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Fossil soldier beetles (Coleoptera: Cantharidae) of the Georg Statz Collection from the Oligocene Rott Formation, Germany

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Abstract

Specimens of the family Cantharidae Imhoff, 1856 from the Georg Statz Collection (latest Oligocene, Rott Formation, Germany) are studied. Six specimens are relatively complete for species-level determinations, including one with a partial aedeagus visible, a first for soldier beetles preserved as compressions. The new species herein described include: Cantharis (Cantharis) bradburyi sp. nov., C. (C.) lidiae sp. nov., C. (C.) rottensis sp. nov., Podistra (Absidia) quies sp. nov., Rhagonycha (Rhagonycha) carolynae sp. nov. and R. (R.) ultramundana sp. nov. Notably, these genera are still found in Germany and the present report thus provides support for earlier occurrences of Cantharis, Podistra, and Rhagonycha from the Eocene Baltic amber.

Keywords: Cantharidae, Oligocene, Rott, Georg Statz, compression fossils, new species

Introduction

The "Statz Collection" was amassed by Georg Statz (1894-1945), a German schoolteacher who gathered a large and impressive collection of fossil insects, arachnids, vertebrates, and plants from the locality of Rott, an area northeast of the Siebengebirge near the present-day town of Hennef (Rhineland, Germany) (Furst, 1959; Gee & Taylor, 2016). Statz later published numerous monographs and articles on his collection (e.g., Statz, 1940, 1944, 1950), which survived World War II and was auctioned to the Natural History Museum of Los Angeles County (NHMLA) (Howard, 1955; Furst, 1959). While the paleobotanical component of the Statz Collection was later transferred to the University of Bonn, approximately 4,300 fossil arthropods (primarily insects) remain in the care of the NHMLA in Los Angeles, California, USA (Hendy & Mertz, 2018, 2019).

The goal of this work is to report six new Cantharidae

Imhoff, 1856 (soldier beetles) from the Statz Collection. Many of these specimens retain both part and counterpart (= "countertype"), as well as characters useful for species-level diagnoses. All specimens have been fossilized in finely laminated shale resulting a highly detailed preservation quality.

Cantharidae have been previously reported from the Rott Formation with four species of the genus *Cantharis* Linnaeus, 1758 (Heyden & Heyden, 1866) having been described from the Krantz and Heymann Collections at the University of Bonn (Heyden & Heyden, 1866; Scudder, 1891; Handlirsch, 1906–1908, 1920–1921; Kirejtshuk & Ponomarenko, 2009–2015; Mitchell, 2013; Fanti, 2017; The Paleobiology Database).

Geological setting

The lacustrine shales of the Rott Formation were deposited in a small, shallow maar lake and now outcrop near the town of Hennef, Germany (Mörs, 1995). The Lagerstätte is known for its diverse and well-preserved flora and fauna (Koenigswald, 1996). The age of this unit is based on mammal biostratigraphy and considered to be latest Oligocene (Chattian) (\sim 24 Ma), while radiometric data suggest an early Miocene (Aquitanian) age range of $20.6-23.0 \pm 0.5$ Ma, although the latter age range is generally considered too young (Scudder, 1891; Mörs, 1995; Grimaldi & Engel, 2005; Gee & Taylor, 2016).

Materials and methods

The specimens described herein were collected by Georg Statz and his family from the latest Oligocene Rott Formation of Germany and are housed in the Invertebrate Paleontology collections (LACMIP) at the Natural History



FIGURE 1. *Cantharis* (*Cantharis*) *bradburyi* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3451 Part A), dorsal view. **B**, Holotype (LACMIP 2533.3451 Counterpart B), habitus.

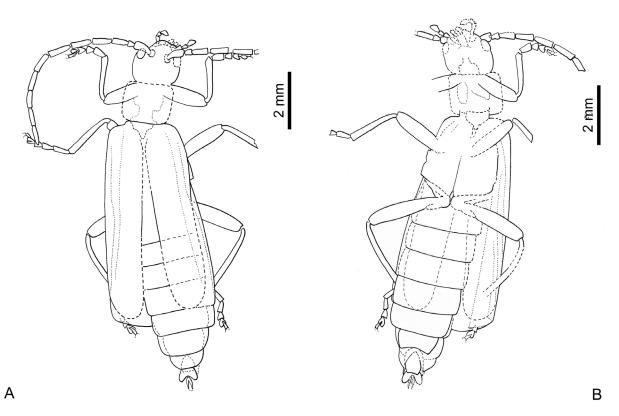


FIGURE 2. *Cantharis* (*Cantharis*) *bradburyi* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3451 Part A), illustration. **B**, Holotype (LACMIP 2533.3451 Counterpart B), illustration.

Museum of Los Angeles County. The terms follow the general literature of the family Cantharidae and Evenhuis (2008). The descriptions of the new species were made by comparing, where present, both part and counterpart for each type specimen. Given sexual dimorphism in the Cantharini, it is possible to assign sex to some specimens. Males are more slender and have longer antennae, while females tend to have larger abdomens with several exposed tergites. Moreover, the last ventrite is narrower and more triangular in males relative to females.

While the precise collecting location of each specimen is unknown (LACMIP locality 2533), the NHMLA's original accession records indicate Statz's collecting events occurred "over a period of 30 years" within the Rott Formation. Recently (2017–2019), the NHMLA digitized the Statz Collection to increase access to both the type and undescribed specimens, the latter of which have been largely unavailable to the research community since its acquistion by the museum in 1955. All LACMIP specimen records relevant to this project can be accessed from the Global Biodiversity Information Facility (GBIF. org) (Hendy & Mertz, 2019), and Integrated Digitized Biocollections (iDigBio.org) (Hendy & Mertz, 2018). Further, a GBIF occurrence download for all LACMIP specimens cited herein is available online (GBIF.org, 07 October 2019). Each specimen was digitally photographed using a Canon 5D Mark III DSLR camera paired with a Canon Macro Photo MP-E 65mm lens attached to a Cognysis StackShot motorized rail. Tethered image capture was then accomplished using Adobe Lightroom and Helicon Focus stacking software. Measurements were taken from a 5mm BioQuip miniscale, which was then digitally redrawn in each photo. Specimen illustrations were hand-drafted and processed using PhotoImpact Viewer SE software.

The new species were compared with images of the holotype of *Cantharis exauctarata* (Heyden & Heyden, 1866) housed at the University of Bonn, Germany (catalog number IGPB-Ro-A-554 Heymann collection). As the original Krantz' collection was sold and dispersed among many institutions, the remaining three holotypes of Heyden & Heyden (1866) were not located.

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) bradburyi sp. nov. (Figs 1–2)

Type material. Holotype: Male, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3451 (Part A, Counterpart B).

Etymology. Named after David Bradbury, a life-long enthusiast of fossil arthropods, generous volunteer of the LACMIP collections, and active member of the Southern California Paleontological Society.

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. The new species is easily distinguished from the subsequent new species by its shorter elytra that are also wider than the pronotum, which has straight margins. Furthermore, Cantharis bradburyi sp. nov. differs from: C. brodiei (Heyden & Heyden, 1866) by its overall larger dimensions, pronotum less transverse, and shorter elytra (surpassing the body in C. brodiei); from C. caduca (Heyden & Heyden, 1866) by the larger dimensions, rounded head (elongated in C. caduca), and different pronotal shape (in C. caduca the pronotum is longer); from C. exauctarata (Heyden & Heyden, 1866) by the pronotum being less rounded at sides, head more rounded, and shorter elytra; and from C. carbonaria (Heyden & Heyden, 1866) by the much narrower pronotum and different length of antennomeres with particularly the second antennomere being much shorter than the third (Heyden & Heyden, 1866; Meunier, 1915; Fanti, 2017). Other Cantharis Linnaeus, 1758 compressions have been described from the nearly coeval Enspel Fossil Lagerstätte, Germany, the early Miocene of Radoboj, Croatia, the Upper/Middle Miocene of Oeningen, Germany, and in the Baltic amber (Fanti, 2017; Fanti & Damgaard, 2018; Kazantsev, 2018; Fanti & Poschmann, 2019).

Description. Adult, winged. Male defined on the basis of the aedeagus being partially visible, as well as by the vaguely triangular and small last sternite. Body length: about 12.0 mm, elytra: 6.5 mm long and 1.8–1.9 mm wide.

Head completely exposed, short, small, rounded. Eyes sub-elliptical, inserted in the upper part and laterally into the head, inter-ocular dorsal distance about 2.8 times greater than eye diameter. Mandibles falciform, slender, without tooth, thin apically. Maxillary palpi 4-segmented; first palpomere stout, rounded; second palpomere robust, longer than first; third palpomere short, about 1.3 shorter than second palpomere; last palpomere securiform with rounded apex. Last labial palpomere securiform. Antennae filiform, 11-segmented, surpassing the half length of elytra and almost reaching apex of elytra; antennomere I (scape) elongated, club-shaped, enlarged apically; II



FIGURE 3. *Cantharis* (*Cantharis*) *lidiae* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3432 Part A), dorsal view. **B**, Holotype (LACMIP 2533.3432 Counterpart B), detail of abdomen, elytra and scutellar shield.

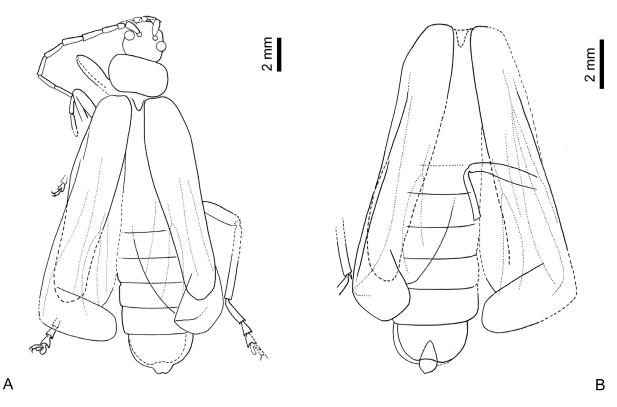


FIGURE 4. *Cantharis* (*Cantharis*) *lidiae* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3432 Part A), illustration. **B**, Holotype (LACMIP 2533.3432 Counterpart B), illustration.

(pedicel) short, vaguely triangular, about 3.0 times shorter than I; III 2.5 times longer than II; IV–VIII sub-equal (VI slightly longer than others), slightly longer than III; IX–X sub-equal, slightly shorter than previous ones; XI filiform, elongated, rounded at apex.

Pronotum as large as head, little rounded at sides, posterior margin straight and not bordered, anterior margin slightly sinuous, anterior and posterior corners slightly rounded, surface with shallow punctation. Scutellar shield triangular-shaped, rounded apically. Elytra very short, leaving four abdominal segments uncovered, much wider than pronotum, slender, parallel-sided, apex rounded, surface smooth. Metathoracic wings little visible, slightly longer than elytra.

Legs slender; coxae roundish, robust; trochanter elongated and rounded apically; femora slender, very slightly curved; tibiae cylindrical, pro- and mesotibiae as long as pro- and mesofemora, metatibiae longer than metafemora; tarsal formula 5-5-5, protarsomere I robust and slightly elongated, meso- and metatarsomere I slender and elongate and about 2.0 times longer than tarsomere II, protarsomere II triangular, meso- and metatarsomere II slightly elongated, tarsomeres III expanded at sides, tarsomeres IV bilobed, V thin, claws not clearly visible. Abdominal segments transverse; metasternum elongated, robust with posterior margin pointed in the middle, penultimate tergite rounded, last tergite strongly bilobed, last sternite vaguely triangular with apical margin wide and concave in the middle, aedeagus partially visible with long parameres and rounded basally.

Remarks. This specimen is exceptionally well-preserved. The mandibles, maxillary palpi, and last labial palpomere are all present, as is the aedeagus (partially), a first for soldier beetles fossilized as compressions. The holotype lacks only the tarsus of the right mesothoracic leg, and the right antenna is truncated at the basal part of antennomere VI. The counterpart is preserved in ventral view and is less complete. Missing anatomy on the counterpart include: on the left mesothoracic leg, part of tibia and entire tarsus; on the right mesothoracic leg, the second (partial), third, fourth, and fifth tarsomeres, as well as the claws; the right prothoracic leg is nearly entirely missing, except the proximal half of the femur; on the left antenna, four apical antennomeres; and, on the right antenna, all but antennomeres I–III.

Cantharis (Cantharis) lidiae sp. nov. (Figs 3–4)

Type material. Holotype: Female, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3432 (Part A, Counterpart B).

Etymology. Named after Lidia Lustig, an avid

geologist and long-time volunteer of the LACMIP collections.

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. The large size is of *C. lidiae* sp. nov. is striking, with only C. carbonaria (Heyden & Heyden, 1866) of comparable dimensions. In fact, C. carbonaria (probably a female: see Fanti, 2017) has a length of about 12 mm in the original description, but indicated to be 20 mm in Meunier's redescription (Heyden & Heyden, 1866; Meunier, 1915). However, the new species is easily recognizable by pronotum more transverse, smooth elytra, and relatively long antennomeres (the length ratio differs between antennomeres II–III in the two species). Other two fossil species of Cantharis from Enspel, Germany, have similar dimensions. C. doernerorum Fanti & Poschmann, 2019 with a size of 19.0 mm is distinguished from C. lidiae sp. nov. by the head more rounded and pronotum less transverse (Fanti & Poschmann, 2019). While, C. zabolica Fanti & Poschmann, 2019 with a probable size of 15.0 mm, has more transverse pronotum as well as more robust and more elongate elytra, and has also a different length of antennomeres (Fanti & Poschmann, 2019).

Description. Adult, winged. Female defined on the basis of the short antennae and the last sternite wide, emarginate and concave at apex. Body length: 20.4 mm, elytra: 10.2 mm long, ~2.1 mm wide.

Head almost completely exposed, rounded, small. Eyes prominently preserved, rounded, inserted in the upper part of the head and not much laterally, inter-ocular dorsal distance 2.1–2.2 times greater than eye diameter. Mandibles stout and elongated. Antennae robust, filiform, 11-segmented, reaching and slightly surpassing the half length of elytra; antennomere I elongated, very robust; II short, robust; III 2.0 times longer than II; IV–IX more slender (except the IV) and longer than previous; X slightly shorter than preceding ones, XI filiform, elongated, apparently rounded at apex.

Pronotum transverse, wider than head, rounded at sides, anterior margin almost straight, posterior margin sinuous and concave in the centre, corners rounded, surface probably with shallow punctation. Scutellar shield triangular-shaped, slightly pointed apically with the margin roundish. Elytra short, leaving two abdominal segments uncovered, wider than pronotum, parallel-sided, apex rounded, surface smooth. Metathoracic wings partially visible, partially folded, slightly longer than elytra, with some veins.

Legs rather short; femora stout, enlarged, slightly curved; tibiae cylindrical, longer than femora; tarsal formula 5-5-5, metatarsomere I elongated, II triangular and 2.0 times shorter than previous, metatarsomere III



FIGURE 5. Cantharis (Cantharis) rottensis **sp. nov.** compression from the Rott Formation, Germany. Holotype (LACMIP 2533.3440), dorsal view.

bilobed and shorter than II, IV bilobed, V thin, claws not clearly visible. Abdominal segments transverse; last sternite wide, rounded and with strongly curved sides, apical margin concave in the middle; last tergite narrows apically subtriangular.

Remarks. Holotype is clearly visible and almost complete, except for the right antenna of which only the first articles are visible (the left is clearly visible except for the tip of the antennomere XI obscured by matrix). The right pro- and mesothoracic legs are missing, and the left ones are incomplete. As for the metathoracic legs, the right is visible almost completely, except for the juncture of the femur and tibia (hidden by matrix), while only tarsomeres are visible on the left. The counterpart lacks the entirety of the head, pronotum, and most of the legs (including all tarsomeres), while everything else from the scutellar shield up to the abdomen is present. No legs are substantially visible, being missing or obscured by the folded wings and elytra, although the apical portion of the tibia and first tarsomere of the left metathoracic leg are visible.

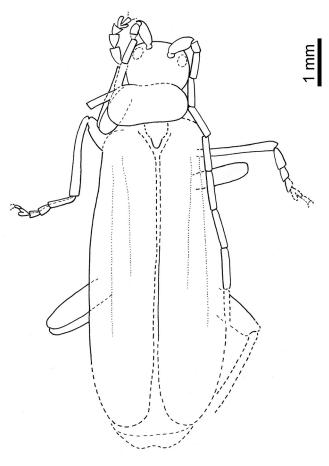


FIGURE 6. Cantharis (Cantharis) rottensis **sp. nov.** compression from the Rott Formation, Germany. Holotype (LACMIP 2533.3440), reconstruction.

Cantharis (Cantharis) rottensis sp. nov. (Figs 5–6)

Type material. Holotype: Probably female, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3440.

Etymology. Derived from the toponym Rott (type locality) + the Latin suffix -*ēnsis*.

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. The new species is easily distinguishable by very transverse pronotum, not present in other fossil species of the genus *Cantharis* (Fanti, 2017), except for *C. lidiae* **sp. nov.**, and *C. zabolica* Fanti & Poschmann, 2019 from Enspel. *C. lidiae* **sp. nov.**, however, is much larger and has shorter elytra, while *C. zabolica* is much larger and has a more elongate head and wider elytra.

Description. Adult, winged. Probably female defined on the basis of the large abdomen. Body length:



FIGURE 7. *Podistra* (*Absidia*) *quies* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3450 Part A), dorsal view. **B**, Holotype (LACMIP 2533.3450 Counterpart B), habitus.

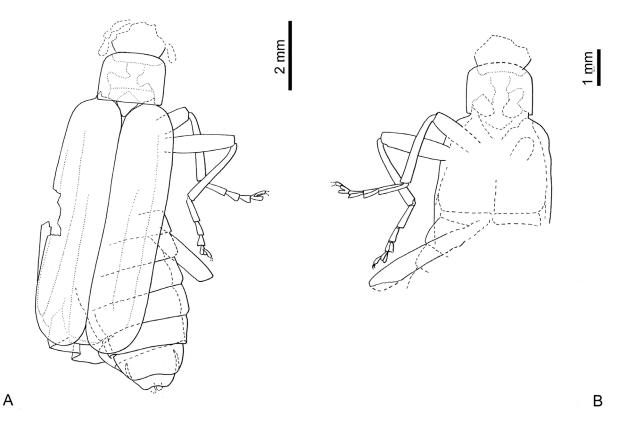


FIGURE 8. *Podistra* (*Absidia*) *quies* **sp. nov**. compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3450 Part A), illustration. **B**, Holotype (LACMIP 2533.3450 Counterpart B), illustration.

8.4 mm, elytra: 5.5 mm long (\sim 4.6 mm visible), \sim 1.3 mm wide. (Body and elytral lengths estimated as the abdomen incomplete).

Head wide, broad, almost completely exposed. Eyes indistinct. Antennae robust, filiform, antennomere XI invisible, inserted far from the eyes, surpassing the metathoracic legs; antennomere I massive; II short, robust, about 2.3 times shorter than previous; III about 2.1 times longer than II; IV–X elongated, sub-equal in length, slightly longer than previous.

Pronotum strongly transverse, almost as large as head, rounded at sides, anterior margin slightly sinuous, posterior margin straight and feebly concave in the middle and not bordered, anterior corners slightly rounded with the posteriors very rounded. Scutellar shield robust, triangular-shaped, rounded apically. Elytra elongated, slender, possibly covering all abdominal segments, wider than pronotum and head, parallel-sided, apex rounded, surface smooth. Metathoracic wings obscured by elytra. Legs rather short; femora robust, slightly curved; tibiae cylindrical, protibiae slightly longer than profemora, meso- and metatibiae longer than meso- and metafemora; protarsomere I robust, protarsomere II triangular and 1.5 times shorter than previous, protarsomere III slightly lobed laterally and shorter than II, IV strongly bilobed, protarsomere V thin, mesotarsomeres more elongated than protarsomeres, claws invisible. Abdominal segments not clearly visible, the last of which is possibly sinuous and concave at apex.

Remarks. With respect to the holotype, most legs are missing or invisible, and preservation of the left antenna is truncated at antennomere V (the right antenna is complete up to the apex of antennomere IX). To our knowledge, no counterpart was collected.

Genus *Podistra* Motschulsky, 1839 Subgenus *Absidia* Mulsant, 1862

Podistra (Absidia) quies sp. nov. (Figs 7–8)

Type material. Holotype: Female, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3450 (Part A, Counterpart B).

Etymology. Derived from the Latin noun $qu\bar{t}e\bar{s}$ = rest, eternal rest, sleep. In reference to the fact that it seems asleep until today. Epithet is to be treated as noun in apposition.

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. No *Podistra* have been previously described from the Oligocene and thus from Rott. The

new species differs from *Podistra* (*Absidia*) *kloevedali* Fanti & Damgaard, 2018 in Baltic amber by its shorter elytra and shorter pronotum, which is flatter especially at the base (Fanti & Damgaard, 2018).

Description. Adult, winged, stout. Female defined on the basis of abdominal size (large). Body length: 10.6 mm, elytra: 7.3 mm long, ~1.2 mm wide.

Head slightly visible, short, almost completely exposed. Eyes sub-elliptical, inserted laterally into the head. Antennae invisible except for the first articles (partially), filiform, with 11 antennomeres assumed.

Pronotum sub-quadrate, slightly wider than head, straight at sides, anterior margin rounded and slightly protruding over the head, posterior margin straight and very faintly bordered, anterior corners rounded, posterior corners almost acute, surface flat and smooth. Scutellar shield elongated, triangular-shaped, rounded apically. Elytra long, robust, covering the abdominal segments except the last two urites, wider than pronotum and head, parallel-sided, strongly rounded at apex, surface with shallow punctation. Metathoracic wings slightly protruding from the elytra.

Legs short and robust; femora robust, faintly curved; tibiae cylindrical, slender, slightly longer than femora, without spurs at apex; tarsomere I slender and elongated, protarsomere II about 1.6 times shorter than protarsomere I, mesotarsomere II about 1.8 times shorter than mesotarsomere I, tarsomere III slightly lobed at sides and shorter than II, tarsomere IV with lobes at sides very elongated, protarsomere V thin, mesotarsomeres more elongated than protarsomeres, claws thin and slightly visible. Abdominal segments strongly transverse, last tergite wide and sinuous apically and concave (in the middle at the apex) with the sides slightly rounded, last sternite wider than last tergite and concave at the apical margin.

Remarks. Holotype lacks all of left legs, while the right legs are well-preserved except for the posterior where only the femur is visible. The head and antennae are not preserved. The matrix containing the counterpart is broken and therefore half of the abdomen is missing such that no sternites or tergites are visible. The subgeneric attribution is uncertain due to the poor preservation of the claws.

Genus *Rhagonycha* Eschscholtz, 1830 Subgenus *Rhagonycha* Eschscholtz, 1830

Rhagonycha (*Rhagonycha*) carolynae sp. nov. (Figs 9–10)

Type material. Holotype: Probably female, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3446 (Part A, Counterpart B).



FIGURE 9. *Rhagonycha* (*Rhagonycha*) *carolynae* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3446 Part A), dorsal view. **B**, Holotype (LACMIP 2533.3446 Counterpart B), habitus.

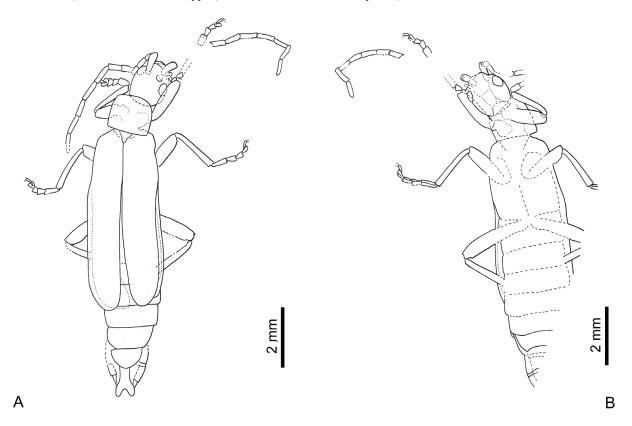


FIGURE 10. *Rhagonycha* (*Rhagonycha*) *carolynae* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3446 Part A), illustration. **B**, Holotype (LACMIP 2533.3446 Counterpart B), illustration.

Etymology. Named after Carolyn Weiss, a dedicated volunteer of the NHMLA with an admirable passion for museum collections, science, and outreach.

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. This is the first *Rhagonycha* described from the Oligocene and Rott. Previously described fossil *Rhagonycha* include: four species from the Baltic amber (Middle Eocene), one from Florissant (latest Eocene), two from Oeningen (Miocene) (of which a paralectotype is cited also from Radoboj, Croatia), and one from Lac Chambon, France (Pliocene) (Fanti, 2017; Fanti & Damgaard, 2018; Fanti & Pankowski, 2018). The new species differs from others by its larger dimensions, with only *Rhagonycha germari* (Heer, 1847) from Oeningen, vaguely similar in size (8.50–9 mm) having longer elytra (Heer, 1847; Fanti, 2017).

Description. Adult, winged. Probably female defined on the basis of the large abdomen and short elytra. Body length: 11.1 mm, elytra: 5.6 mm long, ~2.5 mm wide. Head almost completely exposed, elongated. Eyes rounded, inserted in the upper part and laterally of the head. Mandibles falciform, stout, without tooth, thin apically. Maxillary palpi 4-segmented, with the last palpomere slightly securiform. Antennae filiform, 11-segmented, short, about reaching the metathoracic legs and half of the elytra; antennomere I elongated, clubshaped, very stout; II short, slender, about 1.9 times shorter than I; III–IV sub-equal and the same size of the antennomere II; V–IX sub-equal and longer than previous ones; X slightly shorter than previous ones; XI filiform, elongated, rounded at apex.

Pronotum wider than head, sides straight and slightly narrow anteriorly, posterior margin straight and slightly bordered, anterior margin slightly rounded, anterior corners slightly roundish, surface with punctation. Scutellar shield triangular-shaped, pointed apically. Elytra very short, leaving four abdominal segments uncovered, wider than pronotum, slender, parallel-sided, apex rounded, surface with punctation. Metathoracic wings not well-visible, probably as long as elytra.

Legs rather short; femora enlarged, very slightly curved; tibiae cylindrical, with spur at apex, slightly longer than femora; protarsomere I robust and about 1.7 times longer than II, protarsomere II and III sub-equal in length and not lobed at sides, mesotarsomere I slender and elongate and about 1.6 times longer than mesotarsomere II, mesotarsomere II and III with anterior margin straight, tarsomeres IV bilobed, tarsomeres V thin, claws robust. Abdominal segments transverse; penultimate tergite rounded, last tergite strongly bilobed and concave apically.

Remarks. Holotype is clearly visible, lacking only the right protibia and the first articles of the right antenna (the first antennomere, however, is visible). The tarsomeres of the posterior legs are also obscured by the abdomen. The counterpart lacks the left pro- and mesotarsi, right protibia, last sternites and antennae are less visible than in the holotype.

Rhagonycha (Rhagonycha) ultramundana sp. nov. (Figs 11–12)

Type material. Holotype: Sex undefined, compression fossil in lacustrine shale from the Rott Formation. LACMIP 2533.3448 (Part A, Counterpart B).

Etymology. Derived from the Latin adjective $ultr\bar{a}mund\bar{a}nus$ -a -um ($ultr\bar{a} + mundus = world$) = that is beyond the world, afterlife / netherworld. In reference to the fact that it is of another geologic epoch and that with its fossilization and this description has come to us from "another world".

Type locality and horizon. Germany: Rott am Siebengebirge; Upper Oligocene-upper Chattian: *ca.* 24–23.03 Mya (Winterscheid *et al.*, 2018) or 23.9–24.2 Mya (Mertz *et al.*, 2006).

Diagnosis. *Rhagonycha ultramundana* **sp. nov.** differs from *Rhagonycha carolynae* **sp. nov.** by longer elytra and pronotum narrower anteriorly.

Description. Adult, winged, stout. Sex undefined. Body length: 10.7 mm, elytra: 7.3 mm long, ~1.5 mm wide.

Head almost completely exposed, very wide and short, rounded, with punctation. Eyes rounded, inserted laterally in the upper part of the head. Mandibles falciform, stout, probably without teeth. Antennae partially visible, probably 11-segmented, filiform, short, reaching the metathoracic legs; antennomere I elongated, club-shaped, not particularly enlarged; II short, slender, about 2.3 times shorter than I; III–VI sub-equal in length, very elongated; VII–IX little visible, as long as previous ones or very slightly shorter; X–XI invisible.

Pronotum anteriorly as wide as head and posteriorly slightly wider than head, posterior margin slightly sinuous and not bordered, anterior margin straight and not bordered that partially covers the head, posterior corners strongly rounded, anterior corners slightly rounded, surface probably slightly wrinkled. Scutellar shield short, triangular-shaped, rounded apically. Elytra elongated, covering all abdominal segments, wider than pronotum, slender, parallel-sided, apex rounded. Metathoracic wings slightly longer than elytra.

Legs robust, rather short; femora very stout, slightly curved; tibiae cylindrical, pro- and mesotibiae as long as pro- and mesofemora, metatibiae slightly longer than metafemora; protarsomere I very robust, triangular.



FIGURE 11. *Rhagonycha* (*Rhagonycha*) *ultramundana* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3448 Part A), dorsal view. **B**, Holotype (LACMIP 2533.3448 Counterpart B), habitus.

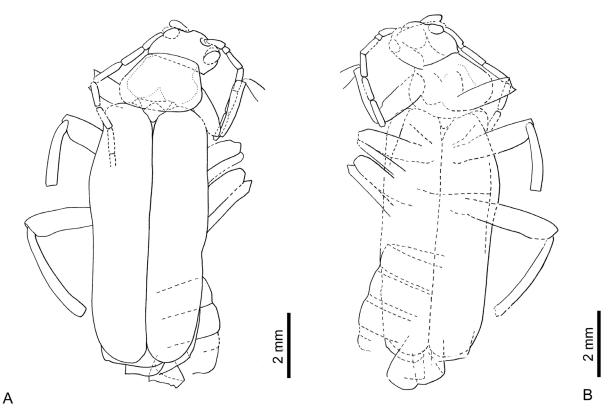


FIGURE 12. *Rhagonycha* (*Rhagonycha*) *ultramundana* **sp. nov.** compression from the Rott Formation, Germany. **A**, Holotype (LACMIP 2533.3448 Part A), illustration. **B**, Holotype (LACMIP 2533.3448 Counterpart B), illustration.

Abdominal segments transverse, not clearly visible except for few parts laterally and with last tergite that appears rounded at the margin and sinuous apically.

Remarks. The holotype's antennae are not clearly visible (particularly the right antenna), the legs are very incomplete (diagnostic characters not preserved).

Discussion

The discovery of additional Cantharidae from the Rott fauna enables several interpretations. Cantharids have been described from the Eocene Baltic amber (Fanti, 2017, 2018; Fanti & Damgaard, 2018; Kazantsev, 2018), and the latest Eocene Florissant Formation (Fanti, 2017). In addition to the Rott fauna, an Oligocene cantharid species of *Malthodes* Kiesenwetter, 1852 is also known from the Brunstatt brown coals of Alsace, France (Förster, 1891).

Occurrences of Cantharis Linnaeus, 1758 and Rhagonycha Eschscholtz, 1830 in the Rott Formation are suggestive of an open environment with low vegetation around the lake, where they likely fed on other insects and abundant pollen (Fiori, 1949). Presently, there are no known species of Malthodes from the Rott Formation, which are purely predatory and more associated with woodland environments. Cantharis and Rhagonycha, on the other hand, are larger and may have been similarly abundant in the late Oligocene as they are in presentday Europe (Köhler & Klausnitzer, 1998; Kazantsev & Brancucci, 2007). The genus Podistra Motschulsky, 1839 contains few species (Kazantsev & Brancucci, 2007) and, until now, was only known from one species and three specimens from the Baltic amber (Fanti, 2017; Fanti & Damgaard, 2018). The lack of *Podistra* diversity from Rott, a landscape which may have been flat or hilly but not high altitude (Mörs, 1995), could be for various reasons. As far as *Podabrus* Dejean, 1833 is concerned, its absence may be due to orography, as this genus typically occurs in montane areas (Bourgeois, 1884-1892; Magis, 1955; Moscardini, 1968). Silis Charpentier, 1825, a hydrophilous taxon, may have been present in the vicinity of the Oligocene lake of Rott, but may have been as uncommon then as it is today (Kazantsev & Brancucci, 2007). It is also possible these absences are due to natural taphonomic or collector-introduced biases.

Significantly, the cantharid fauna of the latest Oligocene Rott Formation is broadly comparable to that of present-day in Germany. These species also provide important calibration points for previous interpretations that confirm these genera have been present since the Eocene with their evolution and diversification continuing

into the Oligocene (Fanti, 2017; Fanti & Damgaard, 2018; Fanti & Pankowski, 2018; Kazantsev, 2018; Kupryjanowicz & Fanti, 2019).

Key to the fossil soldier beetles of the Rott Formation

1	Tarsomeres III lobed at sides
-	Tarsomeres III straight apically9
2	Pronotum not transverse, straight at sides
_	Pronotum transverse, rounded at sides
3	Pronotum sub-quadrate
_	Pronotum elongate
4	Pronotum slightly transverse
	Pronotum strongly transverse and strongly rounded at
-	sides
5	Short elytra leaving some abdominal segments uncovered.
	6
-	Long elytra covered body, head ovoidal elongate
6	Elytra very short, pronotum slightly rounded at sides
_	Elytra longer, pronotum rounded at sides
7	Large size (over 20.0 mm), short elytra
,	
_	Small size (under 9.0 mm), long elytra
8	Elytra longer than body, robust species
O	
	Elytra as long as body or slightly shorter than body, slender
-	
0	species
9	Pronotum slightly narrowed anteriorly, short elytra
-	Pronotum strongly narrowed anteriorly, long elytra
	Rhagonycha ultramundana sp. nov.

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