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Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Cretaceous and Miocene ambers

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Abstract

Beetle larvae represent important components of the modern-day fauna. This should have been the case in the past as well. Yet, fossil beetle larvae are rare, or at least are rare in the literature, as identifying a beetle larva to a narrower taxonomic group is very challenging. This is even more complicated if prominent features have evolved convergently in several lineages. Yet, even in such cases, an ecological interpretation of the fossils is possible if the convergent character is coupled to a specific life habit. For example, different, not closely related, beetle larvae that possess setiferous processes. We here report on three beetle larvae, one from Miocene Mexican and two from Cretaceous Kachin amber, Myanmar. These larvae possess setiferous processes, most similar to the processes of modern representatives of Cucujiformia, especially of the groups Endomychidae, Erotylidae, Cerylonidae and Coccinelidae. Considering the shape of the entire habitus, we see the most similarities between the new larvae and the modern larvae of Endomychidae. However, the new larvae and the larvae of modern representatives differ in certain aspects, most prominently in the body size. The fossils are smaller than their extant counterparts with setiferous processes. Hence the fossils could represent larvae of Endomychidae, but the case remains unclear. Despite this uncertainty, we suggest a lifestyle of the fossil larvae as fungus-eaters on rotting wood. This lifestyle is not only known from extant larvae of Endomychidae, but also from other larvae with similar processes.

Key Words

Endomychidae, fossils, fungus-eating, Myanmar amber, palaeoecology

Introduction

Beetle larvae are very important components of the modern fauna. This importance is caused by the fact that the group of beetles, Coleoptera, is extremely species-rich with only slightly fewer than 400,000 formally described species, and also by the various ecological roles fulfilled by beetle larvae. Given their importance in the modern fauna, it is astonishing that fossil beetle larvae, which could inform us about the evolutionary history of these important faunal components, are relatively underrepresented in the literature.

This under-representation seems to be coupled to the fact that many fossil beetle larvae can prove quite difficult to be interpreted in a phylogenetic or taxonomic frame (Klausnitzer 1978). This has led to controversies over the identification of fossil larvae (e.g. Grimaldi et al. 2005 vs. Beutel et al. 2016; Zippel et al. 2022a vs. Batelka and Engel 2022). Nevertheless, controversies over the phylogenetic interpretation of fossils are also common in adults (Cai et al. 2017 vs. Li et al. 2022a; Clarke et al. 2019). Even more problematic in this respect is that some fossil larvae differ in certain aspects from all known modern forms. In some cases, this may mean that the fossils possess an unusual combination of characters ("chimeras"; Haug et al. 2019a) not found in modern forms, but the individual characters are well-known in different modern larvae (e.g. Zippel et al. 2023). In other cases, the fossil larvae may retain plesiomorphies (see discussions in Haug et al. 2021a and Zippel et al. 2022a; see Batelka and Engel 2022 and Rasnitsyn and Müller 2023 for an alternative view).

Yet, some beetle larvae have rather prominent features that allow the recognition of a fossil as a representative of a specific group with quite some certainty. The aquatic larvae of whirligig beetles (Gyrinidae) are very conspicuous due to their body shape in combination with the lateral processes projecting from their trunk and hence can easily be identified also as fossils (Zhao et al. 2019; Gustafson et al. 2020). Also larvae of water penny beetles (Psephenidae), likewise aquatic, with their often flat and round appearance can be easily identified (Wedmann et al. 2011; Hayashi et al. 2020). Many larvae of false flower beetles (Scraptiidae) have an enlarged trunk end, which provides also a good identifier in the case of fossils (Larsson 1978; Haug and Haug 2019; Zippel et al. 2022b). Larvae of Texas beetles (Brachypsectridae) have quite peculiar processes on their trunk segments and well-specialised head and mouthpart shapes, which have also been identified in fossils preserved in amber from different ages including the Cretaceous (Zhao et al. 2020; Haug et al. 2021b), Eocene (Scheven 2004; Klausnitzer 2009; Haug et al. 2021b) and Miocene (Poinar 1992; Wu 1996; Poinar and Poinar 1999; Woodruff 2002; Scheven 2004; Klausnitzer 2009).

There are other groups of beetles that have larvae with prominent processes on the trunk (Haug et al. 2021b fig. 15 p. 177). Within the group Cucujiformia, larvae of several lineages have setiferous lateral protrusions, apparently as a result of independent convergent evolution. We here report new fossil beetle larvae preserved in about 100-million-year-old Kachin amber, Myanmar and about 25-million-year-old Mexican amber. They also possess lateral protrusions resembling those of different cucujiformian larvae, but also differing from these in certain aspects. We discuss the implications of these new fossils concerning the evolution of larval characters in beetles and the importance of reporting fossil larvae.

Material and methods

Material

At the centre of this study are three new fossil specimens: SNHMB.G 8195, SNHMB.G 8196, and PED 1955. Two specimens (SNHMB.G 8195, with an old depository number MEX 011, and SNHMB.G 8196, with an old depository number BUB 1259) came from one of the authors (PM) and are now deposited in the Staatliches Naturhistorisches Museum Braunschweig, Germany. One specimen (PED 1955) is deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München, Germany. All three specimens were legally purchased.

Specimen SNHMB.G 8195 originates from approximately 25-million-year-old Miocene Mexican amber. Specimens SNHMB.G 8196 and PED 1955 originate from about 100-million-year-old Kachin amber, Myanmar. SNHMB.G 8196 was acquired by one of the authors (PM) in the year 2016. Specimen PED 1955 was acquired from the trading platform ebay.com from the trader burmite-miner.

Three specimens of extant fungus-eating larvae of Endomychidae from the Coleoptera Collection of the Natural History Museum of Denmark, Copenhagen (NHMD) are included for comparison. The specimens were preserved in glass jars and vials filled with ethanol without a depository number, organised alphabetically by the group and the land of origin. The specimen of *Endomychus biguttatus* was collected by Riley, C. J. in Tennessee on 17.02.1890. The specimen of *Endomychus coccineus* was collected under the bark of beech in Bonn, Germany on 1.6.1925. The specimen of *Eumorphus quadriguttatus* was collected in Sarawak in Borneo. Unfortunately, the labels within the vials were not well-readable and therefore we cannot provide more information on the extant specimens.

Documentation methods

All three of the fossil specimens were documented on a Keyence VHX-6000 digital microscope in front of white and black backgrounds. The specimens were 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 (see Haug et al. 2008, 2011; Kerp and Bomfleur 2011) with the built-in HDR function (cf. Haug et al. 2013b). All of the images were further processed with Adobe Photoshop CS2. Drawings of specimens from the literature were drawn with the free software Inkscape.

The extant specimens were photographed in the Coleoptera Collection at the National History Museum of Denmark (NHMD) in Copenhagen with macro-photography equipment. Each specimen was stored with multiple other specimens in 70% ethanol. For photographing purposes, each specimen of interest was placed in a separate Petri dish with 70% ethanol and covered with a coverslip. A Canon Rebel T3i digital camera equipped with a Canon MP-E 65 mm macro lens was used. A Yonguno YN24EX E-TTL twin flash provided illumination. Polarisers were placed on the lens and flashes (perpendicular to each other in order to produce cross-polarised light). Stacks were further processed with Combine ZP (Haug et al. 2008, 2011).

Morphological terminology

The usual 'entomological' terminology within the text is amended with more descriptive morphological terminology within the first description of a specimen. This is done in order to enhance the comprehensibility for non-experts. The descriptive terms apply to all of the specimens but are not repeated to facilitate easier reading of the text.

Results

Description of fossil specimen SNHMB.G 8195

Small larva. Total body length ~1.86 mm. Body oval in dorsal view, flattened dorso-ventrally, parallel-sided (Fig. 1A–C), differentiated into anterior head and posterior trunk. Head partially torn, partially inaccessible, possibly partly retracted under tergite of anterior part of trunk. No stemmata discernible. Labrum (derivative of ocular segment) partly discernible (Fig. 1E) with at least three strong setae on anterior rim (Fig. 1E arrow). Antennae (appendages of post-ocular segment 1) not accessible. Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (appendages of post-ocular segment 3) not accessible. Maxillae (appendages of post-ocular segment 4) with maxillary palp, partially discernible (Fig. 1E). Labium (appendages of post-ocular segment 5) not accessible.

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso- and metathorax). Prothorax sub-rectangular in

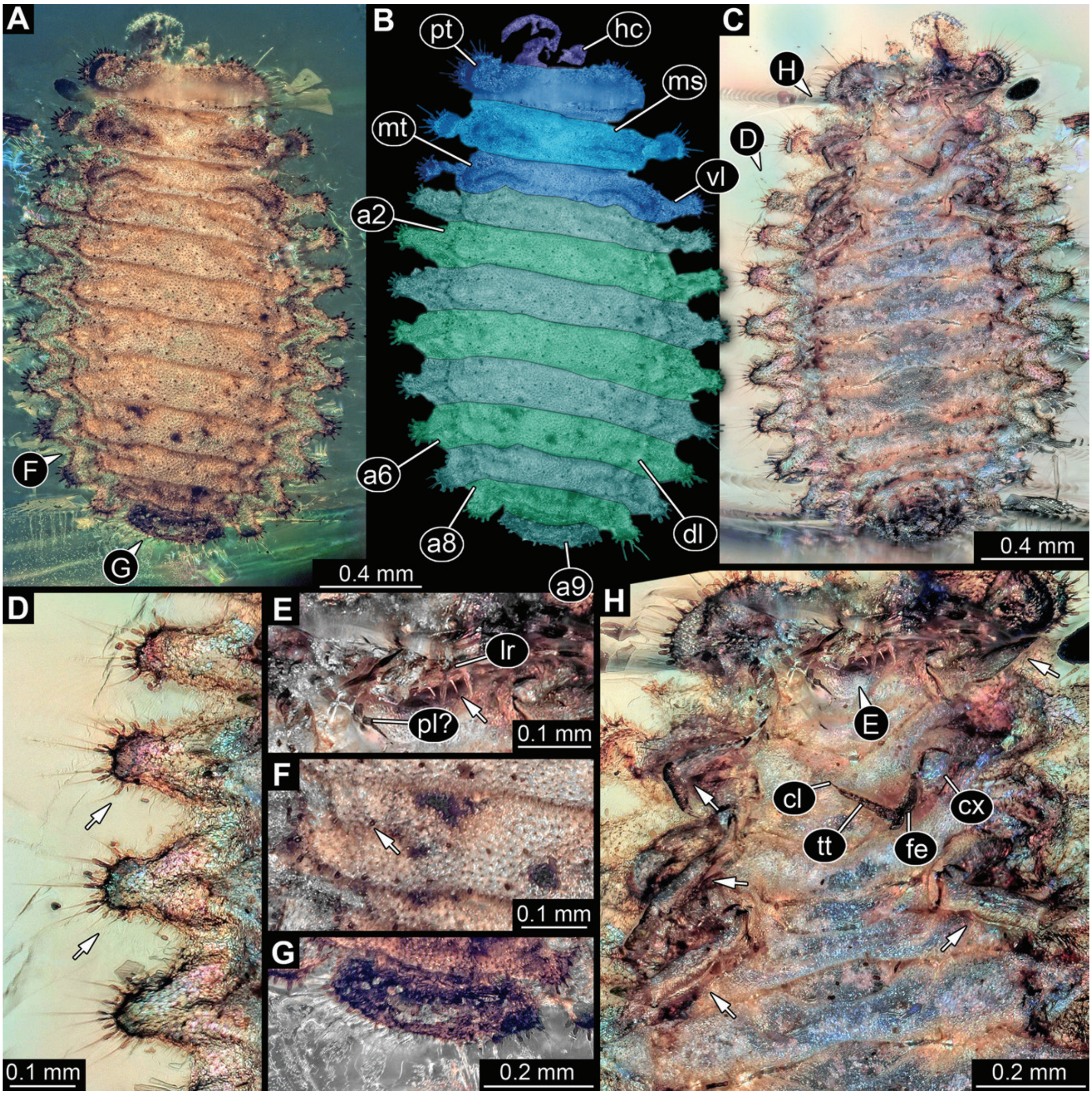

Figure 1. Fossil specimen SNHMB.G 8195, larva of Cucujiformia: **A.** Habitus in dorsal view; **B.** Colour-marked version of **A**; **C.** Habitus in ventral view; **D.** Close-up of lateral processes with specialized hairs (arrows) in ventral view; **E.** Close-up of probable head region in ventral view, arrow marks the strong hairs of possible labrum; **F.** Close-up of body surface in dorsal view, arrow marks the darker coloured wart; **G.** Close-up of abdomen segment 9 in dorsal view; **H.** Close-up of anterior part of the body in ventral view, arrows mark legs. **Abbreviations:** a2–9 = abdomen segments 2–9; cl = claw; cx = coxa; dl = dorso-lateral process; fe = femur; hc = head capsule; lr = labrum; ms = mesothorax; mt = metathorax; pl? = possible palp; pt = prothorax; tt = tibio-tarsus; vl = ventro-lateral process.

dorsal view, wider than long, 4.2× (~0.17 mm long) with convex lateral edges. Meso- and metathorax sub-similar in shape, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge. Mesothorax wider than long, 5.2× (~0.19 mm long; width including lateral processes). Metathorax wider than long, 8.2× (~1.11 mm long; width including lateral processes; Fig. 1A–C). Legs discernible, with five elements (Fig. 1H arrows): coxa (~0.14 mm long), trochanter (~0.08 mm long), femur (~0.16 mm long), tibio-tarsus (~0.14 mm long) and a claw (~0.02 mm long).

Abdomen segments 1–8 sub-similar, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge (Fig. 1D). Abdomen segments 1–8 wider than long (between 0.13–0.19 mm long and between 0.67–1.32 mm wide, including lateral processes). Abdomen segment 9 sub-trapezoid in dorsal view, wider than long, 3.4× (~0.12 mm long) (Fig. 1G). Trunk end (with possible pygopod) not discernible.

Dorsal surface of body bears very short irregularities of integument (asperities), not possible to interpret whether they are short setae or small spines, and small dark-coloured warts (Fig. 1F arrow). Lateral processes of trunk segments bear laterally relatively long tubercles (appear like enlarged warts) with longer simple setae distally (0.11–0.13 mm long). Abdomen segment 9 bears similar tubercles with longer simple setae posteriorly (Fig. 1G).

Description of fossil specimen SNHMB.G 8196

Small larva. Total body length ~2.47 mm. Body oval in dorsal view, flattened dorso-ventrally, parallel-sided (Fig. 2A–C), differentiated into anterior head and posterior trunk. Head semi-circular in dorsal view, partially covered in Verlumung (ventral view). No stemmata discernible. Labrum partly discernible with at least four shorter setae on anterior rim (Fig. 2E). Antennae discernible, elongated in dorsal view (~0.13 mm long), with at least three antennomers (elements of an antenna). Most distal element bears at least four strong setae distally (Fig. 2E). Intercalary segment without externally recognizable structures. Mandibles, maxillae and labium not accessible.

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso- and metathorax; Fig. 2B). Prothorax semi-ovaloid in dorsal view, wider than long, 4.1× (~0.2 mm long) with convex lateral edges drawn out into lateral processes, one per lateral edge. Meso- and metathorax sub-similar in shape, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge. Mesothorax wider than long, 4.4× (~0.22 mm long; width including lateral processes). Metathorax wider than long, 5.2× (~0.2 mm long; width including lateral processes) (Fig. 2A–C). Legs partially discernible, partially covered in Verlumung, with presumed five elements (Fig. 2D arrows): coxa, trochanter (not accessible), femur (partially accessible), tibio-tarsus and a claw.

Abdomen segments 1–7 sub-similar, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge (Fig. 2A–C). Abdomen segment 8 sub-similar, but with lateral edges and lateral processes orientated posteriorly. Abdomen segments 1–8 wider than long (between 0.13–0.18 mm long and between 0.54–1.04 mm wide, including lateral processes). Abdomen segment 9 sub-trapezoid, wider than long, 1.7× (~0.19 mm long), with anterior rim medially convex and posterior rim medially concave in dorsal view (Fig. 2F). Trunk end not accessible, covered by Verlumung (Fig. 2A).

Dorsal surface of body bears short irregularities of integument (asperities) and small dark-coloured warts (Fig. 2C). Anterior and lateral rims of head capsule bear multiple setae. Lateral processes of trunk segments bear laterally tubercles (appear like enlarged warts) with longer fringed setae (setae with distal tip forked in multiple smaller branches), distally (0.05–0.25 mm long) (Fig. 2F). Abdomen segment 9 bears similar tubercles with longer simple setae posteriorly, but also shorter ones which are broader distally and possibly fringed (Fig. 2F).

Description of fossil specimen PED 1955

Small larva. Total body length ~2.41 mm. Body oval, slightly elongated in dorsal view, flattened dorso-ventrally, parallel-sided (Fig. 3A–C), differentiated into anterior head and posterior trunk. Head sub-trapezoid in ventral view, wider than long, 2.4× (~0.13 mm long); partially covered by other inclusions (dorsal view) (Fig. 3C), partially covered by Verlumung (ventral view) (Fig. 3A), possibly partly retracted under anterior part of trunk. No stemmata discernible. Labrum not clearly discernible (Fig. 3A). Antennae only partially accessible, only one antenna partially discernible (Fig. 3A arrow). Intercalary segment without externally recognizable structures. Mandibles not clearly accessible. Maxillae not clearly accessible. Labium not clearly accessible.

Trunk further differentiated into anterior thorax and posterior abdomen (Fig. 3B). Thorax with three segments (pro-, meso- and metathorax). Prothorax sub-rectangular in dorsal view, wider than long, 3.4× (~0.18 mm long) with convex lateral edges. Meso- and metathorax sub-similar in shape, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge. Mesothorax wider than long, 4.2× (~0.17 mm long; width including lateral processes). Metathorax wider than long, 4.8× (~0.17 mm long; width including lateral processes) (Fig. 3A–C). Legs discernible, with five elements (Figs 3A, D): coxa, trochanter, femur, tibio-tarsus and a claw (Fig. 3D arrow).

Abdomen segments 1–8 sub-similar, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, one per lateral edge. Abdomen segments 1–8 wider than long (between 0.15–0.23 mm long and between 0.67–0.84 mm wide, including lateral

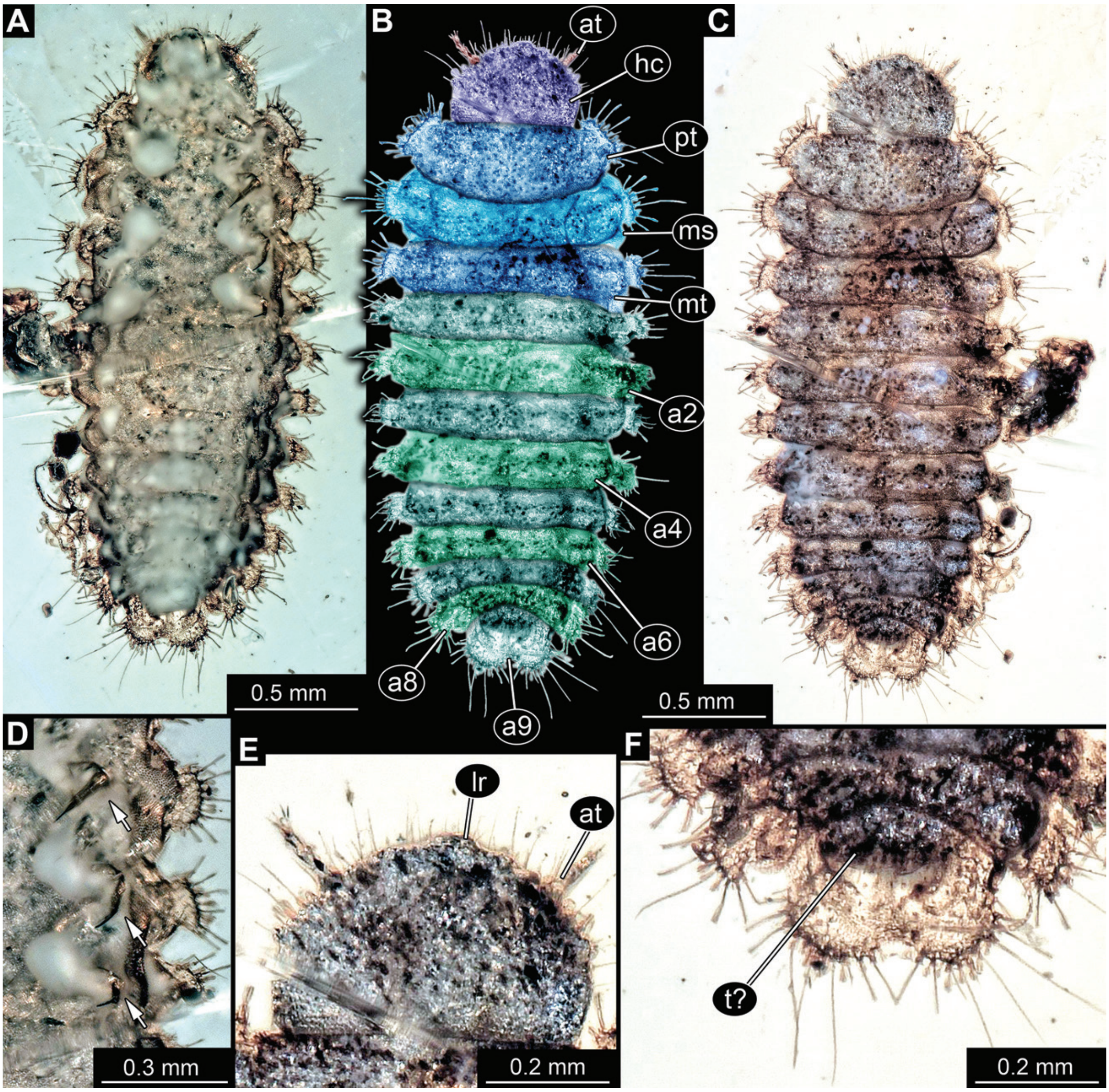

Figure 2. Fossil specimen SNHMB.G 8196, larva of Cucujiformia: **A.** Habitus in ventral view; **B.** Colour-marked version of **C**; **C.** Habitus in dorsal view; **D.** Close-up of legs and lateral processes with hairs in ventral view, arrows mark the legs; **E.** Close-up of head in ventral view; **F.** Close-up of posterior part of abdomen. **Abbreviations:** a2–9 – abdomen segments 2–9; at – antenna; hc – head capsule; lr – labrum; ms – mesothorax; mt – metathorax; pt – prothorax; t? – possible trunk end.

processes). Abdomen segment 9 sub-trapezoid, wider than long, 2.5× (~0.14 mm long), with posterior rim medially concave in ventral view and posteriorly with two processes (possible urogomphi; ~0.09 mm long), cone-shaped (with distal tips posteriorly orientated; Fig. 3E). Trunk end (with possible pygopod) partly discernible in ventral view (Fig. 3E: t?), surrounded by abdomen segment 9, closer to anterior rim of abdomen segment 9 than to its posterior rim.

Dorsal surface of body with paired darker patches per all three thorax and abdomen tergites 1–8. Within patches small dark-coloured warts discernible (Fig. 3C). Similar patches on lateral processes discernible. Lateral processes of trunk segments bear laterally setae which are broader distally and possibly fringed (maximally 0.18 mm long) (Fig. 3F). Abdomen segment 9 bears similar fringed setae along lateral and posterior edge, but also single simple longer setae near posterior processes (Fig. 3A, E).

Description of extant specimen of *Endomychus biguttatus*

Small larva. Total body length ~4.89 mm. Body oval in dorsal view, flattened dorso-ventrally (Fig. 4A, E), differentiated into anterior head and posterior trunk. Head hypognathous (mouth parts facing downwards), ovaloid in ventral view, completely hidden by first sclerite of

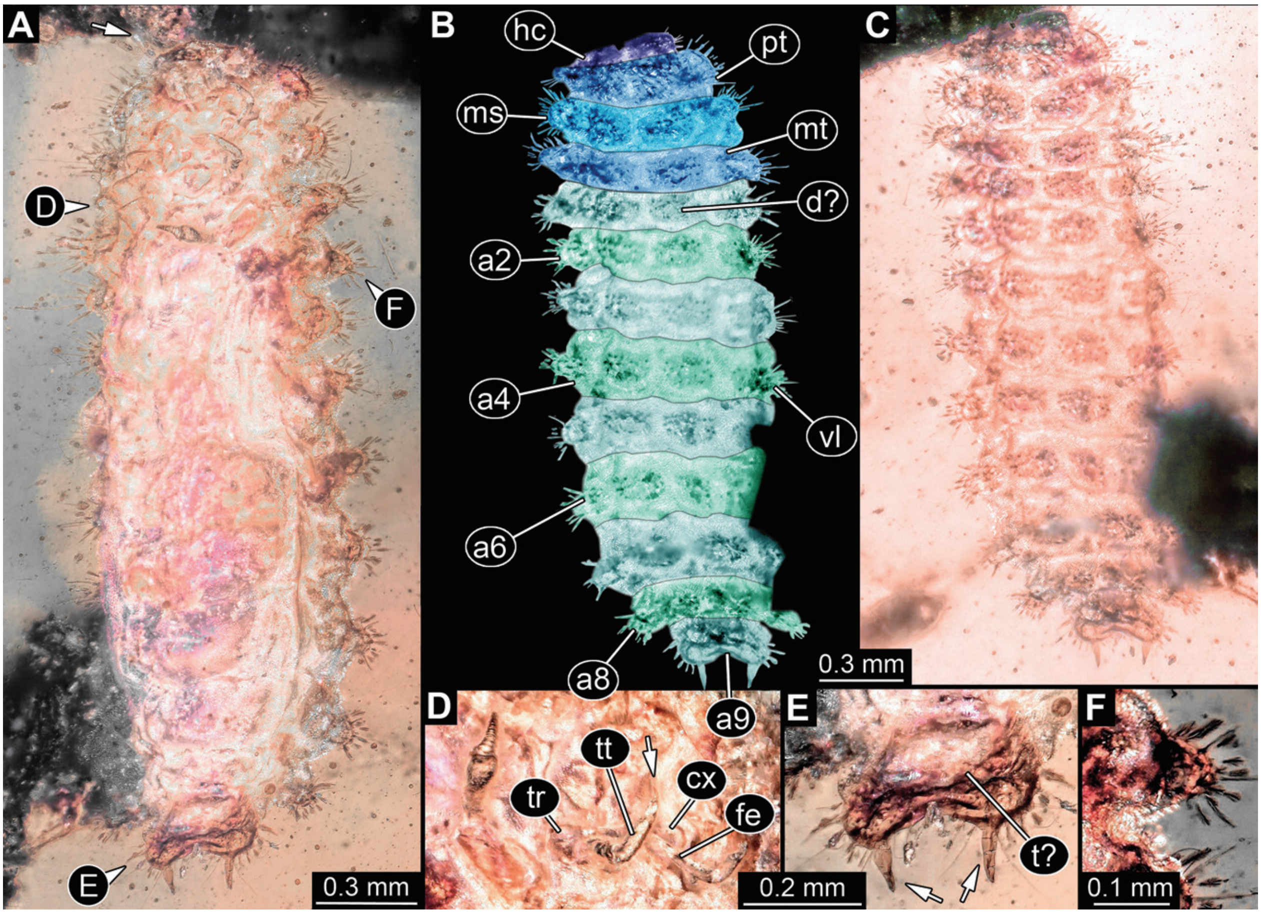

Figure 3. Fossil specimen PED 1955, larva of Cucujiformia: **A.** Habitus in ventral view, arrow marks the possible antenna; **B.** Colour-marked version of **C**; **C.** Habitus in dorsal view; **D.** Close-up of legs in ventral view, arrow marks the claw (image was turned 90 degrees to the right); **E.** Close-up of abdomen segment 9 in ventral view, arrows mark the posterior processes; **F.** Close-up of ventro-lateral processes with specialized hairs. **Abbreviations:** a2–9 – abdomen segments 2–9; cx – coxa; d? – possible dorso-lateral process; fe – femur; hc – head capsule; ms – mesothorax; mt – metathorax; pt – prothorax; t? – possible trunk end; tr – trochanter; tt – tibio-tarsus; vl – ventro-lateral process.

anterior part of trunk in dorsal view, wider than long, 1.8× (~0.51 mm long). No stemmata discernible in ventral view, four stemmata on each side presumed. Labrum discernible, wider than long, with anterior rim medially slightly concave in ventral view (Fig. 4D). Antennae discernible, one partially covered by other body parts, elongated, longer than wide (~0.51 mm long), with three antennomeres (elements of an antenna). Intercalary segment without externally recognizable structures (Fig. 4B). Mandibles not discernible in ventral view. Maxillae discernible, each with cardo proximo-laterally, sub-triangular in ventral view; with stipes in middle, elongate in ventral view; with single endite medially, longer than wide, with multiple short setae; and maxillary palp distally (Fig. 4D). Palp, longer than wide (~0.18 mm long), with three palpomeres (elements of a palp), on membranous area. Labium sub-trapezoid in ventral view, with a pair of palps. Each palp longer than wide (~0.07 mm long), with two palpomeres (elements of a palp) on membranous area (Fig. 4D).

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso- and metathorax). Prothorax semi-circular in dorsal view, with convex posterior edge, wider than long, 2× at maximum width (~1.06 mm long). Lateral edges of prothorax postero-laterally drawn out; medially longitudinal line discernible (Fig. 4A). Meso- and metathorax sub-similar in shape, sub-trapezoid in dorsal view, with convex lateral edges; medially with distinct longitudinal line. Edges of tergite drawn out posteriorly into dorso-lateral processes, one per lateral edge. Mesothorax wider than long, 4.2× (~0.59 mm long; width including lateral processes). Metathorax wider than long, 3.9× (~0.64 mm long; width including lateral processes; Fig. 4). Legs discernible, with five elements (Fig. 4F): coxa (~0.62 mm long), trochanter (~0.22 mm long), femur (~0.47 mm long), tibio-tarsus (~0.55 mm long) and a claw (~0.15 mm long).

Abdomen segments 1–8 sub-similar, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, a dorso-lateral and a ventro-lateral one per edge (Fig. 4G). Abdomen segments 1–8 wider than long (between 0.26–0.39 mm long and between 1.11–2.64 mm wide, including lateral processes). Abdomen

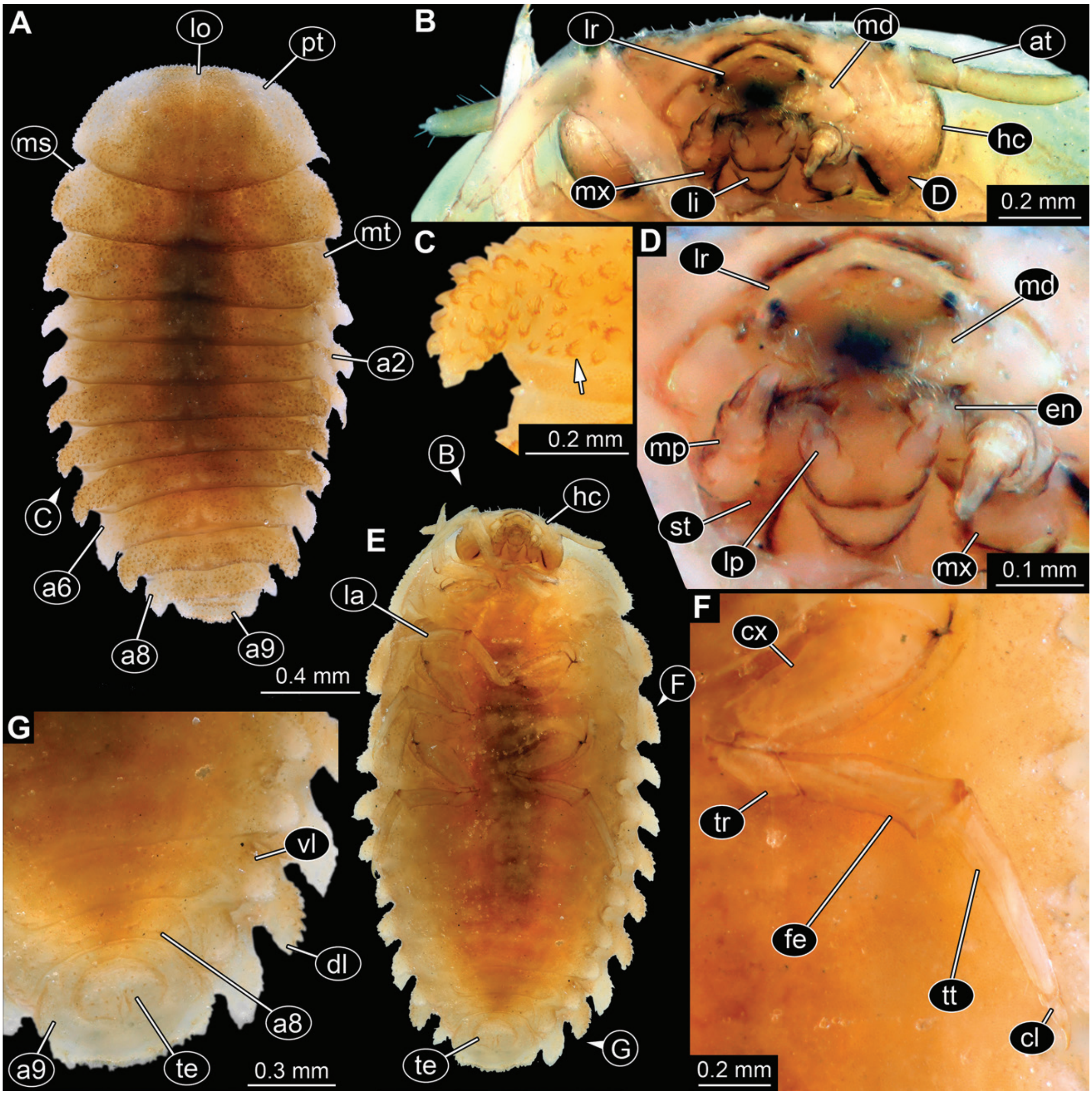

Figure 4. Extant specimen of larva of *Endomychus biguttatus*, Endomychidae: **A.** Habitus in dorsal view; **B.** Close-up of head in ventral view; **C.** Close-up of dorso-lateral process in dorsal view, arrow marks a wart; **D.** Close-up of mouth parts in ventral view; **E.** Habitus in ventral view; **F.** Close-up of a leg in ventral view; **G.** Close-up of posterior part of abdomen in ventral view. **Abbreviations:** a2–9 – abdomen segments 2–9; at – antenna; cl – claw; cx – coxa; dl – dorso-lateral process; en – endite; fe – femur; hc – head capsule; la – locomotory appendages (legs); li – labium; lo – longitudinal line; lp – labial palp; lr – labrum; md – mandible; mp – maxillary palp; ms – mesothorax; mt – metathorax; mx – maxilla; pt – prothorax; st – stipes; te – trunk end; tr – trochanter; tt – tibio-tarsus; vl – ventro-lateral process.

segment 9 sub-trapezoid in dorsal view, wider than long, 4.3× (~0.16 mm long) (Fig. 4A). Trunk end (with possible pygopod) only accessible in ventral view, ovaloid, with indentation medio-posteriorly, dorsally not visible as concealed by abdomen segment 9, closer to anterior rim of abdomen segment 9 than to its posterior rim (Fig. 4G).

Dorsal surface of body, including the processes, bears small darker-coloured warts (Fig. 4C arrow). Abdomen segment 9 bears similar tubercles also posteriorly (Fig. 4).

Description of extant specimen of *Endomychus coccineus*

Small larva. Total body length ~6.44 mm. Body oval in dorsal view, flattened dorso-ventrally (Fig. 5A, D), differentiated into anterior head and posterior trunk. Head hypognathous (mouth parts facing downwards), semi-circular in dorsal view, wider than long, 1.2× (~0.81 mm long), with two lighter lines discernible (arms of moulting suture) (Fig. 5C arrows). Single stemma discernible, but additional three per side presumed (Fig. 5G). Labrum discernible, wider than long (~0.27 mm wide) (Fig. 5C). Antennae discernible, elongated, longer than wide (~0.55 mm long), with three antennomeres (elements of an antenna) (Fig. 5C). Intercalary segment without externally recognizable structures. Mandibles partially discernible, mostly concealed by other mouth parts (Fig. 5G). Maxillae discernible, each with cardo proximo-laterally, sub-triangular in ventral view; with stipes in middle, elongate in ventral view; with single endite medially, longer than wide, with multiple short setae; and maxillary palp distally (Fig. 5G). Palp longer than wide (~0.21 mm long), with three palpomeres (elements of a palp), at proximal part membranous area discernible. Labium sub-trapezoid in ventral view, with a pair of palps. Each palp longer than wide (~0.08 mm long), with two palpomeres (elements of a palp), on proximal part membranous area discernible (Fig. 5G).

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-,

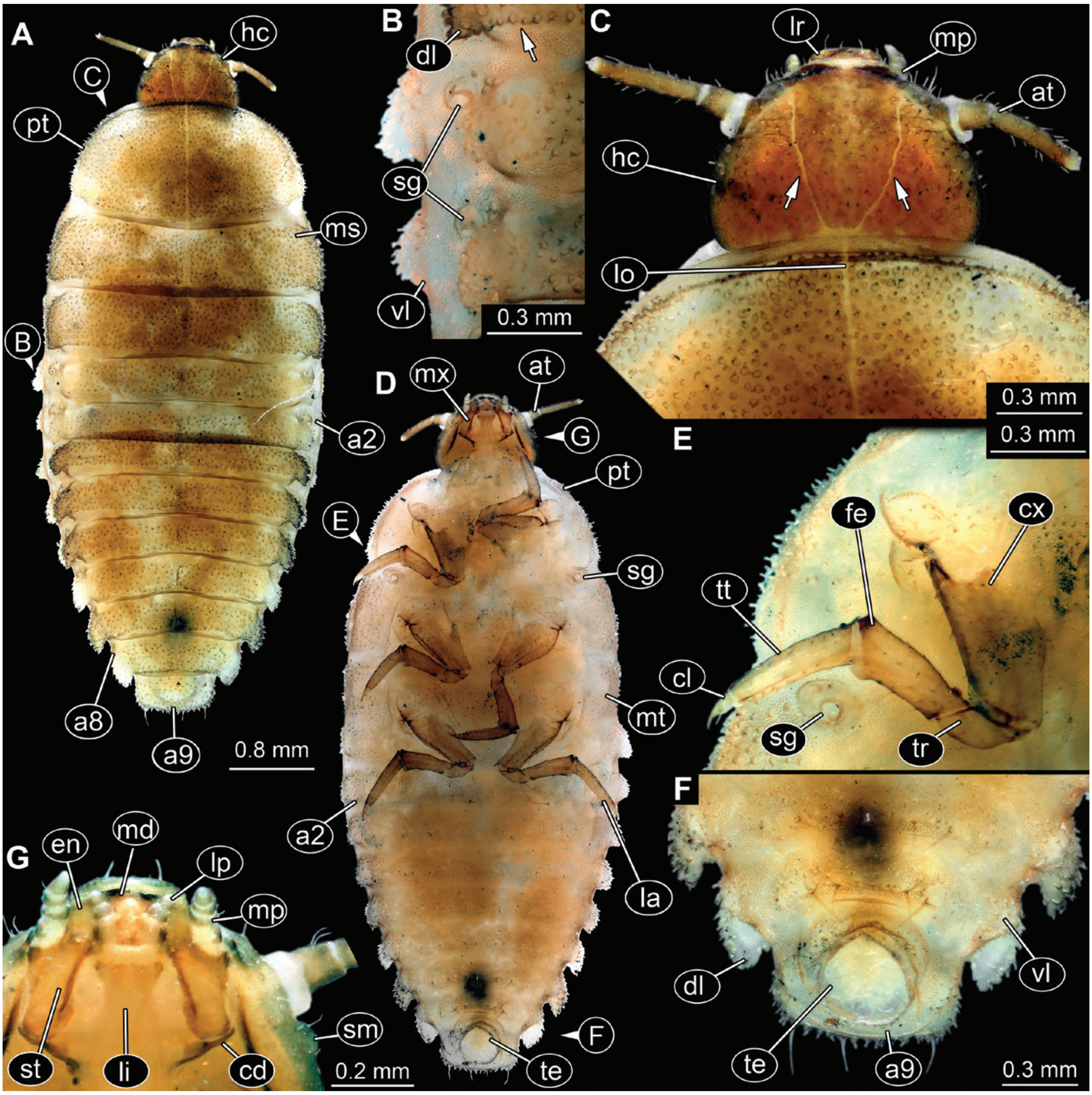

Figure 5. Extant specimen of larva of *Endomychus coccineus*, Endomychidae: **A.** Habitus in dorsal view; **B.** Close-up of lateral processes and stigmata in dorsal view, arrow marks a wart; **C.** Close-up of head in dorsal view, arrows mark the arms of epicranial suture; **D.** Habitus in ventral view; **E.** Close-up of a leg in ventral view; **F.** Close-up of posterior part of abdomen in ventral view; **G.** Close-up of head in ventral view. **Abbreviations:** a2–9 – abdomen segments 2–9; at – antenna; cd – cardo; cl – claw; cx – coxa; dl – dorso-lateral process; en – endite; fe – femur; hc – head capsule; la – locomotory appendages (legs); li – labium; lo – longitudinal line; lp – labial palp; lr – labrum; md – mandible; mp – maxillary palp; ms – mesothorax; mt – metathorax; mx – maxilla; pt – prothorax; sg – stigma; sm – stemma; st – stipes; te = trunk end; tr – trochanter; tt – tibio-tarsus; vl – ventro-lateral process.

meso- and metathorax). Prothorax semi-circular in dorsal view, with posterior edge convex, wider than long, 1.7× at maximum width (~1.22 mm long). Lateral edges of prothorax postero-laterally drawn out; medially with prominent longitudinal line (Fig. 5A). Meso- and metathorax sub-similar in shape, sub-rectangular in dorsal view, with convex lateral edges; medially with prominent longitudinal line. Edges drawn out posteriorly into short dorso-lateral processes, one per lateral edge (Fig. 5A). Mesothorax wider than long, 3.3× (~0.77 mm long; width including lateral processes). Metathorax wider than long, 3.1× (~0.84 mm long; width including lateral processes) (Fig. 5A). Legs discernible, with five elements (Fig. 5E): coxa (~0.69 mm long), trochanter (~0.27 mm long), femur (~0.45 mm long), tibio-tarsus (~0.57 mm long) and a claw (~0.12 mm long).

Abdomen segments 1–8 sub-similar, sub-rectangular in dorsal view, with convex lateral edges drawn out into lateral processes, a dorso-lateral and a ventro-lateral one per edge (Fig. 5A, B, F). Abdomen segments 1–8 wider than long (between 0.19–0.41 mm long and between 1.17–2.74 mm wide, including lateral processes). Abdomen segment 9 sub-rectangular in dorsal view, wider than long, 1.3× (~0.55 mm long) (Fig. 5A). Trunk end (with possible pygopod) only accessible in ventral view, sub-circular in shape, dorsally not visible as concealed by abdomen segment 9, closer to anterior rim of abdomen segment 9 than to its posterior rim (Fig. 5F).

Dorsal surface of body, including the processes, bears small darker-coloured warts (Fig. 5A, C). Abdomen segment 9 bears similar tubercles also posteriorly and some longer simple setae.

Description of extant specimen of *Eumorphus quadriguttatus*

Larva. Total body length ~11.57 mm. Body oval in dorsal view, flattened dorso-ventrally (Fig. 6A), differentiated into anterior head and posterior trunk. Head hypognathous (mouth parts facing downwards), sub-pentagonal in ventral view, partially hidden by first sclerite of anterior part of trunk in dorsal view, wider than long, 2.4× (~1.03 mm long), with two lighter lines discernible (arms of epicranial suture), anterior rim with short setae. Multiple stemmata discernible (Fig. 6B arrows), exact number not obvious. Labrum discernible, wider than long, 2.3× (~0.22 mm wide), sub-pentagonal in ventral view, with anterior rim medially slightly concave and multiple setae antero-laterally (Fig. 6C). Antennae discernible, elongated, longer than wide (~0.8 mm long), with three antennomeres (elements of an antenna), at proximal part membranous area discernible. Intercalary segment without externally recognizable structures. Mandibles partially discernible, mostly hidden by other mouth parts (Fig. 6C). Maxillae partially discernible, with cardo inaccessible; with partially discernible stipes in the middle; with single endite medially, with multiple short setae; and maxillary palp distally (Fig. 6C). Palp longer than wide (~0.38 mm long), with three palpomeres (elements of a palp), at proximal part membranous area discernible. Labium (appendages of post-ocular segment 5) partially discernible, with a pair of palps. Each palp longer than wide (~0.11 mm long), with two palpomeres (elements of a palp), at proximal part membranous area discernible.

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso- and metathorax). Prothorax semi-circular in dorsal view, wider than long, 2.3× at maximum width (~1.7 mm long). Tergite of prothorax bears antero-laterally cone-shaped processes with multiple setae, one per side; medially longitudinal line discernible. Antero-lateral processes ~1.2 mm long. Meso- and metathorax subsimilar in shape, sub-rectangular in dorsal view, with convex lateral edges; medially longitudinal line discernible. Lateral edges of tergites convex, bear antero-laterally cone-shaped processes with multiple setae, one per side. Mesothorax wider than long, 3.6× (~1.35 mm long; width without lateral processes). Metathorax wider than long, 5× (~1.1 mm long; width without lateral processes; Fig. 6A). Antero-lateral processes between 1.64–1.66 mm long. Legs discernible, with five elements (Fig. 6D): coxa (~1.06 mm long), trochanter (~0.53 mm long), femur (~0.89 mm long), tibio-tarsus (~1.49 mm long) and a claw (~0.16 mm long).

Abdomen segments 1–8 sub-similar, sub-rectangular in dorsal view. Lateral edges of tergites convex, bear laterally cone-shaped processes with multiple setae, a dorso-lateral and a ventro-lateral one per edge (Fig. 6A), ventral processes shorter than dorsal ones. Abdomen segments 1–8 wider than long (between 0.74–0.98 mm long and between 3.32–6.44 mm wide, without lateral processes). Abdomen segment 9 only partially accessible in dorsal view, sub-hexagonal in ventral view, wider than long, 1.7× (~0.98 mm long) (Fig. 6E). Postero-lateral edges of abdomen segment 9 posteriorly drawn out into processes (~0.41 mm long) with multiple setae. Trunk end (with possible pygopod) only accessible in ventral view, sub-circular, dorsally not visible while concealed by abdomen segment 9, wider than long, 2.2× (~0.43 mm long), closer to anterior rim of abdomen segment 9 than to its posterior rim (Fig. 6E).

Discussion

Identity of the new fossils: beetle larvae of Cucujiformia

All three new fossils have a segmented body arranged into a head and a trunk, which is further differentiated into a thorax with three leg-bearing segments (and no wings) and an abdomen with legless segments (Figs 1–3). Also, no genitalia or compound eyes are accessible. This character combination indicates that the new fossils are immature stages of the group Holometabola (Lawrence 1991a). In addition, abdomen leg derivatives, such as sometimes seen in Lepidoptera and Hymenoptera, and antennae with

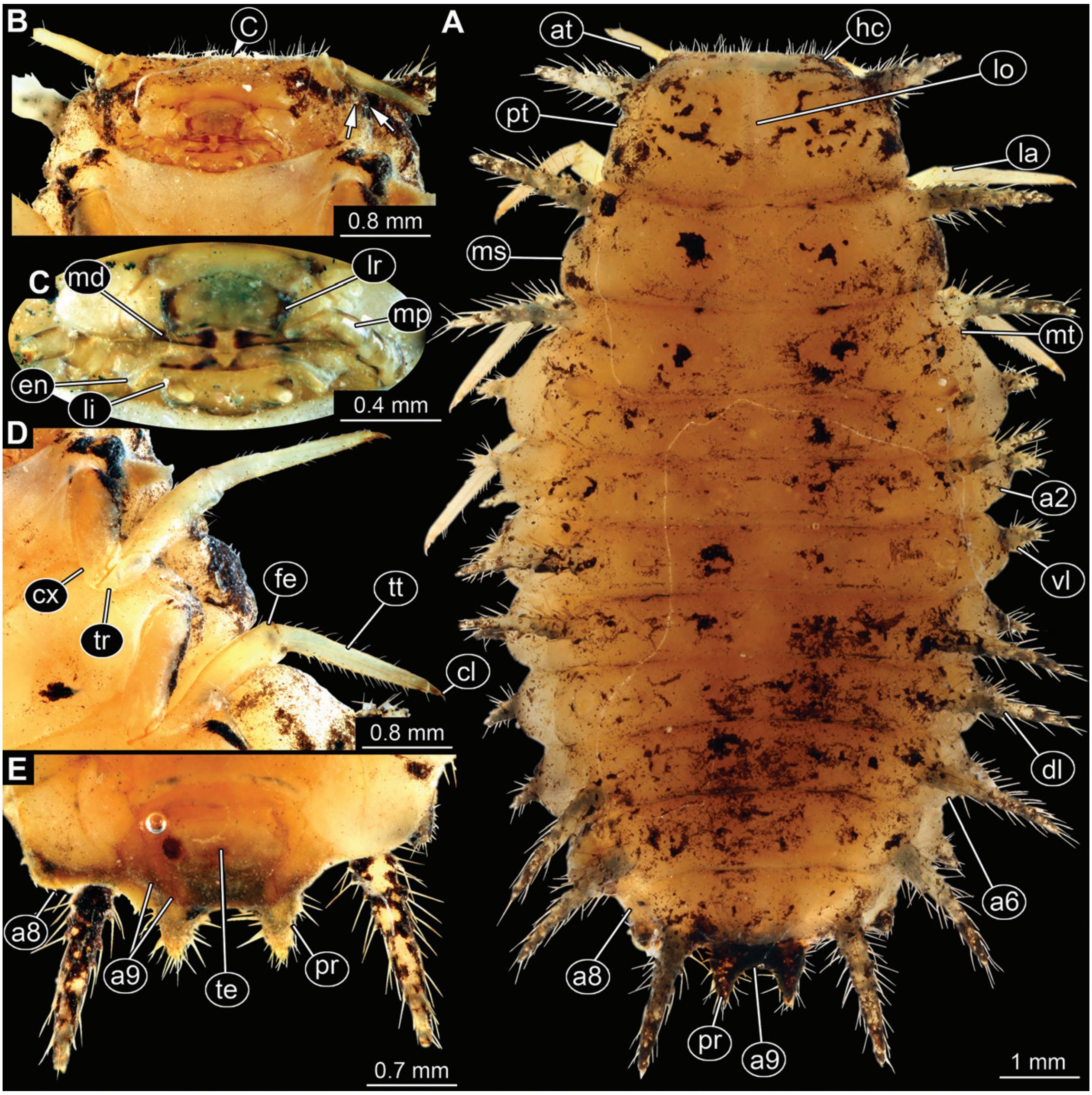

Figure 6. Extant specimen of larva of *Eumorphus quadriguttatus*, Endomychidae: **A.** Habitus in dorsal view; **B.** Close-up of head in ventral view, arrows mark stemmata; **C.** Close-up of mouth parts in ventral view; **D.** Close-up of legs in ventral view; **E.** Close-up of posterior part of abdomen in ventral view. **Abbreviations:** a2–9 – abdomen segments 2–9; at – antenna; cl – claw; cx – coxa; dl – dorso-lateral process; en – endite; fe – femur; hc – head capsule; la – locomotory appendages (legs); li – labium; lo – longitudinal line; lr – labrum; md – mandible; mp – maxillary palp; ms – mesothorax; mt – metathorax; pr – process; pt – prothorax; te – trunk end; tr – trochanter; tt – tibio-tarsus; vl – ventro-lateral process.

more than four elements, such as seen in early lineages of Hymenoptera (Lawrence 1991a), are also not discernible.

The lack of certain characteristics and a strongly sclerotized head capsule (Peterson 1957; Beutel and Lawrence 2005) imply that the new fossils are immature stages of beetles (Coleoptera). More precisely, the legs with five elements imply that these are the immatures of either Myxophaga or Polyphaga. However, the larvae of Myxophaga have spiracle gills on most of the abdomen segments (Beutel 2005), which are not discernible on any of the new fossils. The dorso-ventrally flattened habitus with multiple trunk processes of the new fossil larvae resembles the habitus of some larvae of the group Cucujiformia. More precisely, larvae with such processes are known in Erotylidae (pleasing fungus beetles; Fig. 7E, H; Lawrence 1991b; Ruta et al. 2011; Zaitsev et al. 2016), Cerylonidae (minute bark beetles; Lawrence 1991c), Coccinellidae (ladybird beetles; Kapur 1950; LeSage 1991), or Endomychidae (handsome fungus beetles; Figs 4–6, 7A–D, F, G, I–L; Leschen and Carlton 1988; Lawrence 1991d; Burakowski 1997; McHugh and Pakaluk 1997; Zaitsev 2022a, 2022b) and other ingroups.

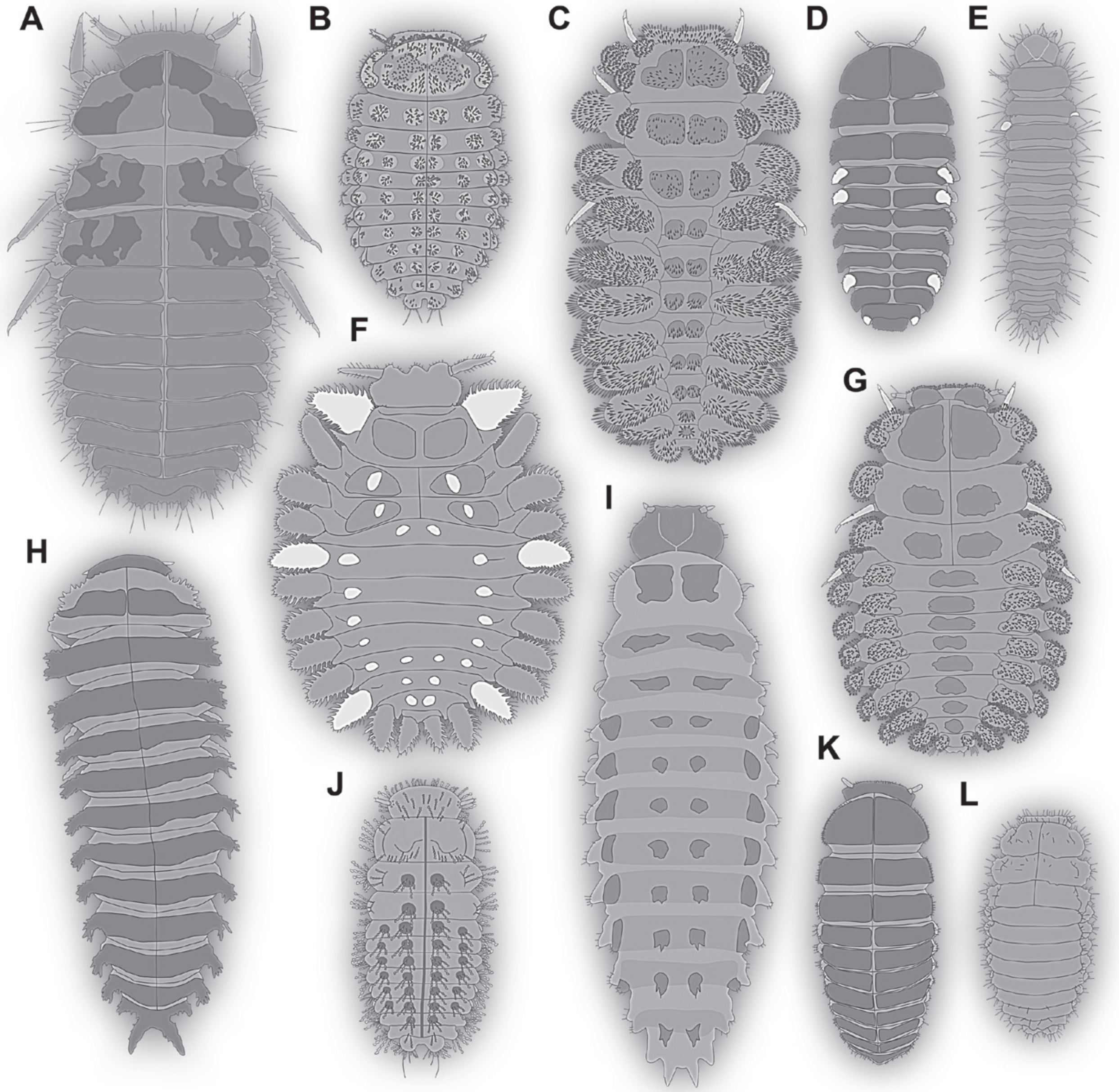

Figure 7. Examples of extant larvae of Endomychidae (**A–D, F, G, I–L**) and Erotylidae (**E, H**) with processes, modified after literature: **A.** *Stenotarsus commodus* from McHugh and Pakaluk (1997 fig. 42 p. 74); **B.** *Mycetina cruciata* from Burakowski (1997 fig. 1 p. 210); **C.** *Andrytus* from McHugh and Pakaluk (1997 fig. 1 p. 60); **D.** *Endomychus coccineus* from Tomaszewska and Zaitsev (2012 fig. 29b p. 89); **E.** *Cryptophilus integer* from Ruta et al. (2011 fig. 2 p. 4); **F.** *Amphisternus corallifer* from Yoshitomi and Sogoh (2018 fig. 1 p. 225); **G.** *Epipocus* from McHugh and Pakaluk (1997 fig. 18 p. 66); **H.** *Episcapha morawitzi* from Zaitsev et al. (2016 fig. 23 p. 372); **I.** *Lycoperdina dux* from Tomaszewska and Zaitsev (2012 fig. 29a p. 89); **J.** First stage larva of *Mycetina cruciata* from Burakowski (1997 fig. 20 p. 212); **K.** Last stage larva of *Ectomychus basalis* from Tomaszewska and Zaitsev (2012 fig. 2 p. 83); **L.** *Mycetina marginalis* from Tomaszewska and Zaitsev (2012 fig. 28c p. 86).

After McKenna et al. (2015) Erotylidae is an ingroup of Cucujoidea; Cerylonidae, Coccinellidae and Endomychidae are all ingroups of Coccinelloidea. Since in both groups, Cucujoidea and Coccinelloidea, processes are present rather often, it could be argued that this overall habitus is ancestral for either both groups or even their shared stem-species (≈ancestor) and has been lost in all other ingroups of Cucujoidea and Coccinelloidea. Nevertheless, it is also possible, if not even more likely, that the ingroups with processes developed them several times independently through convergent evolution.

Convergence is a quite common phenomenon among beetles in general and also beetle larvae (see also Haug et al. 2023b). Coleoptera as a whole and also many ingroups of it are extremely species-rich. This extreme species richness indicates that many lineages underwent rather rapid speciation events. This should have led to many different species with rather similar overall morphology. When several of these species were exposed to similar selective pressures, it should not be surprising that several of these evolved similar morphological traits.

Differences among the extant larvae of Endomychidae and the new fossils

The new fossil larvae resemble in some characters the larvae of extant representatives of Endomychidae (cf. Figs 1–3 and Figs 4–6). Similarities to the modern larvae include the dorso-ventrally flattened body, the antennae morphology in SNHMB.G 8196, the lateral processes and their position on the body, and the specialised setae of the processes (Figs 1–3, 7). Additionally, the shapes of abdomen segment 9 of SNHMB.G 8196 and SNHMB.G 8195 in dorsal view are similar to the shapes of abdomen segment 9 of certain modern larvae.

However, there are multiple differences between the new fossils and the extant larvae of Endomychidae. The new fossil larvae are relatively small in body size compared to the extant larval representatives with lateral processes (Burakowski 1997; McHugh and Pakaluk 1997; Tomaszewska and Zaitsev 2012; Yoshitomi and Sogoh 2018; also to the new extant specimens described here in Figs 4–6). It is possible that not all here described larvae are of the same life stage. Nevertheless, the difference in size between the extant and fossil larvae is obvious. A comparable effect of differences in size over time was already described from larvae of other insect groups (Zippel et al. 2022b), but also adults in Myanmar amber (e.g., Wichard 2021). Hence the fossil larvae could be later-stage larvae of overall small-sized animals.

In addition to the difference in body shape among the new fossils, they also differ in the morphology of the tergite of the abdomen segment 9. Each of the fossils has a different shape of this tergite in dorsal view. The fossil specimen SNHMB.G 8195 has a fan-shaped tergite that has no medial indentation of the posterior rim. A rather similar morphology is present in extant larvae of *Endomychus* (Figs 4, 5 and Leschen and Carlton 1988). The fossil specimen SNHMB.G 8196 has the posterior rim of the tergite medially indented and laterally convex. The tergite seems almost bilobed. A similar morphology is known in extant larvae of *Mycetina* (Tomaszewska and Zaitsev 2012; Zaitsev 2022a). However, the shape of the head capsule of the new fossil and the extant larvae differs greatly (cf. Fig. 2 and Tomaszewska and Zaitsev 2012: fig. 28.c; Zaitsev 2022a: figs 3, 29, 58). Indeed, the specimen SNHMB.G 8196 resembles in some characters the larva of *Sticholotis ruficeps* (Coccinellidae). On one hand, the modern larva has similar lateral processes and head shape to the fossil. On the other hand, the tergite of the abdomen segment 9 of the modern larva differs from the tergite seen in the new fossil (Escalona and Ślipiński 2010, fig. 37). The tergite of abdomen segment 9 is narrow and medially convex but not indented. Among the three new fossils, only the specimen SNHMB.G 8195 has a tergite without the medial indentation. However, the tergite of the larva of *Sticholotis ruficeps* is much narrower than the tergite of the specimen SNHMB.G 8195.

The fossil larva PED 1955 is the most slender one of the new fossils. Its tergite of abdomen segment 9 has a similar shape to that of SNHMB.G 8196, but it has additional posterior processes, which possibly represent urogomphi; see Fig. 3). Urogomphi are rare in extant larvae of Endomychidae (Tomaszewska 2005). A combination of a medially indented posterior rim of abdomen tergite 9 and possible urogomphi (as seen in specimen PED 1955) seems unknown in extant larvae of Endomychidae. The distal parts of the possible urogomphi resemble more those of the larvae of *Omosita nearctica* (Nitidulidae; Williams et al. 2021 their fig. 3) than the known posterior processes of larvae of Endomychidae (for comparison check the larva of *Eumorphus quadriguttatus* in Fig. 6).

Overall, the differences could mean that the fossils are not representatives of the group Endomychidae, they may not even be closely related to the group. As pointed out, there are several groups with larvae carrying lateral processes comparable to those of the fossils (Endomychidae and Erotylidae; Fig. 7; Genung et al. 1980; Carlton et al. 2000; Skelley 2009; Ruta et al. 2011; Zaitsev et al. 2016, Coccinellidae; Ślipiński and Tomaszewska 2005, fig. 10.33.7.B, Escalona and Ślipiński 2010, fig. 37). The new fossils may be more closely related to either of these groups or represent one (or even more) additional lineage(s) that is (are) now extinct, which evolved larvae with such processes. Yet, it is also possible that the morphology of the fossils, with their combinations of characters, is no longer present among the extant larvae of Endomychidae, but that they represent early offshoots of the group. Examples of today's extinct morphologies have been recognised for some groups of Holometabola (Badano et al. 2018, 2021; Haug et al. 2019a, 2019b, 2021c, 2022a; Zippel et al. 2021, 2023). Despite the uncertainty of interpretation and limited access to crucial characters, it seems likely that the new fossils are larvae of the group Cucujiformia, with some implications that the fossil SNHMB.G 8195 is a representative of Endomychidae. However, the relationship of the other two fossils, SNHMB.G 8196 and PED 1955, to the ingroups of Cucujiformia remain uncertain.

Adult representatives of Endomychidae are known in Kachin amber (Tomaszewska et al. 2018, 2022; Li et al. 2022b). Interestingly, even though the evolutionary history of Coccinellidae was traced back to the Cretaceous (McKenna et al. 2019), not a single fossil of Coccinellidae is known from that period. The oldest fossil reported is of an adult from the Eocene French Oise amber (Kirejtshuk and Nel 2012). Additional fossils have been also reported from Eocene Baltic amber (Szawaryn and Szwedo 2018; Szawaryn 2019; Szawaryn and Tomaszewska 2020). Hence, a possible relationship of the specimens to the representatives of Coccinellidae must be interpreted carefully.

Ecology of the new fossils

Many of the extant larvae of Cucujiformia spend most of their immature life in decaying wood infested with fungi. Some of the examples are larvae with setiferous processes of the groups Erotylidae, Cerylonidae and Endomychidae (Leschen and Carlton 1988; Lawrence 1991b, 1991c, 1991d; Burakowski 1997; McHugh and Pakaluk 1997; Leschen et al. 2005; Ruta et al. 2011; Zaitsev et al. 2016; Zaitsev 2022a, 2022b). Few representatives have a dorso-ventrally flattened body that allows them to live within small crevices, often directly underneath the bark (Leschen et al. 2005; Ślipiński and Lawrence 2005; Tomaszewska 2005). Some are even obligatory fungus-feeders and are specialized in a single species of fungi (Tomaszewska 2005). The processes with specialized setae are probably helping in defence or hunting, which would explain why so many larval representatives of Coccinellidae also still have a similar morphology (Ślipiński and Tomaszewska 2005). The processes might also be helpful in feeding upon the fungi-infested wood. If we presume that these larvae are not predaceous (as larvae of Brachypsectridae; Haug et al. 2021b or most of the larvae of Coccinellidae; Ślipiński and Tomaszewska 2005), the processes will unlikely be used for any hunting strategy. Therefore, it is much more likely that the processes have a role in defence mechanisms such as camouflaging. Cloaking as a defence mechanism is one of the behaviours already known from some larvae of Endomychidae (Tomaszewska 2005) and can be seen in other holometabolan larvae as well (Wang et al. 2016; Machado et al. 2019; Haug et al. 2022b, 2022c, 2022d). The processes of the new larvae may help in cloaking themselves with hyphae or spores of the fungi as well. Such camouflage is probably additionally useful to stay unnoticed by a predator (Tomaszewska 2005) and have easier access to food. Similar strategies of decorating with hyphae are also seen in the brood care of some adults of Endomychidae. The female representatives of *Endomychus biguttatus* wrap hyphae around the individual eggs to physically protect them (Leschen 1994).

In some species the first-stage larvae do not have strongly pronounced processes, for example, the first instar of *Endomychus biguttatus* (Fig. 1; Leschen and Carlton 1988, their fig. 3). It has only slightly posteriorly drawn out lateral edges of trunk segments. However, the later stages, which are also much larger in size, have much more pronounced processes. This can naturally be due to the growth of the animal. Alternatively, it is possible that having the processes is of advantage only for the older (often also relatively larger) stages. Smaller larvae might rather have an "escape strategy" than a "camouflage one". If we consider their often small size, the "escape strategy" might be the less costly one since they can easily fit in small crevices in the bark or wood.

Despite the overall uncertainty of the interpretation of the new larvae, it seems likely that they had a similar lifestyle to extant larvae with similar setiferous processes. Therefore it seems most likely that they were wood-associated. In the case of the specimen SNHMB.G 8195, which has many characters similar to the modern larvae of Endomychidae, a similar lifestyle of feeding upon fungi can be presumed as well. However, in the cases of the specimens PED 1955 and SNHMB.G 8196, we cannot surely imply such a lifestyle because some modern representatives of Cucujiformia lead different lifestyles. For example, the modern larvae of Coccinellidae can be mycophagous, phytophagous, or predaceous, but Leschen (2000) and Ślipiński and Tomaszewska (2005) implied that the predaceous lifestyle is likely a derived one. Therefore, even if one of the new fossil specimens would be an early representative of Coccinellidae, a fungus-feeding lifestyle of the fossil representatives would still be possible.

Diversity of ecological roles

Wood-associated lifestyles of specimens preserved in amber are not surprising. In Kachin amber (Cretaceous, Myanmar) many different wood-associated ecological roles have been recognised (Peris 2020; Peris and Rust 2020), including hard-wood borers (Peris 2020; Haug et al. 2021a), soft-wood borers (Zippel et al. 2022b, in press a), submerged wood borers (Zippel et al. in press b), predators of wood-eating larvae (Haug et al. 2021b; Peris et al. 2022), but also larvae that possibly feed on fungi-infested rotting wood (Tomaszewska et al. 2018; Zippel et al. 2023; Haug et al. 2023b). The new fossils add to the latter category but possess a rather different overall appearance than the already known forms.

In younger ambers in the Eocene also numerous wood-associated larvae of different types are known (Larsson 1978; Klausnitzer 2003; Gröhn 2015; Haug et al. 2021b, 2023a; Zippel et al. 2022c). In Miocene amber many of these wood-associated larvae have so far not been reported, besides the "wood predators" (Haug et al. 2021b). Recognising one of the new larvae (specimen SNHMB.G 8195) as a possible wood-associated fungus feeder is, therefore, an important amendment to the Miocene amber fauna.

Conclusion

The three new larvae are an important addition to the amber fauna of the Cretaceous and Miocene. All new fossils are likely larvae of the group Cucujiformia, with characteristic setiferous processes and some other characters shared with modern larvae of Endomychidae. The characteristic setiferous processes are present in many larvae of Cucujiformia, not only in Endomychidae. It seems likely that setiferous processes in the larvae of different ingroups of Cucujifromia evolved as a response to similar selective pressures and are the result of convergent evolution. The processes in the new fossils might have had a function in hunting, but also in defence and camouflaging. They likely helped while, at least some of, the new larvae were feeding on fungi.

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