Pleistocene insects of Western Siberia and adjacent lands

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Abstract

Fossil insect remains from 100 sites assigned to the Pleistocene and Holocene from Western Siberia and adjacent areas of the Ural and Altai Mountains are considered. Most of these locations are assigned to MIS3-1. The beetle faunas from the MISS 5 (Last Interglacial) deposits reflect a climate similar or warmer than present. Latitudinal differentiation in the composition of insect faunas is noted for MIS3 assemblages, with specific "*Otiorrhynchus*" complexes recorded south of 58°N. These faunas share features with modern communities of the Southeastern Altai. Beetle faunas from the last glacial maximum reflect colder climate; in the south, "*Otiorrhynchus*" faunas were preserved. Holocene complexes are similar to modern ones in the same territories.

Keywords

Climate changes; Faunal changes; Holocene; Late Pleistocene; Paleoenvironmental reconstructions; Quaternary period; Sub-fossil insects; The Urals; West Siberia

Key points

- Beetle faunas from MIS 5 are very similar to with modern regional faunas. They represent periods of warming within the Eemian Interglacial (MIS 5e) and Brørup Interstadial (MIS 5c).
- The end of the MIS 3 interstadial was characterized in northern sites by the presence of arctic and subarctic species; subarctic faunas with some dry-adapted species dominated at sites from 59° to 61°.
- Late MIS 3 Faunas from areas south of 58°N were characterized by the dominance of *Otiorhynchus* weevils, as well steppe and cold-adapted beetle species.
- There are no modern analogs for the late MIS 3 West Siberian lowland faunas of and parts of the Urals.
- Faunas from the Last Glaciation (MIS 2) are also geographically distinct in West Siberia Northern zone beetle faunas contain arctic and subarctic taxa reflecting dry, cold climate.
- There are no modern analogs for the MIS 2 beetle faunas of the southern zone. Sites from the foothills of the Altai, include wood-associated beetles, indicating the presence of forest refuges.
- The Late Pleistocene-Holocene transition is characterized by the gradual appearance of boreal forest species in these territories. Holocene insect faunas are virtually the same as modern regional faunas.

Introduction

Insects are one of the important groups of organisms in paleoecological research and are widely used to reconstruct the natural environments of the past. Despite active work in this field, until recently a number of regions of Northern Eurasia remained unstudied. The greatest attention of Russian researchers has been focused on European Russia and North-Eastern Siberia. The latter region is important because it formed the western part of Beringia. As such, the study of Pleistocene insect faunas from North-Eastern Siberia allows us to understand the processes of formation of the faunas of both Eurasia and northwestern North America. However, the central part of the Asian continent has been explored to a much lesser extent. Beginning in the 1990s large collections of fossil insect assemblages have been obtained from an enormous region of north-central Asia, from the Yamal and Gydan peninsulas in the north, to the Altai region in the south. Research on these faunas has provided new, unique data concerning the historical development of regional insect faunas in the Pleistocene and Holocene. Moreover, in the course of these studies, we have identified certain characteristic insect complexes from the Late Pleistocene. These faunas differ significantly from the Quaternary insect faunas of both Europe and Northeastern Siberia. This work allowed the researchers to identify characteristic features of regional insect faunas for specific intervals of the Late Pleistocene and Holocene. The timing of the formation of the characteristic faunas was established at a significant number of locations with similar radiocarbon dates allowing correlation between faunas through certain periods of the late Quaternary.

This chapter reviews studies covering the interval from the Early Late Pleistocene to the Holocene (MIS5-MIS1). Entomological material from Early and Middle Pleistocene deposits is poorly preserved and fragmentary, unlike the finds of beetles from Late Pleistocene and Holocene localities. It is this material that is considered in this chapter.

Preservation and abundance of fossil beetles

Insect remains are widely represented in different types of sediments in the vast regions of the Urals and Western Siberia, from the Yamal and Gydan peninsulas in the north to river valleys in the vicinity of Teletskoye Lake (south-east part of the Altai Mountains). Most of the locations are confined to the river terraces of the Ob Valley and its tributaries: the Agan, Irtysh, Aley, and Isha rivers, and others. Chitin is commonly preserved in clays and silts. However, insect remains are also preserved in sands and buried soils. Unlike the frozen peat of the Arctic, in which insect fossil preservation is excellent, peats of early and middle Pleistocene age from our study regions yield weak, denatured exoskeletal material that is generally in very poor condition. The extraction of insect remains from these intervals requires extra effort.

The field collection of the material and its subsequent laboratory processing was carried out according to standard methods described in the literature (Dudko et al., 2022)—(Fig. 1).

The number of insect fragments recovered from individual samples does not always correlate with the volume of sediment sampled. In some cases, large numbers of insect remains can be extracted from 100 g or less of plant detritus (washed from 2 to 3 L of sediment). Unfortunately, in other cases even very large volumes of sediment yield only a small number of insect remains, even when the sediment sample contains a great deal of plant detritus. Often layers of sediment containing the remains of insects occur in thin beds intercalated among thick layers of inorganic sediments. It is sometimes impossible to sample sufficient volumes of these organic-rich layers. We have found that peat samples yield low numbers of identifiable insect fossils, whereas alluvial detritus more consistently contains large numbers of such specimens. The preservation of insect remains depends on specific taphonomic conditions to a greater extent than on the age of the host sediments. In some cases, perfectly preserved material has been found in middle Pleistocene deposits, whereas Holocene sediments may yield only thin, deformed insect fragments.

Paleoenvironmental interpretations of Late Pleistocene insect faunas

There are a number of difficulties in paleoenvironmental interpretations of insect faunas extracted from Quaternary sediments. We determined the type of species complex based on a classification scheme proposed by Zinovyev (2006). Using the Climate-data.org website (https://ru.climate-data.org/), we estimated paleotemperatures of the study regions. Most often our reconstructions more-or-less matched the modern thermal environments.

We also attempted to use the Mutual Climatic Range (MCR) method to reconstruct the average temperature of the warmest month of July (Tmax) (Bray et al., 2006). The MCR method failed to produce useful results for faunal assemblages that have no modern analog. Beside temperature, other factors certainly influence the distribution of insect species in Central Asia. These include aridity levels of the climate. Dry climate contributes to the suppression of woody vegetation while enhances soil salinization and the consequent formation of saline reservoirs. The latter is related to presence some ground beetles of the genus *Pogonus* and dark beetles of *Centorus* genus.

Non-analog faunas were identified sites in Byelorussia and northeastern Siberia (Alfimov et al., 2003). The occurrence of steppe species in tundra communities is rare for Byelorussia. But in the Kolyma lowland (northeastern Siberia) a variety of steppe species have been found in association with cold-adapted taxa, not only in Quaternary fossil assemblages, but also modern tundra and tundra–steppe communities. Because of this, the species that had originally been characterized purely as steppe inhabitants (hence, dry-adapted), have now been reclassified as cryoxerophilous (both cold- and dry-adapted), able to inhabit the severely cold conditions of arctic tundra–steppe. However, in some cases we cannot adequately explain the joint occurrences of species having dissimilar ecological requirements and types of modern distribution.

Such approaches are justified when Quaternary complexes have modern analogs. During the study of entomological material from the sediments of the period MIS3-2 in locations south of 58°N., complexes that have no modern analogs were described.

Fig. 1 Field sampling of sub-fossil insect material at the Mal'kovo site on the banks of the Tura river, August 2012. Original photo of A.A. Legalov, used with permission.

Fossil beetles localities in the Urals, West Siberia and adjacent lands

The study area covers a vast region from 73° to 50°N and 60° to 93°E; there are three ecological zones (tundra, taiga and steppe) and two transitional bands (forest-tundra and forest-steppe) (Chernov, 1975). Forest-steppe in Western Siberia replaces the belt of broad-leaved (nemoral) forests represented in the European part of Eurasia and in the Southern Urals (Mordkovich, 2014). On level ground, the ecosystem boundaries have a clearly defined latitudinal zonation. The West Siberian Plain is characterized by swamp land that covers large areas.

Medvedev pioneered the study of Pleistocene insect fossils from the Koshelevo site in the Lower Irtysh region. His data were included in Krapivner (1969). Kiselev (1973) studied insect remains from the Mal'kovo site, on the right bank of the Tura River near Tyumen City. No-analog beetle faunas were first described there, characterized by the abundance of *Otiorhynchus* weevils. Kiselev (1988) published an article summarizing Quaternary fossil beetle studies from West Siberia. At the time of this publication, most of these faunas were not accurately dated, greatly complicating subsequent data interpretations. Insect fossils from the Southern Urals, and the Middle and Southern Yamal Peninsula were described by Erokhin and Zinovyev (1991). As a result of Zinoviev's research, fossil insect remains from more than 130 localities were described from the Urals and the northern part of the West Siberian Plain (Zinovyev et al., 2019).

The regional insect faunas are associated with the Late Pleistocene (MIS3-2). This is typical for both the northern and southern parts of the region.

Late Pleistocene events of the central part of Northern Eurasia

The Late Pleistocene is the best-studied period of the Quaternary in the Urals and West Siberia. The beginning of that time marked by the disappearance of Taz (Saalian) (MIS 6) Glaciation (approximately 130 thousand years ago). This was followed by the last interglacial period (MIS 5), including the Eemian warming. MIS 4 cooling brought on the Spartan (Wurm; MIS 4)) Glaciation, which caused the spread of the Scandinavian ice into northwest Russia.. The Last Glacial Maximum (LGM, MIS 2) occurred about 25 thousand years ago. During MIS 5a-4, most of Northwest Eurasia was covered by open landscapes similar to modern Arctic tundra in the north. To the south, landscapes featured open periglacial spaces such as tundra-steppe and steppe communities. Woody vegetation did not form closed forests, although it is likely that sparse woods existed in some regions. This reconstruction is indicated by occurrences of buried wood at latitude 74°N., which have been radiocarbon dated from 46 to 33 ka, and at 71°N—from 52 to 22 ka (Naurzbaev, 2005). These landscapes probably resembled cold savannas or grasslands.

At the Late Pleistocene—Holocene boundary, a number of fairly rapid climatic changes took place in Western Siberia. These events transpired along with the gradual retreat of glacial margins in northwestern Eurasia, combined with large-scale climate oscillations in the Late Glacial period. The boundaries of modern vegetation zones formed during this period (Arkhipov and Volkova, 1994).

Late Pleistocene beetle records, central Northern Eurasia

See Fig. 2.

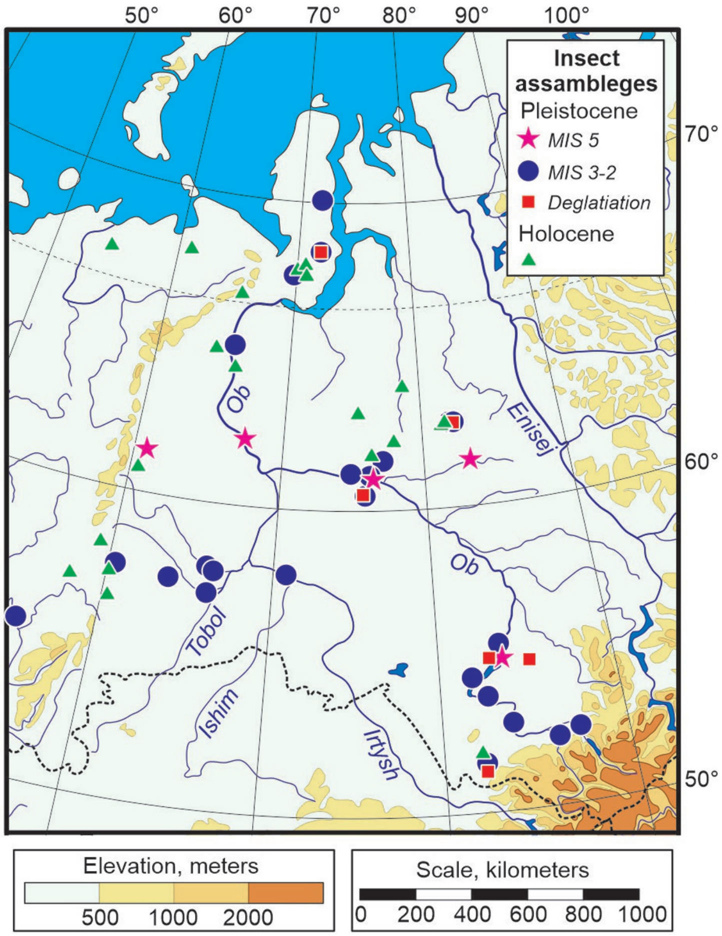

Fig. 2 Localities of late Pleistocene and Holocene insects from West Siberia and surrounding areas. From Gurina AA, Dudko RYu, Zinovyev EV, Legalov AA (2022) Quaternary Palaeoentomology: 10 Years in the South of Western Siberia. 1. Priroda. 6,: 3–11 (in Russian with English abstract).

Insect faunas of the beginning of Late Pleistocene (MIS5-4, 130-80 thousand years ago)

Some fossil assemblages represent MIS 5, But only three are reliably dated to this interval, based on TL and U-Th dating. These fossil assemblages are from are the Karymkary peat bog, the Belaya Gora site, and the Kiryas site (Rusakov et al., 2019). Based on stratigraphic position, the Shipichnoye-2 site has been correlated to MIS 5 (Table 1).

Last interglacial (MIS 5e) insect fossils from Karymkary peat bog (Fig. 3) indicate swampy habitats with woody vegetation and relatively warm, and climate, for which the mean July temperatures (Tmax) were at least 17.7–18 °C (Zinovyev et al., 2019). Thermophilous indicator species include the ground beetle *Trechus secalis* in most samples. This species inhabits floodplain meadows in the lower reaches of the Irtysh River and the middle reaches of the Ob (Koltunov et al., 2009). These localities are situated well to the south of the Karymkary site. Fossil assemblages lying below the interglacial peat deposit are thought to represent the MIS6-5 transition, (Zinovyev, 2012).

Insect assemblages from the Belaya Gora and Kiryas localities are assigned to the Brørup stadial (MIS5c) based on ^{230}Th/U dates. Beetle assemblages from this site show the faunal changes associated with the transition from cool to moderately warm climates during stages MIS 5d-c). One insect assemblages associated with a horizon–dated at 103 ± 9 ka, correlating with the MIS 5c stadial (Rusakov et al., 2019). In summary, fossil insect faunas in from the Belaya Gora site reflect a sequence of climate changes from cold climate at the base of the sequence mean (Tmax ≤7.6 °C) to warm climate (Tmax ≤15 °C).

Insect remains of Kiryas-2 section were found in four samples collected in organic-rich fluvial sediment of the lower part of this section. Detailed descriptions of insect faunas, seeds and plant macrofossils were published earlier (Zinovyev et al., 2019;). U/Th ages of 105–104 ka were obtained for five samples of the Kiryas-K section (Laukhin, 2009).

Fossil insect data indicate a sequence of paleoenvironmental conditions at the Kiryas site. Insect assemblages from the lower part of the exposure indicate cold climate and open ground, with one exception: the presence of the bark beetle *Pityogenes irkutensis*. This species feeds on larch. Climatic analysis of this fauna suggests a Tmax value of 14 °C and a Tmin of −24 °C. These values are found today in North Taiga zone. The peat layer immediately above apparently formed under the same conditions. The upper peat horizon was apparently deposited during MIS3 based on a ^{14}C age of 43.9 ka. This fauna represents severe climate conditions and open landscapes similar to those found in the tundra zone, today, with Tmax of 9.5 °C and Tmin of −25 °C.

Additional samples from Kiryas-2 yielded little evidence of environmental change (Laukhin, 2009). Many water beetles were identified, mainly specimens of *Agabus* and *Gaurodytes* (Dytiscidae) and *Helophorus* (Hydrophilidae). Ground beetles associated with humid, cool climate were abundant, including *Carabus maeander*, *Pterostichus maurusiacus*, *Diacheila polita*, *Amara alpina*, and *Blethisa catenaria*. This fauna indicates an unusually humid climate However, beetle remains recovered from the lowest part of this layer suggest a warm, temperate climate, such as the temperate ground beetle *Trechus secalis*. So, the insect complexes of this layer demonstrate the transition from the conditions of a warmer climate to a cooler one at the MIS5d-e boundary.

The beetle faunas of the Belaya Gora and Kiryas localities reflect the conditions of a cool and humid climate; they are similar to modern insect communities of Western Siberia, at latitudes north of 63°N. The small number of bark beetles may indicate patches of woody vegetation, mainly larch.

Insect complexes from the Shipichnoye-2 site are similar to the fossil beetle faunas of the Karymkarsky Sor locality. The species identified from the Shipichnoye-2 site in the Northern Urals, also inhabit this territory today, indicating the relatively warm conditions of MIS5d.

Despite the differences between the beetle faunas of the sites discussed here, the fossil assemblages have modern analogs living in regions north of the Urals and in West Siberia. Because of the absence of "non-analog" faunal assemblages, it is apparent that the humidity of climate was similar to the modern. However, the July isotherms during the same Brørup simply shifted to the north compared to their current state. The data obtained generally correlate with earlier conclusions based on spore-pollen and carpological analyses for the same time.

The timing and direction of climate change indicated by the insect faunas discussed here are generally consistent with paleoenvironmental reconstructions based on insect fossils from other regions of Northern Eurasia (Kuzmina, 2015).

Insect faunas from MIS3-2

Most of the Late Pleistocene localities of insect fossils in the Urals and western Siberia are attributed to MIS 3-2 (the end of an interstadial and the LGM). In the northern part of the region, reliably dated sites were deposited mainly during MIS 3; in the south, most sites date to MIS2. The presence of a significant number of localities with ^{14}C dates from 35 to 26 ka facilitated the identification of series of regional features from 67°N to 52°N.

Beetle species with modern arctic and subarctic ranges dominate insect faunas at locations north of 61°N. In some localities the single finds of xerophilic insects have been made, including the ground beetles *Carabus sibiricus*, *Poecilus ravus*, and the leaf beetles *Chrysolina aeruginosa* and *C. cavigera*. Taken together, the insect faunal evidence suggests open tundra-like landscapes (possibly with sparse trees) from latitudes of 73–61°N. The faunas are composed of abundant remain of beetle species associated with the Arctic, combined with scattered occurrences of xerophilous (dry-adapted) species. This is quite consistent with the spore and pollen data.

Only one location of this age is known from latitudes 61°-60°N: the Kul'egan-2247 site. The dominant species are arctic and subarctic beetles (*Pterostichus* (*Cryobius*) cf. *pinguedineus*, *P. costatus*, *P. vermiculosus*, *Curtonotus alpinus*, *Tachinus arcticus*, and *T. brevipennis*)—consistent with modern tundra faunas.

Table 1 Localities of Late Pleistocene and Holocene sub-fossil insects from the West Siberia and adjacent areas and their absolute dates.

N	*Locality*	*Coordinates*		*Samples and references*	*Type of dating*	*Laboratory code*	*Absolute age and type of dating*
		N	*E*				
1.	Karymkarskiy peat bog	62°03'	67°22'	Arkhipov and Volkova, 1994	TL		data 131 ± 31 ka BP
2.	Belaya gora	61°27'	82°28'	Rusakov et al., 2019	Th/U (Calibrated		103 ± 9/7 ka (TSD-model)
3.	Syoyakha-Mutnaya	70°01'	71°56'	V.I. Nazarov, personal communication (Zinovyev, 2020)	14C	UPI-716	30,700 ± 1100
4.	430 km of Ob	65°24'	65°38'	Zinovyev, 2006	14C	IPAE-63	24,000 ± 1500
5.	Aganskiy uval-1290/2	61°22'	76°44'	Zinovyev, 2006	14C	IPAE-176	23,300 ± 500
6.	Zelyoniy ostrov	62°29'	81°51'	Sample 1, depth 3,85–4,15 m	14C	SOAN-7550	22,100 ± 325
				Sample 2, depth 1,0–1,4 m		Le-8972	10,780 ± 70
				Sheinkman et al., 2016			
7.	Mega-2169	60°56'	72°20'		14C	SOAN-982	26,285 ± 590
8.	Mega-2172	60°56'	72°20'	Dudko et al., 2022	14C	IOAN-132,	33,100 ± 2300
9.	Lokosovo	60°40'	71°32'		14C	SOAN 956	22,930 ± 650
10.	Kul'egan-2247	60°25'	75°50'	Section I	14C	LOIA-8663	21,815 ± 225
				Section II		LOIA-8664	26,730 ± 250
11.	Andryushino	57°41'	66°08'	Bone	14C	GIN-5337	41,900 ± 800
				Plant detritus		SPb-2413	32,077 ± 1000
				Zinovyev, 2020			
12.	Nizhnyaya Tavda	57°41'	66°12'	Zinovyev, 2006	14C	SOAN 4535	24,820 ± 750
						SOAN 4534	27,400 ± 335
13.	Mal'kovo	56°25'	66°10'	Zinovyev, 2020	14C	GIN-5338	31,800 ± 350
14.	Skorodum	57°47'	70°58'	Zinovyev, 2020	14C	SOAN 4538	26,500 ± 550
15.	Nikitino	57°34'	63°17'	Zinovyev, 2006	14C	SOAN-4537	24,480 ± 580
						SOAN-4536	28,460 ± 800
16.	Shurala	57°28'	60°15'	Zinovyev, 2020	14C	Ki-15505	27,600 ± 150
						Ki-15512	36,700 ± 250
17.	Gornovo	54°54'	55°53'	Dudko et al., 2022	14C	H-1856/1857	29,700 ± 1250
						BashGI-36	28,800 ± 125
	Gornovo-IV	54°54'	55°53'	Dudko et al., 2022		SPb-2895	31,455 ± 1000
18.	Tyurseda-Khadyta	67°26'	69°57'	Zinovyev, 2020	14C	NTUAMS-832	19,325 ± 144
						NTUAMS-118	13,498 ± 98
19.	Agan-1082/2	62°04'	77°32'	Zinovyev, 2020	14C	IPAE-95	13,070 ± 575
20.	Bol'shaya gorka	62°27'	81°33'	Zinovyev, 2020	14C	SOAN-7309	13,390 ± 150
21.	Kul'egan-2241	60°30'	75°45'	Zinovyev, 2005	14C	IPAE-94	10,700 ± 325
22.	Ngoyun	68°32'	72°06'		14C	IPAE-177	14,208 ± 1921
						IPAE-176	1226 ± 17210
						IPAE-175	688 ± 240
23.	Pereval'noye Lake	66°51'	65°41'	Panova, 2011	14C	LU-6425	9030 ± 80
						LU-6424	9270 ± 110
24.	Nyulsaveyto	67°32'	70°10'		14C	IPAE-67k	5620 ± 188
						IPAE-69s	6081 ± 207
						IPAE-69sm	7041 ± 281
						IPAE-71s	7291 ± 219
						IPAE-72	8179 ± 231

25.	Shapkina-1102.	67°28’	54°36’	Zinovyev, 2020	14C	GIN-9443дт	7030 ± 110
						GIN-9443др	5920 ± 50
26.	Vanzevat	64°10’	66°03’	J.S. Waterhouse and L.I. Agafonov, personal communication (Zinovyev, 2020)	14C	B-7064	8350 ± 300
27.	Agan-4068/2	62°06’	77°55’	14C date yr BP	14C	IPAE-96	2200 ± 150977
				14C date yr BP		IPAE-97	0 ± 30011400
				14C date yr BP (Zinovyev, 2005)		IPAE-98	±350
28.	Gorbunovskiy peat bog	57°48’	59°56’	Sample 3	14C	GIN-14125	6990 ± 40
				Sample 2		GIN-14128	8200 ± 40
				Sample 3		GIN-14083	9140 ± 40
				Panova, 2011			
29.	Yakhayadato	67°46’	70°77’	Zinovyev et al., 2001	Date of death of the tree		3050 BCE
30.	Portsy-yakha	67°46’	70°77’	Zinovyev et al., 2001	Date of death of the tree		3004 BCE
31.	Yada-yakhody-yakha-1	67°35’	70°36’	Zinovyev et al., 2001	Date of death of the tree		1794 BCE
32.	Yada-yakhody-yakha-5	67°32’	70°40’	Zinovyev et al., 2001	Date of death of the tree		638 BCE
33.	Yada-yakhody-yakha-8	67°31’	70°40’	Zinovyev et al., 2001	Date of death of the tree		3769 BCE
34.	Shipichnoye-1	61°05’	60°33’	Zinovyev, 2020		SOAN-4539	5770 ± 60
35.	Cheryomukhovo	60°24’	59°57’			SOAN 4798	3210 ± 25
36.	Bogoslovskiy kar’er	57°21’	60°08’	Zinovyev, 2020	14C	GIN-84	4400 ± 60
37.	Ust’-Log	56°57’	57°25’	Zinovyev et al., 2014	14C	SPb_920	2664 ± 100
38.	Zakharovo-1	51°38’	81°19’	Sample 3	14C	SPb-1344	153 ± 25
39.	Ustyanka-1	51°16’	81°30’	Sample 1 (2013) (Gurina et al., 2019)	14C	SPb-1345	10,150 ± 200
				Sample 2 (2020)		SPb-3757	11,636 ± 100
				Sample 3 (2013) (Gurina et al., 2019)		SPb-1346	10,806 ± 100
				Sample 3 (2013), Aspropartheni carinicollis		UCIAMS-225787	12,150 ± 90
				Sample 3 (2013), Otiorhynchus ursus		UCIAMS-225786	14,200 ± 110
40.	Stepnogutovo-2	54°51’	84°53’	.1	14C	SPb-3759	10,470 ± 100
				Sample 6		SPb-3689	10,460 ± 70
				Sample 11		SPb-3758	10,350 ± 100
41.	Bun’kovo	55°04’	82°30’	(Zinovyev et al., 2016)		⊠O⊠H-8806	11,550 ± 125
42.	Lebed’	51°56’	87°06’	Sample 3		SPb-3685	11,956 ± 120
				Sample 1		SPb-3127	13,832 ± 100
43.	Kizikha-1	51°26’	81°36’	Sample 1 (Gurina et al., 2019)		SPb-1347	13,455 ± 150
44.	Novaya Surtaika	52°14’	85°55’	Sample E		SPb-3687	16,404 ± 150
				Sample 1c		SPb-2415	18,248 ± 250
				Sample D		SPb-2299	21,389 ± 400
				Sample A2		SPb-2414	>40,000
45.	Dubrovino	55°27’	83°15’	Sample 1		SPb-1417	19,444 ± 150
46.	Suzun-1	53°44’	82°11’	Sample 1		SPb-3011	21,190 ± 500
47.	Suzun-2	53°44’	82°11’	Sample 2		SPb-3125	16,984 ± 120
48.	Nizhny Suzun	53°43’	82°08’	Sample 2		SPb-3126	23,737 ± 200
49.	Kalistratikha	52°58’	83°37’			SPb-1416	24,438 ± 350
50.	Kizikha -2	51°27’	81°36’	(Gurina et al., 2019)		SPb-1418	26,094 ± 400
51.	Gornovo-IV	54°54’	55°53’	Sample 5 (Dudko et al., 2022)		SPb-2895	31,455 ± 1000

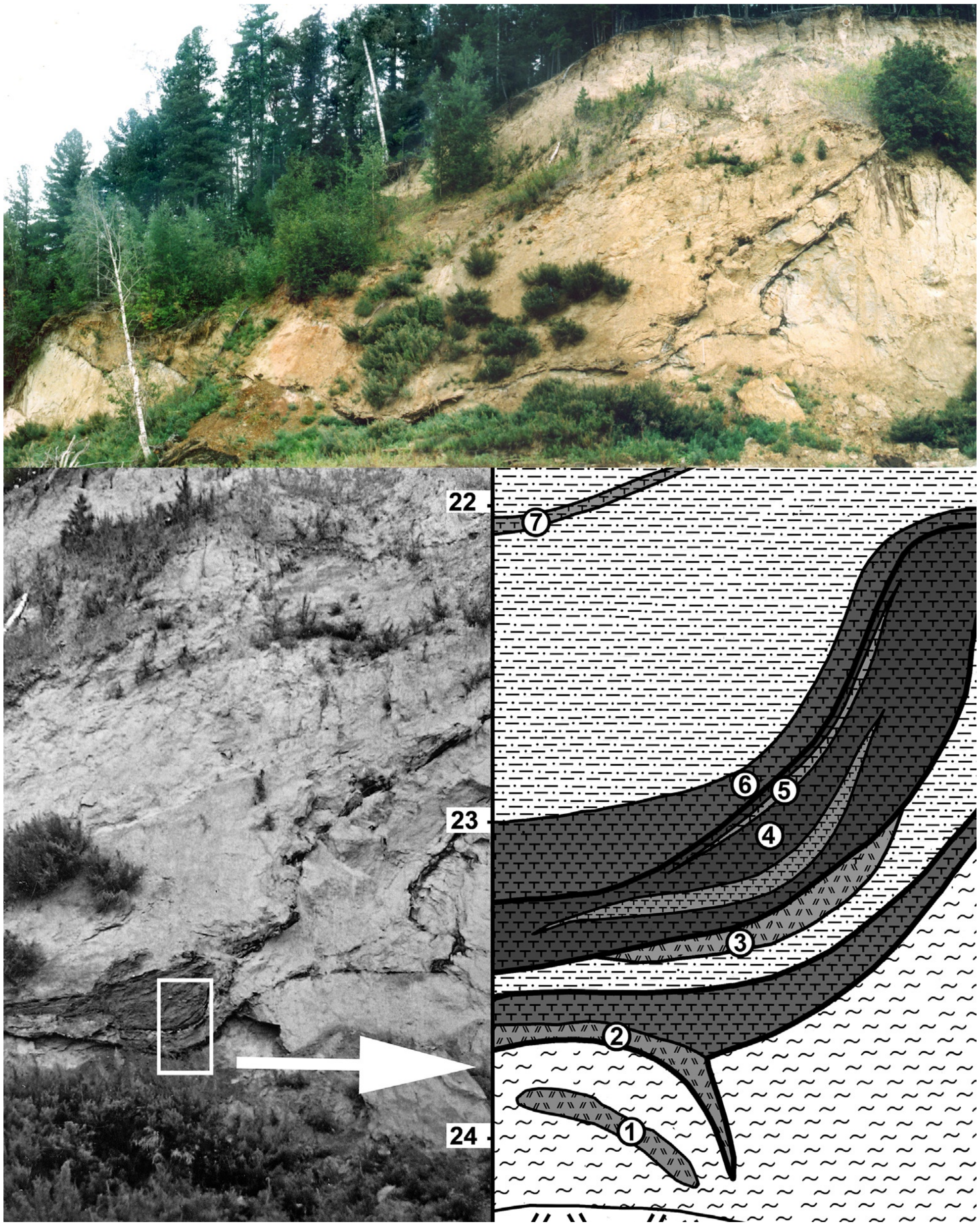

Fig. 3 Photo of the Karymkary peat bog and position of layers with occurrences of subfossil insects (Zinovyev, 2012).

The Kul'egan-2247 fauna contains a greater steppe species component, such as *Poecilus ravus*, *Aclypaea bicarinata*, and *Stephanocleonus eruditus*, whereas weevils of the genus *Otiorhynchus* are generally lacking (Legalov et al., 2016). Occurrences of the bark beetle *Phoelotribus spinulosus*, and the wood-reliant weevils *Hylobius excavatus*, *H. pinastri*, *Pissodes* sp.) indicate the presence of small patches of conifers (pine and spruce). The insect faunas of this site reflect relatively cold and dry climate with landscapes of open ground similar to modern tundra with inclusions of single trees. Steppe-adapted species were found in some of the fossil faunasbut steppe insect are still found in modern tundra and taiga faunas, such as *Carabus sibiricus*, *Polystichus connexus*, and *Chrysolina exathematica* s/sp. *gemmifera*, etc.) (Mikhailov, 2000). The fossil assemblages suggest cool, dry climatic conditions, similar to modern southern tundra regions in the vicinity of 64°N with Tmax of 14 °C.

Beetle faunas have been found in localities located south of 59°N. These have been assigned to the "periglacial" or "Otiorhynchus" type, which includes Non-analog assemblages. Such faunas are found at sites ranging from 59° to 52°N: Gornovo, Mal'kovo, Shurala, Nizhnaya Tavda, Nikitino, Andryushino, Skorodum, Kazakovka, Kizikha-2, Kalistratikha (see Fig. 2).

These beetle faunas are characterized by the large numbers of *Otiorhynchus* weevil specimens (*O. bardus*, *O. ursus*). These beetle are found today in the steppes of the central and eastern Kazakhstan (Fig. 4). *Otiorhynchus* specimens comprise up to 70% of the individuals in localities of this period of Late Pleistocene (Fig. 5). Other steppe species are also well represented, including *Poecilus*

Fig. 4 Modern specimen (left) and associated fossil elytra (right) of weevil *Otiorhynchus bardus* (Gurina et al., 2022). Gurina AA, Dudko RY, Zinovyev EV, Legalov AA (2022) Quaternary Palaeoentomology: 10 Years in the South of Western Siberia. Priroda 6: 3–11 (in Russian with English abstract).

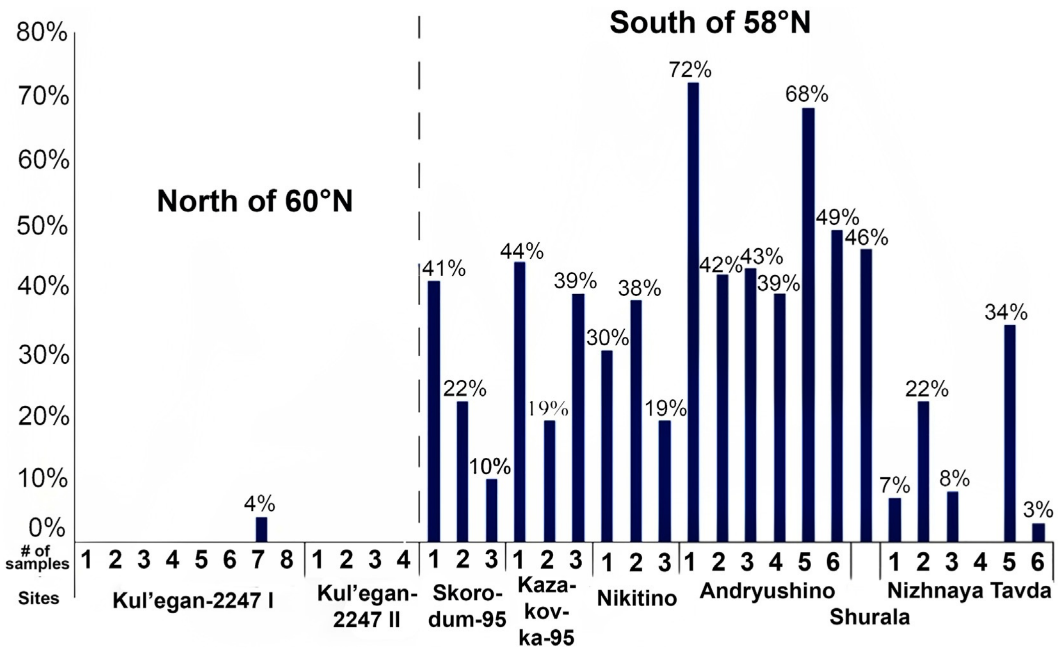

Fig. 5 The percentage ratio of weevils of the genus *Otiorhynchus* in sediments of the northern part of the West Siberian Plain. From Zinovyev EV (2020) Insect faunae of the Urals and West Siberian Plain In Quaternary Period. Unbubl. Ph D. Thesis. Ekaterinburg, Institute of Plant and Animals Ecology. pp. 1–42.

Fig. 6 Modern and fossil elytral specimens of the ground beetle *Pogonus cumanus*. 1, 2—left and right elytra of *P. cumanus* from the Skorodum site (Late Pleistocene); 3—fragment of modern specimen of *P. cumanus*. Original photo of E. Zinovyev.

ravus, *Pseudotaphoxenus tilesii*, *Stephanocleonus eruditus*, *S. foveifrons*, *Aclypaea sericea*, and *A. bicarinata*. Some halophilic (salt pan) beetles (*Pogonus punctatulus*, *P. cumanus*, *Centorus* sp.) also are good indicators of an aridity (Fig. 6).

However, these faunas lack significant numbers of thermophilous beetle taxa (most Tenebrionidae, most species of weevils, ground-beetles, leaf beetles), that characterize modern steppic beetle faunas of Northern Eurasia. Instead, there are significant numbers of cold-adapted beetles that are found today on tundra, forest tundra, and northern taiga forests. These include *Pterostichus* (*Cryobius*) spp., *Curtonotus torridus*, *C. alpinus*, and *Diacheila polita*). Additionally, species beetles adapted to cold/dry conditions (cryoxerophilous species), such the pill beetle *Morychus viridis* and the ground beetle *Cymindis arctica* have been found. The modern range of *C. arctica* is confined to the northeastern Siberia (Kryzhanovskij et al., 1995). One of the characteristic features of these faunas is the lack of wood-associated (xylobiont) species, such as the bark beetle *Phoelotribus spinulosus*).

While these faunas differ sharply from the modern insect faunas of the West Siberian Plain, they do share some features in common with the faunas of the continental regions of the South Siberian mountains, such as the Southeast Altai (Chytrý et al., 2019). We found that 50–60% of the species from regional Late Pleistocene fossil assemblages now live the southern part of the study area (Gurina et al., 2022). Steppe and some subarctic species of insects cohabit these territories, mainly at altitudes of 2200–2400 m, where the steppe belt of the mountains gradually gives way to tundra. There are very few forest species in the composition of such faunas, since larch forests occupy very limited areas and do not form a continuous belt. We also note significant abundance and diversity among the *Otiorhynchus* species in the fossil assemblages. These faunal characteristics match those of the MIS3 period, described above.

Interestingly, *Otiorhynchus bardus* and *O.* cf. *ursus*, that typified MIS3 faunas of the West Siberian Plain, are absent in the modern beetle faunas of the Southeastern Altai. Instead, darkling beetles (Tenebrionidae), abundant in modern steppe faunas of Southern Siberia are nearly absent from the "otiorynchus-type" fossil insect assemblages of most localities. One exception to this is the fossil fauna of the Gornovo site, where at least four species of darkling beetles have been identified. Among them, *Cenorus rufipes* and *C.* cf. *procerus* are classified as halophiles; the rest are typical steppe beetles: *Pedinus* cf. *femoralis* and *Anatolica abbreviata* (Dudko et al., 2022).

Nevertheless, species that occurred in the same Late Pleistocene assemblages cannot be found in the same biotopes at present. This includes the most thermophilous (heat-loving) species, such as carrion beetle *Aclypea sericea*, that do not inhabit regions 1800 m a.s.l. here. The same fossil assemblages contain the most cryophilic species, the ground beetles *Diacheila polita* and *Pterostichus brevicornis* are found today only in the mountain tundra above 2400 m a.s.l. (Dudko et al., 2022). It thus appears that the Southeastern Altai region, has an extracontinental climate with a clearly pronounced influences of macrorelief, since not all cold- and warm-adapted species could live together in the same exact locality. Nevertheless, these species lived together on low-relief regions of the center and south of Western Siberia in the Late Pleistocene. In such environments, thermally contrasting habitats could only exist within a framework of meso- and microrelief. From this we conclude that the degree of continentality associated with the "Otiorhynchus-type" faunas in the West Siberian Plain was significantly higher than it is now.

There was a gradual decrease of cold-loving species in the Late Pleistocene faunas of "periglacial" or "Otiorhynchus-type" in the south of our study region. Fossil sites located between 58° and 55°N contained numerous remains of Arctic and subarctic species, including the ground beetles *Diacheila polita*, *Pterostichus* (*Cryobius*) spp., as well as the weevil *Lepyrus nordenskioldi* (Gurina et al., 2019) (Fig. 7).

Tmax estimates have upper and lower boundaries, and most of the cryophilic species in the fossil assemblages from this locality have Tmax values with significantly lower upper limits with the gap between upper and lower Tmax boundaries for some species of 7–10 °C. Based on their modern ranges, the species from these samples do not share a mutual climatic range, indicating that they could not live together. The MCR method for determining the mean July temperature is problematic for periglacial (tundra-steppe) landscapes, since modern species ranges do not correspond with the actual lower limits of the habitat of thermophilous species. Thus, MCR Tmax estimates appear to be too high. Nevertheless, even the upper limit of Tmax can be very informative for

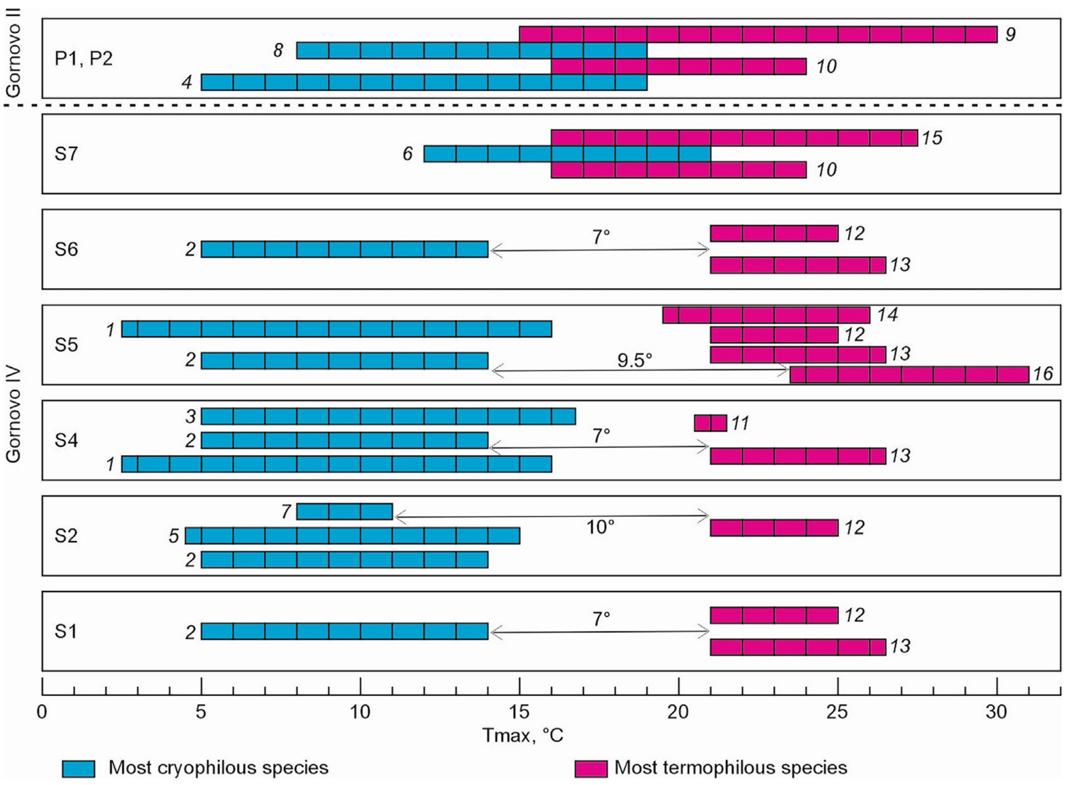

Fig. 7 Tmax range for the most cryophilous (1–8) and most thermophilous (9–16) species from different samples of Gornovo II and Gornovo IV. 1—*Diacheila polita*, 2—*Bembidion dauricum*, 3—*B. hastii*, 4—*Patrobus septentrionis*, 5—*Pterostichus brevicornis*, 6—*P. mannerheimii*, 7—*P. kokeilii*, 8—*P. dilutipes*; 9—*Agonum versutum*, 10—*Platynus livens*, 11—*Cribramara skopini*, 12—*Cymindis kasakh* (Carabidae), 13—*Aclypea bicarinata* (Silphidae), 14—*Anatolica abbreviata* (Tenebrionidae), 15—*Thryogenes festucae*, 16—(Curculionidae) (Dudko et al., 2022). From Dudko RYu, Danukalova GA, Gurina AA, Ivanov AV, Mikhailov YuE, Osipova EM, Prosvirov AS, Solodovnikov AYu, Legalov AA, Zinovyev EV (2022) Insects and molluscs of the Late Pleistocene at the Gornovo site (Southern Ural foreland, Russia): New data on palaeoenvironment reconstructions. 1. *Quaternary International* 632: 154–177. https://doi.org/10.1016/j.quaint.2021.10.003.

reconstructions. However, when Tmax estimates fall below 15 °C this indicates faunal assemblages from relatively cold stages, and the predominance of thermophilous species is associated with the contrast of micro-conditions and the wide distribution of well-heated biotopes.

Within MIS 3 there was a brief period of warm, humid climate from 32 to 30 ka (Volkova et al., 2002). This warming trend is best expressed in beetle faunas from the Gornovo site in the Southern Urals. Here, the thermophilous faunas differ greatly from the distinctive "periglacial" insect assemblages above and below the warming event fauna from the same section.. These "warm" insect faunas are quite similar to those associated with the third (last) warming of MIS 3 (Volkova et al., 2002). Tmax estimates fall between 16 and 19°C. Rapid warming during phases of MIS 3 has also been recorded from insect faunas at two locations in Western and Central Siberia: Seyakha-Mutnaya in the Middle Yamal, dated at 30.7 ± 1 ka, and at the site in the Yenisei valley dated at 39 ± 1.4 ka. The fossil insect assemblage from the Seyakha-Mutnaya site consists of arctic species, including aquatic leaf beetles of the genus *Donacia*, that are atypical for the tundra of the Middle Got Yamal. These aquatic beetles are found today in the northern taiga and forest tundra.

The terminal phase of Pleistocene and the beginning of the Holocene (MIS2-1, 12–8 ka)

The Pleistocene-Holocene transition (11–8 ka) was characterized by climatic instability which brought rapid changes in the composition of regional insect faunas. This climatic transition is clearly marked in faunas from sites north of 60°N. Beetle faunas representing arctic and subarctic conditions were gradually replaced by boreal insect faunas, signaling increased temperatures and higher humidity. In the central part of the study area, a mixture of arctic and subarctic insects dominated some faunas dating to the Pleistocene-Holocene transition including the Kul'egan-2241 site, where boreal insects (*Pterostichus mannerheimi*, *Amara brunnea*, and others) were found in fossil assemblages containing no evidence of woody vegetation (Zinovyev, 2005).

An insect fauna dated at 12.8 ka from the "Zelyoniy ostrov" site also contained boreal species such as *Notiophilus fasciatus*, *Pterostichus adstrictus*, *Calathus micropterus*, and *Chlaenius costulatus*. Beetle species found today in more than one ecosystem include *Clivina fossor*, *Loricera pilicornis*, *Elaphrus riparius*, *Bembidion quadrimaculatum*, *Acidota crenata*, and *Chrysolina lapponica*. Some subarctic beetles were also found, including *Carabus odoratus*, and *Diacheila polita*. The faunal composition of this layer reflects the presence of riparian forests adjoining sandy river banks and riparian shrub associations represented by willows (as indicated by the leaf beetles

Chrysomela lapponica and *Gonioctena* sp., and the weevil *Lepyrus volgensis*) and birch (weevil *Trichapion simile*) (Sheinkman et al., 2016). The presence of single cryophilic species (*C. odoratus*, *D. polita*) suggests that Tmax was 1–2 °C lower than today (Sheinkman et al., 2016), corresponding to a value of 15 °C.

Fossil insect faunas from the southern part of the region were similar to those associated with the MIS 3-2 period. For instance, the beetle fauna of the Bun'kovo locality from Novosibirsk, dated at 11.5 ka reflects the "Otiorynchus" (or "periglacial") type. This fauna includes subarctic, boreal, and steppe beetle species. The dominant group is weevils (Curculionidae), including beetles of the genus *Otiorhynchus*, characterized by a rich species diversity. Among the weevils of genus *Otiorhynchus*, a part has a subarctic and boreal distribution (*O. arcticus* and *O. politus*), whereas the majority (O. *wittmeri*, *O. bardus*, *O. ursus*, *O. subocularis*, *O. relicinus*) occurs in the steppe zone today. Weevils of the genus *Stephanocleonus* were highly diverse, with at least 8 species identified. Comparisons of this fauna with similarly aged faunas from the central and northern parts of the West-Siberian Plain (Kul'egan-2241, "Zelyoniy ostrov") reveal an important difference. The Bun'kovo fauna includes xerophilic species that are almost completely absent in the northern faunas (Zinovyev et al., 2016). Taken together, the data suggest that tundra-steppe landscapes with dry and cold climatic conditions occupied these sites in the past. There is no evidence of forests in the region. However, 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 (Zinovyev et al., 2016).

The most southerly site in the region site, Ustyanka-1, has samples with radiocarbon ages (from 12.1 to 10.1 ka. This beetle fauna contains at least 66 species and differs significantly from the two previous ones. Steppe species predominate here, while hygrophiles, including halobionts (*Dyschiriodes luticola*, *Paratachys centriusstatus*, *Bembidion aspericolle*, *B. gassneri*, and *Megamecus argetatus*) are also numerous. Tundra and forest species are absent. Most of the species are part of the regional modern fauna. Some are known from the steppe zone of Eurasia, in regions south or west of the fossil site. These include*Scarites terricola*, *Paratachys centriustatus*, *Lebia punctata*, *Aclypea calva*, and *Tychius albolineatus*. Only one species was found that now lives north of the region and is characteristic of cold habitats: *Notaris aethiops*. Several species of "Otiorhynchus-type" fauna, such as *Otiorynchus bardus*, *O. ursus*, and *O. obscurus*, were also found in the Ustyanka-1 fauna. The insect fauna from the Ustyanka-1 site contains elements associated with the fauna of the steppe zone of Western Siberia, as well as some thermophilous southern taxa. This combination suggests an environment that was warmer and/or drier than today.

Holocene insect faunas

The species composition of Holocene insect faunas is best studied from the northern part of the study region, where 39 localities are known (Zinovyev, 2020). Only three localities are known in the southern part of the region, and all of them date to the end of the Holocene (Gurina et al., 2022).

In the northern part of the West Siberian Plain, Holocene insect faunas are identical in species composition to modern ones in the same territories. Changes in the composition of plant communities of that time (based on spore-pollen data) showed only a change in the species composition of forests—coniferous or coniferous-deciduous or small-leaved (Panova, 1996). They were not so radical as to cause fundamental changes in the composition of insect faunas of that time. The dynamics of insect faunas related to changes in the landscape and climatic conditions can be observed only at the boundaries of the recent natural zones, such as the boundary between the tundra and taiga. During the Holocene climatic optimum, a number of species associated with forests (including such species as bark beetles *Hylugrops palliatus*, *Phoelotribus spinulosus*, *Orthotomicus suturalis*, and *Polygraphus* sp.) shifted northwards in these boundary territories (Zinovyev et al., 2001). Within the taiga zone, the beetle faunas from studied Holocene samples taken from alluvial and peat deposits are identical to the recent faunas of the corresponding territories. The main changes within individual sections may be attributed to successions related to the meso-landscape dynamics, for example, river bed fluctuations, formation of dead river branches, and subsequent forest development.

At the beginning of the Holocene, the territory of the Urals was inhabited by species associated with southern taiga forests. This includes such species as *Carabus menetriesi*, *Platycerus caraboides*, and *Agelastica alni*, found in Early Holocene deposits of the Gorbunovsky peat bog. These samples are dated 8.5 and 9.2 ka (Zinovyev, 2020) (Fig. 8). At the same time, the influence of the Holocene Climatic optimum (Atlantic period) on the composition of insect assemblages is not reflected in the deposits of alluvial and swamp genesis. The only deposits yielding insect faunas reflecting this thermal event are zoogenic. These layers are more likely to accumulate species inhabiting the zonal upland biotopes. For instance, zoogenic sediments from the Ust'-Log locality dated 2.7 ka have yielded fragments of the woodland dung beetle *Trypocopris veranlis*, found today in the regions south and west of the fossil locality (Zinovyev et al., 2014).

Holocene insect faunas of the south of Western Siberia are also fundamentally different from the Late Pleistocene faunas of the "Otiorhynchus" type (Gurina et al., 2022). The species represented in Holocene sediments are still found in these territories today while most beetles from Late Pleistocene faunas have not been found either in Holocene layers or in modern faunas of the region. Only a small number of common species are noted—the pill beetle *Porcinolus murinus* (Byrrhidae), the leaf beetle *Pachnephorus tessellatus* (Chrysomelidae), the weevil *Otiorhynchus unctuosus* (Curculionidae) and the ground beetle *Olisthopus sturmii* (Carabidae). Such a sharp change in the species composition of insects in sediments reflects the fundamental differences in climatic and, as a consequence, habitat conditions of the late Pleistocene and Holocene in the south of the West Siberian Plain (Gurina et al., 2022).

Fig. 8 Beetle remains from Gorbunovskiy peat bog locality (Early Holocene). 1.—*Carabus menetriesi*—associated elytra; 2.—*Protaetia metallica*—associated elytra; 3.—*Selatosomus melancholicus*—right elytron; 4.—*Thanatophilus dispar*—left elytron; 5.—*Platycerus caraboides*—left elytron; 6.—*Chlaenius sulcicollis*—pronotum. Original photo by Zinovyev E.V.

Conclusions

1. Beetle faunas from the early Late Pleistocene (MIS 5) are mainly correlated with modern regional faunas, showing only their displacement relative to modern boundaries. This makes it possible in some cases to apply paleotemperature reconstructions, while reflecting the periods of warming within the Eem and Brørup stadials.
2. At the end of MIS3 there were clearly pronounced regional differences of between beetle faunas from the central part of the continent. Beetle faunas from localities situated north of 61°N were composed of arctic and subarctic species with single occurrences of xerophilic insects (*Carabus sibiricus*, *Poecilus ravus*, *Chrysolina aeruginosa*, and *C. cavigera*), Between 61° and 59° there were subarctic faunas with much more content of xerophious steppe species. South of 58°N there were characteristic insect faunas. These faunas are defined as "periglacial" or "Otiorhinchus-type" and are characterized by the dominance of weevils of the genus *Otiorhynchus* of the *O. bardus* group, as well as a combination of steppe and cold-adapted beetle species. Today, the westernmost location of this type of fauna is the Gornovo locality in the Southern Urals. There are no modern analogs for such faunas in the flat territories of West Siberia and the surrounding South and middle parts of the Urals. At the end of MIS3, (30–2 ka), a short period of climate humidification is observed, reflected in the change in the composition of fossil assemblages from sites such as the Gornovo locality and the Neptenne site (Yenissei river valley).

3. Regional differences between insect faunas of the Last Glaciation period (MIS 2) are also noted. In the north of the study region, beetle faunas of arctic and subarctic types reflect dry and cold climate, while in the south of the region, non-analog beetle faunas were found. In the foothills of the Altai, the identified faunal assemblages suggest the presence of forest refuges.
4. The Late Pleistocene-Holocene transition is characterized by a gradual warming of the climate and the gradual appearance of boreal forest species in these territories. Faunas of the periglacial or "Otiorhinchus" type were preserved in the south of the region up to the very boundary of the Late Pleistocene—Holocene (Bunkovo location).
5. Holocene insect complexes of the region are similar to regional faunas in the same territories, and they are fundamentally different from Pleistocene beetle communities. The dynamics of insect faunas related to changes in the landscape and climatic conditions can be observed only at the boundaries of the recent natural zones, such as the tundra and the taiga.

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