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Ecological and evolutionary determinants of dental polymorphism in the arctic fox *Vulpes* (*Alopex*) *lagopus*

Elwira Szuma

Mammal Research Institute, Polish Academy of Sciences, ul. gen. Waszkiewicza 1, PL-17-230 Białowieża, Poland (e-mail: eszuma@zbs.bialowieza.pl)

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The influence of some ecological and evolutionary factors on the pattern of dental polymorphism across the geographic range of the arctic fox (*Vulpes* (*Alopex*) *lagopus*) was studied. Dental morphotype characters (groups of morphotypes from A to S) in 12 geographically separate populations of the arctic fox were documented. Two evolutionary trends were observed: (1) simplification of the premolars and lower carnassial (M_1), and (2) increased complexity of the upper carnassial (P^4), third upper incisor (I^3), and third lower molar (M_3). Differences in dental morphology among arctic fox populations appear to be largely explained by evolutionary history, presence or absence of competition with the red fox (*Vulpes vulpes*), and diet, with a lesser influence of geography and climate. With respect to morphology, arctic foxes from the mainland populations of Eurasia and North America, are the most similar, followed by the partly-isolated island populations (Greenland, St. Lawrence Island). The most distinct forms are the arctic foxes from Commander Islands, that exist in permanent isolation.

Introduction

Over the course of its evolutionary history, the arctic fox has expanded its range significantly. Nevertheless, the species has always been associated with open terrains that are environmentally quite homogenous. At present, the arctic fox lives in arctic and alpine areas of tundra in Eurasia, North America, the Canadian archipelagoes, Siberian islands, Greenland, Iceland, and Svalbard. It also occurs in subarctic seas, on the islands of the Aleut archipelago and the Bering Sea, Commander Islands, and coasts of Iceland (Angerbjörn *et al*. 2004).

Within its range, eight subspecies of arctic fox are recognized: *Vulpes* (*Alopex*) *lagopus lagopus*, *V. l. beringensis*, *V. l. fuliginosus*, *V. l. groenlandicus*, *V. l. hallensis*, *V. l. pribilofensis*, *V. l. spitzbergenensis*, *V. l. ungava* (Audet *et al*. 2002). The subspecies *V. l. lagopus* includes the larger part of the total range of the arctic fox. This subspecies is connected mainly with land areas of Eurasia as well as North America. Remaining subspecies are more or less isolated island populations. Two ecotypes of arctic foxes have been distinguished: "coastal foxes" and "lemming foxes" (Braestrup 1941, Tannerfeldt & Angerbjörn 1998). The "coastal" form has a distinctly coastal diet and does not undergo pronounced demographic cycles. The "lemming" foxes live further inland, feed primarily on rodents, and regularly undergo cyclical changes in population size. The pelage of mainland populations of the arctic fox change from dark in summer to white in winter, whereas the coastal populations lack a white winter coat and are instead variably dark all year (Braestrup 1941).

In spite of these morphological and ecological differences, the arctic fox is relatively similar across its range, and has been called a "monolithic" species (Ognev 1931). A lack of physical barriers over most of its geographic range has resulted in almost continuous panmixia especially during winter (Geptner & Naumov 1967). Arctic foxes are known to migrate, and have been recorded to travel over 1000 km (Eberhardt & Hansson 1978, Macpherson 1968), and even as much as 2300 km (Eberhardt *et al.* 1983). A study of the arctic fox mtDNA, conducted by Dalén *et al.* (2005) showed very low genetic variability and a lack of phylogeographic structure with no separate evolutionary units. Based on this they suggested that there is no support for distinguishing subspecies in the arctic fox. However, other studies of the mtDNA and microsatellite data in the whole range of the arctic fox found some geographical pattern of the genetic heterogeneity in the species (Geffen *et al.* 2007). The authors concluded that geographic distance and occurrence of sea ice together affected the pattern the most.

Craniometric studies uncovered an ambiguous picture of size variability in the arctic fox (Zalkin 1944, Bisaillon & DeRoth 1980, Pengilly 1984, Frafjord 1993, Prestrud & Nielsen 1995, Zagrebel'nyi & Puzachenko 2006, Puzachenko & Zagrebel'nyi 2008). Various analyses of skull parameters indicated opposite directions of geographical variation (Frafjord 1993, Daitch & Guralnick 2007). Puzachenko and Zagrebel'nyi (2008) suggested that climate as well as food base could be the main factors affecting this variation.

Szuma (2008) found no clear patterns of size variation in arctic fox dentition that could be explained by latitude or longitude. Similarly, there was no relationship between geography and either skull size or patterns of sexual dimorphism of the dental characters. Other investigations suggested that skull size and metric dental features are influenced by climatic factors, diet, and intra- and interspecies competition (Puzachenko & Zagrebel'nyi 2008, Szuma 2008).

Daitch and Guralnick (2007) used geometrical analysis of the size and shape of the first upper molar (M^1) to distinguish among foxes from Semidi Island, St. Paul Island, Bering Island, Nunivak Island and Siberia. The same authors did not observe any differences in this molar size in other populations, but did observe more significant differences among the populations in the shape of M^1 that they ascribed to differences in the diet. However, the variability of a single tooth does not provide a full view of variation of dentition in the species, and limits the possible explanations of the variability.

A more complete picture of the variation and evolution of dental morphology in arctic foxes is possible through analysis of frequency of dental morphotype characters, as was done for the hare, *Lepus* (Suchentrunk 2004, Suchentrunk & Fux 1996, Suchentrunk *et al.* 1994), marten, *Martes* (Wolsan 1988, 1989), and red fox *Vulpes vulpes* (Szuma 2002, 2004, 2007)

The chronological analysis of the morphometric pattern of variability of dental characters in the Polish population of the red fox over 70 years showed that qualitative dental characters were a more sensitive indicator of changes than patterns of correlation or variation of quantitative characters (Szuma 2003). Diminutive shifts in frequency of morphotypes seem to be a good indicator of evolutionary change in the mammalian dental system. In Szuma (2007), the influence of ecological and evolutionary factors on dental morphology was found, the phylogeographic relationships in the species were uncovered, and evolutionary changes in the *Vulpes vulpes* line were reconstructed.

The dental morphology of the arctic fox has not been so well studied. The arctic fox is closely related to the red fox, which co-occurs and competes with it in the southern part of its range. The literature on the subject of competition and social interactions among these species is abundant (e.g. Hersteinsson & Macdonald 1992, Linnell *et al.* 1999, Tannerfeldt *et al.* 2002). In regions where both species co-occur, in conditions of intensified competition, the arctic fox is dominated by the red fox (Tannerfeldt *et al.* 2002).

It is not known whether patterns of variability of the dental morphotype characters in the arctic fox and the red fox are similar, and what effect competition has on dental morphology of the arctic fox, and how it has responded in the case of total release of the pressure of the stronger competitor (such as in populations from Commander Islands). With this in mind, the goals of this study were to: (1) document the frequency distributions of dental morphotypes across the arctic fox range, (2) compare the patterns of morphotype frequency distributions in the arctic and red fox (using selected populations of the red fox that are sympatric with the arctic fox, Szuma 2007), (3) explore the influence of geographical, climatological, ecological, or evolutionary factors on the pattern of frequency of morphotype characters in the dentition of the arctic fox, as well as (4) attempt to verify phylogeographic relationships in the species range.

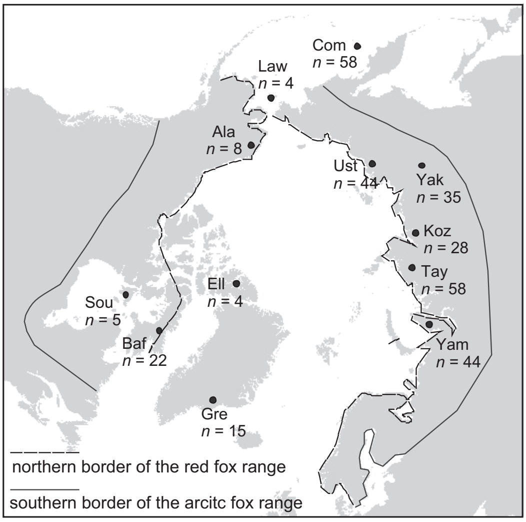

Fig. 1. Distribution of the studied samples of the arctic fox *Vulpes* (*Alopex*) *lagopus.* Abbreviation for particular populations: Ala = Alaska, Baf = Baffin Island, Com = Commander Islands, Ell = Ellesmere Island, Law = St. Lawrence Island, Sou = Southampton Island, Gre = Greenland, Koz = Kozhevnikova Bay, Tai = Taimyr Peninsula, Ust = Ust-Yansk region, Yak = Yakutsk region, Yam = Yamal Peninsula.

Material and methods

Variation in the tooth shape of the arctic fox, *Vulpes* (*Alopex*) *lagopus* was analyzed using 325 skulls from 12 geographically distant populations (Fig. 1). Figure 1 provides the entire list of populations, abbreviations of population names, as well as numbers of individuals (*n*) in particular samples. Because of the small number of specimens in the samples Ell, Law, and Sou, these populations were not statistically analyzed.

Specimens used in the investigations came from scientific collections belonging to: the Zoological Institute, Russian Academy of Sciences in St. Petersburg; the Zoological Museum of the Moscow University; the Siberian Zoological Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences in Novosibirsk; the National Museum of Natural History in Kiev; the Zoological Museum University of Taras Schevchenko in Kiev; the Natural History Museum in London; the Zoological Museum, Amsterdam University.

Dental polymorphisms in the arctic fox were analysed using morphotypes (Fig. 2) earlier defined and illustrated for the red fox (*see* Szuma 2007). The morphotype groups were identified by the letters from A to R, whereas morphotype variants within each group were identified numbers, with higher numbers indicating a more complex morphology. The number of morphotypes in each group ranges from 2 to 5. Definitions of the dental morphotypes that were used in the analysis of dental polymorphism in the arctic fox are listed in Appendix.

Three groups of morphotypes used in the previous work on red foxes were not used in this study (B, N, S). Groups B and N were not considered because the characters could only be coded on a small number of individuals. Group S was omitted because of a lack of variability of the character in the arctic fox. All arctic foxes have the same morphotype S1, which exhibits no traces of a conule in the posterolingual part of the crown of M_1 behind the entoconid.

Geographical variation of the morphotype characters was analysed using the left side of the tooth row. Because the earlier analysis of frequency distributions of the morphotypes in females and males conducted on the sample of red fox from Poland showed a lack of significant differences between sexes (Szuma 2002),

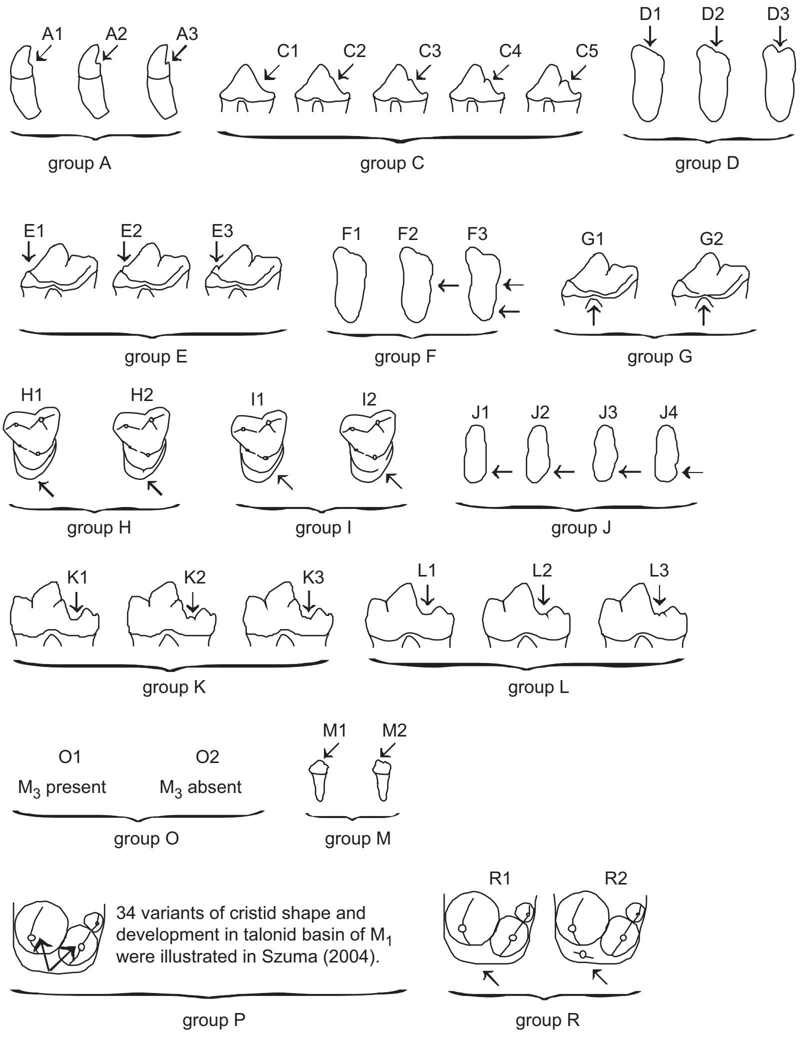

Fig. 2. Depiction of morphotypes of groups from A to R in the arctic fox dentition.

the sexes were combined for each of the arctic fox populations. Moreover, separating the sexes would have resulted in much smaller sample sizes as sex was not recorded for many specimens.

The frequency distribution for 15 groups of the morphotypes were analysed in 12 populations of the arctic fox. These frequency distributions were compared with frequency distributions of the same features in several, previously analysed, northern populations of the red fox from PEC (Pechoro-Illycheskiy Reserve, n = 77), CHU (Chukchi, n = 90), YAK (Yakutsk region, n = 38), KAM (Kamchatka Peninsula, n = 30), MAG (Magadan region, n = 96) (*see* Szuma 2007).

Before variance, multiple regression and principal component analyses were conducted, the frequencies of particular morphotypes were arcsine transformed using MS Excel 2007 to normalize the data. The significance of interpopulation differences in morphological features of teeth of the arctic fox was determined using the Chi-square test (χ^2).

Multiple regression was used to estimate the influence of geographic and climatic factors on variation in the frequency of individual morphotypes. The influence of longitude (LON), latitude (LAT), mean annual temperature (MAT), mean amplitude of temperatures between warmest month (July) and coolest month (January) in the year ($\mathrm{AMT}_{\mathrm{Jun–Jan}}$), as well as mean annual sum of precipitation (MASP) were analysed. Geographic coordinates of every specimen were marked with 1° precision. The geographic coordinates of a population was calculated as the average of geographic coordinates for all specimens belonging to a given population. The climatic data for populations studied were taken from the WorldClimate data base (1996–2004 Buttle and Tuttle Ltd.; http://www.worldclimate.com). Using the geographic coordinates of a population, the closest meteorological station was found in the WorldClimate data base. In this way, every population was assigned a mean annual temperature (with 0.1 °C accuracy) and mean annual sum of precipitation (with 0.1 mm accuracy).

A principal components analysis was used to assess which morphotype features are most important in explaining intrapopulation variation in the arctic fox. Multiple regression was used to determine the proportion of variance explained by the geographic and climatic variables. Finally, a cluster analysis was used to determine levels of similarity among the arctic fox populations, as well as between these and the five northern populations of the red fox *Vulpes vulpes*. All statistical analyses were performed using the Statistica.PL 1997 software package.

Table 1. Interpopulation differences in frequency distributions of the group morphotypes from A to R in the whole range of the arctic fox *Vulpes* (*Alopex*) *lagopus*.

Morphotype group	χ^2	df	p
A	17.475	20	0.621
C (P^2)	60.070	20	< 0.001
C (P^3)	143.950	30	< 0.001
C (P_2)	24.540	20	0.220
C (P_3)	108.568	40	< 0.001
C (P_4)	21.295	20	0.380
D	48.600	10	< 0.001
E	37.190	20	0.011
F	24.495	20	0.221
G	19.266	10	0.037
H	20.273	10	0.027
I	19.455	10	0.035
J	45.994	20	0.001
K	60.582	20	< 0.001
L	14.239	10	0.162
M	62.127	10	< 0.001
O	10.496	10	0.398
P	54.024	30	0.005
R	5.549	10	0.851

Results

Among, the studied groups of morphotypes, statistically significant interpopulational variability ($p > 0.05$) was confirmed in the case of groups A, C (for P^2, P^3, and P_3), D, E, H, J, K, M, and P (Table 1). The comparison of frequency distributions for individual groups of the morphotypes in the arctic fox and co-occurring red foxes showed that these species differ significantly ($p < 0.05$) in the majority of analysed features (Table 2).

In group A in the arctic fox populations, morphotypes A2 and A3 dominate (Fig. 3). In the St. Lawrence population, only specimens with morphotype A2 are present. From Ellesmere Island, only arctic-fox specimens with morphotype A3 were found. Morphotype A1 was observed in only one case in the population of arctic foxes from Ust-Yansk region.

In case of P^2, morphotype C1 has the greatest share (Fig. 4). Only in the populations from Commander Islands and the Yakutsk region do morphotypes C2 and C3 have larger proportions than in the other populations of the arctic fox. On P^3, the share of individual morphotypes of group

Table 2. Differences in frequency distributions of the group morphotypes from A to S in two sympatric foxes: the arctic fox *Vulpes* (*Alopex*) *lagopus* and the red fox *Vulpes vulpes*.

Morphotype group	χ^2	df	p
A	154.999	2	< 0.001
C (P^2)	0.842	2	0.656
C (P^3)	5.042	4	0.283
C (P_2)	34.274	2	< 0.001
C (P_3)	39.506	4	< 0.001
C (P_4)	0.946	2	0.623
D	6.192	2	0.045
E	50.199	2	< 0.001
F	53.662	2	< 0.001
G	3.925	1	0.048
H	61.719	1	< 0.001
I	66.938	1	< 0.001
J	26.282	3	< 0.001
K	37.608	2	< 0.001
L	40.337	2	< 0.001
M	49.266	1	< 0.001
O	5.607	1	0.018
P	192.547	4	< 0.001
R	178.396	1	< 0.001
S	41.617	1	< 0.001

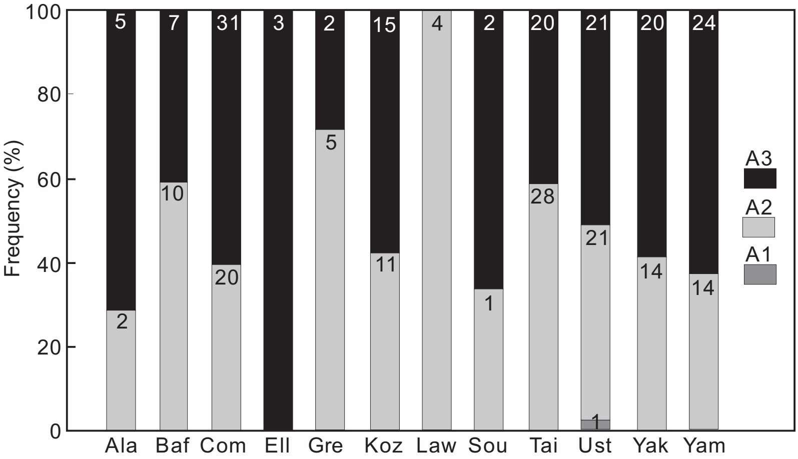

Fig. 3. Frequency distribution of morphotype group A for I^3 in the arctic fox populations. For definitions of the morphotypes *see* Appendix. For illustrations of the morphotypes *see* Szuma 2007 and Fig. 2. For abbreviations *see* Fig. 1.

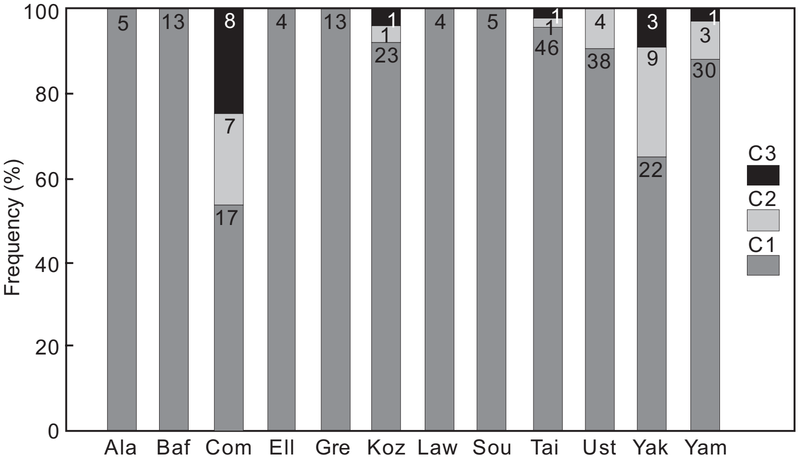

Fig. 4. Frequency distribution of morphotype group C for P^2 in the arctic fox populations. Other explanations as in Fig. 3.

C is more diverse (Fig. 5). Morphotypes C1, C2, and C3 dominate. Only in the arctic foxes from Commander Islands does morphotype C4 dominate (78.6%). P_2 shows a lack of significant variation in the shape ($p > 0.05$) of the crown (Table 1 and Fig. 6). In all the populations morphotype C1 dominates. Only in the arctic foxes from Commander Islands was the share of two different morphotypes noted: C2 (7.1%) and C3 (10.7%). On P_3, the whole scope of C-group morphotypes was observed (Fig. 7). Dominant morphotypes were C1, C2, and C3, while C5 was scarce. Only in case of the arctic foxes from Commander Islands do the morphotype C4 (68.7%) dominate. A lack of a significant inter-population difference ($p > 0.05$) was found in the case of P_4 (Table 1 and Fig. 8). Morphotype C4 dominates in all the populations.

In the arctic fox, morphotypes D2 and D3 illustrate the shape of P^4 (Fig. 9). Morphotype D1 was not found in any population of this fox. Morphotype D2 appears exclusively in the arctic foxes from Commander Islands. Also on Southampton Island and Ellesmere Island only specimens with morphotype D2 were observed.

Group E in the arctic fox is mainly represented by morphotype E1 (Fig. 10). Two remaining morphotypes — E2 and E3 — appear in smaller numbers. In the case of group F, the most numerous morphotype is F2, whereas F1 is the rarest (Fig. 11). The frequency distribution for group G shows that in the arctic fox the morphotype G1 dominates, and it achieves the highest frequency in the Commander Islands population (87.3%; Fig. 12).

The shape of the M^1 crown describes morphotypes of groups H and I. In group H, mor-

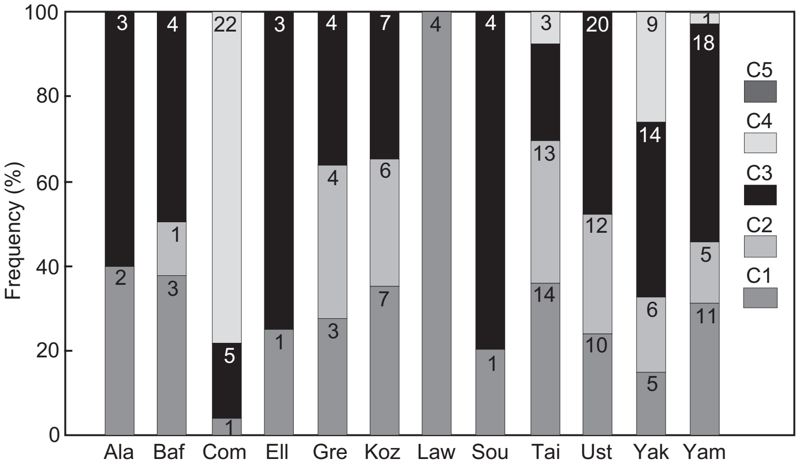

Fig. 5. Frequency distribution of morphotype group C for P^3 in the arctic fox populations. Other explanations as in Fig. 3.

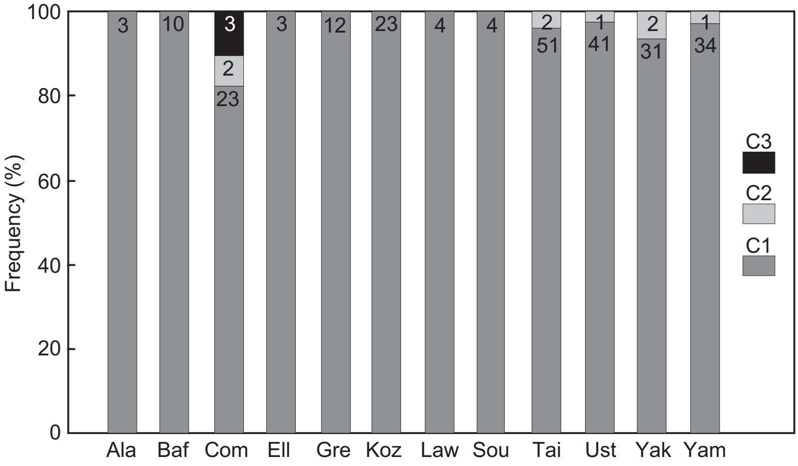

Fig. 6. Frequency distribution of morphotype group C for P_2 in the arctic fox populations. Other explanations as in Fig. 3.

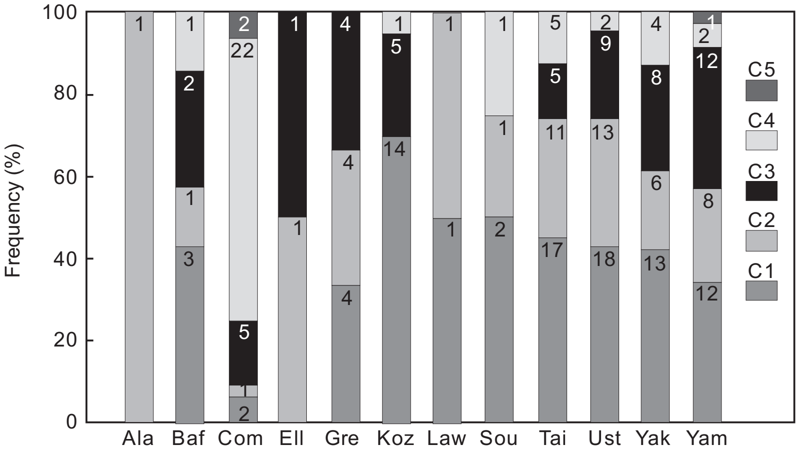

Fig. 7. Frequency distribution of morphotype group C for P_3 in the arctic fox populations. Other explanations as in Fig. 3.

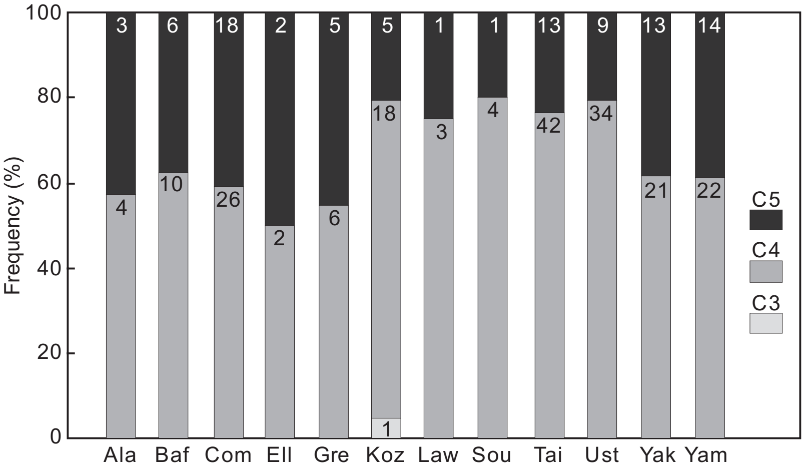

Fig. 8. Frequency distribution of morphotype group C for P^4 in the arctic fox populations. Other explanations as in Fig. 3.

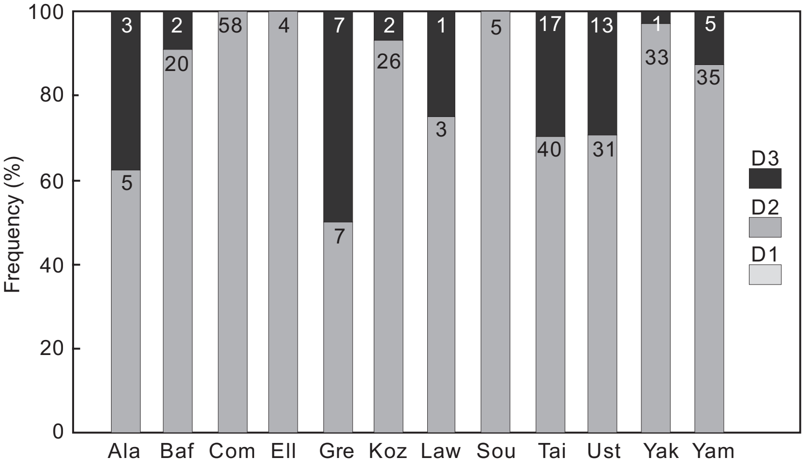

Fig. 9. Frequency distribution of morphotype group D for P^4 in the arctic fox populations. Other explanations as in Fig. 3.

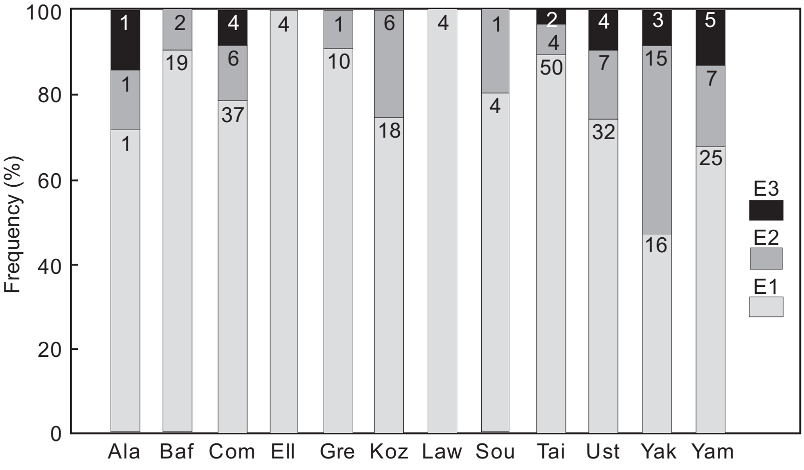

Fig. 10. Frequency distribution of morphotype group E for P^4 in the arctic fox populations. Other explanations as in Fig. 3.

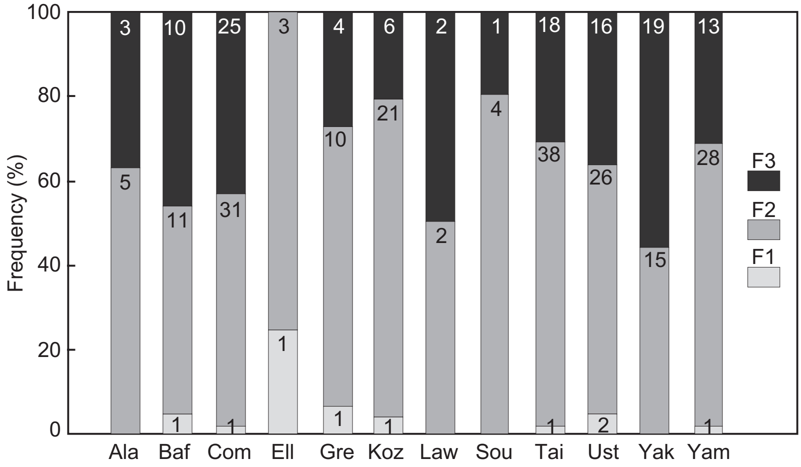

Fig. 11. Frequency distribution of morphotype group F for P^4 in the arctic fox populations. Other explanations as in Fig. 3.

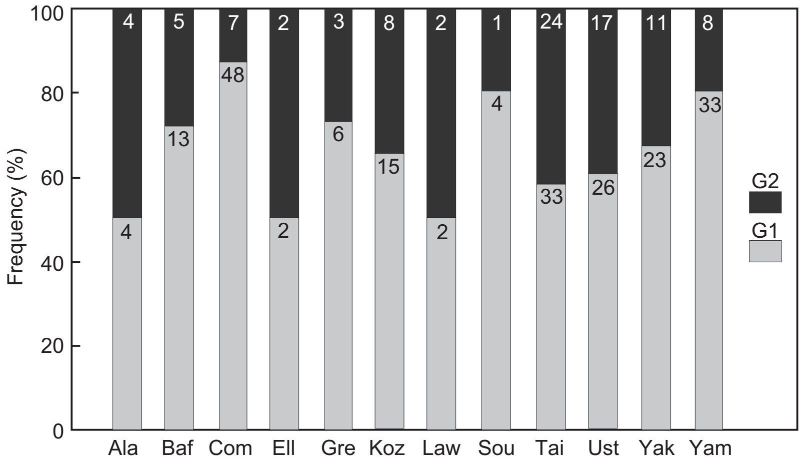

Fig. 12. Frequency distribution of morphotype group G for P^4 in the arctic fox populations. Other explanations as in Fig. 3.

photype H1 dominates (Fig. 13). In less numerous samples of the arctic fox, morphotype H1 achieves the frequency of even 100% (Alaska, Southampton Island, Ellesmere Island, Greenland, St. Lawrence Island). In the case of group I, in the majority of the arctic fox populations morphotype I2 is outnumbered, simultaneously the highest frequency of I2 has been found in the population from Greenland (83.3%; Fig. 14).

The shape of the P_4 crown in the arctic fox is illustrated by morphotypes J1, J2, and J3, with J1 being the dominant (Fig. 15). Next in frequency is morphotype J2; the presence of morphotype J3 was notably reduced and was observed only in the Ust-Yansk-region and Yamal Peninsula populations.

In the case of group K related to the shape of M_1, the dominant morphotype is K2 (Fig. 16). Only in the populations from Commander Islands and St. Lawrence Island does morphotype K1 dominates (71.4% and 75.0%, respectively). The frequency distribution of the morphotypes in group L indicates the dominance of morphotype L1 (Fig. 17).

Frequencies of morphotypes M1 and M2 in the arctic fox, which are connected with the M_3 crown shape, are diverse in individual populations (Fig. 18). Conversely, there are no significant interpopulation differences ($p > 0.05$) in the frequencies of group-O morphotypes, which are related to the presence or absence of M_3 in the arctic fox dentition (Table 1 and Fig. 19).

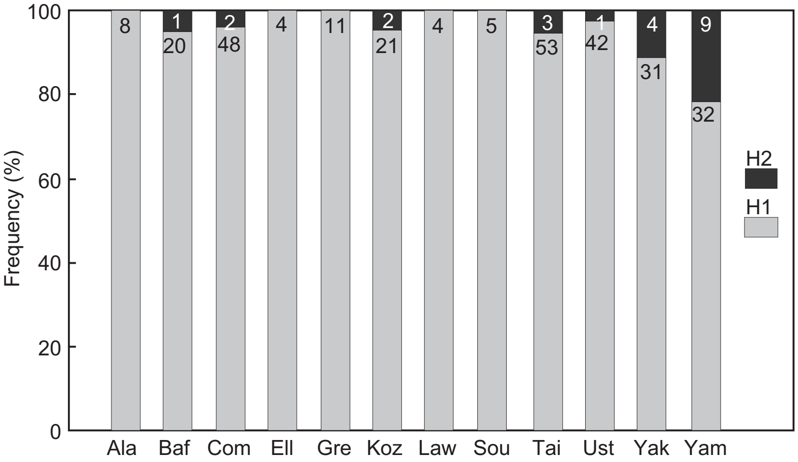

Fig. 13. Frequency distribution of morphotype group H for M^1 in the arctic fox populations. Other explanations as in Fig. 3.

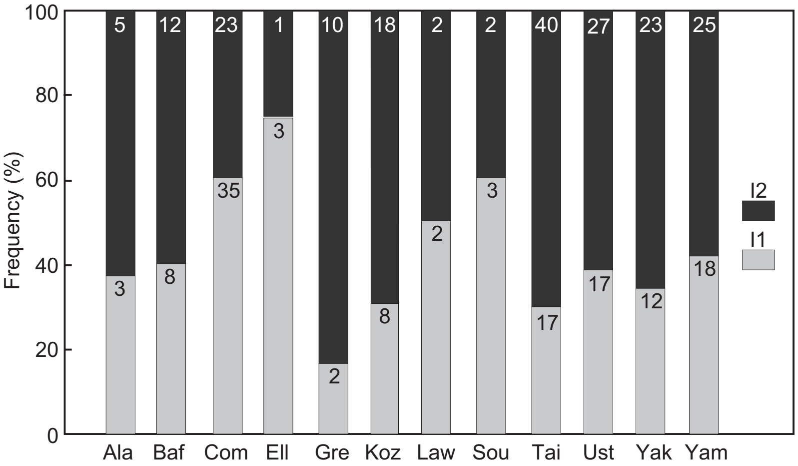

Fig. 14. Frequency distribution of morphotype group I for M^1 in the arctic fox populations. Other explanations as in Fig. 3.

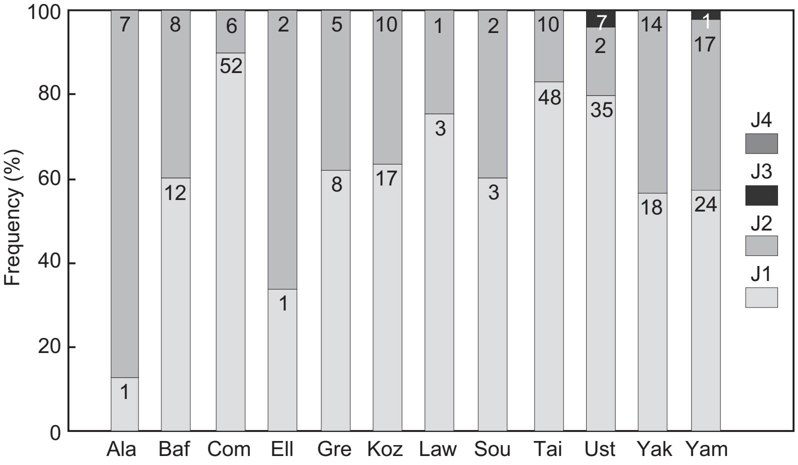

Fig. 15. Frequency distribution of morphotype group J for P_4 in the arctic fox populations. Other explanations as in Fig. 3.

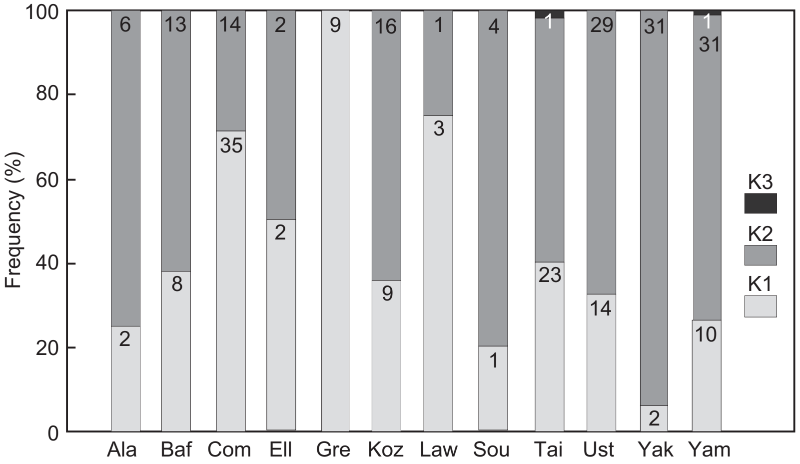

Fig. 16. Frequency distribution of morphotype group K for M_1 in the arctic fox populations. Other explanations as in Fig. 3.

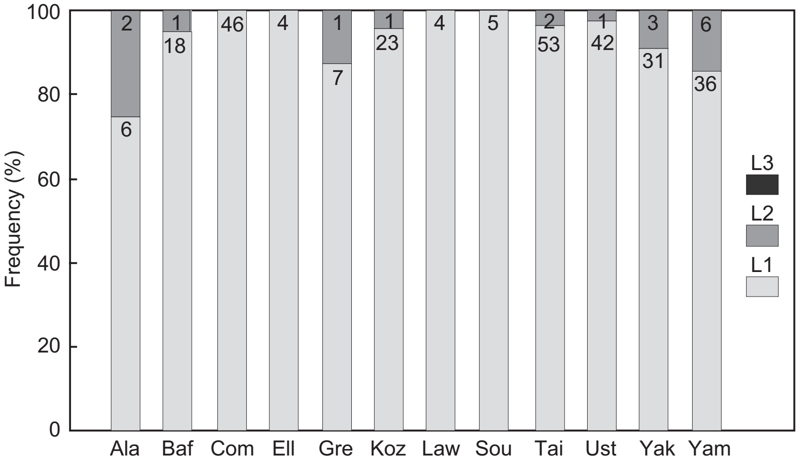

Fig. 17. Frequency distribution of morphotype group L for M_1 in the arctic fox populations. Other explanations as in Fig. 3.

A significant interpopulation difference in the frequency of group-P morphotypes was found (Table 1 and Fig. 20). Morphotype P1 is most common, whereas morphotype P5 is absent altogether. In the case of group R, morphotype R1 dominates (Fig. 21), at the same time morphotype R2 appears in the population from Commander Islands (2.3%) and Kozhevnikova Bay only (4.2%).

The analysis of the influence of geographic and climatic factors on the differences in frequencies of all dental morphotypes showed, that in few cases latitude, mean annual temperatures as well as mean amplitude of temperatures between the warmest month (July) and coolest month (January) in the year had significant ($p < 0.05$) effects (Table 3). Longitude and mean annual sum of precipitation do not affect significantly ($p > 0.05$) frequencies of the morphotypes over the whole range of the arctic fox.

The principal component analysis (PCA) of the morphotypes of group C for upper and lower premolars revealed, that the first component is correlated with factor loadings for P^2 (C1, C2, C3), P^3 (C1, C4), P_2 (C1, C2, C3) and P_3 (C4, C5) (Table 4). Factor loadings for P^3 (C2) and P_3 (C1) are correlated with the second component. The first component explains nearly 48% of the total variance while the second, 21%. Multiple regression of the components and geographical and climatic parameters shows that latitude and mean annual temperature explain the second component only (Fig. 22).

The PCA of the morphotypes related to the

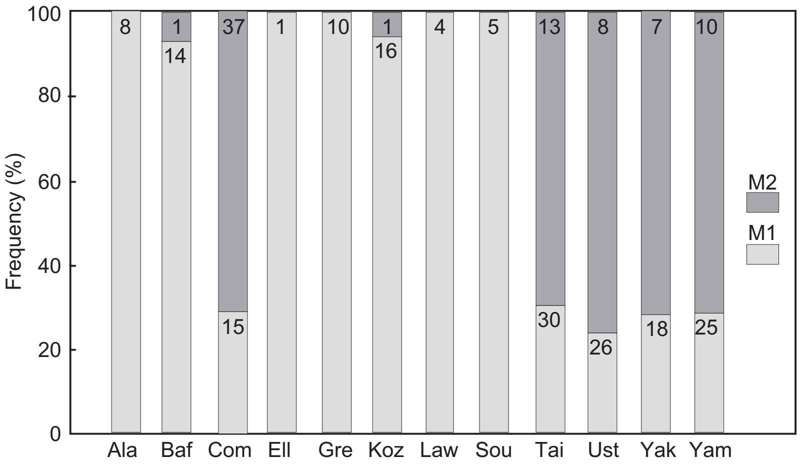

Fig. 18. Frequency distribution of morphotype group M for M_3 in the arctic fox populations. Other explanations as in Fig. 3.

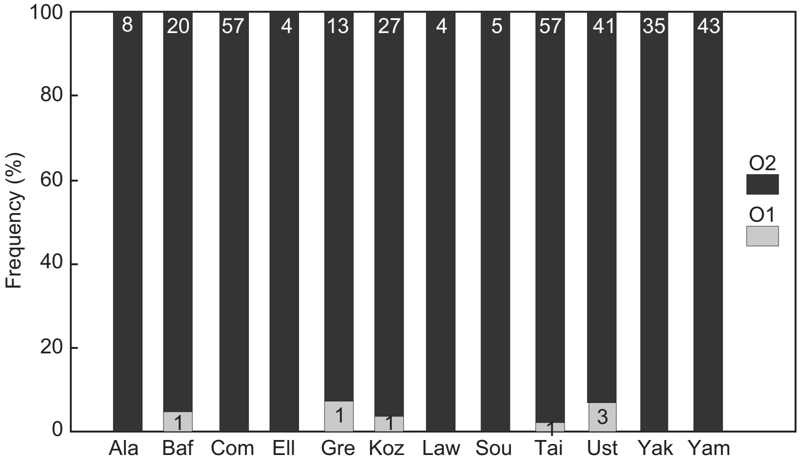

Fig. 19. Frequency distribution of morphotype group O for M_3 in the arctic fox populations. Other explanations as in Fig. 3.

shape of the upper carnassial (groups D, E, F, G) revealed in the case of the first component the highest correlation with factor loadings of morphotypes D2, D3, G1, G2, while the second component presents the highest correlation with factor loadings of morphotypes E1, E2, E3 and F3 (Table 5). The first component explains 40% total variance, whereas the second, 29.5%. As in

Table 3. Geographic and climatic influence on frequency changes of the some morphotypes in the arctic fox *Vulpes* (*Alopex*) *lagopus* range.

Morphotype	R^2	LON		LAT		MASP		AMT		MAT	
		t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
C1 (P^3)	0.68	1.57	0.16	1.84	0.11	–1.26	0.25	–2.13	0.07	2.88	0.02
C2 (P^3)	0.60	0.25	0.81	–2.52	0.04	–0.66	0.53	1.06	0.32	–1.77	0.12
E1 (P^4)	0.54	0.84	0.43	–1.09	0.31	–0.99	0.35	–2.42	0.05	–0.26	0.80
E3 (P^4)	0.69	0.39	0.71	0.65	0.53	–0.77	0.47	2.88	0.02	2.01	0.08
G1 (P^4)	0.57	–1.79	0.12	–1.09	0.31	0.88	0.41	0.74	0.48	–2.43	0.04
G2 (P^4)	0.57	1.79	0.12	1.09	0.31	–0.88	0.41	–0.74	0.48	2.43	0.04
K1 (M_1)	0.62	1.84	0.11	0.88	0.41	–1.23	0.26	–2.80	0.03	0.57	0.59

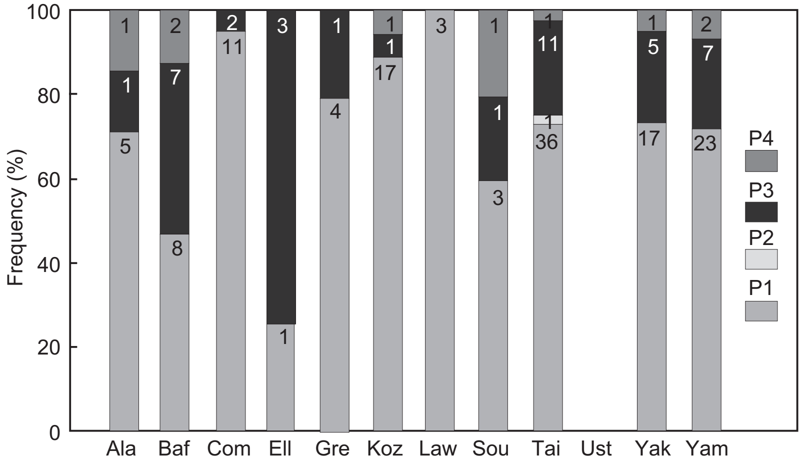

Fig. 20. Frequency distribution of morphotype group P for M_1 in the arctic fox populations. Other explanations as in Fig. 3.

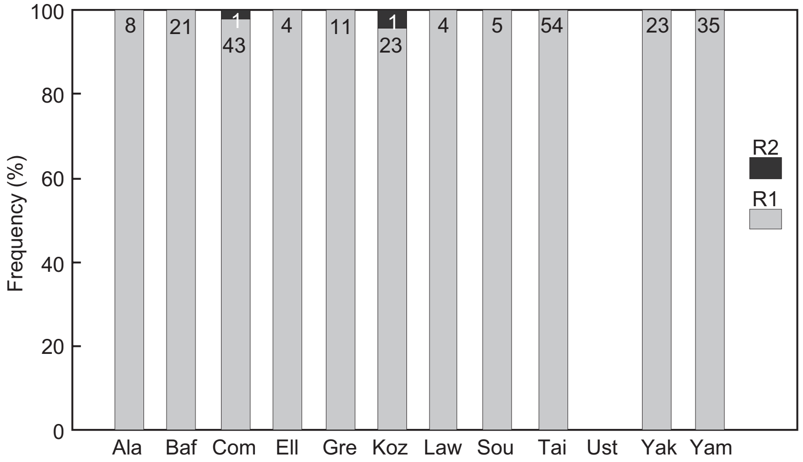

Fig. 21. Frequency distribution of morphotype group R for M_1 in the arctic fox populations. Other explanations as in Fig. 3.

the case of variation in premolars (group-C morphotypes) and also the shape variability of the upper carnassial (P^4) the first component could not be explained by climatic and geographic variables. The second component changes significantly together with mean amplitude of temperatures ($t = -8.24$, $p = 0.001$) and latitude ($t = 2.87$, $p < 0.05$) (Fig. 23).

Among the factor loadings of the morphotypes of groups H, I, J, K, L, P, and R, that describe the shape polymorphism of M^1, P_4, and M_1, loadings of H1, H2, P1, P3, and P4 are significantly ($p < 0.05$) correlated with the first component, while J1, J2, L1, and L2 are significantly ($p < 0.05$) correlated with the second component (Table 6). The first component explains 31% of the variance, while the second, 18%. In the case of morphotypes describing the shape of M^1, P_4, and M_1 no factor explaining the total variance is affected by geographic and climatic parameters (Fig. 24).

Factor loadings obtained for the morphotypes illustrating the shapes of M_1 and M_3 — i.e. O1, O2, and R1 — are significantly ($p < 0.05$) correlated with the first component, whereas M1 and M2 are significantly ($p < 0.05$) correlated with the second component (Table 7). In the case of this set of morphotype characters the first component explains 43% of total variance, while the second, 34%. The first component is only slightly affected by latitude; the second component does not depend on any analysed climatic

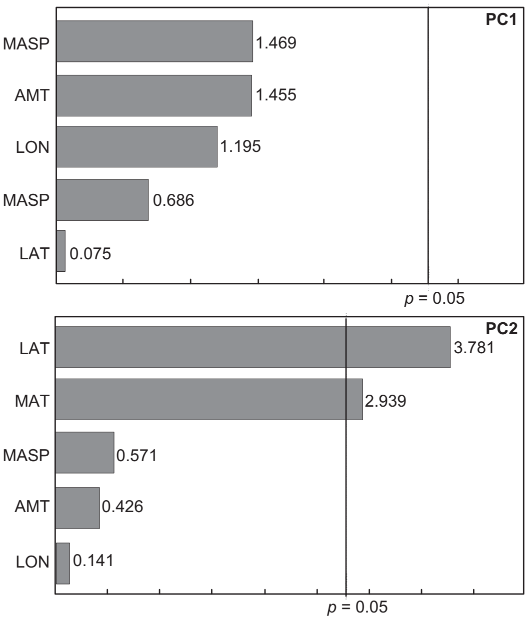

Fig. 22. Dependence of the principal components of the shape of upper carnassials (groups D, E, F, G morphotypes) on geographic and climatic factors in the arctic fox. Indices next to the columns are the Pareto coefficients.

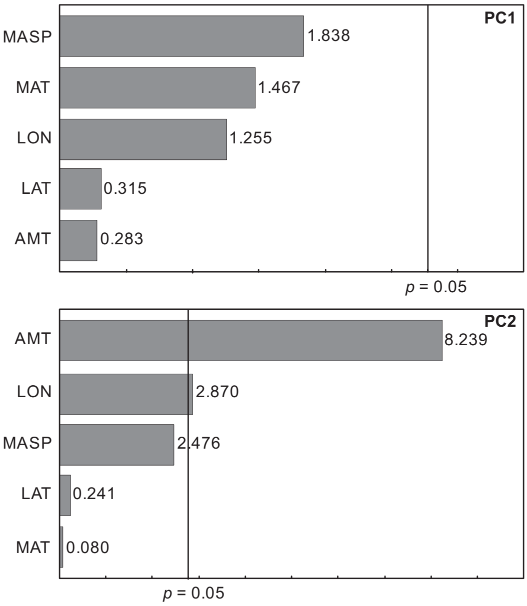

Fig. 23. Dependence of the principal components of the shape of premolars (morphotypes of group C) on geographic and climatic factors in the arctic fox. Indices next to the columns are the Pareto coefficients.

and geographic variables (Fig. 25).

The cluster analysis showed that the greatest similarity among the populations of the arctic fox was observed between the samples from Baffin Island, Kozhevnikova Bay as well as the Taimyr Peninsula. The arctic foxes from the Yakutsk region and Yamal Peninsula show great similarity with each other (Fig. 26). Somewhat

Table 4. Component correlations of the morphotypes of group C on P^2, P^3, P_2, P_3, P_4 with the first and second principal components for the arctic fox *Vulpes* (*Alopex*) *lagopus*.

Morphotype	PC1	PC2
C1 (P^2)	0.942	0.083
C2 (P^2)	–0.865	–0.143
C3 (P^2)	–0.947	0.019
C1 (P^3)	0.819	–0.186
C2 (P^3)	0.123	–0.753
C3 (P^3)	0.666	0.216
C4 (P^3)	–0.947	0.252
C1 (P_2)	0.947	–0.122
C2 (P_2)	–0.854	–0.002
C3 (P_2)	–0.815	0.350
C1 (P_3)	0.118	–0.931
C2 (P_3)	0.535	0.698
C3 (P_3)	–0.330	–0.518
C4 (P_3)	–0.773	0.080
C5 (P_3)	–0.765	0.326
C3 (P_4)	0.165	–0.618
C4 (P_4)	0.059	–0.620
C5 (P_4)	–0.165	0.674

Table 5. Component correlations of the morphotypes of group D, E, F, G on P^4 with the first and second principal components for the arctic fox *Vulpes* (*Alopex*) *lagopus*.

Morphotype	PC1	PC2
D2	–0.942	0.218
D3	0.942	–0.218
E1	0.174	–0.872
E2	–0.325	0.703
E3	0.199	0.711
F1	0.223	–0.591
F2	–0.108	–0.667
F3	0.042	0.770
G1	–0.908	–0.112
G2	0.908	0.112

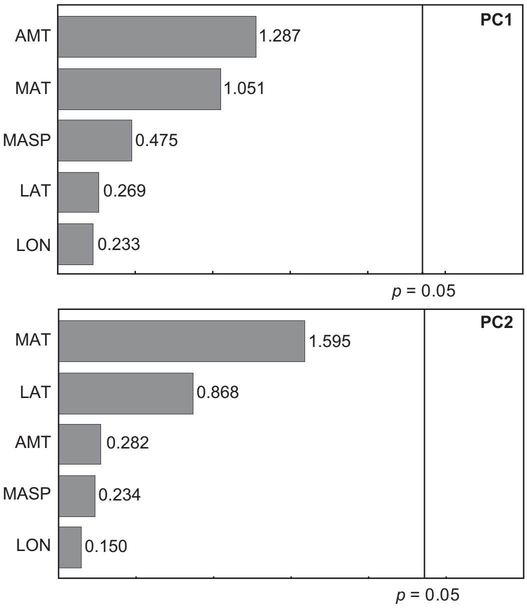

Fig. 24. Dependence of the principal components of the shape polymorphism of carnassials region (groups H, I, J, K, L, P, R morphotypes) on geographic and climatic factors in the arctic fox. Indices next to the columns are the Pareto coefficients.

Table 6. Component correlations of the morphotypes of group H, I on M^1, group J on P_4, groups K, L, P, R on M_1 with the first and second principal components for the arctic fox *Vulpes* (*Alopex*) *lagopus*.

Morphotype	PC1	PC2
H1	–0.868	0.081
H2	0.868	–0.081
I1	–0.608	–0.478
I2	0.608	0.478
J1	0.170	–0.819
J2	–0.176	0.821
J3	0.216	–0.104
K1	–0.111	0.436
K2	0.098	–0.436
K3	0.431	–0.177
L1	–0.458	–0.797
L2	0.458	0.797
P1	0.779	0.108
P2	0.431	–0.177
P3	0.834	0.241
P4	0.785	0.094
R1	0.020	0.202
R2	0.178	–0.166

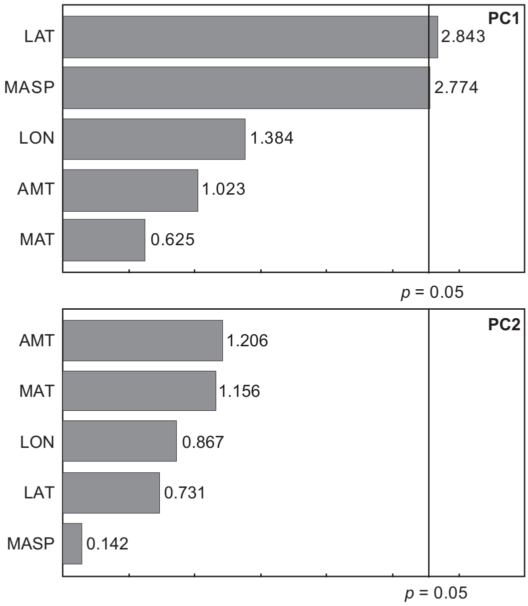

Fig. 25. Dependence of the principal components of the shape M_1 and M_3 (groups M, O, R morphotypes) on geographic and climatic factors in the arctic fox. Indices next to the columns are the Pareto coefficients.

more distant are the arctic foxes from the Greenland and St. Lawrence Island populations. The most distant with respect to dental morphology, and at the same time the most morphologically close to the red fox, is the isolated population of the arctic fox living on Commander Islands.

Discussion

The arctic fox is recognized as a genetically and morphologically homogeneous species. Dalén *et*

Table 7. Component correlations of the morphotypes of group M, O on M_3, group R on M_1 with the first and second principal components for the arctic fox *Vulpes* (*Alopex*) *lagopus*.

Morphotype	PC1	PC2
M1	0.103	0.970
M2	–0.103	–0.970
O1	0.956	0.175
O2	–0.956	–0.175
R1	–0.701	0.318
R2	0.059	–0.477

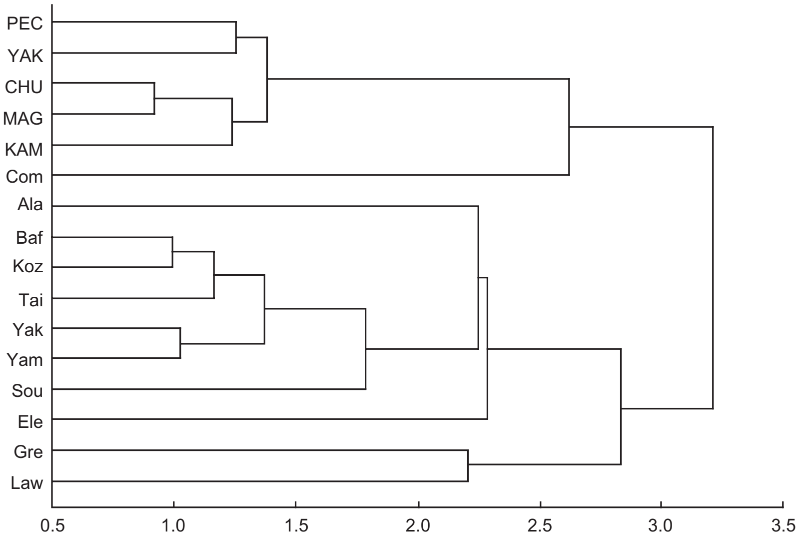

Fig. 26. Tree of Euclidean distance between the populations of the arctic fox and some populations of the red fox (abbreviations in block letters) based on the frequencies of morphotype dental characters.

al. (2005) did not observe significant geographic differences of the arctic fox but did find some differences between the populations they called "coastal" and "lemming" foxes belonging to two ecotypes. Based on comparisons of genetic structure of the arctic foxes from North America and Svalbard, Carmichael *et al*. (2007) suggested the species to be genetically homogeneous throughout its range. These authors argued that the present genetic structure is a result of historical and demographic factors, and also the ability of arctic foxes to migrate long distances. Geffen *et al*. (2007) based on analysis of mtDNA and microsatellite data in the populations of the arctic fox from High Arctic concluded that the present pattern of gene diversity in the species resulted from its great adaptation to long migration on sea ice.

In spite of an absence of definite geographical trends with regard to morphology, Szuma (2008) found statistically significant differences between the arctic fox populations in the sizes of canine and upper carnassials, as well as variation in most metrical tooth characters and in condylobasal skull length. A significant interpopulation variation in the tooth shape was also found. The significant differences between the populations were confirmed in case of the shape of premolars, i.e. P^2, P^3, and P_3 (group C), P_4 (group J), P^4 (group D, E, G), M^1 (group H, I), M_1 (group K, P) as well as M_3 (group M). No significant geographic variation was revealed in frequencies of the following groups of morphotypes: I^3 (group A), P_2 and P_4 (group C), P^4 (group F), M_1 (group L, R), and M_3 (group O). The red fox presents higher geographical variation in the morphotype dental pattern than the arctic fox. In the Palearctic range of the red fox, the significant geographic variation was found in all groups of morphotypes (Szuma 2007). In the arctic fox, similarly to the red fox from Nearctic, there is a significant geographical difference in the frequency of the morphotypes in 12 groups. However, in the arctic fox the set of most variable dental characters is different than in the red fox. The arctic fox shows the greatest geographical variation in the premolars, whereas the red fox from the Nearctic is more variable in groups of morphotypes bounded with P^4 and I^3.

The comparison of frequency distributions of the same set of tooth characters between the populations of the arctic and red foxes (*see* Szuma 2007) suggests that these two closely related predators have evolved in different directions. For example, a premolar region in the arctic fox is characterized by more simple shapes than in the red fox. Also occlusial surface of the lower carnassial in the arctic fox presents less complicate arrangement of crists (P) and cusps (R, S) than in the red fox. Contrary, the crowns of I^3 and P^4 show more complicated shapes in the arctic fox than in the red fox.

The individual regions of dentition in the arctic and the red foxes present more or less separate directions of evolutionary changes. This is indicated by the significant differences in the frequency distributions of the morphotype characters in the red and the arctic foxes, and also different degrees of interpopulation differences in the individual dental features.

As compared with the red fox dentition, in some regions of the arctic fox dentition, there is a tendency to simplify the shape, while in others, there is a tendency toward greater complexity. Also, the comparison of the frequency distributions of the morphotype characters reveals more pronounced reductive tendencies in the arctic fox dentition than in the dentition of the red fox.

A general mesio-distal gradient of the crown size and shape in the premolar region is observed in most groups of mammals. Also in the arctic and red foxes the simplest premolars are situated at the front edge of the cheek tooth-row (P^1, P_1, P^2, P_2), while the most complicated are the last premolars, particularly P^4. However, in the arctic fox, the premolar shape remains simpler than in the red fox. The dominant variant of the P^2 shape in the whole range of the arctic fox is morphotype C1. Only in the arctic foxes from Commander Islands and the Yakutsk region have more complicated shapes of the premolar crown (morphotype C2, C3).

As compared with that in the red fox, the simplifying of the P^3 crown is distinct in the arctic fox. Indeed, different frequency distributions of the morphotypes of group C for this premolar have been found in the red fox and the arctic fox. In the red fox, all variants of the crown shape (morphotypes from C1 to C5) were observed, but in the arctic fox a more complicated variant of the shape — morphotype C4 — occurred in individual populations only and morphotype C5 did not appear at all. The largest share of the C4 morphotype was found in the arctic foxes from Commander Islands, then occasionally the morphotype was observed in the population from the Yakutsk region, while in the Taimyr Peninsula and Yamal Peninsula populations it appears rarely.

On P_2, both in the arctic fox and the red fox, the simplest morphotype of group C, C1, dominates, while morphotypes such as C2 and C3 are rare, except in the population of the arctic fox from Commander Islands where the total share of the morphotypes C2 and C3 equals nearly 20%. In all remaining populations of the arctic fox, only morphotypes C1 and rarely C2 were present. A similar pattern of frequency distribution of the morphotypes of group C (morphotype C1 and rarely C2) appears also in the red fox from Kodiak Island (*V. v. harrimani*) (Szuma 2007).

Similarly, in the case of P_3 there is a difference in frequency distributions of the morphotypes of group C in the red fox and the arctic fox, with the latter tending toward a simpler shape. In the red fox from Siberia, a more folded shape of the P_3 crown dominates (i.e. C3, C4), whereas these two morphotypes are less frequent than the simpler morphotypes C1 and C2 common in the arctic fox populations. The arctic fox populations from Commander Islands are exceptional, because the more complicated shape of crown of P_3 (C3, C4, C5) characterizes over 90% of the individuals.

In the red fox and the arctic fox, the complex variants of the P_4 tooth shape (morphotypes C4 and C5) are observed almost exclusively. However, in the red fox (*see* Szuma 2007) and also in the arctic fox, there were no significant interspecies or interpopulation differences in the frequency distribution of the morphotypes for P_4. In both fox species however, a significant difference was discovered in the occlusial outline of the crown of P_4 (group J). The red fox displayed the full spectrum of group J morphotypes (*see* Szuma 2007), while the arctic fox was lacking the most complicated shape (morphotype J4). Moreover, morphotype J3 appeared in the populations from the Ust-Yansk region and Yamal Peninsula only. Therefore, the crown shape of P_4 in the arctic fox is limited to mostly morphotypes J1 and J2.

In the upper carnassials (P^4), the arctic fox differs from the red fox in exhibiting greater complexity. For example in group D, the dominant morphotype is D2, and in the island populations (Commander Islands, Ellesmere Island and Southampton Island) this variant appears with 100% frequency. The highest frequency of morphotype D3 (50%) was noted in the arctic foxes from Greenland. However, individuals with morphotype D1 were not observed. In the red fox, morphotype D1 is the rarest variant of the shape, but it occurs across almost all of its Eurasian range (Szuma 2007).

Also the distribution of group E morphotypes in the arctic fox showed increased complexity in the shape of the upper carnassial. As in the red fox, the most frequent morphotype in the arctic fox is E1 (*see* Szuma 2007), though in the Yakutsk region and Yamal Peninsula populations, the percentages of morphotypes E3 and E2 are substantial. The frequency distribution of group E morphotypes in the arctic fox is significantly different from that in the red fox (*see* Szuma 2007). In Nearctic populations of the red fox, morphotypes E2 and E3 appear rarely, and in the north and the west of this region they do not occur at all. Also in the Palearctic, the percentage of morphotypes E2 and E3 in the red fox is very low (Szuma 2007). In the arctic fox, the more complicated shape of the anterior part of the P^4 crown could be observed more often than in the red fox. Also the frequency distribution of the morphotypes of group F indicates the larger share of morphotypes which describe the more complicated shape of the P^4 crown. In comparison with the red fox, the fraction of the morphotype F3 in the arctic fox is larger (*see* Szuma 2007).

Only the distribution of group G morphotypes does not show clear evolutionary tendencies. However, there is a significant difference ($p < 0.05$) in the frequency distribution of group G morphotypes among the arctic fox populations. The cingulum continuity (morphotype G1) most often occurs in the arctic foxes from Commander Islands (*V. l. beringensis*, *V. l. semenovi*). In Palearctic red foxes, a considerably larger percentage of morphotype G2 is observed. In Nearctic red foxes, the distribution of this feature is more similar to that observed in the arctic fox (*see* Szuma 2007).

Similarly to group G, the morphotypes of groups H and I that reflect the shape of the crown of M^1 do not show any definite tendencies regarding their complexity. In both groups (H, I), the populations of the arctic fox show weak differences across their range ($p < 0.05$). However, the distributions of these morphotypes in the arctic fox are indeed different ($p < 0.001$) in comparison with those in the red fox. In the arctic fox, morphotype H1 dominates, while the fraction of morphotype H2 is small. Just the opposite occurs in the red fox from the Palearctic region where the frequency of morphotype H2 is relatively high. Only in Nearctic red foxes is the distribution of the group H morphotypes similar to that of the arctic fox. In the populations of the red fox from the western Nearctic (*V. v. harrimani*, *V. v. necator*), morphotype H2 is absent (*see* Szuma 2007). In the arctic fox, the dominant variant of group I morphotypes is I2 whose highest frequency was found in Greenland. Morphotype I1 dominates in the red fox from the Palearctic region. In Nearctic red foxes, the situation is opposite: as in the arctic fox, morphotype I2 dominats (*see* Szuma 2007). The frequency distributions of morphotypes H and I reflect the evolutionary history of *Vulpe*s. Dominance of the primitive morphotype H2 in the Palearctic and reduction of this morphotype in the Nearctic indicate the origin and direction of spreading of the species. Similarly, a low frequency of morphotype H2 in the populations of the arctic fox confirms its later origin. Moreover, studies of the distribution of morphotype I reveal that the primitive is morphotype I1. Morphotype I2 evolved from morphotype I1, and the former is more frequent in the red fox in the Nearctic and also in the evolutionary younger arctic fox.

For M_1, the situation is different from that for P^4. A clear tendency toward simplifying the pattern of the crown of the lower carnassial in the arctic fox is observed as compared with the pattern observed in the red fox. In the case of group K, the dominant fraction is morphotype K2 in both the red and the arctic foxes. Morphotype K1 (lack of entoconulide) is more frequent in the arctic fox than in the red fox, whereas morphotype K3 is observed more frequently in the red fox than in the arctic fox (*see* Szuma 2007). Group K shows significant interpopulation diferences in the range of the arctic fox.

Morphotypes describing the shape of the M_1 talonid (P, R, S) exhibit interpopulation differences in the range of the arctic fox, but the frequency distributions of individual groups of M_1 talonid morphotypes in the arctic fox show a tendency toward simplification when compared with those in the red fox. In the case of group P, morphotypes P3 and P4 dominate in the red fox whereas P1, the simplest variant, dominates in whole range of the arctic fox. In most of the studied arctic fox, morphotype R1 dominates but in the populations from Commander Islands and Kozhevnikova Bay morphotype R2 also appears. Group R in the red fox differs from that in the arctic fox. In most populations of the red fox, morphotype R2 is most common both in Palearctic and Nearctic (*see* Szuma 2007). Moreover, morphotype S2 was not present in the whole range of the arctic fox, whereas in the red fox, especially from the Palearctic region, morphotype S2 is quite common (e.g. Poland, Hungary, Italy, Chukchi, Magadan region). Therefore, a 100% presence of morphotype S1 in all populations of the arctic fox suggests the simplifying of the M_1 crown in the species.

In the distal part of the lower tooth row, the small molar (M_3) is present in foxes. In the red fox dentition, a tendency toward reduction i.e. simplifying, and even oligodonty of the last lower molar was found (Szuma 1999, 2007). Unlike the red fox, in the arctic fox the complicated shape of the M_3 crown (morphotype M2) is observed more often than oligodonty. Morphotype M2 dominates in the populations from Taimyr Peninsula, Yamal Peninsula, the Ust-Yansk region, the Yakutsk region, and Commander Islands, while in the remaining populations of the arctic fox morphotype M1 dominates. In the red fox, the frequency distribution of the morphotypes of group M is also geographically diverse. Morphotype M2 dominates in the Palearctic, while M1 in the Nearctic (Szuma 2007). Regarding morphotypes M, the arctic foxes from Siberia are closer to the foxes from the Palearctic, but the arctic foxes from the Nearctic, and also those from Kozhevnikova Bay are similar to red foxes from the Nearctic.

Significant differences are observed between the arctic fox and the red fox regarding presence/absence of the M_3 polymorphism ($p < 0.05$). In the arctic fox, morphotype O1 occurs more rarely than in the red fox (Szuma 2007), indicating that the field of molar teeth in the arctic fox is genetically and developmentally more stable than in the red fox.

In the arctic fox, a tendency toward increased tooth complexity in the incisor region was observed. In the red fox, morphotype A2 is most common, while morphotype A1 and A3 are less frequent (Szuma 2007). In the arctic fox, the simplest variant of the I^3 shape, i.e. morphotype A1, does not appear at all, while the type associated with a more complicated shape, i.e. morphotype A3, dominates.

In the arctic fox, the dentition morphotype variability seems to be slightly shaped by geographic and climatic factors. Principal component analysis showed that the first component which explains variance in the arctic fox's dentition the most, does not include climatic or geographic factors. Only the variation in the characters connected with regions of lower molars (O1, O2, and R2) reveals a significant dependence on latitude. In some dental features, the second component shows some significant dependencies on geo-climatic variables. For example, variability in such features as C2 on P^3 and C1 on P_3 seems dependent partly on latitude and mean annual temperature. However the characters illustrating P^4 variation (E1, E2, E3, F3), change with latitude and mean annual temperatures. In contrast to that in the arctic fox, dental polymorphism in the red fox is more dependent on geographic and climatic factors (Szuma 2007). In particular, latitude, mean annual temperature, and longitude significantly influence morphotype variation in the red fox dentition. Mean annual amplitude of temperatures as well as mean annual sum of precipitation were less important. This most probably is related to the fact that the range of the red fox is considerably more vast than that of the arctic fox and it includes a wide variety of environments (Larivière & Pasitschniak-Arts 1996). The diet of the red fox changes across this extensive geographic gradient as well. Nevertheless, the analysis of the morphological distances among the populations based on the dental features reflected evolutionary history and exposed the evolutionary tendencies in the red fox dental system (Szuma 2007).

In the case of the arctic fox, the dental morphotype characters were used to analyse the phylogeographic relationships within this species as well. Previously, the same set of dental characters was used to verify the phylogeographic relationships between geographically different populations of the red fox in the broad range of the species (Szuma 2007). That study confirmed intra-species taxonomic relationships as well as indicated similarities and differences between the populations. An analogical analysis in the arctic fox confirmed the close similarity of the mainland populations (areas of Siberia, Baffin Island, *V. l. lagopus*). Somewhat more distant from them are the arctic foxes from Alaska (*V. l. lagopus*) and Ellesmere Island (*V. l. lagopus*), and more distant still are arctic foxes from Greenland (*V. l. groenlandicus*) and St. Lawrence Island (*V. l. lagopus*). The most distinct of the remaining arctic fox populations, and the closest to the red fox from areas of Siberia are the arctic foxes from Commander Islands (*V. l. semenovi*, *V. l. beringensis*). These results reveal the evolutionary history of the arctic fox. They show that the populations of the arctic fox from Commander Islands have long been isolated from the mainland (Ryazanov 2002, Geffen *et al.* 2007). This confirms the high value of F_{ST} between the arctic fox populations from Commander Islands and the mainland (Dzhikiya *et al.* 2007). Dzhikiya *et al.* (2007) showed that the high F_{ST} index and a unique character of the haplotypes indicate that the Bering Island population remains endemic in some traits. Also the pattern of morphotype characters in the arctic foxes from Commander Islands is different from that in the other populations. The closer morphological similarity of the arctic foxes from Commander Islands to the red fox than to populations of the arctic fox suggests, in evolutionary terms, early colonization and a long-lasting isolation of fauna on these islands. It seems that the dental morphotype characters in the arctic fox population from Commander Islands retained derived characters and persisted due to a stable environment and the absence of competition with other predators.

Recapitulating, relative to those of the red fox, the arctic fox teeth tend to show greater complexity in P^4 as well as in I^3, and also greater developmental stability in the molar region (M_3). Simultaneously, the opposite tendency, i.e. crown shape simplification, is observed in the premolar region and in M_1. The similarities and differences in the tooth shape of the arctic fox and the red fox, and thereby of the frequency distributions of the morphotype characters are undoubtedly a result of their common evolutionary history, and also the late origin of the arctic fox in the Nearctic region. Evolutionary tendencies in the arctic fox dentition were most probably the result of competition with the red fox. It is supported by the data on dietary differences between the species (e.g. Barth *et al.* 2000, Frafjord 2000). For example, Frafjord (2000) indicated that the red fox consumes more voles, birds, insects as well as berries, and it has a more diverse diet than the arctic fox. In the arctic fox diet, lemmings dominate as well as carrion of large mammals (e.g. the reindeer *Rangifer tarandus*, fur seal *Callorhinus ursinus*, *see* lion *Eumetopias jubatus*) (Frafjord 2000, Kruchenkova *et al.* 2009). It seems that the differences in the dietary niches between the arctic fox and the red fox can also explain the interspecies differences in their dentition. The more specialized diet of the arctic fox causes simplification of cutting blades in the premolar region and lower carnassial. Growth in complexity of the upper carnassial indicates its essential function in portioning prey. Increase in incisor tooth complexity may improve prey holding ability. The observed tendency toward retention of the lower cheek teeth (M_3), likely reflects adaptation for crushing sea invertebrates. The arctic foxes belonging to the "coastal" form as well as those living on islands rely heavily on ocean resources. Most often these are remains of sea vertebrates or crustaceans and molluscs (Zagrebel'nyi 2000). This also explains the tendencies toward complexity increase in P^4 and growth of the developmental stability and the absence of reduction in M_3.

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Appendix. List of dental morphotypes used to assess of dental polymorphism in the arctic fox (*Vulpes* (*Alopex*) *lagopus*).

Group A describes the variation in form of the cingulum in the linguobasal part of the crown of I^3:

- **morphotype A1**: the cingulum creates an obtuse angle with the occlusal part of the crown;
- **morphotype A2**: the cingulum creates nearly a right angle with the occlusal part of the crown;
- **morphotype A3**: the cingulum assumes a conule shape which is separated from the occlusal part of the crown by a V-shaped notch.

Group C describes the variation in shape of the following premolars: P^2, P^3, P_2, P_3, and P_4:

- **morphotype C1**: the posterior ridge of the protocone (protoconid) without any convexity;
- **morphotype C2**: the posterior slope of the protocone (protoconid) with a small elevation passing smoothly into the ridge;
- **morphotype C3**: the posterior slope of the protocone (protoconid) shows a small elevation which passes anteriorly into the ridge at a right angle;
- **morphotype C4**: the posterior slope of the protocone (protoconid) exhibits a cusp-like elevation separated anteriorly from the ridge by a shallow occlusobasal V-shaped depression;
- **morphotype C5**: the posterior slope of the protocone (protoconid) bears a small but distinct cusp separated anteriorly from the ridge by a clear V- or U-shaped occlusobasal depression.

Group D describes the variation in shape of the anterior part of the crown of P^4:

- **morphotype D1**: no depression in the outline of the anterior part of the crown;
- **morphotype D2**: a small depression in the outline of the anterior part of the crown divides it into the lingual and buccal parts, at the same time the buccal part is visibly shorter and moved backwards in relation to the lingual part;
- **morphotype D3**: a U-shaped depression divides the anterior part of P^4 into two lobes, the anterolingual and anterobuccal lobes, at the same time the buccal lobe is slightly shorter and moved toward back in relation to the lingual lobe.

Group E describes the variation in shape of the anterior edge of paracone in P^4:

- **morphotype E1**: no convexity in the anterobasal part of the edge of the paracone;
- **morphotype E2**: the anterobasal part of the edge of the paracone is slightly opposite, this convexity with the upper part of the edge creates an obtuse angle;
- **morphotype E3**: the anterobasal part of the edge of the paracone possesses a small but distinct cusp separated from the upper part of the ridge by a clear V-shaped occlusobasal depression.

Group F describes the variation in the buccal contour of the crown of P^4:

- **morphotype F1**: the buccal contour of the crown in occlusal view shows no traces of any concavity, the outline in this part is nearly a straight line;
- **morphotype F2**: the buccal contour of the crown in occlusal view shows the presence of a concavity in the middle part, i.e. at the level of the slit between the anterobuccal and distal roots;
- **morphotype F3**: the buccal contour of the crown in occlusal view shows the presence of two concavities, the first occurring in the middle part (as in morphotype F2) and the other lying in the distal part.

Group G describes the variation in shape of the lingual part of the crown of P^4:

- **morphotype G1**: the lingual side of the tooth crown shows a distinct and permanent cingulum line;
- **morphotype G2**: the lingual side of the tooth crown presents a distinct cingulum with a break in the middle part.

continued

Group H describes the variation in shape of the lingual part of the crown of M^1:
morphotype H1: the border of cingulum surrounding the talon is continuous;
morphotype H2: the border of cingulum surrounding the talon has a notch breaking its continuity.

Group I describes the variation in shape of the lingual part of the crown of M^1:
morphotype I1: the anterior and posterior cingulum are continuous lingually in relation to the protocone;
morphotype I2: the anterior and posterior cingulum are not continuous lingually in relation to the protocone.

Group J describes the variation in the crown outline of the lingual part of P_4:
morphotype J1: the lingual contour of the crown in occlusal view does not show any convexities or concavities, it is a straight line nearly;
morphotype J2: the lingual contour of the crown in occlusal view shows the convexity which declines toward the distal part of the crown;
morphotype J3: the lingual contour of the crown in occlusal view shows a convexity, and beyond it a gentle concavity is observed;
morphotype J4: in the lingual contour of the crown in its middle part a convexity is observed, and beyond it occurs an acute, steplike incision.

Group K describes the variation in shape of the posterolingual part of the crown of M_1:
morphotype K1: no traces of the conule presence in the concavity between the metaconid and entoconid on the lingual side of the crown;
morphotype K2: a small singular conule (entoconulid) is present in the concavity between the metaconid and entoconid on the lingual side of the crown;
morphotype K3: two small conules (postmetaconulid and entoconulid) are present in the concavity between the metaconid and entoconid on the lingual side of the crown.

Group L describes the variation in the shape of the posterobuccal part of the crown of M_1:
morphotype L1: no traces of the conule present in the concavity between the protoconid and hypoconid on the buccal side of the crown;
morphotype L2: a small singular conule is present in the concavity between the protoconid and hypoconid on the buccal side of the crown;
morphotype L3: two small conules are present in the concavity between the protoconid and hypoconid on the buccal side of the crown.

Group M describes the variation in the cusp number on the occlusal surface of M_3:
morphotype M1: tooth crown with a singular cusp;
morphotype M2: tooth crown with two cusps.

Group O describes the presence/absence of polymorphism of M_3 in the dentition:
morphotype O1: congenital absence of M_3 in dentition (no traces of earlier presence of the tooth);
morphotype O2: presence of the tooth or its traces in dentition (empty alveolus or the alveolus overgrown by secondary bone tissue).

Group P describes variability in development and shaping of central cristid and other crests on occlusal surface of the talonid basin on M_1 (illustration all variants *see* Szuma 2004):
morphotype P1: no traces of enamel cristids in central part of talonid basin on M_1 (variant P-);
morphotype P2: variants with short fragments of enamel cristids in central part of talonid basin (variants Pa, Pb, Pab, Pi, Pl);
morphotype P3: enamel cristids create partial but not complete join between entoconid and hypoconid (variants Pc, Pcb, Pg: cristid run from hypoconid and it is broken in the central part talonid basin; variants Pd, Pe, Pf, Pid, Pie, Paf, Pad, Phi, Pld, Plf, Ple: cristid runs from the entoconid, and it is broken in central part talonid basin);
morphotype P4: variants with complete or almost complete join between entoconid and hypoconid (variants Phd, Phf: almost complete connection between entoconid and hypoconid; variants Pgf, Pgd, Pcf, Pcd, Pcid, Pgid, Pce: complete connection between entoconid and hypoconid);
morphotype P5: all variants, in which apart from feature of changeable cristid presence, another enamel ridge on the hypoconid is visible; this ridge originates from the mesial part of hypoconid base and runs in direction of the cusp top medially in relation to cristid oblique (variants Pdj, Pgfj, Padj, Pabk, Padk, Pk, Pkd, Pek, Pfk, Pldk, Pcfk).

Group R describes the variation in shape of the posterobuccal part of the crown of M_1:
morphotype R1: no traces of a hypocingulid presence in the posterobuccal part of the crown of M_1;
morphotype R2: a small hypocingulid present in the posterobuccal part of the crown of M1.