



## A new Eocene soldier beetle (Cantharidae) of the genus †*Cacomorphocerus* Schaufuss, 1892 from Baltic amber

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### Abstract

Recent studies of extinct soldier beetles have generated an immense amount of new information. Scientists have described various new species of †*Cacomorphocerus* Schaufuss, 1892, confirming the remarkable diversification and evolution of this genus and the Cantharidae family during the Eocene. In the present work, we describe a new species from Baltic amber. *Cacomorphocerus marki* **sp. nov.**, is the first species of *Cacomorphocerus* discovered with filiform 11-segmented antennae. Based on inclusions in Baltic and Rovno amber, it now appears certain that the genus *Cacomorphocerus* and the tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018 evolved and subsequently went extinct in Europe during the Eocene. Known for more than 100 years from a single species, the genus is now known to be far more morphologically diversified thanks to these recent discoveries.

**Key words:** soldier beetle, fossil, amber, Eocene, taxonomy, evolution

### Introduction

For over a century, the genus †*Cacomorphocerus* Schaufuss, 1892 (Cantharidae Cantharinae) was known from just one species, *C. cerambyx* Schaufuss, 1892. Then a relative explosion of discoveries started in 2010, with all of the new species and specimens found in Baltic or Rovno amber (Kuška & Kania 2010; Kazantsev & Perkovsky 2014; Fanti & Damgaard 2018; Fanti & Kupryjanowicz 2018; Kazantsev 2018; Bukejs *et al.* 2019; Fanti & Pankowski 2019; Poinar & Fanti 2019; Kazantsev & Perkovsky 2020). Based on some of these records as well as information published by Kazantsev (2013), the genus was transferred—independently twice—first by Fanti & Kupryjanowicz (2018) and then by Kazantsev (2018) into the subfamily Cantharinae. In the same period, Fanti & Kupryjanowicz (2018) established the Cacomorphocerini tribe with two genera: *Cacomorphocerus* Schaufuss, 1892 and *Sucinocantharis* Kuška & Kania, 2010 characterized by having strongly modified, saucer-shaped and supernumerary antennomeres, numbering from 12 to 16. That changed with the subsequent discoveries (Fanti & Damgaard 2018) of other similar genera with a greater number of antennomeres (17 and 19), and above all with the discoveries of new species of *Cacomorphocerus* with 11 antennomeres (Poinar & Fanti 2019; Kazantsev & Perkovsky 2020).

### Material and methods

Baltic amber is considered to range in age from the Lutetian to the Priabonian stage of the Middle-Upper Eocene. This amber specimen comes from the Sambian Peninsula in Russia and was purchased from an amber dealer. The photographs of the inclusion were taken using a Canon EOS 70D and MP-E 65mm macro lens and they were assembled with a focus stacking software. Plates were processed using the program PhotoImpact Viewer SE. The specimen was donated to the Smithsonian's National Museum of Natural History (USNM) and assigned the catalog number USNM PAL 770863.

## Systematic treatment

### Family Cantharidae Imhoff, 1856

### Subfamily Cantharinae Imhoff, 1856

### Tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018

### Genus *Cacomorphocerus* Schaufuss, 1892

#### *Cacomorphocerus marki* FANTI & M. G. PANKOWSKI sp. nov.

(Figs. 1–4)

**Description.** Adult, winged, robust, entirely dark brown. Female, based on the last urite rounded and having short antennae. Body length: 7.1 mm; antennal length: about 3.6 mm; pronotum: about 1.35 mm long; elytral length: 5.35 mm.

Head prognathous, transverse, short, robust, slightly convex, covered posteriorly by the pronotum, with very shallow punctation and sparse erect setae. Eyes rounded, convex, prominent, inserted in lateral part of head, interocular distance about 3.0 times greater than eye diameter. Mandibles elongate, falciform, smooth, very large and triangular at base, thin and pointed apically. Maxillary palps 4-segmented, adorned with setae, palpomere I short and robust, almost globular, palpomere II elongate, palpomere III similar to II and slightly shorter, palpomere IV very elongated, thin, securiform, with rounded apex. Labial palps 3-segmented, last palpomere strongly securiform. Antennae 11-segmented, filiform, pubescent with erect setae, rather short and not reaching middle of the elytra, insertion rather far to upper margin of the eyes; scape robust especially at apex and club-shaped; pedicel about two-thirds shorter than scape; antennomere III filiform, about 0.7 times longer than II; antennomeres IV–VII filiform, slightly longer than antennomere III; antennomeres VIII–X nearly equal in length and longer than previous ones; antennomere XI very elongated, cylindrical, thinner and slightly pointed at apex. Pronotum elongated, wider than the head, without shallow punctation and equipped with sparse and erected setae, surface flat, posterior margin wider than the slightly rounded anterior margin, each side narrower at the middle and with a rounded protuberance near the apex, posterior corners slightly rounded, anterior corners strongly rounded. Scutellar shield robust, triangular. Elytra elongate, slightly longer than the last abdominal segment, parallel-sided, completely smooth but adorned with erect setae, wider than the pronotum and the head, apices rounded, suture and sides not bordered. Hind wings slightly infuscate and slightly longer than the elytra, almost completely covered by the elytra. Metasternum sub-rectangular, robust, pubescent; ventrites strongly transverse, pubescent. Last urite short, sinuous, with lobes. Legs slender and long, densely pubescent; coxae elongate and robust; trochanters elongate, vaguely triangular with rounded apex, slightly enlarged in the middle; femora elongate, robust, slightly enlarged and slightly curved; tibiae cylindrical, long, thin, with a spur on the side near the apex, protibiae very slightly shorter than the profemora, mesotibiae very slightly longer than the mesofemora, metatibiae longer than the metafemora; tarsi 5-segmented; tarsomere I elongate with protarsomere more robust than meso- and metatarsomere; tarsomere II shorter than tarsomere I; tarsomere III shorter than tarsomere II and vaguely triangular; tarsomere IV flat, bilobed with large lobes; tarsomere V slender, very elongated and curved; claws thin, elongate, pointed at apex and with an evident and obtuse denticle basally. Male unknown.

**Etymology.** Species named after Mark A. Pankowski, oldest brother of the second author who gave him a deep appreciation of nature by showing him how to find rare species everywhere from rivers to roadsides.

**Holotype.** Female, adult specimen included in a Baltic amber piece: Catalog number USNM PAL 770863, in the Smithsonian's National Museum of Natural History (USNM) in Washington, DC in the USA.

**Type locality.** Quarry in Yantarny, Baltic Sea Coast, Sambian Peninsula, Kaliningrad Region, Russia.

**Type strata.** Baltic amber, Middle-Upper Eocene, Prussian Formation, also known as the "blue earth" formation.

**Syninclusions.** Botanical remains, stellate hairs, gas vesicles (air bubbles), mite (Acarina), and dipteran (Nematocera Culicomorpha).

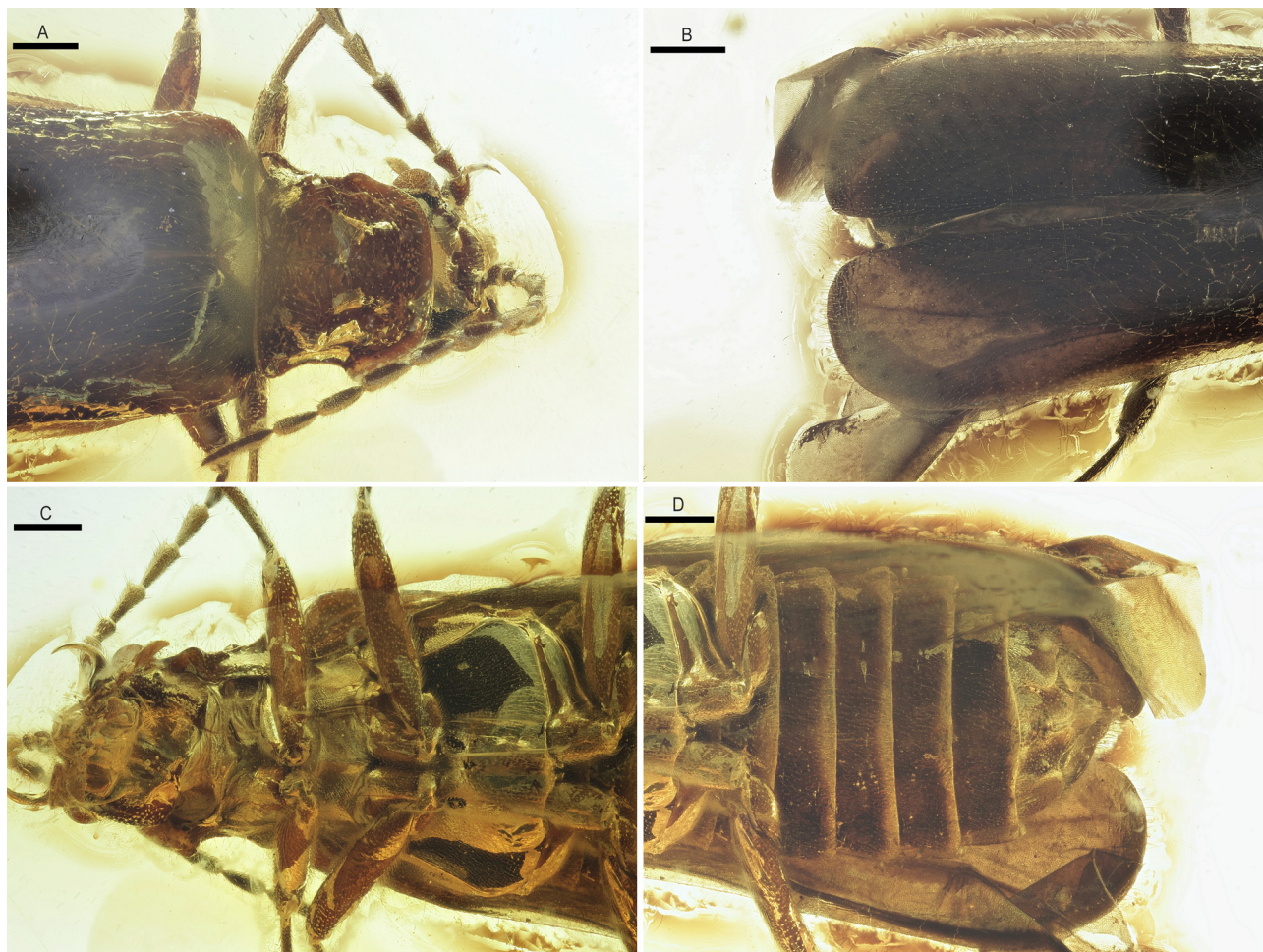
**Differential diagnosis.** The species of *Cacomorphocerus* most commonly have 12 antennomeres, with the

central antennomeres dilated or strongly saucer-shaped (Schaufuss 1892; Kuška & Kania 2010; Fanti & Damgaard 2018; Fanti & Kupryjanowicz 2018; Bukejs *et al.* 2019; Fanti & Pankowski 2019). In another species with 12 antennomeres, the “central antennomeres” are very slightly dilated or almost globular (Parisi & Fanti 2020). *Cacomorphocerus endecacerus* Poinar & Fanti, 2019 from Baltic amber has 11 antennomeres, and it is easily distinguishable from *C. marki* **sp. nov.** by the former’s antennomeres II–VIII that are saucer-shaped or irregular instead of totally filiform as in *C. marki* **sp. nov.** (Poinar & Fanti 2019). Also, *Cacomorphocerus meridionalis* Kazantsev & Perkovsky, 2020 from Rovno amber has 11 antennomeres with the “central antennomeres” strongly modified (Kazantsev & Perkovsky 2020). Both *C. endecacerus* and *C. meridionalis* also have a very different pronotal shape (compared to *C. marki* **sp. nov.**) without a protuberance on each side (Poinar & Fanti 2019; Kazantsev & Perkovsky 2020).



**FIGURE 1.** *Cacomorphocerus marki* **sp. nov.** in Baltic amber. A: Holotype, dorsal view, scale bar = 1.0 mm. B: Holotype, ventral view, scale bar = 1.0 mm.

**Remarks.** The oval piece of amber (approximately 28 x 22 x 4 mm) is extremely transparent and allows an excellent view of the whole inclusion. There are no surface fractures or emulsion (a white cotton-like cloud sometimes found in Baltic amber). The specimen is complete and perfectly preserved in a relaxed and horizontal position. All structures including the mandibles, palps, and claws are clearly visible.



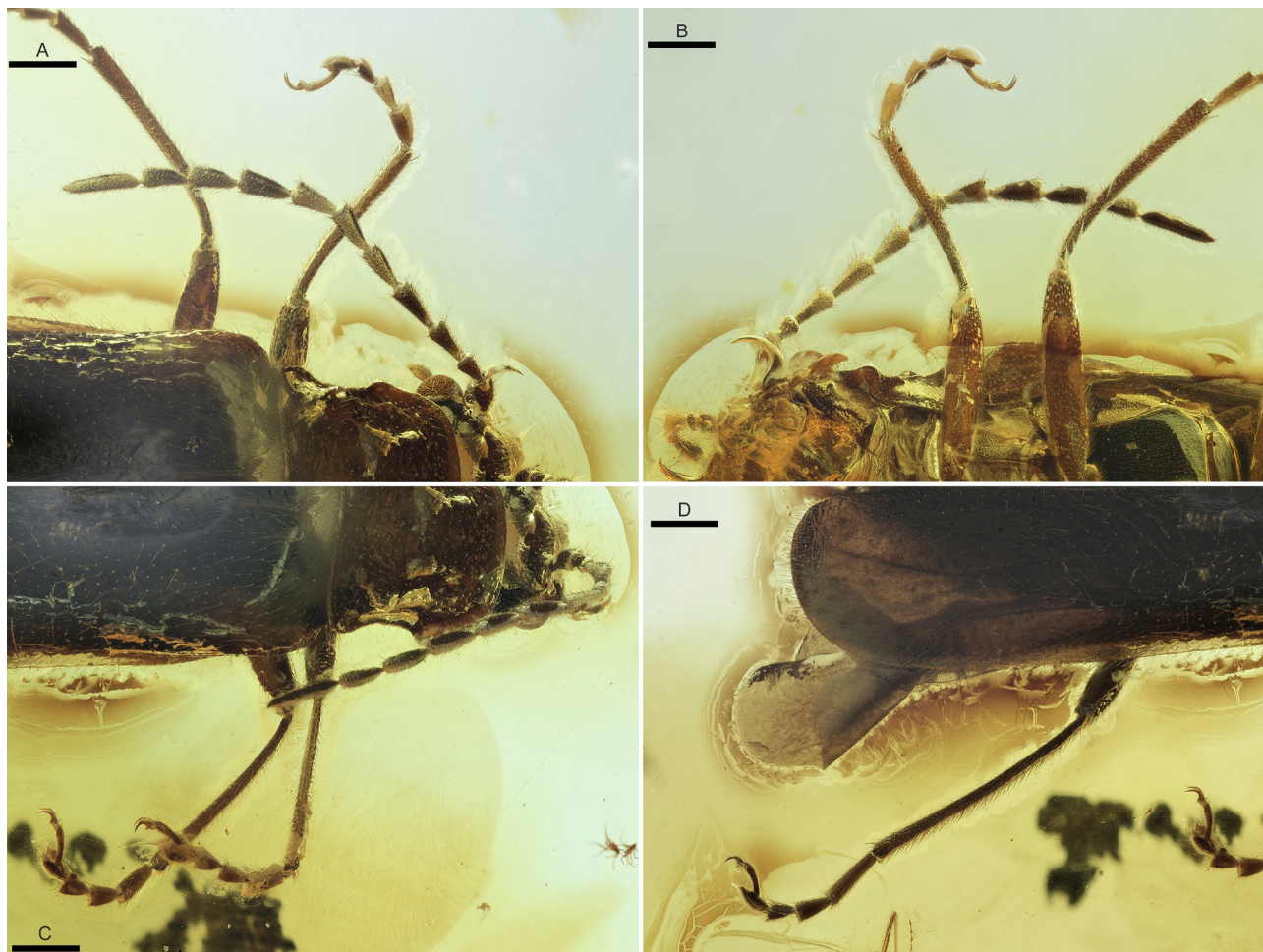
**FIGURE 2.** *Cacomorphocerus marki* sp. nov. in Baltic amber. A: Holotype, detail of head and pronotum, scale bar = 0.5 mm. B: Holotype, detail of elytral apex, scale bar = 0.5 mm. C: Holotype, detail of head, pronotum and metasternum (ventral view), scale bar = 0.5 mm. D: Holotype, detail of urites, scale bar = 0.5 mm.

## Discussion

After a series of recent discoveries, the genus *Cacomorphocerus* now comprises 11 species, including *C. marki* described here, and has been recognized as a part of the subfamily Cantharinae in the tribe Cacomorphocerini Fanti & Kupryjanowicz, 2018. The tribe appears to have evolved and become extinct in the Eocene (Bukejs *et al.* 2019), based on specimens found so far only in Baltic and Rovno amber. This suggests that the tribe's ancestors evolved in Laurasia, perhaps centered in present-day Europe (Fanti & Pankowski 2019). The tribe is characterized by filiform (rarely) or dilated and saucer-shaped antennae, with the latter type most common today in South American representatives of the subfamily Dysmorphocerinae Brancucci, 1980. These are possibly homoplastic traits.

According to Kazantsev & Perkovsky (2020), the diagnostic characters of the various subfamilies of Cantharidae are based on the wing venation, the shape of the maxillary palps, the structure of abdominal segments and especially on the shape of the aedeagus (Brancucci 1980), which obviously can be very rarely seen in fossils. In the Cacomorphocerini tribe, we find antennae with 11-12 articles, sometimes with 15-17 articles and one species with 19 articles. In living soldier beetles, nearly all species have antennae with 11 antennomeres. As Fanti & Pankowski (2019) and Poinar & Fanti (2019) inform us, in fact, only a few extant species of *Heteromastix* Boheman, 1858 (Cantharidae Dysmorphocerinae) and *Pseudosilis* Pic, 1911 (Cantharidae Silinae) have 12 antennomeres. This dem-

onstrates that the presence of supernumerary antennomeres developed several times during the evolution of Cantharidae (Poinar & Fanti 2019) and in various subfamilies. This also confirms that this characteristic was common in the Eocene, and highlights, in our opinion, a particular evolutionary line that easily allows *Cacomorphocerus* and the other related genera to constitute a particular tribe.



**FIGURE 3.** *Cacomorphocerus marki* sp. nov. in Baltic amber. A: Holotype, detail of antenna, dorsal view, scale bar = 0.5 mm. B: Holotype, detail of antenna, ventral view, scale bar = 0.5 mm. C: Holotype, detail of pro- and mesothoracic leg, scale bar = 0.5 mm. D: Holotype, detail of metathoracic leg, scale bar = 0.5 mm.

The genus *Cacomorphocerus* has proven to have a remarkable diversity of forms, both with regard to the antennae and the pronotum. We can define some groupings on the basis of these morphological traits. The most numerous group of species is the *Cacomorphocerus* group *cerambyx* (*C. cerambyx*, *C. jantarius*, *C. wiszniewskii*, *C. madseni* and probably also *C. bentifabrici*), which has antennae consisting of 12 antennomeres with the central ones strongly saucer-shaped and a characteristic elongated pronotum with an evident protuberance (except in *C. bentifabrici*) on each side near the front edge. Another particular grouping is the *Cacomorphocerus* group *eocenicus* (*C. eocenicus* and *C. coleae*) that has antennae with 12 antennomeres slightly modified with the central antennomeres little dilated. Then we have the *endecacerus* group (*C. endecacerus* and *C. meridionalis*), with 11 antennomeres and the central ones saucer-shaped. Finally, we have isolated species: *C. obstinatus* (Parisi & Fanti 2020) with 12 antennomeres (II-IX slightly modified) and *C. marki* sp. nov., with 11 antennomeres that are filiform. As already highlighted by Fanti & Pankowski (2019) and Poinar & Fanti (2019), and also demonstrated by *C. marki* sp. nov., the probable common ancestor of the tribe Cacomorphocerini had antennae of 11 articles that were filiform, as it is already considered to be for beetles in general. The extreme differences in the shape of the antennae would also suggest that the genus *Cacomorphocerus* is polyphyletic. To confirm this, however, we would need more specimens to study to reconstruct the ancestral traits of these fascinating beetles.



**FIGURE 4.** *Cacomorphocerus marki* sp. nov. in Baltic amber. A: Holotype, detail of head, mandibles and palps, ventral view, scale bar = 1.0 mm. B: Holotype, detail of metathoracic leg and last urites, ventral view, scale bar = 1.0 mm.

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