

Cranial Variation in the Siberian Weasel *Mustela sibirica* (Carnivora, Mustelidae) and its Possible Taxonomic Implications

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Alexei V. Abramov, Andrey Yu. Puzachenko, and Ryuichi Masuda (2018) Morphometric variation in 23 cranial characters of 555 Siberian weasels (*Mustela sibirica*) was studied across its whole distribution range. Most of the distribution range in Siberia and China is occupied by medium-sized weasels, whereas the eastern part of the species range - including the Russian Far East, Korea and eastern China - is occupied by the larger form. Specimens from the Pacific islands (Jeju and Tsushima) were morphologically closely related to the western form of *M. sibirica* than to the neighboring continental weasels. The western form can be treated as nominotypical subspecies *M. s. sibirica* Pallas, 1773, whereas the eastern form can be treated as *M. s. manchurica* Brass, 1911. Small-sized weasels from the eastern Himalayan area (Myanmar and southwestern China) form a distinct group within *M. sibirica*, and they were treated as a subspecies; *M. s. moupinensis* (Milne-Edwards, 1874). Specimens from the western Himalayas (Kashmir, Nepal and Sikkim) are morphologically distinct from all other populations of *Mustela sibirica* and can be treated as a separate species *Mustela subhemachalana* Hodgson, 1837.

Key words: Skull variation, *Mustela sibirica*, Subspecies, Taxonomy.

BACKGROUND

The Siberian weasel *Mustela sibirica* Pallas, 1773 has one of the largest distribution ranges in the Palearctic among small mustelid species, with the exception of the stoat *Mustela erminea* Linnaeus, 1758 and least weasel *M. nivalis* Linnaeus, 1766. *Mustela sibirica* is widely distributed across the East Palearctic, from Eastern Europe (Kirov Oblast and Tatarstan in Russia) eastward to the Pacific coast and southward to the Himalayas (from northern Kashmir eastward to northern Myanmar); however, the weasel does not occupy a large part of arid Central Asia (southern

Mongolia and northwest China) (Heptner et al. 1967; Abramov et al. 2016). It occurs in few Pacific islands (Jeju, Tsushima and Taiwan) and it has been introduced to the Japanese islands Honshu, Shikoku and Kyushu (Sasaki 2008). The southern and southwestern limits of its distribution range are poorly known: the records from Laos, Vietnam and Thailand are incomplete and unconvincing (see Abramov et al. 2016).

Geographic variation and intraspecific taxonomy of the Siberian weasel have been poorly investigated. Intraspecific variation in morphological characters, such as coat color and body size, has led to the description of many taxa

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of the species or subspecies rank (see Appendix 1). Across a wide species range there are more than 20 scientific names attributed to *M. sibirica*, and 11 of them have recently been recognized as subspecies (Wozencraft 2005). Most subspecific names are based on pelage characters only, however these characters (color intensity, expression of white and dark spots on the muzzle, etc.) have high individual and seasonal variations throughout most of Palearctic range of the species (Stroganov 1962; Heptner et al. 1967). All previous morphological and genetic studies on *M. sibirica* were based on a rather narrow set of samples, and no studies have covered the whole distribution range of this species.

The aim of the present paper is to study geographical variation across the Siberian weasels' whole distribution range and use any patterns it reveals to elucidate possible taxonomic interpretations. We do this using cranial characters, which are consistent across seasons.

MATERIALS AND METHODS

We have examined 555 (including 416 intact) adult *M. sibirica* skulls (450 males and 105 females) across the species' distribution range. The specimens were separated into 33 geographic samples (Appendix 2). Age classes were defined by scoring morphological features of skull structures (the development of crests, the obliteration of sutures, tooth wear and dentition) used in mustelids (Buchalczyk and Ruprecht 1977).

The studied specimens are deposited in the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), the Zoological Museum of Moscow State University (Moscow, Russia), the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia), B.M. Zhitkov Russian Research Institute of Game Management and Fur Farming (Kirov, Russia), the Natural History Museum (London, UK), National Science Museum (Tokyo, Japan), Swedish Museum of Natural History (Stockholm, Sweden), Shanghai Natural History Museum (Shanghai, China) and the Institute of Zoology and Genofunds of Animals (Almaty, Kazakhstan).

Twenty-three measurements were taken for each skull using digital calipers to the nearest 0.1 mm: condylobasal length (CbL), neurocranium length (NcL), viscerocranium length (VcL), palatal

length (PL), maxillary tooth-row length (MxtL), upper carnassial teeth Pm⁴ length (Pm4L), greatest length between oral border of the auditory bulla and aboral border of the occipital condyles (BcL), length of the auditory bulla (AbL), zygomatic width (ZyW), mastiod width of skull (MW), postorbital width (PoW), interorbital width (IW), width of rostrum (RW), greatest palatal width (GpW), width of the auditory bulla (AbW), width of upper molar M¹ (M1W), cranial height (CH), total length of the mandible (ML), length between the angular process and infradentale (AL), mandibular tooth-row length (MatL), length of lower carnassial teeth M₁ (m1L), height of mandible in the vertical ramus (MaH) and minimal palatal width (MpW). See Abramov and Puzachenko (2009) for the scheme of measurements.

For damaged skulls with incomplete sets of measurements, we used the expectation-maximisation (EM) algorithm (Dempster et al. 1977) to estimate the missing values. The missing data were estimated for males and females separately. In all cases, the missing completely at random hypothesis was accepted. EM uses an iterative process to estimate the means, covariance matrix and correlation of measures with missing values. Grubbs' two-sided test (Stefansky 1972) for revealing outliers in new variables was used. Statistical differences between the measures (average, variance and type of distribution) were tested by comparing the full data set including the missing values filled in by the EM method and the initial data set. No statistical differences were detected between the two data sets. We used estimated values for multivariate analysis only.

As a high degree of sexual size dimorphism (SSD) was observed in Siberian weasel skulls (Abramov and Puzachenko 2009 2012), we investigated the male and female samples separately.

Before the multivariate statistical analysis, all the measures were standardised to exclude the impact of the 'scale' on different measurements according to the following transformation:

$$\bar{x}_i = \frac{x_i - x_{\min}}{x_{\max} - x_{\min}}, \text{ where } \bar{x}_i \text{ is the standardised}$$

variable, \bar{x}_i , x_{\min} , and x_{\max} are observed, minimum, and maximum values of the i -th variable, respectively.

The square dissimilarity matrix contained the Euclidean distances matrix and the similarity matrix of Kendall's tau-b (corrected for ties) measure of association (Kendall 1975); these

were calculated among all pairs of specimens. Two multidimensional morphological spaces (morphospace) were constructed using the Nonmetric Multidimensional Scaling (NMDS) technique (Davison and Jones 1983; NCSS 2007 (Hintze 2007)) based on two types of morphological distance matrices (see more details on our approaches to multivariate statistical analyses in previous publications: Abramov et al. 2009; Baryshnikov and Puzachenko 2011 2012; Abramov and Puzachenko 2012 2016). These morphospaces were constructed to provide a compact representation of the morphological distances between skulls. The Euclidean metric, as a simple geometric distance in the multidimensional space, integrally describes the variability of size. The Kendall's rank measure of association describes, overall, the variability in skull proportions (shapes). The first type of model is based on the Euclidian distance matrix and describes skull size diversity ("size morphospace", SZM model); the second model is based on Kendall's tau-b measures matrix and describes the diversity in their shapes ("shape morphospace", SHM model). The 'best-minimum' dimensionality of an NMDS model was estimated based on 'stress formula 1' (Kruskal's stress) according to the procedure described by Abramov and Puzachenko (2005). In the text, dimensions of SZM based on the Euclidean distances metric were denoted as E1, E2, etc., and dimensions of SHM based on Kendall's rank measure were denoted as K1, K2, etc. The dimensions of SZM and SHM models were used as virtual variables in further geographical samples for UPGMA clustering (PAST v. 3.12, Hammer et al. 2001). We applied canonical discriminant analysis STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA) to clarify which specimens belonged to each morphological cluster.

RESULTS

The SZM model had three dimensions in samples of males and four in females; SHM models had three and two dimensions, respectively (Table 1). The first dimension of SZM for both genders described the general size variation for skulls and was associated with most cranial characters, except for postorbital width (for both sexes) and neurocranium length, interorbital width and minimal palatal width (in females only). These variables correlated with the second or third dimensions of SZM models. The first dimension

of the SHM model (K1) in males mostly correlated with the relative length of the viscerocranial part of the skull. The first dimension E1 in the female SZM model was equal to the E1 in the male model, while the equivalent of the K1 dimension of the male SHM model was K2 in the female model. The K1 dimension had a negative correlation in females with the relative dimensions of teeth.

The relative variance components in the variance of the SZM and SHM coordinates associated with the geographical "factor" were no more than 60% and 47% for the dimensions E1 of SZM models, for males and females, and 37-36% for the dimensions K1 of SHM models. This means geographical differences between specimens are manifested 1) not very clearly and 2) based mainly on the size of cranial characters.

The changes in the E1 and K1 dimensions in the geographical coordinates of males' multidimensional models are shown in figures 1a and 1b, which illustrate the presence of some spatial patterns of skull size and shape variation. We used the sample means of the dimensions E1, E2, E3 and K1 (selected based on their high relative variance values from Table 1) to construct a UPGMA tree for males (Fig. 1C). The cophenetic coefficient for this classification was not high (0.88), which reflects influences of non-hierarchical relationships between the main clusters. However, we choose three groups from the tree that we deemed reasonably distinct. The first cluster was the most separated from the rest of tree, and brings together samples from Nepal and India (G1). The second cluster combined samples mainly from the northern and northwest parts of the species range (G2a). Cluster G2b included the samples mainly from northeast and southeast parts of the range. Several samples ("Burma", "Tsushima", "Sichuan", "Jeju", and "Tyva") were selected for further testing by discriminant analysis. According to the test results, the specimen "Tyva" and "Jeju" most likely belonged to the morphological cluster G2a. According to discriminant analysis results (Appendix 3), the sample from Tsushima consisted of specimens that were similar to Siberian weasels from G2a and G2b. In general, Tsushima weasels had similar general skull sizes as members of G2a, but the shape of skull was more similar to the animals from the G2b cluster. Analysis showed the specimen from Sichuan Province (China) to be between the Burma cluster and cluster G2a. The members of all clusters, except "Nepal-Indian" weasels, were morphologically closely related to each other. The "Burma" Siberian weasels were

more closely related to the northwestern G2a cluster than animals from the G2b cluster. The main differentiation between two numerous G2a and G2b clusters was observed in the general skull size, while differentiation between them in the skull shape was weakly expressed (Fig. 1D).

The skull from Tibet was extremely large and clearly separated from all other samples (Fig. 2B). The samples equivalent to clusters G2a and G2b for males were very closely related in morphological features to females. Moreover, the comparison of cranial variation between males and females (Figs. 1D and 2B) revealed differences between G2a and G2b in sexual dimorphism. The Siberian weasels belonging to the northwestern G2a cluster had a relatively lower SSD than that in the eastern cluster G2b. This finding is in concordance with our previous study (Abramov and Puzachenko 2009). In addition, there was

also a low SSD in the “Nepal-India-Afghanistan” weasels.

There was a relatively small sample size of females, including five samples from the northwest part of the range occupied by weasels from cluster G2a and only one sample from the Russian Far East (Primorsky Krai, Appendix 2), the territory in which animals from the G2b group are mainly distributed. At the same time, there are several interesting specimens that originated from Tibet (Lhasa), India and Afghanistan. Results of UPGMA clustering (Fig. 2A) based on dimensions E1, E2, E4, K1, and K2 with the highest relative variance (Table 1), were further tested with the discriminant analysis (Appendix 3). The discriminant analysis showed that specimens from India and Afghanistan were closely related, despite significant variance in their characteristics.

Table 1. Description of the multidimensional morphological spaces for male and female Siberian weasel skulls. Correlation coefficients among the characters and dimensions of the SZM and SHM models (E, K) are shown; r^2 - coefficients of determination in the linear multiple regression models

Characters	Males							Females						
	SZM model			SHM model			r^2	SZM model				SHM model		r^2
	E1	E2	E3	K1	K2	K3		E1	E2	E3	E4	K1	K2	
CbL	0.96	-0.05	-0.04	0.47	0.05	-0.41	0.96	0.90	-0.13	0.02	0.11	-0.17	0.56	0.85
AL	0.95	-0.06	0.01	0.51	-0.06	-0.35	0.92	0.85	-0.06	-0.03	-0.12	-0.28	0.43	0.75
ML	0.95	-0.11	0.00	0.55	-0.05	-0.33	0.93	0.89	-0.09	0.02	-0.11	-0.26	0.48	0.81
PL	0.92	-0.07	0.01	0.50	-0.01	-0.41	0.89	0.86	-0.08	0.02	-0.06	-0.25	0.48	0.75
MaH	0.89	-0.05	-0.06	0.47	-0.01	-0.17	0.82	0.64	-0.22	-0.03	0.09	0.03	0.39	0.46
MW	0.88	-0.14	-0.14	0.52	0.02	-0.06	0.84	0.75	-0.32	-0.16	-0.20	0.03	0.53	0.78
MatL	0.86	0.10	0.09	0.31	-0.17	-0.43	0.80	0.77	0.29	0.03	-0.12	-0.57	0.30	0.70
MxtL	0.86	0.12	0.16	0.31	-0.23	-0.47	0.82	0.78	0.32	0.01	-0.03	-0.54	0.26	0.70
VcL	0.86	-0.33	0.07	0.71	-0.15	-0.22	0.82	0.78	-0.21	0.35	-0.17	-0.29	0.76	0.85
GpW	0.85	0.08	0.08	0.33	-0.26	-0.12	0.79	0.63	0.21	-0.09	-0.19	-0.29	0.21	0.56
BcL	0.83	-0.02	-0.05	0.32	0.18	-0.47	0.84	0.69	-0.11	0.11	0.56	-0.08	0.59	0.82
ZyW	0.83	-0.30	-0.05	0.63	-0.06	0.03	0.85	0.76	-0.29	-0.04	-0.14	-0.01	0.55	0.69
RW	0.82	-0.28	0.06	0.68	-0.20	-0.07	0.83	0.63	-0.35	0.21	0.03	0.07	0.60	0.58
AbL	0.78	-0.07	-0.02	0.32	0.20	-0.52	0.80	0.71	-0.10	0.02	0.55	-0.05	0.56	0.81
IW	0.77	-0.21	-0.27	0.53	0.00	0.06	0.77	0.45	-0.29	-0.18	-0.49	0.03	0.20	0.53
MpW	0.75	0.08	-0.24	0.27	0.02	-0.02	0.64	0.35	-0.30	-0.21	-0.20	0.14	-0.02	0.40
M1W	0.71	0.40	0.37	0.08	-0.50	-0.30	0.84	0.61	0.50	0.05	-0.17	-0.64	0.13	0.64
CH	0.68	0.28	-0.09	0.07	0.00	-0.12	0.59	0.36	0.22	-0.73	0.28	-0.03	-0.18	0.80
M1L	0.68	0.44	0.37	-0.04	-0.50	-0.33	0.89	0.67	0.51	-0.01	-0.15	-0.68	0.12	0.72
Pm4L	0.68	0.40	0.31	-0.03	-0.46	-0.30	0.76	0.62	0.64	0.09	-0.07	-0.78	0.12	0.80
AbW	0.64	-0.15	-0.24	0.32	0.24	-0.02	0.58	0.54	0.09	-0.33	0.16	-0.13	0.14	0.40
NcL	0.57	0.48	-0.19	-0.19	0.19	-0.27	0.72	0.26	0.13	-0.64	0.25	0.16	-0.31	0.62
PoW	0.29	0.56	-0.69	-0.29	0.17	0.25	0.93	-0.17	-0.26	-0.64	-0.30	0.39	-0.48	0.61
Components of variance, %														
Factor: "Region"	57.4	28.2	17.7	35.5	13.3	15.5		46.9	37.8	1.2	30.2	37.3	23.1	

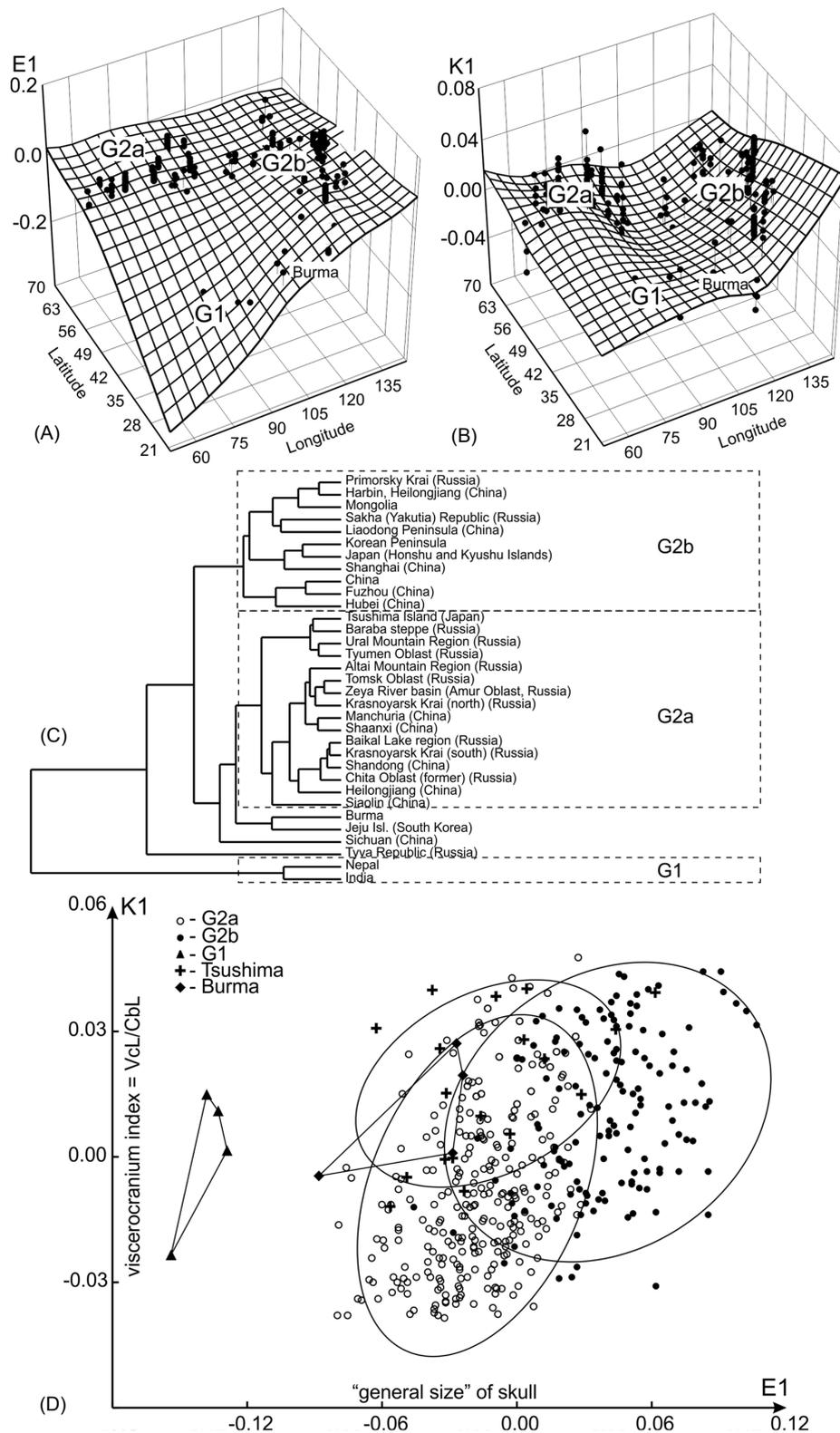


Fig. 1. (A, B) 3D plots of first dimensions of SZM (E1) and SHM (K1) models of male skull variation in geographical coordinates of the samples. (C) UPGMA dendrogram based on means of dimensions E1, E2, E3, and K1 and Euclidian distances between the male samples of *Mustela sibirica*. (D) Scatterplot of geographical groups (males) belonging to the morphological clusters G1 ("Nepal-India"), G2a, G2b, "Burma" and "Tsushima". The ellipses' horizontal and vertical projections onto axes are equal to sample mean (centroid) \pm highest value - lowest value \times 0.95.

DISCUSSION

Studies of morphometric variation make it possible to delimit species and geographic intraspecific variation, mainly in species with wide distribution ranges (Baryshnikov and Puzachenko 2011 2012; Hernández-Romero et al. 2015). The aim of the present study was to elucidate the geographical pattern of intraspecific skull shape and size variation in *M. sibirica* along its distribution range and use morphological differences between the local populations to interpret taxonomies. The results revealed a pattern that supports the hypothesis on cryptic diversity, because skull size and shape are clearly dimorphic when comparing specimens along the whole distribution range. The distribution of the clarified morphological groups of *M. sibirica* is mapped on figure 3.

According to most reviews (Ognev 1931; Heptner et al. 1967; Abramov 2000; Aristov and Baryshnikov 2001), there are two subspecies of Siberian weasel in Russia. Most of the species range in Siberia is occupied by medium-sized weasels belonging to the nominotypical form *M. s. sibirica* Pallas, 1773. The Far Eastern part of the species range is occupied by the larger subspecies, *M. s. manchurica* Brass, 1911. The distribution of two main groups of the Siberian weasel, G2a and G2b (see Fig. 1C and Fig. 3),

correspond well with that of two subspecies. We think that these clusters could be treated as subspecies *M. s. sibirica* and *M. s. manchurica*, respectively. The most essential distinctions between these two clusters were found for males, in viscerocranium length, condylobasal length, total length of the mandible, length between the angular process and infradentale, palatal length, mastoid width of skull, and height of mandible in the vertical ramus (see also Abramov 2000; Abramov and Puzachenko 2009). The female skull sizes were very similar among the subspecies, and differences were found mainly in tooth characters (maxillary tooth-row length, upper carnassial tooth length, width of upper molar M¹, length of lower carnassial tooth) and cranial height. The female skull sizes were very similar among the subspecies, and differences were found mainly in tooth characters (maxillary tooth-row length, upper carnassial tooth length, width of upper molar M¹, length of lower carnassial tooth) and cranial height. Both, the upper and lower carnassial teeth in *M. s. manchurica* females are some shorter than in *M. s. sibirica* (Pm4L: 5.67 ± 0.03 mm vs. 6.0 ± 0.02 mm, $p < 0.01$; M1L: 6.3 ± 0.03 mm vs. 6.5 ± 0.03 mm).

The geographical borders between these subspecies are not clear. Specimens that could formally be attributed to *M. s. sibirica* based on cranial characters are sometimes found within the

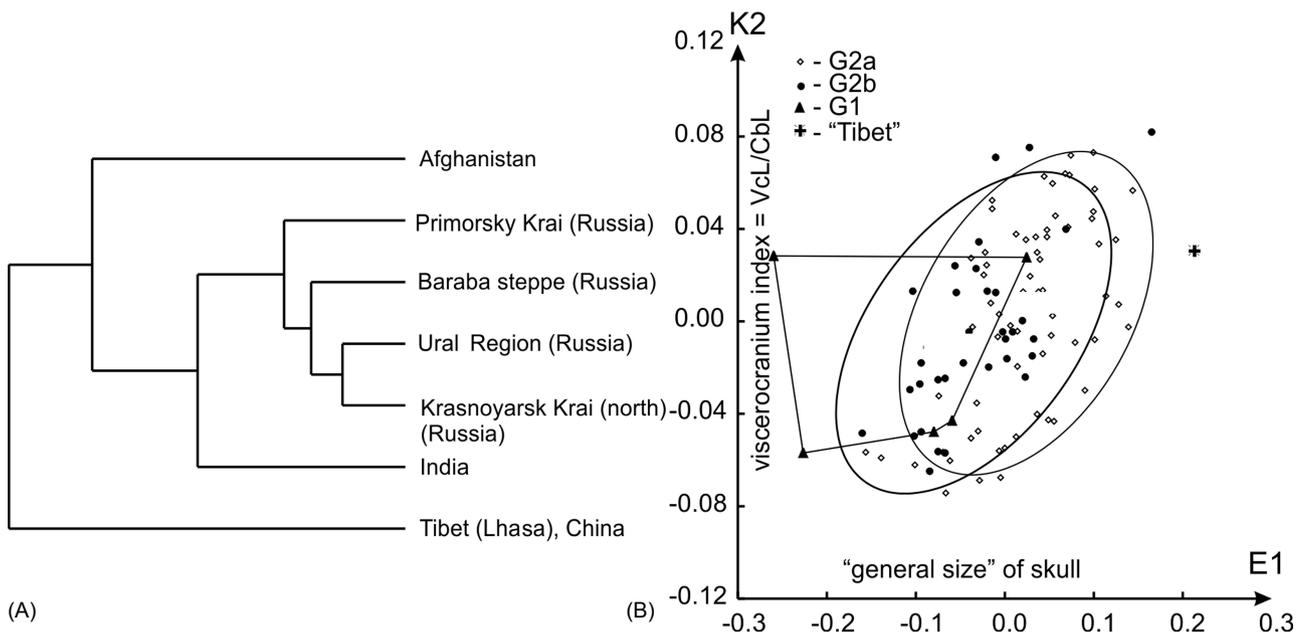


Fig. 2. (A) UPGMA dendrogram based on means of dimensions E1, E3, E4, and K1, K2 and Euclidian distances between the female samples of *Mustela sibirica*. (B) Scatterplot of geographical groups (females) belonging to the morphological clusters G1 ("India-Afghanistan"), G2a, G2b and "Tibet". The ellipses' horizontal and vertical projections onto axes are equal to sample mean (centroid) ± highest value - lowest value × 0.95.

range of *M. s. manchurica* and vice versa. We can thus assume that the eastern form is younger and expanded its range to the west of Siberia and to the south and southwest of Eastern Asia, probably during the Late Pleistocene and the Holocene. This hypothesis is in accordance with the recent geographical distribution of the G2a and G2b morphological forms (see Figs. 1C and 3).

The weasels from the Korean Peninsula are usually considered the distinct subspecies *M. s. coreana* (Domaniewski, 1926) (see Ellerman and Morrison-Scott 1951; Wozencraft 2005), but the subspecies was described based on pelage characters that are slightly different from the nominotypical form (Domaniewski 1926). According to our morphological classification, two subsamples from Korea are very closely related to the samples from Japan (Kyushu and Honshu) and the Shanghai region in China (Fig. 1C), and all of them could be attributed to the Far Eastern subspecies *M. s. manchurica*. Meanwhile, it has been reported that *M. sibirica* was introduced from the Korean Peninsula to Kyushu and Honshu in 1930s-40s (Sasaki 2008). Mitochondrial DNA phylogenetic data revealed that the introduced population of Siberian weasels in western Japan originated from a small founder population from the Korean Peninsula (Masuda et al. 2012). Therefore,

we can conclude that samples from the main Japanese islands originated from populations of the subspecies *M. s. manchurica*. The distributional patterns of *M. s. sibirica* and *M. s. manchurica* in the central and northern areas of mainland China could be affected by the widespread release of the Siberian weasels for rat-control in these parts of country (data from Bosco P. L. Chan, see Abramov et al. 2016).

The distinct taxonomic rank of *M. s. quelpartis* (Thomas, 1908) from Jeju Island (South Korea) was not supported by previous morphological data (Abramov 2006) and mitochondrial DNA analysis (Koh et al. 2012). Our study shows that specimens from Jeju Island are closely related to the western G2a cluster, though they are placed in a separate position on the classification tree (Fig. 1C). Nevertheless, our sample size is too small to conclude the morphological status of the weasels from this insular isolate.

We found morphological differentiation between Tsushima Island and continental populations that are in concordance with previous data (Abramov 2006; Suzuki et al. 2013). The Tsushima sample occupies an intermediate position between the continental *M. s. sibirica* and Far Eastern *M. s. manchurica* (Fig. 1D), being more closely related to the first subspecies based

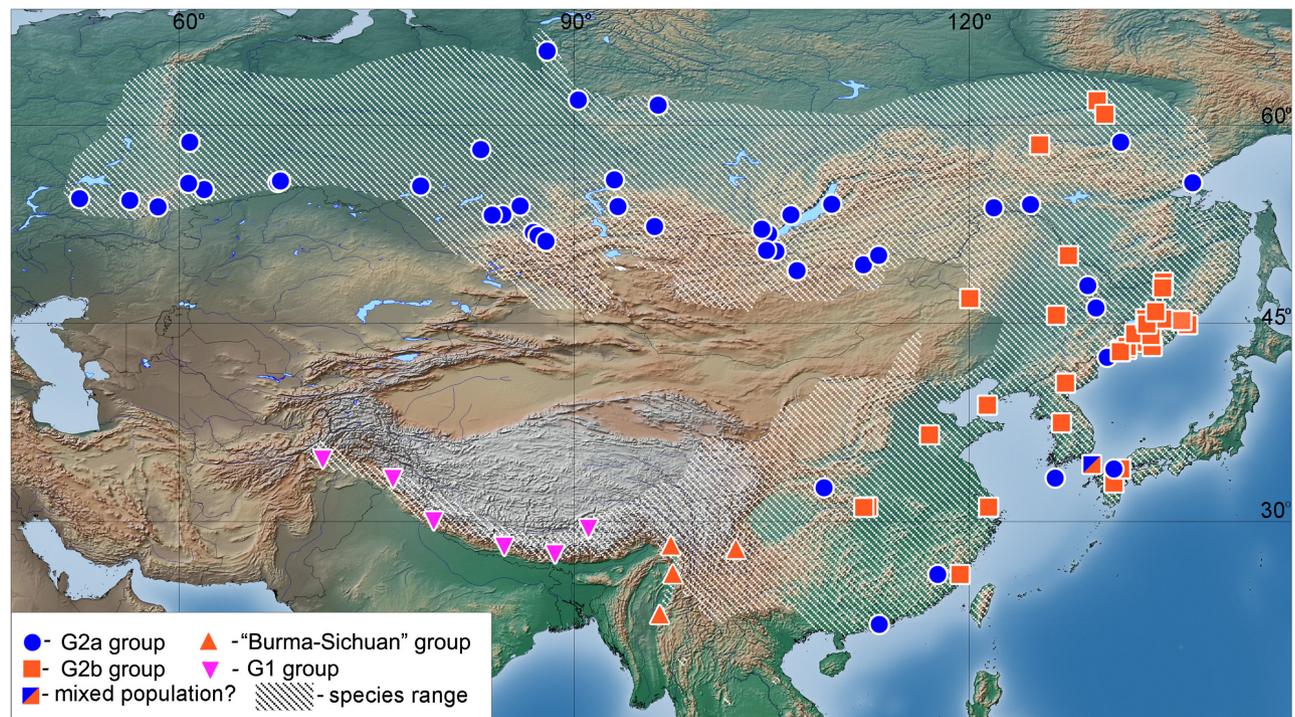


Fig. 3. Species range of the Siberian weasel *Mustela sibirica* (modified from Abramov et al. 2016) and localities of the specimens included in this study. The distribution of the morphological groups is shown.

on the general skull size. Based on genetic data, weasels from Tsushima were included in an *M. sibirica* clade in the phylogenetic trees, and formed a separate subclade closely relating to weasels from the Russian part (Urals and Transbaikalia) of the range (Masuda et al. 2012; Shalabi et al. 2017). In addition, Shalabi et al. (2017) investigated whole sequences of the mitochondrial genome and proposed that *M. sibirica* from Tsushima Island is likely a relict sister lineage to the main Russian continental lineage. This insular population may have multiple origins resulting from two different immigrant waves into the continent. The first wave may have consisted of animals close to *M. s. sibirica*, and the second one to *M. s. manchurica*.

Little is known about the Siberian weasels distributed in the eastern Himalayan part of the species range. Museum specimens from this region are very scarce, and only skins or badly broken skulls exist for most taxa of the Siberian weasel described from this region (see Appendix 1). Our analysis includes the type specimen *M. s. hamptoni* Thomas, 1921 as well as two additional skulls from Myanmar. On the general skull size, these weasels were clearly separate from *M. s. manchurica*, and smaller than the typical *M. s. sibirica*. Unlike the typical *M. sibirica*, they have an elongated rostral part of the skull. On the classification tree (Fig. 1C), weasels of Myanmar are clearly separated from the eastern cluster G2b and more closely related to cluster G2a. The additional discriminant analysis showed that the one specimen from Sichuan Province was most closely related to this group; therefore, we can assume that this subspecies is morphologically valid, and the available name is *M. s. moupinensis* (Milne-Edwards, 1874), which was described from southwestern Sichuan. The distribution range of this taxon covered the mountainous area in southwestern China and northern Myanmar.

Several taxa were described from mountainous regions of northern India, Bhutan and Nepal (Appendix 1). In our samples, all male specimens from India and Nepal were grouped in one cluster G1 (Fig. 1C), which was highly distant from all other Siberian weasels. This cluster was characterized by the smallest skull size, and placed separate from the main group of Siberian weasels on the scatterplot (Fig. 1D). Four female skulls from India were also separated from *M. sibirica* (Fig. 2), but this was not clear in males. In addition, one skull from Afghanistan was most closely related to the Indian sample. The single skull from Lhasa

(Tibet, China) has previously been identified as female, however it is possibly a small male. Within the female sample, this individual has a unique position in the classification tree and is separate from the other females on the scatterplot (Fig. 2). Therefore, if this result is a consequence of sexual size dimorphism only, the specimen from Tibet should be included in the “India-Nepal-Afghanistan” set. Based on these results, we have concluded that weasels occurring in these regions indeed belong to a separate species. On the basis of the Principle of Priority (ICZN 1999, Article 23.1), we could assign the name *Mustela subhemachalana* Hodgson, 1837 to this distinct species. The name *M. subhemachalana* was given to a specimen from Nepal by Hodgson (1837), based on coloration and external characters. Among other color features, the tail tip is darker than the rest of *M. subhemachalana*, contrary to the typical *M. sibirica* (Hodgson 1837; Pocock 1941). Additional study of the samples from the Himalayas is required to clarify the content and phylogenetic relationships of this taxon.

Further systematical revision combined with analysis of geographical variation in genetic markers is needed to investigate the extent to which the observed cranial diversity reflects phylogenetic relationships among currently unclassified species in the Siberian weasel complex.

CONCLUSIONS

An analysis of cranial variation in *M. sibirica* along its distribution range has demonstrated a clear separation between local populations. The results revealed a pattern supporting the hypothesis on cryptic diversity of Siberian weasel. Most of the distribution range in Siberia and China is occupied by the medium-sized weasel (treated here as nominotypical subspecies *M. s. sibirica* Pallas, 1773), whereas the eastern part of the species range, including the Far East, Korea and eastern China, is occupied by the larger form (*i.e.*, *M. s. manchurica* Brass, 1911). Specimens from the Pacific islands (Jeju and Tsushima) were morphologically closely related to the western form *M. s. sibirica* than to the neighboring *M. s. manchurica*. Small-sized weasels from the eastern Himalayan area (Myanmar and southwestern China) form a distinct group within *Mustela sibirica*, and we treated them here as a subspecies: *M. s. moupinensis* (Milne-Edwards, 1874). Specimens

from the western Himalayas (Kashmir, Nepal and Sikkim) are morphologically distinct from all other populations of *Mustela sibirica* and can be treated as a distinct species *Mustela subhemachalana* Hodgson, 1837.

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Appendix 1. List of *Mustela sibirica* synonyms. Type specimens of taxa included in the cranial analysis are marked in bold (download).

Appendix 2. Geographic sampling of the *Mustela sibirica* specimens used for morphological analysis (download).

Appendix 3. The posterior probabilities for specimens from the several geographical samples according to discriminant analysis (download).