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Phylogenetic Evaluation of Three Subspecies from the *Mustela nivalis* Group

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Urmas Saarma and Igor L. Tumanov (2006) Phylogenetic evaluation of three subspecies from the *Mustela nivalis* group. *Zoological Studies* **45**(3): 435-442. Extensive morphological variation has been a foundation for speculation and controversy about the evolutionary history and systematics of the *Mustela nivalis* group. Our aim was to assess the phylogenetic relationship of 3 subspecies of the *Mustela nivalis* group: *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri*. A phylogenetic network, based on partial mtDNA cytochrome b sequences, revealed that all analyzed subspecies belong to the same clade with *M. n. nivalis*. These results support the hypothesis that the *M. nivalis* group can largely be considered a single species with remarkable phenotypic and geographic variations. http://zoolstud.sinica.edu.tw/Journals/45.3/435.pdf

Key words: Mustelids, Cytochrome b, Phylogeny, Speciation, Subspecies.

The Mustelidae is the largest and the most diverse family of the Carnivora. Evolution of the family has progressed rapidly since its origin (Bininda-Emonds et al. 1999). Large-scale adaptive radiation of mustelids had already begun in Eurasia by the late Pliocene. In Eurasia, 12 species are recognized as members of the genus *Mustela*. Based on mitochondrial cytochrome b sequences, the phylogeny of Eurasian mustelids has recently been established (Hosoda et al. 2000, Kurose et al. 2000).

Mustelids exhibit extraordinary variability in morphological characters such as body size, tail length, and fur coloration, to name a few. The distribution of the *M. nivalis* group (MNG) is widespread, covering most of Europe (except Ireland and Iceland), North Africa, a major part of Asia (except for the southern tropical regions and some Arctic islands), and North America (Abramov and Baryshnikov 2000). Based on the high degree of variation in morphology, a large number of subspecies and taxonomic names have been proposed (Ognev 1935, Heptner et al. 1967, Abramov and Baryshnikov 2000). The most pressing challenge is reflected by the frequent disagreement as to 1) how many subspecies there are in the MNG, and 2) if some can considered to be separate species. The subdivision of *M. nivalis* into more than 1 species-level taxon has important implications for understanding the extensive morphological variations within the MNG. The acceptance of subdivisions within *M. nivalis* would imply a major role of natural selection in regulating the size of individuals. Recognition of a single species encompassing such large differences would imply that natural selection highlights the maintenance of size plasticity (Reig 1997). Looking at the diverse morphologies of members of the MNG, it is tempting to consider them as separate species. For example, body weight varies from 35 g in *M. n. punctata* to 250 g in *M. n. heptneri*, and large differences are found in other characteristics of the body and in fur coloration. One possible reason for such remarkable diversity is that members of

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the MNG inhabit different ecosystems. Moreover, climatic changes derived by recurrent ice ages have induced large-scale movements of animal populations (Taberlet et al. 1998, Hewitt 2000). It is conceivable that some populations of the MNG have evolved in allopatry, which has promoted the divergence of morphological characters. Adaptive morphological evolution is often part of the early phase of speciation. E. Mayr (1963) wrote: "Usually morphological differentiation seems to take place more rapidly than the acquisition of isolating mechanisms." It has been speculated that intraguild competition provides an incentive for morphological radiation (Dayan and Simberloff 1994). Concerning the systematic status of the MNG, 2 hypotheses have prevailed among researchers. First, small and large weasels can be considered separate species (Allen 1933). Indeed, recent data relying on the analysis of morphological characters, suggest that the Egyptian weasel *M. n. subpalmata* can be regarded as a separate species (Reig 1997). Second, *M. nivalis* is 1 species with a complicated morphological structure and remarkable geographic variation (Ognev 1935, Heptner et al. 1967, Mandahl and Fredga 1980, Zyll de Jong 1992). However, it is not known whether differences in morphology are reflected in the phylogeny of the MNG. Recently, based on the analysis of coat coloration and karyotypes, 3 major phylogenetic lineages were proposed to exist in Europe (Zima and Cenevova 2002).

In this study we examined the taxonomic status of 3 large subspecies in the MNG. To understand the process of divergence among mustelids, we performed a phylogenetic analysis using mtDNA cytochrome b sequences. Four subspecies of the MNG were used in this investigation: *M. n. nivalis*, *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri*. The morphology and distribution of these subspecies, together with the other subspecies of the MNG, have been extensively reviewed elsewhere (Ognev 1935, Heptner et al. 1967, Abramov and Baryshnikov 2000); here we just provide short descriptions.

Mustela n. nivalis is a small, short-tailed weasel. The mean body length is 178 mm, and relative tail length is 17%-20% (of body length). The coloration is of the *nivalis* type. It is found in Scandinavia, northern European Russia, the Urals, Siberia, Kazakhstan, Mongolia, Sakhalin, the Kuril Is., and Hokkaido.

Mustela n. dinniki is a large, long-tailed weasel with an average body length of 227 mm and a relative tail length of 27%-33%. The coloration is of the *vulgaris* type. It is distributed in the Caucasus area.

Mustela n. boccamela is large, long-tailed weasel. Its average body length is 270 mm, and relative tail length is 35%-39%. The coloration is of the *vulgaris* type. It is distributed in the northern part of the Iberian Peninsula, the Balearic Is., southern France, Italy, Sardinia, and Malta. Several authors also consider the Transcaucasia as a part of the distribution range of this subspecies (Satunin 1905, Heptner et al. 1967). Other systematists believe that the distribution range of *M. n. boccamela* is restricted to Sardinia (Corbet 1978).

Table 1. Identity of the analyzed mustelid specimens

Code	Species or subspecies	GenBank	Locality	References
Sle	*Mustela nivalis*	AF068545	Slovenia	Davison et al. 1999
Hep	*M. n. heptneri*	AY188792	Kazakhstan	this study
Ru1	*M. nivalis*	AB051267	Rostov region, Russia	Hosoda et al. 2000
Din	*M. n. dinniki*	"	Republic of Dagestan	this study
Boc	*M. n. boccamela*	"	Azerbaijan	this study
Twn	*M. nivalis*	AB046612	Taiwan	Hosoda et al. unpubl.
Ala	*M. nivalis*	AF457461	Alaska, USA	Fleming, and Cook 2002
Est	*M. n. nivalis*	AY188793	Estonia	this study
Kor	*M. nivalis*	AB051270	South Korea	Hosoda et al. 2000
Ru2	*M. n. nivalis*	AY188794	Leningrad region, Russia	this study
Ru3	*M. nivalis*	AB051268	Primorje region, Russia	Hosoda et al. 2000
Np1	*M. nivalis*	AB051272	Japan	Hosoda et al. 2000"
Ger	*M. nivalis*	AB051264	Germany	Hosoda et al. 2000"
Np2	*M. nivalis*	AB026106	Japan	Kurose et al. 2000
Erm	*M. erminea*	AB051260	Honshu, Japan	Hosoda et al. 2000
Alt	*M. altaica*	AB051255	Altai Mountains, Russia	Hosoda et al. 2000"

Mustela n. heptneri is a large, long-tailed weasel, with an average length of body of 233 mm and a relative tail length of 27%-32%. The coloration is of the *nivalis* type. It is distributed in Iran, Afghanistan, Turkmenistan, Uzbekistan, Western Tajikistan, and southern Kazakhstan.

MATERIALS AND METHODS

Samples and DNA purification

Skin samples were taken from collections of the Research Institute of Nature Conservation of the Arctic and North, St. Petersburg, Russia and the subspecies were determined by researchers at this institute. Skins were 11-12 y old and had been air-dried, and all specimens were males. One sample of *M. n. boccamela* was from Azerbaijan of the Transcaucasian region, and 3 samples of *M. n. dinniki* were from Dagestan of the Caucasian region. One sample of *M. n. heptneri* was collected in the vicinity of Lake Balkhash, Eastern Kazakhstan, and 1 sample of *M. n. nivalis* was from the Leningrad region of Russia. One muscle sample of *M. n. nivalis* was from Estonia, and was part of the tissue collection of the Institute of Zoology and Hydrobiology, Tartu, Estonia (Table 1). Total genomic DNA was extracted using a QIAamp DNA Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol, including an extraction blank.

PCR and sequencing

A 378-base pair (bp) fragment of the mitochondrial cytochrome b gene was amplified using the primers L14771 (Davison et al. 1999) and H15149 (Irwin et al. 1991). Purified genomic DNA (20-80 ng) and 4 pmol of primers were used for the polymerase chain reaction (PCR). PCR was performed in a total volume of 20 μl. Cycling parameters were 5 min for the denaturation step at 94°C, followed by 35 cycles of 1 min at 94°C, 1 min at 55°C, and 1 min at 72°C with 1 U Platinum *Taq* DNA polymerase (Invitrogen, Carlsbad, USA), 0.2 mM dNTP, and 1.5 mM $MgCl_2$. The PCR product was purified with shrimp alkaline phosphatase and exonuclease I treatment. One unit of both enzymes (USB, Cleveland, USA) was added to 10 μl of the PCR mixture and incubated for 30 min at 37°C, followed by 15 min inactivation at 80°C.

DNA cycle sequencing was performed using a DYEnamic ET Terminator Cycle Sequencing Kit (Amersham Pharmacia Biotech, Uppsala, Sweden). Thirty-three cycles (15 s at 95°C, 15 s at 50°C, and 60 s at 60°C) were performed in a total volume of 10 μl. Sequences were resolved on an ABI PRISM 377 automated DNA sequencer (Applied Biosystems, Foster City, USA). To obtain unequivocal sequences, both chains of the DNA were sequenced using either the L14771 or H15149 primer. All mutations were verified by reextraction, reamplification, and resequencing. New cytochrome b genotypes were submitted to GenBank, including *M. n. heptneri* (Hep)

Table 2. Pairwise distance matrix of analyzed mustelids. Codes refer to those in table 1

Code	Sle	Hep	Ru1(Din, Boc)	Twn	Ala	Est	Kor	Ru2	Ru3	Np1	Ger	Np2	Erm	Alt
Sle														
Hep	0.009													
Ru1 (Din, Boc)	0.006	0.003												
Twn	0.012	0.009	0.006											
Ala	0.012	0.009	0.006	0.006										
Est	0.015	0.012	0.009	0.009	0.003									
Kor	0.015	0.012	0.009	0.009	0.003	0.006								
Ru2	0.018	0.015	0.012	0.012	0.006	0.009	0.009							
Ru3	0.015	0.012	0.009	0.009	0.003	0.006	0.006	0.009						
Np1	0.015	0.012	0.009	0.009	0.009	0.012	0.012	0.015	0.006					
Ger	0.012	0.009	0.006	0.006	0.006	0.009	0.009	0.012	0.003	0.003				
Np2	0.012	0.009	0.006	0.006	0.006	0.009	0.009	0.012	0.009	0.009	0.006			
Erm	0.059	0.056	0.053	0.053	0.053	0.056	0.056	0.060	0.056	0.050	0.053	0.046		
Alt	0.073	0.070	0.066	0.066	0.066	0.070	0.070	0.073	0.070	0.070	0.066	0.059	0.056	

AY188792, *M. n. nivalis* from Estonia (Est) AY188793, and *M. n. nivalis* from Russia (Ru2) AY188794 (Table 1).

Phylogenetic analysis

Consensus sequences were created with the program Consed (Gordon et al. 1998), using sequence data of both DNA strands. Sequences were double-checked by eye.

In addition to 7 sequences obtained in this study, 9 cytochrome b haplotypes of *M. nivalis* and the outgroup sequences of *M. altaica* and *M. erminea* were included from GenBank (Table 1). Sequences were aligned with Clustal W (Thompson et al. 1994), using BioEdit as the sequence editor (Hill 1999). A reduced median-joining network was calculated with the Netw3111 computer software (Bandelt et al. 1999). Maximum parsimony (MP) analysis was conducted with PAUP* 4.0b10 (Swofford 2003), applying a heuristic MP analysis with 1000 random taxon addition replicates and tree bisection-reconnection branch swapping. Relative support for the recovered clades was calculated using the nonparametric bootstrap method (Felsenstein 1985). One thousand bootstrap pseudoreplicates were analyzed under a heuristic search. The neighbor-joining (NJ) method was applied with the Kimura 2-parameter model and 1000 bootstrap pseudoreplicates using MEGA 2.1 (Kumar et al. 2001).

For the maximum likelihood (ML) analysis, Modeltest 3.06 (Posada and Crandall 1998) was used to determine the model of DNA substitution that best fit the data. Model parameters obtained by Modeltest were included in the Nexus file of the dataset, and heuristic ML analyses with NNI branch swapping and 1000 bootstrap pseudoreplicates were conducted in PAUP*. In addition, the ML analysis was performed using PHYLIP 3.62 (Felsenstein 1989). SeqBoot from the PHYLIP package was used to generate 1000 bootstrap pseudoreplicates. The ML analysis was run using PHYML with default settings. The majority rule consensus tree was constructed with Consense from 1000 ML trees in PHYLIP to estimate support for the recovered branches. MrBayes 3.04b (Ronquist and Huelsenbeck 2003) was used for the Bayesian estimation of phylogeny. The HKY model selected by Modeltest was used for the Bayesian inferences. An initial run was performed to determine the burn-in value, which was applied in further analyses to exclude all trees prior to the stable log likelihood estimate. Searches were conducted with 4 simultaneous Markov Chains with over 2 x 10^6 generations, sampling every 100 generations, and ending with a calculation of a 50% majority rule consensus tree. To ensure that the Bayesian inference was not trapped in local optima, the analysis was performed 3 times. Phylogenetic trees were visualized with TreeView 1.6.6 (Page 1996).

Pairwise genetic distances were calculated with Mega 2.1 using the Kimura 2-parameter

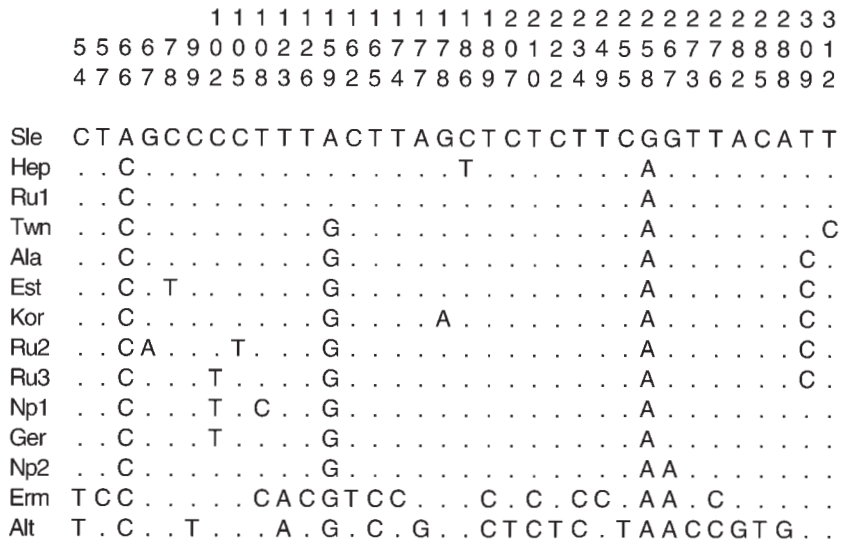

Fig. 1. Cytochrome b sequence (partial, 312 bp) variations in the *Mustela nivalis* group. Haplotype designations are in the left column, with variable sites in the top row. Numbers correspond to positions of the cyt b sequence of *M. nivalis* from GenBank (AB051241). Identity with the 1st sequence is denoted by a dot. *Mustela erminea* (Erm) and *M. altaica* (Alt) were used as outgroups.

model (Kumar et al. 2001).

RESULTS

Eleven samples of twelve years old skins *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri* were successfully used for DNA analysis. A 378-bp fragment of the 5' part of the mitochondrial cytochrome b (cyt b) gene was PCR-amplified, and both strands were sequenced for 7 different specimens: 3 samples of *M. nivalis dinniki*, 1 sample each of *M. n. boccamela* and *M. n. heptneri*, and 2 samples of *M. n. nivalis*. Based on sequences of both strands, a consensus sequence was created for each specimen. The sequences were aligned and trimmed, and as a result, sequences of 312 bp (corresponding to bases 36-348 in the cyt b sequence of *M. n. nivalis*) were used for further analysis (Fig. 1).

Out of 7 sequences analyzed, 4 cyt b haplotypes were found. All 3 specimens of *M. n. dinniki* (Din) together with *M. n. boccamela* (Boc) produced identical sequences. *Mustela n. heptneri* gave a unique haplotype (Hep) as did *M. n. nivalis* specimens from Estonia and Russia (Est and Ru2, respectively). Sequences obtained from GenBank yielded 9 haplotypes. Haplotype Ru1 was identical to haplotypes Din and Boc (Table 1).

Mutations were found at 34 positions and included a total of 84 base changes. Transitions were most common, including 69 mutations at 32 positions, 15 of which were transversions. Most base changes occurred at the 3rd codon positions

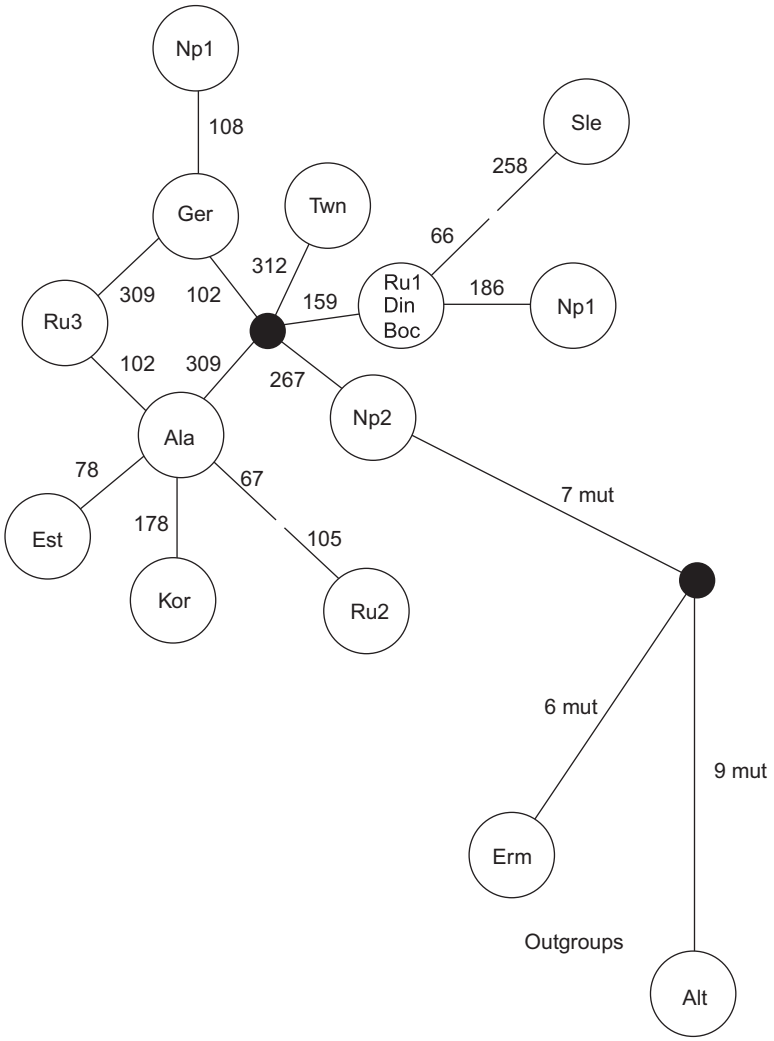

Fig. 2. Reduced median joining network of the *Mustela nivalis* group, based on the partial cytochrome b sequence. For haplotype identity, see table 1. Filled circles are median vectors (genotypes not sampled or extinct). One bar equals 1 mutation. Numbers on the bars are mutations according to figure 1. Number of mutations that separate outgroups from the *M. nivalis* group are on long branches.

(82 mutations at 32 positions). The 1st codon position was altered twice; mutations were not found at the 2nd codon position. Synonymous substitutions were most frequent; only 16 mutations at 4 positions were non-synonymous. Either Ala was changed to Thr, Met to Ile, or Ile to Met (data not shown). Genetic pairwise distances indicated the close relationships among members of the MNG (Table 2).

The reduced median joining analysis grouped all members of the MNG into a single clade in the network. The outgroup sequences of *M. erminea* and *M. altaica* were 13 and 16 mutations apart from the nearest *M. nivalis*. *Mustela n. dinniki* and *M. n. boccamela* were indistinguishable from each other, while *M. n. heptneri* was separated from them by 1 nucleotide change (Fig. 2).

The model HKY selected by Modeltest was used for the ML and Bayesian analyses. All phylogenetic methods gave similar tree topologies, albeit with different levels of statistical support (Fig. 3).

According to the Bayesian inference, *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri* formed a separate clade together with *M. n. nivalis* specimens from Slovenia and Russia.

Our results indicated that *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri* belong to the same clade with *M. n. nivalis* specimens from different locations in Eurasia, whereas *M. erminea* and *M. altaica* are clearly distant from the MNG.

DISCUSSION

It has been emphasized that in the case of species showing considerable phenotypic variation, such as the weasel, it is critical to define the biological or taxonomic groups under consideration, and to verify the genetic identities of different morphotypes observed, before attempting to hypothesize about the species morphological plasticity and systematic status (Reig 1997). While the phenotypic variation has been extensively studied, there are no data available to reveal the phylogenetic relationships among subspecies of the MNG.

Herein, we evaluated the phylogenetic status of different subspecies of the MNG. Partial

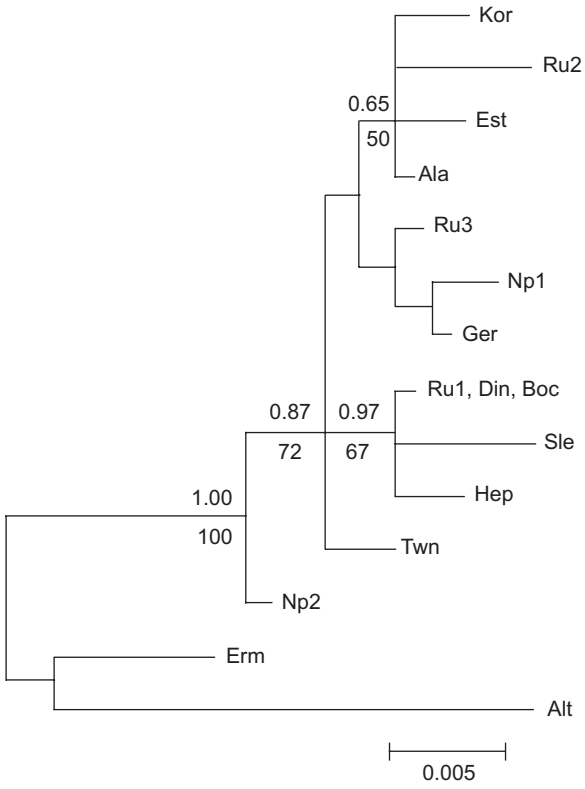

Fig. 3. Phylogeny of the *Mustela nivalis* group (MNG), based on sequences of the mtDNA cytochrome b gene fragment (312 bp). Values above the branches indicate posterior probabilities for Bayesian inferences above 0.6; below the branches are values of the bootstrap support of the neighbor-joining tree which exceed 50%. *Mustela erminea* and *M. altaica* were used as outgroups.

cytochrome b sequences of *M. n. nivalis*, *M. n. dinniki*, *M. n. boccamela*, and *M. n. heptneri* were used to infer the intraspecific phylogeny (due to the rarity of well-preserved samples of the MNG subspecies in museums, we were unable to include more subspecies in this study).

The results demonstrated rather limited mtDNA divergence among the different morphotypes, with all subspecies assigned to a single clade, while the MNG remained clearly distant from the mountain weasel *M. altaica* and the ermine *M. erminea*. The partial cyt b sequence analyzed in this study has enough resolution to produce molecular discrimination at the species level. Longer sequences would certainly place subspecies into a more-distant position, but the relative distances between members of the MNG and well-recognized species of the genus *Mustela*, such as *M. altaica* and *M. erminea* (the closest relatives to the MNG), would most probably remain comparable to our results. Intriguingly, all analyzed subspecies coalesced at the same point, implying a recent common founder. Taking into account the genetic similarity within the MNG and its distance from *M. altaica* and *M. erminea*, these results support the hypothesis that the *Mustela nivalis* group largely represent a single species with a complicated morphological structure and remarkable geographic variations (Ognev 1935, Heptner et al. 1967, Mandahl and Fredga 1980, Zyll de Jong 1992).

Phenotypic variation may result from processes where natural selection favors a particular adaptive morphology, which implies selection for the corresponding genotype and ultimately evolutionary divergence and speciation. Recognition of a single species encompassing large differences suggests that natural selection is highlighting the maintenance of phenotypic plasticity. Results of this study seem to favor the latter opinion.

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