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First records of sub-fossil insects from Quaternary deposits in the southeastern part of West Siberia, Russia

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A B S T R A C T

Data are presented on species composition in Bun'kovo taphocoenosis at the Chik River, Novosibirsk, Russia (55°03′46″ N, 82°29′50″ E) with conventional radiocarbon dating ca 11,550 ± 125 ^{14}C BP. The entomofauna complex is unique by species composition. 90 species of Coleoptera from 15 families, 4 species from 3 families of Hymenoptera (Pamphiliidae, Formicidae, Sphecidae) and pupae of Diptera are recorded. Amongst Coleoptera the most numerous is Curculionidae represented with 41 species, especially *Otiorhynchus* – 10 species and *Stephanocleonus* – 8 species, Carabidae – 21 species and Chrysomelidae – 7 species. Among the species recorded, *Otiorhynchus karkaralensis* (Curculionidae) predominates with 250 specimens present. 80% of the species are not known for this territory at the present time. Species typical of open landscapes such as boggy tundra, cold northern and warm southern steppes are included in the taphocoenosis. Forest species are rare, and humid thermophilic species are completely absent. The Bun'kovo taphocoenosis is closely related to entomofaunal complexes found in older deposits (28,000–24,000 BP) in central part of West Siberia and the Urals based on species composition, but differs in the abundance of *Stephanocleonus*. Similar-age taphocoenosis from central and northern parts of West Siberia are contrasted with Bun'kovo, highlighting the absence of xerophilic species. Based on the beetle species composition, cold and dry climate conditions (at least 4–5 C° cooler than present) and prevalence of dry tundra-steppe landscapes are re-constructed at Bun'kovo. This conclusion is reinforced by palynological data from nearby sites in the southern part of West Siberia. Analysis of modern distribution ranges of the species found in the taphocoenosis shows that species have shifted dramatically from the late Pleistocene to present time because of increasing warmth and humidity during the Holocene. The contemporary distributions include shifts to the north in meso-hygrophilous and mesophilous species, to the east or south in xerophilous species, and to northern, eastern or southern directions in hygrophilous species.

1. Introduction

Quaternary Coleoptera are the most sensitive indicators of paleoclimatic and paleolandscape changes, and therefore are actively used in paleoecological and paleogeographic investigations (Elias, 1994; Sher et al., 2005). Good preservation of isolated beetle parts, the presence of diagnostic characters necessary for identification of species and genera, and the high level of species richness and ecological diversity provides a high level of resolution for paleoecological investigations. Although the relatively low strength of chitin fragments may cause their destruction or reburial (Burkanova et al., 2010), the probability of such reburial is low in comparison with osseous remains of mammals, seeds and plant macrofossils, especially pollen and spores of plants.

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Quaternary insects of many regions in North Eurasia have not been completely studied, despite the importance of broad geographical sampling in efforts to reconstruct accurate paleoclimate sequences. The West-Siberian Plain is a unique region for paleoecological investigations. It encompasses a large area (2500 km from north to south, 1900 km from west to east) located far from maritime influences, and local elevation is relatively constant (not more than 100 m variation). Therefore, zonality is quite regular, depending mostly on latitude and the global climate. Other studies of insects from Pleistocene and Holocene deposits in the central part of Northern Eurasia have been limited to the northern and central parts of the West-Siberian Plain, territories near the Urals, and the Bolshezemelskasya tundra (Kiselev, 1988; Zinovyev, 1997, 2003, 2006, 2008, 2011; Smirnov et al., 1999; Kosintsev et al., 2004), with no publications on Quaternary insects from the southern part of the West-Siberian Plain.

Regular investigations of sub-fossil insect remains from Quaternary locations in the southern part of West-Siberian Plain were started in 2012. One of the best deposits of entomological material was found at the Bun'kovo locality on the Chik River, located in Novosibirsk on the upper Ob River basin (Tsepelev et al., 2013; Tshernyshev et al., 2013). 500 g of dry plant detritus was taken from sample layer for determination of age. An examination of the detritus using a QUANTULUS-1220 (Liquid Scintillation Counters) determined that the conventional radiocarbon age of the deposit was ^{14}C 11,550 ± 125 yrs (COAH-8806) or calibrated age was 13,695–13,108 BP (95.4% probability). This date is close to Pleistocene–Holocene transition. According to regional stratigraphic scale it is Late Pleistocene, which is finished 10300–10200 BP (Arkhipov, 1997). Vasiliev et al. (2002) consider this time as Allerod, but Berger (1990) considers it as Dryas.

2. Insects in taphocoenosis of similar-age deposits of West-Siberian Plain

Four localities with similar-age deposits of insects have been described from West Siberia (Table 1, Fig. 1). The first locality is Ngoyun, located on the Yamal peninsula, while the remaining three localities are Zelyoniy Ostrov, Agan and Kul'egan located within the middle Ob River basin. Data on fossil insects from the new locality, Bun'kovo, represent a new region located in the upper Ob River basin. Material from an additional 6–7 localities, in the region around Kizikha and Ust'yanka, were collected in 2013 and are currently being examined.

Entomofaunal complexes from similar-age deposits of the Ngoyun locality (Erokhin and Zinovyev, 1991) completely coincide with the extant beetle faunas described for this region (Ryabitsev, 2000; Zinovyev and Olshvang, 2003; Chernov et al., 2014) and comprise several arctic species, such as *Pterostichus sublaevis*, *P. costatus*, and *Curtonotus alpinus*. Similarly, the same pattern of extant beetle species were represented in localities found in the middle Ob River basin (Zelenyi Ostrov and Kulyegan-2241 localities) (Zinovyev and Nesterkov, 2003; Zinovyev, 2005). Moderate differences from the modern faunas of the Glubokii Sabun River valley are found for the entomofaunal complex at the Zelenyi Ostrov locality. In particular, fragments of beetles currently distributed northwards from the locality, such as *Carabus odoratus* and *Diacheila polita*, are recorded. Based on the distribution of extant beetle species, we can infer that this fossil deposit indicates a much colder climate at this locality than the present climate.

A similar pattern was found at the Kul'egan-2241 locality (Zinovyev, 2005), where many fossils are still found in the Kul'egan River valley, such as *Pterostichus* (*Cryobius*) *brevicornis* and *D. mannerheimii*. Some ground beetle species suggest a colder climate occurred in the past, including: *Dicheirotrichus mannerheimii*, *Diacheila polita*, *Elaphrus lapponicus* and *Curtonotus torridus*, because they are distributed far to the north of this region (Kryzhanovskii et al., 1995).

From the lower part of the section located in the upper stream of Agan River (Agan-4068/2) beetle faunas considered subarctic and arctic were found, although they were very low in abundance in the sample. These included the ground beetle species *Pterostichus vermiculosus*, *P. costatus*, *Curtonotus alpinus* and the rove beetle *Tachinus arcticus*. These species are currently limited to the tundra and mountain tundra zones.

Botanical data gained from the samples at Kul'egan-2241, Agan-4068/2 and Ngoyun did not corroborate conclusions based on the entomological data (Erokhin and Zinovyev, 1991; Zinovyev, 2005). Coniferous pollen, *Picea* sp. from spruce–birch associations, was recorded in low abundance from Agan-4068/2 (about 12–10,000 years). In contrast, no coniferous pollen was recorded at Kul'egan-2241, even though pine pollen can disperse over hundreds of kilometers. This would suggest that coniferous forests were absent from the Kul'egan River during the end of the late glacial, and subsequent warming during the Dryas and pre-boreal witnessed widespread colonization of parvifoliate trees and their associated insect complexes. Finally, forest-tundra habitat with birch-fir forests and yernik and meadow-bog vegetation was reconstructed for the Ngoyun locality on the Yuribei River (Korona et al., 2014).

Thus, similar-age deposits in the central and northern parts of West-Siberian Plain, suggest: 1. Beetle assemblages from the deposits of similar age characterize cold climate conditions in comparison with modern climate at these sites; these differences could be expressed as a depression of average July temperatures by several degrees, geographical habitat shift of approximately

Table 1
Similar-age deposits of Late Pleistocene insects in West Siberia.

		Coordinates		Taphonomic type	Radiocarbon dates, years BP	Citation
		N	E			
1	Ngoyun	68°32′	72°06′	floodplain	Layer 3 – 11,226 ± 172 (IPAE-176), layer 2 – 10,688 ± 240 (IPAE-175) Layer 3 (depth 3.1–3.15 m) 11,000 ± 50 (Beta-345169), layer 5 (depth 5.75 m) 12,000 ± 50 (Beta-345168)	Zinovyev, 2008 Korona et al., 2014
2	Zelyoniy Ostrov	62°29′	81°51′	floodplain	10,780 ± 10 (Le-8972)	Borodin et al., 2013
3	Agan-4068/2	62°06′	77°55′	floodplain	Layer 3 (top), 9770 ± 300 (IPAE-97), layer 3 (bottom) – 11,400 ± 350 (IPAE-98)	Zinovyev, 2005
4	Kul'egan-2241	60°30′	75°45′	floodplain	10,700 ± 325 (IPAE-94)	Zinovyev, 2005
5	Bun'kovo	55°03′46″	82°29′50″	floodplain	11,550 ± 125 BP (COAH-8806)	Tsepelev et al., 2013; Tshernyshev et al., 2013
6	Kizikha-1	51°26′	81°36′	floodplain	13,455 ± 150 BP (SPb-1347)	under preparation
7	Ust'yanka	51°16′	81°29′	floodplain	10,150 ± 200 BP (SPb-1345); 10,806 ± 100 BP (SPb-1346)	under preparation

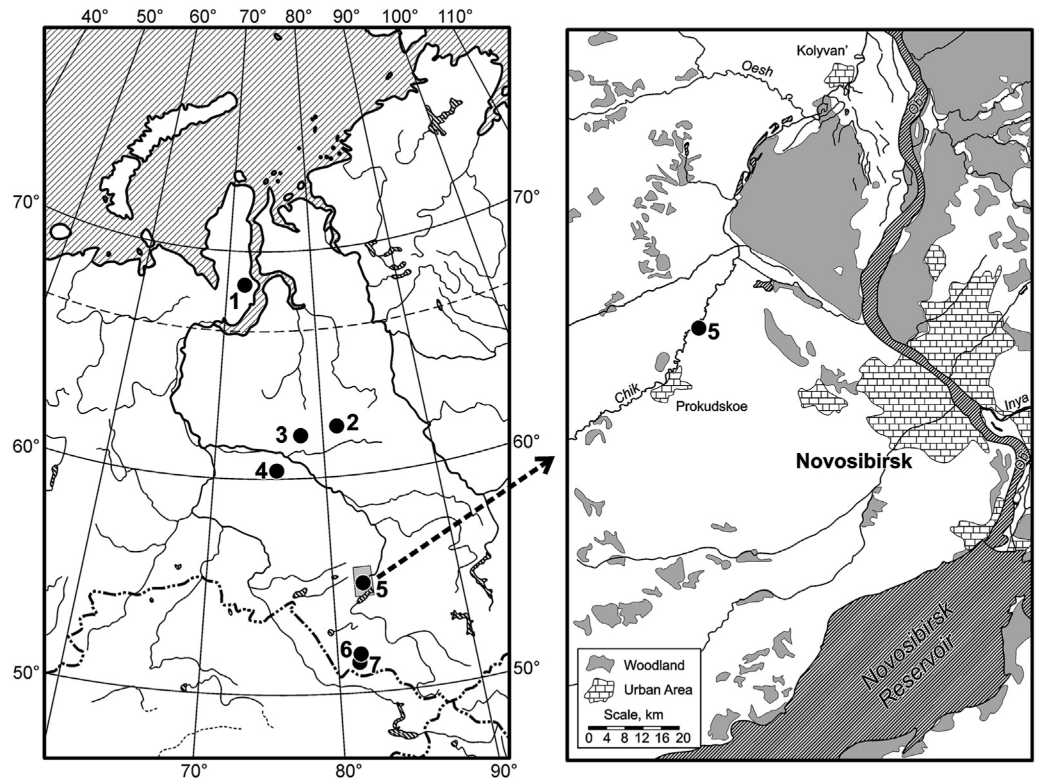

Fig. 1. Locality map of Bun'kovo and similar-age deposits of West Siberia. 1 – Ngoyun, 2 – Zelyoniy Ostrov, 3 – Agan, 4 – Kul'egan-2241, 5 – Bun'kovo, 6 – Kizikha, 7 – Ust'yanka.

100–300 km shifted to the south, and distinct faunal changes with the inclusion of arctic beetle complexes in areas currently occupied by taiga forests; 2. Incompatibility of entomological and paleobotanical data, with the latter reflecting warmer conditions. One explanation is that climate change and distributional changes were extremely rapid, with differential rates of change in plant and insect communities. A second possibility is that the presence of arctic beetle faunas could be misleading. For these beetle species, habitats such as birch-fir forests are equivalent to tundra.

3. Regional setting

Bun'kovo is situated in the forest-steppe zone along the upper tributary of the Ob' River, at the Chik River, near Bun'kovo Village (55°03′46″ N, 82°29′50″ E). Local vegetation is characterized by a combination of birch groves, grass–forb and grass meadows. A continental climate is found at the site, with extreme alterations of daily, seasonal, and annual air temperatures, and annual precipitation of 400–450 mm (about 70% during the warm season). According to long-term observations, average July temperatures are +18.5–19 °C, and the coldest month, January, has averages of −19.5 to −20 °C (Kravtsov, 2002).

Quaternary sediments are widespread and include rich organic material. The Ob' River region has excellent conditions for paleoentomological research, as well as nearby sites such as the Chik River. To date, mainly fossils of mammals, molluscs and paleobotanic material including seeds and plant macrofossils have been studied from this region (Nikitin, 1940; Golubeva, 1960; Bukreeva, 1965; Arkhipov, 1973; Panychev, Orlova, 1973; Vangengeim, 1975; Panychev, 1979; Krivonogov, 1988; Volkova, Klimantov, 1988; Zykin et al., 1989; Volkova, Kul'kova, 1994). Other outcrops from the Chik River have only been examined for large mammal fossils, particularly at sites near Kazakovo Village (Lobachev et al., 2011, 2012).

4. Materials and methods

A vertical section in a 7.6 m cliff is the first terrace above the flood plain of the Chik River near Bun'kovo Village was carefully excavated in 2012, and a layer with a large chitin inclusion was isolated (Table 2, Fig. 2).

Table 2
Description of the section in a 7.6 m cliff on the first terrace above the flood plain of the Chik River near Bun'kovo Village.

Nr of layer	Depth from the surface, m	Description
1	0.0–0.2	Modern soil
2	0.2–0.65	Sandy loam
3	0.65–0.9	Peaty sandy loam with plant macrofossil remains
4	0.9–1.2	Peaty sandy loam with chalkstone inclusions
5	1.2–1.7	Paleosoil with traces of alkalinization
6	1.7–2.3	Dense sandy loam with inclusions of fossilized chalkstone
7	2.3–2.8	Fine-dispersed sandy loam with interlaying of ferrous sandy loam
8	2.8–3.3	Grey-beige loam
9	3.3–3.65	Ferrous loam
10	3.65–7.05	Fine-dispersed sand with inclusions of ferrugination and dark thin layers of sludgy sand
11	7.05–7.6	Intermixed sand with interlaying of dark-glaucous peaty clay filled with detritus and insect remains

Samples for entomological analysis were extracted from the layer after geological description of the locality. Extracted sediment was washed out in a sieve with 0.25 mm mesh; plant detritus from this wash was placed in a plastic bag and labeled with the location, depth of sample and its number. Subsequent processing of the insect sample included drying, separation through a soil sieve column, and then separation of insect sub-fossils under a binocular microscope. Each sub-fossil fragment was studied individually. After washing, all extracted fragments were mounted on 14 × 6 mm entomological cards and pinned as modern insect specimens. The material was identified using taxonomic references for extant species and in comparison to collections held at the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia (ISEA) and Zoological Institute, Saint-Petersburg, Russia (ZISP).

While compiling the list of species, the minimum number of individuals for each species was estimated to ascertain their local abundance (Kiselev, 1987). This material is now being stored at the Institute of Systematics and Ecology of Animals.

5. Results

5.1. Taxonomic composition

At least 95 insect species, mainly Coleoptera (90 species) (Table 3) were discovered at the Bun'kovo site. The remaining taxa include 4 species from 3 families of Hymenoptera (Pamphiliidae, Formicidae, Sphecidae) and a single species of a pupal Diptera. Coleoptera are represented by 15 families, of which the most species rich is Curculionidae – 41 species (43% of all insects recorded), followed by Carabidae – 21 species (22%) and Chrysomelidae – 7 species (7%). The remaining 12 families, including Dytiscidae, Helophoridae, Hydrophilidae, Leiodidae, Silphidae, Staphylinidae, Scarabaeidae, Byrrhidae, Heteroceridae, Elateridae, Coccinellidae and Tenebrionidae, are represented by 1–4 species each. The most species rich genera represented are *Otiorhynchus* (Curculionidae) – 10 species, *Stephanocleonus* (Curculionidae) – 8 species, *Phyllobius* (Curculionidae) and *Bembidion* (Carabidae) – 5 species each.

Table 3
List of insect species of Bun'kovo taphocoenosis.

Family	Nr[a]	Species	Type of fragment									Min number of specimens
			HD	PR	LP	RP	EL	LE	RE	UN	Other	
Coleoptera												
Dytiscidae	1	*Ilibius*? sp.	–	–	–	–	–	1	–	–	–	1
	2	*Hydroporus*? sp.	–	–	–	–	–	–	–	1	–	1
	3	Dytiscidae indet.	1			1		1	1	3	1	1
Carabidae	4	*Pelophila borealis* (Paykull, 1790)	1	–	–	–	–	–	–	–	–	1
	5	*Notiophilus* sp.	1	–	–	–	–	–	–	–	–	1
	6	*Elaphrus sibiricus* Motschulsky, 1844	–	1	–	–	–	–	–	–	–	1
	–	*Elaphrus* sp.	–	–	–	–	–	–	–	1	–	1
	7	*Clivina fossor* (Linnaeus, 1758)	1	4	–	–	–	–	–	1	–	4
	8	*Bembidion almum* J.R. Sahlberg, 1900	–	–	–	–	–	1	–	–	–	1
	9	*Bembidion difficile* (Motschulsky, 1844)	–	–	–	–	–	1	–	–	–	1
	10	*Bembidion humerale* Sturm, 1825	–	–	–	–	–	1	–	–	–	1
	11	*Bembidion kokandicum* Solsky, 1874	–	–	–	–	–	1	2	–	–	2
	12	*Bembidion* cf. *infuscatum* Dejean, 1831	–	–	–	–	–	1	–	–	–	1
	–	*Bembidion* spp.	1	3	–	–	–	–	–	–	–	3
	13	*Pogonus punctulatus* Dejean, 1828	–	–	–	1	–	1	–	–	–	1
	–	*Pogonus* spp.	–	1	–	–	–	2	1	–	–	2
	14	*Patrobus ?septentrionis* Dejean, 1828	2	–	–	–	–	–	1	–	–	2
	15	*Patrobus* sp.	–	–	–	–	–	–	1	–	–	1
	16	*Poecilus ravus* (Lutshnik, 1922)	–	8	–	–	–	2	3	–	–	8
	17	*Poecilus ?major* (Motschulsky, 1844)	–	–	–	–	–	1	1	–	–	1
	–	*Poecilus* (*Derus*) sp.	–	–	1	–	–	–	1	–	–	2
	18	*Pterostichus* (*Cryobius*) sp.	–	–	–	–	–	1	–	–	–	1
	–	*Pterostichus* sp.	–	–	1	–	–	–	–	–	–	1
	19	*Agonum* sp.	–	1	–	–	–	–	–	–	–	1
	20	*Curtonotus* sp.	–	1	–	–	–	–	–	–	–	1
	21	*Harpalus amputatus* (Say, 1830)	–	1	–	–	–	–	–	–	–	1
	22	*Harpalus* spp.	9	1	–	–	–	–	1	–	–	9
	23	*Cymindis arctica* Kryzhanovsky et Emetz, 1979	–	1	–	–	–	–	–	–	–	1
	24	*Cymindis* spp.	3	–	–	–	–	–	–	–	–	3
	–	Carabidae indet.	54	–	7	–	–	3	–	60	10	54
Helophoridae	25	*Helophorus sibiricus* (Motschulsky, 1860)	–	–	–	–	–	–	–	–	1	1
Hydrophilidae	26	*Hydrobius fuscipes* (Linnaeus, 1758)	–	1	–	–	–	–	1	–	1	1
Leiodidae	27	*Leiodes* sp.	–	–	–	–	–	–	1	–	–	1
	–	Leiodidae indet.	–	–	–	–	–	1	–	–	–	1
Silphidae	28	*Aclypea sericea* (Zubkov, 1833)	–	–	1	–	–	1	–	–	–	1
	29	*Aclypea opaca* (Linnaeus, 1758)	–	–	–	–	–	–	1	–	–	1
	30	*Thanatophilus dispar* (Herbst, 1793)	–	1	–	–	–	–	–	–	–	1
	–	Silphidae indet.	–	–	–	–	–	–	1	–	–	1
Staphylinidae	31	*Tachinus* sp.	–	–	–	–	–	–	1	–	–	1
	–	Staphylinidae indet.	1	1	–	–	–	–	–	1	–	1
Scarabaeidae	32	*Aphodius* sp.	2	2	–	–	–	2	1	–	–	2
	33	*Aegialia* sp.	1	–	–	–	–	3	2	–	–	3
	34	*Psammodius* sp.	1	1	–	–	–	–	–	–	–	1
Byrrhidae	35	*Morychus ostasiaticus* Tshernyshev, 1997	–	1	–	–	–	2	4	–	–	4
	36	*Lamprobyrrhulus nitidus* (Schaller, 1783)	–	3	–	–	–	1	3	–	–	3
	37	*Cytilus sericeus* (Forster, 1771)	–	–	–	–	–	–	2	–	–	2
	38	*Porcinolus murinus* (Fabricius, 1794)	–	1	–	–	–	–	2	–	–	2

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Table 3 (*continued*)

Family	Nr[a]	Species	Type of fragment									Min number of specimens
			HD	PR	LP	RP	EL	LE	RE	UN	Other	
	–	Byrrhidae indet.	–	3	–	–	–	1	2	–	3	3
Heteroceridae	39	*Heterocerus fenestratus* (Thunberg, 1784)	–	–	–	–	–	1	–	–	–	1
Elateridae	40	*Hypnoidus* sp.	–	–	–	–	–	–	1	–	–	1
	–	Elateridae indet.	–	1	–	–	–	–	–	1	–	1
Coccinellidae	41	*Coccinella ?nivicola* Mulsant, 1850	–	–	–	–	–	–	1	–	–	1
	–	*Coccinella* sp.	–	2	–	1	–	–	–	–	–	2
Tenebrionidae	42	*Centorus* (*Belopus*) sp.	4	7	–	–	–	3	1	–	–	7
Chrysomelidae	43	*Plateumaris* sp.	–	–	–	–	–	–	–	1	–	1
	44	*Chrysolina ?perforata* (Gebler, 1830) (or *Ch. ?purpurata* (Faldermann, 1833))	1	–	–	1	–	–	–	–	–	1
	–	*Chrysolina* spp.	–	–	2	1	–	–	–	–	–	2
	45	*Chrysomela* sp.	–	–	–	–	–	–	–	–	1	1
	46	*Colaphellus* sp.	–	1	–	–	–	–	–	–	–	1
	47	*Crosita* ? sp.	–	–	1	–	–	–	–	–	–	1
	48	*Phratora*? sp.	–	2	–	–	–	–	–	–	–	2
	49	Alticinae indet.	–	–	–	–	–	1	–	–	–	1
	–	Chrysomelidae indet.	1	2	–	–	–	–	2	–	1	2
Curculionidae	50	*Tournotaris bimaculata* (Fabricius, 1792)	7	17	–	–	1	12	15	3	–	17
	51	*Notaris aethiops* (Fabricius, 1793)	4	3	–	–	–	1	–	–	–	4
	52	*Thryogenes* sp.	–	1	–	–	–	–	–	–	–	1
	53	*Lepyrus nordenskioldi* Faust, 1885	1	1	–	–	–	–	–	–	–	1
	54	*Stephanocleonus luctuosus* Faust, 1895	1	–	–	–	–	–	–	–	–	1
	55	*Stephanocleonus suvorovi* Legalov, 1999	3	–	–	–	–	–	–	–	–	3
	56	*Stephanocleonus foveifrons* Chevrolat, 1873	3	–	–	–	–	–	–	–	–	3
	57	*Stephanocleonus eruditus* Faust, 1890	1	–	–	–	–	–	–	–	–	1
	58	*Stephanocleonus isochromus* Suvorov, 1912	11	–	–	–	–	1	–	–	–	11
	59	*Stephanocleonus leucopterus* (Fischer von Waldheim, 1823)	1	–	–	–	–	–	–	–	–	1
	60	*Stephanocleonus prasolovi* Ter-Minassian, 1990	1	–	–	–	–	–	–	–	–	1
	61	*Stephanocleonus tschuicus* Suvorov, 1912	1	–	–	–	–	–	–	–	–	1
	–	*Stephanocleonus* sp.	–	2	–	–	–	–	–	5	–	5
	62	*Coniocleonus astragali* Ter-Minassian and Korotyaev, 1977	1	–	–	–	–	–	–	–	–	1
	–	Cleonini indet.	–	1	–	–	–	–	1	1	2	1
	63	*Aulacobaris lepidii* (Germar, 1824)	1	1	–	–	–	–	–	–	–	1
	64	*Eubrychius velutus* (Beck, 1817)	–	–	–	–	–	1	–	–	–	1
	65	*Tychius uralensis* Pic, 1902	1	1	–	–	–	–	–	–	–	1
	66	*Eremochorus mongolicus* (Motschulsky, 1860)	1	–	–	–	–	–	–	–	–	1
	67	*Hypera ornata* (Capiomont, 1868)	4	7	–	–	–	–	–	–	–	7
	68	*Hypera* sp.	1	–	–	–	–	–	–	–	–	1
	69	*Trichalophus biguttatus* (Gebler, 1832)	3	–	–	–	–	–	–	1	–	3
	70	*Sitona ovipennis* Hochhut, 1851	7	–	–	–	–	–	1	–	–	7
	71	*Sitona suturalis* Stephens, 1831	1	–	–	–	–	–	–	–	–	1
	72	*Chlorophanus sibiricus* Gyllenhal, 1834	3	–	–	–	–	–	–	–	–	3
	73	*Tanymecus palliatus* (Fabricius, 1793)	2	–	–	–	–	–	–	1	–	2
	74	*Paophilus hispidus* (Faust, 1882)	–	–	–	–	–	1	–	–	–	1
	75	*Eusomatus obovatus* (Boheman, 1839)	–	–	–	–	–	1	1	–	–	1
	76	*Phyllobius femoralis* Boheman, 1843	–	–	–	–	–	1	2	–	3	2
	77	*Phyllobius ? fumigatus* Boheman, 1843	1	–	–	–	–	–	–	–	–	1
	78	*Phyllobius pomaceus* Gyllenhal, 1834	1	–	–	–	–	–	–	–	–	1
	79	*Phyllobius thallasinus* Gyllenhal, 1834	–	–	–	1	–	–	–	–	–	1
	80	*Phyllobius virens* (Faust, 1890)	2	–	–	–	–	–	–	–	–	2
	–	*Phyllobius* sp.	–	–	–	–	–	1	1	–	–	1
	81	*Otiorhynchus wittmeri* Legalov, 1999	8	–	–	–	–	2	1	–	–	8
	82	*Otiorhynchus politus* Gyllenhal, 1834	4	6	–	–	–	1	1	2	–	6
	83	*Otiorhynchus arcticus* (Fabricius, 1780)	–	7	–	–	–	1	2	–	–	7
	84	*Otiorhynchus subocularis* Arnoldi, 1975	–	1	–	–	–	1	1	–	–	1
	85	*Otiorhynchus perplexus* Gyllenhal, 1834	5	5	–	–	–	–	–	–	–	5
	86	*Otiorhynchus obscurus* Gyllenhal, 1834	1	1	–	–	–	–	–	–	–	1
	87	*Otiorhynchus altaicus* Stierlin, 1861	–	7	–	–	–	–	–	–	–	7
	88	*Otiorhynchus karkaralensis* Bajtenov, 1974	250	130	–	–	5	73	49	62	25	250
	89	*Otiorhynchus kasachstanicus* Arnoldi, 1964	–	3	–	–	–	–	–	–	–	3
	90	*Otiorhynchus relicinus* Arnoldi, 1975	–	10	–	–	–	–	–	–	–	10
	–	Curculionidae indet.	2	–	–	–	–	–	–	–	–	2
–	–	Coleoptera indet.	3	2	–	–	–	–	–	8	17	3
Hymenoptera												
Pamphiliidae	91	*Cephalcia lariciphila* (Wachtl, 1898)	1	–	–	–	–	–	–	–	–	1
Formicidae	92	*Formica* cf. *fusca* Linnaeus, 1758	2	–	–	–	–	–	–	–	–	2
	93	*Formica* sp.	1	–	–	–	–	–	–	–	–	1
Sphecidae	94	*Crabro* sp.	1	–	–	–	–	–	–	–	–	1
–	–	Hymenoptera indet.	2	6	–	–	–	–	–	4	3	6
Diptera												
–	95	Diptera indet.	–	–	–	–	–	–	–	–	7	7
–	–	Insecta indet.	2	2	–	–	–	–	–	6	73	2

Abbreviations: HD – head, PR – pronotum, LPR – left part of pronotum, RPR – right part of pronotum, EL (left + right elytra), LE – left elytron, RE – right elytron, UN – underside, sensu Warner et al. (1988).

[a] Undetermined species are not numbered if the fragments may be attributed to any previous species.

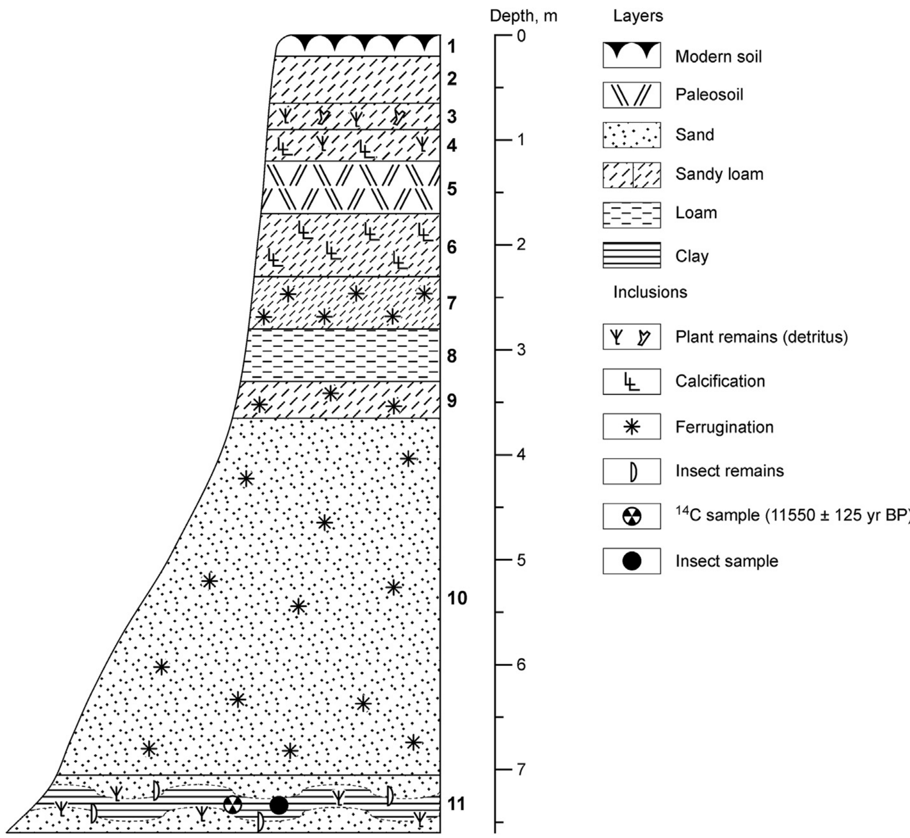

Fig. 2. Scheme of Bun'kovo vertical section at the Chik River.

The most abundant groups in Bun'kovo taphocoenosis are also Curculionidae – about 390 specimens (67% of all insects found) and Carabidae – about 106 specimens (18%). All other insect specimens together represent about 15% of the abundance. The most abundant species is *Otiorhynchus karkaralensis* (Curculionidae) – about 250 specimens (43%), followed by *Tournotaris bimaculata* (Curculionidae) – 17 specimens (3%). 10 additional species, including *Poecilus ravus* (Carabidae), *Centorus* (*Belopus*) sp. (Tenebrionidae), *Stephanocleonus isochromus*, *Hypera ornata*, *Sitona ovipennis*, *Otiorhynchus wittmeri*, *O. politus*, *O. arcticus*, *O. altaicus*, *O. relicinus* (Curculionidae), represent 1% each of the total abundance. All other species are recorded from single sub-fossil fragments.

5.2. Ecological groups

Both terrestrial and aquatic insects are represented in the taphocoenosis. However, only five fragments represent aquatic insects, including predatory Dytiscidae (*Hydroporus* sp., Ilybius sp.) and saprotrophic (detritophage imago) *Helophorus sibiricus* (Helophoridae), *Hydrobius fuscipes* (Hydrophilidae). *Helophorus sibiricus* is distributed in high latitudes and inhabits in temporal water ponds, *Hydrobius fuscipes* is a polyzonal species occurring in many types of stagnant and drift water reservoirs.

Terrestrial insects are represented mainly by phytophagous species (more than 60% of species and about 70% of the total specimens), either associated with vascular plants (Curculionidae, Chrysomelidae, Silphidae – *Aclypea*, Pamphiliidae) or mosses (Byrrhidae). Curculionidae and Chrysomelidae are dominant polyphagous species in the sample, while several oligophagous species (*Colaphellus* sp. and *Aulacobaris lepidii* develop on Brassicaceae (Zaslavskij, 1956); *Hypera ornata* develops on *Astraganus* spp. and *Oxytropis* spp. (Khruleva and Korotyaev, 1999) and three monophagous species (*Eubrychius velutus* develops on *Myriophyllum* spp. (Egorov, 1988), *Tychius uralensis* on *Caragana* spp. (Korotyaev, 1990), and *Cephalcia lariciphila* – on *Larix* spp.) were also present. The sub-fossils include an abundance of species whose larvae develop in plant roots (*Otiorhynchus*), and also species whose larvae develop in plant stems (*Tournotaris bimaculata*), leaves (*Hypera ornata*, *Chrysolina*), acerose leaves (*Cephalcia lariciphila*) and in seeds (*Tychius uralensis*).

Predatory insects are represented mainly by Carabidae, and in single specimens of Staphylinidae, Coccinellidae, and Sphecidae. Imagos of *Harpalus* and *Curtonotus* (Carabidae) were found, as well as ants (Formicidae) which consume both animal and plant food.

Terrestrial saprotrophs are represented by several specimens: *Thanatophilus dispar* (Silphidae), *Aphodius*, *Aegialia*, *Psammodius* (Scarabaeidae). Amongst them, only *Thanatophilus* is a scavenger. A single micetophage, *Leiodes* sp. (Leiodidae), is recorded.

Most of the species at Bun'kovo are known from terrestrial habitats, including soil-dwelling species. Herbivorous beetles that forage on plants include Byrrhidae, some of leaf-beetle species of *Chrysolina*, and the weevils *Otiorhynchus*, *Stephanocleonus*, *Coniocleonus*, and *Eremochorus*. The beetle species present that inhabit plants are mainly associated with grasses. Several *Salix* specialists are present, including *Lepyrus nordenskioldi* (Korotyaev, 1980) and *Chlorophanus sibiricus* (Curculionidae) (Legalov, 1998), and only *Cephalcia lariciphila* (Pamphiliidae) is associated with trees.

5.3. Extant distribution and biotope preferences

Recent entomophauna of the upper Ob River basin strongly differ from the entomofauna collected in the Bun'kovo taphocoenosis (Legalov and Opanassenko, 2000; Dudko and Lyubechanskii, 2002, Bespalov et al., 2010; Legalov, 2010). Most sub-fossil species are absent from the entire upper Ob River basin (Table 4). A few species have their distributional limits in the region and are extremely rare. Only 18% of polyzonal or ecologically valent species are typical residents of the territory, including: *Clivina fossor* (Carabidae), *Hydrobius fuscipes* (Hydrophilidae), *Aclypea opaca*, *Thanatophilus dispar* (Silphidae), *Lamprobyrrhulus nitidus*, *Cytilus sericeus* (Byrrhidae), *Heterocerus fenestratus* (Heteroceridae), *Tournotaris bimaculata*, *Sitona suturalis*, *Tanymecus palliatus*, *Phyllobius pomaceus*, and *Ph. thallasinus* (Curculionidae) (Kryzhanovskii et al., 1995; Tshernyshev, 2006, 2012; Legalov, 2010). The remaining species have their centers of distribution far from Bun'kovo.

Table 4
Modern distribution of species found in Bun'kovo taphocoenosis.

Species	Environs of Bun'kovo (Kochenevskij raion of Novosibirskaya Oblast)	South of West Siberia	Center of distribution (in comparison with Bun'kovo site)
Pelophila borealis (Paykull, 1790)	–	+	North
Elaphrus sibiricus Motschulsky, 1844	–	–	East
Clivina fossor (Linnaeus, 1758)	+	+	+
Bembidion almum J.R. Sahlberg, 1900	–	–	S
Bembidion difficile (Motschulsky, 1844)	–	+	North
Bembidion humerale Sturm, 1825	–	+	West
Bembidion kokandicum Solsky, 1874	–	–	South
Pogonus punctulatus Dejean, 1828			South
Patrobus septentrionis Dejean, 1828	+	+	North
Poecilus ravus (Lutshnik, 1922)	–	–	East
Poecilus major (Motschulsky, 1844)	–	–	East
Harpalus amputatus (Say, 1830)	–	–	East
Cymindis arctica Kryzhanovsky et Emetz, 1979	–	–	East
Helophorus sibiricus (Motschulsky, 1860)	–	–	North
Hydrobius fuscipes (Linnaeus, 1758)	+	+	+
Aclypea sericea (Zubkov, 1833)	–	–	South
Aclypea opaca (Linnaeus, 1758)	+	+	+
Thanatophilus dispar (Herbst, 1793)	+	+	+
Morychus ostasiaticus Tshernyshev, 1997	–	+	East
Lamprobyrrhulus nitidus (Schaller, 1783)	+	+	+
Cytilus sericeus (Forster, 1771)	+	+	+
Porcinolus murinus (Fabricius, 1794)	+	+	South
Heterocerus fenestratus (Thunberg, 1784)	+	+	+
Coccinella nivicola Mulsant, 1850	–	–	East
Centorus (*Belopus*) sp.	–	?	?South
Chrysolina perforata (Gebler, 1830)	–	–	East
Tournotaris bimaculata (Fabricius, 1792)	+	+	+
Notaris aethiops (Fabricius, 1793)	–	+	North
Lepyrus nordenskioldi Faust, 1885	–	–	North
Stephanocleonus luctuosus Faust, 1895	–	–	East
Stephanocleonus suvorovi Legalov, 1999	–	–	South
Stephanocleonus foveifrons Chevrolat, 1873	–	–	East
Stephanocleonus eruditus Faust, 1890	–	–	East
Stephanocleonus isochromus Suvorov, 1912	–	–	South
Stephanocleonus leucopterus (Fischer von Waldheim, 1823)	–	+	East
Stephanocleonus prasolovi Ter-Minassian, 1990	–	–	South
Stephanocleonus tschuicus Suvorov, 1912	–	–	South
Coniocleonus astragali Ter-Minassian et Korotyaev, 1977	–	–	East
Aulacobaris lepidii (Germar, 1824)	+	+	+
Eubrychius velutus (Beck, 1817)	+	+	+
Tychius uralensis Pic, 1902	–	–	South
Eremochorus mongolicus (Motschulsky, 1860)	–	–	South
Hypera ornata (Capiomont, 1868)	–	–	North
Trichalophus biguttatus (Gebler, 1832)	–	–	East
Sitona ovipennis Hochhut, 1851	–	–	North
Sitona suturalis Stephens, 1831	+	+	+
Chlorophanus sibiricus Gyllenhal, 1834	+	+	East
Tanymecus palliatus (Fabricius, 1793)	+	+	+
Paophilus hispidus (Faust, 1882)	–	–	East
Eusomatus obovatus (Boheman, 1839)	–	+	East
Phyllobius femoralis Boheman, 1843	–	–	East
Phyllobius fumigatus Boheman, 1843	–	–	East
Phyllobius pomaceus Gyllenhal, 1834	+	+	+
Phyllobius thallasinus Gyllenhal, 1834	+	+	West
Phyllobius virens (Faust, 1890)	–	–	East
Otiorhynchus wittmeri Legalov, 1999	–	+	East
Otiorhynchus politus Gyllenhal, 1834	–	+	North
Otiorhynchus arcticus (Fabricius, 1780)	–	–	North
Otiorhynchus subocularis Arnoldi, 1975	–	+	South
Otiorhynchus perplexus Gyllenhal, 1834	–	+	South
Otiorhynchus obscurus Gyllenhal, 1834	–	+	South
Otiorhynchus altaicus Stierlin, 1861	–	–	South
Otiorhynchus karkaralensis Bajtenov, 1974	–	–	South
Otiorhynchus kasachstanicus Arnoldi, 1964	–	–	South
Otiorhynchus relicinus Arnoldi, 1975	–	–	South
Cephalcia lariciphila (Wachtl, 1898)	–	–	North

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Eleven species of the "Northern" group (17%, see Table 4) are widely distributed in tundra and taiga zones of Palaearctic and Holartic (Carabidae: *Pelophila borealis*, *Patrobus septentrionis*, Helophoridae: *Helophorus sibiricus*, Curculionidae: *Lepyrus nordenskioldi*) (Korotyaev, 1980; Kryzhanovskii et al., 1995; Bousquet, 2012), and most can be found in the mountains of South Siberia, Mongolia and the Far East (Fig. 3). Only *Otiorhynchus arcticus* (Curculionidae) is known from the north of Europe and the Urals (Fig. 3) (Yunakov et al., 2012). These species prefer areas of tundra and swampy meadows in taiga habitats. *Bembidion difficile* (Carabidae) inhabits banks of streams located chiefly in the taiga zone. *Cephalcia lariciphila* (Pamphiliidae), whose larvae develop exclusively on *Larix* trees, also characterize taiga habitats.

Twenty-one species (32% of identified species) are attributed to an "Eastern" group (Table 4), which is distributed in south Siberia and adjacent regions. *Paophilus hispidus* and *Stephanocleonus luctuosus* (Curculionidae) are known from Minusinskaya Hollow only (Fig. 4). *Morychus ostasiaticus* (Byrrhidae), *Eusomatus obovatus*, and *Otiorhynchus wittmeri* (Curculionidae) – can be found in the western part of south Siberia (Tshernyshev and Dudko, 1997; Tshernyshev, 2006, 2012; Legalov, 2010). *Stephanocleonus leucopterus* is known from the western part of south Siberia to Irkutskaya Oblast in the east and central and east Kazakhstan in the south (Legalov and Opanassenko, 2000). *Poecilus ravus* (see Zinovyev, 2008: Fig. 2), *P. major*, *Chrysolina perforata*, *Stephanocleonus foveifrons*, *S. eruditus*, and *Trichalophus biguttatus* are widespread in the mountains of south Siberia and Mongolia (Voss, 1967; Korotyaev, 1980; Legalov, 2010), while *Trichalophus biguttatus* is found in the South Urals. *Chrysolina perforata*, *Stephanocleonus foveifrons* (Fig. 4), and *S. eruditus* are found in northeast Russia (Korotyaev, 1980). Fragments representing the head and pronotum of *Chrysolina* are provisionally attributed to *Ch. perforata*, but could represent *Ch. purpurata*, which is widespread in central and northern Kazakhstan, southern Siberia and along the Indigirka River in the mountains of northeast Yakutia. *Harpalus amputatus* is distributed in the mountains of south Siberia, southeast Siberia, Mongolia, and North America (Kataev, 1987: Fig. 74). *Cymindis arctica* is known from the mountains of northeast Yakutia only (Fig. 4). *Elaphrus sibiricus*, *Coccinella nivicola*, *Chlorophanus sibiricus*, *Phyllobius femoralis*, *Ph. fumigatus* are widespread in Siberia and Russia's Far East (Korotyaev and Egorov, 1977). Most species, *Poecilus ravus*, *Cymindis arctica*, *Chrysolina perforata*, *Ch. purpurata*, *Paophilus hispidus*, *Trichalophus biguttatus*, *Stephanocleonus* spp., *Phyllobius* spp., *Coniocleonus astragali*, and *Otiorhynchus wittmeri*, are xerophilous and prefer dry steppes, or are found on xerophytic plant associations on slopes with southern aspect. Halophilous species *Poecilus major* and *Harpalus amputatus* inhabit mainly banks of salted lakes. *Morychus ostasiaticus* and *Chlorophanus sibiricus* prefer river flood-lands, and *Elaphrus sibiricus* is found in the banks of stagnant reservoirs.

Nineteen species (29%) are found in steppe habitats of Eurasia, which we refer to as the "Southern" group. *Bembidion almum*, *Pogonus punctulatus*, *Porcinolus murinus*, and *Tychius uralensis* are widespread in steppe and semi-desert zones of Eurasia (Korotyaev, 1990). *Bembidion kokandicum* is found in the mountains of Central Asia and southeast Altai. *Aclypea sericea* inhabit southeastern Russia, including the Chuiskaia steppe of southeast Altai, as well as west and central Kazakhstan (Tsepelev et al., 2013: Fig. 7). Twelve species are distributed locally as follows: *Otiorhynchus karkaralensis* and *O. kasachstanicus* in Kazakhskii Melkosopochnik (Fig. 3) (Arnoldi, 1964; Bajtenov, 1974), *O. obscurus*, and *O. altaicus* in steppe of Altaiskij Krai and Novosibirskaya Oblast (Arnoldi, 1975), *O. subocularis* and *O. perplexus* in the foothills of west Altai (Arnoldi, 1975; Legalov and Opanassenko, 2000), *O. relicinus* in Zaisan Lake basin (Arnoldi, 1975), *Stephanocleonus prasolovi* in the central Altai (Ter-Minassian, 1990), *S. isochromus* in southeastern Altai (Ter-Minassian, 1988), *S. tschuicus* and *S. suvorovi* in southeastern Altai and Tuva (Ter-Minassian, 1988), and *Eremochorus mongolicus* in Tuva and Mongolia (Korotyaev, 1995; Legalov, 2010). Nearly all species of the group are xerophilous and residents of dry steppes. Only *Bembidion kokandicum* inhabits stream banks, and the halophilous species *Pogonus punctulatus* prefers salty ponds and brackish water. Two Euro-Siberian species (Zaslavskij, 1956; Toledano, 1999; Legalov, 2010), *Bembidion humerale* and *Aulacobaris lepidii*, are assigned to a "Western" group.

6. Discussion

The following features of the taphocoenosis can be defined:

1 Phytophagous Coleoptera of the family Curculionidae are the dominant representatives of the entomofaunal complex; weevils (Curculionoidea) occur practically in all Late Cenozoic localities as a dominant group among phytophagous beetles and are an important component of the entomofaunal complexes from the second half of the Mesozoic (Legalov, 2012; Gratshev and Legalov, 2014), with their species richness increasing through time (Legalov, 2013; Gratshev and Legalov, 2014). In Pleistocene and Holocene deposits, Curculionoidea are represented by two families, Brentidae (Apioninae) and Curculionidae (Kuzmina and Matthews, 2012), and in most deposits they are not dominant, because other beetle groups such as Carabidae or Byrrhidae often predominate. Weevils are often less numerous in comparison with ground-dwelling beetle species, however they are notably abundant in a number of localities, including those from the central West-Siberian Plain (Zinovyev et al., 2007). *Otiorhynchus* and *Stephanocleonus* weevil species are the most commonly represented phytophagous beetles, with the species *Otiorhynchus karkaralensis* having the greatest abundance in our sample.
2 The sub-fossil beetles identified at the Bun'kovo locality are not been found in this territory at the present time, but are instead located spread eastward, southward or northward from the locality.
3. The beetles in this taphocoenosis consist of species preferring open landscapes, bog-tundra, and cold northern and warm southern steppes.
4. Humid thermophilic species are absent, and forest specialized species are represented by the single sawfly specimen, *Cephalcia lariciphila*.

The composition of the species represented in the Bun'kovo taphocoenosis is similar to insect groups from earlier deposits in the central part of West-Siberian Plain and Middle Transurals (Zinovyev et al., 2007; Zinovyev, 2011). For example, the localities of Andryushino, Nizhnyaya Tavda, and Skorodum, which are attributed to the late "Karginskoe" time period at the end of Marine Isotope Stage 3 (28,000–24,000 BP), have a dominant representation of weevils including *O. karkaralensis*. Moreover, the proportional representation of *Otiorhynchus* weevils reaches 50% in the deposits of Andryushino locality near the lower Nizhnyaya Tavda River (Zinovyev et al., 2007).

One of the principal differences of the fauna from Bun'kovo is the presence of significant number of East-Siberian components, *Stephanocleonus* weevils. Representatives of this genus as well as the genus *Coniocleonus* are more typical for Pleistocene deposits in northeast Siberia (Kiselev, 1981; Sher and Kuzmina, 2007; Kiselev and Nazarov, 2009; Kuzmina and Matthews, 2012). In the late Quaternary deposits of West Siberia, they are recorded as single finds, for example as *Stephanocleonus eruditus* in the Late

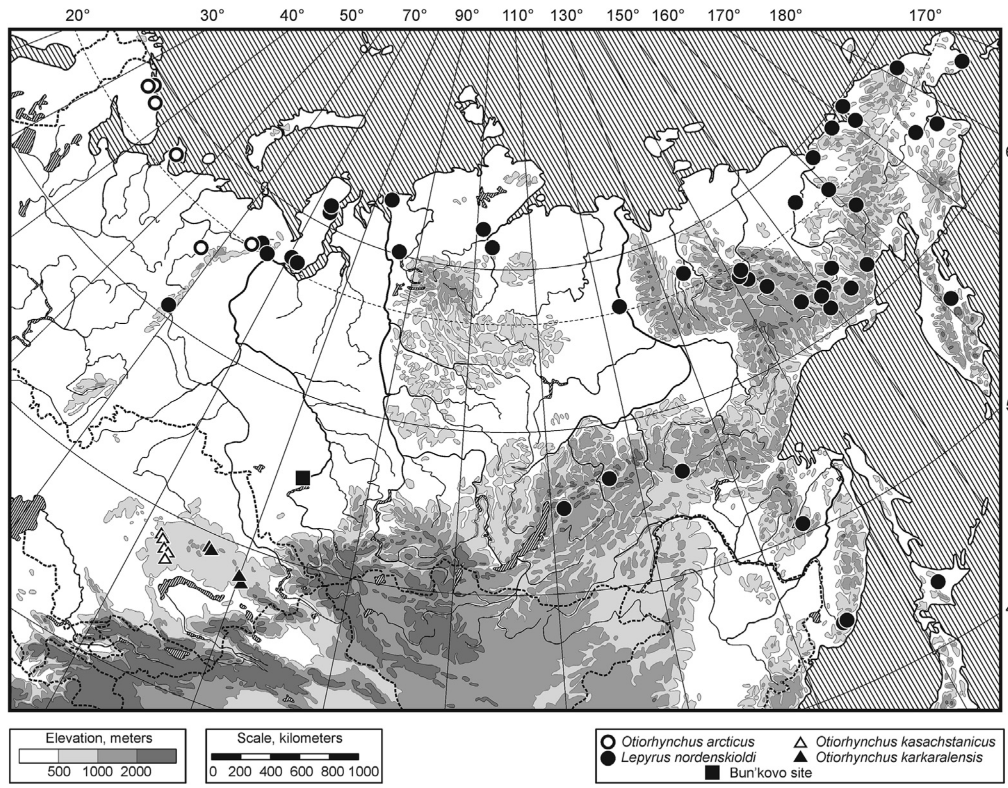

Fig. 3. Modern distribution of the weevils *Lepyrus nordenskioldi*, *Otiorhynchus arcticus*, *O. kasachstanicus* and *O. karkaralensis* in Asia and East Europe. Sensu Arnoldi (1964), Bajtenov (1974), Korotyaev (1980), Khruleva and Korotyaev (2012), Yunakov et al. (2012) and original data from ISEA and ZISP collections.

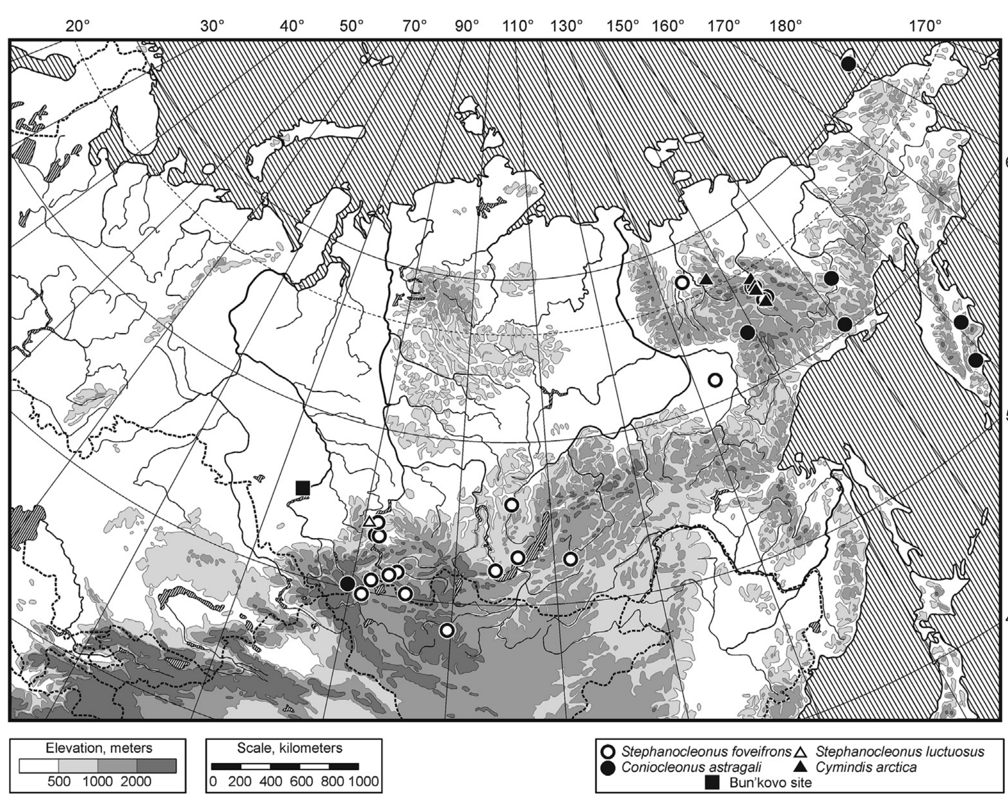

Fig. 4. Modern distribution of the weevils *Stephanocleonus foveifrons*, *S. luctuosus*, *Coniocleonus astragali*, *Cymindis arctica*. Sensu Korotyaev (1980), Ter-Minassian (1988), Khruleva and Korotyaev (1999), Sundukov (2011) and original data from ISEA and ZISP collections.

Pleistocene locality of Kul'egan in the middle Ob River basin. Comparison of the entomocomplex from Bun'kovo with similar-age faunas from the central and northern parts of the West-Siberian Plain (Table 2) show that the principal differences are species that prefer arid landscapes are prevalent in Bun'kovo and almost completely absent in northern faunas of similar age.

The observed combination of a number of steppe species of *Otiorhynchus* and *Stephanocleonus* (8 species each) at Bun'kovo is unusual for both Pleistocene deposits and for local faunas. To illustrate this, several regions of Siberia and Kazakhstan were examined (Table 5). A maximum of 8 *Otiorhynchus* species are recorded in the steppes of west Altai from the upper Ob River to Zaisan Lake. Some species are quite rare, and typically 3 or 4 occur together in sympatry. *Stephanocleonus* species are more typical in southern regions of east Siberia, Tuva and Transbaikalia, and almost completely absent in the West-Siberian Plain. Many *Stephanocleonus* and *Otiorhynchus* are locally distributed and their diversity is caused by vicariance of closely related species. The high number of *Otiorhynchus* and *Stephanocleonus* in Pleistocene deposits indicate that several species possess high dispersal capacity under favourable environmental conditions. Secondly, modern distributions of many local species of *Stephanocleonus* and *Otiorhynchus* are relictual, caused by climate changes in Holocene, and could differ dramatically from the species' past distributions.

A few conclusions on the character of landscapes and regional climatic features at the end of the Pleistocene period and beginning of the Holocene can be proposed on the basis of Bun'kovo species composition. The joint occurrence of northern bog-tundra and xerophilous species in high number, which currently inhabit cryoarid regions of north-eastern Russia, and the absence of humid thermophilic species, suggest that tundra-steppe landscapes, with dry and cold climatic conditions, occupied these sites in the past. The almost complete absence of forest species and species exclusively developing on arboreal vegetation indicate absence lack of forests in the region and open landscapes in the past. The discovery of the sawfly *Cephalcia lariciphila*, which has an obligate association with *Larix* trees, suggests the presence of single trees or groves in the upper Ob' River basin during the Younger Dryas.

The presence of species typically found in southern, moderately warm steppes, especially *Otiorhynchus karkaralensis*, might seem to contradict our conclusion about past conditions being cold. *Otiorhynchus karkaralensis* and *O. kasachstanicus* are endemic to Kazakhskii Melkosopochnik (central Kazakhstan) where average temperatures in July are approximately +19–+20 °C, and 1–2° warmer than in Bun'kovo (Davitaya, 1960). At the same time, average July temperatures in the warmest localities of the tundra species *Lepyrus nordenskioldi* are about +13–+14 °C. A much greater difference in average temperature is observed in January, where ≥−15 °C is required for *Otiorhynchus* and ≤−24 °C for *L. nordenskioldi*. Thus, temperature data based on the recent distribution of these species would suggest that "the mutual climatic range method" (Atkinson et al., 1987; Elias, 1997) could be problematic. What data support our inferences of cold climatic conditions at Bun'kovo for these species? First and foremost, we find a high number of tundra and cryoarid landscape species, whereas we do not find any Tenebrionidae species (except halophilous *Centorus* (*Belopus*) sp.) characteristic of warm arid landscapes. Second, we propose that *Otiorhynchus karkaralensis* prefers colder conditions than currently found in Kazakhskii Melkosopochnik, based on characteristics of its modern and paleodistribution. This species is rare and very localized at present (Fig. 3) (only a few localities are known from central Kazakhstan (Bajtenov, 1974; ZISP collection), but *O. karkaralensis* is dominant in some Pleistocene deposits of central and southern West Siberia, where it found together with cryophilous and xerophilous beetles (Legalov et al., in press). *O. karkaralensis* most likely did not maintain a broader distribution at present due to the presence of other congeners and the increasing humidity of this region. The distribution of *Aclypea sericea* illustrates this extremely well (Tsepelev et al., 2013: Fig. 7). This species is also typical of upper Pleistocene deposits in south Siberia, but now is found in steppe habitats of central Kazakhstan and south-eastern of Russian Plain, and in one microrefugium. This microrefugium, the Chuiskaya Hollow of southeast Altai, is characterized by extremely dry and cold climate conditions, suggesting this species does prefer lower temperatures when they are available. The preponderance of data in our study, therefore, is consistent with cold climatic conditions during the deposition of sub-fossils at Bun'kovo.

During the Middle Dryas (12,000–11,800 BP) southwest Siberia is characterized with extreme deterioration of climate and complete degradation of the arboreal vegetation according to palynological data (Vasiliev et al., 2002). The following period (11,800–11,000 BP) was more warm and humid, although it was cooler than now. Birch and fir trees became part of the vegetative cover. Next, a cooling period led to the disappearance of boreal vegetation in the Late Dryas (11,000–10,200 BP). In spite of the warm Dryas time dated for Bun'kovo according to palynological data, the contradiction of palynological and our entomological data is not significant because the role of trees in landscapes was insignificant.

Examination of the modern species distributions of those taxa found in Bun'kovo shows significant dispersal of the fauna when Holocene climates were warm and humid. Species of different ecological groups shifted their distribution in various directions. The main trend is a shift of mesophilous and mesohygrophilous species to the north. Depending on their degree of cryophily, these species occupy territories in the modern tundra (*Lepyrus nordenskioldi*, *Otiorhynchus arcticus*) and taiga zones (*Pelophila borealis*, *Notaris aethiops*). Shifts of the fauna are less common to mountainous regions of Siberia, most likely because of the altitudinal zonality. Distributional changes of xerophilous species are more variable, though two main trends, in an eastern or southern direction, are observed and coincide with continental climates. The

Table 5
Number of steppes species of *Otiorhynchus* and *Stephanocleonus* in the regions of Siberia and Kazakhstan.

Region	*Otiorhynchus*		*Stephanocleonus*	
	Total[a]	Shared with Bun'kovo taphocoenosis	Total[a]	Shared with Bun'kovo taphocoenosis
Central Kazakhstan	5	2	1	1
Steppe of west Altai	8	6	1	1
South-eastern Altai	4	0	13	3
Tuva	7	0	39	2
Transbaicalia	5	0	35	2
North-east Siberia	1	0	3	2

[a] (Legalov, 2010).

most cryophilic species reduced their distribution and now occur in refugia in northeast Siberia (*Cymindis arctica*), or inhabit wide territories with cold steppes such as Yakutia, Transbaikalia, Tuva and Mongolia (*Stephanocleonus foveifrons*, *S. eruditus*). Less cryophilous species and thermotolerant species are either found in the steppe zone, or are found in dry mountain hollows and foothills. The hygrophilous species variously shifted to the north (*Bembidion difficile*), to the south, or to the east (halophilous *Pogonus punctulatus*, *Poecilus major*).

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