Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 29 (1): 87–94, 2018
OPEN ACCESS
Available online at:
`http://www.italian-journal-of-mammalogy.it`
doi:10.4404/hystrix-00051-2018

Research Article

Shape variation of Palearctic mustelids (Carnivora: Mustelidae) mandible is affected both by evolutionary history and ecological preference

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Keywords:
Mustelidae
mandible
shape
geometric morphometrics
trophic specialization
feeding ecology

Article history:
Received: 26 May 2017
Accepted: 15 December 2017

Acknowledgements
Author thanks the curators and staffs of the Zoological Museum of Moscow Lomonosov State University (Russia), National Museum of Natural History (Kyiv, Ukraine) for kindly providing access to museum collections and help during the visits: Vladimir S. Lebedev and Pavel V. Putshkov, Dmitry V. Ivanoff. Author is especially grateful to Igor Dzeverin, Maria Ghazali, Pavel Gol'din, and Dmitry V. Ivanoff for discussion, help and valuable advice and to anonymous reviewers for their valuable comments that helped highly improve the manuscript.

Abstract

The lower jaws of 14 extant Palearctic mustelid species (290 specimens, Mustelidae,Carnivora) were analyzed through two-dimensional geometric morphometrics using 16 landmarks, in order to explore the relationship between mandibular size, shape and ecology within a comparative context. A principal component analysis and canonical variates analysis were performed on Procrustes fitted coordinates. PC and CV scores of the species means were also displayed with the phylogeny superimposed. Two types of the ascending ramus mandibulae are observed in mustelids — long and narrow one (sea otter-like), and short and wide one (badger-like). Both types of the ramus are present both in closely related species and in species with similar trophic specialization. Carnivorous mustelids (*Mustela*) differ from other trophic groups in relatively large carnassial, increased slicing area of m1, and high mandibular corpus under the canines. More omnivorous mustelids (*Martes*) have the longest and the thinnest lower jaw premolar region. But the lower jaw shape of *Martes flavigula* is closer to meat-eaters. The largest mustelids (*Enhydra lutris*, *Meles meles*, *Gulo gulo*) differ in lower jaw shape although they are all adapted to tough food but they have similar features as strengthened corpus under molar complex. Differences seem to be related with various food objects and with different ancestry and in the case of the wolverine with adaptation to predation. Piscivorous *Lutra lutra* is intermediate in all features and separate from the other groups. *L. lutra* with *Mustela lutreola* have the sloping forward ramus that with the posterior location of masseteric fossa possibly associates with fish consumption. The differences in mandibular traits of the studied species are partly determined both by their evolutionary history and ecological preferences.

Introduction

The mandible is a strong indicator for understanding dietary adaptations in both extant and extinct carnivores (Greaves, 1983, 1985). Two-dimensional shape analysis of mandibles in the geometric morphometrics could be used to explore mandible shape and its association with diet (Raia, 2004; Zelditch et al., 2004). Shape differences of carnivorous jaw (including mustelids) through a geometric morphometric approach have been reported in numerous studies (Meloro, 2011; Meloro et al., 2011; Figueirido et al., 2010, 2011, 2013; Prevosti et al., 2012; Catalano et al., 2014). Their study focused mainly on how mandible shape variation in Carnivora reflected adaptation related to masticatory function and feeding habits. In this work I research the mandible shape variation and adaptation of mandible to diet inside the family Mustelidae.

Extant mustelids display extensive ecomorphological diversity, reflecting the adaptation to different habits and habitats (Koepfli et al., 2008). Generally mustelids, like felids, are solitary hunters killing with a single, penetrating bite. Their jaws are short and powerful and adapted to delivering an accurately placed death bite, focusing mostly on the cervical regions of the prey in order to effect death quickly by neural distress (Ewer, 1973; Biknevicius and Van Valkenburgh, 1996). Mustelids have one of the most powerful bite and more powerful neck musculature among carnivores (Radinsky, 1981a). A high degree of variation is found in dietary strategies, with some species being actually extremely meat-eaters (representatives of the genus *Mustela*), more omnivorous that use a significant amount of invertebrate prey and plant food (genus *Martes*), piscivorous (*Lutra*), and species that eat hard food objects (*Enhydra*, *Gulo*, *Meles*) (Abelentsev, 1968; Ewer, 1973; Aristov and Baryshnikov, 2001). A similarity of feeding ecology within each genus has been shown by these authors.

Dietary hardness and prey size are the main factors affecting the jaw apparatus of Mustelidae. Different feeding behaviors should be reflected in observed differences of jaw shape. However, the design of bone should be recognized as a compromise between mechanical and ancestral factors (Biknevicius and Ruff, 1992) or phylogenetic constraints (Figueirido et al., 2013). Functional aspects, such as diet, are a key factor in the evolution of the carnivore mandible, but also that there is a phylogenetic pattern that cannot be explained by differences in diet alone (Prevosti et al., 2012). It is not clear, whether phylogenetic signal is present in variation of lower jaw shape in Mustelidae or this variation is associated solely with ecological specialization.

The purposes of the present study are: (i) to describe mandible shape differences of the Palearctic Mustelidae through a two-dimensional geometric morphometric approach using a sample of extant species, (ii) to find out how dietary adaptations of mandible are linked to evolutionary history of the groups within this taxon and (iii) to describe quantitatively the trophic specializations of jaw apparatus.

Materials and methods

Mandibles of 290 specimens from 14 species of extant Palearctic mustelids, have been used in geometric morphometric analysis (Tab. 1). I selected only adult and wild caught specimens with fully erupted dentition of both sexes and from different localities. Similar numbers of individuals of each species were sampled. The specimens were collec-

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Hystrix, the Italian Journal of Mammalogy ISSN 1825-5272

doi:10.4404/hystrix-00051-2018
31st May 2018

Table 1 – The studied species and their feeding categories. The feeding classification is from Christiansen and Wroe (2007): 2, omnivores; 3, piscivorous; 4, meat eater specializing in small prey; 5, meat eater specializing in medium-sized prey; 6, meat eater specializing in large prey.

Species	Number of studied specimens	Feeding classification
Sea otter, *Enhydra lutris* (Linnaeus, 1758)	18	3
Wolverine, *Gulo gulo* (Linnaeus, 1758)	19	6
River otter, *Lutra lutra* (Linnaeus, 1758)	20	3
Badger, *Meles meles* (Linnaeus, 1758)	18	2
Pine marten, *Martes martes* (Linnaeus, 1758)	24	4
Stone marten, *Martes foina* (Erxleben, 1777)	23	2
Sable, *Martes zibellina* (Linnaeus, 1758)	22	4
Yellow-throated marten, *Martes flavigula* (Boddaert, 1785)	19	4
White polecat, *Mustela eversmani* Lesson, 1827	23	6
Black polecat, *Mustela putorius* Linnaeus, 1758	24	5
European mink, *Mustela lutreola* (Linnaeus, 1761)	23	5
Siberian weasel, *Mustela sibirica* Pallas, 1773	19	5
Ermine, *Mustela erminea* Linnaeus, 1758	20	6
Weasel, *Mustela nivalis* Linnaeus, 1766	18	6

ted at the National Museum of Natural History (NMNH, Kyiv) and the Zoological Museum of Lomonosov State University (ZM, Moscow).

Mandibles were photographed with a Canon Power Shot SX200IS digital camera in lateral view, oriented with the longest axis of the mandible parallel to the photographic plane. I focused only on the left lateral mandibular side unless it was incomplete or unavailable (8% of the overall sample), I used samples of the right side.

On each mandible photo, a subset of 16 landmarks has been identified and digitized with the software `tpsDig2` (Rohlf, 2010). Landmarks 1 to 6 and 13 to 16 are on the corpus mandibulae, whereas landmarks 7 to 12 are on the ramus mandibulae (Fig. 1). Most of the recognized landmarks are type 2 or type 3 (landmarks 13–16) according to Bookstein (1991).

Specimens were aligned using a full Procrustes fit and projecting the data to the tangent space by orthogonal projection (Dryden and Mardia, 1998; Klingenberg, 2011). Aligning by the principal axis of the mean configuration was used. To examine the main features of shape variation in a sample of specimens (Zelditch et al., 2004) and the arrangement of species in morphospace, principal component analysis (PCA) was performed from the covariance matrix of the aligned coordinates of 290 specimens from 14 species analysed. The major dimensions of shape variation around the mean shape were also explored for some species. Thin plate splines have been applied to visualize shape variation as a wireframe graph. These analyses were performed with MorphoJ 1.04a (Klingenberg, 2011). Canonical variates analysis (CVA) was employed to assess how well the species and trophic groups could be separated based on mandible shape. Species or trophic group assignment was cross-validated by jackknifing procedure. Canonical variates were calculated using a sub-selection of the first five PCs (they explain 83.9% variance). Pairwise squared Mahalanobis distances were estimated for mustelid species and trophic groups; *p*-values for these differences were assessed using the sequential Bonferroni technique. CVA and the estimation of squared Mahalanobis distances were performed on PAST 2.17 (Hammer et al., 2001).

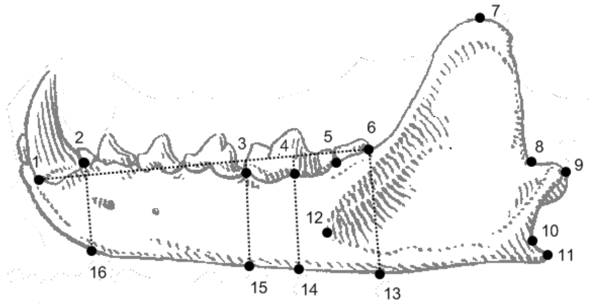

Figure 1 – The position of landmarks on a mandible outline of *Mustela lutreola*.
1, intersection of canine anterior edge and dental bone; 2, intersection of canine posterior edge and dental bone; 3, intersection of carnassial anterior edge and dental bone; 4, projection of the protocone cusp on the m1 baseline; 5, intersection of carnassial posterior edge and dental bone; 6, posterior edge of dentition; 7, tip of the coronoid process; 8, the dorsal extreme between coronoid and condylar process; 9, the most lateral extreme point of the condylar process; 10, the posterior extreme between condylar and angular process; 11, the most lateral extreme point of angular process; 12, the most anterior point of masseter fossa; 13, intersection of the perpendicular to line 1–6 through landmark 6 with ventral edge of mandible; 14, intersection of the perpendicular to line 1–6 through landmark 4 with ventral edge of mandible; 15, intersection of the perpendicular to line 1–6 through landmark 3 with ventral edge of mandible; 16, intersection of the perpendicular to line 1–6 through landmark 2 with ventral edge of mandible. 1–2, anteroposterior diameter of c1; 2–3, length of the premolar row; 3–6, length of the molar row; 2–16, thickness of the mandibular corpus under the canine; 3–15, thickness of the mandibular corpus under the beginning (origin) of the molar row; 4–14, thickness of the mandibular corpus under cutting part of the molar complex; 6–13, thickness of the mandibular corpus under chewing part of the molar complex. The picture of marten mandible is adapted from Novikov (1956).

It was shown that sex differences are pretty important source of variation in mustelids (Dayan and Simberloff, 1994; Loy et al., 2004). The effect of sexual dimorphism in mustelid mandible size and shape has been tested using ANOVA with size or shape as response variable while species and sex as factors. For pairwise comparison mandible shape of males and females of one species with males and females of other species, cross-validation in discriminant function analysis (DFA) was used in MorphoJ (Kovarovic et al., 2011). The analysis was not performed for four species (*Meles meles*, *Mustela lutreola*, *Mustela putorius* and *Mustela eversmani*) because of the lack of information about sex of specimens. Also the analysis was performed not for all specimens of other species for the same reason.

Two-way ANOVA was used to validate the effects of sex and species differences on mandible size. Model testing was performed using the `gvlma` program (Pena and Slate, 2014). The testing showed that the linear model assumptions are not satisfied for these data, therefore permutation test was used to verify the results using `lmPerm` program (Wheeler and Torchiano, 2016). Variance components were obtained using the `VCA` program (Schuetzenmeister, 2016). All these calculations were performed using the R software (R Core Team, 2016). The effects of species, sex and diet on multiple shape (represented by Procrustes coordinates) were evaluated using two-way parametric ANOVA in MorphoJ.

To analyze scaling effects on shape, shape was regressed on size; $\log_{10}$–transformed mandible length was used as a proxy for size. The mandible length was measured as the distance from the anterior edge of the incisors alveoli to the posterior edge of the condylar process. This distance was used to provide a measure of mandible size less abstract than centroid size. The relationship between shape and size was tested for statistical significance using a generalized Goodall's F test, which measures the ratio of explained to unexplained variation in units of Procrustes distance. I also tested the impact of size on a shape for each single species to understand how it changes between species. To test for differences in allometric trajectory, angular comparisons of vector directions of each species with the whole sample were performed.

To investigate whether the morphometric data contain a phylogenetic signal, I used a permutation approach for the Procrustes coordinates for all observations (Klingenberg and Gidaszewski, 2010) using the phylogenetic tree of Koepfli et al. (2008) with a nearly complete generic-level phylogeny of the Mustelidae using a data matrix comprising 22 gene segments. I also display scatter plots of the taxon means of PC scores with the phylogeny superimposed according to the reconstructed ancestral values.

For each species a feeding category was taken from the literature (Christiansen and Wroe, 2007). Diet categories have been assigned as omnivores, piscivorous, meat eaters specializing in small prey (weighing up to 20% of the predator's own body mass), meat eaters specializing in medium-sized prey (up to the predator's own body mass), and meat eaters specializing in large prey (frequently exceeding the predator's own body mass). For the list of species and their feeding category see Tab. 1.

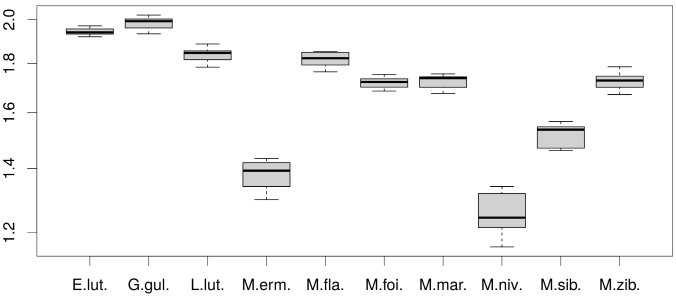

Figure 2 – Mandible size distribution in Palearctic mustelid species. Black string is median, grey box denotes interquartile range, whiskers denote minimum and maximum values. The scaling of Y-axis is logarithmic.

Table 2 – Analysis of Variance. The influence of sex and species, and interaction between the two on mandible size.

	Df	SS	MS	No. of Iterations	p
species	9	7.4897	0.8322	5000	<0.0001
sex	1	0.0817	0.0817	5000	<0.0001
species × sex	9	0.0126	0.0014	5000	0.0266
Residual variation	147	0.0933	0.0006		

Results

Sexual dimorphism in Palearctic mustelids

Mustelid species significantly differ in mandible size (Fig. 2, Tab. 2, $p<0.0001$). Males and females also highly significantly differ in mandible size ($p<0.0001$) and interaction between taxonomy and sex in mandible size is significant too ($p=0.01$).

Variance partitioning showed that species impact is the highest (contribution of species is 96.6%). The contributions of sex and interaction between sex and species are significant but too small (2% and 0.2%, respectively) in comparison with the contribution of taxonomy, so later in this work they are not considered.

Differences in the mandible shape of males and females within a species are not significant for all studied species except for *Mustela sibirica* ($p=0.008$). Pairwise comparisons showed that males and females of one species significantly differ in mandible shape from males and females of other species except for pair of females of weasel and ermine ($p=0.396$).

The influence of taxonomy, sex, diet and phylogeny on mandible shape

Procrustes ANOVA is significant for taxonomy (F=66.71, $p<0.0001$), sex (F=1.74, $p=0.0005$) and diet (F=33.2, $p<0.0001$). The effect of sex differences on mandible shape is significant in the studied mustelid but is not noticeably compared to species and diet differences.

The permutation tests revealed a statistically significant phylogenetic signal present in the mandible shape data ($p=0.0187$, randomization rounds: 10000).

Multivariate variation in mandible shape of Mustelidae

The principal component analysis (PCA) applied to the sample of 290 lower jaws extracts 28 principal components from 16 landmarks. The first three PCs accounted for 69.4% of the total variation.

The first two PCs explain 54.1% of total variance. They are basically associated with the shape changes in the mandibular ramus, the premolar row length, and with displacement of the masseteric fossa (Fig. 3a).

PC1 (30.1% of the total variance) and PC2 (24% of the total variance) separate *M. meles* (negative scores with maximum absolute value of PC1), *Enhydra lutris* (maximum positive value of PC2) and *Lutra lutra* (nearly maximum negative scores of PC2) from the other mustelids (Fig. 3b). *E. lutris* and *M. meles* are opposite in PC1. Mandibles with extreme negative scores of PC1 have widening of mandibular ramus (the angular process is placed more backward and coronoid process is placed more downward). Extreme positive scores of PC2 are associated with elongation of mandibular ramus, the coronoid process is placed more upward and backward. Accordingly the coronoid process varies its position relative to the corpus area, being projected more anteriorly in *Martes* specimens but more posteriorly in *Mustela* specimens, and most posteriorly in *E. lutris* (Fig. 3b). Despite the fact that *E. lutris* and *L. lutra* are in one clade they are opposite in PC2. Unlike *L. lutra*, *E. lutris* has displacing backward masseteric fossa and mandibular ramus tip, shortened mandibular corpus and elevated articular process. *Gulo gulo* is located among *Mustela* in the morphospace of first two axes. PC1 correlates with mandible length (R^2=17.4%, $p<0.0001$) whereas PC2 very poorly correlates (R^2=1.8%, $p=0.023$) with mandible length.

The third PC (15.2% of the total variance) gives some interesting distributions. PC3 describes changes in the premolar row length and height, slicing area and m2 length (Fig. 4a) and separates the meat-eaters (*Mustela*, *Gulo*) from the omnivorous mustelids (*Martes*). Meat-eaters, as opposed to omnivorous, have shorter and higher premolar region, larger carnassial (due to the larger slicing area) and lesser m2. *G.*

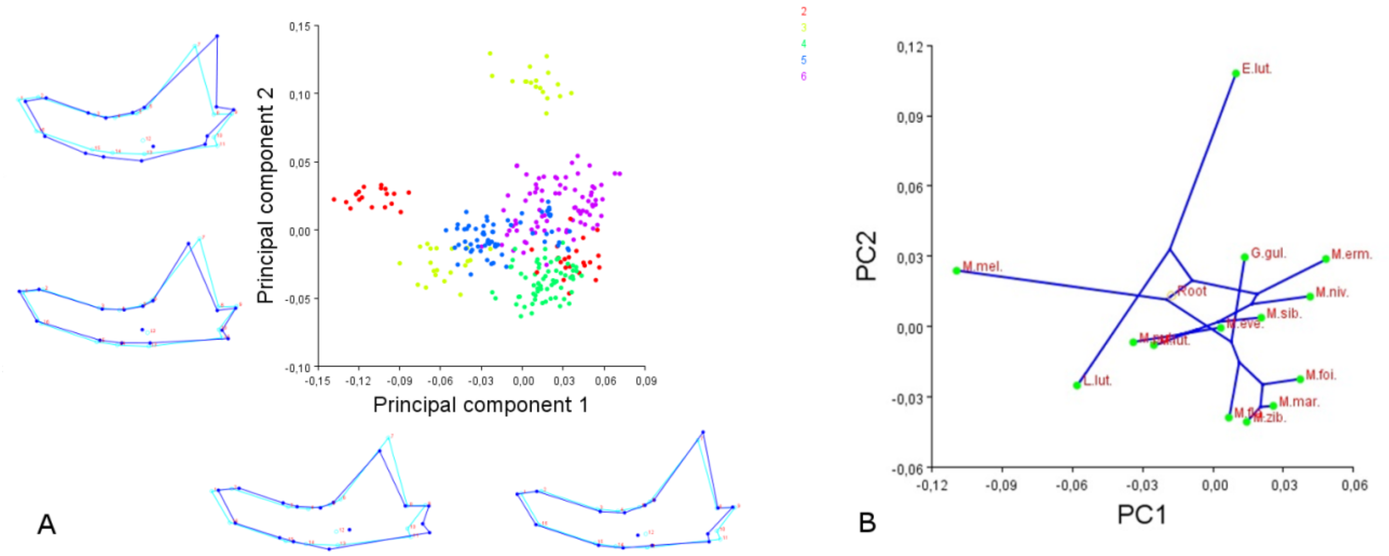

Figure 3 – Mandible shape variation along the first two principal components. A, distribution of mustelid specimens in the morphospace of PC1 and PC2 showing the distribution of diet classes; B, distribution of species average configurations with mapping of phylogeny. Mandible wireframes show the extreme shape changes of PCs from the consensus shape.

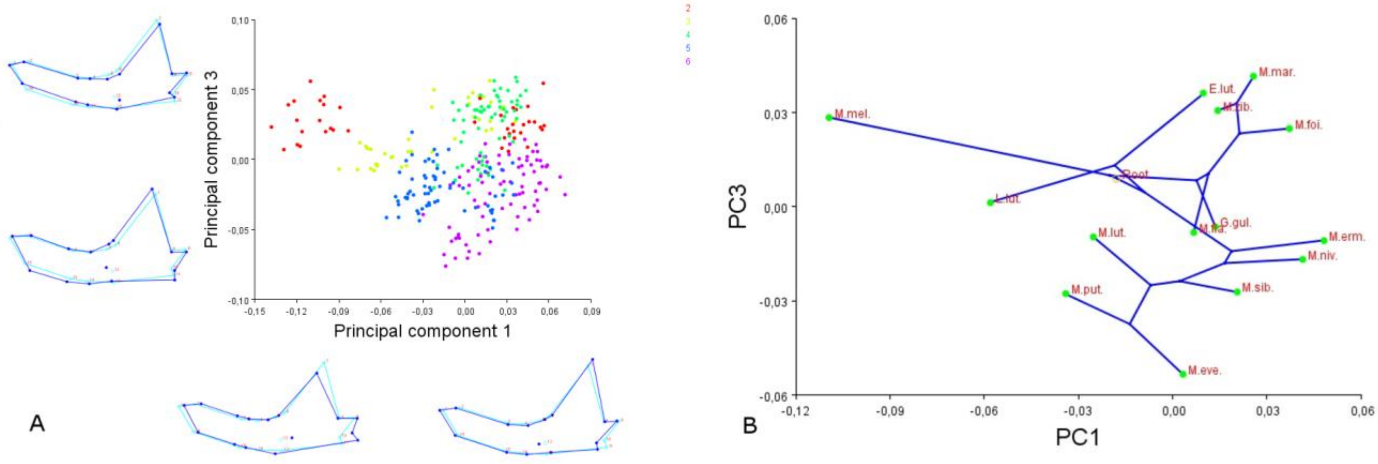

Figure 4 – Distribution of mustelid specimens in the morphospace of PC1 and PC3. A, distribution of mustelid specimens in the morphospace of PC1 and PC3 showing the distribution of diet classes; B, distribution of species average configurations with mapping of phylogeny. Mandible wireframes show the extreme shape changes of PCs from the consensus shape.

gulo, a close relative of *Martes*, is also close to the *Mustela* along PC3 in length and height of mandibular corpus and proportions of the different parts of the molar complex. Noteworthy yellow-throated marten (*M. flavigula*) is placed closer to meat-eaters along PC3 (Fig. 4b) though the other *Martes* are usually omnivorous.

Interspecific and dietary differences

CVA extracted 13 shape data (CVs) from the 16 landmarks, the first three CVs explain 78.6% of the total variance. The first two CVs explain together 59.6% of total variance and they clearly separate specimens into four groups: (i) *Martes*, (ii) *Mustela* + *Gulo*, (iii) *Lutra*, (iv) *Meles* + *Enhydra*. *Mustela* group and *Martes* group overlap widely on the canonical axes (Fig. 5a). *M. meles* and *E. lutris* have the extreme positive scores of the first two axes. They present the shortest mandibles with thin anterior and thick posterior region of corpus and most reduced molar slicing region. *Martes* and *Meles* that are classified to the same trophic group by Christiansen and Wroe (2007) are very distant from each other in the first two axes. Omnivorous *Martes* are opposite to meat-eaters *Mustela* in length of premolar region. The wolverine is among the *Mustela* in the mandible shape.

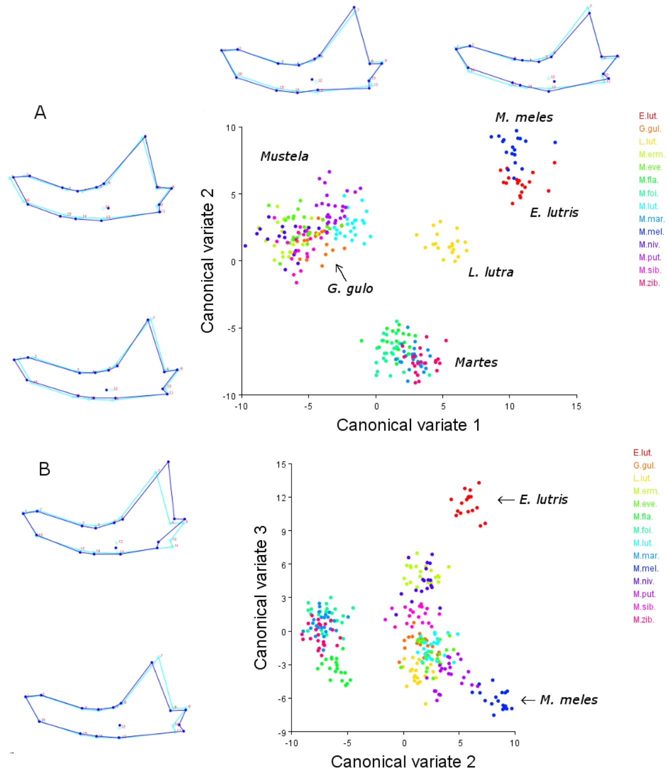

Figure 5 – Distribution of mustelid specimens in the morphospace of the first three canonical variates: A, in the morphospace of CV1 and CV2; B, in the morphospace of CV2 and CV3. Shape changes are shown as the mandible wireframe against the consensus shape.

Sea otter and badger reserve extreme positive and negative scores of CV3 (19% of total variance) associated with mandibular ramus shape (Fig. 5b). Genus *Mustela* is stretched along the third axis: small species have sea otter-like ramus (elongate and narrow ramus) and larger ones have badger-like ramus (short and wide ramus). *Martes* are in the middle between the badger and the sea otter, except yellow-throated marten, which is together with the river otter (*L. lutra*) and black polecat (*M. putorius*) the closest to the badger.

The between-group differences

The differences between Palearctic mustelids are statistically significant (Wilks's lambda <0.0001, $F_{(65,1289)}$=134.4, p<0.0001). This suggests considerable interspecific differences. 243 out of 290 specimens (more than 80%) were correctly assigned to the species after jackknifing procedure. Each species significantly differs from all others with p-values <0.0001. Even for the least differing pairs of mustelid species (*M. zibellina* – *M. martes*, *M. erminea* – *M. nivalis*, *M. nivalis* – *M. sibirica* and *M. foina* – *M. martes*) differences were highly significant (squared Mahalanobis distances are 2.04, 3.04, 4.08 and 4.08, respectively, p<0.0001).

Differences between trophic groups are significant (Wilks's lambda=0.042, $F_{(20,932.9)}$=74.63, p<0.0001), but to a lesser extent than between species. Groups 2 and 3 are heterogeneous, each group is divided into two separate subgroups, and other groups, on the contrary, are overlapped (Fig. 3, 4). The least squared Mahalanobis distances are between two groups omnivores (2 and 4) and between two groups meat-eaters (5 and 6) (3.5 and 3.7, respectively). The greatest difference is between omnivores and meat-eaters — 4 and 6 groups (squared Mahalanobis distance is 45.7).

Allometry effects in variation of mandible shape

The relationship between mandible shape and size is quite noticeable. The multivariate regression of the Procrustes coordinates on $\log_{10}$-transformed mandible length shows that allometry is statistically significant (permutation test with 10000 random permutations, p<0.0001). Log_{10}-transformed mandible length (that is treated here as a proxy for general mandible size) accounts for 11.05% of the variation in shape and associates with such shape changes as reduced molar slicing area, increased second molar, high corpus under second molar, shortened coronoid process, displaced downward and backward front edge of

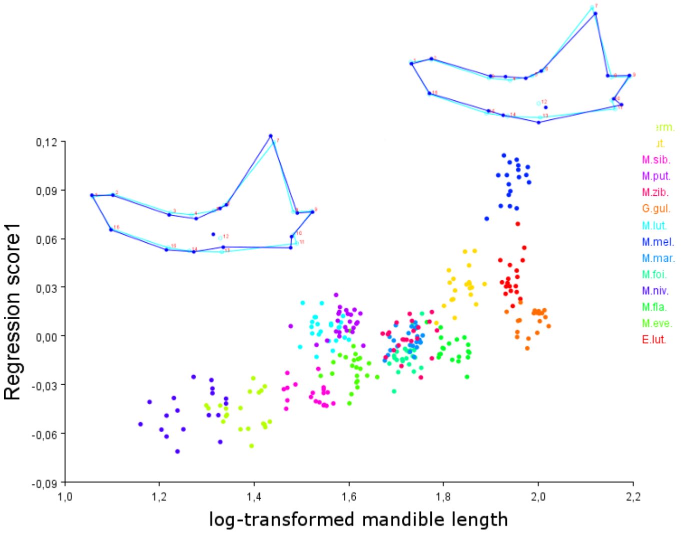

Figure 6 – Allometry of mandible shape, based on multivariate regression of the Procrustes coordinates of shape on $\log_{10}$-transformed mandible length; and the mandible shape changes associated with size.

masseter fossa and upward and backward angular process (acute angular process) with increasing mandible size (Fig. 6).

After exclusion of wolverine, influence of mandible size on shape increases (size accounts for 14.3% of the variation in shape, $p<0.0001$). The plot of Procrustes coordinates without wolverine against mandible size is not very different from the plot with wolverine. But with increasing in size has become more pronounced the higher placement of articular process and decrease in corpus height under the canines. *Enhydra*, *Meles* and *Gulo* are quite differed in shape despite the same size category. In contrast to other large species, wolverine have high mandibular corpus under canine teeth and carnivorous molars (slicing area is larger than crushing one).

Regression models performed independently for each species (Tab. 3) demonstrating that allometric effect impact species differently. The effect of the size on the lower jaw shape is strong and significant in *Mustela* species. In the Siberian weasel mandible size explains the highest percentage of shape variance. Whereas the effect of size in the other species is not significant except for pine marten. However if all *Martes* species are combined in the same sample, mandible size explains almost 23% of shape variance. Differences in the allometric trajectories of most mustelid species from the trajectory of the whole sample are insignificant (Tab. 3). It indicates the same variability trends at the intra- and interspecific level, with the possible exception of several species.

Table 3 – Regressions between mandible shape and $\log_{10}$-transformed mandible length in different species of mustelids. Also angular comparisons of vector directions of each species with the whole sample are shown (possible range of angles 0 to 180 degrees). Significance is highlighted.

Species	% predicted	*p* according to permutation test	Angles (in degrees)	*p*-values (parametric)
E. lutris	7.35	0.2578	74.38	0.078 92
G. gulo	8.0	0.1453	82.14	0.239 58
L. lutra	8.78	0.0877	**64.48**	**0.009 82**
M. meles	9.53	0.0966	**65.49**	**0.012 61**
M. martes	**13.35**	**0.002**	77.18	0.123 68
M. foina	5.35	0.3	**52.71**	**0.000 25**
M. zibellina	7.7	0.0946	80.37	0.192 96
M. flavigula	8.99	0.0897	11.026	0.967 10
M. eversmani	**8.58**	**0.042**	92.7	0.595 71
M. putorius	**12.56**	**0.0005**	84.89	0.322 91
M. lutreola	**22.93**	**<0.0001**	94.2	0.647 05
M. sibirica	**30.42**	**<0.0001**	94.94	0.671 55
M. erminea	**21.75**	**<0.0001**	90.38	0.513 55
M. nivalis	**21.23**	**0.0002**	77.68	0.133 25
Martes spp.	**22.97**	**<0.0001**	89.98	0.499 41
Mustela spp.	**30.27**	**<0.0001**	**59.33**	**0.002 35**

Discussion

Diet classification

The feeding classification of Christiansen and Wroe (2007) was used in the work. These categories consider both food preference and size of prey compared to the size of the predator. Such classification well reflects the main loads on the jaw apparatus from catching the prey. However, not all dietary factors are taken into account by this classification, e.g. food hardness, which affects the way of food processing and differently loads the jaws. Thus, sea otter is clearly specialized not to fish consumption, but to crushing and eating sea urchins that are one of its main foods. The badger is a generalist feeder (Roper, 1994; Rosalino et al., 2005) but, despite its omnivory with earthworms being more or less important depending on the area and season, it also widely consumes plant material, which may include tough food such as nuts, roots, cereals, and cracks chitin sheath of beetles (Kruuk and Parish, 1981; Goszczyński et al., 2000). At that, the consumption of plants can take the first place in the diet (Ewer, 1973; Aristov and Baryshnikov, 2001). This leads to an increase in chewing function and manifests in greater development of masseter muscle in badger compared with other more carnivorous mustelids (Abelentsev, 1968). Sea otter and badger are both the most different species from the other mustelids in mandible shape (Fig. 3, 4, 5). As well as the sea otter is very different in mandible shape from piscivorous (from the river otter in this case), the badger is very different from omnivorous *Martes* species. Badger difference from other omnivorous is also confirmed by tooth microwear (Goillot et al., 2009) that seems to be due to chewing large amount of tough food. Thus classification of *E. lutris* and *M. meles* in feeding category 3 and 2 by Christiansen and Wroe (2007), respectively, is doubtful. Analysis of the mandible shape confirms that these groups are heterogeneous. Each group is divided into two separate, very different in mandible shape, subgroups: group 2 splits into *M. meles* and *M. foina*, and group 3 into *E. lutris* and *L. lutra* (Fig. 3, 4). In the light of the study of effect of diet on the jaw apparatus, a trophic classification should reflect the food items most loading the jaw apparatus (the most hard/tough or large prey). So, another feeding categorization is proposed, which considers feed hardness too: durophagous (species that usually feed on hard or tough food; see Figueirido et al., 2013), piscivorous (fish-eating), omnivorous (feeding on vertebrates as well as invertebrates and plants), and carnivorous (principally or entirely feeding on meat) which can be divided into meat eaters specializing in medium-sized prey, and meat eaters specializing in large prey.

Trophic specializations of the studied mustelid species

From recent researches (Koepfli et al., 2008) mustelid phylogenetic tree is consistently resolved into four primary clades and three monotypic lineages. The authors have shown two bursts of diversification, first during the Miocene, which gave rise to the primary extant clades and lineages, and another during the Pliocene, which gave rise to a large proportion of the species diversity observed today. Most of the extant diversity of mustelids originated in Eurasia and may have been spurred by a combination of faunal turnover events and diversification at lower trophic levels. The mustelid fauna of Africa, North America and South America are composed of taxa from nearly all major clades and lineages, suggesting that in situ speciation has been a relatively minor component in the assembly of these faunas.

In our study the mandible shapes of sea otter, badger, river otter and wolverine are more clearly separated from other mustelids jaw when phylogeny is taking into account. The greatest difference is between *E. lutris* and *L. lutra* in the main associated with length reduction and forward slope of the coronoid and elongation of the mandibular corpus in *L. lutra*. Despite being in one clade they are very different in mandible shape. These significant differences can be explained by adaptation to different diets: piscivorous diet that do not require crushing in the case of the river otter and diet consisting of sea urchins and other tough food in the case of the sea otter. In addition to differences in diet, there are differences in foraging strategies: *L. lutra* is a mouth-oriented predator and *E. lutris* is a hand-oriented predator (see Timm-Davis et al., 2015). Therefore, these two species hardly can be attributed to the same trophic group (but cf. Christiansen and Wroe, 2007).

Martes possess a thin and elongated mandibular corpus related to a developed premolar area due to the larger number of premolar teeth. That is a common feature of omnivorous carnivorans (Biknevicius and Ruff, 1992). Small vertebrate prey and invertebrates, which form a significant component of the diet of martens, are easily captured by the longer jaw and are not expected to load the corpus as much as large vertebrate prey so the jaw is not necessary to additionally strengthen. Interesting, that yellow-throated marten is closer to meat-eaters among the other martens (Fig. 4) by corpus shortening, deepening and curvature, carnassial enlargement especially by the slicing area, an anteriorly displaced masseteric fossa and a lower condylar and angular processes suggesting a more carnivorous food habits. These mandible traits are typical for hypercarnivores (Prevosti et al., 2012). Indeed, *M. flavigula* feeds mainly on small ungulates and mammals being more carnivorous than other *Martes* species but remains largely omnivorous species (Novikov, 1956; Aristov and Baryshnikov, 2001) and even frugivorous in subtropic (Zhou et al., 2008). Prevosti et al. also reports that carnassials are posteriorly placed in hypercarnivores. Contrary to this the carnivorous mustelids have a more anteriorly placed carnassials relatively to condyle that together with short jaws provides the possibility to capture and process larger prey through larger gape and affords some mechanical advantage due to a greater contribution of contralateral masticatory muscle forces to bite force (Biknevicius and Ruff, 1992).

Such mechanical advantage due to short jaw is observed in sea otter and badger. Despite being omnivorous, the badger's mandible is well strengthened, adapted to heavy loads, like the sea otter's mandible. It seems to be due to the consumption of tough plant food that has the same influence on lower jaw adaptations as crushing hard urchins. Sea otter and badger display adaptations for durophagy. Its corpus length and the molar slicing region are reduced. Hard food processing occurs at the enlarged crushing area of molar complex. Such the posterior location of hard food cracking is maximized bite force with the small gape. A common feature to durophagous mustelids is the strengthening of the posterior area of the mandibular corpus. In contrast to them the meat-eaters have a thick anterior part of the corpus.

The difference of the corpus strength between durophagous and carnivorous mustelids are explained by differences in the loads from biting (Figueirido et al., 2013). The meat-eaters use a high canine bite force to capture their prey, and in durophagous the strongest bite force is applied in the molars. Durophages are similar to herbivores on having a higher condyle and an anteriorly placed carnassials with a large talonid that is related to an expansion of the crushing area and reduction of the shearing crests of the molars, strengthening of the posterior portion of the mandibular corpus (Prevosti et al., 2012). Similarity with herbivorous musteloid carnivorans is also evident in short snout (Dumont et al., 2016) which increases the mechanical advantage for food processing. Both herbivorous and carnivorous species have a shorter snout than do omnivorous species.

Wolverine jaw combines the characters of the killing and feeding apparatus of carnivores and durophages. Wolverines can attack large prey such as reindeer using a mustelids-like killing technique and crack bones of large animal carrion (moose for instance) eating even their horns (Abelentsev, 1968; Aristov and Baryshnikov, 2001; see also Hornocker and Hash, 1981; Van Dijk et al., 2008), wherewith have earned the wolverine the name of the "hyaena of the north" (Ewer, 1973). The study of lower molar microwear shows the wolverine as moderate consumer of large bones (Van Valkenburgh et al., 1990). In this connection the wolverines have jaws similar in shape to meat-eaters (*Mustela*) by enlarged slicing region of carnassials and robust anterior region of the corpus and similar to durophages in displacement backward of coronoid and masseteric fossa and how their corpus strengthening under the molar complex.

Strengthen corpus under the crushing region implies similarity in loadings in the lower jaw with durophages. Indeed, wolverine can load their molar corpora heavily cracking bone that is hardly distinguishable from other tough-food consuming categories (Raia, 2004). These similarities in the loads and their effect on the jaw apparatus was also observed between bamboo-feeders and bone-crackers (Figueirido et al., 2013). Sea otter, badger and wolverine are distant relatives, therefore, morphological features of durophages are relatively independent of the phylogenetic legacy. Nevertheless, this similarity in mandible traits required to feed on hard and tough foods represents convergent adaptations toward durophagy (Figueirido et al., 2013). At the same time, mandibles of *E. lutris*, *M. meles* and *G. gulo* demonstrate particular feeding adaptations to three distinct kinds of durophagous since the first uses the jaws to crush urchins, the second — to chew tough food and the third — to crush bones. The differences are observed mainly in the teeth and mandibular ramus shape. Also the carnassials of wolverine are located on the dentary higher than in other mustelids whereby condyle is significantly lower the tooth row (unlike other durophages). Thus wolverine can be attributed to both durophagous and carnivorous trophic groups. Figueirido et al. (2011) attributed wolverine to hypercarnivorous solitary hunters. However, the above mentioned data shows that this mustelid can be considered as hypercarnivorous bone-cracker specialist, too. This is confirmed by the fact that *G. gulo*, which is a highly hypercarnivorous species which relies heavily on carrion, are closer to the living felids and hyaenids than to other mustelids in jaw shape (Figueirido et al., 2011).

Two extreme types of the ascending ramus can be identified among Mustelidae (Fig. 3). These types correspond to the strategies of ramus development — the long and narrow sea otter-like one and the wide and short badger-like one. Within the trophic groups as well as within genera the mustelids have both types of ramus (Fig. 5b). The smallest mustelids, namely weasel and ermine, have the most otter-like ramus unlike black polecat who is together with river otter and yellow-throated marten the closest to badger-like one. Relationship between the mandibular ramus and size is not traced since the smallest and the largest species can have the similar ramus and the largest mustelids (sea otter and badger) have oppositely different types of ramus (see PC1 and PC2 and also CV3 that associated with ramus shape changes and poorly correlates with size, R^2=0.045, *p*= 0.0001). A more detailed study of the ramus characteristics deserves further research.

L. lutra takes an intermediate position between three groups — 1) *Mustela* with *Gulo*, 2) *Martes*, 3) *Enhydra* with *Meles* — by such features as corpus length and molar length including slicing region. River otter is closer to badger on ramus shape (short and wide ramus) although differs from durophages in slope of ramus forward (Fig. 7). Mink (*M. lutreola*) has also the sloping forward ramus but in less measure. Possibly, this trait together with posterior location of masseteric fossa associates with fish consumption by river otter and to a certain extent by mink.

Meloro et al. (2011) reported the strong differentiation in corpus shape between predators and non-predators and confirm the highly adaptive significance of shortening or enlarging molar slicing-crushing area. Mustelids have similar patterns as for the carnivorans in general. Decreasing carnassials length due to reduce of slicing area, shortening mandible thick under the canine region occurs from meat-eaters (*Mustela* and *Gulo*) through *Martes* and *Lutra* to durophagous *E. lutris* and *M. meles* (Fig. 5a). Therefore, the last two mustelids have the shortest lower carnassials and meat-eaters have the longest ones that

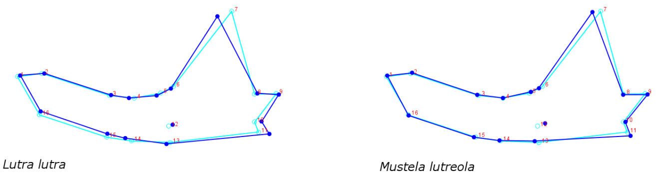

Figure 7 – Mandible shapes of *L. lutra* and *M. lutreola* compared with averaged configuration.

contradict with conclusions of other researches that tough food consumers (including bone-cracking) have a longer lower carnassial than meat-eaters (Raia, 2004). Though, the wolverine as bone-cracker has large carnassials with increased slicing region. The carnivorous and durophagous share a shortening and strengthening of the mandibular corpus (Fig. 5a, see also Meloro et al., 2008; Figueirido et al., 2011, 2013; Prevosti et al., 2012). *Martes* have the longest and the thinnest premolar region in contrast with the others (especially with *Meles*).

Accuracy of the techniques

Our landmark configuration is designed to represent mandibular corpus thickness differences reflecting the different loadings of the canine and lower carnassial regions (Biknevicius and Van Valkenburgh, 1996), differences in the teeth sizes, lengths of premolar and molar regions, and in the ascending ramus, the relative position and sizes of processes. The chosen landmark configuration reveals a strong differentiation among genera in mandibular shape. All *Mustela* are meat specialists in medium-sized and large prey. The genus *Martes* represents more omnivorous, *Lutra* is a fish-eating species. The largest species of Mustelidae — badgers and sea otter — are durophagous. So, mustelids mandible morphology is highly consistent along both phylogenetic origin and ecological specialization.

It is worth taking into account that the mandible is not perfect two-dimensional object. Projections of the curves processes will be slightly different from the actual position. Like sea otter coronoid process which apex is bent interior and therefore the coronoid probably is even longer than that shown in geometry morphometrics. But generally geometric morphometrics allow the interpretation of ecomorphology with a high statistical degree of accuracy. That confirms a number of authors (e.g. Meloro, 2011; Navarro and Maga, 2016).

Correspondence between evolutionary history and trophic specialization

It can be observed both the divergence and convergence as well as the similarity of close relatives in the ecological specialization within Mustelidae. In several cases the species within a clade keep the similar trophic specialization. Species of genera *Martes* and *Mustela* are the examples for such a pattern.

In some cases the closely related species significantly differ on their trophic preferences. For example, river otter and sea otter are both aquatic species having different feeding spectra. On the other hand, sea otter and badger not being close relatives have acquired the similar ecological specialization as a result of convergent evolution. Another example of convergence is ecological similarity of wolverine to *Mustela* as hypercarnivorous species and to *E. lutris* and *M. meles* in their adaptation to hard food consuming despite its evolutionary relationship with *Martes*. Thus we can assume that some species of Mustelidae retain (hold) the ancestry ecological niche during evolution, while others can change it quite radically that is fairly typical for mammals.

Mustelids are one of the most numerous and diverse group of carnivorous mammals. The fact that some species within the same group can change the direction of their ecological specialization indicates that the group retains its plasticity, is not narrowly specialized. It is difficult for more or less specialized species to exceed the limits of a successfully occupied adaptive zone (Schmalhausen, 1939; Simpson, 1944; Dzeverin and Ghazali, 2010). Transition from one adaptation to another within the adaptive zone (often with further specialization) is the most probable trend in evolution of such species (Schmalhausen, 1939; Simpson, 1944; Dzeverin and Ghazali, 2010). Thus, closely related species usually have similar ecological preferences. Such a transition can be accompanied by progressive specialization and the narrowing of the adaptive zone. The progressive specialization is highly probable in evolution of clades, in which the species compete for considerably limited resources (Schmalhausen, 1939; Markov and Naimark, 1998) whereas under the other ecological patterns the progressive specialization is not expected. Numerous lineages and clades preserve an evolutionary potential and ability to occupy various ecological niches within the adaptive zone and sometimes even beyond its bounds (cf. Dzeverin and Ghazali, 2010). On an example of Mustelidae, we see both similarity in trophical adaptations among the closely related species and the successful adaptations to the quite new ecological niches.

Conclusions

Relationships between the jaw shape and trophic specialization within the family Mustelidae are similar to such relationships within order Carnivora on the whole. Ecological features of studied species are partly determined by their evolutionary history.

Two types of the ascending ramus are observed in Palearctic mustelids — long and narrow one (sea otter-like), and short and wide one (badger-like). Both types of the ramus are present both in closely related species and in species with similar trophic specialization. Maximum contribution to the variance of the complex features of the studied species is related to the size of the carnassials, the ratio of slicing/crushing area of molar complex, the height of the mandibular corpus. These features are also highly correlated with the size.

Carnivorous mustelids (*Mustela*) differ from other trophic groups with their large carnassials, increased slicing area of molars, and high mandibular corpus under the canines. Durophagous mustelids (sea otter and badger) are similar by such characteristics as high corpus under the molars, placed posteriorly masseteric fossa, sloping backward coronoid, shortened mandible, and reduced slicing area (with enlarged crushing area of molars). The largest palearctic mustelids are adapted to different food consumption and have the shortest mandibles. More omnivorous mustelids (*Martes*) have the most long and thin mandibles and occupy an intermediate position in carnassials size and in the ratio of the different areas of the molar complex. River otter is intermediate in all characters and separate from the other groups. Wolverine despite the close affinity with *Martes* is close to *Mustela* in the shape of mandible but has durophagous features too.

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Associate Editor: P. Colangelo

Appendix

List of the Specimens Examined by the Author

Enhydra lutris

NMNH 6051, w/n; ZM 153900, 153903, 153905, 153906, 153913, 180675, 180677, 180712, 180726, 180731, 180781, 180795, 180867, 188110, 191478, 191480.

Gulo gulo

NMNH 896; ZM 4770, 12950, 34903, 34905, 34910, 48431, 48442, 84882, 92833, 95903, 95905, 95910, 152554, 188013, 188015, 188017, 188018, 188031.

Lutra lutra

NMNH 27; ZM 12902, 12952, 12958, 29137, 29138, 40254, 48382, 69321, 69342, 76698, 77181, 92196, 92202, 92241, 92244, 92249, 92826, 92830, 92831.

Meles meles

NMNH 16, 864, 867, 868, 870, 872, 875, 878, 893, 1107, 1203, 3150, 3151, 3152, 3153, 3219; ZM 44340, 75418.

Martes martes

NMNH 31, 33, 34, 83, 84, 85, 86, 93, 96, 97, 100, 105, 127, 128, 856, 1668, 4357, 4719, 6110, 6111, 6112, 6115, 6266, 6302.

Martes foina

NMNH 5, 6, 7, 10, 25, 78, 79, 81, 82, 111, 119, 130, 132, 136, 145, 172, 861, 862, 1108, 6123, 6125, 6126, 6127.

Martes zibellina

NMNH 1176, 1177, 1179, 1669; ZM 5770, 5777, 5799, 5817, 5818, 5820, 45121, 57803, 57899, 57943, 58015, 58020, 62471, 62472, 73458, 86448, 89300, 89329.

Martes flavigula

ZM 40696, 40697, 42486, 49207, 69302, 69303, 69304, 69309, 69311, 69312, 77180, 78426, 78427, 92369, 109978, 109983, 109985, 115710, 139099.

Mustela eversmani

NMNH 1, 2, 3, 4, 9, 44, 53, 63, 64, 65, 1042, 1059, 1077, 1078, 2576, 2675, 2842, 5578, 6138, 6156, 6241, 6243, 6244.

Mustela putorius

NMNH 7, 90, 92, 123, 835, 837, 839, 840, 936, 1204, 3765, 3768, 3769, 4720, 5577, 5763, 5797, 6141, 6144, 6157, 6289, A, B, M3861

Mustela lutreola

NMNH 801, 802, 803, 804, 805, 806, 807, 809, 810, 811, 812, 813, 814, 815, 816, 817, 818, 819, 820, 821, 823, 845, 3063.

Mustela sibirica

ZM 27885, 27887, 27902, 41193, 41200, 41219, 41223, 41234, 41238, 41248, 41249, 42475, 76903, 76909, 76951, 77031, 77035, 91758, 123568.

Mustela erminea

ZM 32509, 48606, 8867, 48574, 48614, 48632, 48656, 80847, 101585, 101586, 101588, 162843, 168515, 168516, 168518, 168522, 168524, 171319, 171321, 171331.

Mustela nivalis

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