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Two new species of soldier beetles (Coleoptera: Cantharidae) from Eocene Baltic amber, including one with a rare type of antennae

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Abstract

Two new species of the family Cantharidae from Baltic amber are described and illustrated: *Sucinorhagonycha fabrizioi* **sp. nov.** (Cantharinae, Cacomorphocerini) and *Cantharis* (*Cantharis*) *samsocki* **sp. nov.** (Cantharinae, Cantharini). The former is particularly notable because it has 12 antennomeres, a characteristic that is relatively rare among the world's extant beetles, particularly in soldier beetles. This fascinating characteristic and why it may have evolved are explored here.

Keywords: palaeoentomology, antennomeres, new taxon, fossilized resin

Introduction

Commonly known as soldier beetles, Cantharidae are frequently found as amber inclusions (Spahr, 1981; Alekseev, 2013, 2017; Fanti, 2017a). An extensive variety of species have been described from Agdzhakend, Baltic, Bitterfeld, Burmese, Dominican, Mexican (Chiapas), Rovno, Spanish and Sakhalinian ambers (Wittmer, 1963; Fanti, 2019; Fanti & Damgaard, 2019; Kazantsev & Perkovsky, 2019; Pankowski & Fanti, 2023). Soldier beetles are particularly well known from Baltic amber, with the first fossil taxon of Cantharidae described from this amber in 1892 (Schaufuss, 1892; Kazantsev, 2021). Since then, more than 90 species of Cantharidae from three subfamilies, Cantharinae, Silinae and Malthininae, have been described from Baltic amber (Kazantsev, 2013, 2021; Fanti, 2017a). This fossilized resin comes from the world's largest amber deposit and was formed primarily during the Priabonian of the Eocene (Bukejs *et al*., 2019). Ten genera of soldier beetles found in this prolific amber have living species, including *Cantharis* Linnaeus, 1758 (Coleoptera, Cantharidae) (Kazantsev, 2013; Fanti, 2017a, b; Fanti & Damgaard, 2018; Fanti & M.J. Pankowski, 2018; Fanti & M.K. Pankowski, 2018). This genus has been found only relatively recently in amber, with subsequent discoveries coming in the following years (Fanti, 2017a; Kazantsev, 2018; Fanti & Damgaard, 2019; Fanti & Pankowski, 2020). Prior to this paper, 10 species of *Cantharis* were known from Baltic amber (Fanti, 2017a; Fanti & Pankowski, 2020) and one from Eocene Rovno amber from Ukraine (Fanti & Pankowski, 2023). In addition, two species have been described from Oligocene compression fossils in Enspel, Germany (Fanti & Poschmann, 2019), seven from the Oligocene of Rott, Germany (Heyden & Heyden, 1866; Fanti, 2017a; Fanti & Walker, 2019), two species from the Miocene of Oeningen, Germany, and one species from the Miocene of Radoboj, Croatia (Heer, 1847, 1865; Fanti, 2017a; Fanti & Pankowski, 2023).

Sixteen genera of Cantharidae known from Baltic amber have no living representatives (Kazantsev, 2013; Fanti, 2017a, b; Fanti & Damgaard, 2018; Fanti & M.J. Pankowski, 2018; Fanti & M.K. Pankowski, 2018). These extinct genera include *Sucinorhagonycha* Kuśka, 1996, known from four species in Baltic amber (Kuśka, 1996; Kubisz, 2000; Fanti & M.K. Pankowski, 2018; Kazantsev, 2020; Pankowski & Fanti, 2023) prior to this paper. This genus is characterized by antennae with 12 antennomeres, a feature that is infrequently observed in the world's extant beetles (Nunes *et al*., 2020), particularly among Cantharidae.

Material and methods

Two Baltic amber pieces, each containing one Cantharidae species, were studied. Both pieces came from an amber mine near the village of Yantarny in the Sambian Peninsula, Kaliningrad Region, Russia. They were purchased by the author from online amber dealers and donated to the Smithsonian National Museum of Natural

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History (USNM) in Washington, DC. The pieces were cut and polished to provide a better view of each of the inclusions. The photographs of the *Cantharis* were taken by Marius Veta (Palanga, Lithuania) using a Canon EOS camera on bellows and a macro lens and processed using Zerene Stacker focus stacking software. The photographs of the *Sucinorhagonycha* were taken by Aleksej Damzen (Vilnius, Lithuania) with a Canon EOS 90D camera and Canon MP-E 65mm macro lens and processed using Helicon Focus stacking software. Plates were processed using Ulead PhotoImpact Viewer SE software. Both holotypes are preserved in the Smithsonian National Museum of Natural History.

Systematic palaeontology

Family Cantharidae Imhoff, 1856
Subfamily Cantharinae Imhoff, 1856
Tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018
Genus *Sucinorhagonycha* Kuśka, 1996

***Sucinorhagonycha fabrizioi* sp. nov.**
(Fig. 1)

Holotype. Male, inclusion in Baltic amber. The yellow amber piece measures 37 × 6 × 4 mm. The inclusion is complete and well visible in dorsolateral view. Housed at the Smithsonian National Museum of Natural History (USNM). USNM PAL 787829.

Syninclusions: Air bubbles and botanical remains.

Etymology. Species named in honor of Fabrizio Fanti, a trusted friend, esteemed colleague and respected expert on Cantharidae.

Diagnosis. The specimen can be recognized as a new species based on its pronotum that is slightly longer than wide, whereas it is strongly transverse in *Sucinorhagonycha maryae* M.G. Pankowski & Fanti, 2023 and *S. kulickae* Kuśka, 1996. The new species also has a very raised anterior margin and slightly raised area in the middle, compared with *S. samsockorum* Fanti & M. K. Pankowski, 2018 that has a large and very raised area in the middle and flat margins (Kuśka, 1996; Fanti & M.K. Pankowski, 2018; Pankowski & Fanti, 2023). Furthermore, the new species differs from *S. groehni* Kazantsev, 2020 because the latter species has a different pronotum with the anterior margin less raised, central area flat and posterior part bulged (Kazantsev, 2020).

Locality and horizon. Amber mine near 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. Adult, hind wing developed, elongated. Male, defined on the basis of the last sternite small, narrow and triangular-shaped. Body length: 4.1 mm.

Head rounded, prognathous, short, convex, not completely exposed, slightly wrinkled with shallow punctation and short setae. Eyes rounded, convex, inserted dorsolaterally and near sides of head. Mandibles relatively stout, elongated, strongly curved and falciform, apparently without teeth or denticles. Maxillary palps 4-segmented and unequal in length to one another; last palpomere strongly securiform, almost triangular, conspicuously widened in distal third. Labial palps 3-segmented; last segment elongated, globular in middle, very slightly securiform, with apex thinner and rounded. Antennae with 12 antennomeres, filiform, inserted dorsally and between eyes, not particularly long, slightly surpassing half the length of elytra, all segments pubescent with setae short and long; antennomere I (scape) elongated, club-shaped, noticeably thinner at base; antennomere II short, about 2.0 times shorter than scape, globular and only slightly elongated; antennomere III longer than second antennomere; antennomeres IV–XI subequal, longer than previous one; antennomere XII elongated, about as long as scape, slightly rounded apically. Pronotum very slightly wider than head, anterior margin strongly raised and slightly bordered, posterior margin straight, sides almost straight, corners rounded, surface with shallow punctation and short and sparse pubescence, surface with an evident bulged area shortly after the middle of pronotum. Scutellar shield triangular-shaped with rounded apex. Elytra very elongated, slender, parallel-sided, surpassing the last abdominal segments, wider than pronotum, apex rounded, surface very slightly granulose and equipped with long and erect setae. Hind wings transparent, slightly longer than elytra. Metaventrite elongated, slender, very slightly punctate-rugose, posteriorly very slightly rounded; sternites transverse, short and pubescent; last tergite wide, elongated, rounded apically; last sternite small, narrow, rounded at apex, triangular-shaped. Aedeagus not visible. Legs relatively long, strongly pubescent; coxae very massive, slightly enlarged in middle, very elongated; trochanters slightly elongated, small, rounded apically; femora subcylindrical, almost straight; pro- and mesotibiae shorter than pro- and mesofemora, cylindrical, thin, with at least a spur apically; metatibiae very slightly longer than metafemora. Tarsi 5-segmented; first tarsomere elongated, robust, about 1.3 times longer than second; third tarsomere shorter than second, triangular-shaped and very slightly enlarged at sides; fourth tarsomere bilobed at sides with the lobes not particularly long, curved and rounded at apex; fifth tarsomere elongated, thin; claws simple, very robust at base and very thin apically, long and without lobes or denticles. Female unknown.

Remarks. Based on the last maxillary palps being

FIGURE 1. *Sucinorhagonycha fabrizioi* **sp. nov.** in Baltic amber (USNM PAL 787829). **A**, Holotype, dorsal view. **B**, **C**, Holotype, lateral views.

securiform, elytra comparatively long, antennae filiform, 12-segmented, and claws simple without teeth, the new species belongs in the genus *Sucinorhagonycha* (Kuśka, 1996; Kubisz, 2000; Pankowski & Fanti, 2023).

Family Cantharidae Imhoff, 1856
Subfamily Cantharinae Imhoff, 1856
Tribe Cantharini Imhoff, 1856
Genus *Cantharis* Linnaeus, 1758

***Cantharis* (*Cantharis*) *samsocki* sp. nov.**
(Fig. 2)

Holotype. Female, inclusion in Baltic amber. The yellow amber piece measures 18 × 6 × 3 mm. The inclusion is complete and well visible in dorsolateral view. Housed at the Smithsonian National Museum of Natural History (USNM). USNM PAL 787830.

Syninclusions: Air bubbles, botanical remains, stellate hairs, fungus gnat and a true midge.

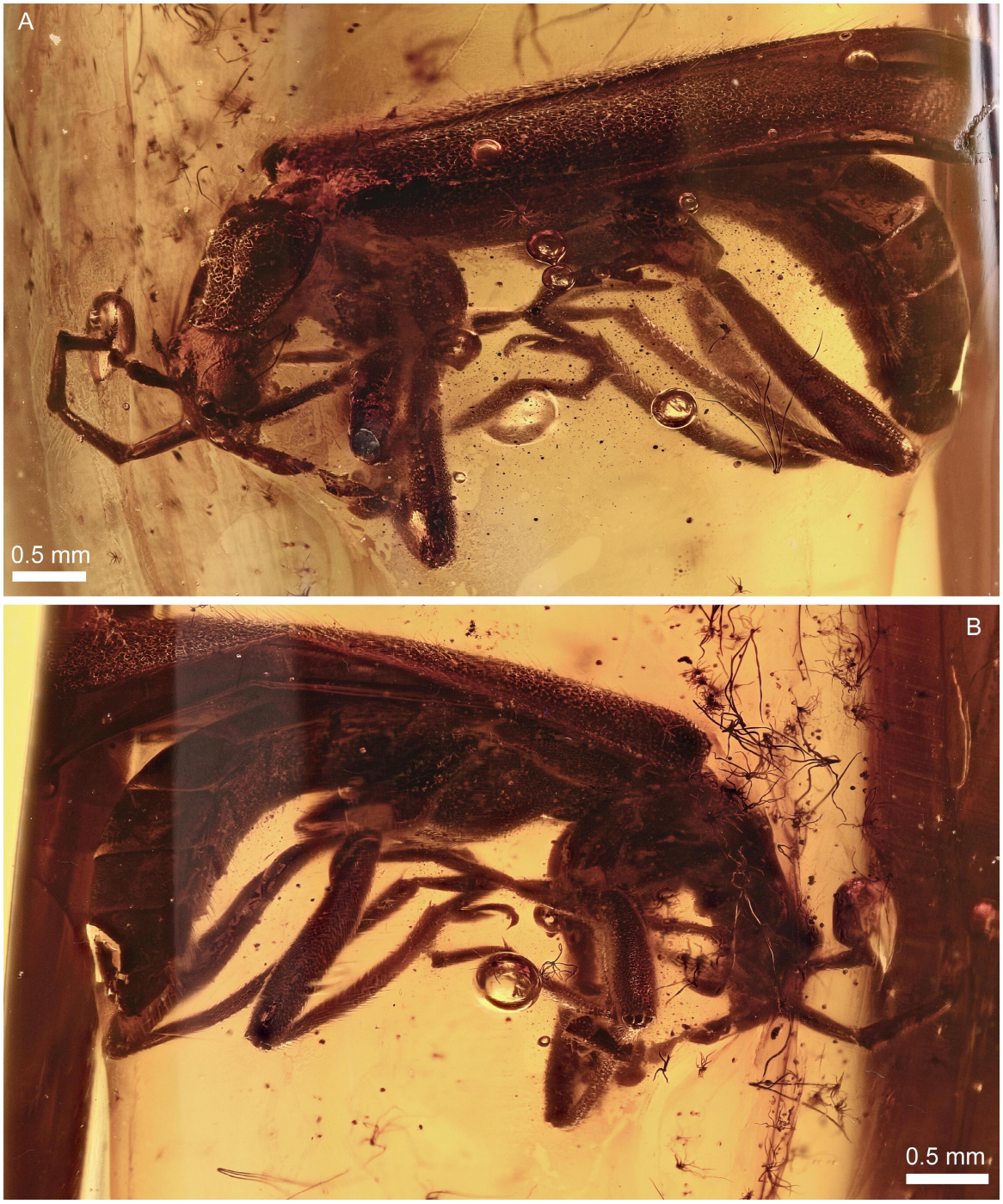

FIGURE 2. *Cantharis (Cantharis) samsocki* **sp. nov.** in Baltic amber (USNM PAL 787830). **A**, Holotype, dorso-lateral view. **B**, Holotype, lateral view.

Etymology. Species named in honor of Frank J. Samsock, grandfather of the author, retired firefighter, and hero.

Diagnosis. Based on its size, claws with a basal tooth and its pronotal shape, the new species appears most similar to *Cantharis raeorum* Fanti & M.G. Pankowski, 2020 from Baltic amber (Fanti & Pankowski, 2020). However, the new species differs based on its pronotum with sides narrower anteriorly (straight in *C. raeorum*) and surface bulged in the posterior part (fairly flat in *C. raeorum*).

Locality and horizon. Amber mine near 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. Adult, winged. Female, based on rounded shape of last sternite and tergite. Body entirely dark brown. Body length: about 6.0 mm.

Head rounded, wide, short, slightly covered by pronotum, wrinkled and equipped with long setae. Eyes relatively large, convex, prominent, inserted in the upper-lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented and unequal in length to one another; last palpomere strongly securiform, very elongated, thinner at base. Labial palps 3-segmented; last segment elongated, securiform. Antennae 11-segmented, filiform, inserted dorsally and between eyes, relatively short, slightly surpassing half of elytra and half of abdomen, all segments pubescent adorned with fitted setae; antennomere I (scape) elongated, curved, club-shaped, thinner at base; antennomere II very short, globular, about 3.1 times shorter than scape; antennomere III elongated, about 1.2 times shorter than scape; antennomeres IV–V subequal, longer than previous one; antennomeres VI–IX subequal, extremely long (the longest); antennomere X slightly shorter than previous ones; antennomere XI elongated, slender, rounded apically. Pronotum very slightly longer than wide, larger at base, approximately as large as head, anterior margin very slightly rounded and slightly bordered, posterior margin almost straight and slightly bordered, sides rounded and narrower anteriorly, corners rounded, surface wrinkled, equipped with scattered short setae and noticeably bulged in the posterior part. Scutellar shield triangular-shaped with rounded apex. Elytra elongated, slender, parallel-sided, covering last abdominal segments, wider than pronotum, apex rounded, wrinkled and equipped with several long setae, suture and sides bordered. Hind wings slightly infuscate, totally covered by elytra. Metaventrite elongated, rectangular, punctate, bulged, equipped with short setae, posteriorly rounded; sternites transverse, very robust and pubescent; last tergite short, slightly protruded in the middle of margin, rounded apically; last sternite smaller than last tergite, strongly rounded with a very small and obtuse point in the middle of margin. Legs relatively long, strongly pubescent; coxae very massive, elongated; trochanters small, elongated, rounded apically; femora subcylindrical, enlarged from the middle to apex, slightly concave and curved in the middle of margin; pro- and mesotibiae shorter than pro- and mesofemora; metatibiae very slightly longer than metafemora. Tarsi 5-segmented, equipped with long setae; first tarsomere extremely elongated, rather thin; second tarsomere elongated, shorter than first; third tarsomere shorter than second; fourth tarsomere bilobed at sides with lobes extremely long, not curved and pointed and very thin at apex; fifth tarsomere very elongated, thin, curved; claws simple, very robust at base and very thin and pointed apically, with very small and obtuse denticle at base. Male unknown.

Remarks. Based on the filiform antennae with 11 antennomeres, securiform last maxillary palpomere, pronotum lacking lateral lobes or teeth, the claws simple with a basal obtuse tooth, and the third bilobed tarsomere, the new species is placed in the genus *Cantharis* (Brancucci, 1980; Constantin, 2014).

Discussion

The genus *Cantharis* today is known widely across the Nearctic, Oriental and Palaearctic regions, with more than 350 extant and extinct species documented (Delkeskamp, 1977; Ramsdale, 2002; Kazantsev & Brancucci, 2007; Fanti & Damgaard, 2019; Fanti & Pankowski, 2020). They are found in meadows and on trees and shrubs. As larvae, they are known to prey on earthworms, soft-tissue insects and snails; adults feed on invertebrates as well as pollen and nectar (Traugott, 2003). The genus is characterized by a medium- to large-sized body (as compared to other Cantharidae), feature aposematic coloration of black and red or black and yellow-orange (Fanti & Pankowski, 2020) and possess 11 antennomeres on each antenna.

In contrast, the extinct genus *Sucinorhagonycha* has 12 antennomeres, a relatively rare feature in Coleoptera, especially among soldier beetles. The genus is a member of the Cacomorphocerini, a tribe characterized by having 11–19 antennomeres (Fanti & Pankowski, 2020). Fanti & Kupryjanowicz (2018) established this tribe with two genera, *Cacomorphocerus* Schaufuss, 1892 and *Sucinocantharis* Kuśka & Kania, 2010, characterized in part by strongly modified antennae with 12 to 16 antennomeres. The tribe was revised with the discoveries (Fanti & Damgaard, 2018) of similar genera with 17 and 19 antennomeres, and a species of *Cacomorphocerus* with 11 antennomeres (Poinar & Fanti, 2019; Kazantsev & Perkovsky, 2020; Fanti & Pankowski, 2020). It is likely that the first members of the Cacomorphocerini possessed 11 antennomeres, although there is always the possibility that the tribe is polyphyletic (Poinar & Fanti, 2019). Because its species have been found only in Baltic and Rovno ambers, the tribe appears to have evolved and gone extinct in the Eocene (Bukejs *et al*.). That seems to indicate that the ancestors of this tribe evolved in Laurasia, very possibly in what is now Europe (Fanti & Pankowski, 2020).

It is not clear what exact factors led the Cacomorphocerini to evolve supernumerary antennomeres. The overwhelming majority of beetle families have antennae with 11 segments, even though their morphologies, localities and habitats differ widely, and many of these species are monomorphic for this characteristic (Beutel & Haas, 2000; Nunes *et al*., 2020). However, there are some interesting exceptions among Coleoptera. For example, among Elateridae, species with

12 antennomeres have been described in some genera of Agrypninae, Elaterinae, and Pityobiinae (Kundrata *et al*., 2020). In Brachypsectridae, the feature has been found in the genus *Asiopsectra* (Kovalev & Kirejtshuk, 2016) and in all 12 known genera of Rhagophthalmidae (Kundrata *et al*., 2022). The firefly family Lampyridae—a family related to soldier beetles—has the largest range of antennomere numbers (7 to 62) among extant beetles, despite having only about 2,500 species in approximately 140 genera (Ferreira *et al*., 2020; Nunes *et al*., 2020). Based on their research, Nunes *et al*. (2020) believe the nine firefly genera with antennomere numbers different from 11 (with 11 being the presumed ancestral condition of Lampyridae) likely represent several independent evolutionary transitions. Among taxa of the genus *Amydetes* Illiger, 1807, which have the largest span of antennomere numbers (24 to 62), larger-sized species tend to have more antennomeres (Nunes *et al*., 2020). Interestingly, the correlation is negatively allometric: The antennomere numbers increase at a smaller rate compared to body size (Nunes *et al*., 2020). Based on their findings, researchers have concluded that sexual selection is probably the ultimate driver of increased antennal surface (Elgar *et al*., 2019; Nunes *et al*., 2020). This larger antennal surface would help males searching for females, especially if the females produce intermittent or tiny amounts of pheromones (Greenfield, 1981; Elgar *et al*., 2019; Nunes *et al*., 2020). However, several firefly species that primarily use pheromones to find mates (because they lack bioluminescence to communicate) have antennae with extra or more elongated branches, instead of more segments, to add antennal surface area (Nunes *et al*., 2020). Therefore, sexual selection cannot be the sole explanation for why supernumerary antennomeres evolved (Nunes *et al*., 2020). These findings could shine a light on the diversity of antennomeres in Cacomorphocerini as well. Sexual selection almost certainly played a role in this extinct tribe evolving supernumerary antennomeres. However, more specimens will need to be discovered to determine what factors shaped these variations.

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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

Beutel, R.G. & Haas, F. (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, 16, 103–141. https://doi.org/10.1111/j.1096-0031.2000.tb00350.x

Brancucci, M. (1980) Morphologie comparée, évolution et systématique des Cantharidae (Insecta: Coleoptera). *Entomologica Basiliensia*, 5, 215–388.

Bukejs, A., Fanti, F. & McKellar, R.C. (2019) A new species of *Cacomorphocerus* Schaufuss, 1892 (Coleoptera: Cantharidae) from Baltic amber with a key to known species. *Palaeontologia Electronica*, 22.2.28A, 1–7. https://doi.org/10.26879/903

Constantin, R. (2014) Observations sur des Cantharidae de France et description de deux espèces nouvelles (Coleoptera, Elateroidea). *Bulletin de la Société entomologique de France*, 119 (1), 91–108. https://doi.org/10.3406/bsef.2014.2570

Delkeskamp, K. (1977) *Coleopterorum Catalogus Supplementa.* Pars 165. Fasc. I. Cantharidae. W. Junk, The Hague, 485 pp.

Elgar, M.A., Johnson, T.L. & Symonds, M.R. (2019) Sexual selection and organs of sense: Darwin's neglected insight. *Animal Biology*, 69, 63–82. https://doi.org/10.1163/15707563-00001046

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. (2019) First fossil soldier beetles (Coleoptera Cantharidae) from Bitterfeld amber, Germany. *Zitteliana*, 93, 89–96.

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. & Damgaard, A.L. (2019) New soldier beetles (Cantharidae) from Baltic, Burmese and Dominican ambers of the Anders Damgaard amber collection. *Baltic Journal of Coleopterology*, 19 (2), 101–125.

Fanti, F. & Kupryjanowicz, J. (2018) Discovery of a new fossil soldier beetle in Eocene Baltic amber, with the establishment of the new tribe Cacomorphocerini. *Annales de Paléontologie*, 104 (2), 149–153. https://doi.org/10.1016/j.annpal.2018.02.001

Fanti, F. & Pankowski, M.G. (2020) Two new species of *Cantharis* Linnaeus, 1758 from Baltic amber, *Zootaxa*, 4878 (3), 401–411.
https://doi.org/10.11646/zootaxa.4878.3.1

Fanti, F. & Pankowski, M.G. (2023) The first species of *Cantharis* from Ukrainian Rovno amber (Coleoptera, Cantharidae). *Zootaxa*, 5323 (2), 293–297.
https://doi.org/10.11646/zootaxa.5323.2.9

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. & Pankowski, M.K. (2019) A new soldier beetle of the extinct tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018. *Zootaxa*, 4651 (3), 589–595.
https://doi.org/10.11646/zootaxa.4651.3.11

Fanti, F. & Poschmann, M. (2019) First soldier beetles (Coleoptera Cantharidae) from the late Oligocene Enspel Fossil-Lagerstätte (SW Germany). *Palaeoentomology*, 2 (4), 363–371.
https://doi.org/10.11646/palaeoentomology.2.4.10

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

Ferreira, S.V, Keller, O. & Branham, M.A. (2020) Multilocus phylogeny support the nonbioluminescent firefly *Chespirito* as a new subfamily in the Lampyridae (Coleoptera: Elateroidea). *Insect Systematics and Diversity*, 4 (6), e2.
https://doi.org/10.1093/isd/ixaa014

Greenfield, M.D. (1981) Moth sex pheromones: An evolutionary perspective. *Florida Entomologist*, 64, 4–17.
https://doi.org/10.2307/3494597

Heer, O. (1847) *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Erste Abtheilung: Käfer. Erster Theil: Käfer*. Wilhelm Engelmann, Leipzig, 229 pp. + [1] + 8 plates. [reprinted in: *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften*. *Nouveaux Mémoires de la Société Helvétique des Sciences Naturelles*, 8]
https://doi.org/10.5962/bhl.title.2469

Heer, O. (1865) *Die Urwelt der Schweiz*. Friedrich Schulthess, Zürich, xxx + 622 pp., 11 plates.

Heyden, C.[H.G.] von & Heyden, L.[F.J.D.] von (1866) Käfer und Polypen aus der Braunkohle des Siebengebirges. *Palaeontographica*, 15 (3), 131–156 (+ p. 157: Dipteren-Larve aus dem Tertiär-Thon von Nieder Flörsheim in Rhein-Hessen) + plates 22–24. [separatum under the title: *Käfer und Polypen aus der Braunkohle des Siebengebirges.—Dipteren-Larve aus dem Tertiär-Thon von Nieder Flörsheim in Rhein-Hessen. Besonderer Abdruck aus den Palaeontographicis, XV.* Theodor Fischer, Cassel, pp. 1–29 + plates 1–3]

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. (2018) New Baltic amber soldier beetles (Coleoptera, Cantharidae, Cantharinae). *Euroasian Entomological Journal*, 17 (2), 146–152.
https://doi.org/10.15298/euroasentj.17.2.11

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. (2021) New species of Baltic amber soldier beetles (Insecta: Coleoptera: Cantharidae). *Russian Entomological Journal*, 30 (2), 153–158.
https://doi.org/10.15298/rusentj.30.2.08

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 (2019) The first Cretaceous beetle from Azerbaijan: *Katyacantharis zherikhini* gen. et sp. n. (Coleoptera, Cantharidae) from Cenomanian Agdzhakend amber. *Palaeoentomology*, 2 (1), 7–12.
https://doi.org/10.11646/palaeoentomology.2.1.2

Kovalev, A.V. & Kirejtshuk, A.G. (2006) *Asiopsectra* gen. n., a second genus of the family Brachypsectridae (Coleoptera, Elateroidea) from the Palaearctic Region. *Insect Systematics & Evolution*, 47, 195–208.
https://doi.org/10.1163/1876312X-47022140

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.

Kundrata, R., Bukejs, A., Prosvirov, A.S. & Hoffmannova, J. (2020) X-ray micro-computed tomography reveals a unique morphology in a new click-beetle (Coleoptera, Elateridae) from the Eocene Baltic amber. *Scientific Reports*, 10: 20158.
https://doi.org/10.1038/s41598-020-76908-3

Kundrata, R., Hoffmannova, J., Hinson, K.R., Keller, O. & Pačková, G. (2022) Rhagophthalmidae Olivier, 1907 (Coleoptera, Elateroidea): described genera and species, current problems, and prospects for the bioluminescent and paedomorphic beetle lineage. *ZooKeys*, 1126, 55–130.
https://doi.org/10.3897/zookeys.1126.90233

Kuśka, A. (1996) New beetle species (Coleoptera: Cantharidae, Curculionidae) from the Baltic amber. *Prace Muzeum Ziemi*, 44, 13–18.

Nunes, V.C.S., Souto, P.M., Minelli, A., Stanger-Hall, K.F. & Silveira, L.F.L. (2020) Antennomere numbers in fireflies (Coleoptera: Lampyridae): unique patterns and tentative explanations. *Zoologischer Anzeiger*, 286, 1–10.
https://doi.org/10.1016/j.jcz.2020.02.006

Pankowski, M.G. & Fanti, F. (2023) Six new species of fossil soldier beetles (Coleoptera: Cantharidae) from Eocene Baltic amber, *Palaeoentomology*, 6 (3), 300–312.
https://doi.org/10.11646/palaeoentomology.6.3.13

Poinar, G.O. Jr. & Fanti, F. (2019) A new fossil soldier beetle (Coleoptera: Cantharidae) of the genus *Cacomorphocerus* Schaufuss, 1892 from Baltic amber. *Palaeodiversity*, 12 (1), 99–105.
https://doi.org/10.18476/pale.v12.a9

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.* 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, pp. 202–218.

Schaufuss, C. (1892) Preussens Bernstein-Käfer. I. Neue Formen aus der Helm'schen Sammlung im Danziger Provinzialmuseum. *Berliner Entomologische Zeitschrift* (1891), 36 (1), 53–64.
https://doi.org/10.1002/mmnd.18910360111

Spahr, U. (1981) Systematischer Katalog der Bernstein- und Kopal-Käfer (Coleoptera). *Stuttgarter Beiträge zur Naturkunde, Serie B*, 80, 1–107.

Traugott, M. (2003) The prey spectrum of larval and adult *Cantharis* species in arable land: an electrophoretic approach. *Pedobiologia*, 47, 161–169.
https://doi.org/10.1078/0031-4056-00179

Wittmer, W. (1963) A new cantharid from the Chiapas amber of Mexico. *University of California Publications in Entomology*, 31, 53 + pl. 3 (p. 59).