

The first neotropical ground beetle (Coleoptera, Carabidae) from the Eocene of Ukraine: finding the first Old World ant nest beetle related to *Eohomopterus* in the Rovno amber

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ABSTRACT: The first record of the tribe Paussini Latreille is reported based on a specimen from late Eocene Rovno amber. It is the first known close relative of the genus *Eohomopterus* (subtribe Carabidomemnina) in the Old World. The recent and Neogene distribution of *Eohomopterus* is Neotropical, with extant representatives in Ecuador, Brazil and the West Indies, and extinct species in Dominican and Mexican amber. The occurrence of the Neotropical Carabidomemnina in Rovno amber and the presence of the Oriental Protopaussini in Dominican amber are of significant interest as evidence of the probable transarctic migrations of their ant host in the early Eocene.



KEYWORDS: amber, ant host, Carabidomemnina, fossil, myrmecophilous, Paussinae.

Most known beetles in Rovno amber belong to the suborder Polyphaga (Bukejs *et al.* 2020; Tshernyshev & Perkovsky 2021; Telnov *et al.* 2021, 2022; Alekseev & Bukejs 2022, 2023a, b; Kazantsev & Perkovsky 2022; Legalov *et al.* 2022a, b, 2023; Vitali & Perkovsky 2022; Yamamoto *et al.* 2022; Lyubarsky *et al.* 2023; Motyka *et al.* 2023; Nabozhenko & Perkovsky 2023) and a few belong to the Archostemata or Adephaga. Examples of Archostemata include *Micromalthus priabonicus* Perkovsky 2016 (Rovno amber) and *Cupes groehni* Kirejtshuk 2005 (Baltic and Rovno amber, Bukejs *et al.* 2021), a new genus and species of thermophile tiger beetle (Matalin *et al.* 2021), an endemic sphodrine species of the extinct genus *Quasicalathus* Schmidt & Will, 2022 in Baltic and Rovno ambers in Schmidt (*et al.* 2022), an extinct lebiine genus known only from Rovno amber with two species (Kirichenko-Babko *et al.* 2022a, b) and the new tropical paussine (Kirichenko-Babko & Perkovsky 2021) described here.

Paussine beetles are commonly known as ‘ant nest beetles’ (Skaife 1954) or ‘flanged bombardier beetles’ (Moore 2006) due to their cuticular flange (flange of Coanda) located at the lateral margin of each elytron near their apex (with the exception of Metriini, see also Deuve 2020). The taxonomy and biogeography of paussids is fairly well examined (e.g., Darlington 1950; Stork 1985; Nagel 1986, 1987b, 2006; Nagel *et al.* 2017; Luna de Carvalho 1989; Ball & McCleve 1990; Ball & Shpeley 1990; Di Giulio *et al.* 2003; Moore 2006, 2008; Fattorini *et al.* 2012, 2013; Moore & Robertson 2014; Robertson & Moore 2016; Deuve 2020). Currently, they are divided into five tribes: Metriini LeConte 1853; Ozaenini Hope 1838; Protopaussini Gestro 1892; Paussini Latreille 1807; and Kryzhanovskianini Deuve 2020. Extant paussids include around 870 species, approximately

600 of which are Paussini, as the largest group of myrmecophilous beetles (Lorenz 2021) and the ‘quintessential Trojan horses of the insect world’ (Moore & Robertson 2014, p. 1). Their geographical distribution has been discussed by Jeannel (1946), Reichensperger (1948), Darlington (1950) and Nagel (1979). They are mainly restricted to the subtropics and tropics, with their highest diversity in the Palaeotropics (Geiselhardt *et al.* 2007).

Most fossil paussines (20 species) are known from the late Eocene Baltic amber (Wasmann 1929). These are placed in six extinct genera: *Arthropterites* Wasmann 1925 (one species); *Cerapterites* Wasmann 1925 (one species); *Eopaussus* Wasmann 1926 (one species); *Pleuarthropterus* Wasmann 1927 (= *Balticarthropterus* Nagel 1987a) (12 species); *Protocerapterus* Wasmann 1926 (two species); and *Succinarthropterus* Kolbe 1926 (three species) (Nagel 1987b; Alekseev 2017; Kirejtshuk & Ponomarenko 2021). They probably belong to the subtribe Carabidomemnina Wasmann 1928 (Paussini) (Geiselhardt *et al.* 2007). The oldest Paussini is a single species reported from the middle Eocene (44–45 Ma) Eckfeld Lagerstätte, belonging to *Pleuarthropterus* (*Balticarthropterus*) (Wappler 2003). Neotropical extinct paussines are described from Miocene Dominican and Mexican ambers (Nagel 1987b, 1997; Solórzano Kraemer 2006). These belong to the three extant genera in two tribes – *Protopaussus* Gestro 1892 in the Protopaussini (one species), *Eohomopterus* Wasmann 1925 (two species) and *Homopterus* Westwood 1841 (one species), both in the Paussini. The oldest paussine *Kryzhanovskiana* Kataev & Kirejtshuk 2019 (originally classified as Metriini, reclassified as Kryzhanovskianini by et Deuve 2020) was described from earliest Cenomanian Kachin amber (Kataev *et al.* 2019). Paussinae has 27 extinct species

belonging to ten genera in three tribes described from the Cretaceous to the Neogene (Kirejtshuk & Ponomarenko 2021; Lorenz 2021): Kryzhanovskianini (one species); Protopaussini (one species); and Paussini (25 species). Nagel (1987b) and Luna de Carvalho (1989) proposed a phylogenetic classification of the fossil paussids; however, their species-level diversity has been insufficiently studied.

1. Material and methods

Ukrainian Rovno amber (Priabonian, 33.9–37.8 Ma) is the southern analogue of Baltic amber found from the north of Volyn and the Rovno and Zhitomir regions (reviewed by Perkovsky *et al.* 2010; Mitov *et al.* 2021). It was redeposited northward to the periphery of the north-western part of the Ukrainian Crystalline Rock Massif (Perkovsky *et al.* 2007).

This paper is based on an amber inclusion from the collection of Nikolai R. Khomych (Rovno) on long-term loan to the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (SIZK), inventory number SIZK L-956, and available for study. It was collected in the Varash district (between Voronki and nearby Luko) of the Rovno Oblast, like most of the important new taxa described from Rovno amber during the last few years (Perkovsky *et al.* 2020; Golub *et al.* 2021; Perkovsky & Nel 2021; Olmi *et al.* 2022; Simutnik *et al.* 2022 and references therein).

The following measurements are in millimetres:

- body length (BL) – from the visible anterior margin of the head to the elytral apex;
- head length (HL) – from the visible anterior part of head to the constriction of neck;
- head width (HW) – maximum width of the head with eyes;
- antennal club length (AL) – of the antennomeres of flagellum;
- pronotal length (PL) – length along the median line from the anterior margin to the pronotal base;
- pronotal width (PW) – maximum width;
- elytral length (EL) – length from the basal border to the apex along the suture; and
- elytral width (EW) – width across the middle of both elytra.

The material was examined with a Leica M165C stereomicroscope and photographed with an attached DFC450 C camera. Photostacking was done with Helicon Focus 6 software. Figures were prepared with Adobe Photoshop CS8. Morphological terminology follows Nagel (1987b, 1997) and Darlington (1950).

Identification was not possible to the species level, as the amber is very dark with many small inclusions of wood and air bubbles and the beetle is located near the surface, positioned such that its ventral morphology cannot be seen (mouthparts, fore coxae and forelegs).

2. Systematic palaeontology

Order Coleoptera

Family Carabidae Latreille 1802

Subfamily Paussinae Latreille 1806

Tribe Paussini Latreille 1806

Subtribe Carabidomemnina Wasmann 1928 (Figs 1–3)

Genus ?*Eohomopterus* Wasmann 1925

Diagnosis. With the combination of characters of the subfamily Paussinae: reduction of the pedicel (antennomere 2), robust

antennae forming a distinct flagellum (antennae club), subapical elytral fold (flange of Coanda) and leg structure. Antennae as in Cerapterina: club with nine free antennomeres (3–11), pronotum without trichome-bearing cleft, elytral base with carina suggesting placement in the Paussini. Belonging to the subtribe Carabidomemnina (comprises two genera, *Carabidomemnus* Kolbe 1924 and *Eohomopterus* Wasmann 1919) by its compact body with glabrous convex surface, flattened antennomeres, elytra with short suture and apex non-truncate, short tibia narrow basally and extended to apex (Nagel 1997). All Baltic amber Paussinae described by Wasmann (1928) have a non-truncate elytral apex (Nagel 1987b).

The Rovno specimen differs from species of *Carabidomemnus* by the short 4 tarsomere, the weakly expanded tarsomeres 2 and 3 (vs *Carabidomemnus* all tarsomeres visible), by the transversally rectangular first flagellomere (antennomere 3) (vs *Carabidomemnus*: relatively small, see Kolbe 1928; Wasmann 1928, 1929) and by the intermediate antennomeres with straight apical and basal margins (Figs 1b, 3b) (vs *Carabidomemnus*: antennomeres 3–8 have a compact crescent shape).

Distinctive features of the Rovno amber species and comparison with known *Eohomopterus* species. The dorsal surface of the Rovno specimen's body is without punctures (vs finely punctate in †*Eohomopterus poinari* and †*Eohomopterus simojovelensis*), and the BL is about 6 mm long (Figs 1, 2). Its antennae are parallel and flattened, reaching the base of the pronotum in turned-back position, and the flagellum is nine-segmented (antennomeres 3–11); AL is about 1.9 mm; the width and height of the last antennomere are 0.67 mm and 0.6 mm, respectively. The first flagellomere (antennomere 3) of the Rovno specimen is transversally rectangular (Figs 1b, 3b), whereas in †*Eohomopterus paulmuelleri* Nagel 1987b and †*E. simojovelensis* Solórzano Kraemer 2006 it is a transverse rhomboid and in †*E. poinari* Nagel 1997 and *Eohomopterus centenarius* Luna De Carvalho 1960 it is transverse and broadly triangular. The exterior and interior apical corners of the Rovno specimen's club articles 4 to 10 have small tooth-shaped prolongations, similar to that of †*E. paulmuelleri* (Nagel 1987b) and †*E. simojovelensis* (Solórzano Kraemer 2006, Figs 3, 4). Its scapus has short setae as in †*E. paulmuelleri*. The head is transverse with protruding eyes. Its anterior has short hairs on the front, distinguishing it from named *Eohomopterus* species, where this character state is known. Unfortunately, the ventral side including the mouthparts are not visible (see above).

The pronotum is slightly cordiform (slightly wider than long: PW/PL = 1.17, with rectangular posterior angles, as in *Eohomopterus aequatoriensis* Wasmann 1899). It has a narrow lateral marginal edge and has small depressions in front of it base on both sides (Fig. 3a). In †*E. poinari* it is also markedly narrowed toward base (Nagel 1997), whereas in †*E. simojovelensis* it is almost rectangular.

The elytral suture is probably short, reaching the elytral middle (elytra slightly open along the suture and the outer side of right elytron is deformed) (Fig. 1a). The elytra are almost twice as long as wide (EL/EW = 1.9) and their basal edge is wider than the pronotal base. The elytral base in the area of the humeri has triangular depressions as in recent and fossil species of *Eohomopterus*, and behind the scutellum of each elytron there is one bristle-bearing pore (Fig. 2a) as in recent species of *Eohomopterus*. The setae of the seria umbilicata is not discernible, as in †*E. paulmuelleri*, vs in †*E. poinari* and †*E. simojovelensis*, where this is visible. The scutellum is elongate triangular (vs equilaterally triangular in †*E. paulmuelleri* and †*E. simojovelensis*) and is without punctures (Fig. 2a).

The structure of the front coxae is an important feature for identifying *Eohomopterus* species (Darlington 1950), which are

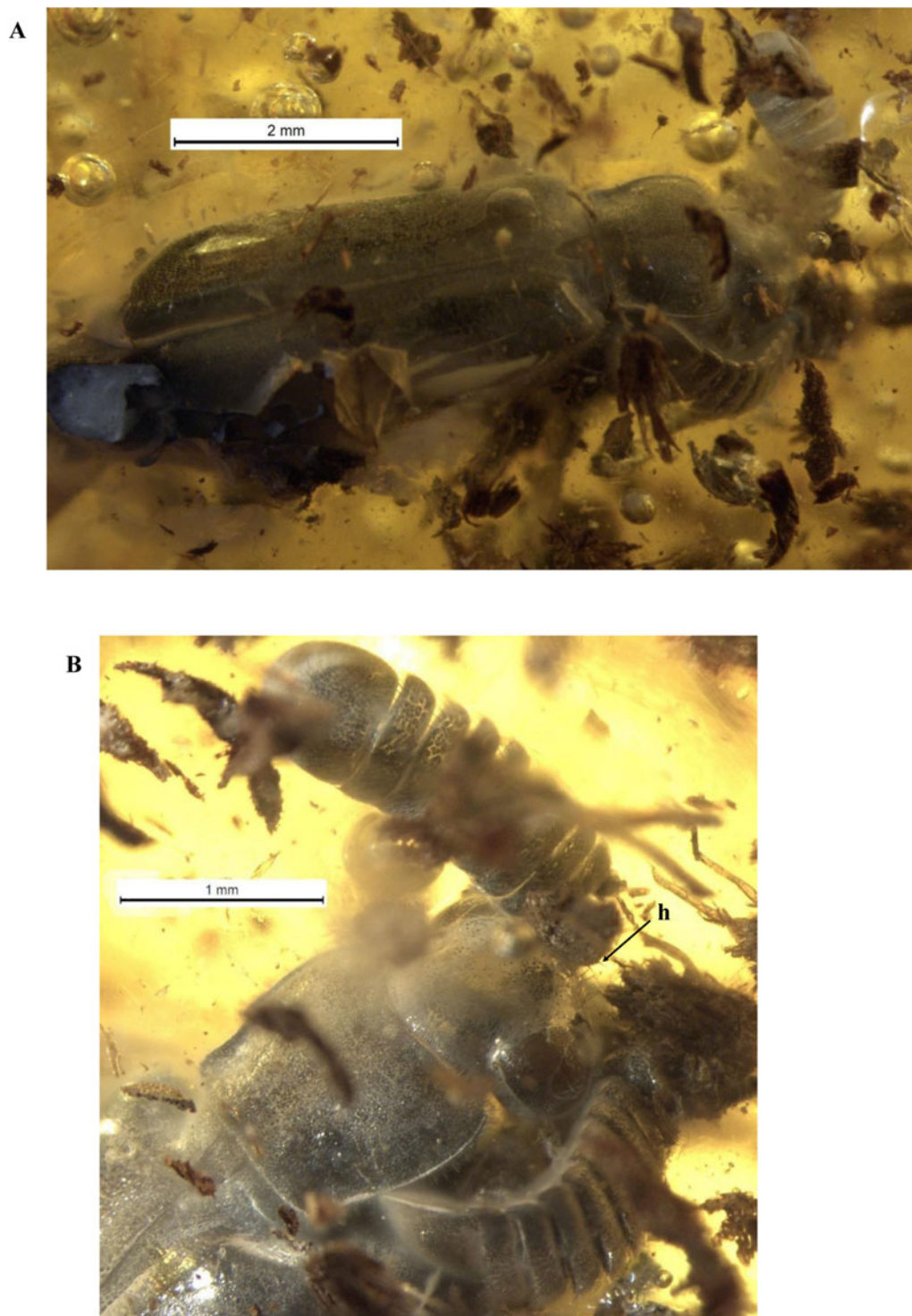


Figure 1 Habitus of the paussine beetle in Rovno amber, dorsal view. (a) Head, antenna and pronotum. (b) Arrow indicates the hairs (h) on the front of the head.

distinguished by a narrow prosternal process in all members; however, in †*E. poinari* (Nagel 1997) and the Rovno specimen this is not visible. The genus *Eohomopterus* is characterised by the emarginated inner margin of its front tibiae, which are apically dilated and have two final spurs; however, this cannot be assessed in the Rovno specimen by preservation (see above). The tibiae of another fossil *Eohomopterus* are rather slender, slightly widened apically (Nagel 1997; Figs 3, 4; Solórzano Kraemer 2006; Fig. 2).

In the Rovno specimen, the visible part of the femora of the right foreleg is broad and short and the femora of the right fore-legs and middle-legs have short pilosity. In the Rovno specimen

the middle tibia (Fig. 2b) is longer than wide (approximately 2.7 times longer than wide), flattened and its proximal end near the femora is narrow as in *E. aequatoriensis*.

The tarsus is slightly longer than the width of the mesotibia at the apex (Figs 2b, 3c). In the right mesotarsus (length about 0.8 mm), tarsomere 5 is longer than 1–3 combined (vs *Carabidomemnus*: all tarsomeres are clearly visible and not reduced), tarsomere 4 is short and tarsomeres 2–3 slightly dilated as in †*E. poinari*. The tarsi have long, simple and distinctly bent claws. The structure of the tarsi of †*E. paulmuelleri* is identical to that of *E. centenarius*: tarsomere 3 is more dilated than tarsomere 2; whereas in *E. aequatoriensis* the 2 and 3 tarsomeres

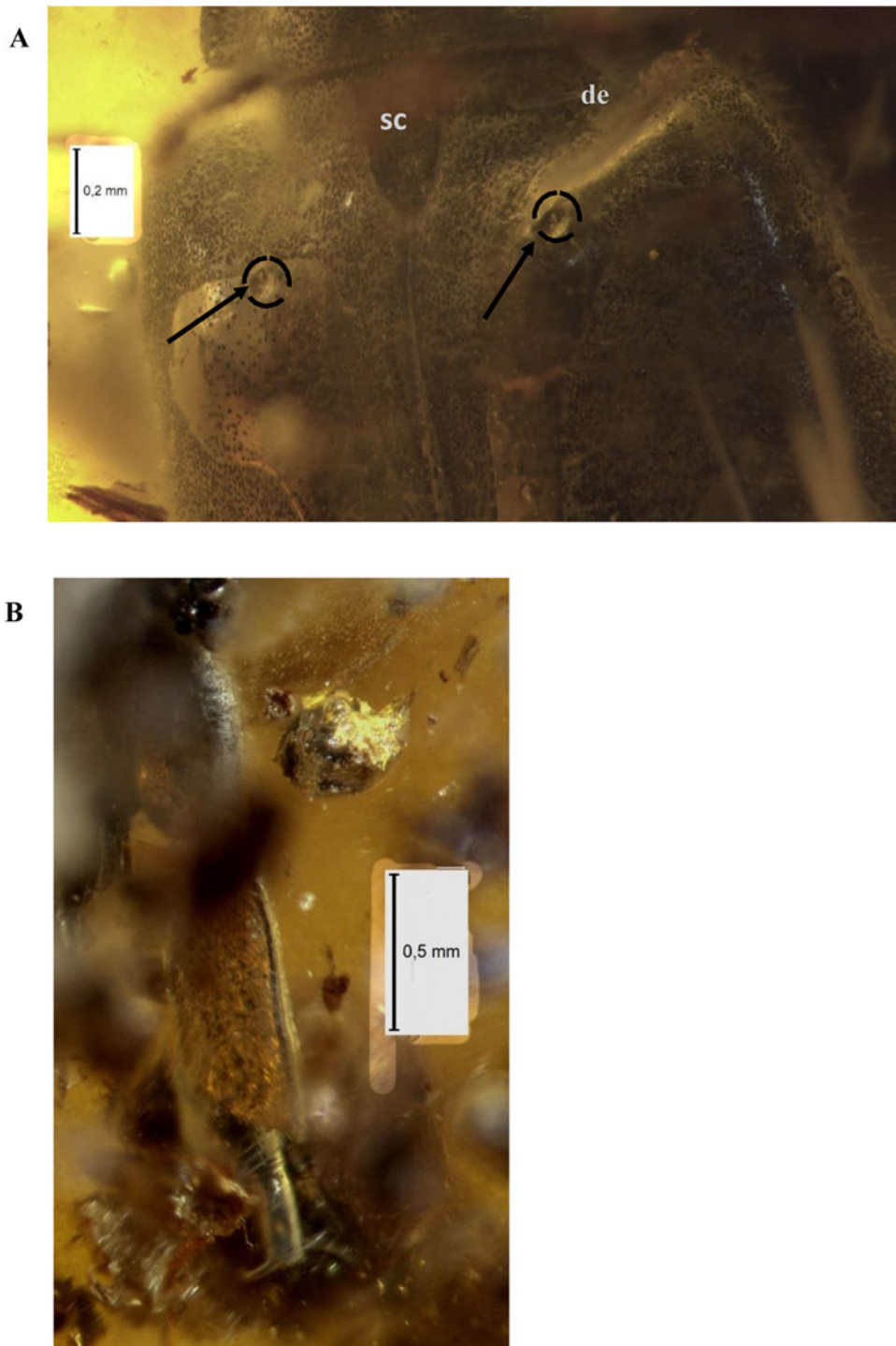


Figure 2 The paussine beetle in Rovno amber. (a) Base of elytra with triangular depressions (de), the elongated scutellum (sc) and two setae in the humeral region and the right middle leg in anterolateral view. (b) The femora, tibia and tarsi. Arrows indicate the setae; circles indicate the setigerous pores.

are extremely strongly lobed, as in †*E. simojovelensis* (Solórzano Kraemer 2006).

In summary, the Rovno amber specimen is distinguished from extant and Neogene species of *Eohomopterus* Wasmann 1919 by the following characteristics:

the transverse rectangular antennomere 3 (1st flagellomere) (Figs 1b, 3b), vs rhomboid in †*E. paulmuelleri* and †*E. simojovelensis* and triangular in †*E. poinari* and *E. centenarius*;

the slightly cordiform pronotum (Figs 1a, b, 3a) as in *E. aequatoriensis*; vs rectangular with broadly rounded

posterior angles in †*E. simojovelensis*, †*E. paulmuelleri* and *E. centenarius*;

the length of the 5th tarsomere equals that of the 1–4th tarsomeres, as in extant *E. aequatoriensis* (Figs 2b, 3c);

the scutellum is elongated triangular; behind it each elytron has one bristle-bearing pore (Fig. 2a) (in other fossil species, this cannot be assessed);

the body surface is without punctures (Fig. 1a) and is glabrous as in *E. aequatoriensis*, vs finely punctate in †*E. poinari* and †*E. simojovelensis*;

the absence of the two punctures on the front of the head between the eyes;

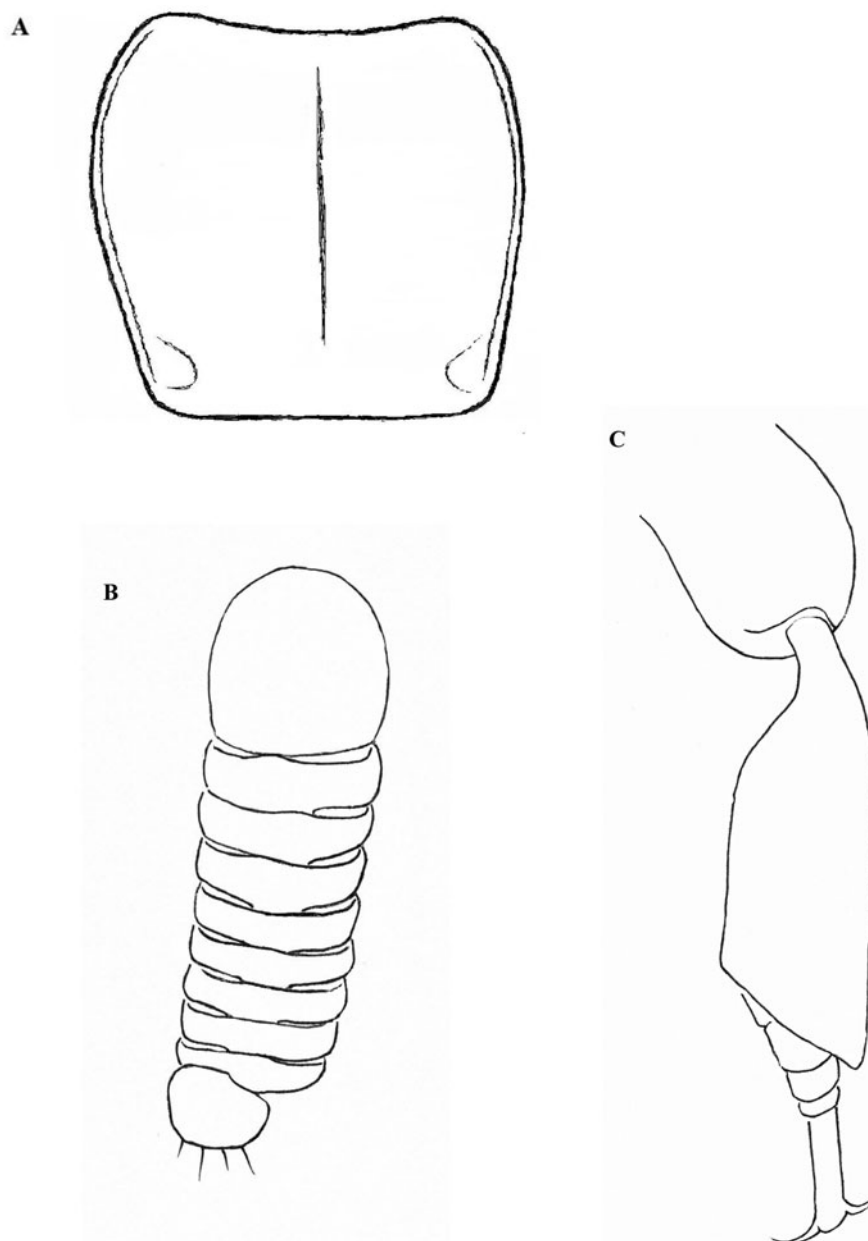


Figure 3 The paussine beetle in Rovno amber (line drawings): (a) The pronotum. (b) The antennae with 9-segmented club. (c) The right middle leg.

the presence of scarce hairs on the front of the head (Fig. 1b); and

the short hairs along the edge of the pronotum and epipleurae of the elytra.

As mentioned above, some diagnostic characters cannot be assessed by preservation (e.g., mouthparts, ventral side of body, the front coxae and the forelegs). Nevertheless, based on the following characters such as its elongated shape of body, flagellum with nine parallel and flattened antennomeres, femora and tibiae of the right middle legs with short setae, tarsomere 4 is very small, the tarsomere 3 not lobed, and the base of elytra with depressions in humeral area (Figs 1, 2), the Rovno specimen is related to extant and Neogene species of *Eohomopterus* Wasmann 1919.

3. Discussion

3.1. Coevolution of paussids with ants

An extraordinary number of myrmecophilous beetle species are known today, belonging to at least 35 families (Vander Meer &

Wojcik 1982; Hölldobler & Wilson 1990; Akino 2002; Orivel *et al.* 2004; Mynhardt 2013); of these, the subfamily Paussinae (Adephaga, Carabidae) is one of the largest. In it species of Protopaussini, Paussini and the subtribe Physeina from Ozaenini are obligate ant predators and symbionts, possessing different adaptations for living with ants (Ball & McCleve 1990; Di Giulio & Vigna Taglianti 2001; Geiselhardt *et al.* 2007; Di Giulio *et al.* 2012; Maurizi *et al.* 2012; Parker 2016).

According to Parker (2016), the Paussini likely represents one of the more ancient clades of myrmecophiles, known from late Eocene Baltic amber (36–37 million years old), little derived within Paussinae (as representatives of Carabidomemnina and Cerapterina) and dominant in the Eocene of Europa (Darlington 1950).

The presence of structures associated with myrmecophily in fossil beetles, such as trichomes, crassate antennae, cephalic horn, or lack of tactile setae, suggest that myrmecophily in paussines already existed in the early Palaeogene (Geiselhardt *et al.* 2007). Given the predominance of trichomes and specialised bristles, it is hypothesised that these beetles produce chemicals from specialised glands concentrated in the antennae, pronotum,

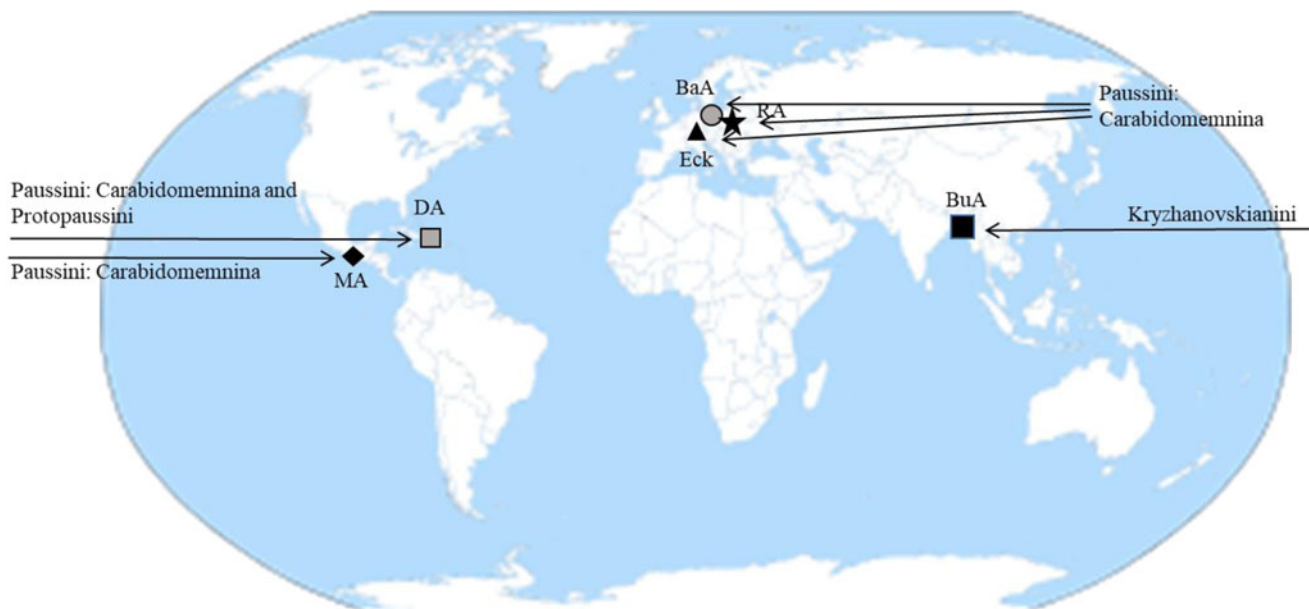


Figure 4 Fossil records of Paussinae: Cretaceous, Kachin (Burmese) amber (BuA, black square); middle Eocene, Eckfeld, Germany (Eck, black triangle); late Eocene, Baltic amber (BaA, grey circle) and Rovno amber (RA, black star); Miocene, Dominican amber (DA, grey square) and Mexican amber (MA, black diamond).

elytra and pygidium (Nagel 1979; Di Giulio *et al.* 2009, 2012; Maurizi *et al.* 2012). This may be part of a complex and effective parasitic strategy along with acoustic mimicry (Geiselhardt *et al.* 2007). There are myrmecophilous paussines stridulatory organs known to live with stridulatory ant hosts and some paussine species with stridulatory organs are known to live with non-stridulatory ants. Adults of the ant subfamilies Ponerinae, Pseudomyrmecinae, Myrmicinae and Ectatomminae are able to produce low-frequency sounds by stridulation (Markl 1965; Ferreira *et al.* 2010), which they use for intraspecific communication and aggregation (Markl & Hölldobler 1978; Baroni-Urbani *et al.* 1988; Hölldobler 1999; Hickling & Brown 2000; Di Giulio *et al.* 2011). It appears that at least among *Paussus* species, anatomical differences of taxonomic value are intimately tied to host–ant interactions and therefore likely to convergently evolve very fast under strong selective pressure (Moore & Robertson 2014).

Probably some fossil paussines from Baltic amber like extant representatives of the subtribe Carabidomemnina (*Carabidomemninus*) were associated with Formicinae and Myrmicinae (Di Giulio *et al.* 2003; Di Giulio & Moore 2004; Di Giulio 2008; Moore *et al.* 2011; Maurizi *et al.* 2012). The Rovno specimen has no stridulatory organs. Based on its morphology it belongs to a ‘defiant’ species (Nagel 1979) that prey upon broods protected from attack by their adult morphology (Darlington 1950; Geiselhardt *et al.* 2007).

3.2. Zoogeographical implication

Both described extant species of *Eohomopterus* are Neotropical: *E. aequatoriensis* (Wasmann 1899) from Ecuador; and *E. centenarius* from Brazil (Lorenz 2021) (another species from the West Indies has not yet been formally described; Moore 2006).

The type species *E. aequatoriensis* was originally assigned to the genus *Homopterus* Westwood 1841 (Wasmann 1899; Nagel 1997). Three extinct species of this genus were described from Miocene amber: *E. paulmuelleri* Nagel 1987b and *E. poinari* Nagel 1997 in Dominican amber; and *E. simojovelensis* Solórzano Kraemer, 2006 in Mexican amber (Nagel 1987b, 1997; Solórzano Kraemer 2006). The distribution of *Eohomopterus* species including fossil records is shown in Fig. 4.

The distribution of extant Paussini is limited by tropical and subtropical regions, even where their ant hosts range further north. For example, the distribution of the paussine *Ceratoderus venustus* Hisamatsu 1963 is limited to the Shikoku, Kyūshū and Yakushima islands (Maruyama 2014), where the winter temperature (coldest quarter mean temperature, CQMT) is 7.4–12°C; while the ant *Crematogaster vagula* Wheeler 1928, associated with the paussine *C. venustus*, is widespread in Honshu (CQMT is 6.1°C). The northern distribution limit of the *Paussus favieri* Fairmaire 1851 in the south of France is further south than the distribution of its ant host (LeMasne 1961).

It is difficult to suggest the possible hosts for neotropical species of *Eohomopterus*, as the only record of an American Paussini species with ants is still apparently that of *Homopterus steinbachi* Kolbe 1920 in a nest of the widespread dominant tropical species *Dolichoderus bispinosus* (Olivier 1792) (Dolichoderinae) (Darlington 1964). Two species of the *bispinosus* group are represented by numerous specimens in Dominican amber (Grimaldi & Agosti 2000) and one undescribed species in Mexican amber (D. A. Dubovikoff, personal communication, 2022). Dolichoderines were dominant ants of the European amber forests (Dlussky & Rasnitsyn 2009; Perkovsky 2016), so Eocene dolichoderine species can be considered the most probable ant hosts of paussines. Most *Dolichoderus* Lund 1831 species are arboreal, building their nests under bark or in dead tree branches (Dlussky & Rasnitsyn 2009).

A *Formica flori* Mayr, 1868 worker ant preserved in the same piece of Baltic amber as *Eopaussus balticus* Wasmann 1926 (Wasmann 1929, Figs 35, 36) was redetermined. The general appearance of the body and the individual morphological structures visible in the photograph (long scapules, the position of the eyes, the structure of the mesosome and petiole) indicate that the ant shown in the photograph is more likely to belong to the species *Yantaromyrmex geinitzi* (Mayr 1868) and not *Formica* (D. A. Dubovikoff, personal communication, 2023).

The climate of the Rovno amber forest was warmer than that of the Baltic amber forest (Mänd *et al.* 2018; Perkovsky 2018; Sokoloff *et al.* 2018; Yamamoto *et al.* 2022; Anisytukin & Perkovsky 2023; Jenkins Shaw *et al.* 2023), a probable reason for the absence in Baltic amber of some cryophobic Rovno taxa

with extant Western Hemisphere distributions; for example, the brentid genus *Toxorhynchus* Scudder 1893 and *Caulophilus* Wolleston 1854 (Nazarenko *et al.* 2011; Bukejs & Legalov 2020) and probably the cerambycid *Poliaenus europaeus* Vitali & Perkovsky 2022 as well (Vitali & Perkovsky 2022).

The confident relationship of the Rovno specimen with *Eohomopterus*, as well as the presence of the Dominican amber *Protopaussus pristinus* Nagel 1997 (extant *Protopaussini* are limited to the Oriental Region tropics and subtropics), testify to transarctic migrations of their hosts in the early Palaeogene, similar to the intercontinental dispersal of giant cryophobic ants from extinct subfamily Formiciniinae (Archibald *et al.* 2011, 2023).

4. Conclusion

The presence of Neotropical Carabidomemmina in Rovno amber as well as of *Protopaussini* in Dominican amber is of significant interest as a probable result of transarctic migrations of host ants in the early Eocene. This unexpected Rovno amber record, like that of the new tribe of wingless pincer wasps (Olmi *et al.* 2022) highlights the significance of the fossil biota of the Rovno amber forest.

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7. Competing interests

The authors declare none.

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