Geographic variation and intraspecific taxonomy of weasel *Mustela nivalis* (Carnivora, Mustelidae)

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Relationships of Holarctic weasels (*Mustela nivalis*), based on cranial variables, sizes and proportions of body and tail, and coloration of summer pelage were analysed. It is possible to divide *M. nivalis* into three groups: large long-tailed weasels with “nivalis”-coloration, weasels of average size with a relatively long tail and “vulgaris”-coloration, and small short-tailed weasels with “nivalis”-coloration. The combination of all characters allows us to divide *M. nivalis* into 19 subspecies, including *M. nivalis rossica* **subsp. n.** (Eastern Europe). The Egyptian weasel (*M. subpalmata*) is regarded by us as a separate species. Large long-tailed weasels with coloration of “nivalis”-type (group *numidica*) are probably closest to the ancestral type of *M. nivalis*. Small weasels (group *nivalis*) appeared later, probably in the boreal regions of the Palaearctic. These weasels could have penetrated North America through Beringia. Another form (*vulgaris-boccamela*) was formed during the Late Pleistocene in the eastern Mediterranean from *numidica*. When weasels of this group occupied Western and Central Europe they displaced small *nivalis* to the north and east.

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Introduction

The weasel (*Mustela nivalis* L., 1766) has a wide distribution covering the whole of Europe (except Ireland and Iceland), North Africa, a major part of Asia (except southern tropical regions and some arctic islands) and North America. The species displays notable variation in this range and, in the opinion of Heptner (Heptner et al., 1967), represents one of the most interesting cases of geographic variability among mammals. A decline in general size of the body is observed from south towards the north (contrary to the well-known Bergmann’s rule), as well as variation in the relative length of tail, change of summer coloration, the sympatric presence of large and small animals, and so on. As a result, during the past 200 years a multitude of different forms of *M. nivalis* with taxonomic status from species to race have been described. Analysis of intraspecific structure is complicated by sexual dimorphism and age variation of animals.

There is no general agreement about *M. nivalis* taxonomy. The arguments concern not only notions of number of subspecies and their association with certain spaces, but also the question of the number of weasel species in Europe, Africa and Asia. Different models have been proposed for the development of geographic variation of *M. nivalis*. Therefore it is necessary to focus on the history of intraspecific taxonomy of Palaearctic weasels.

Historical review

The species *M. nivalis* L., 1766 was described from Sweden. The Province of Västerbotten is regarded as its terra typica. The area is inhabited by small, relatively short-tailed weasels whose colour becomes completely white in the winter. The species was established on a specimen in white winter fur. At the first stage of study of weasels in Europe, other geographic forms, reflecting the major tendencies in spatial variation of *M. nivalis*, were separated: average-sized and moderately long-tailed *M. vulgaris* Erxleben, 1777 from Germany, and very large and long-tailed *M. boccamela* Bechstein, 1800 from Sardinia.

In the middle of the last century it was noted that small short-tailed individuals with infantile features in skull structure occur among large and relatively long-tailed weasels in Central and Southern Europe. This form was named *M. minuta* (Pomel, 1853) (described from the vicinity of Paris). Subsequently other small races were revealed: *M. nivalis caucasica* (Barrett-Hamilton, 1900) for the Caucasus, *M. n. monticola* (Cavazza, 1908) for the Alps. The small weasel was regarded as a separate species existing in Europe sympatrically with a larger one *M. nivalis* (or *M. vulgaris*) (Cavazza, 1908, 1909, 1914, 1915; Cabrera, 1913a, 1914; Zimmermann, 1943; Kalela, 1946; Kahmann, 1951; Kratochvil, 1951; Brink, 1957; Fog, 1969; Lehmann, 1969; etc.).

The small short-tailed weasel inhabiting North America was named *M. rixosa* (Bangs, 1896). Small and short-tailed animals also inhabit Siberia and the Far East, Japan included. J. Allen (1903), who described the Siberian weasel as *Putorius pygmaeus*, noted that this form was obviously closer to *M. rixosa eskimo* (Stone, 1900) from Alaska than to *M. nivalis nivalis* proper from Sweden. Kuroda (1921) placed the Siberian *pygmaea*, and his Japanese form *namiyei*, into the North American species *M. rixosa*. Later G. Allen (1933) joined in one species, *M. rixosa,* all small weasels from different regions of the Holarctic known at that time. These included *M. pygmaea* (J. Allen), *M. caucasica* (Barrett-Hamilton), and *M. monticola* (Cavazza). Zimmermann (1943) also recognized the taxonomic separateness of small Palaearctic weasels, but regarded them as subspecies of *M. minuta* (Pomel). Therefore these researchers regarded small and large weasels as separate species, each possessing a set of geographic races (subspecies).

According to another point of view, which became widely spread after the adoption of polytypic concept of species, there exists in the Holarctic only one species *M. nivalis*, with a complex pattern of geographic variation (Barrett-Hamilton, 1900; Kafka, 1900; Miller, 1912; Ognev, 1928; 1935; Ellerman & Morrison-Scott, 1951; Zimmermann, 1959; Heptner et al., 1967; Mazák, 1970; Corbet, 1978; Mandahl & Fredga, 1980; King, 1990; Zyll de Jong, 1992; Reichstein, 1993; Sheffield & King, 1994). It was emphasised that differences between extreme geographic forms of *M. nivalis* are so great that if material is restricted the forms can appear to be separate species. Some taxonomists, following the opinion of Hall (Hall, 1951; Hall & Kelson, 1959), continued for a long time to regard the weasels of North America as a separate species *M. rixosa*, but currently they are usually included in *M. nivalis* as several subspecies. Some times ago Reig (1997) analysed by multivariate statistics the geographic variation in the skulls of *M. nivalis* from North America, Central Europe and Siberia. He came to the conclusion that there are large differences in cranial size and shape between Alaskan form *eskimo* and other North American subspecies (*rixosa* group sensu Reig). In the opinion of Reig, this suggests that North American weasels should be considered a separate species *M. rixosa* (except Alaskan subspecies *M. nivalis eskimo*).

Trying to explain the joint existence of both large and small ("*minuta*") forms in populations of *M. nivalis* from Central Europe, some researchers regarded the small forms as extreme, dwarf specimens (the "minus-variants") (Kafka, 1900; Miller, 1912; Reichstein, 1957, 1993; Zimmermann, 1959; Frank, 1985). It was proposed that the dwarf weasels of Central Europe are "glacial relicts" of a Pleistocene fauna that came from Siberia and persisted in the European highlands (Zimmermann, 1943; Kratochvil, 1951; etc.). It was assumed that the small European weasel, having survived Ice Age in Europe, is now gradually disappearing because of a gradual mixing with the larger form, surviving only in small isolated groups spread through the distribution range of the large weasel.

As was subsequently shown (Frechkop & Misonne, 1952; Mazák, 1970; Grulich, 1977; Meia & Mermod 1992), all studied specimens of "*minuta*" fit the limits of individual (age, sex) variation of the species *M. nivalis*. There is no doubt, however, about the bordering distribution ranges of small and large weasels. Thus Ognev (1928, 1935) and Novikov (1956), separating within the entire Palaearctic eight subspecies of *M. nivalis*, indicate two subspecies for the Caucasus – the large Caucasian weasel *M. nivalis dinniki* (Satunin, 1907) and small Caucasian weasel *M. nivalis caucasica* (Barrett-Hamilton, 1900). As has been noted by Verestchagin (1942, 1959), the distributions of the two subspecies in the Caucasus overlap, both forms being spread ubiquitously and frequently living side by side.

The large long-tailed weasel of Southern Europe and islands of the Mediterranean Sea is most frequently placed in the subspecies *M. nivalis boccamela* Bechstein, 1800 (Miller, 1912; Ognev, 1928, 1935; Ellerman & Morrison-Scott, 1951; Reichstein, 1957, 1993; Atanassov & Peschev, 1963; Barbu, 1968; Beaucournu & Grulich, 1968; Kratochvil, 1977; Sheffield & King, 1994). Sometimes its distribution range is considered to include also the Transcaucasia (Satunin, 1905, 1911; Heptner et al., 1967). Other systematists believed that the distribution range of *boccamela* is restricted to Sardinia, from where it was described (Frechkop, 1963; Mazák, 1970; Corbet, 1978; Douma-Petridou & Ondrias, 1986).

For Southern Europe, other geographic forms of large weasel have been proposed: *M. n. ibericus* (Barrett-Hamilton, 1900) from the Iberian Peninsula, *M. n. siculus* (Barrett-Hamilton, 1900) from Sicily, *M. n. italicus* (Barrett-Hamilton, 1900) from Italy, *M. n. corsicanus* (Cavazza, 1908) from Corsica, *M. n. galinthias* (Bate, 1905) from Crete. The form *dombrowskii* Matschie, 1901 was described from Romania, and *hungarica* Vásárhelyi, 1943 from Hungary.

The large weasel from the Mediterranean, unlike the small Central European weasel, has been given species status less frequently. Ognev (1928, 1935) placed animals inhabiting Egypt, Malta and the Azores in the species *M. africana* Desmarest (i.e. the form *numidica* (Pucheran, 1855) because the name *africana*, as was shown by Cabrera (1913b), belongs to a species of *Mustela* from South America). He regarded the weasel from Crete as a separate species, *M. galinthias*. Zyll de Jong (1992), having conducted craniometric analysis of *M. nivalis,* arrived at the conclusion that the very large Egyptian weasel is a separate species *M. subpalmata* Hemprich et Ehrenberg, 1833 (see also Reig, 1997). In Egypt (Cairo, Alexandria) *M. subpalmata* leads an exclusively synanthropic mode of life. Frank (1985) believes that these animals were brought there by ancient people and this fact (as well as geographic isolation) is responsible for their distinctive characters in coloration and size.

The taxonomic status and distribution of *M. n. numidica* (Pucheran, 1855) are not quite clear. Large weasels from Morocco, Algeria, Tunisia and the Azores are usually attributed to this form. According to Frechkop (1963), it occurs also in Balearic Islands (Majorca), whereas according to Heptner et al. (1967) it occurs in Malta. Some authors (Cabrera, 1923; Frechkop, 1963; Frank, 1985) gave *M. numidica* specific status on the basis of the structure of the baculum and features of coloration. Frechkop (1963) separated weasels into four species – *M. rixosa*, *M. nivalis*, *M boccamela* and *M. numidica*. To the last-mentioned he attributed also the form *iberica* from the Iberian Peninsula.

Weasels of Central and Eastern Asia have been poorly studied. From this region *M. stoliczkana* Blanford 1877 (Kashgaria), *M. russelliana* Thomas, 1911 (Sichuan) and *M. tonkinensis* Björkegren (Northern Tonkin) have been described as separate species. The forms *stoliczkana* and *russelliana* are currently regarded as subspecies of *M. nivalis* (Ellerman & Morrison-Scott, 1951; Heptner et al., 1967; Corbet & Hill, 1992), although G. Allen, as early as 1938, regarded weasels of southern China (*russelliana, stoliczkana*) as species distinct from *M. nivalis*. The identity of the Vietnamese form *tonkinensis* with the species *M. nivalis* has frequently been doubted (Ellerman & Morrison-Scott, 1951; Heptner et al., 1967), although in recent time it has been regarded as its subspecies (Corbet & Hill, 1992). Björkegren (1942) believes that the species described by him was most closely related to *stoliczkana*.

Many researchers that considered weasels from the standpoint of a single polytypic species *M. nivalis* tried to analyse its geographic variation and reveal intraspecific structure. For the separation of subspecies most frequently general body size, tail length and features of coloration have been used. One of the most logical classifications was proposed by Morozova-Turova (Morozova-Turova, 1965; Heptner et al., 1967). She separated three groups of subspecies: small short-tailed weasels of the group *pygmaea-rixosa* (Northern Europe, Siberia, Mongolia, North-Eastern China, Japan, North America); large long-tailed weasels of the group *boccamela* (Mediterranean, Transcaucasia, Asia Minor, Fore-Asia, Kazakhstan, Middle Asian plains, Kopet-Dag Mountains, Afghanistan); middle-sized weasels of the intermediate group *nivalis* (middle region of Europe, Northern Caucasia, Western Kazakhstan, Urals, mountain area of Middle Asia, except Kopet-Dag Mountains).

In the opinion of Morozova-Turova and Heptner, the nominotypical subspecies of *M. n.*

nivalis inhabiting Northern Europe (except the northern part of Scandinavia, Finland and north of European Russia) is one of the stages in the transition from the small *pygmaea* to a larger *vulgari*s, and further to very large southern weasels of *boccamela* type. The region of mixing and the proportion of transitional individuals are relatively large in both directions, i.e. *pygmaea* and *vulgaris*. Individual variation of this form is high, and along with weasels of "normal size" throughout nearly the entire distribution range of *nivalis*, very small ("*minuta*") forms occur. Separate individuals and small populations of relatively large animals occur. Grulich (1977) held to a similar system of subspecies.

It should be noted that one of the propositions underlying the system of Morozova-Turova and Heptner was erroneous. As a result, the nomenclature appeared to be inaccurate. Heptner indicated that the Swedish province Västerbotten, which is the type locality for *M. nivalis*, is situated between 60° and 61° N. According to his scheme, the form *nivalis* was shifted further south, and small weasels of Northern Europe (Scandinavia, north of European part of Russia) were placed in *pygmaea*. The same concepts of nomenclature were proposed by a number of European authors (Siivonen, 1967; Grulich, 1977; Kratochvil, 1977). In reality Västerbotten Province is situated further north. The Swedish zoologist Stolt (1979) refined the type locality for *M. nivalis* to latitude 64° 30′ N. Therefore the nominotypical subspecies includes small animals of the northernmost parts of the European continent.

The modern system of subspecies for *M. nivalis* according to Reichstein (1993) looks as follows: *nivalis*, *pygmaea*, *rixosa*, *vulgaris*, *boccamela*, *iberica*, *corsicana*, *galinthias*; *M. numidica* is possibly a separate species. Sheffield & King (1997) accepted four Nearctic subspecies – *allegheniensis*, *campestris*, *eskimo*, *rixosa*, and six Palaearctic subspecies – *boccamela*, *namiyei*, *nivalis*, *numidica*, *subpalmata*, *vulgaris*. However Zyll de Jong (1992) accepts for Europe only two subspecies – *M. n. nivalis* (relatively small weasels of northern regions) and *M. n. vulgaris* (middle and southern regions).

Material and methods

The authors studied the collections of 26 zoological museums across the world (see Table 1 for their names and acronyms).

A total of 765 skulls (including 421 complete skulls of adult males) and 1769 skins (including specimens in alcohol and formalin) were examined. The amount of material studied is shown in Table 1. In addition, bacula of 46 specimens were examined.

The skull of the weasel is characterized by a high degree of age and sexual variation in size and proportions (see King, 1980). Therefore, the combined use of data from specimens of different ages and sexes leads, in our opinion, to inaccuracies and errors in comparison of metric parameters from different samples. To preclude such errors as much as possible, skulls of adult males alone were used in statistical analysis. Regarded as adult were specimens with adnate (or unobtrusive) nasal sutures, postorbital width equal to or smaller than preorbital width, and weak (or no) rugosity of braincase (see also Meia, 1990a; Schmidt, 1992). Data on available females and young specimens were also used for comparative analysis, but without the application of multivariate statistics. Twenty-one measurements were made on each skull using sliding callipers with the accuracy of 0.1 mm. The measurement scheme is indicated in Fig. 1.

For statistical analysis, skulls of adult males were divided into the following samples: North-Eastern Europe (n = 27), England (n = 30), France (n = 22), Italy (n = 4), Central Europe (n = 45), Crimea (n = 7), central part of European Russia (n = 13), Spain (n= 15), Southern Europe (n = 21), Greece (n = 1), Crete (n = 2), Malta (n = 2), Corsica (n = 2), Sardinia (n = 4), Sicily (n = 5), Majorca (n = 3), Azores (n = 1), North-Western Africa (n = 5), Egypt (n = 17), Turkey (n = 5), Caucasus (n = 10), Iran (n = 3), Middle Asia (Turkmenistan, Uzbekistan) (n = 21), Kirgizstan (n = 15), Lob-Nor, China (n = 1), Northern Tonkin, Vietnam (n = 1), Yamal (n = 7), Urals (n = 5), Northern Kazakhstan (n = 10), Western Siberia (n = 28), Altai (n = 11), Central Siberia (n = 30), North-Eastern Siberia (n = 14), Kunashir Island (n = 1), Hokkaido (n = 14), Alaska (n = 2), Minnesota (n = 16), Ohio (n = 4). Factor analysis also included one female from Sichuan (type specimen of *M. russelliana*). The means and coefficients of variations for each sample listed in Table 2.

Craniometric characters were analysed with multivariate statistics using the program STATISTICA 4.5 for Windows. The following exterior parameters were used for

Table 1. Material examined (including skins of alcohol- and formalin-preserved specimens)

Collection	Skulls		Skins
	♂♂	♀♀	
Zoological Institute, Saint-Petersburg, Russia (ZIN)	71	11	295
Zoological Museum, Moscow State University, Moscow, Russia (ZMMU)	122	52	381
Institute of Animal Systematics and Ecology, Novosibirsk, Russia	42	12	
Institute of Plant and Animal Ecology, Ekaterinburg, Russia	5		
Department of Zoology, Penza State Pedagogical University, Penza, Russia	4	2	
Institute of Zoology, Yakutsk, Russia	3	1	
Institute of Biological Problems of North, Magadan, Russia	3	8	12
Institute of Zoology, Yerevan, Armenia	5	1	4
Institute of Zoology and Soil, Bishkek, Kirgizstan	13	6	9
Institute of Zoology and Genofunds of Animals, Almaty, Kazakhstan	20	10	13
Kazakh Antiplague Research Institute, Almaty, Kazakhstan	11	2	23
Natural History Museum, London, England (NHM)	112	5	282
Zoological Museum, University of Helsinki, Helsinki, Finland	16	14	82
Swedish Museum of Natural History, Stockholm, Sweden	14	5	1
Basel Museum of Natural History, Basel, Switzerland	9	2	6
Museum National d'Histoire Naturelle, Paris, France	8	1	
Senkenberg Museum, Frankfurt am Main, Germany	14	6	
National Museum (Natural History), Prague, Czech Republic	54		136
Department of Zoology, Charles University, Prague, Czech Republic	2		332
Institute of Vertebrate Biology, Brno, Czech Republic			134
Field Museum of Natural History, Chicago, USA	30	15	
Illinois State Museum, Springfield, USA	3		
Museum of Natural History, John Werner University of Illinois, Urbana, USA	8	6	
Bell Museum of Natural History, University of Minnesota, Saint Paul, USA	11	6	28
The Museum, Faculty of Agriculture, Hokkaido University, Sapporo, Japan	13	5	23
National Science Museum, Tokyo, Japan (NSM)	2		8
Total	595	170	1769

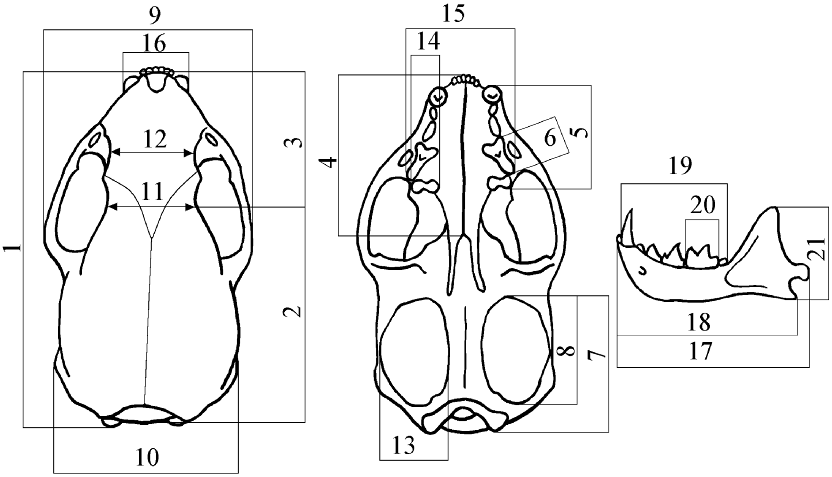

Fig. 1. Cranial measurements of least weasel *Mustela nivalis*. **1**, condylobasal length (CbL); **2**, upper neurocranium length (NcL); **3**, viscerocranium length (VcL); **4**, median palatal length (PtL); **5**, maxillary toothrow length (MxtL); **6**, upper carnassial teeth P^4 length (PuL); **7**, greatest length between oral border of the auditory bulla and aboral border of the occipital condyles (BcL); **8**, greatest diameter of the auditory bulla (AbL); **9**, zygomatic breadth (ZyB); **10**, greatest mastiod breadth (GmB); **11**, least breadth aboral of the supraorbital processes (PoB); **12**, least breadth between the orbits (InB); **13**, least diameter of the auditory bulla (AbB); **14**, upper molar M^1 breadth (MuB); **15**, greatest palatal breadth (GpB); **16**, breadth at the canine alveoli (CaB); **17**, total length of the mandible (TmL); **18**, length between the angular process and infradentale (AmL); **19**, mandibular toothrow length (MatL); **20**, length of lower carnassial teeth M_1 (MlL); **21**, height of mandible in the vertical ramus (MaH).

Table 2. Population means (above) and coefficients of variation (below) for the 21 cranial variables studied

Localities	n	CbL	NcL	VcL	PtL	MxtL	PuL	BcL	AbL	ZyB	GmB	PoB	InB	AbB	MuB	GpB	CaB	TmL	AmL	MatL	M_1L	MaH
NE. Europe	27	33.50	22.78	13.57	13.17	8.62	3.34	14.01	11.58	17.24	15.98	7.85	7.23	5.83	9.83	5.10	2.62	16.50	15.16	10.10	3.58	7.62
		1.0	0.4	1.0	0.3	0.1	0.1	0.2	0.2	0.7	0.3	0.5	0.2	0.1	0.2	0.1	0.1	0.6	0.4	0.2	0.1	0.2
England	30	38.25	22.87	17.12	15.83	10.45	3.87	15.52	12.39	20.63	18.07	8.64	8.44	8.29	11.92	6.80	3.06	19.70	18.51	11.70	4.12	9.24
		1.4	1.1	1.9	0.3	0.2	0.1	0.3	0.3	1.2	0.6	0.2	0.5	0.2	0.3	0.2	0.1	0.5	0.6	0.3	0.1	0.3
France	22	38.10	22.65	17.19	16.08	10.54	3.95	15.36	12.39	20.20	18.00	8.43	8.26	8.20	11.76	6.57	3.24	19.72	18.62	11.98	4.21	9.38
		8.8	2.7	5.1	2.1	0.9	0.1	1.4	0.7	4.9	2.6	0.4	0.9	0.9	1.5	0.7	0.1	3.9	4.0	1.2	0.2	1.3
Italy	4	41.43	23.83	19.42	17.78	11.58	4.25	16.40	13.20	22.03	20.03	8.08	8.93	9.03	12.88	7.07	3.23	22.30	20.95	13.40	4.55	10.58
		1.4	3.8	1.2	0.3	0.1	0.1	0.4	0.1	0.2	0.5	0.1	0.2	1.0	0.1	0.6	0.1	0.8	0.8	0.1	0.1	0.5
C. Europe	45	37.97	23.02	17.19	15.78	10.25	3.86	15.41	12.42	20.14	17.99	8.13	8.13	7.88	11.67	6.48	3.05	19.80	18.44	11.94	4.12	9.46
		8.4	4.3	4.0	2.3	0.8	0.1	1.5	0.9	4.1	2.1	0.6	0.7	0.8	0.9	0.6	0.1	3.8	3.4	1.0	0.1	0.9
Crimea	7	38.41	24.14	17.07	16.10	10.59	3.87	15.73	13.00	20.09	17.79	8.19	8.20	6.90	11.61	5.77	3.03	20.67	18.62	12.12	4.48	9.03
		1.4	0.9	0.3	0.8	0.1	0.1	0.7	0.3	0.7	0.4	0.3	0.1	0.1	0.4	0.2	0.1	0.2	0.2	0.3	0.1	0.3
C. Russia	13	37.34	23.89	16.28	15.21	10.02	3.75	15.34	12.55	19.42	17.72	7.77	7.84	6.75	11.25	5.53	3.00	19.65	18.03	11.85	4.08	8.83
		7.2	2.2	2.7	1.8	0.6	0.1	1.1	0.8	4.8	3.0	0.5	0.5	0.6	0.9	0.4	0.1	2.7	2.3	0.9	0.1	0.8
Spain	15	39.93	22.64	18.26	16.47	10.87	3.97	16.06	12.71	22.01	19.29	8.20	8.53	8.78	12.50	7.10	3.15	20.88	19.69	12.55	4.21	10.17
		2.5	2.7	2.7	1.3	0.2	0.1	0.3	0.2	2.1	1.3	0.3	0.4	0.5	0.6	0.2	0.1	1.1	1.1	0.3	0.1	0.9
S. Europe	17	42.66	25.29	19.81	17.96	11.62	4.23	17.05	13.73	23.28	20.61	8.24	9.13	8.41	13.00	6.77	3.28	23.21	21.58	13.62	4.60	10.96
		8.9	3.7	4.0	2.1	0.9	0.1	1.8	1.1	4.3	3.1	0.7	1.0	1.0	0.8	0.7	0.1	4.0	3.7	1.2	0.1	1.3
Greece	1	45.40	25.10	21.90	19.10	12.20	4.50	18.10	14.30	26.40	22.40	9.30	10.30	10.70	14.30	7.70	3.40	24.10	23.70	14.00	4.60	12.50
Crete	2	44.75	25.85	21.60	19.45	12.90	4.70	17.50	14.05	25.95	22.25	9.45	10.45	11.05	14.55	7.35	3.85	24.60	23.25	14.50	5.20	11.40
		2.8	3.1	1.1	1.0	0.1	0.1	0.2	0.1	1.3	0.3	0.1	0.1	0.1	0.7	0.1	0.1	1.3	1.3	1.1	0.1	0.1
Malta	2	44.00	28.00	22.05	20.70	13.15	4.60	16.00	14.00	25.30	22.00	7.75	9.85	10.55	15.20	6.70	3.70	25.95	24.35	15.70	5.15	12.00
		-	2.0	1.4	2.0	0.6	0.2	0.2	0.1	0.3	0.2	0.1	0.1	0.4	0.5	0.1	0.1	0.8	2.2	0.1	0.1	0.1
Corsica	2	44.90	27.35	21.15	19.50	11.80	4.25	17.60	14.15	24.15	21.60	8.95	9.75	8.90	13.40	6.60	3.60	24.35	22.80	13.85	4.85	11.25
		3.9	5.4	1.8	1.3	0.2	0.1	0.5	0.1	2.6	0.1	0.0	0.1	0.1	1.0	0.1	0.1	3.6	1.3	1.4	0.1	0.1

Table 2 (continued)

Localities	n	CbL	NcL	VcL	PtL	MxtL	PuL	BcL	AbL	ZyB	GmB	PoB	InB	AbB	MuB	GpB	CaB	TmL	AmL	MatL	M_1L	MaH
Sardinia	4	42.30	26.33	18.93	18.40	11.38	4.13	16.63	13.15	23.55	21.45	7.98	9.15	8.75	12.83	7.00	3.38	22.65	21.28	13.56	4.33	10.45
		0.6	0.1	1.1	0.1	0.1	0.1	0.1	0.1	0.7	0.4	0.1	0.1	0.4	0.1	1.6	0.1	0.5	0.1	0.1	0.0	0.4
Sicily	5	42.76	22.73	20.60	18.30	11.82	4.30	16.58	13.08	24.34	20.52	8.34	8.98	9.76	13.10	7.96	3.38	22.72	22.12	13.56	4.54	11.34
		0.8	1.0	0.3	0.1	0.1	0.1	0.2	0.1	0.8	0.6	0.5	0.1	0.1	0.4	0.2	0.1	0.3	1.0	0.1	0.1	0.1
Majorca	3	37.30	23.30	18.47	17.37	11.27	4.23	14.80	13.00	21.70	19.90	7.43	8.83	9.47	12.77	7.00	3.40	22.33	21.43	13.13	4.53	10.07
		4.2	0.7	2.3	2.6	0.7	0.2	101.0	1.7	2.7	2.2	0.8	0.4	0.4	0.4	0.1	0.1	4.2	7.0	0.7	0.2	1.1
Azores	1	42.20	22.70	20.60	18.30	11.30	4.00	16.90	13.40	22.40	21.30	8.70	9.20	9.50	12.70	7.90	3.50	22.90	21.50	12.50	4.20	11.00
NW. Africa	5	43.22	25.08	19.58	18.30	12.00	4.46	17.34	14.06	22.90	20.60	8.48	9.54	9.82	13.36	7.18	3.42	23.58	22.38	13.74	4.76	11.04
		7.5	0.4	6.0	1.7	0.3	0.1	1.4	0.7	3.5	2.8	3.4	0.8	1.2	0.7	0.9	0.1	3.4	3.5	0.6	0.1	1.6
Egypt	17	49.20	26.34	22.94	20.97	13.34	4.70	18.97	14.52	27.36	24.96	8.69	10.69	11.52	15.52	8.26	3.72	27.12	25.55	15.43	4.79	12.85
		1.7	1.4	1.4	0.9	0.3	0.1	0.2	0.3	1.9	0.9	0.5	0.5	0.5	0.3	0.4	0.1	1.5	1.0	0.4	0.1	0.4
Turkey	5	40.60	22.68	19.36	17.02	11.32	4.18	16.38	13.08	21.00	19.38	8.78	8.82	8.04	12.66	6.86	3.30	21.84	20.10	13.08	4.36	10.02
		2.6	2.1	1.9	0.6	0.4	0.1	0.1	0.1	0.2	0.4	0.1	0.3	1.3	0.7	0.8	0.1	0.9	1.2	0.5	0.1	0.1
Caucasus	10	40.76	23.59	18.69	17.06	10.84	3.99	16.13	13.04	21.23	19.03	8.20	8.71	7.49	11.84	6.39	3.03	21.29	19.60	12.69	4.25	9.92
		10.7	5.7	11.5	2.6	2.1	0.3	0.9	0.5	9.9	5.7	0.2	1.4	1.3	2.7	0.3	0.2	9.5	8.9	2.9	0.3	3.1
Iran	3	43.33	24.27	20.07	18.00	12.10	4.47	17.30	13.80	23.63	21.43	9.27	9.60	9.40	13.87	7.97	3.70	23.40	22.37	13.93	4.93	11.50
		2.8	0.4	1.7	0.8	0.4	0.1	0.4	0.3	2.3	0.1	0.9	0.5	0.3	0.1	0.2	0.1	2.4	1.1	0.2	0.1	0.2
Middle Asia	21	41.99	26.11	19.09	18.16	11.74	4.41	17.11	13.90	23.34	20.04	7.89	9.25	8.21	13.45	6.81	3.40	23.33	21.71	13.80	4.74	10.80
		3.6	1.3	1.9	1.2	0.4	0.2	1.3	0.7	4.4	3.0	0.5	0.6	0.6	1.1	1.0	0.1	1.8	1.5	0.7	0.1	0.7
Kirgizstan	15	37.39	23.77	16.59	16.23	10.52	4.05	15.40	12.41	18.99	17.09	7.24	8.14	7.06	11.66	5.75	3.03	20.27	18.99	12.25	4.26	9.35
		1.5	1.3	1.1	0.4	0.3	0.1	0.5	0.6	8.4	1.0	0.8	0.3	0.4	0.6	0.3	0.1	1.0	1.0	0.4	0.1	0.3
Lob-Nor	1	46.10	28.00	21.60	19.20	12.40	5.00	19.30	15.60	25.40	21.20	6.50	9.50	8.80	14.00	7.30	3.70	25.00	23.40	14.90	5.40	12.80
Sichuan	1	29.00	17.10	12.20	10.90	7.80	2.80	11.70	10.10	14.70	13.80	7.20	6.00	5.40	9.60	4.90	2.20	13.30	13.00	7.80	3.40	7.00
N. Tonkin	1	37.30	24.50	15.80	15.70	9.80	3.60	15.00	10.60	18.60	15.50	7.00	7.50	6.10	10.30	4.50	3.00	19.60	18.20	11.20	4.00	9.70

Table 2 (end).

Localities	n	CbL	NcL	VcL	PtL	MxtL	PuL	BcL	AbL	ZyB	GmB	PoB	InB	AbB	MuB	GpB	CaB	TmL	AmL	MatL	M_1L	MaH
Yamal	7	33.94	23.21	13.54	13.56	8.83	3.44	14.37	11.83	18.16	16.19	7.50	7.30	6.36	10.43	5.24	2.59	16.93	15.69	10.51	3.71	7.94
		0.5	0.3	0.4	0.4	0.1	0.1	0.2	0.2	1.3	0.6	0.2	0.1	0.1	0.3	0.3	0.1	0.2	0.4	0.2	0.1	0.2
Urals	5	32.82	22.22	13.32	13.38	8.50	3.32	13.32	10.92	15.28	15.38	7.28	6.88	6.00	9.64	5.24	2.56	16.26	15.10	10.14	3.66	7.60
		2.7	1.4	2.1	0.3	0.1	0.1	0.2	0.1	1.2	2.5	0.8	0.1	0.3	0.1	0.1	0.1	0.4	0.6	0.2	0.1	0.1
N. Kazakhstan	10	33.80	21.30	14.20	13.67	8.53	3.33	13.93	11.37	17.68	14.98	6.73	7.09	6.04	9.28	5.07	2.43	16.80	15.50	10.10	3.60	8.20
		1.1	0.8	0.2	0.1	0.2	0.1	0.4	0.1	0.9	0.8	0.5	0.3	0.1	1.7	0.1	0.1	0.2	0.2	0.2	0.1	0.3
Altai	11	34.11	23.11	13.95	13.49	8.79	3.39	14.21	11.86	17.17	16.25	8.28	7.31	5.83	9.98	5.14	2.60	16.73	15.25	10.47	3.72	7.93
		0.9	1.0	0.1	0.4	0.1	0.1	0.2	0.2	0.2	0.4	0.6	0.1	0.1	0.1	0.1	0.1	0.4	0.3	0.1	0.1	0.1
W. Siberia	28	33.16	22.29	13.50	13.14	8.73	3.37	13.85	11.48	16.73	15.31	7.66	7.14	5.77	9.95	5.07	2.61	16.36	15.01	10.24	3.70	7.59
		1.4	1.0	0.8	0.4	0.2	0.1	0.4	0.3	1.5	0.8	0.4	0.4	0.1	0.3	0.2	0.1	0.7	0.5	0.2	0.1	0.2
C. Siberia	30	32.96	22.43	13.33	13.20	8.62	3.37	14.06	11.62	16.63	15.63	7.56	7.04	5.88	10.00	5.18	2.56	16.39	14.93	10.25	3.60	7.64
		1.0	0.7	0.8	0.3	0.2	0.1	0.3	0.2	1.2	0.4	0.3	0.3	0.2	0.3	0.2	0.1	0.7	0.6	0.2	0.1	0.2
NE. Siberia	14	32.83	22.52	13.17	13.13	8.61	3.35	14.18	11.64	17.14	16.13	7.62	7.06	6.07	10.15	5.34	2.56	16.44	14.91	10.17	3.59	7.67
		1.1	0.6	0.4	0.3	0.1	0.1	0.5	0.6	0.6	0.5	0.3	0.2	0.1	0.1	0.1	0.1	0.4	0.2	0.1	0.1	0.1
Kunashir	1	31.60	22.40	12.30	13.00	8.40	3.00	12.50	10.10	15.90	15.70	7.60	6.30	5.50	9.60	4.50	2.30	16.00	14.50	9.50	3.30	7.20
Hokkaido	15	34.08	22.57	14.29	13.72	8.93	3.41	13.73	11.16	17.45	16.17	7.67	7.43	5.91	10.01	4.97	2.66	17.47	16.21	10.34	3.63	7.99
		3.3	1.7	1.3	1.0	0.3	0.1	0.5	0.4	1.1	0.9	0.3	0.2	0.2	0.4	0.1	0.1	1.3	1.3	0.4	0.1	0.4
Alaska	2	34.45	22.20	13.70	14.30	8.95	3.55	14.35	12.05	17.85	16.10	7.75	7.30	6.70	10.70	5.20	2.45	17.15	15.95	10.65	3.75	8.10
		0.5	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	101.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Minnesota	16	32.08	20.15	13.69	12.64	8.64	3.18	13.11	10.68	16.15	14.93	7.27	6.60	6.38	9.66	5.54	2.53	16.15	14.76	9.90	3.62	7.50
		1.1	1.1	0.6	0.3	0.1	0.1	0.2	0.2	0.7	0.5	0.2	0.2	0.2	0.2	0.1	0.1	0.5	0.5	0.3	0.1	0.2
Ohio	4	31.63	19.00	14.00	12.80	8.58	3.13	13.08	10.60	16.88	15.18	7.10	6.73	6.03	9.48	5.73	2.43	16.28	14.88	9.85	3.30	7.08
		1.0	1.0	0.2	0.1	0.1	0.1	0.2	0.1	0.6	0.2	0.9	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2

comparison of samples from different geographic localities: body length (L), tail length (C), length of hind foot (Pl), relative tail length (C/L), relative foot length (Pl/L). Coloration of summer fur was also studied.

Variability of craniometrical features

Sizes and proportions of skulls of *M. nivalis* from different parts of its world distribution were analysed using principal components analysis. Craniometric features did not show significant correlation with geographic co-ordinates. Similar results have been obtained for North America (Ralls & Harvey, 1985) and for Europe (Meia, 1990b). There is a tendency for increase of average skull size observed from north to south, particularly in Europe (see also Reichstein, 1957), and to some extent from east to west. This tendency disappears in the analysis of features in separate individuals because the range of individual variation in weasels is relatively high; not infrequently within one population animals occur which are close in size to individuals from a different geographic sample. This feature of *M. nivalis* was noted a long time ago and frequently separate taxa were described on this basis. Examples are the supposed forms *minuta* and *monticola* in Europe, *caucasica* in the Caucasus and possibly *pallida* from the mountain areas of Middle Asia.

Craniometric features used in the study appeared to be strongly correlated. In principal components analysis, all characters except the postorbital width were combined in the first factor (total skull size), which accounts for 89.2 percent of the variance (Table 3). The results of comparing samples by mean values on the first two factors are shown in Fig. 2. Samples studied can be divided into three size groups: small, middle and large weasels. They partly correlate with the subspecies groups of Morozova-Turova (1965). The first one includes animals from the north of Scandinavia and European Russia, Urals, the whole of Siberia and North America. Differences within this group, in comparison with the entire range of variation among the samples studied, are very small. It should be noted that weasels from Scandinavia and north-west Russia (*nivalis*) were similar to animals from North-Eastern Siberia (*pygmaea*). Samples from Western and Eastern Siberia (Yakutia) reveal no significant differences between themselves in the craniometric characters studied (t-criterion). Weasels from Yamal, Urals and Northern Kazakhstan in their turn do not differ notably from animals from Finland and north-western regions of Russia on the one hand, and from weasels of Eastern Siberia on the other. Weasels from North America appear at the background of variation of *M. nivalis* quite similar among themselves, and only the form *eskimo* (Alaska) has somewhat larger sizes.

Table 3. Factor loadings from principal component analysis of 21 cranial variables from *Mustela nivalis* males

Variables	Factor 1	Factor 2	Factor 3
Cbl	0.9853	0.0216	-0.0658
NcL	0.7679	0.4947	-0.3587
VcL	0.9833	-0.0672	0.0868
PtL	0.9851	0.0564	0.0402
MxtL	0.9929	-0.0059	0.0392
PuL	0.9811	0.1184	0.0158
BcL	0.9480	0.0857	-0.1197
AbL	0.9398	0.1424	-0.1268
ZyB	0.9886	-0.0332	0.0316
GmB	0.9784	-0.0851	0.0065
PoB	0.4517	-0.7979	-0.3959
InB	0.9867	-0.0804	-0.0073
AbB	0.9010	-0.2679	0.2349
MuB	0.9701	-0.0144	0.0460
GpB	0.9892	-0.0455	0.0147
CaB	0.9429	-0.2153	0.1489
TmL	0.9911	0.0516	0.0401
AmL	0.9924	0.0152	0.0736
MatL	0.9859	0.0984	0.0391
M_1L	0.9385	0.1584	-0.1228
MaH	0.9755	0.0320	0.0968
Expl. Var.	18.7325	1.1053	0.4450
Prp. Totl.	0.8920	0.0526	0.0211

M. nivalis from Western and Central Europe is similar in skull size to weasels of the Ukraine (Crimea included) and the middle and southern regions of European Russia. The same size group includes specimens from Kirgizstan (form *pallida*). To a larger extent, differences between these groups

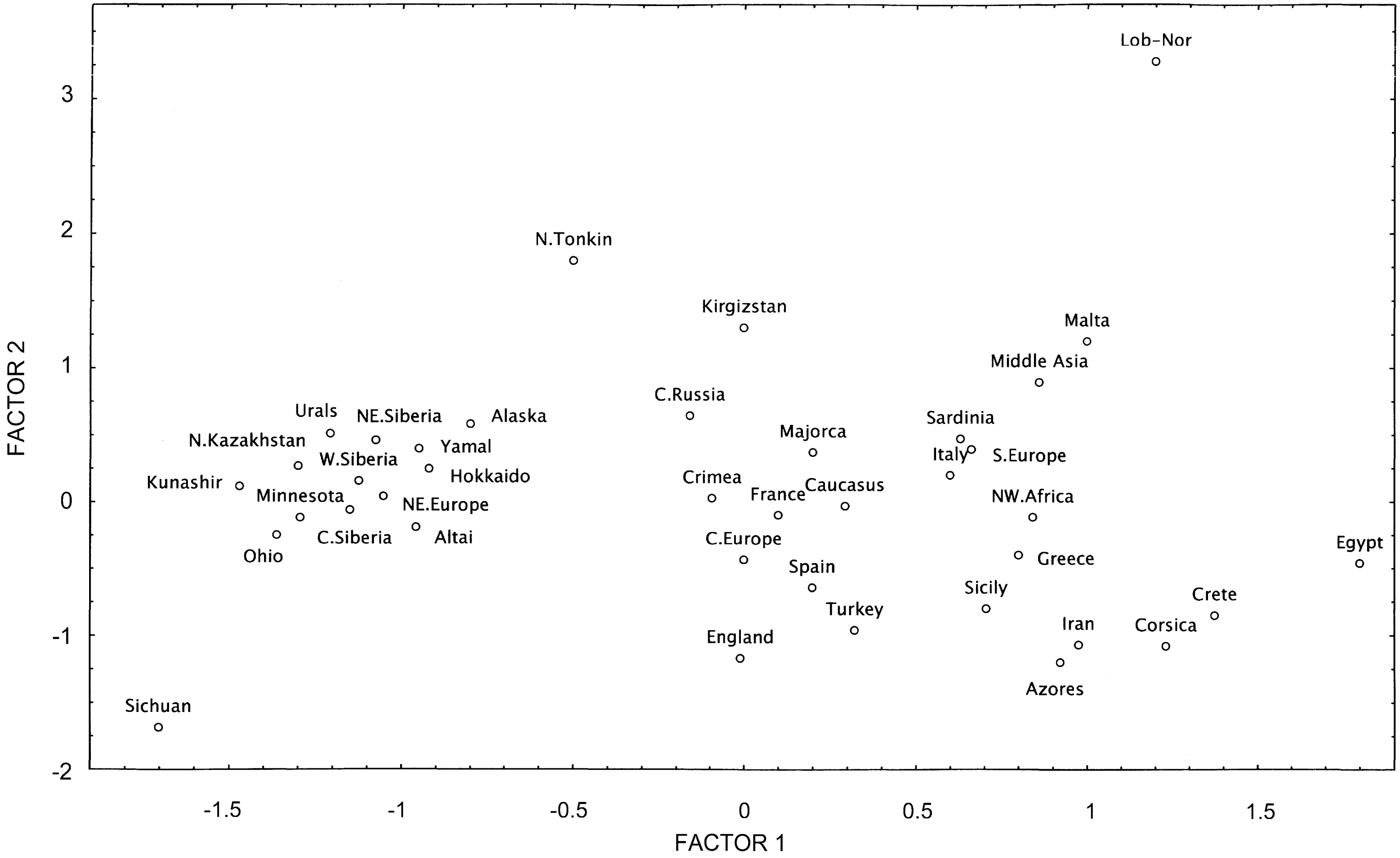

Fig. 2. Results of factor analysis of different geographic samples of male *M. nivalis* based on two factors (Factor 1 and Factor 2).

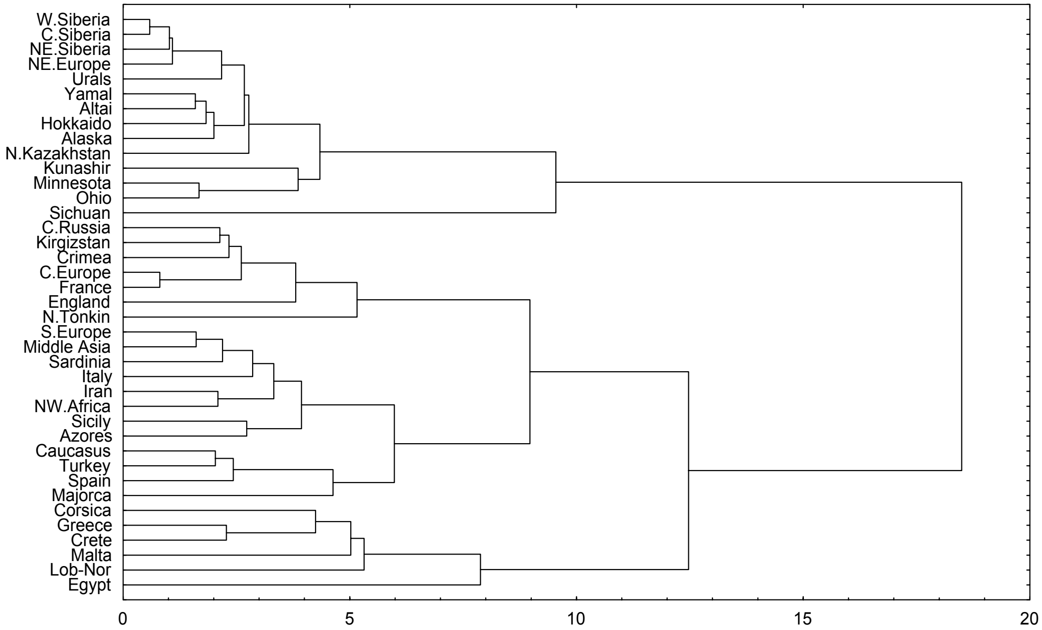

Fig. 3. Distance phenogram summarizing the morphometric relationships (Ward method) among different geographic samples of male *M. nivalis*.

were noted in the size of the postorbital narrowing (factor 2).

In skull size, Vietnamese form *tonkinensis* is closer to the group of small weasels, but is characterized, like *pallida,* by considerable postorbital narrowing.

Large weasels inhabit Southern Europe, North-Western Africa, Fore-Asia and Central Asia. In this group of samples, maximum skull sizes are observed in populations furthest to the south. *M. nivalis* from Bulgaria, Turkey and the Caucasus in mean values of craniometric variables is between Central European and South European animals. Asian weasels (Iran, Turkestan and Western China) are close in skull size to large individuals from Southern Europe.

Among Central Asian weasels the specimen from the vicinity of Lob-Nor Lake, North-Western China (ZIN No. 0.9881) is distinguished by strong postorbital narrowing. This character, as already noted, is related to the animal's individual age. It is beyond doubt that the development of the postorbital constriction is bound by a negative allometric relationship with the general size of the skull. Small weasels have in general juvenile proportions of the skull even in quite adult males. However, in large animals the postorbital constriction may be very sharply pronounced.

The weasel from Egypt attains maximum sizes for *M. nivalis*. This feature of the Egyptian weasel was already noted by Zyll de Jong (1992).

The results of UPGMA cluster analysis of the matrix of Euclidean distances between the samples, are shown in a dendrogram (Fig. 3). Small boreal forms are joined in one cluster (group *nivalis-pygmaea-rixosa*), weasels of average size (group *vulgaris*) form another cluster, while all large forms (group *boccamela*) form a third. The Egyptian weasel (*subpalmata*) is placed in the third cluster, but is distinctly separated from its other members.

Sexual dimorphism of the cranium

In *M. nivalis*, skulls of males are always much larger than those of females. In large subspecies the difference in size is much more pronounced than in small ones (Reichstein, 1957; Heidt, 1970). Reichstein noted also differences in proportions: in females the skull is relatively narrower. Variability in size and shape of the skull in males is higher

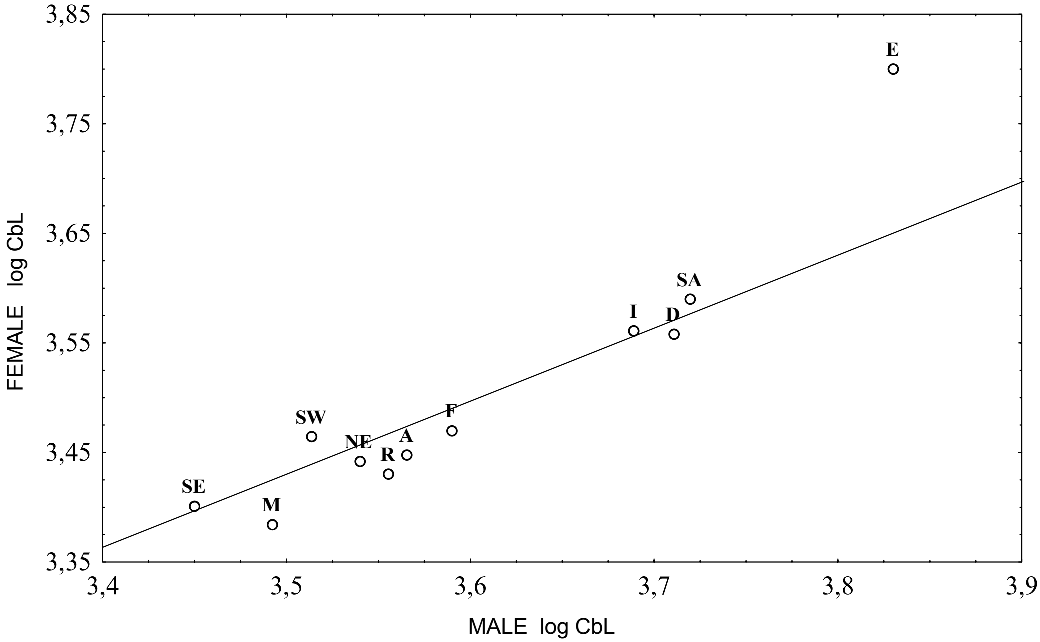

Fig. 4. Sexual dimorphism of size in *M. nivalis* from different localities. A – England, I – Spain, F – France, D – Southern Europe, NE – North-Eastern Europe, R – Central Russia, SA – Middle Asia, SW – Western Siberia, SE – North-Eastern Siberia, M – Minnesota, E – Egypt.

than in females (Reichstein, 1957; Schmidt, 1992). According to Grulich (Beaucournu & Grulich, 1968; Grulich, 1977), sexual dimorphism in the size of the skull of European weasel becomes more pronounced from north to south, i.e. proportionately to the increase in general size of the animals.

The results of investigation of the relationship of size in females and males of *M. nivalis* are shown in Fig. 4. According to this data, the Egyptian weasel alone displays a different relationship between skull sizes of males and females. In this case sexual dimorphism is less pronounced than might be expected in animals of such large size. Similar results for samples from the other populations of *M. nivalis* were obtained by Zyll de Jong (1992). In the opinion of Zyll de Jong, this is an additional argument in favour of the view that *M. subpalmata* is a separate species. For weasels of North America, no correlation has been revealed between the degree of sexual dimorphism and geographical origin (Ralls & Harvey, 1985).

Structure of baculum

The morphology of the baculum (os penis) plays an important role in the systematics of Mustelidae. In the majority of cases in *M. nivalis*, this small bone has a nearly straight shaft, triangular in cross section. The dorsal side is weakly concave. The lower side is flattened with a deep urethral groove which continues in the proximal end of the bone as a hook-like bend. The groove may stretch along the entire length of the baculum or only along its distal half. In small weasels (*nivalis*, *pygmaea, rixosa*) the baculum attains 13-15 mm in length; in the large Turkmenian weasel *heptneri* it is 19-23 mm. The structure of the baculum of *M. nivalis* from different localities is shown in Figs 5, 6.

The baculum of the Berberian weasel (*M. nivalis numidica*) has a different structure (Cabrera, 1923). The shaft is bent upwards in the distal part and is slightly reminiscent of the baculum of ermine *Mustela erminea*, but at the end it has a hook-like bend as in the majority of representatives of the genus *Mustela*. Length of the baculum in the specimen from Algeria was 20.0 mm (NHM No. 57.297a).

Frechkop (1963) assumed that the Spanish (continental) weasel has a baculum of *numidica* type, and on this basis he regarded the name *iberica* as a junior synonym of *numidica*. He also paid attention to the drawing of the baculum of a weasel from France (Cantal and Seine regions) in the work by Didier (1947), in which it does not differ from the typical *numidica*. In the opinion of Frechkop, this indicates that *M. numidica* (in the form of *iberica*) is distributed throughout Spain and into France. In animals from Majorca, the os penis is of the same shape as in *numidica* (Frechkop, 1963).

The shape of the baculum in animals from different islands of the Mediterranean varies slightly. Weasels from Corsica and Sardinia have bacula of shape typical of *M. nivalis*, i.e. with straight shaft and hook on the distal end (Frechkop, 1963; Beaucournu & Grulich, 1968). Zimmermann (1953) gives a drawing of the baculum of a weasel from Crete (*galinthias*); the bend of the shaft is not as pronounced as in *M. numidica* in the drawing of Cabrera (1923). In the opinion of Zimmermann, the differences in the structure of the baculum in continental *M. nivalis* and the Cretan weasel are not great. The specimen studied by us from Crete (NHM No. 45.158) also has an ascending distal part of the shaft, and the terminal hook is well developed; length of the bone is 23.4 mm (Fig. 5D).

Cavazza (1915) noted that in the Alpine form *monticola,* the shaft of the baculum is bent as in *numidica*, and the length of the bone is 14.2 mm (Fig. 5A). Typical *vulgaris* from the same Alpine region has a baculum with a straight shaft, 19 mm in length. Cavazza admits notable variation in the degree of curvature of the shaft.

In *M. subpalmata* (NHM No. 1938.6.34.34) the distal end of the baculum is slightly elevated, but the terminal hook is weakly developed. The urethral groove divides it anteriorly into two lobes, of which the left is larger. Length of os penis is 25.9 mm.

In order to evaluate the systematic value of the noted differences in the shape of the baculum, it is necessary to reveal variability in the structure of the bone from different parts of the distribution range; all the more so, because in other species of *Mustela*, such as the American mink *M. (Neovison) vison*, the degree of curvature of baculum shaft can vary notably even within one population (Elder, 1951).

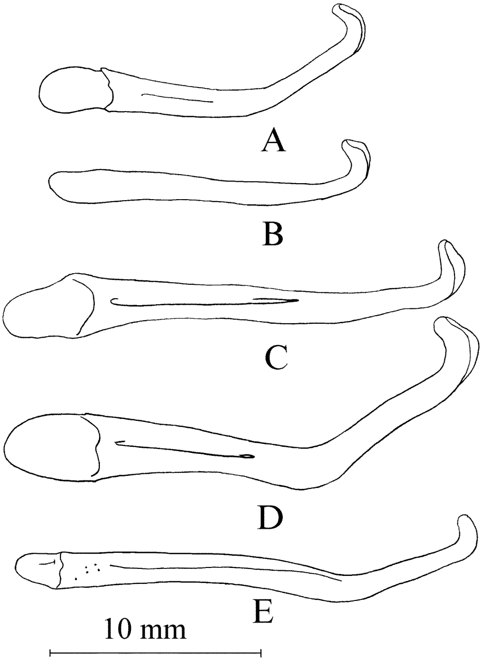

Fig. 5. The structure of baculum (os penis) of *M. nivalis* from different localities. A – *M. n. vulgaris*, Alps (after: Cavazza, 1915, form *monticola*); B – *M. n. nivalis*, ZIN No. O.15710, Leningrad Prov., Russia; C – *M. n. heptneri*, ZIN No. C.44016, Turkmenistan; D – *M. n. numidica*, NHM No. 45.158, Crete; E – *M. n. numidica*, Morocco (after: Cabrera, 1923).

Variability in the curvature of the baculum shaft in weasels was noted in the work of Didier (1947). Kratochvil (1951) indicates changes in the length and shape of the baculum in animals from Czechoslovakia: length varies from 15.3 to 19.45 mm. Curvature of the shaft also varies – it can be straight, evenly bent or elevated in the distal third (reminiscent of *numidica*!). The baculum of a small weasel from Czechoslovakia (form *minuta* in the opinion of Kratochvil) has the shaft curved upwards, as in *monticola*, with length of baculum 13.1 mm. In the opinion of Beaucournu & Grulich (1968), the shaft of the baculum is not always rectilinear in animals of continental Europe; they know a specimen from the west of France (Sarthe),

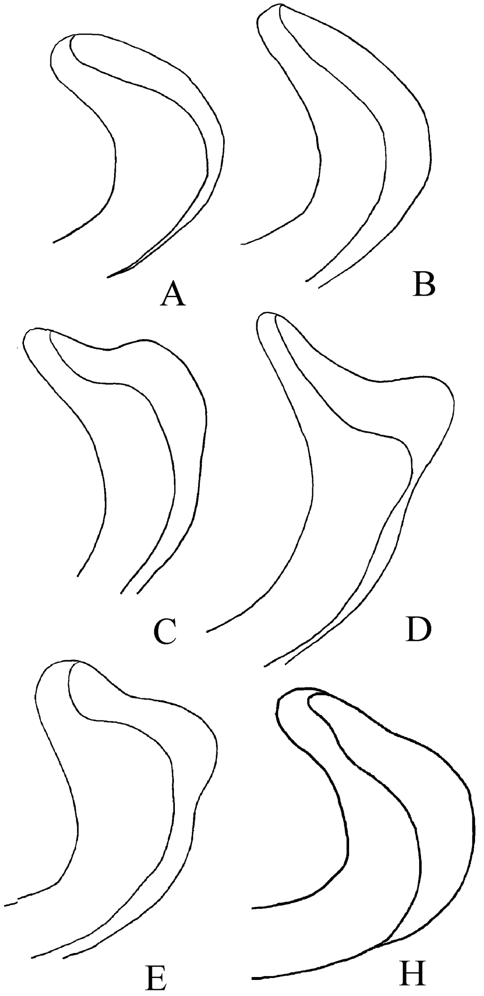

Fig. 6. Variability of structure of distal part of the baculum (hook) of *M. nivalis* from different localities. A – *M. n. nivalis*, ZIN No. O.34175, Yakutia, Russia; B – *M. n. nivalis*, ZIN No. O.15710, Leningrad Region, Russia; C – *M. n. heptneri*, ZIN No. C.44015, Turkmenistan; D – *M. n. vulgaris*, ZMMU No. S-155363, Netherlands; E – *M. subpalmata*, NHM No. 1938.6.34.34, Egypt; H – *M. n. numidica*, NHM No. 57.297a, Algeria.

the baculum of which in its curvature is closer to *numidica* than to *nivalis*. Ognev (1935) gives the drawing of a similar baculum of a weasel from the vicinity of Erevan in Armenia (form *dinniki*), in which the shaft is curved upwards in the distal third, length 19.5 mm.

The data cited do not permit us to regard the curvature of the baculum shaft as a specific character distinguishing *numidica*, *galinthias* and *monticola* from other forms of weasel. Such a shape of the shaft is only the extreme in a range of variability of the baculum in *M. nivalis* (Fig. 5).

Kishida (1936) indicates that the subspecies *M. pygmaea caraftensis* from Sakhalin described by him differs in the structure of baculum from *M. pygmaea pygmaea* and from *M. pygmaea yesoidsuna* Kishida (southern Kuril Islands and Hokkaido), but does not cite any distinctive features.

As is known for other species of Mustelidae, the shape of the distal end of the baculum is often of a species-specific nature (Baryshnikov & Abramov, 1997, 1998). The hook at the distal end of baculum in the specimens studied by us from Egypt and Algeria varies somewhat in shape (Fig. 6). In *numidica*, the left lobe is large, whereas the right one is hardly developed at all. In *subpalmata*, both lobes are notably more developed, although the left one is somewhat stronger. Among specimens from the Ukraine, Leningrad Province, Central Russia, Caucasus and Western Siberia, a hook with strongly developed left lobe occurs most frequently. There are, however, bones with a hook as in the Egyptian weasel or with both lobes well-developed – from Turkmenistan (ZIN No. C.44015) and from Turkey (ZIN No. O.34622). The shape of the hook apparently varies notably. In the collection of ZMMU there is a specimen from the Netherlands (No. S-155363) whose lobes on the hook have taken the shape of wide processes (Fig. 6D); as a result the hook resembles the distal end of the baculum of the Colombian weasel *Mustela* (*Cabreragale*) *felipei* (Izor & de la Torre, 1978).

Body size and relative tail length

The size and proportions of the body (relative tail length, relationship between tail length and hind foot length) have always been a major criterion for the assessment of geographic variation in *M. nivalis* and the separation of subspecies.

Along with an overall high variation of exterior characters, there is a certain tendency towards an increase of body size and relative tail length from north to south and to some

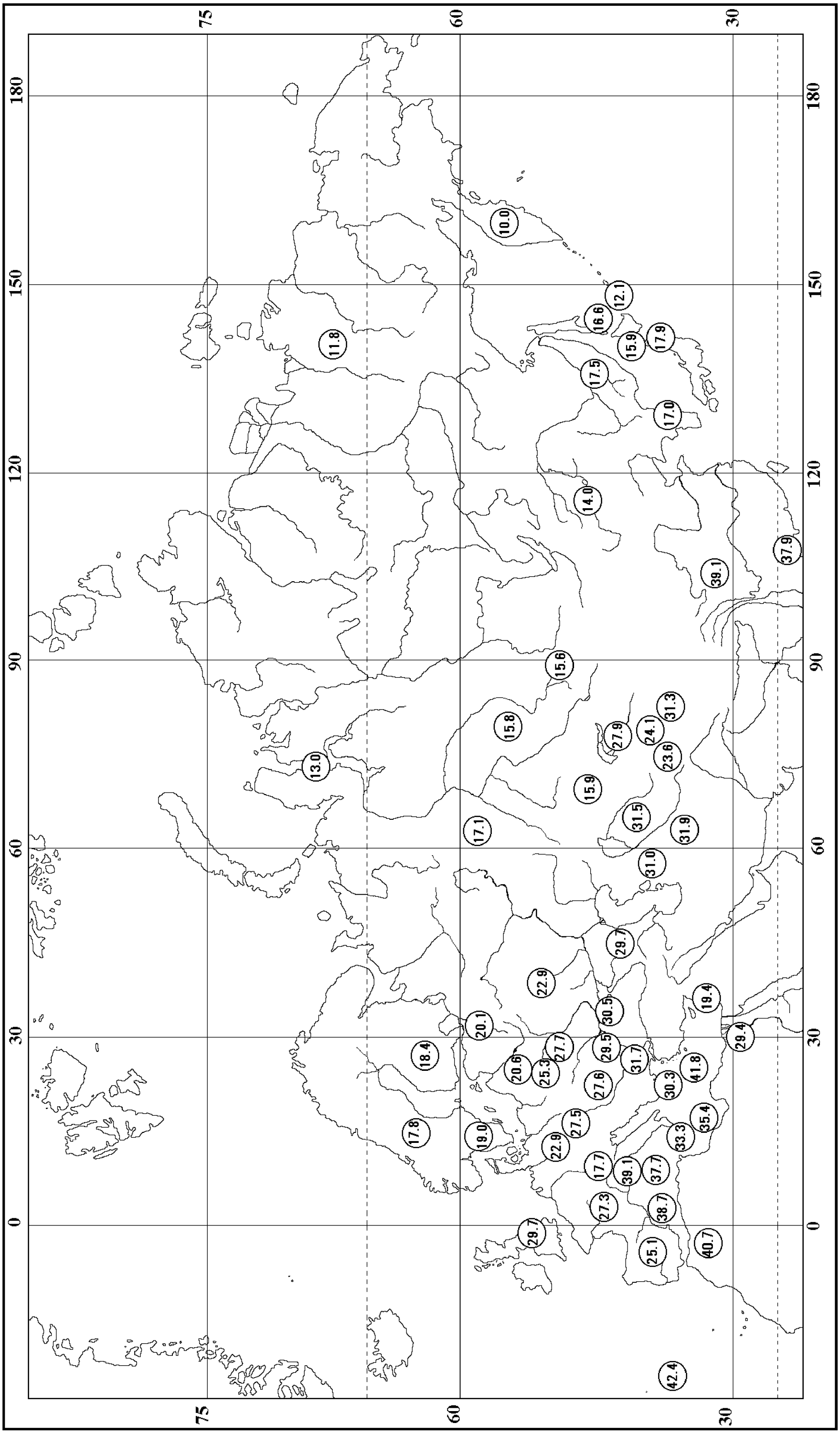

Fig. 7. Geographic variation in the relative length of tail (%) of *M. nivalis* in the Palaearctic.

Table 4. Body length, tail length and relative tail length (C/L) of adult males of *Mustela nivalis* from different localities. Minimum, maximum and means for external measurements, means for relative tail length (%), *n* - number of individuals

Localities	*n*	Length of body (mm)	Length of tail (mm)	C/L (%)	Authors
Northern Europe					
Sweden (northern part)	87	172-227 (202.3)	23-45 (36.1)	17.8	Stolt (1979)
north-western part of European Russia	22	152-195 (177.2)	29-43 (35.8)	20.1	Danilov & Tumanov (1976); our data
Central Europe					
Sweden (southern part)	61	204-266 (233.0)	34-57 (44.2)	19.0	Stolt (1979)
England	46	175-220 (202.0)	40-75 (60.0)	29.7	King (1977)
France (central part)	46	195-253 (217.7)	39-95 (59.8)	27.3	our data
Germany	138	157-204 (180.6)	30-52 (41.3)	22.9	Reichstein (1993)
Bohemia & Moravia	355	156.8-274 (216.7)	35-80 (59.4)	27.5	our data
Switzerland (Alps)	9	208-243 (221.2)	29.2-52 (39.4)	17.7	Cavazza (1914)
Hungary	5	205-250 (222.0)	55-66 (61.2)	27.6	Vásárhelyi (1942); our data
Lithuania	28	182-186 (184.0)	37-39 (38)	20.6	Mitskus & Baranauskas (1990)
Byelorussia	4	179-203 (189.8)	46-52 (48.0)	25.3	our data
Ukraine	14	155-238 (199.8)	43-76.4 (57.2)	27.7	our data
Crimea	13	173-224 (196.3)	44.5-73 (59.6)	30.5	our data
European Russia (central part)	25	130.6-232 (187.5)	26.2-61 (42.8)	22.9	our data
Southern Europe					
Spain	6	220-278 (243.5)	50-67 (60.8)	25.1	Miller (1912); Cabrera (1914)
Roumania	43	181-250 (218.0)	52-76 (64.3)	29.5	Barbu (1968)
Bulgaria	11	189-260 (224.5)	49-85 (71.0)	31.7	Zimmermann (1953); our data
Greece	28	263-382 (335.5)	65-125 (101.7)	30.3	Douma-Petridou & Ondrias (1986)
Crete	2	240-245 (242.5)	93-110 (101.5)	41.8	Zimmermann (1953)
Malta	2	173, 300	62, 105	35.4	Thomas (1895); Miller (1912)
Corsica	3	228-264 (246.3)	88-106 (97.3)	39.5	Beaucournu & Grulich (1968); our data
Sardinia	6	213-245 (226.6)	81-90 (85.2)	37.7	Frechkop (1963); our data
Sicily	3	230-250 (240.0)	70-90 (80.0)	33.3	Barrett-Hamilton (1900)
Majorca	5	191-258 (220.5)	79-98 (84.5)	38.7	Alcover & Jaume (1983); our data
Azores	2	255-266 (260.5)	105-116 (110.5)	42.4	our data
North Africa					
Morocco	3	223-240 (234.3)	89-102 (95.3)	40.7	our data
Egypt	3	398-403 (400.3)	107-129 (117.6)	29.4	Setzer (1958)

Fore Asia & Caucasus					
Caucasus	44	176-265 (215.6)	42-88 (63.5)	29.7	our data
Lebanon	1	360.0	70.0	19.4	Harrison & Lewis (1964)
Afghanistan	3	200-245 (221.7)	64-83 (73.5)	31.9	Niethammer (1973)
Central Asia					
Kazakhstan (northern and central parts)	46	150-192 (173.2)	19-37 (27.9)	15.9	Sludsky et al. (1982); our data
Kazakhstan (south-eastern part)	15	202-254 (228.6)	57-72 (63.6)	27.9	our data
Uzbekistan	10	202-246 (222.0)	66-76 (70.0)	31.5	Palvaniyazov (1974)
Turkmenistan	16	210-266 (233.0)	60-87 (72.3)	31.0	Kalustov (1992)
Western Tadjikistan	3	200-240 (226.7)	50-55 (53.3)	23.6	our data
Kirgizstan (mountains)	8	150-225 (191.9)	28-56 (46.3)	24.1	our data
China, Yarkend (type of *stoliczkana*)	1	309.9	76.2	24.6	Blanford (1877)
Western China (Lob-Nor Lake)	1	250.0	78.0	31.3	our data
Mongolia	?	148-188 (170.0)	17-33 (23.5)	14.0	Bannikov (1952)
Eastern Asia					
Northern Korea (type of *mosanensis*)	1	250.0	43.0	17.0	Mori (1927)
Japan, Hokkaido	31	153-193 (173.8)	23-34 (27.6)	15.9	data of Dr. T. Saitoh; our data
Japan, Honshu	2	160-166 (163.0)	28.5-30.0 (29.3)	17.9	our data
Sichuan (paratype of *russelliana*)	1	138.0	54.0	39.1	Thomas (1911)
Northern Vietnam (type of *tonkinensis*)	1	243.0	92.0	37.9	our data
Siberia					
Western Siberia	31	155-200 (170.2)	18-29.5 (22.7)	15.8	our data
Primorsk Territory	9	153-175 (168.0)	21.2-35 (28.7)	17.5	our data
Kunashir Island	3	170-187.1 (173.7)	15-25.2 (21.0)	12.1	Voronov (1974); our data
Sakhalin	7	155-186 (171.9)	25-30 (28.6)	16.6	Voronov (1974)
Eastern Yakutia	16	142-185 (160.0)	12-24 (17.0)	10.6	Tavrovskiy et al. (1971)
Chukotka & Kamchatka	24	138-180 (158.6)	16-24 (18.2)	12.2	our data
North America					
M. n. eskimo	3	203-230 (212.3)	27-31 (28.7)	13.5	Hall (1951); our data
M. n. rixosa	14	177-208 (194.2)	29-35 (32.7)	16.9	Hall (1951); our data
M. n. campestris	4	225-237 (231.0)	32-39 (36.0)	15.6	Hall (1951)
M. n. allegheniensis	3	191-206 (197.0)	28-37 (32.0)	16.4	Hall (1951)

extent from east to west. This coincides with an analogous pattern of increase of linear parameters of the skull in the same directions (see above). A review of our own data and some from the literature is given in Table 4 and in Fig. 7.

Animals inhabiting the northern part of Scandinavia and European Russia are characterized by small size and a relatively short tail. In the north of Sweden the animals are smaller and have shorter tails than in the south of Sweden; relative tail length is 17.8% and 19% respectively. North-west Russia is inhabited by relatively small but long-tailed weasels (20.1%). Occurring in the same area are separate smaller individuals reminiscent of the European *minuta*. In Central Europe (Great Britain included) and in the central region of Russia, an increase in size of the body and relative length of tail from north to south is observed.

The largest weasels having the longest tails inhabit Southern Europe (Spain, southern France, Italy, Greece) and North-Western Africa (Morocco, Algeria, Tunisia). The islands of the Mediterranean and the Azores are inhabited by even larger sized and longer-tailed weasels. Relative tail length in animals from Morocco, Crete and the Azores is approximately 42%.

M. subpalmata from Egypt is even larger. In body length it exceeds by nearly three times weasels from north-eastern part of the distribution range (Chukotski Peninsula, Kamchatka). The tail is relatively long (30%).

The Caucasus is inhabited by relatively large weasels with relatively long tails, similar in proportions to Middle Asian and Balkan forms. Animals of similar sizes live in Turkey and Iran. It should be noted that smaller specimens of similar proportions occur in the Caucasus relatively frequently. Harrison (Harrison & Lewis, 1964; Harrison, 1968) indicates for weasels from the Lebanon large body sizes, but a relatively short tail (L = 360 mm, C = 70 mm). To judge by small skull size (CbL = 37.7 mm) it is possible that body length is indicated erroneously, and the weasel from Lebanon has the same body proportions as individuals from Asia Minor.

M. nivalis from the Urals and Western Siberia (including the Altai and Sayan Mountains) are small and short-tailed (15.8%), but their tail length exceeds foot length (Stroganov, 1962). Specimens similar in size are known from Northern and Eastern Kazakhstan. South-Eastern Kazakhstan, the plains region of the Middle Asian republics, and Afghanistan are inhabited by large long-tailed weasels, the relative tail length of which is approximately 30%. Mountain areas of Middle Asia (Kirgizstan, Western Pamirs) are inhabited by *M. nivalis* of medium size, with a relatively long tail (form *pallida*). Its exterior is similar to that of the weasel from the central part of European Russia.

The smallest animals having the shortest tails (*pygmaea*) occur in North-Eastern Siberia (Chukotski Peninsula, Kamchatka). Average values of their relative tail length are 11.8%. The tail is normally shorter than or equal to foot length.

In the majority of intraspecific classifications proposed for *M. nivalis*, the ratio “tail length/foot length” is regarded as one of the major demarcation characters between subspecies *nivalis* and *pygmaea*. This is not, however, an absolute character: in samples of *nivalis* rare individuals occur whose tail is not longer than the hind foot (see also Stroganov, 1962). Relative length of foot, unlike relative length of tail, is a sufficiently constant value; in animals of different sizes it constitutes 13-15% of body length (up to 17% in large southern forms). Considering this circumstance we do not attach great taxonomic importance to the ratio of tail length to foot length as has been assumed before (Stroganov, 1962; Heptner et al., 1967; Beaucournu & Grulich, 1968).

Body size and proportion of weasels from the steppes of Transbaikalia and Mongolia (form *kerulenica*) are reminiscent of those in animals from Western Siberia; however, very small specimens, similar to northern *pygmaea*, also occur in Western Transbaikalia.

The weasel from the Far East of Russia is most frequently classified as *pygmaea*. Yudin (1984) believed that this subspecies spreads up to the Chukotski and Kamchatka Peninsulas, and also to Sakhalin and the Kuril Islands. However the animals from the Amur Province and Primorsk Territory are characterized by a longer tail (17.5%) than weasels of the north-east of Siberia and Kamchatka. This feature permitted Stroganov (1962) some time ago to assume the taxonomic separation of the animals as an unnamed subspecies. Similar sizes and proportions were noted in *M. nivalis* from the Little Khingan Mountains (Zimmermann, 1964). The Korean form *mosanensis* is larger and longer-tailed than the one from Primorsk Territory, although it has the same relative tail length (17%).

Differences in general body size and relative tail length in different geographically separated populations of weasels from Siberia are noticeable only on the level of average values of metric characters: the range of individual variability is quite high. Small and short-tailed weasels that are not distinguishable from typical *pygmaea* occur, for example, in the Novosibirsk Province, Altai, Tuva, Transbaikalia (see also Ognev, 1935) and in Mongolia. On the other hand, relatively large long-tailed weasels are known from Eastern Yakutia.

Japanese weasels are close in size to Siberian ones, animals from Honshu being on the average smaller than from Hokkaido (see also Obara, 1991b), but have longer tail (17.9%). Weasels from Sakhalin and Kunashir are also similar in body size to *M. nivalis* from Siberia. In relative tail length, the Sakhalin weasel occupies an intermediate position between West Siberian and Primorsk Territory populations (16.6%). The weasel from Kunashir Island has a shorter tail (12.1%) and is similar to East Siberian animals in this respect. Based on longer tail as compared to typical *pygmaea* (14% as compared to 10%), Kishida (1936) separated weasels from Hokkaido and Kuril Islands as subspecies *yesoidsuna*.

Concerning *M. nivalis* from China very little is known to us. The form *stoliczkana* described from Yarkand (Eastern Turkestan) is characterized by large size and relatively long tail – 24.6% (Blanford, 1877, 1879). Animals from Lob-Nor region that were placed by Russian zoologists (Ognev, 1928, 1935, and others) in *stoliczkana* are somewhat smaller and have a longer tail (31.3%). The subspecies *russelliana* from Sichuan is much smaller with a relatively long tail (39.1% of body length). Form *tonkinensis*, known by one specimen from Northern Vietnam (Tonkin), has a very long tail (45%), the general size of the body being average.

In *M. nivalis* from North America size increases in two directions – from central regions of the continent northwards and southwards (see Ralls & Harvey, 1985). Therefore the southern subspecies *campestris* and *allegheniensis*, and the form *eskimo* from Alaska, are somewhat larger than the typical *rixosa*. According to our data *rixosa* is rather reminiscent in sizes and body proportions of typical *nivalis*, but not of *pygmaea* from Northern Siberia. The Alaskan form *eskimo* resembles the North Siberian weasel in its relative tail length, but is larger. However, in the size and proportions of the skull, North American, Siberian and North European weasels are very similar (Fig. 2).

Characteristics of coloration and moult

The summer pelage of the weasel is two-coloured: brown from above and white from below. Proceeding from the character of the boundary between the colour zones Niethammer (1973) separated two major types of coloration ("minuta" and "nivalis") and showed that they are distributed allopatrically in Europe. The distribution of pigmentation types of *M. nivalis* in the European part of the range was given also in the monograph by King (1990). For the sake of justice it should be noted that Barrett-Hamilton (1900) used features of coloration of the back and belly, and the ability to change colour in winter, in his revision of the subspecies structure of *M. nivalis*.

Frank (1985) refined the characters of both types of coloration and gave them different names: "nivalis" and "vulgaris" respectively. Coloration of "nivalis"-type is characterized by a straight demarcation line between the brown dorsal and white abdominal areas on the neck and along the entire body, there being no pronounced spotted pattern on the ventral side (sometimes 1-3 spots on the breast are present) (Fig. 8 E, F). Animals of this group turn completely white in winter (except those from the southern part of the range).

The "vulgaris"-type is characterized by an indented demarcation line between the areas of brown and white colour, in both the neck and trunk regions (Fig. 8 A, B, C, D). Sometimes the brown field reaches so far on the belly that it may join in some areas, forming transverse bands. There are also dark paired spots on the cheeks behind the mouth; their absence is due to fusion of particularly large spots with the coloration of the upper part of the head. Moreover, brownish spots of different shapes and sizes frequently occur in the regions of the chin, neck, breast and belly. In winter these weasels do not turn white or white only partly.

We present below a review of original and literature data on the spread of types of pigmentation across the distribution range of *M. nivalis*, refining the regions of their distri-

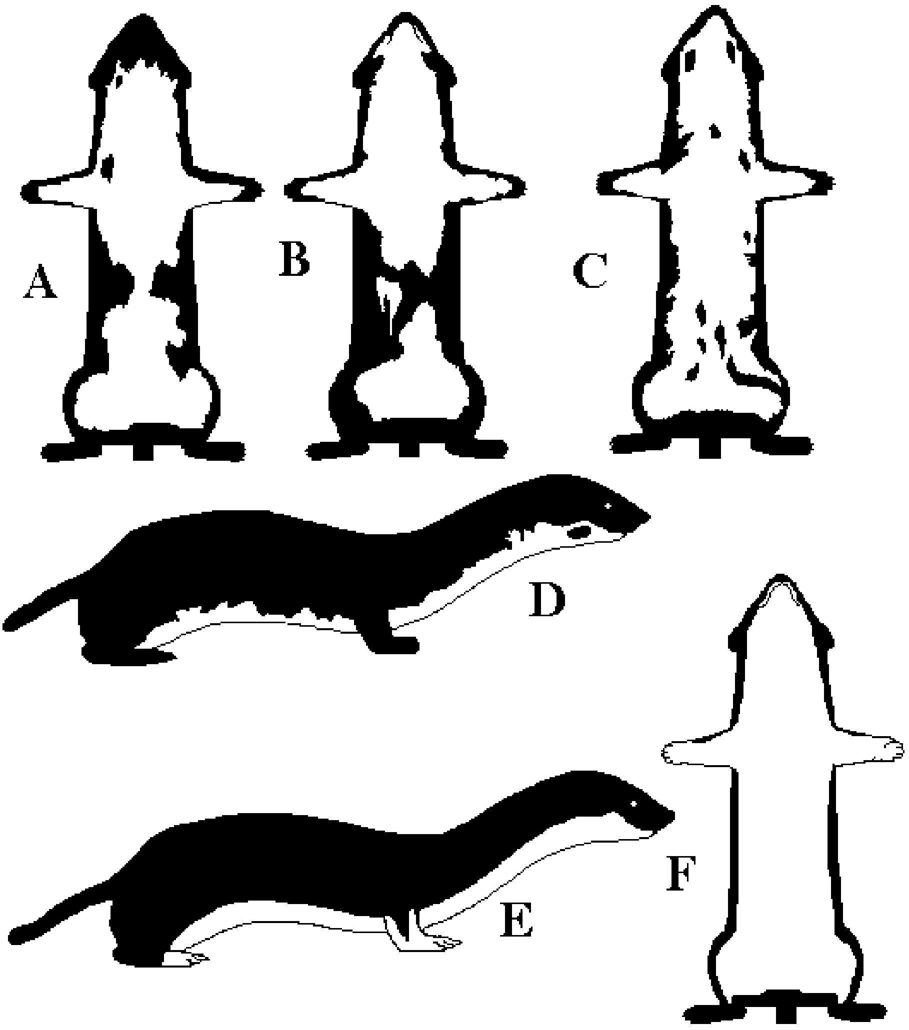

Fig. 8. The coloration of summer pelage of *M. nivalis* (scheme). A, B, C, D – "vulgaris"-type; E, F – "nivalis"-type (after: Frank, 1985; König & Müller, 1989).

bution indicated previously (Niethammer, 1973; King, 1990).

Animals having coloration of "nivalis"-type occupy the major part of the Palaearctic distribution range, i.e. Scandinavia (except southern Sweden), Belarus (Minsk Province, Belovezhskaya Pushcha), Ukraine, Moldavia and European Russia south up to the Northern Caucasia, and also the Urals and Siberia, Primorsk Territory included.

The majority of North American weasels (forms *rixosa, eskimo, campestris*) have "nivalis"-coloration type and white winter fur. The exception is the subspecies *allegheniensis* from the extreme south-western part of the American distribution range, which has coloration of both types. According to the description of Hall (1951), the majority of specimens studied have "vulgaris"-coloration and dark spots on the lower part of the body (see also Frank, 1985). In winter, both white and brown individuals of this form occur. Approximately 20% of weasels of another subspecies, *campestris,* also have "vulgaris"-coloration. Possibly in the USA there is a transitional zone (presumably in the region of Iowa – Illinois) where animals of both types of coloration occur.

The "nivalis"-coloration type is also observed in all small and large animals of Middle Asia and Kazakhstan (*pallida* and *heptneri*). In the collection of the Zoological Institute (St.Petersburg) there is only one specimen of a different type of coloration from this region – from the vicinity of Balkhash Lake, Eastern Kazakhstan (ZIN No. C.25753). The light brown colour of the woolly coat of the back which was the basis for placing the relatively small Middle-Asian mountain weasels into a subspecies *pallida,* in fact strongly varies. Along with the light forms, dark brown weasels also occur here, which in the their range of colours of summer pelage are not discernible from the European ones. As was noted by Shnitnikov (1936), the intensity of coloration is probably subject to individual variation and often depends on local ecological factors.

Weasels from Afghanistan have "nivalis"-coloration type (Niethammer, 1973). Niethammer placed them in subspecies *stoliczkana*, which is, however, incorrect, because the latter has "vulgaris"-coloration. The subspecies occurring in Afghanistan is probably the same as the one noted in former-Soviet Middle Asia, i.e. *M. nivalis heptneri*. It should be noted that previously (see Satunin, 1911), weasels from Turkmenistan were placed in the form *stoliczkana*.

In his description of the form *M. n. kerulenica* (coloration of "nivalis"-type) from steppes of Eastern Mongolia, Bannikov (1952, 1954) noted that only a few specimens have white winter pelage, whereas in the majority of animals the winter fur is only slightly lighter than the summer one. Our data and a number of publications (Allen, 1938; Sokolov & Orlov, 1980) indicate that weasels of Mongolia have purely white winter fur.

Animals from Central Asia (form *stoliczkana* from Western China) have "vulgaris"-type of pigmentation. The weasel from the Little Khingan Mountains in North-Eastern China has the "nivalis"-coloration (Zimmermann, 1964). Animals from the Great Khingan Mountains and from Primorsk Territory have a similar coloration. The Chinese *russelliana* from Sichuan, and Vietnamese *tonkinensis* from Tonkin, have "nivalis"-coloration. New form of weasel from Taiwan Island has "vulgaris"-type of pigmentation.

The relatively large form *mosanensis,* described from north-eastern Korea, has "nivalis"-coloration; its winter coat turns completely white (Mori, 1927). In other parts of the Korean Peninsula (in the south), animals with "vulgaris"-coloration occur (one specimen from Seoul, NSM No. 21751, and also to judge from photographs kindly given to us by Dr. H.S. Han of Korean Wildlife and Research Centre).

The Japanese weasel (*M. n. namiyei*) from Honshu Island has coloration of "nivalis"-type. Kuroda (1921), in the original description of *namiyei*, says nothing about the character of the winter fur, although he had at his disposal specimens obtained at the end of December. The weasel from Hokkaido, Sakhalin and the southern Kurils is often placed in the same subspecies (see Voronov, 1974). The only specimen studied by us from Kunashir Island (ZIN No. C.33772) has "vulgaris"-coloration. Weasels from Hokkaido and southern Sakhalin have "nivalis"-coloration. In Sakhalin (Benjkovskiy, 1961; Benjkovskiy & Benjkovskaya, 1983), a very late whitening of animals in the southern parts of the island is observed (specimens caught in late November – early December had brown fur and the fur turns completely white only after the establishment of snow cover). It is not clear from these data whether white specimens were ever found, or if this is only a supposition. Weasels from Hokkaido have white winter coat.

Coloration of "vulgaris"-type is noted in weasels from the British Isles, Central and Southern Europe (Netherlands, Denmark, Germany, Czech Republic, Poland, Hungary, Slovenia, Serbia, Bulgaria, northern Spain, France, Italy).

The weasels with "nivalis"-coloration were noted in Middle Europe: in the Alps (*monticola*), in Austria, and in Germany – "Western Prussia", Bavaria, and the vicinity of Bonn (Gaffrey, 1943; Kahmann, 1951; Lehmann, 1969; Reichstein, 1993). There are some specimens with "nivalis"-coloration from Bohemia and Moravia. Cavazza (1909) noted that in Italy (Emilia region) one can

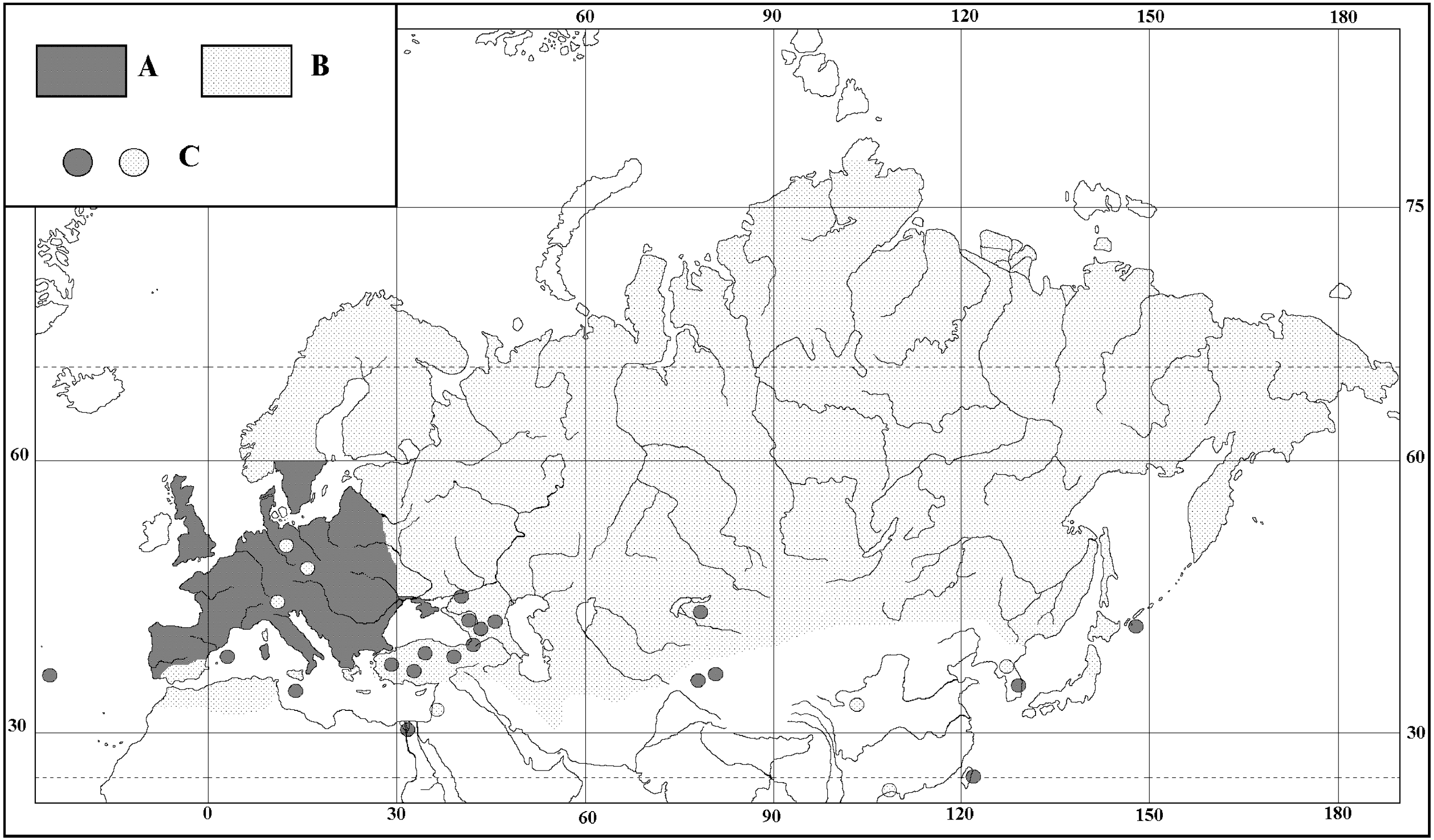

Fig. 9. Distribution of coloration type of *M. nivalis* in Palaearctic. A – “vulgaris”-type, B – “nivalis”-type, C – separate findings.

sometimes find animals with "nivalis"-coloration. He also indicated a specimen from Sardinia having the same coloration. One of the features of the form *hungarica* described from Hungary (Vásárhelyi, 1942) is the ability to retain brown coloration of the winter fur in those latitudes where typical weasels turn white. In this case, as far as one can judge from the photograph in the publication, at least one of the type specimens has coloration of "nivalis"-type.

The boundary of weasels having "nivalis"-coloration apparently passes through western parts of the Ukraine and Moldavia. However, animals from the Crimea have "vulgaris"-coloration. In the monograph of Ognev (1935) it is noted that in the Crimean Peninsula, forms of *nikolskii* do not turn white, whereas in the part of the peninsula adjoining the continent some forms retain brown fur in winter, whereas other forms acquire white fur. The collections of the Zoological Institute of the Russian Academy of Sciences contain weasels from the Askaniya-Nova Reserve (Kherson Province, southern Ukraine) with coloration of "vulgaris"-type, and a winter specimen (from the same area) is almost completely white (with only a brown band on the back). One more specimen with coloration of "vulgaris"-type from the same collection comes from the vicinity of Rostov-on-Don, which possibly indicates a distribution of animals with "vulgaris"-pigmentation along the northern coast of the Azov Sea.

Transitional regions are situated between the major regions of predominance of different types of coloration in Northern and Eastern Europe. Thus in southern Sweden (approximately at 59° N) there is a zone approximately 100 km wide where weasels with both types of coloration occur sympatrically (Stolt, 1979; see also Lönnberg, 1900). In the collection of the Zoological Institute there are specimens from the Transcarpathian Province, of the Ukraine (Perechinsky District) with both types of coloration. Abelentsev (1968) indicated that animals with brown coloration of the back frequently occur in the Carpathian region in winter. Ognev (1935) wrote that the coat of some of the weasels from the Orel Province and from southern Ukraine does not turn white in winter, but the animals of the Odessa Province have white coloration in winter. In the Moscow Province, weasels sometimes occur with coloration reminiscent of "vulgaris"-type, with spots on the cheeks, neck, and breast, and a low demarcation line, but the line itself is straight. The winter fur is completely white. Animals with such a type of coloration are present also in the Yaroslavl and Tver provinces.

Both types of coloration are present in the Caucasus. The "nivalis"-type is more widely spread. Large long-tailed weasels (form *dinniki*) as well as short-tailed forms of smaller size (form *caucasica*) have this type of coloration. In some areas (near Batumi and along the Main Caucasian Ridge) both types of pigmentation occur sympatrically. Here some of the specimens turn white in winter, others retain brown coloration. In Turkey also, both types are present, sometimes in the same region, animals inhabiting the mountains turning completely white in winter (Kasparek, 1988). A specimen from Gorgan, Iran (NHM No. 18.5.74) has "nivalis"-coloration.

Animals with both types of coloration occur in the Iberian Peninsula (Cabrera, 1914). "Vulgaris"-type (*M. nivalis* according to Cabrera) occurs in northern parts of Spain, "nivalis"-type with a straight demarcation line (*M. iberica*) in southern parts of Spain. The sizes of the animals are approximately the same. In central Spain both forms occur near each other. Weasels with "vulgaris"-coloration inhabit the Balearic Islands (Majorca, Menorca) (Alcover & Jaume, 1983).

Weasels of both types of coloration occur with a mosaic distribution in the Mediterranean region. Animals of the highlands of Lebanon have "nivalis"-coloration (Harrison, 1968). The form *siculus*, described for Sicily, is also characterized by "nivalis"-coloration. The same coloration is observed in large long-tailed weasels of Corsica (form *corsicana*), as well as Greece and Crete (form *galinthias*) (see Douma-Petridou & Ondrias, 1986). These authors believed that the subspecies *M. n. galinthias* inhabits also southern Yugoslavia and Bulgaria, but specimens from that region at our disposal have coloration of "vulgaris"-type.

Weasels of North-Western Africa (Algeria, Morocco, Tunisia) have "nivalis"-type of pigmentation (forms *numidica*, *siculus*); weasels of Egypt, Sardinia, Malta and Azores have "vulgaris"-type of coloration.

Hence specimens with "nivalis"-type of coloration occupy a major part of the distribution range of *M. nivalis* (Fig. 9). Coloration of "vulgaris"-type occurs as a solid mass in Europe only, where it separates like a wedge "nivalis"-coloured populations of the Mediterranean and northern regions. In

Asia, the "vulgaris"-type is spread sporadically and evidently does not form a continuous zone.

According to the results of studies conducted by Frank (1985), coat pigmentation of *M. nivalis* is determined by one gene with two alleles. "Nivalis"-type is inherited recessively relative to "vulgaris", so that it should occur in mixed populations relatively seldom. Frank assumes that weasels with "vulgaris"-coloration never turn white in winter, whereas the woolly coat in forms with "nivalis"-coloration, depending on the climatic features of the region, may turn partly or completely white. In the southern parts of the distribution range of *M. nivalis* such animals do not always become purely white in winter.

There is no exact evidence on the possibility of a complete whitening of winter fur of weasels of "vulgaris"-type. King (1977) briefly mentions that white winter coloration is seldom noted in animals of the British Isles. According to the data of Barbu (1968), animals living in Romania and having "vulgaris"-coloration do not become white in winter. Only one specimen had partly white coloration (a dark zone was retained in the middle of the back). We examined 552 specimens from Czech Republic, only two of them have white coloration in winter. Cavazza (1909) discovered only one white specimen (out of 385) from the northern part of Italy. The collections of the Zoological Museum of Moscow University contain winter specimens from the vicinity of Rzeszow (Poland) with brown coloration of "vulgaris"-type as well as completely white ones.

Karyotype

Karyotyped animals from Sweden, Bulgaria, Czechoslovakia, central Italy, Caucasus, Siberia and North America (see Zima & Grafodatskij, 1985) have the same diploid chromosome set of 2n=42. Some researchers indicate 2n=38 for Great Britain (Muldal, 1950) and for Honshu Island (Obara, 1982, 1985). Data for the English weasel are probably erroneous (see also Zima & Grafodatskij, 1985; Peshev et al., 1985).

Karyotypes of a small short-tailed *nivalis* (northern Sweden) and larger long-tailed *vulgaris* (southern Sweden) have the same chromosome number of 2n=42, NF=76 (Mandahl & Fredga, 1980), including 7 pairs of chromosomes with completely heterochromatic arms; the morphology of individual chromosome pairs is identical. The weasel from Western Siberia is karyotypically identical with the Scandinavian one (Grafodatskij et al., 1977). Animals from the High Tatra Mts. have only 6 pairs of autosomes with complimentary heterochromatic arms and differ from the above-mentioned ones in the absence of accessory arms on the 7th pair of autosomes (Zima & Grafodatskij, 1985). The karyotype of a small *minuta* from the same region appeared to be identical to the rest. Based on this evidence, the authors believed that the joining of small Arctic weasels (*pygmaea*) and Central European weasels (*minuta, monticola*) into one taxon (different from *M. nivalis*) is incorrect from the karyological point of view.

For the Bulgarian weasel (vicinity of Sofia), NF=84 (NFa=80) is indicated (Peshev et al., 1985). Animals from Shumava have a similar karyotype (NFa=80) (Zima, 1984). Possibly these additional arms are also determined by the presence of additional heterochromatin.

Animals from Transcaucasia (Armenia) and Northern Caucasia (Kabarda) have similar chromosome sets, with a larger number of arms as compared to the Siberian forms, i.e. NF=82 (NFa=78) (Dzuev & Thamokov, 1976; Dzuev et al., 1979). In *M. nivalis* from the Japanese islands, the karyotype varies. For animals from Hokkaido the usual diploid set of chromosomes 2n=42 is indicated (Tsuchiya, 1979; Obara, 1991a, 1991b) and for weasels from Honshu 2n=38 (Obara, 1982, 1985). Based on these differences, Obara (1991a, 1991b) assumed that two different species live in Japan – *Mustela nivalis* (Hokkaido) and *M. namiyei* (Honshu). Analysis of mitochondrial DNA showed however that difference between the two forms are less than interspecific differences known for the genus *Mustela* and do not exceed subspecific rank (Masuda & Yoshida, 1994).

Increase of the number of arms related to the increase of the portion of two-arm elements in the karyotype is determined by the appearance of "complimentary" heterochromatic arms on separate chromosomal pairs. It is assumed (Grafodatskij et al., 1977; Zima & Grafodatskij, 1985) that increase of the amount of C-heterochromatin is a progressive tendency in the karyotypic evolution of Mustelidae. Therefore karyotypes of the Scandinavian and West-Siberian forms may be regarded as more primitive than those of the Caucasian or European forms. The lowest number of C-heterochromatic blocks (only 5) observed in the Japanese weasel can in all probability be accounted for by its secondary simplification brought about by geographic isolation.

Discussion

Notable variation in the craniological and external characters of *M. nivalis* considerably hinders the study of the taxonomic structure of the species. A gradual increase in the size of the animals from north to south is observed. Relative tail length increases in the same direction. Local distribution of different types of pigmentation of the fur is observed. For separation of size groups (large, average, and small weasels) we used craniometric features. Body sizes indicated on collection labels, in our opinion, are less informative because of the considerable error in the measurements. Therefore groups separated based on body sizes may not always coincide with those that have been obtained on the basis of skull measurements.

As is seen from the data presented above, within the limits of variation of *M. nivalis* there are three major groups: large long-tailed weasels with "nivalis"-coloration (*numidica*), weasels of average and large sizes with a relatively long tail and "vulgaris"-coloration (*boccamela*, *vulgaris*), and small short-tailed weasels with "nivalis"-coloration (*nivalis, pygmaea, rixosa*). Chinese forms (*russelliana, stoliczkana*) drop out of this scheme, but Central Asian material is unfortunately quite scanty even in the largest collections.

Large weasels of the first group occur in Northern Africa and Spain, in the Caucasus, Fore-Asia and Central Asia. Weasels of the second group occur in Europe (except its north-eastern part) and in Eastern Asia (Korea, Vietnam). Small weasels occupy the major part of the distribution range of the species – North America, Northern Europe and northern half of Asia. In both oceanic sectors of Eurasia (Atlantic and Pacific), small forms contact in the south with animals of average size; and in continental regions of Central Asia directly with large weasels.

Occurring in the territory of each group are a certain number of deviating individuals – smaller or larger or with a different coloration. In a study of small samples from a restricted geographical region these deviating forms have sometimes been regarded as separate subspecies or even species. Such is, for instance, the situation with Central European taxa – *trettaui, monticola, dombrowskii* or *hungarica*, or with the form *occidentalis* proposed by Kratochvil (1977) for Western Europe. If the variation of *M. nivalis* is observed over the entire species distribution range, these local differences are levelled. The small specimens are most probably only an ecological form of weasel, formation of which is determined only by local conditions of the environment. Ecological forms (ecotypes) are known also in other mammals (e.g. bank vole *Arvicola terrestris*). Among *M. nivalis* the small ecological form most frequently occurs in mountain regions (Alps, Carpathians, Caucasus), but is known also from other areas (Western Siberia, Moscow Province). The decrease in size of animals may lead to their earlier maturation and as a consequence to abundant progeny. Comparative data available on reproduction of small and large weasels (Frank, 1974) have shown that small Scandinavian weasels (*nivalis*) are capable of producing two broods per year. Pregnancy (5 weeks) and weaning of the young (8-9 weeks) continues in the same periods as in the larger Central European weasel (*vulgaris*). However, in females of the small form, oestrus begins 5 weeks after the first delivery; during the second pregnancy they continue weaning the young of the first brood. Therefore the small weasel may have two broods during 5.5 months. Females of *vulgaris* did not have oestrus until 9-10 weeks after the first delivery, i.e. until the first brood grew up completely. Small North American weasels in captivity are also capable of raising two broods a year (Heidt et al., 1968). This feature of the small weasel may be regarded as an adaptation to conditions of short summer in northern latitudes (see also Frank, 1974). It is quite possible that such an ability is characteristic also of small weasels occurring in mountains in parts of the range of *M. nivalis* situated further south. In any case these small forms ("minus-variants") should not be considered within the framework of geographic variation of the species, because their appearance is not related to the spatial geographic structure of *M. nivalis*, but is determined by other reasons.

Now let us try to explain the change of body size of *M. nivalis* in the process of evolution. It was generally accepted (Nasimovich, 1949; Rosenzweig, 1966, 1968; McNab, 1971), that decrease in size of animals from south to north (contrary to Bergmann's rule) is determined by competition for food between weasel and ermine (*M. erminea*). In accordance with this fact, in the southern regions where the latter is absent, the weasel has large size; and in latitudes situated further north, it has to occupy the ecological niche of a very small carnivore obtaining small rodents in narrow burrows inaccessible to ermine. However, in Northern Caucasia or in the mountains of Middle Asia (Tadjikistan, Kirgizstan) both species coexist, weasel being quite comparable in size to ermine, but their distribution by biotope is different. In Northern Caucasia, for example, they occur in different biotopes: *M. nivalis* in meadow and shrub biotopes, *M. erminea* nearly exclusively in rock streams; areas of their habitation do not overlap (Dobrolubov, 1987). In North America, where three closely related species of mustelids (*M. frenata*, *M. erminea* and *M. nivalis*) are distributed sympatrically, such a relationship (correlation of sizes of the animals and their competitive interaction) has not been observed.

It appears more probable to us that body size in *M. nivalis* has changed under the impact of climatic and landscape conditions (low winter temperatures, long snow cover, life beneath the snow and presence of suitable prey (size and abundance of rodents, the possibility of penetrating underground refuges). It has been shown (King, 1990) that body size in weasels is bound by an inverse correlation with temperature and duration of snow cover.

Proceeding from available data, one can assume the following scheme of the origin and further modification of different forms of *M. nivalis*. Large long-tailed weasels of North-Western Africa, southern Spain, islands of the Mediterranean and Greece, with coloration of "nivalis"-type (group *numidica* sensu Frank, 1985), are probably most close to the original state for the species *M. nivalis*. This is indicated by their similarity to other representatives of the genus *Mustela* (e.g. with ermine) in external features (general size and proportions of the body, coloration), and also by the modern distribution range which is easily explicable from the standpoint of the zoogeographic theory of ousted relicts. Frank (1985) held the same opinion. Large weasels of the group *numidica* were in the past probably more widely spread in continental Europe and also penetrated Asia Minor and Central Asia. To judge by fossil remains from Israel (Dayan & Tchernov, 1988), in the cold epochs of the Late Pleistocene they could have reached the Levant and even Egypt.

Small weasels of the form *nivalis* appeared later, probably in the boreal regions of the Palaearctic. In the Middle Pleistocene in Western Europe forms have been discovered that are transitional between the Early Pleistocene *M. praenivalis* Kormos and modern *M. nivalis* L. (Kurtén, 1968). The joint occurrence of fossil remains of large and small weasel in cave layers is known for the Late Pleistocene of the Caucasus (Mezmaiskaya Cave) and Altai (Denisov Cave) (Baryshnikov & Golovanova, 1989). Small Late Pleistocene *M. nivalis* that cannot be distinguished in size from the Siberian weasel was found in Poland (Netopezhova Cave close to Krakow), in the Crimea (Syren'-1) (Birula, 1930), and in the south of Slovakia (Kafka, 1900), i.e. notably further west than at present. Climatic cooling that began in the Middle Pleistocene evidently led to the necessity for new adaptations in the weasel, i.e. decrease of size (life beneath the snow during the long winter, decrease of fodder supply), and whitening in winter (decrease of heat transfer, camouflage coloration). Therefore in the Late Pleistocene a new biological form of *M. nivalis* appeared: a small predator, well adapted to life in the snow-covered areas of boreal and arctic regions of the Holarctic. These particular weasels could have penetrated North America through Beringia; in the west and south as the areas of continental glaciers increased they could have penetrated Crimea and the Alps.

Another biological form of weasel (*vulgaris-boccamela*) was evidently formed, during the Late Pleistocene in the eastern Mediterranean part of the range from *numidica* that was displaced southwards by the glacier (see also Kratochvil, 1977)."Vulgaris"-coloration could have arisen as a result of an accidental mutation. In warm climate, whitening in winter related to the "nivalis"-type of coloration was not vitally important and coloration of animals changed to "vulgaris"-type. Gradually, weasels of the group *vulgaris-boccamela* occupied the whole of Western and Central Europe, displacing small *nivalis-pygmaea* to the north and east. The appearance of large forms such as *boccamela* within this group could have been local; e.g. this could have been related to the Mediterranean spectrum of prey (abundance of large rodents), or insular isolation.

At the end of the Pleistocene the form *vulgaris* occupied Central and Western Europe (the British Isles and southern Sweden included). The size of the animals declined again, possibly because of the presence of snow cover or the availability of prey of adequate size. This form of average size fuses in Southern Europe with *boccamela* and forms a mixed (contact) zone with *nivalis* in central Sweden, the Alps, Eastern Europe and probably in Turkey. In the opinion of a number of authors (Kratochvil, 1977; Frank, 1985), during dispersal of the southern weasel in the mountain regions of Europe and the Caucasus, relict isolates of small *M. nivalis* (*monticola, caucasica*) were formed. The most credible speculation in our opinion is that animals with "nivalis"-coloration appearing from time to time in the territory of "vulgaris" in Central Europe are ancestral phenotypes permanently present in the populations. It is evident that the mountainous conditions of the Alps particularly favour the survival of specimens with "nivalis"-coloration, therefore their frequency of occurrence here is higher.

Weasels of Iran, Middle Asia and Afghanistan were apparently closer to the form *numidica* than to *nivalis* from Kazakhstan. The subspecies from the Caucasus and Turkey was probably the youngest, and in this territory the transition to "vulgaris"-coloration is still in progress. This process has covered the whole of Central Europe.

The same process as in Europe took place in all probability independently in the southeast of the North American region of *M. nivalis* distribution, i.e. the range of the subspecies *allegheniensis.* It is difficult to say anything about the history of *M. nivalis* in Eastern Asia except that probably the small short-tailed weasel displaced southward forms which had been widely spread in the past, such as *russelliana, tonkinensis* and *mosanensis*.

Frank (1985) made the supposition that the shift from "nivalis"-pigmentation type (related to the possibility of winter change of coloration) to "vulgaris"-type occurred because of the necessity of adaptation to certain climatic conditions (according to Frank, the region of forests of Mediterranean type). Such an adaptive interpretation of the appearance of "vulgaris"-coloration is insufficient for understanding the separate cases of occurrence of "vulgaris"-coloration within the distribution range of weasels with "nivalis"-coloration (Balkhash Region, Caucasus, Turkey, Korea, Kunashir, Western China). In all probability "vulgaris"-coloration is a relatively frequent mutation within the "nivalis"-type. Therefore specimens with this coloration appearing in different remote areas are not related to each other.

The suitability of craniometric or external features (body size, coloration) for the taxonomic analysis of *M. nivalis* has been doubted many times. Either craniological characters or external characters have been used. The results of cytogenetic studies alone proved insufficient. The low karyological variation of populations, and also insufficient information on this species obtained using precise methods of modern systematics, i.e. analysis of mitochondrial DNA, protein electrophoresis, hybridological analysis, barely permit to use these results as additional information. We believe that most promising today is an integrated approach, considering all morphological indices available. Such a combined analysis of craniological and exterior features within the entire species range permits the proposition of a relatively consistent scheme of *M. nivalis* subspecies structure.

Given below is an attempt to revise the intraspecific taxonomy of *M. nivalis* from the data of the present study. Subspecies were separated based upon the differences in size and proportions of the skull and body, features of summer fur coloration and also upon karyological data. As has been noted, the change in size and proportions of body and skull displays a clinal pattern and different types of coloration are dispersed discretely. The combination of these characters permits us to distinguish precise geographical forms which are given subspecific status. Our taxonomic review includes all subspecies of weasel *M nivalis* and also the Egyptian weasel (*M. subpalmata*). We regard the latter, following Zyll de Jong (1992), as a separate species in the subgenus *Gale* Wagner, 1841. Distribution of subspecies of *M. nivalis* is shown in Figs 10, 11.

Taxonomic review

Genus **Mustela** Linnaeus, 1758

Mustela Linnaeus, 1758. Syst. Nat., ed. X, 1: 45. (Type species – *Mustela erminea* Linnaeus. See Miller, 1912: 381).

Subgenus **Gale** Wagner, 1841

Gale Wagner, 1841. Schreb. Säugetn. Suppl., 2: 234. (Type species – *Mustela vulgaris* Erxleben = *M. nivalis* L.).

Mustela (Gale) nivalis Linnaeus, 1766

Mustela nivalis nivalis Linnaeus, 1766

Mustela nivalis Linnaeus, 1766. Syst. Nat., ed. XII, 1: 69.

Mustela punctata Domaniewski, 1926. Ann. Zool. Mus. Polon. Hist. Nat., 5: 55. Darasun, Eastern Transbaikalia. Holotype (skin) was deposited in Polish State Museum of Natural History (now Institut Zoologiczny PAN, Warszawa).

Mustela pygmaea yesoidsuna Kishida, 1936. Doubuts. Zasshi, 48(4): 177. South Kuril Islands and Hokkaido Island. Type not designated.

Mustela pygmaea caraftensis Kishida, 1936. Doubuts. Zasshi, 48 (4): 177. Sakhalin, near Toyohara (=Yuzhno-Sakhalinsk). Type not designated.

Mustela nivalis kerulenica Bannikov. 1952. Bull. Moskovsk. Obsth. Ispyt. Prirody, 57(2): 40. Holotype: skull and skin, ♂, No. S-41755, coll. ZMMU; near Undurkhan, Kerulen River, Mongolia.

Type not designated. This species was described from Västerbotten Province, Sweden.

Diagnosis. Size small. Body length of males 152-230 mm (average 178 mm), tail rather short (17-20% of body length), but longer than hind foot. Condylobasal length of skull of males 29.8-36.4 mm (average 34.0 mm), female average 31.5 mm. Coloration of "nivalis"-type, winter fur white.

Distribution. Scandinavia (except southern Sweden), north of European Russia (southwards probably up to Tver Province), Urals, all of Siberia (except north-eastern part), Northern and Eastern Kazakhstan, Mongolia, Sakhalin, Kuril Islands and Hokkaido.

Remarks. Within its large distribution range the nominotypical subspecies reveals notable variability of exterior features. Length of body and relative length of tail decrease from west to east, but in the Far East there are forms similar to the weasel from the north-western part of Russia.

Mustela nivalis pygmaea (J. Allen, 1903)

Putorius (Arctogale) pygmaeus J.Allen, 1903. Bull. Amer. Mus. Nat. Hist., 19: 176.

Ictis nivalis var. *kamtschatica* Dybowski, 1922. Arch. Towar. Naukow Lwowie, 1: 349. Nomen nudum.

Holotype. Skull and skin, ♀, No. 18322, coll. Amer. Mus. Nat. Hist., New York, USA. Terra typica: Gichiga [=Gizhiga], northern coast of Okhotsk Sea, Eastern Siberia.

Diagnosis. The smallest weasel, tail short, shorter or only slightly longer than hind foot. Body length of males 135-180 mm (average 160 mm); average relative length of tail 12%. Condylobasal length of skull of males 28.0-35.6 mm (average 33.0 mm). Colouring of "nivalis"-type.

Distribution. North-Eastern Siberia, including Kamchatka.

Remarks. We leave this subspecific name only for weasels from the north-east of Siberia. However, it is necessary to note that this form is rather close to the nominotypical subspecies both in the size and proportions of body and skull, except for a shorter tail.

Mustela nivalis rixosa (Bangs, 1896)

Putorius rixosus Bangs, 1896. Proc. Biol. Soc. Washington, 10: 21.

Holotype. Skull and skin, ♀, No. 642 Bangs Coll., coll. Mus. Comp. Zool., Boston, USA. Terra typica: Osler, Saskatchewan, Canada.

Diagnosis. Small-sized weasel. Body length of males 177-208 mm (average 194.2 mm); relative length of tail 17%. Condylobasal length of skull of males 30.9-33.5 mm (32.1 mm). Colouring of "nivalis"-type.

Distribution. Most of Canada and the northern states of the USA, from the south up to central regions of Montana, North Dakota and Minnesota.

Remarks. All subspecies from North America are externally rather similar among themselves (with the allowance of a typical range of variability for a species across its entire range). In the size and proportions of skull, *rixosa,* as well as the other three American forms, is close to *M. nivalis nivalis*. The distribution of North American subspecies is given by Hall (Hall, 1951, 1981; Hall & Kelson, 1959).

Reig (1997) believes that all North American subspecies (except *eskimo*) belong to separate species *M. rixosa*.

Mustela nivalis eskimo (Stone, 1900)

Putorius rixosus eskimo Stone, 1900. Proc. Acad. Nat. Sci. Philadelphia, 52(1): 44.

Holotype. Skull and skin, ♀, No. 848, coll. Mus. Acad. Nat. Sci. Philadelphia, Philadelphia, USA (see Hall, 1951). Terra typica: Point Barrow, Alaska.

Diagnosis. Size small. Body length of males 200-230 mm (average 212 mm); aver-

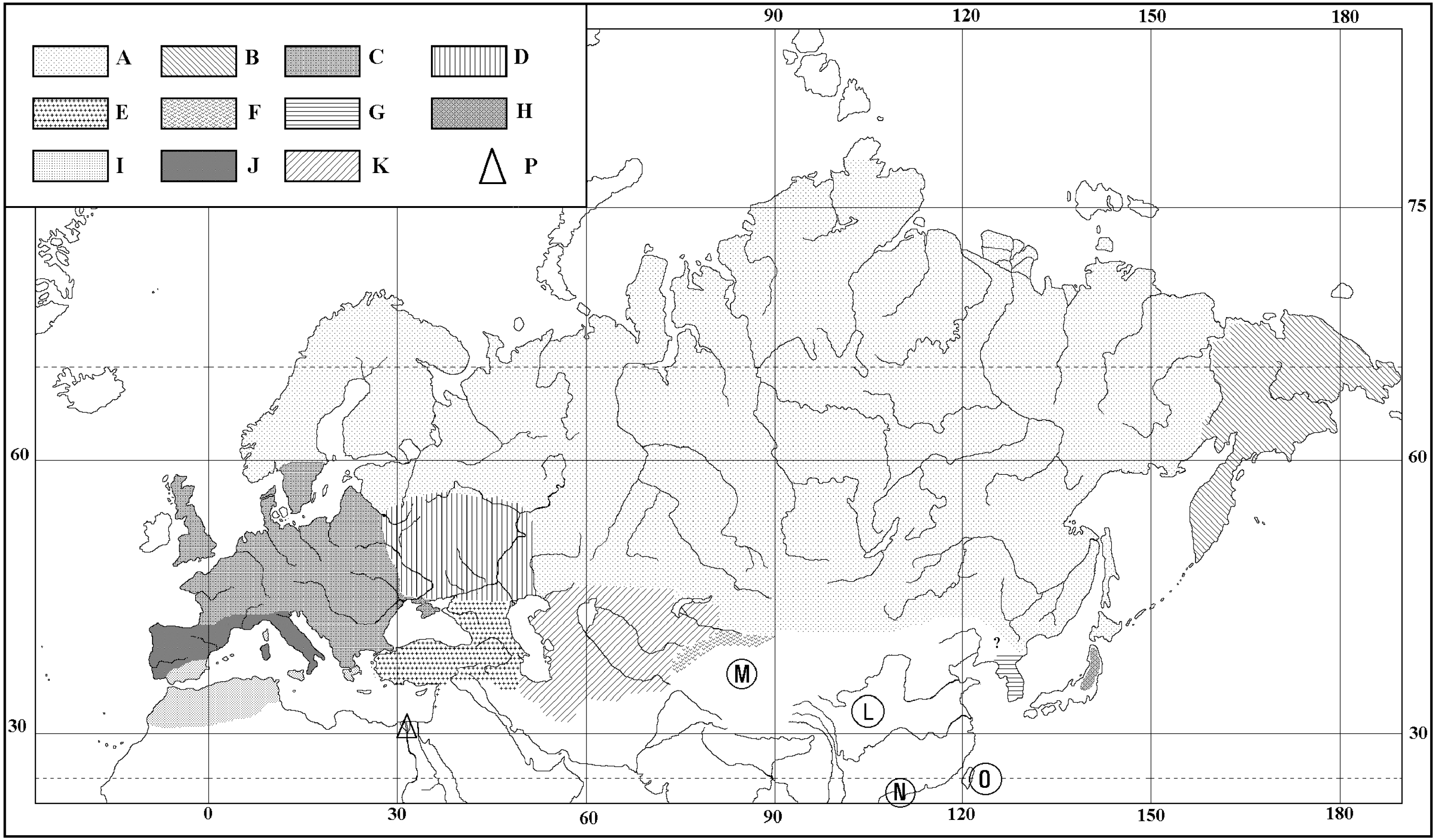

Fig. 10. Distribution of subspecies of *M. (Gale) nivalis* (A-O) and *M. (G.) subpalmata* (P) in the Palaearctic. A – *nivalis*, B – *pygmaea*, C – *vulgaris*, D – *rossica*, E – *caucasica*, F – *pallida*, G – *mosanensis*, H – *namiyei*, I – *numidica*, J – *boccamela*, K – *heptneri*, L – *russelliana*, M – *stoliczkana*, N – *tonkinensis*, O – *M. nivalis* subsp. n.

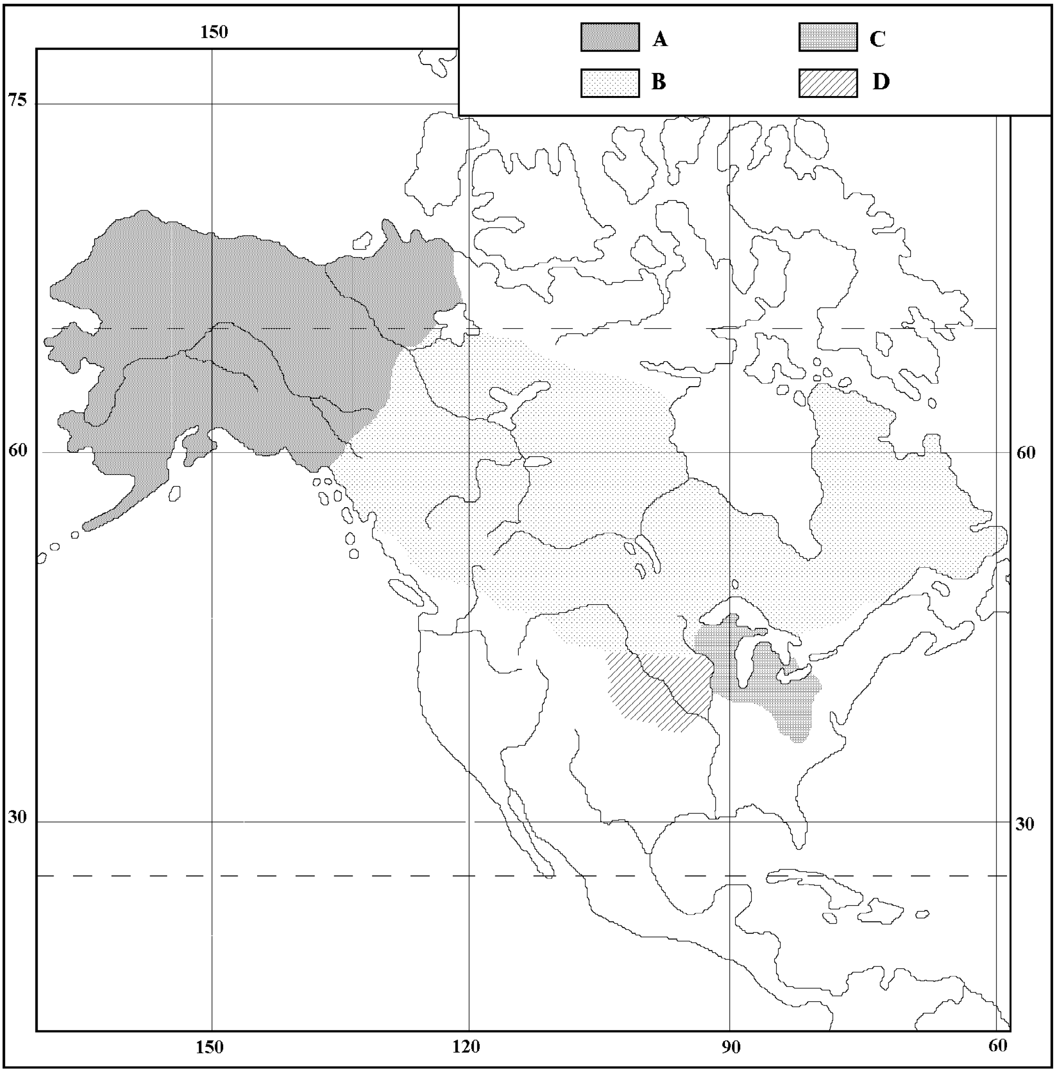

Fig. 11. Distribution of subspecies of *M. (Gale) nivalis* L. in North America (after: Hall, 1951, with additions). A – *eskimo*, B – *rixosa*, C – *allegheniensis*, D – *campestris*.

age relative length of tail 13.5%. Average condylobasal length of skull of males 34.4 mm. Colouring of "nivalis"-type. Winter fur white.

Distribution. Alaska and Yukon Territory in Canada.

Mustela nivalis campestris Jackson, 1913

Mustela campestris Jackson, 1913. Proc. Biol. Soc. Washington, 26: 124,

Holotype. Skull and skin, ♀, No. 171490, coll. Nat. Mus. Natur. Hist., Washington, USA. Terra typica: Beemer, Cuming Co., Nebraska, USA.

Diagnosis. Weasel of medium sizes. Body length of males 225-237 mm (average 231 mm); relative length of tail on average 15.6%. Condylobasal length of skull of males on average 34.7 mm (Hall, 1951). Colouring of "nivalis"-type.

Distribution. USA: South Dakota, Nebraska and Iowa.

Remarks. Hall (1951) points out that about 20% of specimens of *campestris* have coloration of "vulgaris"-type. We assume that these animals may belong to the subspe cies *allegheniensis*; is highly probable also that between both subspecies there is a transient zone (presumably in the region of Iowa – Illinois), where it is appropriate to draw their boundary.

Mustela nivalis allegheniensis (Rhoads, 1901)

Putorius allegheniensis Rhoads, 1901. Proc. Acad. Nat. Sci. Philadelphia, (1900), 52(3): 751.

Holotype. Skull and skin, ♂?, No. 6195, coll. Mus. Acad. Nat. Sci. Philadelphia, Philadelphia, USA. Terra typica: near Beallsville, Washington Co., Pennsylvania, USA.

Diagnosis. Weasel of small sizes. Body length of males 191-206 mm (average 197 mm); relative length of tail on average 16.4%. Condylobasal length of skull of males 30.7-34.6 mm (average 31.8 mm). Colouring of "vulgaris"-type.

Distribution. USA, states Wisconsin, northern parts of Illinois and Indiana, Michigan, Ohio and Pennsylvania.

Remarks. Like other North American forms, *allegheniensis* is closer to the nominotypical subspecies than to the European *M. n. vulgaris*, despite similar character of colouring.

Mustela nivalis vulgaris Erxleben, 1777

Mustela vulgaris Erxleben, 1777. Syst. Regni Animal., 1: 471.

Putorius minutus Pomel, 1853. Cat. Meth. Descr. Vert. Foss. Loire: 51. Near Paris, France. Type not designated.

Mustela nikolskii Semenov, 1899. Zapiski Imper. Akad. Nauk, 8(6): 14. Near Simpheropol, Crimea. This name was given for Crimean weasel, which was described (without scientific name) by Nikolskiy (1892). Type material was stored in the Zoological Cabinet of Saint-Petersburg University, not found now.

Mustela (Ictis) dombrowskii Matschie, 1901. Sitzungsber. Ges. naturf. Freunde Berlin, 1901: 231. Siulnita, Roumania.

Putorius nivalis var. *monticola* Cavazza, 1908. Ricerche sui "*Putorius nivalis*" e sui "*Putorius ermineus*" d'Italia: 37. High mountains of Alps. Type not designated.

Mustela trettaui Kleinschmidt, 1937. Falco, 33(1): 11. Gimmel, Kreis Oels, Silezia [= near Poniatowice (about 40 km NE of Wroclaw), Poland].

Mustela hungarica Vásárhelyi, 1942. Zool. Anz., 137 (1/2): 221. Bükk-Gebirge, Kom. Borsod, Hungary. Preoccupied by *Mustela eversmanni hungarica* Ehik, 1928.

Mustela vásárhelyi Kretzoi, 1942. Földtani Közlöni, 72: 349. New name for *Mustela hungarica* Vásárhelyi, 1942.

Mustela nivalis boccamela natio *occidentalis* Kratochvil, 1977. Acta Sci. Nat. Brno, 11(10): 35. Nomen nudum.

Type not designated. Terra typica: "temperate Europe" (according to Barrett-Hamilton, 1900: 42, near Leipzig, Germany; according to Kleinschmidt, 1937: 11, Göttingen, Germany).

Diagnosis. Size intermediate, notably larger than in the nominotypical subspecies; tail relatively longer. Length of body varies considerably (as a result of the presence of small-sized specimens in populations); body length of males 160 to 290 mm (average 207 mm); relative length of tail 18-30% (average 25%). Condylobasal length of skull of males 30.1-44.5 mm (average 38.3 mm), females average 33.6 mm. Colouring of "vulgaris"-type. In Central Europe animals sometimes occur with "nivalis"-type of colouring. Winter fur is usually brown; coloration of some individuals in winter may be partially or (rarely!) completely white.

Distribution. Southern Sweden, Great Britain, Western and Central Europe, Balkan Peninsula (except Greece), Crimea. Eastern boundary of distribution is not exactly established; as a whole it coincides with the western boundary of the former Soviet Union.

Remarks. In mountain areas of Central Europe, there are populations of rather small-sized weasels, in which specimens with "nivalis"-colouring quite often occur. Kratochvil (1977) suggested the use of the name *monticola* for this form.

Mustela nivalis rossica subsp. n.

Holotype. Skull without mandible, No. O.9866, skin, No. C.83129, ♂ ad, coll. ZIN. **Ukraine**, *Poltava Province*, Poltava District, Rudnoe Village, 3.VII. 1914 (A. Nagulnyak).

Paratypes. **Ukraine**, *Poltava Prov.*, Poltava Distr.: skull, skin, ♂ ad, No. S-28800, coll. ZMMU, Kovan'kovka, 31.III.1934 (Gordienko); skull, ♂ ad, No. S-28828, coll. ZMMU, Bugaevka, 24.X.1934 (Gordienko); skull, ♂ ad, S-28830, coll. ZMMU, Zhuka-Poluzer'e, 28.X.1934 (Gordienko).

Diagnosis. A weasel of medium size, a little larger than the nominotypical subspecies; tail slightly longer. Body length of males 150-238 mm (average 189 mm); relative length of tail 20-30% (average 25%). Condylobasal length of skull of males 31.5-43.8 mm (average 37.7 mm). Colouring of "nivalis"-type; winter fur is usually white.

Distribution. Central and southern part of European Russia, Ukraine, Byelorussia, northern regions of Moldova. In the east, most likely reaches the Urals.

Remarks. Usually the weasel of central and western parts of European Russia is attributed to the subspecies *M. n. vulgaris* (Ognev, 1928, 1935; Novikov, 1956; Polushina, 1964; Morozova-Turova, 1965; Heptner et al., 1967). In fact, in both the size and proportions of skull and body the subspecies described is close to *vulgaris*, however it has a different type of colouring.

Mustela nivalis caucasica (Barrett-Hamilton, 1900)

Putorius nivalis caucasicus Barrett-Hamilton, 1900. Ann. Mag. Nat. Hist., 5: 48.

Putorius nivalis dinniki Satunin, 1907. Izv. Kavkaz. Muz., 3(2-3): 105. Stavropol, Russia. Type in the Museum of Georgia, Tbilisi (see Pavlinov & Rossolimo, 1987).

Holotype. Skull and skin, No. 94.9.2.3, coll. NHM; Mons Hotschal [Khochal-dag], at a height of 12000 feet (Dagestan), Caucasus.

Diagnosis. Size medium; tail rather long. Body length of males 176-265 mm (average 216 mm); length of tail approximately 30% of body length. Condylobasal length of skull of males 34.1-43.4 mm (average 40.7 mm). Most of specimens have colouring of “nivalis”-type, but sometimes animals of “vulgaris”-colouring also occur sympatrically.

Distribution. Caucasus with Ciscaucasia and Asia Minor.

Remarks. It was assumed for a long time that two weasels, small-sized (*caucasica*) and large-sized (*dinniki*), jointly inhabited the Caucasus. The morphological differences between them, however, are insignificant, which was already noted by Satunin (1907). Characterizing animals from Ciscaucasia (Stavropol Territory), Satunin indicated as their differences from the typical Central Russian weasel the large size and much longer tail. Our data also testify that the Caucasian weasel differs genuinely from *M. n. rossica* in the larger sizes of body and skull. The boundary between these subspecies probably passes through the areas of the Don River and Manych River.

Mustela nivalis pallida (Barrett-Hamilton, 1900)

Putorius nivalis pallidus Barrett-Hamilton, 1900. Ann. Mag. Nat. Hist., 5: 48.

Holotype. Skull and skin, ♀, No. 94.9.2.1, coll. NHM. Terra typica: Kokand, Ferghana, Uzbekistan.

Diagnosis. A weasel of small to intermediate size, with rather long tail. Body length of males 150-225 mm (average 191.9 mm); relative length of tail 21-25 % (average 24.1%). Skull rather narrow, its condylobasal length in males 30.8-39.4 mm (average 36.4 mm). Measurements of the holotype: CbL = 38.5 mm, ZyB = 21.0 mm, GmB = 17.7 mm. Colouring of “nivalis”-type. Winter fur white.

Distribution. Tien-Shan and Pamirs-Alai.

Remarks. In the size and proportions of the skull, similar to the typical subspecies, but the exterior is different, the tail somewhat longer. Collection material of this form is very scanty. Probably it is only a small-sized mountain form of a large weasel from plain areas. In this case the name *heptneri* is only a junior synonym of *pallida*. Barrett-Hamilton (1900) regarded also the weasel from Afghanistan as *pallida*.

Mustela nivalis russelliana Thomas, 1911

Mustela russelliana Thomas, 1911. Abstr. Proc. Zool. Soc. London, 90: 4.

Holotype. Skull and skin, ♀, No. 11.2.1.86, coll. NHM. Terra typica: Ta-tsien-lu [= Kanding], at a height 12000 feet, Province Sichuan, China.

Diagnosis. Small-sized, rather long-tailed weasel. Length of body of male 138 mm; length of tail 54 mm (39%). Skull rather narrow. Measurements of holotype: CbL = 29.0 mm, ZyB = 14.7 mm, GmB = 13.8 mm. Colouring of “nivalis”-type.

Distribution. Is known only from high mountains of Sichuan, China.

Mustela nivalis mosanensis Mori, 1927

Mustela nivalis mosanensis Mori, 1927. J. Chosen. Nat. Hist. Soc., 5: 28.

Holotype. Skin, ♀, without coll. No., we do not know the depository of type material. Terra typica: Yengan near Mosan, north-eastern Korea.

Diagnosis. A poorly investigated form of intermediate to large size. Length of body of male (paratype) 250 mm, female (holotype) 225 mm; tail short (17% of length of body). According to the description, it has a colouring of “nivalis”-type; however, animals with the other type of colouring also occur (southern part of Korean Peninsula).

Distribution. Korean Peninsula.

Remarks. The absence of sufficient material on the Korean weasel does not allow us to make a final inference about its taxonomic status. We reserve for this form the name *M. n. mosanensis* as, according to information available, this weasel differs from better investigated animals of adjacent populations (Mongolia, Primorsk Territory) in the size of the body.

Mustela nivalis namiyei Kuroda, 1921

Mustela rixosa namiyei Kuroda, 1921. J. Mammal., 2: 209.

Holotype. Skin without coll. No., sex unknown, depository unknown. Terra typica: Aomori Province, Honshu, Japan.

Diagnosis. Body small-sized; tail short. Length of body 160-166 mm (average 163.0 mm); relative length of tail 17.9%. Condylobasal length of skull of males 31.5-31.9 (average 31.7 mm), female average 30.3 mm (Obara, 1991b). Colouring of "nivalis"-type.

Distribution. Northern part of Honshu, Japan.

Remarks. Subspecific rank of weasel from Honshu Island is beyond question. It has, in particular, diploid set of chromosomes 2n=38, that could be a consequence of the long insular isolation. Differs from animals from Hokkaido Island also in the smaller size of skull and much broader palate (Obara, 1991b).

Mustela nivalis tonkinensis Björkegren, 1941

Mustela tonkinensis Björkegren, 1941. Arkiv Zool., 33B(15): 1.

Holotype. Skull and skin, ♂, No. 63.0148, coll. Swed. Mus. Nat. Hist., Stockholm. Terra typica: Chapa, Northern Tonkin, Vietnam.

Diagnosis. Size medium. Length of body 200 mm; length of tail 90 mm (type specimen). Skull rather narrow. Measurements of holotype: CbL = 37.3 mm, ZyB = 18.6 mm, GmB = 15.5 mm. Colouring of "nivalis"-type.

Distribution. Only one specimen, from Northern Vietnam (Chapa), is known.

Remarks. Some authors (Ellerman & Morrison-Scott, 1951; Heptner et al., 1967) doubted the placement of this form in *M. nivalis* and supposed that it, most likely, belonged to the species *M. kathiah.* We believe that the taxon *tonkinensis* is just a subspecies of *M. nivalis.*

Mustela nivalis numidica (Pucheran, 1855)

Putorius numidicus Pucheran, 1855. Rev. Mag. Zool., 7: 393.

Mustela vulgaris fulva Mina Palumbo, 1868. Ann. Agr. Sci. Palermo, 12: 53. Forest parts of Sicily.

Mustela vulgaris albipes Mina Palumbo, 1868. Ann. Agr. Sci. Palermo, 12: 54. Agricultural parts of Sicily.

Putorius vulgaris var. *meridionalis* Costa, 1869. Ann. Mus. Zool. Univ. Napoli, 1869: 40. Southern Italy.

Putorius ermineus algiricus Thomas, 1895. Ann. Mag. Nat. Hist., 15: 451. Near Algiers, Algeria. Holotype: skull, sex unknown, No. 56.3.12.13, coll. NHM.

Putorius nivalis ibericus Barrett-Hamilton, 1900. Ann. Mag. Nat. Hist., 5: 45. Seville, Spain. Holotype: skull and skin, ♀ ?, No. 95.3.3.10, coll. NHM.

Putorius nivalis siculus Barrett-Hamilton, 1900. Ann. Mag. Nat. Hist., 5: 46. Marsala, Sicily. Holotype: skull and skin, ♂, No. 95.4.4.5, coll. NHM.

Putorius nivalis atlas Barrett-Hamilton, 1904. Ann. Mag. Nat. Hist., 13(76): 323. Atlas Mountains, Morocco. Holotype: skull and skin, ♂, No. 2174, coll. NHM.

Putorius nivalis galinthias Bate, 1905. Proc. Zool. Soc. London, 2: 319. Crete. Holotype: skin, ♂ ?, No. 5.12.2.24, coll. NHM.

Putorius nivalis var. *corsicanus* Cavazza, 1908. Ricerche sui "*Putorius nivalis*" e sui "*Putorius ermineus*" d'Italia: 37. Corsica. Type not designated.

Holotype. Specimen in alcohol, No. C.250, coll. Paris Museum. Terra typica: Tangier (see Barrett-Hamilton, 1900).

Diagnosis. Large, long-tailed weasel. Body length of males 230-380 mm (average 300 mm); relative length of tail 33-42% (average 38%). Condylobasal length of skull of males 39-49 mm (average 44.2 mm). Colouring of "nivalis"-type.

Distribution. Morocco, Algeria, Tunisia, southern Spain, Greece, Corsica, Sicily and Crete.

Mustela nivalis boccamela Bechstein, 1800

Mustela boccamela Bechstein, 1800. Pennant's Ueber. vierfüs. Thiere, 2: 395, 694.

Putorius nivalis italicus Barrett-Hamilton, 1900. Ann. Mag. Nat. Hist., 5: 45, Grezzana, highlands of the Province of Verona, Italy. Holotype: skull, ♂, No. 95.11.11.1, coll. NHM.

Type not designated. Terra typica: Sardinia.

Diagnosis. Large, long-tailed weasel. Length of body is 210-320 mm (average 270 mm); relative length of tail 35-39% (average 37%). Condylobasal length of skull of males 39-45 mm (average 43.5 mm). Colouring of "vulgaris"-type.

Distribution. Northern part of Iberian Peninsula, Balearic Islands, southern

France, Italy, Sardinia, and also, probably, Malta.

Remarks. The weasel from the Azores is close to this subspecies in the size and proportions. Weasels, apparently, were brought to the Azores by seamen in ancient times.

Mustela nivalis heptneri Morozova-Turova, 1953

Mustela nivalis heptneri Morozova-Turova, 1953. Zool. Zh., 32(6): 1268.

Holotype. Skull and skin, ♂, No. S-38822, coll. ZMMU. Terra typica: Islim-Cheshme, Egri-Gek River (tributary of Kushka River), Badhyz, Turkmenistan.

Diagnosis. Large long-tailed weasel. Length of body 200-270 mm (average 233 mm); relative length of tail 27-32%. Condylobasal length of skull of males 40-46 mm (average 42.0 mm). Colouring of "nivalis"-type. Summer coat on the back rather light, pale brown.

Distribution. Iran, Afghanistan, Turkmenistan, Uzbekistan, Western Tadjikistan, Southern Kazakhstan (in north up to Emba River).

Mustela nivalis stoliczkana Blanford, 1877

Mustela stoliczkana Blanford, 1877. J. Asiat. Soc. Bengal, 46(3): 260.

Lectotype (? Barrett-Hamilton, 1900: 49). Skin, without coll. No., depository of type material unknown. Terra typica: Yarkand, Eastern Turkestan [= Xinjiang, China].

Diagnosis. Large weasel. Length of body 250-310 mm (average 280 mm); tail rather long (25-31%). Condylobasal length of skull of males 42.5-46.1 mm (average 44.3 mm). Summer colouring of "vulgaris"-type; fur on back light-brown, pale.

Distribution. Western China. Distribution of this subspecies is not investigated; only the specimens from Yarkand and from region of Lob-Nor Lake are known. Bannikov (1952, 1954) assumed that it was possible to find large weasel, similar to this form, in mountains of the Transaltai Gobi.

Mustela nivalis subsp. n.

Mustela sp. nov. Lin & Harada, 1998. Abstr. Euro-Amer. Mammal Congr., Santiago de Compostela, Spain: 263.

Type not designated. Terra typica: Mt. Houhan (at a height 3200 m), Taiwan.

Diagnosis. Not large weasel; tail rather long (probably about 30-40%). Colouring of "vulgaris"-type.

Distribution. Two specimens from central mountain of Taiwan are known only.

Remarks. This form was described from Taiwan Island as a new (not named) species of *Mustela* (Lin & Harada, 1998). These authors believed the new form is close to *M. erminea.* We have an opportunity to examine the colour photographs of this animal kindly given to us by Dr. T. Oshida (Hokkaido University). Exterior and coloration of this new form is according to *M. nivalis*. Our opinion is confirmed by karyological data (2n = 42, NF = 68) (Lin & Harada, 1998).

Mustela (Gale) subpalmata Hemprich & Ehrenberg, 1833

Mustela subpalmata Hemprich & Ehrenberg, 1833. Symb. Phys. Icon., Mamm., 3(2): k verso.

Type no designated. Terra typica – Cairo and Alexandria (in houses), Egypt.

Diagnosis. Very large and long-tailed weasel. Body length of males 280-403 mm (average 380 mm); relative length of tail 30%. Condylobasal length of skull of males 47.3-51.4 mm (average 49.2 mm). Colouring of "vulgaris"-type.

Distribution. Egypt (probably only Lower Egypt). Inhabits human houses and agricultural places.

Remarks. Based on results of craniometric analysis, Zyll de Jong (1992) has restored specific status for the Egyptian weasel. This researcher believed that an additional argument in favour of specific separateness of *M. subpalmata* is the degree of sexual dimorphism in skull size, distinct from other subspecies of the least weasel. In addition, according to our data, the correlation structure of craniometric measurements of the Egyptian weasel differs in essential features from that of *M. nivalis*. The separation of *M. subpalmata* from the ancestral form could have occurred at an earlier phase of evolution than the division of *M. nivalis* into major groups of geographic forms.

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