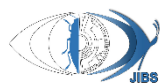


Original Article 

Fifth Baltic amber representative of *Atomaria* Stephens, 1829 (Coleoptera: Cryptophagidae) and an identification key to Eocene species

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ABSTRACT. A new extinct species of the genus *Atomaria* Stephens, 1829 from Baltic amber is described and illustrated: *A. (Anchicera) rasnitsyni* **sp. nov.** from Baltic amber. It is the tenth species of the genus *Atomaria* from the Eocene amber fauna and the fifth species from Baltic amber. The new species is distinguished by the combination of morphological features, particularly the length of the antennae and the shape of the pronotum. An updated key to the species of *Atomaria* known from Eocene ambers is presented. The ecological characteristics of the subgenera of *Atomaria* and their possible influence on the representation of these beetles in Eocene ambers are also discussed. Cryptophagids (19 species) are the most diverse group of mycophagous beetles in European amber.

KEYWORDS: Atomariinae, *Anchicera*, Cretaceous, Mycophagy, Priabonian

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INTRODUCTION

The genus *Atomaria* Stephens, 1829 currently includes two subgenera and approximately 240 species, occurring in all biogeographical realms except Antarctica (Johnson et al. 2007; Pelletier & Hebert 2019; Esser 2021; Otero 2024; Lyubarsky 2025). The genus *Atomaria* Stephens, 1829 comprises two subgenera: the nominotypical *Atomaria* s.str. and *Anchicera* Thomson, 1863. Species of *Anchicera* are characterized by a short, oval body and widely separated antennal insertions, which are attached beneath the lateral margin of the frons, close to the eyes. In contrast, species of subgenus *Atomaria* s.str. typically have an elongated body with subparallel lateral margins, and their antennal insertions are positioned closer to each other. Both subgenera are widely distributed and occur in almost all regions of the world. Extant representatives of both subgenera inhabit leaf litter, decaying hay, and wood-decaying or soil fungi (Leschen 1996). They are also found, albeit sporadically, in stored food products, including those in residential cellars and warehouses, as well as in the burrows and nests of social insects, mammals, and birds.

A total of nine representatives of *Atomaria* (listed below) have been recorded from Baltic, Rovno, and Bitterfeld amber (Lyubarsky & Perkovsky 2013, 2018; Lyubarsky & Bukejs 2022; Lyubarsky et al. 2023a, 2024a, 2024c; Perkovsky & Lyubarsky 2014). Detailed data on the Eocene *Atomaria* records are presented in Table 1.

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Several notes on the Miocene and Lower Cretaceous Cryptophagidae, a change in the taxonomic placement of the genera *Elytrophagus* Zhang, 1989, and *Plastophagus* Zhang, 1989, as well as the description of the Cretaceous genus, *Shixitomaria* Lyubarsky & Perkovsky, 2018, are available in Lyubarsky and Perkovsky (2018). The Mesozoic fauna of Cryptophagidae includes six genera: four genera of Cryptophaginae: *Turgaphagites* Lyubarsky & Perkovsky, 2024 (Barremian-Aptian, Eastern Siberia), *Albocryptophagus* Peris, Lyubarsky & Perkovsky, 2017 (Albian Spanish amber); *Microticus* Lyubarsky, Perkovsky, 2015, and *Ennoticus* Lyubarsky & Perkovsky, 2017 (both Santonian Taimyr amber) (Peris et al. 2017; Lyubarsky & Perkovsky 2017a); and two genera of Atomariinae: *Nganasania* Zherikhin, 1977 (Lyubarsky & Perkovsky 2014, 2017b: two extinct species, Santonian Taimyr amber); *Shixitomaria* (Aptian-Albian, Jiangxi, China). All six genera appear only in the Barremian-Santonian. The Cenozoic fauna differs from the Mesozoic in having a completely different composition of genera. The most comprehensive identification key to Eocene species (updated in the present paper) was presented by Lyubarsky et al. (2024d).

The Eocene amber record of Atomariinae consists exclusively of extant genera. This contrasts with the Mesozoic fauna (Lyubarsky & Perkovsky 2018), where all known genera are different from the extant ones (Lyubarsky & Perkovsky 2018). Until recently, Mesozoic cryptophagid records were almost unknown, but now a general picture of this fauna is emerging (Lyubarsky et al. 2024a, 2024b). The oldest Atomariinae is *Shixitomaria cretacea* (Cai & Wang, 2013) from the Aptian-Albian of the Shixi Formation in southern China (Cai & Wang 2013). This taxon was originally described as *Atomaria*; however, a more detailed examination (Lyubarsky & Perkovsky 2018) revealed discrepancies with the generic characteristics of Cenozoic *Atomaria*, and a new genus was erected for this species (based on traits such as eye size, position of antennal insertion, absence of boss on frons, pronotal structure, and the length of first abdominal ventrite). *Nganasania khetica* Zherikhin, 1977 (Zherikhin 1977; Lyubarsky & Perkovsky 2017b) and *N. taymyrica* Lyubarsky & Perkovsky, 2014 (Lyubarsky & Perkovsky 2014) were described from Santonian Taimyr amber from Yantardakh (Perkovsky & Vasilenko 2019). The genus *Atomaria* was comparatively diverse in Russo-Scandia (Baltic and Bitterfeld amber, but remains unknown from Danish amber), with six described species; it is already more diverse than in Rovno amber (Volhynian Uplift – Chemyreva et al. 2024), where five species are known.

A new cryptophagid is described from Baltic amber. This specimen is assigned to the subgenus *Atomaria* (*Anchicera*) C.G. Thomson, 1863, based on the following character: antennal insertions widely separated. The aim of this study is to describe a new Eocene species of *Atomaria*, incorporate it into an identification key and summary table of the Eocene species of the genus, and discuss the ecological differences between its subgenera in relation to their occurrence in Eocene ambers.

MATERIALS AND METHODS

The studied piece of Baltic amber was mined in Kaliningrad Oblast, Russia, and is of the late Eocene age (Priabonian) (Ross et al. 2026). The amber inclusion was studied, and images were taken using a Leica® Z16 APO stereomicroscope equipped with a Leica DFC 450 camera, or with flash lighting and a P-51 Camlift Driver ver. 2.6.1 controlling a Canon® EOS K2-SC camera. Stacking was performed in Zerene Stacker. Morphological terminology follows Leschen (1996). The holotype (earlier from Karin Nordmann Ernst amber collection) is deposited at the Natural History Museum of Denmark, Copenhagen.

RESULTS

Class Insecta Linnaeus, 1758

Order Coleoptera Linnaeus, 1758

Superfamily Cucujoidea Latreille, 1802

Family Cryptophagidae Kirby, 1826

Subfamily Atomariinae LeConte, 1861

Tribe Atomariini LeConte, 1861

Genus *Atomaria* Stephens, 1829

Subgenus *Anchicera* C.G. Thomson, 1863

Atomaria (Anchicera) rasnitsyni Lyubarsky & Perkovsky, sp. nov.

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[Figs 1–2]

Material examined. **Holotype** NHMD-616938, Yantarnyi, Baltic amber, late Eocene. Syninclusions: stellate hairs. Holotype id deposited at the Natural History Museum of Denmark, Copenhagen.

Etymology. The species is named in honour of the eminent palaeontologist A.P. Rasnitsyn.

Diagnosis. Lateral margins of pronotum visible from above only in basal half of pronotal length; antennae long, antennal club extending beyond base of pronotum when antenna is directed posteriorly; pronotum not or indistinctly narrowed basally, its maximum width at base; 5th antennomere elongated, approximately 1.7 times as long as wide.

Description. Body elongate (Figs 1A, 2A), total length 1.32 mm, maximum width 0.53 mm, moderately convex, covered with slightly curved, decumbent pale pubescence of moderate length. Body, legs and antennae uniformly dark brown. Head transverse, finely punctate dorsally, distance between punctures is greater than a puncture's diameter; facets quite large, significantly larger than diameters of head punctures. Eye well-developed (Fig. 1C). Antennae long (Fig. 1B), slender, with club extending beyond base of pronotum when directed posteriorly (Fig. 1A), flagellomeres elongate, antennomere 1 elongated, slightly curved, 1.5 times as long as antennomere 2, antennomeres 4–6 equal in length, about 1.7 times as long as broad. Antennomere 3 is 1.3 times as long as wide, shorter than antennomeres 4–6, antennomere 7 slightly elongate, about 1.1 times as long as wide, and antennomere 8 slightly wider, subquadrate. Antennomere 9 transverse, 1.25 times as wide as long, slightly narrower than antennomere 10, antennomere 10 distinctly transverse, 1.5 times as wide as long, antennomere 11 widely oval with rounded apex, slightly flattened, twice as long as antennomere 10 (Fig. 1B). Antennal insertions widely separated (Fig. 1C–D). Pronotum slightly transverse (Figs 1A, 2A–B), parallel-sided, widest at base (Fig. 2A), of approximately same width from middle to base, 0.75 times as long as broad, strongly punctured, distance between punctures approximately equal to a puncture's diameter. Pronotal disc slightly convex, anterior margin straight, anterolateral angle without thickening or callosity. Lateral margin visible from above only in basal half of pronotum (Figs 1C, 2B). Base of pronotum with median dorsal depression (Figs 1A, 2B), with basal pits (at the base of the pronotum); posterolateral angles right-angled. Basal margin finely bordered, basal edge slightly lobed. Prosternum finely punctate, distance between punctures greater than puncture diameters (Fig. 1B). Lines on prosternal process absent, prosternal process not vaulted. Longitudinal metasternal line (groove) absent. Scutellar shield small, pentagonal, transverse. Elytra long-oval, approximately parallel-sided, moderately convex, humeral corners rounded, weakly curved at sides (Figs 1A, 2A), maximum width of elytra in first third, 2.6 times as long as pronotum, 1.3 times as long as wide. Elytral surface shiny, moderately densely punctured, punctures on basal part of elytra slightly stronger than those on pronotal disk and separated by approximately 1.5 puncture diameters. Ventrite 1 with intercoxal process wider than long. Femoral line absent. Ventrite 5 evenly arcuate, without crenulations, surface without modifications (Fig. 2C).

Legs. Tibia slender, parallel-sided, with paired terminal spur. Tarsomeres 1 and 5 longest, tarsomere 4 shortest (Figs 1A, 1B, 2C).

Sex. Unknown.

Updated key to extinct Eocene species of *Atomaria (Anchicera)*

- | | | |
|---|---|---|
| 1 | Lateral margins of pronotum visible from above for entire length. Maximum pronotal width before midlength. Antennae long, antennal club extends beyond base of pronotum. 5 th antennomere conical, elongated, 1.5× as long as wide. Body length 1.0–1.1 mm. Baltic amber. | <i>A. groehni</i> Lyubarsky & Perkovsky, 2014 |
| — | Lateral margins of pronotum visible from above only in basal half of pronotum. | 2 |

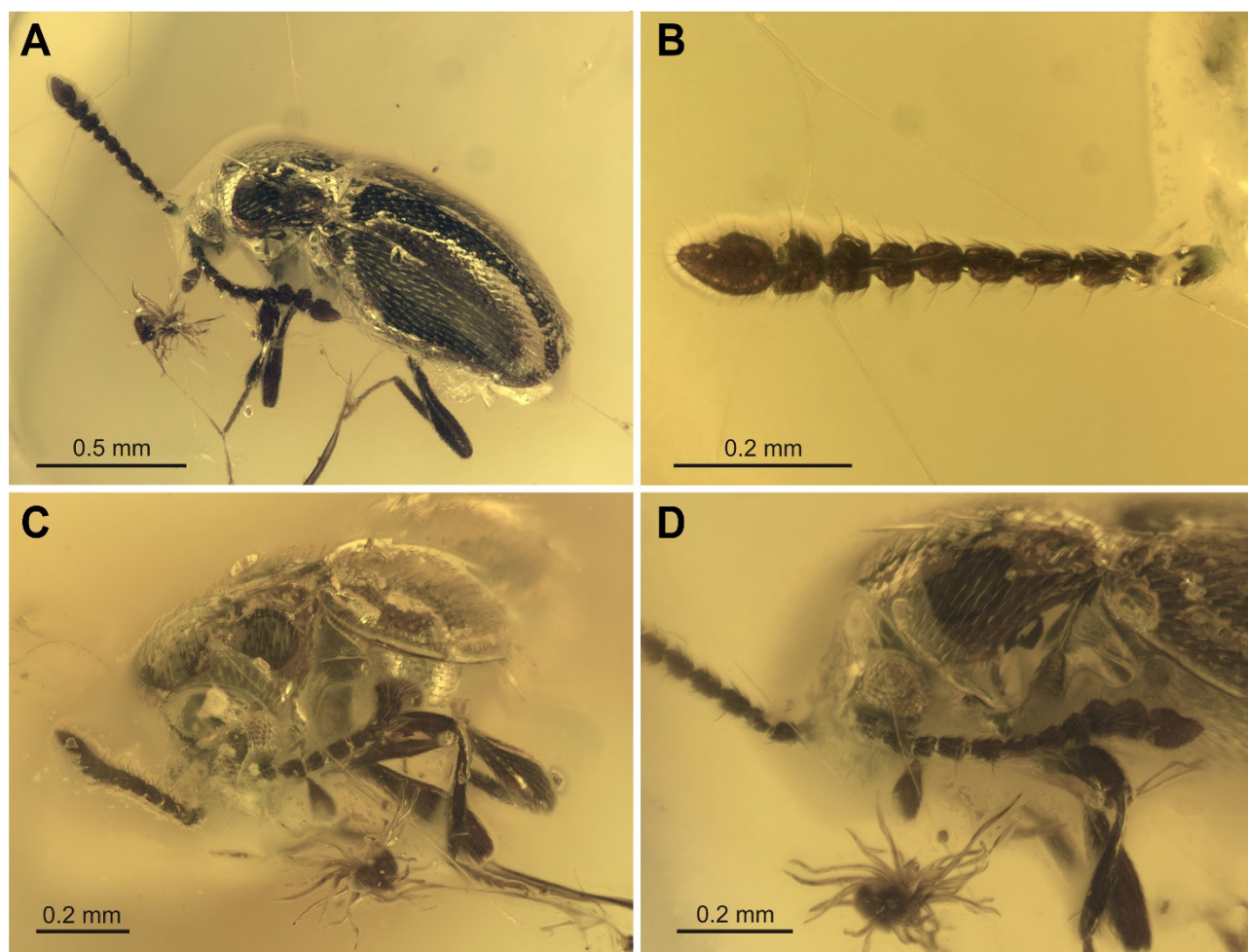


Figure 1. *Atomaria (Anchicera) rasnitsyni* sp. nov., holotype. A. Body, dorsolateral view; B. Antenna; C. Head: face and antenna; D. Head and pronotum, lateral view.

- | | | |
|---|--|---|
| 2 | Antennae short, antennal club not extending beyond base of pronotum when directed posteriorly. | 3 |
| — | Antennae long, antennal club extends beyond base of pronotum when directed posteriorly. | 2 |
| 3 | Pronotum distinctly narrowed basally, maximum pronotal width at its midlength. | 4 |
| — | Pronotum not or indistinctly narrowed basally, maximum width of pronotum at its base. | 5 |
| 4 | Fifth antennomere elongate, 1.5× as long as wide. Body length 1.35 mm. Rovno amber..... | |
| | <i>A. telnovi</i> Lyubarsky, Perkovsky & Vasilenko, 2023 | |
| — | Fifth antennomere subquadrate, 1.1× as long as wide. Body length 1.19 mm. Rovno amber. | |
| | <i>A. perkovskyi</i> Lyubarsky & Bukejs, 2022 | |
| 5 | Fifth antennomere equal in length to antennomere 3. Antennomere 7 subquadrate, approximately as long as antennomeres 6 and 8. Body length 1.35 mm. Bitterfeld amber, Rovno amber. | |
| | <i>A. saxonica</i> Lyubarsky & Perkovsky, 2018 | |
| — | Fifth antennomere longer than third. Seventh antennomere elongated, longer than antennomeres 6 and 8. Body length 1.35 mm. Rovno amber. | |
| | <i>A. archibaldi</i> Lyubarsky & Perkovsky, 2024 | |
| 6 | Pronotum distinctly narrowed basally, maximum pronotal width at its midlength. | 7 |
| — | Pronotum not or indistinctly narrowed basally, maximum width of the pronotum at its base. | 9 |
| 7 | Pronotal disc flat, without transverse depression. Pronotum strongly narrowed basally. Body length 1.65 mm. Baltic amber. | |
| | <i>A. gedanicola</i> Lyubarsky & Perkovsky, 2013 | |
| — | Pronotal disc convex, with distinct transverse depression. Pronotum slightly narrowed basally. | 8 |

- 8 Antennal flagellum stout, $\sim 0.33\times$ as wide as dorsal eye length. Third antennomere $\sim 1.3\times$ longer than wide. Antennomeres 9–10 slightly transverse. Body length 1.46 mm. Baltic amber. *A. propinqua* Lyubarsky, Alekseev & Bukejs, 2023
- Antennal flagellum slender, $\sim 0.2\times$ as wide as dorsal eye length. Third antennomere $\sim 1.8\text{--}2\times$ longer than wide. Antennomeres 9–10 strongly transverse. Body length 1.39–1.57 mm. Baltic amber. *A. alekseevi* Lyubarsky & Bukejs, 2022
- 9 Fifth antennomere subquadrate. Body length 1.65 mm. Rovno amber. *A. bukejsi* Lyubarsky & Perkovsky, 2024
- Fifth antennomere elongated, ~ 1.7 times as long as broad. Body length 1.32 mm. Baltic amber. *A. rasnitsyni* sp. nov.

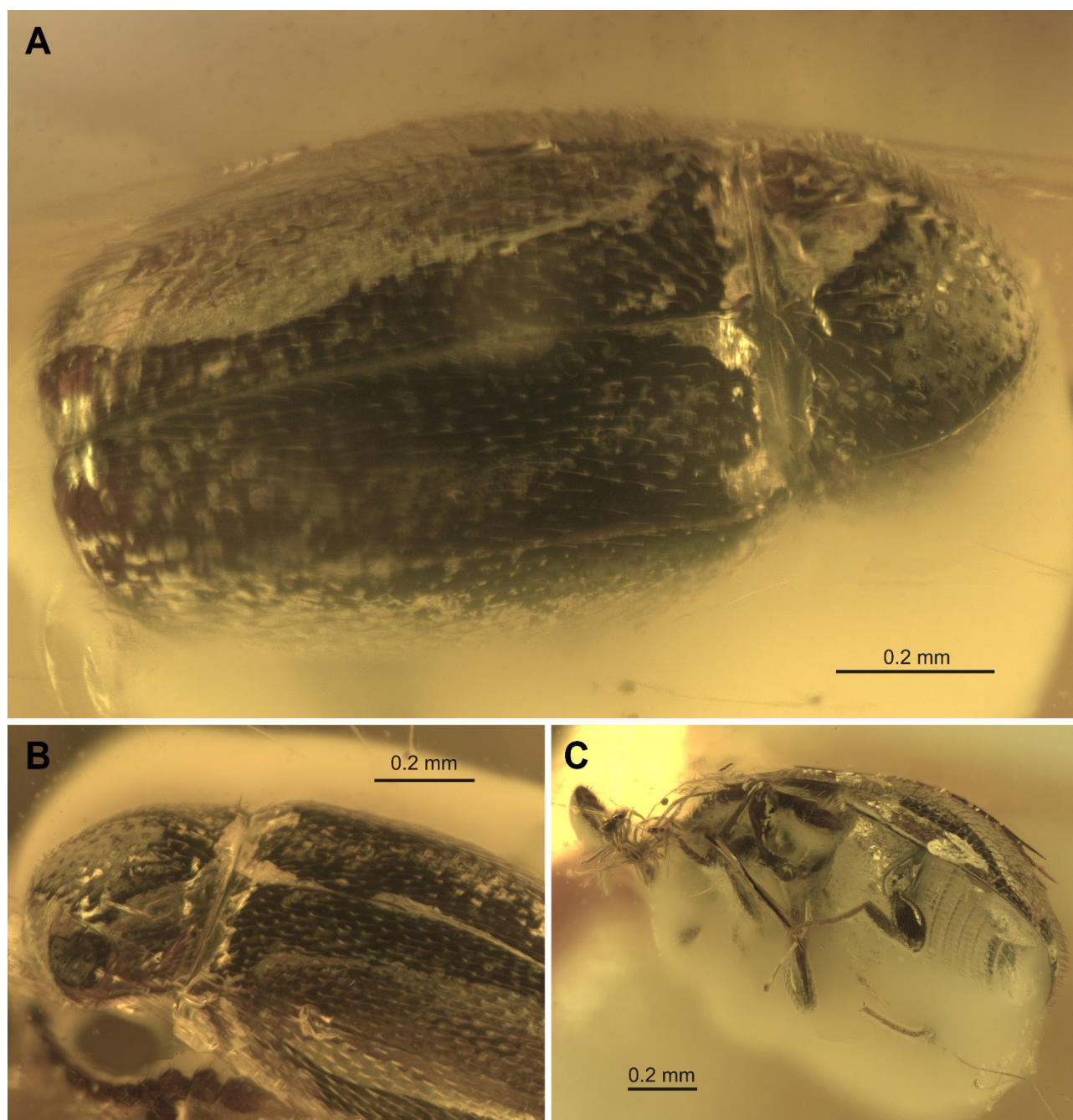


Figure 2. *Atomaria* (*Anchicera*) *rasnitsyni* sp. nov., holotype. A. Dorsal view. B. Pronotum, and anterior part of elytra, dorsolateral view. C. Ventral view.

Table 1. The list of Eocene amber *Atomaria* (*Anchicera*) species.

<i>Atomaria</i> species	Author/year	Amber deposit/locality	Age	Type material	Depository*	Body length (mm)	Original reference
<i>A. alekseevi</i>	Lyubarsky & Bukejs, 2022	Baltic amber	Late Eocene	Holotype No 6831 [MAIG]	MAIG	1.39–1.57	Lyubarsky & Bukejs 2022 Lyubarsky et al. 2024c
<i>A. archibaldi</i>	Lyubarsky & Perkovsky, 2024	Rovno amber	Late Eocene	Holotype SIZK L-425	SIZK	1.31	Lyubarsky et al. 2024d
<i>A. bukejsi</i>	Lyubarsky & Perkovsky, 2024	Rovno amber	Late Eocene	Holotype SIZK CC-2	SIZK	1.65	Lyubarsky et al. 2024d
<i>A. gedanicola</i>	Lyubarsky & Perkovsky, 2013	Baltic amber	Late Eocene	Holotype MAI-897	MAIG	1.65	Lyubarsky & Perkovsky 2013
<i>A. groehni</i>	Lyubarsky & Perkovsky, 2014	Baltic amber	Late Eocene	Holotype GPIH no. 4458	GPIH	1.0–1.1	Perkovsky & Lyubarsky 2014 Lyubarsky & Perkovsky 2021
<i>A. perkovskyi</i>	Lyubarsky & Bukejs, 2022	Rovno amber	Late Eocene	Holotype 6832 [MAIG]	MAIG	1.19	Lyubarsky & Bukejs 2022
<i>A. propinqua</i>	Lyubarsky, Alekseev & Bukejs, 2023	Baltic amber	Late Eocene	Holotype No 062 [ACAB]	VA	1.46	Lyubarsky & Bukejs 2022
<i>A. rasnitsyni</i> sp. nov.	Lyubarsky et al.	Baltic amber	Late Eocene	Holotype NHMD-616938	NHMD	1.32	Current study
<i>A. saxonica</i>	Lyubarsky & Perkovsky, 2018	Bitterfeld and Rovno amber	Late Eocene	Holotype 1223-4	SDEI	1.35	Lyubarsky & Perkovsky 2018 Lyubarsky et al. 2024a
<i>A. telnovi</i>	Lyubarsky, Perkovsky & Vasilenko, 2023	Rovno amber	Late Eocene	Holotype SIZK UA-28149	SIZK	1.35	Lyubarsky et al. 2024c

GPIH – Geological-Palaeontological Institute, University of Hamburg, Germany; **MAIG** – Museum of Amber Inclusions (Muzeum inkluzji wbrusztynie), Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk (Gdańsk, Poland); **NHMD** – Natural History Museum of Denmark, Copenhagen; **SDEI** – Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **SIZK** – Schmalhausen Institute of Zoology, Kyiv, Ukraine; **VA** – Vitalii Alekseev's personal collection, Kaliningrad, Russia.

DISCUSSION

All Eocene species of *Atomaria* belong to the subgenus *Anchicera* Thomson, 1863. This subgenus is very numerous in the extant fauna. Adults of modern *Anchicera* species are most often found on flowers and forest litter, collected in mass in flight on summer evenings, and also found on wood-decaying fungi and mouldy substrates (Leschen 1996). This pattern is supported by a sample of specimens from three different ambers, in which nine fossil species of the subgenus *Anchicera* were identified, whereas no species of the nominotypical subgenus were hitherto found. Misidentification of the subgenus is unlikely, as the two subgenera differ in the position of antennal insertions, a feature that remains discernible even when the antennae are lost. Extant species of the nominotypical subgenus are somewhat more frequently found in concealed habitats associated with fungi; however, this difference is not statistically significant. Many species of the genus *Atomaria* are nidicoles, inhabiting nests and burrows of social insects, mammals, and birds. In the extant fauna, the number of species in the subgenus *Anchicera* is approximately twice that of the nominotypical subgenus. An analysis of the ecology of extant species reveals significant differences between the two subgenera in their associations with animal nests. Species of both subgenera are found with similar frequency in nests and burrows of mammals and birds; however, species of the nominotypical subgenus are encountered much more frequently – approximately four times as often – in the nests of social insects (original data).

The following species of *Anchicera* are recorded from nests and burrows of mammals and birds: *Atomaria* (*Anchicera*) *analisis* Erichson, 1846; *A.* (*A.*) *apicalis* Erichson, 1846; *A.* (*A.*) *fuscata* (Schönherr, 1808); *A.* (*A.*) *mesomela* (Herbst, 1792), *A.* (*A.*) *morio* Kolenati, 1846; *A.* (*A.*) *munda* Erichson, 1846; and *A.* (*A.*) *peltata* Kraatz, 1853. The following species of the nominotypical subgenus were discovered in the nests and burrows of mammals and birds: *Atomaria* (s.str.) *gracilicornis* Reitter, 1888; *Atomaria* (s.str.) *linearis* Stephens, 1830; *Atomaria* (s.str.) *trapeziformis* Johnson, 1970; and *Atomaria* (*A.*) *vespertina* Mäklin, 1853. There are approximately twice as many mammal and bird nidicoles known in the subgenus *Anchicera* as in the nominotypical subgenus; this corresponds with the proportion of species in each of the subgenera within the overall taxonomic diversity. Eight species of the subgenus *Anchicera* were recorded from the nests of social insects (bees, wasps, ants): *A.* (*A.*) *analisis* Erichson; *A.* (*A.*) *apicalis* Erichson; *A.* (*A.*) *atra* (Herbst, 1793); *A.* (*A.*) *fuscata* (Schönherr); *A.* (*A.*) *kamtschatica* Motschulsky, 1845;

A. (A.) lewisi Reitter, 1877; *A. (A.) morio* Kolenati, and *A. (A.) rubella* Heer, 1841; only one species of the nominotypical subgenus was found: *Atomaria* (s.str.) *elongatula* Erichson, 1846 (in a honeybee hive). Thus, the proportion of social-insect nidicoles in the nominotypical subgenus is lower than its proportion of the genus's overall taxonomic diversity. Species of the subgenus *Anchicera* appear to be more closely associated with the nests of social insects than species of the nominotypical subgenus. It may cautiously be suggested that the differences in niche preferences and degree of specialisation observed in extant species were also characteristic of these subgenera during the Eocene. Such differences may account for the unequal representation of known species of the two subgenera in Eocene ambers. However, the ecology of this group remains insufficiently studied, precluding any definitive conclusions.

A total of 19 species in European amber (additionally ten species of late Eocene Cryptophaginae (Lyubarsky & Perkovsky 2020, 2021; Lyubarsky et al. 2024a, 2024e, 2024f) from Rovno, Danish and Baltic amber) which by far does not exhaust the entire diversity of the group in the amber forests of Europe, makes cryptophagids one of the most diverse families of beetles in the European amber fauna (Lyubarsky et al. 2024a). The climate of the European amber-producing forests was equable (Archibald & Farrell 2003; Legalov et al. 2022; Lyubarsky et al. 2023b; Telnov & Perkovsky 2025, 2026), with mild winters and summers that were not hot (Colombo et al. 2020). Cryptophagidae (Lyubarsky & Perkovsky 2014, 2015, 2017a, 2017b) compose a third of the known species of Taimyr amber beetles (Perkovsky & Vasilenko 2019; Perkovsky et al. 2024) and a quarter of the known amber beetle species from the *Baeomorpha* Realm (Siberian and Canadian amber). As climate of Taimyr amber forest was warm temperate (Telnov et al. 2024), not surprising that silken fungus beetles are abundant and diverse in European ambers, as temperate elements strongly dominate in these climates (Legalov et al. 2024; Melnitsky et al. 2024). Some other dominant elements of the Late Cretaceous *Baeomorpha* Region, such as polycentropodid caddisflies (Perkovsky 2022 and references therein), also appear to have been well adapted to life in the Eocene amber forest.

AUTHOR CONTRIBUTIONS

The authors confirm their contribution to the paper as follows: G.Yu. Lyubarsky & E.E. Perkovsky: Conceptualisation, Taxonomic investigation, Visualisation, Writing – original draft, Writing – review and editing; D.V. Vasilenko: Visualisation, Writing – original draft, Writing – review and editing; A.A. Legalov: Writing – original draft, Writing – review and editing. The authors read and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

The type specimen mentioned in this study is deposited at the Natural History Museum of Denmark, Copenhagen, and is available from the curator upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included fossil arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

GENERATIVE AI STATEMENT

No generative AI tools were used in the preparation of this manuscript.

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پنجمین نمایندهٔ سردهٔ *Atomaria* Stephens, 1829 (Coleoptera: Cryptophagidae) در کهربای بالتیک و کلید شناسایی گونه‌های ائوسن

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چکیده: گونه‌ای منقرض‌شده و جدید از سردهٔ *Atomaria* Stephens, 1829 در کهربای بالتیک به نام *A. (Anchicera) rasnitsyni* sp. nov. توصیف و تصاویر آن ارائه شد. این آرایه، دهمین گونه از سردهٔ *Atomaria* در فون کهرباهای ائوسن و پنجمین گونهٔ آن از کهربای بالتیک است. گونهٔ جدید با ترکیبی از ویژگی‌های ریخت‌شناختی، به‌ویژه طول شاخک‌ها و شکل پیش‌گرده، از گونه‌های دیگر متمایز می‌شود. کلید شناسایی به‌روزشده‌ای برای گونه‌های *Atomaria* شناخته‌شده از کهرباهای ائوسن ارائه شد. همچنین ویژگی‌های بوم‌شناختی زیرسرده‌های *Atomaria* و تأثیر احتمالی آن‌ها بر حضور و فراوانی این سوسک‌ها در کهرباهای ائوسن مرور شد. سخت‌بال پوشان خانواده Cryptophagidae، متنوع‌ترین گروه سوسک‌های قارچ‌خوار در کهربای اروپا (۱۹ گونه) هستند.

ویراستار علمی

مصطفی غفوری‌مقدم

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واژگان کلیدی: *Anchicera*، *Atomariinae*، کرتاسه، قارچ‌خواری، پریابونین،