Mammalian Biology 83 (2017) 10–20

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original investigation

Cranial variation and taxonomic content of the marbled polecat *Vormela peregusna* (Mustelidae, Carnivora)

Andrey Yu Puzachenko[a], Alexei V. Abramov[b,*], Viatcheslav V. Rozhnov[c]

[a] *Institute of Geography, Russian Academy of Sciences, Staromonetnyy per., Moscow 109017, Russia*
[b] *Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia*
[c] *A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow 119071, Russia*

ARTICLE INFO

Article history:
Received 11 March 2016
Accepted 10 November 2016
Handled by Daisuke Koyabu
Available online 11 November 2016

Keywords:
Skull variation
Vormela peregusna
Morphospace
Subspecies
Taxonomy

ABSTRACT

Morphometric variation in 26 characters of 245 skulls of the marbled polecat (*Vormela peregusna*) was studied across the distribution range. Morphological diversity was low with respect to both the size and the shape of the skull. The sexual size dimorphism of cranial characters in *V. peregusna* was low compared with other similar-sized mustelids. This finding may be a result of more specialized behaviour, resulting in less intra-specific competition with respect to habitat and food selection. Analysis of the geographic variation of skulls revealed two morphological groups – western and eastern. These groups were treated as distinct subspecies in this study. Nominotypical *V. p. peregusna* (Güldenstädt, 1770) (syn. *sarmatica*, *euxina*) is found in southern and eastern Europe, Asia Minor and Caucasus. The eastern subspecies *V. p. koshewnikowi* Satunin, 1910 (syn. *alpherakii*, *chinensis*, *negans*, *obscura*, *ornata*, *pallidior*, *syriaca*, and *tedshenika*) is found south and east of the Middle East, in Middle and Central Asia and eastward to China. Our data revealed a gradual decrease in the morphological diversity in *Vormela* skulls from west to east in the distribution range. This phenomenon may be explained by the later origin of the eastern subclusters of the marbled polecat. The pattern of geographic variation revealed in this study may reflect the Pleistocene history of the species range formation, rather than a relationship to climate conditions throughout the modern species range.

Introduction

The marbled polecat *Vormela peregusna* (Güldenstädt, 1770) is a small-sized carnivore that is well-adapted to arid and semi-arid open landscapes. This polecat-like mustelid belongs to the subfamily Ictonychinae Pocock, 1921, in the family Mustelidae (Wolsan and Sato, 2010; Sato et al., 2012). The marbled polecat is the only widely distributed Eurasian member of this subfamily, whereas other species have restricted ranges in Africa (*Ictonyx*, *Poecilogale*, *Poecilictis*) and Central and South America (*Galictis* spp., *Lyncodon*). The distribution range of *V. peregusna* extends from south-eastern Europe through Asia Minor, the Middle East, Caucasus and Middle Asia to Mongolia and northern China (Rozhnov, 1999; Wozencraft, 2005; Abramov et al., 2016a).

Throughout this wide distribution range, the marbled polecat displays extreme individual variation, which has led to the naming of many taxa of species or subspecies. Five or six subspecies were recognized in recent reviews (Gorsuch and Lariviere, 2005; Wozencraft, 2005). Ognev (1935) conducted the first taxonomic revision of the marbled polecat. He recognized 3 subspecies – nominotypical (occurs from south Europe to North Caucasus and the Volga River), *V. p. alpherakii* (Iran, Middle Asia, and western Kazakhstan) and *V. p. negans* (eastern Kazakhstan and China). Based on fur coloration, Ognev (1935) divided all populations of *V. peregusna* into 2 groups: a western group (includes *peregusna* and *alpherakii*) and an eastern group (*negans*). Pocock (1936) divided the marbled polecat into six subspecies – *V. p. peregusna* (south-eastern Russia and North Caucasus), *V. p. euxina* (Balkans, Ukraine, and south Russia), *V. p. alpherakii* (Turkmenistan, Afghanistan, and Iran), *V. p. syriaca* (Near East), *V. p. ornata* (Siberia), and *V. p. negans* (China). Although Pocock's revision was based on a few specimens, this system was accepted in most subsequent reviews and checklists (see Table S1).

There are only a few genetic studies of the marbled polecat. Analysis of mitochondrial DNA (Rozhnov et al., 2006, 2008) showed no genetic differences between samples from southern Russia (Kalmykia, Rostov Province), Transcaucasia (Armenia, Azerbaijan), and Middle Asia (Turkmenistan, Uzbekistan). A recent study of

---

* Corresponding author.
E-mail address: a.abramov@mail.ru (A.V. Abramov).

http://dx.doi.org/10.1016/j.mambio.2016.11.007
1616-5047/

the genetic diversity of Turkish populations revealed three distinct haplogroups within the marbled polecat (Ibis and Tez, 2014). The main haplogroup contained haplotypes from Armenia, Azerbaijan, Russia, Turkey (Anatolia), Turkmenistan and Uzbekistan. The second haplogroup consisted of haplotypes from Turkey (Thrace) and Turkmenistan. The third haplogroup contained only the haplotypes from central and eastern Turkey. There was no geographic structuring in the distribution of haplotypes in Turkey; however, all three haplogroups were found in central Turkey. Chromosomal studies revealed that *V. peregusna* had 38 chromosomes throughout the entire studied range, whereas the fundamental number varied from 68 to 72 (Gorsuch and Lariviere, 2005).

The aim of the present study was to study the geographical patterns of cranial diversity in the marbled polecat and elucidate the taxonomic content of this species.

Material and methods

This study was based on 245 skulls of adult *V. peregusna* from 135 localities across the species' distribution range (Fig. 1, Table S2). Age classes were defined by scoring the morphological features of skull structure, such as the development of crests, the obliteration of sutures, and dentition.

Twenty-six measurements were made using a digital sliding caliper to the nearest 0.1 mm. The scheme of the cranial measurements used is shown in Fig. 2. We used the expectation-maximization algorithm (Dempster et al., 1977) to estimate the missing measurements (due to damaged skulls). In all cases, the hypothesis of a random distribution of missing values was accepted.

We examined the collections of the Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg, Russia; the Zoological Museum of Moscow State University, Moscow, Russia; A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia; the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia; A.K. Tembotov Institute of Ecology of Mountain Territories of the Russian Academy of Sciences, Nalchik, Russia; the Institute of Zoology of the Uzbekistan Academy of Sciences, Tashkent, Uzbekistan; the Institute of Zoology of the Bulgarian Academy of Sciences, Sofia, Bulgaria; the Harrison Institute, Sevenoaks, UK; and the Natural History Museum, London, UK. Studied cranial material included the type specimens of *alpherakii*, *chinensis*, *euxina*, *intermedia*, *obscura*, *syriaca* and *tedshenika*.

In the model of morphological space (Puzachenko, 2011, 2013, 2016), the morphological system in the present case was defined as a sample set of marbled polecat skulls (elements), which were defined by a set of 26 measurements. The relationships between the elements of the system were defined by a metric that was a specific method for measuring morphological distances (disparity or similarity) between any pair of elements. Then, we introduced a morphospace as a multidimensional statistical model, which was constructed to provide a compact representation of the morphological distances between elements of a morphosystem. The coordinates (dimensions) of the morphospace did not exactly coincide with any of the original measurements, but any of them could be reproduced (with certain errors) as linear combinations of the modelled coordinates.

We constructed two morphological spaces, as described above, using the Nonmetric Multidimensional Scaling (NMDS) technique (Shepard, 1962; Kruskal, 1964; Davison and Jones, 1983; James and McCulloch, 1990) based on the matrices of morphological distances (Abramov et al., 2009; Abramov and Puzachenko, 2009, 2012 Baryshnikov and Puzachenko, 2011; Puzachenko, 2013). NMDS provides the Euclidian space with *d* coordinates that are orthogonal, and the distance for any pair of microstates is proportional (linear/nonlinear) to the initial morphological distance between individuals. For initial of NMDS algorithm, we use square dissimilarity matrix contained the Euclidean distances and similarity matrix of Kendall's tau-*b* (corrected for ties) rank-order coefficients (Kendall, 1975) between all pairs of skulls. The Euclidean metric integrally describes the variability of skull size, while the Kendall's coefficient is the difference between the probabilities that the observed rank data (ranked standardized variables) describes the coordination of variation in different measurements of two specimens. that is it can be interpreted as an integrated metric of a skull's proportions or shape.

The "best-minimum" dimensionality of the NMDS model (estimation of "degrees of freedom" of a morphosystem) was estimated according to the procedure described earlier in (Kupriyanova et al., 2003; Abramov et al., 2009).

As a result, we have two variants of morphospaces. The first one reproduces the size diversity (SZM model), and the second – diversity of skull proportions (shape) (SHM model). In the text, the coordinates for the SZM model based on the Euclidean distances matrix were denoted as E1, E2, etc., and the coordinates of SHM model based on Kendall's coefficients matrix were denoted as K1, K2, etc. The coordinates of morphospaces used, also, for classification (clustering) of the *V. peregusna* geographical localities.

In this model, the whole set of pairwise distances between elements of a model was defined as the structure of the morphospace. A modelled space, like to common practice in statistical physics, divided into n ($n = 1, 2, 3\ldots k$; $k = logN + 1$, where N is the sample size) equal parts/volumes. Then, for any N and k, we define a sample probability $p_k = n_k/N$ ($p_{k\in}[0;1]$, $\sum_{i=1}^{k} p_i = 1$ is the normality condition). After this operation, a morphospace was defined as a probability space. Note that our model differed critically from the well-known models of morphological space proposed by Foote (1990) or McGhee (2007).

In the proposed model, the term " morphological diversity *sensu lato*" included the full set of statistical properties of the morphological space, had a sense of the function of structure of the morphospace. Thus, it is intended in general case, the diversity can be described by a set of special variables – macroscopic parameters (macroparameters) or state variables.

The dimensionality (d) of the morphospace is the first acceptable macroparameter of the morphological diversity because the coordinates of a modelled morphospace may be interpreted as a pairwise independent order parameter or degree of freedom of a morphosystem in a synergetic sense (Haken, 1983). Based on the probabilistic conditions for a morphospace model, an actual volume of the morphospace occupied of a morphosystem ("morphological niche", James (1982) may be estimated by Shannon-Weaver entropy (Shannon and Weaver, 1949; Hutcheson, 1970): $H = -\sum_{j=1}^{d}\sum_{i=1}^{k} p_i \log_2 p_i$. The next parameter, $H_d = H/d$, is the average entropy and is a normalized variable or average diversity per one degree of freedom of the morphospace. Another parameter of morphological diversity is the measure of organization (MO) of the morphosystem structure: $MO = 1\text{-}E = 1 - [(\sum_{j=1}^{d} H_j)/(d\log_2 k)]$. Here, E is the common evenness (Pielou, 1966) or information redundancy (Shannon, 1948). We used MO as an estimation of the potential constrains of morphological diversity. MO varied from 1 (extremely strong limitation, full deterministic system) to 0 (limitations were absent, nondeterministic, stochastic system).

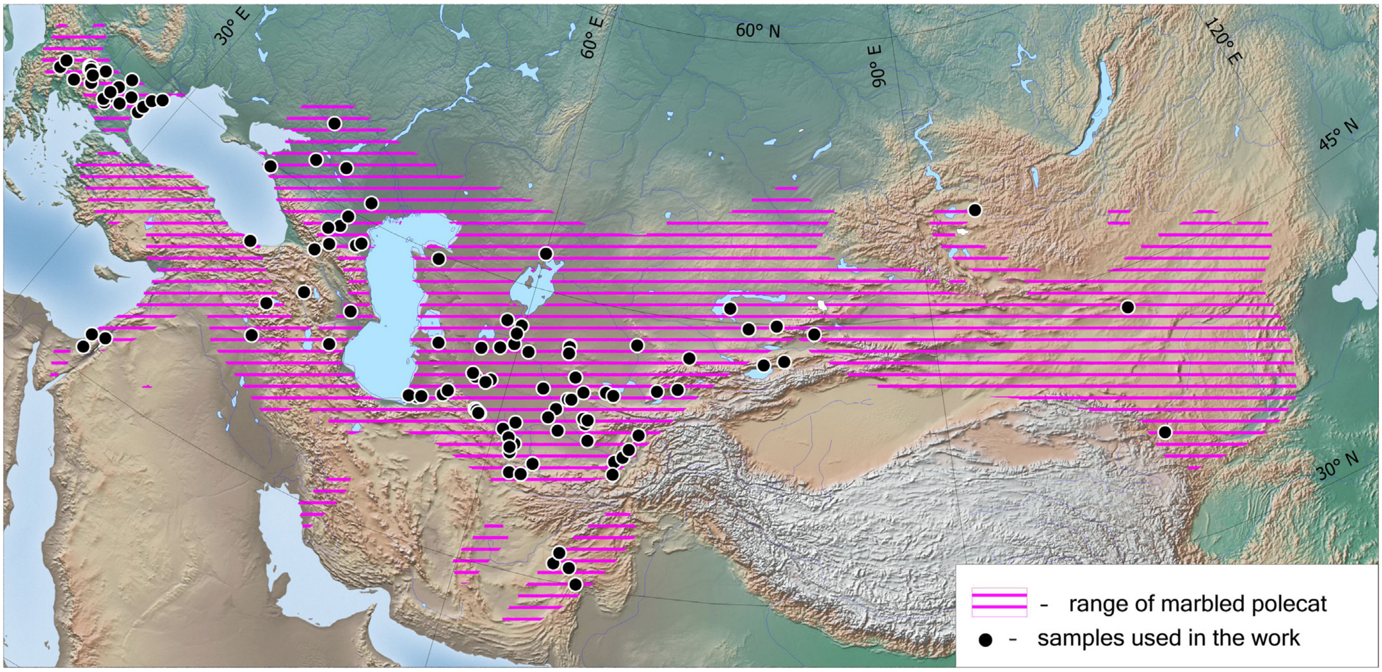

Fig. 1. Range of the marbled polecat (*V. peregusna*) (modified from Abramov et al., 2016a), and localities of the specimens included in this study. The distributions of the morphological groups and subclusters are shown.

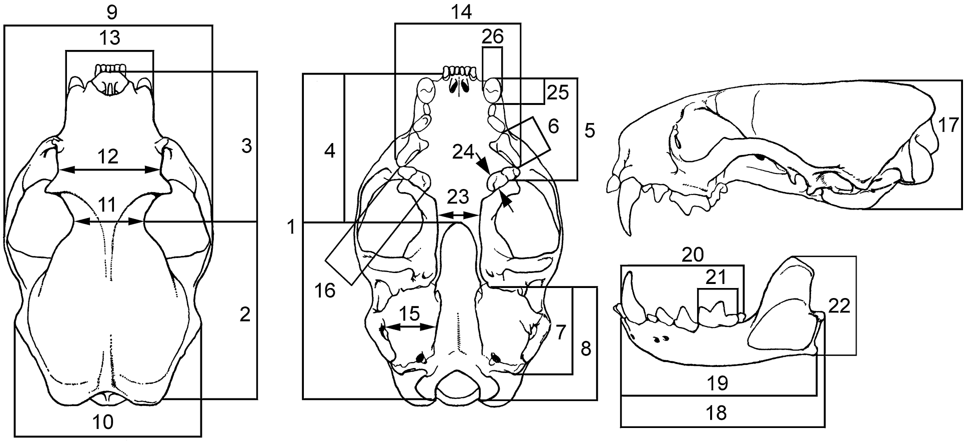

Fig. 2. Skull measurements taken in marbled polecat: 1–condylobasal length (CbL), 2–neurocranium length (NcL), 3–viscerocranium length (VcL), 4–palatal length (PL), 5–maxillary tooth-row length (MxtL), 6–upper carnassial teeth Pm4 length (Pm4L), 7–length of the auditory bulla (AbL), 8–greatest length between the oral border of the auditory bulla and the aboral border of the occipital condyles (BcL), 9–zygomatic width (ZyW), 10–mastoid width of the skull (MW), 11–postorbital width (PoW), 12–interorbital width (IW), 13–width of the rostrum (RW), 14–greatest palatal width (GpW), 15–width of the auditory bulla (AbW), 16–width of upper molar M1 (M1W), 17–cranial height (CH), 18–total length of the mandible (ML), 19–length between the angular process and infradentale (AL), 20–mandibular tooth-row length (MatL), 21–length of lower carnassial teeth m1 (m1L), 22–height of the mandible in the vertical ramus (MaH), 23–minimal palatal width (MpW), 24–length of upper molar M1 (M1L), 25–length of upper canine (CL), 26–width of upper canine (CW).

Sample size (*N*) can significantly influence Shannon's entropy value and other state variables. In particular, it is a very important factor when a small sample size ($N \leq 30$) is used. On a logarithmic scale, the dependence of the state variable and *N* are written as a linear function. The calibration of *H* and *MO* in this case consists of doing the same thing in accordance with the following transformation: $x_{i,cal} = [x_i - (a + b\log_{10}N_i)] + (a + b\log_{10}N_{st})$, where the term of the sum (in square brackets) corresponds to the subtraction of the linear trend of *N* from the current values of *H* or *MO*, and the second term of the sum is the scale constant, which returns the original scale of data. N_{st} is the "standard sample size." N_{st} was selected equals 50, because the computer simulations showed that the entropy increased rapidly within the interval of 15–40 observations when we used random data with a normal distribution, but it increased by only a few percentages within the range from 50 to 100 observations. In the common case, the *i* in calibration equation is about 7 (4–10) random subsamples with different N_i, from 20 to 25 to *N*.

We compared the values of the macroparameters of morphological diversity estimated for *V. peregusna* samples with the parameters of ten other mustelid species from four genera (*Martes, Meles, Mustela,* and *Lutra*).

As a measure of sexual size dimorphism (SSD), we chose the ratio of male size to female size because they are intuitively simple and easily interpretable: $SSD = 100 \times (M_{\text{male}} - M_{female})/(M_{male} + M_{female})$, where *M* is sample mean for the males or females. Average sexual size dimorphism

(ASSD) was calculated as $(\sum_{i=1}^{y} SSD_i)/y$, where y is the number of the skull measures. For a comparative analysis of SSD, we used the data for 12 mustelid species (Baryshnikov et al., 2003; Abramov and Puzachenko, 2005, 2009; Abramov and Puzachenko, 2006 Abramov et al., 2009; Abramov et al., 2016b; Baryshnikov and Puzachenko, 2012).

Statistical analyses were performed using SYSTAT (SYSTAT Inc.) and PAST (Hammer et al., 2001).

Results

Geographical skull variation

The pooled set for both sexes was studied for geographic variation. The SZM model had 4 dimensions, whereas the SHM model had only 3 dimensions (Table 1). The first dimension (E1) describes the general size variation of the skull and associated with most of the characters, except for postorbital width (correlated with axes E2 and E4) and the length of upper molar M1 (correlated with axis E3). High Spearman's coefficient, r, values between cranial characters and axes K1-K3 may indicate a high contribution of allometry in the skull variation.

The morphospace dimensions had no significant correlation with the geographic coordinates. Thus, we did not find clear geographic clines in cranial variation throughout the studied species range. Analysis of Variance (ANOVA) (Table 1) revealed that the variances of axes E3 and K2 associate with geographic location ("geographical factor") in 33.7% and 53.5%, respectively. The relative variance of E1 was determined by SSD in 43%, whereas the dimensions E3 and K1 did not depend on SSD.

The classification of subsamples with more than 2 specimens, based on the means of the E3 and K2 dimensions, was divided into two, Western and Eastern, clusters (Fig. 3A). The Eastern cluster was formed by samples from Middle and Central Asia and the Middle East (Israel), whereas the Western cluster included marbled polecats from southern Russia (North Caucasus, Rostov Province) and Bulgaria. The membership of 13 unclassified specimens was tested by discriminant analysis. Based on these results, animals from Macedonia, Rumania, Turkey, Armenia, Iraq and Kalmykia (southern of Central Russia) were belonged to the Western cluster, whereas animals from Azerbaijan, Iran, southern Siberia (Tyva) and China were classified as members of the Eastern cluster. Surprisingly, the specimen from southern Mongolia was closer to the Western cluster than to the Eastern cluster. The values of the canonical variable CAN 1 for both groups overlapped considerably (Fig. 3B), suggesting relatively low morphological differentiation among the marbled polecat groups.

Nevertheless, two groups significantly ($p < 0.05$) differed in 13 cranial characters (Table 2). The marbled polecat skulls of the Western cluster were smaller than those of the Eastern cluster. The main differences were found in interorbital width, greatest length between the oral border of the auditory bulla and the aboral border of the occipital condyles, and length of upper molar M1. Animals of the Western cluster were significantly larger with respect to a few characters: width of the rostrum, cranial height, and height of the mandible in the vertical ramus.

Two marbled polecat groups were analysed separately (Tables S3–S5). The Western cluster was divided into three subclusters (Fig. 4A): Balkan–Anatolian (specimens from Macedonia, Rumania, Bulgaria and Turkey), East European (specimens from North Caucasus, Kalmykia and Rostov Province) and specimens from Armenia and Iraq. The Balkan–Anatolian cluster had the smallest skulls (Table 3), but this may likely be explained by the larger ratio of males in the Eastern European sample. Two specimens from Armenia and Iraq were characterized by relatively large skulls and had intermediate positions between the two other subclusters. The Eastern cluster was also divided into three subclusters (Fig. 4B). The first subcluster mainly included specimens from the northern

Table 1

Spearman's correlation coefficients for skull measurements of *V. peregusna* and coordinates of the morphospaces: E1–E4 – size diversity morphospace; K1–K3 – shape diversity morphospace; and r^2 – adjusted coefficient of determination for linear multivariate regression models, which characterizes the quality of reproduction of the measurements by the coordinates of the two morphospaces.

Characters	E1	E2	E3	E4	K1	K2	K3	r^2
CbL	0.93	−0.23	−0.06	0.08	0.65	−0.03	0.08	0.93
NcL	0.65	0.36	0.08	0.37	0.03	0.15	−0.14	0.76
VcL	0.86	−0.35	−0.06	−0.15	0.75	−0.04	0.21	0.88
PL	0.87	−0.08	−0.23	0.06	0.49	−0.18	0.16	0.82
MxtL	0.89	−0.01	−0.17	−0.13	0.47	−0.04	0.34	0.85
Pm4L	0.71	0.17	−0.25	−0.11	0.18	−0.04	0.35	0.71
AbL	0.80	−0.21	−0.13	0.31	0.50	−0.13	−0.08	0.79
BcL	0.83	−0.27	−0.13	0.28	0.58	−0.18	−0.08	0.86
ZyW	0.90	−0.16	0.14	−0.03	0.65	0.15	0.04	0.87
MW	0.93	−0.17	0.06	0.02	0.65	0.07	0.06	0.89
PoW	0.16	0.77	0.15	0.41	−0.48	0.19	−0.26	0.83
IW	0.82	−0.22	0.01	0.12	0.62	−0.08	−0.09	0.79
RW	0.80	0.01	0.23	−0.31	0.48	0.33	0.30	0.82
GpW	0.85	0.20	−0.01	−0.16	0.31	0.17	0.34	0.83
AbW	0.77	−0.12	0.00	0.11	0.47	0.01	−0.01	0.64
M1W	0.64	0.30	−0.44	−0.08	0.06	−0.27	0.35	0.74
CH	0.76	0.24	0.29	0.06	0.29	0.36	−0.02	0.79
ML	0.96	−0.13	0.03	−0.08	0.63	0.11	0.20	0.94
AL	0.95	−0.11	0.03	−0.04	0.61	0.11	0.18	0.92
MatL	0.90	0.03	−0.15	−0.12	0.44	−0.02	0.30	0.84
m1L	0.77	0.13	−0.35	−0.10	0.25	−0.17	0.35	0.75
MaH	0.84	−0.08	0.21	−0.08	0.55	0.32	0.14	0.81
MpW	0.69	0.12	−0.01	−0.05	0.27	0.12	0.15	52.2
M1L	0.58	0.24	−0.61	0.01	0.05	−0.44	0.27	0.77
CL	0.72	0.33	0.00	−0.20	0.16	0.13	0.27	0.69
CW	0.70	0.35	0.05	−0.29	0.17	0.22	0.33	0.75
ANOVA, Estimated Relative Variance (%)								
Sexual size dimorphism	42.9	13.2	0.0	0.0	<5	<5	<5	
Geographical factor	27.4	7.7	33.7	13.5	13.1	53.5	7.8	

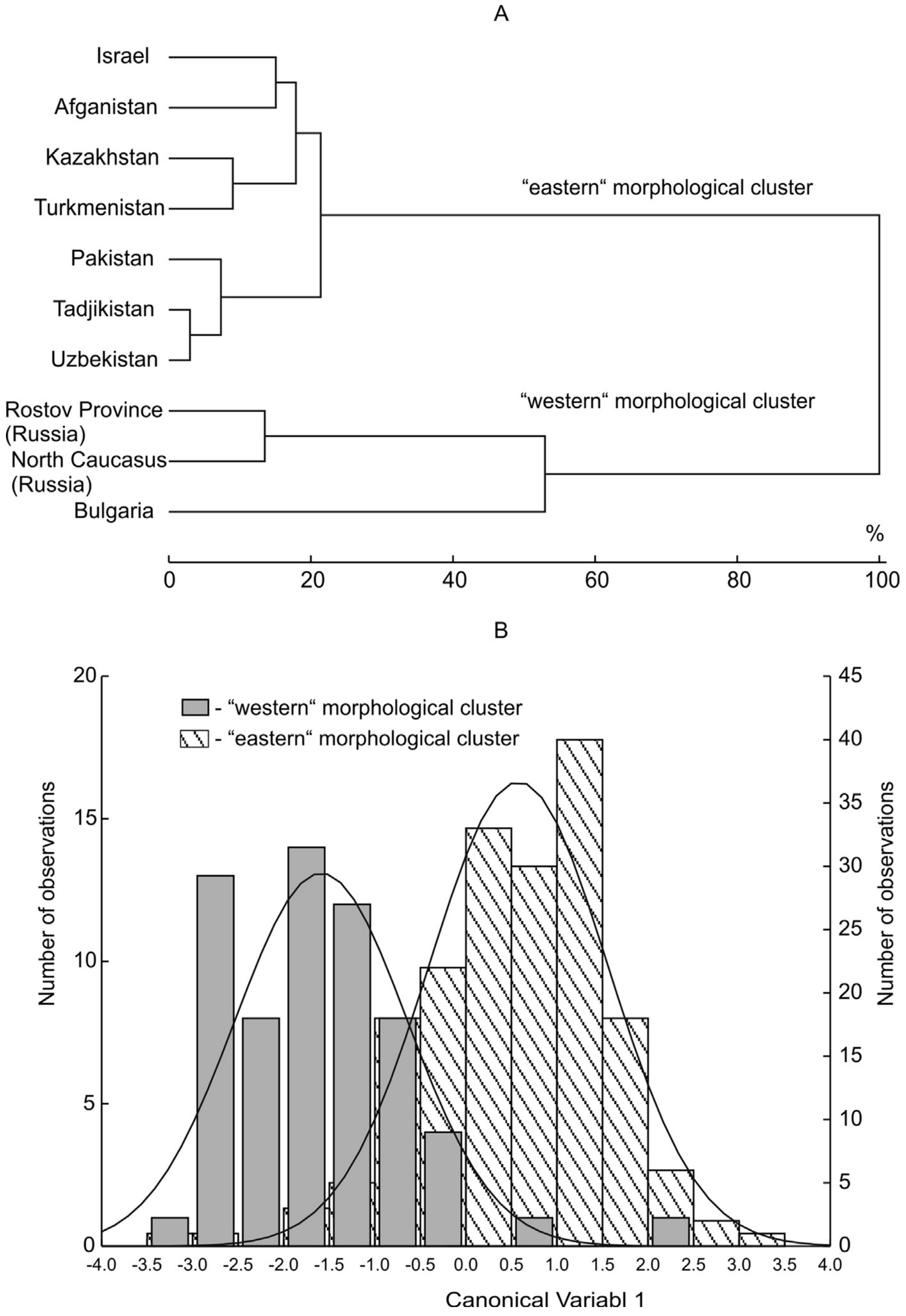

Fig. 3. (A) UPGMA clustering of *V. peregusna* samples with more than 2 specimens based on the means of the E3 and K2 axes of the morphospace models. (B) Distributions of the values of the first canonical variable for the "western" and "eastern" morphological groups of *V. peregusna* skulls.

part of the range (Uzbekistan, Kazakhstan, Tyva, and Mongolia). The second subcluster included specimens from the southern part of the range (Azerbaijan, Turkmenistan, Tajikistan, Iran, Afghanistan, Pakistan, and China) (Fig. S1). Specimens from Israel were considerably separated from the other two eastern subclusters.

The "northern" and 'southern" subclusters of the Eastern cluster were significantly different in most of the cranial characters (Table S2). Skulls from the "northern" subcluster were longer and wider than those from the "southern" subcluster. The specimens from Israel were characterized by very small skull dimensions.

The discriminant analysis of six subclusters illuminating these morphological disparity (Figs. 5A-C). First, four canonical variables (CAN 1–4) were found to be statistically significant (according to χ^2 test, $p < 0.001$) with respect to the classification of these groups. Specimens of the Western and Eastern clusters diverged along the first canonical variable, reflecting the differences in M1L, PL, BcL, RW, and some other characters (Table S6). The Balkan-Anatolian and Eastern European subclusters diverged along the second canonical variable, reflecting differences on MW, CH, MH, ZyW and some other cranial characters. The "northern" and the "southern" subclusters of the Eastern cluster were partly segregated along the third canonical variable. This variable had a significant correlation with the interorbital width. The relative positions of the centroids of six geographical groups are shown on the NJ tree in Fig. 5D.

Sexual size dimorphism

The SSD and ASSD indices were separately analysed for three morphological subclusters (Balkan-Anatolian, northern, and south-

Table 2
ANOVA results of *V. peregusna* skulls from Western and Eastern clusters; M – mean (in mm) and m – standard error. Characters ranged according to the *F* values.

Characters	Clusters				ANOVA	
	Western group		Eastern group			
	M	± m	M	± m	*F*-criterion	*p*
M1L	2.5	0.03	2.7	0.02	30.19	<0.01
IW	14.3	0.16	15.2	0.10	21.29	<0.01
BcL	18.8	0.13	19.5	0.08	19.98	<0.01
RW	13.7	0.13	13.1	0.07	19.66	<0.01
PL	23.8	0.23	24.7	0.10	17.37	<0.01
AbL	15.5	0.13	16.0	0.07	11.93	<0.01
m1L	6.7	0.05	6.8	0.03	9.15	<0.01
CH	21.9	0.16	21.4	0.08	8.93	<0.01
M1W	5.2	0.04	5.4	0.02	8.89	<0.01
AbW	9.1	0.09	9.4	0.05	6.10	0.014
VcL	27.1	0.30	27.9	0.18	5.17	0.023
CbL	53.9	0.38	54.9	0.21	4.54	0.034
MaH	15.8	0.15	15.5	0.08	4.01	0.046
MW	29.3	0.23	29.9	0.14	3.62	>0.05
CL	3.4	0.04	3.4	0.02	1.12	>0.05
ZyW	32.7	0.28	33.1	0.16	0.96	>0.05
AL	33.3	0.20	33.5	0.12	0.91	>0.05
ML	34.3	0.21	34.5	0.13	0.52	>0.05
CW	2.8	0.04	2.7	0.02	0.39	>0.05
PoW	10.9	0.12	11.0	0.06	0.31	>0.05
GpW	19.8	0.13	19.8	0.07	0.24	>0.05
NcL	32.4	0.16	32.5	0.09	0.13	>0.05

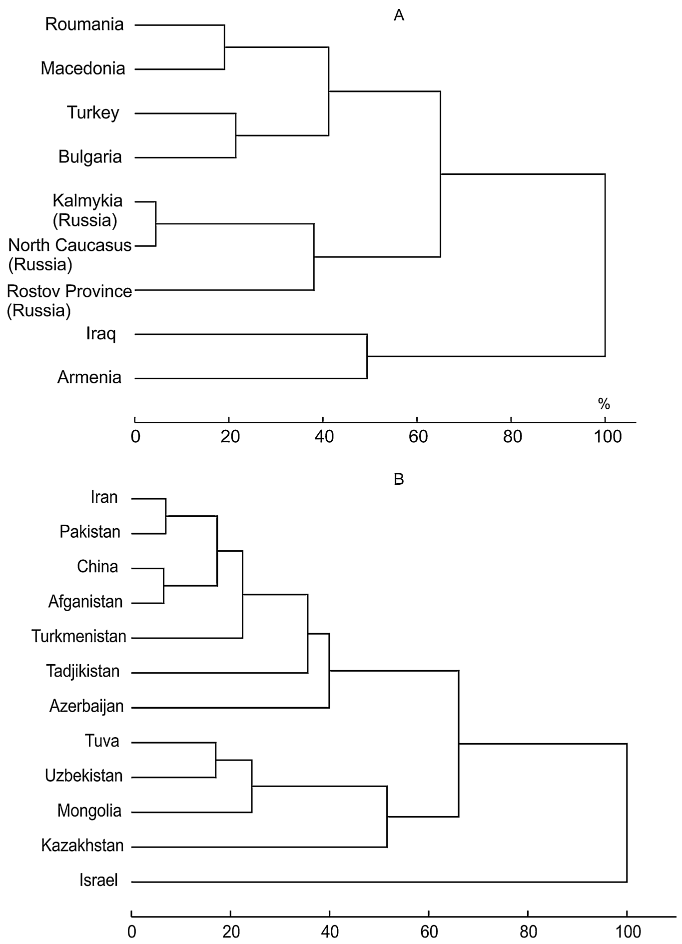

Fig. 4. UPGMA clustering of *V. peregusna* samples with more than 2 specimens based on the means of the coordinates of the morphospace models for the “western” (A) and “eastern” (B) morphological groups.

ern) (Table S7). A significant correlation of the SSD indices (0.89, $p < 0.001$) was found between two subclusters of the Eastern cluster. The comparison of SSD patterns in the Western and Eastern clusters revealed no significant correlation (0.45, $p = 0.02$), reflecting geographical variation in the SSD patterns.

In the Balkan-Anatolian subcluster, high degree of SSD was found for canine length (6.3), viscerocranium length (5.7) and height of the mandible (4.7). SSD was non-significant for some characters (minimal palatal width and postorbital width) in this subcluster. In two subclusters of the Eastern cluster, high SSD was found for canine length (4.9 and 4.6) and width (3.8 and 4.6), interorbital width (3.5) and the length of upper molar M1 (3.3 and 3.5).

Morphological diversity

The dimensionality of the SZM and SHM models varied between 2 and 4 for the different geographical groups. The entropy (H) of SZM and SHM models were higher in the western group than in the Eastern group of marbled polecat (Table 3). The diversity in the Balkan-Anatolian subcluster was significantly higher than that in the “northern” and “southern” subclusters of the Eastern group. The parameter MO was higher in the Eastern group (Table 3), which indicated a stronger constraint on morphological diversity in the eastern part of the species range.

The parameters of morphological diversity of the marbled polecat skull were within the typical range for all of the studied mustelid species (Fig. 7A–C, Table 3), was closer to that of the European polecat (*Mustela putorius*) and European badger (*Meles meles*) (Fig. 7D, Table S9).

Discussion

The variation in skull size and shape is a common phenomenon of the geographic variation in mammals. It can reflect the colonization history, the response to a gradient of environmental conditions, the genetic diversity, or a combination of historical and ecological factors (Eger, 1990; Baryshnikov and Puzachenko, 2012; Hernández-Romero et al., 2015; Korablev et al., 2015). The geographic variation of marbled polecat, both morphological and genetic ones, remains poorly studied yet. The dimensionality of SZM and SHM models depends on a variation of the parameters that are not correlated with a general skull size. The first dimensions of the SZM models for *V. peregusna* describe the general size variation, which is common in the morhometric variation of mammalian skulls and originates from the high correlation between parts of the cranium (see Wiig, 1986). Puzachenko (2016) analysed 76 species of the five mammalian orders (Carnivora, Artiodactyla, Perissodactyla, Rodentia, and Soricomorpha) and found out that the majority of SZM models had three dimensions whereas those of SHM – four dimensions. In the mustelids, the SZM models vary from two (*Mustela erminea, Meles leucurus, M. canescens*) to six (*M. eversmanii, M. lutreola, M. sibirica*) dimensions, while the SHM models vary from two (*Mustela erminea, Lutra lutra*) to four (*Mustela putorius, M. lutreola, M. sibirica*) dimensions (Table S9). The models’ dimensions in *V. peregusna* lie within the range of other mustelids.

The current analysis of the cranial variation in *V. peregusna* has revealed two geographic groups: the western and eastern ones. On the average, specimens from the western group turned out to be smaller than those from the eastern group. The level of morphological differentiation between these groups is not very high and could apparently be treated as subspecific.

The observed disparity in teeth sizes, the interorbital constriction, and the zygomatic width seems to reflect the difference in prey ranges between the western and eastern populations of *Vormela*, as

Table 3
Calibrated (per standard sample $N = 50$) parameters of morphological diversity of *V. peregusna* skulls.

Sample	N	Parameters of morphological diversity							
		size diversity morphospace				shape diversity morphospace			
		d	H bit/ specimen	H_d bit/ dimension/ specimen	MO	d	H bit/ specimen	H_d bit/ dimension/ specimen	MO
All species range (males and females)	245	4	8.83 ± 0.08	2.21 ± 0.025	0.19 ± 0.006	3	7.25 ± 0.07	2.42 ± 0.025	0.11 ± 0.007
males	161	4	8.50 ± 0.09	2.13 ± 0.022	0.19 ± 0.009	4	9.53 ± 0.05	2.38 ± 0.013	0.14 ± 0.003
females	84	4	8.62 ± 0.07	2.16 ± 0.017	0.19 ± 0.005	3	7.34 ± 0.04	2.15 ± 0.017	010 ± 0.005
Western cluster	62	4	8.60 ± 0.16	2.15 ± 0.041	0.21 ± 0.011	3	7.46 ± 0.05	2.49 ± 0.017	0.09 ± 0.011
“Balkan–Anatolian” subgroup	37	4	9.43 ± 0.20	2.36 ± 0.051	0.14 ± 0.007	3	7.58 ± 0.14	2.53 ± 0.046	0.09 ± 0.004
Eastern cluster	182	3	6.68 ± 0.10	2.23 ± 0.035	0.24 ± 0.005	2	4.84 ± 0.046	2.42 ± 0.023	0.14 ± 0.005
“southern” subgroup	106	2	4.66 ± 0.07	2.33 ± 0.033	0.14 ± 0.009	3	7.28 ± 0.08	2.43 ± 0.027	0.10 ± 0.006
“northern” subgroup	74	3	6.53 ± 0.016	2.18 ± 0.055	0.20 ± 0.014	3	7.05 ± 0.13	2.35 ± 0.044	0.13 ± 0.011

it was found in some other mustelids (Dayan et al., 1989; Dayan and Simberloff, 1994; De Marinis, 1995; Abramov et al., 2016b). The marbled polecat occupies a narrow range of habitats (arid open landscapes) throughout the species distribution range (Heptner et al., 1967; Abramov et al., 2016a). The climate continentality increases from the western (Europe, Middle East) to eastern (Cen-

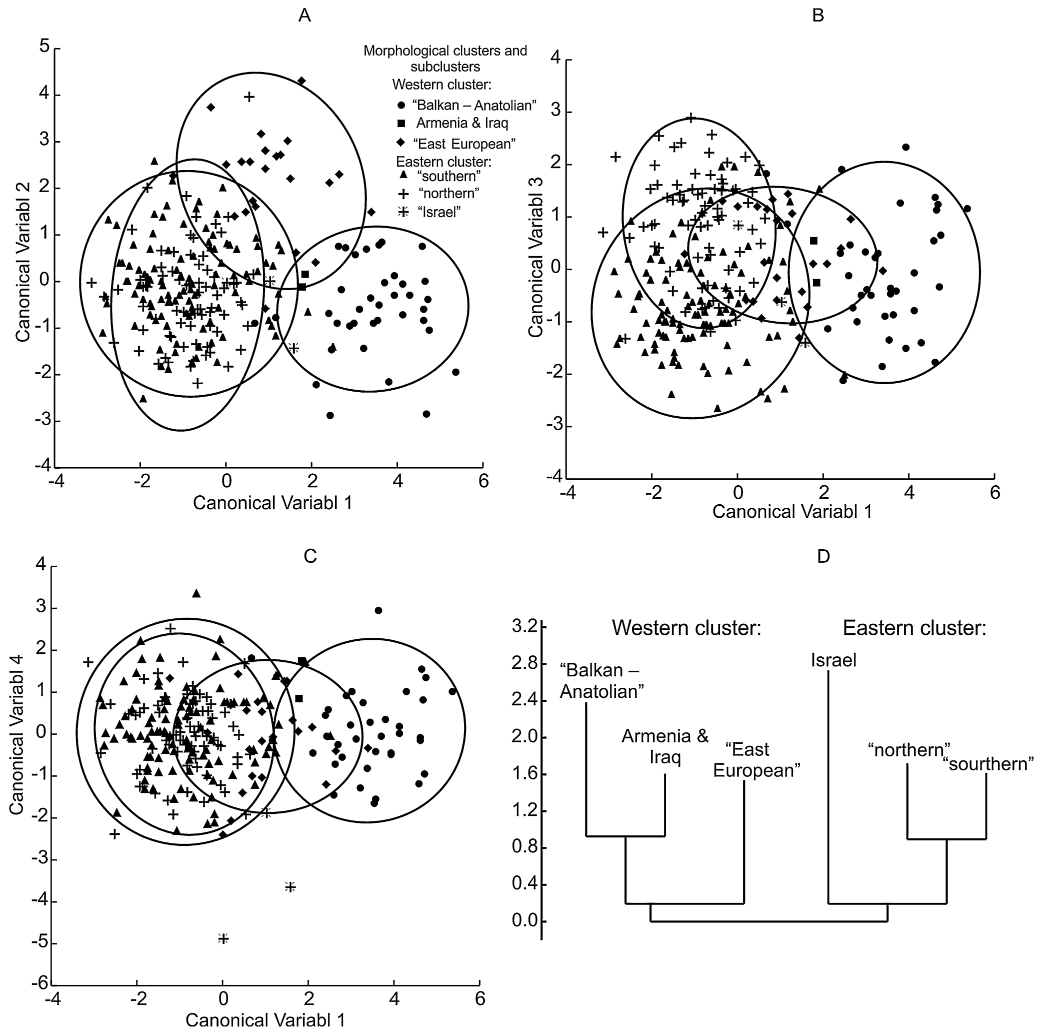

Fig. 5. Results of the discriminant analysis for six morphological subclusters of *V. peregusna* (A-C) and the NJ tree of their centroids (D).

tral Asia, China) part of the species range. Thus, the occurrence of the western and eastern groups of *V. peregusna* seems to depend on ecological and environmental parameters. We have also found out that there is a morphological differentiation between northern and southern populations, albeit not as well statistically significant as the meridional differentiation. Both in the western and eastern groups, the cranial measurements were larger in northern populations than in southern ones, being in concordance with the Bergmann rule. However, the hypotheses about the impact of climatic gradients on the skull size and shape should be interpreted with caution. For instance, in Russia, the otters *Lutra lutra* with smallest skulls were found in northern populations (Baryshnikov and Puzachenko, 2012). In Norwegian otters the skull sizes were shown to increase from south to north, whereas in Sweden they increase from north to south (Yom-Tov et al., 2006, 2010). The continental subspecies of the European badger *Meles meles taxus* has the largest size, whereas the Scandinavian subspecies *M. m. meles* and *M. m. milleri* have relatively small skulls (Abramov et al., 2009). It seems that these examples could be accounted for a colonization history or a phylogenetic pattern rather than for ecological reasons. Eger (1990) considered that the geographic variation in skull size of the North American stoat *M. erminea* could be better explained by climatic factors (temperature and precipitation), whereas the shape variation could be related to the existence of several Pleistocene refugia in Eastern Beringia. The pattern of geographic skull variation in *V. peregusna* seems to be indicative of its historical origin.

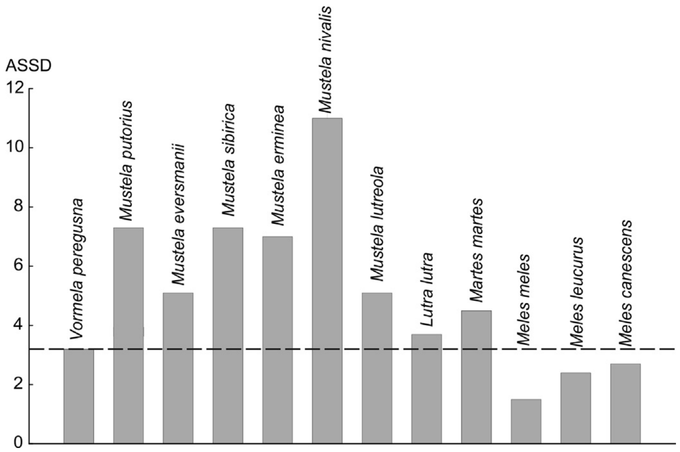

Fig. 6. Average SSD (ASSD) in the marbled polecat (*V. peregusna*) and several other mustelids.

As compared with other mustelids, the marbled polecat shows a relatively low degree of the sexual dimorphism, yet this parameter lies within the mustelid range (Fig. 6, Table S8). The sexual size dimorphism (SSD) is a common phenomenon in Mustelidae (Shubin and Shubin, 1975). The SSD in the mustelids varies from

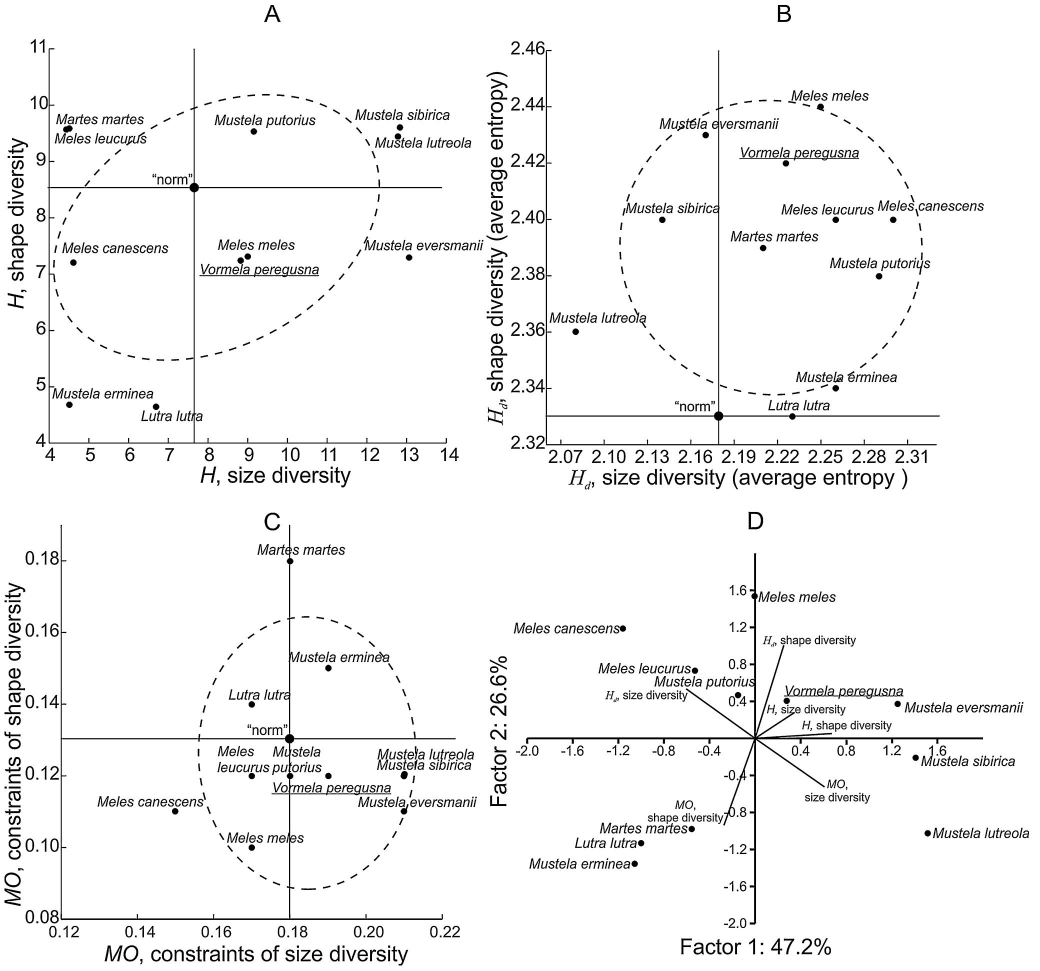

Fig. 7. Scatterplots of parameters of morphological diversity in *V. peregusna* skulls and some other mustelids: entropy (A), average entropy per one morphospace' dimension (B) and the measure of organization (C). Principal component analysis of the marbled polecat and some other mustelids based on parameters of morphological diversity (D). "Norm" – the average of parameters for 72 mammalian species according to Puzachenko (2016).

a relatively low one in *Meles* spp. and *Lutra lutra* to a high SSD in *Mustela nivalis* and *M. sibirica* (Table S8). Our results have confirmed the low SSD in *Vormela*, being in the agreement with previous data (Rozhnov and Abramov, 2006). Several hypotheses were proposed to explain the SSD in Mustelidae: the sexual selection hypothesis argues that a larger male size is beneficial in competition for a female, particularly, in the case of polygamous reproduction that is typical for small mustelids (Ralls and Harvey, 1985; Gittleman and van Valkenburgh,1997; Weckerley, 1998); the resource partitioning model treats the SSD as a result of differences in the diet between males and females (Dayan et al., 1989; Dayan and Simberloff, 1994; Gittleman and Van Valkenburgh, 1997). The available data on the marbled polecat behaviour are not enough to regard the relatively low distinctions in cranial properties between males and females as being related to a low aggressiveness or sociality of this species (see Rozhnov and Abramov, 2006). As compared with other similar-sized mustelids, the low SSD in the marbled polecat could have been caused by its narrow feeding preferences in both sexes and a more specialized behaviour which result in a less intra-specific competition with respect to habitat and food selection (Novikov, 1956; Stroganov, 1962; Heptner et al., 1967; Ben-David et al., 1991).

Most researchers suggested the complicated subspecific classification of *V. peregusna* (Table S1). However, the previous studies were based on a small number of specimens and qualitative comparisons (Ognev, 1935; Pocock, 1936; Heptner et al., 1967). In contrast, our study has compared a large set of specimens from many localities. Based on our data, we propose to divide *V. peregusna* into two subspecies. By and large our results are in the agreement with those of Ognev (1935), who split all the *Vormela* populations into the western and eastern groups, but the taxonomic content of Ognev's and our groupings are different. Our western group fits within the nominotypical subspecies *V. p. peregusna* (Güldenstädt, 1770), which includes *sarmatica* and *euxina* as synonyms. The available name for the eastern group is *V. p. koshewnikowi* Satunin, 1910. As evident from the list of synonyms given below, the three descriptive papers were published in 1910 (Birula, 1910; Miller, 1910; Satunin, 1910). Satunin's paper was published on 9 August 1910, whereas the paper by Miller was published on 19 August 1910, and the paper by Birula was published in October 1910 (see Abramov and Baryshnikov, 1990). Therefore, the names *koshewnikowi* and *tedshenika* proposed by Satunin (1910) have a priority over *alpherakii* and *negans*. The eastern subspecies, *V. p. koshewnikowi* Satunin, 1910; also includes the following synonyms: *alpherakii*, *chinensis*, *negans*, *obscura*, *ornata*, *pallidior*, *syriaca*, and *tedshenika*.

List of synonyms *

(* all misprints in names, years, and localities in the list of synonyms by Gorsuch and Lariviere, 2005 are corrected here).

Mustela peregusna Güldenstädt, 1770: 441. Steppes at lower Don River. Restricted to "Rostov Province, USSR" by Honacki et al. (1982).

Mustela sarmatica Pallas, 1771: 453. Between the Syzran and Medveditsa River, southern Russia [Syzran District, Samara Province, Russia].

Vormela koshewnikowi Satunin, 1910: 59. Ashgabat [Turkmenistan].

Vormela tedshenika Satunin, 1910: 60. Tedzhen Oasis [Tedzhen District, Turkmenistan].

Vormela negans Miller, 1910: 385. Ordos Desert, approximately 100 miles north of Yu-ling-fu, Shensi, China.

Vormela sarmatica alpherakii (not *alpherakyi* as usually written) Birula, 1910: 333. Ashgabat, Turkmenistan.

Vormela peregusna peregusna natio *intermedia* Ognev, 1935: 70. Starogladkovskaya Village, Terek River [= Shelkovskoi District, Chechnya, Russia]. Unavailable name (infrasubspecific rank).

Vormela peregusna euxina Pocock, 1936: 718. Malcoci, Dobrudscha in Rumania [= Tulcea County, Dobruja, Romania].

Vormela peregusna syriaca Pocock, 1936: 720. Tiberias [Israel].

Vormela peregusna ornata Pocock, 1936: 721. Vicinities of Lake Baikal. Likely in error, as the species does not occur there (Novikov, 1956; Stroganov, 1962). Two paratypes labelled as "Siberia."

Vormela peregusna pallidior Stroganov, 1948: 129. Semirechie, Kopal County [Aksu District, Almaty Province, Kazakhstan].

Vormela peregusna obscura Stroganov, 1948: 131. Valley of Vakhsh River, Kuibyshevsk District, Kurgan-Tube Province [= Jomi District, Khatlon Province, Tajikistan].

Vormela peregusna chinensis Stroganov, 1962: 378. China. An exact locality of the holotype is unknown. Stroganov (1962) restricted it to the "lower reach of the Hwang Ho River."

The western subspecies, *V. p. peregusna*, occurs in the south and south-east parts of Europe and the Middle East region. The eastern subspecies, *V. p. koshewnikowi*, is distributed from Middle and Central Asia, eastward to China. We have also placed the populations from eastern Transcaucasia (Iran and Azerbaijan) and Israel to this subspecies. However, the distributions of two subspecies in the southern and eastern parts of the Middle East needs further detailed studies. The specimens from Israel are very peculiar, but a small amount of the available material did not allow us to analyse their specificity.

In addition to the cranial characters (see Table 2), two subspecies differ in their fur colour patterns (see also Ognev, 1935; Heptner et al., 1967). The pelage of the nominotypical subspecies is relatively contrasted, dark brown. Light bands on the back of the head and neck are clearly distinct and are not joined at the front as a collar. The whitish ring around the mouth is small and usually does not connect to the white area under the eyes. There are either a few (1–4) or no yellowish spots on the belly. The eastern subspecies is characterized by lighter fur coloration, with the predominance of yellow colour pelage. There are many yellowish areas and spots in the shabrack. The neck bands usually join at the front as a complete collar. The whitish ring around the mouth is large and usually connects to the white area under the eyes. There are numerous large yellowish spots on the belly.

The pattern of geographic variation revealed in this study seems to reflect the Pleistocene history of species range formation, rather than a relationship to the climate conditions throughout the modern species range. The subfamily Ictonychinae is most likely to be of an African or African/Middle Eastern origin (Spassov and Spiridonov, 1993; Spassov, 2001; Koepfli et al., 2008; Sato et al., 2012). The *Vormela* lineage appears to have evolved in the steppe-like landscapes of southern Europe and Asia Minor in the late Pliocene or Early Pleistocene (Heptner et al., 1967; Kurtén, 1968; Spassov, 2001; Koepfli et al., 2008; Sato et al., 2012). The relatively high genetic diversity found within the Turkish populations showed that *V. peregusna* could have originated from the Anatolian part of Turkey (Ibis and Tez, 2014). Supposedly, during the late Pleistocene, the marbled polecat spread eastward to Central Asia and southward to the Middle East. The low variation of mtDNA found in the populations throughout Eurasia (except Anatolia) is evidence that this colonization could have occurred quickly, during a short period of time after the last glacial age (Rozhnov et al., 2008; Ibis and Tez, 2014). Our data have revealed a gradual decrease in the morphological diversity in *Vormela* skulls from the west to the east. This phenomenon could also be explained by the later origin of the eastern subclusters of the marbled polecat. Further investigations on the molecular biogeography of *V. peregusna* are needed to fully understand the migration routes and colonization history of the species.

Acknowledgements

We are thankful to Paulina Jenkins, Fatimat Tembotova, Natalia Lopatina, Bakhriddin Abdunazarov, Nikolay Spassov, David Harrison and Igor Pavlinov for giving access to the collections under their care. We thank Daisuke Koyabu and two anonymous reviewers for useful comments on previous drafts of this manuscript. This study was supported in part by the Russian Foundation for Basic Research (grants 16-04-00085, 16-54-50004) and the Zoological Institute' Program No. 01201351185.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.11.007.

References

Abramov, A.V., Baryshnikov, G.F., 1990. Catalogue of the type specimens collection of Zoological Institute, USSR Academy of Sciences. Mammals 2 (Carnivora, Proboscidea, Desmostylia. Zool. Inst. USSR Acad. Sci., Leningrad).

Abramov, A.V., Puzachenko, A.Yu., 2005. Sexual dimorphism of craniological characters in Eurasian badgers *Meles* spp. (Carnivora, Mustelidae). Zool. Anz. 244, 11–29.

Abramov, A.V., Puzachenko, A.Yu., 2006. Geographical variability of skull and taxonomy of Eurasian badgers (Mustelidae, *Meles*). Zool. Zh. 85, 641–655.

Abramov, A.V., Puzachenko, A.Yu., 2009. Spatial variation of sexual dimorphism in the Siberian weasel *Mustela sibirica* (Mustelidae, Carnivora). Russ. J. Theriol. 8, 17–28.

Abramov, A.V., Puzachenko, A.Yu., 2012. Species co-existence and morphological divergence in west *Siberian mustelids* (Carnivora, Mustelidae). Mamm. Stud. 37, 255–259.

Abramov, A.V., Puzachenko, A. Yu, Wiig, Ø., 2009. Cranial variation in the European badger Meles meles (Carnivora, Mustelidae) in Scandinavia. Zool. J. Linn Soc. 157, 433–450.

Abramov, A.V., Kranz, A., Maran, T., 2016a. *Vormela peregusna*. IUCN Red List of Threatened Species 2016, e.T29680A45203971.

Abramov, A.V., Puzachenko, A.Yu., Tumanov, I.L., 2016b. Morphological differentiation of the skull in two closely-related mustelids species (Carnivora: Mustelidae). Zool. Stud. 55.

Baryshnikov, G.F., Puzachenko, A.Yu., 2011. Craniometrical variability of cave bears (Carnivora, Ursidae). Quatern. Int. 245, 350–368.

Baryshnikov, G.F., Puzachenko, A.Yu., 2012. Craniometrical variability of the Eurasian otter (*Lutra lutra*: Carnivora: Mustelidae) from the Northern Eurasia. Proc. Zool. Inst. RAS 316, 203–222.

Baryshnikov, G.F., Puzachenko, A.Yu., Abramov, A.V., 2003. New analysis of variability of check teeth in Eurasian badgers (Carnivora, Mustelidae, Meles). Russ. J. Theriol. 1, 133–149.

Ben-David, M., Pellis, S.M., Pellis, V.C., 1991. Feeding habits and predatory behaviour in the marbled polecat (Vormela peregusna syriaca): 1. Killing methods in relation to prey size and prey behaviour. Behaviour 118, 127–143.

Birula, A., 1910. Contributions to systematics and geographic distribution of mammals. Ezhegodn. Zool. Mus. Imper. Acad. Nauk 15, 318–333.

Davison, M.L., Jones, L.E., 1983. Special issue: multidimensional scaling and its applications. Appl. Psychol. MeasurE 7, 373–514.

Dayan, T., Simberloff, D., 1994. Character displacement, sexual dimorphism and morphological variation among British and Irish mustelids. Ecology 75, 1063–1073.

Dayan, T., Simberloff, D., Tchernov, E., Yom-Tov, Y., 1989. Inter- and intra-specific character displacement in mustelids. Ecology 70, 1526–1539.

De Marinis, A.M., 1995. Craniometric variability of polecat *Mustela putorius* L. 1758 from North-Central Italy. Hystrix (n.s.) 7, 57–68.

Dempster, A.P., Laird, N.M., Rubin, D.B., 1977. Maximum likelihood from incomplete data via the EM algorithm. J. R. Stat. Soc. Ser. B 39, 1–38.

Eger, J.L., 1990. Patterns of geographic variation in the skull of Nearctic Ermine (*Mustela erminea*). Can. J. Zool. 68, 1241–1249.

Foote, M., 1990. Nearest-neighbor analysis of trilobite morphospace. Syst. Zool. 39, 371–382.

Gittleman, J.L., Van Valkenburgh, B., 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. J. Zool. 242, 97–117.

Gorsuch, A., Lariviere, S., 2005. *Vormela peregusna*. Mamm. Spec. 779, 1–5.

Güldenstädt, A.J., 1770. Peregusna, nova mustelae species. Nov. Comme. Acad. Sci. Imp Petropol. 14, 441–455.

Haken, H., 1983. An Introduction. Nonequilibrium Phase Transitions and Self-Organization in Physics, Chemistry and Biology. Springer-Verlag, Berlin, Heidelberg, New York.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Pal. Electr. 4 (1), 1–9.

Heptner, V.G., Naumov, N.P., Yurgenson, P.B., Sludsky, A.A., Chirkova, A.F., Bannikov, A.G., 1967. Mammals of Soviet Union Vol. 2 (1). Sirenia and Carnivora, Vysshaya Shkola, Moscow.

Hernández-Romero, P.C., Guerrero, J.A., Valdespino, C., 2015. Morphological variability of the cranium of *Lontra longicaudis* (Carnivora: mustelidae): a morphometric and geographic analysis. Zool. Stud. 54 (50).

Honacki, J.H., Kinman, K.E., Koeppl, J.W. (Eds.), 1982. Allen Press, Inc. and the Assoc. of Syst. Coll, Univ Kansas, Lawrence.

Hutcheson, K., 1970. A test for comparing diversity based on the Shannon formula. J. Theor. Biol. 29, 151–154.

Ibis, O., Tez, C., 2014. Phylogenetic status and genetic diversity of the Turkish marbled polecat, *Vormela peregusna*, (Mustelidae Carnivora: mammalia), inferred from the mitochondrial cytochrome *b* gene. Vertebr. Zool. 64, 285–294.

James, F.C., McCulloch, Ch.E., 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Ann. Rev. Ecol. Syst. 21, 29–166.

James, F.C., 1982. The ecological morphology of birds: a review. Ann. Zool. Fenn 19, 265–275.

Kendall, M.G., 1975. Rank Correlation Methods. Charles Griffin and Co., Ltd, London.

Koepfli, K.-P., Deere, K.A., Slater, G.J., Begg, C., Begg, K., Grassman, L., Lucherini, M., Veron, G., Wayne, R.K., 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biol. 6, 1–22.

Korablev, N.P., Korablev, M.P., Korablev, P.N., Tumanov, I.L., 2015. The factors of morphological variation in craniometrical traits of the American mink (*Neovison vison*). Russ. J. Biol. Invasions 6, 21–36.

Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29, 1–27.

Kupriyanova, I.F., Puzachenko, A.Yu., Agadzhanyan, A.K., 2003. Temporal and spatial components of skull variability of the common shrew, *Sorex araneus* (Insectivora). Zool. Zh. 82, 839–851.

Kurtén, B., 1968. Pleistocene Mammals of Europe. Weidenfeld & Nicolson, London.

McGhee, G.R., 2007. The Geometry of Evolution Adaptive Landscapes and Theoretical Morphospaces. Cambridge Univ. Press, Cambridge.

Miller, G.S., 1910. A new carnivora from China. Proc. US Natl. Mus. 38, 385–398.

Novikov, G.A., 1956. The carnivorous mammals of the USSR. Izd. Acad. Nauk SSSR, Moscow–Leningrad.

Ognev, S.I., 1935. The Mammals of the USSR and Adjacent Countries, vol. 3. Gosizdat, Moscow-Leningrad.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 3, 131–144.

Pocock, R.I., 1921. On the external characters and classification of the Mustelidae. Proc. Zool. Soc. Lond., 837.

Pocock, R.I., 1936. The polecats of the genera *Putorius* and *Vormela* in the British Museum. Proc. Zool. Soc. Lond. 106, 691–723.

Puzachenko, A.Yu., 2011. Information variables of morphometric diversity of mammals. In: Abstracts of IX Congress of Theriological Society of RAS, KMK, Moscow, p. 384.

Puzachenko, A.Yu., 2013. Invariants and dynamics of morphological diversity (A case study of mammalian skull). In: Dr. Sci. Dissertation, IPEE RAN, Moscow.

Puzachenko, A.Yu., 2016. The quantitative patterns of morphological disparity of mammalian skull. Arch. Zool. Mus. Moscow State Univ. 54, 229–268.

Ralls, K., Harvey, P.H., 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biol. J. Linn. Soc. 25, 119–167.

Rozhnov, V.V., 1999. Marbled polecat (*Vormela peregusna*). In: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralík, V., Zima, J. (Eds.), The Atlas of European Mammals. Academic Press, London, pp. 340–341.

Rozhnov, V.V., Abramov, A.V., 2006. Sexual dimorphism of marbled polecat *Vormela peregusna* (Carnivora: Mustelidae). Biol. Bull. 33, 144–148.

Rozhnov, V.V., Meschersky, I.G., Kholodova, M.V., 2006. Molecular genetic study of marbled polecat (*Vormela peregusna*, Carnivora: mustelidae). Dokl. Biol. Sci. 407, 567–570.

Rozhnov, V.V., Meschersky, I.G., Abramov, A.V., 2008. Geographical variation of the marbled polecat *Vormela peregusna* (Carnivora: mustelidae): molecular genetic study. Dokl. Biol. Sci. 418, 27–29.

Sato, J.J., Wolsan, M., Prevosti, F.J., D'Elía, G., Begg, C., Begg, K., Hosoda, T., Campbell, K.L., Suzuki, H., 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Mol. Phyl. Evol. 63, 745–757.

Satunin, K.A., 1910. Über die geographischen rassen des tigeriltisses. Zool. Anz. 36, 58–60.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. Univ Illinois Press, Urbana.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Technol. J. 27, 623–656.

Shepard, B.N., 1962. The analysis of proximities: multidimensional scaling with unknown distance function. Psychometrika 27, 125–140.

Shubin, I.G., Shubin, N.G., 1975. Sexual dimorphism and its pattern in mustelids. Zh. Obshch. Biol. 36, 283–290.

Spassov, N., Spiridonov, G., 1993. *Vormela peregusna* (Güldenstaedt, 1770) —Tigeriltis. In: Stubbe, M., Krapp, F. (Eds.), Handbuch Der Saugetiere Europas. Aula, Wiesbaden, pp. 817–855.

Spassov, N., 2001. Zorillas (Carnivora, Mustelidae, Ictonychini) from the Villafranchian of Bulgaria with a description of new species of Baranogale Kormos, 1934. Geodiversitas 23, 87–104.

Stroganov, S.U., 1948. New data on the systematics of marbled polecat (*Vormela peregusna* Gueldenstaedt). Proc. Zool. Inst. AS USSR 7, 129–132.

Stroganov, S.U., 1962. The mammals of siberia. Carnivora. Nauka Moscow.

Weckerley, F.W., 1998. Sexual size dimorphism: influence of mass and mating systems in the most dimorphic mammals. J. Mamm. 79, 33–52.

Wiig, Ø., 1986. Sexual dimorphism in the skull of minks *Mustela vison*, badgers *Meles meles* and otters *Lutra lutra*. Zool. J. Linn. Soc. 87, 163–179.

Wolsan, M., Sato, J.J., 2010. Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). Cladistics 26, 168–194.

Wozencraft, W.C., 2005. Order carnivora. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammals Species of the World. A Taxonomic and Geographic Reference, vol. 1, 3rd ed. Johns Hopkins Univ Press, Baltimore, pp. 532–628.

Yom-Tov, Y., Heggberget, T.M., Wiig, Ø., Yom-Tov, S., 2006. Body size changes among otters, Lutra lutra, in Norway: the possible effects of food availability and global warming. Oecologia 150, 155–160.

Yom-Tov, Y., Roos, A., Mortensen, P., Wiig, Ø., Yom-Tov, S., Heggberget, T.M., 2010. Recent changes in body size of the Eurasian otter *Lutra lutra* in Sweden. AMBIO 39, 496–503.