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LATE PLEISTOCENE URSIDAE AND MUSTELIDAE REMAINS (MAMMALIA, CARNIVORA) FROM GEOGRAPHICAL SOCIETY CAVE IN THE RUSSIAN FAR EAST

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ABSTRACT

The paleontological collection from Geographical Society Cave located in southern part of Primorskii Territory is found to comprise 5 species of ursids and mustelids: *Ursus arctos, Meles anakuma, Martes zibellina, Gulo gulo* and *Lutra lutra*. Bone remains of brown bear (*Ursus arctos*) predominate; scant tooth-marks of large carnivores on their surfaces suggest bears to have been only occasional prey, dying mainly when overwintering in the cave. The presence of Asian badger (*Meles anakuma*) and true otter (*Lutra lutra*), whose findings are not known northwardly, provide the possibility to regard southern regions of the Russian Far East as a refuge, where these species survived during the Late Pleistocene.

Key words: Late Pleistocene, Mustelidae, Palaeolithic cave sites, Russian Far East, taphonomy, taxonomy, Ursidae

ПОЗДНЕПЛЕЙСТОЦЕНОВЫЕ ОСТАТКИ URSIDAE И MUSTELIDAE (MAMMALIA, CARNIVORA) ИЗ ПЕЩЕРЫ ГЕОГРАФИЧЕСКОГО ОБЩЕСТВА НА ДАЛЬНЕМ ВОСТОКЕ РОССИИ

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РЕЗЮМЕ

В палеонтологической коллекции из пещеры Географического общества на юге Приморского края определены 5 видов из семейств медвежьих (Ursidae) и горностаевых (Mustelidae): *Ursus arctos, Meles anakuma, Martes zibellina, Gulo gulo* и *Lutra lutra*. Преобладают костные остатки бурого медведя (*Ursus arctos*); редкие следы от зубов крупных хищников на их поверхности позволяют предполагать, что медведи были только случайной добычей, а преимущественно погибали в пещере во время зимнего сна. Присутствие азиатского барсука (*Meles anakuma*) и речной выдры (*Lutra lutra*), ископаемые находки которых не известны севернее, позволяют рассматривать юг Дальнего Востока России как рефугиум, где эти виды сохранялись в течение позднего плейстоцена.

Ключевые слова: Поздний плейстоцен, Mustelidae, палеолитические пещерные стоянки, Дальний Восток России, тафономия, таксономия, Ursidae

INTRODUCTION

At present time Ursidae are represented in the southern regions of the Russian Far East by two species: *Ursus thibetanus* G. Cuvier, 1823 and *U. arctos* L., 1758; Mustelidae are found to involve there nine species: *Meles anakuma* Temminck, 1844, *Martes flavigula* (Boddaert, 1785), *M. zibellina* (L., 1758), *Gulo gulo* (L., 1758), *Mustela erminea* L., 1758, *M. sibirica* Pallas, 1773, *M. altaica* Pallas, 1811, *M. nivalis* L., 1766, and recently acclimatized *Neovison vison* (Schreber, 1777) (see Yudin 1984).

Ovodov (1977), in his tentative list of the Late Pleistocene mammals of the southern part of the Russian Far East, which were identified on the basis of bone assemblage from Geographical Society Cave, enumerated seven species of ursids and mustelids: *Ursus arctos*, *U. thibetanus* (?), *Mustela sibiricus*, *Martes flavigula* (?), *Gulo gulo*, *Meles meles* and *Lutra lutra*. *Ursus thibetanus* has been identified by a single phalanx. Affiliation of *Martes flavigula* and *Mustela sibiricus* with the Pleistocene fauna is not confident for me, since these species have no stratigraphic timing; therefore, these species were not included into the present study.

Geographical Society Cave is situated at the Partizanskaya River (former Suchan River) near Nakhodka City in Primorskii Territory (42°52´N; 133°00´E). The detailed description of this cave site has been provided by me earlier (Baryshnikov 2014). The cave was found to contain an extensive bone material as well as non-numerous stone artefacts suggesting visits of ancient humans.

Stone implements and most of the osteological material were found chiefly within layer 4 (Ovodov 1977). However, a larger portion of fossil remains has no precise stratigraphic connection and is associated only with the depth of deposition. Six AMS ^{14}C dates from 34,510 to 48,650 BP were obtained for the hyena bones and further AMS ^{14}C dates from 31,500 to 33,420 BP for the mammoth bones (Kuzmin et al. 2001; Rohland et al. 2005; Stuart and Lister 2014). These dates assign the time of formation of the bone-bearing layer in Geographical Society Cave to a warmer stage of the Late Pleistocene (MIS3).

The remains of a big cat from Geographical Society Cave were referred by Vereshchagin (1971) to tiger, *Panthera tigris* (L., 1758) or cave lion, *P. spelaea* (Goldfuss, 1810). Meantime, I have recently published reviews of fossil Hyaenidae and Canidae from this cave (Baryshnikov 2014, 2015 in press).

In the course of the present study I have reidentified and morphologically characterized for the first time all bone material belonging to families Ursidae and Mustelidae, which is kept at the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg. This material predominantly came from 1966–1967 excavations by N. Ovodov as well as from collections by N. Vereshchagin in 1966 and by the student of local lore E. Leshok in 1972.

Institutional abbreviations. IGDMY, Institute of Geology of Diamond and Precious Metals, Siberian Branch of the Russian Academy of Sciences, Yakutsk, Russia; IPUW, Institute of Paleontology, Vienna University, Austria; MMB, Moravian Museum (Anthropos), Brno, Czech Republic; NHM, Natural History Museum, London, Great Britain; NHMB, Natural History Museum, Humboldt University, Berlin, Germany; NHMP, Natural History Museum, Prague, Czech Republic; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Measurements. Dental measurements: *L* – greatest length, *Lbuc* – buccal length, *Lling* – lingual length, *Lpa* – length of paracon, *Ltrd* – length of talonid, *W* – greatest width. Vertebrates measurements: *BFcr* – breadth of the cranial articular surface, *LCDe* – length in the region of the corpus including the dens, *SBV* – smallest breadth of the vertebra. Limb bones measurements: *Bd* – breadth of the distal end, *BG* – breadth of the glenoid cavity, *Bp* – breadth of the proximal end, *BPC* – breadth across the coronoid process, *Dd* – breadth of the distal end, *Dp* – breadth of the proximal end, *DPA* – depth across the Processus anconaeus, *GB* – greatest breath, *GD* – greatest depth, *GL* – greatest length, *GLP* – greatest length of glenoid process, *SD* – breadth of the diaphysis in medium part. Measurements were taken in accordance with the scheme by von den Driesch (1968).

SYSTEMATICS

Order Carnivora Bowdich, 1821

Family Ursidae Fisher von Waldheim, 1814

Genus *Ursus* Linnaeus, 1758

Ursus arctos Linnaeus, 1758

By the amount of bone remains found in Geographical Society Cave, the brown bear occupies the second place among carnivores, yielding only to wolf (*Canis lupus* L., 1758). Ovodov (1977) counted 175 bone fragments from 9 individuals. In the course of my study, 231 fossil remains were referred to bear.

Description. There is the right mandible fragment with p4, m2, m3 and alveolus of m1 (ZIN 37291-1), found at the depth of 100 cm (Fig. 1A). Margins of this fragment are slightly rolled, and smoothed over; the lower marginal part is broken (probably bitten off by a large carnivore, such as hyena or wolf). Crowns of m2 and m3 are heavily worn, which provide the possibility to ascribe this mandible to an old animal.

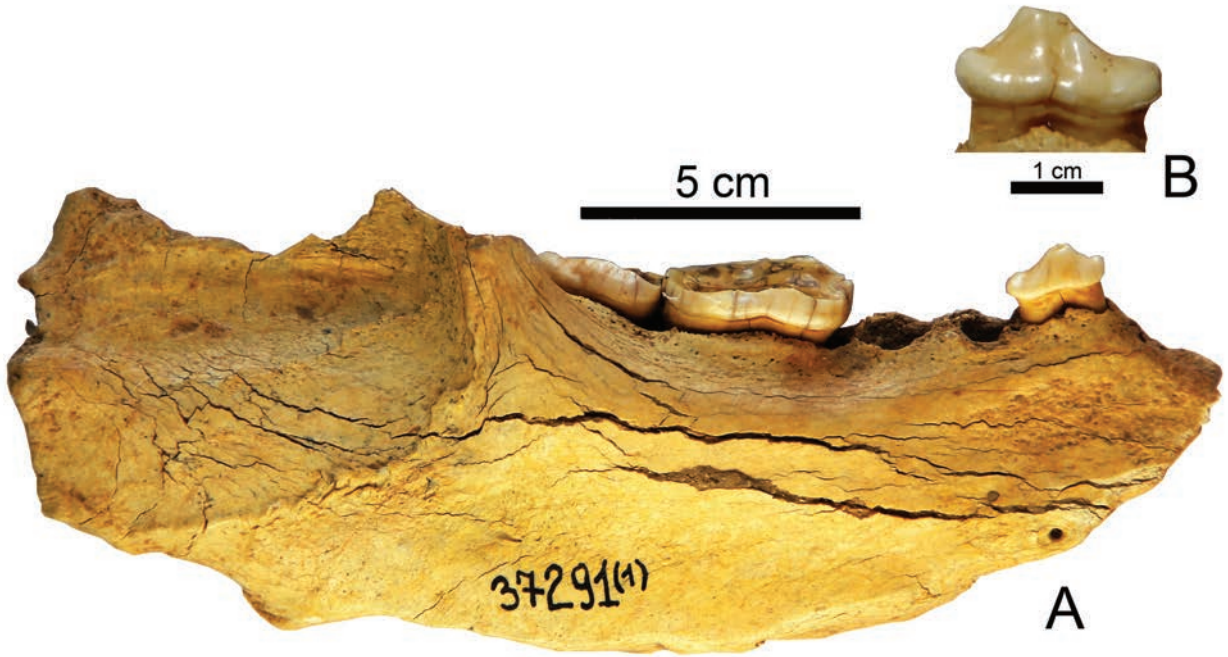

Fig. 1. *Ursus arctos*, right mandible fragment (ZIN 37291-1) from Geographical Society Cave; general aspect (A) and detail of p4 crone (B); buccal (A) and lingual (B) views.

Size of mandible ZIN 37291-1 is very robust; its dimensions noticeably exceed those of fossil brown bears examined by me from various regions of Northern Asia (Table 1). Bears belonging to the recent subspecies *U. a. beringianus* Middendorff, 1851, which inhabit the southern part of the Russian Far East, are one of the largest in Asia. However, even the males of this subspecies have the length of lower tooth row p4-m3 (74.7–90.5 mm, n=12) markedly yielding to that of the specimen from Geographical Society Cave (101.9 mm). Still more pronouncedly ZIN 37291-1 is distinguishable by the dimensions of tooth crowns (especially taking into account their marked wear). By the length of m2, the examined bear exceeds fossil specimens from other localities of Eurasia (Table 1) as well as males of the recent *U. a. beringianus* (24.1–29.0 mm, n=13). The length of m3 in ZIN 37291-1 corresponds to that of the largest recent males of the brown bear from Primorskii Territory (18.5–25.7 mm, n=10).

It was found the bear milk canine (ZIN 37291-20); its length along the lower margin of enamel measuring 7.6 mm, width 5.6 mm. The root is entirely preserved; signs of resorption absent. This points out that the tooth fell into the cave deposits as a consequence of the death of cub and was not a result of the replacement of milk teeth onto permanent ones. By its dimensions, the fossil milk canine does not exceed the bounds of its variation in the recent *U. arctos* (length 5.0–8.6 mm, width 3.7–5.7 mm, n=42; Baryshnikov and Averianov 1992).

Isolated permanent canines are partly broken, several of them demonstrating heavily worn crowns. Five upper canines are represented; their measurements are (mm): length 22.7, 24.3, 24.4, 25.2, 27.2 and width 19.0, 18.0, 19.5, 20.0, 23.1, correspondingly. Males of the recent *U. a. beringianus* are characterized by the width of upper canine 13.6–19.0 mm (n=14) and females 11.8–14.4 mm (n=8). Therefore all specimens found in Geographical Society Cave may be ascribed to males on the basis of robustness of these teeth.

Six lower canines exhibit the following parameters of length: 18.3, 18.5, 20.0, 20.4, 23.2, 24.0 mm and width: 12.2, 14.0, 15.6, 16.8, 17.0, 18.4 mm, correspondingly. In the recent *U. a. beringianus*, the width of lower canine constitutes 13.6–17.7 mm (n=14) in males and 11.6–15.7 mm in females (n=9). Although

Table 1. Measurements (mm) of mandibles of Pleistocene *Ursus arctos*.

Measurements	Middle (?) Pleistocene	Late Pleistocene			
	Mamontovaya Gora, Yakutia, Russia	Geographical Society Cave, Russia	Kyra-Sullar, Yakutia, Russia	Předmosti, Czech Republic	
	IGDMY 677, sen.	ZIN 37291-1, sen.	IGDMY 4967, sen.	MMB n/n, ad.	MMB 12440
Lc1-m3	130.9	–	150.8	164.7	147.7
Lp4-m3	77.9	101.9	84.6	101.2	92.6
Teeth					
Lp4	11.4	17.5	14.6	15.8	14.6
Wp4	7.2	8.9	8.3	9.7	8.0
Lm2	22.3	33.4	26.7	29.5	27.7
Wm2	14.0	19.9	17.4	18.5	18.4
Lm3		25.0			23.7
Wm3		19.7			16.4

the measurements of males and females markedly overlap, it seems to be appropriate to refer three canines to males and three canines to females within the examined fossil sample.

There are also several isolated cheek teeth. All specimens demonstrate heavily worn masticatory surface, which makes it impossible to morphologically characterize them. Tooth measurements are (L/W, mm): M1 ZIN 37291-17 (26.0/18.4), ZIN 37291-18 (25.4/18.7), M2 ZIN 37291-13 (39.6/20.9), m1 ZIN 37291-14 (29.9/14.8), m2 ZIN 37291-15 (29.6/18.7). These dimensions surpass those of specimens from the European localities measured by me (Table 2): meanwhile, similar values are characteristic of the teeth of fossil *U. arctos* from Zhoukoudian 1 in Northern China (Pei 1934).

Lower premolar p4, preserving in mandible ZIN 37291-1 and having no signs of wear, exhibits elongated crown and well defined lingual cingulid. The protoconid is high, with a single apex. The supplementary cusp ("metaconid") is visible at its posterior margin, from the lingual side (Fig. 1B). By the greatest length, the tooth-in-study noticeably surpasses premolars of examined fossil brown bears from various localities of Northern Eurasia (Table 1) as well as the teeth of the recent *U. a. beringianus* (10.8–13.4 mm, n=12). A similar length of p4 was observed in the fossil *U. arctos* (identified as *U. spelaeus*) from Upper Cave at Zhoukoudian (Pei 1940).

The postcranial skeleton is mostly represented by fragments of vertebrae and long bones as well as by metacarpals and metatarsals. The second cervical vertebra, axis, (ZIN 37291-31), is partly broken; its measurements are (mm): LCDe – 77.7, BFcr – 67.1, SBV – 49.6.

Limb bones belong to the adult bears. These bones markedly vary in the size, which implies the presence of males as well as females in the examined material, since males of brown bear are noticeably larger than females. Measurements in most cases surpass those of the recent adult male from Kamchatka (subspecies *U. arctos piscator* Pucheran, 1855), measured for the comparison (Tables 2, 3). This testifies that predominantly males were buried inside Geographical Society Cave.

The robust size of the fossil *U. arctos*, as well as mentions in old publications on the findings of the cave bear (*U. spelaeus* Rosenmüller, 1794) at the Chinese localities (Pei 1940), generated the need to compare the examined material with this species.

On the fragment of ulna (ZIN 37291-33), the zone of tuberosity along the middle part of anterior surface of diaphysis is markedly distanced from the zone of upper tuberosity of the same surface, locating under the incisura radii (Fig. 2A), which discriminates this bone of *U. arctos* from that of *U. spelaeus* (Gromova 1950). The radius (ZIN 37291-32, found at the depth of 140 cm) is more slender than in *U. spelaeus* (Fig. 2B).

The calcaneus (ZIN 37291-62, found at the depth of 30–70 cm) reveals tuber calcanei slightly flattened, whereas the sulcus between coracoid and sustentacu-

Table 2. Measurements (mm) of forelimb bones of *Ursus arctos*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd	GB	GD	BPC	GLP	BG
					Scapula							
Geographical Society Cave, Russia	ZIN 37291-35										80.2	45.6
Kamchatka, recent	ZIN 32672, ♂										77.7	40.7
					Humerus							
Geographical Society Cave, Russia	ZIN 37291-77				37.3							
Kamchatka, recent	ZIN 32672, ♂				33.1							
					Ulna							
Geographical Society Cave, Russia	ZIN 37291-32									48.6		
Kamchatka, recent	ZIN 32672, ♂									52.4		
					Radius							
Geographical Society Cave, Russia	ZIN 37291-32	324.0	46.7		28.2	65.7						
	ZIN 37291-34					71.0						
	ZIN 37291-78		51.3									
Kamchatka, recent	ZIN 32672, ♂	312.0	43.5		31.0	61.5						
					Scapholunatum							
Geographical Society Cave, Russia	ZIN 37291-60							64.6	60.5			
	ZIN 37291-61							64.6	61.9			
	ZIN 37291-79							–	56.4			
Kamchatka, Recent	ZIN 32672, ♂							56.6	50.9			
					Mc1							
Geographical Society Cave, Russia	ZIN 37291-51	91.9	30.5	23.6	14.0	23.6	18.5					
Kamchatka, recent	ZIN 32672, ♂	76.4	24.9	19.9	11.3	19.2	16.1					
					Mc2							
Geographical Society Cave, Russia	ZIN 37291-44	99.0	18.7	32.5	16.4	25.1	19.6					
	ZIN 37291-45	100.4	21.1	33.2	16.7	26.5	20.5					
	ZIN 37291-48	92.1	18.6	30.1	15.7	24.3	21.0					
	ZIN 37291-55	84.2	18.0	28.0	14.5	21.6	21.7					
Kamchatka, Recent	ZIN 32672, ♂	84.1	18.4	26.6	13.4	22.5	17.5					
					Mc3							
Geographical Society Cave, Russia	ZIN 37291-42	99.9	22.8	34.8	16.9	26.9	21.2					
	ZIN 37291-46	–	–	–	17.7	30.5	–					
	ZIN 37291-59	–	22.4	31.0	17.2							
Kamchatka, recent	ZIN 32672, ♂	85.4	17.4	25.3	13.6	21.6	18.7					

Table 2. *Continued*

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd	GB	GD	BPC	GLP	BG
				Mc4								
Geographical Society Cave, Russia	ZIN 37291-41	104.6	25.1	–	18.5	26.8	22.0					
	ZIN 37291-37	–	23.5	36.0	–	–	–					
Kamchatka, Recent	ZIN 32672, ♂	87.8	19.2	28.0	14.0	22.6	19.3					
				Mc5								
Geographical Society Cave, Russia	ZIN 37291-38	105.8	29.2	37.0	17.7	30.1	21.0					
	ZIN 37291-47	95.8	29.2	32.3	17.4	26.5	22.2					
	ZIN 37291-49	86.0	27.9	31.8	16.0	24.3	20.4					
Kamchatka, recent	ZIN 32672, ♂	89.5	25.6	29.2	15.2	26.5	19.8					

Table 3. Measurements (mm) of hindlimb bones of *Ursus arctos*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd	GB
		Tibia						
Geographical Society Cave, Russia	ZIN 37291-76				40.6			
Kamchatka, recent	ZIN 32672, ♂				28.7			
		Calcaneus						
	ZIN 37291-36	105.0						–
Geographical Society Cave, Russia	ZIN 37291-62	81.0						59.3
	ZIN 37291-63	75.1						42.6
Kamchatka, recent	ZIN 32672, ♂	86.1						57.8
		Talus						
	ZIN 37291-64	55.3						67.4
Geographical Society Cave, Russia	ZIN 37291-66	49.2						54.4
	ZIN 37291-65	50.3						53.8
Kamchatka, recent	ZIN 32672, ♂	48.9						51.4
		Mt1						
Geographical Society Cave, Russia	ZIN 37291-58	66.1	24.8	24.6	11.6	18.3	16.8	
Kamchatka, recent	ZIN 32672, ♂	68.9	23.1	26.2	11.3	19.4	14.3	
		Mt2						
Geographical Society Cave, Russia	ZIN 37291-52	89.9	17.2	30.9	14.7	21.7	17.4	
	ZIN 37291-57	75.5	16.8	25.1	13.5	20.4	18.1	
Kamchatka, recent	ZIN 32672, ♂	79.7	14.8	25.6	13.1	21.3	15.7	
		Mt3						
Geographical Society Cave, Russia	ZIN 37291-43	97.7	26.0	36.7	16.7	22.3	18.7	
	ZIN 37291-53	–	–	–	16.3	23.4	20.1	
Kamchatka, recent	ZIN 32672, ♂	85.8	18.3	27.8	12.8	19.9	16.6	
		Mt4						
Geographical Society Cave, Russia	ZIN 37291-50	88.9	21.3	28.7	14.9	22.4	19.2	
Kamchatka, recent	ZIN 32672, ♂	93.4	20.9	27.4	14.0	21.1	17.2	
		Mt5						
Geographical Society Cave, Russia	ZIN 37291-39	109.0	29.5	31.3	15.5	24.9	–	
	ZIN 37291-40	109.9	33.5	34.6	16.2	25.0	19.0	
Kamchatka, recent	ZIN 32672, ♂	93.4	26.8	31.5	14.5	23.6	17.5	

Fig. 2. *Ursus arctos*, right ulna fragment (ZIN 37291-33; A) and left radius (ZIN 37291-32; B) from Geographical Society Cave; medial (A) and dorsal (B) views.

lar facets is narrower and shallower in comparison with *U. spelaeus* (Fig. 3A). Two tali (ZIN 37291-64, 65) exhibit the rough area surrounding the trochlea tali from above and from within to be narrow and not separated by a deep incision from the pronouncedly projected medially caput tali, which is observed in *U. spelaeus* (Fig. 3B, C). The internal crest of the distal articulary capitulum on the metacarpal and metatarsal bones is slightly concave, which is characteristic of the *U. spelaeus*; however, this concavity is less pronounced in the examined specimens (Fig. 4); it should be mentioned that it is observed on bones of the recent *U. arctos* from Kamchatka. Fossil metacarpals and metatarsals are shortened to a lesser degree as compared to *U. spelaeus*.

Taphonomy. I have earlier presumed that the bone assemblage was formed in Geographical Society Cave mainly as a result of the life activity of larger carnivorous animals, predominantly cave hyenas having used the cave as a den (Baryshnikov 2014). It is ascertained by the presence of a large amount of bone fragments gnawed by large animals in the cave cavity.

On the contrary, brown-bear bones found in Geographical Society Cave reveal scarce tooth marks of carnivores. These were detected on the mandibular fragment (ZIN 37291-1) and on several long bones (e.g. on the right humerus, ZIN 37291-77) (Fig. 5A).

The surface of the left tibia fragment (ZIN 37291-76) reveals six short longitudinal indentations (their length is 5.5–7.7 mm), which may be grouped in pairs and interpret as traces of three bites from teeth of a large carnivore (Fig. 5B). Distances between left and right indentations vary from 53.5 mm to 54.5 mm, which corresponds to the distance between lower canines of hyena (*Crocuta ultima*) and brown bear (*Ursus arctos*).

Thus a scarce occurrence of gnawed remains of fossil bear in Geographical Society Cave suggests their accumulation in the cave deposits to be associated not only with the food activity of carnivores (tiger, hyena) but happened also by other way.

As it has been mentioned above, the large size of brown-bear canines and limb bones found in the cave implies that they belong to males. This hypothesis is additionally confirmed by the presence of a baculum fragment (ZIN 37291-30) in the collection; its distal end reveals inconspicuous wavy convolution characteristic of *U. arctos* (Fig. 6A). At the same time, small size of other canines and bones detects the presence of females in the material-in-study.

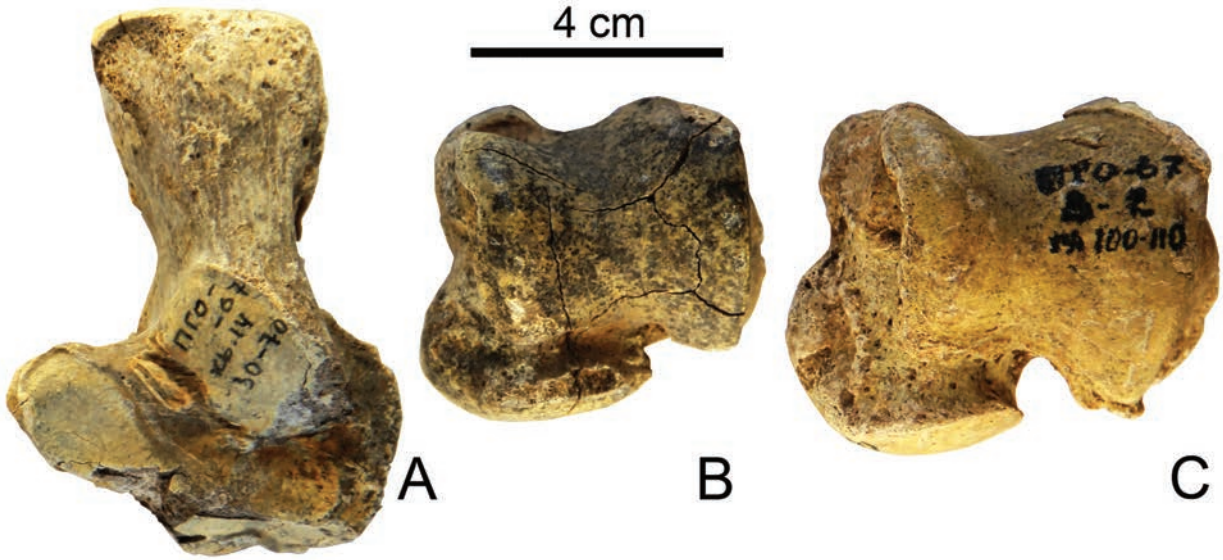

Fig. 3. *Ursus arctos*, left calcaneus (ZIN 37291-62; A), left talus (ZIN 37291-65; B) and left talus (ZIN 27291-64; C) from Geographical Society Cave; dorsal view.

Fig. 4. *Ursus arctos*, metacarpal (A) and metatarsals (B–D) from Geographical Society Cave; lateral (A, C) and medial (B, D) views; A – left mc5 (ZIN 37291-49); B – left mt1 (ZIN 37291-58); C – right mt2 (ZIN 37291-52); D – right mt5 (ZIN 37291-39).

Fig. 5. *Ursus arctos*, fragments of humerus (ZIN 37291-77) in posterior view (A) and tibia (ZIN 37291-76) with traces of carnivorous teeth (B) from Geographical Society Cave.

Fig. 6. *Ursus arctos*, baculum fragment (ZIN 37291-30; A), scapholunatum, right (ZIN 37291-61; B) and left (ZIN 37291-60; C), with pathological changes from Geographical Society Cave and left scapholunatum (ZIN 32672; D) of recent *U. a. piscator* from Kamchatka; lateral (A) and volar (B–D) views.

The examined collection mostly involved fragments of vertebrae and long bones as well as metacarpals, metatarsals, and phalanges (including ungual ones). Several specimens, including axis and radius, as well as short limb bones are preserved intact. This composition of skeletal elements and the presence of baculum (which may be easily lost in a process of butchering carcasses), together with the scarcity of bear bones with the tooth-marks of large carnivores, provide the possibility to assume that several bears perished within the cave cavity instead of were brought inside as a prey. The presence of old animals (ascertained on the basis of heavy wear of the tooth crowns) suggests that death occurred during overwintering as a result of a deficit of fat supply or because of the old age or illness. Presumably, wolves, wolverines, hyenas, and other bears were attracted into the cave by a smell of decay.

Therefore, Geographical Society Cave was a winter den for bears and was mostly used by males. Occasionally, females with cubs also overwintered there (judging from the find of the milk canine of a bear-cub). The indirect evidence of use of the cave as a den may be the presence of pathological signs on several bear bones (on vertebrae and limb bones). For example, the bone overgrowth is pronouncedly developed on the left and right metacarpals (presumably, from a single individual) (Fig. 6B, C). Long period of staying in the wet and cold cave during the winter sleeping might provoke various sicknesses (periostitis or arthritis). Similar signs of disease are often observed on the bones of cave bear (*U. spelaeus*) denned in the European caves (Breuer 1931; Withalm 2004). Bones of hyena, wolf, and tiger found in Geographical Society Cave, disclose no traces of pathological changes.

Discussion. This study revealed that the fossil remains of bear in Geographical Society Cave belong to *U. arctos* and demonstrate reliable morphological difference from bones of *U. spelaeus*. The Late Pleistocene *U. arctos* from the Russian Far East had very large size exceeding that of the adult males of the recent *U. a. beringianus* from Primorskii Territory, whose weight reaches 400 kg (Yudin 1984). Hence, larger Pleistocene bears could, presumably, approach 500–600 kg. This implies to a rich food supplies of the ancient landscapes (various plants, salmon rivers, sea emissions), which provided a possibility for such large animals to accumulate enough fat for overwintering. It should be mentioned that the large size is characteristic for the Late Pleistocene *U. arctos* over the whole Northern Eurasia. On the contrary, recent brown bears are small in the arctic regions of the continental Asia, which may be regarded as an

adaptation to poor food base and very long (almost 7 months) residing of animals at lair (Boeskorov and Baryshnikov 2013).

Huge size of males allowed them to use Geographical Society Cave, which located near the sea coast, as a winter den and not to be afraid of attacks by larger carnivores. Females with cubs, presumably, preferred more secluded earth-dens or rocky shelters located higher, in mountains, where females could escape from males and other dangerous for them predators.

Thus, it may be hypothesized that Geographical Society Cave has been, from time to time, a shelter for large carnivores (hyena, tiger), ancient hominins, and bears. As it was demonstrated by studies in Denisova Cave (Altai, Western Siberia), after the cave had been occupied by hyenas and had become to be visited by ancient humans, bears begun to regard this place as dangerous and became to search their winter dens in other places (Derevianko et al. 2003).

In the Late Pleistocene, *U. arctos* was distributed over the whole territory of Northern Asia, reaching northwardly the Arctic coast of Yakutia and Taimyr Peninsula (Boeskorov and Baryshnikov 2013).

Family Mustelidae Fisher von Waldheim, 1817

Genus *Meles* Brisson, 1762

***Meles anakuma* Temminck, 1844**

Ovodov (1977) ascribed 12 bones of badger to the Pleistocene; however, most of them reveal preservation of the bone substance characteristic of Holocene. There is the only isolated tooth (presumably, found at the depth of 190–210 cm), which I conditionally refer to the fossil material.

Right lower m1 (ZIN 37284, Fig. 7B) has the greatest length 15.6 mm and greatest width 6.9 mm, which is comparable with the maximum values of these dimensions in the recent subspecies *M. anakuma amurensis* Schrenk, 1859 from Primorskii Territory (length 14.1–15.5 mm, width 6.3–6.6 mm, n=7). A similar size of m1 is also recorded in the fossil badgers from Zhoukoudian (Upper Cave, Locality 1 and 3) in Northern China, which were referred to *M. leucurus* Hodgson, 1847 (Zdansky 1925; Pei 1934, 1936, 1940), and Middle Pleistocene *M. chiai* Teilhard, 1940 from Locality 18 at Beijing (Teilhard de Chardin 1940).

ZIN 37284 is characterized by large and nearly equally high paraconid, protoconid, and metaconid.

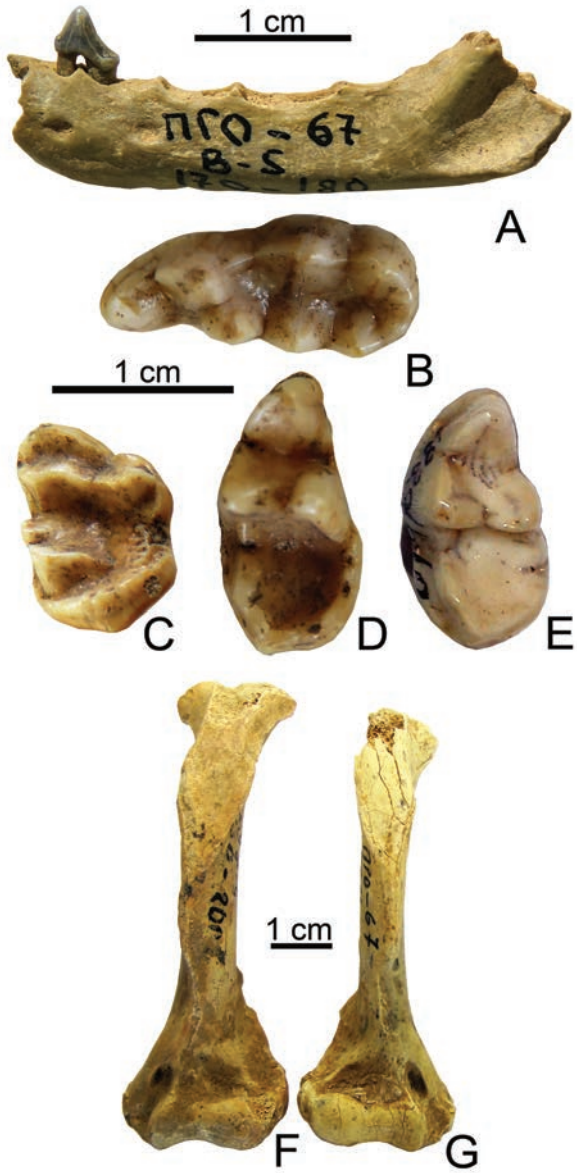

Fig. 7. Mustelidae remains from Geographical Society Cave (A–C, F, G) and Hundsheim, Austria (E); buccal (A), occlusal (B–E) and caudal (F, G) views; *Martes zibellina*: left mandible with p2 (ZIN 37289; A); *Meles meles*: left m1 (ZIN 37284; B) and *Lutra lutra*: left M1 (ZIN 37285-2; C), right m1 (ZIN 37285-1; D), right m1 (IPW HH 1889/6/2, type *simplicidens*; E), left humerus (ZIN 37285-3; F) and right humerus (ZIN 37285-4; G).

Talonid has a deep basin (Fig. 7B). The hypoconid is distanced from protoconid by a wide valley. The hypoconid and entoconid reveal beyond them smaller cuspids linked with each other by the serrated ridge running along the posterior margin of the tooth

crown. The examined tooth is referred to morphotype C3, which is common of the recent *M. a. amurensis* (Baryshnikov and Potapova 1990).

The genus *Meles* was traditionally regarded to include the only species, *M. meles* (L., 1758) (Corbet 1978; Yudin 1984). In the last time, 2 to 4 species are recognized within this genus (Baryshnikov et al. 2003; Abramov 2003; Del Cerro et al. 2010, etc.). The Asian badgers are referred to the single species *M. anakuma*, which is sometimes divided into continental *M. leucurus* and insular *M. anakuma* from Japan. These badgers are similar by their tooth morphology (Baryshnikov et al. 2003); moreover, the results of the latest analysis of mitochondrial DNA (cytochrome b) revealed that a degree of genetic divergence between *M. anakuma* and *M. leucurus* is not great (Koh et al. 2014). Therefore, I refer the East-Asian badgers to the single species, *M. anakuma*.

The recent distribution range of *M. anakuma* in the Russian Far East does not exceed northwardly the bounds of the Amur River basin (Yudin 1984). This species also did not occur in the Late Pleistocene in Northern Asia (Boeskorov and Baryshnikov 2013).

Genus *Martes* Pinel, 1792

Martes zibellina (Linnaeus, 1758)

Sable remains has not been recorded by Ovodov (1977) in the fossil material; however, the right mandible recovered at the depth of 170–180 cm (earlier mistakably referred to *Mustela sibiricus*), reveals the Pleistocene type of fossilization of the bone substance.

The mandible (ZIN 37289, Fig. 1A) keeps only tooth p2; other cheek teeth are lost, being represented only by their alveoli. The fossil specimen is of comparatively small size, which is characteristic of the recent subspecies *M. zibellina princeps* Birula, 1922 from Primorskii Territory. The alveolar length p1-m2 constitutes 27.2 mm, the height in front of m1 is 6.7 mm (in the recent *M. z. princeps* these parameters are equal to 24.6–28.7 mm and 6.2–9.1 mm correspondingly, n=8). The foramina mentales are connivent, as in *M. zibellina*; the distance between them is 4.4 mm. The length of premolar p2 constitutes 4.1 mm, width 2.3 mm (in the recent sables it is measured 3.6–4.7 mm and 2.0–2.5 mm correspondingly, n=6). The tooth is high and double-rooted; there is no supplementary cuspid.

Records of *M. zibellina* are scant in the Late Pleistocene of Eastern Siberia. These are known from the basin of the Lena River southwards of 60°N, from Khaiyrgas Cave (layer 5 and 6) and from Dyuktaiskaya Cave (Boeskorov and Baryshnikov 2013). The sable remains become common there in the Holocene localities. *Martes* sp. is mentioned in the list of species from Zhoukoudian 1 and from the Late Pleistocene layers in Xitaiping Cave near Beijing, China (Pei 1934; Tong et al. 2008).

Analysis of mtDNA sequences of recent *M. zibellina* suggests population size change and expansion of sable in warm Karganian time (near 40 kya). One of its group colonized Kamchatka Peninsula, where it survived the last glaciation (Malyarchuk et al. 2014).

Genus *Gulo* Pallas, 1780

Gulo gulo (Linnaeus, 1758)

Ovodov (1977) reported Geographical Society Cave to contain 12 fossils of wolverine from two individuals. The examined material involves, owing to my calculations, 14 fossil bones and teeth belonging to this species.

Description. There are three maxilla fragments from two individuals: left ZIN 37382 and right ZIN 37283 (probably belonging to a single animal) and left ZIN 37281 from another animal (Fig. 8). One of them (ZIN 37382, 37283) is very large, presumably representing a male. This suggestion corresponds to the size of upper canine (11.9 mm) whose width varies in the recent males from the southern part of the Russian Far East (Zeya River basin and Sakhalin Island) from 8.3 mm to 9.0 mm (n=4). By the length of the tooth row C1-M1 (59.6 mm), wolverine ZIN 37382 resembles the Late Pleistocene subspecies *G. gulo berelekhii* Novikov, 1993 described on the basis of cranium with mandible (ZIN 34907, holotype) from the Berelekh locality in Yakutia, Siberia (Table 4), markedly surpassing animals of the recent subspecies *G. gulo jacutensis* Novikov, 1993 from Eastern Siberia and southern regions of the Russian Far East (Novikov 1993) having this length 49.9–55.8 mm (n=6).

The second individual (ZIN 37281, found at the depth of 120 cm) is somewhat smaller in size and, hence, may be recognized as a female. In the length of P4-M1 (26.4 mm), the specimen markedly surrenders to mandibles from the locality of Berelekh (Table 4).

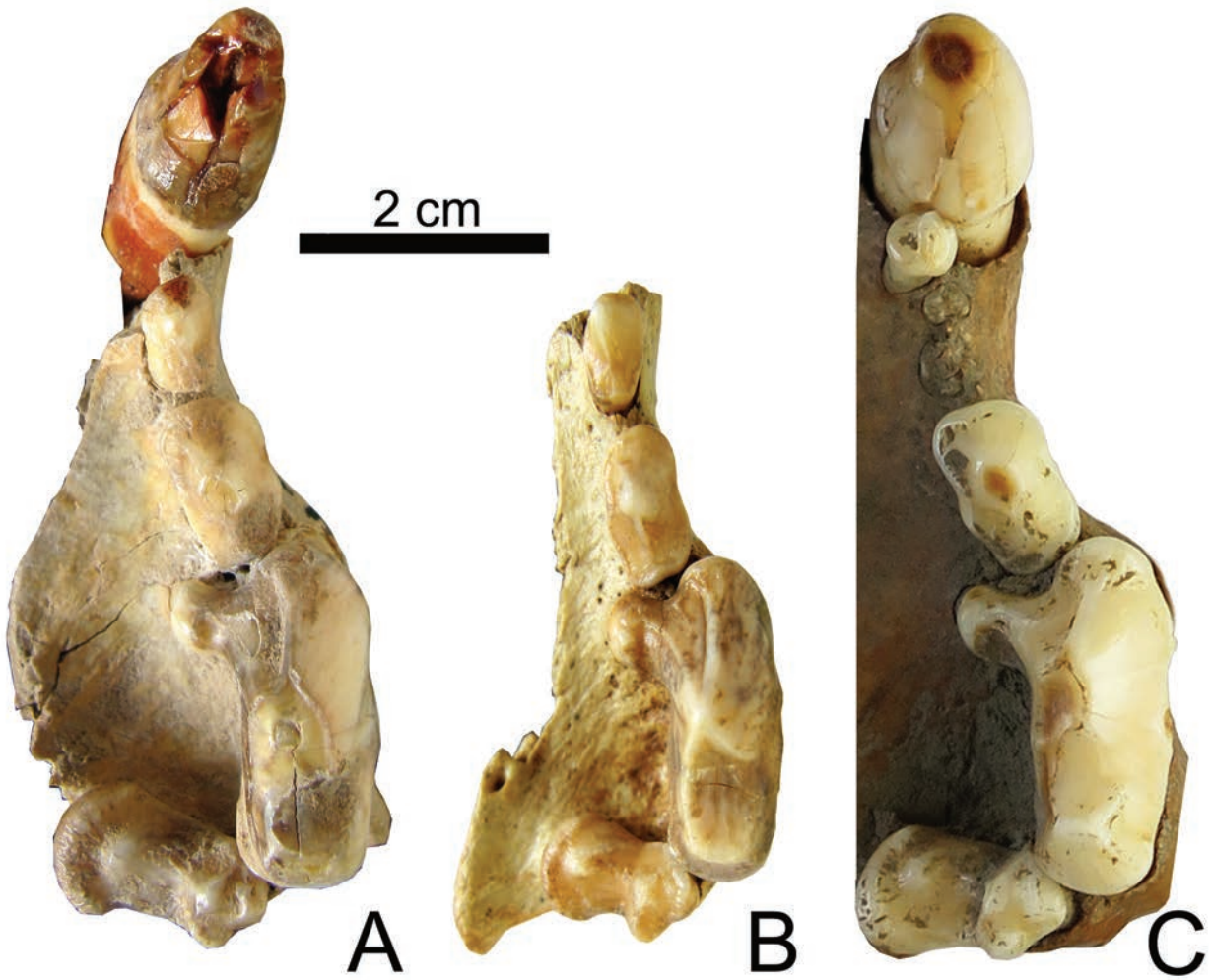

Fig. 8. *Gulo gulo*, left maxilla fragments: ZIN 37282 (A) and ZIN 37281 (B) from Geographical Society Cave, and ZIN 34907, holotype of *G. gulo berelekhii* (C), from locality Berelekh, Siberia; occlusal view.

Two wolverine mandibular fragments were found in Geographical Society Cave: ZIN 37279-1 and ZIN 37280 (the latter specimen was recovered at the depth of 130–140 cm) (Fig. 9). Judging from the size of lower canine, ZIN 37279-1 belongs to a female. The second specimen is larger, representing, probably, a male. Mandibles from Geographical Society Cave and Berelekh River possess alveoli of m2.

Both fossil specimens are larger than mandibles of the recent wolverine from the southern part of the Russian Far East. For example, the height of mandible body before m1 does not exceed 21 mm (18.7–20.9 mm, n=6) in the recent sample; at the same time, in ZIN 37280 this parameter constitutes 22.4 mm. Similarly robust mandibles are recorded in the fossil wolverines from European and Siberian localities (Table 5; Fig. 10).

Metric characteristics of the upper cheek teeth of *G. gulo* from Geographical Society Cave are noticeably surpass those of the recent wolverine from the Russian Far East, their tooth morphology being, nevertheless, similar. P3 demonstrates somewhat different proportions; the ratio between the premolar width and its length constitutes 58.5–61.8% (on the average 60.0%, n=4) in fossil animals from Primorskii Territory and Yakutia, whereas the recent wolverine from Sakhalin Island has the wider tooth, 60.2–69.9% (on the average 66.0%, n=5).

Table 4. Measurements (mm) of upper tooth rows of Late Pleistocene *Gulo gulo*.

Measurements	Geographical Society Cave, Russia			Berelekh River, Yakutia, Russia	Gailenreuth, Germany	Chlupáčova sluj, Konepruse, Czech Republic
	ZIN 37282	ZIN 37283	ZIN 37281	ZIN 34907, holotype *berelekhii*	NHM 21(o. c.)	NHMP R2531
LC1-M1	59.6			59.8		59.7
LP2-P4	41.1	ca41.3	39.1	40.3		
LP4-M1	28.3		26.4	27.8		
Teeth						
LC1	11.9	11.9		12.9		
WC1	9.6	9.0		9.9		
LP1		–		4.5	3.9	
WP1		5.0		4.3	4.5	
LP2	7.7		6.6		7.7	7.8
WP2	4.8		4.7		5.2	5.2
LP3	11.5	11.1	10.2	11.5	11.2	10.3
WP3	6.8	6.5	6.3	7.0	6.8	6.6
LP4	22.6	22.5	21.1	23.1		22.6
LpaP4	15.9	16.0	14.1	15.6		14.7
WP4	13.4	ca11.6	12.7	13.1		ca11.2
LbucM1	7.4		7.0	7.5	7.8	7.9
LlingM1	9.6		8.1	8.4	8.4	8.4
WM1	15.6		13.7	14.3	14.6	14.3

Dimensions of the lower carnassial teeth exceed in the examined material those of representatives of the recent subspecies *G. gulo jacutensis*. For example, the length of lower carnassial tooth m1 constitutes 23.1 mm in ZIN 37280; whereas the recent animals from Sakhalin Island exhibit this parameter varying from 20.0 mm to 22.4 mm (in average 21.56 mm, n=5). By the means of the m1 length 23.70 mm (23.1–24.9 mm, n=3), the fossil wolverine from Primorskii Territory and Yakutia demonstrated no difference from Late Pleistocene *G. gulo* from Europe whose length of m1 constitutes in the examined samples on average 23.39 mm (22.1–24.6 mm, n=7).

The Late Pleistocene *G. gulo* from Northern Eurasia is characterised by lower carnassial tooth m1 slightly wider as compared to the recent wolverine. The ratio between the width of m1 and its greatest length corresponds to 42.2–48.0% (on the average 45.4%, n=10); at the same time, the recent animals from Sakhalin show this ratio to be 42.8–44.5% (in average 43.4%, n=5).

The postcranial skeleton is represented by isolated bones of the hind limb. Their dimensions show the fossil bones do not surpass those of female of the recent wolverine from the southern part of the Russian Far East measured for the comparison (Table 6).

Discussion. The study indicates that the Late Pleistocene *G. gulo* from the Russian Far East differs from the recent representatives of this species by strong mandibles and robust cheek teeth. These features may be regarded as an adaptation to scavenging of larger animals. Fossil *G. gulo* could gnaw thicker bones in comparison with the recent wolverines and participate in the utilization of carcasses of bison, deer or horses as well as those of mammoths and rhinos.

The recent wolverines not only hunt, but readily consume carrion and eat off leftovers after other carnivores (wolf, tiger) (Novikov 1993; Tumanov and Kozhechkin 2012). A similar behaviour, presumably, was characteristic of the wolverine in the Late Pleistocene of Siberia. Excavations of the large

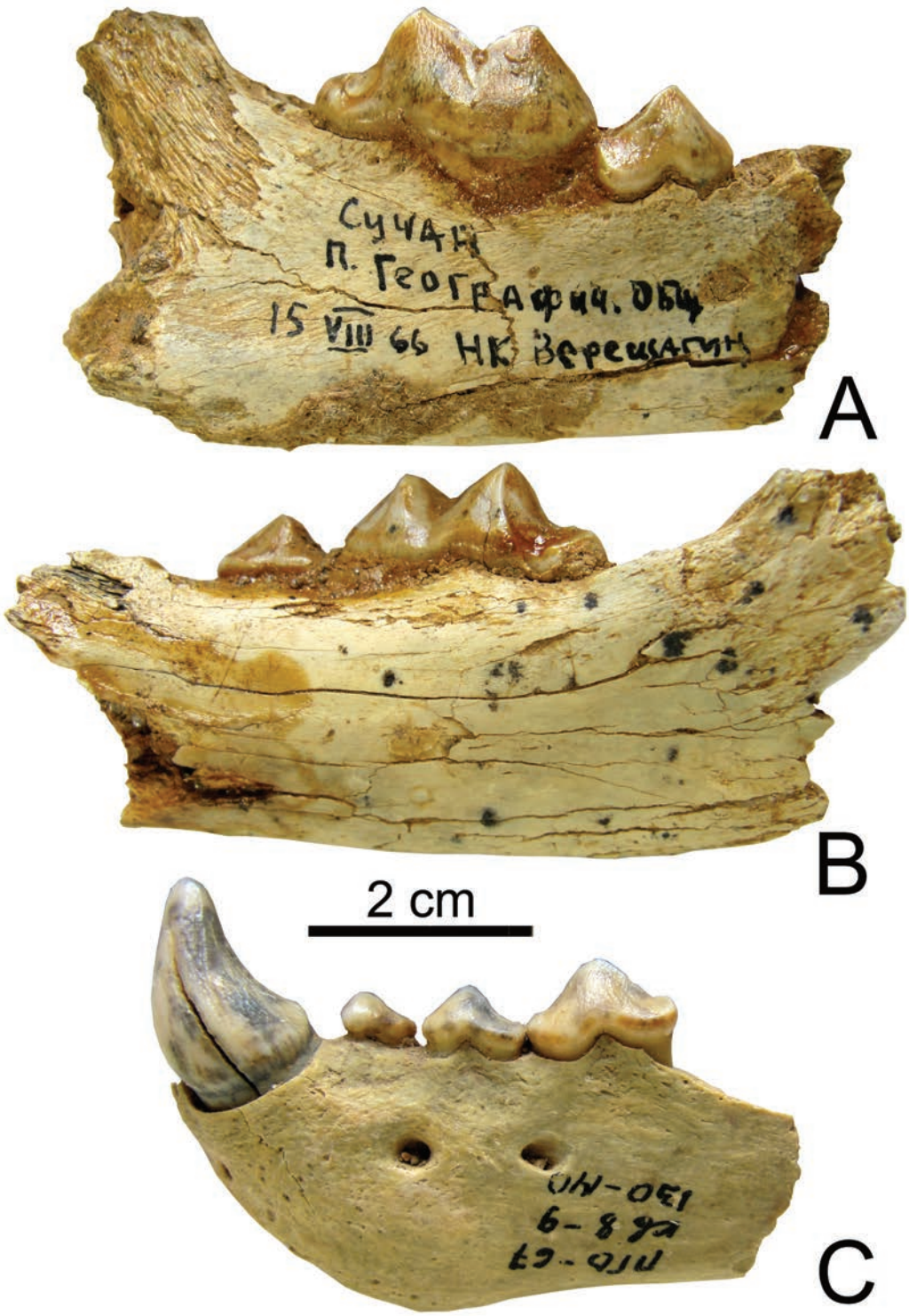

Fig. 9. *Gulo gulo*, mandible fragments: right (ZIN 37280; A, B) and left (ZIN 37279-1; C) from Geographical Society Cave; buccal (A, C) and lingual (B) views.

Table 5. Measurements (mm) of mandibles of Late Pleistocene *Gulo gulo*.

Measure-ments	Geographical Society Cave, Russia		Berelekh River, Yakutiya, Russia		Chlupáčova sluj, Koněpruse, Czech Republic	Srbsko Chlum Komin Cave, Czech Republic	
	ZIN 37279-1	ZIN 37280	ZIN 34906	ZIN 34907, holotype *berelekhii*	NHMP R4377	NHMP R4376	NHMP R4376
Total length			112.6	118.3	107	106.3	105.8
Lc1-m2			ca71.8	ca71	67.3	68.0	67.1
Lp2-m1			51.3	50.8			ca55.2
Lp1-p4	30.0		31.2	31.8			
Lm1-m2		ca28	ca30.3	ca28.8		27.8	28.4
Height of vertical ramus			54.0	59.8	53.1	48.2	53.1
Height before m1		22.4	24.1	23.5		22.1	21.3
Teeth							
Lc1	11.1		13.9		12.8	12.4	11.9
Wc1	10.0		11.9		10.7	10.9	11.1
Lp2	6.1		7.1	7.2	7.0	7.0	7.2
Wp2	4.6		4.7	4.8	5.0	4.5	4.9
Lp3	8.6		9.9	9.2	8.6	8.5	8.4
Wp3	5.7		7.1	6.0	6.3	5.6	5.9
Lp4	12.0	12.4	13.2	13.1	12.6	12.5	12.7
Wp4	7.2	8.2	9.0	8.3	7.4	8.0	7.2
Lm1		23.1	24.9	23.1	24.6	23.2	24.6
Ltrdm1		18.7	19.6	18.5	19.3	18.6	18.8
Wm1		10.9	11.5	10.4	10.4	10.5	10.4

Table 6. Measurements (mm) of fore limb bones of *Gulo gulo*.

Locality	Bones	Museum number	GL	Bp	Dp	SD	Bd	Dd
Geographic Society Cave, Russia	Femur	ZIN 37279-2				10.4		
		ZIN 37279-4		ca37.8		10.6		
Berelekh, Russia		ZIN 34908	149.2	37.7	18.1	11.4	31.2	
Zeya River Region, recent, ♀		ZIN 32110		37.1		10.8		
Geographic Society Cave, Russia	Metatarsal 2	ZIN 37279-6	51.2	7.3	10.4	7.2	10.1	7.7
Zeya River Region, recent, ♀		ZIN 32110	51.4	6.4	9.4	6.1	9.1	7.6
Geographic Society Cave, Russia	Metatarsal 3	ZIN 37279-7	55.8	9.0	11.7	6.5	9.6	7.8
Zeya River Region, recent, ♀		ZIN 32110	57.6	9.4	12.9	6.5	9.5	7.9
Geographic Society Cave, Russia	Metatarsal 5	ZIN 37279-5	53.6	10.9	12.6	6.2	9.4	8.4
Zeya River Region, recent, ♀		ZIN 32110	54.6	10.6	12.5	5.4	9.7	8.3

Fig. 10. *Gulo gulo berelekhii*, right mandibles from locality of Berelekh, Yakutia, Russia; buccal (A, B) and lingual (C, D) views; A, C – ZIN 34907, holotype; B, D – ZIN 34906.

bone assemblage of woolly mammoth (*Mammuthus primigenius* (Blumenbach, 1799)) at the bank of the Berelekh River in Yakutia recovered the wolverine mummy (ZIN 32214) (Fig. 11). Presumably, this animal scavenged on carcasses of giant mammals and perished there (Vereshchagin 1977). Measurements of the mummy reveal that in the length of long limb bones (the greatest length of humerus constitutes 163 mm) the fossil animal was markedly larger than the recent wolverines. In addition, the bone proportions were found to be different: the forearm is shorter than humerus and tibia shorter than femur, whereas the recent animals reveal inverse proportions or these parts of limbs are approximately equal in length. This testifies the shortening of distal portions of limbs in the Pleistocene wolverine from Yakutia, which may be hypothesized as a local adaptation to survival in the extremely cold climate of the ice age in the northern regions of Siberia and Beringia (Boeskorov and Baryshnikov 2013).

Gulo gulo has been widely distributed in the Late Pleistocene in Northern Eurasia, reaching the Arctic coast of Siberia. In China, this species was scant, occurring in the north-eastern regions (Xu and Wei 1987). Middle Pleistocene *Gulo* sp. from Zhoukoudian 1 near Beijing is smaller (measurements of m1: length 19.2 mm, width 8.2 mm; Pei 1934) and exhibits dimensional resemblance to the wolverine from Poland (Deszczowa Cave), which is referred to *G. schlosseri* Kormos, 1914 or is regarded as an intermediate form between *G. schlosseri* and *G. gulo* (Krajcarz 2012).

Late Pleistocene *G. gulo* from Europe and China are characterized by very robust size (Xu and Wei 1987; Döppes 2001) resembling that of wolverines from Yakutia and the Russian Far East. However, metric characteristics of wolverines from the Upper Palaeolithic Mal'ta site in Southern Siberia (Baikal Region), judging from the length of humerus (137 and 140 mm; Ermolova 1978), did not exceed those of the recent animals.

Genus *Lutra* Brisson, 1762

Lutra lutra Linnaeus, 1758

The examined material was found to contain 9 fossil remains of the true otter, which coincides with the data by Ovodov (1977). At least, 3 specimens are present.

Fig. 11. *Gulo gulo berelekhii*, mummy (ZIN 32214) from locality Berelekh, Yakutia, Russia.

Upper canine C1 (ZIN 37285-3) is transversally rounded, of piercing type. It is 6.0 mm in length and 5.5 mm in width (at the basis of the enamel crown), which corresponds to the dimensions of canines in males of the recent *L. lutra* from Primorskii Territory (length 5.5–6.8 mm, width 4.6–5.9 mm, n=17).

Upper molar M1 (ZIN 37285-2, Fig. 7C) is represented on by the crown; the tooth, presumably, was not erupted, belonging to an otter cub. Crown measurements are (mm): buccal length 8.2, lingual length 8.0, anterior width 10.6, and posterior width 10.0. By its size the fossil specimen does not differ from male teeth of the recent *L. lutra* from Primorskii Territory (buccal length constituting 8.0–9.3 mm, anterior width 9.7–10.6 mm, n=17), being comparatively wider. The crown of ZIN 37285-2 exhibits no facets of wear; the stylar shelf is developed. Paracone and metacone are placed on the same longitudinal line; the paracone is longer as compared to metacone, the latter being higher. The inner basin of trigon is wide. Protocone is odontoid. There is a smaller cusp (paraconule) in front of it. The outer margin of talon is bordered with the cingulum, which forms the apically serrated hypocone.

Lower molar m1 (ZIN 37285-1, Fig. 7D) is measured as follows (mm): greatest length 13.7, length of trigonid 7.8, width of trigonid 6.2, width of talonid 7.1. In the recent *L. lutra* from Primoskii Territory the greatest length of m1 varies in males from 12.0 mm to 13.8 mm and the width of talonid varies from 5.7 mm to 7.5 mm (n=17). Therefore, the fossil specimen does not surpass by its size beyond the limits of the recent sample. Paraconid of m1 is shaped like a three-edged dent. Protoconid is larger and higher than paraconid. Metaconid is nearly as high as paraconid; it is divided by a deep valley from protoconid and its apex is shifted slightly backwards with respect to the apex of protoconid. The talonid is wide and reveals a basin. Hypoconid is elongated, trenchant. The place of entoconid is detected by a low ridge (ridge-like entoconid?) with inconspicuously differentiated denticles. The buccal margin of the tooth crown is bordered with a distinct cingulid.

The size and shape of fossil bone fragments from Geographical Society Cave do not differ from those of the recent *L. lutra* from the European Russia (Fig. 7F, G; Table 1). Several bones reveal tooth-marks of carnivores.

The analysis of craniometrical variability has demonstrated a considerable uniformity of the recent river otter in the northern part of its distributional range from the Atlantic to the Pacific, which makes it possible to refer these animals to the nominotypical subspecies *L. lutra lutra* (Baryshnikov and Puzach-

Table 7. Measurements (mm) of limb bones in *Lutra lutra*.

Locality	Bone	Museum number	SD	Bd	DC
Geographical Society Cave	Humerus	ZIN 37285-4	7.1	25.3	
		ZIN 37285-5	8.2	27.6	
		ZIN 37285-6	8.0	–	
European Russia		ZIN 32562, ♂	8.2	30.5	
		ZIN 30129	7.0	25.6	
Geographical Society Cave	Femur	ZIN 37285-9			13.0
European Russia		ZIN 32562, ♂			12.5
		ZIN 30129			10.9
Geographical Society Cave	Tibia	ZIN 37285-7	6.5	17.5	
		ZIN 37285-8	6.0	16.6	
European Russia		ZIN 32562, ♂	7.1	16.7	
		ZIN 30129	6.0	15.3	

enko 2012). However, the analysis of variability of the cheek-tooth morphotypes revealed a difference between western and eastern samples (Gimranov and Kosintsev 2012).

Craniometrical and genetic characters discriminate the otter population from Honshu Island in Japan, which is regarded as a distinct subspecies *L. lutra nippon* Imaizumi et Yoshiyuki, 1989 or even as a species (Imaizumi and Yoshiyuki 1989; Suzuki et al. 1996; Baryshnikov and Puzachenko 2012). By the metric characteristics of M1 (buccal length 7.9–8.3 mm, n=3) and m1 (greatest length 12.1–12.5 mm, n=3) *L. lutra nippon* demonstrates no difference from fossil as well as recent river otter of the Russian Far East.

Middle Pleistocene *L. simplicidens* Thenius, 1965 from the locality of Hundsheim in Austria (IPW HH 1889/6/2, holotype) resembles ZIN 37285-1 by morphology and size of lower carnassial tooth m1 (greatest length 12.8 mm, width of talonid 6.5 mm) (Fig. 7E).

The finding of *L. lutra* in Geographical Society Cave is of great interest. Fossil bones of otter of similar geological age are absent in the northern regions of Eastern Asia. These are also scarce in the Late Pleistocene localities of Europe and are predominantly confined there to the Mediterranean (Willemsen 1992). This may be associated with unfavourable past natural conditions in the Northern Eurasia for the river otter and it could survive during glaciations only within the southern refuges, one of them locating at the place of recent Primorskii Territory. This hypothesis is ascertained by the morphological diversity of *L. lutra* in the southern part of Russian Far East, which suggests the genetic diversity and the presence of several habitat centres in the past history of true otter (Baryshnikov and Puzachenko 2012). The species began to disperse in the post-glacial time northwards up to the Arctic coast.

CONCLUSIONS

The study of paleontological collection from Geographical Society Cave in Primorskii Territory, Russia, revealed the presence of 5 species: *Ursus arctos* (Ursidae), *Meles anakuma*, *Martes zibellina*, *Gulo gulo* and *Lutra lutra* (Mustelidae). All these species are represented in the recent regional fauna. The absence of other ursids and mustelids, occurring now in the southern part of the Russian Far East, in the fossil assemblage, may be associated with imperfect methods of excavations or with the poor preservation of the bones of smaller mustelids (*Mustela erminea*, *M. sibirica*, *M. altaica*, *M. nivalis*) in cave deposits of this region or with the migration of several species (*Martes flavigula*, *Ursus thibetanus*) there later, in Holocene. Bone remains of these later colonizers occur in the uppermost depositions of Geographical Society Cave (layers 1–3), as well as smaller neighbouring caves (Tigrovaya Cave, Letuchaya Mysh, Malaya Pensau, Spiachaya Krasavitsa) (Ovodov 1977).

Taphonomical peculiarities of the examined osteological collection from Geographical Society Cave suggest that mustelids whose remains were found within the cave deposits could be the prey of carnivores (otter) or they came into the cave for scavenging (wolverine). Brown bears, whose bones seldom reveal signs of gnawing by large carnivores, presumably, perished in the cave during overwintering, though several bears might be the prey of big cats or hyenas. The examined bones of ursids and mustelids have no reliable cut-marks from the stone tools; no burnt bone fragments were found. Hominids, presumably, visited this shelter only occasionally.

The Late Pleistocene ursids and large mustelids were represented in the northern regions of the continental Siberia by two species (*Ursus arctos*, *Gulo gulo*); the additional species (*Martes zibellina*) appeared there in the warm epochs (Boeskorov and Baryshnikov 2013). Therefore species diversity observed in the collection from Geographical Society Cave suggest more favourable natural conditions in the Late Pleistocene in the southern part of the Russian Far East, which presumably was a refuge, from where several mustelids (such as *Mustela sibirica*, *Lutra lutra*) spread in Holocene far northwards. At the same time, Asian black bear and Indian marten, associated with broad-leaved and subtropical forests, dispersed there from China and Korean Peninsula.

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