



Three new species of soldier beetles from Baltic amber (Coleoptera, Cantharidae)

FABRIZIO FANTI¹ & MARY K. PANKOWSKI²

¹*via del Tamburino 69, I-53040 Piazze (SI), Italy. E-mail: fantifab@alice.it*

²*16405 Fox Valley Terrace, Rockville, Maryland 20853, USA. E-mail: marykpankowski@gmail.com*

Abstract

Three new species of soldier beetles (Cantharidae) are described from late Eocene Baltic amber from the Kaliningrad Region of Russia on the coast of the Baltic Sea, *i.e.*, *Rhagonycha maryae* **sp. nov.**, *Sucinorhagonycha samsockorum* **sp. nov.** and *Malthodes josephi* **sp. nov.** *Sucinorhagonycha samsockorum* has a few antennomeres that are slightly dentate, making the new species appear intermediate between genus *Sucinorhagonycha* Kuška, 1996, with filiform antennae, and genus *Cacomorphocerus* Schaufuss, 1892, which has saucer-shaped central antennomeres. This suggests that the relationship between the two genera may be closer than previously believed. *Malthodes josephi* is noteworthy because it has cuticular vesicles extruding from its abdominal segments that suggest their use for chemical defense. It is the first time that these vesicles have been discovered in Eocene species of soldier beetles. It is also the first time they have been seen in all extinct and extant species of the subfamily Malthiniinae and its genus *Malthodes* Kiesenwetter, 1852.

Key words: fossil resin, Priabonian, Insecta, soldier beetles, new species

Introduction

Eight genera of soldier beetles present as fossil inclusions in Baltic amber have living representatives. Seven of them, including *Rhagonycha* Eschscholtz, 1830 and *Malthodes* Kiesenwetter, 1852, are widespread and common in the Holarctic region, with about 600–650 known species of *Malthodes* (Delkeskamp 1977; Kazantsev & Brancucci 2007; Fanti 2017b) and about 300–320 taxa of *Rhagonycha* (Delkeskamp 1977; Kazantsev & Brancucci 2007). Only the genus *Themus* Motschulsky, 1858 is present in the Palaearctic region in South Asia from Iran to India, China, Taiwan and in the Oriental region, but not present in Europe or North America today. In the fossil record (Baltic amber), there are 11 genera of the family Cantharidae Imhoff, 1856 that are extinct, including *Sucinorhagonycha* Kuška, 1996 (Fanti 2017a, 2017c; Fanti & Castiglione 2017; Fanti & Kupryjanowicz 2017; Fanti & Pankowski 2018). Many genera in the family Cantharidae have predatory larvae that feed on worms, slugs, and small insects. The adults of many genera are also predatory but supplement their diet with pollen and shoots (Fiori 1949; Ramsdale 2002). In some cases, for example *Chauliognathus* Hentz, 1830 and *Belotus* Gorham in Godman & Salvin, 1881, they appear to be purely pollinivorous and nectarivorous (Ramsdale 2002; Pérez-Hernández 2018). Thus, it is likely that the two described species belonging to the extant genera *Rhagonycha* and *Malthodes* likely fed on insects, as do their counterparts. For the new species of *Sucinorhagonycha*, however, this can only be hypothetical, as there is no extant species of the genus to observe.

Materials and methods

The amber pieces were discovered along the Baltic Sea coast from a quarry near Yantarny, Kaliningrad Region, Russia, and were cleaned and polished before examination. Observations, photographs and measurements were taken with a microscope Olympus DSX100 with Extended Focal Image (EFI) capabilities, or with a camera Canon

70D and macrolens Canon MPE-65mm, with the addition of focus stacking software Helicon Focus. The photos have been processed with the program PhotoImpact Viewer SE, and the reconstruction was drawn free-hand with China ink. All specimens were donated to the Smithsonian Institution's National Museum of Natural History (USNM). The morphological terminology of the male terminalia of the new species of *Malthodes* follows that used in Wittmer (1970, 1979) and Liberti (2011). Based on many recent publications, the age of the Baltic amber is considered here to be of the Upper Eocene (Priabonian, 37.8–33.9 Mya), although the age is still controversial (Cai *et al.* 2016) and sometimes the Prussian Formation “blue earth” (Kosmowska-Ceranowicz 2008) and marine strata containing amber are referred to the Lutetian (47.8–41.2 Mya), Middle Eocene (*e.g.*, Wolfe *et al.* 2009: 44.1±1.1 and 47.0±1.5 Mya).

Systematic treatment

Family Cantharidae Imhoff, 1856

Subfamily Cantharinae Imhoff, 1856

Tribe Cantharini Imhoff, 1856

Genus *Rhagonycha* Eschscholtz, 1830

Subgenus *Rhagonycha* Eschscholtz, 1830

Rhagonycha (Rhagonycha) maryae FANTI & M. K. PANKOWSKI sp. nov.

(Fig. 1)

Description. Adult, winged, slender and elongated. Female, defined on the basis of the large last sternite as wide as last tergite and apically sinuous and concave in the middle. Body length: 3.7 mm; elytra: 3.1 mm; antennae: approximately 2.8 mm. Entirely dark brown including legs and antennae. Head almost completely exposed, rounded, with thin and shallow punctation. Eyes rounded, convex, inserted laterally to the head, inter-ocular dorsal distance about 2.4 times greater than eye diameter. Mandibles not visible. Maxillary palps 4-segmented, unequal in length, with the last palpomere securiform. Labial palps 3-segmented, last segment securiform. Antennae filiform, 11-segmented and with all segments pubescent, relative short, surpassing half of elytra; antennomere I (scape) robust, elongated, club-shaped; antennomere II robust, short, 1.7 times shorter than scape; antennomeres III–V elongated, robust (particularly the third), slightly shorter than first article; antennomeres VI–IX filiform, subequal, thinner and around 0.1–0.2 times shorter than previous three articles; antennomere X filiform, approximately 0.3 times shorter than previous one; antennomere XI filiform as long as antennomeres VI–IX. Pronotum larger basally, trapezoidal, larger than head, posterior corners rounded, posterior margin strongly bordered, anterior margin and sides slightly bordered, sides concave at half length, surface irregular and equipped with short, thick pubescence. Scutellum subquadrate with apex truncate and straight. Elytra slender, parallel-sided, very elongated and completely covering and slightly surpassing the last abdominal segments, wider than pronotum, apex rounded, surface rugose and equipped with many short setae. Posterior wings present, almost completely covered by elytra. Metasternum dark brown, rounded posteriorly, equipped with setae; sternites short, transverse, wrinkled; last sternite wide, rounded and sinuous at apex with central concavity. Legs short and pubescent; coxae massive; trochanters rounded; femora slightly enlarged; tibiae thin, cylindrical, longer than femora. All tarsi 5-segmented; first segment elongated; second tarsomere elongated and longer than first tarsomere; third about 2.3 times shorter than second, straight at apex; fourth tarsomere bilobed at sides; fifth flat and elongated; claws apparently bifid at apex without denticles at base.

Etymology. Species named after Mary L. Pankowski, paternal grandmother of the second author, who provides immense love to her family, supports her community in numerous ways and inspires all with her indomitable spirit of optimism.

Holotype. Female, adult specimen included in Baltic amber, accession No. USNM PAL 712534 in the USNM.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

Type strata. Baltic amber, Upper Eocene, Prussian Formation (Priabonian). Estimated age: 37.8–33.9 Mya.
Syninclusions. Wood remains.

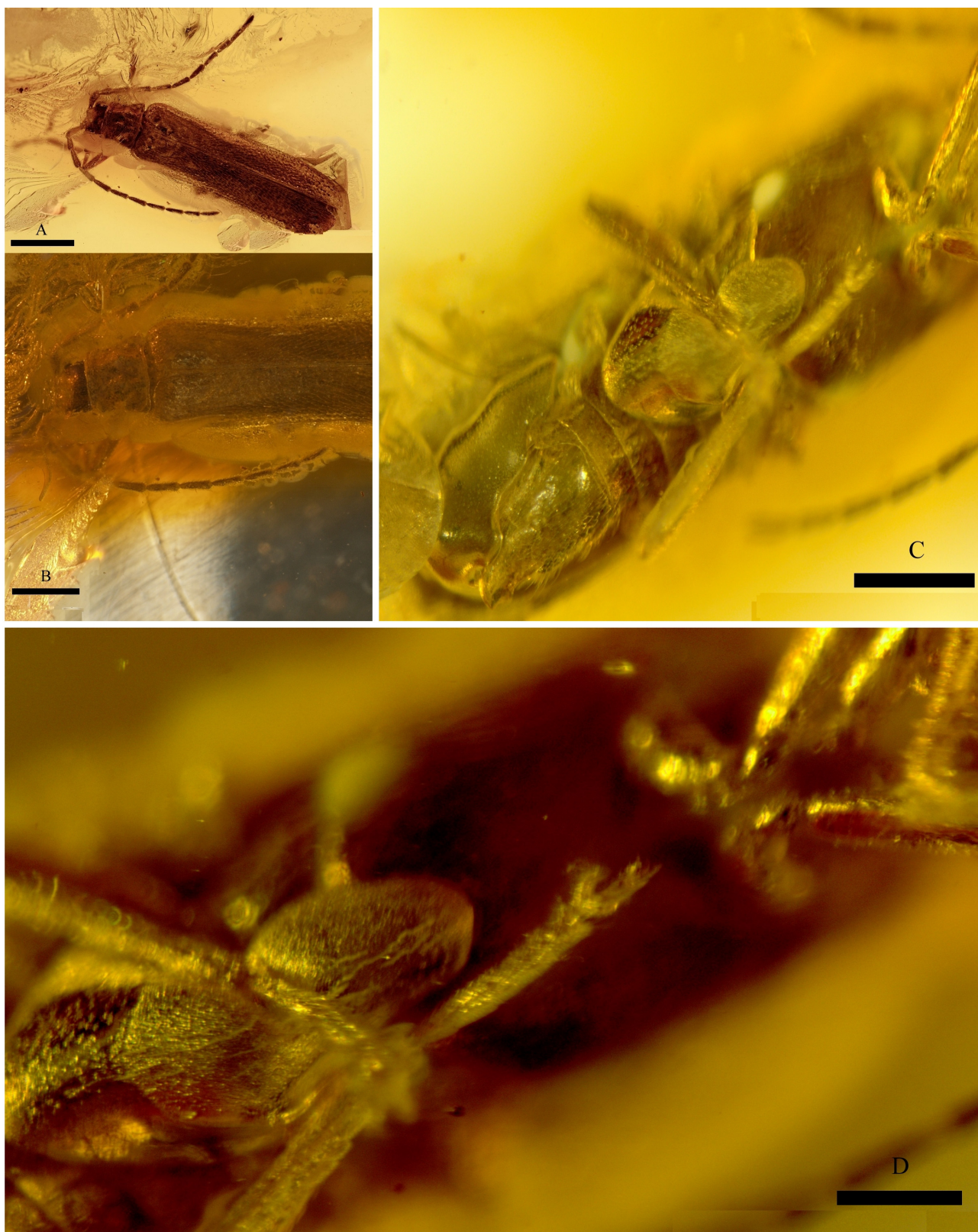


FIGURE 1. *Rhagonycha maryae* sp. nov. in Baltic amber. A: Holotype, dorsal view, scale bar = 1.0 mm. B: Holotype, detail of head, pronotum and left antenna, scale bar = 0.5 mm. C: Holotype, ventral view, scale bar = 0.5 mm. D: Holotype, detail of leg and claws, scale bar = 0.2 mm.

Differential diagnosis. The new species belongs to the genus *Rhagonycha* Eschscholtz, 1830 based on its bifid claws and for its anteriorly narrowed pronotum. Two species of the genus *Rhagonycha* have previously been described from inclusions in Baltic amber: *R. kryshstofovichi* (Yablokov-Khnzorian, 1960) and *R. sucinobaltica* (Poinar & Fanti, 2016). *Rhagonycha kryshstofovichi* initially attributed to the genus *Malchimus* Kiesenwetter, 1863 was then transferred to *Rhagonycha* by Kazantsev (2013) based on the anteriorly narrowed pronotum, the fourth palpomere securiform and unmodified *terminalia*. In the genus *Rhagonycha* males and females possess the same pronotal shape. Thus, because the pronotal shape of *R. maryae* **sp. nov.** is different from *R. kryshstofovichi* and *R. sucinobaltica*, it can be distinguished as a new species. (It's worth noting here that the specimen of *R. maryae* **sp. nov.** is a female because its last sternite is as wide as its last tergite, and it has an apical margin sinuous and concave in the middle. In the males of *Rhagonycha*, the last tergite is triangular and narrower than the last tergite.) *R. kryshstofovichi* is easily distinguishable from *R. maryae* **sp. nov.** based on its larger size (with a body length of 7 mm compared to 3.7 mm for *R. maryae*), different pronotum and different length of the antennomeres (Yablokov-Khnzorian 1960). While the other known species *R. sucinobaltica* Poinar & Fanti, 2016 has similar dimensions (a body length of 3.5 mm), it possesses a different pronotum that is more curved at the sides and less bordered at the posterior margin (Poinar & Fanti 2016). *Rhagonycha maryae* **sp. nov.** also differs from other inclusions in Baltic amber known at a generic level as well as specimens known from mold impression and compression fossils in various rocky sediments (Fanti 2017a).

Remarks. The amber piece measures 19x19x4 mm and weighs 0.8 grams. It has a round shape and is rather flat.

Genus *Sucinorhagonycha* Kuška, 1996

Sucinorhagonycha samsokorum FANTI & M. K. PANKOWSKI **sp. nov.**

(Figs. 2–3)

Description. Adult, winged, elongated, rather robust. Male, defined on the basis of the last sternite very small, narrow, rounded at apex, and separated and away from the last tergite. Body length: 4.5 mm; elytra: 3.3 mm; antennae: approximately 2.5 mm. Head black, elytra blackish to dark brown, pronotum with antennae and legs reddish to dark brown. Head very elongated and narrow, prognathous, completely exposed, wrinkled with shallow punctation and short setae. Eyes subelliptical, convex, inserted dorsally and near the sides of the head. Mandibles robust, elongated, slightly falciform, without teeth or denticles. Maxillary palps 4-segmented and unequal in length; first palpomere massive; second palpomere flat, robust, rounded and enlarged in the middle; third small, thin and short; last palpomere securiform, elongated, rounded externally, apically thin but with a bulbous tip. Labial palps 3-segmented, very elongated; first segment massive; second segment thin; last segment elongated, very slightly securiform with the apex robustly pointed. Antennae 12-segmented, inserted dorsally and between the eyes, very short, reaching and slightly surpassing the humeral zone, all segments pubescent along all margins; antennomere I (scape) filiform and robust, elongated, not club-shaped, slightly enlarged apically; antennomere II robust, short, 2.0 times shorter than scape, concave in the middle on the external side; antennomere III robust, slightly shorter than second article and not concave in the middle; antennomeres IV–V subequal, very slightly shorter than antennomere III, enlarged apically (dentate) on the external side; antennomere VI elongated, robust, approximately 1.5 times longer than antennomeres IV–V and not dentate on the external side; antennomere VII robust and the shortest, concave in the middle on the internal side; antennomere VIII filiform but slightly dentate at the external apex; antennomeres IX–XII filiform, unequal in length with the antennomere XII rounded at apex and the longest. Pronotum subquadrate, slightly longer than wide, very slightly wider than head, corners rounded, margins bordered, in the middle of the pronotum there is a large and very raised (evident) area slightly concave in the center, sides and margins flat after the raised area with shallow punctation and short pubescence. Scutellum not well visible. Elytra very elongated, slender, parallel-sided, completely covering the last abdominal segments, wider than pronotum, apex rounded, surface equipped with long and erected setae. Posterior wings completely covered by elytra. Metasternum blackish, punctate, elongated, posteriorly slightly rounded; sternites and tergites wide, punctate; last tergite short, wide and strongly bent at sides; last sternite small, narrow, rounded at apex. Anterior and median legs short, posterior legs longer; coxae massive, wide at base, elongated; trochanters elongated,

posteriorly triangular; profemora strongly enlarged and slightly curved, meso- and metafemora thin; pro- and mesotibiae shorter than pro- and mesofemora, cylindrical, thin, with two spurs (one very short) and setae; metatibiae longer than metafemora, cylindrical, thin, with spurs and setae. Tarsi 5-segmented and with setae; pro- and mesotarsi with the first segment elongated, 1.5 times longer than second; metatarsi with the first tarsomere approximately 1.9 times longer than second; third tarsomere shorter than second and slightly enlarged apically; fourth tarsomere bilobed at sides with the lobes very long, curved and rounded at apex; fifth tarsomere elongated, thin; claws simple, long and without lobes or denticles.

Etymology. Species named after Frank and Joanne Samsock, maternal grandparents of the second author, who worked hard, dedicated their lives to their family and were excellent role models for their children and grandchildren.

Holotype. Male, adult specimen included in Baltic amber, accession No. USNM PAL 712533 in the USNM.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

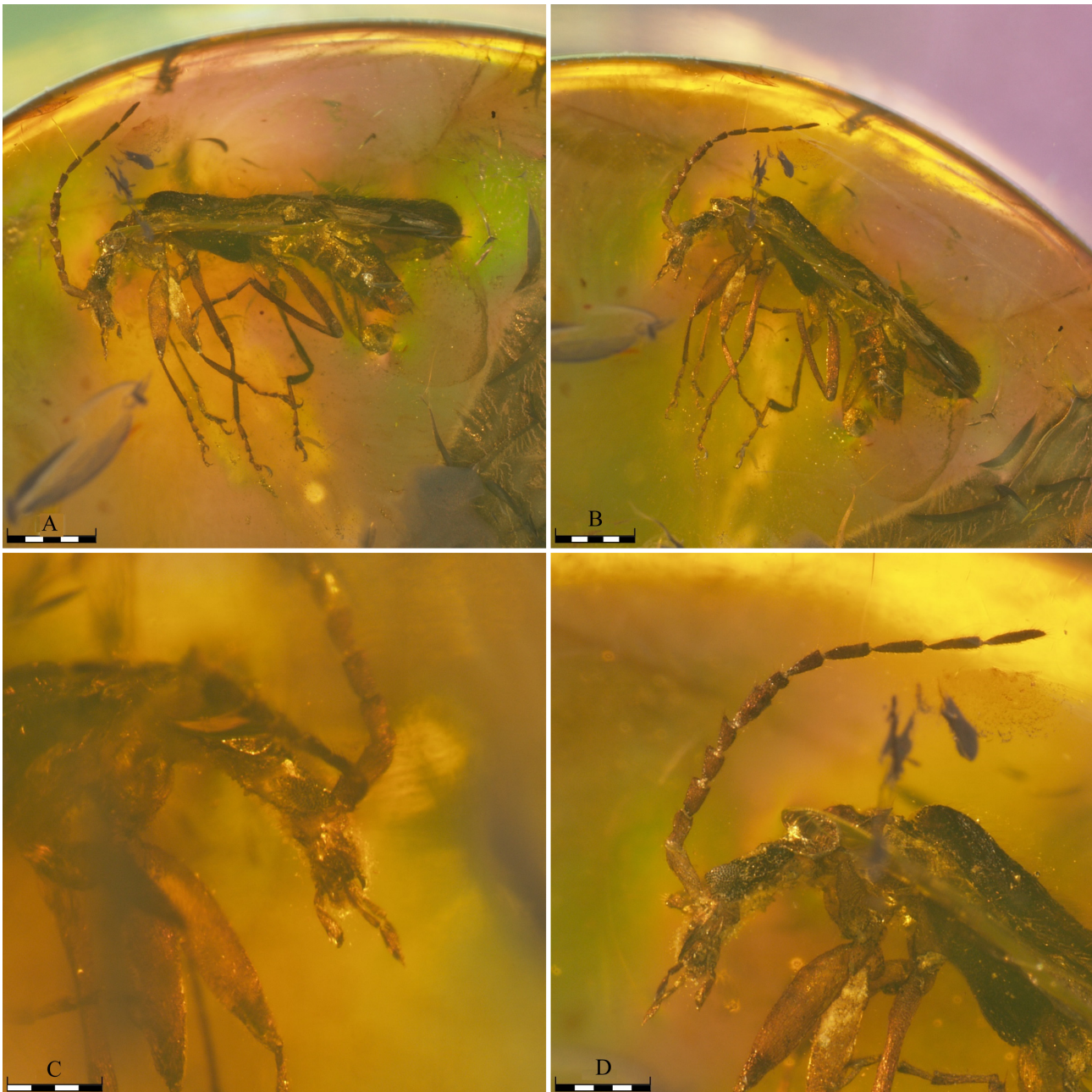


FIGURE 2. *Sucinorhagonycha samsokorum* sp. nov. in Baltic amber. A–B: Holotype, lateral views, scale bar = 1.0 mm. C: Holotype, detail of palps, scale bar = 0.4 mm. D: Holotype, detail of antenna, scale bar = 0.5 mm.

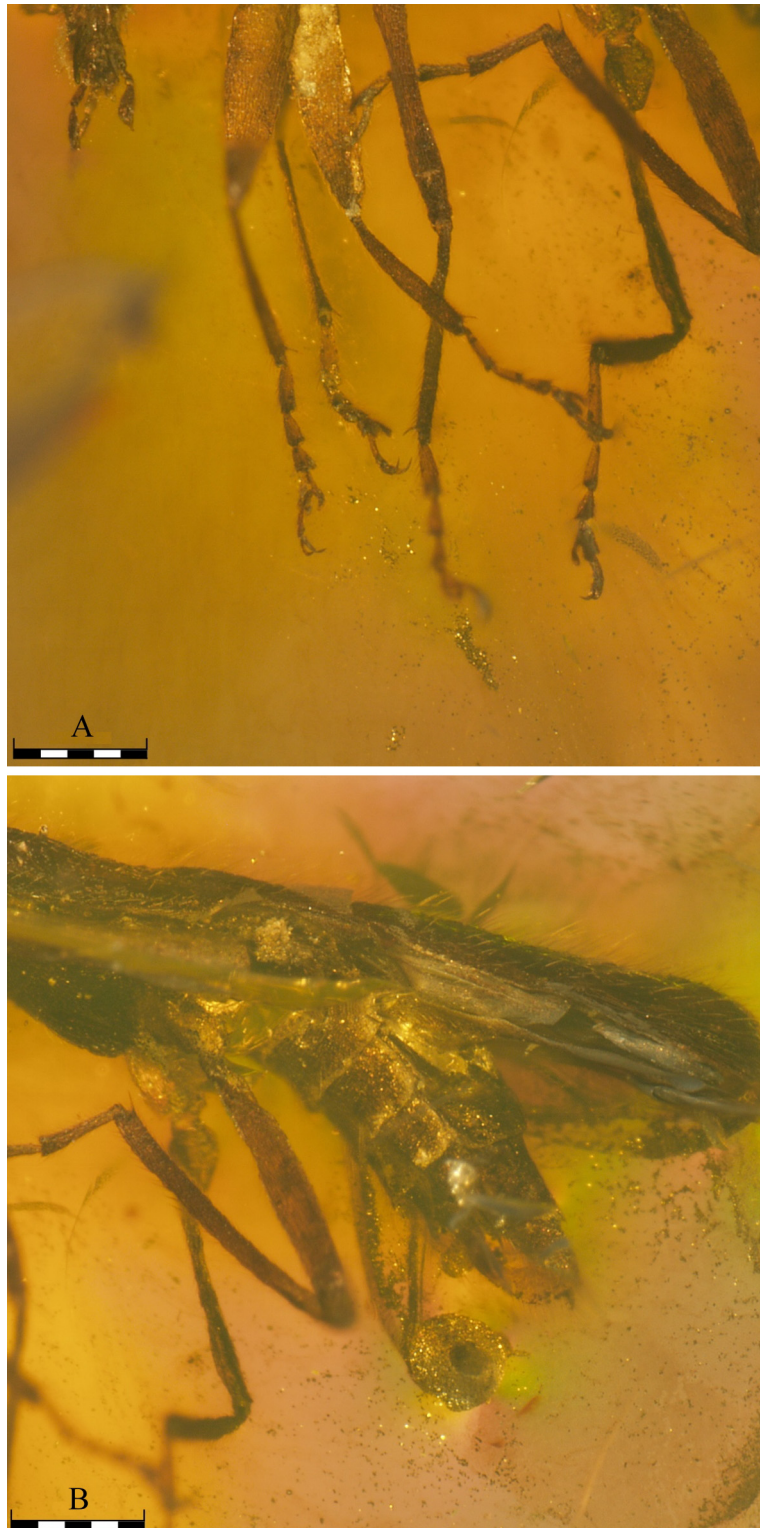


FIGURE 3. *Sucinorhagonycha samsockorum* sp. nov. in Baltic amber. A: Holotype, detail of legs, scale bar = 0.5 mm. B: Holotype, detail of last sternites, scale bar = 0.5 mm.

Type strata. Baltic amber, Upper Eocene, Prussian Formation (Priabonian). Estimated age: 37.8–33.9 Mya.

Syninclusions. Many wood remains and masses of plant fragments (detritus).

Differential diagnosis. Antennae with 12 antennomeres and the claws without lobes of the new species suggest that it belongs to the genus *Sucinorhagonycha*. (For more details, see the key below.) The genus is easily distinguishable from the fossils of the family Cantharidae Imhoff, 1856 with its 12-segmented antennae present

only in *Cacomorphocerus* Schaufuss, 1892 (for the differences, see Discussion section below) and the extant Australian genus *Heteromastix* Boheman, 1858 (Subfamily Dymorphocerinae Brancucci, 1980), which also sometimes has 12 antennal articles (Brancucci 1980; Fanti 2017c), with the antennomeres X–XI strongly modified (Brancucci 1980; Kuška 1996). Only one other species of *Sucinorhagonycha* has been described, *S. kulickae* Kuška, 1996, which is known on the basis of a male and a female found in different Baltic amber pieces (Kuška 1996; Kubisz 2000; Fanti 2017a). *Sucinorhagonycha samsokorum* **sp. nov.** differs from both sexes of *S. kulickae* because its antennal articles IV–V are slightly dentate (compared to filiform in *S. kulickae*), and because its pronotum is not transverse and has two evident central thickenings (while in *S. kulickae* the pronotum has a longitudinal central linear depression and protuberances on the sides). In addition, the male of *S. kulickae* has shorter antennomeres than *S. samsokorum* **sp. nov.**

Remarks. The yellow amber piece has a spherical shape measuring 15x14x11 mm and weighs 1.3 grams. The inclusion is complete and well visible.

Subfamily Malthininae Kiesenwetter, 1852

Tribe Malthodini Böving & Craighead, 1931

Genus *Malthodes* Kiesenwetter, 1852

Subgenus *Malthodes* Kiesenwetter, 1852

Malthodes (Malthodes) josephi* FANTI & M. K. PANKOWSKI **sp. nov.*

(Figs. 4–6)

Description. Adult, winged. Male, based on the last abdominal segments modified and the long antennae. Body length: 2.8 mm; elytra: 1.2 mm; antennae: 2.2 mm. Entirely dark brown including legs and antennae, without yellow spots on elytra. Head completely exposed, strongly rounded, larger than pronotum, equipped with shallow punctation. Eyes rounded, very large and prominent, inserted laterally to the head. Mandibles elongated, falciform, large at base and thin apically, concave on the internal side. Maxillary palps 4-segmented, unequal in length, with the terminal palpomere globular and distally pointed. Labial palps 3-segmented with the last segment globular and pointed. Antennae filiform, 11-segmented, long, surpassing the elytra, not reaching the last abdominal segments; antennomere I (scape) elongated, not club-shaped; antennomeres II–III filiform and approximately 1.4 times shorter than scape; antennomeres IV–X elongated, filiform, subequal in length, slightly longer than antennomeres II–III; antennomere XI thinner and longer than previous one, apically rounded; antennomeres with small setae. Pronotum large, transverse, surface undulating and with shallow punctation, posterior margin straight, anterior margin strongly bordered, sides sinuous, corners rounded. Scutellum triangular-shaped. Elytra wider than pronotum, short, slender, parallel-sided, reaching until the fifth abdominal segment, wide at base and narrower posteriorly to the humeral zone, apex rounded, surface pubescent. Posterior wings wide and long, dark, surpassing the elytra and the abdominal segments. Anterior and median legs very short, posterior legs long; coxae robust; trochanters elongated; femora enlarged; pro- and mesotibiae as long as pro- and mesofemora, metatibiae longer than metafemora, all the tibiae cylindrical and very thin. Tarsi 5-segmented; tarsomere I long and more of two times longer than second; tarsomere III slightly shorter than second; tarsomere IV bilobed; tarsomere V slender; claws simple. Penultimate tergite (tergite 9) elongated and slightly bent at sides; last tergite (tergite 10) short and wide with the sides bent, apically the margin is straight; last sternite (sternite 9) long and flat, large at base and curved after few millimeters, from which start two elongated and separated lobes with rounded apex; two wide and irregular with rounded apex urophysis, each inserted by the penultimate sternite (sternite 8) and located on both sides of the sternite 9. Sternal surface of abdomen punctate and with pubescence.

Etymology. Species named after Joseph M. Pankowski, paternal grandfather of the second author, who always puts his family first, is generous beyond words and who is a friend to all.

Holotype. Male, adult specimen included in Baltic amber, accession No. USNM PAL 712536 in the USNM.

Type locality. Yantarny settlement (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

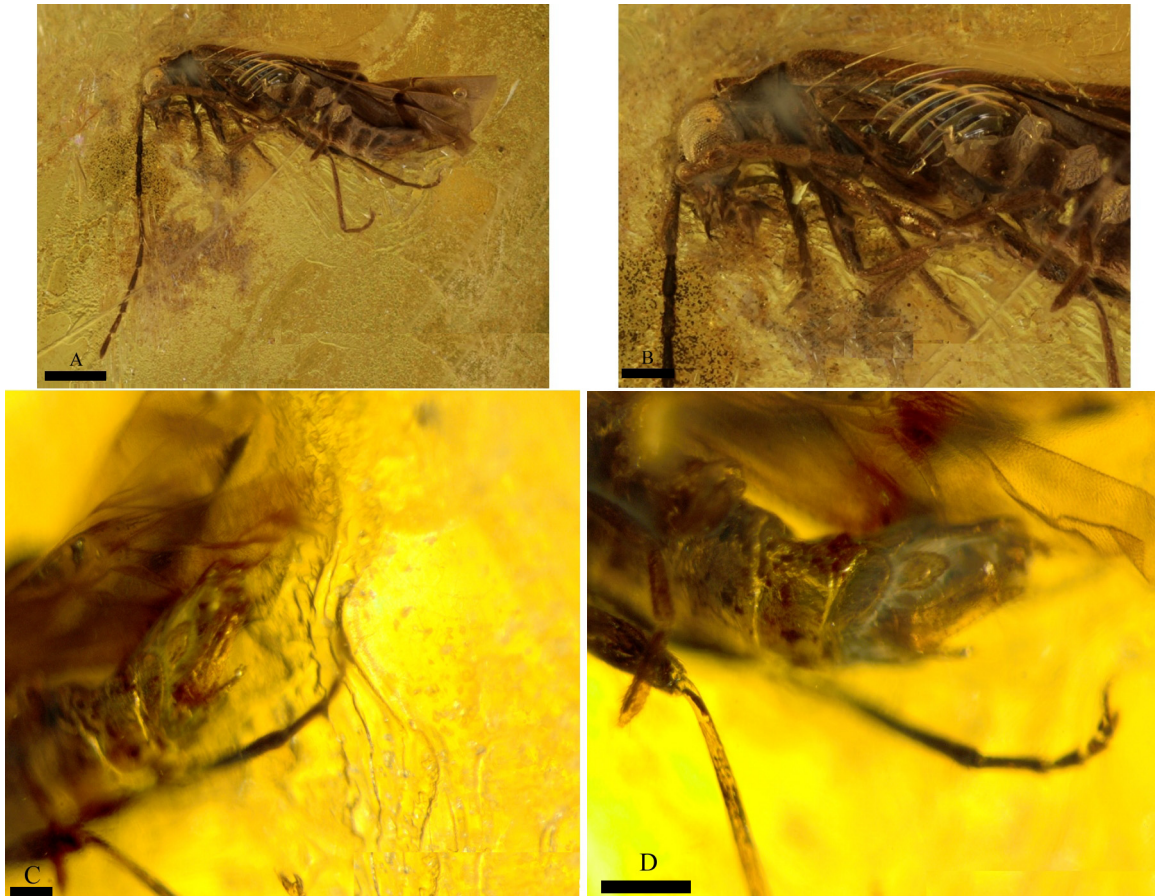


FIGURE 4. *Malthodes josephi* sp. nov. in Baltic amber. A: Holotype, lateral view, scale bar = 0.5 mm. B: Holotype, lateral view, scale bar = 0.1 mm. C: Holotype, detail of *terminalia*, scale bar = 0.1 mm. D: Holotype, detail of *terminalia*, scale bar = 0.2 mm.

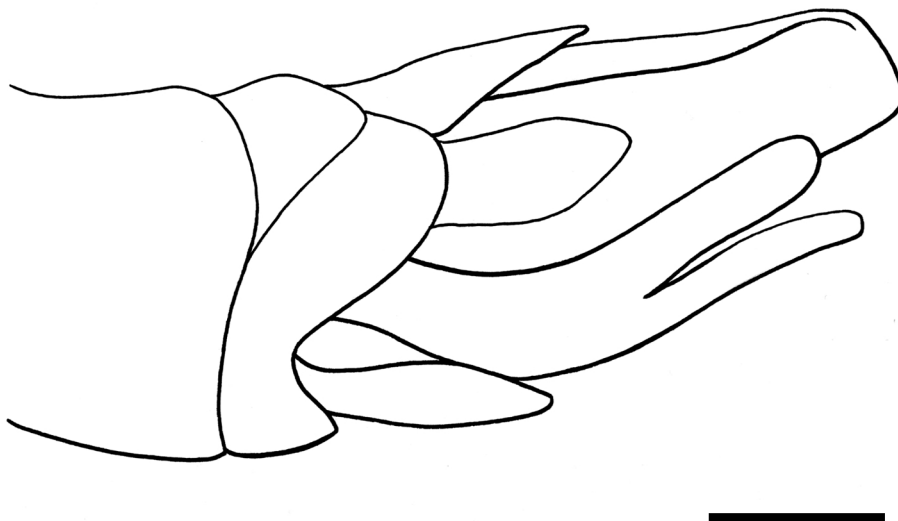


FIGURE 5. *Malthodes josephi* sp. nov. in Baltic amber. Line drawing of the last abdominal segments, scale bar = 0.1 mm.

Type strata. Baltic amber, Upper Eocene, Prussian Formation (Priabonian). Estimated age: 37.8–33.9 Mya.

Syninclusions. Wood remains and air bubbles.

Differential diagnosis. Characters such as the globular and pointed last palpomere, the short elytra and the strongly modified last abdominal segments (both tergites and sternites) suggest that the new species belongs to the genus *Malthodes*. No other fossil of *Malthodes* shows the same features of the *terminalia* of the new species (Fanti & Vitali 2017; Fanti & Michalski 2018), and no extant species of Central-North Europe and Alps is similar. Only the group of *M. alpicola* Kiesenwetter, 1852 (*M. alpicola*, *M. guttifer* Kiesenwetter, 1852, *M. spretus* Kiesenwetter, 1852, *M. bertolinii* Fiori, 1905) might be seen as similar, although not from a strictly anatomical point of view, because of the last sternite (sternite 9) that is shaped as a wide, apically forked membrane (Liberti 2011, 2015, 2016) and possessing a similar last tergite (tergite 10). However, these species are much bigger in size, and tendentially have a yellow spot (more or less evident) on each elytral apex. The group of *M. minimus* (Linnaeus, 1758) is only vaguely similar, with the last tergite lobe-shaped and little developed, and the last sternite without median membrane. The important diagnostic characters of *Malthodes* are based on the male's terminalia and habitus, as the morphology of the fossils is nearly identical to the living species. It is, however, interesting to note that, out of all the fossil species known, only *M. perkovskyi* Kazantsev from Rovno amber (Kazantsev 2010) has the elytra with two yellow spots apically (Förster 1891; Kuška & Kupryjanowicz 2005; Kuška & Kania 2010; Kazantsev & Perkovsky 2014; Fanti 2017b; Fanti & Vitali 2017; Fanti & Michalski 2018). These are indeed present, even if sometimes difficult to see, in many living species (Fender 1951; Wittmer 1970; Liberti 2011, 2015, 2016, 2017).

Remarks. The amber piece measures 28x22x10 mm, is rectangularly shaped and weighs 2.8 grams. The amber is opaque yellow and there are scratches on the surface.

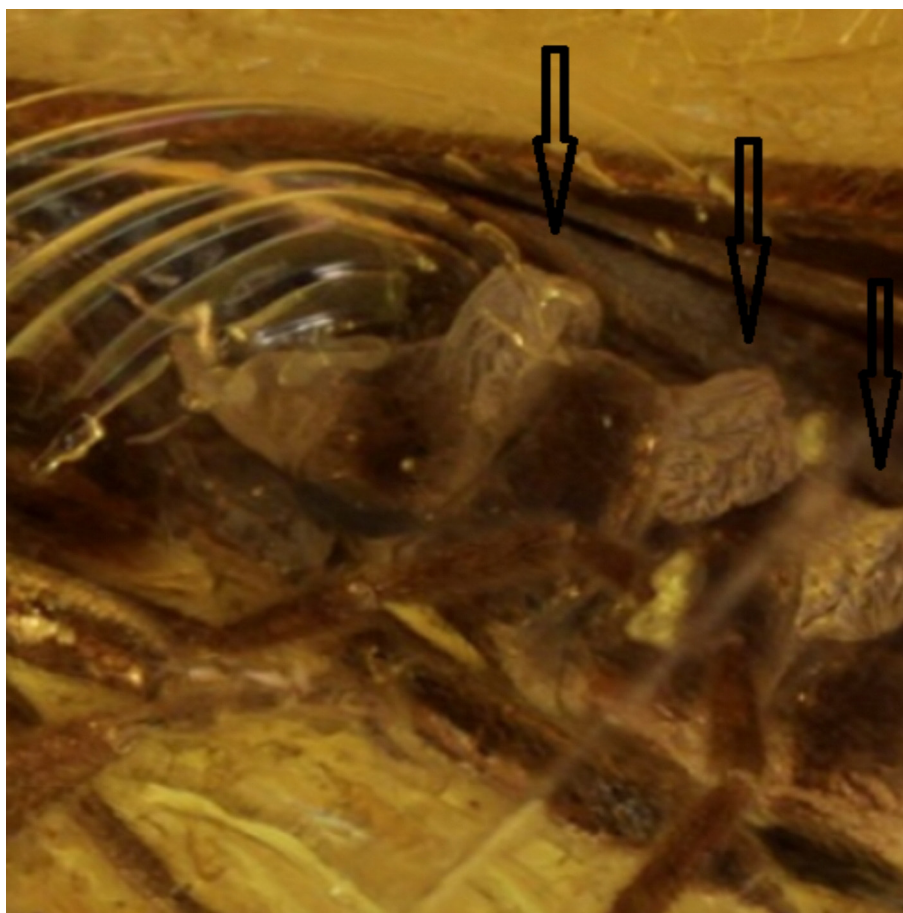


FIGURE 6. *Malthodes josephi* sp. nov. in Baltic amber. Arrows shows cuticular vesicles extruded from the abdominal segments.

Discussion

Genus *Rhagonycha* is common in amber but few species have been described due to their uniform habitus, while

many species of *Malthodes* have been described (Fanti 2017a, 2017b; Fanti & Vitali 2017, Fanti & Michalski 2018). *Malthodes josephi* **sp. nov.** shows at least three extruded cuticular vesicles, and there are probably others that are not visible. They are located in the lateral part of the first sternites, and are sub-quadrangle, large and appear gray and spongy. *M. josephi* **sp. nov.** may have used these vesicles for chemical defense. Many living soldier beetles have chemical compounds, such as diterpenes, alkaloids and acids with toxic properties (Fanti & Vitali 2017), that they use for defensive measures. Soldier beetles with these vesicles are also known from Cretaceous Burmese amber with an age of 99 Mya (Poinar *et al.* 2007; Poinar & Fanti 2016; Fanti *et al.* 2018). However, this is the first time these vesicles have been found in Eocene soldier beetles and in representatives (both extinct and extant) of the subfamily Malthininae. It is very interesting to find these vesicles in the genus *Malthodes* because the species are uniformly black-blackish (or at most with small yellow spots at the elytral apex) and do not show aposematic colorations like other living species from other genera that have these exudates (see *e.g.*, Moore & Brown 1978; Eisner *et al.* 1981; Durvaux *et al.* 2007). *Sucinorhagonycha samsokorum* **sp. nov.** shows interesting intermediate characteristic between both genera *Cacomorphocerus* and *Sucinorhagonycha*. At the first glance, the habitus of the two genera is extremely similar, with the same length of the elytra and the pronotum modified at the sides or on the surface. But *Sucinorhagonycha*, including *S. samsokorum* **sp. nov.**, has claws without lobes and denticles (an important systematic character), while *Cacomorphocerus* has claws fitted with a basal tooth, more or less visible. Both of these genera have antennae with 12 articles (a very rare character in extant species) instead of 11. Furthermore, the antennomeres of the two genera are slightly different. *Cacomorphocerus* possesses “central” antennomeres (III–IX) that are conspicuously saucer-shaped, while *Sucinorhagonycha* has filiform antennae (Schaufuss 1892; Kuška 1996; Kubisz 2000, Kuška & Kania 2010; Kazantsev 2013; Fanti 2017a). The central antennomeres of *S. samsokorum* **sp. nov.** are slightly dentate and widened (with other articles concave in the middle), making them rather similar to those of *Cacomorphocerus*. This would suggest an interesting diversification of the antennal shapes in these two genera and a relationship closer than previously thought. More study—and many more specimens—would be needed to better understand how they are related.

The following key summarizes differences:

- | | | |
|---|---|--|
| 1 | Antennae 12-segmented with all antennomeres filiform or with antennomeres IV–V slightly dentate and antennomeres III and VII modified, claws without basal lobes or denticles | <i>Sucinorhagonycha</i> Kuška, 1996 |
| - | Antennae 12-segmented with antennomeres III–IX saucer-shaped, claws with basal tooth more or less evident and obtuse. | <i>Cacomorphocerus</i> Schaufuss, 1892 |

Acknowledgements

We are indebted to Dale E. Greenwalt (National Museum of Natural History, Washington, D.C., USA) for helping us to measure and photograph the specimens, and Alessio Morelli (Pianella, Pescara, Italy) for the excellent drawing. We are also grateful to Gianfranco Liberti (Uboldo, Varese, Italy) and another anonymous reviewer for their excellent suggestions for improving this paper.

References

- Boheman, C.H. (1858–1859) Coleoptera. Species novas descripsit. In: Virgin, C. (Ed.), *Kongliga Svenska Fregatten Eugénies Resa omkring jorden under befäl af C.A. Virgin, Åren 1851–1853. Vetenskapliga iakttagelser på H.M. Konung Oscar den Förstes befallning utgifna af K. Svenska Vetenskaps Akademien. Andra delen. Zoologi. 1. Insecta*. P.A. Norstedt & Söner, Almqvist et Wiksells, Stockholm, pp. 1–217, pls. I–II. [issued in parts, pp. 1–112 in 1858, pp. 113–218 in 1859].
- Böving, A.G. & Craighead, F.C. (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana*, New Series, 11 (1–4), 1–80, 81–160, 161–256, 257–351, pls. 1–125. [(1): publ. 14 Nov. 1931; (2): 7 Dec.; (3): 9 Dec.; (4): 21 Dec. 1931 (wrappers)].
- Brancucci, M. (1980) Morphologie comparée, évolution et systématique des Cantharidae (Insecta: Coleoptera). *Entomologica Basiliensis*, 5, 215–388.
- Cai, C.-Y., Lü, L., Caron, E., Bortoluzzi, S., Newton, A.F., Thayer, M.K. & Huang, D.-Y. (2016) First Piesticine Rove Beetle in Eocene Baltic Amber (Coleoptera, Staphylinidae, Piesticinae). *Journal of the Kansas Entomological Society*, 89 (4), 345–357.

<https://doi.org/10.2317/0022-8567-89.4.345>

- Delkeskamp, K. (1977) *Coleopterorum Catalogus Supplementa. Pars 165. Fasc. 1. Cantharidae*. W. Junk, The Hague, 485 pp.
- Durvaux, C., Laurent, P., Daloze, D., Braekman, J.-C., Lupoli, R., Dimarcq, J.-L. & Pasteels, J. (2007) A new diterpene enone from the soldier beetle *Cantharis livida* (Coleoptera: Cantharidae). *Arkivoc*, 10, 5–9.
- Eisner, T., Hill, D., Goetz, M., Jain, S., Alsop, D., Camazine, S. & Meinwald, J. (1981) Antifeedant action of Z-dihydromatricaria acid from soldier beetles (*Chauliognathus* SPP.). *Journal of Chemical Ecology*, 7 (6), 1149–1158.
<https://doi.org/10.1007/BF00987634>
- Eschscholtz, J.F.G. von (1830) Nova genera Coleopterorum Faunae Europaeae. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 2 (1), 63–66.
- Fanti, F. (2017a) Catalogo Cantharidae fossili del mondo. *Fossils & Minerals Review*, 2, 1–18 [abbreviated Italian version. Available: 12 March 2017/World catalog of fossil Cantharidae. *Fossils & Minerals Review*, 2 (Special Issue), 1–52, extended English version, available: 25 May 2017].
- Fanti, F. (2017b) *Malthodes michalskii*: a new species of Cantharidae from Baltic amber (Coleoptera). *Giornale italiano di Entomologia*, 14 (62), 685–690.
- Fanti, F. (2017c) New fossil Cantharidae genus and species from Baltic amber (Insecta Coleoptera). *Giornale italiano di Entomologia*, 14 (62), 709–714.
- Fanti, F. & Castiglione, E. (2017) Description of a new genus and species of Cantharidae from Eocene Baltic amber (Insecta, Coleoptera). *Palaeodiversity*, 10, 123–127.
<https://doi.org/10.18476/pale.v10.a8>
- Fanti, F., Damgaard, A.L. & Ellenberger, S. (2018) Two new genera of Cantharidae from Burmese amber of the Hukawng Valley (Insecta, Coleoptera). *Cretaceous Research*, 86, 170–177.
<https://doi.org/10.1016/j.cretres.2018.02.015>
- Fanti, F. & Kupryjanowicz, J. (2017) A new soldier beetle from Eocene Baltic amber. *Acta Palaeontologica Polonica*, 62 (4), 785–788.
- Fanti, F. & Michalski, A.R. (2018) An unusual fossil *Malthodes* with long elytra (Insecta Coleoptera Cantharidae). *Giornale italiano di Entomologia*, 15 (63), 127–132.
- 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. & Vitali, F. (2017) Key to fossil Malthininae, with description of two new species in Baltic amber (Coleoptera Cantharidae). *Baltic Journal of Coleopterology*, 17 (1), 19–27.
- Fender, K.M. (1951) The Malthini of North America (Coleoptera—Cantharidae). *The American Midland Naturalist*, 46 (3), 513–629.
<https://doi.org/10.2307/2421804>
- Fiori, A. (1905) Revisione delle specie italiane a me note del genere *Malthodes* Kiesw. *Rivista Coleopterologica Italiana*, 3 (12), 221–252, 2 tabs.
- 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 Spezialkarte von Elsass-Lothringen*, 3 (5), 335–593 + [1], 6 pls. (+ 6), + [1].
- Gorham, H.S. (1881) Malacodermata. Fam. Telephoridae. In: Godman, F.D. & Salvin, O. (Eds.), *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. III. Part 2 [1880–1886]*. Taylor and Francis, London, pp. 65–106, supplement and tabs.
- Hentz, N.M. (1830) Remarks on the use of the Maxillae in Coleopterous Insects, with an Account of two Species of the Family Telephoridae, and of three of the Family Mordellidae, which ought to be the Type of two distinct Genera. *Transactions of the American Philosophical Society, New Series*, 3, 458–463, 1 pl.
- Imhoff, L. (1856) *Versuch einer Einführung in das Studium der Koleoptern. In zwei Theilen und einem, 25 Tafeln lithographirter Abbildungen nebst Text enthaltenden, Anhänge. Auf Kosten des Verfassers*. Schweighauser, Basel, xxxi + [2] + 1–114 + [2] + 272 pp., 25 pls.
- Kazantsev, S.V. (2010) New *Malthodes* (Insecta: Cantharidae: Coleoptera) from the Rovno Amber (Upper Eocene of Ukraine). *Russian Entomological Journal*, 19 (2), 105–107.
- Kazantsev, S.V. (2013) New taxa of Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae) with synonymic and taxonomic notes. *Russian Entomological Journal*, 22 (4), 283–291.
- 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.
- Kiesenwetter, E.A.H. von (1852) Beiträge zu einer Monographie der Malthinen. *Linnaea entomologica*, 7, 239–324, tabs. 1–2.
- Kiesenwetter, E.A.H. von (1863) *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Vierter Band*. Nicolaische Verlagsbuchhandlung, Berlin, vi + 745 + [1] pp. [issued in parts, pp. 1–178 in 1857; pp. 179–386 in 1858; pp. 387–570 in 1860; pp. 571–745 + [1] in 1863].

- Kosmowska-Ceranowicz, B. (2008) Glowing stone: Amber in Polish deposits and collections. *Przegląd Geologiczny*, 56 (8/1), 604–610, figs. 17–19 (pp. 574).
- 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.
- Kuśka, A. (1996) New beetle species (Coleoptera: Cantharidae, Curculionidae) from the Baltic amber. *Prace Muzeum Ziemi*, 44, 13–18.
- Kuśka, A. & Kania, I. (2010) New soldier beetles (Coleoptera, Cantharidae) from the Eocene Baltic amber. *Zootaxa*, 2400, 49–56.
- Kuśka, A. & Kupryjanowicz, J. (2005) Soldier beetles (Coleoptera: Cantharidae) from Baltic amber. *Polskie Pismo Entomologiczne*, 74, 309–316.
- Liberti, G. (2011) Le specie di *Malthodes* Kiesenwetter, 1852 delle Alpi Marittime e Liguri (Coleoptera, Cantharidae). *Annali del Museo Civico di Storia Naturale "G. Doria"*, Genova, 103, 147–246.
- Liberti, G. (2015) Le specie di *Malthodes* Kiesenwetter, 1852 d'Italia nord-occidentale (Coleoptera, Cantharidae) (*Malthodes* di Lombardia: 2° contributo alla conoscenza dei *Malthodes* italiani). *Annali del Museo Civico di Storia Naturale "G. Doria"*, Genova, 107, 1–151.
- Liberti, G. (2016) Le specie di *Malthodes* Kiesenwetter, 1852 delle Alpi (Coleoptera, Cantharidae) (*Malthodes* del Nord-Est: 3° contributo alla conoscenza del genere *Malthodes* in Italia). *Annali del Museo Civico di Storia Naturale "G. Doria"*, Genova, 108, 89–198.
- Liberti, G. (2017) Le specie appenniniche di *Malthodes* Kiesenwetter, 1852 (Coleoptera, Cantharidae) (*Malthodes* d'Italia peninsulare: 4° contributo alla conoscenza del genere *Malthodes* in Italia). *Annali del Museo Civico di Storia Naturale "G. Doria"*, Genova, 110, 33–164.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Laurentii Salvii, Holmiae, 823 pp.
- Moore, B.P. & Brown, W.V. (1978) Precocinelline and related alkaloids in the Australian soldier beetle, *Chauliognathus pulchellus* (Coleoptera: Cantharidae). *Insect Biochemistry*, 8 (5), 393–395.
[https://doi.org/10.1016/0020-1790\(78\)90027-6](https://doi.org/10.1016/0020-1790(78)90027-6)
- Motschulsky, V. de (1858) Entomologie spéciale. Insectes du Japon. *Etudes Entomologiques*, 6, 25–41, 1 pl. [1857]
- Pérez-Hernández, C.X. (2018) Natural History and Ecology of Soldier Beetles (Coleoptera: Cantharidae) in the Mexican Tropical Dry Forests. *Environmental Entomology*, 47 (3), 535–544.
<https://doi.org/10.1093/ee/nvy012>
- Poinar, G.O. Jr. & Fanti, F. (2016) New fossil soldier beetles (Coleoptera: Cantharidae) in Burmese, Baltic and Dominican amber. *Palaeodiversity*, 9, 1–17.
<https://doi.org/10.18476/pale.v9.a1>
- Poinar, G.O. Jr., Marshall, C.J. & Buckley, R. (2007) One Hundred Million Years of Chemical Warfare by Insects. *Journal of Chemical Ecology*, 33, 1663–1669.
<https://doi.org/10.1007/s10886-007-9343-9>
- Ramsdale, A.S. (2002) Family 64. Cantharidae Imhoff 1856. In: Arnett, R.H. Jr., Thomas, M.C., Skelley, P.E. & Frank, J.H. (Eds.), *American Beetles. Vol. 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, pp. 202–218.
- Schaufuss, C.F.C. (1892) Preussens Bernstein-Käfer. Neue Formen aus der Helm'schen Sammlung im Danziger Provinzialmuseum. *Berliner Entomologische Zeitschrift*, 36 (1), 53–64. [1891]
- Wittmer, W. (1970) Zur Kenntnis der Gattung *Malthodes* Kies. (Col., Cantharidae) (48. Beitrag zur Kenntnis der palaearktischen Cantharidae). *Entomologische Arbeiten aus dem Museum G. Frey*, 21, 13–107.
- Wittmer, W. (1979) 4. Tribus: Malthinini. In: Freude, H., Harde, K.W. & Lohse, G.A. (Eds.), *Die Käfer Mitteleuropas. Band 6. Diversicornia*. Goecke & Evers, Krefeld, pp. 40–51.
- Wolfe, A.P., Tappert, R., Muehlenbachs, K., Boudreau, M., Mckellar, R.C., Basinger, J.F. & Garrett, A. (2009) A new proposal concerning the botanical origin of Baltic amber. *Proceedings of the Royal Society of London Series B - Biological Sciences*, 276 (1672), 3403–3412.
<https://doi.org/10.1098/rspb.2009.0806>
- Yablokov-Khnzorian, S.M. (1960) New beetles from the Baltic amber. *Paleontologicheskii Zhurnal*, 3, 90–101. [in Russian, title: Novye zhestkokrylye iz Baltijskogo yantarya]