The evolutionary history of wood-associated beetle larvae and the contribution of amber fossils

Dissertation zur Erlangung des naturwissenschaftlichen Doktorgrades „Doctor rerum naturalium” an der Fakultät für Biologie der Ludwig-Maximilians-Universität München

Ana Zippel

München, 2023

Diese Dissertation wurde angefertigt
unter der Leitung von Prof. Dr. Joachim T. Haug
im Bereich Zoologie
an der Ludwig-Maximilians-Universität München

Erstgutachter/in: Prof. Dr. Joachim T. Haug
Zweitgutachter/in: PD Dr. Michael Raupach

Tag der Abgabe: 07.08.2023
Tag der mündlichen Prüfung: 25.10.2023

TABLE OF CONTENTS

EIDESSTATTLICHE ERKLÄRUNG

Ich versichere hier mit an Eides statt, dass meine Dissertation selbständig und ohne unerlaubte Hilfsmittel angefertigt worden ist.

München, 02.08.2023

____

Ana Zippel

ERKLÄRUNG

Hiermit erkläre ich, dass diese Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

München, 02.08.2023

____

Ana Zippel

LIST OF PUBLICATIONS AND MANUSCRIPTS INCORPORATED IN THIS DISSERTATION

1. Haug, C., Haug, G. T., **Zippel, A.**, van der Wal, S. & Haug, J. T. (2021). The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4, 390–404. (**Article I**)
https://doi.org/10.11646/palaeoentomology.4.4.14

2. Haug, J.T., **Zippel, A.**, Haug, G.T., Hoffeins, C., Hoffeins, H.-W., Hammel, J.U., Baranov, V. & Haug, C. (2021). Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14, 161–183. (**Article II**)
https://doi.org/10.18476/pale.v14.a8

3. **Zippel, A.**, Baranov, V.A., Hammel, J.U., Hörnig, M.K., Haug, C. & Haug, J.T. (2022). The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10, e13025. (**Article III**)
https://doi.org/10.7717/peerj.13025

4. **Zippel, A.**, Haug, C., Hoffeins, C., Hoffeins, H.-W. & Haug, J.T. (2022). Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia 128, 81–104. (**Article IV**)
https://doi.org/10.54103/2039-4942/17084

5. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (2022) First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96, 219–229. (**Article V**)
https://doi.org/10.1007/s12542-022-00608-8

6. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (2023). The first fossil false click beetle larva preserved in amber. PalZ 97, 209–215. (**Article VI**)
https://doi.org/10.1007/s12542-022-00638-2

7. Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. (early view). Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ. (**Article VII**)
https://doi.org/10.1007/s12542-023-00648-8

8. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (accepted). Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ. (**Article VIII**)

9. **Zippel, A.**, Haug, C., Elverdi, Z, Müller, P. & Haug J.T. (2023). Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Miocene and Cretaceous ambers. Fossil Record 26, 191–207. (**Article IX**)

LIST OF ADDITIONAL PUBLICATIONS AND MANUSCRIPTS

1. **Zippel, A.**, Kiesmüller, C., Haug, G.T., Müller, P., Weiterschan, T., Haug, C., Hörnig, M.K. & Haug, J.T. 2021. Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. Palaeoentomology 4, 475–498.

2. **Zippel, A.**, Haug, C., Gauweiler, J., Hörnig, M.K., Haug, G.T. & Haug, J.T. 2022. A small beetle larva preserved in 23-million-year-old Mexican amber: possible first fossil record of an immature variegated mud-loving beetle. Boletín de la Sociedad Geológica Mexicana 74, A150322.

3. Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. 2022. A modern type of ant-like stone beetle larva preserved in 99-million-year-old Kachin amber. Fragmenta entomologica 54, 193–200.

4. Haug, C., **Zippel, A.**, Hassenbach, C., Haug, G.T. & Haug, J.T. 2022. A split-footed lacewing larva from about 100-million-year-old amber indicates a now extinct hunting strategy for neuropterans. Bulletin of Geosciences 97, 453–464.

5. Haug, C., Posada Zuluaga, V., **Zippel, A.**, Braig, F., Müller, P., Gröhn, C., Weiterschan, T., Wunderlich, J., Haug, G.T. & Haug, J.T. 2022. The morphological diversity of antlion larvae and their closest relatives over 100 million years. Insects 13, 587.

6. Haug, C., Pérez-de la Fuente, R., Baranov, V., Haug, G.T., Kiesmüller, C., **Zippel, A.**, Hörnig, M.K. & Haug, J.T. 2023. The first fossil record of a mantis lacewing pupa, and a review of pupae in Mantispidae and their evolutionary significance. Rivista Italiana di Paleontologia e Stratigrafia 129, 185–205.

7. **Zippel, A.**, Haug, C., Yáñez Iturbe-Ormaeche, B. & Haug, J.T. (in revision). Diversity of archostematan beetle larvae throught time with a new fossil. Palaeodiversity.

LIST OF FIGURES

STATEMENT OF AUTHOR CONTRIBUTIONS

This thesis presents the results from research conducted between 2020 to 2023, carried out under the supervision of Prof. Dr. Joachim T. Haug, Prof. Dr. J. Matthias Starck and PD Dr. Michael Raupach associated with the Ludwig Maximilian University of Munich.

1. Haug, C., Haug, G. T., **Zippel, A.**, van der Wal, S. & Haug, J. T. (2021). The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4, 390–404.

   Conceptualization, JTH and CH; Methodology, JTH, GTH, AZ, SvdW, CH; Formal Analysis and Investigation, JTH, GTH, AZ, SvdW, CH; Writing and Original Draft Preparation, JTH, AZ, CH; Writing - Review and Editing, JTH, GTH, AZ, SvdW, CH; Funding aquisition, JTH; Resources, JTH. All authors have read and agreed to the published version of the manuscript.

2. Haug, J.T., **Zippel, A.**, Haug, G.T., Hoffeins, C., Hoffeins, H.-W., Hammel, J.U., Baranov, V. & Haug, C. (2021). Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14, 161–183.

   Conceptualization, JTH and CH; Methodology, JTH, AZ, GTH, JUH, VB, CH; Formal Analysis and Investigation, JTH, AZ, GTH, JUH, VB, CH; Writing and Original Draft Preparation, JTH, AZ, GTH, VB, CH; Writing - Review and Editing, JTH,, AZ, GTH, VB, CH; Funding aquisition, JTH; Resources, JTH, CH (Christel Hoffeins), H-WH. All authors have read and agreed to the published version of the manuscript.

3. **Zippel, A.**, Baranov, V.A., Hammel, J.U., Hörnig, M.K., Haug, C. & Haug, J.T. (2022). The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10, e13025.

   Conceptualization, JTH; Methodology, JTH, VAB, AZ, JUH, MKH, CH; Formal Analysis and Investigation, JTH, VAB, AZ, JUH, MKH, CH; Writing and Original Draft Preparation, JTH, VAB, AZ, MKH; Writing - Review and Editing, JTH, VAB, AZ, JUH, MKH, CH; Funding aquisition, JTH, MKH; Resources, JTH. All authors have read and agreed to the published version of the manuscript.

4. **Zippel, A.**, Haug, C., Hoffeins, C., Hoffeins, H.-W. & Haug, J.T. (2022). Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia 128, 81–104.

   Conceptualization, JTH and CH; Methodology, JTH, AZ, CH; Formal Analysis and Investigation, JTH, AZ, CH; Writing and Original Draft Preparation, JTH, AZ, CH; Writing - Review and Editing, JTH, AZ, CH; Funding aquisition, JTH; Resources, JTH, CH (Christel Hoffeins), H-WH. All authors have read and agreed to the published version of the manuscript.

5. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (2022) First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96, 219–229.

   Conceptualization, JTH and CH; Methodology, JTH, AZ, CH; Formal Analysis and

Investigation, JTH, AZ, CH; Writing and Original Draft Preparation, JTH, AZ, CH; Writing - Review and Editing, JTH, AZ, CH; Funding aquisition, JTH; Resources, JTH and PM. All authors have read and agreed to the published version of the manuscript.

6. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (2023). The first fossil false click beetle larva preserved in amber. PalZ 97, 209–215.

   Conceptualization, JTH; Methodology, JTH, AZ, CH; Formal Analysis and Investigation, JTH, AZ, CH; Writing and Original Draft Preparation, JTH, AZ, CH; Writing - Review and Editing, JTH, AZ, CH; Funding aquisition, JTH; Resources, JTH and PM. All authors have read and agreed to the published version of the manuscript.

7. Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. early view. Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ.

   Conceptualization, CH, AZ, JTH; Methodology, CH, AZ, PM, JTH; Formal Analysis and Investigation, CH, AZ, PM, JTH; Writing and Original Draft Preparation, CH, AZ, JTH; Writing - Review and Editing, CH, AZ, PM, JTH; Funding aquisition, JTH; Resources, PM and JTH. All authors have read and agreed to the published version of the manuscript.

8. **Zippel, A.**, Haug, C., Müller, P. & Haug, J.T. (SUBMITTED). Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ.

   Conceptualization, CH, JTH, AZ; Methodology, CH, PM, JTH, AZ; Formal Analysis and Investigation, CH, PM, JTH, AZ; Writing and Original Draft Preparation, CH, JTH, AZ; Writing - Review and Editing, CH, PM, JTH, AZ; Funding aquisition, JTH; Resources, PM and JTH. All authors have read and agreed to the published version of the manuscript.

9. **Zippel, A.**, Haug, C., Elverdi, Z, Müller, P. & Haug J.T. (SUBMITTED). Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Miocene and Cretaceous ambers. Fossil Record.

   Conceptualization, CH, JTH, AZ; Methodology, CH, PM, JTH, AZ, ZE; Formal Analysis and Investigation, CH, PM, JTH, AZ; Writing and Original Draft Preparation, CH, JTH, AZ; Writing - Review and Editing, CH, PM, JTH, AZ, ZE; Funding aquisition, JTH; Resources, PM and JTH. All authors have read and agreed to the published version of the manuscript.

Ana Zippel

Prof. Dr. Joachim T. Haug

SUMMARY

Beetles (Coleoptera) comprise more than 380,000 described species and are not only highly taxonomically diverse today but also ecologically and morphologically. The fossil record of beetles is not scarce, however, it is mostly represented by adult specimens. Beetle larvae, especially preserved in amber, have a reputation to be rare, and wood-associated beetle larvae have been claimed to be 'anecdotal'. It has been suggested that small and soft-bodied larvae do not get fossilized easily, especially the larvae leading a hidden way of life within the wood. I wanted to research whether they really are as rare in amber as it seems from the literature. In my thesis, I studied specimens preserved mostly in ~100-million-year-old Kachin, ~40-million-year-old Baltic, and ~25-million-year-old Mexican ambers. Through my contributions, in the form of 9 publications, I demonstrate that wood-associated beetle larvae can actually be considered relatively abundant in ambers. In fact, such finds should not surprise since the fossil larvae probably inhabited areas close to the origin of the plant resin. The resin dripped on the animal, or the animal stumbled or fell in. Once the animal became stuck and engulfed within the resin it became a biological inclusion within hardened and fossilized resin, now considered amber.

However, the fossil record of diverse groups of beetles within ambers seems biased towards adults, especially males. The reports of beetle larvae stay scarce, even though they are of great importance for understanding the evolutionary history of beetles and their biodiversity. In Holometabola, a group including beetles as well, modern representatives have life cycles including an adult, a pupa, and larval stages. Interestingly, most of the lifespan of many extant beetles is spent in the larval stages. Therefore, larvae of beetles not only increase the morphological and often ecological diversity of the group but are a big, if not the biggest, part of the beetle biomass.

In addition, the modern wood-associated beetle larvae have another important role, they help in breaking and decomposing of wood, therefore, enhancing carbon cycling. It seems that wood as a substrate offers many different microenvironments depending on the state it is in. In this study I differentiate several functional groups of modern representatives of beetle larvae that feed on wood in different states: hardwood borers, softwood borers, fungus-infected wood borers, submerged wood borers, and in-wood predators. Even though predators are not directly feeding on wood, they are often encountered within the wood, especially within the galleries and tunnels of wood-feeding larvae that they prey upon. I was wondering whether such differentiation of wood-associated larvae already existed within the extinct representatives of past faunas. In the scope of this thesis I present two publications with possible hardwood borers, three publications considering possible softwood borers (even though, one specimen is likely a larva of Holometabola, but possibly not of Coleoptera), one manuscript with fungus feeders, one publication and one manuscript with submerged-wood borers and two publications with in-wood predaceous beetle larvae. Therefore, the wood habitats were crawling with life also in ecosystems of the past.

Within the incorporated manuscripts and publications, my co-authors and I presented the fossil beetle larvae and their morphological characters on images created with a digital microscope, x-ray microcomputed tomography, and synchrotron radiation micro-computed tomography. The (rendered) images were further processed with programs such as Adobe Photoshop or Inkscape for easier interpretation by readers.

Additionally, many of the new fossil larvae showed morphologies unknown from modern beetle larvae. Hence implying that the morphologies of extinct beetle larvae differed and occupied a different range of morphospace than the morphologies known from the modern beetle larvae. In order to compare the range of morphologies through time within the morphospace we used the pipeline of programs SHAPE that uses an Elliptic Fourier Analysis and a Principal Component Analysis.

1. INTRODUCTION

Beetles (Coleoptera) comprise more than 380,000 formally described species today (Nielsen & Mound 1999, Grove & Stork 2000, Ślipiński et al. 2011, McKenna et al. 2015, McKenna et al. 2019, Cai et al. 2022). The estimated total number of species of beetles in the world is even higher, with estimations ranging from approximately 850,000 mostly up to 1.5 million, with some estimations of up to 4 million species (Stork et al. 2015, Bouchard et al. 2017, Cai et al. 2022). This makes them one of the most successful groups of organisms in the world. This high taxonomic diversity of the group is supported by high ecological and morphological diversity (the latter often referred to as disparity)(Lawrence et al. 2011). There are several explanations discussing the enormous success of beetles. One is paired with the novelty of elytra (Crowson 1981, Lawrence & Britton 1994, Grimaldi & Engel 2005, Hunt et al. 2007), the hard sclerotized forewings of adult beetles. Such hardened forewings gave the early beetles a new advantage against possible predators and pathogens but also from desiccation in dry areas (Lawrence & Newton 1982, Grimaldi & Engel 2005, Gimmel & Ferro 2018). Additionally, the elytra protect the folded hindwings and therefore, enabled beetles to occupy concealed tight spaces without damaging the hindwings (McKenna et al. 2015). Another explanation for the success of beetles is the association with flowering plants (Farrell 1998, Barraclough et al. 1998; Lloyd et al. 2008, McKenna et al. 2015). A further suggestion is that the development of holometaboly indirectly positively influenced diversity (Béthoux 2009, Nicholson et al. 2014, Schachat et al. 2018). In Holometabola, the immatures and the adults show great differences in morphology and therefore are able to exploit habitats with different ecology and often lead very different lifestyles. This is true for all the groups of Holometabola, therefore it should have been advantageous for beetles, as well. A newer reconstruction from McKenna et al. (2019) suggests that beetle diversity resulted from multiple factors. It did not only result from the co-diversification with flowering plants but also from low extinction rates over a long evolutionary history (Labandeira & Sepkoski 1993, Hunt et al. 2007, McKenna et al. 2009, Smith & Marcot 2015) and adaptive radiations of some plant-feeding beetles (Pauchet et al. 2010, Kirsch et al. 2014, McKenna et al. 2016, Salem et al. 2017, Busch et al. 2019). As it seems, some of the plant-feeding beetles gained the ability to digest plant tissues (the cell walls containing cellulose, hemicellulose, and pectin) without additional gut symbionts, which must have boosted their radiation into new habitats (McKenna et al. 2019). This then additionally created new opportunities for predatory beetles and fungus-feeding beetles and possibly boosted their diversification.

1.1. *Origin of beetles*

McKenna et al. (2019) dated the origin of beetles (Coleoptera) near the Lower Carboniferous–Upper Carboniferous boundary (ca. 327 Ma) based on phylogenetic and molecular analyses. Boudinot et al. (2023) agree that beetles originated sometime during the Carboniferous. They also hypothesize that these must have been relatively soft-bodied insects flying with their hind wings, having flexible abdomens, and tegmina (as still possessing real veins) loosely resting over the body.

Unfortunately, the beginnings of beetles are not supported by many fossil findings. Among the earliest fossil records of beetles were the representatives of today extinct group Tshekardocoleidae from Lower Permian (ca. 280 Ma; Ponomarenko 1963, Kukalová 1969, Ponomarenko 1969, Kukalová- Peck & Beutel 2012, Nel et al. 2013, Kirejtshuk et al. 2014, Ponomarenko & Prokin 2015, Yan et al. 2017a, b, 2018, 2020). The representatives of Tshekardocoleidae were assigned to the sister group of Coleoptera by Beutel (1997) and Beutel et al. (2008). Somewhat later Béthoux (2009) interpreted *Adiphlebia lacoana* from the Upper Carboniferous of the USA as the oldest early beetle representative. However, the interpretation was dismissed by Kukalová-Peck & Beutel (2012) and Kirejtshuk et al. (2014) based on the significant characteristics that adult beetles usually lack and the new fossil had, such as long heart-shaped prothoracic shield, hind wings shorter than forewings, tegmina in roof-like position at rest, posteriorly tapering abdomen, shorter than wings. Unfortunately, the relationship of *Adiphlebia lacoana* to other representatives of Coleoptera remains unresolved till now. Yet another fossil, *Coleopsis archaica*, was interpreted as the earliest beetle by Kirejtshuk et al. (2014). Nevertheless, the relationship of this fossil to other beetles was re-interpreted multiple times, as well (Kirejtshuk & Nel 2016, Beutel et al. 2019, Kirejtshuk 2020, Cai et al. 2022, Schädel et al. 2022).

The fossil adult representatives of Tschekardocoleidae resemble extant adult beetles in certain characteristics, for example, their elytra with window punctures resemble the ones in modern representatives of certain adults of Archostemata (Cupedidae and Ommatidae)(Boudinot et al. 2023). Nevertheless, they also greatly differ from any modern adult beetles in antennae with more than 11 elements, presence of pleural suture (suture on pleura extending from proximal part of wings to the proximal part of coxa), morphology of procoxal cavities (coxal cavity can be of 'open'-type when the coxal cavity is closed by the sclerite of mesothorax, or of 'closed'-type when the coxal cavity is closed by expanded sclerite of prothorax; Borror et al. 1989), tegmina venation, venation of hindwings and its transverse foldings, length of abdomen in comparison to elytra and sclerotized ovipositor (Lawrence & Newton 1982). Boudinot et al. (2023) additionally mention that tent-like manner of resting elytra that are longer than the abdomen, and flexible and almost cylindrical abdomen are the plesiomorphies of adults of Tschekardocoleidae.

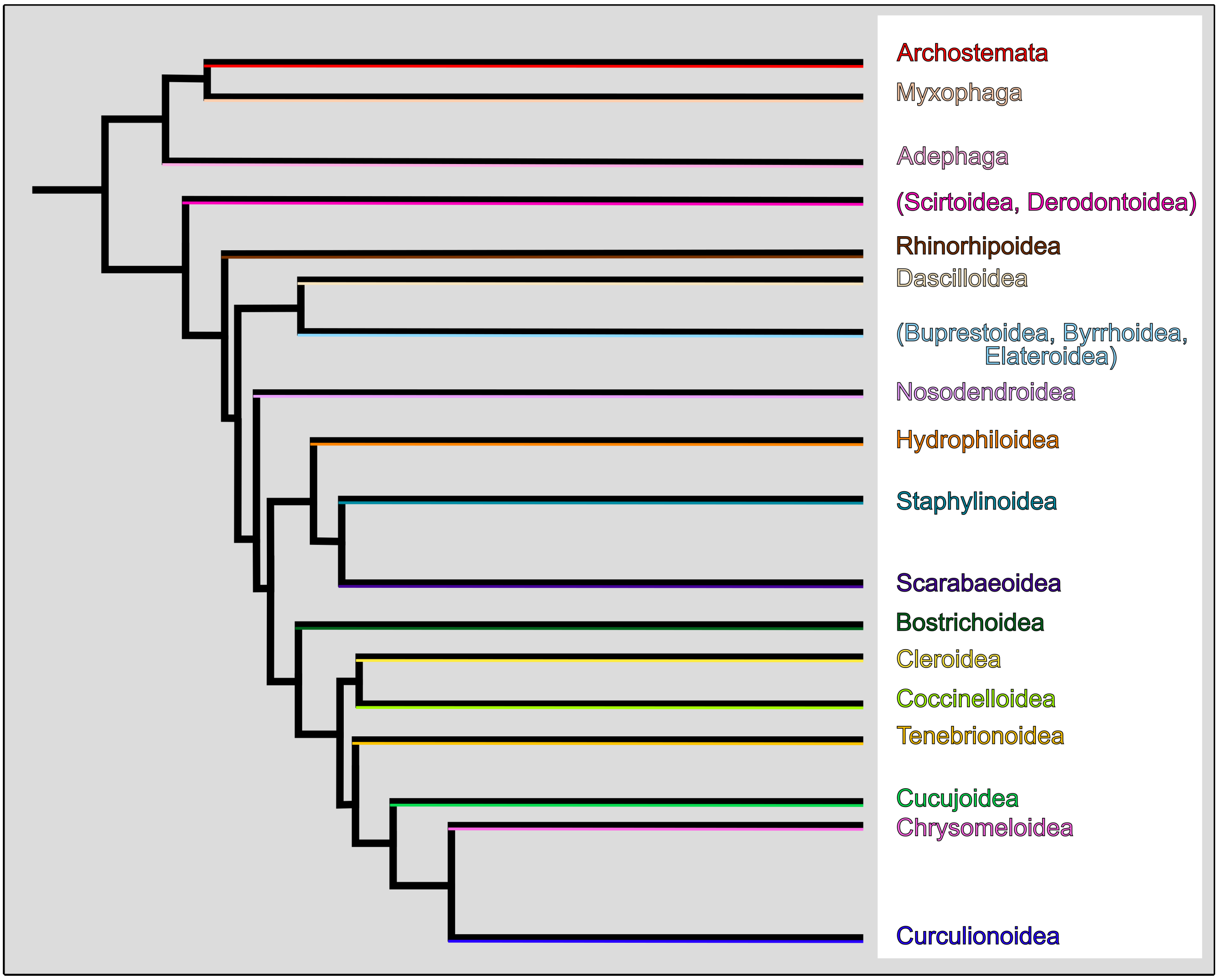

Fig. 1 Simplified phylogenetic tree of Coleoptera based on McKenna et al. (2019).

The first representatives of four extant beetles lineages (Adephaga, Archostemata, Myxophaga, and Polyphaga) (Fig. 1) appeared in a period from Triassic to Cretaceous (Whalley 1987, Grimaldi & Engel 2005, Hunt et al. 2007, Zhang et al. 2018, Lawrence et al. 2011, Prokin et al. 2013, Ponomarenko et al. 2015, Prokin & Bashkuev 2021).

1.2. *Climate and vegetation changes during the diversification of beetles*

As the first representatives of early beetles started to diversify, the continents were united in a single supercontinent Pangea. Throughout the period the climate shifted from cool with relictual glaciation and permanently wetted terrestrial ecosystems to hot and dry with big desert areas (Penney & Jepson 2014, Cai et al. 2022). This resulted in drastic deforestation where the vegetation changed from fern-dominated to being dominated by seed-bearing plants (Penney & Jepson 2014, Prokop et al. 2023). Nevertheless, the ecological communities became more complex, with a higher number of trophic levels (Looy et al. 2014, Benton et al. 2021). Ecological changes in plant composition and climate possibly played a significant role in shaping the early diversification of beetles (Cai et al. 2022). In accordance with this, certain changes in morphological characters, such as the closed sub-elytral space of adult beetles, must have been advantageous for this group during the Permian aridification (Boudinot et al. 2022). In addition, deforestation in the Late Permian must have been of great importance, i.e. a negative impact leading to the extinction of largely xylophagous Permian beetle fauna (Prokop et al. 2023).

At the end of the Paleozoic era and the Permian period, the biggest extinction took place, presumably as a result of high volcanic activity of the Siberian Traps (Penney & Jepson 2014) and widespread ocean anoxia (Payne & Clapham 2012). On the one hand, this led to the great extinction of different plant groups. On the other hand, the surviving and the new groups of plants diversified after this event. In total, such a floral turnover had a distinct impact on the global fauna (Prokop et al. 2023). Nonetheless, some early diverging beetle groups apparently survived this event and diversified in the Mesozoic (Cai et al. 2022). Additionally, during the extinction event, many different environments were left empty by the extinct species and were successively filled by others with similar ecology (Prokop et al. 2023).

At the beginning of the Mesozoic, during the Triassic, the supercontinent Pangea split up into Laurasia and Gondwana leading to changes in the sea currents and cooling off of continents. In addition, the humidity was raising (Penney & Jepson 2014). There was a great increase in the diversity of holometabolan insect groups, for example, Coleoptera, Neuroptera, and Mecoptera (Prokop et al. 2023).

In the Jurassic, the dry areas became even more moist and deserts were replaced by rainforests. Insects were represented either with today extinct groups or with early representatives of extant groups, including the representatives of beetles (Penney & Jepson 2014, Cai et al. 2022). The terrestrial vegetation of mid-Mesozoic was made of representatives of Pinophyta, Cycadophyta, Ginkgophyta, Gnetophyta, and other extinct ingroups of Spermatophyta such as Czekanowskiales, Corystospermales, Caytoniales, Bennettitalens (Labandeira et al. 2007, Labandeira 2010, Friis et al. 2011, Peris et al. 2020).

In the Cretaceous, the continents as we know today already existed but their position differed. This was the period of a warm climate where the dominance of seed-bearing plants was exchanged with the dominance of flowering plants. This event of rapid diversification of flowering plants, but also the events of diversification of different insect groups, squamates, birds, and mammals were united under the term Cretaceous Terrestrial Revolution (Barba-Montoya et al. 2018, Condamine et al. 2020). The earliest occurrence of pollen of flowering plants indicates that these plants originated during the Early Cretaceous (Hughes & McDougall 1987, Labandeira & Sepkoski 1993) and by 112 million years ago flowering plants dominated many habitats (Peris et al. 2020). In total, the insect fauna already comprised many groups, that are still represented in today's fauna (Penney & Jepson 2014), for example, Coleoptera, Neuroptera, and Hymenoptera (Penney &

Jepson 2014). Additionally, there were certain groups present that are today only known from fossil deposits (Penney & Jepson 2014).

The Cretaceous period ended with another big extinction, probably caused by changes in the sea level, high rates of volcanism of the Deccan Trap, and a bolide impact at Chicxulub on the Yucatán Peninsula (MacLeod 2012). It could be expected that after this event, plant-associated insects would have elevated extinction levels. However, Cai et al. (2022) did not find any implications of that. It seems that the mass extinction was hardly devastating for beetles. Possibly, different insect species went extinct but the morphologies they represented survived this event (Whalley 1987, Smith & Marcot 2015, Labandeira et al. 2002, Cai et al. 2022).

In the Paleogene, the position of continents was relatively similar to today´s. However, Europe was an archipelago of islands. In Paleocene and Eocene, the climate was warm and moist, reaching the thermal maximum with global warming as a result. The vegetation was mostly represented by plants known from subtropical and tropical ecosystems. This was followed by subsequent cooling off and aridification at the boundary between Pliocene and Pleistocene. The cooling off of the Earth climaxed with the glaciation in the Pleistocene (Penney 2010, Penney & Jepson 2014).

1.3. Amber and amber-producing forests

Amber is a hardened and fossilized form of a tree resin that originated from extinct forests of different ages. If the resin was preserved under certain conditions and the original organic compounds are polymerized over millions of years we can speak of amber (Penney & Jepson 2014). Amber represents a small window into the extinct worlds of past ecosystems. It provides us with ecological information in the form of palaeogeographical data and cases of 'frozen behaviour' (Arrilo 2007, Poinar 2010).

Amber can contain biological inclusions, such as small animals that were entrapped in the fresh sticky resin or just pieces of animals that were left behind (for example wings, legs, hairs, feathers, and scales). Out of animal inclusions, representatives of Euarthropoda seem to be most common in certain types of amber, with the majority of those being representatives of Insecta (Hoffeins & Hoffeins 2003, Wichard & Weitschat 2004, Penney 2010, Penney & Jepson 2014, Gröhn 2015).

There are ~200 known fossiliferous amber deposits in the world, some with amber already from Mid-Carboniferous amber forests. The fauna presented within a piece of amber can differ immensely, depending on the geological origin and the age of the amber. The earliest ambers with biological inclusions represent the fauna of the Cretaceous and Tertiary (Penney & Jepson 2014). Several deposits from the Cretaceous yielded ambers with insect inclusions such as Raritan New Jersey Amber, Charentes French Amber, Kachin Amber, Canadian Amber, Spanish Amber, and Lebanese Amber (Penney 2010). From the Eocene there are (for example) Bitterfeld Amber, Rovno Amber, Oise Amber, and of course Baltic Amber (Penney 2010). Somewhat younger ambers are known from the Miocene, such as Dominican and Mexican Amber and possibly Australian Cape York Amber (Penney 2010).

Within the scope of this thesis, I further concentrate only on three types of amber because most of the specimens studied came from one of the three deposits. The oldest specimens came from the Kachin amber, dated to the Cretaceous, but younger ambers were also included, such as Eocene Baltic and Miocene Mexican amber.

1.3.1. Mexican Amber

Mexican Amber represents an approximately 15–20 million years old deposit from the southern state of Chiapas of Mexico (Solórzano Kraemer 2007). During the Cenozoic, this area was a coastal area with tropical dry forest as a part of the mangrove region (Langenheim 1967, Bousfield & Poinar 1994). This was implied by the biological inclusions of fossil plants (Graham

1999a, b; Martinez-Hernández 1992; Langenheim 1967), aquatic insects that inhabited epiphytic plants (Solórzano Kraemer 2010), and specimens of Amphipoda that are today closely associated to mangroves (Bousfield & Poinar 1994). The resin of an extinct tree *Hymenaea mexicana* seems to be the origin of Mexican Amber (Poinar & Brown 2002).

1.3.2. Baltic Amber

The exact age of Baltic Amber is still unsure. However, the 'Blue Earth', which the Baltic amber is mostly mined from, indicates the Priabonian (upper Eocene; approximately 34–38 million years old) age (Kosmowska-Ceranowicz et al. 1997). Nevertheless, some layers of the Baltic amber deposits are younger (Lower Gestreifter Sand; upper Oligocene) or even older (Lower Blue Earth; Lutetian). This leads to an estimated age range from 23–48 million years for all Baltic amber-bearing strata (Kosmowska-Ceranowicz et al. 1997, Standke 1998, Kasiński & Kramarska 2008, Standke 2008).

Within the Baltic amber representatives of nine conifer groups, not present in other Eocene floras, were found (Knobloch et al. 1996, Kvaček 2002, Kvaček 2010, Kvaček & Teodoridis 2011). This indicates the presence of coastal lowland swamps mostly influenced by brackish water and mixed conifer-flowering plant forests with meadows that were not affected by periodic flooding and waterlogging in 'Baltic amber forests' (Sadowski et al. 2017). This find suggests that Baltic amber derives from humid warm-temperate forests, as seen in modern East Asia and North America and the upper-Eocene-origin of the amber (Sadowski et al. 2017).

Other than very often plant inclusions of 'stellate hairs' from branched epidermal trichomes, Baltic amber is known for the high proportion of inclusions of the group Euarthropoda (Hoffeins & Hoffeins 2003, Wichard & Weitschat 2004, Weitschat & Wichard 2010). Surprisingly often are the inclusions of mero- and hololimnic animals, i.e. animals that spend parts or their entire life cycle in water (Wichard et al. 2009).

The source of the resin responsible for the Baltic amber remains unknown. There are several suggestions about the tree that was the source of the resin. These include a tree related to the modern representatives of Burseraceae (Kosmowska-Ceranowicz et al. 1993), an extinct relative of the araucarian tree *Agathis australis* (Langenheim 1969), an extinct relative of the modern cedar tree *Cedrus atlantica* or an umbrella pine (*Sciadopitys*)(Wolfe et al. 2009). However, pollen analysis of the amber suggests that the source of the resin was a pine relative, possibly *Pinus succinifera*, as already suggested by Goeppert (1850) and Conwentz (1890).

1.3.3. Kachin Amber

The age of Kachin amber from the Hukawng Valley of Myanmar, the so-called Burmite, has been controversial. At the beginning of the scientific studying of the Kachin amber, it was considered to be Eocene–Miocene in age (Shi et al. 2012). Now it is accepted that it originated in the Cretaceous. The exact age is still under dispute and different methods of age dating resulted in slightly different results, mostly around the border of Albian and Cenomanian (~100.5 mya; Cruickshank & Ko 2003, Feldberg et al. 2021, Shi et al. 2012). Based on the additional research on bivalves the early Cenomanian age seems to be the most likely (Smith & Ross 2016).

The environment in which the Burmese amber originated was tropical with temperatures between 32–55°C (Grimaldi et al. 2002). The suggested marine, estuarine or lagoonal areas of the environment must have been influenced by the volcanic activities nearby. This would have allowed quick burial of fresh resin by volcanic ejecta and ash, and preservation of amber and accompanying organic matter (Cruickshank & Ko 2003, Shi et al. 2012). This suggestion of fast burial is consistent with the signs of a volcanic eruption occurring at ~98.80 mya in the vicinity of the Hukawng Valley (Shi et al. 2012). More on ecology was discussed by Poinar & Poinar (2008) but without supporting many of the suggestions with explanations (Ross 2008).

Interestingly, from all major deposits of Cretaceous amber, Kachin amber contains the extremely species-rich palaeobiota with exceptional diversity and abundance of beetles (Shi et al. 2012). The origin of the resin seems to be an araucarian pine, similar to the extant representatives of *Agathis* (Penney 2010).

1.4. *Wood-associated beetles and trophic groups*

Today almost half of all insect species feed on plants (Schoonhoven et al.1998, Labandeira et al. 2002), with especially many beetle species that feed on tissues of flowering plants (McKenna et al. 2019). The plant-feeding strategies of beetles arose early in their history, probably already in Permian (Carpenter 1992). The earliest fossil record of wood-borings caused by a beetle is from mid- to upper Permian in fungus-decayed wood (Feng et al. 2017, McKenna et al. 2019). It is likely that pure fungal feeding preceded the feeding of wood tissues (Labandeira 2007). It was suggested that at some point the ancient beetles feeding on saprophytic fungi in leaf litter transitioned to feeding upon similar fungi in decaying wood and at some point started feeding on wood tissues only (Grimaldi & Engel 2005, Feng et al. 2017, McKenna et al. 2015, 2019, Peris et al. 2020, Tooker & Giron 2020). They further diversified and also developed types feeding on other plant tissues. The 'new' plant-feeding strategy was quite successful and by the mid-Jurassic herbivorous species doubled beetle diversity (Farrell 1998). The diverse 'new' plant-feeding groups exploited all types of wood, plant organs, and even pollen (Rasnitsyn & Krassilov 1996, Cai et al. 2018, Bao et al. 2019). Cai et al. (2018) reported an adult beetle of Boganiidae with pollen-feeding adaptations (mouthparts and legs) carrying pollen of cycads preserved in mid-Cretaceous Kachin amber. A year later, Bao et al. (2019) reported one of the first beetle pollinators of flowering plants from the mid-Cretaceous. This beetle pollinator was an adult specimen of Mordellidae with pollen grains attached to its body. The specimen had typical pollen-feeding mouthparts seen in the extant adult pollen-feeding representatives of Mordellidae (Bao et al. 2019). The most distal element of the maxillary palp was enlarged and axe-shaped. Such specialized modifications help collect and probably transport pollen grains (Krenn 2005). All major feeding groups of insects were established before the flowering plants 'overtook' the terrestrial ecosystems (Labandeira & Sepkoski 1993). By the beginning of the Paleogene, plant-feeding beetles overshadowed the nonherbivorous groups (Farrell 1998).

Depending on the position where the beetle is feeding, the plant feeding can be differentiated into ectophagy and endophagy. Endophagy in beetles is a type of insect feeding on plant or fungal tissues within a tissue of a plant, whether the tissue is dead or alive (Tooker & Giron 2020). The great diversity of endophytic feeding in beetles was likely driven by nutritional selection pressures (Tooker & Giron 2020). Endophages include a full range of beetles with secluded lifestyles, for example, borers, miners, or gallers (Tooker & Giron 2020). This diversity of lifestyles and taxonomical diversity of beetle endophages is partially connected to the evolution of larvae with prognathous heads and chewing mouthparts that allowed biting into plants and further eating/boring/mining of hidden plant tissues (Labandeira 1997). In addition, the endophagous beetles profit from their hidden way of life in lower mortality due to natural enemies (Hawkins et al. 1997) and heat or moisture stress (Tooker & Giron 2020).

After Nikitsky et al. (1996, 2008) wood-associated beetles (≈ xylobiont beetles) can be associated either with a wood of various states, fungi within a wood, or slime moulds on bark or dead wood (Myxomycetes; Stephenson & Stempen 1994). Based on their food preferences these can be further differentiated into one of four major trophic groups of beetles after Lobanov (Bieliavtsev 2021): phytophages (include: xylophages), mycetophages (include: myxomycetophages, xylomycetophages, sapromycetophages and zoomycetophages), saprophages (include: detritophages, saproxylophages and sapromycetophages) and zoophages (include: predators and parasites with parasitoids). Even though zoophage predators do not directly feed on the wood or wood fungi, they are often encountered within the wood, where they predate on xylophages within their corridors (i.e. predators on Scolytinae or Platypodinae). However, different categories of trophic groups should be used carefully since many categories contain species with mixed types of feeding and are often understood differently among different authors (Bieliavtsev 2021).

Nikitsky et al. (2008) distinguish seven trophic groups in their study based on the nutrition of the xylobiont beetle larvae: 1. true xylophages (including phleophages), 2. saproxylo-mycetophages and saproxylophages, 3. saprophages and sapronecrophages, 4. true myxomycetophages and mycetophages, 5. predators, 6. parasites, and 7. pantophages that feed both as phytophages and as predators. For example, there are records of some larvae of Cerambycidae, that are normally considered truly phytophagous (Craighead 1923, Linsley 1958, 1959), predating on bark beetles or other conspecific larvae (Dodds et al. 2001). Ulyshen (2016) recognized only four, so-called, functional groups: phloem and wood feeders, fungus feeders, detritus feeders, and predators.

The percentages of representatives of each trophic group differ with the region and the environmental conditions (Nikitsky 1993, Kovalev 2014). Additionally, the presence of individuals of certain species can influence the percentage in which the representatives of different trophic groups occur, as well (Gossner et al. 2019). Therefore, knowing which trophic groups are represented within an ecosystem is important because the insect species composition and the percentages of individual trophic groups can be indicators of the state of forest ecosystems (Bieliavtsev 2021).

1.5. Beetle larvae

Holometabola is a megadiverse group of insects that comprises between 830 000–850 000 described species (Wiegmann et al. 2009, Beutel et al. 2022). Within this extremely diverse group larvae differ morphologically and ecologically from their adults (Beutel 2005a, Lawerence et al. 2011, Haug et al. 2015, Badano et al. 2018, Truman 2019, Beutel et al. 2022, Prokop et al. 2023). Furthermore, representatives of Holometabola have also a pupa, an additional life stage between the last larval stage and the adult, with yet another different morphology and ecology. Once these aspects are included, biodiversity of this group is additionally increased. Therefore, beetles, which are also holometabolous, often have larvae leading completely different lifestyles than adults. However, the imaginary lines of larva-pupa-adult are not always clear. An ontogenetic sequence of beetle species can be complex and can comprise many larval stages (Peterson 1951) and adults with retained larval characters (Kundrata & Bocak 2011, McMahon & Hayward 2016, Rosa et al. 2020, Haug et al. early view b: **Article 7**).

So, what is a larva, and which criteria to use when working with immature holometabolous insects? Very different definitions were given by various authors (Hickman 1999, Minelli 2003, Stehr 2009). The general term of a larva often involves free-living sexually immature stages that differ from their corresponding adult (Campbell 1997, Storch et al. 2013, Haug 2018). For more precise terminology Haug (2018) outlined different criteria that are used to identify an immature as a larva. He further differentiates: a) morpho-larva (s.l. or s.str.), b) eco-larva (s.l. or s.str.), c) metamorph-larva, d) apo-larva and e) plesio-larva. All insects, including the Holometabola with their pupa as well, could be interpreted as morpho-larva s.l. where immatures morphologically differ significantly from the corresponding adult (Haug 2018). However, not all can be interpreted as eco-larva s.l. or other.

Unfortunately, the importance of larvae, as counterparts of adults with often different ecology and morphology that add significantly to the biodiversity of beetles, has been often overlooked (Haug et al. 2019, Zippel et al. 2022a: **Article 4**, 2023a). Additionally, in many holometabolan groups, individuals spend longer time as a larva than as an adult. The number of larval stages of beetles can vary drastically depending on the species (and sometimes even within the species; check Esperk et al. 2007), with a minimum of three (Peterson 1951), but often with more (i.e. riffle beetles with seven larval stages, Brown 1987; some roundheaded borers with up to 15 larval stages, Adachi 1994; some darkling beetles with up to 20 larval stages, Park et al. 2014).

Therefore, larvae contribute to the biomass majorly (Haug & Haug 2019). The biomass of insect larvae is so big that the insect larvae are considered a more efficient food source (for animals but also humans) that could level out the environmental impacts of food production systems (Scriber & Slansky1981, Barragan-Fonseca et al. 2017, van Huis & Tomberlin 2017, Lalander et al. 2015, Gligorescu et al. 2019).

There is generally a lack of information on larvae of most of the ingroups of beetles (for example, larvae of Scraptiidae; Minelli et al. 2006, Haug & Haug 2019, Zippel et al. 2022a: **Article 4**) and larvae of many species, and even on the level of supra-specific groups, are still unknown. For example, larvae are still unknown in some groups within Archostemata (Hörnschemeyer 2005), some groups within Myxophaga (Beutel 2005b), for example, Lepiceridae (Arce-Pérez et al. 2005), some ingroups within Carabidae (Arndt et al. 2005), Hydrophilidae (Archangelsky et al. 2005), Decliniidae (Lawrence 2005a), Limnichidae (Hernando & Ribera 2005), Glaresidae, Diphyllostomatidae, Belohinidae, some ingroups of Scarabaeidae (Scholz & Grebennikov 2005), Rhinorhipidae (Lawrence 2005b), some ingroups of Elateridae (Costa et al. 2005a), Plastoceridae (Branham 2005a), Telegeusidae (Lawrence 2005c), Omethidae (Ramsdale 2005), some ingroups of Disteniidae (Svácha & Lawrence 2014a). This effect is possibly present due to biased collecting of generally more available adults in comparison to the harder sampling of often secluded larvae (Buck 1954, Crowson 1955, Hayashi 1962, Vanin et al. 1996, Zippel et al. 2023), the more challenging interpretation based on often very different characters in comparison to the adult ones (Lawrence et al. 2011) or simply due to the decision of taking the easier route of re-investigating the known and 'in trend' topics (Zippel et al. 2022a: **Article 4**).

Beetle larvae have a wide spectrum of morphologies that facilitate the most diverse ecological functions (Böving & Craighead 1931, Peterson 1951, Klausnitzer 1978). A great majority of beetle larvae are terrestrial, with only some groups having aquatic larvae (Peterson 1951). Many beetle larvae feed on plant tissues (whether living or dead), fungi, carrion, and dung, and only some beetle larvae are predaceous or parasitic (including parasitoid larvae) (Stehr 1991).

Beetle larvae are morphologically very diverse and therefore, the body can drastically differ between different groups. Peterson (1951) differentiates several body types: campodeiform (i.e. some larvae of Adephaga, Staphylinoidea), eruciform (i.e. some larvae of Polyphaga), scarabeiform (i.e. some larvae of Scarabaeidea, Lucanidae, Anobiidae, Bostrichidae), vermiform (i.e. some representatives of Eucnemidae), cyphosomatic (i.e. Criocerinae) and limpet-like (i.e. Psephenidae). The mouth parts are mostly of biting type but can differ depending on the source of food (Beutel & Lawrence 2005). Legs are either with six (Archostemata, Adephaga) or five elements (Myxophaga, Polyphaga) (Lawrence 1991, Lawrence et al. 2011).

1.5.1. Importance of wood-associated beetle larvae

Some beetle larvae, apart from adding to biodiversity and biomass, have additional important effects on the ecological communities by promoting wood-decomposition and cycling of elements, especially carbon and nitrogen (Möller 2009, Ulyshen 2016, Zippel et al. 2022a: **Article 4**, 2023b: **Article 6**). The positive influence of insect larvae on the processing of wood material is often underestimated and under-credited. A single larva of *Protaetia lugubris* (Scarabaeidae) can process during its development the astonishing 1000 gramms of wet woody substance (Möller 2009). During wood decomposition, the molecules of cellulose, hemicellulose, and lignin are cut into smaller units until they are returned to the environment in inorganic form (Swift et al. 1979). This subdivision can be achieved by respiration, combustion, or physical degradation (Cornwell et al. 2009). Wood-feeding beetle larvae, among other wood-inhabiting organisms (Ulyshen 2016, Philippe et al. 2022), accelerate the release of bound nutrients within the wood while feeding (Möller 2009). Some beetle larvae fragment the wood and break down the woody tissues either with self-produced wood-decomposing enzymes or with the help of symbionts in their gut (Möller 2009, Ulyshen 2016, McKenna 2019, Martinson 2020). Especially, the larvae that feed in nutrientdeficient tissues may depend on wood-digesting enzymes to help in nutrient assimilation (Hanks 1999). Additionally, by penetrating the wood, the distribution of wood-decomposing fungi over the dying or decaying wood is enhanced (Rayner & Boddy 1988, Möller 2009, Ulyshen 2016), and the aeration within the wood increases. This results in a faster spreading of the fungi, and the development of enzymatic or oxidative degradation processes (Rayner & Boddy 1988). After digestion, the frass of the larvae contains degraded wood substances that positively influence the forest floor, and promote humidification and the stability of soil organic matter (Boddy & Swift 1984, Swift et al. 1984, Szujecki 1987, Möller 2009). The processed wood matter serves further as a food source for some beetles, both the larvae and the adults (sometimes wood gets digested more than once to extract most of it, see Szlávecz & Pobozsny, 1995 and Ulyshen 2016), earthworms, and microbes (Ghilarov 1970, Kühnelt, 1976; Szlávecz & Pobozsny, 1995).

However, the importance of wood-associated beetle larvae is not only positive. Many wood borer larvae cause severe damage to plants and are considered a pest. The influence of insects, both immature and adult, can have drastic impacts on wood ecosystems and negative economic consequences for humans (*e.g.*, bark beetles; Kirkendall et al. 2015, Zippel et al. 2023b: **Article 6**). For example, some species of Scolytinae (bark beetles) evolved complex behavioural patterns that enable them to override the defence systems of healthy trees (Wood 1982). They produce specific pheromones used in communication to simultaneously attack a single tree at once. Once the tree is inhabited, the beetles will reproduce within and therefore weaken the tree even further (Farrell et al. 2001). Heavily-stressed trees have lowered defence reactions, which opens an opportunity for other insects, without such profound mechanisms as in bark beetles, to also successfully colonize the tree (Klepzig et al. 2005, Lombardero et al. 2006, Saint-Germain et al. 2006).

Understanding the biodiversity of tree-associated beetles is, therefore, extremely relevant not only to the forest industry (Bouchard et al. 2017) but also for the comprehension of the global effects that woods have on climate and element cycling. However, only a small portion of xylobiont species is known and has been adequately interpreted (Bouchard et al. 2017).

1.5.2. Fossil beetle larvae

Just as knowledge about the biodiversity of extant beetles can tell us a lot about the state of the ecosystems today, the same can be presumed for the past ecosystems. The interaction between plants and animals is a very old force driving the evolution of both counterparts, and this is especially present in insects (Haug et al. 2021a: **Article 1**). While considering that beetles are holometabolous and the difference between larvae and adults is often immense, fossils of larvae are especially relevant when reconstructing ecological aspects of past faunas (Baranov et al. 2020, Haug et al. early view b: **Article 7**).

Unfortunately, immature fossils are often not preserved completely or the informative morphological characteristics with details are unavailable, which makes them difficult to interpret (Rolfe 1985, Shear & Kukalová-Peck 1990, Klausnitzer 2003, Stehr 2009). This is especially true for the fossils of larvae of Holometabola, such as beetle larvae, which can lead to disagreements about the interpretation within the scientific public [check Kirejtshuk (2020) vs. Boudinot et al. (2023), or Zippel et al. (2022b: **Article 5**) vs. Batelka & Engel (2022), Rasnitsyn & Müller (2023)]. There is a general opinion that many larvae that are relatively small, especially in comparison to adult counterparts, seem to be relatively less often preserved. Shear & Kukalová-Peck (1990) explain this through a taphonomic bias against the preservation of small, terrestrial, nonflying, and poorly sclerotized organisms. A similar conclusion was made for species with wood-associated lifestyles by dos Santos et al. (2021). Supposedly, due to the hidden way of life, such specimens are hardly preserved in the paleontological record and there seems to be only 'anecdotal evidence' for their presence in it (Peris & Rust 2020, dos Santos et al. 2021). Philippe et al. (2022) suggested that organisms that live in wood are less likely to get fossilized because the host wood deteriorates faster through the proliferation of such organisms and the specimens are 'subject to a taphonomic tragedy'.

Therefore, the reconstruction of the evolutionary history of wood-associated insect groups seems especially challenging (dos Santos et al. 2021, Cai et al. 2022). However, there are certain preservation types that prefer exactly small poorly sclerotized organisms (for example, 'Orsten'-type preservation; Waloszek 2003, or the Rhynie chert; Dunlop & Garwood 2018), and the specimens with wood-associated lifestyle are found within various amber deposits relatively often (Haug et al. early view a), as seen within the scope of this thesis (Haug et al. 2021a, b, early view b, Zippel et al. 2022a, b, c, 2023b, in review a, b: **Articles 1–9**). Therefore, the statements made about the poor fossilization of beetle larvae are not in congruence with our findings.

Indeed, it should not be surprising to find wood-associated larvae within amber. The habitat of such larvae was close to the source of tree resin and the entrapment within must have occurred regularly (Zippel et al. 2022a). Therefore, the number of such larvae should be relatively high in different ambers. It seems that the rareness of these larvae within amber is the result of not reporting such larvae. Lately, the interest in fossil larvae of insects seems to change the course for the better, and quite some reports of insect inclusions in amber can be found (e.g. Kirejtshuk & Azar 2008, Ross 2010, Hörnschemeyer 2013, Haug & Haug 2019, Badano et al. 2018, 2021, Baranov 2020, 2021, Peris & Rust 2020, Haug & Haug 2021, 2022, Haug et al. 2022a, b, c, d, early view a, b: **Article 7**, Hörnig et al. 2022, Zippel & Kiesmüller et al. 2021, Zippel et al. 2022d, 2023b: **Article 6**, Amaral et al. 2023).

In addition, traces of wood-borers within fossilized wood (Genise & Hazeldine 2008, Feng et al. 2017, McKenna et al. 2019, Haug et al. early view a) and plant structures that resulted from insect activity within plants, such as galls (Wiegmann et al. 2009), also help to better understand the evolution of insects associated with plants. Such a record of plant-insect relationships provides us with the input of the feeding type, information that we cannot always deduct from the habitus of fossilized insects (Labandeira 2007, Labandeira et al. 2007).

2. THE GOALS OF THIS THESIS

The communities of wood-associated animals are of great importance in breaking down wood into smaller pieces that can further be easily processed, for example, by microorganisms. Wood-associated beetle larvae, also help with the cycling of the elements, especially carbon, in this way. Even though their importance is therefore immense, the presence of these larvae in literature is rather scarce. Their fossil record is often even scarcer, with many larvae of wood-associated beetle ingroups remaining entirely unknown, before the modern fauna. However, are fossil wood-associated beetle larvae as rarely fossilized, as indicated by their scarceness in literature? Do all wood-associated beetle larvae share the same morphological characters? Are there fossil groups that share morphological patterns and possibly have had the same ecological roles within the wood? To answer these questions I set several goals for this study.

The goal of this thesis is to study whether:

- the fossil wood-associated larvae are as rare as presented in the literature. My prediction is that the wood-associated beetle larvae occur much more often in amber as previously thought.
- wood-associated beetle larvae of different groups with similar ecological functions are morphologically similar. I predict that the wood-associated beetle larvae within a single trophic group living under similar conditions have similar ecological functions and share certain morphological patterns.
- wood-associated extant larvae are morphologically similar to fossil larvae of the same groups. My prediction is that fossil wood-associated beetle larvae have similarities to the extant representatives of the lineages but do not yet have all apomorphic characters known from modern counterparts.
- different trophic groups among wood-associated communities already existed in past ecosystems. I predict that specializations for a certain type of feeding within different wood tissues, and therefore different trophic groups, already existed in the past.

To test the predictions, I researched the available literature on wood-associated beetle larvae. Additionally, I visited and studied various museum collections of amber. I also often included extant specimens that were used together with fossil specimens in morphospace analyses. With the morphoshape analyses, I compared different available larval characters. Since the characters, such as mouth parts, that are mostly used for the interpretation of extant beetle larvae, were often not accessible in the fossils, all characters that showed diversity among the groups and were available were taken into consideration. Such comparison among extant and fossil larval specimens was important for understanding the evolution of certain character patterns. I expected that fossil representatives already have some apomorphic characters known also from today´s groups but not all. Therefore, I additionally focused on finding such intermediate forms but also on finding completely unknown morphologies that went extinct somewhere on the way.

3. RESULTS:

3.1. *Article I – a publication*

Haug, C., Haug, G. T., **Zippel, A.**, van der Wal, S. & Haug, J. T. (2021). The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4, 390–404.
https://doi.org/10.11646/palaeoentomology.4.4.14

3.2. *Article II – a publication*

Haug, J.T., **Zippel, A.**, Haug, G.T., Hoffeins, C., Hoffeins, H.-W., Hammel, J.U., Baranov, V. & Haug, C. (2021). Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14, 161–183.
https://doi.org/10.18476/pale.v14.a8

3.3. *Article III – a publication*

Zippel, A., Baranov, V.A., Hammel, J.U., Hörnig, M.K., Haug, C. & Haug, J.T. (2022). The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10, art. e13025.
https://doi.org/10.7717/peerj.13025

3.4. *Article IV – a publication*

Zippel, A., Haug, C., Hoffeins, C., Hoffeins, H.-W. & Haug, J.T. (2022). Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia 128, 81–104.
https://doi.org/10.54103/2039-4942/17084

3.5. *Article V – a publication*

Zippel, A., Haug, C., Müller, P. & Haug, J.T. (2022) First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96, 219–229.
https://doi.org/10.1007/s12542-022-00608-8

3.6. *Article VI – a publication*

Zippel, A., Haug, C., Müller, P. & Haug, J.T. (2023). The first fossil false click beetle larva preserved in amber. PalZ 97, 209–215.
https://doi.org/10.1007/s12542-022-00638-2

3.7. *Article VII – a publication*

Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. (early view). Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ. https://doi.org/10.1007/s12542-023-00648-8

3.8. *Article VIII – a manuscript*

Zippel, A., Haug, C., Müller, P. & Haug, J.T. (in REVISION). Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ.

Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber

Ana **Zippel**[1*], Carolin **Haug**[1,2], Patrick **Müller**[3], Joachim T. **Haug**[1,2]

[1] Ludwig-Maximilians-Universität München, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany; ORCID: CH (https://orcid.org/0000-0001-9208-4229); AZ (https://orcid.org/0000-0002-6509-4445); JTH (https://orcid.org/0000-0001-8254-8472)
[2] GeoBio-Center at LMU, Richard-Wagner-Str. 10, 80333 München, Germany.
[3] Kreuzbergstr. 90, 66482 Zweibrücken, Germany.

[*] corresponding author: ana.zippel@palaeo-evo-devo.info

Abstract

Beetle larvae show high diversity in forms and ecological roles. Beetle larvae are often roughly categorised into certain larval types, for example: campodeiform, onisciform, scarabeiform, or elateriform. Larvae of the latter type are virtually absent from the fossil record. Here we report three amber pieces from Cretaceous Kachin amber, Myanmar (about 100 million years old) that together include nine elateriform beetle larvae. One of the amber pieces has a single specimen included. The specimen is interpreted as a larva of Elateridae, the group of click beetles, possibly of the ingroup Elaterinae; yet accessible details are limited. Eight specimens within the other two amber pieces show certain similarities with larvae of Elateridae, but show significant differences in the trunk end, which bears two lobes armed with hooks in these fossils. This very specific structure is well known in modern larvae of Ptilodactylidae (toed-winged beetles). Therefore, the fossils are interpreted as larvae of Ptilodactylidae. Both types of here reported elateriform larvae represent the first fossil record of larvae of their respective groups. It is well known that larval morphology does not evolve in concert with adult morphology, and a modern-type morphology of the one may precede that of the other. Hence the new fossils are important indicators of the appearance of the modern larval morphologies of their respective lineages. We also briefly discuss the fossil record of larvae of Elateriformia (of which Elateridae and Ptilodactylidae are ingroups) in general.

Key words: Elateridae; click beetles; Ptilodactylidae; toed-winged beetles; Burmese amber; Cretaceous

Declarations

Funding: The study is kindly supported by the German Research Foundation (DFG Ha 6300/6-1) and Volkswagen Foundation with a Lichtenberg Professorship to JTH.

Conflicts of interest/Competing interests: The authors declare that they have no conflicts of interest and no competing interests.

Availability of data and material: All data is provided in the text and the figure.

Code availability: not applicable

Authors' contributions: Conceptualization: Carolin Haug, Joachim T. Haug, Ana Zippel; Methodology: Carolin Haug, Patrick Müller, Joachim T. Haug, Ana Zippel; Investigation: Carolin Haug, Patrick Müller, Joachim T. Haug, Ana Zippel; Writing - original draft preparation: Carolin Haug, Joachim T. Haug, Ana Zippel; Writing - review and editing: Carolin Haug, Patrick Müller, Joachim T. Haug, Ana Zippel; Funding acquisition: Joachim T. Haug; Resources: Patrick Müller, Joachim T. Haug

Introduction

Beetles (Coleoptera) have been considered the most species-rich group of animals, yet this statement is logically incorrect (see Haug et al. 2016 for the comparable case of Insecta). Still the group Coleoptera is indeed extremely species-rich, with more than 380,000 formally described species (e.g. McKenna et al. 2019).

Despite the enormous species richness, people are usually able to recognise most beetles as such, at least adult beetles. Beetles have a quite stereotypic morphology as adults, with strongly sclerotised exoskeleton and elytrae (Beutel and Lawrence 2016), providing a straight line on the back, instead of an oblique one. On the contrary, the larvae can have astonishingly different morphologies. To cope with the enormous form diversity of the larvae, they are often grouped into specific types: there are, for example, campodeiform larvae (Jałoszyński and Kilian 2016), onsiciform ones (Jałoszyński and Beutel 2012; Jałoszyński 2018), or grubs, also known as scarabeiform larvae. The last name also gives a hint that this special larva is also typical for a specific ingroup of beetles, in this case Scarabeidae (dung beetles). A comparable case is that of elateriform larvae, a special type of larvae that occurs in certain species of click beetles (Elateridae, with about 10,000 species; Costa et al. 2010 p. 75; especially in the ingroup Elaterinae, more precisely, Elaterini, Ampedini, or Cebrionini; Hyslop 1917; Schimmel and Tarnawski, 2010 fig. 98 p. 469; Casari and Biffi 2012).

Such a larva is very elongate and slender, all trunk segments are basically tube-shaped. The locomotory appendages (legs) are well developed, but are still short in comparison to the very elongate body. Elateriform larvae occur in few other lineages, for example, in other lineages of beetles, such as false click beetles (Eucnemidae; e.g. Otto 2017 p. 3, fig. 1 p. 8), darkling beetles (Tenebrionidae; e.g. Costa and Vanin 2010 fig. 14 left p. 8), riffle beetles (Elmidae; e.g. Barr et al. 2015 fig. 22 p. 543; González-Córdoba et al. 2020 fig. 3B p. 535; Shepard et al. 2020 fig. 2 p. 4) or toed-winged beetles (Ptilodactylidae; e.g. Stribling 1986 fig. 33 p. 227; Lawrence and Stribling 1992 fig. 12), but also in non-coleopteran lineages, such as butterflies and moths (Lepidoptera; Hoare et al. 2006 fig. 25 p. 578) or some scorpionflies (Mecoptera: Nannochoristidae; Pilgrim 1972 figs. 1–3 p. 153). Yet, most common elateriform larvae seem to be representatives of click beetles.

Click beetle larvae can fulfil numerous ecological roles. Some are, for example, ferocious predators that can also subdue much larger prey, such as the likewise predatory larvae of antlions (Devetak & Arnett 2010). Others are saprophagous or phytophagous. With these ecological roles they are important, and also not rare, components in many habitats.

Click beetles have a quite astonishing fossil record with more than 250 formally described species (recently summarised in Kundrata et al. 2021a tab. A1 pp. 82–88). Of these, 23 species appear to be based on exceptionally preserved specimens in different types of ambers from various ages, including Miocene (Becker 1963; Zaragoza Caballero 1990), Eocene (Iablokoff-Khnzorian 1961; Schimmel 2005; Kirejtshuk and Kovalev 2015; Kundrata et al. 2020) and also Cretaceous ambers (Cockerell 1917; Otto 2019), although only three species have been described from the latter. So far, all of these fossils seem to be adult individuals. Also general books providing overviews over amber from different deposits did not include any elateriform larva.

Toed-winged beetles, on the contrary, have so far quite a scarce fossil record and appear overall understudied (Kundrata et al. 2021b p. 1). Kundrata et al. (2021b) listed five fossil species (their tab. A1 pp. 11–12), each represented by very few specimens (Motschulsky 1856; Chatzimanolis et al. 2012; Alekseev and Jäch 2016; Kirejtshuk et al. 2019). Similarly to the fossil record of click beetles, the fossil record of toed-winged beetles so far includes only adult specimens.

The seeming absence of elateriform larvae is quite remarkable, given the fact that amber in general, and specifically Cretaceous amber has provided numerous types of holometabolan larvae. This includes, for example, larvae of hymenopterans (Lohrmann & Engel 2017), dipterans (Baranov et al. 2020; Liu et al. 2020), lepidopterans (MacKay 1970; Grimaldi & Engel 2005; Xia et al. 2015; Haug and Haug 2021; Gauweiler et al. 2022), lacewings (Pérez-de la Fuente et al. 2012, 2016, 2018, 2019, 2020; Wang et al. 2016; Liu et al. 2016, 2018, 2022; Badano et al. 2018, 2021; Haug et al. 2018, 2019a–c, 2020a–d, 2021a–d, 2022a; Herrera-Flórez et al. 2020; Hörnig et al. 2020, 2022; Zippel et al. 2021; Luo et al. 2022) and their closer relatives (Engel 2002; Perrichot and Engel 2007; Grimaldi & Nascibeme 2010; Haug et al. 2020e, early view; Baranov et al. 2022), but especially also beetles (Kirejtshuk and Azar 2008; Beutel et al. 2016; Batelka et al. 2019; Zhao et al. 2019, 2020; Haug et al. 2021e, f, in press; Zippel et al. 2022a, early view). Given the fact that in the modern fauna elateriform larvae are relatively well known components and that adults of Elateridae are known in Cretaceous Myanmar amber, we should expect to be able to find such larvae also in this type of amber.

We here report the first elateriform larvae from Myanmar amber. We discuss implications of this finding.

Material and Methods

Material

In total, three amber pieces are in the centre of this study: BUB 4275, PED 0369, and PED 0925. All three amber pieces originate from about 100-million-year-old Cretaceous Myanmar Kachin amber from the Hukawng Valley (Cruickshank and Ko 2003; Shi et al. 2012). BUB 4275 comes from the collection of one of the authors (PM), PED 0369 and PED 0925 are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München. The PED specimens were legally acquired via the online platform ebay.com from two different traders (globalburmiteamber, burmite-miner).

The three pieces of amber include in total nine elateriform larvae. BUB 4275 includes a single larva of interest, PED 0369 includes in total three larvae of interest, and PED 0925 includes five larvae of interest. All three amber pieces are filled with additional inclusions such as air bubbles, detritus, or cuticle fragments.

Documentation methods

The specimens were documented on a Keyence VHX-6000 digital microscope in front of white and black background under different illumination settings (cross-polarised co-axial light and low-angle ring light; Haug et al. 2013a, 2018). All images were recorded as composite images (Haug et al. 2008, 2011; Kerp and Bomfleur 2011), combining several images of varying focus and several adjacent image details as well as different exposure times (HDR, cf. Haug et al. 2013b). Images were further processed and colour-marked with Adobe Photoshop CS2. Comparative drawings were prepared in Adobe Illustrator CS2.

Results

Description of specimen BUB 4275

Amber piece with a single beetle larva. Total body length approximately 8.70 mm. Body elongate, cylindrical (Fig. 1a–c), differentiated into anterior head and posterior very elongated trunk. Head prognathous, mouthparts facing forwards, slightly-flattened (Fig. 1d–e), semi-ovoid in antero-lateral view, longer than wide, 1.9× (~ 0.47 mm long). No stemmata discernible. Labrum (derivative of ocular segment), wider than long, antero-medially drawn out into pentagonal (in antero-lateral view) projection (nasale) (Fig. 1d, e). Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna with two elements discernible, shorter than head capsule, 2.8×

(~ 0.17 mm long). Possible further distal antenna element not accessible. Preserved distal element distally wider and with a spine-like process (Fig. 1d, e). Intercalary segment (post-ocular segment 2) without externally recognisable structures.

Mandibles (appendages of post-ocular segment 3) strongly sclerotized, only partially accessible, appear sickle-shaped in antero-lateral view, right mandible ~ 0.32 mm long. A single seta discernible on left mandible (Fig. 1d, e). Maxillae (appendages of post-ocular segment 4) with two major parts discernible: rectangular proximal part, longer than wide (0.19 mm long), and distal palp, ~ 0.13 mm long. Maxillary palp with four elements (Fig. 1d, e). Labium (conjoined appendages of post-ocular segment 5) partially accessible, distal palps discernible in antero-lateral view.

Trunk further differentiated into anterior thorax and posterior abdomen. Thorax with three segments (pro-, meso-, and metathorax). Each thorax segment with a pair of locomotory appendages (legs). Prothorax rectangular in lateral view, longer than wide, 2× (~ 0.67 mm long), also longest segment of thorax. Anterior part of prothorax with a structurally differentiated, possibly more sclerotized region, probably as a ring around the body. Meso- and metathorax sub-similar. Mesothorax wider than long, 1.3× (~ 0.42 mm long). Metathorax slightly wider than long, 1.1× (~ 0.34 mm long) (Fig. 1a–c). Legs discernible, ~ 0.55 mm long (Fig. 1a–c).

Abdomen with nine discernible units. Abdomen segments 1–8 subsimilar, rectangular in lateral view, longer than wide (between 0.56–0.82 mm long and between 0.29–0.37 mm wide). Anterior part of abdomen units 3–9 each with a short, structurally differentiated, possibly more sclerotized region, probably as a ring around the body. Terminal end semi-ovoid in lateral view, longer than proximally wide, 2.1× (~ 0.75 mm long) (Fig. 1a–c).

General description of larvae in amber pieces PED 0369 and PED 0925

Beetle larvae with very elongate, cylindrical body. Body differentiated into anterior head and posterior very elongated trunk. Trunk further differentiated into anterior thorax and posterior abdomen. Head prognathous, mouthparts facing forwards. Thorax with three segments (pro-, meso- and metathorax). Thorax bears on each segment a pair of locomotory appendages (legs). Abdomen with ten discernible units, nine segments and the trunk end. Segment 9 with tergite and sternite forming a single continuous sclerotic structure. Entire sclerotic structure of subtrapezoid shape in lateral view, with sternal region of approximately half the length of tergal region. Trunk end partly overhung by dorsal part of segment 9, hence functionally ventrally articulated to it. Trunk end with two postero-ventrally orientated, thin, spine-like processes and a two-lobed structure (possible pygopod) with multiple hooks (at least five hooks per lobe).

Description of specimen 1 in amber piece PED 0369 (Fig. 2a–c)

Total body length approximately 9.93 mm. Head semicircular in dorso-lateral view, wider than long, 1.3× (~ 0.38 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible in dorso-lateral view. Antennae (appendages of post-ocular segment 1) with at least two elements discernible, longer than head, 1.3× (~ 0.51 mm long) (Fig. 2b, c). Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (appendages of post-ocular segment 3) not discernible. Proximal parts of maxillae (appendages of post-ocular segment 4) not accessible, possible distal part (palp) apparent (Fig. 2c), no details accessible. Labium (appendages of post-ocular segment 5) not accessible. Anterior and lateral rim of head with several long setae (~ 0.32 mm long).

Three thorax segments with prominent dorsal sclerite each (tergite, notum; pro-, meso-, and metanotum). Pronotum trapezoid in dorso-lateral view, longer than wide at anterior end, 2×, and at posterior end, 1.4× (~ 0.94 mm long), longest tergite of thorax. Meso- and metanotum subsimilar, rectangular in dorso-lateral view. Mesonotum wider than long, 1.2× (~ 0.6 mm long). Metanotum wider than long, 1.3× (~ 0.6 mm long) (Fig. 2b, c). Legs not accessible.

Abdomen segments 1–8 subsimilar, rectangular in dorso-lateral view. Segments 1 and 2 shorter than wide (~ 0.68 mm long and between 0.77–0.81 mm wide), segment 5 as long as wide (~ 0.77 mm long), segments 3–4 and 6–8 longer than wide (between 0.82–0.86 mm long and between 0.68–0.78 mm wide). Abdomen segment 9 sub-trapezoid in dorso-lateral view, longer than proximally wide, 2× (~ 1.2 mm long) (Fig. 2b, c). Posterior half of segment 9 bears multiple setae (between 0.17–0.51 mm long). Trunk end largely concealed, partially visible lobe structure (Fig. 2c).

Description of specimen 2 in amber piece PED 0369 (Figs. 2a, 3a)
Total body length unknown due to the inaccessibility of anterior parts of the specimen (Fig. 3a). Head unaccessible. Thorax and its appendages unaccessible. Abdomen segments 2–9 discernible with total length of ~ 5.95 mm. Segments 2–8 subsimilar, rectangular in dorsal view, between 0.51–0.79 mm long and between 0.59–0.67 mm wide. Abdomen segment 9 subtriangular in dorsal view, longer than proximally wide, 1.4× (~ 0.58 mm long) (Fig. 3a). Trunk end not accessible. Posterior half of segment 9 bears multiple setae (between 0.01–0.21 mm long).

Description of specimen 3 in amber piece PED 0369 (Figs. 2a, 3b–d)
Specimen is damaged in the posterior part of abdomen (Fig. 3b). Total body length only estimated to approximately 9.14 mm. Head pentagonal in dorso-lateral view, longer than wide, 1.7× (~ 0.68 mm long) (Fig. 3c). No stemmata discernible. Labrum (derivative of ocular segment) strongly sclerotised, pentagonal in dorso-lateral view, posteriorly wider than long, 1.2× (~ 0.43 mm long) (Fig. 3d). Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna with at least two elements discernible, accessible part shorter than head. Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (appendages of post-ocular segment 3) strongly sclerotized, only partially accessible (Fig. 3c, d). Proximal parts of maxillae (appendages of post-ocular segment 4) only partially accessible, distal part (palp) apparent. Maxillary palp with four elements (Fig. 3d, white arrows). Labium (conjoined appendages of post-ocular segment 5) partially accessible, possible distal palps discernible in dorso-lateral view.

Thorax tube-like in lateral view, with total length of ~ 1.35 mm. Separate thorax segments not discernible (Fig. 3b). Legs not accessible.

Abdomen tube-like in lateral view, with total length of ~ 7.12 mm. Separate abdomen segments 1–8 not clearly discernible. Abdomen segment 9 triangular in lateral view, longer than proximally wide, 2.3× (~ 1.42 mm long) (Fig. 3b). Trunk end largely concealed, partially visible hooks on lobe structure (Fig. 3b, white arrow).

Description of specimen 1 in amber piece PED 0925 (Fig. 4a, b)
Total body length approximately 8.25 mm. Head trapezoidal in lateral view, longer than wide, 1.4× (~ 0.37 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible in lateral view. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible, accessible part shorter than head capsule, 1.7× (~ 0.22 mm long). Number of elements not discernible (Fig. 4b). Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4) and labium (appendages of post-ocular segment 5) not accessible.

Prothorax tube-like in lateral view, anteriorly and posteriorly wider, longer than wide at posterior end, 2.2× (~ 0.78 mm long), also longest segment of thorax. Meso- and metathorax subsimilar, rectangular in lateral view. Mesothorax wider than long, 2.1× (~ 0.25 mm long). Metathorax wider than long, 1.2× (~ 0.47 mm long) (Fig. 4b). Legs discernible, ~ 0.6 mm long (Fig. 4b, white arrows).

Abdomen segments 1–8 subsimilar, rectangular in lateral view. Abdomen segments 1–6 wider than long (between 0.47–0.72 mm long and between 0.7–0.82 mm wide). Abdomen segments

7–8 longer than wide (between 0.8–0.95 mm long and 0.55–0.66 mm wide) (Fig. 4b). Abdomen segment 9 triangular in lateral view, longer than wide at proximal end, 2.5× (~ 1.17 mm long) (Fig. 4b). Trunk end not accessible.

Description of specimen 2 in amber piece PED 0925 (Figs. 4a, 5a, 6c, d)

Total body length approximately 10.87 mm. Head semi-ovoid in lateral view (Fig. 5a), longer than wide, 1.3× (~ 0.51 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not accessible. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible, longer than head, 1.7× (~ 0.86 mm long) (Fig. 5a, white arrow). Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4) and labium (appendages of post-ocular segment 5) not accessible.

Prothorax tube-like, subrectangular in lateral view, longer than wide, 1.8× (~ 1.14 mm long), also longest segment of thorax. Meso- and metathorax subsimilar, wider than long, 1.1× (~ 0.78 mm long) (Fig. 5a). Legs discernible, ~ 1.38 mm long (Fig. 5a).

Abdomen segments 1–8 subsimilar, rectangular in lateral view, longer than wide (between 0.75–0.86 mm long and between 0.51–0.77 mm wide). Abdomen segment 1 widest segment of abdomen. Abdomen segment 9 trapezoidal in lateral view, with convex posterior lateral sides of segment, tergite longer than sternite, 2.4× (tergite ~ 1.38 mm long) (Figs. 5a, 6c). Trunk end partially concealed, with partially visible two postero-ventrally orientated, thin, spine-like processes and lobed structure with hooks (Fig. 6c, d). Body bears setae (between 0.1–0.28 mm long).

Description of specimen 3 in amber piece PED 0925 (Figs. 4a, 5b, c, 6a, b, e, f)

Total body length approximately 9.55 mm. Head (Fig. 6b) semicircular in ventral view, wider than long, 1.3× (~ 0.53 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not discernible, but presumed. Antennae (appendages of post-ocular segment 1) with two elements and a short distal process discernible, longer than head, 1.2× (~ 0.66 mm long). Proximal element longer than distal element, 1.3× (~ 0.34 mm long) (Figs. 5b, c, 6a, b). Intercalary segment (post-ocular segment 2) without externally recognizable structures. Mandibles (paired appendages of post-ocular segment 3) only partially accessible, rectangular in ventral view with serrated gnathal edge, longer than wide, 1.8× (~ 0.31 mm long) (Fig. 6a, b). Maxillae (paired appendages of post-ocular segment 4) with three parts discernible: trapezoidal proximal part, longer than wide, 2.6× (~ 0.27 mm long), distal inner setous part (presumably lacinia and galea), and distal outer part (palp) (~ 0.36 mm long). Maxillary palp with three elements (Fig. 6a, b). Labium (conjoined appendages of post-ocular segment 5) subrectangular in ventral view, wider than long, 1.3× (~ 0.24 mm long), no palps discernible.

Prothorax rectangular in ventral view with convex anterior rim, as wide as long (~ 0.76 mm long). Meso- and metathorax subsimilar, trapezoidal in ventral view. Posterior rim of mesothorax wider than segment is long, 1.5× (~ 0.57 mm long). Posterior rim of metathorax slightly wider than segment is long, 1.1× (~ 0.76 mm long) (Fig. 5b, c). Legs discernible (one leg of metathorax presumably ripped out), with five elements (coxa, trochanter, femur, tibia, and claw), ~ 1.52 mm long (Figs. 5b, c, 6a, b).

Abdomen segments 1–8 subsimilar, rectangular in lateral view. Abdomen segment 1 slightly longer than wide, 1.1× (~ 0.95 mm long). Abdomen segments 2–8 wider than long (between 0.61–0.76 mm long and between 0.72–0.83 mm wide). Abdomen segment 9 elongate, semi-ovoid in ventral view, also longest segment of abdomen, longer than proximally wide, 2.2× (~ 1.27 mm long) (Fig. 6e). Trunk end rectangular in ventral view, wider than long, 4.2× (~ 0.11 mm long) with two postero-ventrally orientated, thin, spine-like processes (~ 0.25 mm long) and two-lobed structure (~ 0.32 mm long) with at least five hooks per lobe (Fig. 6e, f). Body bears setae (between 0.1–0.42 mm long).

Description of specimen 4 in amber piece PED 0925 (Figs. 4a, 7a, b)
Total body length approximately 8.71 mm. Head only partly accessible due to way of inclusion. Appendages of ocular and post-ocular segments not accessible (Fig. 7a).

Pronotum of prothorax semi-ovoid in dorsal view, with anterior rim concave, longer than wide, 1.3× (~ 0.91 mm long). Mesonotum subrectangular in dorsal view, slightly wider than long, 1.1× (~ 0.74 mm long). Metanotum trapezoidal in dorsal view, wider than long, 1.4× (~ 0.54 mm long) (Fig. 7a). One leg discernible, ~ 1.4 mm long (Fig. 7a, white arrow), others not accessible.

Abdomen segments 1–8 subsimilar, rectangular in dorsal view. Abdomen segments 1, 2, and 7 slightly wider than long, 1.2× (between 0.65 and 0.51 mm long). Abdomen segments 3–6 longer than wide (between 0.71–0.8 mm long and between 0.61–0.73 mm wide). Abdomen segment 8 as long as wide (~ 0.57 mm long). Segment 9 triangular in dorsal view, also longest segment of abdomen, longer than proximally wide, 2.7× (~ 1.24 mm long) (Fig. 7b). Trunk end not accessible. Body bears setae (between 0.13–0.45 mm long).

Description of specimen 5 in amber piece PED 0925 (Figs. 4a, 7c, d)
Total body length approximately 9.42 mm. Head pentagonal in dorso-lateral view, longer than wide, 1.3× (~ 0.29 mm long). No stemmata discernible. Labrum (derivative of ocular segment) not accessible. Antennae (appendages of post-ocular segment 1) only partially accessible, only one antenna discernible (Fig. 7c, black arrow), longer than head, 1.3× (~ 0.37 mm long). Mandibles (appendages of post-ocular segment 3), maxillae (appendages of post-ocular segment 4) and labium (appendages of post-ocular segment 5) not accessible (Fig. 7c).

Prothorax trapezoid in dorso-lateral view, longer than posterior rim wide, 1.8× (~ 0.79 mm long), pronotum strongly sclerotized. Mesothorax and metathorax subsimilar, rectangular in dorso-lateral view. Mesothorax slightly wider than long, 1.2× (~ 0.42 mm long). Metathorax as long as wide (~ 0.52 mm long) (Fig. 7c). Legs discernible, ~ 0.62 mm long (Fig. 7c, white arrows).

Abdomen segments 1–8 subsimilar, tube-like, rectangular in dorsal view, longer than wide (between 0.7–0.96 mm long and between 0.48–0.52 mm wide) (Fig. 7c). Segment 9 trapezoidal in dorsal view, also longest segment of abdomen, longer than proximally wide, 2.7× (~ 1.26 mm long). Posterior end of tergite 9 laterally on both sides bearing tufts of hairs (Fig. 7d). Trunk end not accessible. Body bears setae (between 0.18–0.38 mm long).

Discussion

Identity of specimen BUB 4275
The overall morphology of all the here reported specimens is clearly elateriform, immediately identifying these specimens as larval representatives of the group Holometabola. Still, as pointed out, larvae of this general organisation occur in several lineages of Holometabola. We therefore need to use some more details for further identifying them more precisely.

Specimen BUB 4275 is preserved in an unfortunate orientation, prohibiting access to many details. Yet, the overall arrangement of the antennae and mouthparts, although only seen in antero-lateral view, is strongly resembling that in modern larvae of Elaterinae (e.g. Casari and Biffi 2012 fig. 15 p. 69). Despite the limited access to details we therefore see an interpretation of this larva as representatives of Elateridae and also Elaterinae as the most likely one.

As pointed out, the fossil record of Elateridae is relatively rich (Kundrata et al. 2021a). It should therefore not be surprising that there is a fossil record of a possible adult specimen of Elateridae in Myanmar amber (Kundrata et al. 2021a p. 30). The larva can potentially represent an immature of this species, we are therefore refraining from erecting a new species for the larva.

The fact that we cannot further narrow down the interpretation of the larva combined with the fact that modern larvae have a variety of different roles does not allow us to further speculate about the ecological role of the fossil larva.

Identity of the other specimens

The three specimens preserved in PED 0369 do not provide many details. The accessible details, especially of abdomen segment 9, resemble those of the overall better preserved specimens in PED 0925. Very informative details are accessible especially in specimens 2 and 3, mainly of the posterior end. Abdomen segment 9 is elongated, as for example also in many larvae of Elateridae (Hyslop 1917; Costa et al. 2010; Casari and Biffi 2012). Yet, there is a significant difference between the fossils and click beetle larvae: In larvae of Elateridae, the trunk end is positioned far anteriorly on abdomen segment 9; it seems that the trunk end is functionally in contact with abdomen segment 8 and that abdomen segment 9 basically has no real ventral structure. This is different in the fossils; there is clearly a ventral part of abdomen segment 9, reaching to about 50% of the overall length of the dorsal side. Accordingly, the trunk end is positioned further posteriorly.

Also the trunk end in the fossils is very distinct and unlike those of the larvae of Elateridae (cf. Costa et al. 2010, fig. 4.7.12.C, D and Lawrence 2005, fig. 18.9.1.). It basically appears to form two lobes, which are armed with few hooks, giving it almost the appearance of two hands. Such an arrangement of abdomen segment 9 with a two-lobed hooked trunk end is well known in larvae of Ptilodactylidae (LeSage and Harper 1976 fig. 1 p. 234; Stribling 1986 fig. 33 p. 227, figs. 34–39 p. 228), which are also elateriform (Stribling 1986 fig. 33 p. 227). Due to the distinct similarity of this very specific structure, we interpret the new fossils as larvae of Ptilodactylidae, toed-winged beetles.

The fossil specimens in PED 0925 have many details accessible, and therefore a comparison with known extant larval representatives of Ptilodactylidae is possible. The overall appearance of the fossils strongly resembles that of extant representatives of the group *Anchytarsus*. The characters shared by the fossils and extant larvae of *Anchytarus*, but differing in other larvae of Ptilodactylidae, include: a relatively small prognathous head in comparison to the prothorax; moderately long antennae with multiple visible elements; an elongated and rectangular prothorax in lateral view; abdomen segment 9 being the longest one of the abdomen and with dorso-ventrally flattened posterior part; a membranous terminal end with hand-like lobes with hooks; and relatively long setae on all segments. Also, the shape and the position of the antennae (Figs. 4b, 5a, b, 7c) strongly resembles the condition in extant representatives of *Anchytarsus* (Fig. 8a; Lawrence 2005 fig. 18.9.1.C). The mandibles of the fossils appear symmetrical, broad and stout with multiple teeth. The maxillae have distally moderately long palps with multiple elements and setous endites (lacinia and/or galea; Fig. 6b). Therefore, also these mouthparts are similar to extant larvae of *Anchytarsus* (Lawrence 2005 fig. 18.9.2.C). Based on this, we conclude that the specimens within PED 0925 are either larval representatives of *Anchytarsus* or at least closely related representatives within the group of Anchytarsinae. This find would represent the first record of the group Anchytarsinae from the Cretaceous. The larvae in PED 0369 might be conspecific, yet this must remain unclear due to fewer preserved details. Further reaching comparisons on species level are not possible due to inaccessibility of certain details of the terminal ends (Stribling 1986).

Fossil record of Ptilodactylidae

The group Ptilodactylidae was so far represented by very few specimens (Motschulsky 1856; Chatzimanolis et al. 2012; Alekseev and Jäch 2016; Kirejtshuk et al. 2019). The eight specimens reported here therefore expand the fossil record of the group from the perspective of individuals. A taxonomic interpretation of the specimens is much more challenging. As Kundrata et al. (2021b) pointed out, the group Ptilodactylidae seems in urgent need of taxonomic re-working. Also, as in many other beetle groups, it appears that extant larvae are known for relatively few species (see discussion in Haug and Haug 2019). Hence the correspondence of larval morphologies to certain taxonomic groups is not well established (see discussion in Haug and Haug 2019).

There is one formally described species of Ptilodactylidae from Kachin amber, *Aphebodactyla rhetine* (Chatzimanolis et al. 2012) based on an adult male. Although the here reported larvae have strong similarities with modern larvae of the group *Anchytarsus,* it can not be easily excluded that the larvae are those of *Aphebodactyla rhetine.* The new fossils therefore do not necessarily increase the species richness of the fossil record of Ptilodactylidae. Yet, they demonstrate that such beetles are more common than indicated by only adults. Also the presence of a specific adult morphology is not a reliable indicator of a specific larval morphology (Scholtz 2005; Haug et al. 2015). The newly reported larvae resemble a very modern type of larva of Ptilodactylidae. This find demonstrates that this morphology was already present 100 million years ago and indicates a similar ecological role of the larvae.

Possible ecology of larvae of Ptilodactylidae

In extant representatives of Ptilodactylidae, the larvae live close to or in rivers (Alekseev and Jäch 2016 p. 593) and other water bodies (Kundrata et al. 2021b), in moist litter or rotten logs (Chatzimanolis et al. 2012 p. 570), and feed on decaying vegetation or rotting wood (Alekseev and Jäch 2016 p. 593) or possibly on fungi on these substrates (Chatzimanolis et al. 2012 p. 570). We can assume that the fossil larvae had also one of the mentioned life styles. The extant larvae of *Anchytarsus,* which the specimens in PED 0925 strongly resemble, live in an aquatic environment on or within submerged decaying wood, on which they also feed (LeSage and Harper 1976; Lawrence 2005). A xylophagous lifestyle is not restricted to terrestrial environments, but is also quite common among extant aquatic larvae of different insect groups (Cranston and McKie 2006). The fossil record of terrestrial beetle larvae shows that xylophagous lifestyle was already common in the Cretaceous (Haug et al. 2021e; Zippel et al. 2022a, early view), but has so far been relatively rarely reported (Peris and Rust 2020). The modern-appearing morphology of the new fossils of Ptilodactylidae implies that larvae possibly led a similar aquatic xylophagous lifestyle as their extant counterparts. Such a life style is so far quite rare in the fossil record. A fossil larva of Elmidae (like Ptilodactylidae an ingroup of Byrrhoidea) from Eocene Baltic amber that was recently described in Zippel et al. (2022b) also possibly led a xylophagous lifestyle in aquatic environment. It shows that this lifestyle might have been already popular in the past. The new fossils push the time boundary of this type of lifestyle all the way back to Cretaceous.

While both general lifestyles, living in water or inside wood, may appear as not very beneficial for becoming preserved in amber, there are in fact numerous examples for both cases in Myanmar amber. Aquatic organisms include numerous larvae of various lineages of Pterygota (e.g. Sroka et al. 2018; Gustafson et al. 2020; Schädel et al. 2020; Haug et al. 2021g; Zippel et al. 2022b), but also many others (Xing et al. 2018; Salamon et al. 2019; Schädel et al. 2019, 2021a, b; Yu et al. 2019; 2021; Wang et al. 2020; Bolotov et al. 2021). Larvae known to feed on or live inside wood are also well known as amber inclusions (Baranov et al. 2020), especially various types of beetle larvae (Haug & Haug 2019; Peris and Rust 2020; Haug et al. 2021e; Zippel et al. 2022a, early view).

Source of variation among larvae within one amber piece

Two amber pieces that contain multiple specimens of Ptilodactylidae (PED 0369 and PED 0925) contain in total eight larvae of relatively similar sizes (total body length between 8.7–10.9 mm). It is possible that the larvae within one amber piece hatched from the same clutch of eggs, therefore might be conspecific. They do show variation in habitus, but that might be due to different views in which they are accessible.

An additional source of differences might be ontogeny. LeSage and Harper (1976) noted that the species *Anchytarsus bicolor* develops through ten instars. Larval instars were differentiated based on the size of the pronotum. Indeed there is a small variation in size of the whole prothorax among newly described specimens, but the size of the pronotum as a criteria for differentiating the instars cannot be considered here as the new larvae are accessible in different views or are partially hidden by inclusions; therefore, measuring of the same two points on the pronotum was not possible. In addition to size, other characteristics, such as number of setae or hooks on the trunk end, were also changing during the development of the larvae described by LeSage and Harper (1976). Once again, this is not a clear factor we can rely on, since there is a possibility that specimens got damaged during the process of inclusion within the resin. Nevertheless, we presume that the specimens are not first instars, but later ones. Out of these reasons, we cannot clearly say where the variation of the specimens comes from, even within one amber piece.

Fossil record of larvae of Elateroidea

The seeming rareness of larvae of Elateridae in the fossil record is worth some further discussion. Within the larger group Elateroidea, Elateridae is very species-rich and has a quite good overall fossil record (Kundrata et al. 2021a). Still, there is so far only the single larva reported here. Other ingroups of Elateroidea, which are much less species-rich and with a less good fossil record, have a record of at least some fossil larvae, including possible Lycidae and Lampyridae (Haug et al. in review), Cantharidae (Fowler 2019), or Eucnemidae (Chang et al. 2016; Zippel et al. early view). Especially remarkable is the fossil record of larvae of the group Brachypsectridae, which is quite species-poor in the modern fauna, but is known from larvae in amber from the Cretaceous (Zhao et al. 2020; Haug et al. 2021f), Eocene (Scheven 2004; Klausnitzer 2009; Haug et al. 2021f), and Miocene (Wu 1996; Woodruff 2002; Klausnitzer 2009; Poinar 2010; all records recently reviewed in Haug et al. 2021f). The larvae of Brachypsectridae are very prominent and rather easy to identify as such, possibly explaining why these larvae have a (seemingly) better record. We still expect that more fossil larvae of Elateridae should be present in ambers, but simply have not been reported.

Fossil record of larvae of Byrrhoidea and Elateriformia

Although Ptilodactylidae is sometimes still recognised as an ingroup of Dryopoidea (e.g. Kundrata et al. 2021b) most authors seem to consider them an ingroup of Byrrhoidea (e.g. McKenna et al. 2019). Byrrhoidea, like Elateroidea, is a large ingroup of Elateriformia that may even be more species-rich than often anticipated, especially if one recent phylogenetic analysis is considered in which Buprestidae was resolved as an ingroup of Byrrhoidea (McKenna et al. 2019 figs. 1, 2). Even if the position of Buprestidae within Byrrhoidea will not be further supported in future work, the group of Buprestidae stays widely recognised as an ingroup of Elateriformia (e.g. Zhang et al. 2018 fig. 2 p. 3). Larvae of Buprestidae, metallic wood-boring beetles, are known from Cretaceous and Eocene ambers (Haug et al. 2021e and references therein; Haug et al. in press).

Different larvae of Byrrhoidea have also been reported in the fossil record, including: Elmidae (riffle beetles; Eocene amber, Zippel et al. 2022b), Heteroceridae (variegated mud-loving beetles; Miocene amber, Zippel et al. 2022c), Psephenidae (water penny beetles; Cretaceous amber, Bao et al. 2018; Eocene, Wedmann et al. 2011; Miocene, Hayashi and Kawakami 2009; Pleistocene, Hayashi et al. 2020). The findings reported here further expand this record.

Overall it appears that many specialised larval forms are present from early on, in many cases already in the Cretaceous (see also Muona et al. 2020). Yet, many of these early larvae show at least some differences to their modern counterparts (e.g. Haug et al. 2021e, in press; Zippel et al. 2022b, early view). This phenomenon has been not only recognised in beetles, but also in other lineages of Holometabola. In lacewings, for example, there are also very modern-appearing larvae known from the Cretaceous (e.g. Wang et al. 2016; Badano et al. 2018; Haug et al. 2018, 2021d; Haug and Haug 2022), but also more larvae with more plesiomorphic (≈ancestral) characters, and also highly specialised larvae not known before or afterwards (e.g. Badano et al. 2018, 2021; Haug et al. 2019a, b, 2020b). This observation emphasises that it is important to report and describe fossil larvae and not assume the presence of a certain larval morphology based on the presence of a certain adult morphology (Haug et al. 2015; Baranov et al. 2019).

The observable details in the larvae of Ptilodactylidae here appear very similar to those of their modern counterparts. At most, the antennae appear slightly longer in fossil larvae in comparison to those of the modern counterparts. Similar, or even more expressed, cases of this phenomenon are already known from other larvae preserved in Cretaceous amber (Haug et al. 2020e, 2021c). Hence, the new larvae seem to be a case of a very modern-appearing type of morphology back in the Cretaceous.

Acknowledgements

Gideon T. Haug, Neuried, is thanked for his time and efforts invested into the image processing and drawings for this publication. M. Jäch, Vienna, is thanked for his expert advice regarding the manuscript. J. Matthias Starck, LMU Munich, is thanked for long-time support. We thank all people providing low-cost, open-access or open-source software. This is LEON publication #48.

References

Alekseev, V.I., and M. A. Jäch. 2016. *Electrolichas circumbalticus* gen. et sp. nov. (Coleoptera: Byrrhoidea: Ptilodactylidae) from Baltic amber, the first anchytarsine toed-winged beetle described from Europe. *Zootaxa* 4136(3): 593–599. https://doi.org/10.11646/zootaxa.4136.3.10

Badano, D., M. S. Engel, A. Basso, B. Wang, and P. Cerretti. 2018. Diverse Cretaceous larvae reveal the evolutionary and behavioural history of antlions and lacewings. *Nature Communications* 9: 3257. https://doi.org/10.1038/s41467-018-05484-y

Badano, D., M. Fratini, L. Maugeri, F. Palermo, N. Pieroni, A. Cedola, J. T. Haug, T. Weiterschan, J. Velten, M. Mei, A. Di Giulio, and P. Cerretti. 2021. X-ray microtomography and phylogenomics provide insights into the morphology and evolution of an enigmatic Mesozoic insect larva. *Systematic Entomology* 46: 672–684. https://doi.org/10.1111/syen.12482

Bao, T., J. Rust, and B. Wang. 2018. Systematics, phylogeny and taphonomy of Cretaceous Psephenidae (Insecta: Coleoptera) from Burmese amber. *Palaeontographica Abteilung A* 310: 131–159. https://doi.org/10.1127/0375-0442/2018/0086

Baranov, V., C. Hoffeins, H.-W. Hoffeins, and J. T. Haug. 2019. More than dead males: reconstructing the ontogenetic series of terrestrial non-biting midges from the Eocene amber forest. *Bulletin of Geosciences* 94: 187–199.

Baranov, V. A., Y. Wang, R. Gašparič, S. Wedmann, and J. T. Haug. 2020. Eco-morphological diversity of larvae of soldier flies and their closest relatives in deep time. *PeerJ* 8: e10356. https://doi.org/10.7717/peerj.10356

Baranov, V., C. Haug, M. Fowler, U. Kaulfuss, P. Müller, and J. T. Haug. 2022. Summary of the fossil record of megalopteran and megalopteran-like larvae, with a report of new specimens. *Bulletin of Geosciences* 97: 89–108. https://doi.org/10.3140/bull.geosci.1840

Barr, C. B., J. R. Gibson, and P. H. Diaz. 2015. *Typhloelmis* Barr (Coleoptera: Elmidae: Elminae), a new stygobiontic riffle beetle genus with three new species from Texas, USA. *The Coleopterists Bulletin* 69: 531–558.

Batelka, J., J. Prokop, H. Pohl, M. Bai, W. Zhang, and R. G. Beutel. 2019. Highly specialized Cretaceous beetle parasitoids (Ripiphoridae) identified with optimized visualization of microstructures. *Systematic Entomology* 44: 396–407. https://doi.org/10.1111/syen.12331

Becker, E. C. 1963. Three new fossil elaterids from the amber of Chiapas, Mexico, including a new genus (Coleoptera). *Journal of Paleontology* 37: 125–128.

Beutel, R. G., and J. F. Lawrence. 2016. 4. Coleoptera, morphology. In *Coleoptera, Beetles: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)* (Vol. 1), volume eds. R. G. Beutel, and R. A. B. Leschen, 35–40. In *Handbook of Zoology: Arthropoda: Insecta (2nd edition),* eds. R. G. Beutel, and N. P. Kristensen. Berlin, Boston: Walter de Gruyter. https://doi.org/10.1515/9783110373929-007

Beutel, R. G., W. W. Zhang, H. Pohl, T. Wappler, and M. Bai. 2016. A miniaturized beetle larva in Cretaceous Burmese amber: reinterpretation of a fossil “strepsipteran triungulin”. *Insect Systematics & Evolution* 47: 83–91. https://doi.org/10.1163/1876312X-46052134

Bolotov, I. N., O. V. Aksenova, I. V. Vikhrev, E. S. Konopleva, Y. E. Chapurina, and A. V. Kondakov. 2021. A new fossil piddock (Bivalvia: Pholadidae) may indicate estuarine to freshwater environments near Cretaceous amber-producing forests in Myanmar. *Scientific Reports* 11: 6646. https://doi.org/10.1038/s41598-021-86241-y

Casari, S. A., and G. Biffi. 2012. Immatures of *Dicrepidius* Eschscholtz, 1829 and *Dipropus* Germar, 1839 (Elateridae, Elaterinae, Ampedini: Dicrepidiina). *Zootaxa* 3587(1): 65–77.

Chang, H., J. Muona, H. Pu, L. Xu, C. Wang, M. Teräväinen, D. Ren, Q. Yang, X. Zhang, and S. Jia. 2016. Chinese Cretaceous larva exposes a southern Californian living fossil (Insecta, Coleoptera, Eucnemidae). *Cladistics* 32: 211–214. https://doi.org/10.1111/cla.12124

Chatzimanolis, S., M. E. Cashion, M. S. Engel, and Z. H. Falin. 2012. A new genus of Ptilodactylidae (Coleoptera: Byrrhoidea) in mid- Cretaceous amber from Myanmar (Burma). *Geodiversitas* 34: 569–574. https://doi.org/10.5252/g2012n3a6

Cockerell, T. D. A. 1917. Insects in Burmese amber. *Annals of the Entomological Society of America* 10(4): 323–329. https://doi.org/10.1093/aesa/10.4.323

Costa, C., and S. A. Vanin. 2010. Coleoptera larval fauna associated with termite nests (Isoptera) with emphasis on the “bioluminescent termite nests” from Central Brazil. *Psyche* 2010: 723947. https://doi.org/10.1155/2010/723947

Costa, C., J. F. Lawrence, and S. P. Rosa. 2010. 4.7. Elateridae Leach, 1815. In *Coleoptera, Beetles: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (Vol. 2), volume eds. R. A. B. Leschen, R. G. Beutel, and J. F. Lawrence, 75–103. In *Handbook of Zoology, Arthropoda: Insecta, Teilband 39,* eds. N. P. Kristensen, and R.G. Beutel. Berlin: Walter de Gruyter. https://doi.org/10.1515/9783110911213.75

Cranston, P. S., and B. McKie. 2006. Aquatic wood – an insect perspective. In *Insect Biodiversity and Dread Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology,* eds. S. J. Grove, and J. L. Hanula, 9–14. Asheville: United States Department of Agriculture, The

Forest Service.

Cruickshank, R. D., and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* 21(5): 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

Devetak, D., and A. E. Arnett. 2010. A click beetle larva (Coleoptera: Elateridae) preying upon an antlion larva (Neuroptera: Myrmeleontidae). *Entomological News* 121: 514–516. https://doi.org/10.3157/021.121.0515

Engel, M. S. 2002. The smallest snakefly (Raphidioptera: Mesoraphidiidae): a new species in Cretaceous amber from Myanmar, with a catalog of fossil snakeflies. *American Museum Novitates* 2002(3363): 1–22. https://doi.org/10.1206/0003-0082(2002)363<0001:TSSRMA>2.0.CO;2

Fowler, M. J. F. 2019. Eocene world: Imaging fossil insects in Baltic amber. *Bulletin of the Amateur Entomologists' Society* 78: 139–146.

Gauweiler, J., C. Haug, P. Müller, and J. T. Haug. 2022. Lepidopteran caterpillars in the Cretaceous: were they a good food source for early birds? *Palaeodiversity* 15: 45–59. https://doi.org/10.18476/pale.v15.a3

González-Córdoba, M., M. D. C. Zúñiga, and V. Manzo. 2020. La familia Elmidae (Insecta: Coleoptera: Byrrhoidea) en Colombia: riqueza taxonómica y distribución. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 44: 522–553. https://doi.org/10.18257/raccefyn.1062

Grimaldi, D. A., and M. S. Engel. 2005. *Evolution of the Insects.* Cambridge: Cambridge University Press.

Grimaldi, D. A., and P. C. Nascimbene. 2010. Raritan (New Jersey) amber. In *Biodiversity of fossils in amber from the major world deposits*, eds. D. Penney, D. Green, and C. Mellish, 167–191. Siri Scientific Press, Manchester, UK

Gustafson, G. T., M. C. Michat, and M. Balke. 2020. Burmese amber reveals a new stem lineage of whirligig beetle (Coleoptera: Gyrinidae) based on the larval stage. *Zoological Journal of the Linnean Society* 189: 1232–1248. https//doi.org/10.1093/zoolinnean/zlz161

Haug, C., K. R. Shannon, T. Nyborg, and F. J. Vega. 2013b. Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. *Bolétin de la Sociedad Geológica Mexicana* 65: 273–284.

Haug, C., A. F. Herrera-Flórez, P. Müller, and J. T. Haug. 2019a. Cretaceous chimera–an unusual 100-million-year old neuropteran larva from the “experimental phase” of insect evolution. *Palaeodiversity* 12: 1–11. https://doi.org/10.18476/pale.v12.a1

Haug, C., G. T. Haug, A. Zippel, S. van der Wal, and J. T. Haug. 2021e. The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. *Palaeoentomology* 4: 390–404. https://doi.org/10.11646/palaeoentomology.4.4.14

Haug, C., V. A. Baranov, M. K. Hörnig, J. Gauweiler, J. U. Hammel, E. E. Perkovsky, and J. T.

Haug. early view. 35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests. *Palaeobiodiversity and Palaeoenvironments*. https://doi.org/10.1007/s12549-022-00552-0

Haug, C., A. Zippel, P. Müller, and J. T. Haug. in review. Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. *PalZ*.

Haug, G. T., C. Haug, P. G. Pazinato, F. Braig, V. Perrichot, C. Gröhn, P. Müller, and J. T. Haug. 2020a. The decline of silky lacewings and morphological diversity of long-nosed antlion larvae through time. *Palaeontologia Electronica* 23: a39. https://doi.org/10.26879/1029

Haug, G. T., V. Baranov, G. Wizen, P. G. Pazinato, P. Müller, C. Haug, and J. T. Haug. 2021a. The morphological diversity of long-necked lacewing larvae (Neuroptera: Myrmeleontiformia). *Bulletin of Geosciences* 96: 431–457. https://doi.org/10.3140/bull.geosci.1807

Haug, G. T., C. Haug, and J. T. Haug. 2021b. The morphological diversity of spoon-winged lacewing larvae and the first possible fossils from 99 million-year-old Kachin amber, Myanmar. *Palaeodiversity* 14: 133–152. https://doi.org/10.18476/pale.v14.a6

Haug, G. T., C. Haug, S. van der Wal, P. Müller, and J. T. Haug. 2022a. Split-footed lacewings declined over time: indications from the morphological diversity of their antlion-like larvae. *PalZ* 96: 29–50. https://doi.org/10.1007/s12542-021-00550-1

Haug, J. T., and C. Haug. 2019. Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). *PeerJ* 7: e7871. https://doi.org/10.7717/peerj.7871

Haug, J. T., and C. Haug. 2021. A 100-million-year-old armoured caterpillar supports the early diversification of moths and butterflies. *Gondwana Research* 93: 101–105. https://doi.org/10.1016/j.gr.2021.01.009

Haug, J. T., and Haug, C. 2022. 100 million-year-old straight-jawed lacewing larvae with enormously inflated trunks represent the oldest cases of extreme physogastry in insects. *Scientific Reports* 12: 12760. https://doi.org/10.1038/s41598-022-16698-y

Haug, J. T., C. Haug, and M. Ehrlich. 2008. First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). *Palaeodiversity* 1: 103–109.

Haug, J. T., C. Haug, V. Kutschera, G. Mayer, A. Maas, S. Liebau, C. Castellani, U. Wolfram, E. N. K. Clarkson, and D. Waloszek. 2011. Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244: 259–272. https://doi.org/10.1111/j.1365-2818.2011.03534.x

Haug, J. T., C. H. G. Müller, and A. Sombke. 2013a. A centipede nymph in Baltic amber and a new approach to document amber fossils. *Organisms Diversity & Evolution* 13: 425–432. https://doi.org/10.1007/s13127-013-0129-3

Haug, J. T., J. W. Martin, and C. Haug. 2015. A 150-million-year-old crab larva and its implications for the early rise of brachyuran crabs. *Nature Communications* 6: 6417. https://doi.org/10.1038/ncomms7417

Haug, J. T., C. Haug, and R. J. Garwood. 2016. Evolution of insect wings and development – new details from Palaeozoic nymphs. *Biological Reviews* 91: 53–69. https://doi.org/10.1111/brv.12159

Haug, J. T., P. Müller, and C. Haug. 2018. The ride of the parasite: a 100-million-year old mantis lacewing larva captured while mounting its spider host. *Zoological Letters* 4: 31. https://doi.org/10.1186/s40851-018-0116-9

Haug, J. T., P. Müller, and C. Haug. 2019b. A 100-million-year old predator: a fossil neuropteran larva with unusually elongated mouthparts. *Zoological Letters* 5: 29. https://doi.org/10.1186/s40851-019-0144-0

Haug, J. T., P. Müller, and C. Haug. 2019c. A 100-million-year old slim insectan predator with massive venom-injecting stylets – a new type of neuropteran larva from Burmese amber. *Bulletin of Geosciences* 94: 431–440. https://doi.org/10.3140/bull.geosci.1753

Haug, J. T., V. Baranov, M. Schädel, P. Müller, P. Gröhn, and C. Haug. 2020b. Challenges for understanding lacewings: how to deal with the incomplete data from extant and fossil larvae of Nevrorthidae? (Neuroptera). *Fragmenta entomologica* 52: 137–167. https://doi.org/10.13133/2284-4880/472

Haug, J. T., P. G. Pazinato, G. T. Haug, and C. Haug. 2020c. Yet another unusual new type of lacewing larva preserved in 100-million-year old amber from Myanmar. *Rivista Italiana di Paleontologia e Stratigrafia* 126: 821–832. https://doi.org/10.13130/2039-4942/14439

Haug, J. T., M. Schädel, V. A. Baranov, and C. Haug. 2020d. An unusual 100-million-year old holometabolan larva with a piercing mouth cone. *PeerJ* 8: e8661. https://doi.org/10.7717/peerj.8661

Haug, J. T., P. Müller, and C. Haug. 2020e. A 100 million-year-old snake-fly larva with an unusually large antenna. *Bulletin of Geosciences* 95: 167–177. https://doi.org/10.3140/bull.geosci.1757

Haug, J. T., V. Baranov, P. Müller, and C. Haug. 2021c. New extreme morphologies as exemplified by 100 million-year-old lacewing larvae. *Scientific Reports* 11: 20432. https://doi.org/10.1038/s41598-021-99480-w

Haug, J. T., G. T. Haug, A. Zippel, S. van der Wal, P. Müller, C. Gröhn, J. Wunderlich, C. Hoffeins, H.-W. Hoffeins, and C. Haug. 2021d. Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings and their closer relatives over 100 million years. *Insects* 12: art. 860. https://doi.org/10.3390/insects12100860

Haug, J. T., A. Zippel, G. T. Haug, C. Hoffeins, H.-W. Hoffeins, J. U. Hammel, V. Baranov, and C. Haug. 2021f. Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. *Palaeodiversity* 14: 161–183. https://doi.org/10.18476/pale.v14.a8

Haug, J. T., P. Müller, and C. Haug. 2021g. Fossil dragonfly-type larva with lateral abdominal protrusions and implications on the early evolution of Pterygota. *iScience* 24: 103162. https://doi.org/10.1016/j.isci.2021.103162

Haug, J. T., M. S. Engel, P. Mendes dos Santos, G. T. Haug, P. Müller, and C. Haug. early view. Declining morphological diversity in snakefly larvae during last 100 million years. *PalZ*.

https://doi.org/10.1007/s12542-022-00609-7

Hayashi, M., and Y. Kawakami. 2009. Fossil of the genus *Eubrianax* (Coleoptera, Psephenidae) from the Upper Miocene Ningyôtôge formation in Tottori Prefecture, Japan. *Elytra* 37: 99–103.

Hayashi, M., H. Aiba, E. Nakano, Y. Takahashi, and T. Sato. 2020. Fossilized water pennies (Coleoptera: Psephenidae) in the Middle Pleistocene lake deposits in Shiobara site, Tochigi Prefecture, Japan. *Japanese Journal of Systematic Entomology* 26: 84–86.

Herrera-Flórez, A. F., F. Braig, C. Haug, C. Neumann, J. Wunderlich, M. K. Hörnig, and J. T. Haug. 2020. Identifying the oldest larva of a myrmeleontiformian lacewing – a morphometric approach. *Acta Palaeontologica Polonica* 65: 235–250. https://doi.org/10.4202/app.00662.2019

Hoare, R., J. Dugdale, and C. Watts. 2006. The world's thinnest caterpillar? A new genus and species of Batrachedridae (Lepidoptera) from *Sporadanthus ferrugineus* (Restionaceae), a threatened New Zealand plant. *Invertebrate Systematics* 20: 571–583. https://doi.org/10.1071/IS06009

Hörnig, M. K., C. Kiesmüller, P. Müller, C. Haug, and J. T. Haug. 2020. A new glimpse on trophic interactions of 100-million-year old lacewing larvae. *Acta Palaeontologica Polonica* 65: 777–786. https://doi.org/10.4202/app.00677.2019

Hörnig, M. K., C. Haug, P. Müller, and J.T. Haug. 2022. Not quite social – possible cases of gregarious behaviour of immatures of various lineages of Insecta preserved in 100-million-year-old amber. *Bulletin of Geosciences* 97: 69–87. https://doi.org/10.3140/bull.geosci.1818

Hyslop, J. A. 1917. The phylogeny of the Elateridae based on larval characters. *Annals Entomological Society of America* 10: 241–263.

Iablokoff-Khnzorian, S. M. 1961. Novye zhestkokrylye semeystva Elateridae iz baltiyskogo yantayra. *Paleontologicheskii Zhurnal* 1961: 84–97.

Jałoszyński, P. 2018. Morphological Diversity of Immature Scydmaeninae. In *Biology of Rove Beetles (Staphylinidae),* eds. O. Betz, U. Irmler, and J. Klimaszewski, 321–333. Cham: Springer. https://doi.org/10.1007/978-3-319-70257-5_14

Jałoszyński, P., and R. G. Beutel. 2012. Functional morphology and evolution of specialized mouthparts of Cephenniini (Insecta, Coleoptera, Staphylinidae, Scydmaeninae). *Arthropod Structure & Development* 41: 593–607. https://doi.org/10.1016/j.asd.2012.07.002

Jałoszyński, P., and A. Kilian. 2016. Description of the second-and third-instar larva of South African S*tenomastigus longicornis* (Boheman) (Coleoptera: Staphylinidae, Scydmaeninae). *Zootaxa* 4158(2): 151–182. https://doi.org/10.11646/zootaxa.4158.2

Kerp, H., and B. Bomfleur. 2011 Photography of plant fossils—new techniques, old tricks. *Review of Palaeobotany and Palynology* 166: 117–151. https://doi.org/10.1016/j.revpalbo.2011.05.001

Kirejtshuk, A. G., and D. Azar. 2008. New taxa of beetles (Insecta, Coleoptera) from Lebanese amber with evolutionary and systematic comments. *Alavesia* 2(15): e46.

Kirejtshuk, A. G., and A. V. Kovalev. 2015. First fossil representative of the family Omalisidae (Coleoptera, Elateroidea sensu lato) from the Baltic amber. *Paleontological Journal* 49: 1413–1416. https://doi.org/10.1134/S0031030115130031

Kirejtshuk, A. G., A. G. Ponomarenko, A. S. Kurochkin, A. V. Alekseev, V. G. Gratshev, A. V. Solodovnikov, F.-T. Krell, and C. Soriano. 2019. The beetle (Coleoptera) fauna of the Insect Limestone (late Eocene), Isle of Wight, southern England. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 110: 405–492. https://doi.org/10.1017/S1755691018000865

Klausnitzer, B. 2009. Bemerkungen zu rezenten und fossilen Larven (Bernstein) der Gattung *Brachypsectra* LeConte (Coleoptera, Brachypsectridae). *Contributions to Natural History* 12: 721–742.

Kundrata, R., A. Bukejs, A. S. Prosvirov, and J. Hoffmannova. 2020. X-ray micro-computed tomography reveals a unique morphology in a new click-beetle (Coleoptera, Elateridae) from the Eocene Baltic amber. *Scientific Reports* 10: 20158. https://doi.org/10.1038/s41598-020-76908-3

Kundrata, R., G. Packova, A. S. Prosvirov, and J. Hoffmannova. 2021a. The fossil record of Elateridae (Coleoptera: Elateroidea): described species, current problems and future prospects. *Insects* 12: 286. https://doi.org/10.3390/insects12040286

Kundrata, R., G. Packova, K. Kairišs, A. Bukejs, J. Hoffmannova, and S. M. Blank. 2021b. The first *Ptilodactyla* Illiger, 1807 (Coleoptera: Dryopoidea: Ptilodactylidae) described from Eocene Baltic amber. *Biology* 10: 877. https://doi.org/10.3390/biology10090877

Lawrence, J. F. 2005. Ptylodactylidae Laporte, 1836. In *Coleoptera, Beetles: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), Vol. 1*, volume eds. R. A. B. Leschen and R. G. Beutel, 536–542. In *Handbook of Zoology, Arthropoda: Insecta, Teilband 38,* eds. N. P. Kristensen, and R. G. Beutel. Berlin, New York: Walter de Gruyter.

Lawrence, J. F., and J. B. Stribling. 1992. A new genus of Ptilodactylidae (Coleoptera: Elateriformian) from North Queensland, with description of the presumed larva. *Australian Journal of Entomology* 31: 19–27. https://doi.org/10.1111/j.1440-6055.1992.tb00454.x

LeSage, L., and P. P. Harper. 1976. Notes on the life history of the toed-winged beetle *Anchytarsus bicolor* (Melsheimer) (Coleoptera: Ptilodactylidae). *The Coleopterists Bulletin* 30: 233–238.

Liu, H., C. Luo, E. A. Jarzembowski, and C. Xiao. 2022. *Acanthochrysa langae* gen. et sp. nov., a new lacewing larva (Neuroptera: Chrysopoidea) from mid-Cretaceous Kachin amber. *Cretaceous Research* 133: 105146. https://doi.org/10.1016/j.cretres.2022.105146

Liu, X., W. Zhang, S. L. Winterton, L. C. Breitkreuz, and M. S. Engel. 2016. Early morphological specialization for insect-spider associations in Mesozoic lacewings. *Current Biology* 26: 1590–1594. https://doi.org/10.1016/j.cub.2016.04.039

Liu, X., G. Shi, F. Xia, X. Lu, B. Wang, and M. S. Engel. 2018. Liverwort mimesis in a Cretaceous lacewing larva. *Current Biology* 28: 1475–1481. https://doi.org/10.1016/j.cub.2018.03.060

Liu, Y., M. Hakim, and D. Huang. 2020. First stratiomyomorphan larvae in the mid-Cretaceous amber from Myanmar (Diptera: Brachycera). *Cretaceous Research* 106: 104265. https://doi.org/10.1016/j.cretres.2019.104265.

Lohrmann, V., and M. S. Engel. 2017. The wasp larva's last supper: 100 million years of evolutionary stasis in the larval development of rhopalosomatid wasps (Hymenoptera: Rhopalosomatidae). *Fossil Record* 20: 239–244. https://doi.org/10.5194/fr-20-239-2017

Luo, C., H. Liu, and E. A. Jarzembowski. 2022. High morphological disparity of neuropteran larvae during the Cretaceous revealed by a new large species. *Geological Magazine* 159: 954–962. https://doi.org/10.1017/S0016756822000176

MacKay, M. R. 1970. Lepidoptera in Cretaceous amber. *Science* 167: 379–380. https://doi.org/10.1126/science.167.3917.379

McKenna, D. D., S. Shin, D. Ahrens, M. Balke, C. Beza-Beza, D. J. Clarke, A. Donath, H. E. Escalona, F. Friedrich, H. Letsch, S. Liu, D. Maddison, C. Mayer, B. Misof, P. J. Murin, O. Miehuis, R. S. Peters, L. Podsiadlowski, H. Pohl, E. D. Scully, E.V. Yan, X. Zhou, A. Ślipiński, and R. G. Beutel. 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences* 116: 24729–24737. https://doi.org/10.1073/pnas.1909655116

Motschulsky, M. 1856. Voyages: Lettres de M. de Motschulsky à M. Ménétriés. No. 4. *Etudes Entomologiques* 5: 21–38.

Muona, J., H. Chang, and D. Ren. 2020. The clicking Elateroidea from Chinese Mesozoic deposits (Insecta, Coleoptera, Elateroidea). *Insects* 11: 875. https://doi.org/10.3390/insects11120875

Otto, R. L. 2017. Eucnemid larvae of the Nearctic Region. Part VII: Description of the larvae of *Nematodes penetrans* (LeConte, 1852) (Coleoptera: Eucnemidae: Macraulacinae: Nematodini), with notes on its hypermetamorphic life cycle. *Insecta Mundi* 0545: 1–9.

Otto, R. L. 2019. Descriptions of two new elateroid beetles (Coleoptera: Eucnemidae, Elateridae) from Burmese amber. *Insecta Mundi* 702: 1–6.

Pérez-de la Fuente, R., X. Delclòs, E. Peñalver, M. Speranza, J. Wierzchos, C. Ascaso, and M. S. Engel. 2012. Early evolution and ecology of camouflage in insects. *Proceedings of the National Academy of Sciences* 109: 21414–21419. https://doi.org/10.1073/pnas.1213775110

Pérez-de la Fuente, R., X. Delclos, E. Penalver, and M. S. Engel. 2016. A defensive behavior and plant-insect interaction in Early Cretaceous amber–the case of the immature lacewing *Hallucinochrysa diogenesi*. *Arthropod Structure & Development* 45: 133–139. https://doi.org/10.1016/j.asd.2015.08.002

Pérez-de la Fuente, R., E. Peñalver, D. Azar, and M. S. Engel. 2018. A soil-carrying lacewing larva in Early Cretaceous Lebanese amber. *Scientific Reports* 8: 16663. https://doi.org/10.1038/s41598-018-34870-1

Pérez-de la Fuente, R., M. S. Engel, D. Azar, and E. Peñalver. 2019. The hatching mechanism of 130-million-year-old insects: An association of neonates, egg shells and egg bursters in Lebanese amber. *Palaeontology* 62: 547–559. https://doi.org/10.1111/pala.12414

Pérez-de la Fuente, R., M. S. Engel, X. Delclòs, and E. Peñalver. 2020. Straight-jawed lacewing larvae (Neuroptera) from Lower Cretaceous Spanish amber, with an account on the known amber diversity of neuropterid immatures. *Cretaceous Research* 106: 104200. https://doi.org/10.1016/j.cretres.2019.104200

Peris, D., and J. Rust. 2020. Cretaceous beetles (Insecta: Coleoptera) in amber: the palaeoecology of this most diverse group of insects. *Zoological Journal of the Linnean Society* 189: 1085–1104. https://doi.org/10.1093/zoolinnean/zlz118

Perrichot, V., and M. S. Engel. 2007. Early Cretaceous snakefly larvae in amber from Lebanon, Myanmar, and France (Raphidioptera). *American Museum Novitates* 2007(3598): 1–11. https://doi.org/10.1206/0003-0082(2007)3598[1:ECSLIA]2.0.CO;2

Pilgrim, R. L. C. 1972. Aquatic larva and the pupa of *Choristella philpotti* Tillyard, 1917 (Mecoptera: Nannochoristidae). *Pacific Insects* 14(1): 151–168.

Poinar, G. Jr. 2010. Palaeoecological perspectives in Dominican amber. *Annales de la Société entomologique de France (N.S.)* 46(1–2): 23–52. https://doi.org/10.1080/00379271.2010.10697637

Salamon, M. A., J. P. Lin, P. Duda, P. Gorzelak, W. I. Ausich, and T. Oji. 2019. Paleoenvironmental and biostratigraphic implications of echinoderm ossicles trapped within Burmese amber. *Palaios* 34: 652–656. https://doi.org/10.2110/palo.2019.084

Schädel, M., V. Perrichot, and J. T. Haug. 2019. Exceptionally preserved cryptoniscium larvae - morphological details of rare isopod crustaceans from French Cretaceous Vendean amber. *Palaeontologia Electronica* 22: 71. https://doi.org/10.26879/977

Schädel, M., P. Müller, and J. T. Haug. 2020. Two remarkable fossil insect larvae from Burmese amber suggest the presence of a terminal filum in the direct stem lineage of dragonflies and damselflies (Odonata). *Rivista Italiana di Paleontologia e Stratigrafia* 126: 13–35. https://doi.org/10.13130/2039-4942/12720

Schädel, M., M. K. Hörnig, M. Hyžný, and J. T. Haug. 2021a. Mass occurrence of small isopodan crustaceans in 100-million-year-old amber: an extraordinary view on behaviour of extinct organisms. *PalZ* 95: 429–445. https://doi.org/10.1007/s12542-021-00564-9

Schädel, M., M. Hyžný, and J. T. Haug. 2021b. Ontogenetic development captured in amber – the first record of aquatic representatives of Isopoda in Cretaceous amber from Myanmar. *Nauplius* 29: e2021003. https://doi.org/10.1590/2358-2936e2021003

Scheven, J. 2004. *Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut.* Hofheim a. T.: Kuratorium Lebendige Vorwelt.

Schimmel, R. 2005. Die Megapenthini-Arten Süd- und Südostasiens. Vierter Teil: Phylogenese, Zoogeographie und Katalog (Coleoptera: Elateridae). *Pollichia-Buch* 48: 1–411.

Schimmel, R., and D. Tarnawski. 2010. Monograph of the subtribe Elaterina (Insecta: Coleoptera: Elateridae: Elaterinae). *Genus* 21(3): 325–487.

Scholtz, G. 2005. Homology and ontogeny: pattern and process in comparative developmental biology. *Theory in Biosciences* 124: 121–143. https://doi.org/10.1007/BF02814480

Shepard, W. D., S. Clavier, and A. Cerdan. 2020. A generic key to the known larval Elmidae (Insecta: Coleoptera) of French Guiana. *Papéis Avulsos de Zoologia* 60: 1–9. https://doi.org/10.11606/1807-0205/2020.60.special-issue.15

Shi, G, D. A. Grimaldi, G. E. Harlow, J. Wang, J. Wang, M. Yang, W. Lei, Q. Li, and X. Li 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163. https://doi. org/10.1016/j.cretres.2012.03.014

Sroka, P., A. H. Staniczek, and B. C. Kondratieff. 2018. 'Rolling' stoneflies (Insecta: Plecoptera) from mid-Cretaceous Burmese amber. *PeerJ* 6: e5354. https://doi.org/10.7717/peerj.5354

Stribling, J. B. 1986. Revision of *Anchytarsus* (Coleoptera: Dryopoidea) and a key to the New World genera of Ptilodactylidae. *Annals of the Entomological Society of America* 79: 219–234.

Wang, B., F. Xia, M. S. Engel, V. Perrichot, G. Shi, H. Zhang, J. Chen, E. A. Jarzembowski, T. Wappler, and J. Rust. 2016. Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Science Advances* 2: e1501918. https://doi.org/10.1126/sciadv.1501918

Wang, H., M. Schädel, B. Sames, and D. J. Horne. 2020. New record of podocopid ostracods from Cretaceous amber. *PeerJ* 8: e10134. https://doi.org/10.7717/peerj.10134

Wedmann, S., T. Hörnschemeyer, and H. Schmied. 2011. Fossil water-penny beetles (Coleoptera: Psephenidae: Eubrianacinae) from the Eocene of Europe, with remarks on their phylogenetic position and biogeography. *Palaeontology* 54: 965–980. https://doi.org/10.1111/j.1475-4983.2011.01088.x

Woodruff, R. E. 2002. A new species of the beetle genus Brachypsectra from the Dominican Republic, with fossil connections (Coleoptera: Brachypsectridae). *Insecta Mundi* 549: 161–170.

Wu, R. J. C. 1996. *Secrets of a Lost World: Dominican Amber and its Inclusions*. Santo Domingo: Privately published.

Xia, F., G. Yang, Q. Zhang, G. Shi, and B. Wang. 2015. *Amber: Life Through Time and Space.* Beijing: Science Press.

Xing, L., B. Sames, R. C. McKellar, D. Xi, M. Bai, and X. Wan. 2018. A gigantic marine ostracod (Crustacea: Myodocopa) trapped in mid-Cretaceous Burmese amber. *Scientific Reports* 8: 1365. https://doi.org/10.1038/s41598-018-19877-y

Yu, T., U. Thomson, L. Mu, A. Ross, J. Kennedy, P. Broly, F. Xia, H. Zhang, B. Wang, and D. Dilcher. 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences of the United States of America* 116: 11345–11350. https://doi.org/10.1073/pnas.1821292116

Yu, T., T. A. Neubauer, and A. Jochum. 2021. First freshwater gastropod preserved in amber suggests long-distance dispersal during the Cretaceous Period. *Geological Magazine* 158: 1327–1334. https://doi.org/10.1017/S0016756821000285

Zaragoza Caballero, S. 1990. Descripción de una especie nueva fósil de *Glyphonyx* Candèze (Coleoptera: Elateridae, Adrastinae) del ámbar de Simojovel, Chiapas, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie zoología* 61(3): 147– 151.

Zhang, S. Q., L. H. Che, Y. Li, D. Liang, H. Pang, A. Ślipiński, and P. Zhang. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* 9: 205. https://doi.org/10.1038/s41467-017-02644-4

Zhao, X., X. Zhao, E. A. Jarzembowski, and B. Wang. 2019. The first whirligig beetle larva from mid-Cretaceous Burmese amber (Coleoptera: Adephaga: Gyrinidae). *Cretaceous Research* 99: 41–45. https://doi.org/10.1016/j.cretres.2019.02.015

Zhao, X., X. Zhao, E. Jarzembowski, Y. Tian, and L. Chen. 2020. The first record of brachypsectrid larva from mid-Cretaceous Burmese amber (Coleoptera: Polyphaga). *Cretaceous Research* 113: 104493. https://doi.org/10.1016/j.cretres.2020.104493

Zippel, A., C. Kiesmüller, G. T. Haug, P. Müller, T. Weiterschan, C. Haug, M. K. Hörnig, and J. T. Haug. 2021. Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. *Palaeoentomology* 4: 475–498. https://doi.org/10.11646/palaeoentomology.4.5.14

Zippel, A., C. Haug, C. Hoffeins, H.-W. Hoffeins, and J. T. Haug. 2022a. Expanding the record of larvae of false flower beetles with prominent terminal ends. *Rivista Italiana di Paleontologia e Stratigrafia* 128: 81–104. https://doi.org/10.54103/2039-4942/17084

Zippel, A., V. A. Baranov, J. U. Hammel, M. K. Hörnig, C. Haug, and J. T. Haug. 2022b. The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. *PeerJ* 10: e13025. https://doi.org/10.7717/peerj.13025

Zippel, A., C. Haug, J. Gauweiler, M. K. Hörnig, G. T. Haug, and J. T. Haug. 2022c. A small beetle larva preserved in 23-million-year-old Mexican amber: possible first fossil record of an immature variegated mud-loving beetle. *Boletín de la Sociedad Geológica Mexicana* 74: A150322. http://dx.doi.org/10.18268/BSGM2022v74n2a150322

Zippel, A., C. Haug, P. Müller, and J.T. Haug. early view. The first fossil false click beetle larva preserved in amber. *PalZ*. https://doi.org/10.1007/s12542-022-00638-2

Figures

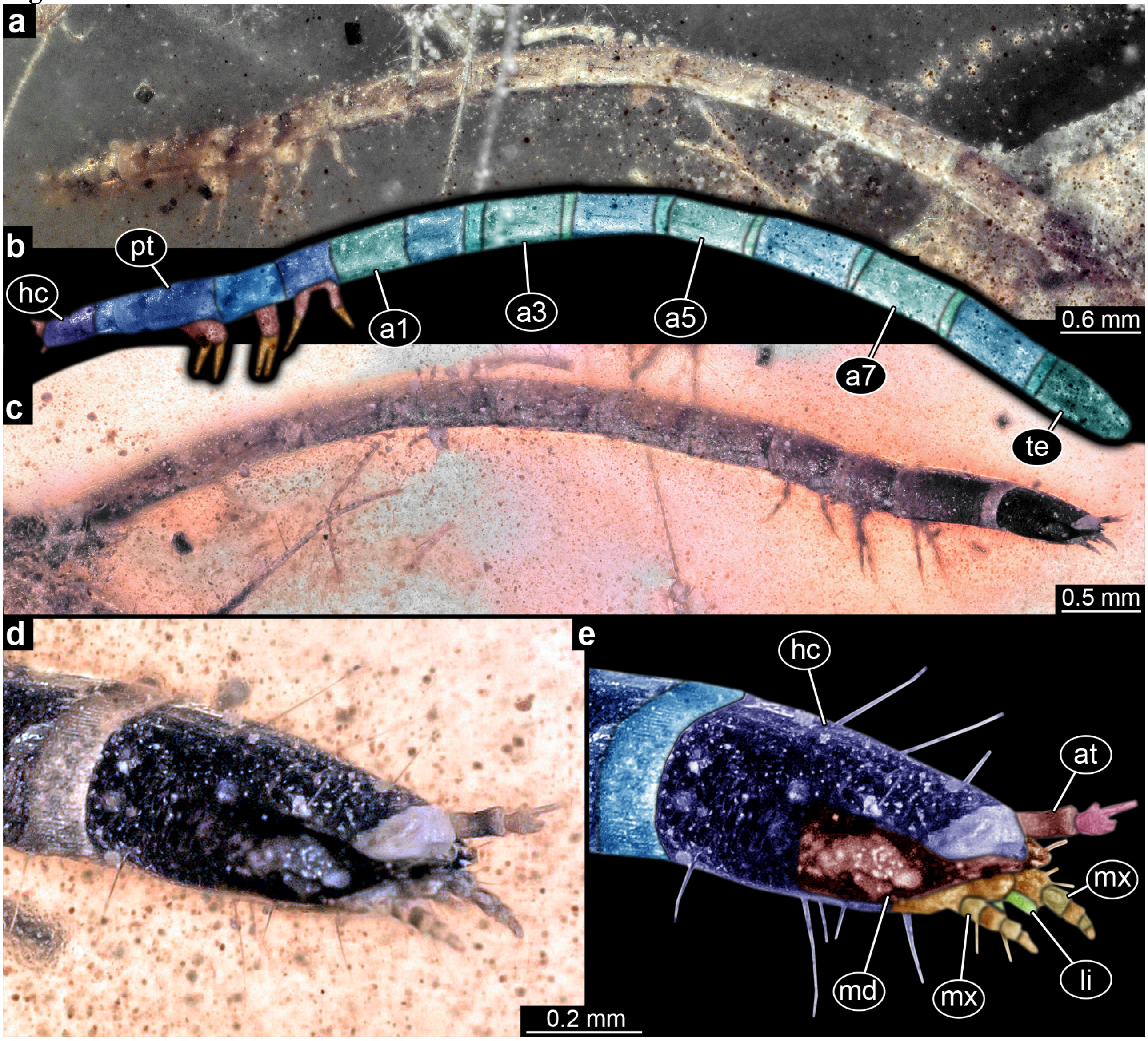

Fig. 1
Fossil specimen BUB 4275, possible larva of Elateridae: **a** Habitus in lateral view; **b** Colour-marked version of **a**; **c** Habitus in antero-lateral view; **d** Head in antero-lateral view; **e** Colour-marked version of head and its mouthparts based on **d**; Abbreviations: a1–a7 = abdomen segments 1–7; at = antenna; hc = head capsule; li = labium; md = mandible; mx = maxilla; pt = prothorax; te = trunk end

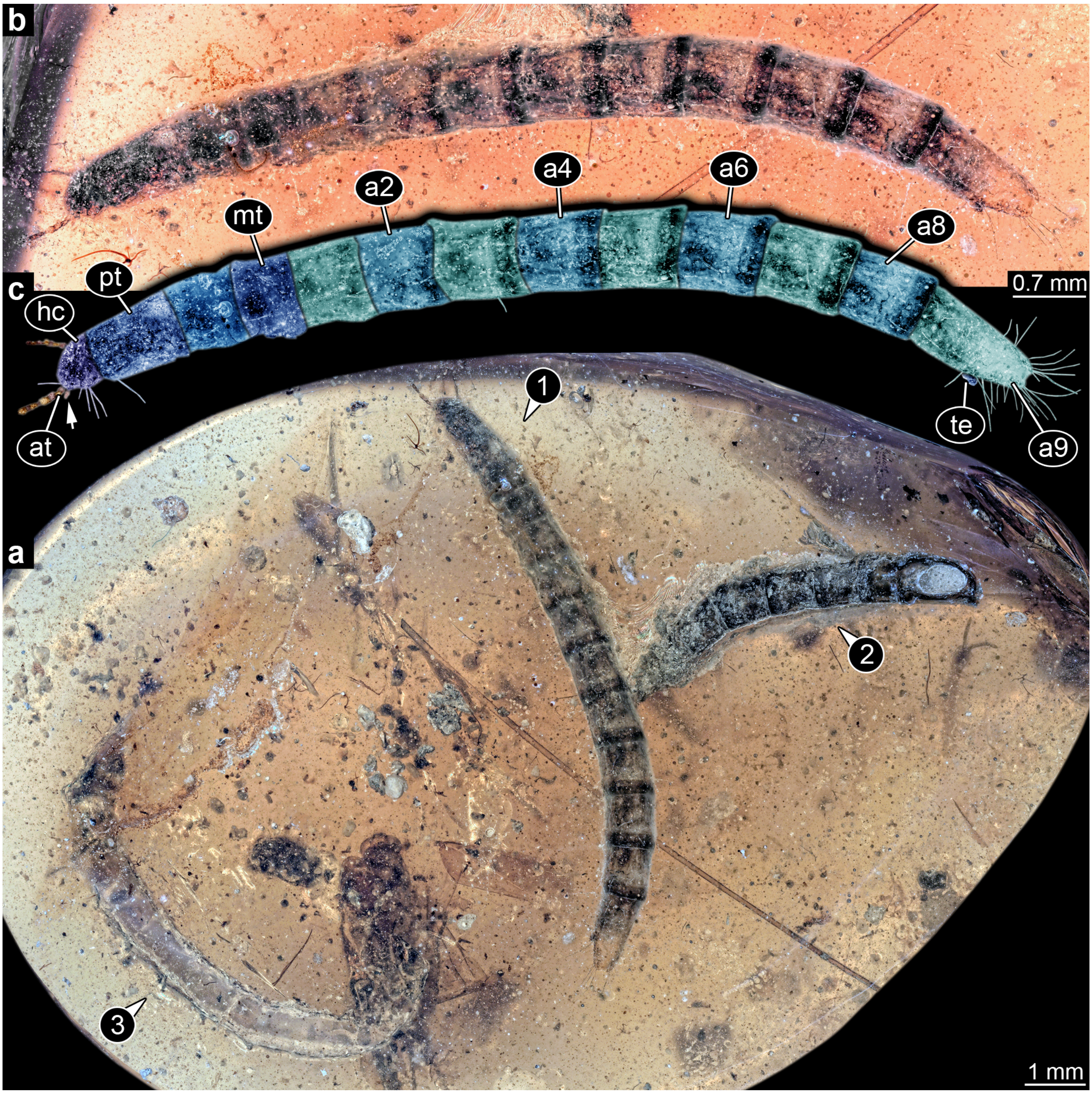

Fig. 2
Amber piece PED 0369 with close-up on specimen 1; **a** Amber piece with various inclusions, three specimens of larvae of Ptilodactylidae are numbered 1–3; **b** Habitus of specimen 1 in dorso-lateral view; **c** Colour-marked version of **b**, palp of maxilla discernible (white arrow); Abbreviations: a2–a9 = abdomen segments 2–9; at = antenna; mt = metathorax; pt = prothorax; te = trunk end

Fig. 3
Specimens 2 and 3 of amber piece PED 0369; **a** Habitus of specimen 2 in dorsal view; **b** Habitus of specimen 3 in dorso-lateral view, hooks of trunk end discernible (white arrow); **c** Head in dorso-lateral view; **d** Colour-marked version of head and its mouthparts based on **c**, palps of maxillae discernible (white arrows); Abbreviations: at = antenna; hc = head capsule; li = labium; lr = labrum; md = mandible; mx = maxilla

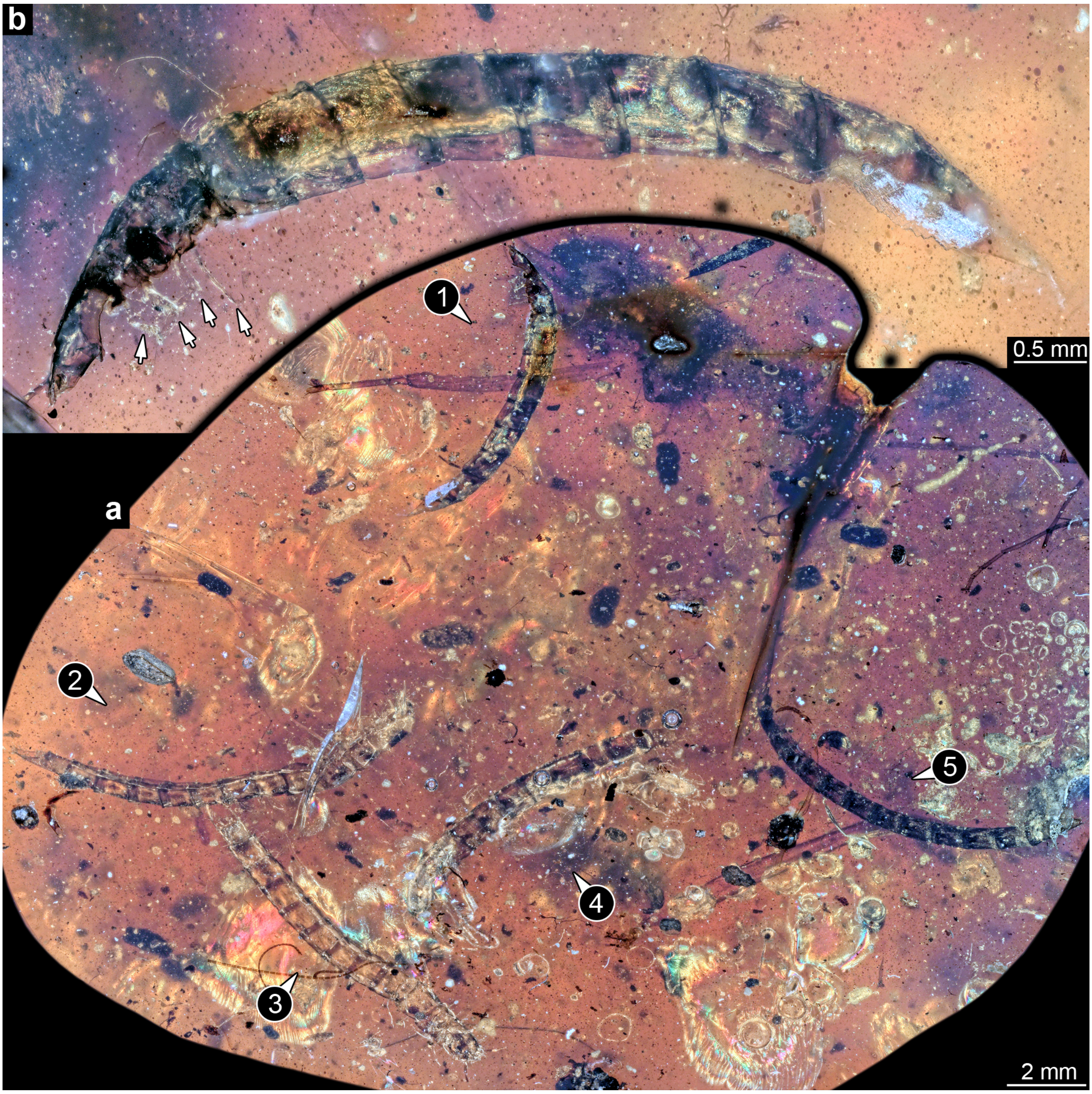

Fig. 4
Amber piece PED 0925 with close-up on specimen 1; **a** Amber piece with various inclusions, five specimens of larvae of Ptilodactylidae are numbered 1–5; **b** Habitus of specimen 1 in lateral view, probable legs discernible (white arrows)

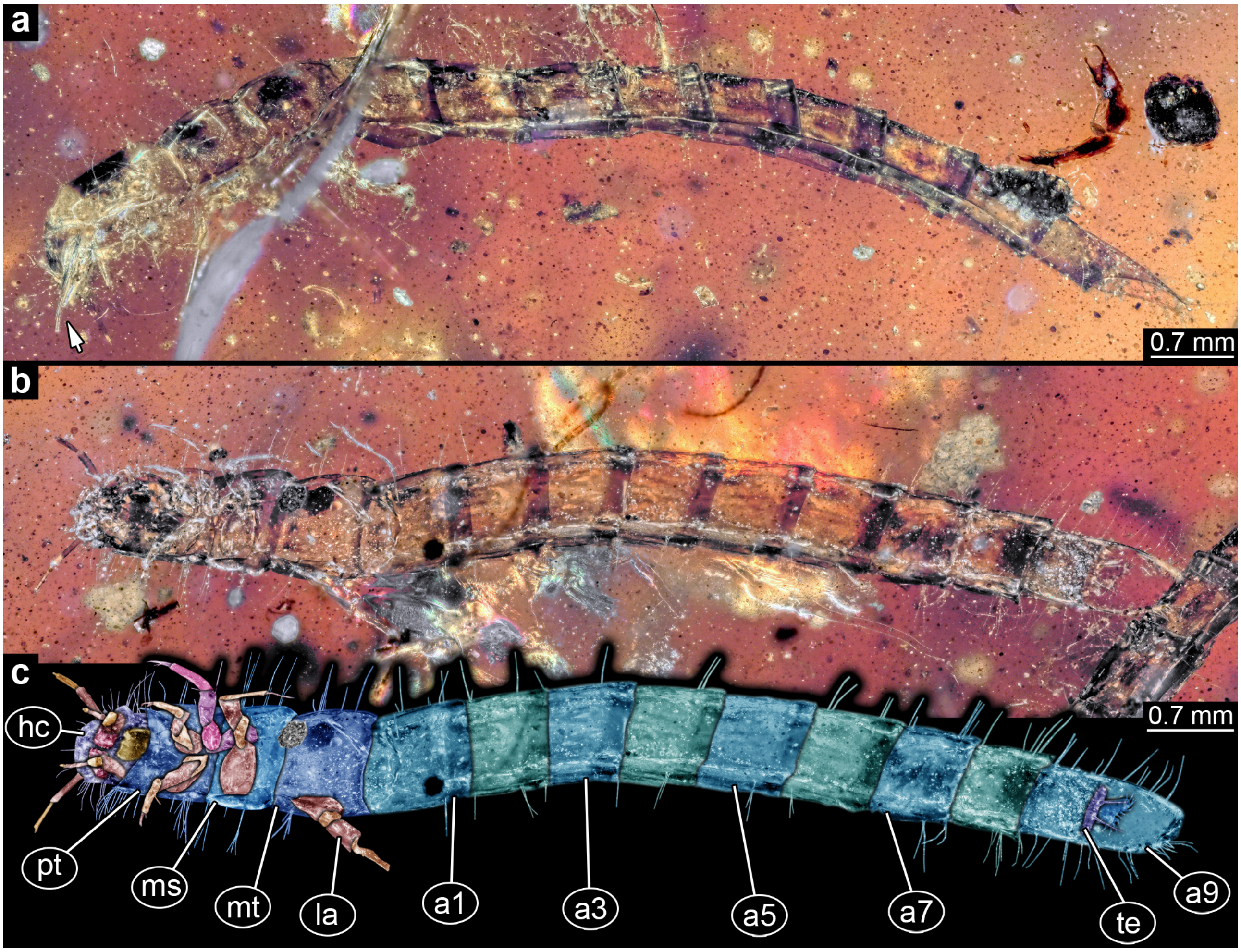

Fig. 5
Specimens 2 and 3 of amber piece PED 0925; **a** Habitus of specimen 2 in lateral view, probable antenna discernible (white arrow); **b** Habitus of specimen 3 in ventral view; **c** Colour-version of **b**; Abbreviations: a1–9 = abdomen segments 1–9; hc = head capsule; la = locomotory appendages (legs); ms = mesothorax; mt = metathorax; pt = prothorax; te = trunk end

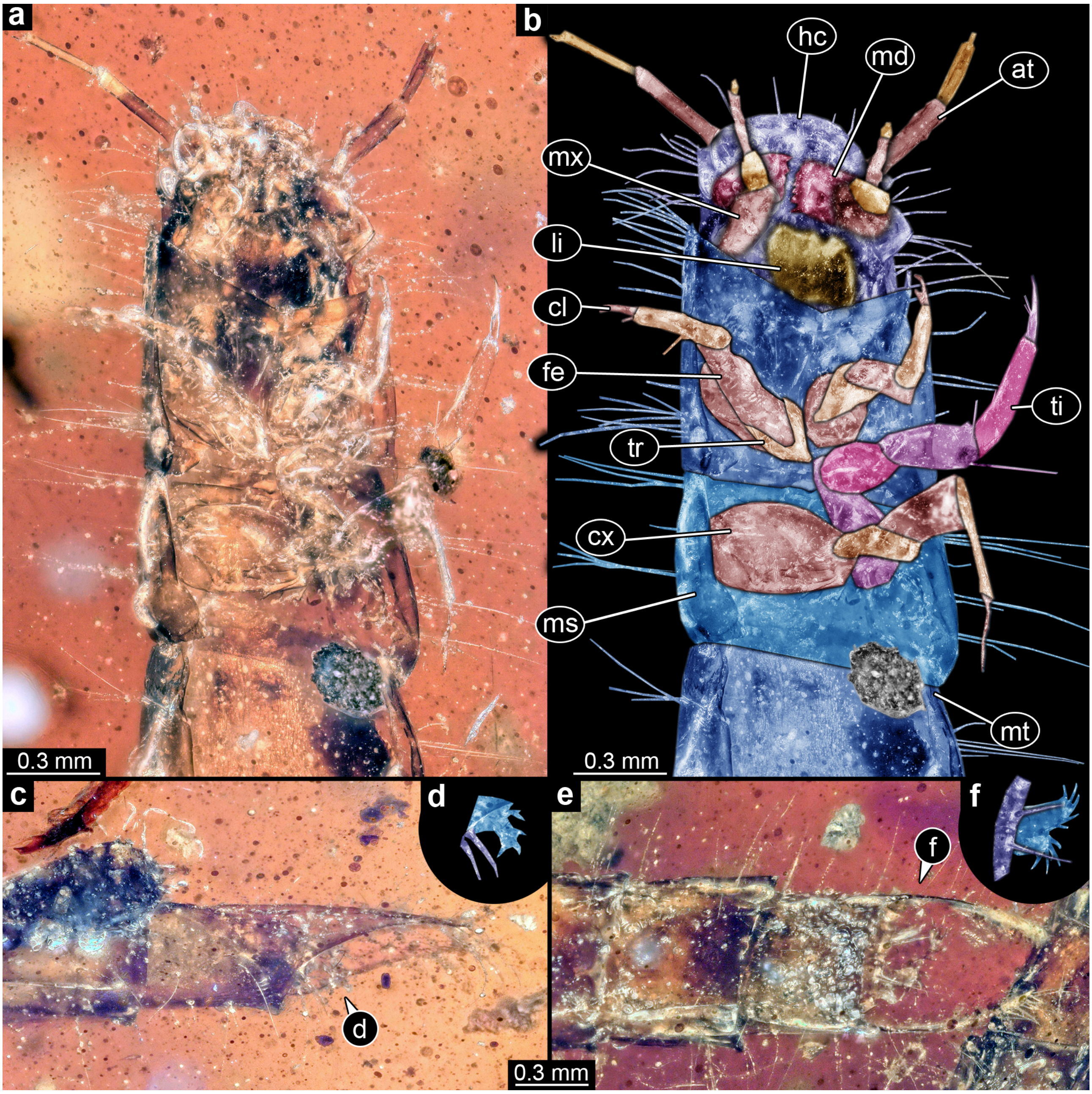

Fig. 6
Close-ups of specimens 2 and 3 of amber piece PED 0925; **a** Close-up of head, pro-, and mesothorax of specimen 3 in ventral view; **b** Colour-marked version of **a**; **c** Close-up of abdomen segment 9 and trunk end of specimen 2; **d** Colour-marked version of trunk end from **c**; **e** Close-up of abdomen segments 8–9 and trunk end of specimen 3; **f** Colour-marked version of trunk end from **e**; Abbreviations: at = antenna; cl = claw; cx = coxa; fe= femur; hc =head capsule; li = labium; md = mandible; ms = mesothorax; mt = metathorax; mx = maxilla; ti = tibia; tr = trochanter

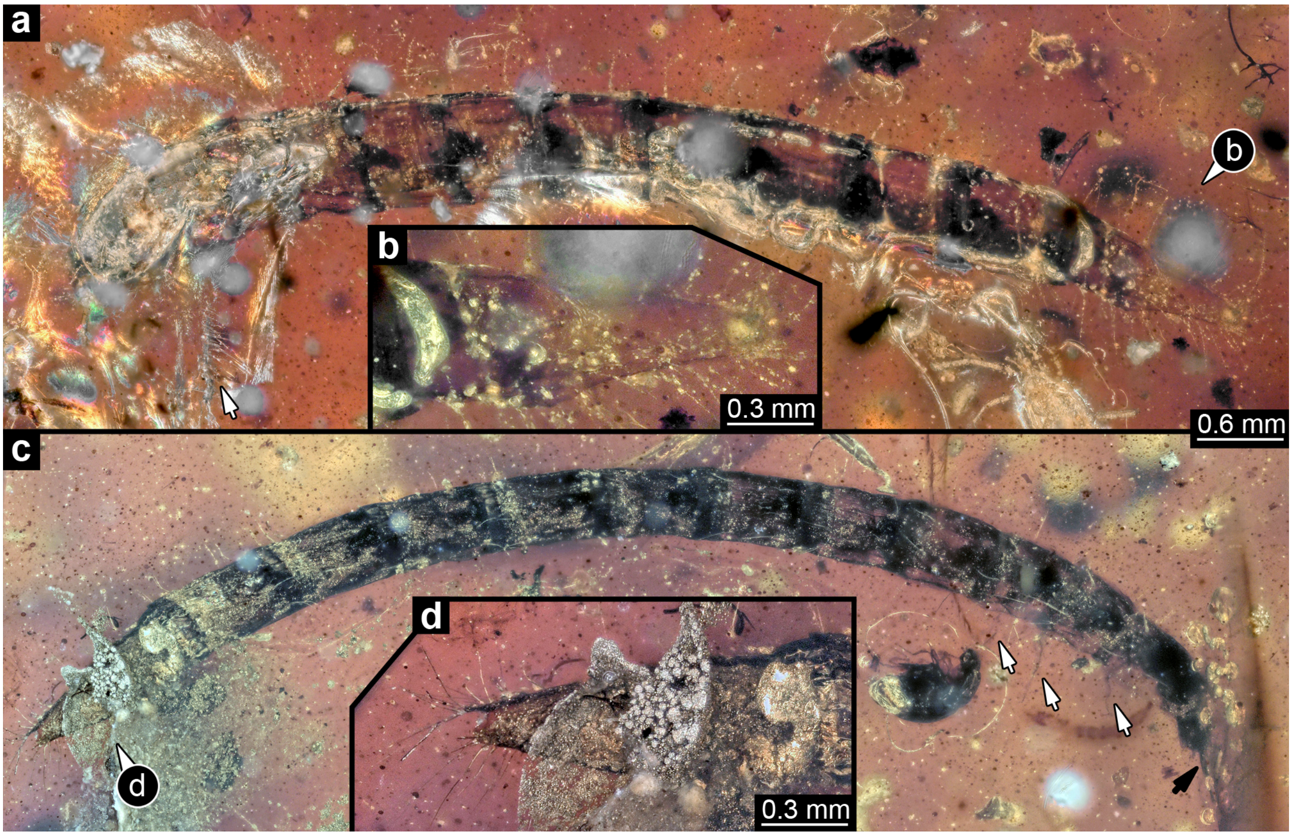

Fig. 7
Specimens 4 and 5 of amber piece PED 0925; **a** Habitus of specimen 4 in dorsal view, probable leg discernible (white arrow); **b** Close-up of abdomen segment 9 of specimen 4; **c** Habitus of specimen 5 in dorso-lateral view, probable antenna (black arrow) and legs (white arrows) discernible; **d** Close-up of abdomen segment 9 of specimen 5 in dorsal view

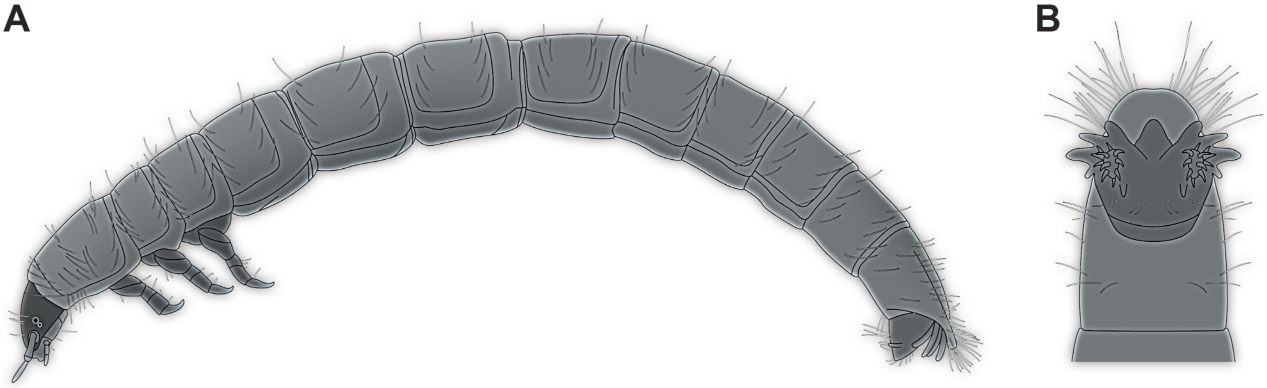

Fig. 8
Schematic representation of extant larva of Ptilodactylidae based on Stribling (1986, fig. 33); **a** Habitus of larva in lateral view; **b** Close-up of abdomen segment 9 and trunk end with lobes and hooks in ventral view

3.9. *Article IX – a manuscript*

Zippel, A., Haug, C., Elverdi, Z, Müller, P. & Haug J.T. (in REVISION). Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Miocene and Cretaceous ambers. Fossil Record.

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

Ana Zippel[1*], Carolin Haug[1,2], Zeynep Elverdi[3], Patrick Müller[4], Joachim T. Haug[1,2]

[1] Ludwig-Maximilians-Universität München (LMU Munich), Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany; CH ORCID https://orcid.org/0000-0001-9208-4229; JTH ORCID https://orcid.org/0000-0001-8254-8472; AZ ORCID https://orcid.org/0000-0002-6509-4445

[2] GeoBio-Center at LMU, Richard-Wagner-Str. 10, 80333 München, Germany.

[3] Istanbul Technical University (İTÜ), Faculty of Science and Letters, Ayazağa Campus, 34469 Maslak-Istanbul, Turkey

[4] Kreuzbergstr. 90, 66482 Zweibrücken, Germany.

[*]corresponding author (ana.zippel@palaeo-evo-devo.info)

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. There are different not closely related beetle larvae that posses setiferous processes. We here report three beetle larvae one from Miocene Mexican and two from Cretaceous Kachin amber, Myanmar. These larvae posses 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 of the new larvae to 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 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; fungus-eating; Myanmar amber; fossils; 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 less 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, that could inform us about the evolutionary history of these important faunal components, are relatively underrepresented in the literature.

The under-representation seems to be coupled to the fact that many fossil beetle larvae can proof 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. 2018). 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. early view). 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 the, likewise aquatic, larvae of water penny beetles (Psephenidae) 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, that 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 implications of these new fossils concerning the evolution of larval characters in beetles and the importance of reporting fossil larvae.

Material and Methods

Material

In 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 lables within 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 in 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 separated 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 a more descriptive morphological terminology within the first description of a specimen. This is done in order to enhance the understandability for non-experts. The descriptive terms apply to all of the specimens but are not repeated for 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 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).

(FIGURE 1.)

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-colored 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).

(FIGURE 2.)

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 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).

(FIGURE 3.)

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 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. 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 membraneous 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 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).

(FIGURE 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 (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, at proximal part membraneous 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-, 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 setaee. (FIGURE 5.)

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). 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, at proximal part membraneous 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 membraneous 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).

(FIGURE 6.)

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 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.)

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. early view a). 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 a 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, the shape of abdomen segment 9 of SNHMB.G 8196 and SNHMB.G 8195 in dorsal view, and the specialised setae of the processes (Figs 1–3, 7).

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; Yoshitomo 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 sizes among 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 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 processess and the head shape to the fossil. On the other hand, the tergite of the abdomen segment 9 of the modern larva differs to the tergite seen in the new fossil (Escalona & 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 larva of *Sticholotis ruficeps* is much narrower than the tergite of the 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 & Tomaszewska 2005, fig. 10.33.7.B, Escalona & Ślipiński 2010, fig. 37). The new fossils may be closer 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 extinct morphologies have been recognised for some groups of Holometabola (Badano et al. 2018, 2021; Zippel et al. 2021, early view, Haug et al. 2019a, 2019b, 2021c, 2022a). 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 stay 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 & Nel 2012). Additional fossils have been also reported from Eocene Baltic amber (Szawaryn & Szwedo, 2018; Szawaryn, 2019; Szawaryn & 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 a life 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 on 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 & 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 &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 mechanism 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). It is possible that the processes of the new larvae help in cloaking themselves with hyphae or spores of the fungi as well. Such a camouflage is probably additionally useful to stay unnoticed by a predator (Tomaszewska 2005) and have an easier access to the food. Similar strategies of decorating with hyphae is also seen in 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, that 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 an 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 that 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. Leschen (2000) and Ślipiński and Tomaszewska (2005) implied that 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 review a), submerged wood borers (Zippel et al. in review b), predators of wood-eating larvae (Haug et al. 2021b; Peris et al. 2022), but also larvae that possibly feed on fungi in rotting wood (Tomaszewska et al. 2018; Zippel et al. early view; Haug et al. early view a). 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, early view b; 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. It is likely that they helped while, at least some of, the new larvae were feeding on fungi. .

Acknowledgements

We thank Artem Zaitsev, Moscow, and an anonymous reviewer for their helpful input and suggestions about the manuscript. This study benefited from the help of various people and institutions; we thank them for their support. Lars Vilhelmsen, Alexey Solodovnikov, and Martin V.

Sørensen, all Copenhagen, are thanked for providing access to specimens at NHMD and their help and support. J. Matthias Starck, Munich, is thanked for long time support. We thank Mike Reich, Braunschweig, for his help with curating of the two new fossil specimens. JTH is kindly supported by the Volkswagen Foundation with a Lichtenberg Professorship and by the German Research Foundation (DFG Ha-6300/6-1). This study also benefited from SYNTHESYS+ grant (DK-TAF-TA4-007) that supported AZ for her three-weeks-stay in Copenhagen, Denmark. We are grateful to all people providing free software used in this project. This is LEON publication #56.

References

Badano D, Engel MS, Basso A, Wang B, Ceretti P (2018) Diverse Cretaceous larvae reveal the evolutionary and behavioural history of antlions and lacewings. Nature Communications 9: art. 3257.
https://doi.org/10.1038/s41467-018-05484-y

Badano D, Fratini M, Magueri L, Palermo F, Pieroni N, Cedola A, Haug JT, Weiterschan T, Velten J, Mei M, di Gulio A, Ceretti P (2021) X-ray microtomography and phylogenomics provide insights into the morphology and evolution of an enigmatic Mesozoic insect larva. Systematic Entomology 46: 672–684.
https://doi.org/10.1111/syen.12482

Batelka J, Engel MS (2022) The ‘first fossil tumbling flower beetle’ larva is a symphytan (Hymenoptera). Acta Entomologica Musei Nationalis Pragae 62: 57–59.
https://doi.org/10.37520/aemnp.2022.005

Beutel RG (2005) Myxophaga Crowson, 1955. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga (partim). 1st ed. Walter De Gruyter, Berlin (NY), 43–44.

Beutel RG, Lawernce JF (2005). 4. Coleoptera, Morphology. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga (partim). 1st ed. Walter De Gruyter, Berlin (NY), 23–27.

Beutel RG, Zhang WW, Pohl H, Wappler T, Bai M (2016) A miniaturized beetle larva in Cretaceous Burmese amber: reinterpretation of a fossil “strepsipteran triungulin”. Insect Systematics & Evolution 47: 83–91.

Burakowski B (1997) Descriptions of larva and pupa of *Mycetina cruciata* (Schaller)(Coleoptera, Endomychidae). Annales Zoologici 47(1–2): 209–214.

Carlton CE, Townsend VR, Van Zandt PA, Mopper S (2000) Description of the larva of *Loberus* *impressus* (Coleoptera: Languriidae: Xenoscelinae) with notes on its natural history. Annals of the Entomological Society of America 93(3): 356–361. https://doi.org/10.1603/0013-8746(2000)093[0356:DOTLOL]2.0.CO;2

Cai CY, Háva J, Huang DY (2017) The earliest Attagenus species (Coleoptera: Dermestidae: Attageninae) from Upper Cretaceous Burmese amber. Cretaceous Research 72: 95–99. https://doi.org/10.1016/j.cretres.2016.12.018

Clarke DJ, Limaye A, McKenna DD, Oberprieler RG (2018) The weevil fauna preserved in Burmese amber—snapshot of a unique, extinct lineage (Coleoptera: Curculionoidea). Diversity 11: art. 1. https://doi.org/10.3390/d11010001

Escalona HE, Ślipiński A (2010). *Sticholotis ruficeps* Weise: new synonymies and description of its mature larva (Coleoptera: Coccinellidae: Sticholotidini). Annales Zoologici 60: 309–318.

Genung WG, Woodruff RE, Grissell EE (1980) *Languria erythrocephalus*: Host plants, immature stages, parasites, and habits (Coleoptera: Languriidae). Florida Entomologist 63: 206–210. https://doi.org/10.2307/3494441

Grimaldi D, Kathirithamby J, Schawaroch V (2005) Strepsiptera and triungula in Cretaceous amber. Insect Systematics & Evolution 36: 1–20.

Gröhn C (2015) Einschlüsse im baltischen Bernstein.Verlag Wachholtz, Kiel, 424 pp.

Gustafson GT, Michat MC, Balke M (2020) Burmese amber reveals a new stem lineage of whirligig beetle (Coleoptera: Gyrinidae) based on the larval stage. Zoological Journal of the Linnean Society 189(4): 1232–1248. https://doi.org/10.1093/zoolinnean/zlz161

Haug C, Shannon KR, Nyborg T, Vega FJ (2013b) Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. Bolétin de la Sociedad Geológica Mexicana 65(2): 273–284.

Haug C, Herrera-Flórez AF, Müller P, Haug JT (2019a) Cretaceous chimera–an unusual 100-million-year old neuropteran larva from the "experimental phase" of insect evolution. Palaeodiversity 12: 1–11.
https://doi.org/10.18476/pale.v12.a1

Haug C, Haug GT, Zippel A, van der Wal S, Haug JT (2021a) The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4: 390–404.
https://doi.org/10.11646/palaeoentomology.4.4.14

Haug C, Posada Zuluaga V, Zippel A, Braig F, Müller P, Gröhn C, Weiterschan T, Wunderlich J, Haug GT, Haug JT (2022b) The morphological diversity of antlion larvae and their closest relatives over 100 million years. Insects 13: art. 587.
https://doi.org/10.3390/insects13070587

Haug C, Zippel A, Hassenbach C, Haug GT, Haug JT (2022a) A split-footed lacewing larva from about 100-million-year-old amber indicates a now extinct hunting strategy for neuropterans. Bulletin of Geoscneces 97: 453–464.
https://doi.org/10.3140/bull.geosci.1861

Haug C, Zippel A, Müller P, Haug JT (early view a) Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ (2023).
https://doi.org/10.1007/s12542-023-00648-8

Haug C, Baranov VA, Hörnig MK, Gauweiler J, Hammel JU, Perkovsky EE, Haug JT (early view b). 35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests. Palaeobiodiversity and Palaeoenvironments.
https://doi.org/10.1007/s12549-022-00552-0

Haug GT, Baranov V, Wizen,G, Pazinato PG, Mueller P, Haug C, Haug JT (2021c) The morphological diversity of long-necked lacewing larvae (Neuroptera: Myrmeleontiformia). Bulletin of Geosciences 96(4): 1–27.
https://doi.org/10.3140/bull.geosci.1807

Haug GT, Haug C, van der Wal S, Müller P, Haug JT (2022c) Split-footed lacewings declined over time: indications from the morphological diversity of their antlion-like larvae. PalZ 96: 29–50. https://doi.org/10.1007/s12542-021-00550-1

Haug JT, Haug C (2019) Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). PeerJ 7: art. E7871. https://doi.org/10.7717/peerj.7871

Haug JT, Haug C, Ehrlich M (2008) First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). Palaeodiversity 1: 103–109.

Haug JT, Haug C, Kutschera V, Mayer G, Maas A, Liebau S, Castellani C, Wolfram U, Clarkson ENK, Waloszek D (2011) Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244: 259–272. https://doi.org/10.1111/j.1365-2818.2011.03534.x

Haug JT, Müller CHG, Sombke A (2013a). A centipede nymph in Baltic amber and a new approach to document amber fossils. Organisms Diversity & Evolution 13: 425–432. https://doi.org/10.1007/s13127-013-0129-3

Haug JT, Müller P, Haug C (2018) The ride of the parasite: a 100-million-year old mantis lacewing larva captured while mounting its spider host. Zoological Letters 4: art. 31. https://doi.org/10.1186/s40851-018-0116-9

Haug JT, Müller P, Haug C (2019b) A 100-million-year old predator: a fossil neuropteran larva with unusually elongated mouthparts. Zoological Letters 5: 1–14. https://doi.org/10.1186/s40851-019-0144-0

Haug JT, Zippel A, Haug GT, Hoffeins C, Hoffeins H-W, Hammel JU, Baranov V, Haug C (2021b) Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14: 161–183. https://doi.org/10.18476/pale.v14.a8

Haug JT, Linhart S, Haug GT, Gröhn C, Hoffeins C, Hoffeins H-W, Müller P, Weiterschan T, Wunderlich J, Haug C (2022d) The diversity of aphidlion-like larvae over the last 130 million years. Insects 13: art. 336.
https://doi.org/10.3390/insects13040336

Hayashi M, Aiba H, Nakano E, Takahashi Y, Sato T (2020) Fossilized water pennies (Coleoptera: Psephenidae) in the Middle Pleistocene lake deposits in Shiobara site, Tochigi Prefecture, Japan. Japanese Journal of Systematic Entomology 26: 84–86.

Kapur AP (1950). The biology and external morphology of the larvae of Epilachninae (Coleoptera, Coccinellidae). Bulletin of Entomological Research 41: 161–208.

Kerp H, Bomfleur B (2011) Photography of plant fossils— new techniques, old tricks. Review of Palaeobotany and Palynology 166: 117–151.
https://doi.org/10.1016/j.revpalbo.2011.05.001

Kirejtshuk AG & Nel A (2012) The oldest representatives of the family Coccinellidae (Coleoptera: Polyphaga) from the lowermost Eocene Oise amber (France). Zoosystematica Rossica 21: 131–144.

Klausnitzer B (1978) Ordnung Coleoptera (Larven). Bestimmungsbücher zur Boden-Fauna Europas, vol 10. Akademie Verlag, Berlin, 378 pp.
https://doi.org/10.1007/978-94-009-9975-6_2

Klausnitzer B (2003) Käferlarven (Insecta: Coleoptera) in Baltischem Bernstein-Möglichkeiten und Grenzen der Bestimmung. Entomologische Abhandlungen 61: 103–108.

Klausnitzer B(2009) Bemerkungen zu rezenten und fossilen Larven (Bernstein) der Gattung *Brachypsectra* LeConte (Coleoptera, Brachypsectridae). Contributions to Natural History 12: 721–742.

Larsson SG (1978) Baltic Amber: A Palaeobiological Study. Entomonograph I. Scandinavian Scientific Press, Klampenborg, 192 pp.

Lawrence JF (1991a) Order Coleoptera. Beetles. Diagnosis. In: Stehr FD (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 144–146.

Lawrence JF (1991b) Order Coleoptera. Beetles. Erotylidae (Cucujoidea)(including Dacnidae). Pleasing fungus beetles. In: Stehr FD (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 473–475.

Lawrence JF (1991c) Order Coleoptera. Beetles. Cerylonidae (Cucujoidea)(= Cerylidae; including Aculagnathidae, Anommatidae, Dolosidae, Euxestidae, Murmidiidae). In: Stehr FD (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 480–481.

Lawrence JF (1991d) Order Coleoptera. Beetles. Endomychidae (Cucujoidea)(including Merophysiidae, Mycetaeidae). In: Stehr FD (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 482–485.

LeSage L (1991) Order Coleoptera. Beetles. Coccinellidae (Cucujoidea). The lady beetles, lady birds. In: Stehr FD (Ed) Immature Insects, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa, 485–494.

Leschen RAB (1994) Ecological and behavioral correlates among mycophagous Coleoptera. Folia Entomologica Mexicana 92: 9–19.

Leschen RAB, Carlton CE (1988) Immature stages of *Endomychus biguttatus* Say (Coleoptera: Endomychidae) with observations on the alimentary canal. *J*ournal of the Kansas Entomological Society 61(3): 321–327.
https://www.jstor.org/stable/25085008

Leschen RAB (2000) Beetles feeding on bugs (Coleoptera, Hemiptera): repeated shifts from mycophagous ancestors. InvertebrateTaxonomy 14: 917–929.

Leschen RAB, Skelley AB, McHugh JV (2005) 10.7. Erotylidae Leach, 1815. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 2: morphology and systematics (Elateroidea, Bostrichiformia,Cucujiformia Partim). 1st ed. Walter De Gruyter, Berlin (NY), 311–319.

Li Y-D, Tomaszewska W, Huang DY, Cai CY (2022b) *Rhomeocalpsua torosa* gen. et sp. nov., a unique lineage of Endomychidae from mid-Cretaceous Burmese amber (Coleoptera: Coccinelloidea). Palaeoentomology 5(2): 146–154. https://doi.org/10.11646/palaeoentomology.5.2.7

Li Y-D, Huang D-Y, Cai C-Y (2022a) "*Attagenus*" *burmiticus* from mid-Cretaceous amber reinterpreted as a member of Orphilinae (Coleoptera: Dermestidae). Palaeoentomology 5(4): 390–394. https://doi.org/10.11646/palaeoentomology.5.4.12

Machado RJ, Gillung JP, Winterton SL, Garzón-Orduña IJ, Lemmon AR, Lemmon EM, Oswald JD (2019). Owlflies are derived antlions: anchored phylogenomics supports a new phylogeny and classification of Myrmeleontidae (Neuroptera). Systematic Entomology 44: 418–450. https://doi.org/10.1111/syen.12334

McHugh JV, Pakaluk J (1997) Review of the larval stages of Epipocinae [Insecta: Coleoptera: Endomychidae]. Annales Zoologici 47(1–2): 59–77.

McKenna DD, Wild AL, Kanda K, Bellamy CL, Beutel RG, Caterino MS, Farnum CW, Hawks DC, Ivie MA, Jameson ML, Leschen RAB, Marvldi AE, McHugh JV, Newton AF, Robertson JA, Thayer MK, Whiting MF, Lawrence JF, Ślipiński A, Maddison DR, Farrell BD (2015) The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology 40: 835–880. https://doi.org/10.1111/syen.12132

McKenna DD, Shin S, Ahrens D, Balke M, Beza-Beza C, Clarke DJ, Donath A, Escalona HE, Friedrich F, Letsch H, Liu S, Maddison D, Mayer C, Misof B, Murin PJ, Niehuis O, Peters RS, Podsiadlowski L, Pohl H, Scully ED, Yan EV, Zhou X, Ślipiński A, Beutel RG (2019) The evolution and genomic basis of beetle diversity. PNAS 116: 24729–24737. https://doi.org/10.1073/pnas.1909655116

Peris D (2020) Coleoptera in amber from Cretaceous resiniferous forests. Cretaceous Research 113: art. 104484. https://doi.org/10.1016/j.cretres.2020.104484

Peris D, Rust J (2020) Cretaceous beetles (Insecta: Coleoptera) in amber: the palaeoecology of this most diverse group of insects. Zoological Journal of the Linnean Society 189(4): 1085–1104. https://doi.org/10.1093/zoolinnean/zlz118

Peris D, Mähler B, Kolibáč J (2022) Review of the Family Thanerocleridae (Coleoptera: Cleroidea) and the Description of Thanerosus gen. nov. from Cretaceous Amber Using Micro-CT Scanning. Insects 13(5): art. 438. https://doi.org/10.3390/insects13050438

Peterson A (1957) Larvae of insects. An Introduction to Nearctic Species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera (Vol. 2). Third edition. Ohio State University, Columbus, Ohio, 416 pp.

Poinar GO (1992) Life in Amber. Stanford University Press, Stanford, California, viii+118 pp.

Poinar GO, Poinar R (1999) The amber forest: a reconstruction of a vanished world. Princeton, Princeton University Press, Princeton, New Jersey, xiii+229.

Rasnitsyn AP, Müller P (2023) Identity of the larva described by Zippel et al. (2022) in the mid-Cretaceous Burmese (Kachin) amber (Hymenoptera, Tenthredinoidea, Blasticotomidae = Xyelotomidae syn. Nov.). Palaeoentomology 6: 13–16. https://doi.org/10.11646/palaeoentomology.6.1.4

Ruta R, Jałoszyński P, Sienkiewicz P, Konwerski S (2011) Erotylidae (Insecta, Coleoptera) of Poland–problematic taxa, updated keys and new records. ZooKeys 134: 1–13. https://doi.org/10.3897/zookeys.134.1673

Scheven J (2004) Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut. Kuratorium Lebendige Vorwelt, Hofheim a. T., 160 pp.

Skelley PE (2009) Pleasing fungus beetles of the West Indies (Coleoptera: Erotylidae: Erotylinae). Insecta Mundi 82: 1–94.

Ślipiński A, Lawrence J (2005) 10.29. Cerylonidae Billberg, 1820. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). 1st ed. Walter De Gruyter, Berlin (NY), 422–432.

Ślipiński A, Tomaszewska W (2005) 10.33. Coccinellidae Latreille, 1802. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). 1st ed. Walter De Gruyter, Berlin (NY), 454–472.

Szawaryn K (2019) Unexpected diversity of whitefly predators in Eocene Baltic amber – new fossil Serangium species (Coleoptera: Coccinellidae). Zootaxa 4571: 270–276.

Szawaryn K, Szwedo J (2018) Have ladybird beetles and whiteflies co-existed for at least 40 Mya? Paläontologische Zeitschrift 92: 593–603.

Szawaryn K, Tomaszewska W (2020) The first fossil Sticholotidini ladybird beetle (Coleoptera: Coccinellidae) reveals a transition zone through northern Europe during the Eocene. Papers in Palaeontology 6: 651–659.
https://doi.org/10.1002/spp2.1321.

Tomaszewska W (2005) 10.32. Endomychidae Leach, 1815. In: Kristensen NP, Beutel RG (Eds) Handbook of zoology, vol. IV Arthropoda: Insecta. In: LeschenRAB, Beutel RG Lawrence JF (volume Eds) Part 38. Coleoptera, vol. 2: morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). 1st ed. Walter De Gruyter, Berlin (NY), 442–454.

Tomaszewska W, Zaitsev AA (2012) Larva of *Ectomychus basalis* Gorham (Coleoptera, Endomychidae, Stenotarsinae) and its phylogenetic implication. Deutsche Entomologische Zeitschrift 59: 81–90.
https://doi.org/10.1002/mmnd.201200005

Tomaszewska W, Ślipiński A, Bai M, Zhang W, Ren D (2018) The oldest representatives of Endomychidae (Coleoptera: Coccinelloidea) from the Upper Cretaceous Burmese amber. Cretaceous Research 91: 287–298.

https://doi.org/10.1016/j.cretres.2018.07.001

Tomaszewska W, Szawaryn K, Arriaga-Varela E (2022) First member of ‘higher Endomychidae’ (Coleoptera: Coccinelloidea) from the Mid-Cretaceous amber of Myanmar and new insights into the time of origin of the handsome fungus beetles. Insects 13: art. 690.
https://doi.org/10.3390/insects13080690

Wang B, Xia F, Engel MS, Perrichot V, Shi G, Zhang H, Chen J, Jarzembowski EA, Wappler T, Rust J (2016) Debris-carrying camouflage among diverse lineages of Cretaceous insects. Science Advances 2: art. e1501918.
https://doi.org/10.1126/sciadv.1501918

Wedmann S, Hörnschemeyer T, Schmied H (2011) Fossil water-penny beetles (Coleoptera: Psephenidae: Eubrianacinae) from the Eocene of Europe, with remarks on their phylogenetic position and biogeography. Palaeontology 54(5): 965–980.
https://doi.org/10.1111/j.1475-4983.2011.01088.x

Wichard W (2021) Overview of the caddisflies (Insecta, Trichoptera) in mid-Cretaceous Burmese amber. Cretaceous Research 119: art. 104707.
https://doi.org/10.1016/j.cretres.2020.104707

Williams KA, Clitheroe C-L, Villet MH, Midgley JM (2021). The first record of *Omosita nearctica* Kirejtshuk (Coleoptera, Nitidulidae) in South Africa, with the first description of its mature larva. African Invertebrates 62: 257–271.
https://doi.org/10.3897/afrinvertebr.62.58842

Woodruff RE (2002) A new species of the beetle genus *Brachypsectra* from the Dominican Republic, with fossil connections (Coleoptera: Brachypsectridae). Insecta Mundi 549: 161–170.
https://digitalcommons.unl.edu/insectamundi

Wu RJC (1996) Secrets of a Lost World: Dominican Amber and its Inclusions. Self-published by the author, Santo Domingo, 222 pp.

Yoshitomi H, Sogoh K (2018) Description of the larva of *Amphisternus corallifer* Gerstaecker

(Coleoptera: Endomychidae), with specimens list of the genus *Amphisternus* preserved in EUMJ. Japanese Journal of Systematic Entomology 24(2): 225–229.

Zaitsev AA, Kompantsev AV, Zaitsev AI (2016) A review of larval Encaustini (Coleoptera: Erotylidae) from Russia. Russian Entomological Journal 25(4): 367–386.

Zaitsev AA (2022a) Larval description of two species of *Mycetina* Mulsant, 1846 (Coleoptera: Endomychidae: Lycoperdininae) from Russian Far East. Russian Entomological Journal 31(4): 392–406.

Zaitsev AA (2022b) Larval description of *Lycoperdina smirnoviorum* Gusakov, 2017 (Coleoptera: Endomychidae: Lycoperdininae). Russian Entomological Journal 31(2): 144–153. https://doi.org/10.15298/rusentj.31.2.09

Zhao X, Zhao X, Jarzembowski E, Wang B (2019) The first whirligig beetle larva from mid-Cretaceous Burmese amber (Coleoptera: Adephaga: Gyrinidae). Cretaceous Research 99: 41–45. https://doi.org/10.1016/j.cretres.2019.02.015

Zhao X, Zhao X, Jarzembowski E, Tian Y, Chen L (2020) The first record of brachypsectrid larva from mid-Cretaceous Burmese amber (Coleoptera: Polyphaga). Cretaceous Research 113: art. 104493.
https://doi.org/10.1016/j.cretres.2020.104493

Zippel A, Kiesmüller C, Haug GT, Müller P, Weiterschan T, Haug C, Hörnig MK, Haug JT (2021) Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. Palaeoentomology 4: 475–498.
https://doi.org/10.11646/palaeoentomology.4.5.14

Zippel A, Baranov VA, Hammel JU, Hörnig MK, Haug C, Haug JT (2022c) The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10: art. e13025. https://doi.org/10.7717/peerj.13025

Zippel A, Haug C, Hoffeins C, Hoff eins H-W, Haug JT (2022b) Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia

128: 81–104.
https://doi.org/10.54103/2039-4942/17084

Zippel A, Haug C, Müller P. Haug JT (2022a) First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96: 219–229.
https://doi.org/10.1007/s12542-022-00608-8

Zippel A, Haug C, Müller P, Haug JT (early view) The first fossil false click beetle larva preserved in amber. PalZ (2022).
https://doi.org/10.1007/s12542-022-00638-2

Zippel A, Haug C, Yanez Iturbe-Ormaeche B, Haug JT (in review a) Diversity of archostematan beetle larvae through time with new possible fossils. Palaeodiversity.

Zippel A, Haug C, Müller P, Haug JT (in review b) Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ.

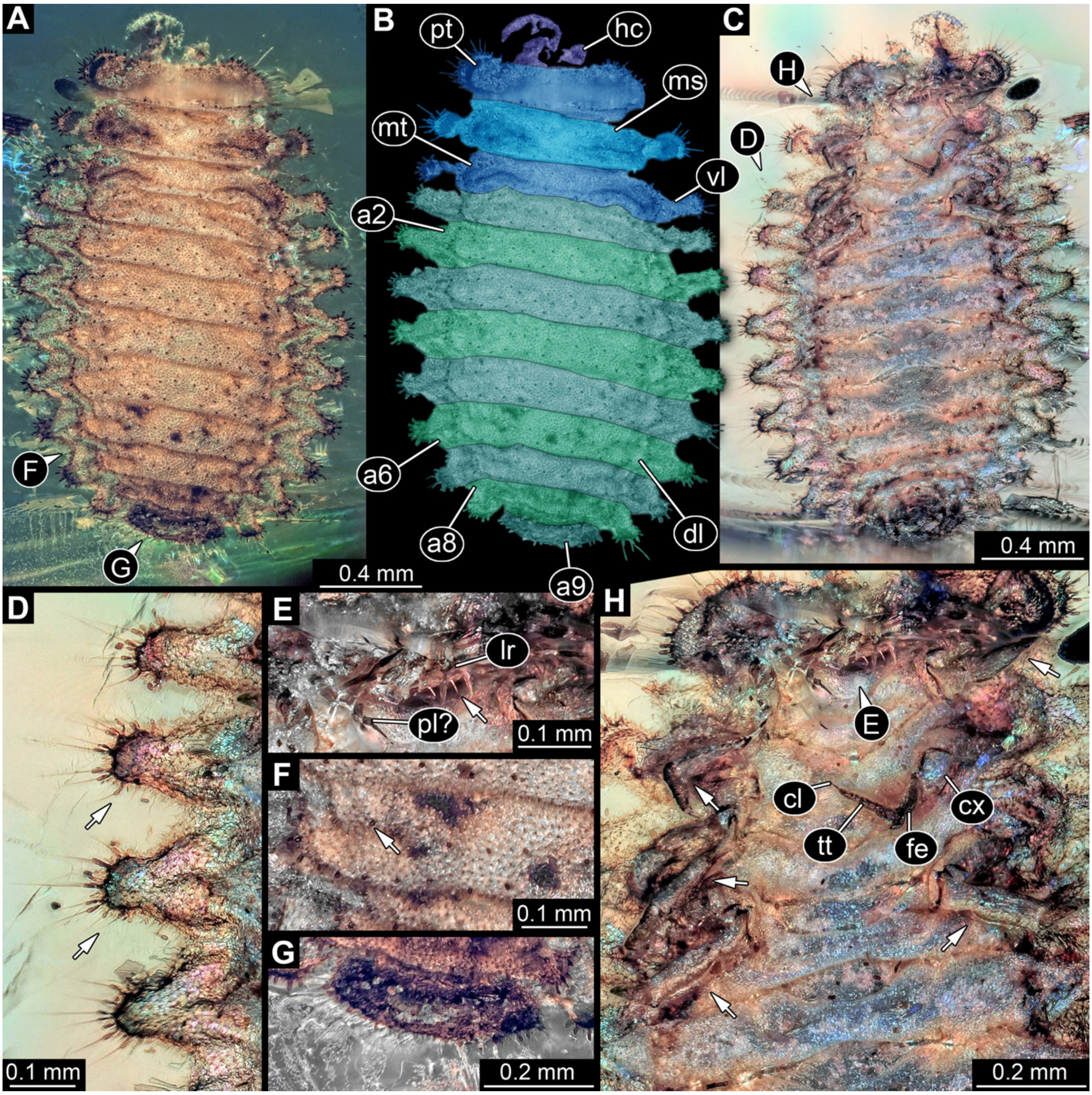

Figure 1.

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.

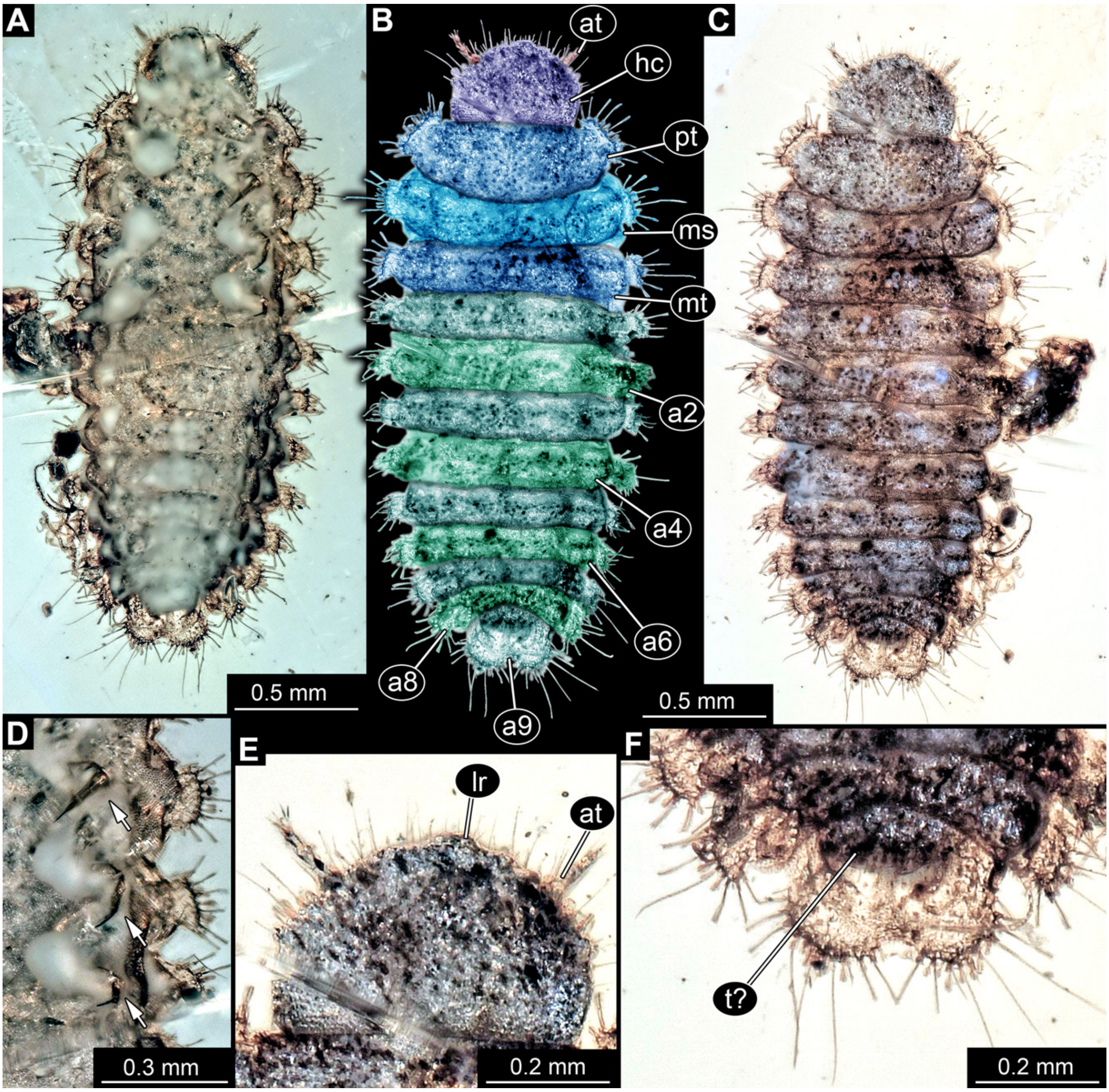

Figure 2.

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.

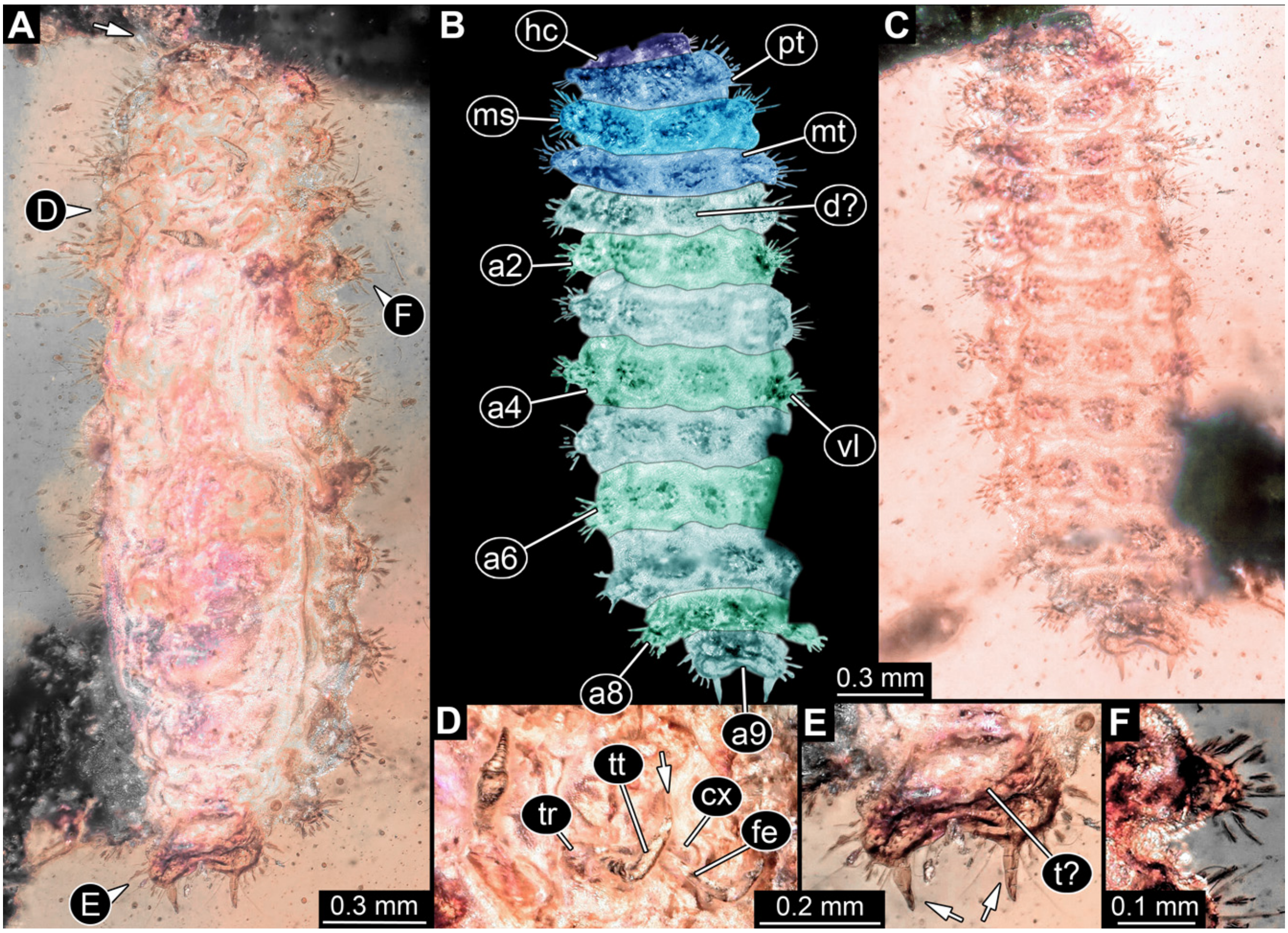

Figure 3.

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.

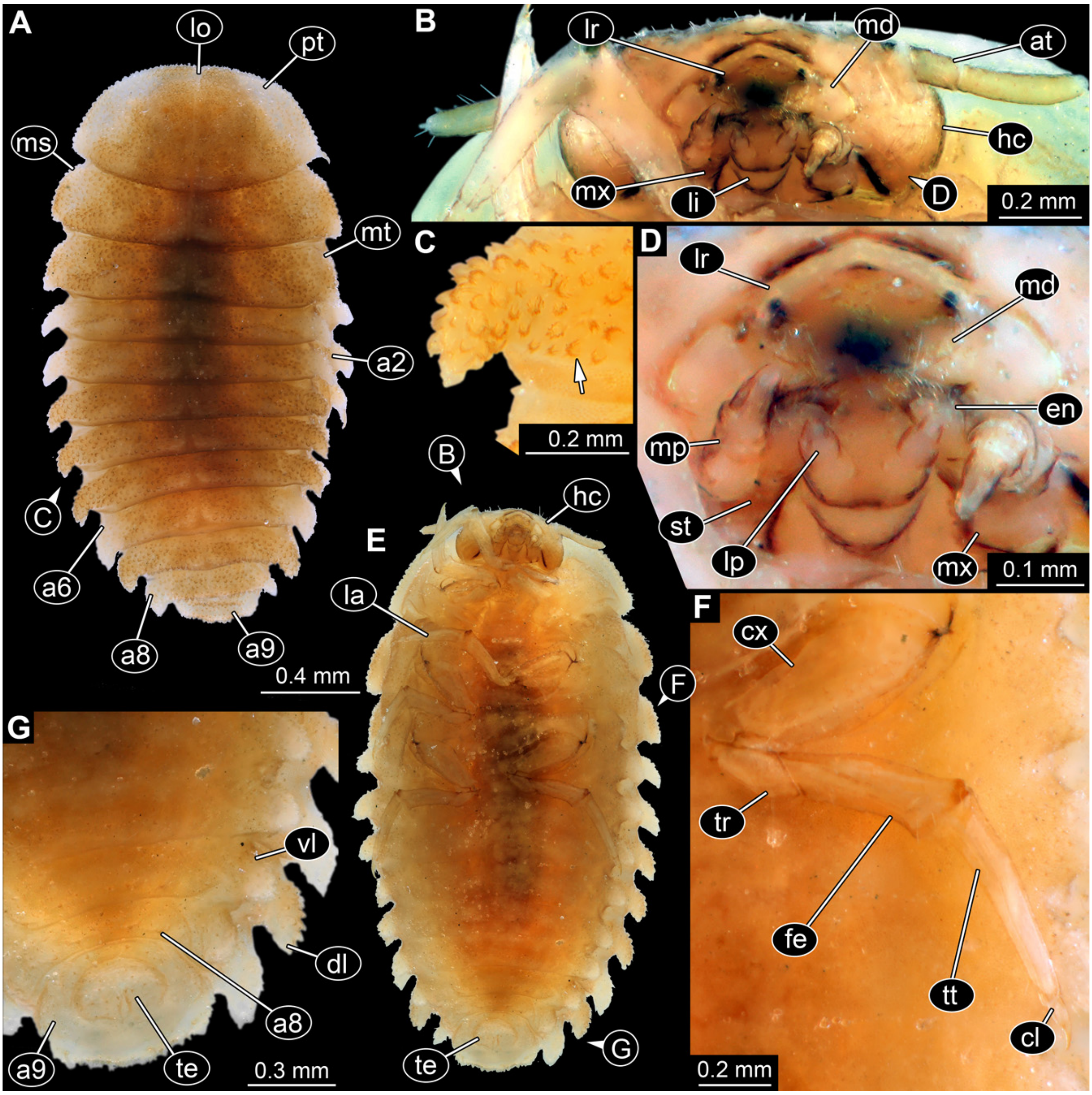

Figure 4.

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.

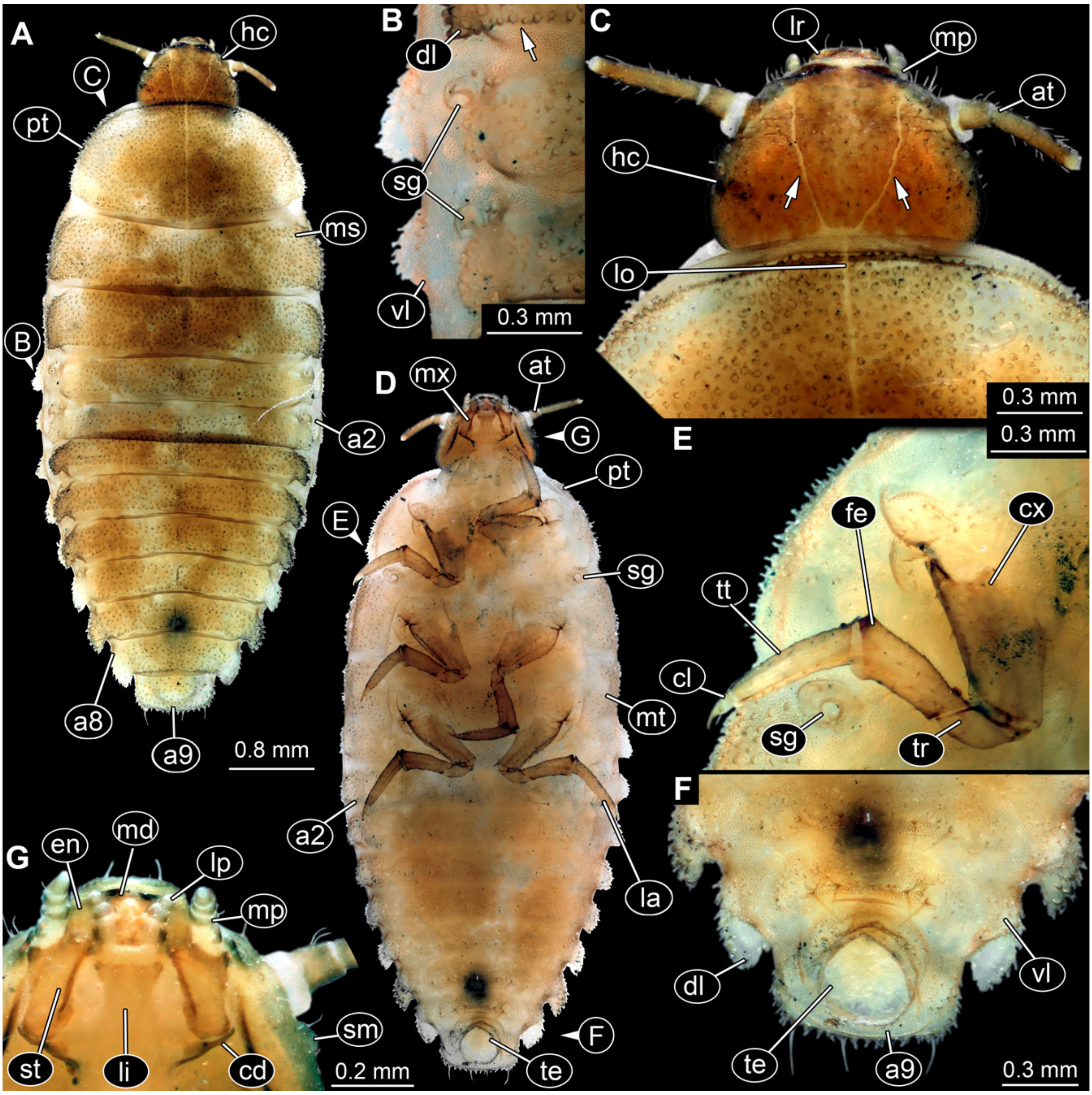

Figure 5.

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.

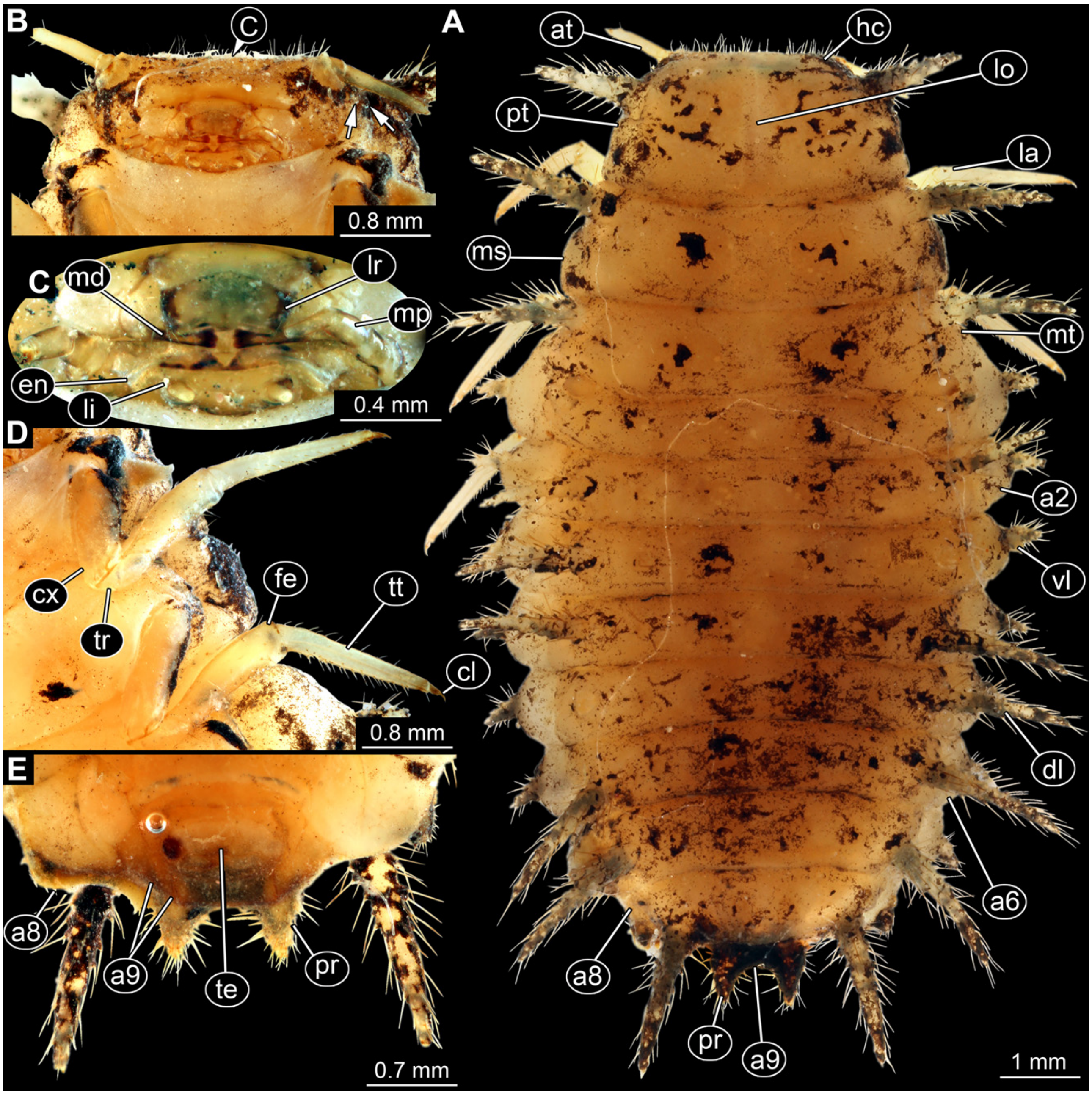

Figure 6.

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.

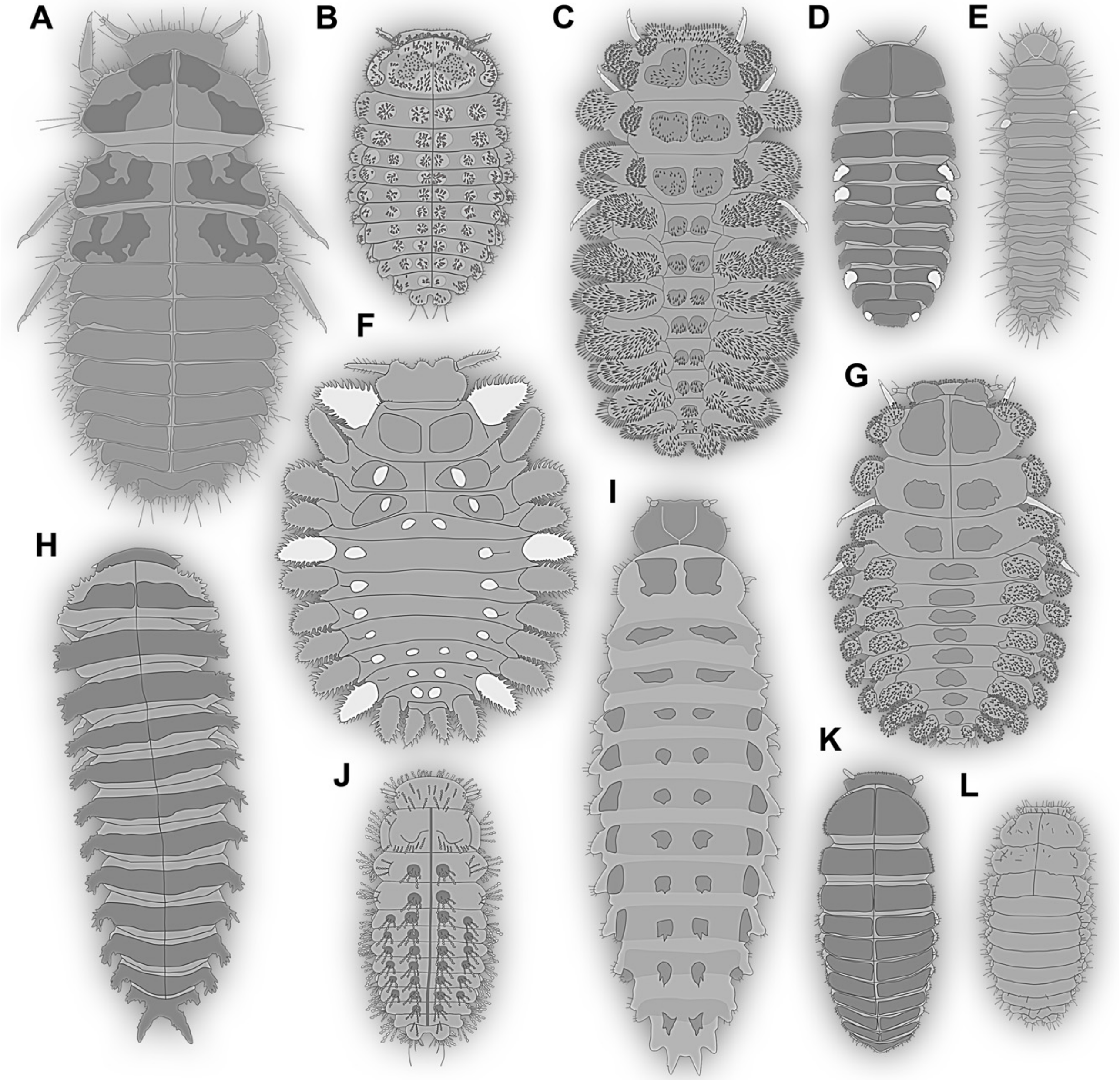

Figure 7.

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 & Pakaluk (1997 fig. 42 p. 74); **B.** *Mycetina cruciata* from Burakowski (1997 fig. 1 p. 210); **C.** *Andrytus* from McHugh & Pakaluk (1997 fig. 1 p. 60); **D.** *Endomychus coccineus* from Tomaszewska & Zaitsev (2012 fig. 29b p. 89); **E.** *Cryptophilus integer* from Ruta et al. (2011 fig. 2 p. 4); **F.** *Amphisternus corallifer* from Yoshitomi & Sogoh (2018 fig. 1 p. 225); **G.** *Epipocus* from McHugh & Pakaluk (1997 fig. 18 p. 66); **H.** *Episcapha morawitzi* from Zaitsev et al. (2016 fig. 23 p. 372); **I.** *Lycoperdina dux* from Tomaszewska & 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 &

Zaitsev (2012 fig. 2 p. 83); **L.** *Mycetina marginalis* from Tomaszewska & Zaitsev (2012 fig. 28c p. 86).

4. DISCUSSION

4.1. *The availability of larvae in amber: rare or forgotten?*

The availability of beetle larvae in amber seems quite limited when researching the literature (Peris & Rust 2020). However, already during the first screenings of the material available in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-University of Munich, Germany, I noticed that among many pieces of amber, quite some bioinclusions were of beetle larvae. To our surprise, many of the larvae were of the groups with high numbers of xylobiont representatives. This was surprising, especially for the wood-boring beetles that have a reputation for being extremely rare in amber (i.e. Bostrichidae, Ptinidae, Curculionidae, Cerambycidae in Cretaceous amber; Peris & Rust 2020). Additional processing of collections in various museums (Naturkundemuseum Stuttgart, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/M., Natural History Museum of Denmark) and specimens from voluntary cooperations with private collectors (Patrick Müller, Christel and Hans-Werner Hoffeins) increased the number of beetle larvae preserved in amber even more. Therefore, I can conclude that the rarity of beetle larvae in the literature is mostly artificial.

Even though there are only several groups with wood-associated representatives described within the scope of this thesis, many more were found and are being processed further (Fig. 2). Possible representatives of wood-associated beetle larvae that I found in different ambers are of the groups:

1) Cupedidae (reticulated beetles, Archostemata) or Micromalthidae (telephone-pole beetles; Archostemata)(Fig. 2B)
2) Buprestidae (jewel beetles or metallic wood-boring beetles; Buprestoidea)(Fig. 2F)
3) Elmidae (riffle beetles; Byrrhoidea)
4) Ptilodactylidae (toe-winged beetles; Byrrhoidea)
5) Brachypsectridae (Texas beetles; Elateroidea)
6) Eucnemidae (false click beetles; Elateroidea)
7) Elateridae (click beetles; Elateroidea)(Fig. 2A)
8) Lycidae (net-winged beetles; Elateroidea)
9) Lampyridae (fireflies; Elateroidea)
10) Cleridae (checkered beetles, Cleroidea)(Fig. 2C)
11) Endomychidae (handsome fungus beetles; Coccinelloidea)
12) Silvanidae (silvan flat bark beetles; Cucujoidea)(Fig. 2H)
13) Mycetophagidae (hairy fungus beetles; Tenebrionoidea)(Fig. 2D)
14) Scraptiidae (false tumbling beetles; Tenebrionoidea)(Fig. 2E)
15) Cerambycidae (long-horn beetles; Chrysomeloidea)
16) Dermestidae (skin beetles; Bostrichoidea)(Fig. 2G)

However, interpreting is very often challenging when it comes to larvae in amber. Pieces of amber have different sets of features depending on the origin. Some pieces of ambers are brittle and break easier, some have more inclusions, and solemn pieces can have grazes, bubbles, and darker oxidized areas concealing the bio-inclusion of interest. These factors in combination with unknown larval representatives of the group in extant fauna make it often impossible to interpret a fossil specimen to the level of species. Nevertheless, such specimens can still, given today´s wide array of methods provide valuable input of at least some informative characters.

During my thesis project, I tried different methods how to achieve the best results that would help us in the interpretation of larval specimens. In some cases, microCT scans and synchrotronCT scans allow us access to concealed details (for example, Haug et al. 2021b: **Article 2**, Zippel et al. 2022c: **Article 3**). In simpler cases where the properties of amber limited the sharpness of

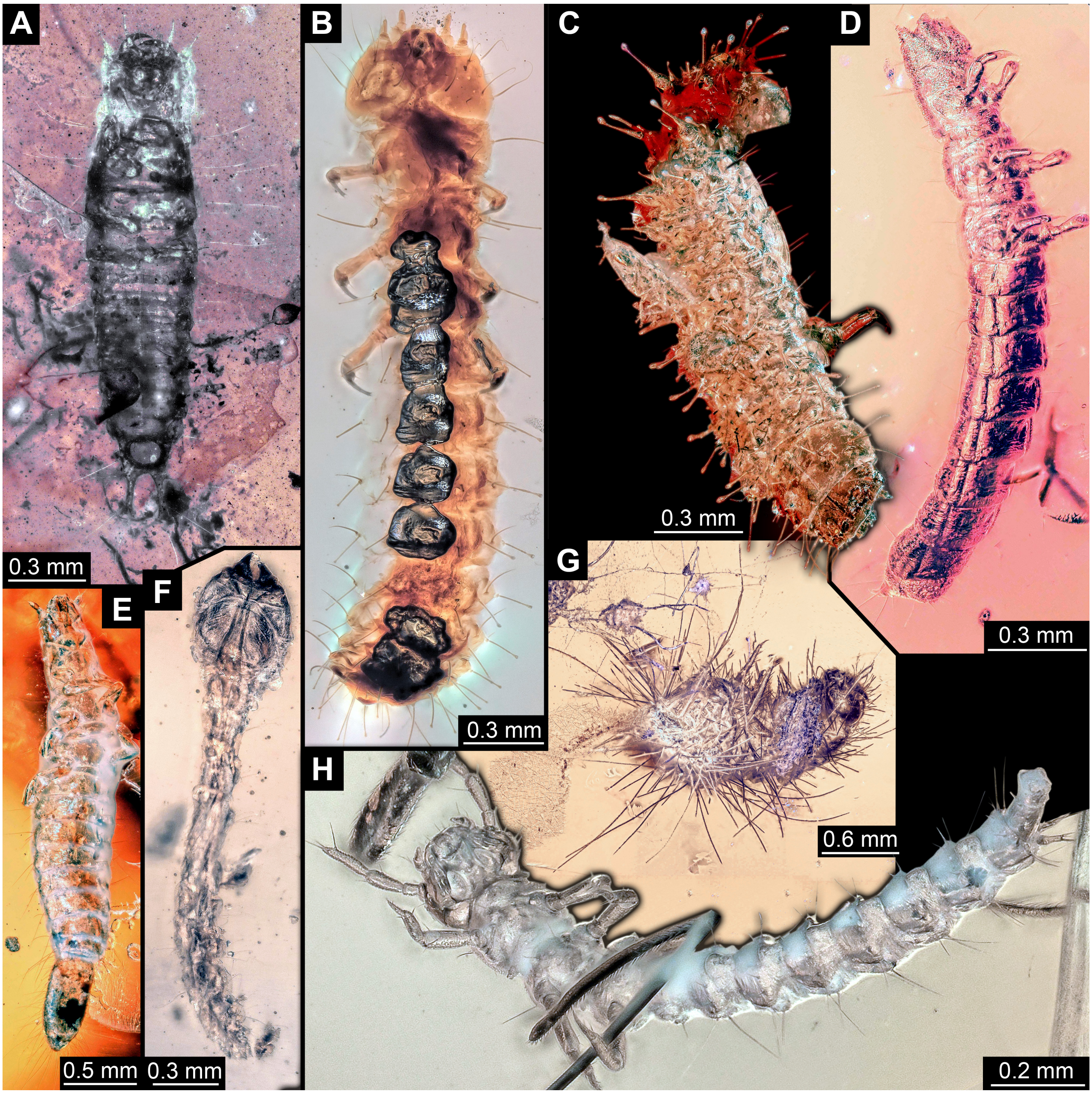

Fig. 2 Diversity of fossil wood-associated beetle larvae within amber. **A.** Larva of Agrypninae (Elateridae) in Cretaceous Kachin amber, dorsal view (PED 0498). **B.** Larva of Archostemata in Eocene Baltic amber, ventral view (PED 1748). **C.** Larva of Cleridae in Eocene Baltic amber, dorso-lateral view (PED 0010). **D.** Larva of Mycetophagidae in Eocene Baltic amber, lateral view (NHMD 153440). **E.** Larva of Scraptiidae in Eocene Baltic amber, ventral view (PED 1478). **F.** Larva of Buprestidae in Cretaceous Kachin amber, dorsal view (PED 1811). **G.** Larva of Dermestidae in Miocene Lausitz amber, dorsal view. **H.** Larva of Silvanidae in Eocene Baltic amber, ventral view (PED 2037). Specimens with the depository number PED are deposited at Palaeo-Evo-Devo Research Group Collection of Arthropods at the Ludwig-Maximilians-Universität München, Germany, and the specimen with the depository number NHMD is deposited in the Amber Collection of the Nature History Museum of Denmark, Copenhagen.

informative characteristics (for example, often small mouth parts), a simple mechanical degradation of material was of help. Additionally, computer software programs (such as Photoshop or ImageJ) that allow playing with colour spectra or saturation were helpful as well. This often resulted in a more informative image (for example, Haug et al. 2021a: **Article 1**, 2022e, Zippel et al. 2022c: **Article 3**). Even a partial find of a fossil larva can be of great importance, for example for a morphometric analysis. Morphometric software, such as SHAPE, enables us to compare biological organs or organisms with a pipeline of programs, for shape aspects and, coupled with that, for functional aspects. This is possible even in cases in which the phylogenetic interpretation remains challenging. With the help of Elliptic Fourier Analysis, it produces a proxy for the shape (resulting in principal components) of informative characters that can be further compared to various parameters. For instance, the stylets and head capsules of lacewing larvae (Haug et al. 2020, 2021c, d, 2022b, f, Zippel & Kiesmüller et al. 2021), body shapes of beetle larvae (Haug et al. 2021a: **Article 1**, b: **Article 2**), shields of crustaceans (Braig et al. 2019, 2023), appendages (Baranov et al. 2022), processes or trunk ends of different groups (Zippel et al. 2022a: **Article 4**). Such analyses already brought new insights into functional biodiversity over time (for example, of lacewings; Haug et al. 2023a). Therefore, 'partial' larvae can still be used for analyses of the shape of certain characters. The presence and diversity of a single character, for example, a mouthpart, compared over time can show us how the occupancy of morphospace changed, indicating changes in ecological functions. In other words, it can show us whether the morphological diversity was greater or smaller in the past (Haug et al. 2023a) and suggest also changes in the diversity of ecological roles.

Therefore, even damaged fossil larvae or the exuviae of larvae (Haug et al. 2021b: **Article 2**), can have a great impact and improve our understanding of the fossil fauna. Therefore, now is a perfect time to start including larvae in science as valuable and ever-present counterparts of adults.

4.2. *Beetle groups with wood-associated larvae*

Wood provides a variety of habitats that differ from each other substantially depending on the state and the position of the wood tissue. The exact anatomy of a tree can differ depending on the group but simplified all trees have several layers: an outer bark, an inner bark also called phloem, a cambium cell layer, sapwood, and heartwood. The outer bark is the tree´s outer insulating protective layer that helps against desiccation, cold, heat, and animals, especially insects. Phloem is a tissue with many pipelines that pass food within the tree. Cambium is the growing part producing new wood (xylem) and bark (phloem). Sapwood is a tissue with many pipelines passing water within the tree, and is also referred to as the 'new wood'. Heartwood is the center of a tree and gives it stability. It is made of old sapwood cells that died therefore often named 'old wood' (Khan 2002). In addition, different wood tissues differ in nutritional quality and other physical properties, such as hardness (Hanks 1999, Möller 2009). In commercial use terms 'softwood' and 'hardwood' differ by the origin of wood, whether it is from conifers or from flowering woody plants. However, in this thesis, the terms 'softwood' and 'hardwood' refer to the actual state of wood that was fed upon and inhabited. Therefore, the term 'softwood' is used for softer woody tissues (such as phloem and cambium between the bark and the wood) and rotting, dying already partially decayed woody tissues, and the term 'hardwood' for the relatively hard, often less nutritional wood (xylem) of often still-living trees.

All of the different parameters are indirectly responsible for a quite versatile beetle fauna within the wood. Most of the taxonomic diversity of wood-feeding beetles is made of species whose representatives feed on subcortical tissues, and the smallest part is represented by few beetle species, whose representatives feed within the woody tissues (Savely 1939, Hanks 1999).

A healthy living tree will have well-coping defence mechanisms to fight off the attack of feeding insects, whether it is physical or chemical (e.g. Klepzig et al. 1996, 2005, Franceschi et al. 2005). Adults of such species often have specialized strategies on how to override the defence of the tree before laying the eggs (e.g. attack the tree on the vulnerable spots or synergize the attack with many conspecific individuals; check Möller 2009). The larvae that feed upon such hardwood with low nutritional value need special traits as well, for example, strong mandibles or special enzymes that cut molecules of polysaccharides (such as cellulose or hemicellulose) into digestible components. Such characteristics may not be needed for living in already partially decomposed soft rotting wood and soft fungus-infested wood. A larva that lives and feeds upon rotting submerged wood will need yet again another set of traits. Therefore, I can assume that wood-associated beetle larvae differ in their morphology when living in hardwood, soft, rotting, fungi-infested wood, or submerged wood. Additionally, an important part of the wood-associated fauna is made of the predaceous larvae of different beetle groups, whether they hunt underneath the bark or within tunnels and galleries made by wood borers.

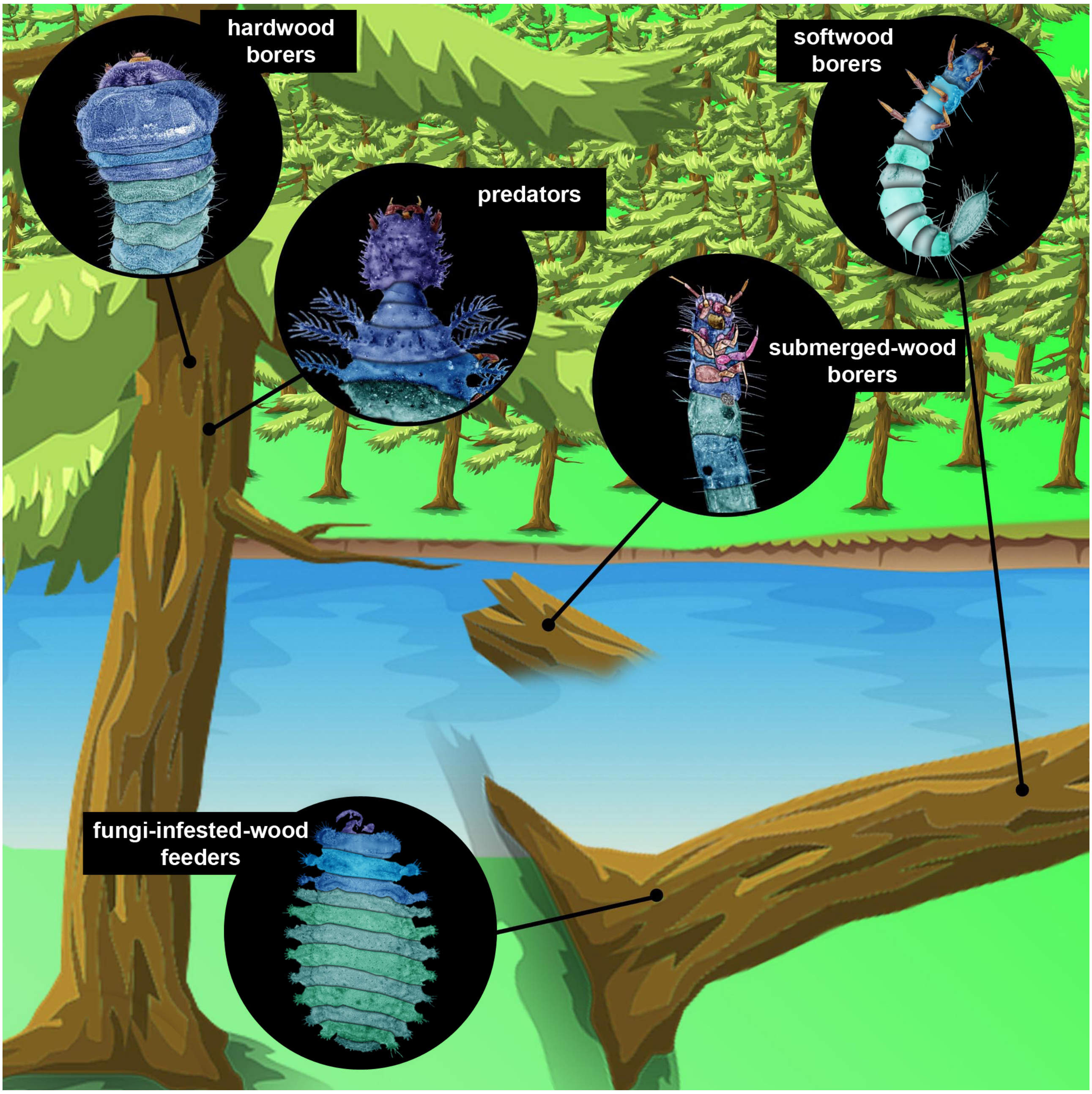

Fig. 3 Diversity of wood-associated groups within fossil ecosystem (adapted after an image from Prof. Dr. J.T. Haug).

Therefore, I recognize five major groups of wood-associated beetle larvae (Fig. 3), extant and fossil, that differ based on their feeding preferences:

1) hardwood borers
2) softwood borers
3) fungi-infested-wood feeders
4) submerged-wood borers
5) predators.

4.2.1. Hardwood-boring beetle larvae

In extant fauna, the hardwood boring larvae are represented, for example, within the groups of Buprestidae (jewel beetles) (Fig. 4A) and Cerambycidae (longhorn beetles) (Fig. 4C). The larvae of Scolytinae (Curculionidae) (Fig. 4B) are not strictly bound to softer wood, but can also be found in living hardwood and the occupation of different types of wood is species related. For example, the species of Scolytinae that grow ambrosia fungi can afford boring deeper into the less nourishing wood while mostly feeding on fungi (Jordal 2014).

The larval representatives of Platypodinae (Curculionidae) are also found within the hardwood but just like some larvae of Scolytinae, they also raise and feed upon ambrosia fungi. Therefore, representatives of both Scolytinae and Platypodinae that actively cultivate fungi (some representatives of Ascomycota) for their feeding are addressed with the term ambrosia beetles. In both cases, the adults of ambrosia beetles excavate the galleries before laying eggs and sometimes nourish the young larvae.

In modern woods, ambrosia beetles represent a generally recognized threat due to their ability to override the defence mechanisms of healthy trees (Jordal 2014). Mass occurrences can cause death of trees on a large scale, even killing entire forests. Even though adults of Scolytinae are already known from Cretaceous Lebanese and Kachin amber (Cognato et al. 2009, Kirejtshuk et al. 2009), the adult fossils of Scolytinae are mostly known from Eocene and Miocene deposits (Peris et al. 2021). The adult representatives of Platypodinae are mostly known from the Miocene (Peris et al. 2021). In Miocene Mexican and Dominican ambers, beetles of Scolytinae and Platypodinae were found in such large numbers (Bright & Poinar 1994, Peris et al. 2015) that their notorious wood-boring activity was interpreted as the main cause of resin production in Miocene amber forests (Peris & Rust 2020).

Another beetle ingroup with larvae that bore into hardwood is Lymexylidae (Fig. 5G). The adults lay the eggs with their long ovipositor under the bark or in bark crevices of weak and sick still-living trees. The first-stage larvae bore galleries into the wood and line them with fungi that they also feed upon (Peris et al. 2021). Interestingly, the larvae of some ingroups actively remove frass from their tunnels with a specialized heavily sclerotized trunk end forming a distinct plate or posteriorly drawn-out process (supposedly part of the abdomen tergite 9)(Fig. 5L). They also use it for closing the entrance to the tunnels (Lawrence 2005d, fig. 8.3.).

The extant hardwood boring larvae of Buprestidae and Cerambycidae are most easily recognized due to their 'simplified' soft bodies with enlarged prothoraxes (Fig. 4A, C, Bellamy & Volkovitsh 2005, Svácha & Lawrence 2014b, Haug et al. 2021a: **Article 1**, early view a). Additionally, a well-sclerotized head capsule, often retracted in the prothorax, with very strong mandibles is discernible (Fig. 4H, K). Legs are mostly short, often having reduced elements, or are completely absent (Bellamy 2003, Bellamy & Volkovitsh 2005, Svácha & Lawrence 2014b). Such specializations in body shape, legs, and setae remind us of the characteristics known from endoparasites (Chiappini & Nicoli Aldini 2011). The larvae, so-called flatheaded borers (Buprestidae) and roundheaded borers (Cerambycidae), are mostly unable to live outside of the wood and can be regarded as obligatory wood inhabitants. Additionally, living trees can suffer great damage from the feeding modus of such larvae, especially if inhabited by larvae of species with high invasive potential (Svácha & Lawrence 2014b). Therefore, the hardwood boring larvae of both Buprestidae and Cermabycidae could easily be referred to as 'plant parasites' (Haug et al. 2021a: **Article 1**). 'Plant parasitism' is a term that is not often used in entomology for a relationship between an insect and a plant (*e.g.*, Labandeira & Li 2021). Nevertheless, in studies about nematodes 'plant parasitism' seems widespread (Bongers et al. 1997, Kumar & Yadav 2020, Topalović et al. 2020).

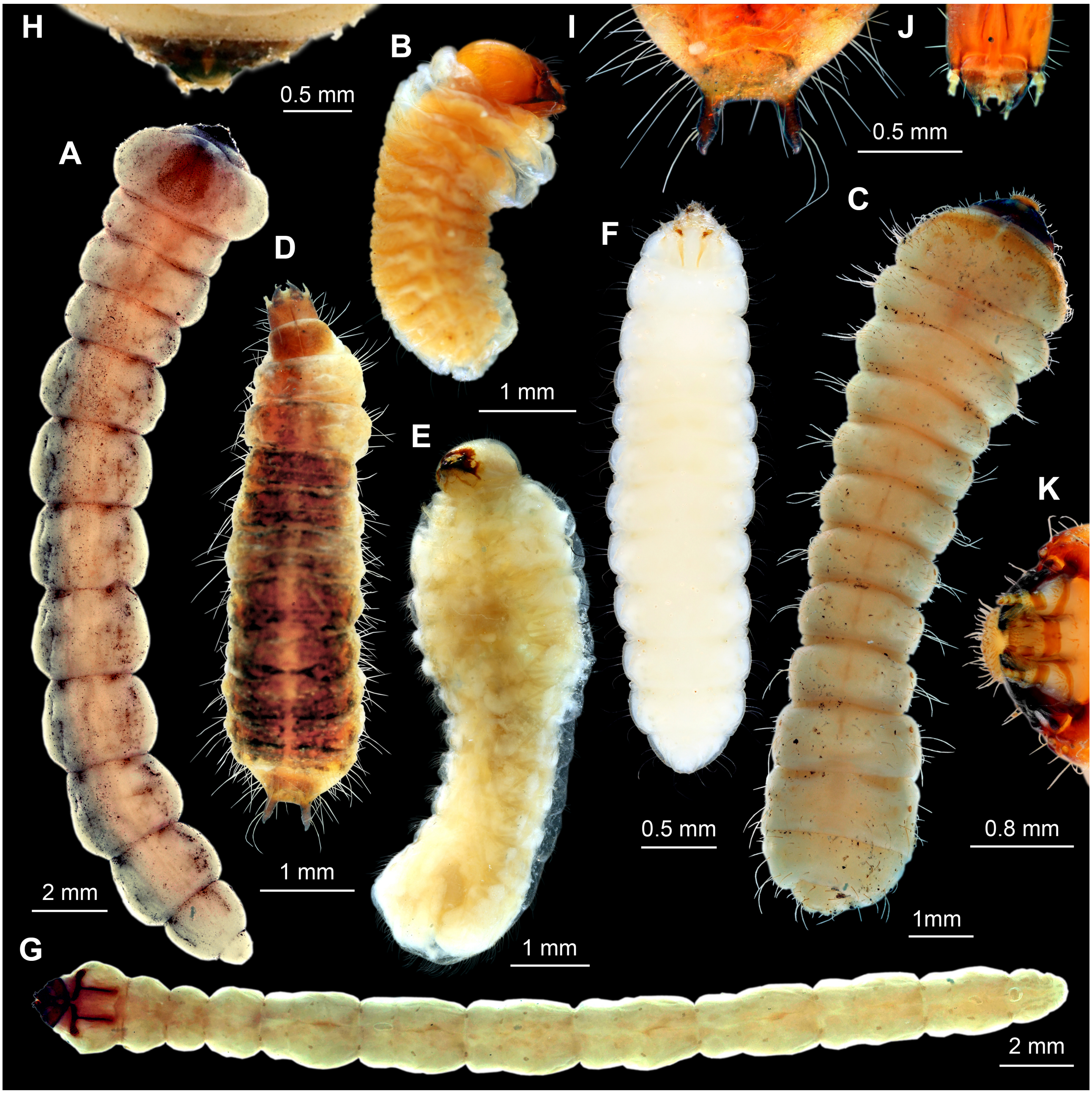

Fig. 4 Extant representatives of wood-associated beetle larvae from the Coleoptera collection of Nature History Museum Denmark, Copenhagen. **A.–G.** Overwievs. **H.–K.** Close-ups. **A.** *Phaenops cyaneus* (Buprestidae). **B.** *Hyastes cunicularius* (Scolytinae, Curculionidae). **C.** *Oplosia cinerea* (Cerambycidae). **D.** *Necrobia ruficollis* (Cleridae). **E.** *Anobium costatum* (Anobiinae, Ptinidae). **F.** *Trixagus meybohmi* (Throscidae). **G.** *Melasis buprestoides* (Eucnemidae). **H.** Head of larva of *Phaenops cyaneus*, dorsal view. **I.** Trunk end of larva of *Necrobia ruficollis*, ventral view. **J.** Head of larva of *Necrobia ruficollis*, ventral view. **K.** Head of larva of *Oplosia cinerea*, ventral view.

Interestingly, some larvae of Eucnemidae bore into hardwood, as well (*Melasis, Isorhipis, Nematodes, Hylochares*; Muona & Teravainen 2008, 2020). Larvae of these groups show quite some similar features to flatheaded and roundheaded borers, such as strong, large mandibles, enlarged segments of thorax with strong muscles, reduced legs, and gripping surface structures (Fig. 4G, Muona & Teravainen 2008).

The larvae that develop in hardwood often share certain characteristics, such as chisel-like strong mandibles, often a head capsule that is retracted into the thorax, cylindrical or sub-cylindrical cross-section of the body, poorly sclerotized cuticle, slightly enlarged pro- and sometimes mesothorax giving them the 'buprestiform' shape of the body, and lack or strong reduction of legs (Jordal 2014, Gimmel & Ferro 2018).

However, did all of these characteristics already exist in fossil larvae of these groups? Are there any hardwood-boring larvae preserved in amber? As I hypothesized, the fossil hardwood boring larvae are not only 'anecdotally' found in amber (Haug et al. 2021a: **Article 1**, early view a, Zippel et al. 2023b: **Article 6**). Even more so, I would dare to say that they are relatively abundant compared to some other groups of animals. During only two and half years, I found in different ambers more than twenty specimens of fossilized larvae with hardwood borers' characteristics (i.e. Haug et al. 2021a: **Article 1**, Zippel et al. 2023b: **Article 6**, Fig. 2F).

The fossil larvae of Buprestidae (Fig. 2F) and Cerambycidae were easily recognized by the enlarged prothorax segments. A darker head region, sometimes with massive heavily sclerotized mandibles, was often discernible, as well. Among these fossil larvae, at least two specimens had relatively long legs (PED 0816 and PED 1130; Haug et al. 2021a: **Article 1**), a characteristic rarely seen in extant specimens. For example, in some late stages of roundheaded borers of Lepturinae (Svácha & Lawrence 2014b, fig. 2.4.20.P). However, the long legs in this group seem to be a derived character (Svácha & Lawrence 2005).

Interestingly, when plotting the results of SHAPE analysis, the body outlines of two fossil specimens with legs plotted (Haug et al. 2021a: **Article 1**; fig. 7; PED 0816 under the number 0501, and PED 1130 under the number 0502) wide apart from each other but also relatively far from the morphospace occupied by the larvae of Cerambycidae. In both cases, specimens plotted relatively close to the borders of the morphospace of larvae of Buprestidae. Considering that the differences between the two specimens with longer legs are substantial, it is not very likely that they both represent fossil larvae of Lepturinae. Additionally, only the later stages of the modern larvae of Cerambycidae have such long legs. In comparison to later stages of modern wood-boring larvae, our specimens were relatively small-sized. Therefore, it does not seem as if they were later stages of larvae.

It is possible that representatives of an extinct sister group of either Cerambycidae or Buprestidae had this character pronounced and that these fossils represent an extinct transitional type of hardwood-boring morphology. Such intermediate morphological types, so-called 'chimeras', are already known from other insect groups (Haug et al. 2019, Baranov et al. 2020).

The fossil larva of Eucnemidae (Zippel et al. 2023b: **Article 6**) that colleagues and I described from Kachin amber also shows a mixture of characters and a morphology not known from the modern fauna. As mentioned, hardwood-boring larvae of Eucnemidae show typical enlargement of prothorax, as well. However, the fossil specimen BUB 3710 has in addition to the enlarged prothorax also the enlarged mesothorax. It has characters that modern hardwood-boring larvae of Eucnemidae do not possess, such as jagged lateral sides of the head and paired setal fields. These characteristics and additional small areoles are mostly present in larvae that bore in the rotten softwood (Leiler 1976).

Similar morphologies of certain characters seen in fossil and modern larvae of Buprestidae and Cerambycidae speak for the similar lifestyle (for example strong opposing chisel-like mandibles). Such finds of larvae are extremely important because finds of adults of these groups do not necessarily automatically imply that the fossil larvae of the groups looked like extant larval representatives or that larvae had the same lifestyle at the time of entrapment of an adult. In addition, the fossilized wood-boring traces in mineralized wood, such as preserved host tissue damage or fossilized faecal pellets, can help us conclude how the extinct larvae exploited plant resources. Sometimes even the gut content in fossils can be of help (Labandeira & Sepkoski 1993). Indeed, fossilized wood with tunnels of hardwood borers has been found and supports furthermore that the hardwood-boring lifestyle was present in these groups (Feng et al. 2017, 2019).

For the fossil larva of Eucnemidae, we cannot imply with certainty that they also led the same lifestyle. On one hand, the 'buprestiform' shape of the body, lack of legs, and bifid structures (serving probably for gripping) speak for such an interpretation. On the other hand, the jagged head, not very large mandibles, and paired setal fields known from 'softwood' larvae speak for the life within the softer rotting wood. This mixture of characteristics in the larva implies a question about the host tree, and whether it is still known today. Possibly, the wood of the host tree was somewhat softer than the wood of the host trees today. Even though the Cretaceous flora and fauna already comprised some extant groups they still differed from the modern ones greatly. Therefore, it is possible that a tree with wood, that this larva with its morphology was specialized to, became extinct. If this highly specialized 'chimera' larval type was only specialized for a single host species that went extinct, it is possible that this larval type stopped existing as well. It is also possible that the fossil larva represents a larval stage that was boring from outer softer layers of wood into the hardwood and therefore needed specializations for both environments. Such an explanation would be supported by the life cycle of some extant representatives that have different life stages developing in different types of wood (e.g. larvae of *Fornax* and *Nematodes*; Muona & Teravainen 2008, or larvae of *Eucnemis*; Muona & Teravainen 2020).

4.2.2. Softwood-boring beetle larvae

The decomposition of wood is a process that involves both abiotic and biotic factors. From the biotic factors, the effects of microorganisms such as bacteria and fungi mostly influence the decay. Such a process mostly starts in unprotected areas that are exposed to abiotic factors and easily approachable to microorganisms (e.g. wounds or surfaces without a bark). The decomposition of wood happens gradually, with different parts of wood being in different states of decomposition. The area under the bark is especially rich in nutrients, relatively soft, and often within reach, therefore, an attractive habitat for macroorganisms such as the larvae of insects.

Some modern beetle larvae also feed on the bark itself or the outer layers of sapwood, for example, some larvae of Ptinidae (some representatives of Anobiinae, see Fig. 4E) (Philips & Bell 2005). Other larval representatives of softwood borers can be found in various stages of decaying wood (Hayashi 1980) and enhance the decomposition process with their saprophagous activities (e.g. larvae of Passalidae, Lucanidae, Aderidae). Depending on the part of the wood they occupy the shape of the body differs. As already mentioned, the wood borers are typically cylindrical or sub-cylindrical in cross-section and the specialized groups living under the bark are dorso-ventrally flattened (Gimmel & Ferro 2018).

The exploitation of rotting wood as a lifestyle is also present within the group of Archostemata. The few known larvae of its ingroups Micromalthidae and Ommatidae spend their life cycles within the rotting wood. There is a scarce fossil record of these larvae and the fossil specimen PED 1748 (Fig. 2B) is a valuable addition to it. The body of the specimen is slightly dorso-ventrally flattened with a prognathous head. This character is well-known from predaceous larvae but also from the wood-feeding larvae, where the forward-orientated mouth parts facilitate the boring of the woody substrate (Labandeira 1997). Additionally, the extant larvae have a strong thick inner medial area (i.e. ridge) of the head capsule. In this way, strong muscles have enough attachment area to inflict a strong bite into the wood. The fossil larva also has a triangular end of the trunk with a posterior heavily sclerotized tip. The sclerotized tip possibly had the same function as the urogomphi of larvae of Eucnemidae, helping them move backward through a dense substrate.

Another group with larvae exhibiting similar morphology of the trunk end is Mordellidae (Zippel et al. 2022b: **Article 5**, fig. 1). Some larvae of Mordellidae are known to bore in soft decaying wood (Zemoglyadchuk & Buialskaya 2020) and even into soft but compact woody substrates (Lawrence 1991, Lisberg & Young 2003). Another larva with the trunk end having a posterior medial sclerotized tip was interpreted in Zippel et al. (2022b: **Article 5**) as a fossil larva of Mordellidae. However, this publication raised several different opinions that the larva is not a larva of a beetle but more so a larva of a hymenopteran (Batelka & Engel 2022, Rasnitsyn & Müller 2023). Indeed, there are larval representatives of certain ingroups and certain life stages of Hymenoptera without obvious abdomen parapodia (e.g. Pamphiliidae, Blasticotomidae) that exhibit similarities with the morphology of the fossil larva from Zippel et al. (2022b: **Article 5**). However, both the extant larvae of Pamphiliidae and fossil representatives of Blasticotomidae show differences, as well (as pointed out by Rasnitsyn & Müller 2023). Since this fossil is preserved in Cretaceous Kachin amber, it is very likely that it is an extinct representative of a group unknown from modern fauna. Disregarding the identity of the larva, it is still very likely that the ecological role of the larva was similar to the ecological role of the modern larvae of Mordellidae, hence being a borer, as suggested by Zippel et al. (2022b: **Article 5**) and Rasnitsyn & Müller (2023).

Even though some representatives can bore into compact woody substrates of softer wood species (Lawrence 1991, Lisberg & Young 2003), the larvae of the softwood borers are mostly associated with rotting wood. The larvae of extant Pythidae (Fig. 5E), Prostomidae, Zopheridae, or, more rarely, Pyrochroidae also live within soft decaying wood and have heavily sclerotized urogomphi at the abdomen segment 9 (Fig. 5I).

The larvae of Scraptiidae also spend their larval development within decaying wood (Crowson 1955, Hayashi 1962, Vanin et al. 1996) where they take part in carbon cycling. Some larvae of Scraptiidae (Scraptiinae) have very prominent processes posteriorly at the trunk end. The exact function of this bulbous process is still not exactly clear but self-defence by autotomy (Švácha 1995) and connection to the saproxylic lifestyle of these larvae (Haug & Haug 2019) have been suggested. The fossil record of these larvae was significantly increased lately (Haug & Haug 2019, Zippel et al. 2022a: **Article 4**). Among the fossils, the first finds from the Cretaceous Kachin amber were reported, as well (Zippel et al. 2022a: **Article 4**; fig. PED 0483 and PED 1108). The reported fossils had bulbous trunk ends that differed in shape, especially the trunk ends of Cretaceous specimens (more triangular). The SHAPE analysis of the trunk ends explained most of the variance was influenced by the length and the shape of the anterior part of the trunk end. Whether the length and shape of the trunk end correlate to the differences in habitat or are species-related or stage-related is still unclear. Therefore, our study (Zippel et al. 2022a: **Article 4**) not only reports such a larva-type from the Cretaceous for the first time but also confirms that a heart-shaped posterior part of the trunk end, as seen in the larva PED 0006 from Haug & Haug (2019) and the new specimen SNSB-BSPG 2018 III 232 (Zippel et al. 2022a: **Article 4**), is not an artefact. Whether the diversity of the trunk ends changed over time is still not clear due to the lack of extant specimens of different larval stages.

Another case of 'chimera' was also reported from Kachin amber including a larva with trilobite-beetle-like processes (Haug et al. early view b: **Article 7**). The modern larvae of Lycidae are found in soft dead wood where they pass through decayed parts and crevices and feed on juices from decaying wood (Bocak & Matsuda 2003, Bocak & Boackova 2005). Even though we expect inhabitants of decomposing trees to have lived close to the source of the resin and therefore would be easily engulfed in it, no unequivocal fossil record of larvae of Lycidae exists. However, the adults are known from the Cretaceous ambers, and the reported specimen BUB 3989 from Kachin amber shares many characters with the modern type of trilobite-like larvae. Nevertheless, processes of this kind are seen in larvae of several ingroups of Elateroidea (e.g. Lampyridae, Cantharidae) and are probably the result of convergent evolution. This fossil may represent a larva of the extinct sister group or an early offshoot of Elateroidea.

In addition, many other larvae of beetles live a saproxylic way of life [e.g. larvae of Oedemeridae (Fig. 5C), Callirhipidae, Lophocateridae, Phloeostichidae, Synchroidae, Stenotracheliade, Trictenotomidae, some larve of Hybosoridae, Scarabaeidae, some larvae of Ptinidae (Fig. 4E), Oxypeltidae, Priasilphidae, Throscidae (Fig. 4F), and Tenebrionidae; Yensen 1980, Philips & Bell 2005]. Gimmel & Ferro (2018) estimated that more than half of all major beetle groups have at least one species with representatives leading a saproxylic lifestyle, making it one of the most common ways of life among extant beetles (Gimmel & Ferro 2018). Peris and Rust (2020) report that more than half of all inclusions within the Cretaceous amber are the saproxylic beetles (based on studies by Peris et al. 2016 and Ross 2019 where mostly, but not only, adult specimens were considered). Therefore, they suggest that the proportion of saproxylic groups in the Cretaceous resembled the proportion of these groups in the modern fauna. However, for a clear assessment of the proportion of softwood-feeding groups in the past the accessibility of mouthparts is crucial. Unfortunately, many specimens in amber do not have these structures discernible, either due to bad preservation, Verlumung, grazes, bubbles, syn-inclusions, or other properties of the amber pieces.

4.2.3. Fungi-infested-wood-feeding beetle larvae

Many beetle larvae feed on fungi and fungi-infested wood (Stehr 1991, Ingham 1992). However, the feeding range of the fungus-feeding larvae often overlaps with one of the larvae that feed upon soft woody tissues (Peris & Rust 2020). Many different fungi and moulds take part in the process of rotting and decomposing dying or dead wood (Fukasawa & Matsukura 2021). There they get intertwined with the wood tissues that some larvae feed upon (Peris & Rust 2020). Therefore, there is no clear line between softwood feeders and fungus feeders, and many groups with representatives feeding on fungi, often have representatives feeding on mixed substrates of softwood and fungi e.g. Ptinidae; Philips & Bell 2005). Köhler (2000) described that representatives of fungus-feeding species tend to have smaller body sizes than representatives of dead wood-feeding species. He also noted that the species that feed on both wood and fungi are of intermediate size.

The fungus-feeders are represented by extremely morphologically diverse larvae in the modern fauna and were already very diverse in the past (Lobanov 2008, Peris & Rust 2020). It seems that fungivorous species dominate among the saproxylic specimens in Spanish amber from the Cretaceous (Peris & Rust 2019). This is not surprising since it was assumed that fungal feeding preceded feeding on plant tissues in beetles (McKenna et al. 2015, 2019, Peris 2020). In some modern representatives of Archostemata (Cupedidae), the larvae feed upon fungi-infested softwood, as well (Hörnschemeyer 2005). Therefore, possibly the same feeding strategy was present in the early larvae of this group. Among adephagan beetles, only some ground beetles (Carabidae: Rhysodinae) feed on moulds and fungi-infested rotting wood. Larvae of Polyphaga commonly feed on fungi. Some larval representatives of Agyrtidae, Eucinetidae, Clambidae, Cerophytidae, and Eucnemidae also feed upon rotting wood infested with fungi. Representatives of Dermestidae (Fig. 5F) are usually scavengers (both adults and larvae) on animal and plant matter and quite some are associated with nests of bees, butterflies, and wasps, but also bird nests and mammal burrows. However, larvae of species of *Orphilus* prefer dry dead fungi-infested wood (Paulian 1942, Lawrence & Ślipiński 2005). Motyka et al. (2022) suggested that feeding on fungi is an ancestral feeding strategy that was shared with a common ancestor with Endecatomidae and stayed retained only within Orphilinae. The fossil record of Dermestidae is relatively abundant (especially from Cenozoic Baltic and Dominican ambers and deposits of Europe and North America; Háva & Prokop 2004, Fig. 2G), with the oldest fossil specimens of elytra from Late Triassic and Early Jurassic deposits (Dunstan 1923) and the first well-preserved fossil from Middle Jurassic Jiulongshan Formation, China (Deng et al. 2017). Interestingly, a single fossil from the Early Oligocene of Florissant, Colorado, USA has been interpreted as a representative of *Orphilus* (Wickham 1912, Háva & Prokop 2004). Most of the fossils of Dermastidae are adults, and only few fossil larvae are known, for example, the larvae of *Trogoderma* from Baltic amber (Háva et al. 2006).

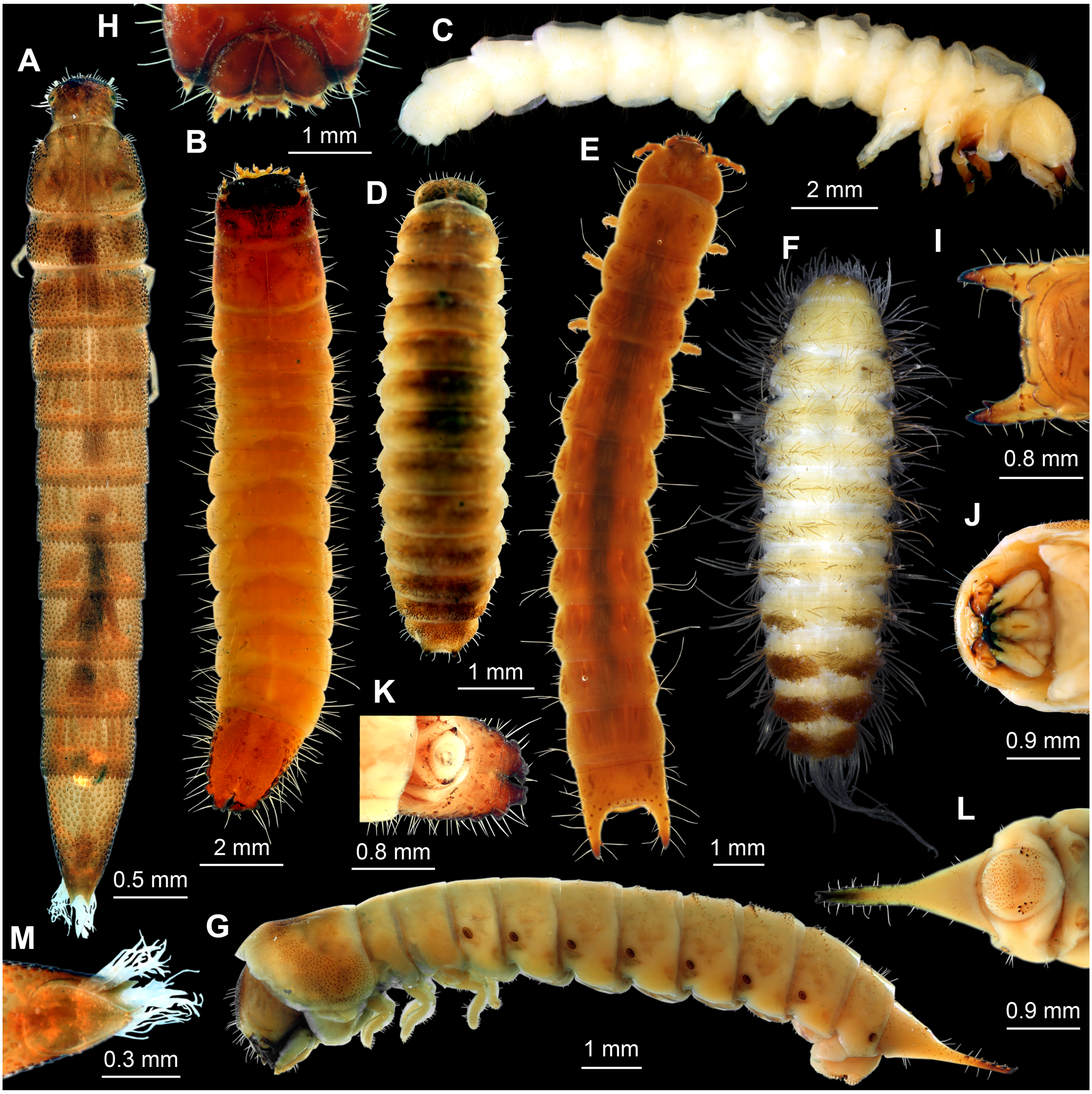

Fig. 5 Extant representatives of wood-associated beetle larvae from the Coleoptera collection of Nature History Museum Denmark, Copenhagen. **A.–G.** Overwievs. **H.–M.** Close-ups. **A.** *Limnius volckmari* (Elmidae). **B.** *Agrypnus murinus* (Elateridae). **C.** *Nacerda melanura* (Oedemeridae). **D.** *Tritoma bipustulata* (Erotylidae). **E.** *Pytho depressus* (Pythidae). **F.** Larva of Dermestidae. **G.** *Hylecoetus dermestoides* (Lymexylidae). **H.** Head of larva of *Agrypnus murinus*, ventral view. **I.** Trunk end of larva of *Pytho depressus*, ventral view. **J.** Head of larva of *Hylecoetus dermestoides*, ventral view. **K.** Trunk end of larva of *Agrypnus murinus*, ventral view. **L.** Trunk end of *Hylecoetus dermestoides*, ventral view. **M.** Trunk end of larva of *Limnius volckmari*, ventral view.

Many groups with fungus-feeding larvae are represented within Cucujiformia in the modern fauna (Leschen et al. 2005, Leschen & Ślipiński 2005). For example, larvae of Lymexylidae (Fig. 5G), Trogossitidae, Biphyllidae, Erotylidae, Monotomidae, Hobartiidae, Cryptophagidae, Priasilphidae, Phloeostichidae, Silvanidae, Nitidulidae, Cerylonidae, Endomychidae, Discolomatidae, Corylophidae, Mycetophagidae, Ciidae, Tetratomidae, Melandryidae, Ulodidae, Tenebrionidae, Mycteridae, Pyrochoridae, Salpingidae, Anthicidae, Brentidae and previously mentioned Scolytinae and Platypodinae (Fig. 4B, Zippel et al. in review b: **Article 9**).

Considering the morphological characters of the fungi-feeding larvae, there are differences often related to the stage of decomposition or the layer of the wood that they feed in. The fungus feeders that feed within crevices of softwood tend to have more cylindrical (Fig. 5D, G) and only slightly dorso-ventrally flattened bodies, whereas the fungus feeders that live under the bark have relatively small and very dorso-ventrally compressed bodies (e.g. Priasilphidae, Discolomatidae, Erotylidae, Cerylonidae, Endomychidae), as already reported by Gimmel and Ferro (2018) and Peris and Rust (2020). In addition, in the larvae of Cucujiformia tergites are often drawn out into lateral processes giving the larvae an oval body outline (e.g. Discolomatidae, Endomychidae). Considering that such processes are present relatively often within this group, the described type of habitus may represent an ancestral condition. However, it is also very likely that the similar habitus developed several times independently as a result of the convergent evolution due to the similar selective pressures in a similar habitat (see Haug et al. early view b: **Article 7**).

Another character of some fungus feeders is the specialized mandible. For example, in larvae feeding upon small fungal particles, such as spores or loose hyphae, mandibles bear small teeth-like structures used for grinding spores or hairs for brushing off these fungal tissues, or spoon-shaped mandibles that help collect spores as seen in larvae of *Hylecoetus dermestoides* (Fig. 5J). A very specialized case of mouth parts used for feeding on fungi or slime moulds can be observed in some larvae of Ceryloninae (Cerylonidae; minute bark beetles). The larvae have stylet-like mandibles that are in some ingroups (*Philothermus, Mychocerus*) enclosed within a 'beak' (Costa et al. 1996, Ślipiński & Lawrence 2005). The larvae were observed on slime moulds, under tree bark, and within the tunnels of wood-boring beetles, where they presumably feed on ambrosia fungi (Ślipiński & Lawrence 2005). The exact way of feeding of these larvae is still uncertain but could be similar to the feeding of some adult fungi-feeding beetles that exhibit similar morphology of the mouth parts (e.g. 'beaks' of adults of Corylophidae, Leiodidae and Eucinetidae). For example, some adults of Corylophidae insert their prolonged mouth parts in the pore tubes of fungi and feed on undetached spores (Ślipiński et al. 2005). Such specialized mouth parts in larvae are not a new invention. Haug et al. (2020b, 2022f) interpreted two mysterious larvae with similar cone-shaped 'beaks' from ~100-million-year-old Kachin amber.

Many wood-associated fungus-feeding larvae often exhibit urogomphi (short processes at the posterior end of the abdomen) pointing dorsally. Such processes help move backwards in narrow spaces (Lawrence et al. 2011). Additionally, the body surface often bears many setae of various sizes and shapes (e.g. scale-like)(Leschen et al. 2005). Sometimes these are used for holding debris, which helps in camouflaging. Cloaking as a defence mechanism is already known from some larvae of Endomychidae (Leschen & Carlton 1993, Tomaszewska 2005). Some females of Endomychidae even cloak their eggs with hyphae to protect them (Leschen 1994).

Many fossil larval representatives of Cucujiformia show similar morphology of dorso-ventrally flattened habitus with processes (Zippel et al. in review b: **Article 9**). As already discussed in the chapter about the hardwood borers, the presence of the same feeding style among the fossil larvae can only be presumed based on the morphological similarities between the fossils and the modern counterparts (mouth parts in particular), fossilized traces of boring activities, or the fossilized fras. Naugolnykh & Ponomarenko (2010) reported tunnel structures in fungus-decayed wood from the Permian. Feng et al. (2017, 2019) described fossilized hardwood with beetle borings and fossilized hyphae, also from the Permian. Therefore, it is possible that beetles already farmed fungi within these tunnels in hardwood. Even though, in such fossils, partial remains of larval mouthparts were found very often, this is not the case here. Specialized structures on mandibles (hairs and small teeth) for feeding on fungal spores or small hyphae, were not accessible in the fossils.

Unfortunately, the body shape sometimes only reveals in what kind of habitat the larvae lived, not necessarily the type of food they ate, and therefore one must be careful with conclusions. For example, in some lineages of Coccinellidae, larvae secondarily developed predatory lifestyles, yet the habitus of some still resembles, for example, the fungus-feeding larvae of Endomychidae (Ślipiński & Tomaszewska 2005, their fig. 10.33.7. vs. Zippel et al. in review b: **Article 9**).

4.2.4. Submerged-wood-boring beetle larvae

Some beetles spend their entire lives or at least some life stages in water. Some of these aquatic larvae are predaceous (Peterson 1951), but there is also a number of xylobiont specialists living on or in submerged wood (Cranston & McKie 2006, Möller 2009). Wood within streams and other bodies of water provides an abundant source of carbon that has a significant role in energy flow and nutrient dynamics. This has further a role in shaping of the biotic communities (Dudley & Anderson 1982, and the references within, Cranston & McKie 2006). Submerged wood provides a large number of protected habitats and can be used for attachment, oviposition, as a refuge, e.g. for pupation, or as an emergence site (Hoffmann & Hering 2000). For the species that are obligate xylophages of submerged wood, wood offers many beneficial properties. For example, habitats within the moist wood protect from desiccation, extreme predation, and strong water currents. In addition, the fluctuations in temperature are more stable and therefore protect against freezing. Considering that not many organisms are able to bore into submerged wood and build galleries within, the competition with other animals should not be very strong either (Hoffman & Hering 2000).

Within Polyphaga there are several groups with aquatic larval representatives that feed upon the decaying submerged wood. These groups are Elmidae (Fig. 5A, LeSage & Harper 1976a, Dudley & Anderson 1982, Hoffman & Hering 2000), Lutrochidae (e.g. *Lutrochus germari* and *Stegoelmis* sp.; Brown 1991, Ide et al. 2005, Valente-Neto & Fonseca-Gessner 2011), Psephenidae (e.g. *Mubrianax, Jaechanax*; Lee et al. 2005), Cneoglossidae (Costa et al. 1999, 2005b), Ptilodactylidae (e.g. *Anchytarsus bicolor*; LeSage & Harper 1976b, Lawrence 2005e), and Eulichadidae (e.g. *Eulichas dudgeoni*; Ivie 2005 HoZ). In addition, based on the gut content of the aquatic larvae of *Elodes marginata* it seems that some representatives of Scirtidae (Warmke & Hering 2000) also live as facultative xylophages. Dudley & Anderson (1982) also found that both adults and the larvae of *Ditylus quadricollis* (Oedemeridae) bore tunnels within submerged logs.

The submerged-wood-boring beetles often have characters not encountered among the terrestrial ones. For example, some adults of xylophagous aquatic species of Elmidae have specially formed mandibles with foveae, a specialization proposed to serve in carrying wood-decomposing organisms (Kodada & Jäch 2005). In larvae, morphological specializations to aquatic and wood habitats are also present. The larvae of Elminae have tracheal areal sacks, which they can use as a tool for buoyancy within the water, strong cuticle, a retractable head, a behaviour that minimizes injuries if they get dislodged, and long legs with strong claws for holding onto the substrate (Fig. 5A, M, Kodada & Jäch 2005). The larvae of Lutrochidae have retractile anal tracheal gills, probably for optimizing oxygen absorption within deep galleries (Valente-Neto & Fonseca-Gessner 2011). The xylophagous larvae of Psephenidae have thick mandibles with distal teeth and more oblong bodies as an adjustment to clinging to narrower submerged twigs and not to stones (Lee et al. 2001, 2007). The larvae of Cneoglossidae and the xylophagous larvae of Ptilodactylidae have tridentate mandibles, osmoregulatory organs well-seen, and hooks at the trunk end, possibly a specialization to staying fixed on the wood in running waters (Costa et al. 1996, Lawrence 2005e).

Surprisingly, aquatic organisms can be well-preserved in modern resins, and also in amber (Schmidt & Dilcher 2007, Bechly & Wichard 2008, Girard et al. 2008, Wichard et al. 2009, Schädel et al. 2020, 2021, Pazinato et al. 2023). It is possible that a resin flows into water-filled tree holes and entraps the organisms living within or that the resin flows down the bark onto the forest floor and into the nearby water (Schmidt & Dilcher 2007). Extant cypress forests produce such underwater resin flows and, due to slow polymerization, successfully entrap small aquatic organisms (Schmidt & Dilcher 2007). Therefore, fossil larvae that lived in aquatic habitats should be occasionally found within ambers. Nevertheless, the fossil record of larvae of Elmidae, Lutrochidae, Psephenidae, Cneoglossidae, Eulichadidae, Scirtidae, and Oedemeridae is very scarce. In the scope of this thesis, I present the first possible larva of Elmidae preserved in Eocene ~40-million-year-old Baltic amber (Zippel et al. 2022c: **Article 3**) and the first larvae of Ptilodactylidae preserved in Cretaceous ~100-million-year-old Kachin amber (Article still in review). Just recently another larva of Elmidae was described, however, this larva was not preserved within amber but fossilized within sediments of the Palana formation of India (Kirejtshuk et al. 2023). The larvae of Psephenidae are known from ambers of different origins: Cretaceous (Bao et al. 2018), Eocene (Wedmann et al. 2011), Miocene (Hayashi & Kawakami 2009), and Pleistocene (Hayashi et al. 2020).

The representatives of the Elmidae and Ptilodactylidae that I present here also show certain characteristics known from modern aquatic wood-boring larvae. The fossil larva of Elmidae has four rows of processes dorsolaterally on the trunk and at the end of the trunk a ventral operculum with two small hooks posteriorly. In addition, there are structures between the ventral and the dorsal sclerite that look similar to the gills of modern counterparts (Zippel et al. 2022c: **Article 3**). A modern larva of *Neolimnus* has similar processes with a similar position on the body (Shepard et al. 2020). Interestingly, the new fossil shares multiple morphologies with representatives of the modern ingroups of Elmidae [cf. the legs of the undetermined larva V and Z, the number and position of processes of the larva of *Neolimnus*, the fringed processes of larvae of *Stegoelmis* and *Potamophilops*, the curvature of the body of the larva of *Xenelmis* in Shepard et al. 2020 with the fossil larva (Zippel et al. 2022c: **Article 3**) and the setous body surface of the larva of *Potamophilus cinereus* in Vanin & Costa (2011) with the body surface of the fossil (Zippel et al. 2022c: **Article 3**, fig. 1F)] but a single larva with all characters is not known from the modern fauna. Therefore, this larva is possibly another 'chimera', representing an extinct morphology with mixed characters seen in the different modern larvae.

The new fossil larvae of Ptilodactylidae represent a modern-appearing morphology. The similarities between the new larvae and the modern larvae of *Anchytarsus* are obvious (cf. Figs. 2–8 within Zippel et al. in review a: **Article 8** and figs. 18.9.1.C and 18.9.2.C in Lawrence 2005e). Therefore, the new fossils are either larval representatives of *Anchytarsus* or closely related representatives within the Anchytarsinae.

On the one hand, the similarities between the fossils and the modern larvae of Ptilodactylidae are clear and therefore it is very likely that they both shared similar lifestyles with aquatic wood-boring habits. On the other hand, for the fossil larva of Elmidae, I cannot say whether it led exactly the same way of life as its modern counterparts. However, the presence of gills implies that this was an aquatic larva. Additionally, the strong claws, the small hooks on the operculum, and the fringed processes might have helped this animal with hanging to woody surfaces in running bodies of water.

4.2.5. Predaceous wood-associated beetle larvae

The wood does not provide a habitat only to xylophagous and mycetophagous insect larvae. Additionally, quite some groups of beetles have predaceous larvae that hunt their prey in wood. The predators developed many different morphologies that ease their hunt in chosen woody habitats whether they hunt under the loose bark of dying or dead trees, within the soft decaying wood, or within the galleries and tunnels bored by the wood borer.

Predaceous larvae associated with wood have some representatives in Carabidae (i.e.

Cicindelinae), Synteliidae, Staphylinidae (i.e. Omaliinae, Pselaphinae, Aleocharinae, Steninae, Staphylininae), Brachypsectridae, Lampyridae, Cantharidae, Chaetosomatidae, Thanerocleridae, Elateridae (i.e. Agrypninae, Fig. 5B), Cleridae (Fig. 4D), Melyridae, Cucujidae, Passandridae, Derodontidae, Trogossitidae, and Monotomidae.

Some larvae within these groups are real specialists and hunt only particular prey. For example, some larvae of Passandridae or Monotomidae feed on the larvae of Scolytinae and Platypodinae, some larvae of Derodontidae prey on representatives of Adelgidae, some larvae of Thanerocleridae hunt only small wood borers, and many others specialize in hunting in tunnels of wood borers (larvae of some Chaetosomatidae, Cleridae, Elateridae, and Bothrideridae).

Predaceous larvae often have well-sclerotized head capsules (Fig. 5H) with strong mandibles, that are often sickle-shaped (Figs. 4J). In addition, they also often have urogomphi that serve a similar function as in fungus-feeders and softwood borers living in narrow spaces (Figs. 4I). The larvae of Elateridae living under the loose bark and in well-decayed wood, have an elateriform and heavily sclerotized body, and bear no urogomphi (Fig. 5B, K, Costa et al. 2005a, Zippel et al. in revision: **Article 8**). However, some larvae of Elateridae that excavate tunnels, either beneath the firm bark or in still compact rotten wood, are slightly dorso-ventrally flattened, have urogomphi , and sometimes additional attachment structures, such as spinose legs and hooks around the trunk end (e.g. Negastriinae). Additionally, In some larvae of Elateridae the whole abdomen tergite 9 together with urogomphi makes a firm plate that armours them within the woody habitat from behind (Fig. 5B, K).

Larvae of Brachypsectridae are dorso-ventrally flattened, with short paddle-shaped antennae, and prognathous heads with strong sickle-shaped mandibles. Such mandibles remind strongly of the stylets (connected mandibles and parts of maxillae) of larvae of Neuroptera. These larvae are also predaceous and have preoral digestion, after which they suck the liquified prey through the channels within the stylets, a morphology known also from the fossils (Haug et al. 2022e, 2023b, Zippel & Kiesmüller et al. 2021). Additionally, the larvae of Brachypsectridae are easily recognized by their specific lateral processes with spines on trunk segments, giving them a comb-like appearance (Haug et al. 2021b: **Article 2**) and specialized scale-like setae covering the body (e.g. Lawrence et al. 2011). The flatness of the body is likely a morphology specialized for the tight spaces under the bark where these larvae sit and wait for their prey (Barber 1905), and the specialized processes might serve a purpose in hunting.

The entire record of larvae of Brachypsectridae has been presented by Haug et al. (2021b: **Article 2**) and it includes fossil larvae from Miocene, Eocene, and Cretaceous ambers. Interestingly, the specimen from Zhao et al. (2020) and the newly described specimen (Haug et al. 2021b: **Article 2**) from the Cretaceous lack paddle-shaped antennae that are known from other fossil and extant representatives. The SHAPE analysis of the body outlines and the outlines of the anterior part of the body revealed no real signal in shifts and losses of body morphology over time. Therefore, it seems that the morphology remained rather unchanged over time. However, there might be a slight indication that there was more variation in morphology 100 million years ago, based on the differences in the branching of lateral processes (Haug et al. 2021b: **Article 2**).

Similar sickle-shaped mandibles with channels for digestive juices are also seen in other predaceous beetle larvae, for example, some larvae of Lampyridae, mostly known for their photic organs emitting light (Lawrence et al. 2011). These lights probably have a function of an aposematic warning signal (Branham 2005b). Even though they inhabit many different habitats, including semi-aquatic and fully-aquatic ones, they can also be found preying within rotting softwood. There they can locate their prey via chemical cues (Schwalb 1960).

Only a single fossil larva of Lampyridae from Dominican amber has been reported (Ferreira et al. 2022). The fossil females, which are often larviform, are still unknown. In the scope of this thesis, I additionally present two larviform specimens which may represent either larvae or larviform females with characteristic laterally drawn-out protrusions and sickle-shaped mandibles.

Nevertheless, the specimens differ from their modern counterparts and could easily represent more ancestral lineages (Haug et al. early view b: **Article 7**).

In addition, there are also groups with larvae that not only prey but also reduce the fitness of the host. As Crowson (1981) suggested, it is challenging to differentiate parasitoids from predators sometimes. If the fitness of the host becomes decreased but the host survives the attack we are talking about parasitic larvae, however, if the host is in the end killed by the activity of the parasite then we are talking about parasitoid larvae. Interestingly, larvae of Bothrideridae and some of Passandridae are parasitizing among other insects also on eggs and larvae or pupae of wood-borers. The extreme case of parasitism among beetles is known from the larvae of Ripiphoridae, which are endoparasitic on wood-boring beetle larvae (Lawrence et al. 2005). There are also ingroups with only some species with larvae parasitizing on wood borers, for example, some larvae of Cleridae, Zopheridae, and Brentidae (Crowson 1981).

We can conclude that relatives of the predators hunting wood borers in modern forests already existed in the past and that more fossil representatives will be discovered in amber over time. After a personal observation, the fossil larvae of Cleridae, or closely-related extinct groups, seem to be well-represented within amber.

4.3. *Phylogeny and evolutionary history of wood-associated beetles*

Humans always had a need to organize and classify the world around them. This need often surpasses the logic and laws of nature, often resulting in so-called 'wastebasket' groups. Such groups tend to contain organisms that are related only by the fact that they 'do not fit' in any of the human-made groups. The 'wastebasket' groups can be seen in almost any bigger group of animals, for example, in beetles the group of Elateridae (Kundrata et al. 2020). Many extinct lineages were also often combined under a single 'wastebasket' group, for example, Protorthoptera (Handlirsch 1906). The chances of misinterpreting specimens as extinct representatives of certain groups known from modern fauna are even higher in fossils. Fossils are mostly partially preserved and the 'usual' taxonomic interpretation based on the 'important' characters (generally based on the adult male extant representatives) is often not possible. Nevertheless, even partial fossils can help us understand more of the history of beetles. For example, many fossils of early beetle lineages are known only from fossilized wings or mouthparts. Yet, even such small parts with only some characters help us to better understand the relationships of early beetles.

In order to better understand relationships between extant representatives of various lineages, including extraordinarily diverse beetles, different phylogenetic trees based on different analyses are made. For example, Lawrence et al. (2011) performed a cladistic analysis based on adult and larval morphological characters and McKenna et al. (2015, 2019) presented timetrees of beetles based on the analyses of DNA sequences. The origin of Coleoptera seems to be monophyletic with a single common ancestor, but the relationships within Coleoptera are more complex and not completely understood. Unfortunately, in such a diverse group, like beetles, even despite strong interest the interrelationships are relatively controversial (Baehr 1979, Kukalová-Peck & Lawrence 1993, Klausnitzer 1975, Beutel 1997, Beutel & Haas 2000, McKenna et al. 2015, Cai et al. 2022, Boudinot et al. 2023). Already the relationships among the four main groups of Coleoptera (Archostemata, Myxophaga, Adephaga, and Polyphaga) differ in interpretation among different authors. Lawrence et al. (2011) consider all four ingroups monophyletic and (Archostemata + Adephaga) a sister group to (Myxophaga + Polyphaga). In newer studies, McKenna et al. (2015, 2019) argued that all four ingroups of Coleoptera were monophyletic and that Archostemata was a sister group to Myxophaga, whereas Adephaga was a sister group to (Archostemata + Myxophaga), and Polyphaga was a sister group to all other ingroups (Adephaga (Archostemata + Myxophaga)).

After McKenna et al. 2019, Polyphaga phylogeny is interpreted as (group including Scirtoidea and Derodontoidea + (Rhinorhipoidea + ((Dascilloidea + group including Byrrhoidea, Buprestoidea, Elateroidea) + (Nosodendroidea + ((Hydrophiloidea + (Staphylinoidea + Scarabaeoidea)) + (Bostrichoidea + ((Cleroidea + Coccinelloidea) + (Tenebrionoidea + (Cucujoidea + (Chrysomeloidea + Curculionoidea)))))))) (Fig. 1). Therefore, Scirtoidea and Derodontoidea are only monophyletic together within a single group. The same is true for Byrrhoidea, which is monophyletic only in a group also including Buprestoidea and Elateroidea. Additionally, Jacobsoniidae were resolved within Staphylinoidea.

Phylogenetic analyses can also help in the timing of diverse evolutionary patterns, such as the diversification of various beetle lineages (McKenna et al. 2019). However, often such implications do not overlap with the fossil record of certain lineages. Additionally, a fossil find of an adult beetle with similar morphology to the extant representatives of the lineage does not necessarily imply that the larval morphology known from the extant representatives would coincide with the fossil larva as well. Haug et al. (2015) showed that such evolutionary independence between larval and adult morphologies can be present, especially in other crustacean groups. Therefore, the fossil finds of certain larval morphologies are important to time the first appearances of certain larval types. For example, the first reports of the 'chimeran' larva-type of Eucnemidae from Kachin Cretaceous amber (Zippel et al. 2023b: **Article 6**) or the larvae of Scraptiidae from the same amber deposit with more triangle-shaped trunk end (Zippel et al. 2022a: **Article 4**) differ from known modern representatives of these groups.

5. CONCLUSIONS & OUTLOOK

One of the goals of this thesis was to re-evaluate the availability of beetle larvae in different ambers. Since the wood-associated larvae were living close to the source of the resin-producing trees, I expected that different ambers will yield many wood-associated beetle larvae. As it showed, the larvae were more than abundant in amber and sometimes well enough preserved for further conclusions about their relationships and ecology.

Further goals were to compare the morphological characters of larvae that lead different lifestyles within the wood of different properties and compare fossil wood-associated larvae with extant. In some fossil specimens, very modern morphologies were present and I was able to draw parallels to the extant specimens. In other fossil specimens known 'modern' morphologies were present in combinations with the yet unknown morphologies in extant specimens. Therefore, the prediction that at least some fossil larvae will not show all apomorphic characters was also true.

I also noticed that larvae exposed to similar selective pressures within the same types of wood and with similar lifestyles shared some similar morphological characters. For example, extant hardwood borers that actively bore their tunnels (the larvae of Buprestidae, Cerambycidae, and some larvae of Eucnemidae; Haug et al. 2021a: **Article 1**, Zippel et al. 2023b: **Article 6**) exhibited enlarged segment/s of thorax and strong cutting mandibles. Additionally, in some representatives, structures for holding onto a substrate, setose areas for moving, and small ampullae that help with living within the hardwood were discernible. The same characters were observed in fossil larvae, however, sometimes in different combinations, unknown from modern counterparts.

In softwood borers, the shape of the body mostly depended on the layer of the softwood, and the stage of wood decomposition, the larvae lived in. The softwood-associated larvae living under the bark were mostly dorso-ventrally flattened, however, the larvae inhabiting decomposing wood with looser textures were of more cylindrical shape (Zippel et al. 2022a: **Article 4**, b: **Article 5**, Fig. 5D, G). The same pattern was noticed for the fungus-feeding larvae. In both groups, representatives often had urogomphi at the abdomen segment 9, possibly helping with moving in narrow spaces, or certain structures/hairs for attachment or possibly defence. Predators and fungus-feeders also displayed a variety of lateral trunk processes likely helping in hunting or camouflaging (Zippel et al. 2021b: **Article 2**, in review b: **Article 9**). Representatives of the different groups showed variability in the shape of their mouth parts, especially the mandibles. For example, the predators often had strong sickle-shaped mandibles, for example in larvae of Brachypsectridae or Lampyridae (Haug et al. 2021b: **Article 2**, early view b: **Article 7**).

The larvae on submerged wood were characterized by gills and processes and structures that help them stay on and in the wood despite the strong water currents. The characters of fossils were also well descernible and comparable with the characters of the extant larvae, allowing us interpretation of the fossils as aquatic larvae (Zippel et al. 2022c: **Article 3**), and in the case of the new fossils of Ptilodactylidae, and also as submerged-wood borers (Zippel et al. in revision a: **Article 8**).

Based on the numerous fossil larvae that I interpreted within the scope of this thesis I can conclude that differences among wood-associated larvae already existed in past ecosystems. As it seems, already in the Cretaceous beetle larvae had a complex network of ecological roles within different wood types. It is likely that they significantly attributed the decomposition of wood and carbon cycling in the Miocene, Eocene, and Cretaceous amber forests, as well. I also managed to show that the evolutionary history of wood-boring beetles had a high diversity of morphologies, often including morphologies that are unknown today, possibly because they went extinct throughout history. Additionally, I showed that the appearance of a certain larval type within a group does not necessarily coincide with the suggested first appearance of the adult morphologies of the same group based on the phylogenetic analyses. This evolutionary independence of larvae and adults of a group was already represented by Haug et al. (2015) in other crustacean groups.

Therefore, modern-appearing adults might already be present in fossil records but the specialized modern-appearing larvae evolved later (Haug et al. 2015, Zippel et al. 2022d).

6. REFERENCES

Adachi, I. (1994). Development and life cycle of *Anoplophora malasiaca* (Thomson)(Coleoptera: Cerambycidae) on citrus trees under fluctuating and constant temperature regimes. Applied Entomology and Zoology 29(4), 485–497.

Amaral, A.P., Gombos, D., Haug, G.T., Haug, C., Gauweiler, J., Hörnig, M.K. & Haug, J.T. (2023). Expanding the fossil record of soldier fly larvae—An important component of the Cretaceous amber forest. Diversity 15, art. 247.

Arce-Pérez, R., Navarrete-Heredia, J.L., & Beutel, R.G. (2005). 6.1. Lepiceridae Hinton, 1936 (= Cyathoceridae) In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, pp. 45. Berlin and New York: Walter de Gruyter.

Archangelsky, M., Beutel, R.G., & Komarek, A. (2005). 10.1. Hydrophilidae (Helophorinae, Epimetopinae, Georissinae, Hydrochinae, Spercheinae, Horelophinae, Horelophopsinae, Hydrophilinae, Sphaeridiinae). In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 158–183. Berlin and New York: Walter de Gruyter.

Arillo, A. (2007). Paleoethology: fossilized behaviours in amber. Geologica Acta 5(2), 0159–166.

Arndt, E., Beutel, R.G., & Will, K. (2005). 7.8. Carabidae Latreille, 1802. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 119–146. Berlin and New York: Walter de Gruyter.

Badano, D., Engel, M.S., Basso, A., Wang, Bo, & Cerretti, P. (2018). Diverse Cretaceous larvae reveal the evolutionary and behavioural history of antlions and lacewings. Nature Communications 9, art. 3257.

Badano, D., Fratini, M., Maugeri, L., Palermo, F., Pieroni, N., Cedola, A., Haug, J. T., Weiterschan, T., Velten, J., Mei, M., Di Giulio, A., & Cerretti, P. (2021). X-ray microtomography and phylogenomics provide insights into the morphology and evolution of an enigmatic Mesozoic insect larva. Systematic Entomology 46, 672–684.

Baehr, M. (1979). Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax der Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). Zoologica 44(130), 1–76.

Bao, T., Wang, B., Li, J., & Dilcher, D. (2019). Pollination of Cretaceous flowers. Proceedings of the National Academy of Sciences, 116(49), 24707–24711.

Barber, H.S. (1905): Illustrations of an undetermined coleopterous larva. Proceedings of the Entomological Society of Washington 7, 117–121.

Batelka, J., & Engel, M.S. (2022). The‘first fossil tumbling flower beetle’ larva is a symphytan (Hymenoptera). Acta entomologica 62, 57–59.

Baranov, V.A., Wang, Y., Wedmann, S., & Haug, J.T. (2020). Ecomorphological diversity of larvae of soldier flies and their closest relatives in deep time. PeerJ 8, art. e10356.

Baranov, V.A., Engel, M.S., Hammel, J., Hörnig, M.K., van de Kamp, T., Zuber, M., & Haug, J.T. (2021) Synchrotronradiation computed tomography uncovers ecosystem functions of fly larvae in an Eocene forest. Palaeontologia Electronica 24, a07.

Baranov, V., Perez-de La Fuente, R., Engel, M.S., Hammel, J.U., Kiesmüller, C., Hörnig, M.K., Pazinato, P.G., Stahlecker, C., Haug., C., & Haug, J.T. (2022). The first adult mantis lacewing from Baltic amber, with an evaluation of the post-Cretaceous loss of morphological diversity of raptorial appendages in Mantispidae. Fossil Record 25, 11–24.

Barba-Montoya, J., Reis, M.D., Schneider, H., Donoghue, P.C.J., Yang, Z. (2018). Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous Terrestrial Revolution. New Phytologyst 218, 819–834.

Barraclough, T.G., Vogler, A.P., & Harvey, P.H. (1998). Revealing the factors that promote speciation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 353(1366), 241–249.

Barragan-Fonseca, K.B., Dicke, M., & van Loon, J.J.A. (2017). Nutritional value of the black soldier fly (*Hermetia illucens* L.) and its suitability as animal feed – A review. Journal of Insects as Food and Feed 3(2), 105–120.

Bechly, G., & Wichard, W. (2008). Damselfly and dragonfly nymphs in Eocene Baltic amber (Insecta: Odonata), with aspects of their palaeobiology. Paleodiversity 1, 37–73.

Bellamy, C.L. (2003). An illustrated summary of the higher classification of the superfamily Buprestoidea (Coleoptera). Folia Heyrovskyana, Supplement 10, 197 pp.

Bellamy, C.L., & Volkovitsch (2005). 17.1. Buprestidae Leach, 1815. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 461–468. Berlin and New York: Walter de Gruyter.

Benton, M.J., Wilf, P., & Sauquet, H. (2022). The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. New Phytologist 233(5), 2017–2035.

Béthoux, O. (2009). The earliest beetle identified. Journal of Paleontology 83(6), 931–937.

Beutel, R.G. (1997). Über Phylogenese und Evolution der Coleoptera (Insecta). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 31, 1–164.

Beutel, R.G. (2005a). 1. Systematic position, basal branching pattern and early evolution. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 1–9. Berlin and New York: Walter de Gruyter.

Beutel, R.G. (2005b). 6. Myxophaga In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B.

Leschen, R.G. Beutel, & J.F. Lawrence, 29–42. Berlin and New York: Walter de Gruyter.

Beutel, R.G., & Haas, F. (2000). Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics 16(1), 103–41.

Beutel, R.G., & Lawrence, J.F. (2005). 4. Coleoptera, Morphology. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 29–42. Berlin and New York: Walter de Gruyter.

Beutel, R. G., Pohl, H., Yan, E. V., Anton, E., Liu, S. P., Ślipiński, A., McKenna, D., & Friedrich, F. (2019). The phylogeny of Coleopterida (Hexapoda)–morphological characters and molecular phylogenies. Systematic Entomology 44(1), 75–102.

Beutel, R.G., Ge, S.-Q., & Hörnschemeyer, T. (2008). On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. Cladistics 24, 270–298.

Beutel, R.G., Friedrich, F., & Economo, E.P. (2022). Patterns of morphological simplification and innovation in the megadiverse Holometabola (Insecta). Cladistics 38(2), 227–245.

Bieliavtsev, M.P. (2021). Ecological groups of xylobiont beetles (Insecta: Coleoptera) in the fresh oak forest of the National Nature Park 'Gomilshanski Lisy' (Kharkiv Region, Ukraine). The Kharkov Entomological Society Gazette 29(2), 31–39.

Bocak, L., & Matsuda, K. (2003). Review of the immature stages of the family Lycidae (Insecta: Coleoptera). Journal of Natural History 37(12), 1463–1507.

Bocak, L., & Bocakova, M. (2005). 4.11. Lycidae Laporte, 1836. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 114–123. Berlin and New York: Walter de Gruyter.

Boddy, L., & Swift, M.J. (1984). Wood decomposition in an abandoned beech and oak coppiced woodland in SE England: III. Decomposition and turnover of twigs and branches. Ecography 7(2), 229–238.

Böving, A.G., & Craighead, F.C. (1931). An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana (NS) 11, 1–351.

Bongers, T., van der Meulen, H., & Korthals, G. (1997). Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. Applied Soil Ecology 6(2), 195–199.

Borror, D.J., Triplehorn, C.A., & Johnson, N.F. (1989). An Introduction to the Study of Insects, 6th Ed. Philadelphia: Saunders College Publishing.

Bouchard, P., Smith, A.B., Douglas, H., Gimmel, M.L., Brunke, A.J., & Kanda, K. (2017). Chapter 11. Biodiversity of coleoptera. In Insect biodiversity: science and society, eds. R.G. Foottit, & P.H. Adler, 337–417. Hoboken, NJ and Chichester: John Wiley & Sons.

Boudinot, B.E., Yan, E.V., Prokop, J., Luo, X.Z., & Beutel, R.G. (2023). Permian parallelisms: reanalysis of† Tshekardocoleidae sheds light on the earliest evolution of the Coleoptera. Systematic Entomology 48, 69–96.

Bousfield, E.L., & Poinar Jr, G.O. (1994). A new terrestrial amphipod from Tertiary amber deposits of Chiapas province, southern Mexico. Historical Biology 7(2), 105–114.

Braig, F., Haug, J. T., Schädel, M., & Haug, C. (2019). A new thylacocephalan crustacean from the Upper Jurassic lithographic limestones of southern Germany and the diversity of Thylacocephala. Palaeodiversity 12, 69–87.

Braig, F., Haug, C., & Haug, J.T. (2023). Phenotypic variability in the shield morphology of wild- vs. lab-reared eumalacostracan larvae. Nauplius, art. 31.

Branham, M.A. (2005a). 4.8. Plastoceridae Crowson, 1972. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 103–104. Berlin and New York: Walter de Gruyter.

Branham, M.A. (2005). 4.15. Lampyridae Latreille, 1817. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 141–149. Berlin and New York: Walter de Gruyter.

Bright, D.E., & Poinar Jr, G.O. (1994). Scolytidae and Platypodidae (Coleoptera) from Dominican Republic amber. Annals of the Entomological Society of America 87(2), 170–194.

Brown, H.P. (1987). Biology of riffle beetles. Annual review of entomology, 32, 253–273.

Brown, H. P. (1991). Lutrochidae (Dryopoidea). In Immature insects, vol. 2, ed. F.W. Stehr, 397–399. Dubuque: Kendall-Hunt Publishing Co.

Buck, F.D. (1954) Coleoptera: Lagriidae, Alleculidae, Melandryidae, Salpingidae, Pythidae, Mycteridae, Oedemeridae, Oedemeridae, Mordellidae, Scraptiidae, Pyrochroidae, Rhipiphoridae, Anthicidae, Aderidae and Meloidae. Handbooks for the Identification of British Insects, 5(9). Royal Entomological Society of London, 30 pp.

Busch, A., Danchin, E.G.J., & Pauchet, Y. (2019). Functional diversification of horizontally acquired glycoside hydrolase family 45 (GH45) proteins in Phytophaga beetles. BMC Evolutionary Biology 19, art. 100.

Cai, C., Escalona, H.E., Li, L., Yin, Z., Huang, D., & Engel, M.S. (2018). Beetle pollination of cycads in the Mesozoic. Current Biology, 28(17), 2806–2812.

Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J. F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M.K., Newton, A.F., Leschen, R.A.B., Gimmel, M.L., Lü, L., Engel, M.S., Bouchard, P., Huang, D., Pisani, D., & Donoghue, P.C. (2022). Integrated phylogenomics and fossil data illuminate the evolution of beetles. Royal Society Open Science 9(3), art. 211771.

Campbell, N.A. (1997). Biologie. Heidelberg, Berlin, Oxford: Spektrum Akademischer Verlag.

1140 pp.

Carpenter, F.M. (1992). Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Superclass Hexapoda. Lawrence: Geological Society of America and University of Kansas Press.

Chiappini, E., & Aldini, R.N. (2011). Morphological and physiological adaptations of wood-boring beetle larvae in timber. Journal of Entomological and Acarological research 43(2), 47–59.

Cognato, A.I., & Grimaldi, D. (2009). 100 million years of morphological conservation in bark beetles (Coleoptera: Curculionidae: Scolytinae). Systematic Entomology 34, 93–100.

Condamine, F.L., Silvestro, D., Koppelhus, E.B., Antonelli, A. (2020). The rise of angiosperms pushed conifers to decline during global cooling. Proceedings of the National Academy of Sciences of the USA 117, 28 867–28 875.

Conwentz, H. (1890). Monographie der Baltischen Bernsteinbäume. Danzig: Naturforschende Gesellschaft. 151 pp.

Cornwell, W.K., Cornelissen, J.H., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., & Zanne, A.E. (2009). Plant traits and wood fates across the globe: rotted, burned, or consumed?. Global Change Biology 15(10), 2431–2449.

Costa, C., Ide, S., & Teixeira, É. P. (1996). Larvae of neotropical coleoptera. Xx: *Glyptolopus quadricostatus* heinze (cerylonidae, ceryloninae). Revista Brasileira de Entomologia 39(4), 771–7.

Costa, C., Vanin, S.A., & Ide, S. (1999). Systematics and bionomics of Cneoglossidae with a cladistic analysis of Byrrhoidea sensu Lawrence & Newton (1995) (Coleoptera, Elateriformia). Arquivos De Zoologia 35(3), 231–300.

Costa, C., Lawrence, J.F., & Rosa, S.P. (2005a). 4.7. Elateridae Leach, 1815. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 75–103. Berlin and New York: Walter de Gruyter.

Costa, C., Vanin, S.A., & Ide, S. (2005b). 18.8. Cneoglossidae Guérin-Méneville, 1843. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 533–536. Berlin and New York: Walter de Gruyter.

Craighead, F.C. (1923). North American cerambycid larvae. Canadian Department of Agriculture Technical Bulletin 27(n.s.), 150 pp., 44 pls.

Cranston, P.S., & McKie, B. (2006). Aquatic wood–an insect perspective. In Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology (Vol. 9), ed. S.J. Grove, & J.L. Hanula, 9–14. Asheville: US Department of Agriculture, Forest Service, Southern Research Station.

Crowson R.A. (1955). The classification of the families of British Coleoptera (part). Entomologist´s Monthly Magazine 86, 56–57.

Crowson RA. (1981). The biology of the Coleoptera. London, UK: Academic Press. 814 pp.

Cruickshank, R.D., & Ko, K. (2003). Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of asian earth Sciences 21(5), 441–455.

Deng, C., Ślipinski, A., Ren, D., & Pang, H. (2017). The oldest dermestid beetle from the Middle Jurassic of China (Coleoptera: Dermestidae). Annales zoologici 67, 109–112.

Dodds, K.J., Graber, C., & Stephen, F.M. (2001). Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). Environmental Entomology 30, 17–22.

dos Santos, M.F.A., Mattos, I., Mermudes, J.R.M., Scheffler, S.M., & Reyes-Castillo, P. (2021). A new passalid fossil (Insecta: Coleoptera) from the Santana Formation (Crato member, Lower Cretaceous), Araripe Basin, NE Brazil: Paleoecological and paleobiogeographic implications. Cretaceous Research 118, art. 104664.

Dudley, T., & Anderson, N.H. (1982). A survey of invertebrates associated with wood debris in aquatic habitats. Melanderia 39, 1–21.

Dunlop, J.A., & Garwood, R.J. (2018). Terrestrial invertebrates in the Rhynie chert ecosystem. Philosophical Transactions of the Royal Society B: Biological Sciences 373(1739), art. 20160493.

Dunstan, B. (1923). Part I. Introduction and Coleoptera, Mesozoic insects of Queensland. Publication of the Queensland Geological Survey, Brisbane 273, 1–88.

Esperk, T., Tammaru, T. & Nylin, S. (2007). Intraspecific variability in number of larval instars in insects. Journal of Economic Entomology 100(3), 627–645.

Farrell, B.D. (1998) ‘Inordinate fondness’ explained: why are there so many beetles? Science 281, 555–559.

Farrell, B.D., Sequeira, A.S., O’Meara, B., Normark, B.B., Chung, J.H., & Jordal, B.H. (2001). The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55, 2011–2027.

Feldberg, K., Gradstein, S.R., Gröhn, C., Heinrichs, J., von Konrat, M., Mamontov, Y.S., Renner, M.A.M., Roth, M., Schäfer-Verwimo, A.Sukkharak, P., & Schmidt, A.R. (2021). Checklist of fossil liverworts suitable for calibrating phylogenetic reconstructions. Bryophyte Diversity and Evolution 43, 14–71.

Feng, Z., Wang, J., Rößler, R., Ślipiński, A., & Labandeira, C. (2017). Late Permian wood-borings reveal an intricate network of ecological relationships. Nature Communications 8, art. 556.

Feng, Z., Bertling, M., Noll, R., Ślipiński, A., & Roessler, R. (2019). Beetle borings in wood with host response in early Permian conifers from Germany. PalZ 93(3), 409–421.

Ferreira, V.S., Solodovnikov, A., Ivie, M.A., & Kundrata, R. (2022). Dominican amber net-winged beetles suggest stable paleoenvironment as a driver for conserved morphology in a paedomorphic lineage. Scientific Reports 12, art. 5820.

Franceschi, V.R., Krokene, P., Christiansen, E., & Krekling, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New phytologist 167(2), 353–376.

Friis, E.M., Crane, P.R., & Pedersen, K.R. (2011). Early flowers and angiosperm evolution. Cambridge: Cambridge University Press. 586 pp.

Fukasawa, Y., & Matsukura, K. (2021). Decay stages of wood and associated fungal communities characterise diversity–decomposition relationships. Scientific Report 11, art. 8972 .

Genise, J.F., & Hazeldine, P.L. (2008). A new insect trace fossil in Jurassic wood from Patagonia, Argentina. Ichnos 4, 1–5.

Ghilarov, M.S. (1970). Soil biocoenoses. In Methods of Study in Soil Ecology*,* ed. J. Phillipson. Paris: Proceedings of the Paris Symposium Organized by Unesco and the International Biological Programme.

Gimmel, M. L., & Ferro, M. L. (2018). General overview of saproxylic Coleoptera. In Saproxylic insects: diversity, ecology and conservation, Zoological Monographs, ed. M.D. Ulyshen, 51–128. Cham: Springer.

Girard, V., Schmidt, A.R., Saint Martin, S., Struwe, S., Perrichot, V., Saint Martin, J.P., Grosheny, D., Breton, G., & Néraudeau, D. (2008). Evidence for marine microfossils from amber. PNAS 105, 17426–17429.

Gligorescu, A., Toft, S., Hauggaard-Nielsen, H., Axelsen, J.A., & Nielsen, S.A. (2019). Development, growth and metabolic rate of *Hermetia illucens* larvae. Journal of Applied Entomology 143, 875–881.

Goeppert, J.H.R. (1850). Monographie der fossilen Coniferen. Leiden: Arnz & Comp. 359 pp.

Gossner, M.M., Falck, K., & Weisser, W.W. (2019). Effects of management on ambrosia beetles and their antagonists in European beech forests. Forest Ecology and Management 437, 126–133.

Graham, A. (1999a). Studies in neotropical paleobotany. XIII. An oligo-miocene palynoflora from Simojovel (Chiapas, Mexico). American Journal of Botany 86, 17–31.

Graham, A. (1999b). The Tertiary history of the northern temperate element in the northern Latin American biota. American Journal of Botany 86, 32–38.

Grimaldi, D.A., Engel, M.S., & Nascimbene, P.C. (2002). Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361, 1–71.

Grimaldi, D., & Engel, M.S. (2005). Evolution of the insects, 1st edn. Cambridge: Cambridge University Press. 755 pp.

Gröhn, C. (2015). Einschlüsse im baltischen Bernstein. Kiel: Wachholtz Verlag, Murmann Publishers. 424 pp.

Grove, S.J., & Stork, N.E. (2000). An inordinate fondness for beetles. Invertebrate Systematics 14(6), 733–739.

Handlirsch A. (1906). Die Fossilen Insekten und die Phylogenie der Rezenten Formen, parts I–IV. Ein Handbuch fur Palaontologen und Zoologen. Leipzig: Wilhelm Engelmann. 640 pp.

Hanks, L.M. (1999). Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annual review of entomology 44, 483–505.

Haug, C., Herrera-Flórez, A.F., Müller, P., & Haug, J.T. (2019). Cretaceous chimera–an unusual 100-million-year old neuropteran larva from the "experimental phase" of insect evolution. Palaeodiversity 12, 1–11.

Haug, C., Haug, G.T., Zippel, A., van der Wal, S., & Haug, J.T. (2021a). The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4, 390–404. (**Article 1**)

Haug, C., Posada Zuluaga, V., Zippel, A., Braig, F., Müller, P., Gröhn, C., Weiterschan, T., Wunderlich, J., Haug, G.T., & Haug, J.T. (2022c). The morphological diversity of antlion larvae and their closest relatives over 100 million years. Insects 13, art. 587.

Haug, C., Zippel, A., Hassenbach, C., Haug, G.T., & Haug, J.T. (2022e). A split-footed lacewing larva from about 100-million-year-old amber indicates a now extinct hunting strategy for neuropterans. Bulletin of Geosciences 97, 453–464.

Haug, C., Zippel, A., Müller, P., & Haug, J.T. (2022a). A modern type of ant-like stone beetle larva preserved in 99-million-year-old Kachin amber. Fragmenta entomologica 54, 193–200.

Haug, C., Braig, F., & Haug, J. T. (2023a). Quantitative analysis of lacewing larvae over more than 100 million years reveals a complex pattern of loss of morphological diversity. Scientific Reports 13, art. 6127.

Haug, C., Baranov, V.A., Hörnig, M.K., Gauweiler, J., Hammel, J.U., Perkovsky, E.E. & Haug, J.T. (early view a). 35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests. Palaeobiodiversity and Palaeoenvironments.

Haug, C., Zippel, A., Müller, P. & Haug, J.T. (early view b). Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ. (**Article 7**)

Haug, G.T., Haug, C., Pazinato, P.G., Braig, F., Perrichot, V., Gröhn, C., Müller, P., & Haug, J.T. (2020a). The decline of silky lacewings and morphological diversity of long-nosed antlion larvae through time. Palaeontologia Electronica 23(2), art. a39.

Haug, G.T., Haug, C., & Haug, J.T. (2021d). The morphological diversity of spoon-winged lacewing larvae and the first possible fossils from 99 million-year-old Kachin amber, Myanmar. Palaeodiversity 14, 133–152.

Haug, G.T., Haug, C., van der Wal, S., Müller, P., & Haug, J.T. (2022b). Split-footed lacewings declined over time: indications from the morphological diversity of their antlion-like larvae. PalZ

96, 29–50.

Haug, J.T. (2018). Why the term „larva“ is ambiguous, or what makes a larva? Acta Zoologica 101, 167–188.

Haug, J.T., & Haug, C. (2019). Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). PeerJ 7, art. e7871.

Haug, J.T., & Haug, C. (2021). A 100 million-year-old armoured caterpillar supports the early diversification of moths and butterflies. Gondwana Research 93, 101–105

Haug, J.T., & Haug, C. (2022). Another strange holometabolan larva from Kachin amber—the enigma of the beak larva (Neuropteriformia). Palaeoentomology 005, 276–284.

Haug, J.T., Labandeira, C.C., Santiago-Blay, J.A., Haug, C., & Brown, S. (2015). Life habits, hox genes, and affinities of a 311 million-year-old holometabolan larva. BMC Evolutionary Biology 15, art. 208.

Haug, J.T., Schädel, M., Baranov, V.A., & Haug, C. (2020b). An unusual 100-million-year old holometabolan larva with a piercing mouth cone. PeerJ 8, art. e8661.

Haug, J.T., Haug, G.T., Zippel, A., van der Wal, S., Müller, P., Gröhn, C., Wunderlich, J., Hoffeins, C., Hoffeins, H.-W. & Haug, C. (2021c). Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings and their closer relatives over 100 million years. Insects 12, art. 860

Haug, J.T., Zippel, A., Haug, G.T., Hoffeins, C., Hoffeins, H.-W., Hammel, J.U., Baranov, V., & Haug, C. (2021b). Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14, 161–183. (**Article 2**)

Haug, J.T., Haug, C., Wang, Y., & Baranov, V. A. (2022d). The fossil record of lepidopteran caterpillars in Dominican and Mexican amber. Lethaia 55(3), 1–14.

Haug, J. T., van der Wal, S., Gröhn, C., Hoffeins, C., Hoffeins, H. W., & Haug, C. (2022f). Diversity and fossil record of larvae of three groups of lacewings with unusual ecology and functional morphology: Ithonidae, Coniopterygidae and Sisyridae. Palaeontologia Electronica 25(2), 1–31.

Haug, J.T., Kiesmüller, C., Haug, G.T., Haug, C., & Hörnig, M.K. (2023b). A fossil aphidlion preserved together with its prey in 40 million-year-old Baltic amber. Palaeobio Palaeoenv 103, 155–163.

Háva, J., & Prokop, J. (2004). New fossil dermestid-beetles (Coleoptera: Dermestidae) from the Dominican amber of the Greater Antilles, with an appendix listing known fossil species of this family. Acta Societatis Zoologicae Bohemicae 68, 173–182.

Háva, J., Prokop, J., & Herrmann, A. (2006). New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber. Acta Societatis Zoologicae Bohemicae 69, 281–287.

Hawkins, C.P., Hogue, J.N., Decker, L.M., & Feminella, J.W. (1997). Channel morphology, water temperature, and assemblage structure of stream insects. Journal of the North American benthological society 16(4), 728–749.

Hayashi, N. (1962). The larval form of Anaspis (Anaspis) funagata Kono (Scraptiidae).(Studies on coleopterous larvae XIV). Entomological Review of Japan 15, 19–21.

Hayashi, N. (1980). Illustrations for identification of larvae of the Cucujoidea (Coleoptera) found living in dead trees in Japan. Memoirs of the Education Institute for Private Schools in Japan 72, 95–147.

Hayashi, M., & Kawakami, Y. (2009). Fossil of the genus Eubrianax (Coleoptera, Psephenidae) from the Upper Miocene Ningyôtôge formation in Tottori Prefecture, Japan. Elytra 37, 99–103.

Hayashi, M., Aiba, H., Nakano, E., Takahashi, Y., & Sato, T. (2020). Fossilized Water Pennies (Coleoptera: Psephenidae) in the Middle Pleistocene Lake Deposits in Shiobara Site, Tochigi Prefecture, Japan. Japanese Journal of Systematic Entomology 26, 84–86.

Hernando, C., & Ribera, I. (2005). 18.5. Limnichidae Erichson, 1846. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 512–518. Berlin, New York: Walter de Gruyter.

Hickman, C.S. (1999). Larvae in invertebrate development and evolution. In The origin and evolution of larval forms, eds. B.K. Hall, & M.H. Wake , 21–59. San Diego, London: Academic Press.

Hörnig, M.K., Haug, C., Müller, P. & Haug, J.T. (2022). Not quite social – possible cases of gregarious behaviour of immatures of various lineages of Insecta preserved in 100-million-year-old amber. Bulletin of Geosciences 97, 69–87.

Hörnschemeyer, T. (2005). 5. Archostemata Kolbe, 1908. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 29–42. Berlin, New York: Walter de Gruyter.

Hörnschemeyer, T. (2013). First fossil larvae of Berothidae (Neuroptera) from Baltic amber, with notes on the biology and termitophily of the family. Zootaxa 3716(2), 236–258.

Hoffeins, C., & Hoffeins, H.-W. (2003). Untersuchungen über die Häufigkeit von Inklusen in Baltischem und Bitterfelder Bernstein (Tertiär, Eozän) aus unselektierten Aufsammlungen unter besonderer Berücksichtigung der Ordnung Diptera. Studia Dipterologica 10, 381–392.

Hoffmann, A., & Hering, D. (2000). Wood-associated macroinvertebrate fauna in Central European streams. International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology 85, 25–48.

Hughes, N.F. & McDougall, A.B. (1987) Records of angiospermid pollen entry into the English Early Cretaceous succession. Review of Palaeobotany and Palynology 50(3), 255–272.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O. St., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., Gómez-Zurita, J., Ribera, I., Barraclough, T.G., Bocakova, M., Bocak, L., & Vogler, A.P. (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science 318, 1913–1916.

Ide, S., Costa, C., &Vanin, S.A. (2005). 18.4. Lutrochidae Kasap & Crowson, 1975. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 508–512. Berlin, New York: Walter de Gruyter.

Ingham, R.E. (1992). Interactions between invertebrates and fungi: effects on nutrient availability. In The Fungal Community: Its Organization and Role in the Ecosystem, eds. G.C. Carroll, & D.T. Wicklow, 669– 690. New York: Marcel Dekker Inc.

Ivie, M.A. (2005). 18.11. Eulichadidae Crowson, 1973. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 547–551. Berlin, New York: Walter de Gruyter.

Jordal, B.H. (2014). 3.7.12. Scolytinae Latreille, 1806. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Phytophaga), vol. 3, eds. R.A.B. Leschen, & R.G. Beutel, 633–642. Berlin, Boston: Walter de Gruyter.

Kasiński, J.R., & Kramarska, R. (2008). Sedimentary environment of amber-bearing association along the Polish-Russian Baltic coastline. Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften 236, 46–57.

Kirejtshuk, A.G., & Azar, D. (2008). New taxa of beetles (Insecta, Coleoptera) from Lebanese amber with evolutionary and systematic comments. Alavesia 2(15), art. e46.

Kirejtshuk, A.G., & Nel, A. (2016). Origin of the Coleoptera and significance of the fossil record. Euroasian Entomological Journal 15, 66–73.

Kirejtshuk, A.G., Azar, D., Beaver, R.A., Mandelshtam, M.Y., & Nel, A. (2009). The most ancient bark beetle known: a new tribe, genus and species from Lebanese amber (Coleoptera, Curculionidae, Scolytinae). Systematic Entomology 34, 101–112.

Kirejtshuk, A.G., Poschmann, M., Prokop, J., Garrouste, R. & Nel, A. (2014) Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tshekardocoleidae). Journal of Systematic Palaeontology, 12, 575–600.

Kirejtshuk, A.G. (2020). Taxonomic review of fossil coleopterous families (Insecta, Coleoptera). Suborder Archostemata: superfamilies Coleopseoidea and Cupedoidea. Geosciences, 10(2), art. 73.

Kirejtshuk, A.G., Patel, P., Rana, R.S., Prokin, A., Nel, A., & Jäch, M.A. (2023). Discovery of the oldest known elmid larva (Coleoptera, Elmidae) from the Lower Eocene of Rajasthan (India, Palana Formation). Palaeoentomology 6(3), 235–241.

Kirkendall, L.R., Biedermann, P.H., & Jordal, B.H. (2015). Evolution and diversity of bark and ambrosia beetles. In Bark beetles: Biology and Ecology of Native and Invasive Species, eds. F.E. Vega, & R.W: Hoffstetter, 85–156. San Diego: Elsevier.

Kirsch, R., Gramzow, L., Theißen, G., Siegfried, B.D., Heckel, D.G., & Pauchet, Y. (2014).

Horizontal gene transfere and functional diversification of plant cell wall degrading polygalacturonases: Key events in the evolution of herbivory in beetles. Insect Biochemistry and Molecular Biology 52, 33–50.

Klausnitzer, B. (1975). Probleme der Abgrenzung von Unterordnungen bei den Coleoptera. Entomologische Abhandlungen 40(2), 269–275.

Klausnitzer, B. (1978). Ordnung Coleoptera (Larven). Berlin: Akademie-Verlag. 378 pp.

Klausnitzer, B. (2003). Käferlarven (Insecta: Coleoptera) in Baltischem Bernstein—Möglichkeiten und Grenzen der Bestimmung. Entomologische Abhandlungen 61, 103–108.

Klepzig, K.D., Smalley, E.B., & Raffa, K.F. (1996). Combined chemical defenses against an insect-fungal complex. Journal of Chemical Ecology 22, 1367–1388.

Klepzig, K.D., Robison, D.J., Fowler, G., Minchin, P.R., Hain, F.P., & Allen, H.L. (2005). Effects of mass inoculation on induced oleoresin response in intensively managed loblolly pine. Tree Physiology 25, 681–688.

Knobloch, E., Konzalová, M., & Kvaček, Z. (1996): Late Eocene flora of the Staré Sedlo Formation in Bohemia (Central Europe). Rozpravy Českého Geologického Ústavu 49, 1–260.

Kodada, J., & Jäch, M.A. (2005). 18.2. Elmidae Curtis, 1830. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 471–496. Berlin, New York: Walter de Gruyter.

Köhler, F. (2000). Totholzkäfer in Naturwaldzellen des nördlichen Rheinlands: vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung. Recklinghausen: Landesanstalt für Ökologie, Bodenordnung und Forsten/Landesamt für Agrarordnung Nordrhein-Westfalen. 352 pp.

Kosmowska-Ceranowicz, B., Kohlman - Adamska , A. & Grabowska , I. (1997). Erste Ergebnisse zur Lithologie und Palynologie der bernsteinführenden Sedimente im Tagebau Primorskoje. Metalla, Sonderheft - Neue Erkenntnisse zum Bernstein 66, 5–17.

Kosmowska-Ceranowicz, B., Krumbiegel, G., Vavra, N. (1993). Glessit, ein tertiäres Hartz von Angiosperman der Familie Burseraceae. Neues Jahrbuch für Geologie und Paläontologie: Abhandlungen 187, 299–324.

Kovalev, A.V. (2014). Fauna of the beetles of the families Throscidae, Eucnemidae, Cerophytidae and Brachypsectridae (Coleoptera) of Russia and neighboring countries. Doctoral dissertation, Zoological Institut RAS, Saint Petersburg. (in Russian). Жесткокрылые семейств Throscidae, Eucnemidae, Cerophytidae и Brachypsectridae (Coleoptera) фауны России и сопредельных стран (Doctoral dissertation, Зоол. ин-т РАН).

Krenn, H.W., Plant, J.D., & Szucsich, N.U. (2005). Mouthparts of flower-visiting insects. Arthropod Structure & Development 34, 1–40.

Kühnelt, W. (1976). Soil Biology: With Special Reference to the Animal Kingdom. London: Faber and Faber. 483 pp.

Kukalová, J. (1969). On the systematic position of the supposed Permian beetles, Tshekardocoleidae, with a description of a new collection from Moravia. Sbornik Geologických Veˇd (P.) 11, 139–144.

Kukalová-Peck, J., & Lawrence, J.F. (1993). Evolution of the hind wing in Coleoptera. The Canadian Entomologist 125(2), 181–258.

Kukalová-Peck, J. & Beutel, R.G. (2012). Is the Carboniferous †*Adiphlebia lacoana* really the "oldest beetle"? Critical reassessment and description of a new Permian beetle family. European Journal of Entomology 109, 633–645.

Kumar, Y., & Yadav, B.C. (2020). Plant-parasitic nematodes: Nature's most successful plant parasite. International journal of research and review 7(3), 379–386.

Kundrata, R., & Bocak, L. (2011). The phylogeny and limits of Elateridae (Insecta, Coleoptera): Is there a common tendency of click beetles to soft-bodiedness and neoteny? Zoologica Scripta 40, 364–378.

Kundrata, R., Packova, G., & Hoffmannova, J. (2020). Fossil Genera in Elateridae (Insecta, Coleoptera): A Triassic Origin and Jurassic Diversification. Insects 11(6), 394.

Kvaček, Z. (2002). Late Eocene landscape, ecosystems and climate in northern Bohemia with particular reference to the locality of Kučlín near Bílina. Bulletin of the Czech Geological Survey 77, 217–236.

Kvaček, Z. (2010). Forest flora and vegetation of the European early Palaeogene – a review. Bulletin of Geosciences 85, 63–76.

Kvaček, Z., & Teodoridis, V. (2011). The late Eocene flora of Kučlín near Bílina in North Bohemia revisited. Acta Musei Nationalis Pragae, Series B, Historia Naturalis 67, 83–144.

Labandeira, C.C. (1997). Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. Annual Review of Ecology and Systematics 28, 153–193.

Labandeira, C. (2007). The origin of herbivory on land: initial patterns of plant tissue consumption by arthropods. Insect science 14(4), 259–275.

Labandeira, C. C. (2010). The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects. Annals of the Missouri Botanical Garden 97(4), 469–513.

Labandeira, C.C., & Sepkoski, J.J. (1993). Insect diversity in the fossil record. Science 261, 310–315.

Labandeira, C.C., & Li, L. (2021). The history of insect parasitism and the Mid-Mesozoic Parasitoid Revolution. In The Evolution and Fossil Record of Parasitism: Identification and Macroevolution of Parasites, eds. K. De Baets & J.W. Huntley, 377–533. Cham: Springer International Publishing.

Labandeira, C.C., Johnson, K.R., & Wilf, P. (2002). Impact of the terminal Cretaceous event on plant–insect associations. Proceedings of the National Acadamy of Sciences of the USA 99, 2061–2066.

Labandeira, C.C., Wilf, P., Johnson, K.R., & Marsh, F. (2007). Guide to insect (and other) damage types on compressed plant fossils. Version 3.0. Washington DC: Smithsonian Institution. 25 pp.

Lalander, C.H., Fidjeland, J., Diener, S., Eriksson, S., & Vinnerås, B. (2015). High waste-to-biomass conversion and efficient *Salmonella spp.* reduction using black soldier fly for waste recycling. Agronomy for Sustainable Development 35, 261–271.

Langenheim, J.H. (1969). Amber: A botanical inquiry. Amber provides an evolutionary framework for interdisciplinary studies of resin secreting plants. Science 136, 1157–1169.

Lawrence, J.F. 1991. Mordellidae (Tenebrionoidea). In Immature insects, vol. 2, ed. F.W. Stehr, 508–509. Dubuque: Kendall-Hunt Publishing Co.

Lawrence, J.F. (2005a). 15.1. Decliniidae Nikitsky et al., 1994. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 431–433. Berlin, New York: Walter de Gruyter.

Lawrence, J.F. (2005b). 4.1. Rhinorhipidae Lawrence, 1988. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 38–42. Berlin, New York: Walter de Gruyter.

Lawrence, J.F. (2005c). 4.1. Telegeusidae Leng, 1920. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 123–126. Berlin & New York: Walter de Gruyter.

Lawrence, J.F. (2005d). 8. Lymexyloidea Fleming, 1821. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 229–235. Berlin & New York: Walter de Gruyter.

Lawrence, J.F. (2005e) 18.9. Ptilodactylidae Laporte, 1836. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 536–542. Berlin & New York: Walter de Gruyter.

Lawrence, J. F., & Newton, A. F. Jr. (1982). Evolution and classification of beetles. Annual Review of Ecology and Systematics 13, 261–290.

Lawrence, J.F., & Britton, E.B. (1994). Australian beetles. Melbourne: Mellbourne University Press. 192 pp.

Lawrence, J.F., & Ślipiński, A. (2005). 6.1. Dermestidae Latreille, 1804. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 198–206. Berlin, New York:

Walter de Gruyter.

Lawrence, J.F., Falin, Z.H., & Ślipiński, A. (2005). Ripiphoridae Gemminger and Harold, 1870. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 538–548. Berlin, New York: Walter de Gruyter.

Lawrence, J.F., Ślipinski, A., Seago, A.E., Thayer, M.K., Newton, A.F., & Marvaldi, A.E. (2011). Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annals of Zoology 61, 1–217.

Lee, C.F., Yang, P.S., & Satô, M. (2001). Phylogeny of the genera of Eubrianacinae and descriptions of additional members of Eubrianax (Coleoptera: Psephenidae). Annals of the Entomological Society of America 94(3), 347–362.

Lee, C.F., Jäch, M.A., & Beutel, R.G. (2005). 18.7. Psephenidae Lacordaire, 1854. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 521–533. Berlin, New York: Walter de Gruyter.

Lee, C.F., Sato, M., Shepard, W.D., & Jaech, M.A. (2007). Phylogeny of Psephenidae (Coleoptera: Byrrhoidea) based on larval, pupal and adult characters. Systematic Entomology 32(3), 502–538.

Leiler, T.E. (1976). Zur Kenntnis der Entwicklungsstadien und der Lebensweise nord und mitteleuropaischer Eucnemiden (Col.). Entomologische Blätter für Biologie und Systematik der Käfer 72, 10–50.

Lesage, L., & Harper, P.P. (1976a). Cycles biologiques d'Elmidae (Coleopteres) de ruisseaux des Laurentides, Quebec. Annales de Limnologie-International Journal of Limnology 12(2), 139–174.

LeSage, L., & Harper, P.P. (1976b). Notes on the life history of the toed-winged beetle *Anchytarsus bicolor* (Melsheimer)(Coleoptera: Ptilodactylidae). The Coleopterists' Bulletin 30(3), 233–238.

Leschen, R.A.B. (1994). Ecological and behavioral correlates among mycophagous Coleoptera. Folia Entomologica Mexicana 92, 9–19.

Leschen, R.A.B., & Ślipiński, A. (2005). 7. Cucujiformia Lameere, 1938. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 227–228. Berlin, New York: Walter de Gruyter.

Leschen, R.A.B., & Carlton, C.E. (1993). Debris cloaking in Endomychidae: a new species from Peru (Coleoptera). Zoological Journal of the Linnean Society 109, 35–51.

Leschen, R.A.B., Skelley, A.B., McHugh, J.V. (2005) 10.7. Erotylidae Leach, 1815. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 311–319. Berlin, New York: Walter de Gruyter.

Linsley, E.G. (1959). The role of Cerambycidae in forest, urban and agricultural environments. The

Pan-Pacific Entomologist 34, 105–124.

Linsley, E.G. (1959). Ecology of cerambycidae. Annual review of entomology 4, 99–138.

Lisberg, A., & Young, D.K. (2003). Descriptions of larva and pupa of *Tomoxia lineella* LeConte with notes on larval habitat (Coleoptera: Mordellidae). The Coleopterists Bulletin 57 (3), 339–344.

Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W.E., Jennings, R., & Benton, M.J. (2008). Dinosaurs and the Cretaceous Terrestrial Revolution. Proceeding of the Royal Society B: Biological Sciences 275, 2483–2490.

Lombardero, M.J., Ayres, M.P., & Ayres, B.D. (2006). Effects of fire and mechanical wounding on Pinus resinosa resin defenses, beetle attacks, and pathogens. Forest Ecology and Management 225, 349–358.

Looy, C., Kerp, H., Duijnstee, I., DiMichele, B. (2014). The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. Sedimentary Record 12, 4–18.

MacLeod, N. (2012). Extinction: K–Pg Mass Extinction. In eLS. Chichester: John Wiley & Sons. https://doi.org/10.1002/9780470015902.a0001656.pub3

Martínez-Hernández, E. (1992). Caracterizacíon ambiental del Terciario de la región de Ixtapa, Est. Chiapas – Un enfoque palinoestratigráfico. Revista, Universidad Nacional Autónoma de México, Instituto de Geología 10, 54–64.

Martinson, V.G. (2020). Rediscovering a forgotten system of symbiosis: Historical perspective and future potential. genes 11, art. 1063.

McKenna, D.D., Sequeira, A.S., Marvaldi, A.E., & Farrell, B.D. (2009). Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences of the USA 106, 7083–7088.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marivaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński,, A., Maddison, D.R., & Farrell, B.D. (2015). The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology 40, 835–880.

McKenna, D.D., Scully, E.D., Pauchet, Y., Hoover, K., Kirsch, R., Geib, S.M., Mitchell, R.F., Waterhouse, R.M., Ahn, S.-J., Arsala, D., Benoit, J.B., Blackmon, H., Bledsoe, T., Bowsher, J.H., Busch, A., Calla, B., Chao, H., Childers, A.K., Childers, C., Clarke, D.J., Cohen, L., Demuth, J.P., Dinh, H., Doddapaneni, H.V., Dolan, A., Duan, J.J., Dugan, S., Friedrich, M., Glastad, K.M., Goodisman, M.A.D., Haddad, S., Han, Y., Hughes, D.S.T., Ioannidis, P., Johnston, J.S., Jones, J.W., Kuhn, L.A., Lance, D.R., Lee, C.-Y., Lee, S.L., Lin, H., Lynch, J.A., Moczek, A.P., Murali, S:C., Muzny, D.M., Nelson, D.R., Palli, S.R., Panfilio, K.A., Pers, D., Poelchau, M.F., Quan, H., Qu, J., Ray, A.M., Rinehart, J.P., Robertson, H.M., Roehrdanz, R., Rosendale, A.J., Shin, S., Silva, C., Torson, A.S., Vargas Jentzsch, I.M., Werren, J.H., Worley, K.C., Yocum. G., Zdobnov, E.M., Gibbs, R.A., & Richards, S. (2016). Genome of Asian longhorn beetle (*Anoplophora glabripennis*), a globaly significant invasive species, reveals key functional and evolutionary innovations at the beetle-plant interface. Genome biology 17, art. 227.

McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath , A., Escalona, H.E., Friedrich, F.,Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019). The evolution and genomic basis of beetle diversity. Proceedings of the National Academy of Sciences 116(49), 24729–24737.

McMahon, D.P., & Hayward,A. (2016). Why grow up? A perspective on insect strategies to avoid metamorphosis. Ecological Entomology 41, 505–515.

Minelli, A. (2003). The development of animal form: Ontogeny, morphology, and evolution. Cambridge: Cambridge University Press. 323 pp.

Minelli, A., Brena, C., Deflorian, G., Maruzzo, D., & Fusco G. (2006). From embryo to adult – beyond the conventional periodization of arthropod development. Development Genes and Evolution 216, 373–383.

Möller, G. (2009). Struktur-und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera-Käfer (Doctoral dissertation). Berlin: Universitätsbibliothek der Freien Universität Berlin, Refubium (Repositorium der Freien Universität Berlin), Dissertationen FU. 284 p.

Motyka, M., Kusy, D., Háva, J., Jahodářová, E., Bílková, R., Vogler, A.P., & Bocak, L. (2022). Mitogenomic data elucidate the phylogeny and evolution of life strategies in Dermestidae (Coleoptera). Systematic Entomology 47, 82–93.

Muona, J., & Teräväinen, M.A. (2008). Notes on the biology and morphology of false click-beetle larvae (Coleoptera: Eucnemidae). The Coleopterists Bulletin 62(4), 475–479.

Muona, J., & Teräväinen, M.A. (2020). Re-assessment of the Eucnemidae larval characters. Papéis Avulsos de Zoologia 60(special issue), art. e202060.

Naugolnykh, S.V., & Ponomarenko, A.G. (2010). Possible traces of feeding by beetles in coniferophyte wood from the Kazanian of the Kama River Basin. Paleontological Journal 44, 468–474.

Nel, A., Roques, P., Nel, P., Prokin, A.A., Bourgoin, T., Prokop, J., Szwedo, J., Azar, D., Desutter-Grandcolas, L., Wappler, T., Garrouste, R., Coty, D., Huang, D., Engel, M.S., & Kirejtshuk, A.G. (2013). The earliest known holometabolous insects. Nature 503(7475), 257–261.

Nicholson, D.B., Ross, A.J., & Mayhew, P.J. (2014). Fossil evidence for key innovations in the evolution of insect diversity. Proceedings of the Royal Society B 281, art. 20141823.

Nielsen, E.S., & Mound, L.A. (1999). Global diversity of insects: the problems of estimating numbers. In Nature and Human Society: The Quest for a Sustainable World eds. P.H. Raven, & T. Williams, 213–222. Washington DC: National Academic Press.

Nikitsky, N.B. (1993). Mushroom-eating beetles (Coloptera, Mycetophagidae) of the fauna of Russia and neighboring countries. Moscow: Moscow State University Press. 183 pp. (in Russian).

Nikitsky, N.B., Osipov, I.N., Chemeris, M.V., Semenov, V.B., & Gusakov, A.A. (1996). Coleoptera: Xylobionts, Mycetobionts, and Scarab Beetles of the Prioksko-Terrasny Nature Biosphere Reserve. Archives of Zoological Museum of Moscow State University 36. Moscow: Moscow State University. 197 pp. (in Russian).

Nikitsky, N.B., Bibin, A.R., & Dolgin, M.M. (2008). Xylophilous beetles (Coleoptera) of the Caucasian State Natural Biosphere Reserve and adjacent territories. Syktyvkar: Russian Academy of Sciences. 254 pp.

Park, J.B., Choi, W.H., Kim, S.H., Jin, H.J., Han, Y.S., Lee, Y.S., & Kim, N.J. (2014). Developmental characteristics of *Tenebrio molitor* larvae (Coleoptera: Tenebrionidae) in different instars. International Journal of Industrial Entomolology 28, 5–9.

Pauchet, Y., Wilkinson, P., Chauhan, R., ffrench-Constant, R.H. (2010). Diversity of beetle genes encoding novel plant cell wall degrading enzymes. PLoS One 5, art. e15635.

Paulian, R. (1942). Larvae of the sub-family Orphilinae and their bearing on the systematic status of the family Dermestidae (Col.). Annals of the Entomological Society of America 35, 35–46.

Payne, J.L., & Clapham, M.E. (2012). End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? Annual Review of Earth and Planetary Sciences 40, 89–111.

Pazinato, P.G., Müller, P., & Haug, J.T. (2023). New species of Tanaidacea from Cretaceous Kachin amber, with a brief review of the fossil record of tanaidacean crustaceans. Fossil Record 26, 39–50.

Penney, D. (2010). Biodiversity of fossils in amber from the major world deposits. Manchester: Siri Scientific Press. 304 pp.

Penney, D., & Jepson, J. E. (2014). Fossil insects: an introduction to Palaeoentomology. Manchester: Siri Scientific Press. 223 pp.

Peris, D. (2020). Coleoptera in amber from Cretaceous resiniferous forests. Cretaceous Research 113, art. 104484.

Peris, D., & Rust, J. (2020). Cretaceous beetles (Insecta: Coleoptera) in amber: the palaeoecology of this most diverse group of insects. Zoological Journal of the Linnean Society 189, 1085–1104.

Peris, D., Solórzano Kraemer, M.M., Peñalver, E., & Delclòs, X. (2015). New ambrosia beetles (Coleoptera: Curculionidae: Platypodinae) from Miocene Mexican and Dominican ambers and their paleobiogeographical implications. Organisms Diversity & Evolution 15, 527–542.

Peris, D., Ruzzier, E., Perrichot,V., & Delclos, X. (2016). Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. Geoscience Frontiers 7(4), 695–706.

Peris, D., Labandeira, C.C., Barron, E., Delclos, X., Rust, J., & Wang, B. (2020). Generalist pollen-feeding beetles during the mid-Cretaceous. Iscience 23(3), art. 100913.

Peris, D., Delclòs, X., & Jordal, B. (2021). Origin and evolution of fungus farming in wood-boring

Coleoptera–a palaeontological perspective. Biological Reviews 96(6), 2476–2488.

Peterson, A. (1951). Larvae of Insects. An Introduction to Nearctic Species. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Larvae of Insects. An Introduction to Nearctic Species. Edward Brothers, Columbus, 416 pp.

Philippe, M., McLoughlin, S., Strullu-Derrien, C., Bamford, M., Kiel, S., Nel, A., & Thévenard, F. (2022). Life in the woods: Taphonomic evolution of a diverse saproxylic community within fossil woods from Upper Cretaceous submarine mass flow deposits (Mzamba Formation, southeast Africa). Gondwana Research 109, 113–133.

Philips, T.K., & Bell, K.L. (2005). 6.4. Ptinidae Latreille, 1802. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 217–225. Berlin, New York: Walter de Gruyter.

Poinar Jr, G. (2010). Palaeoecological perspectives in Dominican amber. Annales de la Société entomologique de France 46, 23–52.

Poinar Jr, G., & Brown, A.E. (2002). *Hymenaea mexicana* sp. nov.(Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. Botanical journal of the Linnean Society 139(2), 125–132.

Poinar, G.O., & Poinar, R. (2008). What bugged the dinosaurs?: insects, disease, and death in the Cretaceous. Princeton: Princeton University Press. 280 pp.

Ponomarenko, A.G. (1963). Palaeozoic cupedid beetles from the European part of the URSS (Coleoptera: Cupedidae). Paleontologicheskij Zhurnal 1, 70–85.

Ponomarenko, A.G. (1969). The historical development of archostematan beetles. (in Russian). Trudy Paleonthologicheskogo Instituta Akademiya Nauk SSSR 125, 1–238.

Ponomarenko, A.G., & Prokin, A.A. (2015). Review of paleontological data on the evolution of aquatic Coleoptera. Paleontological Journal 49, 1383–1412.

Prokin, A.A., & Bashkuev, A.S. (2021). *Trialarva coburgensis* gen. et sp. nov., a remarkable fossil holometabolan larva (Insecta: Coleoptera) from the Triassic of Germany. PalZ 95, 55–60.

Prokin, A.A., Makarov, K.V., Ponomarenko, A.G., & Bashkuev, A.S. (2013). New beetle larvae (Coleoptera: Coptoclavidae, Caraboidea, Polyphaga) from the Upper Triassic of Germany. Russian Entomology Journal 22(4), 259–274.

Prokop, J., Nel, A., & Engel, M.S. (2023). Diversity, Form, and Postembryonic Development of Paleozoic Insects. Annual Review of Entomology 68, 401–429.

Ramsdale, A.S. (2005). 4.16. Omethidae LeConte, 1861. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 149–153. Berlin, New York: Walter de Gruyter

Rasnitsyn, A.P., & Krassilov, V.A. (1996). First find of pollen grains in the gut of Permian insects.

Paleontological Journal 30, 484–90.

Rasnitsyn, A.P., & Müller, P. (2023). Identity of the insect larva described by Zippel et al.(2022) in the mid–Cretaceous Burmese (Kachin) amber (Hymenoptera, Tenthredinoidea, Blasticotomidae= Xyelotomidae, syn. nov.). Palaeoentomology 6, 013–016.

Rayner, A.D., & Boddy, L. (1988). Fungal decomposition of wood. Its biology and ecology. Chichester, Sussex: John Wiley & Sons Ltd. 587 pp.

Rolfe, W.D.I. (1985). Early terrestrial arthropods: a fragmentary record. Philosophical Transactions of the Royal Society of London B, Biological Sciences 309, 207–218.

Rosa, S.P., Costa,C., Kramp, K., & Kundrata, R. (2020). Hidden diversity in the Brazilian Atlantic rainforest: The discovery of Jurasaidae, a new beetle family (Coleoptera, Elateroidea) with neotenic females. Scientific Reports 10, art. 1544.

Ross, A.J. (2008). Book review. What bugged the dinosaurs? By George Poinar Jr And Robert Poinar 2008. Times Higher Education 1841, 50–51.

Ross, A., Mellish, C., York, P., Crighton, B., & Penney, D. (2010). Burmese amber. In Biodiversity of fossils in amber from the major world deposits, ed. D. Penney, 208–235. Manchester: Siri Scientific Press.

Ross, A. J. (2019). Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*, *2*(1), 22–84.

Sadowski, E.M., Schmidt, A.R., Seyfullah, L.J., & Kunzmann, L. (2017). Conifers of the" Baltic Amber Forest" and their palaeoecological significance. Linz: Oberösterreichisches Landesmuseum. 73 pp.

Saint-Germain, M., Buddle, C.M., & Drapeau, P. (2006). Sampling saproxylic Coleoptera: scale issues and the importance of behaviour. Environmental Entomology 35, 478–487

Salem, H., Bauer, E., Kirsch, R., Berasategui, A., Cripps, M., Weiss, B., Koga, R., Fukumori, K., Vogel, H., Fukatsu, T., & Kaltenpoth, M. (2017). Drastic genome reduction in an herbivore's pectinolytic symbiont. Cell 171, 1520–1531.

Savely, H.E. Jr (1939). Ecological relations of certain animals in dead pine and oak logs. Ecological Monographs 9, 321–385.

Schachat, S.R., Labandeira, C.C., Saltzman, M.R., Cramer, B.D., Payne, J.L., & Boyce, C.K. (2018). Phanerozoic pO2 and the early evolution of terrestrial animals. Proceedings of the Royal Society B 285, art. 20172631.

Schädel, M., Mueller, P., & Haug, J.T. (2020). Two remarkable fossil insect larvae from Burmese amber suggest the presence of a terminal filum in the direct stem lineage of dragonflies and damselflies (Odonata). Rivista Italiana di Paleontologia e Stratigrafia 126, 13–35.

Schädel, M., Hyžný, M., & Haug, J.T. (2021). Ontogenetic development captured in amber-the first record of aquatic representatives of Isopoda in Cretaceous amber from Myanmar. Nauplius 29, art.

e2021003.

Schädel, M., Yavorskaya, M., & Beutel, R. (2022). The earliest beetle† Coleopsis archaica (Insecta: Coleoptera) – morphological re-evaluation using Reflectance Transformation Imaging (RTI) and phylogenetic assessment. Arthropod Systematics & Phylogeny 80, 495–510.

Schmidt, A.R., & Dilcher, D.L. (2007). Aquatic organisms as amber inclusions and examples from a modern swamp forest. Proceedings of the National Academy of Sciences, 104(42), 16581–16585.

Scholtz, C., & Grebennikov, V.V. (2005). 13.14. Scarabaeidae. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), vol. 1, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 386–427. Berlin, New York: Walter de Gruyter.

Schoonhoven, L.M., Jermy, T., & van Loon, J.J.A. (1998). Insect-plant Biology: From Physiology to Evolution. London: Chapman & Hall. 409 pp.

Schwalb, H.H. (1960). Beiträge zur Biologie der einheimischen Lampyriden *Lampyris noctiluca* Geoffr. und *Phausis splendidula* LeC. und experimentelle Analyse ihres Beutefang- und Sexualverhaltens. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 88, 399–550.

Scriber, J. M., & Slansky Jr, F. (1981). The nutritional ecology of immature insects. Annual Review of Entomology 26, 183–211.

Shear, W.A., & Kukalová-Peck, J. (1990). The ecology of Paleozoic terrestrial arthropods: the fossil evidence. Canadian Journal of Zoology 68, 1807–1834.

Shepard, W.D., Clavier, S., & Cerdan, A. (2020). A generic key to the known larval Elmidae (Insecta: Coleoptera) of French Guiana. Papéis Avulsos De Zoologia, 60(special), art. e202060(s.i.).15.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., & Li, X. (2012). Age constraint on Burmese amber based on U–Pb dating of zircons. Cretaceous research 37, 155–163.

Ślipiński, S.A., & Lawrence, J.F. (2005). 10.29. Cerylonidae Billberg, 1820. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 422–432. Berlin, New York: Walter de Gruyter.

Ślipiński, S.A., Lawrence, J.F., & Cline, A.R. (2005). 10.34. Corylophidae LeConte, 1852. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, eds. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 472–481. Berlin, New York: Walter de Gruyter.

Ślipiński, S.A., Leschen, R.A.B., & Lawrence, J.F. (2011) Order Coleoptera Linnaeus, 1758. In Animal Biodiversity: An outline of higher-level classification and survey of taxonomic richness, ed. Zhang, Z.-Q. Zootaxa 3148(1), 203–208.

Smith, D.M., & Marcot, J.D. (2015). The fossil record and macroevolutionary history of the beetles. Proceedings of the Royal Society B 282, art. 20150060.

Smith, R.D., & Ross, A.J. (2016). Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 107(2–3), 239–247.

Solórzano Kraemer, M.M. (2007). Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber. Palaeontographica Abteilung A 282, 1–133.

Solórzano Kraemer, M.M. (2010). Mexican amber. In Biodiversity of fossils in amber from the major world deposits, ed. D. Penney, pp. 42–56. Manchester: Siri Scientific Press.

Standke, G. (1998). Die Tertiärprofile der Samländischen Bernsteinküste bei Rauschen. Schriftenreihe für Geowissenschaften 7, 93–133.

Standke, G. (2008). Bitterfelder Bernstein gleich Baltischer Bernstein? - Eine geologische Raum-Zeit-Betrachtung und genetische Schlussfolgerungen. Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften 236, 11–33.

Stehr, F.W. (1991). Immature insects volume 2. Iowa, USA, Kendall/Hunt Publishing Company.

Stehr, F.W. (2009). 148. Larva. In Encyclopedia of insects, eds. V.H. Resh, & R.T. Cardé, 551–552. Burlington, San Diego, London: Academic Press.

Stephenson, S.L., & Stempen, H. (1994). Myxomycetes: A handbook of slime molds. Portland: Timberland Press. 183 pp.

Storch, V., Welsch, U., & Wink, M. (2013). Evolutionsbiologie (3rd ed.). Berlin, Heidelberg: Springer Spektrum. 581 pp.

Stork, N.E., McBroom, J., Gely, C., & Hamilton, A.J. (2015). New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. Proceedings of the National Academy of Sciences of the United States of America 112, 7519–7523.

Švácha, P. (1995). The larva of *Scraptia fuscula* (PWJ Müller)(Coleoptera: Scraptiidae): autotomy and regeneration of the caudal appendage. Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson (eds. J. Pakaluk, & S.A. Ślipiński), 473–489. Varsavia: Muzeum i Instytut Zoologii.

Svácha, P., & Lawrence, J.F. (2014a). 2.3. Disteniidae J. Thomson, 1861. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Phytophaga), vol. 3, eds. R.A.B. Leschen, & R.G. Beutel, 60–77. Berlin, Boston: Walter de Gruyter.

Svácha, P., & Lawrence, J.F. (2014b). 2.4. Cerambycidae Latreille, 1802. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Phytophaga), vol. 3, eds. R.A.B. Leschen, & R.G. Beutel, 77–178. Berlin, Boston: Walter de Gruyter.

Swift, M.J., Heal, O.W., Anderson, J.M.,, & Anderson, J.M. (1979). Decomposition in terrestrial ecosystems (Vol. 5). Berkeley, Los Angeles: University of California Press. 266 pp.

Swift, M. J., Boddy, L., & Healey, I. N. (1984). Wood decomposition in an abandoned beech and oak coppiced woodland in SE England: II. The standing crop of wood on the forest floor with particular reference to its invasion by *Tipula flavolineata* and other animals. Holarctic ecology 7, 218–228.

Szlávecz, K., & Pobozsny, M. (1995). Coprophagy in isopods and diplopods: a case for indirect interaction. Acta Zoologica Fennica 196, 124–128.

Tomaszewska W (2005) 10.32. Endomychidae Leach, 1815. In Handbook of Zoology, Coleoptera, Beetles, Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim), vol. 2, ed. R.A.B. Leschen, R.G. Beutel, & J.F. Lawrence, 442–454. Berlin, New York: Walter de Gruyter.

Tooker, J.F., & Giron, D. (2020). The evolution of endophagy in herbivorous insects. Frontiers in Plant Science 11, art. 581816.

Topalović, O., Hussain, M., & Heuer, H. (2020). Plants and associated soil microbiota cooperatively suppress plant-parasitic nematodes. Frontiers in microbiology 11, art. 313.

Truman, J.W. (2019). The evolution of insect metamorphosis. Current Biology 29(23), R1252–R1268.

Ulyshen, M. D. (2016). Wood decomposition as influenced by invertebrates. Biological Reviews 91, 70–85.

Valente-Neto, F., & Fonseca-Gessner, A.A. (2011). Larvae of *Lutrochus germari* (Lutrochidae: Coleoptera) and *Stegoelmis sp.*(Elmidae: Coleoptera): bore submerged woody debris in Neotropical streams. Zoologia (Curitiba), 28(5), 683–686.

van Huis, A., & Tomberlin, J.K. (2017). Insects as food and feed: from production to consumption. Wageningen: Waningen Academic Press. 447 pp.

Vanin, S.A., & Costa, C. (2011). Description of the larva of *Potamophilops cinereus* (Blanchard) from Southeastern Brazil (Coleoptera, Elmidae, Larainae). Zootaxa 2808, 57–63.

Vanin S.A., Ide S., Casari S.A., & Costa C. (1996). Larvae of Neotropical Coleoptera, XXIV: *Scraptia triangularis* Champion, description of immatures and redescription of adult (Tenebrionoidea, Scraptiidae). Revista Brasileira de Entomologia 40, 89–96.

Waloszek, D. (2003). The 'Orsten'window—a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthropoda. Paleontological Research 7, 71–88.

Warmke, S., & Hering, D. (2000). Composition, microdistribution and food of the macroinvertebrate fauna inhabiting wood in low-order mountain streams in Central Europe. International Review of Hydrobiology 85, 67–78.

Wedmann, S., Hoernschemeyer, T., & Schmied, H. (2011). Fossil water-penny beetles (Coleoptera: Psephenidae: Eubrianacinae) from the Eocene of Europe, with remarks on their phylogenetic position and biogeography. Palaeontology 54(5), 965–980.

Whalley, P. (1987). Insects and Cretaceous mass extinction. Nature 327, p. 562.

Weitschat, W. & Wichard, W. (2010). Baltic Amber. In Biodiversity of fossils in amber from the major world deposits, ed. D. Penney,80–115. Siri Scientific Press, Manchester.

Wichard, W., & Weitschat, W. (2004). Im Bernsteinwald. Hildesheim: Gerstenberg Verlag. 168 pp.

Wichard, W., Gröhn, C., & Seredszus, F. (2009). Aquatic Insects in Baltic Amber. Remagen-Oberwinter: Verlag Kessel. 336 pp.

Wickham, H.F. (1912). A report on some recent collections of fossil Coleoptera from the Miocene shales of Florissant. Bulletin from the Laboratory National History University, Iowa 6, 3–38.

Wiegmann, B.M., Kim, J.W., & Trautwein, M.D. (2009). Holometabolous insects (holometabola). The timetree of life 31, 260–263.

Wolfe, A.P., Tappert, R., Muehlenbachs, K., Boudreau, M., McKellar, R.C., Basinger, J.F., & Garrett, A. (2009). A new proposal concerning the botanical origin of Baltic amber. Proceedings of the Royal Society B, Biological Sciences 276, 3403–3412.

Wood, D.L. (1982). The role of pheromones, kairomones, and allomones in the host selection and colonization of bark beetles. Annual Review of Entomology 27, 411–446.

Yan, E., Beutel, R.G., & Ponomarenko, A.G. (2017a) Peltosynidae - a new beetle family from the middle-late Triassic of Kirghyzia - its affinities to Polyphaga (Insecta, Coleoptera) and the groundplan of the megadiverse suborder. Journal of Systematic Palaeontology 16, 515–530.

Yan, E.V., Beutel, R.G., & Ponomarenko, A.G. (2017b). †Ademosynidae (Insecta: Coleoptera) – a new concept for a coleopteran key taxon and its phylogenetic affinities to the extant suborders. Palaeontologica Electronica 20, 1–22.

Yan, E.V., Lawrence, J.F., Beattie, R., & Beutel, R.G. (2018) At the dawn of the great rise: †Ponomarenkia belmonthensis (Insecta: Coleoptera), a new remarkable late Permian beetle from the southern hemisphere. Journal of Systematic Palaeontology 16, 611–619.

Yan, E.V., Beutel, R.G., Lawrence, J.F., Yavorskaya, M.I., Hörnschemeyer, T., Pohl, H., Vassilenko, D.V., Bashkuev, A.S., & Ponomarenko, A.G. (2020) Archaeomalthus - (Coleoptera, Archostemata) a “ghost adult” of Micromalthidae from upper Permian deposits of Siberia? Historical Biology 32, 1019–1027.

Yensen, E. (1980). A revision of the North American species of *Trixagus kugelann* (Coleoptera: Throscidae) American Entomological Society 101, 125–166

Zemoglyadchuk, A.V., & Buialskaya, N.P. (2020). Description of the larvae of three species of the genus *Mordellistena* (Coleoptera: Mordellidae) with notes on their ecology. Zootaxa 4743(3), 371–381.

Zhang, S.Q., Che, L.H., Li, Y., Liang, D., Pang, H., Ślipiński, A., Zhang, P. (2018). Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. Nature Communications

9, art. 205.

Zhao, X., Zhao, X., Jarzembowski, E., Tian, Y., & Chen, L. (2020). The first record of brachypsectrid larva from mid-Cretaceous Burmese amber (Coleoptera: Polyphaga). Cretaceous Research 113, art. 104493.

Zippel, A., Kiesmüller, C., Haug, G.T., Müller, P., Weiterschan, T., Haug, C., Hörnig, M.K., & Haug, J.T. (2021). Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. Palaeoentomology 4, 475–498.

Zippel, A., Baranov, V.A., Hammel, J.U., Hörnig, M.K., Haug, C., & Haug, J.T. (2022c). The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10, art. e13025. (**Article 3**)

Zippel, A., Haug, C., Gauweiler, J., Hörnig, M.K., Haug, G.T., & Haug, J.T. (2022d). A small beetle larva preserved in 23-million-year-old Mexican amber: possible first fossil record of an immature variegated mud-loving beetle. Boletín de la Sociedad Geológica Mexicana 74, art. A150322.

Zippel, A., Haug, C., Hoffeins, C., Hoffeins, H.-W., & Haug, J.T. (2022a). Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia 128, 81–104. (**Article 4**)

Zippel, A., Haug, C., Müller, P., & Haug, J.T. (2022b). First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96, 219–229. (**Article 5**)

Zippel, A., Cao, Q., & Betz, O. (2023a). Morphology of the abdominal segmental glands and spinning behaviour of Stenus larvae (Coleoptera, Staphylinidae). Arthropod Structure & Development 75, art. 101286.

Zippel, A., Haug, C., Müller, P., & Haug, J.T. (2023b). The first fossil false click beetle larva preserved in amber. PalZ 97, 209–215. (**Article 6**)

Zippel, A., Haug, C., Müller, P., & Haug, J.T. (in REVISION). Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ. (**Article 8**)

Zippel, A., Haug, C., Elverdi, Z, Müller, P., & Haug J.T. (in REVISION). Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Miocene and Cretaceous ambers. Fossil Record. (**Article 9**)

7. ACKNOWLEDGEMENTS:

First of all, I want to thank Prof. Dr. Joachim T. Haug (Munich). Dear Joachim, thank you for giving me the 'once-in-a-lifetime' opportunity that changed my life for the better. Thank you for recognizing my hard work and my potential, and for pushing me into many things I would have not dared on my own. You and your family restored my faith in people, I see now there are many good people ready to help while still persisting in doing what they love with their full hearts. You have been indeed a great mentor. Not only in the scientific manner, where you opened many new horizons for me, thought me so much, and showed me it is ok to agree to disagree, but also as a person and a friend, showing me that there is a place in the academic society for genuine people relying only on their hard work.

Secondly, I want to say a huge thank you to PD Dr. Carolin Haug (Munich). Dear Carolin, I need to thank you for your always-open arms, and your readiness to help with any kind of problem, professional or personal. Thank you for all the lovely cooperations and conversations. I thank you for your endless support and everything else you have done with and for me. Thank you for your honest and caring guidance. After almost three years, I dare to say I see you as a true friend. I am looking forward to future conversations, parties and enjoying life together.

I also want to thank Prof. Dr. J. Matthias Starck and PD Dr. Michael Raupach (both Munich). Dear Prof. Dr. Starck, dear Michael, thank you for agreeing to take this journey with me. I appreciate the honest and constructive critiques and different inputs that helped me widen my views and improve my thesis even more. Thank you for your support.

The next set of 'thank yous' goes to the colleagues that made this journey so much fun. I could have not asked for a more helpful and positive group of colleagues. Dear Dr. Viktor A. Baranov and Ms. Valentyna Inshyna (both Sevilla) I will always remember you as the first colleagues I met after moving to Munich. Thank you for being very welcoming and helpful in those confusing pandemic-driven days. Dear Florian Braig, dear André Pereira do Amaral, dear Jehan Le Cadre (all Munich), the three black-bearded men, and dear Dr. Sofía I. Arce (Munich), thank you for your time, your compassion, and your help. Dear Paula G. Pazinato (Brazil), and Serita van der Wal (Finnland), even though our encounters and cooperations were rare and often short, they were always remembered as nice moments. Thank you for these positive memories. Dear Dr. Marie K. Hörnig (Rostock), dear Christine Kiesmüller (Greifswald) dear Joshua Gauweiler (Greifswald), it is always nice to see you again. Thank you for the cooperation, support, and all the lovely conversations we had. Dear Simon J. Linhard, dear Timo Popp, dear Colin Hassenbach, dear Laura Buchner (all Munich), dear Beñat Yáñez Iturbe-Ormaeche (UK), dear Zeynep Elverdi (Turkey) thank you for your help in imaging and processing of some specimens from my thesis. I also want to thank Ms. Ulrike Wimmer. Dear Ulrike, thank you for your technical support and help with everyday work-related problems.

I wish to show appreciation for the scientists I met over the SYNTHESYS+ project, as well. Dear Prof. Dr. Alexey Solodovnikov, dear Prof. Dr. Lars Vilhelmsen, and Prof. Dr. Martin Vinther Sørensen (all Denmark) thank you for your support and help over the three weeks I spent in the Natural History Museum of Denmark in Copenhagen. Dear Lars, big thank you for lending me all the amber specimens from the Amber Collection I needed.

Additionally, I would like to thank my colleagues from the University of Zagreb and Croatian Natural History Museum (Zagreb) that were extremely willing to help with the samples of extant beetle larvae. The biggest thank you goes to Prof. Dr. Mladen Kučinić (Croatia) that went an

extra mile and brought the specimens directly to Munich. Thank you Prof. Dr. Maria Špoljar, Prof. Dr. Boris Hrašovec, Prof. Dr. Vlatka Mičetić Stanković (all Croatia). I am looking forward to future 'kave' and cooperations that might develop while at them.

I wish to thank private collectors that generously shared their amber specimens with me. Thank you Mr. Patrick Müller (Zweibrücken), Ms. Christel Hoffeins and Mr. Hans-Werner Hoffeins (both Hamburg). I am also thankful to all the people providing open access programs, all the reviewers that helped improve my numerous manuscripts, museum curators, and all the other colleagues that enriched my journey towards my promotion.

I cannot forget to thank my lifelong friends for their support and love over so many years. Dear Andrea Ivanković, dear Suzana Šamec, dear Silvija Matulić, dear Dubravko Pogledić, thank you for being you, every moment together is a blessing. Especially you dear Andi, without your friendly nudge I possibly would have never sent the application for the 'job of my dreams'. Thank you!

In the end, I wish to acknowledge and thank the most important people in my life – my family: my parents, my sister, my two boys and my husband.

Dragi mama i tata, hvala vam na neograničenoj ljubavi, bezbrojnim mogućnostima koje ste mi pružili i stalnoj potpori kada mi je god zatrebala. Hvala vam što ste mi usadili prave vrijednosti i pokazali mi da se za dobre stvari u životu isplati boriti. Nadam se da ste i vi zadovoljni i ponosni na sve moje uspijehe. Volim vas.

My dearest sister, you are the Iva to my Ana, the best sister one can ever wish for. Thank you for everyday support and love, you know I will be there for you the way you always were for me. Volim te.

My dearest Peter and Jakob, my two little larvae, thank you for being childishly honest but also so grown-up patient. It makes me very happy to see how proud you are of mommy´s cool job. Thank you for your understanding and support during my promotion, especially in searching for specimens in the cold creeks. Mommy will have a bit more time for playing now. I love you!

To my husband, Sebastian Zippel, my soulmate and my rock, thank you. You have always been supportive of this path I have chosen and helped me in every way possible. Without you and your endless patience, this would have probably not been doable. We have been through so many situations, some good and some bad, and yet I still look forward to many more with you. I cannot wait to see which new memories the future adventures hold for us. I love you.

Ana Zippel - Curriculum Vitae

Affiliation

LMU Munich, Faculty of Biology, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

ORCiD nr.	0000-0002-6509-4445

Academic education and career

25/10/2023	disputation of PhD studies
01/12/2020 – present	PhD studies and employment, LMU Munich
10/2015 – 07/2020	Master of Science, Tübingen University
07/2003 – 11/2009	Master of Educational Biology, University of Zagreb

Scholarships, awards, external funding

21/09/2023	Young Scientists Award for oral presentation “Specialized morphological characters of wood associated beetle larvae for hunting or defense in deep time” (200 €)
24/10 –11/11/2022	SYNTHESYS+ grant for three-weeks work and stay in Copenhagen, at Natural History Museum of Denmark, funded by European Comission (c. 3,500 €)
01/06 – 29/08/2022	Bachelor student internship through DAAD RISE program funded by the German Federal Foreign Office (c. 2,500 €)
09/2008 – 01/2009	Scholarship for one semester at the Uppsala University, Sweden (c. 2,500 €)

Research visits

11/04 – 16/04/2023	Visit to the insects collection of the Croatian Natural History Museum and Biological Department of University of Zagreb
20/02 – 24/02/2023	Visit to the insects collection of the Staatliches Naturhistorisches Museum Braunschweig
24/10 –11/11/2022	Visit to the amber and insects collection of the Natural History Museum of Denmark
18/11/2021	Visit to the amber collection of the Naturkundemuseum Stuttgart

Contributions at conferences

Zippel, A., Haug, C., & Haug, J.T. 2023. Talk. Wood-associated larvae in different ambers. Paläoentomologentreffen 2023, Frankfurt/Main (04/11 – 05/11/2023).

Zippel, A., Haug, C., Hörnig, M., & Haug, J.T. 2023. Talk. Specialized morphological characters of wood-associated beetle larvae for hunting or defense in deep time. 94. Jahrestagung der Paläontologischen Gesellschaft (PalGes), Jena (18/09 – 22/09/2023).

Zippel, A., Haug, C., Hörnig, M., & Haug, J.T. 2023. Poster. The morphology of mandibles of wood-associated beetle larvae. 94. Jahrestagung der Paläontologischen Gesellschaft (PalGes), Jena (18/09 – 22/09/2023).

Zippel, A., Arce, S.I., Kiesmüller, Linhart, S.J., C., Haug, C., & Haug, J.T. 2023. Talk. Wood boring beetle larvae and the study of plant-parasitism in deep time. 115th meeting of the German zoological society (DZG), Kassel (04/09 – 08/09/2023).

Zippel, A., Haug, C., Yáñez Iturbe-Ormaeche, B., & Haug, J.T. 2022. Talk: What does it take to live in wood? The fossil record of wood-associated beetle larvae and their impact on past ecosystems. 93. Jahrestagung der Paläontologischen Gesellschaft, Stuttgart (19/09 –23/09/2022).

Zippel, A., & Haug, J.T. 2022. Talk: Hidden within the plant: morphology of fossil xylophagous beetle larvae. 5th International Congress on Invertebrate Morphology, Vienna (08/08 – 12/08/2022).

Zippel, A., & Haug, J.T. 2022. Talk: Where to breathe – a comparisson of gill positions among crustaceans. 20. Crustaceologen-Tagung, Kiel (07/04 – 10/04/2022).

Zippel, A., Haug, C., Hoffeins, C., Hoffeins, H.-W., & Haug, J.T. 2021. Poster: The morphology of extant and fossil larvae of false flower beetles with prominent terminal ends. 113. Jahrestagung – DZG 2021, virtually (30/08 – 03/09/2021).

Teaching activities

- Supporting and mentoring of Bachelor and Master students during their theses, LMU Munich (01/12/2020 – present)
- Supporting and mentoring of international DAAD RISE student, LMU Munich (01/06 – 29/08/2022)
- Supporting and mentoring of students during *Arthropoda* course, LMU Munich (18/10 – 05/11/2021)
- Supporting and mentoring of students during *Evolutionary Developmental Biology of Arthropods* course, LMU Munich (29/06 – 16/07/2021)
- Educative programs about plants and environment, Botanical Garden of Tübingen University (04/2018 – 11/2020)
- Practical course *Ecology and Biodiversity Practicum* as an assistant, Tübingen University (07/2017)
- Lecturing and practical programs as a teacher of biology and chemistry, Primary school (5 – 8. Grade), Zagreb (2011 – 2012)
- Educative programs about nature and animals, Zagreb Zoological Garden (02/2010 – 09/2011)

Publications

Peer-reviewed publications in journals

Haug, C., Haug, G.T., **Zippel, A.**, van der Wal, S. & Haug, J.T. 2021. The earliest record of fossil solid-wood-borer larvae—immature beetles in 99 million-year-old Myanmar amber. Palaeoentomology 4, 390–404.

Haug, C., Posada Zuluaga, V., **Zippel, A.**, Braig, F., Müller, P., Gröhn, C., Weiterschan, T., Wunderlich, J., Haug, G.T. & Haug, J.T. 2022. The morphological diversity of antlion larvae and their closest relatives over 100 million years. Insects 13, 587.

Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. 2022. A modern type of ant-like stone beetle larva preserved in 99-million-year-old Kachin amber. Fragmenta entomologica 54(2), 193–200.

Haug, C., **Zippel, A.,** Hassenbach, C., Haug, G.T. & Haug, J. T. 2022. A split-footed lacewing larva from about 100-million-year-old amber indicates a now extinct hunting strategy for neuropterans. Bulletin of Geosciences 97(4), 453–464.

Haug, C., Pérez-de la Fuente, R., Baranov, V., Haug, G.T., Kiesmüller, C., **Zippel, A.**, Hörnig, M.K. & Haug, J.T. 2023. The first fossil record of a mantis lacewing pupa, and a review of pupae in Mantispidae and their evolutionary significance. RIPS 129, 185–205.

Haug, C., **Zippel, A.**, Müller, P. & Haug, J.T. 2023. Unusual larviform beetles in 100-million-year-old Kachin amber resemble immatures of trilobite beetles and fireflies. PalZ.

Haug, J.T., Haug, G.T., **Zippel, A.**, van der Wal, S., Müller, P., Gröhn, C., Wunderlich, J., Hoffeins, C., Hoffeins, H.-W. & Haug, C. 2021. Changes in the morphological diversity of larvae of lance lacewings, mantis lacewings and their closer relatives over 100 million years. Insects 12, art. 860.

Haug, J.T., **Zippel, A.**, Haug, G.T., Hoffeins, C., Hoffeins, H.-W., Hammel, J.U., Baranov, V. & Haug, C. 2021. Texas beetle larvae (Brachypsectridae) – the last 100 million years reviewed. Palaeodiversity 14, 161–183.

Zippel, A., Kiesmüller, C., Haug, G.T., Müller, P., Weiterschan, T., Haug, C., Hörnig, M.K. & Haug, J.T. 2021. Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. Palaeoentomology 4, 475–498.

Zippel, A., Baranov, V.A., Hammel, J.U., Hörnig, M.K., Haug, C. & Haug, J.T. 2022. The first fossil immature of Elmidae: an unusual riffle beetle larva preserved in Baltic amber. PeerJ 10, e13025.

Zippel, A., Haug, C., Gauweiler, J., Hörnig, M.K., Haug, G.T. & Haug, J.T. 2022. A small beetle larva preserved in 23-million-year-old Mexican amber: possible first fossil record of an immature variegated mud-loving beetle. Boletín de la Sociedad Geológica Mexicana 74, A150322.

Zippel, A., Haug, C., Hoffeins, C., Hoffeins, H.-W. & Haug, J.T. 2022. Expanding the record of larvae of false flower beetles with prominent terminal ends. Rivista Italiana di Paleontologia e Stratigrafia 128, 81–104.

Zippel, A., Haug, C., Müller, P. & Haug, J.T. 2022. First fossil tumbling flower beetle-type larva from 99 million-year-old amber. PalZ 96, 219–229.

Zippel, A., Cao, Q., & Betz, O. 2023. Morphology of the abdominal segmental glands and spinning behaviour of Stenus larvae (Coleoptera, Staphylinidae). Arthropod Structure & Development 75, art. 101286.

Zippel, A., Haug, C., Müller, P. & Haug, J.T. 2023. The first fossil false click beetle larva preserved in

amber. PalZ 97, 209–215.

Zippel, A., Haug, C., Elverdi, Z, Müller, P., & Haug J.T. 2023. Possible fungus-eating cucujiformian beetle larvae with setiferous processes from Miocene and Cretaceous ambers. Fossil Record 26, 191–207.

Zippel, A., Haug, C., Müller, P., & Haug, J.T. accepted. Elateriform beetle larvae preserved in about 100-million-year-old Kachin amber. PalZ.

Zippel, A., Haug, C., Yáñez Iturbe-Ormaeche, B., & Joachim T. Haug. in revision. Diversity of archostematan beetle larvae through time with a new fossil. Palaeodiversity.