



Size of the lower carnassial in the arctic and the red fox from Late Pleistocene in Belgium compared to other ancient and extant populations

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Abstract

Lengths, widths, and size proportions (length to width) of the lower carnassial were measured in 45 teeth of the arctic fox and 35 teeth of the red fox from Belgium radiocarbon dated to 46 640–14 120 ka BP. Data the Late Pleistocene foxes from Belgium were compared to 20 ancient and extant populations from Europe, Asia, and North America. The Pleistocene arctic fox from Belgium showed larger carnassial than in all recent samples of this species, whereas the Belgian fossil red foxes were characterized by the carnassial size comparable to that of the recent Siberian red foxes. Both fox species from the Pleistocene of Belgium showed the highest index of the carnassials length to width, which means increase in carnivorous adaptation. We conclude that the higher level of carnivorous specialization reached by the Belgian arctic and red foxes at the end of the Late Pleistocene reflected their scavenging on kills of large carnivores and human hunters (remains of megafauna). Harsh environmental conditions of that period and specific composition of ecosystems led to adapting to a more carnivorous food niche in both foxes.

Keywords *Vulpes lagopus* · *Vulpes vulpes* · Eurasia · North America · Molar size · Carnivore specialization

Introduction

The red fox (*Vulpes vulpes*) and the arctic fox (*Vulpes lagopus*), two closely related species, share a partly common evolutionary history and recent ecological interactions in the most northern areas of the Holarctic. Fossil remains of the arctic and the red fox from the Pleistocene reveal great changes in their ranges (Sommer and Benecke 2005). During the Pleniglacial and the Late-Glacial, both species occurred in almost whole Europe (Baryshnikov 2006; Germonpré and Sablin 2004; Kurtén

1967; Lipecki and Wojtal 2015; Pazanoi 2004; Sommer and Benecke 2005). Fossil remains of the arctic fox were also found in northern Europe, e.g., along the coast of Norway (Frafjord and Hufthammer 1994). At the end of the Pleistocene, the arctic fox become extinct in most areas of Europe. Sub-fossil remains of the arctic fox from the Holocene are restricted to the contemporary European distribution of the species. In the Post-Glacial period, the red fox occurred in almost the whole of Europe (Sommer and Benecke 2005).

The analyses of teeth or long bones of the fossil foxes reveal changes in their adaptations to extreme fluctuations in climate and ecosystem structure during Pleistocene (see Baryshnikov 2006; Germonpré and Sablin 2004). Recently, genetic methods made it possible to reveal the phylogenetic and phylogeographic history of many species (e.g., Baca et al. 2017; Dalén et al. 2007; Knapp 2018; Lorenzen et al. 2011; Niedziałkowska et al. 2014; Niedziałkowska 2017), and the analyses of stable isotope content in bones provided new insights into food niches and habitats of the fossil fauna (e.g., Drucker et al. 2008, Bocherens et al. 2017). Nonetheless, the traditional morphometric approach remains a reliable tool for studying between- and intra-species relationships, phyletic distances, and feeding preferences of mammals (Haba et al. 2008; Korablev and Szuma 2014; Piras et al. 2012; Szuma 2003, 2011).

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The teeth, as the hardest fragments of the mammal skeleton, are the most abundant fossil remains. The most stable and the most specific patterns of the tooth variation are observed in the jugal teeth: premolars and molars. Among them, the first lower molar has a special importance in the dental system of canids because it is the largest tooth, centrally situated in the tooth-row, and it shows the smallest variation in size (Szuma 2000). The crown surface of the lower carnassial is best fitted to the crown surface of the upper carnassial, and it plays a significant role in slicing and grinding food. The mesial part of the tooth — trigonid — is used to slice, whereas the distal part — talonid — is used to grind (Ungar 2010). The length of the lower carnassial is a very good indicator of body size in carnivores (Van Valkenburgh 1990, 1991, 2007). Already Legendre and Roth (1988) showed that correlation of M_1 area and body size in Carnivora is very high and the correlation coefficient r reaches 0.91. Flower (2016) found very high correlation between the length of the M_1 and body mass in modern carnivores ($r_{25} = 0.97$, $p < 0.001$).

Based on the M_1 size and metrical parameters of long bones of fossil red and arctic foxes, Germonpré and Sablin (2004) found that red foxes from the Late Pleistocene of Belgium were larger than the extant foxes in Nordic populations. The Late Pleistocene Belgian arctic foxes had shorter limbs than arctic foxes from recent Siberian populations. This suggests more severe conditions in Belgium during the Late Pleistocene than the recent climate of Siberia. Between 20° N and 60° N, the size of the red fox follows the Bergmann's rule (Huston and Wolverton 2011; Meiri et al. 2004). Size variation of the arctic fox does not show a latitudinal gradient in its contemporary native range (Szuma 2008). Germonpré and Sablin (2004) proposed that the changes in body size of the red fox reflected climatic variations across the time scale. Also during the twentieth century, microevolutionary changes in the dentition of the red fox, corresponding to the growing opportunism in diet of this species, were observed (Szuma 2003).

In this study, we aimed to compare the level of carnivorous specialization in the first lower molar of the red fox and the arctic fox in Late Pleistocene populations from Belgium with other ancient and extant populations in Eurasia and North America. A detailed analysis of size of the first lower molar in fossil and recent material of both foxes could help us understand the evolutionary history and ecological characteristics of the two species. We expected that the lower carnassial of the more northern arctic fox would retain carnivorous characters and stable morphological patterns since the Pleistocene epoch to modern times, whereas the tooth in the red fox would show bigger changes through time and weak carnivorous attributes.

Material and methods

For this study, we used (1) the fossil material of the red fox and the arctic fox from the Late Pleistocene of Belgium, (2) material from extant populations of the two species in Eurasia and North America, and (3) data on the fossil arctic foxes from Baryshnikov (2006).

The Belgian fossil material of the red fox consisted of 35 isolated M_1 that originated from five caves (Trou de Chaleux, Goyet, Trou du Frontal, Trou des Nutons, Trou Magritte). The fossil sample of the arctic fox contained 45 carnassials that were discovered at four caves (Trou de Chaleux, Goyet, Trou des Nutons, Trou Magritte) in Belgium. All these sites are located in the Ardenne Massif and were excavated by Edouard Dupont in the 1860's (Dupont 1873). The material recovered has been stored at the Royal Belgian Institute of Natural Sciences since then. Available ^{14}C dates of the fossil material from the five caves span the period of 46 640–14 120 calibrated years BP (Accelerator Mass Spectrometry, calibration calculated using the Oxcal 3.4 program). Description of caves and list of ^{14}C dates is given in Table 1.

In each fossil M_1 tooth, the crown length (L) and the crown width (W) were measured with a Sylvac digital calliper and recorded to the nearest 0.01 mm. The crown length of the M_1 (LM_1) is the greatest distance between anterior and posterior (mesial and distal) points of the tooth, whereas the width of M_1 (WM_1) is the greatest distance between lingual and buccal points of the tooth crown at the level of talonid part of the tooth (Fig. 1). To obtain a better diagnostic of fox dentition, the carnivorous index — the proportion of LM_1 to WM_1 (LM_1/WM_1) — was calculated. Larger values of that index mean an advantage of food slicing over grinding ability, thus an increase in carnivorous adaptation.

The data on extant red foxes were collected for the Belgian population. Additionally, the earlier published material from 8 populations of the red fox in the Palearctic (Szuma 2007a, b) and 7 populations of the arctic fox in the Holarctic (Szuma 2008, 2011) were used for comparison with the fossil data (Fig. 2). The samples of the red fox were larger than 50 specimens per population. The arctic fox samples varied in size

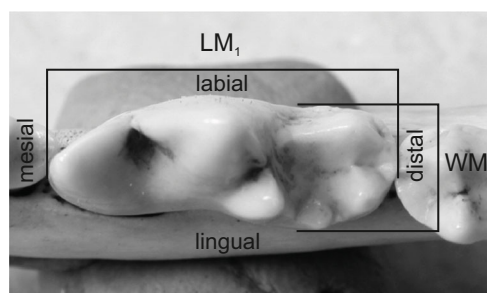
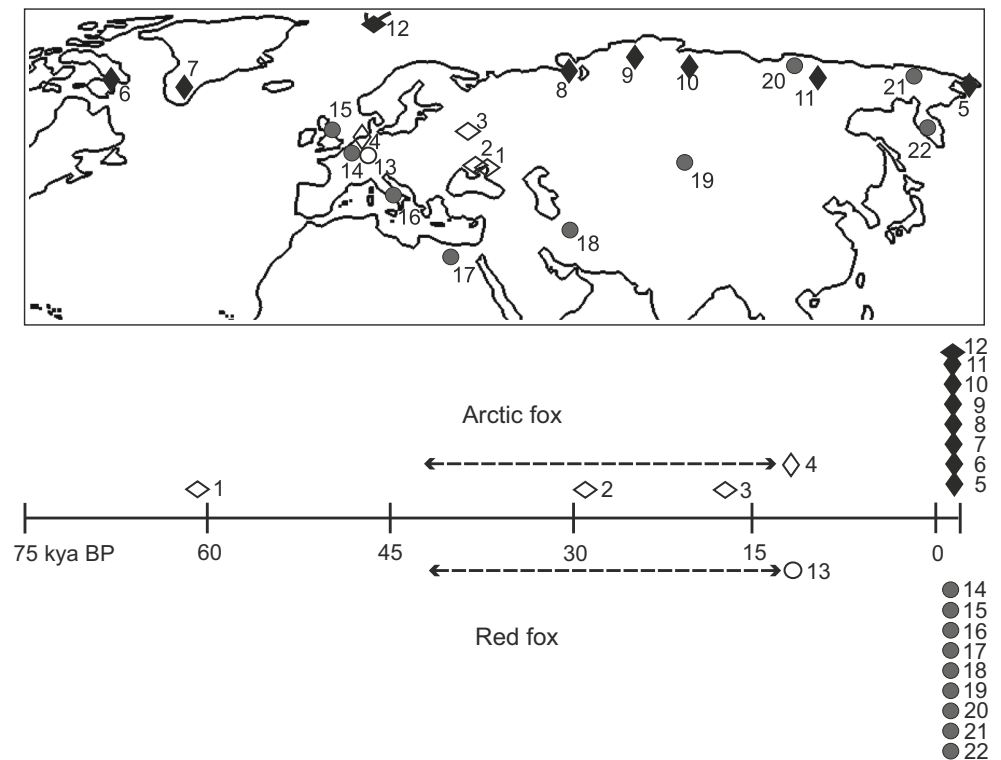


Fig. 1 Linear measurements conducted on the lower carnassials (M_1) of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes*: LM_1 — length of M_1 , WM_1 — width of M_1

Fig. 2 Geographic distribution of the recent and fossil samples of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes* used in the study. Black rhomb — recent populations of the arctic fox measured by Szuma (2011), black rhomb is turned off — recent population of the arctic fox (pop. 12) measured by Baryshnikov (2006), empty rhomb — fossil populations of the arctic fox (pop. 4) measured by Szuma to the study, empty rhomb is turned off — fossil population of the arctic fox (pops 1, 2, 3) measured by Baryshnikov (2006); grey circle — recent populations of the red fox measured by Szuma (2011); empty circle — fossil population of the red fox (pop.13). Population names as in Table S2



from 11 to 58 specimens per population. All measurements on the first lower molars in the fossil and the recent material were carried out in the same way and by the same contractor (E. Szuma). A list of samples, abbreviations of population names, systematic status, and collection name is given in Table S2.

For metric parameters of M_1 in all fossil and extant populations the arithmetic mean, standard deviation, standard error, and coefficient of variation were calculated for each variable (Table S3). The normality of the frequency distributions of each parameter was analyzed with the Shapiro-Wilk's statistic (*SW-W*) (Figs S1–6). In a few samples of the arctic and red foxes, some metric parameters were not normally distributed, so the Kruskal-Wallis test (*K-W*) was used in the between population comparisons. The results of the *K-W* test were compatible with the statistical significances of the interpopulation variation in the arctic and red foxes for each of the metrical characters assessed by the Friedman test. Additionally, the metrical traits of the M_1 among populations of each species were compared with ANOVA and the conservative Tukey *post hoc* test. The Tukey *post hoc* analysis indicated more between population statistically significant variation than the Kruskal-Wallis test.

In most recent populations of the arctic and red fox, we observed statistically significant sexual dimorphism in the size but not size proportions of M_1 (see Table S4). Red fox males are significantly bigger than females, and on average, tooth measurements in males are 3.6% larger than those in females (Szuma 2007b). For obvious reasons, we did not have

information about the sex of the foxes from ancient samples, so all statistical analyses common for ancient and extant populations were carried out excluding sexual divisions.

Principal component analysis (PCA) was performed using LM_1 , WM_1 , and LM_1/WM_1 to visualize distance among populations of each species. Based on the metrical characteristics of the lower carnassials and the Euclidean distances, using UPGMA (unweighted pair-group method using arithmetic averages), trees of the phyletic relationships for the arctic and red foxes were constructed. The spatial arrangements of the populations of both fox species in 2D planes were illustrated by a multidimensional scaling procedure (MDS). In both species, stress levels were very low (the red fox, stress = 0.0000044; the arctic fox, stress = 0.000027), which suggests the matrix of the reconstituted proximity matched well to the matrix of the observed proximity. Statistical analyses were carried out in Statistica.pl version 9.0.

For some comparisons and analyses, data from Baryshnikov (2006) on fox populations in the Russian Federation were used (see Table S5). Baryshnikov's (2006) study included one sample extant population of the arctic fox from Yamal, which was also measured at the Zoological Institute RAS in St. Petersburg by E. Szuma. Mean of the M_1 length obtained by Baryshnikov was 13.92 mm, whereas that by Szuma 13.91 mm. Therefore, we assumed that the measurements were done in the identical way and yielded highly consistent results. On the other hand, we did not include here the

measurements of the Belgian ancient arctic foxes (analyzed in this study) done earlier by Germonpré and Sablin (2004), which yielded rather divergent results. Other technique of measurements was used by the last authors.

Results

The arctic fox

The average length of the lower carnassials in the fossil Belgian sample (population 4 dated 46,6–14,1 kya BP) was the largest (14.21 mm, CV 4.77) among the studied populations (Fig. 3, Table S3). The distribution of the LM_1 did not deviate from normality and was left-skewed (Fig. S1). Arctic foxes from Greenland (pop. 7) had the smallest M_1 (13.52 mm; Figs. 3 and S1). The variation in the mean length of M_1 among the eight populations was statistically significant (Fig. 3). Pairwise comparisons of mean LM_1 revealed statistically significant differences between the ancient Belgian foxes (pop. 4) and all extant populations except for the Bering, Taymyr, and Yamal arctic foxes (pops 5, 8, 9; Table 1).

The average crown width of the M_1 in the Belgian fossil sample was 5.08 mm with CV 6.39 (Table S3). The frequencies of the crown width measures did not differ statistically from normal distribution (Fig. S2). The lowest mean of WM_1 was observed in Greenland (pop. 7; 4.91 mm), whereas the biggest one in Yamal (pop. 8; 5.19 mm) (Fig. 3, Table S3). The mean widths of lower carnassial among the eight populations were significantly differentiated (Fig. 3), yet the pairwise comparisons revealed significant difference between two samples only: Yamal and Greenland (pops 7 and 8; Table 1).

The mean of LM_1/WM_1 index for the fossil arctic foxes from Belgium equalled 2.80 with CV 5.50 (Table S3). The distribution of the index of LM_1/WM_1 for this population did not differ significantly from normality (Fig. S3). The ancient arctic foxes (pop. 4) were characterized by the highest mean LM_1/WM_1 index (Fig. 3). The variation among all populations was statistically significant, and the Kruskal-Wallis test indicated significant differences between population 4 and all extant populations of foxes except for Baffin Land, Greenland, and Taymyr (pops 6, 7, 9; Table 2).

The PCA procedure (which included also three populations from Baryshnikov (2006), i.e., Prolom — pop. 1, Siuren — pop. 2, Yudinovo — pop. 3) showed that 56.6% of the size variation in the lower carnassial in the arctic fox was explained by factor I, whereas 43.3% by factor II (Fig. 4). The loads of factor I correlated significantly with WM_1 (0.78) and LM_1/WM_1 (−0.97), and those of factor II with LM_1 (−0.99). The MDS procedure revealed that populations

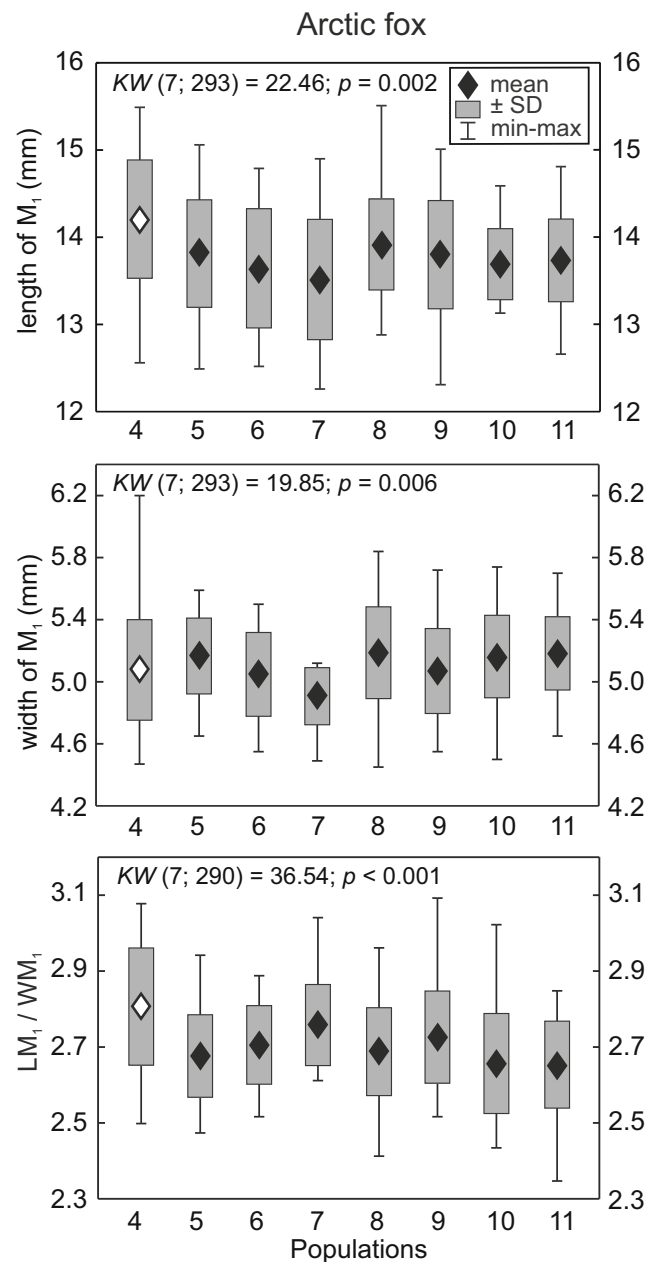


Fig. 3 Size variation of the first lower molar (M_1) in relation to length (LM_1), width (WM_1), and size proportion index (LM_1/WM_1) in one fossil and eight recent populations of the arctic fox *Vulpes lagopus*. Population names as in Table S2

4 (ancient, Belgium) and 7 (extant, Greenland) were distant from each other and from the other populations of the species (Fig. 5). Dimension I showed a distance between populations 4 and 7 and other extant populations of the arctic fox, but dimension II reflected the differentiation between pop. 4 and all extant populations of arctic foxes. The phenogram of the Euclidean distances between the means of the arctic fox samples showed that the ancient arctic foxes from Belgium were separated from all extant populations (Fig. 6).

Table 1 Above diagonal: Variation between populations of the arctic fox (*Vulpes lagopus*) based on the lengths of M_1 were arranged by the z values of the Kruskal-Wallis test. Below diagonal: Variation between populations of the

arctic fox (*Vulpes lagopus*) based on widths of M_1 were arranged by the z values of the Kruskal-Wallis test. Significant differences ($p < 0.05$) were presented in italics. Population names as in Table S2

Pop	4	5	6	7	8	9	10	11
4	*	3.08	3.24	3.24	2.15	3.11	3.54	3.25
5	1.82	*	0.93	1.36	0.78	0.01	1.02	0.54
6	0.05	1.50	*	0.53	1.49	0.92	0.01	0.44
7	0.61	3.04	1.66	*	1.80	1.35	0.57	1.35
8	1.88	0.60	1.89	3.32	*	0.80	1.62	1.21
9	0.18	1.78	0.20	2.04	2.25	*	1.02	0.53
10	1.50	0.00	1.31	2.80	0.50	1.43	*	0.47
11	1.94	0.34	1.66	3.11	0.21	1.90	0.29	*

The red fox

Length and width of the M_1 and the LM_1/WM_1 index in ten populations of the red fox showed a highly significant geographic variation (Fig. 7). The mean LM_1 in the Belgian fossil red foxes (pop. 13) was 15.97 mm, CV 4.83 (Fig. 7, Table S3). Frequency distribution of the LM_1 in population 13 was close to the Gaussian distribution (Fig. S4). The average length of the M_1 was moderate compared to those in all extant populations, and ANOVA revealed a statistically significant variation of LM_1 among populations (Fig. 7). The Kruskal-Wallis test indicated that the LM_1 of ancient red foxes from Belgium (pop. 13) were similar to those in one extant European (pop. 15) and four extant populations from Siberia (pops 19–22; Table 3).

The mean WM_1 of the ancient population 13 was 6.04 mm, CV 7.99 (Table S3), and the frequency distribution was close to normality (Fig. S5). The ancient foxes showed moderate width of M_1 compared to the extant populations (Fig. 7). The variance in the WM_1 among populations was statistically significant (Fig. 7), whereas pairwise comparisons revealed that ancient red foxes were significantly different from three extant pop-

ulations of the species (Egypt, pop. 17; Iran, pop. 18; Kamchatka, pop. 22) (Table 3).

Table 2 Variation between populations of the arctic fox (*Vulpes lagopus*) based on size proportions of M_1 (LM_1/WM_1) were arranged by the z values of the Kruskal-Wallis test. Significant differences ($p < 0.05$) were presented in italics. Population names as in Table S2

Pop	5	6	7	8	9	10	11
4	4.56	2.36	0.72	3.58	2.47	4.61	4.37
5	*	1.20	2.12	0.75	2.33	0.87	0.32
6		*	1.05	0.57	0.51	1.76	1.36
7			*	1.61	0.80	2.52	2.22
8				*	1.40	1.45	0.97
9					*	2.75	2.36
10						*	0.53

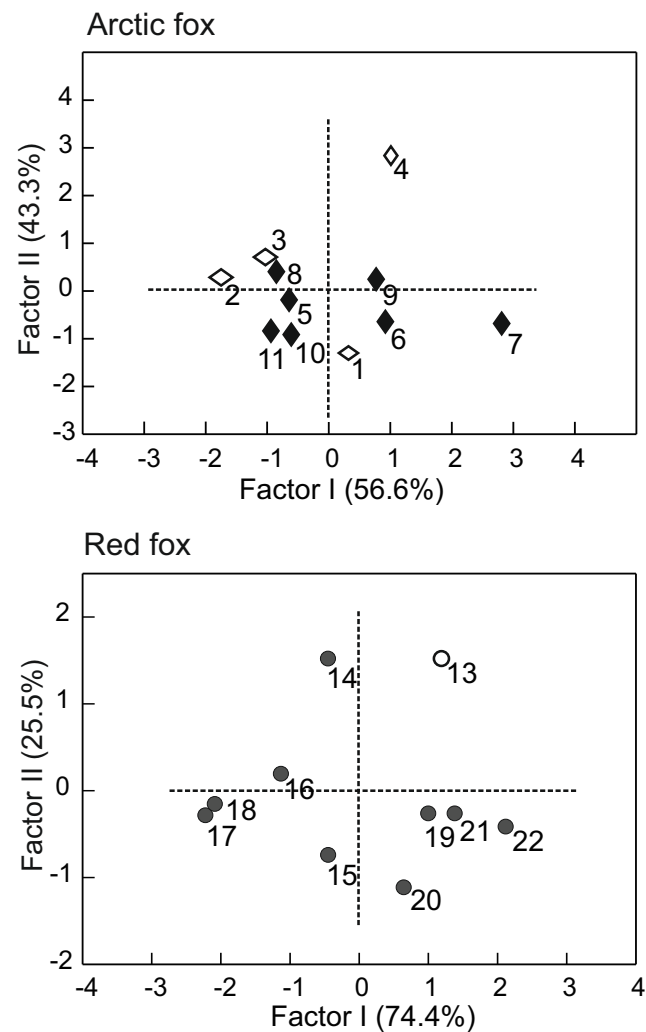


Fig. 4 Distribution of recent and fossil populations of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes* in relation to I and II factors. Analyses were conducted using metric parameters and proportion index in the first lower molar (LM_1/WM_1). Population names as in Table S2

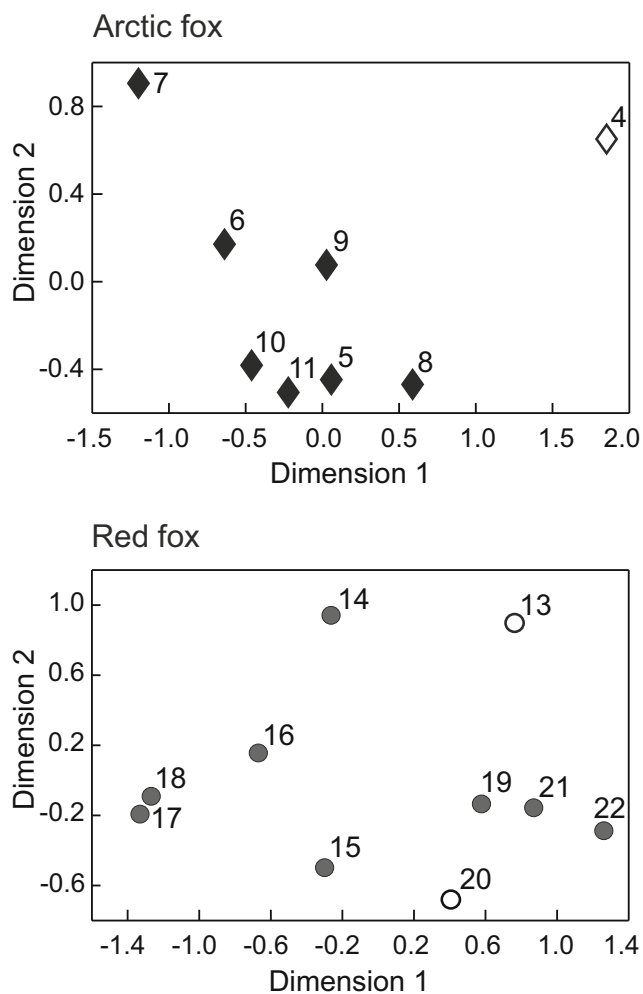


Fig. 5 Configuration of the studied populations of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes* in 2D plane based on metric parameters and proportion index of the first lower molar. Population names as in Table S2

The distribution of the LM_1/WM_1 index in the ancient Belgian foxes (pop. 13) deviated from the Gaussian distribution and showed two peaks (Fig. S6). The mean of the index in the ancient fox population (2.65) was higher than those of all extant populations of the red fox (Table S3, Fig. 7). Also *CV* for the LM_1/WM_1 index in population 13 (5.67) is the highest. ANOVA showed a significant variation in among populations (Fig. 7). The Kruskal-Wallis test revealed that the ancient Belgian foxes differed in respect of LM_1/WM_1 index from all extant populations of red foxes with the exception of Belgian (pop. 14), Italy (pop. 16), Novosibirskaya obl. (pop. 19), Chukchi (pop. 21), and Kamchatka (pop. 22) populations (Table 4).

The PCA based on the size of the lower carnassial in the red fox showed that factor I and II explained 99.9% of the total variance, with factor I accounting for 74.4%

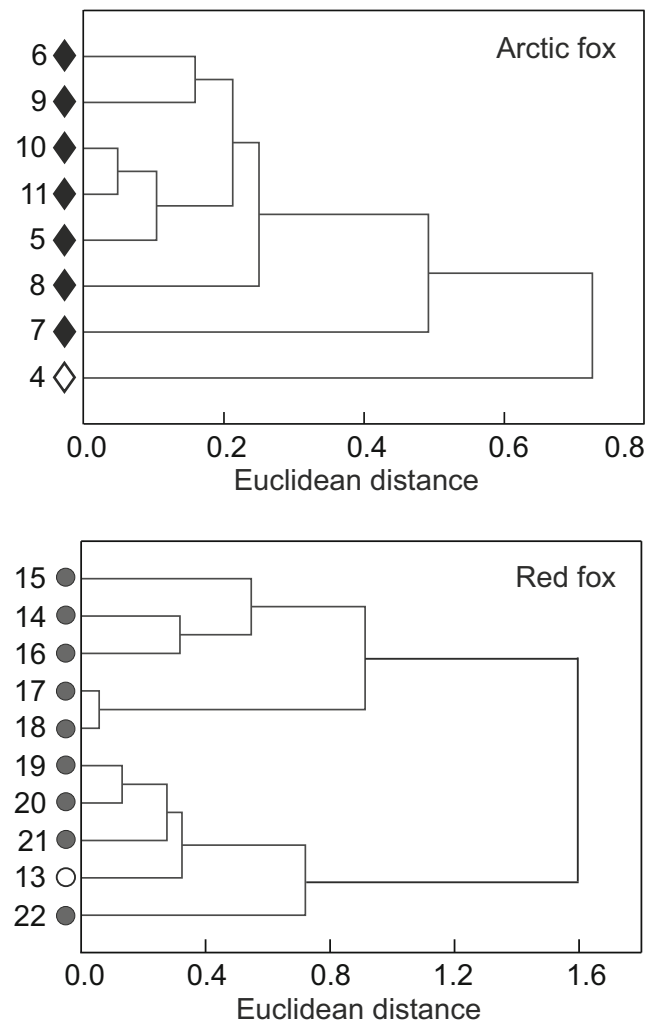


Fig. 6 Tree graphs for the studied populations of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes* based on Euclidean distances with using Ward method calculated on size and proportion parameters of the first lower molar. Population names as in Table S2

and factor II accounting for 25.5% of variance, respectively (Fig. 4). The length and width of the molar were correlated with the factor I (0.99 and 0.90, respectively), whereas index LM_1/WM_1 was related to factor II (factor loading 0.75). The MDS analysis showed that in a 2D plane, the ancient Belgian and the extant Siberian populations were in the same level with respect to dimension I. With regard to dimension II, the ancient and the extant Belgian populations were the closest to each other (Fig. 5). The dispersion of M_1 size vectors along two main factors indicated some differentiation in concentration of the vectors for each population. Also, the phylogenetic tree constructed with the use of Euclidean distances and the UPGMA suggested that the ancient red foxes from Belgium were similar to the extant Siberian populations (Fig. 6).

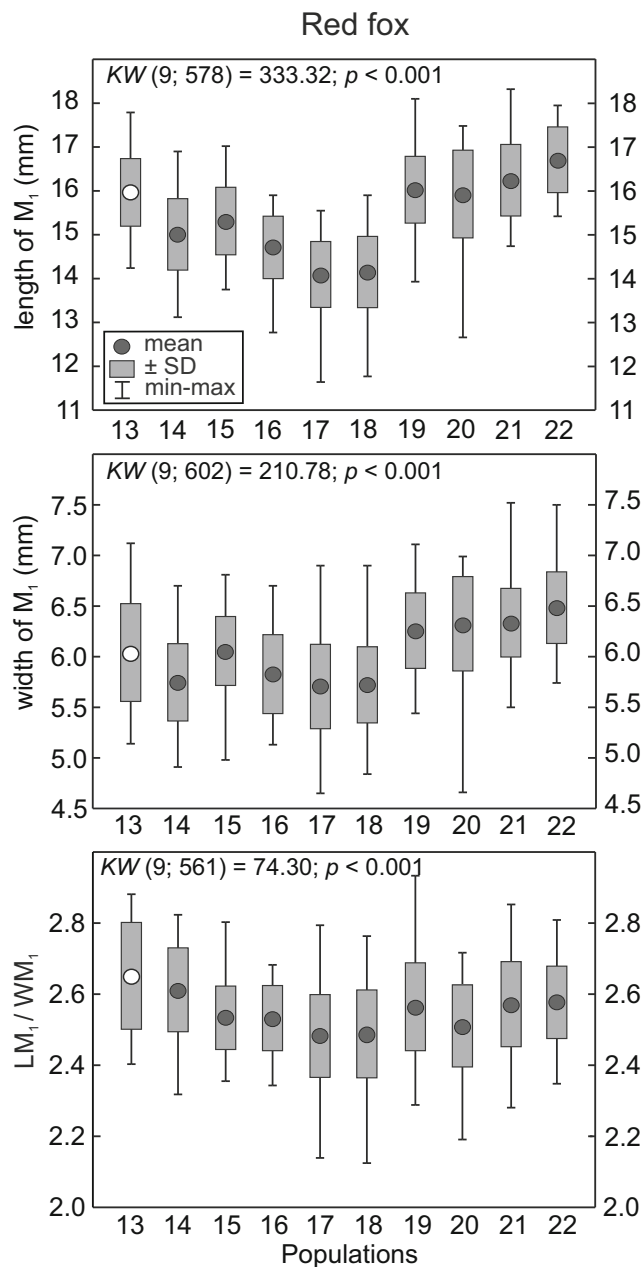


Fig. 7 Size variation of the first lower molar (M_1) in relation to length (LM_1), width (WM_1) and size proportion index (LM_1/WM_1) in one fossil and eight recent populations of the red fox *Vulpes vulpes*. Population names as in Table S2

Comparison of the arctic and the red foxes

For the statistic and graphic analyses of the metrical traits of M_1 in the arctic and red foxes, the means of the metrical features of the molar from three ancient and one extant samples' from Russia (Baryshnikov 2006, Table S5) have been included. Linear plots of the means for all populations of the arctic and red foxes showed differences between the two species. Both length and width of the M_1 were larger in the red fox than those in the arctic fox (Fig. 8). In contrast, the index

of LM_1/WM_1 was smaller in the red fox (Fig. 8). Among the arctic foxes, the Spitsbergen population (pop. 12) was characterized by smaller teeth and a high value of the index of LM_1/WM_1 .

The distribution of mean LM_1 in the ancient and recent populations of the arctic fox showed that the molars of foxes dated between 46 640 BP and 14 120 BP were longer than those of both the older and the younger ones (Fig. 8). The mean width of M_1 in the ancient populations did not differ from those in extant foxes. The index of the proportion of size of the fossil foxes is quite low, with the exception of the population 4 that shows a very high index of carnivore specialization (Fig. 8).

In terms of metric lower carnassials characteristic, the two fox species were very distinctive. It was confirmed by the PCA procedure, where factor I divided the species and explained 84.9% of total variance (Fig. 9).

Discussion

Evolutionary changes in the lower carnassials of the arctic fox

The oldest fossils of the arctic fox progenitor (*V. qiuzhundingi*) were found in the Tibet Plateau and were dated as the Pliocene fossils (ca. 3–4 Myr BP; Wang et al. 2014). In Europe, the arctic fox, a representative species of the Pleistocene, was known since the Saalian Glacial (Sommer and Benecke 2005). Molecular investigations (Dalén et al. 2007) revealed high haplotype diversity of the Late Pleistocene arctic foxes in Europe, which suggested a high effective population size of the species. Dalén et al. (2007) found that at the end of the Pleistocene, the European arctic foxes got extinct. Their discovery has been confirmed by our study on the lower carnassial in fossil foxes: the arctic fox from the late Pleistocene of Belgium appeared significantly distinct from several extant and ancient populations. The Belgian population was characterized by the longest crown and the highest size proportion index of the lower carnassials. The crown length of lower carnassial of that ancestral form of the arctic fox (*V. qiuzhundingi*) reached 16.6 mm, so it was bigger than any of the ancient and extant populations of the arctic fox shown in this analysis.

Size proportions of the M_1 suggest that the fossil arctic foxes of Belgium reached the highest level of carnivorous adaptation among the studied populations.

Among the recent populations of the arctic fox, the highest level of carnivory (highest index of LM_1/WM_1) was observed in the population of Spitzbergen. The diet of the arctic fox in the Franz Josef Island and Alaska was heavily dependent on kill food remnants of the polar bear (*Ursus maritimus* L.): marine mammals and fish (Cahalane 1947; Chesemore

Table 3 Above diagonal: Variation between populations of the red fox (*Vulpes vulpes*) based on lengths of M₁ were arranged by the *z* values of the Kruskal-Wallis test. Below diagonal: Variation between populationsof the red fox (*Vulpes vulpes*) based on widths of M₁ were arranged by the *z* values of the Kruskal-Wallis test. Significant differences (*p* < 0.05) were presented in italics. Population names are listed and explained in Table S2

Pop	13	14	15	16	17	18	19	20	21	22
13	*	<i>4.16</i>	2.95	<i>4.84</i>	<i>8.05</i>	<i>7.66</i>	0.23	0.11	0.89	2.21
14	3.14	*	1.61	1.29	<i>4.41</i>	<i>3.98</i>	<i>5.99</i>	<i>4.12</i>	<i>5.89</i>	<i>6.52</i>
15	0.15	<i>4.01</i>	*	2.69	<i>6.40</i>	<i>5.91</i>	<i>4.47</i>	2.88	<i>4.56</i>	<i>5.42</i>
16	2.03	0.82	2.50	*	2.34	2.01	<i>6.33</i>	<i>4.80</i>	<i>6.33</i>	<i>6.95</i>
17	<i>3.66</i>	0.44	<i>4.77</i>	1.22	*	0.38	<i>11.92</i>	<i>8.09</i>	<i>10.67</i>	<i>10.38</i>
18	<i>3.59</i>	0.38	<i>4.66</i>	1.18	0.06	*	<i>11.21</i>	<i>7.69</i>	<i>10.15</i>	<i>9.98</i>
19	2.38	<i>4.88</i>	2.87	<i>4.88</i>	<i>8.43</i>	<i>8.26</i>	*	0.38	0.93	2.52
20	2.73	<i>6.25</i>	3.01	<i>4.75</i>	<i>6.93</i>	<i>6.84</i>	1.02	*	1.03	2.35
21	2.93	<i>7.14</i>	<i>3.40</i>	<i>5.19</i>	<i>8.07</i>	<i>7.94</i>	1.07	0.12	*	1.60
22	<i>3.61</i>	<i>7.06</i>	<i>4.00</i>	<i>5.55</i>	<i>7.72</i>	<i>7.63</i>	2.18	1.00	1.23	*

1968; Degerbøl and Freuchen 1935). Such a narrow food niche of the arctic fox and extremely difficult environmental conditions in Svalbard and Franz Josef Island (archipelagos above 80° N) played a part in the decrease of its body size and the increase of carnivorous adaptations of its dental system.

Germonpré and Sablin (2004) noticed that the length of the front leg and hind foot in European arctic foxes increased from the Pleniglacial onwards. This size increase could be related to several factors such as the cold conditions of the Late Pleistocene, changes in prey-capture behavior, prey availability, and/or interference competition (Germonpré and Sablin 2004). Based on the size variation in the arctic foxes in their contemporary range, we can conclude that during the Late Pleistocene, arctic foxes adapted to cold by increasing their body size (Germonpré and Sablin 2004) and developing more carnivorous specialization of their dentition.

Lower carnassials in the ancient red fox from Belgium

Compared to the modern red foxes, the size of the lower carnassial from the ancient Belgian population was comparable with its size in some extant Siberian foxes (Novosibirskaya obl., Yakutskaya obl.). Only in the extant red foxes from the most north-eastern areas of Siberia (Kamchatka, Chukchi) did the dimensions of the lower carnassial exceed those in the ancient Belgian foxes. However, Baryshnikov (2015) found a few fossil remains of *V. vulpes* in the Geographic Society Cave (Far East, the warm stage of Late Pleistocene, 34 510–48 650 BP), where the dimensions of a single M₁ far exceeded the fossils of the late Pleistocene Belgian foxes. The length of the M₁ was 18.3 mm and the width 7.0 mm. The size of the tooth was comparable with the dimensions of the largest specimens of the recent red foxes from Chukchi and Kamchatka populations. The carnivorous index of the specimen was 2.61 and was similar to the mean LM₁/WM₁ index in ancient foxes

Table 4 Variation between populations of the red fox (*Vulpes vulpes*) based on size proportions of M₁ (LM₁/WM₁) were arranged by the *z* values of the Kruskal-Wallis test. Significant differences (*p* < 0.05) were marked by bold letters. Population names as in Table S2

Pop	14	15	16	17	18	19	20	21	22
13	0.48	<i>3.73</i>	2.89	<i>5.42</i>	<i>5.24</i>	2.51	<i>3.59</i>	1.95	1.46
14	*	<i>3.85</i>	2.77	<i>5.87</i>	<i>5.64</i>	2.42	<i>3.58</i>	1.72	1.16
15		*	0.35	2.10	1.88	1.92	0.45	1.98	1.92
16			*	2.01	1.84	1.09	0.69	1.28	1.36
17				*	0.21	<i>4.28</i>	1.22	<i>3.95</i>	<i>3.53</i>
18					*	<i>4.02</i>	1.05	<i>3.74</i>	<i>3.36</i>
19						*	1.95	0.40	0.62
20							*	2.06	2.04
21								*	1.95

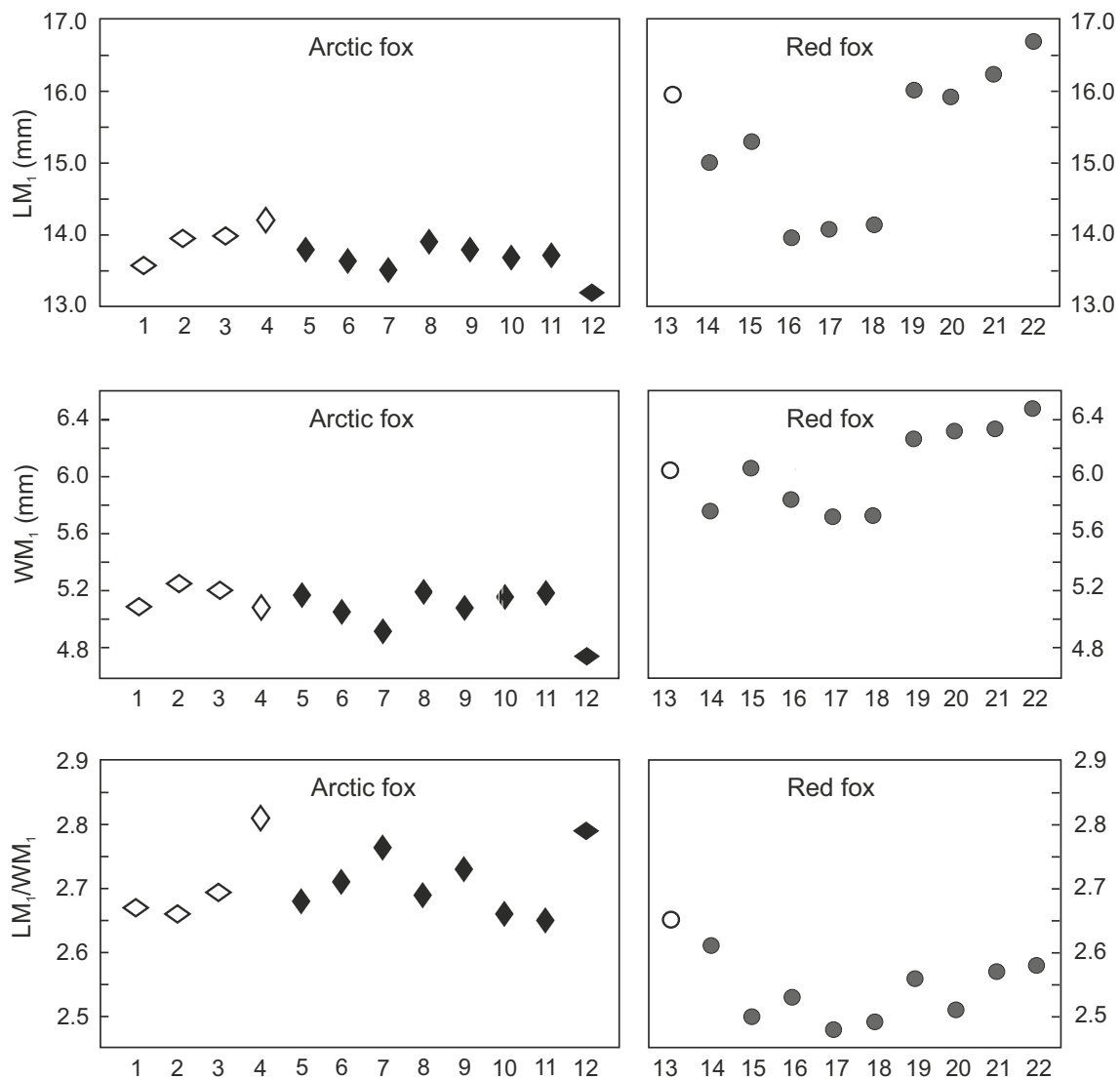


Fig. 8 Distribution of mean lengths (LM_1), mean widths (WM_1), the size proportion indices (LM_1/WM_1) of the lower carnassial in recent and fossil populations of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes*. Population names as in Table S2

from Belgium (2.65). In modern populations of the red fox, the means of the index are below 2.61. This indicates that the red foxes from the Late Pleistocene were characterized by higher level of carnivorous specialization than the modern red foxes. Earlier analyses (Szuma 2003, 2004) the red fox dental system revealed some microevolutionary adaptations of teeth to a more opportunistic diet in the last decades of the twentieth century. Also other authors documented the increasing dietary opportunism in the red fox in Europe (Yom-Tov et al. 2013). Such changes in the food niche of the red fox resulting from adaptation to anthropogenic environments bring on a decrease of carnivorous specialization in their teeth.

Interestingly, in the phyletic tree based on the size of lower carnassials, the Late Pleistocene Belgian foxes grouped with the contemporary populations of red foxes from Central and North-eastern Siberia, and not with the European populations of the

species. Phylogeographic studies on modern and ancient red foxes in Europe suggested some exchange in the fragments of various mtDNA clades in fox population before and after LGM (Teacher et al. 2011; Edwards et al. 2012; Statham et al. 2014).

Variation in carnivorous adaptation of both fox species

The means of crown length and width and the size proportions of the M_1 showed important differences between the two species. The LM_1/WM_1 index indicates the higher level of carnivorous specialization in the arctic fox than in the red fox. The size proportions of the carnassials in the ancient Belgian red foxes show a similarity to those in modern populations of the arctic fox, whereas the ancient arctic foxes from Belgium demonstrate the highest level of carnivorous adaptations. With

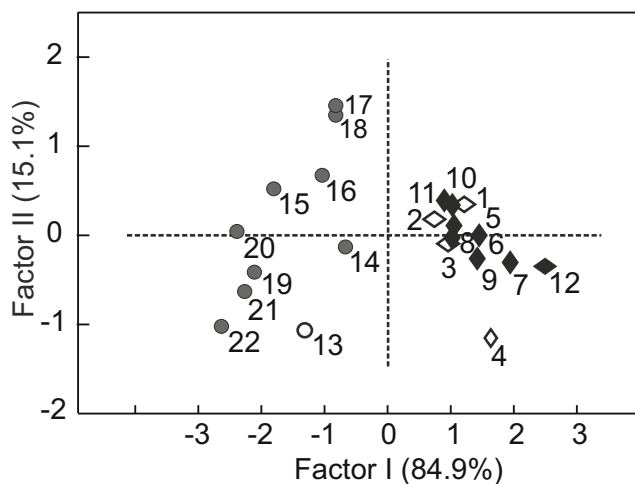


Fig. 9 Common distribution of recent and fossil populations of the arctic *Vulpes lagopus* and red foxes *Vulpes vulpes* in relation to I and II factors. In the PCA used metric parameters and proportion index of the first lower molar (LM_1/WM_1). Population names as in Table S2

regard to LM_1/WM_1 , the fossil arctic foxes from Belgium appeared most similar to the modern population of the species from Spitsbergen. This gives insight into food niche of Belgian arctic foxes during the Late Glacial and Pleniglacial period. Nowadays, the food resources of the arctic foxes in the High Arctic are extremely unpredictable. This translates into very small body size of the arctic foxes in Spitsbergen (condylobasal length of skull, 113–136 mm, Zalkin 1944). Very limited food resources, a weak food niche variation, a high specialization towards scavenging polar bear kills (hard skin, bones, frozen meat from large prey, mainly seals) resulted in small body size and heavy carnivore specialization of the dentition.

During the Late Pleistocene, Belgium was populated by horses (*Equus* sp.), muskoxen (*Ovibos moschatus*), reindeers (*Rangifer tarandus*), woolly rhinoceros (*Coelodonta anticuītatis*), woolly mammoths (*Mammuthus primigenius*), bison (*Bison* sp.), and large carnivores (see Table 1). The proper *Homo sapiens* appeared in Europe around 40 kya BP (Groucutt et al. 2015, Posth et al. 2016). The Upper Palaeolithic people hunted for large herbivores and carnivores (Germonpré 1997; Germonpré and Sablin 2004; Germonpré et al. 2009, 2013a, b; Hämäläinen and Gemonpré 2007). In the Netherlands, Van Kolfschoten (2001) describes the presence of such large mammals as the woolly mammoths, the giant deer (*Megaloceros giganteus*), the elk (*Alces alces*), the aurochs (*Bos primigenius*), the steppe bison (*Bison priscus*), and the muskoxen. Among large carnivores, the cave hyena (*Crocota crocota spelaea*), the cave lion (*Panthera leo spelaea*), the cave bear (*Ursus spelaeus*), and the brown bear (*Ursus arctos*) were present.

The arctic and red foxes could have consumed the remains of the large prey killed by the large predators and they could have actively hunted small mammals. It is possible that the foxes were feeding on the kill sites or even inside the camp sites of the

prehistoric hunters, scavenging the remains of the prey killed by the Palaeolithic people. When we look at the strong carnivorous specialization and teeth size of the arctic fox, we can conclude that the diet of this fox species in great part included large carcasses — the remains of the kills of large carnivores and Upper Palaeolithic people. The large dimensions of the Belgian Late Pleistocene arctic foxes (see Germonpré and Sablin 2004) in contrast to the recent and other ancient samples suggest rich food resources in that period. Thus, we can propose that the diet of the arctic fox of the Late Pleistocene of Belgium was highly differentiated with strong emphasis on the feeding on large carcasses from big prey animals. Similarly, heavy exploitation of mammoths by the Gravettian people from the Předmostí site (Czech Republic) most likely permitted the local arctic foxes to rely on mammoth meat (Bocherens 2015).

In summer, recent arctic foxes have a territorial life, but in winter, they gather near large prey and eat collectively, as do many other species consuming carrion (e.g., hyenas, wolves). Some findings of heavily worn teeth in ancient Siberian arctic foxes (Boeskorov and Baryshnikov 2013) also indicate an obvious adaptation to scavenging behavior. Heavy wear of teeth could have resulted from consumption of frozen meat or from gnawing of big bones (Boeskorov and Baryshnikov 2013).

Interestingly, the ancestor of the arctic fox from the Tibet Plateau (*V. qiuzhudingi*) had very large lower carnassial with highly specialized trigonid and relatively small talonid (Wang et al. 2014), which suggested strong hypercarnivory adaptation of this Pliocene fox. Assuming that the Tibetan Plateau during Pliocene was the origination center for cold-adapted Quaternary Ice Age fauna (Deng et al. 2019), also this fox species most probably showed heavy adaptation for carnivory/scavenging on megafauna prey. Recent research depicted very severe conditions during Pliocene in the Tibet Plateau and the presence of the cold adapted megafauna such as *Coelodonta thibetana* (Deng et al. 2011, 2019).

It seems that the ancient red fox from Belgium could scavenge to some extent the remains of the large prey but more likely its diet was mainly based on hunting for small mammals. The red fox is characterized by a solitary lifestyle and keeps other individuals away from large food resources. Moreover, there are no known findings of the red fox from the northern regions of Siberia for cold epochs of the Late Pleistocene (Boeskorov and Baryshnikov 2013). It seems that the extreme cold conditions of glaciation were not appropriate for this species and it expanded its range into this area only in the postglacial period. The lower carnassial dimensions of the ancient red foxes from Belgium are close to the recent populations of the fox from Siberia. Thus, we can conclude that the food niches of these populations were comparable. The palaeontological records from the Late Pleistocene of the Netherlands include the European moles (*Talpa europaea*), the grey dwarf hamsters (*Cricetulus migratorius*), the arctic lemmings (*Dicrostonyx torquatus*), the European water voles (*Arvicola terrestris*), the narrow-headed

voles (*Microtus gregalis*), the root voles (*Microtus oeconomus*), and the long-tailed ground squirrels (*Spermophilus undulatus*) (Van Kolfshoten 2001). In Belgium, during the Late Pleistocene, the Norwegian, steppe and collared lemmings, and the common and narrow-headed voles were present in varying frequencies, implying the presence of a mosaic landscape with woodland formation, open dry meadows and open humid meadows (Brace et al. 2012; Lagerholm et al. 2014; López-García et al. 2017). The composition of mammal fauna could suggest more open steppe landscape in that period. The records of large mammals such as the mammoth, the horse, the steppe bison, the reindeer, and the woolly rhinoceros support this observation (Germonpré 1997; Germonpré et al. 2013a). It is possible that in Belgium during the end of the Pleistocene, forests encroached in the landscape along rivers, in lower altitudes (cf. Noirel-Schultz 1994; López-García et al. 2017). Such conditions were suitable for coexistence of species from open and wooded areas. Relatively larger carnassials and higher carnivorous specialization of teeth in the arctic and red foxes from Late Pleistocene in Belgium can result from specific food resources of the epoch, abounding in the cold megafauna.

Conclusions

In the Late Pleistocene of Belgium, the arctic and red foxes showed the most carnivorous specialization of the carnassials morphology among other ancient and extant populations of the foxes, which seems to be a result of specific ecological and climatic factors: rich assembly of mammal mega-fauna and extremely harsh environmental conditions during the glacial period. The complete separation of the Late Pleistocene arctic foxes from Belgium from other ancient and extant populations of the species confirmed the earlier finding that the Late Pleistocene arctic fox from north-western Europe was a distinct phylogenetic lineage that got extinct with the climate warming.

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