

## Article

# Diversity Phenomenon of the Danaceinae Malachite Beetle Subfamily (Coleoptera: Dasytidae) in Eocene Baltic Amber with a New Description of an Extinct Genus and Species

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**Abstract:** A new malachite beetle, *Baltamauroania mirabilicornis* gen. et sp. nov., belonging to the tribe Amauroniodini (Coleoptera: Dasytidae) embedded in Eocene Baltic amber is described and illustrated. The new genus differs from the congeners of the tribe Amauroniodini in possessing a black, elongated, and subparallel body and a pronotum with scalloped lateral sides; long and 11-segmented antennae, with three apical antennomeres enlarged and forming a ‘club’ shape, with cylindrical antennomere 1; tarsi shortened and compressed, 5-segmented, with tarsomeres 1 and 2 equal in length, and tarsomere 5 the longest in all legs; pubescence of the dorsal surface consisting of short strong brown semi-erect and fine adpressed setae; punctuation of dorsal surface irregular, elytra lacking grooves; pronotum almost equilateral, slightly elongated, with acute anterior and obtuse posterior angles, with wide margination of basal side and with scalloped and finely margined lateral sides; lateral edges of pronotum weakly rounded, with obtuse protuberance before middle. This is the second extinct genus and third record of the subfamily Danaceinae found in Eocene amber. The fossil records of the family Dasytidae are discussed. Three recent records of different Amauroniodini taxa from Eocene East European amber (Baltic and Rovno) show there to have been a high Danaceinae biodiversity in both the southern coast of the Subparatethys (documented by Rovno amber) and in its northern coast (documented by Baltic amber). The phenomenon of Danaceinae diversity in the Eocene Epoch is discussed.

**Keywords:** Cleroidea; Amauroniodini; *Baltamauroania*; new taxa; fossil resin; paleobiodiversity; Cenozoic



**Citation:** Tshernyshev, S.E.; Lyubarsky, G.Y.; Alekseev, V.; Bukejs, A. Diversity Phenomenon of the Danaceinae Malachite Beetle Subfamily (Coleoptera: Dasytidae) in Eocene Baltic Amber with a New Description of an Extinct Genus and Species. *Diversity* **2023**, *15*, 1077. <https://doi.org/10.3390/d15101077>

Academic Editor: Luc Legal

Received: 14 September 2023

Revised: 7 October 2023

Accepted: 9 October 2023

Published: 11 October 2023



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## 1. Introduction

Members of the Malachite beetle family (Coleoptera, Dasytidae) are distributed worldwide in diverse landscapes, particularly in the Temperate Zone [1,2]. They are well known in amber inclusions as small-to-moderate-sized (1 to 5 mm) beetles with a typically subparallel body, convex pronotum, epignathous head, and dense double pubescence with long erect and short semierect hairs. In comparison with the closely related family Malachiidae, Dasytines can be recognized by their well-sclerotized body; the thorax lacking evaginating vesicles; mostly conical apical maxillary palpomere; elytra mostly completely covering the entire abdomen; legs and antennae rarely modified; tarsomere 1 as long or longer than tarsomere 2 in all legs; and abdominal ventrites 1 and 2 free [1,3]. Representatives of these families in the larval stage are known to be predators of small invertebrates appearing in soil litter [4]. The imagoes are usually residents of flowers [4,5] in meadows and in shrubs in forested areas, but some genera such as *Dasytes* and *Aplocnemus* occur in trees [6–8].

The oldest record of the family Dasytidae, *Protodasytes cretaceus* Tihelka, Huang, Perrihot & Cai, 2021, relates to the Late Cretaceous Epoch and was described from Charentese amber originating from sediments in the Charente-Maritime area of France [3]; according to geological dating, this amber is considered to be early Cenomanian within the Late Cretaceous Epoch, ca. 96 to 100.5 Ma [9,10]. A recent study [11] of poorly preserved remains of a Mesozoic Albian species, *Acanthocnemoides sukatshevae* Zherikhin, 1977, described from Siberian Taimyr amber dated ca. 78 to 115 Ma, and previously attributed to the family Acanthocnemidae [12,13], resulted in its placement in the tribe Danaceini. This decision remains questionable and demands further study due to poorly visible main characteristics necessary to define family attribution of the beetle. This species is probably a member of Acanthocnemidae or an ancestral form of this family which possesses special thermosensitive pores located in characteristic pit of prothorax hypomeron adjacent to the sternopleural suture [14]. Traces of such a structure are visible in the hypomeron of *Acanthocnemoides sukatshevae*, but it is necessary to clarify if this is a natural structure or an artefact which appeared as result of chemical treatment of the amber and its inclusion. In this case, it is better to consider only *Protodasytes cretaceus* as a true Dasytidae reported from Cretaceous fossils.

The findings of Dasytidae in Charentese amber [3], Prionoceridae in Burmese amber [15], and Malachiidae in Burmese amber [16] provide evidence of an old history for these three families, which have existed independently over at least 100 million years since the Cretaceous. Such a long history of independent evolution of these groups provides a new argument for the systematic positioning of them into three separate families [17].

Representatives of Dasytidae are not rare in Eocene amber inclusions and are also known from Florissant Fossil beds, Colorado, USA, where several new taxa have been described: three extinct genera, *Eudasytites* Wickham, 1912, *Aploceble* Majer, 1998, and *Protomauroania* Tshernyshev, 2021; one subgenus *Aploceble* (*Chalcoaploceble*) Tshernyshev, 2012; and 12 fossil species [18–26].

The majority of Eocene Dasytidae belong to extant genera, represented by the species with elongate, subparallel, and slightly convex bodies which are densely covered with double pubescence. Usually, dasytid beetles registered in inclusions are with filiform (*Dasytes*) or serrate (*Aplocnemus*, *Aploceble*) antennae, but the recently described *Protomauroania* Tshernyshev differs in its clubbed antennae [21]. This genus was attributed to the subfamily Danaceinae on the basis of its clubbed antennae; scalloped lateral side of the pronotum; and long, strong, reddish, and semi-erect setae dorsally. Furthermore, the scalloped lateral edges of the pronotum places this genus in the tribe Amauroniodini. This was the first representative of Danaceinae from Baltic amber.

Recently, a small dasytid beetle possessing clubbed antennae was found in Baltic amber; its body is elongate and subparallel, whereas the pronotum has the scalloped lateral edges; the antennae are long, three apical antennomeres are enlarged and form a ‘club’; the tarsi are shortened and compressed, and tarsomere 1 is as long as tarsomere 2; the pubescence of the dorsal surface consists of short, strong, brown semi-erect and fine adpressed hairs. These brown hairs are dissimilar from the adpressed scales typical of recent Danaceinae and can be considered as an ancestral characteristic which has been modified during evolution to form scales such as in the *Danacea* species. The complex of characteristics mentioned above is close to *Protomauroania* Tshernyshev, which was also described from Baltic amber, but *Protomauroania* differs in its small ovoid body which narrows towards the posterior; short antennae with friable club composed of six apical antennomeres; metatarsi with strongly elongated tarsomeres 1–3; short tarsomere 4 and relatively long tarsomere 5; and dorsal body surface densely covered with stiff, semi-erect, long brown setae. Obviously, the newly registered species belongs to a different genus, and both these two genera are different, but belong to one tribe of Danaceinae. This is the third record of this subfamily in the Eocene amber following those of *Protomauroania chaetophorata* Tshernyshev from Baltic amber [21] and *P. mikhailovi* Tshernyshev & Perkovsky, 2021 from Rovno amber [22].

Based on this complex of characteristics, *Baltamauroania mirabilicornis* gen. et sp. nov. is described and illustrated in the tribe Amauroniodini of the subfamily Danaceinae.

## 2. Materials and Methods

The specimen studied here is currently housed in the collection of Vitalii Alekseev (Kaliningrad, Russia) (collection prefix CVIA) and will ultimately be deposited in the Paleontological Institute of Russian Academy of Sciences (Moscow, Russia) for permanent preservation.

In this study, Malachiidae beetles are considered as a family [1,2,17,27,28], but not as subfamilies, such as, for example, in Gimmel et al. [29].

The amber piece with the inclusion was collected from the surf zone of the Baltic Sea coast near Mechnikovo village (the south-western Sambian peninsula, Kaliningrad region, Russia) on 20 June 2016. The amber piece was polished manually with emery papers of different grit sizes, allowing improved views of the included specimen. The beetle inclusion AWI-144 is preserved in a small, polished piece of transparent amber and subsequently embedded in a block of artificial resin by Hans Werner Hoffeins according to the technique described by Hoffeins [30].

Measurements of the holotype were made using an ocular micrometer in a stereoscopic microscope. Reconstruction was made based on free-hand drawings during an examination of the original specimen. The microphotographs were taken using a Canon EOS 4000D camera mounted on a Zeiss microscope. An extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using Helicon Focus software. The resulting images were edited using Adobe Photoshop 7.0.

Nomenclatural acts introduced in the present work are registered in ZooBank ([www.zoobank.org](http://www.zoobank.org) (accessed on 14 September 2023)) under LSID urn:lsid:zoobank.org:pub:8BFC404A-E24D-46C3-8824-8B1AF65B5070.

## 3. Results

### Systematics

Superfamily **Cleroidea** Latreille, 1802

Family **Dasytidae** Laporte de Castelnau, 1840

Subfamily **Danaceinae** C. G. Thompson, 1859

Tribe **Amauroniodini** Majer, 1987

Genus *Baltamauroania* gen. nov.

LSID: urn:lsid:zoobank.org:act:72BB8249-538E-48C4-994A-BE4852BF0C9D

Type species: *Baltamauroania mirabilicornis* sp. nov., by present designation.

**Diagnosis.** Body black, elongate and subparallel, pronotum with scalloped lateral sides. Antennae 11-segmented, long, three apical antennomeres enlarged and in the form of forming a ‘club’, antennomere 1 cylindrical. Tarsi shortened and compressed, all tarsi 5-segmented, tarsomeres 1 and 2 of similar length, and tarsomere 5 the longest in all legs. Pubescence of the dorsal surface consists of short strong brown semierect and fine adpressed hairs. Punctuation of dorsal surface irregular, elytra-lacking grooves. Pronotum almost equilateral, slightly elongated, with acute anterior and obtuse posterior angles, with wide margination of basal side and scalloped and finely margined lateral edges, which are weakly rounded and provided with an obtuse protuberance below the middle of the disc.

**Etymology.** The name is formed from the name of the Baltic Region where the amber inclusion comes from and the name of a closely related extant genus *Mauroania* Majer, 1997. Feminine gender.

**Comparison.** *Baltamauroania* gen. nov. is similar to *Protomauroania* Tshernyshev, described from Baltic amber, but differs by the following combination of characteristics: subparallel and evenly rounded posteriorly body (ovoid and narrowed posteriorly body in *Protomauroania*); antennae elongate, with a loose 3-segmented club (antennae short with friable club composed of six antennomeres in *Protomauroania*); tarsi shortened and compressed; tarsomeres 1 and 2 of similar length in all legs (metatarsi with strongly elongated

tarsomeres 1–3, a short tarsomere 4, and relatively long tarsomere 5 in *Protomauroania*); body evenly covered with short, strong, brown, semi-erect setae and fine adpressed hairs dorsally (body densely covered with stiff, semi-erect, long brown setae in *Protomauroania*).

**Composition.** Type species only.

**Taxonomic assignment.** The new fossil genus is placed in the family Dasytidae within the superfamily Cleroidea based on the the following combination of characteristics listed by Majer [31]: thorax lacking evaginating vesicles; body integument strongly sclerotized; abdominal ventrites lack membranes for contraction; bodies of adults are less flexible than the bodies of Malachiidae which have fast-opening elytra to initiate flight; body dorsal surface with erect or adpressed hairs, rarely with double pubescence; elytra are evenly rounded towards the apex and weakly flattened; most males lack special male characteristics, indicating sexual dimorphism; tarsomeres 1 and 2 equal in length; claws short, without basal appendages; elytra lacking longitudinal carinae, with irregular punctation.

*Baltamauroania mirabilicornis* gen. et sp. nov. is assigned to the tribe Amauroniodini within the subfamily Danaceinae based on the complex of characteristics mentioned above (see Diagnosis).

*Baltamauroania mirabilicornis* sp. nov.

(Figures 1–3)

LSID: urn:lsid:zoobank.org:act:C658927F-9C1A-4FBE-A855-24EA8EF11362

**Type material.** Holotype: No AWI-144 (CVIA); adult, male (due to strongly prominent ‘antennal club’, i.e., dilated three apical antennomeres, and a shape of ultimate ventrite, which is narrow and truncate at apex so that space between the ventrite and the pygidium remains open).

Almost complete beetle (right antennomeres 5–11 and apical segments of left protarsus were ground off during amber processing) is included in a small, transparent amber piece and subsequently embedded in a block of artificial resin to preserve inclusion. Syninclusions: absent.

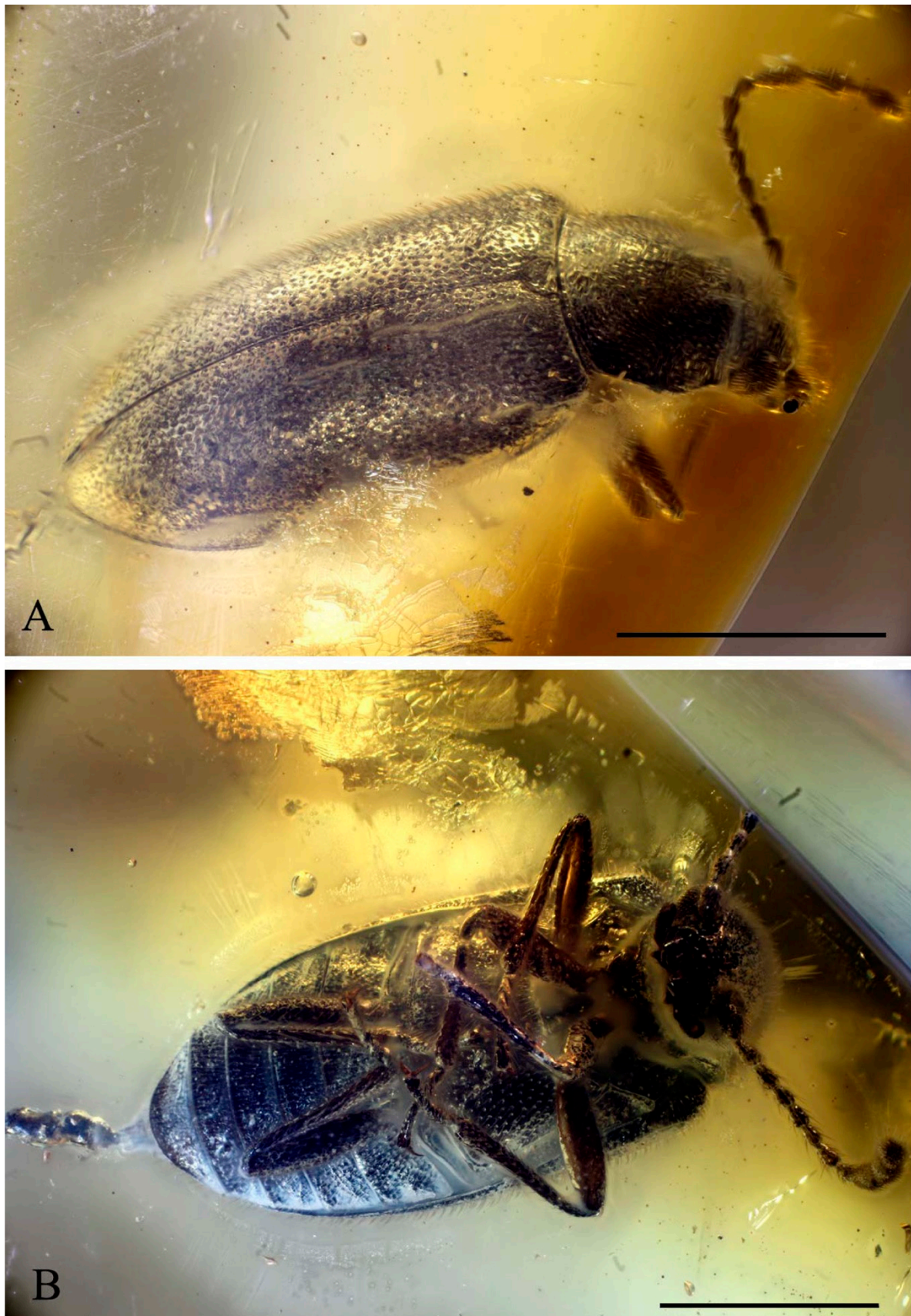
**Type stratum.** Baltic amber; Middle–Late Eocene [32–36].

**Type locality.** Baltic Sea coast near Mechnikovo village (former Neuhäuser), Sambian (Samland) peninsula, Kaliningrad region, W Russia, 20 June 2016, collector: VA. The collection site corresponds to the sampling sector 1.1 ‘Nodems’ [37].

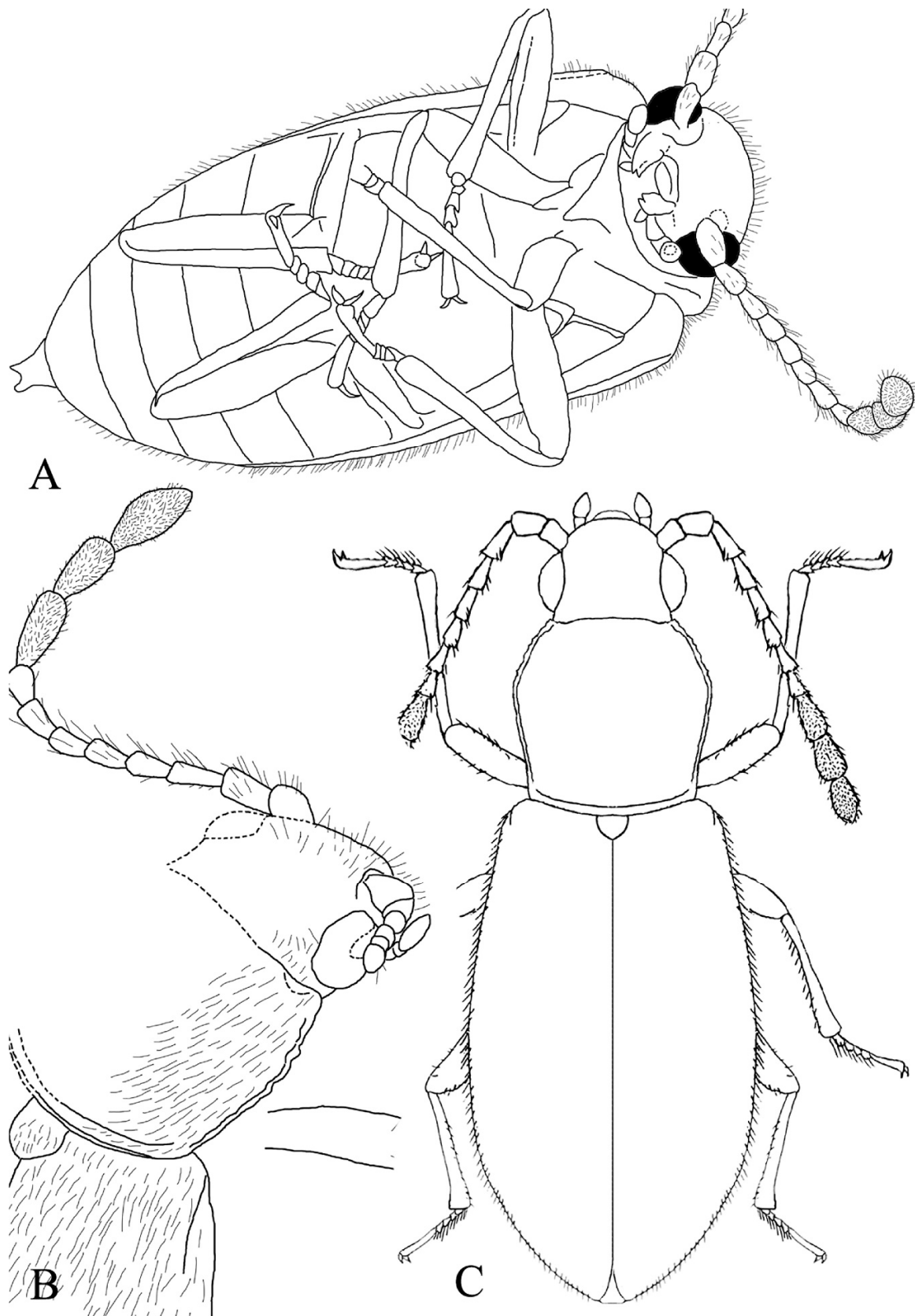
**Description.** Measurements: body length (i.e., length of elytra, pronotum, and head along midline) 3.68 mm, body maximum width across elytra 1.25 mm; head length 0.38 mm, head maximum width at the level of eyes 0.55 mm; pronotum length 0.8 mm, pronotum maximum width 0.75 mm; elytra length 2.5 mm, elytra maximum width 1.25 mm. Body elongated, moderately convex; integument black lacking metallic luster; surface densely covered with strong semi-erect brown setae and fine adpressed hairs.

Head partially retracted into thorax, transverse, about  $1.6\times$  wider (including eyes) than long; finely pubescent by semierect strong hairs; shallowly punctate, distance between punctures  $1.0\text{--}1.5\times$  diameter of one puncture, punctation distinctly denser on periphery. Frons convex. Frontoclypeal suture indiscernible. Mandible with bidentate apex. Compound eyes hemispherical, convex, medium-sized, shallowly impressed near antennal insertion, with fine facets, surface bare, lacking pubescence. Terminal maxillary palpomere large, broadly oval, pointed apically. Antennae inserted close to anterior margin of eyes; antennal insertions exposed in dorsal view, widely separated. Antennae 11-segmented, with loose, 3-segmented club, comparatively long, reaching slightly beyond one-fourth of elytron; all antennomeres elongate,  $2.0\text{--}2.5\times$  longer than wide; with long semierect pubescence; antennomere 1 subcylindrical; antennomeres 2–8 conical, slightly dilated apically; antennomeres 9 and 10 widened, conical, dilated apically, antennomere 9 about  $1.4\times$  wider than antennomere 8; antennomere 11 spindle-shaped, narrowly rounded apically; antennomeres 9–11 densely covered by short and fine pubescence; relative length ratios of antennomeres 1–11 equal to 10:10:7:7:7:7:7:6:10:9:9.

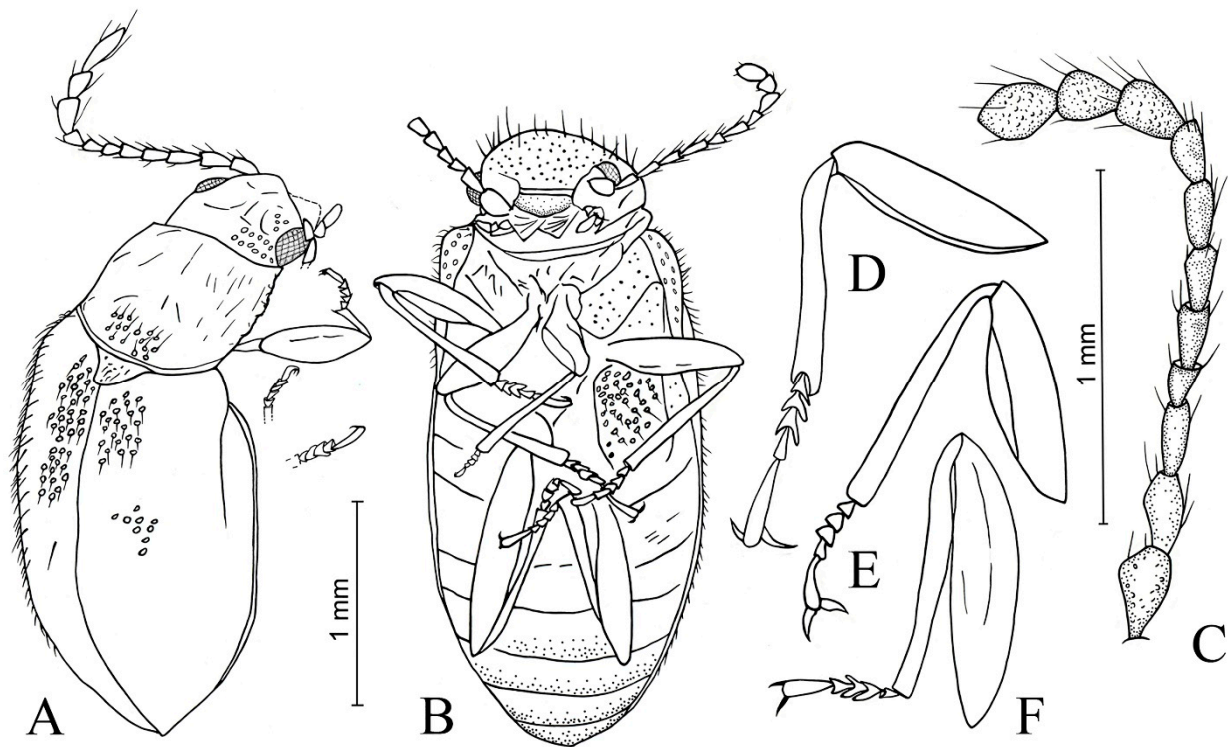




**Figure 1.** Photomicrographs of *Baltamauroania mirabilicornis* gen. et sp. nov., holotype, No AWI-144 (CVIA), habitus: (A) dorso-lateral view; (B) ventral view. Scale bars represent 1 mm.



**Figure 2.** *Baltamauroania mirabilicornis* gen. et sp. nov., holotype, No AWI-144 (CVIA): (A) schematic drawing of the habitus in ventral view; (B) schematic drawing of the lateral margin of the pronotum; (C) reconstruction of the habitus in dorsal view.



**Figure 3.** Schematic drawing of *Baltamauroania mirabilicornis* gen. et sp. nov., holotype, No AWI-144 (CVIA): (A) habitus, dorso-lateral view; (B) habitus, ventral view; (C) right antenna; (D) foreleg; (E) middle leg; (F) hind leg. Scale bars represent 1 mm.

Pronotum weakly elongate  $1.1\times$  longer than wide, narrowed both at base and distally, at base distinctly narrower than elytral base, with the maximal width at the anterior third. Pronotal disc convex. Posterior side strongly and anterior finely marginate, lateral sides scalloped and finely margined. Punctuation on pronotum dense, slightly more widely spaced than on head, distance between punctures equal to  $0.5\text{--}1.0\times$  diameter of one puncture. Posterior angles obtuse; anterior angles acute. Anterior edge weakly rounded, without excision; posterior edge evenly arcuate; lateral edges weakly rounded, with obtuse protuberance before middle, almost straight in posterior two-thirds. Prosternum short anterior of procoxae; with convex disc; sparsely punctate. Prosternal process flat, narrow.

Scutellar shield large, semicircular, as wide as long, finely punctate, and pubescent. Elytra elongate-oval, slightly widened posteriorly, moderately convex, with maximum width in middle,  $2.0\times$  longer than wide, almost  $3.1\times$  as long as pronotum length; completely covering the abdomen; lateral sides slightly rounded; humeri distinct, slightly prominent. Elytral punctuation irregular, coarse and dense; punctures in basal part similar diameter or slightly larger as punctures on pronotum; distance between punctures equal to  $0.5\text{--}1.5\times$  diameter of one puncture. Epipleura narrowed posteriorly, incomplete, extending to about level of abdominal ventrite 2. Mesocoxal cavities subovate, narrowly separated, closed laterally. Meso-metaventral junction straight. Metaventrite with disc convex; covered with coarse, rather dense punctuation.

Legs slender, long, relatively similar in shape, finely punctate, and pubescent. Procoxae large, widely sub-oval, transverse; mesocoxae rounded; metacoxae narrowly oval, strongly transverse. Femora narrowly spindle-shaped, weakly flattened. Tibiae thin, almost straight, slightly dilated apically, nearly as long as femora. Tarsal formula 5-5-5. Tarsi long and thin; tarsomere 1 bilobed, tarsomeres 2-4 simple. In all legs, tarsomere 1 depressed; meso- and metatarsomeres compressed laterally. Claws strong, curved, simple, without appendages, symmetrical.



Abdomen with five visible, freely articulated ventrites, finely punctate and pubescent; intercoxal process rather wide; ventrite 1 longest; ventrite 5 wide and rounded. Relative length ratios of ventrites 1–5 (medially) equal to 25:15:12:10:12.

**Note.** The character state of procoxal cavities (closed or open) is not visible in the examined specimen due to the positioning of the legs in the inclusion.

**Etymology.** The specific epithet *mirabilicornis* is a compound Latin adjective formed from ‘mirabilis’ (strange, wonderful, marvelous) and ‘cornu’ (horn, acute apex), on the basis of the extremely unusual elongate antennal ‘club’ of the beetle.

**Remark.** The included beetle represents an example of stressed behavior in resin [38], namely defecation.

#### 4. Discussion

Representatives of melyrid lineage of the superfamily Cleroidea that include the families Melyridae, Dasytidae, and Rhadalidae are well known from the Eocene, the second of three major worldwide divisions of the Paleogene. Beetles have already been described from Baltic [8,18–21,39–45], Rovno [22,43], and French [46] amber and from imprints in Florissant deposit [23–26,47]. Melyridae lineage of the Cleroidea is reported from Cretaceous Charentese [3] and Burmese amber [48–50] and mentioned from imprints found in Liaoning deposit (Early Cretaceous age, ca. 125 Ma) located near Chaomidian Village, Huangbanjigou: Liaoning Province, China [51].

As mentioned above, amongst the Melyridae-group families, species of the family Dasytidae are more usual in amber inclusions, and several new taxa have been described in the past 100 years: four extinct genera, *Eudasytites* Wickham, 1912; *Aploceble* Majer, 1998 (with the subgenus *Aploceble* (*Chalcoaploceble*) Tshernyshev, 2012); *Protomauroania* Tshernyshev, 2021; and *Protodasytes* Tihelka et al., 2021; and 13 species: *Eudasytites listriiformis* Wickham, 1912; *Eutrichopleurus miocenensis* Wickham, 1917; *Aploceble* (*Aploceble*) *berendti* Majer, 1998; *A. (A.) fuscipes* Majer, 1998; *A. (A.) kunowi* Majer, 1998; *A. (A.) lateantennata* Tshernyshev, 2019; *Protomauroania chaetophorata* Tshernyshev, 2021; *P. mikhailevi* Tshernyshev et Perkovsky, 2021; and *Protodasytes cretaceus* Tihelka et al., 2021 [3,18–23,26].

Furthermore, based on external morphology, some fossil beetles were assigned to the extant genera: *A. (Chalcoaploceble) viridiaeneus* Tshernyshev, 2012; *Aplocnemus (A.) hoffeinso-rum* Tshernyshev, 2019; *A. (Ischnopalpus) baltiensis* Tshernyshev, 2019; *Dasytes (Mesodasytes) ochraceus* Tshernyshev, 2019; *Microjulistus* sp.; *Aplocnemus* sp. and *Psilothrix* sp.; *Xamerpus* sp.; *Malthacodes* sp.; *Pelecophora* sp.; and *Aplocnemus* cf. *tarsalis* C.R. Sahlberg, 1822; and three species closely related to *Dasytes* sp. [18,40]. Majer [18] also identified three inclusions as *incertae sedis* and noted that they belong to a separate genus closely related to *Xamerpus*.

An extinct genus, *Eudasytites* Wickham, and two species, *E. listriiformis* Wickham and *Eutrichopleurus miocenensis* (Wickham), were described from Upper Eocene–Oligocene shale deposits in Florissant Fossil beds, Colorado, USA. The impressions were poorly preserved and indistinct, without legs and antenna. Wickham [23] referred *Eudasytites* to Dasytidae, since the beetle was imprinted from the ventral side and had no distinct male specific structures on the elytra or abdomen, and, therefore, could not be placed in Malachiidae. The characteristics given for the new genus were: ‘slender build and coarse sculpture, with vestiture inconspicuous or wanting’ [23]. The impressions of the other species contrariwise was from dorsal side with distinct elytra and regular punctured rows. This characteristic is close to the recent species *Trichochrous seriellus*, and fossil species described as *T. miocenensis* Wickham. Later, the species was transferred to the genus *Eutrichopleurus* Blaisdell, 1938 [47]. All other Eocene fossil of Dasytidae were found in Baltic and Rovno amber. It should be noted that catalogues [23,40–42,52–54] provide details of effective analysis of impressions and inclusions of fossil insects.

The oldest records of the family Dasytidae relate to two species: *Protodasytes cretaceus* Tihelka, Huang, Perrichot & Cai, 2021, described from Charentese amber of the Late Cretaceous Epoch [3]; and *Acanthocnemoides sukatshevae* Zherikhin, 1977 described from Siberian Taimyr amber of the Mesozoic Albian [11,12].



The genus *Protodasytes* Tihelka, Huang, Perrichot & Cai, 2021, with the type species *Protodasytes cretaceus* Tihelka, Huang, Perrichot & Cai, 2021, was described from Charentese amber discovered in sediments in the Charente-Maritime area of France. This is the oldest record of Dasytidae and the first record in the Cretaceous of Europe [3]. According to geological dating, this amber age is considered as early Cenomanian of the Late Cretaceous Epoch (c. 96 to 100.5 Ma) [9,10]. The external appearance of the beetle in amber, reconstructed using high-resolution X-ray microtomography (micro-CT), looks very similar to *Acanthocnemus*, namely: the shape of the body, black coloration, irregular dense punctation of elytra with typically widened lateral sides in a middle, antennae short with 3-segmented club, legs slender with short and compressed tarsi, and the prothorax hypomeron adjacent to sternopleural suture possesses an elongate pit noticeable in the reconstructed picture (Figure 2B, [3]). This species differs in having longitudinal grooves in lateral sides of the pronotum, typical for the tribe Chaetomalachiini, but was probably used as a primitive thermosensor organ, typical of Acanthocnemidae. Working with the characteristics untypical to any tribes, Tihelka et al. [3] decided to regard this species ‘as a fossil link between the two tribes Dasytini and Listrini’ and to treat the species ‘as tribe *incertae sedis*’.

Recently, the poorly preserved remains of the Mesozoic Albian species *Acanthocnemoides sukatshevae* Zherikhin, 1977 were also re-examined to clarify the attribution of the species to the family Acanthocnemidae [11]. This species was described in Siberian Taimyr amber dated ca. 78 to 115 Ma [55], as a member of the family Acanthocnemidae [12]. To make such a decision in this case was very difficult, since the poorly preserved inclusion was, essentially, only a black contour of the beetle which masked essential characteristics such as tarsomeres and elytral punctation. The only characteristic, the slender antenna with a small club, made it possible to consider this species as belonging to Danaceinae of the family Dasytidae. Kolibač and Perkovsky [11] transferred this species from Acanthocnemidae to Dasytidae, but their decision remains questionable and demands further study of the beetle remains. Very likely, this species is really a member of Acanthocnemidae or an ancestral form of this family which possesses special thermosensitive pores located in a characteristic pit of the prothorax hypomeron adjacent to the sternopleural suture [14].

The largest number of Eocene Dasytidae were probably residents of mixed forests due to the repeated co-occurrence of beetles with stellate fagacean trichomes [20] and original personal observation. Recent Eurasian malachite beetles mainly occur in forest and forest-steppe habitats [6], probably similar to those they inhabited in Paleogene. Dasytid species can be found in coniferous and mixed forests, and, probably, fossil species also occurred in Eocene biocenoses with coniferous trees. Moving to open landscapes, Dasytidae occupied soil litter, whereas the Malachiidae used ecological niches in different plant communities.

Dasytidae species known from Eocene fossils belong both to extinct and extant genera [8]. Beetles with characteristic elongated, subparallel, slightly convex bodies densely covered with double pubescence differ from other similar habitus beetles in possessing filiform (*Dasytes*) or serrate (*Aplocnemus*, *Aploceble*) antennae. These inclusions can be easily attributed to subfamilies Rhadalinae LeConte, 1862 or Dasytinae Laporte de Castelnau, 1840. That is why malachite beetles with clubbed antennae newly discovered in amber inclusions can lead to misidentifications and are, therefore, assigned to Cucujoidea families. After a more detailed morphological study, it is clear that these beetles belong to the Dasytidae subfamily Danaceinae Thomson, 1859. Representatives of this subfamily have demonstrated a high level of evolution adaptation and morphological changes. Typically, this subfamily, represented by small and slightly elongated species densely covered with adpressed scales or scale-shaped chaetae, which prevent drying and overheating, were capable of adapting to open landscapes. The first record of Dasytinae in Baltic amber was the genus *Protomauroania* Tshernyshev [21]. This is a small ovoid beetle with narrowed posteriorly elytra; clubbed antennae; a scalloped lateral side of the pronotum; and long, strong, reddish, semi-erect setae on the upper side of the body. Obviously, this is an ancestral form of recent Danaceinae, demonstrating an initial development of their dense cover as strong semi-erect setae, which was probably modified afterwards to flat scales in *Danacea*. The

scalloped lateral edges of the pronotum made it possible to place this new extinct genus in the tribe Amauroniodini close to the recent genus *Amauronia* Westwood, 1839, for which there was formerly no ancient history evidence of genera of this subfamily. It was the first description of a new extinct genus and species of Danaceinae from Baltic amber. Later, one more species of the genus *P. mikhailovi* Tshernyshev et Perkovsky, 2021 was described from Rovno amber [22]. These records in different amber confirm the widespread and species richness of Danaceinae representatives of Eocene landscapes.

The new genus and species of Dasytinae, *Baltamauroania mirabilicornis* gen. et sp. nov., described herein from Baltic amber, possesses clubbed antennae and pronotum with scalloped lateral sides, but differs in long antennae with only three apical antennomeres which are enlarged and club-shaped; the shortened and compressed tarsi with tarsomeres 1 and 2 equal in length; and pubescence of the dorsal surface consisting of short, strong, brown erect and fine adpressed hairs. Two different genera, *Protomauroania* Tshernyshev and *Baltamauroania* gen. nov., confirm the diversity of Eocene Danaceinae at the generic level.

The characteristics revealed in beetles described from inclusions are considered as typical for the tribe Amauroniodini, and, probably, illustrate an ancestral form for all other representatives of Danaceinae, which, at present, includes three tribes and 20 genera:

1. Tribe Amauroniodini Majer, 1987 (*Amauronia* Westwood, 1839, *Baltamauroania* gen. nov., *Indamauronia* Majer, 1997, *Mauroania* Majer, 1997, *Perisphinctus* Schilsky 1898, *Protomauroania* Tshernyshev, 2021 and *Pseudamauronia* Pic, 1915);
2. Tribe Danacaeomimini Majer, 1987 (*Cyrdobaldus* Majer, 1989, *Cyrdothrix* Majer, 1989, *Danacaeomimus* Champion, 1922, *Piechockia* Majer, 1986, *Schoenia* Majer, 1989);
3. Tribe Danaceini Kiesenwetter, 1863 (*Amecocerus* Solier, 1849, *Danacea* Laporte de Castelnau, 1836, *Haplamaurus* Kirsch, 1865, *Hylodanacaea* Pic, 1926, *Listrocercus* Majer, 1998, *Setigerodasytes* Pic, 1910, *Bilyella* Majer, 1988 and *Hoppingiana* Blaisdell, 1924).

Three recent records of different Amauroniodini taxa from Eocene East European amber (Baltic and Rovno) demonstrate the phenomenon of a high Danaceinae biodiversity in both the southern coast of the Subparatethys (documented by Rovno amber) and on the more northern Fennosarmatian landmass (documented by Baltic amber).

## 5. Conclusions

The newly described genus and species, *Baltamauroania mirabilicornis* gen. et sp. nov., is the third record of the subfamily Danaceinae in Eocene amber, following those of *Protomauroania chaetophorata* Tshernyshev in Baltic amber and *P. mikhailovi* Tshernyshev & Perkovsky in Rovno amber. The discovery of two different genera and at least three distinct species in different ambers confirms the widespread and high level of diversity of Danaceinae in Eocene amberiferous forest landscapes of the Fennosarmatian landmass and in the southern coast of the Subparatethys. This phenomenon of Danaceinae diversity in Eocene fossil remains has only been recorded in the past three years.

Different strategies of adaptation in ecosystems dictate the morphology and bionomy of beetles, but, initially, they were probably connected with trees. The fact that Dasytidae are found in Charentese amber [3], Prionoceridae in Burmese amber [15], and Malachiidae in Burmese amber [16] is clear evidence of the ancient history of these families, which has sustained their independent existence over 100 million years since the Cretaceous to the present day. Such a long existence of independent groups provides a new argument for the systematic positioning of Dasytidae and Malachiidae as separate families, as previously done by Majer [1] and Bocakova et al. [17], and a counterargument for considering them as subfamilies within a single diverse family Melyridae together with Melyridae s.str., as proposed by Lawrence and Leschen [4] and Gimmel et al. [29].

**Author Contributions:** Conceptualization, V.A. and S.E.T.; writing—original draft preparation, review, and editing, S.E.T., G.Y.L., V.A. and A.B.; visualization, S.E.T., V.A. and A.B.; project administration, S.E.T. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The specimen is deposited in the collection of Vitalii Alekseev (Kaliningrad) (collection prefix CVIA) and will ultimately be deposited in the Paleontological Institute of Russian Academy of Sciences (Moscow, Russia) for permanent preservation.

**Acknowledgments:** We are grateful to Mark Seaward (Bradford University, U.K.) for his most helpful advice and linguistic revision of the text, and to Hans-Werner Hoffs (Germany, Hamburg) for the conservation of the studied inclusion. We thank an anonymous reviewer and Gianfranco Liberty for their helpful comments and improvements of our manuscript.

**Conflicts of Interest:** The authors declare no conflict of interest.

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