

Structure of the upper teeth of the red fox (*Vulpes vulpes*) and Arctic fox (*Vulpes lagopus*) and analysis of dental variability in insular forms

Dmitriy O. Gimranov

ABSTRACT. Various polymorphic dental characters of *Vulpes vulpes* and *Vulpes lagopus* have been described on the basis of a detailed description of the occlusal surfaces of P4, M1, and M2. The prevalence of these characters was found to be significantly different between samples of *V. vulpes* and mainland *V. lagopus*, which can be used to determine species in a fossil record. Notably, Commander Islands *V. lagopus* differ from mainland *V. lagopus* in most of the characters. However, some characters of Mednyi Island *V. lagopus* are unique to them and are not found in any other sample. Some samples from Bering Island do not display such specific features. Samples of ancient foxes, *V. praeglacialis* and *V. praecorsac*, have also been studied. Primitive features were observed in both *V. praeglacialis* and *V. praecorsac*, with the latter exhibiting also a number of advanced features. It has also been found that primitive features are prevalent in the maxillary dentition of *V. vulpes*. The insular groups of *V. lagopus* display numerous primitive features, whereas mainland *V. lagopus* demonstrate a substantial number of advanced characters. This combination of primitive and advanced features is typical of insular *V. lagopus* and indirectly suggests that these populations have spent a long time in isolation.

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KEY WORDS: *Vulpes vulpes*, *Vulpes lagopus*, upper teeth, variability, dental characters, insular isolation, diagnosis of species.

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Структура верхних зубов лисицы (*Vulpes vulpes*) и песца (*V. lagopus*) и анализ ее изменчивости у островных форм

Д.О. Гимранов

РЕЗЮМЕ. На основе детального изучения коронарных поверхностей P4, M1 и M2 описаны зубные признаки у *V. vulpes* и *V. lagopus* обладающие полиморфизмом. Частота встречаемости зубных признаков существенно различалась между *V. vulpes* и материковым *V. lagopus*. Это может быть использовано при идентификации ископаемых остатков этих близкородственных видов. Островные (Командорские) *V. lagopus* отличаются от материковых *V. lagopus* по многих признакам, в то время как некоторые особенности строения зубов *V. lagopus* с о. Медный уникальны для них и не встречаются в других выборках. У некоторых песцов с острова Беринга подобные особенности не прослеживаются. Для понимания эволюционного характера признаков исследовались зубы древних форм *V. praeglacialis* и *V. praecorsac*. Примитивные черты в строении зубов наблюдались как у *V. praeglacialis*, так и у *V. praecorsac*, но у последнего имеется и ряд продвинутых характеристик. Среди всех изученных современных выборок примитивные состояния зубных признаков преобладают у *V. vulpes*. Островные группы *V. lagopus* демонстрируют многочисленные примитивные особенности в строении зубов, в то время как материковые *V. lagopus* демонстрируют значительное число продвинутых состояний. Такое сочетание примитивных признаков с прогрессивными характерно для островных *V. lagopus* и косвенно свидетельствует о том, что эти популяции долгое время находятся в изоляции.

КЛЮЧЕВЫЕ СЛОВА: *Vulpes vulpes*, *Vulpes lagopus*, верхние зубы, изменчивость, зубные признаки, островная изоляция, диагностика видов.

Introduction

Both the red fox (*Vulpes vulpes* L., 1758) and Arctic fox (*Vulpes lagopus* L., 1758) are widely spread species. *V. vulpes* are distributed throughout Northern Eurasia, except in tundra and Arctic zones, whereas *V. lagopus* mostly populate inland and Arctic island territories.

Besides overlapping in the past, the areas of these two species are currently overlapping (Aristov & Baryshnikov, 2001). Remains of both *V. vulpes* and *V. lagopus* are commonly found in Pleistocene and Holocene faunas (Vereshchagin & Kuzmina, 1982; Kuzmina & Sablin, 1993; Sommer & Benecke, 2004; Kosintsev *et al.*, 2016). However, differentiating these two species on the basis of fossil isolated specimens is complicated (Benes, 1975; Lanoe, 2012). Generally, extensive variability is observed in the morphological structures of living and fossil members of the Canidae family. In particular, extensive variability has been observed in the dental morphology of members of the genus *Vulpes* (Szuma, 2007, 2011; Tedford *et al.*, 2009; Perini *et al.*, 2010; Prevosti, 2010; Gimranov *et al.*, 2015; Gimranov, 2017; Szuma & Germonpré, 2020a, b). Therefore, in many cases, some important dental characters cannot be used to describe a species or population without a preliminary study of their variability. Previous investigations have attempted to describe the variability of the dental morphology of the *V. vulpes* and *V. lagopus* using Eurasian collections of these species (Szuma, 2000, 2002, 2003, 2007, 2011; Gimranov *et al.*, 2015; Gimranov, 2017). However, E. Szuma considered these variations only as a tendency to form either more complicated or more simplified morphotypes within a single character. Similar to other researchers who studied this topic (Gimranov *et al.*, 2015; Gimranov, 2017), Szuma did not discuss the evolutionary nature of the variability of dental characters.

However, both authors provide us with quite extensive information on the variability of the upper cheek teeth of different members of the *Vulpes* genus (Szuma, 2002, 2007, 2011; Gimranov, 2017). Szuma (2007, 2011) proven that the P4 *V. vulpes* and *V. lagopus* were found to have variable lingual cingulum, protocone position and plesioconule, while M1 had variable lingual cingulum and hypocone. Gimranov (2017) also comes to this conclusion and complements it: in P4 the *V. vulpes*, *V. corsac* and *V. lagopus* are variable metacone of P4, with an occlusal shape and protocone complex in M1. Gimranov (2017) also evaluated the variability of M2 and highlighted the different morphotypes for this tooth.

Studying the morphological variability of recent *V. vulpes* and *V. lagopus* from Northern Eurasia, we found significant differentiation in the dental characters between mainland *V. lagopus* and Commander Islands *V. lagopus* (Gimranov, 2014). The presence of such differentiation in *V. lagopus* (exterior, dimensional, and genetic) has been frequently discussed by researchers (Heptner *et al.*, 1967; Džikija *et al.*, 2007; Geffen *et al.*, 2007; Szuma, 2008, 2011; Ploshnitsa *et al.*, 2012, 2013; Nanova & Proa, 2017; Martín-Serra *et al.*, 2019a; Proa

& Nanova, 2019). The reasons for these differences are clearly related to the island specificity of these animals and their isolation from the mainland community. Studying the dental morphology and comparatively analyzing the dental characters of the members of the Vulpini tribe can provide us with an opportunity to analyze island forms in terms of island isolation.

Thus, the aims of this study are to describe the morphology of occlusal surfaces of the teeth of two *Vulpes* species (*V. vulpes* and *V. lagopus*) and to evaluate the variation of the dental characters of Commander Islands *V. lagopus* populations from the viewpoint of the influence of island isolation.

Materials and methods

Cranial samples of *V. vulpes* and *V. lagopus* from different parts of Russia and other countries were studied. Data were obtained from collections of the Zoological Museum of Moscow State University (Moscow), Zoological Institute of the Russian Academy of Sciences (Saint Petersburg), and the Museum of the Institute of Plant and Animal Ecology (Yekaterinburg).

The localities and sample sizes for *V. vulpes* were as follows: Armenia ($n = 10$); Austria ($n = 1$); Azerbaijan ($n = 3$); Belarus ($n = 12$); Bulgaria ($n = 1$); Georgia ($n = 4$); Germany ($n = 6$); Kazakhstan ($n = 5$); Kyrgyzstan ($n = 3$); Mongolia ($n = 13$); Romania ($n = 5$); Russia, Amur Region ($n = 6$), Arkhangelsk Region ($n = 9$), Astrakhan Region ($n = 3$), Volgograd Region ($n = 5$), Vologda Region ($n = 9$), Voronezh Region ($n = 10$), Irkutsk Region ($n = 10$), Kaliningrad Region ($n = 5$), Kamchatka Territory ($n = 10$), Kirov Region ($n = 5$), Krasnodar Territory ($n = 16$), Krasnoyarsk Territory ($n = 17$), Leningrad Region ($n = 12$), Magadan Region ($n = 4$), Moscow Region ($n = 6$), Murmansk Region ($n = 6$), Novgorod Region ($n = 2$), Novosibirsk Region ($n = 1$), Orenburg Region ($n = 12$), Primorye Territory ($n = 11$), Pskov Region ($n = 4$), Republic of Altai ($n = 6$), Republic of Kalmykia ($n = 4$), Republic of Sakha (Yakutia, $n = 15$), Republic of Tatarstan ($n = 6$), Republic of Tuva ($n = 5$), Rostov Region ($n = 5$), Samara Region ($n = 4$), Saratov Region ($n = 10$), Smolensk Region ($n = 8$), Tver Region ($n = 7$), Tyumen Region ($n = 2$), Udmurt Republic ($n = 3$), Khabarovsk Territory ($n = 6$), Chelyabinsk Region ($n = 16$), and Chukotka Autonomous Area ($n = 12$); Tajikistan ($n = 5$); Turkmenistan ($n = 15$); Ukraine ($n = 15$); and Uzbekistan ($n = 10$).

The localities and sample sizes for *V. lagopus* were as follows: Norway ($n = 12$) and Russia, Arkhangelsk Region ($n = 30$), Kamchatka Territory (Bering Island, $n = 30$; Mednyi Island, $n = 13$), Krasnoyarsk Territory ($n = 35$), Republic of Sakha (Yakutia, $n = 30$), Chukotka Autonomous Area ($n = 30$), and Yamal–Nenets Autonomous Area ($n = 12$). Table 1 shows a list of the characters discussed in this study. The following published data was used to describe dental occlusal surfaces and determine the characters' grades (Butler, 1939; Hershkovitz, 1971; Tedford *et al.*, 1995, 2009;

Table 1. Description of the characters and states of the teeth.

	Characters	State		Description
P4	Lingual cingulum	A	Complete	
		B	Incomplete	
		C	Present under the metacone blade	
		D	Absent	
	Cingulum around the protocone	E	Complete	
		F	Incomplete	
		G	Present only at the posterior part of the protocone	
		H	Absent	
	Protocone crests	I	Anterior crest	Present
			Absent	
		J	Posterior crest	Present
		K	Inner crest	Absent
	Anterior cingulum	L		Extends on the labial side of the crown
		M		Extends to the anterolabial corner of the crown
		N		Developed only on the anterior side
		O		Developed only at the base of the anterior paracone crest
	Lingual paracone crest	P		Rises from the base of the protocone to the top of the paracone
		Q		Extends from the base of the protocone to the paracone base
		R		Absent
		S		Present
	Parastyle	T		Absent
		U		Very large
		V		Medium size
		W		Small
	Plesioconule	X		Absent
		A	Complete	
		B	Incomplete	
		C	Very large	
M1	Developed of the parastyle (Ps)	D	Medium size	
		E	Small or absent	
		F		Cingulum complete, extends to the hypocone
		G		Cingulum does not extend to the hypocone
	Cingulum behind the metaconule	H		Absent
		I	Complete	
		J	Incomplete	
		K	Absent	
	Inner crest of the paracone	L	Present	
		M	Absent	
		N	Small	
		O	Large	
	Hypocone	P		Large, divided into two parts by an inner groove
		Q		Large, divided into three parts by inner grooves
		R		Double-cusped
		S		Present
	Inner crest of the hypocone	T		Absent
		U		No contact with metaconule
		V		Contact with metaconule is present
		A		
M2	Metacone	B		Metacone length equal to paracone length
		C		Metacone length is slightly smaller than paracone length
		D		Metacone length half as less as paracone length
		E		Complete, with a cusp-like metaconule
	Postprotocrista	F		Complete, with a ridge-like metaconule
		G		Incomplete postprotocrista, with a reduced metaconule
		H		Not developed
		I		Reduced
	Lingual cingulum around the protocone	J		Complete
		K		Incomplete
		L		Present
		M		Absent
	Protocone and paraconule separation	N		Large
		A		Small
		B		
		C		
	Hypocone	D		
		E		
		F		
		G		

Rabeder, 1999). In particular, we noted that, in the Canidae family, the posterolingual cingulum of M1 and M2 is referred to as the hypocone (Wang *et al.*, 1999; Tedford *et al.*, 2009). In this study, we followed Tedford and Wang and used the term “hypocone.”

None of the samples were categorized on the basis of sex, as previous research has shown that dental morphotype variation of the *V. vulpes* and *V. lagopus* is not significantly associated with sex (Szuma, 2002; El'kina, 2007). Only individuals with unworn teeth were included in the analysis, and individuals displaying different character states in the left and right teeth were excluded.

To define the relationships (primitive or derived) between the character states studied, we used the state matrices of the dental characters published by Wang (1994), Wang *et al.* (1999), Tedford *et al.* (1995, 2009), and Prevosti (2010). Table 1 shows a list of the studied characters and their states for P4 and M1–M2. The structure of the teeth of *V. praeglacialis* (Kormos, 1932) and *V. praecorsac* (Kormos, 1932) was discussed on the basis of published images and descriptions (Del Campana, 1913; Kormos, 1932; Thenius, 1954; Viret, 1954; Odintzov, 1965; Kurten, 1968; Bonifay, 1971; Rabeder, 1976; Kurtén & Crusafont-Pairot, 1977; Jánossy, 1986; Wiszniewska, 1989; García & Arsuaga, 1999; Caleros *et al.*, 2006; Garrido, 2008; Madurell-Malapeira *et al.*, 2009; Petrucci *et al.*, 2013; Koufos, 2014, 2018; Rook *et al.*, 2017). We also had the opportunity to study some of the collections listed above at the Hungarian Natural History Museum (five samples of *V. praeglacialis* from Early Pleistocene localities, Villány, Hungary), the Hungarian Institute of Geology and Geophysics (three samples of *V. praeglacialis* and two samples of *V. praecorsac* from Early Pleistocene localities, Villány, Hungary), and the Department of Palaeontology of the University of Vienna (15 samples of *V. praeglacialis* and five samples of *V. praecorsac* from Early Pleistocene localities, Deutsch Altenburg 2C, Austria).

Notably, *Alopex* (which is the same as *V. lagopus*) has been previously treated as a separate genus. However, at present, it is considered a subgenus of *Vulpes* (Wilson & Reeder, 2005; Abramov & Khlyap, 2012).

Results

P4 — In *V. vulpes*, the lingual cingulum (Fig. 1) is either completely developed (48.9%, state A) or incompletely developed (44.2%, state B; Tab. 2), whereas the lingual cingulum in mainland *V. lagopus* is strongly reduced (40.9%, state C). In the island populations of *V. lagopus*, the completely developed form is predominant (66.7% and 69.2%, state A).

The lingual cingulum around the protocone is present only at the posterior part of the protocone in *V. vulpes* and mainland *V. lagopus* (81.8% and 96.2%, state G), whereas in the island forms of *V. lagopus*, the cingulum around the protocone is frequently less complete (73.3% and 61.5%, state G).

The anterior protocone crest is absent (state I “absent”) in both *V. vulpes* and mainland and Bering Island *V. lagopus* but quite prevalent in Mednyi Island *V. lagopus* (38.5%, state I “present”). On the other hand, the posterior protocone crest is almost always present in *V. vulpes* (95.3%, state J “present”). In mainland and Bering Island *V. lagopus*, this feature is observed in approximately half of the cases (57% and 46.7%, state J “present”). In Mednyi Island *V. lagopus*, this character is very frequent (76.9%, state J “present”).

The inner protocone crest is almost ubiquitous in *V. vulpes* (93.4%, state K “present”) and completely fixed in the island populations of *V. lagopus* (100% and 100%, state K “present”). However, this character is often absent in mainland *V. lagopus* (22.6%, state K “absent”).

The anterior cingulum in *V. vulpes* is less developed (17.4%, states L and M) than in the island populations of *V. lagopus* (96.7% and 61.5%, states L and M). Mainland *V. lagopus* exhibit almost equal frequencies of developed (47.2%, states L and M) and weakly developed (52.8%, state N) anterior cingulum.

The lingual paracone crest in *V. vulpes* is complete in the majority of the individuals (94.2%, state P) but typically incomplete or absent in mainland *V. lagopus* (46.5%, state Q; 52.2%, state R). This character is often absent in Bering Island *V. lagopus* (76.7%, state R) but is totally absent in Mednyi Island *V. lagopus* (100%, state R).

The parastyle (Fig. 2) is usually absent (state T) in all species and forms studied (Tab. 2). The parastyle is very rarely present in mainland *V. lagopus* (2.5%, state S) and Bering Island *V. lagopus* (3.3%, state S). The same holds true for the plesioconule (Fig. 2) in *V. vulpes* (96.8%, state X) and Mednyi Island *V. lagopus* (100%, state X). This character is occasionally found in a weakly pronounced form in mainland (17.0%, state W) and Bering Island (26.7%, state W) *V. lagopus*.

M1 — The lingual cingulum around the protocone (Tab. 3, Fig. 3) is often complete in *V. vulpes* (70.0%, state A) and the island populations of *V. lagopus* (80% and 84.6%, state A), whereas the incomplete variant of this character is predominant in mainland *V. lagopus* (66.7%, state B).

The parastyle is small (state D) and mostly absent (state E) in almost all species and forms studied. The cingulum behind the metaconule is typically well developed in *V. vulpes* (91.9%, state G) and the island populations of *V. lagopus* (70% and 84.6%, state G) and is mainly absent in mainland *V. lagopus* (91.2%, state H).

The inner crest of the paracone in *V. vulpes* is often complete and well developed (98.9%, state I), whereas the reduced variant (state O or K) is predominant in all individuals of *V. lagopus* studied.

The separation of the paraconule from the preprotocrista was not studied in the island populations of *V. lagopus*. This character is frequent in *V. vulpes* (98.4%, state L) and moderately prevalent in mainland *V. lagopus* (50%, state L).

In all species and forms studied, the hypocone is predominantly large and well developed (Fig. 4, state O).

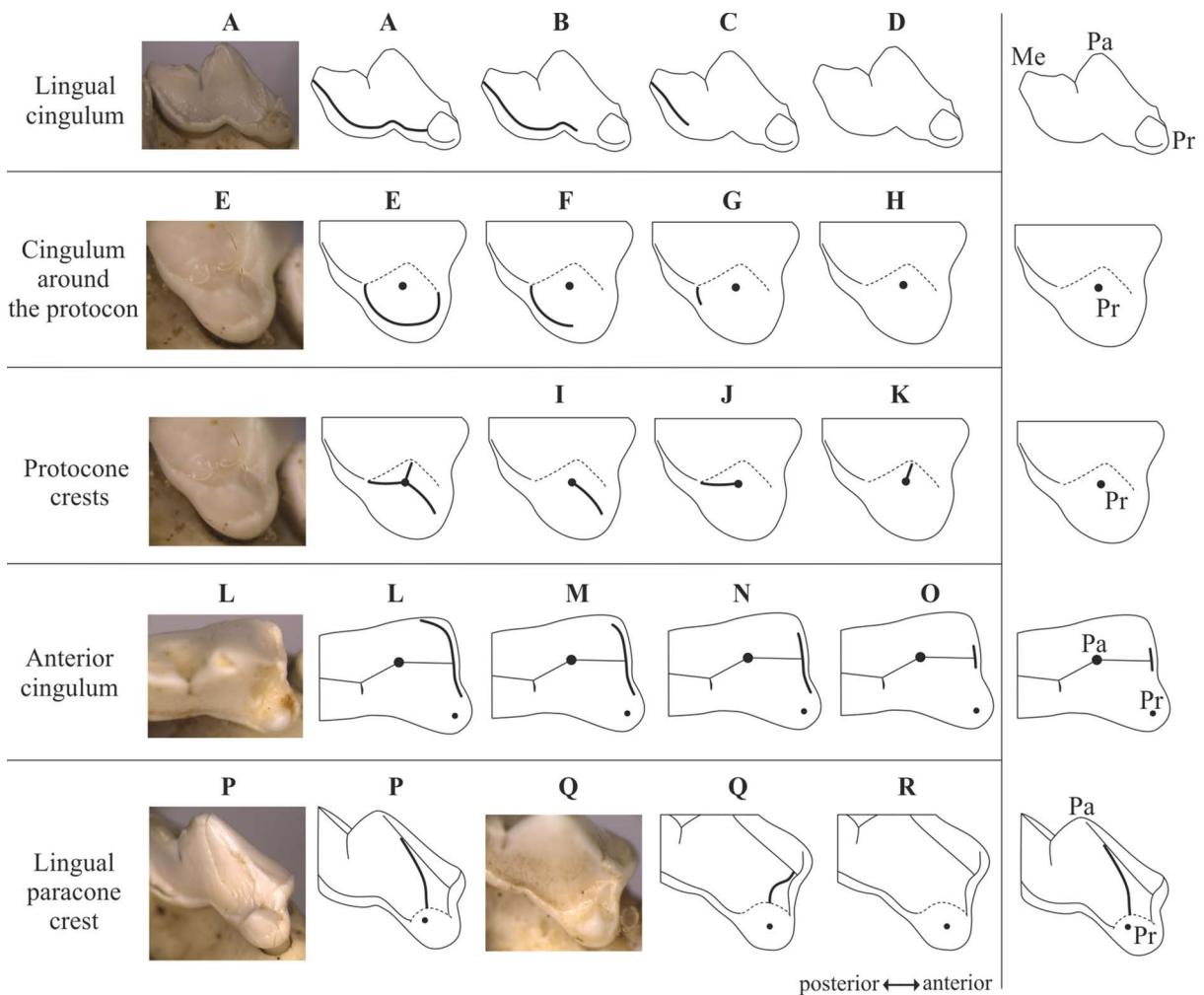


Fig. 1. States of the characters of the P4 in *V. vulpes* and *V. lagopus*. Pa — Paracone, Me — Metacone, Pr — Protocone. Lingual view: states A–D and P–R, occlusal view: states E–O.

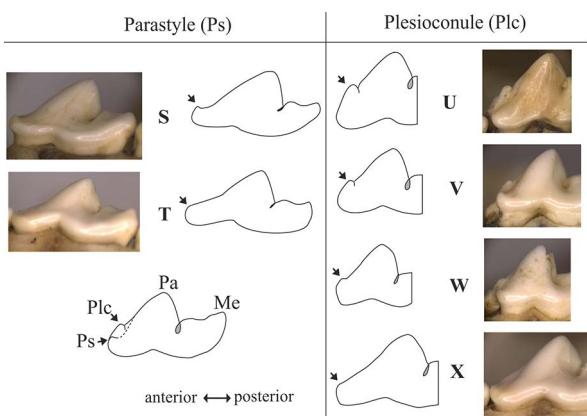


Fig. 2. States of the characters of the P4 in *V. vulpes* and *V. lagopus*. Pa — Paracone, Me — Metacone, Ps — Parastyle, Plc — plesioconule (labial view).

Notably, in *V. vulpes*, the cusp often displays an inner groove (22.9%, state P).

The inner crest of the hypocone is frequently absent in the majority of *V. vulpes* (88.4%, state T) and Bering Island *V. lagopus* (93.9%, state T) specimens. In mainland and Mednyi Island *V. lagopus*, this character is also frequently absent (71.1% and 76.9%, respectively).

The posterior cingulum of the hypocone is often not connected to the metaconule in *V. vulpes* (98.9%, state U) and the insular populations of *V. lagopus* (80.0% and 100%, state U). However, in mainland *V. lagopus*, it merges with the metaconule in half of the cases (54.4%, state V).

M2 — In *V. vulpes*, the metacone length (Tab. 4, Fig. 5) is typically large, only slightly smaller than the paracone length (75.1%, state B). In mainland and Bering Island *V. lagopus*, the metacone length is frequently two times smaller than the paracone length (73.9% and 70.0%, state C), whereas in Mednyi Island *V. lagopus*, a large metacone is predominant (46.2%, state B). The metacone and paracone lengths in Mednyi Island *V. lagopus* are most frequently equal (15.4%, state A).

The postprotocrista in *V. vulpes* is often complete, with a ridge-like metaconule (55.5%, state E). In

Table 2. Frequencies of the characters of the P4 in members of the genus *Vulpes*. 1 — *V. vulpes* (all), 2 — *V. lagopus* (mainland), 3 — *V. lagopus* (Bering Island), 4 — *V. lagopus* (Mednyi Island), 5 — *V. praeglacialis*, 6 — *V. praecorsac*.

Characters	State	1		2		3		4		5		6	
		%	n	%	n	%	n	%	n	%	n	%	n
Lingual cingulum	A	185	48.9	17	10.7	20	66.7	9	69.2	19	7		
	B	167	44.2	50	31.4	9	30.0	4	30.8	0	0		
	C	26	6.9	65	40.9	1	3.3	0	0.0	0	0		
	D	0	0.0	27	17.0	0	0.0	0	0.0	0	0		
<i>n</i>		378		159		30		13		19		7	
Cingulum around the protocone	E	32	8.4	1	0.6	3	10.0	0	0.0	0	0		
	F	37	9.7	5	3.2	5	16.7	5	38.5	0	0		
	G	311	81.8	151	96.2	22	73.3	8	61.5	2	0		
	H	0	0.0	0	0	0	0.0	0	0.0	18	7		
<i>n</i>		380		157		30		13		20		7	
Protocone crests	I	Present	2	0.5	2	1.3	0	0.0	5	38.5	1	0	
		Absent	378	99.5	157	98.7	30	100.0	8	61.5	17	7	
	<i>n</i>		380		159		30		13		18		7
	J	Present	362	95.3	90	57.0	14	46.7	10	76.9	18	7	
		Absent	18	4.7	68	43.0	16	53.3	3	23.1	1	0	
	<i>n</i>		387		158		30		13		19		7
	K	Present	355	93.4	123	77.4	30	100.0	13	100.0	18	6	
		Absent	25	6.6	36	22.6	0	0.0	0	0.0	2	1	
	<i>n</i>		387		159		30		13		20		7
Anterior cingulum	L	0	0.0	2	1.3	0	0.0	0	0.0	11	2		
	M	66	17.4	73	45.9	29	96.7	8	61.5	7	5		
	N	283	74.7	84	52.8	1	3.3	5	38.5	2	0		
	O	30	7.9	0	0.0	0	0.0	0	0.0	0	0		
<i>n</i>		379		159		30		13		20		7	
Lingual paracone crest	P	358	94.2	2	1.3	1	3.3	0	0.0	15	0		
	Q	6	1.6	74	46.5	6	20.0	0	0.0	3	0		
	R	16	4.2	83	52.2	23	76.7	13	100.0	2	7		
<i>n</i>		380		159		30		13		20		7	
Parastyle	S	0	0.0	4	2.5	1	3.3	0	0.0	1	2		
	T	380	100.0	155	97.5	29	96.7	13	100.0	20	5		
<i>n</i>		380		159		30		13		21		7	
Plesioconule	U	1	0.3	1	0.6	0	0.0	0	0.0	1	1		
	V	6	1.6	4	2.5	0	0.0	0	0.0	3	1		
	W	5	1.3	27	17.0	8	26.7	0	0.0	2	0		
	X	368	96.8	127	79.9	22	73.3	13	100.0	15	5		
<i>n</i>		380		159		30		13		21		7	

mainland and Bering Island *V. lagopus*, absence of the metaconule is the main variant (81.0% and 73.3%, state G). Mednyi Island *V. lagopus* frequently display a particular (reduced) morphology of the protocone (76.9%, state H).

In *V. vulpes*, the lingual cingulum around the protocone is often complete (84.7%, state I), contrary to all *V. lagopus* samples (Tab. 4). Bering Island *V. lagopus* are considered an exception, as they display a high rate of well-developed lingual cingula around the protocone (43.3%, state I).

The separation of the paraconule from the preprotocrista was not studied in the island populations of *V. lagopus*. This character is typically absent in *V. vulpes* (92.4%, state L) and mainland *V. lagopus* (91.7%, state L).

The hypocone is large and well developed in most cases in all *V. vulpes* and *V. lagopus* samples (from 76.7% to 100%, state M). Notably, mainland and Bering Island *V. lagopus* frequently exhibit a reduced, small hypocone (22.6% and 23.3%, state N).

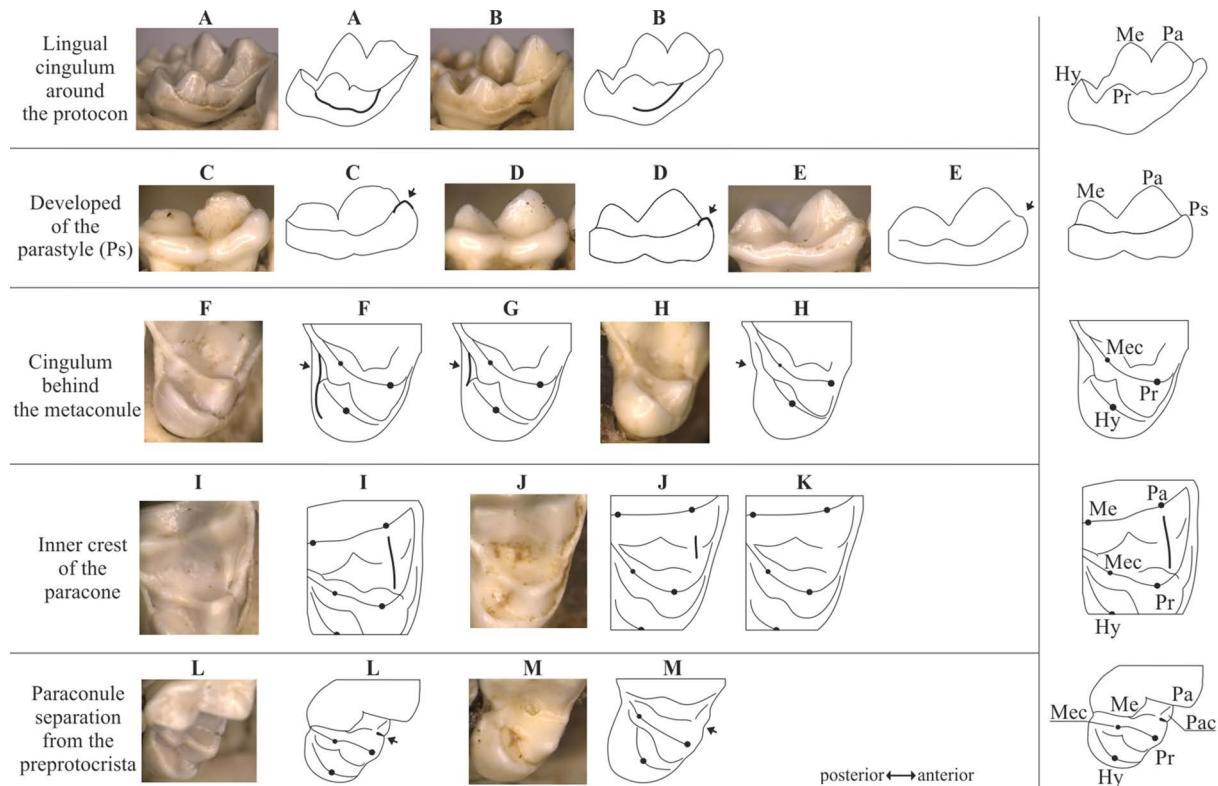


Fig. 3. Character and state of the M1 in *V. vulpes* and *V. lagopus*. Pa — Paracone, Me — Metacone, Pr — Protocone, Hy — hypocone, Ps — Parastyle, Mec — metoconule, Pac — paraconule. Anterior view: state A–B, labial view: states C–E, occlusal view: states F–M.

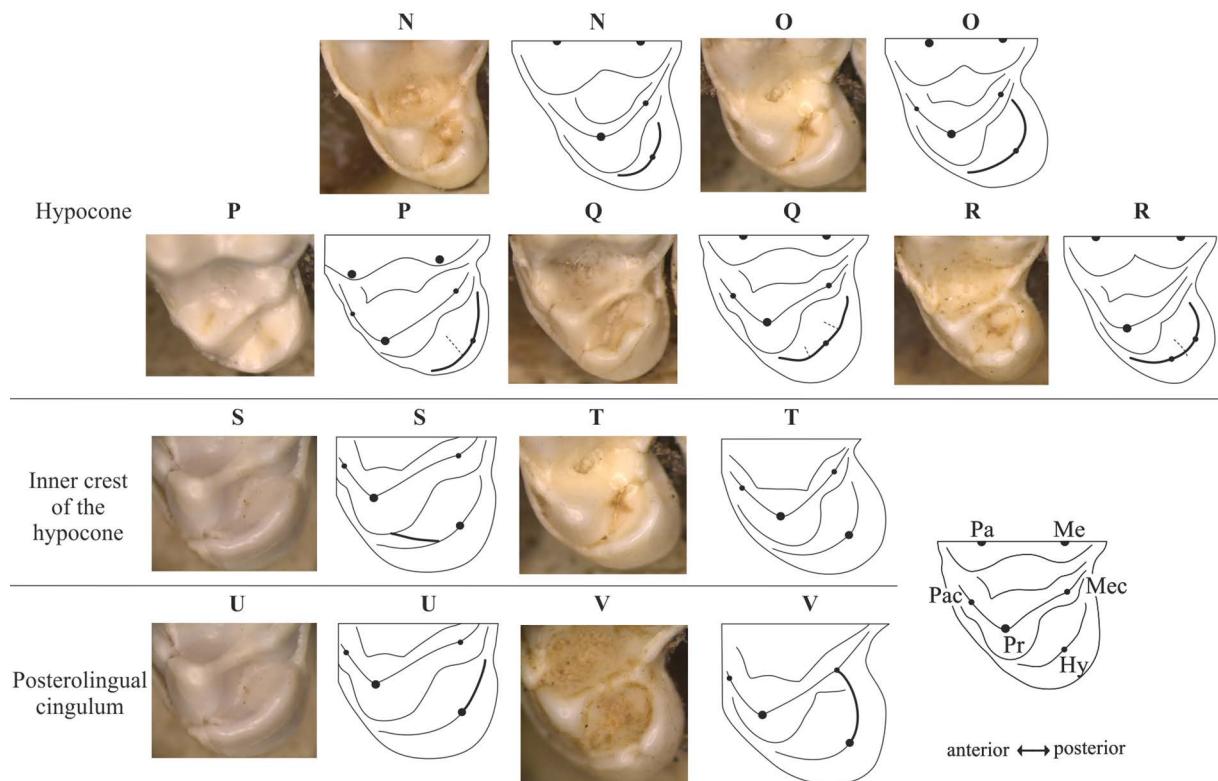


Fig. 4. Character and state of the M1 in *V. vulpes* and *V. lagopus*. Pa — Paracone, Me — Metacone, Pr — Protocone, Hy — hypocone, Mec — metoconule, Pac — paraconule (occlusal view).

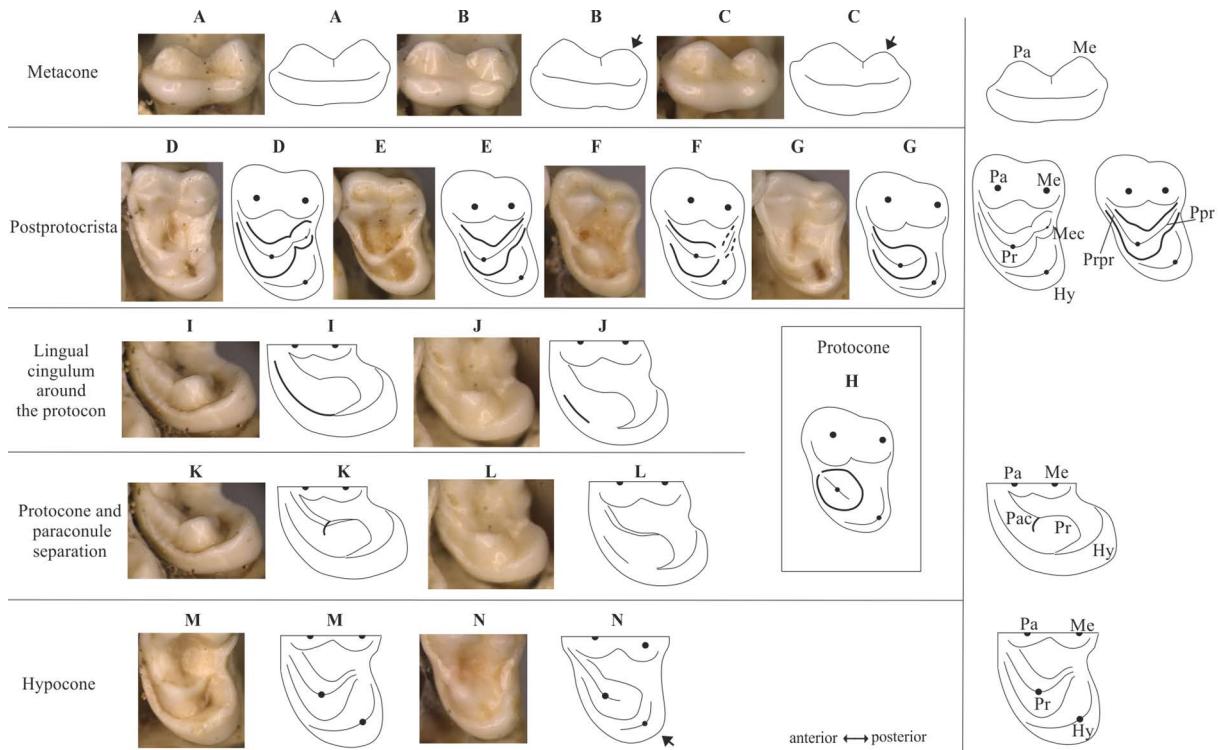


Fig. 5. Character and state of the M2 in *V. vulpes* and *V. lagopus*. Pa — Paracone, Me — Metacone, Pr — Protocone, Hy — hypocone, Mec — metoconule, Pac — paraconule. Labial view: states A–C, occlusal view: states D–N.

Discussion

Interspecific variability

P4 — The results of this study show that *V. vulpes* can be distinguished from mainland *V. lagopus* on the basis of most of the characters studied. The most important characters for distinguishing between these two species are the lingual cingulum, posterior and inner protocone crests, development of the anterior cingulum, and shape of the lingual paracone crest of P4. The island samples of *V. lagopus* display a similarity to *V. vulpes* in terms of the morphology of the lingual cingulum and the crests of the protocone. The frequency of the anterior cingulum helps differentiate the island populations of *V. lagopus* from both *V. vulpes* and mainland *V. lagopus*. Mednyi Island *V. lagopus* were found to be the most particular population differing from all the other groups of *Vulpes* in terms of the morphology of the cingulum around the protocone, anterior protocone crest, and anterior cingulum of P4. The morphotype typical of the island populations of *V. lagopus* can be broadly outlined as follows: complete lingual and anterior cingula, tendency toward a high frequency of complete cingula around the protocone, and presence of all three protocone crests. Except for the well-developed anterior cingulum and the presence of the anterior protocone crest, all of these characters are typical of *V. vulpes* as well. The shape of the lingual paracone crest is probably a unique feature of *V. vulpes*, which is mostly absent in *V. lagopus*. As previously shown, the

complete lingual cingulum is more dominant than the discontinuous lingual cingulum (grades G1 and G2; Szuma, 2007) in *V. vulpes* from Northern Eurasia. Further, it was demonstrated that complete lingual cingula (grade G1; Szuma, 2011) are more frequently found in mainland *V. lagopus* than discontinuous lingual cingula (grade G1; Szuma, 2011). Our results demonstrate that a more detailed consideration of the morphology of the lingual cingulum in *V. vulpes* and *V. lagopus* is important for distinguishing between the two species. Variants of the morphology of the plesioconule of P4 were also described for *V. vulpes* and *V. lagopus* (Szuma, 2007, 2011). In *V. vulpes* from Northern Eurasia, a simple morphology without a pronounced plesioconule (grade E1; Szuma, 2007) is predominant, an observation that is in good agreement with our data (Tab. 2). Variants of P4 with a pronounced plesioconule (grades E2 and Ex3; Szuma, 2011) are more commonly found in mainland *V. lagopus*, which is also in line with the results of the present study (Tab. 2). Although a variation of some characters of P4 in *V. vulpes* and *V. lagopus* has been described earlier (Gimranov, 2017), in our previous studies, we did not consider the plesioconule and parastyle separately. It is of note, however, that the parastyle is extremely uncommon in *V. vulpes* and *V. lagopus* from Northern Eurasia.

M1 — Mainland *V. lagopus* can be distinguished from *V. vulpes* on the basis of most characters of the upper first molar: a developed lingual cingulum around the protocone, a cingulum behind the metaconule, and

Table 3. Frequencies of the characters of the M1 in members of the genus *Vulpes*. 1 — *V. vulpes* (all), 2 — *V. lagopus* (mainland), 3 — *V. lagopus* (Bering Island), 4 — *V. lagopus* (Mednyi Island), 5 — *V. praeglacialis*, 6 — *V. praecorsac*.

Characters	State	1		2		3		4		5		6	
		n	%	n	%	n	%	n	%	n	n		
Lingual cingulum around the protocon	A	266	70.0	53	33.3	24	80.0	11	84.6	8	1		
	B	114	30.0	106	66.7	6	20.0	2	15.4	2	4		
<i>n</i>		380		159		30		13		10	5		
Developed of the parastyle (Ps)	C	1	0.3	1	0.6	0	0.0	0	0.0	1	1		
	D	46	12.1	6	3.8	2	6.7	1	7.7	8	4		
	E	333	87.6	152	95.6	28	93.3	12	92.3	1	0		
<i>n</i>		380		159		30		13		10	5		
Cingulum behind the metaconule	F	18	4.7	0	0.0	0	0.0	0	0.0	0	0		
	G	349	91.9	14	8.8	21	70.0	11	84.6	7	3		
	H	13	3.4	145	91.2	9	30.0	2	15.4	3	2		
<i>n</i>		380		159		30		13		10	5		
Inner crest of the paracone	I	376	98.9	2	1.3	0	0.0	0	0.0			10	5
	J	1	0.3	128	80.5	30	100.0	13	100.0				
	K	3	0.8	29	18.2	0	0.0	0	0.0	0	0		
<i>n</i>		380		159		30		13		10	5		
Paraconule separation from the preprotocrista	L	373	98.4	6	50.0	—	—	—	—	8	5		
	M	6	1.6	6	50.0	—	—	—	—	0	0		
<i>n</i>		379		12		—		—		8	5		
Hypocone	N	0	0.0	1	0.7	0	0.0	0	0.0	0	2		
	O	281	73.9	138	90.2	29	96.7	12	92.3	6	3		
	P	87	22.9	11	7.2	0	0.0	1	7.7	2	0		
	Q	1	0.3	0	0.0	0	0.0	0	0.0	0	0		
	R	11	2.9	3	2.0	1	3.3	0	0.0	2	0		
<i>n</i>		380		153		30		13		10	5		
Inner crest of the hypocone	S	44	11.6	46	28.9	2	6.7	3	23.1	—	—		
	T	335	88.4	113	71.1	28	93.3	10	76.9	—	—		
<i>n</i>		379		159		30		13		—	—		
Posterolingual cingulum	U	376	98.9	72	45.6	24	80.0	13	100.0	9	5		
	V	4	1.1	86	54.4	6	20.0	0	0.0	1	0		
<i>n</i>		380		158		30		13		10	5		

separation of the paraconule from the preprotocrista. The island populations of *V. lagopus* exhibit a cingulum behind the metaconule and a posterolingual cingulum, similar to *V. vulpes*. The frequency of an incomplete inner crest of the paracone is similar between the island populations of *V. lagopus* and mainland *V. lagopus*. All samples are broadly similar in terms of the prevalence of the main variants of the hypocone and the inner crest of the hypocone. It has been shown previously that two morphological variants are prevalent in *V. vulpes* from Northern Eurasia: without separation by a groove (grade H1; Szuma, 2007) and with a fully developed protocone cingulum (grade I1; Szuma, 2007). Our results confirm those findings. Szuma also demonstrated that hypocones without groove separation (grade H1; Szuma, 2011) and with incomplete protocone cingula (grade I2; Szuma, 2011) are predominant in mainland *V. lagopus*. This is also in good agreement with the results of the present study. The variation of some characters of M1 in *V. vulpes* and *V. lagopus* described previously (Gimranov,

2017) can be elaborated on by the results obtained for the hypocone in this study.

M2 — According to the three characters of the second upper molar, it is possible to differentiate *V. vulpes* from mainland *V. lagopus*. The diagnostic characters are the size of the metacone, the morphology of the postprotocrista, and the development of the lingual cingulum around the protocone. Although the hypocone does not display significant differences between the species, it exhibits a reduction tendency in *V. lagopus*. The morphologies of the metacone and protocone complex are very similar between mainland and Bering Island *V. lagopus*. However, Mednyi Island *V. lagopus* appear to be closer to *V. vulpes* in terms of the metacone morphology and display a particularity in the shape of the protocone as state H (reduced protocone) is not found in any other sample. An opposite scenario was observed for the lingual cingulum around the protocone: Mednyi Island *V. lagopus* are similar to their mainland conspecifics, whereas Bering Island *V. lagopus* display a similarity to *V. vulpes*.

Table 4. Frequencies of the characters of the M2 in members of the genus *Vulpes*. 1 — *V. vulpes* (all), 2 — *V. lagopus* (mainland), 3 — *V. lagopus* (Bering Island), 4 — *V. lagopus* (Mednyi Island), 5 — *V. praeglacialis*, 6 — *V. praecorsac*. * — one specimen has a double hypocone.

Characters	State	1		2		3		4		5		6	
		n	%	n	%	n	%	n	%	n	n		
Metacone	A	8	2.1	1	0.6	0	0.0	2	15.4	0	0		
	B	284	75.1	40	25.5	9	30.0	6	46.2	6	1		
	C	86	22.8	116	73.9	21	70.0	5	38.5	0	0		
<i>n</i>		378		157		30		13		6	1		
Postprotocrista	D	50	14.4	1	0.6	2	6.7	0	0.0	2	0		
	E	193	55.5	8	5.1	2	6.7	0	0.0	3	1		
	F	81	23.3	21	13.3	4	13.3	0	0.0	1	0		
	G	24	6.9	128	81.0	22	73.3	3	23.1	0	0		
	H	0	0.0	0	0.0	0	0.0	10	76.9	0	0		
<i>n</i>		348		158		30		13		6	1		
Lingual cingulum around the protocon	I	320	84.7	16	10.1	13	43.3	2	15.4	6	1		
	J	58	15.3	143	89.9	17	56.7	11	84.6	0	0		
<i>n</i>		378		159		30		13		6	1		
Protocone and paraconule separation	K	29	7.6	1	8.3	—	—	—	—	—	—		
	L	351	92.4	11	91.7	—	—	—	—	—	—		
<i>n</i>		380		12		—		—		—	—		
Hypocone	M	357	94.4	123	77.4	23	76.7	13	100.0	6*	0		
	N	21	5.6	36	22.6	7	23.3	0	0.0	0	1		
<i>n</i>		378		159		30		13		6	1		

Evolutionary interpretation of the results

The following are the earliest members of the genus *Vulpes* described from the Pliocene in Eurasia: *V. praecorsac* from Ukraine (Odintzov, 1965), *V. qiuzechengi* from the Tibetan Plateau (Wang *et al.*, 2014), and *V. beihaiensis* from China (Qiu & Tedford, 1990).

Four species were described from the Early Pleistocene in Europe: *V. alopecoides* (Forsyth Major, 1875; Del Campana, 1913; Viret, 1954; Kurtén & Crusafont-Pairot, 1977; Garrido, 2008; Petrucci *et al.*, 2013; Koufos, 2014), *V. praeglacialis* (Kormos, 1932; Bonifay, 1971; Rabeder, 1976; Jánossy, 1986; García & Arsuaga, 1999; Moigne *et al.*, 2006; Madurell-Malapeira *et al.*, 2009; Koufos, 2018), *V. praecorsac* (Kormos, 1932; Jánossy, 1986; Rabeder, 1976; Gasparik & Pazonyi, 2018), and *V. angustidens* (Thenius, 1954).

Many of the abovementioned authors thought that *V. alopecoides*, *V. praeglacialis*, and *V. praecorsac* are direct ancestors of *V. vulpes* and *V. lagopus*. However, according to other data, the ancestor of *V. lagopus* inhabited Asia in the Early Pliocene (Wang *et al.*, 2014).

Recently, a new paper by Lucenti and Madurell-Malapeira (2020) on ancient foxes was published. In that study, the authors combined all the findings on foxes from the Pleistocene in Europe into one species, *V. alopecoides* (Del Campana, 1913). However, we believe that it is important to leave the division between *V. praeglacialis* and *V. praecorsac* in this paper.

P4 — The primitive state of P4 in the Canidae family includes a developed anterior cingulum (Tedford *et al.*, 2009) and the absence of the parastyle (Wang *et al.*, 1999). On the other hand, the advanced state of P4 manifests as a reduction or absence of the anterior cingulum and presence of the parastyle and plesioconule.

In our opinion, the presence of a developed lingual cingulum in P4 is a primitive feature of Vulpini (Tab. 2). This conclusion is also based on the fact that the lingual cingulum is fairly developed in *V. praeglacialis* and *V. praecorsac*, fossil members of the genus *Vulpes*. Those fossil species lack a cingulum around the protocone, an anterior protocone crest, a parastyle, and a plesioconule and exhibit inner and posterior protocone crests and, finally, a fairly developed anterior cingulum of P4 (Kormos, 1932; Rabeder, 1976). Such a combination is predominant in modern *V. vulpes* and not typical of mainland *V. lagopus*. Notably, *V. praeglacialis* exhibit a fairly developed lingual paracone crest, which is rather absent in *V. praecorsac* and *V. lagopus*. This indicates that *V. praeglacialis* and *V. praecorsac* are different species.

We, hence, conclude that *V. vulpes* display numerous primitive morphological features in P4 and that mainland *V. lagopus* appear to be advanced in most characters. As previously mentioned, the island populations of *V. lagopus* tend to be morphologically similar to *V. vulpes*, meaning that Bering Island and Mednyi Island *V. lagopus* retained a primitive morphological state of

P4. This observation indirectly suggests their long-term isolation from mainland populations.

M1 — The primitive complex of M1 in the Canidae family includes a developed parastyle and a well-developed protocone cingulum, as well as the presence of a paraconule and metaconule in the protocone crest and also the presence of a developed hypocone. The advanced state of the tooth is marked by an enlargement or reduction in the hypocone, an enlargement (to the size of the protocone) or reduction (slight) in the para- and metaconules, a substantial reduction in the parastyle, and an enlargement of the paracone with respect to the metacone (Tedford *et al.*, 1995, 2009). In our opinion, the primitive state in Vulpini includes the presence of differentiated para- and metaconules of moderate size. This observation is supported by data on the morphology of M1 in the possible ancestral species, *V. praeglacialis* and *V. praecorsac* (Tab. 3). Both exhibit a small but fairly pronounced parastyle, a paraconule separated from the preprotocrista, and a posterolingual cingulum that does not merge with the metaconule. However, the development of the protocone and metaconule cingula differs between *V. praeglacialis* and *V. praecorsac*. In *V. praeglacialis*, the cingulum is complete and developed, whereas in *V. praecorsac*, the protocone cingulum is commonly incomplete and the metaconule cingulum is often absent (Kormos, 1932; Rabeder, 1976). Notably, the morphology of the hypocone differs between *V. praeglacialis* and *V. praecorsac* as well. The former predominately exhibit a developed hypocone and accessory elements (grooves) in the hypocone in some cases, whereas the latter display a developed hypocone as well but a reduced hypocone, without accessory elements in both cases. In both *V. praeglacialis* and *V. praecorsac*, we found a well-pronounced metaconule and a paraconule separated from the preprotocrista (morphotypes B2 and C2; Gimranov, 2017). The dental features of *V. praeglacialis* are generally more primitive. Interestingly, contrary to that, *V. praecorsac* already acquired a number of advanced characters: reduction or absence of the protocone and metaconule cingula and reduction of the hypocone.

Hence, we conclude that *V. vulpes* display numerous primitive morphological features in M1, namely, complete protocone and metaconule cingula, paraconule separation from the preprotocrista, and a posterolingual cingulum that does not merge with the metaconule. On the contrary, mainland *V. lagopus* display a number of advanced characters. Notably, the primitive morphology of the parastyle (fairly large) is extremely rare in all the recent samples. The island populations of *V. lagopus* are similar to *V. vulpes* in six characters and to mainland *V. lagopus* in only four characters of M1. The similarity between the island populations of *V. lagopus* and *V. vulpes* suggests that the former retained many primitive features of dental morphology.

M2 — The evolutionary transformations of M2 in the Canidae family are broadly similar to those of M1. The primitive state includes the presence and development of the parastyle, paraconule, and metaconule, as well as a developed protocone crest and hypocone. The

advanced morphology of M2 is marked by a reduction in the hypocone and parastyle, a lesser development of the para- and metaconules, and a reduction in the protocone crest (Tedford *et al.*, 1995, 2009). The protocone complex and protocone cingulum are similar between *V. praeglacialis* and *V. praecorsac*, with both morphological elements being fairly developed in those species. In ancient species, the metacone is slightly smaller than the paracone (Tab. 4). The difference between the two species is the presence of a developed hypocone in *V. praeglacialis* and the reduction of this cusp in *V. praecorsac* (Kormos, 1932; Rabeder, 1976). As no parastyle was detected in the specimens of recent *Vulpes*, this character was not discussed further.

We, hence, conclude that *V. vulpes* display numerous primitive morphological features in M2: The metacone is slightly smaller than the paracone, and the protocone complex, protocone cingulum, and hypocone are well developed. Mainland *V. lagopus*, on the other hand, display numerous advanced features, including a combination of characters opposite to those of *V. vulpes*. Notably, the insular morphs of *V. lagopus* are not as similar to *V. vulpes* in terms of M2 morphology as it was observed for P4 and M1. Only two characters, the large metacone and large hypocone, display a similarity between *V. vulpes* and *V. lagopus* from Mednyi Island. Mainland and Bering Island *V. lagopus* exhibit a tendency toward a reduction in the hypocone. The latter are similar to an extent to *V. vulpes* in terms of the protocone cingulum morphology and to mainland *V. lagopus* in terms of the protocone morphology. The shape of the protocone in Mednyi Island *V. lagopus* is peculiar and unique from that observed in other studied groups. In general, a remarkable combination of primitive and advanced features exists in the dentition of the island populations of *V. lagopus* complemented by features unique to these populations.

Both North American and Northern Eurasian *V. lagopus* are fairly homogenous genetically and display a low level of genetic differentiation (Dalen *et al.*, 2005; Carmichael *et al.*, 2007). Molecular data also suggest that Commander Islands *V. lagopus* strongly differ genetically from mainland populations (Geffen *et al.*, 2007; Džikija, 2008). The results of morphological studies on recent *V. lagopus* corroborate the findings of molecular genetics (Puzachenko & Zagrebelsky, 2008; Szuma, 2008, 2011; Nanova, 2015; Nanova *et al.*, 2017; Nanova & Proa, 2017; Martín-Serra *et al.*, 2019b). A previous study on the nonmetric characters of maxillary teeth (Gimranov, 2014) showed that Mednyi Island *V. lagopus* populations are clearly distinct from other modern groups of the same species. Szuma (2011) demonstrated that Commander Islands *V. lagopus*, according to the prevalence of different dental morphotypes, are very similar to *V. vulpes* and occupy the same branch of the Euclidean distance tree. The results of this study confirm the particularity and isolated position of the island populations of *V. lagopus* with respect to the mainland populations of this species. The dentition of the island groups represents

a mixture of primitive, advanced, and unique features. One explanation for this phenomenon is the possible bottleneck event that might have taken place either as a result of long-term isolation on the islands or during the initial settlement of the islands at the turn of the Holocene (Goltsman *et al.*, 2005; Džikija, 2008; Nanova *et al.*, 2017; Proa & Nanova, 2019). Another potential factor that could have led to a change in dentition might be the narrow range of food resources available on the islands. In our opinion, the modern dental pattern of *V. lagopus* from the Commander Islands is a result of the interplay of a complex of factors, including both factors mentioned above. One unquestionable observation, however, is that contact with mainland polar fox populations was lost a long time ago, when mainland *V. lagopus* still had many primitive features in their upper dentition. We assume that the island populations of *V. lagopus* stopped coming into contact with mainland *V. lagopus* at the end of the Late Pleistocene.

Conclusion

Our detailed description of the occlusal surfaces of P4, M1, and M2 revealed a number of polymorphic dental characters, some of which are typical of *V. vulpes* while others are typical of *V. lagopus* (nine characters for P4, eight characters for M1, and five characters for M2). The frequency of the characters is significantly different between *V. vulpes* and mainland *V. lagopus*, and thus these characters can be used to distinguish between species.

It was observed that the island populations of *V. lagopus* differ from mainland *V. lagopus* in most of the characters. Mednyi Island *V. lagopus* are the most specific group as they display a number of unique dental features not found in other populations. However, this is not the case for Bering Island *V. lagopus*.

Primitive features of P4, M1, and M2 are found in both *V. praeglacialis* and *V. praecorsac*. However, the latter also exhibit a number of advanced features, indicating that *V. praeglacialis* and *V. praecorsac* are different species. Primitive features are also prevalent in the maxillary dentition of *V. vulpes*. Although the same applies to the island populations of *V. lagopus*, their mainland conspecifics display numerous advanced features. It can be concluded that the island populations inherited the primitive features from their mainland ancestors in the past. However, to understand the population history of the island populations of *V. lagopus*, it is important to understand the fact that they have retained these primitive features in combination with many advanced ones and also acquired some unique derived characters. This observation indirectly suggests the long-term isolation of the island populations of *V. lagopus*. However, the exact time of the last contact between them and the ancestral mainland populations can only be determined after studying Pleistocene *V. lagopus*.

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