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ORIGINAL PAPER

35 million-year-old solid-wood-borer beetle larvae support the idea of stressed Eocene amber forests

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Abstract

Eocene amber is an important window into the past about 35 million years ago. The large quantities of resin produced by this forest of the past, resulting in amber, triggered the idea of a forest under stress. Recent findings of higher abundances of hoverfly larvae in Eocene amber, in the modern fauna often associated with wood-borer larvae, provided a hint that wood-borer larvae may have contributed to this stress. Yet, so far only few such larvae have been reported. We have compiled a dozen additional wood-borer larvae in amber, including a giant one of at least 35 mm length in Rovno amber. Heavily damaged fossils furthermore indicate that larger larvae of this type were prone to oxidation and that, at least some, enigmatic tube-like tunnels in larger amber pieces may represent remains of large wood-borer larvae. This find strongly indicates that wood-borer larvae were not rare, but common in the Eocene amber forest, which is compatible with the high abundances of hoverfly larvae and further supports the idea of a forest under stress. Whether the possible higher abundances of wood-borer larvae were the cause of the stress or a symptom of an already stressed forest remains so far unclear.

Keywords Cerambycidae · Buprestidae · Rovno amber · Baltic Eocene · Fossil ecosystems

Introduction

Amber provides a unique view into past ecosystems, preserving animals in an almost life-like manner. Therefore, fossils preserved in amber are an ideal source for any comparison with the modern fauna. Still, many aspects of the amber forest remain unclear, for example the factors leading to the large amount of resin production in the amber forests (Penney 2016). It has been suggested that the extensive production of resin at least in some amber forests was a result of stress (McKellar et al. 2011; Seyfullah et al. 2018). More precisely, water stress of the resin-producing trees might have been the cause (Martínez-Delclòs et al. 2004; Labandeira 2014; Seyfullah et al. 2018), possibly mediated by drought, flood diseases, wildfires, or plant parasites (though the impact of plant parasites has been questioned: Peris et al. 2016; Peris and Rust 2020; but see also Peris 2020 and Peris et al. 2021).

Baranov et al. (2021) recently reported a large number of hoverfly larvae (Syrphidae) of the group Volucellini preserved in Baltic amber. These larvae resemble modern hoverfly larvae that co-occur with wood-borer moth larvae (Cossidae, Lepidoptera), feeding on the plant juices that seep after the moth larvae have damaged the plants (Speight 2010). Other extant larvae of Volucellini are associated with nests of eusocial hymenopterans (Marshall 2012). Such hymenopterans are rare in ambers, making it unlikely that the fossil larvae of

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Volucellini had such a life style (Baranov et al. 2021). Presumably, the hoverfly larvae represent an indirect indication of the presence of a specific type of plant parasites, namely wood-borer larvae in the Eocene amber forest; in fact, also larger abundances of them might be expected (see discussion in Baranov et al. 2021). Although in the modern fauna these seem mostly wood-borer larvae of the group Lepidoptera, also other types of wood-borer larvae could be expected to co-occur with the hoverfly larvae.

Actual fossils of solid-wood-borer larvae (mostly larvae of Buprestidae and Cerambycidae; for details see discussion in Haug et al. 2021) have so far only been occasionally reported in amber (e.g. Larsson 1978; Klausnitzer 2003; Nel et al. 2004; Peris 2020; Peris and Rust 2020). Larvae associated with rotting, i.e. dead wood seem to be more common (e.g. Micromalthidae: Kirejtshuk and Azar 2008; Perkovsky 2016; Eucnemidae: Chang et al. 2016; Scraptiidae: Haug and Haug 2019; Zippel et al. 2022a,b). Furthermore, larvae boring in solid wood have only rarely been figured (one specimen of Buprestidae in Cretaceous New Jersey amber: Grimaldi and Engel 2005, fig. 10.36, p. 381; two specimens of Cerambycidae in Eocene Baltic amber: Bachofen-Echt 1949; Gröhn 2015). Only recently, some larvae clearly representing solid-wood borers (Buprestidae and Cerambycidae) have been described with some detail from the Cretaceous, based on four specimens in 99 million-year-old Myanmar amber (Haug et al. 2021).

Overall, these finds provide a conflicting impression of the situation in amber forests. We have indirect indicators that the trees were under stress; this stress might have (partly) been caused by wood-borer larvae (but see also contradictory studies above), which then should have been a rather common component of the fauna. However, such larvae have so far only very rarely been found, indicating that they were not a common component.

Here we report new larvae of the beetle groups Buprestidae and Cerambycidae, representing solid-wood borers, from Eocene ambers (Baltic and Rovno amber; c. 35 million years old; for age determination, see, e.g. Perkovsky et al. 2010; Sukhomlyn et al. 2021; Matalin et al. 2021). We demonstrate that solid-wood-borer larvae seem to be much more common in ambers than so far anticipated.

Material and Methods

Material

In total, 13 specimens preserved in twelve pieces of amber were investigated. Ten amber pieces with eleven specimens are from Baltic amber, possibly some from the Yantarny mine, Kaliningrad Oblast, Sambian Peninsula (Russia), but the exact origin is unclear: SNSB-BSPG 2018 III 80 (Staatliche Naturwissenschaftliche Sammlungen Bayerns—Bayerische Staatssammlung für Paläontologie und Geologie, München), NHMD-157126 (Natural History Museum of Denmark, Copenhagen), SMF Be 8018, SMF Be 10595 (both Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main), PED 1393, PED 1394 (with two specimens), PED 1410, PED 1477, PED 1601, PED 1602 (all publicly accessible at the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München). All PED specimens were legally purchased from various traders: Marius Veta, Vilnius, ambertreasure4u.com; AmberTreeLab via the platform etsy.com; Jonas Damzen, Vilnius, amberinclusions.eu; Rafiq A. Bhat, Pahalgam, Stars Magic Gems.

Two additional amber pieces with two specimens are Ukrainian Rovno amber, both from Varash district, Rovno Oblast: SIZK L-957 (Schmalhausen Institute of Zoology, Kiev) and PED 1479. The PED piece was legally purchased from a private collector and officially exported.

For comparison, an extant solid-wood-borer beetle larva of Cerambycidae was documented. The specimen is part of the collection of the Centrum für Naturkunde (CeNak), Leibniz-Institut zur Analyse des Biodiversitätswandels (LIB) Hamburg (ZMH 828298).

Some newly prepared volume renders of specimens of hoverfly larvae reported by Baranov et al. (2021) are shown for background information (Fig. 1a–e). For details about these specimens and methods, see Baranov et al. (2021).

Methods

Amber specimens were mostly documented with optical methods. Most specimens were documented on a Keyence VHX-6000 digital microscope with standardised settings (Haug et al. 2019). All images are composite images (Haug et al. 2011), including imaging under different exposure times (Haug et al. 2013a). Some images are stereo anaglyphs based on virtual surfaces (Haug et al. 2013b, 2019). Larger amber pieces were scanned entirely with a flat-bed scanner (Haug et al. 2013c).

X-ray micro-computed tomography (μCT) of PED 1479 was performed using an XRadia MicroXCT-200 (Carl Zeiss Microscopy GmbH, Jena, Germany) equipped with switchable scintillator-objective lens units. Scanning parameters were: (1) overview: 0.39x objective, x-ray source settings: 40 kV, 8 W, exposure time 5.5 s, binning 2, image stack properties: 1024 x 1024 px, system-based calculated pixel size of 37.25 μm; (2) head: 0.39 x objective, x-ray source settings: 40 kV, 8 W, exposure time 5 s, binning 2, image stack properties: 1024 x 1024 px, system-based calculated pixel size of 25.96 μm. Tomographic images were reconstructed using XMReconstructor (Carl Zeiss Microscopy GmbH, Jena, Germany), resulting in image stacks (TIFF format). Tiff image

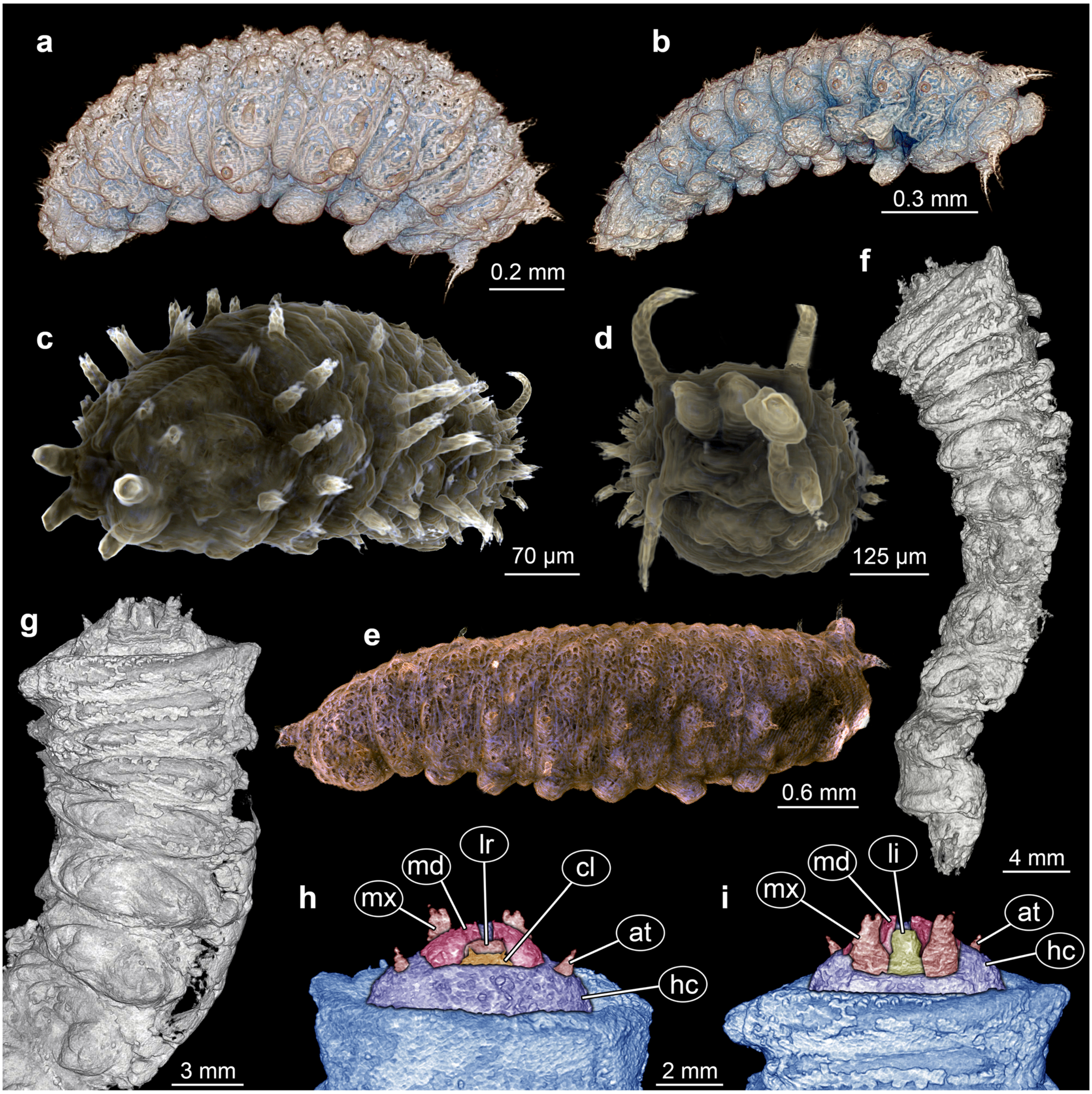

Fig. 1 Volume renders of SRμCT and μCT scans of fossils from Eocene amber. **a–e** Hoverfly larvae of the group Volucellini. **a, b** Dip-00889. **a** Latero-ventral view. **b** Ventral view. **c, d** Dip-00895. **c** Oblique frontal view. **d** Terminal view. **e** Dip-00894, lateral view. **f–i** PED 1479, Rovno amber, giant larva of longhorn beetle (Cerambycidae). **f** Habitus in ventral view. **g** Close-up on anterior body region. **h** Close-up on head region in dorsal view. **i** Close-up on head region in ventral view. Abbreviations: *at* antenna; *cl* clypeus; *hc* head capsule; *li* labium; *lr* labrum; *md* mandible; *mx* maxilla

stacks were postprocessed in Fiji (Schindelin et al. 2012). Volume renderings based on μCT data were generated using Amira 6 (FEI, Thermo Fisher Scientific) and Drishti 2.7 (Limaye 2012).

The extant specimen was documented with a super-macro-photographic setup (Canon EOS 650D + MP-E 65 mm) in its original storage liquid (70% ethanol). Lighting was provided by two Yongnuo Digital Speedlite YN560EX II flashes equipped with polarisation filters. Another polarisation filter was placed in front of the lens and arranged perpendicular to those on the flashlights, providing cross-polarized light (Haug et al. 2011). Also these images were recorded as composite images.

The larvae of Volucellini were scanned at the PETRA III (DESY Hamburg). For details of the methods, see Baranov et al. (2021).

Results

The screening of the above mentioned collections revealed an unexpected wealth of wood-borer larvae. Among the discovered specimens is a very large larva of at least 35 mm in length (Figs. 1f, g, 2b) preserved in a large piece of Rovno amber (Fig. 2a). Details of the head are not well accessible with light microscopy, but with μCT. Antennae short, clypeus and labrum well developed, prominent mandibles, other mouthparts small without prominent endites, palps only short (Fig. 1h, i). The head is distinctly surrounded by the anterior trunk (prothorax). The body is rather soft with distinct folds, but without sclerites. Ventrally, the anterior trunk segments (thorax) bear three pairs of tiny legs (Fig. 2c). Overall this arrangement is very similar to that in extant larvae of Cerambycidae (longhorn beetles; Fig. 2d).

Very similar appearing larvae occur in different body sizes. These reach from tiny ones (Fig. 3b), probably

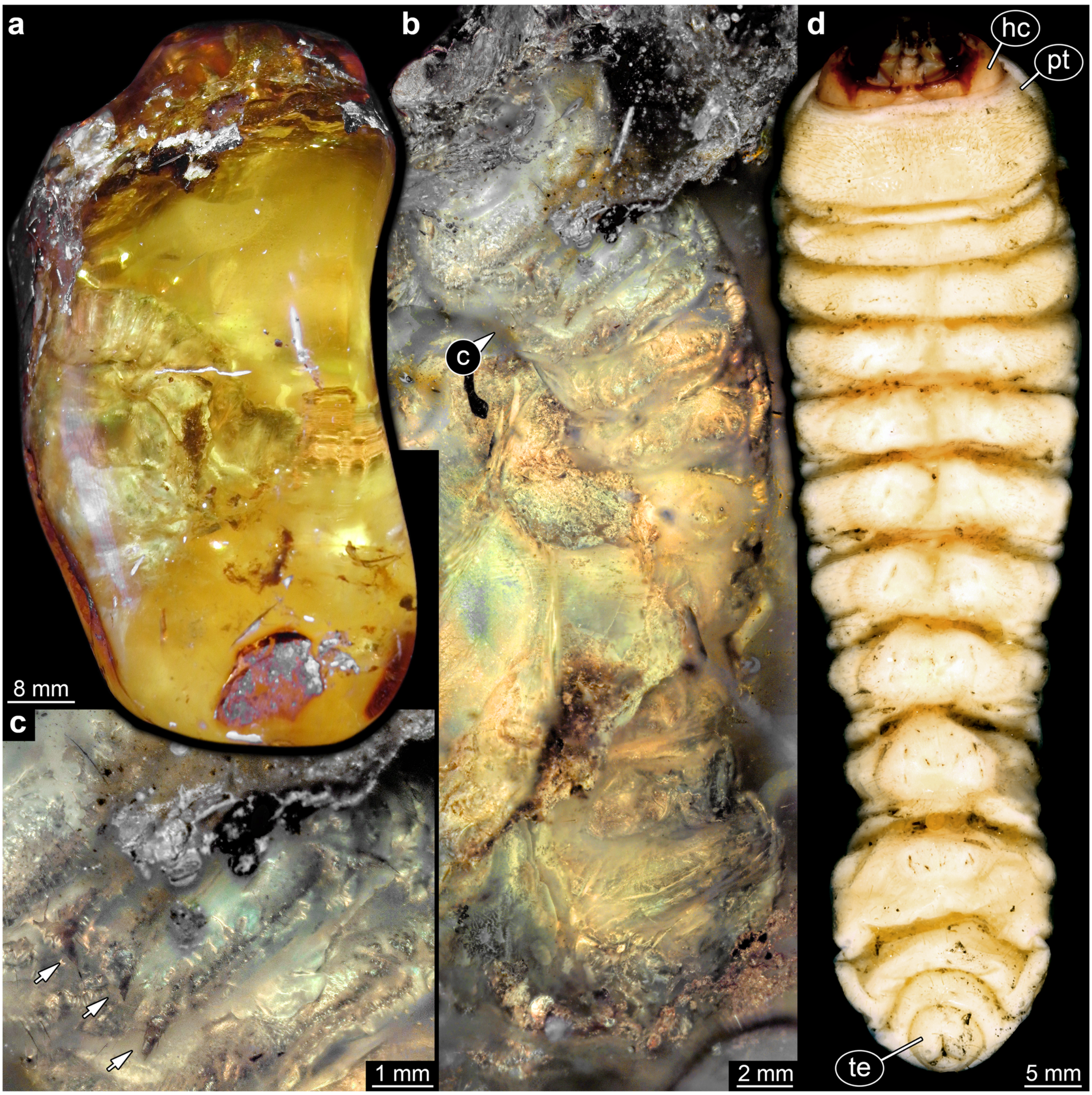

Fig. 2 PED 1479, Rovno amber, giant larva of longhorn beetle (Cerambycidae), continued and extant comparison. **a** Overview of entire amber piece. **b** Overview of specimen. **c** Detail of small legs (arrows). **d** Extant larva of Cerambycidae for comparison (ZMH 828298). Abbreviations: *hc* head capsule; *pt* prothorax

Fig. 3 Additional specimens of wood-borer larvae in Eocene ambers. **a–d, g, i** Cerambycidae, **e, f, h** Buprestidae. **a** Rovno amber, SIZK L-957. **b–i** Baltic amber. **b** NHMD-157126. **c** PED 1410. **d** PED 1393. **e, f** PED 1394. **e** Specimen 1. **f** Specimen 2. **g** SMF Be 8018. **h** SNSB-BSPG 2018 III 80. **i** PED 1477

representing early stage larvae as mentioned in Larsson (1978) and Klausnitzer (2003), over slightly larger ones (Fig. 3e–h) and some of almost one centimetre in size (Fig. 3c, d) up to further specimens reaching into the centimetre range (Figs. 3a, i, 4a, b, h).

An important detail of the larger specimens is that many of them are incomplete (Fig. 4). Larger animals are often not fully embedded into the amber as the resin flow was only partly able to cover them (e.g. birds: Xing et al. 2017, 2019, 2020; lizards: Daza et al. 2016; Čerňanský et al. 2022). After the carcass is rotten, this leaves a large cavity in the amber. While well preserved in the area where the specimen is embedded inside the amber, the other side is often heavily damaged (compare two sides of the same specimen: Fig. 4c vs. Fig. 3d; Fig. 4d vs. Fig. 3i; Fig. 4e vs. Fig. 3a). The inclusion is exposed here and appears to oxidise and simply crumble away.

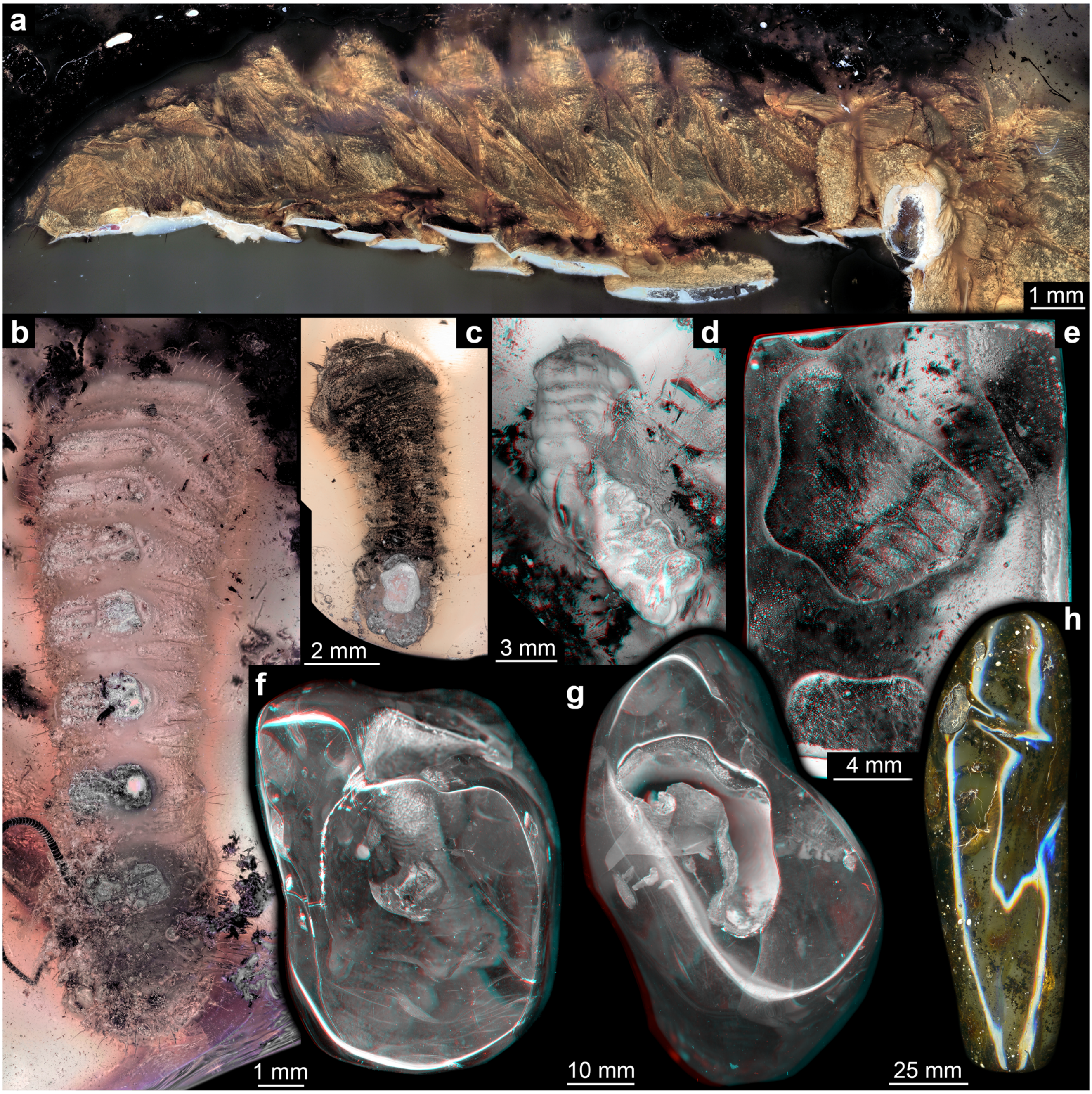

Fig. 4 Additional specimens of wood-borer larvae in Eocene ambers. **a–e** Cerambycidae. **a** PED 1601, partial specimen. **b** SMF Be 10595. **c–e** Backsides of some larvae showing their damaged condition. **c** PED 1393. **d, e** Stereo anaglyphs (please use red-cyan glasses to view). **d** PED 1477. **e** SIZK L-957. **f, g** PED 1602, stereo anaglyphs, with tube-like tunnel in large amber piece, possibly representing remain of a wood-borer larva. **h** Overview of large amber piece, PED 1601 (in **a**)

There are rather large amber pieces with tube-like tunnels through them with a heavily oxidised and entirely destroyed surface (Fig. 4f, g). These tubes are in the size range of some of the larger larvae reported here. We suggest that one possible origin of these tubes is that originally a wood-borer larva was embedded, but not fully. It then rotted and the surface of the inclusion became heavily oxidised, leaving no detail of the original larva.

Discussion

Identity of the specimens

Convergent specialisation to wood boring seems to lead to similar morphologies in beetle larvae and other larvae of Holometabola. The larvae reported here are interpreted either as larvae of the group Buprestidae (jewel beetles; Fig. 3e, f, h) or Cerambycidae (longhorn beetles; Figs. 2, 3a–d, g, i). Many modern jewel beetle larvae have a distinct V-shaped fold on the prothorax, well apparent in some of the fossils (Fig. 3e, f, h)

Longhorn beetle larvae may look on a first glance very similar to moth larvae of the group Castniidae; yet in the latter the first pair of legs is much further anterior (Sarto i Monteys and Aguilar 2005a p. 2) than in longhorn beetle larvae, similar to the condition in many of the fossils (Fig. 3b, d, i). Also, in longhorn beetle larvae there is a distinct fold separating the posterior part of the prothorax; such a fold is well apparent in most of the fossils (Fig. 3b, c, g), but absent in extant larvae of Castniidae. Furthermore, in larvae of Castniidae only four pairs of prominent creeping processes are present in the posterior trunk (abdomen; Alario 2005 fig. 5 p. 245; Sarto i Monteys and Aguilar 2005a p. 2, 2005b fig. 11a p. 72; Lopez-Vaamonde and Lees 2010 p. 990 right) with the corresponding segments being larger, while in the fossils and modern longhorn beetle larvae more segments bear creeping welts and are more similar in size (Figs. 2, 3a–d, g, i). All these characters therefore support that the fossils are indeed larvae of Buprestidae and Cerambycidae. The assumed relationship of the larvae and their morphology strongly indicate that these are solid-wood borers.

Wood-borers seem not to be rare in Eocene amber

So far, few sources have mentioned solid-wood-borer beetle larvae in Eocene ambers (Larsson 1978; Klausnitzer 2003; Nel et al. 2004) and in only two cases specimens have been figured (Bachofen-Echt 1949 p. 115 fig. 102, specimen not found in museum collections in Munich and Vienna; Gröhn 2015 p. 272). We were able to compile no less than twelve additional solid-wood-borer beetle larvae from Eocene ambers, including rather small specimens of about 2 mm (Fig. 3b), to a specimen of at least 35 mm in length (Fig. 2). Ambers seem to tend to preserve smaller specimens (though the situation seems to be more complex and also includes different preservation potential due to differences in behaviour, e.g. Penney 2002; Penney and Langan 2006; Solórzano Kraemer et al. 2015, 2018). A larva of several centimetres in size is therefore quite unusual. The specimen might indeed represent the so far largest beetle larva (or even holometabolan larva) preserved in amber.

These finds demonstrate that solid-wood-borer larvae may be not as rarely preserved in ambers as assumed. Larval forms preserved in amber seem to be less intensely studied than adults (examples for adults in Eocene amber: Larsson 1978; Bellamy 1995; Vitali 2009a, b, 2014; Vitali and Perkovsky 2022) as these are less easy to be interpreted in a phylogenetic framework. Adults of solid wood-borer beetle larvae have been found in Eocene ambers quite often in comparison to the occurrence of such adults in modern resins (Zherikhin et al. 2009).

The dominance of studying adults also applies to the fossils here. Despite the fact that further reaching phylogenetic interpretations are difficult for beetle larvae, it remains important to emphasise that in holometabolans such as beetles often major parts of the lifetime are spent as larvae and that the major interactions with other components of the ecosystem occur in this phase. Hence, the ecological impact of larvae should not be underestimated. Furthermore, it is important that presence of adults is not a good direct indicator for presence of larvae of distinct eco-types (see discussion in Baranov et al. 2019), but the direct finding of these larvae clearly allows to draw conclusions about their ecological role. Yet, biased search for adults may only be one factor leading to the impression that wood-borer larvae would be rare.

Another factor may indeed be preservation. The often damaged condition of the larger larvae hints to the possibility that at least some, if not many, of the heavily oxidised tubes preserved in larger pieces of amber may represent remains of larger wood-borer larvae, which would make these even more common. In other words, solid-wood-borer larvae seem not to have been rare in the Eocene amber forest fauna.

This possibility might fit with the rather large abundances of hoverfly larvae of the group Volucellini, which also co-occur with plant parasites in the modern fauna (see above). Together, both factors would fit into a picture of an amber forest under stress, causing the trees to produce larger amounts of resins, which ultimately led to amber (McKellar et al. 2011; Baranov et al. 2021; but see also above). However, it remains difficult to draw causal conclusions here. It currently remains unclear whether such a possibly higher abundance of solid-wood-borer larvae was the stressor for the trees or just a symptom for an already stressed forest due to another stressor (see also discussion in Peris 2020). Some modern larvae of Buprestidae and Cerambycidae also have slightly different ecological roles as leaf miners or root feeders (e.g. Bellamy and Volkovitsh 2005; Grebennikov 2013; see discussion in Haug et al. 2021). If the fossil larvae had such roles, at least in part, they would have still represented stressors for the trees, but would not have had an influence on the density of hoverfly larvae.

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Data availability statement The SRμCT and μCT datasets analysed during the current study are available in the repository www.morphdbase.de under the following links:
Dip-00889 (Fig. 1a, b): https://www.morphdbase.de/?V_Baranov_20210130-S-7.1
Dip-00895 (Fig. 1c, d): https://www.morphdbase.de/?V_Baranov_20210130-S-5.1
Dip-00894 (Fig. 1e): https://www.morphdbase.de/?V_Baranov_20220922-M-56.1
PED 1479 (Fig. 1f–i): https://www.morphdbase.de/?V_Baranov_20220927-S-17.1 and https://www.morphdbase.de/?V_Baranov_20220927-S-18.1

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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