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THE ROLE OF INVASIONS IN EVOLUTION OF COMMENSAL TAXA OF *MUS MUSCULUS* SENSU LATO SPECIES GROUP

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One of most important evolutionary consequences of commensalisms and invasions in house mice is formation of hybrid zones of different kinds: a narrow 16-50 km wide zone of introgressive hybridization between *M. musculus* and *M. domesticus* in Central Europe, a well-studied "tension zone" of secondary contact; large complex hybrid zone in Trans-Caucasus – presumably hybrid events can occur here at different times and were "superposed" on gene pool of ancient autochtonous population; large zones of gene introgression in Asia between *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus;* hybridization of different commensal taxa in large cities. Formation of these hybrid zones were consequence of invasions of commensal taxa of house mice and colonization of new territories by human agency. These zones are absolutely different in term of time and history of their formation and role of humans. It is possible to predict different ways of evolution in hybrid populations: (i) stabilization of hybrid genome, (ii) formation of premating reproductive isolation arise between parental taxa and hybrid population because of reinforcement and (iii) "dediffirentitiation" of closely related taxa. The analysis of different kinds of hybridization supports the hypothesis of "dediffirentitiation".

Key words: house mice, invasions, hybridization, commensal species.

Introduction

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 and Schwarz 1943 – *M. macedonicus* Petrov and 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. spretus*, *M. macedonicus* and *M. spicilegus* [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 during 30 last years. On the other hand it was demonstrated two large divergent groups in *Mus musculus* s.l. [Boursot et al., 1993; Sage et al., 1993]. The one group includes the aboriginal wildliving species *M. spicilegus* – *M. macedonicus* – *M. spretus*. The other one includes commensal genetic groups: *M. m. musculus*, *M. m. domesticus*, *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, 2004]. According to many authors *M. musculus* includes subspecies well distinguished on the bases of external and cranial morphology, morphology of chromosomes, these subspecies have some taxon-specific RAPD-markers. Many of them distributed

on the territory of the f. USSR (*M. m. wagneri* Eversmann 1948, *M. m. gansuensis* Satunin 1903 (= *raddei* Kastschenko 1910), *M. m. manchu* Thomas 1909, *M. m. musculus* and some other – Argiropulo, 1940; Yakimenko et al., 2003; Spiridonova et al., 2008]. Commensal taxa of *Mus musculus* s.l. species group hybridize in zones of their contacts.

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 wildliving (*M. spicilegus* and *M. macedonicus*) [Mezhzherin, Kotenkova 1989]. It should be noted that in Trans-Caucasus *M. macedonicus* is sympatric with hybrid population of *M. musculus* and *M. domesticus*.

The aim of this review is evaluation of the importance of commensalisms and invasions by human agency in evolution of *Mus musculus* s.l. species group on the bases of own and literature data.

Two periods of house mice evolution

Within the last decade of the XX century much progress has been made in the search of ancestor populations and motherland of the commensal taxa of *M. musculus* species group. 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 Pakistani and Indian populations occupy a genetically central position with respect to the peripheral species. Din et al. (1996) interpreted these results as retention of ancestral genetic polymorphism and identified northern India as the probable cradle of commensal species. *M. musculus* and *M. domesticus* lineages probably started to differentiate a few hundred thousand years ago in isolated mountain areas, and they may have colonized the peripheral parts of their ranges only recently. By our opinion it is possible to divide evolutionary history of commensal species of *Mus musculus* s.l. species group in two main periods. The first one began after their differentiation and beginning of dispersal from northern India and continued up to their transfer to commensal species. The second period began after development of commensalism. At this time human press turned into one of the main factors of evolution of commensal species and its influence enhanced at the present stage. Here the main attention will be concentrated on the second period. According to opinion of J.Klein et al. (1987) and some other investigators *M. musculus* and *M. domesticus* began to associated with man independently in different ancient agricultural centers: in the near East and in China. According to opinion of other authors commensal *M. domesticus* began its coexistence with humans approximately 10 000 years ago on the territory of Israel. One of the main questions is: why *M. musculus* and *M. domesticus*, but not other species occupied new habitat of early human dwellings and became commensal? One explanation was suggested by Auffray et al. (1988). In Israel *M. macedonicus* lived from Middle Pleistocene, *M. domesticus* colonized Middle-East during the latest glacial period, 10 000 years ago. Representatives of *M. domesticus* could be in competition with *M. macedonicus* for outdoor environment and were excluded by *M. macedonicus* into newly created by man habitats. We analyzed the most part of available literature concerned of distribution and ecology of island populations of commensal taxa of house mice and concluded that these species occupied islands and live there with association of humans. In the case of invasion of the island by other rodent wildliving species it excluded house mice

from most parts of natural habitats up to their elimination. But house mice were more competitive than other small mammals in human dwellings. These data support the hypothesis of Auffray et al. (1988) and give us opportunity to suppose that after appearance of human dwellings in some situations house mice can be excluded from natural habitats by more competitive species of small mammals. But it is not enough to become commensal.

There are two alternative view points concerned of preadaptive behavior in commensal species. According one of them some ethological characters of commensal species can be preadaptations to man-made environment. According to other these characters are result of long evolution of mice during their cohabitation with man. We suggested the compromise hypothesis that some behavioral characters of commensal species from the one hand were preadaptations, but on the other hand they change in the course of evolution under human pressing. If idea of preadaptation will be rejected, it is very difficult to explain why just house mice but not other species of small mammals can occupy new habitat of early human dwellings and become commensal. Result of long evolution, because mice should continually adopt to human pressing. Commensal environment changed very quick, small houses were changed to multistory sky-scrapers. People worked out new methods of control for management of pest rodents. As result evolutionary changes and new adaptations of commensal species of house mice should be very effective and rather quick. One of the examples can be different strategy of exploratory behavior of commensal and wildliving taxa. In our previous comparative studies of exploratory behaviour in large enclosures with different interiors (including enclosures having many features in common with a human dwelling), commensal populations, from the one hand, outdoor populations of the same species and wildliving species of *Mus* from the other hand had different strategies for exploring their environment [Kotenkova et al., 1994]. Although commensal populations investigated the floor and practically all objects in the enclosure, outdoor populations and wildliving species investigated the floor and only some of the available objects. There were many other qualitative and quantitative differences between commensal and outdoor populations. These differences and adaptive character of exploratory behavior in genus *Mus* reviewed by Meshkova et al. (1994). From our previous results we conclude that strategy and some features of exploratory behaviour (number and character of upright postures, the pace, number and features of climbing, the number and type of contacts with different objects) were adaptations to commensal or outdoor living conditions. From the one hand, these behavioral adaptations can be result of long existence in very complex and unstable man-made environment. On the other hand some characters of exploratory behavior can be preadaptation to this environment.

M. domesticus is invasive and wide spread species and occupied now western Europe, northern Africa. It colonized by means of people also Australia, some parts of America and many islands. *M. musculus* is a widespread and polytypic commensal species found in Eastern Europe and Asia. Figure 1 demonstrated some parts of areas of some species of *Mus musculus* s. l. In Russia *M. musculus* colonized many parts of Sibiria and Primorski Territory during last two century.

It is possible to put one taxon after another according to decreasing of level of commensalism and ecological plasticity (Fig.2).

M. castaneus – earlier was considered as obligatory commensal species, but later it was demonstrated that really individuals of this species can establish also outdoor populations. *M. musculus* and *M. domesticus* can establish commensal and outdoor populations. Annual cycle of commensal species is different in different climatic conditions. For example *M. musculus* can live in human dwellings only

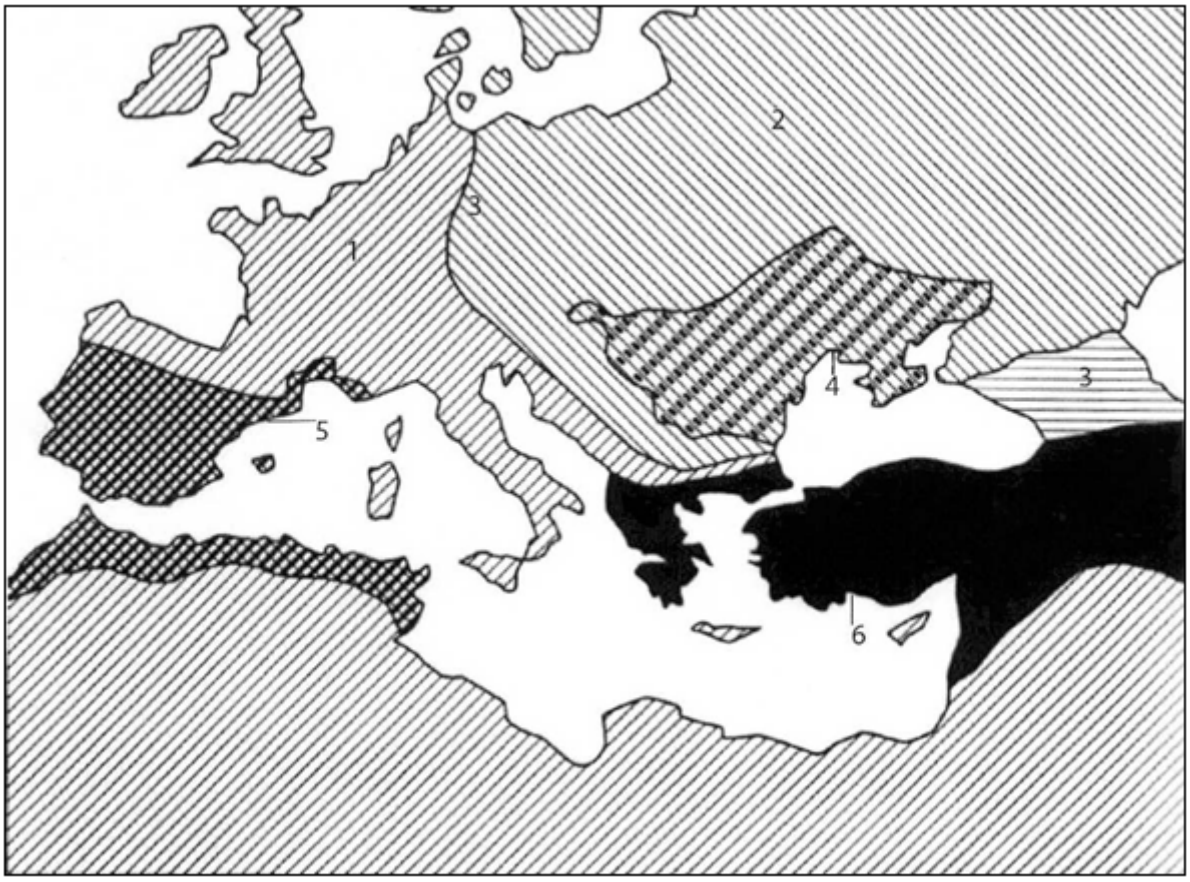

Fig.1. Ranges of commensal and wildliving species of *Mus musculus* s.l.
Legends: 1 – *M. domesticus*, 2 – *M. musculus*, 3 – hybrid zone of *M. musculus* and *M. domesticus*. Areas of sympatry: 4 – *M. musculus* and *M. spicilegus*, 5 – *M. domesticus* and *M. spretus*, 6 – *M. domesticus* and *M. macedonicus*.

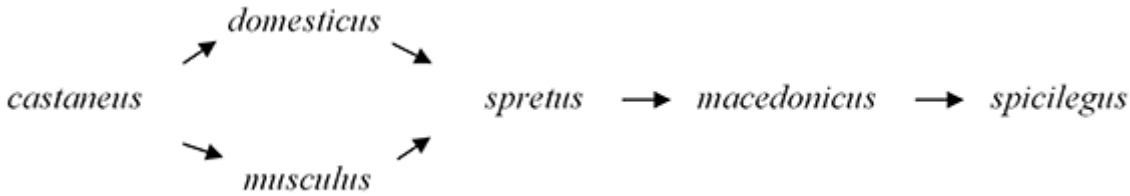

Fig.2. Decreasing of the level of commensalism and ecological flexibility of different species of *Mus musculus* sensu lato species group.

(in the north of the area), establishes permanent outdoor populations in summer and indoor populations in winter in cold-temperate zone or lives outdoor during all year in southern parts of the area. *M. spretus* is wildliving species, but sometimes can visit human dwellings, *M. macedonicus* and *M. spicilegus* are wildliving species and the last is well adopted to agroecosystems. A distinctive character of *M. spicilegus* is its grain-hoarding activity and construction of special mounds in which to store food and live for the winter.

Evolutionary consequences of commensalisms and invasions: Hybrid zones and speciation

Analysis of own and literature date concerned of investigations of hybrid populations of house mice support the point of view that hybridization have important role in evolution of house mice. There are some different kinds of hybridization in commensal taxa of house mice.

1. A narrow 16-50 km wide zone of introgressive hybridisation between *M. musculus* and *M. domesticus* in Central

Europe (Fig.1), a well-studied "tension zone" of secondary contact [Boursot et al, 1993; Sage et al., 1993].

2. Large complex hybrid zone in Trans-Caucasus (Fig.1) [Mezhzherin et al., 1998; Orth et al., 1996] – presumably hybrid events can occur here at different times and were "superposed" on gene pool of ancient autochtonous population [Milishnikov et al., 2004].

3. Large zones of gene introgression in Asia between *M. castaneus*, *M. domesticus* and various subspecies of *M. musculus* [Yakimenko et al., 2003].

4. Hybrid origin of *M. m. molossinus* of Japanese island [Yonekawa et al., 1988].

5. Hybrid origin of population at Lake Casitas, California, intermediate between *M. domesticus* and *M. castaneus* [Orth et al., 1998].

6. Hybridization of different commensal taxa in large cities [Milishnikov et al., 1994]. Allozyme variation of commensal mice in large cities (Brno, Moscow and Samarkand) was higher than in other populations.

Formation of these hybrid zones were consequence of invasions of commensal taxa of house mice and colonization of new territories by human agency. It is possible to predict different ways of evolution in hybrid populations: (i) stabilization of hybrid genome, (ii) formation of premating reproductive isolation arise between parental taxa and hybrid population because of reinforcement and (iii) "dediffirentitiation" of closely related taxa. The analysis of different kinds of hybridization supports the hypothesis of "dediffirentitiation" and demonstrates that now this process really exists in populations of commensal taxa.

Analysis of hybrid populations of commensal house mice demonstrates the particular significance of hybridization 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.

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