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Biochemical systematics of House mice from the central Palearctic region

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Abstract

The systematic status of eight subspecies and one species differentiation of house mice of the genus *Mus* has been examined at 29 loci using electrophoretic analysis of proteins. The data obtained for the central Palearctic region were compared with the biochemical groups of mice of the genus *Mus* from Western Europe. Genetic groups corresponding to species *(Mus musculus mus-culus - M. spicilegus),* to semi-species *(M. m. domesticus - M. m. musculus; M. spicilegus - M. ab-botti)* and to subspecies *(M.m. musculus* s. str., *M.m. wagneri, M.m. sewertzowi)* could be detected in the USSR.

Key words: *Mus musculus* - *Mus spicilegus* - House mice - Systematics - Electrophoresis of proteins

1 Introduction

The systematics of the mice genus *Mus* have advanced during the last two decades owing to the methods of biochemical and molecular genetics, especially the electrophoresis of enzymes and proteins (MINEZAWA et al. 1981; SAGE 1981; THALER et al. 1981 a; BONHOMME et al. 1984; BONHOMME 1986). The investigation of gene variation of *Mus musculus* has demonstrated that in the Palearctic region seven forms at different levels of genetic divergence can be recognized. The first level is represented by sympatric forms reproduc-tively isolated from each other in nature. There are *Mus musculus domesticus* and *M. spretus* in South France and Spain (BRITTON and THALER 1978; BONHOMME et al. 1984) and *M.m. musculus* and *M. spicilegus* in Rumania (THALER et al. 1981 b). The second level of genetic divergence was observed in parapatric forms having stable zones of hybridization at the boundaries of their ranges. Such zones of hybridization were established for the semi-species *Mm musculus domesticus* and *M.m. musculus* in Denmark (SELANDER et al. 1969), in different parts of Western Europe (BONHOMME et al. 1984), and in Bulgaria (VANLER-BERGHE et al. 1988).

For the USSR the systematics of the mice genus *Mus* is not yet understood well. Different authors described more than twenty species and subspecies (see PAVLINOV and Ros-SOLIMO 1987). ARGIROPULO (1940) revised the taxonomy of *Mus musculus* and concluded that there are five subspecies in the USSR. Until recently, it has not been clear whether the observed genetic discreteness detected in the house mouse by protein electrophoresis corresponds to subspecies distinguished on the basis of geographical and morphological characters. The recent studies carried out in the USSR have essentially confirmed the evidence obtained in Western and Southern Europe. Reproductive isolation and genetic divergence of *M.m. musculus* and *M. spicilegus* were found in Ukraine and in Moldavia (MEZHZHERIN 1987, 1988; MEZHZHERIN and ZAGORODNYUK 1989; MILISHNIKOV et al. 1989). In the Primorski territory there is a hybrid zone between *M.m. musculus* and *M.m. castaneus* (FRISMAN 1988). Methods of biochemical systematics were used to prove that *M. tataricus (= M. abbotti)* is distributed in Transcaucasus (MEZHZHERIN and KOTENKOVA 1989; MILISHNIKOV and RAFIEV 1990). However, the taxonomy of genus *Mus* of Eastern Europe, Transcaucasus and Central Asia remains obscure. This paper presents some new data con-

cerned with the biochemical systematics of the genus *Mus* in the USSR. The major problems caused by variety led us to study the entire central Palearctic region with the aim to estimate the genetic divergence of the subspecies and their ecological forms.

Material and methods

The house mice (n = 290) were collected from 25 localities of central Palearctic region in the USSR (Fig. 1). The classical systematic description of house mice as well as geographic principles were used to identify eight subspecies and one species (HEPTNER 1930; ARGIROPULO 1940; BOBRINSKYI et al. 1965): *Mus musculus musculus* L., 1758 (n = 92); *Mus musculus wagneri* Eversmann, 1848 (n = 67); *Mus musculus sewertzowi* Kashkarov, 1922 (n = 31); *Mus musculus tomensis* Kastschenko, 1899 (n = 7); *Mus musculus formosovi* Heptner, 1930 (n = 19); *Mus musculus praetextus* Brants, 1827 (n = 24); *Mus musculus tataricus* Satunin, 1908 (n = 5); *Mus hortulanus* Nordmann,.184Q = *Mus spicilegus* Petenyi, 1882 (n = 38). The measurements of the skull and the trunk of the various house mouse taxa under investigation are given in Table 1.

Electrophoresis in 7,5 % polyacrylamide gel was used to study the following enzymes: xanthine dehydrogenase (XDH; EC 1.1.1.204), alcohol dehydrogenase (ADH; EC 1.1.1.1) in liver, lactate dehydrogenase (LDH-A.B; EC 1.1.1.27), malate dehydrogenase (MOR-1,2; EC 1.1.1.37), malic enzyme (MOD-1,2; EC 1.1.1.40), isocitrate dehydrogenase (IDH-1,2; EC 1.1.1.42), 6-phosphogluconate dehydrogenase (PGDH; EC 1.1.1.44), glucose-6-phosphate dehydrogenase (GPD-X; EC 1.1.1.49), aspartate aminotransferase (AAT-1,2; EC 2.6.1.1), superoxide dismutase (SOD-1,2; EC 1.15.1.1), alphaglycerophosphate dehydrogenase (GDC-1; EC 1.1.1.8), sorbitol dehydrogenase (SDH; 1.1.1.14), phosphoglucomutase (PGM-2; EC 5.4.2.2), esterase (ES-1,3,6,10; EC 3.1.1.1) in kidneys and muscles, esterase (ES-2,5^), transferins (Tf), albumins (Alb), postalbumins (Post) in blood serum and hemoglobin (Hb) in nemolysate. Nonspecific esterases, phosphoglucomutase and plasma proteins were analysed using disc-electrophoresis technique (DAVIS 1964), whereas the rest was studied in Tns-EDTA-borate (pH 8,5) buffer system (PEACOOK et al. 1965). The loci are designated according to the official nomenclature used for laboratory strains of *M. musculus* s. lato.

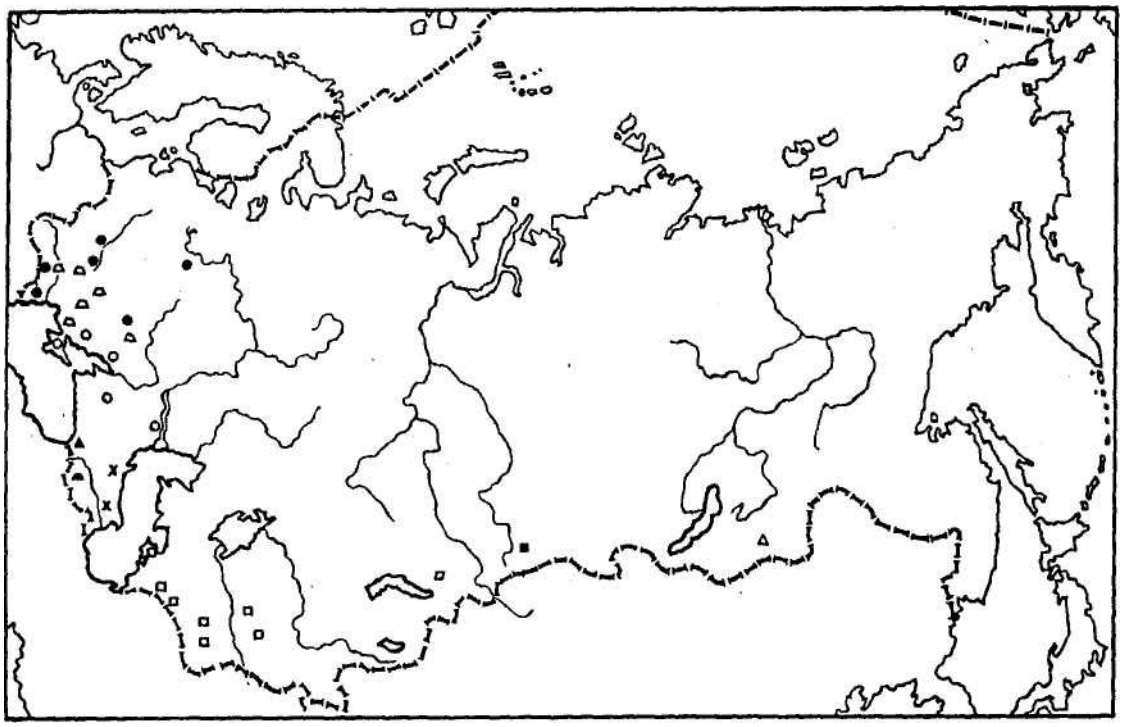

Fig. 1. Localities of collection of different species and subspecies of house mice: 1 = *M. m. musculus, 2 = M. m. wagneri, Ъ — M.m. sewertzowi,* 4 = *M.m. tomensis,* 5 = *M. m. raddei,* 6 = *M.m. formosovi,* 7 = *M.m. praetextus,* 8 = *M. spicilegus,* 9 = *M.m. tataricus* (= *M. abbotti)*

Eleven of the 29 loci proved mono-morphic in all populations under the above-described electrophore-tic conditions: SOD-1,2; GPD-X, IDH-2, PGD, ES-a, GDC-1, MOR-1,2; LDH-A, Tf, Post.

SOD. Two zones of activity were observed SOD-1 following staining for MOD, IDH and other dehydrogenases and SOD-2 after staining for PGM. Under the electrophoretic conditions used SOD-1, which is diagnostic for *M. spicilegus* and *M. m. musculus* (THALER et al. 1981b; BONHOMME et al. 1984; MILISHNIKOV et al. 1989), was invariant in both taxa. According to MILISHNIKOV et al. (1989) SOD-2 is also diagnostic for this pair of species but only with disc-electrophoresis. This enzyme showed a single electrophoretic variant in all investigated taxa.

Alb. After electrophoresis of liver tissue extracts a difference in electrophoretic mobility was identified between *M. m. mnsculns* and *M. spicilegns* (HUBNER 1991, pers. comm.). In 9 of the 10 individuals of *M. spicilegus* from different regions a more mobile albumin (Alb 101) than in *M. m mnsculus* (Alb 100) was identified. *M. m. tataricus* possesses another allelic variant of this protein with most slow mobility (Alb 98).

£5-6. Both, kidneys and muscles, present multiple band pheno-types of this enzyme with two main zones of activity. This enzyme is controlled by a multiple loci system (NASH and DEIMLING 1982). Disk-electrophoresis demonstrated that *M. spicilegus* and *M. m. tataricus* have more rapidly migrating allozymes of both main zones (ES-6b) than *M. musculus* s. lato (ES-6a).

XDH. Only one zone of activity was observed due to the pre-

Table 2. Allelic variation among house mice taxa at 29 loci

Locus	Allcle	*m.m.*	*m. w.*	***m. t.***	***m. torn.***	*m. r.*	*m.pr.*	***m.f.***	***m.sp.***	***m. tat.*** t
ES-2	null	0.23	0.24	0.54	1.00	0.86	0.21	0.03	1.00	0.40
	100	0.66	0.69	0.46		0.14	0.37	0.97		0.60
	103	0.11	0.07				0.52			
	104									
ES-1	98	1.00	1.00	0.03	1.00	1.00	0.23	0.89	1.00	1.00
	100			0.97			0.77	0.11		
ES-3	91 95				1.00	1.00	1.00	1.00	0.06	
	99	0.02	0.13	0.97					0.33	0.20
	100								0.61	
	105	0.98	0.87	0.03						0.80
	110									
ES-10	100	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00
	104							0.05		
	110									
"Es-6"	a b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PGM-2	95 99				1.00	1.00		1.00	0.20	1.00
	100	0.33	0.02	0.11			0.22		0.76	
	105								0.0+	
		0.67	0.98	0.89			0.78			
IDH-1	95	1.00	1.00	0.98	1.00	1.00	0.19	0.50	1.00	1.00
	100			0.02			0.81	0.50		
	102									
SDH	100	1.00	1.00	1.00	1.00	-	0.88	1.00	1.00	1.00
	101						0.06			
	105						0.06			
ADH	-100	0.67	0.43	0.48	0.86		0.25	0.20	0.90	1.00
	-105	0.33	0.57	0.52	0.14		0.75	0.80	0.10	
AAT-1	90	1.00	1.00	0.02	1.00	1.00	0.03	1.00	1.00	1.00
	100			0.98			0.97			
AAT-2	-95	0.15	0.85	0.02	1.00	1.00	1.00	1.00	1.00	1.00
	-100	1.00		0.98						
MOD-1	98	0.79	0.89	0.70	1.00	0.29	0.84	0.04	0.90	1.00
	100	0.18	0.02	0.26		0.57	0.16	0.80	0.10	
	101	0.03	0.09	0.04		0.14		0.16		
	103									
XDH	99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	100									
MOD-2	98	0.98	1.00	1.00	1.00	1.00	0.80	0.75	0.05	1.00
	100	0.02					0.20	0.25	0.95	
	102									
Hbb	d	0.57	0.45	0.24	0.43	1.00	0.50	0.20	1.00	1.00
	P	0.13	0.26	0.76	0.57		0.50	0.19		
	s	0.30	0.29					0.61		
LDH-B	95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.08	1.00
	100								0.92	
Alb	98 .	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.10	1.00
	100								0.90	
	101									
	n	13	7	8	7	7	8	6	10	4

n- number of mice which albumin locus investigated in tissue extract. m.m. – Mus musculus musculus s.str., m.w. M.m. wagneri, m.s. –M.m. sewertzowi, m.tom. – M.m. tomensis, m.r. – M.m. raddei, m.pr. – M.m. praetextus, m.f. – M.m.formosivi, m.sp. – M. spicilegus, m.tat.-M.m. tataricus

Table 3. **Genetic distance matrix for house mice taxa** Values corresponding to NEI'S genetic distance index

Taxa		9	8	7	6	5	4	3	2	1
M. m. musculus	1	0.367	0.314	0.068	0.046	0.019	0.047	0.005	0.009	X
M. m. wagneri	2	0.356	0.321	0.057	0.039	0.013	0.049	0.001	X	
M. m. sewertzowi	3	0.386	0.340	0.052	0.019	0.027	0.032	X		
M. m. tomensis	4	0.443	0.371	0.104	0.051	0.003	X			
M. m. raddei	5	0.452	0.378	0.045	0.017	X				
M. m. praetextus	6	0.335	0.283	0.02	X					
M. m.formosovi	7	**0.309**	0.260	X						
M. spicilegus	8	0.093	X							
M. m. tataricus	9	X								

sence of a single locus. XDH proved monomorphic in all the taxa but had different mobility in *M. musculus* on one hand, and in *M. spicilegus* and *M. m. tataricus* on the other in 6 % polyacrylamide gel.

The allele frequency distribution found for 18 variable loci is shown in Table 2. NEI'S (NEI 1975) genetic distance (D) was calculated to investigate the genetic relationships between the house mice taxa. The resulting matrix is shown in Table 3. The phenogramme (Fig. 2) showing genetic relationships among the taxa was derived by UPGMA (SNEATH and SOKAL 1973).

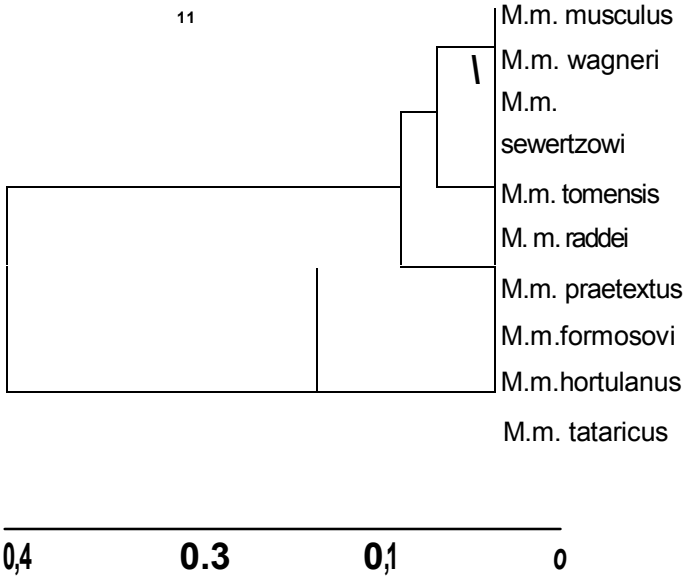

Fig. 2. Phenogramme of genetic distances in the species and subspecies of genus *Mus*

Discussion

Two main levels of genetic divergence in house mice taxa were found (Fig. 2). The first one is the interspecific differentiation between *M. spicilegus* and *M, m, tataricus* on one and *M. musculus s.* lato on the other side. The average NEI'S genetic distance D is 0.351 ± 0.015. The second level is expressed by the intraspecific differences within *M. musculus* s. lato and between *M. m. tataricus* and *M. spicilegus* (average genetic distance is 0.036 ± 0.006). There are further three genetically determined groups within *M. musculus* s. lato. The first group consists of three western Palearctic subspecies: *M. m. musculus, M. m. wagneri, M. m. sewertzowi* (D = 0.005), the second includes two eastern Palearctic forms: *M. m. tomensis* and *M. m. raddei* (D = 0.003) and the third consists of transcaucasian taxa: *M. m.formosovi* and *M. m. praetextus* (D = 0.002). The distribution of genetic distances among these, groups is not symmetrical (Fig. 2) and is between eastern-western Palearctic sub-

species significantly lower (D = 0.02 + 0.006) than between the transcaucasian forms (D = 0.056 + 0.008). The variation of allozymes confirmed that all the species are isolated from the mound-building mice. This was demonstrated in Rumania for *M. m. musculus* and *M. spicilegus* too (THALER et al. 1981 b). The above conclusion was drawn on the basis of the following observations: 1. high values of genetic distance between the two forms; 2. presence of fixed allelic differences in the loci: IDH-1; ES-1,2,6,10; XDH 2 for the pair of species *M. m. musculus* and *M. spicilegus.,* and in ES-3,6,10; Alb, PGM-2, XDH between *M. m. tataricus* and *M. m. formosovi;* 3. the absence of hybrid heterozygotes in sympatric populations even from the same habitats.

The important character of the alleles in IDH-1, ES-1, ES-2 in *M. m. formosovi* and in *M. m. praetextus* distinguish these two subspecies from the other forms but demonstrates their genetic similarity with *M. m. domesticus.* This suggestion is also confirmed by several morphological features of these mice. The individuals of both forms are large long-tailed mice. The back and belly of *M. m. formosovi* is grey (almost black) and zygomatic plates are of the same shape as those of *M. m. domesticus* in Germany (KRAFT 1984/85). *M. m. praetextus* is characterized by more light colour of back and white belly, round zygomatic plates and seems to be transitional between *M. m. domesticus* and *M. m. musculus. M. m. domesticus* and *M. m. musculus* build narrow hybrid zones in Denmark (SELANDER et al. 1969), Western Europe (BONHOMME et al. 1984) and Bulgaria (VANLERBERGHE et al. 1988) at their range limits. Hence, it is logical to consider *M. m. formosovi* as belonging to *M. m. domesticus.* The gradual decrease in the frequencies of the alleles of the loci IDH-1, ES-1, ES-2 and the variation in colour and in some ratios of the body in the same direction provide proof for the existence of such a hybrid zone in Trancaucasus. Analysis of the distribution of the dark belly long-tailed mice in the above region (previously classified as *M. m. formosovi* (HEPTNER 1930; SVIRIDENKO 1936; ARGIROPULO 1940; SHIDLOVSKYI 1962) suggests the presence of a pronounced boundary between short-tailed, white belly *M. m. wagneri* and long-tailed, dark belly *M. m. domesticus.* In the north, this boundary may be located in main Caucasus, whereas east of Transcaucasus it might be situated in the continental steppe region of North Caucasus. This fact demonstrates the importance of ecological factors in the establishment and in the maintenance of stable and narrow hybrid zones in house mice. Temperature and humidity appear of particular importance.

M. bactrianus is well distinct from other forms of mice, morphologically and genetically (MARSHALL 1977; BONHOMME et al. 1984). This form is distributed in Centra] Asia adjacent to the USSR. The electrophoretic studies of house mice in Middle Asia, Turkmenia and eastern Transcaucasus where *M. bactrianus* occurs have failed to detect populations with alleles typical for *M. bactrianus.* In most cases mice classified as subspecies *M. m. sewertzowi* and *M. m. praetextus* were characterized by alleles typical of *M. m. musculus.* However, some individuals had alleles of the loci AAT-1 and ES-1,3 that could be identical to those observed in *M. bactrianus.* This fact as well as morphological features of the subspecies and primarily the round form of the zygomatic plate [a characteristic of *M. bactrianus* (MARSHALL 1977)] may suggest an admixture of genes from south palearctic mice during the formation of populations of house mice in Middle Asia, Turkmenia and eastern Transcaucasus. However, the admixture of genes of these forms is negligible with respect to *M.m. musculus* and hence it would be more reasonable to consider mice of the desert zone of Central Asia and Turkmenia only as a subspecies of the latter one, and classify *M. m praetextus* as a hybrid form between *M. m. musculus* and *M. m. domesticus* with a possible introduction of a certain fraction of genes from south Central Asia mice.

The genetic investigation of *M. m. wagneri, M. m. raddei, M. m. tomensis* indicates that they have alleles specific for *M. m. musculus* s. lato. The differences observed between them appear mainly in conventionally polymorphic loci. Consequently these subspecies can be considered only as geographic forms of *M. m. musculus* s. lato.

As a result of our studies the following hierarchical system of the house mice in the central Palearctic region can be developed corresponding in its main features with the concepts of systematics of house mice proposed recently (MARSHALL 1986).

The first level is a species differentiation. It is characterized by the fixation of alternative alleles and reproductive isolation in sympatric conditions. The substantial morphological and ecological differences are caused by genetic factors. *Mus musculus* s. lato includes synathropic or wild forms with a specific "mouse" odour. In natural conditions they hibernate in simple burrows. They have sufficiently wide arcus zygomaticus, narrow ramus superior arcus zygomaticus (Table 1) and a relatively high skull with long incisive holes and a short row of upper molars. The crown M^1 does not cover the protruding forward root, M^3 is small (0.65 x 0.63 mm). *Mus spicilegus* s. lato (= *spretoides)* are wild forms without "mouse" odour. Morphological features include relatively narrow arcus zygomaticus, wide ramus superior arcus zygomaticus (Table 1), the skull with short incisive holes and a long row of upper molars. The crown M^1 covers the root, M^3 is relatively large (0.75 X 0.73 mm).

The second level is a differentiation of semi-species. There are parapatric forms which have genetic differences and narrow hybrid zones at the limits of the species ranges whose stability ensures the existence of the forms. *Mus musculus domesticus (M. m. formosovi, M. m. praetexttis) are* the large long-tailed mice (Ca - 90-100%, PI - 17-18 mm, Au - 13-15 mm). The colour of the back is almost black with grey belly without a distinctive transition upon the back and often with albino spots. Hybrids demonstrate a continuous transition in colouring from *M. m. musculus* to *M. m. domesticus. M. musculus* s. lato are small,~mter.mediate and large short-tailed mice (CA - 60-100%, PI - 14-17,5 mm, Au - 12-14 mm), their belly is grey or white with a transition to a darker colour of the back. *Mus spicilegus* are small mice with a homogenous grey coloration of the fur (occasionally/ light bellied), with no admixture of red colours. The main character of *M, spicilegus* is grain-storing activity. In autumn 4-14 mice work together to construct mounds with a supply of food and remain to live in these mounds for the winter (BRAUNER 1899; NAUMOV 1940). The fore-part of zygomatic plate is not characterized by a protruding angular form. *Mus abbotti* (= *tataricus)* is a larger form with greyish-brown colour of the fur on the back and purely white belly, which builds no mounds, the fore-part of the zygomatic plate having the shape of a protruding angle.

The third level is the one of subspecies differentiation. There are no clear genetic differences between allopatric morphologically differing populations and no exact borders between areas. There is only gradual change from one form to the other. The differences are mainly originated by geographic separation of the populations with respect to natural-climatic zones. *Mus musculus musculus* s. str. is a synanthropic form, the fur having two colours with an admixture of red hues, expecially distinctive on the sides, and a grey or white belly. The body size and length of tail are average (CA- 70-100%). *M. m. wagneri (M. m. raddei)* can be a synantropic or a wild form. It inhabits steppes of eastern Ukraine, Crimea, North Caucasus, Kazakhstan, Transbaikal. They are short-tailed mice (Ca - 60-80%) with contrasting two-colour fur: reddish-grey back and a white belly. *M. musculus sewertzowi* is synantropic or wild. It dweels Central Asia and Turkmenia. It is characterized by large size, short tail (CA - 80%), the colour of the back is sandy-light, the belly is white.

Unfortunately we have failed to clarify the problem concerning the status of *M. abbotti* (= *tataricus)* in our systematic studies. Genetic differences between *M. spicilegus* and *M. abbotti* favour the separate species hypothesis. However, these differences are substantially lower than the ones generally seen between rodents species. The observed morphological differences from *M. spicilegus* give, according to KRATOCHVIL (1986), ground to consider *M. abbotti* to be a species. However, to date it is difficult to determine the status of *M. abbotti* in the systematics of house mice, since it is not clear yet, whether this

form is allospecies, semi-species or subspecies, e. g. whether it has: 1. reproductive isolation in the zone of sympatry with *M. spicilegus, 2.* restricted hybridization in a narrow zone, or 3. continuous transition from one to the other.

Could this mean that populations from Macedonia to Turkey are linked via the Armenian populations to grain-storing mice from Ukrainia through Serbia? Perhaps not, since hybrids between Armenian and Moldavian grain-storing mice support the "separate species" hypothesis. The hybrids die at an age of 3-4 months (LAVRENCHENKO et al. 1989; LAVRENCHENKO 1990).

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Zusammenfassung

Biochemische Systematik van Hausmaus-Arten aus dem Zentrum der palaarktischen Region

Elektrophoretische Analysen von Proteinmustern, die von 29 Genloci determiniert werden, wurden verwendet, urn den systematischen Status von acht Differenzierungen auf Unterart- und Art-Ebene in der Gattung *Mus* zu bestimmen. Die Daten aus der palaarktischen Region der UdSSR wurden mit biochemischen Daten aus Westeuropa verglichen. Genetische Gruppen im Species-Status *(Mus musculus musculus — Mus musculus spicilegus),* aber auch im Differenzierungsgrad von Semispecies *(Mus musculus domesticus - Mus musculus musculus; Mus spicilegus - Mus abbotti)* und von Subspecies *(Mus musculus musculus* s. str. - *Mus musculus wagneri — Mus musculus sewertzowi)* konnten dabei in der UdSSR beobachtet werden.

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