ЭВОЛЮЦИЯ ГЕНОМА
Оригинальное исследование/ Original article
УДК 575.222.7:575.224.232

Вавиловский журнал генетики и селекции. 2019;23(2):239-243
DOI 10.18699/VJ19.488

A meiotic mystery in experimental hybrids of the eastern mole vole (*Ellobius tancrei*, Mammalia, Rodentia)

V.G. Tambovtseva[1] ✉, S.N. Matveevsky[2], A.A. Kashintsova[2], A.V. Tretiakov[2], O.L. Kolomiets[2], I.Yu. Bakloushinskaya[1] ✉

[1] Koltzov Institute of Developmental Biology, RAS, Moscow, Russia
[2] Vavilov Institute of General Genetics, RAS, Moscow, Russia
✉ e-mail: lynx1994@gmail.com; i.bakloushinskaya@idbras.ru

Chromosomal rearrangements can lead to the formation of new stable karyotypes, nevertheless changing the architectonics of the nucleus. The differences in locations might promote Robertsonian (Rb) translocations and encourage meiotic drive in favour of changed chromosomes or against them. We hypothesized that hybridization and meiotic drive may produce new chromosomal forms in *Ellobius tancrei*. We crossed two forms with 2*n* = 50, and two pairs of different Rb metacentrics with partial (monobrachial) homology. In 10 years of inbred crossings (sister–brother), we got 9 generations of hybrids (262 litters, 578 animals). In the first hybrid generation, two trivalents, a tetravalent and 20 bivalents were revealed at meiotic prophase I. Hybrids of the first generation had lower fertility, fertility increased starting from the third generation. Instead of returning to parental karyotypes, starting from the second generation, hybrids obtained new chromosome sets, with different 2*n* (48, 49, 51, 52) and combinations of Rb metacentrics. Analysis of F4, F7 and F9 hybrids revealed that synapsis of homologous parts take place despite the presence of heterozygotes and monobrachial homology of Rb metacentrics. The most common meiotic disturbance was delayed synapsis, which resumed later compared to the homologous crossings. The late synaptic adjustments nevertheless provide a proper segregation of chromosomes and normal sets in the gametes. Therefore, some cells pass through meiosis successfully and promote viable gametes. We proved the hypothesis that origin of monobrachially homologous Rb translocations may lead to divergence in several generations, due to meiotic drive.
Key words: Robertsonian translocations; synaptonemal complex; hybridization; meiotic drive.

For citation: Tambovtseva V.G., Matveevsky S.N., Kashintsova A.A., Tretiakov A.V., Kolomiets O.L., Bakloushinskaya I.Yu. A meiotic mystery in experimental hybrids of the eastern mole vole (*Ellobius tancrei*, Mammalia, Rodentia). Vavilovskii Zhurnal Genetiki i Selektsii = Vavilov Journal of Genetics and Breeding. 2019;23(2):239-243. DOI 10.18699/VJ19.488

Особенности мейоза у экспериментальных гибридов слепушонок (*Ellobius tancrei*, Mammalia, Rodentia)

В.Г. Тамбовцева[1] ✉, С.Н. Матвеевский[2], А.А. Кашинцова[2], А.В. Третьяков[2], О.Л. Коломиец[2], И.Ю. Баклушинская[1] ✉

[1] Институт биологии развития им. Н.К. Кольцова Российской академии наук, Москва, Россия
[2] Институт общей генетики им. Н.И. Вавилова Российской академии наук, Москва, Россия
✉ e-mail: lynx1994@gmail.com; i.bakloushinskaya@idbras.ru

Хромосомные перестройки могут приводить к формированию новых устойчивых кариотипов, изменяя при этом архитектонику ядра. Различия в локализации хромосом, вероятно, обусловливают неслучайность робертсоновских (Rb) транслокаций и влияют на мейотический драйв как в пользу измененных хромосом, так и против них. Мы предположили, что благодаря гибридизации и мейотическому драйву могут возникать новые хромосомные формы у слепушонок *Ellobius tancrei*. Был поставлен эксперимент по гибридизации двух форм с одинаковым 2*n* = 50, но с разными робертсоновскими метацентриками. За десять лет инбредных скрещиваний (сестра–брат) получено девять поколений гибридов (262 помета, 578 животных). У гибридов первого поколения сохранялось диплоидное число 2*n* = 50, но в силу неполной (монобрахиальной) гомологии в профазе мейоза I помимо 20 бивалентов были выявлены два тривалента и один тетравалент. Гибриды первого поколения имели более низкую плодовитость по сравнению с родительскими формами. Начиная с третьего поколения плодовитость повышалась. Вместо возвращения к родительским кариотипам гибриды второго и последующих поколений получили новые наборы хромосом, отличающиеся диплоидным числом (48, 49, 51, 52) и комбинациями робертсоновских метацентриков. Анализ мейоза у гибридов F4, F7 и F9 показал, что гомологичный синапсис хромосом может быть затруднен из-за наличия гетерозигот и монобрахиальной гомологии, однако некоторые клетки успешно проходят мейоз, что приводит к формированию жизнеспособных гамет и рождению гибридов. Проведенный нами эксперимент воспроизводит процессы, происходящие в естественных условиях,

и дает основания считать мейотический драйв основным механизмом, обеспечивающим диверсификацию и быструю фиксацию возникающих хромосомных форм в природе.
Ключевые слова: робертсоновские транслокации; синаптонемный комплекс; гибридизация; мейотический драйв; видообразование.

Introduction

The role of chromosomal rearrangements in speciation is still a matter of considerable debate (Faria, Navarro, 2010; Dobigny et al., 2017). It is well illustrated in a large number of studies that chromosomal rearrangements can lead to the formation of new balanced karyotypes, nevertheless changing the architectonics of the nucleus and its functioning (Qumsiyeh, 1999; Shapiro, 2002; Graphodatsky et al., 2011; Romanenko et al., 2018). However, direct mechanisms of new karyotype fixation are still in the scale. In general terms, a transformation of chromatin structures may alter the genetic system of the species, due to the modulation accessibility of transcription factors to DNA binding sites, thus regulating gene expression. A concept of chromosome territories proposes a non-random distribution of chromosomes in nuclei; the nuclear architecture constitutes the basis for gene expression regulation (Cremer T., Cremer C., 2001).

Robertsonian (Rb) translocations join two acrocentrics into one metacentric chromosome. This is the most common type of chromosomal rearrangements in mammals (King, 1993). Translocations restructure the organization of the nuclei, especially when chromosomal territories of fused acrocentrics are located far from each other (Berríos et al., 2017). These changes unavoidably influence the hybrids' fertility because of different Rb fusions inherited from parents. In the case of partial, or monobrachial, homology, which originated by the combination of different acrocentrics in Rb biarmed chromosomes, meiosis in hybrids should become more complicated (Baker, Bickham, 1986). These hybrids' gametes reveal the formation of complex chains in meiotic prophase I. As a result, we observe the reduction of fertility in hybrids, and this may be treated as a starting point of full or partial reproductive isolation. That is why chromosomal rearrangements, including Rb translocations, are considered to be some of the mechanisms of speciation (King, 1993).

Fixation of new karyotype variations might occur by non-random chromosomal segregation, for example, when a new Rb metacentric fixes in generations instead of homologous acrocentric chromosomes. This may be a perfect illustration for a conception of meiotic drive (Sandler, Novitski, 1957; de Villena, Sapienza, 2001; Lindholm et al., 2016). Previously it was believed that monobrachial homology causes full reproductive isolation and leads to complete sterility of hybrids. The reason was that chromosome disjunction after multivalent formation cannot be balanced and resulted in aneuploid gametes and inviable zygotes production (Baker, Bickham, 1986). However, recently it was shown for different groups of animals that species and forms with monobrachially homologous chromosomes are naturally occurring (Nunes et al., 2011; Potter et al., 2017).

Our research was focused on the eastern mole vole (*Ellobius tancrei* Blasius, 1884, Rodentia, Mammalia) noted for wide karyotypic variability caused by Rb translocations (Vorontsov et al., 1980; Lyapunova et al., 1984, 2010), unique sex chromosomes (XX♂/XX♀) and an enigmatic sex determination system (Bakloushinskaya, Matveevsky, 2018). The ancestral karyotype of this species contains 52 acrocentric chromosomes and a pair of submetacentrics, but the diploid number can be reduced to $2n = 30$ by Rb translocations and fixation of new Rb metacentrics (Bakloushinskaya et al., 2013). Our study of natural variability in *E. tancrei* enables us to hypothesize that hybridization and meiotic drive may produce new chromosomal forms, and the aim of the present study was an evaluation of this hypothesis experimentally.

Material and methods

For the experimental crossing, we chose two individuals of *E. tancrei* from a natural habitat, and their progeny, a line of strictly inbred hybrids F1–F9. We crossed two forms with $2n = 50$, and two pairs of Rb metacentrics: 2Rb(4.12) and 2Rb(9.13), nicknamed 'Khodza Obi-Garm', according to the closest settlement in the Varzob River Valley, and 2Rb(2.18) and 2Rb(5.9), in the form which was named 'Voidara', according to the closest settlement in the Surkhob River Valley (Tajikistan). The homology of Rb chromosomes had been previously verified by chromosome painting (Bakloushinskaya et al., 2010; Matveevsky et al., 2015). During 10 years of inbred crossings (sister–brother), despite reduced fertility, we got, in total, 9 generations of hybrids (262 litters, 578 animals). For the presented research, we used data on F1–F9 hybrids, 50 animals in total.

Analysis of fertility and the experimental design were carried out using a database accumulating data from breeding and field logs. Animals were treated according to established international protocols, such as the Guidelines for Humane Endpoints for Animals Used in Biomedical Research, and Regulations for Laboratory Practice in Russian Federation, and under the supervision of the Ethics Committee for Animal Research of the Koltzov Institute of Developmental Biology, RAS.

For all the specimens under analysis, we prepared slides, using fixed cells from bone marrow for mitotic metaphases and suspensions of spermatocytes to study meiosis (Ford, Hamerton, 1956; Graphodatsky, Radjabli, 1988). G-banding was carried out for all preparations of metaphase chromosomes, using trypsin treatments, in order to identify Rb metacentrics, according to Seabright (1971). The suspensions and spreads of spermatocytes were made as described by Kolomiets et al. (2010) or Peters et al. (1997). Immunostaining was designed as in our previous studies (Kolomiets et al., 2010; Matveevsky et al., 2016). Synaptonemal complexes (SC) and centromeres in pachytene spermatocytes were detected using antibodies to axial SC elements – SYCP3 (Abcam, UK) – and the kinetochores (ACA, Antibody Incorporated, USA). The slides were analyzed with an Axioimager D1 microscope (Carl Zeiss, Jena, Germany). Images were processed using Adobe Photoshop CS3 Extended.

Results

We had previously demonstrated (Matveevsky et al., 2015) that parental forms possessed two types of $2n = 50$ karyo-

types with two different pairs of Rbs: 2Rb(4.12) and 2Rb(9.13) in 'Khodza Obi-Garm', and 2Rb(2.18) and 2Rb(5.9), in 'Voidara'. F1 hybrids had $2n = 50$, NF = 56, but all the Rb metacentrics were different: Rb(9.13), Rb(2.18), Rb(5.9) and Rb(4.12). In the first hybrid generation, monobrachial homology leads to formation of two trivalents [(2/2.18/18) and (4/4.12/12)], and a tetravalent (5/5.9/9.13/13) in meiotic prophase I (Matveevsky et al., 2015, 2017) (Fig. 1, *a*, Fig. 2, *a*). Hybrids of the first generation had lower fertility, but did not exhibit any health problems, and their longevity was the same as the parental ones' (up to seven years).

Hybrid fertility began to increase in the third generation. We have specially focused on the most intrigued result, which was the emergence in hybrids of new chromosome sets, with different $2n$ (48, 49, 51, 52) and combinations of Rb metacentrics (see Fig. 1, *b–d*). For example, all the progeny of F2, No. 26432, ♂, $2n = 48$, 2Rb(4.12), 2Rb(2.18), 1Rb(5.9), 1Rb(9.13) (see Fig. 1, *c*, *d*) and No. 26433, ♀, $2n = 52$, 2Rb(5.9) got karyotypes identical to F1 hybrids, $2n = 50$, 1Rb(9.13), 1Rb(5.9), 1Rb(2.18), 1Rb(4.12). In meiosis, they demonstrated the same meiotic disturbances, such as the presence of a tetravalent and two trivalents in the pachytene and diakinesis, anaphase bridges, etc. (see Fig. 1, *a*, *h* and Fig. 2, *a*). When we crossed these F3 mole voles, whose karyotype was identical to F1, we appeared to return to the initial crossings. That was the reason for a long-term experiment, because we had to override a high level of heterozygosity, which appeared continuously. Anyway, the substitution of F2 chromosomal sets determined descent generations' variety and appeared to be the first step in the emergency of new balanced chromosomal forms.

G-banding analysis revealed that 4 Rb metacentrics described for these crossings seem to have different evolutionary destinies. Three of them – Rb(9.13), Rb(2.18) and Rb(4.12) – have a tendency to fix in generations, while Rb(5.9) reveals negative dynamics. The smallest Rb(9.13) has an advantage

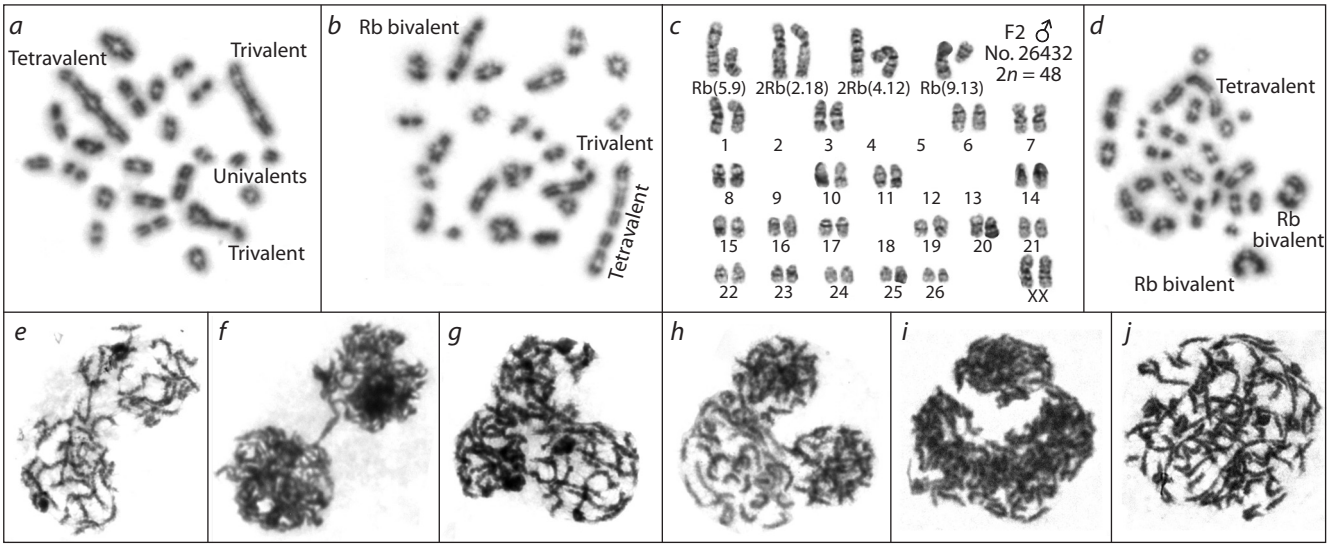

Fig. 1. Meiotic and mitotic chromosomes of *E. tancrei* hybrids (F1–F9).

a, F1, No. 26182, $2n = 50$: 1Rb(5.9), 1Rb(2.18), 1Rb(4.12), 1Rb(9.13), diakinesis; *b*, F2, No. 26453, $2n = 49$: 2Rb(4.12), 1Rb(5.9), 1Rb(2.18), 1Rb(9.13), diakinesis; *c*, F2, No. 26432, $2n = 48$: 2Rb(2.18), 2Rb(4.12), 1Rb(5.9), 1Rb(9.13), karyotype and diakinesis; *d*, abnormalities in meiosis; *e*, F2, No. 26335, $2n = 49$: 2Rb(2.18), 2Rb(9.13), 1Rb(4.12), anaphase I bridge; *f*, F3, No. 26140, $2n = 51$: 2Rb(9.13), 1Rb(2.18), anaphase I bridge; *g*, F2, No. 26139, $2n = 50$: 2Rb(9.13), 1Rb(4.12), 1Rb(2.18); *h*, F3, No. 26436, $2n = 50$: 1Rb(4.12), 1Rb(5.9), 1Rb(9.13), 1Rb(2.18); *i*, F9, No. 26995, $2n = 50$: 2Rb(9.13); *j*, F9, No. 26995, $2n = 50$: 2Rb(9.13), a polyploid cell. Magnification (*a*, *b*, *d–j*): 1000×.

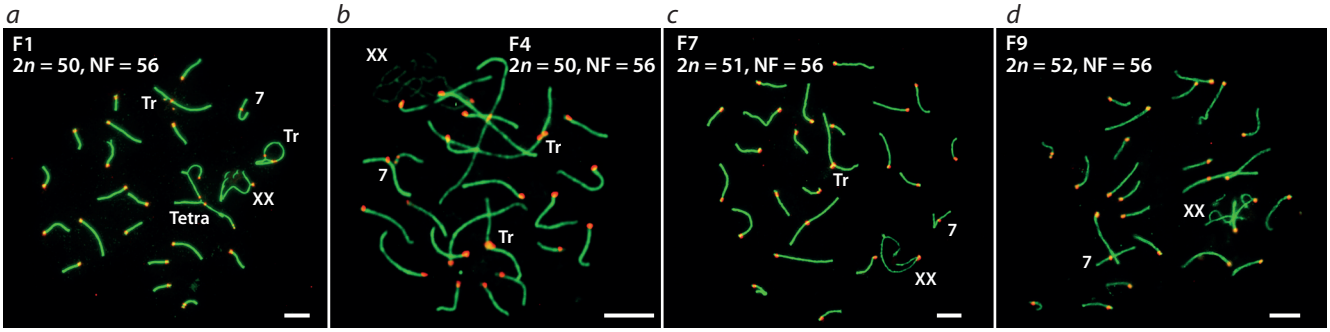

Fig. 2. Chromosome synapsis in pachytene spermatocytes of *E. tancrei* hybrids of different generations.

Axial SC elements were identified using anti-SYCP3 antibodies (green), anti-ACA for kinetochores (red). Tetra: tetravalent; Tr: trivalent; XX: male sex chromosomes. Bivalent No. 7 is an exclusive non-Rb submetacentric in all forms and hybrids of *E. tancrei*. NF: number of chromosome arms.
a, F1, No. 26990, $2n = 50$, NF = 56: 19 bivalents, 1 tetravalent, 2 trivalent, sex (XX) bivalent; *b*, F4, No. 26572. $2n = 50$: 21 bivalents, 2 trivalents, sex (XX) bivalent; *c*, F7, No. 26986, $2n = 51$: 23 bivalents, 1 trivalent, sex (XX) bivalent; *d*, F9, No. 26995. $2n = 52$: 25 bivalents, sex (XX) bivalent. Bar (*a–d*) = 5 μm.

compared to others. In F7–F9, it seems to be in a stable homozygotic state. As the Rb metacentrics started to fix and produce new karyotypes, we observed reduction of the number of complicated figures (trivalents, tetravalents) in meiosis (see Fig. 1, *e–g* and Fig. 2, *b–d*), despite the presence of other deviation (see Fig. 1, *f*, *i*, *h*). In F2 we first noted specimens, homozygotic by one or two pairs of Rb metacentrics. These hybrids also showed minimum abnormalities in the pachytene (see Fig. 2, *d*) and diakinesis, but there were other abnormalities, such as polyploid cells. The ploidy of such cells was rather difficult to count, most cells were probably tetraploid ones (see Fig. 1, *j*). Some animals were somatic mosaic, for example, F7 No. 26986 had $2n = 50–51$ 2Rb(9.13), 1Rb(2.18), 0–1 Rb(4.12) in bone marrow cells. In all spermatocytes studied we distinguished $2n = 51$ only (see Fig. 2, *c*).

Analysis of SCs in F1, F4, F7 and F9 hybrids proved that synapsis and recombination of homologous parts take place, despite the presence of heterozygotes and monobrachial homology of Rb metacentrics (see Fig. 2). Such synapsis is a prerequisite for the proper chromosome disjunction. Most probably, the base for a balanced chromosome segregation is a cis configuration for Rb trivalents, which we observed regularly. Therefore, some cells passed through meiosis successfully and promoted the efficient number of viable gametes.

Discussion

The hypothesis of meiotic drive as a prominent mechanism of quick fixation of chromosomal rearrangements expects preferential inheritance of Rb metacentrics. What is more, some previous Rb inheritance research conducted on shrews (Searle, Wójcik, 1998) suggests that large Rb metacentrics have an advantage compared to smaller ones, but other studies on domestic mice did not prove that (Castiglia, Capanna, 2000). However, those studies did not observe the cases of hybrids with Rb chromosomes having monobrachial (partial or single arm) homology. Our data are mainly consistent with the hypothesis of meiotic drive, but the thesis concerning the dynamics of fixation of large and small Rb metacentrics was not proved. Rb metacentrics of the line under investigation can be split into two groups: small (Rb(9.13) and Rb(4.12)) and large (Rb(5.9) and Rb(2.18)). We observed clear positive dynamics of inheritance and fixation only for Rb(9.13), the smallest of represented Rb metacentrics. Moreover, large Rb(5.9), also containing acrocentric 9, is the only one which revealed negative dynamics. Such a "competition" for the acrocentrics and an advantage of the smaller Rb metacentric made it clear that our results are at variance with some of the previous studies. So, this matter needs follow-up investigations. Preferential inheritance of the smaller chromosomes may be explained by a specific architectonics of the interphase nucleus, which is still unknown for mole voles. Another possible reason is a less complicated picture of meiosis, due to the compactness of chromosomes. For two other Rb metacentrics – Rb(4.12) and Rb(2.18) – the observed segregation was almost Mendelian. But it still confirms the hypothesis of meiotic drive: despite the fact that the acrocentric karyotype is prone to Rb translocations, chromosomal rearrangements are still serious mutations. They change the architectonics and functioning of the nucleus in unexpected ways, so the probability of their fixation in generations is not high. That is why the absence of negative selection may be interpreted as the effect of meiotic drive.

We have observed all possible prophase I SC combinations in *E. tancrei* heterozygous spermatocytes previously (Bogdanov, Kolomiets, 2007; Matveevsky, Kolomiets, 2016). Some complicated figures – trivalents and a tetravalent – were observed in meiosis of mole voles of all studied generations, F1–F9. But we revealed a clear tendency of reduction of their number. All F1 individuals have the same chromosomal chains in prophase I. In F2 homozygotization started, so only a few animals showed the same level of meiotic abnormalities. In F3, some specimens demonstrated normal process of meiosis, not disturbed by monobrachial homology and multivalent formation. In all generations under analysis, abnormalities of late stages of meiosis seem to be the same. They can be summed up as disturbance of synchronism and spatial distribution of chromosomes.

A particularly interesting output of this experiment was a meiotic solution for heterozygotes, carrying Rb metacentric and homologous acrocentrics. The most common meiotic disturbance was delayed synapsis, which resumed later comparing to the homologous crossings. The late synaptic adjustments nevertheless provide a proper segregation of chromosomes and normal sets in the gametes. The question of a lower rate of recombination due to delayed synapses is still open; apparently, it may lead to negative consequences in an evolutionary perspective. It should be noted that the impact of different SC combination on the meiotic progression is significantly variable (Ratomponirina et al., 1988; de la Fuente et al., 2007; Berríos et al., 2017). Some aspects about it were discussed early (Bakloushinskaya et al., 2010; Matveevsky et al., 2015). Another interesting phenomenon was an occurrence of numerous polyploid pachytenes in hybrid meiosis. Possibly, the consequences of chromosome abnormalities, which we observed in the prophase I, might be opposite ones. Longevities and fissions at the zygotene are most probably precursors for new chromosome changes, otherwise abnormalities at the anaphase lead to cell elimination and disappear under natural selection.

It was possible to get a pure line in three generations, if cross animals with identical karyotypes, but we decided to make a 'black box' with a sister–brother breeding system to avoid artificial selection. As a result, we got heterozygous progeny for many generations, but the endpoint appeared to be more similar to natural selection. The main result was an emergence of new balanced chromosomal set and lack of meiotic disturbances.

Conclusion

To conclude, we want to highlight the fact of formation and fixation of new karyotypes in inbred line of *Ellobius tancrei* with monobrachially homologous Rb metacentrics. This model shows the way for origin of new stable chromosomal forms which may occur in wild as well. In several generations, it may lead to divergence and can be treated as early stages of speciation.

References

Baker R.J., Bickham J.W. Speciation by monobrachial centric fusions. Proc. Natl. Acad. Sci. USA. 1986;83:8245-8248. DOI 10.1073/pnas.83.21.8245.

Bakloushinskaya I., Matveevsky S. Unusual ways to lost Y chromosome and survive with changed autosomes: a story of mole voles

Ellobius (Mammalia, Rodentia). OBM Genetics. 2018;2(3). DOI 10.21926/obm.genet.1803023.

Bakloushinskaya I.Yu., Romanenko S.A., Graphodatsky A.S., Matveevsky S.N., Lyapunova E.A., Kolomiets O.L. The role of chromosome rearrangements in the evolution of mole voles of the genus *Ellobius* (Rodentia, Mammalia). Russ. J. Genetics. 2010;46:1143-1145. DOI 10.1134/S1022795410090346.

Bakloushinskaya I., Romanenko S.A., Serdukova N.A., Graphodatsky A.S., Lyapunova E.A. A new form of the mole vole *Ellobius tancrei* Blasius, 1884 (Mammalia, Rodentia) with the lowest chromosome number. Comp. Cytogenet. 2013;7:163-169. DOI 10.3897/CompCytogen.v7i2.5350.

Berríos S., Fernández-Donoso R., Ayarza E. Synaptic configuration of quadrivalents and their association with the XY bivalent in spermatocytes of Robertsonian heterozygotes of *Mus domesticus*. Biol. Res. 2017;50(1):38. DOI 10.1186/s40659-017-0143-6.

Bogdanov Yu.F., Kolomiets O.L. Synaptonemal Complex – Indicator of the Dynamics of Meiosis and Chromosome Variation. Moscow: KMK Scientific Press, 2007. (in Russian)

Castiglia R., Capanna E. Contact zones between chromosomal races of *Mus musculus domesticus*. 2. Fertility and segregation in laboratory-reared and wild mice multiple heterozygous for Robertsonian rearrangements. Heredity. 2000;85:147-157. DOI 10.1046/j.1365-2540.2000.00743.x.

Cremer T., Cremer C. Chromosome territories, nuclear architecture and gene regulation in mammalian cells. Nat. Rev. Genet. 2001;2(4):292-301. DOI10.1038/35066075.

de la Fuente R., Parra M.T., Viera A., Calvente A., Gómez R., Suja J.Á., Rufas J.S., Page J. Meiotic pairing and segregation of achiasmate sex chromosomes in eutherian mammals: the role of SYCP3 protein. PLoS Genet. 2007;3(11):e198. DOI 10.1371/journal.pgen.0030198.

de Villena F.P., Sapienza C. Female meiosis drives karyotypic evolution in mammals. Genetics. 2001;159:1179-1189.

Dobigny G., Britton-Davidian J., Robinson T.J. Chromosomal polymorphism in mammals: an evolutionary perspective. Biol. Rev. 2017;92(1):1-21. DOI 10.1111/brv.12213.

Faria R., Navarro A. Chromosomal speciation revisited: rearranging theory with pieces of evidence. Trends Ecol. Evol. 2010;25:660-669. DOI 10.1016/j.tree.2010.07.008.

Ford C.E., Hamerton J.L. A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain Techn. 1956;31:247-251. DOI 10.3109/10520295609113814.

Graphodatsky A.S., Radjabli S.I. Chromosomes of Farm and Laboratory Mammals. Atlas. Novosibirsk: Nauka Publ., 1988. (in Russian)

Graphodatsky A.S., Stanyon R., Trifonov V.A. The genome diversity and karyotype evolution of mammals. Mol. Cytogenet. 2011;4:22. DOI 10.1186/1755-8166-4-22.

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

Kolomiets O.L., Matveevsky S.N., Bakloushinskaya I.Yu. Sexual dimorphism in prophase I of meiosis in mole vole (*Ellobius talpinus* Pallas) with isomorphic (XX) chromosomes in males and females. Comp. Cytogenet. 2010;4:55-66. DOI 10.3897/compcytogen.v4i1.25.

Lindholm A.K., Dyer K.A., Firman R.C., Fishman L., Forstmeier W., Holman L., Johannesson H., Knief U., Kokko H., Larracuente A.M., Manser A., Montchamp-Moreau C., Petrosyan V.G., Pomiankowski A., Presgraves D.C., Safronova L.D., Sutter A., Unckless R.L., Verspoor R.L., Wedell N., Wilkinson G.S., Price T.A.R. The ecology and evolutionary dynamics of meiotic drive. Trends Ecol. Evol. 2016;31:315-326. DOI 10.1016/j.tree.2016.02.001.

Lyapunova E.A., Bakloushinskaya I.Y., Saidov A.S., Saidov K.K. Dynamics of chromosome variation in mole voles *Ellobius tancrei* (Mammalia, Rodentia) in Pamiro-Alay in the period from 1982 to 2008. Russ J. Genetics. 2010;46:566-571. DOI 10.1134/S1022795410050091.

Lyapunova E.A., Ivnitskii S.B., Korablev V.P., Yanina I.Yu. Complete Robertsonian fan of the chromosomal forms in the mole-vole superspecies *Ellobius talpinus*. Doklady Akademii Nauk SSSR = Proceedings of the Academy of Sciences of the USSR. 1984;274:1209-1213. (in Russian)

Matveevsky S., Bakloushinskaya I., Kolomiets O. Unique sex chromosome systems in *Ellobius*: How do male XX chromosomes recombine and undergo pachytene chromatin inactivation? Sci. Rep. 2016;6,29949. DOI 10.1038/srep29949.

Matveevsky S., Bakloushinskaya I., Tambovtseva V., Romanenko S., Kolomiets O. Analysis of meiotic chromosome structure and behavior in Robertsonian heterozygotes of *Ellobius tancrei*: a case of monobrachial homology. Comp. Cytogenet. 2015;9(4):691-706. DOI 10.3897/CompCytogen.v9i4.5674.

Matveevsky S.N., Kolomiets O.L. Synaptonemal complex configurations in Robertsonian heterozygotes. Tsitologia. 2016;58(4):309-314.

Matveevsky S., Kolomiets O., Bogdanov A., Hakhverdyan M., Bakloushinskaya I. Chromosomal evolution in mole voles *Ellobius* (Cricetidae, Rodentia): Bizarre sex chromosomes, variable autosomes and meiosis. Genes. 2017;8(11):306. DOI 10.3390/genes8110306.

Nunes A.C., Catalan J., Lopez J., da Graça Ramalhinho M., da Luz Mathias M., Britton-Davidian J. Fertility assessment in hybrids between monobrachially homologous Rb races of the house mouse from the island of Madeira: implications for modes of chromosomal evolution. Heredity. 2011;106:348-356. DOI 10.1038/hdy.2010.74.

Peters A.H., Plug A.W., van Vugt M.J., De Boer P. A drying-down technique for the spreading of mammalian meiocytes from the male and female germline. Chromosome Res. 1997;5(1):66-68.

Potter S., Bragg J.G., Blom M.P., Deakin J.E., Kirkpatrick M., Eldridge M.D., Moritz C. Chromosomal speciation in the genomics era: disentangling phylogenetic evolution of Rock-wallabies. Front. Genet. 2017;8:10. DOI 10.3389/fgene.2017.00010.

Qumsiyeh M.B. Structure and function of the nucleus: anatomy and physiology of chromatin. Cell. Mol. Life Sci. 1999;55:1129-1140.

Ratomponirina C., Brun B., Rumpler Y. Synaptonemal complexes in Robertsonian translocation heterozygous in lemurs. In: Brandham P.E. (Ed). Kew Chromosome Conference 3. London: HMSO, 1988;65-73.

Romanenko S.A., Serdyukova N.A., Perelman P.L., Trifonov V.A., Golenishchev F.N., Bulatova N.S., Stanyon R., Graphodatsky A.S. Multiple intrasyntenic rearrangements and rapid speciation in voles. Sci. Rep. 2018;8:14980. DOI 10.1038/s41598-018-33300-6.

Sandler L., Novitski E. Meiotic drive as an evolutionary force. Am. Nat. 1957;91:105-110.

Seabright M. A rapid banding technique for human chromosomes. Lancet. 1971;2:971-972. DOI 10.1016/S0140-6736(71)90287-X.

Searle J.B., Wójcik J.M. Chromosomal evolution: the case of *Sorex araneus* In: Wójcik J.M., Wolsan M. (Eds.). Evolution of Shrews. Białowieża: Mammal Research Institute PAS, 1998;219-268.

Shapiro J.A. Genome organization and reorganization in evolution: formatting for computation and function. Ann. N. Y. Acad. Sci. 2002;981:111-134. DOI 10.1111/j.1749-6632.2002.tb04915.x.

Vorontsov N.N., Lyapunova E.A., Borissov Y.M., Dovgal V.E. Variability of sex chromosomes in mammals. Genetica. 1980;52/53:361-372.

ORCID ID

V.G. Tambovtseva orcid.org/0000-0002-2607-4169
S.N. Matveevsky orcid.org/0000-0002-5808-7685
I.Yu. Bakloushinskaya orcid.org/0000-0002-5808-7685

Acknowledgements. This study was funded in part by the IDB RAS Government basic research program No. 0108-2019-0007, VIGG RAS State Assignment Contract No. 0112-2019-0002, Program of the Russian Academy of Sciences' Presidium No. 41 'Biodiversity of Natural Systems and Biological Resources of Russia', and the Russian Foundation for Basic Research No. 16-04-01447.

Conflict of interest. The authors declare no conflict of interest.

Received November 22, 2018. Revised December 17, 2018. Accepted December 17, 2018.