



The House mice, *Mus musculus* s. l., hybrid zone of Transcaucasus

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Abstract

A description of the hybrid zone of house mice species of the Transcaucasus is given on the basis of allozymic data and morphological characters. It is demonstrated that the hybrid zone in the Transcaucasus is formed by three parapatric species: *M. musculus*, dwelling mainly in the north Caucasus; *M. domesticus*, inhabiting the area from western Transcaucasus to eastern Ciscaucasus; *M. praetextus*, widely represented in steppe regions of Azerbaijan. The main features of this hybrid zone are: (i) unusually high range of gene introgression throughout the entire Transcaucasus; (ii) a sharp boundary between *M. musculus* and the gene introgression zone between *M. musculus*, *M. domesticus*, and *M. praetextus*, stretching along the climatic boundary between continental and subtropical regions; (iii) the existence of a transitional zone in the Central Transcaucasus between *M. praetextus* and *M. domesticus*. The results obtained are discussed with regard to the hybrid zones of Europe and Eastern Asia. Two main features of Asian hybrid zones are emphasised: their unusually large width as compared to European examples and their localisation in climatic zones similar to the subtropics.

Key words: *Mus musculus*, hybrid zones, biochemical and morphological variation

Introduction

In recent years, the interest in the systematics of Palearctic representatives of the genus *Mus* has increased due to the introduction of biochemical systematic methods and the discovery of introgressive hybridisation between different forms (SELANDER et al. 1969; SELANDER 1970; HUNT and SELANDER 1971; VANLERBERGHE et al. 1986, 1988; NANCE et al. 1990), whose species status is discussed (MARSHALL 1986, 1991; BONHOMME 1986; Mezherin 1994).

Evidence obtained in Europe confirms the existence of a stable narrow hybrid zone between *M. musculus* and *M. domesticus*, several dozens kilometres wide, which passes throughout Europe, from Jutland across the Alps to the Balkans (HUNT and SELANDER 1973; BONHOMME et al. 1983; KRAFT 1984; VANLERBERGHE et al. 1986, 1988; KRSTUFEK 1991). The geography of hybrid zones in Asia, where along with *M. musculus* Linnaeus, 1758, distributed virtually ubiquitously in the temperate and continental zone, there also occur southern species: *M. domesticus* Ruddy, 1772, *M. praetextus* Brants, 1827 and *M. castaneus* Waterhouse 1843, which have received little attention. In addition to analysis of hybridisation between northern and southern species, it would be interesting to compare southern forms with one another, since the southern forms display considerable morphological differences (MARSHALL 1977) and they are also differentiated at the biochemical level (SAGE 1981; BONHOMME et al. 1984).

A good possibility for analyses of hybrid zones of northern and southern species on the one hand, and European and Asian ones, on the other, is provided by the Caucasian region. In fact, this region combines the areas of three forms. *M. musculus* comes from the north, *M. domesticus* (syn. *M. m. formosovi* Heptner, 1930) penetrates from the south and the south-west, and *M. praetextus* from the south-east (SATUNIN 1905, 1909; HEPTNER 1930; VERESCHAGIN 1957; SHIDLOVSKI 1947, 1958, 1976; MEZHHERIN and KOTENKOVA 1989, 1992).

The main aim of the present study is the presentation of data on allozymic variability in house mice from the Caucasus; identification of morphological characters which appear to be diagnostic for *M. musculus*, *M. domesticus*, *M. praetextus* in this region; revision of museum collections on the basis of the distinctive features obtained; and, in the final analysis, specification of the range of these subspecies in the Caucasus.

Material and methods

Material

House mice from different regions of the Caucasus were analysed by method of protein and enzyme polyacrylamide gel-electrophoresis. Twelve specimens from Adjara (Georgia), 8 house mice from Armenia, and 15 mice from Azerbaijan were investigated from the Transcaucasus region, 8 specimens from the Krasnodar region (Russia), and 7 from the Daghestan (Russia) in the Northern Caucasus region. Besides Caucasian mice, 3 individuals of *M. domesticus* from the Konstanz Lake region (Germany), 2 specimens of *M. praetextus* from Syria (type locality of this species), and 7 mice of *M. musculus* from Poland, and 112 from the Ukraine were examined as controls.

The house mice museum collections from the Caucasian region were investigated. The collections of the Zoological Institute of the Russian Academy of Sciences (N = 44), of the Moscow State University (N = 107), of the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (N = 127), and of the Kiev State University (N = 35) were analysed. All Caucasian house mice samples are presented in figure 1.

Species diagnostics

Biochemical identification: Trapped mice were brought alive to the laboratory, where they were killed immediately before electrophoretic procedures. Diagnostics of *M. musculus*, *M. domesticus* species pair were carried out by identification of alleles at three biochemical loci (Es-1, Es-2, Idh-1). Identification of Transcaucasus house mice from representatives of *M. spicilegus* s. l. was performed by the following loci: Es-2, Es-15, Es-10, and Alb. Description of standard acrylamide electrophoresis methods and gel staining has been published earlier (MEZHHERIN and KOTENKOVA 1992).

Morphological identification: Diagnostics of the pair *M. musculus*, *M. domesticus* of museum collections were performed by two well-known characters: belly colouration and relative length of tail and body (ORSINI et al. 1983; KRAFT 1984; Marshall 1986). For diagrams reflecting geographic variations of the mentioned morphological features, we used not less than three adult specimens for every record. Besides the above mentioned characters, we analysed the shape of the zygomatic plate and occlusal surface of the first lower molar, which have a diagnostic significance in identifications of *M. musculus*, *M. domesticus* (ORSINI et al. 1983; KRAFT 1984; KRATOCHVIL 1986).

The distinction of *M. musculus* s. l. from representatives of *M. spicilegus* s. l. was performed in the museum collections by the zygomatic coefficients (ORSINI et al. 1983) and the relative length of the tail.

Results

Biochemical data

The frequencies of alleles of 28 loci of house mice from different regions are presented in table 1. Three reliable diagnostic loci for *M. musculus*, *M. domesticus* species have been

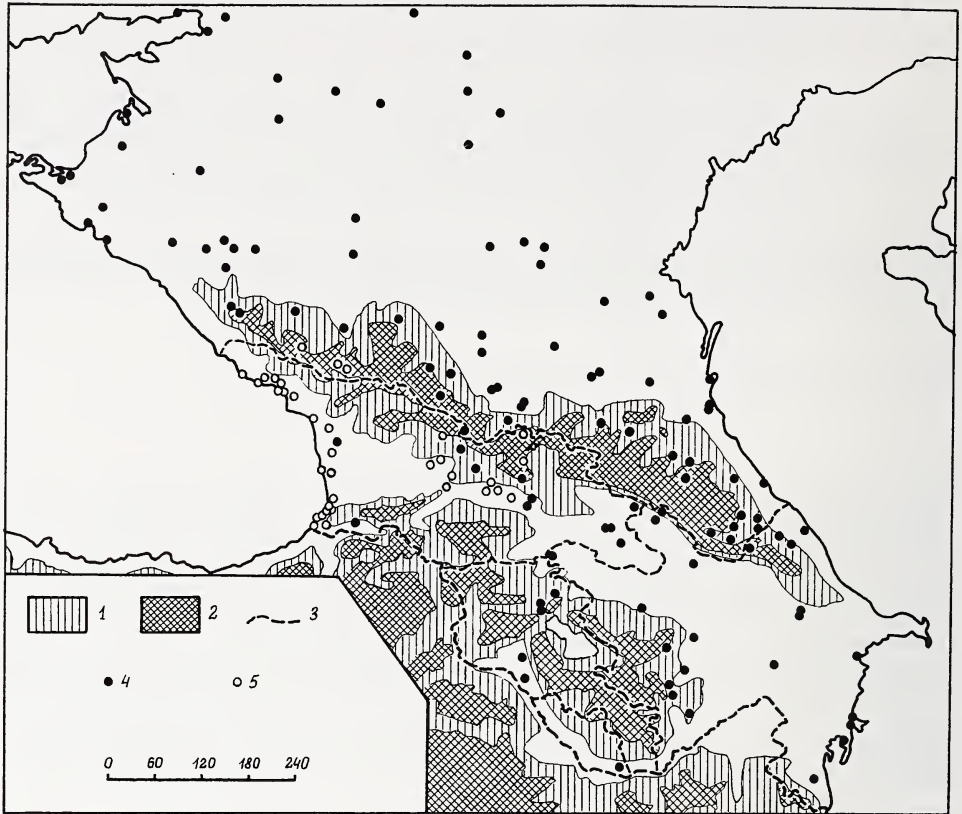


Fig. 1. Localities of house mice collection in Ciscaucasus and Transcaucasus. 1: highland from 1000 m to 2000 m above sea level; 2: highland more than 2000 m above sea level; 3: state borders; 4: localities of house mice collection in museums of Russia and the Ukraine; 5: localities of black-bellied mice collection (after: SHIDLOVSKI 1947, 1958).

found in this study corresponding to previous data (SELANDER et al. 1969; THALER et al. 1981; BONHOMME et al. 1984).

Es-1: This locus is considered as diagnostic for *M. musculus*, *M. domesticus* after investigations performed in Europe (SELANDER et al. 1969; SELANDER 1971; THALER et al. 1981; BONHOMME et al. 1984; VANLERBERGHE et al. 1988). Among 290 individuals of *M. musculus*, which were investigated by the authors from the European part of the former USSR, Central Asia, and Siberia (MEZHHERIN and KOTENKOVA 1989, 1992; MEZHHERIN et al. 1992) and according to other data (FRISMAN et al. 1990), the Es-1¹⁰⁰ allele was fixed. The slow allelic variant Es-1⁹⁸, which was fixed in *M. domesticus* and *M. spicilegus* s.l. (THALER et al. 1981; BONHOMME et al. 1984), was revealed in two individuals from Central Asia (MEZHHERIN and KOTENKOVA 1992). In the Transcaucasus region the allelic variant was predominant while in the mice of Adjara it has been fixed (Fig. 2). The mean frequency of this allele in Transcaucasus house mice populations was 0.60 ± 0.04 ($t = 12.5$; $p < 0.001$) in contrast to the eastern Europe house mouse populations where allele Es-1⁹⁸ was not found.

Es-2: This locus as well as Es-1 is traditionally used in the analysis of European hybrid zone (SELANDER et al. 1969; SELANDER 1971; VANLERBERGHE et al. 1988), although the allelic variant intrinsic to *M. domesticus*, is always represented in *M. musculus* popula-

Table 1. Allelic frequencies of house mice species *Mus musculus* s. lato from different regions

Loci	Alleles	<i>musc.</i> Poland	<i>musc.</i> Ukraine	<i>musc.</i> Kras- nodar region	<i>musc.</i> Da- ghestan	<i>praet.</i> Sirya	<i>praet.</i> Azer- baijan	<i>dom.</i> Adjaria	<i>dom.</i> Arme- nija	<i>dom.</i> Ger- many
Aat-1	90						0.03		0.10	
	100	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.90	
Aat-2	-90	0.37	0.15							1.00
	-100	0.63	0.65	1.00	1.00	1.00	1.00	1.00	1.00	
Adh	-100	0.38	0.67	0.70	0.72	1.00	0.25	0.16	0.20	
	-105	0.62	0.33	0.30	0.28		0.75	0.84	0.80	1.00
Idh-1	95					1.00	0.19	0.50	0.52	
	100	1.00	1.00	1.00	1.00		0.81	0.50	0.48	1.00
Es-1	98					1.00	0.23	0.89	0.84	1.00
	100	1.00	1.00	1.00	1.00		0.77	0.11	0.16	
Es-2	null		0.23	0.25			0.21			
	100	1.00	0.66	0.75	0.58		0.37	0.03	0.52	
	103		0.11		0.42	1.00	0.52	0.97	0.48	1.00
Es-3	95		0.10							1.00
	100	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	
Es-10	100	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00
	105							0.05		
Mod-1	98							0.04		
	100	0.50	0.79	0.67	0.76		0.84	0.80	0.50	
	101	0.50	0.18	0.33	0.24	1.00	0.16	0.16	0.50	1.00
Pgm-2	103		0.03							
	95	0.27	0.20	0.15	0.21		0.22		0.05	
	100	0.73	0.80	0.85	0.79	1.00	0.78	1.00	0.95	1.00
Sdh	100	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00
	101						0.06			
	105						0.06			
Hbb	d	0.44	0.57	0.55	0.46		0.50	0.20	0.15	
	p	0.28	0.13	0.45	0.54	1.00	0.50	0.19	0.35	
	s	0.28	0.30					0.61	0.50	1.00

Loci: Alb, Es-15, Es-9, Gdc-1, Gpd-x, Hba, Idh-2, Ldh-A, Ldh-B, Mor-1, Mor-2, Pgdh, Post, Sod-1, Sod-2, Tf were monomorphic under used electrophoretic conditions.

tions at low frequencies (THALER et al. 1981; BONHOMME et al. 1984; MEZHHERIN 1987; MEZHHERIN and KOTENKOVA 1992; FRISMAN et al. 1990). In the Russian and Central *M. musculus* populations its frequencies do usually not exceed 10% (MEZHHERIN and KOTENKOVA 1992; FRISMAN et al. 1990) while in Transcaucasus populations the allele predominates and in Adjaria it is even fixed (Fig. 3). The mean frequency of Es-2¹⁰³ allele in Transcaucasus house mice was (0.657 ± 0.02) in comparison to investigated eastern Europe populations where its frequency was significantly lower (0.11 ± 0.007; $t = 25.0$; $p \leq 0.001$).

Idh-1: As well as the above-mentioned alleles, the slow migrating allele Idh-1⁹⁵ is likewise characteristic for the southern house mice species (Asian populations of *M. domesticus*, *M. praetextus*, and *M. castaneus*, and representatives of *M. spicilegus* s.l.: THALER et al. 1981; BONHOMME et al. 1984, 1989; FRISMAN et al. 1990; BRITTON-DAVIDIAN 1991). In the territory of the former USSR, in European, northern Caucasian, Middle-Asian, and Siberian house mice populations the slow migrating allele was never recorded (MEZHHERIN 1987; MEZHHERIN and KOTENKOVA 1989, 1992; MEZHHERIN et al. 1992;

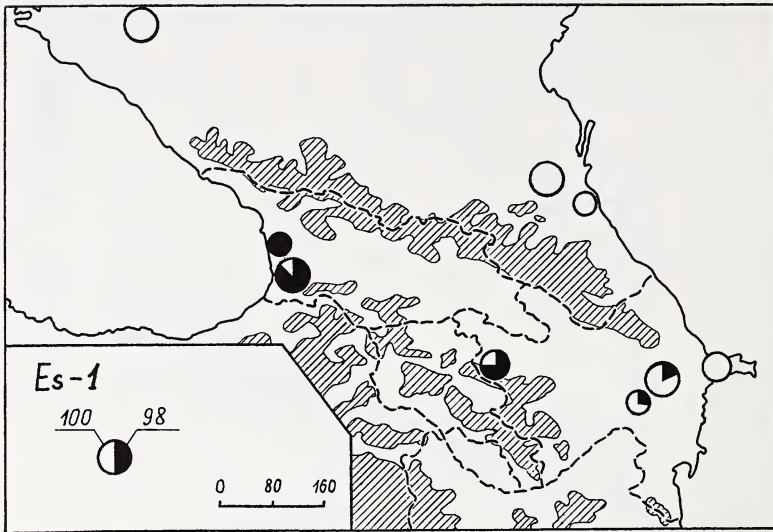


Fig. 2. Diagram of geographic distribution of Es-1 alleles in the Caucasus region. The scale of maps Figs. 2-6: 1 : 800 000; shaded areas are highland more than 2 000 m above sea level.

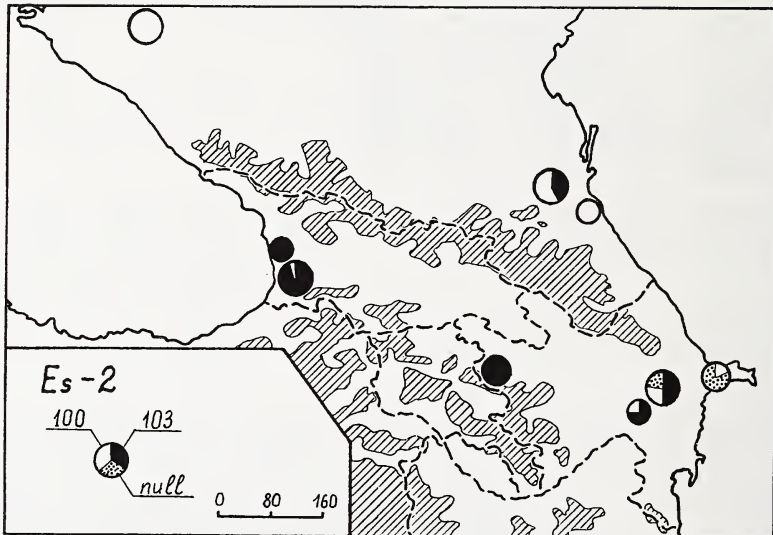


Fig. 3. Diagram of geographic distribution of three alleles of Es-2 locus in the Caucasus region.

MILISHNIKOV et al. 1989, 1990; FRISMAN et al. 1990). The appearance of this allele was found only in the Transcaucasus (Fig. 4), where mean frequency was 0.371 ± 0.041 ($t = 9.04$; $p < 0.001$). In addition, this allele at high frequencies was found in the south of the Russian Far East (FRISMAN and KOROBITSINA 1990), where gene introgression took place from *M. castaneus* to *M. musculus*.

In addition to the alleles of the above-mentioned loci, the Transcaucasian house mice populations can be characterised by Sod-1^a, Pgm-1^a, Gpd-1^a (MILISHNIKOV et al. 1990;

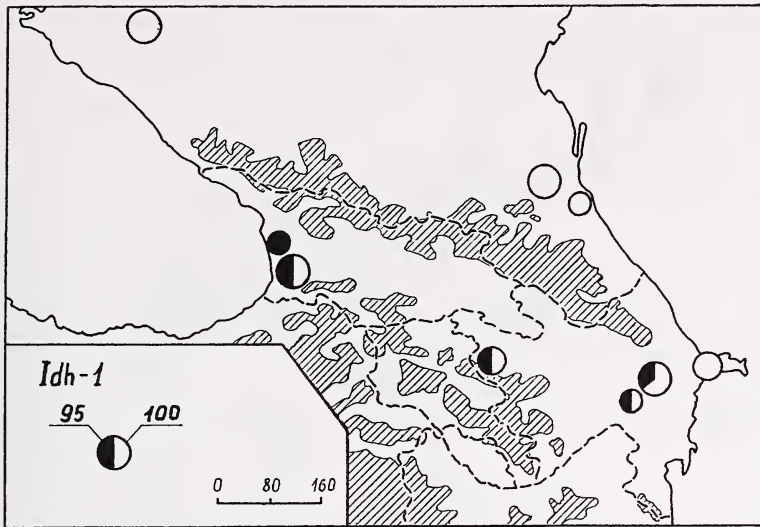


Fig. 4. Diagram of geographic distribution of two alleles of Idh-I locus in the Caucasus region.

FRISMAN et al. 1990), and Mod-2^a (MEZHHERIN and KOTENKOVA 1992). In Transcaucasus populations they are met together with the Es-1⁹⁸, Es-2¹⁰³, and Idh-1⁹⁵ proving the existence of *M. musculus* and *M. domesticus* gene introgression in this region.

Comparison of eastern Transcaucasus white-bellied *M. praetextus* with western dark-bellied *M. domesticus* yielded no considerable difference at the biochemical gene level, except for the Hbb locus. The allele Hbb^s, predominating in western European *M. domesticus* (BRITTON-DAVIDIAN 1989), is represented at a high frequency in the occidental Transcaucasus form also. Therefore, we suggest a direct relationship between the Transcaucasian *M. domesticus* populations and the European ones. Predominance of the Hbb^p and absence of Hbb^s in the oriental transcaucasus populations within white-bellied house mice indicate their Asian origin, where very similar gene distribution of Hbb locus is observed (MIYASHITA et al. 1985).

Morphological variation

Presence of at least two forms of house mice belonging to the species group *M. musculus* s.l. has been traditionally recognised in the Transcaucasus region (SATUNIN 1905, 1909; HEPTNER 1930; ARGIROPULO 1940; VERESTSCHAGIN 1959; SHIDLOVSKI 1947, 1958, 1976). They were the occidental dark-bellied mouse *M. m. formosovi* (syn. *M. domesticus*) and the oriental white bellied form identified by many authors as *M. m. praetextus*, *M. m. bactrianus*, *M. m. tataricus* (partim!). Revision of collections confirms this concept in general, although the pattern of variability of belly colouration has proven to be far more complicated (Fig. 5). Dark-bellied mice with no distinct belly and back colouration occur in the moist subtropics of Adjara. In central Georgia and Armenia mostly dark-bellied specimens with distinct albino spots of diverse shape are distributed. In Daghستان, where *M. m. formosovi* was described, the most diversified colour variants of typical *M. musculus*, *M. domesticus*, and *M. praetextus* and their combinations occur. In steppe regions of central Azerbaijan exclusively white-bellied mice with a brown back are found (Fig. 5). These mice were recognised by SHIDLOVSKI (1976) as *M. m. praetextus*. External

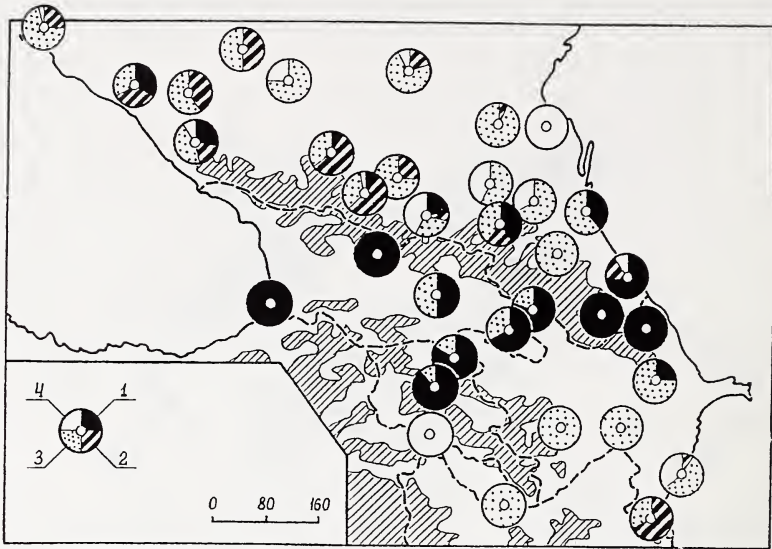


Fig. 5. Diagram of geographic distribution of different types of belly's colouration in the Caucasus region. 1: black belly mice; 2: dark-grey belly mice; 3: light grey belly mice; 4: white belly mice.

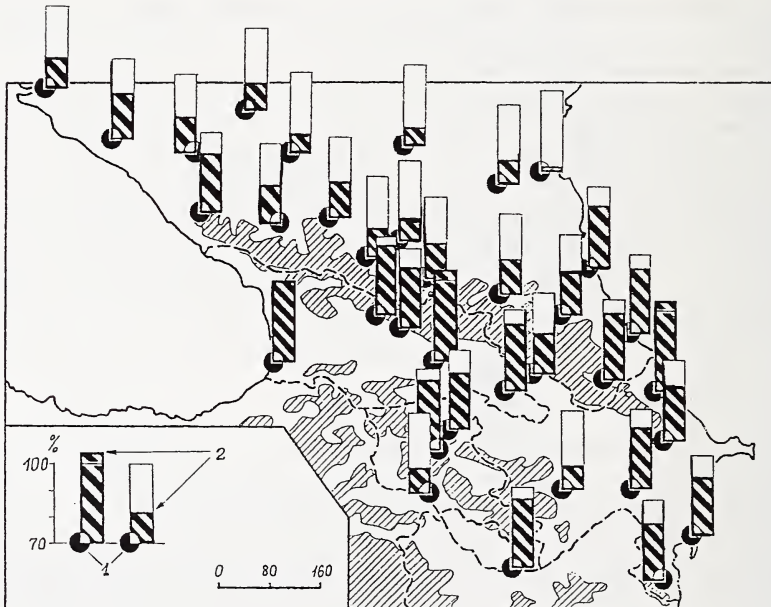


Fig. 6. Diagram of geographic distribution of house mice with different length of tail in the Caucasus region.

morphology of the house mice from Azerbaijan do not differ in appearance from those from Syria. These are large white-bellied mice with a tail equal or longer than body. The colouration on the back varies from sand-coloured to brown. In addition, on the edge of the distribution ranges of *M. domesticus* and *M. praetextus*, on the borders of Azerbaijan,

Georgia, and Armenia mostly grey-bellied mice occur. Their coloration contrasts with both dark-bellied occidental and white-bellied oriental forms. Most likely, they resulted from hybridisation between *M. domesticus* and *M. praetextus*.

The geographical variation of the relative tail length of the house mice of the Caucasus is presented in figure 6. Considerably long-tailed are mice from Transcaucasus and Daghestan, whose relative tail length varies within 90–110%. In the North Caucasus, in the regions of the Great Caucasus and the Black Sea coast, the tail is always shorter than the body (80–90%). In dry continental regions of the North Caucasus, and particularly in semideserts, mice have the shortest tails (70–80%).

Measurements of skull and body of the Cis- and Transcaucasus mice are given in table 2. Virtually all the measurements of the Ciscaucasian mice are smaller than those of the Transcaucasian ones. On this background considerable differences are found in the Transcaucasian population, too. House mice from the western Transcaucasus show a greater ear length and interorbital distance than those from the eastern Transcaucasus. In general, occidental specimens appear rougher than oriental *M. praetextus*, largely due to a thick tail and massive skull.

Table 2. Measurements of main characters of the skull and body in three house mice species

Characters	Species		
	<i>M. musculus</i> Northern Caucasus	<i>M. domesticus</i> Adjaria	<i>M. praetextus</i> Azerbaijan
Length of body (mm)	78.8 ± 1.11	81.7 ± 1.34	80.3 ± 1.15
Length of tail (mm)	64.4 ± 2.18	81.4 ± 2.24	75.0 ± 1.58
Length of foot (mm)	15.9 ± 0.11	16.9 ± 0.12	16.9 ± 0.10
Height of ear (mm)	13.0 ± 0.1	14.4 ± 0.14	13.8 ± 0.22
Relative length of tail (%)	82.0 ± 2.0	100.0 ± 3.10	93.0 ± 2.0
Condylbasal length (mm)	20.0 ± 0.16	20.7 ± 0.24	20.6 ± 0.19
Length of foramina incisiva (mm)	4.8 ± 0.08	4.9 ± 0.06	4.9 ± 0.08
Length of upper molars (mm)	3.2 ± 0.02	3.2 ± 0.02	3.3 ± 0.04
Infraorbital width (mm)	3.6 ± 0.05	3.7 ± 0.04	3.4 ± 0.03

The traditional shape of the masseteric plate is used as a diagnostic character of house mice species (MARSHALL 1977; ORSINI et al. 1983; KRAFT 1984; KRATOCHVIL 1986). In the Central Asian house mice species *M. bactrianus* (= *M. praetextus*), the anterior edge of the plate is round, while specimens of *M. domesticus* have the shape of a protruding angle, and in *M. musculus* the anterior edge is slightly a rounded or angular in shape. A comparative analysis of this morphological characteristic of Transcaucasus house mice and *M. musculus* from North Caucasus and Ukraine, *M. domesticus* from Germany, and *M. praetextus* from Syria (Fig. 7) indicates that the western Transcaucasian mice have a masseteric plate most similar to that of European *M. domesticus*. House mice from eastern Transcaucasus have a rounded plate outline, similar in shape to that of *M. bactrianus* (= *M. praetextus*).

A notable morphological characteristic of *M. domesticus* is the pattern of an occlusal surface of the first lower molar (ORSINI et al. 1983; KRAFT 1984). Of all transcaucasian mice analysed by electrophoresis, only some individuals from Georgia demonstrated the occlusal surface of M_1 , in shape similar to that of *M. domesticus* (Fig. 8). The remainder of the mice from the region shows patterns usual for *M. musculus*. The populations of *M. musculus* from the northern Caucasus demonstrate a pattern typical for this species.

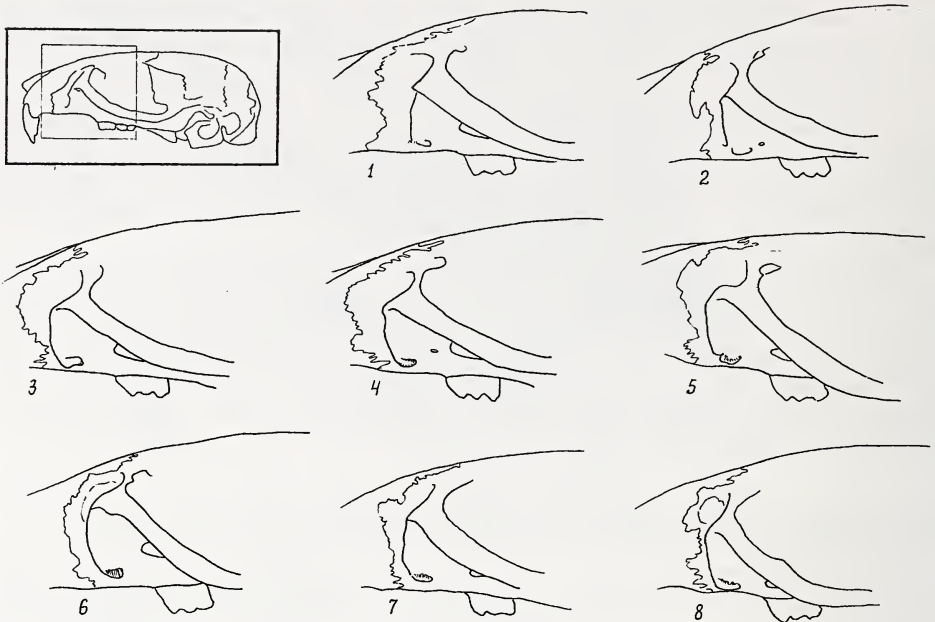


Fig. 7. Shape of masseter plates in house mice from different regions (collection of Zoological Museum of the Institute of Zoology, National Academy of Sciences of the Ukraine). *M. domesticus*: 7: Germany (No 10031); 8: Germany (No 10032); 5: Georgia (No 700); *M. praetextus*: 3: Syria (No 10033); 4: Syria (No 10030); 6: Azerbaijan (No 437); *M. musculus*: 1: Ukraine, Kiev (No 33); 2: Ukraine, steppe region.

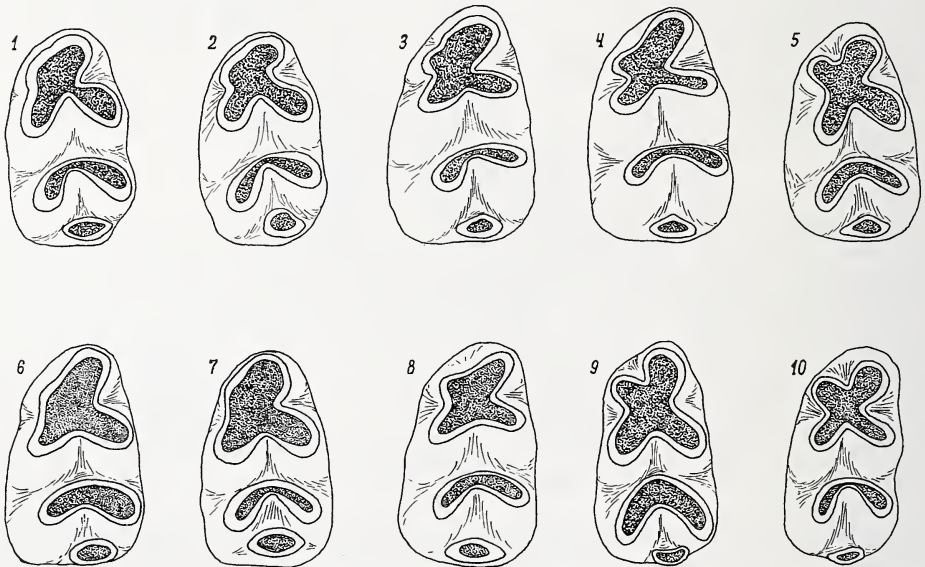


Fig. 8. Variation of M_1 occlusal surface in house mice from different regions (collection of the Zoological Museum of Institute of Zoology, National Academy of Sciences of the Ukraine): *M. domesticus* 1: Germany (No 10031); 2: Germany (No 10032); 6: Georgia (No 557); 7: Georgia (No 558); 8: Georgia (No 700); *M. praetextus* 3: Syria (No 10033); 4: Syria (No 10030); 5: Azerbaijan (No 436); *M. musculus* 9: Ukraine, Kiev (No 13); 10: Ukraine, steppe region (No 33).

Generalisation of geographic variation data according to climatic zones

In the occidental part of the Transcaucasus with a moist subtropical climate, where genes of *M. domesticus* predominate, house mice are characterised by dark bellies, sometimes with white spots, and by tails equal or longer than heads and bodies together, while in the oriental Transcaucasus, with a climate similar to dry subtropics, populations of white-bellied and rather long-tailed mice occur with a relatively high level of *M. domesticus* genes. Typical *M. musculus* populations dwell in continental steppe regions of the Ciscaucasus. These mice have all morphological and genetic characteristics inherent to this species. The climate of Daghestan is intermediate between the Cis- and Transcaucasus. The gene pool of these populations is practically identical to *M. musculus*, but some specimens have certain morphological features (mainly the tail length and belly colouration) typical for *M. domesticus*.

Discussion

Taxonomy of Caucasus house mice

High frequency of alleles $Es-1^{98}$, $Es-2^{103}$, $Idh-1^{95}$, large body size, relatively long tail, belly colouration, and some cranial features of the house mice dwelling in the Transcaucasus prove their identity to southern house mice species (*M. domesticus* or *M. praetextus*).

The sharp contrast between mice dwelling in the eastern and western parts of the Transcaucasus indicates the existence of two southern house mice species in this region. There are also two forms occurring in the Transcaucasus. Specimens of the occidental form, *M. m. formosovi* Heptner, 1930, are characterised by: large body size; dark belly and back with albino spots, and lacking a distinct borderline of colouration; usually tail longer than head and body, long feet and ears; fairly massive skull with a wide interorbital space; masseter plate in the angular form. In some mice from the most southern localities a characteristic three looped pattern on the occlusal surface of the M_1 was found. All of these features confirm the identity of *M. m. formosovi* to *M. domesticus*. In the Caucasus region it occurs in Georgia, Armenia and penetrates into Daghestan. The second geographic form is traditionally identified in Transcaucasus under different names, such as: *M. m. bactrianus* Blyth, 1846 (SATUNIN 1905), *M. m. tataricus* Satunin, 1909 (HEPTNER 1930; ARGIROPULO 1940; VERESCHAGIN 1957), or *M. m. praetextus* (SHIDLOVSKY 1976). It is a large white-bellied mouse with a tail length, equalling to that of head and body, large hind feet, and moderate ear lengths. The skull is not massive, the interorbital space is of intermediate width, and the masseter plate is round in shape. It mainly occurs in Azerbaijan steppes.

Mice living in Ciscaucasus and, probably in some semidesert and mountainous regions of the Transcaucasus, were identified as *M. m. wagneri* Eversmann, 1848 by SATUNIN (1905); *M. m. hortulanus* Nordmann, 1840 by ARGIROPULO (1940), and VERESCHAGIN (1957), and *M. m. musculus* by SHIDLOVSKY (1976). The specimens can be characterised by: a rather small body size; grey or white belly contrasting with the back; short tail (60–90%) and feet; and small ears. The skull has a small size, narrow interorbital width, an angular or slightly rounded masseteric plate. The occlusal surface of M_1 has a four looped pattern.

The *M. musculus*–*M. domesticus* hybrid zone

As noted above (MILISHNIKOV et al. 1990), the main peculiarity of the Transcaucasian hybrid zone consists in an unusually great extent of introgression of *M. musculus* and *M. domesticus*. While in Europe the hybridisation zone does not exceed several dozens

kilometres (HUNT and SELANDER 1973; KRAFT 1984; VANLERBERGHE et al. 1988), in the Transcaucasus it is more than several hundred kilometres. In this case, it is quite probable, that the geographic distribution of *M. musculus* genes is not limited by the border of the former USSR but extends still farther south throughout Asia Minor to the Mediterranean, where they are regularly recorded at low frequencies (THALER et al. 1981; BRITTON-DAVIDIAN 1990).

The distribution of individuals morphologically identical with *M. domesticus*, and having genes inherent to this species, is limited within the territory of the former USSR to the Transcaucasus, since in the north of the Great Caucasian Ridge genetically and morphologically homogeneous *M. musculus* populations occur. A sharp boundary in the distribution is most likely due to climatic transition from the subtropics of the Transcaucasus to the continental steppe regions of the northern Caucasus. Thus, climatic boundaries in this region determine the subdivision of superspecies *M. musculus* s.l. into the southern forms *M. domesticus* and *M. praetextus* and the northern *M. musculus*. While the northern species is homogeneous genetically and morphologically, the southern forms represent a complicated hybrid complex, including genes of both *M. musculus* and *M. domesticus*. Thus, in this region there is no clear subdivision into *M. musculus* and *M. domesticus* as in the case of Europe. It should be emphasised that this boundary is not only geographical, passing along the Great Caucasus but rather climatic. This is confirmed by penetration of *M. domesticus* genes into southern Daghestan, where the climate is similar to subtropical, and by penetration at the biochemical level of homogeneous *M. musculus* specimens (FRISMAN et al. 1990) to eastern Azerbaijan on the Apsheron Peninsula, in the region with dry continental climate.

The geographical distribution of different house mice species in the Transcaucasian region supports the importance of climatic borders (KLEIN et al. 1987) in the determination of house mice areas and attachment of *M. musculus* to continental regions and *M. domesticus* to moist ones, similar to subtropical conditions.

The *M. domesticus*–*M. praetextus* hybrid zone

The presence of grey-bellied mice in the Central Transcaucasus, sharply contrasting in colouration with occidental dark-bellied and oriental white-bellied forms, indicates hybridisation of *M. praetextus* and *M. domesticus*. In this case the hybrid zone is also not limited by several dozens kilometres, since grey-bellied long-tailed mice occur not only in the Central Transcaucasus (the border of Georgia and Azerbaijan in this case), but also in the south of Azerbaijan (in the Lenkoran). In this region fairly dark-bellied mice live along with white-bellied. This fact is due to penetration of *M. domesticus* along the mountaineous regions of the Small Caucasus or, presumably, their import by man.

Analysis of habitat preferences resulted in the following. As compared with *M. praetextus*, *M. domesticus* (*M. m. formosovi*) is more closely connected in the Transcaucasus with human structures (SHIDLOVSKI 1976), which accounts for its penetration throughout the Great Caucasus and Daghestan. *M. praetextus* is an indigenous form, dwelling mostly in steppe landscapes (SHIDLOVSKI 1976). It is distributed in Azerbaijan, where there are true steppes. Thus, each of the species is associated with its own habitat: *M. domesticus* is a synantropous form, living in the immediate vicinity of human houses, and *M. praetextus* is a more indigenous steppe form, which presumably penetrated from Iran, where similar specimens inhabit natural landscapes (SCHWARTZ and SCHWARTZ 1943), similar to Azerbaijanian ones. Hence, in contrast to the *M. musculus*–*M. domesticus* species, the *M. domesticus*–*M. praetextus* introgression zone is stabilised by landscape-biotopical factors.

Comparative characteristics of European and Asian hybrid zones

On the basis of biochemical genetical studies of both European and Asian hybrid zones, it was possible to analyse the structure and genetic processes in these zones in detail.

The European zone is a result of hybridisation of two species, *M. domesticus* and *M. musculus*. Its width is approximately a few dozen kilometres and does not exceed 50 kilometres (SELANDER et al. 1969; KRAFT 1984; VANLERBERGHE et al. 1986, 1988; NANCE et al. 1990). There is a tendency toward limitation of hybridisation in the European zone. Thus, a previous study showed that mitochondrial DNA introgression occurs in one direction only, that is from *M. musculus* to *M. domesticus* (VANLERBERGHE et al. 1988). Moreover, it has been shown (VANLERBERGHE et al. 1986, 1988; NANCE et al. 1990) that no chromosome introgression occurs. There has been a direct observation supporting assortive breeding in hybrid *M. musculus* and *M. domesticus* species performed in Bulgaria (VANLERBERGHE et al. 1988; NANCE et al. 1990). This has been confirmed by heterozygous deficit at diagnostic loci.

Hybridisation in the Transcaucasus takes place among three parapatric species, *M. musculus*, *M. domesticus*, and *M. praetextus*. The width of this hybrid zone is more than several hundred kilometres. This circumstance transformed it from a hybrid zone into a zone of gene introgression. There is a narrow transitional zone along the Great Caucasus between the homogeneous Ciscaucasus *M. musculus* populations and the Transcaucasus zone of gene introgression. This border between the zone of hybridisation and homogeneous *M. musculus* populations corresponds well to the subdivisions by climatic zones. Thus, specimens of the northern species dwell in drier and more continental re-

Table 3. Comparative characteristics of hybrid house mice zones of Europe and Asia

Characteristics	Hybrid zones		
	Europe	Transcaucasus	Eastern Asia
Hybridising species	<i>M. musculus</i> – <i>M. domesticus</i>	<i>M. musculus</i> – <i>M. domesticus</i> – <i>M. praetextus</i>	<i>M. musculus</i> – <i>M. castaneus</i>
Width of hybrid zone	not more than 50 kilometres	more than 300 kilometres	more than 1 000 kilo- metres in latitude
Expressiveness of border between hybrid zone and parental species	border is well- expressed	only the border be- tween <i>M. musculus</i> and introgression zone	sharp transition between parental species and hy- brid zone is absent
Intrapopulation mechanisms limiting interbreeding	present	not found	absent
Correspondence geography of hybrid zone to climate borders	<i>M. musculus</i> dwells in drier continental regions while <i>M. domesticus</i> prefers moister regions with oceanic climate	accumulations of <i>M. domesticus</i> genes and morphological fea- tures take place in sub- tropical regions	higher concentrations of <i>M. castaneus</i> genes and expressiveness of some morphological features are observed in warmer and moister climate
Possible mechanisms of hybrid zone stability	first of all, there are biological barriers	climate factors, biologi- cal barriers are unknown	only climatic factors
General characteristics	typical hybrid intro- gressive zone between parapatric species	complicated formation which is not presented by classical narrow hybrid zone	gradual transitional zone between two species identified at biochemical gene level

gions while specimens with genes and morphological characteristics of southern forms occur only in subtropical regions. No tendencies toward limitation of gene flow in the Transcaucasus between specimens of the three species were found.

Gene introgressions between the eastern Asian house mouse form *M. castaneus* and the northern Palearctic *M. musculus* have been found in Japan (BONHOMME et al. 1989) and in some parts of the Russian Far East (FRISMAN et al. 1990), initially in the Vladivostok region (FRISMAN and KOROBITSINA 1990). The estimated width of introgression zones was at least three hundred kilometres. These observations were confirmed by morphological investigations also. Thus, in the Russian Far East localities, where alleles of *M. castaneus* predominate, specimens are characterised by a long tail and "castaneus"-like belly coloration (FRISMAN et al. 1990). The geographical distribution of house mice species in eastern Asia (BONHOMME 1986) and data concerning the localisation of the hybrid zone suggest that the zone of gene introgression in a North-South direction between *M. castaneus* and *M. musculus* can be more than one thousand kilometres wide.

Comparison of hybrid zone biological peculiarities confirms significant differences in structure of European and Asian hybrid zones, especially, in their sizes. So, in Europe the *M. musculus* – *M. domesticus* hybrid zone width does not exceed some tens kilometres. In the Transcaucasus, where hybridisation takes place between *M. musculus*, *M. domesticus*, and *M. praetextus*, it is more than 300 hundred kilometres. In eastern Asia the interstitial zone between *M. musculus* and *M. castaneus* most probably is more than one thousand kilometres. Therefore, the concept of narrow hybrid "zone" is not appropriate for Asian territories. Actually, these are zones of gradual transitions between the above-mentioned species. It can be characterised by gradual changing of the gene frequencies and intermediate morphological features of specimens according to climate.

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Zusammenfassung

Die Hybridzone der Hausmäuse Mus musculus s.l. in Transkaukasien

Die Hybridzone der Hausmausarten in Transkaukasien wird auf der Grundlage von Allozymdaten und morphologischen Merkmalen beschrieben. Es wird aufgezeigt, daß die Hybridzone in Transkaukasien von drei parapatrischen Arten gebildet wird: *M. musculus*, hauptsächlich im Nordkaukasus beheimatet, *M. domesticus*, die vom westlichen Transkaukasien bis zum östlichen Kaukasusvorland zu finden ist und *M. praetextus*, weit verbreitet in den Steppen Aserbaidshans. Wesentliche Besonderheiten dieser Hybridzone sind: 1) die ungewöhnliche Ausdehnung der Zone der Genintrogressionen; sie umfaßt das gesamte Transkaukasien; 2) die schmale Grenze zwischen *M. musculus* und der Zone der Genintrogressionen zwischen *M. musculus*, *M. domesticus* und *M. praetextus*, die sich entlang der Klimagrenze zwischen der kontinentalen und subtropischen Region erstreckt und 3) das Vorhandensein einer Übergangszone zwischen *M. praetextus* und *M. domesticus* in Zentraltranskaukasien. Die gewonnenen Ergebnisse werden im Vergleich mit den Besonderheiten der Hybridzonen in Europa und Ostasien dargestellt. Der Schwerpunkt liegt dabei auf zwei wesentlichen Besonderheiten der Hybridzonen Europas und Asiens, ihrer nach europäischen Maßstäben ungewöhnlichen Breite und ihrer Lokalisierung in Gebieten mit nahezu subtropischem Klima.

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