

## Late Middle Pleistocene small mammals from south-east of Western Siberia

Dmitriy G. Malikov\* & Semion E. Golovanov

**ABSTRACT.** The present paper fills the gap in the Middle Pleistocene fossil record of small mammals in the southeast of Western Siberia. We describe small mammals faunas from localities of the second half of the Middle Pleistocene. Faunal remains were derived from alluvial deposits from three geological sections in the Cis-Altai Plain. The small mammals localities occupy a clear stratigraphic position between the deposits of the lower Middle Pleistocene and the loess-paleosol deposits of the Upper Pleistocene. We describe a rich faunal association of the post-Vyatkinian (=post-Tiraspolian/post-Cromerian) appearance. The fauna is dominated by steppe species of small mammals, *Spermophilus* sp., *Lagurus lagurus*, and *Stenocranius gregalis*. The evolutionary level of small mammal fauna is in good agreement with stratigraphic structure of geological sections. The most probable age of this fauna is the first half of the late Middle Pleistocene (MIS 11-9). The steppe lagurine and the narrow-headed vole morphology are in good agreement with this dating. Open steppe landscapes were reconstructed for the studied faunal localities.

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**KEY WORDS:** small mammals, late Middle Pleistocene, Cis-Altai Plain, West Siberian Plain, biostratigraphy.

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## Мелкие млекопитающие позднего среднего плейстоцена юго-востока Западной Сибири

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**РЕЗЮМЕ.** Заполнен пробел в ископаемой летописи мелких млекопитающих среднего плейстоцена юго-востока Западной Сибири. Приведено описание фаун мелких млекопитающих из местонахождений второй половины среднего плейстоцена. Остатки фауны происходят из аллювиальных отложений из трёх геологических разрезов на Предалтайской равнине. Местонахождения мелких млекопитающих занимают чёткое стратиграфическое положение между отложениями нижнего среднего плейстоцена и лессово-почвенными отложениями верхнего плейстоцена. Описан богатый комплекс фауны послевяткинского (послетираспольского/послекромерского) облика. Основу фауны составляют степные виды мелких млекопитающих — *Spermophilus* sp., *Lagurus lagurus* и *Stenocranius gregalis*. Эволюционный уровень мелких млекопитающих хорошо согласуется со стратиграфическим строением геологических разрезов. Наиболее вероятный возраст этой фауны первая половина позднего среднего плейстоцена (MIS 11-9). Морфология остатков степной пеструшки и узкочерепной полёвки хорошо согласуется с такой датировкой. Для изученных местонахождений фауны реконструированы открытые степные ландшафты.

**КЛЮЧЕВЫЕ СЛОВА:** мелкие млекопитающие, поздний средний плейстоцен, Предалтайская равнина, Западно-Сибирская равнина, биостратиграфия.

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## Introduction

The south of Western Siberia is an important region for the study of evolution of Siberian ecosystems in the Neogene and Quaternary periods. Representative faunistic complexes of small and large mammals characterize main stages of the Neogene and Quaternary of Siberia. However, stages of the Quaternary are known very unevenly. From a biostratigraphic aspect, the best documented stage is Early Pleistocene. Three complexes of small mammals were described (Zazhigin, 1980) in the south of Western Siberia: Podpusk-Lebyazhian (=Khaprovian/Middle Villafranchian), Kizikhian (later abolished by Zazhigin (1998)), and Razdolian (=Tamanian/Late Villafranchian). The transitional stage between faunas of the Early and Middle Pleistocene known as the fauna of the Petropavlovka–Karaj–Dubina type, originally described from Eastern Europe (Markova, 1982; Rekovets, 1994), was subsequently recognized in Western Siberia too (Krukover, 2007).

For the first half of Middle Pleistocene in the south of Western Siberia, V.S. Zazhigin (1980) described the Vyatkinian complex of small mammals. The major sites of this unit are located on the left bank of the Ob River. The lower boundary of this complex is determined by the disappearance of *Allophaiomys* Kormos 1932 and *Prolagurus pannonicus* Kormos 1932, first appearance of *Lagurus transiens* Yanossy, 1962 and a presence of *Myospalax* Laxmann 1773. There are only two species of *Mimomys* Forsyth-Major 1902 voles left in this complex (*Mimomys intermedius* Newton, 1881 and *M. pusillus* Mehely, 1914), and genus *Allophaiomys* is completely replaced by *Microtus* cf. *nivaloides* Forsyth-Major, 1902 and *Stenocranius* ex gr. *hintonigregaloides* (Galkina, 1975; Zazhigin, 1980; Krukover, 2007). This association correlates with Tiraspolian fauna in Eastern Europe and Cromerian fauna in Western Europe. The Vyatkinian complex is the last complex of small mammals for the southeast of Western Siberia that is different from the modern fauna at the genus level (Zazhigin, 1980).

There are no recognized complexes of small mammals for the Middle and Late Pleistocene in the south of Western Siberia. This is due to a deficiency of material with a reliably established stratigraphic position, as well as to the fact that species from this faunistic complex are similar to the modern fauna. The main distinguishing feature of the faunas of this time is the presence of the genus *Arvicola* Lacépède 1799, whereas *Mimomys* is completely absent (Krukover, 2007).

For a long time, large localities of fauna that could be firmly dated to the second half of the Middle and the beginning of the Late Pleistocene were not discovered in the south of Western Siberia (Zazhigin, 1980). There are also almost no geochronometrically dated sections containing the fauna of rodents of this time. There are only few collections of the remains of small mammals from burrows dated on the basis of loess-soil stratigraphy (Krukover, 2007; Zykina & Zykina, 2012), and some alluvial (Adamenko, 1974; Zazhigin, 1980;

Panychev, 1979) and caves localities (Dupal, 2004; Serdyuk, 2019; Agadjanian *et al.*, 2021) with radiocarbon and luminescence dating. In this paper we present the small mammals fauna data from three geological sections dated to the end of the Middle Pleistocene (Middle Neopleistocene in Russian General Stratigraphic Scale of the Quaternary).

## Regional stratigraphy and chronology. Geological sections

In this article, we adhere to the Stratigraphic scheme of the southeast Western Siberia (Arkhipov *et al.*, 2000) revised based on loess-paleosol stratigraphy (Zykina & Zykina, 2012). We also follow the International Stratigraphic Chart (ISC) with the lower boundary of the Quaternary at 2.588 Ma BP, and the subdivision of the Pleistocene into Lower, Middle, and Upper subseries (Head *et al.*, 2008). The boundary between the Lower and the Middle Pleistocene is drawn at the level of 0.774 Ma BP.

In this study we consider the small mammal fauna of the second half of the Middle Pleistocene (Middle Neopleistocene of the Russian scale) from the Tobol interglacial (=Likhvin interglacial in Eastern Europe; =Holstenian interglacial in Western Europe; =Hoxnian interglacial in Great Britain) in Western Siberia (MIS 11, 424–374 ka), prior to the beginning of the Kazantsevo interglacial (=Mikulino interglacial in Eastern Europe; =Eemian interglacial in Western Europe; =Ipswichian in Great Britain) in Western Siberia (MIS 5e, ~130 ka).

The second half of the Middle Pleistocene (Middle Neopleistocene) in the region includes the deposits of the Tobol (MIS 11, 424–374 ka) and Shirta (MIS 9, 337–300 ka) interglacials and Samarovo (MIS 10, 374–337 ka), and Taz (MIS 8-6, 300–~130 ka) glacial horizons. These deposits can best be characterized at the south of Western Siberia by the loess-soil sequence compiled by V.S. Zykina & V.S. Zykina (2012). The time of the Tobolsk interglacial corresponds to the Shadrkha pedocomplex. This is followed by the Samarovo glacial with Shibaevo loess deposits. In the following Shirta interglacial, the Shipunovo pedocomplex was formed. During the Taz glacial, the Chulym (MIS 8, 300–243 ka) and Suzun (MIS 6, 191–~130 ka) loess, and the Koinikha (MIS 7, 243–191 ka) pedocomplex were formed (Zykina & Zykina, 2012).

**Solonovka section**, the section is associated with the deposits of the southeastern slope of the Anui Ridge, exposed in the coastal cliff of the left slope of the valley of the Peschanaya River, 1.5 km downstream from the Solonovka village (52.017°N, 84.65°E). The geological structure, conditions for section formation, and preliminary data on the Middle Pleistocene fauna were published by Zykina *et al.* (2017). Small mammals remains originate from alluvial deposits represented by uneven-grained gravel in the basal part of the middle bed of the section. Sediments containing rodent remains overlie clayey silts containing remains of *Equus nalai-*

**Table 1.** Species composition of small mammals from Solonovka, Petropavlovskoe and Malinovka-4 localities

Species	localities		
	Petropavlovskoe	Solonovka	Malinovka-4
<i>Ochotona</i> sp.	–	1	–
<i>Spermophilus</i> sp.	10	16	13
<i>Allactaga</i> sp.	–	1	–
<i>Ellobius talpinus</i>	3	3	–
<i>Cricetus cricetus</i>	–	1	–
<i>Myospalax myospalax</i>	2	2	1
<i>Craseomys rufocanus</i>	1	1	–
<i>Clethrionomys cf. rutilus</i>	1	1	–
<i>Lagurus lagurus</i>	31	6	16
<i>Eolagurus luteus</i>	7	2	2
<i>Stenocranius gregalis</i>	11	20	1
<i>Alexandromys oeconomus</i>	2	4	3
<i>Microtus</i> sp.	10	9	7
Total	78	67	43

*khaensis* Kuznetsova, Zhegallo, 1996, dating to the Vyatkinian time. The upper part of the section is formed of subaerial deposits of Upper Pleistocene (Zykin *et al.*, 2017). The material was collected in expeditions in 2016, 2017, and 2019. The sixty-seven small mammals remains were identified in the localities (Tab. 1).

**Petropavlovskoe section**, the section is associated with the deposits of the southeastern slope of the Kolyvan Ridge, exposed in the coastal cliff of the left slope of the valley of the Anui River, on the northeastern outskirts of the village Petropavlovskoe (52.083°N, 84.113°E). The geological structure and formation conditions of the Petropavlovsk section have been described (Zykina *et al.*, 2018). The upper part of the section is formed of subaerial Upper Pleistocene deposits covering, a 11.7 m thick bed of lacustrine and alluvial deposits. Remains of small mammals originate from a bed of alluvial sand at the depth of 21–22.5 m. The sands occur on blue silts which yielded a tooth of *Mammuthus trogontherii* Pohling, 1885 (Adamenko, 1974). This allows date this silts sediments to the Vyatkinian time. The material was received during the 2017 expedition. 78 small mammals remains were studied at the localities (Tab. 1).

**Malinovka section**, belongs to the Priobie Loess Plateau and is exposed on the left bank of the Ob River, 1 km upstream from Malinovka village (53.417°N, 82.733°E). The total thickness of the section is 57–57.5 m. The section contains four localities of small mammal remains (Zudin *et al.*, 1977; Krukover, 2007; Zykina & Zykin, 2012; and others). The lower part of the section is represented by dense, brown, reversely magnetized clays of the Kochkovo Suite of Early Pleistocene. The clays contain a paleosol that yielded remains of small mammals of the Razdolian complex (Malinovka-1 locality). Kochkovo clays are overlain by a loess-soil series. The upper fossil soil (Malinovka pedocomplex)

yielded remains of rodent fauna at an evolutionary level intermediate between Razdolian and Vyatkinian complexes (Malinovka-2 locality). Above the Malinovo pedocomplex, there is an alternation of sands, silty sands, loams, and loess of the Evsino pedocomplex. The upper fossil soil is characterized by the fauna of the Vyatkinian faunal complex (Malinovka-3 locality). Above, there are cross-bedded sands containing remains of rodents, the Malinovka-4 locality. The material was collected during the field work in 2013. Forty-three remains of micromammals were studied at the localities (Tab. 1).

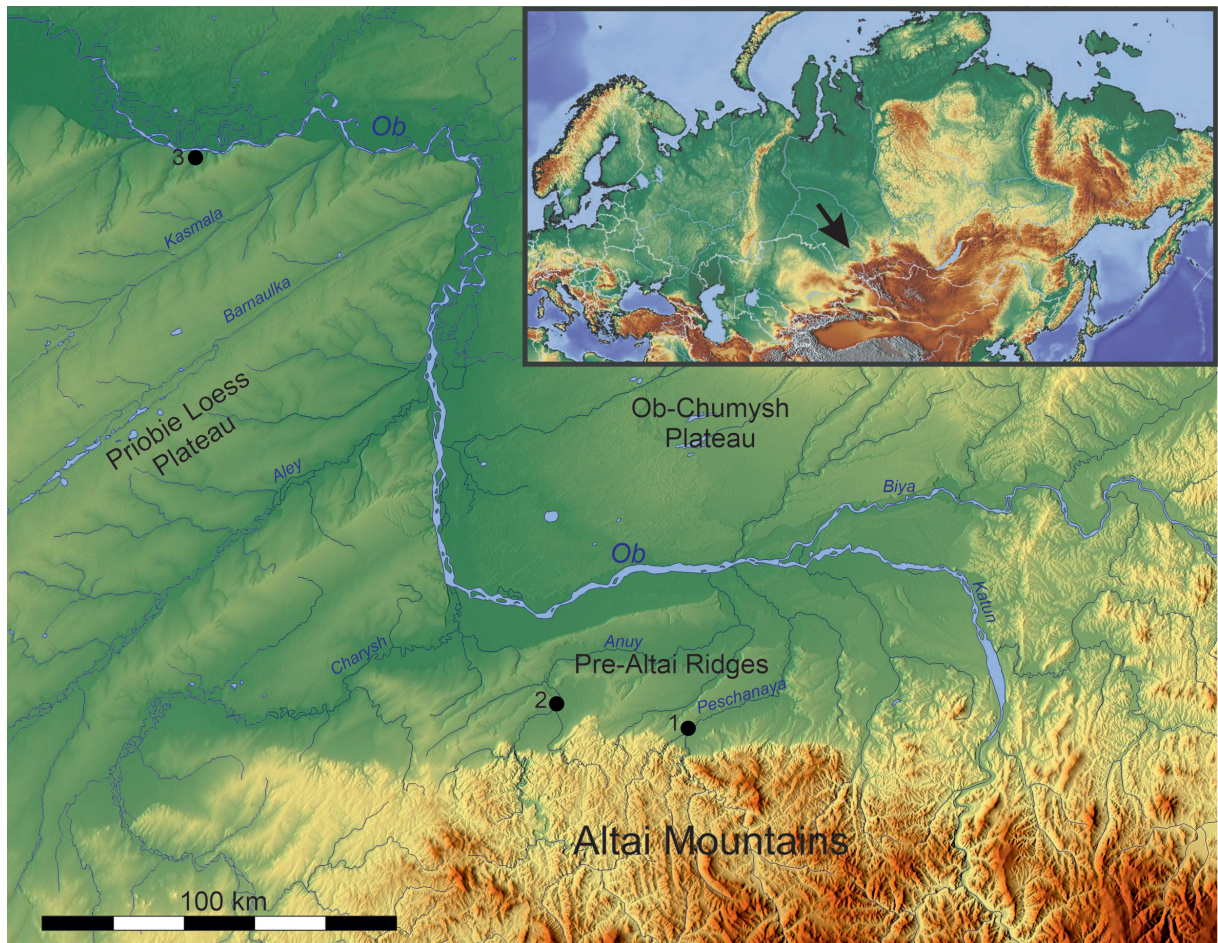
## Material and methods

We studied remains of small mammals fauna from three geological sections of the Late Middle Pleistocene in the south of Western Siberia. The geographical area of material collection is the Cis-Altai Plain, located between the Altai Mountains in the south and the Salair Ridge in the east, northeast and north. This is the southeastern edge of the West Siberian Plain. The material was collected in three localities (Fig. 1): Solonovka (the Peschanaya River), and Petropavlovskoe (Anui River), and Malinovka (Ob River). All the materials are stored in the Laboratory of paleoclimatology, Cenozoic geology and mineral indicators of climate, Sobolev Institute of Geology and Mineralogy RAS, in different years of research.

The material was collected by wet screening the deposits using the mesh size of 0.5 and 1 mm, with 0.5 mm sieves used for sandy sediments with a low clay content, and 1 mm, for clayey deposits. This is done to maximize the efficiency of collecting faunal remains. The obtained concentrate was manually sorted to extract remains of mammals and mollusks.

The identification and measurement of remains is carried out under laboratory conditions on Altami CM0745-T binocular microscope, the samples were





**Fig. 1.** Map of the investigated small mammal localities: 1 — Solonovka; 2 — Petropavlovskoe; 3 — Malinovka-4. The arrow shows the location of the Cis-Altai Plain in Eurasia.

photographed with a UCMOS05100KPA camera. The taxonomy of small mammals mainly follows A.A. Lisovsky *et al.* (2019), taxonomy of narrow-headed vole and red-backed vole mainly follows B. Kryštufek & G.I. Shenbrot (2022). The main morphotypes of m1 tooth of *Lagurus lagurus* (Pallas, 1773) and *Stenocranius gregalis* (Pallas, 1779) were identified after Bolshakov *et al.*, 1980; Smirnov *et al.* (1986) and Rekovets (1994). Statistical processing of the measurement results was done using the Past software package version 4.04 (Hammer *et al.*, 2001).

The analysis of paleoenvironment was conducted using a part of bioclimatic method by Hernández Fernández (2001). A connection of many small mammals species to certain climatic zones makes them a good basis for landscape and climatic reconstructions. Bioclimatic method developed by M. Hernández Fernández (2001) was used to improve accuracy of the ecological interpretation from small mammal remains from Cis-Altai Plain. We used both the part of original (Hernández Fernández, 2001) and modified methods. In particular, a different classification of environmental zones by A.K. Markova *et al.* (2019)

was applied comparing to the original methodology (Golovanov & Malikov, 2021). The original classification focused on global climatic zones and corresponding zonobiomes. The classification includes zones of tropical deciduous forests and evergreen tropical rainforests, highly unlikely for Western Siberia in the Pleistocene. At the same time, the original methodology lumps steppes and cold deserts into the same zone. In our opinion, the classification by A.K. Markova *et al.* (2019) more accurately reflects the landscape and ecology of small mammals in the West Siberian region.

The bioclimatic method is based on the degree of species specialization in the fossil faunistic complex, expressed through a climatic restriction index (*CRI*). The index is calculated by the formula:  $CRI_i = 1/n$ , where  $n$  is the number of climatic zones inhabited by a species, and  $i$  is the climatic zone  $i$  in which the species occurs. If the species does not live in a certain climatic zone, then the index value in this zone will be equal to zero. The sum of the different *CRI* of a species will be equal to one. Consequently, the more zones a species inhabits, the lower *CRI* value will characterize each specific zone in which the species lives. On the basis

of *CRI* of all species from the localities, calculating bioclimatic component (*BC*). This component reflecting the share that the climatic zone occupies in the bioclimatic spectrum of the faunal complex. *BC* is calculated by the following formula:  $BC_i = (\sum CRI_i)100/S$ , in which *i* — climate zone *i*, and *S* — number of species in the locality. Thus, it is possible to determine in what landscape-climatic conditions the faunistic complex existed, which will be expressed in the predominance of *BC* of certain climatic zones in the general bioclimatic spectra.

Bioclimatic spectra for the Petropavlovskoe and Solonovka localities were calculated based on the collections of small mammals remains from V.S. Sobolev Institute of Geology and Mineralogy SB RAS. Calculations for the Malinovka-4 locality were partially based on materials from the collection of the V.S. Sobolev Institute of Geology and Mineralogy SB RAS and partially on the basis of the published data (Krukover, 1992). The data on modern voles of the Altai Territory were taken from publication (Makarov, 2017; Dupal, 2004). The non-vole small mammals (Soricidae, Sminthinae, and Muridae) that were not found in fossil communities were excluded from the analysis. This is done to compare the data directly.

## Results

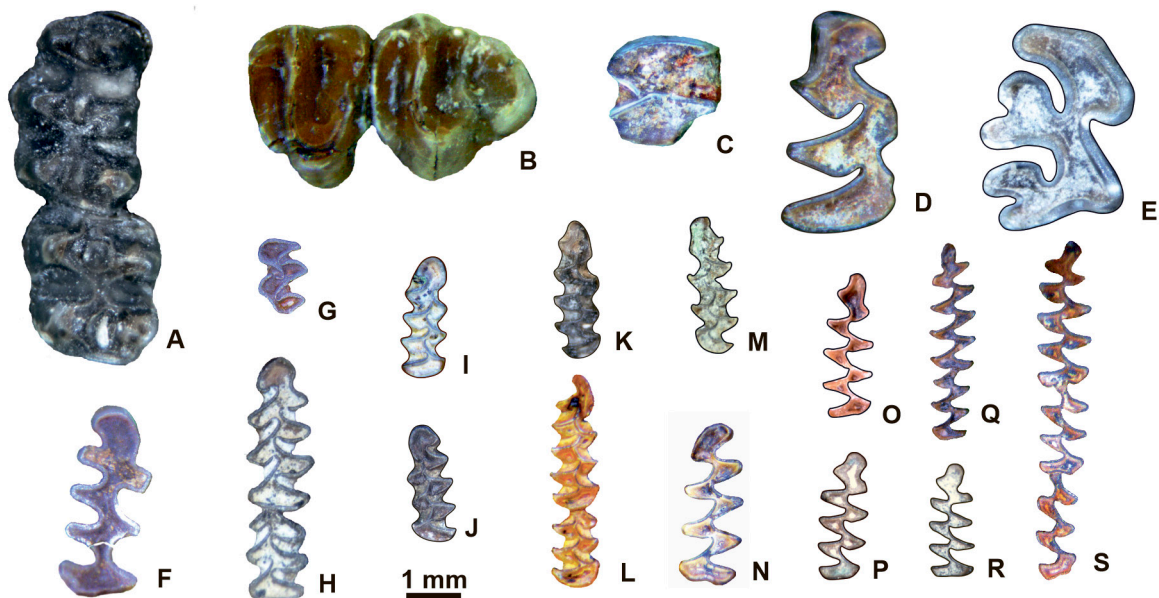
The studied material is mostly represented by single remains. The ground squirrel, steppe lagurine and narrow-headed vole remains are prevail in the collection. The following species of small mammals have been

identified by now (Fig. 2): *Ochotona* sp., *Spermophilus* sp., *Allactaga* sp., *Ellobius talpinus* (Pallas, 1770), *Cricetus cricetus* (Linnaeus, 1758), *Myospalax myospalax* (Laxmann, 1773), *Craseomys rufocanus* (Sundevall, 1846), *Clethrionomys cf. rutilus* (Pallas, 1779), *Lagurus lagurus*, *Eolagurus luteus* (Eversmann, 1840), *Stenocranius gregalis*, *Alexandromys oeconomus* (Pallas, 1776). The previously mentioned collared lemming *Dicrostonyx* sp. (Malikov & Golovanov, 2020) was determined erroneously. Morphology of rodent remains indicates a geological age of the fauna with the most informative being the remains of steppe lagurine and narrow-headed voles.

### Narrow-headed voles *Stenocranius gregalis* (Pallas, 1779)

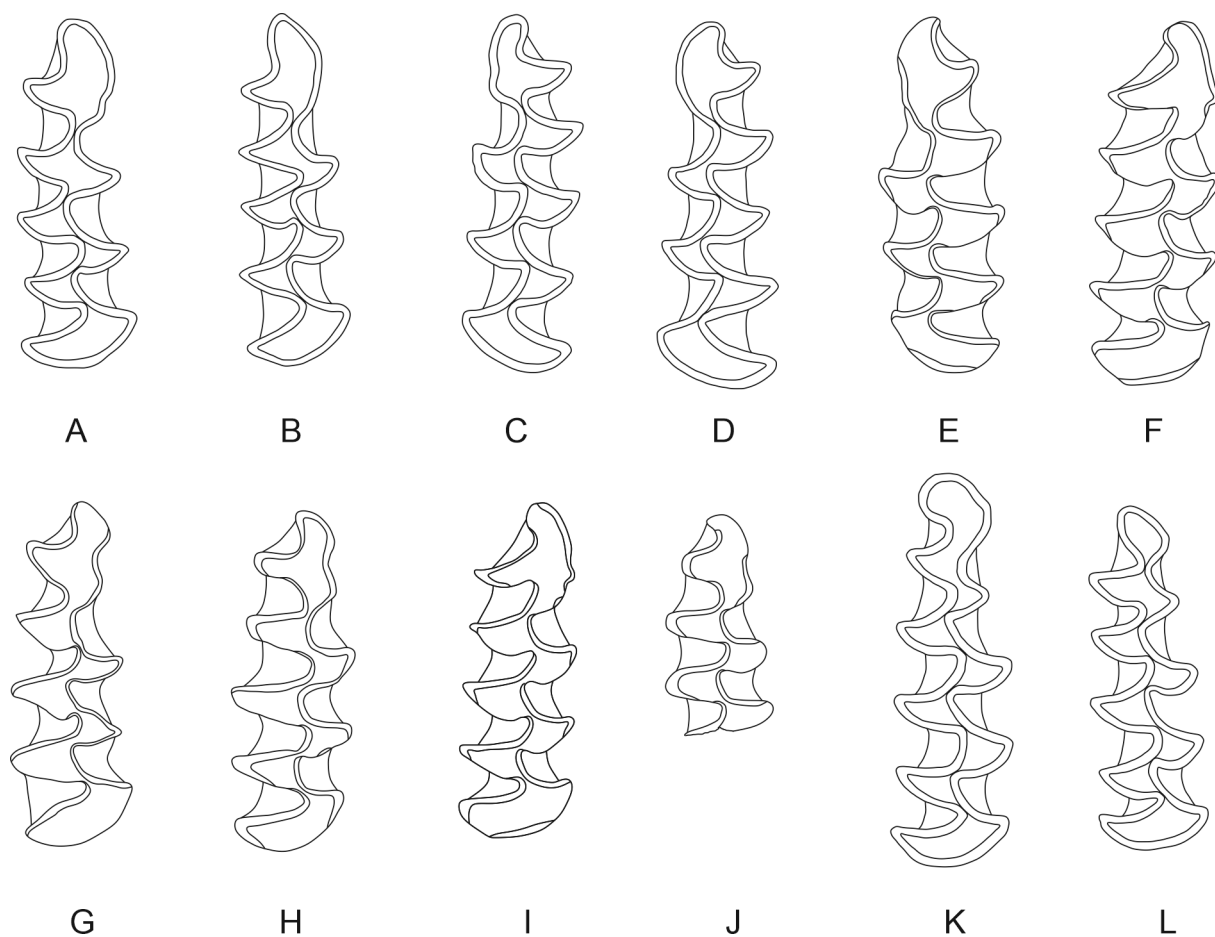
The 20 m1 teeth of the narrow-headed vole *Stenocranius gregalis* were identified in the studied localities (Fig. 2, K–M). Rootless teeth, cement accumulations in the reentrant angles. Isolated prisms with "Pitymys" configuration: T5 is isolated from the anteroconid loop. The enamel is differentiated according to the "Microtus"-type. For the studied teeth, the presence of all three morphotypes of the anteroconid loop m1 was noted "gregaloid-microtid" variants with a complicated anteroconid shape prevail in the sample (Fig. 3, E–J).

Among studied localities, the largest number of m1 teeth of the narrow-headed vole was found in the Solonovka locality (13 specimens). Less representative samples were in Petropavlovskoe (6 specimens) and Malinovka-4 (1 specimen) localities. Measurements of the tooth from the Malinovka-4 locality are almost identical



**Fig. 2.** Small mammals remains from localities of the Cis-Altai Plain. A — *Cricetus cricetus*; B — *Spermophilus* sp.; C — *Ochotona* sp.; D — *Myospalax myospalax*; E — *Allactaga* sp.; F — *Ellobius talpinus*; G — *Clethrionomys cf. rutilus*; H — *Craseomys rufocanus*; I, J — *Alexandromys oeconomus*; K, L, M — *Stenocranius gregalis*; N — *Eolagurus luteus*; O, P, Q, R, S — *Lagurus lagurus*. Exemplars: A, C, D, E, F, G, I, K — teeth from Solonovka locality; B, H, J, M, N, P, Q, R, S — teeth from Petropavlovskoe locality; L, O — teeth from Malinovka-4 locality.





**Fig. 3.** Molars of narrow-headed vole, m1: A, B — *S. hintoni-gregaloides* early Middle Pleistocene, Kuznetsk basin, Bachatsk quarry (Dupal, 1987, fig. 3: 4,6); C, D — *S. cf. gregalis* late Middle Pleistocene, Kuznetsk basin, Novosergeevo quarry (Dupal, 1987, fig. 3a); E-J — *S. gregalis* late Middle Pleistocene, Petropavlovskoe (E-H), Malinovka-4 (I) and Solonovka (J); K, L — *S. gregalis* recent, Altai Region, Pavlovsky District (Dupal, 1987, fig. 3b).

to the mean values of Solonovka teeth (Appendix 1). The teeth from the Petropavlovskoe locality are somewhat smaller than the specimens from Solonovka, the difference in mean crown length reaching 0.3 mm (Appendix 1). This difference in m1 length is similar to the difference between the length of this tooth in young (males:  $2.42 \pm 0.01$ ; females:  $2.42 \pm 0.01$ ) and overwintered (males:  $2.67 \pm 0.02$ ; females:  $2.71 \pm 0.03$ ) animals in modern populations (Dupal & Abramov, 2010). However, the pattern of the chewing surface of the narrow-headed vole tooth, formed at a young age, persists throughout the life of the animal (Dupal & Abramov, 2010). Thus, the morphology of the m1 tooth is more reliable parameter than its size. The similarity of the morphological structure in teeth of narrow-headed vole and the correlation in the geological structure of the Solonovka and Petropavlovskoe sections make it possible to consider the entire fauna in a single complex. It is possible that different ontogenetic stages of animals are represented in the studied localities. In the morphology of the m1 occlusal surface, the studied voles are closest to the *S. cf.*

*gregalis* of the Middle Pleistocene of the Novosergeevo quarry of Kuznetsk basin (Fig. 3, C, D). Our samples differ from *S. hintoni-gregaloides* of the Cis-Altai Plain and Kuznetsk basin (Fig. 3, A, B) by the complete separation of T5 and T6 enamel triangles, and a more complex structure of the anteroconid loop, with a predominance of the "gregaloid-microtid" morphotype. In contrast to the modern narrow-headed voles of the Altai Territory (Dupal, 1987), the buccal prism (T6) is nearly undeveloped on the anteroconid, and the lingual prism is widely fused with the anterior cap. Thus, the structure of the m1 chewing surface of the narrow-headed vole from the Solonovka, Petropavlovskoe, and Malinovka-4 localities significantly differs both from the voles of the early Middle Pleistocene (Early Neopleistocene) and from the recent voles of the south of the West Siber. The size of the m1 in narrow-headed vole from the Solonovka, Petropavlovskoe and Malinovka-4 localities showed differences from recent representatives of the species inhabiting this territory (Appendix 2). By most measurements, the sample studied turned out to be close to the voles of

**Table 2.** Mean values of coronary length m1 tooth and significance of differences in the Pleistocene vole forms (adapted from Dupal, 1998, 2000a)

Species	Locality	n	M±m	t
<i>S. hintoni</i>	Priobie Loess Plateau	17	2.41±0.02	
	Kuznetsk basin	8	2.40±0.05	
<i>S. hintoni-gregaloides</i>	Priobie Loess Plateau	28	2.50±0.02	3.2**
	Kuznetsk basin	16	2.52±0.03	
<i>S. gregaloides</i>	Priobie Loess Plateau	21	2.62±0.02	4.3***
<i>S. gregalis</i>	Cis-Altai Plain*	20	2.63±0.05	
	Priobie Loess Plateau	98	2.64±0.01	
	Kuznetsk basin	16	2.68±0.03	3.8**
<i>S. gregalis</i> modern	Priobie Loess Plateau	22	2.67±0.03	

\* — this paper; significance level: \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

the Late Pleistocene of the Priobie Loess Plateau (Dupal, 2000b). However, voles from the described localities are, on average, slightly smaller than specimens from the Upper Pleistocene sediments. Narrow-headed voles from late Middle Pleistocene of Khudyakov locality on the Tobol River (Zazhigin, 1980) and Kuznetsk basin (Dupal, 1987), are much larger than the sample studied by us (Appendix 3). This well correlates with the data of Recent voles, with narrow-headed voles of Kuznetsk basin being on the average larger than in the Altai Territory (Dupal, 2000a).

For a more accurate determination of the position of the studied samples in the *S. hintoni*–*S. gregalis* phylogeny series, it is useful to estimate the crown length of m1. Dupal (1998) showed a consistent increase of the length of m1 from the end of the Early Pleistocene to the present. Thus, the estimated mean length of the tooth, along with the morphotypes ratio of the sample, allows us to assess the evolutionary level of the sample under study. In terms of crown length of m1, narrow-headed voles from the Solonovka, Petropavlovskoe, and Malinovka-4 localities occupy an intermediate position between *S. gregaloides* Hinton, 1923 of the early Middle Pleistocene and *S. gregalis* of the Late Pleistocene of the Priobie Loess Plateau (Tab. 2).

The morphology of m1 in voles from the studied localities differs well from *S. gregaloides*, and its structure is similar to that of narrow-headed voles. Thus, it is likely that the differences in size of m1 between our sample and *S. gregaloides* are caused by evolutionary differences. What accounts for slight differences in size between the studied sample and the voles of the Late Pleistocene of the Priobie Loess Plateau (Dupal, 1998) is not yet clear. Perhaps these differences are due to a smaller sample from the Solonovka, Petropavlovskoe, and Malinovka-4 localities ( $n=20$  versus  $n=98$  from Priobie Loess Plateau). An increase in the sample size is necessary to address this question.

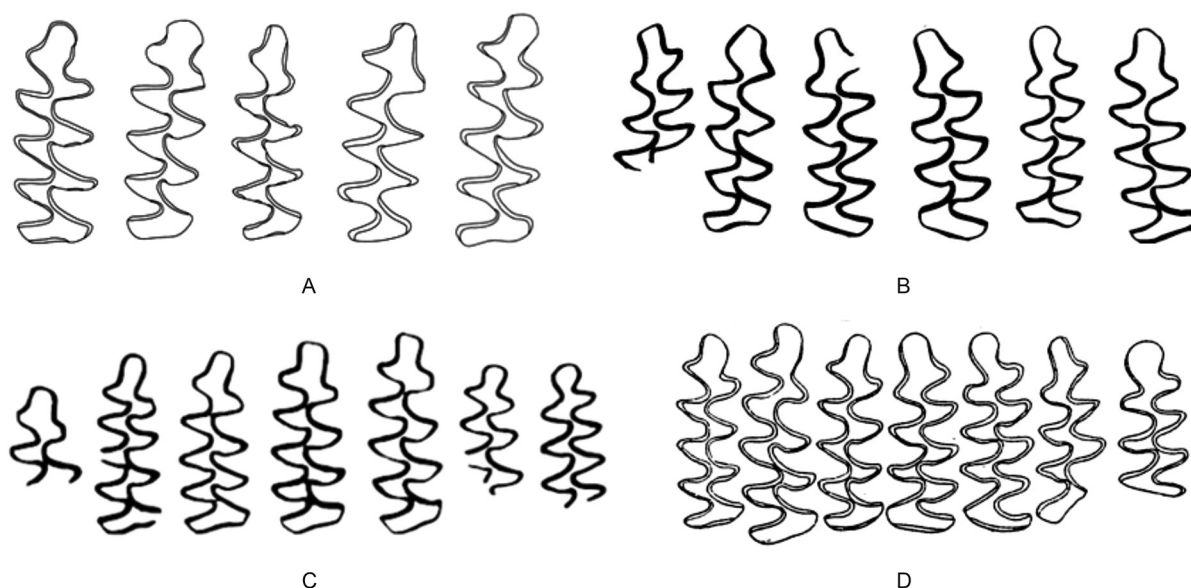
#### Steppe lagurine (=steppe lemming) *Lagurus lagurus* Pallas, 1773

The remains of steppe lagurines are represented by isolated teeth and fragments of lower jaws

(Fig. 2, O–S). In total, six M3 and 13 m1 teeth and their fragments were identified, of which three are juvenile. There are no roots and cement in their molars. The enamel is differentiated according to the "Microtus"-type: the thinner walls occur on the convex (trailing) edges of prisms. Always thinner are the inner parts of the reentrant angles, triangle prisms of the are isolated. Among the studied m1 molars, the anteroconid neck was formed in seven specimens ("*lagurus*" morphotype). The anteroconid neck begins to form only in four specimens ("*transiens*" morphotype). Thus, both "*lagurus*" and "*transiens*" m1 teeth morphotypes of steppe lagurines were found in the Cis-Altai Plain localities (Fig. 4).

Four m1 molars of the *Lagurus lagurus* were found in each locality Malinovka-4 and Petropavlovskoe, and only one m1 tooth was found in the Solonovka locality (Appendix 3). In all three localities m1 are of large size values up to 2.78 (Solonovka), 2.75 (Petropavlovskoe), and 2.65 (Malinovka-4) mm, and smaller size is 2.05 (Petropavlovskoe) and medium size 2.43 (Malinovka-4) mm. Small amount of material in the studied localities does not allow to make a detailed comparison and assessment of the ratio of *L. lagurus* morphotypes. It is possible that teeth of both young and adult animals are represented in the studied localities, which is also confirmed by the records of juvenile teeth. They correspond to morphology of *S. gregalis*. Thus, geological data and information on the morphology of the narrow-headed vole from the studied localities makes it possible to consider this fauna as a single complex even despite the difference in the average values of the m1 teeth of *L. lagurus*.

In terms of the anteroconid morphology and the size of m1, specimens of the Cis-Altai Plain show a high similarity with the *Lagurus transiens* Janossy, 1962 remains from the Krasnoselka locality of Ukraine (Rekovets, 1994) of the Late Tiraspol age (early Middle Pleistocene). At the same time, specimens from the Solonovka, Petropavlovskoe, and Malinovka-4 localities are significantly larger than the *L. transiens* remains from the Vyatkino locality (Zazhigin, 1980) located on the Cis-Altai Plain too.



**Fig. 4.** Molars of steppe lagurine, m1: A — *Lagurus lagurus* from Solonovka, Petropavlovskoe and Malinovka-4 locality; B — *Lagurus transiens* from Vorona fossil soil in Kolkotova Balka section (Markova *et al.*, 2021, fig. 5); C — *Lagurus ex gr. transiens-lagurus* from Priluki locality (Markova & Puzachenko, 2017, text-fig.4: 30-36); D — *Lagurus lagurus* Morozovka-2 locality (Rekovets, 1994, fig. 24a).

The studied specimens differ significantly from the steppe lagurine from Vyatkinno not only in size (Appendix 4), but also the morphology. For example, in the Vyatkinno locality, teeth of the "lagurus" morphotype are not described; the re-entrant angles on the anteroconid loop are very weakly expressed, especially on the lingual side (Zazhigin, 1980). In the specimens under this study, the re-entrant angles of the anteroconid loop are well developed, and even "lagurus" morphotype m1 are encountered.

The m1 of *L. lagurus* from the Priluki locality in Ukraine (Markova & Puzachenko, 2017) has a similar morphology and similar size characteristics (Tab. 3). Similar remains have been described from other localities in Eastern Europe: Morozovka-2 locality in Ukraine (Rekovets, 1994), in the Kolkotova Balka section from the Vorona paleosol deposits (Markova *et al.*, 2021). All these localities date from the beginning of the second half of the Middle Pleistocene (MIS 11-9).

The lower molars m1 of *L. lagurus* from the Cis-Altai Plain localities look more primitive than those of steppe lagurines from the Kosika section on the Lower Volga, characterizing the end of the Middle (MIS 7) and the beginning of the Late (MIS 5) Pleistocene (Zastrozhnov *et al.*, 2020). The steppe lagurines remains from the Late Pleistocene (MIS 5) of Yagodnoe and Spasskoe localities from the Middle Volga region (Svitoch *et al.*, 2021) are also of a more progressive appearance. The "transiens" morphotype teeth are found in single specimens in these localities, in contrast to the Cis-Altai Plain localities where they are common. First lower teeth, m1,

of the Cis-Altai Plain steppe lagurines are larger than those of *L. lagurus* of the Late Pleistocene (Tab. 3). This also allows us to consider them as an earlier evolutionary stage in the development of steppe lagurines.

On this basis, we identify the studied specimens as *L. lagurus*. It is possible that the studied material characterizes one of the earliest stages of the formation of the *L. lagurus* species on the Cis-Altai Plain.

#### Landscape reconstruction

A bioclimatic analysis of faunal associations at the Petropavlovskoye, Solonovka, and Malinovka-4 localities revealed the predominance of open biotopes in the bioclimatic spectra (Fig. 5, A). Original methodology shows the transition from the Pleistocene steppe-desert communities of small mammals to modern forest-in-trozonal communities, at least in the eastern, foothill part of the Cis-Altai Plain. For the Solonovka (68%), Malinovka-4 (76%), and Petropavlovskoe (65%) localities the most probable ecological zone is the steppe-desert zone. The use of bioclimatic method with a more detailed classification of ecological zones for the studied region shows the predominance of the steppe, forest-steppe, and semi-desert parts of the BS in fossil communities (Fig. 5, B). Steppe, forest-steppe, and semi-desert zones account for 86% of the BS in the Malinovka-4 locality, 79% in the Petropavlovskoe locality, and 80% in the Solonovka locality. All other ecological zones occupy a much smaller part of BS.

The obtained bioclimatic spectra represent data on faunal complexes from the studied localities. In all



**Table 3.** Mean crown length and width in first lower molar, m1, of the Pleistocene and modern steppe lagurine

Age	Locality and region	length				width			
		n	min	M	max	n	min	M	max
Late Pleistocene (MIS 3)	Kabazi V/95, Crimean Mts.*	6	2.6	2.73	2.8	6	0.85	0.9	0.95
Late Pleistocene (MIS 3)	Starosele/94, Crimean Mts.*	1		2.55		1		0.85	
Late Pleistocene (MIS 3)	Arapovichi, Upper Dnieper basin*	18	2.2	2.41	2.65	18	0.75	0.86	1.15
Late Pleistocene (MIS 5e)	Malyutino, Seim River basin*	16	2.4	2.43	2.75	16	0.7	0.87	0.95
Late Pleistocene (MIS 5e)	Shkurlat, Crimean Mts.**	35	2.2	2.49	2.8	35	0.6	0.85	1.05
Late Middle Pleistocene (MIS 9)	Priluki, Sula River basin*	15	2.4	2.52	2.75	15	0.75	0.86	1
Late Middle Pleistocene	Cis-Altai Plain***	8	2.05	2.47	2.78	8	0.68	0.79	0.95
Late Middle Pleistocene (MIS 11)	Gun'ki II, Psel River basin*	48	2.1	2.35	2.65	50	0.65	0.84	1.05
Modern	Ryazan and Voronezh districts*	47	2.2	2.27	2.6	51	0.75	0.8	0.9
Modern	Southern Ukraine*	20	2.15	2.32	2.55	20	0.8	0.9	1
Modern	Astrakhan steppe, W. Kazakhstan*	20	2	2.48	2.75	20	0.8	0.87	0.95
Modern	Kazakhstan*	30	2.2	2.38	2.63	35	0.65	0.8	1
Modern	Southern Trans-Urals****	30	2.05	–	2.65	30	0.7	–	1.1

\* — Markova, 1999; \*\* — Markova, 2000; \*\*\* — this paper; \*\*\*\* — Borodin, 2009

three localities, a significant share of the remains belongs to ground squirrels, narrow-headed voles, and steppe vole, i.e. species that live mainly in steppe environments (Gromov & Erbaeva, 1995). In addition, the obtained distribution in the BS of the studied faunal localities is in good agreement with their geographic distribution. Thus, the largest part of open biotopes (76 or 86%) belongs to the Malinovka-4 locality. This Cis-Altai Plain is the most remote from the mountainous regions and is located in the north of the Cis-Altai Plain (Fig. 1). In the Solonovka and Petropavlovskoe localities a share of open biotopes species decreases (68 or 79 and 65 or 80%, respectively), and species of closed forest biotopes show higher numbers. It agrees with the absence of forest voles remains in the Malinovka-4 locality and a scarce of the same voles in the Solonovka and Petropavlovskoe localities. It should be noted that the complete absence of cold-loving species as the *Lemmus* or *Dicrostonyx* may indicate the formation of all three localities in a warm, probably interglacial period.

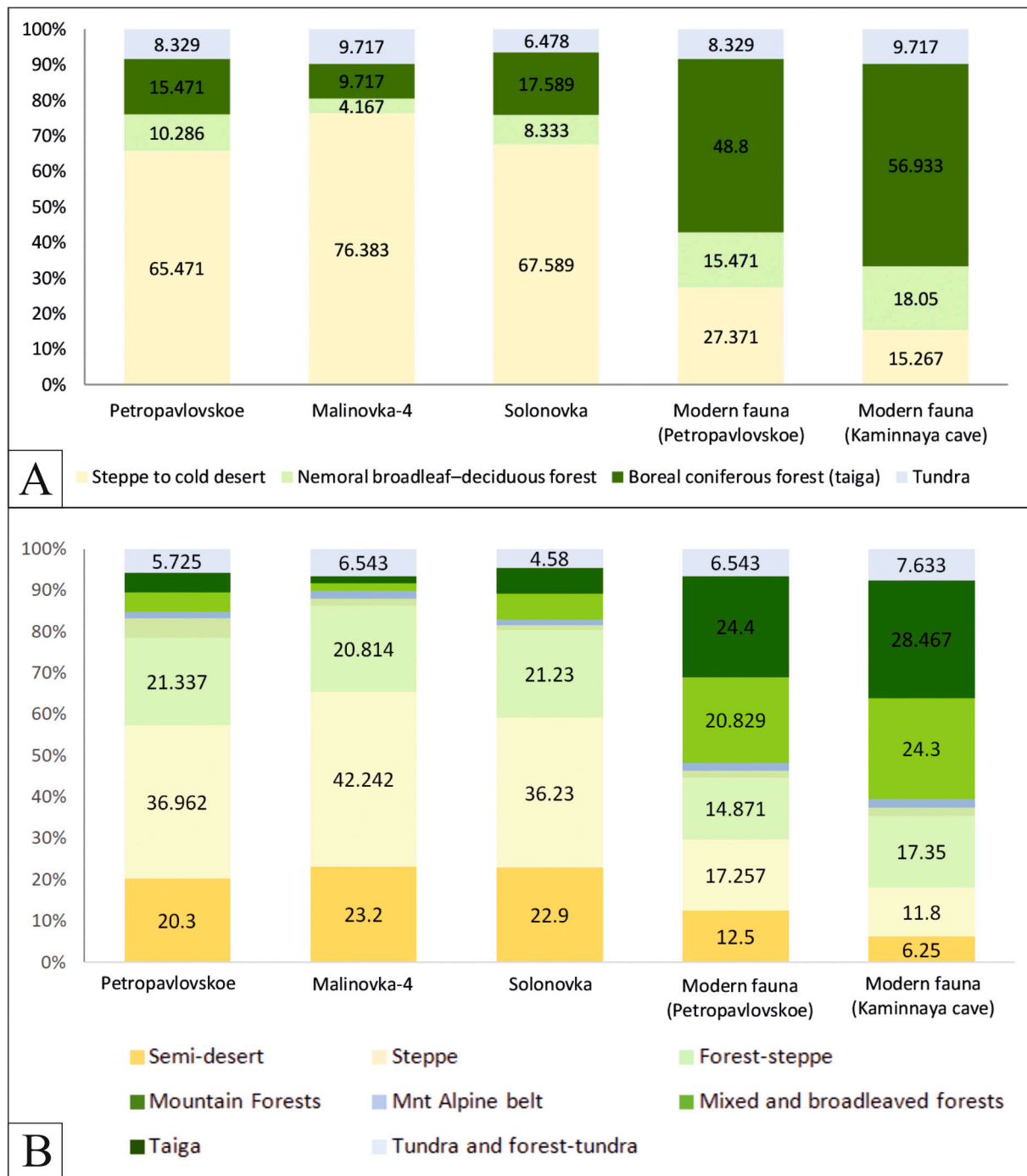
The application of bioclimatic method to modern small mammal fauna of the Cis-Altai Plain (Makarov, 2017) shows a significant difference with the data for the second half of the Middle Pleistocene. In modern communities steppe-desert zone accounts for an average of 21% in bioclimatic spectra. In fossil communities this zone accounts for an average of 70% (Appendix 5). When using a detailed classification the steppe, forest-steppe and semi-desert zones in fossil faunistic associations account for 82% of the BS. In the modern fauna of the Petropavlovskoe region, these zones account for only 45% (Appendix 6). There is a noticeable trend towards the expansion of closed forest landscapes. It accounts for 44% in modern fauna against 8% in fossil associations.

## Discussion

Paleontological data, together with data on paleosol stratigraphy and magnetostratigraphy, make it possible to estimate the age of the studied small mammal faunas. The deposits containing remains of small mammals in the sections under study overlie the sediments containing remains of the *Equus nalaikhaensis* (Zykin *et al.*, 2017) and *Mammuthus trogontherii* (Adamenko, 1974). In addition, for the Malinovka section, a paleomagnetic study of the Malinovka-4 locality placed it in the Brunhes Chron, whereas the underlying sediments belong to the Matuyama Chron (Zudin *et al.*, 1977). The section was also characterized by paleontological and paleosol data (Krukover, 2007; Zykina & Zykin, 2012). Thus, the mammalian fauna of the Solonovka, Petropavlovskoe, and Malinovka-4 localities has a post-Vyatkinian (=post-Tiraspolian/post-Cromerian) age, which matches the overall composition of these faunas. The narrow-headed vole and the steppe lagurine morphology makes it possible to date the fauna of the studied localities more accurately.

The first lower molars of *Stenocranius gregalis* and *Lagurus lagurus* from the Cis-Altai Plain localities look more primitive than in the same species from the Kosika section of the Lower Volga, dated to the end of the Middle (MIS 7) through the beginning of the Late (MIS 5) Pleistocene (Zastrozhnov *et al.*, 2020). Remains of steppe lagurines from the Late Pleistocene (MIS 5) Yagodnoe and Spasskoe localities from the Middle Volga region (Svitoch *et al.*, 2021) are also of a more progressive appearance. In these localities, the "transiens" morphotypes in steppe lagurines are less numerous compared to the Cis-Altai Plain localities.

The narrow-headed voles described here occupy an intermediate position between *S. gregaloides* of



**Fig. 5.** Histogram of the bioclimatic spectra of late Middle Pleistocene and modern fauna in (A) original method of Hernández Fernández (2001), and (B) its adapted version (Golovanov, Malikov, 2021).

the early Middle Pleistocene and *S. gregalis* of the Late Pleistocene of the Priobie Loess Plateau. General morphology of narrow-headed vole teeth structure are most similar to *S. gregalis* of the late Middle Pleistocene of Kuznetsk basin and the Tobol River (Zazhigin, 1980; Dupal, 1987). This is in good agreement with the fact that this species characterizes the post-Vyatkinian

(=post-Tiraspolian/post-Cromerian) faunas of various regions of Eurasia.

Thus, we believe that the faunas from the studied Cis-Altai Plain localities cannot be dated to the Late Pleistocene. This is in good agreement with the occurrence of fauna localities below the loess-soil deposits of the Upper Pleistocene (Zykin *et al.*, 2017; Zykina *et*

*al.*, 2018). The Upper Pleistocene age of the loess-soil deposits of the Solonovka section was confirmed by OSL-dating (Meshcheryakova *et al.*, 2022).

We compare our fauna with the fauna of the Priluki locality (Markova & Puzachenko, 2017) in Eastern Europe dated to the Kamenka interglacial (MIS 9). The Priluki locality contains the steppe lagurines remains of the transitional type of *Lagurus ex gr. transiens-lagurus*. We found a steppe lagurine with a similar morphology in the Cis-Altai Plain localities. Both the steppe lagurine and the narrow-headed vole of the studied sections have a morphology similar to the voles obtained from Vorona paleosol in the Kolkotova Balka section, also dating from the Kamenka interglacial (Markova *et al.*, 2021). The fauna of the Morozovka-2 locality in Ukraine (Rekovets, 1994) is another locality with which the Solonovka, Petropavlovskoe, and Malinovka-4 sections fauna can be correlated. The Morozovka-2 locality most probable dates to the middle part of the Middle Pleistocene too: MIS 11-9 (Krokhmal' *et al.*, 2021). A similar correlation has already been proposed for the Malinovka-4 locality earlier (Krukover, 2007). Here we confirm it using more abundant material.

Thus, it is most likely that the faunas from the Solonovka, Petropavlovskoe and Malinovka-4 localities can be dated to the first half of the late Middle Pleistocene (beginning of the Middle Neopleistocene), MIS 11-9. This is confirmed by the data on the geological structure of the Solonovka section (Zykin *et al.*, 2017). In this section, sediments containing the small mammals fauna remains occur below the fossil soil horizon. Loess-like deposits presumably correlating to the Chulym loess (MIS 8) occur above this paleosol.

No remains of the water voles were found in the studied sections. This hampers dating of the obtained small mammal associations because a significant part of the biostratigraphic correlations of the Middle and Upper Pleistocene sediments is based on water voles (Heinrich, 1990; von Koenigswald & van Kolfschoten, 1996; and others). The water vole *Arvicola kalmankensis* Zazhigin, 1980 was described for the second half of the Middle Pleistocene in the south of Western Siberia (Zazhigin, 1980). In terms of its evolutionary level, this vole corresponds to the transitional stage between *A. mosbachensis* Schmidtgen, 1911 and the modern *A. terrestris* L., 1758. The identification of *Alexandromys oeconomus*, a species that lives in humid landscapes, makes it possible to expect a water vole to be found in the future.

Also noteworthy is the absence of lemmings in the Pleistocene of the Cis-Altai Plain, whereas *Lemmus* and *Dicrostonyx* remains are known both in the surrounding mountains (Dupal, 2004; Agadzhanyan *et al.*, 2021) and in the Kuznetsk Basin (Galkina, 1975). It is most likely that the described faunas of the Cis-Altai Plain reflect one of the warm intervals of the second half of the Middle Pleistocene (MIS 11 or 9). At the same time, lemmings could not get to Altai Mountains bypassing the Cis-Altai Plain. Thus, a more detailed study of the sediments of the cold intervals of the Middle and Late

Pleistocene allows us to expect finds of *Lemmus* and *Dicrostonyx* in the future.

Application of both original bioclimatic discriminant analysis and its adapted version for fossil and modern small mammal communities showed similar results. The data shows the absolute dominance of open landscapes on the territory of the Cis-Altai Plain in the second half of the Middle Pleistocene. Thus, during this period steppe, forest-steppe and semi-desert landscapes were present in the region. Later there was a transition to modern, more closed landscapes. The transition from the Pleistocene steppe and forest-steppe landscapes to more closed modern forest zones was also noted in the areas adjacent to the Cis-Altai Plain (Dupal, 2004). Similar to the fossil fauna, specialized tundra species are completely absent in the modern fauna. Apparently, the conditions of the region during the period of the formation of fossil complexes were more arid in comparison with modern times.

This landscape-climatic reconstruction for Middle Pleistocene localities is confirmed by palynological data on the Solonovka section. Palynological data show the presence of a wide range of grassland plants like wormwoods (*Artemisia*), grasses (Poaceae), sedges (Cyperaceae), pigweeds (Chenopodiaceae) and Asteraceae, indicating a close occurrence of open steppe landscapes (Zykin *et al.*, 2017). Conifer pollen dominates in the arboreal group and the leaved trees are almost absent. Palynological samples were taken from levels younger than the layer with remains of small mammals. However, the palynological data characterize the same lithological bed which yielded bone remains. Thus, the palynological data confirm the assumption of the forest-steppe ecosystem, with the dominance of open steppe landscapes (Zykin *et al.*, 2017).

## Conclusions

The described small mammal localities in the south of Western Siberia are associated with alluvial deposits of the late Middle Pleistocene. The age model of the studied deposits is defined by faunal remains of the early Middle Pleistocene, and the stratigraphic control of the overlying loess-paleosol series of the Upper Pleistocene.

The following small mammal species have been identified: *Ochotona* sp., *Spermophilus* sp., *Allactaga* sp., *Ellobius talpinus*, *Cricetus cricetus*, *Myospalax myospalax*, *Cruseomys rufocanus*, *Clethrionomys cf. rutilus*, *Lagurus lagurus*, *Eolagurus luteus*, *Stenocranius gregalis*, *Alexandromys oeconomus*. This fauna is younger than the Vyatkinian (=Tiraspolian/Cromerian) faunal complex of the first half of the Middle Pleistocene. The upper boundary of the fauna distribution is clearly defined by the upper Suzun loess sediments correlated with MIS 6. The age of the described small mammal faunas is reliably determined as the second half of the Middle (MIS 11-7) Pleistocene. The most probable age of the fauna from the Solonovka, Petropavlovskoe, and Malinovka-4 localities is the first



half of the late Middle Pleistocene (beginning of the Middle Neopleistocene), MIS 11-9.

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## Appendix 1. Dimensions of the m1 in narrow-headed vole from Solonovka, Petropavlovskoe, and Malinovka-4 sites

Measurements localities	Solonovka n=13		Petropavlovskoe n=6		Malinovka-4 n=1
	lim	M±m	lim	M±m	
L	2.5-2.95	2.74±0.06	2.25-2.6	2.45±0.05	2.77
W	0.83-1.03	0.94±0.06	0.83-1.07	0.93±0.04	0.9
L of ACC	1.17-1.57	1.34±0.04	1.23-1.33	1.28±0.02	1.43
W of ACC	0.7-0.97	0.86±0.02	0.73-1.0	0.84±0.04	0.87
L of AC	0.73-1.03	0.85±0.02	0.65-0.93	0.78±0.04	0.93
W of AC	0.63-0.8	0.71±0.02	0.57-0.67	0.62±0.02	0.68
Lingual L of ACC	0.83-1.2	0.99±0.04	0.87-1.03	0.98±0.03	1.17
Buccal L of ACC	1.0-1.33	1.18±0.04	1.07-1.2	1.13±0.02	1.27

## Appendix 2. Dimensions of the m1 of narrow-headed vole in the south-east of Western Siberia

Measurements (Dupal, 1987)	Predaltai plain (Solonovka, Petropavlovskoe, Malinovka-4)			late Middle Pleistocene		Priobie Loess Plateau, Late Pleistocene (Dupal, 2000b) n=98	Modern, Altai Territory, Pavlovsky district (Dupal, 2000a) n=22	
				Tobol river, Khudyakovo (Zazhigin, 1980) n=10	Kuznetsk basin, Fomikha village (Dupal, 1987) n=16			
	n	lim	M±m	lim	M±m			
L	13	2.25-2.95	2.63±0.05	2.45-2.8	2.68	2.68±0.03	2.64±0.01	2.67±0.03
W	17	0.83-1.07	0.93±0.02	0.9-1	0.98	0.94±0.01	0.97±0.01	0.99±0.01
L of ACC	18	1.17-1.57	1.33±0.03	1.3-1.65	1.5	1.37±0.03	1.35±0.01	1.41±0.02
W of ACC	18	0.7-1	0.86±0.02	-	-	0.89±0.01	0.90±0.01	0.92±0.02
L of AC	20	0.65-1.03	0.83±0.02	0.75-1	0.92	0.84±0.02	0.94±0.01	0.9±0.02
W of AC	19	0.57-0.8	0.68±0.02	-	-	0.65±0.01	0.68±0.01	0.75±0.01
Lingual L of ACC	15	1-1.33	1.17±0.02	-	-	1.19±0.02	1.17±0.01	1.28±0.02
Buccal L of ACC	16	0.83-1.2	1±0.03	-	-	0.97±0.02	1.04±0.01	1.06±0.02

## Appendix 3. Dimensions of the m1 of steppe lagurine in Solonovka, Petropavlovskoe, and Malinovka-4 localities

Measurements	Solonovka	Petropavlovskoe		Malinovka-4	
	n=1	n=4	M±m	n=4	M±m
L	2.78	2.05; 2.2; 2.43; 2.75	2.36±0.08	2.43; -; 2.5; 2.65	2.53±0.08
W	0.83	0.68; 0.73; 0.85; 0.95	0.8±0.02	0.8; -; 0.75; 0.75	0.77±0.02
L of ACC	1.6	1.1; 1.2; 1.35; 1.48	1.28±0.13	1.28; 1.33; 1.48; 1.48	1.39±0.09
L of AC	1.05	0.7; 0.78; 0.85; 0.93	0.81±0.08	0.78; 0.8; 0.88; 0.9	0.84±0.03
W of AC	1.0	0.63; 0.75; 0.88; 0.88	0.78±0.09	0.73; 0.63; 0.73; 0.83	0.73±0.05



## Appendix 4. Dimensions of the m1 of steppe lagurine of the Middle and Late Pleistocene

Measurements	Predaltai plain (Solonovka, Petropavlovskoe, Malinovka-4)			<i>L. transiens</i> , Vyatkino (Zazhigin, 1980) n=16		<i>L. transiens</i> Krasnoselka (Rekovets, 1994) n=6		<i>L. lagurus</i> Morozovka-2 (Rekovets, 1994) n=50		<i>L. cf. lagurus</i> Shkurlat (Markova, 2000) n=35		Southern Trans-Urals, modern (Borodin, 2009) n=30
	n	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim	M±m	lim
L	8	2.05-2.78	2.47±0.2	2.15-2.5	2.35	2.45-2.6	2.52±0.05	2.3-2.95	2.58±0.1	2.2-2.8	2.49	2.05-2.65
W	8	0.68-0.95	0.79±0.07	0.85-0.95	0.9	0.8-0.9	0.85±0.05	0.75-1	0.86±0.11	0.6-1.05	0.84	0.7-1.1
L of ACC	9	1.1-1.6	1.36±0.13	-	-	1.35-1.5	1.4±0.05	1.2-1.65	1.44±0.07	1.15-1.6	1.33	-
L of AC	9	0.7-1.05	0.85±0.08	0.7-0.8	0.75	0.7-0.9	0.79±0.06	0.7-1.05	0.88±0.07	0.7-0.9	0.79	-
W of AC	9	0.63-1.0	0.78±0.1	0.5-0.6	0.55	0.65-0.9	0.77±0.08	0.6-0.9	0.78±0.06	-	-	-

## Appendix 5. Bioclimatic signal of the late Middle Pleistocene and modern fauna using the original method of Hernández Fernández

(2001)

Species	Climatic restriction index (CRI)			
	Nemoral broadleaf–deciduous forest	Steppe to cold desert	Boreal coniferous forest (taiga)	Tundra
Solonovka	10.286	65.471	15.471	8.329
Petropavlovskoe	4.167	76.383	9.717	9.717
Malinovka-4	8.333	67.589	17.589	6.478
Modern fauna (Petropavlovskoe)	15.471	27.371	48.8	8.329
Modern fauna (Kaminnaya cave)	18.05	15.267	56.933	9.717

## Appendix 6. Bioclimatic signal of the late Middle Pleistocene and Modern fauna by the adapted method (Golovanov &amp; Malikov, 2021)

Species	Climatic restriction index (CRI)										
	Arctic desert	Tundra and forest-tundra	Taiga	Mixed and broadleaved forests	Forest-steppe	Steppe	Semi-desert	Desert	Mountain Forests	Mnt Alpine belt	Mnt steppe
Solonovka	-	4.58	6.25	6.25	21.23	36.23	22.9	-	1.25	1.25	-
Petropavlovskoe	-	5.725	4.687	4.687	21.337	36.962	20.3	-	4.687	1.562	-
Malinovka-4	-	6.543	1.786	1.786	20.814	42.242	23.2	-	1.786	1.786	-
Modern fauna (Petropavlovskoe)	-	6.543	24.4	20.829	14.871	17.257	12.5	-	1.786	1.786	-
Modern fauna (Kaminnaya cave)	-	7.633	28.467	24.3	17.35	11.8	6.25	-	2.083	2.083	-