

First fossil species of ship-timber beetles (Coleoptera, Lymexylidae) from Eocene Rovno amber (Ukraine)

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Abstract

A new lymexylid fossil species, †*Raractocetus sverlilo* Nazarenko, Perkovsky & Yamamoto, **sp. nov.**, is described from late Eocene Rovno amber of Ukraine. This new species is similar to species of the recent genera *Atractocerus* Palisot de Beauvois and *Raractocetus* Kurosawa in the ship-timber beetle subfamily Atractocerinae, but differs in pronotal and elytral features. Notably, the new species is one of the smallest attractocerines known to date. This is the first member of the family Lymexylidae found in Rovno amber. Our finding sheds further light on the paleodiversity of attractocerine beetles, highlighting a peculiar distribution during the Eocene. Only one extant attractocerine specimen has been reported from Europe (Greece), while three species from Eocene European amber forests with equable climate are known now, including two species from the otherwise tropical genus *Raractocetus*. Our finding of the *Raractocetus* beetle from Rovno amber is of significant biogeographically because it indicates the wide distribution of the genus in the Eocene European amber forests.

Key Words

Atractocerinae, Lymexyloidea, new species, paleobiogeography, paleoclimate, paleodiversity, *Raractocetus*, systematics

Introduction

Extant ship-timber beetles (Lymexylidae) include approximately 70 species of 12 genera in four subfamilies (Lawrence 2020), including 17 Palaearctic species and only 5 known in Europe (Cuccodoro 2007). Currently, Lymexylidae are placed within the cucujiformian superfamily Tenebrionoidea (e.g. Lawrence 2020) or in its own superfamily Lymexyloidea (e.g. Bouchard et al. 2010; Zhang et al. 2018). All known members of the family develop in wood as larvae and mutualism with fungi has been reported for a few species (Batra and Francke-Grosmann 1961; Wheeler 1986; Young 2002; Lawrence 2010; Casari and Albertoni 2013; Toki 2021), although more rigorous study and evidence are needed if the other unstudied lymexylid beetles are strongly connected with

fungi (Lawrence 2010). Recently, Peris et al. (2021) discussed a potentially crucial role of the lymexylids as wood-boring insects, with a special emphasis on the insect–fungus mutualism, more specifically the cultivate ambrosia fungi and their associations. Moreover, Peris et al. (2021) considered that Lymexylidae might actually be one of the ambrosia beetles based on the fact that some of their larvae feed primarily on symbiotic ambrosia fungi in tunnels or caves in woody tissues following the criteria by Kirkendall et al. (2015).

The fossil records of Lymexylidae are relatively rare and scarce, mostly known from fossiliferous resins (e.g. Heer 1865; Wickham 1911; Kirejtshuk 2008; Wolf-Schwenninger 2011; Chen 2019; Yamamoto 2019; Chen and Zhang 2020; Nazarenko et al. 2020). The earliest Lymexylidae fossil is known from the Lower

Cretaceous Crato Formation in Brazil (Wolf-Schweninger 2011). Five species in four genera of the subfamily Atractocerinae have recently been described from mid-Cretaceous Burmese (Kachin) amber (Chen 2019; Yamamoto 2019; Chen and Zhang 2020), with some unstudied material (e.g. Peris 2020, 2021; Yamamoto, pers. obs.). The family is relatively rare in Eocene Baltic amber and is represented definitively only by adults (Kirejtshuk 2008; Yamamoto 2019). So far, three extinct species of the recent attractocerine genus *Raractocetus* Kurosawa have been described from Kachin and Eocene Baltic ambers (Yamamoto 2019).

Late Eocene Rovno amber from Ukraine is the southern coeval of the famous Baltic amber (Sokoloff et al. 2018), and more than 300 arthropod species have already been described from there (Perkovsky 2018; Bukejs et al. 2020; Colombo et al. 2021a, 2021b; Khaustov et al. 2021a, 2021b and references therein). Fewer than 48% of Rovno hymenopteran species (Simutnik et al. 2020, 2021; Colombo et al. 2021a, 2021b, 2021c; Radchenko et al. 2021, our data), 32% of caddisfly species (Melnitsky et al. 2021a, 2021b, 2021c), 24% of Nematocera (Gilka et al. 2021), and less than 15% of beetle species (Legalov et al. 2021a, 2021b; Kirichenko-Babko et al. 2021, 2022; Kupryjanowicz et al. 2021; Lyubarsky and Perkovsky 2021; Telnov et al. 2021; Tshernyshev and Perkovsky 2021; Perkovsky et al. 2022; this paper) are shared with Baltic amber fauna. Nearly all studied Rovno amber inclusions from the Rovno Region were collected from Klesov and the Horyn River Basin (Perkovsky et al. 2010; Perkovsky 2017a; Mitov et al. 2021), except new collections from Varash District (former Vladimirets and Zarechnoye Districts) in the Rovno Region and the former Manevichi District in the Volyn Region (Styr, Veselukha, and Stokhod River Basins). These new collections (mostly from Kuchotskaya Volya, Voronki, and Velyki Telkovichichi) revealed a number of new species of hymenopterans, termites, cockroaches, caddisflies, beetles, neuropterans, and snakeflies (e.g. Jałoszyński and Perkovsky 2019, 2021; Legalov et al. 2019, 2021b; Perkovsky and Makarkin 2019, 2020; Makarkin and Perkovsky 2020; Lyubarsky and Perkovsky 2020; Perkovsky et al. 2020; Anisyutkin and Perkovsky 2021; Melnitsky et al. 2021a; Matalin et al. 2021; Perkovsky and Nel 2021, etc.) and some species recorded previously from Baltic amber (Perkovsky and Olmi 2018; Martynova et al. 2019; Mamontov et al. 2020; Simutnik et al. 2020) or from both Baltic and Bitterfeld ambers (Radchenko and Perkovsky 2018, 2020).

Here, we describe a new *Raractocetus* species for the first time from Rovno amber from the Varash District, Ukraine. We discuss paleobiogeographical, paleoecological, and morphological features based on the new species.

Material and methods

The amber fossil studied here came from Voronki (former Vladimirets District), Rovno Region, Ukraine. The

holotype of †*Raractocetus sverlilo* sp. nov. is relatively well preserved, embedded in a parallelogram-shaped piece of amber (53 × 46 × 13 mm). Recent studies suggested the late Eocene age of Rovno amber, with a different geological background from Baltic amber (Perkovsky 2016a, 2018; Mänd et al. 2018). The generic classification of Atractocerinae generally follows that of Yamamoto (2019) and Lawrence (2020). The holotype of †*R. sverlilo* sp. nov. is deposited in the I.I. Schmalhausen Institute of Zoology (SIZK), National Academy of Sciences of Ukraine, Kiev, Ukraine, with the assigned number SIZK L-814. We compared the new species with the previously described three fossil species of *Raractocetus* by Yamamoto (2019), of which deposited in the insect collection of the Gantz Family Collections Center, Field Museum of Natural History (FMNH), Chicago, IL, USA, with consecutive numbers from FMNHINS-3965988 to FMNHINS-3965991. Observations were made using MBS-9 and Leica M165C stereomicroscopes. Images were taken with a Leica M165C equipped with a Canon EOS 500D or Leica Z16 APO stereomicroscope equipped with a Leica DFC 450, and later processed with Helicon Focus for focus stacking. The figures were edited and assembled using Photoshop Elements 15. This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending LSID to the prefix '<http://zoobank.org/>'. The LSIDs for this publication are: urn:lsid:zoobank.org:pub:B6791E34-7D6E-4956-9E8C-BED11F-2CFA6F; urn:lsid:zoobank.org:act:CBAD43C7-ECAF-4637-BC1E-67E23F216E7E.

Systematic paleontology

Superfamily Lymexyloidea Fleming, 1821

Family Lymexyloidea Fleming, 1821

Subfamily Atractocerinae Laporte, 1840

Genus *Raractocetus* Kurosawa, 1985

†*Raractocetus sverlilo* Nazarenko, Perkovsky & Yamamoto, sp. nov.

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Figs 1–4A, C, D

Holotype. SIZK L-814, female. The beetle inclusion can be observed from multiple angles, except obliquely. Near the inclusion there are cracks that partially cover the lower part of the body. Syninclusions: Scaptiidae (Coleoptera), Mymaridae (Hymenoptera), 3 Dolichopodidae (Diptera), larva of Syrphidae (Diptera), Lepidoptera, and Acari.

Etymology. The name of the species is derived from the Russian name, сверлило (*sverlilo*), for Lymexyloidea.

Type strata. Rovno amber, Upper Eocene.

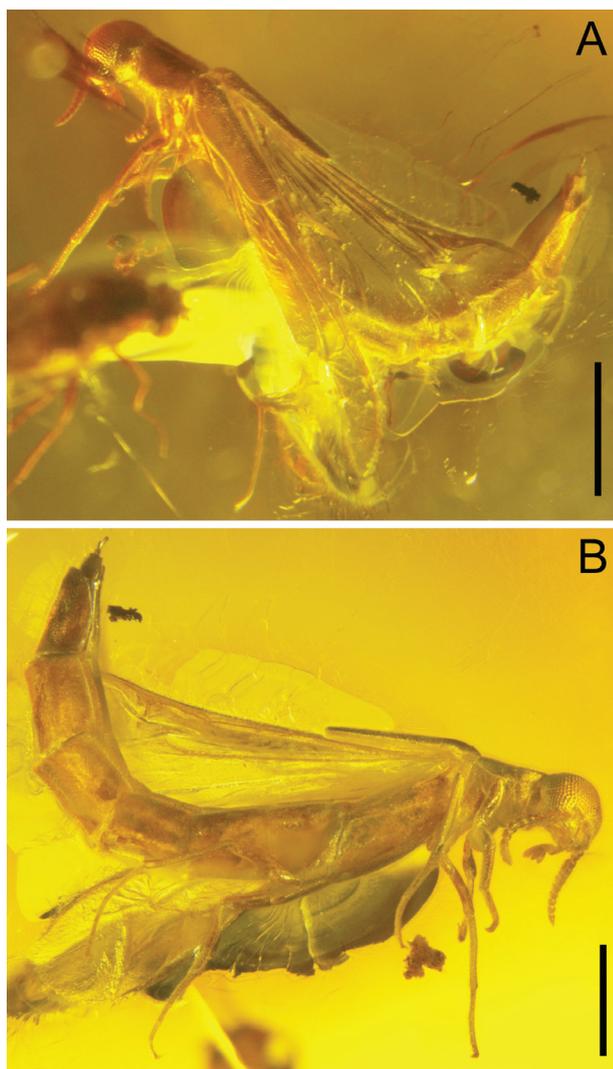


Figure 1. †*Raractocetus svertilo* sp. nov., female, holotype, SIZK L-814. **A.** General habitus, dorsolateral view; **B.** General habitus, ventrolateral view. Scale bars: 1.0 mm.

Type locality. Voronki locality (Varash district), Rovno Region, Ukraine.

Description. Measurements: body length ca. 7.1 mm, head length 0.60 mm, head width 0.70 mm, pronotum length 0.60 mm; elytra length 1.30 mm, elytra width 0.41 mm, hindwing length ca. 4.20 mm, hindwing width 1.10 mm; length of protibia 0.37 mm, mesotibia 0.67 mm, metatibia 0.78 mm; length of protarsus ca. 0.44 mm, mesotarsus 0.71 mm, metatarsus 1.10 mm; lengths of 4–7th sternites, respectively 0.77 mm, 0.86 mm, 0.80 mm and 0.86 mm.

Female. Body small, narrowly elongate, abdomen arcuate dorsally curved. Color uniformly yellowish brown, in some areas with cuticles darker. Surface leathery, covered with dense, very short protruding pubescence in most areas; legs and thoracic sternites mostly covered with dense setae.

Head broadly oval, rather vertical, 1.3 times shorter than pronotum, slightly wider than prothorax. Eyes large, nearly contiguous, occupying almost entire visible surface

of head capsule; anterior margin cut out, covering partly of antennal insertion; vertex areas each diverging to form rather triangle shape of eyes. Antennae 11-segmented, relatively short and thick, 1.2 times as long as head and 1.5 times as long as pronotum; left antenna fully visible and observable, whereas right one partially appressed with only 7 last antennomeres clearly visible; first two antennomeres each slightly transverse, rounded, similar in shape and size, with visible part of first antennomere 1.6 times as wide as its length, of second 1.3 times; 3rd to 11th antennomeres forming flagellum with somewhat fusiform club; 3rd antennomere 1.25 times wider than second, its length almost equal to its width, next two antennomeres approximately equal to it in width, fourth 1.5 times wider than its length, fifth 2 times wider than its length, sixth 1.1 times narrower than 5th, 1.3 times wider than its length, its width slightly decreasing towards apex, seventh 1.14 times narrower than sixth and 1.17 times wider its length, 8th approximately equal in length and width, 1.14 times narrower than 7th, 9th almost same width, 1.17 times wider than its length, 10th 1.1 times narrower than 9th, 1.17 times as long as wide, 11th cone-shaped, pointed, 1.18 times narrower than 10th and 2 times as long as wide. Mouthparts partially visible. Clypeus transverse. Mandibles small, inconspicuous. Maxillary palpus with at least 7 short branched appendages (i.e., maxillary palporgan *sensu* Wheeler 1986), each slightly to moderately longer than penultimate maxillary palpomere.

Pronotum short, without maculation, anterior margin rounded; complete longitudinal groove along midline present, but with interruption just behind middle of furrow (see Fig. 4A, C, *ipf*). Mesoscutellum relatively narrow, details not visible.

Mid- and hindlegs somewhat long, slender; forelegs rather short, robust, moderately thickened, profemora, protibiae, and protarsi approximately equal in length; protibiae without spur, mesotibiae and metatibiae each with one spur (indistinct on mesotibia); procoxae thick, robust, more or less cylindrical; protibiae robust, 4 times as long as wide, protarsi 1.1 times as long as protibiae, 1.35 times as long as pronotum; mesofemora 0.38 times narrower than profemora; mid- and hindlegs long and thin; mesotibiae and metatibia 1.1 times longer than pronotum and 1.8 times as long as protibiae; metacoxae strongly projecting posteriorly, metatibiae feebly curved externally. Tarsi 5-segmented, metatarsi slightly longer than metatibiae; protarsi with 1st and 5th protarsomeres very long, 2nd and 3rd short and inconspicuous, approximately equal in length, 4th protarsomere shorter than each of them; meso- and metatarsi with first segments longest, second ones about 2.3 times shorter than them, 3rd and 5th segments slightly shorter than 2nd, 4th about 1.8 times shorter than 3rd. Claws simple, widely separated.

Elytra short, 2.45 times as long as pronotum, and 3.4 times as long as its maximum width, each nearly subparallel sided, exposing most part of abdomen; outer elytral margins gently arcuate each with very shallow median emargination (Fig. 4D, *oe*), whereas inner margin

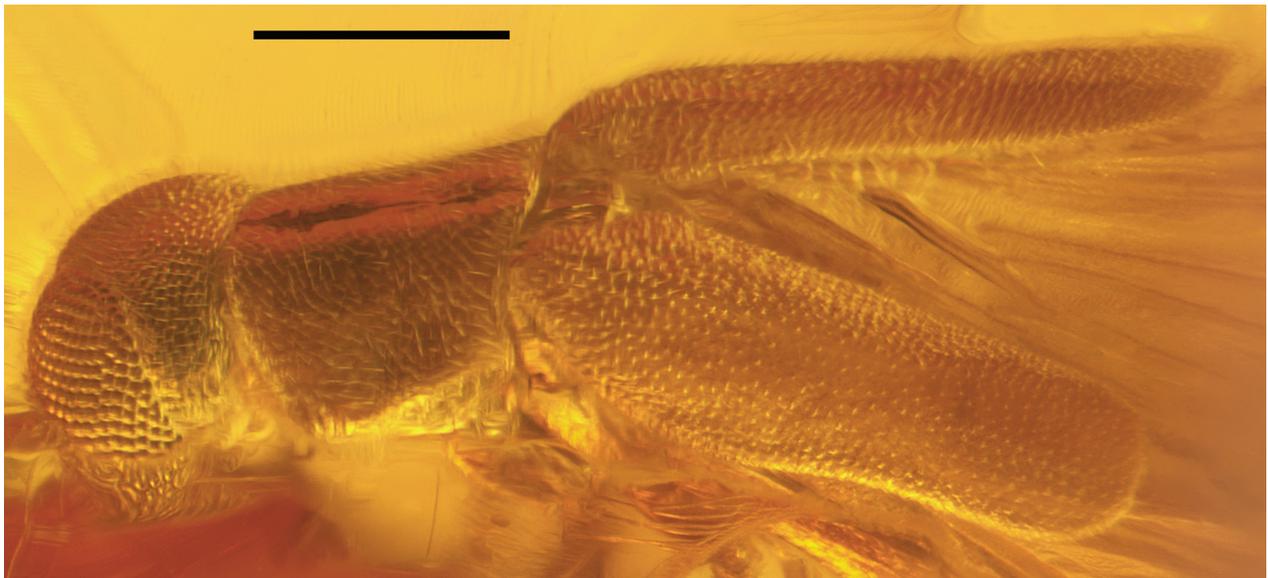


Figure 2. †*Raractocetus sverlilo* sp. nov., female, holotype, SIZK L-814: forebody, dorsolateral view. Scale bar: 0.5 mm.

straight, not extending beyond metacoxae; surface covered with dense, short obliquely protruding pubescence.

Hindwings fully developed, entire, 2.7 times as long as elytra; their apices not covering last two visible abdominal tergites; venation with details remaining unclear, but with visible veins of C-Sc-R, radial-medial (r-m), medial and cubital veins, and part of anal veins. Metaventrite distinctly elongate.

Abdomen narrowly elongate, nearly subparallel-sided, weakly tapering posteriorly, uniformly bent dorsally as preserved; abdominal segments II–VII visible. Abdominal segment VIII and ovipositor partially protruding. Styli exposed, weakly clavate, their apices with sparse long bristles.

Male unknown.

Comparison. †*Raractocetus sverlilo* Nazarenko, Perkovsky & Yamamoto, sp. nov. can be assigned to Atractocerinae based on the markedly reduced brachelytrous elytra with largely exposed hindwings, large bulging eyes, and distinctly modified maxillary palp organ in the female (Paulus 2004; Yamamoto 2019). The new fossil species is placed in the genus *Raractocetus* by having a rather vertical head, which is slightly wider than the pronotum, and large and subcontiguous eyes in the frontal view (Kurosawa 1985; Paulus 2004). This new species is similar to described fossil representatives of the genus from Eocene Baltic amber and mid-Cretaceous Burmese (Kachin) amber based on the strongly projecting metacoxae, length and shape of the pronotum, elytral shape, wing venation, antennal details and appendages of the maxillary palps of the female (Yamamoto 2019), and possibly its smaller body size as well. Interestingly, †*R. sverlilo* sp. nov. has a much smaller body (ca. 7.1 mm) than recent attractocerine species (less than half in body length, see Lawrence 2020), but it is similar in size to the mid-Cretaceous species †*R. fossilis* Yamamoto, 2019 (ca. 7.6 mm). Nevertheless, the individual size of adult ship-timber beetles may depend of larval feeding

and therefore, the reason for such the small sizes in the fossil lymexylid species are still unclear. More study is needed to discuss the possible miniaturization phenomenon as seen in the extinct ship-timber beetles. The new species differs from the three extinct species currently assigned to *Raractocetus* mainly by the pronotal and elytral shapes, together with the structures of a longitudinal furrow along midline of the pronotal disc. It is readily distinguished from †*R. balticus* Yamamoto, 2019 from Baltic amber, by its markedly smaller body (†*R. balticus*, ca. 11.1 mm body length), the presence of the interruption on the pronotal furrow (see Fig. 4A, C, *ipf* vs. †*R. balticus* in Fig. 4B), non-linear (i.e., shallowly emarginate) outer margins of the elytra (Fig. 4D, *oe*) and possibly by seemingly thicker antennae. Furthermore, †*R. sverlilo* sp. nov. is distinguished from †*R. extinctus* Yamamoto, 2019 and †*R. fossilis* from Kachin amber by having a smaller body size (†*R. extinctus* ca. 13.4 mm body length), simple coloration without any types of maculation, rounded anterior margin of the pronotum, more conspicuous and deeper longitudinal pronotal furrow, the presence and straight elytral inner edges with their different shapes of elytral emargination along outer margins of elytra, additionally by seemingly thicker antennae and protibiae.

Discussion

Here, we described the first lymexylid beetle from the Ukrainian Rovno amber. Our discovery of the attractocerine genus *Raractocetus* in Rovno amber suggests a potentially widespread distribution of this genus in the late Eocene in Europe, as previously suggested by Yamamoto (2019) based on †*R. balticus* from Baltic amber. The only two recent species of *Raractocetus* are distributed in the Oriental Region and Australia respectively (Lawrence 2020). The entire subfamily

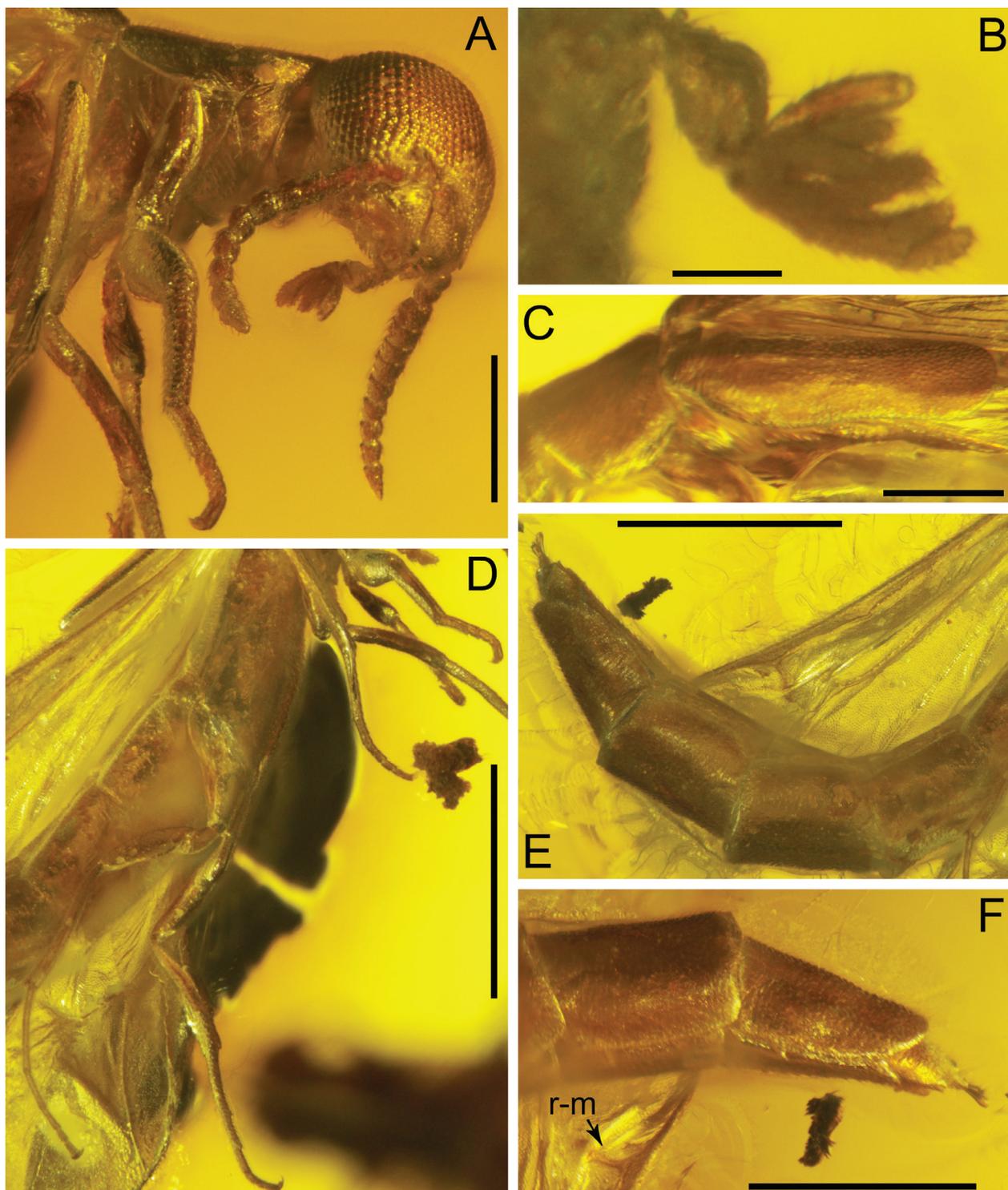


Figure 3. †*Raractocetus sverlilo* sp. nov., female, holotype, SIZK L-814. **A.** Head and prothorax, dorsoventral view; **B.** Maxillary palporgan with branches; **C.** Pronotum and left elytron, dorsolateral view; **D.** Metaventrite and legs, ventrolateral view; **E.** Abdomen in posterior half, ventrolateral view; **F.** Abdominal terminalia with styli, lateral view. Scale bars: 0.5 mm (A, C); 0.1 mm (B); 1.0 mm (D–F). Abbreviation: r-m, radial-medial vein.

Atractocerinae is represented now in Europe by the single species *Urtea graeca* Paulus, 2004 from Greece only (Paulus 2004). Hence, finding *Raractocetus* in European ambers is of great significance when considering the paleobiogeography of the genus and subfamily. Extant *Raractocetus* feed on both living (Lawrence 2020) and

dead trees. In addition, a scraptiid syninclusion may indicate that the new species possibly fed on dead trees because nearly all the members of Scraptiidae develop in dead wood. Numerous scraptiid larvae in Rovno amber (V. K. Odnosum, Kiev, pers. com.) were also found together in the same amber with larvae and adults of the

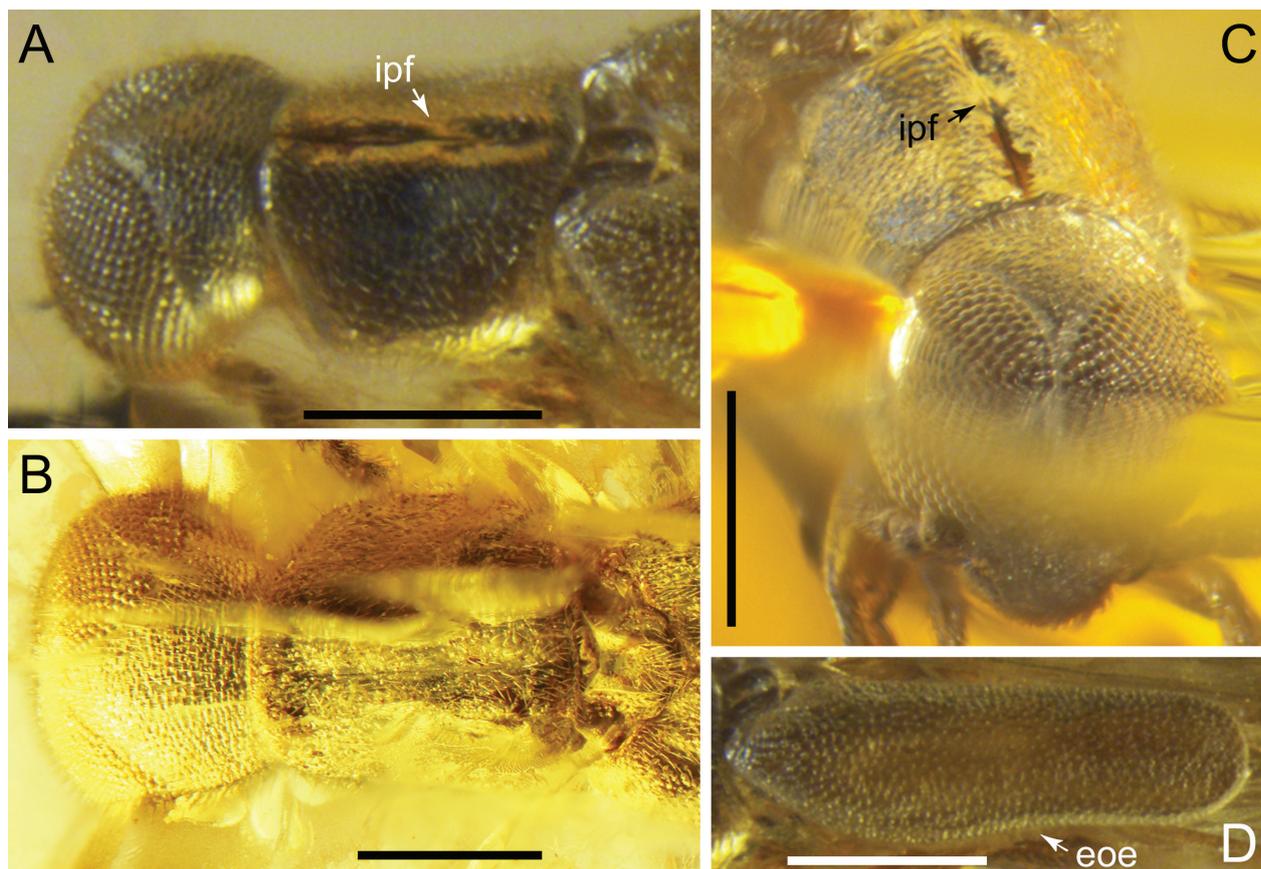


Figure 4. Morphological comparison of two Eocene *Raractocetus* species. †*Raractocetus sverlilo* sp. nov., female, holotype, SIZK L-814 (A, C, D) and †*R. balticus* in Eocene Baltic amber, female, holotype, FMNHINS-3965991 (B). A. Head, pronotum and mesoscutellum, dorsolateral view; B. Head, pronotum and mesoscutellum, dorsal view; C. Head and pronotum, frontal view; D. Elytron, dorsolateral view. Scale bars: 0.5 mm (A–D). Abbreviations: eoe, shallow median emargination along outer elytral margin; ipf, interrupted longitudinal furrow on pronotum.

wood-boring Micromalthidae beetle, *Micromalthus priabonicus* Perkovsky, 2016 (Perkovsky 2016b).

The Oriental species of *Raractocetus* occurs in tropical India, Sri Lanka, Myanmar, Thailand, Sumatra, Java, Sulawesi, Sarawak and the Philippines (Wheeler 1986 and references therein) and in subtropical Taiwan (Kurosawa 1985); it was reported to feed on the oriental plants *Buchanania latifolia* Roxb. (Anacardiaceae) and *Dipterocarpus zeylanicus* Thwaites (Dipterocarpaceae) (Wheeler 1986 and references therein). Australian species feeds in Western Australia on the several myrtaceous trees, mostly *Eucalyptus* (Clarke 1925; Lawrence 2020) and was most important pest for commercial timber there (Clarke 1925). All localities of Australian species (Lawrence 2020) have a cold month mean temperature (CMMT) higher than 11 °C, except the Australian Capital Territory and a nearby (70 km) locality in New South Wales with a CMMT = 5.5 °C and a single locality in South Australia with a CMMT = 7.4 °C. The Baltic amber forest is thought to have grown in a climate with mild winters (Archibald and Farrell 2003), although extant Holarctic genera prevail in its entomofauna (Perkovsky 2017b; Radchenko and Perkovsky 2021 and references therein). As the CMMT was lower than 5.5 °C, this might account

for Baltic amber *Raractocetus* being so rare; for comparison, in Arnaia (Chalkidiki, Greece), where the holotype of *Urtea graeca* was found, the CMMT is 5 °C, and still only the holotype of this species has been reported. The climate of the Rovno amber forest was warmer than that of the Baltic (Perkovsky 2017b, 2018; Mänd et al. 2018), and therefore, it could be possible to speculate that *Raractocetus* as well as many other thermophilic beetles, e.g. Smicripidae (Kupryjanowicz et al. 2019), should have been more common in the amber-producing forest but more evidence is needed to assess this hypothesis.

The morphology of †*R. sverlilo* sp. nov. generally agrees well with the three fossil *Raractocetus* species from Baltic and Kachin amber, more than with the extant species, which have different geographical and geological backgrounds. For example, they share similar structures in the metacoxae and its inner areas strongly project posteriorly (Fig. 3D). In most primitive Atractocerinae, the metacoxae project very strongly posteriorly (see also Paulus 2004), such as in the fossils *Cratoatractocerus* (Wolf-Schwenninger 2011) and *Vetatractocerus* (Yamamoto 2019) and the extant *Urtea* Paulus, *Fuscicornis* Philippi (Chile) and *Leptonetron* Lawrence (Tasmania, in continental Australia outside of Victoria and New South

Wales known only from Brisbane (Queensland) and Pemberton in extreme southwestern Western Australia). The very strongly projecting metacoxae in Cenozoic Atractocerinae correlate with seasonal subtropical and even temperate climate and importance of the shorter pupal stage. This stimulates premature eclosion of adult that in turn results in imaginal juvenilization which is accompanied with elongation of metacoxae in Polyphaga (Tikhomirova 1991). A pair of elytra of Eocene species also remarkably reduced as in the extant species (also a possible result of juvenilization, as a retention of pupal short elytra, cf Tikhomirova 1991: fig. 10, 9), and the elytra shows species-specific variation in shape and size (Yamamoto 2019; this study). Compared to the Kachin amber taxa, the specimens from European ambers lack distinct colored markings, maculation, or patterns on the head, pronotum, and elytra (Yamamoto 2019; this study). Of note, such color patterns appear to play a role in the mimicry of various Hymenoptera, particularly certain nocturnal wasps (Kurosawa 1985). If correct, then the ecological and behavioral strategies of species from European and Kachin ambers might differ. Such color patterns are sometimes not preserved in fossils or even appeared as artefact. Nevertheless, it is noteworthy to mention here that Eocene species had no evident color pattern as seen in the Myanmar amber fossils (Yamamoto 2019; this study). The discovery of †*R. sverlilo* sp. nov. opens a new window on the paleobiogeography and paleoecology of lymexylid beetles.

Data availability

The sole fossil material (holotype) of †*Raractocetus sverlilo* sp. nov. described in the paper is deposited in the I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine (SIZK). The remaining material of the other three fossil species of *Raractocetus* are deposited in the insect collection of the Gantz Family Collections Center, Field Museum of Natural History (FMNH), Chicago, IL, USA. All data are included in the description. Higher-resolution images are also available through the Zenodo repository (<https://doi.org/10.5281/zenodo.5913279>).

Author contributions

SY and EEP designed the study. SY, EEP and VYN identified and described the specimen. SY and VYN produced the photos. SY edited and assembled the figures. SY, VYN, DVV and EEP prepared the paper and contributed to the editing.

Competing interests

The authors declare that they have no conflict of interest.

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