

Late Pleistocene insects from the Dubrovino site at Ob River (West Siberia, Russia) and their paleoenvironmental significance

**Anna A. Gurina, Roman Yu. Dudko, Sergey E. Tshernyshev,
Eugeny V. Zinovyev, and Andrei A. Legalov**

ABSTRACT

A blue-grey clay loam lens with plant and insect remains was found in an exposure of the Ob River, 2 km upper Dubrovino village in Novosibirskaya Oblast of Russia. Conventional radiocarbon dating of the Dubrovino deposit is ca 19,444±159 ¹⁴C BP (23,234±338 cal yr BP) and coincides with Sartan glaciation period (MIS 2). Ninety-two Coleoptera species, dominated by fragments of Curculionidae and Carabidae are represented in the Dubrovino deposit. Species of the tundra-steppe fauna are dominant, followed by meadow-dwelling taxa and coniferous forest taxa. A comparison of the Dubrovino assemblage with the previously studied late Pleistocene Kalistratikha and Bunkovo fossil assemblages showed that tundra-steppe landscapes with coniferous groves and sparse meadow vegetation were typical for this area from the end of Kargin interglacial (MIS 3) through the end of the Sartan glaciation (MIS 2).

Anna A. Gurina. Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Frunze Street 11, Novosibirsk 630091, Russia. auri.na@mail.ru

Roman Yu. Dudko. Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Frunze Street 11, Novosibirsk 630091, Russia. rdudko@mail.ru

Sergey E. Tshernyshev. Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Frunze Street 11, Novosibirsk 630091, Russia and Tomsk State University, Lenina Prospekt 36, Tomsk 634050, Russia. sch-sch@mail.ru

Eugeny V. Zinovyev. Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences, Vos'mogo Marta Street 202, Yekaterinburg 620144, Russia. zin62@mail.ru

Andrei A. Legalov*. Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Frunze Street 11, Novosibirsk 630091, Russia and Tomsk State University, Lenina Prospekt 36, Tomsk 634050, Russia. fossilweevils@gmail.com

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INTRODUCTION

Insect remains in Quaternary deposits have typically been found in the temperate and high latitudes, and are especially well-preserved in permafrost regions. These fossils are widely used for the reconstruction of past environments (Nazarov, 1984; Elias, 1994; Coope and Lemdahl, 1995; Sher et al., 2005). Chitin is poorly preserved in tropical and subtropical regions, although insect diversity and abundance is much greater there (Buckland and Coope, 1991).

Late Pleistocene insects are known from deposits on the southern part of the West Siberian Plain and have recently been described from sites in the territory of Novosibirskaya Oblast and Altaiskii Krai (Tsepelev et al., 2013; Tshernyshev et al., 2013; Zinoviyev et al., 2016; Kuzmina, 2017; Gurina et al., 2018). One of the fossil deposits was discovered in the bank of Ob River near Dubrovino Village (ca 55°27' N), with calibrated radiocarbon age of 23,234±338 cal BP (SPb-1417), that coincides with Marine isotope stage 2 (MIS 2) and the Sartan glaciation period according to Siberian regional scale. Similar age Quaternary insect deposits have not previously been described from the southern and central parts of the West Siberian Plain. This paper presents data on the fossil Coleoptera from this deposit as well as a paleoenvironmental reconstruction based on the insect faunal assemblage.

STUDY AREA

The Dubrovino deposit is located in the southern part of forest zone of West Siberian Plain (Figure 1). Pine forests including *Pinus sibirica* Du Tour, *Betula pendula* Roth., *B. alba* L., *Sorbus sibirica* Hedl. and rarely with *Larix sibirica* Ledeb. are represented in the studied area. The regional climate is continental with great changes in air temperature on a daily, seasonal and annual basis; the annual precipitation ranges from 380–430 mm. The average temperature of the warmest month, July, is +19.3 °C, and the coldest, January, is –17.7 °C (Luchitskaia et al., 2014).

GEOLOGICAL SETTINGS

The deposit is located on the right bank of the Ob River, 2 km above Dubrovino village in Moshkovskii District of the Novosibirskaya Oblast of Russia, 40 km north of Novosibirsk city. The site coordinates are: 55°27'07.0" N, 83°15'17.7" E. The deposit is in a 13 m cliff. The lower part of the sequence, at 12.6–12.9 m depth, contains alluvial

detritus with insect remains. Samples for entomological and radiocarbon analysis were taken from this organic-rich deposit in August 2014. A sedimentary description of the Dubrovino deposit profile is presented in Table 1 and Figure 2.

MATERIAL AND METHODS

Sampling methods follow those of Coope (1959) with later updates (Medvedev, 1968; Morgan, 1969, 1988; Nazarov, 1984; Kiselev et al., 1987). For geological description of the profile and to prevent contamination by modern insect fragments, the upper layer in the cliff was cleaned to produce a fresh exposure. The layer of sediments containing detritus and insect remains was placed in a large volume of filtered river water. The suspension was then washed through the sieve with cell diameter 0.3 mm. The sediment, containing a mixture of plant detritus and insect fragments, was

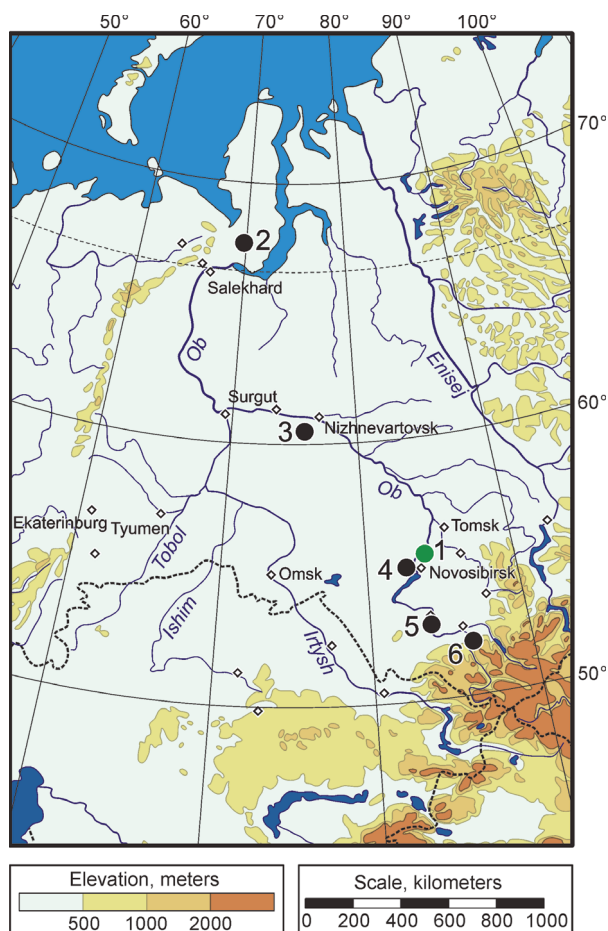


FIGURE 1. Locality map of Dubrovino site and similar-age late Pleistocene deposits from the West Siberian Plain. 1, Dubrovino; 2, Tyurseda-Khadyta; 3, Kul'egan-2247; 4, Bun'kovo; 5, Kalistratikha; 6, Novaya Surtaika.

TABLE 1. Description of the Dubrovino section.

Layer No.	Elevation (m)	Thickness (m)	Description
8	12.7–13.0	0.3	Modern soil
7	12.0–12.7	0.7	Sandy loam consistent, dry, whitish, with ferruginous interlayer in lower part
6	7.1–12.0	4.9	Horizontal alternation of medium and coarse-grained sands
5	6.9–7.1	0.2	Interlayer with fine and compact light-grey sand
4	4.4–6.9	2.5	Alternation of medium sands and coarse-grained sands; in right side coarse-grained sands are turning into sandy gravel with fragments fragment of cbivalve shells
3	0.4–4.4	4.0	Alternation of fine-grained sands, loamy sands and grey-brown loams
2*	0.1–0.4	0.3	Grey loam with a streak of alluvial detritus
1	0–0.1	>0.1	Rufous clay extending under water surface

*Sample upper 0.2 m (12.6–12.8 m from the surface) with insect remains and phytodetritus for dating.

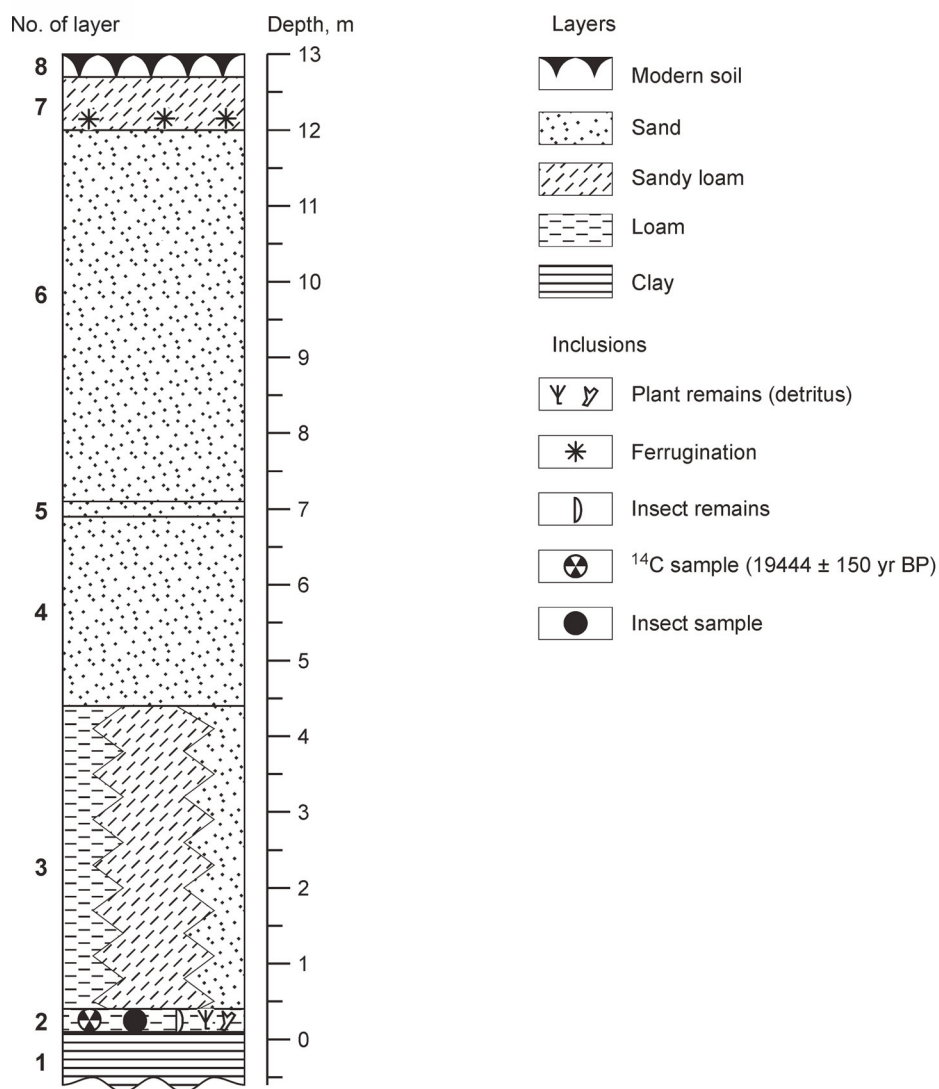


FIGURE 2. Stratigraphic diagram of the Dubrovino section on the Ob River.

examined, and the insect remains were placed in a vial with 30% alcohol. Other detritus containing chitin was collected in a plastic bag. Further study of these samples took place in the laboratory. The sample was sieved meshes of 3 mm, 1 mm and 0.3 mm, respectively. The sieved fractions were air-dried, and the remaining insect fragments were picked under a binocular microscope.

The fragments were mounted with water-soluble glue onto entomological cards or placed in general plate, as each fragment was given a number entered into a digital database. Each fragment was then studied and identified by taxonomic specialists of the different beetle groups.

The sample was dated by radiocarbon analysis, yielding an age of $19,444 \pm 159$ ^{14}C BP (SPb-1417). The calibrated age using the Calpal Online (<http://www.calpal-online.de>) is $23,234 \pm 338$ cal yr BP. This age coincides with the beginning of MIS 2 or Sartan glaciation of the late Pleistocene.

RESULTS

Taxonomic Composition of Beetles in the Dubrovino Assemblage

Fossil beetle results are presented in Table 2. Photos of fossil insects are presented in Figures 3-4. A total of 92 beetle species from 15 families were identified from the Dubrovino deposit. The faunal composition was as follows: 74% of the fauna were weevils and carabids (33 and 34 species, respectively), 6% were pill beetles (Byrrhidae, 5 species), and each of the remaining 12 families were represented by just 1–3 species. The majority of species in the assemblage are typical of late Pleistocene deposits from the southern and central parts of West Siberia (Zinovyev, 2011, Legalov et al., 2016; Zynovyev et al., 2016), but a number of species are recorded here for the first time, namely: *Nebria* cf. *rubrofemorata* Shilenkov, 1975; *Trechus* cf. *compactulus* Belousov and Kabak, 1996; *Pterostichus* cf. *tomensis* (Gebler, 1847); *Aphodius multiplex* Reitter, 1867; *Stephanocleonus favens* Faust, 1884; *S. isochromus* Suvorov, 1912; *Lixus paraplecticus* (Linnaeus, 1758); *Ceutorhynchus ignitus* Germar, 1823; *Otiorhynchus beatus* Faust, 1890; and *O. janovskii* Korotyayev, 1990.

The majority of fragments (N = 1050, 72%) from the deposit belong to Curculionidae, next numerous (201 fragments, 14%) are Carabidae, and fragments of remaining species share 13%. *Otiorhynchus* Germar, 1822 specimens are the most numerous (897 fragments, 55%), dominated by two closely related species *O. altaicus* Stierlin,

1861; and *O. ursus* Gebler, 1844 (550 fragments, 39%), and also *O. obscurus* Gyllenhal in Schoenherr, 1834 (84 fragments); and *O. politus* Gyllenhal in Schoenherr, 1834 (51 fragments). Also abundant are *Tournotaris bimaculata* (Fabricius, 1787) (Curculionidae) (65 fragments, 5%); and *Poecilus* (*Derus*) spp. (Carabidae) (31 fragments, 2%).

Ecological Groups

The ecological preferences of the insects found in the Dubrovino deposit are diverse and represent members of steppe, forest, tundra, meadow, water and saline species-complexes.

The steppe complex is the best-represented, based on the number of species and specimens. Xerophilous and meso-xerophilous beetles typical of steppe habitats, including *Poecilus ravus* (Lutshnik, 1922); *Poecilus fortipes* (Chaudoir, 1850); *Pterostichus macer* (Marsham, 1802); *Cymindis arctica* Kryzhanovskij and Emetz, 1979; *Metadonus distinguendus* (Boheman in Schoenherr, 1842); *Tychius albolineatus* Motschulsky, 1860; *Stephanocleonus eruditus* Faust, 1890; *S. favens*; *S. fossulatus* (Fischer von Waldheim, 1823); *S. isochromus*; *S. leucopterus* (Fischer von Waldheim, 1823); *Phyllobius femoralis* Boheman in Schoenherr, 1842; *Otiorhynchus beatus*; *O. altaicus*; *O. ursus*; *O. obscurus*; *O. unctuosus* Germar, 1823. Most of these are known from other late Pleistocene assemblages in the south and central part of the West Siberian Plain that have also yielded cold-dry environmental reconstructions (Zinovyev, 2011; Tshernyshev et al., 2013; Zinovyev et al., 2016; Legalov et al., 2016).

Forest species are represented in the fossil assemblage by only four species, i.e., *Notiophilus fasciatus* Mäklin, 1855; *Pterostichus tomensis*; *Hylobius excavatus* (Laicharting, 1781); and *Pisodes insignatus* Boheman in Schoenherr, 1843. These are typical of coniferous (taiga) forests and indicate the presence of conifers in the study region at the beginning of MIS 2.

Cold-adapted boreo-arctic species that inhabit tundra and forest-tundra ecotone regions include *Diacheila polita* (Faldermann, 1835); *P. (Cryobius)* spp.; *Notaris aethiops* (Paykull, 1792); *Lepyryus nordenskioldi* Faust in Sahlberg, 1887; and *Hypera ornata* (Capiomont, 1868).

Species typical of various meadow habitats are as follows: *Trechus compactulus*; *Olisthopus sturmii* (Duftschmid, 1812); *Phyllobius virideaeris* (Laicharting, 1781); *Polydrusus amoenus* (Germar, 1823); *Otiorhynchus grandineus* Germar, 1823; and *O. politus*.

TABLE 2. Species composition and number of insect fragments in Dubrovino taphocoenosis. HD = head, PR = pronotum, EL = elytra, OT = other fragments, N_{min} = minimum number of specimens.

No.	Species	Distribution*	Type of fragment				N _{min}
			HD	PR	EL	OT	
Carabidae							
1	<i>Notiophilus</i> cf. <i>aquaticus</i> (Linnaeus, 1758)	+	-	-	2	-	2
2	<i>Notiophilus fasciatus</i> Mäklin, 1855	North	-	-	1	-	1
-	<i>Notiophilus</i> sp.	-	-	-	1	-	1
3	<i>Nebria</i> cf. <i>rubrofemorata</i> Shilenkov, 1975	East	-	-	1	-	1
4	<i>Nebria subdilata</i> Motschulsky, 1844	East	-	-	1	-	1
5	<i>Diacheila polita</i> (Faldermann, 1835)	North	-	-	1	-	1
6	<i>Elaphrus</i> cf. <i>riparius</i> (Linnaeus, 1758)	+	1	2	-	-	2
-	<i>Elaphrus</i> sp.	-	-	-	2	1	1
7	<i>Clivina fossor</i> (Linnaeus, 1758)	+	-	2	2	-	2
8	<i>Trechus</i> cf. <i>compactulus</i> Belousov and Kabak, 1996	East	-	-	2	-	2
9	<i>Trechus</i> sp. 1	-	-	-	3	-	2
10	<i>Bembidion</i> (<i>Plataphodes</i>) cf. <i>fellmanni</i> (Mannerheim, 1823)	North	-	-	1	-	1
-	<i>Bembidion</i> (<i>Plataphodes</i>) sp.	-	-	-	1	-	1
11	<i>Bembidion</i> (<i>Plataphus</i>) sp.	-	-	-	2	-	2
12	<i>Bembidion</i> (<i>Peryphus</i>) <i>dauricum</i> (Motschulsky, 1844)	East	-	-	4	-	3
13	<i>Bembidion</i> (<i>Asioperypus</i>) spp.	-	4	-	-	-	4
14	<i>Bembidion</i> (<i>Pamirium</i>) sp.	South	-	-	1	-	1
-	<i>Bembidion</i> sp.	-	-	-	1	4	1
15	<i>Pogonus iridipennis</i> Nicolai, 1822	South	-	1	-	-	1
16	<i>Pogonus punctulatus</i> Dejean, 1828	South	-	3	3	-	3
17	<i>Patrobus</i> cf. <i>septentrionis</i> Dejean, 1828	+	-	-	1	-	1
18	<i>Poecilus</i> (<i>Derus</i>) cf. <i>ravus</i> (Lutshnik, 1922)	East	-	6	9	-	5
19	<i>Poecilus</i> (<i>Derus</i>) sp. 1	-	-	12	6	-	11
20	<i>Poecilus</i> (<i>Poecilus</i>) <i>fortipes</i> (Chaudoir, 1850)	+	-	1	-	-	1
21	<i>Pterostichus</i> (<i>Lyperopherus</i>) <i>mirus</i> (Tschitschérine, 1894)	East	-	1	-	-	1
30	<i>Pterostichus</i> (<i>Adelosia</i>) <i>macer</i> (Marsham, 1802)	South	-	1	-	-	1
22	<i>Pterostichus</i> (<i>Cryobius</i>) cf. <i>brevicornis</i> (Kirby, 1837)	North	-	2	1	-	2
23	<i>Pterostichus</i> (<i>Cryobius</i>) spp.	North?	-	3	6	-	4
24	<i>Pterostichus</i> (<i>Petrophilus</i>) cf. <i>tomensis</i> (Gebler, 1847)	East	-	2	-	-	2
25	<i>Pterostichus</i> (<i>Petrophilus</i>) sp. 1	-	-	2	-	-	2
-	<i>Pterostichus</i> spp.	-	-	2	3	-	4
26	<i>Amara</i> (<i>Amara</i>) sp.	-	-	-	1	-	1
27	<i>Amara</i> (<i>Bradytus</i>) <i>aurichalcea</i> Germar, 1823	North	-	1	-	-	1
28	<i>Curtonotus</i> sp.	-	-	4	3	-	4
29	<i>Agonum</i> sp.	-	-	-	1	-	1
30	<i>Olisthopus sturmii</i> (Duftschmid, 1812)	+	-	-	1	-	1
31	<i>Harpalus</i> spp.	-	2	3	-	-	3
32	<i>Cymindis</i> cf. <i>arctica</i> Kryzhanovskij and Emetz, 1979	East	1	5	-	-	5
-	<i>Cymindis</i> spp.	-	1	-	1	-	1
-	Carabidae indet.	-	25	-	7	55	-

TABLE 2 (continued).

No.	Species	Distribution*	Type of fragment				N _{min}
			HD	PR	EL	OT	
Hydrophilidae							
33	<i>Cymbiodyta marginella</i> (Fabricius, 1792)	+	-	-	-	1	1
34	<i>Cercyon</i> sp.	-	-	-	1	-	1
Helophoridae							
35	<i>Helophorus</i> spp.	-	-	-	6	-	3
Leiodidae							
36	Leiodidae indet.	-	-	-	1	-	1
Silphidae							
37	<i>Thanatophilus</i> spp.	-	-	1	4	-	2
-	Silphidae indet.	-	1	5	1	-	5
Staphylinidae							
38	<i>Tachinus</i> sp.	-	-	-	-	1	1
39	Omaliinae indet.	-	-	1	-	-	1
-	Staphylinidae indet.	-	-	3	1	-	3
Scarabaeidae							
40	<i>Aegialia</i> cf. <i>abdit</i> a Nikritin, 1975	North	-	-	1	-	1
41	<i>Aphodius multiplex</i> Reitter, 1867	South	1	-	-	-	1
42	<i>Aphodius dictinctus</i> (O.F. Müller, 1776)	+	-	-	1	-	1
43	<i>Aphodius</i> sp.	-	4	7	15	2	8
Byrrhidae							
44	<i>Lamprobyrrhulus nitidus</i> (Schaller, 1783)	+	1	3	5	-	3
45	<i>Morychus ostasiaticus</i> Tshernyshev, 1997	East	-	-	4	2	2
46	<i>Porcinolus murinus</i> (Fabricius, 1794)	South	-	-	1	-	1
47	<i>Simplocaria elongata</i> J. Sahlberg, 1903	North	-	-	1	-	1
48	<i>Cytilus sericeus</i> (Foerster, 1771)	+	-	-	1	1	1
Elateridae							
49	<i>Hypnoidus</i> sp.	-	-	1	3	-	2
50	Elateridae indet.	-	-	-	4	4	2
Coccinellidae							
51	<i>Coccinella</i> sp.	-	-	1	-	1	1
52	<i>Scymnus</i> sp.	-	-	-	1	-	1
Tenebrionidae							
53	<i>Centorus rufipes</i> (Gebler, 1833)	South	-	7	-	-	7
Anobiidae							
54	<i>Xyletinus</i> sp.	-	-	-	1	-	1
Chrysomelidae							
55	<i>Hydrothassa hannoveriana</i> (Fabricius, 1775)	North	-	-	1	-	1
56	Chrysomelidae indet.	-	-	3	2	1	3
Brentidae							
57	<i>Mesotrichapion punctirostre</i> (Gyllenhal in Schoenherr, 1839)	South	-	-	3	-	2
58	Apioninae indet.	-	-	-	19	6	10

TABLE 2 (continued).

No.	Species	Distribution*	Type of fragment				N _{min}
			HD	PR	EL	OT	
Curculionidae							
59	<i>Tournotaris bimaculata</i> (Fabricius, 1787)	+	13	19	12	23	19
60	<i>Notaris aethiops</i> (Paykull, 1792)	North	18	1	-	1	18
61	<i>Thryogenes nereis</i> (Paykull, 1800)	+	1	1	1	-	1
62	<i>Hylobius excavatus</i> (Laicharting, 1781)	North	-	-	1	-	1
63	<i>Pissodes insignatus</i> Boheman in Schoenherr, 1843	East	-	-	1	-	1
64	<i>Lepyrus nordenskioldi</i> Faust in Sahlberg, 1887	North	1	-	-	-	1
65	<i>Lepyrus</i> sp.	-	-	-	-	1	1
66	<i>Lixus paraplecticus</i> (Linnaeus, 1758)	+	-	-	2	-	1
67	<i>Stephanocleonus eruditus</i> Faust, 1890	East	4	-	2	-	4
68	<i>Stephanocleonus favens</i> Faust, 1884	East	1	-	-	-	1
69	<i>Stephanocleonus fossulatus</i> (Fischer von Waldheim, 1823)	East	1	-	-	-	1
70	<i>Stephanocleonus isochromus</i> Suvorov, 1912	East	2	-	-	-	2
71	<i>Stephanocleonus leucopterus</i> (Fischer von Waldheim, 1823)	South	1	-	-	-	1
72	<i>Coniocleonus</i> sp.	-	-	-	-	1	1
-	Cleonini gen. sp.	-	-	-	2	-	-
73	<i>Ceutorhynchus ignitus</i> Germar, 1823	+	-	-	1	-	1
74	<i>Tychius albolineatus</i> Motschulsky, 1860	South	-	-	1	-	1
75	<i>Hypera ornata</i> (Capiomont, 1868)	North	-	1	-	-	1
	<i>Hypera</i> sp.	-	-	-	-	1	1
76	<i>Metadonus distinguendus</i> (Boheman in Schoenherr, 1842)	+	1	1	-	-	1
77	<i>Trichalophus biguttatus</i> (Gebler, 1832)	East	1	-	-	-	1
78	<i>Sitona</i> sp.	-	2	14	-	-	14
79	<i>Chlorophanus sibiricus</i> Gyllenhal in Schoenherr, 1834	+	-	-	-	1	1
80	<i>Phyllobius femoralis</i> Boheman in Schoenherr, 1842	East	1	-	-	-	1
81	<i>Phyllobius virideaeris</i> (Laicharting, 1781)	+	3	1	2	-	3
	<i>Phyllobius</i> spp.	-	-	4	14	6	7
82	<i>Polydrusus amoenus</i> (Germar, 1823)	North	7	-	-	-	7
83	<i>Otiorhynchus arcticus</i> (O. Fabricius, 1780)	North	-	1	-	-	1
84	<i>Otiorhynchus beatus</i> Faust, 1890	East	-	-	2	-	1
85	<i>Otiorhynchus grandineus</i> Germar, 1823	East	-	-	2	-	1
86	<i>Otiorhynchus janovskii</i> Korotyaev, 1990	East	-	2	13	-	7
87	<i>Otiorhynchus altaicus</i> Stierlin, 1861	South	220	165	103	82	220
88	<i>Otiorhynchus ursus</i> Gebler, 1844	South			13		
89	<i>Otiorhynchus obscurus</i> Gyllenhal in Schoenherr, 1834	South	19	41	13	11	41
90	<i>Otiorhynchus politus</i> Gyllenhal in Schoenherr, 1834	North	4	11	6	18	11
91	<i>Otiorhynchus pullus</i> Gyllenhal in Schoenherr, 1834	South	1	6	2	-	6
92	<i>Otiorhynchus unctuosus</i> Germar, 1823	South	-	1	11	-	6
-	<i>Otiorhynchus</i> sp.	-	-	-	-	19	-
-	Coleoptera indet.	-	17	3	-	5	-
-	Hymenoptera indet.	-	5	-	-	7	5

* Modern distribution in comparison with the Dubrovino site.



FIGURE 3. Subfossil beetle fragments from the Dubrovino assemblage; pronotum (1-4, 6, 10-12), head (5), and elytron (7-9, 13-15). 1, *Elaphrus* cf. *riparius* (Linnaeus, 1758); 2, *Pogonus punctulatus* Dejean, 1828; 3, *Pterostichus* cf. *brevicornis* (Kirby, 1837); 4, *Cymindis* cf. *arctica* Kryzhanovskij et Emetz, 1979; 5, *Aphodius multiplex* Reitter, 1867; 6, *Cymbiodyta marginella* (Fabricius, 1792); 7, *Trechus* cf. *compactulus* Belousov et Kabak, 1996; 8, *Bembidion dauricum* (Motschulsky, 1844); 9, *Olisthopus sturmii* (Duftschmid, 1812); 10, *Pterostichus macer* (Marsham, 1802); 11, *P. mirus* (Tschitschérine, 1894); 12, *Amara aurichalcea* Germar, 1823; 13, *Porcinolus murinus* (Fabricius, 1794); 14, *Morychus ostasiaticus* Tshernyshev, 1997; 15, *Poecilus* cf. *ravus* (Lutshnik, 1922). Scale bars are 1 mm increments. Figure parts 1-9 and 10-15 correspond to upper and the bottom scale bars, respectively.



FIGURE 4. Subfossil beetle fragments from the Dubrovino assemblage; elytra (1-2, 7, 11, 13, 17), pronotum (3-4, 6, 8, 15), head (5, 9, 14, 16), and rostrum (10, 12). 1, *Otiorhynchus altaicus* Stierlin, 1861; 2-3, *O. obscurus* Gyllenhal in Schoenherr, 1834; 4, *O. pullus* Gyllenhal in Schoenherr, 1834; 5-6, *O. politus* Gyllenhal in Schoenherr, 1834; 7, *O. beatus* Faust, 1890; 8, *Stephanocleonus eruditus* Faust, 1890; 9, *S. isochromus* Suvorov, 1912; 10, *S. favens* Faust, 1884; 11, *Pissodes insignatus* Boheman in Schoenherr, 1843; 12, *Trichalophus biguttatus* (Gebler, 1832); 13, *Tychius albolineatus* Motschulsky, 1860; 14, *Phyllobius femoralis* Boheman in Schoenherr, 1842; 15, *Metadonus distinguendus* (Boheman in Schoenherr, 1842); 16, *Notaris aethiops* (Paykull, 1792); 17, *Tournotaris bimaculata* (Fabricius, 1787). Scale bars are 1 mm increments.

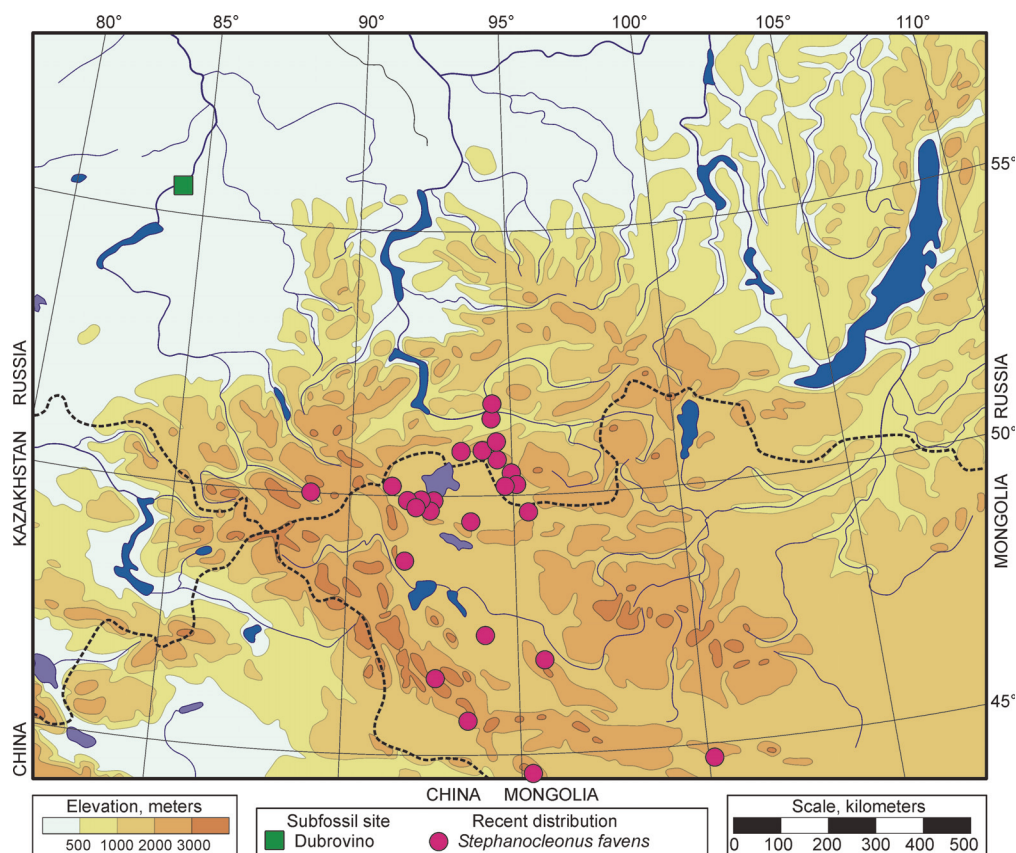


FIGURE 5. Late Pleistocene and modern ranges of *Stephanocleonus favens* Faust, 1884.

Quite diverse and abundant complex of species associated with moist habitats includes riparian species from the banks of streams (*Nebria rubrofemorata*; *N. subdilatata* Motschulsky, 1844), and species that occur near edge of shallow, standing water [*Elaphrus riparius* (Linnaeus, 1758); *Cymbiodyta marginella* (Fabricius, 1792); *Cercyon* sp.; *Tournotaris bimaculatus* (Fabricius, 1787); and *Notaris aethiops*]. *Pterostichus mirus* (Tschitschérine, 1894); *Amara aurichalcea* Germar, 1823; and *Aegialia abdita* Nikritin, 1975 inhabit river valleys, and *Helophorus* spp. represents the only aquatic beetle found.

The following species are associated with saline habitats: *Pogonus iridipennis* Nicolai, 1822; *Pogonus punctulatus* Dejean, 1828; and *Centorus rufipes* (Gebler, 1833).

Most of the phytophagous species from the assemblage feed plants of different families. Several species are associated with *Carex* L. (*Tournotaris bimaculatus*; *Notaris aethiops*), legumes (*Tychius albolineatus*; *Hypera ornata*; *Sitona* sp.), Brassicaceae (*Ceutorhynchus ignitus*), Umbelliferae (*Lixus paraplecticus*), chenopodiaceous

(*Metadonus distinguendus*) and *Salix* L. (*Lepyrus* spp.; *Chlorophanus sibiricus* Gyllenhal in Schoenherr, 1834). Two species that feed exclusively on *Larix* Mill. (*Hylobius excavatus* and *Pissodes insignatus*) and several moss-feeding species (Byrrhidae) were found. A significant share of fragments belong to predatory Carabidae (28 species) and Coccinellidae (2 species).

Comparison of the Fossil Species Composition with the Contemporary Fauna of the Region

The recent fauna of the upper Ob River territory is distinctly different from those found in the Dubrovino deposit. Only a quarter of the species occur today in the upper Ob River north of Novosibirsk (Table 2). Actually, these species range in different zones and have a broad ecological tolerance. Most of the species identified from the study site are absent in the upper Ob River region today. These species range to North, South or East from the region (Table 2).

Eastern species represent the highest proportion (28%) of the fossil assemblages. The recent range of eastern species includes the mountains of South Siberia. Some of them inhabit high elevation

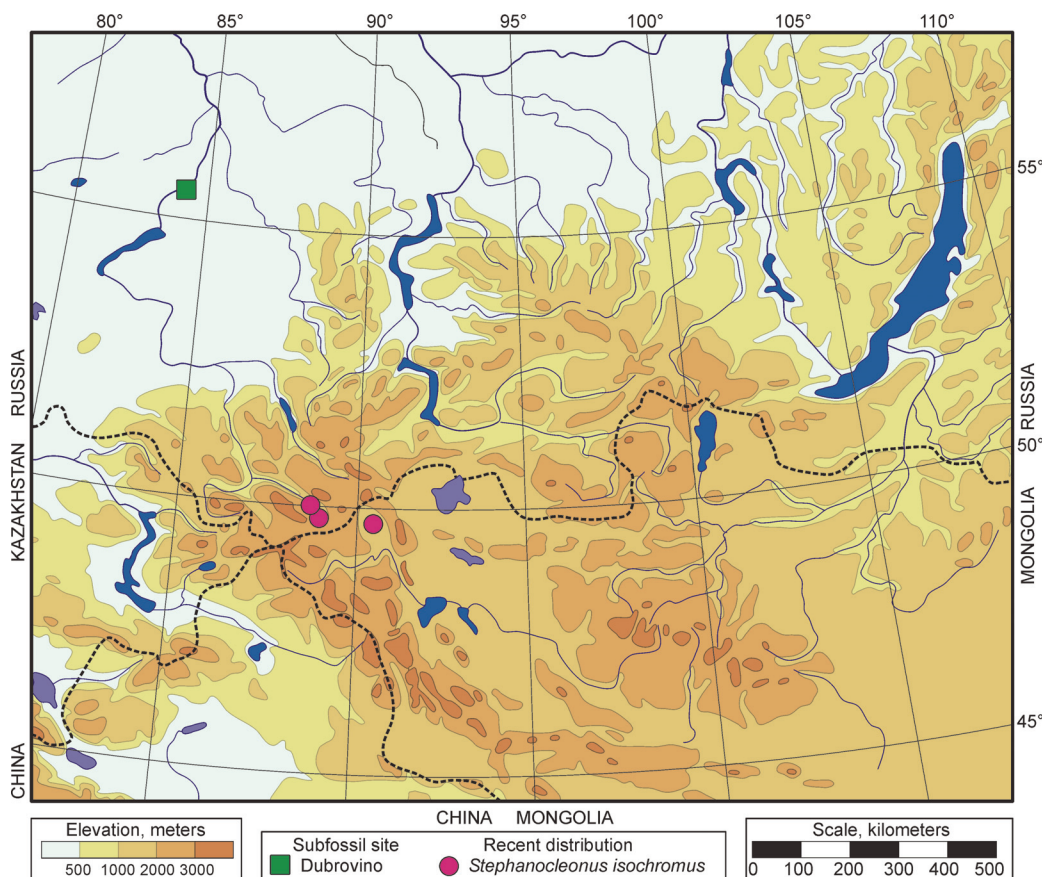


FIGURE 6. Late Pleistocene and modern ranges of *Stephanocleonus isochromus* Suvorov, 1912.

landscapes like mountain tundra or taiga (*Nebria rubrofemorata*; *Pterostichus tomensis*). Another species are the endemics of the mountain depressions and inhabit mostly steppe landscapes (Figures 5-7). Northern or boreal species were comparable with the recent ones. These are adapted to cold climatic conditions. Finally, southern species contribute one-fifth of the total species identified. These species are adapted to dry climatic conditions.

Reconstruction of MIS 2 Conditions at the Fossil Site

The species composition of insects in the Dubrovino deposit allows the reconstruction of a colder and more arid MIS 2 climate with strong steppic influences. The species with modern ranges to the north of the fossil site (*Diacheila polita*; *Pterostichus* (*Cryobius*) spp.; *Notaris aethiops*; *Lepyryus nordenskioldi*; and *Hypera ornata*) are indicators of colder-than-modern climate. The species of the steppe complex with modern ranges to south and sometimes to east from the Dubrovino site are indicators of dry climate. At the same time,

the presence of forest-dwelling beetle species, including wood-feeding beetles, indicates the existence of forest vegetation in close proximity to the site. Thus, there may have been steppe landscapes at the site, developed under cold climatic conditions during the Last glaciation (MIS 2).

DISCUSSION

It is useful to compare the fossil insect fauna identified from the Dubrovino site with fossil assemblages from other sites in the central and southern parts of the West Siberian Plain (Figure 1) (Zinovyev, 2006, 2016; Zinovyev et al., 2016; Dudko et al., 2017; Gurina et al., 2018). The closest assemblage, in terms of chronology and locality, is from the Novaya Surtaika site on the right bank of the Isha River near its confluence with the Katun River in the foothills of the Northern Altai (52°14' N, 85°55' E; 21,389±400 ¹⁴C BP [SPb-2299] and 18,248±250 ¹⁴C BP [SPb-2415], or 25,648±603 cal yr BP and 21,918±390 cal yr BP). The Novaya Surtaika fauna includes the cold-adapted beetles, i.e., *Diacheila polita*; *Pterostichus*

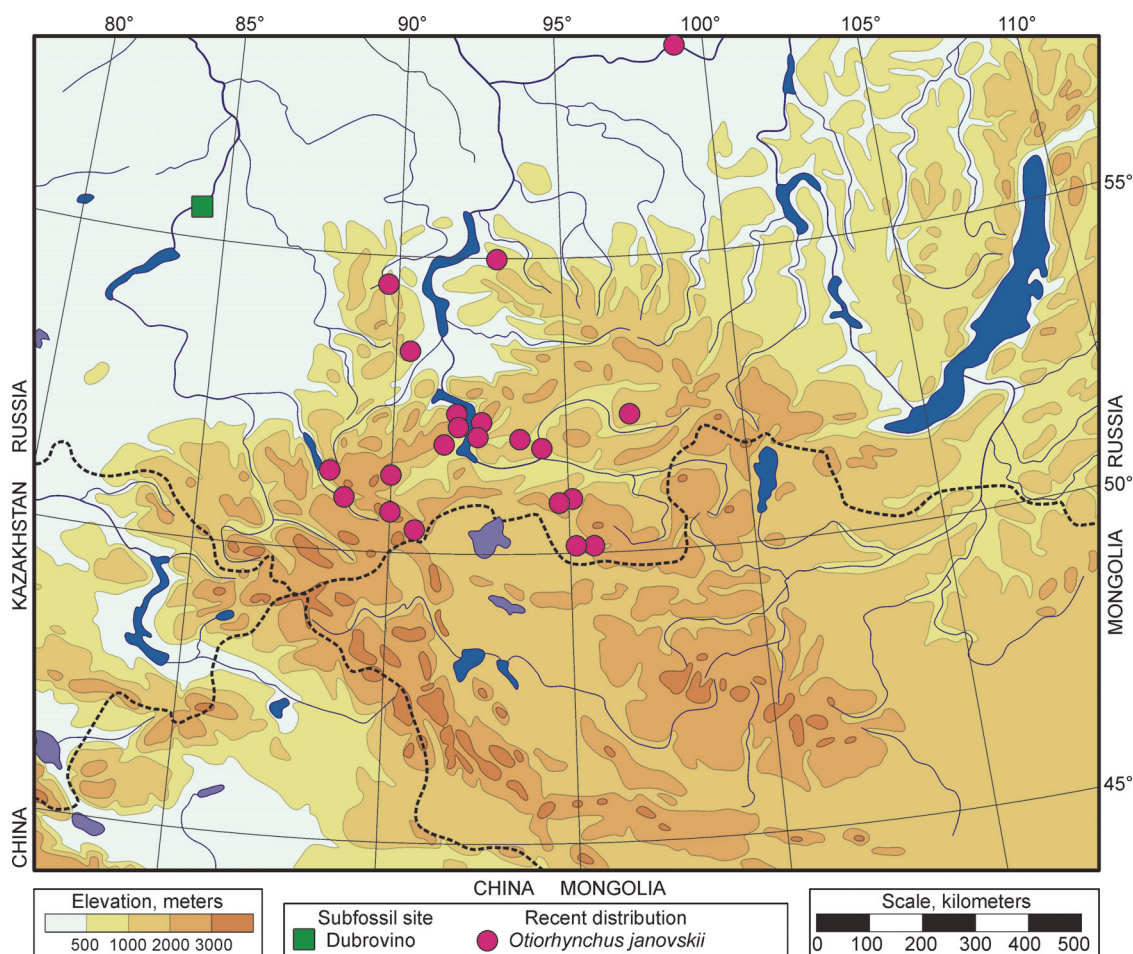


FIGURE 7. Late Pleistocene and modern ranges of *Otiorynchus janovskii* Korotyaev, 1990.

(*Cryobius*) sp.; *Hemitrichapion tschernovi* (Ter-Minassian, 1973); and *Cymindis vaporariorum* (Linnaeus, 1758), characterizing a colder climate than today. In addition, this complex includes beetle species typical of modern subalpine meadows of the humid regions of Atai-Sayan mountains (*Notiophilus jakovlevi* Tschitschérine, 1903; *Pterostichus drescheri* (Fischer von Waldheim, 1817); *Eutrichapion rhomboidale* (Desbrochers des Loges, 1870); *Notaris altaicus* (Legalov, 1997); *Otiorynchus grandineus*; and bark beetle species, i.e., *Phloeotribus spinulosus* (Rey in Eichhoff, 1883) and *Polygraphus poligraphus* (Linnaeus, 1758), developing on fir. The species composition of the assemblage allows us to conclude that environmental conditions in the foothills of the Northern Altai during MIS 2 coincide with the modern environments of the Central Altai region, at the elevation ca 1,700 m a.s.l. The presence of forest species indicates that this region served as a refugium for boreal, moisture-loving fauna (Dudko et al., 2017).

The sample from the center of the Kul'egan-2247 profile (60°25' N, 75°50' E; 21,815±225 ¹⁴C BP [SOAN-6837] or 26,091±553 cal yr BP) relates to the MIS 2 period in the central part of the West Siberian Plain. Cold-adapted, boreo-arctic and arctic beetle species predominate, including *Pterostichus costatus* (Ménétriés, 1851); *P. (Cryobius)* spp.; *Tachinus* cf. *arcticus* (Motschulsky, 1860); and *Curtonotus alpinus* (Paykull, 1790). Specimens of *Morychus* cf. *viridis* Kuzmina and Korotyaev, 1987 were also found. Steppe species were completely absent. The species composition of the assemblage reflects cold climate conditions in an open landscape much like modern tundra (Zinovyev, 2006).

Similar fossil insect assemblages have been described from the Tyurseda-Khadyta site in South Yamal (67°26' N, 69°57' E; 23,090±295 and 20,970±690 cal yr BP), and dominated by cold-adapted species such as *Tachinus* cf. *arcticus*; *Curtonotus alpinus*; *Pterostichus (Cryobius)* spp.; *Chrysolina* cf. *septentrionalis* (Ménétriés, 1851);

Lepyrus nordenskioldi; *Notaris aethiops*; and *Isochnus arcticus* (Korotyaev, 1977). The species composition of the Tyurseda-Khadyta assemblage reflects cold climate conditions and moss-dwarf shrub tundra landscapes (Zinovyev, 2016).

Thus, fossil beetle assemblages from the northern and central parts of the plain are all indicative of arctic environments associated with cold climate and tundra-like open landscapes. While in the south, there were likely areas of dry steppe formed under cold dry climate. In the region of the Altai foothills climate was cold but with moisture levels favourable for the development of woody vegetation. The Dubrovino fossil assemblage agrees with the reconstruction of cold climate in the central part of North Eurasia during MIS 2 (Volkova and Mikhailova, 2001).

The species composition of the Dubrovino assemblage is similar to that of the Kalistratikha (52°58' N, 83°37' E; the end of MIS 3: 24,438±350 ¹⁴C BP [SPb-1416] or 29,222±567 cal yr BP) and Bunkovo (55°04' N, 82°30' E; the end of MIS 2: 11,550±125 ¹⁴C BP [SOAN-8806] or 13,515±398 cal yr BP) assemblages. Phytophagous beetles, especially the weevils *Otiorhynchus altaicus* (= *O. karkaralensis* Bajtenov, 1974) and *O. ursus* (= *O. kasachstanicus* Arnoldi, 1964), dominate these assemblages (Zinovyev et al., 2016; Gurina et al., 2018). The meadow complex is poorly represented, dominated by *O. politus*. Only a single species characterizes the forest complex. These facts indicate the presence of specific tundra-steppe landscapes with interspersed sparse coniferous trees and sparse meadow vegetation in the southern territories of the West Siberian Plain.

The results of Quaternary insect studies from deposits of the Last Glacial Maximum (beginning and middle period of MIS 2) from the territories of Western and Eastern Europe, and North-East Siberia, also indicate cold climatic conditions (Nazarov, 1979, 1984; Ponel, 1995; Kasse et al., 1998; Ponel et al., 2003; Sher et al., 2005).

The time interval ca 23,000–22,000 cal yr BP is considered the coldest period of the late Pleistocene in the Northern Hemisphere. This was the time of maximum glaciation north-west Eurasia and exposed shelves of the Arctic Ocean, extending from the British Islands in the west to the Novosibirsk Islands in the east (Hughes et al., 2016) that

caused the formation of glacier-dammed lakes in the lowlands of West Siberia.

The climate was cold and dry due to large volumes of water frozen in continental ice sheets (Arkhipov and Volkova, 1994; Volkova et al., 2002; Simakova, 2006; Markova and Puzachenko, 2008; Simakova and Puzachenko, 2008; Hudges et al., 2016). The widest distribution of open tundra-type landscapes like periglacial forest-tundra, tundra-steppes or cold steppes with typical vertebrate faunas is characteristic of MIS 2 (ca 24,000–21,000 BP) (Simakova and Puzachenko, 2008).

CONCLUSION

A fossil insect assemblage from the Dubrovino site reflects cold and dry climate associated with the development of open landscapes with specific forest-steppe vegetation that differs from any modern environment. This reconstruction is supported by a number of cold- and dry-adapted species that are absent from this region today. Thus, the studied assemblage has no modern analogue, as the fossil assemblage species do not occur together in a single region today. Their modern ranges include localities that are north, south and east of the fossil locality. The characteristics of the fossil assemblage are compatible with the environmental conditions of the last (Sartan) glacial maximum in West Siberia, as reconstructed on the basis of entomological, vertebrate and palaeobotanical data (Arkhipov and Volkova, 1994; Borodin, 1996; Zinovyev, 2008). All these proxies clearly indicate the existence of cold-dry climate in the study region during MIS 2.

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