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Late Pleistocene Canidae remains from Geographical Society Cave in the Russian Far East

Gennady F. Baryshnikov

ABSTRACT. The analysis of bone remains of canids from the Upper-Pleistocene deposits of Geographical Society Cave in Primorskii Territory, Russia, revealed the presence of 4 species: *Nyctereutes procyonoides*, *Canis lupus*, *Cuon alpinus*, and *Vulpes vulpes*. Their accumulation is associated predominantly with the food activity of larger carnivores (*Crocuta ultima*, *Panthera tigris*), which used the cave as a den. No reliable signs of utilization of canids by ancient people were detected.

KEY WORDS: Canidae, Late Pleistocene, Paleolithic cave sites, Russian Far East, taphonomy, taxonomy.

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Позднеплейстоценовые остатки псовых (Canidae) из пещеры Географического общества на Дальнем Востоке России

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РЕЗЮМЕ. Анализ костных остатков канид из верхнеплейстоценовых отложений пещеры Географического общества (Приморский край, Россия) показал присутствие 4 видов: *Nyctereutes procyonoides*, *Canis lupus*, *Cuon alpinus* and *Vulpes vulpes*. Их накопление связано преимущественно с пищевой активностью крупных хищников (*Crocuta ultima*, *Panthera tigris*), использовавших пещеру как свое логово. Нет достоверных следов утилизации канид древним человеком.

КЛЮЧЕВЫЕ СЛОВА: Canidae, поздний плейстоцен, палеолитические пещерные стоянки, Дальний Восток России, тафономия, систематика.

Introduction

Recent Canidae are known to be represented in the southern part of the Russian Far East by four species: *Nyctereutes procyonoides* (Gray, 1834), *Canis lupus* L., 1758, *Cuon alpinus* (Pallas, 1811), and *Vulpes vulpes* (L., 1758). *Cuon alpinus* disappeared from this region during last decades. Ovodov (1977) included these species into his preliminary list of the Late Pleistocene mammals from the Geographical Society Cave situated at Partizanskaya River (former Suchan River) near Nakhodka City in Primorskii Territory (42°93′N, 133°05′E).

In the present study, I re-identified and morphologically characterized all canid material from this cave for the first time. The present material is housed in the Zoological Institute of Russian Academy of Sciences in Saint Petersburg and came predominantly from 1966–1967 excavations by N. Ovodov and from the collection of the local history researcher E. Leshok from 1972.

Fossil large mammal remains from Geographical Society Cave are referred to hyena, wolf, mammoth, woolly rhino, horse, bison, deer, elk, goral, and other inhabitants of forest and grassy or rocky landscapes. This implies a great biological and taxonomical diversity of the Late Pleistocene fauna in the southern part of the Russian Far East. The cave yielded scarce stone artifacts indicating visits of ancient hominins. It is not yet known who these visitors were.

A detailed description of the cave site has been earlier provided by Baryshnikov (2014). The stone implements and significant osteological material are mainly associated with the layer 4 (Ovodov, 1977). However, a greater part of fossil records has no stratigraphical connection, being characterized only by a depth of their occurrence. Hyena bones provided six AMS ^{14}C dates, from 34510 to 48650 BP (Kuzmin *et al*., 2001; Rohland *et al*., 2005; Stuart & Lister, 2014), which refer a time of the formation of bone-bearing layer in Geographical Society Cave to the warm stage of the Late Pleistocene (MIS 3).

Institutional abbreviations: GMMKU — Geology-Mineralogy Museum of Kazan University, Kazan, Russia; GMY — Geological Museum, Yakutsk, Russia; ISAK — Institute of Systematics and Evolution of Animals, Krakow, Poland; NHM — Natural History Museum, London, Great Britain; NHMB — Natural History Museum, Berlin, Germany; NHMP — National Museum, Prague, Czech Republic; ZIN — Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Fig. 1. *Nyctereutes procyonoides*, right mandible (ZIN 37290) from Geographical Society Cave, buccal view.

Measurements. Dental measurements**:** *L* — greatest length, *Lpa* — length of paracon, *Ltrd* — length of talonid, *W* — greatest width. Vertebrae measurements: *BFcd* — breadth of the caudal articular surface, *BFcr* — breadth of the cranial articular surface, *BPacd* — breadth between processi articulares caudales, *GL* — greatest length of atlas, *H* — height, *LAd* — length of the dorsal arch, median, *LAPa* — length of the arch including the prosessus articularis caudalis, *LCDe* — length in the region of the corpus including the dens. Limb bones measurements: *Bd* — breadth of the distal end, *BG* — breadth of the glenoid cavity, *Bp* — breadth of the proximal end, *Dd* — breadth of the distal end, *Dp* — breadth of the proximal end, *DPA* — depth across the processus anconaeus, *GB* — greatest breath, *GL* — greatest length, *GLP* — greatest length of glenoid process, *LAR* — length of the acetabulum on the rim, *SD* — breadth of the diaphysis in medium part, *SDO* — smallest depth of the olecranon, *SH* — smallest height of the shaft of ilium, *SLC* — smallest length of neck of the scapula. Measurements were taken in accordance with the scheme by von den Driesch (1976).

Systematic part

Family *Canidae* Fisher, 1817
Genus *Nyctereutes* Temminck, 1838
Nyctereutes procyonoides (Gray, 1834)

Ovodov (1977) found four bones of raccoon dog in the Pleistocene deposits of Geographical Society Cave. No remains were reliably associated with the lower levels. I provisionally referred to this level the left mandible (ZIN 37290), based on the degree of its fossilization.

The specimen ZIN 37290 exhibits three incisors, a canine, alveolus of p1, and cheek teeth p2–m2 (Fig. 1). Alveolus of m3 is absent. The mandible is high and has

Table 1. Measurements (mm) of mandibles of *Nyctereutes procyonoides*.

Measurements	Late Pleistocene	*N. p. ussuriensis*, recent		*N. p. viverrinus*, recent
	Geographical Society Cave, Russia	Primorskii Territory		Honshu, Japan
	ZIN 37290	ZIN 2684, ♂	ZIN 9270	ZIN 32542
Lc1–m2	52.2	48.3	51.3	48.6
Lp2–m2	38.9	36.4	39.2	36.7
Lp1–p4	ca25	22.5	24.3	22.0
Lm1–m2	19.8	18.0	19.8	18.7
Height behind m1	16.9	13.8	14.4	12.9
Height behind p2	11.0	10.4	10.4	9.0
Teeth				
Lc1	6.3	5.3	6.4	5.8
Lc1	4.3	3.5	4.0	3.7
Lp2	5.9	5.3	5.6	5.4
Wp2	2.6	2.6	2.8	2.4
Lp3	6.4	6.2	6.4	6.0
Wp3	2.8	2.8	3.1	2.5
Lp4	8.4	7.0	7.4	6.9
Wp4	3.6	3.4	3.9	3.5
Lm1	13.3	12.1	13.0	12.4
Ltldm1	4.0	3.9	4.4	4.3
Wm1	5.1	4.7	5.5	5.2
Lm2	6.5	5.6	7.2	6.5
Wm2	4.2	3.9	4.3	4.2

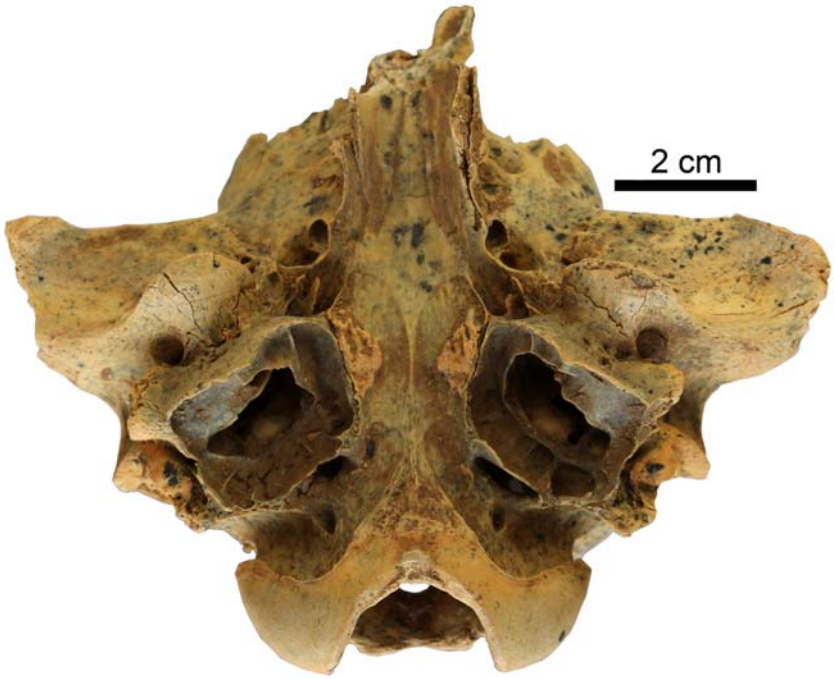

Fig. 2. *Canis lupus*, cranial fragment (ZIN 37265) from Geographical Society Cave, ventral view.

preangular lobe, which is characteristic of *N. procyonoides*. Cheek teeth are apically worn. By its dimensions, the fossil finding approaches to the largest specimens of the continental subspecies *N. p. ussuriensis* (Matschie, 1907), which now occurs in the southern part of the Russian Far East, and exceeds the size of mandibles of the insular subspecies *N. p. viverrinus* Temminck, 1838 from Japan (Tab. 1). Especially impressive seems to be a pronounced height of the body of mandible and a marked length of carnassial tooth. Even larger size of m1 was observed in the fossil *N.* cf. *sinensis* from Zhoukoudian (Locality 3) in China (Pei, 1936).

Among the premolars p2–p4, only p4 bears well pronounced posterior accesory cusp. The lower carnassial tooth m1 has a large metaconid. Talonid of this tooth is characterized by wide and deep basin divided into two parts by transverse ridges running from hypoconid and entoconid. The latter is smaller than hypoconid and is shifted farther backwards. Hypoconulid is not developed. The molar m2 shows a high metaconid and rather small talonid with depression in inner part.

Genus *Canis* Linnaeus, 1758
Canis lupus Linnaeus, 1758

By the number of bone remains found in the cave, wolf occupies the first place among Carnivora. Ovodov (1977) points out 390 bones from 13 individuals. I have counted 392 wolf specimens.

Description. *Skull fragments*. There is the rostral part of cranium with P2 and P3 (ZIN 37274-2), which breadth in the area of canines is nearly 50 mm, as well as the upper part of neurocranium (ZIN 37274-1) with minimal width 40.5 mm. Ones more fragment represents the part of basicranium (ZIN 37265) with open auditory bullae and with both occipital condyles (Fig. 2). The breadth at occipital condyles is 48.4 mm; the mastoid breadth is nearly 83 mm. Inner margins of auditory bullae run non-parallel as in the recent *C. lupus*, being, however, more pronouncedly approximated to each other.

Mandibles are high. Their height behind m1 constitutes 30.2–37.2 mm (mean 34.14 mm, *n*=5), the height behind p2 varies from 26.9 mm to 31.8 mm (mean 29.14 mm, *n*=11). By these dimensions, mandibles exceed not only the examined specimens from the Late Pleistocene of Europe (Tab. 2), but also the mandibles from the Late Pleistocene of Yakutia in Russia. In the latter, the height behind m1 is 26.0–34.7 mm (mean 30.13 mm, *n*=7) and the height behind p2 is 23.3–29.7 mm (mean 25.97 mm, *n*=8). Mandibles of the recent *C. lupus* from Primorskii Territory are also markedly lower, their height behind m1 is evaluated as 26.2–33.6 mm in males (mean 29.26 mm, *n*=8) and as 23.6–27.6 mm in females (mean 25.75 mm, *n*=8), whereas the height behind p2 corresponds to 21.8–25.9 mm in males (mean 24.12 mm, *n*=8) and 18.6–23.9 mm in females (mean 21.14 mm, *n*=8).

Upper teeth. By their shape, upper and lower incisors reveal no difference from those of the recent *C. lupus* (Fig. 3). Their dimensions vary depending on the degree of wear and, probably, on sex. The measurements of upper incisors are: I1 (L=6.8 mm, W=6.2 mm, *n*=1), I2 (L=7.6, 7.8, 8.8, 9.5 mm, W=7.0, 6.1, 7.8, 8.7 mm, correspondingly; *n*=4) and I3 (L=9.9, 10.2, 10.2 mm, W=7.5, 8.2, 8.8 mm, correspondingly; *n*=3). The

Table 2. Measurements (mm) of upper tooth rows of Late Pleistocene *Canis lupus*.

Measure-ments	Geographical Society Cave, Russia		Khaptashinsky Yar, Yakutia, Russia	Gailenreuth, Germany		Srbsko Chlum-Komín Cave, Czech Republic	
	ZIN 37267, sen.	ZIN 37266, ad.	GMY 3728, ad.	NHM 404b	NHM 403	NHMP R3717	NHMP R5228
LP4–M2	44.9	45.8	47.4	49.3	43.4	46.2	46.9
LM1–M2	24.4	25.5	25.8	27.3	24.0		
Teeth							
LP4	25.5	25.4	26.7	26.8	23.8	26.6	25.8
LpaP4	17.3	16.7				17.8	17.2
WP4	15.0	13.4	13.4	16.3	15.0	15.2	15.5
LM1	16.2	15.7	16.2	17.8	15.9	16.4	16.7
WM1	19.8	18.2	20.5	21.0	18.0	19.7	19.7
LM2	8.2	7.6	9.5	9.7	7.9	8.3	8.8
WM2	11.0	10.6	12.9	12.6	10.7	11.8	11.5

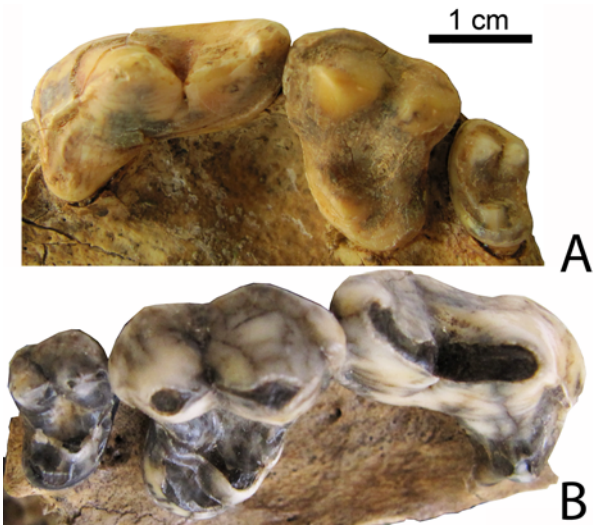

Fig. 3. *Canis lupus*, upper teeth row P4-M2 from Geographical Society Cave, Russia (A) and from Srbsko Chlum-Komín Cave, Czech Republic (B); occlusal view.
A — ZIN 37266, left; B — NHMP R3717, right.

largest specimens exceed maximum size of incisors in the recent *C. lupus* from Primorskii Territory.

Males of *C. lupus* are known to be larger than females; the difference in size is well apparent in the dimensions of canines. In the sample of the recent wolf from Primorskii Territory, the anterior-posterior length of the male upper canine constitutes 12.7–14.5 mm and width 7.4–8.8 mm (*n*=9). In females the upper canine varies from 11.6 mm to 12.8 mm in length and from 6.8 to 8.0 mm in width (*n*=8). The fossil sample contains six male canines exceeding 13.0 mm (13.1–14.9 mm) in length and 9.0 mm (9.3–10.0 mm) in width. Two specimens (W=8.1, 8.9 mm) are referred to female.

A single P2 (L=14.0 mm, W=6.2 mm) bears a distinct posterior accessory cusp. P3 markedly varies in size. Maximum length of ZIN 37274-3 exceeds that of P3 in all Pleistocene wolves measured (Tab. 4). The posterior cusp is well developed; a knob-like postcingulum is well defined behind it.

The upper carnassial tooth P4 is typical of *C. lupus*. The greatest length (25.4–28.0 mm, *n*=3) somewhat surpasses this dimension in the recent wolf from Primorskii Territory (22.1–26.1 mm, *n*=20). The protocone is slender and is located far ahead of the level of the paracone apex. The length of metastylar blade, with regards of the tooth greatest length, does not differ from that of other measured fossil specimens.

M1 is densely crowded to P4. By the length and width, M1 resembles the Pleistocene *C. lupus* from Northern Eurasia (Tab. 4). The paracone is higher than metacone. The protocone is shifted to the anterior margin of talon. The hypocone is diminished. Paraconule is not developed. Metaconule is ridge-like. The lingual cingulum is well differentiated.

M2 is more pronouncedly diminished, with regards to the relative size of this tooth, than in other examined wolves. The ratio between the length of M2 and that of P4 is calculated as 29.9 and 32.1% respectively (*n*=2), whereas that of the measured fossil specimens from other regions constitutes 31.2–38.3% (mean 35.4%, *n*=9). This index calculated for the recent wolf from Primorskii Territory varies from 31.2% to 38.3% (mean 34.7%, *n*=20). M2 is not densely crowded to M1 and more markedly shifted lingual as compared to *C. lupus* from the Late Pleistocene of Europe (Fig. 3).

Lower teeth. Dimensions of lower incisors: i1 (L=5.9 mm, W=4.6 mm), i2 (L=7.1, 7.5, 7.9 mm, W=6.1, 6.2, 6.5 mm, correspondingly; *n*=3) and i3 (L=7.3, 7.5, 7.8 mm, and W=6.6, 7.0, 8.0 mm, correspondingly; *n*=3).

Males of the recent wolf from Primorskii Territory have the length of lower canine 12.5–14.5 mm and width 8.0–9.6 mm (*n*=10). The female canine length is 11.1–12.8 mm and width 7.5–8.3 mm (*n*=7). The fossil sample is found to involve 9 male lower canines with the length exceeding 13.0 mm (13.0–15.2 mm) and width exceeding 8.5 mm (8.5–9.8 mm). Females were recognized by four canines (L=11.8–13.0 mm, W=8.1–8.2 mm).

The lower premolar p1 is single-cuspid (L=5.8-6.8 mm, W=5.5–5.3 mm, *n*=3). The premolar p2 reveals

Table 3. Measurements (mm) of mandibles of Late Pleistocene *Canis lupus*.

Measure-ments	Geographical Society Cave, Russia						Obman-chivoye, Yakutia, Russia	Gailenreuth, Germany		Srbsko Chlum-Komín Cave, Czech Republic	
	ZIN 37268	ZIN 37269	ZIN 37273	ZIN 37270	ZIN 37272	ZIN 37271	GMY 5171	NHM 404c	NHM 403a	NHMP R3720	NHMP R5159
Lc1–m3	123.8							117.8		116.6	113.7
Lp1–m3	99.2		101.8					97.5	103.0		
Lp2–m2	87.8	87.8	89.7	88.4	86.0	87.6		85.4	85.1		
Lp1–-p4	52.8	34.6	55.5	54.9				52.3	53.7		
Lm1–m3	46.5		48.3		47.3			47.7		45.6	44.8
Height behind m1	36.8	35.0	35.9		32.4		34.7	34.0	31.0		
Height behind p2	30.1	27.4	29.5	30.1	28.1	28.7	29.7	26.0	27.2	26.3	28.5
Teeth											
Lc1	14.5			15.7			14.6				12.7
Wc1	10.3			10.1			9.1				8.2
Lp1	6.0								5.5		
Wp1	5.1								4.9		
Lp2	12.7	13.1		13.8	13.1	14.1	12.4	13.1	12.8	13.7	12.8
Wp2	6.7	6.4		6.6	6.1	6.5	7.1	7.0	6.3	6.6	6.1
Lp3	14.2	15.3		15.3		15.0		14.1	14.4	14.8	14.2
Wp3	7.1	7.4		7.6		7.4		7.4	7.1	7.2	6.5
Lp4	16.1	17.1		16.9		16.9	15.3	17.1	15.8	16.9	16.0
Wp4	8.9	8.4		8.1		8.4	8.6	8.9	8.1	8.7	7.9
Lm1	30.7	–	30.3	31.3	28.6	30.5	29.8	30.4	28.1	28.9	28.1
Ltldm1	7.1	6.4	8.7	7.7	8.1	8.3	6.3	8.6	7.3	6.1	6.0
Wm1	11.8	11.9	12.5	12.2	12.3	12.3	12.3	12.6	12.1	12.0	11.0
Lm2	11.5	12.1		11.6	11.9	11.6	11.5	11.4	11.2	10.0	11.6
Wm2	9.0	9.2		8.3	9.1	8.7	8.6	8.8	8.1	8.5	7.9

Table 4. Measurements (mm) of upper cheek teeth of Late Pleistocene *Canis lupus*.

Localities	Museum number	LP3	WP3	LP4	LpaP4	WP4	LM1	WM1	LM2	WM2
Geographical Society Cave, Russia	ZIN 37267			25.5	17.3	15.0	16.2	19.8	8.2	11.0
	ZIN 37266			25.4	16.7	13.4	15.7	18.2	7.6	10.6
	ZIN 37274-3	18.9	8.4	28.0	19.3	16.0				
	ZIN 37274-2	15.7	7.3							
	ZIN 37274-4								9.6	12.4
Khaptashinsky Yar, Siberia, Russia	GMY 3728	17.5	7.3	26.7	–	13.4	16.2	20.5	9.5	12.9
	GMY 3729						16.5	19.4	8.2	11.8
Omolon River, Siberia, Russia	SESC 10	17.0	7.5	25.1	-	15.5	16.3	20.4	9.2	11.9
Karmalki, Russia	GMMK n/n	16.3	7.6	24.8	17.2	13.2	17.0	20.3	9.5	14.7
Kostenki, Russia	ZIN 36233			27.2	18.4	14.6	17.6	20.6		
Zoolithen (Gailenreuth), Germany	NHM 404b			26.8	–	16.3	17.8	21.0	9.7	12.6
	NHM 403			23.8	–	15.0	15.9	18.0	7.9	10.7
	NHM 24			24.9	–	12.4	15.8	20.0		
	NHMB 2001	17.4	8.3				16.6	20.3	10.0	12.0
	NHMB 28929	16.3	7.2	26.4	17.9	14.5	17.2	20.0	8.9	12.4
	NHMB 30370	15.4	6.5	23.9	16.5	13.1	15.8	19.5	8.3	12.0
Wierzchowska Górna, Poland	ISAK 6029	17.4	7.0	25.1	16.5	15.7	16.5	21.1	9.2	13.7
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R3717	17.7	7.2	26.6	17.8	15.2	16.4	19.7	8.3	11.8
	NHMP 5229			25.2	17.0	15.6			9.2	12.6
	NHMP 5228			25.8	17.2	15.5	16.7	19.7	8.8	11.5
	NHMP 504						18.0	21.3	8.9	13.8
	NHMP 4161	16.9	6.6							

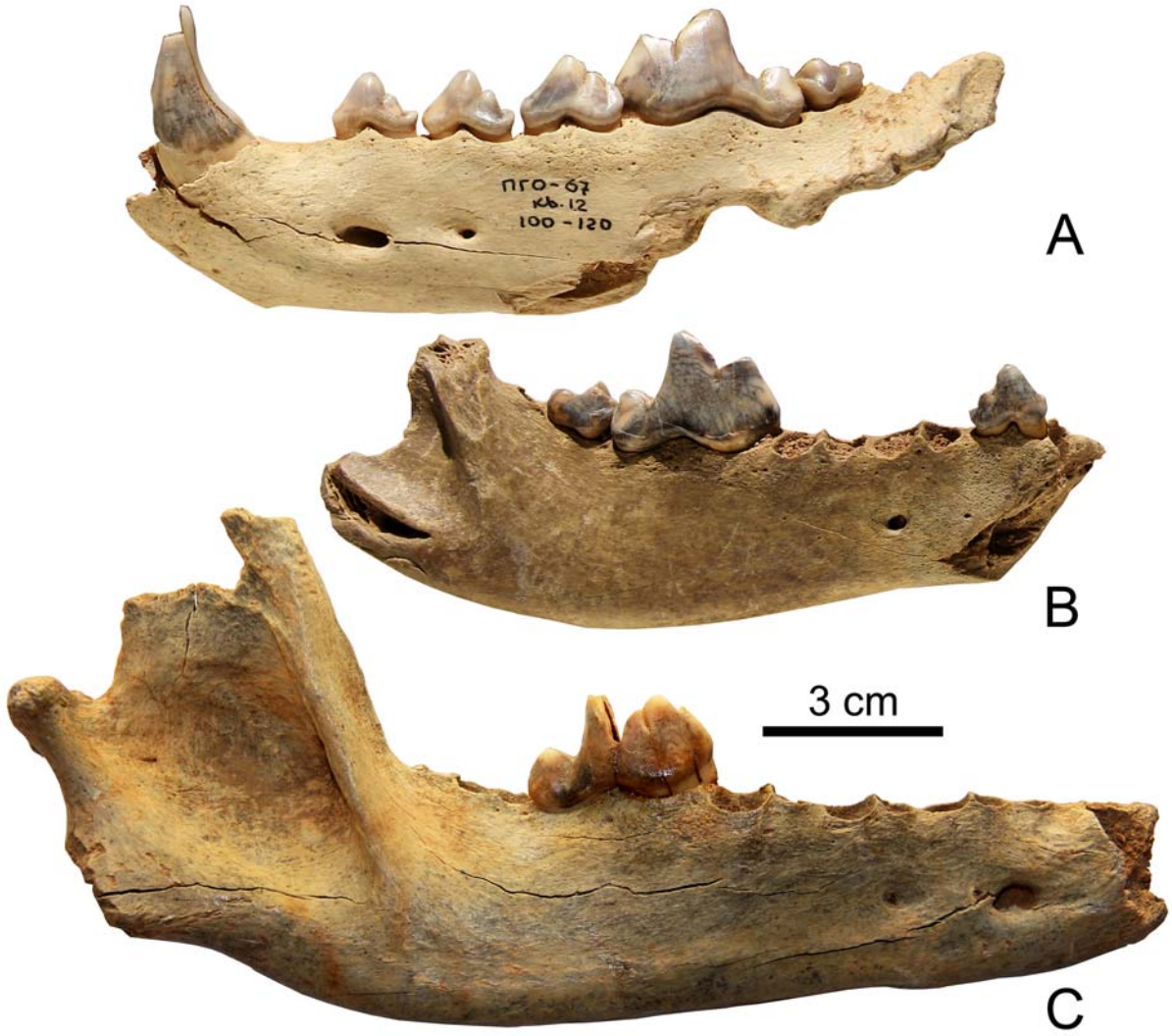

Fig. 4. *Canis lupus*, left (A) and right (B, C) mandibles from Geographical Society Cave, buccal views.
A — ZIN 37270; B — ZIN 37272; C — ZIN 37373.

the posterior accessory cusp (well-defined in 4 specimens and poorly developed in 6 specimens). All specimens of p3 show posterior accessory cusp and distinct postcingulid. Premolar p4 is larger in comparison with p2 and p3 and reveals higher located posterior accessory cusp. The principal cusp is lower than paraconid of m1 (Fig. 4A). Small additional tubercle is visible. Dimensions of premolars are given in Tab. 4.

The length of lower carnassial m1 in the collection from Geographical Society Cave varies from 28.3 mm to 30.8 mm (*n*=11) (Tab. 5), which corresponds to this dimension range in the recent wolf from Primorskii Territory (26.2–30.4 mm, n=18). However, the mean value of this length in the fossil sample (29.50 mm) surpasses that of the recent animals (27.72 mm). The explanation of this seems to be a noticeable difference in male/female ratio in compared samples — the fossil sample consists mainly from the male teeth. Males of the recent wolf from Primorskii Territory have the lower carnassial measured 26.2–30.4 mm in length (*n*=9), whereas females exhibit the length of this tooth 26.2–27.9 mm (*n*=9). The fossil sample provisionally includes 8 male specimens, with the length exceeding 28.8 mm, and 3 female teeth.

The fossil m1 is shaped typically of *C. lupus* (Fig. 5). Paraconid and protoconid are apically pointed. The metaconid is well developed, locating near the posterior margin of protoconid. The talonid constitutes less than 1/3 of the tooth greatest length (22.7–30.9%, mean 26.0%, *n*=10). The talonid of the recent-wolf specimens from Primorskii Territory was found to be somewhat longer (23.7–34.3%, mean 28.8%, *n*=18). The talonid basin is deep and opened lingual. The talonid cusps, hypoconid and entoconid, are distinct, single-pointed; the hypoconid is markedly higher than entoconid. The hypoconid is directly adjoined to the poste-

Table 5. Measurements (mm) of lower cheek teeth of Late Pleistocene *Canis lupus*.

Localities	Museum number	Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Ltldm1	Wm1	Lm2	Wm2
Geographical Society Cave, Russia	ZIN 37268	13.9	6.5	15.0	7.3	17.1	8.2	30.8	7.0	12.5	12.0	9.3
	ZIN 37269	13.4	6.4	15.5	7.6	17.1	8.5	–	6.2	12.2	11.8	9.2
	ZIN 37273							30.4	8.3	12.6		
	ZIN 37270	14.0	6.6	15.2	7.3	17.0	8.0	30.7	7.6	12.2	11.4	8.4
	ZIN 37272	13.1	6.6					28.5	8.3	12.2	12.3	8.8
	ZIN 37271	14.1	6.5	14.9	7.4	17.0	8.5	30.9	7.8	12.3	11.6	8.7
	ZIN 37274-5	14.3	7.1	16.3	8.1							
	ZIN 37274-7	13.1	6.4	15.5	7.6	17.5	9.3					
	ZIN 37274-8	13.4	6.6	14.8	7.2	17.2	8.4					
	ZIN 37274-9	13.2	6.5			16.7	8.5					
	ZIN 37274-6	13.7	7.3									
	ZIN 37274-254			14.3	7.2							
	ZIN 37274-257			15.0	8.1							
	ZIN 37274-17			14.7	7.6	17.0	8.6					
	ZIN 37274-10					16.4	8.4	28.8	7.3	12.4	11.0	8.0
	ZIN 37274-11					15.9	7.8	29.0	6.7	11.1		
	ZIN 37274-12					17.0	8.6	29.4	–	12.9		
	ZIN 37274-19					16.0	9.5					
	ZIN 37274-13							28.3	8.2	11.3		
	ZIN 37274-15							–	7.4	13.1	11.9	8.5
	ZIN 37274-16							29.3	6.9	11.9	12.3	8.9
	ZIN 37274-22							28.4	8.0	11.0		
Zoolithen (Gailenreuth), Germany	NHM 403a	12.8	6.3	14.4	7.1	15.8	8.1	28.1	7.3	12.1	11.2	8.1
	NHM 404	12.6	6.3	14.3	7.1	16.5	8.5	29.0	7.2	12.1	11.6	8.9
	NHM 404c	13.1	7.0	14.1	7.4	17.1	8.9	30.4	8.6	12.6	11.5	8.6
	NHM 23			13.7	5.9			27.8	7.1	11.1	11.8	8.0
	NHM 403b							29.7	8.0	11.4		
	NHMB 2001			14.9	7.3	16.1	8.9	30.0	7.3	11.6	11.5	8.6
	NHMB 28962			15.1	7.6	17.7	9.1	30.5	8.1	12.9	12.3	9.5
	NHMB 28963	12.4	5.9	14.8	7.0	16.8	8.4	30.6	9.0	11.6		
	NHMB 30370					17.0	8.7	ca28.0	7.4	11.7	11.6	8.7
Srbsko Chlum-Komín Cave, Czech Republic	NHMP 3720	13.7	6.6	14.8	7.2	16.9	8.7	28.9	6.1	12.0	12.0	8.5
	NHMP 4254	13.1	6.1	14.6	6.5			27.7	7.2	10.9		
	NHMP 6265	13.1	6.4	14.6	6.7	16.6	8.4	28.4	7.5	12.0	11.2	8.5
	NHMP 5159	12.8	6.1	14.2	6.5	16.0	7.9	28.1	6.0	11.0	11.6	7.9
	NHMP 5158	13.0	5.9	14.3	6.4	16.0	7.7				11.6	7.3

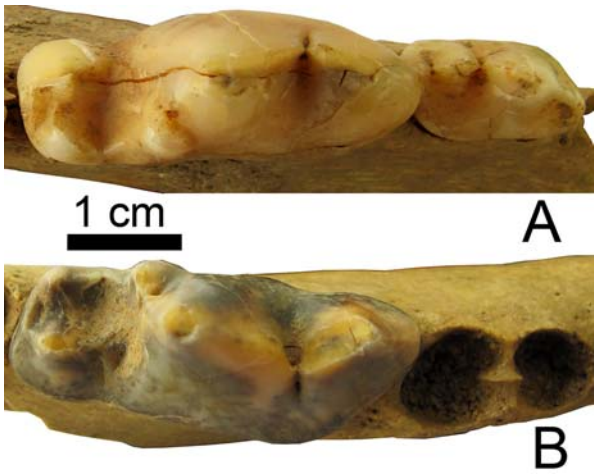

Fig. 5. *Canis lupus*, lower teeth p4 and m1 from Geographical Society Cave, occlusal view.
A — ZIN 37274-11, left; B — ZIN 37274-13, right.

rior margin of protoconid (n=12) or shifted backwards with respect to the latter (n=5). Entoconulid is absent. Two specimens having, nevertheless, a miniature accessory cuspid in front of the entoconid are present. The place of hypoconulid is detected by a transverse ridge.

The crown of m2 is characterized in the fossil material by the robust protoconid. The metaconid is lower and shifted backwards. The hypoconid, which is present on the talonid, is distanced from the protoconid by a deep valley. Entoconid is not developed. The lingual cingulid is visible in the anterior part of the tooth crown.

The last lower molar m3 is lost in all mandibles, but its alveoli are detected (excepting a single specimen).

Postcranial bones. Almost all elements of skeleton were found, including cervical vertebrae represented by two atlases and six axes (Tab. 6, Fig. 6). Long bones of limbs are mostly broken; however, several of them as

Table 6. Measurements (mm) of cervical vertebrae of Late Pleistocene *Canis lupus* from Geographical Society Cave, Russia.

Museum number	GL	BFcr	BFcd	LAd	H	LCDe	LAPa	BPacd	SBV
Atlas									
ZIN 37274-25	49.0	48.9	37.6	19.9	33.7				
ZIN 37274-179		44.7	37.5	20.8	33.7				
Axis									
ZIN 37274-26		34.5	–			60.1	60.7	36.0	24.8
ZIN 37274-180		35.5	25.8			59.5	58.9	ca35	23.9
ZIN 37274-181		36.4	22.7			60.7	58.2	–	27.0
ZIN 37274-182		34.9	22.9			57.2	55.9	33.1	26.7
ZIN 37274-183		40.6	–			–	–	–	29.2

Fig. 6. *Canis lupus*, cervical vertebrate from Geographical Society Cave, dorsal (A) and lateral (B) views.
A — atlas, ZIN 37274-25; B — axis, ZIN 37274-26.

well as many short limb bones remained intact (Fig. 7–10). These bones do not differ in their shape from corresponding bones of the recent *C. lupus*, being nevertheless more robust (Tab. 7–10).

Comparison. In the tooth size and morphology, the fossil wolf from Geographical Society Cave is similar to the recent subspecies *C. lupus coreanus* Abe, 1923 from Primorskii Territory, exhibiting however somewhat different proportion of the cranium. In spite of equal length of the lower carnassial with the recent specimens, the fossil mandibles reach a greater height. This suggests the reinforcement of tooth-bone strength

Fig. 7. *Canis lupus*, hind limb bones from Geographical Society Cave, dorsal (B, C) and lateral (A) views.
A — ulna, ZIN 37274-27; B — radius, ZIN 37274-29; C — radius, ZIN 37274-28.

Fig. 8. *Canis lupus*, right metacarpals from Geographical Society Cave, lateral (A, C, E, G) and medial (B, D, F, H) views.
A, B — Mc 2, ZIN 37274-37; C, D — Mc3, ZIN 37274-38; E, F — Mc4, ZIN 37274-39; G, H –Mc5, ZIN 37274-40.

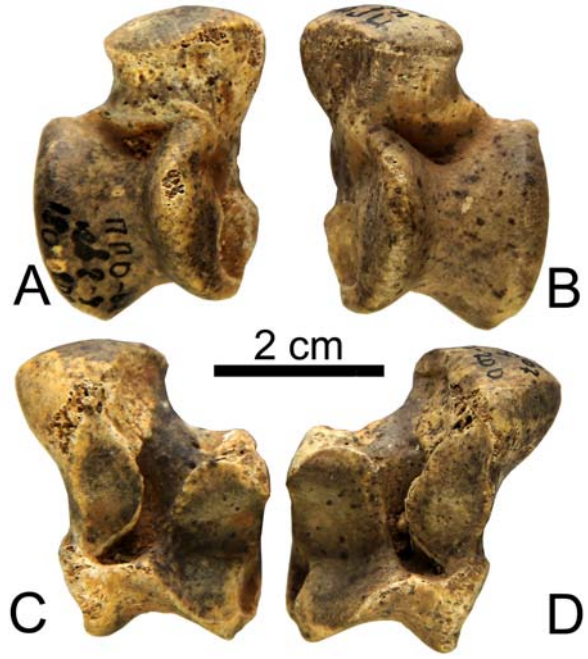

Fig. 9. *Canis lupus*, talus from Geographical Society Cave, dorsal (A, B) and ventral (C, D) views.
A, C — ZIN 37274-43, left; B, D — ZIN 37274-41, right.

and, hence, a capacity to gnawing thicker bones of potential prey. The Late Pleistocene wolf presumably consumed a large carrion in the southern part of the Russian Far East, as it has been already hypothesized for the fossil wolf on the basis of perished mammoths, rhinos, and bison carcasses present here (Leonard *et al*., 2007; Baryshnikov *et al*., 2010).

The tooth size of *C. lupus*, *C. lupus variabilis* Pei, 1934 and *C. chihliensis* Zdansky, 1924 from Early and Middle Pleistocene of China (Shanshenmiaozui, Ningyang, Zhoukoudian 1) is considerably smaller than that of the wolf from Geographical Society Cave (Pei, 1934; Zhang, 2001; Tong *et al*., 2012). Smaller teeth have also *C. lupus* specimens from the layer G in Grotta Ramanelli, Italy, which was dated between 69 and 40 thousand years (Sardella *et al*., 2014).

Taphonomy. Fossil remains of wolf are the most common among the canids in the material from Geographical Society Cave. The minimal number of indi-

Fig. 10. *Canis lupus*, right metatarsals from Geographical Society Cave, lateral (A, C, E, G) and medial (B, D, F, H) views.
A, B — Mt 2, ZIN 37274-45; C, D — Mt 3, ZIN 37274-46; E, F — Mt4, ZIN 37274-47; G, H — Mt5, ZIN 37274-48.

Table 7. Measurements (mm) of hind limb bones in *Canis lupus*.

Locality	Museum number	GL	Bp	SD	Bd	SLC	GLP	BG	SDO	DPA
Scapula										
Geographical Society Cave, Russia	ZIN 37274-185					34.6	41.5	26.3		
	ZIN 37274-186					34.8	40.7	25.2		
	ZIN 37274-187					32.1	35.1	21.5		
	ZIN 37274-189					29.1	37.4	22.0		
	ZIN 37274-255						33.6	21.6		
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5383					33.4	41.9	26.4		
Humerus										
Geographical Society Cave, Russia	ZIN 37274-192			17.7	44.4					
	ZIN 37274-193				41.9					
	ZIN 37274-196				45.8					
	ZIN 37274-195				43.0					
	ZIN 37274-197				40.3					
	ZIN 37274-198				39.2					
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5162	200.4		15.9	40.3					
	NHMP R5183	201.2		16.0	40.3					
Ulna										
Geographical Society Cave, Russia	ZIN 37274-27								27.8	32.3
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5387								27.6	34.8
Radius										
Geographical Society Cave, Russia	ZIN 37274-29	195.7	21.7	16.4	28.7					
	ZIN 37274-28	218.2	25.6	18.9	35.0					
	ZIN 37274-206		24.8	17.2						
	ZIN 37274-258			16.8						
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5170	198.4	22.8	16.8	30.4					
	NHMP R5386	198.5	25.3	17.5	32.8					
Mongolia, recent, ♀	ZIN 24365	199.6	19.1	14.1	26.9					

Table 8. Measurements (mm) of metacarpals in *Canis lupus* (to be continued).

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Mc2							
Geographical Society Cave, Russia	ZIN 37274-37	79.7	11.9	15.2	10.1	13.2	11.0
	ZIN 37274-55	84.6	12.5	16.0	10.0	13.4	12.7
	ZIN 37274-56	77.8	10.5	14.2	9.2	12.4	11.1
	ZIN 37274-57	81.5	10.9	15.5	9.4	13.9	11.3
	ZIN 37274-58	85.6	13.6	16.0	11.0	14.1	13.1
	ZIN 37274-59	84.5	12.5	15.5	10.7	13.9	12.5
	ZIN 37274-60		10.4	13.3	8.4		
	ZIN 37274-61	78.5	10.3	13.8	8.8	12.1	10.4
	ZIN 37274-62		9.6	13.8	9.3		
	ZIN 37274-229	76.9	10.7	13.4	8.6	11.9	10.4
	ZIN 37274-230	81.1	11.6	14.6	9.0	12.7	11.0
Gailenreuth Cave, Germany	NHM 222	76.7				13.3	
	NHM 222	72.8				12.9	
	NHM 403	73.2				11.6	
	NHM 403	76.8				12.8	
	NHM 403	80.7				13.3	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5214	75.7	11.0	13.4	8.2	12.0	10.9
Mongolia, recent, ♀	ZIN 24365	73.7	10.1	12.2	7.0	10.6	9.5

Table 8 (continued).

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Mc3							
Geographical Society Cave, Russia	ZIN 37274-38	86.7	12.1	15.6	9.4	12.6	12.8
	ZIN 37274-76		11.3	14.6	9.3		
	ZIN 37274-77		11.2	14.7	8.7		
	ZIN 37274-37	87.6	11.9	15.7	9.2	12.6	12.9
	ZIN 37274-78	90.0	11.5	14.8	8.6	11.7	12.1
	ZIN 37274-79	87.7	11.1	14.6	8.6	12.1	11.7
	ZIN 37274-80		11.9	14.5	9.7		
	ZIN 37274-81		11.6	15.1			
	ZIN 37274-82		10.7	14.6	8.0		
Gailenreuth Cave, Germany	NHM 222	86.6				11.3	
	NHM 222	90.0				12.5	
	NHM 222	78.1				10.5	
	NHM 403	98.7				13.7	
	NHM 403	84.3				12.1	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5390	88.4	13.1	16.7	8.5	12.4	13.6
Mongolia, recent, ♀	ZIN 24365	84.2	9.8	14.0	7.1	9.7	10.5
Mc4							
Geographical Society Cave, Russia	ZIN 37274-64	94.2	11.8	17.0	9.7	12.6	14.0
	ZIN 37274-65	90.5	11.3	14.4	9.2	12.0	12.7
	ZIN 37274-66	88.9	10.3	15.3	8.3	11.2	12.0
	ZIN 37274-63	98.1	11.4	14.3	7.8	10.4	11.4
	ZIN 37274-67		10.0	17.3	8.5		
	ZIN 37274-68		10.8	17.1	9.1		
	ZIN 37274-73		11.5	16.7	10.1		
	ZIN 37274-69	91.9	9.7	15.4	8.3	11.6	11.7
	ZIN 37274-39	95.7	12.2	16.8	9.2	12.6	13.6
	ZIN 37274-70	93.1	9.7	15.0	8.4	11.1	10.6
	ZIN 37274-71	87.0	9.6	13.8	7.7	10.8	11.7
	ZIN 37274-72		10.0	16.6	8.7		
	ZIN 37274-74		9.8	14.8	8.3		
	ZIN 37274-83	86.2	9.4	15.1	7.9	11.8	
	ZIN 37274-75		9.2	14.8	7.8		
Gailenreuth Cave, Germany	NHM 222	94.5				11.9	
	NHM 222	95.1				11.4	
	NHM 403	81.6				11.0	
	NHM 403	88.1				11.1	
	NHM 403	75.7				10.9	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5213	87.3	11.5	14.8	8.0	11.4	12.3
	NHMP R5214	86.9	11.2	14.5	8.3	11.5	12.2
	NHMP R601	89.3	11.2	14.9	8.2	12.2	12.0
Mongolia, recent, ♀	ZIN 24365	83.8	9.0	13.7	6.4	9.3	10.6
Mc5							
Geographical Society Cave, Russia	ZIN 37274-49	72.9	13.6	14.5	9.4	13.1	11.0
	ZIN 37274-53	75.6	13.7	16.1	9.7	13.0	11.2
	ZIN 37274-54		16.5	15.8	11.5		
	ZIN 37274-50	76.0	13.4	13.3	9.9	12.8	10.5
	ZIN 37274-40	72.8	13.2	14.1	9.3	13.3	10.7
	ZIN 37274-51		12.6	14.1	9.8		
	ZIN 37274-52	69.0	14.4	12.9	9.4	12.8	
	ZIN 37274-260				9.2	10.9	10.3
Gailenreuth Cave, Germany	NHM 222	74.9				12.9	
	NHM 222	72.6				12.9	
	NHM 403	65.0				13.1	
	NHM 403	76.0				13.5	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5211	71.6	14.3	15.3	8.9	12.7	11.3
Mongolia, recent, ♀	ZIN 24365	72.3	12.2	11.5	8.1	10.7	10.2

Table 9. Measurements (mm) of hind limb bones in *Canis lupus*.

Locality	Museum number	GL	Bp	SD	Bd	SH	LAR	GB
Pelvis								
Geographical Society Cave, Russia	ZIN 37274-214					26.8	26.5	
	ZIN 37274-213					25.9	26.5	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R3737					24.6	28.5	
Tibia								
Geographical Society Cave, Russia	ZIN 37274-222	217.8	ca38	19.9	29.4			
	ZIN 37274-223			18.3	32.3			
	ZIN 37274-221			17.4	30.6			
	ZIN 37274-225				30.1			
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5173	219.8	45.3	17.2	29.3			
Mongolia, recent, ♀	ZIN 24365	217.6	37.8	13.0	24.4			
Calcaneus								
Geographical Society Cave, Russia	ZIN 37274-33	61.3						24.4
	ZIN 37274-228	62.6						26.3
	ZIN 37274-32	58.5						26.1
	ZIN 37274-220	56.7						24.3
	ZIN 37274-30	53.7						21.1
	ZIN 37274-32	58.3						26.1
Tigrovaya Cave, Russia	ZIN 65	56.7						22.5
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R4160	57.4						23.0
	NHMP R5314	56.2						22.4
Mongolia, recent, ♀	ZIN 24365	50.9						19.6
Talus								
Geographical Society Cave, Russia	ZIN 37274-41	35.9						32.4
	ZIN 37274-42	34.4						–
	ZIN 37274-43	34.7						29.3
Mongolia, recent, ♀	ZIN 24365	30.0						19.6

viduals is 8 (calculated on the basis of the Mt3). The collection comprises almost all elements of the skeleton, including fragments of vertebrae and ribs; several cervical vertebrae and long bones (two radii and one tibia) as well as many short limb bones are intact (Figs 6–10).

Adult individuals predominate (except one subadult represented by a bone fragment with an unfused epiphysis). No juveniles are present. Males are most common (see above). Their prevalence, as well as the absence of juveniles, suggests that Geographical Society Cave was not used by wolves as a den for raising offspring, although these animals often create brood shelters in the Primorskii Territory in rock niches or beneath flat rocks (Yudin, 2013).

Many wolf bones have been gnawed by larger carnivores. Among metapodial bones, gnawed specimens constitute 33% (n=88). Several mandibles show the lower margin characteristically broken (Fig. 4A). Similar damage was observed on the hyena mandibles (Baryshnikov, 2014). In both cases, mandibles may have been gnawed by hyenas *Crocuta ultima* (Matsumoto, 1915), which presumably used the cave as a den for protecting their cubs. No traces of gnawing by larger carnivores are observable on the cervical vertebrae.

Eight of the wolf humeri are represented only by the distal end, which occasionally exhibits tooth-marks (Fig. 11C). There is an interesting group of calcanei with traces of gnawing from carnivore teeth on the lateral margin (Fig. 12). The width of the tooth punctures ranges from 4.8 mm to 8.8 mm (mean of 6.5 mm, n=4), which exceeds dimensions of punctures produced by wolves (Sala *et al*., 2014). The damage to the humeral and heel bones may have been caused by large carnivores such as hyenas or tigers detaching the distal portions of limbs, which have low value as food. The distal portions of limbs typically remain unbroken in places where tigers have consumed prey (Yudin & Yudina, 2009). It is therefore not surprising to find large fragments of radii, ulnae, and tibiae, as well as metacarpals, metatarsals and phalanges, intact after being detached from wolf carcasses.

The pattern of preservation is characteristic of natural mortality in a cave or for animals brought to a cave as a prey.

A part of the wolf bones exhibit minute traces of gnawing probably produced by hyena cubs (Fig. 13), which may have gnawed, in their cave-den, bones lying on the cave floor. There is a bone fragment with traces of acidic corrosion, which has been derived from the

Table 10. Measurements (mm) of metatarsals in *Canis lupus*.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Mt2							
Geographic Society Cave, Russia	ZIN 37274-106	80.8	11.6		9.3	11.3	9.0
	ZIN 37274-107		11.5	18.7	9.2		
	ZIN 37274-45	92.4	13.0	20.0	11.2	12.9	12.1
Gailenreuth Cave, Germany	NHM 222	89.3				12.5	
	NHM 222	91.8				13.7	
	NHM 403	85.0				12.0	
	NHM 403	87.3				13.6	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R4200	86.6	12.2	18.1	8.7	11.5	11.0
	NHMP R5199	81.0	12.3	16.5	8.5	12.9	10.7
	NHMP R5187	81.0	12.3	17.1	9.6	11.7	12.0
Mongolia, recent, ♀	ZIN 24365	82.0	9.7	14.9	6.1	9.9	9.4
Mt3							
Geographic Society Cave, Russia	ZIN 37274-94	104.4	14.0	18.7	9.7	13.1	12.8
	ZIN 37274-95	93.9	13.6	18.4	10.1	–	11.2
	ZIN 37274-99		11.6	17.3	8.8		
	ZIN 37274-97		13.5	18.6			
	ZIN 37274-98	96.1	13.3	19.0	9.8	13.0	12.7
	ZIN 37274-96	104.1	13.3	19.5	9.7	12.3	12.0
	ZIN 37274-46	103.5	14.8	19.5	10.4	13.3	14.0
	ZIN 37274-100	102.0	13.3	18.6	9.9	12.0	11.9
	ZIN 37274-101	101.2			10.5	13.0	13.2
	ZIN 37274-102	96.6			9.9	13.3	
	ZIN 37274-103		11.4	17.3	9.2		
	ZIN 37274-104	91.0	11.7	16.5	9.6	12.0	
Gailenreuth Cave, Germany	NHM 222	86.6				11.3	
	NHM 222	90.0				12.5	
	NHM 222	78.1				10.5	
	NHM 403	98.7				13.7	
	NHM 403	84.3				12.1	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5200	90.7	12.5	17.2	9.6	11.9	12.1
	NHMP R5188	90.1	12.3	17.1	9.6	11.7	12.0
Mongolia, recent, ♀	ZIN 24365	91.1	11.2	15.2	8.4	9.6	10.6
Mt4							
Geographic Society Cave, Russia	ZIN 37274-93		12.8	17.3			
	ZIN 37274-47	105.3	13.6	18.6	9.9	12.6	13.4
	ZIN 37274-91	106.5			10.1	12.5	13.0
	ZIN 37274-92		13.7	18.9			
Gailenreuth Cave, Germany	NHM 222	101.3				11.2	
	NHM 403	105.0				11.7	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5411	85.6	9.8	13.3	7.5	11.1	12.4
	NHMP R5216	96.7	11.5	15.7	7.7	11.0	12.2
	NHMP R5300	81.7	10.6	17.2	9.3	12.1	13.4
	NHMP R5201	92.8	11.5	15.6	9.1	11.2	11.6
	NHMP R5189	93.0	11.0	16.2	8.9	10.9	11.7
Mongolia, recent, ♀	ZIN 24365	93.2	10.6	14.5	7.1	9.3	10.3
Mt5							
Geographic Society Cave, Russia	ZIN 37274-48	97.0	12.7	15.4	9.9	12.3	12.0
	ZIN 37274-89	88.3	10.3	13.7	9.1	10.7	10.0
	ZIN 37274-90	86.8	11.4	15.5	8.6	11.9	10.9
	ZIN 37277-10		10.8	13.4	8.9		
Gailenreuth Cave, Germany	NHM 222	84.9				11.6	
	NHM 222	86.8				11.9	
	NHM 222	89.6				13.2	
	NHM 403	91.6				12.2	
Srbsko Chlum-Komín Cave, Czech Republic	NHMP R5202	82.7	10.9	13.9	9.3	11.9	10.4
	NHMP 5190	82.0	10.9	14.1	8.8	12.1	10.3
Mongolia, recent, ♀	ZIN 24365	82.4	11.8	10.1	6.8	8.9	9.3

Fig. 11. *Canis lupus*, distal fragments of humerus, caudal view.
A — ZIN 37274-194, right; B — ZIN 37274-190, right; C — ZIN 37274-193.

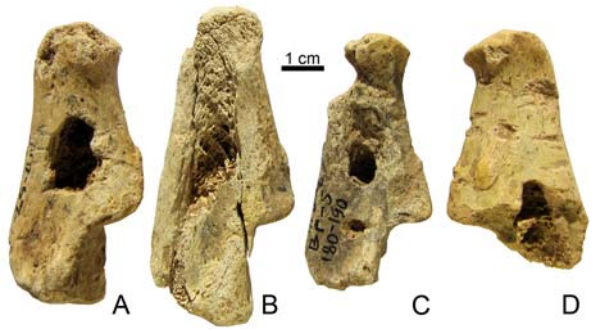

Fig. 12. *Canis lupus*, calcanei with signs of gnawing by large carnivores (presumably, by hyenas), lateral view.
A — ZIN 37274-32, right; B — ZIN 37274-33, right; C — ZIN 37274-31, right; D — ZIN 37274-34, left.

Fig. 13. *Canis lupus*, radius proximal fragments with signs of gnawing by large carnivores (presumably, by cup of hyenas), dorsal view (ZIN 37274-36, left and ZIN 37274-35, right).

stomach of a hyena. Most probably wolves (alive or dead) were the hyena prey and were brought into the cave by hyenas for consumption or for feeding their cubs. Pleistocene hyenas were larger than wolves, formed clans with complex social behavior, and likely represented dangerous competitors for the canids in the contest for hunting territory and available shelters.

Another potential source of the accumulation of wolf remains in the cave may be the tiger, *Panthera tigris* (L., 1758) or cave lion, *P. spelaea* (Goldfuss, 1810), whose bone remains were also found in Geographical Society Cave (Vereshchagin, 1971). Recent wolves are known to abandon tiger habitat in Primorskii Territory, being forced out by a stronger competitor (Kostoglod, 1982). This occurred in Lazovskii Nature Reserve; a tiger killed a wolf but neglected to consume it (Valova *et al*., 1989). In Pleistocene, wolves, most probably, became the prey of tigers only occasionally; therefore the role of this large cat in the accumulation of wolf bones in the cave was insignificant.

I have not observed reliable signs of modification by stone tools on the wolf bones or examples of burnt specimens.

Genus *Cuon* Hodgson, 1838
Cuon alpinus (Pallas, 1811)

In number of bone remains recovered in Geographical Society Cave, *Cuon alpinus* is noticeably inferior to *Canis lupus*. Ovodov (1977) counted 20 specimens of the red wolf; the examined material seems to confirm only 10 fossil remains.

There is the mandibular fragment (ZIN 37276) with p4 and m1 and alveoli of p2, p3 and m2 (Tab. 11, Fig. 14). By its height in front of m1 (25.2 mm), ZIN 37276 corresponds to the largest fossil specimens of *C. a. caucasicus* from Kudaro 3 Cave in Caucasus (Baryshnikov, 2012); however, the greatest length of its m1 does not differ from that in the majority of m1 specimens from the Caucasian collection. The length of p4–m1 (33.8 mm) is similar to maximum values of this dimension in the recent subspecies *C. a. alpinus* from the Russian Far East.

Table 11. Measurements (mm) of mandibles of *Cuon alpinus* and *Vulpes vulpes*.

Measurements	*C. alpinus*			*V. vulpes*	
	Geographical Society Cave		Primorskii Territory, recent	Geographical Society Cave	Primorskii Territory, recent
	ZIN 37276	ZIN 37277-6	ZIN 18262, ♂	ZIN 37286	ZIN 16706, ♂
Lc1–m3, alv				ca77	72.8
Lp1–m3				67.6	59.9
Lp1–p4				37.8	34.2
Lp4–m1	34.0		34.5	alv28.7	25.8
Lm1–m2				26.3	23.5
Height behind m1	26.1		23.8	17.4	14.5
Height behind p2	23.6		20.4	14.9	12.5
Teeth					
Lp4	13.9		13.7		
Wp4	6.2		6.5		
Lm1	21.6	22.5	22.9	18.3	15.8
Ltldm1	5.5	6.5	5.9	6.0	5.0
Wm1	9.1	10.9	8.5	7.0	6.4
Lm2				8.3	7.2
Wm2				6.1	5.5

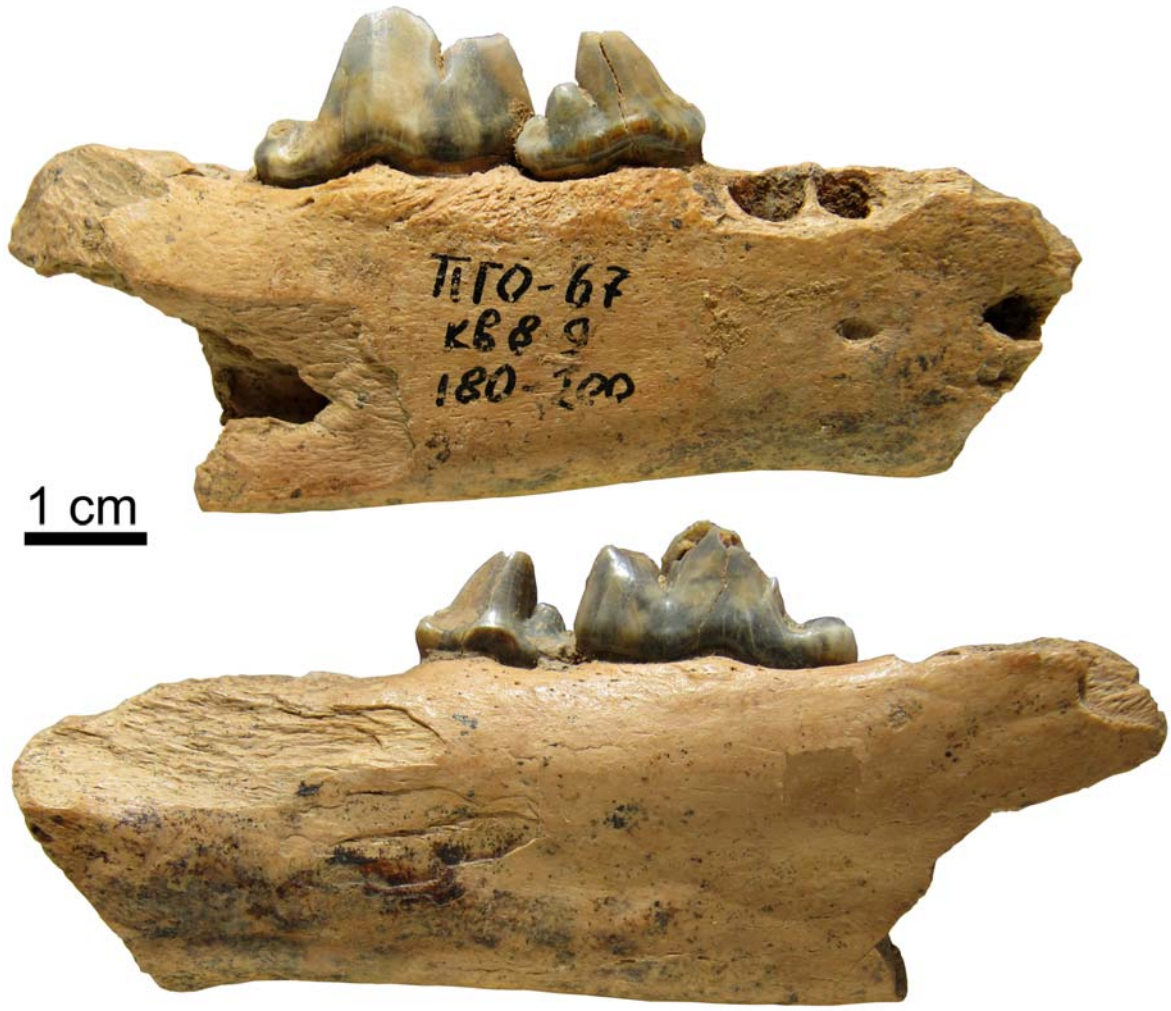

Fig. 14. *Cuon alpinus*, right mandible (ZIN 37276) from Geographical Society Cave, buccal (A) and lingual (B) views.

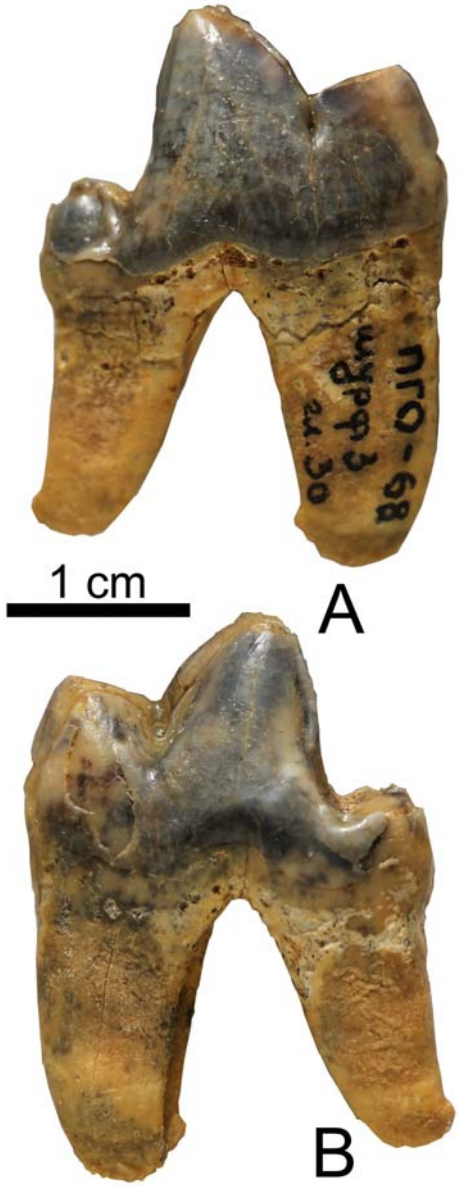

Fig. 15. *Cuon alpinus*, right lower molar m1 (ZIN 37277-6) from Geographical Society Cave, buccal (A) and lingual (B) views.

The lower premolar p4 is characterized by the high protoconid with a large accessory cusp at its base. A still smaller cuspid is observed behind the accessory cusp.

The lower carnassial m1 may be narrow (ZIN 37276) or somewhat widened (ZIN 37277-6) and exceed teeth of *C. a. caucasicus* in the width. By the length it corresponds to this tooth of the fossil *C. alpinus* from Upper Cave at Zhoukoudian in China (Pei, 1940). In both m1 specimens from Geographical Society Cave, metaconid is practically absent (Fig. 14, 15). The talonid is short; the robust hypoconid is shifted to its middle part. An inconspicuous transverse crest is present on the lingual side of hypoconid in ZIN 37277-6. The anterior-internal part of talonid is shaped as a small platform. Entoconid is not developed, but there is a rather low, serrated ridge along the talonid lingual margin. The crown buccal side bears a weak cingulid.

Several postcranial bones were found. The metacarpal 5 (ZIN 37277-15) is smaller and more slender as compared to the same bone of *C. lupus* (Tab. 12). In addition, there is a marked crest on the plantar side, which is inconspicuously defined in *C. lupus* (Fig. 16). The tibia (ZIN 37277-8) reveals smaller size than tibias of *C. lupus*, corresponding to that of *C. a. caucasicus* (Baryshnikov, 2012). Both tali (ZIN 37277-12, 37277-13) differ from the analogous bones of *C. lupus* by smaller size and by more pronouncedly backwards extended extremity of upper trochlea in the area of its sulcus (Fig. 17).

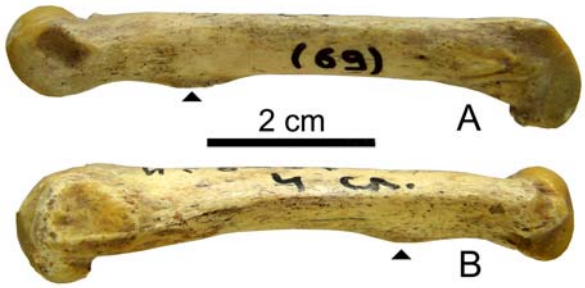

Fig. 16. *Cuon alpinus*, right metacarpal 5 (ZIN 37277-15) from Geographical Society Cave, medial (A) and lateral (B) views. Plantar ridge mark of up arrow.

Table 12. Measurements (mm) of hind limb bones of Late Pleistocene *Cuon alpinus* from Geographical Society Cave.

Bone	Museum number	GL	Bp	Bd	SD	Bd	Dd	GLP	BG	GB
Hind limb										
Scapula	ZIN 37277-7							33.6	21.6	
Radius	ZIN 37277-9				16.6					
Mc5	ZIN 37277-15	62.5	12.6	13.4	8.7	12.2	11.5			
Fore limb										
Tibia	ZIN 37277-8				15.2	27.7				
Calcaneus	ZIN 37277-10	52.3								21.7
	ZIN 37277-11	50.9								22.7
Talus	ZIN 37277-12	31.3								25.5
	ZIN 37277-13	30.1								27.2

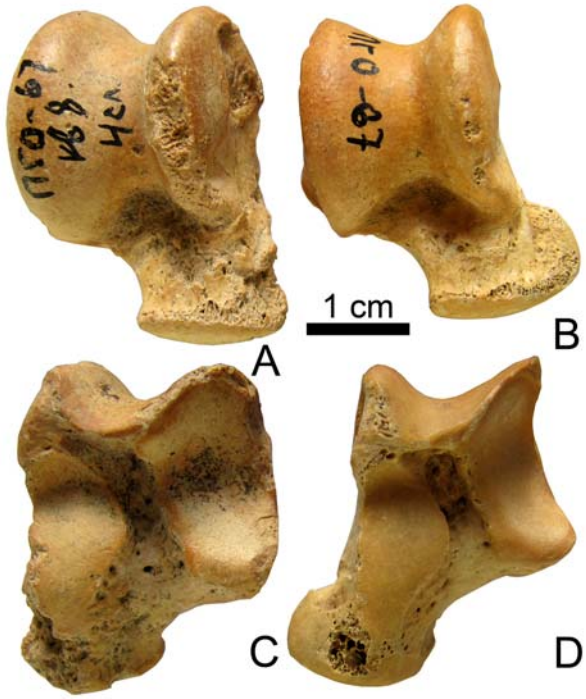

Fig. 17. *Cuon alpinus*, right tali from Geographical Society Cave, dorsal (A, B) and ventral (B, C) views.
A, C — ZIN 37277-12; B, D — ZIN 37277-13.

Genus *Vulpes* Frisch, 1775
Vulpes vulpes (Linnaeus, 1758)

Ovodov (1977) referred 19 bones of the red fox to 4 individuals. The material examined by me comprises 17 fossil remains of *V. vulpes*.

The right mandible (ZIN 37286-1) is large (Tab. 11). Its height behind the m1 as well as length of m1 and m2 markedly exceed those of fossil mandibles from Kudaro caves in Caucasus (Baryshnikov, 2012) as well as mandibles of the recent *V. vulpes dolichocrania* Ognev, 1926 from Primorskii Territory.

The upper dentition is represented by the isolated canine (ZIN 37286-4), two premolars P3 (ZIN 37286-9, 37286-6), and the molar M2 (ZIN 37286-2). The canine (L=6.7 mm, W=4.5 mm) corresponds by its size to canines of the recent *V. vulpes*. P3 is shaped ordinary of *V. vulpes*. Dimensions of both specimens (L=8.9, 9.3, W=3.6, 3.9, mm, correspondingly, *n*=2) resemble those of the recent red fox. The M2 does not differ by its length (6.2 mm) and width (8.9 mm) from the teeth of the recent *V. vulpes*. The paracone is markedly higher and larger than metacone. A well-defined cingulum is extended at bases of both cusps. The protocone is rather small and distanced from the paracone. The metaconule is smaller and adjoined to the metacone. There is a minute accessory cusp between the protocone and metaconule, so as three cusps enclose lingually the talon basin. The cingulum forms a high and elongated elevation, hypocone, on the lingual margin of the crown. The tooth exhibits 3 roots.

Fig. 18. *Vulpes vulpes*, right mandible fragment (ZIN 37286-1); buccal (A) and lingual (B) views.

The dimensions of the lower canine ZIN 37286-3 (L=8.6 mm, W=5.1 mm) make it possible to assign it to a female. There are also two lower premolars p2 (ZIN 37286-5 and 37286-8). Their size (L=8.7, 8.9 mm, W=3.8, 3.8 mm, respectively, *n*=2) is corresponds to that of the recent *V. vulpes.*

The tooth m1 from the mandible ZIN 37286-1 reveals a very high protoconid (Fig. 18). The metaconid is distinct and well separated from the posterior margin of protoconid. The talonid is characterized by the basin opened lingual. The hypoconid is robust and undivided. The entoconid is markedly smaller and lower and more pronouncedly shifted backwards with regard to hypoconid. Hypoconulid is not developed. The lower premolar m2 from specimen ZIN 37286-1 has a high protoconid and lower metaconid. Apices of both cusps lay on the same level in the lateral view. The depression (talonid basin) is placed behind these cusps, being surrounded by hypoconid, entoconid, and a miniature entoconulid. The crown has a cingulid visible in its anterior-external angle.

Bones of postcranial skeleton resemble by their size and morphology those of the recent *V. vulpes* (Tab. 13).

Conclusions

The analysis of paleontological collection from Geographical Society Cave ascertains the presence of the fossil remains of four canid species: *Nyctereutes procyonoides*, *Canis lupus*, *Cuon alpinus,* and *Vulpes vulpes*. These species occur in Primorskii Territory at present time (with exception for the recently extinct dhole). Therefore, the canid species diversity did not undergo changes in the southern part of the Russian Far East from the Late Pleistocene until now, i.e. over 40 thousands years.

Wolf (*Canis lupus*) was widely distributed in the Late Pleistocene in Siberia: from Altai and Sayan Mountains to the Arctic coast northwards. Red fox (*Vulpes vulpes*) was confined predominantly to the southern regions of Siberia, not migrating far northwards (Boesko-

Table 13. Measurements (mm) of limb bones in Late Pleistocene *Vulpes vulpes* from Geographical Society Cave.

Bone	Museum number	GL	Bp	SD	Bd	SDO	DPA	BPC	SLC	GLP	BG
Hind limb											
Scapula	ZIN 37286-17								19.0	20.7	12.8
Humerus	ZIN 37286-10			7.8	20.5						
Ulna	ZIN 37286-15					14.1	17.2	9.5			
Radius	ZIN 37286-14		12.9	8.9							
Mc4	ZIN 37286-16	52.2	5.7	4.2	6.4						
Fore limb											
Tibia	ZIN 37286-12		22.0	9.3							
	ZIN 37286-11			8.8	17.0						
	ZIN 37286-13				16.0						

rov & Baryshnikov, 2013). Dhole (*Cuon alpinus*), presumably, occurred in the southern mountain ranges of Southern Siberia; no finds of its dens or its cubs is known there in the historical time, which suggests only occasional occurences of these animals during their long migrations. The raccoon dog (*Nyctereuites procyonoides*) is recorded in the Late Pleistocene of Asiatic Russia only in the localities of Primorskii Territory. Therefore, the Late Pleistocene canid complex established on the basis of the collections from Geographical Society Cave involves hunters of mid-size ungulates (*Canis lupus*, *Cuon alpinus*), a hunter of rodents and birds (*Vulpes vulpes*), and a gatherer of smaller vertebrates and invertebrates (*Nyctereutes procyonoides*), which testifies the former abundance of fauna in the southern part of the Russian Far East.

A part of canid remains may have been accumulated in the Geographical Society Cave as a result of natural mortality of animals within the cave cavity. Nevertheless, the main source of bone accumulation appears to be a hunting activity of larger carnivores: hyena (*Crocuta ultima*) and large cats (*Panthera tigris*/ *P. spelaea*). Wolves and hyenas could also take a part in the modification of the bone assemblage in the cave. No traces of canid utilization by ancient people have been detected, suggesting the cave was used by hominins as a short-termed shelter.

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References

Baryshnikov G. 2012. Pleistocene Canidae (Mammalia, Carnivora) from the Paleolithic Kudaro caves in the Caucasus // Russian Journal of Theriology. Vol.11. No.2. P.77–120.

Baryshnikov G. 2014. Late Pleistocene hyena *Crocuta ultima ussurica* (Mammalia, Carnivora, Hyaenidae) from the Paleolithic site in Geographical Society Cave in the Russian Far East // Proceeding of the Zoological Institute RAS. Vol.318. P.197–225.

Baryshnikov G., Mol D. & Tikhonov A. 2010. Finding of the Late Pleistocene Carnivora in Taimyr Peninsula (Russia, Siberia) with paleoecological context // Russian Journal of Theriology. Vol.8. No.2. P.107–113.

Boeskorov G.G. & Baryshnikov G.F. 2013. [Late Quaternary Carnivora of Yakutia]. Saint-Petersburg: Nauka. 199 p. [in Russian].

Driesch A., von den. 1976. A guide to the measurement of animal bones from archaeological sites // Peabody Museum Bulletin. Vol.1. P.1–136.

Kostoglod V.E. 1980. [Wolf] // Rastitel'nyi i Zhivotnyi Mir Sikhote-Alinskogo Zapovednika. Moscow: Nauka. P.228–230 [in Russian].

Kuzmin Y.V., Baryshnikov G.F., Timothy J., Orlova L.A. & Plicht J. van der. 2001. Radiocarbon chronology of the Pleistocene fauna from Geographic Society Cave, Primorye (Russian Far East). Current Research in the Pleistocene. Vol.18. P.106–108.

Leonard J.A., Vila C., Fox-Dobbs K., Koch P.L., Wayne R.K. & Van Valkenburgh B. 2007. Megafaunal extinctions and the disappearance of a specialized wolf ecomorph // Current Biology. Vol.17. P.1146–1150.

Ovodov N.D. 1977. [Late Quaternary fauna of mammals (Mammalia) of south of Ussiry region.] // Yudin B.S. (ed.). Fauna i Sistematika Pozvonochnykh Sibiri. Novosibirsk: Nauka. P.157–177. [in Russian].

Pei W.C. 1934. On the Carnivora from Locality 1 of Choukoutien // Palaeontologia Sinica. Ser.C. Vol.8. P.1–216.

Pei W.C. 1936. On the mammalian remains from Locality 3 at Choukoutien // Palaeontologia Sinica. Ser.C. Vol.7. No.5. P.1–108.

Pei W.C. 1940. The Upper Cave Fauna of Choukoutien // Palaeontologia Sinica. Ser.C. Vol.10. P.1–84.

Rohland N., Pollack J.L., Nagel D., Beauval C., Airvaux J., Pääbo S. & Hofreiter M. 2005**.** The population history of extant and extinct hyenas // Molecular Biology and Evolution. Vol.22. No.12. P.2435–2443.

Sala N., Arsuaga J.L. & Haynes G. 2014. Taphonomic comparison of bone modifications caused by wild and captive wolves (*Canis lupus*) // Quaternary International. Vol.330. P.126–135.

Sardella R., Bertè D., Iurino D.A., Cherin M. & Tagliacozzo A. 2014. The wolf from Grotta Romanelli (Apulia, Italy) and its implications in the evolutionary history of *Canis lupus* in the Late Pleistocene of Southern Italy // Quaternary International. Vol.328–329. P.179–195.

Stuart A.J. & Lister A.M., 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. Quaternary Science Reviews. Vol.96. P.108–116.

Tong H.-W., Hu N. & Wang X.-M. 2012. New remains of *Canis chihliensis* (Mammalia, Carnivora) from Shanshenmiaozui, a Lower Pleistocene site in Yangyuan, Hebei // Vertebrate PalAsiatica. Vol.50. No.4. P.335–360.

Valova Z.G., Vasil'ev N.G., Zhivotchenko V.I., Makovkin L.I., Oliger T.I., Prisyazhniuk V.E., Prisyazhniuk N.P., Solomkina N.V., Khramtsov V.S. & Shaldybin S.L. 1989. [Lazovsky Reserve]. Moscow: Agropromizdat. 206 p. [in Russian].

Vereshchagin N.K. 1971. [The cave lion and his history in Holarctic and in territory of USSR] // Trudy Zoologicheskogo Instituta AN SSSR. Vol.49. P.123–199 [in Russian with English summary].

Yudin V.G. 2013. [The Wolf of the Far East of Russia]. Vladivostok: Dalnauka. 412 p. [in Russian].

Yudin V.G. & Yudina E.V. 2009. [The Tiger of the Far East of Russia]. Vladivostok: Dalnauka. 485 p. [in Russian].

Zhang Zh.-Q. 2001. Fossil mammals of early Pleistocene from Ningyang, Shandong Province // Vertebrate PalAsiatica. Vol.39. No.2. P.139–150.