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Fossil Fauna of Small Mammals from Imanay Cave, Southern Urals, Russia

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Abstract—The fossil fauna of small mammals from the Imanay cave deposits (53°02′ N, 56°26′ E), Southern Urals, Russia, was studied. Species of open habitats prevailed, the narrow-headed vole (*Microtus* (*Stenocranius*) *gregalis*) being dominant. Two types of fauna were identified that characterize its composition and structure at the end of the Late Pleistocene and, presumably, in the Early Holocene. A codominant species of the first type of fauna (lower and middle cave deposits) was the steppe lemming (*Lagurus lagurus*). This type was characterized by a sharp predominance (83.0–92.2%) of steppe species and a low proportion (1.5–3.9%) of forest mammal species. Open landscapes must have dominated and been common in the Late Glacial in the southern part of the Ural Mountains. The pika (*Ochotona* sp.) co-dominated in the fauna of the second type (upper cave deposits), with relatively high proportions of forest species (14.3–21.4%) indicating the appearance of forest formations in the Late Glacial or Early Holocene in this area. Samples of the first lower molars of narrow-headed voles were characterized by a high proportion of teeth (>50%) with simple variants of the structure of the anteroconid cap ("gregaloid" morphotype). High proportions (up to 51.6%) of the "transiens" morphotype were recorded among the first lower molars of the steppe lemming. Among the teeth in the lower half of the cave deposits, rootless cemented first lower molars (m1) and third upper molars (M3) were found with wide merging triangles T4–T5 (m1) and T2–T (M3). This structure of the chewing surface of the molars was typical of the ancient voles *Microtus* (*Stenocranius*) *gregaloides* and *M.* (*Terricola*) *arvalidens* from the fauna of the first half of the Early Pleistocene and the second half of the Middle Pleistocene.

Keywords: small mammals, Late Glacial, Holocene, Southern Urals

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INTRODUCTION

The Late Pleistocene period was characterized by multiple sharp climate fluctuations (Dansgaard et al., 1993; Wohlfarth et al., 2008; Rasmussen et al., 2014; etc.), which had a great impact on vertebrate populations. During this relatively short geological period, significant changes occurred in the ranges of species (Sommer and Nadachowski, 2006; Sommer and Zachos, 2009; Markova et al., 2008; Cooper et al., 2015; Baca et al., 2017), as well as the extinction of many species of large mammals (Stuart and Lister, 2007; Stewart, 2008; Pacher and Stuart, 2009; etc.). Of particular interest is the history of the development of the mammalian fauna on the territory of the Ural region, a unique biogeographic crossroads of northern Eurasia, currently inhabited by representatives of the European, Siberian, and transpalearctic fauna (Bol'shakov et al., 2000). The results of numerous studies of the Late Pleistocene fauna of this area, combined with data on the development of the environment, provide a complex picture of the dynamics of species in the past and raise new issues on certain aspects of the Quaternary history of the Urals.

Among the caves of the southern part of the Southern Urals, Imanay cave discovered in 2009 on the territory of Bashkiria National Park (Meleuzovskii district, Republic of Bashkortostan, Russia), stands out in terms of the richness of faunal finds. A rich complex of remains of Pleistocene–Holocene mammals was found near the cave entrance and inside (Gimranov et al., 2016; Yakovlev et al., 2016; Gimranov and Kosintsev, 2020). Numerous bones of large cave lions and cave bears were found in the deposits of the cave (Sotnikova and Gimranov, 2017; Gimranov et al., 2016, 2017, 2018, 2021). The thermal properties, gran-

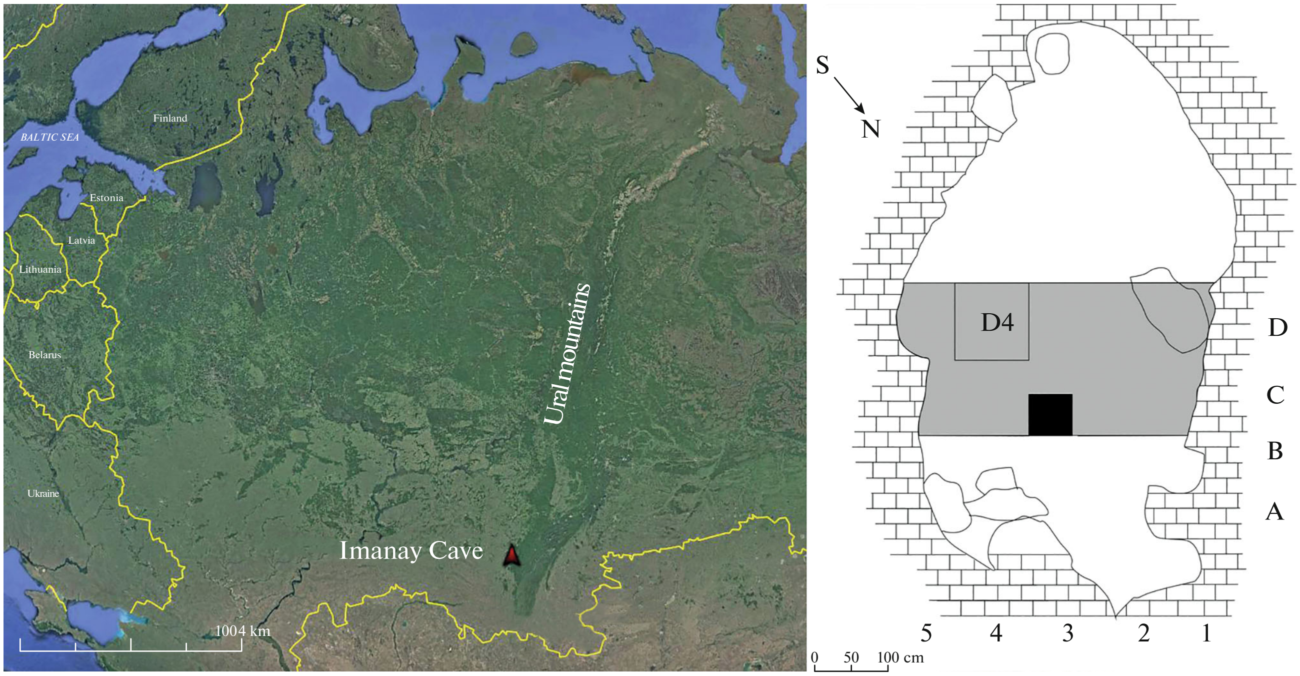

Fig. 1. Geographical location of Imanay Cave (Southern Urals, Russia) and the scheme of the central grotto of the cave with the designation of the studied areas of the excavation (D4 and exploration pit (black square)). The area of the entire excavation is highlighted in gray. The excavation squares are marked with numbers and letters.

ulometric, phase, chemical, and normative-mineral compositions of the eluvial soils of the cave have been studied in detail, and the mineralogical and geochemical features of cave fossilization of fossil bones of cave bears and lions have been revealed (Silaev et al., 2018, 2020). A complex of stone tools attributed to the Middle Paleolithic (Mousterian culture) was found in the deposits of the cave (Kotov et al., 2020). Based on the results of the study of the bone remains of small mammals from the floor surface and from the deposits of the exploration pit of the cave (2013), it was concluded that the deposition of this material (to a depth of 65 cm) occurred at the end of the Late Pleistocene and in the early Holocene, followed by the introduction of Late Holocene bones (Yakovlev et al., 2016). As a result of subsequent excavations of this cave (2016), numerous bone remains of small mammals were found in deposits down to a depth of 120 cm, the number of which proved to be significantly higher in the lower half of the exposed deposits. It has been suggested that the lower half of the exposed deposits of the cave was formed no later than the middle of the Late Pleistocene. This assumption was based on the results of radiocarbon dating of bones of large mammals (from a depth of 0.0–0.1 m, 26 320 ± 1790 years ago (GIN-14244); from a depth of 0.1–0.2 m, 34250 ± 120 years ago (IGAN-8464), 38210 ± 200 BP (IGAN-8466), and 46 260 ± 350 BP (IGAN-8465); from a depth of 0.2–0.3 m, 31 150 ± 110 BP (IGAN-8462)), the predominant localization of which was recorded in the upper half of the cave deposits.

In this article, we present the results of a study of the fossil fauna of small mammals from the 2016 excavation of Imanay Cave. The objectives of this study are to determine the time period of the formation of cave deposits and characterize the composition and structure of small mammal communities (Euliphotyphla, Chiroptera, Lagomorpha, Rodentia) corresponding to this period in the southern part of the Ural Mountains.

The meaning of the term “fossil fauna” in this work is interpreted as “a set of species of one particular locality” (Agadzhanyan, 2009). In this paper, “fauna types” are considered as certain phases (chronological stages) of fauna development, characterized by the quantitative predominance of certain taxa.

MATERIALS AND METHODS

Imanay Cave is located 7 km northeast of the village of Nugush (53°02′ N, 56°26′ E) (Fig. 1). The corridor-type cave is about 100 m long. The first part of the cave is a narrow hole (0.7 × 0.3 m) 18 m long, followed by a corridor (2 × 2 m) 75 m long, ending in a grotto measuring 5 × 6 × 5.6 m (Gimranov et al., 2016). An excavation with a total area of 9.5 m^2 was laid in the central grotto of the cave. The deposits consist of two layers: layer 1 is grayish loam with limestone crumbs, single embers and accumulations of embers, individual pieces of red ocher, flint items; layer thickness, 0.6 m; layer 2 is brown loam with single limestone stones and individual blocks; stripped thickness is 0.6 m (Gimranov et al., 2021).

The fauna of small mammals was studied from square D4 (Fig. 1). From the studied deposits of 12 conditional horizons (depth 0–120 cm) of this part of the central grotto, the taxonomic affiliation of 15430 teeth and jaws of mammals from four orders Eulipotyphla, Chiroptera, Lagomorpha, and Rodentia was established (Table 1). The fossil bone material is highly fragmented and is mainly represented by isolated teeth.

Radiocarbon dating of the samples was carried out at the Laboratory of Radiocarbon Dating and Electron Microscopy, Center for Collective Use, Institute of Geography, Russian Academy of Sciences, Moscow, and the Center for Applied Isotope Research, University of Georgia, United States. Two radiocarbon dates were obtained for the D4 square deposits from the bones of small mammals: 13255 ± 60 IGAN 9116 (depth 50–60 cm) and 17100 ± 50 IGAN 9117 (100–110 cm). Uncalibrated dates are given.

The first lower molars of narrow-headed voles (*Microtus* (*Stenocranius*) *gregalis*) and steppe lemmings (*Lagurus lagurus*) are differentiated according to the morphotypes of the unpaired antheroconid loop (Bol'shakov et al., 1980; Yakovlev, 2015). The first lower molars of gray voles (*Microtus agrestis*, *M. arvalis*) were identified using classification functions (Markova and Borodin, 2005). The species identification of a single tooth (M3) of a representative of the tribe Lemmini was carried out according to the accepted techniques (Smirnov et al., 1997; Ponomarev et al., 2015). The digitization of the material was carried out using a VEGA 3 LMH scanning electron microscope at the Laboratory of the Geology of Mineral Deposits, Mining Institute, Ural Branch, Russian Academy of Sciences.

All identified species of rodents from the deposits of the cave are assigned to certain ecological groups based on the ecological preferences of recent species (Markova, 2008). Six groups were identified: steppe species: *Spermophilus* sp., *Sicista subtilis*, *Microtus gregalis*, *Lagurus lagurus*, *Allocricetulus eversmanni*, and *Cricetulus migratorius*; semi-desert species: *Allactaga major*, *Alactagulus* sp., *Ellobius talpinus*, and *Eolagurus luteus*; forest species: *Sylvaemus* sp., *Craseomys rufocanus*, *Myodes* sp., and *Microtus agrestis*; meadow: *Cricetus cricetus* and *Microtus arvalis*; intrazonal species: *Arvicola amphibius* and *Alexandromys oeconomus*; and tundra species: *Lemmus sibiricus*.

RESULTS

Taphonomic features. Bone material from the studied deposits is highly fragmented. All bones of the postcranial skeleton of small mammals (humerus, ulna, radius, femur, tibia, pelvis) are fragmented. Complete skulls and mandibles are missing. All teeth of rodents are presented in an isolated form, and some of the teeth of insectivorous mammals and bats are preserved in fragmented mandibles. Bone material throughout the depth of the deposits is yellow. Single bones have internal dark gray spots and rare external punctate black mineral formations. Depigmented teeth of shrews are rare. Based on the high degree of fragmentation of the bone material, it can be assumed that the bones of small mammals are of excremental origin. Zoogenic deposits were formed as a result of the activity of the predatory mammals (fox, Arctic fox) that used the inner grotto of the cave as a temporary shelter.

The composition and structure of the fauna. The largest number of certain taxa of small mammals (18–22) was found in the upper conditional horizons of deposits (0–20 cm) and in the middle part of deposits (50–80 cm) (Table 1). Teeth of narrow-headed voles predominate throughout the entire depth of the deposits, and steppe lemmings or pikas (*Ochotona* sp.) are codominant species. These three taxa account for 57.0–74.7% of the total number of identified teeth and jaws of small mammals in the deposits of the upper conditional horizons (0–30 cm) and 81.5–90.5% in the deposits of the middle and lower conditional horizons (30–120 cm). In the upper conditional horizons (0–30 cm), narrow-headed voles are codominants of pikas (19.8–23.4% of the total number of teeth and jaws of all species of small mammals); in the middle and lower conditional horizons (30–120 cm), the codominant species is different, the steppe lemming (16.4–40.5%), while the proportion of pika teeth becomes significantly smaller (4.4–10.9%). In addition to these differences, a larger proportion of shrews and red-backed voles can be noted in the deposits of the upper horizons compared to those in the middle and lower horizons (3.8–9.0 and 6.3–8.7%, 0.0–1.3 and 0.9–3.7%, respectively). The teeth of the yellow steppe lemming (*Eolagurus luteus*) are rare in the upper horizons (0–20 cm) and make up from 1.5 to 7.6% in the underlying deposits. The share of skeletal remains of most of the remaining taxa, determined by the teeth, is less than 1% throughout the entire depth of the deposits.

Among the teeth of rodents in the lower half of the deposits, rootless cemented first lower molars (m1) were found with a wide confluence of anteroconid triangles T4 and T5 (Fig. 2). Such a “pitimis” structure of the masticatory surface with certain forms of an unpaired loop of the antheroconid region is characteristic of the ancient voles *Microtus* (*Stenocranius*) *gregaloides* and *M.* (*Terricola*) *arvalidens* from the fauna of the first half of the Early Pleistocene and second half of the Middle Pleistocene (Maul and Markova, 2007). Teeth with fusion of T2 and T3 were found among rootless cemented third molars (M3) of voles. In terms of preservation and color characteristics, these teeth are similar to the teeth of other small mammal species found in the investigated deposits of the cave.

Table 1. Taxonomic composition and number of bone remains of mammals (Euliphotyphla, Chiroptera, Lagomorpha, and Rodentia) from the deposits of the D4 square of Imanay Cave

Taxon/depth of deposits, cm	110–120	100–110	90–100	80–90	70–80	60–70	50–60	40–50	30–40	20–30	10–20	0–10
Talpa sp.	1	1	–	1	1	1	–	1	–	–	–	1
Crocidura sp.	1	1	–	–	–	–	–	–	–	2	1	2
Sorex araneus Linnaeus 1758	–	–	–	–	–	–	2	–	–	2	4	–
Sorex isodon Turov 1924	–	–	–	–	–	–	–	–	–	–	–	1
Sorex tundrensis Merriam 1900	–	4	5	–	7	3	4	3	2	–	3	11
Sorex minutus Linnaeus 1766	–	–	–	–	–	–	–	–	–	–	–	1
Sorex sp.	1	3	3	2	4	7	19	4	2	6	24	21
Eptesicus nilssonii (Keyserling & Blasius 1839)	–	–	–	–	–	–	1	1	–	–	–	1
Plecotus auritus (Linnaeus 1758)	–	3	–	–	–	–	1	–	1	–	2	2
Chiroptera	1	–	2	1	4	1	2	–	1	1	5	
Ochotona sp.	13	102	88	37	158	141	230	68	29	37	68	73
Lepus sp.	–	–	–	–	1	–	2	3	–	–	1	–
Spermophilus sp.	–	–	2	–	3	4	5	1	–	–	1	3
Sicista subtilis Pallas 1773	–	–	–	–	–	–	1	–	–	–	–	–
Sicista sp.	–	–	–	–	–	–	1	–	–	–	–	2
Allactaga major (Kerr 1792)	–	–	2	–	1	–	1	–	–	–	–	–
Alactagulus sp.	–	–	–	2	1	4	10	2	–	–	1	–
Cricetus cricetus Linnaeus 1758	2	8	10	4	22	5	11	6	–	–	3	11
Allocricetulus eversmanni Brandt 1859	2	4	5	2	1	6	24	1	2	2	1	8
Cricetulus migratorius Pallas 1773	7	2	5	3	15	14	39	2	1	–	–	–
Ellobius talpinus Pallas 1770	3	9	9	3	21	12	22	6	6	1	9	12
Lemmus sibiricus Kerr 1792	–	–	–	–	–	–	–	–	–	–	–	1
Craseomys rufocanus Sundevall 1846 (M2)	–	1	1	1	–	–	–	–	–	–	2	2
Myodes glareolus Schreber 1780 (M2)	2	6	1	2	4	4	7	–	2	–	2	4
Myodes rutilus Pallas 1779 (M2)	–	–	3	–	–	–	–	–	–	–	–	–
Craseomys sp., *Myodes* sp.	9	31	12	8	20	22	47	10	7	10	22	23
Lagurus lagurus Pallas 1773	61	494	410	259	830	837	1667	262	68	3	31	32
Eolagurus luteus Eversmann 1840	14	27	41	15	52	64	165	52	4	12	1	–
Arvicola amphibius (Linnaeus 1758)	–	1	–	–	–	–	3	–	2	–	5	8
Alexandromys oeconomus (Pallas 1776) (m1)	1	5	–	2	4	5	8	3	2	–	3	–
Microtus (*Stenocranius*) *gregalis* Pallas 1779 (m1)	28	122	98	46	159	167	345	93	20	13	12	20
cf. *Microtus* (*Stenocranius*) *gregaloides* Hinton 1923 (m1)	1	4	2	2	6	2	4	3	–	–	–	–
cf. *Microtus* (*Terricola*) *arvalidens* Kretzoi 1958 (m1)	–	–	–	1	–	–	–	–	–	–	–	–
Microtus arvalis (Pallas 1779) (m1)	–	2	2	–	5	1	–	3	1	–	2	1
Microtus agrestis (Linnaeus 1761) (m1, M2)	–	2	3	–	1	2	4	2	–	1	2	4
Microtus ex gr. *agrestis–arvalis* (m1)	–	1	6	3	7	3	6	2	1	–	–	2
Microtus sp.	119	612	466	435	1161	978	2159	332	167	85	148	194
Sylvaemus sp.	–	1			–	–	1	–	–	–	4	1
Σ (number of remains)	266	1446	1176	828	2488	2284	4791	860	318	175	357	441
N (number of taxa)	15	19	17	17	20	18	22	16	13	11	20	21

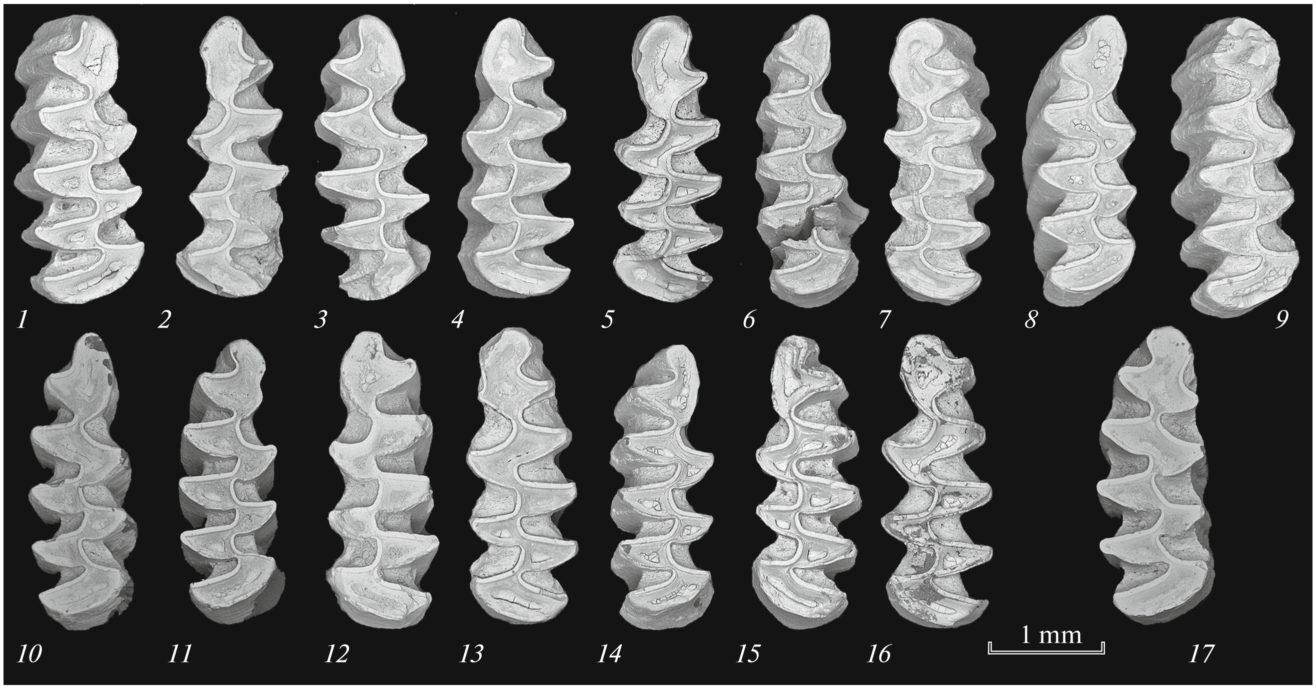

Fig. 2. Teeth of voles from the deposits of the D4 square of Imanay Cave. cf. *Microtus* (*Stenocranius*) *gregaloides* (Hinton 1923): (*1*, *2*) depth of 40–50 cm; (*3–5*) 50–60 cm; (*6–9*) 70–80 cm; (*10*, *11*) 80–90 cm; (*12*) 90–100 cm; (*13–15*) 100–110 cm; (*16*) 110–120 cm. cf. *Microtus* (*Terricola*) *arvalidens* Kretzoi 1958: (*17*) 80–90 cm.

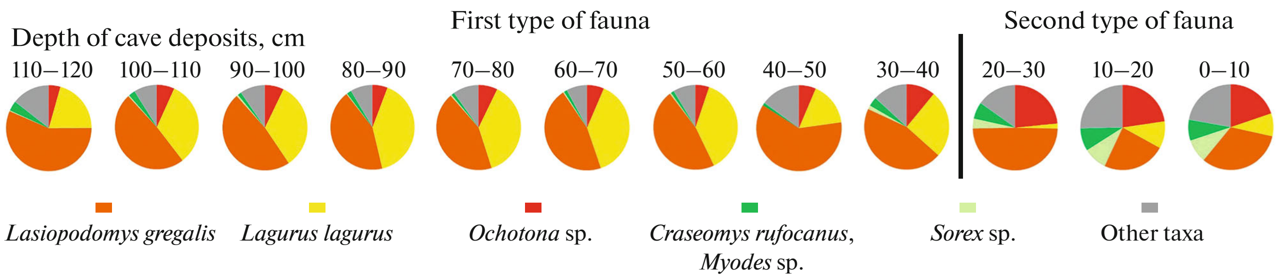

Fig. 3. Two types of fossil fauna differentiated by the ratios of the number of skeletal remains of the dominant taxa of small mammals. Imanay Cave, D4 square.

The fauna of small mammals from the studied deposits can be conditionally divided into two types according to the proportion of dominant species (Fig. 3). In the first type of fauna (deposits of conditional horizons from a depth of 30–120 cm), the teeth of narrow-headed voles and steppe lemmings constitute the bulk of the identified teeth; forest species are represented by single teeth of red-backed voles and fragments of the lower jaws of shrews. The second type is typical for the deposits of the upper conditional horizons (depth 0–30 cm), where the teeth of narrow-headed voles and pikas dominate, and conventionally forest species (red-backed voles and shrews) are common.

Taxonomic Notes

Order Rodentia Bowdich 1821

Family Cricetidae Fischer von Waldheim 1817

Subfamily Arvicolinae Gray 1821

Genus *Microtus* Schrank 1798

Subgenus *Stenocranius* Kastshenko 1901

Microtus (*Stenocranius*) *gregalis* Pallas 1779

Material. 1123 isolated first lower molars (m1) were identified, 236 m1 were measured.

Description and comparison. Rootless teeth with deposits of external cement in the reentrant angles. "Microtus"-type of enamel (the thickness of the enamel is noticeably thinner on the posterior walls of the loops). Tooth length ranges from 2.15 to 3.30 mm.

In the studied samples of teeth, a similar distribution of frequencies for all groups of morphotypes was recorded (Fig. 4; Table 2). The samples are dominated

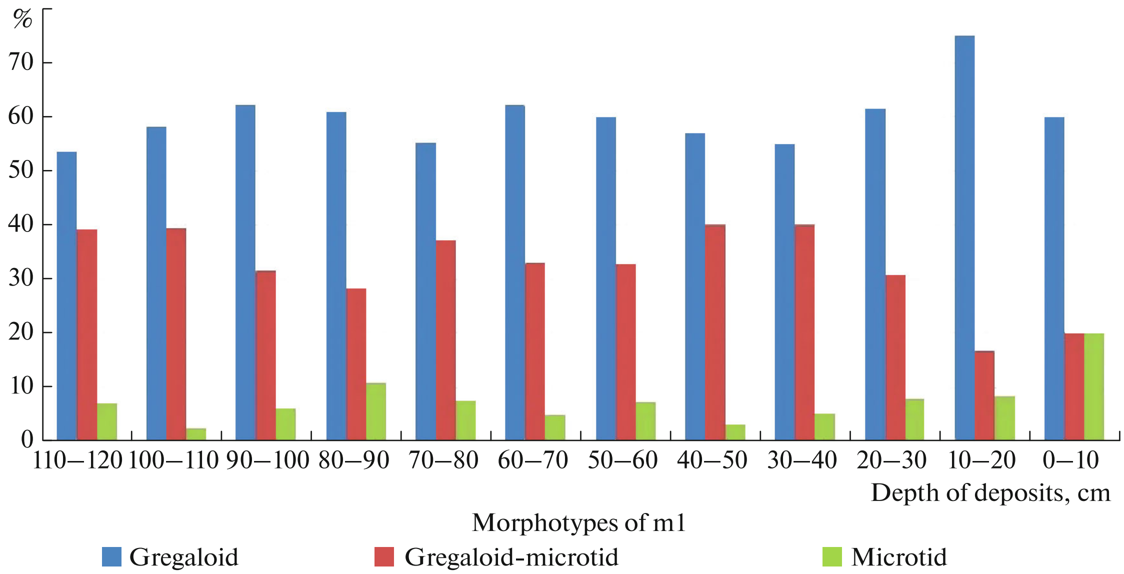

Fig. 4. Ratio of morphotypes of the first lower molars (m1) of *Microtus* (*Stenocranius*) *gregalis*. Imanay Cave, D4 square.

(more than 50% of all m1 species) by teeth of a simple structure of an unpaired loop of the antheroconid complex, without a reentrant angle on the buccal side ("gregaloid" morphotype). Teeth with a complex structure of the loop, on the buccal side of which the reentrant angle is more than 20° ("microtid" morphotype), are not numerous. Teeth with complex morphs account for about 10% or less, except for a sample from the uppermost horizon. The predominance of the "gregaloid" morphotype was also recorded in Late Glacial–Early Holocene samples of narrow-headed vole teeth from the Baislan-Tash cave and Maksyutovsky grotto, located approximately 30 km southeast of Imanay Cave on the right bank of the Belaya River (Table 2). Previously, the dominance of teeth with the "gregaloid" morphotype was recorded in samples of teeth from deposits of the Middle Pleistocene and the first half of the Late Pleistocene of the Southern Urals (Smirnov et al., 1990; Fadeeva et al., 2019; Yakovlev, 2020). However, Late Glacial samples of teeth of the species from localities in the northern mountainous part of the Southern Urals have a slightly different morphological appearance with a predominance of the "gregaloid-microtid" morphotype (Smirnov et al., 1990). Teeth samples of modern subspecies of narrow-headed voles from the territory of the Urals (with the exception of the Yamal sample) are dominated by teeth of a complex structure ("microtid" morphotype) (Golovachev et al., 2001).

The limits of tooth length from fossil samples from the localities in the southern part of Southern Urals (Klimovka, Maksyutovsky grotto, Baislan-Tash and Imanay caves) are 2.15–3.30 mm. The lower limit of the size range is higher (2.30 mm) in the fossil samples from the localities in the northern part of the Southern Urals (Gruzdevka, Gornova, Krasnyi Yar, Ignatievskaya, and Prizhim II caves, Ustinovo canopy). The size limits of tooth length in fossil narrow-headed voles of the Southern Urals are closest to those of the modern sample of the northern subspecies *M. g. gregalis* from the vicinity of Mount Krasnyi Kamen' (Northern Urals) (Table 2).

Genus Lagurus Gloger 1841

Lagurus lagurus (Pallas 1773)

Material. 4954 isolated molars were identified, 233 m1 were measured.

Description and comparison. Rootless, cementless molars. Enamel of the microtus type. The size range of teeth length ranges from 2.10 to 2.65 mm.

The samples of the first lower molars of steppe lemmings from the deposits of Imanay Cave differ from all previously studied fossil samples of the species from the territory of the Southern Urals by the high proportion (28.0–51.6%) of the "transiens" morphotype, which is characteristic of the teeth of the Early–Middle Pleistocene species *Lagurus transiens* Janossy 1962 (Fig. 5; Table 3). For the territory of the Urals, fossil samples of thte teeth of steppe lemmings were previously found, where the maximum number of teeth of the "transiens" structure constitutes no more than a third of the number of all teeth in the sample (Table 3).

The first lower molars of steppe lemmings from the deposits of Imanay Cave differ from other fossil samples of the species from the Southern Urals by their relatively small size (Table 3). Similar m1 sizes are typical for modern steppe lemmings from the territories of the Volga region and Kazakhstan (Maleeva and

Table 2. Ratio of morphotypes and sizes of the first lower molar (m1) in the teeth samples of *Microtus* (*Stenocranius*) *gregalis* from fossil and modern localities of the Urals

Locality	Layer, depth, cm	Radiocarbon dating/period	N	Morphotypes m1			Length of m1 (mm) (minimum–average–maximum [n])	Source
				gregaloid	gregaloid-microtid	microtid		
Yamal (*M. g. major*)	–	Modern times	59	6.8	55.9	37.3	2.68–2.96–3.30 [59]	Golovachev et al., 2001
Krasnyi Kamen' (*M. g. major*)	–		109	–	23.8	76.2	2.38–2.69–3.05 [107]	
Payuta (*M. g. major*)	–		81	1.2	42.0	56.8	2.55–2.94–3.23 [81]	
Bredy (*M. g. gregalis*)	–		42	–	33.3	66.7	2.25–2.51–2.90 [42]	
Kamyshlovsky (*M. g. gregalis*)	–		42	4.7	40.5	54.8	2.08–2.50–2.88 [42]	
Ustinovo	L. 1	4380 ± 170 IPAE 47	29	6.9	65.5	27.6	2.30–2.61–2.80 [22]	Smirnov et al., 1990
	L. 3	12400 ± 300 IPAE 49	24	20.8	55.3	23.9	2.35–2.75–3.10 [16]	
Prizhim II	L. 1–3	16650 ± 400 IPAE 32, 17070 ± 1017 IEMAE 700	68	33.8	53.0	13.2	2.35–2.74–3.15 [67]	
	L. 6–8	21085 ± 630 IPAE 37	86	30.2	55.9	13.9	2.40–2.74–3.25 [83]	
Ignatievskaya II	L. 2	14038 ± 490 IEMAE 366	177	30.5	54.2	15.3	2.53–2.69–3.25 [175]	
Baislan-Tash	225–450	9616 ± 62 IEMAE 1340, 13560 ± 250 GIN 10853	61	57.4	27.9	14.7	2.50–2.73–3.13 [44]	Yakovlev et al., 2006; Danukalova et al., 2011; this article
Maksyutovsky grotto	L. 2	15650 ± 150 SOAN 7755	27	44.4	40.7	14.8	2.50–2.71–3.02 [15]	
Imanay D4	50–60	13255 ± 60 IGAN 9116	345	60.0	32.8	7.2	2.15–2.65–3.30 [141]	
	100–110	17100 ± 50 IGAN 9117	122	58.2	39.3	2.5	2.30–2.63–2.95 [95]	
Ignatievskaya V excavation of 1985	160–195	>27500 IPAE 21	34	47.1	41.2	11.7	2.40–2.71–3.15 [34]	Smirnov et al., 1990
	195–255		64	39.1	53.0	7.8	2.30–2.66–3.10 [64]	
	255–315		39	61.5	30.8	7.7	2.35–2.61–3.00 [40]	
	315–400		201	42.8	50.7	6.5	2.25–2.60–3.30 [196]	
excavation of 2014	325–400	End of the Middle Pleistocene (?)–beginning of Late Pleistocene	594	52.1	37.1	10.8	2.30–2.64–3.30 [254]	Fadeeva et al., 2019
	400–520		311	73.2	23.2	3.6	2.20–2.58–2.90 [105]	
Gornova	–	First half of Late Pleistocene	34	38.2	32.4	29.4	2.35–2.61–2.87 [13]	Yakovlev, 2020
Klimovka	–	Middle Pleistocene	27	37.1	44.4	18.5	2.3–2.67–3.2 [15]	
Gruzdevka	–	Middle Pleistocene	21	52.4	23.8	23.8	2.5–2.71–3.0 [7]	
Krasnyi Yar	–	First half of Middle Pleistocene	77	59.7	27.3	13.0	2.45–2.68–3.0 [40]	

A dash indicates the absence of data. N is the number of teeth in samples for morphotypic analysis, and n is the number of teeth in samples for morphometric analysis.

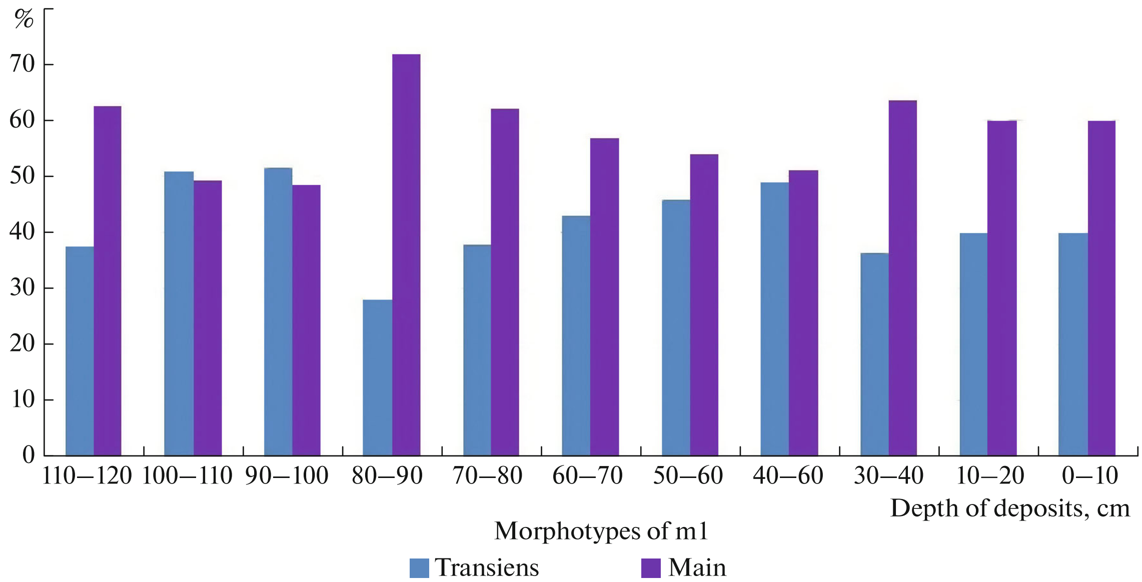

Fig. 5. Ratio of morphotypes of the first lower molars (m1) of *Lagurus lagurus*. Imanay Cave, D4 square.

Vorob'eva, 1973); however, in these samples, the proportion of teeth of the "transiens" morphotype is significantly smaller (<7%).

DISCUSSION

Imanay Cave is included in the southern group of caves in the mountainous part of the Southern Urals, located in the latitudinal areas of the Belaya and Nugush river valleys (Danukalova et al., 2011, 2020). For this territory, the small mammal fauna of the second half of the Late Pleistocene and Middle and Late Holocene has been known so far (Danukalova et al., 2002; Yakovlev, 2003, 2014; Yakovlev et al., 2004, 2006; Bachura and Kosintsev, 2010; Kosintsev and Bachura, 2013; Kosintsev et al., 2018; etc.). The Late Pleistocene and Middle Holocene fauna of this territory is dominated by narrow-headed voles, steppe lemmings, and pikas, while the Late Holocene fauna is dominated by red-backed voles. At the end of the Late Holocene, white-toothed shrews, pikas, jerboas, gray hamsters, Eversmann's hamsters, mole voles, yellow steppe lemmings, steppe lemmings, and narrow-headed voles disappeared from this territory. Currently, only representatives of forest and intrazonal species of small mammals inhabit this region (Danukalova et al., 2011).

Two types of fauna of Imanay Cave (Fig. 6) identified by the share of dominant species were compared with the Late Glacial and Holocene fauna of other localities situated on the banks of the Belaya River, about 30 km southeast of the cave.

The first type of fauna (lower and middle conditional horizons) of Imanay Cave and the fauna of the lower deposits of the Maksyutovsky grotto (layer 2, 15650 ± 150 SOAN-7755) (Danukalova et al., 2011) were formed in the Late Glacial and are characterized by a sharp predominance of steppe rodent species, narrow-headed voles, and the codominance of the steppe lemming. The bone remains of these rodent species amount to 70.9–84.4% in the middle and lower deposits of Imanay Cave and 62.8–68.6% in the deposits of the Maksyutovsky grotto.

The fauna of the second type (upper conditional horizons) of Imanay Cave and the fauna of the third (135–225 cm) and fourth (225–450 cm) layers of the studied deposits of Baislan-Tash Cave (52°54′ N, 56°51′ E) are very close. In the Baislan-Tash cave, the third layer is dated to the Middle Holocene (7140 ± 170 GIN-10854), while the lowest fourth layer is assigned to the Late Glacial–Early Holocene (9616 ± 62 IEMAE-1340; 13560 ± 250 GIN-10853) (Yakovlev et al., 2006). The compared faunas are characterized by the dominance of narrow-headed voles, codominance of pikas and steppe lemmings, and significant proportions of shrews and red-backed voles.

The presence of steppe, forest, intrazonal, meadow, and semi-desert rodent species is characteristic of all the examined faunas of the southern group of the southern mountainous part of the Southern Urals. Only one tooth of the tundra species *Lemmus sibiricus* was found in the upper deposits of Imanay Cave. In these upper deposits of the cave, as well as in the deposits of Baislan-Tash Cave, the proportion of bone remains of meadow and forest species is about 30% or more (Fig. 7). Among the skeletal remains of small mammals in the middle and lower layers of deposits of the D4 square of Imanay Cave, a significant proportion consists of steppe species (83.0–92.2%), while the number of remains of forest and

Table 3. Ratio of morphotypes and sizes of the first lower molar (m1) in the samples of *Lagurus lagurus* teeth from the Southern Urals

Locality	Layer, depth, cm	Radiocarbon dating/period	*N*	Morphotypes: transiens	Morphotypes: main – transitional	Morphotypes: main – lagurus	Length of m1 (mm) (minimum–average–maximum [*n*])	Source
Volga river region	–	Modern times	29	6.7	66.7	26.6	2.17–2.40–2.69 [29]	Maleeva and Vorob'eva, 1973
North Kazakhstan	–		30	6.7	73.3	20.0	1.99–2.36–2.69 [30]	
Baislan-Tash	225–450	9616 ± 62 IEMAE 1340; 13560 ± 250 GIN 10853	29	21.1	39.5	39.5	2.32–2.63–3.00 [29]	Yakovlev et al., 2006; Danukalova et al., 2011; this study
Maksyutovsky grotto	L. 2	15650 ± 150 SOAN 7755	8	12.5	25.0	62.5	2.55–2.69–2.90 [6]	
Imanay D4	50–60	13255 ± 60 IGAN 9116	174	43.0	42.3	14.7	2.10–2.45–2.65 [86]	
	100–110	17100 ± 50 IGAN 9117	59	50.8	28.8	20.3	2.20–2.45–2.65 [35]	
Ignatievskaya V (excavation of 2014)	325–400	End of Middle Pleistocene (?)–beginning of Late Pleistocene	70	34.3	17.1	48.6	2.25–2.52–2.90 [36]	Fadeeva et al., 2019
	400–430		19	21.1	21.1	57.9	2.45–2.54–2.70 [6]	
Gornova	–	First half of Late Pleistocene	39	2.6	30.8	66.6	2.35–2.56–2.75 [25]	Yakovlev, 2015
Klimovka	–	Middle Pleistocene	16	18.8	31.3	50.0	2.30–2.65–2.87 [10]	
Gruzdevka	–	Middle Pleistocene	18	16.7	16.7	66.7	2.27–2.55–2.78 [9]	
Krasnyi Yar	–	First half of Middle Pleistocene	519	18.1	41.4	40.5	2.20–2.61–3.02 [100]	

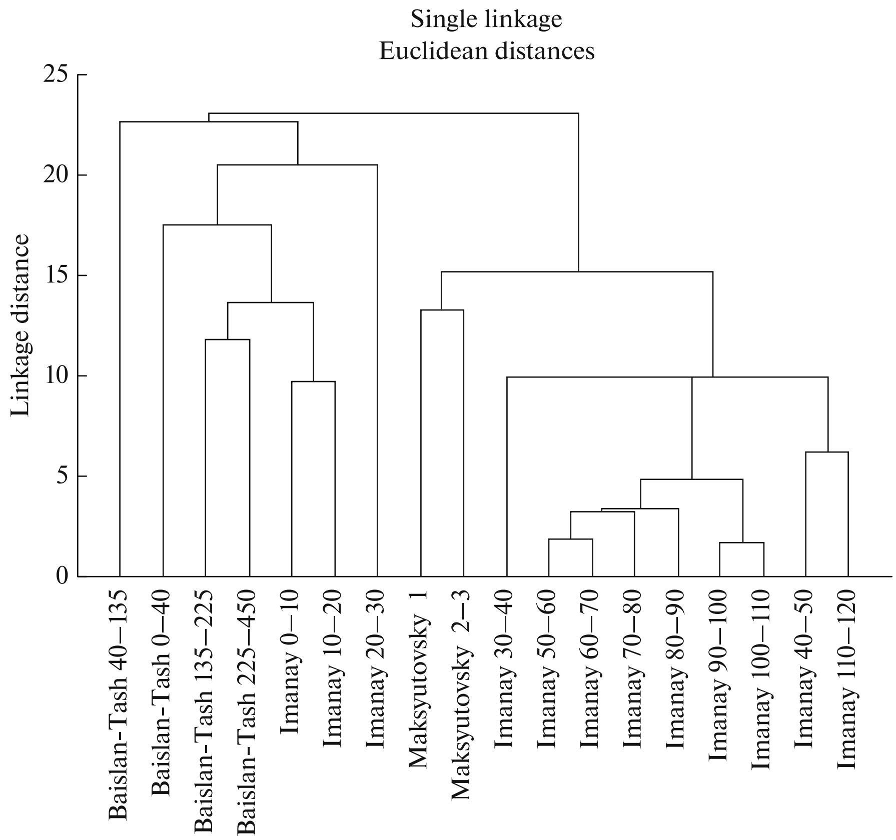

Fig. 6. Cluster analysis of fossil faunas of the southern group of caves in the mountainous part of the Southern Urals (Imanay Cave, D4 square (depths in cm); Baislan-Tash Cave (depths in cm); Maksyutovsky grotto (numbers of layers).

meadow representatives is relatively small (2.2–6.5%) (Fig. 7). Such ratios of the skeletal remains of species from different ecological groups from these deposits of Imanay Cave are closer to those from the deposits of the Maksyutovsky grotto (steppe, 74.6%; forest and meadow, 5.3–16.6%). The large proportion of intrazonal species (18.7%) in the Late Glacial deposits of the Maksyutovsky grotto compared to that in the middle and lower deposits of Imanay Cave (up to 6.1%) is probably due to the location of the grotto on the river bank.

The morphotypic characteristics of the samples of fossil first lower molars of the narrow-headed vole from Imanay and Baislan-Tash caves and Maksyutovsky grotto are very similar (Table 2). The morphology of the teeth of this species from deposits of the second half of Late Pleistocene from the localities of the southern group of caves in the mountainous part of the Southern Urals (Imanay, Bayslan-Tash, Maksyutovsky grotto) is similar to that from the deposits of the Middle Pleistocene and the first half of the Late Pleistocene from the localities of the northern group of plain and mountainous parts of the Southern Urals (Gruzdevka, Krasnyi Yar, Gornova, Ignatievskaya cave). All these samples of fossil teeth of the species are characterized by a great proportion of teeth of a simple structure of the anteroconid segment, which distinguishes them from the fossil samples of the second half of Late Pleistocene–Holocene of the northern group of localities (Ignatievskaya Cave, Prizhim II, Ustinovo) and modern samples of teeth of narrow-headed voles from the territories of the Northern and Southern Urals.

Samples of the first lower molars of steppe lemmings from the deposits of Imanay Cave are characterized by a high proportion of "transiens" morphotype teeth (28.0–59.7%). The teeth of this morphotype make up about 30% of the combined sample of teeth of the species from the deposits of the first half of the Late Pleistocene of Ignatievskaya Cave. The proportion of such teeth in the deposits of Baislan-Tash Cave and the Maksyutovsky grotto is significantly lower. In addition, the teeth of steppe lemmings from the deposits of Imanay Cave are smaller in size compared to the teeth from all other previously studied samples from the Southern Urals. Additional studies are required to understand the reasons for the significant difference in the morphological characteristics of the first lower molars of steppe lemmings from the Late Pleistocene localities of the Southern Urals.

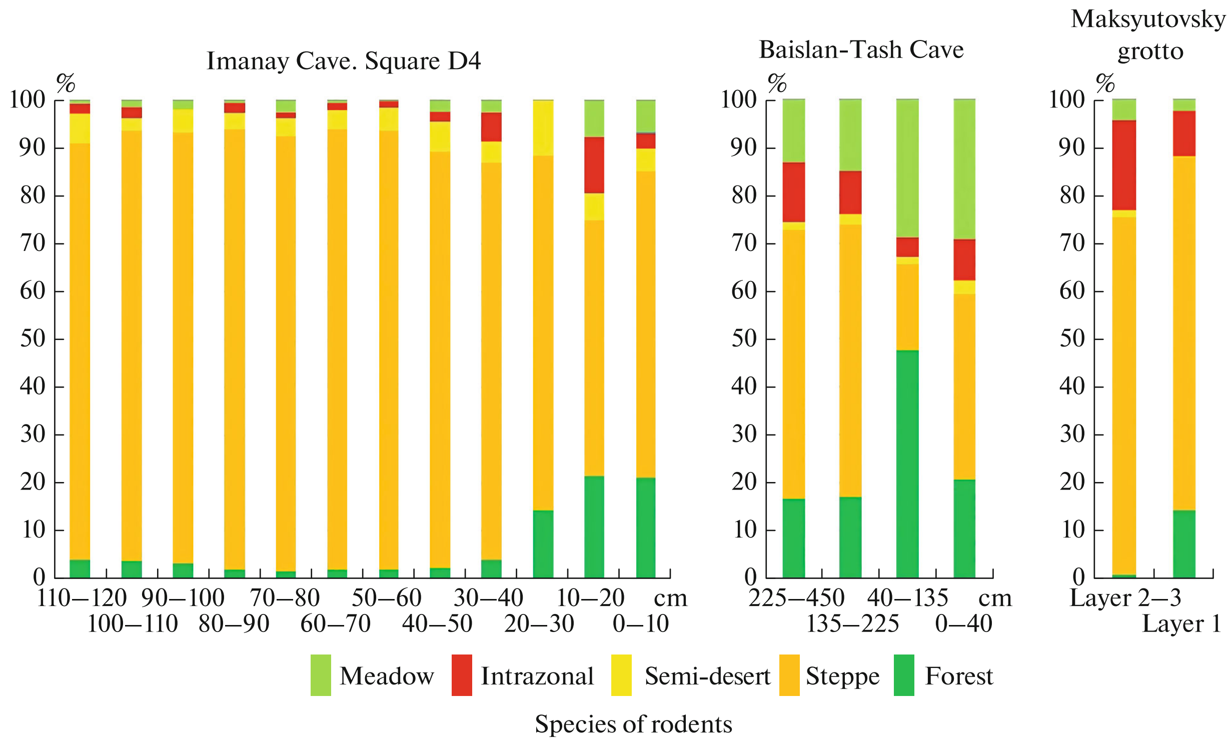

Fig. 7. Correlation between the amounts of bone remains of rodents from various ecological groups (in accordance with their modern habitats) in the deposits of the southern group of caves in the mountainous part of the Southern Urals.

CONCLUSIONS

Thirty-two taxa of mammals from four orders (Eulipotyphla, Chiroptera, Lagomorpha, and Rodentia) were identified in the studied deposits of Imanay Cave. A single dominant species, *Microtus gregalis*, was found in all conditional horizons of the Imanay Cave deposits. The lower and middle parts of the deposits are characterized by the codominance of *Lagurus lagurus*; in the upper horizons of the deposits, another codominant is *Ochotona* sp. The lower and middle parts of the deposits of the Imanay cave, judging by radiocarbon dates, were formed in the Late Glacial period. The composition and structure of the fauna from these deposits (the first type of fauna) are very close to those of the Late Glacial fossil fauna of the Maksyutovsky grotto. The fauna (second type) of the upper conditional horizons of the cave comprises a relatively higher proportion of forest species, similar to that in the fauna of the lower horizons of the deposits of Baislan-Tash Cave (Late Glacial–Early Holocene). Samples of the first lower-molar teeth of the narrow-headed voles from the Late Glacial deposits of the southern group of localities in the mountainous part of the Southern Urals (Imanay and Bayslan-Tash caves, Maksyutovsky grotto) are characterized by a high proportion of teeth of a simple structure ("gregaloid" morphotype). However, the samples of teeth of the steppe lemmings from the deposits of Imanay Cave differ from other Late Glacial samples of the Southern Urals by their small size and the relatively high proportion of teeth of the "transiens" morphotype. The features of fossil fauna of Imanay Cave also include findings of teeth with a "pitymys" structure of the chewing surface, which is characteristic of ancient (Early–Middle Pleistocene) species of voles, but their preservation, identical with the teeth of other species of small mammals from the deposits, excludes the version of the material being redeposited.

Based on the compositions and structures of the distinguished types of fauna, it can be concluded that, in the southern part of the Ural Mountains in the Late Glacial, open steppe landscapes existed, which, presumably, at the end of this period or in the early Holocene were transformed into forest–steppe landscapes.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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