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Authors: Zippel, Ana, Haug, Carolin, Iturbe-Ormaeche, Beñat Yáñez, and Haug, Joachim T.

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Diversity of archostematan beetle larvae through time with new fossils

Ana Zippel, Carolin Haug, Beñat Yáñez Iturbe-Ormaeche & Joachim T. Haug

Abstract

Archostemata is a species-poor group of beetles. However, the morphological diversity of the group is still not completely grasped since many ingroups are only known by the adult representatives. *Micromalthus debilis* is often the most discussed representative of this group in literature and stands as an example of a complex and unique life cycle. The rest of the known representatives do not have such specialised life cycles. However, in many groups, only the ecology of the adults is known and the few known larvae show specialisations of softwood-borers. Here we summarise the known larvae of Archostemata and report a new fossil from Eocene Baltic amber. The new specimen shows many morphological characters known from modern larvae of Archostemata (e.g., the broad head or the distinct posteromedian indentation of the head capsule) and is highly likely a larval representative of the group, and therefore, represents the first larva of Archostemata from the Eocene. We also study and discuss two additional unidentified fossil specimens with similar body outlines originating from Cretaceous Myanmar amber. Additionally, we analysed all the available specimens with quantitative methods, both fossil and modern, new and from literature.

Keywords: Archostemata; *Cretomalthus*; Micromalthidae; Cupedidae; shape analysis.

1. Introduction

Coleoptera (beetles) is an extremely species-rich group with more than 380.000 formally described species (Zhang 2011, 2013; McKenna et al. 2019; Boudinot et al. 2023). However, this extreme taxonomic diversity is unevenly distributed within the group. In comparison, Polyphaga comprises over 320,000 described species (Beutel & Leschen 2005), whereas the lineage of Archostemata is represented by only about 40 species in the extant fauna (Lawrence 1999; Hörnschemeyer 2016d).

In the modern fauna Archostemata comprises *Crowsoniella relicta* (single species of Crowsoniellidae; Hörnschemeyer 2016a), 31 species of Cupedidae (Hörnschemeyer & Yavorskaya 2016), *Micromalthus debilis* (single species of Micromalthidae; Hörnschemeyer 2016b), six species of Ommatidae (Hörnschemeyer & Beutel 2016) and *Sikhotealinia zhiltzovae* (single species of Jurodidae; Hörnschemeyer 2016c), in total 40 extant species. Additional adult fossils of extinct beetle lineages with morphological characters known from modern archostematan beetles were reported already from the Permian (Ponomarenko 1969, 2003; Yan et al. 2020; Boudinot et al. 2023). Ponomarenko (1969) interpreted an extinct lineage of beetles with such morphologies, that of Tshekardocoleidae, as part of Archostemata s.l. However, the lineage was later interpreted as the earliest branching lineage of the early coleopterans by Beutel (1997), Ponomarenko (2003), Beutel et al. (2008), and Boudinot et al. (2023) and the similarities between the archostematans and the early beetles were discussed only as plesiomorphies (Beutel 1997; Beutel et al. 2008, 2019). Together with other early lineages of Coleoptera (such as Permocupedidae), Tshekardocoleidae played an important role in the early diversification of beetles (Boudinot et al. 2023) and their phylogenetic position influences the position of Archostemata and other beetle groups on the phylogenetic tree of beetles (Boudinot et al. 2023). The position of Archostemata is still debated and has been differently interpreted by several authors (Beutel 1997; Beutel et al. 2008, 2019, Lawrence et al. 2011; McKenna et al. 2015, 2019; Cai et al. 2022; Boudinot et al. 2023). Therefore, the fossil record of Archostemata considerately enhances the understanding of Coleoptera evolution. Unambiguous representatives of Archostemata are known from the Mesozoic, when the species diversity of the group was the highest (Hörnschemeyer 2016d; Jarzembowski et al. 2017, 2018, 2019; Li et al. 2019, 2020; Song et al. 2022).

Yet, many aspects of the biology of archostematan beetles are still largely unknown. As for many beetles and other groups of Holometabola, archostematans spend a considerable part of their life cycle in their larval forms, which differ significantly in morphology and ecology from their corresponding adults. Most of the adults of Archostemata have an incompletely sclerotised elytra with window-like punctures or reticulation. The body is covered with scales, often with colourful patterns. The body of larvae of Archostemata is elongated with legs with six elements (Hörnschemeyer 2010). All larvae have a head capsule with a posterior rim that is concave with an indentation medially (posteromedial emargination) and a strong inner cuticular thickening of the medial part of the head capsule (endocarina). Additionally, the moulting suture of the head (ecdysial suture) is reduced or absent. The mandibles of the larvae have distinct teeth and distinct cutting areas of the mandibles (Yavorskaya et al. 2015). However, larvae remain unknown for most archostematan species (Hörnschemeyer 2016d), for example, the larvae of *C. relicta* and *S. zhiltzovae* and most species of Cupedidae and Ommatidae (Hörnschemeyer 2016a, 2016c; Hörnschemeyer & Beutel 2016; Hörnschemeyer & Yavorskaya 2016). Extant larvae are only known for *M. debilis* (Hörnschemeyer 2016b) and five species of Cupedidae (Hörnschemeyer & Yavorskaya 2016); in addition, larvae, presumably of a species of *Omma*, have been reported for Ommatidae (Lawrence 1999; Grebennikov 2004).

Known larvae of Cupedidae feed on fungus-infected wood (Hörnschemeyer & Yavorskaya 2016). The entire (and very complex) life cycle of *M. debilis* including the larval phase (with so-called triungulin larvae with legs and legless cerambycoid and curculionid larvae) takes place in rotting wood (Hörnschemeyer 2016b; Perotti et al. 2016). For the larvae of Ommatidae, it has been generally assumed, based on the collection data of the adults, that they are also associated with dead wood or tree roots (Hörnschemeyer 2010). Hence it appears that the representatives of Archostemata were coupled to the evolution of wood-consuming larvae. This is an important ecological function that helps to cycle carbon back into the system.

The fossil record of wood-borer larvae, including archostematan larvae is still scarce (Peris & Rust 2020; Haug et al. 2021). A single larva possibly related to *M. debilis* has been reported from ca. 130-million-year-old Lebanese amber (*Cretomalthus acracrowsonorum* Kirejtshuk & Azar, 2008). The single specimen of *C. acracrowsonorum* would therefore be a fossil representative of another species of Micromalthidae. *M. debilis* has also been reported from the fossil fauna. Rozen (1971) reported three first larval stages of the species from Mexican Chiapas amber of the late Oligocene or the early Miocene. Unfortunately, there are no images of these specimens; hence, these important finds cannot be further considered here. Additionally, Kirejtshuk (2020) reported a single larva from deposits from Tshekarda, Russia (ca. 279–272 million years old). He interpreted the specimen as a larva of Tshekardocoleidae based on a general appearance similar to extant larvae of Cupedinae (e.g., the shape of the head capsule and shape of the truncated median process at the trunk end). However, the specimen does not have many morphological characters accessible and is possibly the representative of another insect group (Boudinot et al. 2023).

Here we summarise the known and figured larvae of Archostemata, and describe a new fossil larva. We also discuss two additional unidentified fossil specimens from Cretaceous Myanmar amber with similar body outlines and some morphological characteristics of larvae of Archostemata. Additionally, we analysed with quantitative methods all the available specimens, both fossil and modern, new and from literature.

2. Material and methods

2.1. Material

In total, three new pieces of amber were included in this study, PED 0904, PED 0964 and PED 1748. The pieces are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München, Germany. PED 1748 originates from approximately 35–40-million-year-old Eocene Baltic amber (Figs. 1–3) and PED 0904 and PED 0964 originate from approximately 100-million-year-old Cretaceous Myanmar amber (Suppl.-Fig. 1). The new specimens were legally acquired from the trading platform ebay.com from the traders rmvveta (Baltic amber; see also ambertreasure4u.com) and burmite-miner (Myanmar amber).

Here we describe, identify and analyse the new fossil PED 1748 with quantitative methods. Together with the fossil PED 1748 we also analyse the body outlines of two unidentified new fossils, PED 0904 and PED0964, the larvae of Archostemata from the literature, and the possible larva of Tshekardocoleidae. The new unidentified fossils were included in the shape analysis due to their overall similar habitus to the known larvae of Archostemata. Unfortunately, the lack of accessible details did not allow further identification of the specimens based on the morphological characters.

2.2. Documentation methods

All of the new specimens used in the analysis were documented on Keyence VHX-6000 digital microscope in front of white and black backgrounds. The specimens were also documented with different illumination settings: cross-polarised co-axial and low-angle ring light (Haug et al. 2013a, 2018). All images were recorded as composite images (Haug et al. 2008, 2011; Kerp & Bomfleur 2011) with the HDR function (cf. Haug et al. 2013). In addition, the specimen PED 1748 was documented as a stack of images and was processed following Haug et al. (2009), resulting in stereo images. All of the images were further processed with Adobe Photoshop CS2. We used the stereo anaglyphs from the stacks (Suppl.-Figs. 2, 3) for interpreting the details of overlapping mouthparts and the structures of the head capsule (Fig. 3). Drawings of specimens from the literature were drawn in the free software Inkscape. The outlines for the SHAPE analysis were also drawn in Inkscape.

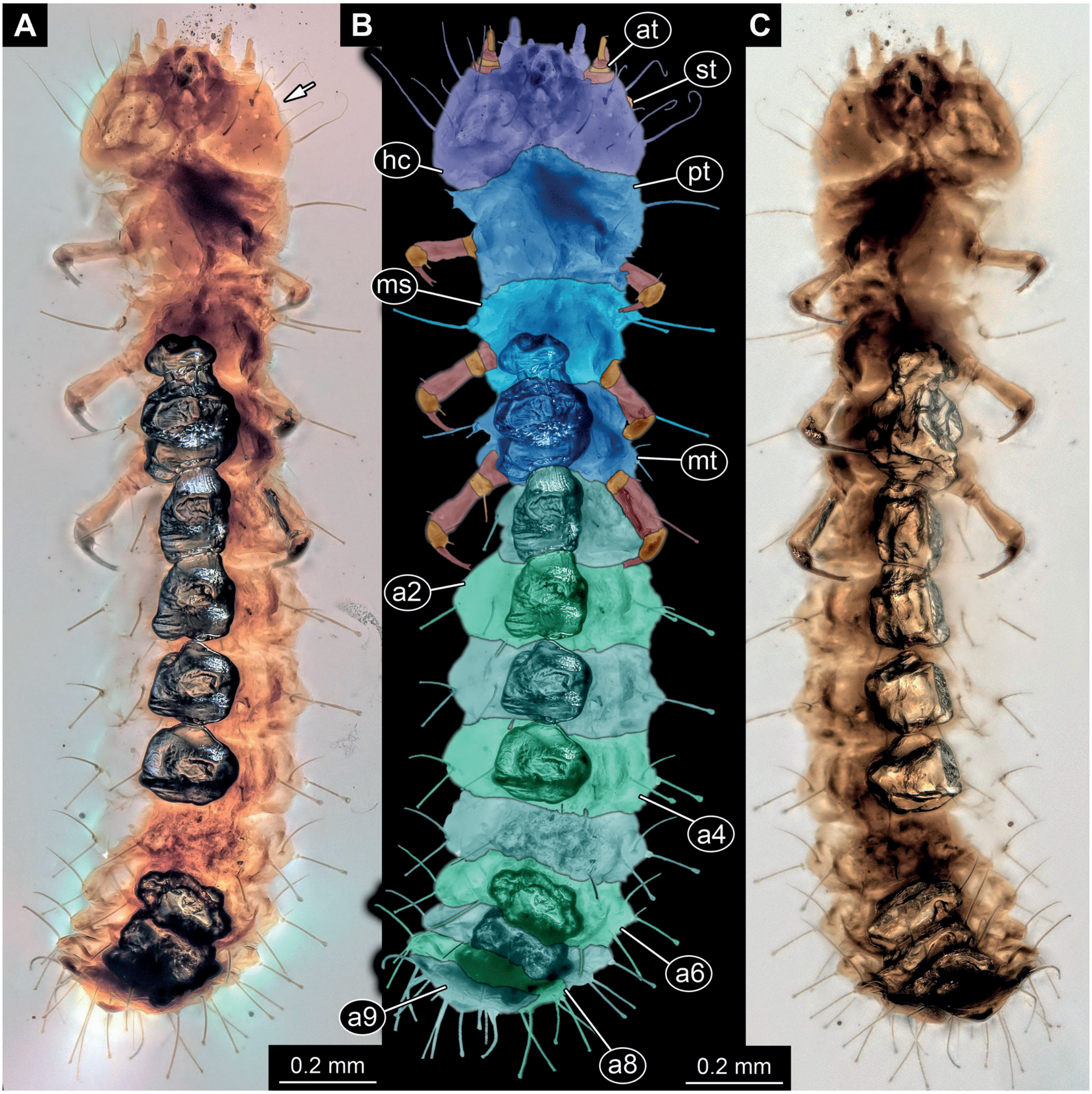

Fig. 1. Fossil specimen PED 1748, larva of Archostemata. **A** – Habitus in dorsal view, photographed with polarised light on white background (a white arrow marks a stemma); **B** – colour-marked version of **A**; **C** – habitus in ventral view, photographed with ring light on white background. Abbreviations: a2–9 = abdomen segments 2–9; at = antenna; hc = head capsule; ms = mesothorax; mt = metathorax; pt = prothorax; st = stemma.

2.3. Shape analysis

Beetle larvae preserved in amber often do not have many identifying characters accessible due to a damage, other inclusions, or Verlumung. However, the outline of, for example, a body, processes, or mouth parts showed to be characteristic for certain insect groups. The larvae of Archostemata, especially the larvae of the ingroup Micromalthidae, show differences in the habitus morphology not only considering their antennae, mouth parts or legs but also the body shape. We compare here the shape of the head, thorax and abdomen in extant and fossil larvae

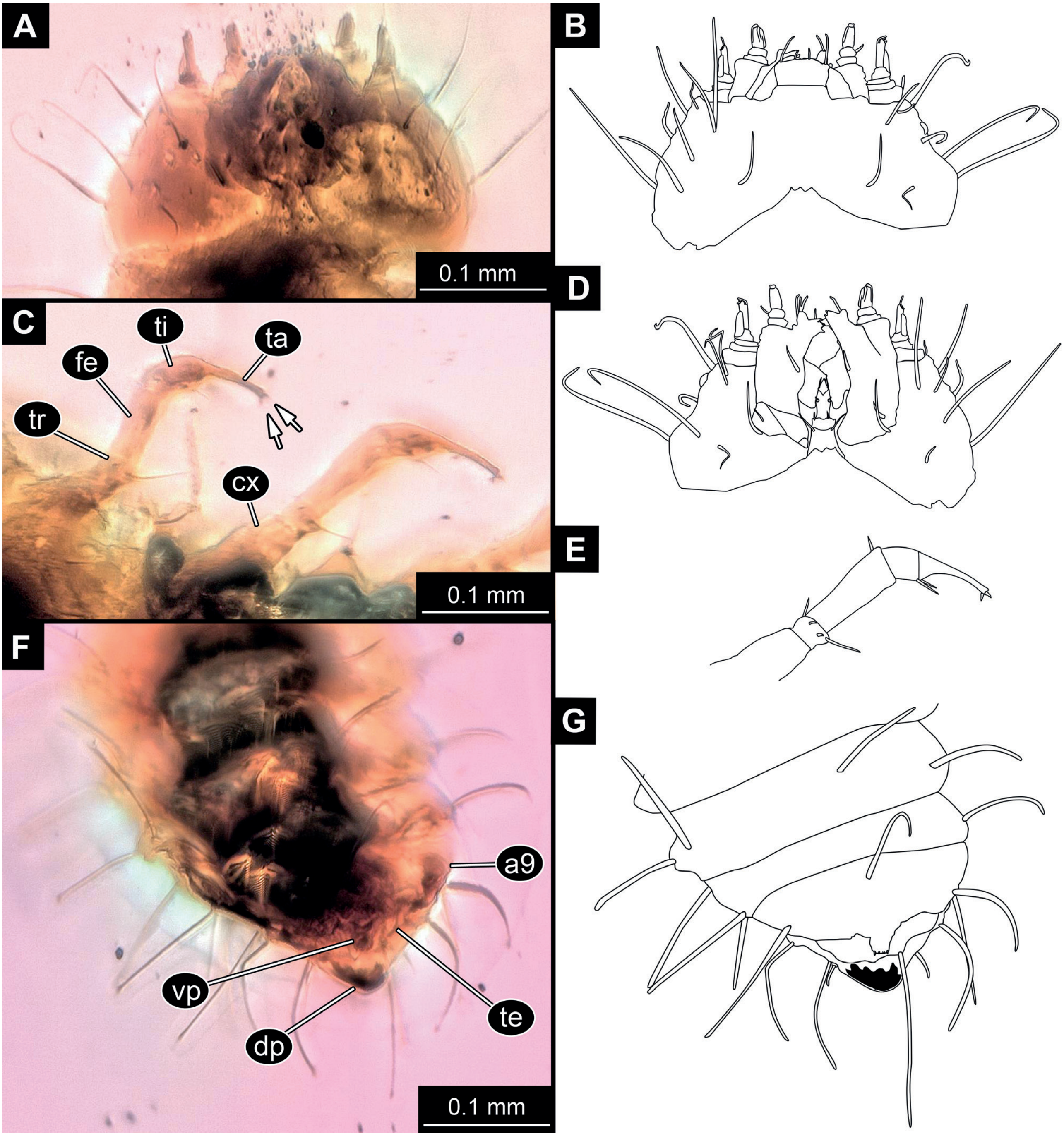

Fig. 2. Close-ups of fossil specimen PED 1748. **A** – Close-up of head in ventral view; **B** – drawing of head in dorsal view (based on the stereo images in Suppl.-Fig. 2); **C** – close-up of legs on pro- and mesothorax (white arrows mark two claws) in ventral view; **D** – drawing of head in ventral view (based on the stereo images in Suppl.-Fig. 2); **E** – drawing of a leg of metathorax in dorsal view (based on Fig. 1C); **F** – close-up of trunk end with a small ventral and strongly sclerotised dorsal process in ventral view; **G** – drawing of trunk end in ventral view. Abbreviations: a9 = abdomen segment 9; cx = coxa; dp = dorsal process; fe = femur; ta = tarsus; te = trunk end; ti = tibia; tr = trochanter; vp =ventral process.

of Archostemata, possible fossil larva of Tshekardocoleidae (with similar body outline to some larvae of Cupedidae), and two unidentified beetle larvae with similar body outline (large head in comparisson to entire body, triangular-shaped posterior end of abdomen). Three of the analysed larvae are the new fossils PED 1748, PED 0964, and PED 0904. Unfortunately, the identifying characters of mouth parts or trunk end of PED 0964 and PED 0904 are obscurred and inaccessible and therefore the specimens remain not further identifiable than to the level of Coleoptera. In total, we included 27 body outlines in the analysis: one specimen from the Permian, three from the Cretaceous, one from the Eocene and 22 extant specimens. The outlines were redrawn in dorsal or ventral view in Inkscape. First, we drew the outline of the body, filled it with colour into a shape and if needed the shape of the specimen was straightened segment by segment as described in Haug et al. (2021). We only used one half of each shape and saved them as bitmap files. The halfed shapes make alignment in the SHAPE software pipeline easier because the halfed shapes have more similar longest eclipses (Braig et al. 2024a). We then processed the bitmap files with the program package SHAPE (National Agricultural Research Organisation of Japan; Iwata & Ukai 2002). The program analyses the data with an Elliptic Fourier Analysis and a Principal Component Analysis (PCA). Before the analyses themselves, we alligned the specimens within the program based on the option of the longest radius with the marker set at the tip of the trunk end of the body. Each specimen was manually re-checked for alignment to avoid any error due to misalignment (Braig et al. 2019, 2024b). We used the resulted PC values to plot the first two most effective dimensions orthogonal to each other.

3. Results

3.1. Description of specimen PED 1748

Amber piece with a single beetle larva. Total body length ~1.45 mm. Body elongate, slightly flattened dorso-ventrally, parallel-sided (not tapering or widening; Fig. 1A–C), differentiated into anterior head and posterior elongated trunk. Head prognathous (mouth parts facing forwards; Fig. 1), head capsule semi-circular in dorsal view with posterior rim with concave indentation medially, at widest point wider than medially long, 2.2× (~0.14 mm long). Dorsal moulting line (ecdysial suture) and thickening (dorsal endocarina) are not discernible. One stemma discernible, on right lateral side of head capsule in dorsal view (Fig. 1B, Suppl.-Fig. 2A, B: white arrow). Lateral sides of head capsule bear at least four long setae and several shorter setae each (Fig. 2A, B, D). Labrum (derivative of ocular segment) subrectangular in dorsal view, together with subhexagonal clypeus as clypeo-labral complex, clypeo-labral suture discernible (Fig. 2B, 3, Suppl.-Fig. 2A, C). Anterior rim of labrum bears four simple setae (Fig. 2B, 3, Suppl.-Fig. 2A, C), two lateral ones longer than median ones. Antennae (appendages of post-ocular segment 1) with four elements (antennomeres) discernible (Fig. 2A–C, 3, Suppl.-Fig. 2A, C), head capsule longer than antennae, 2.3× (antennae ~0.06 mm long). Proximal (antennomere 1) and two middle elements (antennomere 2 and 3), wider than long, proximal element ~0.04 mm wide. Element 3 (antennomere 3) with sensory appendix, as long as the element 3 is wide. Most distal element (antennomere 4) almost as long as all three other elements together (antennomeres 1–3), bearing one longer seta at the very tip and possibly several shorter ones close by (Fig. 3: at Suppl.-Fig. 2B). Intercalary segment (post-ocular segment 2) without externally recognisable structures.

Mandibles (appendages of post-ocular segment 3) strongly sclerotised, ~0.09 mm long, with three teeth distally discernible (Fig. 3: white arrows, Suppl.-Fig. 2D–G). Maxillae (appendages of post-ocular segment 4) ~0.13 mm long, with several major parts discernible: rectangular in ventral view lateroproximal part, wider than long, with several sclerites (possibly subdivided cardo); rectangular in ventral view middle part (stipes), longer than wide, with median endites (probable galea bearing distal setae and bilobed lacinia) and a distal palp with at least three elements (palpomeres; whole palp ~0.08 mm long). Most proximal and middle elements (palpomeres 1 and 2) wider than long, middle bearing seta antero-laterally; most distal element (palpomere 3) longer than the proximal and middle two together, bearing multiple short setae at the very tip. Labium (conjoined appendages of post-ocular segment 5) longer than wide, ~0.14 mm long, with several parts discernible, parted with abaxial lines into: proximal part (postmentum), bears one strong seta laterally on each side; middle part (mentum), and distal part (prementum) with disto-laterally two small labial palps, possibly with two small elements each. Labium at the functionally anterior end with ligular sclerite (ligula). Ligula triangular at the functionally anterior tip in ventral view (Fig. 3, Suppl.-Fig. 3).

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso- and metathorax). Pronotum (tergite of pronotum) subpentagonal in dorsal view, wider than long, 1.6× (~0.14 mm long), anterior rim medially convex, posterior rim narrower than anterior (Fig. 1A–C). Meso- and metathorax similar, rectangular in dorsal view, smaller than prothorax. Mesothorax wider than long, 2.1× (~0.11 mm long). Metathorax wider than long, 2.3× (~0.11 mm long) (Fig. 1A–C). Each thoracic segment with a pair of locomotory appendages (legs). Legs ~0.23 mm long (Figs. 1B, 2C, E), with six elements each: coxa, trochanter, femur, tibia, tarsus and claws. Trochanter bears

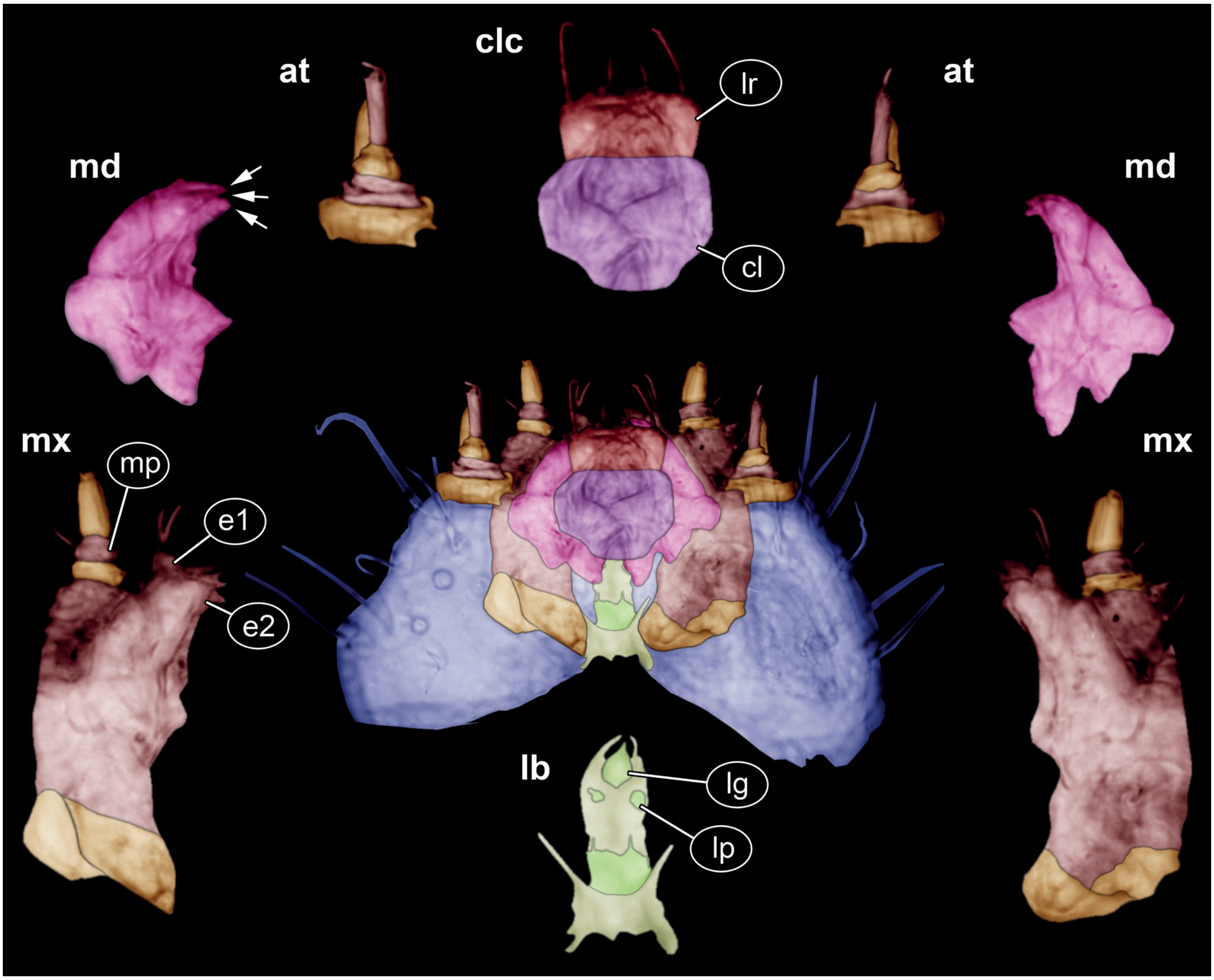

Fig. 3. Colour-marked close-up of head of fossil specimen PED 1748 in ventral view (based on stereo images from Suppl.-Fig. 2); mouth parts are additionally presented separated from the head capsule. White arrows point out three teeth of mandible. Abbreviations: at = antenna; cl = clypeus; clc = clypeo-labral complex; e1–2 = endite 1–2; lb = labium; lg = ligula; lr = labrum; lp = labial palp; md = mandible; mp = maxillary palp; mx = maxilla.

two setae, two small spines discernible in between. Femur bears one longer spine-like seta latero-distally. Tibia bears two-spine-like setae close together medio-distally. Two claws subequal in length (~0.01 mm) (Fig. 2C, E). Pronotum bears laterally one long seta per side, meso- and metanotum each bear two setae per side, of which one seta more ventral. Longer setae somewhat wider at the distal end than in the middle.

Abdomen with nine discernible segments and partially accessible trunk end (Fig. 2F, G). Tergites of segments 1–8 subsimilar, subhexagonal in dorsal view, middle of lateral rims slightly drawn outwards, wider than long (between 0.07–0.13 mm long and between 0.24–0.3 mm wide). Abdomen segment 9 subtriangular in dorsal view, wider than long, 1.7× (~ 0.14 mm long), with tergite with heavily sclerotised posteromedian process (Figs. 1A–C, 2F, G). Ventrite of abdomen segment 9 in ventral view with posteromedian process, narrower than posteromedian process of tergite, distally with four small spine-like setae (Fig. 2F, G). Paired processes of abdomen segment 9 (urogomphi) not discernible. Abdomen segment 1 bears laterally one long seta per side (possibly not all discernible) and one long seta ventrally. Abdomen segments 2–8 bear laterally three setae per side, of which one more ventrally and one more dorsally are longer than third shorter seta in between, also each segment bears two ventral long setae (Fig. 1C). Tergite of abdomen segment 9 with multiple lateral setae and at least one pair of setae ventrally (Fig. 2F, G). Longer setae somewhat wider at the distal end than in the middle. No details of trunk end observable.

3.2. Larvae of Archostemata in literature

Here we list sources that described and visualised larvae of Archostemata. The list is in chronological order and provides information on whether the image is an original, an adaptation or a copy. We used the specimens of larvae with enough details and either ventral or dorsal overview (numbered under Specimen nr.) as templates for our schemes (Fig. 4) and outlines for the SHAPE analysis.

1) Snyder (1913) provided numerous images (drawings and micrographs) of different developmental stages of *Tenomerga cinerea* (in the text under an old synonym *Cupes concolor*; Cupedidae). Among these are three overview micrographs of a larva of *T. cinerea* in ventral, lateral and dorsal views (pl. 1, fig. 1c). Since all three views are of the same larva, only the dorsal overview was further considered here (Fig. 4: Specimen 1).

2) Barber (1913a) provided numerous images (drawings and micrographs) of different developmental stages of *Micromalthus debilis* (Micromalthidae). The overview micrograph of a triungulin stage of *M. debilis* in almost perfect ventral view (pl. 3, fig. 2) was further considered (Fig. 4: Specimen 2).

3) Barber (1913b) provided some additional text on the larvae of Archostemata but provided no additional images of outer morphology and could not be further considered here.

4) Böving (1929) provided numerous drawings of *T. cinerea* (in the text under an old synonym *C. concolor*; Cupedidae; pl. 16) and *M. debilis* (pl. 17). Although overview images were provided (pl. 16, fig. E; pl. 17, fig. J), these are in lateral view and could not be further considered here.

5) Böving & Craighead (1931) re-figured (pls. 1, 2) drawings from Böving (1929).

6) Scott (1938) provided numerous drawings of several live stages of *M. debilis* (fig. 1, p. 636), as well as numerous micrographs. The drawings included a dorsal outline of a legless larva (fig. 1a) that was further considered here (Fig. 4: Specimen 3). The micrographs also included images of larvae, yet either the details are not sufficient, or the orientation is not ideal to further consider these here.

7) Fukuda (1938) provided a drawing of the larval stages of *Tenomerga mucida* (in the text under an old synonym *C. clathratus;* Cupedidae). The drawing included two larvae in dorsal overview that we further considered here (fig. 1, Fig. 4: Specimen 4; and fig. 2; Fig. 4: Specimen 5).

8) Pringle (1938) provided numerous drawings of several different larval stages of *M. debilis*. Images included a dorsal overview of a triungulin larva (fig. 1a, p. 278) that we considered here (Fig. 4: Specimen 6) and a cerambycoid legless larva (fig. 2a, p. 281) we further considered as well (Fig. 4: Specimen 7).

9) Scott (1941) cited some larvae of Archostemata but provided no additional images of the outer morphology of our interest and could not be further considered here.

10) Peterson (1957) provided drawings of a legless larva of *M. debilis*, including a dorsal overview (fig. C51K, p. 187) that we further considered here (Fig. 4: Specimen 8). There are several versions of this book, available to our knowledge 1951, 1953, 1957 and 1960. The version available to us was from 1957. Reference to pages and figures may only be correct for this version.

11) Neboiss (1968) provided drawings of the dorsal and ventral habitus of a pupa of *D. varians* (in the text under an old synonym *Cupes varians;* Cupedidae) found in a decayed spruce tree (*Picea abies*). In addition, drawings of separated mouth parts, a leg, a claw and part of the abdomen segment 9 of the larva were also provided. However, a dorsal or ventral overview of a larva was not provided and therefore cannot be further considered here.

12) Ross & Pothecary (1970) provided numerous drawings of a stage one larva of *Priacma serrata* (Cupedidae; figs. 3–9, p. 348). These included a dorsal overview (fig. 3) that we further considered here (Fig. 4: Specimen 9).

13) Rozen (1971) mentioned two larvae were preserved in Mexican amber, yet none of these were figured; therefore, they cannot be further considered here.

14) Kühne (1972) provided numerous images of various larvae of *M. debilis.* Yet, most of the images are not sufficiently detailed to be further considered here, including the triungulin larva in lateral view (fig. 2.1. specimen from the left). We only considered two specimens (fig. 1.b, here in Fig. 4: Specimen 10; and fig. 2.2. specimen from the left, here in Fig. 4: Specimen 11).

15) Crowson (1981) mentioned a larva of *Micromalthus* from Lebanese amber, however no description is provided. Since it is the same larva that was later described by Kirejtshuk & Azar (2008) and they supported the description by multiple photographs this specimen is only considered once (see later).

16) Neboiss (1984) provided multiple images of specimens of Cupedidae, but since only adults were presented, the specimens were not further considered here.

17) Costa et al. (1988) provided several drawings of different developmental stages (pl. 1). Images included a triungulin larva of *M. debilis* in dorsal view (Fig. 4: Specimen 12).

18) Lawrence (1991a) provides a drawing of a larva of *T. cinerea* (in the text under an old synonym *T. concolor*) in dorsal view (fig. 34.67a, p. 299) that we further considered here (Fig. 4: Specimen 13).

19) Lawrence (1991b) provides a drawing of a cerambycoid larva of *M. debilis* in dorsal view (fig. 34.68a, p. 301) and multiple SEM micrographs of different body parts of several specimens of *M. debilis*. The dorsal overview of the larva was further considered here (Fig. 4:

Specimen 14). In the text, Lawrence (1991b) also mentions that there are fossil larvae of *M. debilis* from the Oligocene of Europe among his unpublished material but we did not manage to find those and therefore the specimens were not considered here further.

20) Lawrence (1999) provided drawings of a putative larva of *Omma* sp. (Fig. 4: Specimen 15). Drawings included a dorsal overview (fig. 12, p. 377). For comparison, details of other archostematan larvae were provided as SEM micrographs (figs. 14–16, p. 382), yet it did not include an overview image and can therefore not be further considered here.

21) Philips & Young (2000) provide general descriptions of both, the adults and the larvae, of Micromalthidae. Only a drawing of an adult specimen of *M. debilis* in dorsal view (fig. 1.2, p. 22) is provided and therefore cannot be further considered here.

22) Young (2000) provides general descriptions of both, the adults and the larvae, of Cupedidae. Only the drawings of the adult specimens of *T. cinerea* (fig. 1.1, p. 19) and *P. serrata* (fig. 2.1, p. 20) in dorsal views are provided and therefore cannot be further considered here.

23) Beutel & Hörnschemeyer (2002a) provided several images of different developmental stages of *M. debilis*. Images included an overview drawing of a larva in dorsal view (fig. 2, p. 171) that we further considered here (Fig. 4: Specimen 16).

24) Beutel & Hörnschemeyer (2002b) provided several images of different developmental stages of *Rhipsideigma raffrayi* (Cupedidae). Images included an overview drawing of a larva in dorsal view (fig. 2, p. 54) that we further considered here (Fig. 4: Specimen 17).

25) Grebennikov (2004) provided numerous drawings of larvae of Archostemata. Most of these are drawings of details (e.g., head capsule, mouth parts, legs). A dorsal overview (fig. 74, p. 286) was provided for a later stage larva of *D. varians* (Cupedidae) that we further considered here (Fig. 4: Specimen 18). There are also details available for the head, thorax segments and first and two last units of the abdomen in dorsal view.

26) Grimaldi & Engel (2005) provided several SEM micrographs of different developmental stages of *M. debilis* (fig. 10.5, p. 364). Two images showed: a triungulin larva in dorsal view (fig. 10.5.: the middle left image) that we further considered here (Fig. 4: Specimen 19) and a triungulin larva in ventral (fig. 10.5: middle right image) view that we further considered here (Fig. 4: Specimen 20). Based on the scale and the small differences in the legs' positions and hairs in both specimens we concluded that these are not two overviews of the same specimen. Another drawing shows a fossil larval specimen from Lebanese amber (fig. 10.6, p. 365) that we only considered once based on photographs with more information than the drawing available here (see later under Kirejtshuk & Azar 2008). Grimaldi & Engel (2005: 365) also mentioned archostematan triungulin larvae preserved in Baltic amber and Mexican amber and cite Rozen (1971) for it. However, in Rozen (1971) only the two larvae from Mexican amber are mentioned.

27) Kirejtshuk & Azar (2008) provided numerous images of a fossil triungulin-type larva of *Cretomalthus acracrowsonorum* (possibly Micromalthidae). This included a dorsal overview (fig. 1, p. 18; pl. 1A, p. 19) that we further considered here (Fig. 4: Specimen 21). The specimen in amber is the same fossil specimen previously only drawn by Grimaldi & Engel (2005) and we will only consider it here once. We decided to redraw the specimen after Kirejtshuk & Azar (2008) because the photographs give more information than the drawing in Grimaldi & Engel (2005).

28) Liebherr & McHugh (2009) provided several drawings of larvae of Archostemata. A larva of *T. cinerea* (in the text under an old synonym *T. concolor*) in dorsal view (fig. 15, p. 218) was here redrawn from Lawrence (1991a) and the two larvae of *M. debilis* together with a paedogenic specimen in dorsal view (figs. 16–18, p. 218) were redrawn, what seems to be, after Pringle (1938). Therefore, these larvae were not considered once again.

29) Hörnschemeyer et al. (2010) provided multiple images of fossil adult specimens of *M. debilis* and a schematic life cycle of *M. debilis*, including different larval stages (fig. 5, p. 309) based on Barber (1913a, b) and Scott (1938). Therefore, these larvae were not considered once again.

30) Lawrence et al. (2011) provided images of several species of Archostemata. *M. debilis* was only represented by scanning electron micrographs of details of adults and a larva (figs. 9F, p. 90, 56B, p. 137, 59I, p. 140, 83F, p. 164). No overview of the habitus of a larva was presented and therefore cannot be further considered here. *D. varians* was presented by an overview macrophotograph of the larva in the lateral view (fig. 69D, p. 150). Although an overview image is provided, it is in the lateral view and could not be further considered here. Larva of *T. cinerea* (Cupedidae) was presented only by macrophotographs (head – fig. 64I, p. 145) and scanning electron macrographs (head – figs. 74D, p. 155, 77D p. 158, trunk end – fig. 83E, p. 164) of details. Since there were no overviews of the larval habitus in ventral or dorsal view the specimens cannot be further considered here.

31) Normark (2013) redrew the schematic life cycle of *M. debilis* (fig. 1B, p. R430) after Hörnschemeyer et al. (2010).

32) Yavorskaya et al. (2015) provided numerous images of a first stage larva of *T. mucida* (Cupedidae). These included an SEM micrograph of the entire larva in dorsal view (fig. 1A, p. 240) that we further considered here (Fig. 4: Specimen 22).

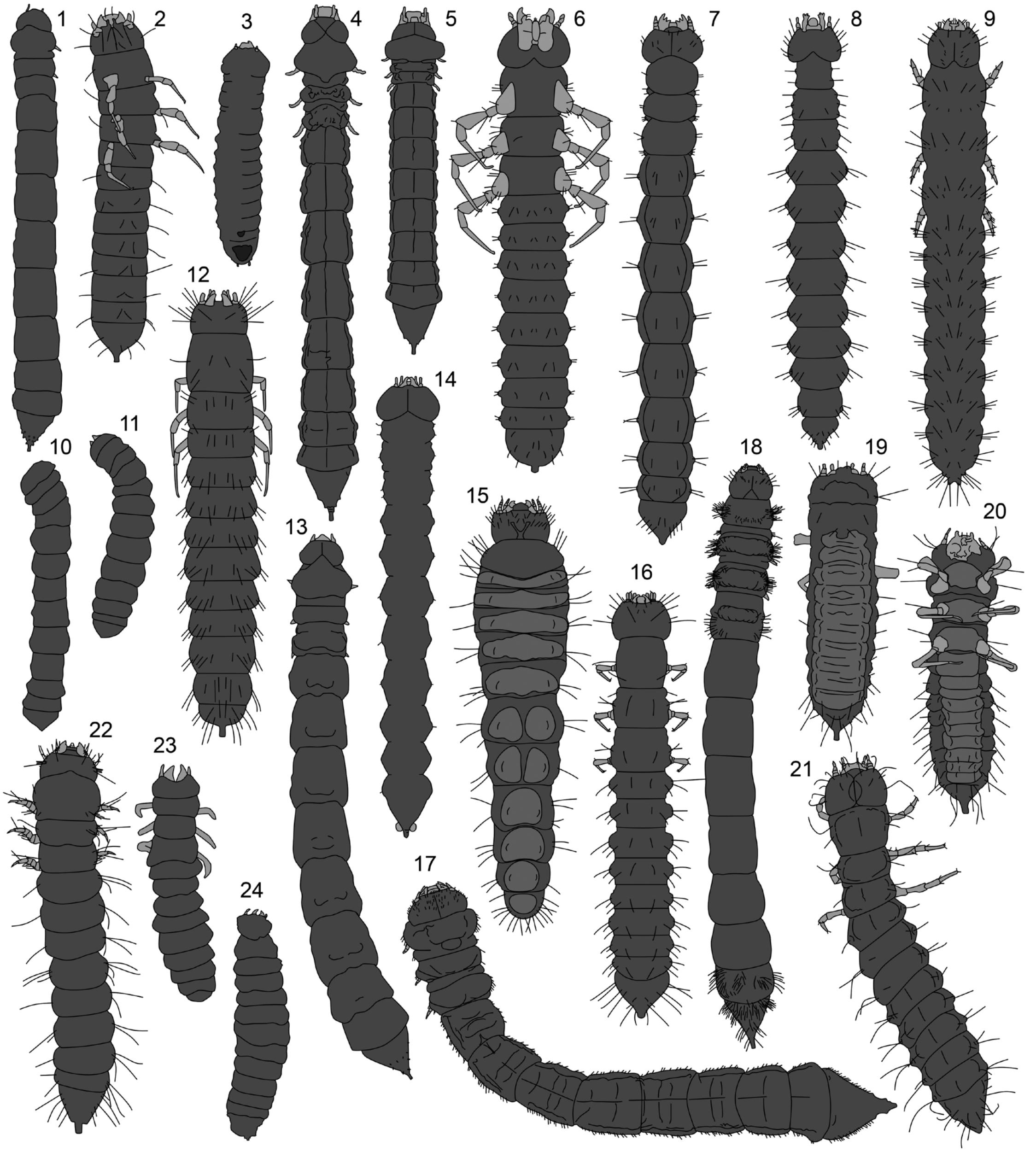

Fig. 4. Known extant and fossil larvae of Archostemata, redrawn from literature; 1) extant larva of *Tenomerga cinerea* from Snyder (1913, pl. 1, fig. 1C); 2) extant triungulin larva of *Micromalthus debilis* from Barber (1913a, pl. 3, fig. 2); 3) extant "legless" larva of *M. debilis* from Scott (1938, fig. 1A); 4) extant larva of *Tenomerga mucida* from Fukuda (1938, fig. 1); 5) another extant larva of *T. mucida* from Fukuda (1938, fig. 2); 6) extant triungulin larva of *M. debilis* from Pringle (1938, fig. 1A); 7) extant cerambycoid larva of *M. debilis* from Pringle (1938, fig. 2A); 8) extant cerambycoid larva of *M. debilis* from Peterson (1957, fig. C51K); 9) extant larva of *Priacma serrata* from Ross & Pothecary (1970, fig. 3); 10) extant cerambycoid larva from Kuehne (1972, fig. 1b); 11) another extant cerambycoid larva from Kuehne (1972, fig. 2, 2. from left); 12) extant triungulin larva of *M. debilis* from Costa et al. (1988, fig. 1); 13) extant larva of *T. cinerea* from Lawrence (1991a, fig. 34.67a); 14) extant cerambycoid larva of *M. debilis*, from Lawrence (1991b, fig. 34.68a); 15) extant larva of *Omma* from Lawrence (1999, fig. 12); 16) extant triungulin larva of *M. debilis* from Beutel & Hörnschemeyer (2002a, fig. 2); 17) extant larva of *Rhipsideigma raffrayi* from Beutel & Hörnschemeyer (2002b, fig. 2); 18) extant larva of *D. concolor* from Grebennikov (2004, fig.74); 19) extant triungulin larva of *M. debilis* from Grimaldi & Engel (2005, fig. 10.5, middle left); 20) another extant triungulin larva of *M. debilis* from Grimaldi & Engel (2005, fig. 10.5, middle right); 21) fossil larva of *Cretomalthus acracrowsonorum* from Kirejtshuk & Azar (2008, fig. 1); 22) extant larva of *T. mucida* from Yavorskaya et al. (2015, fig. 1A); 23) extant triungulin larva of *M. debilis* from Perotti (2016, fig. 1); 24) possible fossil larva of Tshekardocoleidea, a representative of early beetles from Kirejtshuk (2020, fig. 3A).

33) Hörnschemeyer (2016b) provided an overview of a triungulin, cerambycoid and paedogenic specimens of *M. debilis* (fig. 5.7, p. 51) and a scheme of its life cycle (fig. 5.6). The specimen of triungulin larva (fig. 5.7H, p. 51) is the same as in Beutel & Hörnschemeyer (2002a) and the scheme of the life cycle same as in Hörnschemeyer et al. (2010). The cerambycoid larva is presented in a dorsal view as a SEM micrograph but unfortunately, the trunk end of the abdomen is unavailable (fig. 5.7J, p. 51). Therefore, these larvae were not considered once again.

34) Hörnschemeyer & Beutel (2016) refigured the specimen of *Omma* from Lawrence (1999). Therefore, this specimen was not considered once again.

35) Hörnschemeyer & Yavorskaya (2016) provided overviews of two specimens of larvae of Cupedidae but they are both refigured from other sources; *R. raffrayi* (fig. 5.5A, p. 48) after Hörnschemeyer & Beutel (2002b) and *T. mucida* (fig. 5.5D–F, p. 48) after Yavorskaya at al. (2015). Therefore, these larvae were not considered once again.

36) Perkovsky (2016) reported a single piece of Rovno amber with 76 representatives of Micromalthidae, two of which are adults and 74 larvae. Based on the characters of the adults he erected a new species *Micromalthus priabonicus*. However, this important find has been supported with only images of the adults, whereas the larval specimens should be presented in another publication that is unfortunately still unavailable. Therefore, none of the larvae of the new species were further included in our analyses.

37) Perotti et al. (2016) provided a life cycle of *M. debilis* with different larval stages in several micrographs (fig. 1, p. 2). However, only the image of the triungulin larva was furthermore considered here (Fig. 4: Specimen 23).

38) Kirejtshuk (2020) provided several images of adult specimens of Archostemata and a single image of a possible larva that he interpreted as one of Tshekardocoleidae in dorsal view (his specimen PIN 1700/4747; fig. 3A, p. 14; but see Boudinot et al. 2023) that we also include here (Fig. 4: Specimen 24).

3.3. Shape analysis

The shape analysis of 27 specimens (24 specimens from the literature and the three complete new fossils) resulted in six effective Principal Components (PCs). All the values and measurements can be found in the electronic Supplementary-Table 1 (see digital version at https://bioone.org/journals/Palaeodiversity/volume-17/issue-1/pale.v17.a3).

PC1 explains 63.3% of the total variance. It is mostly influenced by the width of the body. High values indicate a wider body and a medially rounded posterior part. Low values indicate a narrower body with a medially more drawn-out and pointier posterior part of the body (Suppl.-Fig. 4).

PC2 explains 22.61% of the total variance. It is mostly influenced by how wide the "middle part" of the body is (thorax and anterior part of the abdomen). High values indicate a narrower "middle part" compared to the rest of the body, making it slightly concave laterally and low values indicate a wider "middle part" making it slightly convex.

PC3 explains 3.53% of the total variance. It is mostly influenced by how round are the anterior and posterior parts of the body and whether the thorax is more concave or convex laterally. High values indicate a medially rounder head, a wider trunk end, and a slightly laterally concave thorax. Low values indicate a medially pointier head, a narrower trunk end, and a slightly laterally convex thorax.

PC4 explains 2.71% of the total variance. It is mostly influenced by the width of the anterior part of the body and how much the trunk end of the body is drawn out medio-posteriorly. High values indicate a wide anterior part of the body and a medio-posteriorly drawn-out trunk end. Low values indicate a narrower anterior part of the body and a more rounded trunk end of the body.

PC5 explains 1.87% of the total variance. It is mostly influenced by the width of the anterior trunk. High values indicate a broad anterior part of the trunk and low values indicate a narrower anterior part of the trunk.

PC6 explains 1.37% of the total variance. It is mostly influenced by the width of the anterior part of the head capsule. High values indicate a narrower head. Low values indicate a wider head.

When plotting the principal components 1 and 2, the areas occupied by both, extant and fossil specimens overlap in the morphospace (Fig. 5C). However, the overlap is only true for the fossils and some of the specimens of *M. debilis* (Fig. 5A). Interestingly, all the fossil specimens plot on the right half of the scatter plot (Fig. 5C) and do not overlap with any of the larvae of other Archostemata groups such as Ommatidae or Cupedidae (Fig. 5B, C). All of the specimens of Cupedidae and a single specimen of Ommatidae plot on the left half of the scatter plot (Fig. 5A, B). This is especially pronounced in a single specimen of *D. variens* that plots in the left lower quadrant of the scatter plot, with the lowest PC1 values of all the specimens included (Fig. 5A). Also the three specimens of *T. mucida* plot left of the Y-axis in a diagonal pattern (Fig. 5A), either slightly above the X-axis or underneath it, depending of the width of the "middle part" of the body (represented by different PC2 values). The single specimen of *P. serrata* plots in the lower left quadrant of the plot (Fig. 5A). The single specimen of *R. raffrayi* also plots

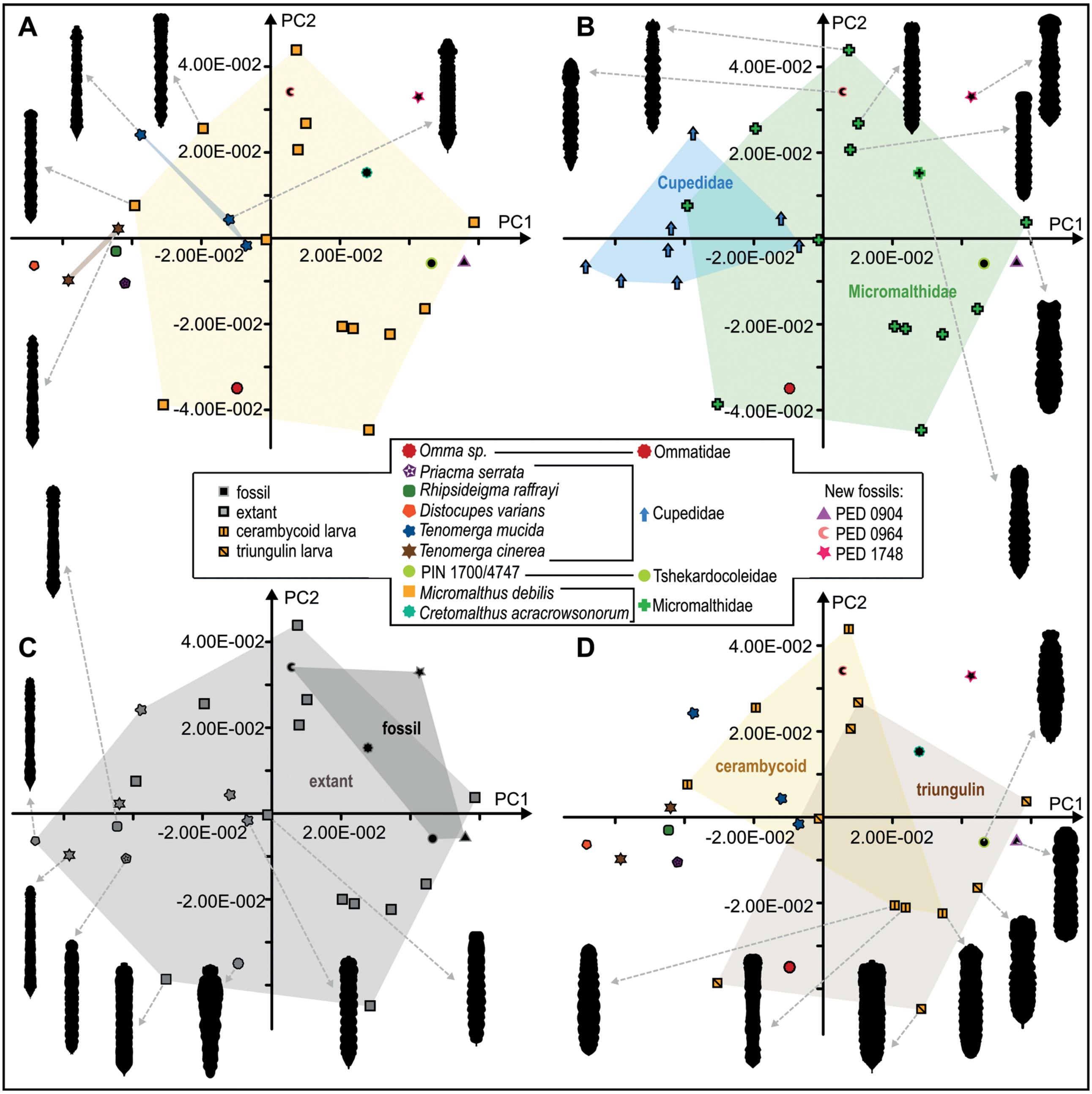

Fig. 5. Scatter plot PC2 over PC1 with body outlines of specimens from literature and three new fossils, presented in four panels (outlines within one quadrant of scatter plot are presented separately per panel), with each panel emphasizing different parameters. **A** – Different species of the sample; yellow convex hull representing the morphospace occupancy of the representatives of *M. debilis*, dark blue of *T. mucida* and brown of *T. cinerea*; other species are only represented here by a single specimen each; **B** – different groups of Archostemata; green convex hull representing the morphospace occupancy of the representatives of Micromalthidae and light blue of Cupedidae; other groups are represented by single specimens; **C** – different ages of specimens; dark grey convex hull representing the morphospace occupancy of the fossils and light grey of the extant specimens; **D** – different larval stages of *M. debilis*; beige convex hull representing the morphospace occupancy of legless cerambycoid and brown of triungulin larvae with legs.

in the lower left quadrant (Fig. 5A) between the specimens of *T. cinerea* and a single specimen of *P. serrata*. The single representative of Ommatidae plots relatively far from all the specimens in the lower left quadrant relatively close to the Y-axis (Fig. 5A, B). Only one specimen of a triungulin larva of *M. debilis* plots somewhat close by the larva of Ommatidae (Fig. 5D).

Some fossil specimens plot in the lower right quadrant of the scatter plot, relatively close to the X-axis (for example, the possible fossil larva of Tshekardocoleidae and the new fossil PED 0904; Fig. 5C). Both these fossils plot between the two triungulin-type larvae of *M. debilis* (Fig. 5D). The other fossils plot in the upper right quadrant of the scatter plot (for example, the fossil larva of *C. acracrowsonorum*, and new fossils PED 0964 and PED 0748). Of the three fossils in the upper right quadrant, only the specimen PED 0964 plots relatively close to some larvae of Micromalthidae (two triungulin larvae and one legless larva; Fig. 5D), whereas the specimen of *C. acracrowsonorum* and the specimen PED 0748 stand alone in the middle of the quadrant (Fig. 5). The new fossil PED 1748 seems to plot the furthest from any other specimen, with the fossil specimen of *C. acracrowsonorum* seeming to be the closest to it (Fig. 5).

4. Discussion

4.1. Identity of the new specimen PED 1748: beetle larva

The new fossil has certain features that identify it as a representative of Insecta, for example, the segmented body arranged into a head and trunk with three leg-bearing segments (thorax) followed by several legless segments (abdomen). No wings are present on the thorax segments. These characters in combination with the lack of genitalia or compound eyes indicate that the specimen is either a specimen of the early lineages of non-flying insects or, more likely, an immature stage within the group of Holometabola (Lawrence 1991c). Especially the lack of abdomen leg derivates, which are sometimes present in older insect lineages, makes the interpretation of the specimen as a larva of Holometabola more plausible. The campodeiform body with a strongly sclerotised head capsule (Peterson 1957; Beutel & Lawrence 2005) with an indented posterior rim separates the new fossil from the larvae of Trichopetara, Megaloptera, Raphidioptera and Neuroptera (Lawrence 1991c). Even though some Mecoptera (Nannochoristidae) have legs with six elements, their habitus is generally elateriform (Pilgrim 1972), which is not the case in the new fossil. Most of the larvae of Lepidoptera and Hymenoptera have additional abdomen legs (leglets, parapods, pseudopods) that the new fossils do not have. The new fossil has a prognathous head, different to the "typical lepidopteran head" that is mostly hypognathous sphere-shaped with specific sclerites above the 'ecdysial suture' and with a spinneret (Lawrence 1991c). Many larvae of hymenopterans are legless (especially of the ingroup Vespina), also with a hypognathous head and, additionally, with reduced maxillary palps with one element. Some larvae of the early lineage of Hymenoptera have either abdomen prolegs or more than four elements in the antennae (antennomeres) (Lawrence 1991c: 145). All of these characters are not present in the new fossils. Therefore, the characters of our new specimen imply that the new specimen is indeed an immature beetle (Coleoptera).

4.2. Identity of the new specimen PED 1748: larva of Archostemata

The legs of the fossil PED 1748 have six elements, due to the separation of tarsus and claws. Among beetle larvae legs with separated claws are characteristic for larvae of Archostemata and Adephaga, whereas larvae of Myxophaga and Polyphaga usually have legs with a tarsungulum, conjoined claw and tarsus (Beutel & Lawrence 2005) and therefore differ from the new fossil larva. However, the interpretation of the new larva as a larva of either Adephaga or Archostemata requires further comparison. Most characteristics of larval representatives of Archostemata are inner structures such as muscles and the hindgut (Yavorskaya et al. 2015). These are very often not available in fossils. This is also the case here and only some characters can be further discussed here. Therefore, we describe here all accessible morphological characters and compare those with the larvae of Archostemata from the literature. The characters mentioned by Yavorskaya et al. (2015) such as a posterodorsal and posteroventral medial emargination of the head capsule are characters discernible in the new fossil PED 1748. The fossil has a wider than long and laterally rounded head, a head shape more similar to that of extant larvae of Cupedidae and Micromathidae (Yavorskaya et al. 2015) than of larvae of Adephaga.

Nevertheless, the morphologies of mouth parts and legs indicate that the new fossil is indeed a larva of Archostemata and not of Adephaga. Adephagan larvae have mouth parts shaped differently from the new fossil, coupled often with the predatory way of life and extraoral ingestion. Even though the mouth parts of the new fossil are partially obscured by debris in ventral view, the translucence of the new specimen facilitates the observation on several stack images (Figs. 2, 3, Suppl.-Fig. 2). Even ligula (Figs. 2, 3, Suppl.-Fig. 2) is discernible on the stack images.

However, the translucence of the fossil can also be an obstacle, for example, here in the case of endocarina. The endocarina of the new fossil is not obvious, possibly due to the multiple overlapping of structures of mouth parts, especially the labium (Fig. 1). Another character in which the new fossil differs from larvae of Adephaga are prominent processes (urogomphi) on the trunk end. These processes (urogomphi) seen in larvae of Adephaga are not discernible in the new larva. The triangular-shaped abdomen segment 9 of the new larva is also more similar to the morphology of some extant larvae of Archostemata (Lawrence 1999). The sclerotised posterior median processes of the abdomen segment 9 additionally support the interpretation of the new fossil as a larva of Archostemata.

4.3. Morphological diversity among larvae of archostematan specimens from literature

We see a certain morphological diversity of larvae within Archostemata. We can expect that it should be even higher, due to the still unknown larvae of Jurodidae and Crowsoniellidae.

Micromalthus debilis is the only species of Micromalthidae today, however, other species have been erected based on fossil specimens. The species *Archaeomalthus synoriacos* was erected based on an adult specimen from the Upper Permian Babiy Kamen' locality (Yan et al. 2020). Two species were erected based on fossils from the Cretaceous: *Cretomalthus acracrowsonorum* based on a larva from Lebanese amber (Kirejtshuk & Azar 2008) and *Protomalthus burmaticus* based on an adult female from Kachin amber, Myanmar. Two more species *Micromalthus priabonicus* and *Micromalthus eocenicus* were erected based on Eocene fossils: *M. priabonicus* based on two adult specimens and 74 larvae from Eocene Rovno amber of Ukraine (Perkovsky 2016) and *M. eocenicus* based on an adult female specimen from Eocene of France (Kirejtshuk et al. 2010). A specimen of an adult female of a supposed species *Micromalthus anansi* erected by Perkovsky (2007) was later synonymised under *M. debilis* by Hörnschemeyer et al. (2010).

Even though today there is only one extant species of Micromalthidae, *M. debilis*, the species is represented with morphologically highly diverse specimens due to a unique life cycle with numerous morphotypes of different larvae (Hörnschemeyer et al. 2010; Normark 2013; Perotti et al. 2016). The larvae range from slightly flattened forms with functional legs, so-called triungulin larvae, to legless forms, so-called cerambycoid larvae and rare curculionid larvae. The morphological difference among the extant larvae of this ingroup can also be seen in the shape of the head (Hörnschemeyer 2016d), but also in body shape (Fig. 5A, B). The larvae of Cupedidae are known in the extant fauna from five species: *Distocupes varians*, *Tenomerga cinerea*, *T. mucida*, *Priacma serrata* and *Rhipsideigma raffrayi* (Hörnschemeyer 2016d; Hörnschemeyer & Yavorskaya 2016). Until now, not a single fossil larva of the group Cupedidae has been identified, even though today this group is represented with the highest number of species within Archostemata (Neboiss 1984; Young 2000). The larvae of Cupedidae mostly show differences in the shape of mouth parts, the number of antennae elements, and the number of leg claws (Neboiss 1968; Grebennikov 2004; Hörnschemeyer 2016a). However, one should keep in mind that not many specimens have been described and they do not all represent the same larval stage.

4.4. Possible relationship of fossil specimen PED 1748 within Archostemata

The new fossil PED 1748 (Fig. 1) resembles the larva of *C. acracrowsonorum* (Kirejtshuk & Azar 2008), which can also be seen from the shape analysis (Fig. 5). PED 1748 has accessible important characters such as details of the mouth parts due to the slight translucence of the body. The specimen has a posterior edge of the head capsule strongly medially indented, stronger than in *C. acracrowsonorum* (Fig. 4: specimen 21) and most of the specimens from the literature (Fig. 4: specimens 2, 6, 12, 16, 19, 20).

Specimen PED 1748 has one stemma on each side (Fig. 1B, Suppl.-Fig. 2B: arrow), however, the larva was not accessible in the lateral view and the possibility of additional stemmata is not completely excluded. The morphology with a single stemma on each side is known from modern triungulin larvae of *M. debilis* from Hong Kong (Pollock & Normark 2002) and early stages of Priacminae and Cupedinae (Grebennikov 2004). Besides the specimens from Hong Kong no other described modern representatives of *M. debilis* have stemmata (Grebennikov 2004). The morphology with two stemmata per side is known from the fossil larva of *C. acracrowsonorum* (Kirejtshuk & Azar 2008). The morphology with four stemmata per side is known from extant later stage larvae of *Omma* (Grebennikov 2004). Therefore, if the new fossil specimen PED 1748 has only one pair of stemmata, it may be an early stage larva.

In both, the larva of *C. acracrowsonorum* and specimen PED 1748 the antennae have four elements (antennomeres) each. However, in the new fossil, the third antennomere and a prominent sensory lobe at this antennomere are more similar in appearance to those of modern triungulin larva of *M. debilis* (cf. Fig. 2 and Grebennikov 2004, fig. 3, p. 276) than to those of *C. acracrowsonorum*. The labium of the new specimen resembles in shape the labium of the modern larve of *M. debilis* (Böving & Craighead 1931; Lawrence 1991c, fig. 117, p. 273). The labium is not only slender, but the labial palps are very small. Interestingly, the ligula is not wedge-shape as known from larvae of *M. debilis* (Böving & Craighead 1931; Lawrence 1991c, his figs. 34.68i p. 301, 117 p. 273), *T. cinerea* (Lawrence 1999) and representatives of *Cupes* (Böving & Craighead 1931; Lawrence 1991b), but triangular in ventral view, similar to the ligula of *T. mucida* (Yavorskaya et al. 2015).

The leg elements of PED 1748 also show different proportions than in the larva of *C. acracrowsonorum,* but they all end with two claws of the same length. Among modern larvae of Archostemata, paired claws are also present in larvae of *M. debilis* (Hörnschemeyer 2010) and *Tenomerga* (Böving 1929). The other known larvae of Cupedidae have unpaired claws (Beutel et al. 2008). The process of the abdomen tergite 9 has a darker strongly sclerotised area in PED 1748, known also from the triungulin larvae of *M. debilis,* the larva of *C. acracrowsonorum* (Kirejtshuk & Azar 2008) and larvae of Cupedidae (Beutel & Hörnschemeyer 2002a). However, the new larva also has a sternite of the abdomen segment 9 drawn out medioposterally, in the shape of a truncated process (Fig. 2F, G). Such a process of the sternite is unknown from larvae of Cupedidae (Böving & Craighead 1931; Beutel & Hörnschemeyer 2002b; Yavorskaya et al. 2015). The triungulin larvae of *Micromalthus* have both, tergite and sternite, drawn out posteriorly into a process that in lateral view looks like forceps; nevertheless, the morphology still differs greatly from the morphology of the new specimen (Lawrence et al. 2011).

Due to the combination of characters that this larva shares with *C. acracrowsonorum*, *M. debilis* but also some representatives of Cupedidae we cannot identify this larva further than being a larva of Artchostemata. Considering that the new fossil larva unites different characters today present in larvae of different groups of Archostemata, this chimera may be an immature representative of the extinct sister group of today known groups of Archostemata. However, it is also possible that it is an extinct representative of one of the modern groups because the immatures of many modern groups of Archostemata are still unknown. For example, the group Micromalthidae today has only one species, but had more in the past. We can therefore not exclude that the larva is conspecific with one of these known species. Therefore, we did not erect a new species based on this larval specimen.

4.5. Shape analysis

In the scatter plot all the fossil larvae plot on the right side, which has higher PC1 values (Fig. 5C, Suppl.-Fig. 1). This pattern indicates that all the fossils have wider body outlines and medially more rounded posterior part of the body (Fig. 5C, Suppl.-Fig. 1). This find underlines that the larvae of Cupedidae, that completely plot in the left half of the scatter plot, have more slender body outline with a medially more drawn out posterior part of the body (Fig. 5B, Suppl.-Fig. 1). The only species that scatter over all four quadrants is *M. debilis* (Fig. 5A). On the one hand, this pattern is not surprising due to the complex life cycle of the species, with morphologically diverse legless cerambycoid-type, and leg-bearing campodeiform triungulin-type larvae (Pringle 1938; Scott 1938; Kühne 1972; Costa et al. 1988; Beutel & Hörnschemeyer 2002a; Grimaldi & Engel 2005; Normark 2013; Hörnschemeyer 2016b; Perotti et al. 2016). On the other, it is indeed surprising that the triungulin-type larvae also plot quite scattered (Fig. 5D). This pattern additionally shows that there is also a high morphological diversity among the same type of larvae (the triungulin-type) within the representatives of *M. debilis.* This also demonstrates that the high morphological diversity is not only recognisable by the presence or absence of appendages but also the body shape and other characteristics. The wide geographic distribution of *M. debilis*, with many separate populations (Pollock & Normark 2002) may explain the differences that we see in the scatter plot (Fig. 5). In addition, not a single specimen of the highly variable larvae of *M. debilis* plots as far left in the scatter plot as the rather slender larvae of *D. varians* and *T. cinerea;* no matter which type they represent (Fig. 5A, D).

Considering the PC2, the lower half of the plot is occupied by larvae that have a wider "middle part" of the body. The single specimen of *Omma* plots quite low in the left half of the plot and therefore obviously has a relatively wide "middle part" of the body. Only a single specimen of triungulin larvae of *M. debilis* has a more convex "middle part" than the *Omma* specimen and plots even lower in the quadrant with lower PC2 values (Fig. 5A). That the only representative of *Omma* in this study plots relatively separate from the other larvae was to be expected due to its rather unique morphology among the larvae within the group of Archostemata (Hörnschemeyer & Beutel 2016). In the lower half of the plot, there is a group of larvae: a single specimen of *P. serrata,* a single specimen of *Rhipsideigma raffrayi,* a single specimen of *D. concolor* and one of the two specimens of *T. cinerea*, all of which are relatively slender (Fig. 5). Another specimen of *T. cinerea* plots slightly above the X-axis but still quite left. Two out of three specimens of *T. mucida* plot mostly around the X-axis on the left side of the plot: the third specimen is an exception and plots somewhat higher, above the X-axis. This means that most of the specimens have no great difference in the width of the "middle part" and the rest of the body. Two fossil larvae, PED 0904 (Suppl.-Fig. 1) and the possible larva of Tshekardocoleidea from the Permian (Kirejtshuk 2020, fig. 3, p. 14; PIN 1700/4747) also plot in the lower half of the plot but relatively close to the X-axis. They differ from the specimens of *Tenomerga* in having much higher values of PC1, as they have much wider bodies. The upper half of the plot is occupied by larvae with a narrower "middle part" of the body, but an overall generally wider body. Interestingly, two of the three new fossils (PED 0964 and PED 1748; Figs. 1, Suppl.-Fig. 1C) plot relatively high in the upper half of the plot (Fig. 5A); the two specimens have a relatively wide head capsule making the rest of the body seem much narrower (Figs. 1, Suppl.-Fig. 1). The single larva of *Cretomalthus acracrowsonorum* also plots in the upper right quadrant relatively far away from all the other specimens (Fig. 5A–D). This shows that the body shape of the specimen differs from that of all the other larvae. However, the larva of *C. acracrowsonorum* plots within the area of the morphospace occupied by Micromalthidae (among the triungulin larvae of *M. debilis* and the new fossil PED 1748; Fig. 5D). Hence, there must be certain similarity of the body shape of the fossil and that of modern larvae of Micromalthidae (Fig. 5B).

Specimen PED 1748 (Fig. 1) plots relatively far out in the upper right quadrant (Fig. 5A), closest to the fossil of *C. acracrowsonorum* and not too far from some triungulin specimens of *M. debilis.* This emphasises that there are certain similarities in body shape among these larvae as well.

However, when looked at as a whole, the occupancy of the morphospace in the past was much smaller than today, but this is likely an artefact due to the low number of available specimens. Still, the left part of the plot is left completely unoccupied by fossils. This could be a real signal, possibly indicating that the representatives of Cupedidae diversified only later.

4.6. Relationship of unidentified new fossil specimens to other analysed larvae

Two fossil larvae, PED 0904 (Suppl.-Fig. 1A, B) and PED 0964 (Suppl.-Fig. 1C) plot relatively far apart from each other, however, both of the not further identified larvae plot very close to other representatives of Archostemata, to representatives of Micromalthidae to be precise (Fig. 5B). The specimen PED 0904 also plots relatively close to the possible larva of Tshekardocoleidae but very far from the larvae of Cupedidae or Ommatidae. Interestingly, the only new specimen that we were able to identify as a larva of Archostemata plots the furthest of all the other extant specimens of Archostemata. And even though the body shape of the two unidentified specimens resembles the most the body shape of extant larvae of Micromalthidae, we cannot exclude that the similar body shape is a result of convergent evolution. The similar overall shape of a body can be found in representatives of different groups that have similar ecological roles (e.g., larvae of Buprestidae vs. Cerambycidae, Endomychidae vs. Coccinellidae; discussed in Haug et al. 2021; Zippel et al. 2023a).

4.7. Fossil record of wood-borer beetle larvae

Wood-borer and wood-feeding beetle larvae have been suggested to be rather rare in the fossil record (Peris & Rust 2020). This rarity is surprising considering that wood-associated beetle larvae have a very important ecological role as decomposers and are involved in carbon cycling (Zippel et al. 2022a). Thus they should be expected to be rather common. In addition, the original habitat of these insects was likely within the wood which was likely also the source of the plant resin. Therefore, it should be expected that findings of such beetle larvae within amber are more numerous. Possibly this is another effect of not reporting larvae rather than of the unavailability of such larvae (Baranov et al. 2020, 2021). There are some more examples of such wood-associated beetle larvae, for example: larvae of jewel beetles (Buprestidae; Grimaldi & Engel 2005 fig. 10.36, p. 381; Haug et al. 2021, figs. 2–4; Haug et al. 2023), long horn beetles (Cerambycidae; Gröhn 2015: 272; Haug et al. 2021, figs. 5–6; Haug et al. 2023), false click beetles (Eucnemidae; Chang et al. 2016; Zippel et al. 2023b, fig. 1) and false flower beetles (Scraptiidae; Haug & Haug 2019, figs. 1–3; Zippel et al. 2022a, figs. 2–16). In addition, there are some fossil larvae of groups in which only some extant larvae are known to be wood-borers and hence the fossil larvae may be wood borers, but the case is less clear in, for example, riffle beetles (Elmidae; Hinton 1973; LeSage & Harper 1976; Merritt & Cummins 1996; Valente-Neto & Fonseca-Gessner 2011; Kodada & Jäch 2016) or toed-winged beetles (Ptilodactylidae; Chatzimanolis et al. 2012; Alekseev & Jäch 2016; Zippel et al. 2024). Elmidae are represented only by two fossil larvae (Zippel et al. 2022b; Kirejtshuk et al. 2023) and Ptilodactylidae (Zippel et al. 2024, figs. 1–7) are represented by only eight fossil larvae.

We should expect to find many more representatives of wood-boring larvae within different types of amber in the future since the decomposition of dead wood seems to be one, if not the most, common way of life in extant beetles (Gimmel & Ferro 2018) and must have been similar in the past, too (Tate et al. 1993; Grove 2002). Considering that the group Archostemata is one of the oldest lineages of the beetles, a wood-feeding lifestyle is likely one of the oldest ways of life in beetle larvae.

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Addresses of the authors:

Ana Zippel (Corresponding author), Ludwig-Maximilians-Universität München (LMU Munich), Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany; zippel@biologie.uni-muenchen.de; ORCID: https://orcid.org/0000-0002-6509-4445.

Carolin Haug, Ludwig-Maximilians-Universität München (LMU Munich), Biocenter, Großhaderner Str. 2,
82152 Planegg-Martinsried, Germany & GeoBio-Center at LMU, Richard-Wagner-Str. 10, 80333 München, Germany;
ORCID: https://orcid.org/0000-0001-9208-4229.

Beñat Yáñez Iturbe-Ormaeche, The University of Edinburgh, School of Biological Sciences, Roger Land Building,
The King's Buildings, Alexander Crum Brown Road, EH9 3FF, Edinburgh, UK;

Joachim T. Haug, Ludwig-Maximilians-Universität München (LMU Munich), Biocenter, Großhaderner Str. 2,
82152 Planegg-Martinsried, Germany & GeoBio-Center at LMU, Richard-Wagner-Str. 10, 80333 München, Germany;
ORCID: https://orcid.org/0000-0001-8254-8472.

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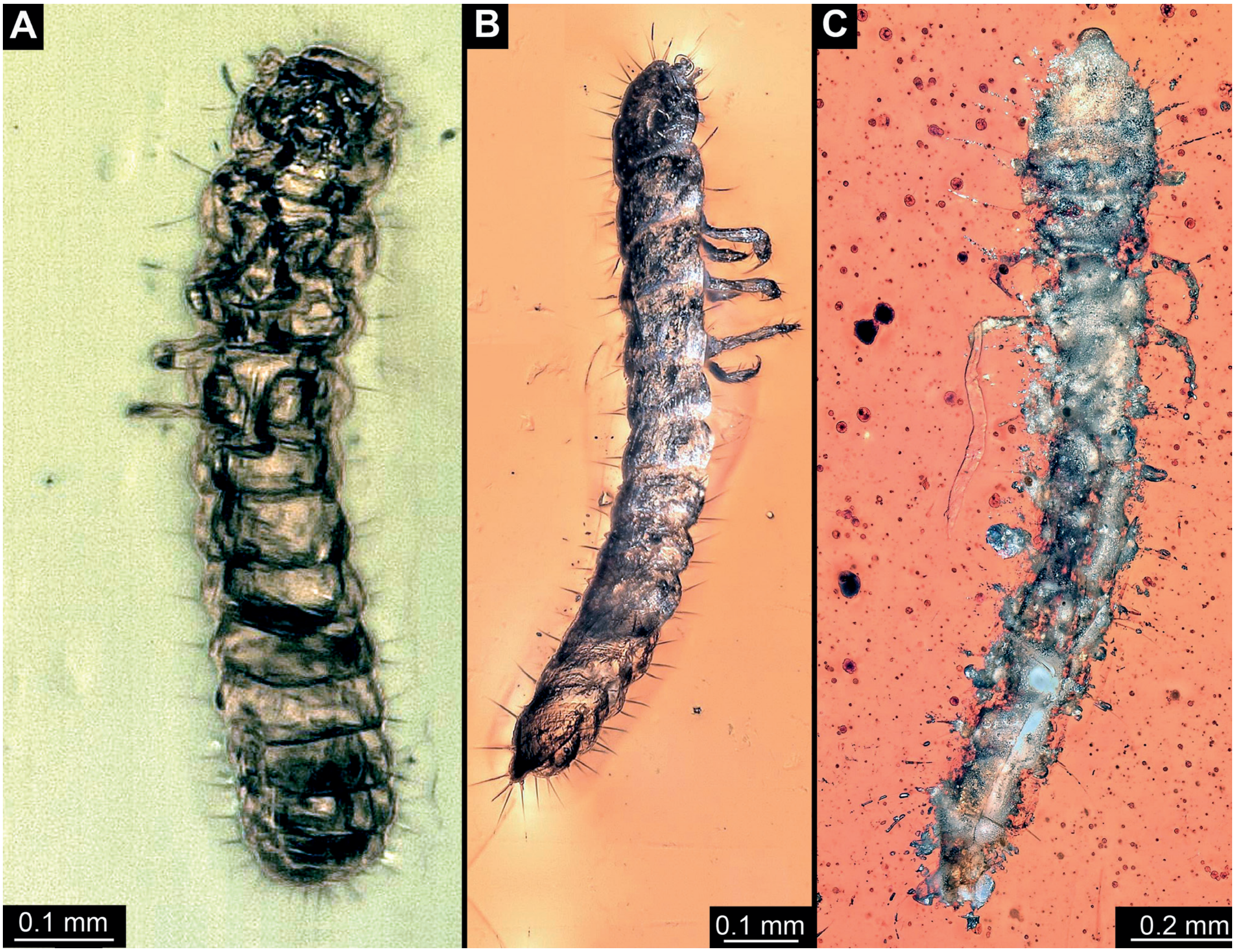
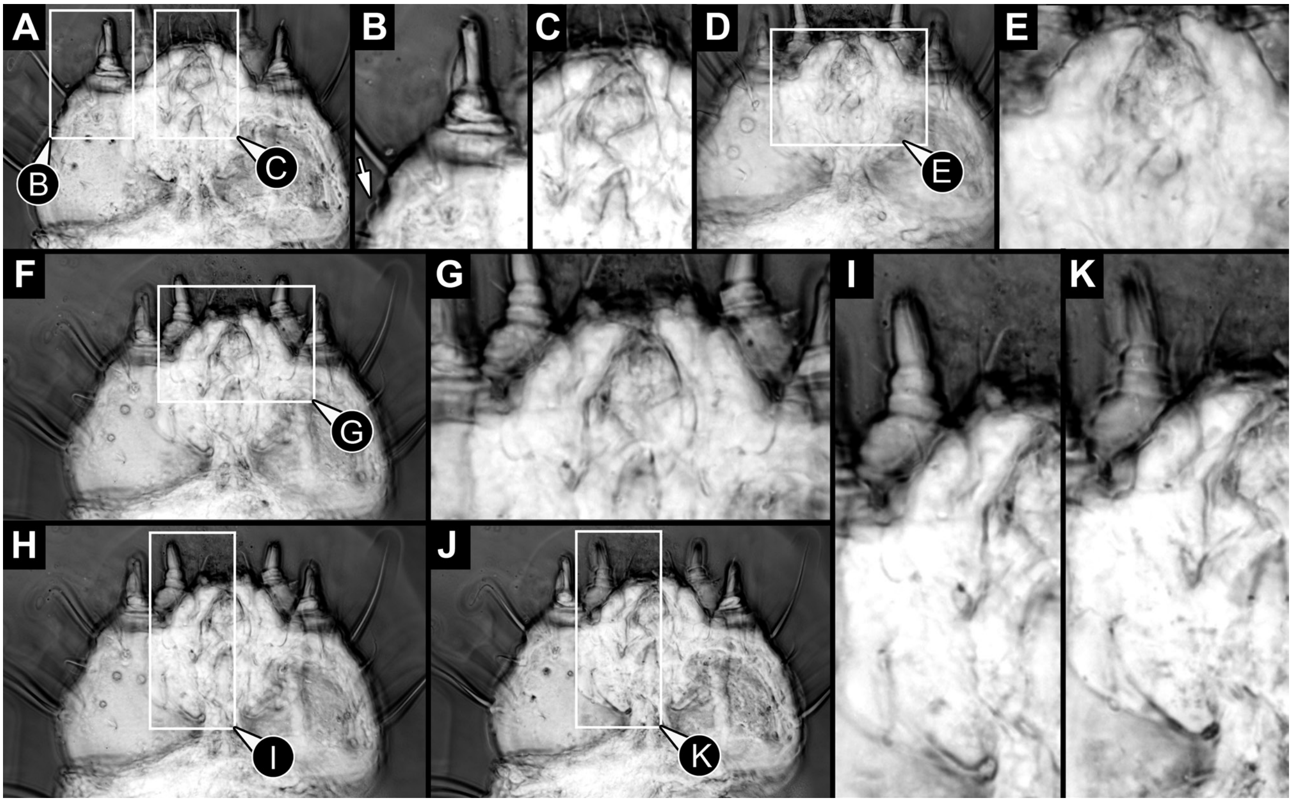
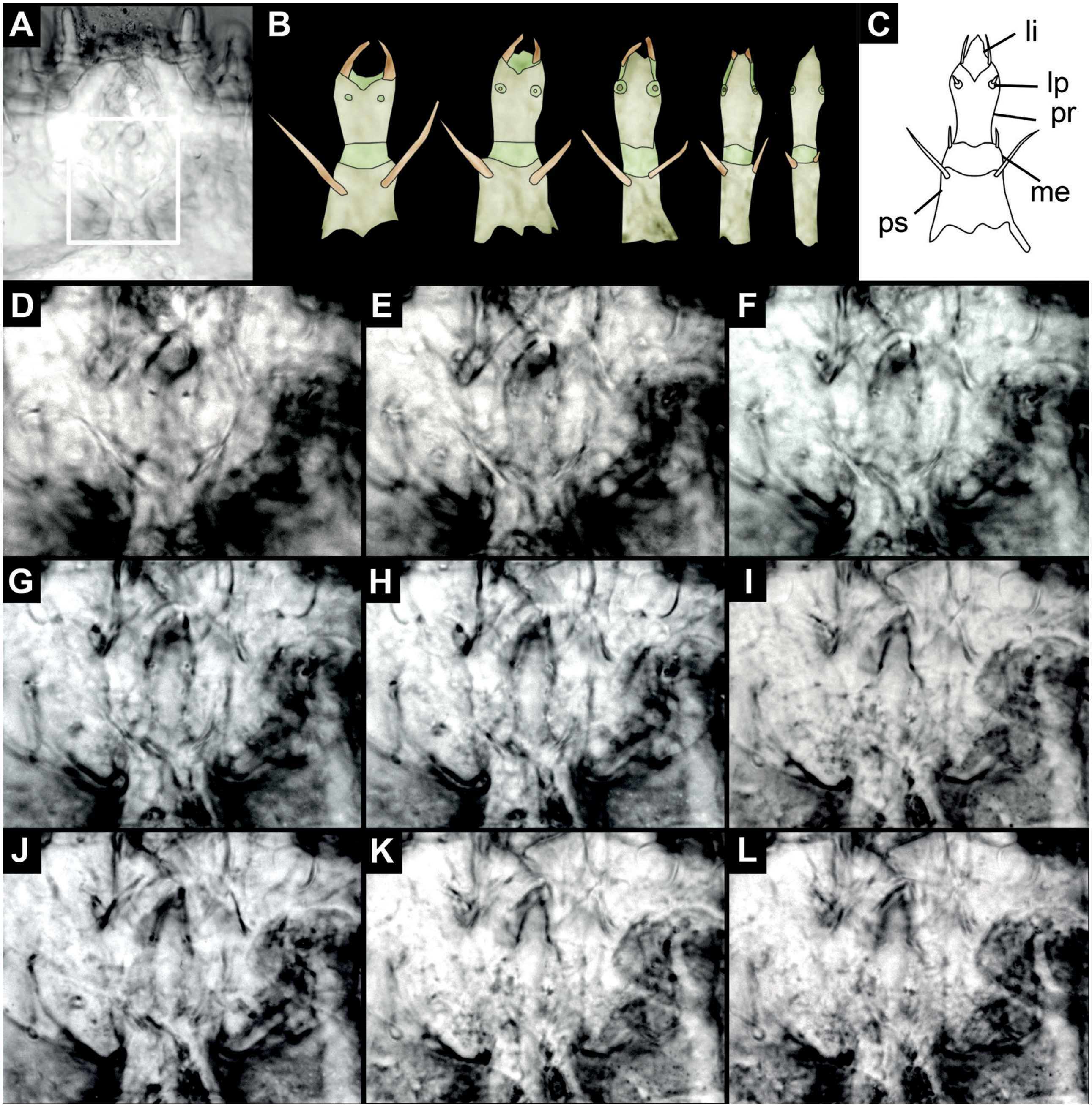


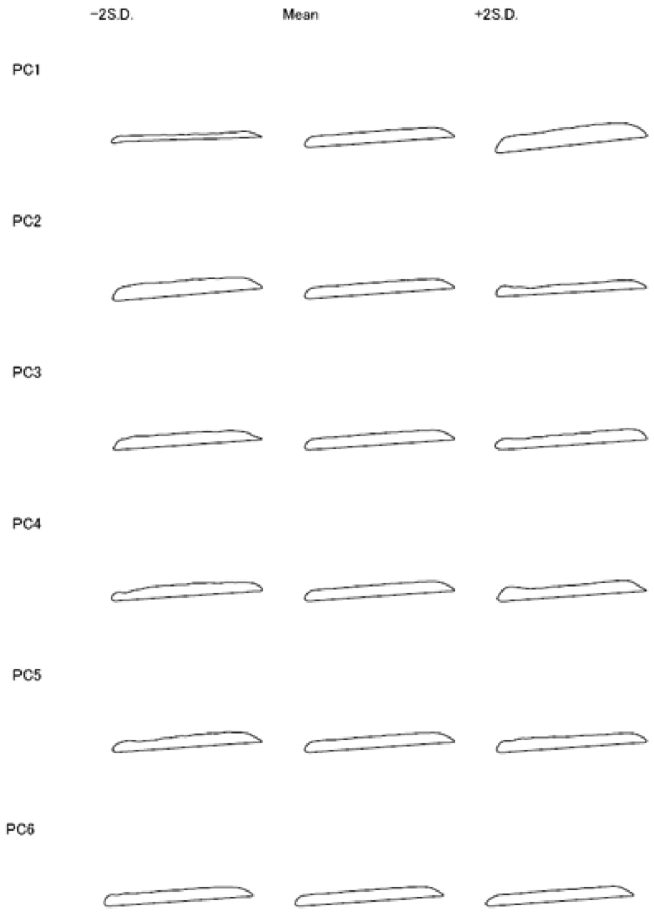
Suppl.-Fig. 1. Two new not further identified fossil specimens of Coleoptera used in the SHAPE analysis. **A** – Fossil specimen PED 0904 in ventral view preserved in Cretaceous Kachin amber; **B** – fossil specimen PED 0904 in lateral view; **C** – fossil specimen PED 0964 in ventral view preserved in Cretaceous Kachin amber.



Suppl.-Fig. 2. A stack of stereo images of the head of the fossil specimen PED 1748. **A** – Most dorsal image in the stack, antenna and clypeo-labral complex surrounded by a white square each; **B** – close-up of antenna (white arrow marks stemma); **C** – close-up of clypeo-labral complex; **D** – dorsal middle image in the stack, mandibles surrounded by a white square; **E** – close-up of mandible, focus on distal part; **F** – middle image in the stack, mandibles surrounded by a white square; **G** – close-up of mandibles, focus on the proximal part; **H** – ventral middle image in the stack, maxilla surrounded by a white square; **I** – close-up of maxilla, focus on the palp and endites; **J** – most ventral image in the stack, maxilla surrounded by a white square; **K** – close-up of maxilla, focus on proximal part.



Suppl.-Fig. 3. A stack of stereo images of the labium of the fossil specimen PED 1748. **A** – Overview of mouthparts with a white sqare surrounding labium; **B** – close-up color-version of stack from most ventral towards most dorsal, left towards right; **C** – drawing and interpretation of the stack images of labium; **D–L** – stack of close-up stereo images of labium with D being the most ventral and L being the most dorsal. Abbreviations: li = ligula; lp = labial palp; me = mentum; pr = prementum; ps = postmentum.



Suppl.-Fig. 4. Graphical representation of the factor loadings of the principal component analysis of all studied specimens.