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PAST DISTRIBUTION OF THE MARMOTS IN THE SOUTH-EAST OF WESTERN SIBERIA

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Three marmot species currently inhabit the south-east of Western Siberia: steppe marmot (*Marmota bobak* Müller 1776), gray marmot (M. baibacina Kastschenko 1899) and forest-steppe marmot (*M. kastschenkoi* Stroganov et Yudin, 1956). We reconstructed the past ranges of these three species using original and previously published data on marmot remains from 43 Holocene localities and records of marmot historical distribution. Species discrimination of marmot remains was conducted using discriminant analysis of skull morphometric characteristics. Results suggest that throughout the Holocene, the northern extent of marmot distribution reached the southern limit of the forest zone. In the Ob river valley, it stretched above the treeline and then crossed the Yenisei River at 56° N. At the end of the Late Holocene the northern limit of marmot distribution in the Yenisey valley shifted to the south-west. Discriminant analysis of remains from the Aidashinskaya cave of Lower Chulym (56°12' N; 90°18' E) suggests the presence of gray and forest-steppe marmots. Neither species now inhabits the area. One skull and mandible from the Aidashinskaya cave was attributed to gray marmot, and one skull and three mandibles were attributed to forest-steppe marmot. We can assume that in the Late Holocene the range of the gray marmot has retreated to the south-east and the range of the forest-steppe marmot has shifted to the west. The eastern boundary of the steppe marmot was most likely limited to the Irtysh river valley. Range fragmentation in all three species was caused by spread of farming in the last 100-150 years and extirpation of remaining populations of marmots.

The current distribution of the three marmot species, steppe marmot, gray marmot, and forest-steppe marmot, extend across or stop in the territory of the south-east of Western Siberia and adjacent regions of Altai and Kazakhstan. The eastern part of the steppe marmot range extends from the flat steppes of Central Kazakhstan to the left bank of Irtysh river, where it overlaps with the western part of the gray marmot range. The most northern colonies of gray marmot occur in the Northern Altai near the Cherga settlement (51°34' N). Further to the east the gray marmot's range extends to the Abakan riverhead and the south-east districts of the Tyva Republic (Bibikov&Berendyaev, 1978; Ognev, 1947). The forest-steppe marmot's range extends along the right bank of the Ob river beginning at the Tom river mouth (56°N) in the north and continuing to the south boundary of the forest-steppe zone, at the confluence of the Biya and Katun' rivers (52°N). At the present time, there is no overlap between its range and that of the gray marmot (Taranenko, 2011). The Mongolian marmot (*Marmota sibirica* Radde 1862) occupies an adjacent region of southern Tyva and the Mongolian Altai (Gromov&Erbaeva, 1995).

The problem of species identification arises during the investigation of subfossils of the *Marmota* genus obtained from the territory of south-east Western Siberia. The difficulty is due to the morphological similarity of steppe, gray, and forest-steppe marmots, who are phylogenetically close to each other. In the past, some authors regard this taxon as one species with two subspecies – steppe and gray marmots (Bibikov, 1986). Others

referred to steppe and gray marmots as separate species but considerfed forest-steppe marmot a subspecies of gray marmot (Laptev&Yudin, 1952; Gromov&Erbaeva, 1995), or even as the same species (Ognev, 1947). Recent investigations have shown that genetically, steppe, gray, and forest-steppe marmots represent three closely related but still taxonomically separate 'bobak'-type species (Brandler et al., 2010).

Modern representatives of the Marmota genus morphologically differ by fur color and density, length of awn hairs, skull structure, and by the form of their tooth crowns (Gromov, 1965; Galkina et al. 1970; Galkina et al., 2005). Because this study worked with subfossil material not all of these characteristics could be used for species identification. Assessment of morphotypic and morphometric features of the cranium and mandible is the optimal diagnosis method for identifying steppe vs grey marmots (Gasilin&Kosintsev, 2011) . This method was also used to identify potential members of the third species – forest-steppe marmot - samples from which were also present in the ofsubfossil material from the study area. The range of the Mongolian marmot is further to the south-east (Fig.1) so it was not included in the analysis.

The aim of the study was to investigate the history of the range of the Marmota genus with a focus on three representative species, steppe marmot, gray marmot, and forest-steppe marmot, in the territory of the south-east of Western Siberia during the Holocene.

Materials and methods

The study area was in the subtaiga, forest-steppe, and steppe zones of the south-eastern part of the Western Siberian Plain, the Salair Ridge, the Kuznetsk Alatau, and the East Sayan Mountains also (Fig.1).

We investigated subfossil materials from zoogenic deposits and mixed complexes from deposits in karst cavities, and from archaeological sites.

Zoogenic material was dated using the base of deposit's stratigraphy data and by the accompanying fauna subfossils. Some of the material collected had a very wide date range – the whole Holocene (10300–300 years B.P.). Other samples were dated with the help of archaeological methods (Troitskaya&Novikov, 2004). Some sites possessed radiocarbon dates (Table 5). The dates of marmot samples were correlated with climate-stratigraphy subdivisions of the Holocene (Khotinsky et al., 1991) for analysis. The subfossil bones of marmots from a total of 45 sites were explored (Fig.1).

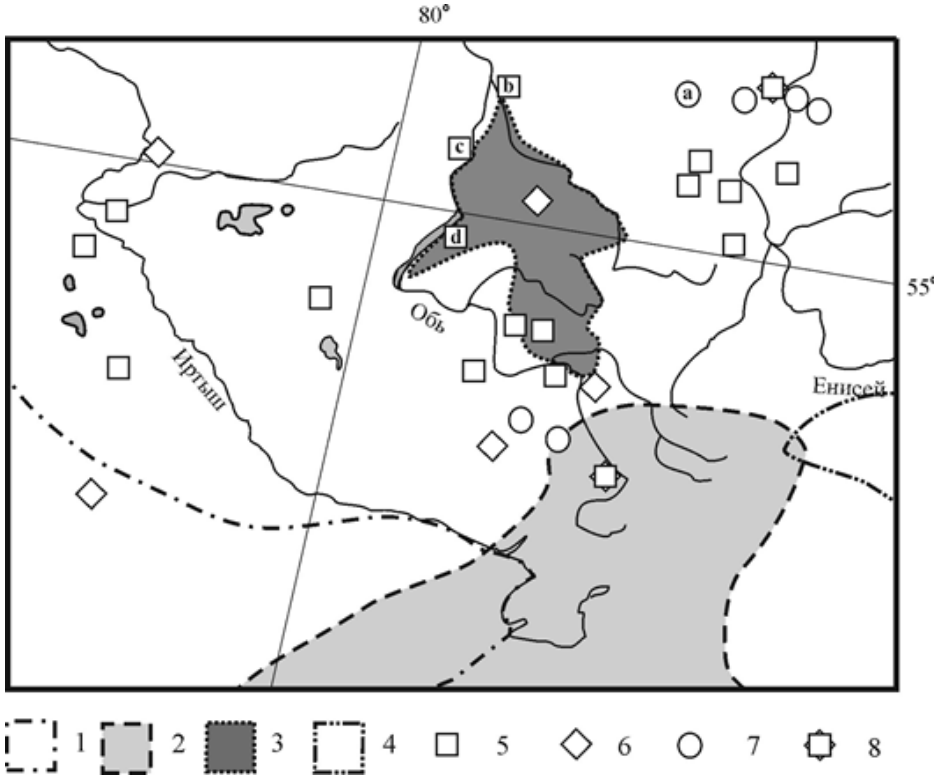

Figure. 1. *Modern boundaries of the ranges of representatives of the genus Marmota and the location of their remains in the southeast of Western Siberia. 1 - north-eastern border of the range of steppe marmot (Marmota bobak); 2 - northern border of the range of gray marmots (M. baibacina); 3 - the range of forest-steppe marmot (M. kastschenkoi); 4 - the western border of the range of Mongolian marmot (M. sibirica); 5 - samples of marmots dating from the late Holocene, Subboreal period; 6 - samples of marmots dating from the Subatlantic period of the Holocene; 7 - samples of marmots dating from the late Pleistocene-Holocene; 8 - samples of marmots dating from the Subboreal and Subatlantic periods of the Holocene; a - Aidashinskaya cave; b - Chekist settlement; c - Elovskoye settlement; d - Milovanovo 3 settlement.*

To develop a method for identifying recent species we used craniums with mandibles from 68 steppe marmot (from the collection of the Zoological Institute of the Russian Academy of Sciences [RAS]), 58 gray marmot(from the collection of the Museum of the Institute of Plant and Animal Ecology, Ural Branch of the RAS and the Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch of the RAS [ISEA SB RAS]) and 51 forest-steppe marmot(from the collection of the Museum of ISEA SB RAS and Zoological Museum of Tomsk State University). We took 20 measurements (Fig. 2) from the skulls (Gasilin&Kosintsev, 2011). The set of cranial measurements (Gasilin&Kosintsev, 2011) was supplemented by measurements 26–29 (Fig. 3) whereas measurements 4–7 were not taken and were not analyzed because it is rare to find subfossil mandibles with teeth.

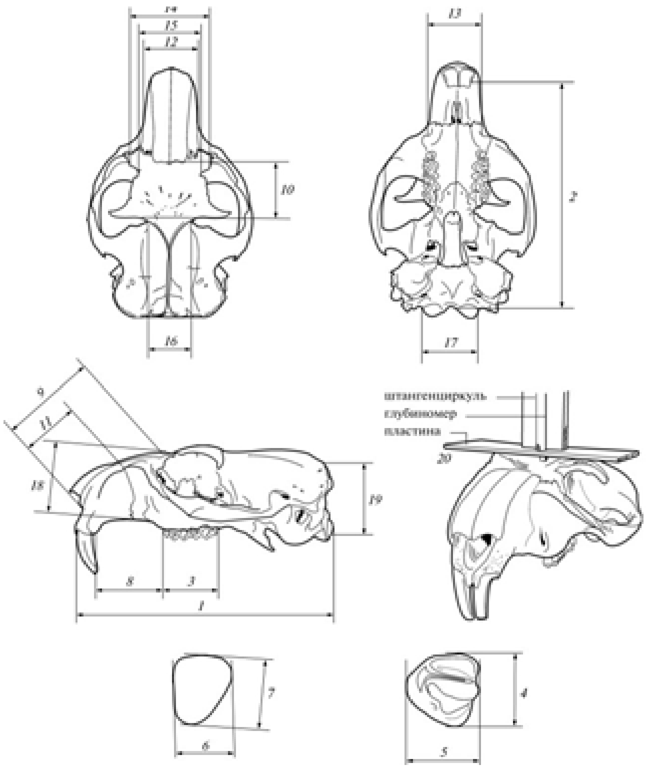

Fig. 2. *Skull measurements used for this study (Gasilin &Kosintsev, 2011).*

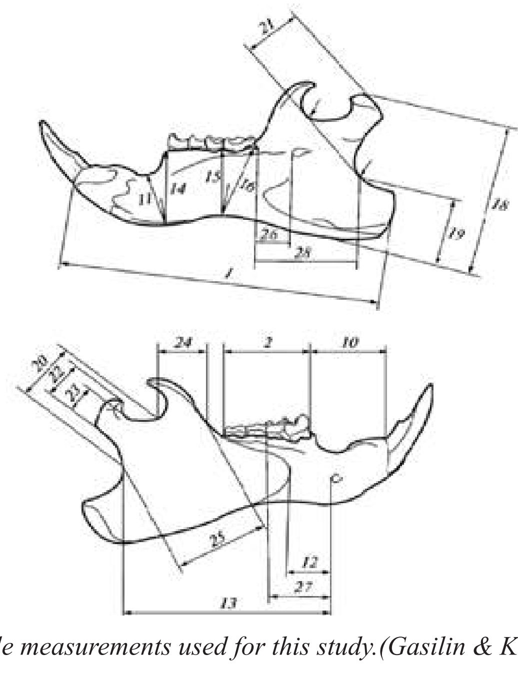

Fig. 3. *Mandible measurements used for this study.(Gasilin & Kosintsev, 2011)*

The samples used for species identification included the whole and fragmented skulls (n=4) and mandibles (n=18) from four sites located in the territory of the Russian Federation. All skulls and 14 mandibles were found in Aidashinskaya cave, located in Krasnoyarsk region ner Achinsk town (56°12'N; 90°18'E). Osteological material from this cave covered a wide date range - the whole Holocene (Ovodov, 1980). Four mandibles were found in archaeological sites from the Late Bronze Age - the end of Subboreal period (SB3, 3200-2600 years B.P.) - in the settlements Elovskoe (n=2), Chekist (n=1) and Milovanovo 3 (n=1). The settlement Elovskoe is located in Kozhevnikovsky district of the Tomsk region (55°34'N; 83°25'E); Chekist is located in the Tomsk district of Tomsk region (56°22'N; 84°29'E), and Milovanovo 3 in the Ordynsky district of the Novosibirsk region (54°5'N; 81°33'E).

Measurements were conducted with the help of electronic caliper accurate to 0.1 mm. The software package Statistica 6 was used for statistical calculations.

Discriminant analysis with standard and single-step inclusion of variants was used to determine the species of recent and subfossil samples. The sexual dimorphism of marmots by dimensional features was not greater than the interspecies differences (Cardini, 2004). Thus, sexual dimorphism did not interfere with the results of species identification, so sex identification was not included in analysis. Statistical models for species classification were specially built for almost every subfossil cranium or mandible because most samples were fragmented. Besides morphometric characteristics, lacrimal bone morphotype analysis of the subfossil cranium was also used for species identification(Fig. 4).

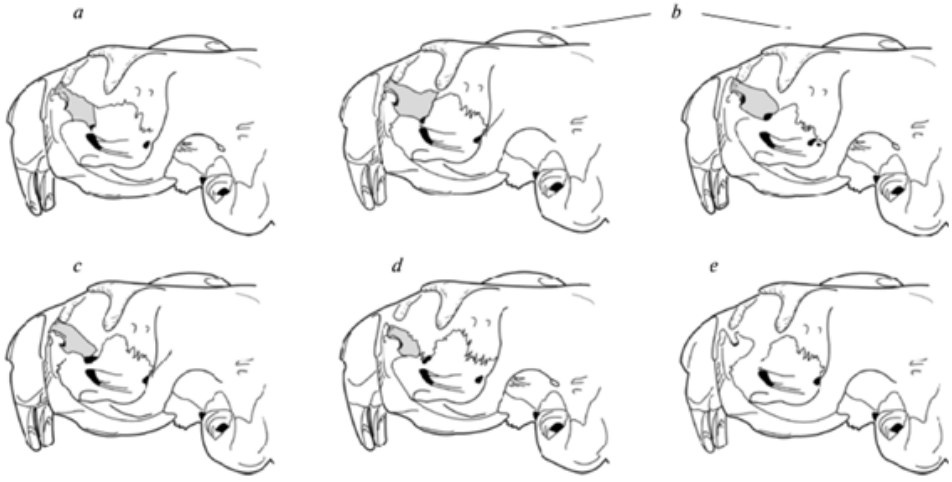

Fig. 4. *Morphotypes of the position of the lacrimal bone in representatives of the genus Marmota used in this study (Gasilin & Kosintsev, 2011)*

Results and discussion

The diagnostics of recent representatives of *Marmota*

Morphotypic characteristics. The results of the analysis showed that lacrimal bone morphotypes *a, b, c, d* and *e* occurred in steppe marmot samples, morphotype b in gray

marmot samples (Gasilin&Kosintsev, 2011) and morphotypes *a, b* and *c* in forest-steppe marmots. The frequencies of these morphotypes in forest-steppe and steppe marmots was virtually equal while b was the most common morphotype among all three species (Table 1).

Table 1. *Percent of samples showing each morphotype of lacrimal bone position for each marmot species; steppe (Marmota bobak), gray (M. baibacina) and forest-steppe (M. kastschenkoi) .*

Species	% of samples showing each morphotype					# of samples
	a	b	c	d	e	
M. bobak	14±2,6	68	9±2,2	8±2,1	1±0,1	173
M. baibacina	0	100±0	0	0	0	218
M. kastschenkoi.	18±5,3	74±6,1	8±3,8	0	0	52

Morphotypes d and e appear to be diagnostic of steppe marmot. The absolute predominance (100%) of morphotype b in gray marmot suggests that the occurrence of this morphotype can be used to determine the presence of gray marmots. An occurrence of >75% of samples with the b morphotype (68% and 74% of steppe and forest-steppe marmots had morphotype b in the sample population) may indicate the presence of gray marmots.

Morphometric characteristics. Metric data from recent marmot samples constituted learning groups used in standard and single-step with inclusion discriminant analysis. Correct identification of sampling on the total assortment of characteristics both for cranium and mandible was 97–98%. The validity of the resulting statistical model was examined with the help of test groups that included three mandibles of known species. All test samples were identified correctly. Thus, the model appears to be effective in discriminating between the three species based on cranium and mandible measurements. The degree of differentiation of forest-steppe marmot from grey and steppe marmots based on cranium and mandible measurements was close to 100% (Fig. 5).

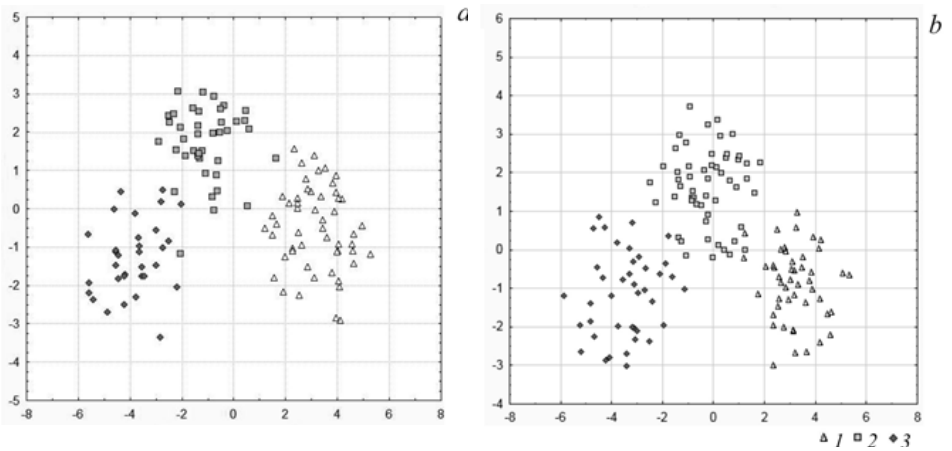

Fig. 5. *Distribution of recurrent cranium (a) and mandible (b) measurements in the space of discriminant axes: 1–steppe marmot (Marmota bobak); 2–gray marmot (M. baibacina); 3–forest-steppe marmot (M. kastschenkoi).*

Determining the species of subfossil cranium remains.

Lacrimal bones were not common in the sampled subfossil skulls and only displayed morphotype b. Thus, it was not possible to determine marmot species based on the lacrimal bone morphology of the sample population.

Using morphometric characteristics, two craniums and four mandibles from two sites were identified to species level. Samples from the Chekist and Milovanovo sites could not be identified to species level. The marmot mandibles from the Elovskoe settlement belonged to forest-steppe marmot. Of particular interest were the subfossil remains from Aidashinskaya cave. Two species were identified there, with one cranium and one mandible belong to gray marmots, and one cranium and three mandibles to forest-steppe marmots.

The area reconstruction of the *Marmota* genus.

Marmot remains were found at one Early Holocene site (9680–8860 years B.P.), 14 Middle Holocene sites (3800–2600 years B.P.), seven Late Holocene sites (2500–300 years B.P.), and 23 sites dated from sometime during the Holocene.

The most northern occurrence of *Marmota* from Priirtyshje was documented at the Isakovsky 1 burial ground (55°27'N), dated by archaeological and radiocarbon dating as from beginning of the Subatlantic period of the Late Holocene. The most northern occurrence of *Marmota* from Priobye was from the Chekist settlement (56°36'N), dated from the end of the Subboeral period (SB3, 3200–2600 years B.P.) of the Holocene. Sites of *Marmota* bones from the Yenisei river basin were found at about 56°20'N (the caves Eleneva and Karaul'naya 1), and dated as Early (PB–BO, 9600-8000 years B.P.) and Middle Holocene (AT, 8000–5000 years B.P.). The most northern occurrence of *Marmota* from the samples, dated as from sometime during the Holocene, were from theAudashinskaya cave (56°12'N) and from caves on the Yenisei river (Ledopadnaya, Kazyreevskie and others nearby at 56°N). There data show that the northern boundary of *Marmota* distribution in the Early and the Middle Holocene was between 56 and 57°N in the south-east of Western Siberia. At the beginning of the Late Holocene the range extended to 55°27'N in Priirtyshje. The northern extent of *Marmota*'s range in Priobye hasn't shifted latitude between modern days and the end of the Middle Holocene. The edge of *Marmota*'s range along the Yenisey river in the Late Holocene isn't precisely known. In the 18th and 19th centuries, the distribution of *Marmota* did not change in Priirtyshje, and signs of marmot habitation have been documented at 55°N (Ognev, 1947). Although the range of marmots was unchanged over time in Priobye, along the Yenisei river up to the beginning of the 17th century t there is no record of marmots occurring in the Krasnoyarsk outskirts or on the right bank of Yenisei river.

In the central and southern parts of the study area there were numerous Middle Holocene sites with marmot remains and a few Late Holocene sites (Fig. 1). Marmots occurred here in the 18th and 19th centuries as well. In the description of Kolyvanskie plants there is reference to the abundance of marmots in the Altai forest-steppe territory in 1730 . In the middle of 18th century, P.S. Pallas encountered a great number of marmots on the woodless slopes between the Aley and Talovka rivers (Kirikov, 1966). All these data seem to indicate that the southern boundary range of *Marmota* hasn't substantially changed over the last few thousand years.

The area reconstruction of separate species

According to findings at the Elovskoe settlement, the forest-steppe marmot has inhabited the region of Novosibirsk Priobye and partly Tomsk Priobye since the end of Subboreal period of the Holocene. However, the range of the forest-steppe marmot was considerably larger during the Subboreal period than it is today.. Its range extended to the east at least as far as upstream of the Chulym river, where the remains of forest-steppe marmot were found in the Aidashinskaya cave. The forest-steppe marmot was initially identified as a gray marmot by the first scientists to document it. Since then, it has also been identified as a subspecies of gray marmot (Ognev, 1947). As a result, it is challenging to differentiate the historical, and recent, southern boundary of the forest-steppe marmot's range from that of the northern edge of the gray marmot's historical range. The forest-steppe marmot appears to have had a limited range over the last few centuries. There was sharp decrease in its population size in the middle of the 20th century due to systematic hunting (Laptev, 1958). According to data from the Western Siberian Branch of "VNIIOZ" the forest-steppe marmot's population hasn't undergone considerable changes in recent years and has showed some signs of increase (The resolution…, 2014).

The first written record of the distribution of gray marmot in the Altai Mountains appeared at the beginning of the 20th century. According to the records of different authors (Ognev, 1947; Yudin et al., 1979), gray marmot inhabited a large part of the Altai Mountains during this time. It was absent only in taiga districts of the northern and partly the north-eastern parts of the Altai and also in the forest south-west of the Ust-Koksinskiy district of Altai Republic. The boundaries of the gray marmot's range experienced some fluctuations during this time. The main cause was usually direct extermination by man (Yudin et al., 1979). It is challenging to assess the range of the gray marmot over the 21st century due to lack of data.

ubfossil bones confirmed to be those steppe marmot were absent. Written records on its distribution from the south-east of West Siberia are from the 19th century. During that time the northern edge of its range came up to 55°N, on the Irtysh river. At the end of the 19th century steppe marmot was recorded in the Omsk town outskirts (Ognev, 1947). The decline of the steppe marmot population and the shift of its range began in 1865, when mass peasant migrations to the forest-steppe zone began (Kirikov, 1966). From that time the steppe marmot's range shifted to what it is today, retreating to the south and dividing into isolated pockets. According to data from the Western Siberian Branch of "VNIIOZ", in 2008, the population of steppe marmot showed increases and its range appeared less patchy (Mashkin, 2009).

Conclusion

The analysis of the results of subfossil cranium remains from Holocene sites, together with records from the 19th and 20th centuries made it possible to reconstruct shifts in the range of *Marmota* over time in the south-east of Western Siberia in the Holocene. We used discriminant analysis to identify the species of marmot cranium remains. This method allowed us to differentiate forest-steppe marmots from gray and steppe marmots with close to 100% confidence.

The distribution of marmot remains indicates that the northern boundary of *Marmota*'s range during the Holocene extended along the south boundary of the forest zone, to

the basin of the Ob river, across the mountains of Southern Siberia, and over the Yenisei river at a latitude of about 56°N, extending to its east bank. Written records did not confirm the presence of marmots in basin of Chulym river or in the outskirts of Krasnoyarsk city. It may be the marmot's range retreated from the area before Russian colonization, i.e. more than 300 years B.P. By the time of Russian colonization, the range extended to the basin of the Yenisei river had been to the south and west to the Western Sayan Mountains, and marmots had disappeared from the east bank of the Yenisei river. In the first third of the 20th century the northern boundary extending to the basin of the Irtysh river was displaced to the south (Ognev, 1947).

Species identification of marmot cranium remains showed that the range of gray and forest-steppe marmots was larger in the past and included the upper stream of the Chulym river (56°12'N; 90°18'E). The current range of the gray marmot is now considerably further south (between 51° and 52°N). Forest-steppe marmots inhabit more western territories (between 85° and 86°E) in the indicated district (Fig.1). The edge of the steppe marmot's range in the Holocene is not well known. During the last 100 to 150 years the range of all three species contracted and fragmented due to the expansion of agriculture and active extirpation of marmots by humans.

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