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A remarkable new fossil *Malthodes* (Coleoptera, Cantharidae, Malthininae) from Baltic amber

MADELINE V. PANKOWSKI

Rockville, Maryland 20853, USA. madelinepankowski@gmail.com; https://orcid.org/0000-0002-9430-0121

Abstract

A remarkable new soldier beetle, *Malthodes* (*s. str.*) *susanbuttsae* **sp. nov.**, is described and illustrated from Eocene Baltic amber. This fossil species exhibits exceptional preservation of the terminal abdominal segments, which are highly variable at the species level among males of this genus. Also provided is a brief discussion examining the various factors that may have shaped the modifications of the terminal urites of *Malthodes* males.

Key words: soldier beetle, taxonomy, palaeoentomology, new species, Eocene

Introduction

Cantharidae, known as soldier beetles, are a family of straight-sided, soft-bodied beetles in the superfamily Elateroidea (McKenna *et al.* 2019; Cai *et al.* 2022; Pankowski & Fanti 2023). They comprise over 140 extant and 32 fossil genera, with more than 5,500 species living today (Delkeskamp 1977; Brancucci 1980; Bocak *et al.* 2013; Motyka *et al.* 2023; Pankowski & Fanti 2024; Fanti 2025a, 2025b).

Soldier beetles today occupy a broad array of different habitats throughout the world. Many species are known to lay their eggs in soil or leaf litter (Pankowski & Fanti 2023). Their larvae eat tiny insects, slugs, worms, and other larvae; adults often are found on plants, shrubs, and trees, feeding on insects like aphids as well as pollen and nectar (Ramsdale 2002; Pankowski & Fanti 2023).

The genus *Malthodes* Kiesenwetter, 1852 is one of the most diverse of the family. A member of the subfamily Malthininae, the genus includes over 600 living species in the Holarctic region (Delkeskamp 1977), as well as numerous fossil species, with more than 30 preserved in Baltic, Rovno, and Bitterfeld ambers from the Eocene (Delkeskamp 1977; Brancucci 1980; Kazantsev & Brancucci 2007; Pankowski & Fanti 2024; Fanti 2025a). Today *Malthodes* species are known to be predators throughout their lives, feeding as adults on small insects such as aphids while living on conifers or decideous trees as well as herbaceous plants (Ramsdale 2002; Parisi & Fanti 2024), with some possibly supplementing their diet with pollen. Males of the genus exhibit modifications of their last abdominal segments (both tergites and sternites), which are used to hold the female during mating. These modifications differ widely among species, allowing males to be distinguished relatively easily, whereas females remain difficult to classify without an associated male (Fender 1951). In this paper, we describe a new *Malthodes* species from Baltic amber, a remarkable specimen with unique last abdominal segments that are exceptionally preserved.

Material and Methods

The specimen was found in an amber mine on the Baltic Sea coast in the Yantarny settlement (formerly Palmnicken), Sambia (Samland) Peninsula, Kaliningrad Region, Russia. Baltic amber was created independently in two stages, the Bartonian and Priabonian, with most of the horizon of the Prussian Formation formed 35.6 million to 38 million years ago during the Priabonian (Bukejs *et al.* 2019). The inclusion was photographed by Aleksej Damzen and Jonas

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Damzen (Vilnius, Lithuania) with a Canon 90D camera with a macro lens (Canon MPE-65 mm). Extended depth of field at high magnifications was achieved by stacking multiple images from a range of focal planes using Helicon Focus v. 6.0.18 software, and the final images were edited to create figures using Adobe Photoshop 7.0. The plates were processed with PhotoImpact Viewer SE. The illustration of the specimen's last abdominal segments was made freehand by Alessio Morelli with China ink.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758 Superfamily Elateroidea Leach, 1815 Family Cantharidae Imhoff, 1856 Subfamily Malthininae Kiesenwetter, 1852 Tribe Malthodini Böving & Craighead, 1931 Genus *Malthodes* Kiesenwetter, 1852 Subgenus *Malthodes* Kiesenwetter, 1852

Malthodes susanbuttsae M. V. PANKOWSKI & FABRIZIO FANTI sp. nov.

(Figs. 1–3)

Description. Adult, winged, slender. Male defined on the basis of last urites (both tergites and sternites) strongly modified (Figs. 1–3). Body length: about 4.7 mm (from head to the apex of last sternite); elytra length: 2.0 mm; pronotum length: 0.4 mm; head length: 1.0 mm. Entirely dark brown, elytra without yellow spots at apex.

Head exposed, small, rather rounded, wrinkled, equipped with several short setae and shallow punctation. Eyes large, prominent, convex, rounded, inserted in lateral-upper part of head. Mandibles falciform, very elongated. Maxillary palpi 4-segmented, with last palpomere robust, globular, and distally pointed. Labial palpi 3-segmented, with last palpomere globular and distally pointed. Antennae filiform, 11-segmented, moderately long, slightly surpassing elytra, just reached last tergite; antennomere I elongated, rather robust, club-shaped; antennomere II short, about 2.4 times shorter than antennomere I; antennomere III about 1.4 times longer than antennomere II; antennomeres IV–IX elongated, sub-equal in length and shape, longer than previous one, shorter than scape; antennomere X, slightly shorter than previous ones; antennomere XI elongated, rounded at apex; all antennomeres equipped with several short setae. Pronotum strongly transverse, wider than head, surface irregular (not flat) with very minute punctation and several short setae, sides straight but slightly enlarged anteriorly, anterior margin bordered and slightly rounded, posterior margin straight and strongly bordered, corners rounded. Elytra short, wider than pronotum, smooth, equipped with several setae, parallel-sided (slightly dehiscent posteriorly), rounded at apexes, without apical yellow spots. Hind wings infuscate, noticeably exceeding elytra and last abdominal segments. Legs slender, pubescent; coxae short and robust; trochanters rather robust, short, with rounded apex; femora enlarged, slightly curved; tibiae cylindrical and thin, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsi 5-segmented, pubescent; tarsomere I elongated; tarsomere II shorter than tarsomere I; tarsomere III shorter than tarsomere II; tarsomere IV strongly bilobed with lobes rounded at apex; tarsomere V thin, elongated, slightly curved; claws simple without tooth. Metasternum rectangular with posterior margin straight. Sternites transverse and pubescent, three abdominal segments with an extruded cuticular vesicle. Last tergite (tg10) slightly modified, equipped with a few long setae, robust, lobed, triangular-shaped, contrasts with strongly modified last sternite (st9), which in basal part is elongated, broad, and flat, and at apex (laterally) bifurcated with these parts strongly pubescent and thin, cylindrical and above all exceptionally long and curved.



FIGURE 1. *Malthodes (Malthodes) susanbuttsae* **sp. nov.** holotype, in Baltic amber. A, habitus, dorsal view; B, habitus, ventral view. Scale bars = 1.0 mm.



FIGURE 2. *Malthodes (Malthodes) susanbuttsae* **sp. nov.** holotype, in Baltic amber. A, detail of last tergites; B, detail of last sternites. Scale bars = 0.5 mm.



FIGURE 3. *Malthodes (Malthodes) susanbuttsae* sp. nov. holotype, in Baltic amber. A, reconstruction of last abdominal segments, ventral view; B, reconstruction of last abdominal segments, dorsal view.

Etymology. Species named after Dr. Susan Butts, Director of Collections & Research at the Yale Peabody Museum, for her unwavering dedication to studying and preserving our prehistoric past.

Holotype. Male, in Baltic amber, deposited under accession number YPM IP.463895 at the Yale Peabody Museum in New Haven, Connecticut, USA (ex coll. Jonas Damzen: JDC-5976).

Type locality and type horizon. Yantarny mine, Sambian Peninsula, Kaliningrad Region, Russia. Middle Eocene: Bartonian-Priabonian (41.0–33.9 Mya).

Syninclusions. An Araneae (YPM IP.463896 at the Yale Peabody Museum), an Empididae (YPM IP.463897), a Dolicophodidae (YPM IP.463898), an unidentified Diptera (YPM IP.463899), air bubbles, and botanical remains.

Systematic placement. The pronotal shape, short elytra, the last maxillary palpomere globular and distally pointed, and the last abdominal segments strongly modified place this species in the genus *Malthodes* Kiesenwetter, 1852 and its nominotypical subgenus (Wittmer 1970; Brancucci 1980; Liberti 2011; Kupryjanowicz & Fanti 2019).

Differential diagnosis. The exceptionally distinctive shapes of the last abdominal segments of *M. susanbuttsae* **sp. nov.** are not observed in any fossil *Malthodes* (Fanti 2017, 2025a). Slightly similar forms of the last abdominal segments can be found in just a few *Malthodes* species living in the western Palearctic and North America (Fender 1951; Kaszab 1955a, 1955b; Wittmer 1970, 1992; Liberti 2011, 2015, 2016, 2017, 2021, 2023; Liberti & Poggi 2018; Diéguez Fernández 2021; Kazantsev 2021, 2024), such as *Malthodes flexuosus* Fender, 1951, found in Oregon in the United States (Fender 1951); and *Malthodes forcipifer* (Kiesenwetter, 1852), observed in Spain, Portugal, and France (Diéguez Fernández 2021). However, these last abdominal segments do not closely resemble those of *M. susanbuttsae* **sp. nov.**

Remarks. The yellowish amber piece measures approximately 63x23x8 mm, and weighs 6.3 grams. The inclusion is complete. Female of the new species is unknown.

Discussion

Malthodes Kiesenwetter, 1852 is an important genus in evolutionary studies, particularly in understanding the environmental and ecological forces that can drive speciation (Pankowski & Fanti 2024). The genus *Malthodes* is characterized, along with a few others in the Cantharidae family (Malthininae Malthodini), such as *Prosthaptus* Gorham, 1900 (Delkeskamp 1977) and *Frostia* Fender, 1951 (Fender 1951; Delkeskamp 1977), by the remarkable modification of the last abdominal segments, both tergites and sternites. These fascinating adaptations are believed to have evolved for reproductive purposes (Magis 1963). The specific environmental factors driving these modifications remain unknown (Pankowski & Fanti 2024). However, researchers have hypothesized that such changes may be influenced by topographical factors, such as orography (Wittmer 1970; Brancucci 1980); ecological conditions, including soil humidity and the quality of litter and humus (Liberti 2021; Pankowski & Fanti 2022; Parisi & Fanti 2025); and variables in the climate, particularly thermal gradients (Pankowski & Fanti 2022).

According to Sadowski *et al.* (2017), the region where Baltic amber was formed during the Eocene had minimal orographic variation but exhibited significant environmental diversity. The diverse habitats included coastal swamps and mixed mesophytic angiosperm-conifer forests, forming a "mosaic-like landscape" (Sadowski 2017; Sadowski *et al.* 2017). This, combined with warmer temperatures, is believed to have spurred a high biodiversity in the region, including a wide variety of *Malthodes* species (Pankowski & Fanti 2022, 2023; Parisi & Fanti 2024).

The substantial presence of *Malthodes* species in Baltic, Rovno, and Bitterfeld amber deposits (Fanti 2017, 2025a) shows speciation was far more extensive in the Eocene than in present-day Central and Northern Europe, where species diversity is lower due at least in part to the region's much colder climate today compared to 40 million years ago (Parisi & Fanti 2020; Pankowski & Fanti 2024). Despite these insights, little is known about what specific factors promoted such a diversity of last male abdominal segments (Pankowski & Fanti 2024). These structures feature a variety of different forms (bifurcated, lobed, pennate, etc.), yet their adaptive role remains unclear (Fanti & Sontag 2019; Pankowski & Fanti 2024). While modifications to male genitalia are fairly well-documented among insect species, variations in the last abdominal segments are comparatively less common. Such modifications have been observed in groups like Diptera (Tipulidae) and certain Odonata, among others (Cordero-Rivera & Córdoba-Aguilar 2010; Eberhard & Gelhaus 2024). Despite their morphological differences, these structural changes appear to serve a common function in species of *Malthodes*: grasping and securing the female's abdominal apex during

copulation (Fender 1951; Magis 1963; Brancucci 1980, Pankowski & Fanti 2024). In some species of insects, this grasping ability provides an apparent advantage to males by allowing them to maintain prolonged contact with the female, increasing their reproductive success (Han *et al.* 2010). While this might explain the evolutionary benefit of prehensile structures accompanying genitalia, it does not fully account for their astonishing morphological diversity (Pankowski & Fanti 2024). Other hypotheses, such as how these different structures may have resulted in mechanical isolation between species, may also help explain their variation. Further discoveries will be crucial, especially considering that male abdominal structures in *Malthodes* species were already highly diversified in the Eocene, the period when the genus is believed to have originated and quickly begun evolving into new species (Fanti 2021; Fanti & Pankowski 2024; Parisi & Fanti 2024).

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