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## Six new species of fossil soldier beetles (Coleoptera: Cantharidae) from Eocene Baltic amber

MAXIMILIAN G. PANKOWSKI<sup>1,\*</sup> & FABRIZIO FANTI<sup>2</sup>

<sup>1</sup>16405 Fox Valley Terrace, Rockville, Maryland 20853, USA

<sup>2</sup>Via del Tamburino 69, I-53040 Piazze (SI), Italy

✉ [maxgpankowski@gmail.com](mailto:maxgpankowski@gmail.com); <https://orcid.org/0000-0001-9397-3415>

✉ [fantifab@alice.it](mailto:fantifab@alice.it); <https://orcid.org/0000-0003-2002-108X>

\*Corresponding Author

### Abstract

We describe and illustrate six new species of the family Cantharidae from Baltic amber: *Sucinorhagonycha maryae* **sp. nov.** (Cantharinae, Cacomorphocerini), *Podistra madelineae* **sp. nov.** (Cantharinae, Cantharini), *Malthinus (Malthinus) karenpankowskiae* **sp. nov.** (Malthininae, Malthinini), *Malthinus (Malthinus) pauljohnsoni* **sp. nov.** (Malthininae, Malthinini), *Malthodes (Libertimalthodes) betseyae* **sp. nov.** (Malthininae, Malthodini) and *Malthodes (Malthodes) greenwalti* **sp. nov.** (Malthininae, Malthodini). These new taxa add to the astonishing palaeodiversity documented in Baltic amber, demonstrating the wide range of organisms thriving in European forests and wooded areas during the Eocene. Extant species of *Malthodes*, *Malthinus* and *Podistra* also provide important clues to how these extinct taxa lived, fed and reproduced some 35–40 million years ago.

**Keywords:** new species, palaeoentomology, Cantharidae, Eocene, resin

### Introduction

Known as soldier beetles, Cantharidae are soft-bodied beetles in the superfamily Elateroidea (McKenna *et al.*, 2019; Cai *et al.*, 2022). This cosmopolitan family is found on every continent except the Antarctica, with more than 5,000 species (Bouchard *et al.*, 2009) and about 150 genera (Fanti & Damgaard, 2018). Soldier beetles are also extensively documented in the fossil record, especially in amber (Spahr, 1981; Alekseev, 2013, 2017; Fanti, 2017a). Species have been described from Agdzhakend, Baltic, Bitterfeld, Burmese, Dominican, Mexican, Rovno, Sakhalinian and Spanish ambers. The most common amber is from the Baltic region, and Cantharidae are frequently found as inclusions. Ten

genera of soldier beetles discovered in Baltic amber have extant species, while 16 genera are extinct (Kazantsev, 2013; Fanti, 2017a, b; Fanti & Damgaard, 2018; Fanti & M.J. Pankowski, 2018; Fanti & M.K. Pankowski, 2018). This amber was formed primarily during the Priabonian, the last stage of the Eocene (Bukejs *et al.*, 2019).

Six species of Cantharidae from four different genera are described below. Three of these genera have living representatives: *Malthinus* Latreille, 1806; *Malthodes* Kiesenwetter, 1852 and *Podistra* Motschulsky, 1839. Hundreds of *Malthinus* are alive today primarily in the Holarctic region, with a smaller number of species in the Oriental and Neotropical regions (Švihla, 2009; Pankowski & Fanti, 2022). In the fossil record, *Malthinus* species have been found only in Baltic amber (Kuška & Kania, 2010; Fanti, 2017a; Fanti & Damgaard, 2018; Pankowski & Fanti, 2022). Another extant genus, *Malthodes*, has over 600 species living in Europe, Asia, North Africa and North America (Delkeskamp, 1977; Kazantsev & Brancucci, 2007; Fanti & M.K. Pankowski, 2018). This genus is also abundant in the fossil record, especially in Eocene ambers (Fanti, 2021). Multiple species have been discovered in Baltic amber (Fanti & Sontag, 2019; Parisi & Fanti, 2019, 2020; Fanti, 2021), two species in Rovno amber from the Ukraine (Kazantsev, 2010; Kazantsev & Perkovsky, 2014) and two species in Bitterfeld amber from Germany (Fanti, 2019a). Other species have been described from compression fossils: one found in the Brunstatt brown coal deposits from the Oligocene in France (Förster, 1891) and another species from the Miocene deposits of Vlădiceni, Romania (Pintilioaie *et al.*, 2021). The third extant genus, *Podistra*, lives today in the Palaearctic region (Delkeskamp, 1977; Kazantsev, 1998; Kazantsev & Brancucci, 2007; Fanti, 2021); two species also are found in the United States (Fender, 1972; Delkeskamp, 1977; Ramsdale, 2002; Fanti, 2021). In

the fossil record, a few species of *Podistra* have been described from Baltic amber (Fanti & Damgaard, 2018, 2020; Fanti, 2020, 2021), with other specimens identified to the generic level in this amber, and another species found in the Oligocene deposits of Rott, Germany (Fanti & Walker, 2019). Finally, the fourth genus documented in this paper is extinct: *Sucinatorhagonycha* Kuška, 1996. Prior to our study, this genus was known from just three species in Baltic amber (Kuška, 1996; Kubisz, 2000; Fanti & M.K. Pankowski, 2018; Kazantsev, 2020).

## Material and methods

The specimens are embedded in Baltic amber pieces from the Sambian Peninsula, Kaliningrad region, Russia. They were donated to the Smithsonian National Museum of Natural History (USNM) in Washington, DC, USA, where they are currently preserved. The pieces were cut and polished to provide a better view of each of the inclusions. The specimens were examined using a Carton stereomicroscope 0.8–40x. Photographs were taken by Aleksej Damzen (Vilnius, Lithuania) with a Canon EOS 70D camera and Canon MP-E 65mm macro lens. Plates were processed using a PhotoImpact Viewer SE program.

## Systematic palaeontology

**Family Cantharidae Imhoff, 1856**

**Subfamily Cantharinae Imhoff, 1856**

**Tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018**

**Genus *Sucinatorhagonycha* Kuška, 1996**

***Sucinatorhagonycha maryae* sp. nov.**

(Fig. 1)

**Holotype.** Female, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787823.

Syninclusions: Air bubbles and debris.

**Etymology.** Species named in honor of Mary K. Pankowski, the first author's elder sister and trusted advisor.

**Diagnosis.** The specimen clearly belongs to the genus *Sucinatorhagonycha* based on its securiform last maxillary palpomere, long elytra, filiform and 12-segmented antennae, the pronotum without lobes at the sides, and the simple claws without lobes and denticles.

Based on its transverse pronotum, the new species described here is most similar to *S. kulickae* Kuška, 1996, but it differs from the latter species in the length of the

antennomeres; in particular, the antennomere V of the new species is long and distinctly longer than III, while it is very short and as long as the third in *S. kulickae*. The new species is also significantly larger than the holotype of *S. kulickae*, which is only 4.5 mm in length (Kuška, 1996; Fanti & Pankowski, 2018; Kazantsev, 2020). Kubisz (2000) describes the female of *S. kulickae*; however, given the enormous difference with the holotype (a male), we are convinced that it is a different species.

**Locality and horizon.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Description.** Female, defined on the basis of the short antennae and last sternite small and rounded. Body length: about 7.0 mm. Body entirely dark brown.

Adult, winged, elongate. Head elongate, rounded at sides, not completely exposed, wrinkled with shallow punctation and short setae. Eyes rounded, convex, located in upper lateral part of head.

Mandibles robust, elongate, falciform. Maxillary palps 4-segmented and unequal in length, with the last palpomere strongly securiform. Labial palps 3-segmented, with the last palpomere strongly securiform. Antennae 12-segmented, filiform, relatively short, reaching to about half of elytra, all segments pubescent; antennomere I (scape) club-shaped, enlarged apically; antennomere II robust, short, about 2.0 times shorter than scape; antennomere III robust, longer than second; antennomere IV robust, longer than antennomere III; antennomeres V–VII robust, the longest except for the scape; antennomeres VIII–IX robust, subequal, slightly shorter than previous ones; antennomere X slightly shorter than previous ones; antennomere XI shorter than antennomere X; antennomere XII elongate, equal to or very slightly longer than antennomeres V–VII, rounded at apex. Pronotum transverse, wider than head, corners rounded, margins and sides straight and bordered, surface with large and deep punctation and equipped with many setae. Scutellum wide, triangular shaped, with rounded apex. Elytra very elongate, slender, parallel-sided, surpassing the last abdominal segments, wider than pronotum, apex rounded, surface wrinkled and equipped with long setae. Hind wings transparent, longer than elytra. Metasternum elongate, punctate; sternites and tergites punctate and transverse; last tergite elongate, rounded at apex; last sternite much smaller than last tergite, rounded at apex. Legs short, thin; coxae massive, robust, elongate; trochanters elongate, rounded at apex; femora almost straight, profemora sturdier than meso- and metafemora, cylindrical; tibiae cylindrical, thin, with apical spur, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae as long as metafemora. First tarsomere elongate; second tarsomere about 1.9 times shorter than first; third tarsomere shorter than





**FIGURE 1.** *Sucinorhagonycha maryae* sp. nov. in Baltic amber. Holotype (USNM PAL 787823). **A**, Dorsal view. **B**, Dorso-lateral view. **C**, Lateral view. Scale bars = 0.5 mm.



second, triangular shaped, with apical margin straight; fourth tarsomere bilobed at sides with the lobes very long, curved; fifth tarsomere elongate, thin, curved; claws simple, without lobes or denticles. Male unknown.

**Remarks.** The yellow rectangular and elongate amber piece measures approximately  $20 \times 6 \times 8$  mm. The inclusion is complete. The legs and head on the ventral side have white emulsion. The surface has some oxidation.

**Tribe Cantharini Imhoff, 1856**

**Genus *Podistra* Motschulsky, 1839**

***Podistra madelineae* sp. nov.**

(Fig. 2)

**Holotype.** Female, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787824.

Syninclusions: Air bubbles, detritus and botanical fragments.

**Etymology.** Species named in honor of Madeline Pankowski, the first author's younger sister and valued partner in palaeontological projects.

**Diagnosis.** The last maxillary palpomere securiform, the long elytra and the rectangular pronotum place this taxon in the genus *Podistra*. Based on the absence of the basal tooth of claws but with an obtuse enlargement, the species could be placed in the subgenus *Pseudoabsidia*.

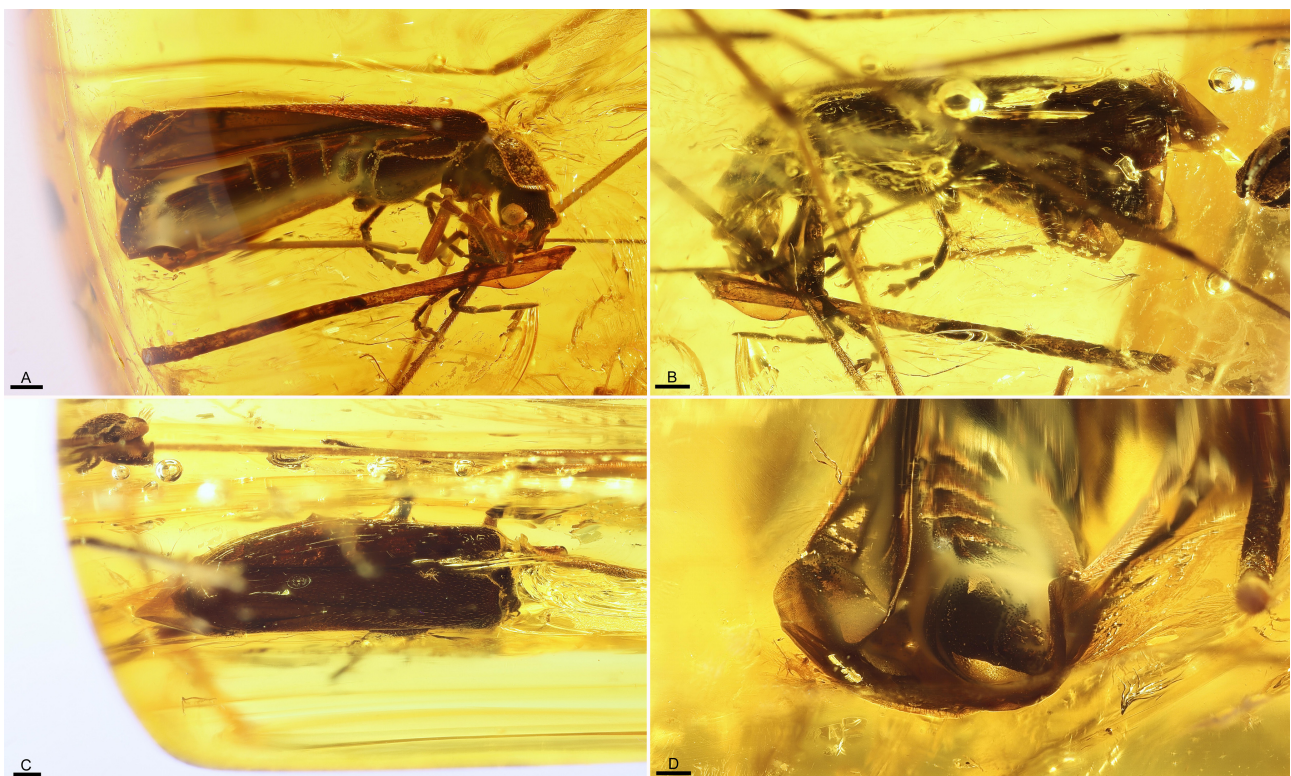
However, this subgenus has recently been synonymized with the subgenus *Podistra* (Kazantsev, 2023), and the taxonomy of the subgenera remains largely unclear.

The new species is most similar to *Podistra guthriei* Fanti, 2021 but is significantly larger than that species (7.5 mm vs. 5.7 mm). Antennomeres III–V of the new species also are not subequal, unlike in *P. guthriei* (Fanti, 2021).

**Locality and horizon.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Description.** Female, defined on the basis of the short antennae and the last sternite small and rounded. Body length: about 7.5 mm. Head black, other body parts entirely dark brown.

Head not completely exposed, wide, rounded, equipped with scattered short setae and without punctation. Eyes relatively small, rounded, located in upper lateral part of the head. Mandibles falciform. Maxillary palpi 4-segmented, with the last palpomere securiform. Labial palpi 3-segmented with the last palpomere securiform. Antennae 11-segmented, filiform, short, surpassing the humeral region of the elytra, inserted close to the upper part of the eyes, all antennomeres pubescent with short and long setae; antennomere I elongate, club-shaped, enlarged apically; antennomere II short, slightly



**FIGURE 2.** *Podistra madelineae* sp. nov. in Baltic amber. Holotype (USNM PAL 787824). **A, B,** Lateral views, scale bars = 0.5 mm. **C,** Dorsal view, scale bar = 0.5 mm. **D,** Detail of last abdominal segments, scale bar = 0.1 mm.



elongate, rather robust, about 2.4–2.5 times shorter than antennomere I; antennomere III about 1.4 times longer than antennomere II; antennomere IV robust, longer than previous one; antennomeres V–X subequal and shorter than previous ones; antennomere XI filiform, elongate, rounded apically. Pronotum longer than wide, rectangular, about as wide as head, surface slightly granulous and equipped with several setae and slightly bulged in the posterior part, anterior margin rounded and not bordered, posterior margin and sides straight and slightly bordered, propleura small and rounded. Scutellum very wide, triangular shaped, with apex slightly rounded, equipped with scattered setae. Elytra wider than pronotum, elongate, covering and slightly surpassing the last abdominal segments, surface slightly wrinkled and equipped with scattered and long setae, parallel-sided, rounded apically. Hind wings semitransparent, slightly longer than elytra. Legs short, relatively robust, densely pubescent; coxae robust, elongate, rounded apically; trochanters elongate with rounded apex; femora slightly enlarged, straight, cylindrical; tibiae thin, cylindrical, with apical spur that is short and robust, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae slightly longer than metafemora. First tarsomere elongate and robust; second tarsomere shorter than first tarsomere; third tarsomere triangular-shaped, with apical margin straight; tarsomere IV conspicuously widened, very shortly bilobed; tarsomere V thin, elongate, curved; claws simple without teeth but

with an obtuse enlargement at base. Metasternum elongate, equipped with scattered long setae, rounded apically. Sternites transverse, wide, pubescent. Last sternite short, small, rounded. Male unknown.

**Remarks.** The yellow, nearly square amber piece measures approximately  $12 \times 11 \times 8$  mm. The specimen is bent. One posterior leg is not preserved and the last sternite is partially covered by a white emulsion.

**Subfamily Malthininae Kiesenwetter, 1852**

**Tribe Malthinini Kiesenwetter, 1852**

**Genus *Malthinus* Latreille, 1806**

**Subgenus *Malthinus* Latreille, 1806**

***Malthinus (Malthinus) karenpankowskiae* sp. nov.**

(Figs 3, 4)

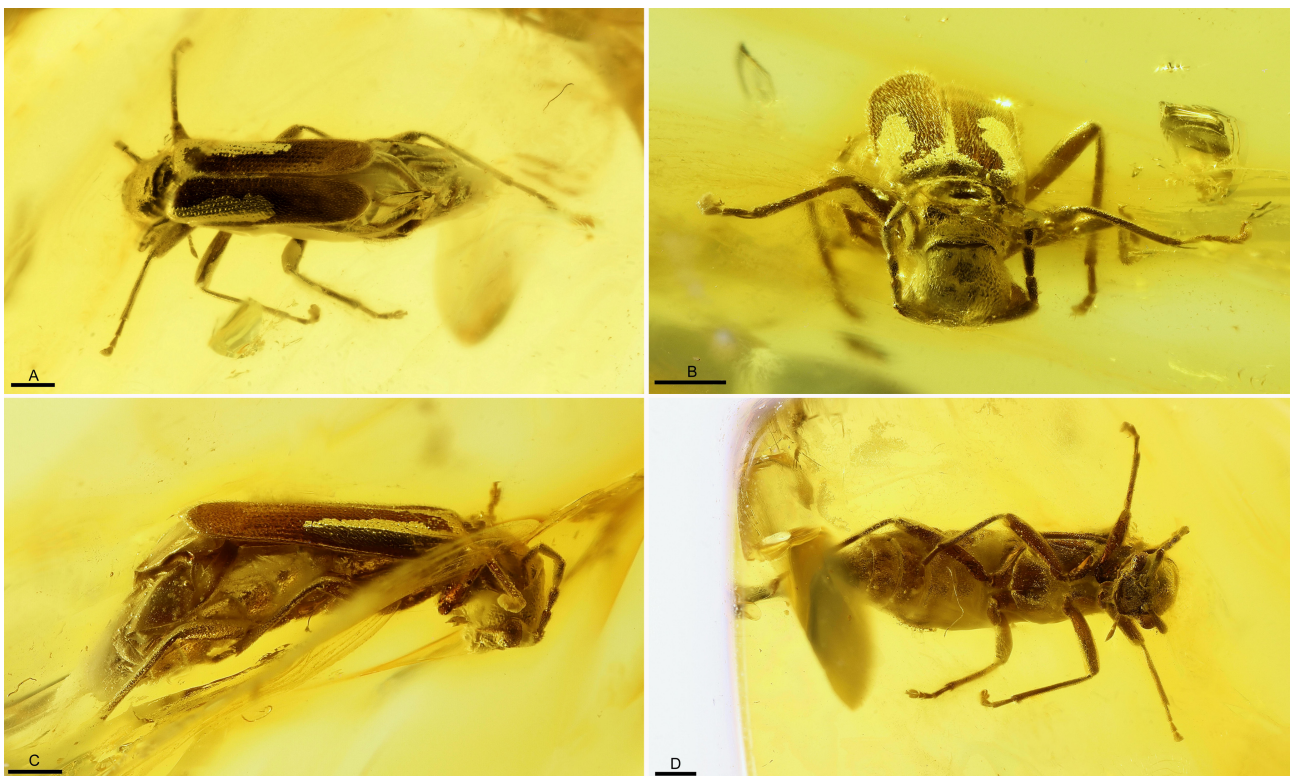
**Holotype.** Female, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787825.

Syninclusions: A few small debris.

**Etymology.** Species named in honor of Karen Pankowski, the fearless, caring mother of the first author.

**Diagnosis.** The globular and distally pointed last maxillary palpomere, the short elytra, head restricted behind the eyes, and the elytra with impressed punctuation clearly place this taxon in the genus *Malthinus*.

Only three fossil species of *Malthinus* have been



**FIGURE 3.** *Malthinus (Malthinus) karenpankowskiae* sp. nov. in Baltic amber. Holotype (USNM PAL 787825). **A**, Dorsal view. **B**, Detail of head and pronotum. **C**, Lateral view. **D**, Ventral view. Scale bars = 0.5 mm.





**FIGURE 4.** *Malthinus (Malthinus) karenpankowskiae* sp. nov. in Baltic amber. Holotype (USNM PAL 787825). **A**, Detail of head and pronotum. **B**, Detail of head and metasternum. Scale bars = 0.3 mm.

described previously to this paper, all from Baltic amber (Kuška & Kania, 2010; Fanti & Damgaard, 2018; Pankowski & Fanti, 2022). The new species described here is easily distinguished from these other *Malthinus* species by its strongly transverse pronotum with no expansion posteriorly or narrowing anteriorly.

**Locality and horizon.** Amber mine in the Yantary settlement, Sambian Peninsula, Kaliningrad region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Description.** Female, defined on the basis of wide and rounded last sternite. Body length: about 5.0 mm. Body entirely dark brown without yellow spots on elytra.

Adult, alate, slender. Head completely exposed, strongly narrowed behind eyes, very wrinkled, with deep

punctuation, interocular dorsal distance about 3.5 times greater than eye diameter. Eyes convex, sub-elliptical, located in upper lateral part of the head. Mandibles falciform, elongate, thin. Maxillary palpi 4-segmented, with last palpomere globular-elongate and apically pointed. Labial palpi 3-segmented, with last palpomere globular and apically pointed. Antennae filiform, 11-segmented, short, reaching about half of the elytra; antennomere I elongate, slightly club-shaped; antennomere II about 2.1 times shorter than antennomere I; antennomere III slightly shorter and sturdier than antennomere II; antennomere IV longer than previous one; antennomeres V–X subequal, slightly shorter than previous one; antennomere XI elongate, very slightly pointed; all antennomeres covered by short setae. Pronotum strongly transverse, slightly wider than head,



equipped with short setae and sparse punctation, anterior and posterior margins straight and bordered (anterior margin strongly bordered), sides straight, anterior corners slightly acute, posterior corners rounded. Scutellum triangular shaped, pointed apically. Elytra short, revealing four abdominal segments uncovered, wider than pronotum, covered with deep punctation in rows and short setae, parallel-sided, not dehiscent, rounded at apex. Hind wings slightly infusate, exceeding elytra and not reaching last abdominal segment. Metasternum with slightly rounded posterior margin, covered with dispersed and short setae and very shallow punctation. Sternites transverse, wide, with shallow punctation and short pubescence. Last tergite and last sternite wide, small and rounded. Legs slender, pubescent; coxae elongate, stout; trochanters elongate with rounded apex; femora enlarged, rather straight; tibiae cylindrical and thin, equipped with apical spurs, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsomere I thin, elongate; tarsomere II about 2.0 times shorter than tarsomere I; tarsomere III short; tarsomere IV strongly bilobed; tarsomere V elongate, slightly curved, slender; claws simple without tooth. Male unknown.

**Remarks.** The yellow squared amber piece measures approximately  $9 \times 9 \times 8$  mm. The inclusion is slightly bent but complete; the head and antennae are folded and some parts of the beetle are covered with white emulsion.

*Malthinus (Malthinus) pauljohnsoni* sp. nov.  
(Fig. 5)

**Holotype.** Female, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787826.

Syninclusions: Botanical fragments, stellate hairs, small air bubbles and a Diptera (with eggs).

**Etymology.** Species named in honor of Dr. Paul Johnson, a professor at South Dakota State University who is always happy to provide his invaluable expertise on beetle taxonomy.

**Diagnosis.** This species belongs to the genus *Malthinus* based on its globular and distally pointed last maxillary palpomere, the short elytra, head restricted behind the eyes and the elytra with impressed punctuation.

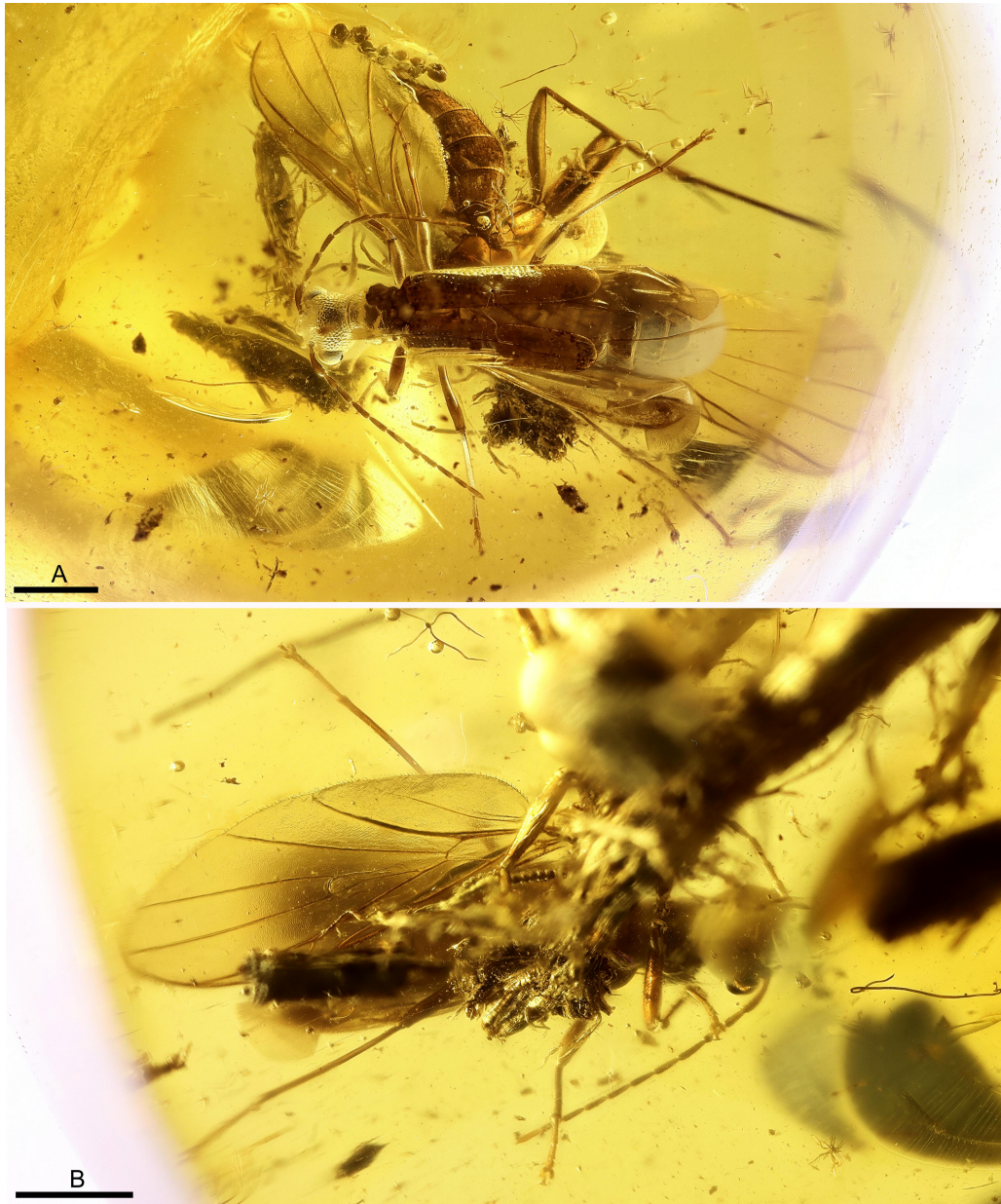
Only three fossil species of *Malthinus* have been described so far, all from Baltic amber (Kuška & Kania, 2010; Fanti & Damgaard, 2018; Pankowski & Fanti, 2022). *Malthinus rifbjergi* Fanti & Damgaard, 2018 and *Malthinus danieli* Kuška & Kania, 2010 are the most similar to the new species described here, but they have the pronotum only narrower anteriorly (Kuška & Kania, 2010; Fanti & Damgaard, 2018), where in *Malthinus pauljohnsoni* sp. nov. the pronotum is widely expanded before the posterior corners.

**Locality and horizon.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Description.** Female, defined on the basis of the short antennae and wide and rounded last sternite. Body length: about 4.9 mm. Body entirely dark brown without yellow spots on elytra.

Adult, alate, slender. Head completely exposed, strongly narrowed behind eyes, very strongly wrinkled, with deep and wide punctation, interocular dorsal distance about 2.5–2.6 times greater than eye diameter. Eyes large, convex, rounded, located in the upper lateral part of head. Mandibles falciform, elongate, thin. Maxillary palpi 4-segmented, with last palpomere globular and apically pointed. Labial palpi 3-segmented, with last palpomere globular and apically pointed. Antennae filiform, 11-segmented, short, surpassing half of elytra but not reaching the elytral apex; antennomere I elongate, slightly club-shaped; antennomere II about 2.1 times shorter than antennomere I; antennomeres III–IX subequal, very slightly longer and slender than antennomere II; antennomere X very slightly shorter than previous ones; antennomere XI elongate, very slightly pointed; all antennomeres covered by short setae. Pronotum longer than wide, narrower than head, slightly punctate, equipped with short setae, anterior margin straight and strongly bordered, posterior margin undulate, sides with a wide expansion before the posterior corners. Scutellum wide with truncate apex, enlarged in the middle. Elytra short, revealing three and a half abdominal segments uncovered, wider than pronotum, covered with deep punctation (smaller punctation close to the elytral apex) in rows and some setae, parallel-sided, rounded at apex. Hind wings slightly infusate, clearly exceeding elytra and slightly exceeding last abdominal segment. Metasternum with straight posterior margin, covered with dispersed and short setae and very shallow punctation. Sternites transverse with shallow punctation. Last tergite and last sternite wide and rounded. Legs slender, pubescent; coxae short, stout; trochanters elongate with rounded apex; femora enlarged, rather straight; tibiae cylindrical and thin, equipped with apical spurs, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsomere I thin, elongate; tarsomere II about 1.8 times shorter than tarsomere I; tarsomere III very short, rounded; tarsomere IV strongly bilobed; tarsomere V elongate, slightly curved, slender; claws simple without tooth. Male unknown.

**Remarks.** The yellow amber piece measures approximately  $18 \times 13 \times 10$  mm. The inclusion is complete. The last tergites and ventral part of the head are covered with white emulsion.



**FIGURE 5.** *Malthinus (Malthinus) pauljohnsoni* sp. nov. in Baltic amber. Holotype (USNM PAL 787826). **A**, Dorsal view. **B**, Ventral view. Scale bars = 1.0 mm.

**Tribe Malthodini** Böving & Craighead, 1931

**Genus *Malthodes*** Kiesewetter, 1852

**Subgenus *Libertimalthodes*** Kupryjanowicz & Fanti, 2019

*Malthodes (Libertimalthodes) betseyae* sp. nov.

(Fig. 6)

**Holotype.** Male, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787827.

**Syninclusions:** Air bubbles (some quite large), botanical fragments and detritus.

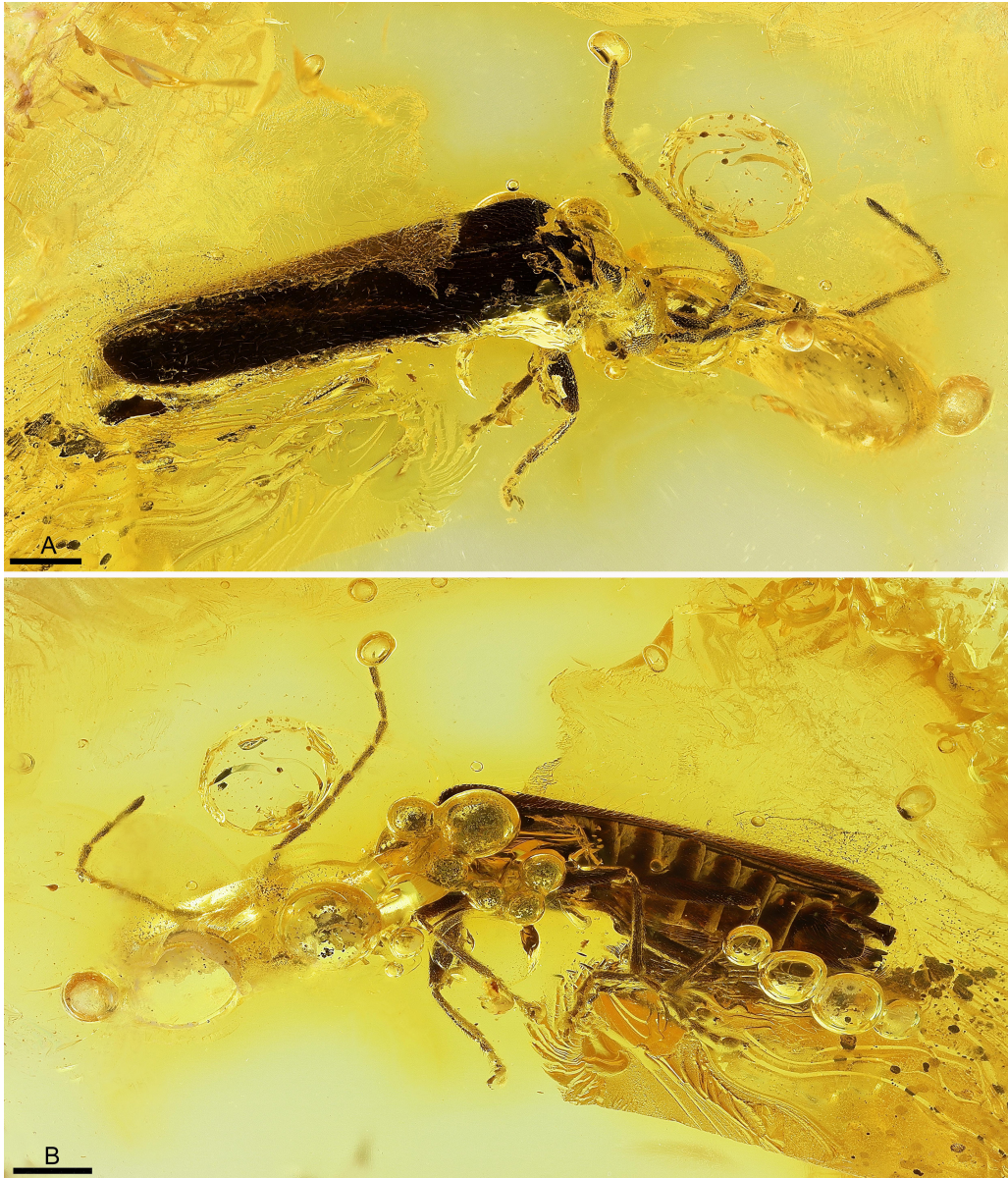
**Etymology.** Species named after Betsey Kim, great

aunt of the first author who spent her life teaching and inspiring hundreds of schoolchildren in Tallahassee, Florida.

**Diagnosis.** The globular and distally pointed last maxillary palpomere, the elongate and smooth elytra, the head rounded behind the eyes, the unmodified last abdominal segments, and the robust and large aedeagus place this species in the genus *Malthodes* and its subgenus *Libertimalthodes* (Brancucci, 1980; Fanti, 2019b).

*Malthodes (Libertimalthodes) betseyae* sp. nov. is similar to *M. (L.) elytratus* Kupryjanowicz & Fanti, 2019, but the new species differs in its slightly longer antennae, its pronotum transverse with sides straight, and by its last sternite not rounded at the sides and with a deeper central apical concavity (Kupryjanowicz & Fanti, 2019).





**FIGURE 6.** *Malthodes (Libertimalthodes) betseyae* sp. nov. in Baltic amber. Holotype (USNM PAL 787827). **A**, Dorsal view. **B**, Ventral view. Scale bars = 0.5 mm.

**Locality and horizon.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

**Description.** Male, defined on the basis of a small part of visible aedeagus. Body length: about 4.0–4.1 mm. Body entirely dark brown without yellow spots on elytra.

Head exposed, wide, rounded, slightly granulous with shallow punctation and several setae. Eyes large, rounded, located in upper lateral part of head. Mandibles not well visible. Maxillary palps 4-segmented, with the last palpomere globular and distally pointed. Labial palps 3-segmented with the last palpomere globular and pointed. Antennae filiform, 11-segmented, relatively

long, slightly surpassing half the length of elytra; antennomere I club-shaped, robust, enlarged apically; antennomere II rather long, about 2.0–2.1 times shorter than scape; antennomere III slightly longer than second; antennomere IV slightly longer than third; antennomeres V–VI subequal, slightly longer and slightly thinner than previous one; antennomeres VII–X filiform, subequal, slightly shorter than previous ones; antennomere XI elongate, filiform, apically rounded; all antennomeres with several setae. Pronotum transverse, wider than head, surface flat, equipped with several short setae and with small and shallow punctation, anterior margin slightly rounded, posterior margin straight and bordered, sides straight, corners strongly rounded. Scutellum triangular-



shaped, rounded at apex. Elytra elongate, wider than pronotum, parallel sided, apex rounded, surface slightly granulous and equipped with scattered and long setae and without punctation. Posterior wings about as long as elytra, completely covered by elytra. Legs relatively short, rather robust, pubescent; coxae wide and rounded; trochanters elongate, rounded at apex; femora robust, subcylindrical, slightly curved; tibiae shorter than femora, cylindrical, thin, with spur at apex. Tarsomeres robust; tarsomere I elongate; tarsomere II about 1.8 times shorter than first; tarsomere III shorter than second, triangular shaped; tarsomere IV strongly bilobed with lobes curved; tarsomere V elongate and flat; claws simple without lobes or teeth. Metasternum with short pubescence and slightly granulous. Abdominal segments transverse, wide, with sparse and long setae, slightly granulous; ultimate sternite wide, robust, elongate, with sides not rounded and rather straight, apical margin with a small and deep concavity in the middle; last tergite barely visible, small. Aedeagus slightly extruded, large, wide, parameres–laterophyses elongate, enlarged and squared apically. Female unknown.

**Remarks.** The yellow amber piece, rounded and flat, measures approximately 12 × 11 mm. The inclusion is complete with the head and pronotum barely visible in ventral views, due to the presence of large air bubbles. The surface of the amber has numerous fractures.

**Subgenus *Malthodes* Kiesenwetter, 1852**

***Malthodes (Malthodes) greenwalti* sp. nov.**  
(Figs 7, 8)

**Holotype.** Male, inclusion in Baltic amber, housed at the Smithsonian National Museum of Natural History, USNM PAL 787828.

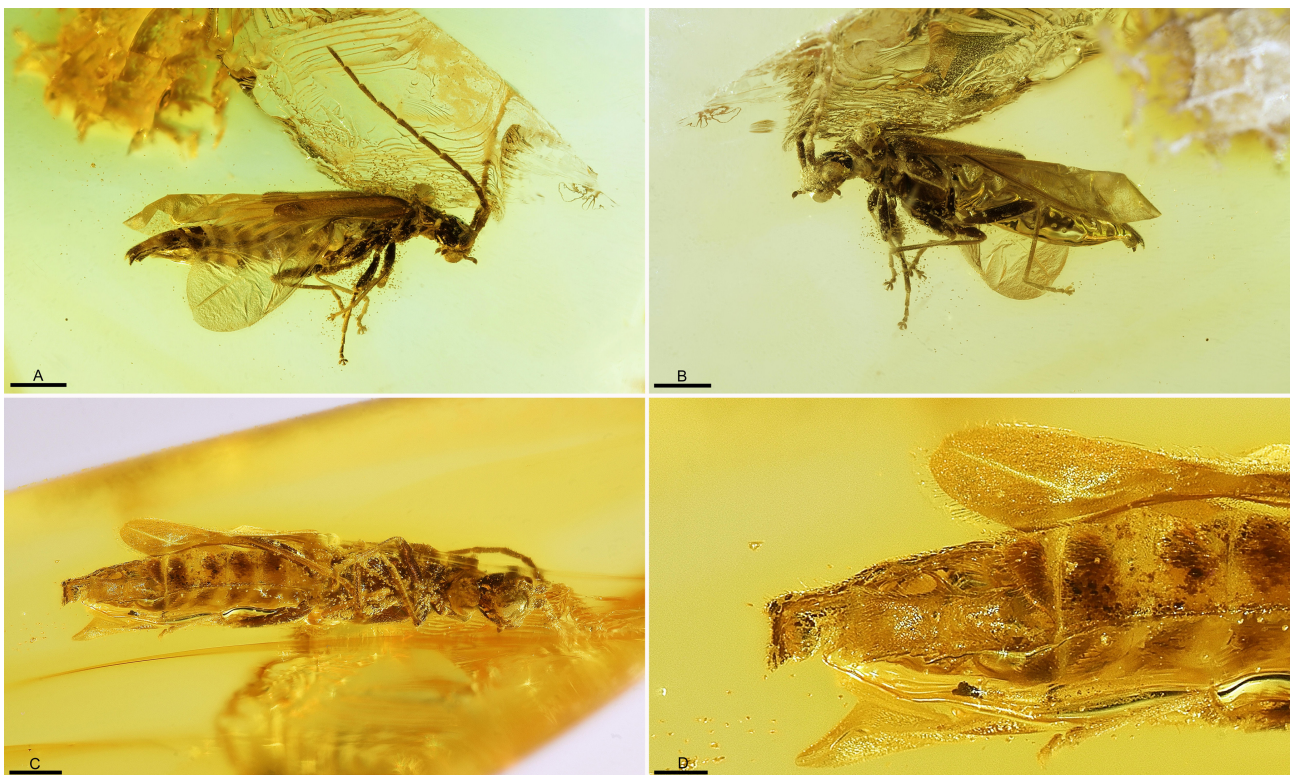
Syninclusions: Small air bubbles and debris.

**Etymology.** Species named in honor of Dr. Dale Greenwalt, researcher at the Smithsonian National Museum of Natural History, former president of the Washington Paleontological Society and much-admired mentor to the first author.

**Diagnosis.** This species belongs to the genus *Malthodes* based on its globular and distally pointed last maxillary palpomere, the very short and almost smooth elytra, head rounded behind the eyes, and the strongly modified last abdominal segments.

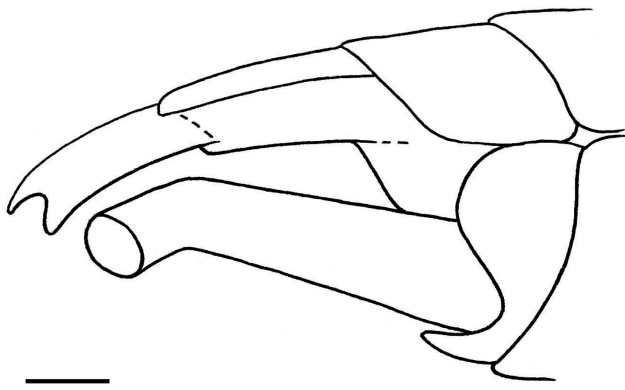
The new species is easily distinguished based on its last sternite (st9) that is elongated, wide and slightly folded and rounded in the apical margin. These features are not present in any known fossil *Malthodes*.

**Locality and horizon.** Amber mine in the Yantarny settlement, Sambian Peninsula, Kaliningrad Region, Russia. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).



**FIGURE 7.** *Malthodes (Malthodes) greenwalti* sp. nov. in Baltic amber. Holotype (USNM PAL 787828). **A**, Dorso-lateral view, scale bar = 0.5 mm. **B**, Lateral view, scale bar = 0.5 mm. **C**, Detail of last sternites, scale bar = 0.3 mm. **D**, Detail of last sternites, scale bar = 0.1 mm.





**FIGURE 8.** *Malthodes (Malthodes) greenwalti* sp. nov. in Baltic amber. Holotype (USNM PAL 787828). Line drawing of the last abdominal segments, scale bar = 0.1 mm.

**Description.** Male, defined on the basis of the last urites strongly modified. Body length: 3.1 mm. Body entirely dark brown without yellow spots on elytra.

Head exposed, small, rounded, covered by dispersed setae. Eyes large, prominent, convex, rounded, located in the upper lateral part of head. Mandibles falciform, elongate. Maxillary palpi 4-segmented, with last palpomere globular and distally pointed. Labial palpi 3-segmented, with last palpomere globular and distally pointed. Antennae filiform, 11-segmented, not particularly long, surpassing the apex of elytra and half of abdomen; antennomere I very elongate, slightly club-shaped; antennomere II globular and only slightly elongate, short, about 2.1 times shorter than antennomere I; antennomere III short, about 1.3 times longer than antennomere II; antennomeres IV slightly longer than previous one; antennomeres V–IX subequal in length, slightly longer than antennomere IV; antennomere X slightly shorter than previous ones; antennomere XI elongate, thin, rounded at apex; all antennomeres covered by short and long setae. Pronotum transverse, wider than head, surface almost flat at center and slightly folded at sides and barely punctate with many short setae, sides straight and bordered and narrower before the posterior corners, posterior and anterior margins straight and strongly bordered, corners rounded. Elytra very short (revealing six tergites uncovered), wider than pronotum, covered with very shallow punctation and several short setae, parallel-sided, strongly rounded at apexes. Hind wings transparent, clearly exceeding the elytra and almost reaching the last abdominal segment. Legs slender, pubescent; coxae short, stout; trochanters elongate with rounded apex; femora enlarged, slightly curved; tibiae cylindrical and thin, protibiae longer than profemora, mesotibiae shorter than mesofemora, metatibiae longer than metafemora. Tarsomere I thin, elongate; tarsomere

II about 1.4 times shorter than tarsomere I; tarsomere III shorter than second; tarsomere IV strongly bilobed; tarsomere V elongate, slightly curved, slender; claws simple without tooth. Metasternum subquadrate, slightly elongate, with the posterior margin protruded in the middle, covered with dispersed and short setae. Sternites transverse and pubescent. Penultimate tergite (tg9) wide, subrectangular; last tergite (tg10) narrower than penultimate tergite, elongate, slightly curved, with sides at apex with lobes that are short, robust and rounded; last sternite (st9) elongate, wide, almost flat, with the apical margin slightly folded and rounded. Aedeagus not visible. Female unknown.

**Remarks.** The yellow rectangular and elongated amber piece measures approximately  $23 \times 8 \times 4.5$  mm. The left antenna of the specimen is preserved until the seventh antennomere.

## Discussion

Baltic amber is the most common amber in the world today, with the greatest diversity of described inclusions, yielding more than 3,000 species of insects, arachnids, amphibians, molluscs, plants and other organisms (Briggs, 2018). This exceptional biodiversity could be due to a number of factors, such as the Eocene's warmer temperatures, which may have favored speciation (Erwin, 2009). It also could be a result of the broad range of habitats where Baltic amber formed, including meadows, coastal lowland swamps and angiosperm-conifer forests (Sadowski, 2017; Parisi & Fanti, 2020; Pankowski & Fanti, 2022).

Nearly 100 Cantharidae species have been discovered in this prolific amber. Because three of the genera highlighted in this paper have living relatives, they shed important light on how their Eocene counterparts lived and fed in the forests of Europe. Females lay their eggs in clusters in soil. Larvae of many species feed on the ground, eating small insects, worms and slugs. Adults are observed on trees, shrubs and flowers, often feeding on arthropods but also supplementing their diet with nectar, pollen and shoots (Fiori, 1949; Ramsdale, 2002; Fanti & Pankowski, 2018).

Looking at specific genera, *Podistra* are likely predators of arthropods, probably augmenting their diet with nectar and pollen (Fanti, 2020). *Podistra* are found mostly at high altitudes (Fanti, 2020). The forests where Baltic amber formed were at a lower altitude, providing evidence that *Podistra* species can evolve to live in flatter areas given favorable environmental conditions (Fanti, 2020). *Malthodes* and *Malthinus* species today are frequently observed in forests, wooded areas and

environments rich in bushes and shrubs (Fanti & Damgaard, 2018). They search for tiny insects on leaves and branches and are comparably small as well, with bodies generally below 3–4 mm but up to about 5.5 mm in *Malthinus* (Fanti & Damgaard, 2018). Thus, their Eocene ancestors were more likely to become trapped in the resin oozing from trees (Fanti & Damgaard, 2018). Together with the thousands of other organisms entombed in Baltic amber, they help to paint a vivid portrait of the Northern European landscape during the Eocene—deepening our understanding of biogeography and the evolution of life, and offering critical insights into our changing world today.

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## References

- Alekseev, V.I. (2013) The beetles (Insecta: Coleoptera) of Baltic amber: the checklist of described species and preliminary analysis of biodiversity. *Zoology and Ecology*, 23 (1), 5–12. <https://doi.org/10.1080/21658005.2013.769717>
- Alekseev, V.I. (2017) Coleoptera from the middle-upper Eocene European ambers: generic composition, zoogeography and climatic implications. *Zootaxa*, 4290 (3), 401–443. <https://doi.org/10.11646/zootaxa.4290.3.1>
- Bouchard, P., Grebennikov, V.V., Smith, A.B.T. & Douglas, H. (2009) *Biodiversity of Coleoptera*. Wiley-Blackwell Publishing Ltd, Oxford, 632 pp.
- Brancucci, M. (1980) Morphologie comparée, évolution et systématique des Cantharidae (Insecta: Coleoptera). *Entomologica Basiliensia*, 5, 215–388.
- Briggs, D.E.G. (2018) Sampling the insects of the amber forest. *Proceedings of the National Academy of Sciences*, 115 (26), 6525–6527. <https://doi.org/10.1073/pnas.1807017115>
- Bukejs, A., Alekseev, V.I. & Pollock, D.A. (2019) Waidelotinae, a new subfamily of Pyrochroidae (Coleoptera: Tenebrionoidea) from Baltic amber of the Sambian peninsula and the interpretation of Sambian amber stratigraphy, age and location. *Zootaxa*, 4464 (2), 261–273. <https://doi.org/10.11646/zootaxa.4464.2.8>
- Cai, C.Y., Tihelka, E., Giacomelli, M., Lawrence, J.F., Ślipiński, A., Kundrata, R., Yamamoto, S.H., Thayer, M.K., Newton, A.F., Leschen, R.A.B., Gimmel, M.L., Lü, L., Engel, M.S., Bouchard, P., Huang, D.Y., Pisani, D. & Donoghue, P.C.J. (2022) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science*, 9, 211771. <https://doi.org/10.1098/rsos.211771>
- Delkeskamp, K. (1977) *Coleopterorum Catalogus Supplementa. Pars 165. Fasc. I. Cantharidae*. W. Junk, The Hague, 485 pp.
- Erwin, D.H. (2009) Climate as a driver of evolutionary change. *Current Biology*, 19 (14), R575–R583. <https://doi.org/10.1016/j.cub.2009.05.047>
- Fanti, F. (2017a) Catalogo Cantharidae fossili del mondo. *Fossils & Minerals Review*, 2, 1–18 [abbreviated Italian version] / World catalog of fossil Cantharidae. *Fossils & Minerals Review*, 2 (Special Issue), 1–52 [extended English version].
- Fanti, F. (2017b) New fossil Cantharidae genus and species from Baltic amber (Insecta Coleoptera). *Giornale Italiano di Entomologia*, 14 (62), 709–714.
- Fanti, F. (2019a) First fossil soldier beetles (Coleoptera Cantharidae) from Bitterfeld amber, Germany. *Zitteliana*, 93, 89–96.
- Fanti, F. (2019b) New fossil *Malthodes* Kiesenwetter, 1852 of the subgenus *Libertimalthodes* Kupryjanowicz & Fanti, 2019 from Baltic amber (Coleoptera: Cantharidae). *Palaeodiversity*, 12, 65–68. <https://doi.org/10.18476/pale.v12.a5>
- Fanti, F. (2020) Two new fossil soldier beetles from the Baltic amber (Coleoptera: Cantharidae). *Studies and Reports, Taxonomical Series*, 16 (1), 13–19.
- Fanti, F. (2021) Two new *Malthodes* and a new *Podistra* from Eocene Baltic amber (Coleoptera, Cantharidae). *Baltic Journal of Coleopterology*, 21 (1), 1–9.
- Fanti, F. & Damgaard, A.L. (2018) Fossil soldier beetles from Baltic amber of the Anders Damgaard amber collection (Coleoptera Cantharidae). *Baltic Journal of Coleopterology*, 18 (1), 1–32.
- Fanti, F. & Pankowski, M.J. (2018) A new fossil soldier beetle (Coleoptera, Cantharidae, Silinae) from Eocene Baltic amber. *Zootaxa*, 4370 (2), 189–193. <https://doi.org/10.11646/zootaxa.4370.2.7>
- Fanti, F. & Pankowski, M.K. (2018) Three new species of soldier beetles from Baltic amber (Coleoptera, Cantharidae). *Zootaxa*, 4455 (3), 513–524. <https://doi.org/10.11646/zootaxa.4455.3.7>
- Fanti, F. & Sontag, E. (2019) A new fossil soldier beetle (Coleoptera: Cantharidae: Malthininae) from Baltic amber. *Zootaxa*, 4629 (4), 583–588. <https://doi.org/10.11646/zootaxa.4629.4.6>
- Fanti, F. & Walker, L.J. (2019) Fossil soldier beetles (Coleoptera: Cantharidae) of the Georg Statz Collection from the Oligocene Rott Formation, Germany. *Palaeoentomology*, 2 (5), 491–504. <https://doi.org/10.11646/palaeoentomology.2.5.13>



- Fender, K.M. (1972) The genera *Podistra* and *Pseudoabsidia* in North America (Coleoptera: Cantharidae). *The Coleopterists Bulletin*, 26 (1), 13–16.
- Fiori, G. (1949) Contributi alla conoscenza morfologica ed etologica dei Coleotteri. IV. *Cantharis livida* Lin. (Cantharidae). *Bollettino dell'Istituto di Entomologia dell'Università degli Studi di Bologna*, 17, 265–274.
- Förster, B. (1891) Die Insekten des “Plattigen Steinmergels” von Brunstatt. *Abhandlungen zur Geologischen Specialkarte von Elsass-Lothringen*, 3 (5), 335–593 + [1], 6 pls., (6) + [1].
- Kazantsev, S.V. (1998) On *Podistra* complex of Russia and adjacent territories. *Zoologicheskii Zhurnal*, 77 (6), 689–695. [In Russian with English summary, translated into English in 1999: *Entomological Review*, 78 (3), 391–397]
- Kazantsev, S.V. (2010) New *Malthodes* (Insecta: Cantharidae: Coleoptera) from the Rovno Amber (Upper Eocene of Ukraine). *Russian Entomological Journal*, 19 (2), 105–107. <https://doi.org/10.15298/rusentj.19.2.02>
- Kazantsev, S.V. (2013) New taxa of Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae) with synonymic and taxonomic notes. *Russian Entomological Journal*, 22, 283–291.
- Kazantsev, S.V. (2020) New Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae) with some taxonomic notes. *Palaeoentomology*, 3 (3), 260–268. <https://doi.org/10.11646/palaeoentomology.3.3.7>
- Kazantsev, S.V. (2023) Do the Palaearctic subgenera of *Podistra* Motschulsky, 1839 really occur in North America: description of *P. (Pidostris)*, subgen. nov. (Coleoptera: Cantharidae). *Zootaxa*, 5263 (3), 389–400. <https://doi.org/10.11646/zootaxa.5263.3.4>
- Kazantsev, S.V. & Brancucci, M. (2007) Family Cantharidae Imhoff, 1856 (1815). In: Löbl, I. & Smetana, A. (Eds), *Catalogue of Palaearctic Coleoptera. Vol. 4. Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea, Cucujoidea*. Apollo Books, Stenstrup, pp. 234–298.
- Kazantsev, S.V. & Perkovsky, E.E. (2014) A new *Malthodes* and some other interesting soldier beetles (Coleoptera: Cantharidae) from Late Eocene Rovno amber. *Russian Entomological Journal*, 23 (2), 113–116. <https://doi.org/10.15298/rusentj.23.2.03>
- Kubisz, D. (2000) Fossil beetles (Coleoptera) from Baltic amber in the collection of the Museum of Natural History of ISEA in Kraków. *Polskie Pismo Entomologiczne*, 69, 225–230.
- Kupryjanowicz, J. & Fanti, F. (2019) New subgenus and three new species of soldier beetles from the Eocene of Baltic amber. *Palaeontologia Electronica*, 22.2.22A, 1–14. <https://doi.org/10.26879/895>
- Kuška, A. (1996) New beetle species (Coleoptera: Cantharidae, Curculionidae) from the Baltic amber. *Prace Muzeum Ziemi*, 44, 13–18.
- Kuška, A. & Kania, I. (2010) New soldier beetles (Coleoptera, Cantharidae) from the Eocene Baltic amber. *Zootaxa*, 2400 (1), 49–56. <https://doi.org/10.11646/zootaxa.2400.1.5>
- McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 116 (49), 24729–24737. <https://doi.org/10.1073/pnas.1909655116>
- Pankowski, M.G. & Fanti, F. (2022) Two new fossil species of soldier beetles (Coleoptera, Cantharidae, Malthininae) from Baltic amber. *Zootaxa*, 5165 (4), 548–556. <https://doi.org/10.11646/zootaxa.5165.4.6>
- Parisi, F., Fanti, F. (2019) A new fossil *Malthodes* Kiesenwetter, 1852 from the Eocene Baltic amber (Coleoptera Cantharidae). *Zootaxa*, 4652 (1), 189–195. <https://doi.org/10.11646/zootaxa.4652.1.13>
- Parisi, F. & Fanti, F. (2020) Baltic amber: A new *Cacomorphocerus* Schaufuss, 1892 with two specimens preserved in a single piece, and four new *Malthodes* Kiesenwetter, 1852. *Zootaxa*, 4778 (3), 546–560. <https://doi.org/10.11646/zootaxa.4778.3.6>
- Pintilioaie, A.-M., Fanti, F. & Ionesi, V. (2021) First finding of a fossilized Cantharidae (Insecta: Coleoptera) from the Middle Miocene deposits in Romania. *Travaux du Muséum National d'Histoire Naturelle “Grigore Antipa”*, 64 (1), 73–80. <https://doi.org/10.3897/travaux.64.e64706>
- Ramsdale, A.S. (2002) Family 64. Cantharidae Imhoff 1856 (pp. 202–218). In: Arnett, R.H. Jr., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds), *American Beetles, 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, 880 pp.
- Sadowski, E.-M. (2017) Towards a new picture of the ‘Baltic amber forest’ - flora, habitat types, and palaeoecology. Thesis, Göttingen, v + 319 pp.
- Spahr, U. (1981) Systematischer Katalog der Bernstein- und Kopal-Käfer (Coleoptera). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 80, 1–107.
- Švihla, V. (2009) New species of the subfamily Malthininae (Coleoptera: Cantharidae) from the western Palaearctic Region. *Acta Entomologica Musei Nationalis Pragae*, 49 (2), 191–216.