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Finding of the Late Pleistocene carnivores in Taimyr Peninsula (Russia, Siberia) with paleoecological context

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ABSTRACT. The fossil bone remains of wolf (*Canis lupus*) and brown bear (*Ursus arctos*) from the permafrost of the Taimyr Peninsula have been examined. By the dimensions of the skull, the Late Pleistocene *C. lupus* resembles recent wolves of the Eurasian tundra, but exceeds them in the zygomatic width and length of the tooth row as well as possesses wider premolars. These peculiarities of the cranial and dental morphology suggest the Late Pleistocene wolves from north Siberia to consume more carrion than the recent wolves. Fossil remains of *U. arctos* were found far to north of the modern limits of brown bear distributional range in Taimyr. The robust size provides the possibility to presume that the Late Pleistocene brown bears ate a lot of animal proteins. The abundance of the representatives of the megafauna (mammoth, rhino, bison, musk-ox, etc.) in the arctic zone of Siberia as well as the absence of specialized mammal scavengers (hyenas) led the wolf and brown bears to be, most probably, among the main consumers of the large carcasses.

KEY WORDS: Carnivora, Pleistocene, Siberia, paleoecology.

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Находка на полуострове Таймыр (Сибирь, Россия) позднеплейстоценовых хищных млекопитающих и их палеоэкологическая интерпретация

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РЕЗЮМЕ. Изучены ископаемые кости волка (*Canis lupus*) и бурого медведя (*Ursus arctos*), найденные в мерзлоте на полуострове Таймыр. По величине черепа позднеплейстоценовый C. lupus сходен с современным волком из тундровой зоны Евразии, но отличается от него скуловой шириной, длиной зубного ряда и более широкими премолярами. Такая специализация черепной и зубной морфологии свидетельствует о том, что на севере Сибири позднеплейстоценовые волки потребляли больше падали, чем современные. Ископаемые останки *U. arctos* найдены севернее современной границы распространения бурого медведя на Таймыре. Крупные размеры предполагают, что значительную часть питания бурого медведя в позднем плейстоцене составляли животные корма. Обилие представителей мегафауны (мамонт, носорог, бизон, овцебык и др.) в арктической зоне Сибири и отсутствие здесь специализированных падальщиков (гиен), по всей видимости, кормиться волкам и бурым медведям на крупной падали.

КЛЮЧЕВЫЕ СЛОВА: Carnivora, плейстоцен, Сибирь, палеоэкология.

Introduction

Large carnivorous mammals (Carnivora) took an important place in the mammoth steppe biome of the Late Pleistocene of Northern Eurasia consuming ungulates as a pray and carrion. Carnivora fossil remains are scarce in the Siberian permafrost; therefore, each finding is important to provide the paleoecological information.

The Cerpolex/Mammuthus expedition, which has been organized to search frozen mammoth carcasses in the Taimyr Peninsula, revealed in 2000, 2001, and 2003 several fossil bones of carnivores north to 74°N that is one of the northernmost records of the Pleistocene Carnivora in the Eurasia.

The skull fragment (CERPOLEX 2000/131) and right mandible (CERPOLEX 2000/132) of the wolf (*Canis lupus*) as well as the second cervical vertebra (axis) (CERPOLEX 2003/680) of the brown bear (*Ursus arctos*) were found near the Taimyr Lake south to the Cape Sabler. The wolf bones seem to belong to a

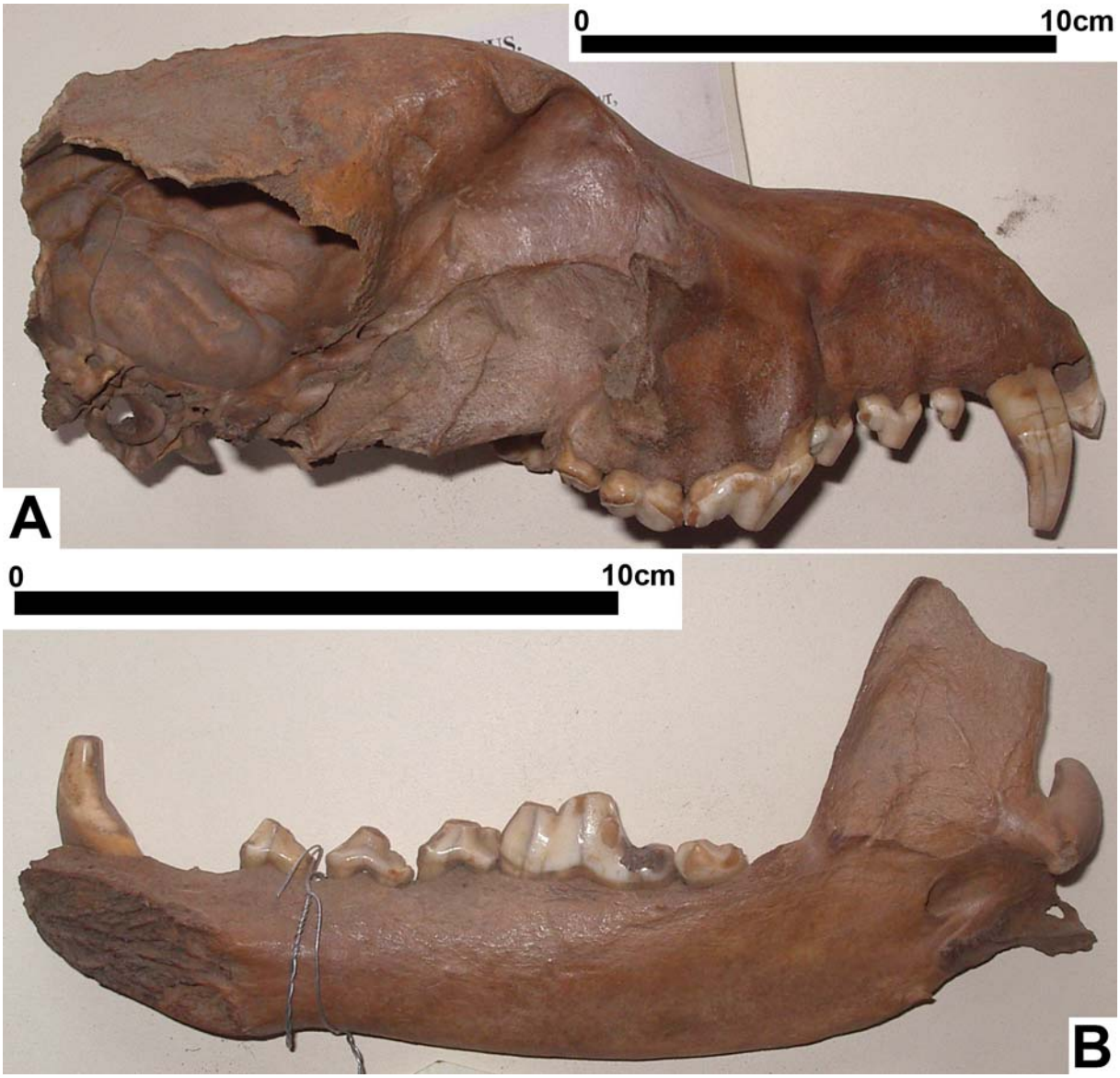

Figure 1. Wolf (*Canis lupus*). Skull fragment (A) and mandible (B).

single adult individual. The skull was dated by radiocarbon as 16,220 +/- 50 BP (MacPhee *et al*., 2002).

Another brown bear bone is a metatarsal IV (CERPOLEX 2003/872) was found farther to north, in a site at the Leningradskaya River (76°23′N, 102°01′E). It possesses radiocarbon date 12,500 +/- 70 BP (GrA 19290).

The examined material is kept at the museum of Khatanga settlement (Krasnoyarsk Territory, Russian Federation). For comparison, the collections of Zoological Institute, Russian Academy of Sciences in St. Petersburg (ZIN) and Natural History Museum in London (NHM) were used.

Description

Wolf (*Canis lupus* L. 1758). The occipital portion of the skull is absent as well as one of zygomatic arks (Fig. 1). Upper cheek teeth, two incisors, and one canine are present. Bone tissue is dense, weakly fossilized and colored pale brown. Tooth enamel of creamy color. Apices of tooth cusps are worn.

Right mandible was preserved nearly entirely, with only apex of coronal process being broken. Lower teeth, besides incisors and m3, present. There is no the premolar p1 as well as signs of its alveoli. Bone coloration and tooth wear corresponding to those of the skull.

Skull dimensions and rather small size of upper and lower canines testify its belonging to a female. The fossil skull does not differ by its size from female skulls of the recent wolf from northern Siberia (Tabs 1, 2). However both upper and lower tooth rows are longer as a result of increasing the premolar length, whereas posterior molars are, on the contrary, diminished. In

Table 1. Size of skulls and upper teeth of *Canis lupus* (females).

Measurements, mm*	Late Pleistocene		Recent				
	Lake Taimyr, Russia	Bernburg, Germany	Yamal Peninsula and Taimyr, Siberia (coll. ZIN)				
	CERPOLEX 200/131	NHM 38144	n	min	max	M	SD
Viscerocranium length (8)	146.7	149.5	5	130.2	148.9	140.34	7.09
Greatest length of the nasals (10)	89.3		5	83.2	98.3	90.04	5.69
Median palatal length (13)	122.1	126.1	5	115.7	128.2	119.60	5.12
C1–M2 length	109.2	109.5	5	96.8	105.4	99.88	3.45
P4–M2 length	47.0		5	45.9	48.0	46.98	0.87
Zygomatic breadth (30)	ca147.4	ca129.6	5	125.9	138.5	133.54	5.12
Least breadth of skull (31)	42.0	44.9	5	39.5	45.6	43.48	2.35
Frontal breadth (32)	49.2	47.5	5	41.9	49.0	45.38	2.86
Greatest palatal breath (34)	87.2	81.2	5	72.4	81.0	77.82	3.43
Breadth at the canine alveoli (36)	47.2		5	41.7	46.7	44.82	2.01
Greatest inner height of the orbit (37)	38.0	37.1	5	33.7	37.7	35.28	1.57
Upper teeth							
C1 length	13.0		4	13.3	15.2	14.07	0.94
C1 width	8.7		4	8.2	9.7	8.92	0.78
P1 length	7.4		5	6.7	8.4	7.54	0.64
P1 width	5.6		5	4.5	5.7	5.06	0.46
P2 length	14.5	14.5	4	13.5	14.6	14.00	0.45
P2 width	6.5	6.3	4	5.5	6.0	5.77	0.26
P3 length	16.6	15.7	4	15.0	16.7	15.82	0.74
P3 width	7.5	7.2	4	6.0	7.1	6.65	0.48
P4 length	25.6	25.5	5	23.4	26.0	24.72	1.16
P4 length of metastylar blade	7.7	8.1	5	7.5	9.8	8.52	0.92
P4 width	15.1	12.8	5	12.1	14.5	13.32	1.00
M1 length	15.9	16.7	5	15.9	17.2	16.48	0.49
M1 width	21.1	20.2	5	20.1	21.2	20.64	0.53
M2 length	8.3	9.7	5	8.8	10.5	9.64	0.64
M2 width	13.2	13.4	5	13.4	14.8	14.12	0.68

* Skull measurements according von den Driesch (1976). Abbreviation: M — mean value, max — maximal value, min — minimal value, n — number of specimens, SD — standard deviations.

spite of the only zygomatic ark is preserved, one may note that the skull width in the Late Pleistocene wolf exceeded that of the recent animals. The increasing of the skull width points out the pronounced development of the temporalis muscle.

Upper incisors are robust (I1 length 7.5 mm, width 5.6 mm, I2 length 8.8 mm, width 7.5 mm), whereas canine are weakly developed for the animal of such size. In the length of the carnassials, the fossil wolf demonstrates no difference from the recent wolf, notwithstanding its premolars are wider and more robust. The ratio of width and length of the upper premolar P3 (45.23%) exceeds average ratio in the recent animals (44.16%, n=20). Trenchant metastylar blade of the upper carnassial tooth P4 in the fossil wolf is comparatively shorter, constituting 30% of total tooth length (on average 34.3%, n=6, in the recent Siberian females).

The wolf from the Late Pleistocene of Western Europe belongs to the subspecies *C. lupus spelaeus* Goldfuss, 1821 established on the basis of findings from Zoolithen (=Gailenreuth) Cave in Germany. The female skull from the locality of Bernburg in Germany (NHM 38144) possesses comparatively wide P3 (45.8%) and short metastylar blade of P4 (31.8%), as in the fossil wolf from the Taimyr Peninsula.

The East European subspecies, *C. lupus brevis*, was described basing on the material from the Upper Paleolithic site of Kostenki 1 (layer 1); this animal being larger is size than the extant wolf from the tundra zone of Eurasia (Kuzmina & Sablin, 1995). P3 of the type male skull (ZIN 34327) is comparatively wide (45.7% of tooth length), the metastylar blade of P4 being not diminished (34.6% of the tooth length). The rostral skull portion is comparatively short, like that in the Taimyr skull.

C. lupus brevis is distinguished from the recent wolves by short limb bones. Presumably, its fore and hind limbs were, at least, 5 cm shorter (Kuzmina & Sablin, 1995: 57). This peculiarity is pronounced in the length of humerus, radius, and tibia as well as in the length of metacarpal and metatarsal bones. The length of the metatarsal 3 from Kostenki 1 is 87.8–98.4 mm (n=7) and 83.0–99.8 mm (n=8) in Zoolithen Cave, testifying the shortening of limbs to be characteristic of

Table 2. Size of mandible and lower teeth of *Canis lupus* (females).

Measurements, mm *	Late Pleistocene		Recent				
	Lake Taimyr, Russia	Zoolithen, Germany	Yamal Peninsula and Taimyr, Siberia (coll. ZIN)				
	CERPOLEX 200/132	NHM 403a	n	min	max	M	SD
Total length (1)	176.9		5	170.1	183.6	176.54	5.00
c1–m3 length	120.9		5	111.6	116.9	114.22	2.51
m1–m3 length	46.9		5	43.5	49.4	46.14	2.24
Height of the mandible behind m1 (19)	30.6	31.0	5	28.2	30.5	29.28	0.87
Height of the mandible between p2 and p3 (20)	24.7	27.2	5	22.7	26.0	24.44	1.21
Lower teeth							
c1 length	13.8		5	13.9	15.2	14.52	0.59
c1 width	9.3		5	8.9	10.5	9.60	0.60
p2 length	12.4	12.8	4	11.3	13.4	12.30	0.93
p2 width	6.4	6.3	4	5.9	6.4	6.15	0.21
p3 length	14.5	14.4	4	12.3	14.3	13.35	0.85
p3 width	7.0	7.1	4	6.1	6.8	6.52	0.31
p4 length	16.3	15.8	4	15.0	16.2	15.60	0.50
p4 width	8.6	8.1	4	7.1	8.3	7.87	0.57
m1 length	28.7	28.1	5	25.7	29.7	28.00	1.50
m1 length of trigonid	22.2	20.8	5	19.2	21.1	20.16	0.88
m1 width	11.7	12.1	5	10.3	11.3	11.02	0.41
m2 length	11.0	11.2	5	11.6	14.4	12.78	1.05
m2 width	8.9	8.1	5	9.0	10.2	9.46	0.44

* Table of symbols see in Table 1.

the West European fossil wolf as well. Most probably, the subspecies *C. lupus spelaeus* Goldfuss and *C. lupus brevis* Kuzmina et Sablin are synonyms.

Both the European fossil skulls examined are characterized in the enlargement of the anterior premolars and diminution of upper posterior teeth in size, i.e. these skulls demonstrate the same characters of dentition as the fossil wolf from Taimyr (Tabs 1, 2).

The widely spaced zygomatic arcs and robust premolars point out the reinforcement of masticatory apparatus. Such the reinforcement, together with weak canines, suggests the considerable portion of carrion and bones in the diet of the Pleistocene Siberian wolves.

Notably, the Pleistocene *C. lupus* from eastern Beringia by the skull shape, tooth wear, and isotopic data is also reconstructed as specialized hunter and scavenger of extinct North American megafauna (Leonard *et al*., 2007). In addition, East-Beringian wolves genetically differ from any modern Northern American wolf, and instead they appear most closely related to Late Pleistocene wolves of Eurasia. This uniquely adapted and genetically distinct wolf ecomorph suffered extinction in the Late Pleistocene, along with other megafauna.

The adaptation of *C. lupus* to scavenging differs from the hyena-like specialization of *C. dirus* Leidy, 1858 from Late Pleistocene of North America (Nowak, 1979; Kurtén & Anderson, 1980). In spite of the American species possesses widely spaced zygomatic arcs, its premolars are not so massive (the width of P3 with regard of the tooth length constitutes in average 43.57%, n=3), the upper carnassial tooth P4 being more robust, and upper molars not diminished (Merriam, 1912).

Brown bear (*Ursus arctos* L., 1758). The brown bear remains are represented by the second cervical vertebra (axis) and right metatarsal 4 (Figs 2, 3).

Axis (=epistropheus) is complete, belonging to the adult individual. The color of bone beige grayish; engraved traces of plant roots are visible. The vertebral foramen is not as circular as that in polar bear (*U. maritimus* Phipps, 1774), the arch is longer, caudal

Figure 2. Axis of brown bear (*Ursus arctos*).

Figure 3. Metatarsal 4 of brown bear (*Ursus arctos*).

articulating processes are not so widely spaced (Tab. 3). These characters allow the attribution of the fossil vertebra to *U. arctos*.

Metatarsal 4 is complete. The bone is colored grey, the bone tissue being dense, but its surface stronger eroded as compared to other findings examined. Most probably, it had lied on the ground for a longer time. In the proportions, the metatarsal 4 from Taimyr is similar to specimens of *U. arctos*. *U. maritimus* possesses broader proximal and distal portions of the bone that is associated with the broadening of foot in this species (Tab. 4). In the cave bear (*U. spelaeus* Rosenmüller, 1794) this bone is comparatively shorten, with the concave anterior margin of the proximal articular ridge.

The modern boundary of the distributional range of *U. arctos* runs on the south of Taimyr approximately from the mouth of the Yenisei River towards the mouth of the Khatanga River, involving left tributaries of the Dudypta River (71°30′N) as well as the Novaya River basin (72°30′N) (Heptner *et al*., 1967). Bears often overstep forest limits, penetrating to the tundra in the years of plenty of berries. Occasionally, animals run as far as 74°N (Zavatsky, 1993); however, we failed to find any information on the occurrence of the brown bear north to the Byrranga Mountains. Therefore the finding at the Leningradskaya River, which flows into the Tol Gulf of Kara Sea, originates from the pronouncedly more northern place (nearly 400 km) from the modern limit of regular habitats of *U. arctos*.

Both bones of *U. arctos* from Taimyr Peninsula are characterized in the very large size similar to that of the recent brown bear from Kamchatka (*U. arctos piscator* Pucheran, 1855). Most probably, these bones belong to the fossil subspecies *U. arctos priscus* Goldfuss, 1818 described from the Zoolithen Cave in Germany, which

Table 3. Size of axis of brown and polar bears.

Measurements, mm *	*Ursus arctos*			*Ursus maritimus*
	Lake Taimyr, Late Pleistocene	Bashkiriya, Recent	Kamchatka, Recent	Taimyr Peninsula, Recent
	CERPOLEX 2003/680	ZIN 15726, female	ZIN 32672, male	ZIN 8226, male
Length in the region of the corpus including the dens (LCDe)	81.1	67.7	73.6	74.9
Length of the arch (LAPa)	100.8	77.0	90.8	70.5
Breadth of the Facies articularis cranialis (BFcr)	74.6	54.3	62.7	59.7
Breadth across the Processus articularis caudales (BPacd)	56.2	42.1	59.9	54.1
Smallest breadth of the vertebra (SBV)	59.5	40.6	46.7	42.8
Breadth of the Facies terminalis caudalis (BFcd)	51.8	34.2	37.5	36.4
Height (H)	99.5	71.5	88.9	76.3

* Bone measurements according von den Driesch (1976).

Table 4. Size of metatarsal IV of brown and polar bears.

Measurements, mm *	*Ursus arctos*			*Ursus maritimus*
	Lake Taimyr, Late Pleistocene	Bashkiriya, Recent	Kamchatka, Recent	Russian Arctic, Recent
	CERPOLEX 2003/872	ZIN 15726, female	ZIN 32672, male	ZIN 15639
Greatest length (GL)	104.1	88.2	93.1	100.3
Breadth of the proximal end (Bp)	24.2	19.2	20.7	21.4
Depth of the proximal end (Dp)	28.8	23.8	27.5	27.6
Smallest breath in middle diaphysis (SD)	18.2	11.8	13.8	12.5
Breadth of the distal end (Bd)	22.5	18.1	20.7	23.7
Depth of the distal end (Dd)	20.3	16.0	17.2	19.8

* Bone measurements according von den Driesch (1976).

Figure 4. The mammoth bones gnawed by predators. Berelekh River, Yakutia. Photo N. Vereschagin.

demonstrates a large size. In Siberia, the fossil skull found at the mouth of Yana River in Yakutia has been referred to this subspecies (Baryshnikov & Boeskorov, 2005).

The size of the recent brown bears was shown to depend on the proportion of the animal proteins in their diet. Animals from the North American sea-coast, consuming salmons, twice exceed the weight of bears inhabiting inland regions and eating mainly plants (Hilderbrand *et al*., 1999). The role of animal proteins increases as well in the bears inhabiting Chukotka tundra in the northeastern Siberia (Chernyavskyi & Kretchmar, 2001). In the taiga of Middle Siberia, the brown bear only seldom haunts the elk (predominantly calves), often feeding, however, their carcasses (Zavatsky, 1993).

The large size of the Late Pleistocene *U. arctos* from Taimyr makes it possible to suggest the considerable portion of the animal proteins in its diet. In the arctic conditions, nourishing meet food had been necessary for storing the fat for long overwintering. The brown bear was capable to haunting ungulates, but, presumably, consumed carrion. Analogically, in the western Beringia, the short-faced bear, *Arctodus simus* (Cope, 1879) was a scavenger (Matheus, 1995, 2003). Presumably, this species competed with *U. arctos* for a meet food (Barnes *et al*., 2002).

Conclusion

The examination of the fossil bones of the wolf and brown bear from the Taimyr Peninsula provides the possibility to suggest these animals to consume carcasses of large animals in the Late Pleistocene of the Siberian arctic zone. This conclusion quite corresponds to the data on the mammoth steppe, occupying the vast territories of the Northern Eurasia, Alaska, and Yukon Territory, to have a high biological productivity, being characterized in the diversified megafauna (wooly mammoth, wooly rhino, steppe bison, musk-ox, and several species of horses and deer) (Guthrie, 1982, 2001). The ecological structure of the mammoth fauna paradox resembled that of the modern African savanna (Vereshchagin & Baryshnikov, 1992). In the both cases, the specialized scavengers, osteophagous (the cave hyena in the Eurasia and spotted hyena in the Africa) occur on the top of trophic pyramid.

The abundance of large herbivores in the Late Pleistocene of Northern Siberia suggests them to be a regular source of carrion as a result of their mortality by starvation, floods, bad weather. This led many carnivores of mammoth fauna to become scavengers or osteophagous. The analysis of a large assemblage of the mammoth bones at the Berelekh River in Yakutia has demonstrated that 19% of bones posses traces of carni-

vore gnawing (Fig. 4) (Vereshchagin, 1977). Meantime, the certain bones revealed this proportion to increase up to 42.5%. The absence of hyenas in the north of Eurasia provided a niche for scavengers, which was occupied by wolves, brown bears, and wolverines (*Gulo gulo* L.). In the severe environmental conditions of the Late Pleistocene arctic zone of Eurasia, the carrion had been one of the principal food sources for these animals.

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