

Quantitative comparisons of cranial shape and size in adults of *Felis silvestris*, *Vulpes vulpes*, *Mustela putorius* and *Mustela nivalis* from the West Carpathians (Slovakia)

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Abstract. Morphometric analyses of cranial form were performed on samples of four species of carnivorous mammals to investigate patterns of interspecific variation, and intraspecific sexual and regional differences in the skull shape and size. Comparing the skulls of the Wild Cat and the Red Fox, there was no agreement between the patterns of variation between male and female samples. In the Wild Cat, there was significant variation in cranial size and shape between the sexes. Skulls of males and females of foxes did not differ in size. The differences in skull shape between male and female foxes may partially indicate the behavioural separation between the sexes.

The regional differences in skull shape and size were studied in mustelids. The Weasels in general exhibited the greater degree of regional skull variability than the Western Polecats, both in the skull size and shape.

Key words: craniometry, principal component analysis, *Vulpes vulpes*, *Felis silvestris*, *Mustela putorius*, *M. nivalis*

Introduction

One important goal of biological morphometry is the quantitative comparison of animal species or populations as trajectories that react to short-term ecological responses (Jolicouer 1959, 1963 a,b; Garaj 1994, Lynch *et al.* 1996). Univariate studies such as those of Sládek (1991, 1992) atomize the animal morphology and treat each trait as the product of independent evolutionary mechanisms. Yet, morphological features of an organism are not autonomous, changes in diverse aspects of morphology are coordinated (Zelditch *et al.* 1992). Consequently, morphology is best described by multivariate techniques which accommodate the inter-correlated nature of form (Thorpe and Leamy 1983, Thorpe 1988). The need for a composite measure of body size and shape led directly to the application of multivariate statistics, particularly principal component analysis (Strauss 1987). In a multivariate sense, form has two independent components: size and

shape (Jolicouer 1960, 1963 a,b). In this study, we inquire about sexual and environmental contributions to the intraspecific variability of skull size and shape of some carnivores.

Recent comparative morphometric analyses of cranium in carnivores have shown that a large portion of variability in size and shape parameters is found below the level of the species (Jolicouer 1959; Sládek 1991, Lynch *et al.* 1996). It has been suggested that this high-specific variability adjusts size and mainly shape of the skull to temporal and spatial changes in environmental conditions (Martinková 1996). Additionally, many morphometric analyses have shown that the cranial shape and size differ between sexes (Scherling 1989; Lynch and O'Sullivan 1993; Simoens *et al.* 1994 a, b). The objective of this study was to describe regional and sexual variation in the skull form of four species of carnivores living in Slovakia. We examine variation between mustelids from North- and South-Slovakia. We show the role of sexual dimorphism in these populations. Morphology of skull was examined within a context of correlated structures. In this way, similarities among populations, and those groups of animals which possess unique and perhaps adaptively modified patterns of cranium form could be identified.

Material and Methods

The skulls used for this study are held in the collections of Slovakian museums in Košice, Ružomberok, Liptovský Mikuláš and Tatranská Lomnica). We measured 54 crania of adult wild cats, 48 foxes, 28 polecats, and 27 weasels. 44 cranial measurements were taken - measured with vernier callipers graduated to 0.1 mm. The measurements were taken according to definitions given in Driesch (1976). These were:

- V1 - Total length: Akrokranion-Prosthion (A-P)
- V2 - Condylbasal length: aboral border of the occipital condyles-Prosthion (P)
- V3 - Basal length: Basion-Prosthion (Ba-P)
- V4 - Basicranial axis: Basion-Synsphenion (Ba-Sy)
- V5 - Basifacial axis: Synsphenion-Prosthion (Sy-P)
- V6 - Neurocranium length: Basion-Nasion (B-Na)
- V7 - Upper neurocranium length: Akrokranion-Frontal midpoint (A-F)

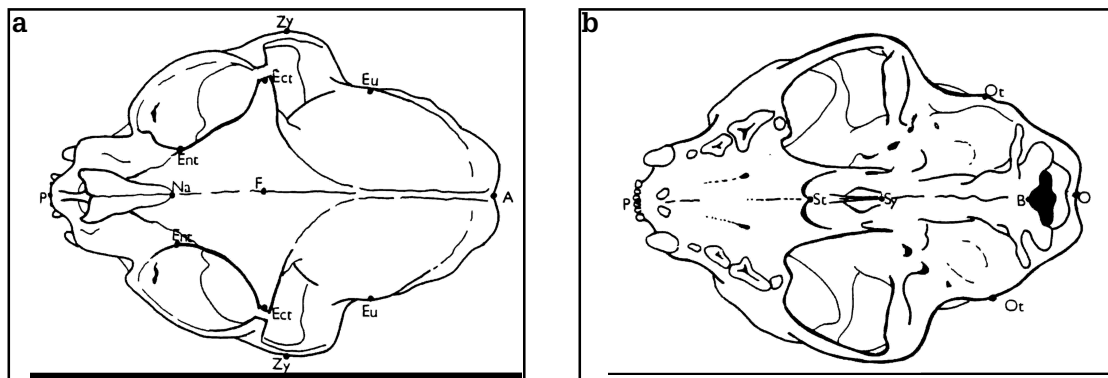


Fig.1. The sets of morphological distance measurements used to quantify cranial form. Cranium of cat is used as a model; a - norma dorsalis, b - norma ventralis. Abbreviations are given in the Material and methods.

- V8- Viscerocranium length: Nasion-Prothion (Na-P)
- V9- Facial length: Frontal midpoint-Prothion (F-P)
- V10- Maximum length of the nasals: Nasion-Rhinion (Na-Rh)
- V11- Length of braincase. This measurement can be taken only when the cribriform is preserved. One insert a thin ruler through the foramen magnum; the front end must reach the cribriform plate and the measurement is read off against the Basion
- V12- „Snout“ length: oral border of the orbits (median)-Prosthion (P)
- V13- Median palatal length: Staphylion-Prosthion (St-P)
- V14- Palatal length: the median point of intersection of the line joining the deepest indentations of the Choanae-Prosthion (P)
- V15- Length of the horizontal part of the palatine: Staphylion-Palatinoorale
- V16- Length of the horizontal part of the palatine corresponding to 13.
- V17- Length of cheektooth row (measured along the alveoli on the buccal side)
- V18- Length of the molar row (measured along the alveoli on the buccal side)
- V19- Length of the promolar row (measured along the alveoli on the buccal side)
- V20- Length of the carnassial, measured at the cingulum
- V21- Maximum breadth of the carnassial. Until now the breadth of the carnassial has been measured without medial projection. Because this distance is difficult to measured exactly we propose to leave it out and to measure only the maximum breadth
- V22- Length to the carnassial alveolus
- V23- Length and breadth of M^1 , measured at the cingulum
- V24- Length and breadth of M^2 , measured at the cingulum
- V25- Maximum diameter of the auditory bulla: from the most aboral point of the bulla on the suture with the paraoccipital process up to the external carotid foramen
- V26- Maximum mastoid breadth = maximum breadth of the occipital triangle: Otion-Otion (Ot-Ot)
- V27- Breadth dorsal to the external auditory meatus
- V28- Maximum breadth of the occipital condyles
- V29- Maximum breadth of the bases of the paraoccipital processes
- V30- Maximum breadth of the foramen magnum
- V31- Height of the foramen magnum: Basion-Opisthion (B-O)
- V32- Maximum neurocranium breadth = maximum breadth of the braincase: Euryon-Euryon (Eu-Eu)
- V33- Zygomatic breadth: Zygon-Zygon (Zy-Zy)
- V34- Least breadth of skull = least breadth aboral of the supraorbital processes = breadth at the postorbital constriction: Frontostenion-Frontostenion (Fr-Fr).
- V35- Frontal breadth: Ectorbitale-Ectorbitale (Ec-Ec)
- V36- Least breadth between the orbits: Entorbitale-Entorbitale (En-En)
- V37- Maximum palatal breadth: measured across the outer borders of the alveoli
- V38- Least palatal breadth: measured behind the canines
- V39- Breadth at the canine alveoli
- V40- Maximum inner height of the orbit
- V41- Skull height. The two pointers of the slide gauge are placed basally on the basis of the skull (on the basioccipital) and dorsally on the highest elevation of the sagittal crest
- V42- Skull height without the sagittal crest the slide gauge is placed in the same position as for M^{38} but the upper pointer is placed beside the sagittal crest on the highest point of the braincase
- V43- Height of the occipital triangle: Akrokranium-Basion (A-B)
- V44- Height (length) of the canine, measured in a straight line from pointy to point. This measurement is only possible if the tooth can be removed from the jaw

We explored patterns of variation using principal component analysis, a sensitive multivariate technique which summarizes the primary trends of variation within a data set, reducing these trends to a small number of independent variables that incorporate the original information. Principal components (PCs) were computed from the covariance matrix of logarithmically transformed data. The logarithmic transformation produces a covariance matrix independent of scaling, but preserves allometries (Jolicoeur 1963 a,b; Strauss 1985, Lynch *et al.* 1996). The significance of a component is determined by the sum of the positive eigenvalues of the covariance matrix (the variance) of the component. If the correlations of the variables on axis are of the same sign, the axis can be taken to represent general size. Our

samples of each species contained individuals that varied significantly in body size; consequently the first component (PC1) was a measure of "general size". In all of our among-group analyses, a substantial amount of residual variation was accounted for by PC2 to PCx, which described contrasts in the skull shape. The loadings and their signs (component weights) indicate the degree to which individual morphometric measurements contribute to shape differences.

Specimens of foxes and cats were pooled by sex to form statistically comparable samples. In weasels and polecats we always compared two different regional samples. PC scores of two pooled groups of crania were compared by one-way analysis of variance. All means are presented + SE unless otherwise noted; statistical significance was accepted at $P \leq 0.05$, and tests were two tailed.

Results

Cranial variation between sexes - comparison of the Red Fox and Wild Cat

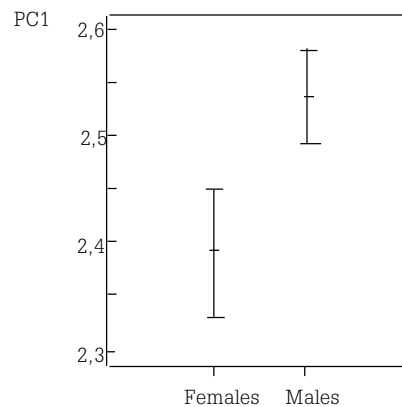


Fig.2. Males of Wild Cats differ from females in having greater size (PC1) of cranium than females.

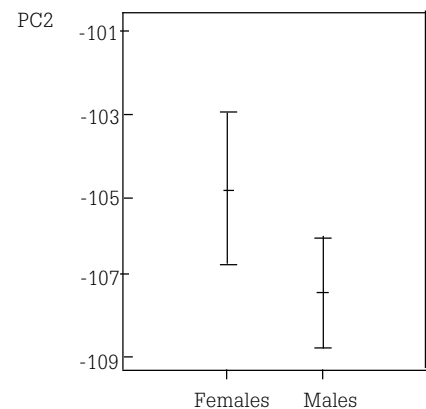


Fig.3. Sexes of *Felis silvestris* differed in the skull shape. For details see Results.

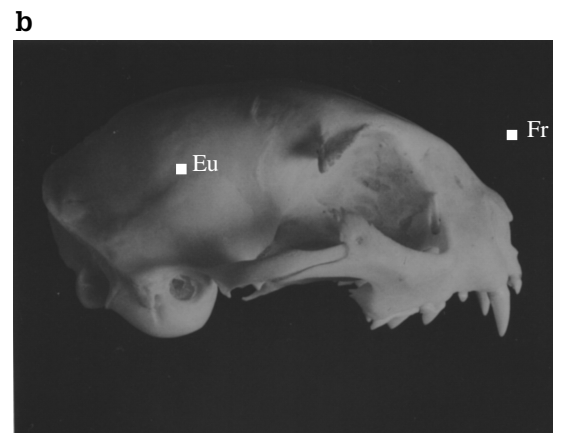
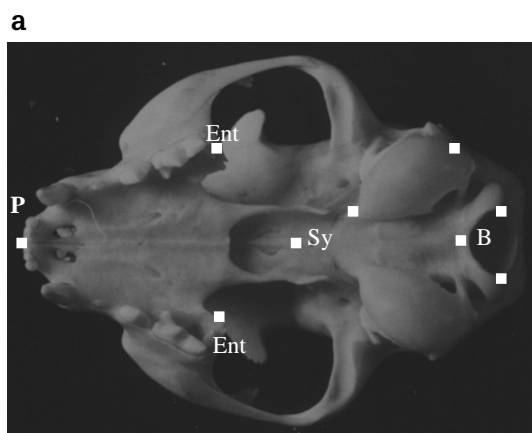


Fig.4. The female crania possessed relatively long carnassial and short basifacial axis, while in males, there was *vice-versa* trend in the skull shape ; a - norma ventralis, b - norma lateralis. For abbreviations see Material and methods.

The first within-group principal component is a highly consistent measure of general size in both species, despite their rather large differences in form (see Fig.9). For both species, size vectors (PC1) have positive loadings for all characters and account for 54% of total variance in the Wild Cat, and for 29% (more measured variables than in cats) in the Red Fox (Table1). In cats, the crania significantly differ between sexes. Males differ from females in having greater size of cranium than females (Fig.2.). In the foxes, there was not statistically significant difference in the size (mean PC1 scores) of crania between sexes. PC2 describes the significant shape difference between the skulls of the Wild Cat males and females (Fig. 3.). The component accounted for 11% of the variation within samples. The female crania possessed relatively long carnassial and short basifacial axis, while in males, there was *vice-versa* trend in the skull shape (Fig.4.a,b). In general, there was greater degree of sexual dimorphism in the size and shape of skull of *Felis silvestris* than in the form of skull of *Vulpes vulpes*. PC8 - shape component was the only component which separated the samples of crania of the Red Foxes (Fig. 5.). It accounted for 3% of the sample variation. The frontal

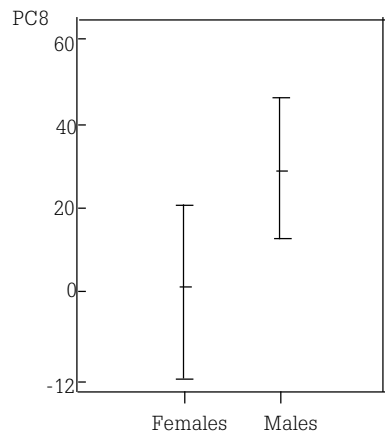


Fig.5. Significant skull shape difference between sexes in the Red Foxes. For details see Results and Fig.6.

region of the female skull was relatively wide with wide M_2 , while skulls of males are relatively deep-bodied in their basal region having relatively higher orbit and longer carnassials (Fig. 6).

Skull morphological variation within two species of the East Slovakian mustelids

Crania of weasels from South-East Slovakia were significantly larger than the crania of animals from North-East (more mountain) Slovakia (one-way ANOVA for PC1 scores of the two groups: $F=4.7$, $d.f.=24$, $P=0.04$). In the Western Polecats, there was not found difference in the skull size between samples from the North- and South-East Slovakia

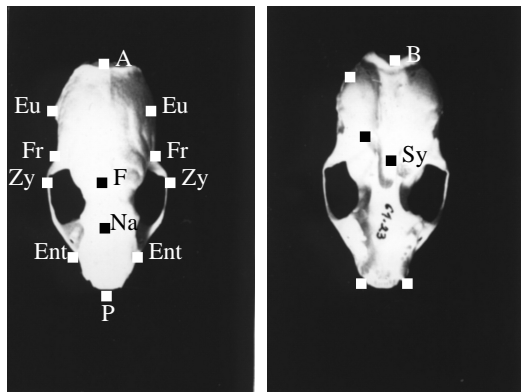


Fig.7. Markers of geographic variation of the skull shape of *Mustela nivalis*; a - norma dorsalis, b - norma ventralis. For details see Results

($F=0.03$, $d.f.=25$, $P=0.86$). The first principal component accounted for 33% of the skull variation within the sample of weasels, and 66% in polecats (Table1). The skull shape of weasels varied greatly (23% of the variation on PC2), compared to PC2 value of polecats of 12% in the same East Slovakian region. The second component significantly (one-way ANOVA: $F=7.1$, $d.f.=24$, $P=0.01$) separated the animals from North-(shorter neurocranium, longer height of foramen magnum) and South-East Slovakia (longer and narrower neurocranium, and wider

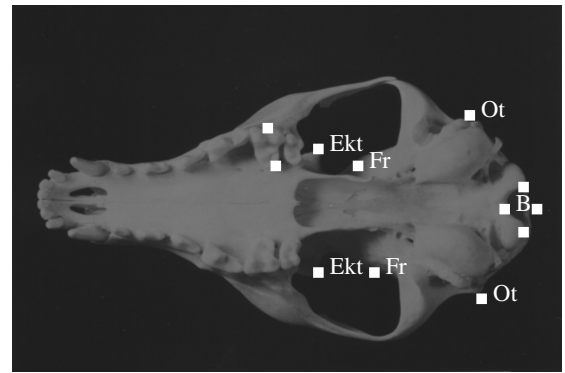


Fig.6. The frontal region of the fox female skull was relatively wide with wide M_2 , while skulls of males are relatively deep-bodied in their basal region having relatively higher orbit and longer carnassials; **norma ventralis**.

and longer splanchnocranium (Fig. 7a,b). In general, the same shape trend was observed in the Western Polecats. Although the skulls of polecats less varied in the shape between the two regions than the skulls of weasels, the trend in the shape variation was comparable. The south-east Slovakian polecats had a relatively longer splanchnocranium and shorter neurocranium while their north counterparts had a longer neurocranium and shorter splanchnocranium (Fig. 8a,b). As shown in Table 1, these characters are among those that load most heavily on PC5 that accounts 2.4% of sample variation (one-way ANOVA of PC5 scores between the two pooled groups: $F=6.8$, $d.f.=25$, $P=0.015$).

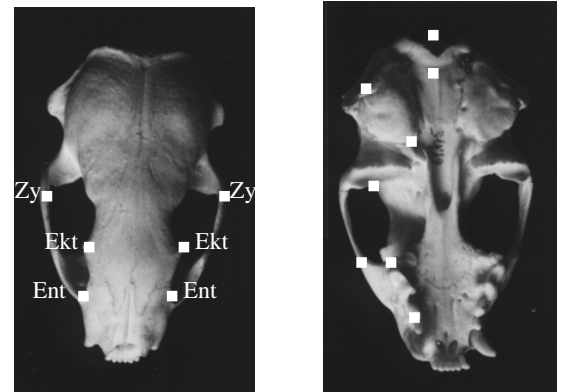


Fig.8. Markers of geographic variation of the skull shape of *Mustela putorius*; a - norma dorsalis, b - norma ventralis. For details see Results.

Discussion

Among the mammals, Carnivora are perhaps those that are readily suitable to studies of variation in the skull size and shape (Fig.9). The differences in the skull form are evident among European species, thus the intraspecific variation in the skull may be effectively studied.

Martinková (1996) used available data from literature (Sládek *et al.* 1972, Kratochvíl 1973 for the examination of skull variation between Wild Cat

	<i>Felis silvestris</i>		<i>Vulpes vulpes</i>		<i>Mustela nivalis</i>		<i>Putorius putorius</i>	
	PC1	PC2	PC1	PC8	PC1	PC2	PC1	PC5
V1	0,172	-0,109	0,168	-0,048	0,138	0,005	0,192	0,097
V2	0,165	-0,112	0,167	-0,054	0,137	0,006	0,173	-0,058
V3	0,094	-0,072	0,181	-0,059				
V4	0,297	0,168	0,159	0,052	0,086	-0,331	0,168	-0,570
V5	0,143	-0,266	0,185	-0,083	0,138	0,012	0,181	0,038
V6	0,168	-0,091	0,129	-0,094	0,128	0,027	0,197	-0,000
V7	0,147	-0,023	0,157	0,097	0,214	0,049	0,201	-0,141
V8	0,197	-0,090	0,214	-0,058	0,427	-0,102	0,186	-0,605
V9	0,159	-0,124	0,220	-0,104				
V10			0,187	-0,082				
V11	0,230	-0,095	0,219	-0,050	0,223	0,032	0,234	-0,139
V12	0,177	-0,125	0,183	-0,044	0,156	0,008	0,188	0,037
V13	0,164	-0,117	0,091	-0,019				
V14			0,221	-0,006				
V15			0,220	0,030				
V16	0,150	-0,009	0,151	-0,026	0,098	0,067	0,211	-0,087
V17			0,054	0,031				
V18	0,165	-0,039	0,182	-0,091	0,135	0,006	0,185	0,113
V19	0,236	0,499	0,181	0,199				
V20			0,112	0,032				
V21	0,238	0,383	0,244	0,239				
V22			0,087	0,039				
V23			0,130	-0,053				
V24			0,051	0,143				
V25			0,102	-0,347				
V26	0,154	-0,132	0,074	0,283	0,087	0,035	0,083	-0,037
V27	0,133	-0,125	0,090	0,008	0,160	0,038	0,186	0,065
V28			0,091	0,022				
V29	0,131	0,019	0,060	0,025	0,120	0,023	0,160	0,108
V30			0,130	0,602				
V31	0,093	0,004	0,025	0,038	0,129	0,058	0,114	-0,146
V32	0,165	0,380	0,032	0,259	0,153	0,831	-0,019	-0,093
V33	0,089	0,086	0,037	-0,015	0,082	0,003	0,151	0,041
V34	0,201	-0,129	0,169	-0,115	0,207	0,031	0,254	-0,018
V35	0,086	0,209	-0,028	-0,119	0,044	-0,121	0,146	-0,128
V36	0,148	-0,096	0,265	-0,158	0,200	0,045	0,278	-0,127
V37	0,382	0,128	0,267	-0,149	0,262	-0,006	0,250	-0,111
V38	0,110	-0,122	0,091	0,088	0,134	-0,001	0,166	-0,119
V39			0,069	0,079				
V40	0,154	-0,187	0,192	0,003	0,479	-0,326	0,148	-0,062
V41	0,097	-0,155	0,055	0,224	0,100	0,037	0,229	0,038
V42			0,058	0,152				
V43			0,034	0,088				
V44	0,135	-0,189	0,120	-0,019	0,168	-0,018	0,204	-0,002

Table 1. Principal components, which summarize the primary trends of variation size and shape of skull.

specimens from different regions. Cranium size in cats showed marked interlocality variation. Cranium size decreased from the West Carpathian to East Carpathian stations. In all localities, males had larger skull than females. Martinková notes that the great variation in the skull size of Wild Cats may be caused by interbreeding with domestic cats, which are smaller than most Wilds.

In *Mustela putorius*, there is also significant morphological variation in the skull size among samples from across Europe (Fig. 10.). In all localities, males had larger skulls than females, and in both sexes, the size of cranium decreased from easterly to westerly stations. There was significant interdependence between the factor "locality" and factor "sex" (Martinková 1996). Differences in skull morphology between male and female mustelids may allow dietary separation between the sexes (Lynch and O'Sullivan 1993).

In Weasels, we found that throughout East Slovakia the cranium shape exhibited striking patterns of ecogeographic variation - from northerly to south-

erly stations. Martinková (1996) compared the shapes of weasel crania from Slovakia, Hungary, and Frankfurt region, Germany (Széky 1973). The shape component separated the samples into three groups. The crania mainly differed in relative maximum length - condylus occipitalis, mastoid width, neurocranium width, and height of foramen magnum.

In our study, we confirmed that phenotypic cranial variation results from a complex nexus of interactions between genes (e.g. difference between males and females) and the environment (geographic differences in the skull form). By encompassing this complexity this study provides insight into the evolutionary processes maintaining patterns of phenotypic diversity. It is also showed that skull size in carnivores is a phenotypically plastic trait. Phenotypic plasticity in cranium size and shape may produce "new morphologies" in response to variable environmental pressures and thus create patterns of local and continental morphological diversity. It is obvious that further work must be done on morphologic and genetic variation between carnivore populations.

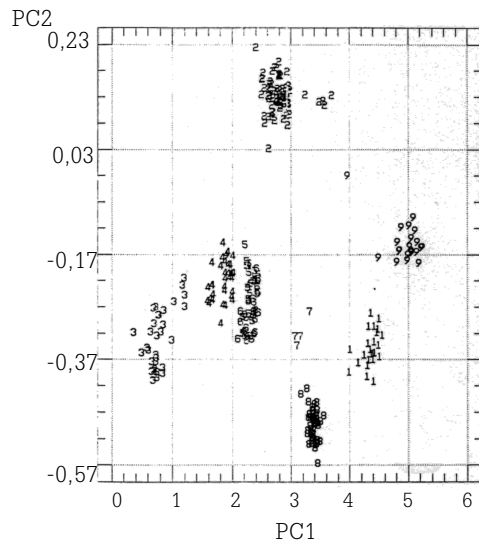


Fig.9. Scatterplot of inter-species variation in the first two principal components of variation in crania dimensions of carnivores from East Slovakia. PC1 represents size, with large to right; PC2 represents shape, from elongated skulls (bottom) to fat (top). Species are as follows: 1 - *Canis* sp., 2 - *Felis* sp., 3 - *Mustela* sp., 4 - *Mustela (Putorius)* sp., 5 - *Martes martes*, 6 - *Martes foina*, 7 - *Meles meles*, 8 - *Vulpes vulpes*, 9 - *Ursus arctos*. After Martinková (1996).

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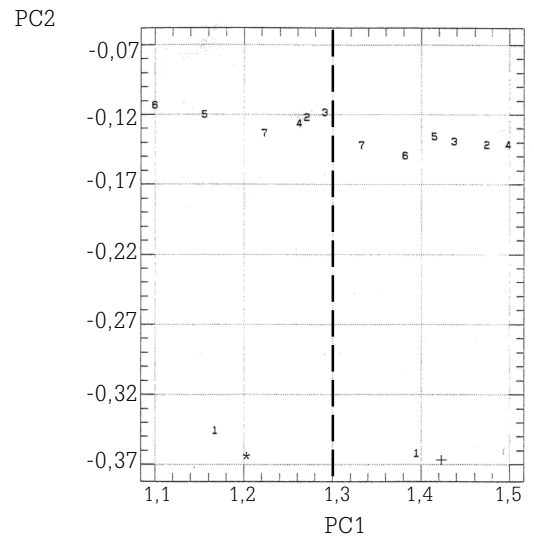


Fig. 10. Plots of principal components analysis (PC2 - skull shape versus PC1 skull size) of males (+) and females (*) of seven European Western Polecat populations. Samples are as follows: 1- East Slovakia, 2 - Hungary, 3 - Frankfurt region, Germany, 4 - Bratislava region, Slovakia, 5 - Warsaw region, Poland, 6 - Moscow region, Russia, 7 - Ukraine. After Martinková (1996) and Széký (1973).

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