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Quaternary small mammal faunas from the west Siberian plain

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Abstract. During the Pleistocene, zonal complexes of small mammals existed on the west Siberian plain. These included the northern tundra-like faunas, the southern steppe and forest-steppe faunas, and the central "non-analogue" faunas. Paleontological material allows us to state that the modern steppe complex of small mammals is of autochthonous origin and that the formation of the modern tundra and forest complexes was determined by the geological history of the northern territories and by global climatic shifts during the Pleistocene and Holocene. The modern taiga zone is new to the west Siberian plain and might be a result of the degradation of the "non-analogous" Pleistocene faunas.

Key words: Paleoecology, west Siberian plain, Quaternary, small mammals.

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I. INTRODUCTION

The west Siberian plain is one of the largest plains in the world covering about three million square kilometers. Sedimentary processes, mostly active during the Quaternary, are responsible for the formation of the relief of this area (GVOZDETSKI & MICHAILOV 1963). For this reason Pleistocene and Holocene deposits of marine and continental origin are widely distributed, the latter often including the remains of animals and plants.

The study of fossil small mammal faunas of the west Siberian plain began relatively recently. It was only towards the end of the 1960s that mass occurrences of small mammal fossils began to be found in this region (MALEEVA 1970; MOTUZKO 1975; GALKINA 1977, 1980; ZAZHIGIN 1980; BORODIN & SMIRNOV 1984; SMIRNOV et al. 1986). Today, about one hundred sites with small mammals are known (Fig. 1). Almost all these sites are of alluvial type, and therefore the species lists need to be interpreted carefully, taking into account taphonomic peculiarities (SMIRNOV et al. 1986). Another difficulty is the limited comparisons that exist between the west Siberian plain and the European faunas, both as regards geographic and chronologic aspects.

Nevertheless, the data available can be used to investigate a whole complex of problems, both,stratigraphical and biological, that are reflected in the works of the above mentioned authors. The material allows us to note some peculiarities in the geographical distribution of small mammal faunas and the evolution of some rodent taxa during the Quaternary period in this region.

In this paper we will deal mainly with the study of the history of the faunal complexes of the west Siberian plain using all the known material.

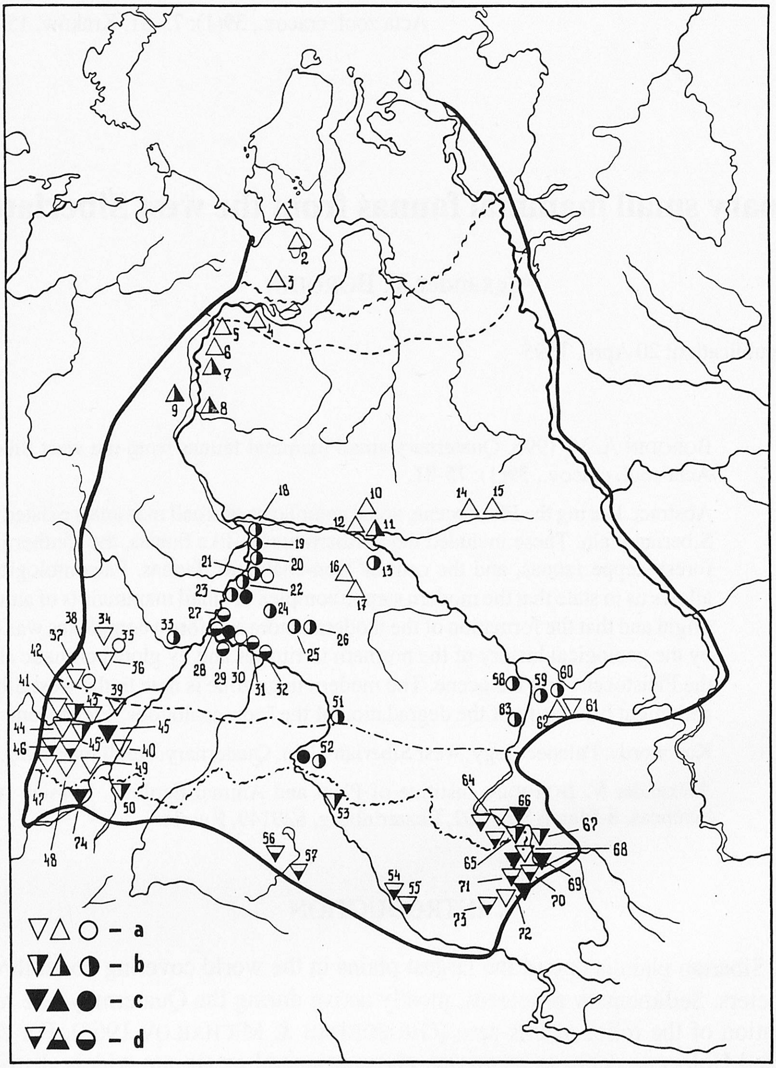

Fig. 1. The Pleistocene sites of small mammal faunas of the West-Siberian plain. 1 – Nyamuyu-Nado, 2 – Ngoyun, 3 – Lyabtosyo, 4 – Gornokazymsk, 5 – Pelyach-Yugan, 6 – 430-th Km, 7 – Khashgort, 8 – Kazym-Mys, 9 – Beryosovo, 10 – Agansky Uval-1290/2, 11 – Kiryas, 12 – Mega, 13 – Kulyegan, 14 – Kolyalki, 15 – Komses-Egan, 16 – Malyi Yugan III, 17 – Malyi Yugan II, 18 – Semeika, 19 – Chembakchino, 20 – Gornopravdinsk, 21 – Bobrovka, 22 – Demyanskoye, 23 – Koshelevo, 24 – Yarsino, 25 – Shakhmatovka I, 26 – Shakhmatovka II, 27 – Nadzy, 28 – Chornaya, 29 – Isker, 30 – Yakushinsky Yar, 31 – Skorodum, 32 – Romanovo, 33 – Nizhnaya Tavda, 34 – Lebyodkino, 35 – Rechkalovo, 36 – Merkushino, 37 – Kolchedanka, 38 – Dolmatovo, 39 – Dolgovskoye, 40 – Verchnaya Alabuga, 41 – Balandino, 42 – Stepnoye, 43 – Myasskoye, 44 – Korkino, 45 – Baturino, 46 – Kochkar, 47 – Streletskoye, 48 – Bobrovskoye, 49 – Vvedenka, 50 – Novopokrovka, 51 – Kartashovo, 52 – Novotroitskoe, 53 – Tatarka, 54 – Lebyazhye, 55 – Podpusk, 56 – Ashchily-airyk, 57 – Iliinka, 58 – Krivosheino, 59 – Kubayevo, 60 – Mazalovo, 61 – Mariinsk, 62 – Vtoraya Pristan, 63 – Urtam, 64 – Shelabolicha, 65 – Malinovka, 66 – Gonba, 67 – Kalmanka, 68 – Belovo, 69 – Vyatkino, 70 – Razdolye, 71 – Machanovo, 72 – Kisikha, 73 – Troitskoe, 74 – Rudnyi. (References: 22, 27, 58, 63, 64 – Krukover 1992; 28 – Motuzko 1975; 34-37, 43, 47, 49 – Maleeva & Stefanovski 1988; 51-57, 59-62, 67, 69-74 – Zazhigin 1980; 64-66 – Zudin et al. 1977). The bounderies of the modern climatic zones: ~ ~ tundra – forest-tundra, – – – forest-tundra – taiga, – · – taiga – forest-steppe, ~ · ~ forest-steppe – steppe. Δ – tundra-like faunas, ○ – non-analogue faunas, ∇ – steppe and forest-steppe faunas, a – Late Pleistocene, b – Middle Pleistocene, c – Early Pleistocene, d – Late Pliocene.

II. ZONALITY OF THE QUATERNARY FAUNAS OF THE WEST SIBERIAN PLAIN

The limited relief of the west Siberian plain leads to a strongly pronounced landscape zonality (tundra, forest-tundra, taiga, forest-steppe, steppe). The topography does not strongly influence this zonality, the main factors instead being insolation (latitude dependent) and hydrological regime. We have every reason to believe that the formation of the Quaternary ecosystems (and therefore the distribution of different species of small mammals) was mainly determined by the same factors.

The fossil small mammal faunas found in the plain may be placed in at least three groups on the basis of species composition: 1) local faunas represented by species classified as ancestors of the modern tundra species or as forms indicating tundra conditions; 2) faunas having acquired the name of "mixed", "periglacial" , "disharmonious", "non-analogue" (SEMKEN 1974, 1988) or "discomformable" (SHER 1990), including both tundra species and some steppe forms, as well as intrazonal and some forest forms. 3) faunas without lemmings that in some cases could be considered steppe faunas and in others forest-steppe faunas.

Fig. 1 shows that the distribution of these groups is independent of age and is in accordance with features that could be interpreted as the result of the climatic zonality of the landscape.

The sites of the first group are located in the northern part of the west Siberian plain. This territory stretches from the modern southern tundra to the northern part of the middle taiga zone. In these faunas, small mammals are represented by the genera *Lemmus, Dicrostonyx* and *Microtus* (*M. gregalis* and *M. middendorffii*). No other species of small mammals have been found in this region (SMIRNOV et al. 1986).

Local faunas characterising the interval from the Middle Pleistocene to the end of the Late Pleistocene differed in the evolutionary level of the voles (evolution from *Dicrostonyx ocaensis* to *D. gulielmi*; complication of *M. gregalis* morphotypes) and in the ratios of vole species reflecting local ecological conditions. This is seen in the Late Pleistocene faunas (Table I). The Agansky Uval-1290/2 site (radiocarbon date 23,300±500, IERiZh-176) is located at 61°N; 430th km site (radiocarbon date 24000±1500, IERiZh-63) at 66°N and Ngoyunat site at 69°N.

The sites of the second faunistic group belong to the middle part of the Plain (between 61 and 56°N). The time interval represented by the remains of the second group is upper Villafranchian to Late Pleistocene (SMIRNOV et al. 1986; KRUKOVER 1992), much longer than that of the first group.

A difference in species diversity is also evident. A general feature of the local faunas of this group is the coexistence of steppe, tundra and forest elements. The genera *Desmana*, *Erinaceus*, *Talpa*, *Sorex*, *Ochotona*, *Spermophilus* and *Sicista*, together with voles, make up the faunas of this zone. The oldest faunas include *Clethrionomys* ex gr. *rutilus-glareolus*, *C. major* BORODIN, 1988 [the ancestral form of the Late Pleistocene *C. rufocanus* (BORODIN 1988)], *Prolagurus pannonicus*,

Table I

Ratio of the molars of different species (%) in the Late Pleistocene faunas of the West-Siberian Plain according with the latitude of sites: Agansky Uval-1290/2 – 61°N, 430-th Km – 66°N, Ngoyun – 69°N

Species	Ratio (%)		
	Agansky Uval-1290/2	430-th Km	Ngoyun
Dicrostonyx cf. gulielmi SANFORD, 1870	5.03	35.39	53.61
Lemmus sibiricus KERR, 1792	11.17	30.27	37.11
Microrus gregalis PALLAS, 1778	76.80	32.32	7.42
M. ex gr. middendorffii POLYAKOV, 1881	7.00	2.02	1.86

Lemmus cf. *sibiricus*, *Dicrostonyx meridionalis* SMIRNOV & BORODIN, 1986 (comparable with *D. antiquitatis*), several *Mimomys* species (e. g., *M. pusillus* and *M. intermedius*) and *Allophaiomys pliocaenicus* (late form). The Late Pleistocene faunas include *Clethrionomys* ex gr. *rutilus-glareolus*, *C. rufocanus*, *Lagurus lagurus*, *Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Arvicola terrestris*, *Microtus gregalis*, *M. oeconomus*, *M. agrestis* and *M. middendorffii*. In certain cases the proportion of forest forms may be considerable. Southwards, the decreasing percentage of lemming remains is notable, as well as the increasing total diversity. The percentage of steppe elements also decreases. These trends are seen both in the *Allophaiomys-Mimomys* faunas and in faunas where the evolutionary level of the voles is close to modern. No faunal changes that could be related to the Glacial/Pluvial cycles are seen. The number of forest species increases from north to south.

It is possible to observe differences in species content of faunas of the same geological age and geographic location. Table II shows data on the species found in faunas from the Middle Pleistocene deposits of the altitudinally lower part of the Irtysh river.

The sites are situated close to each other, and the differences in species content must therefore be explained by features such as the alluvial type of fossil accumulation and the landscape and climatic changes that occurred over geologically short intervals from the moment of deposition of one site until the formation of the next.

It must be noted, that during some periods of the Pleistocene the faunas of non-analogous type spread far south beyond the boundaries mentioned, along the mountain regions framing the west

Table II

Species content of the Mid-Pleistocene faunas from the sites of the same geological age and geographical position. Numbers indicate the number of molars

Species		Sites	
		Semeika	Chembakchino
Sorex sp.		14	5
Lepus sp.		4	1
Ochtona ex *gr. hyperborea* PALLAS, 1811		58	71
Spermophilus sp.		–	1
Gen. *Clethrionomys*		38	39
Cl. ex *gr. glareolus* SCHREBER, 1780	M/1	6	6
Cl. cf. *rutilus* PALLAS, 1779	M/1	4	6
Lagurus transiens JÁNOSSY, 1962		–	7
Dicrostonyx cf. *henseli* HINTON, 1910		75	135
Lemmus cf. *sibiricus* KERR, 1795		180	580
Arvicola aff. *terrestris* LINNAEUS, 1758		10	–
Gen. *Microtus*		521	990
M. gregalis PALLAS, 1778	M/1	53	124
M. oeconomus PALLAS, 1778	M/1	79	86
M. agrestis LINNAEUS, 1761	M/1	2	2
M. ex *gr.arvalis-agrestis*	M/1	5	12
M. ex *gr. middendorffii* POLYAKOV, 1881	M/1	20	23

Siberian plain. Data relevant to this issue can be found in GALKINA (1977) for the southwestern part of the plain and SMIRNOV (1992) for the Urals.

The sites of the third group of faunas are located mainly to the south of 56°N. The most detailed descriptions dealing with the southwestern part of the plain have been published by GALKINA (1977, 1980), ZAZHIGIN (1980), KRUKOVER (1992) and, for the Trans-Urals, by MALEEVA & STEFANOVSKI (1988) and myself.

The Late Pliocene faunas of this group include the genera *Sorex*, *Drepanosorex*, *Desmana*, *Ochotona*, *Castor*, *Marmota*, *Spermophilus*, *Cricetulus*, *Sicista*, *Allactaga*, *Alactagulus*, *Prosiphneus*, *Cricetus*, *Clethrionomys* (*Clethrionomys* ex gr. *sokolovi*), *Borsodia* (late form), *Mimomys* and *Allophaiomys*. The Pleistocene faunas include *Erinaceus*, *Desmana*, *Sorex*, *Ochotona*, *Sicista*, *Spermophilus*, *Marmota*, *Allactaga*, *Alactagulus*, *Cricetulus*, *Ellobius*, *Myospalax*, *Clethrionomys*, *Lagurus*, *Eolagurus*, *Arvicola*, *Microtus* (*M. gregalis*, *M. oeconomus*, *M. arvalis* and, in the Middle and Late Pleistocene, *M. agrestis*).

It is obvious, that alongside the forest-steppe elements a considerable proportion of certain faunas consists of species considered to be indicators of semidesert biotopes. Generally, this group of faunas can be characterised by the fact, that within the time interval from the Late Pliocene to the Pleistocene the species composition of the faunas varied from forest-steppe to steppe-semidesert.

It is possible to observe an overlap between the above mentioned three faunistic complexes (Fig. 1). On the basis of the present data, overlap between faunas of different ages could be due to varying environmental conditions during different stages of the Pleistocene. The environmental gradient that influenced biological diversity in an east-west direction is rather stable, whereas the north-south gradient is more variable in a historical context. The dynamics of environmental change led to changes in the species composition of the faunas and shifts in the boundaries of the complexes.

Nevertheless, we conclude that even taking into consideration a certain pulsation of boundaries the nuclei of the specified geographical complexes remained within the studied region during the Quaternary period, though the species composition and boundaries of the distributions of the zonal complexes differed considerably from those of today.

III. HISTORICAL ROOTS OF THE MODERN ZONAL COMPLEXES

The autochthonous origin of the forest-steppe and steppe faunas of the west Siberian plain and the origin of the steppe zone of the Late Pliocene have been previously discussed (e. g., GALKINA 1980; ZAZHIGIN 1980; MALEEVA & STEFANOVSKI 1988).

A problem that calls for further discussion is the history of the modern tundra and taiga faunas. In view of the historical roots of the modern zonal faunas and of the mixed faunas in place during the whole Quaternary period, it is necessary to emphasise the considerable differences between the geographic histories of the west Siberian plain and Europe and central Siberia. Besides possible covering glaciations during cold periods the character of the zonal faunas may during warm periods have been significantly influenced by marine transgressions (VELICHKO 1993). These would not only determine the climate of the region, but also lead to the existence of a number of large, insular ecosystems isolated from each other for a long time.

As we have already seen, the tundra-like faunas of small mammals were characteristic of the northern part of the plain during at least the Middle to Late Pleistocene period.

General problems of the history of tundra ecosystems have been previously discussed by SHVARTZ (1963) on the basis of modern material and by KOWALSKI (1980) on the basis of paleontological data. Work by neontologists on the modern west Siberian tundra has highlighted the unsaturated trophic chains of tundra ecosystems suggesting that these ecosystems are rather young (SHVARTZ 1963). This assumption is in contradiction to the data of paleontologists, which indicate that the tundra complexes are ancient. This contradiction disappears if we remember two principal arguments:

1) Pleistocene small mammal tundra-like complexes were the part of the mammoth biota and thus the northern Pleistocene ecosystems differed from the modern ones; 2) The development of the ecosystems is closely connected with the geological history of this territory.

In this paper we have noted that the tundra-like small mammal complex was distributed more widely than the modern boundaries of the forest-tundra zone.

As regards the west Siberian plain, Pleistocene faunas recovered from areas today covered by tundra and forest-tundra are older than the Kazantzevo (=Eemian) transgression (about 100,000 years ago) and can not be considered ancestral to modern tundra faunas. At that time this region was covered by water. Later, the main part of the region was covered by Zyryanian (=early Weichselian) ice sheets. During the Sartanian (=late Weichselian) the fauna that evolved toward the end of the Karginsky was distributed on a few islands. Thus, the modern tundra faunas were probably formed during the last part of the Late Pleistocene and the Holocene as a result of the expansion of mammals from insular refugia and the northward expansion of species living in riverine environments as they gradually migrated to the north.

The region that is covered by the modern tundra zone of the west Siberian plain was formed only after the Sartanian and was inhabited by representatives of the northern mammoth biota (this biota was degraded during the Pleistocene/Holocene transition) and also by species such as *Arvicola terrestris*, *Microtus oeconomus*, *Clethrionomys rutilus* and others, that moved northwards along with the intrazonal biotopes.

One unresolved issue concerns the problem of the historical roots of the modern forest zone in the west Siberian plain. Figure 1 indicates that the tundra-like small mammal complex was present in the northern part of this zone, and the "non-analogue" complex in the southern part. We must suppose that the northern part of this region could have been partially covered by an ice sheet during the cold periods and then be transformed into large islands or peninsulas during warm periods as a result of transgressions.

These processes probably provided the physical geographic conditions necessary for the preservation of zonality during the Pleistocene.

The "non-analogue" faunas include practically all the species of small mammals (or their ancestral forms) currently living in the forest-taiga zone of the west Siberian plain.

Judging from the available paleontological data we are inclined to consider the modern taiga fauna of the west Siberian plain as the result of a degradation of the "non-analogue" faunistic complex of the Late Pleistocene and Early Holocene of this region. The modern aspect of the taiga fauna evolved in the Holocene.

Thus, the geological history of the region predetermined the specific character of ecosystem formation and therefore the small mammal faunistic complexes of the west Siberian plain differ from those of Europe and east Siberia. This should be taken into consideration when studying the evolution and phylogeny of west Siberian species and also when constructing regional biostratigraphical schemes and correlations.

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