

## Evolutionary implications of morphological variation in the lower carnassial of red fox *Vulpes vulpes*

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Research on the morphological variability of the occlusal surface of M<sub>1</sub> talonid in the red fox *Vulpes vulpes* (Linnaeus, 1758) in the Holarctic has been carried out on 2271 specimens originating from 42 populations. The Nearctic was represented by 666 specimens belonging to 13 populations, whereas Palearctic was represented by 1605 specimens from 29 populations. Analyses of the developmental level and formation of cristids between the hypoconid and entoconid allowed the differentiation of 34 shape variants of the occlusal surface of the talonid in the red fox. Because of the complicated variation of cristids, 34 variants were assigned to 5 morphotypes of group P. In the Palearctic and Nearctic a significant geographic variation occurred of P morphotypes and their variants. Primitive variants of the talonid structure on M<sub>1</sub> are predominant in populations from the south of the Asian range of the red fox, while more progressive characters of the occlusal surface of the lower carnassial are typical of the northern and centrally located red fox populations in the Palearctic and Nearctic. The geographic differentiation is probably connected with different Pleistocene histories of particular populations.

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### Introduction

A penetrating analysis of the dental polymorphism within a species, or between closely related species, enables detection of phylogenetic relationships and evolutionary tendencies. Morphological analyses discerns complex variation of the occlusal surface of cheek teeth. The morphotypic variability of the occlusal surface in premolars or molars, has been analyzed to reveal the evolutionary, taxonomic, and phylogenetic relationships of many rodents, such as: *Citellus parryi* (Serdyuk 1979), *Chionomys* (Nadachowski 1991, 1992), or leporids, eg: *Hypolagus beremendensis* (Fladerer and Reiner 1996), *Lepus europeaeus* (Suchentrunk 1994), *Lepus nigricollis* and *L. peguensis* (Suchentrunk 2004). In Carnivora morphotypic analyses of teeth were carried out on cheek teeth in the genus *Martes* (Wolsan 1988, 1989), early European *Mustelida* (Wolsan 1993), *Meles* (Baryshnikov and Potapova 1990, Baryshnikov *et al.* 2002). Moreover, the polymorphism of cheek teeth and I<sup>3</sup>

in the Polish population of the red fox (Szuma 2002) has been described, and then, following the study on morphotypic character occurrence, a microevolutionary analysis of the dentition in *Vulpes vulpes* (Linnaeus, 1758) was conducted (Szuma 2003).

A particular role in the dentition of the carnivores, including the red fox, is played by the carnassial pair ( $P^4$  and  $M_1$ ). These teeth are the largest and have the most complex shape of the occlusal surface.

The first lower molar in the fox is characterised by the presence of a strongly developed talonid. From the buccal side the talonid has a well-shaped hypoconid, and from the lingual side, a slightly smaller entoconid. From the hypoconid a ridge, so-called cristid obliqua, runs in the mesial direction, and in the distal direction – a postcristid. In the distal part of the talonid the postcristid is present, which sometimes disappears and sometimes joins the entoconid. The entocristid (see: Photo 1) runs from the entoconid in the mesial direction. Between the cusps, hypoconid and entoconid, there is a depression, the talonid basin. The lateral surfaces of the hypoconid and entoconid from the talonid basin side in Carnivora are usually smooth. Sometimes on these surfaces there appear enamel ridges (= cristids) of a defined course. The variation in the shapes and cristid courses in the talonid basin region have not been described, but their variable occurrence, both in

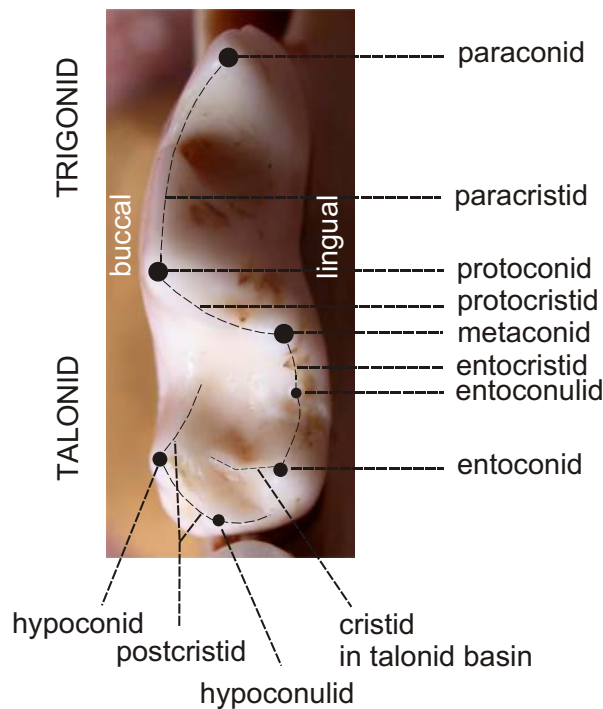


Photo 1. Occlusal structure of  $M_1$  in the red fox (MRI PAS 168933).

foxes and other species of the Canidae family, has been indicated (Tedford *et al.* 1995). The earlier research in the polymorphism of the  $M_1$  crown shape concerned such features as the variable presence of entoconulid on  $M_1$  (Degerböl 1933, Kurtén 1967, Pulliainen *et al.* 1972, Szuma 2002, 2003), or the variable presence or absence of the hypoconulid and postcingulid (E. Szuma, unpubl.). Taking into account the significant role of  $M_1$  in the dental system, the complex tooth-crown shape with the simultaneous low level of variation in the size and shape, as well as the high level of fitting of the  $M_1$  crown shape to the crown of the opposing upper carnassial  $P^4$  (Szuma 2000), one may suppose that the variation in the shape of talonid surface is a significant indicator of evolutionary transformations in the fox dentition. Initial observations indicate that the polymorphism in the talonid surface shape may also be a reliable diagnostic feature enabling to identification of the *Vulpes vulpes* species having a single tooth as a sample.

The aim of this paper is: (1) to describe the variation of the talonid surface shape on  $M_1$ ; (2) to detect the geographic variation in the shape of talonid in contemporary populations in the Holarctic range of the red fox; and (3) to identify the features indicated in the reconstruction of dentition evolution of *Vulpes vulpes*.

## Material and methods

The polymorphism of talonid shape on  $M_1$  was analyzed on 2271 specimens of the red fox *Vulpes vulpes*. The sample included 42 populations from the northern hemisphere. The population names, the numbers of individuals studied, and distribution are shown on a schematic map (Fig. 1). This map provides data on climatic zones of the northern hemisphere based on the climatic world division by Berg dated 1938 (Martyn 1985). North America is represented by 666 individuals belonging to 13 populations, whereas Eurasia and North Africa by 1605 specimens from 29 populations. Only individuals without tooth wear were included in the study. The analysis of the frequency distribution of morphotypes was carried out on left  $M_1$ 's. Males and females were evaluated together because of a low numerical representation of some populations, and because of the formerly established lack of sexual dimorphism in the qualitative characters in the Polish population of the red fox (Szuma 2002).

The studied specimens came from scientific collections belonging to the following institutions: American Museum of Natural History in New York; Field Museum of Natural History in Chicago; Hungarian Natural History Museum in Budapest; Mammal Research Institute, Polish Academy of Sciences in Białowieża; Museo di Storia Naturale e del Territorio, Università di Pisa; Museum of Vertebrate Zoology, University of California in Berkeley; Natural History Museum in Berne; Natural History Museum in London; Natural History Museum, University of Florence; Siberian Zoological Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences in Novosibirsk; Smithsonian Institutions, National Museum of Natural History in Washington DC; Zoological Institute, Russian Academy of Sciences in St. Petersburg; Zoological Museum, Amsterdam University; Zoological Museum of Moscow University; National Museum of Natural History in Kiev; Zoological Museum, Taras Shevchenko University in Kiev.

The research in the shape variation of the occlusal surface of  $M_1$  talonid in its central part allowed to differentiate 34 shape variants (Fig. 2). To simplify the procedure of obtaining a statistic conclusion, all these shape variants were classified into 5 morphotypes: P1, P2, P3, P4, and P5. Morphotype P1 is characterized by a complete absence of cristid traces in the central part of  $M_1$  talonid (variant P-). Morphotype P2 covers variants with the presence of short fragments of enamel ridges in the central part of the talonid basin (variants Pa, Pb, Pab, Pi, and Pl). Morphotype P3 is created by a group of shape variants of the enamel ridges forming partial, not complete, connections between the entoconid

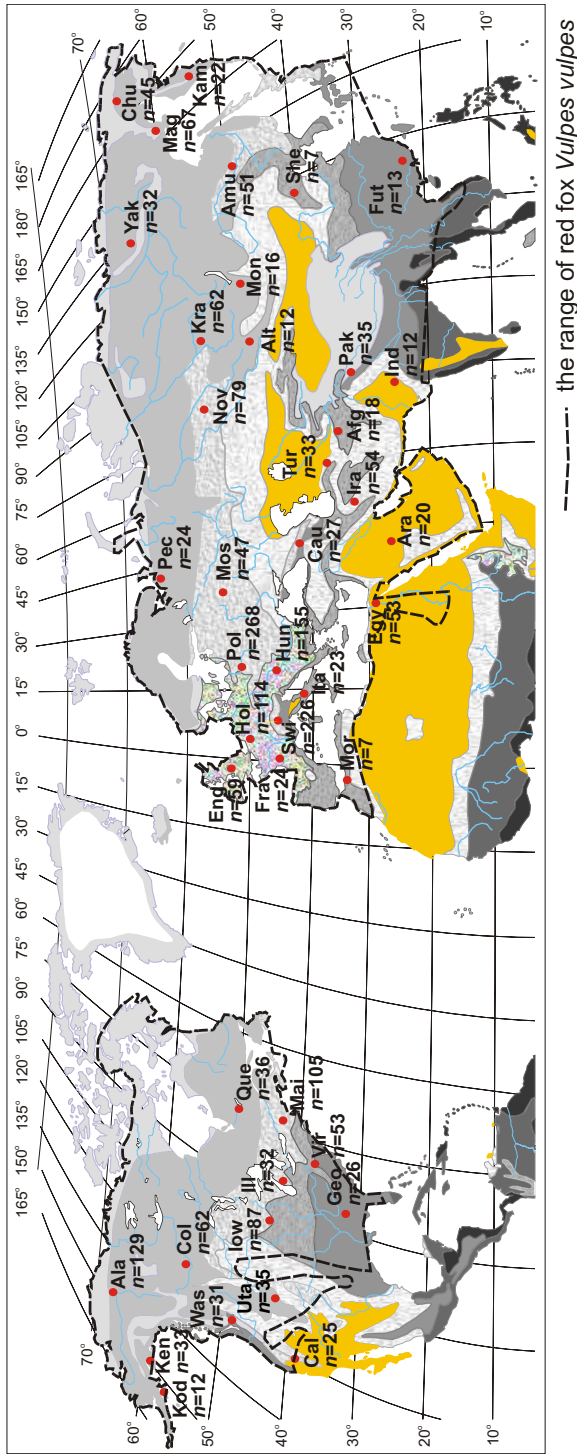


Fig. 1. Distribution and numbers of individuals in the studied populations of the red fox in Holarctic. North America: Ala - Alaska, Cal - California, Col - British Columbia, Geo - Georgia, Ill - Illinois, Iow - Iowa, Ken - Kenai Peninsula, Kod - Kodiak Island, Que - Quebec, Uta - Utah, Wyoming, Ver - Vermont, Vir - Virginia, Was - Washington. Eurasia: Afg - Afghanistan, Alt - Altai, Amu - Amur, Ara - Saudi Arabia, Cau - Caucasus, Chu - Chukchi, Egy - Egypt, Eng - Great Britain, Fra - France, Fut - Futsing province, China, Hol - Holand, Hun - Hungary, Ind - India, Ira - Iran, Ita - Italy, Sardinia, Cyprus, Kam - Kamchatka, Kra - Krasnoyarskaya oblast', Mag - Magadan, Mon - Mongolia, Mor - Morocco, Mos - Moscovskaya oblast', Nov - Novosibirskaya oblast', Pak - Pakistan, Pec - Pechoro-Ilycheskii zapovednik, Arkhangelskaya oblast', Pol - Poland, Shen - Shensi province, China, Swi - Switzerland, Tur - Turkmenistan, Yak - Yakutskaya oblast'.

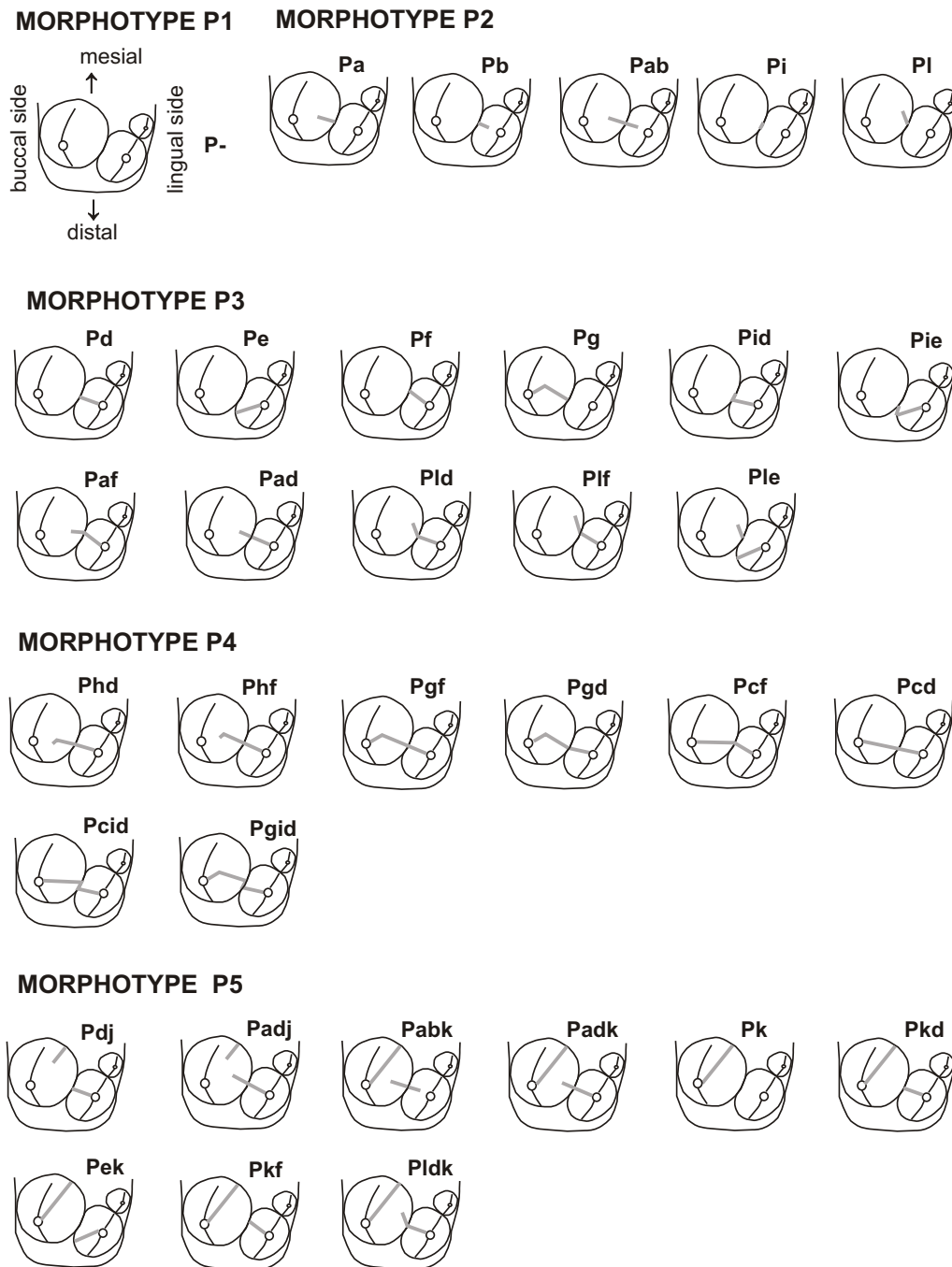


Fig. 2. Variation in the shape and developmental level of enamel ridges in the central part of  $M_1$  talonid in the red fox. The course of the studied cristids is marked with the thick grey line.

and hypoconid (variant Pg – where the cristid runs from the hypoconid and ends in the central part of the talonid basin, and variants Pd, Pe, Pf, Pid, Pie, Paf, Pad, Pld, Plf, Ple – where the cristid emerges on the entoconid and ends in the central part of the talonid basin). Morphotype P4 is composed by variants of cristid shapes with a complete or almost complete connection between the entoconid and hypoconid. An almost full connection of the entoconid and hypoconid forms cristid variants Phd and Phf. The complete connection is present in variants Pgf, Pgd, Pcf, Pcd, Pcid, Pgid. Morphotype P5 gathers the variants where apart from the feature of variable cristid presence and shape, another enamel ridge on the hypoconid is visible. This ridge originates from the mesial part of hypoconid base and runs into the direction of the cusp top medially in relation to cristid obliqua. This morphotype P5 covers variants Pdj, Padj, Pabk, Padk, Pk, Pkd, Pek, Pkf, and Pldk (Fig. 2).

## Results

Frequency distributions of the morphotype of group P (Fig. 3) in the populations of the red fox from the Palearctic show a highly significant interpopulation variation ( $\chi^2 = 206.99$ ;  $p < 0.001$ ). The populations of the Nearctic have a lower interpopulation variation but also statistically significant ( $\chi^2 = 83.24$ ;  $0.001 < p < 0.01$ ). In the Palearctic fox populations from the temperate climatic zone of Europe are characterized by a low share of morphotype P1 (from 0.0% in France to 18.6% in Great Britain). A higher share of morphotype P1 is typical of populations from the southern edges of the red fox range in Asia (from 22.2% in Iran and Afghanistan to 35.0% in Saudi Arabia). Like the European ones, populations from North Africa show a low level of morphotype P1 occurrence (0.0% in Morocco, 7.5% in Egypt). Populations from Central Asia and Far East have an intermediate share of morphotype P1 (from 8.9% in Chukchi to 30.4% in Novosibirskaya oblast'). In the Nearctic the frequency of morphotype P1 varies between 3.1% (Illinois) to 24.1% (Iowa), although the frequency changes of this morphotype do not suggest any definite geographical tendency. Morphotype P2 has a low share in the populations of both the Palearctic and Nearctic. Merely in the former region, the morphotype was present in 15.4% of red foxes in Altai. In the remaining populations morphotype P2 was either absent or occurred sporadically. The percentage of morphotype P3 in the Palearctic ranges from 16.7% (Pechoro-Illycheskii zapovednik) to 57.1% (Morocco), while in the Nearctic from 22.2% (Quebec) to 91.7% (Kodiak Island). Morphotype P3 in the Palearctic does not show any definite geographic gradient. In the Nearctic fox populations from the northern part of the range have a lower share of morphotype P3 (Quebec – 22.2%, British Columbia – 46.8%) than in the populations from the south (California – 72.0%, Georgia – 73.1%). A high occurrence of morphotype P3 is visible in the insular population from Kodiak Island (91.7%). Frequency of morphotype P4 in the Palearctic varies from 16.7% (India) to 75.0% (Pechoro-Illycheskii zapovednik), whereas in the Nearctic from 8.0% (California) to 58.3% (Quebec). In the Palearctic the lower share of morphotype P4 is characteristic of the populations from the south of the range (from 16.7% in India to 35.0% in Saudi Arabia). A higher level of morphotype P4 occurrence can be observed in red foxes of Europe and Siberia. The north-south gradient of morphotype P4 frequency appears in the Nearctic. The populations from the south are charac-

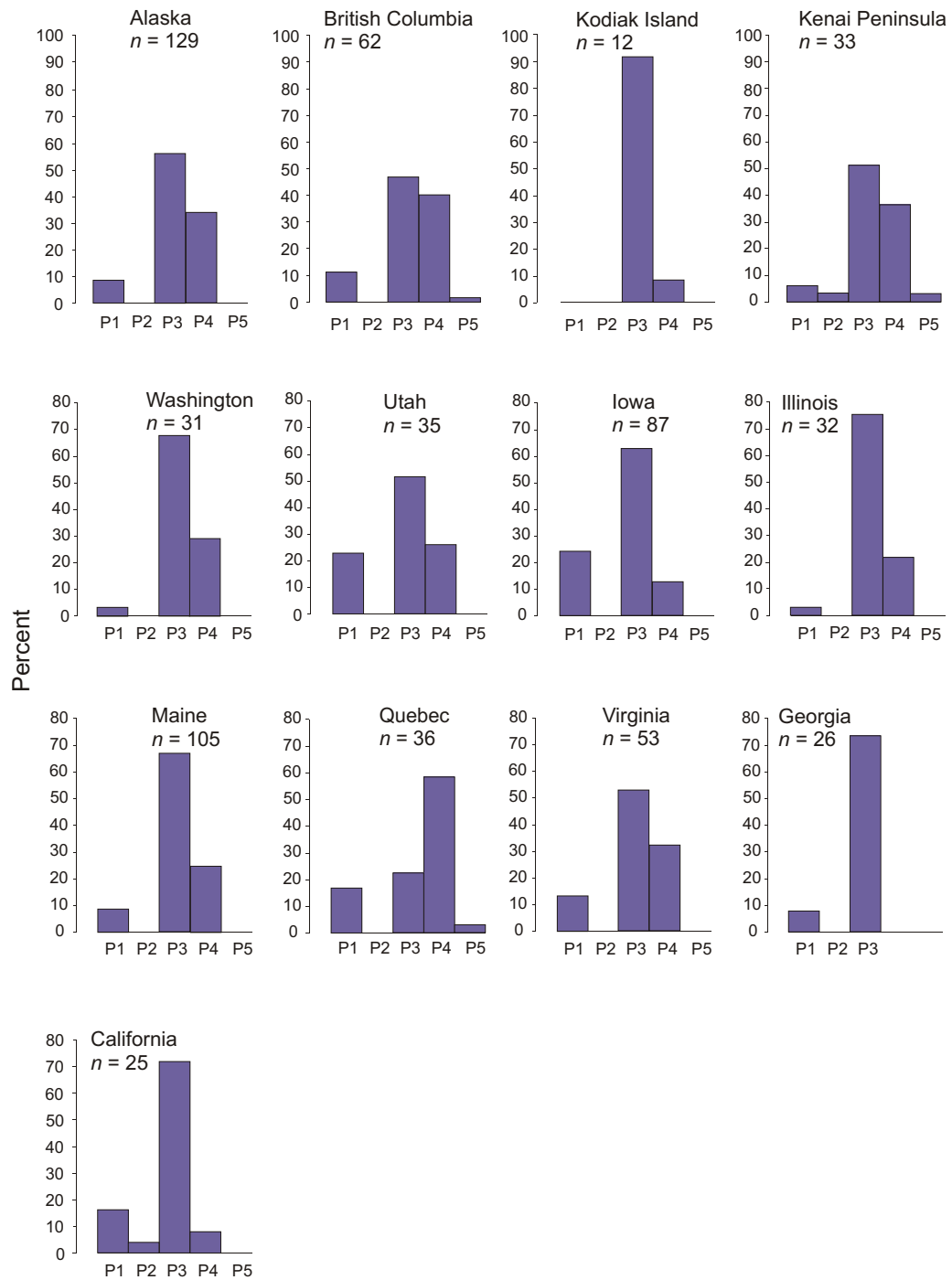


Fig. 3. Frequency distribution of morphotypes of group P in 42 populations of the red fox.

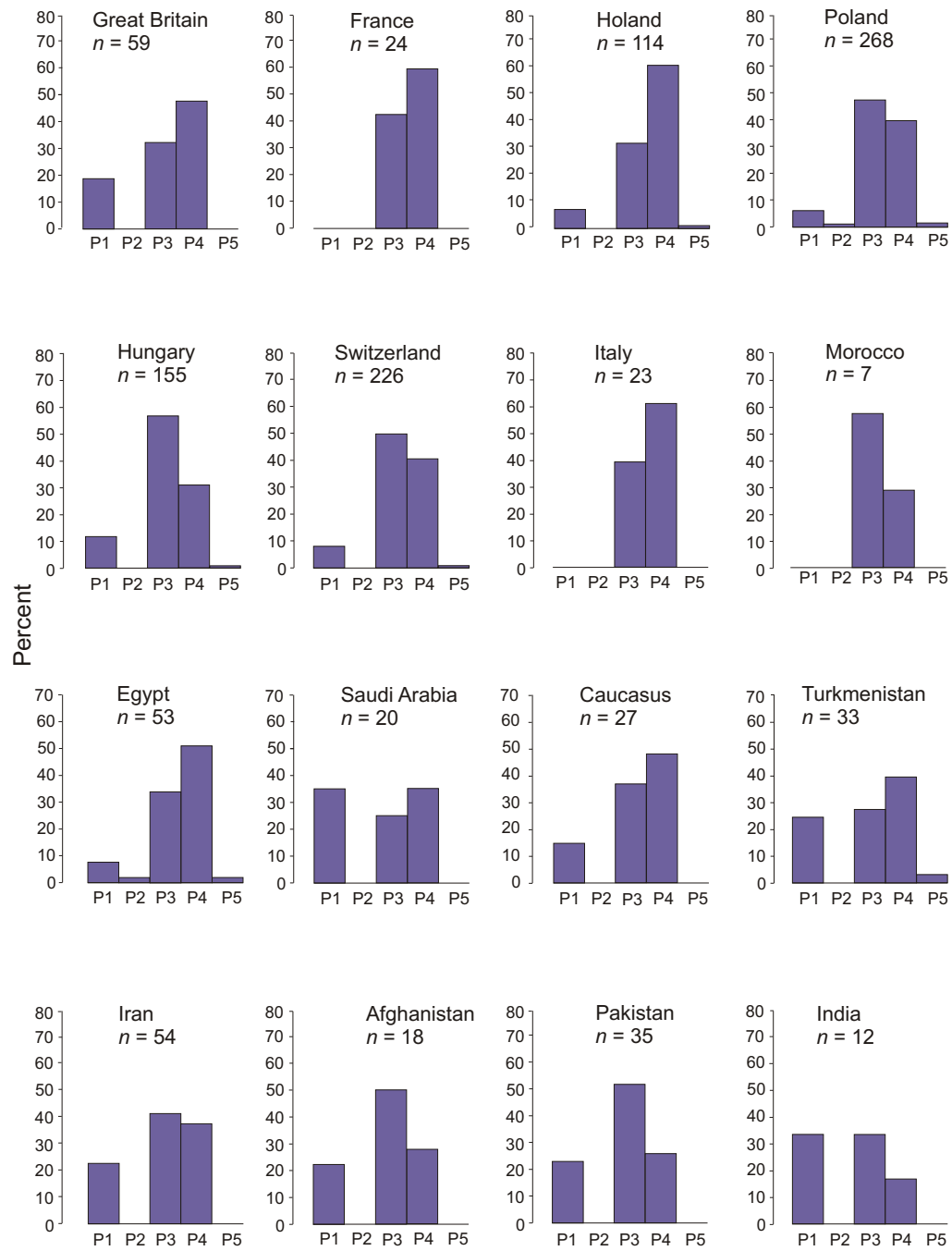


Fig. 3 continued.



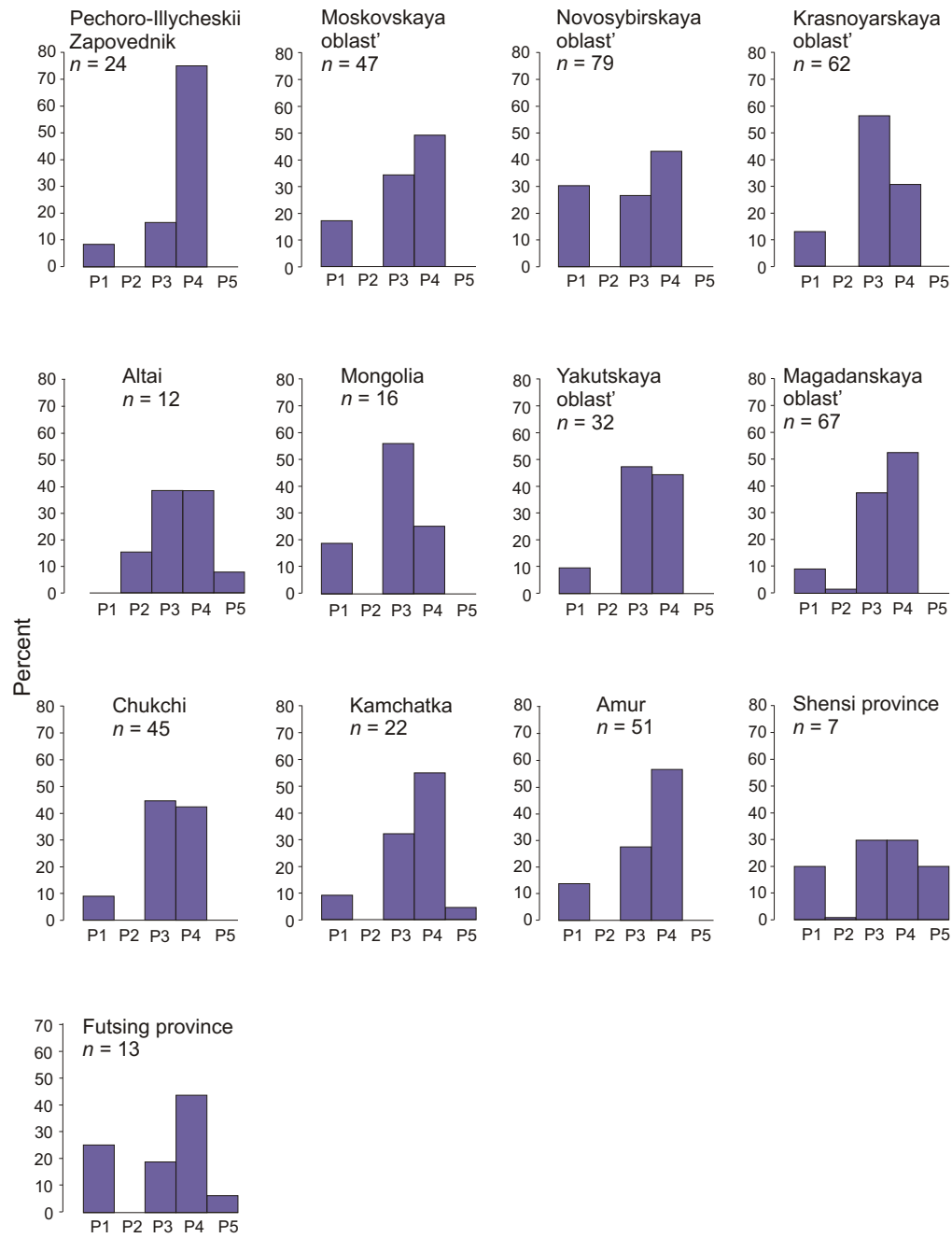


Fig. 3 – concluded.

Table 1. Share of frequency of particular variants of group P in 42 populations of the red fox.

	n	P1			P2			P3							Pld	Plf	Ple
		Pa	Pb	Pab	Pi	Pl	Pd	Pe	Pf	Pg	Pid	Pie	Paf	Pad			
Alaska	129	8.5					15.5		1.6	0.8	0.8		3.9	31.8	2.3		
Brithish Columbia	62	11.3					16.1		1.6	1.6			3.2	21.0	3.2		
Kodiak Island	12						25.0		8.3					58.3			
Kenai Peninsula	33	6.1					15.2						15.2	18.2	3.0		
Washington	31	3.2					19.4	3.2	3.2				16.1	22.6	3.2		
Utah	35	22.9					20.0	2.9	8.6				2.9	14.3	2.9		
Iowa	87	24.1					28.7	2.3	6.9				11.5	12.6	1.2		
Illinois	32	3.1					25.0		9.4				12.5	25.0		3.1	
Maine	105	8.6					12.4	1.0					14.3	38.1	1.0		
Quebec	36	16.7					5.6			5.6			5.6	2.8			2.8
Virginia	53	13.2		1.9			20.8	1.9	3.8				3.8	20.8	1.9		
Georgia	26	7.7					19.2	3.9	3.9				23.1	19.2	3.9		
California	25	16.0					36.0	8.0	4.0					24.0			
Great Britain	59	18.6		1.7			8.5		5.1				8.5	10.2			
France	24						12.5		4.2				8.3	16.7			
Holand	114	7.0					5.3		0.9				7.9	16.7	0.9		
Poland	268	6.0				0.4	14.9	1.9	3.0	0.8			1.5	23.9	1.5		
Hungary	155	11.6		0.6			9.7	1.3	1.9	0.6			5.2	12.3			
Switzerland	226	8.0		0.9	0.4		18.1	0.4	0.4				7.1	23.5			
Italy	23						13.0	8.7					4.4	13.0			
Morocco	7			14.3			14.3		28.6					14.3			
Egypt	20	7.6		1.9	1.9		13.2	1.9					3.8	15.1			
Saudi Arabia	27	35.0		5.0			15.0						5.0	5.0			
Caucasus	53	14.8					11.1		3.7			3.7	3.7	14.8			
Turkmenistan	33	24.2		6.1			12.1		3.0			3.0	3.0	9.1			
Iran	54	22.2					13.0		9.3			9.3	9.3	9.3			
Afghanistan	18	22.2					11.1		16.7			16.7	5.6	16.7			
Pakistan	35	22.9					28.6		2.9			2.9	5.7	14.3			
India	12	33.3		16.7			16.7		8.3			8.3	4.2	12.5			
Pechoro-Ilycheskii zap.	24	8.3															
Moskovskaya oblast'	47	17.0					14.9	4.3	2.1			4.3	4.3	6.4	2.1		
Nowosybirskaya oblast'	79	30.4					11.4	2.5				11.4	8.9	8.9	3.8		
Krasnoyarskaya oblast'	62	12.9					17.7	1.6				17.7	3.2	29.0	4.8		
Altai	12				8.3		8.3	8.3	16.7								
Mongolia	16	18.8					18.8							37.5			
Yakutskaya oblast'	32	9.4					12.5	3.1				3.1		25.0	3.1		
Magadanskaya oblast'	67	9.0					16.4	3.0	1.5				1.5	9.0	6.0		
Chukchi	45	8.9		4.4			2.2	8.9					2.2	24.4	6.7		
Kamchatka	22	9.1					9.1	9.1					9.1		4.5		
Amur	51	13.7			2.0		5.9	2.0			2.0			9.8	5.9		2.0
Shensi province	7	14.3											14.3	14.3	14.3		
Futsing province	13	30.8		7.7	7.7												



terized by a low share of morphotype P4. Its frequency is higher in the north of the range. Only the isolated population from Kodiak Island does not subject to the geographic gradient and shows a low percentage of morphotype P4 occurrence (8.3%).

Morphotype P5 appears sporadically over the whole Holarctic range of the red fox. In the Nearctic it is present in the populations of the north, ie Quebec, British Columbia and Kenai Peninsula. In the Palearctic the highest share of P5 was noted in the populations from China: Shensi province (20.0%) and Futsing province (6.3%), as well as in Altai (7.7%). In the remaining populations morphotype P5 is absent or occasional.

The frequency distribution of particular variants of group P morphotypes is presented in Table 1. In the Nearctic the most frequently observed variants of P3 morphotype are Pd, Pad, and Paf. From among morphotype P4 variants, Pcd and Pcf are predominant. In the north and in the center of the Nearctic, other quite frequent variants of morphotype P4 are: Pgd, Pgf, and Phf. Moreover, in the populations from the north of the range the presence of variants of morphotype P5 was noted. In the populations from the south (Virginia, Georgia, California) variants Pgd, Pgf, and Phf were not registered.

In the Palearctic the most frequently observed variants of morphotype P3 are Pad, Pd, and Paf. Morphotype P4 is mainly represented by variants Pcd and Pcf. Moreover, in the European populations and the ones from the northern Asian range one can observe a frequent presence of variants Pgf, Pgd, and sometimes Phf. On the contrary, in the populations from the southern part of the range (Futsing province, Pakistan, India, Afghanistan, Iran, Turkmenistan) variants Pgd and Phf were not found.

## Discussion

The morphological structure of the occlusal surface of the lower carnassial next to P<sup>4</sup> shows the highest level of complexity in the dental system of carnivorous mammals. In foxes M<sub>1</sub> has a set of cusps and enamel ridges typical of tribosphenic molars. So far the level of hypoconid and entoconid formation has been indicated in considerations on the structure of talonid in placental mammals (Van Valen 1994), but the question of cristid presence and development between the hypoconid and entoconid has been addressed sporadically. Sometimes this junction is named transverse crest (Tedford *et al.* 1995). Observations of dentition fragments of fossilized foxes show a significant occurrence of cristids within the talonid basin of M<sub>1</sub>. These cristids are likely to help in studying evolutionary processes in the phyletic line *Vulpes* (D. V. Ivanov and M. V. Sotnikova, unpubl.). Research in the shape variation in the dentition of contemporary foxes in 42 populations evenly covering almost all the red fox natural range have allowed differentiation of 34 variants in cristid shapes within the talonid basin. Frequency distributions of particular variants and the degree of cristid formation show a significant

interpopulation variation, both in the Palearctic and Nearctic. The higher interpopulational variability in foxes in the Palearctic probably results from a higher number of analyzed populations. In addition, the picture of interpopulation variation in the Nearctic is influenced by the episodes of red fox introduction from England to the territory of the United States of America in the end of the 18th and at the beginning of the 19th centuries (Goszczyński 1995, Larivière and Pasitschniak-Arts 1996, Wilson and Ruff 1999), or by fox resettlements from eastern North America to California taking place at the beginning of the previous century (Lidicker 1991).

In spite of the factors blurring the image of the natural geographic variation of the red fox, the research in  $M_1$  talonid shape polymorphism revealed the existence of visible geographical trends, both in the Palearctic and Nearctic.

The simplest variant of group P morphotype (P-), distinguished for the total lack of enamel ridges on the surface of the talonid basin and the medial surfaces of hypoconid and entoconid, is most often observed in the southern areas of the Asian range. Populations from the central and northern parts of the Asian range, as well as from Europe and North Africa, show a lower occurrence of the P- variant. Although variation in the frequency of this simplest variant of  $M_1$  talonid in North America does not show a definite geographical direction, the isolated population of Kodiak Island (*V. v. harrimani*) is characterized by a complete absence of this variant.

A higher degree of enamel edge development on the talonid is described by morphotypes P3, P4, and P5. Both the distinguished morphotypes and variants within these morphotypes show definite geographic tendencies, in the Palearctic and Nearctic alike. The P3 morphotype and particular variants do not manifest any significant geographic variation in the Palearctic region. In the Nearctic, on the contrary, one can find a north-south gradient of morphotype P3 frequency. Populations from the north and center of the Nearctic range show a high percentage of variants Pad, Pd, and Paf, whereas in the south the share of these variants diminishes. In comparison with the North American populations, foxes from Kodiak Island present a very high share of Pld variant, which is more infrequently observed in other populations. Variant Pld makes morphotype P3 very common among foxes in Kodiak Island.

Variants describing the highest level of talonid structure complexity (P4 morphotype) in the Palearctic most often appear in the north and center of the range, and in the south the percentage of P4 morphotype decreases. This results from the Pgd variant disappearance in the populations from south and south-eastern Asia. At the same time no variant of P5 morphotype emerges in the south of the Asian range. Single variants of this morphotype are found in some populations in Europe, Central Asia, and Far East.

Also in the Nearctic P4 morphotype presents a north-south gradient of frequency. More and more complex variants of P4 morphotype (Pcf, Pgf, Phf) are observed in the north and center of the Nearctic range of the red fox, while the

share of morphotype P4 variants diminishes towards the south. Like in the Palearctic, single variants of P5 morphotype are found in populations from the north and sometimes the center of the range, and they do not appear in the south at all.

Tedford *et al.* (1995) indicate that the presence of a full junction between the hypoconid and entoconid (transverse crest) is the final step in the morphocline leading to the carnassial talonid structure typical of living Canini. In modern canines, including the red fox, the direction of evolutionary change in the structure of the lower carnassial is related to the adaptations to hypocarnivory. It is connected with an enlargement of the talonid and an increase in complexity of the forming structures. This shows that variants of the occlusal structure of M<sub>1</sub> belonging to P1 and P2 morphotypes are primitive characters in the *Vulpes vulpes* line, whereas variants belonging to morphotypes P4 and P5 are progressive at this stage of the species evolution. This analysis suggests that the more primitive initial features of dentition are predominant in populations of the southern part of the Asian range of the red fox. The more advanced in development and complexity talonid is typical of the populations from the north and central part of the Palearctic and Nearctic ranges.

Similarly, a north-southern geographic gradient in some dental characters was observed by Nadachowski (1992) in populations of *Chionomys*. The 'northern' high mountain populations of *Chionomys* are morphologically advanced, while the 'southern' groups preserve primitive traits. This gradient is probably associated with different Pleistocene histories and different recolonisation patterns of the groups. The 'northern' populations colonized the high mountain territories relatively late, in most cases after the retreat of the glaciers, and then underwent distinct morphological changes. The 'southern' populations occupy lower altitudes and/or inhabit areas which have never been covered by ice-sheet. So, they preserved the primitive traits. This explanation can be applied to the geographic gradient of the talonid in the red fox too. The accordance of the observed gradients in the red fox range with the above explanation can be confirmed by the morphotype frequency and variants of the talonid shape even in the most isolated population of the red fox – Kodiak Island. This 'northern' population in North America presents complete absence of primitive character (P-) and also a relatively high frequency of a more advanced and new feature – variant Pld.

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