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NEW LATE EOCENE CHRYSOMELIDAE (INSECTA: COLEOPTERA) FROM BALTIC, ROVNO AND DANISH AMBERS

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Abstract: New fossil taxa of Chrysomelidae are described: from Baltic amber, *Succinispa stainesi* Nadein gen. et. sp. nov. (Cassidinae: Oposispini); from Danish (Scandinavian) amber, *Psyllototus viking* Nadein sp. nov. (Galerucinae: Alticini), *Calomicroides danicus* Nadein gen. et sp. nov. (Galerucinae: Galerucini: Luperina), *Paleomolpus hirtus* Nadein gen. et sp. nov. (Eumolpinae: Eumolpini); from Rovno amber (Ukraine, Klesov), *Archealtica convexa* Nadein gen. et sp. nov. (Galerucinae: Alticini), *Taphioporus rovnoi* Moseyko and Perkovsky sp. nov. (Eumolpinae: Euryopini). Leaf beetles in succinites are represented by four species of extant 'Holarctic' (temperate) genera in contrast to one species of a Recent 'tropical' genus. Faunal composition of leaf beetles of late Eocene succinites supports the opinion of Archibald and Farrell (2003) that arthropods with different climatic preferences preserved in Baltic amber were able to co-exist under an extinct equable climate with temperate summers and mild winters.

Key words: Chrysomelidae, Rovno amber, Danish amber, Baltic amber, palaeoclimate.

THE family Chrysomelidae (leaf beetles) is one of the most species-rich groups of phytophagous Coleoptera and is worldwide in distribution. It comprises over 35 000 species arranged in approximately 2000 genera and 12 subfamilies (Leschen and Beutel 2014). The geological history of leaf beetles and their palaeodiversity have been summarized by Santiago-Blay (1994) and R. C. McKellar and M. E. Engel (pers. com.). So far, nine subfamilies of Chrysomelidae have been recorded from fossil resins (Bukejs and Nadein 2015). More new taxa of leaf beetles from Baltic, Rovno and Danish ambers are described in the present paper.

MATERIAL AND METHODS

The Rovno amber collection is housed in the Schmalhausen Institute of Zoology, Kiev, Ukraine (SIZK); the Danish amber collection housed in the Zoological Museum, University of Copenhagen (ZMUC); and the Baltic amber collection of the Palaeontological Institute of the Russian Academy of Sciences (PIN).

All observations were made using a Leica MZ7.5 stereomicroscope, with measurements made using an ocular micrometre. The photographs were taken using a Leica MZ12 stereomicroscope and an AxioCam MRc5 digital camera.

Synchrotron X-ray microtomography (SR-μCT) was performed at the ID19 beamline of ESRF (experiment LS-2342; European Synchrotron Radiation Facility, Grenoble, France). The set energy is 19.5 keV, voxel size of 1.4 μ and 4998 projections. Synchrotron data were reconstructed using DRISHTI 2.5.1 software (Limaye 2014).

SYSTEMATIC PALAEONTOLOGY

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Order COLEOPTERA Linnaeus, 1758
Suborder POLYPHAGA Emery, 1886
Family CHRYSOMELIDAE Latreille, 1802
Subfamily CASSIDINAE Gyllenhal, 1813
Tribe OPOSISPINI Uhmann, 1939

Genus SUCCINISPA Nadein nov.

LSID. urn:lsid:zoobank.org:act:92EB21FC-167E-42C1-B5D5-68A9C825C4A1

Type species. Succinispa stainesi Nadein sp. nov.

Derivation of name. The name derives from 'succinite', a variety of fossil resin of Baltic amber, and '*ispa*', part of generic name *Hispa*, a common ending in hispines names; gender feminine.

Diagnosis. Body without long, stiff spines, head without frontal horn between antennae, clypeus well-developed, antenna 11-segmented, antennomere 3 the longest, pronotum without protruding anterior and posterior angles and without impression, elytra with scutellar row of punctures, elytral punctuation regularly striate, elytra costate, abdominal ventrite 5 with semicircular flat area.

Tribal attribution to Oposispini is based on strong similarity to the genera *Oposispa* Uhmann, 1939 and *Sucinagonia* Uhmann, 1939, in particular to the presence of a scutellar row of punctures, to the body shape, to the structure and number of antennomeres (third antennomere the longest), to the shape of the pronotum, and to the costate elytra with regular punctural rows.

The new genus differs from *Oposispa* as follows: antennomere 3 twice as long as previous (not longer in *Oposispa*), antennomeres 3–7 without long pubescence, pronotum uniformly and densely punctured, scutellar punctural row with three punctures (six in *Oposispa*), two outer intercostal spaces with three punctural rows each (all intercostae with two rows each in *Oposisipa*), metaventrite and abdomen punctate (impunctate in *Oposispa*), last abdominal ventrite with flat semicircular microsculptured area (absent in *Oposispa*). From *Sucinagonia*, this new genus differs in the absence of impressions on the pronotal base, and in that antennomere 2 is longer than the first, the anterior angles of the pronotum are not produced, the scutellum is not emarginate apically, and abdominal ventrite 5 lacks a setose semicircular impression (with a flat semicircular microsculptured area).

Description

Body. Elongate, narrow, not flattened.

Head. Nearly as wide as pronotum, hypognathous-opisthognathous; vertex broad, convex; frons between antennal sockets transversely raised; clypeus broad; labrum short; eyes large; genae very short.

Antennae. 11-segmented, *c.* 2.4 times shorter than body; antennomere 3 very long; antennomeres 7–10 short.

Prothorax. Narrow, cylindrical; pronotal lateral margins parallel-sided; posterior margin medially with rectangular projection; lateral carinae present; angles of pronotum not produced; hypomera convex; prosternum narrow, with intercoxal prosternal process broad.

Elytra. Elongate, medially narrowed, apically wider than basally; humeral calli produced; elytral punctures arranged in 11 striate rows, including scutellar and marginal rows; punctural rows separated by three costae; elytral margin without denticles or spines; epipleura narrow.

Scutellum. Small, rectangular. Metepisterna not visible, covered by elytra. Metaventrite two times longer than abdominal ventrite 1, without distinct median line.

Abdominal. Ventrite 1 longer than following, with intercoxal medial process acute; ventrites 2–4 equal in length.

Legs. Short; femora and tibiae thick; tarsomeres very broad; claw tarsomere deeply inserted in tarsomere 3.

Succinispa stainesi Nadein sp. nov.
Figure 1

LSID. urn:lsid:zoobank.org:act:50A0690E-E210-418F-9419-C664D734DBB6

Derivation of name. The new species is named after the outstanding specialist in Hispinae, Charles L. Staines (Smithsonian Institution).

Holotype. PIN 964/1311; donated from the collection of Victor A. Gusakov, coll. Nr. 029C98, Zvednyi Sity, Moscow Region, Russian Federation. Specimen in a transparent irregular-shaped piece, weight 3 g.

Syninclusions (other inclusions occurring in the same piece of amber). Hymenoptera: Scelionidae.

Locality and age. Village of Jantarnyi, Kaliningrad Region, Russia; Baltic amber, late Eocene.

Description

Body. Length 5.2 mm, width 2 mm. Elongate, narrow, convex, not flattened, in general parallel-sided, visible coloration dark metallic.

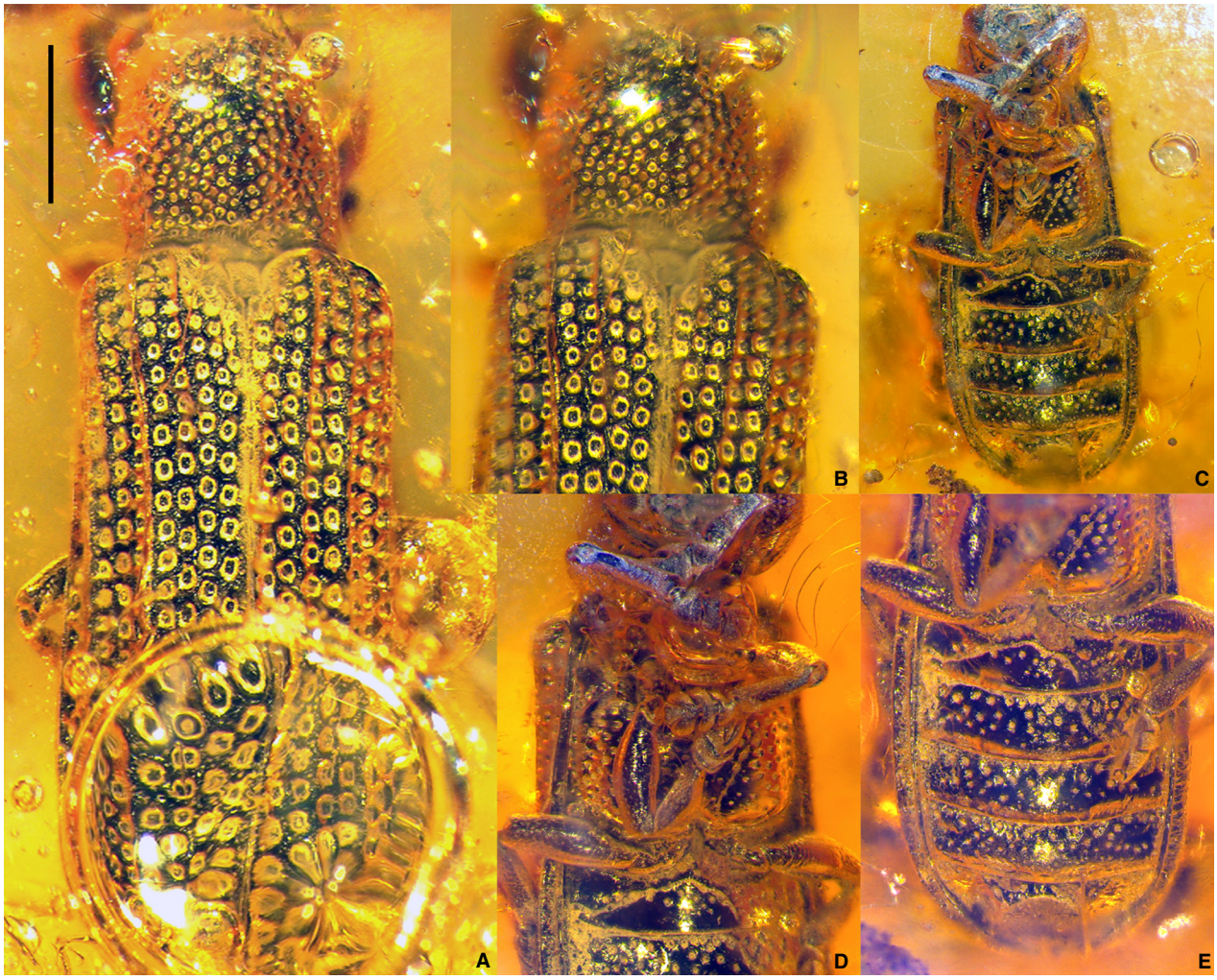

FIG. 1. *Succinispa stainesi* Nadein gen, et sp. nov., holotype PIN 964/1311. A, body, dorsal view. B, pronotum and elytral base, dorsal view. C, body, ventral view. D, thorax, ventral view. E, metathorax and abdomen, ventral view. Scale bar represents 1 mm. Colour online.

Head. Nearly as wide as pronotum, of intermediate hypognathous–opisthognathous position; vertex very broad, convex, covered with large and deep punctures, with distance between punctures not exceeding diameter of puncture, with interstices flat and smooth; frons between antennal sockets transversely raised, frontal area covered with large and deep punctures, distance between antennal socket and mouth opening slightly longer than socket diameter, distance between socket and margin of eye equal to socket diameter; clypeus broad and smooth; labrum short and transverse, medially notched; eyes large, convex, slightly longer than wide, distance between eyes about twice longer than longitudinal diameter of eye; genae very short, at least twice shorter than antennal socket diameter.

Antennae. 11-segmented, short, *c.* 2.4 times shorter than body; antennomere 1 short and globose; antennomere 2 longer and thick; antennomere 3 very long, nearly twice longer than two preceding combined; antennomere 4 twice shorter than third; antennomere 5 slightly shorter than preceding; antennomere 6 shorter than fifth; antennomeres 7–10 short, thick, gently wider than long, shorter than antennomere 6; last antennomere slightly longer, as long as wide, broadly conical.

Thorax. Prothorax narrow, 1.1 times longer than wide, cylindrical; anterior margin strongly produced, rounded; lateral margins parallel-sided, weakly rounded; posterior margin medially with rectangular projection, with posterior margin of projection truncate; lateral carinae present, smooth, weakly raised, gently thickened; anterior and posterior angles not produced. Hypomera convex. Prosternum moderately narrow; intercoxal prosternal process broad. Pronotal, hypomeral and prosternal surfaces evenly covered with large and deep punctures, their size smaller than those of elytra, with distance between punctures less than diameter of puncture; interpunctural spaces smooth and raised. Scutellum small, rectangular, longer than wide; apex truncate; surface smooth.

Mesepimera and mesepisterna covered with large and deep punctures. Metepisterna not visible, covered by elytra. Metaventrite two times longer than abdominal ventrite I, convex, covered with deep punctures, without distinct median line.

Elytra. Elongate, 3.4 times longer than pronotum, 2.1 times longer than wide, in dorsal view basally somewhat wider than medially, basally nearly rounded, apically rounded, medially narrowed, apically wider than basally. Humeral calli strongly produced. Punctures arranged in 11 striate rows, including scutellar and marginal rows; scutellar row short, containing three punctures; punctural rows separated by three costae in the following way: two rows (and scutellar) – two rows – three rows – three rows (including marginal); internal and middle costa moderately raised, outer costa strongly raised and elytral side behind outer costa nearly vertically sloping; punctures very deep and much larger than those of pronotum, with distance between punctures always less than diameter of puncture; interpunctural spaces raised. Elytral margin gradually widened and flattened from base to apex, visible from above, except not visible at the very base under humeral calli; marginal edge smooth, without denticles or spines. Epipleura narrow, weakly concave; surface rough; basal third narrower than elytral puncture; middle third wider than basal third, about as wide as diameter of elytral puncture.

Abdomen. Ventrite 1 slightly longer than following, with intercoxal medial process elongate, acute apically; ventrites 2–4 equal in length, their anterior and posterior margins weakly curved; ventrite 5 slightly longer than preceding, nearly straight apically, medially with semicircular flat area covered with fine, silky, and whitish microsculpture; surface of ventrites covered with punctures varying in size and distance between them, with punctures deep and distinctly smaller than those of elytra, with average distance between punctures equal to average diameter of puncture; interstices smooth, shining, flat.

Legs. Short; femora and tibiae thick; tarsomeres very broad, much wider than tibia, nearly of equal width with each other, with tarsomeres 1–3 wider than long, with tarsomere 3 deeply bilobed, with claw tarsomere widely triangular, deeply inserted in tarsomere 3 and slightly exceeding the lobes of tarsomere 3; femora somewhat swollen; tibiae gradually widening apically; tibiae and femora covered with minute and sparse punctures and very short setae.

Subfamily GALERUCINAE Latreille, 1802
Tribe ALTICINI Newman, 1834

Genus PSYLLOTOTUS Nadein *in* Nadein and Perkovsky, 2010

Type species. Psyllototus progenitor Nadein *in* Nadein and Perkovsky, 2010; Rovno amber.

Psyllototus viking Nadein sp. nov.
Figures 2–3

LSID. urn:lsid:zoobank.org:act:71AC38C1-9F08-4EAC-904B-BDA566BA6C0D

Derivation of name. The species epithet refers to the origin of the fossil specimen and to the Danish tribes that were among those known as Vikings during the eighth to the eleventh centuries.

Holotype. Chrysomelidae Th. Hansen/16-1 1961/Halticinae (ZMUC); specimen a rectangular piece of dark colour, weight after treatment 0.07 g; syninclusions are absent.

Locality and age. Denmark, Danish (Scandinavian) amber; late Eocene.

Description

Body. Length 2.3 mm, width 1.2 mm. Slender, elongate, convex; dorsum with dark metallic lustre.

Head. Moderately sized; vertex without clear punctation, covered with fine microgranulation; ocular sulci distinct; frons narrow; frontal ridge distinctly raised, long and sharp; anterofrontal ridge thin, slightly raised, straight; eyes large, round-elliptic, convex; antennal socket placed very close to eye margin, with distance between sockets not exceeding diameter of socket; labrum small and transverse.

Antennae. 11-segmented, filiform, with fifth antennomere longer than previous and following (left antenna with 10 antennomeres complete, with 11th antennomere missing; right antenna missing eight antennomeres with three antennomeres present).

Prothorax. Narrower than elytral base. Pronotum convex; anterior margin straight; posterior margin evenly convex; lateral margins converging anteriorly, with lateral edge slightly rounded and with thin margin; anterofrontal callosities weakly protruding; pronotal punctures dense and shallow, with unclear margins; interstices somewhat convex and rough, microgranulated.

Elytra. Elongate, convex, slightly wider than pronotal base; humeral calli moderately protruding; epipleura clearly visible along whole length, internal margin of each with row of sparse punctures; surface covered with deep, small punctures arranged in regular striae that are clearly visible along whole length; distance between punctures not exceeding diameter of punctures; striae somewhat grooved, with distance between striae equal to about twice diameter of puncture; interstitial space convex, covered with easily visible secondary punctation. *Scutellum* small, triangular, with acute apex. Hind wings partially exposed.

Legs. Pro- and mesofemora straight, long, narrow, as well as pro- and mesotibiae; protibia curved; protarsi with thin, long first tarsomere (indicating sex of specimen is likely to be female). Metafemur elongate, strongly swollen, covered with dis-

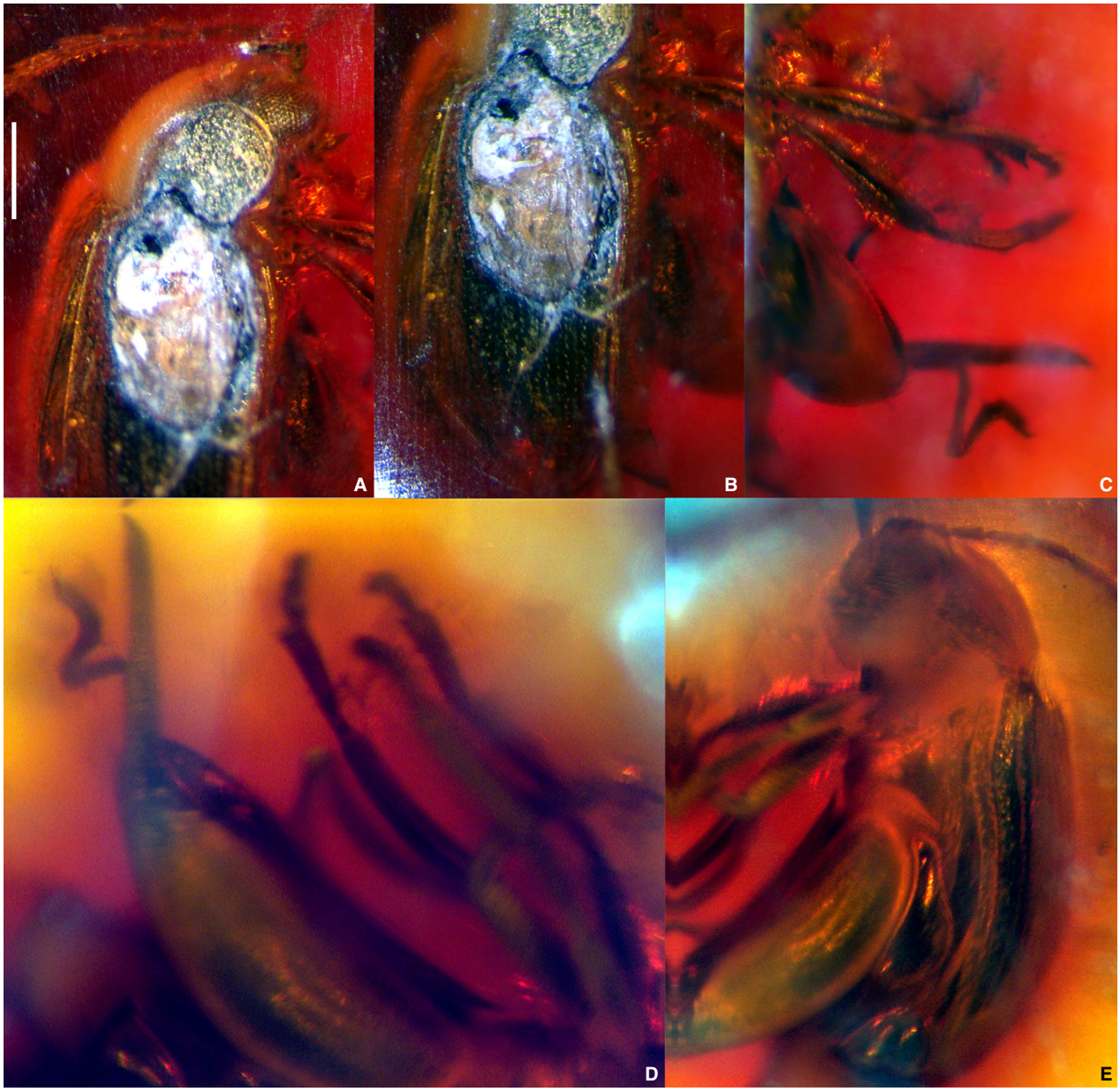

FIG. 2. *Psyllototus viking* Nadein sp. nov., holotype ZMUC 16-1 1961. A, anterior half of body, right side, dorsolateral, view. B, base of prothorax and elytra, right side, dorso-lateral, view. C, legs, right-side view. D, legs, left-side view. E, body, left side, lateral view. Scale bar represents 0.5 mm. Colour online.

tinct shagreen-like sculpture, with sparse punctation and short setae; metatibia long, as long as metafemur, straight, narrow, with apical half dorsally dentate on each side, with large and acute spur at apex; metatarsus attached at middle of metatibia; metatarsomere 1 half as long as metatibia; metatarsomere 2 one-third shorter than first; following tarsomeres half as long as preceding.

Remarks. Psyllototus is a fossil genus closely related to the recent *Psylliodes* Latreille, 1829, from which it differs in having 11-segmented antennae, while *Psylliodes* bears 10-segmented antennae. Three species, *Psyllototus progenitor* Nadein *in* Nadein and Perkovsky, 2010 from Rovno amber, *Psyllototus doeberli* Bukejs and Nadein, 2013 and *Psyllototus groehni* Bukejs and Nadein, 2014 from Baltic amber have been described. The new species is a fourth representative of the genus.

The new species generally resembles *P. progenitor*, from which it differs in the narrow frontal ridge, slightly rounded lateral margins of the pronotum, less protruding

FIG. 3. *Psyllototus viking* Nadein sp. nov., holotype ZMUC 16-1 1961, synchrotron X-ray microtomography volume reconstruction. A, body, ventral view. B, body, left side, lateral view. C, anterior view. D, body, dorsal view. E, body, right side, lateral view. F, body, left side, ventrolateral view. G, posterior view. Scale bar represents 0.5 mm. Colour online.

anterolateral callosities of the pronotum, and acute apex of the scutellum. From *P. doeberli*, the new species differs in many characters, such as thinner antennomeres, denser punctation of the pronotum and elytra, straight metatibia, and medially inserted metatarsus (insertion at distal third in *P. doeberli*).

Genus ARCHEALTICA Nadein nov.

LSID. urn:lsid:zoobank.org:act:C2FFA382-786B-44C8-8750-54B8AC4E1E13

Type species. Archealtica convexa Nadein sp. nov.

Derivation of name. The genus name is formed from the words 'arkhaios' (Ancient Greek, meaning old, ancient) and '*Altica*' (type genus of the tribe Alticini and a common ending of generic names in flea beetles); gender feminine.

Diagnosis. Body oval, convex. Head hypognathous; ocular sulci distinct; frontal calli convex, well delimited from frons; frontal ridge long and raised; labrum as long as wide; eyes round, convex; antennal sockets situated extremely close to eye margin; antennae filiform, 11-segmented, with antennomeres 7–11 about as long as wide. Pronotum broad and convex, with antebasal short longitudinal furrows. Elytra convex, without convex humeral calli; punctures arranged in 11 striae; epipleura flat, horizontal. Legs moderately long and narrow; metatarsomere 1 shorter than following three tarsomeres combined; metatibia with apical spur very short. Abdominal ventrites 2–4 very short.

Remarks. The new genus strongly resembles the Palaearctic genus *Minota* Kutschera, 1859, which is distributed mostly in Europe, with several species known from the Himalayas, China and Japan. From this genus, *Archealtica* differs in the shape of frontal calli, which are not delimited from the vertex, the globose eyes, the very short distance between the antennal socket and eye margin, the more raised frontal ridge, the longer labrum, the more triangular shape of the scutellum, the thinner legs, especially the thinner metafemora, the absence of distinct secondary punctation, the metatibia that lacks an easily visible and moderately long apical spur, antennomere 2 that is longer than the third, and antennomere 5 that is slightly longer than either the previous or following. The new genus is also similar to *Paraminota* Scherer, 1989 from Nepal, from which it differs in the long and raised frontal ridge, position of the antennal socket (very closely to margin of eye), well-developed pronotal longitudinal impressions, and the presence of striate punctures on the elytra. It is also similar to another Nepalese genus, *Paraminotella* Döberl and Konstantinov, 2003, from which the new one differs in the same characters mentioned for the previous genus, including the presence of pronotal longitudinal impressions and the much shorter metatibial apical spur.

Archealtica convexa Nadein sp. nov.
Figures 4–5

LSID. urn:lsid:zoobank.org:act:102FEDA4-FAAA-4E56-88BA-3132968F36FE

Derivation of name. The specific name is derived from the Latin word *convexus* (convex), referring to the convex body shape.

Holotype. K-15868 (SIZK); specimen in a transparent, rectangular piece, which before treatment measured 56 × 33 × 27 mm and weighed 20 g.

Syninclusions. K-15862 Dolichopididae; K-15863 Brachycera; K-15864 Diptera; K-15865 Staphylinidae; K-15866 Psychodidae; K-15867 Megaspilidae; K-15868 Dolichopididae; K-15869 Collembola, Symphypleona, Psocoptera (larva), Acari, Diptera (head of Nematocera).

Locality and age. Klesov, Ukraine, Rovno amber; late Eocene.

Description

Body. Length 2.0 mm, width 1.2 mm. Oval, convex. Colour dark with possible metallic lustre.

Head. Hypognathous, slightly longer than wide. Vertex convex, without visible punctation; ocular sulci distinct, deep, reaching antennal sockets; large setiferous pores situated on vertex above ocular sulci in middle between frontal callus and margin of pronotum; frontal calli convex, nearly rectangular, well delimited from frons, not clearly delimited from vertex; frontal ridge long, slightly wider and flatter between antennal sockets, then narrow and raised, reaching anterior margin of frons, the latter without ridge. Labrum as long as wide; labial palpi about twice longer than labrum, last palpomere with acute apex. Eyes round and convex. Antennal sockets situated extremely close to eye margin, with distance between antennal sockets longer than diameter of socket.

Antennae. Filiform, 11-segmented, reaching middle of the body; antennomere 2 longer than either third or fourth; antennomere 5 slightly longer than previous and following; antennomeres 1–6 about 2–2.5 times longer than wide; antennomeres 7–11 distinctly wider than previous, about as long as wide.

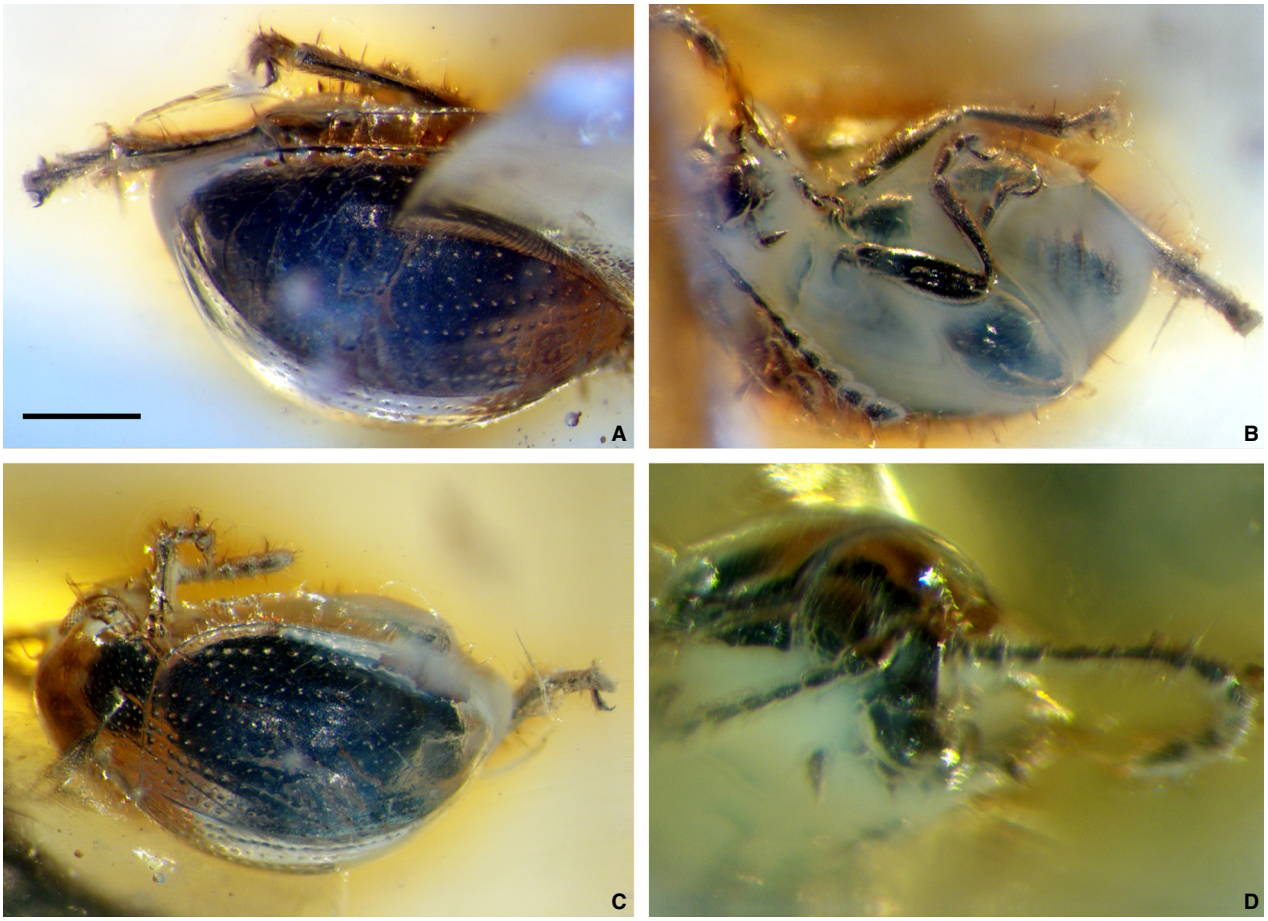

FIG. 4. *Archealtica convexa* Nadein gen. et sp. nov., holotype SIZK K-15868. A, left elytron, dorsolateral view. B, body, ventrolateral view. C, body, dorsolateral view. D, head, anterolateral view. Scale bar represents 0.5 mm. Colour online.

Pronotum. Wide, very convex, basally almost as wide as elytra. Base of pronotum with antebasal, short, longitudinal furrows, these narrow, moderately deep, straight, situated at a distance from lateral margin slightly longer than length of furrow. Surface of pronotum covered with small and distinct punctures, distance between them larger than diameter of punctures; surface between punctures flat with smooth and very fine microsculpture. Lateral carina of pronotum distinct; anterior and posterior angles not large and projecting; posterior margin of pronotum evenly curved.

Elytra. Oval, very convex; without convex humeral calli. Punctures arranged in 11 striae; sutural stria short, not reaching middle of elytra; striae 7–9 not covering humeral area; punctures in striae somewhat larger than those of pronotum, with discal punctures deep and distinct, with those towards apices becoming shallower, smaller and less distinct; striae not reaching elytral apices; distance between striae about 3–4 times diameter of puncture; interstices flat or weakly convex, covered with smooth and fine microgranulation; secondary punctation absent. Epipleura flat, horizontal, evenly broad from base to apical third, then narrowed before apex.

Abdomen. Ventrites 2–4 very short.

Legs. Moderately long, not shortened; fore and middle legs narrow; tibiae thin, not distinctly thickened apically; metafemur about twice longer than wide; metatibia not thickened, very slightly curved; metatarsomere 1 short, shorter than following three tarsomeres combined.

Tribe GALERUCINI Latreille, 1802
Subtribe LUPERINA Gistel, 1848

Genus CALOMICROIDES Nadein nov.

LSID. urn:lsid:zoobank.org:act:7614428B-FA3B-42C8-B7C7-C15F542C231A

Type species. Calomicroides danicus Nadein sp. nov.

Derivation of name. The generic name is derived from the genus name *Calomicrus* Stephens, 1831, to which the new genus is similar; gender masculine.

FIG. 5. *Archealtica convexa* Nadein gen. et sp. nov., holotype SIZK K-15868, synchrotron X-ray microtomography volume reconstruction. A, body, dorsal view. B, body, ventral view. C, pronotum and elytral base, dorsal view. D, body, right side, lateral view. E, body, left side, lateral view. F, anterior view. G, posterior view. Scale bar represents 0.5 mm. Colour online.

Diagnosis. Body ovate, glabrous; punctation confused; head narrower than pronotum, antennal sockets situated between eyes, frontal area triangular, frontal calli present, supraocular sulcus present, antennae filiform; pronotum without impressions, posterolateral setiferous callosities large; elytra without callosities and costae, pygidium covered by elytra, humeral calli and epipleura present; tibiae thin, tibial apices without projections and emarginations; metaventrite 1 very long; metatarsomere 1 not longer than following combined.

Remarks. Other than Alticini, there are only two described species of fossil Galerucini: *Leptonesiotes virkkii* Santiago-Blay *et al.*, 1996, from Dominican amber (middle Miocene) and *Calomicrus eocenicus* Bukejs and Bezdek, 2014, from Baltic amber. Beyond this, some putative records from Recent genera are known for Baltic amber: *Galeruca* sp., *Galerucella* sp., *Luperus* sp., *Luperodes* sp., and *Monolepta* sp. (Santiago-Blay 1994). The present finding is the second described species known for the late Eocene and from the Old World.

Tribal assignment of a new taxon is hard to determine, since some important diagnostic characters (ventral side of prothorax, position of procoxae, large portion of head and abdomen, claw tarsomere) are hidden. Because of this, the taxonomic position of a new genus is regarded as *insertae sedis* until clarification. It is worth of mentioning that the position of antennal sockets, absence of pronotal impressions, glabrous dorsum and long metatarsomere 1 resemble representatives of the subtribe Luperina.

The new genus generally resembles some recent European representatives of the genera *Calomicrus* and *Luperus* Geoffroy, 1762. However, the combination of characters in the specimen under question differs from all the European and Oriental genera. *Calomicroides* can be easily separated from *Luperus* by the much shorter antennae, with antennomere 3 not longer than the second. Among European genera, the new one is closest to *Calomicrus*, from which it differs in the broader and more convex body, light coloration, longer frontal part of the head, larger posterolateral angles of the pronotum, wider epipleura that are clearly visible from lateral view along the entire length, and longer metatarsomere 1. Among Oriental genera, the new one is supposedly close to *Monolepta* Chevrolat, 1837, which is distributed widely in the Afrotropical and Oriental Regions. From *Monolepta*, it differs in the wider epipleura, shorter metatarsomere 1 and the absence of a long spur at the apex of the metatibia.

Calomicroides danicus Nadein sp. nov.
Figure 6

LSID. urn:lsid:zoobank.org:act:15084FE3-A33F-49BE-9540-81EDF6A97D3F

Derivation of name. The specific epithet refers to origin of the amber specimen.

Holotype. Chrysomelidae Børge Mortensen/11-7 1960 (ZMUC)/ Galerucinae; specimen in a rectangular piece of dark colour, with weight after treatment being 0.65 g; syninclusions are absent.

Locality and age. Denmark, Danish (Scandinavian) amber; late Eocene.

Description

Body. Length 3.3 mm, width 2.0 mm. Ovoid, yellowish; dorsum glabrous, covered with irregular dense punctures.

Head. Slightly narrower than pronotum; vertex large and convex; frontal calli well-developed and convex; antennal insertions situated between eyes and behind anterior margin of eyes, with distance between them not exceeding diameter of fossa; frontal area large, triangular, smooth, somewhat elevated, medially convex in ridge-like elevation, slightly penetrating between antennal insertions; eyes moderate-sized, roundish, convex, delineated from vertex by deep sulcus.

Antennae. 11-segmented, filiform, without modifications, with antennomeres thin, not widened apically, on average 2–3 times longer than wide; antennomere 1 shorter than two following antennomeres together; antennomere 2 slightly shorter than third; antennomere 5 longer than preceding and following; antennomeres 6–10 of equal length; last antennomere slightly longer than preceding, with acute apex.

Thorax. Pronotum transverse, moderately narrower than elytral base, without impressions; anterior edge straight, without distinct margin; anterolateral setiferous callosities weakly projecting; posterior edge with distinct margin; posterolateral setiferous callosities very large, strongly projecting; posterior margin convex, medially straight; lateral edges rounded, with widened margins. Mesoventrite very short. Metaventrite very long and convex, tree times longer than abdominal ventrite 1, covered with small and sparse punctures.

Elytra. Elongate, gradually widened apically, evenly convex, without basal callosities or longitudinal ridges; humeral calli present; epipleura present, reaching sutural angles of elytra, visible laterally along entire length, gradually narrowing towards apices, widest at basal third; scutellum small, triangular.

Abdomen. Ventrites 1 and 2 nearly as equal in length, ventrite 3 slightly shorter than previous; pygidium covered by elytra.

Legs. Thin and long; mesocoxae situated close to each other and probably contiguous; tibiae thin, gradually and weakly thickened apically, covered with short setae; tibial apices without projections or emarginations; metatibial apical spur minute and poorly visible; metatarsomere 1 hardly as long as following combined.

Subfamily EUMOLPINAE Hope, 1840
Tribe EURYOPINI Lefèvre, 1885

Genus TAPHIOPORUS Moseyko and Kirejtshuk, 2013

Type species. Taphioporus balticus Moseyko and Kirejtshuk, 2013, Baltic amber.

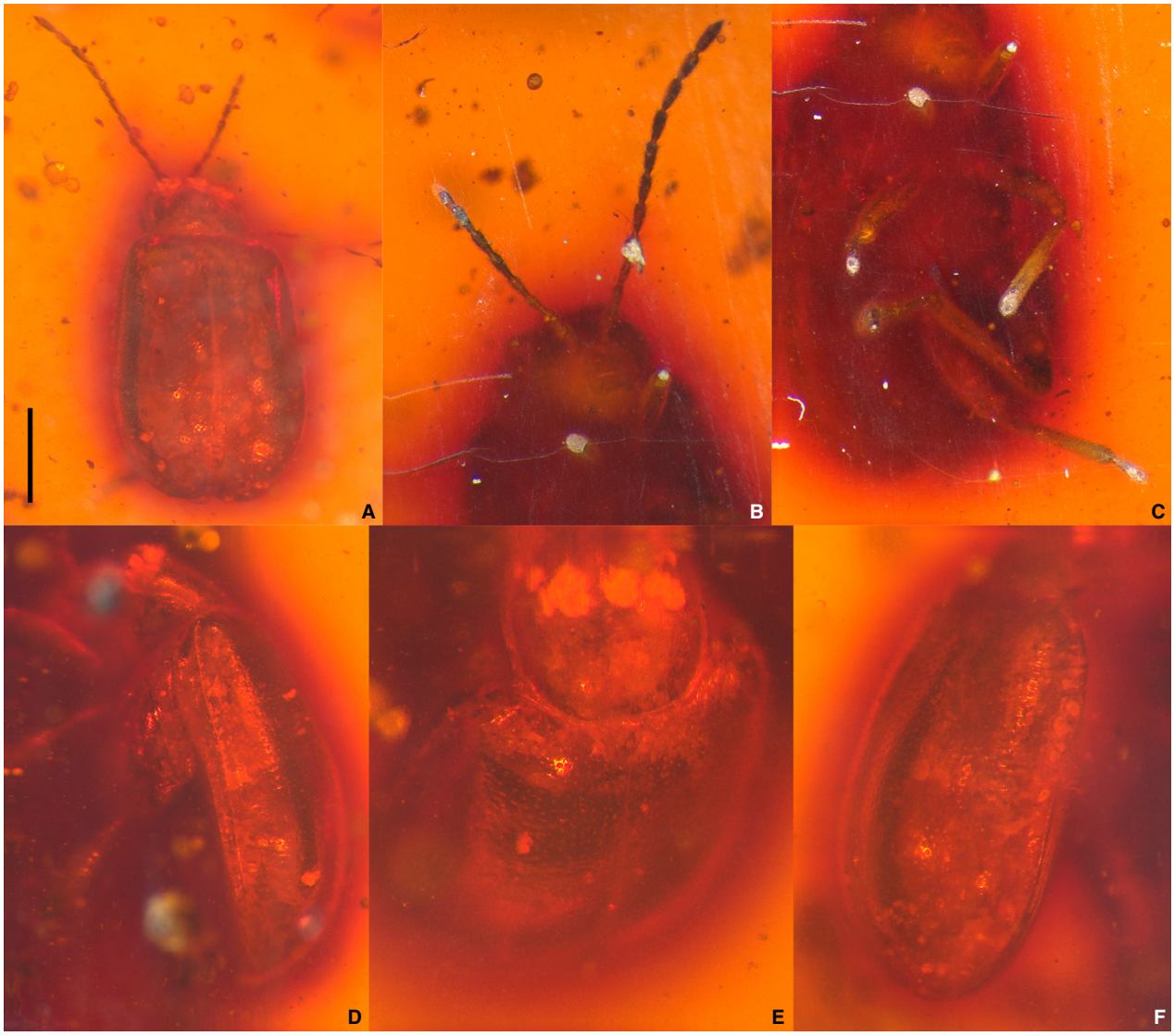

FIG. 6. *Calomicroides danicus* Nadein gen. et sp. nov., holotype ZMUC 11-7 1960. A, body, dorsal view. B, head, ventral view. C, body, ventral view. D, body, left side, lateral view. E, pronotal and elytral base, dorsal view. F, body, right side, dorsoventral view. Scale bar represents 1 mm. Colour online.

Taphioporus rovnoi Moseyko and Perkovsky sp. nov.
Figure 7

LSID. urn:lsid:zoobank.org:act:4DEBCCCF-0BA5-40B2-BBFD-79A43DAF2C94

Derivation of name. Epithet formed from the 'Rovno amber', from which the new species is described.

Holotype. K-7122 (SIZK); specimen in a transparent irregular-shaped piece, weighing 18.7 g after primary treatment.

Syninclusions. K-7117 Phoridae; K-7118 Anobiidae; K-7119 Trombidiidae; K-7120 Theridiidae; K-7121 Oribatei (Liacaridae), Drepanosiphidae; K-7123 Chironomidae, Tanypodinae, Acari; K-7124 Diptera (Brachycera); K-7125 Collembola, Symphypleona; K-7126 Erythraeidae (*Erythraeus*?); K-7127 Diptera (Cyclorrhapha), elytra of Coleoptera, Acari; K-7128 Chironomidae, Orthocladiinae, Scydmaenidae, Tipuloidea legs, Trombodioidea; K-7129 Bethylidae; K-7130 *Lasius schiefferdeckeri* Mayr; K-7131 Parasitengona, Oribatei (Galumnoidea?).

Locality and age. Klesov, Ukraine, Rovno amber; late Eocene.

Description

Body. Length 2.8 mm, width 1.6 mm. Bare, without scales or setae, elongate oval, completely black with feeble golden lustre which is probably an artefact.

FIG. 7. *Taphioporus rovnoi* sp. nov., holotype SIZK K-7122. A, body, dorsal view. B, body, anterior view. C, body, ventral view. D, body, dorsolateral view. Scale bar represents 0.5 mm. Colour online.

Head. Covered with small punctures separated by distance equal to diameter of puncture. Paraocular grooves slightly curved parallel to edge of eye, not deep.

Antennae. Subfiliform, about two-thirds as long as body; preapical antennomeres about twice as long as broad; second antennomere subequal in length to third and only slightly shorter than first.

Thorax. Pronotum about 1.3–1.5 times as wide as long (not precisely measurable), with maximum width in anterior half; covered with small punctures separated by distance equal to diameter of puncture. Lateral carina of prothorax distinctly bent. Hypomera covered with small punctures separated by distance greater than diameter of puncture. Sides of anterior edge of prosternum quite S-shaped, with inner parts more convex. Seta at anterior angle of prothorax placed on convex part at the front

of this angle. Metepisterna and metaventrite with well-developed edges.

Elytra with 12 longitudinal rows of moderate punctures.

Abdomen. Punctured.

Legs. Femora with very small and difficult to observe tooth on ventral side. All tibiae without preapical emargination. Claws appendiculate.

Remarks. The new species is similar to only one other species of *Taphioporus*, *T. balticus* Moseyko and Kirejtshuk, 2013, but the head, pronotum and hypomera are distinctly punctured. The taxonomic position of the genus *Taphioporus* was discussed in detail in the original description (Moseyko and Kirejtshuk 2013).

Tribe EUMOLPINI Hope, 1840

Genus PALEOMOLPUS Nadein nov.

LSID. urn:lsid:zoobank.org:act:99C43CC1-5243-44FF-A6C5-8DF558B2D852

Type species. Paleomolpus hirtus Nadein sp. nov.

Derivation of name. The generic name derives from the Ancient Greek word 'palaios' (old, ancient) and '*-molpus*' (part of '*Eumolpus*', the type genus of the subfamily); gender masculine.

Diagnosis. Body narrow, dorsum pubescent, eyes without emargination, antennae filiform and long, frons and vertex without grooves, last segment of maxillary palpi acute, lateral margins of pronotum with carinae, anterolateral margin of prothorax concave, humeral calli of elytra not produced, elytral punctuation confused, pygidium partially exposed, legs long and thin, femora without tooth, tibiae without preapical emargination or acute projections, tarsal claw with large denticle.

Remarks. The new genus belongs to the tribe Eumolpini because of following combination of characters: simple apices of meso- and metatibiae; carinate and irregularly curved sides of prothorax; appendiculate claws (after Chen 1940; Selman 1965; Moseyko and Kirejtshuk 2013). Among the genera of the recent European fauna, there are no genera that are morphologically similar to the new one. Hair coverage of elytra makes it quite similar to some genera of the tribe Adoxini. Within Adoxini, the American genera *Glyptoscelis* LeConte, 1859 and *Myochrous* Erichson, 1847 have modified prothoracic sides slightly similar to those in *Paleomolpus,* but have a convex anterolateral margin of prothorax ('propleurae') and a body covered by scales. Within the tribe Eumolpini, the new genus belongs to the group of American and Australian genera, close to *Colaspis* Fabricius, 1801 because of elongate body, concave 'propleurae', long antennae with preapical segments more than three times as long as wide and acute last segment of maxillary palpi. Within this section, *Paleomolpus* similar to Recent genera *Colaspis*, *Geloptera* Baly, 1861 and *Hypoderes* Lefévre, 1877 because of having irregularly curved sides of prothorax (in *Geloptera* and *Hypoderes* it is also dentate). From all these genera, *Paleomolpus* differs by completely confused elytral punctation, even on apex of elytron. From *Colaspis* and *Geloptera*, it differs also by having hairy elytra.

The new genus can easily be distinguished from the fossil eumolpine genus *Aoriopsis* Moseyko *et al.*, 2010 (Oise amber), due to the confused punctation of the elytra and the short claw tarsomere. From both fossil genera *Acolaspoides* Moseyko *et al.*, 2010 (Oise amber) and *Taphioporus* Moseyko and Kirejtshuk, 2013 (Baltic and Rovno amber), it differs in the pubescent dorsum and confused punctation of the elytra.

Paleomolpus hirtus Nadein sp. nov.
Figures 8–9

LSID. urn:lsid:zoobank.org:act:FA6E638F-7C80-4F2E-9468-D8A2CCBAFD79

Derivation of name. The specific epithet refers to the pubescent dorsum of the new species.

Holotype. Chrysomelidae Børge Mortensen/21-3 1961 (ZMUC); specimen in a rectangular piece of dark colour, having weight after treatment 0.31 g; syninclusions are absent.

Locality and age. Denmark, Danish (Scandinavian) amber; late Eocene.

Description

Body. Length 3.5 mm, width 1.7 mm. Slender, narrow, shining, with metallic lustre; dorsum pubescent.

Head. Broad, seemingly as broad as pronotum; vertex large and broad, flat, densely and roughly punctate and wrinkled, covered with short, sparse, appressed setae; frons broad, flat, more or less broadly trapezoidal, punctured and wrinkled, probably weakly raised between antennal insertions, in space between eyes as long as eye diameter; antennal insertion located immediately in front of eye, with distance between insertions about four times diameters of insertion; eyes moderately sized, round and convex, without emargination, not delimited from frons by groove; genae short; labial palpi long, with last palpomere long, acute, about three times longer than wide.

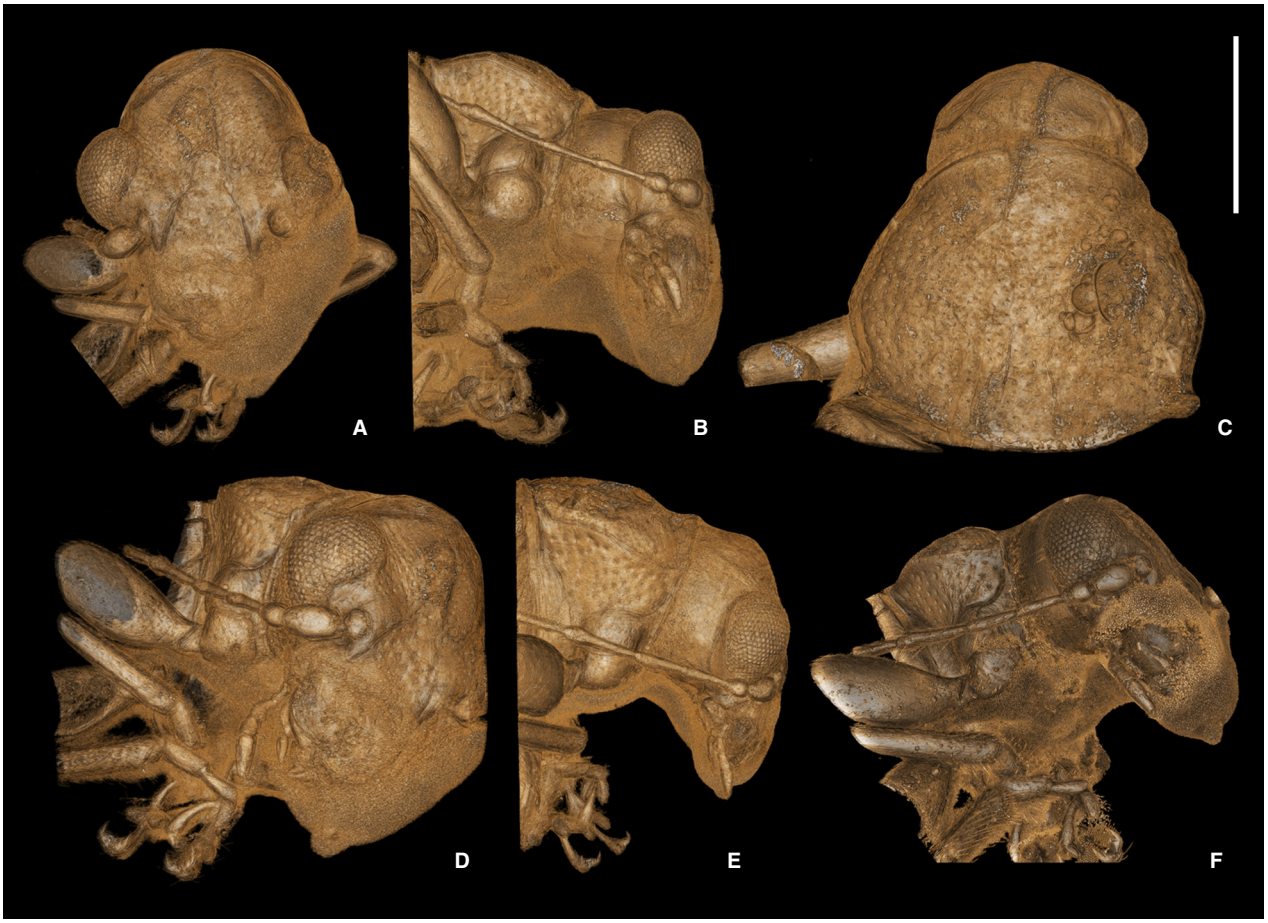

FIG. 8. *Paleomolpus hirtus* Nadein gen. et sp. nov., holotype ZMUC 21-3 1961, synchrotron X-ray microtomography volume reconstruction. A, head, frontal view. B, head and prothorax, ventrolateral view. C, pronotum, dorsal view. D, head and prothorax, anterolateral view. E, head and prothorax, lateral view. F, head and prothorax, ventrolateral view. Scale bar represents 1 mm. Colour online.

Antennae. Filiform, 11-segmented, short, reaching middle of body; apices of antennomeres with long setae; antennomere 1 short and swollen, shorter than two following combined; antennomere 2 about half as long as those following; antennomeres 3–4 of equal length; antennomeres 4–11 long and thin, about 4–5 times as long as wide; antennomere 5 longer than preceding and following; last antennomere sharply acute apically.

Pronotum. Slightly shorter than elytral base, convex, cylindrical; posterior margin raised; lateral margin with carina; hypomera punctate, anterolateral margin of prothorax concave; pronotal surface covered with short, sparse setae, as well as with dense, deep punctures; interstices convex.

Elytra. Convex, without produced humeral calli; punctation confused or with weak traces of rows on disc, apically totally confused; punctures dense, large, deep, larger than those on pronotum; interstices rough, convex, transversely wrinkled; setae covering elytral surface short, comparatively dense, either appressed or semi-erect; epipleura very narrow in apical third.

Abdomen. Ventrites sparsely pubescent, depressed, broad, scale-shaped; 1–3 short, of equal length; ventrite 4 longer than preceding; pygidium probably partially exposed.

Legs. Long and thin; femora short, weakly swollen medially, narrowed apically; femoral surface shagreened, densely pubescent; metafemur without process or tooth; tibiae long, thin, gradually widened towards apex, without longitudinal ridges, apical part simple, without emargination or spur, surface covered with dense setae; tarsi short; tarsomere 1 moderately broad, about 2.5 times as long as wide, shorter than following tarsomeres combined; tarsomere 2 short; tarsomere 3 not deeply bilobed; claw tarsomere short, shorter than first, not longer than third; tarsal claw basally with large denticle.

Subfamily CRYPTOCEPHALINAE Gyllenhal, 1813
Tribe CRYPTOCEPHALINI Gyllenhal, 1813

Material. Chrysomelidae G.V. Henningsen/19-11 1958 (ZMUC); weight after treatment 0.29 g.

FIG. 9. *Paleomolpus hirtus* Nadein gen. et sp. nov., holotype ZMUC 21-3 1961, synchrotron X-ray microtomography volume reconstruction. A, body, dorsal view. B, body, dorsolateral view. C, body, ventral view. D, body, left side, ventrolateral view. E, body, right side, ventrolateral view. F, posterior view. Scale bar represents 1 mm. Colour online.

Locality and age. Denmark, Danish (Scandinavian) amber; late Eocene.

Remarks. The specimen is embedded in an irregularly shaped piece of dark colour. The ventral surface is damaged and exposed, due to a cleft fringe of the amber piece, but the dorsal surface is clearly visible. Generic assignment is hard to determine due to strong damage of large portions of specimen, especially to the head, legs and ventral side. Nonetheless, the specimen is described as follows.

FIG. 10. Cryptocephalinae gen. sp., ZMUC 19-11 1958; body, dorsolateral view. Scale bar represents 0.5 mm. Colour online.

Description

Body. Length 3.0 mm, width 1.7 mm; robust, cylindrical (Fig. 10). Vertex punctate; eye large, flat, elongate. Pronotum nearly as wide as elytral base, convex, with anterior margin broad and raised, with lateral margin equipped with well-developed, slightly explanate carina, with shape rounded in dorsal view, medially curved downwards in lateral view, with posterior margin broad and strongly raised, its fringe transversely, densely, regularly folded (wrinkled); pronotal surface covered with large, deep punctures, with distance between punctures not exceeding diameter of puncture, with interstices convex, smooth, with a row of punctures along lateral margin. Scutellum very small, rectangular, not projecting. Elytra convex, cylindrical, with punctation arranged in 12 rows; scutellar row short, containing 9–10 punctures; next row shorter, with 5–6 punctures and joined with scutellar row; other 10 rows complete, some of them joined before apex; punctures in basal half large, slightly irregularly placed, with interstices between rows smooth, weakly convex, with transverse wrinkles; punctures in apical half smaller, arranged regularly, groove-like, with interstices between rows smooth and costate.

Cryptocephalinae are poorly represented in fossil resins, being described recently from Baltic amber (*Cryptocephalus groehni* Bukejs and Chamorro, 2015) and from Dominican amber (*Cryptocephalus kheelorum* Bukejs and Chamorro, 2015).

DISCUSSION

Definition, area and time of origin of Baltic amber

The fossil flora and fauna of Baltic amber are extremely rich and well explored (more than 3000 described species of arthropods, according to Weitschat and Wichard 2010). They constitute one of the most important reference points for deciphering the history of the entire non-marine past biota. However, the term 'Baltic amber' is somewhat confusing, particularly with respect to the time-and-space allocation and environmental interpretation of particular varieties of amber. Baltic amber belongs to the *succinite* type, under which we consider here all mid-Cenozoic ambers from northern and eastern Europe, including those from Rovno, Jutland, Gdansk, and 'classic' materials from Kaliningrad that are distinguished by their yield of succinic acid. As a result, important characteristics of the Baltic amber in a more restrictive sense (the one mined from the so-called Blue Earth of the Prussian Formation in the Samland Peninsula of the Kaliningrad Oblast of Russia), such as its age, duration of accumulation, source area, climate, relief, hydrography and vegetation, all are the subject of long-lasting debates. The age of the Blue Earth horizon has been defined variously, ranging from Lower Priabonian (36–37 Ma; Aleksandrova and Zaporozhets 2008; Kosmowska-Ceranowicz 2012) to Lutetian (41–48 Ma; Grimaldi and Engel 2005; Weitschat and Wichard 2010) or even Ypresian (54–48 Ma; Bauer *et al.* 2005), that is from the early (Bauer *et al.* 2005; Weitschat and Wichard 2010) to late Eocene (50 vs. 35 Ma; Rasnitsyn and Quicke 2002; Perkovsky *et al.* 2007).

Additional controversy arises because amber mostly occurs in secondary deposits and can therefore be older than the source rocks. The geographical area of the origin of Baltic amber (*s.s.*) is also variously delimited, ranging from all of Russo-Scandia (Weitschat and Wichard 2002, 2010) to the exclusively eastern Fenno-Scandian Upland (Perkovsky 2011). The suggested palaeoclimate of the source time and area of Baltic amber varies from hot and rather dry (paratropical), when based on the Lutetian (middle Eocene) age as proposed by Weitschat and Wichard (2002, 2010), to the equable climate (of lower seasonality, with a warm summer and mild winter) that is compatible with the less warm late Eocene age (Archibald and Farrell 2003; Dlussky and Rasnitsyn 2009; Perkovsky *et al.* 2012). In order to explain the observed combination of subtropical and temperate species in the inclusions, the palaeolandscape of Baltic amber source territory was suggested to be a combination of highland and lowland areas (Ulmer 1912). However, findings of specimens of warm-loving and temperate taxa included in one and the same piece of amber make this hypothesis inappropriate (Archibald and Farrell 2003; Perkovsky 2013) and support the alternative hypothesis of equable climate. Even the source plant producing the resin for Baltic amber is not identified with certainty; it has been suggested to be either *Pinus* (Weitschat and Wichard 2010), or *Pseudolarix* (Anderson and LePage 1996), or perhaps *Sciadopitys* (Wolfe *et al.* 2009).

Wheeler's dilemma

The contradictory composition of the Baltic amber fauna was noted more than a century ago by Wheeler (1910), who mentioned controversial co-occurrence of thermophilic and temperate ant genera there. Although the opinion that the Baltic amber arthropod fauna is a mixture of Recent temperate and tropical genera is widespread (Archibald and Farrell 2003), Zherikhin *in* Popov *et al.* (2001) concluded that insect groups with true tropical affinities are absent (Termitidae), or very rare (Mastotermitidae; Curculionidae: Brentinae, Platypodinae; etc.) in the Baltic amber. Instead, he claimed that temperate groups like snake-flies of the extant families Raphidiidae and Inocelliidae, winter crane flies (Trichoceridae), or aphids (Heie 1967; Kulicka and Wegierek 1996) prevail in Baltic amber. High prevalence of temperate taxa is also found for the Baltic amber fauna of ants (Dlussky and Rasnitsyn 2009; Perkovsky 2011). Nevertheless, thermophilous insect species do exist in Baltic amber and other succinites, and their presence calls for explanation. Archibald and Farrell (2003) discuss three possible explanations: (1) Baltic amber preserves a mixture of different faunas that were replacing one another following climate change during the existence of amber forest; (2) different faunas existed simultaneously in different climatic conditions of lowlands and mountains, but the respective inclusions from different landscapes have been mixed during transport and burial of resin; and (3) arthropods with different climatic preferences preserved in Baltic amber were able to co-exist under an equable climate with temperate summer and mild winter. Archibald and Farrell (2003) strongly and reasonably favour the third alternative; ancillary evidence from the flora supports it too (Pimenova 1937).

Danish amber

The late curator of the Zoological Museum at Copenhagen, S. G. Larsson, indicated that considerable amounts of Baltic amber have been found in the Miocene lignite deposits of Jutland (Larsson 1978). In his opinion, this Miocene lignite amber and the coastal amber of west Jutland originated in the amber forests of south Sweden in the western side of the southern Scandinavian water-shed, which is significantly more westward than the supposed area of origin of Baltic amber in a strict sense (mostly Samlandian). Unfortunately, Larsson's ideas about a southern Scandinavian source of Danish amber received little attention and were superseded by the widely accepted views of a single geographical source for all fossil resins of the succinite type that was supposedly some area far to the east of southern Sweden. However, evidence of a geographically independent source of the recently discovered Rovno amber (Perkovsky *et al.* 2007, 2010, and see below), along with the observed stronger similarity between arthropod assemblages of the Rovno and Danish ambers than between either of these and the amber from Gdańsk Bay (Dlussky and Rasnitsyn 2009; Perkovsky 2011), brings us back to Larsson's hypothesis which deserves more attention and thorough testing. The most contrasting differences are features of the well-studied assemblages of notably temperate aphids in the Baltic and Danish ambers. In spite of manifold larger collections, the Baltic amber yields only about as many aphid species (47) as the Danish amber (45), and only 21 of them are in common (Heie 1967, 1972; Heie and Wegierek 2011).

In view of the special features of the 'Baltic amber' found in Denmark, it is important to abandon a more inclusive and perhaps misleading broad concept of 'Baltic amber' as Eocene succinite resins found in the Baltic Sea Basin, in favour of the restrictive and precise definition of Baltic amber as the amber found only in Gdańsk Bay.

Rovno amber

Rovno amber is found predominantly in the lower part of the Mezhygorje Formation (the lowest Oligocene; Perkovsky *et al.* 2010). In the south of Byelorussia, amber is found mostly in Quaternary deposits (Perkovsky and Bogdasarov 2009). The specific composition of the fossil fauna found as inclusions in Rovno amber (Perkovsky *et al.* 2007), which includes more than 200 species not found in Baltic amber, indicates that the sedimentary basin source of Rovno amber was independent from that of Baltic amber (for details, see Perkovsky *et al.* 2003; Dlussky and Rasnitsyn 2009; Perkovsky and Rasnitsyn 2013). Just as the Baltic region sediments with epidote indicate that the fossil resins originated from Fennoscandia, the sediments with andalusite and tourmaline minerals indicate the Ukrainian Shield as the source for amber found in Gorka Lubartowska (southern Poland), and extracted in Klesov, Ukraine; Rovno amber (succinite) extracted in Klesov stretches to Belarus in the area of Gatcha–Osova (Kosmowska-Ceranowicz 2009). The age of Rovno amber, like the age of Danish amber, has always been considered to be the same as that of Baltic amber (Kosmowska-Ceranowicz 1999; Perkovsky *et al.* 2003).

Palaeoclimate and faunal composition of leaf beetles of succinites

Leaf beetles in succinites (Table 1) are represented by four species of extant 'Holarctic' (temperate or primarily temperate) genera (*Crepidodera decolorata* Nadein and

TABLE 1. Fossil Chrysomelidae from late Eocene resins

Taxon	Origin
Cassidinae	
Oposispini	
Oposispa scheeli Uhmann, 1939	Baltic amber
Sucinagonia javetana Uhmann, 1939	Baltic amber
Succinispa stainesi gen. and sp. nov.	Baltic amber
Anisoderini	
Protanisodera glaesi Quiel, 1909	Baltic amber
Gonophorini	
Electrolema baltica Schaufuss, 1892	Baltic amber
Criocerinae	
Criocerina pristina Germar, 1813	Baltic amber
Chrysomelinae: Chrysomelini	
Paleophaedon minutus Nadein *in* Nadein and Perkovsky, 2010	Rovno amber
Cryptocephalinae	
Cryptocephalus groehni Bukejs and Chamorro, 2015	Baltic amber
Cryptocephalinae gen. sp.	Danish amber
Eumolpinae	
Eumolpini	
Paleomolpus hirtus gen. et sp. nov.	Danish amber
Colaspoides eocenicus Moseyko and Kirejtshuk, 2013	Baltic amber
Euryopini	
Taphioporus rovnoi sp. nov.	Rovno amber
Taphioporus balticus Moseyko and Kirejtshuk, 2013	Baltic amber
Galerucinae	
Galerucini	
Calomicrus eocenicus Bukejs and Bezdek, 2014	Baltic amber
Calomicroides danicus gen. et sp. nov.	Danish amber
Alticini	
Psyllototus progenitor Nadein *in* Nadein and Perkovsky, 2010	Rovno amber
Psyllototus doeberli Bukejs and Nadein, 2013	Baltic amber
Psyllototus groehni Bukejs and Nadein, 2014	Baltic amber
Psyllototus viking sp. nov.	Danish amber
Crepidodera decolorata Nadein and Perkovsky, 2010	Rovno amber
Crepidodera svetlanae Bukejs, 2014	Baltic amber
Manobiomorpha eocenica Nadein *in* Nadein and Perkovsky, 2010	Rovno amber
Archealtica convexa Nadein, gen. et sp. nov.	Rovno amber
Ambraaltica baltica Bukejs and Konstantinov, 2013	Baltic amber
Paolaltica eocenica Biondi, 2014	Baltic amber
Lamprosomatinae: Lamprosomatini	
Succinoomorphus warchalowskii Bukejs and Nadein, 2015	Baltic amber
Archelamprosomius balticus Bukejs and Nadein, 2015	Baltic amber
Archelamprosomius kirejtshuki Bukejs and Nadein, 2015	Baltic amber

Perkovsky, 2010; *Crepidodera svetlanae* Bukejs, 2014; *Calomicrus eocenicus* Bukejs and Bezdek, 2014; *Cryptocephalus groehni* Bukejs and Chamorro, 2015), in contrast to one species of a Recent 'tropical' genus (*Colaspoides eocenicus* Moseyko and Kirejtshuk, 2013; for definitions for 'Holarctic' and 'tropical' genera, see Dlussky and Rasnitsyn 2009). A similar pattern is characteristic of the more extensively studied and more abundant ants in succinites. A total of 21 'Holarctic' species of ants and 19 'tropical' species are known from Baltic amber; for Danish amber, the numbers are 7 and 7; and for Rovno amber, they are 11 and 14 (Dlussky and Rasnitsyn 2009; Perkovsky 2011). Two more species of leaf beetles belong to Recent tribes of the subfamily Cassidinae with 'tropical' ranges (*Protanisodera glaesi* Quiel, 1909 (Anisoderini) and *Electrolema baltica* Schaufuss (Gonophorini)), and four more species are placed in fossil genera related to Recent 'tropical' genera (*Taphioporus balticus* Moseyko and Kirejtshuk, 2013, *Taphioporus rovnoi* Moseyko and Perkovsky sp. nov., *Manobiomorpha eocenica* Nadein *in* Nadein and Perkovsky, 2010 and *Paolaltica eocenica* Biondi, 2014). Additional 'Holarctic' genera have been recorded from Baltic amber, but their generic placements warrant further investigation.

Thus, there is a paradoxical combination of 'Holarctic' and 'tropical' leaf beetles found in succinites. This is possibly explained by past equable climate, with warm winters and cool summers (Archibald and Farrell 2003). The Chrysomelidae succinite fauna differs radically from that of the middle Eocene deposits of Messel and Eckfeld in central Europe. These are associated with a paratropical climate and totally lack 'Holarctic' elements, in contrast to the 'tropical' species.

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