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RESEARCH ARTICLE

First record of soft-winged flower beetles (Coleoptera, Malachiidae) in a late Pleistocene deposit from West Siberia with a review of known Quaternary data

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Abstract

Soft-winged flower beetles (Coleoptera, Malachiidae), *Apalochrus femoralis pallipes* Motschulsky, 1860 and *Ebaeus* Erichson, 1840 species, are recorded for the first time from Quaternary fossils in the deposit Ustyanka-1 near Ustyanka river, the right tributary of Alei river in Altaiskii Krai, West Siberia, Russia. The strata containing malachiid fragments belong to the warm phase of the late glacial succession. It is shown that soft-winged flower beetles are typical of Holocene deposits and practically unknown from cold phases of the Pleistocene, except in the case of *Protapalochrus* Evers, 1987 which has been recorded from the Pleistocene. Illustrations of the external appearance of both male and female of the beetles, and sub-fossil remains of *Apalochrus femoralis pallipes* Motschulsky, 1860 and three species from the *Ebaeus rufipes*-group distributed in the region are given, together with details of their position within the Ustyanka-1 deposit. Data on the Malachiidae in Quaternary deposits of the Northern Hemisphere are briefly reviewed.

Keywords
Coleoptera, Cleroidea, Malachiidae, *Apalochrus femoralis pallipes*, *Ebaeus rufipes*-group, West Siberia, sub-fossils, Quaternary deposit, Pleistocene – Holocene transition

Introduction

Insects of different groups are poorly represented in Quaternary deposits, whereas Coleoptera are the exception since they are well preserved due to the sclerotized parts of their bodies, such as pronotum, elytra or head which are suitable for identification of species or species-group (Elias 1994; Kuzmina 2017). Furthermore, Coleoptera are prevalent in all types of landscapes, usually in high numbers. However, body parts of soft-winged flower beetles (Coleoptera, Cleroidea: Malachiidae) are weakly sclerotized, and are not abundant, especially in northern regions (Tshernyshev 2012b). Thus, malachiids are rarely recorded in sub-fossil deposits, and each new discovery in deposits of different age located in various regions are particularly interesting in terms of understanding the faunogenesis of the group.

In the Northern Hemisphere, insects in Quaternary deposits have been well studied in the different regions in Europe, such as England, France and Belarus (Coope et al. 1971; Nazarov 1984; Coope and Lemdahl 1995), West Siberia and the Urals (Zinovyev 2008, 2011), and the north-eastern part of Asia and the northern part of North America (Kuzmina and Matthews 2012). A high number of malachiids, for at least 10 species, are known from western Europe, where they occur in late glacial deposits and have been recorded from the whole of the Holocene. For the late glacial period, *Anthocomus coccineus* (Schaller) and *Micrinus dimorphus* Abeille de Perrin were recorded from deposits in France (Ponel et al. 1999, 2007), and *Cordylepherus viridis* (Fabricius), *Anthocomus* sp. and *Malachius* sp. from England (Ashworth 1973; Rose et al. 1980). From the Holocene deposits of western Europe, malachiids were recorded from 30 deposits – eight species, *Anthocomus coccineus* (Schaller), *A. fasciatus* (Linnaeus), *Axinotarsus ruficollis* (Olivier), *Cerapheles terminatus* (Ménétries), *Clanoptilus marginellus* (Olivier), *Cordylepherus viridis* (Fabricius), *Malachius aeneus* (Linnaeus) and *Malachius bipustulatus* (Linnaeus) from England (Girling 1980; Robinson 1981, 2006; Osborne 1997; Kenward 2005), and four species, *Anthocomus coccineus* (Schaller), *Cerapheles terminatus* (Ménétries), *C. lateplagiatus* (Fairmaire) and *Malachius* sp. from France (Ters et al. 1971; Andrieu-Ponel and Ponel 1999). In the deposits of northern, central and southern Europe, malachiids were recorded as single species, such as a *Malachius* sp. from the late glacial in Italy (Ponel and Lowe 1992; Ponel 1997) and Switzerland (Coope and Elias 2000), and from the late Holocene in Norway (Barrett et al. 2007). In the Quaternary deposits of eastern Europe, the Malachiidae are known from the most south-eastern regions only, the only specimen, an almost completely intact beetle, from the middle Neopleistocene Singil deposit of the lower reaches of Volga river, being identified as *Malachius* ex group *bipustulatus* (Linnaeus) (Bidashko and Proskurin 1987). No malachiids have been recorded in the northern regions of eastern Europe, despite the intensive study of sub-fossil insects in the region (Nazarov 1984).

Only a few soft-winged flower beetle species were found in the Quaternary deposits of North America, all in Holocene strata, namely *Attalus* sp., *Collops* sp. and Malachiidae indet. in Yukon (Kuzmina and Matthews 2012; Kuzmina et al. 2014), *Attalus tusconensis* March. (Elias 1992) and Malachiidae indet. (Devender, Hall 1994) in Mexico.

Sub-fossil fragments of Malachiidae in northeast Siberia area are frequently recorded and known from 35 deposits in early, middle and late Pleistocene and Holocene strata, and identified as *Troglocollops arcticus* (L. Medvedev) (Kuzmina and Matthews 2012; Kuzmina 2015), currently regarded as *Protapalochrus arcticus* (L. Medvedev) (Tshernyshev 2016). No malachiid species have been found in Siberia and the remaining territory of northeast Asia. During the 2013 expedition to the south-east part of West Siberia, Russia, the only elytron was discovered in the Ustyanka-1 deposit in the Pleistocene – Holocene transition stratum (Gurina et al. 2019a), later identified as an *Ebaeus* sp. Repeated collections from this deposit in 2020 extracted more fragments of this species, as well as elytra of *Apalochrus femoralis pallipes* Motschulsky, 1860, as presented and discussed below.

Region, Material and Methods

Location and description of the sections

The deposit Ustyanka-1 (Fig. 1) is located on the right bank of the Ustyanka River, right tributary of the Alei River in the Loktyovskii District of the Altaiskii Krai region of Russia, 8 km NNE of Pokrovka Village. The sample with a Malachiidae fragment was taken on 6 August 2013 by E.V. Zinovyev and K.A. Tsepelev from layer 9, section II of the deposit. A description of the section at 51°15'37.4"N, 81°28'57.4"E made by E.V. Zinovyev is as follows:

layer 1, 0.00-0.90 m, humified horizon (chernozem);

layer 2, 0.90-1.85 m, light-beige loamy sand with interlayers and ferruginous lenses;

layer 3, 1.85-1.86 m, interlayer of coarse-grained sand and gravel;

layer 4, 1.86-2.00 m, light-beige loamy sand;

layer 5, 2.00-2.03 m, alternating coarse-grained sand and gravel;

layer 6, 2.03-2.88 m, light-grey loam, dense, with vertical ferruginous striae;

layer 7, 2.88-3.48 m, coarse-grained sand and reddish-brown gravel with grey-green loam with small lenses;

layer 8, 3.48-4.08 m, green-grey loam, dense, with ferruginous spots;

layer 9, 4.08-5.28 m, blue-grey clay with alluvial detritus and insect remains; the layer is partly below the shore line.

Two samples for entomological analysis were obtained from the layer 9, namely: sample 2 at a depth pf 5.00-5.20 m and sample 3 at 4.48-4.70 m.

Other fragments of Malachiidae were extracted on 2 July 2020 by A.A. Gurina, R. Yu, E.R. Dudko and N.N. Golosova, from layer 11 of section I (Fig. 2). A description of the section at 51°15'38.0" N, 81°28'57.2" E made by A.A. Gurina and R.Yu Dudko is as follows:

layer 1, 0.00-0.64 m, soil-plant layer;
layer 2, 0.64-1.01 m, light-beige loamy sand;
layer 3, 1.01-1.05 m, interlayer with ferruginous sand and gravel;
layer 4, 1.05-1.75 m, dark-grey loamy sand with ferruginous vertical inclusions;
layer 5, 1.75-2.05 m, interlayer of strongly ferruginous sand and gravel;
layer 6, 2.05-3.49 m, beige loam with ferruginous vertical inclusions;
layer 7, 3.49-3.54 m, light-beige coarse-grained sand;
layer 8, 3.54-3.70 m, light-beige loam with inclusions of shells;
layer 9, 3.70-4.00 m, brown loam;
layer 10, 4.00-4.10 m, interlayer of brown and grey-blue loam with inclusions of plant detritus;
layer 11, 4.10-5.62 m, blue and blue-grey clay with interlayers of dark-grey loam and mollusc shells in the upper portion of the layer and a coarse sand in the lower; alluvial plant detritus and insect remains included; remaining 22 cm of the layer located below the shore line. 32 samples each of 4-6 cm were extracted from layers 10-11 serially.

Figure 1. Common view of the bluff Ustyanka-1 Site, July 2020.

Sampling

Sampling methods follow those of Coope (1959) with modifications of Gurina et al. (2019c). The sediment, containing a mixture of plant detritus and insect fragments, was sieved (3 mm meshes) in filtered river water. In the laboratory, the concentrate obtained was washed with tap water and fractioned via meshes of 2 mm, 0.6 mm and 0.3 mm, respectively. The extracted fragments including well preserved malachiids parts were clearly visible on the sieve; these were air dried, and the insect fragments were selectively removed under a binocular microscope Carl Zeiss Stemi 2000. After washing first with "Sanelit" synthetic detergent, then with running water with the aid of a syringe, the fragments were mounted with water-soluble glue onto entomological boards. Each numbered fragment was into a digital database, and the specimens deposited in the collection in the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia.

Radiocarbon dating

Four radiocarbon dates were obtained for the basal layer (blue-grey clays) of the Ustyanka-1 site. Two of these 10150±200 ^{14}C BP (SPb-1345) and 10806±100 ^{14}C BP (SPb-1346), using liquid scintillation counting for measuring ^{14}C activity, were undertaken by M.A. Kul'kova in Herzen State Pedagogical University, Saint-Petersburg. For the dating 100 g of dry herbal remains were used. The other two dates, measured by accelerator mass spectrometry, were undertaken by Keck-CCAMS Group, Irvine, California, USA. For the dating beetle remains of *Asproparthenis carinicollis* (Gyllenhal, 1834) and *Otiorhynchus ursus* Gebler, 1845 were used. Dates of 12150±90 ^{14}C BP (UCIAMS-225787) were obtained for *Asproparthenis carinicollis* (Gyllenhal) and 14200±110 ^{14}C BP (UCIAMS-225786) for *Otiorhynchus ursus* Gebler. Obtained radiocarbon dates were calibrated using the Calib Rev 8.1.0. software and curve IntCal20, range ± σ.

Illustrations

Illustrations for the species have been prepared using specimen from the following localities: *Apalochrus femoralis pallipes* Motschulsky, 1860, neotype, male – Kazakstan, Kokshetau, near Ruzaevka, *Ebaeus pedicularius atrotibialis* (Tshernyshev 2003), holotype, male, paratype, female – Russia, West Siberia, Gornyi Altai, near Kosh-Agach, *E. rufipes* Morawitz, 1861 – Russia, West Siberia, Gornyi Altai, near Kosh-Agach, *E. ukokus* Tshernyshev, 2006 – Russia, West Siberia, Gornyi Altai, Ukok Plateau.

The beetles were studied using an Amscope trinocular stereomicroscope (Ultimate Trinocular Zoom Microscope 6.7X-90X Model ZM-2TY) and digital photographs were taken using a Carl Zeiss Stemi 2000 trinocular microscope and the AxioVision 6.0 program.

Figure 2. Position of the samples with Malachiidae fragments in the layer 11, section I of Ustyanka-1, July 2020.

Results and discussion

Fragment definition

Nine fragments of soft-winged flower beetles were extracted from the Quaternary deposit Ustyanka. One fragment, elytron, was found in sample 2 of section II, 2013, depth 5.0-5.2 m, and eight fragments (1 pronotum and 7 elytra) were extracted from samples 16, 19, 20, 22 and 25 of section I, 2020, depth 4.76-5.35 m (Fig. 2).

Two elytra clearly belong to the Asian subspecies *A. femoralis pallipes* Motschulsky, 1860 of the genus *Apalochrus* Erichson, 1840. This subspecies differs from the nominative subspecies by its smaller size, pale-yellow antennae and coxae, and green-blue metallic lustre of the upper surface. Elytra from the deposit were parallel and rounded at the apex with a typical complete and distinct suture, with dense slightly coarse punctures, demonstrating typical characters of the genus *Apalochrus* Erichson, small size and green-blue colouration are characteristic of *A. femoralis pallipes* Motschulsky which is widely distributed in Asian steppes and steppe meadows and occurs on cereal plants.

One pronotum and six elytra from the deposit belong to the genus *Ebaeus* Erichson, 1840 from the tribe Ebaeini. The elytra are typical of the females, being slightly ovoid and narrowed at apex, with indistinct suture, apices lacking impression or appendages. In males, elytral apices are impressed and bear two appendages, the inner as a transparent oval plate on vertical pedicle, and the outer as an oval or cup-shape plate that close the inner one from outer side. The suture in the elytra from the deposit is distinctly visible only in the middle due to the elytra being impressed, punctures that are fine and smoothed. The pronotum transverse, with specific emargination near scutellum, finely punctured and monochromously dark, while the elytra are dark with a yellow spot at the apices near the suture. Fragments of the genus *Ebaeus* Erichson were found in the deposit with the main differential characters as follows: pronotum uniformly dark, transverse, elytra large, almost completely dark with yellow spots at apex, surface of the elytra and the pronotum with blue metallic lustre and finely punctured. 10 species of dark coloured *Ebaeus* Erichson with female elytra similar to those found in the deposit are known in Inner Asia, namely *Ebaeus adyri* Tshernyshev, 2007 (Kazakhstan, Tarbagatai), *E. basipes* Abeille de Perrin, 1891 (Transcaspian, Turkmenistan), *E. erythropus* Peyron, 1877 (Kazakhstan; Kyrgyzstan; Mongolia; West Siberia), *E. fischeri* Fleischer, 1909 (Turkestan), *E. legalovi* Tshernyshev, 2009 (Primorie, Ussuri), *E. milkoi* Tshernyshev, 2006 (Kyrgyzstan, Alaj Mountain Range), *E. pedicularius* (Linnaeus, 1758) (from Europe to Central Asia and West Siberia), *E. rufipes* Morawitz, 1861 (Europe, Kazakhstan, Turkmenistan, S Russia, West Siberia), *E. transbaikalicus* Pic, 1912 (Mongolia, East Siberia), and *E. ukokus* Tshernyshev, 2006 (Russia: West Siberia, Gornyi Altai, Ukok Plateau). Of three of the above, *E. pedicularius atrotibialis* Tshernyshev, 2003, *E. rufipes* Morawitz, 1861 and *E. ukokus* Tshernyshev, 2006, the elytra of females are the most similar to those found in the deposit by the colouration, but significantly shorter them.

Nearly all dark-coloured *Ebaeus* Erichson species are residents of arborescent-shrub landscapes, and occur on willows, elms or poplars in river valleys, or on bushes in steppes and meadows (Tshernyshev 2003, 2006, 2007). This is the first record of fragments of the tribe Ebaeini being recorded from Quaternary deposits. Recent representatives of the tribe are typical residents of open and intrazonal landscapes, the imago preferring arborescent-shrub vegetation on river banks, but occasionally can be found on cliff stones.

Malachiidae Fleming, 1821

Apalochrini Mulsant and Rey, 1867

Apalochrus Erichson, 1840

Species of the genus previously attributed to *Paratinus* Abeille de Perrin, 1891 and recently transferred to *Apalochrus* Erichson, 1840 (Mayor 2003) differ from the congeners by the almost complete absence of the specific characters in males, which differ from the females by slightly wider antennae, shorter body, and sometimes the presence of a comb in anterior tarsus.

Six species and subspecies that are distributed mainly in Inner Asia are included in *Apalochrus* Erichson, but only the nominative subspecies is widely distributed in steppes and meadows of Europe (Tshernyshev 2016), namely *A. femoralis femoralis* Erichson, 1840 (Europe: Austria, Czech Republic, Denmark, Finland, France, Germany, Hungary, Latvia, Sweden, Turkey, Ukraine, European part of Russia); *A. femoralis pallipes* Motschulsky, 1860 (Kazakhstan, Asian part of Russia); *A. flavicollis* Schaufuss, 1870 (Afghanistan, Tajikistan, Kazakhstan, ?S. Russia); *A. fulvicollis* (Gebler, 1845) (Kazakhstan, Kyrgyzstan, Russia: Kalmykia, South Urals); *A. notatus* (Zoubkoff, 1833) (Kazakhstan, Mongolia) and *A. turkestanicus* Pic, 1907 (Turkestan?, China: Inner Mongolia) (Tshernyshev 2016).

Typical characters of *Apalochrus* Erichson species are as follows: pronotum elongate and narrowed to base, elytra almost completely parallel, slightly expanded and evenly rounded distally, punctures fine and distinct, suture complete; antennae filiform, slightly flattened, legs simple, short. One subspecies, *Apalochrus femoralis pallipes* Motschulsky, 1860, is recorded from the region, and differs by its green-blue metallic lustre, pale-yellow antennae and coxae, and relatively smaller size.

Apalochrus femoralis pallipes Motschulsky, 1860

Sub-fossil material. Site Ustyanka-1 (2020), section I, sample 20 (depth 5.00-5.06 m) – fragments No. 22 (right elytron) (Fig. 3c) and No. 23 (left elytron) (Fig. 3b).

Comparative material. Neotype, male: Kazakhstan: Kokchetavskaya Oblast': env. of Ruzaevka vill., 54°04'N, 44°52'E, sweeping in a field of wheat, 28.VI.1982, G. Sukacheva leg. (Fig. 3a).

Fragment description. Left elytron, black with green-blue metallic lustre, narrow, expanded and rounded posteriorly, densely and deeply punctured, suture entire, sizes: 0.44 mm at base near humerus, 0.77 mm at widest part near apices, 2.25 mm length; right elytron looks similar to the left, sizes: 0.45 mm at base near humerus, 0.73 mm at widest part near apices, 2.28 mm length.

Distribution. Asia: Kazakhstan – Transcapian steppes, Kokchetavskaya, Vostochno-Kazakhstanskaya Oblast', Russia: South Urals – Orenburgskaya Oblast', West Siberia – Tyumenskaya, Omskaya, Novosibirskaya Oblast', Altaiskii Krai.

Habitat. Cereal steppes and meadows of Inner Asia.

Notes. For a detailed description of the subspecies see Tshernyshev 2016: 363–365, Figs 3–4, 15–18, 19.

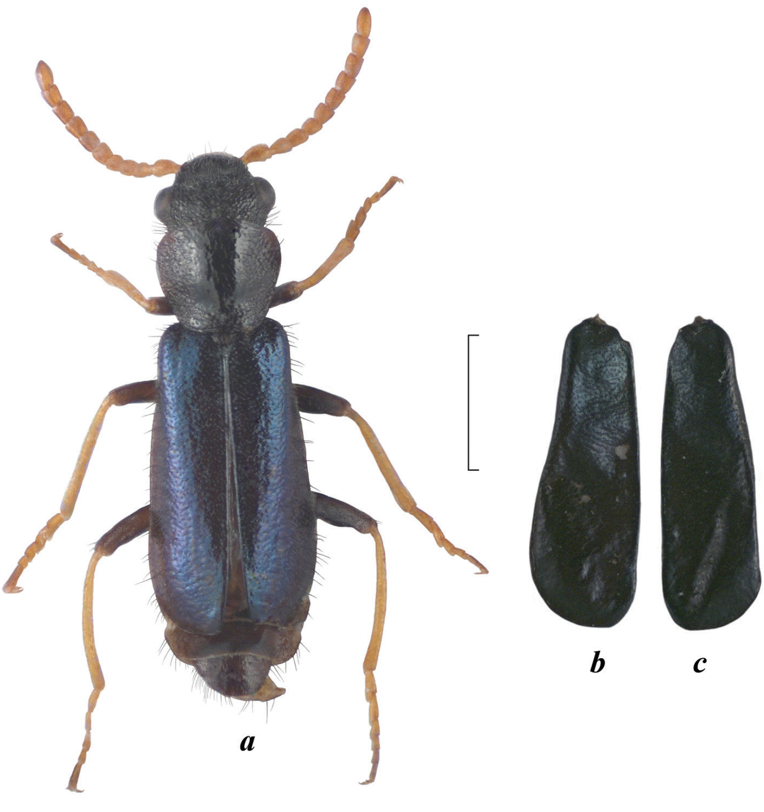

Figure 3. *Apalochrus femoralis pallipes*: **a**, general view of the neotype; **b**, **c**, sub-fossil fragments from the Ustyanka-1.

Ebaeini Portevin, 1931

Ebaeus Erichson, 1840

The genus is widely distributed in Eurasia, Africa, SE Asia, and America. Characteristics of the genus are as follows: **males** – anterior tarsi with a comb above the second tarsomere, antennae filiform or weakly serrate, pronotum transverse or equilateral with evenly rounded lateral sides, anterior side slightly protruding, posterior with emargination above scutellum; disk of pronotum convex lacking transverse depression basely, slightly impressed at basal angles; elytral apices impressed and possessing two appendages, one as transparent oval plate on pedicle inside the impression, and other one lamellate oval or cup-shape, external, covering the inner appendage from outer side, shape of appendages is species specific; posterior tibiae simple, not curved or strongly widened posteriorly; **females** – elytral apices simple, not impressed or appendiculate, narrowed and rounded distally like pointed end of egg. In dark coloured species elytral apices often with yellow or orange spot. Colouration of species strongly diverse, usually as combination of dark areas with weak metallic lustre and light background usually yellow or orange (Tshernyshev 2003).

Several species of dark-coloured *Ebaeus* Erichson are recorded from the region, amongst them three, *E. pedicularius atrotibialis* Tshernyshev, 2003, *E. rufipes* Morawitz, 1861 and *E. ukokus* Tshernyshev, 2006, are the most similar to those found in the deposit (Tshernyshev 2003). The remaining species from Central and North Asia with dark coloured pronotum and elytra differ from the deposit fragments by the following charateristics: *Ebaeus adyri* Tshernyshev, 2007 from Kazakhstan has yellow margination to elytra, in females also has a yellow spot near the middle of suture; *E. basipes* Abeille de Perrin, 1891 from Turkmenistan is small in size and has a wide yellow colouration of elytral apices; *E. erythropus* Peyron, 1877 occurring in the study region has uniformly dark coloured elyta, in females sometimes with narrow yellow margination of apices; *E. fischeri* Fleischer, 1909 from Kazakhstan and Kyrgyzstan, apart from its small size and lacking yellow spot on apices, has a bright blue metallic lustre of upper surface; *E. legalovi* Tshernyshev, 2009 only known from Primorie, Ussuri, is a small beetle with green metallic lustre of dark colouration; *E. milkoi* Tshernyshev, 2006 from Kyrgyzstan is uniformly black without a metallic lustre and lacks yellow spots in the apices; and *E. transbaikalicus* Pic, 1912, occurring in East Siberia, the Russian Far East and East Mongolia is also small, with blue metallic lustre and lacks yellow spots in apices of elytra.

Ebaeus sp.

Sub-fossil material. Site Ustyanka-1 (2013), section II, sample 2 (depth 5.00-5.20 m) – fragment No. 2-13 (right elytron) (Fig. 4k); site Ustyanka-1 (2020), section I, sample 16 (depth 4.76-4.82 m) – fragment No. 10 (left elytron) (Fig. 4h); ibidem, sample 19 (depth 4.94-5.00 m) – fragments No. 13 (right elytron) and No. 14 (base of left elytron); ibidem, sample 20 (depth 5.00-5.06 m) – fragment No. 21 (right elytron) (Fig. 4i); ibidem, sample 22 (depth 5.12-5.19 m) – fragment No. 2 (right elytron) (Fig. 4j); ibidem, sample 25 (depth 5.30-5.35 m) – fragment No. 6 (pronotum) (Fig. 4g).

Fragment description. Sample 16 (2020), No.10 left elytron, black with weak violet-blue metallic lustre, narrow, ovoid narrowed distally with narrowed and rounded apex and yellow spot near suture; suture thin and indistinct, scutellum emargination wide; punctures fine and sparse, hardly visible, sizes: 0.6 mm at base near humerus, 0.86 mm at widest part near apices, length 2.64 mm; sample 2 (2013), No.2-13 right elytron, apparently looks similar to left one (mentioned above), yellow spot on apex slightly transverse, sizes: 0.68 mm at base near humerus, 0.94 mm at widest part near apices, length 2.95 mm; sample 20 (2020), No.21 right elytron, in comparison with the other fragments relatively more strongly narrowed at apex, with round yellow spot near suture, sizes: 0.62 mm at base near humerus, 0.93 mm at widest part near apices, length 2.76 mm; sample 22 (2020), No.2 right elytron, black with a weak blue metallic lustre, narrow, almost completely not widened, narrowed and rounded distally, apex completely yellow, punctures fine and sparse, indistinct, suture thin, indistinct, scutellum emargination wide, sizes: 0.69 mm at base near humerus, 0.86 mm at widest part near apices, length 2.95 mm; sample 25 (2020), No.6 pronotum, transverse, 1.5 times as wide as long, convex lengthwise and slightly depressed at basal angles, anterior side weakly protruding, posterior with distinct emargination above scutellum, sides evenly rounded, with thin margination, surface finely and densely punctured, black with a weak green-blue metallic lustre, sizes: width 1.44 mm, length 0.93 mm.

Discussion. It is difficult to refer the fragments from the deposit to one of the known species of the genus *Ebaeus* Erichson due to the considerably larger size of elytra and pronotum, and their colouration with distinct violet-blue metallic lustre. Probably, this is one of independent and undescribed species which could be defined if male elytra are found.

Ebaeus pedicularius atrotibialis Tshernyshev, 2003

Material. Russia, Republic of Altai: Mountain Altai, Kosh-Agach district, 6 km NE of Ortolyk village, valley of Tedtuyaryk river, sweeping on poplars, 3.VII.2003, S.E. Tshernyshev leg. – ♂, holotypus, ♀, allotypus; (Fig. 4e, f).

Distribution. Russia: South Siberian mountains.

Habitat. Collected from poplar and elm leaves and stems near mountain river.

Notes. The main characteristics that differentiate the subspecies from the nominative one is the larger size, angular yellow colouration of elytral apices, shape of the outer appendage and black colouration of hind tibiae. Sizes are closer to those in sub-fossil fragments, but smaller. For a detailed description of the subspecies see Tshernyshev 2003: 294, 297, Figs 47-53.

Ebaeus rufipes Morawitz, 1861

Material. Russia, Republic of Altai: Mountain Altai, Kosh-Agach district, 6 km NE of Ortolyk village, valley of Tedtuyaryk river, sweeping on poplars, 3.VII.2003, S.E. Tshernyshev leg. – ♂, ♀; (Fig. 4a, b).

Distribution. Russia: South Siberian mountains.

Habitat. Collected from poplar and elm leaves and stems near mountain river.

Notes. The species is similar to that extracted from sub-fossil deposit, but differs in its smaller size and weaker green metallic lustre to dark colouration of surface.

Ebaeus ukokus Tshernyshev, 2006

Material. Russia, Republic of Altai: Mountain Altai, Kosh-Agach district, Ukok Plateau, Zhumaly valley, 2300 m a.s.l., 26-29.VI.2007, E. Guskova & R. Yakovlev leg. – ♂, ♀; (Fig. 4c, d).

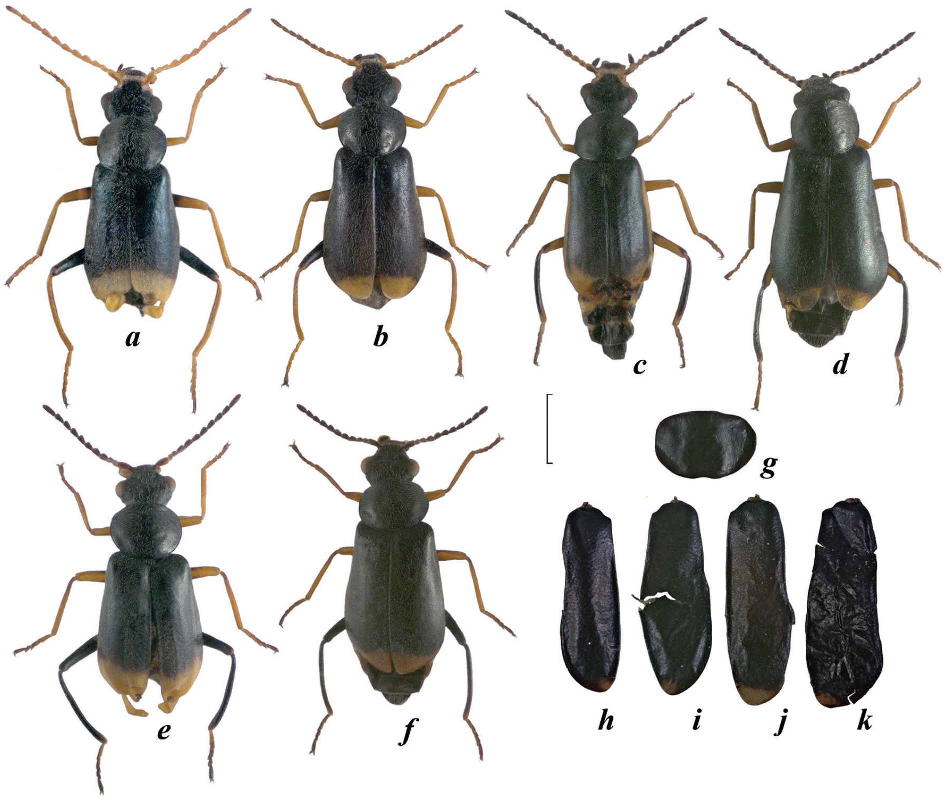

Figure 4. *Ebaeus* spp. upper side (**a–f**) and sub-fossil fragments from the Ustyanka-1 (**g–k**): **a**, **b**, *E. rufipes*; **c**, **d**, *E. ukokus*; **e**, **f**, *E. pedicularius atrotibialis*; **g–k**, *Ebaeus* sp.: pronotum (**g**), left elyton (**h**), right elytra (**i**, **j**, **k**). **a**, **c**, **e** – males, **b**, **d**, **f**, **h**, **i**, **j**, **k** – females.

Distribution. Russia: Mountains of South Siberia.

Habitat. Collected in alpine meadow and tundra, and from stones near high altitude mountain lake and rivers.

Notes. Females of the species are much similar to deposit fragments, but size is smaller. Lateral sides of elytra are yellow in male.

Dating and reconstructions

The sample was dated by radiocarbon analysis of plant detritus, yielding an age of: 10806±100 ^{14}C BP (SPb-1346) (sample 3, 2013) and 10150±200 ^{14}C BP (SPb-1345) (sample 1, 2013), and coincides with the calibrated age 12698-12838 cal yr BP and 11390-12099 cal yr BP, the end of late glacial – beginning of Holocene.

Insect assemblages from samples 1, 2 and 3 are similar and represented by at least 66 Coleoptera species (Gurina et al. 2019a). Steppe species prevail in the assemblages, with a high share of hygrophilous and halobiont species, such as *Dyschiriodes luticola* (Chaudoir, 1850), *Paratachys centriustatus* (Reitter, 1894), *Bembidion aspericolle* (Germar, 1829), *B. gassneri* Netolitzky, 1922 (Carabidae) and *Megamecus argentatus* (Gyllenhal, 1840) (Curculionidae), but tundra and forest species are completely absent. Main part of species revealed from the deposit is typical of modern fauna of the region, and several species are known from steppe zone of Eurasia and distributed southerly or westerly of the location of the deposit Ustyanka-1, namely: *Scarites terricola* Bonelli, 1813, *Paratachys centriustatus* (Reitter), *Lebia punctata* Gebler, 1843 (Carabidae), *Aclypaea calva* (Reitter, 1898) (Silphidae), *Tychius albolineatus* Motschulsky, 1860 (Curculionidae).

The Ustyanka-1 insect assemblage strongly differs from late Pleistocene deposits of south-east regions of West-Siberian Plain in species composition (Zinovyev et al. 2016; Gurina et al. 2018, 2019b, 2019c). Nevertheless, some species of the assemblage, such as weevils *Otiorhynchus ursus* Gebler, 1844 and *O. altaicus* Stierlin, 1861, are typical of the late Pleistocene but not the recent fauna of the region, their presence allow supposed them re-deposited, although this is not typical to insect remains (Kuzmina 2017). For the verification of this hypothesis, fragments of two Curculionidae species from sample 3 were dated via the AMS method. As a result, a date of 12150±90 ^{14}C BP (UCIAMS-225787) was determined for the fragment of *Asproparthenis carinicollis* (Gyllenhal, 1834), the species typical of modern fauna of steppe zone of West-Siberian Plain, and a date of 14200±110 ^{14}C BP (UCIAMS-225786) for *Otiorhynchus ursus*, a resident of the late Pleistocene landscape in the region. Calibrated data are 13857-14170 cal yr BP and 17099-17370 cal yr BP.

The AMS data gained demonstrated that (1) previous dating results, were probably somewhat younger due to contemporary carbon penetration of the sample, (2) the insect assemblage from Ustyanka-1 coincides with a warm stage of the late glacial period (Bølling or Allerød), and (3) part of fragment assemblage has probably been re-deposited from Sartan layers (MIS-2).

The first insect assemblage of the late glacial warm stage revealed in the region corresponds with the present-day steppe zone fauna of West Siberia in terms of species composition, which allows one to re-construct the former climate that was warmer and/or drier than those today. The deposit site was surrounded with open steppe landscapes, and presence of a large number of halophilous species of beetles is evidence of strong salinization of the site. Both Malachiid species found in the deposit support these reconstructions.

Comparison of Malachiidae from Quaternary deposits of different regions

Data on soft-winged flower beetles in Quaternary deposits are fragmentary, mainly due to the irregular study of insects in such deposits of different regions, and the specificity of the group.

To date, insects in Quaternary deposits have been relatively well studied in West and Central Europe and some northern regions (Scandinavian countries, Belorussia, northern and central regions of West Siberia, NE Siberia, North Canada and Alaska (Nazarov 1984; Elias 1994; Zinovyev 2008, 2011; Kuzmina and Matthews 2012). However, malachiid beetles have not been recorded from deposits in the northern part of the West-Siberian Plain and Belorussia, and from North Europe there is known one record of *Malachius* sp. from the Holocene in Norway (Barrett et al. 2007). Several reasons explain this phenomenon, such as taphonomic factors, especially the soft and thin cuticle which dictates fragment preservation in deposits and the naturally low numbers of malachiid beetles in northern regions (Tshernyshev 2012b). On the contrary, in West Europe they frequently occur in deposits, being known from 50 localities with more than 100 samples which contain malachiid beetle fragments (Ters et al. 1971; Ashworth 1973; Girling 1980; Rose et al. 1980; Osborne 1997; Ponel et al. 1999, 2007; Kenward 2005; Robinson 2006; Bugs… 2020). It is difficult to explain the unexpected fact that all Quaternary records mentioned above relate to the Holocene or the end of Pleistocene, the deglaciation time, i.e. warm stages of the Quaternary period. To date, no malachiid fragment has been recorded from cryochrons of West Palaearctic. The only record of soft winged flower beetles from deposits of East Europe relates to the Singil warm stage (MIS11) (Bidashko and Proskurin 1987). This regularity is conforming by new recordings for south-eastern regions of West Siberia. No malachiid fragments were found in more than 10 Pleistocene deposits studied in recent years (MIS-3 and MIS-2) (Legalov and Dudko 2016; Zinovyev et al. 2016; Gurina et al. 2018, 2019b, 2019c). The only soft-winged flower beetle fragments were found in several samples of the late glacial warm stage Ustyanka-1 deposit. In North America malachiid beetles are only recorded from Holocene layers (Elias 1992; Devender and Hall 1994; Kuzmina and Matthews 2012; Kuzmina et al. 2014). An unexpected exception to the rule is North East Siberia, where a poor species diversity of Malachiids is found in deposits; only Apalochrini, represented by *Protapalochrus arcticus* (L. Medvedev), has been regularly recorded from both the Holocene and the Pleistocene deposits (Kuzmina and Matthews 2012); this species currently occurs in the region, preferring relic tundra-steppes of North East Siberia, cold and dry landscapes widely located during glacial periods (Tshernyshev 2012 a,b; Chernov at al. 2014).

The malachiid beetles registered in Quaternary deposits are typical for recent regional faunas, and it is appropriate result, because differences in species distribution were revealed for cold periods of Pleistocene, while Holocene fauna was similar to that at the present time (Nazarov 1984; Elias 1994; Kuzmina 2017). Thus, the assemblages of Malachiidae beetles in deposits reflect the contemporary fauna of the regions, those for Europe being Malachiini represented by *Anthocomus* Erichson, 1840, *Axinotarsus* Motschulsky, 1854, *Cerapheles* Mulsant and Rey, 1867, *Clanoptilus* Motschulsky, 1854, *Cordylepherus* Evers, 1985, *Micrinus* Mulsant and Rey, 1867 and *Malachius* Fabricius, 1775, and for East Asia by Apalochrini *Protapalochrus arcticus* (L. Medvedev). Newly found fragments from the deposit in West Siberia revealed representatives of two tribes, Apalochrini and Ebaeini.

All malachiids registered in Quaternary deposits of Europe, *Anthocomus coccineus* (Schaller), *A. fasciatus* (Linnaeus), *Axinotarsus ruficollis* (Olivier), *Cerapheles terminatus* (Ménétries), *C. lateplagiatus* (Fairmaire), *Clanoptilus marginellus* (Olivier), *Cordylepherus viridis* (Fabricius), *Micrinus dimorphus* Abeille de Perrin, *Malachius aeneus* (Linnaeus) and *M. bipustulatus* (Linnaeus) belong to the tribe Malachiini and are typical representatives of the European fauna. Two species, *Micrinus dimorphus* Abeille de Perr. and *Cerapheles lateplagiatus* (Fairmaire), recorded from France, Italy, Portugal and Spain, could be regarded as endemic for southern Europe, *Axinotarsus ruficollis* (Olivier) is widespread in the southern Europe and reaches North Africa, four species, *Cerapheles terminatus* (Ménétries), *Anthocomus coccineus* (Schaller), *A. fasciatus* (Linnaeus) and *Clanoptilus marginellus* (Olivier) are widely distributed in south-western to south-eastern regions of Europe, and three species, *Cordylepherus viridis* (Fabricius), *Malachius aeneus* (Linnaeus) and *M. bipustulatus* (Linnaeus) are widely distributed in the forest-steppe zone of Eurasia from Europe to East Siberia and Mongolia. The presence of these species in Quaternary deposits of Europe define the specificity of the fauna formation of the region due to the number of species and rich diversity of Malachiini, while in the Oriental region they are almost absent.

Different tendencies in the Quaternary fauna are noticeable in deposits of the north-eastern part of Eurasia, with only one Apalochrini representative, *Protapalochrus arcticus* L. Medvedev (= *Troglocollops arcticus* (L. Medvedev) (Tshernyshev 2016), being recorded (Kuzmina 2015). Apalochrini are diverse in south-east Asia, Australia and Africa and represented by a number of locally distributed genera, but only one genus, *Collops* Erichson, 1840, is recoreded from America. Representatives of the tribe are typical for Eurasia and more diverse in Asian regions with endemic genera *Protocollops* Evers, *Simoderus* Abeille de Perrin, *Troglocollops* Wittmer and *Pectapalochrus* Tshernyshev.

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Authors contribution

The authors contributed equally to the study design, analysis and manuscript preparation.

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