New subgenus and three new species of soldier beetles from the Eocene of Baltic amber

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ABSTRACT

One fossil subgenus and three fossil species of soldier beetles: Libertimalthodes subg. nov., Cantharis (Cantharis) dougi sp. nov., Malthodes (Libertimalthodes) elytatus sp. nov. and Malthodes (Malthodes) nublar sp. nov., are described from Eocene Baltic amber. The deposit appears to be comparatively rich in inclusions of Cantharidae. The new subgenus differs from the nominotypical subgenus in possessing elytra that are elongated and covering the last abdominal urites, a huge aedeagus and the last abdominal sternite that is wide and little modified. Furthermore, the new species has an aedeagus that is almost completely extruded, which is a rare feature to find in fossils of soldier beetles. Malthodes nublar sp. nov. is characterized by short elytra and has a different shape of the terminalia, while Cantharis dougi sp. nov. has a different pronotal shape than in known fossil species. Malthodes aphidiphagus Fanti and Michalski, 2018, is transferred from the nominotypical subgenus Malthodes to the new subgenus Libertimalthodes.

INTRODUCTION

The number of taxa of Cantharidae preserved in Baltic amber is very high with 51 species described and also some extinct lineages (Fanti, 2017a, 2017b; Fanti and Damgaard, 2018; Fanti and Kupryjanowicz, 2018), and it seems probable that during the Eocene many more species of the family lived in Northern Europe and the Baltic region than currently inhabit the region. In this paper we describe a new species of Cantharis Lin-
naeus, 1758, and two new species of *Malthodes* Kiesenwetter, 1852, one of which is a new subgenus and is currently only known from fossil material. The new subgenus shows a peculiar character in that it has the aedeagus almost completely exposed and clearly visible: this is a useful aspect because the aedeagus, along with the shape of claws, tarsomeres and antennae, are important characters in the systematics of the family Cantharidae. A key to the subgenera of *Malthodes* is provided in Appendix 1. The genus *Malthodes* Kiesenwetter, 1852, is widespread throughout the Holarctic and the subfamily Malthininae Kiesenwetter, 1852, to which it belongs, is considered more recent than the other subfamilies of soldier beetles (Brancucci, 1980). Recently a probably related genus has been described from the Cretaceous Burmese amber (Hsiao et al., 2016); this finding demonstrates that our understanding of evolutionary changes in the Cantharidae is limited, also due to the scarcity of the fossil remains from the Cretaceous. The discovery of specimens of *Malthodes* with long elytra, which is a character currently known only in the fossil remains of the Eocene Epoch and with some aedeagus aspects similar to the subfamily Cantharinae Imhoff, 1856, supports an older origin.

**MATERIAL AND METHODS**

The examined material originated from the Kaliningrad Region, Russia, near the village of Yantarny (Sambian Peninsula). Here, hundreds of tons of amber have been extracted in open-cast mines (at a depth of 12—60 m) since the middle of the seventeenth century, with pronounced industrialization since 1874 (Małka, 2010) and mechanization since around 1930. The amber pieces with the inclusions are deposited in the J. Kupryjanowicz collection at the Andrzej Myrcha Center of Nature, University of Białystok, Poland (UCP UwB). The specimens were polished, mounted on the microscope’s ball table, and we used a removable and re-usable rubber adhesive (Faber Castell Tack-it Removable Reusable Adhesive) to slide-mounting were used during the observation. Digital photographs were taken in the Laboratory of Evolutionary Biology and Insect Ecology at the Institute of Biology, University of Białystok (Poland). Images were obtained with an Olympus DSX110 stereo-microscope and a camera with a colour CCD image sensor (1/1.8 inch, 2.01 megapixels), equipped with a DSXPLFL 3.6x lens. The specimen drawings were made using CorelDrawX6. Morphological terms and acronyms of the last abdominal segments of *Malthodes*, follow Liberti (2011, 2015).

**SYSTEMATIC PALAEONTOLOGY**

Order COLEOPTERA Linnaeus, 1758
Superfamily ELATEROIDEA Leach, 1815
Family CANTHARIDAE Imhoff, 1856
Subfamily CANTHARINAE Imhoff, 1856
Tribe CANTHARINI Imhoff, 1856
Genus Cantharis Linnaeus, 1758
Subgenus Cantharis Linnaeus, 1758
*Cantharis (Cantharis) dougi* sp. nov.

**Type material.** Holotype: probably male, in Baltic amber, deposited under accession number UCP UwB 1679. The yellow amber piece measures 15 x 6 x 4 mm, and the inclusion is only slightly folded, with a white emulsion on the eye and opaque emulsion on the ventral side (particularly surrounding sternum and head). Syninclusions consist of wood remains and a stellate hair.

**Type horizon.** Middle Eocene (Lutetian) (47.8—41.2 Mya) to late Eocene (Priabonian) (37.8—33.9 Mya).

**Type locality.** Russia, Kaliningrad Region, Yantarny mine.

**Etymology.** New species is named in honour of Doug Lundberg (Colorado Springs, USA), amber expert and dear friend of one of the authors (J. Kupryjanowicz).

**Differential diagnosis.** Three species of *Cantharis* have been described from amber deposits: *Cantharis* (s. str.) *sucinonigra* Kuśka, 1992, and *C. (Cyrtomoptila) sucinokotejai* (Kuśka, 1996) have similar size (6.0 mm) but different coloration and pronotal shape than *C. dougi* sp. nov. *C. sucinonigra* has a red pronotum that is roundish at sides, while *C. sucinokotejai* has almost square pronotum, and has thorax and femora black-brown with tibiae and tarsi yellow-brown (Kuśka, 1992, 1996; Fanti, 2017a, 2017b). Whereas, *Cantharis* (*Cyrtomoptila*) *mikkelsenorum* Fanti and Damgaard, 2018, has a larger body size and a pronotum sub-rectangular with sinuous lateral margins and with ripples in the middle (Fanti and Damgaard, 2018).

**Description.** Adult, winged, probably male (defined on basis of last sternite, which appears triangular and narrower than last tergite). Body length: 6.5 mm; head: 0.88 mm; pronotal length: 0.92 mm; scutellar shield: 0.33 mm long, 0.30 mm wide near the base; elytra: 4.5 mm long, width at humeri: 0.62 mm, width near apex: 0.95 mm;
antennae: 4.8 mm long, with antennomere I: 0.36 mm, antennomere II: 0.12 mm.

Head black, pronotum brown, elytra along with legs and antennae dark brown. Head not completely exposed, short and roundish, covered with scattered long setae. Eyes large, rounded and convex. Mandibles elongated, without tooth, robust at base, pointed at apex. Maxillary palp 4-segmented, with first palpomere short, second palpomere elongate, third palpomere slightly longer than first, and last palpomere slender and securiform, all palpmeres with long setae. Labial palp 3-segmented.

Antennae 11-segmented, short, reaching near midlength of elytra, filiform, with short setae; scape long, cylindrical, robust, club-shaped; antennomere II short, 3.0 times shorter than scape; antennomere III longer than second; antennomere IV elongate, filiform, about as long as scape; antennomeres V—VIII subequal, elongate, longer than scape; antennomeres IX—XI about one-third shorter than previous antennomeres.

FIGURE 1. Cantharis (s. str.) dougi sp. nov. in Baltic amber (holotype, No. UCP UwB 1679) lateral view, scale bar equals 1 mm (1), ventro-lateral view, scale bar equals 1 mm (2), detail of head and pronotum (in dorsal view), scale bar equals 400 μm (3), detail of elytra, scale bar equals 1 mm (4).
Pronotum transverse, wider than head, sub-rectangular, equipped with scattered setae, anterior and posterior margins bordered and sinuous, surface undulate, slightly swollen at center and flatter near the margins, sides almost straight. Scutellar shield subtriangular with very round apex.

Elytra wider than pronotum, elongate, covering last abdominal segment, equipped with numerous setae, narrower at humeri and wider near rounded apex. Hind wings dark, reaching last abdominal segments.

Sternum subquadrate, punctate, slightly elongate. Abdominal ventrites transverse, robust, slightly pubescent, with last ventrite triangular and narrow.

Legs covered with long thick pubescence; coxae slightly elongate; trochanters triangular; femora cylindrical and only slightly flat, long, not curved; tibiae very thin, slightly sturdier at apex, cylindrical, as long as femora, equipped with single acute and long spur at apex. Tarsi 5-segmented equipped with many and long setae; first tarsomere

FIGURE 2. *Cantharis (s. str.) dougi* sp. nov. in Baltic amber (holotype, No. UCP UwB 1679) detail of head and pronotum in lateral view, scale bar equals 400 μm (1), detail of mandible and palps, scale bar equals 300 μm (2), detail of protarsum, scale bar equals 100 μm (3), detail of mesotarsi, scale bar equals 200 μm (4).
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Elongate, as long as second and third combined, 0.52 mm long; second tarsomere shorter, enlarged ventrally, length 0.32 mm; third tarsomere slightly shorter than second, bilobed at sides, and 0.21 mm long; fourth tarsomere short and bilobed at sides, 0.18 mm long; fifth thin and elongate, length with claws about 0.26 mm; claws simple with single small and obtuse tooth at base.

Subfamily MALTHININAE Kiesenwetter, 1852
Tribe MALTHODINI Böving and Craighead, 1931
Genus Malthodes Kiesenwetter, 1852
Subgenus Libertimalthodes subg. nov.

Etymology. New subgenus is named in honour of Gianfranco Liberti (Uboldo, Italy), expert on soldier beetles (particularly Malthodes), as well as dear friend and mentor of an author (F. Fanti) on these beetles, plus the addition of the genus Malthodes Kiesenwetter, 1852. Gender: masculine.

Type species. Malthodes (Libertimalthodes) elytratus sp. nov. New subgenus is established based upon two species: Malthodes elytratus sp. nov. and M. aphidiphagus Fanti and Michalski, 2018.

Diagnosis. Malthininae features found in new subgenus include: globular and pointed last maxillary palpomere, general habitus, and last urites modified (similar to extant Malthodes). Differences from nominotypical subgenus include: elytra elongate, covering and slightly surpassing last abdominal segments, and large aedeagus, which is very wide and about as long as last two sternites combined. Furthermore, last sternite is little modified, and antennae of males are short. The other subgenus Podistrina Fairmaire, 1875, with doubtful validity (Brancucci, 1980), is characterized by elongate head, longitudinal pronotum, absence of hind wings, and elytra that are particularly short (Brancucci, 1980).

Distribution. Currently known only from Eocene Baltic amber. Malthodes (Libertimalthodes) elytratus sp. nov. Figures 3-5

Type material. Holotype: male, in Baltic amber, deposited under accession number UCP UwB 1684. Piece was cut from larger nugget with dimensions 100 x 30 x 11 mm, and reduced to dimensions of 20 x 5 x 3 mm, making the inclusion of new Malthodes highly visible. Syninclosures consist of wood remains, air bubbles, two stellate hairs, Ceratopogonidae (2 specimens), Psocoptera (1 specimen), Acarina (1 specimen), Collembola (1 specimen), and Coleoptera - Scirtidae (1 specimen).

Type horizon. Middle Eocene (Lutetian) (47.8—41.2 Mya) to late Eocene (Priabonian) (37.8—33.9 Mya).

Type locality. Russia, Kaliningrad Region, Yantarny mine.

Etymology. Specific epithet is Latin elytratus = “equipped with elytra”, which refers to long elytra.

Differential diagnosis. Only fossil Malthodes aphidiphagus Fanti and Michalski, 2018 is similar to Malthodes (Libertimalthodes) elytratus subg. et sp. nov. in possessing elongate elytra (Fanti and Michalski, 2018). However, new species is easily recognizable based upon its last sternite being both wide and roundish, with different shape of the posterior most tergites, slender habitus, wider and more elongate aedeagus, and slightly smaller body size (3.7 mm instead of 4.0 mm).

Description. Adult, male (defined on basis of visible aedeagus), winged and with slender habitus. Body length: 3.7 mm; head: 0.4 mm long; pronotum: 0.45 mm long; elytra: 2.6 mm long. Entirely dark brown-reddish, with elytra lacking yellow spots at apex.

Head exposed, rounded, as wide as pronotum, equipped with long setae. Eyes large, rounded, convex, and inserted laterally in upper part of head, interocular dorsal distance about 1.5 times greater than eye diameter. Mandibles short, robust, wide at base. Maxillary palp 4-segmented with terminal palpmere robust, globular and distally pointed. Labial palp 3-segmented, with last palpmere globular and pointed.

Antennae filiform, 11-segmented, very short, reaching humeral zone of elytra; antennomere I club-shaped, robust; antennomere II short, globular-elongate, about 2.0 times shorter than first article; antennomeres III—V filiform, longer than antennomere II and with antennomeres III—VI sturdier than others; antennomere XI filiform, rounded at apex.

Pronotum sub-quadrate in shape, covered with setae, surface irregular and slightly punctate, anterior and posterior margins slightly bordered, sides undulate. Scutellar shield short, triangular-shaped, rounded at apex.

Elytra slightly wider than pronotum in region of humeri, elongate and surpassing posterior most urites, wide at humeri, narrower at center, width secondary widening near apex, surface pubescent, apex rounded. Hind wings dark, almost completely covered by elytra.
Legs slender; coxae robust and elongated; trochanters triangular; femora robust, enlarged, slightly curved ventrally; tibiae slightly longer than femora, cylindrical, thin, without spurs at apex and equipped with short setae. Tarsi 5-segmented; tarsomere I elongate; pro- and mesotarsomere II slightly shorter than pro- and mesotarsomere I; metatarsomere II about 1.5 times shorter than I; metatarsomere III about as long as II; tarsomeres IV bilobed; tarsomeres V elongate and slender; claws simple with obtuse tooth at base.

Metasternum elongate and apically rounded, without punctuation or pubescence. Abdominal sternites transverse and slightly pubescent.

Penultimate sternite strongly transverse; last sternite very wide, with sides strongly rounded and apically undulate with a central depression-concavity equipped with long setae on all the surface. Aedeagus almost completely extruded, huge, wide, and as large as last sternite at its base, with long dorsal shield slightly folded at apex, parameres
(laterophyses) long and robust with apex slightly enlarged and globular.

Female unknown.

Subgenus *Malthodes* Kiesenwetter, 1852
*Malthodes* (*Malthodes*) *nublar* sp. nov.

**FIGURE 4.** *Malthodes* (*Libertimalthodes*) *elytratus* subgen. et sp. nov. in Baltic amber (holotype, No. UCP UwB 1684) detail of head and palps (in frontal view), scale bar equals 200 μm (1), detail of palps, scale bar equals 100 μm (2), detail of metatarsus, scale bar equals 500 μm (3), detail of metatarsus, scale bar equals 100 μm (4).

Type material. Holotype: male, in Baltic amber, deposited under accession number UCP UwB 1683. Amber piece measures 20 x 4 x 4 mm, with surrounding amber transparent and inclusion extremely visible, well-preserved, and complete. Syninclusions consist of wood remains and air bubbles.

**Type horizon.** Middle Eocene (Lutetian) (47.8—41.2 Mya) to late Eocene (Priabonian) (37.8—33.9 Mya).

**Type locality.** Russia, Kaliningrad Region, Yantar mine.

**Etymology.** Specific epithet is in homage to "Isla Nublar", fictional island setting of Jurassic Park,
novel of Michael Crichton and film directed by Steven Spielberg. Epithet is to be treated as noun in apposition.

**Differential diagnosis.** No fossil *Malthodes* shows combination of features found in new species described herein (Fanti, 2017b, 2017c, 2018; Fanti and Vitali, 2017; Fanti and Damgaard, 2018; Fanti and Michalski, 2018; Fanti and Pankowski, 2018).

Only *Malthodes ceranowiczae* Kuśka and Kupryjanowicz, 2005, has similar total body length (2.7 mm), but last tergite in this species is smaller and shorter, and last sternite exhibits stronger caudal fork (Kuśka and Kupryjanowicz, 2005). Furthermore, generally comparable species, such as *Malthodes caenozoicus* Fanti and Vitali, 2017, are smaller (1.8 mm total body length), with shorter antennae, shorter elytra, differences in shape of last sternite, and more elongate urophysis (Fanti and Vitali, 2017).

**Description.** Adult, male. Body length: 2.4 mm; head: 0.39 mm long, and 0.41 mm wide; pronotum: 0.3 mm long and 0.5 mm wide; elytra: 1.3 mm long; antennae: 1.7 mm long. Entirely dark brown - testacean with head darker and without yellow spots on elytra.

Head completely exposed, rounded, pubescent, narrower than pronotum. Eyes large, rounded, convex, dorsal interocular distance about 3.7 times greater than eye diameter, eyes inserted laterally relative to surface of head. Maxillary palp 4-segmented, with terminal palpomere globular and distally pointed. Labial palp 3-segmented, with last palpomere globular and pointed.

Antennae filiform, 11-segmented, relatively short, not reaching apex of elytra; antennomere I elongate, more robust at apex; antennomere II about 1.5 times shorter than antennomere I; antennomeres III—X filiform, longer than antennomere II; antennomere XI filiform, rounded at apex.

Pronotum strongly transverse, surface slightly punctate and pubescent, margins and sides narrowly bordered. Scutellar shield small, short, triangular, widest anteriorly, and with apex straight.

Elytra as wide as pronotum, short, parallel-sided, not narrowed at apex, reaching base of seventh abdominal segment, with apex rounded, and surface slightly wrinkled and pubescent. Hind wings very elongate, dark, surpassing elytra and abdominal urites in length.

Legs robust; coxae very robust, elongate, and curved; trochanters elongate, triangular at apex; femora enlarged, slightly curved at base; tibiae longer than femora, thin and equipped with short setae. Tarsi 5-segmented; tarsomere I elongate and slightly enlarged at apex; protarsomeres I and II nearly equal in length; meso- and metatarsomere II half length of I; tarsomeres III roundish, robust and slightly shorter than second; tarsomeres IV bilobed; tarsomeres V elongate and slender; claws simple.

Metasternum subtrapezoidal in shape. Sternites transverse and slightly pubescent.

Penultimate tergite (tg9) robust, sub-quadrate in shape; last tergite (tg10) sub-quadrate, with straight margin, distally equipped with setae, narrower than tg9; penultimate sternite (st9) short, transverse, with sides slightly rounded, equipped with setae on the central part, and with two long laminate urophysis at sides; last sternite (st9) elongate, not exceeding half of length of tg10, narrow, flat, not curved, slightly forked at apex, and equipped with long setae. Aedeagus partially extruded and slightly longer than st9, with long lobes globular and rounded at apices.

Female unknown.

**DISCUSSION**

*Malthodes (Libertimalthodes) elytratus* subg. et sp. nov. exhibits a head that is globular, a distinctive pronotal shape, and modified posterior abdominal urites that show it is clearly related to the genus *Malthodes* Kiesenwetter 1852. The latter genus is extremely variable, but the differences in elytral lengths (particularly when it is combined...
with the very large aedeagus and the little modified posterior abdominal segments) can be a useful character in support of the new subgenera, much as it has been informative in the related subgenus *Indomalthinus* Brancucci in Wittmer and Brancucci, 1978, which has slightly longer elytra, and small differences in the pronotum with respect to the nominotypical subgenus (Brancucci, 1978). *Malthodes* species traditionally have short elytra that leave some abdominal segments uncovered (Brancucci, 1980; Liberti, 2011), but we can also find species with more elongate elytra, such as *Malthodes rectus* LeConte, 1881 (in North America), or species of the *brevicollis*-group in Europe (Liberti, 2016, 2017), for example. However, *Malthodes* (*Libertimalthodes*) *elytratus* subg. et sp. nov. displays elongate elytra, which completely cover and overtake the abdomen. It is widely accepted that the shape of the aedeagus is an important phylogenetic character among the genera of soldier beetles (Brancucci, 1980; Liberti, 2011), and this feature even has some importance at the family level for many beetles (Schilthuizen et al., 2016). The morphology of the posterior most abdominal

**FIGURE 6.** *Malthodes* (s. str.) *nublar* sp. nov. in Baltic amber (holotype, No. UCP UwB 1683) dorsal view, scale bar equals 400 μm (1), ventral view, scale bar equals 400 μm (2), lateral view, scale bar equals 500 μm (3), lateral view, scale bar equals 500 μm (4).
segments and the aedeagus were studied for the first time, in a broad way, by Magis (1963, 1964). In these works, the posterior structures of the abdomen are compared with those of representatives of the genus *Rhagonycha* Eschscholtz, 1830, revealing that the aedeagus of *Malthodes* members is considerably shorter, the tegmen is reduced, and variations in the median lobe are most diagnostic. Subsequently, the aedeagus was studied by Wittmer (1970, 1979), Brancucci (1980), and Liberti (2011, 2015, 2016, 2017). The aedeagus is scarcely visible in other fossil records for the family Cantharidae, and we find it marginally visible in: *Cacomorphocerus jantaricus* (Kuśka and Kania, 2010), and *Malthodes aphidiphagus* Fanti and Michalski, 2018, and exposed to a slightly larger extent in: *Kuskaella macroptera* Fanti and Kupryjanowicz, 2017, *Malthodes rovnoensis* Kazantsev and Perkovsky, 2014, and the new *Malthodes* species with short elytra described herein. Currently, only two specimens with the aedeagus almost completely extruded are known, belonging to *Sucinorhagonycha kulickae* Kuśka, 1996, and *Mimoplatycis bicolor* Fanti and Vitali, 2017 (Kuśka, 1996;
Kuśka and Kania, 2010; Kazantsev and Perkovsky, 2014; Fanti and Kupryjanowicz, 2017; Fanti and Vitali, 2017; Fanti and Michalski, 2018). Small dimensions and globular shape of the aedeagus are present in the known species and in *Malthodes nublar* sp. nov., but not at all in *Malthodes (Liberti-malthodes)* subg. nov. In fact, *Liberti-malthodes* members possess an aedeagus more similar to the subfamily Cantharinae Imhoff, 1856, in terms of its large size, the elongate shape of the dorsal shield (“pièce basale” of Brancucci), and long, robust parameres-laterophyses (see: Magis, 1971; Brancucci, 1980). Conversely, the apparent lack of an internal sac, shows similarity to the Malthininae, and *Malthodes*. The range of variation observed within features of the aedeagus in the genus *Malthodes* suggests that further material and studies may ultimately support elevation of the new subgenus *Liberti-malthodes* to a higher taxonomic rank.

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**REFERENCES**


APPENDIX 1.

Key to the subgenera of *Malthodes*:

(1) Aedeagus small and globular; elytra very short or short enough to leave at least the last abdominal segments uncovered………………………………………………………………………………2

Aedeagus large and elongate; elytra long enough to cover and slightly surpass the last abdominal segment; posteriormost urites little modified……………………………………*Libertimalthodes* subg. nov.

(2) Elytra short; metathoracic wings tend to be present………………*Malthodes* Kiesenwetter, 1852

Elytra very short; wings absent; head elongate; pronotum longitudinal….*Podistrina* Fairmaire, 1875