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Pleistocene and modern distribution of the subterranean rodent *Myospalax myospalax* (Rodentia, Myospalacidae) in response to environmental factors

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ABSTRACT

The question of the modern and past distribution of Siberian zokor *Myospalax myospalax* (Laxmann, 1773) continues to be an unresolved puzzle. This Western Siberian endemic species belongs to the family Myospalacidae, a group of subterranean rodents. The distribution of *M. myospalax* went through dramatic changes due to mass hunting in the first half of the 20th century and later development of agriculture. Because of this, data from various studies executed in different years do not always match, making it difficult to determine the natural limiting factors in the distribution of Siberian zokors. In turn, paleontological data from different regions are fragmentary and have not been summarized in a single study. We aimed to review the past and modern distribution of *M. myospalax* and examine its relationship with environmental factors such as climate and soils distribution. We hypothesized that this species may be a good indicator of past environmental conditions because of its special habitat characteristics. We gathered and revised published data to reconstruct the distribution before the anthropogenic influence of the 20th century and during the Pleistocene and Holocene epochs. The modern preanthropogenic range was compared with the distribution of soil complexes and provinces. We also examined *M. myospalax* molars from Late Pleistocene – Holocene localities and compared them with the modern population. The Siberian zokor distribution data provided herein will be useful for researchers from other regions who use fragmentary or doubtful data on the topic. We also identified climatic and soil parameters of *M. myospalax* habitat. These parameters can be used to reconstruct past environmental conditions from paleontological findings of the Siberian zokor.

Key words: biogeography, climate reconstruction, Myospalacidae, paleobiogeography, Western Siberia, zokors

Распространение подземных грызунов *Myospalax myospalax* (Rodentia, Myospalacidae) в плейстоцене и в современности как ответ на изменение экологических факторов

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РЕЗЮМЕ

Распространение алтайских цокоров *Myospalax myospalax* (Laxmann, 1773) остаётся предметом научных дискуссий как относительно состояния современного ареала, так и палеоареалов в геологическом прошлом. Данный вид является западносибирским эндемиком и относится к семейству цокоровых (Myospalacidae), группе подземных грызунов, ведущих одиночный и территориальный образ жизни. Ареал алтайских цокоров претерпевал сильные изменения в 20 веке, следствием чего стало его сокращение и разорванность. В исследованиях за разные года приводимые ареалы алтайских цокоров часто могут не совпадать друг с другом, что затрудняет определение лимитирующих факторов для данного вида. В свою очередь, данные по ископаемым находкам *M. myospalax* являются фрагментарными и до настоящего момента не были рассмотрены в рамках одной публикации. В настоящей работе проведена ревизия данных по распространению *M. myospalax* с целью определения связи между ареалом алтайских цокоров и такими факторами окружающей среды, как климат и распределение почв. В работе реконструирована зона максимального распространения алтайских цокоров в 19–20 веках. Зона максимального распространения была сопоставлена с распространением почвенных комплексов и провинций, что позволило установить ряд климатических и почвенных параметров, характерных для местообитания данного вида. В работе обобщены авторские и ранее опубликованные данные по ископаемым находкам *M. myospalax*. Исследованы моляры *M. myospalax* из местонахождений позднего плейстоцена и голоцена, с последующим сравнением с рецентными выборками и остатками из местонахождений среднего плейстоцена. На основе полученных результатов выдвинуто предложение об использование данного вида в качестве палеоклиматического индикатора.

Ключевые слова: биогеография, климатические реконструкции, Myospalacidae, палеобиогеография, Западная Сибирь, цокоры

INTRODUCTION

The increase in human presence in the territory of Western Siberia in the 20th century had a strong impact on the fauna of this region (Shmygleva 2017). A good example of this influence is Siberian zokor *Myospalax myospalax* (Laxmann, 1773). This species is a member of the family Myospalacidae, a group of subterranean rodents with solitary and territorial behavior. Although some researchers consider zokors to be a subfamily within the family Spalacidae, we favour the opinion that it is a separate family based on anatomical differences and modern molecular data (Liu et al., 2022). *Myospalax myospalax* is endemic to Western Siberia, and its range is the most distant from the range of other zokor species. The closest geographical “neighbor” of Siberian zokor in the zokor’s family is *M. aspalax* (Pallas, 1776), and the distribution areas of these two species are at a distance of 1000 km from each other (Gromov and Erbaeva 1995; Puzachenko et al. 2009).

In the first half of the 20th century, Siberian zokors were a desired prey for local hunters (Ognev 1947; Laptev and Losev 1949; Makhmutov 1983). In the second half, the areas inhabited by *M. myospalax* became the object of agrarian program of the Soviet Union (Makhmutov 1983; Shmygleva 2017). These factors led to the degradation and fragmentation of the range of this species (Galkina et al. 1969; Makhmutov 1983; Butkauskas et al. 2020). In some areas, information about the presence of *M. myospalax* is outdated and has remained only as historical data (Ognev 1947; Laptev and Losev 1949). Additionally, some data are doubtful in their original validity (Czerski 1873; Ognev 1947). In different studies, the distribution of Siberian zokors does not always match (Galkina et al. 1969; Alexeeva 2006; Butkauskas et al. 2020). Because of controversy and fragmentary data, *M. myospalax* remains a less studied species compared to other species of the family (Liu et al. 2022; Zhang et al. 2022; Kang et al. 2023). Recently studies have revealed differences in the evolution of the West Siberian zokor's lineage and other lineages (Golovanov and Zazhigin 2023). It has also been shown that the West Siberian lineage developed morphological features characteristic of *M. myospalax* at the beginning of the Middle Pleistocene. Since then, evolutionary differences in the West Siberian lineage have been defined at the chronological subspecies level.

Our main goal was to provide a more accurate paleo- and biogeographic characterization of the species *M. myospalax* and to determine the relationship between geographic distribution and environmental factors. To achieve this goal, we reviewed the published data and combine them to give the most accurate biogeographic characterization of the species before intensive anthropogenic influence in the 20th century. We hypothesized that a species distributed in such a restricted territory must have strict natural limiting factors. These factors can be detected and subsequently used to reconstruct environmental conditions in the past only by reconstructing the natural range of the Siberian zokor. Our additional goal was to study the morphology of Late Pleistocene – Holocene *M. myospalax* molars as one of the main indicators of their evolution. To examine the morphological differences between modern and fossil specimens, we used a number of morphometric methods. We wanted to determine whether it is possible to date the Late Pleistocene and Holocene localities of Siberian zokor without depending on other methods.

MATERIAL AND METODS

In the biogeographic part, we used data on the distribution of Siberian zokors from the XIX century to the present (Czerski 1873; Ognev 1947; Laptev and Losev 1949; Galkina et al. 1969; Galkina and Nadeev 1980; Makhmutov 1983; Gromov and Erbaeva 1995; Ovodov and Martynovich 2001; Puzachenko et al. 2009; Butkauskas et al. 2020). Based on these data, the area of maximum distribution of *M. myospalax* in historical times before intensive anthropogenic influence was reconstructed (Fig. 1, Table 1). This area connects modern isolated ranges of Siberian zokor according to their ecological preferences and historical data into one general area. This approach allows us to give the most complete ecological characterization and to display the migration paths of this species. Some of the data we analyzed were controversial, so the least reliable data were not taken into account. The data of S.I. Ognev (1947) on the distribution of *M. myospalax* in the area of the Tom River, west of Lake Chany, and on the right bank of the Ob and Katun rivers were not used. These data were not confirmed in subsequent studies, have an unclear origin, and in some cases were given without factual evidence (Laptev and Losev 1949; Galkina et al. 1969; Makhmutov 1983). For example, I.D. Czerski discovered a skull of the Siberian zokor in the surroundings of Omsk (Czerski 1873), which is quite unique for this region. In his work Czerski notes, although this skull was excavated in the area of Omsk, there is no certainty that zokors are present in this territory in modern times. However, S.I. Ognev (and other researchers after him) used this finding as evidence of the modern distribution of zokors in this area (Ognev 1947; Laptev and Losev 1949; Makhmutov 1983; Ovodov and Martynovich 2001; Puzachenko et al. 2009). Later, no data confirming the distribution of *M. myospalax* in the surroundings of Omsk in historical times were obtained. Most likely, this find is a Pleistocene locality. Unfortunately, the age of this locality cannot be established from the given description, so we do not use it in our analysis.

To characterize the distribution of *M. myospalax* in the Pleistocene and Holocene, our data were used along with those already published (Adamenko and Zazhigin 1965; Galkina et al. 1969; Motuzko 1970, 1975; Zazhigin 1980; Galkina and Nadeyev 1980; Makhmutov 1983; Krukover 1992; Arkhipov et al. 1997; Andrenko et al. 1999; Shunkov and Agadzhanyan 2000; Ovodov and Martynovich 2001; Ovodov et al. 2003; Shpansky 2005; Rusanov and Orlova 2013; Kolyamkin et al. 2021; Malikov and Golovanov 2022; Samandrosova 2023; Leshchinskiy et al. 2023; Golovanov and Malikov 2023; Golovanov and Zazhigin 2023). In Table 2, we summarize 12 Late Pleistocene – Holocene localities with remains of Siberian zokors studied in our paper. These localities were discovered by G.G. Rusanov in 1992–2012 during the expeditions of the geological survey GDP-200 in the Altai Mountains and Pre-Altai plain and dated by biostratigraphic (definitions by A.V. Shpansky) and geochronological methods. We studied the remains of zokors from these localities in 19 samples of skulls with upper molars, lower jaws with molars and separate isolated molars. All samples are stored in the Paleontological Museum of Tomsk State University. For comparison with these samples, we used collections of modern and fossil zokors (first half of

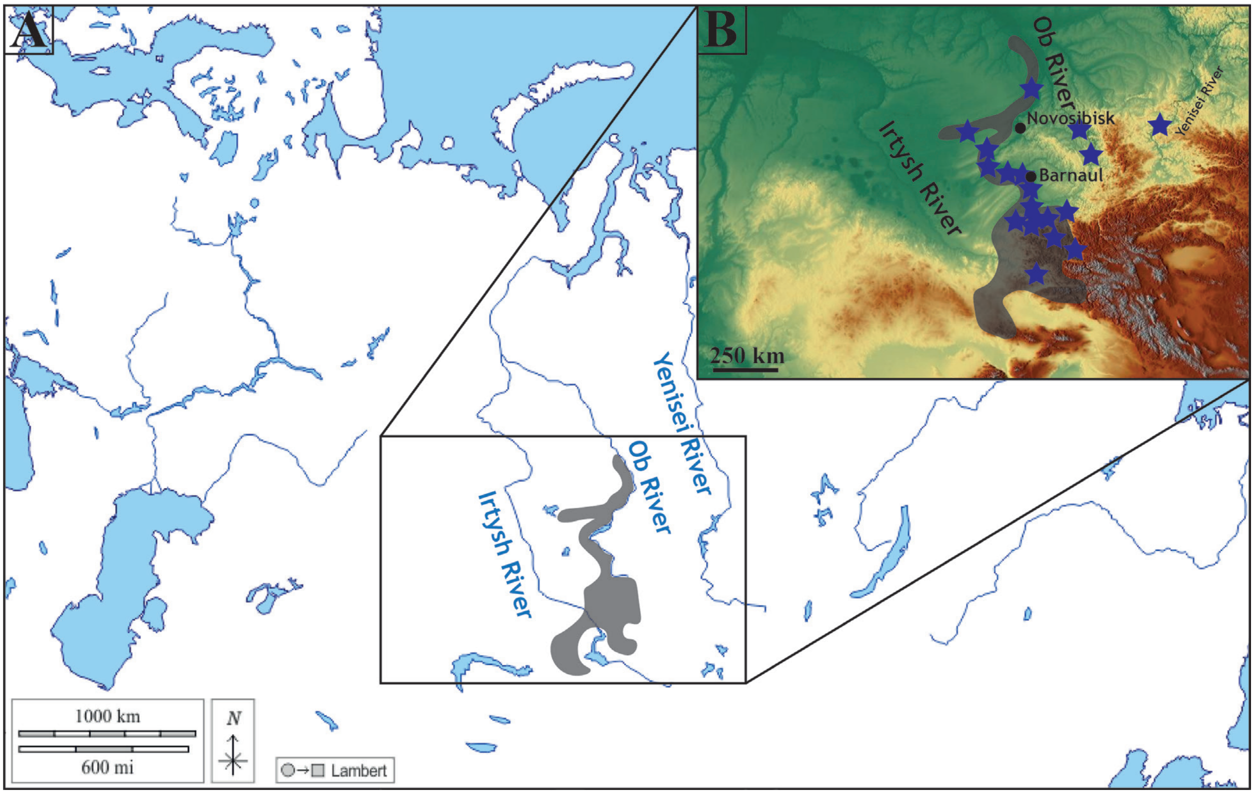

Fig. 1. A – Reconstructed area of maximum distribution of *Myospalax myospalax* in historical times in Western Siberia (area indicated by gray). Map adapted from https://d-maps.com/. B – Reconstructed area of maximum distribution applied to the relief map. Stars indicate localities with remains of *Myospalax myospalax*. Map adapted from https://maps-for-free.com/.

the Middle Pleistocene, localities Belovo-2, Gonba-2, Gonba-3 and Malinovka-3) stored in the Zoological Museum of Moscow State University, the Zoological Institute of the Russian Academy of Sciences, and the Center of Collective Use "Collection GEOCHRON" of the Institute of Petroleum Geology and Geophysics of the Siberian Branch of the Russian Academy of Sciences. Remains of Siberian zokor from localities of the first half of the Middle Pleistocene were collected and dated according to the associated fauna by A.A. Krukover (1992). Later, zokors from these localities were revised and described as chronological subspecies *M. myospalax krukoveri* Golovanov and Zazhigin, 2023 (Golovanov and Zazhigin 2023).

For the description of molars, we used terminology presented in the studies of L.P. Liu et al. (2014) and Ch. Qin et al. (2021) (Fig. 2A). Morphometric analysis (Fig. 2A) and geometric morphometric methods (Fig. 2B) were used to detail the morphological characterization. In morphometric analysis, we used the length, width and width of the dentin field between the turning points of LRA2 (second lingual reentrant angle) and BRA1 (first buccal reentrant angle) of the upper M1. Measurements were made from photographs using the tpsUtil ver.1.82 and tpsDig2 ver.2.32 programs (Rohlf 2015). Morphometric analysis was performed using one-way ANOVA, Kruskal–Wallis test and principal component analysis (PCA) with visualization of the results as a graph for the first two principal components in Past.4.04 software (Hammer et al., 2001). To choose an appropriate statistical method, the Shapiro–Wilk test was performed and showed that the distribution of length departed significantly from normality (W=0.942, p=0.048). Based on this, a Kruskal–Wallis test was used for length variability. The Shapiro–Wilk test did not show evidence of nonnormality for width variability (W=0.974, p=0.575) or variability of width of the dentin field between the turning points of LRA2 and BRA1 (W=0.976, p=0.645). After visual examination of the histograms of these parameters and the QQ plots, we decided to use a one-way ANOVA. The

Table 1. The main boundaries of the maximum distribution of *Myospalax myospalax* in historical time.

Maximum distribution of *Myospalax myospalax*	Geographical description	References
Northern boundary	Mouth of the Chaya River (left tributary of the Ob river)	Laptev and Losev 1949; Gromov and Erbaeva 1995
Western boundary	Eastern edge of Lake Chany (Northern part of the range) Alei River (Central part of the range) Eastern part of the Chingiztau Ridge (Southern part of the range)	Laptev and Losev 1949; Galkina and Nadeev 1980 Ognev 1947; Laptev and Losev 1949; Galkina et al. 1969; Galkina and Nadeev 1980; Puzachenko et al. 2009; Butkauskas et al. 2020 Ognev 1947; Makhmutov 1983
Eastern boundary	Left bank of the Ob river (Northern part of the range) Left bank of the Katun River (Central part of the range) Arshaty village in northeastern Kazakhstan, Markakol Lake area (Southern part of the range)	Laptev and Losev, 1949; Galkina et al., 1969; Galkina and Nadeev, 1980; Puzachenko et al., 2009; Butkauskas et al., 2020 Laptev and Losev, 1949; Galkina and Nadeev, 1980; Butkauskas et al., 2020 Ognev, 1947; Makhmutov, 1983
Southern boundary	Western part of Tarbagatai Mountains, eastern part of the Chingiztau Ridge	Ognev, 1947; Makhmutov, 1983; Puzachenko et al., 2009; Butkauskas et al., 2020

samples were homoscedastic (Levene's test, $p > 0.05$). Geometric morphometric analysis was performed by drawing the curve on the contour of the chewing surface of the upper M1 in the program tpsDig2 ver.2.32. Along the curve, we placed 200 semi-landmarks at an equal distance from each other. All semi-landmarks were converted to landmarks using tpsUtil ver.1.82 (Rohlf 2015). The first semi-landmark of the curve was placed on the buccal edge of the metacone and can be considered a type 2 landmark after conversion (Wärmländer et al. 2018). From the first semi-landmark, the curve was drawn first along the lingual side, then along the buccal side, and closed at the first point. Statistical analysis was performed with MorphoJ 1.07 (Klingenberg 2011) using the Procrustes method and canonical variate analysis (CVA). The results of the analysis are presented in a graph, where canonical variate 1 (54.805% variability) and canonical variate 2 (45.195% variability) were used as axes.

RESULTS

Biogeography of *Myospalax myospalax*

Based on the analyzed data, the northern boundary of the area of maximum distribution of *M. myospalax* in historical times is limited to 58°N, and the area itself extends southward along the territories adjacent to the left bank of the Ob River to Novosibirsk (Fig. 1). Near Novosibirsk, the reconstructed area extends from the banks of the Ob River westward to Lake Chany (Table 1). South of Novosibirsk, the area again extends along the left bank of the Ob River. From the Alei River (left tributary of the Ob), the range expands to the foothill and mountain territories of Altai. Here, the range is limited by the Alei River in the west and the left bank of the Katun River in the east. The southern part of the reconstructed area extends to the Southern Altai, the surroundings of Lake Markakol, the western part of the Tarbagatai mountain ridge and the Chingiztau ridge with a southern boundary to 47°N. Taking into account the ecological preferences of Siberian zokors and actual data (Makhmutov 1983), we can assume that the Tarbagatai and Altai parts of the range should connect along mountain and foothill sections to the west of Lake Zaisan.

The distribution of *M. myospalax* from 47° to 58°N matches the distribution of steppe ecosystems of Western Siberia (Mordkovich 2014). However, it should be considered that the range of Siberian zokors is limited to meadow biotopes. This is clearly noticeable in the north of the range, where the main distribution of *M. myospalax* is along the left bank of the Ob River and some adjoining rivers (Laptev and Losev 1949; Galkina et al. 1969; Galkina and Nadeyev 1980). There are historical data on the distribution of zokors in the area of Lake Chany, where they do not occur at the present time (Laptev and Losev 1949). On the basis of these data, we suggest that the distribution of *M. myospalax* followed the valleys of the Chulym (Novosibirsk Region) or Bagan Rivers. In mountainous areas, this species is also characterized by its distribution along river valleys with meadow biotopes (Makhmutov 1983). In general,

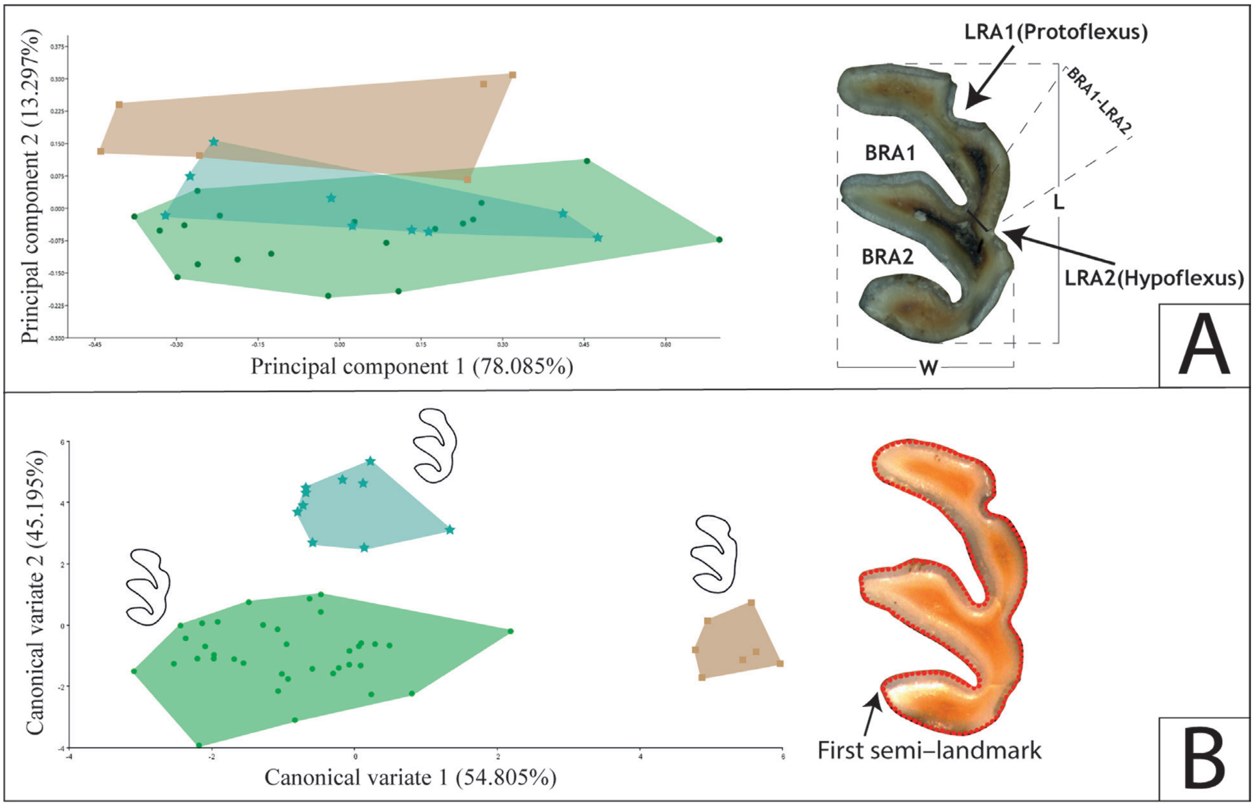

Fig. 2. A – Graph by the first two principal components, representing the results of the morphometric analysis (left). A sample of modern *Myospalax myospalax* is marked by green points, a sample of *M. myospalax krukoveri* from localities of the first half of the Middle Pleistocene is marked by brown squares, and a sample of *M. myospalax* from localities of the Late Pleistocene and Holocene is marked by blue stars. On the right, the scheme of labels of the lingual (LRA) and buccal (BRA) reentrant angels in the structure of the chewing surface of the upper M1 of *M. myospalax* and the parameters used for morphometric analysis are displayed. B – Graph displaying the results of the canonical variation analysis of the geometric morphometric method (left). On the right is the plot of 200 semi-landmarks along the contour of the upper M1, which was used in the analysis.

the range of *M. myospalax* has a narrow longitudinal shape, extending from flat meadow steppes in the north to mountain-meadow ecosystems in the south.

The reconstructed range of Siberian zokor belongs to the following soil provinces: Pre-Altai steppe (H6), Pre-Altai (L4), Western Siberian forest-steppe (M3), and Pre-Altai forest-steppe (M4) (Urusevskaya et al. 2020). Soil province maps are available at the website – https://soil-db.ru/. A number of soil complexes are distinguished within these provinces. The range of *M. myospalax* mostly matches the distribution of chernozems and is limited in the west to the distribution of hydromorphic and semi-hydromorphic soils (Urusevskaya et al. 2020). If we take the climatic parameters in the northernmost province (L4) and the southernmost (H6) plains province as habitatparameters, the resulting range will be characteristic of meadow and true steppes (Mordkovich 2014).

The habitat parameters of atmospheric and soil conditions for the distribution of Siberian zokors are distinguished along the northern flat part of their range. However, these parameters are also characteristic of the southern mountainous part of the range, as the change in the latitudinal-zonal gradient from north to south is compensated by an increase in the altitudinal gradient. This ratio of latitudinal and altitudinal gradients contributes to the fact that *M. myospalax* inhabits a relatively narrow temperature range (Nikol'skii 2008). A.A. Nikol'skii (2008) showed that the average annual temperature amplitude in *M. myospalax* burrows reaches 32°C with negative temperatures and 23°C without them. Since Siberian zokors move to deeper parts of burrows at

Table 2. Characteristics of 12 Late Pleistocene – Holocene localities with studied remains.

Localities	Type of sediment	Radiocarbon dating	Age
Observation point 62 51°14'14"N 85°15'54"E	Yellowish-gray sandy loam		Late Pleistocene – Holocene
Observation point 182 51°06'54"N 85°15'13"E	Proluvium deposits: rubbles cemented by yellow-gray sandy loam		Late Pleistocene – Holocene
Observation point 2065 51°44'43"N 84°05'38"E	Brownish-gray dense loam with columnar separations, porous, loess-like		Late Pleistocene – Holocene
Observation point 2054 51°30'11"N 84°28'18"E	Brownish dense loess-like loam with columnar separations, containing gravel, rare rubbles and separate blocks of granite		Late Pleistocene – Holocene
Observation point 6517 51°40'24"N 83°18'22"E	Yellowish-gray porous carbonatized loam with columnar separations	11690 ± 90 years (SOAN-4391) from the underlying layers	Holocene
Observation point 6595 51°28'31"N 83°11'19"E	Dense gray humusy loam with interlayers filled with gravel and poorly rounded pebbles	6200 ± 240 years (SOAN-8131) from the basal part of the layer with remains	Holocene
Observation point 6601 51°27'26"N 83°10'05"E	Yellowish-gray dense sandy loam with inclusions of gravel		Holocene
Observation point 6602 51°27'27"N 83°09'52"E	Yellowish-gray sandy loam very dense, with grus interlayers of 2 to 20 cm thick of grus, gravel and poorly rounded pebbles		Holocene
Observation point 6611 51°29'24"N 83°12'48"E	Yellowish-gray dense carbonate porous loam with columnar separations of loess-like type, with rare inclusions of gravel and rubble	5735 ± 130 years (SOAN-8132) from the basal part of the layer with remains	Holocene
Observation point 4029 51°49'00"N 82°56'32"E	Yellowish, dense, porous carbonatized loess-like loams containing large amounts of diagenetic carbonate nodules, gravel and rubble		Late Pleistocene – Holocene
Observation point 4031 51°48'04"N 82°55'48"E	Yellow, dense, porous carbonate loam containing carbonate nodules, grus, individual rubble debris and rare lenslike interlayers of sandy-grus material		Late Pleistocene
Observation point 4068 51°35'51"N 82°49'44"E	Yellowish carbonate loams with carbonate nodules, dense, porous, loess-like, with columnar separations, with inclusions of small gravel and grus		Late Pleistocene – Holocene

negative near-surface temperatures, their temperature niche will be characterized by the second value (Nikol'skii 2008).

Paleobiogeography of *Myospalax myospalax*

Most Pleistocene and Holocene localities of *M. myospalax* are located within the reconstructed area of the preanthropogenic range (Fig. 1) (Adamenko and Zazhigin 1965; Galkina et al. 1969; Motuzko 1970, 1975; Zazhigin 1980; Galkina and Nadeyev 1980; Makhmutov 1983; Krukover 1992; Andrenko et al. 1999; Shunkov and Agajanian 2000; Ovodov and Martynovich 2001; Ovodov et al. 2003; Shpansky 2005; Samandrosova 2023; Malikov and Golovanov 2022; Golovanov and Malikov 2023). The localities from which the remains were studied in our work also belong to this category. There are some published data on zokor localities outside the reconstructed area (Fig. 1). In particular, the Middle Pleistocene – Holocene localities are in the Kuznetsk Basin (Galkina et al. 1969, Galkina and Nadeyev 1980), near Krasnoyarsk (Andrenko et al. 1999; Ovodov and Martynovich 2001; Kolyamkin et al. 2021), and on the right bank of the Katun River (Malikov and Golovanov 2022).

The distribution of *M. myospalax* was previously analyzed for the second half of the Middle Pleistocene (Golovanov and Malikov 2023). It was revealed that in the Pre-Altai Plain, the most western localities of zokors are restricted to the area of 82°E on the left bank of the Ob River (Golovanov and Malikov 2023). The distribution of *M. myospalax* up to this boundary was also noted in the first half of the Middle Pleistocene (Galkina et al. 1969; Zudin et al. 1977; Zazhigin 1980; Krukover 1992; Arkhipov et al. 1997). It should be noted that this boundary is most likely due to the lack of paleontological data for the Middle Pleistocene in the region. The data on the presence of zokors in the territory of the Kuznetsk Basin and near Krasnoyarsk in the Middle and Late Pleistocene are interesting (Galkina et al. 1969; Galkina and Nadeyev 1980; Andrenko et al. 1999; Ovodov and Martynovich 2001). It has been suggested that their extinction in these areas was related to aridization and cooling of the climate, resulting in intensive freezing of soils (Galkina and Nadeyev 1980). Additionally, in the area around Krasnoyarsk are known remains of Holocene age zokors, which have been interpreted as evidence for the existence of an isolated population of *M. myospalax* in this area (Ovodov and Martynovich 2001). This population was most likely isolated during the last glacial period and completely extinct in the Late Holocene.

Some of the studied collections are from localities that are dated to the Late Pleistocene – Holocene. Data from these localities, together with literature sources, allow us to reconstruct the Late Pleistocene – Holocene paleoareal more westward than is possible for the Middle Pleistocene and more eastward than is presently occurring. The most valid western occurrences of Siberian zokor fossils were noted in the area of the village of Mamontovo (Barabinsk Lowland, Wolchya Griva) (Galkina et al. 1969; Samandrosova 2023). The burrows in this section, corresponding to the burrows of zokor, have been dated to Holocene age (Leshchinskiy et al. 2023). The eastern boundary in the Altai Mountains is determined by finds of *M. myospalax* on the right bank of the Katun River in the area of the village of Novosurtayevka (Malikov and Golovanov 2022). Deposits containing zokor remains were dated to the end of the Late Pleistocene. The most northern fossil finds of Siberian zokor occur at the Krivosheino (Tomsk Region), Kurtak (Krasnoyarsk Region) and Gosudarev Log (Krasnoyarsk Region) sites (Fig. 1) (Andrenko et al. 1999; Ovodov and Martynovich 2001; Shpansky 2005; Kolyamkin et al. 2021). The Gosudarev Log site is also the most eastern locality of *M. myospalax* (Fig. 1B).

Distribution of *Myospalax myospalax* compared to the distribution of other rodent species

Some patterns in the distribution of Siberian zokor relative to other rodent species in the second half of the Middle Pleistocene have already been noted earlier (Golovanov and Malikov 2023). In particular, the joint occurrence of zokor and mole vole remains is typical for Middle Pleistocene alluvial localities of the Pre-Altai Plain. Similar to Siberian zokors, mole voles are subterranean rodents, but they prefer arid steppes (Gromov and Erbaeva 1995; Markova et al. 2018). The modern range of the northern mole vole *Ellobius talpinus* (Pallas, 1770) in its northeastern part is limited to the left bank of the Ob River and the Altai Mountains (Gromov and Yerbaeva 1995). Data from cave localities show that in the Late Pleistocene, the mole vole inhabited the territory of the northwestern Altai region together with zokors (Shunkov and Agadzhanyan 2000; Dupal 2004). The modern ranges of *M. myospalax* and *E. talpinus* overlap only in the territory of the Pre-Altai Plain, while in the Pleistocene, the boundary between ranges could pass through the territory of the Northwest Altai. It is important to note that the remains of Siberian zokors and mole voles are present together in alluvial and cave-type localities (Zazhigin 1980; Krukover 1992; Golovanov and Malikov 2023). In localities associated with burrows in paleosoil layers in sections on the left bank of the Ob River, there are remains of zokors but no remains of mole voles (Krukover 1992).

There are almost no localities where the zokor remains would occur together with the remains of modern tundra inhabitants – West Siberian lemming and Arctic lemming (Zazhigin 1980; Krukover 1992; Golovanov and Malikov 2023). At present, the ranges of these species and the range of *M. myospalax* are separated by a vast taiga zone acting as a natural barrier. However, in the Middle and Late Pleistocene, a transition zone existed between the northern tundra and southern steppe zones (Shpansky 2018). This zone is identified by localities with rodent fauna of mixed tundra-steppe composition, referred to as the tundra-steppe complex or nonanalog complex (Kosintsev et al. 2004). In most of the Western Siberian localities of the tundra-steppe complex, remains of Siberian zokors were not found (Krukover 1992; Shpansky 2018). The exception is the Urtam and Krivosheino localities, which are the northernmost Western Siberian localities containing remains of zokor (Krukover 1992; Shpanskii 2018). It has been suggested that these localities can be dated to the second half of the Middle Pleistocene (Motuzko 1970, 1975).

Morphology of *Myospalax myospalax* molars from Late Pleistocene and Holocene localities

Recent studies have revealed differences between the Middle Pleistocene *M. m. krukoveri* and the modern population of *M. myospalax* (Golovanov and

Zazhigin 2023). *M. m. krukoveri* is defined by the less developed lingual (M1-M3) and buccal (m2-m3) reentrant angles of the molars at the adult stage. Zokor remains from Late Pleistocene and Holocene localities have a greater similarity with modern *M. myospalax* compared with the Middle Pleistocene samples. Relatively marked reentrant angles on the lingual side of the upper molars and on the buccal side of the lower m2 and m3 correspond to those of modern *M. myospalax*.

Morphometric (Fig. 2A) and geometric morphometric analyses (Fig. 2B) confirm the differences between the molars of *M. m. krukoveri* and *M. myospalax* of the Late Pleistocene – Holocene, with greater similarity of the last with the modern population. In principal component analysis by linear measurements, PCA 1 is largely responsible for the variation in length and width in the studied samples. PCA 2 is largely responsible for the variation in the width of the dentin field between the turning points of LRA2 and BRA1. The three groups of samples from different stratigraphic levels are weakly separated by the first component. The greatest divergence occurs by the second component, which is interpreted as less separated dentin fields in the *M. m. krukoveri* group than in the other two groups. A group of samples from Late Pleistocene – Holocene localities is on a graph between modern and Middle Pleistocene zokors but overlaps more with the modern sample. The results of the Kruskal–Wallis test for length variability showed no significant difference between sample medians (p=0.728). The results of the one-way ANOVA of the width and width of the dentin field between the turning points of LRA2 and BRA1 parameters showed a significant difference between samples (width: F=3.228, df_B =2, df_W=31, p=0.053; width of the dentin field between the turning points of LRA2 and BRA1: F=11.02, df_B=2, df_W=31, p=0.0002). In the graph representing the results of the geometric morphometric analysis, the Late Pleistocene – Holocene *M. myospalax* group has a greater divergence from the Middle Pleistocene sample group than from the modern sample.

DISCUSSION

Zokor molars are a good (and sometimes the only) tool for identifying species affiliation and evolutionary differences (Teilhard de Charden 1942; Zheng 1994; Liu et al. 2014). Since the end of the Early Pleistocene, the Western Siberian zokor phyletic line has developed specific ontogenetic traits unique to this lineage (Golovanov and Zazhigin 2023). The paleontological localities studied here, together with published data, indicate the absence of migration of species from other zokor phylogenetic lineages into the Western Siberian region (Adamenko and Zazhigin 1965; Galkina et al. 1969; Zazhigin 1980; Galkina and Nadeyev 1980; Makhmutov 1983; Krukover 1992; Arkhipov et al. 1997; Andrenko et al. 1999; Shunkov and Agajanian 2000; Ovodov and Martynovich 2001; Ovodov et al. 2003; Rusanov and Orlova 2013; Malikov and Golovanov 2022; Leshchinskiy et al. 2023; Golovanov and Zazhigin 2023). The *M. myospalax* molars from localities dated to the Late Pleistocene – Holocene that we studied have greater similarity with the modern samples than with Middle Pleistocene *M. m. krukoveri*. This conclusion is supported by morphometric (Fig. 2A) and geometric morphometric analyses (Fig. 2B) and proves the correctness of the first dating of these localities.

Zokors are predominantly subterranean, do not hibernate and are territorial solitary animals (Makhmutov 1983; Bazhenov 2017; Zhou et al. 2022). Modern populations of *M. myospalax* inhabit open landscapes with sufficient underground phytomass and a moderate climatic regime, which corresponds to meadow biotopes (Galkina and Nadeyev 1980; Makhmutov 1983). The results of studies of habitats of individuals plateau zokors *Eospalax baileyi* (Thomas, 1911) (family Myospalacidae) revealed that the size of their home habitat (burrow length) negatively correlates with the level of subterranean biomass (Zhou et al. 2022). This pattern is probably true for the Siberian zokor. Soil characteristics and the degree of its freezing and aridization also affect the distribution of *M. myospalax* (Galkina and Nadeyev 1980; Agadjanian 2009). Determining the climatic and soil parameters of *M. myospalax* habitat is impossible without understanding the dynamics of its areal. Anthropogenic influence had a strong impact on the range of Siberian zokor, which makes it difficult to characterize its ecological niche. Combining all the available data on the distribution of *M. myospalax* allowed us to reconstruct its range as it may have been before the anthropogenic impact (Fig. 1). The correlation of this area with soil provinces and complexes (Urusevskaya et al. 2020) revealed certain patterns.

Based on the characteristics of soil provinces, we give the ranges of temperature parameters that can be considered as habitat conditions for the modern Siberian zokor. In particular, these are the range of sums of t>10°C: 1630–2130; range of duration of periods with t>10°C: 110–129 days; range of duration of frost-free periods: 102–124 days; range of sum of precipitation per year: 355–455 mm; range of duration of periods with t>10°C in soil at a depth of 20 cm: 3.5–4.5 months; range of depth of t<0°C penetration into soil: 104–167 cm. The given parameters directly influence the underground and aboveground phytomass and burrowing activity of *M. myospalax*. Therefore, we consider it valid to reconstruct the above parameters in the geological past based on the remains of *M. myospalax*. Meadow and true steppes are typical for these temperature ranges in Western Siberia (Mordkovich 2014). Other studies have also noted the association of *M. myospalax* with meadow biotopes (Galkina et al. 1969; Galkina and Nadeyev 1980; Makhmutov 1983). Comparison of the reconstructed distribution of *M. myospalax* with soil complexes revealed a negative correlation with the distribution of hydromorphic and semihydromorphic soils in the northwestern part of the Siberian zokor range. In the Pleistocene and Holocene, *M. myospalax* was much more widespread than in the 20th and early 21th centuries (Fig. 1B). This is indicated by records of zokor remains in the Kuznetsk Basin, Krasnoyarsk Region, and the right bank of the Katun River (Galkina et al. 1969; Galkina and Nadeyev 1980; Andrenko et al. 1999; Ovodov and Martynovich 2001; Malikov and Golovanov 2022). The migration of Siberian zokors to these regions most likely occurred along mountain valleys. The main part of the localities with the remains of Siberian zokor belongs to the reconstructed area of the maximum distribution of *M. myospalax* in historical time.

Siberian zokor should be considered a species sensitive to climate change. The Quaternary period is characterized by periods of glacial and interglacial epochs, the change of which must have influenced the distribution of *M. myospalax*. During the interglacial epochs, this species could spread to the plain part of Western Siberia, where conditions were favorable for it. The Irtysh River and hydromorphic and semihydromorphic soil complexes could have acted as natural barriers to their westward spreading. Due to climate cooling and aridization during glacial epochs, Siberian zokors must have migrated to the southern mountainous areas of the Altai-Sayan mountain region, which are characterized by high biotopic diversity (Puzachenko and Markova 2020). This hypothesis is supported by the fact that subaerial localities of *M. myospalax* in the territory of the Pre-Altai Plain are associated with paleosoil layers corresponding to interglacial epochs (Krukover 1992; Zykina and Zykin 2012).

There are certain patterns in the distribution of Siberian zokor (both in the modern and Pleistocene time) relative to the distribution of other rodent species. In Western Siberian alluvial and cave sites, zokor remains are found together with remains of mole voles (Zazhigin 1980; Krukover 1992; Shunkov and Agadzhanyan 2000; Dupal 2004; Golovanov and Malikov 2023). Mole voles are also specialized burrowing animals, but in contrast to zokors, they prefer arid and semidesert environments (Markova et al. 2018). The modern range of *E. talpinus* overlaps with the reconstructed “preanthropogenic” range of *M. myospalax* only in the territory of the Pre-Altai Plain (Gromov and Erbaeva 1995). In contrast to the Siberian zokor, *E. talpinus* is absent in mountainous Altai areas, and the eastern boundary of the range of this species occurs in the territory of the Pre-Altai Plain. Thus, the Pre-Altai Plain is an ecotone zone in the distribution of *M. myospalax* and *E. talpinus*. The explanation for this may be the mosaic structure of biotopes of this territory, where both semiarid conditions, suitable for mole voles, and meadow biotopes, necessary for Siberian zokor, are presented. The fact that the remains of these species are present together in alluvial and cave localities indicates a similar landscape heterogeneity in the Pleistocene.

Another discovered pattern is the almost complete absence of localities where the remains of zokors and mole voles were found together with the remains of West Siberian lemming. West Siberian lemmings are confined to mesic-wet habitat types with a distribution in Northern Eurasia in the permafrost region (Gromov and Erbaeva 1995; Markova et al. 2017). In the Pleistocene, the range of *Lemmus sibiricus* (Kerr, 1792) (family Cricetidae) extended much farther south and reached the Middle Irtysh and Middle Ob regions (Zazhigin 1980; Krukover 1992). The absence of zokor remains in the Irtysh localities can be explained by both too low temperatures and the presence of hydromorphic soils in the area between the Irtysh and Ob rivers. The Krivosheino locality, dated to the Middle Pleistocene, is near the northern boundary of the modern distribution of Siberian zokor and one of the northernmost localities with their remains. Together with the Urtam locality, these are the only localities where remains of Siberian zokor and West Siberian lemming occur together (Shpansky 2005). These localities mark a possible ecotone zone between the paleoranges of *M. myospalax* and *L. sibiricus*. In a broader interpretation, this zone can be represented as an ecotone between Pleistocene tundra-steppe and steppe of modern type with meadow biotopes.

CONCLUSION

Molars from the studied Late Pleistocene – Holocene localities are more similar to molars of modern *M. myospalax* than to those of Middle Pleistocene *M. m. krukoveri*. The absence of large samples for the second half of the Middle Pleistocene does not allow us to establish a clear stratigraphic boundary between *M. m. krukoveri* and *M. myospalax* of the modern type. However, as in the case of many chronological subspecies, this boundary is in principle difficult to define, since evolutionary changes are seen in large samples and accumulate gradually.

If we exclude the anthropogenic factor in the historical distribution of *M. myospalax*, specific patterns are revealed. In addition to large water and forests barriers, it can be assumed that hydromorphic and semihydromorphic soils also limited the distribution of Siberian zokors. The dependence on the productivity of underground phytomass and subterranean habitats affects the relatively narrow ranges of climatic and soil parameters suitable for the survival of *M. myospalax*. Even before great anthropogenic influence, the range of this species was ribbon-shaped along river valleys with the center in the western part of the Altai Mountains.

During some stages of the Pleistocene, *M. myospalax* was distributed over a much larger area than in historical times. Presumably, the majority of localities outside the Altai-Sayan mountain region are either confined to warm epochs (plain part of Western Siberia and Kuznetsk Basin) or are evidence of localized refugiums (Krasnoyarsk area). Thus remains of the Siberian zokor may serve as an indicator of the absence of cold or arid environments in the geological past and also allow reconstructing certain climatic and soil parameters.

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