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

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ABSTRACT. The analysis of bone remains of canids from the Upper-Pleistocene deposits of Geographical Society Cave in Primorskiy 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.

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 Primorskiy 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 14C 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.
Measurements. Dental measurements: \( L \) — greatest length, \( Lpa \) — length of paracon, \( Lrd \) — length of talonid, \( W \) — greatest width. Vertebræ measurements: \( BFcd \) — breadth of the caudal articular surface, \( BFcr \) — breadth of the cranial articular surface, \( BPacd \) — breadth between processi articularia caudales, \( GL \) — greatest length of atlas, \( H \) — height, \( LAd \) — length of the dorsal arch, median, \( LAPa \) — length of the arch including the processus 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 proximal end, \( Dp \) — breadth of the distal end, \( DPA \) — depth across the processus anconaeus, \( GB \) — greatest breadth, \( GL \) — 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. assuriensis, recent | N. p. viverrinus, recent |
|--------------|------------------|--------------------------|--------------------------|
|              | Geographical Society Cave, Russia | ZIN 2684, 6 | 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        |
| Lc2          | 6.3              | 5.5                      | 6.0                      | 5.7        |
| Lp2          | 5.9              | 5.3                      | 5.6                      | 5.4        |
| Wp2          | 5.9              | 6.2                      | 6.4                      | 6.0        |
| Lp3          | 6.4              | 6.2                      | 6.4                      | 6.0        |
| Wp3          | 2.8              | 2.8                      | 3.1                      | 2.5        |
| Lp4          | 8.4              | 7.0                      | 8.4                      | 6.9        |
| Wp4          | 3.6              | 3.4                      | 3.9                      | 3.5        |
| Lm1          | 13.3             | 12.1                     | 13.0                     | 12.4       |
| Lm2          | 13.3             | 12.1                     | 13.0                     | 12.4       |
| Wm1          | 5.1              | 4.7                      | 5.5                      | 5.2        |
| Wm2          | 6.5              | 5.6                      | 7.2                      | 6.5        |
| Wm3          | 4.2              | 3.9                      | 4.3                      | 4.2        |
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 accessory 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*.

| Measurements | Geographical Society Cave, Russia | Khaptashinsky Yar, Yakutia, Russia | Gailenreuth, Germany | Srbsko Chlum-Komin 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 | LpaP4 | WP4 | LM1 | WM1 | LM2 | WM2 |
|--------|-----|-------|-----|-----|-----|-----|-----|
|        | 25.5 | 17.3 | 15.0 | 16.2 | 19.8 | 8.2 | 11.0 |
|        | 25.4 | 16.7 | 13.4 | 15.7 | 18.2 | 7.6 | 10.6 |
|        | 26.7 | 13.4 | 16.2 | 20.5 | 9.5  | 12.9 | 12.9 |
|        | 26.8 | 16.3 | 17.8 | 21.0 | 9.7  | 12.6 | 12.6 |
|        | 23.8 | 15.0 | 15.9 | 18.0 | 7.9  | 10.7 | 10.7 |
|        | 26.6 | 15.2 | 16.4 | 19.7 | 8.3  | 11.8 | 11.8 |
|        | 25.8 | 15.5 | 16.7 | 19.7 | 8.8  | 11.5 | 11.5 |

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

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.

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, 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 lower carnassial 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=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=9). 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.
Table 3. Measurements (mm) of mandibles of Late Pleistocene Canis lupus.

| Measurement | Geographical Society Cave, Russia | Obman-chioye, Yakutia, Russia | Gailenreuth, Germany | Srbsko Chlum-Komín Cave, Czech Republic |
|-------------|----------------------------------|-----------------------------|-------------------|---------------------------------|
| Lc1–m3      | ZIN 37268 123.8                  | ZIN 37270 117.8             | NHM 404c 116.6    | NHMP R3720 113.7                |
| Lp1–m3      | ZIN 37269 99.2                   | ZIN 37272 101.8             | NHM 403a 97.5     | NHMP R5159 103.0                |
| Lp2–m2      | ZIN 37273 87.8                   | ZIN 37271 89.7              | NHMP R3720 85.4   | NHMP R5159 85.1                 |
| Lp1–p4      | ZIN 37270 52.8                   | ZIN 37272 55.5              | NHMP R3720 52.3   | NHMP R5159 53.7                 |
| Ln1–m3      | ZIN 37274 46.5                   | ZIN 37271 48.3              | NHMP R3720 47.7   | NHMP R5159 45.6                 |

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

| Localities                  | Museum number | LP3 | WP3 | 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| 7.7  | 6.3 | 10.6 |
| ZIN 37274-3                 | 18.9          | 8.4 | 28.0| 19.3  | 16.0|      |     |      |     |
| ZIN 37274-2                 | 15.7          | 7.3 |     |       |     |      |     |      |     |
| 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 | NNM 404b 26.8 | 16.3| 17.8| 21.0  | 9.7 | 12.6 |     |      |     |
| NNM 403                    | 23.8          | 15.0| 15.9 | 18.0  | 7.9 | 10.7 |     |      |     |
| NNM 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 | 8.9 | 12.4 |
| NHMB 30370                 | 15.4          | 6.5 | 23.9 | 16.5  | 13.1| 15.8 | 8.3 | 12.0 |
| Wierzchowska Góra, 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 | 9.7 | 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 |     |      |     |      |     |      |     |
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 (∑=11) (Tab. 5), which corresponds to this dimension range in the recent wolf from Primorskii Territory (26.2–30.4 mm, ∑=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 (∑=9), whereas females exhibit the length of this tooth 26.2–27.9 mm (∑=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%, ∑=10). The talonid of the recent-wolf specimens from Primorskii Territory was found to be somewhat longer (23.7–34.3%, mean 28.8%, ∑=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.

| Locality                  | Museum number | Lp2 | Wp2 | Lp3 | Wp3 | Lp4 | Wp4 | Lm1 | Lldm1 | 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 | 30.4| 8.3   | 12.6| 11.8| 9.2 |
|                           | ZIN 37273    | 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 | 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 | –   | –   | 28.5| 8.3   | 12.2| 12.3| 8.8 |
|                           | ZIN 37274-7  | 13.1| 6.4 | 15.5| 7.6 | 17.5| 9.3 | 11.5| 6.2   | 11.6| 6.9 | 12.1 |
|                           | ZIN 37274-8  | 13.4| 6.6 | 14.8| 7.2 | 17.2| 8.4 | –   | –     | 11.4| 6.9 | 12.1 |
|                           | ZIN 37274-9  | 13.2| 6.5 | 16.7| 8.5 | –   | –   | 28.5| 8.3   | 12.2| 12.3| 8.8 |
|                           | ZIN 37274-6  | 13.7| 7.3 | –   | –   | 14.3| 7.2 | –   | –     | 11.6| 6.9 | 12.1 |
|                           | ZIN 37274-254| 14.3| 7.2 | –   | –   | 15.0| 8.1 | –   | –     | 11.6| 6.9 | 12.1 |
| Geographic Society Cave, Russia | ZIN 37274-257| 14.7| 7.6 | 17.0| 8.6 | –   | –   | 28.8| 7.3   | 12.4| 11.0| 8.0 |
|                           | 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 | 12.6| 11.5| 8.6 |
|                           | ZIN 37274-12 | 17.0| 8.6 | 29.4| 6.7 | 12.9| 11.4| 8.8 |
|                           | ZIN 37274-19 | 16.0| 9.5 | –   | –   | 28.3| 8.2 | 11.3| 6.2   | 11.6| 6.9 | 12.1 |
|                           | ZIN 37274-13 | 17.2| 8.4 | 28.9| 6.1 | 12.0| 12.0| 8.5 |
|                           | ZIN 37274-15 | 12.9| 6.9 | 11.9| 6.3 | 11.6| 6.9 | 8.5 |
|                           | ZIN 37274-16 | 29.3| 8.0 | 11.0| 6.3 | 11.6| 6.9 | 8.5 |
|                           | ZIN 37274-22 | 29.3| 8.0 | 11.0| 6.3 | 11.7| 6.9 | 11.6| 6.9 | 8.5 |
| Geographical Society Cave, Russia | ZIN 37274-256| 13.7| 6.3 | 14.4| 7.1 | 15.8| 8.1 | 28.1| 7.3   | 12.1| 11.2| 8.1 |
|                           | 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 | –   | –   | 28.8| 7.3 | 12.4| 11.0| 8.0 |
|                           | NHM 403b     | 14.9| 7.3 | 16.1| 8.9 | 30.0| 7.3 | 12.9| 11.6| 8.6 |
|                           | NHMB 2001    | 15.1| 7.6 | 17.7| 9.1 | 30.5| 8.1 | 12.9| 11.6| 9.5 |
|                           | NHMB 28962   | 12.4| 5.9 | 14.8| 7.0 | 16.8| 8.4 | 30.6| 9.0   | 11.6| 6.9 | 12.1 |
|                           | NHMB 28963   | 17.0| 8.7 | ea28.0| 7.4 | 11.7| 11.6| 8.7 |
| Zoolithen (Gaillenreuth, Germany) | 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 | 16.9| 8.7 | 28.9| 6.1   | 12.0| 12.0| 8.5 |
|                           | 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    | 13.0| 5.9 | 14.3| 6.4 | 16.0| 7.7 | 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| 6.3 |

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.
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 vertebrae 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 (Shanshenmiaozi, Ningy- ang, 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-
### 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    |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-255 | 33.4| 41.9| 26.4|     |     |     |     |     |     |
| **Humerus**                           |               |     |     |     |     |     |     |     |     |     |
| Geographical Society Cave, Russia     | ZIN 37274-192 | 17.7|     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-193 |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-196 |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-195 |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-197 |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-198 |     |     |     |     |     |     |     |     |     |
| 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  |     |     |     |     |     |     |     |     |     |
|                                       | NHMP R5387    |     |     |     |     |     |     |     |     |     |
|                                       | ZIN 37274-27  | 27.8|     |     |     |     |     |     |     |     |
|                                       | NHMP R5387    | 27.6|     |     |     |     |     |     |     |     |
| **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|     |     |     |     |     |
|                                         | NHMP R5387    |     |     |     |     |     |     |     |     |     |
| Mongolia, recent, $\ddagger$            | 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|     |     |     |     |     |
|                                       | NHM 222       | 72.8|     |     |     |     |     |
|                                       | NHM 403       | 73.2|     |     |     |     |     |
|                                       | NHM 403       | 76.8|     |     |     |     |     |
|                                       | NHM 403       | 80.7|     |     |     |     |     |
| **Srbsko Chlum-Komín Cave, Czech Republic** | NHMP R5214 | 75.7| 11.0| 13.4| 8.2 | 12.0| 10.9|
| **Mongolia, recent, $\ddagger$**      | ZIN 24365     | 73.7| 10.1| 12.2| 7.0 | 10.6| 9.5 |
| Locality                          | Museum number | GL  | Bp  | Dp  | SD  | Bd  | Dd  |
|-----------------------------------|---------------|-----|-----|-----|-----|-----|-----|
| **Geographical Society Cave, Russia** |                |     |     |     |     |     |     |
| Mc3                               | 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, $^\gamma$**   | 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 37274-70 | 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 |     |     |     |
| **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, $^\gamma$**   | 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, $^\gamma$**   | 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 | Pelvis | Tibia    | Calcaneus | Talus         |
|---------------------------------------|---------------|--------|----------|-----------|--------------|
| Geographical Society Cave, Russia     | ZIN 37274-214 |        |          |           |              |
|                                       | ZIN 37274-213 |        |          |           |              |
| Srbsko Chlum-Komin Cave, Czech Republic | NHMP R3737    | 26.8   | 28.5     |           |              |
| Geographical Society Cave, Russia     | ZIN 37274-222 | 217.8  | 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-Komin 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         |

**Notes:**
- The number of individuals is 8 (calculated on the basis of the Mt3).
- The pattern of preservation is characteristic of natural mortality in a cave or for animals brought to a cave as a prey.
- 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 | 81.5 | 18.7 | 9.2 |
| | ZIN 37274-45 | 92.4 | 20.0 | 11.2 | 12.9 | 12.1 |
| | NHM 222 | 89.3 | 125 |
| | NHM 222 | 91.8 | 13.7 |
| | NHM 403 | 85.0 | 12.0 |
| | NHM 403 | 87.3 | 13.6 |
| 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 |
| Mongolia, recent, | ZIN 24365 | 82.0 | 14.9 | 6.1 | 9.9 | 9.4 |
| | ZIN 24365 | 91.0 | 11.7 | 16.5 | 9.6 | 12.0 |
| | NHM 222 | 86.6 | 11.3 |
| | NHM 222 | 90.0 | 12.5 |
| | NHM 222 | 90.3 | 13.7 |
| | 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 |
| **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 | 14.6 | 17.3 | 9.2 |
| | ZIN 37274-102 | 96.6 | 13.3 |
| | ZIN 37274-103 | 91.0 | 11.7 | 16.5 | 9.6 | 12.0 |
| | ZIN 37274-104 | 91.0 | 11.7 | 16.5 | 9.6 | 12.0 |
| | NHM 222 | 86.6 | 11.3 |
| | NHM 222 | 90.0 | 12.5 |
| | NHM 222 | 90.3 | 13.7 |
| | 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 |
| **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 | 11.6 | 17.3 | 8.8 |
| | ZIN 37274-92 | 13.7 | 18.9 |
| | NHM 222 | 101.3 | 11.2 |
| | NHM 403 | 105.0 | 11.7 |
| | 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 | 10.4 | 11.7 |
| Mongolia, recent, | ZIN 24365 | 91.1 | 11.2 | 15.2 | 8.4 | 9.6 | 10.6 |
| | ZIN 24365 | 91.1 | 11.2 | 15.2 | 8.4 | 9.6 | 10.6 |
| | 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 | 11.6 | 17.3 | 8.8 |
| | ZIN 37274-92 | 13.7 | 18.9 |
| | NHM 222 | 101.3 | 11.2 |
| | NHM 403 | 105.0 | 11.7 |
| | 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 |
| **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 |
| | NHM 222 | 84.9 | 11.6 |
| | NHM 222 | 86.8 | 11.9 |
| | NHM 222 | 89.6 | 13.2 |
| | NHM 403 | 91.6 | 12.2 |
| | NHMP R5202 | 82.7 | 10.9 | 13.9 | 9.3 | 11.9 | 10.4 |
| | NHMP R5190 | 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 |
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 Primorski 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.

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 *p*4 and *m*1 and alveoli of *p*2, *p*3 and *m*2 (Tab. 11, Fig. 14). By its height in front of *m*1 (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 *m*1 does not differ from that in the majority of *m*1 specimens from the Caucasian collection. The length of *p*4–*m*1 (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 |
| Lc1–m3, alv  | ZIN 37276    | ZIN 37277-6 | ZIN 18262, ♂ | ZIN 37286 |
| Lp1–m3       | 67.6         | 59.9        |               |              |
| Lp1–p4       | 37.8         | 34.2        |               |              |
| Lp4–m1       | 34.0         | 34.5        | alv 28.7      | 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**

| Teeth | *C. alpinus* | *V. vulpes* |
|-------|--------------|-------------|
| Lp4   | 13.9         | 13.7        |
| Wp4   | 6.2          | 6.5         |
| Lm1   | 21.6         | 22.5        |
| L1dm1 | 5.5          | 6.5         |
| Wm1   | 9.1          | 10.9        |
| 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.
The lower premolar p4 is characterized by the high protoconid with a large accessory cusp at its base. A still smaller cusp 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 37276-6. 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 postcrania 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).

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|     |     |
| M5        | 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|     |     |     |     |     |     |     |     |
|           | ZIN 37277-11  | 50.9|     |     |     |     |     |     |     |     |
| Talus     | ZIN 37277-12  | 31.3|     |     |     |     |     |     | 25.5|     |
|           | ZIN 37277-13  | 30.1|     |     |     |     |     |     |     | 27.2|

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

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

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 metacone is smaller and adjoined to the paracone. There is a minute accessory cusp between the protocone and metacone, 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.

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. Hypoclypid 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 hypoclypid, entoconid, and a miniature entoclypid. 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).

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

**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 |      |

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 occurrences of these animals during their long migrations. The raccoon dog (*Nyctereutes 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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