

Hybrid zones of house mice of genus *Mus* (Rodentia, Muridae) in Russia and neighbouring countries: role of hybridisation in evolution of commensal taxa

Elena V. Kotenkova

ABSTRACT. The significance of hybridisation in the evolution and diversification of commensal taxa of *Mus musculus* s.l. species group is discussed. Allozyme analysis has shown that Transcaucasian populations of commensal house mice possess an admixture of *musculus* and *domesticus* genes. This region is either a zone of secondary contact between *musculus* and *domesticus*, with very wide introgression of *domesticus* genes into the genome of *musculus*, or these are relict populations descended from non-differentiated forms with ancestral polymorphism. The main feature of this zone is the unusually large extent of *domesticus* genes, which occur throughout the entire Transcaucasia (about 350 000 km²). Data and observations favour the view suggest that Transcaucasian house mouse populations are relicts of an early-differentiated form of *M. musculus*, preserving much of the ancestral gene pool. The second possible hypothesis is that populations of Transcaucasia are result of hybridisation of ancient not finally differentiated forms of house mice. It is possible that ancient “oriental” lineage and ancient form of *musculus* were colonised the Transcaucasia and mixed in this territory. The Adzharian populations would then be a product of contact between these forms and early of fully differentiated *M. domesticus* from Turkey. Large zones of hybridisation are present also in other regions of Asia. Analysis of hybrid populations of house mice in Russia demonstrates the particular significance of hybridisation in the evolution of commensal taxa. This enhanced role in commensals is linked to their unique ability to expand their geographic ranges through human agency and even survive as commensals in areas that are beyond their physiological tolerance.

KEY WORDS: hybridisation, *Mus musculus* species group, commensalism, hybrid zones

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Зоны гибридизации домовых мышей рода *Mus* (Rodentia, Muridae) России и сопредельных территорий: роль гибридизации в эволюции синантропных таксонов

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РЕЗЮМЕ. Обсуждается значение гибридизации в эволюции и разнообразии синантропных домовых мышей группы видов *Mus musculus* s.l. Анализ аллозимов показал, что для популяций синантропных домовых мышей Закавказья характерно наличие генов как *musculus*, так и *domesticus*. В этом регионе находится либо зона вторичного контакта между *musculus* и *domesticus* с широкой интродукцией генов *domesticus* в геном *musculus*, либо популяции Закавказья представляют собой реликтовые популяции до конца не дифференцированных предковых форм, сохранивших высокое генетическое разнообразие. Характерная черта этой зоны – относительно равномерное распределение генов *domesticus* по большой территории (около 350 000 км²). Ряд данных подтверждают точку зрения, согласно которой популяции Закавказья представляют собой реликтовую форму, близкую к *Mus musculus*, сохранившую предковый генетический пул. Вторая возможная гипотеза — популяции Закавказья представляют собой результат гибридизации древних до конца не дифференцированных форм домовых мышей. Возможно, Закавказье было колонизовано двумя формами: “oriental” и *musculus*, которые скрещивались в этом регионе. Популяции Аджарии, возможно, возникли в результате гибридизации этих форм и ранней уже дифференцированной формой *domesticus* из Турции. Большие по площади зоны гибридизации обнаружены в других регионах Азии. Анализ гибридных популяций домовых мышей России демонстрирует особую важность гибридизации в эволюции синантропных таксонов. Такая существенная роль гибридизации в эволюции синантропных таксонов домовых мышей объясняется их уникальной способностью расширять ареал, расселяясь с помощью человека, и даже выживать благодаря синантропному образу жизни в регионах, где их существование в природе невозможно из-за климатических условий.

КЛЮЧЕВЫЕ СЛОВА: гибридизация, группа видов *Mus musculus*, синантропия, зоны гибридизации.

Introduction

The process of speciation, the significance of introgressive hybridisation in the evolution and diversification of mammals are important problems of evolutionary theory. The *Mus musculus* s.l. species group includes closely related taxa in different stages of divergence: sympatric species (*Mus musculus* Linnaeus, 1758 – *M. spicilegus* Peternyi, 1882; *M. domesticus* Schwarz & Schwarz, 1943 – *M. macedonicus* Petrov & Ruzic, 1983; *M. domesticus* – *M. spretus* Lataste, 1883); parapatric taxa which hybridise in zones of their contact (*M. musculus* – *M. domesticus* – *M. castaneus* Waterhouse, 1842) and allopatric species (*M. spicilegus* – *M. macedonicus* – *M. spretus*) (Thaler *et al.*, 1981; Bonhomme *et al.*, 1984; Sokolov *et al.*, 1990; Boursot *et al.*, 1993; Sage *et al.*, 1993). As a result the *Mus musculus* s.l. has served as model group in studies of microevolution (Boursot *et al.*, 1993; Sage *et al.*, 1993). In addition, this species group has been valuable in studies concerning of precopulatory isolating mechanisms and their formation in phylogenetic ontogenesis (Kotenkova & Naidenko, 1999). It was demonstrated two large divergent groups in *Mus musculus* s.l. (Boursot *et al.*, 1993; Sage *et al.*, 1993). The first ones includes commensal genetic groups: *M. m. musculus*, *M. m. domesticus*, and *M. m. castaneus*. One approach is to give them subspecies status (Boursot *et al.*, 1993). The alternative approach is to classify all genetic groups as species: *M. musculus*, *M. domesticus*, and *M. castaneus* and after Sage *et al.* (1993) we consider these as distinct species. One of the reasons of such classification consists of high morphological and in part chromosomal polymorphism of *M. musculus* (Kotenkova, 2000, 2003). According to many authors *M. musculus* includes subspecies well distinguished on the bases of external morphology, morphology of chromosomes and cranial morphology (*M. m. wagneri* Evermann, 1948, *M. m. raddei* Kastchenko, 1910, *M. m. musculus* and some other — Argiropulo, 1940; Vinogradov & Gromov, 1952; Lavrenchenko, 1994; Yakimenko *et al.*, 2000). Commensal taxa of *Mus musculus* s.l. species group hybridise in zones of their contacts. There is a narrow 16–50 km wide zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central Europe, a well-studied “tension zone” of secondary contact (Boursot *et al.*, 1993; Sage *et al.*, 1993).

Intensive systematic studies, involving the investigation of allozyme variation and morphological analysis of both genetically marked individuals and other museum specimens have revealed three species of the genus *Mus* in the territory of the former Union of Soviet Social Republics (USSR). One is commensal (*Mus musculus*), while two are free-living (*M. spicilegus* and *M. macedonicus*) (Mezhzherin & Kotenkova 1989, 1992; Frisman *et al.*, 1990). Some populations of house mice had high levels of genetic polymorphism, sometimes extending across large zones (e.g. Transcaucasia, Primorski Territory, Tuva, and Transbaikalia) (Mezhzherin *et al.*, 1994, 1998; Yakimenko *et al.*, 2000).

The aims of this work are (i) evaluation of the interdependence of commensalism and hybridisation in evolution of *Mus musculus* s.l. species group, (ii) revision and discussion of origin of commensal Transcaucasian populations of house mice possessing high levels of genetic variability.

Origin of Transcaucasian Populations of House Mice

1. Protein polymorphism

Allozyme analysis has shown that Transcaucasian populations of commensal house mice possess an admixture of *musculus* and *domesticus* genes (Mezhzherin & Kotenkova, 1989; Milishnikov *et al.*, 1990; Mezhzherin *et al.*, 1998). This region is either a zone of secondary contact between *musculus* and *domesticus*, with very wide introgression of *domesticus* genes into the genome of *musculus* (Mezhzherin & Kotenkova, 1989; Frisman *et al.*, 1990; Mezhzherin *et al.*, 1994, 1998), or these are relict populations descended from non-differentiated forms with ancestral polymorphism (Milishnikov *et al.*, 1990). The main feature of this zone is the unusually large extent of *domesticus* genes, which occur throughout the entire Transcaucasia (about 350 000 km²) (Mezhzherin *et al.*, 1998).

Within the last decade much progress has been made in the study of populations of the *M. musculus* species group in India and Pakistan (Boursot *et al.*, 1996; Din *et al.*, 1996). Populations of house mice from the northern part of the Indian subcontinent are more heterozygous than samples from any other regions. They also contain the majority of the alleles that exist in the various differentiated species at the periphery of the wider geographic range of the group. According to a neighbour-joining analysis using Nei's genetic distances, and a factorial correspondence analysis of allelic composition, the Pakistanian and Indian populations occupy a genetically central position with respect to the peripheral species. Boursot *et al.* (1996) and Din *et al.* (1996) interpreted these results as a retention of ancestral genetic polymorphism and identified northern India as possible cradle of this commensal species. *Mus musculus* and *M. domesticus* lineages probably started to differentiate a few hundred thousand years ago in isolated mountain areas, and they may have colonised the peripheral parts of their ranges only recently. In a related publication Orth *et al.* (1996) reiterated the view that the Transcaucasian region is a zone of secondary contact between *M. musculus* and *M. domesticus*. However, a hybrid origin of Transcaucasian populations of house mice is doubtful in the light of some facts, which will be discussed below.

In Transcaucasian populations of commensal house mice allozyme variation were studied in whole by different investigators in more than 200 individuals (Mezhzherin & Kotenkova, 1989, 1992; Milishnikov *et al.*, 1990; Frisman *et al.*, 1990; Mezhzherin *et al.*, 1992, 1994, 1998; Orth *et al.*, 1996). On the basis of these data

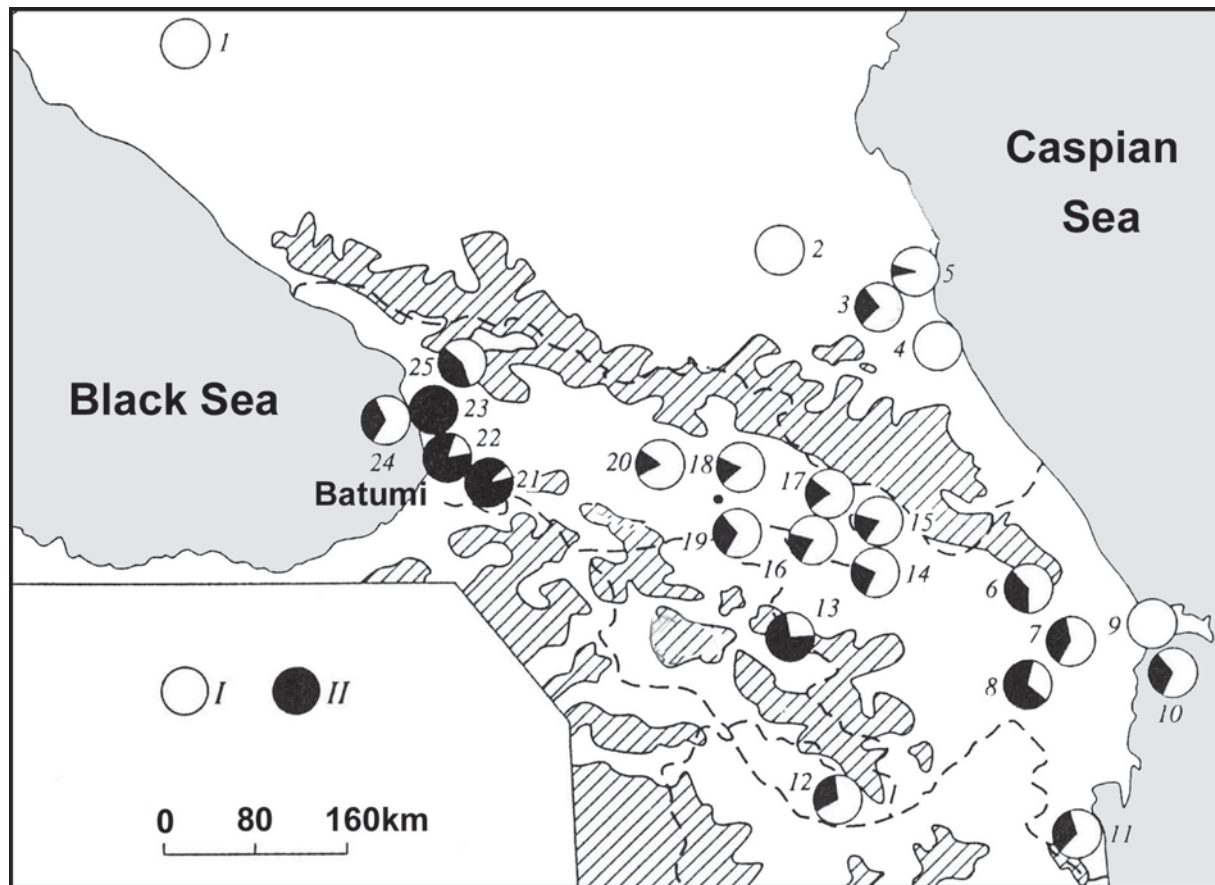


Figure 1. Geographic distribution of “*musculus*” and “*domesticus*” alleles in Transcaucasia. I — “*musculus*” alleles, II — “*domesticus*” alleles.

1 — Viselkovskii District, Krasnodar Territory, n=8 (Mezhzherin *et al.*, 1992, 1998); 2 - city Grozny, n=7 (Frisman *et al.*, 1990); 3 — coast of Sulak River, Dagestan, n=5 (Mezhzherin *et al.*, 1992, 1998); 4 — coast of Caspian Sea, Dagestan, n=2 (Mezhzherin *et al.*, 1998); 5 — city Makhachkala, Dagestan, n=3 (Milishnikov *et al.*, 1990; Rafiev, 1990); 6 — village Ismaili, Azerbaijan, n=4 (Mezhzherin *et al.*, 1998); 7 — village Eshindibi, Azerbaijan, n=10 (Mezhzherin & Kotenkova, 1989; 1992; Mezhzherin *et al.*, 1992, 1994, 1998); 8 — Azerbaijan, n=5 (Mezhzherin *et al.*, 1998); 9 — city Baku, Azerbaijan, n=20 (Milishnikov *et al.*, 1990; Rafiev, 1990); 10 — Apsheron Peninsula, n=6 (Frisman *et al.*, 1990); 11 — Lenkoran' District, Azerbaijan, n=7 (Rafiev, 1990); 12 — Megri, Armenia, n=13 (Orth *et al.*, 1996); 13 — Armenia, n=8 (Mezhzherin *et al.*, 1998); 14 — Vashvalan, Georgia, n=5 (Orth *et al.*, 1996); 15 — Didich-Chiragui, Georgia, n=4 (Orth *et al.*, 1996); 17 — Lagodehi, Georgia, n=13 (Orth *et al.*, 1996); 18 — Lissy, Georgia, n=4 (Orth *et al.*, 1996); 19 — city Tbilisi, Georgia, n=4 (Orth *et al.*, 1996); 20 — Gori, Georgia, n=7 (Orth *et al.*, 1996); 21 — Helvachaury, Georgia, n=7 (Orth *et al.*, 1996); 22 — Botanical garden of Batumi, Adzharia, n=12 (Mezhzherin & Kotenkova, 1989, 1992; Mezhzherin *et al.*, 1994, 1998); 23 — Kobulety, Adzharia, n=4 (Mezhzherin *et al.*, 1998); 24 — Kobulety, Adzharia, n=32 (Rafiev, 1990); 25 — Gantiadi, Abkhazia, n=7 (Orth *et al.*, 1996).

geographic distribution of “*musculus*” and “*domesticus*” genes in Transcaucasian populations of commensal house mice were reconstructed (Fig. 1). Authors investigated different number of allozymes and these evaluations can be modified in the case of other set of diagnostic loci for *musculus* and *domesticus*, but it is possible to assume that gene distribution presented in Fig. 1 is adequate real situation. There are no good pronounced genetic gradient suggesting introgression of *domesticus* genes from the west to the east of Transcaucasia, but in south-western Georgia (Batumi, Kobulety) house mice possess predominantly *domesticus* genotype. Populations of Transcaucasia contain some alleles that are not found in peripheral populations of *M. musculus* and *M. domesticus*. Allele Pgm-2¹²⁰ was found only in Transcaucasia (Orth *et al.*, 1996), Pakistan and Deli popula-

tions (Din *et al.*, 1996). According to Milishnikov *et al.* (1990, 1994) and Rafiev (1990) in populations of Transcaucasia were found five alleles (Got-1⁸⁰, Gsr⁷⁰, Mod-2¹²⁵, Np-1⁸⁵, Pgd¹²⁵), which were found also only in population of *M. musculus* from Middle Asia with low frequency. In whole different authors investigated allozyme variation (21–34 loci) in 12 samples (n=77) from Turkmenistan, three samples from Uzbekistan (n=44) and two samples (n=22) from Tajikistan (Frisman *et al.*, 1990; Mezhzherin *et al.*, 1992; Milishnikov *et al.*, 1994). Morphologically these mice were detected as *Mus musculus wagneri* Eversmann, 1948. They were short-tailed; colour of back was pale straw; colour of belly was pure white or whitish; border between coloration of back and belly is distinct (Frisman *et al.*, 1990; Mezhzherin *et al.*, 1992; Milishnikov *et al.*, 1994). Alleles of diagnostic

loci in house mice of this territory correspond to *M. musculus* and mice from Middle Asia were similar to those from European part of Russia (Frisman *et al.*, 1990; Mezhzherin *et al.*, 1992). In two samples (n=5) from Turkmenistan Prager *et al.* (1998) detected only B allele in *Zfy-2*, along with only *musculus* mtDNA. Middle Asian populations showed high levels of genetic diversity (Milishnikov *et al.*, 1994) and authors considered this fact as presumably related to their proximity to ancient centre of *M. musculus* origin. Some localities from Turkmenistan were not far from the east and south east coast of Caspian Sea. The presence of five alleles mentioned above in populations of Transcaucasia and Middle Asia support the idea of common origin of house mice of these territories. Boursot *et al.* (1996) suppose that *M. m. musculus* (= *M. musculus* according to our terminology) originated in Transcaucasia or east of the Caspian Sea. It is possible to suppose that the territory to the east of Caspian Sea can be the cradle of this species and ancient form of *musculus* could have colonised the Transcaucasia not only round the north (Boursot *et al.*, 1996), but also round the south cost of Caspian Sea. Probably the “oriental” lineage (according to terminology of Boursot *et al.*, 1996) colonised Transcaucasia from north of India other routes than ancient form of *musculus*. The presence in Transcaucasia *praetextus*-like phenotypes (see below) and *domesticus* alleles of diagnostic loci supports this possibility.

Transcaucasian sample from Kobulety (Adzharia) was the most numerous and includes 32 specimens (Milishnikov *et al.*, 1990; Rafiev, 1990). There was no found deficit of heterozygotes in this locality. The correspondence between expected and real frequency of heterozygotes of diagnostic loci were demonstrated in population of Kobulety. The fact supports the evidence of genetic balance in this population.

2. Morphology

Presence of at least two commensal forms of house mice has been traditionally recognised in the Transcaucasian region (Heptner, 1930; Argiropulo, 1940; Shidlovskii, 1947, 1958, 1976; Vereshchagin, 1959). They were the occidental dark-bellied mice *M. m. formosovi* (Heptner, 1930) and oriental white-bellied form identified by many authors as *M. m. praetextus*, *M. m. bactrianus*, and *M. m. tataricus*. In this work we use *M. d. praetextus*, because according to Marshall (1998) lectotype of *M. bactrianus* Blyth, 1946, described from Kandagar, Afghanistan, and holotype of *M. d. praetextus* Brants, 1827, described from Syria, do not differ and *M. bactrianus* should now be considered as synonym of *M. d. praetextus*. Revision of collections of genetically marked individuals and other museum specimens (collections of zoological museums of Moscow, St. Petersburg, Kiev and others) confirms this concept in general, although the patterns of variability of coloration and length of the tail have proven to be far more complicated (Mezhzherin *et al.*, 1994, 1998). Commensal popula-

tions of Transcaucasian house mice were divided into three phenotypes (Mezhzherin *et al.*, 1998): (i) phenotype *musculus* – not large mice, coat colour varies and can be gray, reddish or brownish, tail is shorter than body, they are distributed in northern parts of Caucasus and have diagnostic loci of *musculus*; (ii) phenotype *domesticus* – large, long-tailed, very dark, sometimes practically black mice with dark or black belly sometimes with albino sports, they are distributed in moist subtropics of Adzharia, central Georgia, some parts of Armenia and Dagestan; genotype is intermediate between *musculus* and *domesticus*; (iii) phenotype *praetextus* – large, long-tailed, white-bellied mice with light brown or red back, they are distributed in steppe regions of central Azerbaijan, genotype is intermediate between *musculus* and *domesticus*. External morphology of the house mice from Azerbaijan not differs from those of Syria (15 specimens from St. Petersburg Zoological Institute and two genetically investigated individuals; Mezhzherin *et al.*, 1998). There are also intermediate phenotypes in many localities of Transcaucasia.

Of all Transcaucasian mice analysed by electrophoresis, only some individuals from Georgia demonstrated the occlusal surface of m1, in shape similar to that of *M. domesticus*. The remainder of 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 (Mezhzherin *et al.*, 1998).

According to multiple-factor analysis of cranial morphology commensal populations of Transcaucasia are similar to *Mus musculus* from European part of Russia (Lavrenchenko, 1994). Author investigated more than 700 individuals (*M. m. musculus*, *M. m. wagneri*, *M. m. raddei*, *M. domesticus*, *M. m. bactrianus*, *M. spicilegus*, and *M. macedonicus*) of 32 samples from different localities of Russia, Bulgaria, Afghanistan, Mongolia, and Cuba.

3. Reproduction, exploratory and sexual behaviour in the light of concept of low fitness of hybrids

Traditionally hybridisation is considered as negative process because hybrids have genomic disruption and as result lower fitness than either parental genotypes. The European hybrid zone is considered a “tension zone” (Boursot *et al.*, 1993; Sage *et al.*, 1993). The “tension zone” model develops from a balance between the zone-widening effect of dispersal and the narrowing effect of negative selection on heterozygotes. Evidence that negative selection might be acting comes from increased loads of intestinal parasites in hybrids (Sage *et al.*, 1986; Moulina *et al.*, 1991) and unique variants of nonmetric skeletal traits from contact zone in Denmark (Schnell & Selander, 1981). According to our preliminary data Transcaucasian house mice reproduce in laboratory and the litter size is similar with litter size of *M. musculus*. There were no found any indications of lower fitness in

behavioural experiments. In pair encounters (male and oestrous female) on neutral territory Transcaucasian males try to copulate with intra- and interspecific females (Transcaucasian females, females of *M. musculus* and *M. spicilegus*) and were more active than males of *M. musculus* and *M. spicilegus* (Potanskyi & Kotenkova, 1992). In other experiment a comparative analysis of exploratory behaviour in different commensal taxa of the *Mus musculus* species group was conducted in a 4 x 4 x 1.5 m enclosure (Kotenkova *et al.*, 2003). The interior of the enclosure imitated a room with table, chair, plants, shoes and some other objects. The exploratory behaviour of the Transcaucasian house mice was more similar to that of *M. musculus* there being two significant differences with *M. musculus* from Moscow and only one difference with *M. musculus* from the Kerch Peninsula. They differed significantly from *M. domesticus* in four behavioural patterns. Previous experimental analysis of exploratory behaviour of commensal and free-living mice has demonstrated some differences in patterns of exploratory behaviour, which closely correlate with ecology and lifestyle of species (Kotenkova *et al.*, 2003). If exploratory behaviour in commensal and outdoor mice is an adaptation to their living conditions, and the Transcaucasian populations show similar patterns and strategy to differentiated commensal species, we can suppose that these results support the idea that Transcaucasian house mice are well adapted to commensal living conditions.

4. Are Transcaucasian house mice hybrids or not?

In summary, a hybrid origin of Transcaucasian populations of commensal house mice is doubtful in the light of following facts.

1. There are no clear genetic gradients suggesting introgression of *domesticus* genes from the west to the east of Transcaucasia (Fig.1).

2. In all populations of Transcaucasia (except southwestern Georgia) only “*musculus*” type of Y-chromosome has been found (Orth *et al.*, 1996).

3. Populations of Transcaucasia have allele (Pgm-2¹²⁰) that was not found in other populations of *M. musculus* and *M. domesticus* except populations of Pakistan and Deli (Din *et al.*, 1996; Orth *et al.*, 1996). Transcaucasian house mice have some alleles (Got-1⁸⁰, Gsr⁷⁰, Mod-2¹²⁵, Np-1⁸⁵, Pgd¹²⁵), that were found also only in populations of *M. musculus* from Middle Asia with low frequency (Rafiev, 1990; Milishnikov *et al.*, 1994). Only in Transcaucasia were found two alleles (Sod-1¹³⁰ in Adzharia and Me-1¹²⁰ in Baku) that were not found in populations of *M. musculus* and *M. domesticus* (Milishnikov *et al.*, 1990).

4. In population of Kobulety there was no found deficit of heterozygotes. The correspondence between expected and real frequency of heterozygotes of diagnostic loci was demonstrated for this population (Rafiev, 1990).

5. According to multiple-factor analysis of cranial morphology commensal populations of Transcaucasia (from Adzharia) are similar to *M. musculus* from European part of Russia (Lavrenchenko, 1994).

6. There were no found some facts supported lower fitness or lower fecundity of commensal Transcaucasian house mice (Potanskyi & Kotenkova, 1992; Kotenkova *et al.*, 2003).

7. In a comparative analysis of exploratory behaviour in eight populations of different species and subspecies of house mice, the Transcaucasian population was similar to populations of *M. musculus* (Kotenkova *et al.*, 2003).

These facts favour the point of view that populations of Transcaucasia are relicts of an early-differentiated form (presumably related to *M. musculus*), preserving much of ancestral gene pool. The second possible hypothesis is that populations of Transcaucasia are result of hybridisation of ancient not finally differentiated forms of house mice. May be ancient “oriental” lineage (according to terminology of Boursot *et al.*, 1996) and ancient form of *musculus* were colonised the Transcaucasia and mixed in this territory. This hybrid complex can exist and has own evolutionary development. The Adzharian population would then be a product of contact between these forms and ancient or modern *M. domesticus* from Turkey that was investigated by Gunduz *et al.* (2000). According to Prager *et al.* (1998) and Gunduz *et al.* (2000) in Turkey and Iran that adjacent with Transcaucasia *domesticus* and *castaneus* mtDNA patterns are distributed. This model can only be considered a working hypothesis.

The following facts support hybridisation of Transcaucasian house mice with one of the form *M. m. domesticus* in Adzharia: only in this region “*domesticus* genotype” (allozymes and mtDNA haplotypes) predominated (Mezhzherin *et al.*, 1994, 1998; Orth *et al.*, 1996; Prager *et al.*, 1998) and “*domesticus* type” of Y-chromosome (Orth *et al.*, 1996) was found; only in Adzharia were found mice with the occlusal surface of m1, in shape similar to that of *M. domesticus*. The remainder of mice from Transcaucasia show patterns *domesticus* and *musculus* mtDNA haplotypes followed more or less the allozymic transition (Orth *et al.*, 1996) and usual for *M. musculus* shape of m1 (Mezhzherin *et al.*, 1998).

Hybrid Zones of Eastern Asia

Large zones of hybridisation are present also in Asia. Genetic investigations of commensal house mice demonstrated large hybrid zones in the south of Primorskii Territory, Tuva and Transbaikalia (Frisman & Korobitsyna, 1990; Frisman *et al.*, 1990; Frisman *et al.*, 1990). According to Yakimenko *et al.* (2000) there are a minimum of three large hybrid zones in Primorskii Territory, Amur Province and Sakhalin. Investigation of allozyme variation, karyotypes and mtDNA support that *M. musculus* and *M. castaneus* hybridise in these territories (Korobitsyna *et al.*, 2000; Yakimenko & Korobitsyna, 2000). In Primorskii Territory have been found alleles typical for

domesticus. In whole it was demonstrated that the taxa involved in the formation of these hybrid zones are *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus*. The hybrid zone of Primorskii Territory is very young, dating to the last 30–40 years of the 19th Century at a time when the territory of Primorskii Territory was settled by people from Amur Province; the European part of Russia, Siberia, and China. In Primorskii Territory house mice can not live outside human houses, formation and structure of this hybrid zone was closely connected with their transition by people.

Hybrid Zones and Speciation

There are some different kinds of hybridisation in commensal taxa of house mice.

1. A narrow 16–50 km zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central Europe, a well-studied “tension zone” zone of secondary contact (Boursot *et al.*, 1993; Sage *et al.*, 1993).

2. Large zones of gene introgression in Asia between *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus* (Frisman & Korobitsyna, 1990; Frisman *et al.*, 1990; Yakimenko *et al.*, 2000).

3. Hybrid origin of *M. m. molossinus* of Japanese Islands (Yonekawa *et al.*, 1988), according to Sage *et al.* (1993) this is possible example of stabilised hybrid genome.

4. Hybrid origin of population at Lake Casitas, California, intermediate between *M. musculus* and *M. castaneus* (Orth *et al.*, 1998).

5. Hybridisation of different commensal taxa in large cities (Milishnikov, 1994; Milishnikov *et al.*, 1994). Allozyme variation of commensal mice in large cities (Brno, Moscow and Samarkand) was higher than in other populations.

It is possible to predict different ways of evolution in hybrid populations: stabilisation of hybrid genome, formation of pre-mating reproductive isolation arise between parental taxa because of reinforcement and “dedifferentiation” of closely related taxa. The analysis of different kinds of hybridisation supports the hypothesis of “dedifferentiation” (Mezhzherin *et al.*, 1994) and demonstrates that now this process really exists in commensal populations of house mice.

Analysis of hybrid populations of commensal house mice demonstrates the particular significance of hybridisation in the evolution of commensal taxa. This enhanced role in commensals is linked to their unique ability to expand their geographic ranges through human agency and even survive as commensals in areas that are beyond their physiological tolerance.

According to Golenishev & Malikov (2003) hybridisation can be important factor of evolution not only in commensal, but also in wild living rodents.

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