ISSN 1062-3590, Biology Bulletin, 2016, Vol. 43, No. 8, pp. 759–775. © Pleiades Publishing, Inc., 2016.
Original Russian Text © I.Yu. Bakloushinskaya, 2016, published in Zoologicheskii Zhurnal, 2016, Vol. 95, No. 4, pp. 376–393.

Chromosomal Rearrangements, Genome Reorganization, and Speciation

I. Yu. Bakloushinskaya

Koltzov Institute of Developmental Biology, Russian Academy of Sciences, Moscow, 119334 Russia
e-mail: i.bakloushinskaya@idbras.ru

Received October 19, 2015

Abstract—Historical analysis of studying chromosome changes in evolution allows better understanding of the current level of research in this area. Reorganizations of the genetic system due to chromosomal rearrangements have important evolutionary consequences and may lead to speciation. Despite the complexity of evaluating the primacy of chromosome changes in speciation events, such phenomena are possible and occur in nature, as recent studies have demonstrated.

Keywords: evolution, species, mutations, genome structure

DOI: 10.1134/S1062359016080057

INTRODUCTION

Discussion of the role of chromosomal rearrangements in evolution began over 50 years ago and continues today. What determines the interest in this problem? One of the possible explanations is that chromosomes are unusual and interesting structures because they combine morphological and genetic traits within the same structure and, therefore, can be considered as elementary particles of variation and heredity at the same time. According to Darwin, new species can evolve through natural selection on the basis of variation and due to heredity (Darwin, 1859, 1991 (the 6th edition, translation into Russian)). In the middle of the 19th century, the material basis of heredity was not known. The term "genome" was introduced by Winkler (1920) before the discovery of the role of DNA (Watson and Crick, 1953) to designate the haploid set of chromosomes and the protoplasm, which constitute the material basis of the species. For a long time, this term has combined two levels of genetic information: the genes and the chromosomes. According to modern notion, the genome is the sum of the entire inheritable genetic material; i.e., in addition to DNA (packed into chromosomes), it includes RNA and various epigenetic factors such as DNA methylation, histone modifications, etc., which do not affect the DNA nucleotide sequence but change gene expression (Korochkin, 2006). Importantly, epigenetic changes can be passed to future generations (Szyf, 2015).

Despite the rapid development of biology (first of all, genetics) in the past 150 years, the simplest and, perhaps, therefore the most difficult question as to how and why the transition from polymorphism to speciation occurs still remains unanswered. The changes in the chromosome sets are not always accompanied by changes in the nucleotide composition or the amount of DNA, for example, inversions and various types of translocations include changes in the position of chromosomal fragments (inversions) or whole chromosomes (Robertsonian translocations). Many researchers believe that the chromosome set variability cannot be the basis of speciation and that changes accumulate after the emergence of species and isolation of their genomes. This is the classic approach of population genetics, which prevailed in the works of the adherents of the synthetic theory of evolution (Lewontin, 1974), including its latest modifications. Current data have forced researchers to reconsider this standpoint, because it has become clear that the concept of adaptability applies not only to the organism as a whole but also to the genome, the structure of which changes under the control of selection (Shapiro, 2009, 2013).

Starting from the early studies on evolutionary genetics, the key question in the genomic era remains the same: how does the genetic diversity of species occur and why is its level not the same (Leffler et al., 2012; Romiguier et al., 2014). The main argument against chromosomal speciation is that different chromosomal polymorphism is a common phenomenon

frequently encountered in natural populations (Dobigny et al., 2015). At the body level, aberrations may occur in different tissues; moreover, the liver normally has polyploid tissue. It may seem that, on the one hand, the chromosome set is a fairly variable trait; on the other hand, the changes in it are not related to speciation (in other words, polymorphism occurs and is maintained but has no evolutionary consequences). It is concluded from this premise that chromosomal rearrangements cannot play an initiating role in speciation. The author of this review in no way intended to solve the problem of chromosomal speciation; the purpose of this article is to demonstrate the changes in the standpoints regarding the material basis of variation and heredity, namely, the role of structural changes in the genome (primarily chromosomal rearrangements) in evolution. The basic idea is that the reorganization of the genetic system, which occurs as a result of chromosomal rearrangements, may have evolutionarily important consequences and may lead to speciation.

THE CHROMOSOMAL THEORY OF HEREDITY: THE EMERGENCE OF CYTOGENETICS

The level of knowledge about the structure of the nucleus has long remained insufficient to understand the fundamental role of chromosomes in genome functioning both in the interphase nucleus and in the process that ensures the transmission of genetic information from generation to generation (i.e., in meiosis). According to the apt words of Ferguson-Smith (2015), the recognition of the chromosomal theory of heredity has turned cytologists, who are engaged in studying the nucleus and chromosomes, into cytogeneticists. It is believed that the chromosomal theory of heredity was formulated in 1915 (Morgan et al., 1915). The role of chromosomes in the transmission of hereditary information has long been limited to the role of a carrier that contains the genes, and the properties of the carrier itself had no informational value. However, like any other concept, the chromosomal inheritance theory was based on earlier data of many researchers. The term "chromosome" was introduced by Waldeyer to designate the intensely stained structures of the nucleus that are well seen during cell division (Waldeyer, 1888). McClung in his article published in 1902 (McClung, 1902) emphasized the importance of nuclear structures as a factor of heredity and made the assumption that the unpaired accessory chromosome in the male soldier bug, which was discovered in 1891 by Henking (Henking, 1891), may be responsible for sex determination. In fact, this was the first demonstration of the association between the phenotype (sex) and the chromosome set. The works by Stevens and Wilson on the study of chromosome sets and sex chromosomes (Stevens, 1905; Wilson, 1905), the studies by Bateson (Bateson, 1902), Sutton (Sutton, 1903), Morgan et al. and Sturtevant, Muller, and Bridges (Morgan et al., 1915; Morgan, 1919; Muller, 1914) on the analysis of variation and inheritance, as well as the later theoretical generalizations by Dobzhansky (Dobzhansky, 1937 (translation Dobzhansky, 2010)) were a basic step in the development of genetics. Due to these studies, the formation of the "new synthesis" (known as the "synthetic theory of evolution" in the Russian literature) was made possible. The possibility of chromosomal speciation, the primacy of chromosome changes, and further diversification as a result of these changes was considered within the framework of this concept.

The concept of the karyotype was formulated by Delone (1922) and discussed in more detail by Levitskii in his book *The Material Basis of Heredity*: "If the external characteristics of an organism are generally referred to as the "phenotype," then the term "karyotype" will be suitable specifically for its nuclear characteristics. The concept of the karyotype as the sum of "characters," on the one hand, is part of the concept of the phenotype, but on the other hand, it is very closely related to the concept of the "genotype," i.e., the combination of hereditary factors or genes of an organism" (Levitskii, 1978, p. 78). The karyotype as the sum of quantitative (the number of chromosomes and their size) and qualitative (the morphology of chromosomes) traits of the chromosome set is a species-specific trait. Undoubtedly, the karyotype is a morphological trait, similarly to any quantitative (the number of teeth) and qualitative (the shape and structural characteristics of chromosomes or the tooth surface structure) trait. Furthermore, unlike many traits that may vary with changes in the diet, age, and season (fur coloration), the number and shape of chromosomes is a trait that remains unchanged during ontogeny, which allows diagnostics at different stages of development of an organism.

The understanding that chromosome sets are carriers of genetic information made it possible to show the evolutionary consequences of hybridization between different species and even genera at the beginning of the 20th century, when plant chromosomes were actively studied (Navashin, 1927). *Raphanobrassica* is the product of a classic experiment performed on the basis of chromosome analysis data; as a result of hybridization, an intergeneric hybrid was obtained, which made it possible to substantiate the possibility of the origin of new species as a result of hybridization and polyploidy in plants (Karpechenko, 1927).

CHROMOSOMAL SPECIATION AND EVOLUTION OF GENETIC SYSTEMS

Basic Ideas

In 1939, Darlington in his book *The Evolution of Genetic Systems* wrote: "I have attempted to show genetics as the study of systems of heredity and varia-

tion, systems which rest on the basis of the chromosomes and are related to one another by processes of natural selection" (Darlington, 1939, p. V). This relatively small book deals with the issues that remain relevant today: the levels of genome integration, the emergence of meiosis and sexual reproduction, and the necessity of crossing-over. Moreover, it contains revolutionary ideas such as interlocking in evolution, external stability and internal changes (to the problem of cryptic species and the uneven pace of evolution), the lag in adaptation (delayed adaptation), selection at the germ cell level, the "struggle" of genes (to the genome integrity problem), and others. After considering the main processes, Darlington concluded: "selection therefore acts on the genetic system at every level, gene or chromosome, cell and individual, and in every stage and process, haploid and diploid, mitotic and meiotic, embryonic and adult" (Darlington, 1939, pp. 130–131). Of particular value is the idea of a lag in adaptation (delayed adaptation); for example, both improvement and deterioration of the quality of gametes does not affect (gives no advantage and does not reduce viability) the adaptability of individuals, influencing only the adaptability of the offspring and, therefore, is not a "direct" adaptation.

Chronologically, the initiating role of chromosomal rearrangements in speciation was first proposed in an article by Wallace, in which he formulated the hypothesis of the triad (Wallace, 1953). He considered the inversions that occurred in geographically isolated populations as chromosome rearrangements. A necessary condition was the secondary contact of the emerged forms; due to introgression, the adaptive linkage groups were destroyed, as a result of which the hybrids were sterile. Since this concept was formulated for one group of organisms (*Drosophila*) and for one type of rearrangements, it obviously had limitations and was not widespread.

Almost simultaneously, the article by Mayr "Change of genetic environment and evolution" was published, which covered an extremely wide range of issues (Mayr, 1954). At first glance, this work is not directly related to chromosomal speciation; however, it presents the basic modern views on the role of chromosomal rearrangements in evolution. Mayr considered the role of a sudden ("revolutionary") change in the genetic basis, primarily in peripheral isolates, which often significantly differ from the main range of a species. "Isolating a few individuals (the "founders") from a variable population which is situated in the midst of the stream of genes which flows ceaselessly through every widespread species will produce a sudden change of the genetic environment of most loci. This change, in fact, is the most drastic genetic change (except for polyploidy and hybridization) which may occur in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable "genetic revolution." Furthermore, this "genetic revolution," released by the isolation of the founder population, may well have the character of a chain reaction. Changes in any locus will in turn affect the selective values at many other loci, until finally the system has reached a new state of equilibrium" (Mayr, 1954, p. 170). It can be seen that, in this paragraph, several provisions are set forth at once, which currently form the basis of population genetic and evolutionary studies. However, in the same article Mayr speaks about the role of linkage groups and chromosomes. He writes that, if something new is introduced into a well-balanced system, it can be discarded by selection (here Mayr referred to the theory of stabilizing selection by Schmalhausen), thereby as it were rejecting the very possibility of chromosomal speciation. However, after the introduction of the concept of genetic revolution, it is clear that this concept also applies to chromosomal rearrangements (or, more precisely, to the system chromosomal mutations).

In 1959, at the conference "Darwin's Days in Leningrad," Vorontsov made a report "Species of Palearctic hamsters in *statu nascendi*," which was then published in the form of an article (Vorontsov, 1960). This paper shows that, in nature, there are two ways of speciation: (1) "normal" (or, using today's terminology, gradualistic), which starts with the spatial isolation and changes in allele frequencies and ends with reproductive isolation, and (2) "genetic" (or, using today's terminology, punctualism on the basis of chromosomal speciation), which starts with the appearance of chromosomal rearrangements and the emergence of reproductive isolation and ends with divergence in allele frequencies and phenotypic divergence. On the basis of the study of the divergence of closely related forms of hamsters, it was shown that changes in chromosome numbers (particularly via Robertsonian rearrangements) can not only complete the process of ecological and morphological differentiation of species through genetic isolation but also themselves serve as a basis for morphological divergence of related forms. Due to the presence of genetic isolation, genetic mutations will accumulate very quickly in such populations, which eventually may lead to the formation of a new species differing not only in the chromosome number but also in a whole complex of morphological and ecological features (Vorontsov, 1999, pp. 550–552).

The idea of the possibility of "genetic" speciation was supported by the well-known Swiss cytogenetics Matthey (1960), who described karyotypes for a large number of mammal species. Nevertheless, the work by Vorontsov has not received an international fame. A peculiar "reference book" of cytogenetics is the articles and books by White (1968, 1978, 1978a, 1982). Today, the Australian cytogenetic school remains one of the leading cytogenetic schools.

Description and Analysis of Chromosome Sets: From Routine Staining to Identification of Homology

In the 1960s, an active phase of description and analysis of chromosome sets of animals and plants began, which continues to the present time. The number of both the original descriptions (determination of chromosome numbers) and summaries on the chromosome numbers is steadily increasing. The level of knowledge varies considerably due to methodological issues and different numbers of species in groups. This is especially clearly demonstrated by the statistical section of a specialized journal, *Comparative Cytogenetics*, which publishes increasingly more articles on the chromosomes of fish and insects. The karyotypes of mammals are studied best of all, which can be undoubtedly explained by the interest in human genetics (see the summaries by Vorontsov, 1958, 269 species of mammals, 10 volumes of the *Atlas of the Chromosomes of Mammals* by Hsu and Benirschke, 1967–1977; Matthey, 1973; Chiarelli and Capanna, 1973; Orlov and Bulatova, 1983, *Atlas of Mammalian Chromosomes*, 2006). The description of the human karyotype and various studies published in numerous atlases, journals, and monographs on human cytogenetics are of great medical importance because many syndromes (e.g., Down syndrome) are caused by disturbances in chromosome sets and mutations in individual chromosomes. The introduction of new techniques has made it possible to improve the image under the microscope and to determine more accurately the number, shape, and various structural features of chromosomes due to the development of differential stains. In the early 1990s, not only the methodological approaches but also the worldview and the understanding of how the genome is organized and how it works changed. The breakthrough caused by the development of DNA analysis techniques has made it possible to perform phylogenetic reconstructions, which have led to a revision of the system of the organic world and necessitated the creation of public databases (Simpson and Roger, 2004; Bininda-Emonds et al., 2007; Katz et al., 2012; Hinchliff et al., 2015). The widespread introduction of the chromosomal painting or Zoo-FISH methods (Telenius et al., 1992; Scherthan et al., 1994; Ferguson-Smith, 1997; Wienberg and Stanyon, 1997; Graphodatsky, 2007) made it possible to pass from the description of similarity (number, shape, and differential staining pattern) to the analysis of homology and to solve difficult taxonomic issues both at the species and higher (up to the class) levels, which was brilliantly shown, for example, for mammals (Murphy et al., 2004; Ferguson-Smith and Trifonov, 2007; Graphodatsky et al., 2011). Certainly, the development of the methodology of phylogenetic reconstructions based on the structure of chromosome sets is very difficult; nevertheless, some progress in this direction has already been made (Robinson et al., 2008). The obtained data arrays can and should be understood from the evolutionary point of view.

Some Chromosomal Speciation Concepts

Numerous data indicate that there are patterns of mutation process at the level of karyotype restructuring. White introduced the term "karyotypic orthoselection" to explain the nonrandom occurrence of chromosomal rearrangements of the same type in similar karyotypes and gave five possible explanations for this phenomenon (White, 1978):

(1) *Similar chromosomal rearrangements had similar phenotypic effects which were adaptive in the same environment*. In our opinion, this statement is debatable; apparently, this conclusion was made because originally this concept was formulated for taxonomically close groups. However, it is obvious that the possibility to transform an acrocentric set to a metacentric one will also be retained for unrelated groups that definitely do not live under similar conditions.

(2) *The limits to the size and number of chromosomes in a cell were imposed by the dimensions of the spindle and cytoplasm and the mechanics of cell division*. This is also quite a controversial statement, primarily because corresponding cytological data are missing, and some features of the meiotic systems of organisms also remain undetermined.

(3) *The internal architecture of the chromosome and the distribution of satellite DNA, heterochromatin, and ribosomal DNA* (satDNK and rDNA, e.g., in *Mus* see Garagna et al., 2001) *may impose restrictions on chromosome form*. This statement is the most interesting and promising.

(4) *The regularities in the architecture of the interphase nucleus may have adaptive effects and so influence the types of rearrangements that were selected*. No doubt, this provision should be considered in conjunction with paragraph 3.

(5) *The location of chiasmata was an orthoselective process, for their distribution could modify the types of rearrangements that were produced after breaks were formed*. This provision was also confirmed by modern studies.

King (1993) believes that these criteria can be reduced to two: the propensity of the karyotype to initiate particular types of chromosomal rearrangements and the structural organization of the karyotype, which permitted the fixation of these changes. This simplification does not seem logical. For example, it is obvious that the division of a metacentric chromosome into two acrocentric chromosomes will be hampered if the respective pericentromeric regions, required for the formation of the centromere and, possibly, the telomeric regions, are lost. However, in such a situation, inversions may occur, which will lead to the formation of acrocentrics, which then (at the second step) will fuse to form metacentrics. The main

conclusion of the leading theorists of the chromosomal speciation is that random mutations are the basis for nonrandom processes and that orthoselection is determined by the peculiarities of the genome of each specific group.

In the model of chromosomal speciation, which was called stasipatric speciation (White, 1978, 1978a), the chromosomal change is primary and does not require the geographical isolation of populations; the latter is secondary both in importance and in the timeline. In this concept, the issue of fixation of a new form is solved by the genetic drift between multiple isolated and semi-isolated demes. An important aspect of this concept is the statement that the efficiency of chromosomal rearrangements in the sterility barrier formation is the same during their fixation in the population, and later as a postcopulative isolating mechanism. White did not consider the possibility of synergistic effects arising from multiple chromosomal rearrangements; this factor may be the cause of a much more severe disturbance in the fertility of hybrids.

The model proposed by Baker and Bickham (1986)—speciation by centric fusions—is one of the most interesting models of chromosomal speciation. Centric fusions have a minimal impact on the euchromatic part of the genome and usually do not cause serious problems in the production of balanced gametes in heterozygotes. Therefore, it is logical to assume that centric fusion should be one of the most common types of chromosomal rearrangements involved in evolution. It is believed that these rearrangements are most characteristic of mammals (King, 1993). The model is based on identification of metacentric chromosomes with partial homology (namely, with homology in one of the arms of metacentric chromosomes, i.e., monobrachial homology) in different founder populations. The metacentric chromosomes with monobrachial homology are the result of independent fusions of acrocentric chromosomes.

One of the requirements of this model is the presence of externally isolated subpopulations and certain conditions. For example, a connection between these subpopulations and the peripatric founder population or some other small externally isolated population as well as the fixation of different chromosomal rearrangements in two independent subpopulations is required; this model considers only one type of chromosomal rearrangements (the centric fusions) and is inapplicable to other types of chromosomal rearrangements.

According to this model, different chromosomal centric fusions are fixed in some isolated populations, with meiotic disturbances in each population being minimal. However, if these two populations enter hybridization and the same centric fusions that almost did not cause meiotic disturbances in the fixed state are combined in the heterozygote, they lead to reproductive isolation due to numerous disturbances in meiosis. In the individuals that are heterozygous for the two-armed chromosomes with monobrachial homology, quadrivalents of more complex multivalents, which cannot segregate properly, are formed, thereby leading to a drastic decline in fertility. On the other hand, heterozygotes for simple centric fusions form trivalents in meiosis, which usually segregate normally and do not cause marked disturbances; however, in some cases (e.g., in humans), they leads to a different degree of reduction in the number of normal gametes (Godo et al., 2015). The criticism (Futuyma and Mayer, 1980; Templeton, 1981; Nei et al., 1983) coming from population geneticists, who traditionally deny the possibility of speciation by changes in the chromosome sets, does not apply to speciation through the fixation of chromosomes with monobrachial homology, because the emergence of such metacentric chromosomes leads to a decrease in the fertility of interpopulational hybrids, which ensures reproductive isolation between the daughter populations. For this model, it is not important which factor caused the fixation of centric fusions—selection (i.e., individuals carrying the rearrangements have a certain advantage) or stochastic processes, although this is often the most important issue in other models.

One of the most interesting aspects of speciation by monobrachial fusions is that reproductive isolation can be achieved between two or more populations with differing karyotypes, despite the fact that these emerging species retain reproductive compatibility with populations that have the primitive acrocentric karyotype. Species of complexes *Rhogeessa tumida* (Bickham and Baker, 1979; Baker et al., 1985; Baird et al., 2009), *Mus musculus* (Gropp et al., 1972; Capanna, 1982; Capanna and Garagna, 2004; Garagna et al., 2014), *Rattus rattus* (Yoshida, 1980; Baverstock et al., 1983), *Ellobius tancrei* (Bakloushinskaya et al., 2010), *Sorex araneus* (Searle, 1984; Zima et al., 1998; Searle et al., 2007; Shchipanov and Pavlova, 2016), wallabies of the genus *Petrogale* (Potter et al., 2015), etc., are examples of differences in fusions with monobrachial homology. The greater the number of fusions with monobrachial homology in which species differ, the higher the effectiveness of reproductive isolation. It is believed that the second hybrid generation practically cannot be obtained in the presence of even one pair of such metacentrics, and the gene flow can proceed only through the parental forms. A variant of male and first-generation hybrid sterility and partial female fertility is also known (Potter et al., 2015). However, our studies of the mole vole genetics showed that, in the case of hybridization of forms with monobrachial homology, the sterility of the first-generation hybrids can be overcome, despite the significant disturbances in the chromosome synapsis in the prophase of meiosis I (Matveevsky et al., 2015).

Interestingly, the groups for which the presence of gene flow is shown are usually used as arguments against the chromosomal speciation; that is, forms and

even species are not completely isolated from each other. Is this a paradox? A complete absence of gene flow (i.e., complete reproductive isolation) is undoubtedly an indisputable indicator of the genetic isolation of gene pools of two species; however, the converse is not true. That is, the presence of a gene flow cannot be considered as a basis for the uniting (taxonomic) of two species into one. This situation is perfectly illustrated by the study on the house mice (Nunes et al., 2012) and wallaby (Potter et al., 2015). Interestingly, for *Sorex araneus*, both the presence of a gene flow between different chromosome races (Horn et al., 2012) and its restriction (Polly et al., 2013) were shown, which seems quite logical. The analysis of the genetic mechanisms of speciation and the use of a large number of genetic markers made it possible to analyze more comprehensively the changes in the genome. Furthermore, it was shown that part of the genome may remain stable, whereas the other part may be involved in hybridization and introgression (Noor and Bennett, 2009). As a result, the establishment of specific independence is possible in the presence of a gene flow under parapatric conditions (the so-called divergence-with-gene-flow model) (Ayala and Coluzzi, 2005; Pinho and Hey, 2010). The mathematical model developed by Bazykin (1969, 1972) makes it possible to estimate the evolutionary consequences for equal and unequal fitness of heterozygotes, as well as at a reduced gene flow in separate parts of the range. According to this model, disruptive selection at any, even relatively small change in the fertility of heterozygotes may lead to the emergence of new species. In fact, it makes it possible to substantiate the possibility of speciation in the case of occurrence of changes in chromosomes and fertile hybrids between the original and new forms. A similar scenario in the case of occurrence of chromosomal rearrangements was proposed in the model with the assessment of the effective size of demes (Lande, 1979).

A large number of other models of chromosomal speciation has been developed, the most interesting of which, in our opinion, are two: the emblematic model by Capanna (1982) and the model of chain processes by White (1978a). Both models are fully based on *Mus musculus domesticus* data. The emblematic model clearly defines the role of monobrachial homology in the formation of reproductive isolation. It should be noted that the idea of the unequal effect of different Robertsonian translocations on fertility was expressed in one of the first studies on chromosomal variation in *Mus* by Gropp et al. (1972). Interestingly, speciation in *Mus* is the result of commensal relationships with humans, determining the existence of a population divided into microdemes, which promotes the fixation of centric fusions through inbreeding and genetic drift in microdemes.

White (1978a), speaking about the chain processes of speciation, considers the establishment of reproductive isolation through successful fixation of numerous chromosomal rearrangements and does not reduce them only to the centric fusions. According to White, the chain process is a modification of the stasipatric model and sympatric speciation. Differences in meiotic disturbances in hybrids of different types, including those determined by the monobrachial homology of metacentrics, were not considered in this model.

According to the hypothesis proposed by Stegnii (1993), systemic mutations encompass a group of mutations that determine the spatial organization of chromosomes, namely, the chromosome–membrane relations. The evolutionary consequences of systemic mutations are determined by the fact that such mutations occur in the generative tissues, which removes the issue of fixing a single mutation. A very interesting and modern idea is that ontogeny may be accompanied by repeated reorganization of the architectonics of interphase nuclei of stem cells, which ensures morphological and functional differences of cellular systems and tissues at the regulatory level. Thus, Goldschmidt (1940) considered systemic mutations as structural, whereas Stegnii, who assessed the structure not only as a linear (DNA sequence) but also as a regulatory (spatial organization) formation, believes that it is an irreversible rearrangement of the regulatory system that leads to a speciation event. The issue of the mechanism of saltational changes (in this case, the mechanism of system mutations) is important for both approaches. The possibility to distinguish the discriminating trait (in this case, the chromosome set structure) is important for taxonomists; for the closed-genome concept it is important to understand the mechanisms leading to the separation of genomes (this is also the chromosome set structure, the nucleus structure, and the genome structure).

NUCLEAR STRUCTURE CHARACTERISTICS AS THE BASIS OF SPATIAL AND FUNCTIONAL INTERACTIONS OF CHROMOSOMES

The attempt to determine the role of chromosomal rearrangements in speciation makes it necessary to study the structure and function of the nucleus. Modern studies of the nuclear structure, which allowed identification of chromosomal territories, whose existence had been predicted by Rabl and Boveri (Rabl, 1885; Boveri, 1909), were made possible due to the development of innovative techniques such as DNA sequencing, ultra-high resolution microscopy, and analysis of living cells. These studies have established the relationship between the size, position, and function of chromosomes (Cremer et al., 2001, 2015; Parada and Misteli, 2002; Laat and Grosveld, 2003; Gavrilov and Razin, 2015). It was shown that, in the interphase nucleus, chromosomes occupy a certain area, the relative position of which is important for the regulation of gene expression. In the mammalian

nucleus, chromosomes or their regions rich in genes are located more centrally, whereas the poorer chromosomes and regions are located in the periphery (Mahy et al., 2002). Exon and intron gene regions are also distributed radially; exons are located at a distance from the periphery of the nucleus (Boyle, 2011). The orderliness of chromosome territories allows the formation of transcription "factories," which often include DNA molecules of different chromosomes. As a result, the reorganization of chromosome territories (e.g., changes in the location of chromosomes upon their fusion or segregation) can cause changes in transcriptional activity (Wendt and Grosveld, 2014), and influence the recombination, which, in turn, leads to phenotype modification (including not only the morphological but also other, such as ecological or ethological, characteristics). Data on the relationship between translocations and interchromosomal associations, which are required for transcription, were obtained (Branco and Pombo, 2006).

Mammalian chromosomes are divided into different regions with transcriptional and structural differences: C-, R-, and T-bands (Craig and Bickmore, 1993). R-bands (G-band negative regions) are rich in GC, replicate early in the S phase, have a high concentration of CpG islands and genes, and exhibit a high recombination and transcriptional activity (Holmquist, 1992). Conversely, G-bands (R-negative) are rich in AT, replicate late in S phase, and contain more DNA repeats and a lower concentration of genes (these are primarily tissue-specific genes). The nucleolus undoubtedly plays a major organizing role. The chromosomes carrying the nucleolus organizer regions are associated with the nucleolus, thus being sufficiently rigidly fixed in space (Qumsiyeh, 1999).

The spatial organization and functioning of chromosomes are certainly interrelated. The R- and G-band patterns along the metaphase chromosomes, when it is decondensed in the interphase, are clearly associated with replication and transcription (Jackson, 1995). Transcribed genes are found in the early replicating parts of the genome, chromatin regions that are generally more decondensed in the interphase. Since each chromosome occupies a specific domain, G-chromatin of the chromosome is more condensed and is located in the periphery of the nucleus and in the perinuclear area, whereas R-chromatin regions are arranged more diffusely and are located in the inner part and in the periphery of chromosomal domains (Qumsiyeh, 1999).

Modern studies of the nuclear structure showed that the distribution of chromosomes in the nucleus along a radial ray depends not only on size but also on the density of genes. For example, human chromosome 19, which has a high density of genes, is often located in the inner part of the lymphocyte nucleus, whereas chromosome 18, which is similar in size, as well as the Y chromosome, which is also characterized by a low density of genes, are usually found in the nuclear periphery (Croft et al., 1999; Cremer et al., 2001). It was shown that the same position of these chromosomes is characteristic of the Old World monkeys, although the evolutionary paths of different groups of primates diverged 30 million years ago (Tanabe et al., 2002). The fact of retaining a certain position of chromosomes in the nucleus for such a long evolutionary history demonstrates the important role of the position of chromosomes in the nucleus for genome functioning. In human fibroblasts, chromosomes are distributed only with respect to size; in these cells, both chromosome 18 and the Y chromosome are located in the central part of the nucleus rather than in its periphery. In general, the nonrandom distribution of chromosomes along the radial ray (the larger chromosomes are located more peripherally, whereas the smaller chromosomes are located closer to the central part of the nucleus) is the most general consistent pattern (Sun et al., 2000; Kozubek et al., 2002). The hypothesis of mutual positioning of chromosomes relative to each other was also put forward; in fact, this means the extrapolation of data on the ordering of chromosome arrangement in mitosis (mitotic rosettes) to the interphase nucleus. The sizes of chromosome territory only in the first approximation are determined by the content of DNA; they are also influenced by other factors, such as the transcriptional status (Croft et al., 1999; Mahy et al., 2002).

The nucleus architecture itself can determine a predisposition to certain rearrangements: mutual spatial arrangement of chromosomes may enable or, conversely, hamper translocations. In mammalian evolution, rearrangements of a certain type arose and were fixed in certain phylogenetic lineages (Baker et al., 1987; Qumsiyeh, 1994). This phenomenon of karyotypic orthoselection can be explained by the nuclear positional effects. Other well-known examples include the emergence of a set of specific chromosomal rearrangements in carcinogenesis, which accompany the presumable initial genetic change in cancer. Changes in the position of a DNA segment, when, as a result of rearrangement, it gets from one chromatin environment to another, can change its ability to interact with early replication and transcription factors in the restructuring positioning segment changes in the nucleus and chromatin architecture in general.

For unknown reasons, rearrangements in the genome that have an evolutionary significance occur unevenly both in time (i.e., in phylogenetic lineages) and in the genomic space (i.e., in certain regions of the genome) (Farre et al., 2015). These regions, known as the "evolutionary breakpoint regions," do not have a specific nucleotide composition. The breakpoint regions are largely confined to those genomic regions where the long noncoding DNA segments (the so-called spacers) are located. They can usually be identified in the analysis of spatial interaction of the so-

called open (i.e., uncondensed) chromatin in the nucleus (Berthelot et al., 2015).

THE CENTROMERE: THE MOST MYSTERIOUS PART OF THE CHROMOSOME

The centromere is the chromosome domain in the primary constriction region. In this region, sister chromatids are interconnected. Spindle fibers, which ensure the movement of chromosomes to the division poles, are attached to the constriction region. This definition applies to the monocentric chromosomes, whereas the holocentric chromosomes lack such a region (the so-called diffuse centromere is observed). Some objects with monocentric chromosomes were also shown to contain multiple centromeric domains (Neumann et al., 2012). Despite the fact that the shape of chromosomes is an inherited trait, recent studies showed that there is no universal DNA sequence that ensures centromere formation. Paradoxically, it was found that the centromere is formed by both genetic and epigenetic mechanisms, cooperation between which has not yet been described (Plohl et al., 2014; Catania and Allshire, 2014). In different phyletic lineages, significant differences in the organization of the centromeric chromatin are observed (Steiner and Henikoff, 2015). This is particularly interesting because the centromere function is vitally important for the organism, the growth and functioning of which is impossible without the chromosome disjunction, and the failure of this process can lead to various diseases, primarily cancers (Thompson et al., 2010). The most important proteins that ensure the function of the centromere are histones of the CENH3 group (CENP-A in mammals, CID in *Drosophila melanogaster*, and Cse4 in yeast *Saccharomyces cerevisiae*). The development of immunocytochemical analysis techniques has made it possible to identify the proteins that form various structures in the course of meiosis (such as the synaptonemal complex proteins), to analyze the process of recombination, etc. Originally, the terms centromere (Darlington, 1936) and kinetochore (Schrader, 1939) were synonymous, because they designated the chromosome region to which the spindle fibers attach during cell division in mitosis and meiosis; however, currently these terms define different structures. The kinetochore is a complex protein structure that is formed in the centromeric region and ensures the attachment of spindle fibers. Studies performed in the 1960s at the electron-microscopy level showed that this is a three-layer structure (Brinkley and Stubblefield, 1966; Jokelainen, 1967). According to recent data, the kinetochore is formed by approximately 100 proteins (Hori and Fukagawa, 2012). There is no doubt that such a high level of complexity of this structure is determined by its important function (Sacristan and Kops, 2015).

No less important are the changes in the position of centromeres and the emergence of new centromeres (the so-called evolutionarily new centromeres, or neocentromeres), which were first described in humans (Voullaire et al., 1993). Usually, a large number of repeats formed by sequences of two types—satellite DNA and transposons—accumulate in DNA in the chromosome region, where the centromere is located. A characteristic feature of neocentromeres is the absence of repeats. For example, in horses, the chromosome region carrying neocentromeres does not contain satellite DNA (Wade et al., 2009). Apparently, the evolution of primates (primarily the higher primates, including humans) was strongly associated with the formation of neocentromeres (Montefalcone et al., 1999; Stanyon et al., 2008, 2010). The formation of neocentromeres was shown for different groups of mammals (Rocchi et al., 2012) and often leads to the divergence and formation of new species, as in the case of sibling species of mole voles (Bakloushinskaya et al., 2012). For humans, the emergence of neocentromeres was shown to be correlated with certain diseases, including cancer (Marshall et al., 2008; Pfau and Amon, 2012).

HETEROCHROMATIN VARIATION

Usually, in analyzing the role of chromosomal rearrangements in evolution, the changes in the euchromatin part of the genome are estimated. However, currently, the role of heterochromatin in speciation is being reconsidered. Heterochromatin was described more than 70 years ago as genetically inert chromatin or as a ballast or junk component of the genome that is a late-replicated part of chromatin, depleted in genes but rich in transposable elements (Prokof'eva-Bel'govskaya, 1986). However, recent data show that the role of heterochromatin is quite significant and that it is probably involved in ensuring the integrity of the genome (Vermaak and Malik, 2009). Moreover, experiments on *Drosophila* demonstrated that heterochromatin is involved in speciation (Ferree and Barbash, 2009). The chromosomal races of the pygmy wood mouse are a difficult but interesting model to study both the initial stages of speciation and the role of heterochromatin in this process. The role of changes in the composition and quantity in speciation has been investigated insufficiently. There is evidence pointing to the possible involvement of heterochromatin in speciation, for example, in the pygmy wood mouse (*Sylvaemus uralensis*). Chromosomal races of this species differ from each other in the number of major pericentromeric heterochromatic segments in the karyotype and the nuclear genome size (Bogdanov, 2001; Bogdanov and Rozanov, 2005). The strong correlation between these two traits indicates that heterochromatin variations in *S. uralensis* are accompanied by elimination (or, conversely, accumulation) by repeating DNA sequences. This assumption was confirmed by fluorescence in situ hybridization (FISH) of DNA fragments derived from the pericen-

tromeric C-band of one of the chromosomes of an individual belonging to the East European chromosomal form, with the chromosomes of the pygmy wood mice of all chromosomal forms and races. It was shown that variations in the size of pericentromeric heterochromatic segments, in general, are associated with variation in the number of repeating DNA sequences; i.e., they are quantitative in nature (Karamysheva et al., 2010). A comparative analysis of species of the genus *Sylvaemus* by fluorescence in situ hybridization with the metaphase chromosomes of DNA samples derived from the pericentromeric C-segments showed that the homology of DNA sequences forming the pericentromeric regions of chromosomes and C-segments decreases with a decrease in the relatedness of species (Rubtsov et al., 2011).

POLYPLOIDY IN ANIMALS

Genomic mutations typically include those rearrangements that radically alter the genome (i.e., primarily polyploidization). It is obvious that the evolutionary role of genome duplications is sufficiently high, because they make it possible to increase the complexity of differentiation of an organism and increase the complexity of its structure by recruiting new genes (Holland and García-Fernandez, 1996). During the evolution of vertebrates, genome duplication occurred twice (three times only in fish (Teleostei)) (Van de Peer et al., 2009). The ancient group Acipenseridae passed through the stage of tetraploidization; traces of this process were detected using modern molecular cytogenetic techniques (Romanenko et al., 2015).

In recent years, interest in the problem of polyploidy in mammals has revived. Earlier, in the 1970s, Vorontsov and Lyapunova put forward a hypothesis about the ploidy of a series of chromosome numbers in mole voles—17 (18)–36–54 (*E. lutescens, E. fuscocapillus*, and *E. talpinus*) (Vorontsov et al., 1969). However, they also showed that the karyotype structure analysis did not confirm this hypothesis: the karyotypes of species with low chromosome numbers were metacentric, whereas the karyotype of the 54-chromosome species was acrocentric. Another hypothesis proposed the alloploid origin of the golden hamster *Mesocricetus auratus* ($2n = 44$) from *Cricetus cricetus* ($2n = 22$) and *C. griseus* ($2n = 22$) (Darlington, 1953). Later, this assumption was not confirmed in the study of the DNA content in these species (Sherudilo and Semeshin, 1969). The heteromorphy of sex chromosomes was the main argument against speciation by polyploidy (more precisely, hybridization with an alloploid formation). Indeed, polyploidization in vertebrates is associated with parthenogenetic reproduction, with the loss of heteromorphic sex chromosomes, or with the development of a sex determination system depending on the environmental conditions (Orr, 1990; Mable, 2004).

Furthermore, genome duplication may disturb the dose compensation mechanisms (Otto and Whitton, 2000). The description of the highest diploid number in mammals *Tympanoctomys barrerae* ($2n = 102$) caused a revival of interest in this issue (Gallardo et al., 1999). The study of the genome of this species, which was performed by Gallardo, showed that the genome of *Tympanoctomys barrerae* is twice as large as in the closely related species of the genera *Octomys* and *Octodontomys* (Gallardo et al., 2003). Moreover, the species *Pipanacoctomys aureus* ($2n = 92$), which was described relatively recently (Mares et al., 2000), is apparently also an allotetraploid (Gallardo et al., 2004). The analysis of meiosis, which was performed by the same authors, showed that 51 bivalents are observed in *T. barrerae*. They also showed that, in males, XY sex chromosomes conjugate in the end-to-end manner, whereas the extra X chromosomes conjugate apparently completely and, therefore, are indistinguishable from the autosomal bivalents. These data, as well as the results of genomic in situ hybridization (GISH), testify to allopolyploidy (Suárez-Villota et al., 2012).

Polyploid genomes inevitably face complex problems such as the change in the level of gene expression, which is primarily reflected on the processes of development, sex determination, and adaptability of the unbalanced genome (Wertheim et al., 2013). It is not surprising that cases of polyploidy in higher vertebrates are extremely rare.

THE ROLE OF OTHER GENETIC ELEMENTS IN THE EMERGENCE OF CHROMOSOMAL REARRANGEMENTS

Barbara McClintock (McClintock, 1984) noted that various kinds of stress, such as inbreeding or environmental changes, can increase the frequency of mutations, due to the activity of transposable elements. The only case when a positive correlation between the activity of transposable elements *Ulysses* and *Penelope*, hybrid dysgenesis, and significant chromosomal differences between species was described for the *Drosophila* group *virilis* (Evgen'ev et al., 2000). Thus, the role of RNA interference in the regulation of hybrid dysgenesis syndrome, induced by transposable elements, and the possibility of chromosomal speciation was shown. However, it is likely that transposable elements are literally the "driving force" of evolution (Böhne et al., 2008; Chalopin et al., 2015).

Evidence that the noncoding RNAs can be a factor and, at the same time, the information component that causes chromosomal rearrangements (Brown et al., 2012) is steadily accumulating. Studies of the role of small RNAs are particularly important for analyzing the causes of oncological diseases, which are accompanied by massive chromosomal rearrangements; however, evolutionary consequences are also possible.

POSSIBLE MECHANISMS OF INHERITANCE OF CHROMOSOMAL REARRANGEMENTS

Why are altered chromosomes inherited? First of all, this is possibly due to the peculiarities of meiosis. The emergence of meiosis is an aromorphosis that made possible sexual reproduction: the stably occurring reduction in the number of chromosomes allowed formation of haploid gametes and restored the diploid number after their fusion. Meiosis and sexual reproduction ensure the continuity of generations and allow maintaining the genetic unity of a species (Bogdanov, 2008). The importance of meiosis, which makes it possible to increase the genetic diversity through recombination, can hardly be overestimated. At the same time, mechanisms that eliminate the "defective" chromosomes (e.g., pachytene arrest (the death of cells at the pachytene stage due to blockage of the formation of the sex vesicle)) and ensure the genome stability of a species have formed (Homolka et al., 2007). However, there are also mechanisms (such as meiotic drive) that ensure the preferential inheritance of individual chromosomes (de Villena and Sapienza, 2001; Wu et al., 2005).

THE ROLE OF MEIOTIC DRIVE IN FIXATION OF CHROMOSOMAL REARRANGEMENTS

Meiotic drive is defined as disturbance in the distribution of chromosomal rearrangements in meiosis, namely, their preferential transmission (over 50%) in one direction and subsequent elimination of one of the variants of gametes, i.e., linked inheritance rather than the transmission of single genetic elements (Chevin and Hospital, 2006), which, in turn, leads to the divergence of populations (Orr and Irving, 2005). Even a very low level of meiotic drive can increase the probability of fixation of even those rearrangements that lead to a decrease in viability and fertility (Walsh, 1982). The meiotic drive concept was introduced by Sandler and Novitski (1957). Meiotic drive is usually explained by the asymmetry of meiosis in mammalian females, because polar bodies are formed during the oocyte development and after fertilization and escape from the dictyotene (i.e., after the resumption of meiosis). If rearranged chromosomes get primarily into the oocyte nucleus rather than into the polar bodies, a rapid fixation of the rearrangement will be observed. Undoubtedly, meiotic drive may occur during spermatogenesis due to the spatial segregation of parental genomes (Mayer et al., 2000). It should be noted that, in any case, cells with such unbalanced or compositionally new chromosome sets will undergo rigorous selection during meiosis.

Gamete competition can be considered a form of meiotic drive (Lyttle, 1981, 1982). In this case, we are speaking of the differentiation of chromosome sets, because rearrangements almost always cause certain disturbances in meiosis; if these disturbances are overcome in at least some of the cells, among a large number of offspring we will find individuals with the rearranged chromosome sets. Most likely, such a mechanism may take place during the fixation of sex chromosomes with rearrangements as well as B chromosomes, whose role in the evolution of the genome remains obscure (Makunin et al., 2014).

INBREEDING

As King wrote, "empirically, it would seem unlikely that a chromosomal variant which was negatively heterotic would have much chance of fixation in a population because of the reduced fertility in carries. Nevertheless, such rearrangements do reach fixation and it is simply a matter of expanding our concept of population genetics to account for these phenomena" (King, 1993, p. 117). Thus, we will obtain the basis of the chromosomal speciation concept.

The role of inbreeding in the evolutionary process has long been estimated as important by leading researchers. In formulating the concept of the interaction of selection and genetic drift, Wright (1931) considered small populations, i.e., introducing the factor of inbreeding. The hypothesis proposed by Carson (1982) on coadapted heterozygous systems also includes inbreeding as a mechanism that, along with genetic drift and selection, is required for fixation of new genetic systems. Grant (1985) and a number of other researchers also believe that the fixation of a new gene combination can be achieved in some small colonies due to selection and genetic drift more rapidly that due to selection alone in large populations.

Inbreeding can be caused by various factors, such as insufficient population size or limitations resulting from uneven dispersal in a large population (Bateman, 1950). Autogamy is also a mating type that can be regarded as inbreeding.

According to some researchers, chromosomal evolution is realized in small inbred demes (Wilson et al., 1975; Bush et al., 1977; Larson et al., 1984). These authors believe that a new chromosomal rearrangement can be fixed only under certain very stringent conditions. It is more likely that this may happen in a small population, in which the level of inbreeding is sufficiently high, rather than in a large panmictic population. A rearrangement can be fixed if ten or fewer individuals remain reproductively isolated for some time (for at least two generations). It should also be noted that a rearrangement may not reduce the viability of heterozygotes and may give some advantage to homozygotes, which will contribute to its distribution (Wilson et al., 1975).

ARE THERE SPECIAL "SPECIATION GENES"?

The discovery of the role of the *PRDM9* gene (Mihola et al., 2009) has slightly opened the "black box," in which the speciation genes are stored (Orr

et al., 2004). Why is this gene considered nearly the only "speciation gene" known? The fact is that it is actively involved in recombination, one of the most important genetic processes. In eukaryotes (at least in the species studied in this direction), recombination sites are not evenly distributed along the chromosome; instead, they are clustered in certain regions, the so-called recombination hotspots (Parvanov et al., 2010). The PRDM9 protein puts an "epigenetic mark" (H3K4me3—trimethylation of lysine 4 in histone H3) at certain sites of the chromosome where a DNA break for subsequent crossing-over should occur. In the case of mutation, the protein and label will be absent, and breaks in other sites, as was shown in mutant mice, lead to disturbances in meiosis (Brick et al., 2012) and sterility. It can be seen that the only speciation gene known to date fulfills its function in meiosis, which once again emphasizes the role of chromosomes in speciation.

As was rightly noted by Shapiro (2002), it is clear that the time has come to reconsider the negative attitude of the evolutionary theory to genomic rearrangements. Rapid genome transformations may be the only chance for a species to overcome a crisis situation (e.g., a sharp change in environmental conditions). From this standpoint, those species whose evolution is based solely on independent random changes are very vulnerable. Such a radical change of the basic provisions, in our opinion, fits the system of a biological species, the evolution of which cannot and should not be limited to one way of speciation due to the priority of one isolation mechanism. As for any model, these limitations are artificial. Recently, ideas about the structure and function of genetic material have changed radically. In particular, within the modern genetics concept, the gene cannot be regarded as a linear unbreakable functional unit. Conversely, "functional domains can be assembled from spatially separated chromatin regions, which form loops and associate to form spatially complex binding sites for proteins that either activate or repress transcription" (Golubovsky, 2000, p. 110). Modern data on the structure of the cell nucleus confirm the existence of complex dynamic relationships between the chromosomal structure (including rearrangements) and function (including the regulation of gene expression). The hypothesis about the initiating role of chromosomal rearrangements in speciation agrees well with the concept of the existence of genetic systems, changes in the regulatory part of which may lead to radical changes in the operation of the system and, as a consequence, to a change in the phenotype (including not only morphological but also ecological and ethological characteristics).

We believe that, at the current level of knowledge, it can be postulated that the chromosomal rearrangements, including the Robertsonian translocations, can lead to the formation of a balanced karyotype, having changed the nucleus architecture, and transform the genetic system of a species. From this standpoint, the chromosomal speciation, as a variant of the genetic speciation, is a real phenomenon.

It is gradually becoming clear that the study of speciation cannot be limited only to the analysis of characteristics of reproductively active individuals. The "conflictual speciation" concept has been formulated recently, the key point of which is the formation of reproductive isolation as a by-product of selection, the main subjects of which are the genome and the systems that form it, i.e., DNA and chromosomes (Shapiro, 2005; Maheshwari and Barbash, 2011; Crespi and Nosil, 2013; Presgraves, 2013). Chromosome rearrangements change the structure and spatial position of linkage groups, which affects the transcriptional activity of genes and recombination. Various evolutionary consequences, such as the presence or absence of a genetic flow between chromosomal forms, have a logical explanation within the framework of this concept. Such a pathway seems equally possible along with "speciation genes," especially taking into account the fact that, to date, this status was shown only for the *Prdm9* gene—the only hybrid sterility gene identified in mammals (Baudat et al., 2010; Brick et al., 2012). Single "speciation genes" are only an initiating component; then (particularly, due to the hitchhiking effect), the mutations associated with them reduces the genetic flow, which leads to divergence. Genetic drift and meiotic drive are usually regarded as stochastic processes, in contrast to natural selection. At the same time, these processes cannot be called random: they follow the patterns associated, first of all, with the structure of the genome organization. The study of these processes may provide a clue to understanding the mechanisms of occurrence of uneven changes in the genome and the inconsistency of phenotypic and genetic variability. The creative role of hybridization in speciation was shown in a number of recent studies (Lavrenchenko and Bulatova, 2015; Lukhtanov et al., 2015; Schumer et al., 2015; Arias et al., 2016). This does not contradict the modern concept of a species, in which a species is regarded as a system that allows the passage of a genetic information flow rather than as a completely closed genetic system (Mayr, 1996).

This review has only allowed giving some ideas about the diversity and interdependence of the genetic basis of speciation. Undoubtedly, the term "chromosomal speciation" should not be interpreted literally (Faria and Navarro, 2010) but, rather, should be regarded as a convenient designation for the complex evolutionary processes that are initiated by chromosomes and involve the latter.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project no. 14-04-00785a.

REFERENCES

Arias, C.A., Van Belleghem, S., and McMillan, W.O., Genomics at the evolving species boundary, *Curr. Opin. Insect Sci.*, 2016, vol. 13, pp. 7–15.

Atlas of Mammalian Chromosomes, O'Brien, S.J., Menninger, J.C., and Nash, W.G., Eds., Wiley, 2006.

Ayala, F.J. and Coluzzi, M., Chromosome speciation: humans, drosophila, and mosquitoes, *Proc. Natl. Acad. Sci. U. S. A.*, 2005, vol. 102, pp. 6535–6542.

Baird, A.B., Hillis, D.M., Patton, J.C., and Bickham, J.W., Speciation by monobrachial centric fusions: a test of the model using nuclear DNA sequences from the bat genus *Rhogeessa, Mol. Phylogenet. Evol.*, 2009, vol. 50, pp. 256–267.

Baker, R.J., Bickham, J.W., and Arnold, M.L., Chromosomal evolution in *Rhogeessa* (Chiroptera, Vespertilionidae): possible speciation by centric fusions, *Evolution*, 1985, vol. 39, pp. 233–243.

Baker, R.J., Quimsiyeh, M.B., and Hood, C.S., Role of chromosomal banding patterns in understanding mammalian evolution, in *Current Mammalogy,* Genoways H.H., Ed., New York: Plenum Press, 1987, pp. 67–96.

Baker, R.J. and Bickham, J.W., Speciation by monobrachial centric fusions, *Proc. Natl. Acad. Sci. U. S. A.*, 1986, vol. 83, pp. 8245–8248.

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.

Baklushinskaya, I.Yu., Romanenko, S.A., Grafodatskii, A.S., Matveevskii, S.N., Lyapunova, E.A., and Kolomiets, O.L., The role of chromosome rearrangements in the evolution of mole voles of the genus *Ellobius* (Rodentia, Mammalia), *Russ. J. Genet.*, 2010, vol. 46, no. 9, pp. 1143–1145.

Bateman, A.J., Is the gene dispersion normal?, *Heredity*, 1950, vol. 4, pp. 353–363.

Bateson, W., *Mendel's Principle of Heredity, a Defense*, Cambridge, 1902.

Baudat, F., Imai, Y., and de Massy, B., Meiotic recombination in mammals: localization and regulation, *Nature Rev. Genet.*, 2013, vol. 14, pp. 794–806.

Baverstock, P.R., Watts, C.H.S., Gelder, M., and Jahnke, A., G-banding homologies of some Australian rodents, *Genetics*, 1983, vol. 60, pp. 105–117.

Bazykin, A.D., The effect of disruptive selection on a spatially extended population. I. Equal fitness of homozygotes. II. Unequal fitness of homozygotes. III. A heterogeneous area that includes a site with a reduced gene migration, in *Problemy evolyutsii* (Problems of Evolution), Novosibirsk: Nauka, 1972, vol. 2, pp. 219–232.

Bazykin, A.D., Hypothetical mechanism of speciation, *Evolution*, 1969, vol. 23, no. 4, pp. 685–687.

Berthelot, C., Muffato, M., Abecassis, J., and Crollius, H.R., The 3D organization of chromatin explains evolutionary fragile genomic regions, *Cell Rep.*, 2015, vol. 10, pp. 1913–1924.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., et al., The delayed rise of present-day mammals, *Nature*, 2007, vol. 446, pp. 507–512.

Bogdanov, A.S., Chromosomal differentiation of populations of pygmy wood mouse *Sylvaemus uralensis* in the eastern part of the species range, *Zool. Zh.*, 2001, vol. 80, no. 3, pp. 331–342.

Bogdanov, Yu.F., Evolution of meiosis in unicellular and multicellular eukaryotes. Aromorphosis at the cellular level, *Zh. Obshch. Biol.*, 2008, vol. 29, pp. 102–107.

Bogdanov, A.S. and Rozanov, Yu.M., Variability in size of the nuclear genome in pygmy wood mouse *Sylvaemus uralensis* (Rodentia, Muridae), *Russ. J. Genet.*, 2005, vol. 41, no. 10, pp. 1123–1129.

Böhne, A., Brunet, F., Galiana-Arnoux, D., Schultheis, C., and Volff, J.N., Transposable elements as drivers of genomic and biological diversity in vertebrates, *Chromosome Res.*, 2008, vol. 16, pp. 203–215.

Boveri, T., Die Blastomerenkerne von *Ascaris megalocephala* und die Theorie der Chromosomenindividualität, *Arch. Zellforschung. B*, 1909, pp. 181–268.

Boyle, S., Rodesch, M.J., Halvensleben, H.A., Jeddeloh, J.A., and Bickmore, W.A., Fluorescence in situ hybridization with high-complexity repeat-free oligonucleotide probes generated by massively parallel synthesis, *Chromosome Res.*, 2011, vol. 19, pp. 901–909.

Branco, M.R. and Pombo, A., Intermingling of chromosome territories in interphase suggests role in translocations and transcription-dependent associations, *PLoS Biol.*, 2006, vol. 4, no. 5, p. 780.

Brick, K., Smagulova, F., Khil, P., Camerini-Otero, R.D., and Petukhova, G.V., Genetic recombination is directed away from functional genomic elements in mice, *Nature*, 2012, vol. 485, pp. 642–645.

Bridges, C.B., Non-disjunction as proof of the chromosome theory of heredity, *Genetics*, 1916, vol. 1, pp. 107–163.

Brinkley, B.R. and Stubblefield, E., The fine structure of the kinetochore of a mammalian cell in vitro, *Chromosoma*, 1966, vol. 19, pp. 28–43.

Brown, J.D., Mitchell, S.E., and O'Neill, R.J., Making a long story short: noncoding rnas and chromosome change, *Heredity*, 2012, vol. 108, pp. 42–49.

Bush, G.L., Case, S.M., Wilson, A.S., and Patton, J.L., Rapid speciation and chromosomal evolution in mammals, *Proc. Natl. Acad. Sci. U. S. A.*, 1977, vol. 74, pp. 3942–3946.

Capanna, E. and Castiglia, R., Chromosomes and speciation in *Mus musculus domesticus, Cytogenet. Genome Res.*, 2004, vol. 105, pp. 375–384.

Capanna, E., Robertsonian numerical variation in animal speciation: *Mus musculus* an emblematic model, in *Mechanism of Speciation*, Barigozzi, C., Ed., New York: Alan Liss, 1982, pp. 155–177.

Carson, H.L., Speciation as a major reorganization of polygenic balances, in *Mechanism of Speciation*, Barigozzi, C., Ed., New York: Alan Liss, 1982, pp. 411–433.

Catania, S. and Allshire, R.C., Anarchic centromeres: deciphering order from apparent chaos, *Curr. Opin. Cell Biol.*, 2014, vol. 26, pp. 41–50.

Chalopin, D., Naville, M., Plard, F., Galiana, D., and Volff, J.N., Comparative analysis of transposable elements

highlights mobilome diversity and evolution in vertebrates, *Genome Biol. Evol.*, 2015, vol. 7, pp. 567–580.

Chevin, L.-M. and Hospital, F., The hitchhiking effect of an autosomal meiotic drive gene, *Genetics*, 2006, vol. 173, pp. 1829–1832.

Craig, J.M. and Bickmore, W.A., Chromosome bands—flavours to savour, *BioEssays*, 1993, vol. 15, pp. 349–354.

Cremer, M., von Hase, J., Volm, T., Brero, A., Kreth, G., et al., Non-random radial higher-order chromatin arrangements in nuclei of diploid cells, *Chromosome Res.*, 2001, vol. 9, pp. 541–567.

Cremer, T., Cremer, M., Hübner, B., Strickfaden, H., Smeets, D., et al., The 4D nucleome: evidence for a dynamic nuclear landscape based on co-aligned active and inactive nuclear compartments, *FEBS Lett.*, 2015, vol. 589, no. 20, part A, pp. 2931–2943.

Crespi, B. and Nosil, P., Conflictual speciation: species formation via genomic conflict, *Trends Ecol. Evol.*, 2013, vol. 28, pp. 48–57.

Croft, J.A., Bridger, J.M., Boyle, S., Perry, P., Teague, P., and Bickmore, W.A., Differences in the localization and morphology of chromosomes in the human nucleus, *J. Cell Biol.*, 1999, vol. 145, pp. 1119–1131.

Cytotaxonomy and Vertebrate Evolution, Chiarelli, A.B. and Capanna, E., Eds., London: Acad. Press, 1973.

Darlington, C.D., Polyploidy in animals, *Nature*, 1953, vol. 171, no. 4344, pp. 191–194.

Darlington, C.D., The external mechanics of chromosomes, *Proc. Roy. Soc. Lond., Ser. B: Biol. Sci.*, 1936, vol. 121, pp. 264–319.

Darlington, C.D., *The Evolution of Genetic Systems*, Cambridge: University Press, 1939.

Darwin C., *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, London: John Murray, 1859.

Darwin, C.R., *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 6th ed., London: John Murray, 1872.

Delone, L.N., Comparative karyological study of species *Muscari* Mill. and *Bellevalia* Lapeyr., *Vestn. Tiflis. Bot. Sada*, 1922, vol. 2, no. 1, pp. 1–32.

Dobigny, G., Britton-Davidian, J., and Robinson, T.J., Chromosomal polymorphism in mammals: an evolutionary perspective, *Biol. Rev.*, 2015. doi 10.1111/brv.12213

Dobzhansky, F., *Genetika i proiskhozhdenie vidov* (Genetics and the Origin of Species), Moscow–Izhevsk, 2010.

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

Evgen'ev, M., Zelentsova, E., Poluectova, H., Lyoziin, G., Velikodvorskaya, V., et al., Mobile elements and chromosomal evolution in the *virilis* group of *Drosophila, Proc. Natl. Acad. Sci. U. S. A.*, 2000, vol. 97, pp. 11337–11342.

Faria, R. and Navarro, A., Chromosomal speciation revisited: rearranging theory with pieces of evidence, *Trends Ecol. Evol.*, 2010, vol. 25, pp. 660–669.

Farré, M., Robinson, T.J., and Ruiz-Herrera, A., An integrative breakage model of genome architecture, reshuffling and evolution, *BioEssays*, 2015, vol. 37, pp. 479–488.

Ferguson-Smith, M.A., Genetic analysis by chromosome sorting and painting: phylogenetic and diagnostic applications, *Eur. J. Hum. Genet.*, 1997, vol. 5, pp. 253–265.

Ferguson-Smith, M.A., History and evolution of cytogenetics, *Mol. Cytogenet.*, 2015, vol. 8, p. 19. doi 10.1186/s13039-015-0125-8

Ferguson-Smith, M.A. and Trifonov, V., Mammalian karyotype evolution, *Nature Rev. Genet.*, 2007, vol. 8, pp. 950–962.

Ferree, P.M. and Barbash, D.A., Species-specific heterochromatin prevents mitotic chromosome segregation to cause hybrid lethality in *Drosophila*, *PLoS Biol.*, 2009, vol. 7, no. 10, p. 2310.

Futuyma, D.J. and Mayer, G.C., Non-allopatric speciation in animals, *Syst. Biol.*, 1980, vol. 29, pp. 254–271.

Gallardo, M.H., Bickham, J.W., Honeycutt, R.L., Ojeda, R.A., and Köhler, N., Discovery of tetraploidy in a mammal, *Nature*, 1999, vol. 401, p. 341.

Gallardo, M.H., Bickham, J.W., Kausel, G., Köhler, N., and Honeycutt, R.L., Gradual and quantum genome size shifts in the hystricognath rodents, *J. Evol. Biol.*, 2003, vol. 16, pp. 163–169.

Gallardo, M.H., Kausel, G., Jiménez, A., Bacquet, C., González, C., et al., Whole-genome duplications in South American desert rodents (Octodontidae), *Biol. J. Linn. Soc.*, 2004, vol. 82, pp. 443–451.

Garagna, S., Marziliano, N., Zucotti, M., Searle, J., Capanna, E., and Redi, C.A., Pericentromeric organization at the fusion point of mouse Robertsonian translocation chromosomes, *Proc. Natl. Acad. Sci. U. S. A.*, 2001, vol. 98, pp. 171–175.

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

Gavrilov, A.A. and Razin, S.V., Compartmentalization of the cell nucleus and spatial organization of the genome, *Mol. Biol.* (Moscow), 2015, vol. 49, no. 1, pp. 21–39.

Godo, A., Blanco, J., Vidal, F., Sandalinas, M., Garcia-Guixè, E., and Anton, E., Altered segregation pattern and numerical chromosome abnormalities interrelate in spermatozoa from Robertsonian translocation carriers, *Reprod. Biomed. Online*, 2015, vol. 31, pp. 79–88.

Goldschmidt, R., *The Material Basis of Evolution*, New Haven: Yale Univ. Press, 1940.

Golubovsky, M.D., *Vek genetiki: evolyutsiya idei i ponyatii* (The Age of Genetics: The Evolution of Ideas and Concepts), St. Petersburg: Borei Art, 2000.

Grant, V., *The Evolutionary Process: A Critical Review of Evolutionary Theory*, New York: Columbia Univ. Press, 1985.

Graphodatsky, A.S., Comparative chromosomics, *Mol. Biol.* (Moscow), 2007, vol. 41, no. 3, pp. 361–375.

Graphodatsky, A.S., Trifonov, V.A., and Stanyon, R., The genome diversity and karyotype evolution of mammals, *Mol. Cytogenet.*, 2011, vol. 4, pp. 22–37.

Gropp, A., Winking, H., Zech, L., and Muller, H.J., Robertsonian chromosomal variation and identification of metacentric chromosomes in feral mice, *Chromosoma*, 1972, vol. 39, pp. 265–288.

Henking, H., Über Spermatogenese und deren Beziehung zur Eientwicklung bei *Pyrrhocoris apterus* L., *Zeit schrift für wissenschaftliche Zoologie. B*, 1891, pp. 685–736.

Hinchliff, C., Smith, S., Allmanb, J., Burleighc, J., Chaudharyc, R., et al., Synthesis of phylogeny and taxonomy into a comprehensive tree of life, *Proc. Natl. Acad. Sci. U. S. A.*, 2015, vol. 112, no. 41, pp. 12764–12769.

Holland, P.W.H. and Garcia-Fernandez, J., *Hox* genes and chordate evolution, *Dev. Biol.*, 1996, vol. 173, pp. 382–395.

Holmquist, G.P., Chromosome band, there chromatin flavor and their functional features, *Am. J. Hum. Genet.*, 1992, vol. 51, pp. 17–37.

Homolka, D., Ivanek, R., Capkova, J., Jansa, P., and Forejt, J., Chromosomal rearrangement interferes with meiotic X chromosome inactivation, *Genome Res.*, 2007, vol. 17, pp. 1431–1437.

Hori, T. and Fukagawa, T., Establishment of the vertebrate kinetochores, *Chromosome Res.*, 2012, vol. 20, pp. 547–561.

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.

Hsu, T.C. and Benirschke, K., *An Atlas of Mammalian Chromosomes*, Springer Science and Business Media, 1967–1977, vols. 1–10.

Jackson, D.A., Nuclear organization: uniting replication foci, chromatin domains and chromosome structure, *BioEssays*, 1995, vol. 17, pp. 587–591.

Jokelainen, P.T., The ultrastructure and spatial organization of the metaphase kinetochore in mitotic rat cells, *J. Ultrastructure Res.*, 1967, vol. 19, pp. 19–44.

Karamysheva, T.V., Bogdanov, A.S., Kartavtseva, I.V., et al., Comparative FISH analysis of C-positive blocks of centromeric chromosomal regions of pygmy wood mice *Sylvaemus uralensis* (Rodentia, Muridae), *Russ. J. Genet.*, 2010, vol. 46, no. 6, pp. 712–724.

Karpechenko, G.D., Polyploid hybrids *Raphanus satrivus* L. × *Brassica oleracea* L. (on the problem of experimental speciation), *Trudy Prikl. Bot. Genet. Selekts.*, 1927, vol. 17, no. 3, pp. 305–410.

Katz, L.A., Grant, J.R., Parfrey, L.W., and Burleigh, J.G., Turning the crown upside down: gene tree parsimony roots the eukaryotic tree of life, *Syst. Biol.*, 2012, vol. 61, pp. 653–660.

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

Korochkin, L.I., What is epigenetics, *Russ. J. Genet.*, 2006, vol. 42, no. 9, pp. 958–965.

Kozubek, S., Lukásová, E., Jirsová, P., Koutná, I., Kozubek, M., et al., 3D structure of the human genome: order in randomness, *Chromosoma*, 2002, vol. 111, pp. 321–331.

de Laat, W. and Grosveld, F., Spatial organization of gene expression: the active chromatin hub, *Chromosome Res.*, 2003, vol. 11, pp. 447–459.

Lande, R., Effective deme sizes during long-term evolution estimated from rates of chromosomal rearrangement, *Evolution*, 1979, vol. 33, pp. 234–251.

Larson, A., Prager, E.M., and Wilson, A.C., Chromosomal evolution, speciation and morphological change in vertebrates: the role of social behavior, in *Chromosomes Today*, Bennett, M.D., Gropp, A., and Wolf, U., Eds., London: George Allen and Unwin., 1984, vol. 8, pp. 215–228.

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.*, 2016, vol. 6, no. 3, pp. 232–244.

Leffler, E.M., Bullaughey, K., Matute, D.R., Meyer, W.K., Segurel, L., et al., Revisiting an old riddle: what determines genetic diversity levels within species?, *PLoS Biol.*, 2012, vol. 10, p. e1001388.

Levitskii, G.A, *Material'nye osnovy nasledstvennosti* (The Material Basis of Heredity), Kiev: Gosizdat, 1924 (republication: Levitskii, G.A., *Tsitologiya rastenii. Izbrannye trudy* (Plant Cytology. Selected Works), Moscow: Nauka, 1976).

Lewontin, R., *The Genetic Basis of Evolutionary Change*, Columbia Univ. Press, 1974.

Lukhtanov, V.A., Shapoval, N.A., Anokhin, B.A., Saifitdinova, A.F., and Kuznetsova, V.G., Homoploid hybrid speciation and genome evolution via chromosome sorting, *Proc. Roy. Soc. Lond. B: Biol. Sci.*, 2015, vol. 282, no. 1807, p. 20150157.

Lyttle, T.W., A theoretical analysis of the effects of sex chromosome aneuploidy on X and Y chromosome meiotic drive, *Evolution*, 1982, vol. 36, pp. 822–831.

Lyttle, T.W., Experimental population genetics of meiotic drive system. III. Neutralization of sex-ratio distortion in drosophila through sex chromosome aneuploidy, *Genetics*, 1981, vol. 98, pp. 317–334.

Mable, B., 'Why polyploidy is rare in animals than in plants': myths and mechanisms, *Biol. J. Linn. Soc.*, 2004, vol. 82, pp. 453–466.

Maheshwari, S. and Barbash, D.A., The genetics of hybrid incompatibilities, *Ann. Rev. Genet.*, 2011, vol. 45, pp. 331–355.

Mahy, N.I., Perry, P.E., Gilchrist, S., Baldock, R.A., and Bickmore, W.A., Spatial organization of large-scale chromatin domains in the nucleus: a magnified view of single chromosome territories, *J. Cell Biol.*, 2002, vol. 139, pp. 1597–1610.

Makunin, A.I., Dementyeva, P.V., Graphodatsky, A.S., Volobouev, V.T., Kukekova, A.V., and Trifonov, V.A., Genes on B chromosomes of vertebrates, *Mol. Cytogenet.*, 2014, vol. 7, p. 99.

Mares, M.A., Braun, J.K., Bárquez, R.B., and Díaz, M., Two new genera and species of halophytic desert mammals from isolated salt flats in Argentina, *Occasional Papers Museum of Texas Tech University*, 2000, no. 203, pp. 1–27.

Marshall, O.J., Chueh, A.C., Wong, L.H., and Choo, K.A., Neocentromeres: new insights into centromere structure, disease development, and karyotype evolution, *Am. J. Hum. Genet.*, 2008, vol. 82, pp. 261–282.

Matthey, R., Chromosomes, heterochromosomes and comparative cytology of the palaearctic Cricetinae (Rodentia), *Caryologia*, 1960, vol. 13, pp. 199–223.

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

Matveevsky, S., Bakloushinskaya, I., Tambovtseva, V., Romanenko, S., and Kolomiets, O., Analysis of meiotic chromosome structure and behavior in Robertsonian heterozygotes of *Ellobius tancrei*: a case of monobrachial

homology, *Comp. Cytogenet.*, 2015, vol. 9, no. 4, pp. 691–706.

Mayer, W., Fundele, R., and Haaf, T., Spatial separation of parental genomes during mouse interspecific (*Mus musculus–M. spretus*) spermiogenesis, *Chromosome Res.*, 2000, vol. 8, pp. 555–558.

Mayr, E., Change of genetic environment and evolution, in *Evolution as a Process*, Huxley, J., Hardy, A.C., and Ford, E.B., Eds., London: Allen and Unwin, 1954, pp. 157–180.

Mayr, E., What is a species, and what is not?, *Philos. Sci.*, 1996, vol. 63, pp. 262–277.

McClintock, B., The significance of responses of the genome to challenge, *Science*, 1984, vol. 226, pp. 792–801.

McClung, C.E., "The Accessory Chromosome—Sex Determinant?," *Biol. Bull.*, 1902, vol. 3, pp. 43–84.

Mihola, O., Trachtulec, Z., Vlcek, C., Schimenti, J.C., and Forejt, J., A mouse speciation gene encodes a meiotic histone H3 methyltransferase, *Science*, 2009, vol. 323, pp. 373–375.

Montefalcone, G., Tempesta, S., Rocchi, M., and Archidiacono, N., Centromere repositioning, *Genome Res.*, 1999, vol. 9, pp. 1184–1188.

Morgan, T.H., *The Physical Basis of Heredity*, Philadelphia: J.B. Lippincott, 1919.

Morgan, T.H., Sturtevant, A.H., Muller, H.J., and Bridges, C.B., *The Mechanism of Mendelian Heredity*, New York: Holt, 1915.

Muller, H.J., A gene for the fourth chromosome of *Drosophila, J. Exp. Zool.*, 1914, vol. 17, pp. 325–336.

Murphy, W.J., Pevzner, P.A., and O'Brien, S.J., Mammalian phylogenomics comes of age, *Trends Genet.*, 2004, vol. 20, pp. 631–639.

Navashin, M.S., Ob izmenenii chisla i morfologicheskikh priznakov khromosom u mezhvidovykh gibridov, *Trudy po prikladnoi botanike, genetike i selektsii*, 1927, vol. 17.

Nei, M., Maruyama, T., and Wu, C.I., Models of evolution of reproductive isolation, *Genetics*, 1983, vol. 103, pp. 557–579.

Neumann, P., Navrátilová, A., Schroeder-Reiter, E., Koblížková, A., Steinbauerová, V., et al., Stretching the rules: monocentric chromosomes with multiple centromere domains, *PLoS Genet.*, 2012, vol. 8, p. e1002777.

Noor, M.A. and Bennett, S.M., Islands of speciation or mirages in the desert? Examining the role of restricted recombination in maintaining species, *Heredity*, 2009, vol. 103, pp. 439–444.

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

Orr, H.A., "Why polyploidy is rare in animals than in plants" revisited, *Am. Nat.*, 1990, vol. 136, pp. 759–770.

Orr, H.A. and Irving, S., Segregation distortion in hybrids between the Bogota and United States subspecies of *Drosophila pseudoobscura, Genetics*, 2005, vol. 169, pp. 671–682.

Orr, H.A., Masly, J.P., and Presgraves, D.C., Speciation genes, *Curr. Opin. Genet. Dev.*, 2004, vol. 14, pp. 675–679.

Parada, L. and Misteli, T., Chromosome positioning in the interphase nucleus, *Trends Cell Biol.*, 2002, vol. 12, no. 9, pp. 425–432.

Parvanov, E.D., Petkov, P.M., and Paigen, K., *Prdm9* controls activation of mammalian recombination hotspots, *Science*, 2010, vol. 327, pp. 835–835.

Van de Peer, Y., Maere, S., and Meyer, A., The evolutionary significance of ancient genome duplications, *Nature Rev. Genet.*, 2009, vol. 10, pp. 725–732.

Pfau, S.J. and Amon, A., Chromosomal instability and aneuploidy in cancer: from yeast to man, *EMBO Rep.*, 2012, vol. 13, pp. 515–527.

Pinho, C. and Hey, J., Divergence with gene flow: models and data, *Ann. Rev. Ecol. Evol. Syst.*, 2010, vol. 41, pp. 215–230.

Plohl, M., Meštrović, N., and Mravinac, B., Centromere identity from the DNA point of view, *Chromosoma*, 2014, vol. 123, pp. 313–325.

Polly, P.D., Polyakov, A.V., Ilyashenko, V.B., Onischenko, S.S., White, T.A., et al., Phenotypic variation across chromosomal hybrid zones of the common shrew (*Sorex araneus*) indicates reduced gene flow, *PLoS One*, 2013, vol. 8, p. e67455.

Potter, S., Moritz, C., and Eldridge, M.D., Gene flow despite complex Robertsonian fusions among rock-wallaby (*Petrogale*) species, *Biol. Lett.*, 2015, vol. 11, p. 20150731. doi 10.1098/rsbl.2015.0731

Presgraves, D.C., Hitchhiking to speciation, *PLoS Biol.*, 2013, vol. 11, no. 2, p. e1001498. doi 10.1371/journal.pbio.1001498

Prokof'eva-Bel'govskaya, A.A., *Geterokhromaticheskie raiony khromosom* (Heterochromatic Chromosome Regions), Moscow: Nauka, 1986.

Qumsiyeh, M.B., Evolution of number and morphology of mammalian chromosomes, *J. Hered.*, 1994, vol. 1985, pp. 455–465.

Qumsiyeh, M.B., Structure and function of the nucleus: anatomy and physiology of chromatin, *Cell. Mol. Life Sci.*, 1999, vol. 55, pp. 1129–1140.

Rabl, C., Über Zellteilung, *Morphologisches Jahrbuch.*, 1885, vol. 10, pp. 214–330.

Robinson, T.J., Ruiz-Herrera, A., and Avise, J.C., Hemiplasy and homoplasy in the karyotypic phylogenies of mammals, *Proc. Natl. Acad. Sci. U. S. A.*, 2008, vol. 105, pp. 14477–14481.

Rocchi, M., Archidiacono, N., Schempp, W., Capozzi, O., and Stanyon, R., Centromere repositioning in mammals, *Heredity*, 2012, vol. 108, pp. 59–67.

Romanenko, S.A., Biltueva, L.S., Serdyukova, N.A., Kulemzina, A.I., Beklemisheva, V.R., et al., Segmental paleotetraploidy revealed in sterlet (*Acipenser ruthenus*) genome by chromosome painting, *Mol. Cytogenet.*, 2015, vol. 8, p. 90.

Romiguier, J., Gayral, P., Ballenghien, M., Bernard, A., Cahais, V., et al., Comparative population genomics in animals uncovers the determinants of genetic diversity, *Nature*, 2014, vol. 515, no. 7526, pp. 261–263.

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, no. 9, pp. 1096–1110.

Sacristan, C. and Kops, G.J., Joined at the hip: kinetochores, microtubules, and spindle assembly checkpoint signaling, *Trends Cell Biol.*, 2015, vol. 25, pp. 21–28.

Sandler, L.R. and Novitski, E., Meiotic drive as an evolutionary force, *Am. Nat.*, 1957, vol. 120, pp. 510–532.

Scherthan, H., Cremer, T., Arnason, U., Weier, H.U., Lima-de-Faria, A., and Fronicke, L., Comparative chromosome painting discloses homologous segments in distantly related mammals, *Nat. Genet.*, 1994, vol. 6, pp. 342–347.

Schrader, F., Kinetic regions in chromosomes, *Nature*, 1939, vol. 143, p. 122.

Schumer, M., Cui, R., Rosenthal, G.G., and Andolfatto, P., Reproductive isolation of hybrid populations driven by genetic incompatibilities, *PLoS Genet.*, 2015, vol. 11, p. e1005041.

Searle, J.B., Three new karyotypic races of the common shrew *Sorex araneus* (Mammalia: Insectivora) and a phylogeny, *Syst. Zool.*, 1984, vol. 33, pp. 184–194.

Searle, J.B., Hausser, J., Zima, J., Fredga, K., Wójcik, J.M., et al., The ISACC heritage, *Russ. J. Theriol.*, 2007, vol. 6, pp. 123–167.

Shapiro, J.A., Genome organization and reorganization in evolution: formatting for computation and function, *Ann. N.Y. Acad. Sci.*, 2002, vol. 981, pp. 111–134.

Shapiro, J.A., A 21st century view of evolution: genome system architecture, repetitive DNA, and natural genetic engineering, *Gene*, 2005, vol. 345, no. 1, pp. 91–100.

Shapiro, J.A., Revisiting the central dogma in the 21st century, *Ann. N.Y. Acad. Sci.*, 2009, vol. 1178, no. 1, pp. 6–28.

Shapiro, J.A., Rethinking the (im)possible in evolution, *Progr. Biophys. Mol. Biol.*, 2013, vol. 111, pp. 92–96.

Shchipanov, N.A. and Pavlova, S.V., Evolutionary and taxonomic differentiation of species of shrews in the "araneus" species group of the genus *Sorex*. Communication 1. Levels of chromosomal differentiation, *Biol. Bull.* (Moscow), 2016, vol. 43 (in press).

Sherudilo, A.I. and Semeshin, V.F., Comparison of chromosome sets and the amount of DNA in the nucleus of some Palearctic hamsters, in *Materialy ko II Vses. soveshch. po mlekopitayushchim. Mlekopitayushchie, evolyutsiya, kariologiya, sistematika, faunistika* (Proceedings of the II All-Union Conference on Mammals: Mammals, Evolution, Karyology, Systematics, and Faunistics), Novosibirsk, 1969, p. 110.

Simpson, A.G. and Roger, A.J., The real 'kingdoms' of eukaryotes, *Curr. Biol.*, 2004, vol. 14, no. 17, pp. R693–R696.

Stanyon, R. and Bigoni, F., Primate chromosome evolution: with reference to marker order and neocentromeres, *Russ. J. Genet.*, 2010, vol. 46, pp. 1226–1233.

Stanyon, R., Rocchi, M., Capozzi, O., Roberto, R., Misceo, D., et al., Primate chromosome evolution: ancestral karyotypes, marker order and neocentromeres, *Chromosome Res.*, 2008, vol. 16, pp. 17–39.

Stegnii, V.N., *Arkhitektonika genoma, sistemnye mutatsii i evolyutsiya* (Genome Architectonics, System Mutations, and Evolution), Novosibirsk: Izd. Novosibirsk. Gos. Univ., 1993.

Steiner, F.A. and Henikoff, S., Diversity in the organization of centromeric chromatin, *Curr. Opin. Genet. Dev.*, 2015, vol. 31, pp. 28–35.

Stevens, N.M., *Studies in Spermatogenesis with Especial Reference to the "Accessory Chromosome*," Washington, D.C.: Carnegie Institution, 1905.

Suárez -Villota, E.Y., Vargas, R.A., Marchant, C.L., Torres, J.E., Köhler, N., et al., Distribution of repetitive DNAs and the hybrid origin of the red vizcacha rat (Octodontidae), *Genome*, 2012, vol. 55, pp. 105–117.

Sun, H.B., Shen, J., and Yokota, H., Size-dependent positioning of human chromosomes in interphase nuclei, *Biophys. J.*, 2000, vol. 79, pp. 184–190.

Sutton, W.S., The chromosomes in heredity, *Biol. Bull.*, 1903, vol. 4, pp. 231–250.

Szyf, M., Nongenetic inheritance and transgenerational epigenetics, *Trends Mol. Med.*, 2015, vol. 21, pp. 134–144.

Tanabe, H., Müller, S., Neusser, M., von Hase, J., Calcagno, E., et al., Evolutionary conservation of chromosome territory arrangements in cell nuclei from higher primates, *Proc. Natl. Acad. Sci. U. S. A.*, 2002, vol. 99, pp. 4424–4429.

Telenius, H., Pelmear, A.H., Tunnacliffe, A., Carter, N.P., Behind, A., et al., Cytogenetic analysis by chromosome painting using DOP–PCR amplified flow-sorted chromosomes, *Genes Chromosomes Cancer*, 1992, vol. 4, pp. 257–263.

Templeton, A.R., Mechanisms of speciation—a population genetics approach, *Ann. Rev. Ecol. Syst.*, 1981, vol. 12, pp. 23–48.

Thompson, S.L., Bakhoum, S.F., and Compton, D.A., Mechanisms of chromosomal instability, *Curr. Biol.,* 2010, vol. 2, pp. R285–R295.

Vermaak, D. and Malik, H.S., Multiple roles for heterochromatin protein 1 genes in Drosophila, *Ann. Rev. Genet.*, 2009, vol. 43, pp. 467–492.

de Villena, F.P.M. and Sapienza, C., Female meiosis drives karyotypic evolution in mammals, *Genetics*, 2001, vol. 159, pp. 1179–1189.

Vorontsov, N.N., The significance of the study of chromosome sets for the systematics of mammals, *Byull. Mosk. Obshch. Ispytat. Prirody, Otdel. Biol.*, 1958, vol. 63, pp. 5–86.

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

Vorontsov, N.N., *Razvitie evolyutsionnykh idei v biologii* (The Development of Evolutionary Ideas in Biology), Moscow: Izd. Otdel UNTs DO MGU, Progress-Traditsiya, ABF, 1999.

Vorontsov, N.N., Lyapunova, E.A., Zakaryan, G.G., and Ivanov, V.G., Karyology and taxonomy of the genus *Ellobius* (Microtinae, Rodentia), in *Materialy ko II Vses. Soveshch. po mlekopitayushchim. Mlekopitayushchie, evolyutsiya, kariologiya, sistematika, faunistika* (Proceedings of the II All-Union Conference on Mammals: Mammals, Evolution, Karyology, Ssystematics, and Faunistics), Novosibirsk, 1969, pp. 127–129.

Voullaire, L.E., Slater, H.R., Petrovic, V., and Choo, K.H., A functional marker centromere with no detectable alpha-satellite, satellite III, or CENP-B protein: activation of a latent centromere?, *Am. J. Hum. Genet.*, 1993, vol. 52, pp. 1153–1163.

Wade, C.M., Giulotto, E., Sigurdsson, S., Zoli, M., Gnerre, S., et al., Genome sequence, comparative analysis, and population genetics of the domestic horse, *Science*, 2009, vol. 326, pp. 865–867.

Waldeyer, W., Über Karyokinese und ihre Beziehungen zu den Befruchtungsvorgängen, *Archiv für mikroskopische Anatomie*, 1888, vol. 32, no. 1, pp. 1–122.

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

Walsh, J.B., Rate of accumulation of reproductive isolation by chromosome rearrangements, *Am. Nat.*, 1982, vol. 120, pp. 510–532.

Watson, J.D. and Crick, F.H.C., Molecular structure of nucleic acids, *Nature*, 1953, vol. 171, pp. 737–738.

Wendt, K.S. and Grosveld, F.G., Transcription in the context of the 3D nucleus, *Curr. Opin. Genet. Dev.*, 2014, vol. 25, pp. 62–67.

Wertheim, B., Beukeboom, L.W., and Van de Zande, L., Polyploidy in animals: effects of gene expression on sex determination, evolution and ecology, *Cytogenet. Genome Res.*, 2013, vol. 140, pp. 256–269.

White, M.J.D., Models of speciation. New concepts suggest that the classical sympatric and allopatric models are not the only alternatives, *Science*, 1968, vol. 159, pp. 1065–1070.

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

White, M.J.D., Chain processes in chromosomal speciation, *Syst. Biol.*, 1978a, vol. 27, pp. 285–298.

White, M.J.D., Rectangularity, speciation, and chromosome architecture, in *Mechanism of Speciation*, Barigozzi, C., Ed., New York: Alan Liss, 1982, pp. 75–103.

Wienberg, J. and Stanyon, R., Comparative painting of mammalian chromosomes, *Curr. Opin. Genet. Dev.*, 1997, vol. 7, pp. 784–791.

Wilson, E.B., The chromosomes in relation to the determination of sex in insects, *Science*, 1905, vol. 22, pp. 501–502.

Wilson, A.C., Bush, G.L., Case, S.M., and King, M.C., Social structuring of mammalian populations and rate of chromosomal evolution, *Proc. Natl. Acad. Sci. U. S. A.*, 1975, vol. 72, pp. 5061–5065.

Winkler, H., *Verbreitung und Ursache der Parthenogenesis im Pflanzen—und Tierreiche*, Jena: Verlag Fischer, 1920.

Wright, S., Evolution in Mendelian populations, *Genetics*, 1931, vol. 16, pp. 97–159.

Wu, G., Hao, L., Han, Z., Gao, S., Latham, K.E., et al., Maternal transmission-ratio distortion at the mouse om locus results from meiotic drive at the second meiotic division, *Genetics*, 2005, vol. 170, pp. 327–334.

Yoshida, T.H., *Cytogenetics of Black Rat. Karyotype Evolution and Species Differentiation,* Tokyo: Univ. of Tokyo Press, 1980.

Zima, J., Lukáčová, L., and Macholán, M., Chromosomal evolution in shrews, in *Evolution of Shrews*, Wójcik, J. and Wolsan, M., Eds., Mammal Res. Inst. Polish Ac. Sci. Bialoveza, 1998, pp. 175–218.

Translated by M. Batrukova