Palaeoentomology 007 (1): 112–131
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.7.1.8
http://zoobank.org/urn:lsid:zoobank.org:pub:AD916FD2-2F9E-4FCD-8608-157DA23C8F99

First record of insects from the oldest and older Dryas of Altai (Russia). Coleoptera assemblages from Lebed River

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Abstract

Subfossil remains of insects found in the Lebed site (52.25220°N, 87.15692°E) located on the Lebed River, Altai Republic are recorded. The calibrated radiocarbon dates for two layers of these deposits were 16,461–17,056 cal BP, and 13,520–14,077 cal BP, which correspond to the oldest and older Dryas (Late Pleistocene). Insect assemblages of these deposits are mainly represented by Coleoptera, which are noteworthy there for high taxonomic and ecological diversity and include several endemic and relic species. At least 120 beetle species from 17 families have been found altogether, of them, 37 species are recorded for the Pleistocene deposits of Western Siberia for the first time. Three families, Carabidae, Staphylinidae and Curculionidae are most abundantly represented in the examined Lebed site. Ecologically, this beetle assemblage is dominated by species that are currently confined to the taiga belt and alpine meadows of the Altai Mountains; aquatic and near-water species are also well represented. The studied assemblages are rather different from the previously studied Pleistocene insect fauna in the south of the West Siberian Plain. The taxonomic and ecological compositions of the beetle fauna of Lebed site suggest its existence under humid palaeoclimate that was significantly colder than modern climate in this area.

Keywords: Western Siberia, insects, palaeoenvironment, Late Pleistocene, deglaciation

Introduction

Quaternary insects of West Siberian Plain were studied for more than 50 years during which significant material has been processed from almost 100 localities of the late Pleistocene and the Holocene ages from 67.5°N in the north to 51°N in the south (Kiselev, 1973; Kiselev *et al*., 1982; Zinovyev, 2011, 2020; Gurina *et al*., 2019, 2023). These findings were actively used in reconstructions of the climate and landscapes of that time. In particular, in the south of this territory, in a dry and cold climate and prevailing open steppe landscapes of the late Pleistocene, a peculiar periglacial insect fauna which has no close modern analogues, has been revealed (Zinovyev, 2011; Gurina *et al*., 2019).

At the same time there are almost no data on the Quaternary insects from the adjacent territories of the Altai-Sayan mountain system. Preliminary results of the single study of the Quaternary insects of the Novaya Surtaika locality on Isha River in the foothills of Northern Altai have already showed high specificity of this region (Dudko *et al*., 2017). Based on these data, as well as on the study of the plant macroremains (Panychev, 1979; Ponomareva, 1973; Rusanov & Orlova, 2013), it can be assumed that relatively mild and humid conditions existed in the mountains of the North-Eastern Altai and

 Submitted: 20 Oct. 2023; accepted by D.-Y. Huang: 5 Feb. 2024; published: 27 Feb. 2024

Kuznetsk Alatau throughout the Pleistocene. The search of the new Quaternary insect localities in this region gave a positive result. The first of such locations found in this region on Lebed River and related by radiocarbon dating to the period of deglaciation, are studied in this paper. The purpose of the study is to characterize the newly found assemblages in comparison with the modern fauna of this region and with other late Quaternary fauna of insects. Also, we aimed to identify the closest analogues and reconstruct the climate and biotopes of the study area during the oldest and older Dryas.

Regional setting—Lebed site

Modern environment

The Lebed locality (52.25220°N, 87.15692°E) is placed on the left bank of Lebed River, 900 m below the road bridge near the village of Turochak, 10 km away from its mouth (confluence with Biya River). The area is a strongly erosive dissected medium-altitude plateau (with altitudes of 600–1000 m). Most of the territory (about 70%) is occupied by the very specific type of boreal forest, known as "Chernevaya taiga" or black taiga, characterized by tall-grass aspen-fir and secondary tall-grass birch-aspen forests with bushes. Intrazonal pine forests predominate in Biya valley. The Lebed river valley and its tributaries are characterized by specific plant communities—so called "sogra"—hummocky grass and moss swamps, in some places overgrown with birch, aspen, and pine crooked forests (Kuminova, 1960; Ogureeva, 1980). The studied area is now characterized by a mild climate with high rainfall reaching up to 40 mm even in the driest month. The greatest amount of precipitation, 187 mm, falls in July, and the average amount of precipitation per year is 1,344 mm. The average temperatures of the warmest month, July, are +16.4 °C, and the lowest average temperatures of January are around -15.6 °C (Climate data; Melnikova, 1965).

Geological settings

The first description of the section of the lacustrine-alluvial deposits was made by Baryshnikov and Maloletko in 1971 and published by Rusanov & Orlova (2013). In their description, 5 layers of light gray clays, each 0.1–0.35 m thick, are distinguished, alternating with layers of medium- and coarse-grained sands. These clay layers correspond to lacustrine deposits, one of them (12.8 m from the surface, 3.15 m from the water edge) is saturated with various plant remains. A radiocarbon date of 13750 ± 70 BP (SOAN-576) was obtained for this layer and the flora was described by E.A. Ponomareva (Rusanov & Orlova, 2013) as follows: «*Chara* sp., Bryales gen. ind., *Sphagnum* sp., *Picea obovata* Ledb., *P*. sp., *Pinus sibirica* Mayr., *P*. *silvestris* L., Pinaceae gen. ind., *Selaginella selaginoides* Link., *Sparganium simplex* Huds., *Potamogeton perfoliatus* L., P. sp., Gramineae gen. ind., *Carex* ex gr. A, *C*. ex gr. B, *Alnus glutinosa* Gaerth.,

TABLE 1. Description of the Lebed section-I.

Layer No	Depth of bed, m	Thickness, m	Description
1	0.0–0.3	0.30	Modern soil
2	0.3–0.5	0.20	Gray coarse-grained sand with interlayers of dark brown sand
3	0.5–0.75	0.25	Light gray sandy loam with interlayer of buried soil in upper part
4	0.75–0.85	0.10	Light brown sand horizontally layered
5	0.85–1.95	1.10	Light gray texture less sandy loam with spots of ferrugination
6	1.95–4.25	2.30	Brown-rufous loam, lighter in the lower part, with spots of ferrugination
7	4.25–4.65	0.40	Interbedding of medium-grained sands and light gray clays
8	4.65–5.45	0.80	Coarse-grained dark brown sand with thin interlayers (1–2 cm) of light gray clay
9	5.45–6.65	1.20	Dark brown coarse sand with gravel
10	6.65–6.85	0.20	Brown medium-grained sand
11	6.85–6.95	0.10	Light gray clay
12	6.95–8.7	1.75	Dark brown coarse-grained sand
13	8.7–9.1	0.40	Light gray clay with interlayers of ferrugination
14	9.1–9.25	0.15	Brown medium-grained sand with interlayers of light gray clay
15	9.25–9.55	0.30	Light gray clay, blue clay in the lower part, with thin interlayers of ferrugination
16	9.55–9.85	0.30	Brown rufous sand horizontally layered
17	9.85–9.9	0.05	Light gray clay with dark thin interlayers
18	9.9–10.05	0.15	Dark brown medium-grained sand, with thin (2 cm) interlayer of light gray clay in the lower part
19	10.05–13.05	>3.00	Dark brown wet sand, goes under the water level

FIGURE 1. Section-II at Lebed locality and the samples S1–S4 position.

Juncus gerardii Loisel., *Betula nana* L., *B.* sp., *Salix* sp., *Rumex* sp., *Papaver nudicaule* L., *Rorippa palustris* (D.C.) Bess., *Allium* sp., *Cerastium* sp., Caryophyllaceae gen. ind. (? *Stellaria* sp.), *Linum* sp., *Viola* sp., *Euphorbia* sp., *Matricaria* sp., Umbelliferae gen. ind., and *Nepeta* sp.».

We surveyed the Lebed locality in July 2019. The section I was described by Zinovyev (Table 1); the description is generally similar to the previous one (Rusanov & Orlova, 2013). The general character of the deposits corresponds well to the description of Baryshnikov (Rusanov & Orlova, 2013). Several layers of light gray clays are also expressed in the lower part of the section. The thickest of them, layers 13 and 15, are well traced along the strike of the cliff. To the right of the main excavation, they gradually acquire a blue color, indicating the anaerobic conditions of the sediments, where interlayers of plant detritus also appear. The section II was performed 10 m to the right of the section I (Fig. 1). The lower and, especially, the upper part of the section in this place is heavily turfed and thus are inaccessible for research; therefore, only its middle part is described (Table 2). Layers of light grey clays 15 and 13 correspond to the lake deposit (Rusanov & Orlova, 2013), while a layer 14 of sand interbedded with clays shows that probably the lake was connected to the main river channel at this time, which may have been related to climatic changes.

Materials and methods

Sampling

Samples for the entomological analysis were taken from layers and interlayers saturated with plant detritus (Dudko *et al*., 2022). A total of 4 samples were taken (S1–S4), numbered from bottom to top, from layers 15, 14, and 13 (Fig. 1, Table 3). Each sample was taken in several repetitions (sub-samples). The volume and number of sub-samples were determined based on the concentration of insect fragments in the sediments in order to obtain a representative material. At a low concentration of plant residues and insect fragments in the sediments, the samples were enriched by wet filtration through a 0.3 mm sieve

TABLE 2. Description of the Lebed section-II.

Layer No	Depth of bed, m	Thickness, m	Description
1–12	0.0–8.7	8.70	Covered by talus
13	8.7–9.0	0.30	Blue clay with two interlayers of plant detritus in the upper and near lower parts (Samples S3 and S4)
14	9.0–9.25	0.25	Brown medium-grained sand with interlayers of light gray clay and interlayer of plant detritus at the boundary of layers 14 and 15 (Sample S2)
15	9.25–9.55	0.30	Blue clay, with interlayer of plant detritus in the upper part (Sample S1)
16	9.55–9.85	0.30	Brown rufous sand horizontally layered
17	9.85–9.95	0.10	Light gray sand
18	9.95–10.05	0.10	Interbedded dark brown sand and light gray clay
19	10.05–	>0.5	Dark brown wet sand, excavated thickness is 0.5 m

TABLE 3. Samples of the Lebed section-II for entomological and radiocarbon analysis.

Sample No	Layer	Depth of sample, m	Description	Number of treatment sub-samples	Volume, litres	Radiocarbon date (BP), laboratory code	Calibrated date, cal BP
S4	13	8.70–8.72	Lens of plant detritus	3	3	-	-
S3	13	8.92–8.95	Interlayer of plant detritus (peat)	3	6	11956±120 (SPb-3685)	13520–14077
S2	Boundary of 14 and 15	9.22–9.25	Lens of plant detritus	2	7	-	-
S1	15	9.25–9.30	Blue clay saturated with plant detritus	3	12	13832±100 (SPb-3127)	16461–17056

(samples S1 (partly), S2, S3 (partly)) (The volume of the samples is given in the Table 3). At a high concentration of plant residues, they were placed in plastic bags without washing (samples S1 (partly), S3 (partly), S4).

In addition to the main method, a visual inspection of the layers, opened with a knife or spatula, was additionally carried out. Thus, several large fragments of insects were found in the same layers as the main samples.

Treatment

In the laboratory, the samples were washed with tap water and separated into fractions by wet sieving through sieves with a mesh size of 2 mm, 0.6 mm, and 0.3 mm. Fractions were dried at room temperature. Fragments of insects were selected from them under a binocular microscope CarlZeissStemi 2000. Fragments of good quality (whole or halves of heads, elytra, pronotum, terminalia, *etc*.) were washed with a detergent, then in running water (in a jet of water from a syringe) and glued on cardboard dies with water-soluble glue. Fragments "of little use for identification" (fragments of the exoskeleton, sternites of the abdomen, legs, antennal segments, etc.) were placed in plastic jars for storage and were not taken into account in this work.

The determination of the material was carried out by comparing fragments with modern specimens. For comparison, the collections of the following institutions were used: Institute of Systematics and Ecology of Animals Siberian Branch of RAS (Novosibirsk), Institute of Plant and Animal Ecology, Ural Branch of RAS (Yekaterinburg), Zoological Institute of RAS (St. Petersburg), Paleontological Institute of RAS (Moscow), Zoological Museum of Moscow M.V. Lomonosov State University, Moscow Pedagogical State University, Papanin Institute for Biology of Inland Waters, RAS (Borok).

To estimate the number of individuals of each species in the samples, the Nmin (MNI *sensu* Elias, 1994) indicator (the minimum number of individuals) was used (Gurina *et al*., 2018, 2023).

When comparing the species composition, the Szymkiewicz-Simpson pairwise similarity index was used: $Ks = c / \min(a, b) \times 100\%$; where a and b are the number of species in the first and second samples, respectively, c is the number of common species in these samples (Pesenko, 1982; Magurran, 2004).

Radiocarbon dating

Radiocarbon dating was carried out on plant detritus (100 g each) from samples S1 (layer 15) and S3 (layer 13) at Herzen State Pedagogical University of Russia, St. Petersburg. Obtained radiocarbon dates were calibrated in the Calib Rev 8.1.0. software, using curve IntCal20, range $\pm 2\sigma$ (Table 3). Obtained dates were congruent with the previously published dating according to the earlier geological study of the Lebed site (Rusanov & Orlova, 2013).

Results

In total, 405 Coleoptera fragments, three fragments of parasitic Hymenoptera, and one Diptera puparium were processed from the Lebed locality. Since the fragments of the last two orders could not be determined even down to families, and also due to their clear predominance, only Coleoptera are used in the analysis (Figs 2, 3). The ratio of the main types (head, pronotum, elytron) of beetle fragments H:P:E = 17:92:279 differs significantly from the expected 1:1:2, towards a decrease in the relative number of pronotums and, especially, head capsules. Such a bias during burial is probably due to the lower sinking capacity of the fragments capable of holding air bubbles.

The subfossils are attributed to at least 268 specimens. In total, 120 Coleoptera species from 17 families (Tables A1, 4) are found and 83 species are determined to species

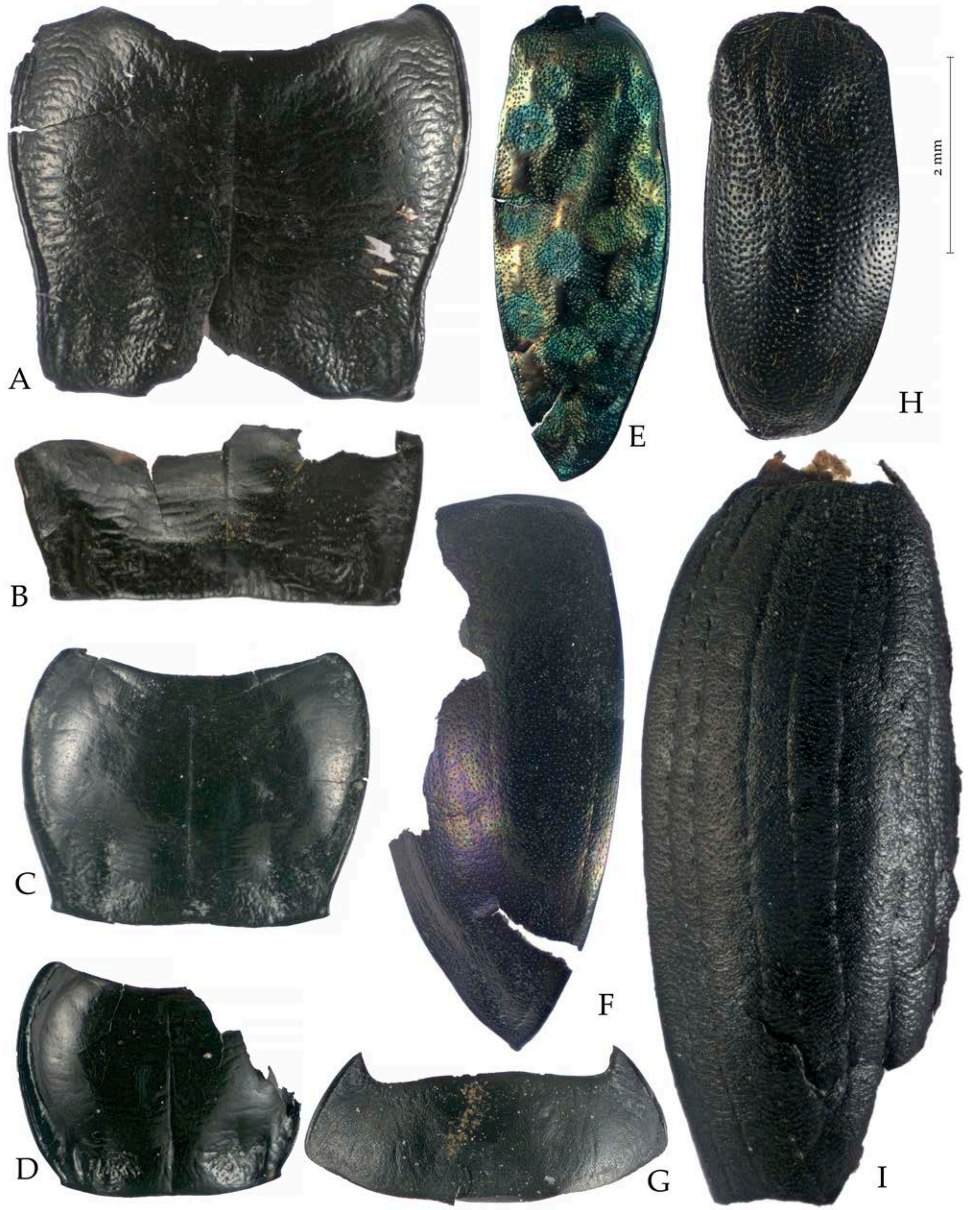

FIGURE 2. Carabidae (**A–E**), Byrrhidae (**F**), Dytiscidae (**G**), Chrysomelidae (**H**) and Curculionidae (**I**) remains from the Lebed deposit. **A**, *Pterostichus drescheri*. **B**, *P. tomensis*. **C**, *P. adstrictus*. **D**, *P. ehnbergi*. **E**, *Elaphrus angusticollis*. **F**, *Byrrhus* cf. *mordkovitshi*. **G**, *Ilybius* cf. *erichsoni*. **H**, *Bromius obscurus*. **I**, *Trichalophus maklini*. **A–D**, **G**, pronotum; **E**, **F**, **H**, **I**, elytra.

or species-group level. Three families are most abundantly represented in the locality: Carabidae (37 species, Nmin = 93), Staphylinidae (33 species, Nmin = 59), and Curculionidae (21 species, Nmin = 43). There are no dominants in the locality. The maximum Nmin = 15 was noted in *Aegialia* sp. (Scarabaeidae), which is only 5.6%

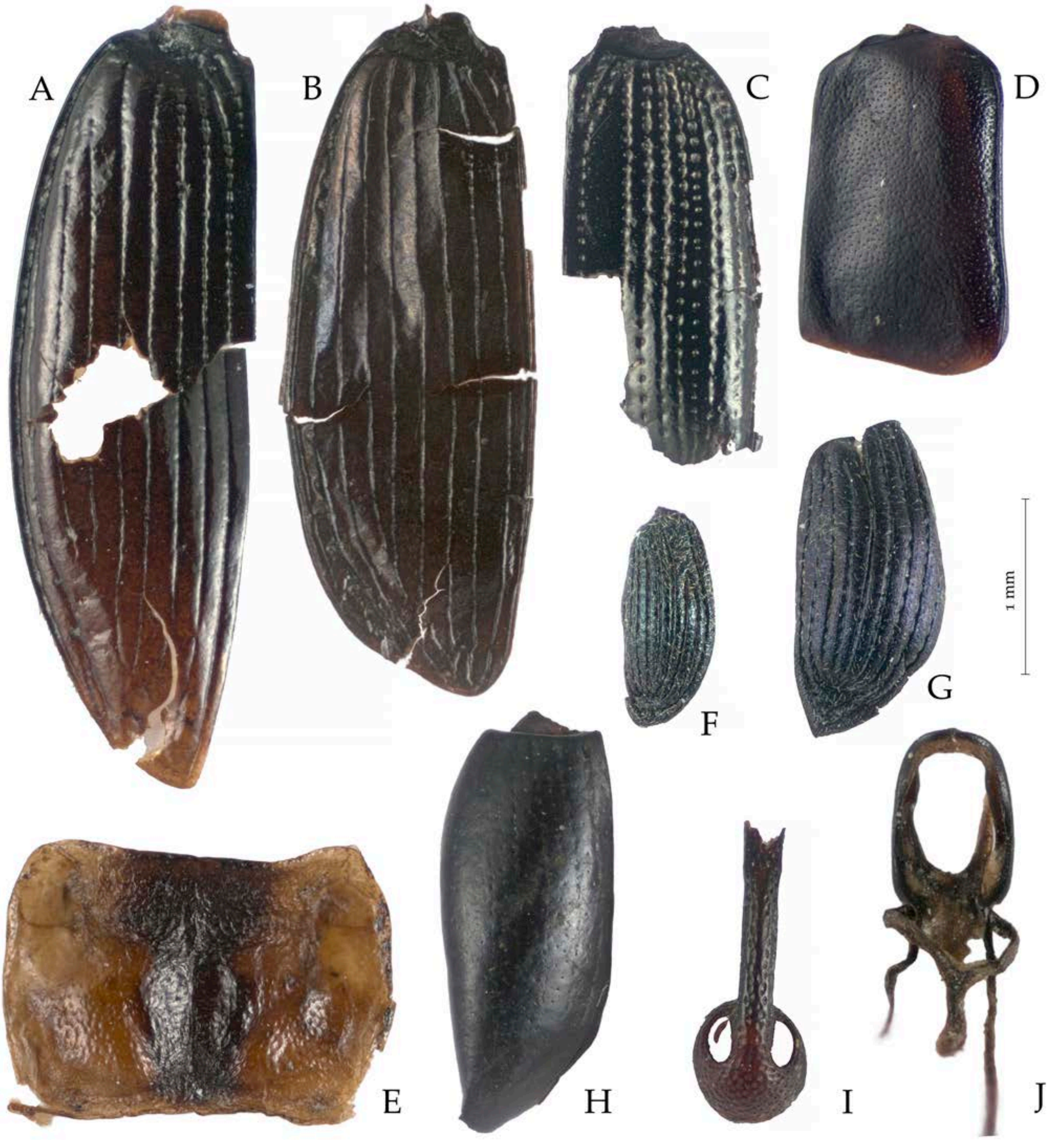

FIGURE 3. Carabidae (**A–C**), Staphylinidae (**D**), Cantharidae (**E**), Brentidae (**F**, **G**) and Curculionidae (**H–J**) remains from the Lebed deposit. **A**, *Patrobus obliteratus*. **B**, *Agonum alpinum*. **C**, *Notiophilus semistriatus*. **D**, *Tachinus rufipes*. **E**, *Podabrus* cf. *alpinus*. **F**, *Hemitrichapion tschernovi*. **G**, *Eutrichapion rhomboidale*. **H**, *Notaris altaica*. **I**, *Thryogenes nereis*. **J**, *Hylobius gebleri*. **A–D**, **F–H**, elytra; **E**, pronotum; **I**, head; **J**, aedeagus.

and which probably includes more than one species. The following species are also relatively numerous: *Clivina fossor* and *Trechus* sp. (Carabidae) (Nmin =7); *Agonum alpinum* (Carabidae), *Tachinus rufipes* (Staphylinidae), *Trichalophus maklini*, *Otiorhynchus grandineus* (Curculionidae) (Nmin = 6). Most of the species are represented by single specimens: 64 species Nmin = 1, 27 species Nmin = 2. The absence of dominants also manifests itself in high values of the Simpson index (1–D = 0.998). The high species diversity is also reflected in the values of the Shannon index (H = 4.72).

The samples differ markedly both in the number of fragments found in them and in the number of identified species (Table 4). This is due to both different saturation of insect remains (Nmin / Volume) and different volumes of samples. Coleoptera from samples S1, S3, and S4 are

TABLE 4. Indexes of biodiversity of subfossil Coleoptera from the Lebed site.

Index	In total	S1	S2	S3	S4
Fragments number	405	180	28	120	77
Nmin	268	120	24	69	55
Nmin / Volume, liter^{-1}	9.6	10.0	3.4	11.5	18.3
Species number	120	67	20	44	36
Families number	17	11	11	12	9
Simpson (1–D)	0.9883	0.9874	0.9881	0.9842	0.9837
Shannon (H)	4.72	4.35	3.37	4.03	3.82

represented by quite rich samples (36–67 species each), sufficient for analysis. The sample S2 (a small lens of detritus extracted as a whole) that includes only 28 fragments of 20 species of Coleoptera, can be considered together with sample S1 (see Table 3), since it was taken in the same layer.

Comparison of the similarity of species composition at the level of subsamples is presented on the graph of principal coordinates, constructed using the Szymkiewicz-Simpson index (Fig. 4). It shows that the species composition of subsamples of one sample is generally similar, and the clusters corresponding to four samples can be traced only at the trend level.

Most of the species were collected by the main method described above (Sampling section). Layer-by-layer examination of the deposit and rough washing of additional subsamples added several good quality fragments and four species of Coleoptera: *Bembidion* (*Asioperyphus*) sp., *Patrobus obliteratus*, *Pterostichus adstrictus*, and *Otiorhynchus krattereri*. All fragments found during deposit examination were isolated, *i.e*., the beetles were disintegrated into fragments before entering the burial.

Discussion

Taxonomical composition and diversity

The Coleoptera assemblage of the Lebed site is characterized by high taxonomic diversity. This can be judged based on the high ratio of the number of species recorded here (120 species, 82 identified) to the number of individuals (Nmin = 268). For comparison, in Western

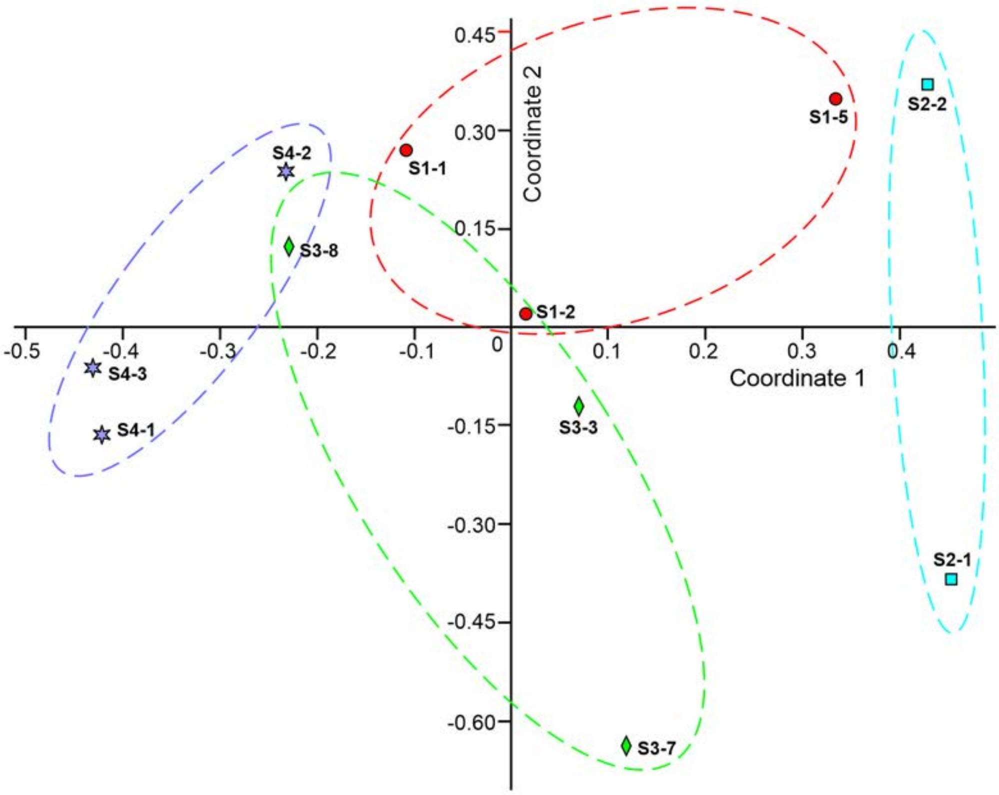

FIGURE 4. Comparison of the similarity of species composition at the level of subsamples by the Szymkiewicz-Simpson index.

Siberia and adjacent territories, where more than ten late Pleistocene localities with a large number of individuals are known (Zinovyev, 2020), only two of them include a larger number of species. In particular, 95 species (Nmin = 575) are known from the periglacial beetle assemblages Gornovo-IV from Southern Cis-Urals (Dudko *et al*., 2022) and 105 species (Nmin = 463) from the Suzun-1 complex in the south of the West Siberian Plain (Gurina *et al*., 2023).

High species diversity is even better reflected by indices accounting for the evenness of the sample. For the Lebed deposit the Shannon index is 4.72, while in most comparable communities it takes values of 1.5–3.5 and rarely exceeds 4.5 (Magurran, 2004). This indicates not only a significant number of species in Lebed, but also their high evenness. The absence of dominants in the deposit is also reflected by a very high (close to 1) value of the Simpson index (0.9883). The high values of the diversity indices suggest that the resulting list of Coleoptera species represents a small part of the truly rich fauna. Consequently, the deduced environmental conditions were quite favourable for beetles, probably relatively mild. One can also assume a high diversity (or heterogeneity) of biotopes that existed in the area where the examined material was deposited.

In addition to the large number of species, taxa of higher rank are also diverse in the Lebed deposit. At least 86 genera and subgenera, 54 subfamilies and tribes, as well as 17 families of beetles have been identified there. Of them, the families Cantharidae and Laemophloeidae were not recorded earlier in the Pleistocene of Western Siberia at all. The large, species-rich families Carabidae, Staphylinidae and Curculionidae (Löbl & Löbl, 2015, 2017; Alonso-Zarazaga *et al*., 2023), which predominate in the number of species in the recent fauna of the region, are represented differently in Quaternary deposits. Carabidae are characteristic of most stratigraphic units, especially in the northern regions, where they predominate (Zinovyev *et al*., 2023). Curculionidae, on the contrary, pre-dominate in the southern regions and form the basis of the late Pleistocene periglacial fauna of the West Siberian Plain (Gurina *et al*., 2019; Dudko *et al*., 2022). Staphylinidae in Western Siberia are most diverse and numerous in Holocene deposits. They are moderately represented (5–15%) in Late Pleistocene deposits of the northern part of the West Siberian Plain. In most localities in its southern part they are absent or are represented singly; only sometimes (Nizhnyaya Tavda, Suzun-1) they are among the dominants (Zinovyev, 2020a, b; Gurina *et al*., 2023).

The representation of major families in different samples is uneven (Table A1). It is particularly peculiar in the sample S3, where Staphylinidae are almost absent. At the same time, species diversity indices in that sample remain as high as in other samples (Table 4). This is probably due to some taphonomic factors, but the reason remains unclear.

Faunistic comparison

Comparison with late Pleistocene complexes of Western Siberia

Despite the relatively good knowledge of the late Quaternary insects of Western Siberia, Lebed is the first insect site from the low elevations of Northern Altai, and one of the few in Western Siberia dating back to the deglaciation period. Therefore, it is expected to have a high degree of originality and little similarity with other deposits. Indeed, almost half of the identified species (37 species) there were not previously recorded in the late Pleistocene of Western Siberia (asterisked in Table A1), 22 were previously recorded only in 1–2 sites, and 24 were more or less common in the Pleistocene of the region. Among them there are polyzonal *Clivina fossor*, *Patrobus septentrionis* (Carabidae) and *Tournotaris bimaculata* (Curculionidae) characteristic of many Quaternary deposits, as well as the arctic-boreal *Pterostichus brevicornis* (Carabidae), *Notaris aethiops* and *Otiorhynchus politus* (Curculionidae).

In Western Siberia, there are eight known localities that have radiocarbon dates close to the Lebed deposit. These are Ngoyun on the Yamal Peninsula, Agan-4068/2, Agan-1082/2, Kul'egan-2241, Zelenyi Ostrov in the Middle Ob region, Bunkovo in the Upper Ob region, Kizikha-1 and Ust'yanka in the very south of the West Siberian Plain (Table 5). As can be seen from the table, the Lebed insect assemblages have little similarity to these localities. No common species were found between Lebed and the northernmost site (Ngoyun), while the similarity of the Lebed assemblages with the rest is low (5–18%) and it is mainly due to shared species generally characteristic of Pleistocene deposits of Western Siberia. The assemblages Zelenyi Ostrov and Kul'egan-2241 from the older Dryas of the Middle Ob region shows somewhat higher similarity (25–26%) with Lebed due to the addition of several taiga species such as *Carabus aeruginosus*, *Pterostichus adstrictus*, *P. dilutipes* (Carabidae) and *Chrysomela lapponica* (Chrysomelidae).

In the southern part (51–58°N) of the West Siberian Plain, during the end of MIS 3 and MIS 2 (*i.e*., the last glacial maximum), a very unique periglacial (tundra-steppe) fauna of insect existed. The Coleoptera assemblages of this territory have been relatively well studied. Based on 16 sites, about 350 species have been identified here (Zinovyev, 2003, 2011, 2020b; Gurina *et al*., 2019a, b, 2023; Dudko *et al*., 2022). This complex, represented by a significant number of steppe and tundra species, was formed in a dry and cold climate. Its moderate similarity (35 common species) with the Lebed site is mainly due to

TABLE 5. Comparison of insect assemblages of the Lebed site with similar age and nearby located late Pleistocene sites of Western Siberia.

Site [7,14,17,22–25]	Coordinates N	E	^{14}C, BP (code)	Determinate species Number	Common with Lebed	Similarity, Ks (%)
Ngoyun	68°32′	72°06′	11226 ± 172 (IPAE-176) 10688 ± 240 (IPAE-175)	8	0	0
Zelenyi Ostrov	62°29′	81°51′	10780 ± 70 (Le-8972)	38	10	26
Agan-4068/2	62°06′	77°55′	11400 ± 350 (IPAE-98)	19	3	16
Agan-1082/2	62°04′	77°32′	13070 ± 575 (IPAE-95)	38	7	18
Kul'egan-2241	60°30′	75°45′	10700 ± 325 (IPAE-94)	28	7	25
Bunkovo	55°04′	82°30′	11550 ± 125 (SOAN-8806)	65	9	14
Kizikha-1	51°26′	81°36′	13455 ± 150 (SPb-1347)	19	3	16
Ust'yanka-1	51°16′	81°29′	10150 ± 200 (SPb-1345) 10806 ± 100 (SPb-1346)	38	2	5
Lebed	52°15′	87°09′	11956±120 (SPb-3685) 13832 ± 100 (SPb-3127)	83	83	100
Kalistratikha	52°58′	83°37′	24438 ± 350 (SPb-1416)	29	10	34
Novaya Surtaika	52°14′	85°55v	16404±150 BP (SPb-3687)	25	17	68

intrazonal riparian species (*Nebria gyllenhali*, *Elaphrus angusticollis*, 4 species of Bembidion (Carabidae), *Hypnoidus* cf. *rivularius* (Elateridae), *etc*.), as well as polyzonal and arctoboreal species characteristic of many Pleistocene localities. At the same time, the species similarity of periglacial assemblages of individual sites and the Lebed assemblage of insects is usually 15–25%. A noticeably greater similarity (34%) is shown by the Kalistratikha deposits (Table 5). This deposit in the Upper Ob region in the very South-East of the West Siberian Plain, approximately 120 km from the Altai Mountains, has the closest location (about 250 km) to the Lebed. The increased level of similarity between Kalistratikha and Lebed is due to the fact that, in addition to the species of the periglacial complex, Coleoptera which are now characteristic of the Altai Mountains, also are noted in both sites. Such species are *Bembidion gebleri*, *Pterostichus drescheri*, *P*. *maurusiacus* (Carabidae), *Trichalophus maklini* (Curculionidae).

Material from the Novaya Surtaika site from the foothills of Northern Altai (85 km from the Lebed) is currently only partially processed (Dudko *et al*., 2017). From the layer classified as MIS 2 deposits, 25 species of beetles were identified, 17 of which were also recorded at the Lebed deposit (Table 5). This indicates a likely very high similarity of the corresponding faunas.

Thus, the originality of the fauna of insect of the Lebed site, in comparison with other late Pleistocene deposits, is determined to a greater extent by its geographical location in the low mountains of Altai, and to a lesser extent by the age of the sediments.

Comparison with modern beetle faunas

The level of knowledge of the modern fauna of Altai is uneven for various groups of Coleoptera. For example, Staphylinidae are relatively poor studied. Therefore, our comparison is based on the families Carabidae (Dudko & Lomakin, 1996; Dudko, 1998; Dudko *et al*., 2002; Dudko & Lyubechansky, 2002; Dudko & Zinchenko 2009; Luzyanin *et al*., 2022) and Curculionidae (Legalov, 1996, 2020a, b, 2021a, b, c, 2022; Legalov & Dudko, 2006; Legalov & Reshetnikov, 2020). The Coleoptera collection of the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian Academy of Sciences was also studied in addition to the published data.

Comparison of the species composition of the Lebed locality with the modern fauna of insect of the studied region and adjacent territories shows its highest similarity with the fauna of insect of the Altai-Sayan mountains as a whole, quite high similarity (73%) with the fauna of the West Siberian Plain, but more interesting to analyse indexes with some sub-regions (Fig. 5, Table 6).

The highest similarity is found with the faunas of insects of highly humid sub-regions: Kuznetsk Alatau (82%), North-Eastern Altai (73%) and Western Altai (71%) (Table 6). Such high values of similarity coefficients suggest that almost all species from the deposit have remained in the subregion since the end of the Pleistocene, *i.e*. the data obtained do not reveal significant changes in species ranges. On the contrary, for lowland late Pleistocene assemblages changes in species ranges are very characteristic (Zinovyev, 2020b; Dudko *et al*., 2022). As an exception, single fragments of two species

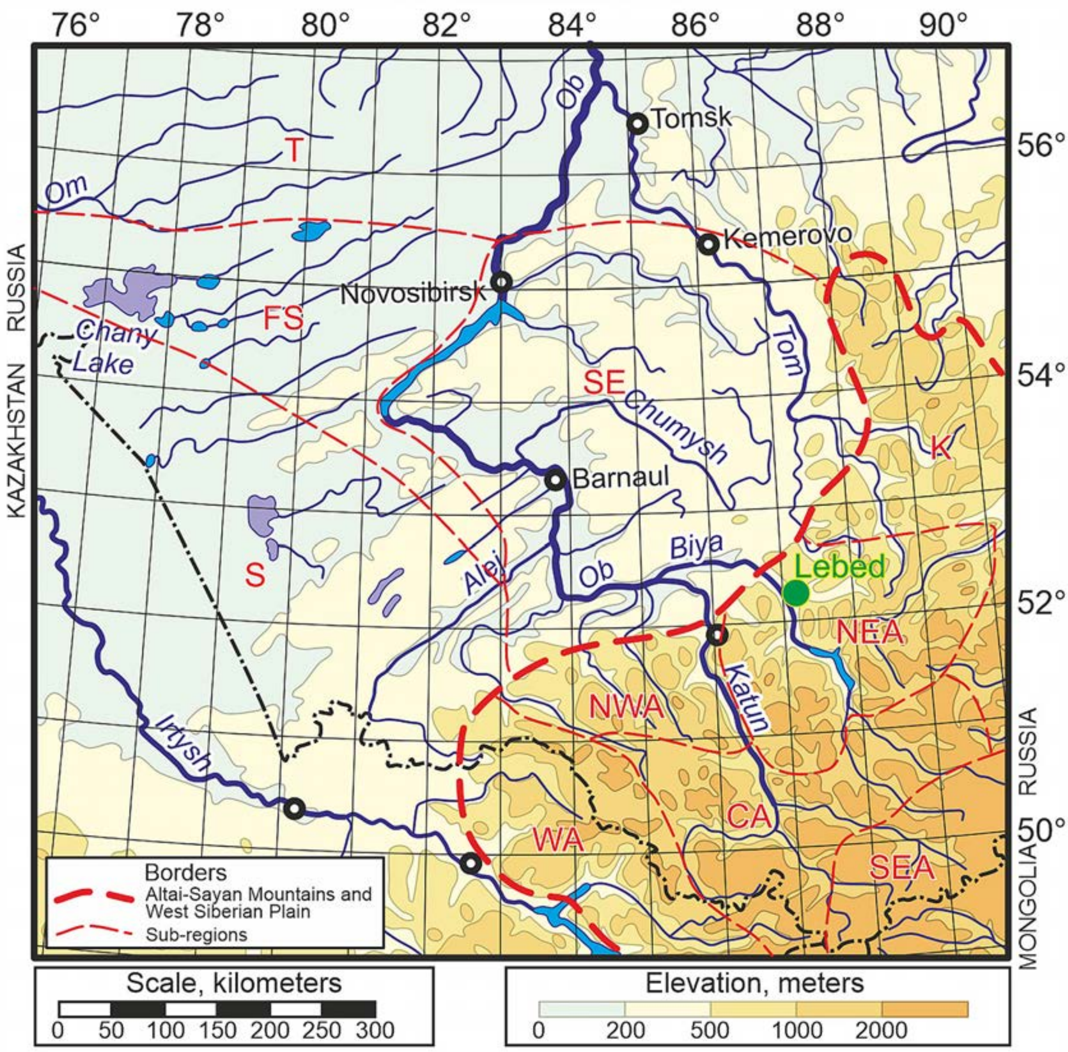

FIGURE 5. Map of regions and sub-regions adjacent with the Lebed site. West Siberian Plain: T, FS, S—taiga, forest steppe and steppe zones respectively, SE—south-eastern part (Upper Ob River, Salair Ridge and Kuznetsk depression); Altai-Sayan Mountains: K—Kuznetsk Alatau, NEA, NWA, WA, CA, SEA—North-Eastern, North-Western, Western, Central and South-Eastern Altai respectively (Dudko, 1998).

TABLE 6. Similarity indexes (Ks) of Coleoptera assemblage from Lebed site and modern faunas of sub-regions of Altai-Sayan Mountains and West Siberian Plain, %.

Region, sub-region	Lebed, in total	S1	S2	S3	S4
Altai-Sayan Mountains	96	98	85	98	96
Kuznetsk Alatau	82	84	69	88	96
North-Eastern Altai	73	79	62	80	80
Western Altai	71	77	62	76	64
North-Western Altai	55	56	54	66	60
Central Altai	65	65	62	78	60
South-Eastern Altai	45	49	46	46	48
West Siberian Plain	73	77	77	73	68
South-eastern part	52	58	62	56	44
Taiga zone	51	56	38	54	60
Forest-steppe zone	27	21	38	29	36
Steppe zone	12	9	31	15	12

were found in the sample S2. *Morychus* cf. *ostasiaticus* is a species characteristic of the Pleistocene assemblages; at present its distribution extends from Western to Eastern Siberia and Mongolia and its more numerous in the arid mountain depressions of Southern Siberia (Tshernyshev & Dudko, 1997; Jaeger & Pütz, 2006; Tshernyshev, 2006). *Otiorhynchus* aff. *ursus* is also a species characteristic of the periglacial fauna of insects of south of Western Siberia; at present its distribution is poor known and limits by East Kazakhstan and extreme west of Altai territory (Dudko *et al*., 2022). For other species, the explanation of their lack in the modern fauna of insect of the region may be the poor knowledge of the group in the region.

Of the considered mountain subregions, weak similarity between the Lebed (45%) and South-Eastern Altai, a region characterized by an extreme hyper-continental arid climate, was revealed. On the contrary, the recent fauna of this particular subregion is most similar to the periglacial assemblages of the West Siberian Plain (Gurina *et al*., 2019b; Dudko *et al*., 2022), which once again confirms the difference between the Lebed site and the lowland late Pleistocene localities.

The fauna of modern subregions of the West Siberian Plain are also less similar to the Lebed subfossil coleopteran fauna. Even in the south-eastern part of West Siberian Plain adjacent to the deposit, only about half of the species composition of the Lebed assemblages occurs. A particularly low similarity (12%) is observed between Lebed and the arid steppe zone of the West Siberian Plain (Table 6).

Ecological analysis

Trophic groups

Predatory beetles, such as ground beetles (43 species) and rove beetles (33 species), predominate in the Lebed assemblages according to trophic relationships. Phytophages are presented by 42 species. Saprophages are poorly represented (two species). *Dermestes depressus* is associated with bumblebee nests. Among the phytophages, mono- and oligophages suggest the presence of the following representatives of 14 plant families: Pinaceae: *Larix* sp. (*Hylobius excavatus*), *Picea* sp. (*Hylobius excavatus*, *Polygraphus polygraphus*, *Phloeotribus spinulosus*), *Pinus* sp. (*Hylobius abietis*), Asteraceae (*Chrysolina graminis*, *Phyllobius virideaeris*, *Otiorhynchus* spp.), Brassicaceae (*Ceutorhynchus erysimi*), Crassulaceae: *Rhodiola rosea* (*Hylobius gebleri*), Cyperaceae: *Carex* sp. (*Notaris aethiops*), Fabaceae: *Oxytropis* sp. (*Hemitrichapion tschernovi*), *Lathyrus gmelinii* (*Eutrichapion rhomboidale*), Lamiaceae (*Chrysolina graminis*), Onagraceae: *Chamaenerion angustifolium* (*Bromius obscurus*), Polygonaceae: *Rumex* sp. (*Gastrophysa viridula*), Ranunculaceae: *Ranunculus* and *Caltha* (*Hydrothassa marginella*), Salicaceae: *Salix* sp. (*Chrysomela lapponica*, *Gonioctena nivosa arctica* / *linnaena,* Saxifragaceae: *Bergenia crassifolia* (*Trichalophus maklini*, *Hylobius gebleri*), Typhaceae: *Typha latifolia* (*Tournotaris bimaculata*), and Violaceae: *Viola* sp. (*Orobitis cyanea*). Compared to the data in Ponomareva (Rusanov & Orlova, 2013), who noted one family of gymnosperms and 18 families of angiosperms, our research confirms the presence of the family Pinaceae and adds the genus *Larix* for gymnosperms. It also confirms the presence of eight families of angiosperms, namely Asteraceae, Brassicaceae, Cyperaceae (*Carex* sp.), Lamiaceae, Polygonaceae (*Rumex* sp.), Salicaceae (*Salix* sp.), and adds Typhaceae (*Typha latifolia*) and Violaceae (*Viola* sp.). Five angiosperm families, Crassulaceae (*Rhodiola rosea*), Fabaceae (*Oxytropis* sp., *Lathyrus gmelinii*), Onagraceae (*Chamaenerion angustifolium*), Ranunculaceae (*Ranunculus* and *Caltha*), and Saxifragaceae (*Bergenia crassifolia*) are suggested for the first time.

Reconstructed biotopes

Since most of the species from the sediments now inhabit North-Eastern Altai and Kuznetsk Alatau, there is reason to believe that biotopes similar to modern biotopes of that region were present in the studied area in the late Pleistocene. At the same time, it is necessary to take into account the vertical vegetation zonality of mountains. In these sub-regions, taiga is developed as black (with a predominance of fir and aspen) and dark coniferous (significant participation of Siberian pine) forests (Ogureeva, 1980). The alpine zone is represented by alpine or subalpine meadows and mountain tundra. Various intrazonal biotopes are formed near water bodies. Mesophytic meadows are present in the foothills (Fig. 6).

Coniferous forests

A large number of beetle species from the list are those that in modern conditions are found both in taiga forests and alpine (subalpine) meadows. This is due to the specifics of Altai-Sayan dark coniferous forests where herbaceous layer is well defined (Ogureeva, 1980). This tall grass in the forests is similar in the species composition to alpine and subalpine meadows. Therefore, it is difficult to reconstruct the degree of forest development based only on Coleoptera. However, in all samples there are species associated specifically with forest vegetation. Namely, weevils *Hylobius abietis* which prefers development on *Pinus* and *H. excavates* which is usually associated with *Larix,* bark beetles *Phloeotribus spinulosus* and *Polygraphus polygraphus* that are species obligately associated with *Picea*. *Leptophloeus alternans* (Laemophloeidae) habitat is in tunnels made by bark beetles mainly in spruce (Hägglund & Hjältén, 2018). *Quedionuchus* cf. *glaber*

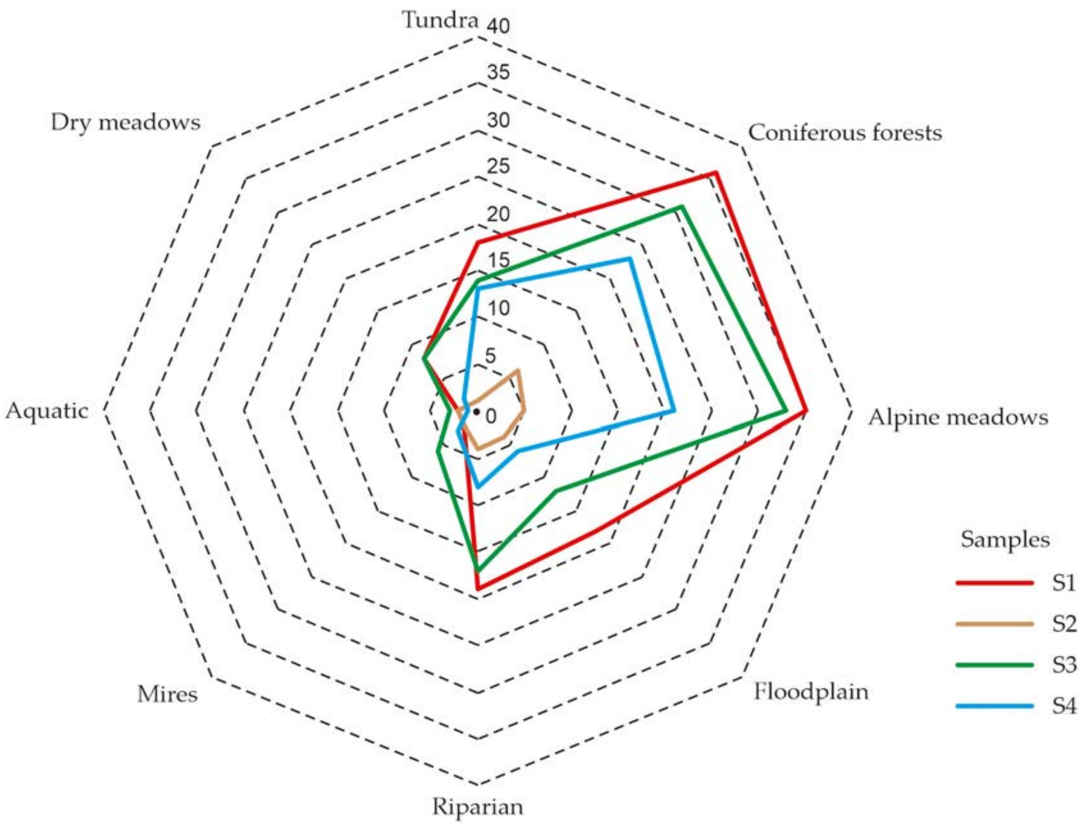

FIGURE 6. Ecological composition of Coleoptera from different samples of the Lebed site.

(Staphylinidae) is a forest species found mainly under the bark of conifers in shaded places (Brunke *et al*., 2020). In addition, forest species include *Carabus aeruginosus* and *Pterostichus adstrictus*. In particular, *Pterostichus adstrictus* is a pyrophilic species that prefers burnt dry coniferous forests (Martikainen *et al*., 2006) and not still recorded from North-Eastern Altai and Kuznetsk Alatau.

Tall grass meadows
Meadows similar to modern alpine or subalpine ones were probably well represented. This is evidenced by the large number of species characteristic of the herbaceous layer of various biotopes, such as *Notiophilus jakovlevi*, *Trechus dudkorum*, *Agonum alpinum*, *Harpalus nigritarsis* (Carabidae), *Podabrus* cf. *alpinus* (Cantharidae), *Hylobius gebleri*, *Trichalophus maklini*, *Otiorhynchus grandineus* (Curculionidae), as well as some specific alpine species, such as *Patrobus obliteratus* (Carabidae) and *Notaris altaica* (Curculionidae). In addition, the high diversity of Coleoptera from the Lebed taphocenosis also suggests a high diversity and patchiness of biotopes (see above).

Tundra
Several species from Lebed taphocenosis (especially in sample S1) are characteristic of modern mountain (sometimes also zonal) tundra. These are *Carabus henningi*, *Pterostichus brevicornis*, *P. ehnbergi*, *P. subaeneus* (Carabidae), *Hypnoidus rivularius* (Elateridae), *Chrysomela lapponica* (Chrysomelidae), *Hemitrichapion tschernovi*, *Eutrichapion rhomboidale* (Brentidae) and *Otiorhynchus politus* (Curculionidae). However, they are all equally characteristic of other landscapes such as alpine meadows, dark coniferous forests or swamps, but not of specifically tundra. Thus, the reconstruction of tundra communities from entomological data remains controversial.

Dry meadows
Four most xerophilous species preferring steppe biotopes, but occurring also in dry meadows (*Chrysolina graminis artemisiae* (Chrysomelidae), *Ceutorhynchus erysimi*, *Phyllobius contemptus* and *Otiorhynchus* af. *ursus* (Curculionidae)) are represented in the locality. The weak representation of the steppe group and the abundance of humid species make the reconstruction of steppe biotopes unlikely, but dry meadows could well have formed on warm slopes of southern exposure.

Intrazonal biotopes
Aquatic (*Gyrinus opacus*, *Ilybius* cf. *erichsoni*, *I. obtusus*, *Helophorus* cf. *sinoglacialis*, *H. sibiricus* and *Ochthebius* cf. *kaninensis*), riparian (*Nebria* cf. *gyllenhali*, *Bembidion* (*Plataphus*) cf. *fellmanni*, *B. difficile*, *etc*.), floodplain (*Aegialia* spp., *Hypnoidus gibbus*, *Simplocaria*

semistriata, *etc*.) and mire (*Patrobus* cf. *septentrionis*, *Thryogenes nereis*, *etc*.) species are widely represented in the studied taphocenosis. At the same time, the halophilic complex, which is very characteristic for late Pleistocene of the south of West Siberian Plain, is completely absent at the Lebed site.

Altitude distribution

Most species from the sediments are now found in a wide range of altitudes, from foothills to highlands. However, a significant number of species from the Lebed site in the region are now confined to high and medium elevations of the mountains. They are absent at low elevations. There is more than a dozen such species and they are present in all samples: *Notiophilus semistriatus*, *Bembidion mckinleyi*, *Patrobus obliteratus*, *Pterostichus brevicornis*, *P*. *ehnbergi*, *P*. *subaeneus*, *Agonum* cf. *consimile*, *Harpalus nigritarsis* (Carabidae), *Aclypea souverbii* (Silphidae), *Aphodius* cf. *piceus* (Scarabaeidae), *Byrrhus* cf. *mordkovitshi* (Byrrhidae), *Chrysomela lapponica* (Chrysomelidae), *Hemitrichapion tschernovi* (Brentidae). The presence of these species indicates that the climate of the studied time was significant colder than the present one.

Apparently, the modern climatic conditions of the mid elevations of North-Eastern Altai in terms of temperature indicators could be similar to the late Pleistocene conditions of the low mountains. At the same time, the presence of xerophilous species in the sediments, which are absent in the region now, does not allow for a close analogy.

Refugium of humid fauna

North-Eastern Altai and Kuznetsk Alatau are the most humid subregions of the Altai-Sayan Mountains. Apparently, relatively mild conditions here persisted throughout the Pleistocene, against the background of the hyper-continentality of most of Eurasia. Species sensitive to dry conditions and significant temperature fluctuations could survive in such places. The fact that there are many endemics in these subregions indicates long-term isolation. The presence of a significant number of endemic and subendemic species in the Lebed taphocenosis is factual confirmation of the existence of these species here at the very end of the Pleistocene. So, *Trechus* cf. *dudkorum*, *Patrobus obliteratus*, *Pterostichus* cf. *subaeneus* (Carabidae), *Helophorus* cf. *sinoglacialis* (Helophoridae), *Byrrhus* cf. *mordkovitshi* (Byrrhidae), *Notaris altaica* (Curculionidae) are endemic, and *Notiophilus jakovlevi*, *Pterostichus drescheri*, *P*. *ehnbergi*, *P*. *tomensis* (Carabidae) and *Aegialia matalini* (Scarabaeidae) are subendemic of the Altai-Sayan Mountains.

An even more convincing indicator of the significance of the region as a refugium is the presence of relict taxa. In particular, the forest flora (Kuminova, 1960; Polozhii & Krapivkina, 1985) and fauna (Dubatolov & Kosterin, 2000; Dudko, 2011) of the Altai-Sayan Mountains include several species that have a disjunctive range, the main part of which covers the regions of Europe or East Asia. There are especially many such species in the North-Eastern and Western Altai, as well as in the Kuznetsk Alatau. Until now, the question of the origin of these species in Siberia remains is open. The first explanation for this phenomenon is the assumption that these species are relics of the tertiary more wide-spread broad-leaved forests (Kuminova, 1960; Polozhii & Krapivkina, 1985). Other researchers argue for a much younger age of disjunctions, namely the Holocene climatic optimum (Dubatolov & Kosterin, 2000). A very likely point of view is that faunal turnover took place more than once and we are talking about relicts of different ages (Dudko, 2011). This problem is beyond the scope of this article, but evidence of confirmation of the presence of such species in deposit of different ages can help to understand the faunogenesis of these taxa.

Four species of Coleoptera from Lebed site have a disjunctive modern range and are distributed in the Altai-Sayan Mountains, isolated from the main part of the range. The main distribution of the ground beetle *Notiophilus semistriatus* is in Nearctic, while in the Palearctic it is represented by isolated areas: along the Pacific coast, in the Baikal region, in the Kuznetsk Alatau and in the Western Altai (Dudko, 2011). *Aclypea souverbii* (Silphidae), *Eutrichapion rhomboidale* (Brentidae) and *Otiorhynchus krattereri* (Curculionidae) have their main range in the mountains of Eastern Europe, but are also known from the Altai-Sayan region (Nikolajev, 2010; Kizub & Slutsky, 2019; Legalov, 2020b; Alonso-Zarazaga *et al*., 2023). All these species are cold-adapted and are not associated with broad-leaved forests. The disjunction can be explained by their association with humid regions.

Comparison of samples

An analysis of the taxonomic composition of different samples from the Lebed locality shows the range of their similarity of 23–56%. On the one hand, this indicates significant differences between different samples (Fig. 7). However, the low values of similarity indices are largely due to insufficient sampling for the high level of diversity, and many species are represented by singletons. On the other hand, assemblages demonstrate significant similarity in ecological composition, both in the biotopic occurrence of species and in their altitudinal distribution. Based on this, we can assume similar climatic conditions during the formation of these deposits.

In general, the similarity of the preferences of the beetle assemblages confirms the similar landscape and climatic conditions in the oldest (S1 and S2) and older (S3 and S4) Dryas.

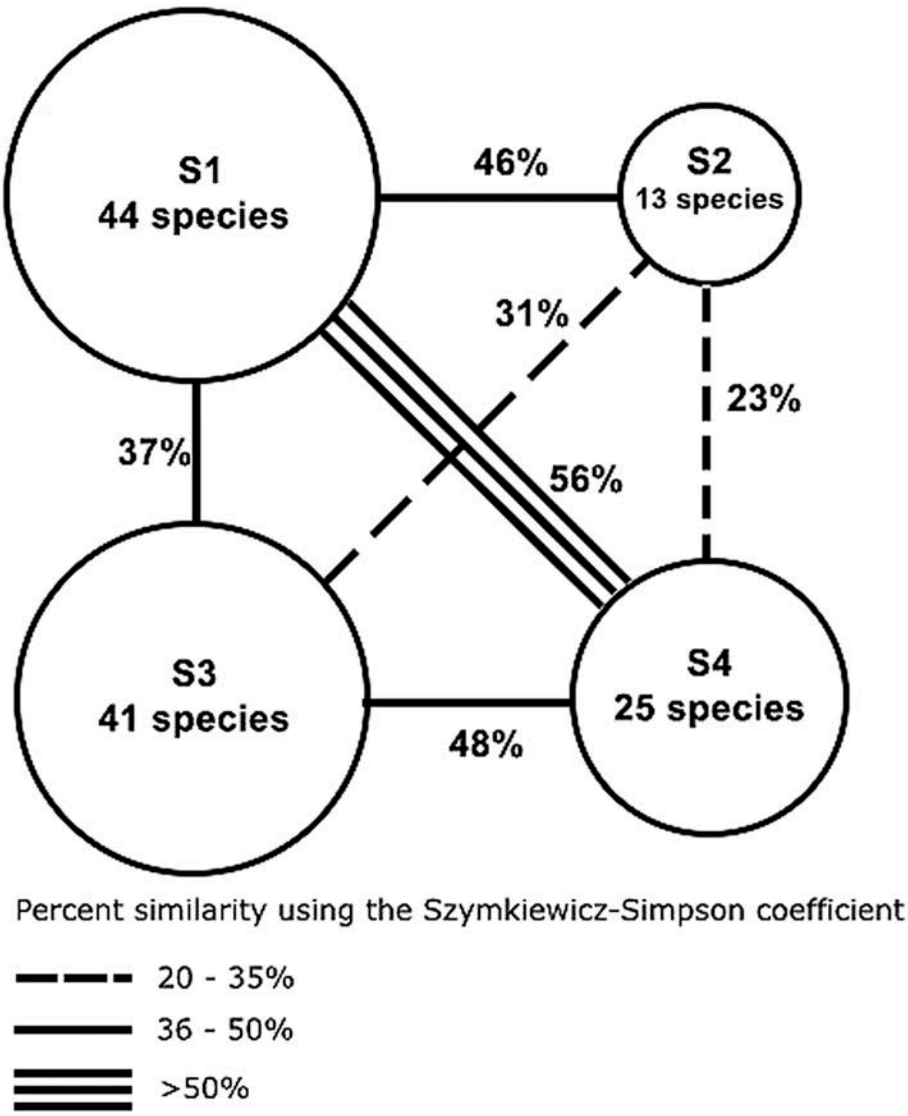

FIGURE 7. Similarity graph of insect assemblages between the samples of Lebed.

Conclusions

A subfossil beetle assemblages found in the Lebed locality in the low mountains of north-eastern Altai is highly unique. Coleoptera are the most abundant and diverse there, represented by 120 species from 17 families. Of these, Carabidae, Staphylinidae and Curculionidae are represented by the largest number of species and are found in all four samples collected from the locality. The species composition of the assemblages is most consistent with the modern fauna found in the middle elevations of the north-eastern Altai and Kuznetsk Alatau and includes several endemic and relic species. Comparison of the Lebed beetle assemblages with the previously studied late Pleistocene fauna of insect of the West Siberian Plain shows similarities due to shared eurytopic species with wide distribution ranges. Based on the known ecological preferences of the identified species in modern conditions, alternating dark coniferous forests and open tallgrass meadows are reconstructed for the studied area during sedimentation. Based on the same type of evidence, the climate is hypothesized as humid and significantly colder than it is in the studies area now. Taking into account ecological preferences of Coleoptera species and radiocarbon age of the two layers (13832±100 BP and 11956±120 BP) the deposits are correlated with the oldest and older Dryas.

Acknowledgments

The authors are sincerely grateful to M.A. Kulkova (A. Herzen Russian State Pedagogical University, St. Petersburg) for determining the radiocarbon age, A.S. Prosvirov, A.V. Ivanov, V.K. Zinchenko for identification of Elateridae and Scarabaeidae. The study of A.G. was carried out under the Russian Science Foundation (grant No.23-74-01024), study of R.D. was carried out under the Federal Fundamental Scientific Research Program (grant No.1021051703269-9-1.6.12), the study of A.L. was supported by the Tomsk State University Development Programme (Priority-2030), the study of A.P. were carried out under the framework of the Russian state research project No.121051100109-1, the study of E.Z. was carried out under a government contract with the Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences (research subject FUWU-2022-0005).

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Appendix—TABLE A1. Subfossil Coleoptera of the Lebed site.

No.	Family / Species	Nmin				No of fragments	
		S1	S2	S3	S4	H-P-E-O	In total
	Gyrinidae	**-**	**-**	**1**	**-**	**1-0-0-1**	**2**
1	*Gyrinus opacus* Sahlberg, 1819*	-	-	1	-	1-0-0-1	2
	Dytiscidae	**-**	**1**	**1**	**-**	**0-2-0-0**	**2**
2	*Ilybius* cf. *erichsoni* (Gemminger et Harold, 1868)*	-	1	-	-	0-1-0-0	1
3	*I. obtusus* Sharp, 1882*	-	-	1	-	0-1-0-0	1
	Carabidae	**41**	**4**	**29**	**19**	**7-36-81-1**	**125**
4	*Notiophilus jakovlevi* Tschitschérine, 1903	2	-	1	-	0-1-2-0	3
5	*N. semistriatus* Say, 1823*	-	-	1	-	0-0-1-0	1
6	*Nebria* cf. *gyllenhali* (Schönherr, 1806)	2	-	-	-	0-2-0-0	2
7	*Carabus* cf. *aeruginosus* Fischer von Waldheim, 1820	-	-	2	-	0-0-2-0	2
8	*C.* cf. *henningi* Fischer von Waldheim, 1817	1	-	-	-	0-0-1-0	1
-	*Carabus* sp.	-	-	2	2	2-0-1-1	4
9	*Elaphrus angusticollis* R.F. Sahlberg, 1844	1	-	-	-	0-0-1-0	1
10	*Clivina fossor* (Linnaeus, 1758)	1	1	3	2	0-2-6-0	8
11	*Dyschiriodes* cf. *subarcticus* (Lindroth, 1961)*	1	-	-	1	0-0-3-0	3
12	*Trechus* cf. *dudkorum* Belousov & Kabak, 1996*	-	-	-	2	0-0-2-0	2
13	*Trechus* spp.	4	-	2	1	2-4-4-0	10
14	*Asaphidion pallipes* (Duftschmid, 1812)	2	-	-	-	0-0-2-0	2
15	*Bembidion* (*Semicampa*) *schueppelii* Dejean, 1831*	2	-	2	-	0-0-4-0	4
16	*B.* (*Notaphus*) sp.1*	-	-	-	1	0-0-1-0	1
17	*B.* (*Plataphus*) cf. *fellmanni* (Mannerheim, 1823)	2	-	-	-	0-0-2-0	2
18	*B.* (*P.*) *difficile* (Motschulsky, 1844)	3	-	1	1	0-0-6-0	6
19	*B.* (*P.*) *gebleri gebleri* (Gebler, 1833)	1	1	1	-	0-1-3-0	4
20	*B.* (*P.*) aff. *coelestinum* (Motschulsky, 1844)*	1	-	-	-	0-1-1-0	2
21	*B.* (*P.*) cf. *coelestinum* (Motschulsky, 1844)*	-	-	1	2	0-1-2-0	3
22	*B.* (*Peryphus*) *femoratum* Sturm, 1825 / ?*B. cruciatum* Dejean, 1831*	-	-	1	-	0-0-1-0	1
23	*B.* (*Terminophanes*) *mckinleyi* Fall, 1926	1	-	-	-	0-0-1-0	1
24	*B.* (*Asioperyphus*) sp.	-	-	1	-	0-0-1-0	1
25	*B.* (*Ocydromus*) *scopulinum* (Kirby, 1837)	-	-	1	-	0-0-1-0	1
-	*Bembidion* spp.	1	2	1	-	2-2-0-0	4
26	*Patrobus obliteratus* Gebler, 1848*	1	-	-	-	0-0-1-0	1
27	*P.* cf. *septentrionis* Dejean, 1828	1	-	-	-	0-0-1-0	1
-	*Patrobus* sp.	1	-	-	-	0-0-1-0	1
28	*Pterostichus* (*Plectes*) *drescheri* (Fischer von Waldheim, 1817)	1	-	1	-	0-1-1-0	2
29	*P.* (*Cryobius*) *brevicornis* (Kirby, 1837)	1	-	1	-	0-1-1-0	2
30	*P.* (*Cryobius*) spp.	3	-	1	-	0-2-6-0	8
31	*P.* (*Eosteropus*) *maurusiacus* (Mannerheim, 1825)	-	-	1	-	0-1-0-0	1
32	*P.* (*Bothriopterus*) *adstrictus* Eschscholtz, 1823	-	-	1	-	0-1-0-0	1
33	*P.* (*Petrophilus*) *dilutipes* (Motschulsky, 1844)	1	-	1	2	0-3-1-0	4
34	*P.* (*P.*) *ehnbergi* Poppius, 1908*	-	-	1	2	0-3-0-0	3
35	*P.* (*P.*) cf. *subaeneus* (Chaudoir, 1850)*	2	-	-	-	0-0-2-0	2
-	*P.* (*P.*) *subaeneus* / ?*P. monticoloides* Shilenkov, 1995	1	-	-	-	0-1-0-0	1
36	*P.* (*P.*) *tomensis* (Gebler, 1847)	1	-	1	1	0-2-1-0	3
-	*P.* (*Petrophilus*) spp.	-	-	1	2	0-0-4-0	4
-	*Pterostichus* spp.	-	-	1	-	1-0-0-0	1
37	*Calathus melanocephalus* (Linnaeus, 1758)	3	-	1	1	0-2-3-0	5
38	*Agonum alpinum* Motschulsky, 1844*	3	1	2	-	0-2-5-0	7
39	*A. consimile* (Gyllenhal, 1810) / ?*A. exaratum* (Mannerheim, 1853)	-	-	-	1	0-0-1-0	1
40	*Harpalus* cf. *nigritarsis* C.R. Sahlberg, 1827	-	-	1	-	0-1-0-0	1
-	Carabidae indet.	3	1	1	1	0-2-5-0	7
	Helophoridae	**1**	**-**	**1**	**-**	**0-0-2-0**	**2**
41	*Helophorus* cf. *sinoglacialis* Angus, Ryndevich & Zhang, 2017*	1	-	-	-	0-0-1-0	1
42	*H. sibiricus* (Motschulsky, 1860)	-	-	1	-	0-0-1-0	1
	Hydraenidae	**1**	**1**	**-**	**1**	**0-0-4-0**	**4**
43	*Ochthebius* cf. *kaninensis* Poppius, 1909*	1	1	-	1	0-0-4-0	4
	Silphidae	**-**	**-**	**1**	**-**	**0-1-1-0**	**2**
44	*Aclypea souverbii* (Fairmaire, 1848)*	-	-	1	-	0-1-0-0	1
-	Silphidae indet.	-	-	1	-	0-0-1-0	1
	Staphylinidae	**40**	**6**	**3**	**10**	**0-29-38-0**	**67**
45	*Eusphalerum* sp.	2	-	-	1	0-0-3-0	3
46	*Geodromicus* sp.*	1	-	-	-	0-1-0-0	1
47	*Olophrum* sp.1	5	-	-	-	0-1-7-0	8

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Appendix—TABLE A1. (Continued)

No.	Family / Species	Nmin				No of fragments	
		S1	S2	S3	S4	H-P-E-O	In total
48	*Olophrum* sp.2	2	-	-	-	0-0-2-0	2
49	*Olophrum* sp.3	2	-	-	-	0-0-2-0	2
50	*Omalium* sp.1	1	-	-	-	0-1-0-0	1
51	*Omalium* sp.2	1	1	-	-	0-2-0-0	2
52	*Phloeostiba* sp.1	-	1	-	-	0-1-0-0	1
53	*Phloeostiba*? sp.2	1	-	-	-	0-1-0-0	1
54	Omaliinae indet. sp.1	1	-	-	-	0-1-0-0	1
55	Omaliinae indet. sp.2	-	2	-	-	0-0-1-0	1
56	Mycetoporinae indet. sp.1	-	-	-	1	0-1-0-0	1
57	Mycetoporinae indet. sp.2	-	-	-	1	0-1-0-0	1
58	*Tachinus rufipes* (Linnaeus, 1758)	4	-	-	2	0-1-7-0	8
59	*Pella*? *humeralis* (Gravenhorst, 1802)*	1	-	-	-	0-1-0-0	1
60	Aleocharinae indet. sp.1	2	-	-	-	0-2-0-0	2
61	Aleocharinae indet. sp.2	1	1	-	-	0-2-0-0	2
62	Aleocharinae indet. sp.3	2	-	-	-	0-1-2-0	3
63	Aleocharinae indet. sp.4	1	-	1	-	0-2-0-0	2
64	Aleocharinae indet. sp.5	-	1	-	-	0-1-0-0	1
65	Aleocharinae indet. sp.6	-	-	-	1	0-1-0-0	1
66	Aleocharinae indet. sp.7	-	-	-	2	0-0-3-0	3
67	*Bledius* sp.1	2	-	-	-	0-2-1-0	3
68	*Bledius* sp.2	1	-	-	-	0-0-1-0	1
69	Oxytelinae indet. sp.1	1	-	-	-	0-0-2-0	2
70	*Stenus* sp.1	1	-	-	1	0-1-1-0	2
71	*Stenus* sp.2	1	-	-	-	0-0-1-0	1
72	*Ocypus* sp.	-	-	1	1	0-0-2-0	2
73	*Philonthus* sp.1	1	-	-	-	0-1-0-0	1
74	*Philonthus* sp.2	1	-	1	-	0-0-2-0	2
75	*Quedionuchus* cf. *glaber* (O. Müller, 1776)*	1	-	-	-	0-0-1-0	1
76	*Quedius* sp.1	3	-	-	-	0-3-0-0	3
77	*Quedius* sp.2	1	-	-	-	0-1-0-0	1
	Scarabaeidae	**8**	**2**	**9**	**-**	**1-1-25-0**	**27**
78	*Aphodius* cf. *piceus* Gyllenhal, 1808*	-	-	3	-	0-0-3-0	3
-	*Aphodius* sp.	1	-	-	-	0-0-1-0	1
79	*Aegialia matalini* Gusakov, 2003*	-	-	1	-	0-1-0-0	1
-	*Aegialia* sp.	7	2	6	-	1-0-21-0	22
	Byrrhidae	**4**	**1**	**-**	**5**	**0-0-11-0**	**11**
80	*Morychus* cf. *ostasiaticus* Tshernyshev, 1997	-	1	-	-	0-0-1-0	1
81	*Byrrhus* cf. *mordkovitshi* Tshernyshev & Dudko, 1997*	1	-	-	5	0-0-7-0	7
82	*Simplocaria semistriata* (Fabricius, 1794)*	3	-	-	-	0-0-3-0	3
	Elateridae	**3**	**-**	**1**	**1**	**0-0-7-0**	**7**
83	*Hypnoidus* cf. *gibbus* (Gebler, 1847)*	-	-	1	-	0-0-1-0	1
84	*Hypnoidus* cf. *rivularius rivularius* (Gyllenhal, 1808)	2	-	-	1	0-0-4-0	4
85	*Oedostethus* cf. *simplicipunctatus* (Tsherepanov, 1956)*	1	-	-	-	0-0-2-0	2
	Cantharidae	**-**	**-**	**1**	**-**	**0-1-0-0**	**1**
86	*Podabrus alpinus* (Paykull, 1798) / ?*P. annulatus* (Mannerheim, 1825)*	-	-	1	-	0-1-0-0	1
	Dermestidae	**-**	**1**	**-**	**-**	**0-1-0-0**	**1**
87	*Dermestes depressus* (Gebler, 1830)*	-	1	-	-	0-1-0-0	1
	Laemophloeidae	**-**	**-**	**-**	**1**	**0-0-2-0**	**2**
88	*Leptophloeus* cf. *alternans* (Erichson, 1846)*	-	-	-	1	0-0-2-0	2
	Chrysomelidae	**5**	**1**	**6**	**3**	**0-10-18-1**	**29**
89	*Chrysomela lapponica* Linnaeus, 1758	1	1	-	-	0-0-3-0	3
90	*Gastrophysa viridula* (De Geer, 1775)*	-	-	1	-	0-1-1-0	2
91	*Hydrothassa marginella* (Linnaeus, 1758)*	-	-	2	-	0-0-2-0	2
92	*Chrysolina graminis artemisiae* (Motschulsky, 1860)	1	-	-	-	0-2-0-0	2
93	*Gonioctena nivosa arctica* Mannerheim, 1853 / ?*G. linnaena* (Schrank, 1781)*	-	-	1	-	0-1-0-0	1
94	*Bromius obscurus* (Linnaeus, 1758)*	-	-	2	-	0-0-2-0	2
-	Chrysomelidae indet.	5	-	3	3	0-6-10-1	17

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Appendix—TABLE A1. (Continued)

No.	Family / Species	Nmin				No of fragments	
		S1	S2	S3	S4	H-P-E-O	In total
	Brentidae	**3**	**1**	**2**	**-**	**0-1-8-0**	**9**
95	*Eutrichapion rhomboidale* (Desbrochers des Loges, 1870)	2	-	2	-	0-0-6-0	6
96	*Eutrichapion* sp.1	-	1	-	-	0-0-1-0	1
97	*Hemitrichapion tschernovi* (Ter-Minasian, 1973)	1	-	-	-	0-0-1-0	1
-	Brentidae indet.	-	-	1	-	0-1-0-0	1
	Curculionidae	**11**	**4**	**14**	**14**	**6-9-59-1**	**75**
98	*Notaris (Erirhinus) aethiops* (Paykull, 1792)	1	-	-	-	1-0-0-0	1
99	*N. (Notaris) altaica* (Legalov, 1997)	-	-	-	1	0-0-1-0	1
100	*Tournotaris bimaculata* (Fabricius, 1787)	-	1	3	2	0-2-7-0	9
101	*Thryogenes nereis* (Paykull, 1800)	-	1	-	-	1-0-0-0	1
102	*Hylobius (Callirus) abietis* (Linnaeus, 1758)	-	1	-	-	0-0-1-0	1
103	*H. (C.) gebleri* Boheman, 1834*	-	-	1	1	0-0-1-1	2
104	*H. (Hylobius) excavatus* (Laicharting, 1781)	1	-	-	1	0-0-2-0	2
105	*Ceutorhynchus erysimi* (Fabricius, 1787)	1	-	-	-	0-0-1-0	1
106	*Glocianus* sp.*	-	-	-	1	0-0-2-0	2
-	Ceutorhynchini indet.	1	-	-	-	1-1-0-0	2
107	*Orobitis cyanea* (Linnaeus, 1758)*	-	-	1	-	0-0-1-0	1
108	*Tychius* sp.	1	-	-	-	0-1-0-0	1
109	*Trichalophus maklini* (Faust, 1890)	4	-	1	1	0-2-10-0	12
110	*Phyllobius (Pterygorrhynchus) contemptus* Schönherr, 1832*	-	-	1	-	0-0-1-0	1
111	*Ph. (Metaphyllobius) pomaceus* Gyllenhal, 1834	-	-	-	1	0-1-0-0	1
112	*Ph. (Subphyllobius) virideaeris* (Laicharting, 1781)	1	-	-	-	1-0-0-0	1
-	*Phyllobius* sp.	-	-	1	-	0-0-1-0	1
113	*Otiorhynchus (Amosilnus) grandineus* Germar, 1823	1	-	3	2	0-0-10-0	10
114	*O. (A.) oberti* (Faust, 1887)*	-	-	-	1	0-1-0-0	1
115	*O. (Podonebistus)* af. *ursus* Gebler, 1844	-	1	-	-	0-0-1-0	1
116	*O. (Prilisvanus) krattereri* Boheman, 1842*	-	-	1	-	0-0-1-0	1
117	*O. (Stupamacus) politus* Gyllenhal, 1834	1	-	3	2	1-1-8-0	10
118	*Polydrusus amoenus* (Germar, 1823)	-	-	-	1	0-0-2-0	2
-	Curculionidae indet.	3	1	4	1	1-0-10-0	11
	Scolytidae	**3**	**2**	**-**	**2**	**0-0-8-0**	**8**
119	*Phloeotribus spinulosus* (Rey, 1883)	3	2	-	-	0-0-6-0	6
120	*Polygraphus polygraphus* (Linnaeus, 1758)	-	-	-	1	0-0-1-0	1
-	Scolytidae indet.	-	-	-	1	0-0-1-0	1
-	Coleoptera indet.	3	-	5	2	2-1-14-13	30
	Coleoptera in total	**120**	**24**	**69**	**55**	**17-92-279-17**	**405**

Notes: Nmin—minimum number of individuals. S1–S4—samples. Type of fragments: H—head, P—pronotum, E—elytron, O—other. *recorded for the Pleistocene of Western Siberia for the first time.