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Mammalian Cytogenetics and Its Contribution to the Development of Chromosomal Diagnoses and the Species System

V. N. Orlov[a], **E. A. Lyapunova**[b], **M. I. Baskevich**[a], **I. V. Kartavtseva**[c],
V. M. Malygin[d], **and N. Sh. Bulatova**[a, *]

[a] *Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia*
[b] *Koltsov Institute of Developmental Biology, Russian Academy of Sciences, Moscow, 113994 Russia*
[c] *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences, Vladivostok, 690022 Russia*
[d] *Department of Biology, Moscow State University, Moscow, 119234 Russia*
**e-mail: bulatova.nina@gmail.com*

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Abstract—A review of studies on the chromosome sets of Palaearctic mammals carried out by Russian karyologists and an important contribution to improving the taxonomy of mammals were made for the first time. For many mammal species, the process of speciation was associated with variability in the number and morphology of the chromosomes; therefore, the karyotypes are often used as diagnostic peculiarities of morphologically similar cryptic species (sibling species). The prospects for cytogenetic studies in the field of speciation (particularly, an enhancement of reproductive isolation, initiated by chromosomal rearrangements, by selection) are discussed.

Keywords: karyotype, "chromosome species", animal cytogenetics, speciation

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INTRODUCTION

The conclusion of T. Dobzhanskii about the "genetic basis of classification" (Dobzhansky, 1937) has subsequently been confirmed many times. The chromosome sets are discrete and combine morphological and genetic peculiarities; therefore, they are of interest for use in biological classification. At the end of the 1940s, the chromosome sets of 134 species and subspecies of mammals were characterized in Matthey's first summary on vertebrate chromosomes (Matthey, 1949), and 176 species were included in Makino's atlas (Makino, 1951). In the 1950s, the results were summarized and important generalizations were made about the evolution of chromosomes and their role in speciation (Wallace, 1953; White, 1954, 1957). But the idea of using the chromosome sets in the taxonomy of animals was developed for the first time in the article by Vorontsov (1958) "The importance of studying chromosome sets for the taxonomy of mammals," in which information about the chromosomes of 269 mammalian species was collected. Even seven years after publication, this work did not lose its relevance and was published as a separate book in English by the Smithsonian Institution (Washington, United States). This "...review on the karyosystematics of vertebrates made at the very beginning of N. Vorontsov's scientific career (at the age of 24!) made his name recognizable in domestic and world science and made him a recognized authority in the theoretical systematics of animals" (Yablokov, 2017, p. 11).

In 1959, Vorontsov made a report "Species of Palaearctic hamsters in statu nascendi," which was subsequently published as an article (1960), at the conference "Darwin Days in Leningrad." The hamsters captured and given to R. Matthey were the material for this publication. A "genetic" method of speciation was substantiated in the article: "Based on the study of the divergence of closely related forms of hamsters, it was demonstrated that changes in the chromosome numbers (especially through Robertsonian translocations) can not only complete the process of ecological and morphological differentiation of species by genetic isolation, but also serve itself as a basis for morphological divergence of similar forms" (cited by Vorontsov, 1999, p. 552).

The studies of chromosome sets of mammals from the populations on the territory of our country on regular laboratory base started in the Institute of Cytology and Genetics, Siberian Branch, Academy of Sciences of the USSR, Novosibirsk (N.N. Vorontsov, E.A. Lyapunova, and S.I. Radjabli) and at Moscow State University, Moscow (V.N. Orlov). The first works were published in the middle of the 1960s

(Vorontsov and Radjabli, 1967; Vorontsov et al., 1967; Orlov and Alenin, 1968).

The karyological direction in the taxonomy developed rapidly; in 1969, it was represented by the established school at the 2nd All-Union Meeting on Mammals. The meeting program included a report by N.N. Vorontsov "Problems of modern taxonomy of mammals" and 33 reports in the sections related to the study of karyotypes. The printed collection of materials "The Mammals: Evolution. Karyology. Taxonomy. Fauna" was prepared for this meeting. At subsequent congresses of the All-Union (All-Russia) Theriological Society (the 1st congress in January, 1973), karyological works constantly occupy a prominent place among the reports of the "Taxonomy" section. The first stage of extensive karyological studies of mammals in the country was characterized as karyosystematics (Orlov, 1970, 1974).

The centers of karyological studies of mammals arose in many cities: in Nalchik (A.K. Tembotov, R.I. Dzuev), Magadan (F.B. Chernyavskii, A.I. Kozlovskii), Saratov (A.I. Belyanin), Yekaterinburg (E.A. Gileva), and Vladivostok (N.N. Vorontsov, E.A. Lyapunova). A karyosystematic direction developed at the Institute of Ecology and Evolution, Russian Academy of Sciences, in Moscow (V.E. Sokolov, V.N. Orlov). In the 1990s, the Institute of Developmental Biology, Russian Academy of Sciences (N.N. Vorontsov), became a new center of mammalian karyology in Moscow; in the 2000s, studies on meiosis in mammals were launched in the Institute of Cytology and Genetics (Siberian Branch, Russian Academy of Sciences, P.M. Borodin) and the Institute of General Genetics, Russian Academy of Sciences (O.L. Kolomiets). In Novosibirsk, a new Institute of Molecular and Cellular Biology (Siberian Branch, Russian Academy of Sciences) became a leader in molecular cytogenetics (A.S. Graphodatsky, V.A. Trifonov). Throughout these years, the Department of Mammals, Zoological Institute, Russian Academy of Sciences, in St. Petersburg has been connected with these centers by common interests.

In the 1970s–1980s, studies of the karyotypes of wild mammals became widespread. The lists of chromosome numbers of mammals compiled by Matthey (1973) included 1560 forms; the list of E.Yu. Ivanitskaya (Orlov and Bulatova, 1983: Supplement)—2050 forms. At present, this number is apparently over 3000. Currently known data indicate both the stability of the chromosome sets and the accumulation of chromosomal rearrangements in the evolution of species. Intrapopulation polymorphism was described in approximately eight dozen mammalian species (that is, less than 4%) (Lyapunova and Kartavtseva, 1976). Among the chromosomal rearrangements in the evolution of karyotypes, centric connections, pericentric inversions, extra chromosomes, deletions, and duplications that are often associated with heterochromatin and that are known for both sex chromosomes and autosomes were described (Orlov and Bulatova, 1989). Changes associated with reciprocal and nonreciprocal translocations, as well as tandem fusions, were detected less frequently than others (Dobigny et al., 2017). Since the 1970s, the development of methods for differential staining of chromosomes consistently increased the resolving levels of chromosomal differentiation for studying issues of taxonomy and phylogenetic relationships of species.

The monographs and atlases on karyosystematics and cytogenetics (Orlov, 1974; Anbinder, 1980; Orlov and Bulatova, 1983; Graphodatsky and Radjabli, 1988; Gileva, 1990; Meier et al., 1996; Dzuev, 1998; Kartavtseva, 2002; Safronova et al., 2018; Stanyon and Graphodatsky, 2012; Searle et al., 2019; Graphodatsky et al., 2020) and chapters in international publications on cytogenetics (Graphodatsky, 1989; Orlov and Bulatova, 1989; Yang and Graphodatsky, 2009; Pavlova and Searle, 2018; Borodin et al., 2019; Bulatova et al., 2019; Fedyk et al., 2019) have been published. Data on species karyotypes became routinely included in monographs by species and systematic reports.

The aim of this review is to sum up some results of the development of the karyological direction in the taxonomy of mammals in our country and the contribution of cytogenetic studies to the concept of species and improving the system of mammalian species.

CYTOGENETIC DIFFERENTIATION OF POPULATIONS AND IMPROVING THE SYSTEM OF MAMMALIAN SPECIES

The problem of creating a taxonomic system of organisms (which is a reflection of the evolutionary process) remains relevant to this day. There is no doubt that the use of different approaches and methods (both classical and relatively new, primarily genetic) allows to expand significantly our understanding of the degree of differentiation of closely related forms (that have not yet been assigned the species status) and of the phylogenetic relationships of supraspecific taxa. The construction of such a system implies the identification of patterns of speciation (a key process of evolution).

Chromosome sets are less susceptible to convergence as compared with the traits usually used in the work with museum collections. Karyological analysis allows us, on the one hand, to identify cases of relatedness of morphologically widely divergent species and, on the other, to establish cases of reproductive isolation of the forms previously classified as a single polytypic species. Data accumulated on the basis of studying cytogenetics of mammalian populations formed the basis for the development of ideas about the chromosomal pathway of speciation. Unlike morphological and molecular differences, cytogenetic differences between the populations directly correlate with disturbances in hybrid fertility. Among many dozens of works devoted to chromosomal speciation (see Vorontsov and Lyapunova, 1989), the monographs of White (1978) and King (King, 1993) should be highlighted.

In the experimental work of geneticists in the first half of the 20th century, a model for the emergence of hybrid sterility when crossing individuals from different populations differing in gene mutations was developed. Later, this model was called the Bateson–Dobzhansky–Muller (BDM) model (Coyne and Orr, 2004). But this model can also be used to explain the occurrence of hybrid sterility when crossing individuals that differ by chromosomal rearrangements (Borodin and Polyakov, 2008).

According to the BDM model, the ancestral species is subdivided into geographically isolated populations, in which gene differences (or different chromosomal rearrangements) are accumulated. Chromosomal rearrangements can be accumulated and fixed in a population only if the fertility of heterozygotes and homozygotes does not differ. With a secondary contact of isolated populations (in which different chromosomal rearrangements were accumulated), complex figures of conjugating chromosomes are formed in meiosis I of hybrids, including translocation crosses, chains and rings of chromosomes, crossover chromatids, and other deviations from normal meiosis. Over decades of cytogenetic studies, it was convincingly demonstrated that such "complex heterozygotes" inevitably have lower fertility as compared with homozygotes; therefore, their distribution is limited to hybrid zones. All models of chromosomal speciation are based on the reduced fertility of "complex heterozygotes" (see the review Bakloushinskaya, 2016). The chromosomal speciation does not necessarily imply the accumulation of morphological differences. Therefore, reproductively isolated species that do not differ in morphological traits can arise, with which taxonomists work; these are cryptic species (or sibling species).

In the 1960s–1970s, taxonomists largely exhausted the possibilities of the development of a taxonomy of Palaearctic mammals using morphological approaches and started using cytogenetic methods in their works. The identification of cryptic species became a necessary link in the description of biological diversity and, at the same time, attracted attention to a new level of discussion of the concepts of species and speciation. The grey voles *Microtus arvalis* Pall. and *M. subarvalis* Meyer, Orlov et Skholl became the first discovery of two cryptic species living together over a large part of the range (Meier et al., 1969, 1972). Over the past 50 years, taxonomists have never been able to discover reliable craniological traits of these species or establish significantly the senior synonym of *M. subarvalis* from the preserved museum collections.

A cohabitation of cryptic mammalian species is directly associated with olfactory communication (the predominant method of communication among mammals). Not only species living together, but also allopatric morphologically similar species found in many mammalian taxa using predominantly chromosomal markers (by which it is possible to judge the degree of reproductive isolation of the compared forms) are of equal interest. Recognition of the species rank of such cryptic forms identified geographically but substituting and karyologically distinct requires additional evidence of reproductive isolation, confirmation by experimental hybridization, or the use of quantitative criteria developed for molecular comparisons (Baker and Bradley, 2006). The existence of cryptic species proves the superiority of the biological species concept as compared with the morphological one and is consistent with the evolutionary (phylogenetic) species concept (Cracraft, 1983).

From the example of individual genera from four orders of Palaearctic mammals, we will demonstrate the contribution of karyological studies to the identification of cryptic species, phylogenetic relationships of populations of the same species, and improvement of the system of mammalian species.

Genus *Sorex* L. Cytogenetic studies demonstrated the leading role of the karyotype in the diagnosis of many shrew species. The "araneus" group out of nine Palaearctic and Nearctic shrew species is characterized by the same sex trivalent in males and almost complete homology of the chromosome sets by G-banding of the chromosomes with clear differences in karyotypes. Four species from the "araneus" group are known on the territory of Russian Federation (*Sorex araneus* L., *Sorex satunini* Ogn., *Sorex tundrensis* Mer., and *Sorex daphaenodon* Thos.). A detailed analysis of karyotypes of the Palearctic species *S. tundrensis* demonstrated its differences from the Nearctic *S. arcticus* Kerr, with which it was previously combined (Ivanitskaya and Kozlovskii, 1985).

The taxonomic structure of the previous large polytypic species of the common shrew (*S. araneus* s. lato) was revised in recent decades using cytogenetic methods. Five cryptic species were identified (*S. araneus* L., *S. granarius* Mill., *S. coronatus* Mill., *S. satunini* Ogn., and *S. antinorii* Bon.), and the phylogenetic relationships between them were discussed (Orlov et al., 2011; Searle et al., 2019). A karyotype close to the initial one for the superspecies is preserved in *S. granarius*. In this species, all autosomes are acrocentric (except for a pair of the smallest ones), while the other species have common or unique centric autosome associations. Modern isolated species of this superspecies have common Robertsonian fusions, which indicates the existence of a common ancestral polymorphic species in the Pleistocene and free distribution of chromosomal rearrangements throughout its range. There are two species from the former *S. araneus* s. lato in the fauna of the Russian Federation.

S. araneus ($2n = 20–33$, NFA = 36). For the species, karyotype polymorphism by 37 centric chromosome fusions (out of which five are common with *S. satunini*, *S. coronatus*, and *S. antinorii*) was demonstrated. In the range, 76 chromosomal races were identified differing in centric chromosome fusions and to varying degrees isolated by narrow and wide hybrid zones (Bulatova et al., 2019). Approximately half of all chromosomal races are distinguished by fixed centric fusions, which indicates the monophyletic origin of such population groups.

S. satunini ($2n = 24–25$, NFA = 42) (Kozlovskii, 1973; Borisov and Orlov, 2012). The chromosome set differs from the common shrew karyotype by Robertsonian fusions of three pairs of chromosomes and a centromere shift in three pairs of chromosomes. Therefore, complex heterozygotes disrupting gametogenesis should arise in meiosis. A contact zone with the common shrew without hybridization was described (Stakheev et al., 2020).

When comparing the karyotypes of four shrew species of the “caecutiens” group (*S. caecutiens* Laxm., *S. isodon* Tur., *S. unguiculatus* Dobs., and *S. roboratus* Holl.) with similar karyotypes ($2n = 42$, NFA = 66–68), a complete homology of autosomes and sex chromosomes (identity in the location of G-bands) was found, and only some autosomes can differ from each other in the position of centromeres as a result of inversions (Kozlovskii and Orlov, 1971; Ivanitskaya et al., 1986; Biltueva et al., 2000).

Karyological studies proved the species independence of shrews of the “minutus” group distinguished by significant rearrangements in the karyotype: *S. minutus* L., $2n = 42$, NF = 54 (Orlov and Alenin, 1968; Biltueva et al., 2000); *S. volnuchini* Ogn., $2n = 40$, NF = 56 (Kozlovskii, 1973a); *S. gracillimus* Thos., $2n = 36$, NF = 60 (Ivanitskaya et al., 1986). The closest findings of the small shrew and Volnukhin shrew without the traits of hybridization were made in the neighboring valleys of the small Kagalnik and Eya rivers (south of the Lower Don) (Stakheev et al., 2010). In the Amphiberingian “cinereus” group, the karyological diagnosis of the species was clarified and the absence of the Nearctic *S. cinereus* species on the territory of the Russian Federation was demonstrated (Ivanitskaya and Kozlovskii, 1985).

Genus *Ovis* L. The first genetic studies in the 1970s of various morphological forms of mountain sheep of the genus *Ovis* demonstrated their division into three monophyletic chromosomal forms: the group of “musimon” subspecies, mouflons ($2n = 54$, NF = 60); the group of “vignei” subspecies, urials ($2n = 58$, NF = 60); and the group of “ammon” subspecies, arkhars and argali ($2n = 56$, NF = 60) (Vorontsov et al., 1972; Nadler et al., 1973; Korobitsyna et al., 1974; Orlov, 1978). Initially, researchers proposed to give these chromosomal forms species status, which was not subsequently supported due to the absence of reproductive isolation. According to the results of differential G-staining, two pairs of large marker metacentrics were identical in all rams studied (Lyapunova et al., 1997; Bunch et al., 1998). The connection of the most northern isolated form of mountain sheep *O. severtzovi* Nasonov to the arkhar–argaloid group “ammon” ($2n = 56$) was demonstrated (Lyapunova et al., 1997), which was an additional justification for the need to protect this small population. The monophyletic origin of each of the three chromosomal forms of mountain sheep was subsequently confirmed by phylogeographic study (Kuznetsova et al., 2002).

Genus *Ochotona* Link. The analysis of karyotypic characteristics of pikas of the genus *Ochotona* allowed researchers not only to diagnose the species of this genus, but also to come closer to understanding the supraspecific structure of the genus (Vorontsov and Ivanitskaya, 1973; Orlov et al., 1978; Formozov et al., 1999, 2004; Formozov and Baklushinskaya, 1999, 2011). In this group, the chromosome numbers often coincide. Several species have $2n = 38$ and $2n = 40$, but the morphology of chromosomes, the number and distribution of heterochromatin blocks, and the nucleolar organizer are species-specific.

Genus *Spermophilus* Cuvier. The study of the chromosome sets of ground squirrels allowed confirmation of the species independence of *S. xanthoprymnus* Bennett ($2n = 42$) and *S. citellus* L. ($2n = 40$) (Vorontsov and Lyapunova, 1969, 1972; Lyapunova and Vorontsov, 1970). The presence of two chromosomal forms in *S. suslicus* Güld. (deserving species status) was demonstrated (Vorontsov and Lyapunova, 1969; Frisman et al., 1999). Between the Volga and the Dnieper, there is a form with $2n = 34$, and there is a form with $2n = 36$ on the right-hand side of the Dnieper (Tsvirka et al., 2000). For allopatric karyomorphs, the electrophoretic analysis of 15 allozyme protein systems demonstrated that the forms are clearly distinguished at two loci (*Alb* and *Tf*). Thus, the division of *S. suslicus* into two karyotypic forms is accompanied by differentiation of these forms at the allozyme level. Long-tailed ground squirrels (considered as a single species *S. undulatus* Pall.) are divided into two (*S. parryi* Rich. ($2n = 32$) and *S. undulatus* Brandt ($2n = 34$)) (Lyapunova, 1969; Vorontsov and Lyapunova, 1970). Using the methods of differential chromosome staining, differences of karyotypes with $2n = 36$ in *S. pygmaeus* Pall and *S. musicus* Menet. were demonstrated, which can be considered species-specific (Tsvirka and Korablev, 2014).

Genus *Marmota* Blumenbach. The chromosome sets of six Palaearctic species of marmots were described. Their homology was demonstrated in all species ($2n = 36–38$, NF = 70), with the exception of *M. camtschatica* Pall. ($2n = 40$, NF = 70) (Lyapunova and Vorontsov, 1969). The Kashchenko marmot

(*M. kastschenkoi* Stroganov et Judin) was isolated from *M. baibacina* Kast. based on a single chromosomal rearrangement (2*n* = 36) (Brandler, 2003), but is more often considered as a subspecies or semispecies (Steppan et al., 2011).

Genus *Sicista* Gray. The chromosomal studies of birch mice were a stimulus for subsequent taxonomic revisions and description of karyologically discrete geographically substitutive cryptic species in their composition. Using karyological data, such species were found in the groups of allopatric species identified on the basis of the peculiarities of male genitalia: “subtilis,” “betulina,” “tianschanica,” and “caucasica” (Sokolov and Kovalskaya, 1990).

The group “betulina” includes two geographically replaced karyologically discrete cryptic species: *S. betulina* Pall. (2*n* = 32) and *S. strandi* Formosov (2*n* = 44; NF = 52) (Sokolov et al., 1989), the degree of chromosomal differentiation of which is sufficient to conclude that they are reproductively isolated.

The group “caucasica” (a group of monochromatic birch mice of the Caucasus) (Sokolov and Kovalskaya, 1990) includes six geographically isolated chromosomal forms considered within four sibling species: *S. caucasica* Vinog. (2*n* = 32, NF = 48; 2*n* = 32, NF = 46); *S. kluchorica* Sokolov et al. (2*n* = 24, NF = 44); *S. kazbegica* Sokolov et al. (2*n* = 42, NF = 52; 2*n* = 40, NF = 50), and *S. armenica* Sokolov et Baskevich (2*n* = 36, NF = 52) (Sokolov et al., 1981, 1986; Sokolov and Baskevich, 1988; Baskevich and Malygin, 2009). The 42-chromosomal *S. kazbegica* (ancient) and 24-chromosomal *S. kluchorica* (the youngest in the group) are the most isolated among the compared species of the “caucasica” group from the Greater Caucasus: their G-stained chromosomes differ in nine non-Robertsonian translocations and two pericentric inversions. Two geographically isolated intraspecific forms of *S. kazbegica* (the karyotypes of which differ by a single tandem translocation), as well as two forms of *S. caucasica* (the chromosome sets of which differ by a single pericentric inversion) are the closest to each other (Sokolov and Baskevich, 1992; Baskevich et al., 2004, 2015).

The species *S. tianschanica* Salen., in which the geographic variability of the karyotype was detected, was allocated to a separate group (Sokolov and Kovalskaya, 1990). Three variants of the karyotype were described, confined to different isolated habitats within the species range: the terskei form (2*n* = 32, NF = 54: central and northern Tien Shan), the talgar form (2*n* = 32, NF = 56: Trans-Ili Alatau), and djungar form (2*n* = 34, NF = 54: Dzungarian Alatau, Tarbagatai) (Sokolov et al., 1982, 1987; Sokolov and Kovalskaya, 1990a). It was suggested that there was a possible species level of differences between the geographically replaced karyomorphs found in the Tien Shan Mountains that make up the “tianschanica” group (Sokolov and Kovalskaya, 1990a). This hypothesis was convincingly confirmed by subsequent molecular studies (Lebedev et al., 2021).

Previously, it was believed that there are only two morphologically similar species in the “subtilis” group: *S. subtilis* s. str. and *S. severtzovi* Ogn. (Sokolov et al., 1986a). The use of the methods of differential chromosome staining opened up new opportunities for studying the systematic diversity of this group (Aniskin et al., 2003; Baskevich et al., 2010, 2011). Cytogenetic studies of birch mice of the “subtilis” group in the Middle Don basin led to the discovery of a series of five largely divergent chromosomal forms (cryptic species): *S. subtilis* s. str. (2*n* = 24, NF = 40–46), *S. severtzovi* (2*n* = 26, NF = 48), *S. nordmanni* (2*n* = 26, NF = 48), *Sicista* sp. n. 1 (2*n* = 22–26, NF = 41–46), and *Sicista* sp. n. 2 (2*n* = 16–22, NF = 28–31). Differences in the karyotypes of varying degrees of complexity at the level of G-banding were determined by 10–29 structural rearrangements of the chromosomes (Kovalskaya et al., 2011).

In addition, the form cimlanica (2*n* = 22, NF = 35–36) was described from the lower reaches of the Don (Tsimlyansk sands); initially, it was considered as a subspecies of the dark birch mouse *S. severtzovi cimlanica* (Kovalskaya et al., 2000), and later species status was postulated for it by the level of chromosomal differentiation (Lebedev et al., 2020). Obviously, additional studies on cryptic birch mouse species are needed.

Genus *Myospalax* Laxmann. The karyological study confirmed the concept of a narrow species in zokors (Lyapunova et al., 1974). Chromosomal data support the species isolation of *M. myospalax* Laxm. (2*n* = 44, NFA = 80–84) and *M. aspalax* Thomas (2*n* = 62, in the population from the Russian Federation, NFA = 113–114; from Mongolia, NFA = 110–112) (Lyapunova et al., 1974; Martynova and Vorontsov, 1975; Vorontsov and Martynova, 1976; Martynova, 1976; Orlov and Baskevich, 1978).

A controversial position in the genus system of the form *M. epsilanus* Thomas (*M. psilurus* Milne-Edwards subspecies or a separate species) was clarified on the basis of a comprehensive analysis, which includes comparative karyology of two isolated populations of the group “*M. psilurus–M. epsilanus*” from the Russian Far East and Transbaikalia (Puzachenko et al., 2014; Tsvirka et al., 2015). All studied zokors have 2*n* = 64; however, there are significant differences in the karyotype structure between the populations from the Transbaikalia region (“epsilanus”) and the Russian Far East (“psilurus”) (Tsvirka et al., 2015). The karyological peculiarities of these forms were supplemented by electrophoretic and molecular data, and the genetic distances between them were comparable to differences between a pair of closely related species *M. aspalax* and *M. armandii* (Tsvirka et al., 2015). Previously, a species-specific karyotype (2*n* = 62–66) was demonstrated in *M. armandii*

(Puzachenko et al., 2011). A comparative analysis of karyotypes and genetic studies of the genus *Myospalax* allowed the suggestion of the origin of the Altai zokor (*M. myospalax*) ($2n = 44$) independently of *M. aspalax* ($2n = 62$) and from *M. psilurus* ($2n = 64$) (Martynova, 1983).

Genus *Calomyscus* Thomas. The taxonomy of the genus *Calomyscus* is still unclear. A difference in the karyotypes by the number of chromosomes of hamsters from Nakhichevan ($2n = 32$) and Turkmenistan ($2n = 30$) allowed researchers to revise the morphological characteristics and describe a new species from Nakhichevan (*C. urartensis* Vor. et Kart.) (Vorontsov et al., 1979). The analysis of karyotypes of these species using G-banding of chromosomes demonstrated not only differences by the number of chromosomes, but also the absence of homologous chromosome fusions that formed double-armed chromosomes of different species (Graphodatskii et al., 1989). In the same work, the chromosomal morphs of *Calomyscus* were described: (A) $2n = 44$; (B) $2n = 44$; (C) $2n = 30$; (D) $2n = 32$. Later, one of 44 chromosomal forms was given a new species name *C. firiusaensis* Meyer et Malikov (Meier and Malikov, 2000). For new chromosomal forms, $2n = 37$, NFA = 44; $2n = 50$, NFA = 50; $2n = 52$, NFA = 56, the taxonomic status is still unclear (Romanenko et al., 2021).

Genus *Cricetulus* Milne-Edwards. At the first stages of karyological studies of this genus in the 1960s, differences in the karyotypes of good morphological species (*C. migratorius* Pall ($2n = 22$) and *C. barabensis* Pall. ($2n = 20$)) were described, and differences in the karyotypes of controversial species that were morphologically very similar (*C. barabensis* Pall. ($2n = 20$) and *C. griseus* Milne-Edwards ($2n = 22$)) were found (Matthey, 1973). In the 1970s, the karyotypes of a good morphological species *C. longicaulatus* Milne-Edwards ($2n = 24$) (Orlov et al., 1978) and two cryptic species of a superspecific group *C. barabensis* s. l. (*C. pseudogriseus* Iskhakova ($2n = 24$) (Orlov and Iskhakova, 1975) and *C. sokolovi* Orlov et Malygin ($2n = 20$) (Orlov and Malygin, 1988)) were described.

The use of the methods of differential chromosome staining in the studies of the genus *Cricetulus* started with a comparative study of the karyotypes of *C. migratorius* and *C. barabensis* with the karyotypes of other species of the Cricetinae subfamily. The analysis of G-banding demonstrated that both species have chromosome pairs with similar G-band patterns and differ in a small number of rearrangements. At the same time, the karyotypes of *Cricetulus migratorius* and *Cricetus cricetus* are more similar to each other than the karyotypes of *C. migratorius* and *C. barabensis* by the number of similar pairs and the nature of chromosomal rearrangements (Radjabli, 1975).

In recent years, the karyotype of *C. sokolovi* was studied using the FISH method, which demonstrated the rearrangement of many chromosomes; according to phylogenetic analysis of the cyt *b* gene, this species was sister to all species of the *C. barabensis* s. l. group (Poplavskaya et al., 2017).

According to FISH data (Romanenko et al., 2007), as well as data on the variability of structural heterochromatin (Vakurin et al., 2014), significant differences in the chromosome structure of all described chromosomal forms in the group *C. barabensis* s. l. and the error of classifying them as a single species were demonstrated. New information about the absence of intensive hybridization in the contact zones of *C. barabensis* and *C. pseudogriseus* and differences in the location of nDNA repeats in the chromosomes of *C. barabensis* and *C. griseus* confirm the species status of these forms (Poplavskaya et al., 2012; Ivanova et al., 2022).

Genus *Lemmus* Link. The species of this genus have predominantly 50 acrocentric chromosomes in a diploid set ($2n =$ NF $= 50$). In the karyotype of *L. sibiricus chrysogaster* J.A. Allen ($2n = 50$, NF $= 54$), there are two pairs of subtelocentric autosomes (in addition to 46 acrocentrics). In the genome of *L. s. chrysogaster*, there is more C-heterochromatin than in all other studied forms of the genus *Lemmus*. In hybrid females *L. s. chrysogaster* × *L. lemmus* and *L. s. sibiricus* × *L. amurensis*, the desynapsis of some chromosomes occurs during the first meiotic division, which indicates the genetic divergence of the parental forms. The cytogenetic peculiarities of *L. s. chrysogaster* confirm its species independence (Gileva et al., 1984).

Genus *Dicrostonyx* Gloger. In the 1970s, a significant chromosomal polymorphism was discovered in morphologically similar Holarctic populations of collared lemmings (Raush and Raush, 1972; Gileva, 1973, 1975; Kozlovskii, 1974). Later, it was found that the diploid number of permanent A-chromosomes (larger) in the Palaearctic varies from 28 to 50, while a different number of small additional B-chromosomes is noted in the karyotypes of many populations. In the continental tundra of the Palaearctic, four chromosomal races of *D. torquatus* Pall. were described (Gileva, 1983; Fredga et al., 1999). The ranges of the races II and III partially overlap without hybridization; therefore, their reproductive isolation is possible. The distribution of race I and the nominative subspecies, as well as the distribution of races II, III, and IV and the *chionapaeus* subspecies, coincides.

The collared lemmings of Wrangel Island were described as a new species *D. vinogradovi* Ogn. (Chernyavskii and Kozlovskii, 1980). In the population of Wrangel Island, $2n$ is reduced to 28 chromosomes, NF $= 50$, and B chromosomes are absent (Kozlovskii, 1974; Chernyavskii and Kozlovskii, 1980). The reproductive isolation of lemmings from Wrangel Island and the continental tundra of the Palaearctic was demonstrated in the experimental crosses (Chernyavskii and Kozlovskii, 1980; Gileva et al., 1994).

Based on the variability of mitochondrial cyt *b* gene, the Holarctic genus *Dicrostonyx* is subdivided into two groups: North American (including the Wrangel Island population) and Eurasian (Fedorov et al., 1999). But *D. vinogradovi* is a sister species relative to all studied populations of North America (including Alaska) (Smirnov and Fedorov, 2003); consequently, it can be considered as a representative of a separate evolutionary line in the North American group of collared lemmings. Since the time of isolation of Palaearctic and Nearctic collared lemmings is estimated as one million years or more (Fedorov and Goropashnaya, 1999), the isolation of the evolutionary line of *D. vinogradovi* from non-Arctic populations could be equally long. Therefore, it is possible that the lemmings of Wrangel Island could be a cryptic species in the composition of the Nearctic group of this genus, and it is advisable to keep the species *D. vinogradovi* Ogn. in the list of mammals of the Russian Federation.

Genus *Alticola* Banford. Using classical cytogenetic methods (including the methods of differential chromosome staining (G-, C-banding)), it is possible to cover a part of the genus species (*A. argentatus* Sev., *A. barakshin* Bann., *A. lemminus* Miller, *A. macrotis* Radde, *A. semicanus* G. Allen, and *A. strelzowi* Kast.) and make only an indirect contribution to the construction of its natural system. At the same time, a conservative karyotype, in which, as a rule, all autosomes (with the exception of the smallest pair) and heterochromosomes are represented by acrocentrics ($2n = 56$, NF = 58) (which is also typical for representatives of other genera of the tribe *Prometheomyini*), was noted for all karyotyped species and subspecies of *Alticola*. However, interpopulation and intersubspecific variability of the karyotype (associated with variability in the amount of heterochromatin in some pairs of autosomes and heterochromosomes) was detected in a number of karyologically studied *Alticola* species (Yatsenko, 1980; Bykova et al., 1978). For example, variability in the morphology of the 1st pair of autosomes and heterochromosomes was noted in the species of the subgenus *Alticola* (*A. barakshin*, *A. semicanus*, and *A. strelzowi*) belonging to the same group "stoliczkanus" (Yatsenko, 1980), or the pairs of autosomes nos. 1, 5, and 9 and heterochromosomes were variable in the karyotype in *A. lemminus* (a representative of the subgenus *Ashizomys* Miller) (Bykova et al., 1978). The use of molecular cytogenetic FISH methods in relation to some representatives of the genus *Alticola* (*A. barakshin*, *A. olchonensis* Litvin., *A. strelzowi*, and *A. tuvinicus* Ogn.) confirms the idea about the conservation of euchromatin regions of the chromosomes and the role of heterochromatin variations in the formation of *Alticola* (Romanenko, 2019).

Genus *Ellobius* Fischer. The subdivision of *Ellobius fuscocapillus* Blyth into two species with significant differences in the chromosome sets was confirmed: standard diploid in *E. fuscocapillus* ($2n = 36$) and with an unusual system of sex chromosomes (XO) in *E. lutescens* Thomas ($2n = 17$) (Vorontsov et al., 1969; Lyapunova and Vorontsov, 1978). Three sibling species were identified (instead of one species): *E. talpinus* Pall. ($2n = 54$, NF = 54), *E. tancrei* Blasius ($2n = 54$, NF = 56), and *E. alaicus* Vorontsov et al. 1969 ($2n = 52$, NF = 56). All three cryptic species are allopatric; hybridization, if any, is local, and no widespread introgression was demonstrated (Vorontsov et al., 1969; Yakimenko and Lyapunova, 1986).

Most of the range from Ukraine to Mongolia is inhabited by species with $2n = 54$, without a submetacentric chromosome (*E. talpinus* s. str., NF = 54), and with a submetacentric chromosome (*E. tancrei*, NF = 56), which has a neocentromere (Bakloushinskaya et al., 2012). A Robertsonian fan in the mole voles *E. tancrei*, localized in a narrow area of the valley of the Surkhob River and the upper reaches of the Vakhsh River (Pamir–Alai), was a cytogenetic discovery (Lyapunova et al., 1984).

In the valley of the Surkhob–Vakhsh River, numerous variants of karyomorphs that arose during the fixation of Robertsonian translocations (including partially homologous) were described (Bakloushinskaya et al., 2012; Romanenko et al., 2019). No such wide variation of the chromosomes ($2n$ from 54 to 30) over a limited range was observed in any species. There is no doubt that an intensive process of chromosomal speciation is taking place here. Out of three different forms with $2n = 32–34$, each acquired its own range. *E. alaicus*, for which the chromosomal variability was only recently described ($2n = 52–48$) and its range was significantly expanded (from the Pamir–Alai to the Tien Shan), progressed the furthest in this direction (Bakloushinskaya et al., 2019; Tambovtseva et al., 2022). The chromosomal rearrangements in this species occur in "real time": for example, the Robertsonian translocation was fixed in the population in Tajikistan over 30 years of observations; the diploid number changed from 50 to 48. Most likely, such a rapid formation of Robertsonian translocations can be associated with special chromosome contacts in meiosis found in this species (Matveevsky et al., 2020).

The study of meiosis in the hybrids of different forms and species of the mole voles started in the 1980s, when "complex heterozygotes" (chains of conjugating chromosomes formed in the hybrids with a large number of translocations) were demonstrated for the first time (Bogdanov et al., 1986). Later, "complex heterozygotes" were discovered in different variants of intraspecific hybrids; in the case of interspecific hybrids (*E. tancrei* × *E. talpinus*), namely the analysis of meiosis allowed the identification of the reason for the reproductive isolation of these two cryptic species (Matveevsky et al., 2020a).

For the cryptic species *E. talpinus* and *E. tancrei,* zones of secondary contact in nature are unknown. *E. tancrei* and *E. alaicus* have a narrow contact zone. Single hybrids were described, but widespread introgression is unknown (Bakloushinskaya et al., 2019; Tambovtseva et al., 2022). Intraspecific chromosomal forms of *E. tancrei* cannot interbreed with each other due to the presence of nonhomologous fusions, but probably they produce hybrids with the original form (like house mice in the Rhaetian Alps). This leads to the formation of diverse karyotypes, "mini-fans" within each of the three forms described (Romanenko et al., 2019) and the emergence of some gene flow between the forms due to backcrossing. Such a system can hardly be called allopatric hybridization; the forms live parapatricly with the initial 54-chromosomal *E. tancrei*. Up to present, there is significant variability in the karyotypes of the mole voles with the complete absence of morphological and ecological differentiation in the Pamir–Alai (Lyapunova et al., 1980).

Genus *Alexandromys* Ognev. Based on morphological and genetic data, 12 species of East Asian voles were recently isolated from the genus *Microtus* into an independent genus *Alexandromys* (Abramson and Lisovskii, 2012). The cryptic species of this genus (*A. maximowiczii* Schrenk, *A. mujanensis* Orlov et Kovalskaya, and *A. evoronensis* Kovalskaya et Sokolov) are included in the superspecific group "maximowiczii" and differ by the number and morphology of chromosomes (Meier et al., 1996); moreover, the last two species were identified on the basis of karyological peculiarities (Orlov and Koval'skaya, 1978; Kovalskaya and Sokolov, 1980). Two vole species (*A. maximowiczii* and *A. evoronensis*) have intra- and interpopulation variability in the structural chromosomal rearrangements, which supported description of the diversity of chromosomal forms for the first species ($2n = 38–44$) (Kovalskaya et al., 1980; Kartavtseva et al., 2008); for the second, there were two chromosomal races in three isolated populations of the southern part of the Russian Far East: evoron ($2n = 38–41$, NF = 54–59) and argi ($2n = 34, 36, 37$, NF = 51–56) (Kartavtseva et al., 2021). The unique polymorphism of these races consisted in multiple structural rearrangements of the chromosomes of 11 pairs, including both centromeric and tandem fusions. For the argi race, the tandem fusion of two double-armed chromosomes and one double-armed chromosome with the formation of a large double-armed chromosome in the heterozygous state was detected. At this stage, we observe a process of incomplete speciation with the involvement of chromosomal transformations in the isolated populations (Kartavtseva et al., 2021). Morphological and chromosomal analysis of the northern subspecies (in Khabarovsk krai and Yakutia) of Maximowicz's vole cast doubt on its belonging to this species (Vorontsov et al., 1988). Further morphological and genetic studies allowed the identification of this subspecies first as an independent species (Gromov's vole (*A. gromovi*)) (Sheremetyeva et al., 2009), and its discovery on Bolshoi Shantar Island in the Sea of Okhotsk allowed researchers to give a new Latin species name (*A. shantaricus*) (Dokuchaev and Sheremetyeva, 2017).

Using the methods of molecular phylogenetics (Bannikova et al., 2010; Haring et al., 2011), the composition of the subgenus *Alexandromys* was clarified: a number of taxa, the phylogenetic position of which was in doubt, were assigned to it (*A. mongolicus* Radde 1861, *A. middendorffii* Poljakov 1881, and *A. limnophilus malygini*) (Courant et al., 1999).

The position of *A. limnophilus* Büchner in different molecular reconstructions of the genus *Alexandromys* is estimated ambiguously: *A. limnophilus* is considered as a sister taxon to *A. fortis* Büchner (Bannikova et al., 2010) or as a basal species in the "middendorffii" group (Lyssovsky et al., 2018) of the subgenus *Alexandromys*, or as a sister species to *A. oeconomus* Pall. (Steppan and Schenk, 2017), but already in the composition of another subgenus *Oecomicrotus* (Krystufek and Shenbrot, 2022). According to chromosomal data, the karyotypes of *A. limnophilus* ($2n = 38$) and *A. oeconomus* ($2n = 30$) are easily homologated, and they were estimated as cryptic species (Malygin et al., 1990). To a certain extent, differences in the karyotypes correlate with the results of molecular reconstruction (Steppan and Schenk, 2017). At the same time, another group of chromosomal data supports the proximity of the 30-chromosomal *Alexandromys* species (*A. oeconomus*, *A. kikuchii* Kuroda, *A. montebellis* Milne-Edwards) due to the similarity of their karyotypes and unique (synaptic) behavior of heterochromosomes in the meiotic prophase (Borodin et al., 1995; Mekada et al., 2001). These data are consistent with data obtained by Bannikova et al. (2010), but contradict the molecular reconstructions of some other researchers.

Genus *Microtus* Schrank (Subgenus *Terricola* Fatio). At present, the karyotypes of almost all representatives of the subgenus have been studied, and it has been demonstrated that the number of chromosomes varies from $2n = 32$ to $2n = 62$. The high level of karyological diversity detected in the subgenus *Terricola* was a trigger mechanism for taxonomic revisions of the taxon, in the composition of which the cryptic forms were later discovered at different stages of their taxonomic differentiation (Ivanov and Tembotov, 1972; Khatukhov et al., 1978; Lyapunova et al., 1988; Akhverdyan et al., 1992).

Thus, 12 morphologically similar karyomorphs of the subgenus are known in the Caucasus region and two cryptic species of pine voles are recognized: (1) the pine vole *M.* (*T.*) *majori* Thomas, which is represented by a forest form with a stable karyotype ($2n = 54$, NF = 60) widespread in the Greater and Lesser Caucasus; (2) the Dagestan vole *M.* (*T.*) *daghestanicus* Shidl., which unites subalpine voles of the Greater and Lesser Caucasus. In this species, 11 karyomorphs with different numbers of chromosomes $2n = 54, 53, 52, 46, 45, 44, 43, 42$ "A," 42 "B," 40, and

38 are known, but with a stable number of chromosome arms NF = 58 (the so-called Robertsonian fan) (Akhverdyan et al., 1992).

Different chromosomal forms of *M.* (*T.*) *daghestanicus* are allopatric or sympatric, and hybrid forms occur in their contact zones. Most fan forms can interbreed, producing fertile offspring; however, reproductive isolation was experimentally demonstrated for some forms (Mambetov and Dzuev, 1988). Therefore, some researchers consider the forms with $2n = 38$ and $2n = 42$“A” (with a range in the Lesser Caucasus) as an independent species *M.* (*T.*) *nasarovi* Shidl. (Khatukhov et al., 1978). However, this point of view found no support among taxonomists (Krystufek and Shenbrot, 2022).

The ranges of *M.* (*T.*) *daghestanicus* and *M.* (*T.*) *majori* overlap over a significant area of the Greater and Lesser Caucasus. Hybridization was not noted in any case of their cohabitation (Khatukhov et al., 1978; Baskevich et al., 1984), which confirms their species status. This conclusion is supported by data on hybridization. Thus, the experimental hybridization between these species revealed almost complete sterility of hybrid males and females (Mambetov and Dzuev, 1988).

The Caucasian endemic *M.* (*T.*) *daghestanicus*, characterized by a wide Robertsonian type chromosomal polymorphism, is included in the same group with the wideranged European—Asia Minor species *M.* (*T.*) *subterraneus* Selys-Long. Three geographically replacing karyomorphs, differing both in the number of the chromosomes and in their morphology, were found in the composition of this species (Baskevich et al., 2018; Bogdanov et al., 2021). In the underground voles inhabiting the northern part of their range in Europe, the karyotype consists of 54 chromosomes, while southern European populations are characterized by a 52-chromosome karyotype. Initially, a species level of differences was postulated for these geographically replacing karyomorphs of Eastern Europe: it was proposed to consider them as cryptic species *M.* (*T.*) *dacius* ($2n = 52$) and *M.* (*T.*) *subterraneus* ($2n = 54$) (Zagorodnyuk, 1992). However, the results of experimental hybridization and a later analysis of the cyt *b* gene polymorphism allowed the establishment of their conspecificity (Baskevich et al., 2018; Bogdanov et al., 2021).

The third karyotype variant in the underground vole ($2n = 54$, NF = 60) was detected in the northern part of Asia Minor: it differs from the 54-chromosome European karyotype by the morphology and peculiarities of localization of the X chromosome heterochromatin (Macholan et al., 2001). Recently, a high level of isolation by molecular markers (cyt *b*, fragments of *BRCA1*, *XIST*, *IRBP* nuclear genes) was discovered in the sample from Samsun located within the range of this karyomorph (Bogdanov et al., 2021), and this form is considered as the cryptic species *M.* (*T.*) *fingeri* Neuchauser 1936 in the latest taxonomic summary of the voles (Krystufek and Shenbrot, 2022).

Genus *Microtus* (subgenus *Microtus* s. str.). The taxonomic structure of the large polytypic species *Microtus arvalis* Pall. was completely revised according to the results of karyological studies and hybridization experiments (Malygin, 1983; *Obyknovennaya polevka: vidy-dvoiniki,* 1994; Meier et al., 1996). In this species, co-living cryptic species (*Microtus arvalis* Pall ($2n = 46$, NF = 84) and *M. subarvalis* Meyer et al. ($2n = 54$, NF = 56)) were for the first time identified for mammals (Meier et al., 1969, 1972). Subsequently, the name *M. subarvalis* was replaced by the senior synonym *M. rossiaemeridionalis* Ogn. (Malygin and Yatsenko, 1986). The study of a parapatric contact zone of two 46-chromosomal taxa in the European part of Russia started (Meier et al., 1997). Simultaneously, the allopatric and cryptic forms of the common vole with $2n = 46$ and NF = 72 were discovered (Orlov and Malygin, 1969), for which the species name *M. obscurus* Eversmann was later proposed (Malygin, 1983). The species isolation of *obscurus* is indicated both by the analysis of meiosis (a complete suppression of crossing over in heteromorphic regions of the chromosomes, which should lead to a limitation of the gene flow in the contact zone between *M. arvalis* and *M. obscurus*) (Basheva et al., 2014) and molecular differences of these forms (Lavrenchenko et al., 2009; Bulatova et al., 2010). The FISH method revealed the molecular markers of cytogenetic differentiation of these cryptic taxa (Bulatova et al., 2013). The polytypy of 46-chromosomal karyotype at the sites of interstitial telomeric sequences (ITS) and ribosomal DNA (rDNA) emphasizes the genetic isolation of *M. arvalis* and *M. obscurus*. The ranges of *M. obscurus* and *M. rossiaemeridionalis* partially overlap, and they behave as sympatric species in this area.

The species independence of four geographically isolated forms was demonstrated: *M. transcaspicus* Sat. ($2n = 52$, NF = 54), *M. ilaeus* Thomas ($2n = 54$, NF = 80) (Lyapunova and Mirokhanov, 1969; Malygin, 1983; Meier et al., 1996), *M. kermanensis* Rog. ($2n = 54$, NF = 56) (Golenishchev et al., 2001), and *M. mystacinus* de Filip. ($2n = 54$, NF = 56) (Bikchurina et al., 2021).

Genus *Microtus* (subgenus *Sumeriomys* Argyropulo). An interest in studying the karyotype of *Microtus schidlovskii* Arg. was caused by uncertainty of the systematic position of large voles from Transcaucasia. These voles were considered by various authors as a small form of *M. guentheri* Danford et Alston or as a subspecies of *M. socialis* Pall. The analysis of chromosome sets supported the conclusion that *M. schidlovskii* ($2n = \mathrm{NF} = 62$) belongs to the group *M. socialis* ($2n = \mathrm{NF} = 62$), but not to *M. guentheri* ($2n = 54$, NF = 56). Data on hybridization of *M. socialis* and *M. schidlovskii* demonstrated male sterility in F_1 hybrids and reduced fertility in females. This confirmed the species independence of *M. schidlovskii* in the Caucasus (Akhverdyan et al., 1991, 1991a). The description of a karyotype with a different number of chromosomes ($2n = 60$) in *M. schidlovskii* from Armenia indicates the possibility of new discoveries in this taxonomic group (Mahmudi et al., 2022).

Genus *Meriones* Illiger. The karyotypes of gerbils of eight species of the genus on the territory of the former Soviet Union and Mongolia were described for the first time by employees in numerous works of two laboratories under the leadership of N.N. Vorontsov (Novosibirsk, Vladivostok) and V.N. Orlov (Moscow). Information about these publications is given in a review work by Korobitsyna and Kartavtseva (1984). The use of the methods of differential staining of the chromosomes of the studied species gave confirmation of the stability of the number of chromosomes, demonstrating their species specificity, and to identify a geographical variability in the amount and localization of C-positive heterochromatin for *M. tristrami* Thomas (Korobitsyna et al., 1984), *M. libycus* Licht. (Korobitsyna and Kartavtseva, 1992), and *M. meridianus* Pall. (Korobitsyna and Kartavtseva, 1988). A possible association of the duplicated heterochromatin material of the chromosomes with different resistance of individuals to the plague microbe was suggested. For *M. tristrami* of Azerbaijan, intraspecific groupings with different resistance to the plague microbe can also be marked by the peculiarities of redistribution of C-heterochromatin. Data on the presence of intraspecific variability of the 15th pair of chromosomes of *M. meridianus* (inversions, deletions–duplications, translocations) allowed the revision of the subspecies structure. Most likely, individuals distributed on the territory of Mongolia belong to an independent species *M. psammophilus*, which was demonstrated by molecular-genetic methods (Neronov et al., 2009).

Genus *Apodemus* Kaup. Chromosomal and morphological studies allowed the clear separation of *Apodemus speciosus* Temm. into two species and demonstrated that the Japanese mouse (*A. speciosus*) lives only on the islands of the Japanese archipelago; on the mainland, the East Asian mouse is found (*A. peninsulae* Thomas = *A. giliacus*) (Vorontsov et al., 1977).

Genus *Sylvaemus* Ognev. The use of chromosome peculiarities to clarify the systematic position is promising even in the cases when the sympatric forms do not differ in the number of chromosomes and G-banding, as in the genus *Sylvaemus* ($2n = 48$) (Chelomina et al., 1998; Kartavtseva, 2002). Since differences in the position of heterochromatic blocks and NOR can be markers of inversions, they can also be associated with the disruption of meiosis in hybrids.

In some regions of Eastern Europe, three species of the genus *Sylvaemus* are common: *S. flavicollis* Melchior, *S. sylvaticus* L., and *S. uralensis* Ogn. Diagnostic differences between these species in the location of heterochromatic blocks and NORs, as well as differences between *S. sylvaticus* of Western and Eastern Europe, were demonstrated (Orlov et al., 1996a, 1996b). Since this species has not yet been studied from the type locality (Sweden, Uppsala), its nomenclature remains unclear. The relationship between *S. uralensis* Ogn from Eastern Europe and *S. microps* Kratochvil et Rosicky described from the Carpathians also remains unclear.

For two species *S. uralensis* Ogn. and *S. ponticus* Sviridenko (living together in the Caucasus), diagnostic differences in heterochromatic blocks present in the populations of both the eastern (Kozlovskii et al., 1990) and western parts of the forest belt (Baskevich et al., 2004a) were demonstrated.

According to some estimations, the degree of differentiation of species from the genus *Sylvaemus* has the smallest value at the morphological level, the highest values at the isozyme level, and average values at the molecular and chromosomal levels (FISH analysis of C-positive regions of the chromosomes) (Rubtsov et al., 2011).

Genus *Mus* L. For *Mus musculus musculus* L. (in which Robertsonian-type polymorphism is unknown, unlike *Mus musculus domesticus* Schwarz et Schwarz (Kapanna, 1988)), variability in the amount and distribution of autosomal heterochromatin was described (Bulatova et al., 1984; Yakimenko and Korobitsyna, 2007). To distinguish a number of species and subspecies taxa of *Mus* house mice with the same diploid number ($2n = 40$), the peculiarities of the morphology of sex chromosomes with pericentromeric heterochromatin can be used. The karyotype of *M. spretus* Lataste is distinguished by a miniature Y chromosome, while one of the variants of the X chromosome (‘*molossinus*’ type) is typical not only for *M. m. molossinus* living in Japan, but also for all studied *Mus m. musculus* L. samples from the territory of the former Soviet Union, while a plesiomorphic variant of the X chromosome ‘*domesticus*’ is found in *M. m. domesticus*, *M. m. hortulanus* Nord., *M. abbotti* Water., and *M. spretus* Lataste (Korobitsyna et al., 1993). Along with data on mtDNA variability, cytogenetic characteristics were a basis for reconstructing the settlement routes of different groups of house mice in Eurasia (Suzuki et al., 2015).

In the above examples of cytogenetic differentiation of the populations, we noted the associated hybrid disorders that can lead to the emergence of reproductive isolation. For intraspecific taxonomy and microevolutionary studies, it is extremely important to use the chromosomal rearrangements also as indices of a monophyletic origin of the population groups (chromosomal forms). Any fixed chromosomal rearrangements (that is, reaching a frequency in the populations close to 100%) indicate the genealogical relationship of such population groups (Baker and Bradley, 2006). Therefore, it becomes possible to compare the phenotypic similarity of the populations and their kinship and to estimate the role of the past evolution of the species in the formation of its modern geographic variability.

In the evolutionary taxonomy, the construction of monophyletic taxa or the existence of a certain correspondence between the classification and phylogeny of the organisms is considered to be the main task. But such a task is not posed in intraspecific taxonomy due to the absence of information about the phylogenetic relationships of the populations. Taxonomists estimate only the similarities and differences of the populations; therefore, a subspecies is not considered as a "unit of evolution" except in rare cases of isolates (Mayr, 1969).

The traces of the past refugial structure of the species are leveled out in the processes of resettlement of populations during warm interglacial periods (such as the Holocene). The traces of the past refugial structure of the species are preserved by phylogroups and populations with chromosomal rearrangements. If geographic or genetic isolation is required for the preservation of phylogroups, then the boundaries of chromosomal forms can persist under conditions of free gene flow (Horn et al., 2012).

For example, the monophyletic origin of three groups of subspecies of mountain sheep (*Ovis ammon* L.) (initially demonstrated on the chromosomes) was also confirmed by molecular data, since these groups of sheep in their evolution were geographically isolated (although a weakening of the gene flow in their hybridization zones is not excluded). On the contrary, molecular differences between the populations are erased in the modern single range of the common shrew (*Sorex araneus*). At the same time, the chromosomal rearrangements indicating a monophyletic origin of some chromosomal races are preserved. At present, such chromosomal races are separated by narrow hybrid zones.

CYTOGENETIC DIFFERENTIATION OF POPULATIONS AND FORMATION OF ETHOLOGICAL ISOLATION BY SELECTION: PROSPECTS OF STUDIES

At the first stages of cytogenetic studies of *Drosophila* and mammals, the reproductive isolation with small chromosomal differences was explained by saltation (rapid) speciation. But the sterility of hybrids is completely optional for the emergence of complete reproductive isolation. The process of the formation of reproductive isolation consists of two stages: (1) the occurrence of adaptability fitness of hybrid individuals and (2) the formation of ethological isolation of contacting populations by selection. Even in the case of a slight decrease in the fertility of heterozygotes caused by chromosomal differences, selection is capable of forming ethological isolation or preferential crossing within each form, up to a complete reproductive isolation of contacting forms (Coyne and Orr, 2004).

In the world literature, the enhancement of genetic isolation by natural selection, which forms ethological isolation, is called "reinforcement" (there is no Russian term) (Coyne and Orr, 2004). As a consequence of "reinforcement," no sterile hybrids are known in natural populations of mammals, while the experimental crossings of the species reproductively isolated in nature sometimes produce fertile offspring. Information began to accumulate that in many species (from *Drosophila* to mammals), there is no direct dependence between the value of genetic differences (genetic or chromosomal) and the level of ethological isolation formed by selection. Therefore, in the study of the processes of speciation, attention should be paid to even slight disturbances of meiosis in hybrids. Studies of the formation of reproductive isolation by selection are just beginning and represent a promising direction of evolutionary studies.

According to the Bateson–Dobzhansky–Muller (BDM) model, the emergence of isolated populations is a condition for the formation of genetic isolating mechanisms. Such conditions have arisen many times in the history of ecosystems on Earth. The climate of the planet in the Pleistocene (last two million years) is called glacial due to a periodic long-term decrease in the average annual temperatures by 6–8°C (as compared with the middle of the 20th century). In the last 420000 years of the history of the Earth alone, four long-term coolings are known (each lasting from 70000 to 110 000 years) (Petit et al., 1999). During the periods of glaciation, the ranges of many species in temperate regions of Europe were reduced and fragmented (Hewitt, 1996). The same processes took place in Asia. Neutral chromosomal rearrangements (accumulated in the populations) could have been fixed in small isolated populations of glacial refugia (Orlov et al., 2017).

The relatively rapid chromosomal evolution in the populations of house mice from Western Europe (*Mus musculus domesticus*) over the past three thousand years can be considered only as an exception. The accumulation of chromosomal rearrangements can be explained by increased frequency of interchromosomal exchanges and other mutations in pericentromeric regions of the chromosomes (Garagna et al., 2014); their rapid fixation, by a demic structure of the populations of this commensal species (Lavrenchenko and Bulatova, 2015). In the mole vole *E. alaicus*, the fixation of Robertsonian translocation in the population of Tajikistan occurred extremely rapidly (over three decades) (Matveevsky et al., 2020a).

During the modern warm and relatively short (12000 years) period in the history of the Earth (Holocene), various zones of "allopatric hybridization" arose between previously isolated populations (Mayr, 1963). The use of this term is useful, when it is necessary to emphasize that the hybrid zone arose as a result of secondary contact. Modern geographical isolates are known on the periphery of the species range, while the zones of allopatric hybridization can be found in any part of the species range. Their location is determined by the past refugial structure of the species.

The zones of allopatric hybridization are frequently considered as key objects for studying the processes of speciation and estimating the degree of isolation of contacting populations (Jiggins and Mallet, 2000). The hybrid zones between the chromosomal races of the common shrew are a good example of the zones of "allopatric hybridization" in mammals.

There are several ways to estimate the isolation of contacting populations. First of all, it is possible to estimate the intensity of hybridization using cytogenetic or molecular markers in the study of contact zones. The species status of contacting forms is indicated by the absence of hybridization, for example, in the contact zones of *Cricetulus barabensis* and *C. pseudogriseus* (Poplavskaya et al., 2012). The gene flow can also be interrupted in a narrow hybrid zone (for example, of the common shrew and *Sorex antinorii* Bon. in the Alps (Yannic et al., 2009)) or in a fairly wide (up to 30 km) hybrid zone of the house mice *Mus m. musculus* and *M. m. domesticus* (Bímová et al., 2011).

To estimate the degree of reproductive isolation in the contact zones (first of all, ethological), the traditional methods of studying behavioral isolation are used, when contacting forms are compared in vitro on individuals taken from the zones of allopatry and hybridization. For example, ethological isolation in the above-mentioned zone of allopatric hybridization of house mice (Bímová et al., 2011) and ethological isolation of phylogroups of the common vole (*Microtus arvalis*) (Beysard et al., 2015) were demonstrated in this way. Such direct methods for estimating the ethological isolation of contacting forms are limited to the species that are convenient to work with in vitro.

For a quantitative estimation of the assortativity of crosses (ethological isolation) in the zones of allopatric hybridization, it is possible to use the deficiency of heterozygotes (inbreeding index, F_{IS}) (Jiggins and Mallet, 2000) or the degree of assortativity of crosses (R index) (Orlov et al., 2019), that is, the deviations of detected chromosome frequencies from those expected during random crossing according to the Hardy–Weinberg (taking into account the Wahlund effect). Among mammals, three model objects are known, on which the role of centric chromosome associations in the occurrence of reproductive isolation was studied in recent decades: the Western European house mouse, common shrew, and species of the genus of mole voles.

In the common shrew, dozens of hybrid zones are known between the chromosomal races, with different centric chromosome fusions (zones of parapatric hybridization). The structure of some hybrid zones (including those on the territory of the Russian Federation) was described in detail (review by Fedyk et al., 2019). The indices of heterozygote deficiency and assortativity of crosses were calculated in 11 hybrid zones between the chromosomal races and in the hybrid zone between the cryptic species of the Bonaparte shrew (*Sorex antinorii* Bon.) and the Vaud chromosomal race of the common shrew (Orlov et al., 2019).

An association between the assortativity of crosses and complication of the configuration of conjugating chromosomes in meiosis is clearly traceable. In the hybrid zones with "simple heterozygotes," conjugation of three chromosomes in meiosis I, the inbreeding index is close to 0, and the frequency of homozygotes and heterozygotes corresponds to those expected under the assumption of a random crossing according to Hardy–Weinberg. Intrapopulation chromosomal polymorphism by one–three centric chromosome fusions (accompanied by "simple heterozygotes") is frequently found in common shrew populations.

In hybrid zones of the chromosomal races of the common shrew with "complex heterozygotes" (rings out of 4–5 chromosomes) in meiosis I, a significant deficiency of heterozygotes is noted, while the proportion of assortative crosses (R) in the hybrid zone between individuals of the same chromosomal form approaches half of all crosses (0.37–0.55) (Orlov et al., 2019).

In hybrid zones with more "complex heterozygotes" (chains out of 9–11 conjugating chromosomes and rings out of six chromosomes) (for example, between the chromosomal races Novosibirsk/Tomsk (Polyakov et al., 2011), Seliger/Moscow (Bulatova et al., 2011), Seliger/Western Dvina (Orlov et al., 2013), and Pechora/Kirillov (Pavlova and Shchipanov, 2014)), the portion of assortative crossings increases significantly (to 0.86–0.96). But even in such hybrid zones, the gene flow is not interrupted (Grigor'eva et al., 2015), although it is reduced, judging by significant morphometric differences in the jaw apparatus in the shrews of contacting populations of chromosomal races (Orlov et al., 2013a).

In the contact zone in the Alps of the Vaud chromosomal race of the common shrew and Bonaparte shrew, complete genetic isolation (while maintaining a narrow hybrid zone) is reached with nine different centric fusions and heterozygotes with the chains out of seven and 11 conjugating chromosomes (Yannic et al., 2009) with $R = 0.995$ (Orlov et al., 2019). Consequently, complete interruption of the gene flow in this hybrid zone occurs with the same heterozygotes as in many genetically non-isolated chromosomal races of the common shrew. Most likely, complete genetic isolation in this case is reached by an increase in the ethological isolation. Although the modern contact between the common shrew and the Bonaparte shrew occurred relatively recently, at the end of the 19th century (Yannic et al., 2009), the isolation of these cryptic species is dated back to the mid-Pleistocene (Mackiewicz et al., 2017).

The isolating effect of chromosomal rearrangements depends entirely on their type. The cryptic species *M.* (*T.*) *majori* and *M.* (*T.*) *daghestanicus* in the sympatry zone in the Western Caucasus differ in the centromere position in the first two pairs of autosomes (transposition), pericentric inversion in the 26th pair of autosomes, and paracentric inversion of the X chromosome (Baskevich et al., 2015). At present, there is not enough data to derive a general rule for the correlation of the chromosomal differences and hybrid sterility. It is well known that hybrid disorders can be also accompanied by gene differences. However, differences in the karyotypes are a taxonomic trait, which makes it possible to calculate the deficiency of heterozygotes in the zones of allopatric hybridization and to estimate the degree of reproductive isolation of contacting forms based on these indices.

CONCLUSIONS

Since the 1970s, the development of the methods for differential staining of chromosomes (and subsequently the FISH analysis) consistently increased the resolving levels of cytogenetic differentiation for studying the issues of the taxonomy and phylogenetic relationships of the species. Cytogenetic studies significantly changed the taxonomy of mammals. It was found that many species that were traditionally considered as large polytypic are complexes of morphologically similar, but genetically well distinguished and reproductively isolated species. The identification of cryptic (hidden siblingspecies is a necessary link in the description of biological diversity and at the same time attracts attention to a new level of discussion of the concepts of species and speciation.

For a taxonomist, the study of the chromosomes is interesting as a study of nuclear structures, a change in the composition, shape, and number of which leads to genetic isolation. Only at the end of the 20th century it was demonstrated that the sterility of hybrids is not required at all for the occurrence of complete reproductive isolation. The process of the emergence of reproductive isolation consists of two stages, including the emergence of reduced adaptability of hybrid individuals and the formation of ethological isolation of contacting populations by selection. It was demonstrated that, even in the case of a slight decrease in the fertility of heterozygotes (caused by chromosomal differences), selection can form an ethological isolation, preferential crossing within each form, up to complete reproductive isolation of contacting forms. The study on the formation of reproductive isolation by selection is just a beginning and represents a promising direction of evolutionary studies.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

Abramson, N.I. and Lisovskii, A.A., Subfamily Arvicolinae, in *Mlekopitayushchie Rossii: sistematiko-geograficheskii spravochnik* (Mammals of Russia: Systematic and Geographical Reference Book), *Tr. Zool. Muz. Mosk. Gos. Univ.*, 2012, vol. 52, pp. 127–141.

Akhverdyan, M.R., Vorontsov, N.N., and Lyapunova, E.A., On the species independence of Shidlovsky's plateau vole *Microtus schidlovskii* Argyropulo, 1933 (Rodentia, Cricetidae) from western Armenia, *Biol. Zh. Arm.*, 1991, vol. 44, pp. 260–265.

Akhverdyan, M.R., Vorontsov, N.N., and Lyapunova, E.A., Flat-mountain Schidlovsky's vole *Microtus schidlovskii* (Rodentia, Cricetidae)—an independent species of the fauna of Armenia, *Biol. Zh. Arm.*, 1991a, vol. 44, pp. 266–271.

Akhverdyan, M.R., Lyapunova, E.A., and Vorontsov, N.N., Karyology and systematics of bush voles of the Caucasus and Transcaucasia (Terricola, Arvicolinae, Rodentia), *Zool. Zh.*, 1992, vol. 71, pp. 96–110.

Anbinder, E.M., *Kariologiya i evolyutsiya lastonogikh* (Karyology and the Evolution of Pinnipeds), Moscow: Nauka, 1980.

Aniskin, V.M., Bogomolov, P.L., Kovalskaya, Yu.M., Lebedev, V.S., Surov, A.V., and Tikhonov, I.A., Karyological differentiation of birch mice of the "subtilis" group (Rodentia, Sicista) in the southeast of the Russian Plain, in *Materialy Mezhdunarodnogo soveshchaniya "Sistematika, filogeniya i paleontologiya melkikh mlekopitayushchikh"* (Materials of the International Meeting "Systematics, Phylogeny, and Paleontology of Small Mammals"), St. Petersburg: Zool. Inst. Ross. Akad. Nauk, 2003, pp. 27–29.

Atlas of Mammalian Chromosomes, Graphodatsky, A.S., Perelman, P.L., and O'Brien, S.J., Eds., USA: Wiley-Blackwell, 2020, 2nd ed.

Baker, R.J. and Bradley, R.D., Speciation in mammals and the genetic species concept, *J. Mamm.*, 2006, vol. 87, pp. 643–662.

Bakloushinskaya, I.Yu., Chromosomal rearrangements, genome reorganization and speciation, *Zool. Zh*., 2016, vol. 95, pp. 376–393.

Bakloushinskaya, I.Yu., Matveevsky, S.N., Romanenko, S.A., Serdukova, N.A., Kolomiets, O.L., et al., A comparative analysis of the mole vole sibling species *Ellobius tancrei* and *E. talpinus* (Cricetidae, Rodentia) through chromosome painting and examination of synaptonemal complex structures in hybrids, *Cytogenet. Genome Res*., 2012, vol. 136, pp. 199–207.

Bakloushinskaya, I., Lyapunova, E.A., Saidov, A.S., Romanenko, S.A., O'Brien, P.C.M., et al., Rapid chromosomal evolution in enigmatic mammal with XX in both sexes, the Alay mole vole *Ellobius alaicus* Vorontsov et al. 1969 (Mammalia, Rodentia), *Comp. Cytogenet*., 2019, vol. 13, pp. 147–177.

Bannikova, A.A., Lebedev, V.S., Lissovsky, A.A., Matrosova, V., Abramson, N.I., et al., Molecular phylogeny and evolution of the asian lineage of vole genus *Microtus* (Rodentia: Arvicolinae) inferred from mitochondrial cytochrome *b* sequence, *Biol. J. Linn. Soc*., 2010, vol. 99, pp. 595–613.

Basheva, E.A., Torgasheva, A.A., Golenischev, F.N., Frisman, L.V., and Borodin, P.M., Chromosome synapsis and recombination in the hybrids between chromosome races of the common vole *Microtus aravalis*: "*arvalis*" and "*obscurus,*" *Dokl. Biol. Sci*., 2014, vol. 456, pp. 206–208.

Baskevich, M.I. and Malygin, V.M., Chromosomal approaches in studying the patterns of formation of genetic and taxonomic diversity of rodents of the Caucasus using the example of birch mice, *Sicista* (Rodentia, Dipodoidea) fauna of the Caucasian region, in *Gornye ekosistemy i ikh komponenty. Materialy III mezhdunarodnoi konferentsii, 24–29 avg. 2009 g., Nal'chik* (Mountain Ecosystems and Their Components. Proc. III Int. Conf., August 24–29, 2009, Nalchik), Moscow: KMK, 2009, part 2, pp. 204–210.

Baskevich, M.I., Lukyanova, I.V., and Kovalskaya, Yu.M., On the distribution of two forms of bush voles *Pitymys majori* Thomas and *Pitymys daghestanicus* Schidl. in the Caucasus, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol*., 1984, vol. 89, pp. 29–33.

Baskevich, M.I., Okulova, N.M., Potapov, S.G., and Varshavskii, A.A., Diagnosis, distribution, and evolution of Caucasian birch mice (Rodentia, Dipodoidea, *Sicista*), *Zool. Zh*., 2004, vol. 83, pp. 220–233.

Baskevich, M.I., Potapov, S.G., Okulova, N.M., and Balakirev, A.E., Diagnosis of mice of the genus *Apodemus* (Rodentia, Muridae) from the western part of the Greater Caucasus under symbiotopic conditions, *Zool. Zh*., 2004a, vol. 83, pp. 1261–1269.

Baskevich, M.I., Oparin, M.L., Cherepanova, E.V., and Avilova, E.A., Chromosomal differentiation of the steppe mouse, *Sicista subtilis* (Rodentia, Dipodoidea) in the Saratov Volga region, *Zool. Zh*., 2010, vol. 89, pp. 749–757.

Baskevich, M.I., Sapelnikov, S.F., and Vlasov, A.A., New data on the chromosomal variability of the dark birch mouse (*Sicista severtzovi*, Rodentia, Dipodoidea) from the Central Black Earth Region, *Zool. Zh*., 2011, vol. 90, pp. 59–66.

Baskevich, M.I., Potapov, S.G., and Mironova, T.A., Cryptic species of rodents of the Caucasus as models in the study of problems of species and speciation, *Zh. Obshch. Biol*., 2015, vol. 75, no. 4, pp. 333–349.

Baskevich, M.I., Bogdanov, A.S., Khlyap, L.A., Shvarts, E.A., and Litvinova, E.M., Taxonomic interpretation of allopatric mammalian forms on the example of two karyoforms of *Microtus* (*Terricola*) *subterraneus* (Rodentia, Arvicolinae) from Eastern Europe, *Dokl. Biol. Sci*., 2018, vol. 480, pp. 119–123.

Beysard, M., Krebs-Wheaton, R.K., and Heckel, G., Tracing reinforcement through asymmetrical partner preference in the European common vole *Microtus arvalis, BMC Evol. Biol*., 2015, vol. 15, pp. 170–181.

Bikchurina, T.I., Kizilova, E.A., Borodin, P.M., Golenishchev, F.N., and Mahmoudi, A., Reproductive isolation between taxonomically controversial forms of the gray voles (*Microtus*, Rodentia; Arvicolinae): cytological mechanisms and taxonomical implications, *Front. Genet*., 2021, vol. 12, p. 653837.

Biltueva, L.S., Perelman, P.L., Polyakov, A.V., Zima, J., Dannelid, E., et al., Comparative chromosome analysis in three *Sorex* species: *S. raddei, S. minutus* and *S. caecutiens, Acta Theriol*., 2000, vol. 45, suppl. 1, pp. 119–130.

Bímová, B.V., Macholán, M., Baird, S.J.E., Munclinger, P., Dufková, P., et al., Reinforcement selection acting on the European house mouse hybrid zone, *Mol. Ecol*., 2011, vol. 20, pp. 2403–2424.

Bogdanov, Yu.F., Kolomiets, O.L., Lyapunova, E.A., Yanina, I.Yu., and Mazurova, T.F., Synaptonemal complexes and chromosome chains in the rodent *Ellobius talpinus* heterozygous for the ten Robertsonian translocations, *Chromosoma* (Berl.), 1986, vol. 94, pp. 94–102.

Bogdanov, A., Khlyap, L., Kefelioğlu, H., Selcuk, A.Y., Stakheev, V.V., and Baskevich, M.I., High molecular variability in three pine vole species of the subgenus *Terricola* (*Microtus*, Arvicolinae) and plausible source of polymorphism, *J. Zool. Syst. Evol. Res*., 2021, vol. 59, pp. 2519–2538.

Borisov, Yu. and Orlov, V., A comparison of the chromosome G-banding pattern in two *Sorex* species, *S. satunini* and *S. araneus* (Mammalia, Insectivora), *Comp. Cytogenet*., 2012, vol. 6, pp. 267–271.

Borodin, P.M. and Polyakov, A.V., Genes, chromosomes, and speciation, in *Sovremennye problemy biologicheskoi evolyutsii: Trudy konferentsii k 100-letiyu Gos. Darvinovskogo muzeya* (Modern Problems of Biological Evolution. Proc. Conference on the 100th Anniversary of the State Darwin Museum), Moscow: GDM, 2008, pp. 136–148.

Borodin, P.M., Sablina, O.V., and Rodionova, M.I., Pattern of X-Y chromosome pairing in Microtine rodents, *Hereditas*, 1995, vol. 123, pp. 17–23.

Borodin, P.M., Fedyk, S., Chetnicki, W., Torgasheva, A.A., Pavlova, S.V., and Searle, J.B., Meiosis and fertility associated with chromosomal heterozygosity, in *Shrews, Chromosomes and Speciation*, Searle, J.B., Polly, P.D., and Zima, J., Eds., Cambridge: Cambridge Univ. Press, 2019, Chapter 7, pp. 217–270.

Brandler, O.V., On the species independence of the forest-steppe marmot *Marmota kastschenkoi* (Rodentia, Marmotinae), *Zool. Zh*., 2003, vol. 82, pp. 1498–1505.

Bulatova, N.Sh., Orlov, V.N., and Kotenkova, E.V., New data on the variability of heterochromatin in house mouse populations, *Dokl. Akad. Nauk SSSR*, 1984, vol. 275, p. 758.

Bulatova, N.Sh., Golenishchev, F.N., Kovalskaya, Yu.M., Emel'yanova, L.G., Bystrakova, N.V., et al., Cytogenetic study of the parapatric contact zone between two 46-chromosomal forms of the common vole in European Russia, *Russ. J. Genet.*, 2010, vol. 46, pp. 443–448.

Bulatova, N., Jones, R.M., White, T.A., Shchipanov, N.A., Pavlova, S.V., and Searle, J.B., Natural hybridization between extremely divergent chromosomal races of the common shrew (*Sorex araneus*, Soricidae, Soricomorpha): hybrid zone in European Russia, *J. Evol. Biol.*, 2011, vol. 24, pp. 573–586.

Bulatova, N.Sh., Pavlova, S.V., Romanenko, S.A., Serdyukova, N.A., Golenishchev, F.N., et al., Molecular cytogenetic markers of cryptic species and hybrids of the common vole superspecies complex *Microtus arvalis* s. l., *Tsitologiya*, 2013, vol. 55, pp. 268–270.

Bulatova, N.S., Biltueva, L.S., Pavlova, S.V., Zhdanova, N.S., and Zima, J., Chromosomal differentiation in the common shrew and related species, in *Shrews, Chromosomes and Speciation*, Searle, J.B., Polly, P.D., and Zima, J., Eds., Cambridge: Cambridge Univ. Press, 2019, Ch. 5, pp. 134–184.

Bunch, T.D., Vorontsov, N.N., Lyapunova, E.A., and Hoffmann, R.S., Chromosome number of Severtzov's sheep (*Ovis ammon severtzovi*): G-banded karyotype comparisons within *Ovis, J. Hered.*, 1998, vol. 89, pp. 267–269.

Bykova, G.V., Vasilyeva, I.A., and Gileva, E.A., Chromosomal and morphological diversity in 2 populations of Asian mountain vole, *Alticola lemminus* Miller (Rodentia, Cricetidae), *Experientia*, 1978, vol. 34, pp. 1146–1148.

Chelomina, G.N., Pavlenko, M.V., Kartavtseva, I.V., Boeskorov, G.G., Lyapunova, E.A., and Vorontsov, N.N., Genetic differentiation of Caucasian wood mice: comparison of isozymic, chromosomal, and molecular divergence, *Russ. J. Genet.*, 1998, vol. 34, pp. 151–162.

Chernyavskii, F.B. and Kozlovskii, A.I., Species status and history of collared lemmings (*Dicrostonyx*, Rodentia) of Wrangel Island, *Zool. Zh.*, 1980, vol. 60, pp. 266–273.

Courant, F., Brunet-Lecomte, P., Volobouev, V., Chaline, J., Quéré, J.-P., et al., Karyological and dental identification of *Microtus limnophilus* in a large focus of alveolar echinococcosis (Gansu, China), *Compt. Rend. Acad. Sci. Paris*, 1999, vol. 322, pp. 473–480.

Coyne, J.A. and Orr, H.A., *Speciation*, Sunderland: Sinauer Associates, Inc., 2004.

Cracraft, J., Species concepts and speciation analysis, in *Current Ornithology*, Johnston, R.F., Ed., New York: Plenum, 1983, vol. 1, pp. 159–187.

Dobigny, G., Britton-Davidian, J., and Robinson, T.J., Chromosomal polymorphism in mammals: an evolutionary perspective, *Biol. Rev.*, 2017, vol. 92, pp. 1–21.

Dobzhansky, T., *Genetics and the Origin of Species*, New York: Columbia Univ. Press, 1937.

Dokuchaev, N.E. and Sheremet'eva, I.N., The identity of gray voles (Cricetidae, Rodentia) from Bolshoi Shantar Island, Sea of Okhotsk, with Gromov's vole (*Alexandromys gromovi* Vorontsov et al. 1988), *Biol. Bull.* (Moscow), 2018, vol. 45, pp. 783–788.

Dzuev, R.I., *Khromosomnye nabory mlekopitayushchikh Kavkaza* (Chromosome Sets of Mammals of the Caucasus), Nal'chik: El'brus, 1998.

Evolutionary Dynamics of Mammalian Karyotypes, Stanyon, R. and Graphodatsky, A., Eds., Basel: Karger, 2012.

Fedorov, V.B. and Goropashnaya, A.V., The importance of ice ages in diversifications of Arctic collared lemmings (*Dicrostonyx*): evidence from the mitochondrial cytochrome *b* region, *Hereditas*, 1999, vol. 130, pp. 301–307.

Fedorov, V., Fredga, K., and Jarrel, G., Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian Arctic, *J. Evol. Biol.*, 1999, vol. 12, pp. 134–145.

Fedyk, S., Pavlova, S.V., Chetnicki, W., and Searle, J.B., Chromosomal hybrid zones, in *Shrews, Chromosomes and Speciation*, Searle, J.B., Polly, P.D., and Zima, J., Eds., Cambridge: Cambridge Univ. Press, 2019, Chapter 8, pp. 271–312.

Formozov, N.A. and Baklushinskaya, I.Yu., On the species status of Hoffmann's pika (*Ochotona hoffmanni* Formozov et al. 1996) and its inclusion in the fauna of Russia, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1999, vol. 104, pp. 68–72.

Formozov, N.A. and Baklushinskaya, I.Yu., Manchurian pika (*Ochotona mantchurica scorodumovi*) from the Shilka and Argun interfluves: karyotype and taxonomic issues of pika species of the Amur region and adjacent territories, *Zool. Zh.*, 2011, vol. 90, pp. 490–497.

Formozov, N.A., Lisovskii, A.Yu., and Baklushinskaya, I.Yu., Karyological diagnosis of pikas (*Ochotona*, Lagomorpha) of the Putorana Plateau, *Zool. Zh.*, 1999, vol. 78, pp. 606–612.

Formozov, N.A., Baklushinskaya, I.Yu., and Ma, Yu., Taxonomic status of the Alashan pika, *Ochotona argentata* (Alashan Ridge, Ningxia Hui Autonomous Prefecture, China), *Zool. Zh.*, 2004, vol. 83, pp. 995–1007.

Fredga, K., Fedorov, V., Jarrel, G., and Jonsson, L., Genetic diversity in Arctic lemmings, *AMBIO*, 1999, vol. 28, pp. 261–269.

Frisman, L.V., Korablev, V.P., Lyapunova, E.A., Vorontsov, N.N., and Brandler, O.V., Allozyme differentiation of heterochromosomal forms of the speckled ground squirrel (*Spermophilus suslicus* Guld 1770, Rodentia), *Russ. J. Genet.*, 1999, vol. 35, pp. 307–313.

Garagna, S., Page, J., and Fernandez-Donoso, R., The Robertsonian phenomenon in the house mouse: mutation, meiosis and speciation, *Chromosoma*, 2014, vol. 123, pp. 529–544.

Gileva, E.A., B chromosomes, unusual inheritance of sex chromosomes and sex ratio in the Arctic lemming *Dicrostonyx torquatus torquatus* Pall., 1779, *Dokl. Akad. Nauk SSSR*, 1973, vol. 213, pp. 952–955.

Gileva, E.A., Karyotype of *Dicrostonyx torquatus chionapaeus* Allen and the unusual chromosomal mechanism of sex determination in Palearctic lemmings, *Dokl. Akad. Nauk SSSR*, 1975, vol. 224, pp. 697–700.

Gileva, E.A., A contrasted pattern of chromosome evolution in two genera of lemmings, *Lemmus* and *Dicrostonyx* (Mammalia, Rodentia), *Genetics*, 1983, vol. 60, pp. 173–179.

Gileva, E.A., *Khromosomnaya izmenchivost' i evolyutsiya* (Chromosomal Variation and Evolution), Moscow: Nauka, 1990.

Gileva, E.A., Kuznetsova, I.A., and Cheprakov, M.I., Chromosome sets and taxonomy of true lemmings (*Lemmus*), *Zool. Zh.*, 1984, vol. 63, pp. 105–114.

Gileva, E.A., Khopunova, S.E., Novokshanova, T.G., and Zibina, E.V., Chromosomal speciation and folliculogenesis in the semisterile interspecific hybrids of the varying lemmings, *Zh. Obsch. Biol.*, 1994, vol. 55, pp. 700–707.

Golenischev, F.N., Meyer, M.N., and Bulatova, N.Sh., The hybride zone between two karyomorphs of *Microtus arvalis* (Rodentia, Arvicolidae), *Proc. Zool. Inst. Russ. Acad. Sci.*, 2001, vol. 289, pp. 89–94.

Graphodatsky A.S., Conserved and variable elements of mammalian chromosomes, in *Cytogenetics of Animals*, Halnan, C.R.E., Ed., Oxon, UK: CAB International Press, 1989, pp. 95–124.

Graphodatsky, A.S. and Radzhabli, S.I., *Khromosomy sel'skokhozyaistvennykh i laboratornykh mlekopitayushchikh. Atlas* (Chromosomes of Agricultural and Laboratory Mammals. Atlas), Novosibirsk: Nauka, 1988.

Graphodatsky, A.S., Radzhabli, S.I., Meier, M.N., and Malikov, V.G., Comparative cytogenetics of hamsters of the genus *Calomyscus* (Rodentia, Cricetidae), *Zool. Zh.*, 1989, vol. 68, pp. 151–157.

Grigoryeva, O.O., Borisov, Yu.M., Stakheev, V.V., Balakirev, A.E., Krivonogov, D.M., and Orlov, V.N., Genetic structure of the common shrew *Sorex araneus* L. 1758 (Mammalia, Lipotyphla) in continuous and fragmented areas, *Russ. J. Genet.*, 2015, vol. 51, pp. 607–618.

Haring, E., Sheremetyeva, I.N., and Kryukov, A.P., Phylogeny of Palearctic vole species (genus *Microtus*, Rodentia) based on mitochondrial sequences, *Mamm. Biol.*, 2011, vol. 76, pp. 258–267.

Hewitt, G.M., Some genetic consequences of ice ages, and their role in divergence and speciation, *Biol. J. Linn. Soc.*, 1996, vol. 58, pp. 247–276.

Horn, A., Basset, P., Yannic, G., Banaszek, A., Borodin, P.M., et al., Chromosomal rearrangements do not seem to affect the gene flow in hybrid zones between karyotypic races of the common shrew (*Sorex araneus*), *Evolution*, 2012, vol. 66, pp. 882–889.

Ivanitskaya, E.Yu. and Kozlovskii, A.I., Karyotypes of Palaearctic shrews of the subgenus *Otisorex* with comments on the systematics and phylogeny of the "*cinereus*" group, *Zool. Zh.*, 1985, vol. 64, pp. 950–953.

Ivanitskaya, E.Yu., Kozlovskii, A.I., Orlov, V.N., Kovalskaya, Yu.M., and Baskevich, M.I., New data on karyotypes of shrews from the fauna of the USSR (*Sorex*, Soricidae, Insectivora), *Zool. Zh.*, 1986, vol. 65, pp. 1228–1236.

Ivanov, V.G. and Tembotov, A.K., Chromosome sets and taxonomic status of bush voles of the Caucasus, in *Fauna, ekologiya i okhrana zhivotnykh Severnogo Kavkaza* (Fauna, Ecology, and Conservation of Animals of the North Caucasus), Nal'chik, 1972, vol. 1, pp. 45–71.

Ivanova, N.G., Kartavtseva, I.V., Stefanova, V.N., Ostromyshenskii, D.I., and Podgornaya, O.I., Tandem repeat diversity in two closely related hamster species—the Chinese hamster (*Cricetulus griseus*) and striped hamster (*Cricetulus barabensis*), *Biomedicines*, 2022, vol. 10, p. 925.

Jiggins, C.D. and Mallet, J., Bimodal hybrid zones and speciation, *Trends Ecol. Evol.*, 2000, vol. 15, pp. 250–255.

Kapanna, E., Karyotype variability and chromosomal speciation in *Mus domesticus, Zool. Zh.*, 1988, vol. 67, pp. 1699–1713.

Kartavtseva, I.V., *Kariosistematika lesnykh i polevykh myshei (Rodentia: Muridae)* (Karyosystematics of Wood and Field Mice (Rodentia: Muridae)), Vladivostok: Dal'nauka, 2002.

Kartavtseva, I.V., Sheremetyeva, I.N., Korobitsina, K.V., Nemkova, G.A., Konovalova, E.V., et al., Chromosomal forms of *Microtus maximowiczii* (Schrenk, 1859) (Rodentia, Cricetidae): variability in 2n and NF in different geographic region, *Russ. J. Theriol.*, 2008, vol. 7, pp. 89–97.

Kartavtseva, I.V., Sheremetyeva, I.N., and Pavlenko, M.V., Multiple chromosomal polymorphism of "Evoron" chromosomal race of the Evoron vole (Rodentia, Arvicolinae), *Russ. J. Genet.*, 2021, vol. 57, pp. 70–82.

Kartavtseva, I.V., Sheremetyeva, I.N., and Pavlenko, M.V., Intraspecific multiple chromosomal variations including rare tandem fusion in the Russian Far Eastern endemic Evoron vole *Alexandromys evoronensis* (Rodentia, Arvicolidae), *Comp. Cytogenet.*, 2021a, vol. 15, pp. 393–411.

Khatukhov, A.M., Dzuev, R.I., and Tembotov, A.K., New karyotypic forms of bush voles (*Pitymys*) of the Caucasus, *Zool. Zh.*, 1978, vol. 57, pp. 1566–1570.

King, M., *Species Evolution. The Role of Chromosome Change*, Cambridge: Cambridge Univ. Press, 1993.

Korobitsyna, K.V. and Kartavtseva, I.V., Some issues of the evolution of the karyotype of gerbils of the subfamily Gerbillinae, Alston 1876 (Rodentia, Cricetidae), in *Evolyutsionnye issledovaniya. Makroevolyutsiya* (Evolutionary studies. Macroevolution), Vladivostok: DVNTs Akad. Nauk SSSR, 1984, pp. 113–139.

Korobitsyna, K.V. and Kartavtseva, I.V., Variability and evolution of the karyotype of gerbils (Rodentia, Cricetidae, Gerbillinae). Message I. Karyotypic differentiation of midday gerbils of the fauna of the USSR, *Zool. Zh.*, 1988, vol. 67, pp. 1889–1899.

Korobitsyna, K.V. and Kartavtseva, I.V., Variability and evolution of the karyotype of gerbils (Rodentia, Cricetidae, Gerbillinae). Message 2. Heterochromatin and its intraspecific and intrapopulation variability in the red-tailed gerbil *Meriones libycus, Zool. Zh.*, 1992, vol. 71, pp. 83–95.

Korobitsyna, K.V., Nadler, C.F., Vorontsov, N.N., and Hoffmann, R.S., Chromosomes of the Siberian snow sheep, *Ovis nivicola*, and implications concerning the origin of amphiberingian wild sheep (subgenus *Pachyceros*), *Quat. Res.*, 1974, vol. 4, pp. 235–245.

Korobitsyna, K.V., Korablev, V.P., and Kartavtseva, I.V., Intraspecific and intrapopulation autosomal polymorphism of the Asia Minor gerbil *Meriones tristrami* Thomas, 1892 (Gerbillinae, Cricetidae, Rodentia, in *Voprosy izmenchivosti i zoogeografii mlekopitayushchikh* (Problems of Variability and Zoogeography of Mammals), Vladivostok: DVNTs Akad. Nauk SSSR, 1984, pp. 3–13.

Korobitsyna, K.V., Yakimenko, L.V., and Frisman, L.V., Genetic differentiation of house mice in the fauna of the former USSR: results of cytogenetic studies, *Biol. J. Linn. Soc.*, 1993, vol. 48, pp. 93–112.

Kovalskaya, Yu.M. and Sokolov, V.E., A new species of vole (Rodentia, Cricetidae, Microtinae) from the Lower Amur region, *Zool. Zh.*, 1980, vol. 59, pp. 1409–1446.

Kovalskaya, Yu.M., Khotolkhu, N., and Orlov, V.N., Geographical distribution of chromosomal mutations in the structure of the species *Microtus maximowiczii* (Rodentia, Cricetidae), *Zool. Zh.*, 1980, vol. 59, pp. 1862–1867.

Kovalskaya, Y.M., Aniskin, V.M., Bogomolov, P.L., Surov, A.V., Tikhonov, I.A., et al., Karyotype reorganization in the *subtilis* group of birch mice (Rodentia, Dipodidae, *Sicista*): unexpected taxonomic diversity within a limited distribution, *Cytogenet. Genome Res.*, 2011, vol. 132, pp. 271–288.

Kovalskaya, Yu.M., Tikhonov, I.A., Tikhonova, G.N., Surov, A.V., and Bogomolov, P.L., New findings of chromosomal forms of mice of the *subtilis* group and description of *Sicista severtzovi cimlanica* subsp. n. (Mammalia, Rodentia) from the middle reaches of the Don River, *Zool. Zh.*, 2000, vol. 79, pp. 954–964.

Kozlovskii, A.I., Somatic chromosomes of two species of shrews of the Caucasus, *Zool. Zh.*, 1973, vol. 52, pp. 571–576.

Kozlovskii, A.I., Results of a karyological examination of allopatric forms of the small shrew (*Sorex minutus*), *Zool. Zh.*, 1973a, vol. 52, pp. 390–398.

Kozlovskii, A.I., Karyological differentiation of northeastern subspecies of collared lemmings, *Dokl. Akad. Nauk SSSR*, 1974, vol. 219, pp. 981–984.

Kozlovskii, A.I. and Orlov, V.N., Karyological confirmation of the species independence of *Sorex isodon* Turov, *Zool. Zh.*, 1971, vol. 50, pp. 1056–1062.

Kozlovskii, A.I., Nadzhafova, R.S., and Bulatova, N.Sh., Cytogenetic hiatus between sympatric forms of forest mice of Azerbaijan, *Dokl. Akad. Nauk SSSR*, 1990, vol. 315, pp. 219–222.

Krystufek, B. and Shenbrot, G., *Voles and Lemmings (Arvicolinae) of the Palaearctivc Region*, Maribor: Univ. Press, 2022.

Kuznetsova, M.V., Kholodova, M.V., and Lushchekina, A.A., Phylogenetic analysis of sequences of the *12S* and *16S* rRNA mitochondrial genes in the family Bovidae: new evidence, *Russ. J. Genet.*, 2002, vol. 38, pp. 942–950.

Lavrenchenko, L.A. and Bulatova, N.Sh., The role of hybrid zones in speciation: a case study on chromosome races of the house mouse *Mus domesticus* and common shrew *Sorex araneus, Biol. Bull. Rev.*, 2015, vol. 6, no. 3, pp. 232–244.

Lavrenchenko, L.A., Potapov, S.G., Bulatova, N.Sh., and Golenishchev, F.N., A genetic study of natural hybridization between two forms of the common vole (*Microtus arvalis*) with the use of molecular and cytogenetic methods, *Dokl. Biol. Sci.*, 2009, vol. 426, pp. 222–224.

Lebedev, V., Poplavskaya, N., Bannikova, A., Rusin, M., Surov, A., and Kovalskaya, Yu., Genetic variation in the *Sicista subtilis* (Pallas, 1773) species group (Rodentia, Sminthidae), as compared to karyotype differentiation, *Mammalia*, 2020, vol. 84, pp. 185–194.

Lebedev, V.S., Kovalskaya, Yu.M., Solovyeva, E.N., Zemlemerova, E.D., Bannikova, A.A., et al., Molecular systematics of the *Sicista tianschanica* species complex: a contribution from historical DNA analysis, *PeerJ*, 2021, vol. 9, p. e10759.
https://doi.org/10.7717/peerj.10958

Lissovsky, A.A., Petrova, T.V., Yatsentyuk, S.P., Golenishchev, F.N., Putincev, N.I., et al., Multilocus phylogeny and taxonomy of East Asian voles *Alexandromys* (Rodentia, Arvicolinae), *Zool. Scr.*, 2018, vol. 47, pp. 9–20.

Lyapunova, E.A., Description of the chromosome set and confirmation of species independence of *Citellus parryi*, in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 53–54.

Lyapunova, E.A. and Kartavtseva, I.V., On mutant karyotypes with a description of the normal karyotype of *Mesocricetus raddei, Zool. Zh.*, 1976, vol. 50, pp. 1414–1418.

Lyapunova, E.A. and Mirokhanov, Yu.M., Chromosome set and species independence of *Microtus transcaspicus*, in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 141–143.

Lyapunova, E.A. and Vorontsov, N.N., New data on the chromosomes of Eurasian marmots, in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 36–40.

Lyapunova, E.A. and Vorontsov, N.N., Chromosomes and some issue of the evolution of the ground squirrel genus *Citellus* (Rodentia, Sciuridae), *Experientia*, 1970, vol. 26, pp. 1033–1038.

Lyapunova, E.A. and Vorontsov, N.N., Genetics of mole voles (*Ellobius* Rodentia). Communication I. Karyological characteristics of four *Ellobius* species, *Genetika*, 1978, vol. 14, pp. 2012–2024.

Lyapunova, E.A. and Zholnerovskaya, E.I., Chromosome sets of some sciurids, in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 57–60.

Lyapunova, E.A., Vorontsov, N.N., and Martynova, L.Ya., Cytogenetical differentiation of burrowing mammals in the Palearctic, in *Symposium Theriologicum II, Proc. Int. Symp. on Species and Zoogeography of European Mammals*, Praha: Publ. House Academia, 1974, pp. 203–215.

Lyapunova, E.A., Vorontsov, N.N., Korobitsina, K.V., Ivanitskaya, E.Yu., Borisov, Yu.M., et al., A Robertsonian fan in *Ellobius talpinus, Genetica* (Hague), 1980, vols. 52/53, pp. 239–247.

Lyapunova, E.A., Ivnitskii, S.B., Korablev, V.P., and Yanina, I.Yu., Complete Robertsonian fan of chromosomal forms of mole voles of the superspecies *Ellobius talpinus, Dokl. Akad. Nauk SSSR*, 1984, vol. 274, pp. 1209–1213.

Lyapunova, E.A., Akhverdyan, M.R., and Vorontsov, N.N., Robertsonian fan of chromosome variation in subalpine voles of the Caucasus (*Pitymys*, Microtinae, Rodentia), *Dokl. Akad. Nauk SSSR*, 1988, vol. 273, pp. 1204–1208.

Lyapunova, E.A., Bunch, E.D., Vorontsov, N.N., and Khoffmann, R.S., Chromosome sets and systematic position of the Severtsov ram (*Ovis ammon severtzovi* Nasonov 1914), *Zool. Zh.*, 1997, vol. 76, pp. 1083–1093.

Macholan, M., Filippucci, M.G., and Zima, J., Genetic variation and zoogeography of pine voles of the *Microtus subterraneus/majori* group in Europe and Asia Minor, *J. Zool.*, 2001, vol. 255, pp. 31–42.

Mackiewicz, P., Moska, M., Wierzbicki, H., Gagat, P., and Mackiewicz, D., Evolutionary history and phylogeographic relationships of shrews from *Sorex araneus* group, *PLoS One*, 2017, vol. 12, p. e0179760.

Mahmoudi, A., Golenishchev, F.N., Malikov, V.G., Arslan, A., Pavlova, S.V., et al., Taxonomic evaluation of the "irani–schidlovskii" species complex (Rodentia: Cricetidae) in the Middle East: a morphological and genetic combination, *J. Comp. Zool.*, 2022, vol. 300, pp. 1–11.

Makino, S., *An Atlas of the Chromosome Numbers in Animals*, Iowa State College Press, 1951, 2nd ed., 1st Am. ed.

Malygin, V.M., *Sistematika obyknovennykh polevok* (Taxonomy of Common Voles), Moscow: Nauka, 1983.

Malygin, V.M. and Yatsenko, V.N., Nomenclature of sibling species of common voles (Cricetidae, Rodentia), *Zool. Zh.*, 1986, vol. 65, pp. 579–591.

Malygin, V.M., Orlov, V.N., and Yatsenko, V.N., Species isolation of *Microtus limnophilus*, relationship with *M. oeconomus* and distribution of the species in Mongolia, *Zool. Zh.*, 1990, vol. 69, pp. 115–128.

Mambetov, A.Kh. and Dzuev, R.I., Taxonomic aspects of hybridization of the genus *Pytimys* of the Caucasus, in *Problemy gornoi ekologii* (Problems of Mountain Ecology), Nalchik: KBGU, 1988, pp. 29–57.

Martynova, L.Ya., Chromosomal differentiation of three species of zokor (Rodentia, Myospalacidae), *Zool. Zh.*, 1976, vol. 55, pp. 1265–1267.

Martynova, L.Ya., Genetic aspects of speciation of two groups of burrowing rodents: zokor and mole rats, in *III S"ezd Vsesoyuznogo Teriologicheskogo obshchestva, tezisy dokladov* (III Congress of the All-Union Theriological Society, Abstracts of Papers), Moscow, 1983, pp. 34–35.

Martynova, L.Ya. and Vorontsov, N.N., Population cytogenetics of zokor (Rodentia, Myospalacinae), in *Sistematika i tsitogenetika mlekopitayushchikh. Vsesoyuznyi simpozium* (Systematics and Cytogenetics of Mammals), Moscow, 1975, pp. 13–15.

Matthey, R., *Les Chromosomes des Vertébrés*, Lausanne: F. Rouge, 1949.

Matthey, R., The chromosome formulae of eutherian mammals, in *Cytotaxonomy and Vertebrate Evolution*, Chiarelli, A.B. and Capanna, E., Eds., Academic, 1973, pp. 531–616.

Matveevsky, S., Kolomiets, O., Bogdanov, A., Alpeeva, E., and Bakloushinskaya, I., Meiotic chromosome contacts as a plausible prelude for robertsonian translocations, *Genes*, 2020, vol. 11, p. 386.

Matveevsky, S., Tretiakov, A., Kashintsova, A., Bakloushinskaya, I., and Kolomiets, O., Meiotic nuclear architecture in distinct mole vole hybrids with Robertsonian translocations: chromosome chains, stretched centromeres, and distorted recombination, *Int. J. Mol. Sci.*, 2020a, vol. 21, p. 7630.

Mayr, E., *Animal Species and Evolution*, Harvard: Harvard Univ. Press, 1963.

Mayr, E., *Principles of Systematic Zoology*, New York: McGrow Hill Book Co., 1969.

Meier, M.N. and Malikov, V.G., New species and new subspecies of mouse-like hamsters of the genus *Calomyscus* (Rodentia, Cricetidae) from southern Turkmenistan, *Zool. Zh.*, 2000, vol. 79, pp. 219–223.

Meier, M.N., Orlov, V.N., and Skholl', E.D., Using data from karyological, physiological and cytological analyzes to identify new species in rodents (Rodentia, Mammalia), *Dokl. Akad. Nauk SSSR*, 1969, vol. 188, pp. 1411–1414.

Meier M.N., Orlov V.N., and Skholl', E.D., Twin species in the group *Microtus arvalis* (Rodentia, Cricetidae), *Zool. Zh.*, 1972, vol. 51, pp. 724–738.

Meier, M.N., Golenishchev, F.N., Radzhabli, S.I., and Sablina, O.V., *Serye polevki (podrod Microtus) fauny Rossii i sopredel'nykh territorii* (Gray Voles (Subgenus *Microtus*) of the Fauna of Russia and Adjacent Territories), Tr. Zool. Inst. Ross. Akad. Nauk, St. Petersburg, 1996, vol. 232.

Meier, M.N., Golenishchev, F.N., Bulatova, N.Sh., and Artobolevskii, G.V., On the distribution of two chromosomal forms of *Microtus arvalis* in European Russia, *Zool. Zh.*, 1997, vol. 76, pp. 487–493.

Mekada, K., Harada, M., Lin, L.K., Koyasu, K., Borodin, P.M., and Oda, S.-I., Pattern of X-Y chromosome pairing in the Taiwan vole, *Microtus kikuchii, Genome*, 2001, vol. 44, pp. 27–31.

Nadler, C.F., Korobitsina, K.V., Hoffmann, R.S., and Vorontsov, N.N., Cytogenetic differentiation, geographic distribution, and domestication in Palearctic sheep (*Ovis*), *Z. Saugetierekunde*, 1973, vol. 38, pp. 109–125.

Neronov, V.M., Abramson, N.I., Warshavsky, A.A., Karimova, T.Y., and Khlyap, L.A., Chorological structure of the range and genetic variation of the midday gerbil (*Meriones meridianus* Pallas, 1773), *Dokl. Biol. Sci.*, 2009, vol. 425, pp. 135–137.

Obyknovennaya polevka: vidy-dvoiniki Microtus arvalis Pallas, 1779, M. rossiaemeridionalis Ognev, 1924 (Common Vole: Twin Species *Microtus arvalis* Pallas, 1779 and *M. rossiaemeridionalis* Ognev, 1924), Moscow: Nauka, 1994.

Orlov, V.N., Evolutionary aspects of chromosomal differentiation of mammals, *Zool. Zh.*, 1970, vol. 49, pp. 813–830.

Orlov, V.N., *Kariosistematika mlekopitayushchikh* (Karyosystematics of Mammals), Moscow: Nauka, 1974.

Orlov, V.N., Systematics of mountain sheep and the origin of domestic sheep according to karyological data, in *Ekologo-morfologicheskie osobennosti dikikh rodichei domashnikh ovets* (Ecological and Morphological Features of Wild Relatives of Domestic Sheep), Moscow: Nauka, 1978, pp. 5–16.

Orlov, V.N. and Alenin, V.P., Karyotypes of some species of shrews of the genus *Sorex* (Insectivora, Soricidae), *Zool. Zh.*, 1968, vol. 47, pp. 1071–1074.

Orlov, V.N. and Baskevich, M.I., Chromosome set of the Transbaikal zokor (*Myospalax aspalax* Pall. 1766) from the MPR, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1978, vol. 83, pp. 57–59.

Orlov, V.N. and Bulatova, N.Sh., *Sravnitel'naya tsitogenetika i kariosistematika mlekopitayushchikh* (Comparative Cytogenetics and Karyosystematics of Mammals), Moscow: Nauka, 1983.

Orlov, V.N. and Bulatova, N.Sh., Population cytogenetics of animals, *Sov. Sci. Rev. F. Physiol. Gen. Biol.*, 1989, vol. 3, pp. 61–96.

Orlov, V.N. and Iskhakova, E.N., Taxonomy of the superspecies *Cricetulus barabensis* (Rodentia, Cricetidae), *Zool. Zh.*, 1975, vol. 54, no. 4, pp. 597–604.

Orlov, V.N. and Kovalskaya, Yu.M., *Microtus mujanensis* sp. n. (Rodentia, Cricetidae) from the Vitim River basin, *Zool. Zh.*, 1978, vol. 57, pp. 1224–1232.

Orlov, V.N. and Malygin, V.M., Two forms of the 46-chromosome common vole, *Microtus arvalis*, in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 143–144.

Orlov, V.N. and Malygin, V.M., A new hamster species *Cricetulus sokolovi* sp. n. (Rodentia, Cricetidae) from the Mongolian People's Republic, *Zool. Zh.*, 1988, vol. 67, pp. 304–308.

Orlov, V.N., Radzhabli, S.I., Malygin, V.M., Khotolkhu, N., Kovalskaya, Yu.M., et al., Karyotypes of mammals of Mongolia, in *Geografiya i dinamika rastitel'nogo i zhivotnogo mira MNR* (Geography and Dynamics of the Flora and Fauna of the MPR), Moscow: Nauka, 1978, pp. 149–164.

Orlov, V.N., Bulatova, N.Sh., Nadjafova, R.S., and Kozlovsky, A.I., Evolutionary classification of European wood mice of the subgenus *Sylvaemus* based on allozyme and chromosome data, *Bonner Zool. Beitr.*, 1996, vol. 46, pp. 191–202.

Orlov, V.N., Kozlovskii, A.M., Nadzhafova, R.S., and Bulatova, N.Sh., Chromosomal diagnoses and the place of genetic taxa in the evolutionary classification of wood mice of the subgenus *Sylvaemus* of Europe (*Apodemus*, Muridae, Rodentia), *Zool. Zh.*, 1996a, vol. 75, pp. 88–102.

Orlov, V.N., Balakirev, A.E., and Borisov, Yu.M., Phylogenetic relationships of Caucasian shrew *Sorex satunini* Ogn. (Mammalia) in the superspecies *Sorex araneus* inferred from the data of karyological analysis and the mtDNA *cyt b* gene sequencing, *Russ. J. Genet.*, 2011, vol. 47, pp. 711–719.

Orlov, V.N., Borisov, Yu.M., Cherepanova, E.V., and Milishnikov, A.N., Assortative mating in the hybrid zones of the common shrew (*Sorex araneus,* Mammalia) chromosome race West Dvina, *Dokl. Biol. Sci.*, 2013, vol. 451, pp. 217–220.

Orlov, V.N., Sycheva, V.B., Cherepanova, E.V., and Borisov, Yu.M., Craniometric differences between karyotypic races of the common shrew *Sorex araneus* (Mammalia) as a result of limited hybridization, *Russ. J. Genet.*, 2013a, vol. 49, pp. 417–427.

Orlov, V.N., Cherepanova, E.V., Krivonogov, D.M., Shchegol'kov, A.V., and Borisov, Yu.M., Zonal and refugial stages in the evolution of species: the example of the common shrew, *Sorex araneus* L. (Soricidae, Soricomorpha), *Usp. Sovrem. Biol.*, 2017, vol. 138, pp. 119–134.

Orlov, V.N., Krivonogov, D.M., Cherepanova, E.V., Shchegol'kov, A.V., and Grigor'eva, O.O., Assortative crossing in hybrid zones between chromosomal races of the common shrew, *Sorex araneus* L. (Soricidae, Soricomorpha), *Usp. Sovrem. Biol.*, 2019, vol. 139, pp. 315–325.

Pavlova, S.V. and Searle, J.B., Chromosomes and speciation in mammals, in *Handbook of Zoology. Mammalian Evolution, Diversity and Systematics*, Zachos, F. and Asher, R., Eds., Berlin–Boston: De Gruyter, 2018, Ch. 2, pp. 17–38.

Pavlova, S.V. and Shchipanov, N.A., A hybrid zone between the Kirillov and Petchora chromosomal races of the common shrew (*Sorex araneus* L. 1758) in northeastern European Russia: a preliminary description, *Acta Theriol.*, 2014, vol. 59, pp. 415–426.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., et al., Climate and atmospheric history of the past 420000 years from the Vostok ice core, Antarctica, *Nature*, 1999, vol. 399, pp. 429–436.

Polyakov, A., White, T., Jones, R., Borodin, P.M., and Searle, J.B., Natural hybridization between extremely divergent chromosomal races of the common shrew (*Sorex araneus*, Soricidae, Soricomorpha): hybrid zone in Siberia, *J. Evol. Biol.*, 2011, vol. 24, pp. 1393–1402.

Poplavskaya, N.S., Lebedev, V.S., Bannikova, A.A., Meshcherskii, I.G., and Surov, A.V., Divergence of karyoforms in the supraspecific complex *Cricetulus barabensis* sensu lato and their relationships in natural contact zones, *Zh. Obshch. Biol.*, 2012, vol. 73, pp. 183–197.

Poplavskaya, N., Romanenko, S., Serdyukova, N., Trifonov, V., and Yang, F., Karyotype evolution and phylogenetic relationships of *Cricetulus sokolovi* Orlov et Malygin 1988 (Cricetidae, Rodentia) inferred from chromosomal painting and molecular data, *Cytogenet. Genome Res.*, 2017, vol. 152, no. 2, pp. 65–72.

Puzachenko, A.Yu., Pavlenko, M.V., Korablev, V.P., and Tsvirka, M.V., Armand's zokor (*Myospalax armandii* Milne-Edwards, 1867), a new species in the fauna of Russia, in *Teriofauna Rossii i sopredel'nykh territorii (IX s"ezd Teriologicheskogo obshchestva). Materialy mezhdunarodnogo soveshchaniya (1–4 fevralya 2011 g.)* (Theriofauna of Russia and Adjacent Territories (IX Congress of the Theriological Society). Proc. Int. Meet. (February 1–4, 2011)), Moscow: KMK, 2011, p. 386.

Puzachenko, A.Yu., Pavlenko, M.V., Korablev, V.P., and Tsvirka, M.V., Karyotype, genetic and morphological variability in North China zokor *Myospalax psilurus* (Rodentia, Spalacidae, Myospalacinae), *Russ. J. Theriol.*, 2014, vol. 13, pp. 27–46.

Radjabli S.I., Karyotypic differentiation of Palaearctic hamsters (Rodentia, Cricetinae), *Dokl. Akad. Nauk SSSR*, 1975, vol. 225, pp. 697–700.

Raush, R.L. and Raush, V.R., Observation on chromosomes of *Dicrostonyx torquatus stevensoni* Nelson and chromosomal diversity in varying lemmings, *Z. f. Saugetierkunde*, 1972, vol. 37, pp. 372–374.

Romanenko, S.A., Chromosomal organization and evolution of rodent genomes (Rodentia, Mammalia), *Extended Abstract of Doctoral (Biol.) Dissertation*, Novosibirsk, 2019.

Romanenko, S.A., Lyapunova, E.A., Saidov, A.S., O'Brien, P.C., Serdyukova, N.A., et al., Chromosome translocations as a driver of diversification in mole voles *Ellobius* (Rodentia, Mammalia), *Int. J. Mol. Sci.*, 2019, vol. 20, p. 4466.

Romanenko, S.A., Volobouev, V.T., Perelman, P.L., Lebedev, V.S., Serdukova, N.A., et al., Karyotype evolution and phylogenetic relationships of hamsters (Cricetidae, Muroidea, Rodentia) inferred from chromosomal painting and banding comparison, *Chromosome Res.*, 2007, vol. 15, pp. 283–297.

Romanenko, S.A., Malikov, V.G., Mahmoudi, A., Golenishchev, F.N., Lemskaya, N.A., et al., New data on comparative cytogenetics of the mouse-like hamsters (*Calomyscus* Thomas 1905) from Iran and Turkmenistan, *Genes*, 2021, vol. 12, p. 964. https://doi.org/10.3390/genes12070964

Rubtsov, N.B., Karamysheva, T.V., Bogdanov, A.S., Likhoshvai, T.V., and Kartavtseva, I.V., Comparative FISH analysis of C-positive regions of chromosomes of wood mice (Rodentia, Muridae, *Sylvaemus*), *Russ. J. Genet.*, 2011, vol. 47, pp. 1096–1110.

Safronova, L.D., Cherepanova, E.V., Malygin, V.M., and Sergeev, E.G., *Atlas sinaptonemnykh kompleksov (SK-kariotipov) nekotorykh vidov mlekopitayushchikh* (Atlas of Synaptonemal Complexes (SC Karyotypes) of Some Mammalian Species), Moscow: KMK, 2018.

Shrews, Chromosomes and Speciation (Cambridge Studies in Morphology and Molecules: New Paradigms in Evolutionary Biology), Searle, J.B., Polly, P.D., and Zima, J., Eds., Cambridge: Cambridge Univ. Press, 2019.

Sheremetyeva, I.N., Kartavtseva, I.V., Kryukov, A.P., Voita, L.L., and Haring, E., Chromosomal and morphological variability of *Microtus maximowiczii* (Rodentia, Cricetidae) in the territory of Russia and reinstatement of *Microtus gromovi* Vorontsov, Boeskorov, Lyapunova et Revin 1988, stat. nov., *J. Zool. Syst. Evol. Res.*, 2009, vol. 47, pp. 42–48.

Smirnov, N.G. and Fedorov, V.B., Holarctic collared lemmings: traces of their spread as related to the history of the Arctic biota, *Russ. J. Ecol.*, 2003, vol. 34, no. 5, pp. 332–338.

Sokolov, V.E. and Baskevich, M.I., A new species of monochromatic mice (Rodentia, Dipodoidea) from the Lesser Caucasus, *Zool. Zh.*, 1988, vol. 67, pp. 300–304.

Sokolov, V.E. and Baskevich, M.I., A new chromosomal form of monochromatic mice from North Ossetia (Rodentia, Dipodoidea, *Sicista*), *Zool. Zh.*, 1992, vol. 71, pp. 94–103.

Sokolov, V.E. and Kovalskaya, Yu.M., System of the genus *Sicista* and chromosomal forms of the Tien Shan mouse, *S. tiancshanica* Salensky 1903, in *Tezisy dokladov V S"ezda Vsesoyuznogo teriologicheskogo obshchestva* (V Congress of the All-Union Theriological Society, Abstracts of Papers), Moscow, 1990, part 1, pp. 99–100.

Sokolov, V.E. and Kovalskaya, Yu.M., Karyotypes of birch mice of the Northern Tien Shan and Sikhote-Alin, *Zool. Zh.*, 1990a, vol. 69, pp. 152–157.

Sokolov, V.E., Baskevich, M.I., and Kovalskaya, Yu.M., Revision of monochromatic birch mice (Rodentia, Dipodidae), *Zool. Zh.*, 1981, vol. 60, pp. 1386–1393.

Sokolov, V.E., Kovalskaya, Yu.M., and Baskevich, M.I., Systematics and comparative cytogenetics of some species of birch mice of the genus *Sicista* of the fauna of the USSR (Rodentia, Dipodoidea), *Zool. Zh.*, 1982, vol. 61, pp. 102–108.

Sokolov, V.E., Baskevich, M.I., and Kovalskaya, Yu.M., *Sicista kazbegica* sp. n. (Rodentia, Dipodidae) from the basin of the upper reaches of the Terek River, *Zool. Zh.*, 1986, vol. 65, pp. 949–952.

Sokolov, V.E., Baskevich, M.I., and Kovalskaya, Yu.M., Variability of the karyotype of the steppe birch mouse, *Sicista subtilis* Pallas 1778 and justification for species independence of *S. severtzovi* Ognev 1935 (Rodentia, Zapodidae), *Zool. Zh.*, 1986a, vol. 65, pp. 1684–1692.

Sokolov, V.E., Kovalskaya, Yu.M., and Baskevich, M.I., Review of karyological research and the problems of systematics in the genus *Sicista* (Zapodidae, Rodentia, Mammalia), *Folia Zool.*, 1987, vol. 6, pp. 35–44.

Sokolov, V.E., Kovalskaya, Yu.M., and Baskevich, M.I., On the species independence of the Strand mouse *Sicista strandi* Formosov (Rodentia, Dipodoidea), *Zool. Zh.*, 1989, vol. 68, pp. 95–106.

Stakheev, V.V., Balakirev, A.E., Grigor'eva, O.O., Shestak, A.G., Potapov, S.G., et al., Distribution of cryptic species of shrews of the genus *Sorex* (Mammalia), diagnosed by molecular markers, in the area between the Don and Kuban, *Povolzh. Ekol. Zh.*, 2010, no. 4, pp. 11–14.

Stakheev, V.V., Makhotkin, M.A., Grigor'eva, O.O., Kornienko, S.A., Makarikov, A.A., et al., First data on the contact zone and hybridization between the cryptic species of shrews *Sorex araneus* and *S. satunini* (Eulipotyphla, Mammalia), *Dokl. Biol. Sci.*, 2020, vol. 494, pp. 251–254.

Steppan, S.J. and Schenk, J.J., Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates, *PLoS One*, 2017, vol. 12, p. e0183070.

Steppan, S.J., Kenagy, G.J., Zawadzki, C., Robles, R., Lyapunova, E.A., and Hoffmann, R.S., Molecular data resolve placement of the olympic marmot and estimate dates of trans-beringian interchange, *J. Mammal.*, 2011, vol. 92, pp. 1028–1037.

Suzuki, H., Yakimenko, L.V., Usuda, D., and Frisman, L.V., Tracing the eastward dispersal of the house mouse, *Mus musculus, Genes Environ.*, 2015, vol. 37, pp. 1–9.

Tambovtseva, V., Bakloushinskaya, I., Matveevsky, S., and Bogdanov, A., Geographic mosaic of extensive genetic variations in subterranean mole voles *Ellobius alaicus* as a consequence of habitat fragmentation and hybridization, *Life*, 2022, vol. 12, p. 728.

Tsvirka, M.V. and Korablev, V.P., On the issue of chromosomal speciation using the example of little (*Spermophilus pygmaeus* (Pallas 1778) and Caucasian Mountain (*Spermophilus musicus* (Menetries 1832)) ground squirrels (Rodentia, Sciuridae), *Zool. Zh.*, 2014, vol. 93, pp. 917–925.

Tsvirka, M.V., Korablev, V.P., Lyapunova, E.A., and Vorontsov, N.N., Differences in cytogenetic characteristics in the zones of sympatry of 36-chromosomal ground squirrels, in *Sistematika i filogeniya gryzunov i zaitseobraznykh. Sbornik statei* (Systematics and Phylogeny of Rodents and Lagomorphs), Moscow, 2000, pp. 177–179.

Tsvirka, M.V., Pavlenko, M.V., Korablev, V.P., and Puzachenko, A.Yu., Genetic and morphological differentiation and systematic of North China zokor *Myospalax psilurus* (Rodentia, Spalacidae), in *Modern Achievements in Population Evolutionary and Ecological Genetics: Program and Abstracts of Int. Symp.*, 2015, p. 49.

Vakurin, A.A., Kartavtseva, I.V., Korablev, V.P., and Pavlenko, M.V., Features of cytogenetic differentiation of hamsters *Cricetulus barabensis* and *Cricetulus pseudogriseus* (Rodentia, Cricetidae), *Zool. Zh.*, 2014, vol. 93, pp. 877–886.

Vorontsov, N.N., The importance of studying chromosome sets for the taxonomy of mammals, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1958, vol. 63, pp. 5–86.

Vorontsov, N.N., Species of Palaearctic hamsters (Cricetinae, Rodentia) in statu nascendi, *Dokl. Akad. Nauk SSSR*, 1960, vol. 132, pp. 1448–1451.

Vorontsov, N.N., *Razvitie evolyutsionnykh idei v biologii* (Development of Evolutionary Ideas in Biology), Moscow: UNTs DO Mosk. Gos. Univ., Progress-Traditsiya, ABF, 1999.

Vorontsov, N.N. and Ivanitskaya, E.Yu., Comparative karyology of pikas (Lagomorpha, Ochodontidae) of the Northern Palearctic, *Zool. Zh.*, 1973, vol. 52, pp. 584–588.

Vorontsov, N.N. and Lyapunova, E.A., Chromosomes of Palaearctic ground squirrels (*Citellus*, Marmotinae, Sciuridae, Rodentia), in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Taxonomy), Novosibirsk, 1969, pp. 41–47.

Vorontsov, N.N., Lyapunova, E.A., Zakaryan, G.G., and Ivanov, V.G., Karyology and systematics of the genus *Ellobius* (Microtinae, Rodentia), in *Mlekopitayushchie: Evolyutsiya. Kariologiya. Faunistika. Sistematika* (Mammals: Evolution. Karyology. Faunistics. Systematics), Novosibirsk, 1969, pp. 127–129.

Vorontsov, N.N. and Lyapunova, E.A., Chromosome numbers and speciation in terrestrial sciurids (Sciuridae, Xerinae, Marmotinae) of the Holarctic, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1970, vol. 75, pp. 112–126.

Vorontsov, N.N. and Lyapunova, E.A., Cytogenetic evidence of the existence of Transcaucasian-Sonoran disjunctions of the ranges of some mammals, *Zool. Zh.*, 1972, vol. 51, pp. 1697–1704.

Vorontsov, N.N. and Lyapunova, E.A., Two ways of speciation, in *Evolutionary Biology of Transient Unstable Populations*, Fontdevila, A., Ed., Berlin: Springer-Verlag, 1989, pp. 220–245.

Vorontsov, N.N. and Martynova, L.Ya., Population cytogenetics of the Altai zokor *Myospalax myospalax* Laxm. (Rodentia, Myospalacinae), *Dokl. Akad. Nauk SSSR*, 1976, vol. 230, pp. 447–449.

Vorontsov, N.N. and Radzhabli, S.I., Chromosome sets and cytogenetic differentiation of two forms of mole voles of the superspecies *Ellobius talpinus* L., *Tsitologiya*, 1967, vol. 9, pp. 846–852.

Vorontsov, N.N., Radjabli, S.I., and Lyapunova, K.L., Karyological differentiation of allopatric forms of hamsters of the *Phodopus sungorus* superspecies and heteromorphism of sex chromosomes in females, *Dokl. Akad. Nauk SSSR*, 1976, vol. 172, pp. 703–705.

Vorontsov, N.N., Korobitsina, K.V., Nadler, Ch.F., Khoffman, R., Sapozhnikov, G.N., and Gorelov, Yu.K., Cytogenetic differentiation and species boundaries in real sheep (*Ovis* s. str.) of the Palaearctic, *Zool. Zh.*, 1972, vol. 51, pp. 1109–1122.

Vorontsov, N.N., Bekasova, T.S., Kral, B., Korobitsyna, K.V., and Ivanitskaya, E.Yu., On the species affiliation of Asian wood mice of the genus *Apodemus* of Siberia and the Far East, *Zool. Zh.*, 1977, vol. 56, pp. 437–449.

Vorontsov, N.N., Kartavtseva, I.V., and Potapova, E.G., Systematics of mouse-like hamsters of the genus *Calomyscus* (Cricetidae). I. Karyological differentiation of sibling species from Transcaucasia and Turkmenistan and a review of species of the genus *Calomyscus, Zool. Zh.*, 1979, vol. 58, pp. 1213–1224.

Vorontsov, N.N., Boeskorov, G.G., Lyapunova, E.A., and Revin, Yu.V., New chromosomal form and variability of molars in the vole *Microtus maximoviczii, Zool. Zh.*, 1988, vol. 67, pp. 205–214.

Vorontsov, N.N., Boeskorov, G.G., Mezhzherin, S.V., Lyapunova, E.A., and Kandaurov, A.S., Systematics of forest mice of the subgenus *Sylvaemus* of the Caucasus (Mammalia, Rodentia, Apodemus), *Zool. Zh.*, 1992, vol. 71, pp. 119–131.

Wallace, B., On co-adaptation in drosophila, *Am. Nat.*, 1953, vol. 87, pp. 343–358.

White, M.J.D., *Animal Cytology and Evolution*, Cambridge: Cambridge Univ. Press, 1954.

White, M.J.D., Some general problems of chromosomal evolution and speciation in animals, *Surv. Biol. Prog.*, 1957, vol. 3, pp. 109–154.

White, M.J.D., *Modes of Speciation*, San Francisco: Freeman, 1978.

Yablokov, A.V., Preface, *Nikolai Vorontsov. Vospominaniya i razmyshleniya* (Nikolai Vorontsov. Memories and Reflections), Moscow: Novyi khronograf, 2017, pp. 8–14.

Yakimenko, L.V. and Korobitsyna, K.V., Variability of chromosome 1 with HSR insertions in natural and synanthropous populations of house mouse *Mus musculus* L. 1758, *Russ. J. Genet.*, 2007, vol. 43, pp. 899–904.

Yakimenko, L.V. and Lyapunova, E.A., Cytogenetic confirmation of the belonging of common mole voles from Turkmenistan to the species *Ellobius talpinus* s. str., *Zool. Zh.*, 1986, vol. 65, pp. 946–949.

Yang, F. and Graphodatsky, A.S., Animal probes and zoo-FISH, in *Fluorescence In Situ Hybridization (FISH)—Application Guide*, Liehr, T., Ed., Berlin: Springer-Verlag, 2009, Ch. 29, pp. 323–346.

Yannic, G., Basset, P., and Hausser, J., Chromosomal rearrangements and gene flow over time in an inter-specific hybrid zone of the *Sorex araneus* group, *Heredity*, 2009, vol. 93, pp. 1–10.

Yatsenko, V.N., C-heterochromatin and chromosomal polymorphism of the Gobi-Altai vole (*Alticola stolizkanus barakschin* Bannikov 1948, Rodentia, Cricetidae), *Dokl. Akad. Nauk SSSR*, 1980, vol. 254, pp. 1009–1010.

Zagorodnyuk, I.V., Geographical distribution and population levels of *Terricola subterraneus* on the territory of the USSR, *Zool. Zh.*, 1992, vol. 71, pp. 86–97.

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