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The fragmented distribution range of *Microtus tatricus* and its evolutionary implications

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A b s t r a c t . *Microtus tatricus* occurs in the Carpathian Mountains of Slovakia, Poland, Ukraine and Romania – a list of current distribution records is given. The species' distribution range is insular on the scale of its entire distribution and fragmented within each mountain range inhabited. The overall altitudinal range is 650–2350 m a.s.l., with the largest number of collecting sites situated between 1100–1700 m a.s.l. The total range size of *M. tatricus* was estimated as 840 km^2 and the total population size at between 200,000–250,000 individuals. A possible reduction in the species' distribution range is discussed.

Key words: Rodentia, Arvicolidae, *Microtus multiplex* complex, mountains, subalpine habitat, phylogeny, colonisation history, molecular species identification

Introduction

The Tatra vole, *Microtus tatricus* (Kratochvíl, 1952), is species endemic to the Carpathian mountain range. It is the only autochthonous mammalian species in the Carpathians (M i t c h e l l - J o n e s et al. 1999), and one of the region's two known vertebrate endemics (the other being the urodele *Triturus montandoni*) (B a r u š et al. 1992).

Palaeontological data indicate that *Allophaiomys pliocaenicus*, that lived between 1.8 and 1.4 million years ago (Mya) is the most recent common ancestor of genus *Microtus* (B r u n e t - L e c o m t e & C h a l i n e 1992, N a d a c h o w s k i & Z a g o r o d n y u k 1996, N a d a c h o w s k i & G a r a p i c h 1998, C h a l i n e et al. 1999). The lineage presumed to lead to *M. tatricus* includes *M. arvalidens* (0.95 Mya), *M. vaufreyi* (0.6 Mya) and/or *M. vergrannensis* (0.35 Mya) (C h a l i n e et al. 1999). These species were more widespread than the extant species of the *Microtus multiplex* complex to which *M. tatricus* belongs (K r a t o c h v í l 1964, 1970, Z a g o r o d n y u k 1989, K r y š t u f e k et al. 1996). *Microtus tatricus* was the first species to diverge from the common and widespread ancestor of this complex (K r a t o c h v í l 1964, M a t t h e y 1964, H a r i n g et al. 2000) followed by the divergence of *M. multiplex*, *M. liechtensteini* and *M. bavaricus*. Speciation probably occurred against a background of the fragmentation and reduction of the distribution range of the ancestral species induced by vegetational responses to climate change. Extant populations retreated to the mountains (H a i t l i n g e r 1970, D u d i c h et al. 1981, Z a g o r o d n y u k & Z i m a 1992). *Microtus tatricus* is first known from the Early Holocene of the Veľká Fatra Mts in Slovakia (D u d i c h et al. 1981) – there are no records from the Pleistocene.

The habitat occupied by *M. tatricus* is either relatively open, humid areas in climax upper montane forest – usually located in inverse valleys (K r a t o c h v í l 1964, K r a t o c h v í l

& G a i s l e r 1967, F l o u s e k et al. 1985, Z a g o r o d n y u k 1989, Z a g o r o d n y u k et al. 1992), or humid rocky meadows in the subalpine zone (R o s i c k ý & K r a t o c h v í l 1955, P e l i k á n 1955, K o w a l s k i 1960, J u r d í k o v á et al. 2000). No reports on population size fluctuations or of population outbreaks are known. In this respect, the Tatra vole is a true K-selected inhabitant of mountains where, in contrast to Arctic species, cyclic population fluctuations are not known (H a p p o l d 1998).

M. tatricus is listed in the 2000 IUCN Red List of Threatened Species as Lower Risk/Near Threatened (I U C N 1996) and in the Appendix II of the Bern Convention.

This work summarises all the distribution data over the whole distribution range of *M. tatricus* and evaluates the altitudinal distribution of the species in respect of the evolutionary history of its fragmented distribution range.

Methods

Distribution range was estimated by summarising the known records of *M. tatricus* from published sources and personal communications. The size of the distribution range was calculated as the sum of the areas of mountain ranges where *M. tatricus* occurs. One fourth of the area of each occupied mountain range was taken as an approximate and rough estimate of habitats potentially useful for colonisation by the species; only this area was used to calculate the distribution range size.

The data on the relative abundance of *M. tatricus* among other small mammals and its density were either taken from published data, or calculated as the number of individuals of the species divided by the total number of trapped animals or trapping area without any edge effect correction, respectively.

New records were obtained by trapping in Slovakia in 1999 and 2000. Morphological measurements unambiguously distinguished *M. tatricus* from *M. arvalis*, *M. agrestis* and sexually active *M. subterraneus*. Young and sexually inactive *M. subterraneus* were identified by restriction fragment length polymorphism (RFLP) analysis of the cytochrome b (*cyt b*) gene. Fingertip tissue samples were collected during the marking of live animals. *Cyt b* was amplified by the polymerase chain reaction (PCR) using the primers L14727-SP: 5'-GAC AGG AAA AAT CAT CGT TG-3' and H-ISO-SP: 5'-AGT AGT TTA ATT AGA ATG TCA GC-3' (M. J a a r o l a , pers. comm.). A 50 µl PCR reaction consisted of 5 µl of 10× Buffer, 5 µl 10× dNTPs (2mM), 3 µl $MgCl_2$ (25mM), 5 µl of each primer (10 µM) and 2U Taq polymerase. Template DNA and water were added with regard to the DNA concentration of each sample. DNA was denatured for seven min at 95°C and amplified for 35 cycles of 93°C/1 min, 48°C/1 min and 72°C/3 min. PCR was completed by 10 min at 72°C. The resulting PCR product was incubated for one hour at 37°C with *Sau3AI* (*MboI*) and *BamHI* separately, and analysed on 2% agarose gels stained by ethidium bromide. RFLP analysis with both enzymes unambiguously distinguished *M. tatricus* and *M. subterraneus*, *Sau3AI* showing two haplotypes for each species. Each haplotype within a species was derived from the other by loss/gain of one restriction site. Neither *M. tatricus* haplotype could be easily derived from any *M. subterraneus* haplotype.

Results

All the 13 individuals collected were shown to be *M. tatricus* by the RFLP analysis of the *cyt b* gene and morphological measurements.

According to available published data, the Tatra vole was found in Slovakia (SK), Poland (PL), Ukraine (UA) and Romania (RO). In decreasing order by the number of collected individuals, *M. tatricus* localities are found in the High Tatra Mts-SK (including the Western, High, and Belianske Tatras) (around 1,250 specimens), Oravské Beskydy Mts-SK, PL (including Pilsko and Babia Gora) (34), Veľká Fatra Mts-SK (30), Eastern Carpathians-UA (20), Low Tatra Mts-SK (14), Rodnei Mts-RO (5), Malá Fatra Mts-SK (5), Kremnické vrchy Mts-SK (4), Ciucas Mts-RO (4), Muránska planina Plateau-SK (3), Chočské vrchy Mts-SK (3), Maramureş Mts-RO (2), and Calimani Mts-RO (1) (Fig. 1, Appendix). All the mountain ranges lie within the geographical limits of the Carpathians. Around 480 specimens originated from a series of expeditions lead by J. K r a t o c h v í l to the Roháčska dolina Valley in the Western Tatra Mts in the early to middle 1960s (e.g. K r a t o c h v í l 1970, protocols deposited at the Institute of Vertebrate Biology, Brno, Czech Republic). Another 327 individuals are known only from osteological material (D u d i c h et al. 1981, O b u c h et al. 1985) including 316 individuals found in the site Muráň I in Belianske Tatra Mts (S c h a e f f e r 1974). These data are not included in further analysis.

The lowest known occurrence of *M. tatricus* is at 600–650 m a.s.l. in cold inverse valleys in the Veľká Fatra Mts (D u d i c h et al. 1981, K l e i n e r t 1983), and the highest is at 2,343 m a.s.l. in Sedlo Váhy Pass in the High Tatra Mts (K r a t o c h v í l 1952). The histogram of localities at different elevations is bimodal with the maximum number of localities at an elevation of c. 1,650 m a.s.l., but with another peak at c. 900–1150 m a.s.l. (Fig. 2). However, these results should be treated with caution as the histogram summarises trapping effort and thus possibly the preferences of various authors and does not represent a systematic study of the altitudinal distribution of the species. The number of individuals captured did not increase significantly with elevation (linear regression, $F = 1.34$, $P > 0.05$, Fig. 3, Appendix) nor did species population density ($F = 0.73$, $P > 0.05$, Fig. 3;

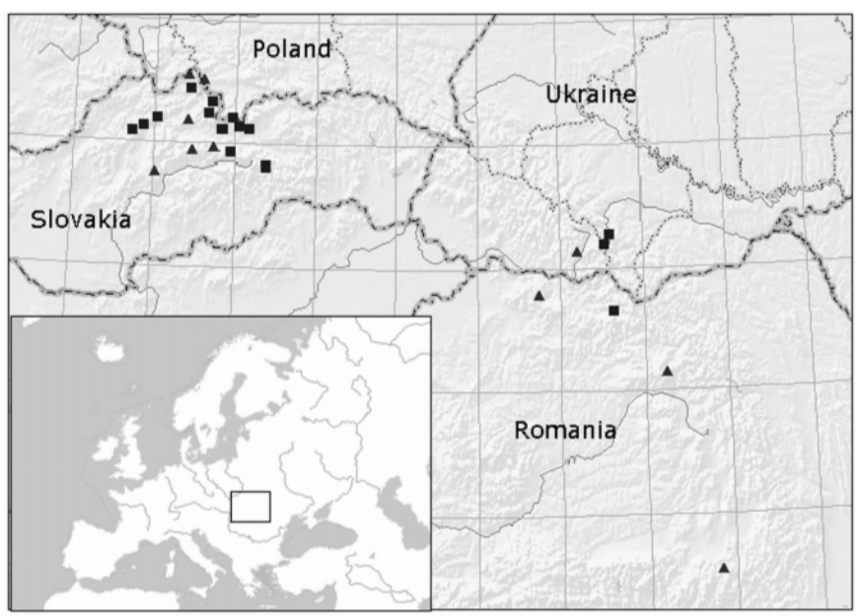

Fig. 1. The distribution range of *Microtus tatricus*. ▲ = locality with a single record, ■ = localities with multiple records.

Kratochvíl & Gaisler 1967, Juchiewicz et al. 1986, Jurdíková et al. 2000, N. Martínková, S. Martínek, A. Zahradníková, unpubl.). However, the relative abundance of *M. tatricus* in the assemblage of other small mammals increased significantly with increasing elevation ($F = 5.31$, $P = 0.03$, $R^2(\%) = 16.9$, Fig. 3; Pelikán 1955, Kratochvíl & Gaisler 1967, Zima et al. 1984, Flousek et al. 1985, Obuch et al. 1985, Štollmann & Dudich 1985, Juchiewicz et al. 1986, Zagorodnyuk et al. 1992, Kadlečík et al. 1995, N. Martínková, S. Martínek, A. Zahradníková, unpubl.).

The species' distribution range area was approximately 840 km^2. Thus, if the median of species population density is 2.6 individuals/ha ($\bar{x} = 6.2$; range: 0.17-28.6; N = 19, Kratochvíl & Gaisler 1967, Juchiewicz et al. 1986, Jurdíková et al. 2000, N. Martínková, S. Martínek, A. Zahradníková, unpubl.) overall population numbers could be approximately 200,000–250,000 individuals.

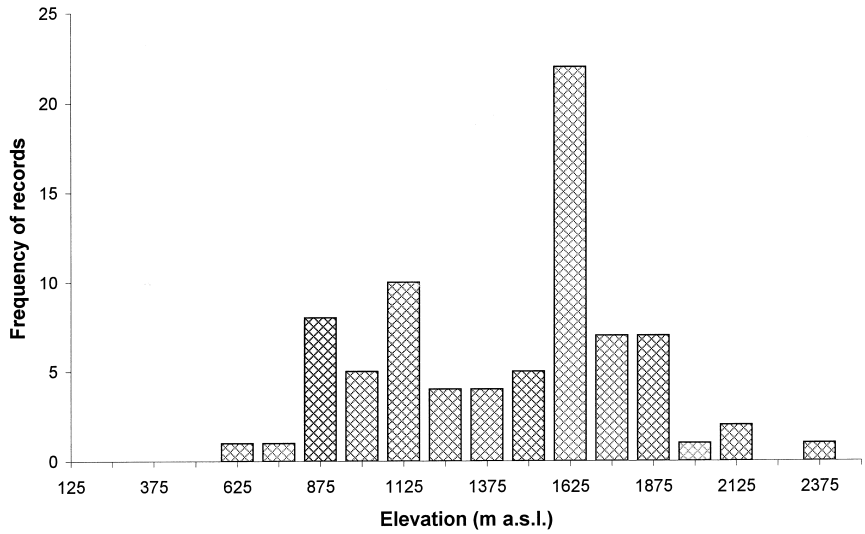

Fig. 2. The frequency of occurrence of localities of *M. tatricus* as dependent on the locality altitude.

Discussion

The present analysis shows that the distribution range of *M. tatricus* is roughly divided into two distant regions – the western in Slovakia and Poland and the eastern in Ukraine and Romania. Thus, the species' range is insular at both the level of the entire distribution range as well as within the mountain ranges occupied (Jurdíková et al. 2000). This fragmentation may be a consequence of the landscape's altitudinal structure and/or habitat heterogeneity.

The localities for *M. tatricus* in the valleys of Veľká Fatra, Muránska planina, or Kremnické vrchy all lie at the bottom of valleys below 1100 m a.s.l. – the first hypsometric limit (Niethammer 1982). Recently, the species' altitudinal distribution limit was placed as 800 m a.s.l. (Mitchell-Jones et al. 1999), but *M. tatricus* has never been found on some Carpathian mountains that exceed this altitude, e.g. Spišská Magura, Čergov.

The Tatra vole utilises a wide range of habitats (Haitlinger 1981, Jurdíková et al. 2000). Alpine meadows do not occur on many uninhabited mountains, but the inverse cold valleys at lower altitudes also occur on mountains from which the species is absent.

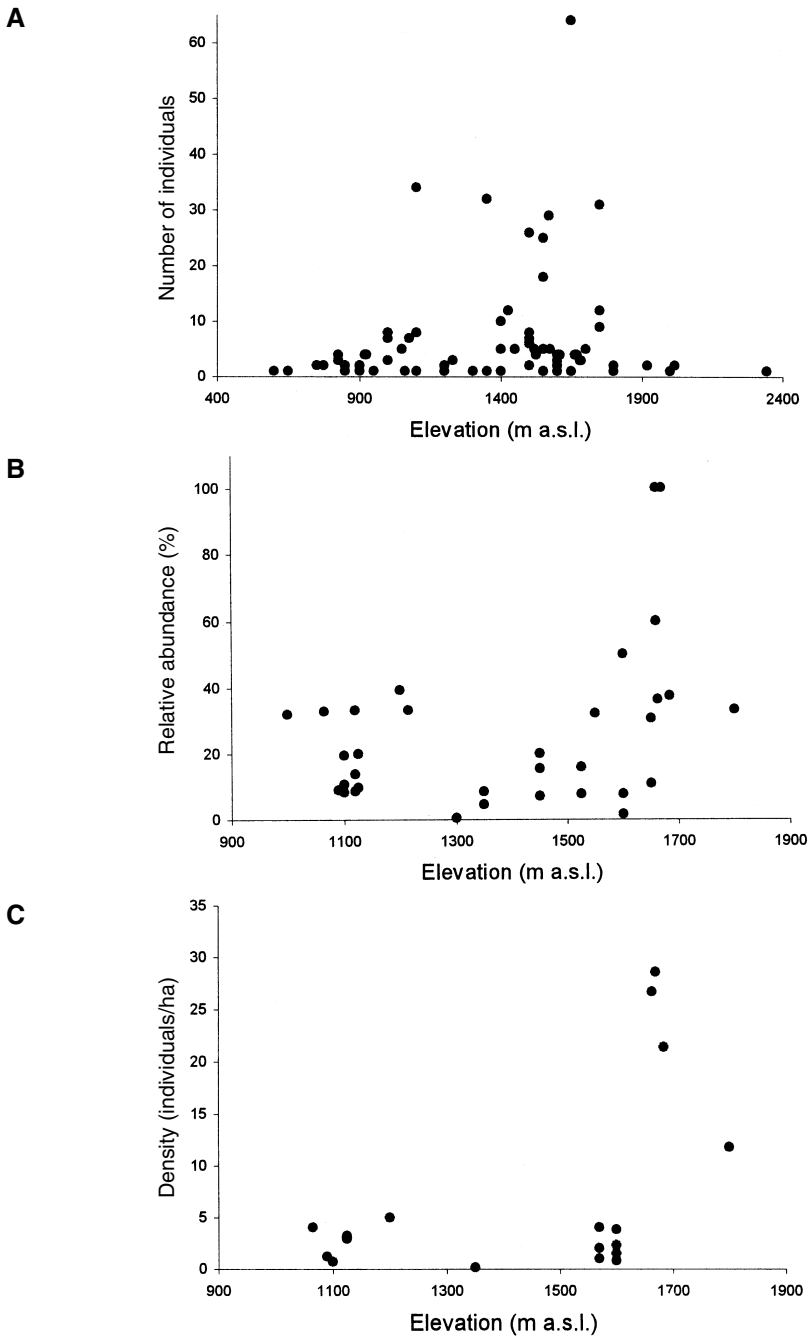

Fig. 3. The altitudinal distribution of *M. tatricus* based on (a) number of individuals caught regardless of the trapping effort, (b) relative abundance of the species amongst other small mammals, and (c) species density.

The reason for the species' irregular and insular distribution may be explicable in the evolutionary history of the species. Three hypotheses could be proposed. Firstly, the end of

Appendix. Full list of localities of *M. tatricus* occurrence ordered from west to east. * indicates osteological material.

	Mountain range	Locality	Elevation	Number	Year	Source
	Veľká Fatra	Blatnická dolina	800	1	1992	Štollmann et al. 1994
	Veľká Fatra	Blatnická dolina, Rakytovské potoky	800	3	1992	Štollmann et al. 1994
*	Veľká Fatra	Bystrická dolina	800	3	1978	Dudich et al. 1981
*	Veľká Fatra	Dolný Harmanec			2001	J. Obuch
	Veľká Fatra	Havranovo, ŠPR Borišov	750-800	2	1989	Kadlečík et al. 1995
	Veľká Fatra	Ľubochnianska dolina		11	1980	Dudich et al. 1981
	Veľká Fatra	Ľubochnianska dolina	900-1200	5	1980	Dudich et al. 1981
	Veľká Fatra	Ľubochnianska dolina	800-850	7	1980	Dudich et al. 1981
	Veľká Fatra	Ľubochnianska dolina	500	1	1980	Kleinert 1983
	Veľká Fatra	Ľubochnianska dolina	600	2	1980	Kleinert 1983
	Veľká Fatra	Ľubochnianska dolina	1000	4	1980	Kleinert 1983
	Veľká Fatra	Oružná dolina	1500	1	1980	Štollman & Dudich 1990
	Veľká Fatra	Oružná dolina	1200	1	1981	Štollman & Dudich 1990
	Veľká Fatra	Prašnica	650	1	1980	Dudich et al. 1981
	Veľká Fatra	Široký úplaz	900	1	1989	Kadlečík et al. 1995
	Veľká Fatra	ŠPR Skalná alpa	1220-1460	2	1986	Kadlečík 1989
	Veľká Fatra	Vyšná Revúca	1220-1520	1	1988	Kadlečík 1992
*	Malá Fatra	Malý Fatranský Kriván	1600	4	1977	Dudich et al. 1981
	Malá Fatra	Vrátna - Za kraviarskym	850	1	1998	A. Dudich
	Kremnické vrchy	Horný Turček	890-950	4	1979	Dudich et al. 1981
	Kremnické vrchy	Turčocká dolina	1050	2	1981	A. Dudich, A. Štollmann
*	Chočské vrchy	Choč		3	1977	Dudich et al. 1981
*	Chočské vrchy	Vyšný Kubín - kaňon		1	1977	Obuch 1981
	Oravské Beskydy	Babia Gora	1200	1	1980	Haitlinger 1983
	Oravské Beskydy	Babia Gora	1200-1600	10	1980	Haitlinger 1981
	Oravské Beskydy	Babia Gora	850			Haitlinger 1981
	Oravské Beskydy	Mutnianska píla	850	2	1978	A. Dudich, A. Štollmann
	Oravské Beskydy	Mutnianska píla	1200	7	1980	A. Dudich, A. Štollmann
	Oravské Beskydy	Pilsko	1300-1550	12	1968-69	Haitlinger 1970
	Oravské Beskydy	Pilsko	900-1100	7	1978	Dudich et al. 1981
	Oravské Beskydy	Slaná voda, Borsučie	850-1000	4	1963	Dudich et al. 1981
	Oravské Beskydy	ŠPR Babia hora	1400	4	1963	Dudich & Štollmann 1993
	Oravské Beskydy	ŠPR Babia hora	1310	1	1984	Karaska & Kocian 1993

Appendix. Continued.

Mountain range	Locality		Elevation	Number	Year	Source
Oravské Beskydy	ŠPR Babia hora		860–1710	8	1985	Karaska & Kocian 1993
Low Tatra	Bystrá dolina		1680	3	1988	Bituší k 1996
Low Tatra	Bystrá dolina		1670	4	2000	N. Martínková, A. Zahradníková
Low Tatra	Demänovská dolina, Jasná		1250	1	1963	Dudich 1970
Low Tatra	Demänovská dolina, Jasná-Dereše		1700	32	1984	Štollman & Dudich 1990
Low Tatra	Demänovská dolina, Luková		1750	3	1963	Dudich 1970
Low Tatra	Horný Jelenec		700	1	1989	Štollman & Dudich 1990
Low Tatra	Kosodrevina - Chopok		1450	1	1982	Štollman & Dudich 1990
Low Tatra	Kotliská		1700	1	1982	Štollman & Dudich 1990
Low Tatra	Kozie chrbty		1450	1	1989	A. Dudich, A. Štollmann
Low Tatra	Krčahovo, Jánska dolina	N 48°58', E 19°40'	1300	1	1976	Zagorodnyuk & Zima 1992
Low Tatra	Ludárová dolina		1600	1	1983	Bituší k 1996
Low Tatra	Patociny - Prašivá		1000	3	1979	Dudich et al. 1981
Low Tatra	Východná, Čierny Váh		830	1	1984	A. Dudich, A. Štollmann
Low Tatra		N 49°00', E 19°26'		1	1981	Haring et al. 2000
Western Tatra	Bobrovecká dolina		1350	5	1993	A. Dudich, A. Štollmann
Western Tatra	Bobrovecká dolina		1500	26	1977	Dudich et al. 1981
Western Tatra	Bobrovecké plesá		1500–1600	25	1977	Štollmann & Dudich 1985
Western Tatra	Prvé Roháčske pleso		1570	29	1996–99	D. Žiak, N. Martínková, Ľ. Kocian
Western Tatra	Roháčska dolina		1100	34	1955–60	Kratochvíl 1969
Western Tatra	Roháčska dolina		1050–1250	480	1963–64	Kratochvíl 1970
Western Tatra	Roháčska dolina		1300–1400	32	1969–74	Zima et al. 1984
Western Tatra	Roháčska dolina			16	1970's	Hrabě 1972
Western Tatra	Roháčska dolina			1/2 of 41	1970's	Hrabě 1974
Western Tatra	Roháčska dolina - Ťatliakova chata		1500	7	1962	V. Hanák, V. Mazák
Western Tatra	Roháčska dolina - Ťatliakova chata		1520	5	1962	V. Hanák, V. Mazák
Western Tatra	Roháčska dolina - Ťatliakova chata		1550	5	1962	V. Hanák, V. Mazák
Western Tatra	Roháčska dolina - Ťatliakova chata		1600	3	1973	V. Vohralík
Western Tatra	Smutná dolina		1684	3	2000	N. Martínková, S. Martínek
Western Tatra	Tichá dolina		1150	1	1982	Štollmann & Dudich 1985
Western Tatra	Tichá dolina		1200	8	1982	Štollmann & Dudich 1985

Appendix. Continued.

	Mountain range	Locality	Elevation	Number	Year	Source
	Western Tatra	Tretie Roháčske pleso	1663	4	2000	N. Martínková, S. Martínek
	Western Tatra	Zuberec - Kozinec	1350	1	1977–78	Štollmann & Dudich 1985
	Western Tatra	Zuberec - Pribisko	1000–1200	8	1977	Dudich et al. 1981
	Western Tatra	Žabi Wierch	1350	1	1982	Juchiewicz et al. 1986
	Western Tatra		1400–1800		1981–1985	Kocian et al. 1985
	High Tatra	Dolina 5 Stawów	2000	1	1954	Kowalski 1960
	High Tatra	Dolina Zeleného plesa	1500–1600	18	1951	Kratochvíl 1952
	High Tatra	Furkotská dolina	1550–1600	5	1949	Kratochvíl 1952
	High Tatra	Furkotská dolina	1800	1	1949	Kratochvíl 1952
	High Tatra	Furkotská dolina	1500–1550	4	1955	Pelikán 1955
	High Tatra	Hala Gasienicowa	1500	6	1954–55	Kowalski 1960
	High Tatra	Hala Gasienicowa	1500	8	1968–69	Haitlinger 1970
	High Tatra	Malá Studená dolina	1500–2000	12	1950	Kratochvíl 1952
	High Tatra	Malá Studená dolina		1/2 of 41	1970's	Hrabě 1974
	High Tatra	Malá Studená dolina	1600–1700	64	1973–75	Zima et al. 1984
	High Tatra	Mengusovská dolina, Popradské pleso	1550	1	1950	Kratochvíl 1952
	High Tatra	Morské Oko	1400	1	1934	Kowalski 1960
*	High Tatra	Muráň I	1400–2200	316	1970's	Schaeffer 1974
	High Tatra	Ostrva	1650	1	1955	Pelikán 1955
	High Tatra	Päť Spišských plies	2016	2	1946	Kratochvíl 1952
	High Tatra	Sedlo Váha	2343	1	1950	Kratochvíl 1952
	High Tatra	Tatranská Polianka	1650	2	1990	B. Chovancová
	High Tatra	Tatranská Polianka	1650	3	1991	A. Dudich, A. Štollmann
	High Tatra	Uhorcie Kasprowe	1700	5	1953–55	Kowalski 1960
	High Tatra	Veľká Studená dolina	1400–1600	2	1949	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1700–1800	9	1949	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1800	2	1949	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1600	2	1949	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1350–1450	5	1949	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1700–1800	31	1950	Kratochvíl 1952
	High Tatra	Veľká Studená dolina		3	1950	Kratochvíl 1952
	High Tatra	Veľká Studená dolina	1520–1700	4	1955	Pelikán 1955
	High Tatra	Veľká Studená dolina	1450	5	1955	Pelikán 1955

Appendix. Continued.

	Mountain range	Locality	Elevation	Number	Year	Source
	High Tatra	Veľká Studená dolina	1800	2	2000	N. Martínková
	High Tatra	Žabie plesá	1920	2	1950	Kratochvíl 1952
	High Tatra	Žólta Turnia	1600	4	1953-59	Kowalski 1960
	High Tatra			18	1955-59	J. Pelikán
	Belánske Tatra	Monkova dolina	1140–1850	5	1988	Tomaškovič 1989
	Belánske Tatra	Skalné vráta	1600	4	1978-83	Zima et al. 1984
	Belánske Tatra	Skalné vráta N 49°12', E 20°18'	1600	1	1990's	Zagorodnyuk & Zima 1992
	Belánske Tatra	Zadné Meďodoly	1200	1	1987	A. Dudich, A. Štollmann
	Belánske Tatra	Zadné Meďodoly	1400	1	1987	A. Dudich, A. Štollmann
*	Muránska planina	Hrdzavá dolina		1	1979	Dudich et al. 1981
	Muránska planina	Za Nihovom	900	2	1983	Kováčik & Štollmann 1984
*	Muránska planina	Dolina Zlatnica, Zlatná na Horehroní			2001	J. Obuch
*	Muránska planina	Jelenia priepasť			2001	J. Obuch
	Eastern Carpathians	Massiv Boržava, Svalavskij rajon, Verchnie Boržavy, Golovcin		1	1950	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Černogora, 10 km E of Jasina	800-1100	1	1972	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Černogora, 8-12 km NE of Ust-Goverla, river Goverlanka, Tovstyj Grun	900, 1070, 1260	7	1988–90	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Černogora, Gat-Balcatul, river Goverlanka		1	1951	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Černogora, Mt. Goverla, Breskul N 48°20', E 24°20'	1060	1	1990's	Zagorodnyuk & Zima 1992
	Eastern Carpathians	Massiv Černogora, river Goverlanka, Petros	1000	3	1963	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Černogora, Ust-Goverla, river Goverlanka	750	2	1982	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Krasna, 18 km N of Širokij Lug	600	1	1989	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Svidovec, 18 km WNW of Jasina		1	1975	Zagorodnyuk et al. 1992
	Eastern Carpathians	Massiv Svidovec, Kvasovskij Mencul	1000-1400	2	1964	Zagorodnyuk et al. 1992
	Maramureş Mts	Valea Runcu		2	1998	Murariu & Rădulet 1998
	Rodnei Mts	Brsa-Fintina	1230	3	1983	Flousek et al. 1985
	Rodnei Mts	Brsa-Fintina	850	2	1983	Flousek et al. 1985
	Calimani Mts	Mt. Negoiul Unguresc, peak and SE slope	2044	1	1986	J. Flousek, Z. Flousková
	Ciucas Mts	Pasul Bratocea (mountain pass), 1 km WSW of Ramura Mica	1100	4	1988	J. Flousek, Z. Flousková

glaciation was accompanied by the retreat of steppe-tundra and the emergence of taiga and boreal conifer forests (Jankovská 1991, Adams & Faure 1997). During that period, the ecosystem became fragmented and surrounding new ecosystems probably did not allow interpopulation dispersal. In this case, some small populations may have become extinct and never recolonised the area. This follows the predictions of the model of stochastic extinction of small isolated populations within metapopulation theory (Angelstam et al. 1987, Hanski et al. 1996, Jaarola et al. 1999, Fox & Fox 2000). Surviving populations retreated to the mountains where they are found today.

Secondly, distribution range reduction still continues, and thus *M. tatricus* disappeared from the other Carpathian mountains relatively recently. This is supported by the fact that, except for the High Tatra Mts and partially Oravské Beskydy and Veľká Fatra, *M. tatricus* is found only in very small numbers despite extensive small mammal research in the area, *i.e.* in Muránska planina Plateau (M. Uhrín, N. Martínková, unpubl. data) or the northern macroslopes of the Eastern Carpathians (Zagorodnyuk et al. 1992). In other mountain ranges *M. tatricus* was found exclusively or primarily as osteological material, *i.e.* Chočské vrchy Mts and Malá Fatra Mts (Appendix).

Alternatively, *M. tatricus* can occur in mountain ranges where zoological research was not extensively carried out. In Romania, the species was found at several localities despite low trapping efforts (Flousek et al. 1985, Murariu & Rădulet 1998, J. Flousek, Z. Flousková, unpubl. data).

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LITERATURE

ADAMS J. M. & FAURE H. 1997: Preliminary vegetation maps of the world since the last glacial maximum: an aid to archaeological understanding. *J. Arch. Sci. 24: 623–647.*

ANGELSTAM P., HANSSON L. & PEHRSSON L. 1987: Distribution borders of field mice *Apodemus*: the importance of seed abundance and landscape composition. *Oikos 50: 123–130.*

BARUŠ V., KRÁL B., OLIVA O., OPATRNÝ E., REHÁK I., ROČEK Z., ROTH P., ŠPINAR Z. & VOJTKOVÁ L. 1992: Fauna ČSFR. Obojživelníci – Amphibia [Fauna of Czechoslovakia. Amphibians – Amphibia]. *Academia, Praha 340 pp. (in Czech with English summary).*

BITUŠÍK P. 1996: Comments on the small mammals fauna (Insectivora, Rodentia) of subalpine zone of Ďumbier National Nature Reserve. *Ochrana prírody 14: 153–157 (in Slovak with English summary).*

BRUNET-LECOMTE P. & CHALINE J. 1992: Morphological convergences versus biochemical divergences in the Holarctic ground voles: *Terricola* and *Pitymys* (Arvicolidae, Rodentia). *N. Jb. Geol. Paläont. Mh. 12: 721–734.*

CHALINE J., BRUNET-LECOMTE P., MONTUIRE S., VIRIOT L. & COURANT F. 1999: Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaeoecological history and evolutionary data. *Ann. Zool. Fennici 36: 239–267.*

DUDICH A. 1970: Mikromammalia Demänovskej doliny [Small mammals of the Demänovská dolina valley]. *Ochrana fauny 10: 10–18 (in Slovak).*

DUDICH A., KOVÁČIK J., ŠTOLLMANN A. & OBUCH J. 1981: Ďalšie poznámky o rozšírení *Sicista betulina* Pallas, 1779 a *Pitymys tatricus* Kratochvíl, 1952 (Mammalia, Rodentia) v Západných Karpatoch [Additional notes on distribution of *Sicista betulina* Pallas, 1779 and *Pitymys tatricus* Kratochvíl, 1952 (Mammalia, Rodentia) in the West Carpathians]. *Biológia (Bratislava) 36: 659–668 (in Slovak).*

DUDICH A. & ŠTOLLMANN A. 1993: Materiály k faune drobných cicavcov (Insectivora, Rodentia) Babej hory (Oravské Beskydy) [Small mammal fauna (Insectivora, Rodentia) from Mt. Babia hora (Oravské Beskydy Mts)]. *XXVII. TOP Oravská priehrada 1991 – Prehľad odborných výsledkov: 95–102 (in Slovak).*

FLOUSEK J., FLOUSKOVÁ Z. & TOMÁŠOVÁ K. 1985: To the knowledge of small mammals (Insectivora, Rodentia) in the Rodnei Mts. (Rumania). *Věst. čs. Společ. zool. 49: 6–17.*

FOX B. J. & FOX M. D. 2000: Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecol. Biogeog. 9: 19–37.*

HAITLINGER R. 1970: *Pitymys* McMurtrie, 1831, from the Beskid Żywiecki and the Sudetes. *Acta Theriol. 15: 365–370.*

HAITLINGER R. 1981: *Pitymys tatricus* Kratochvíl, 1952, in Poland. *Przegląd Zoologiczny 25: 405–407 (in Polish with English summary).*

HAITLINGER R. 1983: *Hirstionyssus tatricus* Mrciak, 1958 and several other species of Acarina new for Polish fauna or rarely collected on mammals in Poland. *Przegląd Zoologiczny 27: 323–326 (in Polish with English summary).*

HANSKI I., MOILANEN A. & GYLLENBERG M. 1996: Minimum viable metapopulation size. *Am. Nat. 147: 527–542.*

HAPPOLD D. C. D. 1998: The subalpine climate at Smiggin Holes, Kosciusko National Park, Australia, and its influence on the biology of small mammals. *Arctic Alp. Res. 30: 241–251.*

HARING E., HERTZIG-STRASCHIL B. & SPITZENBERGER F. 2000: Phylogenetic analysis of Alpine voles of the *Microtus multiplex* complex using the mitochondrial control region. *J. Zool. Syst. Evol. Research 38: 231–238.*

HRABĚ V. 1972: The bacula of *Pitymys tatricus* Kratochvíl, 1952, and *P. subterraneus* (de Sélys-Longchamps, 1836) from the High Tatra Mts. *Zool. listy 21: 145–155.*

HRABĚ V. 1974: Tarsal glands of *Pitymys subterraneus* (de Sél.-Long.) and *Pitymys tatricus* Krat. (Microtidae, Mammalia). *Zool. listy 23: 97–105.*

IUCN 1996: 1996 IUCN Red List of Threatened Animals. *IUCN, Gland, Switzerland, 368 pp.*

JAAROLA M., TEGELSTRÖM H. & FREDGA K. 1999: Colonization history in Fennoscandian rodents. *Biol. J. Linn. Soc. 68: 113–127.*

JANKOVSKÁ V. 1991: The development of the vegetation in inner Carpathian basins of the Tatra – foreland cover at the end of glacial period till the present time. *Zborník prác o TANAP-e 31: 73–84 (in Czech with English, German, Polish and Russian summaries).*

JUCHIEWICZ M., ZEMANEK M., BIENIEK M. & SIUTA E. 1986: Small rodent communities in the Tatra Mountain forests. *Acta Theriol. 31, 32: 433–447.*

JURDÍKOVÁ N., ŽIAK D. & KOCIAN Ľ. 2000: Habitat requirements of *Microtus tatricus*: microhabitat and macrohabitat. *Výskum a ochrana cicavcov na Slovensku 4: 41–49.*

KADLEČÍK J. 1989: Contribution to the knowledge of mammal fauna (Mammalia) of the National Nature Reserve Skalná alpa. *Ochrana prírody 10: 259–270 (in Slovak with English summary).*

KADLEČÍK J. 1992: Note on the mammal fauna (Mammalia) of the Suchý vrch in Veľká Fatra. *Ochrana prírody 12: 297–308 (in Slovak with English summary).*

KADLEČÍK J., DUDICH A., OBUCH J. & ŠTOLLMANN A. 1995: On the mammalian fauna (Mammalia) of the Belianska dolina Valley and the Borišov Nature Reserve in the Veľká Fatra Mts. *Ochrana prírody 13: 311–320 (in Slovak with English summary).*

KARASKA D. & KOCIAN Ľ. 1993: Contribution to the knowledge of small ground mammals in the Slovak part of the Babia hora. *Ochrana prírody 13: 365–374 (in Slovak with English summary).*

KLEINERT J. 1983: Epigeic macrofauna of the region Čierny kameň and Ľubochnianska dolina Valley in the Veľká Fatra Mts. *Ochrana prírody 4: 105–117 (in Slovak with Russian, English and German summaries).*

KOCIAN Ľ., KOCIAN A., KOCIANOVÁ E. & HALÁK K. 1985: Beitrag zur Kenntnis der Wirbeltiere der subalpinen und alpinen Zone der Westtatra-Roháče und ihre bioindikatorische Bedeutung. *Oravské múzeum 2: 83–97 (in Slovak with German summary).*

KOVÁČIK J. & ŠTOLLMANN A. 1984: Occurrence of the Tatra pine vole, *Pitymys tatricus* Kratochvíl, 1952 in Muránska planina (Slovakia). *Lynx (Praha) 22: 89 (in Slovak with English summary).*

KOWALSKI K. 1960: *Pitymys* McMurtrie 1831 (Microtidae, Rodentia) in the Northern Carpathians. *Acta Theriol. 4: 81–91.*

KRATOCHVÍL J. 1952: The voles of genus *Pitymys* in ČSR. *Acta Sc. Nat. Brno 24(8): 155–194 (in Czech with English and Russian summaries).*

KRATOCHVÍL J. 1964: Die systematische Stellung von *Pitymys tatricus* Kratochvíl, 1952. *Z. Säugetierkd. 29: 230–235.*

KRATOCHVÍL J. 1969: Der Geschlechtszyklus der Weibchen von *Pitymys subterraneus* und *P. tatricus* (Rodentia) in der Hohen Tatra. *Zool. listy 18: 90–120*.

KRATOCHVÍL J. 1970: *Pitymys*-Arten aus der Hohen Tatra (Mam., Rodentia). *Acta Sc. Nat. Brno 4(12): 1–63.*

KRATOCHVÍL J. & GAISLER J. 1967: Die Sukzession der kleiner Erdsäugetiere in einem Bergwald *Sorbeto-Piceetum. Zool. listy 16: 301–324.*

KRYŠTUFEK B., GRIFFITHS H. I. & VOHRALÍK V. 1996: The status and use of *Terricola* Fatio, 1867 in the taxonomy of Palaearctic "pine voles" (*Pitymys*) (Rodentia, Arvicolinae). *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Biologie 66: 237–240*.

MATTHEY R. 1964: La formule chromosomique et la position systématique de *Pitymys tatricus* Kratochvíl (Rodentia-Microtinae). *Z. Säugetierkd. 29: 235–241*.

MITCHELL-JONES A. J., AMORI G., BOGDANOWICZ W., KRYŠTUFEK B., REIJNDERS P. J. H., SPITZENBERGER F., STUBBE M., THISSEN J. B. M., VOHRALÍK V. & ZIMA J. 1999: The atlas of European mammals. *Academic Press, London, 484 pp*.

MURARIU D. & RĂDULET N. 1998: Mammalian fauna (Mammalia) from Maramureş Depression, Romania. *Trav. Mus. natl. Hist. nat. "Grigore Antipa" 15: 609–621*.

NADACHOWSKI A. & GARAPICH A. 1998: *Allophaiomys* evolutionary stage in extant *Microtus*. *Paludicola 2: 91–94*.

NADACHOWSKI A. & ZAGORODNYUK I. 1996: Recent *Allophaiomys*-like species in the Palaearctic: Pleistocene relicts or a return to an initial type. *Acta. Zool. Cracov. 39: 387–394.*

NIETHAMMER J. 1982: *Microtus tatricus* (Kratochvíl, 1952) – Tatra-Wühlmaus. In: Niethammer J. & Krapp F. (eds), Handbuch der Säugetiere Europas, Band 2/I, Rodentia II. *Akademische Verlagsgesellschaft, Wiesbaden: 491–496.*

OBUCH J. 1981: Recentné osteologické nálezy z oblasti Choča [Recent osteological records from the Choč region]. *Liptov 6: 257–270 (in Slovak).*

OBUCH J. et al. 1985: Contribution to the inventory research of vertebrates (Vertebrata) in the State Nature Reserve Suchý in the Protected Territory Malá Fatra. *Ochrana prírody 6: 215–230 (in Slovak with Russian, English and German summaries).*

PELIKÁN J. 1955: Zahlzustand einiger Kleinsäuger in der Hohen Tatra im Frühjahr 1955. *Folia Zool. Ent. 4: 295–302 (in Czech with Russian and German summaries).*

ROSICKÝ B. & KRATOCHVÍL J. 1955: Die Kleinsäuger des Tatra-National-parks. *Ochrana přírody 10(2): 2–16 (in Czech with German summary).*

SCHAEFFER H. 1974: Eine Fauna der Hohen Tatra aus dem 18. Jahrhundert (= Muran I). *Bonn. Zool. Beitr. 25: 231–282.*

ŠTOLLMANN A. & DUDICH A. 1985: Contribution to the knowledge of fauna of the small ground mammals (Insectivora, Rodentia) of the Western Tatra Mts. *Zborník prác o TANAP-e 26: 161–172 (in Slovak with Russian, German and English summaries).*

ŠTOLLMANN A. & DUDICH A. 1990: Hmyzožravce (Insectivora) a hlodavce (Rodentia) pripravovanej ŠPR Chabenec v Nízkych Tatrách [Rodents and insectivores of the prepared State Nature Reserve Chabenec in the Nízke Tatry Mts]. In: Vartíková E. (ed.), 25. TOP 1989 Tále – Prehľad odborných výsledkov. *Banská Bystrica, Bratislava: 195–204 (in Slovak).*

ŠTOLLMANN A., JANIČINA P., DUDICH A. & KADLEČÍK J. 1994: Hmyzožravce (Insectivora) a hlodavce (Rodentia) ŠPR Veľká Skalná vo Veľkej Fatre [Insectivores and rodents of the State Nature Reserve Veľká Skalná in the Veľká Fatra Mts]. In: Turiec 1992 – Zborník odborných výsledkov inventarizačných výskumov v povodí rieky Turiec. *Martin: 193–198 (in Slovak).*

TOMAŠKOVIČ M. 1989: Inventarizácia drobných zemných cicavcov v modelovej doline v Belánskych Tatrách [Survey of small mammals in a model valley of the Belánske Tatry Mts]. *M.Sc. Thesis, VŠLD Zvolen, 57 pp. (in Slovak).*

ZAGORODNYUK I. V. 1989: Taksonomiya, rasprostranenie i morfologicheskaya izmenchivost' polevok roda *Terricola* [Taxonomy, distribution and morphological variation in voles of the subgenus *Terricola*]. *Vestnik Zool. 5: 3–14 (in Russian).*

ZAGORODNYUK I. V., VORONTSOV N. N. & PESKOV V. N. 1992: Tatra vole (*Terricola tatricus*) in the Eastern Carpathians. *Zool. Zh. 71(6): 96–105 (in Russian with English summary).*

ZAGORODNYUK I. V. & ZIMA J. 1992: *Microtus tatricus* (Kratochvíl, 1952) in the Eastern Carpathians: cytogenetic evidence. *Folia Zool. 41: 123–126.*

ZIMA J., HRABĚ V., ŠTĚRBA O. & SCHLAMP M. 1984: Small mammals of the Kotlina siedmych prameňov Valley in the Belianske Tatra Mts. *Zborník prác o TANAP-e 25: 29–46 (in Czech with Russian, German and English summaries).*