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EARLY-STAGE FOSSIL LARVA OF SHIP-TIMBER BEETLES WITH DEFENSIVE PLATE-LIKE ABDOMEN IN BALTIC AMBER

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Abstract: Ship-timber beetles (Lymexyloidea) are represented by elongated adults with specialised maxillae and larvae with specific morphologies of their abdomen end. They are leading wood-associated lifestyles, with larvae spending most of their life within wood. With strong mandibles and saw-like asperities on their bodies they manage to bore into the hard wood and expell the wood rests. Even though the group does not comprise many species today, there are multiple fossil reports of adult ship-timber beetles. However, larvae have so far only been described in the literature for extant species. The only mentionings of possible fossil larvae date back to the 19th and early 20th centuries. Here, I report an early-stage larva of Hylecoetidae. Based on the morphology of the mandibles, the numerous asperities on the body, and a specialised plate-like abdominal segment IX, all of which resemble features found in modern larvae of *Elateroides dermestoides* associated with boring into wood, this Eocene fossil larva likely shared a hardwood-associated lifestyle.

INTRODUCTION

Beetles occupy almost all continental ecosystems known to mankind today, they can be found even in the environments that are low on nutrients, such as xylem of trees. Several groups, such as jewel beetles (Buprestidae), longhorn beetles (Cerambycidae), false click beetles (Eucnemidae) and ship-timber beetles (Lymexylidae and Hylecoetidae), have some representatives that spend either part of their life cycle or their entire life within hard, nutrient-poor, undecomposed wood (Ratzerburg 1839;Lawrence 2010). Over a long time, some of these beetles evolved specialised structures (Haug et al. 2021, 2023; Zippel et al. 2023), behaviours (Egger 1974), and even endosymbiosis with microorganisms that help them exploit and digest the hardwood tissues (Graham 1967; McKenna et al. 2019) or a mutualism with ectosymbionts that provide a

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more nutritional food source within the self-made wood galleries (Lehenberger et al. 2021; Peris et al. 2021). Morphologically these larvae show great diversity, but also exhibit several similar features such as strongly sclerotised mandibles for processing tough wood tissues, an enlarged prothorax, a reduction in length of appendages (whether the length of antennae, legs or both), and additional adaptations for anchoring while chewing through tough material or defence (Lawrence et al. 2011). The shared morphological traits of larvae among these diverse, distantly related groups likely reflect strong selective pressures imposed by life in tough wood, and the distinctive morphologies of ship-timber beetle larvae are no exception.

Extant ship-timber beetles occur worldwide and are currently represented by less than 100 described species (Goczał et al. 2024). Following the phylogenomic study of Batelka et al. (2024), ship-timber beetles comprise two major lineages: Lymexylidae (Atractocerinae and Lymexylinae) and Hylecoetidae (Melittommatinae and Hylecoetinae) whose representatives occur in different regions of the world (Lawrence 2010). Some adults of ship-timber beetles are also wood-associated and can be found under bark, on wooden surfaces or in rotten wood (Pfeil 1859; Lawrence 2010). Adult females lay their eggs in bark crevices, old boring holes of already emerged adults, or under the bark with a long ovipositor (Pfeil 1859; Lawrence 2010). Larvae of this group are wood borers, and already the first-stage larvae are well-equipped with strong mandibles for boring into wood (Pfeil 1859; Fulmek 1930; Grandi 1962; Burakowski & Kilian 2005; Casari & Albertoni 2013). The larvae show morphological differences depending on the group, but also the stage of ontogenetic development (Fig. 1). Earlier larvae have shorter, cylindrical bodies (Fig. 1B, E–F, K–L) and the later larvae have long slender bodies (Egger 1974; Fig. 1A, D, G–J, M). Additionally, the later-stage larvae lose stemmata, that are present in earlier stages of Lymexyloidea (Kolibáč 2002; Casari & Teixeira 2011; Casari & Albertoni 2013). The morphology of the abdominal segment IX is especially interesting: it differs between larvae of various groups, but it also changes within different larval stages of a single species (Wheeler 1986). Early larvae of *Elateroides dermestoides* (Linnaeus, 1761), exhibit an oval, plate-like sclerite with crenellations and urogomphi-like paired processes (Grandi 1962, Fig. 1K–L), whereas later larvae, in dorsal view, have abdominal segment IX forming a thin, concave, elongated process surrounded by tooth-like asperities; the two most posterior teeth are also the longest (Egger 1974, Fig. 1J). In both cases, these specialised structures are used for expelling bored wood material from the tunnels (Grandi 1962; Egger 1974). Lyngnes (1958) also suggests that the plate-like structure not only expels debris but also enables the transfer of small particles, such as fungal spores, into the interior of the gallery. Moreover, the oval shape of the plate-like sclerite of the early larva may also serve as a defensive mechanism (Lawrence et al. 2011). The plate-like sclerite can serve as a functional door, blocking the tunnel to potential predators, a defence mechanism known as cryptic phragmosis (Wheeler & Hölldobler 1985).

The fossil record of ship-timber beetles is scarce and is mostly based on specimens preserved in various resins (Fig. 2). And yet, the earliest fossil record comes from the Cretaceous Crato Formation in Brasil (Wolf-Schwenninger 2011). Most fossil specimens of Lymexyloidea from the Cretaceous Kachin Myanmar amber represent Atractocerinae (e.g., Chen 2019; Chen & Zhang 2020; Nazarenko et al. 2020; Li et al. 2022). In contrast to Myanmar amber, representatives of Atractocerinae are relatively rare in Eocene (e.g., Yamamoto 2019; Nazarenko et al. 2020; Yamamoto et al. 2022; Kirejtshuk 2025) and Miocene ambers. Only a single report of larval and adult specimens of Atractocerinae is known from the Miocene Dominican amber (Grimaldi & Engel 2005).

Fossil representatives of Melittommatinae are limited to a single specimen in Baltic amber (Kirejtshuk 2008) and one from the Florissant Formation (Wickham 1911). Fossils of Lymexylinae are only mentioned in older literature from the 19th and early 20th centuries. Menge (1856) reported finding larvae of Lymexylinae, possibly of *Lymexylon* Fabricius, 1775, in the Eocene Baltic amber (Fig. 2). Additional notes on adult fossils of Lymexylinae from the Eocene Baltic amber appear in lists by Berendt (1845), Klebs (1889), Handlirsch (1907), but the whereabouts of these specimens are not clear.

Fossil representatives of Hylecoetinae, including *Elateroides* Schaeffer, 1766 (formerly treated under the synonym *Hylecoetus* Latreille, 1806), were briefly discussed by Heer (1865) and listed by Handlirsch (1907). The fossils mentioned by Heer (1865) represent larvae from the Miocene Upper

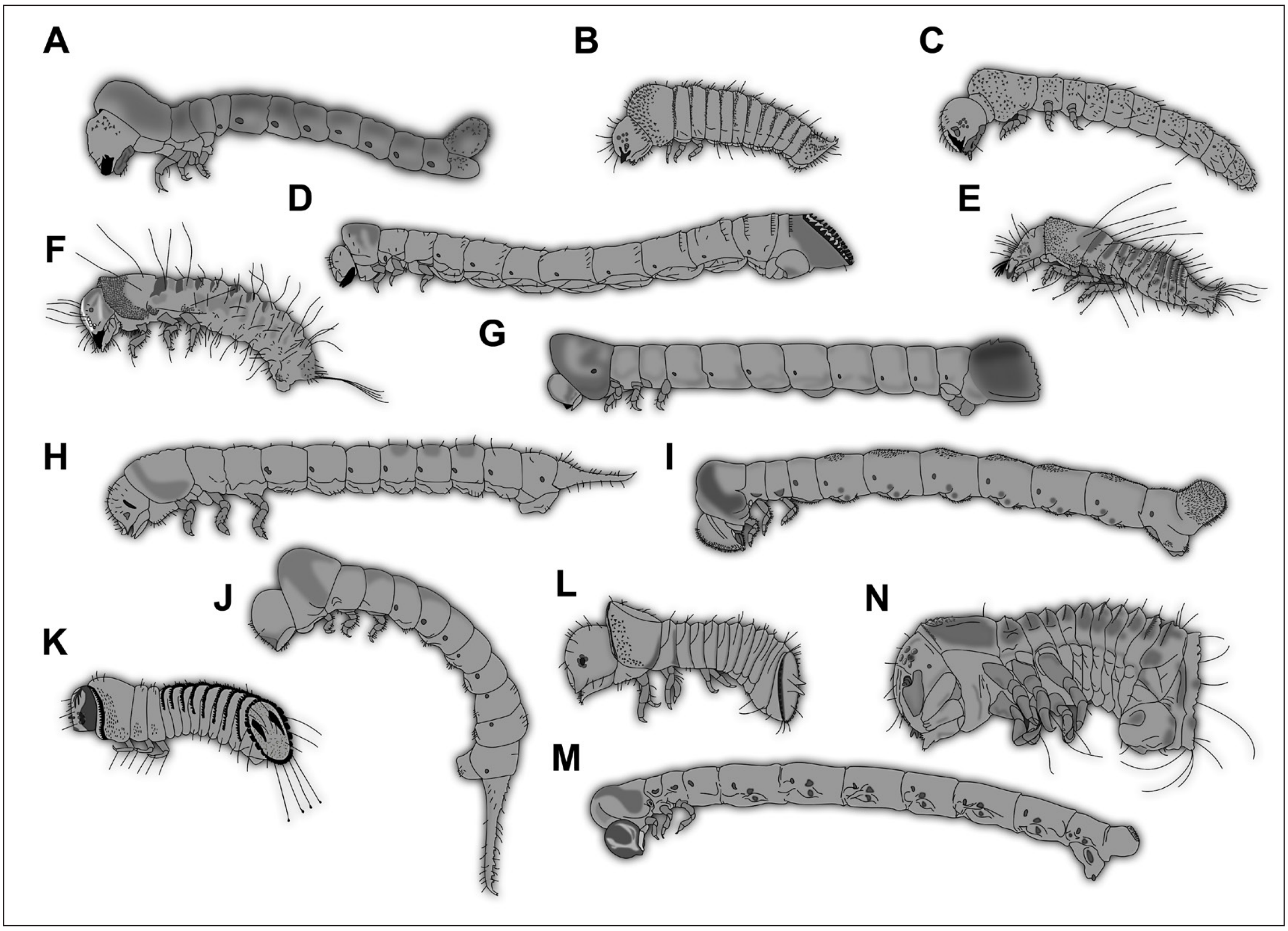

Fig. 1 - Diversity of larvae of Lymexyloidea, based on the published specimens from literature: A–C) Different-stage larvae of *Lymexylon navale* (after Burakowski & Kilian 2005): A) Later-stage larva. B) First-stage larva. C) Second-stage larva. D) Later-stage larva of *Melittomma sericeum* (Harris, 1841)(after Böving & Craighead 1931). E) First-stage larva of *Atractocerus brasiliensis* (after Casari & Albertoni 2013). F) First-stage larva of *Raractocetus emarginatus* (after Fulmek 1930). G) Later-stage larva of *Protomelittomma insulare* (after Gahan 1908). H) Later-stage larva of *Elateroides lugubris* (after Peterson 1951). I) Later-stage larva of *A. braseliensis* (after Casari & Teixeira 2011). J –L) Different-stage larvae of *E. dermestoides*. J) Later-stage larva (after Wheeler 1986). K) First-stage larva (after Egger 1974). L) First-stage larva (after Germer 1912). M) Later-stage larva of *R. emarginatus* (after Fulmek 1930). N) New fossil of first-stage larva of Hylecoetidae, possibly Hylecoetinae.

Freshwater Molasse of the North Alpine Foreland Basin at the Öhningen Lagerstätte. Unfortunately, no images of these fossil larvae assigned to *Hylecoetus cylindricus* Germer, 1912, were provided by Heer (1865). Subsequent taxonomic revision based on adult specimens has shown that *Hylecoetus cylindricus* is a younger synonym of *Ichnea marginella* (Klug, 1842), a species now placed in Cleridae (Opitz 2010). As the original fossil larvae cannot be re-evaluated, their assignment to Hylecoetinae cannot be verified. Handlirsch (1907) reported adult and larval specimens of Hylecoetinae (*Hylecoetus* sp.) but did not provide a detailed description of the fossils, either. Therefore, larval specimens of Hylecoetinae have not yet been described in detail from any fossil Lagerstätte.

This contribution reports an early larva of fossil ship-timber beetles and represents the first detailed description of such a specimen in literature. The new larva shows many similarities to extant early-stage larvae of *E. dermestoides* (Grandi 1962; Egger 1974; Fig. 1K–L).

MATERIALS AND METHODS

Material

A single new fossil specimen preserved in Baltic amber (the specimen lable reads: Baltischer Bernstein; Eozän: Lutetium, "Samland") was investigated and documented for the present study. The specimen (SNSB-BSPG_III_2018_34) is a part of

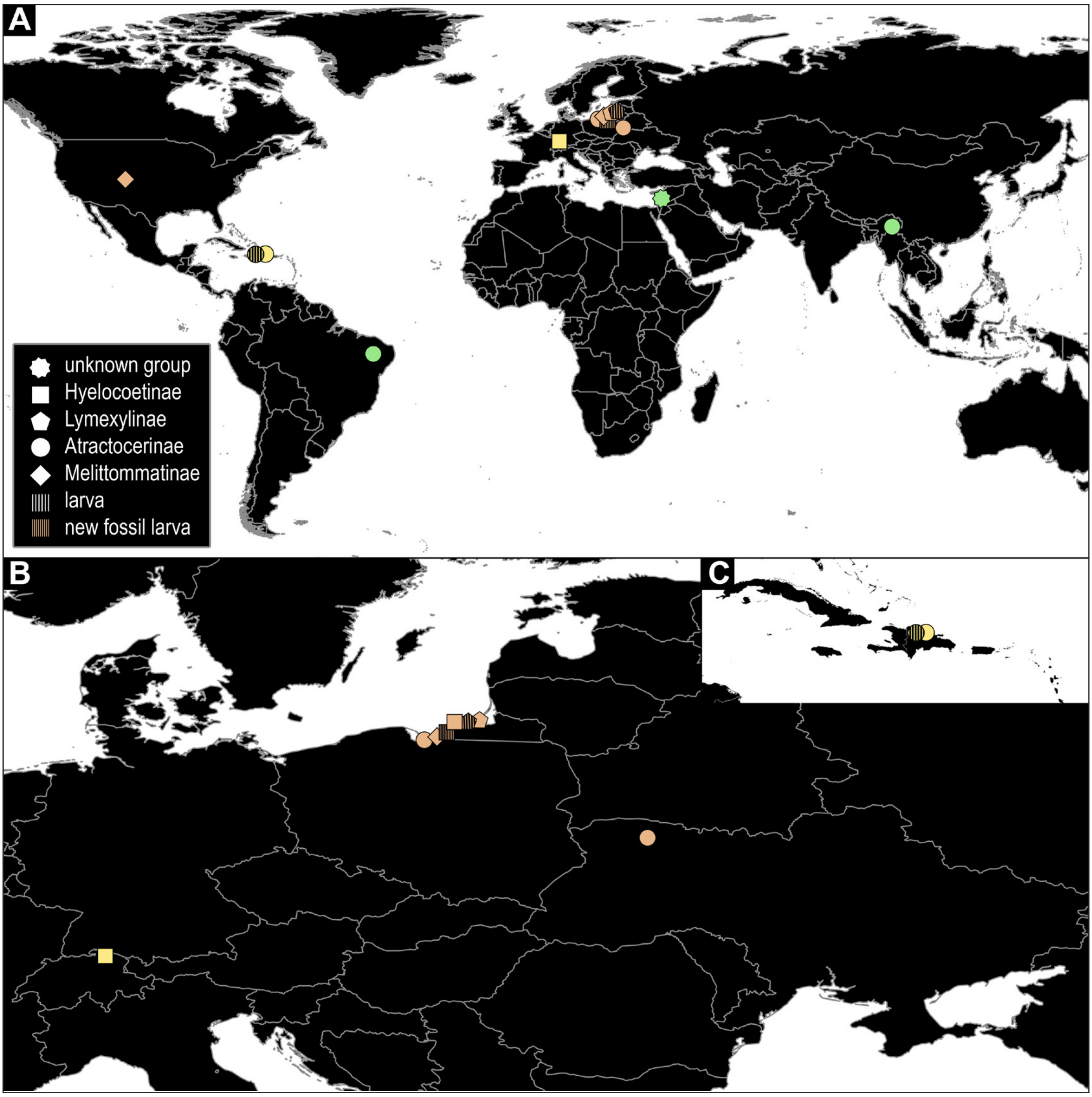

Fig. 2 - Occurrence of Lymexyloidea in the fossil record (adults and larvae) based on the geological locality where they were collected (processed in QGIS on a Natural Earth map). A) Occurrences all over the world. B) Close-up on the occurrences in Europe. C) Close-up on the occurrences from the Dominican Republic. Different colours represent different geological time slices: Cretaceous = green; Eocene = orange; Miocene = yellow. Occurrence data was mapped based on the information from: Menge 1856, Heer 1865, Handlirsch 1907, Klebs 1910, Wickham 1911, Grimaldi et al. 2002, Grimaldi & Engel 2005, Kirejtshuk 2008, Wolf-Schwenninger 2011, Kirejtshuk & Azar 2013, Chen 2019, Yamamoto 2019, Chen & Zhang 2020, Nazarenko et al. 2020, Yamamoto et al. 2022, Kirejtshuk 2025.

the Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany. The specimen used to be part of Krylov & Laging collection. Since 2018, it has been deposited in the Bayerische Staatssammlung fur Paläontologie und Geologie, München, Germany.

Documentation of material

The amber specimen SNSB-BSPG_III_2018_34 was studied in the lab of the Palaeo-Evo-Devo Research Group at the Ludwig-Maximilians-Universität München. For better availability of morphological characters the amber piece was ground with sandpapers of different grits and polished with a polishing paste (Polyboy). The specimen was documented with Keyence VHX-6000 digital microscope at different magnifications, with different illumination settings (ring light, coaxial polarised light, transmitted light) and on different backgrounds (black, white, glass). The newly obtained images were automatically stacked using the built-in Stack and HDR software. Images were further processed with Photoshop CS2. Measuring of the specimen was done with the software ImageJ. Camera lucida of the new specimen, that served as the basis for the drawing (Fig. 1N), and all the other drawings of larvae of Lymexyloidea were done with the digital drawing program Inkscape.

Producing the map

The world map of fossil representatives of Lymexyloidea (Fig. 2) was produced in QGIS (QGIS.org. 2026) using Natural Earth, a free provider of vector and raster map data (@naturalearthdata.com; licensed CC-0 1.0 Public Domain). To precisely place the coordinates, an Excel table containing the location coordinates of presumed Lagerstätten where fossils were found was imported within QGIS. For reports from the 19th and early 20th centuries, coordinates were inferred based on the available information and contemporary knowledge of these Lagerstätten. Large, colourful geometric symbols representing the fossil finds were placed over the smaller points created in QGIS to facilitate identity and to convey the age and ontogenetic stage of the fossils. These symbols were created in Inkscape. Additional labels, lines and the legend were added in Photoshop CS2.

Results

Description of the new specimen

Specimen available in ventral (Fig. 3A), dorsal (Fig. 3G), lateral (Figs. 1N, 4A), posterior (Fig. 3C) and anterior (Fig. 3E) views. Body sub-cilindrical in lateral view, part of anterior trunk region dorsally slightly concave (Fig. 4A). Total body length around 0.9 mm, measuring from anterior tip of labrum to posterior tip of trunk end. Head hypognathous, mouthparts pointing antero-ventrally. Head capsule semicircular in ventral and dorsal view, wider than long, 1.8× (maximum width near anterior rim of thorax ~0.34 mm, maximum length medially ~0.19 mm; Fig. 3A–B). Posterior edge of head capsule retracted under the next segment. Moulting suture not clearly discernible due to preservation, possibly only left arm discernible (Fig. 3E: arrow). Head capsule bearing sparsely scattered setae. Five stemmata on each side discernible (Figs. 3B, E, 4A: white arrows, B, E), single smaller structure on each side, possibly an additional small lens, discernible ventral to the stemmata (Fig. 4A, B–C: arrows, E). Both antennae minute, approximately 0.03 mm long, composed of three elements and sensory process (sensorium; Figs. 3A: black arrows, B, 4B: black arrows, E). Sensorium conical in shape in ventral view, ultimate antenna element longer than sensorium (Fig. 4B). Labrum parted from clypeal region by labro-clypeal suture (Fig. 3E). Mouthparts partially accessible: mandibles partially hidden by other mouthparts, heavily sclerotised, broad and stout (Figs. 3A, E, 4C, E); maxillae longer than wide, 3.7× (at widest ~0.05 mm wide). Each maxilla with triangular cardo (likely split into two sclerites) in ventral view, elongated stipes, longer than wide, endite (mala) and palp (Fig. 4C, E). Articulating area triangular in ventral view (Fig. 4C, E). Each mala bears spine-like setae distally (at least three discernible), slightly indented on outer lateral side (Fig. 4C, E). Each maxillary palp composed of three elements (palpomeres) and a large proximal area (palpifer; Fig. 4C, E). Labium longer than wide, with a pair of palps, each composed of two elements (palpomeres) of approximately same length, each on palpifer, and with elongated ligula, longer than labial palps (Fig. 4C, E).

All thorax segments (pro-, meso- and metathorax), wider than long, with lateral sides of tergites curved ventrally (Figs. 3A–B, G, 4A). Prothorax enlarged, largest thorax segment, wider than long, 1.6×; longer than length of meso- and metathorax together, 1.8× (prothorax ~0.3 mm long dorsally). Anterior rim of pronotum with a line of sclerotised saw-like protrusions (Figs. 3E, 4A: black arrow), rest of dorsal surface with spines and asperities. Mesothorax wider than long, 5.4× (maximum width ~0.4 mm), metathorax wider than long, 5× (maximum width 0.35 mm). Lateral sides of segments bear scarce setae. Each thorax segment with a pair of legs (length ~0.3 mm), each composed of five elements, the most distal one being a strong relatively long claw-like tarsungulus with at least a single seta, but with two presumed (Figs. 3A–B, 4A, D). Several

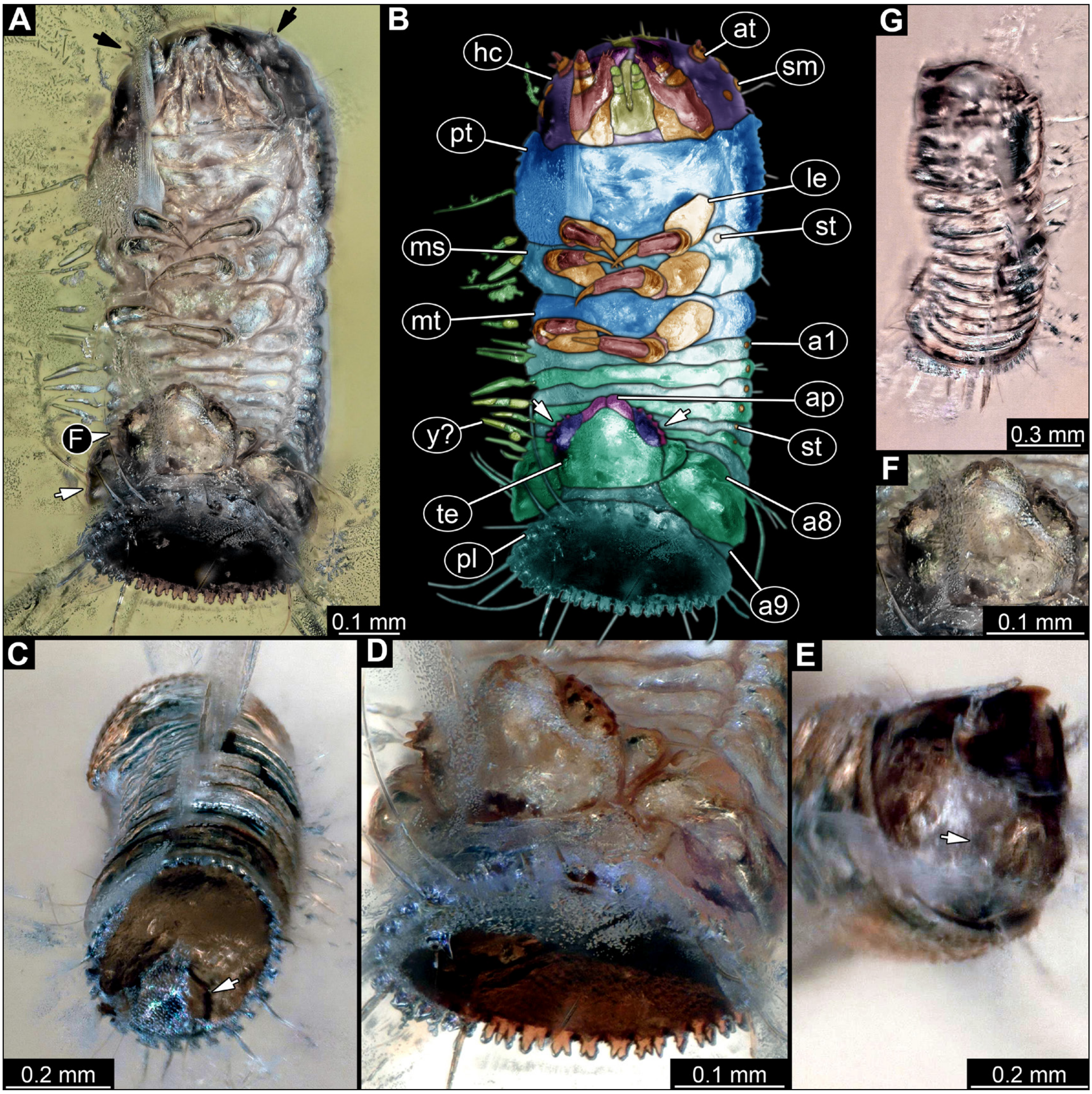

Fig. 3 - New fossil specimen of first-stage larva of Hylecoetidae: A–F) Documented on white background under ring light. G) Documented on white background under coaxial polarised light. A) Habitus in ventral view, white arrow marks lobe-like formation of lateral parts of abdominal segments VIII and IX, black arrows mark antennae. B) Colour-marked version of A, white arrows mark structures on the trunk end with blunt teeth. C) Habitus in posterior view, with close-up on the plate-like sclerite, arrow marks the hexagonal line (possibly a suture or a cuticular ridge) on it. D) Close-up of plate-like sclerite with crenellations and the trunk end. E) Head in dorso-lateral view, arrow marks possible moulting suture. F) Close-up of trunk end, with anal papillae and structures on the trunk end with blunt teeth, from A. G) Habitus in dorsal view. Abbreviations: a1–a9 = abdominal segments I–IX; ap = anal papilla; at = antenna; hc = head capsule; le = legs; ms = mesothorax; mt = metathorax; pl = plate-like sclerite of abdominal segment IX; pt = prothorax; sm = stemma; st = stigma (spiracle); te = trunk end; y? = possible fungal ectosymbionts (yeasts?).

long simple setae in area of legs discernible, likely bore by each leg of meso- and metathorax (Fig. 4D: arrows).

Abdomen with eight wider than long segments (Fig. 3G), modified abdominal segment IX with a circular plate postero-dorsally and trunk end (Figs. 3A–D, F, 4A). Segments I–VIII wider than long (width 0.05–0.08 mm), with segment V being shortest (~0.05 mm long). Segments I–VIII with lateral sides of tergites curved ventrally, each segment with line of saw-like asperities throughout whole width of tergite (Fig. 3C), laterally bear scarcely scattered setae. Segment IX with slightly concave circular plate oriented posteriorly, rim of plate circled with large convex teeth (Fig. 3C–D), each with two or more tips distally (having an effect of crenellation; Fig. 3C–D), and bearing several longer setae (~0.2 mm long), rest of surface with punctures and small asperities. Ventral medial part of plate in posterior view with a hexagon-like darker line (possible suture or cuticular ridge), partially indiscernible due to preservation (Fig. 3C: arrow). Lateral sides of abdominal segments VIII and IX form a lobe-like structure on each side (Fig. 3A: arrow). Trunk end orientated antero-ventrally, with pentagonal tergite, with anal papillae at its tip and antero-laterally orientated protrusions with several sparsely arranged blunt teeth (Fig. 3B: arrows, D, F) and bearing several short setae.

Discussion

Identity of new fossil: larva of Lymexyloidea

There are several characters, or better yet, the lack of which that reveal that the here reported specimen is a beetle larva. The presence of simple eyes (stemmata) and lack of complex compound eyes, together with the lack of wings or genital organs indicate that the specimen is a larva. A well-developed head capsule with antennae composed of three elements, five stemmata on each side, strong mandibles for chewing, legs with five elements, most distal one being a tarsungulus, and an abdomen with nine segments and a trunk end further on indicate it is a larva of a polyphagan beetle (Wheeler 1991). Already the large pronotum that covers part of the head capsule and the modified abdominal segment IX distinguish this larva from most of the other beetle larvae (Wheeler 1991). Both of these morphological characters can be seen in larvae of Lymexyloidea (Böving & Craighead 1931; Klausnitzer 1978; Wheeler 1991; Lawrence 2010). Some early-stage larvae of Lymexyloidea (in literature identified as L_1 larvae) exhibit a short, cylindrical body and an oval, plate-like abdominal segment IX with multiple asperities and cuticular protrusions; these are the larvae of Hylecoetidae (Fig. 1K–L). Other early-stage larvae of Lymexyloidea, the larvae of Lymexylidae, also have a modified abdominal segment IX, but instead of a plate with crenellations, they exhibit an abdominal segment IX with a dorsally-concave sclerite that posteriorly ends in either a pair of urogomphi (Burakowski & Kilian 2005) or a single tooth-like median process directed upwards (Casari & Albertoni 2013; Fig. 1B, E–F). Later-stage larvae (for example, L_3–L_6 larvae) are mostly very elongated but also retain a modified abdominal segment IX (Gahan 1908; Fulmek 1930; Casari & Teixeira 2011). However, the shape of this modified abdominal segment differs from that in early stages (Fig.1A, D, H–J, M). Wheeler (1991) differentiates three structural types of abdominal segment IX in later-stage larvae of Lymexyloidea: the “long sword-like spinose” type (e.g., *Elateroides;* Saalas 1923*;* Burgers & Heijerman 2018), the “large bulbous with dense asperities” type (e.g., *Atractocerus* Palisot de Beauvois, 1801; Casari & Teixeira 2011), and the “cylindrical truncate with large teeth around apical rim” type (e.g., *Melittomma* Murray, 1867; Gahan 1908). Considering that the new fossil SNSB-BSPG_III_2018_34 is not strongly elongated, possesses stemmata, and exhibits neither the types of abdominal segment IX suggested by Wheeler (1991) nor the plate-like abdominal segment IX described by Kolibáč (2002) in a later-stage larva of *E. dermestoides,* it can be identified as a first-stage larva of Lymexyloidea, more precisely, a larva of Hylecoetidae (sensu Batelka et al. 2025).

Identity of new fossil: likely a first instar larva of Hylecoetinae

Even though the ship-timber beetles (Lymexyloidea) are taxonomically speaking relatively small, with fewer than 100 species distributed worldwide (65 species according to Lawrence 2020, 70 regarding to Goczał et al. 2024, or 84 species according to Li et al. 2022), few early-stage larvae have been described. Known early-stage larvae include *E. dermestoides* (Grandi 1962; Egger 1974), *Lymexylon navale* (Linnaeus, 1758) (Burakowski & Kilian 2005), *Raractocetus emarginatus* (Laporte, 1836) (in Fulmek 1930 under old name *Atractocerus emarginatus* Laporte, 1836), and *Atractocerus brasiliensis* Lepeletier & Audinet-Serville, 1825 (Casari & Albertoni 2013). Unfortunately, early-stage larvae of Melittommatinae, the sister group of Hylecoetinae (sensu Batelka et al. 2025) remain undescribed. As discussed above, the morphology of all known early-stage larvae differs markedly from that of later stages (Fig. 1). All known early stages have stemmata, although their number and position vary. The new fossil specimen appears to have five stemmata, similar to the

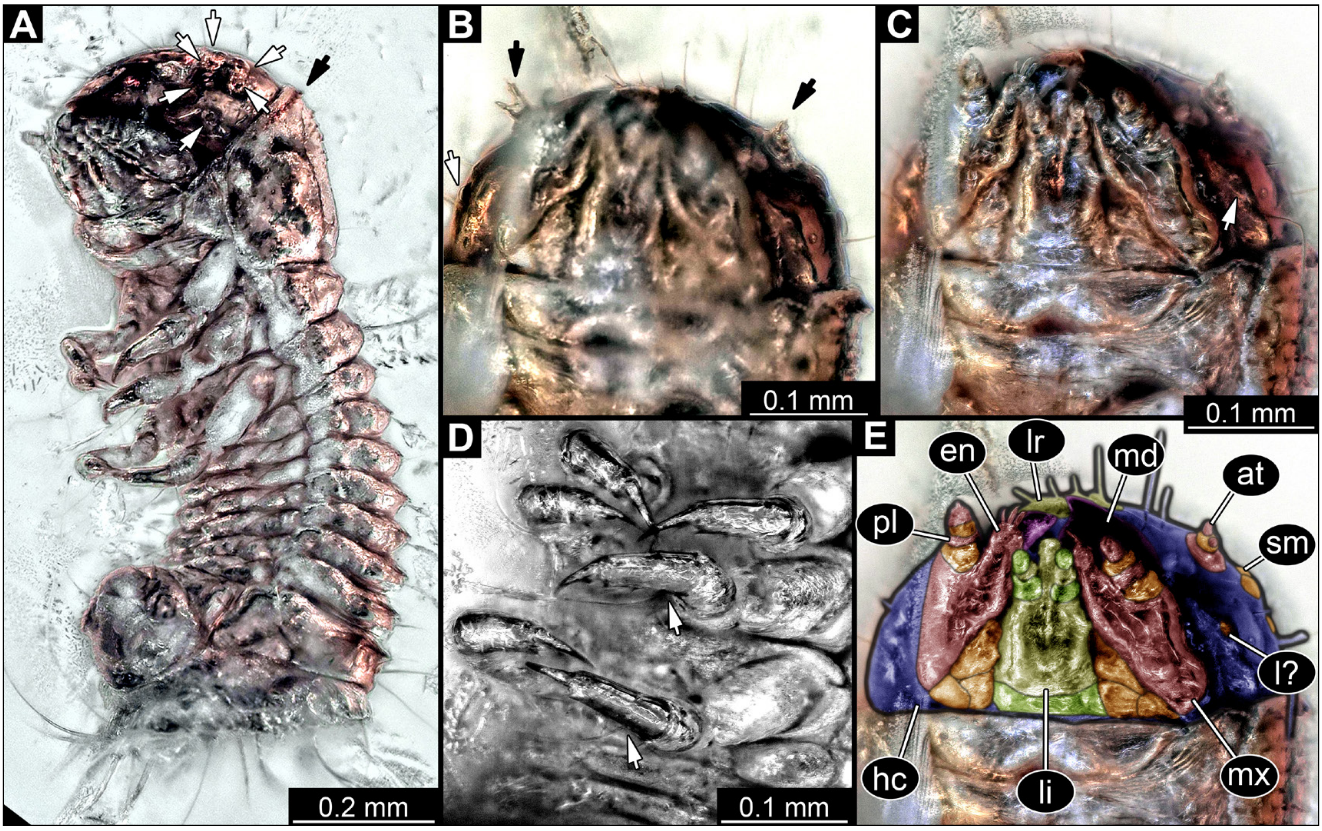

Fig. 4 - New fossil specimen of first-stage larva of Hylecoetidae: A) Documented on white background under ring light. B–E) Documented on transparent background under ring and transmitted light. D) Image was additionally desaturated and its contrast was enhanced. A) Habitus in lateral view, white arrows mark stemmata and a possible lenticular structure, black arrow marks a line of saw-like asperities on the anterior rim of pronotum. B) Close-up of head in ventral view, with focus on antennae (black arrows) and a possible additional lenticular structure (white arrow). C) Close-up of head in ventral view, with focus on mouthparts. D) Close-up of legs in ventral view, white arrows mark the spot where simple setae are attached. E) Colour-marked version of C. Abbreviations: at = antenna; en = endite; hc = head capsule; l? = possible additional lenticular structure; li = labium; lr = labrum; md = mandible; mx = maxilla; pl = palp; sm = stemma.

larva described by Egger (1974). Additionally, several images show a structure that appears to reflect light in a manner similar to the other stemmata (Fig. 4A–C, E). However, due to preservation limitations, it remains unclear whether this structure represents an additional small lens or merely a sensory structure or cuticular elevation. The structure is positioned ventrally relative to the other stemmata (Fig. 4A–B: white arrow), in a position similar to that of the lenticular structure described by Grandi (1962). Such a lenticular structure has not been reported in other early-stage larvae of Lymexyloidea and may represent either an autapomorphy of *Elateroides* or a potential synapomorphy of whole Hylecoetidae (Hylecoetinae + Melittommatinae); however, this cannot be confirmed until an early-stage larva of *Melittomma* is described.

Antennae also differ among early-stage larvae, with early larvae of *E. dermestoides* (Grandi 1962) and early larvae of *R. emarginatus* (Fulmek 1930) having three elements, whereas early larvae of *Atractocerus* are possessing only two elements (Casari & Albertoni 2013). In the new fossil, the antennae are composed of three elements, although the first element of the antenna is short and broad, resembling a membranous ring (Fig. 4B–C, E). The maxillary palps of the new specimen also resemble those of the larvae of *E. dermestoides,* with three relatively large elements and the first element positioned on a prominent palpifer (Grandi 1962; Fig. 4C, E).

Posterior plates of abdominal segment IX in early-stage larvae of *Atractocerus* (da Costa Lima 1953; Casari & Albertoni 2013) differ considerably from those of larvae of *E. dermestoides.* All early larvae of *E. dermestoides* described by Grandi (1962) and Egger (1974) have the abdominal segment IX with an oval-shaped plate that has its rim crenellated. A very similar morphology is present in the new fossil specimen SNSB-BSPG_III_2018_34. Based on the strong resemblance of the new fossil to the early larvae of *E. dermestoides* it is possible that the fossil specimen is also a representative of *Elateroides*. However, once again, this assignment cannot be confirmed until early-stage larvae of *Melittomma* are described, which would clarify whether the observed resemblance is shared across the entire Hylecoetinae + Melittommatinae lineage.

However, several differences distinguish the fossil from known extant early-stage larvae of *Elateroides*. The fossil lacks the two horn-like protrusions on the oval plate of the abdominal segment IX (urogomphi?), present in the representatives of other early larvae of *Elateroides*. It also bears additional asperities and darker lines, possibly corresponding to sutures or cuticular ridge-like structures. The trunk end differs as well from that of extant specimens, where the anal region is not so clearly defined into lobes (anal papilae) as in the new fossil one. In the new fossil it seems that not only the plate of the abdominal segment IX serves as a sealing mechanism of the tunnel opening but that portions of abdominal segment VIII and IX together also form a lobe-like protrusions (Fig. 3A: white arrow) that possibly add to the tightness and stability of the sealing defence mechanism. Additionally, there are differences in setal patterns, such as small setae on the legs or very long setae on the labrum as seen in some specimens of *Atractocerus* that were not discernible here. Taken together, these observations indicate that SNSB-BSPG_III_2018_34 is an early-stage larva of Hylocoetidae with many morphological characters shared with modern larvae of Hylocoetinae. Due to lack of information on other early-stage larvae of this group, its assignment to Hylecoetinae and *Elateroides* must be considered tentative.

Ecology of the new fossil – xylem borer

Larvae of ship-timber beetles are wood borers that bore their tunnels deep into hard wood (Clark 1925). Only seldom do they bore their tunnel galleries close to the surface in the cambium of trees (Lawerence 2016). Since the new fossil larva has many similarities to modern early larvae of *Elateroides* that also bore in hard wood, it can be implied that the new larva led similar lifestyle. The presence of compact strongly sclerotised mandibles (Fig. 3E) and asperities on the anterior rims of trunk segments (Figs. 3C, 4A: black arrow) imply that this larva was able to chew on tough wood and also use the saw-like asperities to build and shape tunnels in hard wood. The antero-lateral structures with blunt teeth at the trunk end (Fig. 3B: arrows) together with the rest of the trunk end seen in the new specimen very likely served as anchoring structures while boring, similar to the behaviour seen in extant specimens of *E. dermestoides*. The position of saw-like cuticular asperities, the shape of the dorsal side of the trunk, and the shape of the trunk oval plate are also extremely similar to these characters of extant larvae of *E. dermestoides,* and therefore, very likely had similar functionality and likely operated in the same way as specialised mechanism for boring and filing holes in recently dead trees described by Egger (1974).

Ecology of the new fossil – possible fungi groomer

Mycophagy is a widespread lifestyle in Coleoptera (Crowson 1981; Wheeler 1986). Ambrosia beetles sensu stricto (representatives of Scolytinae and Platypodinae) received their name after the tendencies of adults to spread and groom ambrosia fungi within the tunnels they bore. However, symbiosis of beetles with ambrosia fungi is known for other beetles, as well, such as Hylecoetidae and Bostrichidae (Peris et al. 2021). In case of Hylecoetidae, at least larvae of some species are the cultivators of ambrosia fungi in the tunnels (Peris et al. 2021). For example, modern larvae of *E. dermestoides* have a symbiotic relationship with fungus *Alloascoidea hylecoeti* (Batra & Francke-Grosmann, 1961) Kurtzmann & Robnett 2013 (Batra & Francke-Grosmann 1961; Francke-Grosmann 1967; Graham 1967; Wheeler 1986; Toki 2012). Adult females carry fungi in their mycetangia (specialised structures for transport of fungal spores) positioned at the distal end of their ovipositor. During oviposition, females apply secretions containing fungal spores onto their eggs (Francke-Grosmann 1967) and early-stage larvae obtain the spores from the egg surface. Additionally, the hatched larvae were observed to exhibit a special twisting behaviour that enhances chances of yeast spore transfer (Wheeler 1986; Peris et al. 2021). The early-stage larvae carry these spores on their integument and bring them into the tunnels where they later tend to them and use them as a food source (Wheeler 1986). Considering that the new larva shares many morphological characters with modern counterparts, it is likely that they led a similar lifestyle, as well. Therefore, it is possible that already approximately 40 million years ago these larvae nourished a symbiotic relationships with fungi Ascomycota. The new specimen exhibits unidentified structures (Fig. 3B: y?) on the short lateral setae on one side of the body. Some of these structures display a consistent and spatially organised morphology, including small horn-like protrusions at their most distal ends and bud-like lateral protrusions. While repeating patterns alone do not exclude preservation artefacts, the regularity and consistency of these features may be more consistent with a biological origin, such as fungal symbionts, particularly as similar morphologies have been illustrated in previous studies (e.g. Batra & Fancke-Grosmann 1961, their figs. 1–9, Hoog & Sybren 2011, their fig. 16.3, Toki 2021, his figure 1c–f). However, this suggestion is strongly presumptive and due to the visibility limitations of this amber piece, even with higher magnifications, no final diagnosis on this topic can be delivered here.

Defence mechanisms – phragmosis

Specialised plate of abdominal segment IX seen in the new specimen (Fig. 3A–D) strongly resembles the one in extant *E. dermestoides*. Therefore, it is very likely that the new specimen used this particular morphological feature in the same way, for collecting and pushing of the wood debris and defence. Additional setae, asperities and teeth on the plate-like tergite (Fig. 3C–D) possibly add to the camouflage of the plate in the early stages of boring into wood since it optically might resemble the bark of a tree they are boring into, especially if the surface is covered in wood debris and possibly fungal hyphae. The phragmosis, a defence mechanism where a part of a body is used to block the entrance, is already known from other insects (e.g., Abbot 2022; Bishoff et al. 2023). This behaviour occurs also within wood-associated beetles such as bark-gnawing beetles (Li et al. 2025), and even in other ambrosia beetles, however, this was reported from adult specimens (e.g., keyhole ambrosia beetles; Flechtmann & Cognato 2011; Bentz & Jönsson 2015). Therefore, it is not surprising that wood-boring larvae have evolved similar defence mechanisms, in which they close the boring hole or other parts of the tunnel with a specialised structure to protect the vulnerable parts of their body. In early-stage larvae, the boring holes are very narrow and are not enlarged as part of a defensive strategy but also to maintain a consistent microclimate within the tunnels that promotes fungal growth (Eggert 1974). As a result, the larvae cannot turn around to defend with their mouthparts. They also continue to remove frass from the tunnels by moving backwards toward the tunnel opening (Eggert 1974; Burgers & Heijerman 2018, their fig. 14). Only full-grown larvae enlarge the tunnel, allowing them to turn around and move toward the bark in order to pupate near the opening hole. This behaviour was described by Simmonds (1965) in later-stage larvae of *Protomelittomma insulare* (Fairmaire, 1893) (old name *Melittomma insulare*, Fairmaire, 1894). Therefore, these observations suggest that selective pressures have favoured the evolution of this passive but effective defence structures in early stages of these larvae.

CONCLUSION

A new fossil larva of ship-timber beetles (Lymexyloidea) is described from approximately 40-million-year-old Eocene Baltic amber. The larva measures approximately 0.9 mm in length and, although differing in some respects from modern larvae, exhibits numerous characters shared with extant early-stage larvae of Hylocoetidae, from which only the early-stage larvae of *Elateroides dermestoides* are known. Shared morphological characters include the presence of five stemmata on each side, short antennae composed of three elements, maxillary palps with three elements with first element seated on a large palpifer, an oval plate-like tergite of abdominal segment IX with a crenellated ring of tooth-like cuticular structures, and a trunk end bearing paired specialised structures with blunt teeth. Based on these morphological similarities, the new specimen very likely had the same wood-boring lifestyle known from modern representatives and, in addition, possibly used its plate-like tergite as defensive mechanism (phragmosis).

Data Availability Statement: The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access

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