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Polymorphism and Mosaicism of B Chromosome Number in Korean Field Mouse *Apodemus peninsulae* (Rodentia) in the Russian Far East

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Abstract—A karyotype analysis of the *Apodemus peninsulae* ($n = 355$) from 41 trapping points from the Russian Far East has allowed us to identify B chromosomes in 87.9% of the animals, 61.7% of which are mosaics. Different levels of variability in the B chromosome numbers have been studied, including both the inter- and intrapopulational, as well as intraindividual variability (mosaicism). It was found that the frequencies of the occurrence of individuals with B chromosomes and mosaicism between different population samples were not constant. The range of the modal B chromosome number variability and variation of the xB index (zero to four; on average, the xB amounted to 1.67) were studied for the first time in different samples and populations of this species. Individuals with the predominant numbers of B chromosome (as a rule, zero to two) were revealed in both groups of animals (with stable and mosaic karyotypes), but the frequency was different in geographical regions. The spectra of B chromosome variability were wider in mosaics (zero to seven) compared to animals with stable karyotypes (zero to four). The importance of this for species of the high frequency of individuals with B chromosomes and with mosaicism has been discussed. The adaptive role of the low number of B chromosomes (one to two), as well as the imbalance of the B chromosome system for the species as a whole is assumed.

Key words: *Apodemus peninsulae*, the Russian Far East, B chromosomes, mosaics, xB index.

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INTRODUCTION

The number of publications that indicate the presence of supernumerary (B) chromosomes in mammals of different taxonomic ranges has increased each year. Out of 55 mammalian species with B chromosomes, 42 species belong to rodents (Vujošević, Blagojević, 2004). The Korean field mouse *Apodemus peninsulae* (Thomas, 1906) is widespread in the forest and/or steppe zones of Siberia, the Russian Far East, Mongolia, China, Korea, and Japan (Hokkaido island) and can serve a model object in studies on polymorphism for supernumerary chromosomes in natural mammalian populations. The karyotype of this species contains 48 acrocentric chromosomes that form a gradually descending row. The chromosomal polymorphism of *A. peninsulae* is connected with the presence of additional chromosomes. This species is unique in that the animals have with a high frequency B chromosomes differing by the number and dimensional-morphological types both between different individuals and between cells of the same individual (mosaicism), which allows one to study the B chromosome system at different levels of species variability, i.e., interpopulational, inrapopulational, and intraindividual. Thus, the frequency of individuals with B chromosomes in the Far East populations of *A. peninsulae* can vary from 0 to 1.0 and, in the Siberian populations, from 0.99 to 1.0 (Kartavtseva et al., 2000; Kartavtseva and Roslik, 2004). Additionally, this species has one of the highest spectra of variations of the number of B chromosomes among mammals, i.e., 0–24. The maximal revealed number of B chromosomes in natural populations of the Korean field mouse of Siberia amounts to 24, while Pribaikalie has 14, Transbaikalia has 9, Mongolia has 13, China has 14, Japan has 13, South Korea has 6, and the Russian Far East has 7 (Kartavtseva and Roslik, 2004). There is information on the variability of the mean number of B chromosomes per individual (xB index) for some populations of the Korean field mouse of Siberia (Borisov, 1990b, 1990c, 1990d; 2008; Borisov et al., 2007) and Transbaikalia (Roslik et al., 2005). These data are absent for mice of the Russian Far East, as well as of Mongolia, China, Korea, and Japan, which makes it different to compare data throughout the entire area of the species.

Mosaicism for the number of B chromosomes in *A. peninsulae* was first described in mice of the Tomsk oblast and the Krasnoyarsk region (Volobuev, 1979; Radzhabli and Borisov, 1979). Further studies have also shown the presence of mosaics in other areas of this species (Volobuev, 1980; Volobuev and Timina, I980; Timina et al., 1980; Bekasova et al., 1980; Koh, 1986; Borisov, 1990a, 1990b, 1990c, 1990d; Wang et al., 2000; Roslik et al., 2003, 2005; Kartavtseva and Roslik, 2004). The frequency of mosaics varied from 0.05 in South Korea (Koh, 1986) to 0.85 in populations of the Russkii island of the Primorskii region (Kartavtseva and Roslik, 2004). However, until now, information about distribution of the numbers of chromosomes in individuals with mosaic karyotypes has been nearly absent. It has also remained unstudied whether the frequencies of animals with B chromosomes and with mosaic karyotypes are constant over time in a certain population.

The present work deals with studying the B chromosome system over time and space in natural populations of *A. peninsulae* in the Russian Far East. Here, the results of a study of individual and inter- and intrapopulational variability are presented based on a comparative analysis of population samples of three geographic regions for several frequency indexes, i.e., spectra of variations of modal numbers, the xB index, the fraction of individuals with B chromosomes, the fraction of individuals with stable and mosaic karyotypes, and interindividual variations of the number of B chromosomes in individuals with stable and mosaic karyotypes.

MATERIALS AND METHODS

The materials for this study were chromosome preparations of 355 individuals (207 males and 148 females) of Korean field mouse trapped between 1980 and 2008 in the continental populations of the Russian Far East (table).

The standard procedure of obtaining cell suspensions using the direct method from red bone marrow is used in the work (Ford and Hamerton, 1956). The mitotic division of the cell was stimulated 24 h before sacrifice with subcutaneous injection (0.5 ml per 25 g of the animal body weight) of a solution of baker's yeast (Lee and Elder, 1980). 30 min prior to sacrifice, the animals were injected intraperitoneally with colchicine (Merck), 1 ml of 0.04% solution per 100 g of the animal body weight. The bone marrow from the femoral bone was washed out into a centrifuge test tube using a medical syringe filled with a hypotonic solution (0.56% KCl) and was incubated for 20–25 min at room temperature. After hypotonia, the cell sediment was fixed with a mixture of 96% ethanol and glacial acetic acid (3 : 1). Preparations were made by dropping the cell suspensions onto chilled, moist object glasses. The dried slides were stained with 2% acetoorcein or 2% azur-eosin (Giemsa dye, Merck, Germany).

The stained chromosomal slides were analyzed under the following microscopes: NU, Jenaval, Axioplan-2-imaging (Carl Zeiss, Germany), and Axioscop (Carl Zeiss, Germany). In photographing, a Micrat-300 film and photo nozzles Practica and Pentacon (at the final magnification ×1000) were used. To study some of the chromosomal slides, as well as to record and process microimages, we used a Canon Power Shot A95 digital camera and an AxoiCam HR CCD-camera and AXIOVISION software (Carl Zeiss MicroImaging GmbH, Germany).

In each animal, 10–69 metaphase plates were studied. In mosaics, the number of counted cells was no less than 22 to estimate with high statistical significance (90–95%) that these metaphases are cell clones according to the recommendations developed to analyze human mosaicism (Hook, 1977).

The mean number of B chromosomes per individual (the xB index) was determined based on animal modal chromosome numbers in each place of trapping. For this index, we used the designation "xB index" after other authors (Zima and Macholán, 1995).

To recognize stable or mosaic karyotypes in the animals, we used the criterion of counting cell clones, which was developed for the study of the fox bone-marrow cells with B chromosomes (Belyaev et al., 1974a). Animals with stable karyotypes usually had constant numbers of chromosomes in all analyzed metaphases. In these mice, as a rule, small deviations (2–4%) from the modal number were of hypoploid character. In mosaics, deviations from the modal number exceeded the percent of aneuploid cells with B chromosomes in animals with the stable karyotype. In cases when these deviations in hypoploid cell classes were 10% or more relative to all metaphase of the individual animal, while deviations in hyperploid cell classes were 5% and higher, we considered these cell classes to be the cell clones. Animals with two or more cellular clones were classified as mosaics, while those with one clone were considered to have stable karyotypes.

In some cases, in mosaics, apart from modal numbers with B chromosomes, animals without B chromosomes were also presented. If, in mosaics, the number of metaphase plates with 48 chromosomes numerically exceeded the number of metaphase plates with, e.g., 1–2 B chromosomes (49, 50, etc.), we ascribed them to the column with a modal number of 0 B chromosomes. To distinguish the actual number of individuals without B chromosomes from the total number of individuals with a modal number of 0 B chromosomes, the separate column presents the number of animals in whose karyotypes B chromosomes (nB) are revealed (table).

RESULTS AND DISCUSSION

Frequency of occurrence of animals with B chromosomes. The standard chromosome set in all studied *A. peninsulae* consisted of 48 chromosomes (A chromosomes) constantly present in all cells; they are

Spectrum of chromosomal variability and the mean frequency of B chromosomes per individual (xB index) in Korean field mouse of the Russian Far East

No.	Place and year of trapping	Distribution of individuals with modal number of B chromosomes								n	nB	xB
		0	1	2	3	4	5	6	7			
1	Magadan oblast (MO): Magadan city, 1998			1						1	1	2.0
2	Amur oblast (AO): Vill. Belogorye, 1986		1	2	1					4	4	2.0
	Jewish Autonomous Oblast (JAO):											
3	JAO: Birakan city, 1991	1	1	1						3	3	1.0
4	JAO: Birobidzhan city, total		**3**	**3**	**6**					**12**	**12**	**2.25**
	the same place, 2004		*1*	*1*						*2*	*2*	*1.5*
	the same place, 2005		*1*		*3*					*4*	*4*	*2.5*
	the same place, 2006		*1*	*2*	*1*					*4*	*4*	*2.0*
	the same place, 2008				*2*					*2*	*2*	*3.0*
I	Total AO + JAO: 2–4	1	5	6	7					19	19	2.0
	Khabarovsk region (KR):											
5	KR: Settl. Krasnoe, total	**9**	**2**	**5**						**16**	**9**	**0.75**
	the same place, 1980	*3*		*1*						*4*	*1*	*0.5*
	the same place, 1981	*4*	*1*	*1*						*6*	*3*	*0.5*
	the same place, 1982	*1*								*1*	*1*	*0*
	the same place, 1996	*1*	*1*	*3*						*5*	*4*	*1.4*
6	KR: Lake Evoron, total	**2**	**1**	**9**	**3**	**2**			**1**	**18**	**17**	**2.39**
	the same place, 2001	*1*		*8*	*1*	*2*				*12*	*11*	*2.25*
	the same place, 2002	*1*	*1*	*1*	*2*				*1*	*6*	*6*	*2.67*
7	KR: Settl. Solnechnyi, 2001	1								1	0	0
8	KR: Komsomolsk-on-Amur city, total	**4**	**1**	**3**	**2**	**1**				**11**	**8**	**1.5**
	the same place, 1983	*4*		*2*	*1*					*7*	*4*	*1.0*
	the same place, 2001		*1*	*1*	*1*	*1*				*4*	*4*	*2.5*
9	KR: Settl. Pivan’, total	**2**	**1**	**1**						**4**	**3**	**0.75**
	the same place, 1983	*1*		*1*						*2*	*2*	*1.0*
	the same place, 1994	*1*	*1*							*2*	*1*	*0.5*
10	KR: Vill. Mariinskoe, 1996					1				1	1	4.0
11	KR: Vill. Malyshevo, 1986	3	3	6		1				13	11	1.46
12	KR: Settl. Zavety Il’icha, 1986		1	1	1					3	3	2.0
II	Total KR: 5–12	21	9	25	6	5			1	67	52	1.55
	Primorskii region (PR):											
13	PR: Vill. Krasnyi Yar, 1996			1						1	1	2.0
14	PR: Vill. Melnichnoe, 1980	1	1	1	1	1				5	5	2.0
15	PR: Vill. Blagodatnoe, Sikhote-Alin Reserve, 1989		1	1		1				3	3	2.33
16	PR: Settl. Rudnaya Pristan’, total	**1**	**4**	**5**	**2**	**2**				**14**	**14**	**2.0**
	the same place, 1990	*1*	*2*	*1*	*1*					*5*	*5*	*1.4*
	the same place, 1991		*1*	*2*						*3*	*3*	*1.67*
	the same place, 1993		*1*	*2*	*1*	*2*				*6*	*6*	*2.67*
17	PR: Dalnegorsk city, total	**10**	**13**	**13**	**1**					**37**	**35**	**1.14**
	the same place, 1982	*2*		*2*						*4*	*4*	*1.0*
	the same place, 1983	*6*	*2*	*2*						*10*	*9*	*0.6*
	the same place, 1987			*1*						*1*	*1*	*2.0*
	the same place, 1990	*2*	*4*	*7*						*13*	*12*	*1.38*
	the same place, 1991		*7*	*1*	*1*					*9*	*9*	*1.33*
18	PR: Settl. Khrustalnyi, 1986	1	2	2	1					6	5	1.5
19	PR: Settl. Olga, 1999			1						1	1	2.0

Table. (Contd.)

No.	Place and year of trapping	Distribution of individuals with modal number of B chromosomes								n	nB	xB
		0	1	2	3	4	5	6	7			
20	PR: Settl. Chuguevka, 1984		1			1				2	2	2.5
21	PR: Sinii Khrebet, Vill. Bussevka, 1987		1		1	1				3	3	2.67
22	PR: upper reaches of the Arsenyevka river, 1996	2	4	1						7	5	0.86
23	PR: Vill. Nikolaevka, 1998		1		1					2	2	2.0
24	PR: Vill. Kamenushka, Ussuriiskii Reserve, total	**17**	**30**	**24**	**9**	**5**				**85**	**71**	**1.7**
	the same place, 1987		*4*	*1*						*5*	*5*	*1.2*
	the same place, 1989	*1*	*2*	*1*						*4*	*3*	*1.0*
	the same place, 1990	*3*	*5*	*2*	*1*	*1*				*12*	*9*	*1.33*
	the same place, 1992					*1*				*1*	*1*	*4.0*
	the same place, 1995	*1*	*1*		*1*					*3*	*3*	*1.33*
	the same place, 1996	*3*	*8*	*9*	*3*	*1*				*24*	*21*	*1.63*
	the same place, 1997	*1*	*3*	*6*	*1*					*11*	*10*	*1.64*
	the same place, 1998		*1*	*4*	*3*	*2*				*10*	*10*	*2.6*
	the same place, 1999	*8*	*6*	*1*						*15*	*9*	*0.53*
25	PR: upper reaches of the Granitnaya river, 2000	2	1		4				1	8	6	2.5
26	PR: Vill. Novonezhino, 1999		4	1		1				6	6	1.67
27	PR: Vill. Lukyanovka, 1990	1	1			2				4	4	2.25
28	PR: Vill. Kuchelinovo, 1989		1	1		1				3	3	2.33
29	PR: Settl. Novoligovsk, 1996					1				1	1	4.0
30	PR: Settl. Avangard, total		**3**	**2**	**2**	**2**				**9**	**9**	**2.33**
	the same place, 1986			*1*		*1*				*2*	*2*	*3.0*
	the same place, 1994		*1*		*1*					*2*	*2*	*2.0*
	the same place, 1996		*1*							*1*	*1*	*1.0*
	the same place, 1997		*1*	*1*						*2*	*2*	*1.5*
	the same place, 2001				*1*	*1*				*2*	*2*	*3.5*
31	PR: Vladivostok City, total	**2**	**2**	**3**	**1**	**1**				**9**	**7**	**1.67**
	the same place, 1988			*1*	*1*					*2*	*2*	*2.5*
	the same place, 1992		*1*	*2*		*1*				*4*	*4*	*2.25*
	the same place, 1998	*2*	*1*							*3*	*1*	*0.33*
32	PR: Vill. Turii Rog, 1986	1	6							7	6	0.86
33	PR: Vill. Barabash-Levada, 1985					1				1	1	4.0
34	PR: Settl. Pogranichnyi, 2000	1								1	0	0
35	PR: Vill. Fadeevka, 2000		1							1	1	1.0
36	PR: Vill. Nezhino, Ananyevka river, 1990		4	1	3					8	8	1.88
37	PR: Kedrovaya Pad Reserve, total	**3**	**6**	**10**	**6**	**2**	**2**			**29**	**26**	**2.14**
	the same place, 1994		*3*	*3*						*6*	*6*	*1.5*
	the same place, 1995		*2*	*2*	*2*	*2*				*8*	*8*	*2.5*
	the same place, 1996	*3*	*1*	*5*	*4*		*2*			*15*	*12*	*2.2*
38	PR: Vill. Ryazanovka, 1992		2			2				4	4	2.5
39	PR: Settl. Kraskino, 1996		1	2						3	3	1.67
40	PR: Station Khasan, 1997		1	1						2	2	1.5
41	PR: Gamov Peninsula, 1981, 1982, 1987–1990	1	3		1	1				6	6	1.67
III	Total PR: 13–41	43	94	70	33	25	2	0	1	268	240	1.68
	Total: 1–41	65	108	102	46	30	2	0	2	355	312	1.67

Note: n is the number of studied individuals; nB is the number of individuals with B chromosomes. Bold indicates the total values of the number of individuals and of xB for samples of animals analyzed for several years, while, below, italics indicate values of these parameters for each trapping year.

acrocentric by their morphology and have very small arms, which is possible see in metaphases with weak and intermediate degree of DNA spiralization of the chromosomes (Fig. 1a). The variable part of karyotype is represented by 0–7 B chromosomes that are predominantly meta- or submetacentrics by morphology and vary in size from large, middle, and small to mini chromosomes that are two to three times smaller than the smallest A chromosomes (Figs. 1b, 1c). Supernumerary chromosomes are revealed in karyotypes of the majority of animals (n = 312 or 87.9%). Portions of these individuals in the Khabarovsk Region (77.6%, n = 52) and Primorskii region (89.6%, n = 240) differed insignificantly. In karyotypes of all mice of Magadan (n = 1), the Amur oblast (n = 4), and the Jewish Autonomous Oblast (n = 15), B chromosomes are found with 100% frequency. The addition of new material to the previously obtained data on the occurrence of individuals with B chromosomes in Korean field mice of the Far East (Roslik et al., 2003; Kartavtseva and Roslik, 2004) did not change these parameters, which seems to argue in favor of the stability of this frequency in geographical regions.

For the first time, we analyzed the variability of the frequency of the occurrence of animals with B chromosomes in samples of different years from 11 populations of three geographic regions (table). Thus, in four samples of population no. 4 of the Jewish Autonomous Oblast, B chromosomes were present in karyotypes of all individuals. In four populations of the Khabarovsk region (5, 6, 8, and 9), this parameter changed in samples from different years. As a rule, in different samples, a few individuals without B chromosomes were present, although, for other years, only animals with B chromosomes were revealed. A similar pattern was also observed in the Primorskii Region (17, 24, 31, and 37). In population 24, the variability of the portion of individuals with B chromosomes was earlier noted in samples of different year seasons (Kartavtseva, 1999). In the Primorskii region, populations were found (16 and 30) in which a constantly high (100%) frequency of animals with B chromosomes was recorded in all samples. It should be noted that, in population 30, due to its constantly low density (around 5%), the samples were scanty (1–2 individuals each). It is possible that during the years of a rise of the population density, we will be able to detect also the animals without B chromosomes.

The obtained chromosomal data indicate that the Korean field mouse of two regions (Khabarovsk and Primorskii) is characterized by variation of the fraction of individuals with B chromosomes – both during different years of study of one population and in different populations. It seems that variation of frequency of individuals with B chromosomes is non-random phenomenon. Similar frequency variations have been also described in other mammalian species. It is known that frequency of individuals with B chromosomes in several Yugoslavian populations of *S. flavicollis* can be changed during different seasons of the year (Blagojević and Vujošević, 1995; Vujošević and Blagojević, 1995). However, there also is opposite information that this frequency of the same species can remain constant for 5 years or more (Vujošević, 1992). Similar evidence for the constancy of B chromosomes and their morphological types for 3–9 years of study have been noted in populations of the Arctic lemming *Dicrostonyx torquatus* of the Polar Ural, north of Yakutia, and west of Chukotka (Gileva, 2004).

As shown above, all populations of the Korean field mouse on the whole are characterized by predominance of the B chromosome-containing animals. Upon analyzing our and the literature data and calculating the mean frequency of the occurrence of individuals with B chromosomes for the species *A. peninsulae* on the whole, we found that it has a rather high value, i.e., 82% (n = 1207). The high frequency of individuals with B chromosomes has also been revealed in other animals; for instance, in Arctic lemmings, this amounts to 0.90, n = 86 (Gileva, 2004). In the European yellow-necked mouse, this frequency is somewhat lower, i.e., 45%, n = 652 (Wójcik et al., 2004); 33%, n = 995 (Vujošević et al., 2005); and 20.5%, n = 44 (Rovatsos et al., 2008). It is rather important that, in the yellow-necked mouse, it is possible to detect specific DNA profiles characteristic of individuals with B chromosomes (regardless of their number), these profiles being absent in mice without B chromosomes (Tanić et al., 2000). The high frequency of animals with B chromosomes in *A. peninsulae* and some other species of the *Apodemus* genus seems to imply the existence of some mechanisms of its maintenance and accumulation. It seems that the presence of a meiotic drive in B chromosomes can be suggested in the Korean field mouse, as in many animal species (Camacho et al., 2000). The mechanism of this chromosomal drive may be based on the structural and morphological peculiarities of B chromosomes of *A. peninsulae* (Rubtsov et al., 2004, 2005). The presence of extra chromosomal material in genome of the majority of individuals of the wood mice allows one to suggest that B chromosome-bearing animals seem to have certain selectional advantages over mice without these structures, especially in periods of a sharp decrease (for different reasons) in the population density.

Variability of the modal number of B chromosomes. For the first time for the Korean field wood mouse of the Russian Far East, we studied modal chromosome numbers whose range of variability was 48–55. We noticed that, in each particular population, individuals with a certain modal number of B chromosomes predominated (table). This tendency is particularly clearly traced in the population, in which relatively large mouse samples have been studied. For instance,

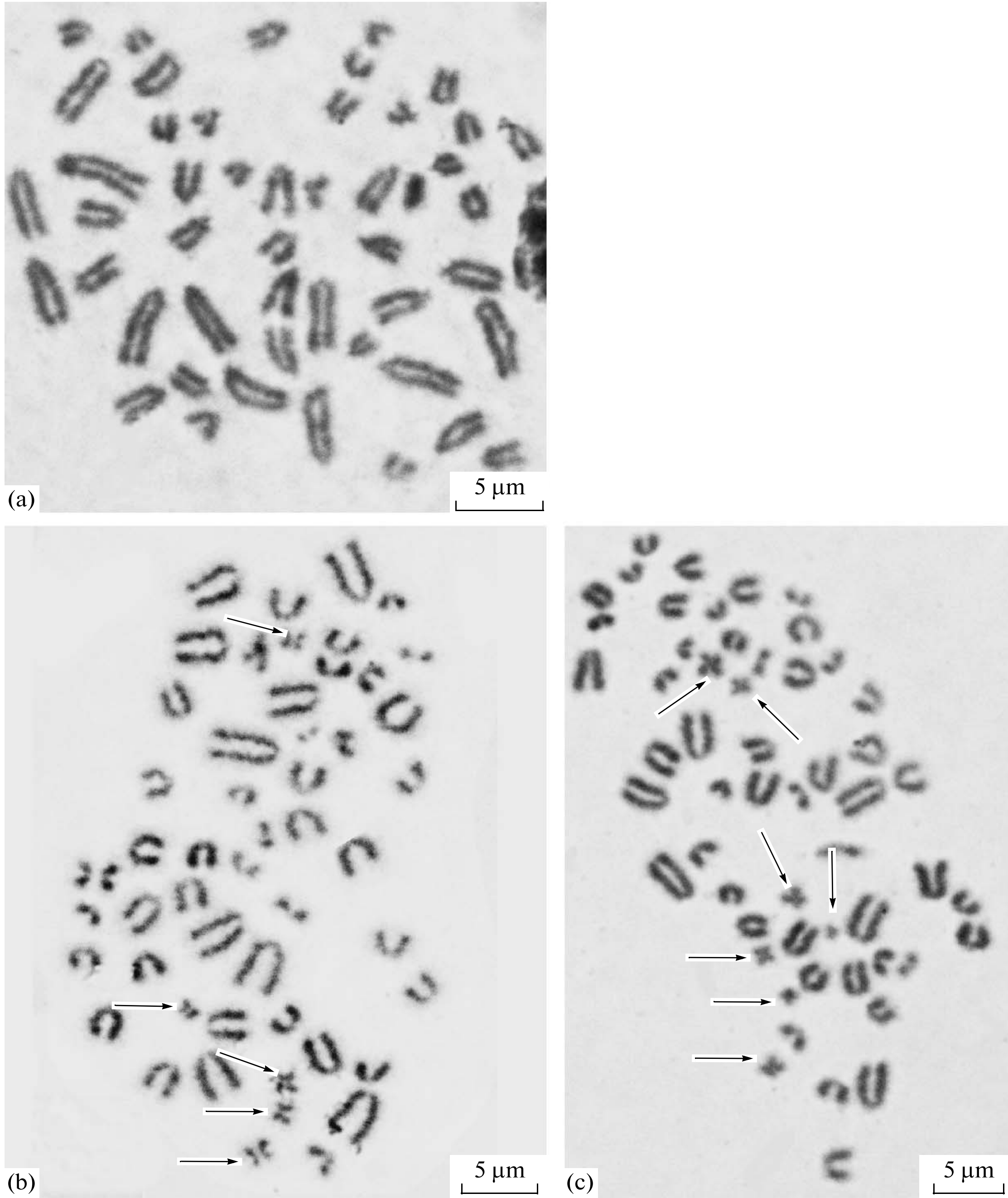

Fig. 1. Metaphase plates of *A. peninsulae* from the Primorskii region: (a) animal without B chromosomes (1230 ♂, population 34), $2n = 48$; (b, c) individual with mosaicism (1212 ♂, pop. 25) with two modal cell clones; (b) $2n = 48 + 5$ B chromosomes; (c) $2n = 48 + 7$ B chromosomes. The standard set is represented by acrocentric chromosomes descending in size. B chromosomes (indicated by *arrows*) by morphology are meta- or submetacentrics, classified by size of medium, small, and mini.

in the south-western population of the Primorskii region (population 25), animals with 3 B chromosomes are found more freqeuntly (50%), while, in population 11 of the Khabarovsk region, 46.2% of mice had two B chromosomes each. This tendency for certain numbers of B chromosomes to dominate has been noted for individual samples of one population taken for different years. Thus, in population 6 of the Khabarovsk region in 2001, individuals with two B chromosomes are dominant (58.3%), while, in 2002, individuals with three B chromosomes dominate (33.3%). In animals of the Kedrovaya Pad Reserve (population 37), in 1994 and 1995, individuals with one and two, and one, two, three, and four B chromosomes, respectively, were found with equal probability, while, in 1996, mice with two (33.3%) and three B chromosomes were slightly dominant (26.7%). In the Ussuriiskii Reserve (population 24) in 1990, individuals with predominately one B chromosome were observed (41.7%), whereas, in 1996–1998, individuals with two B chromosomes were observed (the percentage of these individuals amounted to 37.5, 54.5, and 40%, respectively) and, in 1999, individuals without B chromosomes were dominate (53.3%).

By summarizing data on geographic regions, it can be seen that, in populations of the Amur oblast and the Jewish Autonomous Oblast, animals with three (36.8%) and two (31.6%) B chromosomes are dominant. In the Khabarovsk region, animals with two B chromosomes (37.3%) and without B chromosomes (31.3%) are dominant, while, in the Primorskii region, animals with one (35.1%) and two B chromosomes are dominant (26.1%). A narrowing of the numerical spectra of B chromosomes has been revealed in animals of the Amur oblast and the Jewish Autonomous Oblast compared to mice of the Khabarovsk and Primorskii regions. The common tendency for animals of the three regions is the frequency of the occurrence of mice with two B chromosomes; however, the frequency of these individuals somewhat differs (table).

By generalizing the literature data on modal numbers of mice of other regions, we also have noted that each region is characterized by its own values of this characteristic. Thus, in East Siberia, individuals with four, five, and seven B chromosomes occur more often (Borisov, 1990c), while, in the Tomsk Oblast, individuals with two and nine B chromosomes are more common (Volobuev, 1980; Timina et al., 1980; Roslik and Kartavtseva, 2003). In the Krasnoyarsk region, individuals with 21 and 22 B chromosomes dominate (Borisov, 1990c); in the Western Sayans, individuals with five, six, and three B chromosomes dominate (Borisov, 1990b), in the Altai mountains, individuals with two, three, five, and six B chromosomes dominate (Borisov, 2008); in Pribaikalie, individuals with three and nine to ten B chromosomes dominate (Borisov, 1990d); in Mongolia, individuals with three, four, and six B chromosomes dominate (Borisov and Malygin, 1991); in Buryatia, individuals with four B chromosomes dominate (Borisov and Malygin, 1991); in the Tyva and Chita oblasts, individuals with five and six B chromosomes dominate (Roslik and Kartavtseva, 2003; Roslik et al., 2005); in China, individuals with zero, one, and six B chromosomes dominate (Wang et al., 2000); in South Korea, individuals with two and three B chromosomes dominate (Koh, 1986; Abe et al., 1997); and, in natural populations of Japan, individuals with six and seven B chromosomes dominate (Hayata, 1973; Abe et al., 1997).

Variability of the mean number of B chromosomes per individual (xB index). In the present work, the xB index is presented for the first time for each location in which mice from Far-East populations were trapped calculated from the individual modal numbers of chromosomes. In various geographical Far-Eastern populations of the Korean field mouse, the xB index varied from 0 to 4. In the Far-Eastern populations of the species, this index is equal, on average, to 1.67. Deviations from the mean value in particular geographic regions were insignificant. Thus, in the Magadan and Amur oblasts and the Jewish Autonomous Oblast, this xB index amounted to 2.0; in the Khabarovsk region, the index was equal to 1.55; and, in the Primorskii region, the index was 1.68 (table).

Small average values of the xB index of 2.3–4.0 close to the Far-Eastern populations of *A. peninsulae* have been noted in several occasional Siberian populations of southern Pribaikalie, southwestern Transbaikalia, western Sayans, eastern Siberia (Borisov, 1990b, 1990c, 1990d), and the Chita oblast (Roslik et al., 2005). In the majority of other Siberian populations, the values of this index were the higher, i.e., 4.5 in the Chita oblast (Roslik et al., 2005) and the Altai mountains (Borisov, 2008), 13.2 in the Krasnoyarsk region (Borisov, 1990c) and maximally 20.7 in the Maina village of the Krasnoyarsk region (Volobuev, 1980; Timina et al., 1980). Data about high modal numbers of chromosomes also argue in favor of the high xB index values for animals of Japan (from Hokkaido island) (Hayata, 1973; Abe et al., 1997), central China (Wang et al., 2000), and Mongolia (Borisov and Malygin, 1991). In other species of the *Apodemus* genus, in which supernumerary chromosomes are revealed, as a rule, the xB index seldom exceeds 1.0 (Wójcikk et al., 2004).

As can be seen from the table data, in samples from various years of trapping, from 11 populations (4, 5, 6, 8, 9, 16, 17, 24, 30, 31, and 37) the xB index either varied or remained nearly unchanged. Using the example of a 9-year-long study of karyotypes of individuals of the Ussuriiskii Reserve (population 24), it can be determined that the xB index in 1987, 1989, and 1990 changed weakly and was equal to 1.2, 1.0, and 1.33, respectively. In 1992, the index rose to 4.0; in 1995, it decreased to 1.33, then again rose gradually. In 1996 and 1997, the index amounted to 1.63 and 1.64, respectively, and, in 1998, the index was 2.6; then, in 1999, it fell sharply to a minimal value of 0.53. A similar pattern of the cyclical increase and decrease in the xB index was also observed in other populations (table). The question of why animals with some certain numbers of B chromosomes are dominant during different years remains open. The suggestions offered on this matter are quite different and speculative. For the yellow-necked mouse, an attempt was made to find a connection between the frequency of individuals with B chromosomes, the xB index, and the degree of industrial pollution; however, the correlation has not been established (Zima et al., 1999). The majority of mice studied in this work were from ecologically clean regions; however, a small part were from zones of industrial crises (populations 16 and 17). No differences in the xB index have been found between these populations. Variations in the number of B chromosomes are likely to be connected with the population density (Vujošević and Blagojević, 1995; Kartavtseva, 1999; Wójcik et al., 2004). Among these suggestions, there is also a hypothesis about a connection between B chromosomes with a certain viral disease (tick-borne encephalitis) whose bearers in nature are small rodents (Bekasova and Vorontsov, 1975; Kartavtseva and Roslik, 2004). There are data that viral infections in the bank vole can cause the increased frequency of mutations (Gileva et al., 2001).

Variations in the xB index for different years of studies have been demonstrated for populations of the same species in samples from the Teletskoe lake (Altai mountains), where this index rose from 2.3 in 1980 to 6.5 in 2002 (Borisov et al., 2007). One of the causes for the sharp increase in the xB index in the samples might possibly be the technogenic effect. Highly toxic, unrefined liquid propellant (heptyl and its derivatives) is disposed in this region and can negatively affect plants and animals, although the action of viral mutagenesis on the mouse's organism also cannot be ruled out (Borisov, 2008).

On the other hand, there are data in the favor of the constancy of the xB index. Thus, for instance, it has been shown on individuals of laboratory colonies of two subspecies of the Arctic lemmings that the xB values are close with those of from the natural populations, from which ancestors of the colonies originated, in spite of differences in the vivarium maintenance of the animals and the natural conditions (Gileva, 2003, 2004). Taking into account the xB index constancy, as well as the extremely rare incidence in Arctic lemmings of mitotically unstable mosaics (1.9–3.8%), it is logical to suggest that the system of B chromosomes in this species seems to be well balanced and steady, unlike the B chromosome system in the Korean field mouse.

Distribution of the number of B chromosomes in cells of animals with stable karyotypes and in mosaics. Karyotypes of 219 (61.7%) studied animals were mosaic, while that of 136 (38.3%) were stable. Animals with stable karyotypes were both with (n = 93) and without B chromosomes.

In the group of mice with the stable karyotype, the variability of the number of B chromosomes has been noted to be zero to four. In the Magadan oblast and the Jewish Autonomous Oblast, out of six of these individuals, 66.7% had two B chromosomes in each karyotype. In the Khabarovsk region (n = 26), 57.7% of mice were without B chromosomes, while 26.9% had two B chromosomes. In the Primorskii region (n = 104), 30.8% individuals had one B chromosome, 26.9% had no B chromosomes, and 23.9% had two B chromosomes (Fig. 2a). A common feature of this group is the presence in different regions of individuals with two B chromosomes; the frequency of these individuals in regions varies.

In the group of mosaics, more diverse spectra of combinations of numbers of B chromosomes were revealed; in the range variability (zero to seven) they significantly exceeded those in the group of mice with stable karyotypes. Maximal numbers of B chromosomes (five to seven) were only recorded in a small number of mosaics. In the Jewish Autonomous Oblast and Amur oblast (n = 14), 21.4% of individuals with mosaicism had one to two and two to four B chromosomes, and 14.3% of animals had zero to one and two–three B chromosomes (Fig. 2b, white columns). In the Primorskii region (n = 164), mosaics with the following numerical spectra of B chromosomes were dominant: one to two (19.5% of individuals), zero to two (17.1%), and zero to one (15.2%) (Fig. 2b, dark columns). In the Khabarovsk region (n = 41), individuals with both mice of the above-mentioned regions spectra of B chromosomes were dominant, including zero to one (19.5%); one to two (17.1%); and somewhat different numbers of chromosomes, i.e., one to three (17.1%), two to three (14.6%), and zero to two (12.2%) (Fig. 2b, grey columns). A common characteristic of this group is the presence in all three regions of mosaics with one to two, zero to two, and zero to one B chromosomes; however, the frequencies of these individuals in regions differ somewhat. Spectra of combinations of the number of B chromosomes in mosaics on the whole are more diverse compared to the group of mice with stable karyotypes. Although these spectra are often similar in their number of B chromosomes, they also included higher numbers of B chromosomes absent in animals with stable karyotypes. The authors that study Siberian populations of the same species have the similar opinion that spectra of the variability of B chromosome numbers are higher in the group of mosaics (Volobuev, 1980; Timina et al., 1980). Most likely, mosaics make the greatest contribution to variability and the appearance of the wider spectra of variations in the number of B chromosomes.

The fact that high proportions of mosaics are constantly maintained in populations of the Korean field mouse and some mammalian species can indicate that the variants of combinations of a certain number of B chromosomes in mosaics can play some adaptive role at some particular moment of survival by the population of unfavorable environmental conditions. Periodically changing life conditions are the cause of cyclic transformations in the structure of a species population as a result of natural selection. With changes in habitation conditions during the season, the frequencies of individuals with genotypes that are most adaptive to some particular conditions increase (Altukhov, 2003); parallelism should also not be forgotten. Thus, individuals of *A. peninsulae* from different geographic regions and different habitats that belong to different subspecies (e.g., those from Siberia, Mongolia, and Hokkaido) are similar in number but different in compositional variants of the B chromosome system (Kartavtseva and Roslik, 2004).

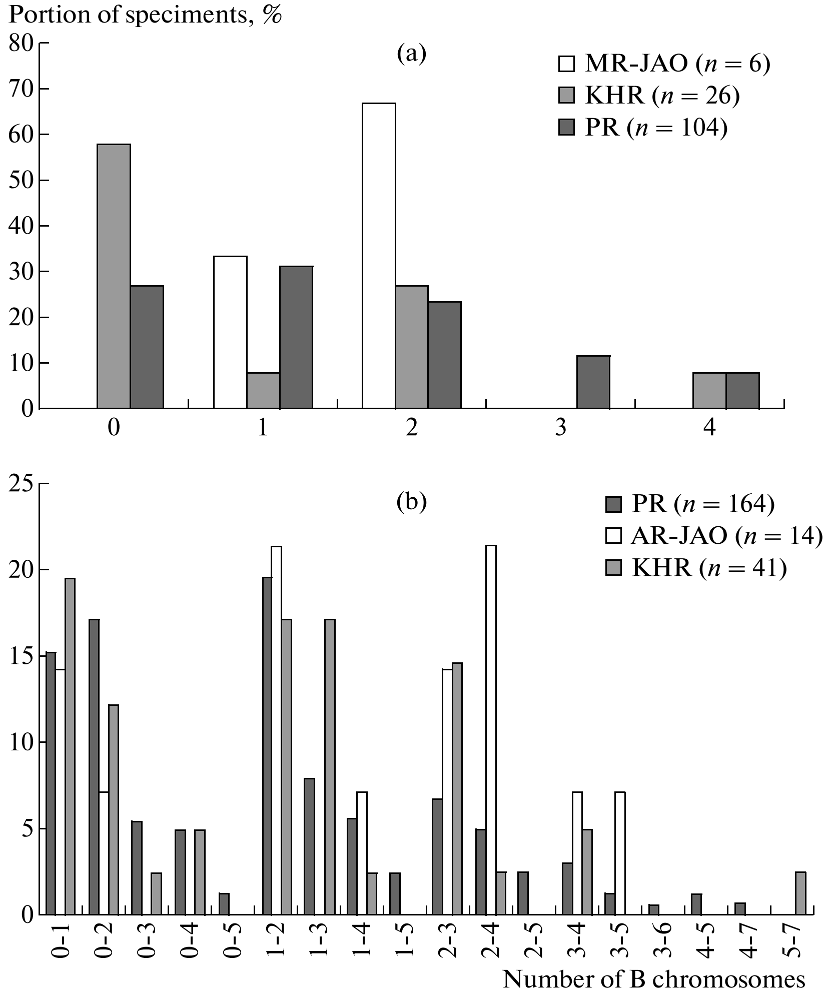

Fig. 2. Distribution of animals for number of B chromosomes in different geographical regions of the Russian Far East: (a) proportion of individuals with stable karyotypes; (b) proportion of individuals with mosaicism. Columns white: pooled data for populations of the Magadan (MO), Amur (AO) oblasts, and the Jewish Autonomous Oblast (JAO); grey: Khabarovsk region (KR); dark: Primorskii region (PR).

There are data about the coupling of the number of B chromosomes and the character of mosaicism with phenotypical effects in animals. No effect of supernumerary chromosomes has been revealed on the fertility and vital ability of female Vulpes vulpes foxes (Belyaev et al., 1974a). However, a correlation was found between the behavior of silver foxes and the character of variations in their number of B chromosomes. Statistically significant differences have been shown between groups of animals selective in behavior for the domesticating effect and aggressiveness as compared to the nonselected animals. An increase was shown in the percentage of individuals with mosaicism (up to 72.7% in tame foxes and to 67.7% in the aggressive foxes compared to 43.6% and 56.0% in nonselected foxes) and the appearance of the high-clone animals in the group of tame foxes (Belyaev et al., 1974b). It is possible that, in the raccoon dog *Nyctereutes procyonoides procyonoides* of farm breeding, the same situation can be observed as in silver foxes. In this species, a high level of mosaicism of 92.3% (Szczerbal et al., 2005) (or 76.9% by the criterion of the present work) has been revealed; most likely, this is also due to the breeding of animals in captivity. The selectively significant phenotypical effects (change in linear body size and/or craniometrical features) connected with the presence of B chromosomes were also noted in the Arctic lemmings (Gileva, 1982, 2003, 2004) and the yellow-necked mouse (Blagojević and Vujošević, 2000; Jojić et al., 2007). Thus, B chromosomes in mammals seem to participate in the genetic control of several qualitative features, including growth and development.

The phenomenon of mosaicism is well known in the medical literature dealing with studies on abnormalities of human autosomes and sex chromosomes. In patients with various chromosomal aberrations, the level of mosaicism is 1–75% (Hassold et al., 1988;

Akbari et al., 1998; Hassànzadeh et al., 2005; Araújo and Ramos, 2008). In human embryos the percentage of mosaics with various chromosomal abnormalities can reach 100% (Malmgren et al., 2002). The negative effect of aneuploidy for pair 21 autosomes on the phenotypical manifestation is leveled in individuals with mosaicism who have mixed trisomy-21 and normal cells. The higher the fraction of cells with normal karyotype, the lower the phenotypical manifestation of the syndrome (Werner et al., 1982). By extrapolating these results to our data, it can be suggested that the maximal numbers of B chromosomes (five to seven) revealed in mosaics of *A. peninsulae*, most likely do not bear an adaptive load. As was shown above, karyotypes of the Far-East *A. peninsulae* contain predominantly zero to two B chromosomes. Animals with three to four B chromosomes are found two to four times less often and mosaics with five and seven B chromosomes are discovered even less frequently. Obviously, animals with one to two B chromosomes have certain selectional advantages over mice with higher numbers of B chromosomes. The non-Mendelian inheritance of B chromosomes leading to the mitotic instability of their number is a factor in the increase in frequency of B chromosomes in natural populations. However, the spread of these B chromosomes in populations still is not unlimited. There seem to exist some mechanisms controlling preservation in the Far East mice certainly not high numbers of B chromosomes. A similar pattern of restriction in cells of the number of B chromosomes and of the highest frequency of the presence of metaphases with certain chromosome numbers has been revealed in the silver foxes. They have seldom been noted to have chromosomal numbers higher than 38, where B = 4 (Belyaev et al., 1974a, 1974b).

Excess genetic material expressed in maximal numbers of B chromosomes can probably produce a negative effect on the organism of the bearer. However, the detection of the widest spectra of the numbers of B chromosomes and the maximal numbers of B chromosomes, particularly in mosaics, which indicates mosaicism for B chromosomes, seems to be very important for the organism, since it probably results in a decrease in the negative action of the excessive DNA material of B chromosomes.

FISH analysis of B chromosomes of *A. peninsulae* from several populations of the Primorskii and Khabarovsk regions has shown the similarity of these structures in their DNA composition and their probable origin by amplification of the pericentromeric regions of sex chromosomes as well as has revealed differences in origin of B chromosomes of the Far-Eastern and Siberian populations (Rubtsov et al., 2004, 2005). Since the composition of B chromosomes in mice of the Far-Eastern populations as compared with that in mice of the Siberian populations has turned out to be relatively uniform, the question arises of whether the amount of DNA in B chromosomes (number, size) or the combination of variants of different dimensional and morphological types of B chromosomes is more important for the Far-East *A. peninsulae*. So far, no answer to this question has been obtained; however, for other types of animals, e.g., grasshoppers *Eyprepocnemis plorans*, there are data that some of the main morphotypes of B chromosomes have an endemic character of spreading (Bakkali et al., 1999; Cabrero et al., 1999; Dzyubenko et al., 2006).

In conclusion, it can be stated that, due to many years of study, samples of the Korean field mouse of the Russian Far East, there was analyzed interpopulational, intrapopulational polymorphism, and mosaicism for the number of B chromosomes. B chromosomes are found in karyotypes of the majority of studied animals (87.9%), of which 61.7% were mosaics. We have for the first time revealed inconsistencies in the frequencies of the presence of animals with B chromosomes in different samples of this species, as well as to studied the range of variability of modal numbers of B chromosomes (zero to seven) and variations in the xB index (zero to four), not only in individuals of different populations, but also in samples of the same population. Based on an analysis of two animal groups, i.e., those with the stable karyotypes and mosaics, the predominance of mice with certain numbers of B chromosomes (as a rule, zero to two) was shown, but with different frequencies in three geographic regions. In mosaics, a wider spectra of variability has been noted in the number of B chromosomes (zero to seven), unlike animals with stable karyotype (zero to four). Rather low numbers of B chromosomes (one to two) seem to play an adaptive role, unlike the maximal numbers of B chromosomes (five to seven), although the latter are present with a low frequency in mosaics.

Based on a study of the number characteristics of B chromosomes in samples of different years and in different natural continental populations of the Korean field mouse of the Russian Far East, we have suggested that, on the whole, the system of B chromosomes of this species seems to be imbalanced and unstable. However, the balance of the *A. peninsulae* B chromosome system in regards to its morphological and dimensional characteristics should only be discussed after studying these parameters.

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