

A new tribe of Galerucinae leaf beetle (Insecta: Coleoptera: Chrysomelidae) from the Upper Cretaceous Taimyr amber[☆]



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ABSTRACT

The new tribe Taimyralticipi trib. nov., new genus *Taimyraltica* gen. nov. and new species *Taimyraltica calcarata* sp. nov. (Coleoptera: Chrysomelidae: Galerucinae) are described from Upper Cretaceous (Santonian) Taimyr amber of northern Siberia (Yantardakh locality). The new genus shares characters with genera of the tribe Alticipi (small size, transverse antebasal groove on pronotum, regular punctate-striate elytra) and the Galerucini (narrow, non-swollen metafemora). A possible apomorphy of the new genus and tribe is a large and acute metatibial spur, erect and oriented transversely to the longitudinal axis of tibia. This character state is unknown in recent and fossil genera of Galerucinae. Early evolution and divergence of leaf beetles are discussed, and a Jurassic and Early Cretaceous subfamily radiation is proposed. Fossil galerucines are reviewed. The oldest *Phyllotreta* is recorded from the lower Miocene of Izarra (Spain). Our findings show an extreme rarity of Phytophaga in Taimyr amber from Yantardakh. Absence of Phytophaga was recorded earlier at Obeschayuschiy (Santonian–Campanian) of the Magadan Region) and compared with their much larger share in Khetana (north of Khabarovsk Krai); we find nearly the same differences between Taimyr amber from Yantardakh and Canadian amber. In Obeschayuschiy this appears due to the Mesophytic character of the flora. It is assumed that the Santonian amber gymnosperm forest of the Khatanga Basin had the same character.

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1. Introduction

Chrysomelidae, or leaf beetles, are representatives of Phytophaga – the mega-diverse beetle group characterized by herbivory. The Mesozoic history of herbivory is insufficiently studied, but it has been suggested that it was intensifying in the Early Cretaceous (Zherikhin, 2002). The mid-Cretaceous extinction affected all major herbivore guilds (Zherikhin, 2002), and created additional opportunities for Phytophaga. It is not yet clear if the first appearance of undoubted leaf beetles in the Early Cretaceous Jehol Biota (Yixian Formation, NE China, Kirejtshuk et al., 2015) was driven by the origin of angiosperms, but there is little doubt that this was the case for younger chrysomelid lineages. That is one reason why the Late Cretaceous is so important in chrysomelid history.

Descriptions of new taxa of fossil leaf beetles from the Cenozoic (especially those of the European upper Eocene ambers) have

recently experienced rapid growth (e.g., Nadein and Perkovsky, 2010; Bukejs, 2014; Nadein et al., 2016). In contrast, Jurassic and Cretaceous leaf beetles are still mostly unknown, and most of the records and descriptions are questionable (Santiago-Blay, 1994). The taxonomic positions of some described Cretaceous taxa have been recently revised, e.g., subfamily Protoscelinae Medvedev, 1968 from the Jurassic of Karatau was transferred to the family Anthribidae (Legalov, 2013). Herbivory damage found on leaves of *Zingiberopsis* (Zingiberaceae) from the latest Cretaceous (~65 Ma) and associated with the hispine ichnotaxon *Cephaloleichnites strongii* Wilf et al., 2000 was questioned by García-Robledo & Staines (2008), and Labandeira et al. (1995) mention a coryphoid palm bud supposedly bored by a hispine leaf beetle larva from the Maastrichtian of USA (Zherikhin, 2002). *Donacia* Fabricius, 1775 (Donaciinae) which feed on aquatic and semiaquatic angiosperms was found in the Maastrichtian–Danian Tsagan Formation (Amur region) (Bieńkowski, 2015). Rasnitsyn and Zherikhin (2002) indicated a Maastrichtian age for these fossils, but the clay with bedded plant and insects remains where this fossil was found lies 37 m above the K-T boundary (Vršanský et al., 2013). Still, some latest

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undescribed Cretaceous records from Brazil, China and France were mentioned by Kirejtshuk et al. (2015). The only indication of leaf beetles in the Late Cretaceous of the Southern Hemisphere is based on elytra (Craw and Watt, 1987), and appears rather doubtful.

Thus, reliable published findings of Mesozoic leaf beetles (Fig. 1) are limited to the Cretaceous: the palm seed beetle *Mesopachymerus antiqua* Poinar, 2005 (Bruchinae) from Grassy Lake (Canadian amber: Campanian, 78–79 Ma) and the extinct monotypic tribe Mesolpinini Kirejtshuk, Moseyko et Ren, 2015 (Chrysomelinae) with five species described from the Lower Cretaceous of the Yixian Formation (Liaoning, China) (125–133 Ma). Here we describe a new species, genus and tribe of the leaf beetle subfamily Galerucinae from Santonian Taimyr amber at Yantardakh (northern Siberia) (Fig. 1).

The subfamily Galerucinae (Coleoptera: Chrysomelidae) is a group of jumping and non-jumping leaf beetles composed of about 1100 genera and over 15,000 species (Nadein and Beždek, 2014), mostly angiosperms-feeders. It is represented from the Eocene to the Pliocene as both compression fossils and inclusions in fossil resins (Santiago-Blay, 1994; Nadein et al., 2016; Kirejtshuk and Ponomarenko, 2017). Current data on the Galerucinae from fossil resins are presented in Table 1.

2. Material and methods

This study is based on a single specimen embedded in Upper Cretaceous Taimyr amber from Yantardakh in northern Siberia. Its location, stratigraphy and age were discussed by Perkovsky and Makarkin (2015, fig. 1) and Rasnitsyn et al. (2016). The amber piece is 4.5 × 4.2 × 2 mm after preparation.

Terminology in general follows Nadein and Beždek (2014). Photographs were taken with a Leica M205C stereomicroscope with an attached Leica DFC425 digital camera.

The specimen is housed in the Paleontological Institute of the Russian Academy of Sciences (Moscow, PIN).

3. Systematic paleontology

Order Coleoptera
Suborder Polyphaga

Superfamily Chrysomeloidea Latreille, 1802

Family Chrysomelidae Latreille, 1802

Subfamily Galerucinae Latreille, 1802

Tribe **Taimyralticini** Nadein, trib. nov.

Type genus: *Taimyraltica* Nadein, gen. nov.

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Description and diagnosis. Body shortly elongate, moderately convex (Fig. 2A, E); head hypognathous, eyes without emargination (Fig. 2B); antennae short, attached closely, anteriorly between eyes, with 11 antennomeres (Fig. 2B), filiform, apical antennomeres thickened; pronotum transverse, narrower than elytral base, with lateral margin, antebasal transverse furrow (Fig. 2B); anterior coxal cavities closed, procoxae shortly transverse; elytra with regular puncture rows (Fig. 2C), intervals between rows convex; hind wings fully developed (Fig. 2D); abdominal ventrites without modifications; hind femora not swollen (Fig. 2D), its length/width ratio 3.0, tibiae simple, apex of hind tibia obtuse, metatibial spur large, acute (Fig. 2D), erect, transversely oriented to longitudinal axis of tibia, tarsal claws simple, claws widely spaced. The new tribe differs from Alticini and Galerucini by metatibial spur structure (see Discussion).

Attribution to Galerucinae is based on the combination of the following characters (Nadein and Beždek, 2014): body elongate, head hypognathous, without constriction behind eyes, antennal insertions situated between eyes at distance from anterior margin of frons, eyes without emargination, pronotum with lateral margin, not constricted, pronotal base with transverse furrow, procoxae transverse, elytra regularly punctured, pygidium not vertical.

Genus ***Taimyraltica*** Nadein gen. nov.

Type species: *Taimyraltica calcarata* Nadein sp. nov.

LSID: urn:lsid:zoobank.org:act:62C09FB2-D55C-44A9-A52D-61711-959E20B

Derivation of name. The genus name combines the name of amber and the name of the type genus of tribe Alticini.

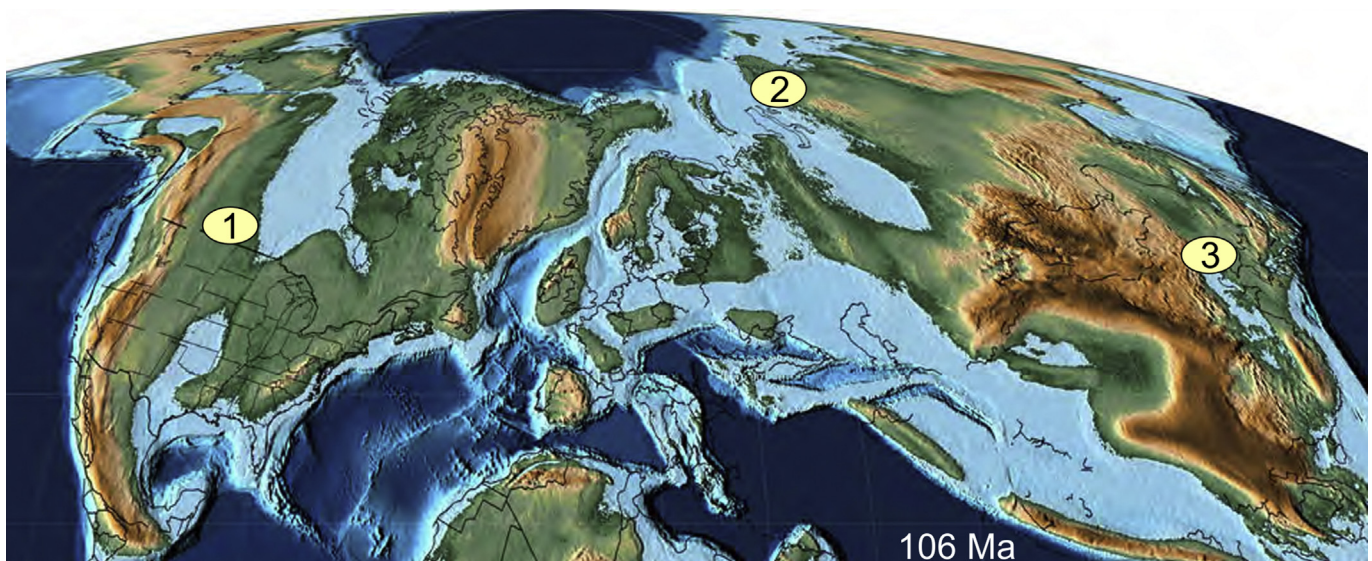


Fig. 1. Localities with named Cretaceous leaf beetles. 1, Grassy Lake, Canadian amber (*Mesopachymerus antiqua* Poinar, 2005). 2, Yantardakh, Taimyr amber (*Taimyraltica calcarata* Nadein, gen. et sp. nov.). 3, Liaoning, Yixian Formation (tribe Mesolpinini Kirejtshuk, Moseyko et Ren, 2015). Map is modified from Scotese (2014).

Table 1

A list of known Galerucinae from fossil resins.

Species	Series/Stage	Locality	References
<i>Taimyraltica calcarata</i> Nadein, gen. et sp. nov.	Upper Cretaceous, Santonian	Yantardakh, Taimyr amber	This paper
<i>Crepidocnema yantarica</i> Moseyko, Kirejtshuk et Nel 2010	lowermost Eocene	Oise amber	Moseyko et al. (2010)
<i>Calomicroides danicus</i> Nadein in Nadein et al., (2016)	upper Eocene	Danish amber	Nadein et al. (2016)
<i>Calomicrus eocenicus</i> Bukejs et Bezděk 2014	upper Eocene	Baltic amber	Bukejs and Bezděk (2014)
<i>Ambraaltica baltica</i> Bukejs et Konstantinov, 2013	upper Eocene	Baltic amber	Bukejs and Konstantinov (2013)
<i>Sucinolivolvia torpida</i> Bukejs, Biondi et Alekseev, 2015	upper Eocene	Baltic amber	Bukejs et al. (2015)
<i>Paolaltica eocenica</i> Biondi, 2014	upper Eocene	Baltic amber	Biondi (2014)
<i>Crepidodera svetlanae</i> Bukejs, 2014	upper Eocene	Baltic amber	Bukejs (2014)
<i>Crepidodera tertiotertiaria</i> Bukejs, Biondi et Alekseev, 2016	upper Eocene	Baltic amber	Bukejs et al. (2016)
<i>Crepidodera decolorata</i> Nadein et Perkovsky, 2010	upper Eocene	Rovno amber	Nadein and Perkovsky (2010)
		Bitterfeld amber	Bukejs et al. (2016)
<i>Archealtica convexa</i> Nadein in Nadein et al., (2016)	upper Eocene	Rovno amber	Nadein et al. (2016)
<i>Manobiomorpha eocenica</i> Nadein in Nadein and Perkovsky (2010)	upper Eocene	Rovno amber	Nadein and Perkovsky (2010)
<i>Psyllototus progenitor</i> Nadein in Nadein and Perkovsky (2010)	upper Eocene	Rovno amber	Nadein and Perkovsky (2010)
<i>Psyllototus viking</i> Nadein in Nadein et al., (2016)	upper Eocene	Danish amber	Nadein et al. (2016)
<i>Psyllototus doeberli</i> Bukejs et Nadein, 2013	upper Eocene	Baltic amber	Bukejs and Nadein (2013)
<i>Psyllototus groehni</i> Bukejs et Nadein, 2014	upper Eocene	Baltic amber	Bukejs and Nadein (2014)
<i>Neocrepidodera antiqua</i> (Gressitt, 1971)	lower-middle Miocene	Mexican amber	Gressitt (1971)
<i>Leptonesiotes virkkii</i> Santiago-Blay, Poinar et Craig, 1996	middle Miocene	Dominican amber	Santiago-Blay et al. (1996)
<i>Wanderbiltiana wawasita</i> Santiago-Blay, Sawini, Furth, Craig et Poinar, 2004	middle Miocene	Dominican amber	Santiago-Blay et al. (2004)
<i>Acallepitrix</i> sp.	middle Miocene	Dominican amber	Santiago-Blay and Craig (1999)

Description. Body shortly elongate, moderately convex (Fig. 2A). Head large, not broader than pronotum; eyes large, head behind eyes visible; antennae short, not reaching half of body, filiform, with 11 antennomeres (Fig. 2B), attached closely to each other anteriorly between eyes.

Pronotum transverse, convex anteriorly, less convex basally, anterior half of pronotum distinctly broader than posterior, lateral margin nearly straight in lateral view (Fig. 2B), anterior angles of pronotum swollen, antebasal furrow present (Fig. 2B), not reaching lateral sides of pronotum, pronotal surface punctate (Fig. 2B), hypomeral suture visible, anterior coxal cavities closed, prosternum transverse; procoxae shortly transverse.

Elytra shortly-elongate (Fig. 2C), convex, humeral calli well developed, elytral surface punctate, punctures arranged in very regular rows (Fig. 2C); epipleurae present, in basal half broadest, gradually narrowing towards elytral apices, fully visible from lateral view. Hind wings fully developed (Fig. 2D). Abdomen not longer than elytra, or at most last abdominal ventrite slightly exposed, five ventrites visible, all ventrites without modifications (Fig. 2A).

Metasternum shortly transverse, twice shorter than ventrites combined, metanepisterum long and narrow.

Legs long, thin (Fig. 2A); femora elongate, narrow, hind femora not swollen (Fig. 2D), 3.5 times longer than wide, tibiae straight, widened weakly, gradually towards apex, apex of hind tibia obtuse, outer, inner margin of metatibial tip bears short, dense bristles, metatibial spur very large, acute, erect, oriented transversely to longitudinal axis of tibia (Fig. 2D), tibial spurs of pro-, mesotibia small. Metatarsus shorter than tibia (Fig. 2A), metatarsomere 1 not elongate, last tarsomere twice longer than third tarsomere, tarsal claws long, simple, claws widely spaced.

Taimyraltica calcarata Nadein sp. nov.

Fig. 2

LSID: urn:lsid:zoobank.org:act:68020470-7169-4B51-A1CF-5D78-E99D31F0

Derivation of name. The specific name is derived from the Latin *calcar* (spur) for the peculiarly large and strongly transversely erect spur of the metatibia of the new species.

Material. Holotype, PIN 3311/1203, collected in 2012 during a PIN expedition. A nearly complete specimen, the head is visible in

lateral view, the left side is almost completely visible, the right side is partially exposed and damaged. Syninclusions: PIN 3311/1204, Ephemeroptera; PIN 3311/1204a, Acari.

Locality and horizon. Russia: Krasnoyarskiy Krai: Taimyrskiy (Dolgano-Nenetskiy) District: Taimyr Peninsula: right bank of the Maimecha River in 3 km upstream from its confluence with the Kheta River (a left tributary of the Khatanga River), Yantardakh Hill (Yantardakh) [71.307222°N, 99.562778°E]. Upper Cretaceous, Santonian (Kheta Formation).

Description. Body coloration light, apparently yellowish (Fig. 2A), without visible metallic luster; dorsum glabrous, ventrum covered with very sparse, small, short hairs, body length 2.0 mm, width about 1.0 mm. Head nearly as long as pronotum (Fig. 2A), vertex of head convex, punctate, frontal part between eyes convex and elevated, apparently ridge-shaped, labrum large, transverse, mandibles large, distinctly exposed; eyes round (Fig. 2A); antennomeres from the 3rd gradually thickening from basal to apical (Fig. 2B), antennomeres 3–7th elongate, about 2.5–3 times longer than wide, 3 apical antennomeres distinctly thicker, at most length twice width, last antennomere thickest, 1.8 times longer than wide, 1.3 times longer than previous, apex nearly obtuse.

Pronotum 2.5 times shorter than elytra, covered with large, moderately deep punctures (Fig. 2B), surface between punctures smooth, glabrous, distance between punctures varies, in average about diameter of puncture, antebasal furrow impunctate (Fig. 2B), interspace between furrow, posterior margin of pronotum convex, impunctate; lateral margin narrow, smooth; hypomera with wavy surface in basal half, anterolateral angles of pronotum somewhat enlarged, moderately swollen (Fig. 2B), posterolateral angles not enlarged.

Elytral punctures large, deep (Fig. 2C), larger than pronotal, puncture rows regular, not double or confused, punctures in rows dense, distance between punctures less than diameter of puncture, in apical parts of puncture rows sparser, intervals between rows convex (Fig. 2C), smooth, glabrous, distance between puncture rows not exceeding diameter of puncture.

Abdominal ventrites nearly impunctate or with rather sparse, small punctures.

Femora covered with rather sparse, small hairs, tibiae covered with short, moderately dense hairs, tibial apex covered with longer hairs and bristles, metatibial spur very large, acute, erect, oriented

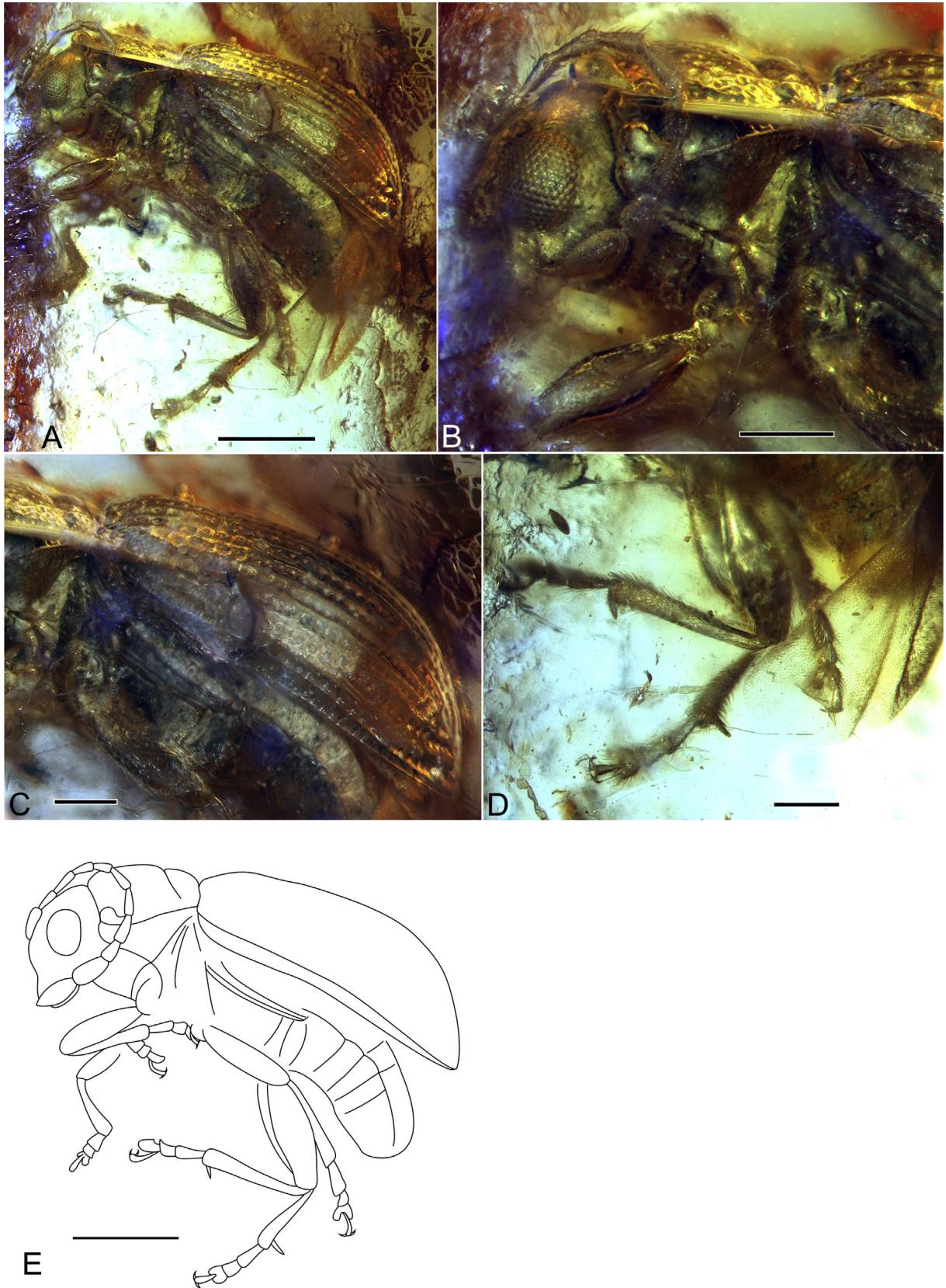


Fig. 2. *Taimyraltica calcarata* Nadein, gen. et sp. nov., holotype PIN 3311/1203. A, general view, lateral. B, Head, lateral. C, Elytra, lateral. D, Hind legs. E, general view outline. Scale bars: A, E, 0.5 mm. B, C, D, 0.2 mm.

transversely to longitudinal axis of tibia (Fig. 2D); tarsomeres covered ventrally with dense, short setae (Fig. 2A); metatarsus 1.6 times shorter than metatibia (Fig. 2D), metatarsomere I 2.5 times shorter than following tarsomeres combined, moderately thick, twice as long as wide, metatarsomere II 1.3 times shorter than previous, last tarsomere very long, bent (Fig. 2D), hardly shorter than first.

4. Discussion

4.1. Comparative morphology and phylogenetic position of *Taimyraltica*

Taimyraltica gen. nov. resembles genera of the tribe Alticini, with which they share the following combination of characters: small size (length 2.0 mm), antennae comparatively short, pronotum with antebasal transverse furrow, elytra with regular puncture rows with convex intervals, abdominal ventrites without modifications; but differs from them by the narrow, not swollen metafemora with length/width ratio 3.5, which is usually characteristic of tribe Galerucini. In most flea beetles, the metafemora are enlarged and swollen, indicating the ability to jump (Nadein and Betz, 2016). The new genus is similar to those of the tribe Galerucini by lacking swollen metafemora. The other characters occur in Galerucini sporadically and have never been recorded in the same combination.

Traditionally, attribution to the tribes Galerucini and Alticini has been usually based on the absence or presence of the jumping apparatus, which was believed to be the only reliable diagnostic character. Nevertheless, there is an informal group of so-called 'problematic' or 'transitional' genera of Alticini (e.g., *Acrocrypta* Baly, 1862, *Chalaenosoma* Jacoby, 1893, *Chaloenus* Westwood, 1861, *Hespera* Weise, 1889, *Luperomorpha* Weise, 1887, *Nonarthra* Baly, 1862, *Orthaltica* Crotch, 1873, *Sjoestedtinia* Weise, 1910) which possess a mixture of 'galerucine-' and 'alticine-type' morphological characters (*sensu* Furth and Suzuki, 1994, 1998). Some of these genera are typically alticine-like but lack jumping ability (as probably in the present case), while the others have a galerucine appearance but are able to jump. Therefore, attribution of these genera to a tribe based solely on this character seems unreliable. Molecular phylogenetic analysis of Galerucinae has partially resolved this situation (Ge et al., 2011, 2012; Nie et al., 2017), indicating that jumping ability and its corresponding morphological leg modifications originated several times in the Galerucinae (Ge et al., 2011, 2012). Detailed examination of 'problematic' and 'transitional' genera resulted in transferring some 'traditional' jumping flea beetle genera (e.g., *Acrocrypta*, *Hespera*, *Luperomorpha*, *Nonarthra*) from the tribe Alticini to the Galerucini (Nie et al., 2017).

Non-swollen metafemora indicate the possible absence of the jumping apparatus, and the general alticine-like appearance of *Taimyraltica* gen. nov. makes it similar to the 'transitional' genera *sensu* Furth and Suzuki (1994, 1998). Without the ability to use molecular-based phylogenetic analysis, resolution of the phylogenetic affinities of the new genus remains problematic.

A unique feature and possible apomorphy of *Taimyraltica* gen. nov. is its large and transversely erect metatibial spur. In Alticini and Galerucini, the apical spur of the tibiae is usually small and acute, attached apically, and more or less corresponds to the longitudinal axis of the metatibia. The transverse position of the metatibial spur is unknown in both Galerucini and the Alticini. The modified metatibiae and spurs are known only for the few genera of Alticini, and represented by the subapical position of the spur in e.g. *Psylliodes* Berthold, 1827 and *Argopistes* Motschulsky, 1860, bifid spur in *Dibolia* Latreille, 1829 and related genera (Nadein, 2015), a very long and serrate spur of *Serraphula* Jacoby, 1897 (Biondi and

D'Alessandro, 2010), and in the extreme case a very long spur and very short tibia in the genus *Aphthonoides* Jacoby, 1885 (Döberl, 2005). The modifications of the metatibial spur in the Galerucini are unknown (Mohamedsaid and Furth, 2011). Thus, establishment of the new tribe is based on the unique combination of characters that it possesses (see description of the tribe) and a presumed apomorphy: the large and transversely erect apical metatibial spur.

4.2. Fossil Galerucinae

Leaf beetles of the subfamily Galerucinae are found as compression fossils and inclusions from the Cretaceous to Pliocene of Europe, Asia and North America (Santiago-Blay, 1994; Kirejtshuk and Ponomarenko, 2017). Besides *Taimyraltica calcarata* gen. et sp. nov., the only known possible Mesozoic occurrence is the putative *Halticophana westwoodi* Handlirsch, 1906 (name given by Handlirsch for 'Haltica' of Westwood (1854)) from the Lower Cretaceous of the Lower Purbecks horizon of Durlstone Bay (UK), which was attributed to Chrysomelidae according to Westwood's figure (1854, Pl. 18, fig. 12) without any supporting evidence.

Paleocene records are very scarce and limited to the description of the putative *Altica dryophylorum* (Piton, 1940) from Menat (France). The oldest reliable appearance of fossil Alticini is recorded in the lowermost Eocene Oise amber (Moseyko et al., 2010), with the single described genus and species *Crepidocnema yantarica* Moseyko et al., 2010. Four more genera and species were discovered in lowermost Eocene Cambay amber (Nadein and Perkovsky, in prep.).

Galerucinae of the late Eocene are much more numerous due to preservation in Baltic, Rovno, Bitterfeld, and Danish ambers. To date, nine genera and 13 species have been described (Table 1) and some other records belonging to recent genera such as *Altica* Geoffroy, 1762, *Galeruca* Geoffroy, 1762, *Galerucella* Crotch, 1873, *Luperodes* Motschulsky, 1858, *Luperus* Geoffroy, 1762, *Monolepta* Chevrolat, 1836, *Ochrosis* Foudras, 1860 are known mostly from Baltic amber (Spahr, 1981); 57% of described late Eocene amber species belong to extant genera (Table 1). Eocene galerucine compression fossils have been discovered in many localities in Europe and North America. For example, three species of the extinct genus *Eogaleruca* Haupt, 1956 have been described from the middle Eocene (Lutetian) of Geiseltal (Germany). According to Wappler (2003), Alticini (Galerucinae) comprises 77% of all leaf beetles in the middle Eocene (Lutetian) of Eckfeld (Germany). Leaf beetles have been found in the upper Eocene Florissant Lagerstätte (Colorado, U.S.A.) where several species of the extant genera *Dia-brotica* Chevrolat, 1836 and *Trirhabda* LeConte, 1865, as well as *Luperodes submonilis* Wickham, 1914a, *Altica renovata* (Wickham, 1914b), *Oryctocirtites protogaeum* Scudder, 1876, *Plectro-trophanes hageni* Wickham, 1914b, *Prochaetocnema florissantella* Wickham, 1914b, *Systema florissantensis* Wickham, 1913 have been described. They are also known from Brunstatt (France) and Kleinkembs (Germany): *Agelasa sessilis* Förster, 1891, *Altica magna* (Förster, 1891), *A. dubia* (Förster, 1891), *Galerucella affinis* Förster, 1891, *G. emarginata* Théobald, 1937, *Psylliodes defiguratus* Théobald, 1937 and *?Psylliodes difficilis* (Förster, 1891).

Oligocene galerucines are known only from upper Oligocene of Rott (Germany): *Luperus fossilis* Schlechtendal von, 1894 and *Galerucella serrata* Meunier, 1919.

Miocene fossils of Galerucinae are less numerous than the Eocene ones. Those in amber are *Neocrepidodera antiqua* (Gressitt, 1971) from Simojovel (Miocene Mexican amber) and *Leptonesiotes virkkii* Santiago-Blay et al., 1996, *Wanderbiltiana wawasita* Santiago-Blay et al., 2004 and *Acallepitrix* sp. (Santiago-Blay and Craig, 1999) from middle Miocene Dominican amber. Galerucines in Miocene compression fossils are represented by *Galeruca*

gemmifera Heer, 1879 and *G. buchi* Heer, 1865 from the middle Miocene of Oeningen (Germany), as well as *Altica tholimorpha* (Zhang et al., 1994), *Derorthaea curtiantenna* Zhang et al., 1994, *Disosebaethe pona* Zhang et al., 1994 from the middle Miocene Shanwang Formation (China). A flea beetle (Alticini) was briefly described and illustrated, but not named from the lower Miocene of Izarra, Spain (Arillo and Ortuño, 1997a, fig. 2; Barrón, 1999). Izarra fossils appear preserved as three dimensional moulds where the body has completely disappeared (Barrón et al., 2002). According to the description and figure (body shape, small head, narrowed pronotum, confusedly punctate elytra and exposed pygidium) this beetle belongs to the genus *Phyllotreta* Chevrolat, 1837, its first fossil record. Flea beetles of the genus *Phyllotreta* consume glucosinolate-containing plants of the families Brassicaceae, Resedaceae, Tropaeolaceae, and Capparaceae (Beran et al., 2014). Izarra is also known as the oldest locality where gregarious Acrididae were found in the Eastern Hemisphere (Arillo and Ortuño, 1997b), and so the appearance of *Phyllotreta* is associated with the origin of grassland biomes (Zherikhin, 1994).

A large variety of subfossil records of Galerucinae are known from Europe, Asia and North America from the Pliocene to the Holocene that mostly belong to recent genera and species (for details see Kirejtshuk and Ponomarenko, 2017; Santiago-Blay, 1994). A few extinct species have been described, for example, *Apteropeda grossa* Théobald, 1935 and *Aphthona puncticollis* Piton, 1939 from Pliocene of Cantal (France), however their taxonomic attribution is in need of revision.

4.3. Early evolution and radiation in leaf beetles

Estimates of the times of origin of the Chrysomelidae and its subfamily radiation based on molecular clock analyses calibrated with paleontological records have yielded widely differing dates. Gómez-Zurita et al. (2007) place the origin of its subfamilies after the Cretaceous. McKenna et al. (2015) and Haddad and McKenna (2016) suppose the origin of the family near the Jurassic/Cretaceous boundary and subfamily diversification throughout the Cretaceous. Kergoat et al. (2011) and Wang et al. (2013, 2014) date the family origin in the Middle Jurassic and suggest that all of its subfamilies originated before the Albian.

These results are not definitive and are sometimes contradicted by subsequent fossil data. Further, time estimations and dating may be influenced by inclusion of the subfamily Protoscelinae from the Late Jurassic and the ichnotaxon *Cephaloleichnites strongii* (see Introduction) in molecular clock calibration in Gómez-Zurita et al. (2007), Farrell (1998), Hunt et al. (2007), McKenna and Farrell (2009), Wang et al. (2014). Another issue is the rather long time of radiation at the subfamily level estimated by Wang et al. (2014, fig. 5), where divergence of Chrysomelinae, Spyllopirinae, Criocerinae and Donaciinae are dated as Late Jurassic, and Cryptocephalinae, Cassidinae and Galerucinae diverging around the middle Cretaceous. Another hypothesis was presented by McKenna et al. (2015), with divergence of major phylogenetic lineages dated as Early Cretaceous. Subfamily radiation estimates from around the middle Cretaceous is, however, contradicted by the recent discovery of the subfamily Chrysomelinae in the Lower Cretaceous (Kirejtshuk et al., 2015).

It appears that the evolution of leaf beetles began in close association with angiosperms, and its real success was first achieved when angiosperms began to dominate. This was expressed in the diversification of groups of chrysomelids of high taxonomic rank (Wang et al., 2013). One of the leading factors was, apparently, the ability to fully consume the cell walls of plants, which constitute the largest reservoir of organic carbon on earth. This was made possible by the acquisition, as a result of horizontal transfer from

ascomycete fungi, of the ability to produce their own plant cell wall degrading enzymes which target pectin, cellulose and hemicelluloses (Kirsch et al., 2014). Leaf beetles may not have been able to realize this potential when feeding on Mesozoic gymnosperms and ferns (Zherikhin, 2002). As pointed out by Ponomarenko (2006, pp. 265–266) “Green tissues of cryptogams and gymnosperms are difficult to consume, because of abundant skeletal elements, and a herbivore has to process a huge volume of green tissue to obtain appreciable amount of proteins. This result in massive vegetation damage, which is particularly well observable now when phytophagous insects cause much higher losses in gymnosperm stands compared to the angiosperm ones. ... With the spread of angiosperms, the abundance of damaged leaves has risen strikingly”. At the same time, initially entomophilous angiosperms have become more valuable as a source of nutrition, with more diverse and easily accessible carbon-containing polymers. We suppose that the most crucial phases of leaf beetle evolution was connected with the Cretaceous Terrestrial Revolution (Ignatov et al., 2016), although details of their presumed coevolution with angiosperms are not clear, and so every new discovery of leaf beetles in the Cretaceous is important.

It is significant that also associated with the Cretaceous Terrestrial Revolution is the shift from faunas dominated mostly by Caridae (=Ithyceridae sensu Legalov, 2015) and, to a lesser extent, Nemonychidae, to Brentidae/Curculionidae-dominated faunas (Legalov, 2012; Davis et al., 2013); this is evident in Mesozoic ambers as well (Legalov, 2012; Peris et al., 2014).

4.4. Paleocological implications

Taimyraltica gen nov. is the first representative of the suborder Phytophaga from Taimyr amber from more than 6500 inclusions. Now Obeschayuschiy (Santonian–Campanian, Magadan Oblast, 60.2° N, 150.5° E; paleocoordinates 65.5° N, 133.8° E; Gromov et al., 1993; Herman, 2011a) is the only known Upper Cretaceous Lagerstätte with a rich entomofauna lacking Phytophaga. In contrast to the flora of Khatanga Basin, the Ola flora of Obeschayuschiy is well studied and is characterized as a Mesophytic flora of dominant gymnosperms and ferns (Herman, 2011a,b). Angiosperms in this flora are extremely rare, which, in our opinion, provides an explanation for the absence of Phytophaga. This contrasts with the middle Cretaceous of Khetana (Ulya flora, the north of the Khabarovsk Krai, Golovneva, 2013) where gymnosperms predominate, but angiosperms are nevertheless diverse and not uncommon, and there is a rich and diverse assemblage of Phytophaga.

As was shown in the well-studied the Arman' flora (Turonian–Coniacian of Magadan Region), remnants of a relatively old Mesophytic and advanced Cenophytic plants are separate, and forests characterized by these two types repeatedly alternate (Herman, 2011b). According to Samylina (1974) angiosperms and advanced ferns and conifers concurrently formed discrete plant communities: “It is likely that communities of Mesophytic and Cenophytic type coexisted ... in the study area ... being in turn able to replace each other ...” (Samylina, 1974, p. 27). It is important that the Arman' flora is not a unique example of unmixed Mesophytic and Cenophytic plant remains in burials (Herman, 2011b). Herman (2011a) proposed the modern ecological succession in the river floodplain of one of the small meandering rivers of Alaska (Herman, 2011a, figure 9.8) as an analogy of the way that the Cretaceous angiosperms replaced the coniferous-fern vegetation existing in the interior of Asia along the river valleys. There conifers do not have time to grow on newly formed river foreland and only later and at some distance from the river bed replace coastal willow-poplar vegetation, forming a mature coniferous forest (Herman, 2011a).

Apparently, the Yantardakh amber forest, as in Obeschayuschiy, belonged to the Mesophytic flora dominated by gymnosperms and ferns (Herman, 2011a), which is the possible reason for the extreme rarity of Phytophaga, with *Taimyraltica* gen. et sp. nov. as the first record in more than 6500 inclusions. Inclusions of the Kheta Formation were hypothesized to be rapidly buried in deltaic sediments and reflect the fauna that inhabited the river bank (Zherikhin and Sinitshenkova, 2002). It can be assumed that the basalts of the Putorana Plateau did not favor the formation of wide river floodplains (as today), and so the angiospermal element in the amber forest could be minimal.

Interestingly, that first fossil representative of the modern scydmaenine genus *Eutheia* Stephens, 1830 (Staphylinidae) (Jałoszyński and Perkovsky, 2016) associated with deciduous litter from temperate regions of northern hemisphere was also found in the collections from Yantardakh from 2012, in contrast to collections from the 1970s of equal size.

Two species of Sisyridae were described from the new Yantardakh collections of 2012 (Perkovsky and Makarkin, 2015; Makarkin and Perkovsky, 2016) as well as four new taxa of caddis flies, including the first Cretaceous Dipseudopsidae known from Asia (Ivanov and Melnitsky, 2017). Another family of caddisflies, Psychomyiidae its first Santonian occurrence (Ivanov and Melnitsky, 2017), and also the first Late Cretaceous Simuliidae from Asia (Perkovsky and Sukhomlin, 2016). It can be assumed that the characters of the watercourses and, consequently, the river valleys with amber forests, which became the source of the material collected by the 2012 expedition, were somewhat different from those collected in Yantardakh in the 1970s.

The most convincing evidence in support of the hypothesis that the extreme rarity of Phytophaga of Kheta Formation was caused by its Mesophytic flora, is provided by comparison with Canadian amber. Among 1630 arthropod specimens of Cedar Lake Canadian amber cataloged by Skidmore (1999), four representatives of Phytophaga beetles have been found (O. Lonsdale, pers. comm., 2017), i.e., the proportion of Phytophaga in Canadian amber is 16 times higher. The paleolatitude of the Canadian amber forest was much lower than that of Yantardakh, and the presence of palm seed beetles at the former suggests that average winter temperatures there were $>8^{\circ}\text{C}$ (Archibald et al., 2014). Therefore, one can suppose that angiosperm abundance and diversity was higher in Canadian amber forest. Zherikhin (2002) indicated that though no quantitative comparative data are available, anecdotal observation indicates that the frequency of all principal damage traces on the Late Cretaceous leaves in temperate Siberia appears to be distinctly lower than in warmer Kazakhstan, Europe and USA.

The only plant described directly from Taimyr amber is a moss of the extinct genus *Taimyrobryum* Ignatov et al., 2016 (Bryopsida insertae sedis) from Yantardakh. However, trophic association of Galerucinae with mosses, ferns, and coniferous is uncommon (Jolivet and Hawkeswood, 1995; Nadein, 2009, 2013); moreover it is likely that *Taimyrobryum* belongs to epiphyte mosses which have no record of being fed up on by galerucines.

The record of extant angiosperm families in the Upper Cretaceous of Taimyr is limited to the Platanaceae, Cercidiphyllaceae, and Araceae (Golovneva, 2012), with Cercidiphyllaceae only found in the Kheta Formation. Platanaceae were found in both the Ledyana (below the Kheta Formation) and Mutino Formations (above the Kheta Formation); the aquatic Araceae as well as extinct aquatic genus *Cobbania* are found in the Mutino Formation (Golovneva, 2012). Araceae as well as Platanaceae and Cercidiphyllaceae are relict families, abundant and well represented in Cretaceous, and so their trophic association with *Taimyraltica* gen. nov. cannot be excluded. However, no extant Galerucinae have been reported consuming Platanaceae and Cercidiphyllaceae. Some extant

Galerucinae have trophic associations with Araceae, for example, genus *Oides* Weber, 1801 (China, South-East Asia), *Meristoides* Laboisière, 1929 (South-East Asia) on *Alocasia*; and *Sangariola* Jakobson, 1922 (Russian Far East, Korea, China and Japan) on *Symplocarpus* (Jolivet and Hawkeswood, 1995). However, Araceae of the Khatanga Depression (found in the Mutino Formation) were aquatic, while aquatic plants are uncommon host plants for Galerucinae (Jolivet and Hawkeswood, 1995). For this reason, a trophic association of *Taimyraltica* gen. nov. with Araceae appears unlikely.

5. Conclusions

1. Establishment of the new tribe Taimyralticini is based on a unique combination of characters shared with tribes Alticini and Galerucini, and the supposed apomorphy of the transversally erect position of the metatibial spur.
2. A second genus of leaf beetles from the Late Cretaceous has been found, dating from the most important period for the evolution of the family Chrysomelidae, immediately following the Cretaceous Terrestrial Revolution. This led to the predominance of angiosperms, with which the vast majority of leaf beetles are associated.
3. For the first time, the absence of Phytophaga in Obeschayuschiy (Santonian-Campanian of the Magadan Region) and their extreme rarity in retinites of the Kheta Formation are compared. In Obeschayuschiy this is due to the fact that the flora is characterized as Mesophytic. It is assumed that the Santonian amber forest of the Khatanga Basin had the same Mesophytic character. Phytophaga are 16 times less represented in Yantardakh Taimyr amber than in Canadian amber.
4. The known occurrences of Cretaceous leaf beetles support the hypothesis of an Late Jurassic to Cretaceous origin and subfamily radiation of Chrysomelidae.
5. The oldest *Phyllotreta* sp. is recorded from the lower Miocene of Spain (Izarra, Álava); the genus is trophically associated with Brassicaceae, Resedaceae, Tropaeolaceae, and Capparaceae. Izarra is also known as the oldest locality where gregarious Acrididae were found (at least in Eastern Hemisphere), so the appearance of *Phyllotreta* is associated with the genesis of grass biomes (Zherikhin, 1994).

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