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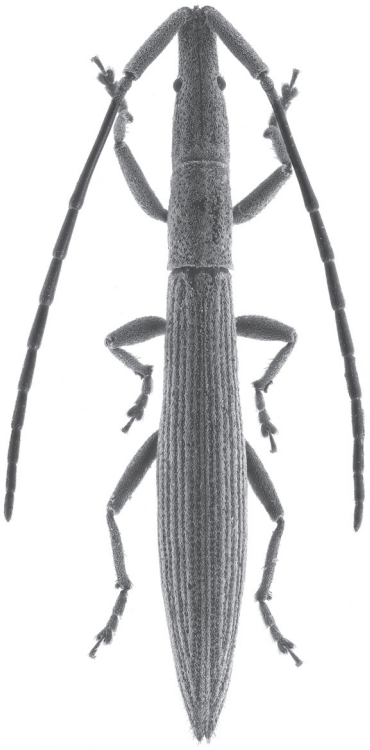

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A new species and a key to *Isomira* Mulsant, 1856 (Coleoptera: Tenebrionidae: Alleculinae) from Eocene Baltic amber

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Abstract. Based on a single well-preserved specimen from Eocene Baltic amber, a new comb-clawed beetle *Isomira lobanovi* **sp. n.** (Alleculinae: Alleculini: Gonoderina) is described and illustrated. The new species belongs to the subgenus *Mucheimira* Novák, 2016, with extant species distributed in South China, Himalaya and the south of Arabian Peninsula. *Isomira lobanovi* **sp. n.** is the most similar to *I.* (*Mucheimira*) *avula* Seidlitz, 1896 from Baltic amber, but differs from the latter by the following characters: antennae longer, distinctly moderately serrate; antennomere 11 clearly longer than antennomere 10; antennomere 3 with sharply obliquely truncate apical margin. A key to fossil species of *Isomira* Mulsant, 1845 from Baltic amber is given. The Mesozoic species *Jurallecula grossa* Medvedev, 1969 must be excluded from the subtribe Alleculina and considered as Alleculini incertae sedis. Two late Eocene species of *Isomira* from the Florissant Formation (North America) have no distinct characters of the genus, and one of them, "*Isomira*" *aurora* Wickham, 1914 would be better interpreted as Coleoptera incertae sedis. The subgenus *Mucheimira* is considered as a basal group in the genus *Isomira*. Two Triassic taxa, *Menephiloides minensis* Fujiyama, 1973 and *Adelidium cordatum* Tillyard, 1918, are proposed to interpret as Coleoptera incertae sedis.

Key words: Tenebrionidae, Alleculinae, *Isomira*, Baltic amber, Eocene, new species, key.

Новый вид и определительная таблица *Isomira* Mulsant, 1856 (Coleoptera: Tenebrionidae: Alleculinae) из эоценового балтийского янтаря

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Резюме. Описан новый вид жуков-пыльцеедов *Isomira lobanovi* **sp. n.** (Alleculinae: Alleculini: Gonoderina) на основании хорошо сохранившегося экземпляра из балтийского янтаря (пос. Янтарный, Калининградская область, Россия). Новый вид относится к подроду *Mucheimira* Novák, 2016, современные виды которого обитают в Гималаях, Южном Китае и на юге Аравийского полуострова. *Isomira lobanovi* **sp. n.** близок к *I.* (*Mucheimira*) *avula* Seidlitz, 1896, также известному из балтийского янтаря, но отличается от него следующими признаками: антенны более длинные, отчетливо умеренно пильчатые; антенномер 11 заметно длиннее 10-го; антенномер 3 с резко скошенным вершинным краем. Составлена определительная таблица трех видов рода *Isomira* Mulsant, 1845, известных из балтийского янтаря. Мезозойский вид *Jurallecula grossa* Medvedev, 1969 должен быть исключен из подтрибы Alleculina и рассматриваться как Alleculini incertae sedis. Два эоценовых вида *Isomira* из североамериканской формации Флориссант не имеют четких родовых признаков, а один из них, "*Isomira*" *aurora* Wickham, 1914, лучше интерпретировать как Coleoptera incertae sedis. Подрод *Mucheimira* рассматривается как базальная группа в роде *Isomira*. Два триасовых таксона, *Menephiloides minensis* Fujiyama, 1973 и *Adelidium cordatum* Tillyard, 1918, предлагается интерпретировать как Coleoptera incertae sedis.

Ключевые слова: Tenebrionidae, Alleculinae, *Isomira*, балтийский янтарь, эоцен, новый вид, определительная таблица.

Introduction

The alleculine genus *Isomira* Mulsant, 1856 comprises 81 extant species and subspecies from the Palaearctic and the transitional Palaearctic-Afrotropical zone in the south of the Arabian Peninsula [Novák, 2020] and 28 ones from the Nearctic and the transitional Nearctic-Neotropic zone [Bousquet et al., 2018]. Four species were described from the Afrotropical, Capean and Malgassy regions (Madagascar, Congo, South Africa) [Fairmaire, 1897; Pic, 1910, 1915, 1954]. Some species are known from the Indo-Malayan Region [Pic, 1923, 1934]. Two extinct species, *I.* (s. str.) *hoffeinsorum* Nabozhenko in Nabozhenko, Chigray et Bukejs, 2019 and *I.* (*Mucheimira*) *avula* Seidlitz, 1896 are known from Eocene Baltic amber [Kirejtshuk et al., 2008; Kirejtshuk, Ponomarenko, 2018; Nabozhenko et al., 2019]. The latter taxon, originally described from Baltic amber [Seidlitz, 1896], was twice erroneously listed as an extant species from Germany and Austria [Novák, Pettersson, 2008; Novák, 2020].

The genus is well differentiated and divided into seven subgenera [Bousquet et al., 2015] with the largest nominotypical one, widely distributed in the North Hemisphere [Bousquet et al., 2018; Novák, 2020]. The first revision of *Isomira* was made by Seidlitz [1896]. Later, several authors added important taxonomic

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and morphological contributions for Europe [Hölzel, 1958; Weise, 1974], Middle Asia [Dubrovina, 1973], the Caucasus [Iablokoff-Khnzorian, 1976], former USSR [Dubrovina, 1982], China and the Near East [Muche, 1981, 1982]. Campbell [1968] revised species of the genus from the Western Hemisphere. Russian authors added a great contribution to the knowledge of larvae of *Isomira* [Striganova, 1961; Dubrovina et al., 1979; Dubrovin, Kompantseva, 1990, 1992]. The most important taxonomic additions and changes were recently published by Novák [2009, 2014, 2016, 2019], who changed the rank of the *Asiomira* Dubrovina, 1973 from subgenus to genus, erected a new subgenus *Mucheimira* Novák, 2016 and described many new taxa from the Palaearctic Region.

A new extinct species of *Isomira* from Baltic amber belonging to the subgenus *Mucheimira* is here described.

Material and methods

The specimens (including the holotype of the new species) examined is deposited in the collection of the Museum of Amber Inclusions (Muzeum inkluzji w Bursztynie), Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk (Gdańsk, Poland) [MAIG]. The amber piece was polished by hand, allowing improved views of the included specimen, and was not subjected to any supplemental fixation.

Observations of the specimens were made using a Nikon SMZ 745T stereomicroscope. The photographs were taken using a Canon 70D camera with a macro lens (Canon MP-E 65mm). Extended depth of field at high magnifications was achieved by combining multiple images from a range of focal planes using Helicon Focus v. 6.0.18 software.

We calculated the dorsal ocular index (distance between eyes / distance across eyes × 100) [Campbell, Marshall, 1964] after 3D modeling the image of the sample using Helicon Focus 7.6.4. So, the index is approximate.

Systematic Paleontology

Family Tenebrionidae Latreille, 1802
Subfamily Alleculinae Laporte, 1840
Tribe Alleculini Laporte, 1840
Subtribe Gonoderina Seidlitz, 1896
Genus *Isomira* Mulsant, 1856

The studied specimen under consideration belongs to the genus *Isomira* of the tribe Alleculini and the subtribe Gonoderina based on the combination of the following characters: five abdominal ventrites (inner sternite and ventrite VIII are hidden, unlike Cteniopodini with externally visible sclerites in male and female), weakly serrate antennae (species of Cteniopodini are with filiform or moniliform antennae, while the majority of Alleculini have serrate antennae), simple penultimate tarsomere (the majority of Alleculina have lobed or bilobed penultimate tarsomere, but species of Gonoderina are with simple one). The specimen has not distinct rows of deep strial punctures or clear impressed striae unlike the majority of gonoderine genera. Only two genera have the mentioned above complex of characters: *Isomira* and *Asiomira*. The fossil specimen examined distinctly differs from Middle East species of the genus *Asiomira* by the subequal length of antennomeres 2 and 3.

Isomira (*Mucheimira*) *lobanovi* **sp. n.**
(Figs 1–6, 9)

Material. Holotype, ♂ (MAIG), collection number "6704" (ex. coll. Jonas Damzen JDC 9351): a complete beetle with the partially exposed metathoracic wings and apical portion of aedeagus is included in a transparent, yellow amber piece with approximate dimensions of 35 × 13 × 12 mm; preserved without supplementary fixation. Organic syninclusions: few small stellate fagacean trichomes.

Type stratum. Baltic amber from Eocene amber-bearing Blue Earth layers; a predominantly Bartonian age has been interpreted for the extinct central European resin-producing forests [Szwedo, Sontag, 2009; Bukejs et al., 2019].

Type locality. Yantarny (formerly Palmnicken), Sambian (Samland) Peninsula, Kaliningrad Region, Russia.

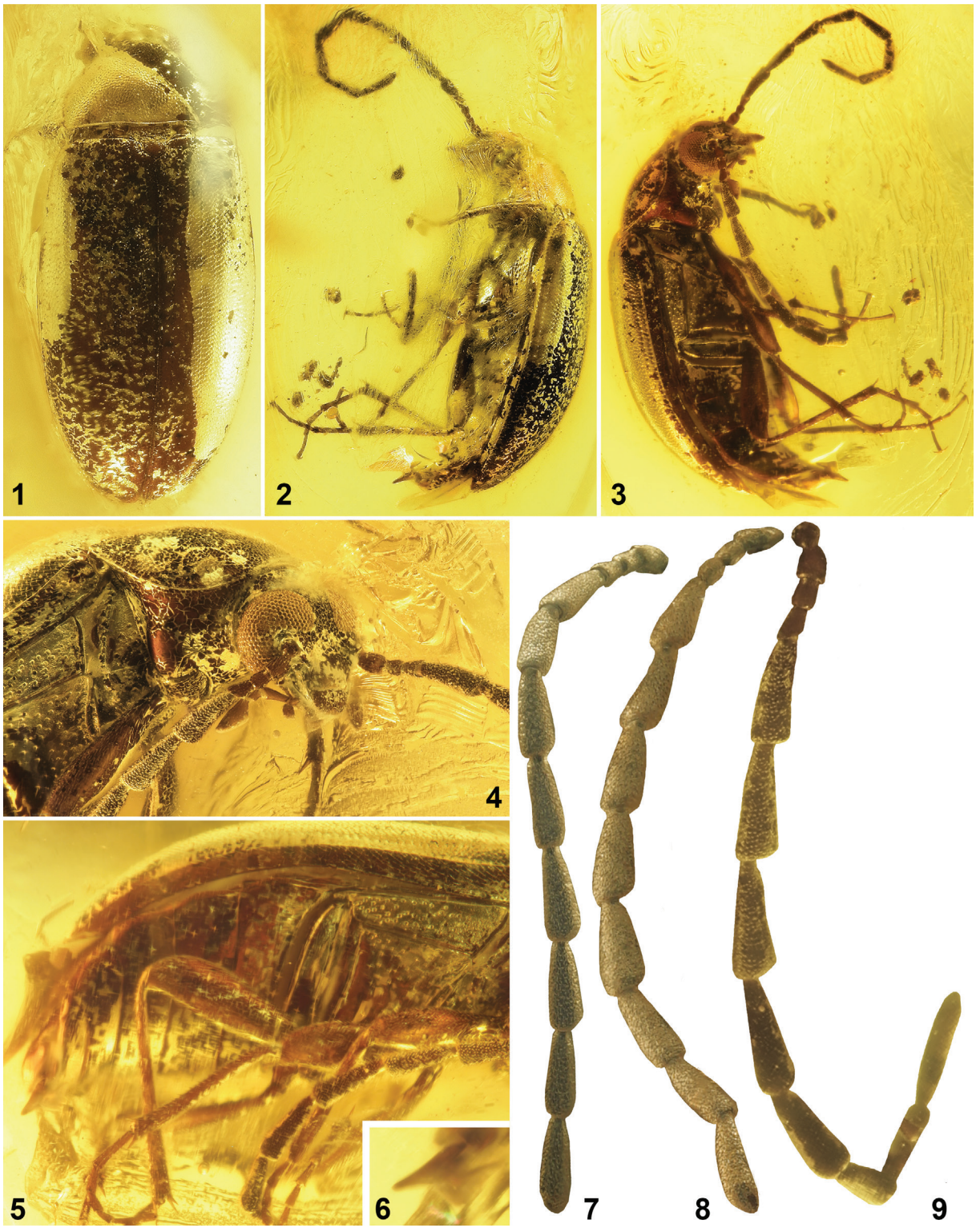
Description. Measurements: body length 4.5 mm, body maximum width 1.9 mm; pronotum length 0.7 mm, pronotum maximum width 1.5 mm; elytral length 3.5 mm, elytral maximum combined width 1.9 mm.

Body elongate-oval, subparallel sided, slightly convex; dorsal surface regularly pubescent with recumbent, short setae (Fig. 1).

Head with coarse and dense punctation, distance between punctures smaller than one puncture diameter; anterior margin emarginate, about 2 times as wide as frons between eyes; lateral margins widely sinuate between epistoma and genae. Frons separated from epistoma by suture-shaped impressed wrinkle. Compound eyes large, convex, reniform, widely emarginate at inner margin; wider dorsally and narrower ventrally; dorsal ocular index 15; eyes ventrally reaching to laryngeal emargination. Maxillary palpomere 1 small, about 0.4 times as long as palpomere 2; palpomere 2 subconical, slightly dilated apically, elongate, 2.7 times as long as wide; palpomere 3 nearly as long as wide, slightly dilated apically, with oblique apical margin; palpomere 4 securiform, apical margin strongly obliquely truncate (Fig. 4), elongate, 2.1 times as long as wide; length ratios of maxillary palpomeres 1–4 equal to 8 : 20 : 11 : 28. Antennae long (nearly reaching middle of abdominal ventrite 3), moderately serrate, inserted between and close to anterior inner margin of eyes (Fig. 9); scape cylindrical, 1.3 times as long as wide; pedicel cylindrical, 1.2 times as long as wide, slightly narrower and shorter than scape; antennomere 3 subconical, about 1.5 times as long as wide, slightly dilated apically, with oblique apical margin; antennomeres 4–10 elongate, dilated apically, subequal in length and shape, joined asymmetrically; antennomere 11 elongate, with pointed apex; length ratios of antennomeres 1–11 equal to 11 : 9 : 11 : 32 : 36 : 36 : 36 : 36 : 32 : 29 : 41.

Pronotum bell-shaped, strongly transverse, 2.1 times as wide as long, widest at middle. Lateral margins very weakly rounded, almost parallel sided in posterior half, and in anterior half they sharply narrowed to anterior margin; anterior margin weakly rounded; base straight laterally and slightly rounded at middle. Anterior angles rounded; posterior angles weakly obtuse. Anterior margin with distinct bead medially; posterior margin with distinct bead; lateral margins with narrow bead. Pronotal punctation fine and dense, not rasp-like, distance between punctures distinctly smaller than a puncture diameter; interspaces microsculptured. Prohypomera and prosternum before procoxae apparently impunctate. Prosternal process narrow, about 0.5 times as wide as diameter of procoxa.

Scutellum moderately large, subtriangular, with slightly convex lateral margins, transverse, 1.4 times as wide as long, punctate.



Figs 1–9. *Isomira* (*Mucheimira*) spp. from Baltic amber, males, habitus and details of structure.

1–6, 9 – *I. lobanovi* **sp. n.**; 7, 8 – *I. avula*. 1 – habitus, dorsal view; 2 – habitus, lateral view (left side); 3 – habitus, lateral view (right side); 4 – head, prothorax and sclerites of pterothorax, latero-frontal view; 5 – abdomen, middle and hind tibiae; 6 –apical piece of the aedeagus, lateral view; 7 – right antenna, view from lateral side; 8 – left antenna, view from below; 9 – right antenna, view from above.

Рис. 1–9. *Isomira* (*Mucheimira*) spp. из балтийского янтаря, самцы, общий вид и детали строения.

1–6, 9 – *I. lobanovi* **sp. n.**; 7, 8 – *I. avula*. 1 – габитус, вид сверху; 2 – габитус, вид сбоку (левая сторона); 3 – габитус, вид сбоку (правая сторона); 4 – голова, проторакс и склериты птероторакса, вид сбоку и спереди; 5 – брюшко, средние и задние ноги; 6 – апикальная доля эдеагуса, вид сбоку; 7 – правая антенна, вид с боковой стороны; 8 – левая антенна, вид снизу; 9 – правая антенна, вид сверху.

Elytra elongate-oval, subparallel sided, widest at middle, 4 times as long as pronotum; with weakly visible striae of fine, longitudinal punctures; interstriae densely covered with fine rasp-like punctation. Epipleura wide, not reaching elytral sutural angle, sharply narrowing before apex, near middle of abdominal ventrite 5; covered with fine punctation. Hind wings present. Mesepisterna and mesepimera with coarse, sparse, round punctures, distance between punctures greater than one puncture diameter. Metepisterna and metaventrite with coarse, moderately dense, round punctation, distance between punctures 0.5–2 times as a puncture diameter (disc of metaventrite and anterior portion of metepisterna with sparser and finer punctures) (Fig. 5).

Legs long and slender, with fine and dense punctation; regularly pubescent with fine, recumbent setae. Femora clavate, flattened. Tibiae thin and straight (pro- and mesotibiae weakly curved in lateral view); with simple fine suberected setiform spines (not strong sparse spines); with two short apical spurs of subequal length. Length ratios of tarsomeres (from basal to apical) equal to 5 : 4 : 3 : 3 : 8 (protarsi), 9 : 5 : 4 : 3 : 8 (mesotarsi), 14 : 5 : 3 : 8 (metatarsi). Tarsal claws serrate, symmetrical, large, strongly divergent. Protarsal claws with four teeth.

Abdomen covered with fine dense punctation and fine recumbent setation; length ratios of abdominal ventrites equal to (?)5 : 6 : 5 : 4 : 4 (medially).

Apical piece of aedeagus narrowly-triangular, with pointed apex (Fig. 6).

Differential diagnosis. This species belongs to the subgenus *Mucheimira* by the very large eyes and short distance between eyes in male and presence of subequal and short antennomeres 2 and 3. The subgenus *Mucheimira* is characterized by sexual dimorphism in ocular index between male and female [Novák, 2016]. The ocular index of female is not defined, but *I. lobanovi* **sp. n.** is very close to *I.* (*Mucheimira*) *avula* by many characters and similar form of apical piece of aedeagus and differs only by the structure of antennae. As a result, the new species is included into the mentioned subgenus. Differences between *I. avula* and *I. lobanovi* **sp. n.** are indicated in the key below. The new species differs from all extant congeners in the distinctly serrate antennae and from *I.* (*Mucheimira*) *stoetzneri* Muche, 1981 and *I.* (*Mucheimira*) *murzini* Novák, 2009 additionally in the shorter body (4.5 mm, unlike more than 7 mm in both mentioned species [Novák, 2009, 2014]). Apical piece of aedeagus subacute and slightly curved in lateral view, the most similar to that in *I.* (*Mucheimira*) *sichuanica* Novák, 2009 [Novák, 2009: fig. 19].

Etymology. The species is named in memory of Dr Andrei Lvovich Lobanov, known specialist on Cerambycidae and the founder of the largest coleopteran website "Beetles and coleopterists".

A key to *Isomira* known from Eocene amber

1(2). Antennomere 3 about twice as long as antennomere 2. Male and female with subequal eye sizes .... *I. hoffeinsorum*

2(1). Antennomeres 2 and 3 short, subequal in length. Male with distinctly larger eyes than female.

3(4). Antennae very weakly serrate (Figs 7, 8), antennomere 3 with straight anterior margin, ultimate and penultimate antennomeres subequal in length ..... *I. avula*

4(3). Antennae distinctly serrate (Fig. 9), antennomere 3 with oblique anterior margin, ultimate antennomere 1.4 times as long as penultimate one .... *I. lobanovi* **sp. n.**

Discussion

The tribe Alleculini is interpreted as the most ancient group within Alleculinae, originally associated with forest [Ogloblin, Znojko, 1950; Dubrovin, Kompantseva, 1990]. The alleculine lineage is known in the fossil records since the late Jurassic [Medvedev, 1969; Kirejtshuk et al., 2008; Kirejtshuk, Ponomarenko, 2018; Nabozhenko, 2019]. Medvedev [1969] preliminary included the Jurassic species *Jurallecula grossa* Medvedev, 1969 to the subfamily Alleculinae in Alleculidae (now the tribe Alleculini in Alleculinae), and noted that it has some important characters of the Nearctic subfamily Lystronychinae (now the subtribe Xystropodina in Alleculini according to Bousquet et al. [2015]), but additional material of better preservation is required for a clear definition of its systematic position. *Jurallecula grossa* does not belong to the subtribe Alleculina because it has not lobed penultimate tarsomeres. Thus, this species was erroneously included to the latter subtribe by Nabozhenko [2019] and it must be interpreted as a member of the tribe Alleculini incertae sedis. The cteniopodine lineage (the tribe Cteniopodini) appears in the fossil record in the early Cretaceous simultaneously with the appearance of angiosperms [Nabozhenko et al., 2015; Chang et al., 2016].

The gonoderine branch appears in the fossil record only in Eocene. All seven known fossil species of the subtribe Gonoderina are known from deposits of the Upper Eocene: Baltic amber, 41.2–37.8 Ma (Bartonian) and Florissant, 37.8–33.9 Ma (Priabonian). Two genera, *Isomira* and *Gonodera* Mulsant, 1856, are the most diverse in the Upper Eocene deposits of Europe and North America; the third Nearctic genus *Capnochroa* LeConte, 1862 is represented by only one species from the Florissant Formation [Nabozhenko, 2019]. Two species of *Isomira* from the Florissant Formation scarcely belong to this genus. The first one, *I. florissantensis* Wickham, 1914, is more or less similar to Alleculinae and has subserrate antennae [Wickham, 1914a: fig. 7] with subequal, moderately long antennomeres 3 and 4 (but slightly shorter than 4–9 ones); this species can be doubtfully interpreted as *Isomira*. The second one, *I. aurora* Wickham, 1914 cannot be reliably assigned to any beetle family, because its description is poorly informative, and according to it the head of the holotype having no details, trapezoidal pronotum, part of elytra and part of not serrate antennae [Wickham, 1914b: fig. 6]. This species was not included in catalogues of fossil Tenebrionidae [Kirejtshuk et al., 2008; Kirejtshuk, Ponomarenko, 2018; Nabozhenko, 2019], because it would be better interpreted as Coleoptera incertae sedis.

Isomira is one of the few groups of Alleculini, whose adults switched their lifestyle to diurnal one and feed on flowers of Angiosperms. The extinct species from amber and some extant Asian ones (subgenera *Mucheimira* and *Paraisomira* Dubrovina, 1982) of the genus demonstrate several characters supposing a nocturnal lifestyle: thickened or weakly serrate antennae and large eyes. Extinct *I. hoffeinsorum* from Baltic amber has very large eyes, although belongs to nominotypical subgenus. This feature makes it possible to suggest that large eyes and the nocturnal lifestyle were characteristic of ancestral

forms of *Isomira*, as well as for most extant Gonoderina. Serrate antennae probably are a symplesiomorphy within the subfamily Alleculinae, because this character occurs in all modern tribes. The majority of extant Cteniopodini have filiform antennae, but some taxa have antennae partly serrate (for example *Podonta antennata* Muche, 1965; personal communication by Vladimír Novák). Two known Mesozoic Cteniopodini have distinctly serrate antennae [Nabozhenko et al., 2015; Chang et al., 2016]. Thus, *Mucheimira* probably is a basal branch of the genus *Isomira* possessing a complex of the characters among extinct and extant taxa. This subgenus possibly was widely distributed in the North Hemisphere during the Paleogene, but to the present time only some exclaves have survived in East Asia (Himalayas, South China) and in the south of the Arabian Peninsula [Novák, 2020].

A taxonomic position of some Triassic taxa interpreted as Tenebrionidae

Menephiloides Fujiyama, 1973

Type species: *Menephiloides minensis* Fujiyama, 1973 by original designation [Fujiyama, 1973: 378]. Monotypic genus.

Type stratum. Omine, Japan, Hazegatani coal mine, Monomoki Formation, Carnian, Upper Triassic (235–221.5 Ma).

This genus was originally included under question in the family Tenebrionidae. Fujiyama [1973] tried to compare the single elytron of *M. minensis* with those in *Menephilus* Mulsant, 1854 (Stenochiinae: Cnodalonini) and *Tenebrio* Linnaeus, 1758 (Tenebrioninae: Tenebrionini). In fact, the elytron of this species has 10 striae without scutellary striole, which is uncharacteristic for Tenebrionidae. *Menephiloides minensis* specially was not included in the fossil records [Kirejtshuk at al., 2008; Kirejtshuk, Ponomarenko, 2018; Nabozhenko, 2019]. However Bao and Antunes-Carvalho [2020] still wrote that it is Tenebrionidae. Here we propose to interpret *Menephiloides minensis* as Coleoptera incertae sedis.

Adelidium Tillyard, 1918

Type species: *Adelidium cordatum* Tillyard, 1918 by original designation [Tillyard, 1918: 752]. Monotypic genus.

Type stratum. New South Wales, Australia, Glenlee railway cutting, Anisian, Middle Triassic (247–242 Ma).

This genus was included in the family Tenebrionidae without any comparison with tenebrionid taxa. Tillyard [1918] suggested that *A. cordatum* possibly closely related to some *Ademosyne* Handlirsch, 1906 (Archostemata: Ademosynidae) from the Upper Triassic Ipswich Coal Measures (Queensland, Australia). In fact, characters of wide and very convex single elytron of *Adelidium* with eight or nine visible striae without scutellary striole can be interpreted very widely. The taxon distinctly does not belong to the family Tenebrionidae, which is known reliably only from the Late Jurassic. *Adelidium cordatum* specially was not included in the fossil records [Kirejtshuk at al., 2008; Kirejtshuk, Ponomarenko, 2018; Nabozhenko 2019]. However Bao and Antunes-Carvalho [2020] still wrote that it is Tenebrionidae. Here we propose to interpret *Adelidium cordatum* as Coleoptera incertae sedis.

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