Article

Quantitative morphology of fossil adephagan beetle larvae including a first record from the Jehol biota does not indicate major diversity losses over time

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Abstract

Coleoptera is a hyper-diverse group of animals with about 400,000 formally described species. Also the morphological diversity of beetles is very high, not only in the adults, but also in the larvae. To understand the evolutionary origin of this enormous diversity, investigations of fossils are crucial, but especially for the larvae such fossil are still scarce. In this study, we present 15 new fossil larvae from different deposits of Cretaceous to Miocene age, which we interpret as larvae of the beetle ingroup Adephaga. Most of these are three-dimensionally preserved and either embedded in amber or silicified. One specimen is a compression fossil, which is very rare for beetle larvae, and represents the first report of an adephagan beetle larva from the Early Cretaceous Jehol biota of China. Of all previously known and new fossil adephagan larvae and of selected extant ones the shapes of the head capsules and mandibles were compared with quantitative morphology methods (elliptic Fourier analysis and principal component analysis). The shapes of the fossil larvae lie all within the morphospace of those of the extant larvae, which indicates that the highest diversity in this aspect is present in the modern fauna, hence no diversity loss occurred. Other lineages of Holometabola show similar patterns, with indications of larval diversifications already in the Cretaceous, further specialisation afterwards, and no major losses. This pattern may be a reason for the enormous species richness of certain holometabloan groups in the modern fauna.

Key words: Adephaga, Coleoptera, Cretaceous, quantitative morphology, biodiversity

Introduction

Coleoptera, the group of beetles, rules the organismic world, at least when we restrict our view to animals. The large species richness of beetles is in fact that of polyphagan beetles with far over 300,000 formally described species (McKenna *et al.* 2019). However, also adephagan beetles comprise more than 45,000 formally described species (McKenna *et al.* 2019) and likely have already been part of the early diversification events of Holometabola. Many beetles have rather stereotypical appearance when they are adults, especially concerning the sclerotised and non-overlapping forewings (elytra) with a distinct median line, a reason why many people appear to be able to identify them as beetles (though without any more detailed identification). On the contrary, the larvae of beetles seem to be more variable concerning their overall appearance, for example, some are elongate worm-shaped without any lateral structures, while others possess prominent laterally protruding gills, long legs, strongly exposed mouthparts, or spine-like protrusions on the trunk region; coupled to that, they appear more diverse concerning their ecological functions (e.g. Introduction in Stehr 1991 p. xv).

To understand the enormous evolutionary success of beetles, looking into the past should be informative. Hence, the fossil record of beetles needs to be further explored. Adult beetles, as outlined above, can be rather easily recognised as such also as fossils. In addition, their hardened forewings, elytra, seem to have a high preservation potential, often being the only remnant of a fossil beetle (Kundrata *et al.* 2020; Schädel *et al.* 2022 and references therein). Therefore, it should not be surprising that the fossil record of adult beetles reaches into the Late Palaeozoic with undoubted finds in the Permian and possible older finds (e.g. Schädel *et al.* 2022; Goczał & Beutel 2023; see recent summary in Beutel *et al.* 2024).

The fossil record of beetle larvae, which would be important for understanding the ecological functions better, is very scarce. Even in amber, which can preserve very soft individuals and those of minute size, beetle larvae are relatively underrepresented (e.g. Klausnitzer 2003). This situation is likely coupled to the taxonomic challenges when dealing with beetle larvae. Ultimately this leads to a situation in which quite some fossils are present in amber, but they are simply not reported. Beetle larvae in sedimentary rocks seem even rarer than those in amber and so far remain true exceptions (Wang *et al.* 2009; Prokin *et al.* 2013; Kirejtshuk 2020 fig. 3). In other lineages closely related to beetles (Neuroptera, Raphidioptera) a focussed search for fossil larvae and a comparison in a quantitative morphological frame, circumventing many challenges coupled to taxonomic issues, has been successfully used to study changes in diversity (e.g. Haug *et al.* 2022a, 2023).

Here we report new fossils of adephagan beetle larvae, including a first report from the Early Cretaceous Jehol biota, China. We furthermore aim at establishing a quantitative morphological frame as a basis for comparing diversity of adephagan beetle larvae over time.

Material and methods

Material

In total, we report 15 new fossil individuals here, all interpreted as larvae of the group Adephaga. One specimen is a compression fossil deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, with repository number NIGP206314. It was collected from tuffaceous mudstone in the Lower Cretaceous Yixian Formation at Huangbanjigou outcrop, Beipiao City, Liaoning Province, northeastern China. The Yixian Formation has yielded abundant fossils belonging to the scope of the Early Cretaceous Jehol Biota.

Five amber pieces originate from Late Cretaceous Kachin amber, Myanmar, and contain six individuals. Four amber pieces are part of the collection of one of the authors (PM) under repository numbers BUB 3996, BUB 4214, BUB 4777 and BUB 4828, the latter containing two individuals). One amber piece is part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany, under repository numbers PED 2552. The specimen was legally purchased on the trading platform ebay.com from the trader burmite-miner.

Three amber pieces originate from Eocene Baltic amber. Two are deposited at the Senckenberg Naturmuseum Frankfurt under repository numbers SMF Be 289 and SMF Be 372. One specimen is part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany under repository numbers PED 1954. It was legally purchased via the trading platform etsy.com from the trader AmberusShop.

One amber piece originates from Mexican amber. It is part of the collection of one of the authors (PM) under repository number MEX 009.

Four silicified specimens originate from the Miocene Barstow formation, Mojave desert, USA. One specimen is deposited at the Smithsonian National Museum of Natural History, Washington D.C. under repository number USNM 561990; the specimen is glued onto a triangular piece of cardboard, which is needled. Two specimens are from the Museum of the University of Tübingen (MUT). They are mounted with glue in a Franke cell onto numbered grids. The object slide has the repository number GEO-Ps-24626. The two specimens sit on grid positions 17 and 36. The fourth specimen is mounted with glue in a Franke cell. It is part of the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany under repository numbers PED 4417. It was legally purchased on the trading platform ebay.com from the trader sdfossils.

Documentation methods

All specimens besides USNM 561990 were documented on a Keyence VHX-6000 digital microscope. For the amber specimens the surface was covered with a drop of glycerol and a cover slip. All images are composite images combining several focus layers per image detail into a sharp image and combing several image details into one large panorama. In addition, the HDR function was used in most cases. Specimen USNM 561990 was documented with a DCM 510 ocular camera mounted onto a Nikon SMZ-U microscope. As the specimen has a rather high relief, it was documented with a stack of images instead of a single image, which was then fused to a single image with the software CombineZM.

Shape analysis

For a broader comparative frame we used all fossils of adephagan larvae with accessible mandibles. Extant counterparts were chosen from the groups Dytiscidae, Gyrinidae, and Carabidae, also here representatives with prominent mouthparts. Most of these specimens come from literature data (details in Supplementary Table 1 and Supplementary Text 1).

Larvae are much less often reported and depicted than their adult counterparts. This phenomenon is coupled to the fact that palaeontological research, as already pointed out, has still a strong focus on taxonomy, and taxonomy is focused on adults, leading to the fact that many experts largely ignore larvae (making suggestions by Beutel & van Vondel 2024 not executable). This habit is furthermore unfortunate as the larvae often are the more important life phase concerning, for example, biomass, diversity of ecological roles, or positions in the food web.

Luckily at least some adephagan beetle larvae have been reported that provide enough detail to use them in a quantitative morphological analysis. Few specimens are known in the Miocene (Palmer 1957), but only one larva of Dytiscidae is usable for the analysis. Eocene ambers (especially Baltic amber) have provided larvae of Dytiscidae, Gyrinidae, and Carabidae (Weitschat & Wichard 2002; Wichard *et al.* 2009; Gröhn 2015), in total ten specimens. Nine specimens have been recovered from Cretaceous Kachin amber, Myanmar (Zhang 2017; Zhao *et al.* 2019; Gustafson *et al.* 2020; Liu *et al.* 2023a, b; Rosová *et al.* 2023; Li *et al.* 2024). Five usable specimens were found in older sedimentary deposits (Wang *et al.* 2009; Prokin *et al.* 2013). In total, these are 25 specimens of informative fossil adephagan larvae from the literature. Of the 15 specimens newly described here, 14 could be included in the shape analysis.

There are few more fossils preserved, but which can not be used in the here performed analysis. Especially unfortunate is the condition of certain larvae of Dytiscidae, known in the extant fauna and in Baltic amber, that have a complex nasale. Due to this structure it was not possible to effectively align the mandibles for these (they would cross with protrusions of the nasale), and we therefore had to exclude some fossils (Wichard *et al.* 2009).

The outline of the head capsule and mandible were digitally drawn using Adobe Illustrator CS2 or Adobe Photoshop CS2. The head capsule was halved medially; in fossils the better preserved half was used as a basis. The mandible was oriented in a standardised way (Haug *et al.* 2023).

Further analysis was performed with the software package Shape (see details in Braig *et al.* 2019), including an elliptic Fourier analysis (EFA) of the outline of head capsule with mandible of 166 specimens, 127 extant ones and 39 fossil ones (Supplementary Table 1), followed by a principal component analysis (PCA). Values of the first two principal components explaining most of the variation (PC1 and PC2) were plotted against each other using OpenOffice Calculator, then re-drawn and visualised with different versions of Adobe Photoshop.

Description

The central new finding of this contribution is in fact the new larva from the Jehol biota, and a more detailed description is provided for this specimen. For other specimens only short descriptions with highlights of observed details are provided.

Results

New specimen from the Jehol biota NIGP206314

Body elongate, organised into distinct head and trunk (Fig. 1A, B). Head in dorsal view wider than long. Anterior margin medially drawn out (labrum?; Fig. 1C, D). Lateral margins straight. Posterior margin indented. No clear indications of eyes apparent. Antenna elongate, about as long as head capsule, with at least five elements (antennomeres), possibly more. No external structures of intercalary segment apparent (Fig. 1C, D).
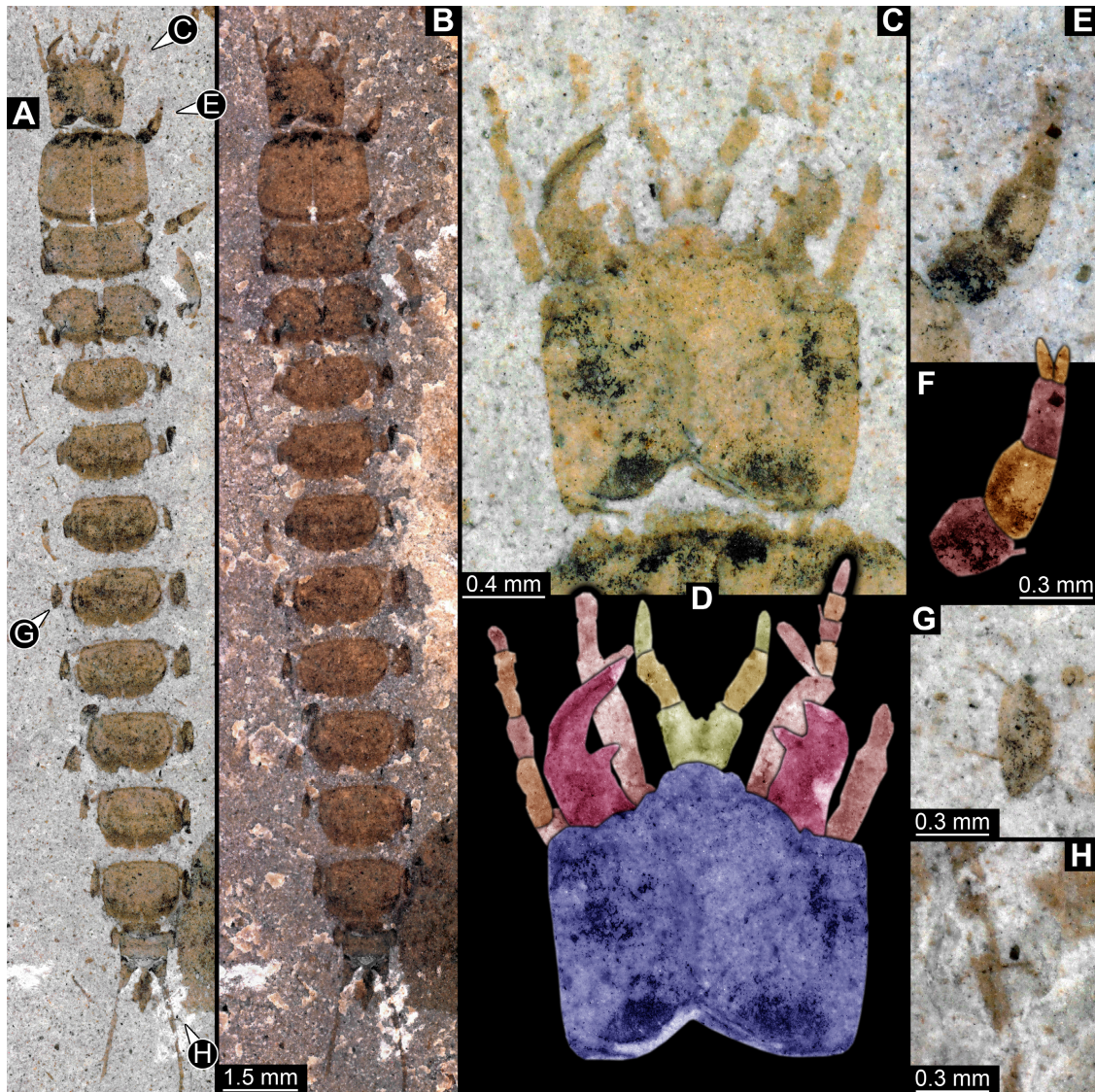

FIGURE 1. NIGP206314, Jehol biota. **A**, **B**, Overview in dorsal view. **A**, Dry conditions. **B**, With thin alcohol film. **C**, Close-up of head. **D**, Colour-marked version of **C**. **E**, First pair of legs. **F**, Colour-marked version of **E**. **G**, Sclerite flanking tergite of abdomen with setae. **H**, Detail of urogomphus with setae.

Mandible prominent, but shorter than head capsule; overall sickle-shaped, but with prominent tooth on the inner margin. Maxilla elongate. Proximal part (stipes?) elongate, about as long as mandible; disto-medially with a prominent endite (galea?). Distally with palp with four elements (palpomeres; Fig. 1C, D).

Trunk with twelve units indicated by dorsal sclerites (tergites), eleven segments and trunk end (amalgam of several segments and growth zone; Fig. 1A, B). Tergite 1 (pronotum) longer and wider than head capsule, wider than long, anterior and posterior rims rounded, slightly protruding. Medially with a distinct suture (moulting suture). First pair of legs with three major elements (femur, tibia tarsus?) and a pair of distal claws apparent (Fig. 1E, F).

Tergite 2 (mesonotum) about as wide as pronotum, but shorter; lateral rims appear more complex, either having

flanking sclerites or broken pieces. Also with median suture. Pieces of second pair of legs present, similar to first pair of legs. Tergite 3 (metanotum) similar to mesonotum.

Tergites 4–10 (of abdomen segments 1–7) sub-similar, narrower than preceding tergites, but about as long; posterior rim with small indentation (indication of suture?). Flanking sclerites well apparent, in well preserved cases with two prominent setae (Fig. 1G). Tergite 11 (of abdomen segment 8) more elongate than preceding ones, posterior rim rounded and drawn out.

Trunk end narrower and shorter, roughly rectangular in dorsal view, wider than long. Postero-laterally with a protruding elongate structure on each side (urogomphus), at least as long as two of the anterior abdomen tergites. With few setae preserved (Fig. 1H), possibly originally with numerous setae. Postero-median structure interpreted as remains of protruding anal membrane (pygopod), longer than trunk end, but incompletely preserved, no further details available.

New specimen from Kachin amber PED 2552

Elongate larva with prominent mouthparts (Fig. 2A–C, E). Legs with a pair of claws each (Fig. 2D). Abdomen segments with prominent feathery gills.
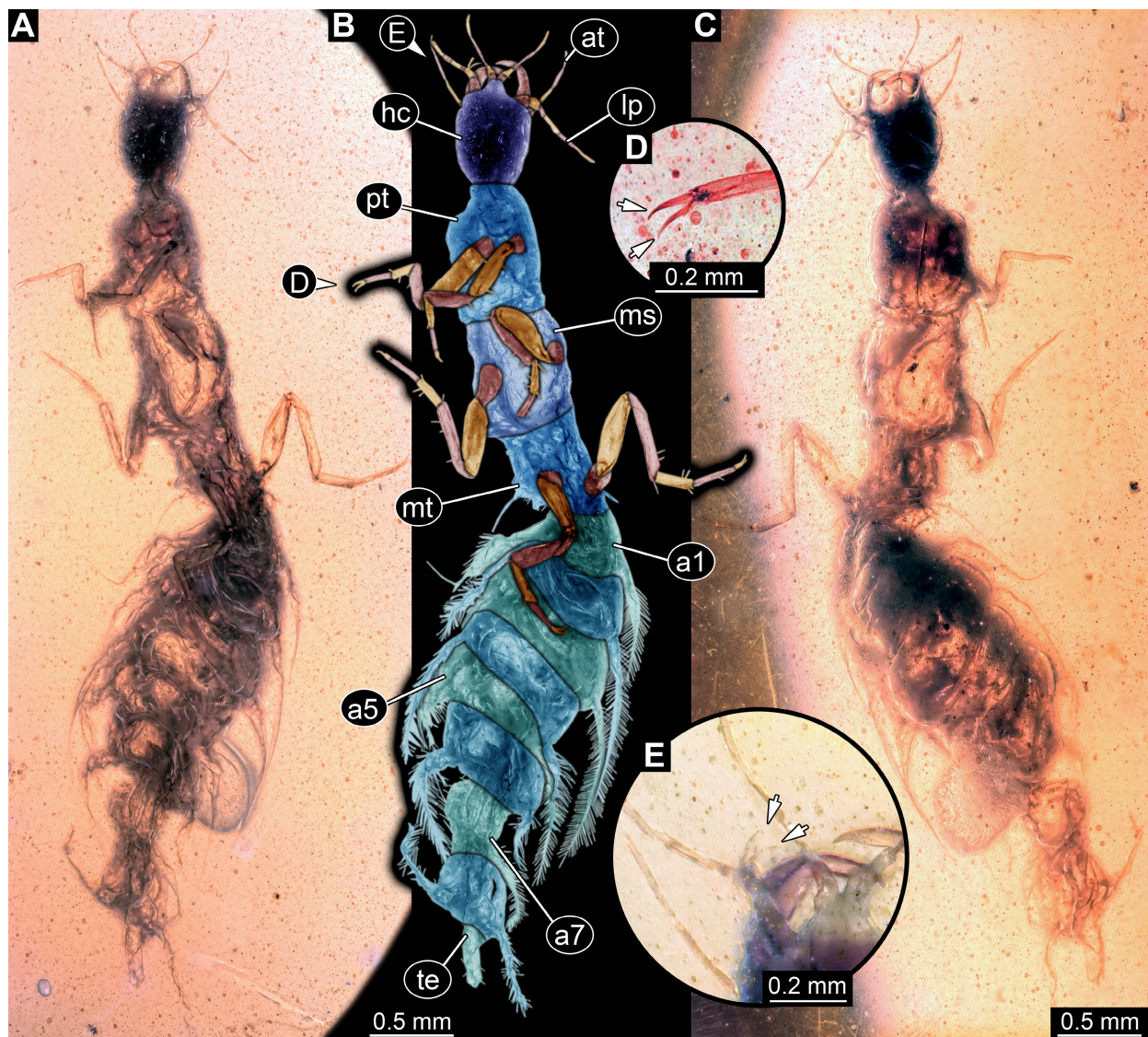

FIGURE 2. PED 2552, Kachin amber. **A**, Overview in ventral view. **B**, Colour-marked version of **A**. **C**, Overview in dorsal view. **D**, Distal end of first pair of legs, arrows mark claws. **E**, Close-up of mouthparts, arrows mark claws. Abbreviations: a1–a7 = abdomen segment 1–7; at = antenna; hc = head capsule; lp = palp of labium; ms = mesothorax; mt = metathorax; pt = prothorax; te = trunk end.

New specimen from Kachin amber BUB 4828a

Preserved together with a second specimen (see next point). Elongate larva (Fig. 3A, C) with prominent mouthparts (Fig. 3B, D). Legs with a pair of claws each (Fig. 3A). Abdomen segments with prominent feathery gills.
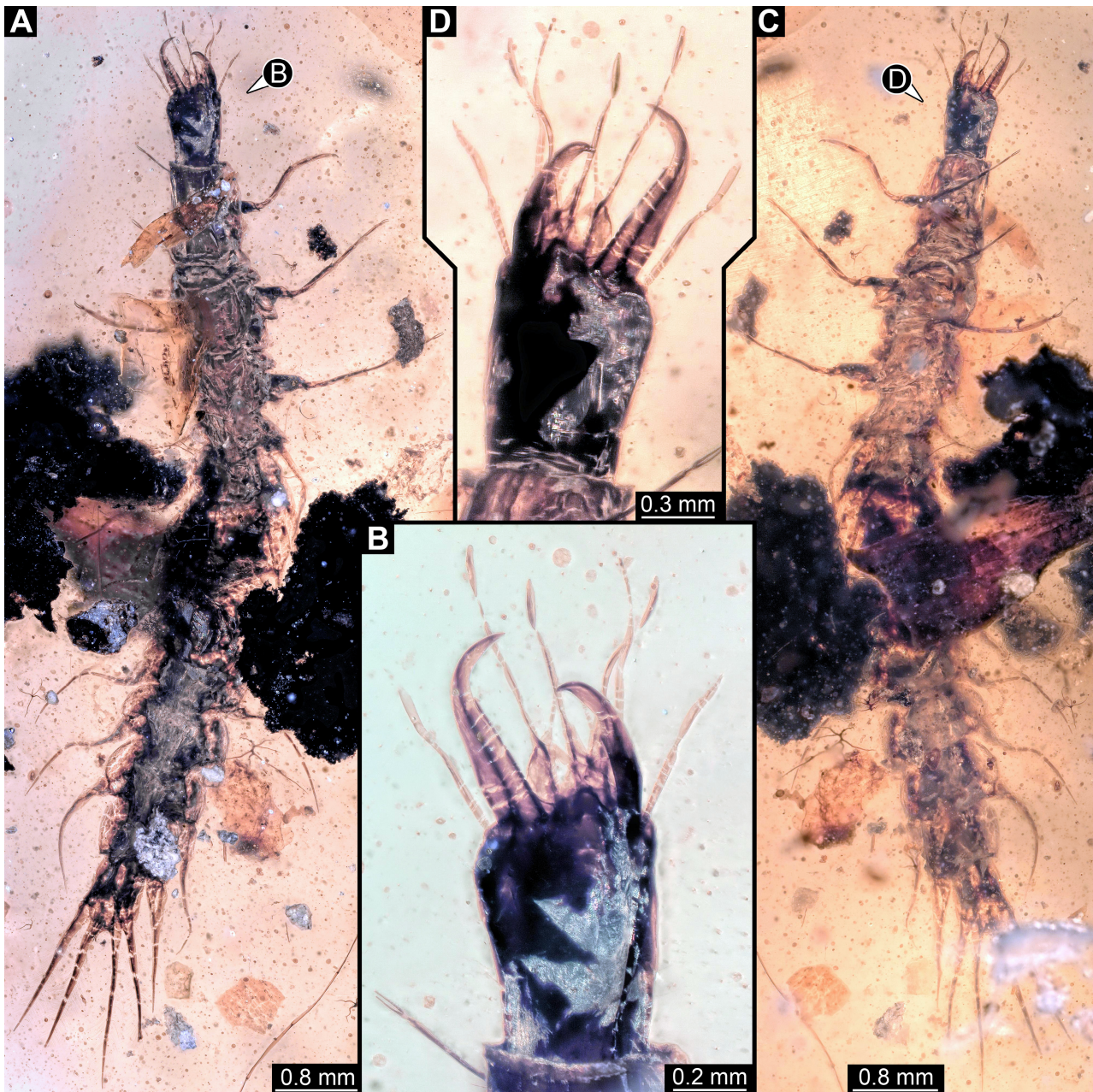

FIGURE 3. BUB 4828a, Kachin amber. **A**, Overview in dorsal view. **B**, Close-up of head in dorsal view. **C**, Overview in ventral view. **D**, Close-up of head in ventral view.

New specimen from Kachin amber BUB 4828b

Preserved together in the same amber with the preceding specimen. Incompletely preserved (Fig. 4A, C). Only head and anterior two trunk segments, the posterior one strongly damaged. Mouthparts prominent (Fig. 4B, D), legs distally each with a pair of claws.
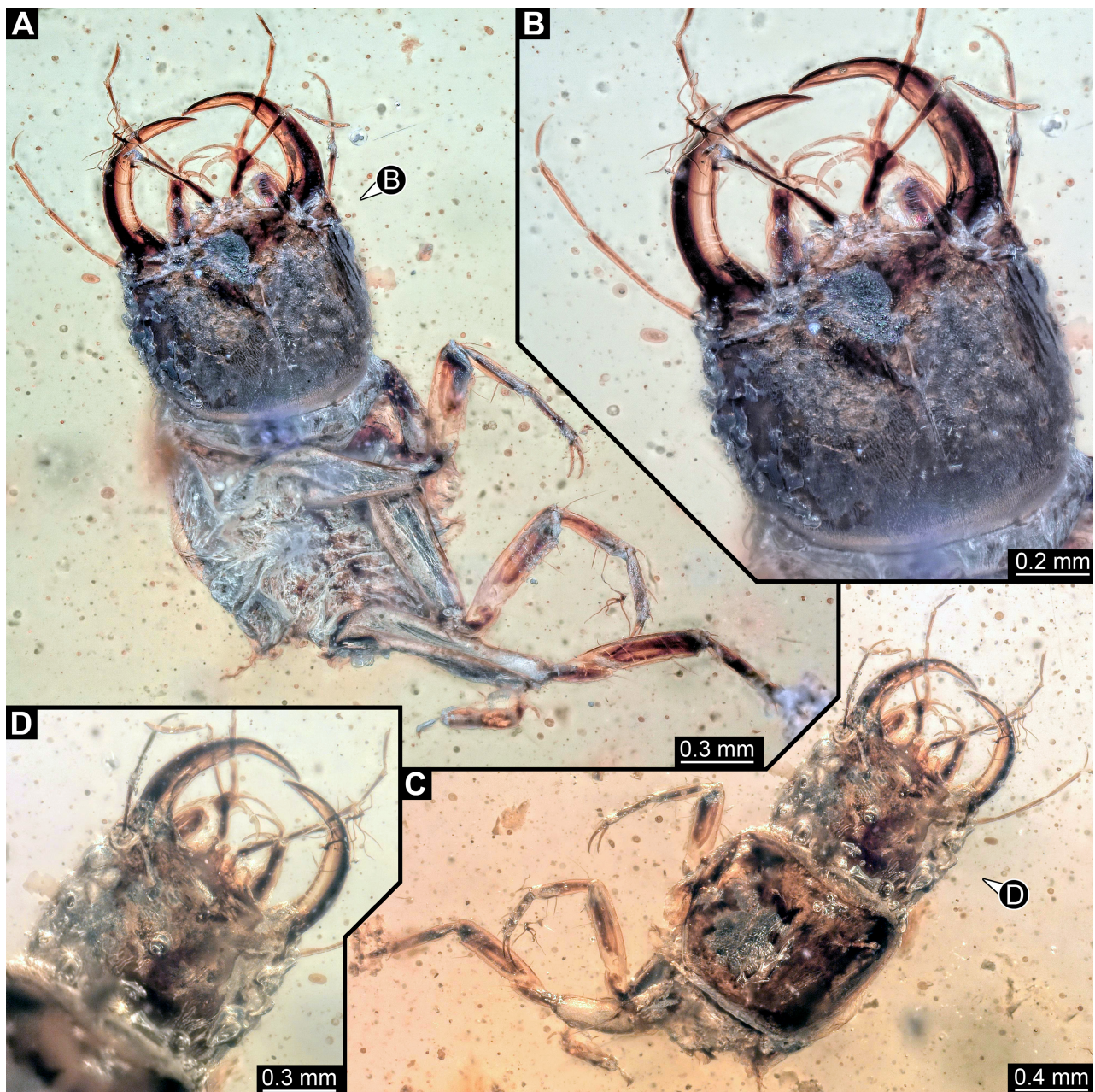
FIGURE 4. BUB 4828b, Kachin amber. **A**, Overview in ventral view. **B**, Close-up of head in ventral view. **C**, Overview in dorsal view. **D**, Close-up of head in dorsal view.

New specimen from Kachin amber BUB 4214

Elongate larva with prominent mouthparts (Fig. 5A). Anterior body sharply bent sidewards, concealing some structures such as legs. Head well accessible (Fig. 5B) Abdomen segments with prominent feathery gills.

New specimen from Kachin amber BUB 3996

Elongate larva with prominent mouthparts (Fig. 5C, D). Legs with a pair of claws each (Fig. 5C). Abdomen segments with prominent feathery gills (Fig. 5C).
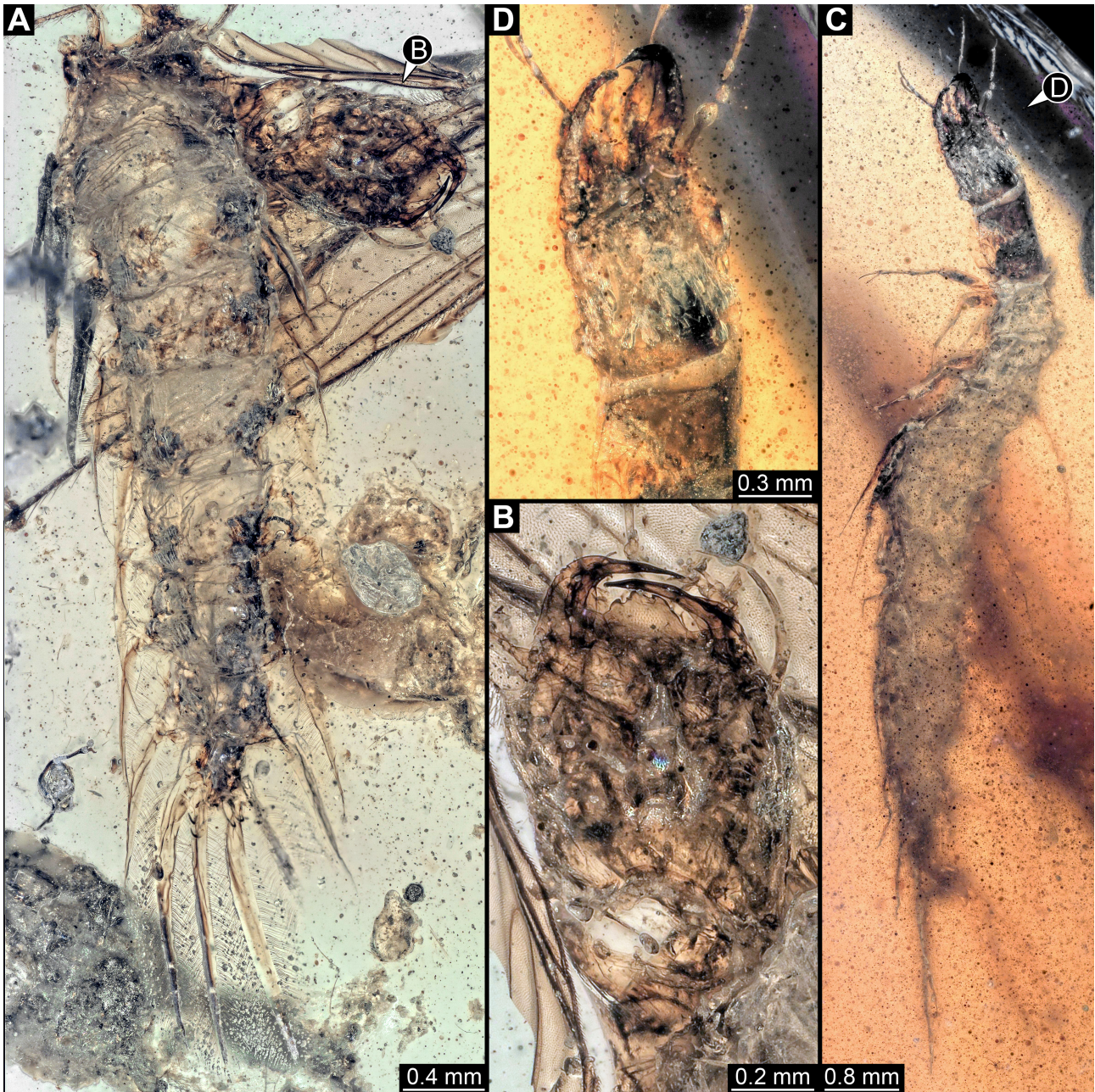
FIGURE 5. Two specimens in Kachin amber. **A**, **B**, BUB 4214. **A**, Overview in dorsal view. **B**, Close-up of head in dorsal view. **C**, **D**, BUB 3996. **C**, Overview in dorsal view. **D**, Close-up of head in dorsal view.

New specimen from Kachin amber BUB 4777

Elongate larva with prominent mouthparts (Fig. 6A, B). Legs entangled, distal parts not accessible (Fig. 6A). Abdomen segments with prominent feathery gills (Fig. 6A). Trunk end with four posterior-extending hook-like protrusions (Fig. 6A).
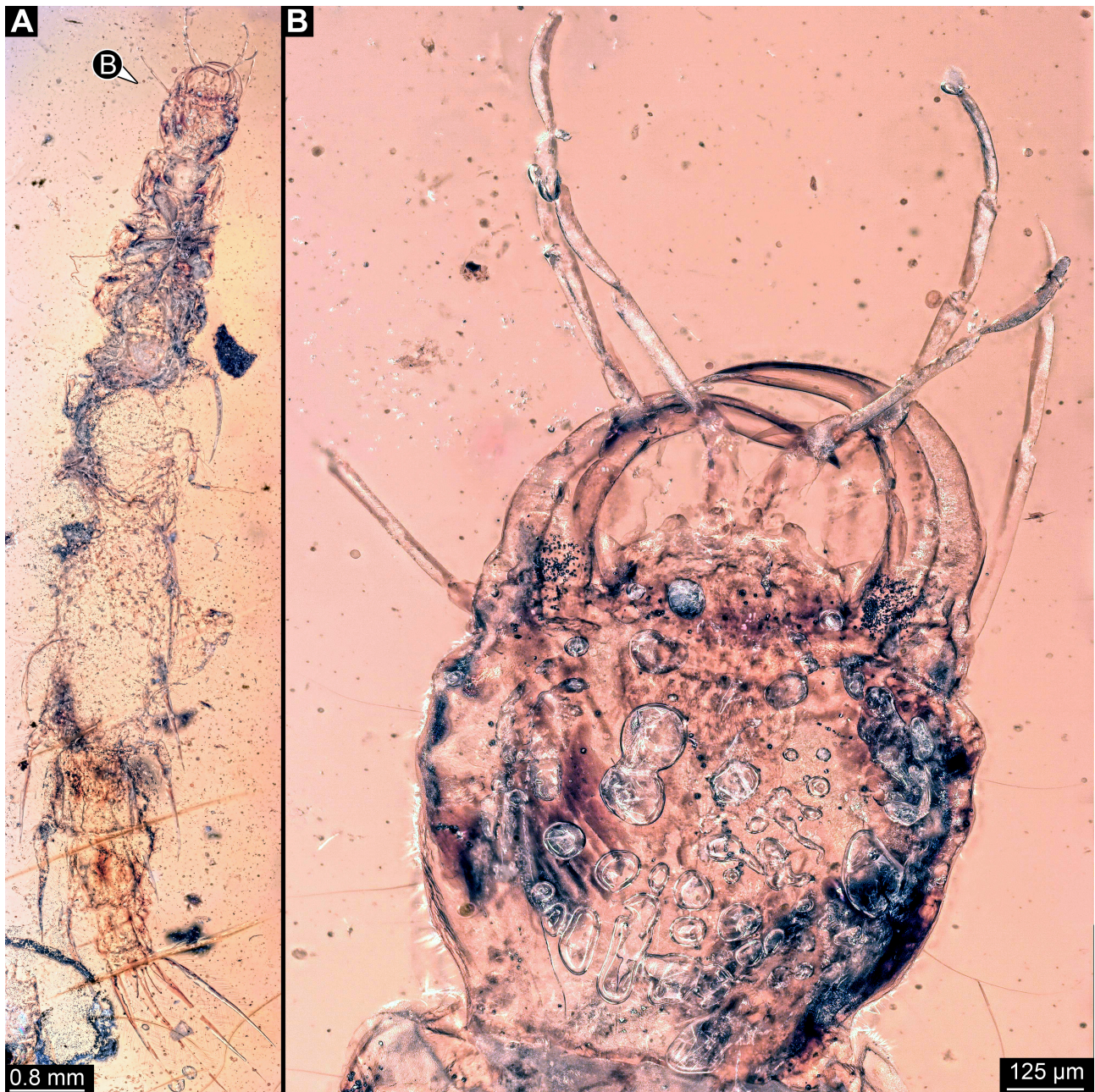
FIGURE 6. BUB 4777, Kachin amber. **A**, Overview in ventral view. **B**, Close-up of head in ventral view.

New specimen from Baltic amber SMF Be 289

Elongate larva with prominent mouthparts (Fig. 7A–C). Legs not accessible. Abdomen segments with prominent feathery gills (Fig. 7A). Trunk end partly outside of the amber, hence not fully preserved; details concealed by Verlumung.

New specimen from Baltic amber SMF Be 372

Elongate larva (Fig. 7D). Head incompletely preserved. Legs with a pair of claws each (Fig. 7D). Abdomen segments with prominent feathery gills (Fig. 7D). Trunk end with four posterior-extending hook-like protrusions (Fig. 7E).
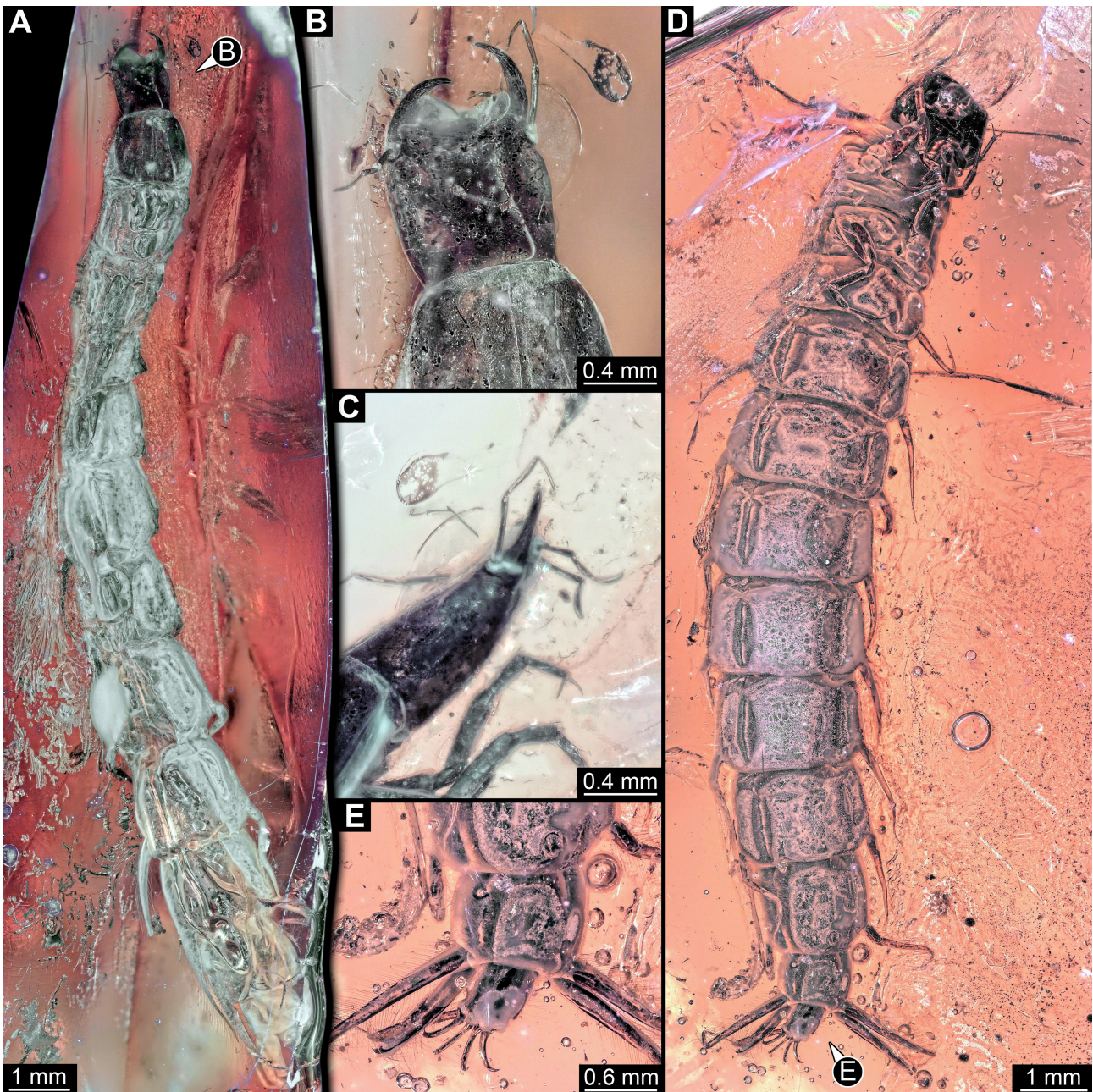
FIGURE 7. Two specimens in Baltic amber. **A–C**, SMF Be 289. **A**, Overview in dorsal view. **B**, Close-up of head in dorsal view. **C**, Head in lateral view. **D**, **E**, SMF Be 372. **D**, Overview in ventral view. **E**, Trunk end with claw-like protrusions.

New specimen from Baltic amber PED 1954

Larva less elongate than preceding ones (Fig. 8A, C). Head wider, also with prominent mouthparts, but antennae and palps shorter than in preceding specimens (Fig. 8B, D, E). Legs also distally with a pair of claws each (Fig. 8A, C).
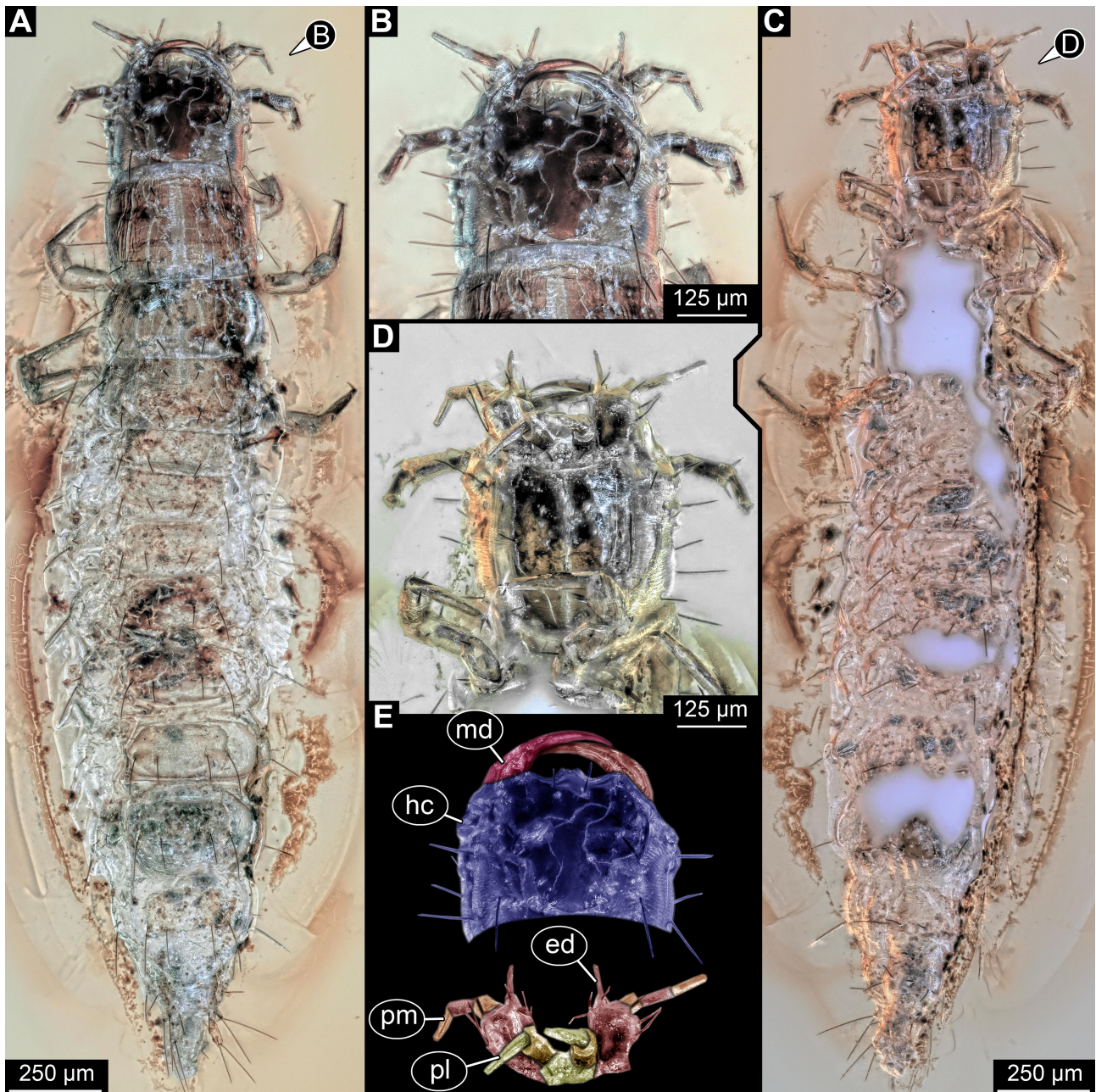
FIGURE 8. PED 1954, Baltic amber. **A**, Overview in dorsal view. **B**, Close-up of head in dorsal view. **C**, Overview in ventral view. **D**, Close-up of head in ventral view. **E**, Colour-marked mouthparts. Abbreviatons: ed = endite; hc = head capsule; md = mandible; pl = palp of labium; pm = palp of maxilla.

New specimen from Mexican amber MEX 009

Accessible from three oblique orientations (Fig. 9A–C). Body overall with long setae. Mouthparts prominently projecting forward (Fig. 9B, C). Legs with a pair of claws each (Fig. 9D). Trunk end with a pair of prominent setose urogomphi (Fig. 9C).
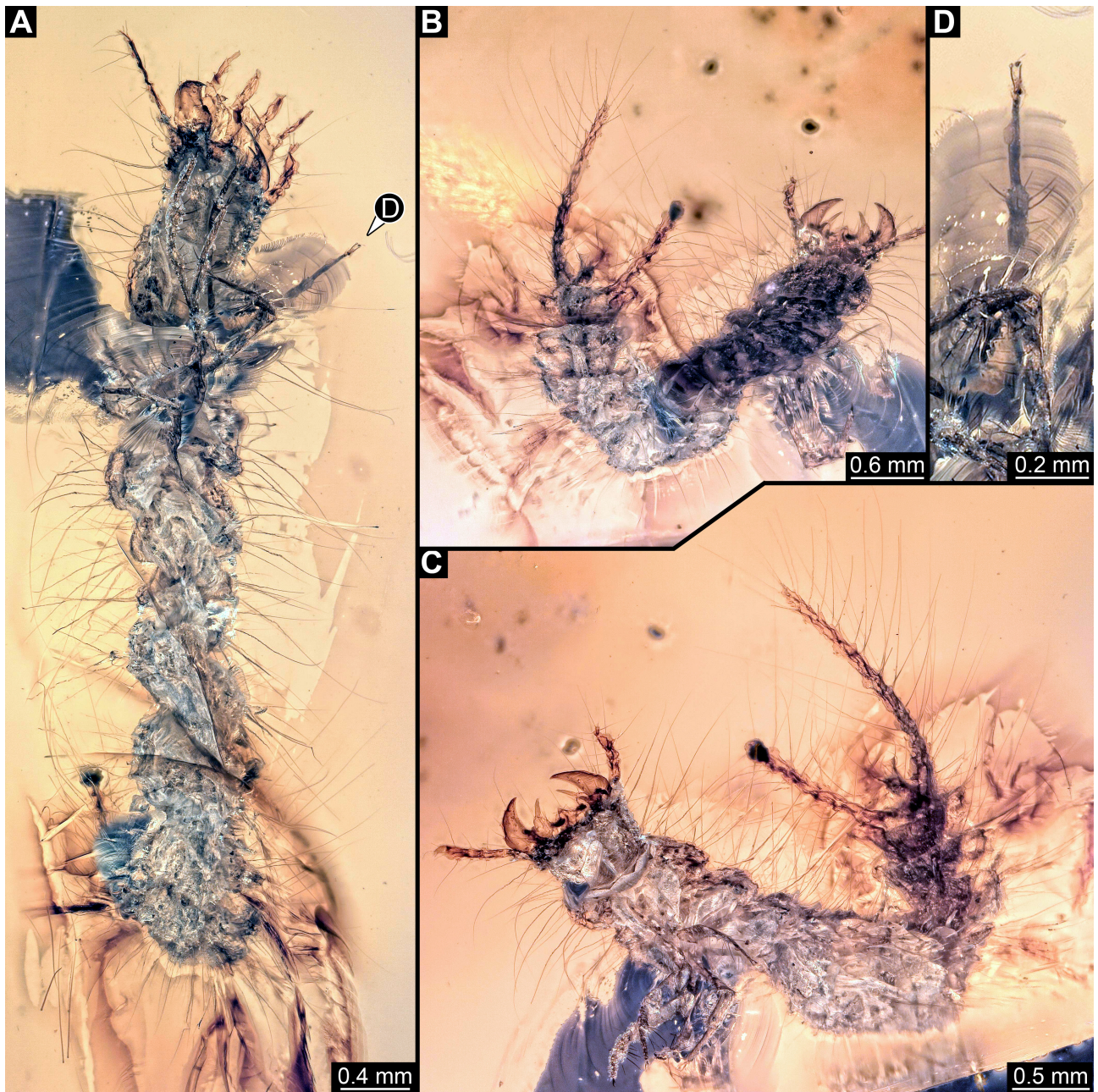
FIGURE 9. MEX 009, Mexican amber. **A–C**, Overview in three different oblique directions. **D**, Leg with distal claws.

New specimens from Barstow, Mojave Desert

Three specimens only preserving the head (GEO-Ps-24626, 17 and 36, Fig. 10A, E; PED 4417, Fig. 10B), fourth specimen more complete (USNM 561990, Fig. 10C, D). Heads of all specimens largely similar. With prominent forward-protruding structure (labrum?), roughly triangular in dorsal view, but with bulging sides. Mandible simple sickle-shaped, slightly shorter than labrum.
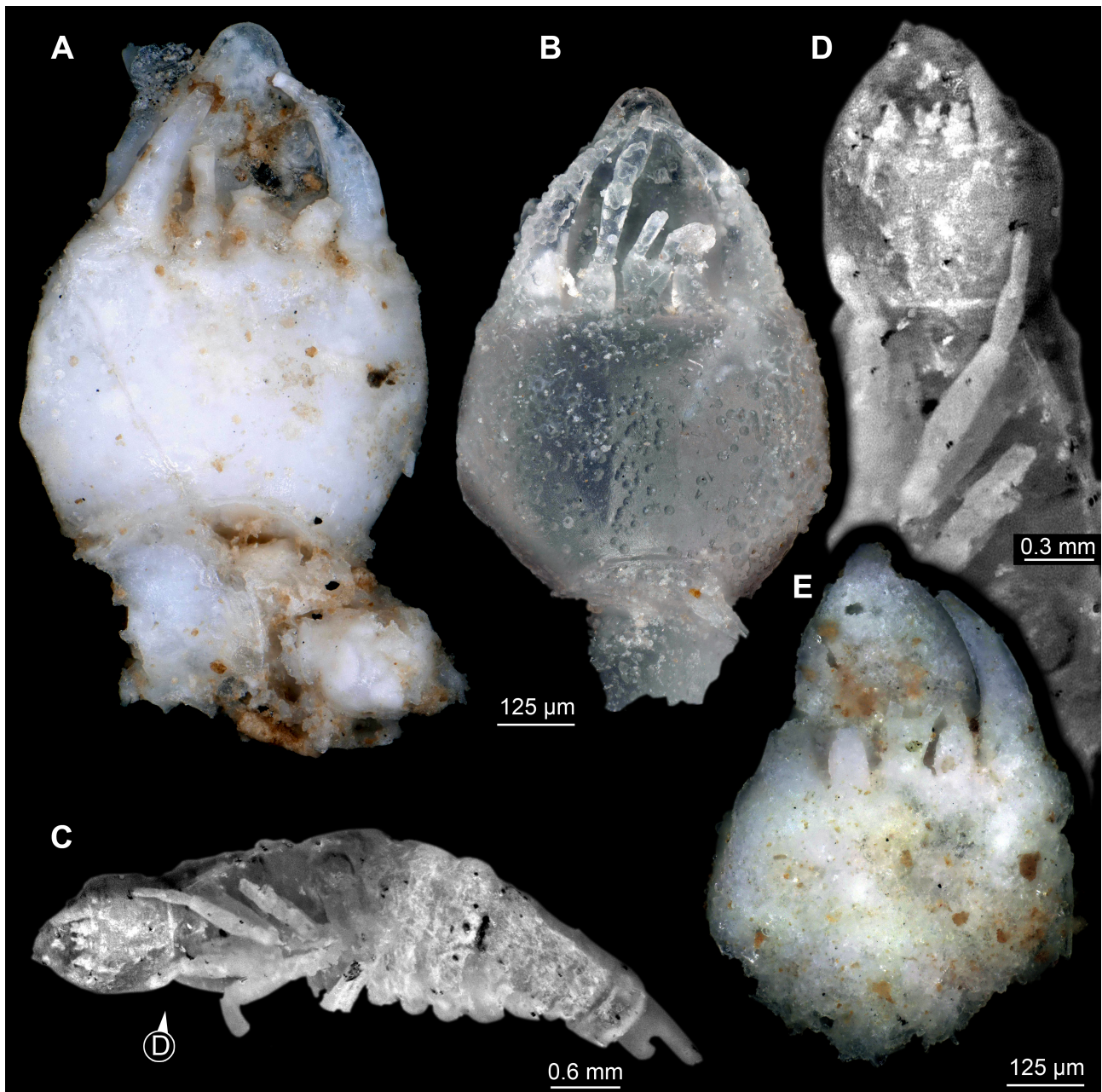
FIGURE 10. Specimens from Barstow, Mojave Desert, all in ventral view. **A**, GEO-Ps-24626, 17, head. **B**, PED 4417, head. **C, D**, USNM 561990. **E**, GEO-Ps-24626, 36, head.

Shape analysis

The PCA of the shape analysis resulted in five effective principal components (PCs) together representing over 92% of the data variation (PC1 = 63.6%, PC2 = 14.9%, PC3 = 6.4%, PC4 = 5.6%, PC5 = 1.9%). The largest variation appears to be in the expression of the nasale, which occurs in different PCs, and relative length and thickness of the mandibles. All details of the results of the shape analysis are presented in Supplementary Files 1–7.

Discussion

Identity of the specimens

Polyphagan beetle larvae are characterised by a lower number of leg elements than adephagan and archostematan beetle larvae (either tarsus and claw form a continuous structure, the tarsungulum/tarsungulus, or tibia and tarsus form a continuous structure, the tibiotarsus, see discussion in Lawrence 1991 p. 162). This condition is not present in the fossils reported here, as far as it is observable. Myxophagan beetle larvae bear special types of gills (Beutel *et al.* 2014 p. 411), which are not apparent in the fossils. Archostematan larvae have highly specialised morphologies, mostly adapted to wood-boring (Hörnschemeyer & Yavorskaya 2016). The overall morphology of the new fossils is most compatible with an interpretation as adephagan beetle larvae, including for example the strongly forward-protruding and anteriorly inserting mouthparts (Lawrence 1991 p. 158).

The silicified beetle larvae resemble already known larvae from the same locality (Palmer 1957) and therefore are interpreted as larvae of Dytiscidae. Many of the new larvae preserved in amber have distinct lateral gills on the abdomen segments. This feature identifies them as representatives of Gyrinidae. The remaining larvae, including the specimen from the Jehol biota, resemble larvae of ground beetles (Carabidae; e.g. Casale *et al.* 2010 fig. 1). Yet, many crucial characters are not accessible. We therefore tentatively interpret them as larvae of Carabidae.

Patterns of loss and gain in the fossil record

Loss of biodiversity, due to extinction events, as well as gain of biodiversity, due to radiations and diversifications, are patterns of interest for the modern society. We hope that we can learn from such processes in the past in order to mitigate the decline of biodiversity in the modern fauna that is currently observed.

Recognising such gains and losses is far from simple. Gains can be reconstructed based on phylogenetic analysis if the time tree is well calibrated. Recognising gains from fossils is more challenging as the absence of certain fossils in the past may not mean they have not been there, but it could mean that these fossils have simply not been preserved.

Losses can not be well detected from phylogenetic reconstructions as the nature of phylogeny is the increase of lineages over time, when viewed from the extant fauna as terminals. Yet also recognising losses using fossils can be challenging. The central unit for counting diversity is still the species (or higher taxonomic units). Comparing different time slices of the past can be compared in this way relatively effectively, although the classical problem of splitters vs. lumpers will bias such an analysis to a certain degree, due to a persistent lack of a species concept over time (Haug & Haug 2017). Yet, the problem becomes even stronger expressed when comparing past faunas to extant ones, as the extant species richness for most lineages outshines the species richness of any past fauna, besides certain exceptions such as for Brachiopoda, Cephalopoda, or Pterosauria. Therefore, the central idea comparing losses and gains in the past to modern losses (and gains?) is very challenging.

Instead of using species, quantifying morphologies by using morphometrics has proven an effective alternative that can recognise differences and allows recognising losses even in comparison to the modern fauna (e.g. Haug *et al.* 2022a, 2023). Another advantage of such an approach is that taxonomically challenging fossils such as immatures (including larvae) as the ecologically often more important life phase can be considered.

The fossil record of adephagan beetle larvae

Our contribution expands the so far scarce record of adephagan larvae immensely, by adding 15 new specimens (14 of which could be used in the analysis). Especially the find of the larva from the Jehol biota was a major one, as larvae from sedimentary deposits are still very rare. This window is especially important as amber tends to preserve smaller specimens, and fossils in sedimentary rocks are often significantly larger.

Also the larva from Mexican amber is quite important. While Mexican amber is in principle a productive one, larvae seem still to be quite rare.

The new findings demonstrate that there are more such larvae available, but are not considered for reporting. There are, for example, numerous specimens in different collections that might represent larvae of Carabidae. Yet,

due to structural similarities with, for example, larvae of Staphylinidae, it remains problematic to more reliably identify them when certain details are obscured. A solution could be to consider simply all larvae of beetles for a comparison, but to set up such a dataset will still take more time.

Patterns of loss and gain in adephagan larvae

Our analysis does not identify a single fossil larva plotting outside the area occupied by extant larvae (Fig. 11B). This result indicates that the highest diversity of adephagan larval morphology is found in the modern fauna. Only Jurassic larvae of the now extinct group Coptoclavidae (Fig. 11A) separate slightly from other forms, but still plot within the area of extant larvae.

Interestingly the oldest larvae plot in an area where all three considered modern groups (Gyrinidae, Dytiscidae, Carabidae) overlap. Furthermore, Gyrinidae, the supposed sister group to the remaining adephagan groups, occupies exactly this area and does not derive from it (Fig. 11A). We can therefore expect that this area represents the ancestral type of morphology for adephagan larvae. Larvae of Dytiscidae and Carabidae derived from this ancestral morphology over time.

Already in the Cretaceous we see rather derived shapes of larvae of Carabidae with higher PC2 values (Fig. 11A, B). We see slightly more extreme values in the modern fauna, yet given the small sample size in the Cretaceous this might be just a bias of the sampling. The same applies to the fact that in the Eocene and Miocene such extreme forms are missing (Fig. 11B).
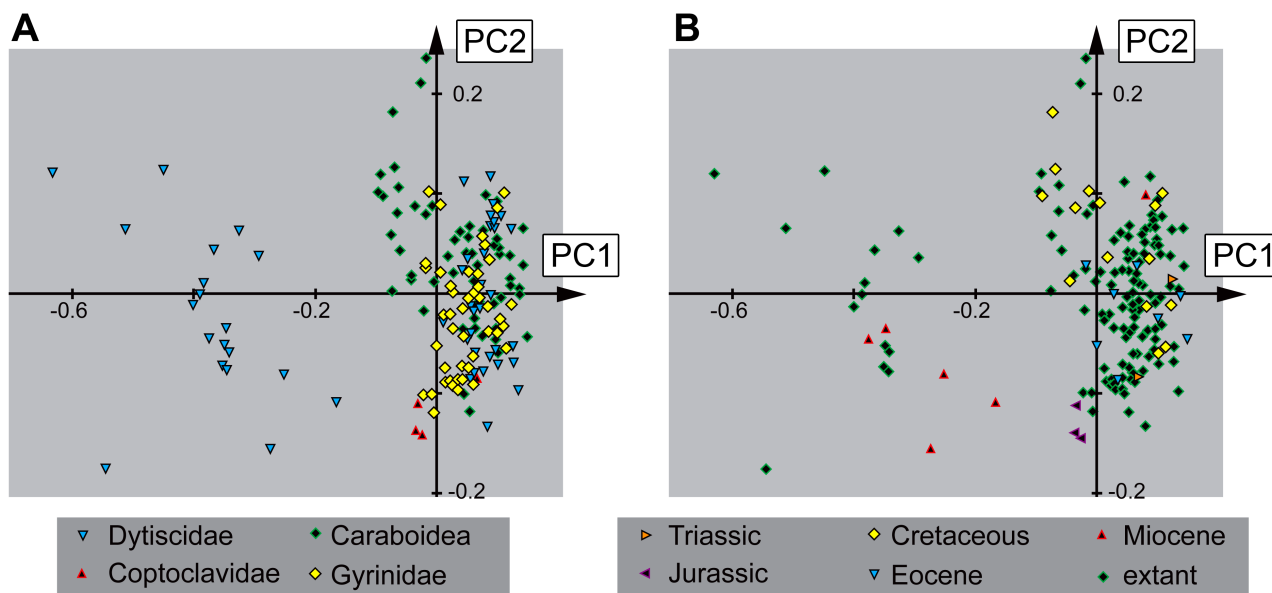

FIGURE 11. Scatterplot of results of shape analysis with principal component 2 (PC2) over principal component 1 (PC1). **A**, Systematic groups marked. **B**, Age of specimens marked.

We lack specialised larvae of Dytiscidae in older deposits, i.e. larvae with strongly expressed nasale. This forward-projecting structure forms a distinct grasping aid specialised for holding prey that is hard to grasp such as the egg-shaped ostracodan crustaceans (Hayashi & Ohba 2018). In the Miocene we have clear cases of such morphologies (Fig. 10; Palmer *et al.* 1957). As pointed out, we have already such forms in the Eocene, but could not include them in the analysis. Still such morphologies seem to be still absent in the Cretaceous.

Overall these patterns indicate no recognisable losses, but instead gains in morphologies over time, Carabidae having diversified their larval morphologies (and ecologies) already by the Cretaceous, Dytiscidae only after the Cretaceous. While this result needs to be taken with care due to the rather low sample size, it already provides a signal that needs to be further explored.

Patterns of losses

Other groups of Neuropteriformia (of which Adephaga and Coleoptera in general are ingroups) such as Neuroptera and Raphidioptera have seen losses of larval morphologies, indicated by larval morphologies known from the fossil record which are no longer present in the modern fauna (e.g. Haug *et al.* 2022a, 2023). Other lineages of Holometabola show more similar patterns to what we recovered here for Adephaga, with indications of larval diversifications already in the Cretaceous, but further specialisation afterwards (Haug & Haug 2021; Gauweiler *et al.* 2022; Haug *et al.* 2022b).

This pattern may be a clue to the phenomenon to the enormous species richness of the four hyperdiverse lineages (Coleoptera, Hymenoptera, Lepidoptera, Diptera). They did not suffer from major losses, leading to an enormous species richness in the modern fauna.

Often Adephaga is considered to be less significant in comparison to Polyphaga. Yet, with about 40,000 species Adephaga is already much more species-rich than most other lineages considered ecologically important. As the oldest fossils of adephagan larvae available reach back into the Triassic (Prokin *et al.* 2013), they seem to have been successful since quite some time.

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Supplementary information:
SUPPLEMENTARY TABLE 1. Information on specimens included into the shape analysis.
SUPPLEMENTARY TEXT 1. References for Supplementary Table 1.
SUPPLEMENTARY FILES 1–7. Results of the shape analysis