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Late Pleistocene arctic fox (*Alopex lagopus*) from Crimea, Ukraine

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Abstract

The teeth and bone fragments of *Alopex lagopus* of early Weichselian age from Mousterian layers of grotto Prolom 2 in Crimea have been studied. The Crimean fossil arctic fox was found to be smaller than the late Weichselian subspecies, *A. l. rossicus,* from the East European Plain, but it seems to be similar in dimensions to the recent insular subspecies, *A. l. spitzbergenensis*. From the latter, the Crimean arctic fox differs in the relatively longer carnassial teeth and relatively wider m1. In the Late Pleistocene of Europe, a progressive increase in size of *A. lagopus* is observed, that makes it possible to recognize two subspecies, stratigraphically replacing one another. The arctic fox from Prolom 2 is presumably referable to the subspecies *A. l. meridionalis*, while the animals from another Crimean Upper Paleolithic site, Siuren 1, are referred to *A. l. fossilis*.

1. Introduction

At the present time, the arctic fox, *Alopex lagopus* (L.), is confined to a circumpolar range, inhabiting the northernmost regions of Eurasia and North America. The nominotypical subspecies *A. l. lagopus* is known to occupy the Eurasian mainland and adjacent islands. A smaller subspecies, *A. l. spitzbergenensis* (Barrett-Hamilton et Bonhote), occurs in Spitsbergen and Franz Josef Land. Two larger subspecies, *A. l. beringensis* (Merriam) and *A. l. semenovi* Ognev, are found in the Commander Islands (Heptner et al., 1967).

In the late Pleistocene, the arctic fox was spread far to the south, reaching Spain and the southern part of France in Western Europe (Kurtén, 1968). In Eastern Europe, the southernmost records came from the Crimea, but the arctic fox has not been found in the Northern Caucasus. In Siberia it is known from the Altai Mountains (Denisova Cave) (Baryshnikov, 1999).

Several species and subspecies of small fossil foxes (*Vulpes meridionalis*, *Vulpes moravicus*, *Leucocyon lagopus fossilis*) described by Woldřich (1878) have been later synonymized with *A. lagopus* (Stehlin and Dubois, 1933, etc.). Beneš (1975) suggested that the material ascribed earlier to "*Vulpes*" *meridionalis* Woldřich (not Nordmann 1858) belongs to the arctic fox from the early Würm (interstadial W1/2), whereas the material formerly attributed to "*Leucocyon*" *lagopus fossilis* Woldřich belongs to the arctic fox from the late Würm stadials (W2 and W3). Consequently, both the names of Woldřich may be used for subspecies of *A. lagopus* from the Late Pleistocene. Thus, for Western Europe, two temporal subspecies are documented: *A. lagopus meridionalis* Woldřich (early Weichselian) and *A. l. fossilis* Woldřich (late Weichselian).

The fossil subspecies *A. l. rossicus* has been described from the Upper Paleolithic site Eliseevichi in Bryansk Province of the European Russia (Kuzmina and Sablin, 1993). *A. l. rossicus* has been also found in other sites of the same age in this region (Yudinovo, Kostenki), so it may be regarded as a marker for the late Weichselian in Eastern Europe (Fig. 1). This subspecies is similar to the recent mainland arctic fox in the length of the lower carnassial tooth m1, but it differs in its width: m1 in the fossil subspecies is relatively narrower (Sablin, 1994). In addition, its limb bones are smaller than in *A. l. lagopus* from the Eurasian tundra, being only somewhat larger as compared to *Vulpes corsac* L.

Fossil remains of arctic fox have been recorded in many Paleolithic sites of Crimea, either Mousterian

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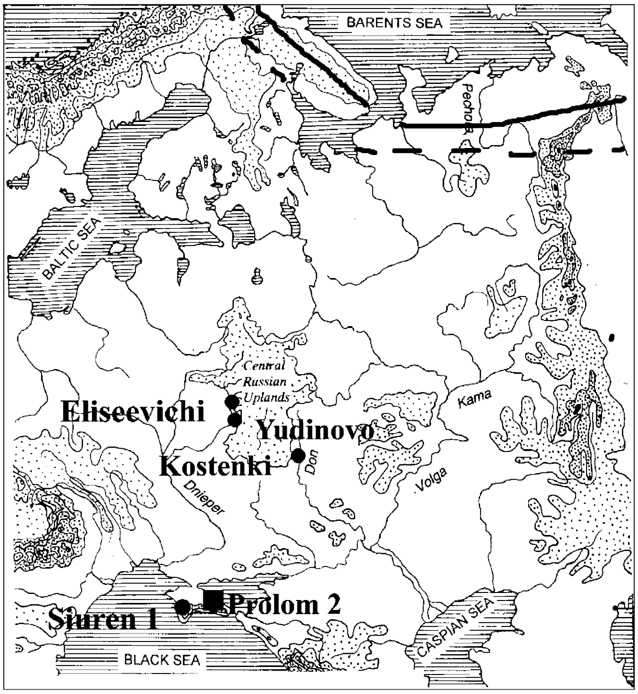

Fig. 1. Distribution of the arctic fox, *Alopex lagopus* in Eastern Europe. Bone remains from the early Weichselian sites are marked with solid squares, and the late Weichselian sites are marked by solid circles. Southern boundary of the modern breeding area and summer range is marked by continuous line, and winter range is marked by a dashed line. (Modern range boundaries, Heptner et al., 1967). Dotted areas show uplands and mountains.

(Adzhi-Koba, Kiik-Koba, Kosh-Koba) or Upper Paleolithic (Siuren 1) (Gromova and Gromov, 1937). This material has never been a subject of thorough study; in particular, the taxonomic position of the Crimean *A. lagopus* was not defined. The focus of this paper is the examination of the collection from the Mousterian levels in the grotto Prolom 2, which was collected by Dr. Yu. G. Kolossov, Kiev (excavations of 1982 and 1985).

2. Locality and material

The rather small grotto, Prolom 2 (45°07′N, 34°42′E), is located on the left bank of the Kuchuk-Karasu River near Belogorsk City at 22 m above river level. In ancient time, the site was beneath the cliff, but later that rocky peak was destroyed, fallen blocks now lying over the second cultural layer. The thickness of the crumbly deposits approaches 2 m. Four cultural layers of Mousterian age, containing numerous stone tool industries, were identified (Kolossov et al., 1993).

More than 3500 bone fragments of large mammals have been identified from Prolom 2. Many bones demonstrate signs of activity of cave hyenas which used the grotto as a den (Enloe et al., 2000). Approximately 400 bones in the assemblage have been referred to the arctic fox. These are mandible fragments, postcranial bones, and isolated teeth. The bones and teeth of the arctic fox were found in all layers of the grotto; approximately $\frac{1}{3}$ of them were enclosed in layer 2.

The faunal composition, as well as dental measurements of horses, are consistent with the first half of the Weichselian glacial period, older than 60 000 years ago (Eisenmann and Baryshnikov, 1995). The archeological evidence dates the second and third cultural levels as 75 000–45 000 years ago, suggesting an earlier age for the fourth layer (Kolossov et al., 1993; Chabai, 1998).

Two most representative samples from two Upper Paleolithic sites were used for comparison: Siuren 1 in Crimea and Yudinovo from East European Plain. The multilayer site in grotto Siuren 1, situated on the right bank of the Belbek River, contains Aurignacian industries. In the collection excavated by G. Bonch-Osmolowski in 1927–1928, the limb bones of the arctic fox predominate; cheek teeth are rare. For layer 2, a date, 17 100 ± 700 (GIN-8081), was obtained. Radiocarbon dates for modern excavations are 29 950 ± 700 (OxA-5155) for level Fb1 and 28 450 ± 600 (OxA-5154) for level Ga (Otte et al., 1996). The Yudinovo site has produced a series of radiocarbon dates from 12 300 to 18 630 years ago (Sinitsyn et al., 1997).

In addition, two tooth samples of *A. lagopus* from Spitsbergen (together with a specimen from Franz Josef Land) and Yamal Peninsula have been examined in order to compare the fossil arctic fox from Prolom 2 with recent insular and mainland populations.

Most material from Prolom 2 is housed at the Institute of Zoology, National Academy of Sciences of Ukraine in Kiev (with the exception of several specimens). Other specimens are deposited at the Zoological Institute, Russian Academy of Sciences in St. Petersburg (ZIN).

3. Methods

Measurements were taken with dial calipers with an accuracy of 0.5 mm. The tooth measurements have been processed with the help of Discriminant Analysis and Cluster Analysis from STATISTICA, 6.0. In the Discriminant Analysis I used the forward stepwise method.

4. Results

4.1. Sexual dimorphism

The frequency distributions of the lower carnassial length were examined for evidence of sexual dimorphism in *A. lagopus*. The distribution was unimodal in all the samples, with the exception of material from the Yamal Peninsula, which has demonstrated some bimodality (Fig. 2), possibly explained by higher sexual dimorphism in this population. The results do not indicate apparent sexual dimorphism in the tooth size of *A. lagopus*, so the samples were not divided into males and females in the present study.

4.2. Mandibles

There are several mandible fragments with preserved cheek teeth (Fig. 3). The dimensions of mandible fragments are given in Table 1. The specimens from Prolom 2 and Siuren 1 do not differ in size. In the length of p1–m3, the Late Pleistocene Crimean *A. lagopus* is similar to recent animals from Spitsbergen (44.3–51.5 mm, $M = 49.19$ mm, $n = 11$), being markedly smaller than arctic foxes from Yudinovo (48.6–54.9 mm, $M = 51.93$ mm, $n = 16$) and Yamal Peninsula (48.5–55.1 mm, $M = 52.38$ mm, $n = 20$).

4.3. Upper cheek teeth

The dimensions of the upper cheek teeth from Prolom 2 are shown in Tables 2 and 3. Only sparse data for P4 and for upper molars (M1 length 6.9, 7.4 mm, width 8.5, 8.7 mm; M2 length 4.6 mm, width 6.8 mm) are known for Siuren 1. Tooth sizes do not differ from those from Prolom 2.

The Late Pleistocene *A. lagopus* from the Crimean sites resembles, in the mean width of M1, the modern sample from Spitsbergen ($M = 9.40$ mm, $n = 12$). M1 is larger in the samples from Yudinovo ($M = 9.80$ mm, $n = 20$) and Yamal Peninsula ($M = 10.05$ mm, $n = 20$). In the ratio of mean length of P4 to mean width of M1, the examined samples form two groups: Yamal Peninsula and Spitzbergen (123%); and Yudinovo and Prolom 2 (128–129%). Therefore, in the Late Pleistocene *A. lagopus,* the upper carnassial tooth P4 is relatively longer as compared to that in living arctic foxes.

A discriminant analysis was based on three measurements of P4 (greatest length, length of metastylar blade, greatest width). This analysis indicated that the sample from Prolom 2 significantly differs from samples from Yudinovo ($P<0.0093$) and Yamal Peninsula ($P<0.00006$), but resembles that from Spitsbergen. The classification matrix of discriminant analysis demonstrates that only the Yamal Peninsula sample keeps most of its specimens (92%). Almost 71% of dental variation is explained by the first canonical axis, 25% by the second. The first canonical variate (Root 1) discriminates greatest width, and the second axis (Root 2) the length of metastylar blade and greatest length.

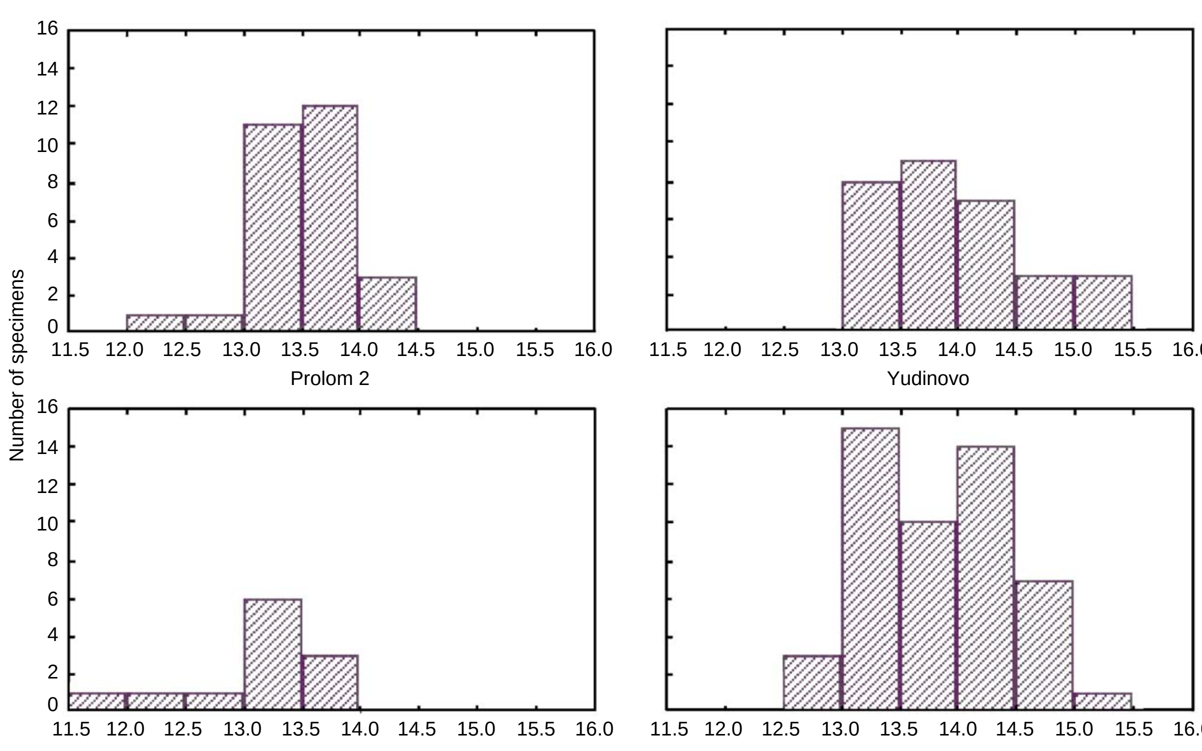

Fig. 2. Frequency distribution of greatest length of lower carnassial tooth m1.

Fig. 3. Mandible fragments of Late Pleistocene *Alopex lagopus* from grotto Prolom 2; ZIN 34596 (A, B) and ZIN 34598 (C, D). Labial (B, C) and lingual (A, D) views.

Table 1
Dimensions of mandibles of Late Pleistocene *Alopex lagopus* from the Crimea

Measurements (mm)	Prolom 2				Siuren 1	
	n	lim	*M*	SD	*n*	lim
Length total		85.7	—	—		
Alveolar length p1–m3	8	46.9–51.5	48.58	1.72	2	49.1, 49.6
Alveolar length p1–p4	8	28.2–30.7	29.05	0.79	2	28.9, 29.0
Length p4–m1	2	22.0, 22.0	—	—		
Alveolar length m1–m3	2	21.5, 21.6	—	—	2	20.1, 20.3
Length m1–m2	6	17.7–19.3	18.57	0.53		
Height between p2 and p3	27	9.4–11.7	10.24	0.65		
Height behind m1	18	12.0–14.4	12.84	0.66	2	12.1,12.1

lim—sampling limits, *M*—mean, *n*—number of specimen, SD—standard deviation.

The scatterplot of canonical scores shows the difference between Prolom 2 and Yudinovo/Yamal Peninsula in the first canonical axis and between Prolom 2 and Spitsbergen in the second axis (Fig. 4). The cluster analysis of samples based on squared Mahalanobis distances divided the samples into three groups: Prolom 2, Spitsbergen and Yudinovo/Yamal Peninsula (Fig. 5). As a result, the arctic foxes from Yudinovo and Yamal Peninsula are found to be very similar.

In the greatest length of P4, the sample from Prolom 2 occupies the intermediate position between the insular sample from Spitsbergen and two mainland ones from Yudinovo/Yamal Peninsula. However, the metastylar blade of P4 in Prolom 2 is relatively longer, so, in this characteristic, the Crimean *A. lagopus* is distinguished from other material analyzed.

4.4. Lower cheek teeth

The dimensions of the lower cheek teeth from Prolom 2 are given in Tables 4 and 5. There are several m2 from Siuren 1 which are larger ($M = 5.80$ mm, $n = 3$) than specimens from Prolom 2, but not larger than those from Yudinovo ($M = 5.80$ mm, $n = 20$) and Yamal Peninsula ($M = 5.71$ mm, $n = 20$). In m2 length ($M = 5.32$ mm, $n = 12$), the recent insular subspecies *A. l. spitzbergenensis* is as small as the fossil arctic fox from Prolom 2.

In Prolom 2, the ratio between m1 length and m2 length is approximately 2.57, being in other samples (including Siuren 1) relatively smaller.

Discriminant analysis, based on three measurements of m1 (greatest length, length of talonid, greatest width), indicated that the sample from Prolom 2 differs from other samples ($P<0.0003$), except for Siuren 1. Seventy six percent of dental variation is explained by the first canonical axis, 18% by the second. The first canonical variate (Root 1) discriminates all the measurements, and on the second axis (Root 2) the length of talonid and greatest width contributes to discrimination.

The scatterplot of canonical scores demonstrates the difference between Prolom 2 and Yudinovo/Yamal Peninsula in the first canonical axis and between Prolom 2 and Spitsbergen in the second axis (Fig. 6). The cluster analysis of samples based on squared Mahalanobis distances demonstrates the isolated position of the Spitsbergen sample (Fig. 7). The arctic fox from Spitsbergen is characterized by relatively narrower m1 (in average 35.8% against 37–38% in other samples).

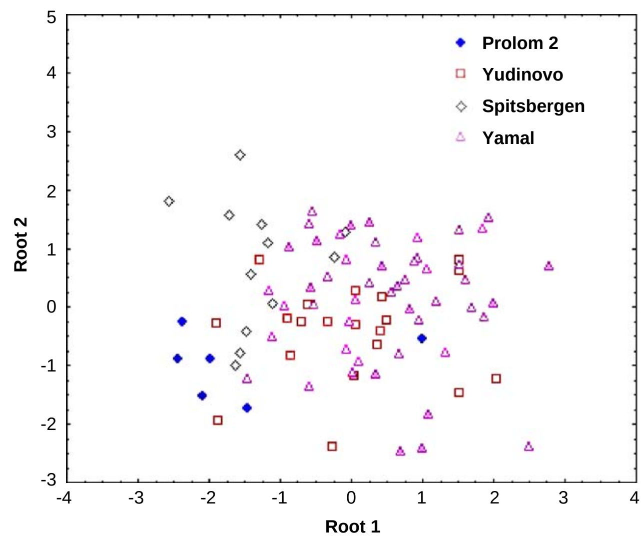

Fig. 4. Scatterplot of canonical scores for upper carnassial tooth P4.

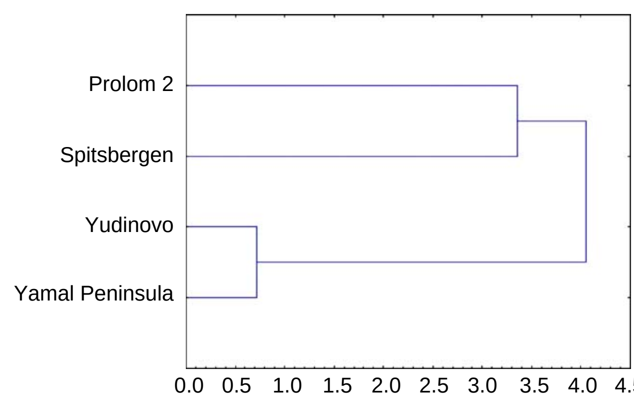

Fig. 5. Hierarchical tree plot of the geographical samples for upper carnassial tooth P4 based on squared Mahalanobis distances.

Table 2
Dimensions of upper cheek teeth of Late Pleistocene *Alopex lagopus* from Prolom 2

Measurements (mm)	*n*	lim	*M*	SD
Length M1–M2	2	11.1, 11.3	—	—
P2 length	2	7.1, 7.6	—	—
Width	2	2.7, 3.0	—	—
P3 length	1	7.9	—	—
Width	1	3.0	—	—
M1 length	9	7.0–8.6	7.60	0.68
Width	9	8.9–10.3	9.42	0.57
M2 length	4	3.7–5.1	4.32	0.58
Width	4	5.5–6.8	6.02	0.60

lim—sampling limits, *M*—mean, *n*—number of specimen, SD—standard deviation.

Table 3
Dimensions of upper carnassial tooth P4 of *Alopex lagopus*

Localities	Measurements (mm)											
	Greatest length				Length of metastylar blade				Greatest width			
	n	lim	*M*	SD	*n*	lim	*M*	SD	*n*	lim	*M*	SD
Late Pleistocene												
Prolom 2	6	11.7–12.8	12.15	0.37	6	4.5–5.3	4.85	0.33	8	5.4–7.0	5.75	0.55
Siuren 1	2	12.0, 12.3	—	—	2	4.5, 4.6	—	—	2	6.5, 6.5	—	—
Yudinovo	20	11.6–13.6	12.55	0.49	20	4.3–5.4	4.78	0.28	20	5.5–7.4	6.50	0.53
Recent												
Spitsbergen	12	10.6–12.3	11.64	0.56	12	4.0–4.8	4.37	0.28	12	5.5–6.6	5.99	0.32
Yamal Peninsula	50	11.4–14.4	12.42	0.57	50	4.1–5.9	4.76	0.36	50	5.8–7.9	6.81	0.48

lim—sampling limits, *M*—mean, *n*—number of specimen, SD—standard deviation.

The greatest length of m1 in Prolom 2 increases from lower layers 3–4 ($M = 13.40$ mm, $n = 10$) to the upper layer 2 ($M = 13.68$ mm, $n = 18$), further increasing in Siuren 1 ($M = 13.97$ mm, $n = 6$).

In the Upper Paleolithic sites of European Russia, the mean value of the m1 greatest length was calculated as 14.00 mm for Yudinovo (Table 5) and 14.2 mm ($n = 48$) for Kostenki (Sablin, 1994). Nearly the same length of m1 is observed in the recent specimens from Yamal Peninsula ($M = 13.91$ mm).

The recent insular subspecies *A. l. spitzbergenensis* occupies an isolated position because of pronouncedly smaller m1 length ($M = 13.20$ mm).

4.5. Limb bones

Males of the arctic fox are larger than females, this difference being observed in the limb bone measurements (Kuzmina and Sablin, 1993). In the collections from Prolom 2 and Siuren 1, bones are strongly fragmented, which makes it impossible to unfailingly attribute their sex. The bone dimensions from both Crimean sites are shown in Tables 6 and 7.

As Kuzmina and Sablin (1993) have observed, limb bones in the fossil subspecies *A. l. rossicus* from Yudinovo are somewhat shorter compared with those

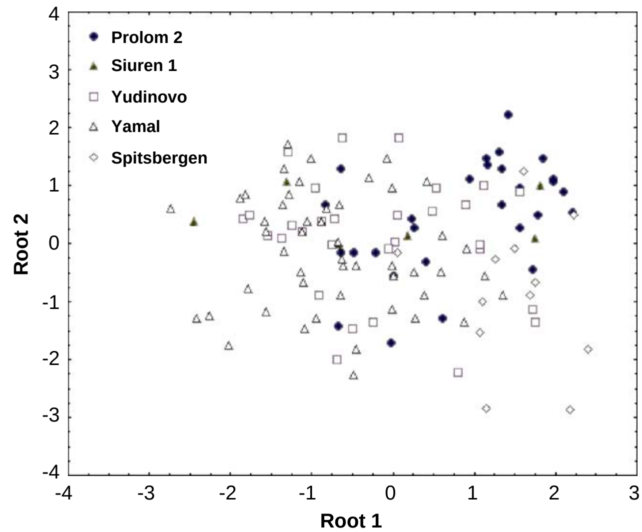

Fig. 6. Scatterplot of canonical scores for lower carnassial tooth m1.

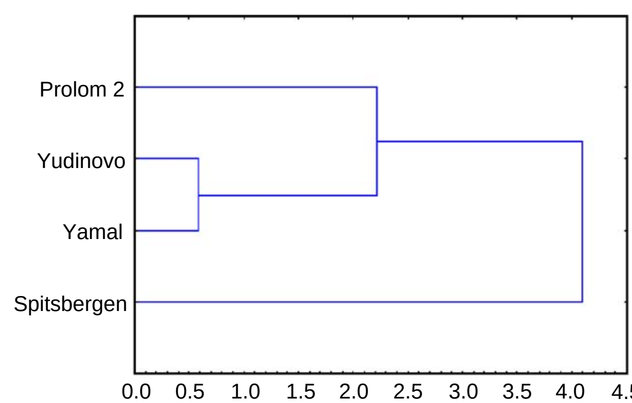

Fig. 7. Hierarchical tree plot of the geographical samples for lower carnassial tooth m1 based on squared Mahalanobis distances.

Table 4
Dimensions of lower cheek teeth of Late Pleistocene *Alopex lagopus* from Prolom 2

Measurements (mm)	n	lim	M	SD
p1 length	3	3.4–3.9	3.60	—
Width	3	2.2–2.4	2.27	—
p2 length	5	6.5–7.0	6.74	0.21
Width	5	2.5–3.0	2.82	0.25
p3 length	10	7.2–9.0	8.25	0.52
Width	10	2.8–3.8	3.09	0.30
p4 length	7	8.5–9.2	8.86	0.24
Width	7	3.4–4.2	3.81	0.27
m2 length	18	4.7–6.4	5.28	0.48
Width	17	3.4–4.5	3.92	0.25

lim—sampling limits, M—mean, n—number of specimen, SD—standard deviation.

Table 5
Dimensions of lower carnassial tooth m1 of *Alopex lagopus*

Localities	Measurements (mm)											
	Greatest length				Length of talonid				Greatest width			
	n	lim	M	SD	n	Lim	M	SD	n	lim	M	SD
Late Pleistocene												
Prolom 2	28	12.5–14.2	13.58	0.35	28	3.1–4.2	3.55	0.34	28	4.7–5.5	5.08	0.20
Siuren 1	6	13.2–14.6	13.97	0.51	6	3.2–4.4	3.80	0.44	6	4.8–5.7	5.25	0.35
Yudinovo	30	13.1–15.5	14.00	0.62	30	3.3–4.3	3.88	0.30	30	4.6–5.7	5.20	0.29
Recent												
Spitsbergen	12	12.0–14.0	13.20	0.57	12	3.2–3.9	3.58	0.22	12	4.3–5.2	4.73	0.25
Yamal Peninsula	50	12.7–15.5	13.91	0.59	50	3.6–4.6	4.03	0.26	50	4.8–5.8	5.29	0.25

lim—sampling limits, M—mean, n—number of specimen, SD—standard deviation.

of recent *A. l. lagopus*. At the same time, these subspecies differ markedly in the length of p1–m3 as well as in the length of m1. Analogous results have been obtained for the Belgian material (Germonpré and Sablin, 2004). Thus, Late Pleistocene arctic foxes possessed comparatively shorter limbs.

The postcranial bone dimensions in Prolom 2 indicate that early Weichselian representatives of *A. lagopus* in Crimea were very small animals, smaller than the fossil arctic fox from Yudinovo as well as those from Weinberghöhlen and Gönnersdorf in Germany (Heller, 1955; Poplin, 1976). The measurements show that the distal portions of fore and hind limbs were especially short. Average values of the length of metacarpals and metatarsals in Prolom 2 correspond to minimal values of those in *A. l. rossicus*.

In Siuren 1, the arctic fox is larger, approaching in limb length animals from Yudinovo. However, distal portions of limbs are relatively short.

5. Discussion

The analysis of sexual dimorphism in fossil arctic fox has demonstrated an insignificant shift of the peak of frequency distribution towards large teeth observed in

Table 6
Sizes of bones of the forelimb of Late Pleistocene *Alopex lagopus* from Crimea

Bone	Measurement (mm)*	Prolom 2				Siuren 1			
		n	lim	*M*	SD	*n*	Lim	*M*	SD
Scapula	SLC	8	11.5–14.0	12.44	0.94	6	12.5–14.9	13.97	0.87
	GLP	12	13.5–15.7	14.42	0.64	7	14.3–16.8	15.59	0.76
	BG	13	7.7–9.9	8.51	0.70				
Humerus	GL	1	92.7	—	—				
	Dp	5	20.0–21.9	21.10	0.74				
	SD	7	6.2–6.6	6.37	0.18	2	6.2, 6.6	—	—
	Bd	18	14.8–17.2	15.90	0.68	18	15.3–18.4	16.79	1.03
Ulna	SDO	2	10.0, 10.9	—	—	7	10.3–12.8	11.76	1.04
	DPA	3	12.2–12.8	12.53	—	7	12.3–15.3	14.04	1.11
	BPC	10	6.1–7.4	6.62	0.36	7	6.7–7.6	7.11	0.35
Radius	GL	1	83.7	—	—	2	88.9, 93.1	—	—
	Bp	14	8.5–10.3	9.28	0.45	6	9.0–10.4	9.43	0.54
	SD	8	6.1–6.8	6.45	0.32	6	6.2–7.5	6.83	0.55
	Bd	17	11.3–13.2	12.23	0.50	9	11.9–13.7	12.70	0.65
Metacarpal 2	GL	8	28.8–36.4	31.34	2.39	8	29.4–38.5	34.46	3.32
FC	Bp	11	3.8–4.9	4.09	0.29	8	3.8–5.3	4.65	0.54
	SD	10	3.2–3.6	3.28	0.14	8	5.5–6.4	6.01	0.33
	Bd	8	4.9–5.3	5.09	0.15	8	5.1–6.1	5.72	0.32
	Dd	8	4.1–4.7	4.37	0.27	8	4.3–5.3	4.87	0.32
Metacarpal 3	GL	1	36.1	—	—	6	39.3–43.7		
	Bp	3	3.6–4.5	4.00	—	6	4.4–4.8	4.60	0.17
	SD	3	2.9–3.6	3.13	—	6	3.2–3.7	3.47	0.21
Metacarpal 4	GL	3	35.2–36.3	35.60	—	2	38.4, 42.1	—	—
	Bp	5	3.9–4.5	4.08	0.25	2	4.7, 5.0	—	—
	SD	4	2.7–3.2	2.90	0.22	2	3.4, 3.7	—	—
	Bd	3	4.4–5.0	4.60	—	2	5.3, 6.1	—	—
	Dd	4	4.1–4.8	4.42	0.30	2	5.4, 5.5	—	—
Metacarpal 5	GL	10	27.3–31.3	29.26	1.12	7	28.4–36.1	32.30	2.84
	Bp	10	5.5–6.2	5.87	0.27	7	5.3–7.0	6.16	0.64
	SD	11	3.5–3.9	3.74	0.12	7	3.5–4.3	3.97	0.27
	Bd	10	5.4–6.2	5.59	0.23	7	5.5–6.3	5.93	0.32
	Dd	10	4.0–4.9	4.37	0.27	7	4.4–5.1	4.77	0.22

lim—sampling limits, *M*—mean, *n*—number of specimen, SD—standard deviation.
Measurement abbreviations: Bd—breadth of the distal end, Bp—breadth of the proximal end, BG—breadth of the glenoid cavity, BPC—breadth across the coronoid process, Dd—depth of the distal end, Dp—depth of the proximal end, DPA—depth across the Processus anconaeus, GL—greatest length, GLP—greatest length of the glenoid process, SD—smallest breadth of the diaphysis, SDO—smallest depth of the olecranon, SLC—smallest length of the neck of the scapula.
*After Driesch von den (1976).

Table 7
Sizes of bones of the hindlimb of Late Pleistocene *Alopex lagopus* from Crimea

Bone	Measurement (mm)*	Prolom 2				Siuren 1			
		n	lim	*M*	SD	*n*	lim	*M*	SD
Pelvis	LA	3	12.1–12.5	12.33	—	5	11.7–13.9	12.68	0.93
	SH	1	10.0	—	—	5	9.6–10.8	10.18	0.55
Femur	GL	1	97.3	—	—	1	103.9	—	—
	Bp	1	21.7	—	—	1	23.9	—	—
	DC	2	9.7, 10.5	—	—	4	9.8–10.8	10.35	0.42
	SD	1	7.8	—	—	2	7.2, 8.4	—	—
	Bd	6	16.6–18.3	17.13	0.61	2	16.4, 17.5	—	—
Patella	GL	1	13.3	—	—				
	GB	1	8.2	—	—				
Tibia	GL	1	105.7	—	—	1	117.4	—	—
	Bp	7	15.7–18.0	16.90	0.85	3	17.9–18.9	18.60	—
	SD	6	6.6–7.7	7.02	0.41	1	7.6	—	—
	Bd	19	11.9–13.9	12.60	0.59	9	11.8–13.9	13.03	0.71
	Dd	20	7.8–10.4	8.73	0.58				
Calcaneus	GL	19	23.4–27.0	24.66	0.76	12	23.6–28.2	26.02	1.82
	GB	21	9.1–10.2	9.68	0.34	12	8.9–11.3	10.13	0.72
Astragalus	GL	9	14.0–16.4	14.69	0.78	6	14.5–16.1	15.43	0.74
Metatarsal 2	GL	5	40.0–43.2	41.62	1.28	10	40.0–48.4	44.93	3.03
	Bp	6	4.4–5.2	4.80	0.32	10	4.9–6.7	5.46	0.51
	SD	6	3.3–3.9	3.50	0.23	10	3.1–4.0	3.65	0.29
	Bd	5	5.0–5.9	5.36	0.36	10	4.9–6.1	5.55	0.45
	Dd	5	4.0–4.7	4.40	0.25	10	4.6–5.3	4.87	0.24
Metatarsal 3	GL	5	44.5–47.7	46.02	1.46	4	45.5–50.8	48.47	2.21
	Bp	14	4.4–5.4	5.00	0.31	4	4.3–5.7	4.95	0.58
	SD	8	3.0–4.0	3.66	0.31	4	3.6–4.1	3.90	0.24
	Bd	5	4.7–5.5	5.14	0.35	4	4.8–5.2	5.00	0.18
	Dd	5	4.7–5.0	4.84	0.13	4	4.8–5.6	5.20	0.33
Metatarsal 4	GL	3	45.5–49.7	47.83	—	5	46.7–57.6	50.14	4.30
	Bp	8	4.3–5.3	4.86	0.43	5	4.6–5.8	5.14	0.45
	SD	5	3.2–3.9	3.48	0.34	5	3.2–4.0	3.44	0.33
	Bd	3	4.5–4.7	4.63	—	5	4.4–5.6	4.88	0.46
	Dd	3	4.7–4.8	4.73	—	5	4.6–6.1	5.10	0.58
Metatarsal 5	GL	5	42.7–47.5	44.92	2.17	3	44.9–50.0	47.27	—
	Bp	13	4.5–6.6	5.16	0.53	3	5.0–6.1	5.47	—
	SD	8	2.9–3.5	3.31	0.23	3	3.4–4.1	3.83	—
	Bd	5	4.7–5.8	5.32	0.41	3	5.6–5.8	5.67	—
	Dd	5	4.1–4.7	4.42	0.22	3	4.4–4.9	4.67	—

lim—sampling limits, *M*—mean, *n*—number of specimen, SD—standard deviation.
Measurement abbreviations: DC—depth of the Caput femoris, LA—length of the acetabulum including the lip, SH—smallest height of the shaft of ilium; other abbreviations see in Table 6.
*After Driesch von den (1976).

the samples from Prolom 2 that, perhaps, indicates slight predominance of males. The frequency distribution of lower canine width has the same pattern. The predominance of males identified from Prolom 2 is especially well represented in material from the lower layers 3 and 4. This may be associated with seasonal peculiarities of life of the arctic fox. According to modern observations in the Taimyr Peninsula (Yakushkin, 1985), adult males are the first to depart the places where they were raised, and begin migrating to the south. The ratio of migrating males in the autumn is about 60–70% of the total. Probably male arctic foxes reached the Crimea in autumn, earlier than females. At the beginning of fur hunting season, they became regular victims of settlers during the formation of the lower layers in Prolom 2. Crimea presumably was the winter grounds for arctic foxes, which might have migrated there from the East European Plain.

The early Weichselian *A. lagopus* from Prolom 2 resembles the subspecies *A. l. spitzbergenensis* from the arctic islands in size. In the late Weichselian, arctic foxes became larger in Crimea, approaching the size of *A. l. rossicus* and *A. l. lagopus*. This may be confirmed by the progressive increase of m1 length in *A. lagopus* from the early to late Weichselian of Eastern Europe.

Few data are available on the early history of the arctic fox. Its presumed ancestor, *Vulpes praeglacialis* Kormos from the early Middle Pleistocene grotte de l'Eskale in France, is similar to *A. lagopus* from Prolom 2 in the length of m1, but the limb bones of *V. praeglacialis* are distinctly larger (Bonifay, 1971).

A small *A. lagopus*, which is similar in the size of m1 and m2 to the specimens from Prolom 2, is also documented by only scant remains in the early Middle Pleistocene sites of Schweinskopf and Hummerich in Germany (Turner, 1990). A very small *A. lagopus* (average length of m1 12.6 mm, $n = 4$) is recorded from the late Middle Pleistocene of grotte de Fontechevade in France (Arambourg, 1958).

More records are available for the Late Pleistocene of Western Europe. Beneš (1975), when studying the *A. lagopus* remains from Czech localities, revealed the increasing size of the arctic fox during the Last glacial. This researcher gave the mean values of m1 length for "*Vulpes*" *meridionalis* from Čertova Díra in the Czech Republic ($M = 12.6$ mm, $n = 8$) as well as for the arctic foxes from localities Pekárna and Pod hradem attributed to early Würm (W1/2). In these dimensions, *A. lagopus* from the early Weichselian of Western Europe is somewhat smaller as compared with that in Prolom 2.

For the late Weichselian *A. lagopus* in the Czech Republic, more robust size is characteristic (Beneš, 1975). The greatest length of m1 in Čertova Díra ($M = 14.1$ mm, $n = 6$) is very similar to that in Yudinovo, but in Pekárna (Würm 3), it is markedly smaller ($M = 12.7$ mm, $n = 12$). Two m1s from Předmost possess length 14.4 and 14.7 mm (Fladerer, 2001).

Thus, progressive increase in size in *A. lagopus* is observed in the Late Pleistocene of Western and Eastern Europe. Beneš (1975) has suggested that it is well explained by Bergmann's rule that would predict increasing body size due to transition from a warm to a cold climatic phase of the Weichselian. However, in Eurasia, the largest arctic foxes are from the Commander Islands, being provided throughout a year by sea waste products (Heptner et al., 1967). Presumably, the body size of arctic fox is partially dependant on the quality of forage.

Morphology (small size and short limbs) of *A. lagopus* from Prolom 2 is probably explained by unfavorable environmental conditions for this species (e.g., scarcity of food). It may be considered as a "maintenance phenotype" in Geist's (1987) interpretation.

The insular subspecies, *A. l. spitzbergenensis,* from Spitsbergen and Franz Josef Land, living in the conditions of polar desert, demonstrates the narrowest lower carnassial tooth m1. This character may be a marker of its predominant miophagy (meat diet). In Late Pleistocene *A. lagopus,* that tooth is wider, reflecting consumption of more diverse food including plants, as in the living animals of the Eurasian tundra.

6. Conclusion

The present study characterizes the fossil *Alopex lagopus* from the grotto Prolom 2 as a small arctic fox with the relatively short limbs. During the late Pleistocene, the size of this species increased in Crimea, since the arctic fox from the younger site, Siuren 1, is larger than that from Prolom 2.

The fossil arctic foxes from Western and Eastern Europe, which originated from stratigraphically similar levels, demonstrate similarity in their tooth dimensions. This raises a possibility of synonymizing *A. l. fossilis* Woldřich with *A. l. rossicus* Kuzmina et Sablin, in spite of the fact that the taxon "*Leucocyon*" *lagopus fossilis* was established on the basis of a single isolated canine (Woldřich, 1878: Taf. VI, Fig. 26).

Thus, I tentatively refer the animals from Prolom 2 to the subspecies *A. l. meridionalis* Woldřich, and the arctic fox from Siuren 1 to *A. l. fossilis* Woldřich.

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