calibration functions; here, we defaulted to 12 harmonics for the stylets.

We quantified the morphospace again in the R-statistics environment, using the package dispRity (ver. 1.6.0 [180]). First, we grouped the specimens by their geological age, discarding Eocene and Miocene specimens due to their small sample sizes. We then used the sum of variance across all dimensions of the morphospace as a measure of morphological diversity for each group (also called “disparity” [181]). We also measured position within the morphospace to test for differences in the general morphology of the time slices. To quantify position, we measured the ratio of distance from point to group centroid and distance from group centroid to morphospace centroid. For both metrics, we bootstrapped results, corrected for sample size, and then used Welch’s two-sample *t*-test with Bonferroni correction for multiple testing to check for significant differences between groups.

3. Results

3.1. Short Descriptions of New Specimens of *Macleodiella*

- (1) Specimen 0812 (PED 1068) is poorly visible due to dirt in the amber. Visible in dorsal view (Figure 1I). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae (Figure 1J) Each stylet has three larger teeth, and two smaller teeth between the proximal tooth and the middle tooth are recognizable. Antennae are incompletely preserved. Only the head and anterior parts of the trunk (parts of the thorax) are preserved; the further posterior part is outside of the amber piece.

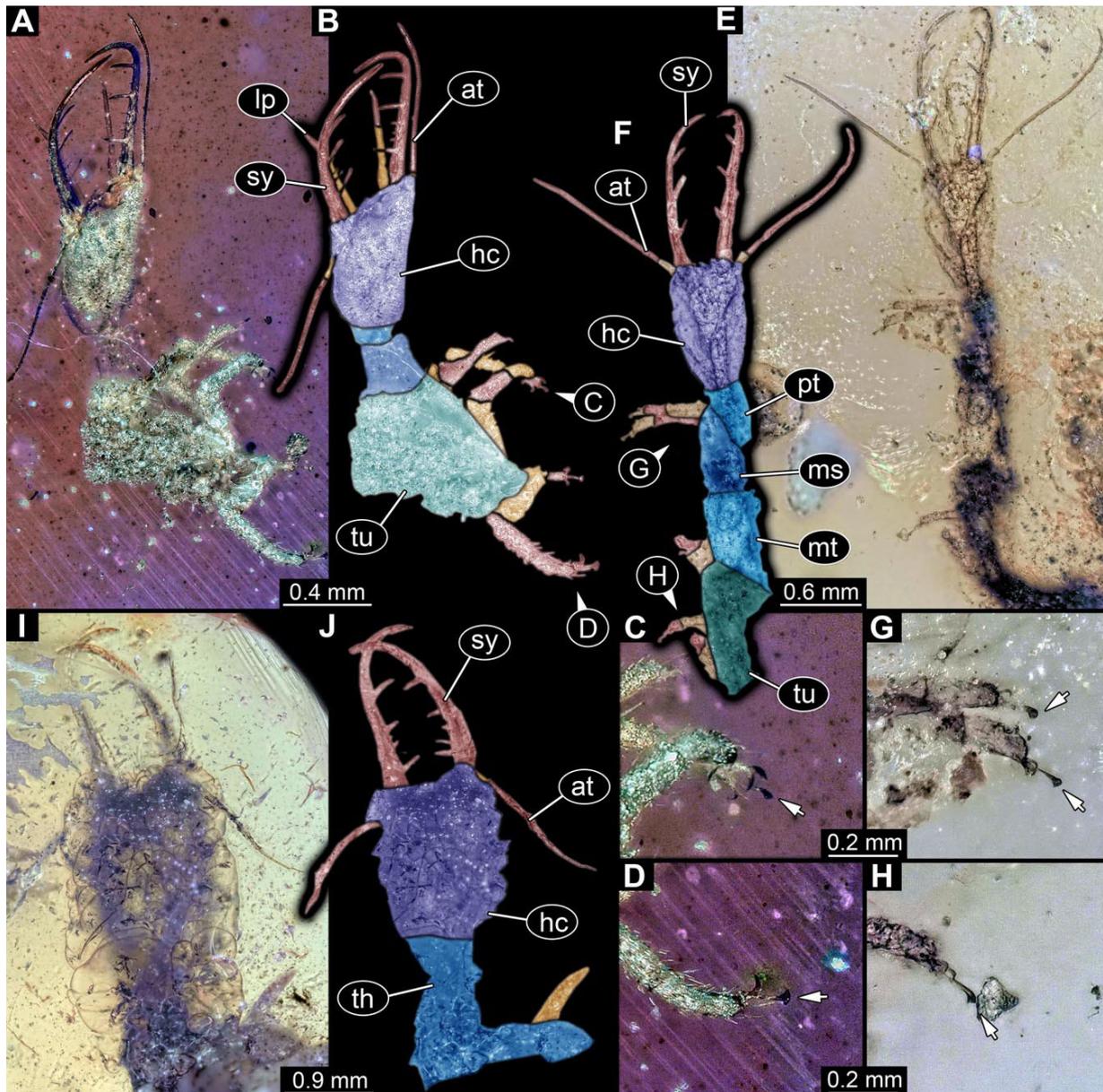


Figure 1. Larvae of the *Macleodiella* type. (A–D) PED 2292 (specimen 0815). (A) Overview. (B) Colour-marked version of (A). (C,D) Details of legs; arrows mark empodia. (E–H) PED 1334 (specimen 0813). (E) Overview. (F) Colour-marked version of (E). (G,H) Details of legs; arrows mark empodia. (I,J) PED 1068 (specimen 0812). (I) Overview. (J) Colour-marked version of (I). Abbreviations: at = antenna; hc = head capsule; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; th = thorax; tu = trunk.

- (2) Specimen 0813 (PED 1334) is visible in dorsal view (Figure 1E). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae (Figure 1F). In each stylet, three larger teeth are recognizable. Antennae elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 1G,H). The posterior part of the trunk (abdomen) is missing.
- (3) Specimen 0814 (PED 2274) is well preserved and accessible from both sides, dorsal (Figure 2B,C) and ventral (Figure 2A). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets, and labial palps, and antero-laterally projecting antennae. In each stylet three larger teeth are recognizable. Labial palps are elongate and shorter than stylets, with at least two elements each; the distal element is slightly leaf-shaped. Antennae elongate and longer than stylets. The first trunk segment (prothorax) is elongate. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 2D). The posterior part of the trunk (abdomen) has at least eight units: seven segments and a trunk end (most likely several conjoined segments). The abdomen is slender and elongate, roughly cone-shaped.

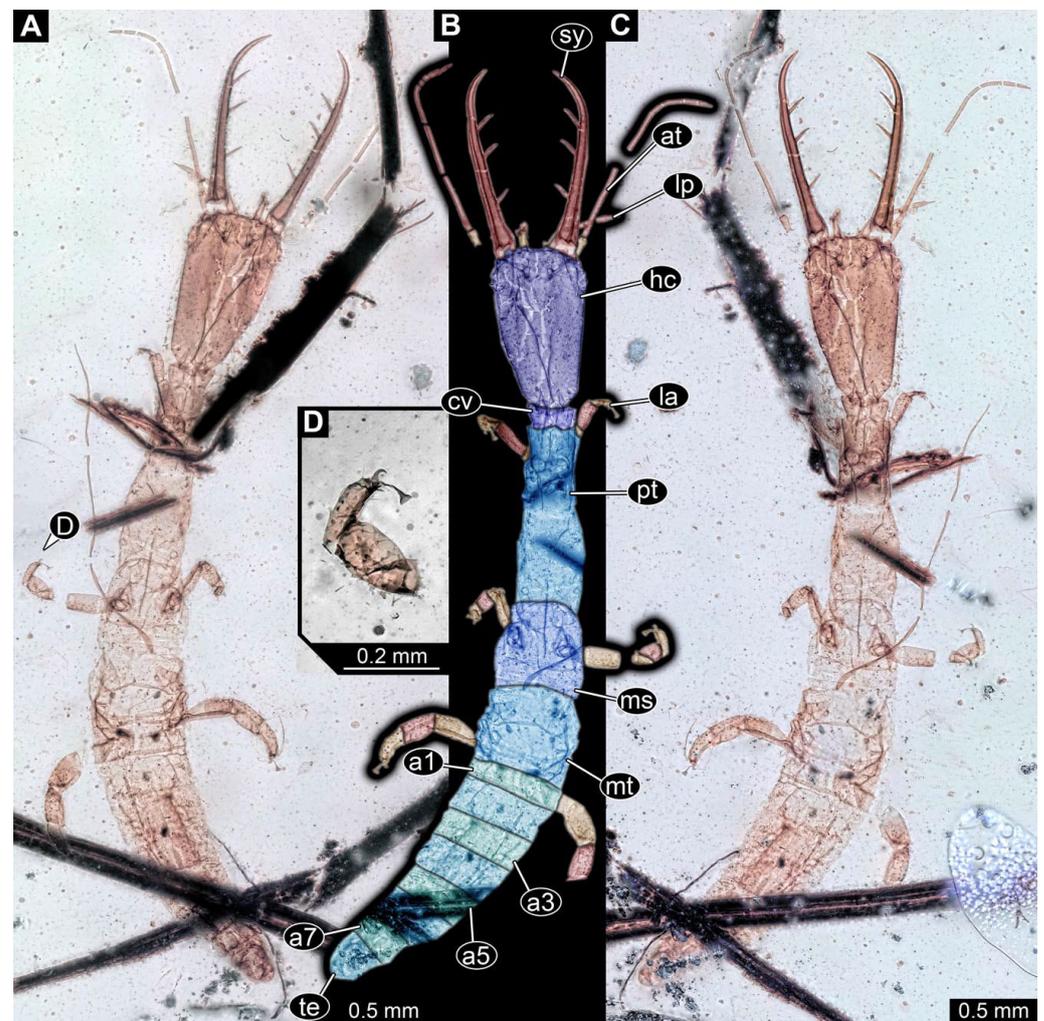


Figure 2. Larva of the *Macleodiella* type, PED 2274 (specimen 0814). (A) Ventral view. (B) Colour-marked version of the dorsal view. (C) Dorsal view. (D) Close-up of leg with empodium. Abbreviations: a1–7 = abdomen segments 1–7; at = antenna; cv = cervix; hc = head capsule; la = locomotory appendage (leg); lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; te = trunk end.

- (4) Specimen 0815 (PED 2292) is incompletely preserved. Visible in dorsal view (Figure 1A,B). Body with a distinct head and trunk. Head with forward projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae (Figure 1A,B). Each stylet has three larger teeth, and three smaller teeth between the proximal tooth and the middle tooth are recognisable. Labial palps are elongate and shorter than stylets, with at least two elements each. Antennae are elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 1C,D). The posterior part of the trunk (abdomen) is missing.
- (5) The amber piece PED 1885 includes the remains of several specimens (Figure 3). Specimen 0816 (Figure 3A) is more completely preserved, allowing us to recognise the subdivision into head, anterior trunk (thorax), and posterior trunk (abdomen). Head with stylets and antennae. Specimen 0817 (Figure 3F) is also more complete, allowing us to recognise the head (with stylets and labial palp) and trunk. Other remains are collectively addressed (“specimen 0818”); remains include four mandibles (Figure 3B–E), meaning that these are at least the remains of two specimens but could also be the remains of up to four specimens. The piece therefore includes the remains of four to six specimens.

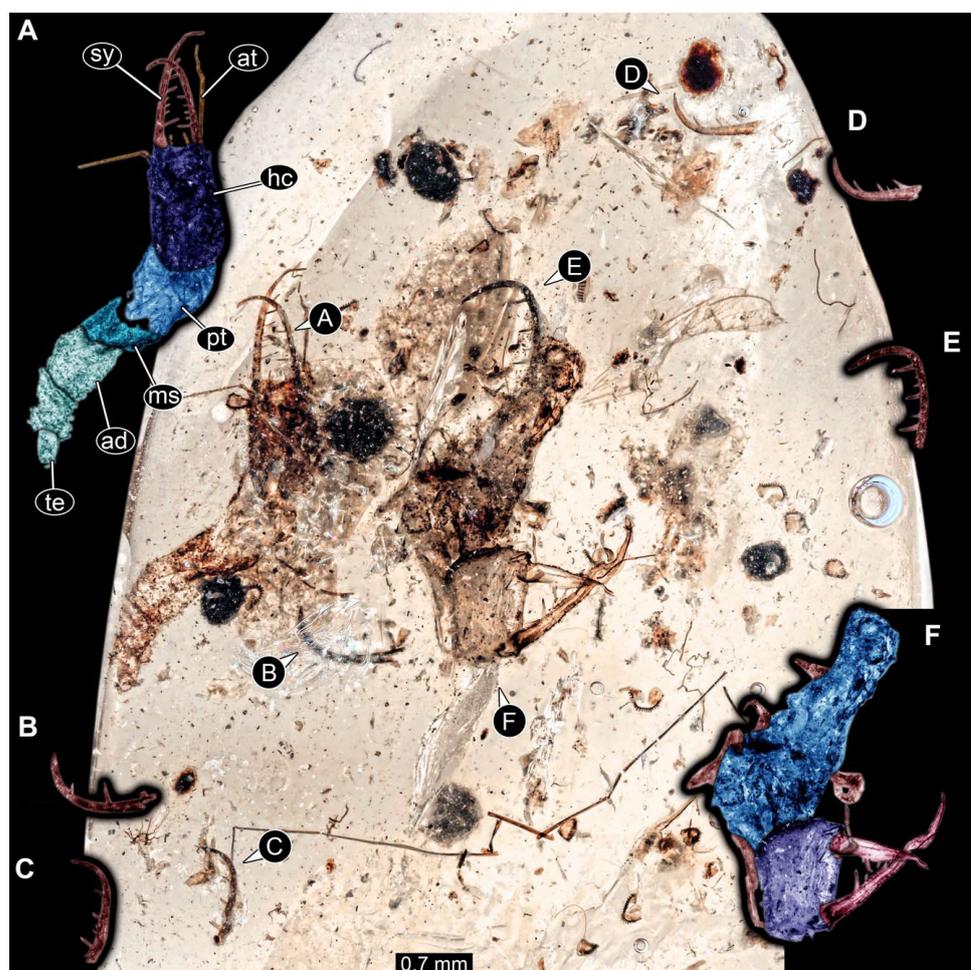


Figure 3. Amber piece (PED 1885) with numerous remains of larvae of the *Macleodiella* type. Central image: overview with positions of specimens in the amber marked. (A) Specimen 0816, colour-marked. (B–E) Isolated mandibles, colour-marked. (F) Specimen 0817, colour-marked. Abbreviations: ad = abdomen; at = antenna; hc = head capsule; ms = mesothorax (and metathorax?); pt = prothorax; sy = stylet; te = trunk end.

3.2. Short Descriptions of Specimens of Superfang Type 1

- (6) Specimen 0842 (BUB 3067) is poorly preserved (Figure 4A,B). Only the distal parts of the mandibles are preserved. Bearing at least seven teeth (Figure 4C). Other parts are unknown.

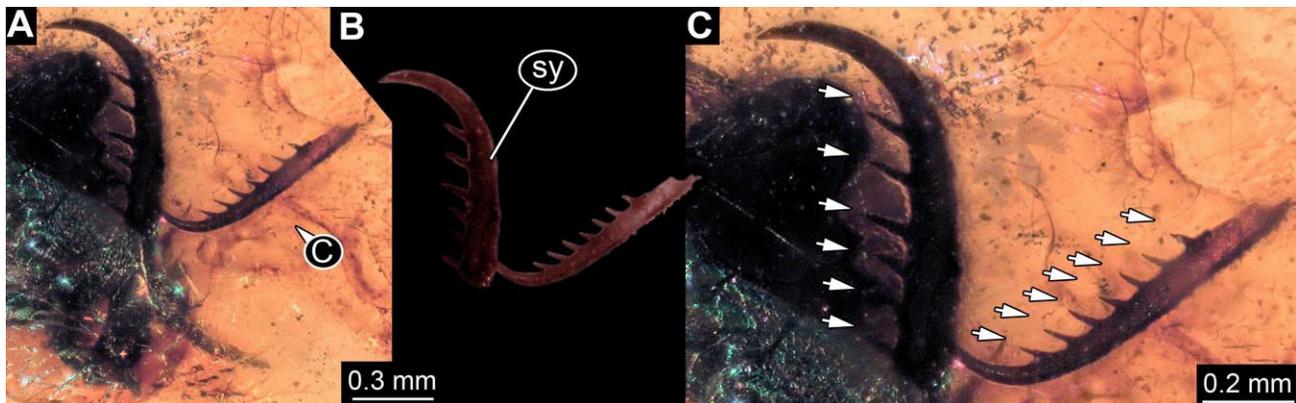


Figure 4. Remains of larvae of the superfang type 1, BUB 3067 (specimen 0842). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on stylets; arrows mark teeth. Abbreviation: sy = stilet.

- (7) Specimen 0843 (BUB 3392) is relatively well preserved in dorsal view (Figure 5A,B). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets are partly damaged and incomplete, each with eight teeth preserved (Figure 5D); laterally, they bear short setae. The second distal tooth is the longest. Labial palps are elongate and shorter than stylets, with at least two elements each. Antennae elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 5C). The posterior part of the trunk (abdomen) is slender and elongate, roughly cone-shaped. Head, trunk, and legs bear numerous shorter setae; abdomen has especially long setae (Figure 5E).
- (8) Specimen 0844 (BUB 3398) is relatively well preserved in dorsal (Figure 6A,B) and ventral views (Figure 6D). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets are partly damaged, with eight teeth; proximo-medially with some setae; laterally bearing short setae. The second distal tooth is the longest (Figure 6C). Labial palps are elongate, shorter than stylets, with at least two elements each (Figure 6F). Antennae elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 6E). The posterior part of the trunk (abdomen) is slender, elongate, and roughly cone-shaped; the posterior end seems to be turned downward. The head, trunk, and legs bear numerous shorter setae; the abdomen has especially long setae.
- (9) Specimen 0845 (PED 0372) is relatively well preserved in dorsal (Figure 7A) and ventral views (Figure 7B,C). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets are partly damaged, with eight teeth; proximo-medially with some setae; laterally bearing short setae. The second distal tooth is the longest (Figure 7E). Labial palps are elongate and shorter than stylets, with at least two elements each. Antennae elongate longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 7D). The posterior part of the trunk (abdomen) is not

preserved. The head, trunk, and legs bear numerous shorter setae; the abdomen has especially long setae.

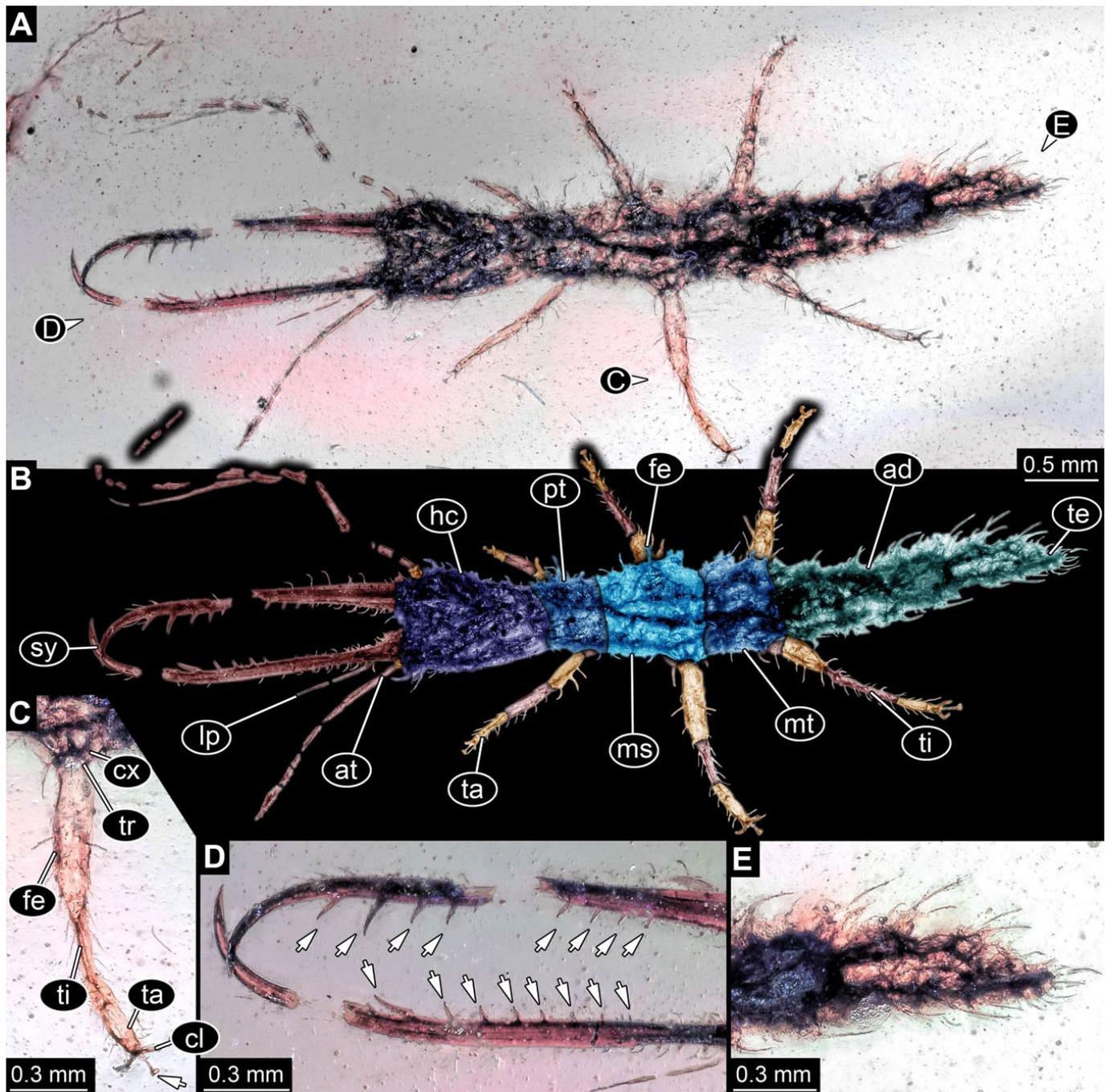


Figure 5. Larva of the superfang type 1, BUB 3392 (specimen 0843). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on locomotory appendage (leg); arrow marks empodium. (D) Close-up on stylet; arrows mark teeth. (E) Close-up on trunk end. Abbreviations: ad = abdomen; at = antenna; cl = claw; cx = coxa; fe = femur; hc = head capsule; la = locomotory appendage (leg); lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

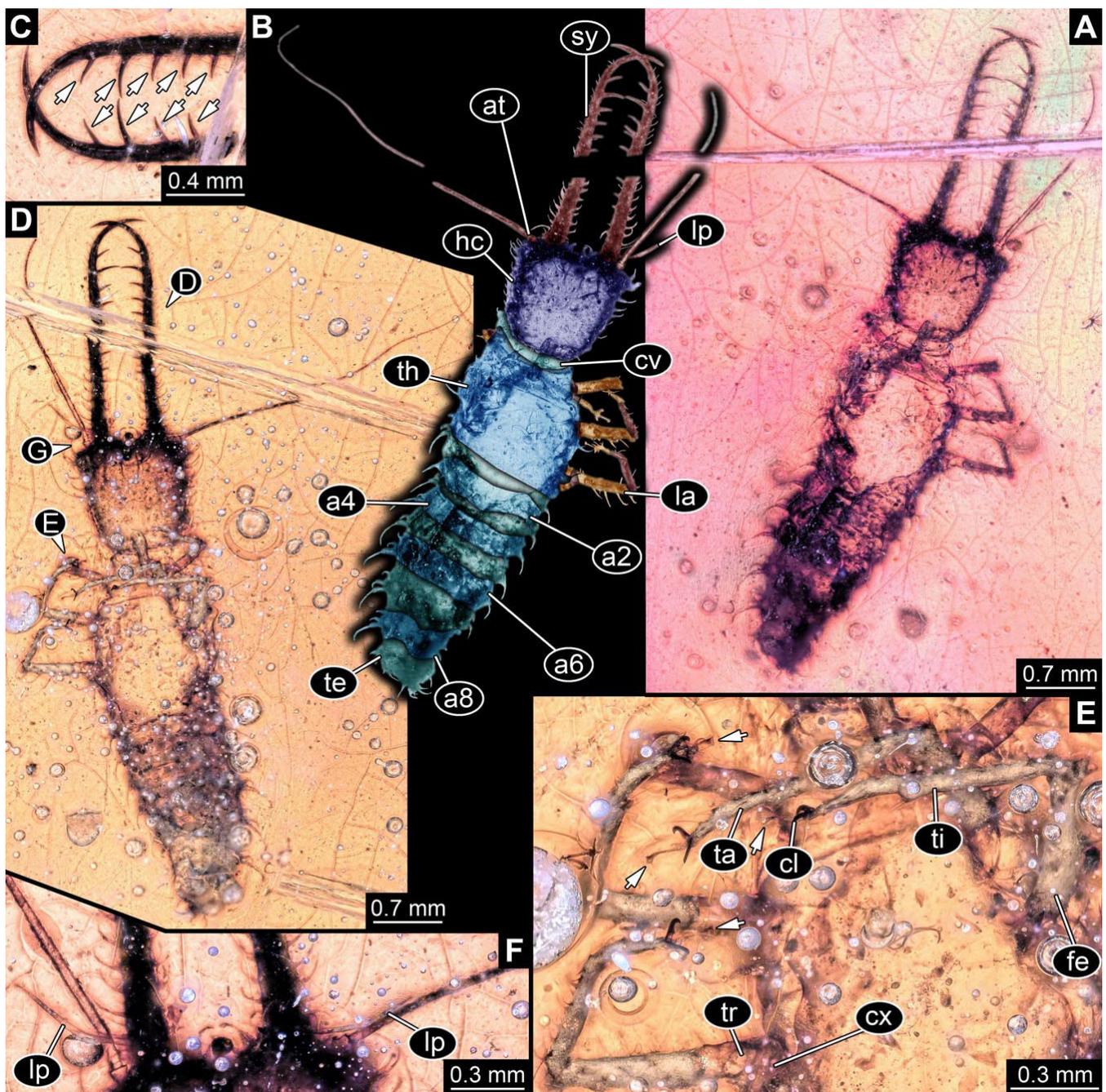


Figure 6. Larva of the superfang type 1, BUB 3398 (specimen 0844). (A) Dorsal view. (B) Colour-marked version of A. (C) Close-up on the tips of stylets; arrows mark teeth. (D) Ventral view. (E) Close-up on locomotory appendages; arrows mark empodia. (F) Close-up on the anterior region of the head. Abbreviations: a2–8 = abdomen segments 2–8; at = antenna; cl = claw; cx = coxa; fe = femur; hc = head capsule; la = locomotory appendage (leg); lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

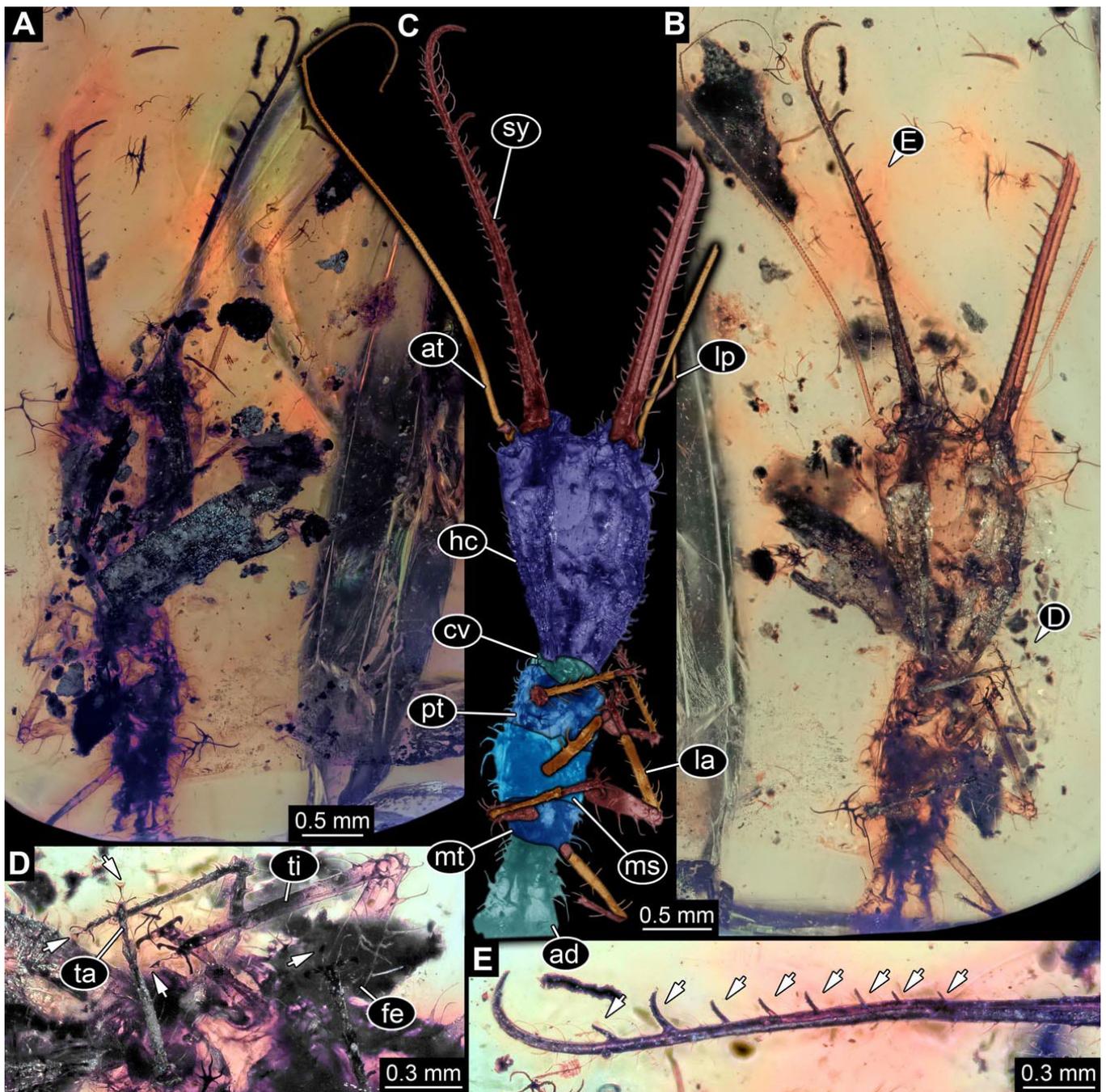


Figure 7. Larva of the superfang type 1, PED 0372 (specimen 0845). (A) Dorsal view. (B) Ventral view. (C) Colour-marked version of B. (D) Close-up on locomotory appendages; arrows mark empodia. (E) Close-up on stylet; arrows mark teeth. Abbreviations: ad = abdomen; at = antenna; cv = cervix; fe = femur; hc = head capsule; la = locomotory appendage (leg); lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; ti = tibia.

- (10) Specimen 0846 (PED 0658) is relatively well preserved in dorsal view (Figure 8A,B). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets largely outside the amber. Labial palps are elongate and shorter than stylets, with at least two elements each (Figure 8D). Antennae elongate longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 8C). Posterior part of trunk

(abdomen) stouter, roughly cone-shaped. The head, trunk, and legs bear numerous shorter setae; the abdomen has especially long setae.

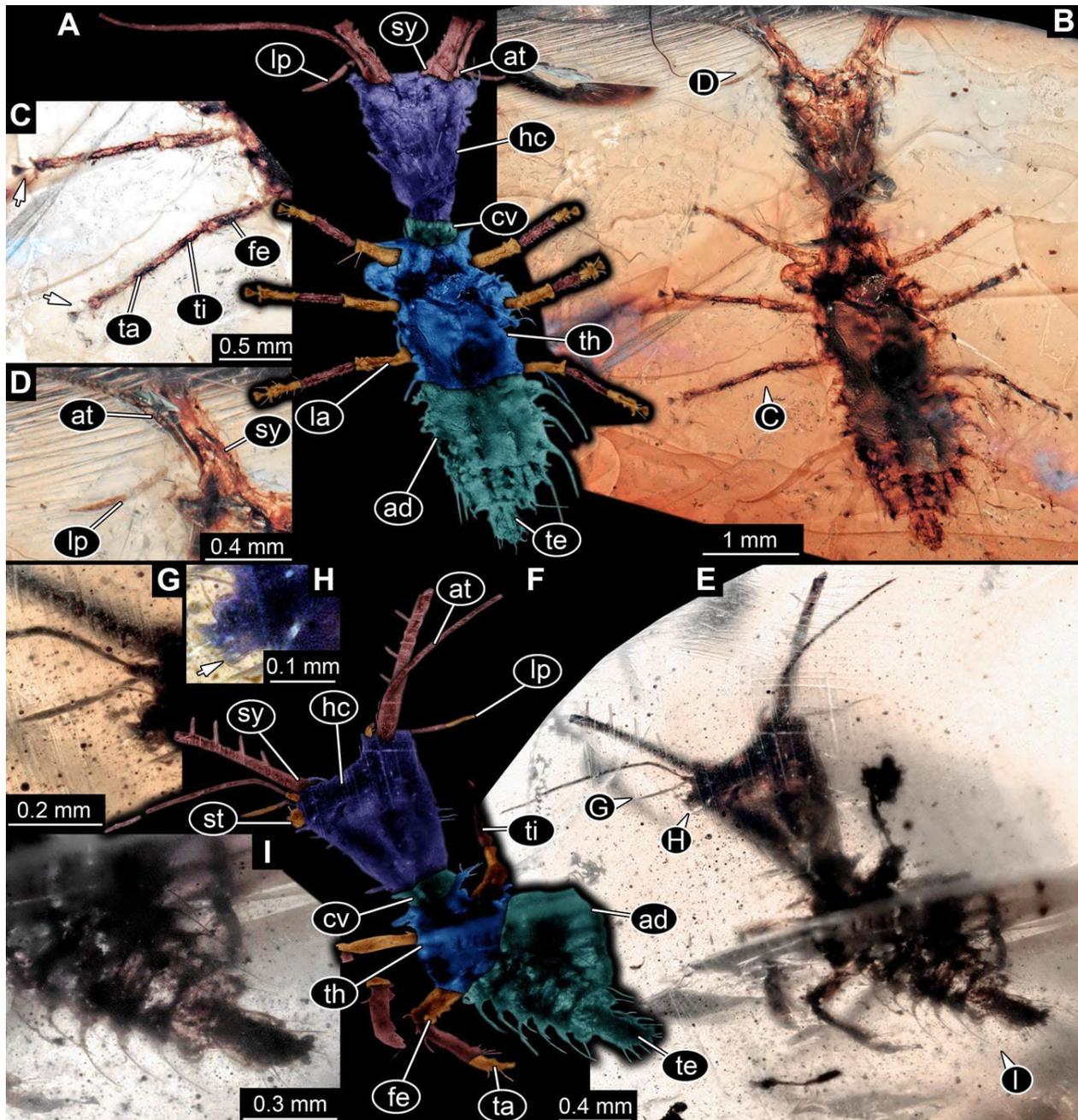


Figure 8. Larvae of the superfang type 1. (A–D) PED 0658 (specimen 0846). (A) Overview, colour-marked. (B) Overview. (C) Close-up on locomotory appendages; arrows mark empodia. (D) Close-up on the anterior region of the head. (E–H) PED 1185 (specimen 0848). (E) Overview. (F) Colour-marked version of (E). (G) Close-up on the anterior region of the head. (H) Close-up on the eye region. (I) Close-up on trunk end. Abbreviations: ad = abdomen; at = antenna; cv = cervix; fe = femur; hc = head capsule; la = locomotory appendage (leg); lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; st = stemmata; sy = stylet; ta = tarsus; te = trunk end; th = thorax; ti = tibia.

- (11) Specimen 0848 (PED 1165) is relatively well preserved in dorsal view (Figure 8E,F). Body with a distinct head and trunk. Head with lateral projections with eyes (Figure 8H); head also with forward projecting mouthparts, the stylets and labial

- palps, and antero-laterally projecting antennae. Stylets distally outside the amber, proximally with at least four shorter teeth. Labial palps elongate shorter than stylets, with at least two elements each (Figure 8G). Antennae elongate longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Posterior part of trunk (abdomen) stouter, roughly cone-shaped (Figure 8I). The head, trunk, and legs bear numerous shorter setae; the abdomen has especially long setae.
- (12) Specimen 0849 (PED 2255) is relatively well preserved in latero-dorsal (Figure 9C) and latero-ventral views (Figure 9A,B). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets with eight teeth; proximo-medially with some setae. Two distal teeth are the longest. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs). Legs have trumpet-shaped attachment structures distally (empodia; Figure 9D). The posterior part of the trunk (abdomen) is damaged.

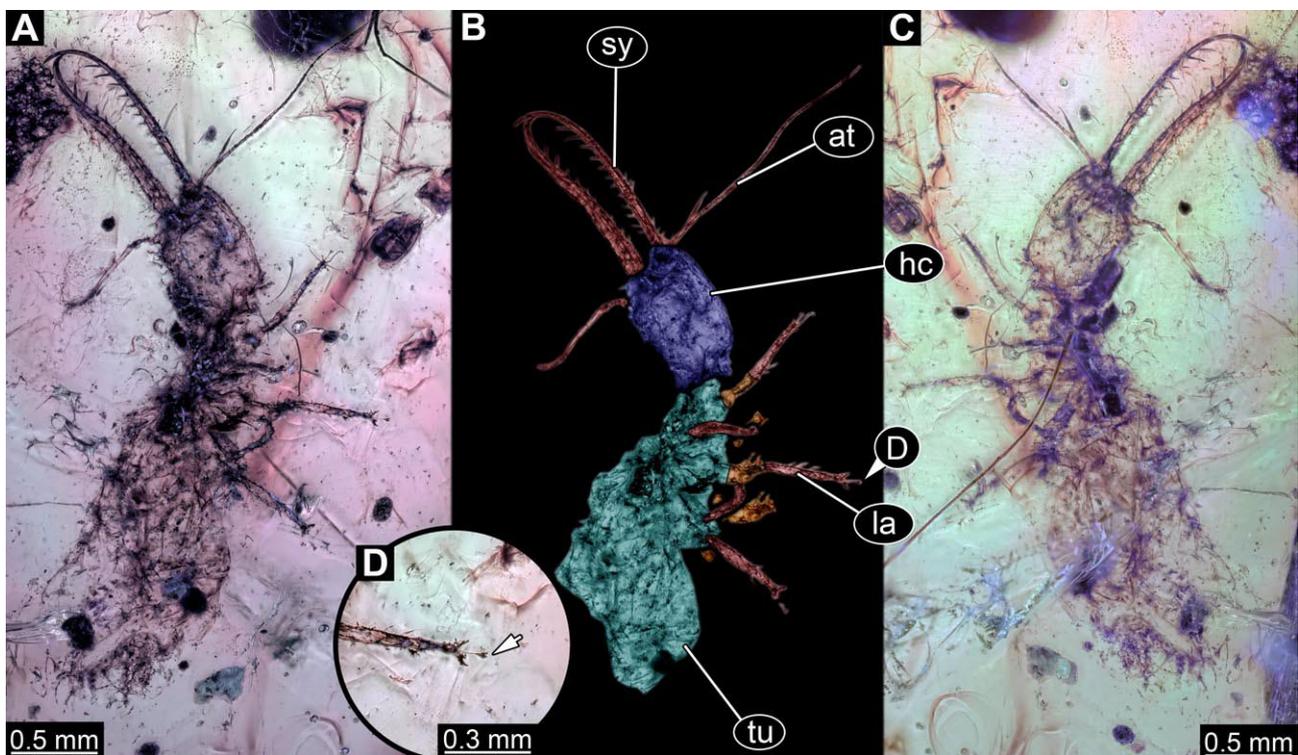


Figure 9. Larva of the superfang type 1, PED 2255 (specimen 0849). (A) Latero-ventral view. (B) Colour-marked version of (A). (C) Latero-dorsal view. (D) Close-up on the distal part of the locomotory appendages; the arrow marks the empodium. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; sy = stylet; tu = trunk.

- (13) Specimen 0850 (PED 2708) is relatively well preserved in ventral view (Figure 10A,B). Body with a distinct head and trunk. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Stylets with eight teeth. The second distal tooth is the longest (Figure 10C). Labial palps are not well preserved. Antennae elongate and longer than stylets. Anterior trunk segments (thorax) with pairs of locomotory appendages (legs) and distal parts outside the amber (Figure 10D). The posterior part of the trunk (abdomen) is outside the amber.

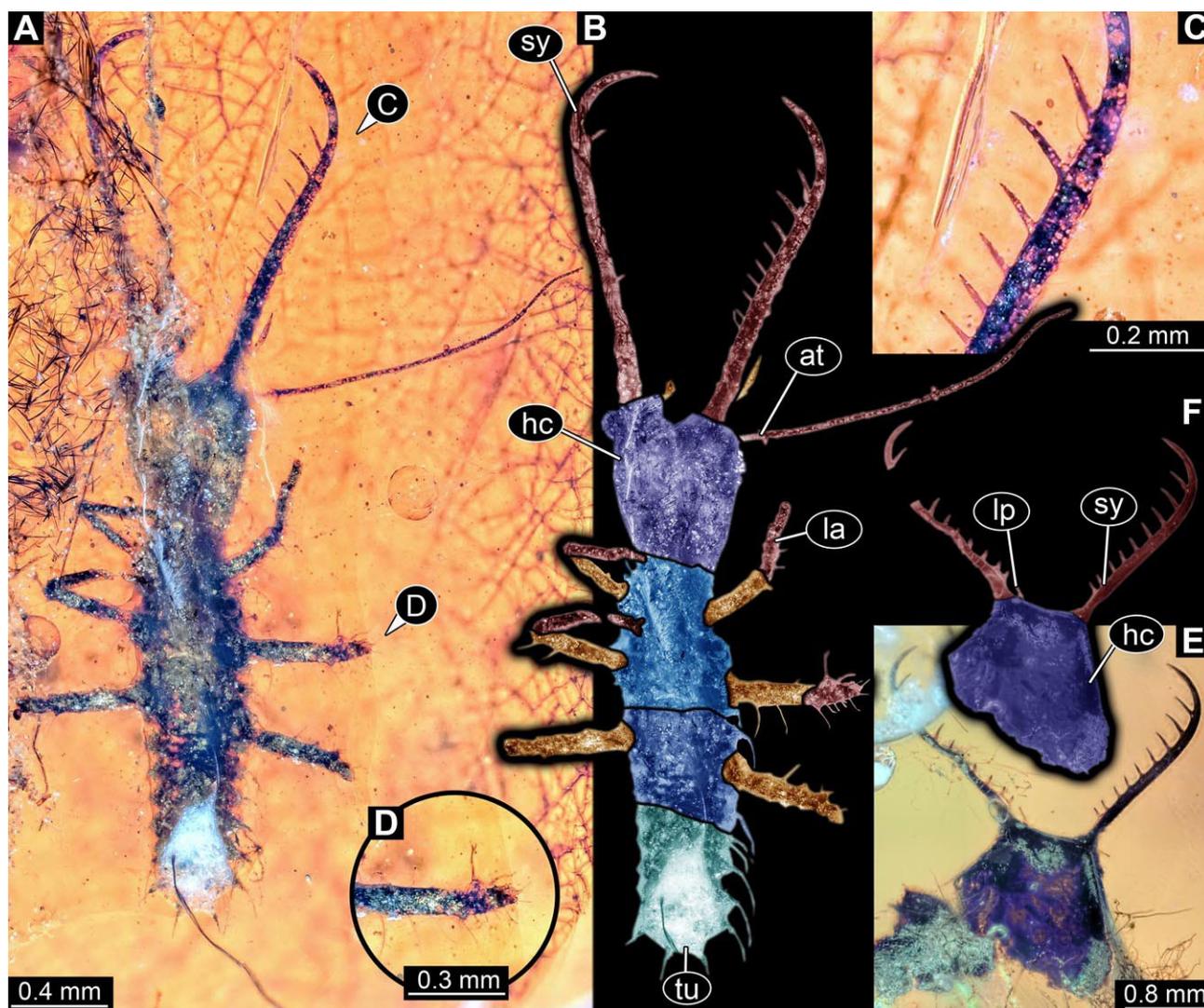


Figure 10. Larvae of the superfang type 1. (A–D) PED 2708 (specimen 0850). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the distal part of the stylet. (D) Close-up on the distal part of locomotory appendages. (E,F) PED 2780 (specimen 0851). (E) Overview. (F) Colour-marked version of (E). Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

(14) Specimen 0851 (PED 2780) is incompletely preserved (Figure 10E). Only the head with forward-projecting mouthparts, the stylets, is present. Stylets with nine teeth. Distal teeth are longer than proximal ones (Figure 10F).

3.3. Short Descriptions of Specimens of Superfang Type 2

(15) Specimen 0861 (PED 0361) is incompletely preserved (Figure 11A,B). Mostly head with forward-projecting mouthparts and stylets. Stylets with six teeth. Distal teeth are significantly longer than proximal ones. In addition, distal parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 11C).

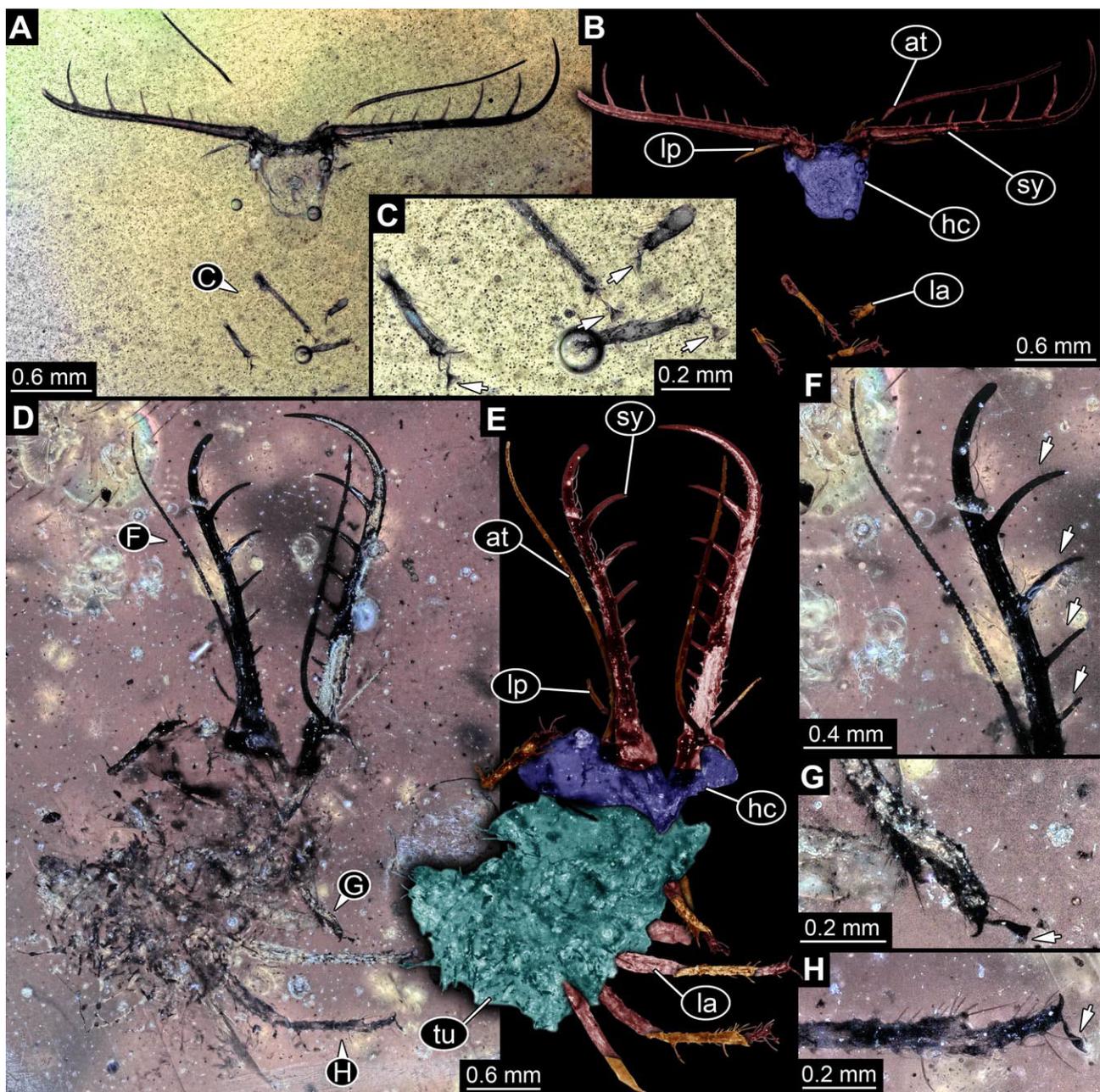


Figure 11. Larvae of the superfang type 2. (A–C) PED 0361 (specimen 0861) (A) Overview. (B) Colour-marked version of (A). (C) Close-up on distal parts of locomotory appendages; arrows mark empodia. D–H. PED 0112 (specimen 0863). (D) Overview. (E) Colour-marked version of D. (F) Close-up on the distal part of the stylet; arrows mark teeth. (G,H) Close-up on the distal part of locomotory appendages; arrow marks the empodia. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (16) Specimen 0862 (PED 0088) is incompletely preserved (Figure 12A–C). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth (Figure 12E). Distal teeth are significantly longer than proximal ones, with a few setae medio-proximally and numerous laterally (Figure 12E). Labial palps are elongate and shorter than stylets. Antennae are elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are

better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 12D).

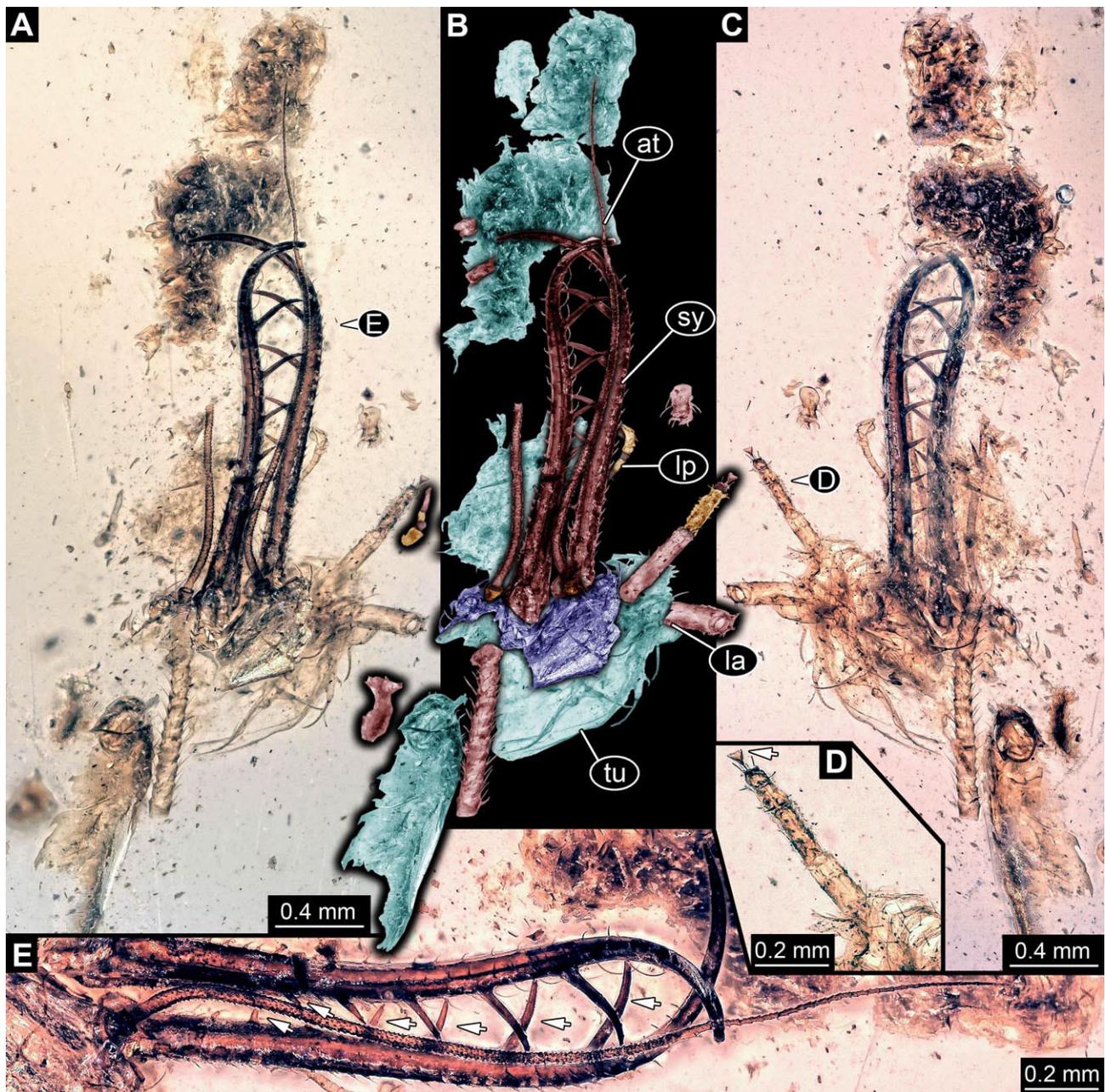


Figure 12. Larva of the superfang type 2, PED 0088 (specimen 0862). (A) Overview, one side. (B) Colour-marked version of (A). (C) Overview, other side. (D) Close-up on the distal part of the locomotory appendage; the arrow marks the empodium. (E) Close-up on stylets; the arrows mark the teeth. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

(17) Specimen 0863 (PED 0112) is incompletely preserved (Figure 11D,E). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones (Figure 11F), with a few setae medio-proximally and latero-proximally. Labial palps are elongate and shorter than stylets. Antennae are elongate and longer

- than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 11G,H).
- (18) Specimen 0864 (PED 0054) is incompletely preserved (Figure 13A,B). Originally more complete, but damaged during transport (Figure 13C). Most likely representing exuvia; the main body is strongly crumpled. Head with antero-lateral eyes (Figure 13F) and forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae is better preserved. Stylets with few teeth. Distal teeth are significantly longer than proximal ones, with a few setae medio-proximally and latero-proximally. Labial palps are elongate and shorter than stylets (Figure 13E). Antennae are elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 13D). Trunk ends are slender with prominent setae (Figure 13G).

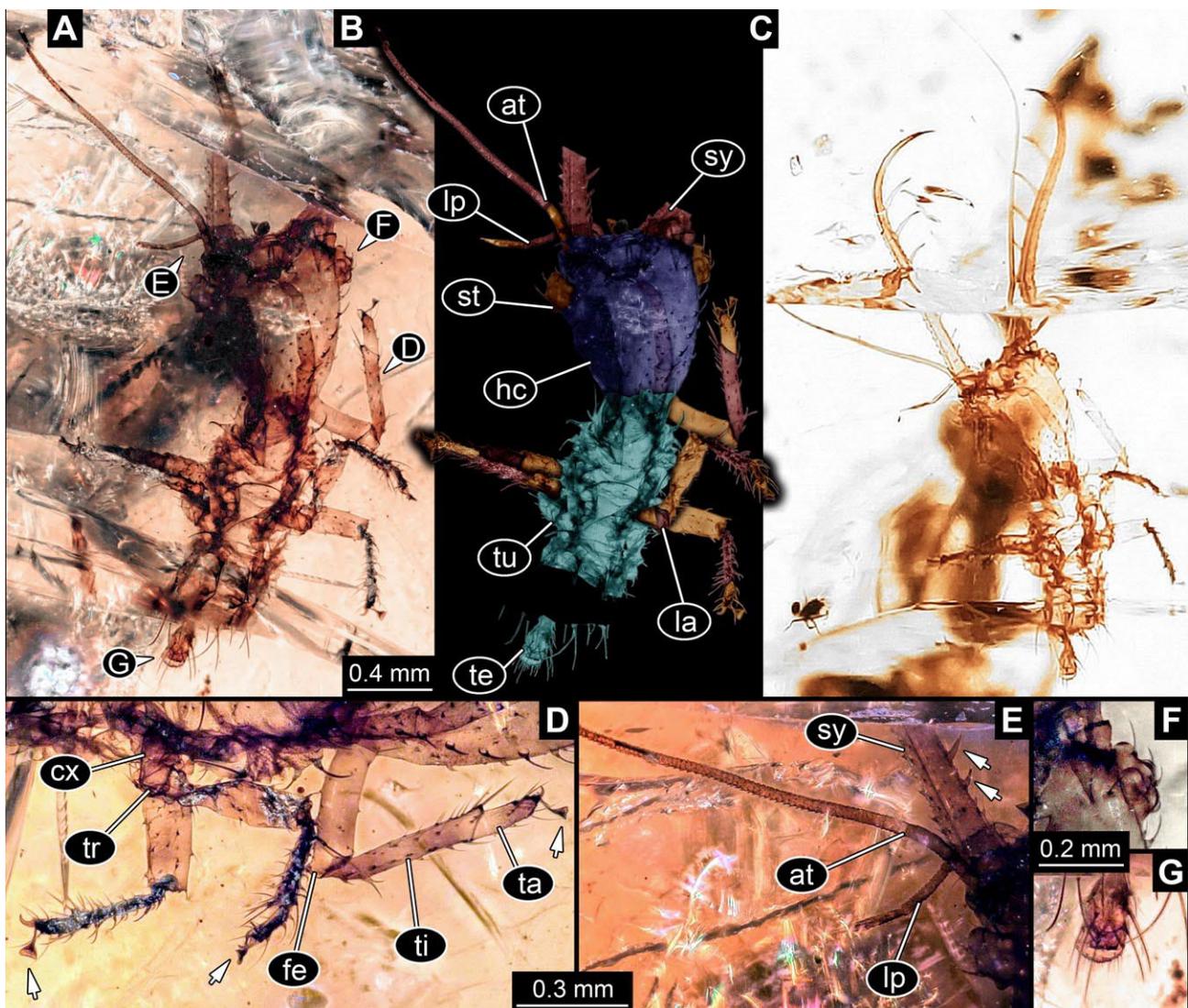


Figure 13. Larva of the superfang type 2, PED 0054 (specimen 0864). (A) Overview. (B) Colour-marked version of (A). (C) Overview before transport damage (image kindly provided by the trader). (D) Close-up on distal parts of locomotory appendages; arrows mark empodia. (E) Close-up on the anterior region of the head. (F) Close-up on the eye region. (G) Close-up on the trunk end. Abbreviations: at = antenna; cx = coxa; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; st = stemmata; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter; tu = trunk.

- (19) Specimen 0865 (PED 0339) is incompletely preserved (Figure 14A,B). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth (Figure 14D). Distal teeth are significantly longer than proximal ones (Figure 14D), with few setae medio-proximally. Labial palps are elongate and shorter than stylets. Antennae are elongate, longer than stylets, with at least three distinct elements (Figure 14D). In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 14C).

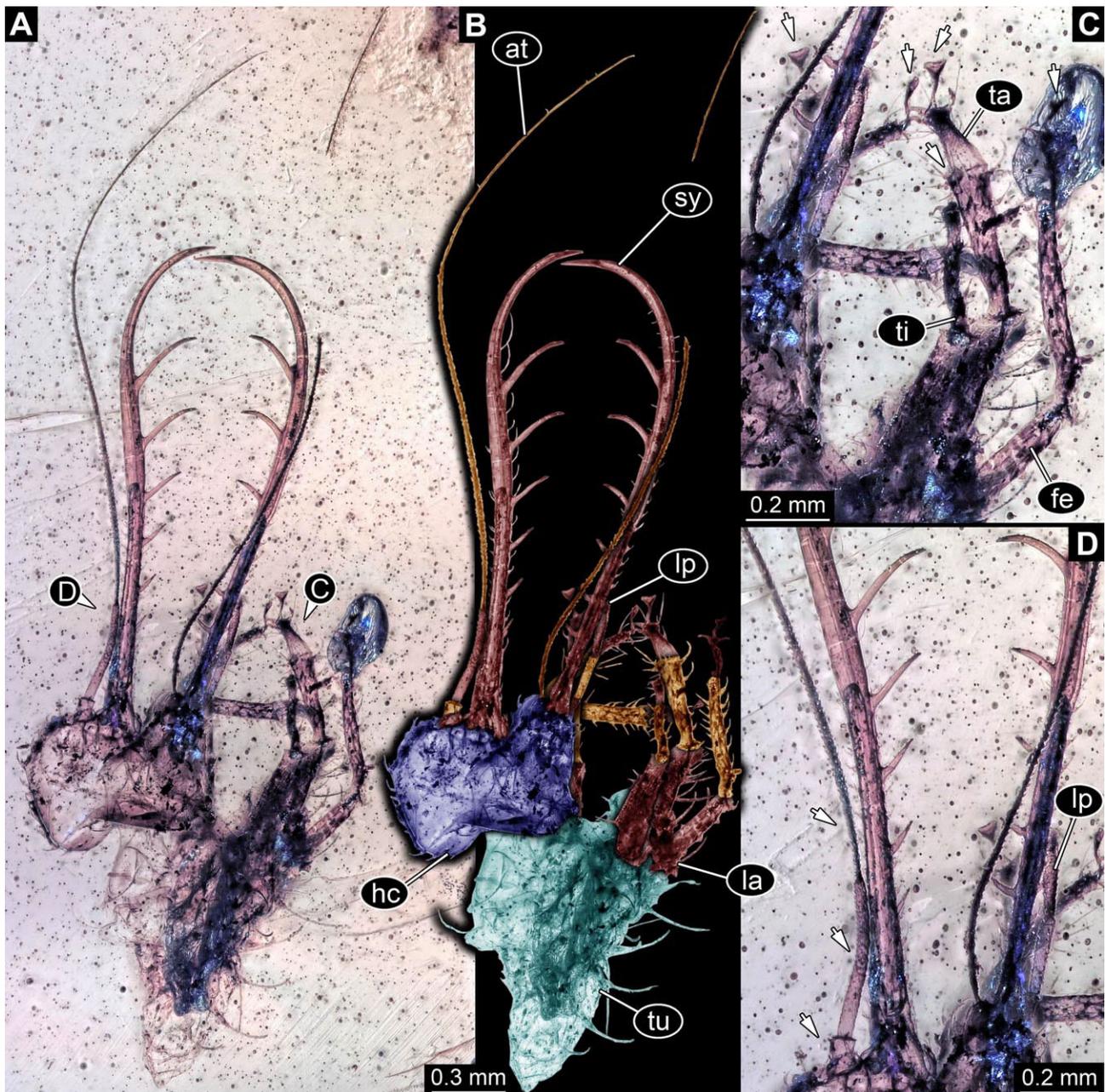


Figure 14. Larva of the superfang type 2, PED 0339 (specimen 0865). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the distal part of locomotory appendages; arrows mark empodia. (D) Close-up on the anterior region of the head; arrows indicate the three elements of the antenna. Abbreviations: at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; ta = tarsus; ti = tibia; tu = trunk.

- (20) Specimen 0866 (PED 0394) is incompletely preserved (Figure 15A,B,D). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with a few setae medio-proximally and more laterally. Labial palps are elongate and shorter than stylets. Antennae are elongate and longer than stylets, with at least three distinct elements (Figure 15B). In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 15C,E,F).

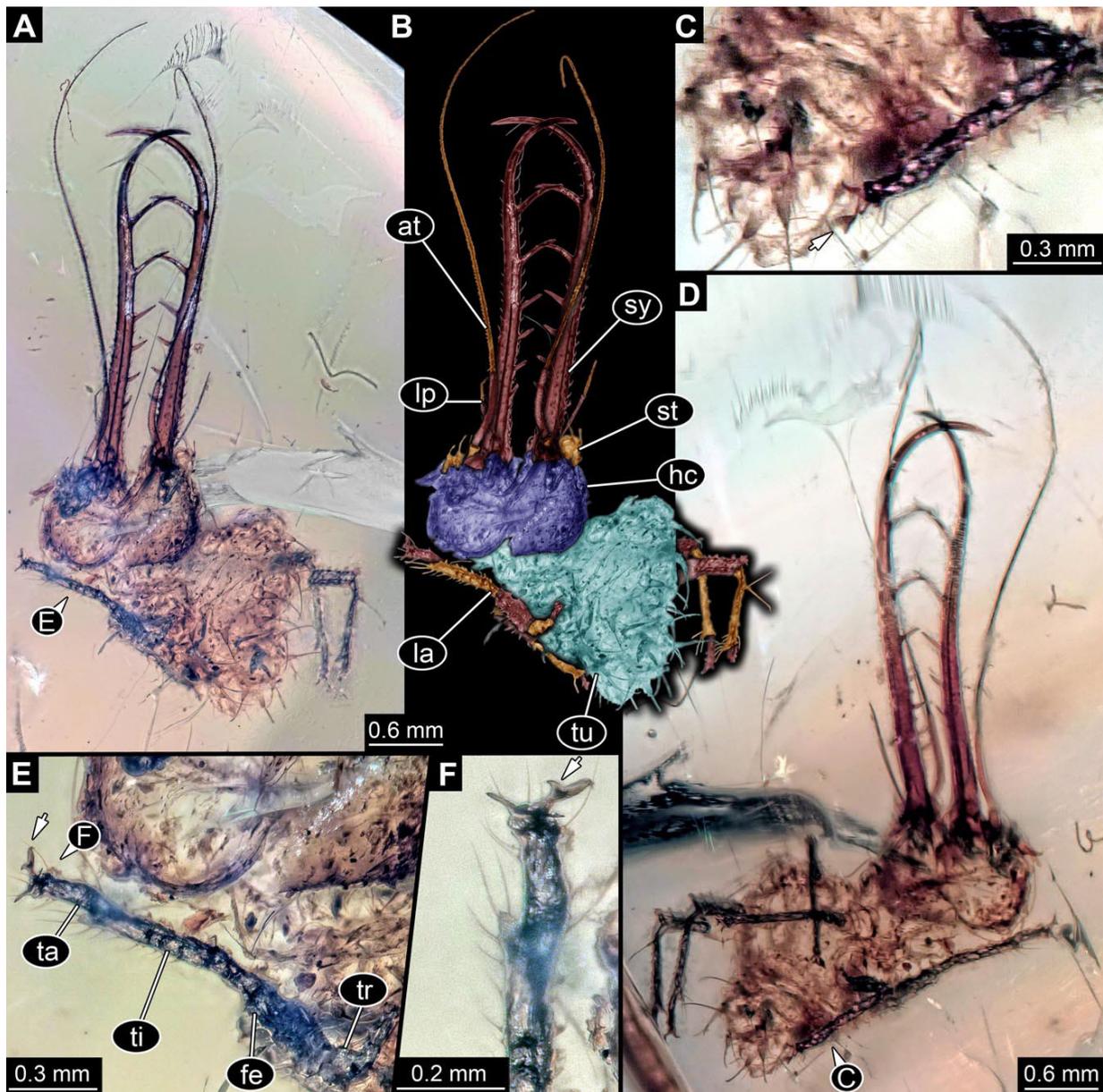


Figure 15. Larva of the superfang type 2, PED 0394 (specimen 0866). (A) Overview, one side. (B) Colour-marked version of (A). (C) Close-up on the distal part of the locomotory appendage; the arrow marks the empodium. (D) Overview, other side. (E,F) Close-up on distal part of locomotory appendage; arrow marks empodium. Abbreviations: at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; st = stemmata; sy = stylet; ta = tarsus; ti = tibia; tr = trochanter; tu = trunk.

- (21) Specimen 0867 (PED 0510) is incompletely preserved (Figure 16A,B). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with a few setae medio-proximally and more laterally. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 16C).

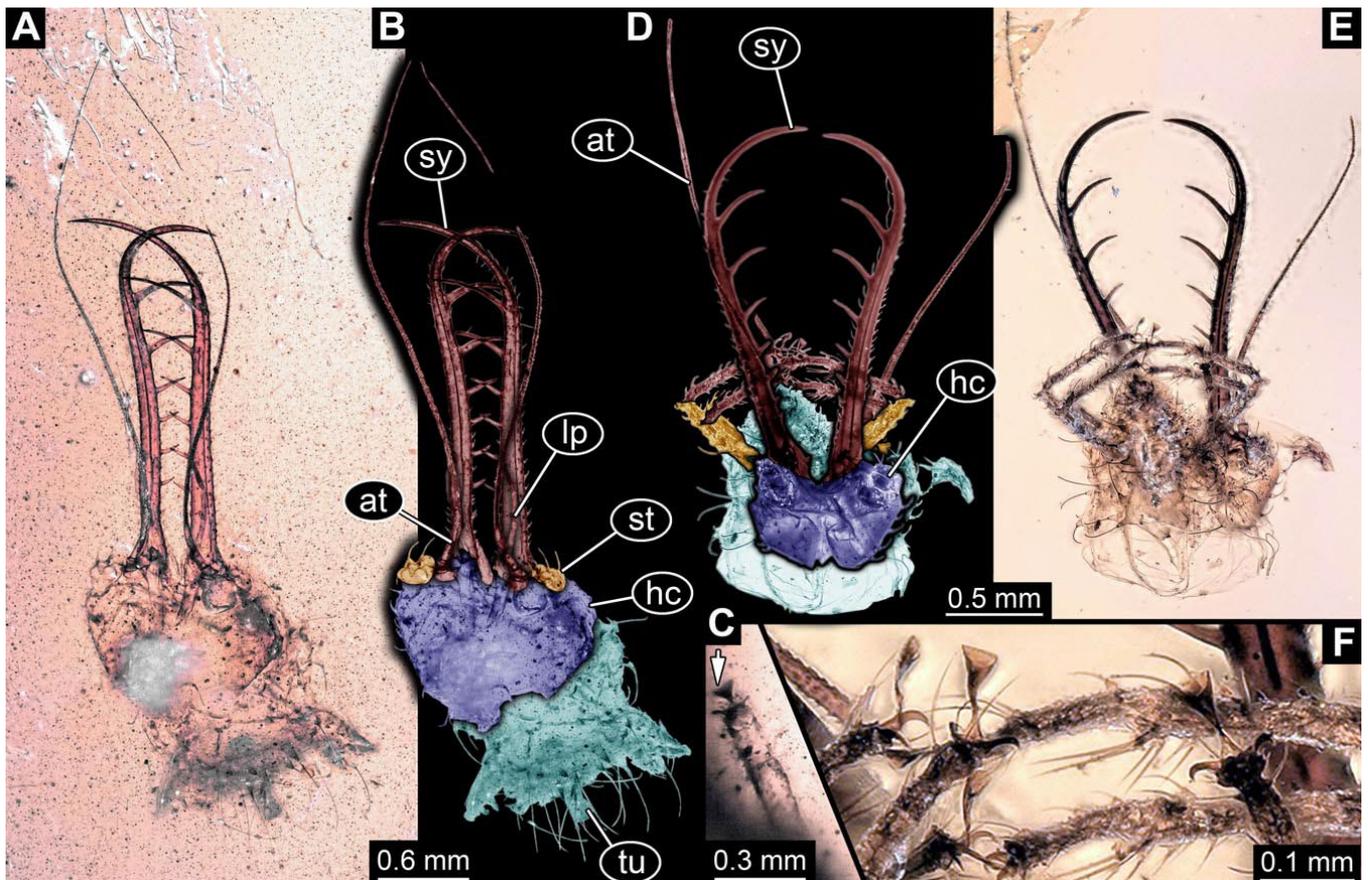


Figure 16. Larvae of the superfang type 2. (A–C) PED 0510 (specimen 0867). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the distal part of the locomotory appendage; the arrow marks the empodium. (D–F) PED 0630 (specimen 0868). (D) Overview. (E) Colour-marked version of (D). (F) Close-up on the distal part of the locomotory appendage with empodia. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; st = stemmata; sy = stylet; tu = trunk.

- (22) Specimen 0868 (PED 0630) is incompletely preserved (Figure 16D,E). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with one distinct socketed seta proximally. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (empodia; Figure 16F).
- (23) Specimen 0869 (PED 0657) is incompletely preserved (Figure 17A,B). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with at least five teeth (Figure 17C). Distal teeth are

significantly longer than proximal ones, with one distinct socketed seta proximally. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Trunk with bulbous projections bearing longer setae (Figure 17D).

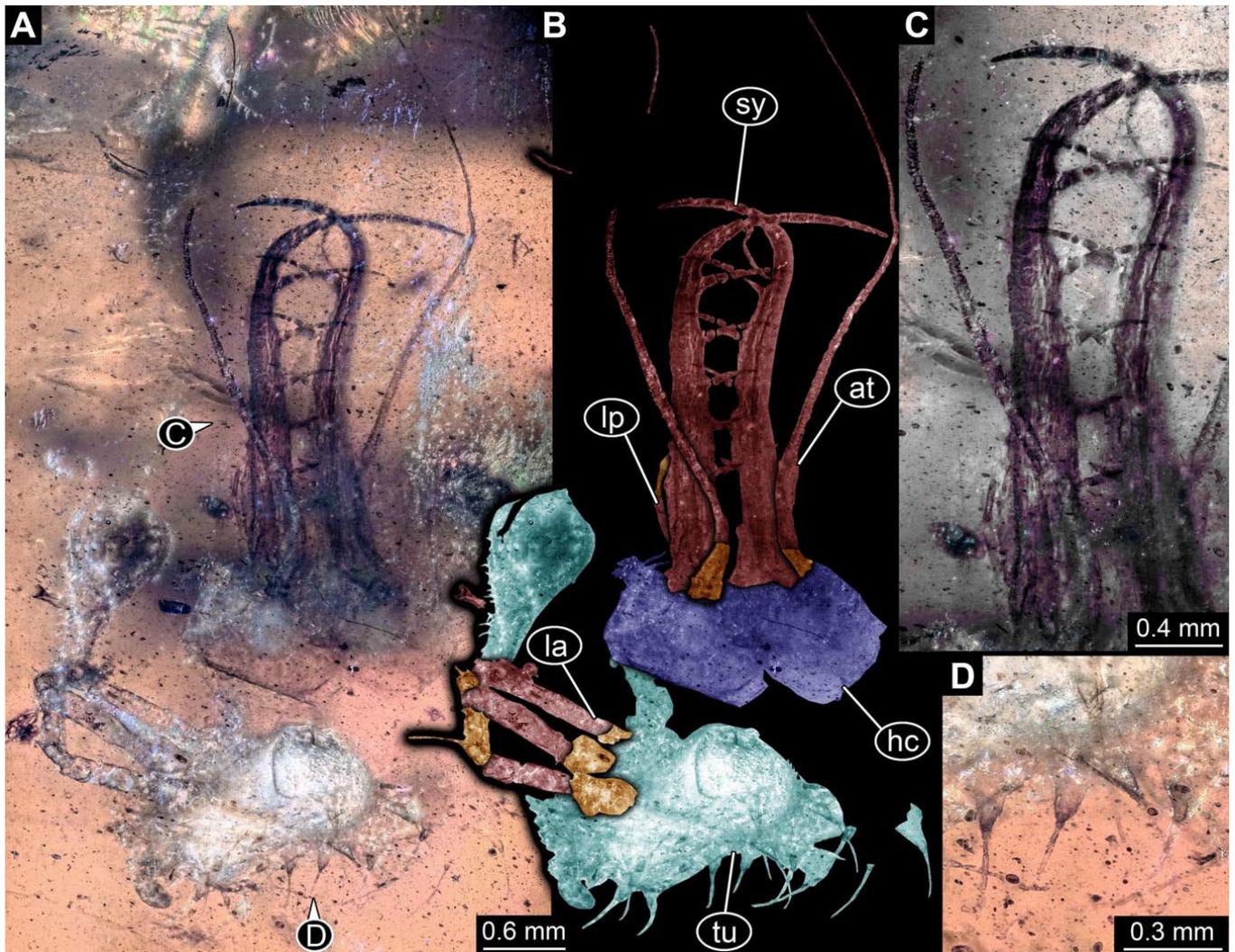


Figure 17. Larva of the superfang type 2, PED 0657 (specimen 0869). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on stylets. (D) Close-up on trunk processes. Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (24) Specimen 0870 (PED 0671) is incompletely preserved (Figure 18A,B). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with at least five teeth. The distal teeth are significantly longer than the proximal ones, with setae between the teeth. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally.

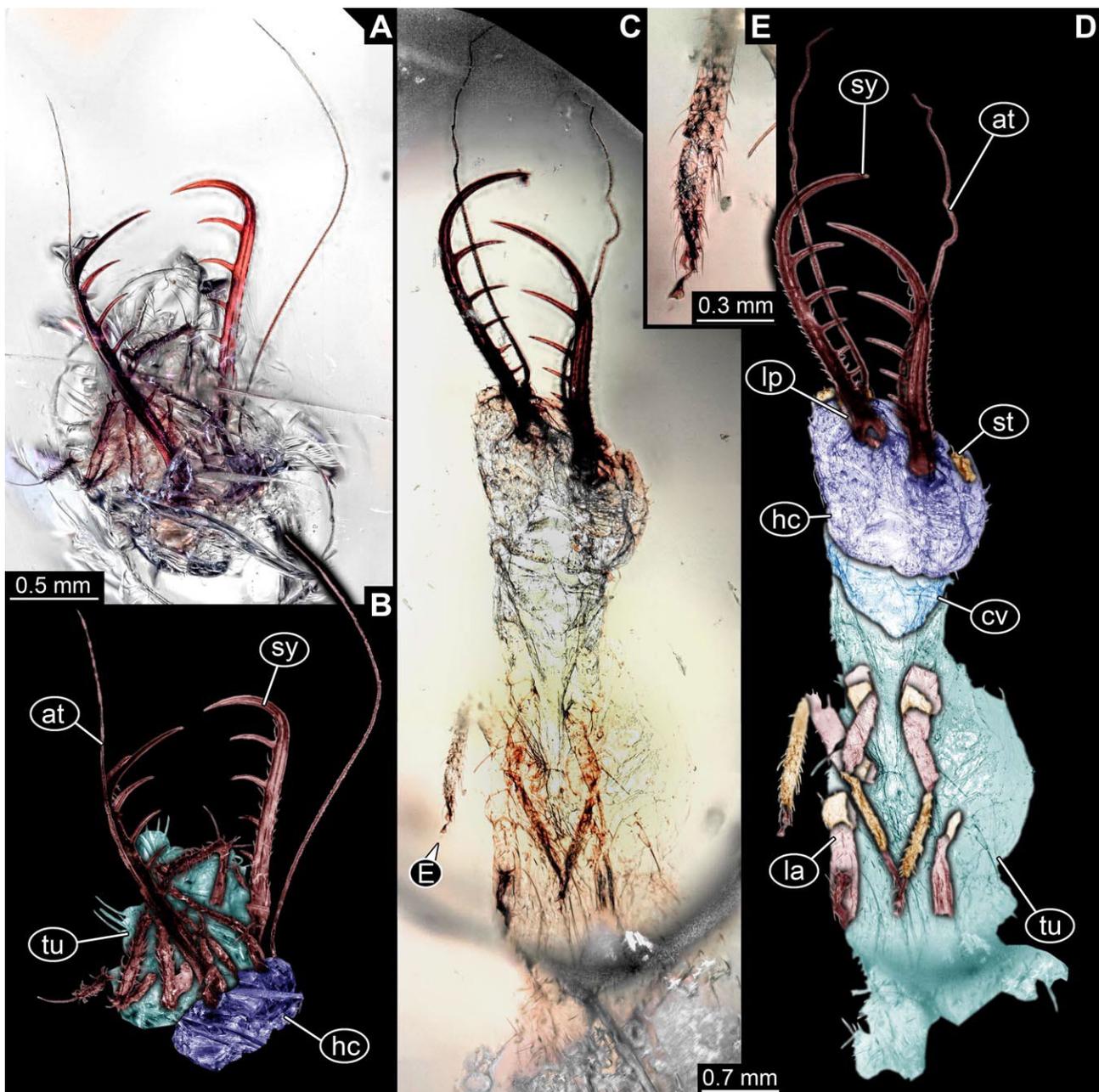


Figure 18. Larvae of the superfang type 2. (A,B) PED 0671 (specimen 0870). (A) Overview. (B) Colour-marked version of (A). (C–E) PED 0739 (specimen 0871). (C) Overview. (D) Colour-marked version of (C). (E) Close-up on the distal part of the locomotory appendage. Abbreviations: at = antenna; cv = cervix; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (25) Specimen 0871 (PED 0739) is incompletely preserved (Figure 18C,D). Most likely representing exuvia; the main body is slightly crumpled. Forwardly projecting mouth-parts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with at least five teeth. Distal teeth are significantly longer than proximal ones; with setae between the teeth, there are more setae laterally. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (Figure 18E).
- (26) Specimen 0872 (PED 0784) is incompletely preserved (Figure 19A,B). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting

mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. The distal teeth are significantly longer than the proximal ones, with setae between the teeth. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are better preserved. Legs have trumpet-shaped attachment structures distally (Figure 19C).

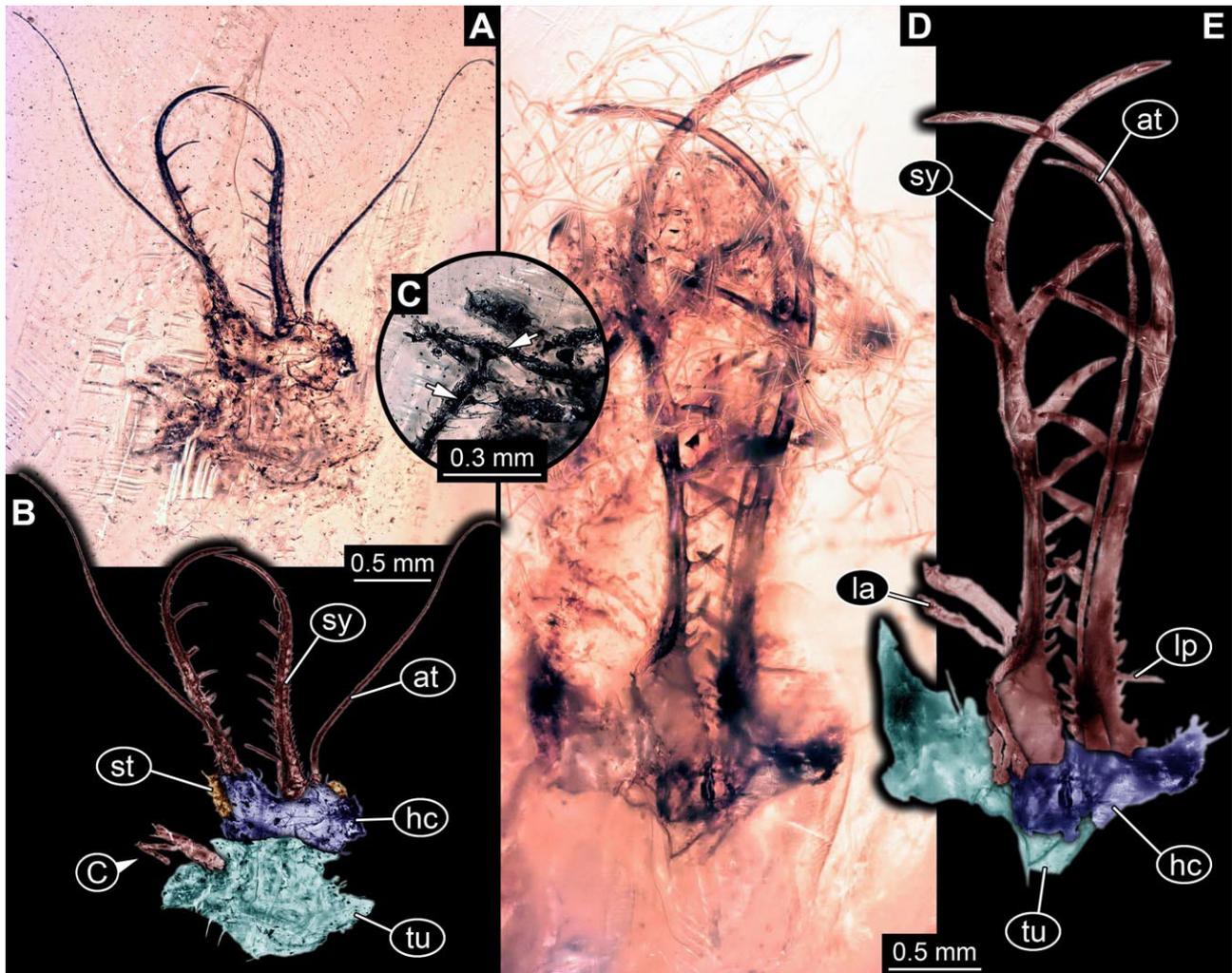


Figure 19. Larvae of the superfang type 2. (A–C) PED 0784 (specimen 0872). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the distal part of the locomotory appendage; the arrows mark the empodia. (D,E) PED 0963 (specimen 0873). (D) Overview. (E) Colour-marked version of (D). Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (27) Specimen 0873 (PED 0963) is incompletely preserved (Figure 19D,E). Most likely representing exuvia; the main body is strongly crumpled. Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with setae between the teeth and more setae laterally. Labial palps are elongate and shorter than stylets. Antennae are elongate, shorter than stylets, and most likely incomplete. In addition, parts of locomotory appendages (legs) are preserved.
- (28) Specimen 0874 (PED 1034) is incompletely preserved (Figure 20A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with antero-lateral

projection, bearing eyes (Figure 20C). Forwardly projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae are better preserved. Stylets with at least five teeth (Figure 20E). The distal teeth are significantly longer than the proximal ones, with setae between the teeth. Labial palps are elongate and shorter than stylets. Antennae are elongate, shorter than stylets, and most likely incomplete. In addition, parts of locomotory appendages (legs) are preserved (Figure 20D).

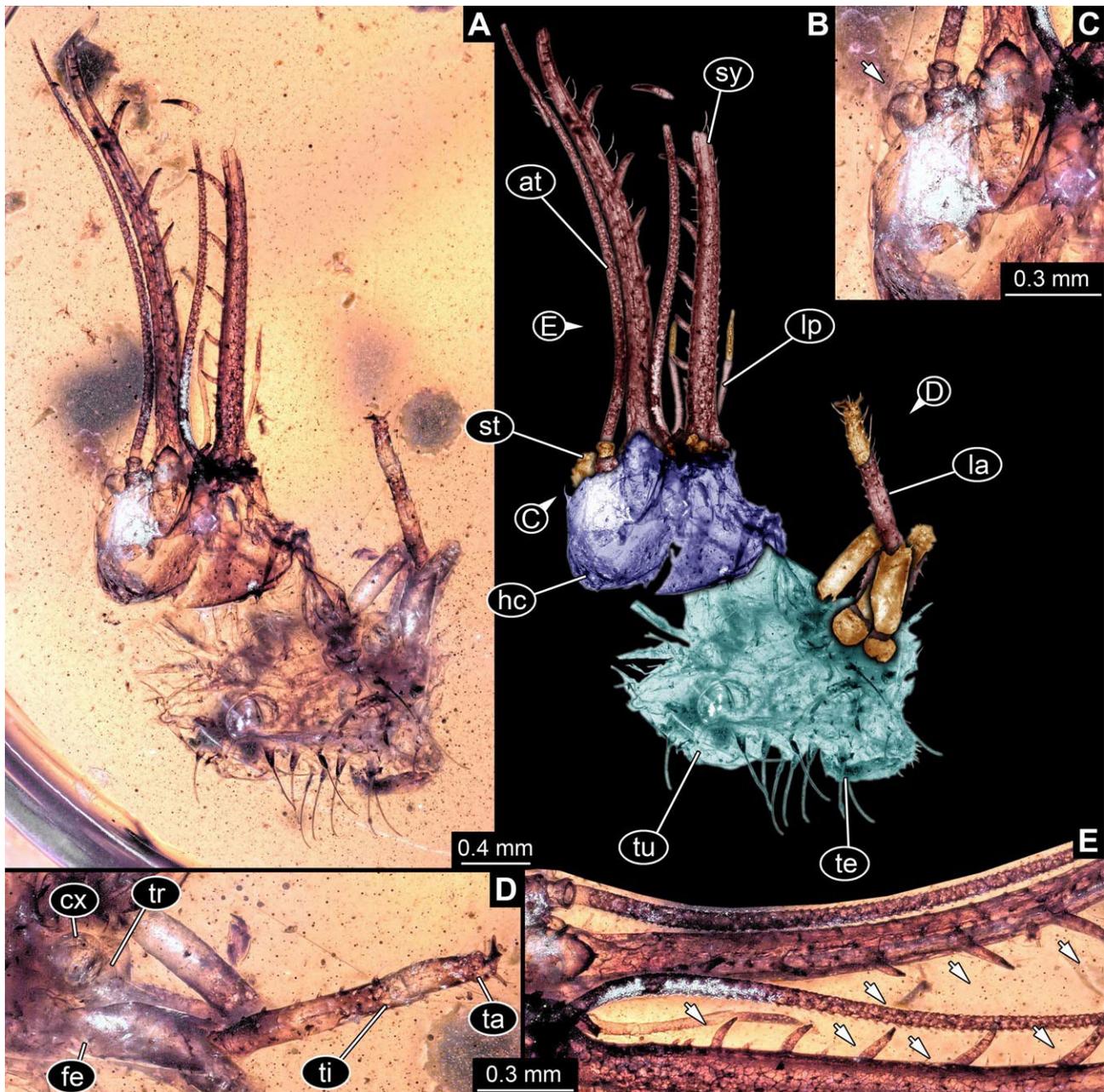


Figure 20. Larva of the superfang type 2, PED 1034 (specimen 0874). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the eye region. (D) Close-up on the locomotory appendage. (E) Close-up on stylet; arrows mark teeth. Abbreviations: at = antenna; cx = coxa; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; st = stemmata; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter; tu = trunk.

(29) Specimen 0876 (Weiterschan BuB 9) is incompletely preserved (Figure 21C,D). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting

antennae is better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with setae between the teeth; laterally with numerous setae. Labial palps are elongate and shorter than stylets. Antennae are elongate, shorter than stylets, and most likely incomplete. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 21E).

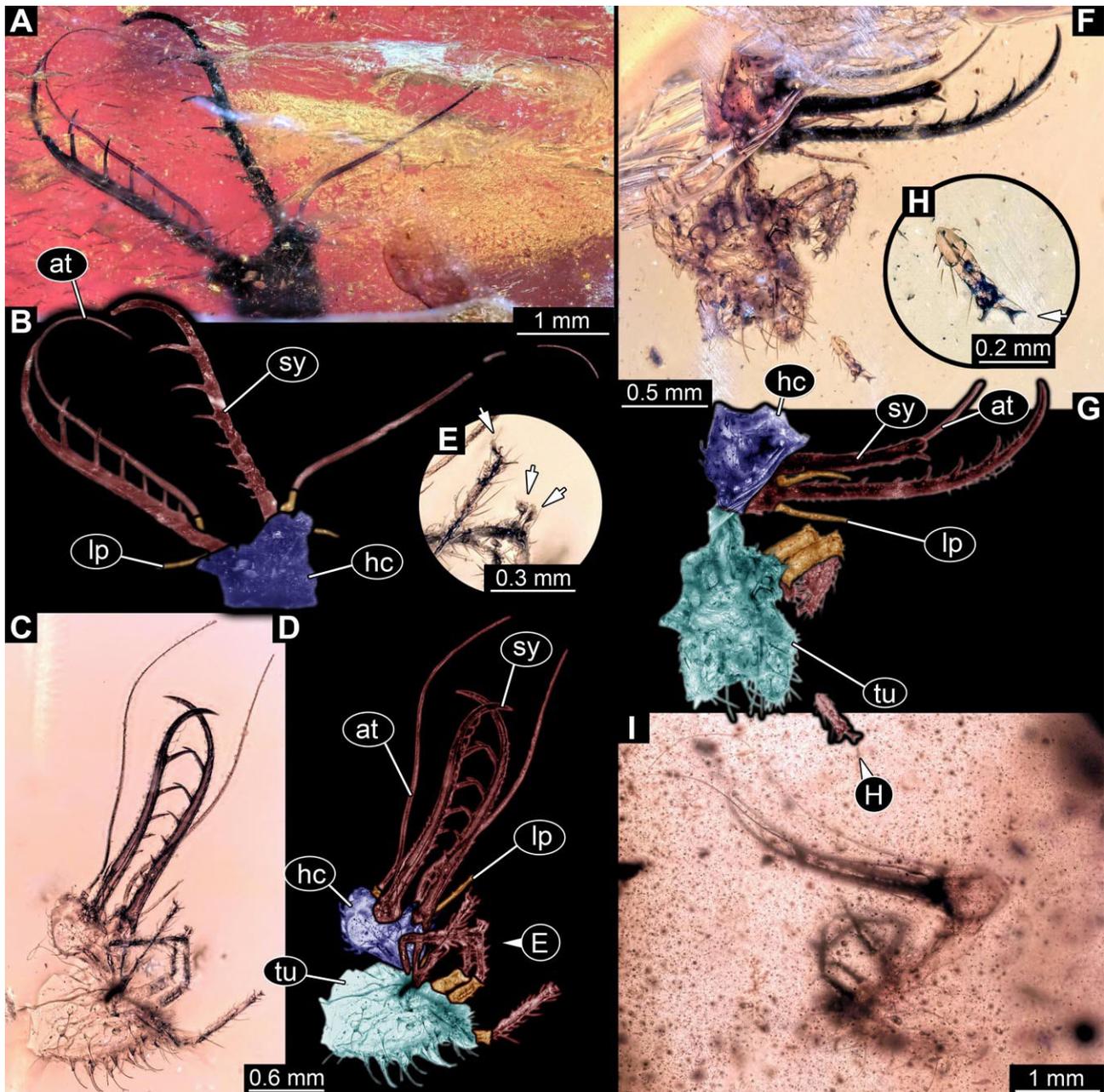


Figure 21. Larvae of the superfang type 2. (A,B) PED 1739 (specimen 0935). (A) Overview. (B) Colour-marked version of (A). (C–E) Weilerschan BuB 9 (0876). (C) Overview. (D) Colour-marked version of (C). (E) Close-up on distal parts of locomotory appendages; arrows mark empodia. (F–H) PED 2633 (specimen 0943). (F) Overview. (G) Colour-marked version of (F). (H) Close-up on distal parts of locomotory appendages; arrow marks empodium. (I) PED 1822 (specimen 0937). Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

(30) Specimen 0877 (PED 1110) is incompletely preserved (Figure 22A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting

mouthparts, the stylets and labial palps and antero-laterally projecting antennae is better preserved. Stylets with few teeth. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are preserved.

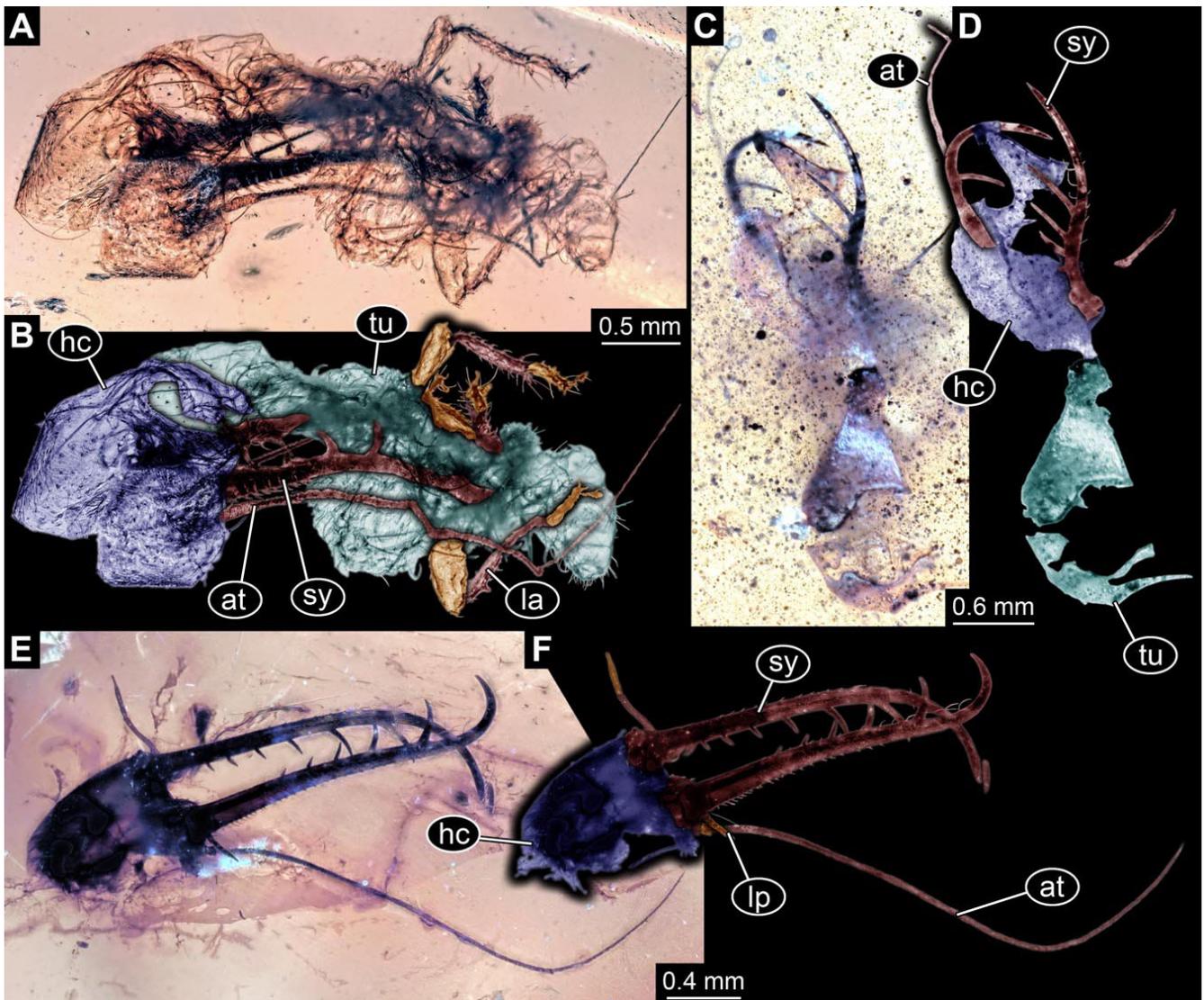


Figure 22. Larvae of the superfang type 2. (A,B) PED 1110 (specimen 0877). (A) Overview. (B) Colour-marked version of (A). (C,D) PED 1242 (specimen 0878). (C) Overview. (D) Colour-marked version of (C). (E,F) PED 1255 (specimen 0879). (E) Overview. (F) Colour-marked version of (E). Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (31) Specimen 0878 (PED 1242) is incompletely preserved (Figure 22C,D). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets with few teeth. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are preserved.
- (32) Specimen 0879 (PED 1255) is incompletely preserved (Figure 22E,F). Mostly head preserved, with forward projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae better preserved. Stylets with six teeth and numerous setae laterally. Labial palps are elongate and shorter than stylets. Antennae elongate and longer than stylets.
- (33) Specimen 0880 (PED 1293) is incompletely preserved (Figure 23A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting

mouthparts, the stylets and labial palps and antero-laterally projecting antennae is better preserved. Stylets with six teeth; one prominent seta proximally. Distal teeth are significantly longer than proximal ones; laterally, there are numerous setae. Labial palps are elongate and shorter than stylets (Figure 23C). Antennae are elongate, shorter than stylets, and most likely incomplete. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 23D).

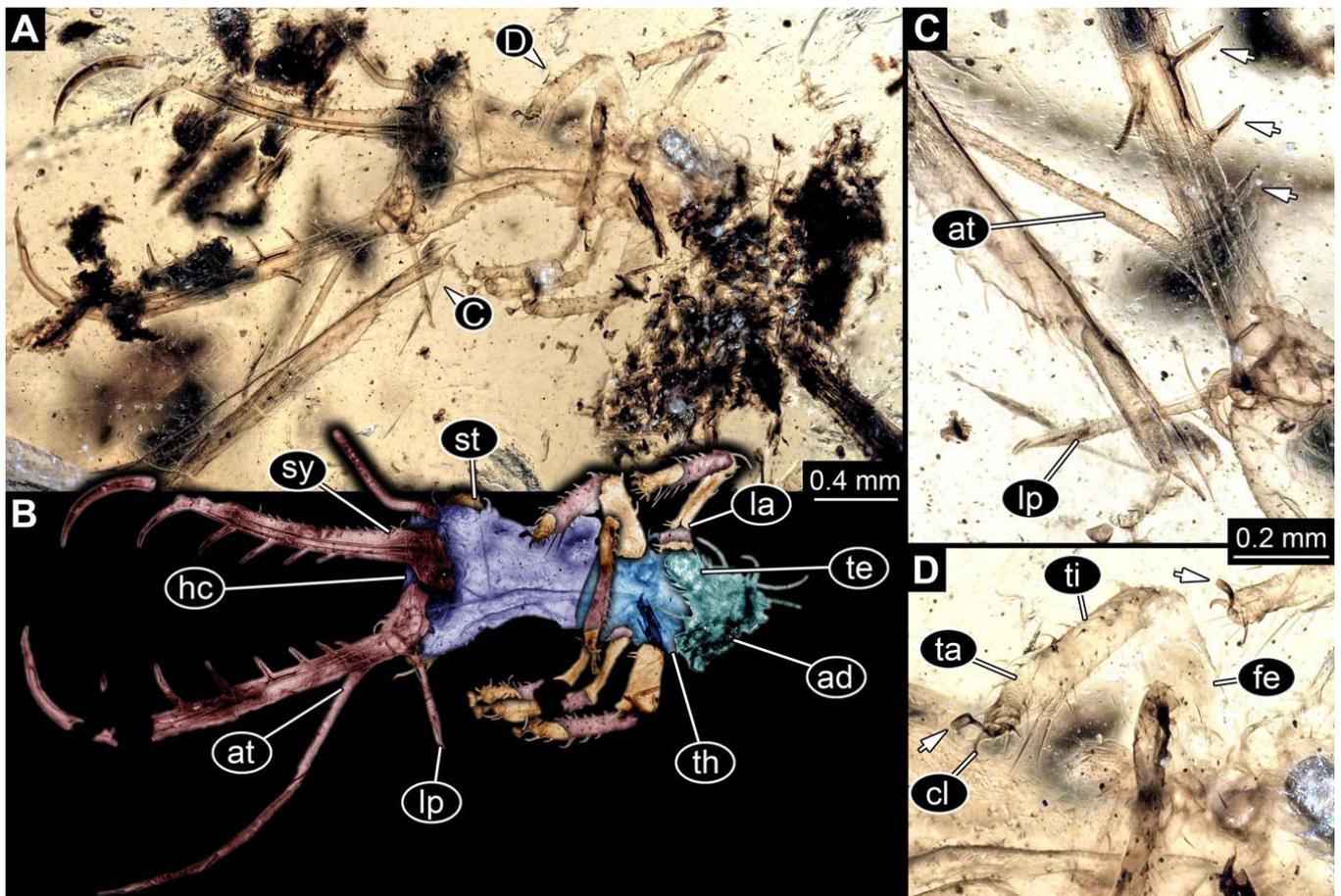


Figure 23. Larva of the superfang type 2, PED 1293 (specimen 0880). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the anterior head region; arrows mark teeth. (D) Close-up on distal parts of locomotory appendages; arrows mark empodia. Abbreviations: ad = abdomen; at = antenna; cl = claw; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; ta = tarsus; th = thorax; ti = tibia; tu = trunk.

(34) Specimen 0931 (PED 1327) is incompletely preserved (Figure 24A–C). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets with six teeth (Figure 24D). Distal teeth are significantly longer than proximal ones. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 24E).

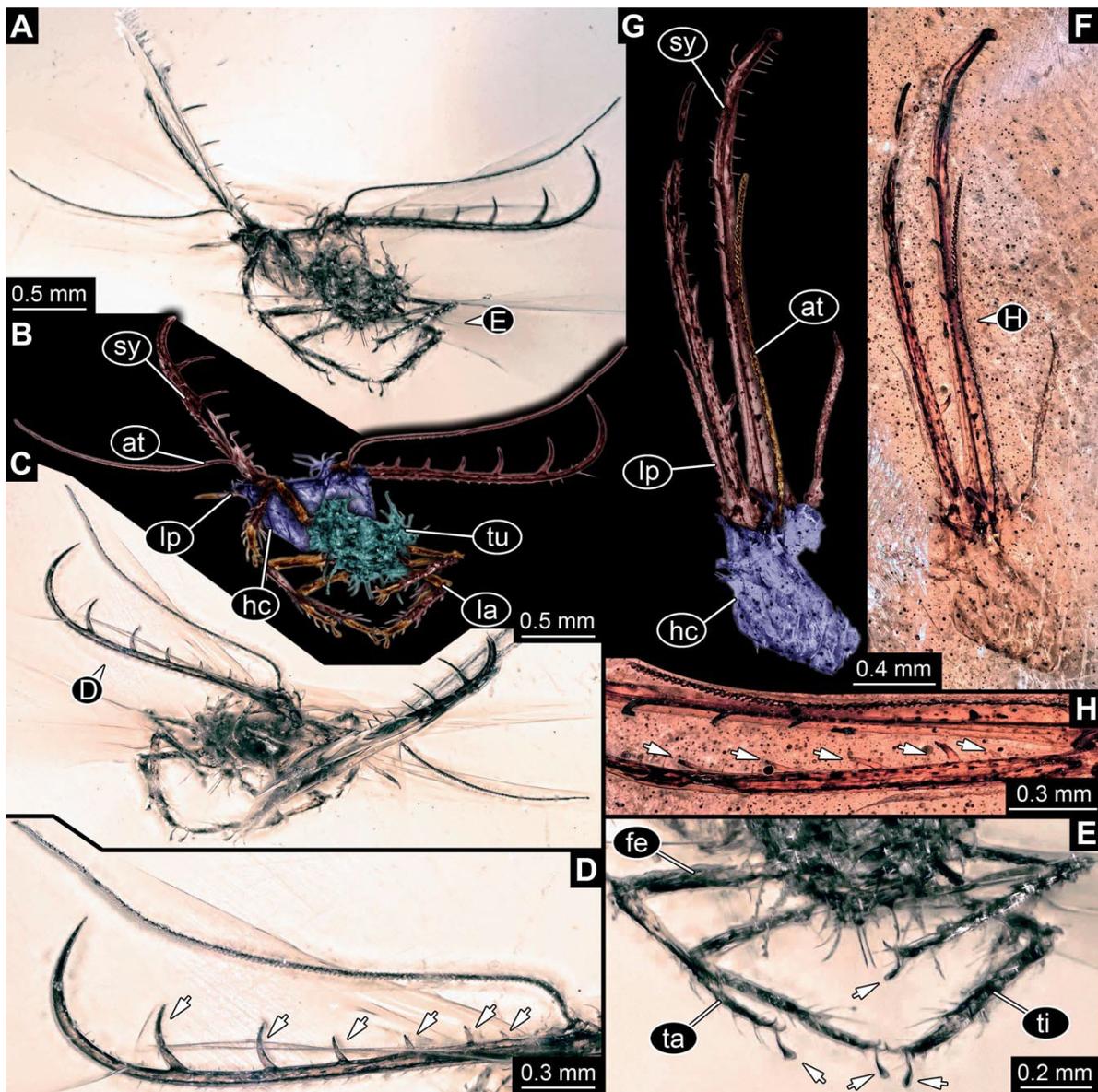


Figure 24. Larvae of the superfang type 2. (A–E) PED 1327 (specimen 0931). (A) Overview, one side. (B) Colour-marked version of (A). (C) Overview, other side. (D) Close-up on stylet; arrows mark teeth. (E) Close-up on distal parts of locomotory appendages; arrows mark empodia. (F–H) PED 1367 (specimen 0932). (F) Overview. (G) Colour-marked version of (F). (H) Close-up on stylet; arrows mark teeth. Abbreviations: at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; ta = tarsus; ti = tibia; tu = trunk.

- (35) Specimen 0932 (PED 1367) is incompletely preserved (Figure 24F,G). Mostly head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae better preserved. Stylets have at least five teeth (Figure 24H); laterally, they have numerous setae. Antennae are elongate, shorter than stylets, and most likely incomplete.
- (36) Specimen 0933 (PED 1409) is incompletely preserved (Figure 25A,B). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones; laterally, there are numerous setae. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 25C,D).

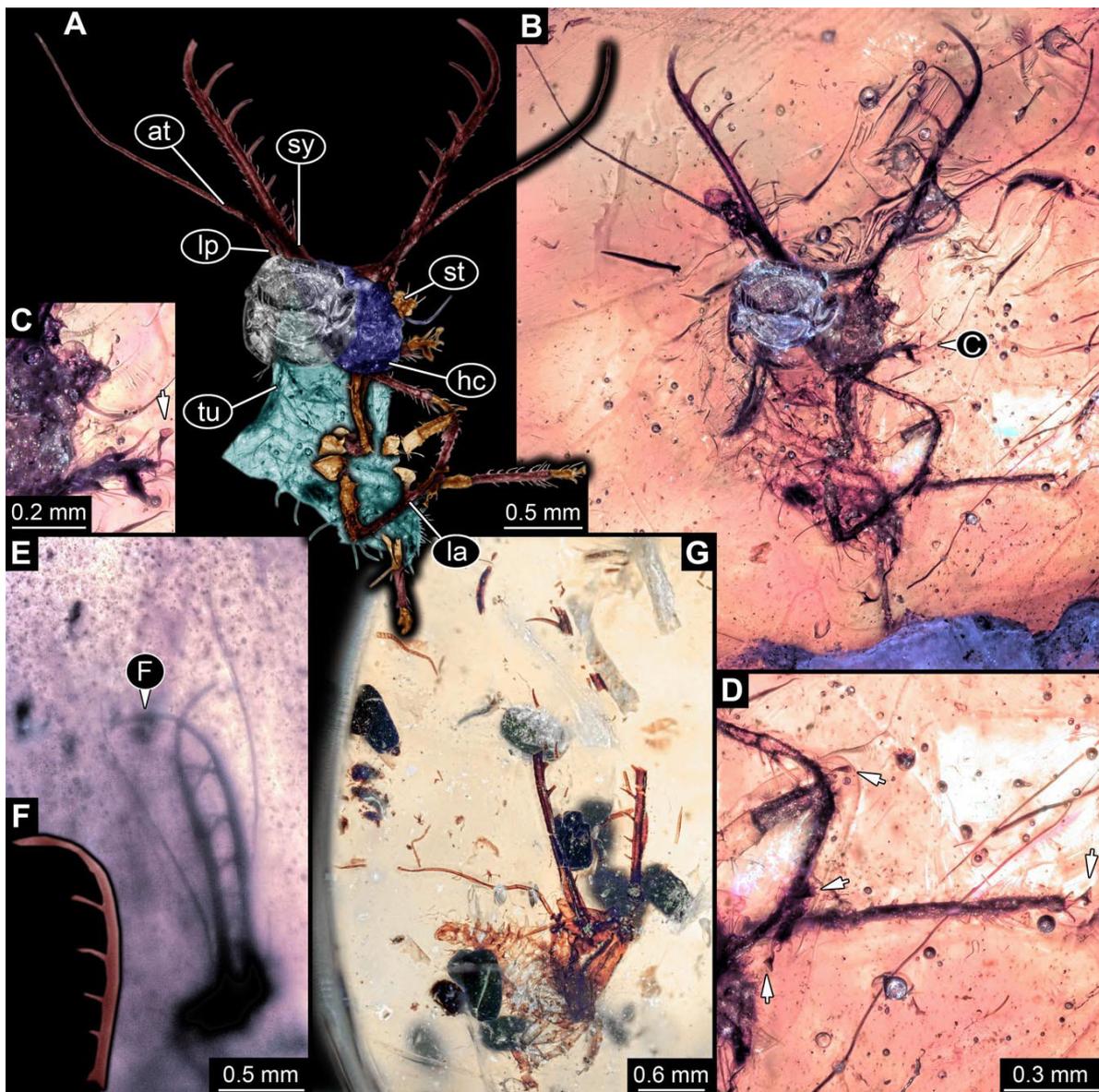


Figure 25. Larvae of the superfang type 2. (A–D) PED 1409 (specimen 0933). (A) Overview, colour-marked. (B) Overview. (C,D) Close-up on distal parts of locomotory appendages; arrows mark empodia. (E,F) PED 1610 (specimen 0934). (E) Overview. (F) Colour-marked stylet. (G) PED 1810 (specimen 0936). Abbreviations: at = antenna; hc = head capsule; la = locomotory appendage; lp = labial palp; st = stemmata; sy = stylet; tu = trunk.

- (37) Specimen 0934 (PED 1610) is poorly preserved (Figure 25E,F). Head hardly recognizable, mostly stylets apparent. Stylets with at least five teeth.
- (38) Specimen 0935 (PED 1739) is incompletely preserved (Figure 21A,B). Mostly head with forward projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones. Labial palps are elongate and shorter than stylets. Antennae are elongate, shorter than stylets, and most likely incomplete.
- (39) Specimen 0936 (PED 1810) is incompletely preserved (Figure 25G). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets are broken, with few teeth. Antennae are elongate but incomplete. In addition, parts of locomotory appendages (legs) are preserved.

- (40) Specimen 0937 (PED 1822) is incompletely preserved (Figure 21I). Most likely representing exuvia; main body strongly crumpled; amber in addition very dirty. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae. Antennae elongate and longer than stylets. In addition, parts of locomotory appendages (legs) are preserved.
- (41) Specimen 0938 (PED 1971) is incompletely preserved (Figure 26A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting mouthparts, the stylets, is better preserved. Stylets with at least five teeth. Distal teeth are significantly longer than proximal ones. In addition, parts of locomotory appendages (legs) are preserved.

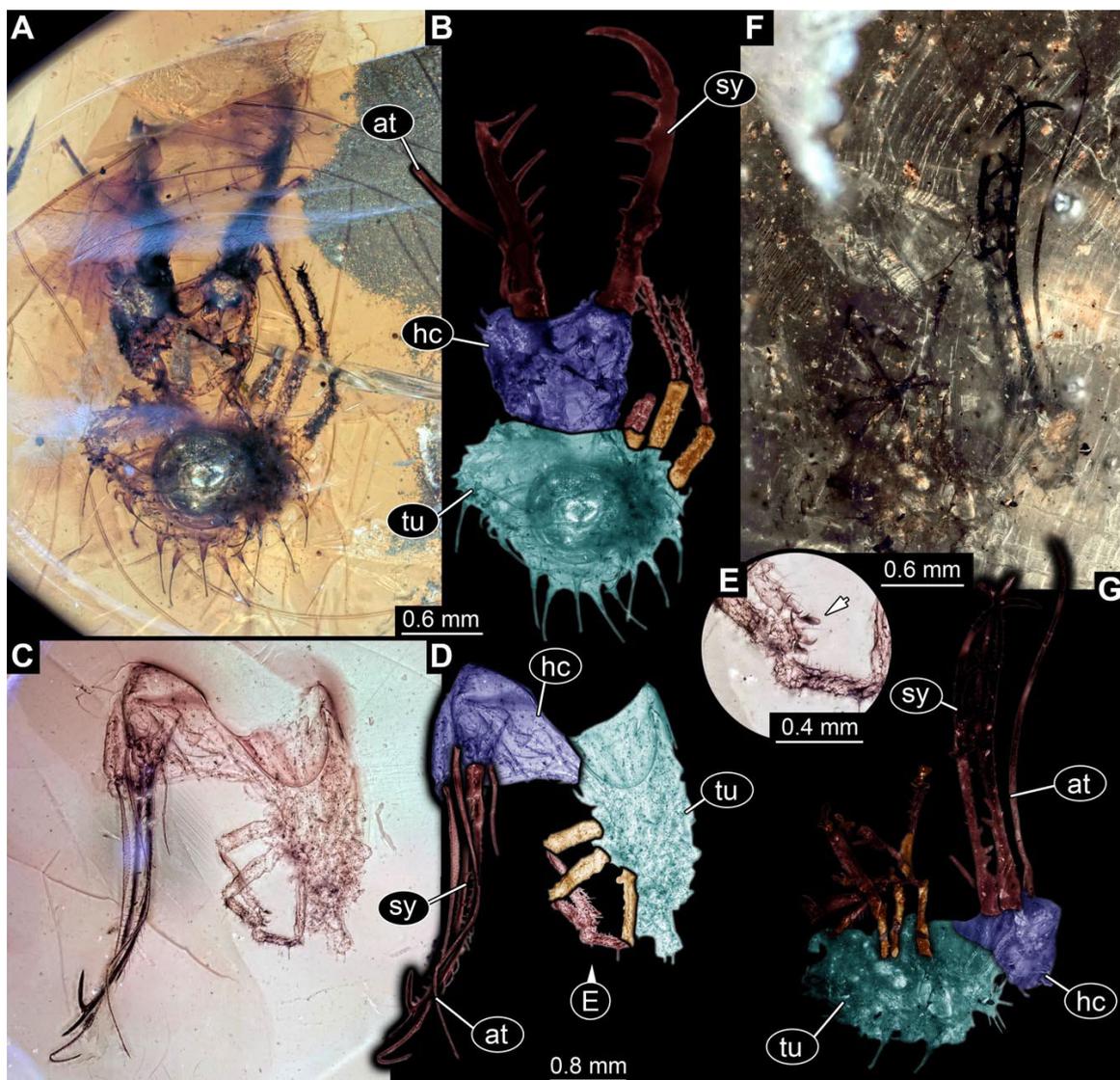


Figure 26. Larvae of the superfang type 2. (A,B). PED 1971 (specimen 0938). (A) Overview. (B) Colour-marked version of (A). (C–E). PED 2190 (specimen 0939). (C) Overview. (D) Colour-marked version of (C). (E) Close-up on distal parts of locomotory appendage; arrow marks empodium. (F,G) BUB 3371 (specimen 0941). (F) Overview. (G) Colour-marked version of (F). Abbreviations: at = antenna; hc = head capsule; sy = stylet; tu = trunk.

- (42) Specimen 0939 (PED 2190) is incompletely preserved (Figure 26C,D). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting mouthparts, the stylets, is better preserved. In addition, parts of locomotory ap-

pendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 26E).

- (43) Specimen 0940 (BUB 3381) is incompletely preserved (Figure 27A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae is better preserved. Stylets with six teeth (Figure 27C). Distal teeth are significantly longer than proximal ones; setae between teeth; also laterally, with numerous setae. Labial palps are elongate and shorter than stylets. Antennae are elongate, longer than stylets, with at least three elements (Figure 27E). In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 27D).

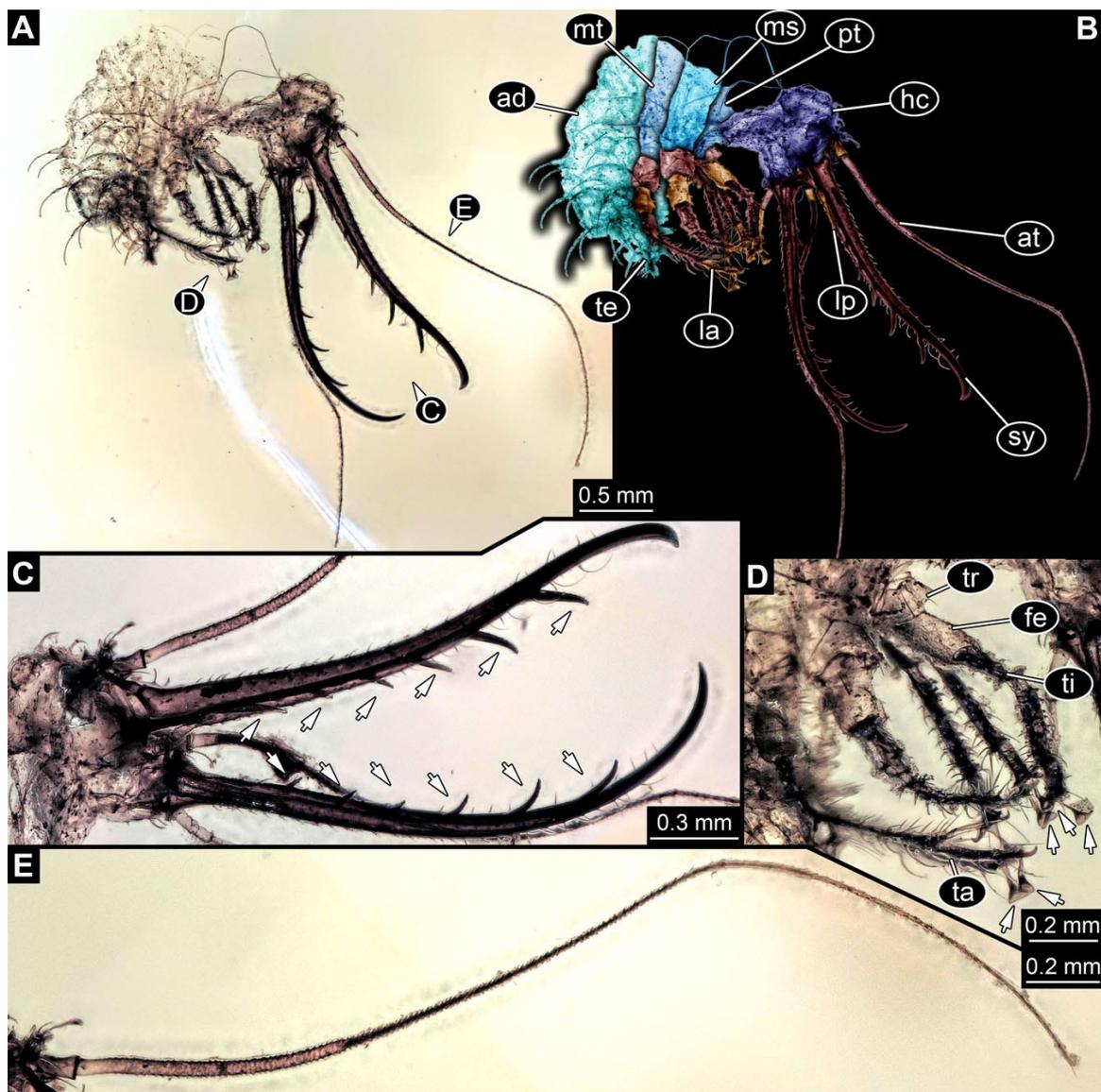


Figure 27. Larva of the superfang type 2, BUB 3381 (specimen 0940). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on stylets; arrows mark teeth. (D) Close-up on distal parts of locomotory appendages; arrows mark empodia. (E) Close-up on the antenna. Abbreviations: ad = abdomen; at = antenna; fe = femur; hc = head capsule; la = locomotory appendage; lp = labial palp; ms = mesothorax; mt = metathorax; pt = prothorax; sy = stylet; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter.

- (44) Specimen 0941 (BUB 3371) is incompletely preserved (Figure 26F,G). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets are broken with few teeth. Antennae are elongate but incomplete. In addition, parts of locomotory appendages (legs) are preserved.
- (45) Specimen 0943 (PED 2633) is incompletely preserved (Figure 21F,G). Most likely representing exuvia; the main body is strongly crumpled. Head with forward-projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae is better preserved. Stylets with six teeth. Distal teeth are significantly longer than proximal ones, with setae between the teeth; laterally with numerous setae. Labial palps are elongate and shorter than stylets. Antennae are elongate, shorter than stylets, and most likely incomplete. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 21H).

3.4. Short Descriptions of Partly Unclear Specimens, Most Likely Superfang Type 2

- (46) Specimen 0847 (PED 0716) is incompletely preserved (Figure 28E,F). Most likely representing exuvia; the main body is strongly crumpled. The head with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae is better preserved. Stylets are broken off distally. Antennae incomplete. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 28G).

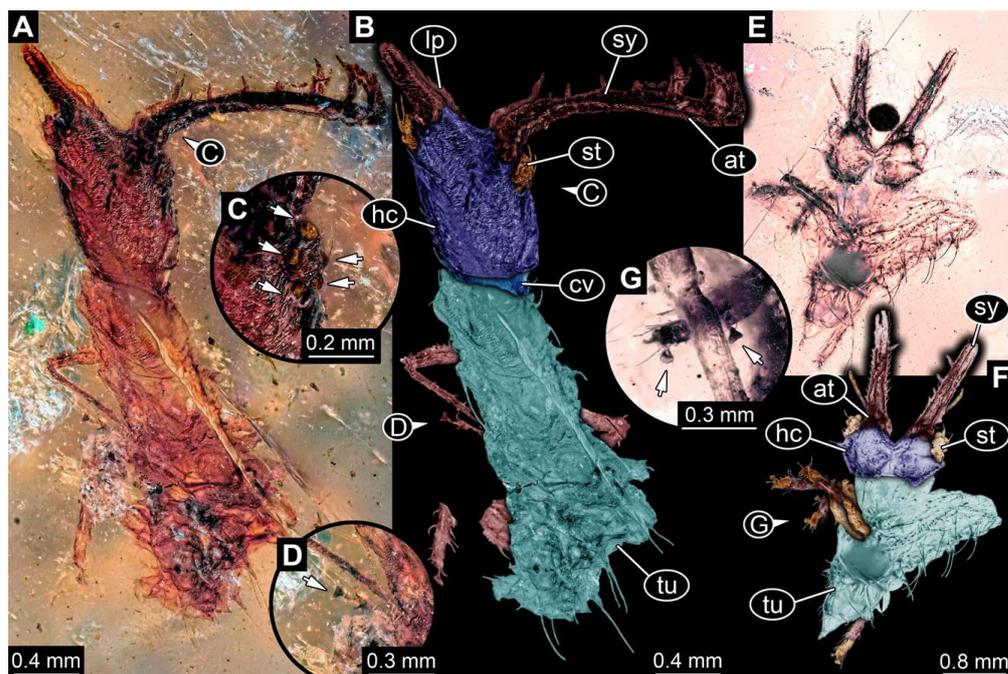


Figure 28. Possible larvae of the superfang type 2. (A–D) PED 0586 (specimen 0875). (A) Overview. (B) Colour-marked version of (A). (C) Close-up on the eye region. (D) Close-up on distal parts of locomotory appendages; arrow marks empodium. (E–G). PED 0716 (specimen 0847). (E) Overview. (F) Colour-marked version of (E). (G) Close-up on distal parts of locomotory appendages; arrows mark empodia. Abbreviations: at = antenna; cv = cervix; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; tu = trunk.

- (47) Specimen 0875 (PED 0586) is incompletely preserved (Figure 28A,B). Most likely representing exuvia; the main body is strongly crumpled. Head with eyes (Figure 28C), forward projecting mouthparts, the stylets and labial palps, and antero-laterally projecting antennae is better preserved. Stylets with six teeth; stylets deformed. Distal teeth are significantly longer than proximal ones; setae between teeth; also laterally

with numerous setae. Labial palps elongate and shorter than stylets. Antennae elongate. In addition, parts of locomotory appendages (legs) are preserved. Legs have trumpet-shaped attachment structures distally (Figure 28D).

3.5. A Short Description of a New Specimen of *Kuafupolydentes hui*

- (48) Specimen 0903 (PED 2335) is incompletely preserved in dorsal (Figure 29C) and ventral views (Figure 29A,B). Mostly head with antero-lateral projections with eyes. Also, forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae are better preserved. Stylets with few blunt teeth (Figure 29A); laterally with numerous setae. Antennae are elongate, shorter than stylets, with two (or three?) elements each.

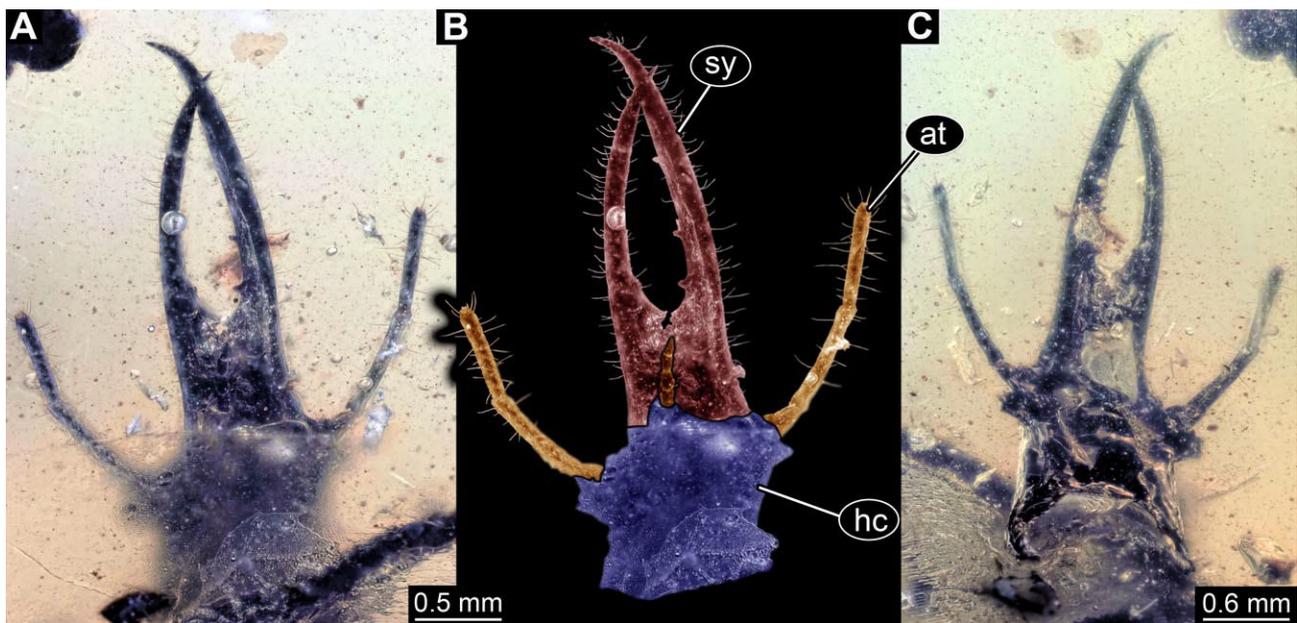


Figure 29. Larva of *Kuafupolydentes hui*, PED 2335 (specimen 0903). (A) Overview, ventral view. (B) Colour-marked version of (A). (C) Overview, dorsal view. Abbreviations: at = antenna; hc = head capsule; sy = stylet.

3.6. Short Descriptions of Specimens of a New Type of Larva: 4–5 Teeth Type

- (49) Specimen 0855 (PED 0476) is incompletely preserved (Figure 30A,B). Most likely representing exuvia; main body crumpled. Head broad; with eyes, forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae better preserved. Stylets with four teeth; numerous setae between teeth; also laterally numerous setae. Antennae are elongate but short and thin (filiform). In addition, parts of locomotory appendages (legs) are preserved. Legs distally with claws (Figure 30C).
- (50) Specimen 0856 (PED 1326) is incompletely preserved (Figure 30D,E). Most likely representing exuvia; main body crumpled. Head broad, with forward-projecting mouthparts, the stylets, and antero-laterally projecting antennae better preserved. Stylets with four teeth; numerous setae between teeth; also laterally numerous setae. Antennae are elongate but short and thin (filiform). In addition, parts of locomotory appendages (legs) are preserved. Legs distally with claws (Figure 30F).
- (51) Specimen 0857 (PED 1337) is poorly preserved (Figure 30G,H). Most likely representing exuvia; main body crumpled. Head broad, with forward-projecting mouthparts and stylets. Stylets with few teeth preserved; laterally with some setae. In addition, parts of locomotory appendages (legs) are recognisable.

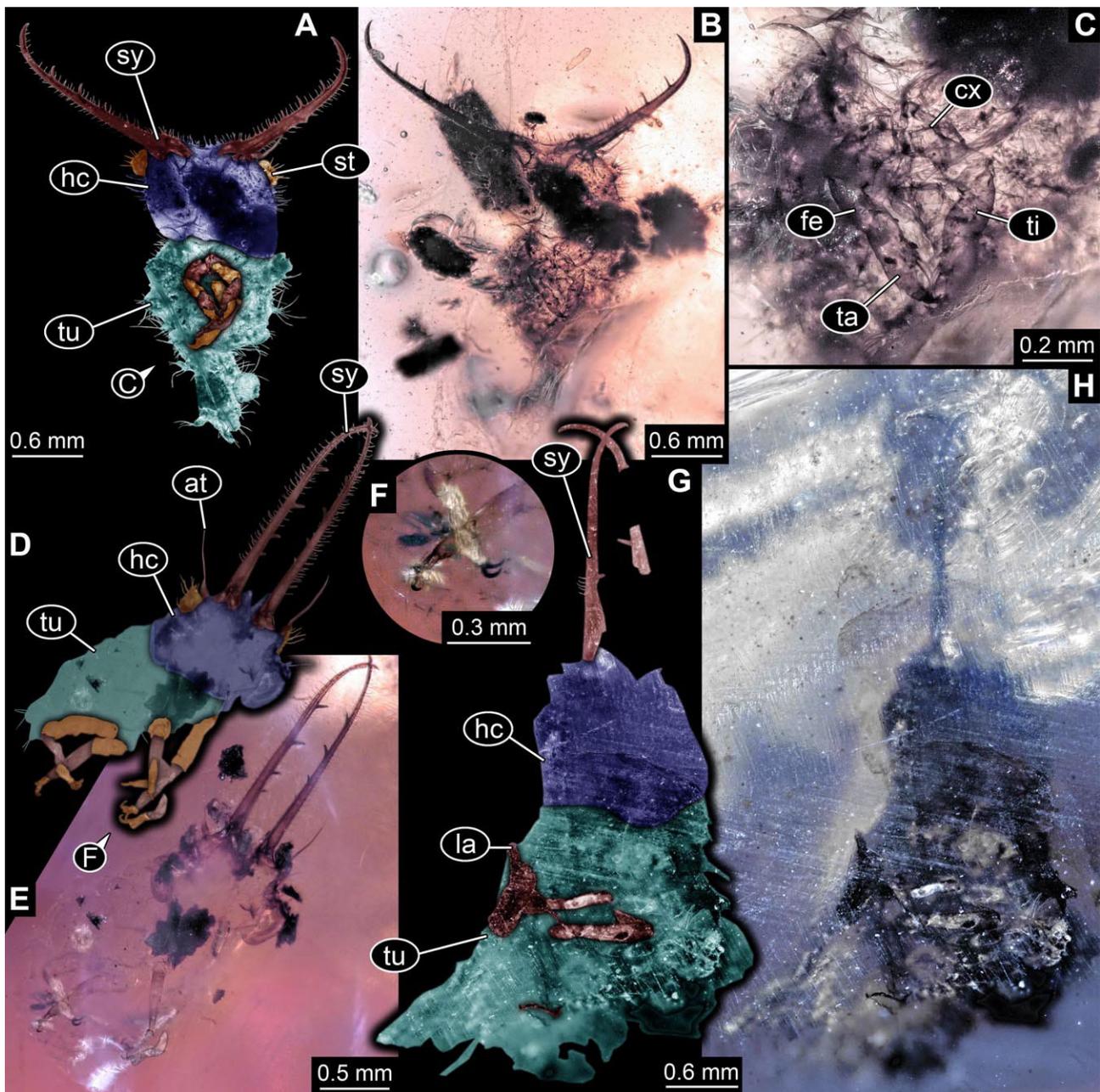


Figure 30. Larvae of the 4–5 teeth type. (A–C) PED 0476 (specimen 0855). (A) Overview, colour-marked. (B) Overview. (C) Close-up on locomotory appendages. (D–F) PED 1326 (specimen 0856). (D) Overview, colour-marked. (E) Overview. (F) Close-up on locomotory appendages. (G,H) PED 1337 (specimen 0857). (G) Overview, colour-marked. (H) Overview. Abbreviations: at = antenna; cx = coxa; hc = head capsule; la = locomotory appendage; lp = labial palp; sy = stylet; ta = tarsus; ti = tibia; tu = trunk.

- (52) Specimen 0858 (Weiterschan BuB 30) is incompletely preserved (Figure 31A). Most likely representing exuvia; main body crumpled. Head broad, with forward-projecting mouthparts, the stylets. Stylets with four teeth; numerous setae between teeth; also laterally numerous setae (Figure 31C,D). In addition, parts of locomotory appendages (legs) are preserved. Legs distally with claws (Figure 31B).

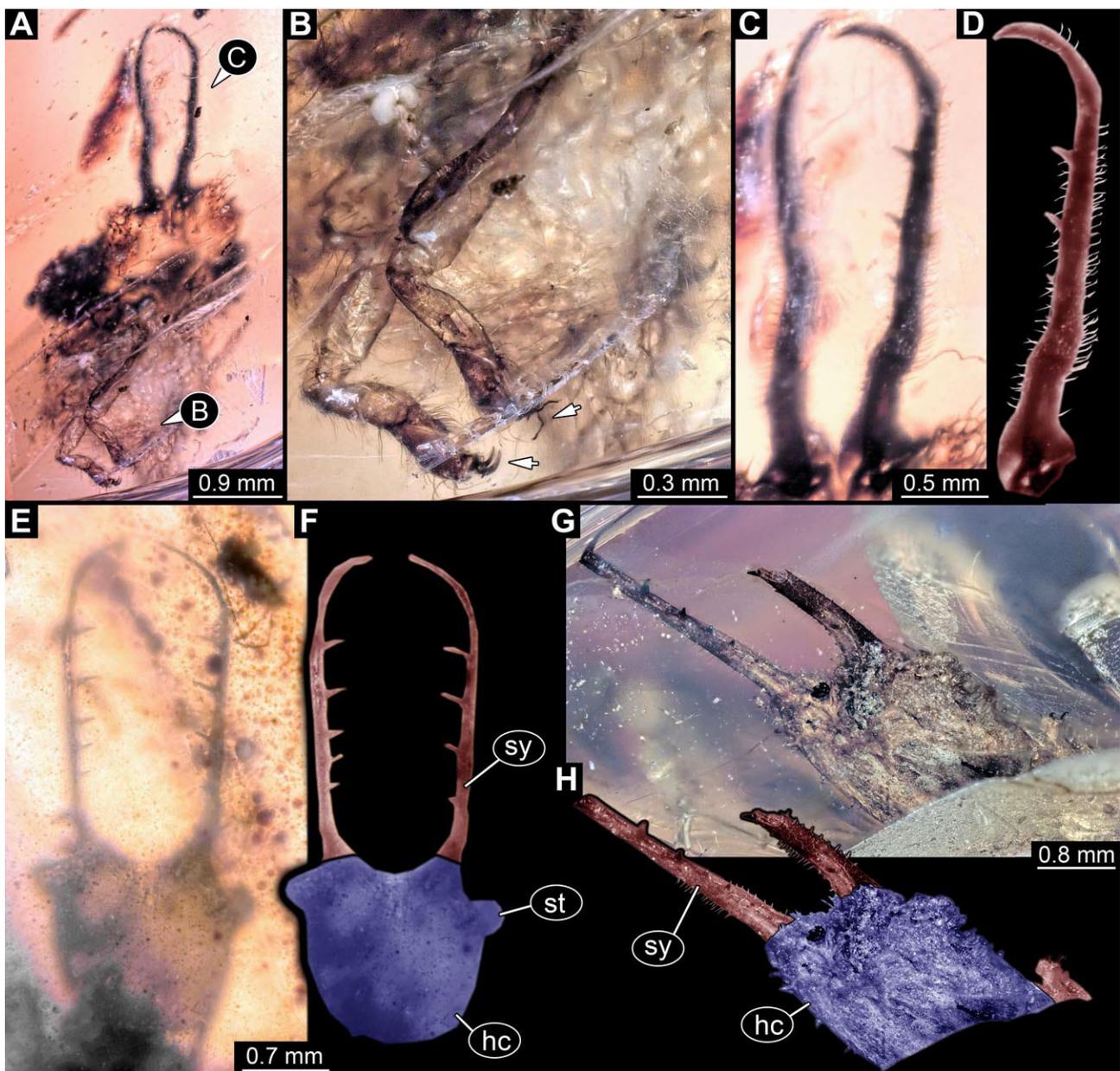


Figure 31. Larvae of the 4–5 teeth type. (A–D) Weiterschan BuB 30 (specimen 0858). (A) Overview. (B) Close-up on locomotory appendages; arrows mark claws. (C) Close-up on stylets. (D) Colour-marked version of (C). (E,F) PED 2599 (specimen 0942). (E) Overview. (F) Colour-marked version of (E). (G,H) Weiterschan BuB 1 (specimen 0944). (G) Overview. (H) Colour-marked version of (G). Abbreviations: hc = head capsule; st = stemmata; sy = stylet.

- (53) Specimen 0942 (PED 2599) is incompletely preserved (Figure 31E,F). Mostly head with forward-projecting mouthparts, the stylets. Stylets with five teeth.
- (54) Specimen 0944 (Weiterschan BuB 1) is incompletely preserved (Figure 31G,H). Mostly head with forward-projecting mouthparts, the stylets. Stylets are distally broken off.

3.7. Morphospace of the Head Capsule

The PCA of the EFA of the head capsule resulted in 15 principal components (PCs), describing over 99% of the morphological variation within the head capsule data set (PC1 = 68.9%; PC2 = 8.6%; PC3 = 6.3%; PC4 = 4.8%; PC5 = 3%; PC6 = 1.9%; PC7 = 1.6%; following eight PCs each less than 1%). The morphospace was created by plotting the first

two PCs, since they covered the most variation in the data (77.5%). The results of the analysis, including the graphical component loadings, are provided in the Supplementary Materials.

PC1 is dominated by the differences between the wide and slim head capsules (Figure 32). Positive values mainly represent slim head capsules widening anteriorly, while negative values mainly represent wide head capsules with antero-lateral notches (Figure 32). PC2 is dominated by the differences between anteriorly wider and posteriorly wider head capsules (Figure 32). Positive values mainly represent head capsules that are anteriorly widening with a slimmer posterior region, while negative values mainly represent posteriorly widening head capsules with anteriorly slimmer regions.

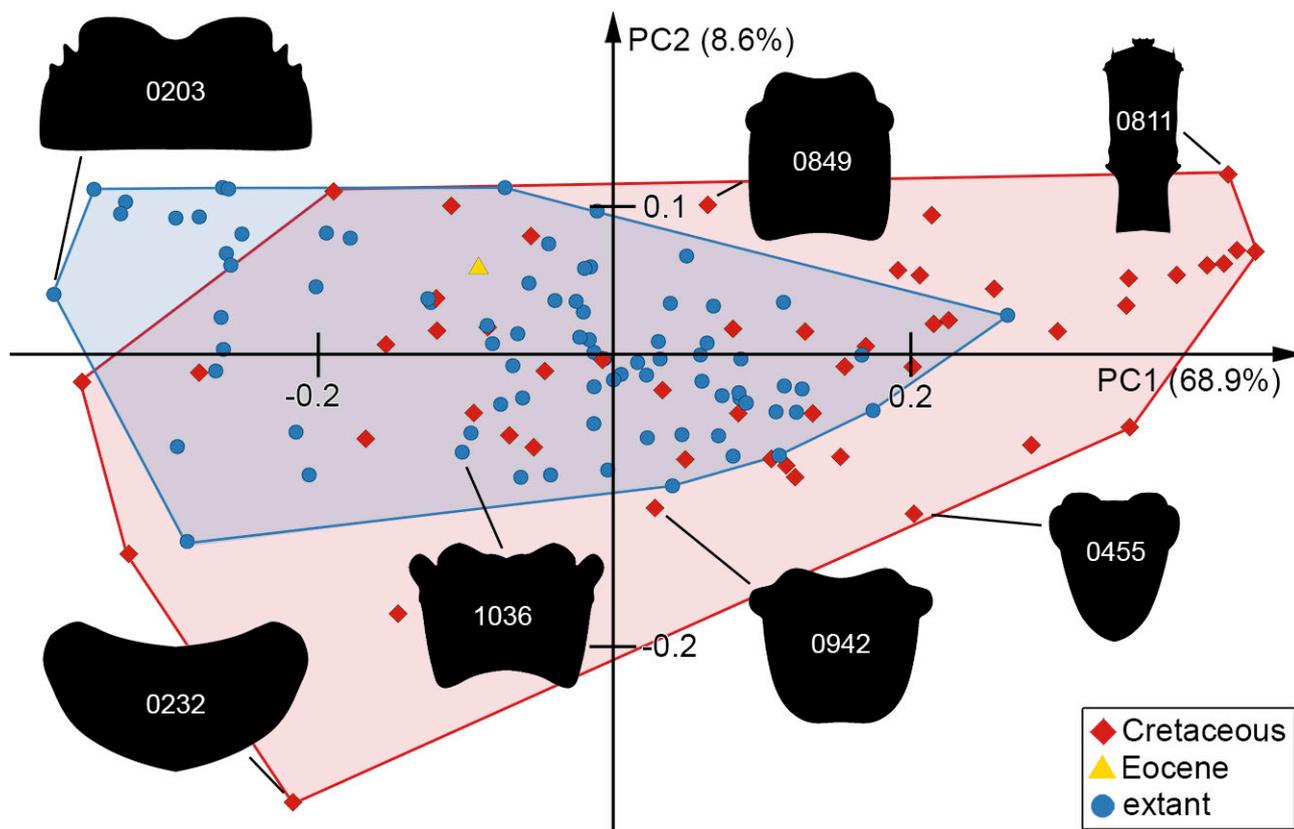


Figure 32. Morphospace is represented by scatter plots of the principal components (PCs) 1 and 2 of the head capsule.

Three of the four time slices are represented in this morphospace. The cluster of Cretaceous specimens plots throughout the whole morphospace, exclusively covering the far-right areas as well as the lower left corner, indicating slim morphologies on the right as well as morphologies that are round and extend antero-laterally. The one Eocene representative plots close to the centre of the morphospace, indicating a median morphology. The extant representatives also cover large areas of the morphospace but show some exclusivity towards the top left, indicating wide and square-shaped head capsules.

When considering all 15 dimensions of the morphospace, we found significant differences in the size of occupied morphospace between the Cretaceous and extant representatives (Welch Two Sample *t*-test; *p*-value < 0.001), with the Cretaceous specimens occupying a larger area. Similarly, we found that the two groups were significantly different in their position within the morphospace (Welch Two Sample *t*-test; *p*-value < 0.001).

3.8. Morphospace of the Head and Stylets with Teeth

The PCA of the EFA of the head and stylets with teeth resulted in 27 PCs, describing over 99% of the morphological variation within the head and stylets data set (PC1 = 38.6%;

PC2 = 23.9%; PC3 = 8.4%; PC4 = 5.1%; PC5 = 4.2%; PC6 = 3.4%; PC7 = 2.4%; PC8 = 2.1%; PC9 = 1.7%; PC10 = 1.4%; PC11 = 1.0%; following 17 PCs each less than 1%). The morphospace was created by plotting the first two PCs, since they covered the most variation in the data (62.4%). The results of the analysis, including the graphical component loadings, are provided in the Supplementary Materials.

PC1 is dominated by the spination of stylets and head shape (Figure 33). Positive values mainly represent slim head capsules and stylets with teeth, while negative values mainly represent head capsules with lateral protrusions and fewer teeth on the stylets (Figure 33). PC2 is dominated by the position of stylets and teeth on the stylets (Figure 33). Positive values mainly represent laterally attaching stylets with median teeth, while negative values mainly represent medially attaching stylets with distal teeth.

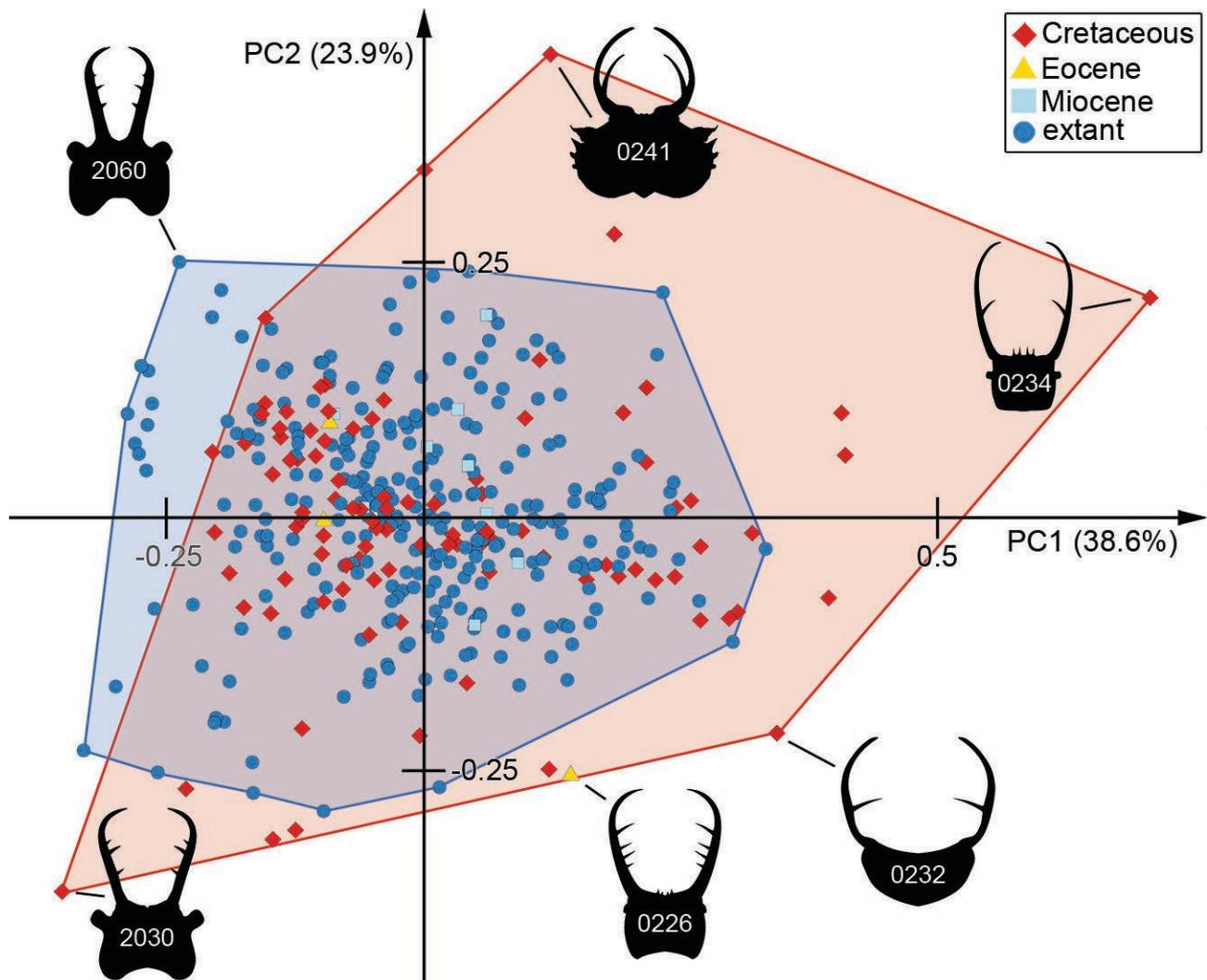


Figure 33. Morphospace is represented by scatter plots of the principal components (PCs) 1 and 2 of the head capsule and stylets with teeth.

All four time slices are represented in this morphospace. The cluster of Cretaceous specimens plots throughout the whole morphospace, showing some outliers towards the top right and bottom left corners, indicating some long stylets and wide heads. One Eocene representative plots at the bottom of the morphospace, showing long stylets with multiple teeth; the other two plot in the centre. The Miocene representatives plot around the centre of the morphospace as well. The extant representatives also cover large areas of the morphospace but show some exclusivity towards the top left, indicating head capsules extending postero-laterally with stout stylets.

When considering all 27 dimensions of the morphospace, we found significant differences in the size of occupied morphospace between the Cretaceous and extant representatives (Welch Two Sample *t*-test; *p*-value < 0.001), with the Cretaceous specimens occupying a larger area. Similarly, we found that the two groups were significantly different in their position within the morphospace (Welch Two Sample *t*-test; *p*-value < 0.001).

3.9. Morphospace of the Stylets with Teeth

The PCA of the EFA of the stylets with teeth resulted in nine effective PCs (PC1 = 25.3%; PC2 = 17.7%; PC3 = 14.6%; PC4 = 10.4%; PC5 = 6.3%; PC6 = 5.8%; PC7 = 4.3%; PC8 = 3.7%; PC9 = 2.8%). The morphospace was created by plotting the first two PCs, since they covered the most variation in the data (43.0%). The results of the analysis, including the graphical component loadings, are provided in the Supplementary Materials.

PC1 is dominated by the spination of stylets (Figure 34). Positive values mainly represent stylets without teeth, while negative values mainly represent stylets with teeth (Figure 34). PC2 is dominated by the size of the teeth on the stylets and the curvature (Figure 34). Positive values mainly represent strongly curved stylets with long teeth, while negative values mainly represent straight stylets with short teeth.

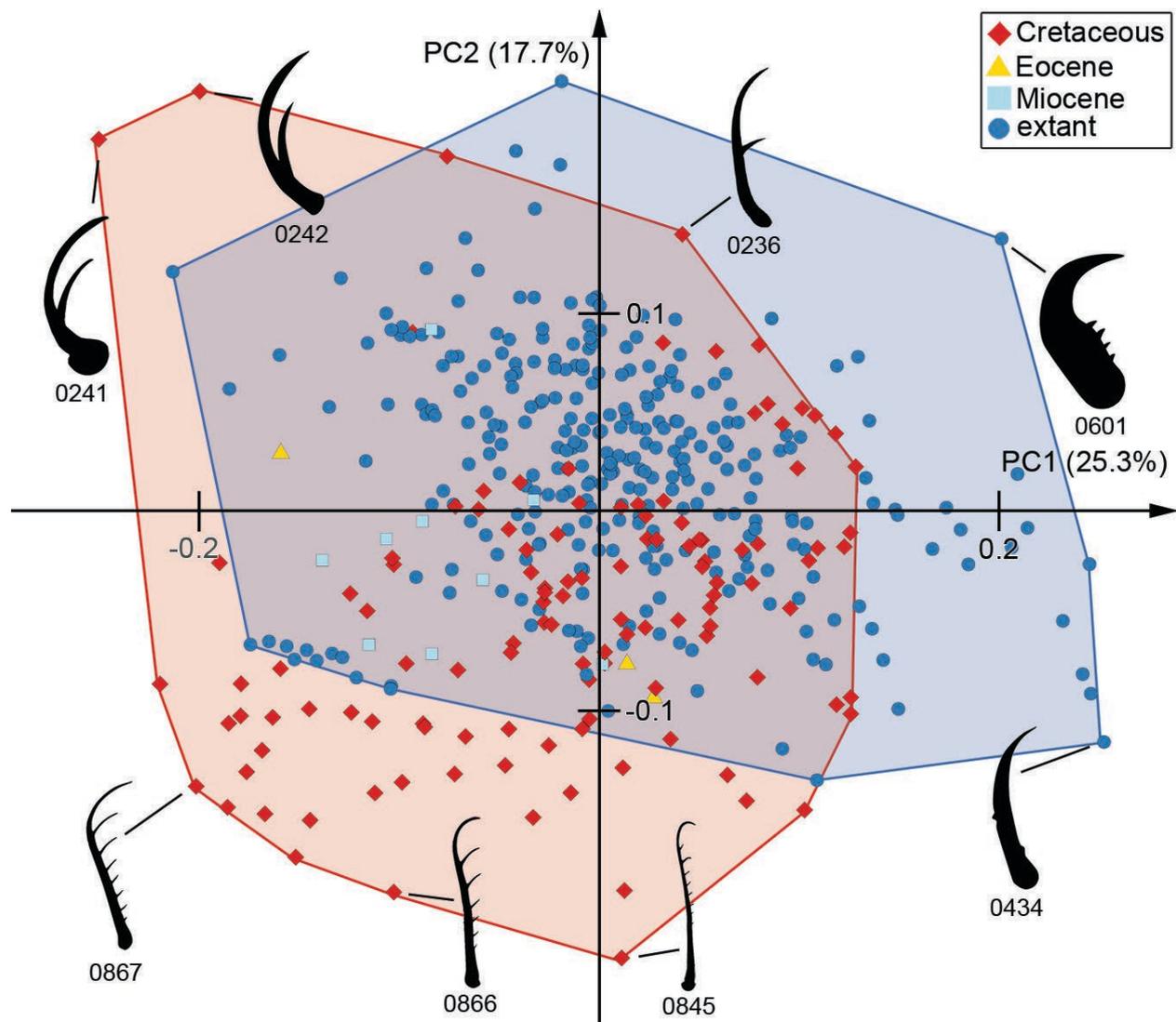


Figure 34. Morphospace is represented by scatter plots of the principal components (PCs) 1 and 2 of the stylets with teeth.

All four time slices are represented in this morphospace. The cluster of Cretaceous specimens plots mainly on the bottom of the morphospace, with some outliers on the top left, indicating long and straighter stylets with many short teeth. The Eocene representatives plot within the main cluster in the morphospace. The Miocene representatives plot at the bottom left of the morphospace, indicating straighter stylets with smaller teeth. The extant representatives cover large areas of the morphospace, but mainly on the top, indicating more curved stylets with fewer but longer teeth.

When considering all nine dimensions of the morphospace, we found significant differences in the size of occupied morphospace between the Cretaceous and extant representatives (Welch Two Sample *t*-test; *p*-value < 0.001), with the Cretaceous specimens occupying a larger area. Similarly, we found that the two groups were significantly different in their position within the morphospace (Welch Two Sample *t*-test; *p*-value < 0.001).

4. Discussion

4.1. Identity of the Specimens

The newly reported fossil represents several distinct morphotypes. The first morphotype is that of *Macleodiella*, for which one species has been formally described [75], but the material likely includes more than one species [94]. Specimens can be well recognised based on elongate head capsules and stylets with three teeth, the distal two teeth being closer together. The second morphotype has been nicknamed superfang type 1 [80,85]. The stylets are much longer than the head capsule, and there are numerous smaller teeth on the stylets, mostly eight. The third morphotype is superfang type 2 [85]. The main difference from superfang type 1 is a lower number of teeth, usually six, that are quite prominent. The fourth morphotype has been formally described as *Kuafupolydentes hui* [95]. It is characterised by a few short and especially blunt teeth. A new, fifth morphotype is reported here; it is characterised by an overall appearance resembling owlions, concerning a rather broad head and an absence of the empodium, but additionally bearing four or five teeth on the stylets.

The first three morphotypes bear empodia on their legs, a plesiomorphic character today only present in long-nosed antlions, i.e., larvae of Psychopsidae. Therefore, these three morphotypes occur in species that are part of the early divergence of Myrmeleontiformia [75,80,85]. The other two morphotypes may already be more derived, but they also represent now extinct morphotypes of Myrmeleontiformia with tooth-bearing stylets.

4.2. A New Detail of *Macleodiella*-Type Larvae

The specimens reported here did not add new morphological details in comparison to earlier studies [75,94]. Yet, a new aspect reported here is the co-occurrence of several specimens in close proximity—four to six specimens in a single and rather small amber piece—indicating that these specimens must have been close together in real life. Such cases of several lacewing larvae in a single amber piece are rare [105], as lacewing larvae in general do not aggregate; instead, they show strongly aggressive behaviour including cannibalism (see discussion in [182]). The most common case of the preservation of several specimens together in one amber piece would be a hatching event. However, the new specimens are larger than the known smallest specimens, making a hatching event an unlikely explanation. Some larvae of lacewings do perform group defence ([36], their Figure 41), but only in stage 1 larvae [182,183]. A possible reason for later-stage larvae being preserved together could be a relatively high density of such larvae in a certain area.

4.3. New Details on Superfang Type 1 Larvae

The original specimen of the superfang type 1 [80] was incompletely preserved, concerning most appendages besides the stylets. The new specimens reported here demonstrate that the antennae are quite long, longer than the stylets, and that the legs bear prominent trumpet-shaped empodia.

4.4. New Details on Superfang Type 2 Larvae

Most newly reported specimens of superfang type 2 largely resemble the original three specimens [85]. All of them appear to represent moult remains (exuvia), preserving mostly the prominent stylets in an undistorted way. This preservation makes it challenging to estimate other aspects of their morphology. The sometimes preserved trunk end resembles that of superfang type 1 larvae in being slender and likewise setose. Yet, different from superfang type 1, many setae seem to have been arising from bulbous protrusions.

The most remarkable aspect of the new larvae is that we have compiled here at least 31 specimens (possibly 33) of this type. This number indicates that this type of larva was, in fact, quite common. The assumption that it was a common form makes it even more unusual that all these finds are exuviae. With our current knowledge, we cannot offer a biological explanation for this observation.

4.5. A New Type of Larva: 4–5 Teeth

The new type of larva, like superfang type 2 larvae, seems to be only represented by exuviae (the question remains as to why). Unlike the superfang-type larvae and the *Macleodiella*-type larvae, the 4–5 teeth larvae appear to lack an empodium, a more derived character state. Also, the broader head region is likely a more derived state, possibly indicating a closer relationship either to Nymphidae or even owlions.

4.6. Tokogenetic Relationships

As pointed out, all five morphotypes treated here are larvae of early lineages of Myrmeleontiformia that are now extinct. This also accounts for different fossil adults, which have been formally attributed to distinct groups such as Kalligrammatidae or Babinskaiidae [41,111–113,184].

It seems therefore likely that some of the five larval morphotypes discussed herein, as well as larvae formally described as *Cladofer huangi* [75] and *Ankyloleon* [76,98], represent larval stages of Kalligrammatidae or Babinskaiidae. Hence, any taxonomic treatment of the fossil larvae remains challenging. For connecting the larvae of fossil holometabolans to the adults, pupae are crucial. Ideally, these should be pupae preserved together with larval exuviae and pharate adults, or adults preserved in the process of eclosion [185]. So far, pupae of lacewings are extremely scarce in the fossil record [186], making such connections currently non-existent.

4.7. Diversity of Shapes through Time

As for earlier comparisons [44], the analysis through time is confined to a comparison of modern-day fauna to that of the Cretaceous, as sample sizes for the other time slices are still too small. When considering all three analysed subsets (head + stylet, head capsule, and stylet), the morphological diversity of the Cretaceous larvae is always significantly larger than that of the modern-day fauna, indicating severe losses of ecological functions after the Cretaceous. The positions of the occupied areas in the morphospaces are different as well, indicating that not only losses occurred but also that some new morphologies evolved after the Cretaceous.

For the head with stylets, a large part of the morphospace is only filled by Cretaceous larvae (in the lower left, upper middle, and upper right; Figure 33). These areas are occupied by larvae of Nymphidae, but also some superfang type 2 larvae. On the contrary, there are also areas only occupied by extant larvae (in the upper left), representing morphologies that must have evolved after the Cretaceous. All these specimens are owlions, more traditionally interpreted as owlflies (“Ascalaphidae”).

For the head capsule alone, the picture is not significantly different. In the upper left corner of the morphospace, extant owlions occupy an area where no fossil larvae plot (Figure 32). The lower left and upper right areas are occupied only by fossils; also in this case, some larvae of Nymphidae plot here, but much more of the *Macleodiella*-type larvae.

For the stylets, there are smaller areas in which only extant larvae plot (middle right; Figure 34). These specimens are long-necked antlions, i.e., larvae of Crocinae (thread-winged lacewings), that bear smaller teeth. Some areas are only occupied by fossils, which are again larvae of Nymphidae (upper left), but mostly by the larval types treated in this contribution (lower right).

Overall, the comparison indicates that the significant loss of lacewing diversity since the Cretaceous included the loss of many of the morphotypes treated in more detail in this study. The loss of these morphotypes also indicates a significant loss of specific ecological functions that were fulfilled by larvae with these specific morphologies.

4.8. Convergent Evolution

When looking especially at the analysis of head and stylet, a further point needs to be discussed. Many of the here-treated fossil larvae plot close to the centre of the morphospace, slightly to the right. From the modern side, the owlion larvae plotted here are those traditionally treated as antlions (“Myrmeleontidae”). The similarity seems to account for more elongate head capsules and relatively long stylets. As argued earlier [187], the slender heads and longer stylets have more reach but less maximum force, and it appears that there was significant selection against this type of morphology. It appears that comparable morphologies have been lost in several lineages [187].

Yet, if indeed many selective pressures act against this type of morphology, why should this type of morphology re-appear in modern-day antlions? The main weakness of low-force stylets is that it is necessary to hunt smaller prey items, but to counteract the lower body mass of each item, more of them need to be caught. This strategy can prove challenging for an ambush predator, as it demands a high number of prey items passing close by the predator.

However, many extant antlion larvae build an additional structure to catch prey, a funnel-shaped pit [188–192]. These pits increase the area significantly in which prey items become available compared to “normal” ambush predators, partly circumventing the challenge of having sufficient prey items nearby.

Could the superfang larvae and other early myrmeleontiformian larvae also have used such pits? This seems unlikely. Antlion larvae have special setae for digging [193,194]. Such setae seem absent in the early larvae. *Macleodiella*-type larvae, for example, seem to be more or less “naked” with little body setation. Superfang type larvae (1 and 2) have prominent setae, yet these appear more similar to setae used for camouflaging (as, for example, known in certain modern-day aphid lions, i.e., larvae of Chrysopidae; [69,195–197]).

4.9. Resilience in Lacewing Larvae

Convergent evolution could buffer losses in diversity to certain degrees through “redundancy” [198–200]. In the case of lacewing larvae, we can see here, like in earlier studies [44], that convergent evolution of larval forms indeed led to the re-appearance of morphologies that went extinct after the Cretaceous. Yet, this post-Cretaceous radiation and diversification, especially of owlions, could not fully reinstall the diversity of myrmeleontiformians that resulted from the radiation before the late Cretaceous. The latter also produced numerous “experimental morphologies” [78]. The larvae dealt with in this study could be interpreted to fall into this “experimental” category.

The impossibility of recovering the diversity was most likely due to the losses in various myrmeleontiformian ingroups, which seem to have simply been too drastic. This holds true especially for the lineages of Psychopsidae and Nymphidae, but also in other early diverging lineages of the antlion-like lacewings, including those of the larvae of *Macleodiella*, superfang (1 and 2), *Kuafupolydentes*, and 4–5 teeth types.

It remains to be tested whether larval forms of other lineages of Holometabola that diversified after the Cretaceous could have taken over the functions that were performed by lacewing larvae in the Cretaceous. For example, ground beetles do not seem to have

been diversified in the Cretaceous [201–203]. Alternatively, the specific ecological functions that got lost could have been coupled, for example, to now extinct prey items.

Supplementary Materials: The following supporting information can be downloaded: <https://www.mdpi.com/article/10.3390/d15121219/s1> and <https://doi.org/10.5281/zenodo.10276908> (accessed on 6 December 2023), Supplementary File S1. Table listing information on all specimens. File S2. Outcome of the principal component analysis of stylets. File S3. Graphical representation of the factor loadings of the principal component analysis of stylets. File S4. Outcome of the principal component analysis of heads and stylets. File S5. Graphical representation of the factor loadings of the principal component analysis of heads and stylets. File S6. Outcome of the principal component analysis of heads. File S7. Graphical representation of the factor loadings of the principal component analysis of heads. File S8. Files resulting from the shape analysis of the stylets, including chain codes, aligned shapes, and principal component analyses. Figures 1–31 in high resolution are available at <https://doi.org/10.5281/zenodo.10276908>.

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