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A new species of Eupariini from Eocene Baltic amber (Coleoptera: Scarabaeidae: Aphodiinae)

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Abstract

Based on 10 specimens from Late Eocene Baltic amber, an extinct species of Eupariini (Coleoptera: Scarabaeidae: Aphodiinae), *Airapus lithuanicus* Tamutis, Alekseev, & Bukejs **new species**, is described and illustrated. The new species is compared with two known fossil representatives of Aphodiinae from Baltic amber. The generic placement of these two species, *Saprosites succini* (Zang, 1905) and *Ataenius europaeus* Quiel, 1910, is discussed, as are details of paleoecology for the new species.

Key words: beetles, Airapus, palaeontology, Paleogene, fossil resin

Dedication

We dedicate the current study to the 100th anniversary of Restoration of the State of Lithuania.

Introduction

The ground-dwelling Aphodiinae (Coleoptera: Scarabaeidae), which occur in terrestrial habitats throughout the world, are rarely fossilized in amber. Over the last hundred years, only two species belonging to this subfamily, *Saprosites succini* (Zang, 1905) and *Ataenius europaeus* Quiel, 1910 have been described from Baltic amber. The first species was originally described in *Aphodius* Illiger (Aphodiini) and was subsequently transferred by Quiel (1910) to *Ataenius* Harold (Eupariini), and by Kolbe (1925) to *Saprosites* Redtenbacher (Eupariini). This generic placement was catalogued in the works of Hieke & Pietrzeniuk (1984), Krell (2000), Alekseev & Alekseev (2016), and Alekseev (2017). The present record of the third species, representing the extant genus *Airapus* Stebnicka & Howden, 1996 (Eupariini), is of great interest in the study of the evolution of this group.

Material and methods

Ten scarabaeid inclusions from two Baltic amber pieces were examined during the current study. The first amber piece "KZM-0001" containing the holotype and eight paratypes is deposited in the Kaunas T. Ivanauskas Zoological Museum (Kaunas, Lithuania) [KZM]. All specimens are included in one medium-sized yellow piece with approximate dimensions of $55 \times 30 \times 20$ mm and were numbered according to the following scheme: 1, holotype; 2–9, paratypes (Fig. 3). Additional animal syninclusions include one specimen of Staphylinidae (Coleoptera: Staphylininae: possibly Philonthini), one specimen of Elateridae (Coleoptera), one small specimen of Hymenoptera, one small spider (Araneae), and one mite (possibly Trombidioidea). Observations of these

specimens were made using a Leica MZ16 stereomicroscope. The photographs were taken using a Motic SMZ – 168 stereomicroscope equipped with a Nikon D3100 digital camera.

The second amber piece "3891" containing a paratype is currently housed in the private collection of Andrzej Górski (Bielsko-Biała, Poland) [CAG] and will subsequently be deposited in the collection of the Museum of Natural History, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland [ISZP]. The complete beetle is included in a small, yellow, subquadratic amber piece with approximate dimensions of $27 \times 20 \times 3$ mm. Syninclusions consist of a few stellate Fagaceae trichomes, some pieces of organic material, and small gas vesicles. Observations of this specimen were made using a Nikon SMZ 745T stereomicroscope. The photographs were taken using a Nikon SMZ 745T stereomicroscope with a Nikon DSFi1 digital camera. Extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using Helicon Focus software.

The amber piece "KZM-0001" originated from Yantarny Village [formerly Palmnicken] of the Sambian [Samland] peninsula in Kaliningrad Region (Russia). The amber piece "3891" [CAG] was collected on the Baltic Sea coast near Gdańsk (Poland).

The amber pieces were polished by hand, allowing improved views of the included specimens, and were not subjected to any supplemental fixation. Measurements were taken using an ocular micrometer (expressed in millimeters).

Systematic Palaeontology

Genus Airapus Stebnicka & Howden, 1996

Remarks. The species under consideration belongs to *Airapus* based on a combination of the following characters: (1) mesocoxae widely separated and flattened, (2) mesofemora relatively long, (3) mesosternum flattened, (4) mesotibiae and metatibiae with longitudinal lines, (5) metatarsomere 1 long, (6) lateral pronotal sides explanate, and (7) elytra with 1 or 2 humeral denticles.

Airapus lithuanicus Tamutis, Alekseev, & Bukejs, new species

(Figs. 1-8)

Type material. Holotype: "0001-01" [KZM], adult, complete, sex unknown. Ventral side of specimen almost completely obscured by "milky" opacity.

Paratype: "0001-02" [KZM], adult, complete, sex unknown. Elytra, pronotum, right mesotibiae and metatibiae, and tarsi visible in dorsal view; ventral part of specimen almost completely obscured by "milky" opacity.

Paratype: "0001-03" [KZM], adult, complete, sex unknown. Dorsal and ventral sides partially obscured by "milky" opacity; left side of dorsal surface visible; ventral view has anterior parts of protibiae and tarsi, ventral side of mesofemorae, and metathoracic legs visible.

Paratype: "0001-04" [KZM], adult, complete, sex unknown. Dorsal side of specimen partially and ventral side completely obscured by "milky" opacity; only left side of pronotum and basal part of elytra visible.

Paratype: "0001-05" [KZM], adult, complete, sex unknown. Dorsal side of specimen completely and ventral side partially obscured by 'milky" opacity; only anterior part of head, both sides of prothorax (including episternum and epipleura), mesothorax and metathorax, ventral sides of legs, and medial part of abdomen visible in ventral view.

Paratype: "0001-06" [KZM], adult, complete, sex unknown. Dorsal side of specimen partially and ventral side completely obscured by "milky" opacity; only dorsal part of pronotum and most of elytra visible.

Paratype: "0001-07" [KZM], adult, complete, sex unknown. Dorsal and ventral sides completely obscured by "milky" opacity, but punctation and sculpture of medial part of pronotum and elytra clearly visible.

Paratype: "0001-08" [KZM], adult, complete, sex unknown. Dorsal side of specimen partially and ventral side completely obscured by "milky" opacity; only part of pronotum and medial part of elytra visible.

Paratype: "0001-09" [KZM], adult, complete, sex unknown. Dorsal and ventral sides almost without "milky" opacity, but position of specimen in amber piece renders most body regions incompletely visible, except for front of head, right side of pronotum, left mesothoracic and metathoracic legs.

Paratype: "3891" [CAG], adult, complete, sex unknown. Dorsal and ventral sides relatively clearly visible; only ventral part of head and prothorax slightly obscured by "milky" opacity.

Type strata. Baltic amber, mid-Eocene to Upper Eocene.

Type locality. Southeastern Baltic Sea coast.

Etymology. The specific epithet "*lithuanicus*" [Lithuanian] is toponymic adjective derived from the name of the Baltic country Lithuania.

Differential diagnosis. *Airapus lithuanicus* differs from Aphodiinae previously described from Baltic amber in possessing mesotibiae and metatibiae with longitudinal lines and two apical spurs, as well as possessing suite of characters mentioned in Table 1.

Within *Airapus*, the newly described fossil species differs from extant congeners (Stebnicka & Howden 1996; Stebnicka 1998) in the combination of the following characters: sides of pronotum explanate, pronotal lateral margins crenulate and setose, pronotal base not bordered, pronotal posterior angles widely rounded, clypeal anterior margin slightly upturned and rounded on each side of anteromedial emargination, head finely and densely punctate, humeri with single small denticle, and head and pronotum without distinct setation.



FIGURES 1–2. *Airapus lithuanicus* **new species**: 1—habitus, dorsal view (left—holotype "0001-01" [KZM]; right—paratype "0001-02" [KZM]); 2 – habitus, ventral view (paratype "0001-05" [KZM]). Scale bars = 1 mm.

TABLE 1. Character matrix for identification of Eupariini from Baltic amber.

	Airapus lithuanicus new species	Ataenius europaeus Quiel	Saprosites succini (Zang)
Base of pronotum	not bordered	bordered	finely bordered
Punctation of pronotum	punctures smaller in anterior half	punctures deep and large	punctures smaller in anterior half
Punctation of head	dense and fine	dense and coarse	dense and fine
Apical spurs of mesotibiae and metatibiae	two, unequal in length	one	two, unequal in length
Pronotum	transverse	transverse	as long as wide
Scutellum	triangular	triangular	semicircular
Elytral base	narrower than pronotum	narrower than pronotum	as wide as pronotum



FIGURES 3–4. *Airapus lithuanicus* **new species**: 3—general view of amber piece "0001" [KZM] with specimen numeration (1—holotype; 2–9—paratypes); 4—habitus, frontal view (paratype "0001-09"). Scale bar: 5 mm for Fig. 3; 0.5 mm for Fig. 4.



FIGURES 5–6. *Airapus lithuanicus* **new species**, paratype "3891" [CAG]: 5—habitus, dorsal view; 6—habitus, ventral view. Scale bars = 1 mm.

Description. *Habitus*. Body moderately convex, elongate, almost parallel-sided; reddish brown to black in color, with lighter appendages (especially visible in paratype "0001-03"); apparently glabrous dorsally. Body length without head (head turned downwards) 3.4–4.0 mm, length with head about 4.1–4.8 mm, maximum width 1.5–2.0 mm. Holotype: "0001-01" 3.4 mm long without head (approximately 4.1 mm with head) and 1.7 mm wide; paratypes: "0001-02" 3.5 mm long (approximately 4.2 mm long with head), and 1.7 mm wide; "0001-03" 3.4 mm

long (approximately 4.1 mm long with head), and 1.7 mm wide; "0001-04" 3.4 mm long (approximately 4.1 mm long with head), and 1.6 mm wide; "0001-05" 3.4 mm long (approximately 4.1 mm long with head), and 1.6 mm wide; "0001-06" 3.5 mm long (approximately 4.2 mm long with head), and 1.7 mm wide; "0001-07" 3.4 mm long (approximately 4.1 mm long with head), and 1.6 mm wide; "0001-08" 3.7 mm long (approximately 4.4 mm long with head), and 1.6 mm wide; "0001-08" 3.7 mm long (approximately 4.4 mm long with head), and 1.7 mm wide; "0001-09" 3.6 mm long (approximately 4.3 mm long with head), and 1.6 mm wide; "3891" 4.0 mm long (approximately 4.8 mm long with head), and 2.0 mm wide.

Head. Transverse, slightly convex, narrower than pronotal anterior margin; finely and densely covered with simple, round punctures, distance between punctures smaller than diameter of one puncture (punctures on vertex distinctly sparser). Clypeus dilated, covering mouthparts; anterior margin widely rounded toward obtuse angle on each side of shallow anteromedial emargination. Genae protruding, margin with few very short, stout setae. Compound eye moderately large and convex, visible in dorsal view. Maxillary palpus with 4 palpomeres; apical palpomere elongate, subcylindrical with narrowed apical half, $3.5 \times$ as long as wide, and about $2.7 \times$ as long as penultimate palpomere. Labial palpus with 3 palpomeres; short, minute; apical palpomere subcylindrical, slightly tapered, nearly as long as palpomeres 1-2 combined. Antennae with 3 antennomere club.

Thorax. Pronotum tranverse, $1.6 \times$ as wide as long; disc evenly and slightly convex, with lateral sides narrowly explanate and flat (width of flattened area reaches about 1/13 of pronotal width); densely covered with small punctures, with distance between punctures approximately $0.5-1.5 \times$ diameter of single puncture; punctures distinctly finer and sparser in anterior one-third of pronotal length. Lateral margins nearly straight, distinctly upturned, not bordered, without marginal line, crenulate; bearing sparse, scale-like, erect setae; posterior margin moderately convex, not bordered; anterior margin slightly convex. Anterior angles rounded, slightly protruding; posterior angles widely rounded.

Scutellum triangular (as long as anterior width), rounded apically.

Elytra parallel-sided, moderately convex, elongate, $1.4 \times$ as long as combined width, about $2.5 \times$ as long as pronotum, widest behind mid-length; elytral base narrower than pronotum; lateral margins bearing short, sparse setae. Humerus with single, small, sharp denticle. Each elytron apparent with 10 deep, punctate striae; punctures elongate (nearly twice as long as width); distance between punctures about $1.5-2.5 \times$ diameter of single puncture in basal one-third of elytra. Interstriae distinctly convex; granulate medially, granulation of interstriae 1–3 less distinct, granulation of interstriae 4–8 more conspicuous; and covered with fine, sparse secondary punctation. Epipleura wide at humeri and gradually narrowed toward elytral apex, reaching elytral apex.

Hypomeron finely, densely punctate. Mesosternum flattened, less elevated than metasternum; with convex triangular area above meso-metasternal suture, and top of triangle with very fine mesosternal carina. Mesosternum and mesocoxae finely and densely punctate (almost equal to prosternal punctation). Disc of metasternum almost flat with midline impressed; with sparse, moderately large punctures (distinctly larger than punctures of prosternum and mesosternum), distance between punctures $1-3\times$ diameter of single puncture; lateral metasternal triangle broad, shallow, distinctly wrinkled. Procoxae and metacoxae apparently contiguous, mesocoxae widely separated by distance about equal to width of mesofemora. Mesocoxae subparallel-sided, flattened, with distinct longitudinal elevated line laterally; separated from base of elytral epipleuron by distinct mesepimeron.

Abdomen. With five visible ventrites, punctation similar to punctation of metasternal disc. Ventrites 2–3 equal in length; ventrite 4 slightly shorter, $0.6 \times$ as long as ventrite 3 medially; anterior margin of ventrite 4 slightly concave.

Legs. Protibia rather short, nearly as long as profemora, impunctate; with terminal spur, slightly arcuately downward; with three large, outer denticles in apical half and with few short, small denticles in basal half. Profemora wide, perimarginal groove deep, posterior margin with marginal line. Mesotibiae and metatibiae weakly expanded apically, with three longitudinal setigerous lines and punctures; with two terminal spurs of unequal length, longest spur distinctly shorter than tarsomere 1 and about $2\times$ longer than shortest spur; apex of mesotibia and metatibia with fringe of spine-like accessory setae that are unequal in size. Mesofemora with sharp posterior marginal line, anterior margin arcuate; coarsely punctate with two distinct sizes of punctures (small punctures situated among large punctures), and punctures slightly larger than those of metasternum. Metafemora narrower, $1.3\times$ as long as mesofemora, and covered with sparser punctation. Tarsal formula 5-5-5, slender, setigerous. Mesotarsi and metatarsi with basal tarsomere about as long as tarsomeres 1–4 combined. Claws fine, simple, symmetrical, acute.



FIGURES 7–8. *Airapus lithuanicus* **new species**, paratype "3891" [CAG]: 7—details of forebody, ventral view; 8 —apical portion of elytra with setose lateral margin, dorsal view. Scale bar: 0.5 mm for Fig. 7; 0.25 mm for Fig. 8.

Discussion

Systematic notes. The systematic placement of *Saprosites succini* (Zang) appears to be questionable (according to Hieke & Pietrzeniuk (1984) the holotype is housed in the Kühl collection at the Berliner Museum für Naturkunde, Germany). In the original description, Zang (1905) noted that this species was close to such taxa as *Rhyssemus* or *Euparia*, and did not represent a true example of *Aphodius*. Unfortunately, the illustration and original description lacked sufficient characters for definitive generic assignment. Some characters mentioned for this specimen by Zang (1905) could suggest placement in the tribe Odontolochini. These features include: "*Körper stark gewölbt, walzenförmig*" [body is strongly convex and cylindrical]; "*Kopf stark geneigt, mit fast vertikaler Stirn*" [head is strongly deflexed with almost vertical frons]; and "*Pronotum etwa solang wie breit, fast kugelig gewölbt*" [pronotum is about as long as wide, almost ball-shaped]. The proposal of any new generic combination or formal transfer in tribe Odontolochini as *insertae sedis* is unreasonable because we have not studied the holotype. Therefore, we choose to continue including *Saprosites succini* within *Saprosites* Redtenbacher (Eupariini), as it was proposed by Kolbe (1925).

The second species known from Baltic amber, *Ataenius europaeus* Quiel, is close to the new species described herein, and most likely also belongs to the genus *Airapus*. However, the most important generic characters of the ventral part of the body and legs were not mentioned by Quiel (1910). The relevant images are also absent in the original description. Two syntypes of *A. europaeus* in amber originally deposited in the collection of Königsberg museum were apparently lost during World War II. Therefore, the generic placement of this taxon could be not assessed or corrected.

Re-examination and detailed re-descriptions of the Zang and Quiel type specimens are needed for the correct generic placement of the above-mentioned species. In the Tertiary, the Aphodiinae fauna had different biogeographical distributions than they do today, therefore, a wide range of the Recent fauna have to be taken into consideration in the tribal and generic classification of fossil material.

Distributional and ecological notes. All known inclusions of Eupariini in Baltic amber represent extinct species belonging to extant genera currently found in tropical regions. The genus *Airapus* contains 23 extant species that are distributed in subtropical and tropical areas of Malaysia, Indonesia, Papua New Guinea, Australia, New Caledonia, Fiji, and Micronesia (Stebnicka 2000). The genera *Saprosites* and *Ataenius* are pantropical (Stebnicka 2009a, 2009b, 2012) and contain hundreds of species worldwide.

The life history of *Ataenius* species is poorly known, but some records indicate that they are humus-feeders and root-feeders in soil, with a few species attracted to decaying vegetation and animal dung (Verdú & Galante 1999; Galante *et al.* 2003). Some species have been recorded in ant nests and animal burrows. *Saprosites* and *Airapus* are also mostly saprophagous, or facultatively coprophagous. Saprophages feed upon dead and decaying plant material that includes leaf litter and moss in forest and scrub lands, logs and tree stumps, rotting fruits, nuts, mushrooms, fallen flowers, compost, and occasional accumulations of flood debris and piles of grass cuttings. The saprophagous adult aphodiines have been divided into two groups (Stebnicka 2001): species adapted for "hard saprophagy" using hard organic substances (*e.g.*, dead wood, leaf litter, mushrooms, and spores), and species adapted for "soft saprophagy" (using semiliquid and liquid contents of decaying vegetation). The second category includes most species of *Saprosites* and *Ataenius*. Similar natural history connected with substrates in hollow old trees or forest litter can be assumed for the fossil species.

Inclusion of nine conspecific Aphodiinae beetles in one piece of Baltic amber is unique and may be a source of additional information. The taphocoenose, consisting of different species with active dispersal, can be classified as heterogeneous (Wichard 2009). Unfortunately, the reason for aggregation of these species and specimens can be only speculated. Swarming, or another type of sexual behavior, is improbably for aphodiines based on the lack of observances for extant species. Most likely, the co-occurrence of multiple conspecific individuals in one fossilized resin piece is based on the availability of food, resulting a specimen accumulation around the bait-substrate for "social" feeding of the beetles. This could have taken place near a localized food source, such as a hollow tree with a nest, excrements, or the carcass of a small vertebrate. The Staphylinidae specimen could be a predator, consuming eggs and larvae of flies and beetles (Jo & Smitley 2003) in the hypothesized environment. Meanwhile, the presence of an Elateridae, a Hymenoptera, and a spider is considered incidental and based on the general habitat type only. Amber pieces like KZM-0001 (so-called "zoological park" pieces in common parlance) are especially interesting for palaeoecological studies and conclusions about palaeohabitats in the Eocene amber forest. The statistical study of syninclusions, as performed by Sontag (2003), provides a broader perspective, and is a promising addition to Baltic amber research.

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References cited

- Alekseev, V.I. (2017) Coleoptera from the middle-upper Eocene European ambers: generic composition, zoogeography and climatic implications. *Zootaxa*, 4290 (3), 401–443. https://doi.org/10.11646/zootaxa.4290.3.1
- Alekseev, V.I. & Alekseev, P.I. (2016) New approaches for reconstruction of the ecosystem of an Eocene amber forest. *Biology Bulletin*, 43, 75–86.

https://doi.org/10.1134/S1062359016010027

- Galante, E., Stebnicka, Z.T. & Verdú, J.R. (2003) Rhyparinae and Aphodiinae (Coleoptera: Scarabaeidae) of the southern states of Mexico (Chiapas, Oaxaca, Puebla and Veracruz). *Acta Zoologica Cracoviensia*, 46, 283–312.
- Hieke, F. & Pietrzeniuk, E. (1984) Die Bernstein-Käfer des Museums für Naturkunde, Berlin (Insecta, Coleoptera). *Mitteilungen aus dem Zoologischen Museums in Berlin*, 60, 297–326.
- Jo, Y.-K. & Smitley, D.R. (2003) Predation of Ataenius spretulus (Coleoptera: Scarabaeidae) eggs and grubs by species of Carabidae and Staphylinidae on golf courses in Michigan. Environmental Entomology, 32, 1370–1376. https://doi.org/10.1603/0046-225X-32.6.1370
- Kolbe, H.J. (1925) Vergleichender Blick auf die rezente und fossile Insektenwelt Mitteleuropas, und eine Erinnerung an meine Abhandlung über "Problematische Fossilien aus dem Culm". *Deutsche Entomologische Zeitschrift, Berlin,* 1925 (2), 147–162.

https://doi.org/10.1002/mmnd.192519250206

Krell, F.T. (2000) The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera: Polyphaga). *Invertebrate Taxonomy*, 14, 871–905.

https://doi.org/10.1071/IT00031

- Quiel, G. (1910) Bemerkungen über Coleopteren aus dem baltischen Bernstein. *Berliner Entomologische Zeitschrift*, 55, 181–192.
- Sontag, E. (2003) Animal inclusions in a sample of unselected Baltic amber. *Acta Zoologica Cracoviensia*, 46 (suppl. Fossil Insects), 431–440.
- Stebnicka, Z.T. (1998) The Aphodiinae of New Guinea, the Bismarck Archipelago and the Solomon Islands (Coleoptera: Scarabaeoidea). *Invertebrate Taxonomy*, 12, 833–895. https://doi.org/10.1071/IT97006
- Stebnicka, Z.T. (2000) New synonyms in the Micronesian Eupariini (Coleoptera: Scarabaeidae: Aphodiinae). Acta Zoologica Cracoviensia, 43, 333–334.
- Stebnicka, Z.T. (2001) Aphodiinae (Insecta: Coleoptera: Scarabaeidae). *Fauna of New Zealand*, 42. Manaaki Whenua Press, Landcare Research, Lincoln, Canterbury, New Zeland, 64 pp.
- Stebnicka, Z.T. (2009a) *Aphodiinae of Australia (Coleoptera: Scarabaeidae). Iconography.* Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, Kraków, Poland, 187 pp., XXVI+10 plates.
- Stebnicka, Z.T. (2009b) *The tribe Eupariini of New Word (Coleoptera: Scarabaeidae: Aphodiinae). Iconography 2.* Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, Kraków, Poland, 135 pp., XIX + 7 plates.
- Stebnicka, Z.T. (2012) A revision of the Indonesian species of Saprosites Redtenbacher, 1858 (Coleoptera: Scarabaeidae: Aphodiinae: Eupariini). Acta Zoologica Cracoviensia, 55, 13–45. https://doi.org/10.3409/azc.55 2.13
- Stebnicka, Z.T. & Howden, H.F. (1996) Revision of Australian genera in the tribes Odontolochini, Psammodiini, Rhyparini, Stereomerini and part of the Euparini (Coleoptera: Scarabaeoidea: Aphodiinae). *Invertebrate Taxonomy*, 10, 97–170. https://doi.org/10.1071/IT9960097
- Verdú, J.R. & Galante, E. (1999) Larvae of *Ataenius* (Coleoptera: Scarabaeidae: Aphodiinae): Generic characteristics and species descriptions. *European Journal of Entomology*, 96, 57–68.
- Wichard, W. (2009) Taphozönosen im Baltischen Bernstein. Denisia, 26, zugleich Kataloge der oberösterreichischen Landesmuseen, Neue Serie, 86, 257–266.
- Zang, R. (1905) Über Coleoptera Lamellicornia aus dem baltischen Bernstein. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1905, 197–205.