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Coat colour and chromosome variation in central European populations of the weasel (*Mustela nivalis*)

† *Dedicated to the memory of our friend Huw Idwal Griffiths (1958–2002)*

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A b s t r a c t . The frequencies of two hereditary coat colour types were determined in a sample of weasels, *Mustela nivalis* (n=1280) from the Czech and Slovak Republics. White pelage was found in four (0.49%) individuals collected in the period between October and April (n=824). All the other individuals studied had type II *vulgaris* coloration, characterised by an irregular border between the upper brown part of the body and the white underbelly. Distal white coloration on the feet and upper lip appeared to be unreliable in distinguishing between the two basic types of weasel summer coat. The karyotypes of five weasels from different parts of the Czech Republic contained large heterochromatic arms in six pairs of autosomes. The absence of a large heterochromatic arm in autosomal pair No. 7 differentiates the chromosomal complement of the central European weasels from those occurring in the northern parts of their range. The same karyotype found in Czech weasels was also found in an individual from European Turkey. Comparison of the available data on coat colour and chromosomal variation confirmes the existence of three major phylogenetic lineages of weasels in Europe.

Key words: weasel, pelage coloration, karyotype, systematics

Introduction

The weasel (*Mustela nivalis* L., 1766) is a species that shows an extraordinary degree of individual, seasonal and geographic variation (R e i c h s t e i n 1993) and the species' extreme variation in body size has led to a rather confused intraspecific taxonomy. R e i c h s t e i n ' s (1957) revision resulted in the currently prevailing opinion that all weasel populations belong to a single Holarctic species (W o z e n c r a f t 1993). F r a n k (1985) suggests that particular characters of weasels from western parts of North Africa, the Iberian peninsula and certain Mediterranean islands could justify their separation as *M. numidica* (Pucheran, 1855). However, V a n Z y l l d e J o n g (1992) proposed separate specific status for populations from Egypt, i.e. *M. subpalmata* Hemprich et Ehrenberg, 1833. The most recent revision (by R e i g 1997) concludes that although North American weasels should be treated as separate species, *M. rixosa* (Bangs, 1896), Alaskan populations represent a subspecies of *M. nivalis*.

Body size represents a character with direct adaptive significance, and its current state and variation are most likely dependent on environmental selection pressures. The extraordinarily large extent of intraspecific size variation in the weasel can be explained by the need for effective division and exploitation of the limited environmental resources

available. Under this scenario individual size morphotypes and sexual dimorphism have roles as separate members of a foraging guild. This produces further character displacement and results in an increase in the extent of size variation (Rosenzweig 1968, King & Moors 1979, Meia & Mermod 1993). The comparison of size components of body and cranial dimensions in individual geographic populations should result in an estimate of the similarity of selection pressure in various areas with similar environmental conditions, but will not reveal real phylogenetic relationships. As a result, multiple discriminant function analyses utilising size-free data have been used to demonstrate shape change in the phylogenetic divergence of geographic populations. In this way, Van Zyll de Jong (1992) differentiated European weasels into two subspecific groups: *M. n. nivalis* and *M. n. vulgaris*. The former group inhabits the Boreal Zone of the Holarctic, the latter the Temperate Zone and the Mediterranean area. Meia & Mermod (1993) doubted the validity of taxonomic classifications of weasels on the basis of body size characters, and concluded that only one or two subspecies were recognisable in Europe. Reig (1997) divided *M. nivalis* into two groups: *M. n. eskimo* (Stone, 1900) from Alaska, and the nominate subspecies from the Palaearctic.

Reichstein (1957), Niethammer (1973), Kratochvíl (1977) and Stolt (1979) underlined the phylogenetic significance of the distribution of the two basic types of weasel coloration. These differ particularly in the course of the line formed at the junction of the dorsal brown and ventral white fur. The line is straight on the neck and at the sides of body in the type I, whereas it has an irregular zigzag pattern in the type II. A brown spot on the cheek is usually present in the type II, and other brown spots can occur along the borderline between brown and white fur. White feet are usually found in the animals with the type I coloration, while brown feet occur in the type II. The winter change of pelage can result in a complete whitening of the coat, but regular moulting into a white winter coat is only characteristic of certain populations. Frank (1985) confirmed the hereditary character of the individual types of coloration and of pelage change, and placed European weasels into three groups. The *M. n. numidica* group has a type I coloration and large body size, lacks a white winter coat, and occurs in the south-western parts of the species' European range (including certain other parts of the Mediterranean). The *M. n. nivalis* group includes populations adapted to hard winter conditions and which inhabit northern Europe and mountain areas; they typically have type I coat coloration, winter change is common, and body size is small. The last group is *M. n. boccamela/vulgaris* which inhabits the Temperate Zone and some regions of the Mediterranean. This form characteristically has type II coloration, white winter fur occurs only rarely, and has an intermediate body size. Despite this, there are few quantitative data on the frequencies of the individual types of coloration in natural populations belonging to this group.

The karyotype of the weasel is polytypic (see review by Zima & Král 1984). The nature of karyotypic variation was elucidated by the study of differentially stained chromosomes in populations from Sweden (Fredga & Mandahl 1973, Mandahl & Fredga 1980), Siberia (Grafodatskij et al. 1977), Japan (Obara 1982, 1985), Alaska (Jarell 1983) and Slovakia (Zima & Grafodatskij 1985). The karyotypes observed in individual geographic populations differ in their diploid numbers and in the numbers of large heterochromatic arms. In Scandinavia, Siberia and Alaska, seven autosomal pairs possessing large heterochromatic arms were recorded, in Slovakia there are six pairs and in a population from Japan only five. The diploid number of

chromosomes is lower in a population from Aomori Pref. (Honshu Island, Japan) as a result of two non-reciprocal translocations (O b a r a 1982, 1985). The only report on the banded karyotype of weasels from central Europe is that of Z i m a & G r a f o d a t s k i j (1985) and is based on the examination of four individuals collected at a single site in Slovakia.

In this paper, we examine two non-metrical characters, coloration pattern and karyotype, with the aim of revealing their patterns of variation in weasel populations from central Europe.

Material and Methods

The study of coat colour variation was based on the examination of skins kept in following institutions: Department of Zoology, Charles University, Praha (DZCU); Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno (IVB); Silesian Museum, Opava (SM); National Museum, Praha (NM). Altogether, 1,280 specimens were studied (1,080 males, 200 females). The majority of the specimens originated from the Czech Republic, although 13 specimens were collected in Slovakia.

Diagnostic characters differentiating coat colour types (I – *nivalis*, II – *vulgaris*) were used according to F r a n k (1985). Within type II some other discrete variants were recorded:
– fore feet distally white, and all other parts brown (wff)
– hind feet distally white, and all other parts brown (whf)
– fore and hind feet distally white, and all other parts brown (wffhf)
– upper lip white, and all other parts brown (wul)
– fore feet and upper lip white, and all other parts brown (wfful)
– hind feet and upper lip white, and all other parts brown (whful)
– fore and hind feet and upper lip white, and all other parts brown (wffhful)
– fore and hind feet and upper lip brown, i.e. the standard coloration of the type II (st)

The occurrence of a white winter coat was recorded in specimens collected between October 1st and April 30th – a period that should include the autumn and spring moults (K r a t o c h v í l 1951, K i n g 1979, S t o l t 1979, M o š a n s k ý 1983).

The frequencies of coat colour variants were analysed by χ^2 tests of homogeneity using BMPDns software. The same formula was used to test the hypothesis of homogeneity and independency. If null frequencies occurred, the classes were united and the derived table was analysed. The normal distribution of data was obtained after calculation of residual values, and the significance of homogeneity deviations was tested using the normalised residuals.

Karyotypes were examined in five individuals from the Czech Republic (a male – Kateřina, Cheb District, 12°25'E 50°09'N; a male – Zámeček, Most District, 13°34'E 50° 41'N; a female – Liběchov, Mělník District, 14°27'E 50°25'N; a male – Pohořelice, Břeclav District, 16°02'E 48°59'N; a female – Skalní mlýn, Blansko District, 16°43'E 49°22'N), and one individual from European Turkey (a male – Dupnisa Magarasi, Kirklareli District, Istranca Mts., 27°50'E 41°55'N). The type II – *vulgaris* coat coloration pattern was present in all the individuals examined karyotypically. Chromosomes were studied using short-term cultivation of bone marrow cells by the application of colchicin, hypotonic treatment with calium chloride and fixation in Carnoy's mixture (3 : 1 methanol : glacial acetic acid). Slides were stained with Giemsa and C- and G- banded after S u m n e r (1972) and S e a b r i g h t (1971), respectively. A minimum of 20 metaphase cells was examined for each individual and for each banding technique used. Individual chromosomal pairs were arranged in the karyotype following M a n d a h l & F r e d g a (1980).

Results

Coat colour

The sample of weasels collected in the winter period contained four individuals with white coloration (no. M495/DZCU – a male collected in January 1958 in Dolní Beřkovice near Mělník, 14°27'E 50°24'N; no. 46/IVB – a male, collected on April 8,1950 near Prostějov, 17°07'E 49°28'N; no. 4247/SM – a male, collected on October 17, 1974 in Hošťálkovice near Opava, 18°13'E 49°51'N; no. 1325/SM – a male, collected on February 23, 1962 near Bardejov, 21°17'E 49°17'N). However, in specimen No. 46/IVB the white coat coloration was only partial due to the presence of brown spots on the head. Thus, white coat coloration was recorded in 0.49% of individuals collected in the period between the autumn and spring pelage change.

No individual with a type I – *nivalis* coloration was recorded, and all the individuals in summer coat (n=1276) had type II – *vulgaris* coloration. Standard type II coloration was recorded in 367 individuals (28.8%) the remainder displaying various variants. Altogether, 852 individuals (66.8%) had white upper sides to the fore feet, 47 individuals (3.7%) had at least partially white hind feet, and 418 individuals (32.8%) had a white upper lip. The variants observed were found in various combinations in the specimens studied (Table 1).

The frequencies of the individual variants revealed some geographical variation among samples originating from different parts of the Czech Republic. The frequency of white coloration in both feet and the upper lip increased significantly in the sample from central Bohemia (NR = 2.45), while white coloration of both feet increased in northern and southern Bohemia (NR = 2.39 and 2.50, respectively) and white coloration of the upper lip increased in eastern Bohemia (NR = 2.35) relative to all the other samples. The frequencies of the coloration variants were significantly different between the samples from central Bohemia and northern Moravia (χ^2 = 20.26, D.F. = 7, P = 0.005), northern Bohemia and northern Moravia (χ^2 = 14.26, D.F. = 7, P = 0.05) and southern Bohemia and northern Moravia (χ^2 = 12.80, D.F. = 7, P = 0.08). However, the overall analysis showed that distribution of the frequencies among geographic samples was homogeneous (χ^2 = 60.40, D.F. = 49, $P_{0.95}$ = 0.13). The frequencies of the variants were significantly different between males and females (χ^2 = 44.58, D.F. = 7, P < 0.01). Significantly lower frequencies of white fore feet and upper lip were recorded in females than in males (normalised residuum NR = -3.08), whereas the standard variant of coloration type II was significantly more frequent in males than in females (NR = -2.08).

Table 1. Frequencies of the variants found within coloration type II (see Material and Methods for abbreviations).

colour variant of type II	no. of individuals (%)
wff	477 (37.4)
whf	1 (0.1)
wffhf	13 (1.0)
wul	54 (4.2)
wfful	331 (25.9)
whful	2 (0.2)
wffhful	31 (2.4)
st	367 (28.8)
total	1276 (100.0)

C h r o m o s o m e s

A diploid number of 42 chromosomes was found in all the individuals examined. Three groups of autosomes could be distinguished according to their size and centromere position. The first group comprised five pairs of large meta- and submetacentric autosomes (nos. 1–5). The three largest pairs were submetacentric, the other two metacentric. The second group comprised eight pairs of medium-sized autosomes (nos. 6–13), including five submetacentric and three subtelo- or acrocentric pairs. The last group comprised seven pairs of small size (nos. 14–20). Three pairs were acrocentric and one of them possessed a prominent secondary constriction (no. 14). The remaining pairs were biarmed but exact determination of the centromere position was sometimes equivocal because of small autosome size; we cannot exclude interindividual or interpopulation variation in the centromeric position in certain of these small autosomal pairs. The X chromosome was submetacentric and its size was similar to that of the 9th autosomal pair. The biarmed Y chromosome was the smallest element in the complement (Fig. 1).

Distinct centromeric C-positive bands were found in the large submetacentric autosome No. 3, in the metacentric autosome No. 4, in four submeta- and subtelocentric autosomes from the second group (Nos. 7,9,10,12), in most autosomes of the third group, and in the X chromosome. Faint telomeric C-positive bands were apparent in the short arm of the subtelocentric pairs No. 10 and 12, and an intercalar C-positive band was present in the short arm of the metacentric pair No. 4. The Y chromosome was completely C-heterochromatic, but the staining was less intensive than in autosomal heterochromatin. C-heterochromatic large autosomal arms were observed in three pairs of the first group

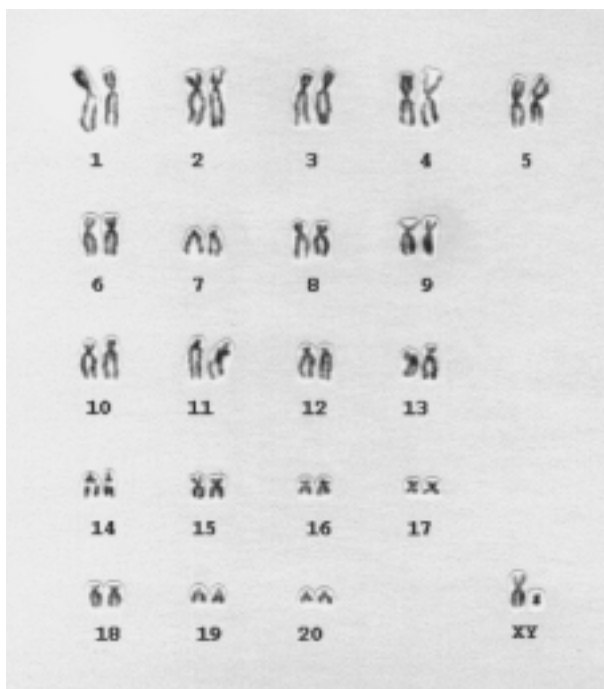

Fig. 1. Conventionally stained karyotype of a male weasel from European Turkey.

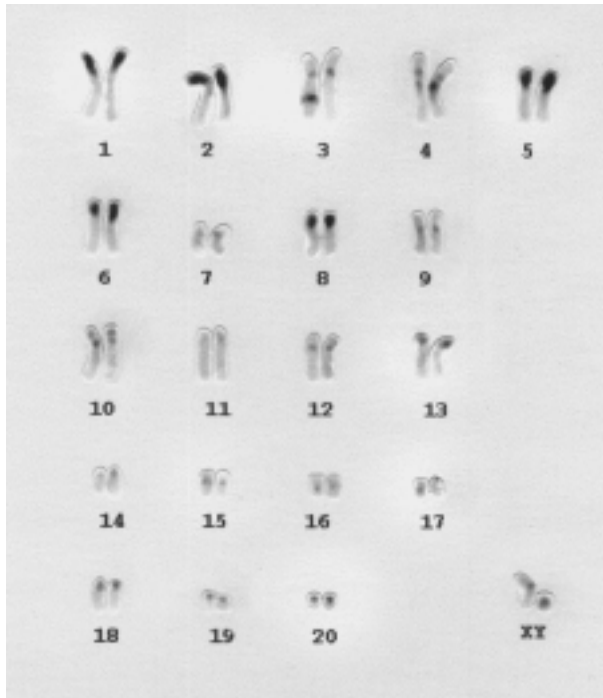

Fig. 2. C-banded karyotype of a male weasel from Kateřina, Czech Republic.

(No. 1,2,5), and in three pairs of the second group (No. 6,8,13). Altogether, six autosomal pairs with large heterochromatic arms were found in the karyotypes studied (Fig. 2). The C-heterochromatic large arm was absent in the autosomal pair No. 7 identified by G-banding.

Discussion

The discovery of the hereditary nature of the coloration types in weasels opened up the possibility of mapping the frequencies of individual presumptive alleles in geographical populations. Both of the F r a n k ' s (1985) basic differentiating criteria (i.e. the line between the upper brown and white under part of body, and the white winter pelage) were usually considered together as belonging to a single set of characters. F r a n k (1985) supposed that both characters were determined either by a single locus or by two closely linked loci. It seems more appropriate to evaluate frequencies of both the alleles separately, supposing that each character is determined by a separate locus with two or more alleles. It is likely that evolutionary forces influencing changes in allele frequencies are distinctly different between the two characters. The ability to effect seasonal pelage changes is probably of direct adaptive significance, as it provides protective coloration in winter. The distribution of the alleles at this locus should therefore be related to natural selection, and the effective forces of this selection are apparently similar to those determining small body size. The allele for the white winter coat is widespread, or even fixed, in populations inhabiting higher latitudes and altitudes. Central Europe is an area with relatively diverse climatic conditions and altitudinal variation, so it is not surprising that relatively low white winter coat allele frequencies are

maintained. Our estimate of the frequency of winter white coloration in the Czech and Slovak populations (0.49%) is in accordance with the few published data available. K r a t o c h v í l (1951) found only one white-coloured individual among 250 Czechoslovak weasels (0.4%), C a v a z z a (1914) reported one white individual from 385 northern Italian weasels (0.3%), B a r b u (1968) found one white animal amongst 85 weasels (1.2%) in a Romanian sample, and M o š a n s k ý (1983) found two white individuals out of 34 weasels from eastern Slovakia (5.7%).

Another situation can be expected in the case of the presumptive locus determining the character of the colour limit between the upper and under part of body. It is difficult to imagine any adaptive difference between the two basic types of coloration, and the frequencies of both types are apparently driven by drift rather than selection. Our study indicates that the allele for type I – *nivalis* is probably absent in the area under study, particularly in the Czech Republic. The independent nature of both the loci determining the main character of coat colour variation in European weasels is supported by two specimens collected in Białowieża in Poland (Nos. 3461/SM, 3462/SM). One specimens was in white winter coat, whereas the other had a summer coat with the type II – *vulgaris* colour pattern. This suggests the simultaneous co-occurrence of both alleles in a single population and supports the separate nature of the respective loci.

Type-II coloration is phenotypically rather variable and one might suppose that certain variants of this type may also be hereditary and hence of phylogenetic importance. Our results do not support this view. The frequencies of individual variants observed within the type II coloration did not show any obvious geographic or environmental pattern. Therefore, the geographic as well as sexual variation observed probably resulted from random shifts in phenotype. However, the variation observed within type II can be used to make the original definition and diagnostic features proposed by F r a n k (1985) more precise. We have demonstrated that white coloration in the feet and the upper lip is relatively common in populations which otherwise show the type II coloration. Therefore, these character variants should not be considered as being diagnostic. The criterion that remains reliable for distinguishing between both summer coat types is the line between the dorsal brown and ventral white fur.

New data on the karyotypes of several weasels from the Czech Republic and one individual from European Turkey confirms the findings of Z i m a & G r a f o d a t s k i j (1985) on the chromosome complement of Slovak weasels. The common feature of all these karyotypes is the presence of large heterochromatic arms in only six autosomal pairs, and their absence from autosomal pair No. 7. Finding the same chromosomal characteristics in nine individuals from five geographically distant areas of the Czech Republic and Slovakia strongly indicates that this complement is widespread in central Europe. The presence of the same karyotype in European Turkey also shows that this karyotype can occur in Balkan populations and, perhaps, in other areas of south-eastern Europe. However, although the chromosomes of the weasel have been studied in several parts of south-eastern and eastern Europe and Asia Minor (P e s h e v et al. 1985, B a k e r et al. 1996, C o l a k et al. 1999) these studies reported only conventionally stained chromosomes, and the number of C-heterochromatic arms cannot be estimated precisely.

Karyotypic divergence between weasel populations reveals a pattern of polytypic heterochromatin variation over a large area (Fig. 3). Heterochromatic segments consist of repetitive DNA, the importance of which in gene expression and genome regulation is

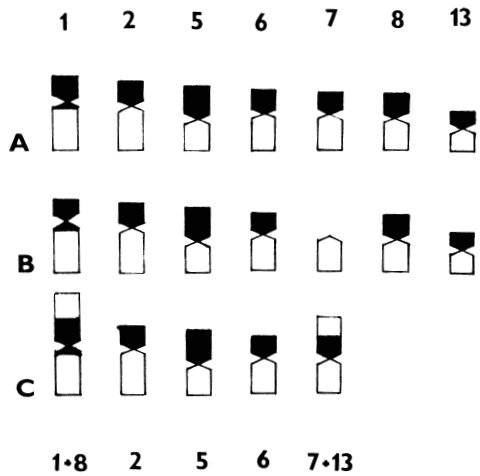

Fig. 3. Karyotypic differences between weasels from different geographic areas. The number designate individual autosomal pairs, black sections indicate heterochromatin. A – Scandinavia, Siberia, Alaska (G r a f o d a t s k i j et al. 1977, F r e d g a & M a n d a h l 1980, J a r r e l l 1983); B - central Europe and European Turkey (Z i m a & G r a f o d a t s k i j 1985, this paper); C - Japan, Aomori Pref. (O b a r a (1982).

unclear (J o h n & M i k l o s 1979). K i n g (1993) suggested that quantitative changes in heterochromatin do not result in negative heterosis, a prerequisite for the formation of reproductive barriers during speciation. The ranges of the two main karyotypic races of *M. nivalis* can thus usefully indicate the pattern of phylogenetic divergence, but the karyotypic difference itself is unlikely to lead to any reproductive problems in possible hybrids.

The known range of populations with seven large heterochromatic arms includes northern Europe, Siberia and Alaska, and it is similar to the range of small-bodied northern populations included in the *M. nivalis* group. Despite this, it seems that we cannot simply identify any karyotypic race with either a specific size morphotype or a weasel subspecies. M a n d a h l & F r e d g a (1980) studied the karyotype of both size morphotypes (*M. n. vulgaris* and *M. n. nivalis*) occurring in southern and northern Sweden, respectively, and found the same complement and number of heterochromatic autosomal arms. Similarly, Z i m a & G r a f o d a t s k i j ' s (1985) examination of individuals with different body sizes (including extremely small animals) revealed a similar result. Furthermore, data presented in this paper shows that, in central Europe, the karyotype found in small-sized individuals from the mountains is the same as in larger individuals from lower altitudes.

Nevertheless, the pattern of variation in cranial morphology, coat coloration and karyotype characteristics in populations of European weasels is rather similar in individual character sets. This similarity inheres particularly in a single pattern of basic divergence, suggesting the existence of only few phylogenetic lineages that are largely discussed in the recent literature (F r a n k 1985, R e i c h s t e i n 1993). The weasels of northern Europe (confined to taiga and tundra habitats) are typically small, have a white winter pelage, a type I coat coloration, and the presence of seven heterochromatic autosomal arms. Central European populations (confined to deciduous forest habitats) are bigger but more variable in size, white pelage occurs only exceptionally in winter, the type II summer coat coloration is widespread, and there are only six heterochromatic autosomal arms in the karyotype. This lineage may also include populations from south-eastern and western Europe – e.g. British

weasels rarely turn white in winter and type II of coat coloration prevails (King 1979). The third lineage is represented by populations from south-western Europe, the southern parts of the Balkans and certain Mediterranean islands. This group has the largest body size amongst European weasels, they never change coat colour in winter, and the summer coat is of type I. Some authors (Van Zyll de Jong 1992, Meia & Mermod 1993) do not recognise the last lineage (*M. n. numidica*) as being a separate phylogenetic group, thus data on the karyotype constitution (which are still lacking from this part of the species' distribution range) could contribute significantly to the clarification of this problem.

The congruence in the variation pattern between the individual character sets is far from absolute, as exemplified in the study of Scandinavian weasels. We therefore suppose that these character sets evolved largely independently, and that their development has been subject to varied evolutionary forces. It is possible that the introduction of appropriate molecular markers will shed more light on this traditional problem.

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LITERATURE

BAKER, R. J., HAMILTON, M. J., VAN DEN BUSSCHE, R. A., WIGGINS, L. E., SUGG, D. W., SMITH, M. H., LOMAKIN M. D., GASCHAK, S. P., BUNDOVA, E. G., RUDENSKAYA, G. A. & CHESSER, R. K., 1996: Small mammals from the most radioactive sites near the Chornobyl nuclear power station. *J. Mammal., 77: 155–170.*

BARBU, P., 1968: Systématique et écologie de la belette *Mustela nivalis* L. provenant de quelques forets des districts d'Ilfov et de Prahova – Roumanie. *Trav. Mus. Hist. Nat. "Gr. Antipa", 8: 991–1002.*

CAVAZZA, F., 1914: Ricerche intorno al *Putorius nivalis monticola* e alla sua distributione geographica. *Boll. Mus. zool., Anat. comp., Torino, 29: 1–19.*

COLAK, E., YIĞIT, N., SÖZEN, M. & ÖZKURT, S., 1999: A study of *Mustela nivalis* Linnaeus, 1766 (Mammalia: Carnivora) in Turkey. *Tr. J. Zool., 23: 119–122.*

FRANK, F., 1985: Zur Evolution und Systematik der kleinen Wiesel (*Mustela nivalis* Linnaeus, 1766). *Z. Säugetierkd., 50: 208–225.*

FREDGA, K. & MANDAHL, N., 1973: Autosomal heterochromatin in some carnivores. *Nobel Symp., 23: 104–117.*

GRAFODATSKY, A. S., TERNOVSKY, D. V., ISAENKO, A. A. & RADJABLI, S. I., 1977: Constitutive heterochromatin and DNA content in some mustelids (Mustelidae, Carnivora). *Genetika, 13: 2123–2128 (in Russian, with a summary in English).*

JARREL, G. H., 1983: Holarctic similarity of chromosomes in the weasel, *Mustela nivalis*: G- and C- banding in an Alaskan specimen. *Mamm. Chrom. Newsl., 24: 207–212.*

JOHN, B. & MIKLOS, G. L.G., 1979: Functional aspects of satellite DNA and heterochromatin. *Int. Rev. Cytol., 58: 1–114.*

KING, C. M., 1979: Moult and colour change in English weasels (*Mustela nivalis*). *J. Zool., Lond., 189: 127–134.*

KING, C. M. & MOORS, P.J., 1979: On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia, 39: 129–150.*

KING, M.,1993: Species evolution. The role of chromosome change. *Cambridge University Press, Cambridge, England.*

MANDAHL, N. & FREDGA, K., 1980: A comparative chromosome study by means of G-, C-, and NOR-bandings of the weasel, the pygmy weasel and the stoat (*Mustela*, Carnivora, Mammalia). *Hereditas, 93: 75–83.*

MEIA, J.-S. & MERMOD, C., 1992: Taxonomie et variation de taille des hermines et des belettes en Europe: revue de littérature et commentaire. *Revue suisse Zool., 99: 109–118.*

MOŠANSKÝ, A., 1983: Die Teriofauna der Ostslowakei und der Katalog der mammaliologischen Sammlungen des Ostslowakischen Museums – II. Teil (Carnivora, Mustelidae). *Zborník Východoslovenského múzea v Košiciach, prírodné vedy, 23: 225–240 (in Slovak, with a summary in German).*

OBARA, Y., 1982: Comparative analysis of karyotypes in the Japanese mustelids, *Mustela nivalis namiyei* and *M. erminea nippon*. *J. Mammal. Soc. Japan, 9: 59–69.*

OBARA, Y., 1985: Karyological relationships between two species of mustelids, the Japanese ermine and the least weasel. *Japan. J. Genet., 60: 157–160.*

PESHEV, D., SPASOV, N. & GERASIMOV S., 1985: On the karyotype of the weasel *Mustela nivalis* L., 1766 (Mammalia, Mustelidae) from Bulgaria. *Zool. Anz., Jena, 215: 156–158.*

REIG, S., 1997: Biogeographic and evolutionary implications of size variation in North American least weasels (*Mustela nivalis*). *Can. J. Zool., 75: 2036–2049.*

REICHSTEIN, H., 1957: Schädelsvariabilität europäischer Mauswiesel (*Mustela nivalis* L.) und Hermeline (*Mustela erminea* L.) in Beziehung zu Verbreitung und Geschlecht. *Z. Säugetierkd., 22: 151–182.*

REICHSTEIN, H., 1993: *Mustela nivalis* – Mauswiesel. In: Stubbe, M. & Krapp, F. (eds), Handbuch der Saügetiere Europas. Band 5/II. *AULA Verlag, Wiesbaden: 571–626.*

ROSENZWEIG, M. L., 1968: The strategy of body size in mammalian carnivores. *Am. Midl. Nat., 80: 299–315.*

SEABRIGHT, M., 1971: A rapid banding technique for human chromosomes. *Lancet, 7731: 971–972.*

STOLT, B.-O.,1979: Colour pattern and size variation of the weasel *Mustela nivalis* L. in Sweden. *Zoon, 7: 179–180.*

SUMNER, A. T., 1972: A simple technique for demonstrating centromeric heterochromatin. *Exptl. Cell Res., 75: 304–306.*

VAN ZYLL DE JONG, C. G., 1992: A morphometric analysis of cranial variation in Holarctic weasels (*Mustela nivalis*). *Z. Säugetierkd., 57: 77–93.*

WOZENCRAFT, W.C., 1993: Order Carnivora. In: Wilson, D. E. & Reeder, D. M. (eds), Mammal species of the world: a taxonomic and geographic reference, 2nd ed. *Smithsonian Inst. Press, Washington: 279–348.*

ZIMA, J. & KRÁL, B., 1984: Karyotypes of European mammals I. *Acta Sc. Nat. Brno, 18 (9): 1–51.*

ZIMA, J. & GRAFODATSKIJ, A. S., 1985: C-heterochromatic arm variation in the weasel, *Mustela nivalis* (Mustelidae, Carnivora). *Folia Zool., 31: 125–132.*