

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Quaternary rodent and insect faunas of the Urals and Western Siberia: Connection between Europe and Asia

Alexandr Borodin*, Evgenia Markova, Evgeniy Zinovyev, Tatiana Strukova, Maria Fominykh, Sergey Zykov

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, ul. 8 Marta, 202, Yekaterinburg 620144, Russia

ARTICLE INFO

Article history:

Available online 22 August 2011

ABSTRACT

The biogeographic groups of rodent (arvicoline) and beetle species in the modern fauna of the Urals and Western Siberia based on the longitudinal patterns of their present-day distribution are established. Occurrence of species of the Transpalearctic, West Palearctic (European), East-Palearctic, and Central-Palearctic faunal groups is estimated at different stages of the Late Quaternary development of the present-day fauna of the region. The border between the European and East-Palearctic faunal groups represents a vast territory where the ranges of the species included in those groups intersect. The border territory includes the Ural Mountains and the lowlands lying west and east of it (the East-European Plain and the West Siberian Plain). The biomes of those territories represent the North-Eurasian corridors providing migrations of species from the different faunal complexes in the west–east, east–west, and north–south directions. The importance of the study area for faunal correlations throughout the continent is determined by presence of the key arvicoline taxa traditionally used for correlation purposes (taxa *Dicrostonyx*, *Lagurus*, *Microtus gregalis*), and by the gradual change in faunal composition along the latitudinal gradient of environment at any given stage of the Quaternary. Transzonal faunal correlations within the Urals and Western Siberia integrating the evolutionary morphological studies of the key taxa and assessment of the faunal successions may serve as a basis for Trans-Eurasian correlation.

© 2011 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Nowadays, the Urals and Western Siberia represent a biogeographic crossroads in the Northern Eurasia where the ranges of European, Siberian and transpalearctic faunal elements intersect (Bol'shakov et al., 2000; Kozyrev et al., 2000; Zinovyev and Olshwang, 2003; Ravkin et al., 2009, etc.). The Urals has been suggested by Hewitt (1996, 2004) as a possible suture zone, i.e. an area with a clustering of contact zones, hybrid zones, and phylogeographic breaks (Remington, 1968; Swenson and Howard, 2005). According to the studies on clustering of contact zones and phylogeographic breaks (Hewitt, 2004; Swenson and Howard, 2004, 2005; Swenson, 2006), the distribution of species and genetic diversity within species are differently patterned within and among regions and biomes in relation to the histories of climatic changes and to geographical background. The patterns of geographical distribution of extant species and genetically distinct forms within species appear to reflect the biogeographical specificity of the Urals and Western Siberia determined by the

geographical position and geological history of the region during the Quaternary. Formation of modern biomes took place on the basis of the Pleistocene biomes that had been drastically transformed during the Late Quaternary, namely at the Late Pleistocene–Holocene transition. As compared to the European territory, which is relatively well-studied with respect to paleogeographic patterns and faunal relationships in the Late Quaternary (Markova, 1998; Taberlet et al., 1998; van der Made, 2011), the central part of Northern Eurasia has received much less consideration.

This paper brings attention to the following issues. First, do the different faunal elements (rodents and insects) reflect the same biogeographic patterns? Second, how is the crossroads position of the region is reflected in the Late Quaternary fossil record? Third, what are the perspectives of the region for faunal correlations throughout Europe and Asia? Four, how can the data on present-day distribution of the key taxa be used for biostratigraphical and paleoecological purposes?

To address those issues, the focus is on the two model groups – arvicoline rodents and beetles that represent homoiothermal and poikilothermal components of the biota. Those groups represent traditional objects of biostratigraphical, biochronological, and paleoecological studies (Agadjanian, 1979; Medvedev, 1979). Arvicolines are commonly employed in Quaternary biostratigraphy due

* Corresponding author. Fax: +7 343 2431584.

E-mail address: bor@ipae.uran.ru (A. Borodin).

to their rapid evolution, abundant fossil record, and wide geographical ranges. Their remains provide paleoenvironmental and paleoclimatic evidence on a number of levels (from the major vegetation types at regional and continental scales to local environments). Beetles are strictly confined by temperature conditions and show high levels of ecological and morphological stability. Beetle species are attributed to particular layers of terrestrial phytocenoses that allows their use as indicators of soil, humidity, insolation, and vegetation type.

The Quaternary history of fauna of the region can be divided into three stages (Smirnov, 1992, 1993, 2001): 1) gradual transformations of biomes during the Pleistocene; 2) revolutionary biotic changes (Upper Pleistocene–Holocene transition), and 3) recent (Holocene) stage of development of the biomes. This study focuses on the Late Pleistocene and Holocene stages of development of the present-day biomes in the region. Since the Late Pleistocene, the insects and rodents of the Urals and Western Siberia are represented by modern species that makes it possible to use the data on their zonal-biotopical requirements to reconstruct the landscape, climatic and environmental characteristics of the quaternary ecosystems and enables direct comparison of geographic distributions in living and extinct forms within the same species.

The study is aimed to outline directions and extent of transcontinental and regional faunal interchange through the territory of the Urals and Western Siberia during the Late Quaternary, and the development of present-day biomes of the regions (based on the key rodent and insect taxa).

2. Regional setting

The Ural Mountains represent a mountain system in the middle of Eurasia stretching from the Arctic coast in the north to the Mugodzhir Hills of Kazakhstan in the south. Geographically, the Ural Mountains mark the northern part of the border between the continents of Europe and Asia. The West Siberian Plain formed by the Trans-Ural peneplain that to the east transforms into an accumulative plain is one of the largest plains in the world, providing an opportunity to assess both the climatic gradients and the differences in geological history reflected in sedimentation characteristics (Arkhipov et al., 1977; Stefanovsky, 1997).

Latitudinal landscape zonality is strongly pronounced in the West Siberian Plain, where the tundra (arctic and subarctic), forest-tundra, taiga, forest-steppe, and steppe biomes are distinguished (Ilyina et al., 1985). In the Ural Mountains, the same biomes are present, although the latitudinal zonation is complicated by altitudinal gradients in elevated areas (Olenev, 1965). In Western Siberia, the large river valleys provide the pathways for the interosculation of southern and northern faunal elements.

Through the Quaternary, there were considerable differences from the modern geographical situation in the study area related to glaciations. The most recent radiocarbon data suggest that during the last 40,000 years the territory of the Ural-Siberian Arctic has not been covered by ice-sheets or ice-dammed water (Astakhov, 2009). According to the current knowledge of the Quaternary ice sheet history (Svendsen et al., 2004), as many as 4 major glaciations have been recorded in the Barents and Kara sea region during the last 150,000 years, but the glacier coverage was limited and did not expand onto the mainland. Thus, during the last 150,000 years the northern and central territories of the Western Siberia were not ice- or water-covered as previously believed (Arkhipov, 1965, 1997; Velichko, 1984).

During the Late Pleistocene, the territory experienced pronounced continental climate that could be regarded as arid and cool (Astakhov, 2009). Tundra-, tundra-steppe, and steppe-like

formations existed over the major part of the study area (Borodin, 1996; Smirnov, 2001). In the Holocene, the climate turned more humid due to the Flandrian transgression that has led to decline of the arid biomes, and formation of the taiga zone (Astakhov, 2009).

Zonal pattern of distribution of small mammal faunas was present in Western Siberia at all stages of the Quaternary (Borodin, 1996). Based on data known for the Ural Mountains, a zonal pattern in distribution of small mammal faunas is described by Smirnov (2001). Zonal distribution of sub-fossil insect faunas of this area is known for MIS 3 (Zinovyev, 2007, 2011).

The main source of materials for biostratigraphic and biochronological purposes is represented by fluvial and lacustrine-and-fluvial deposits in the West Siberian Plain and by karst cavities in the Ural Mountains. Moreover, there are some additional sources of faunal materials such as peat bogs with sub-fossil insect assemblages, and small mammal remains from the deposits of the infillings of burrows (Borodin et al., 1997). Because of the differences in sedimentation processes, the Quaternary fossil records in the two regions are not uniformly documented. In Western Siberia, the best documented is the southern part of the plain where the fossil record characterizes the entire time span from the Eopleistocene to the end of the Late Pleistocene. In the northern part of Western Siberia (Arctic zone), all the localities of micromammal and insect faunas are not older than Late Pleistocene. In the Ural Mountains, all the localities known up to the present are not older than the beginning of the Late Pleistocene.

There are four regional stratigraphic schemes developed for the region: the Urals and Trans-Urals (Stefanovsky, 1997); the Western Siberia without Trans-Urals (Unificirovannaya..., 2000) the Southern Pre-Urals and Southern Urals (Danukalova, 2010); and the Northern Pre-Urals (Shik et al., 2004).

3. Materials and methods

Much paleontological deduction is based on the principle of actualism, which implies using the present as the key to the past. At the same time, the principle of historicism provides a basis for understanding the processes in modern ecosystems. The two principles are indissolubly conjoined when one needs to deal with distribution patterns in recent animal species and in their direct ancestors (Smirnov, 1988; Benton and Harper, 2009). This paper uses both neontological and paleontological approaches in order to outline directions and extent of transcontinental and regional faunal interchange through the territory of the Urals and Western Siberia (Fig. 1) during the Late Quaternary development of present-day biomes of the regions. Distribution patterns of the key rodent and insect taxa in the modern biomes are compared with those inferred from the paleozoological analysis of the Late Pleistocene–Holocene sites known in the Urals and Western Siberia.

The analyzed material includes the authors' collections and also some published data (Fig. 2, Table 1). A total of 91 localities of small mammals were analyzed. To analyze the sub-fossil insect assemblages, the key localities (20 of 111 known for the study area) with the most representative insect faunas with radiocarbon dates were chosen (Table 1). In the steppe zone in the study area there are no localities of sub-fossil insects, in contrast to the steppes of lower reaches of Volga and Ural Rivers, where numerous insect faunas are described (Bidashko and Proskurin, 1987; Bidashko, 1994; Bidashko et al., 2005).

The data on modern distribution of rodent and insect taxa is taken from the literature (Medvedev, 1982; Andreeva and Eryomin, 1991; Kryzhanovskij et al., 1995; Borodin, 1997; Pavlinov et al., 2002; Zinovyev and Olshwang, 2003; Shenbrot and Krasnov, 2005; Zinovyev, 2006, 2007; Berdyugin et al., 2007; Markova et al., 2010). The chorological classification proposed by Chernov

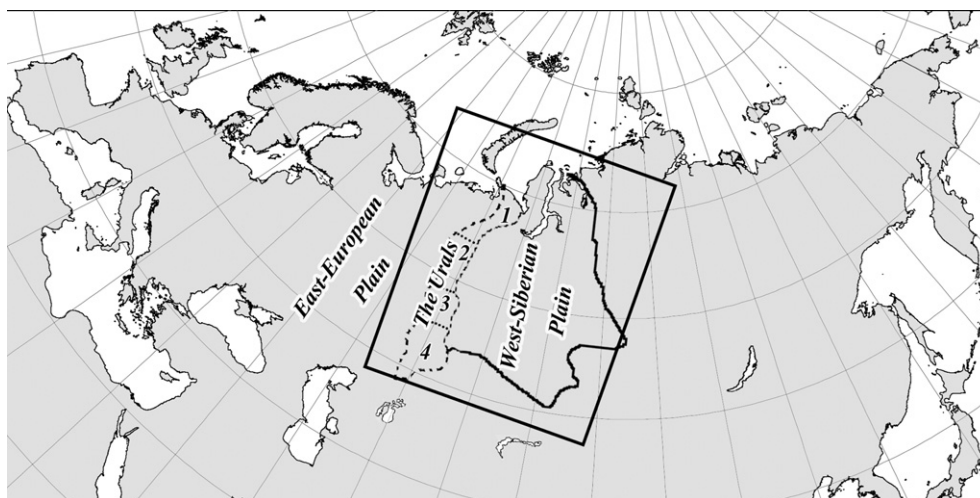


Fig. 1. Map showing general situation of the study area (indicated by a quadrangle frame) in the Northern Eurasia. Solid line – the border of the West-Siberian Plain, dashed line – the border of the Ural Mountains; figures indicate the areas of the Ural Mountains: 1 – Polar Urals, 2 – Northern Urals, 3 – Middle Urals, 4 – Southern Urals.

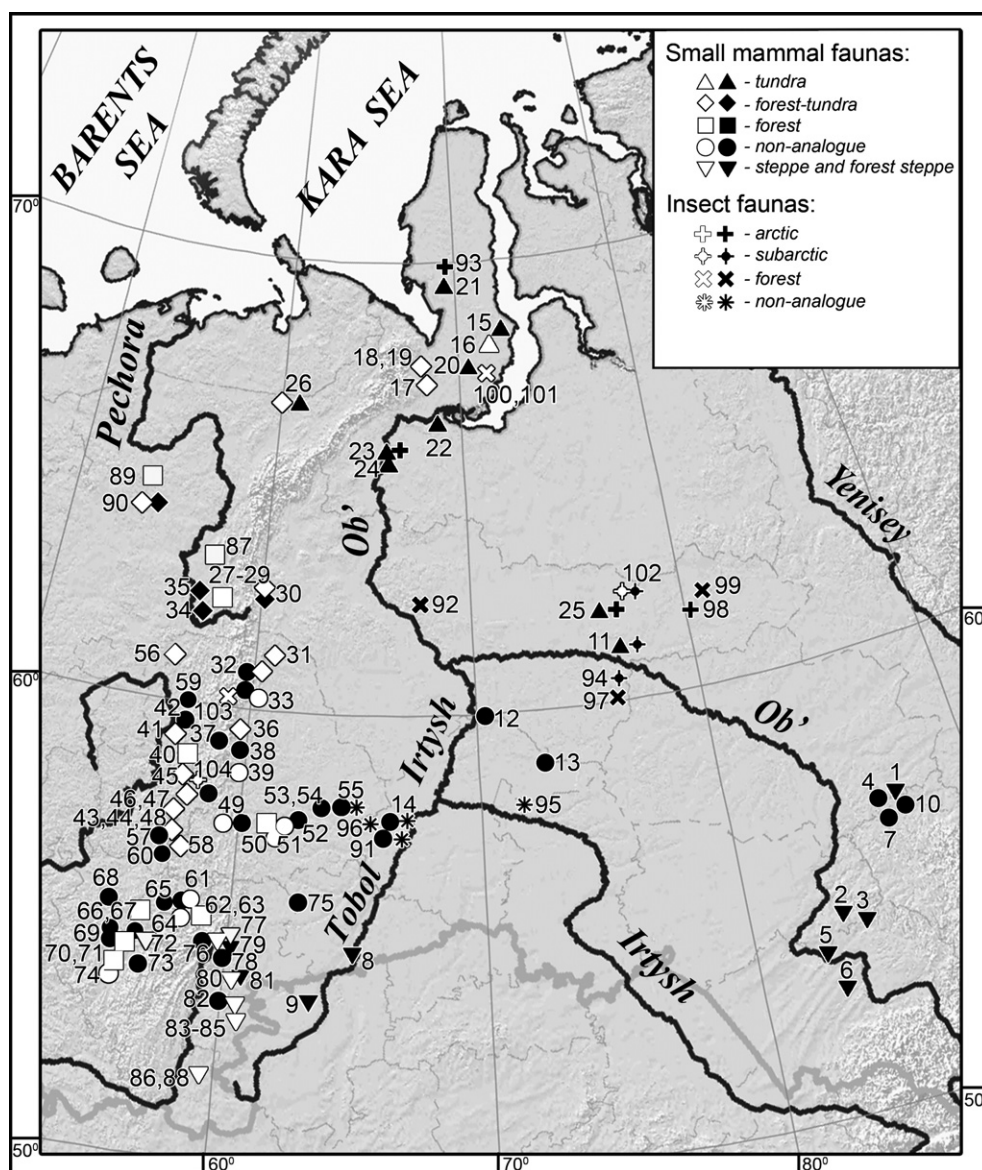


Fig. 2. The Late Pleistocene and Holocene sites of small mammal and beetle faunas in the Ural Mountains and West-Siberian Plain. Black signs indicate the sites of the Late Pleistocene age, white signs indicate the Holocene sites; 1–104 – identification numbers of the sites in Table 1.

Table 1

The Late Pleistocene and Holocene sites of arvicoline rodents (a) and beetles (b) in the Ural Mountains and Western Siberia. Taphonomic types of the sites: f – fluvial and lacustrine-and-fluvial type, k – karst cavities, nk – non-karst rocks, b – burrows of *Alopex lagopus*; p – peat bogs.

No	Arvicolines/ Beetles	Locality	Taphonomic type	Radiocarbon dates (when available), years BP	Citation
1	a	Mariinsk	f	—	Zazhigin, 1980
2	a	Shadrinskovo	f	—	Zazhigin, 1980
3	a	Tal'menka	f	—	Zazhigin, 1980
4	a	Shumikha	f	—	Zazhigin, 1980
5	a	Shelabolikha	f	—	Krukover, 2007
6	a	Belovo	f	—	Krukover, 2007
7	a	Alexeevskiy	f	—	Zazhigin, 1980
8	a	V. Alabuga	f	—	Stefanovsky et al., 2003
9	a	Vvedenskoe	f	—	Stefanovsky et al., 2003
10	a	Vtoraya Pristan'	f	—	Zazhigin, 1980
11	a, b	Mega	f	26,285 ± 590 (SOAN 982) 33,100 ± 2300 (IOAN 132)	Smirnov et al., 1986; Zinovyev, 2011
12	a	Bobrovka II (Gornyi Denshik)	f	—	Smirnov et al., 1986
13	a	Dem'yanka-Ostrov	f	—	Smirnov et al., 1986
14	a, b	Nizhnyaya Tavda (N. Tavda)	f	24,820 ± 750 (SOAN 4535) 27,400 ± 335 (SOAN 4534)	Strukova, 2003; Zinovyev, 2006, 2011
15	a	Ngoyun	f	Layer 8 – 14,208 ± 192 (IPAE-177)	Unpublished data
16	a	Nyamuyu-Nado I	f	—	Smirnov et al., 1986
17	a	Zveroboy	k	Layer 4 – 4100 ± 200 (GIN-9006)	Smirnov et al., 1999
18	a	Yangana-Pe 4	k	Bottom – 1720 ± 120 (GIN-10,157)	Smirnov and Golovachov, 1999
19	a	Yangana-Pe-3	k	23–103 cm – 2459 ± 80 (GIN-10,214)	Smirnov and Golovachov, 1999
20	a	Lyabtose	f	>33,316 (IPAE-64)	Unpublished data
21	a	Burrows of <i>Alopex lagopus</i>	b	—	Borodin et al., 1997
22	a	Gornokazymsk	f	—	Smirnov et al., 1986
23	a, b	430 km, 430 km "a"	f	24,000 ± 150 (IPAE-63)	Smirnov et al., 1986; Zinovyev, 2011
24	a	Pel'yakh-Yugan	f	—	Smirnov et al., 1986
25	a, b	Aganskiy Uval 1290/1	f	23,300 ± 500 (IPAE-176)	Borodin et al., 2001
26	a	Pymva-Shor	k	Layer 3 – 8500 ± 250 (GIN-9005), Layer 4 – 10,000 ± 250 (GIN-9004), Layer 5 – 11,125 ± 80 (TUa-1394)	Smirnov et al., 1999
27	a	Shezhim	k	—	Smirnov and Sadykova, 2003
28	a	Pikhtovka	k	—	Smirnov and Sadykova, 2003
29	a	Iordanskogo 1,2,3	k	—	Smirnov and Sadykova, 2003
30	a	Ushma-1	k	—	Teterina and Ulitko, 2002
31	a	Ushminskaya (Shaytan-Yama I)	k	—	Smirnov, 1996
32	a	Shaytanskaya (Ivdel river)	k	Layer 9 – 14,485	Smirnov, 1996
33	a	Cheremukhovo-1 sections 1, 2, 4	k	Section 1, 2: layer 5 – 4930 ± 75 (SBRAS – 5137); layer 12, horizon 53 – 28,520 ± 850 (AA-36,469), Section 4, layer 2 – 18,784 ± 379 (IEMEG-1259)	Strukova et al., 2005; Bachura and Strukova, 2002
34	a	Medvezhya Cave	k	Horizon A – 12,230 (LE-3059), horizon B – 16,130 (LE-3060), 17,980 ± 200 (LE-3061)	Smirnov, 1996; Bachura and Kosintsev, 2007
35	a	Studenaya Cave	k	—	Kochev, 1993
36	a	Lisya Cave	k	7213 ± 86 (IEMEG – 1338)	Bachura and Kosintsev, 2007
37	a	Zhilishche Sokola	k	—	Smirnov, 1996
38	a	Kakva-4	k	12,800 ± 300 (GIN-9444)	Smirnov et al., 1999
39	a	Lobvinskaya Cave	k	—	Smirnov, 1995
40	a	Bolshaya Makhnevskaya Cave	k	3628 ± 86 (IEMEG -1385)	Fadeeva and Smirnov, 2008
41	a	Makhnevskaya Ledyanaya Cave	k	<i>Arvicola terrestris</i> – 36,480 (+350, –310) (GrA-35,460)	Fadeeva and Smirnov, 2008
42	a	Makhnevskaya – 2	k	Horizon 6 – 11,146 ± 282 (IEMEG -1377), Horizon 9 – 24,811 ± 426 (IEMEG -1376)	Fadeeva and Smirnov, 2008
43	a	Kamen' Koziy	k	9467 ± 252 (IEMEG – 1332)	Fadeeva and Smirnov, 2008
44	a	Kamen' Lazarevskiy	k	—	Fadeeva and Smirnov, 2008
45	a	Kamen' Gorelyi	k	—	Fadeeva and Smirnov, 2008
46	a	Rasik	k	Horizon 21 – 12,680 ± 180 (GIN-10,569) Horizon 24 – 13,250 ± 180 (GIN-10,568) Horizon 27 – 13,330 ± 120 (GIN-10,567) Horizon 30 – >38,400 (GIN-10,566)	Fadeeva and Smirnov, 2008
47	a	Bolshoy Glukhoy	k	Horizon 13 – 10,607 ± 158 (IEMEG -1049), Horizon IX – 38,200 ± 900 (GIN-8404)	Smirnov, 1993; Fadeeva and Smirnov, 2008
48	a	Shaytanskiy (Chusovaya river)	k	Horizon 22 – <i>Clethrionomys rufocanus</i> 9970 ± 50 (CAMS-35,891) <i>Dicrostonyx</i> 12,530 ± 60 (CAMS-35,890)	Smirnov and Sadykova, 2003; Fadeeva and Smirnov, 2008
49	a	Shaytanoozerskiy Kamennyi Ostrov I	nk	Layer 4–5 – 22,460 ± 340 (SBRAS -3824), Layer 5 – 23,170 ± 1420 (SBRAS-3825)	Borodin et al., 2000b
50	a	Bosonogaya Cave	k	—	Strukova, 2003
51	a	Mironovskaya III Cave	k	Horizon 13 – 5340 ± 80 (Ki-15,949) Horizon 25 – 9380 ± 130 (Ki-15,942)	Rupysheva and Strukova, 2010

(continued on next page)

Table 1 (continued)

No	Arvicolines/ Beetles	Locality	Taphonomic type	Radiocarbon dates (when available), years BP	Citation
52	a	Pershinskaya I Cave	k	Layer 3 – 7380 ± 150 (SOAN -3824), Layer 6 – 15,580 ± 130 (GIN-11,225)	Strukova, 2000, 2003
53	a	Lebedkino	f	–	Strukova, 2000
54	a	Rechkalovo	f	25,500 ± 400 (GIN-11,226)	Borodin et al., 2003
55	a, b	Nikitino	f	24,480 ± 550 (SOAN 4537) 28,460 ± 800 (SOAN 4536)	Stefanovsky et al., 2002
56	a	Dyrovaty Kamen' (Vishera river)	k	–	Fadeeva and Smirnov, 2008
57	a	Verkhnegubakhinskaya Cave	k	–	Fadeeva and Smirnov, 2008
58	a	Peschera Tain	k	–	Fadeeva and Smirnov, 2008
59	a	Dolgogo Kamnya 1 Cave	k	–	Fadeeva and Smirnov, 2008
60	a	Dyrovaty Kamen' (Chusovaya river)	k	–	Smirnov, 1993
61	a	Dyrovaty Kamen' (Serga river)	k	Horizon 11 – 9327 ± 158 (IEMEG-1072)	Smirnov, 1993
62	a	Bazhukovo III	k	–	Smirnov, 1993
63	a	Tavra Rock-shelter	k	–	Smirnov, 1993
64	a	Oleniy	k	Layer 2 – 4840 ± 109 (IEMEG-180), Layer 2a – 5440 ± 117 (IEMEG-181), Layer 4 – 5122 ± 92 (IEMEG-182)	Smirnov, 1993
65	a	Arakaevo VIII	k	Layer 12 – 15,739 ± 590 (IEMEG-230)	Smirnov, 1993
66	a	Sukhorechensky Rock-shelter	k	Horizon 1–2 – 248 ± 158 (IPAE-107), Horizon 3–5 – 921 ± 204 (IPAE -110), Horizon 7–8 – 2047 ± 132 (IPAE-112), Horizon 9–12 – 3210 ± 121 (IPAE-114)	Smirnov, 1993
67	a	Bagyshkovo	k	3060 ± 124 (IPAE -145)	Smirnov, 1993
68	a	Bobylek	k	Layer 2a – 14,200 ± 400 (IPAE-164)	Smirnov, 1993
69	a	Idrisovskaya Cave	k	Horizon 8 – <i>M. gregalis</i> 21,970 ± 80 (CAMS-35,883) <i>Lagurus lagurus</i> 35,820 ± 390 (CAMS-35,881)	Smirnov et al., 1990; Smirnov and Sadykova, 2003
70	a	Ignatievskaya Cave (sections 2, 5)	k	Layer 2 – 14,038 ± 490 (IEMEG -366), Layer 3 – >27,500 (IEMEG-723)	Smirnov et al., 1990
71	a	Prizhim II	k	10–20 sm – 16,650 ± 400 (IPAE-32), 50–60 sm – 21,085 ± 630 (IPAE-37)	Smirnov et al., 1990
72	a	Serpievskaya I	k	50–60 sm – 16,585 ± 598 (IEMEG-722)	Smirnov et al., 1990
73	a	Serpievskaya II	k	30–40 sm – 25,200 ± 1800 (IPAE-46)	Smirnov et al., 1990
74	a	Sim I, III	k	–	Smirnov et al., 1990
75	a	Tyulenevo	f	–	Zykov and Maksimova, 2004
76	a	Ustinovo	k	Layer 1 – 4380 ± 170 (IPAE-47), Layer 3 – 12,400 ± 300 (IPAE-49)	Smirnov et al., 1990
77	a	Sukharysh Cave	k	–	Smirnov, 1992
78	a	Yuzhnyi	f	–	Stefanovsky et al., 2003
79	a	Miasskoe	f	–	Stefanovsky et al., 2003
80	a	Kamenka	k	–	Smirnov, 1992
81	a	Streletskoe	f	–	Stefanovsky et al., 2003
82	a	Syrtinskaya Cave	k	Layer 1 – 4029 ± 51 (IEMEG -1337), Horizon 13 – 13,990 ± 340 (SBRAS-5134), Horizon 18 – 17,160 ± 190 (SBRAS-5132), Horizon 24 – 22,050 ± 200 (SBRAS-5133)	Kuzmina, 2006; 2009
83	a	Verkhnyaya Gusikha	k	–	Kuzmina, 2006
84	a	Khudolaz	k	–	Kuzmina, 2006
85	a	Chernyshevskaya-III, V	k	–	Kuzmina, 2006
86	a	Alekseevskaya Cave	k	Horizon 1 – 1470 ± 90 (GIN-11,330), horizon 2 – 2550 ± 100 (GIN-11,331), horizon 3 – 4990 ± 100 (GIN-11,332), horizon 4 – 8100 ± 240 (GIN-11,333), horizon 5 – 8450 ± 200 (GIN-11,334)	Kuzmina, 2006, 2009
87	a	Sobinskaya Cave	k	–	Smirnov and Sadykova, 2003
88	a	Verblyuzhka-1	k	–	Kuzmina, 2006
89	a	Pizhma-1	k	Layer 5 – 9940 ± 150 (GIN-10,570)	Ponomarev et al., 2005
90	a	Sedyu-1	k	Layer 1 – 10,560 ± 280 (GIN-3224)	Kryazheva and Ponomarev, 2008
91	a, b	Mal'kovo	f	31,800 ± 350 (GIN-5338)	Maleeva and Stefanovski, 1988
92	b	Karymkary	p	131,000 ± 31,000 (TL date)	Arkhipov and Volkova, 1994
93	b	Syoyakha-Mutnaya (Se-Yakha)	f	30,700 ± 1100 (UPI-716)	Zinovyev, 2011
94	b	Kul'egan-2247	f	Point I – 21,815 ± 225 (SOAN-6837), Point II – 26,730 ± 250 (LOIA-8663)	Zinovyev, 2006
95	b	Skorodum	f	26,500 ± 550 (SOAN 4538)	Zinovyev, 2003
96	b	Andriyshino	f	41,900 ± 800 (GIN-5337)	Stefanovsky et al., 2007
97	b	Kul'egan-2241	f	10,700 ± 325 (IPAE-94)	Zinovyev, 2005
98	b	Bol'shaya Gorka	f	13,390 ± 150 (SOAN 7309)	Zinovyev, 2005
99	b	Zelyonyi ostrov	f	10,780 ± 70 (Le-8972)	Zinovyev and Nesterkov, 2003
100	b	Yadayakhodykha-4	f	3533 YR BP (Dendrochronological data)	Zinovyev et al., 2001
101	b	Yadayakhodykha-8	f	3769 YR BP (Dendrochronological data)	Zinovyev et al., 2001

Table 1 (continued)

No	Arvicolines/ Beetles	Locality	Taphonomic type	Radiocarbon dates (when available), years BP	Citation
102	b	Agan-4068/2	f	Layer 2 – 2200 ± 150 (IPAE-96), layer 3 (top), 9770 ± 300 (IPAE-97), layer 3 (bottom) – 11,400 ± 350 (IPAE-98)	Zinovyev, 2005
103	b	Loz'va-1	f	5770 ± 60 (SOAN-4539)	Zinovyev and Fadeyev, 2002
104	b	Shurala	f	27,600 ± 150 (Ki 15,505)	Zinovyev, 2011

(1975) for terrestrial animals was used. Following Chernov, species distribution pattern is considered to be (a) zonal when a species is confined to zonal habitats within a single zone, (b) polyzonal when a species is distributed in zonal habitats of two or more zones, (c) intrazonal when a species occurs in intrazonal habitats within a single zone, and (d) intrapolyzonal when a species is confined to intrazonal biotopes of two or more zones. Habitats are considered to be 'zonal' when related to zonal vegetation types (in Russian, plakor areas), 'extrazonal' when related to plakor vegetation of one zone penetrating into another zone (such as forests penetrating into tundra through the river valleys), 'intrazonal' when habitats are included in zonal vegetation but do not form an independent zone being more influenced by specific characteristics of local environments than by regional macroclimate (such as bogs, flood-plain vegetation, etc.), and 'azonal' when habitats are not strictly confined to any particular zone and could be found in different zones (for example, meadows, stony outcroppings, and other biotopes widely distributed over many zones).

Characterization of the species ranges considered the approaches of Smirnov (1988) and Brown et al. (1996). The major emphasis was on geographic characteristics such as range limits, longitudinal/latitudinal spread, and disjunct vs. continuous pattern of distribution. Patterns of intraspecific genetic differentiation of arvicoline rodents inferred from molecular and/or karyological data (Fedorov et al. 1999, 2003, 2008; Brunhoff et al., 2003; Haynes et al., 2003; Jaarola and Searle, 2004; Abramson, 2007) were also considered.

4. Rodent faunas

4.1. Key taxa

Arvicolinae species are commonly used as biostratigraphical, biochronological, and biozonational markers in interregional faunal correlations within the Quaternary, and are widely employed for paleoecological purposes (Smirnov et al., 1990; Maul and Markova, 2007). The present-day arvicoline fauna of the Urals and West Siberian Plain includes 15 native species: (*Ellobius* (*Ellobius*) *talpinus* Pallas, 1770, *Clethrionomys* (*Craseomys*) *rufocanus* Sundevall, 1846, *Clethrionomys* (*Clethrionomys*) *glareolus* Schreber, 1780, *Clethrionomys* (*Clethrionomys*) *rutilus* Pallas, 1779, *Lagurus* *lagurus* Pallas, 1773, *Myopus* *schisticolor* Lilljeborg, 1844, *Lemmus* *sibiricus* Kerr, 1792, *Dicrostonyx* *torquatus* Pallas, 1778, *Arvicola* *terrestris* Linnaeus, 1758, *Microtus* (*Pallasinus*) *oeconomus* Pallas, 1776, *Microtus* (*Alexandromys*) *middendorffi* Poljakov, 1881, *Microtus* (*Stenocranius*) *gregalis* Pallas, 1779, *Microtus* (*Microtus*) *agrestis* Linnaeus, 1761, *Microtus* (*Microtus*) *arvalis* Pallas, 1778 (obscurus form), *Microtus* (*Microtus*) *rossiaemeridionalis* Ognev, 1924 (= *Microtus* *levis* Miller, 1908), and one introduced species – *Ondatra* *zibethica* Linnaeus, 1766.

This paper follows the taxonomy and nomenclature proposed by Pavlinov (2003) with some minor changes. In particular, *Clethrionomys* Tilesius, 1850 is used as a valid name for red-backed voles according to the latest taxonomic interpretation by Tesakov et al. (2010).

Besides the species occurring in the present-day fauna of the Urals and West Siberian Plain, there are several taxa that are known for the Late Pleistocene and Pleistocene–Holocene transition (Smirnov et al., 1986; Borodin, 1996, 2009). Among those, the genus *Eolagurus* Argyropulo, 1946 has disappeared from the region due to range contraction. There are several extinct taxa: †*Dicrostonyx* *gulielmi* Sanford 1870, †*Dicrostonyx* *henseli* Hinton 1910, and †*Microtus* (*Pallasinus*) *?malei* Hinton 1907. Taxonomic status of the extinct taxa is rather problematic (see Zazhigin, 2003; Borodin, 2009 for details).

This study primarily focuses on the native species. However, the data on *O. zibethica*, acclimatized in the region in the 20th century, can also be used for taphonomic inferences and dating of the bone-bearing layers of Late Holocene age.

4.2. Present-day distribution patterns in arvicolines

4.2.1. Zonal patterns of species distribution

Zonal patterns of species distribution and zonal complexes of small mammals in the study area are widely discussed from both neontological (e.g., Shvarz and Pavlinin, 1960; Ravkin et al., 2009), and paleontological viewpoints (e.g., Vangengeim, 1977; Borodin, 1996; Smirnov, 2001; Smirnov et al., 2007). In general, all the arvicoline species known for the study area can be divided into the three groups according to their distribution in modern landscape-geographic zones: 1) species with zonal pattern of the present-day distribution, 2) intrapolyzonal species, 3) polyzonal species.

4.2.1.1. Species with zonal pattern of distribution. This group includes the species which are restricted to one of the modern biomes in the study area. Among those, *D. torquatus*, *L. sibiricus*, *M. middendorffi* are confined to tundra, *M. schisticolor*, *C. rutilus*, *C. rufocanus* inhabit boreal forests (taiga zone). *L. lagurus* and *E. talpinus* are restricted to the modern steppe zone. At present, those species are clearly confined to zonal types of habitats (although they could also be found in azonal and intrazonal biotopes within the respective zone). Where available, they can use extrazonal elements of landscape to expand their ranges to a neighboring zone. This kind of dispersal is the most typical for *C. rutilus* which occurs in water-flood forests of southern tundra (Borodin, 1997), forest parks, and gardens, and for *C. rufocanus*, which is found in urban lands (Chernousova, 2001).

4.2.1.2. Intrapolyzonal species. The group includes the species related to intrazonal biotopes, and distributed in several zones (*M. oeconomus*, *A. terrestris*). *M. oeconomus* primarily inhabits boreal forest zone, and partially subarctic tundra, forest-steppe, and steppe zones. *A. terrestris* inhabits intrazonal biotopes in all zones from subarctic tundra to steppe. Both species do not avoid anthropogenically transformed areas. *O. zibethica*, introduced in the region in the 20th century, should also be included in the group of intrapolyzonal species.

4.2.1.3. Polyzoal species. The group includes widespread species whose modern ranges encompass more than one landscape-

geographic zone where they are confined to zonal habitats, or azonal landscapes within particular zones. Those are the species related to nemoral and boreal forests (*C. glareolus*, *M. agrestis*), steppe and tundra (*M. gregalis*), forest-steppe and azonal landscapes in steppes, nemoral and southern boreal forests (*M. arvalis obscurus* and *M. rossiaemeridionalis*). *C. glareolus* is an inherent species of nemoral forests that occurs in wide range of zonal habitats; it is also present in boreal forests of the Urals and Western Siberia. In the taiga zone, *C. glareolus* is considered to be more common in grass forest habitats, being more abundant in secondary forests than in native dark coniferous forests (Koneva, 1983). *M. agrestis* is often regarded as a species of the taiga complex (Smirnov et al., 2007). However, the species occurs in a wide range of habitats throughout Europe where it could be regarded as polyzonal (van Kolfshoten, 1995), inhabiting woods, grasslands, upland heaths, dunes, marshes, peat bogs and riverbanks, tending to prefer damp areas. Here, *M. agrestis* is considered as a species of azonal forest habitats with a polyzonal pattern of distribution. In the study area, *M. agrestis* has expanded its modern range through flood-plain forests into subarctic tundra, and forest-steppe. *Clethrionomys* voles are related to zonal forest habitats. *C. glareolus* expands its range using extrazonal elements of landscape such as flood-plain forests in forest-steppe, and steppe. Both *C. glareolus* and *M. agrestis* also occur in forest parks and gardens (Chernousova, 2001). *M. arvalis obscurus* and *M. rossiaemeridionalis* expand their ranges using azonal elements of landscape including those of natural (meadows), and anthropogenic origin (agricultural lands, inhabited territories, deforested areas, uncultivated grounds, etc.). *M. gregalis* inhabits river valleys in subarctic tundra, steppe, forest-steppe (zonal and azonal habitats), and alpine meadows (Gromov and Polyakov, 1977).

4.2.2. Present-day longitudinal patterns of arvicoline species distribution

According to the modern distribution maps (Pavlinov et al., 2002; Shenbrot and Krasnov, 2005), the longitudinal distribution patterns of the arvicoline species known for the study area based on the range limits are as follows:

- I. **Transcontinental pattern of distribution.** The only species of arvicolines inhabiting the Eurasian continent from the Atlantic to the Pacific coast is the anthropogenically introduced species *O. zibethica*, the modern range of which encompasses the whole Holarctic.
- II. **West Palearctic (“European”) group.** Modern ranges of the species included in this group reach the Atlantic coast as a western limit, eastward to Siberia to approximately 98°E (*C. glareolus*), 105°E (*M. arvalis obscurus*), 133°E (*M. agrestis*), and 135°E (*A. terrestris*). The group includes the species with polyzonal (*C. glareolus*, *M. agrestis*, *M. arvalis obscurus*), and intrapolyzonal distribution (*A. terrestris*).
- III. **East-Palearctic group.** Modern ranges of the species included in this group reach the Pacific coast or Beringia as an eastern limit and extend westward to the Northern Urals (*M. middendorffi*), to northern European Russia (*D. torquatus*, *L. sibiricus*, and *M. gregalis*), to Northern Europe (*C. rutilus*, *C. rufocanus*, *M. schisticolor*), and to Northern and Central Europe (*M. oeconomus*, isolated populations), but do not reach Western Europe and the Atlantic coast. Some of the species included in this group occur in the western parts of North America (*M. oeconomus*, *C. rutilus*). The group includes inhabitants of tundra (*D. torquatus*, *L. sibiricus*, *M. middendorffi*), boreal forests (*C. rutilus*, *C. rufocanus*, *M. schisticolor*), steppe and tundra (*M. gregalis*), and also one intrapolyzonal species (*M. oeconomus*).

- IV. **Central-Palearctic group.** This includes the species distributed in the central (continental) part of Northern Eurasia. These are the species with zonal steppe (*E. talpinus*, *L. lagurus*), and polyzonal patterns of distribution (*M. rossiaemeridionalis*).

The shape of the species' ranges is considered according to Brown et al. (1996). The species included in the groups II and III have long ranges with east–west distances greater than north–south distances. The north–south distance gradually changes with longitude. Thus, the species included in group II (West Palearctic group) have longer north–south distances in the western parts of their ranges whereas the eastern portions of the ranges are rather attenuated. In *M. arvalis* and *C. glareolus*, the distribution appears to be attenuated starting from Western Siberia, whereas in *M. agrestis* and *A. terrestris*, the range narrowing occurs only in Eastern Siberia.

The species of group III (Eastern Palearctic group) exhibit a reverse pattern of range shape, having the attenuated portions in the western parts of their ranges. It is especially pronounced in the species related to the boreal forest zone (*C. rutilus*, *C. rufocanus*, *M. schisticolor*), and in *M. oeconomus*.

Isolated populations outside the main range of the species included in groups II and III are usually confined to the territories where the range experiences attenuation (in the east for the western group and in the west for the eastern group). This could be regarded as indirect evidence of colonization–extinction dynamics, ecological limiting factors, or a combination.

A disjunct (patchy) range is known for *M. gregalis* (included in group III), usually regarded as a result of the decline of the species in some parts of its ancient range.

In group IV (Central-Palearctic group), all the species have ranges with almost equal north–south and east–west distances. The steppe species (*L. lagurus*, *E. talpinus*) have relatively small ranges confined to the center of Northern Eurasia, whereas *M. rossiaemeridionalis* is more widely distributed. The latter is known as a facultative synanthropic species (Tikhonova et al., 2009). Occasional introduction of *M. rossiaemeridionalis* by human is known for Svalbard, and hypothesized for the isolated populations outside the modern continuous range (Sokolov and Bashenina, 1994).

4.2.3. Spatial vs. genetic patterns of intraspecies differentiation

Comparison of the patterns of species distribution with the patterns of intraspecific genetic differentiation established three patterns in the arvicolid species known for the study area.

- 1) The species which are represented in the Urals and Western Siberia by the most eastern phylogeographic lineage (and/or genetically distinct form) known for the species. These are the species of West Palearctic group.

M. agrestis is represented in the study area by the eastern mtDNA lineage (Jaarola and Searle, 2004). The highest genetic diversity (based on molecular genetic markers) is found in the European part of the species range.

M. arvalis in the study area is represented by the eastern karyotypic form (*obscurus*). In general, the *obscurus* form is considered to belong to the eastern mtDNA lineage (Haynes et al., 2003; Heckel et al., 2005; Tougaard et al., 2008). The highest genetic diversity (based on molecular genetic markers) is found in the European part of the species range (within *arvalis* form).

C. glareolus in the study area is represented by the eastern (Uralian) lineage that inhabits the territories from European Russia to the eastern limit of the species range (Western Siberia

and Altai) (Deffontaine et al., 2005). The highest genetic diversity (based on molecular genetic markers) is found in the European part of the species range.

- 2) In the Eastern Palearctic group, *L. sibiricus* and *M. schisticolor* are represented in the study area by the most western mtDNA phylogeographical groups known for the species. In *L. sibiricus*, the western mtDNA phylogeographical group (Fedorov et al., 2003) is distributed from the western limit of the species range to the Lena River. In *Myopus*, the western clade (mtDNA) is distributed from the western limit of the species range to the Yenisey River (Fedorov et al., 2008).

Phylogeographic studies in *M. gregalis* have shown that genetic distance between the narrow-skulled vole from the northern (Yamal peninsula) and the southern (Omsk, Novosibirsk) parts of Western Siberia is less pronounced than the distance between those and the more eastern populations of the species (Mongolia, Buryat Republic, Chita region) (Abramson, 2007).

For *M. middendorffi*, there are no phylogeographic data available. There are subspecies – *M. middendorffi ryphaeus* (Northern Urals and Yamal), *M. middendorffi middendorffi* (from the Taz River basin to the Kolyma River), and *M. middendorffi hyperboreus* which is distributed from the Taymyr peninsula to the Kolyma River and is sometimes regarded as a separate species *Microtus hyperboreus* (Gromov and Polyakov, 1977).

- 3) Two species (*M. oeconomus* and *D. torquatus*) exhibit phylogenetic splits between the populations occurring in the regions extending eastward and westward of the Ural Mountains. In *D. torquatus*, there are two different phylogeographic groups established based on mtDNA in the study area: the most western group occurs in the north of European Russia, and another one in the north of Western Siberia (Fedorov et al., 1999). For *M. oeconomus*, the Urals is a border between the North European and Central Asian mtDNA lineages (Brunhoff et al., 2003).

4.3. Modern vs. paleontological patterns of arvicoline species distribution

From the Late Pleistocene to Holocene and modern time, the arvicoline species known for the study area experienced either range contractions or expansions. The north–south changes in the species ranges could be traced from their northernmost and southernmost findings in the Late Pleistocene and Holocene sites.

The species of tundra habitats (*D. torquatus*, *L. sibiricus*, *M. middendorffi*) have experienced significant northwards range contraction since the Late Pleistocene to Holocene and the present. The southern boundaries of the tundra species' distributions based on the southernmost findings in the fossil record (Maleeva and Stefanovski, 1988; Smirnov et al., 1990, 1999; Smirnov, 1993; Borodin et al., 2000a,b,c; Fadeeva and Smirnov, 2008), and based on modern data (Shenbrot and Krasnov, 2005; Berdyugin et al., 2007) are as follows (Late Pleistocene/Holocene/Modern): *D. torquatus* – 52°55' N/54°54' N–56°33' N/63° N; *L. sibiricus* – 54°50' N/56°33' N/65° N, *M. middendorffi* – 57°08' N/60°24' N/62° N.

The steppe and semi-desert species (*Eolagurus luteus*, *L. lagurus*, *E. talpinus*) have experienced southwards range contraction in the study area. The northern boundaries of distribution based on the fossil record (Smirnov, 1996; Strukova, 2000; Teterina and Ulitko, 2002) and modern data are as follows (Late Pleistocene/Holocene/Modern): *E. luteus* – 57°41' N/57°27'–60°42' N/48°50' N; *L. lagurus* – 60°42' N/59°36'–60°44' N/about 55°50' N; *E. talpinus* – 56°14' N/57°27' N–57°29' N/about 56° N. The most significant southwards range contraction is found in *E. luteus*, which nowadays occurs in semi-deserts of Eastern Kazakhstan, China, and Mongolia,

where the species is confined to the mosaic of intrazonal biotopes with forbs avoiding extremely dry or wet habitats and gramineous herb associations (Ismagilov and Bekenov, 1969). *E. luteus* became extinct in the study area (between 60° N and 51° N) during the Holocene. In the more southern areas (Northern Kazakhstan), extinction of the yellow steppe lemming took place in the 19th century (Kalabukhov, 1970).

The present-day distribution of arvicoline taxa nowadays confined to tundra (*Dicrostonyx*, *L. sibiricus*, *M. middendorffi*), steppe (*L. lagurus*), and semi-desert (*E. luteus*) and the most latitudinally distant sites where those species are recorded in the Late Pleistocene assemblages are shown in Fig. 3.

Another pattern of range contraction is known for *M. gregalis* (Chaline, 1972; Smirnov et al., 1986; Rekovets, 1994; Khenzykhenova, 1996; Maul and Markova, 2007; Markova et al., 2010). Disjunction of the ancient continuous range of the species has led to the present-day polyzonal pattern of its distribution, so that the species is present in modern tundra and steppe zones in the study area. The present-day distribution (dashed area) of *M. gregalis* and the sites where this species is recorded in the Late Pleistocene assemblages are shown in Fig. 4.

Intapolyzonal species in the study area appear to have widened their range to the north from the Late Pleistocene to the Holocene and present time. In the Late Pleistocene faunas, the most northern findings of *M. oeconomus* and *A. terrestris* are known at about 60° N (Borodin et al., 2000a,b,c). In the Holocene faunas (including those of Early-, Mid-, and Late-Holocene time) they are known from latitudes to 67° N in the Urals (Smirnov et al., 1999). *A. terrestris* is also known from the Late Holocene bone-bearing layers of burrows of *Alopex lagopus* at the same latitude (about 67° N) in the Yamal Peninsula (Borodin et al., 1997). Nowadays, *A. terrestris* reaches above 70° N using the big river valleys, and *M. oeconomus* is present at least to 75° N (Shenbrot and Krasnov, 2005).

Clethrionomys species appear to have widened their range to the north from the Late Pleistocene to Holocene. Based on the fossil data (Smirnov, 1995, 1996; Smirnov et al., 1999; Borodin et al., 2000a,b,c; Teterina and Ulitko, 2002; Fadeeva and Smirnov, 2008), and modern distribution of the species (Shenbrot and Krasnov, 2005; Berdyugin et al., 2007), the most northern findings are as follows (Late Pleistocene/Holocene/Modern): *C. rufocanus* – 61°53' N/67°08'–67°43' N/above 68° N; *C. rutilus* – 60°24' N/59°38'–60°24' N/above 68° N; *C. glareolus* – 58°55' N/59°28' N/about 65° N in the Urals and 55° N in the east of Western Siberia (Berdyugin et al., 2007); *Clethrionomys* ex gr. *rutilus-glareolus* – 60°42' N/67°43' N/65–68° N.

The fossil remains of *M. schisticolor* are known from 54°50'–60°42' N in the Late Pleistocene, and 56°45'–67°43' N during the Holocene (Smirnov, 1993; Smirnov et al., 1999; Smirnov and Sadykova, 2003; Fadeeva and Smirnov, 2008). Nowadays it inhabits the altitudes from 54° to 62° in the Urals and reaches the Arctic Ocean through the river valleys (Berdyugin et al., 2007).

The northernmost findings of *M. agrestis* in the Late Pleistocene, Holocene and modern faunas – 60°42' N/67°08'–67°43'/68° N (Smirnov, 1993; Smirnov et al., 1999; Smirnov and Sadykova, 2003; Berdyugin et al., 2007; Fadeeva and Smirnov, 2008). Thus, *M. agrestis* is present in the northernmost localities known for the study area from the Early Holocene. The faunas comprising *M. agrestis* include also tundra and forest species (Smirnov et al., 1999). Nowadays, *M. agrestis* is present in forest-tundra, and in flood-plain biotopes in the southern tundras. The most southern findings of *M. agrestis* in the study area (Late Pleistocene/Holocene/Modern) are: 54°5' N/51°23'–52°08' N/52° N.

M. arvalis sensu lato is known in the sites between 51°23' and 57°39' N during the Late Pleistocene and the entire Holocene. A considerable increase in abundance of common voles described for

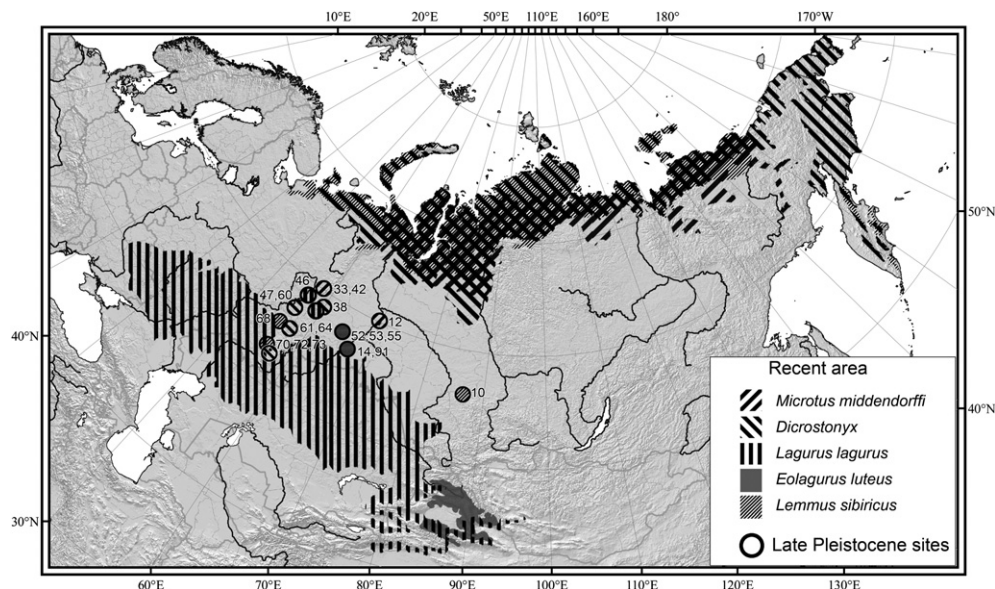


Fig. 3. Map showing the present-day distribution (dashed areas) of arvicoline taxa nowadays confined to zonal tundra (*Dicrostonyx*, *Lemmus sibiricus*, *Microtus middendorffi*), steppe (*Lagurus lagurus*), and semi-desert (*Eolagurus luteus*), and the most latitudinally distant sites where these species are recorded in the Late Pleistocene assemblages (dashed circles). Identification numbers of the sites are given in Table 1.

the Late Holocene faunas of the Middle and Southern Ural Mountains coincides with increased anthropogenic effect on natural ecosystems (Smirnov et al., 1990; Smirnov, 1993). At present, the northern limit of the common voles' distribution occurs at least at 60° N in the Urals (based on the southernmost karyologically dated findings of *M. arvalis obscurus* (Markova et al., 2010)). In Western Siberia, the northernmost findings of *M. arvalis* sensu lato are known at 61° N (Starikov et al., 2009). Near the northern limit of their distribution, the common voles are primarily confined to anthropogenically transformed biotopes and human settlements. Based on that, it is possible to suggest that expansion of the common voles' range to the north is relatively recent. However, common voles might constitute a part of remains identified as

Microtus ex gr. *arvalis-agrestis* in the localities of the Late Pleistocene and Holocene age at latitudes from 57°23' to 60°32' N (Fadeeva and Smirnov, 2008 and others).

To assess the longitudinal changes in distribution patterns of the arvicoline species during the Late Pleistocene and Holocene, the data on their occurrence in the localities of the Urals and Western Siberia (Table 1) are compared with those known for Europe and Eastern Siberia (Chaline, 1972; Sutcliffe and Kowalski, 1976; Nadachowski, 1982; Sher, 1984; Rekovets, 1994; Markova et al., 1995; Khenzykhenova, 1996; Maul and Markova, 2007; Panasenkov and Tiunov, 2010; Erbaeva et al., 2011). Three patterns of longitudinal range dynamics could be detected.

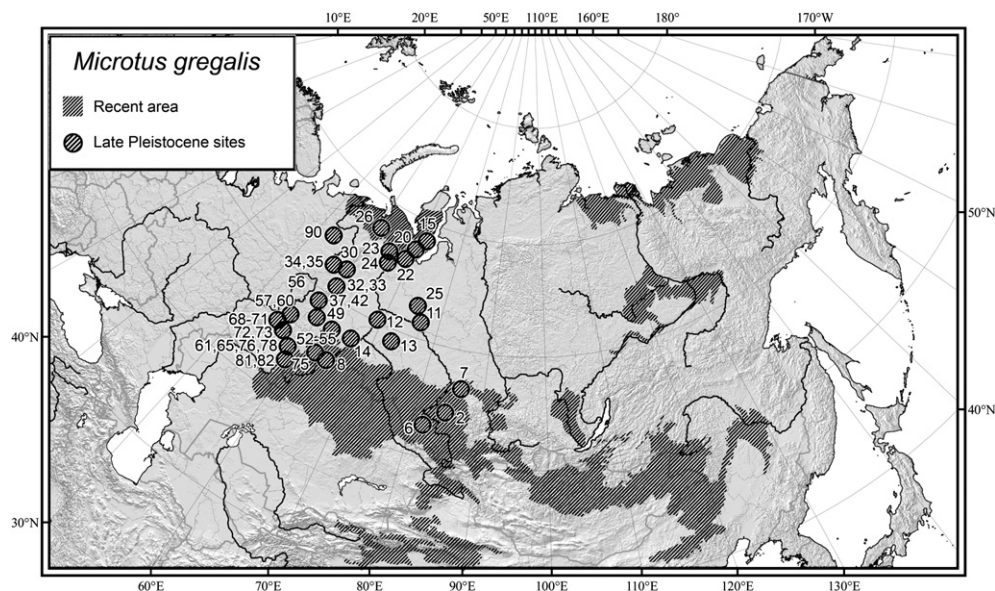


Fig. 4. Map showing the present-day distribution (dashed area) of arvicoline species *Microtus gregalis* confined to modern tundra, forest-steppe, and steppe and the sites where this species is recorded in the Late Pleistocene assemblages (dashed circles). Identification numbers of the sites are given in Table 1.

First, there is a group of species that exhibited the longitudinal range contractions from the Late Pleistocene to the Late Holocene and modern time. These are all the species of tundra habitats (*D. torquatus*, *L. sibiricus*, *M. middendorffi*) and steppe–semi-desert landscapes (*L. lagurus*, *E. luteus*, *E. talpinus*). The changes in their limits reflect the changes in zonality patterns from the Late Pleistocene to the present time, namely the decline of the specific Pleistocene biome called Mammoth Steppe (Guthrie, 2001), or tundra-steppe inhabited by the hyperboreal mammal complex in the study area (Smirnov, 2001). Another species whose range dynamics from the Late Pleistocene to Holocene and present day are strongly related to the tundra-steppe biome is *M. gregalis*. The major westward expansion is dated to the Late Glacial when the species was present in the fauna of the British Isles (Sutcliffe and Kowalski, 1976), southern France (Chaline, 1972; Villa et al., 2010) and Spain (Cuenca-Bescós et al., 2010). The easternmost findings of *M. gregalis* in the Late Pleistocene are known from the Aldan River valley (Simonov and Tesakov, 2007). Range contraction is also detected in the intrapolyzonal species *M. oeconomus*, the westernmost findings of which are known in the Late Pleistocene of Spain (Cuenca-Bescós et al., 2010).

Second, there are several species that do not show considerable longitudinal changes in their distribution during the studied time span (Late Pleistocene and Holocene). These are the species of boreal forests (*M. schisticolor*, *C. rutilus*, *C. rufocanus*), *M. agrestis*, and intrapolyzonal species (*A. terrestris*). Although no substantial longitudinal changes could be detected in the distribution patterns, the abundance and occurrence vary significantly within the ranges of those species during the Late Pleistocene and Holocene.

A third group of species has exhibited range expansion from the Late Pleistocene to the Late Holocene and modern time. Those are *C. glareolus* and *M. arvalis* sensu lato, natural expansion of which in the Urals and Western Siberia has proceeded during historical time. Thus, *C. glareolus* widens its range using deforested areas in the boreal forests, and the common voles widely use different kinds of anthropogenically transformed areas to expand their range. Both *C. glareolus* and *M. arvalis* represent the West Palearctic elements in the fauna of the study area.

The species of West Palearctic group increased their occurrence from the Late Pleistocene to Holocene, as revealed in northern, middle and southern parts of the study area (Fig. 5). Here, occurrence rate is calculated as the total number of records of a particular species in fossil assemblages of a given time span on a given territory. The species of the East-Palearctic group slightly decreased their occurrence from the Late Pleistocene to the Late Holocene. However, the species composition in the western and eastern groups of arvicoline has not changed from the Late Pleistocene to modern time.

The Central-Palearctic group is represented in the fauna of the central and southern parts of the region during the Late Pleistocene and Holocene as could be traced from the overall occurrence of the species (Fig. 5). However, one of the central palearctic species (*E. luteus*) has disappeared from the study area in the Holocene. *O. zibethica* has been successfully introduced and underwent transcontinental dispersal in the Eurasia during less than 100 years.

5. Insect faunas

5.1. Key taxa

The focus is on beetles, the most readily discovered insects in the fossil record. The present-day fauna of beetles of the investigated area is not perfectly studied. Approximately 1500 beetle species are described in the Urals and Western Siberia: it is possible that the real number of species amounts to about 10,000. The most

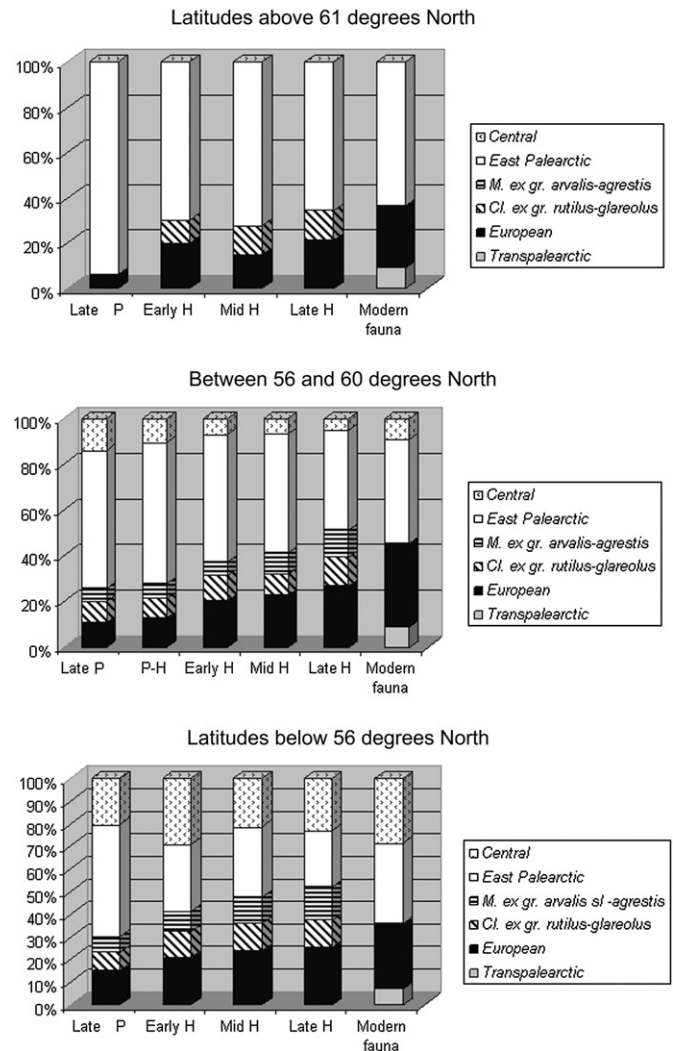


Fig. 5. Percentage occurrence of West (European), East, and Central-Palearctic groups of arvicoline species in the sites of the Urals and West Siberia in the Late Pleistocene (P) and Holocene (H), and proportion of species of those groups in the modern fauna of the region. The species that are problematic to assign to one of the groups due to the lack of criteria for diagnostics of their fossil remains are given separately.

numerous groups are ground beetles (Carabidae), which include about 300 described species (real number may be estimated as 400–500), and rove beetles (Staphylinidae), which include about 100 described species (real taxonomic diversity may be estimated as 600–800 species). Species diversity and their zonal distribution were described (Chernov, 1975, 1978; Korobeinikov, 1987; Volkovich and Alekseev, 1988; Andreeva and Eryomin, 1991; Kryzhanovskij et al., 1995; Mordkovitch and Lujbetchanskij, 1999; Kozyrev et al., 2000; Mikhailov, 2000; Zinovyev and Olshwang, 2003; Zinovyev, 2007).

5.2. Present-day distribution patterns in beetles

5.2.1. Zonal patterns of species distribution

Despite the lack of information on the modern beetle faunas, it is possible to determine some key species typical to zonal, poly-zonal, inazonal, and intrapolyzonal habitats (Medvedev, 1982; Kryzhanovskij et al., 1995; Mikhailov, 2000; Nikolaev and Kozminykh, 2002).

5.2.1.1. *Species with zonal pattern of distribution.* Distributed within one zone and include the species of zonal and intrazonal habitats.

a) Zonal habitats within one zone

The group includes the species with zonal pattern of distribution; these insects are subdivided into several sub-groups: arctic (ground beetles *Pterostichus vermiculosus*, *Amara alpina*, rove beetles *Micralymma discksoni*, *Tachinus arcticus*, leaf beetles *Chrysolina subsulcata*, *Chrysolina tolli*); boreal (ground beetles *Notiophilus reitteri*, *Pterostichus dilutipes*, *Pterostichus adstrictus*, *Carabus aeruginosus*, weevils *Rhyncholus ater*, *Callirus albosparsus*, *Callirus abietis*, bark beetle *Phloeotribus spinulosus*), nemoral (carrion beetle *Dendroxena quadrimaculata*, longhorn beetle *Rosalia alpina*), and steppe group (ground beetles *Carabus bessarabicus*, *Poecilus advena*, *Poecilus crenuliger*, *Poecilus ravus*, *Poecilus hanhaicus*, *Cymindis lateralis*, *Amara fodinae*, *Harpalus steveni*, *Harpalus circumpunctatus*, dark beetles *Tentyria nomas*, *Belopus* spp., leaf beetle *Pallasiola absinthii*, etc.). These species are clearly confined to zonal types of habitats and restricted to particular zones; in some cases these insects may inhabit extrazonal elements of landscape in a neighboring zone.

b) Intrazonal habitats

These insects inhabit intrazonal biotopes (according to the classification of Chernov (1975)) within one landscape-geographic zone – mainly flood-plains and bogs. It includes inhabitants of arctic (*Pterostichus costatus*, *Amara glacialis*), boreal (*Trechus rivularis*) and steppe (*Agonum lugens*, *Agonum viridicupreum*) zones.

5.2.1.2. *Species with polyzonal pattern of distribution.* The group includes insects whose modern ranges encompass more than one landscape-geographic zone. These species may be related to two or more natural zones. Some of them inhabit mainly zonal habitats within these zones. These insects inhabit tundras and boreal forests (ground beetles *Pterostichus* (*Cryobius*) *pinguedineus*, *Stereocerus haematopus*, *Stereocerus rubripes*, *Amara torrida*, *Amara hyperborea*, *Dicheirotichus mannerheimi*, weevils *Sitona borealis*, *Hemitrichapion tschernovi*), nemoral and boreal forests (ground beetles *Pterostichus oblongopunctatus*, *Calathus micropterus*, *Tachyta nana*, *Trachypachus zetterstedti*, *Harpalus latus*, dark beetles *Scaphidema metallicum*, *Diaperis boleti*), forest and steppe (ground beetles *Carabus aurolimbatus*, *Carabus stscheglowi*, *Carabus estreicherii*, *Harpalus anxius*, *Harpalus froelichi*, *Amara convexiuscula*, dark beetle *Opatrum sabulosum*, leaf beetle *Entomoscelis adonidis*), steppe and tundra (ground beetles *Carabus sibiricus*, *Polystichus connexus*, leaf beetle *Chrysolina exathematica gemmifera*). Other species have wide ecological requirements and widespread distribution. Their modern ranges encompass more than two zones and they may live both in zonal and azonal habitats (ground beetles *Carabus arvensis*, *Notiophilus aquaticus*, *Agonum sexpunctatum*, ladybird *Coccinella septempunctata*, etc.).

5.2.1.3. *Intrapolyzonal species.* This group includes the species related to intrapolyzonal biotopes not restricted by single natural zones – willow thickets, sedge and equisetum plant associations in flood-plains (leaf beetles *Plagioderia versicolora*, *Hippuriphila moderei*, weevils *Notaris aethiops*, *Tournotaris bimaculatus*, *Grypus equiseti*), clay and sand beaches of rivers (ground beetles *Bembidion obliquum*, *Bembidion striatum*, *Bembidion velox*, *Bembidion argentiolum*, click beetle *Hypnoidus rivularis*), meadows (leaf beetle *Chrysolina graminis*), and bogs (*Agonum ericeti*).

5.2.2. *Present-day longitudinal patterns of beetle species distribution*

Based on the data of modern distribution of beetles (Korotyaev, 1980; Medvedev, 1982; Kryzhanovskij, 1983, 2002; Gorodkov, 1984; Kryzhanovskij et al., 1995; Anderson et al., 2000; Nikolaev and Kozminykh, 2002; The Genus *Carabus* in Europe, 2003; Catalogue of Palaearctic Coleoptera, 2006; Checklist of Beetles of the British Isles, 2008), several longitudinal patterns can be established:

- I. **Transpalearctic group.** These species distributed from the Atlantic coast of Europe (namely, Ireland, France) to the Pacific coast; some species have Holarctic distribution. The group includes inhabitants of the forest (ground beetles *P. oblongopunctatus*, *C. micropterus*), itrapolyzonal (ground beetles *Pelophila borealis*, *Nebria rufescens*, *Patrobus septentrionis*), polyzonal (*C. arvensis*) and tundra habitats (Holarctic ground beetle *A. alpina*).
- II. **Western (“European and Euro-Ob”) group.** Modern ranges of the species included in this group reach the Atlantic coast as a western limit and reach the Urals and Western Siberia as their eastern limit (ground beetles *Carabus nitens*, *Carabus glabratus*, *Cychrus caraboides*, *Platynus livens*, *A. ericeti*, leaf beetle *Chrysolina varians*). The group includes the species of zonal (nemoral and boreal zones) and intrazonal habitats.
- III. **Eastern (“East-Palearctic”) group.** Modern ranges of the species included in this group reach the Pacific coast or Beringia as an eastern limit and extend westward to Eastern and Northern Europe, but do not reach Western Europe and the Atlantic coast. The group includes inhabitants of the boreal forests (ground beetles *Carabus maeander*, *Carabus tuberculosus*, *Carabus canaliculatus*), intrazonal (ground beetle *Nebria subdilatata*), and tundra habitats (ground beetles *Pterostichus sublaevis*, *Pterostichus agonus*, *P. costatus*, leaf beetles *C. tolli*, *C. subsulcata*). Some species of this group inhabit mainly steppe zone, but have isolated localities in plain and mountainous tundras of the Polar Urals and Yamal (weevil *Coniocleonus ferrugineus*, leaf beetles *Cryptocephalus orochona*, *C. exathematica gemmifera*).
- IV. **Central (“Central-Palearctic”).** These species distributed in the central part of the Northern Eurasia from Transbaikalia, Altai and Sayan Mountains to the Urals and European part of Russia (ground beetles *Carabus schoenherri*, *C. sibiricus*, *C. aurolimbatus*, *Carabus loschnikovi*, *P. dilutipes*). The group includes the species of mesic and arid habitats. *C. sibiricus* inhabit steppes, dry biotopes in forest-steppe (slopes of hills, relict steppe plots), open habitats in tundras and sandy ravines in taiga.

The present-day beetle fauna of this region clearly corresponds to latitudinal zonality, taking into account the widest distribution of intrazonal and intrapolyzonal landscapes, such as bogs and flood-plains. In general, the fauna has a transitional character between European and East Siberian faunas, although the transpalearctic species predominate (Volkovich and Alekseev, 1988; Kryzhanovskij, 2002).

There are numerous examples of west boundaries of the East-Palearctic beetle species' distribution and east borders for West Palearctic species in the study area. These borders are the Ural Mountains (East-Palearctic and Beringian beetles – *C. canaliculatus*, *Bradycellus glabratus*, *Carabus vietinghoffi*, *Bembidion infuscatum*; West Palearctic beetles – *Pterostichus quadrimaculatus*, *Licinus cassideus*, *Bembidion humerale*, etc.) and West Siberian Plain (East-Palearctic – *C. tuberculosus*, *C. maeander*, *Pterostichus laticollis*, *N. subdilatata*; West Palearctic – *C. glabratus*, *C. caraboides*, *Patrobus atrorufus*, *C. varians*). The Urals is considered as a boundary for the

distribution of some morphologically similar species (sibling species), in particular carabids *Pterostichus aethiops* (European beetle) and *Pterostichus maurasiacus* (Central-Palearctic beetle) (Kryzhanovskij, 2002).

Some species exhibit disjunctive distribution, such as *C. sibiricus*. Not long ago it was considered as a steppe species (Kryzhanovskij, 1983). Nowadays this species was found in South Yamal (Korobeinikov, 1987; Andreeva and Eryomin, 1991; Kozyrev et al., 2000; Zinovyev and Olshwang, 2003) and in the Vakh River valley (A.G. Men'shikov, personal communication). A similar type of distribution is known for *P. connexus*, *C. exathematica gemmifera*, that indicates their larger areas in the past (Samko, 1932; Mikhailov, 2000; Zinovyev and Olshwang, 2003; Zinovyev, 2006).

There are also nemoral species with disjunctive ranges, such as carrion beetle *Dendroxena quadripunctata* (distributed in central and South Europe, South Urals and has isolated population in Altai mountains and south of Central Siberia); rhyssodid beetle *Rhysodes sulcatus* (nemoral forests of South Europe, found in South Urals and Altai mountains); longhorn beetle *R. alpina* (nemoral forests of South Europe, found in South Urals) (Kryzhanovskij, 1983, 2002; Nikolaev and Kozminykh, 2002).

5.3. Modern vs. paleontological patterns of beetle species distribution

From the Late Pleistocene to Holocene and modern time, the processes of range dynamics can be observed not only in the single species (Fig. 6) but also in the entire insect complexes. Sub-fossil insect faunas from the Late Pleistocene are represented mainly by cryophilous (zonal and intrazonal arctic and polyzonal arcto-boreal) species (Zinovyev, 2007). Their amount declines southwards, whereas zonal (boreal, steppe) and polyzonal (including intrapolyzonal) insects increase their abundance.

In the Eemian Interglacial (MIS 5e) locality Karymkary, the thermophilous insect faunas of boreal intrazonal type are determined with the presence of ground beetle *Trechus secalis*, and some species which are not found in the study area during other periods of the Pleistocene. Neither arctic nor arcto-boreal carabids

(*Pterostichus* (*Cryobius*) spp.) were recovered from these sites (Zinovyev, 2007).

Entomological data on the Early Valdai Glaciation (MIS 5a and 4, 105,000–50,000 BP) are rather incomplete. The insect faunas from the sites of this age (e.g., Andryushino) belong to arctic and non-analogue types (Zinovyev et al., 2007).

The most complete information was obtained for the period of the end of MIS 3 in the study area between 67° N and 57° N. Previous results (Zinovyev, 2007) allow the outlining of some elements of natural zonality.

At the sites lying north of 61° N, cryophilous arctic and arcto-boreal species (including *P. costatus*, *P. sublaevis*, the subgenus *Cryobius* of the genus *Pterostichus*) dominated during this interval, whereas sub-boreal steppe species (*P. rarus*, *Chrysolina perforata* and *Chrysolina aeruginosa*) were either absent or rare. Between 61° N and 59° N, the sub-fossil beetle faunas of this age are of subarctic type with the presence of a single sub-boreal steppe species (*P. rarus*).

The MIS 3 interstadial faunas from sites situated south of 59° N contain sub-fossil beetle assemblages of a non-analogue type characterized by combinations of species which are not found together in present-day faunas. The main feature of this faunal type is a combination of arctic, arcto-boreal and sub-boreal steppe insects. These faunal assemblages contain arctic and arcto-boreal ground beetles of the *Pterostichus* (*Cryobius*) group, *A. alpina*, and the steppe species *Poecilus major*, *P. rarus*, *P. hanhaicus*, *Blitophaga sericea*, *Aclypaea bicarinata*, *C. perforata*, *Colaphellus sophiae*, and *Porcynolus murinus*. These faunas could be classified as non-analogue and are indicative of tundra-steppe. However, their species composition differs from that in the relict tundra-steppe communities existing today in the Eastern Siberia. In particular, the Western Siberian sub-fossil insect assemblages of that age contain the weevil *Otiorhynchus politus*, and some halophilous species of the genus *Pogonus* (Zinovyev, 2007) which are not known for the East Siberian faunas.

Analysis of longitudinal characteristics suggests that during MIS 3 many East Siberian species occurred in the study area. Present-day ranges of these species do not reach Western Siberia and

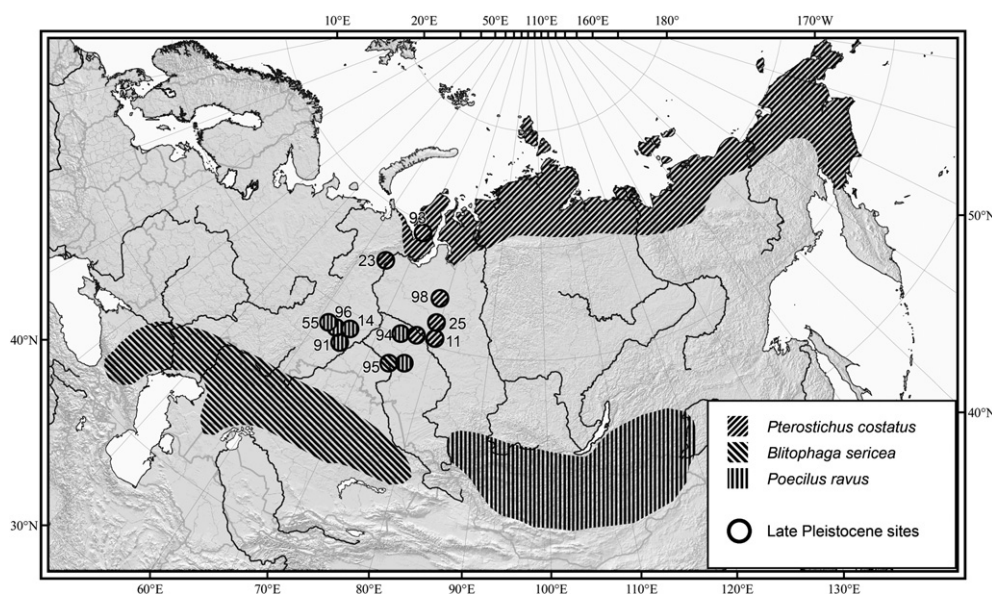


Fig. 6. Map showing the present-day distribution (dashed areas) of beetle taxa nowadays confined to East-Palearctic tundra (*Pterostichus costatus*), Central-Palearctic steppe (*Blitophaga sericea*), and East-Palearctic steppe (*Poecilus rarus*) and the Late Pleistocene sites where these species are recorded in the deposits dated back to the end of MIS 3 (dashed circles). Identification numbers of the sites are given in Table 1.

Urals (Korotyaev, 1980; Kryzhanovskij et al., 1995). In particular, the pill beetle *Morychus viridis* has been found in most of the Western Siberian sites of MIS3. However, the modern range of this beetle covers territories of East Siberia from Chukotka to Yana River (Kuzmina and Korotyaev, 1987). Sher and Kuzmina (2007) have claimed *M. viridis* as "...a real symbol of the Pleistocene biota in North-Eastern Siberia". The East Siberian species found in Pleistocene sites of the Urals and Western Siberia and absent in the modern fauna are ground beetles *P. rarus*, *P. hanhaicus*, *Pseudotaphoxenus dauricus*, *Amara minuta*, weevils *Sterhanocleonus eruditus*, *Tournotaris ochoticus*.

After the Late Pleistocene–Holocene transition (MIS2–MIS 1), the processes of afforestation and water logging caused reductions in the ranges of arctic and arcto-boreal species and the disappearance of some sub-boreal steppe species. During the same time, the expansion of polyzonal and boreal species occurred over the territories of the Urals and Western Siberia (ground beetles *C. micropterus*, *P. oblongopunctatus*, etc.); the majority of these insects have transpalearctic types of longitudinal distribution. Moreover, several European beetles (e.g., *C. nitens*, *C. glabratus*, *C. caraboides*, *P. livens*) have appeared here during the Holocene because they have never been found in the Late Pleistocene beetle assemblages in the study area. However, some species of the European group were already present in the study area in the Late Pleistocene (e.g.,

a ground beetle *A. ericeti*, which was found in MIS 3 sites of the northern part of the Western Siberia (Zinoviyev, 1988)). Most of the East-Palearctic species left this territory (*M. viridis*, *P. rarus*, *P. hanhaicus*, *A. minuta*) or could survive this time in the northern edge of this region, in the Polar Urals, Yamal, Gydan, lower Ob' River (e.g., *C. sibiricus*, *C. exathematica gemmifera*).

6. Comparison between arvicoline and beetle data

The biogeographic groups of arvicolines and selected insect species in the modern fauna of the Urals and Western Siberia based on the longitudinal patterns of their present-day distribution are shown in Table 2.

The Transcontinental (Transpalearctic) group is well represented among native beetles in the study area and includes zonal tundra, forest, and intrapolyzonal species (Table 2). Among arvicolines, no native species with transcontinental pattern of distribution are found in the modern fauna of the region. This could be explained by faster evolution rates in rodents (namely, in Arvicolinae) as compared to all the members of the order Coleoptera.

The West Palearctic ("European") group of beetles includes intrapolyzonal, azonal, forest, and steppe species (Table 2). The same biotopic groups are found in the European arvicolids, but without steppe species. Modern distribution of the West Palearctic

Table 2
Biogeographic groups (I–IV) of arvicoline species and selected beetle species in the modern fauna of the Ural Mountains and Western Siberia based on the longitudinal patterns of their present-day distribution.

Pattern of distribution (habitat affinity)	Arvicoline species	Beetle species
I. Transpalearctic (Transcontinental) group		
Intrapolyzonal (intraazonal)	<i>Ondatra zibethica</i> – non-native (introduced) species	<i>Nebria rufescens</i> , <i>Patrobus septentrionis</i> , <i>Lebia cruxminor</i> , <i>Hydrothassa hannoverana</i> , <i>Plagioderma versicolora</i> , <i>Tournotaris bimaculatus</i> , <i>Grypus equiseti</i>
Polyzonal (azonal)	–	<i>Carabus arvensis</i> , <i>Notiophilus aquaticus</i> , <i>Poecilus versicolor</i> , <i>Chrysolina graminis</i> , <i>Coccinella septempunctata</i>
Zonal (zonal tundra):	–	<i>Amara alpina</i>
Polyzonal within tundra and boreal forests (intraazonal)	–	<i>Pelophila borealis</i> , <i>Diacheila polita</i>
Polyzonal (nemoral and boreal forest habitats)	–	<i>Pterostichus oblongopunctatus</i> , <i>Calathus micropterus</i> , <i>Tachyta nana</i> , <i>Trachypachus zetterstedti</i>
II. West Palearctic (European) group		
Intrapolyzonal (intraazonal)	<i>Arvicola terrestris</i>	<i>Platynus longiventris</i> , <i>Platynus krynickii</i> , <i>Chrysolina varians</i> , <i>Agonum ericeti</i>
Intrapolyzonal within nemoral and boreal forests (intraazonal)	–	<i>Carabus menetriesi</i> , <i>Leistus ferrugineus</i> , <i>Platynus livens</i> , <i>Agonum duftschmidi</i> , <i>Bembidion mannerheimi</i> , <i>Bembidion humerale</i> , <i>Patrobus atrorufus</i>
Polyzonal within nemoral and boreal forest (zonal forest and azonal habitats)	<i>Clethrionomys glareolus</i> <i>Microtus agrestis</i>	<i>Carabus nitens</i> , <i>Carabus glabratus</i> , <i>Cychrus caraboides</i> , <i>Paradromius longiceps</i> , <i>Pterostichus quadrifoveolatus</i>
Polyzonal (azonal)	<i>Microtus arvalis</i> sensu stricto	<i>Poecilus lepidus</i> , <i>Poecilus cupreus</i> , <i>Polystichus connexus</i>
Zonal (steppe)	–	<i>Licinus cassideus</i> , <i>Pterostichus macer</i>
III. East-Palearctic group		
Intrapolyzonal (intraazonal)	<i>Microtus oeconomus</i>	<i>Amara aurichalcea</i>
Intraazonal within boreal forests (intraazonal)	–	<i>Nebria subdilatata</i> , <i>Bembidion infuscatum</i> , <i>Oodes prolixus</i>
Zonal within boreal forests (zonal and azonal forest habitats)	<i>Myopus schisticolor</i> , <i>Clethrionomys rutilus</i> , <i>Clethrionomys rufocanus</i>	<i>Carabus maeander</i> , <i>Carabus tuberculatus</i> , <i>Carabus canaliculatus</i> , <i>Pterostichus laticollis</i>
Zonal (steppe)	–	<i>Poecilus rarus</i>
Polyzonal (tundra and steppe zonal habitats)	<i>Microtus gregalis</i>	<i>Chrysolina exathematica gemmifera</i>
Polyzonal (tundra and boreal forests)	–	<i>Morychus viridis</i> , <i>Stereocerus haematopus</i> , <i>Stereocerus rubripes</i>
Intraazonal within tundra zone (intraazonal)	–	<i>Pterostichus costatus</i> , <i>Chrysolina tolli</i> , <i>Chrysolina subsulcata</i>
Zonal (zonal tundra)	<i>Dicrostonyx torquatus</i> , <i>Lemmus sibiricus</i> , <i>Microtus middendorffi</i>	<i>Pterostichus sublaevis</i> , <i>Pterostichus agonus</i> , <i>Carabus truncaticollis</i>
IV. Central-Palearctic group		
Zonal (steppe):	<i>Ellobius talpinus</i> , <i>Lagurus lagurus</i>	<i>Poecilus advena</i> , <i>Poecilus crenuliger</i> , <i>Poecilus aralensis</i> , <i>Poecilus nitens</i>
Zonal (boreal forests)	–	<i>Carabus schoenherri</i> , <i>Carabus aurolimbatus</i> , <i>Pterostichus dilutipes</i> , <i>Pterostichus drescheri</i> , <i>Pterostichus uralensis</i> , <i>P. magus</i>
Polyzonal (azonal)	<i>Microtus rossiaemeridionalis</i>	–
Polyzonal (tundra and steppe zonal habitats):	–	<i>Carabus sibiricus</i>

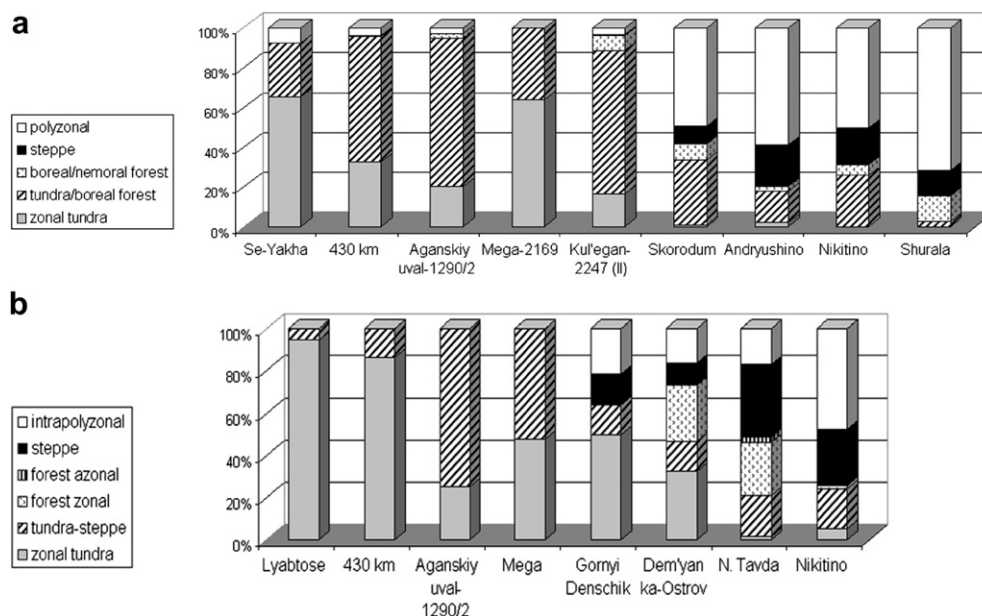


Fig. 7. Proportion of different habitat groups among beetle (a) and arvicoline (b) species in the key sites in the Western Siberia (between 57° and 73° N) dated back to the end of MIS3 – beginning of MIS2. Sites are ordered from the north to the south according to the latitude; names of the sites are given in Table 1.

beetles is not limited by the Ural Mountains. Their ranges reach the Middle Ob', Siberian Uval Hills, and Novosibirsk region in the Western Siberia (*Carabus menetriesi*, *P. livens*, *C. varians*, *Dlochrysa fastuosa*, *Bytiscus betulae*, *Bagous lutosus*, *Lagria hirta*, *Agathidium varians*), where some European beetles could be regarded as common species. Distribution of the West Palearctic arvicolines exhibits the same tendency so that their ranges stretch over the Ural Mountains and reach Western Siberia and Altai (*C. glareolus*, *M. arvalis*), and North-Eastern Siberia (*A. terrestris*, *M. agrestis*).

The Central-Palearctic group of beetles represents a variety of biotopic groups including the steppe, boreal, and tundra-steppe species. The arvicolines of the Central group are represented by the steppe, and azonal species only (Table 2).

The Eastern ("East-Palearctic") group is represented by intrazonal, boreal, and tundra species of arvicolids and beetles, and also by the steppe beetles. At present, the Ural Mountains represent a western range limit for the East-Palearctic carabids. Only the arctic and arcto-boreal species cross the Urals in its polar part (e.g., *Carabus ermaki*, *Pterostichus parens*, *P. vermiculosus*, *P. dilutipes*, et al.), whereas the western limit of the boreal beetles do not cross the eastern slope of the Ural Mountains (e.g., *C. canaliculatus*, *B. glabratus*, *Synuchus congruus*, *B. infuscatum*). The Urals represents a western border for the two East-Palearctic species of voles – *M. middendorffi*, and *M. gregalis*. The species of the Eastern group which do not cross the Ural Mountains at present could be spread much further west in the Late Pleistocene. In particular, *M. gregalis* and *C. maeander* are known from the Late Pleistocene localities of the British Isles (Morgan, 1973; Sutcliffe and Kowalski, 1976).

Along with similarities in the beetle and arvicoline data, there are certain distinctivenesses related to the differences in the species reachness and diversity that are much higher in beetles than in arvicolines. This is especially pronounced in the species related to the steppe biotopes. The modern steppe beetles from the Western, Eastern, and Central-Palearctic groups are related to Mediterranean, Transbaikalian/Mongolian, and Kazakhstan sources respectively. In arvicolines, the steppe forms are represented by the species of the Central-Palearctic group only.

The classification given in Table 2 includes all the arvicoline species known for the modern fauna of the Urals and Western

Siberia; however, it is far from being exhaustive with respect to beetle taxa. In particular, there are beetle species distributed in the subalpine belt of the Central-Palearctic. For example, *Carabus karpinskii* and *Chrysolina lagunovi* in the modern fauna are recorded exclusively in the Southern (*C. karpinskii*) and Southern/Northern (*C. lagunovi*) Ural Mountains (Kryzhanovskij and Matveev, 1993; Gorbunov and Olshwang, 2008). The ground beetle *Cymindis mannerheimi* is nowadays distributed in the subalpine belt of the Pamir, Northern Tien-Shan, and Western Altai (Kryzhanovskij et al., 1995). In the Late Pleistocene, *C. mannerheimi* had a much wider range that was established based on the findings in the localities of the Trans-Urals, Western Siberia and in the lower Yana River (unpublished data).

Comparisons of fossil data on beetles and arvicolines are possible for the territories between 57° N and 72° N (in contrast to arvicoline data, the fossil beetle assemblages are not known from south of 57° N in the study area). Fig. 7 shows the proportions of different biotopic groups among beetles and arvicolids in the key localities in the Western Siberia dated back to the end of MIS3 – beginning of MIS2. Here, proportions are calculated based on the percentage of different biotopic groups of species found in a given locality. The comparison shows that both beetles and arvicolids reveal similar geographic trends from the most northern localities to the southern ones.

6.1. Paleocological and biostratigraphical implications of the data on modern distribution of the key taxa

The data on modern distribution of the key species provide information to fill the gaps in the fossil record. For example, the disjunctive modern ranges of the nemoral beetle species (*Xylodrepa quadripunctata*, *Rhyzodes sulcatus*, etc.) allow reconstruction of the continuous areas of their distribution in the past. Knowledge of the environmental preferences of those species with disjunctive modern ranges may provide some ideas about the past environments which have not been yet revealed by the fossil vertebrate and beetle record, but are important for understanding the faunal connections between the west and east sectors of Palearctic. Pollen data suggest the existence of a continuous forest zone with broad-

leaved trees stretching through Western Siberia and Europe during MIS 5e (Arkhipov and Volkova, 1994). However, there is practically no evidence to confirm the existence of the nemoral forest zone based on the vertebrate or beetle fossil data. In the beetle fossil record, the only exception is a single finding of the Far-East species *Phymatopoderus latipennis* in the deposits of Mikulino age in Belarus (Nazarov, 1984). Probably, this could be related to the taphonomic background in the nemoral forest zone as compared to tundra and steppe.

Another example of using the present-day patterns of species distribution to complement the species record in fossil assemblages of a particular region could be seen in the arvicoline species *M. oeconomus*. Nowadays, isolated populations outside the continuous range of *M. oeconomus* are confined to the westernmost part of the present-day distribution area of the species in Northern and Eastern Europe. That pattern of distribution could be regarded as indirect evidence of colonization–extinction dynamics of the species in Europe supported by direct evidence from the Late Pleistocene sites in Southwestern Europe (Cuenca-Bescós et al., 2010) and British Isles (Sutcliffe and Kowalski, 1976).

On the other hand, the data on the species' expansions caused by human provides some clues to the dispersal potential of a particular species. One of the examples of eastward expansion of beetles caused by human influence is the modern dynamics of the ground beetle *Carabus nemoralis*. This species was described in Sweden in the end of the 18th century. At present, this beetle reaches the Urals, southern Western Siberia, Kazakhstan, and North America (Lindroth, 1972; Kabak and Kolov, 2010).

The data on human-caused dispersal of *O. zibethica* in Northern Eurasia suggest the high potential rates of a rodent invader to become successfully incorporated into the natural communities throughout the continent. However, no native arvicoline species with transcontinental patterns of distribution are found in modern fauna of Northern Eurasia. This could be explained by the fast evolution rates in Arvicolinae, resulting in numerous speciation events during the Pleistocene.

The importance of the study area for faunal correlations throughout the continent is determined by presence of the key arvicoline taxa traditionally used for correlation purposes (taxa *Dicrostonyx*, *Lagurus*, *M. gregalis*), and by the gradual change in faunal composition along the latitudinal gradient of environment at any given stage of the Quaternary. Based on the key taxa and their latitudinal range overlaps, four zones could be proposed according to the south–north gradient: 1) *Lagurini* zone; 2) *Lagurus*–*M. gregalis* zone; 3) *Lagurus*–*M. gregalis*–*Dicrostonyx* zone; 4) *M. gregalis*–*Dicrostonyx* zone. *Eolagurus*, *Arvicola*, and *Clethrionomys* could be used as additional taxa for faunal correlations south of 60° N, and *Lemmus* could serve as an additional clue for correlations through the northern territories. Transzonal faunal correlations within the Urals and Western Siberia integrating the evolutionary morphological studies of the key taxa and assessment of the faunal successions may serve as a basis for Trans-Eurasian correlation.

7. Conclusions

Analysis of the longitudinal patterns of the present-day distribution of arvicoline and beetle species in the modern fauna of the Urals and Western Siberia allows establishment of four biogeographic groups, including 1) transcontinental, 2) West Palearctic (“European”), 3) East-Palearctic, and 4) Central-Palearctic species.

Investigation of the Late Pleistocene and Holocene arvicoline and beetle assemblages from the 104 sites in the Urals and Western Siberia shows that the crossroads position of the Urals and Western Siberia is reflected not only in the modern fauna but also in the Late Pleistocene and Holocene fossil micromammal and beetle record.

The different faunal elements (arvicolines and beetles) reveal the same biogeographic patterns.

The East-Palearctic group of arvicolines constitutes a core of the fauna in the high and middle latitudes of the Urals and Western Siberia. South of 56° N, the Western, Eastern and Central groups are almost equally represented. However, the role of European species in the arvicoline fauna has become more important from the Late Pleistocene to the Late Holocene and present day in the northern, middle, and southern parts of the region.

Transpalearctic species constitute a core of modern beetle fauna of the Urals and Western Siberia within the boreal zone, whereas the Central-Palearctic beetles dominate in steppes, and the East-Palearctic species prevail in tundras. Dominance of the Transpalearctic beetle species and appearance of the most of European boreal and intrazonal elements in the fauna of boreal zone appear to have been gradually formed since the end of Late Pleistocene and Holocene to the present.

Based on distribution patterns of arvicoline and beetle taxa, zoogeographically the border between the European and East-Palearctic faunal groups represents a vast territory where the ranges of the species included in those groups intersect. That border territory includes the Ural Mountains and the lowlands lying east (West Siberian Plain) and west (East-European Plain) of it. The biomes of those territories represent the North-Eurasian corridors providing migrations of the species from the different faunal complexes in west–east, east–west, and north–south directions. Those corridors have been opened when the respective biome was continuous, and they might have been interrupted when the biome was fragmented.

The data on present-day distribution of the key taxa provide a considerable contribution to the understanding of the past biome dynamics, and to reconstructing the gaps in the fossil record (for example, based on the disjunct distribution patterns caused by a decline of the ancient continuous range). On the other hand, the data on expansions via anthropogenically transformed habitats could be used in order to assess the dispersal rates of a particular species and to suggest the potential rates of biotic transformations.

Comparison of modern ranges of the key taxa with the ranges inferred from the fossil data suggests that migrations of the East-Palearctic group goes to the west through the northern latitudes. The West Palearctic group goes to the east primarily via the southern part of the region. Taking into account that the latitudinal gradient of the environmental conditions has been an inherent characteristic of the study area during the Late Quaternary, zonal biomes of the Urals and Western Siberia could be regarded as the key territories to undertake faunal correlations throughout Eurasia, and to correlate the European and Asian stratigraphic schemes.

Arvicolines are employed in Quaternary biostratigraphy due to their rapid evolution, abundant fossil record, and wide geographical ranges. Beetles are strictly confined to temperature conditions and show high levels of ecological and morphological stability. Beetle species are attributed to particular layers of terrestrial phytocenoses, allowing their use as indicators of soil, humidity, insolation, and vegetation type. This study confirms that arvicoline rodents and beetles are now important objects of paleoecological, biostratigraphical, and biochronological studies, providing the possibility to integrate regional data sets into the continental-scale frameworks.

Acknowledgements

We wish to thank the anonymous reviewers for their constructive suggestions. The study was supported by the Russian

Foundation for Basic Research, research grant 10-04-96102, the RAS Program “Biosphere Origin and Evolution”, Federal Target Program “Scientific and scientific-pedagogical personnel of innovative Russia” (02.740.11.0279), the grant for Support of Leading Scientific Schools of Russia (3260.2010.4), and the Young Scientists Grant from the Ural Branch of RAS.

References

- Abramson, N.I., 2007. Filogeografiya: Itogi, problemy, perspektivy. ([Phylogeography: results, issues and perspectives]). Informatsionnyi Vestnik Vsesoyuznogo Obshchestva Genetikov i Selektionerov. ([The Bulletin of the All-Union society of Geneticist and Selectionist]) 11 (2), 307–331 (in Russian with English abstract).
- Agadjanian, A.K., 1979. Izuchenie istorii melkikh mlekopitayushchikh. ([The study of small mammal history]). In: Sokolov, V.E., Dinesman, L.G. (Eds.), *Chastnye metody izucheniya istorii sovremennykh ekosistem* [Special Methods of Studying the History of Recent Ecosystems]. Nauka Publishing House, Moscow, pp. 164–193 (in Russian).
- Anderson, R., McFerran, D., Cameron, A., 2000. The Ground Beetles of Northern Ireland (Coleoptera-Carabidae). Ulster Museum Publication No. 279, Belfast.
- Andreeva, T.R., Eryomin, P.K., 1991. Ecologo-faunisticheskii obzor zhuzhelic (Coleoptera, Carabidae) Uzhnogo Yamala. ([An eco-faunistic review of the ground beetles (Coleoptera, Carabidae) of the South Yamal]). In: *Ecologicheskie grupirovki zhuzhelic (Coleoptera, Carabidae) v estestvennykh i antropogennykh landshtafah Urala* [Ecological groups of ground beetles (Coleoptera, Carabidae) in Natural and Antropogenic Landscapes of the Urals]. USSR Academy of Sciences Press, Sverdlovsk, pp. 3–17 (in Russian).
- Arkhipov, S.A., 1965. Paleogeografiya Zapadno-Sibirskoi nizmennosti v antropogennom periode. Opyt sostavleniya seriya paleogeograficheskikh kart. ([Paleogeography of West Siberian lowland in quaternary period. Experience of construction of series of paleogeographic maps]). In: *Osnovnye problemy izucheniya chetvertichnogo perioda* [Principal Problems of Study of Quaternary Period]. Nauka Publishing House, Moscow, pp. 157–169 (in Russian).
- Arkhipov, S.A., 1997. Record of Late Pleistocene geological events in West Siberia. *Russian Geology and Geophysics* 38 (12), 1891–1911.
- Arkhipov, S.A., Votakh, M.R., Golbert, A.V., Gudina, V.I., Dovgal, L.A., Yudkevich, A.I., 1977. Posledneye oledeneniye v Nizhnem w Priobye. ([The Last Glaciation in the Lower Ob River Region]). Nauka, Novosibirsk (in Russian).
- Arkhipov, S.A., Volkova, V.S., 1994. Geologicheskaya istoriya, landshtafy i klimaty pleistocena Zapadnoi Sibiri. ([Geological History, Landscapes and Climates of the Pleistocene in West Siberia]). United Institute of Geology, Geophysics and Mineralogy Siberian Branch of the Russian Academy of Sciences, Novosibirsk (in Russian).
- Astakhov, V.I., 2009. Glavnye rubezhi pozdnego pleistocena Uralo-Sibirskoy Arktiki. ([Main Landmarks of the Late Pleistocene of the Ural–Siberian Arctic]). In: *Fundamental'nye problemy quater: itogi izucheniya i osnovnye napravleniya dal'neyshikh issledovaniy*. ([In: Fundamental Problems of the Pleistocene: Results of Investigations and Main Directions for Further Studies]). Academ. Publ. House “GEO”, Novosibirsk (in Russian) 50–52.
- Bachura, O., Kosintsev, P., 2007. Late Pleistocene and Holocene small- and large-mammal faunas from the Northern Urals. *Quaternary International* 160, 121–128.
- Bachura, O.P., Strukova, T.V., 2002. Mammal remains from Cheremukhovo-1 locality (excavation 4). In: Kosintsev, P.A. (Ed.), *Pleistocene and Holocene Faunas of the Urals (Biota of the Northern Eurasia in the Cainozoic, Iss. 2)*. Ripheus Press, Chelyabinsk, pp. 37–55 (in Russian with English abstract).
- Benton, M.J., Harper, D.A.T., 2009. Introduction to Paleobiology and the Fossil Record. Wiley-Blackwell, Chichester, West Sussex.
- Berdugin, K.I., Bol'shakov, V.N., Balakhonov, V.S., Pavlinin, V.V., Paskhal'nyi, S.P., Shtro, V.G., 2007. Mlekopitayushchie Polyarnogo Urala. ([Mammals of Polar Ural Mountains]). Ural State University Press, Yekaterinburg (in Russian).
- Bidashko, F.G., 1994. Rekonstruksiya prirodnoi obstanovki pleistocena Severnogo Prikaspiya po paleontologicheskim dannym [Reconstruction of Pleistocene Paleoenvironment of Northern Prikaspiyskaya Lowland on Fossil Insect Data]. Ph.D. thesis, Moscow State University, Moscow, Russia (in Russian).
- Bidashko, F.G., Proskurin, K.P., 1987. The entomological and carpological reconstruction of the bio-environment of the Singilian (Middle Pleistocene) of the Lower Volga. *Paleontological Journal* 21, 66–72.
- Bidashko, F.G., Baymyrzaev, K.M., Bragina, T.M., Zharkova, V.I., 2005. Rekonstruksiya uslovii obitaniya gigant'skogo olenya (*Megaloceros giganeus* Nehring, 1891) nizovii reki Ural [Reconstruction of habitat conditions of the giant deer (*Megaloceros giganeus* Nehring, 1891) from the Ural lower reach. Biological diversity of Asian steppes. Proceedings, International conference, Kostanay, pp. 17–20 (in Russian with English abstract)].
- Bol'shakov, V.N., Berdugin, K.I., Vasil'eva, I.A., Kuznetsova, I.A., 2000. Mlekopitayushchie Sverdlovskoi oblasti. Spravochnik-opredelitel. ([Mammals of Sverdlovsk Oblast: a Reference Book and Index]). Yekaterinburg Publishing, Yekaterinburg (in Russian).
- Borodin, A.V., 1996. Quaternary small mammal faunas from the West Siberian Plain. *Acta Zoologica Cracoviensis* 39 (1), 75–81.
- Borodin, A.V., 1997. Sootnoshenie chislennosti melkikh mlekopitayushchikh v razlichnykh biotopakh doliny reki Khadytayakha (Yuzhnyi Yamal) po rezul'tatam otlovov davilkami i v pishevom ratsione khishnykh ptits i pests. ([Relative abundance of small mammals in different biotopes in Khadytayakha River valley (Southern Yamal Peninsula) based on the results of snap-trapping and in the diets of birds of prey and polar foxes]). In: Kosintsev, P.A. (Ed.), *Materialy po istorii i sovremennomu sostoyaniyu fauny severa Zapadnoi Sibiri* [Materials on the History and Modern State of the Fauna of the North of Western Siberia]. Ripheus Press, Chelyabinsk, pp. 91–105 (in Russian).
- Borodin, A.V., 2009. Opredelitel' zubov polevok Urala i Zapadnoy Sibiri (Pozdnyi pleystotsen-sovremennost. ([A Diagnostic Guide to Teeth of Arvicolines of the Urals and Western Siberia (Late Pleistocene – Modern Time)]). Ural Branch of the Russian Academy of Sciences Publishing, Yekaterinburg (in Russian).
- Borodin, A.V., Erokhin, N.G., Markova, Samokhina, E.A., 1997. Ostatki melkikh mlekopitayushchikh iz otlozheniy nor pests. ([Small mammal remains from the deposits of burrows of Arctic fox]). In: Kosintsev, P.A. (Ed.), *Materialy po istorii i sovremennomu sostoyaniyu fauny severa Zapadnoi Sibiri* [Materials on the History and Modern State of the Fauna of the North of Western Siberia]. Ripheus Press, Chelyabinsk, pp. 91–105 (in Russian).
- Borodin, A.V., Strukova, T.V., Stefanovsky, V.V., 2003. Fossil remains of small mammals from alluvial and lake deposits of the Trans-Urals. In: Smirnov, N.G. (Ed.), *Quaternary Paleozoology in the Urals*. Publishing House of the Ural State University, Yekaterinburg, pp. 73–85 (in Russian with English abstract).
- Borodin, A.V., Kosintsev, P.A., Strukova, T.V., Nekrasov, A.E., 2000a. Mammals, birds and fish from the site Cheremukhovo 1 (section 2). In: Kosintsev, P.A. (Ed.), *Pleistocene and Holocene Faunas of the Urals (Biota of the Northern Eurasia in the Cainozoic, Iss. 1)*. Ripheus Press, Chelyabinsk, pp. 59–80 (in Russian with English abstract).
- Borodin, A.V., Strukova, T.V., Trofimova, S.S., Zinoviev, E.V., 2001. Reconstruction of mammoth environments at different stages of the pleistocene in the West Siberian Plain. *The World of Elephants. Proceedings of the 1st International Congress, Roma, Italy*, pp. 267–271.
- Borodin, A.V., Strukova, T.V., Kosintsev, P.A., Nekrasov, A.E., Panova, N.K., 2000b. New data on the natural environment of the Middle Urals in the Late Quaternary time (the Shaytanoozerskiy Kamennyi Ostrov site). In: Kosintsev, P.A. (Ed.), *Pleistocene and Holocene Faunas of the Urals (Biota of the Northern Eurasia in the Cainozoic, Iss. 1)*. Ripheus Press, Chelyabinsk, pp. 17–35 (in Russian with English abstract).
- Borodin, A.V., Strukova, T.V., Ulitko, A.I., Chairkin, S.E., Bachura, O.P., 2000c. Cheremukhovo 1 – a new historical, ecological and archaeological site in the North Urals (Location and stratigraphy). In: Kosintsev, P.A. (Ed.), *Pleistocene and Holocene Faunas of the Urals (Biota of the Northern Eurasia in the Cainozoic, Iss. 1)*. Ripheus Press, Chelyabinsk, pp. 36–58 (in Russian with English abstract).
- Brown, J.H., Stevens, G.C., Kaufman, D.M., 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Reviews, Ecological Systematics* 27, 597–623.
- Brunhoff, C., Gakbreath, K.E., Fedorov, V.B., Cook, J.A., Jaarola, M.J., 2003. Holarctic phylogeography of the root vole (*Microtus oeconomus*): implications for the late Quaternary biogeography of high latitudes. *Molecular Ecology* 12 (4), 957–968.
- Catalogue of Palaearctic Coleoptera. In: Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea, vol. 3, 2006. Stenstrup: Apollo Books.
- Chaline, J., 1972. Les rongeurs du Pleistocene moyen et superieur de France (Systematique – Biostratigraphie – Paleoclimatologie). Cahiers de Paléontologie. Conseil National Recherche Scientifique, Paris, pp. 1–410.
- Checklist of Beetles of the British Isles, 2008. United Kingdom, Somerset.
- Chernousova, N.F., 2001. Specific features of the dynamics of murine rodent communities under the effects of urbanization: 1. Dynamics of species composition and abundance. *Russian Journal of Ecology [Ekologiya]* 32 (3), 186–192 (in Russian).
- Chernov, Yu.I., 1975. Prirodnyaya zonal'nost' i zhivotnyi mir sushi. ([Natural Zonality and the Terrestrial Animal World]). Nauka Publishers, Moscow (in Russian).
- Chernov, Yu.I., 1978. Struktura zhivotnogo naseleniya Subarktiki. ([Structure of the Animal Population in the Subarctic]). Nauka Publishers, Moscow (in Russian with English summary).
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennásar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International* 212, 109–119.
- Danukalova, G.A., 2010. The refined quaternary stratigraphic scale of the fore-Urals and main events in Southern Urals region. Stratigraphy and Geological Correlation. ([Stratigraphiya. Geologicheskaya Korrelyatsiya]) 18 (3), 331–339 (in Russian).
- Deffontaine, V., Libois, R., Kotlík, P., Sommer, R., Nieberding, C., Paradis, E., Searle, J.B., Michaux, J.R., 2005. Beyond the Mediterranean peninsulas: evidence of central European glacial refugia for a temperate forest mammal species, the bank vole (*Clethrionomys glareolus*). *Molecular Ecology* 14, 1727–1739.
- Erbajeva, M.A., Khenzykhenova, E.I., Alexeeva, N.V., 2011. Late Pleistocene and Holocene environmental peculiarity of the Baikalian region, based on mammal associations and deposits. *Quaternary International* 237, 39–44.
- Fadeeva, T.V., Smirnov, N.G., 2008. Melkie mlekopitayushchie Permskogo Predural'ya v pozdnem pleistocene i golocece. ([Small Mammals in the Perm Pre-Urals during the Late Pleistocene and Holocene Periods]). Goshchitskiy Publishers, Yekaterinburg (in Russian).

- Fedorov, V.B., Fredga, K., Jarrell, G., 1999. Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian Arctic. *Journal of Evolutionary Biology* 12, 134–145.
- Fedorov, V.B., Goropashnaya, A.V., Boeskorov, G.G., Cook, J.A., 2008. Comparative phylogeography and demographic history of the wood lemming (*Myopus schisticolor*): implications for late Quaternary history of the taiga species in Eurasia. *Molecular Ecology* 17, 598–610.
- Fedorov, V.B., Goropashnaya, A.V., Jaarola, M., Cook, J.A., 2003. Phylogeography of lemmings (*Lemmus*): no evidence for postglacial colonization of Arctic from the Beringian refugium. *Molecular Ecology* 12, 725–731.
- Gorbunov, P.Yu., Olshwang, V.N., 2008. Zhuki Srednego Urala. Spravochnik-opredelitel'. ([The Beetles of the Middle Urals. Diagnostic Guide]). Sokrat Publishing House, Yekaterinburg (in Russian).
- Gorodkov, K.B., 1984. Tipy arealov nasekomykh tundry I lesnykh zon Evropeiskoy chasti. ([The Types of Insect Faunas of the Tundra and Forest Zones of the European Part of the USSR]). In: *Arealnye nasekomykh Evropeiskoy chasti SSSR* [Insects Natural Habitats of the European Part of the USSR]. Nauka Publishers, Leningrad, pp. 3–20 (in Russian).
- Gromov, I.M., Polyakov, I.Ya., 1977. Fauna SSSR. Mlekopitayushchie. Tom III(8) Polevki (Microtinae). ([Fauna of the USSR. Mammals. vol. III(8) Voles (Microtinae)]. Nauka Publishers, Moscow-Leningrad.
- Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20, 549–574.
- Haynes, S., Jaarola, M., Searle, J.B., 2003. Phylogeography of the common vole (*Microtus arvalis*) with particular emphasis on the colonization of the Orkney archipelago. *Molecular Ecology* 12, 951–956.
- Heckel, G., Burri, R., Fink, S., Desmet, J.F., Excoffier, L., 2005. Genetic structure and colonization processes in European populations of the common vole *Microtus arvalis*. *Evolution* 59 (10), 2231–2242.
- Hewitt, G.M., 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58, 247–276.
- Hewitt, G.M., 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B-Biological Sciences* 359, 183–195.
- Ilyina, I.S., Lapshina, E.I., Lavrenko, N.N., 1985. Rastitel'nyi pokrov Zapadno-Sibirskoi ravniny. ([Vegetation Cover of the West Siberian Plain]). Nauka, Novosibirsk (in Russian).
- Ismagilov, M.I., Bekenov, A., 1969. Usloviya prebyvaniya i ekologiya zheltogo pestrushki (*Lagurus luteus*) v Zajsanskoy kotlovine. ([Habitat Conditions and Biology of the Yellow Steppe Lemming (*Lagurus luteus*) in the Zajsan Hollow]). *Russian Journal of Zoology*. ([Zoologicheskii zhurnal]) 48 (12), 1869–1877 (in Russian).
- Jaarola, M., Searle, J.B., 2004. A highly divergent mitochondrial DNA lineage of *Microtus agrestis* in southern Europe. *Heredity* 92, 228–234.
- Kabak, I.I., Kolov, S.V., 2010. Materialy k rasprostraneniyu nekotorykh vidov zhuzhelits (Coleoptera, Carabidae) v Central'nom i Yugo-Vostochnom Kazakhstane. ([Notes on the Distribution of Some Ground-beetles (Coleoptera, Carabidae) in Central and South-Eastern Kazakhstan]). *Euroasian Entomological Journal*. ([Evraziatskii entomologicheskii zhurnal]) 9 (1), 29–32 (in Russian).
- Kalabukhov, N.I., 1970. Some peculiarities in adaptation in the steppe and yellow lemmings (*Lagurus lagurus* Pall. and *L. luteus* Eversm.). *Russian Journal of Ecology* [Ekologiya] 1, 69–76 (in Russian).
- Khenzykhenova, F.I., 1996. Late Pleistocene small mammals from the Baikal region (Russia). *Acta Zoologica Cracoviensis* 39 (1), 229–234.
- Kochev, V.A., 1993. Pleistocenovye gryzuny Severo-Vostoka Evropy i ikh stratigraficheskoe znachenie. ([Pleistocene Rodents from the North-east of Europe and their Stratigraphic Significance]). Nauka, St. Petersburg (in Russian).
- van Kolfschoten, T., 1995. On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe. *Acta Zoologica Cracoviensis* 38 (1), 73–84.
- Koneva, I.V., 1983. Gryzuny i zaytseobraznye Sibiri i Dal'nego Vostoka. ([Rodents and Lagomorphs of Siberia and Far East]). Nauka, Novosibirsk (in Russian).
- Korobeinikov, Yu.I., 1987. Ekologo-faunisticheskaya kharakteristika zhuzhelits Uzhnogo Yamala. ([Eco-faunistic characteristics of ground-beetles of the southern Yamal Peninsula]). In: *Fauna i ekologiya nasekomykh Urala* [Fauna and ecology of insects of the Urals], pp. 33–44. Sverdlovsk (in Russian).
- Korotyaev, B.A., 1980. [Materials on the weevil fauna (Coleoptera, Curculionidae) of the North-East of the USSR]. In: *Issledovaniya po entomofaune Severo-Vostoka SSSR* [Entomological Investigations of the North-East of the USSR]. Far East Science Centre of the USSR Academy of Sciences, Vladivostok, pp. 23–50 (in Russian).
- Kozyrev, A.V., Kozminykh, V.O., Eshunin, S.L., 2000. Sostav lokal'nykh faun zhuzhelits (Coleoptera, Carabidae) Urala i Priural'ya. ([Structure of ground-beetles local faunas (Coleoptera, Carabidae) of the Ural and Pre-Urals]). *Bulletin of the Perm University, Biology* 2, 165–215 (in Russian).
- Krukover, A.A., 2007. Quaternary arvicolid faunas of the southern West Siberian Plain. *Courier Forschungsinstitut Senckenberg* 13 (12), 93–98.
- Kryazheva, I.V., Ponomarev, D.V., 2008. Melkie mlekopitayushchie pozdnego pleistocena i golocena iz mestonakhozhdeniy Sed'uy 1, 2 (Yuzhny Timan). ([Small mammal remains of the Late Pleistocene and Holocene from the localities of Sed'uy 1, 2 (Southern Timan)]). *Vestnik* [Bulletin] 7, 15–17 (in Russian).
- Kryzhanovskij, O.L., 1983. Zhuki podotryada Adephaga: semeistva Rhysodidae, Trachypachidae; semeistvo Carabidae (vvodnaya chast', obzor fauny SSSR). ([Beetles of Adephaga suborder: families Rhysodidae and Trachypachidae; family Carabidae (introduction, review of USSR fauna)]. In: *Fauna SSSR, Zhestkokrylye. Tom I(2)* [Fauna of USSR. Beetles. vol. I(2)]. Nauka Publishers, Leningrad (in Russian).
- Kryzhanovskij, O.L., 2002. Sostav i rasprostraneniye entomofaun zemnogo shara. ([Composition and Distribution of Entomofaunas of the Globe]). KMK Publishers, Moscow (in Russian).
- Kryzhanovskij, O.L., Matveev, A.B., 1993. A new species of Carabus from the South Urals (Coleoptera, Carabidae). *Zoosystematica Rossica* 2 (1), 143.
- Kryzhanovskij, O.L., Belousov, I.A., Kabak, I.I., Kataev, B.M., Makarov, K.V., Shilenkov, V.G., 1995. A Checklist of the Ground Beetles of Russia and Adjacent Lands (Insecta, Coleoptera, Carabidae). Pensoft Publishers, Sofia, Moscow.
- Kuzmina, S., Korotyaev, B., 1987. Novyi vid zhukov-pilil'schikov roda Morychus Er. (Coleoptera, Byrrhidae) s Severo-Vostoka SSSR. ([New species of the pill beetle genus *Morychus* Er. (Coleoptera, Byrrhidae) from the Northwest of the USSR]). *Entomological Review* 66 (2), 342–344 (in Russian).
- Kuzmina, E.A., 2006. Dinamika soobshchestv melkikh mlekopitayushchikh Yuzhnogo Zaural'ya v pozdnem pleistocene i golocene [The dynamics of small mammal communities from Southern Trans-Urals in Last Pleistocene and Holocene periods]. Ph.D. thesis, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Science, Yekaterinburg, Russia (in Russian).
- Kuzmina, E.A., 2009. Late Pleistocene and Holocene small mammal faunas from the South Trans-Urals. *Quaternary International* 201, 25–30.
- Lindroth, C.H., 1972. Changes in the Fennoscandian Ground-beetle fauna (Coleoptera, Carabidae) during the twentieth century. *Annales Zoologica Fennici* 9, 49–64.
- van der Made, J., 2011. Biogeography and climatic change as a context to human dispersal out of Africa and within Eurasia. *Quaternary Science Reviews* 30, 1353–1367.
- Maleeva, A.G., Stefanovski, V.V., 1988. Fauna melkikh mlekopitayushchikh iz pozdnepleistocenovykh mestonakhozhdeniy vostochnogo sklona Urala i Zaural'ya. ([Small mammal faunas from the late Pleistocene sites of the Eastern Urals and Trans-Urals]). In: *Sovremennoe sostoyaniye i istoriya zhivotnogo mira Zapadno-Sibirskoy nizmennosti* [The Contemporary Composition and History of the Animals of the West Siberian Lowland], pp. 81–97. Sverdlovsk (in Russian).
- Markova, A.K., 1998. Early Pleistocene small mammal faunas of Eastern Europe. In: *van Kolfschoten, Th., Gibbard, P.L. (Eds.), The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, Haarlem*, pp. 313–326.
- Markova, A.K., Smirnov, N.G., Kozharinov, A.V., Kazantseva, N.E., Simakova, A.N., Kitaev, L.M., 1995. Late Pleistocene distribution, diversity of mammals in Northern Eurasia (Paleofauna database). *Paleontologia i Evolucio* 28–29, 1–143.
- Markova, E.A., Yalovskaya, L.E., Zykov, S.V., 2010. Taxonomic identity of voles of the "Arvalis" Group (Genus *Microtus*, Arvicolinae, Rodentia) at the Northern boundary of their distribution in the Urals. *Doklady Biological Sciences* 432 (4), 212–215 (in Russian).
- Maul, L.C., Markova, A.K., 2007. Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe. *Quaternary International* 160, 81–99.
- Medvedev, L.N., 1979. Koleopterologicheskii analiz. ([Coleopterological analysis]). In: *Sokolov, V.E., Dinesman, L.G. (Eds.), Chastnye metody izucheniya istorii sovremennykh ekosistem* [Special Methods of Studying the History of Recent Ecosystems]. Nauka Publishing House, Moscow, pp. 128–135 (in Russian).
- Medvedev, L.N., 1982. Listoedy Mongolii. ([Leaf Beetles of Mongolia]). Nauka Publishers, Moscow (in Russian).
- Mikhailov, Yu.E., 2000. New distributional records of Chrysomelidae from the Urals and Western Siberia (on some "less interesting" faunistic regions) (Insecta: Coleoptera). *Faunistische Adhandlungen* (Staatliches Museum fur Teirkunde, Dresden) 22, 23–37.
- Mordkovich, V.G., Lujbetchanskij, I.I., 1999. Zonal-catena order of ecological ordination in carabids (Coleoptera, Carabidae) from the West Siberian Plain. *Advances in Current Biology* 118, 205–215.
- Morgan, A., 1973. Late Pleistocene environmental changes indicated by fossil insect faunas of the English Midlands. *Boreas* 2, 173–212.
- Nadachowski, A., 1982. Late Quaternary Rodents of Poland with Special Reference to Morphotype Dentition Analysis of Voles. Państwowe Wydawnictwo Naukowe, Warszawa – Kraków.
- Nazarov, V.I., 1984. Rekonstruktsiya landshaftov Belorussii po paleoentomologicheskim dannym. ([Reconstruction of the Landscapes of Belorussia on the Basis of Paleontomological Data]). Nauka Publishing House, Moscow (in Russian).
- Nikolaev, G.V., Kozminykh, V.O., 2002. Zhuki-mertvoedy (Coleoptera: Agyrtidae, Silphidae) Kazakhstana, Rossii i ryada sopredel'nykh stran: Opredelitel'. ([Carrion Beetles (Coleoptera: Agyrtidae, Silphidae) of Russia, Kazakhstan and Adjacent countries: Identification Guide]). Kazak University Publishing, Almaty (in Russian).
- Olenev, A.M., 1965. Ural i Novaya Zemlya. ([The Urals and Novaya Zemlya]). Mysl', Moscow, 216 pp. (in Russian).
- Panasenko, V.E., Tiunov, M.P., 2010. Naselenie melkikh mlekopitayushchikh (Mammalia: Eulipotyphla, Rodentia, Lagomorpha) na yuzhnom Sihotje-Alin v pozdnem pleistocene i golocene. ([The population of small mammals (Mammalia: Eulipotyphla, Rodentia, Lagomorpha) in the South Sikhote Alin in the Late Pleistocene and Holocene]). *Bulletin of the Institute of Biology and Soil Sciences* 6, 60–67.
- Pavlinov, I.Ya., 2003. Systematics of Recent Mammals. Moscow University Publisher, Moscow.

- Pavlinov, I.Ya., Kruskop, S.V., Warschavsky, A.A., Borisenko, A.V., 2002. Terrestrial Animals of Russia. The Guide. KMK Scientific Press, Moscow (in Russian).
- Ponomarev, D.V., Smirnov, N.G., Golovachov, I.B., Kourova, T.P., Kuzmina, E.A., 2005. Fauna melkikh mlekopitayushchikh iz grot Pizhma 1 (Srednii Timan). ([Small Mammal's Fauna from Pizhma 1 (the Meddle Timan)]. In: Palaeontological collected papers №6, Syktyvkar, pp. 86–97 (in Russian).
- Ravkin, Yu.S., Bogomolova, I.N., Tsybulin, S.M., Panov, V.V., Onischenko, S.O., Il'yashenko, V.B., Vartapetov, L.G., Babina, S.G., Chesnokova, S.V., 2009. Prostranstvenno-tipologicheskaya neodnorodnost' naseleniya melkikh mlekopitayushchikh Zapadnoi Sibiri. ([Spatial and typological inhomogeneity of small mammal communities in plains and mountains of West Siberia]). Contemporary Problems of Ecology 2 (3), 275–283 (in Russian).
- Rekovets, L.I., 1994. Melkie mlekopitayushchie antropogena yuga Vostochnoi Evropy. ([Anthropogene Small Mammals of Southern East Europe]). Naukova Dumka, Kiev (in Russian).
- Remington, C.L., 1968. Suture-zones of hybrid interaction between recently joined biotas. In: Dobzhansky, T., Hecht, M.K., Steere, W.C. (Eds.), Evolutionary Biology. Plenum Press, New York, pp. 321–428.
- Rupysheva, T.A., Strukova, T.V., 2010. Fauny melkikh mlekopitayushchikh vostochnogo sklona Srednego Urala v rannem i srednem golocene [Small mammal faunas from eastern slope of the Middle Urals in early and middle Holocene]. The dynamics of ecosystem in Holocene. Proceedings, Second All-Russian Scientific conference, Yekaterinburg, pp. 165–200.
- Samko, K.P., 1932. Zametki o skakunakh i zhuzhelitsakh (Cicindelidae and Carabidae) Tobol'skoi fauny. ([Some notes on Coleoptera (Cicindelidae and Carabidae) of the Tobolsk fauna]). Bulletin of the Perm Scientific-Research Institute 8 (3), 123–143 (in Russian).
- Shenbrot, G.I., Krasnov, B.R., 2005. An Atlas of the Geographic Distribution of the Arvicoline Rodents of the World (Rodentia, Muridae: Arvicolinae). Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel.
- Sher, A.V., 1984. The role of Beringian Land in the development of Holarctic mammalian fauna in the Late Cenozoic. In: Kontrimavichus, V.L. (Ed.), Beringia in the Cenozoic Era. Amerind Publishing Co. Pvt. Ltd., New Delhi, pp. 296–316.
- Sher, A.V., Kuzmina, S.A., 2007. Late Pleistocene beetle records from Northern Asia. In: Beetle Records: Late Pleistocene of Northern Asia. Elsevier, pp. 94–115.
- Shik, S.M., Borisov, B.A., Zarrina, E.P., 2004. Proekt regional'noi stratigraficheskoi skhemy neopleistotsena Evropeiskoi Rossii. ([The project of the regional stratigraphic scheme of the Neopleistocene of the European part of Russia]). Byulleten' Komissii po izucheniyu chetvertichnogo perioda. ([The Bulletin of Committee for Quaternary Research]) 65, 102–114 (in Russian).
- Shvarz, S.S., Pavlinin, V.N., 1960. Opyt glireogeographicheskogo raionirovaniya Urala. ([The Experience of the Glireogeographical Zoning of Urals]). In: Trudy Instituta biologii AN SSSR, Ural'skii filial. ([Proc. of the Institute of biology AS USSR, Ural Branch]), vol. 14, pp. 83–96 (in Russian).
- Simonov, K.A., Tesakov, A.S., 2007. The voles from the Middle Pleistocene Chujsky site on the river Aldan. In: Sovremennaya Rossiyskaya paleontologiya: klassicheskie i noveishie metody [The Modern Russian Paleontology: a Classic and Newest Methods]. Proceedings, IV. Russian Scientific School of Young Science-Paleontologist, Moscow, Russia, pp. 36–37 (in Russian).
- Smirnov, N.G., 1988. Chorological method in studies of Pleistocene mammals in the West Siberia. In: Sovremennoe sostoyanie i istoriya zhivotnogo mira Zapadno-Sibirskoi nizmennosti [The Contemporary Composition and History of the Animals of the West Siberian Lowland]. Nauka Publishers, Ural Branch, Sverdlovsk, pp. 5–20 (in Russian).
- Smirnov, N.G., 1992. Problemy istoricheskoi ekologii mlekopitayushchikh Severnoi Evrasii. ([Problems of mammal historical ecology of Northern Eurasia]). In: Yekovaya dinamika biogeocenozov [The Secular Dynamics of Biogeocenoses]. Nauka Publishers, Moscow, pp. 17–35 (in Russian).
- Smirnov, N.G., 1993. Melkie mlekopitajushchie Srednego Urala v pozdnem pleistocene i golocene. ([Small Mammals of the Middle Urals in Late Pleistocene–Holocene]). Nauka Publishers, Yekaterinburg (in Russian).
- Smirnov, N.G., 1995. Data to studying of historical dynamics of the rodents diversity in the taiga regions of the Middle Urals. In: Materialy po istorii sovremennoi bioty Srednego Urala [Materials on the History of the Modern Biota of the Middle Urals], pp. 24–57. Yekaterinburg (in Russian).
- Smirnov, N.G., 1996. Small mammal diversity in the Northern Urals over the Late Pleistocene and Holocene. In: Materials and Investigations of the History of the Modern Fauna of the Urals: Scientific Papers. Yekaterinburg Publishing House, Yekaterinburg, pp. 39–83.
- Smirnov, N.G., 2001. Zonal distribution of mammals in the Urals over the Late Pleistocene time. In: Rozanov, A.Yu. (Ed.), Mammoth and Its Environment: 200 Years of Investigations. GEOS Publishing, Moscow, pp. 209–219.
- Smirnov, N.G., Golovachov, I.B., 1999. Holocene history of small mammals in the Urals. In: Benecke, N. (Ed.), The Holocene History of the European Vertebrate Fauna – Modern Aspects of Research. Rahden/Westf., Leidorph, pp. 209–221.
- Smirnov, N.G., Sadykova, N.O., 2003. Istochniki pogreshnostei pri faunisticheskikh rekonstruktsiyakh v chetvertichnoy paleozoologii. ([Sources of errors in faunistic reconstructions in quaternary paleozoology]). In: Ushakova, K.I. (Ed.), Chetvertichnaya paleozoologiya na Urale [Quaternary Paleozoology in the Urals]. Ural State University, Yekaterinburg, pp. 98–115 (in Russian).
- Smirnov, N.G., Bol'shakov, V.N., Borodin, A.V., 1986. Pleistocenovye gryzuny Severa Zapadnoi Sibiri. ([The Pleistocene Rodents of the North of Western Siberia]). Nauka Publishers, Moscow (in Russian).
- Smirnov, N.G., Kuz'mina, E.A., Golovachov, I.B., Fadeeva, T.V., 2007. The narrow-skulled vole (*Microtus gregalis* Pall.) in the dynamics of zonal rodent communities of northern Eurasia. Russian Journal of Ecology [Ekologiya] 2, 117–123 (in Russian).
- Smirnov, N.G., Andreicheva, L.N., Korona, O.M., Zinov'yev, E.V., Golovachov, E.V., Pavlov, P.Yu., Hufthammer, A.-K., 1999. Materialy k kharakteristike bioty Priural'skoi Subarktiki v golocenovom optimume. ([Materials to characterize the biota of the Pre-Ural Subarctic during the Holocene Optimum time]). In: Biota Priural'skoi Subarktiki v pozdnem Pleistocene i golocene [Pre-Urals Subarctic in Late Pleistocene and Holocene], pp. 23–60. Yekaterinburg (in Russian).
- Smirnov, N.G., Bol'shakov, V.N., Kosintsev, P.A., Panova, N.K., Korobeynikov, Yu.I., Ol'shvang, V.N., Erokhin, N.G., Bykova, G.V., 1990. Istoricheskaya ekologiya zhivotnykh gor Yuzhnogo Urala. ([Historical Ecology of Animals in the Southern Urals]). Ural Branch of the USSR Academy of Sciences Publishing, Sverdlovsk (in Russian).
- Sokolov, V.E., Bashenina, N.V., 1994. Obyknovennaya poljevka: vidy-dvoyniki. ([Common Vole: the Sibling Species]). Nauka Publishers, Moscow (in Russian).
- Starikov, V.P., Ibragimova, D.V., Nakonechny, N.V., 2009. Melkie mlekopitajushchie okolovodnykh i pereuvlazhnyennykh biotopov Surguta. ([Small mammals from the flood-plain and overwetting biotopes of Surgut]). In: Ekologiya i prirodopol'zovanie v Yugre [Ecology and Nature Management in the Yugra]. Proceedings, Scientific practical conference. Surgut State University, Surgut, pp. 143–145 (in Russian).
- Stefanovsky, V.V., 1997. The Quaternary Stratigraphic Scheme of the Urals. In: The Regional Stratigraphic Scheme of the Urals: Explanatory Notes, pp. 97–139. Yekaterinburg (in Russian).
- Stefanovsky, V.V., Borodin, A.V., Strukova, T.V., 2003. Correlation of the Upper Neopleistocene alluvial and lacustrine sections of Southern Trans-Urals region on the biostratigraphic data. Stratigraphy and Geological Correlation. ([Stratigraphiya. Geologicheskaya Korrelyatsiya]) 11 (4), 87–100.
- Stefanovsky, V.V., Zinov'yev, E.V., Trofimova, S.S., Korona, O.M., 2007. Alluvial'nye komplekxy v nizhnem techenii reki Tavda (Severnoye Zaural'e). ([The alluvial complexes in lower reaches of Tavda River (the Northern Transuralia)]). Ural'sky Geologicheskyy Zhurnal. ([Urals Geological Journal]) 56 (2), 5–25 (in Russian).
- Stefanovsky, V.V., Zinov'yev, E.V., Trofimova, S.S., Strukova, T.V., 2002. Nikitino – astratotipicheskii razrez rezhevskogo alluvial'nogo kompleksa v Srednem Zaural'e. ([Nikitino – parastratotypical site of Rezh' alluvial complex in the Middle Transuralia]). Ural'sky Geologicheskyy Zhurnal. ([Urals Geological Journal]) 1, 7–19 (in Russian).
- Strukova, T. V., 2000. Typology of Late Pleistocene and Holocene small mammal faunas of the Middle Trans-Urals. Biosphere and Mankind. Proceedings, Young Scientists' Conference, Devoted to the Memory of N.V. Timofeev-Resovsky. Ekaterinburg Publishing, Ekaterinburg, pp. 251–260 (in Russian).
- Strukova, T.V., 2003. Stepnaya pestrushka (*Lagurus lagurus* Pall.) i uzkocherepnaya polevka (*Microtus gregalis* Pall.) v chetvertichnykh faunah Srednego i Yuzhnogo Zaural'ya [A steppe lemming (*Lagurus lagurus* Pall.) and a narrow-skulled vole (*Microtus gregalis* Pall.) in Quaternary faunas of the Middle and South Trans-Urals]. Ph.D. thesis, Institute of Plant and Animal Ecology, Ural Branch of RAS, Yekaterinburg, Russia (in Russian).
- Strukova, T.V., Bachura, O.P., Borodin, A.V., Stefanovsky, V.V., 2005. Mammal fauna first found in alluvial-speleogenic formations of the Late Neopleistocene and Holocene, Southern Urals, locality Cheremukhovo-1. Stratigraphy and Geological Correlation. ([Stratigraphiya. Geologicheskaya Korrelyatsiya]) 13 (6), 125–136 (in Russian).
- Sutcliffe, A.J., Kowalski, K., 1976. Pleistocene rodents of the British Isles. Bulletin of the British Museum (Natural History) Geology 27, 33–147.
- Svendsen, J.I., Alexandersson, H., Astakhov, V., Demidov, J., Dowdeswell, J.A., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H., Ingólfsson, Ó., Jakobsson, M., Kjær, K., Larsen, E., Lokrantz, H., Luunka, E.P., Lysa, A., Mangerud, J., Maslenikova, O., Matushkov, A., Murray, A., Möller, P., Niessen, F., Saarnisto, M., Siegert, M., Stein, R., Spielhagen, R., 2004. Ice sheet history of northern Eurasia. Quaternary Science Reviews 22, 1229–1271.
- Swenson, N.G., 2006. Gis-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone. Journal of Evolutionary Biology 19 (3), 717–725.
- Swenson, N.G., Howard, D.J., 2004. Do suture zones exist? Evolution 58, 2391–2397.
- Swenson, N.G., Howard, D.J., 2005. Clustering of contact zones hybrid zones and phylogeographic breaks in North America. American Naturalist 166, 581–591.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G., Cosson, J.-F., 1998. Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology 7, 453–464.
- Tesakov, A.S., Lebedev, V.S., Bannikova, A.A., Abramson, N.I., 2010. *Clethrionomys* Tiliensis, 1850 is a valid name for red-backed voles and Myodes Pallas, 1811 is a younger synonym of Lemmus Link, 1795. Russian Journal of Theriology 9 (2), 83–86.
- Teterina, A.A., Ulitko, A.I., 2002. Novye mestonakhozhdeniya pozdnepleistocenovykh i golocenovykh faun mlekopitayushchikh v karstovykh polostyakh na Severnom Urale. ([New Localities of the Late Pleistocene and Holocene mammal faunas in Karst Caves of the Northern Urals]). In: Fauna Urala v Plistocene i Golocene [Fauna of the Urals in the Pleistocene and Holocene], pp. 155–182. Yekaterinburg (in Russian).
- The Genus Carabus in Europe, 2003. A synthesis. In: Turin, H., Penev, L., Casale, A. (Eds.), Fauna Europaea Vertebrata, vol. 2. Pensoft Publ., Sofia-Moscow.

- Tikhonova, G.N., Tikhonov, I.A., Surov, A.V., Bogomolov, P.L., 2009. Structure of small mammal communities in Moscow parks and public gardens. *Russian Journal of Ecology [Ekologiya]* 40 (3), 213–217 (in Russian).
- Tougaard, C., Renvoisé, E., Petitjean, A., Quéré, J.-P., 2008. New insight into colonization processes of common voles: inferences from molecular and fossil evidence. *PLoS ONE* 3 (10), e3532. doi:10.1371/journal.pone.0003532.
- Unificirovannaya regional'naya stratigraficheskaya shema chetvertichnykh otlozhenii Zapadno-Sibirskoi ravniny [The Unified Stratigraphic scheme for the territory of Western Siberia], 2000. Nauka, Novosibirsk, 7 pp. (in Russian).
- Vangengeim, E.A., 1977. Paleontologicheskoe obosnovanie stratigrafii antropogena Severnoi Evrazii. ([Paleontological Basis of the Quaternary Stratigraphy of North Eurasia]). Nauka Publishers, Moscow (in Russian).
- Velichko, A.A., 1984. Late Quaternary Environments of the Soviet Union. University of Minnesota Press, USA.
- Villa, P., Sánchez Goñi, M.F., Bescós, G.C., Grün, R., Ajas, A., García Pimienta, J.C., Lees, W., 2010. The archaeology and paleoenvironment of an Upper Pleistocene hyena den: an integrated approach. *Journal of Archaeological Science* 37, 919–935.
- Volkovich, M.G., Alekseev, A.V., 1988. Sravnitel'naya kharakteristika fauny zlatok (Coleoptera, Buprestidae) Severnoi Evrazii. ([Comparative characteristics of the fauna of buprestids (Coleoptera, Buprestidae) of Northern Eurasia]). In: Svyazi entomofaun Severnoi Evropy i Sibiri [The Connections between Entomofaunas of the Northern Europe and Siberia]. ZIN AS USSR Publishing, Leningrad, pp. 42–58 (in Russian).
- Zazhigin, V.S., 1980. Gryzuny pozdnego pliocena i antropogena yuga Zapadnoi Sibiri. ([The Rodents of the Late Pliocene and Anthropogene of the South of West Siberia]). Nauka, Moscow (in Russian).
- Zazhigin, V.S., 2003. O kopytnykh lemmingakh (*Dicrostonyx*, Microtinae, Rodentia) Oigos-Jara Vostochnoi Sibiri i o vidovom statuse srednepleistocenovogo vida roda *Dicrostonyx*. ([About an arctic lemmings (*Dicrostonyx*, Microtinae, Rodentia) from the Oigos-Jar of Eastern Siberia and about the status of the Middle-Pleistocene species of genus *Dicrostonyx*]). In: Nokol'skii, P.A., Pitul'ko, V.V. (Eds.), Estestvennaya istoriya Rossiiskoi Vostochnoi Arktiki v pleistocene i golocene [Natural History of Russian Eastern Siberia in Pleistocene and Holocene Time]. GEOS, Moscow, pp. 14–26 (in Russian).
- Zinovyev, E.V., 1988. Iskopatnye zhestkokrylye mestonakhozhdeniya "Protoka Mega". ([Fossil beetles from the protoka Mega site]). In: Sovremennoe sostoyanie i istoriya zhivotnogo mira Zapadno-Sibirskoi nizmennosti [The Contemporary Composition and History of the Animals of the West Siberian Lowland]. Nauka Publishers, Ural Branch, Sverdlovsk, pp. 119–122 (in Russian).
- Zinovyev, E.V., 2003. Kharakteristika pozdnekarginiskikh entomokompleksov Nizhnego Priirtys'ya na primere mestonakhozhdenii Skorodum-95 i Kazakovka-95. ([Late Karginian fossil insect assemblages of the lower reaches of the Irtysh river, as exemplified by sites Skorodum-95 and Kazakovka-95]). *Evrasiatskii entomologicheskii zhurnal*. ([Eurasian Entomological Journal]) 2, 83–93 (in Russian).
- Zinovyev, E.V., 2005. Materialy k kharakteristike rannegolocenovykh entomokompleksov Srednego Priobya. ([Early Holocene entomocomplexes from the middle reaches of the Ob River in West Siberia]). *Evrasiatskii entomologicheskii zhurnal*. ([Euroasian Entomological Journal]) 4 (4), 283–292 (in Russian).
- Zinovyev, E.V., 2006. Problems of ecological interpretation of Quaternary insect faunas from the central part of northern Eurasia. *Quaternary Science Reviews* 25, 1821–1840.
- Zinovyev, E.V., 2007. A history of ground-beetle faunas of West Siberia and the Urals during the Late Pleistocene to Holocene. Back to the Roots and Back to the Future. Towards a New Synthesis amongst Taxonomic, Ecological and Biogeographical Approaches in Carabidology. Proceedings, XIII European Carabidologists Meeting. Blagoevgrad, Bulgaria, pp. 241–254.
- Zinovyev, E.V., 2011. Sub-fossil beetle assemblages associated with the "mammoth fauna" in the Late Pleistocene localities of the Ural Mountains and West Siberia. In: Kotze, D.J., Assmann, T., Noordijk, J., Turin, H., Vermeulen, R. (Eds.), Carabid Beetles as Bioindicators – Biogeographical, Ecological and Environmental Studies, vol. 93. ZooKeys, pp. 140–169.
- Zinovyev, E.V., Fadeyev, F.A., 2002. Rekonstrukciya uslovii formirovaniya golocenovykh otlozhenii mestonakhozhdeniya Loz'va-1 (Severnyi Ural) na osnove entomologicheskikh dannykh. ([Reconstruction of Holocene sediment deposits at the Loz'va-1 site (North Urals) based on insect data]). In: Pleistocenovye i golocenovye fauny Urals [Urals Fauna in the Pleistocene and Holocene Times]. Ripheus Press, Chelyabinsk, pp. 167–177 (in Russian).
- Zinovyev, E.V., Nesterkov, A.V., 2003. Novye dannye k izucheniuyu chetvertichnykh nasekomykh territorii Zapovedno-Prirodnogo parka "Sibirskie Uvaly". ([New data to studying the Quaternary insects from the Natural Reserve park "Sibirskie Uvaly"]). In: Ekologicheskie issledovaniya vostochnoi chasti Sibirskikh Uvalov [Ecological Researches of the Eastern Part of "Sibirskie Uvaly"]. Priobie Publishers, Nizhnevartovsk, pp. 66–82.
- Zinovyev, E.V., Olshwang, V.N., 2003. Zhuki severa Zapadno-Sibirskoi ravniny, Pri-polyarnogo i Polyarnogo Urals. ([Beetles of the Northwest Siberian Plain, Sub-Polar and Polar Urals]). *Nauchnyi vestnik: Biologicheskoye resursy Polyarnogo Urals*. ([Scientific Journal: Biological Resources of the Polar Urals]) 3, 37–60 (in Russian).
- Zinovyev, E.V., Gilev, A.V., Khantemirov, R.M., 2001. Changes in the entomofauna of the southern Yamal Peninsula in connection with shifts of the northern timberline in the Holocene. *Entomological Review* 81 (9), 1146–1152 (Translated from: *Entomologicheskoe Obozrenie* 80, 843–851).
- Zinovyev, E.V., Korona, O.M., Stefanovsky, V.V., 2007. Rekonstrukciya uslovii formirovaniya pozdnepleistocenovykh otlozhenii mestonakhozhdeniya Andryushino (nizov'ya reki Tavda River) po entomologicheskim i karpologicheskim dannym. ([Reconstruction of formation of Late Pleistocene layers from Andryushino site (low reaches of Tavda River) on the basis of sub fossil insect and carpological data]). *Uralsky Geologicheskyy Zhurnal*. ([Urals Geological Journal]) 56 (2), 27–43 (in Russian).
- Zykov, S.V., Maksimova, E.G., 2004. Tyulenevo – novoe allyuvial'noe mestonakhozhdenie neopleistocenovykh pozvonochnykh Yuzhnogo Zaural'ya [Tyulenevo – a new alluvial site of neopleistocene vertebrate mammals from the Southern Trans-Urals]. In: Sovremennaya Rossiyskaya paleontologiya: klassicheskie i noveishie metody [The modern Russian paleontology: a classic and newest methods]. Proceedings, First Russian scientific school of young science-paleontologist, Moscow, Russia, pp. 36–37 (in Russian).