B Chromosomes in Populations of Mammals Revisited

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Abstract: The study of B chromosomes (Bs) started more than a century ago, while their presence in mammals dates since 1965. As the past two decades have seen huge progress in application of molecular techniques, we decided to throw a glance on new data on Bs in mammals and to review them. We listed 85 mammals with Bs that make 1.94% of karyotypically studied species. Contrary to general view, a typical B chromosome in mammals appears both as sub- or metacentric that is the same size as small chromosomes of standard complement. Both karyotypically stable and unstable species possess Bs. The presence of Bs in certain species influences the cell division, the degree of recombination, the development, a number of quantitative characteristics, the host-parasite interactions and their behaviour. There is at least some data on molecular structure of Bs recorded in nearly a quarter of species. Nevertheless, a more detailed molecular composition of Bs presently known for six mammalian species, confirms the presence of protein coding genes, and the transcriptional activity for some of them. Therefore, the idea that Bs are inert is outdated, but the role of Bs is yet to be determined. The maintenance of Bs is obviously not the same for all species, so the current models must be adapted while bearing in mind that Bs are not inactive as it was once thought.

Keywords: supernumerary chromosomes; additional chromosomes; chromosome polymorphism; evolution

1. Introduction

The presence of supernumerary or B chromosomes (Bs) is the oldest known chromosome polymorphism [1], and yet, after more than a century of research, the biological importance of Bs is still to be better determined. The knowledge about Bs in mammals is more recent and dates since 1965 when they were found in the greater glider, *Petauroides* (*Schoinobates*) *volans* by Hayman and Martin [2] and in the red fox, *Vulpes vulpes* by Moore and Elder [3].

A complex collection of diverse chromosomes, such as Bs, is difficult to describe. Yet, Bs are defined as dispensable supernumerary chromosomes which do not recombine with members of the basic A chromosome set (As), and do not follow the rules of Mendelian segregation law [4]. This definition assembles a pool of various chromosomes that do not share a complete set of features but only the mentioned dispensability, which alludes that a regular growth and development take place with or without Bs. A typical B chromosome is seen as a supernumerary, heterochromatic chromosome, smaller and morphologically different from chromosomes of the standard set, that does not evoke visible phenotypic effects. Nevertheless, the Bs that do not fit either partly or entirely into this picture are far from being atypical. In reality, when it comes to Bs, being out of the ordinary is considered to be a rule.

The earlier Beukeboom's estimate that 15% of all species carry Bs seems to be too high. The more accurate calculation stating that only 3% of karyologically studied extant species, across the majority of taxonomic groups carry Bs, was given by D'Ambrosio et al. [5]. Although it was thought that species with Bs in mammals are many times less frequent than in plants, it seems that this is not well grounded. According to the data that Jones [6] summarized, there are 1252 plant species with Bs that make about 2.4% of karyotypically studied plant species [7]. In the first review of Bs in mammals Volobujev [8] listed 14 species, but the next year he expanded list to 25 species [9]. Vujošević [10] increased the list to 34 species, and in 2004 we recorded fifty-five species carrying Bs [11]. There are nearly 70 species with Bs that were mentioned by Trifonov et al. [12], but the very list of species was not presented. As it can be seen in Table 1, the number of mammalian species carrying Bs has increased to 85. At the same time, the list of documented mammalian species has also increased from 4629 [13] to 6399 extant ones [14]. It appears that ~1.9% of 4380 karyotypically studied mammalian species (according to chromosome number database [15]) are featured by presence of Bs. We gave all species proper names according to the list of Burgin et al. [14], but even in such a detailed list, some species remain questionable. Besides adding new species to the list, we also removed some due to either being listed multiple times under different names, or incorrectly mentioned as species with Bs, such as the pocket gopher, *Thomomys umbrinus* [16].

Despite the vast body of knowledge on Bs within mammalian species, the question of what factors determine the distribution of Bs across different species is yet to be answered. Why are Bs present in some species and not in others? Is there some innate property of the genome, or karyotype, which determines whether a species is likely to carry Bs or not? As passed two decades witnessed huge progress in application of molecular techniques, we decided to re-examine the data on Bs in mammals, and to suggest the future directions of the research.

2. Morphological Characteristics and Size of B Chromosomes

B chromosomes were sorted in three categories [8,10,11] based on their size in relation to chromosomes from the standard set (Table 1). The most frequent Bs are of the same size (II) as the chromosomes from A set (52 species, 65.0%), so they cannot be recognized using standard cytogenetic techniques. In this category, the size of Bs often corresponds to the size of the smallest chromosome in the genome. Furthermore, about less than half (39 species, 48.8%) of species have Bs that are smaller than the smallest chromosomes of the standard set. They belong to category I. Ungulates and bats have only Bs from this category (Table 1). There are two primate species that possess micro Bs, but there is still a debate if human small supernumerary marker chromosomes (sSMC) could be considered as B chromosomes [17].

The rarest (3.5%) of the species are the ones with Bs either larger or the same size as the largest chromosomes from the standard complement (III): *Uromys caudimaculatus* [18], *Holochilus brasiliensis* [19] and *Apodemus peninsulae* [20]. Additionally, the presence of different types of Bs in the same genome contributes to a large variability of Bs. Eleven species from Table 1 show variation in size and morphology of Bs, so there are different types that are recognised. This variation is well studied in *A. peninsulae* where five classes with different morphological types of Bs are present.

Among Bs from type II, metacentrics and submetacentrics are more present (62.7%) than acrocentrics. Hewitt [21] noted that large Bs tend to be mitotically stabile while the small ones have an opposite tendency. It means that the intraindividual variability rises with the decrease in size of Bs (see more details in Section 3).

Table 1. List of species with B chromosomes.

ORDER / Species	Common Name (◊)	2n	NFa	X/Y	No. Bs	Bs Morphology Size *	Bs Morphology Cent. Position †	References
PERAMELEMORPHIA								
Echymipera kalubu	Common Echymipera	13–14 XX/X0	26	M/A	1–5	I	M	[22]
DIPROTODONTIA								
Petauroides (Schoinobates) volans	Greater glider	22	38	M/A	1–8	I	mi	[2,23]
INSECTIVORA								
Crocidura leucodon	Bicolored shrew	28	52	SM/SM, A	1	II	A	[24]
Crocidura malayana	Malayan shrew	38	62	SM/M	1–2	II	M	[25]
Crocidura suaveolens	Lesser shrew	40	46	M/A	1	II		[26]
Sorex bedfordiae	Lesser stripe-backed shrew	24	44	A/A	1–2	II	M	[27]
CHIROPTERA								
Myotis macrodactylus	Big-footed Myotis	44	56	M/A	1	I	mi	[28]
Nyctalus leisleri	Lesser Noctule	44	54	M/A	1–3	I	mi	[29]
Pipistrellus tenuis (mimus)	Least Pipistrelle	38	50	M/A	2–4	I	mi	[30]
PRIMATES								
Alouatta seniculus	Red howler monkey	46	64	M/A	1–3	I	A	[31,32]
A.seniculus macconelli		47–49			1–3			[33]
Homo sapiens	Human	46	78	SM/A	2	I	mi	[34,35]
CARNIVORA								
Atelocynus microtis	Short-eared dog	74	72	SM/SM	2	I	mi	[36]
Chrysocyon brachyurus	Maned wolf	76	72	SM/SM	1	II	A	[37]
Nyctereutes p. procyonoides	Raccoon dog	54	62	M/M	1–4	II	A, SM	[38]
Nyctereutes p. viverinus		38	62	M/M	1–5	II	A	[39]
Vulpes (Alopex) lagopus	Arctic fox	50	92	M/A	1	II	M	[40]
Vulpes bengalensis	Bengal fox	60	68	M/A		I	mi	[41]
Vulpes pallida	Pale fox							[42]
Vulpes vulpes (fulvus)	Red fox	34	64	M/A	1–10	I	A, M	[3,43]
ARTIODACTYLA								
Capreolus pygargus	Siberian roe deer	70	72	SM/A	1–14	I	mi	[44,45]
Mazama americana	Red brocket	42–53	42–52	SM/A	2–5	I	mi, A	[44,46]
Mazama bororo	Small red brocket	34	46	M	4–6	I	mi, A	[47,48]
Mazama gouazoubira	Gray brocket	69–70 70	68–69 68	M, A/A, mi A/M	1–2 1–3	I I	mi, A	[47,49,50]
Mazama nana	Brazilian dwarf brocket	36	54	M/mi	1–6	I	mi, A	[47,51]
Mazama nemorivaga	Amazonian brown brocket	67–69	69–72	SM/A,M	2–7	I	mi	[52]
Moschus moschiferus (sibiricus)	Siberian musk deer	58	56	A/A	1–2	-	-	[53]
RODENTIA								

Table 1. *Cont.*

ORDER Species	Common Name (◊)	2n	NFa	X/Y	No. Bs	Bs Morphology Size *	Bs Morphology Cent. Position †	References
Acomys ngurui		59–61	68	M/A,SM	1	II	SM	[54,55]
Acomys spinosissimus	Spiny mouse	59–61		A/SM	1	II	A	[54]
Akodon mollis	Soft grass mouse	22	42	M/A	1	II	M	[56]
Akodon montensis (arviculoides)	Montane Akodont	24	42	A/A	1–3	II	SM	[57,58]
Apodemus agrarius	Striped field mouse	48	54	A/A	1	I, II	mi, A	[59]
Apodemus argenteus	Small Japanese field mouse	46	48	A/A	1	I, II	mi, SM	[60]
Apodemus flavicollis	Yellow-necked field mouse	48	46	A/A	1–9	II	A	[61,62]
Apodemus mystacinus	Eastern broad-toothed field mouse	48	50	A/A	2	-	-	[63]
Apodemus peninsulae (giliacus)	Korean field mouse	48	46	A/A	1–30	I, II, III	mi, A, SM, M	[64,65]
Apodemus sylvaticus	Long-tailed field mouse	48	46	A/A	1–3	II	A	[66]
Bandicota indica	Greater bandicoot rat	44/45 XX/XO	84	SM/A	1–3	II	SM	[67]
Bandicota savilei	Savile's bandicoot rat	43	58	SM	1	I	SM	[68]
Berylmys berdmorei	Berdmore's Berylmys	40	62	A	1	II	M	[68]
Blarinomys breviceps	Brazilian shrew mouse	29–50	50	A	2	II	M	[69]
Chaetodipus (Perognathus) baileyi	Bailey's pocket mouse	46	64	M/M	1–10	II	M	[70]
Dasymys rufulus	West African shaggy rat	36, 38 39, 40	42–50	A,SM, M/A, SM, M	1–3	II	M	[71]
Dasyprocta fuliginosa	Black Agouti	64	118	M/SM	1	II	SM	[72]
Dasyprocta leporina	Red-rumped Agouti	64	118	M/M	1	I	M	[72]
Dasyprocta prymnolopha (nigriclunis)	Black-rumped Agouti	64	118	M/SM	1	II	M	[72]
Dasyprocta sp.	-	64	118	M/SM	1	II	M	[72]
Dicrostonyx groenlandicus (kilangmiutak)	Northern collared lemming	48		M/SM	1–3	I, II	A, M	[73]
		47–50	48	A, M/A,SM	1–8	II	M	[74]
Dicrostonyx torquatus	Palearctic collared lemming	44	56	A, SM/A	1–42	II	SM, M	[74,75]
Golunda ellioti	Indian bush rat	54	54	SM/A	1–4	II	A	[76]
Grammomys (Thamnomys) dolichurus	Woodland thicket rat	54	68	SM/A	4-7	II	A, M	[77]
Grammomys macmillani (Thamnomys gazellae)	Macmillan's thicket rat	54	70	SM/A	2–17	I	mi	[78]
Holochilus brasiliensis	Web-footed marsh rat	48	58	A/A	1–2	II, III	SM, M	[79]
Holochilus chacarius	Chaco marsh rat	48–56	56–60		1–2	II		[80]
Holochilus venezuelae	-	44	56	A/A	1	II	M	[81]
Holochilus vulpinus	-	36	58	A/A	1–3	II	A	[19]
Mastacomys fuscus	Broad-toothed rat	48	56	SM/SM	1	II	A	[82]
Mastomys erythroleucus	Guinea multimammate mouse	38	54	SM/SM	2	II	A	[83]
Mastomys natalensis	Natal multimammate mouse	32	54	M/A	1	II	SM	[84]
Melomys burtoni	Grassland Melomys	48	50	A/A	1–8	I, II	mi, A, SM, M	[85]
Melomys capensis	Cape York Melomys	48	50	A/A	3–6	-		[85]
Melomys cervinipes	Fawn-footed Melomys	48	50	A/A	4–13	I, II	SM, A	[82]
Microtus gregalis	Narrow-headed vole	36	50	M/A	1–4	II	A	[86]
Microtus longicaudus	San bernardino long-tailed vole	56	84	M/A	1–14	I	M	[87]
Mus cookii	Ryley's spiny mouse	40	38	A/A	1	I, II	A, M	[68]

Table 1. *Cont.*

ORDER Species	Common Name (◊)	2n	NFa	X/Y	No. Bs	Bs Morphology Size *	Cent. Position †	References
Mus shortridgei	Shortridge's mouse	46	46	A/A	1–3	I, II	A, M	[88]
Nannospalax (Spalax) leucodon	Lesser blind mole rat	60	74	SM/M	1–3	I	mi, A	[89]
Nectomys rattus	Common water rat	52	50	A, SM/A, SM	1–3	II	A, SM, M	[90]
Nectomys squamipes	South American water rat	56	54	A, SM/A, SM, M	1–3	II	A, SM	[91]
Oecomys concolor	Natterer's Oecomys	60	62		1–2	I	SM	[92]
Oligoryzomys (Oryzomys) fornesi	Fornes colilargo	62–66	64	SM/SM	1–2	I	A	[93]
Oligoryzomys flavescens	Yellow pygmy rice rat	64	64	SM/SM	1–2	I	mi	[94]
Otomys irroratus	Southern African vlei rat	28	44	M/SM	2–4	II	SM, M	[95]
Proechimys sp.		26			1	I	mi	[96]
Rattus fuscipes	Bush rat	38	58	A/A	1–3	II	M	[82,97]
Rattus norvegicus	Brown rat	42	60	A/A	1	II	A	[98]
Rattus rattus	House rat	42	60–64	A/A	1–3	II	M	[99]
Rattus r. diardii		42			1–4	II	M	[100]
Rattus r. frugivorus		38			1–3	II	M	[101]
Rattus r. kandianus		40			1	II	M	[102]
Rattus r. tahnezumi		42			1	II	M	[102]
Rattus r. thai		42			1-6			[103]
Rattus tunneyi	Pale field rat	42	60	A/A	1	II	M	[104]
Reithrodontomys megalotis	Southern marsh harvest mouse	42			1–7	I	mi	[105]
Reithrodontomys montanus	Plains harvest mouse	36	72	M/A, SM	1	I	SM	[106]
Sigmodon hispidus	Hispid cotton rat	52	50	A/M	3–4	-		[107]
Sooretamys angouya (Oryzomys angouya, O. buccinatus, O. ratticeps)		58	60	A/A	2	I, II	mi, SM	[108–110]
Thallomys nigricauda	Black-tailed tree rat	48	60			-		[111]
Thomomys bottae	Animas mountains pocket gopher	76	130	SM/mi	6–12	I	mi	[112]
Trinomys (Proechimys) iheringi	Ihering's spiny rat	60	116	SM/SM	1–6	I	mi	[113,114]
Tscherskia (Cricettilus) triton	Greater long-tailed hamster	28	30	A/M	1–2	II	A	[112,113]
Uromys caudimaculatus	White-tailed giant rat	46	50	A/A	2–12	II, III	A, SM, M	[18,115]

2n—diploid number, NFa—fundamental number of autosomes, X/Y—morphology of sex chromosomes; * Category: I—Bs smaller than chromosomes from A set, II—same as A, III—larger than A; † mi—micro Bs, M—metacentric, SM—submetacentric, A—acrocentric chromosomes; (◊) Mammal Diversity Database [116].

3. Frequency of B Chromosomes

A large variability of Bs in mammalian species is displayed on all levels: intra-individual, intra- and inter-populational. The most common for mammals is frequent appearance of intraindividual variability that can feature the same tissue or appear between different tissues. Mosaicism for the number of Bs was scored in *Echymipera kalubu* [22], *Rattus rattus* [103], *V. vulpes* [117], *Myotis macrodactylus* [28], *A. peninsulae* [118], *Dicrostonix torquatus* [119], *Trinomys iheringi* [113], *Nictereutes procionides viverinus*, *Capreolus pygargus* [44], *Alouatta seniculus* [32], *Dasyprocta fuliginosa*, *Dasyprocta leporine*, *Dasyprocta prymnolopha* [72], *Apodemus flavicollis* [11], *Nictereutes procionides procyonides* [120], *Mazama nana* [51], *Mazama americana* [51], *Grammomys macmillani* [78], *Acomys ngurui*, *Tscherskia triton* [121] and *Mazama nemorivaga* [52].

The mosaicism for the number of Bs is extensively studied in Korean field mouse, *A. peninsulae*, first noticed in early studies [122] and then confirmed in different areas of species' wide distribution [123,124]. The frequency of mosaics extends from 0.05 in South Korea [125] to even 0.85 in populations from Primorskii region and Hokkaido [123]. Furthermore, it has been found that the variability of B chromosome numbers is higher in the group of mosaics [8,124,126].

The great variability produced by intraindividual mosaicism is also characteristic for genus *Mazama*. In this genus, Bs appear in five out of eight species [51]. For instance, in *M. americana*, Abril et al. [127] found Bs in all 18 studied animals with intraindividual variability from 0–6 Bs. The same occurrence happened in *M. nana* [51] and in *M. nemorivaga* [52] where all studied animals had 0–7 Bs. Besides Bs, genus *Mazama* is featured with other kinds of chromosome polymorphisms, involving autosomes and sex chromosomes. This is also the case with *Acodon montensis* [128]. On the other hand, genus *Apodemus* with one third of species with Bs is karyotypically very stable.

A presence of one B chromosome is the most common situation, but the number of Bs per animal can vary widely. The highest number of Bs, which counted 42, was found in *D. torquatus* [75]. Up to 30 Bs in a single animal have been detected in *A. peninsulae* [65], while there have been 17 Bs identified in *Thamnomys gazellae* (now *Grammomys macmillani*) [78]. The average maximal number of Bs per specimen found in 85 mammalian species is 4.88 (Table 1).

There are some species with Bs whose populations cover wide geographic areas. The yellow-necked field mouse, *A. flavicollis*, common in the Western Palearctic region, has showed Bs presence almost everywhere through its range with frequencies ranging from 0.07 to 0.94 [62,129–138]. The frequency of animals with Bs in different geographic regions varies, but rules cannot be established easily. The variation in frequency of Bs that is generally present in *A. flavicollis* is also characteristic for small areas. For instance, we studied Bs presence in 40 populations from Serbia and the frequencies ranged from 0.11 to 0.67 [66,133,139–142]. Generally, the frequency of animals with Bs increases with altitude towards harsher climatological conditions [141,143]. However, this trend was not confirmed in the samples from Poland [138].

Shellhammer [144] suggested that the most reasonable explanation of great B frequency variation in southern marsh harvest mouse, *Reithrodontomys megalotis*, is a general increase in genetic variability towards the periphery of species distribution. The same was proposed for Bailey's pocket mouse, *Chaetodipus baileyi* [70], while Boyeskorov et al. [145] found the highest B frequency in *A. flavicollis* (0.81) in a peripheral area of its distribution. A north-to-south increase in frequency of Bs was found in grassland Melomys, *Melomys burtoni* [85].

Besides being found in almost all studied populations, Bs in *A. peninsulae* are often present in all individuals. For instance, in the populations in East Asia, the frequency of animals with Bs vary from 0 to 1.0, while in the Siberian populations, from 0.99 to 1.0 [123,146]. So far, the only exceptions are Sakhalin Island and Stenina Island, where Bs repeatedly have not been found [146,147]. The distribution of Bs varies significantly between populations [62,148–152], however, these differences are still largely unexplained. The difference in the maximal number of Bs between regions is also evident varying from 30 in Siberia [65], to 6 in South Korea [123]. Roslik and Kartavtseva [124] established variability in modal number of Bs. Each population is characterized by a certain modal

number of Bs. This number is also specific for regions. Roslik and Kartavtseva [153] documented the presence of clinal decreasing in frequency of rare B morphotypes from East to Northwest in the studied area.

Contrary to such high frequencies of Bs in *A. peninsulae* and *A. flavicollis*, Zima and Macholán [62] found that the frequency of animals with Bs in populations of long-tailed field mouse, *A. sylvaticus*, is very low (2.4%). Such sporadic occurrence of Bs is characteristic for another species from the same genus, the striped field mouse, *Apodemus agrarius* [59]. While *A. peninsulae* and *A. flavicollis* are typical forest-dwelling species, *A. sylvaticus* is limited to the edges of forests and *A. agrarius* is a typical field mouse.

4. Structure and Composition of B Chromosomes

The newly discovered facts about Bs are mostly concerning their structure. Bs were for a long time seen as chromosomes without genes or, at least without active ones, due to a prevailing absence of their visible phenotypic effects. Although the counterevidence was repeatedly suggested, they were generally ignored until recently when technological advances [154] in genome analysis and sequencing armed investigators with a variety of new technical approaches to shake this dogmatic view. Molecular studies represent Bs as assemblage of various repeated sequences originating from one or more A chromosomes [155–157] or even from all [158]. Non-coding repetitive sequences or mobile elements present in both A and B chromosomes prevail but some of them are more frequent in Bs [159]. Some paralogs of genes located on A chromosomes could be found on Bs as intact or as degenerate sequences [154]. Unique sequences specific for Bs are rarely found [23,160,161]. Yet, thanks to the new technology, the list of genes identified on Bs is promisingly increasing.

The previous studies on mammalian Bs that were based mostly on differential staining revealed that 60% of them are C positive [11]. Those studies showed that when different types of Bs are present they could be C positive or C negative, such as in *A. peninsulae* and *M. nana* [51,162]. Furthermore, the analyses of molecular DNA composition of Bs in *A. peninsulae* [163] showed a presence of two specific forms of chromatin with presumed autonomous origin. Besides that, homology to the heterochromatic region of sex chromosomes and pericentromeric DNA of autosomes was established [163–165].

Molecular composition of Bs for 19 mammalian species is presented in Table 2. A presence of ribosomal genes (rDNA) was detected in 5 species by using silver staining and fluorescent in situ hybridization (FISH). Telomeric repeats are most frequently found on Bs (12 species), but centromeric were detected in only three cases. The presence of molecular markers specific for Bs was found in *P. volans* [23] and *A. flavicollis* [160].

Table 2. Current data on molecular composition of B chromosomes in mammalian species.

Species	Found on B Chromosome	Method	References
Petauroides volans	centromeric regions, B specific regions	FISH, PCR	[23]
Nyctereutes procyonoides procyonoides	interstitial telomeric sequences	FISH	[166]
	rDNA (NOR)	FISH, silver staining	[167]
	C-KIT	FISH	[168]
	Kdr, *RPL23A* pseudogene	FISH, PCR	[169]
	rDNA	PRINS (primed in situ DNA synthesis)	[170]
	Lrig1	FISH	[171]
	Ret		
	Lrig1 *Ret*	FISH	
	C-KIT (no transcriptional activitiy)	PCR, RT-PCR	[172]
	100 sequences located on B, homologous to genes involved in cell proliferation, differentiation, neuron sinapse, cell junction	sequencing of microdissected B	[173]
Nyctereutes procyonoides viverrinus	interstitial telomeric sequences	FISH	[166]
	three types of B-specific heterochromatin	FISH	[173]
	C-KIT	FISH	[168,169,171]
	Kdr *RPL23A* pseudogene	FISH, PCR	[169]
Vulpes vulpes	*C-KIT*	FISH	[168,171]
	RPL23A pseudogene	PCR	[169]
	Mdn1, *Ctndd2*	FISH	[171]
	49 sequences located on B, homologous to genes associated with cell division machinery, cell cycle control functions, microtubule, centrosomes, cell differentiation, proliferation	sequencing of microdissected B	[173]
Capreolus pygargus	*Tnni3k*, *Fpgt*, *Lrriq3*	FISH, flow-sorted DNA libraries derived from Bs	[174,175]
	9 genes located on B	re-analyzed data from [175]	[173]

Table 2. *Cont.*

Species	Found on B Chromosome	Method	References
Mazama gouazoubira	55 sequences located on B, homologous to genes associated with functional clusters associated with ATP-binding/kinase, mitochondria, cell cycle, Zn-ion binding/Zn-finger, membrane, cell proliferation/ differentiation, positive regulation of protein kinase activity	sequencing of microdissected B	[175]
	107 sequences located on B homologous to genes	re-analyzed data from [175]	[173]
Acomys sp.	telomeric repeat	FISH	[54]
Akodon montensis (arviculoides)	rDNA (NOR)	silver staining	[57,108]
	telomeric repeat, rDNA (NOR)	FISH, silver staining	[176]
Apodemus flavicollis	rDNA (NOR)	silver staining	[177]
	B specific regions	AP-PCR RT-PCR	[160] [178]
	rDNA	RT-PCR	[179]
	Vrk1	ISSR-PCR, sequencing	[180]
	38 sequences located on B, homologous to genes associated with microtubule, cell cycle proteins, and less significant nucleotide-binding, membrane and metal binding proteins. Satellite repeats, MurSatRep1, ERVL (MaLR), ERVK LTRs and transposable elements.	sequencing of microdissected B	[181]
	101 sequences located on B homologous to genes	re-analyzed data from [181]	[173]
Apodemus peninsulae	telomeric repeat, two types of B arm-specific repeats	FISH	[164] [163]
	two types of B-specific chromatin	FISH	[181]
	repetitive elements	FISH	[182]
	centromeric repeats, 32 sequences located on B homologous to genes associated with cell division machinery, cell cycle control, nucleotide-binding, laminin and EGF-like domain-containing, cytoskeleton and ion-bindings proteins, LINE L1 elements, centromeric repeats, satelite repeats MurSatRep1, ERVK and ERVL (MaLR) LTRs.	sequencing of microdissected Bs	[181]
	152 sequencies located on Bs homologous to genes	re-analyzed data from [181]	[173]
Blarinomys breviceps	telomeric repeats, ITSs	FISH	[69]

Table 2. *Cont.*

Species	Found on B Chromosome	Method	References
Holochilus brasilensis	OSHR, telomeric repeats	FISH	[183]
Nanospalax leucodon	telomeric repeat	FISH	[89]
Nectomys sp.	ITBs	FISH	[184]
Nectomys rattus	OSHR	FISH	[183]
Nectomys squamipes	OSHR, ITS	FISH	[183]
Rattus rattus	rDNA	FISH	[185]
	telomeric repeat	FISH	[186]
Reithrodontomys megalotis	telomeric repeat, LINE elements, centromeric repeats	FISH	[187]
Sooretamys angouya	rDNA (NOR)	silver staining	[108]
Trinomys iheringi	telomeric repeats	FISH	[114]

FISH—fluorecent in situ hybridization; RT-PCR—real time-PCR; rDNA (NOR)—ribosomal DNA (nucleolus organizer region); AP-PCR—arbitrarily primed-PCR; ISSR-PCR—inter simple sequence repeat-PCR; EGF—epidermal growth factor; LINE—long interspersed nuclear element; ERVK—endogenous retrovirus-K; ERVL—endogenous retroviruses-related; LTRs—long terminal repeats; ITS—interstitial telomeric sequences; OSHR—Oryzomyini shared heterochromatin region; ITBs—interstitial telomeric bands.

The first autosomal gene found on Bs of mammals was proto-oncogene receptor tyrosine kinase (*C-KIT*). It was found in three unrelated species, the red fox, *V. vulpes*, the Chinese and Japanese raccoon dog, *N. procyonoides* [168,169] and *M. gouazoubira* [175] but not in *A. flavicollis* [179]. Another gene (*Vrk1*) was found in two *Apodemus* species. By using ISSR-PCR, Bugarski-Stanojević et al. [180] found a part of *Vrk1* gene on Bs of *A. flavicollis*. The presence of this gene was confirmed upon isolation by microdissection [181] and additional 37 genes or parts of genes were found on Bs of this species. The Bs in *A. flavicollis* have similar structure as pericentromeric region of sex chromosomes [188]. Through comparison of gene groups in Bs of six mammalian species from different families, Makunin et al., [173] confirmed enrichment with genes related to cell-cycle, development and genes functioning in the neuron synapse. They pointed that the presence of genes on Bs involved in cell-cycle regulation and tissue differentiation could be important for the B chromosome formation.

There are also findings that propose the existence of regulatory interactions between coding sequences of A and B-chromosomes. Bugno-Poniewierska et al. [189], from studies of Bs in Chinese raccoon dogs and red fox determined that DNA methylation may maintain the transcriptional inactivation of DNA sequences situated on Bs. This could be the way to avoid some negative effects of Bs presence. Trifonov et al. [174] found, for the first time, the protein coding sequences on Bs of the Siberian roe deer, *C. pygargus*, which are not fully inactivated. Earlier, the gene expression in *A. flavicollis* showed elevated expression of three DNA fragments in the presence of Bs [178]. So, B'chromosome could be seen as a repository of various information which could be used depending on the selection pressure that a B carrier faces.

5. Origin of Bs in Mammals

There are several hypotheses proposed to explain the route of B chromosomes appearance [174,185,190]. In general, the source of Bs are chromosomes of the standard set, both autosomes and sex chromosomes, yet their origin from interspecies hybrids has also been proven in certain cases [191,192], but not in mammals. Whatever the source of their origin is, all proto-Bs must instantaneously pass through inactivation to avoid synapsis with the source chromosome. At present, a series of molecular processes are known as good candidates to achieve this condition, for instance mechanisms of sex chromosomes inactivation and epigenetic mechanisms. Bs can follow the same process operating in meiotic sex chromosome inactivation (MSCI) during the meiotic prophase I. Vujošević and Blagojević [11] proposed that B chromosomes are absent in birds due to genome reduction. Moreover, it appears that the sex chromosome specific silencing is absent in birds, although not yet been completely elucidated [193,194]. The same situation is found in egg laying monotremes [195] that also lack Bs. What is frequently overlooked in attempts to explain the initial steps of Bs origin is the possibility of simultaneous origin of proto-Bs in a population [11] that is far more probable in mammals due to their social organisation and population dynamics. This could promote spread of proto-Bs in populations.

The origin of Bs in mammalian species was based rather on presumptions than on facts. The circumstantial evidence come and is expected from molecular studies of Bs DNA contant. Sex chromosomes are proposed as a source of Bs in *E. kalubu* [22], *Dycrostonix groenlandicus* [196] and *Apodemus argenteus* [60]. In *A. peninsulae* a homology of heterochromatic region of Bs, sex chromosomes and autosomes was established [163–165]. Upon generation of microdissected DNA probes followed by FISH on metaphase chromosomes, another study found that Bs in *A. flavicollis* originate from pericentromeric region of sex chromosomes [188]. While there are five different types of Bs [197] with different origin (including sex chromosomes) in *A. peninsulae*, it was shown that all Bs in *A. flavicollis* have the same DNA contant regardless of their number or geographical distance which indicates a common origin from sex chromosomes [188]. Furthermore, whenever two or more types of Bs are present in one species, it appears that they do not have the same origin. A multiple origin of Bs in *A. peninsulae* was suggested by Matsubara et al., [198] based on the presence of 18S/28S rRNA genes only on meta- or submetacentric Bs. Some recent findings offer evidences for single origin of Bs in

this species also [181]. A different origin for two types of Bs was also found in the harvest mouse, *R. megalotis*, by Peppers et al. [187].

Based on comparative cytogenetic studies [67,199] it was suggested that Bs in *Bandicota indica*, *R. rattus* and *Rattus fuscipes* originated before the divergence of these species occurred. Different origin was assumed for Bs in two species of Carnivora, *N. procyonides* and *V. vulpes* [163,173] based on molecular data.

A two-step appearance of Bs was proposed for *A. peninsulae* [164]. The first step is the destabilization of pericentromeric regions, produced by the invasion of DNA sequences from euchromatic parts of A chromosomes, which leads to a formation of microchromosomes in high frequency, and thus make proto-Bs. The second step is the insertion and amplification of new DNA sequences. Similar steps were proposed by Rubtsov et al. [200] that assumed that the origin of Bs start with a loss of a greater part of q arm of an ancestor autosome followed by subsequent evolution of Bs that includes additional constitutional rearrangements. Makunin et al. [175], by using sequencing of isolated Bs of two mammalian species, showed that Bs originate as segmental duplications of specific genomic regions, and subsequently passes through pseudogenization and a repeat accumulation.

Presently, it seems that the new data describing the molecular composition of Bs incites more questions than suggests answers to the old ones.

6. Behaviour of B Chromosomes during Meiosis and their Transmission

The number of species whose meiotic behaviour of Bs was studied increased just slightly in last 15 years but there are new details for some already studied species. Currently, the meiotic behaviour is known for 25 species and univalent Bs are present in all of them. Besides univalents, bivalents appear in 13 species, and multivalents in 7, while assimetrical bivalents are present in 6 species. There are 5 species (*A. peninsulae*, *D. groenlandicus*, *N. procyonides*, *C. baileyi* and *V. vulpes*) where all four mentioned types of configurations are found.

When a different type of Bs is characteristic for the same species, their meiotic behaviour is often type dependent. So Hyata [64] found that both paring and non-paring among Bs occur in *A. peninsulae*. He showed that small macro- and microchromosomes in most cases do not follow Mendelian inheritance, yet other types of supernumeraries do follow it. Further meiotic studies in this species [197] showed that Bs are able to form axial elements and synaptonemal complexes in prophase of the first meiotic division. The same authors found that univalents of dot like Bs of different morphology are obviously not homologous, while metacentric Bs showed a partial homology. Univalent Bs are commonly associated with sex bivalent. Ishak et al. [201] noticed an absence of transcriptional activity in Bs of this species during pachytene. Karamysheva et al. [202], through the use of 2D analysis of pachytene in *A. peninsulae*, found three types of configurations: synapsed bivalents, univalents, and univalents that contain the foldback structure. During meiosis, Bs in *A. flavicollis* appear as univalents, bivalents or, depending on number, combinations of both, but never as a pair with the members of A set [130,203]. In the same species, Banaszek and Jadwiszczak [204] found that Bs behave in non-Mendelian fashion during meiosis I of males.

In *N. squamipes* analysis of the synaptonemal complex revealed auto-pairing of univalent Bs [184]. In the Northen collared lemming, *D. groenlandicus*, it was found that, besides univalents, bivalents and trivalents Bs can make synaptic associations with the Y chromosome [196]. Studies of synaptonemal complex in *M. americana* by Aquino el al. [46] revealed the presence of both univalents and bivalents. Univalents appear in two forms: as autopaired or just univalents.

When Bs appear as univalents in the silver fox, they show a folding-back behaviour that ends as intrachromosomal pairing [205], which indicates the presence of repeated DNA sequences. Sosnowski et al. [206] conducted experiments with spermatocytes of the red fox and the Chinese raccoon dog, and found that Bs that conjugate together form diverse structures, such as bivalents, trivalents, and tetravalents. Sosnowski et al. [206] also concluded that the increase in the number of Bs in spermatocytes of the Chinese raccoon dog corresponds with the lack of conjugation more

frequent. Basheva et al. [43] studied A- and B-chromosome pairing and recombination in the silver fox using electron and immunofluorescent microscopy. They found the same distribution of the foci along B- and A-bivalents and proved, for the first time, that meiotic recombination occurs in mammalian B chromosomes

The accumulation of B chromosomes in mammals appears to be a rarer event than expected. One of the reasons for sure is the lack of studies. Furthermore, Bs in some cases could maintain themselves without the apparent drive. In males, the evidences for accumulation of Bs were found in *C. baileyi* [207], *V. vulpes* [208], *A. peninsulae* [162,197,209], and in the greater long tailed hamster, *T. triton* [121]. In the latter, Bs were found in males only and the increase in number of Bs in germline cells was observed.

In lemmings, univalent Bs were eliminated from the polar body and incorporated into secondary oocytes [210,211]. The evidence of accumulation of Bs has been obtained in females of *R. rattus* [212,213] and *R. fuscipes* [97] by means of controlled crosses. In the case of experimental crosses done by Stitou et al. [213] in *R. rattus*, males showed Mendelian transmission rates, while only a slight accumulation of Bs happened in females.

Palestis et al. [214], following the theory of centromeric drive, based on a different ability of the two meiotic poles for capturing centromeres [215], showed that Bs in mammals are more common in species with acrocentric chromosomes. Since then, the number of mammalian species with Bs increased, therefore this theory is not valid anymore. The number of species with Bs with predominantly acrocentric chromosomes in standard set is just slightly larger, so it seems that such explanation for origin of Bs is reasonable only in proven cases.

Karamysheva et al. [202] studied nuclear organization of Bs in *A. peninsulae*. They showed that additional volume of heterochromatic regions of chromosomes and extra centromeres modify 3D architecture of interphase nuclei. The location of Bs in meiosis appeared not to be random, and unpaired Bs had a tendency to form a common compartment with unpaired part of the sex bivalent, and thus avoided pachytene check point.

7. The Effects of B-Chromosomes

Apart from few exceptions, Bs do not cause visible phenotypic manifestations at individual level. This makes the search for observable effects in mammals rather difficult. But even such a small amount of data, together with new findings of genes on Bs, raises objections to the idea of Bs genetic inertness. It has been found that Bs presence influences cell division, degree of recombination, development, some quantitative characteristics, host-parasite interactions and behaviour.

A new and interesting data came from three-dimensional studies of Bs behaviour during division in both somatic and germ cells. Kociucka et al. [216] studied three-dimensional positioning of B chromosomes in fibroblast nuclei of the red fox and the Chinese raccoon dog, and found that small Bs of the red fox are dominantly positioned in the interior of the nucleus, while the medium-sized Bs of the Chinese raccoon dog are in the peripheral area of the nucleus as well as in intermediate and interior locations. The data was in agreement with the chromosome size dependent theory [216]. But in the nuclei of the Korean field mouse all Bs, irrespective of their size, were located on nuclear periphery in common compartments with C-positive regions of A chromosomes [202]. They suppose that, at least for the Bs of the Korean field mouse, the DNA content is more important parameter that determines where Bs will be located inside the nucleus.

As we pointed earlier, Basheva et al. [43] proved that in the silver fox recombination occurs between B chromosomes which increases variability in the specimens that carry them. In earlier studies, the presence of B chromosomes was associated with increased chiasma frequency in Bailey's pocket mouse, *C. baileyi* [207] and *R. fuscipes* [199]. In both species this increase is not influenced by the number of Bs yet only by their presence.

Gileva [211] recorded a reduction of body and skull sizes in *D. torquatus* that carry numerous Bs, and proposed that this could be reflected as a negative selective value in extreme climate conditions.

Positive correlations between number of Bs and body weight were established in males of two species: *N. p. viverinus* [217] and *A. flavicollis* [62,218]. Effects of Bs presence are extensively studied in *A. flavicollis* and, in general, it was found that they influence the development of some morphometric characters, mostly cranial ones [140]. One of the two regions of the mandible shows almost a triple increase in intensity of integration in B carriers [219]. Furthermore, the maintenance of Bs in the same species was studied by examining their effects on 3 components of cranial variability: canalization, developmental stability, and morphological integration. It was suggested that B carriers follow different developmental pathway for generating covariations of cranial traits [220]. This specific developmental pathway is more sensitive to modifications caused by natural selection, which could be beneficial to B carriers under variable environmental conditions. It was previously established that reaction of animals with Bs to environmental changes differ from those without them [221]. Nonmetric traits analyses show that the population density influences, at the same time, both the variation in the frequency of specimens with Bs and the developmental homeostasis.

Adnađević et al. [222], by analysing effect of recorded endoparasites and parasite life-cycle stages in *A. flavicollis* on expression levels of genes *MHC II-DRB*, *IL-10* and *Tgf-β*, found that the presence of Bs is associated with lower expression level of *Tgf-β* gene. Although the influence of host genetic background on parasite infection has already been well established, this is the first study in mammals that correlates presence of Bs with immune response. Curiously enough, the presence of Bs in this species plays an important role in infrapopulations of their certain endoparasites by shifting sex balance to higher proportion of males [223].

Shellhammer [144] from studies on *R. megalotis* was the first to propose that Bs could have an effect on behaviour. The behaviour and the presence of Bs were connected in foxes through a series of experimental crosses [224–226]. It appeared that groups of foxes selected for specific behaviour differs significantly in frequency of mosaics for Bs.

8. Maintenance of B Chromosomes

The mostly discussed question about Bs during a century of research was the way they are maintained in populations through time. Two schools of thought grouped around two models giving opposite explanations of the way Bs are retained in natural populations. Both models assume that the frequency of specimens with Bs in population is at equilibrium but the explanations how this equilibrium is reached and kept are different. The model firstly named parasitic and then selfish [227] claims that Bs are maintained by balance of accumulation and elimination due to detrimental effects. Contrary to this, the heterotic model [228] suggests that, in the absence of mechanism of accumulation, a small number of Bs could offer an adaptive advantage to carriers, while a large number could be harmful. Currently, the parasitic model is predominant, mostly because the search for adaptive significance of Bs was mostly ineffective. Furthermore, the convergence of this paradigm partly comes from the popular theory of selfish or parasitic DNA, irresistible to some scientists. The number of cases with proved Bs accumulation, which is prerequisite for parasitic model, although larger than the number of cases without accumulation, is still very small in comparison with the known number of species with Bs. For instance, the accumulation of Bs was studied in about 70 plant species and among them 42 (60%) manifested accumulation mechanism [4] which makes only 3.4% of plant species with Bs. Furthermore, detailed studies are largely directed on commercially important species that possess Bs, like maize and rye, and pests such as grasshoppers, so the number of extensively studied species groups is rather small. In attempt to include species without mechanism of Bs accumulation into parasitic model, Camacho et al. [229] proposed that all Bs are initially parasitic, and later on, through arm race with A genome, may become neutral. From this stage they can disappear or become parasitic again. One of their arguments against heterotic Bs is that it is unexpected that Bs could be beneficial in the first step, so a drive is necessary to establish themselves in population. Yet, if Bs appear simultaneously in population, these arguments are not plausible. Therefore, when models are assessed it is not good to stay frozen within a particular paradigm.

Temporal analyses of B frequency and transmission in mammals are scarce. The frequency of animals with Bs was the same in two successive years in *Rattus rattus diardi* [100]. During 8 years of study, equilibrium frequencies of Bs in populations of *A. flavicollis* at one locality were maintained in spite of fluctuations in population density [11,230]. Zima and Macholan [62] and Wojcik et al. [138] also found the equilibrium during a three-year study in the same species. Contrary to stable frequency from year to year, seasonal changes in frequency of animals with Bs could escape from equilibrium in stress situations [231] or could keep it when there is no tough competition present [232]. Thus, though frequencies of Bs could significantly differ through a year, their values stay the same between years [230].

B chromosome frequencies in *A. peninsulae* show temporal variation. Comparison of Bs from the population from Altai Republic, trapped in the 1980 and 2002 showed that a mean number of Bs in this population increased almost threefold in the period of 22 years [200]. This increase was mainly due to the rise of numbers of small and large bi-armed Bs (by factors of 7.0 and 5.3, respectively) and a slight increase in the number of medium-sized biarmed B chromosomes (by a factor of 1.6). Nonetheless, Borisov et al. [233] found that the number of Bs and theirs morphotypes were stable over the period of 30 years in certain populations.

Direct or indirect evidences for B drive in mammals are provided for seven species only: *C. baileyi* [208], *V. vulpes* [209], *R. rattus* [212,213], *D. torquatus* [211], *R. fuscipes* [97], *A. peninsulae* [197], and *T. triton* [121]. In 3 of them, B drive is operating in females thus supporting the theory of centromeric drive [214]. Thomson [97] showed that the maintenance of Bs in *R. fuscipes* supports the parasitic model very well.

The maintenance of Bs in populations can be explained in terms of their contribution to overall genetic diversity of the species possessing them, and it might be arguable under the heterotic model [142]. The increased variability widens the probability that species will survive in changing environmental situations. In *A. flavicollis*, an increased frequency of animals with Bs is found in more extreme climatic conditions [141]. Frequency of B chromosomes and quality of habitat are negatively correlated indicating that B chromosomes in this species are mentioned due to the effects that they exert at the level of populations [143]. Possible adaptive effects of Bs were also postulated by Blagojević et al. [234] upon comparison of head morphology in three populations of this species that have Bs at different frequencies. Adnađević et al. [235], by using amplified fragment length polymorphism (AFLP) markers, made a comparison of populations of *A. flavicollis* settled in ecologically distinct habitats differing in frequency of Bs, and found that the greatest genetic diversity is in the population settled in optimal conditions for this species featured by the lowest frequency of animals with Bs. The majority of loci that are subject of directional selection, feature either population with lower or with a higher frequency of Bs. They suggested that the different frequency of B carriers in populations is related to adaptive differentiation to diverse habitats. Tokarskaia et al. [45] found that the presence of Bs is positively correlated with heterozygosity for random amplification of polymorphic DNA (RAPD) loci, in populations of the Siberian roe deer, *C. pygargus*, thus indicating influence of Bs on the genetic variation of the species. All these findings support the heterotic model of Bs maintenance.

Theoretically, inbreeding is harmful to parasitic Bs but beneficial to mutualistic ones. Social organization of rodent populations and some other mammalian groups supports inbreeding which opens new possibilities for the existence of beneficial Bs.

Extensive population studies of two species of the same genus *Apodemus* best illustrate that the present models do not exclude each other but rather call for further adjustments. If we try to fit the maintenance of Bs in *A. peninsulae* and *A. flavicollis* into the current models, *A. peninsulae* will follow the parasitic (or selfish) model, while Bs in *A. flavicollis* will better fit into heterotic model. But when we go into details, it seems that neither *A. peninsulae* nor *A. flavicollis* fit quite well into proposed models. *A. peninsule* do not have populations at equilibrium and tolerance for Bs is so great that it is not easy to say when Bs become detrimental. Furthermore, five different types of Bs present in this species, have different outcomes. Some types are inherited in almost a Mendelian fashion. On the other hand, Bs

in *A. flavicollis* brings adaptive advantage in certain situations and in some environments. In other situations (and environments) they could be neutral or deleterious. Therefore, it could be hypothesized that the adaptive advantage of these Bs is not general, but it is dependent on events through which the individual or population is passing. The existing models need to be very much adjusted, but the adjustment must be based on detailed and intensive studies in natural populations.

9. Conclusions

After more than a century, it appears that B chromosomes research suffers from an unbalanced approach. That is also true for research of Bs in mammals. Population studies are a very difficult task and are still largely avoided. Even rarer attempts are made to resolve effects of Bs in different species that carry them. While molecular breaks into DNA composition of Bs are rapidly increasing, the number of species included in them is still scarce. Namely, a more detailed molecular composition is known for only six mammalian species. Although the confirmed presence of genes on Bs, in all cases, disproved the claims that Bs are inert, the gathered knowledge and data are not sufficient to explain the significance of Bs to their carriers. Are the paths of evolution of As and Bs opposite, or do the lanes of the same highway promise a greater success in adapting to environmental changes? This is yet to be resolved, but the answer seems to be inclining towards the latter statement.

References

1. Wilson, E.B. Studies on chromosomes. V. The chromosomes of Metapodius. A contribution to the hypothesis of the genetic continuity of chromosomes. *J. Exp. Zool.* **1906**, *6*, 147–205. [CrossRef]
2. Hayman, D.L.; Martin, P.G. Supernumerary chromosomes in the marsupial *Schoinobates volans* (Ker). *Aust. J. Biol. Sci.* **1965**, *18*, 1081–1082. [CrossRef] [PubMed]
3. Moore, J.W.; Elder, R.L. Chromosome of the fox. *J. Hered.* **1965**, *56*, 142–143. [CrossRef]
4. Jones, R.N. B chromosomes in plants. *New Phytol.* **1995**, *131*, 411–434. [CrossRef]
5. D'Ambrosio, U.; Alonso-Lifante, M.P.; Barros, K.; Kovařík, A.; Mas de Xaxars, G.; Garcia, S. B-chrom: A database on B-chromosomes of plants, animals and fungi. *New Phytol.* **2017**. [CrossRef] [PubMed]
6. Jones, N. New species with B chromosomes discovered since 1980. *Nucleus* **2017**, *60*, 263–281. [CrossRef]
7. Rice, A.; Glick, L.; Abadi, S.; Einhorn, M.; Kopelman, N.M.; Salman-Minkov, A.; Mayzel, J.; Chay, O.; Mayrose, I. The chromosome counts database (CCDB)—A community resource of plant chromosome numbers. *New Phytol.* **2015**, *206*, 19–26. [CrossRef] [PubMed]
8. Volobujev, V.T. The B-chromosome system of mammals. *Genetica* **1980**, *52/53*, 333–337. [CrossRef]
9. Volobujev, V.T. The B-chromosome system of the mammals. *Caryologia* **1981**, *34*, 1–23. [CrossRef]
10. Vujošević, M. B-chromosomes in mammals. *Genetika* **1993**, *25*, 247–258.
11. Vujošević, M.; Blagojević, J. B chromosomes in populations of mammals. *Cytogenet. Genome Res.* **2004**, *106*, 247–256. [CrossRef] [PubMed]
12. Trifonov, V.A.; Dementyeva, P.V.; Beklemisheva, V.R.; Yudkin, D.V.; Vorobieva, N.V.; Graphodatsky, A.S. Supernumerary chromosomes, segmental duplications, and evolution. *Russ. J. Genet.* **2010**, *46*, 1094–1096. [CrossRef]
13. Wilson, D.E.; Reeder, D.M. *Mammal Species of the World: A Taxonomic and Geographic Reference*, 2nd ed.; Smithsonian Institutions: Washington, DC, USA; London, UK, 1993; pp. 1–12, ISBN 1-56098-217-9.

14. Burgin, C.J.; Colella, J.P.; Kahn, P.L.; Upham, N.S. How many species of mammals are there? *J. Mammal.* **2018**, *99*, 1–14. [CrossRef]

15. Diploid Numbers of Mammalia. Available online: http://www.bionet.nsc.ru/labs/chromosomes/mammalia.htm (accessed on 25 July 2018).

16. Patton, J.L.; Sherwood, S.W. Genome evolution in pocket gophers (Genus *Thomomys*) I. Heterochromatin variation and speciation potential. *Chromosoma* **1982**, *85*, 149–162. [CrossRef] [PubMed]

17. Liehr, T.; Mrasek, K.; Kosyakova, N.; Ogilvie, C.M.; Vermeesch, J.; Trifonov, V.; Rubtsov, N. Small supernumerary marker chromosomes (sSMC) in humans; are there B chromosomes hidden among them. *Mol. Cytogenet.* **2008**, *1*, 12. [CrossRef] [PubMed]

18. Baverstock, P.R.; Wats, C.H.S.; Hogarth, J.T. Heterochromatin variation in Australian rodent *Uromys caudimaculatus*. *Chromosoma* **1976**, *59*, 397–403. [CrossRef]

19. Nachman, M.W. Geographic patterns of chromosomal variation in South American marsh rats, *Holochilus brasiliensis* and H. vulpinus. *Cytogenet. Cell Genet.* **1992**, *61*, 10–17. [CrossRef] [PubMed]

20. Kartavtseva, I.V.; Pavlenko, M.V. Chromosome Variation in the Striped Field Mouse *Apodemus agrarius* (Rodentia, Muridae). *Rus. J. Genet. C/C Genet.* **2000**, *36*, 162–174.

21. Hewitt, G.M. Orthoptera. In *Animal cytogenetics. 3. Insecta 1 Orthoptera*; John, B., Ed.; Gebr. Borntrager: Berlin, Germany, 1979; pp. 1–170.

22. Hayman, D.L.; Martin, P.G.; Waller, P.F. Parallel mosaicism of supernumerary chromosomes and sex chromosomes in *Echymipera kalabu* (Marsupialia). *Chromosoma* **1969**, *27*, 371–380. [CrossRef] [PubMed]

23. McQuade, L.R.; Hill, R.J.; Francis, D. B-chromosome systems in the greater glider, *Petauroides volans* (Marsupialia: Pseudocheiridae). *Cytogenet. Genome Res.* **1994**, *66*, 155–161. [CrossRef] [PubMed]

24. Atanassov, I.N.; Chassovnikarov, T.G. Karyotype characteristics of *Crocidura leucodon* Herman, 1780 and *Crocidura suaveolens* Pallas, 1811 (Mammalia: Insectivora: Soricidae) in Bulgaria. *Acta Zool. Bulg.* **2008**, *2*, 71–78.

25. Ruedi, M.; Maddalena, T.; Yong, H.; Vogel, P. The Crocidura fuliginosa species complex (Mammalia: Insectivora) in peninsular Malaysia: Biological, karyological and genetical evidence. *Biochem. Syst. Ecol.* **1990**, *18*, 573–581. [CrossRef]

26. Meylan, A.; Hausser, J. Position citotaxonomique de quelques museragines du genere *Crocidura* au Tessisn (Mammalia: Insectivora). Origine du dessin dentarie "*Apodemus*" (Rodentia, Mammalia). *CR Acad. Sci. Paris* **1974**, *264*, 711.

27. Motokawa, M.; Wu, Y.; Harada, M. Karyotypes of six Soricomorph species from Emei Shan, Sichuan Province, China. *Zool. Sci.* **2009**, *26*, 791–797. [CrossRef] [PubMed]

28. Obara, Y.; Tomiyasu, T.; Saitoh, K. Chromosome studies in the Japanese vespertilionid bats. I. Karyotypic variation in *Myotis macrodactylus* Temmink. *Jpn. J. Genet.* **1976**, *51*, 201–206. [CrossRef]

29. Volleth, M. Comparative analysis of the banded karyotypes of the European *Nyctalus* species (Vespertilionidae, Chiroptera). In *Prague Studies in Mammology*; Horáček, I., Vohralík, V., Eds.; Charles University Press: Prag, Czech Republic, 1992; pp. 221–226.

30. Bhatnagar, V.S.; Srivastava, M.D.L. Somatic chromosomes of four common bats of Allahabad. *Cytologia* **1974**, *39*, 327–334. [CrossRef] [PubMed]

31. Yunis, E.J.; De Caballero, O.M.T.; Ramirez, C.; Ramirez, Z.E. Chromosomal variations in the Primate *Alouatta seniculus seniculus*. *Folia Primatol.* **1976**, *25*, 215–224. [CrossRef] [PubMed]

32. Vassart, M.; Guedant, A.; Vie, J.C.; Keravec, J.; Seguela, A.; Volobouev, V.T. Chromosomes of *Alouatta seniculus* (Platyrrhini, Primates) from French Guiana 331–334. *J. Hered.* **1996**, *87*, 331–334. [CrossRef] [PubMed]

33. Oliveira, E.H.C.; De Lima, M.M.C.; Sbaloqueuro, I.J.; Dasvila, A.F. Analysis of polimorphic NORs in *Alouatta* species (Primates, Atelidae). *Caryologia* **1999**, *52*, 169–175. [CrossRef]

34. Walzer, S.M.D.; Breau, G.; Gerald, P.S. A chromosome survey of 2400 normal new born. *J. Pediatr.* **1969**, *74*, 438–448. [CrossRef]

35. Huang, B.; Crolla, J.A.; Christian, S.L.; Wolf-Ledbetter, M.E.; Macha, M.E.; Papenhausen, P.N.; Ledbetter, D.H. Refined molecular characterization of the breakpoints in small inv dup(15) chromosomes. *Hum. Genet.* **1997**, *99*, 11–17. [CrossRef] [PubMed]

36. Hsu, T.C.; Benirschke, K. *An Atlas of Mammalian Chromosomes 4*; Springer: Berlin, Germany, 1970; p. 178.

37.　Pieńkowska-Schelling, A.; Schelling, C.; Zawada, M.; Yang, F.; Bugno, M.; Ferguson-Smith, M. Cytogenetic studies and karyotype nomenclature of three wild canid species: Maned wolf (*Chrysocyon brachyurus*), bat-eared fox (*Otocyon megalotis*) and fennec fox (*Fennecus zerda*). *Cytogenet. Genome Res.* **2008**, *121*, 25–34. [CrossRef] [PubMed]

38.　Makinen, A.; Fredga, K. Banding analyses of the somatic chromosomes of raccoon dogs, *Nyctereutes procyonides*, from Finland. In Proceedings of the 4th Colloquium on the Cytogenetics of Domestic Animals, Uppsala, Sweden, 10–13 June 1980; pp. 420–430.

39.　Ward, O.G. Chromosomes studies in Japanese raccoon dogs: X chromosomes, supernumeraries, and heteromorphism. *MCN* **1984**, *25*, 34.

40.　Mäkinen, A.; Lohi, O.; Juvonen, M. Supernumerary chromosome in the chromosomally polymorphic blue fox, *Alopex lagopus*. *Hereditas* **1981**, *94*, 277–279. [CrossRef]

41.　Bhatnagar, V.S. Microchromosomes in the somatic cells of *Vulpes bengalensis* Shaw. *Chromosom. Inf. Serv.* **1973**, *15*, 32.

42.　Chiarelli, A.B. The chromosomes of the Canidae. In *Wild Canids Their Systematic Behaviour Ecology and Evolution*; Fox, M.W., Ed.; Van Nonstrand Reinhold: New York, NY, USA, 1975; pp. 40–53.

43.　Basheva, E.A.; Torgasheva, A.A.; Sakaeva, G.R.; Bidau, C.; Borodin, P.M. A- and B-chromosome pairing and recombination in male meiosis of the silver fox (*Vulpes vulpes* L., 1758, Carnivora, Canidae). *Chromosom. Res.* **2010**, *18*, 689–696. [CrossRef] [PubMed]

44.　Neitzel, H. Chromosome evolution of Cervidae: Karyotypic and molecular aspects. In *Cytogenetics*; Obe, G.B.A., Ed.; Springer: Berlin, Germany, 1987; pp. 90–112.

45.　Tokarskaia, O.N.; Efremova, D.A.; Kan, N.G.; Danilkin, A.A.; Sempere, A.; Petrosian, V.G.; Semenova, S.K.; Ryskov, A.P. Variability of multilocus DNA markers in populations of the Siberian (*Capreolus pygargus* Pall.) and European (*C. capreolus* L.) roe deer. *Genetika* **2000**, *36*, 1520–1530. [PubMed]

46.　Aquino, C.I.; Abril, V.V.; Duarte, J.M.B. Meiotic pairing of B chromosomes, multiple sexual system, and Robertsonian fusion in the red brocket deer *Mazama americana* (Mammalia, Cervidae). *Genet. Mol. Res.* **2013**, *12*, 3566–3574. [CrossRef] [PubMed]

47.　Duarte, J.M.B.; Jorge, W. Chromosomal polymorphism in several populations of deer (Genus Mazama) from Brazil. *Arch. Zootec.* **1996**, *45*, 281–287.

48.　Duarte, J.M.B.; Jorge, W. Morphologic and cytogenetic description of the small red brocket (*Mazama bororo* Duarte, 1996) in Brazil. *Mammalia* **2003**, *67*, 403–410. [CrossRef]

49.　Valeri, M.P.; Tomazella, I.M.; Duarte, J.M.B. Intrapopulation Chromosomal Polymorphism in *Mazama gouazoubira* (Cetartiodactyla; Cervidae): The Emergence of a New Species? *Cytogenet. Genome Res.* **2018**. [CrossRef] [PubMed]

50.　Rossi, R.V.; Bodmer, R.; Duarte, J.M.B.; Trovati, R.G. Amazonian brown brocket deer *Mazama nemorivaga* (Cuvier 1817). In *Neotropical Cervidology: Biology and Medicine of Latin American Deer*; Duarte, J.M.B., Gonzalez, S., Eds.; Funep: Jaboticabal, Brazil; IUCN: Gland, Switzerland, 2010; pp. 202–210, ISBN 978-85-7805-046-7.

51.　Abril, V.V.; Duarte, J.M.B. Chromosome polymorphism in the Brazilian dwarf brocket deer, *Mazama nana* (Mammalia, Cervidae). *Genet. Mol. Biol.* **2008**, *31*, 53–57. [CrossRef]

52.　Fiorillo, B.F.; Sarria-Perea, J.A.; Abril, V.V.; Duarte, J.M.B. Cytogenetic description of the Amazonian brown brocket *Mazama nemorivaga* (Artiodactyla, Cervidae). *Comp. Cytogenet.* **2013**, *7*, 25–31. [CrossRef] [PubMed]

53.　Sokolov, V.E.; Prikhodko, I.V. Taxonomy of the musk deer moschus-moschiferus (Artiodactyla, Mammalia). *Izv. Akad. Nauk SSSR. Ser. Biol.* **1998**, *1*, 37–46.

54.　Castiglia, R.; Makundi, R.; Corti, M. The origin of an unusual sex chromosome constitution in *Acomys sp.* (Rodentia, Muridae) from Tanzania. *Genetica* **2007**, *131*, 201–207. [CrossRef] [PubMed]

55.　Castiglia, R.; Annesi, F. Cytotaxonomic considerations on the sex chromosome variation observed within *Acomys ngurui* Verheyen et al. 2011 (Rodentia Muridae). *Zootaxa* **2012**, *3493*, 35–38.

56.　Lobato, L.; Cantos, G.; Araujo, B.; Bianchi, N.O.; Merani, S. Cytogenetics of the South American akodont rodents (Cricetidae) X. *Akodon mollis*: A species with XY females and B chromosomes. *Genetica* **1982**, *57*, 199–205.

57.　Yonenaga-Yassuda, Y.; Assis, M.F.L.; Kasahara, S. Variability of the nucleolus organizer regions and the presence of the rDNA genes in the supernumerary chromosome of *Akodon aff. arviculoides* (Cricetidae, Rodentia). *Caryologia* **1992**, *45*, 163–174. [CrossRef]

58. Hass, I.; Soares, A.; Balieiro, P.; Miranda, M.L.P.; Alegri, C.K.; Dornelles, S.S.; Marques, D.; Sbalqueiro, I.J. *Akodon montensis* karyotype variability, in a sample of São Francisco do Sul—SC, arising 0–3 supernumerary chromosomes. In Proceedings of the 60 °Congresso Brasileiro de Genética, Guarujá, Brazil, 26–29 August 2014.

59. Kartavtseva, I.V. Description of B-chromosomes in karyotype of field mouse *Apodemus agrarius*. *Tsitol. Genet.* **1994**, *28*, 96–97. [PubMed]

60. Obara, Y.; Sasaki, S. Fluorescent approaches on the origin of B chromosomes of *Apodemus argenteus* hokkaidi. *Chrom. Sci.* **1997**, *1*, 1–5.

61. Soldatović, B.; Savić, I.; Seth, P.; Reichstein, H.; Tolksdorf, M. Comparative karyological study of the genus *Apodemus*. *Acta Vet.* **1975**, *25*, 1–10.

62. Zima, J.; Macholán, M. B chromosomes in the wood mice (genus *Apodemus*). *Acta Theriol.* **1995**, *40* (Suppl. 3), 75–86. [CrossRef]

63. Belcheva, R.G.; Topashka-Ancheva, M.N.; Atanassov, N. Karyological studies of five species of mammals from Bulgarian fauna. *Comptes Rendus l'Académie Bulg. des Sci.* **1988**, *42*, 125–128.

64. Hayata, J. Chromosomal polymorphism caused by supernumerary chromosomes in field mouse, *Apodemus giliacus*. *Chromosoma* **1973**, *42*, 403–414. [CrossRef] [PubMed]

65. Borisov, Y.M.; Afanasev, A.G.; Lebedev, T.T.; Bochkarev, M.N. Multiplicity of B microchromosomes in a Siberian population of mice *Apodemus peninsulae* (2n = 48 + 4–30 B chromosomes). *Russ. J. Genet.* **2010**, *46*, 705–711. [CrossRef]

66. Vujošević, M.; Živković, S. Numerical chromosome polymorphism in *Apodemus flavicollis* and *A. sylvaticus* (Mammalia: Rodentia) caused by supernumerary chromosomes. *Acta Vet.* **1987**, *37*, 81–92.

67. Gadi, I.K.; Sharma, T.; Raman, R. Supernumerary chromosomes in *Bandicota indica nemorivaga* and a female individual with XX/X0 mosaicism. *Genetica* **1982**, *58*, 103–108. [CrossRef]

68. Badenhorst, D.; Herbreteau, V.; Chaval, Y.; Pagès, M.; Robinson, T.J.; Rerkamnuaychoke, W.; Morand, S.; Hugot, J.P.; Dobigny, G. New karyotypic data for Asian rodents (Rodentia, Muridae) with the first report of B-chromosomes in the genus Mus. *J. Zool.* **2009**, *279*, 44–56. [CrossRef]

69. Ventura, K.; Sato-Kuwabara, Y.; Fagundes, V.; Geise, L.; Leite, Y.L.R.; Costa, L.P.; Silva, M.J.J.; Yonenaga-Yassuda, Y.; Rodrigues, M.T. Phylogeographic structure and karyotypic diversity of the Brazilian shrew mouse (*Blarinomys breviceps*, Sigmodontinae) in the Atlantic forest. *Cytogenet. Genome Res.* **2012**, *138*, 19–30. [CrossRef] [PubMed]

70. Patton, J.L. A complex system of chromosomal variation in the pocket mouse, *Perognathus baileyi* Merriam. *Chromosoma* **1972**, *36*, 241–255. [CrossRef] [PubMed]

71. Volobouev, V.T.; Sicard, B.; Aniskin, V.M.; Gautun, J.C.; Granjon, L. Robertsonian polymorphism, B chromosomes variation and sex chromosomes heteromorphism in the african water rat *Dasymys* (Rodentia, Muridae). *Chromosome Res.* **2000**, *8*, 689–697. [CrossRef] [PubMed]

72. Ramos, R.S.L.; Vale, W.G.; Assis, F.L. Karyotypic analysis in species of the genus *Dasyprocta* (Rodentia: Dasyproctidae) found in Brazilian Amazon. *An. Acad. Bras. Cienc.* **2003**, *75*, 55–69. [CrossRef] [PubMed]

73. Van Wynsberghe, N.R.; Engstrom, M.D. Chromosomal variation in collared lemmings (*Dicrostonyx*) from the western Hudson Bay region. *Musk-Ox* **1992**, *39*, 203–209.

74. Gileva, E.A. B-chromosomes, unusual inheritance of sex chromosomes and sex ratio in the varying lemming, *Dicrostonyx torquatus* Pall. (1779). *Proc. Natl. Acad. Sci. USA* **1973**, *213*, 952–955.

75. Chernyavsky, F.B.; Kozlovsky, A.I. Species status and history of the Arctic lemming (*Dicrostonyx*, Rodentia) of Wrangel Island. *Zoo. Zhurnal* **1980**, *59*, 266–273. (In Russian)

76. Rao, K.S.; Aswathanrayana, N.V.; Prakash, K.S. Supernumerary (B) chromosomes in Indian bush rat *Golunda ellioti* (Gray). *MCN* **1979**, *20*, 79.

77. Roche, J.; Capanna, E.; Civitelli, M.; Ceraso, A. caryotypes des rongeurs de Somalie. *Monit. Zool. Ital. Suppl.* **1984**, *19*, 259–277. [CrossRef]

78. Civitelli, M.V.; Consentino, P.; Capanna, E. Inter- and intra-individual chromosome variability in *Thamnomys* (*Grammomys*) *gazellae* (Rodentia, Muridae) B-chromosomes and structural heteromorphisms. *Genetica* **1989**, *79*, 93–105. [CrossRef] [PubMed]

79. Freitas, T.R.O.; Mattevi, M.S.; Oliveira, L.F.B.; Souza, M.J.; Yonenaga-Yassuda, Y.; Salzano, F.M. Chromosome relationship in three representatives of the genus *Holochilus* (Rodentia, Cricetidae) from Brazil. *Genetica* **1983**, *61*, 13–20. [CrossRef]

80. Vidal, O.R.; Riva, R.; Baro, N. Los cromosomas. del genero *Holochilus*. 1. Polimorfismo en *H. chacarius* Thomas (1906). *Phys. (B. Aires) Ser. C* **1976**, *35*, 75–85.

81. Sangines, N.; Aguilera, M. Chromosome polymorphism in *Holochilus venezuelae* (Rodentia: Cricetidae): C- and G-bands. *Genome* **1991**, *34*, 13–18. [CrossRef]

82. Baverstock, P.R.; Wats, C.H.S.; Hogarth, J.T. Chromosome evolution in Australian Rodents. I. The Pseudomyinae, the Hydrmyinae and the *Uromys/Melomys* group. *Chromosoma* **1977**, *61*, 95–125. [CrossRef] [PubMed]

83. Denys, C.; Lalis, A.; Aniskin, V.; Kourouma, F.; Soropogui, B.; Sylla, O.; Doré, A.; Koulemou, K.; Beavogui, Z.B.; Sylla, M.; et al. New data on the taxonomy and distribution of Rodentia (Mammalia) from the western and coastal regions of Guinea West Africa. *Ital. J. Zool.* **2009**, *76*, 111–128. [CrossRef]

84. Denys, C.; Lalis, A.; Lecompte, É.; Cornette, R.; Moulin, S.; Makundi, R.H.; Machang'u, R.S.; Volobouev, V.; Aniskine, V.M. A faunal survey in Kingu Pira (south Tanzania), with new karyotypes of several small mammals and the description of a new Murid species (Mammalia, Rodentia). *Zoosystema* **2011**, *33*, 5–47. [CrossRef]

85. Baverstock, P.R.; Watts, C.H.S.; Adams, M.; Gelder, M. Chromosomal and electrophorectic studies of Australian *Melomys* (Rodentia:Muridae). *Aust. J. Zool.* **1980**, *28*, 553–574. [CrossRef]

86. Kovalskaja, Y.M. B-chromosomes and XO-males in narrow-skulled vole, *Microtus/Stenocranius/gregalis* from North Mongolia. In Proceedings of the 7th All-Union Conference, Nalchik, Sverdlovsk, Russia; 1988; Volume 1, pp. 73–74.

87. Judd, S.R.; Cross, S.P. Chromosomal variation in *Microtus longicaudus* (Merriam). *Murrelet* **1980**, *61*, 2–5. [CrossRef]

88. Gropp, A.; Marshall, J.; Markvong, A. Hriomosomal findings in the spiny mice of Thailand (genus *Mus*) and occurrence of a complex intraspecific variation in *M. shortridgei*. *Z. Saugetierkd.* **1973**, *38*, 159–168.

89. Ivanitskaya, E.; Sözen, M.; Rashkovetsky, L.; Matur, F.; Nevo, E. Discrimination of 2n = 60 *Spalax leucodon* cytotypes (Spalacidae, Rodentia) in Turkey by means of classical and molecular cytogenetic techniques. *Cytogenet. Genome Res.* **2008**, *122*, 139–149. [CrossRef] [PubMed]

90. Maia, V.; Yonenaga-Yassuda, Y.; Freitas, T.R.O.; Kasahara, S.; Sune-Mattevi, M.; Oliviera, L.F. Supernumerary chromosomes, Robertsonian rearrangement and variability of the sex chromosomes in scaly-footed water rat *Nectomys squamipes* (Cricetidae, Rodentia). *Genetica* **1984**, *63*, 121–128. [CrossRef]

91. Yonenaga-Yassuda, Y.; do Prado, C.R.; Mello, D.A. Supernumerary chromosomes in *Holochilus brasiliensis* and comparative cytogenetic analysis with *Nectomys squamipes* (Cricetidae, Rodentia). *Rev. Bras. Genet.* **1987**, *X*, 209–220.

92. Andrades-Miranda, J.; Oliveira, L.F.B.; Zanchin, N.I.T.; Mattevi, M.S. Chromosomal description of the rodent genera *Oecomys* and *Nectomys* from Brazil. *Acta Theriol.* **2001**, *46*, 269–278. [CrossRef]

93. Myers, P.; Carleton, M.D. The species *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixime ou Rat Tarse Noir". *Publ. Mus. Univ. Mich.* **1981**, *161*, 1–141.

94. Sbalqueiro, I.J.; Mattevi, M.S.; Oliveira, L.F.B.; Solano, M.J.V. B chromosome system in populations of *Oryzomys flavescens* (Rodentia, Cricetidae) from southern Brazil. *Acta Theriol. (Warsz)* **1991**, *36*, 193–199. [CrossRef]

95. Contrafatto, G.; Meester, J.; Bronner, G.; Taylor, P.J.; Willan, K. Genetic variation in the african rodent sub-family Otomyinae (Muridae). iv: Chromosome G-banding analysis of *Otomys irroratus* and *O. angoniensis*. *Isr. J. Zool.* **1992**, *38*, 277–291.

96. Barros, R.M.S. *Variabilidade Cromossômica em Proechimys e Oryzomys (Rodentia) do Amazonas*; Universidade de São Paulo: São Paulo, Brazil, 1978.

97. Thomson, R.L. B chromosomes in *Rattus fuscipes* II. The transmission of B chromosomes to offspring and population studies: Support for the "parasitic" model. *Heredity* **1984**, *52*, 363–372. [CrossRef]

98. Yosida, T.H. Studies on the karyotype differentiation of the Norway rat. *Proc. Jpn. Acad.* **1986**, *62*, 65–68. [CrossRef]

99. Wahrman, J.; Gourevitz, P. The chromosome biology of the 2n = 38 black rat, *Rattus rattus*. In *Chromosomes Today 4*; Wahrman, J., Lewis, K.R., Eds.; John Wiley and Sons: New York, NY, USA, 1973; pp. 433–434.

100. Yong, H.S.; Dhaliwal, S.S. Supernumerary (B-) chromosomes in the Malayan house rat, *Rattus rattus* diardii (Rodentia, Muridae). *Chromosoma* **1972**, *36*, 256–262. [CrossRef] [PubMed]

101. Ladron de Guevara, R.G.; de la Guardia, R.D. Frequency of chromosome polymorphism for pericentric inversions and B-chromosomes in Spanish populations of *Rattus rattus frugivorus*. *Genetica* **1981**, *57*, 99–103. [CrossRef]

102. Yosida, T.H. Population survey of B-chromosomes in black rat. *Ann. Rep. Nat. Inst. Genet.* **1976**, *26*, 33.

103. Gropp, A.; Marshall, J.; Flatz, G.; Olbrich, M.; Manyanondha, K.; Santadust, A. Chromosomenpolymorphismus durch uberzahuge Autosomen Beobachtungen an der hausratte (*R. rattus*). *Z. Saugetierkd.* **1970**, *35*, 363–371.

104. Baverstock, R.P.; Watts, S.C.H.; Hogarth, T.J.; Robinson, C.A.; Robinson, J.F. Chromosome evolution in Australian rodents. II. The Rattus group. *Chromosoma* **1977**, *61*, 227–241. [CrossRef] [PubMed]

105. Blanks, G.A.; Shellhammer, H.S. Chromosome polymorphism in California populations of harvest mice. *J. Mammal.* **1968**, *49*, 726–731. [CrossRef]

106. Robbins, L.W. Sex chromosome polymorphisms in *Reithrodontomys montanus* (Rodentia: Cricetidae). *Southwest. Nat.* **1981**, *26*, 201–202. [CrossRef]

107. Zimmerman, E.G. Karyology, systematics and chromosomal evolution in the rodent genus *Sigmodon*. *Michigan State Univ. Publ. Mus. Biol. Ser.* **1970**, *4*, 385–394.

108. Silva, M.J.J.; Yonenaga-Yassuda, Y. B chromosomes in Brazilian rodents. *Cytogenet. Genome Res.* **2004**, *106*, 257–263. [CrossRef] [PubMed]

109. Suárez-Villota, E.; Di-Nizo, C.; Neves, C.; de Jesus Silva, M.J. First cytogenetic information for *Drymoreomys albimaculatus* (Rodentia, Cricetidae), a recently described genus from Brazilian Atlantic Forest. *Zookeys* **2013**, *303*, 65–76.

110. Gordon, D.H. Discovery of another species of tree rat. *Transvaal Museum Bull.* **1987**, *22*, 30–32.

111. Gordon, D.H.; Rautenbach, I.L. Species complexes in medically important rodents: Chromosome studies of *Aethomys*, *Tatera* and *Saccostomus* (Rodentia: Muridae, Cricetidae). *S. Afr. J. Sci.* **1980**, *76*, 559–561.

112. Hafner, J.C.; Hafner, D.J.; Patton, J.L.; Smith, M.E. Contact zones and the genetics of differentiation in the pocket gopher *Thomomys bottae* (Rodentia: Geomyidae). *Syst. Zool.* **1983**, *32*, 1–20. [CrossRef]

113. Yonenaga-Yassuda, Y.; DeSouza, M.J.; Kasahara, S.; L'Abbate, M.; Chu, H.T. Supernumerary system in *Proechimys iheringi iheringi* (Rodentia, Echimydae), from the state of Sao Paulo, Brazil. *Caryologia* **1985**, *38*, 179–194. [CrossRef]

114. Fagundes, V.; Camacho, J.P.M.; Yonenaga-Yassuda, Y. Are the dot-like chromosomes in *Trinomys iheringi* (Rodentia, Echimyidae) B chromosomes? *Cytogenet. Genome Res.* **2004**, *106*, 159–164. [CrossRef] [PubMed]

115. Baverstock, P.R.; Gelder, M.; Jahnke, A. Cytogenetic studies of the Australian rodent *Uromys caudimaculatus*, a species showing extensive heterochromatin variation. *Chromosoma* **1982**, *84*, 517–533. [CrossRef] [PubMed]

116. Mammal Diversity Database. Available online: www.mammaldiversity.org (accessed on 10 July 2018).

117. Belayev, D.K.; Volobouev, V.T.; Radjabli, S.I.; Trut, L.N. Polymorphism and mosaicism for additional chromosomes in silver foxes. *Genetika* **1974**, *X*, 58–67.

118. Bekasova, T.S.; Vorontsov, N.N.; Korobitsyina, K.V.; Korablev, V.P. B-chromosomes and comparative karyology of the mice of the genus *Apodemus*. *Genetica* **1980**, *52/53*, 33–43. [CrossRef]

119. Gileva, E. Chromosomal diversity and the aberrant genetic system of sex determination in the artic lemming, *Dicrostonyx torquatus* Pallas, 1779. *Genetica* **1980**, *52/53*, 99–103. [CrossRef]

120. Szczerbal, I.; Kaczmarek, M.; Switonski, M. Compound mosaicism, caused by B chromosome variability, in the Chinese raccoon dog (*Nyctereutes procyonoides procyonoides*). *Folia Biol.* **2005**, *53*, 155–159. [CrossRef]

121. Borisov, Y.M. The Polymorphism and distribution of B chromosomes in germline and somatic cells of *Tscherskia triton* de Winton (Rodentia, Cricetinae). *Russ. J. Genet.* **2012**, *48*, 538–542. [CrossRef]

122. Radzhabli, S.I.; Borisov, Y.M. B-chromosomes system variants among continental forms of *Apodemus peninsulae* (Rodentia, Muridae). *Dokl. Akad Nauk SSSR* **1979**, *248*, 979–981.

123. Kartavtseva, I.V.; Roslik, G.V. A complex B chromosome system in the Korean Field mouse *Apodemus peninsulae*, Cytogenet. *Cytogenet. Genome Res.* **2004**, *106*, 271–278. [CrossRef] [PubMed]

124. Roslik, G.V.; Kartavtseva, I.V. Polymorphism and mosaicism of B chromosome number in Korean field mouse *Apodemus peninsulae* (Rodentia) in the Russian Far East. *Cell Tissue Biol.* **2010**, *4*, 77–89. [CrossRef]

125. Koh, H. Systematic studies of Korean Rodents: II. A chromosome analysis in Korean field mice, *Apodemus peninsulae peninsulae* Thomas (Muridae, Rodentia), from Mungyong, with the comparison of morphometric characters of these Korean Field Mice to sympatric striped. *Korean J. Syst. Zool.* **1986**, *2*, 1–10.

126. Volobujev, V.T.; Timina, N.Z. Unusally high number of B-chromosomes and mosaicism by them in *Apodemus peninsulae* (Rodentia, Muridae). *Tsitologia* **1980**, *14*, 43–45.

127. Abril, V.V.; Carnelossi, E.A.G.; González, S.; Duarte, J.M.B. Elucidating the evolution of the red brocket deer *Mazama americana* Complex (Artiodactyla; Cervidae). *Cytogenet. Genome Res.* **2010**, *128*, 177–187. [CrossRef] [PubMed]

128. Malleret, M.; Labaroni, C.; García, G.V.; Ferro, J.; Marti, D.A.; Lanzone, C. Chromosomal variation in Argentine populations of *Akodon montensis* Thomas, 1913 (Rodentia, Cricetidae, Sigmodontinae). *Comp. Cytogenet.* **2016**, *10*, 129–140. [PubMed]

129. Kral, B.; Herzig-Straschil, B.; Štreba, O. Karyotypes of certain small mammals from Austria. *Folia Zool.* **1979**, *28*, 5–11.

130. Rovatsos, M.T.; Mitsainas, G.P.; Tryfonopoulos, G.A.; Stamatopoulos, C.; Giagia-Athanasopoulou, E.B. A chromosomal study on Greek populations of the genus *Apodemus* (Rodentia, Murinae) reveals new data on B chromosome distribution. *Acta Theriol. (Warsz)* **2008**, *53*, 157–167. [CrossRef]

131. Sablina, O.V.; Radzabli, S.I.; Golenisev, F.N. B-chromosomes in the karyotype of *A. flavicollis* from Leningrad district. *Zool. J.* **1985**, *LXIV*, 1901–1903.

132. Giagia, E.; Soldatović, B.; Savić, I.; Zimonjić, D. Karyotype study of the genus *Apodemus* (Kaup 1829) populations from the Balkan peninsula. *Acta Vet.* **1985**, *35*, 289–298.

133. Vujošević, M.; Blagojević, J.; Radosavljević, J.; Bejaković, D. B chromosome polymorphism in populations of *Apodemus flavicollis* in Yugoslavia. *Genetica* **1991**, *83*. [CrossRef]

134. Nadjafova, R.S.; Bulatova, N.S.; Chasovnikarova, Z.; Gerassimov, S. Karyological differences between two *Apodemus* species in Bulgaria. *Z. Saugetierkd.* **1993**, *38*, 232–239.

135. Wolf, U.; Voiculescu, I.; Zenzes, M.T.; Vogel, W.; Engel, W. Chromosome polymorphism in Apodemus flavicollis, possibly due to creation of a new centromere. In *Modern Aspects of Cytogenetics: Constitutive Heterochromatin in Man*; Pfeiffer, A., Ed.; Schattauer F. K.: Stuttgart, Germany; New York, NY, USA, 1972; pp. 163–168.

136. Ramalhinho, M.G.; Libois, R. First report on the presence in France of a B-chromosome polymorphism in *Apodemus flavicollis*. *Mammalia* **2002**, *66*, 300–303.

137. Castiglia, R. Cytogenetic analysis of *Apodemus flavicollis* in Italy: First report of B chromosomes and X chromosome heteromorphism. *Mammalia* **2003**, *67*, 1–3. [CrossRef]

138. Wójcik, J.M.; Wójcik, A.M.; Macholán, M.; Piálek, J.; Zima, J. The mammalian model for population studies of B chromosomes: The wood mouse (*Apodemus*). *Cytogenet. Genome Res.* **2004**, *106*, 264–270. [CrossRef] [PubMed]

139. Vujošević, M.; Blagojević, J. New localities with B chromosomes in *Apodemus flavicollis* (Rodentia, Mammalia). *Arch. Biol. Sci.* **1994**, *46*, 15.

140. Blagojević, J.; Vujošević, M. Do B chromosomes affect morphometric characters in yellow-necked mice *Apodemus flavicollis* (Rodentia, Mammalia)? *Acta Theriol. (Warsz)* **2000**, *45*, 129–135. [CrossRef]

141. Vujošević, M.; Blagojević, J. Does environment affect polymorphism of B chromosomes in the yellow-necked mouse *Apodemus flavicollis*? *Z. Saugetierkd.* **2000**, *65*, 313–317.

142. Vujošević, M.; Blagojević, J.; Jojić-Šipetić, V.; Bugarski-Stanojević, V.; Adnađević, T.; Stamenković, G. Distribution of B chromosomes in age categories of the yellow-necked mouse *Apodemus flavicollis* (Mammalia, Rodentia). *Arch. Biol. Sci.* **2009**, *61*, 653–658. [CrossRef]

143. Vujošević, M.; Jojić, V.; Bugarski-Stanojević, V.; Blagojević, J. Habitat quality and B chromosomes in the yellow-necked mouse *Apodemus flavicollis*. *Ital. J. Zool.* **2007**, *74*, 313–316. [CrossRef]

144. Shellhammer, H.S. Supernumerary chromosomes of the harvest mouse, *Reithrodontomys megalotis*. *Chromosoma* **1969**, *27*, 102–108. [CrossRef] [PubMed]

145. Boyeskorov, G.; Zagorodnyuk, I.; Belyanin, A.N.; Lyapunova, E.A. B-chromosomes in *Apodemus flavicollis* from eastern Europe. *Pol. Ecol. Stud.* **1994**, *20*, 523–526.

146. Kartavtseva, I.V.; Roslik, G.V.; Pavlenko, M.V.; Amachaeva, E.Y.; Sawaguchi, S.; Obara, Y. The B-chromosome system of the Korean field mouse *Apodemus peninsulae* in the Russian Far East. *Chromosom. Sci.* **2000**, *4*, 21–29.

147. Ostromyshenskii, D.I.; Kuznetsova, I.S.; Podgornaya, O.I.; Kartavtseva, I.V. Appearance of B chromosomes like structures in *Apodemus peninsulae* primary cell culture. *Res. J. Zool.* **2018**, *1*, 1.

148. Volobuev, V.T. Karyological analysis of three Siberian populations of *Apodemus peninsulae* (Rodentia, Muridae). *Dokl. AN SSSR* **1979**, *248*, 1452–1454.

149. Borisov, Y.M. Variation of the cytogenetic structure of the population of *Apodemus peninsulae* (Rodentia, Muridae) in western Sayan Mountains. *Genetika* **1990**, *26*, 1484–1491. [PubMed]

150. Borisov, Y.M. Cytogenetic differentiation of the population of *Apodemus peninsulae* (Rodentia, Muridae) in eastern Siberia. *Genetika* **1990**, *26*, 1828–1839. [PubMed]

151. Borisov, Y.M. Cytogenetic Structure of the Population of *Apodemus peninsulae* (Rodentia, Muridae) on the bank of lake Teletskoe (Altai). *Genetika* **1990**, *26*, 1212–1220.

152. Borisov, Y.M.; Malygin, M.V. Cline variability of B-chromosome system in *Apodemus peninsulae* (Rodentia, Muridae) from the Buryatia and Mongolia. *Citologija* **1991**, *33*, 106–111.

153. Roslik, G.V.; Kartavtseva, I.V. Geographic differentiation of B chromosomes in *Apodemus peninsulae* (Rodentia) from the east Asia. In Proceedings of the International Symposium: Modern Achievements in Population, Evolutionary, and Ecological Genetics, Vladivostok, Russia, 3–9 September 2017.

154. Ruban, A.; Schmutzer, T.; Scholz, U.; Houben, A. How next-generation sequencing has aided our understanding of the sequence composition and origin of B chromosomes. *Genes* **2017**, *8*, 294. [CrossRef] [PubMed]

155. Page, B.T.; Wanous, M.K.; Birchler, J.; Ames, A. Characterization of a maize chromosome 4 centromeric sequence: Evidence for an evolutionary relationship with the B chromosome centromere. *Genetics* **2001**, *159*, 291–302. [PubMed]

156. Cheng, Y.-M.; Lin, B.-Y. Cloning and characterization of maize B chromosome sequences derived from microdissection. *Genetics* **2003**, *164*, 299–310. [PubMed]

157. Bugrov, A.G.; Karamysheva, T.V.; Perepelov, E.A.; Elisaphenko, E.A.; Rubtsov, D.N.; Warchałowska-Śliwa, E.; Tatsuta, H.; Rubtsov, N.B. DNA content of the B chromosomes in grasshopper *Podisma kanoi* Storozh. (Orthoptera, Acrididae). *Chromosom. Res.* **2007**. [CrossRef] [PubMed]

158. Valente, G.T.; Nakajima, R.T.; Fantinatti, B.E.A.; Marques, D.F.; Almeida, R.O.; Simões, R.P.; Martins, C. B chromosomes: From cytogenetics to systems biology. *Chromosoma* **2017**, *126*, 73–81. [CrossRef] [PubMed]

159. Lamb, J.C.; Meyer, J.M.; Corcoran, B.; Kato, A.; Han, F.; Birchler, J.A. Distinct chromosomal distributions of highly repetitive sequences in maize. *Chromosom. Res.* **2007**, *15*, 33–49. [CrossRef] [PubMed]

160. Tanić, N.; Dedovic, N.; Vujošević, M.; Dimitrijević, B. DNA profiling of B chromosomes from the yellow-necked mouse *Apodemus flavicollis* (Rodentia, Mammalia). *Genome Res.* **2000**, *10*, 55–61. [PubMed]

161. Schmid, M.; Ziegler, C.G.; Steinlein, C.; Nanda, I.; Schartl, M. Cytogenetics of the bleak (*Alburnus alburnus*), with special emphasis on the B chromosomes. *Chromosom. Res.* **2006**, *14*, 231–242. [CrossRef] [PubMed]

162. Wang, J.; Zhao, X.; Qi, H.; Koh, H.S.; Zhang, L.; Guan, Z.; Wang, C. Karyotypes and B chromosomes of *Apodemus peninsulae* (Rodenita, Mammalia). *Acta Theriol. Sin.* **2000**, *20*, 289–296.

163. Trifonov, V.A.; Perelman, P.L.; Kawada, S.I.; Iwasa, M.A.; Oda, S.I.; Graphodatsky, A.S. Complex structure of B-chromosomes in two mammalian species: *Apodemus peninsulae* (Rodentia) and *Nyctereutes procyonoides* (Carnivora). *Chromosom. Res.* **2002**, *10*, 109–116. [CrossRef]

164. Karamysheva, T.V.; Andreenkova, O.V.; Bochkarev, M.N.; Borisov, Y.M.; Bogdanchikova, N.; Borodin, P.M.; Rubtsov, N.B. B chromosomes of Korean field mouse *Apodemus peninsulae* (Rodentia, Murinae) analysed by microdissection and FISH. *Cytogenet. Genome Res.* **2002**, *96*, 154–160. [CrossRef] [PubMed]

165. Rubtsov, N.B.; Karamysheva, T.V.; Andreenkova, O.V.; Bochkaerev, M.N.; Kartavtseva, I.V.; Roslik, G.V.; Borisov, Y.M. Comparative analysis of micro and macro B chromosomes in the Korean field mouse *Apodemus peninsulae* (Rodentia, Murinae) performed by chromosome microdissection and FISH. *Cytogenet. Genome Res.* **2004**, *106*, 289–294. [CrossRef] [PubMed]

166. Wurster-Hill, D.H.; Ward, O.G.; Davis, B.H.; Park, J.P.; Moyzis, R.K.; Meyne, J. Fragile sites, telomeric DNA sequences, B chromosomes, and DNA content in raccoon dogs, *Nyctereutes procyonoides*, with comparative notes on foxes, coyote, wolf, and raccoon. *Cytogenet. Genome Res.* **1988**, *49*, 278–281. [CrossRef] [PubMed]

167. Szczerbal, I.; Switonski, M. B chromosomes of the Chinese raccoon dog (*Nyctereutes procyonoides procyonoides* Gray) contain inactive NOR-like sequences. *Caryologia* **2003**, *56*, 213–216. [CrossRef]

168. Graphodatsky, A.S.; Kukekova, A.V.; Yudkin, D.V.; Trifonov, V.A.; Vorobieva, N.V.; Beklemisheva, V.R.; Perelman, P.L.; Graphodatskaya, D.A.; Trut, L.N.; Yang, F.; et al. The proto-oncogene C-KIT maps to canid B-chromosomes. *Chromosom. Res.* **2005**, *13*, 113–122. [CrossRef] [PubMed]

169. Yudkin, D.V.; Trifonov, V.A.; Kukekova, A.V.; Vorobieva, N.V.; Rubtsova, N.V.; Yang, F.; Acland, G.M.; Ferguson-Smith, M.A.; Graphodatsky, A.S. Mapping of KIT adjacent sequences on canid autosomes and B chromosomes. *Cytogenet. Genome Res.* **2007**, *116*, 100–103. [CrossRef] [PubMed]

170. Wnuk, M.; Oklejewicz, B.; Lewinska, A.; Zabek, T.; Bartosz, G.; Slota, E.; Bugno-Poniewierska, M. PRINS detection of 18S rDNA in pig, red fox and Chinese raccoon dog, and centromere DNA in horse. *Hereditas* **2010**, *147*, 320–324. [CrossRef] [PubMed]

171. Becker, S.E.D.; Thomas, R.; Trifonov, V.A.; Wayne, R.K.; Graphodatsky, A.S.; Breen, M. Anchoring the dog to its relatives reveals new evolutionary breakpoints across 11 species of the Canidae and provides new clues for the role of B chromosomes. *Chromosom. Res.* **2011**, *19*, 685–708. [CrossRef] [PubMed]

172. Li, Y.M.; Zhang, Y.; Zhu, W.J.; Yan, S.Q.; Sun, J.H. Identification of polymorphisms and transcriptional activity of the proto-oncogene KIT located on both autosomal and B chromosomes of the Chinese raccoon dog. *Genet. Mol. Res.* **2016**, *15*, 1–6. [CrossRef] [PubMed]

173. Makunin, A.; Romanenko, S.; Beklemisheva, V.; Perelman, P.; Druzhkova, A.; Petrova, K.; Prokopov, D.; Chernyaeva, E.; Johnson, J.; Kukekova, A.; et al. Sequencing of supernumerary chromosomes of red fox and raccoon dog confirms a non-random gene acquisition by B chromosomes. *Genes* **2018**, *9*, 405. [CrossRef] [PubMed]

174. Trifonov, V.A.; Dementyeva, P.V.; Larkin, D.M.; O'Brien, P.C.; Perelman, P.L.; Yang, F.; Ferguson-Smith, M.A.; Graphodatsky, A.S. Transcription of a protein-coding gene on B chromosomes of the Siberian roe deer (*Capreolus pygargus*). *BMC Biol.* **2013**, *11*, 90. [CrossRef] [PubMed]

175. Makunin, A.I.; Kichigin, I.G.; Larkin, D.M.; O'Brien, P.C.M.; Ferguson-Smith, M.A.; Yang, F.; Proskuryakova, A.A.; Vorobieva, N.V.; Chernyaeva, E.N.; O'Brien, S.J.; et al. Contrasting origin of B chromosomes in two cervids (Siberian roe deer and grey brocket deer) unravelled by chromosome-specific DNA sequencing. *BMC Genom.* **2016**, *17*, 618. [CrossRef] [PubMed]

176. Soares, A.A.; Castro, J.P.; Balieiro, P.; Dornelles, S.; Degrandi, T.M.; Sbalqueiro, I.J.; Ferreira Artoni, R.; Hass, I. B Chromosome diversity and repetitive sequence distribution in an isolated population of *Akodon montensis* (Rodentia, Sigmodontinae). *Cytogenet. Genome Res.* **2018**, *154*, 79–85. [CrossRef] [PubMed]

177. Boyeskorov, G.G.; Kartavseva, I.V.; Belyanin, A.N.; Liapunova, E.A. Nucleolus organizer regions and B-chromosomes of wood mice (Mammalia, Rodentia, *Apodemus*). *Russ. J. Genet.* **1995**, *31*, 156–163.

178. Tanić, N.; Vujošević, M.; Dedović-Tanić, N.; Dimitrijević, B. Differential gene expression in yellow-necked mice *Apodemus flavicollis* (Rodentia, Mammalia) with and without B. chromosomes. *Chromosoma* **2005**, *113*, 418–427. [CrossRef] [PubMed]

179. Rajičić, M.; Adnađević, T.; Stamenković, G.; Blagojević, J.; Vujošević, M. Screening of B chromosomes for presence of two genes in yellow-necked mice, *Apodemus flavicollis* (Mammalia, Rodentia). *Genetika* **2015**, *47*, 311–321. [CrossRef]

180. Bugarski-Stanojević, V.; Stamenković, G.; Blagojević, J.; Liehr, T.; Kosyakova, N.; Rajičić, M.; Vujošević, M. Exploring supernumeraries—A new marker for screening of B-chromosomes presence in the yellow necked mouse *Apodemus flavicollis*. *PLoS ONE* **2016**, *11*, e0160946. [CrossRef] [PubMed]

181. Makunin, A.I.; Rajičić, M.; Karamysheva, T.V.; Romanenko, S.A.; Druzhkova, A.; Blagojević, J.; Vujošević, M.; Rubtsov, N.B.; Graphodatsky, A.S.; Trifonov, V.A. Low-pass single-chromosome sequencing of human small supernumerary marker chromosomes (sSMCs) and *Apodemus* B chromosomes. *Chromosoma* **2018**, *127*, 301–311. [CrossRef] [PubMed]

182. Matsubara, K.; Yamada, K.; Umemoto, S.; Tsuchiya, K.; Ikeda, N.; Nishida, C.; Chijiwa, T.; Moriwaki, K.; Matsuda, Y. Molecular cloning and characterization of the repetitive DNA sequences that comprise the constitutive heterochromatin of the A and B chromosomes of the Korean field mouse (*Apodemus peninsulae*, Muridae, Rodentia). *Chromosom. Res.* **2008**, *16*, 1013–1026. [CrossRef] [PubMed]

183. Ventura, K.; O'Brien, P.C.M.; do Nascimento Moreira, C.; Yonenaga-Yassuda, Y.; Ferguson-Smith, M.A. On the Origin and evolution of the extant system of B chromosomes in Oryzomyini Radiation (Rodentia, Sigmodontinae). *PLoS ONE* **2015**, *10*, e0136663. [CrossRef] [PubMed]

184. De Jesus Silva, M.J.; Yonenaga-Yassuda, Y. Heterogeneity and meiotic behaviour of B and sex chromosomes, banding patterns and localization of (TTAGGG)n sequences by fluorescence in situ hybridization in the neotropical water rat *Nectomys* (Rodentia, Cricetidae). *Chromosome Res.* **1998**, *6*, 455–462. [CrossRef] [PubMed]

185. Stitou, S.; Díaz de La Guardia, R.; Jiménez, R.; Burgos, M. Inactive ribosomal cistrons are spread throughout the B chromosomes of *Rattus rattus* (Rodentia, Muridae). Implications for their origin and evolution. *Chromosome Res.* **2000**, *8*, 305–311. [CrossRef] [PubMed]

186. Cavagna, P.; Stone, G.; Stanyon, R. Black rat (*Rattus rattus*) genomic variability characterized by chromosome painting. *Mamm. Genome* **2002**, *13*, 157–163. [CrossRef] [PubMed]

187. Peppers, J.A.; Wiggins, L.E.; Baker, R.J. Nature of B chromosomes in the harvest mouse *Reithrodontomys megalotis* by fluorescence in situ hybridization (FISH). *Chromosome Res.* **1997**, *5*, 475–479. [CrossRef] [PubMed]

188. Rajičić, M.; Romanenko, S.A.; Karamysheva, T.V.; Blagojević, J.; Adnađević, T.; Budinski, I.; Bogdanov, A.S.; Trifonov, V.A.; Rubtsov, N.B.; Vujošević, M. The origin of B chromosomes in yellow-necked mice (*Apodemus flavicollis*)—Break rules but keep playing the game. *PLoS ONE* **2017**, *12*, e0172704. [CrossRef] [PubMed]

189. Bugno-Poniewierska, M.; Solek, P.; Wronski, M.; Potocki, L.; Jezewska-Witkowska, G.; Wnuk, M. Genome organization and DNA methylation patterns of B chromosomes in the red fox and Chinese raccoon dogs. *Hereditas* **2014**, *151*, 169–176. [CrossRef] [PubMed]

190. Jones, R.N.; Houben, A. B chromosomes in plants: Escapees from the A chromosome genome? *Trends Plant Sci.* **2003**, *8*, 417–423. [CrossRef]

191. Sapre, A.B.; Deshpande, D.S. Origin of B chromosomes in Coix L. through spontaneous interspecific hybridization. *J. Hered.* **1987**, *78*, 191–196. [CrossRef]

192. McAllister, B.F. Isolation and characterization of a retroelement from B chromosome (PSR) in the parasitic wasp *Nasonia vitripennis*. *Insect Mol. Biol.* **1995**, *4*, 253–262. [CrossRef] [PubMed]

193. Guioli, S.; Lovell-Badge, R.; Turner, J.M.A. Error-Prone ZW Pairing and no evidence for meiotic sex chromosomeinactivation in the chicken germ line. *PLoS Genet.* **2012**, *8*, e1002560. [CrossRef] [PubMed]

194. Gu, L.; Walters, J.R. Evolution of sex shromosome dosage compensation in animals: A beautiful theory, undermined by facts and bedeviled by details. *Genome Biol. Evol.* **2017**, *9*, 2461–2476. [CrossRef] [PubMed]

195. Daish, T.J.; Casey, A.E.; Grutzner, F. Lack of sex chromosome specific meiotic silencing in platypus reveals origin of MSCI in therian mammals. *BMC Biol.* **2015**, *13*, 106. [CrossRef] [PubMed]

196. Berend, S.A.; Hale, D.W.; Engstrom, M.D.; Greenbaum, I.F. Cytogenetics of collared lemmings (*Dicrostonyx groenlandicus*). II. Meiotic behavior of B chromosomes suggests a Y-chromosome origin of supernumerary chromosomes. *Cytogenet. Genome Res.* **2001**, *95*, 85–91. [CrossRef] [PubMed]

197. Kolomeits, O.L.; Borbiev, T.E.; Safronova, L.D.; Borisov, Y.M. Synaptonemal analysis of B-chromosome behaviour in meiotic prophase I in the East-Asiatic mouse *Apodemus peninsulae* (Muridae, Rodentia). *Cytogenet. Cell Genet.* **1988**, *48*, 183–187. [CrossRef] [PubMed]

198. Matsubara, K.; Nishida-Umehara, C.; Tsuchiya, K.; Nukaya, D.; Matsuda, Y. Karyotypic evolution of *Apodemus* (Muridae, Rodentia) inferred from comparative FISH analyses. *Chromosom. Res.* **2004**, *12*, 383–395. [CrossRef] [PubMed]

199. Thomson, R.L.; Westerman, M.; Murray, N.D. B chromosomes in *Rattus fuscipes* I. Mitotic and meiotic chromosomes and the effects of B on chiasma frequency. *Heredity (Edinb)* **1984**, *52*, 355–362. [CrossRef]

200. Rubtsov, N.B.; Borisov, Y.M.; Karamysheva, T.V.; Bochkarev, M.N. The mechanisms of formation and evolution of B chromosomes in Korean field mice *Apodemus peninsulae* (Mammalia, Rodentia). *Russ. J. Genet.* **2009**, *45*, 389–396. [CrossRef]

201. Ishak, B.; Maetz, J.L.; Rumpler, Y. Absence of transcriptional activity in the B-chromosomes of *Apodemus flavicollis* during pachytene. *Chromosoma* **1991**, *100*, 278–281. [CrossRef]

202. Karamysheva, T.V.; Torgasheva, A.A.; Yefremov, Y.R.; Bogomolov, A.G.; Liehr, T.; Borodin, P.M.; Rubtsov, N.B. Spatial organization of fibroblast and spermatocyte nuclei with different B-chromosome content in Korean field mouse, *Apodemus peninsulae* (Rodentia, Muridae). *Genome* **2017**, *60*, 815–824. [CrossRef] [PubMed]

203. Vujošević, M.; Radosavljević, J.; Živković, S. Meiotic behavior of B chromosomes in yellow necked mouse *Apodemus flavicollis*. *Arch. Biol. Sci.* **1989**, *41*, 39–42.

204. Banaszek, A.; Jadwiszczak, K.A. B-chromosomes behaviour during meiosis of yellow-necked mouse, *Apodemus flavicollis*. *Folia Zool.* **2006**, *55*, 113–122.

205. Świtoński, M.; Gustavsson, I.; Höjer, K.; Plöen, L. Synaptonemal complex analysis of the B-chromosomes in spermatocytes of the silver fox (*Vulpes fulvus* Desm.). *Cytogenet. Genome Res.* **1987**, *45*, 84–92. [CrossRef]

206. Sosnowski, J.; Łukasiewicz, A.; Migalska, L.; Wojnowska, M.; Polański, Z. Different levels of a lack of X-Y chromosome pairing in pachytene spermatocytes of red fox (*Vulpes vulpes*) and Chinese raccoon dog (*Nyctereutes procyonoides procyonoides*). *Ann. Anim. Sci.* **2011**, *11*, 71–81.

207. Patton, J.L. B-chromosome system in the pocket mouse, *Perognathus baileyi*: Meiosis and C-band studies. *Chromosoma* **1977**, *60*, 1–14. [CrossRef] [PubMed]

208. Radjabli, S.I.; Isaenko, A.A.; Volobuev, V.T. Investigation of the nature and role of additional chromosomes in silver fox. *Genetika* **1978**, *XIV*, 438–443.

209. Borisov, Y.M. Increase in the number of the B-chromosomes and variants of their system in mouse *Apodemus peninsulae* in Mountain Altai population over 26 years. *Genetika* **2008**, *44*, 1227–1237. [CrossRef] [PubMed]

210. Gileva, E.A.; Chebotar, N.A. Fertile X0 males and females in the varying lemming, *Dicrostonyx torquatus* Pall. (1779). *Heredity (Edinb)* **1979**, *42*, 67–77. [CrossRef]

211. Gileva, E. The B chromosome system in the varying lemming *Dicrostonyx torquatus* Pall., 1779 from natural and laboratory populations. *Russ. J. Genet.* **2004**, *40*, 1399–1406. [CrossRef]

212. Yosida, T.H. Some genetic analysis of supernumerary chromosomes in the black rat in laboratory matings. *Proc. Jpn. Acad.* **1978**, *50*, 440–445. [CrossRef]

213. Stitou, S.; Zurita, F.; Díaz de la Guardia, R.; Jiménez, R.; Burgos, M. Transmission analysis of B chromosomes in *Rattus rattus* from Northern Africa. *Cytogenet. Genome Res.* **2004**, *106*, 344–346. [CrossRef] [PubMed]

214. Palestis, B.G.; Burt, A.; Jones, R.N.; Trivers, R. B chromosomes are more frequent in mammals with acrocentric karyotypes: Support for the theory of centromeric drive. *Proc. R. Soc. B Biol. Sci.* **2004**, *271*, S22–S24. [CrossRef] [PubMed]

215. Pardo-Manuel de Villena, F.; Sapienza, C. Female meiosis drives karyotypic evolution in mammals. *Genetics* **2001**, *159*, 1179–1189. [PubMed]

216. Kociucka, B.; Sosnowski, J.; Kubiak, A.; Nowak, A.; Pawlak, P.; Szczerbal, I. Three-dimensional positioning of B chromosomes in fibroblast nuclei of the red fox and the Chinese raccoon dog. *Cytogenet. Genome Res.* **2013**, *139*, 243–249. [CrossRef] [PubMed]

217. Wurster-Hill, D.H.; Ward, O.G.; Kada, B.H.; Whittmore, S. Banded chromosome studies and B chromosomes in wild-caught raccoon dogs, *Nyctereutes procyonides viverinus*. *Cytogenet. Cell Genet.* **1986**, *42*, 85–93. [CrossRef]

218. Zima, J.; Piálek, J.; Macholán, M. Possible heterotic effects of B chromosomes on body mass in a population of *Apodemus flavicollis*. *Can. J. Zool.* **2003**, *81*, 1312–1317. [CrossRef]

219. Jojić, V.; Blagojević, J.; Ivanović, A.; Bugarski-Stanojević, V.; Vujošević, M. Morphological integration of the mandible in yellow-necked field mice: The effects of B chromosomes. *J. Mammal.* **2007**, *88*, 689–695. [CrossRef]

220. Jojić, V.; Blagojević, J.; Vujošević, M. B chromosomes and cranial variability in yellow-necked field mice (*Apodemus flavicollis*). *J. Mammal.* **2011**, *92*, 396–406. [CrossRef]

221. Blagojević, J.; Vujošević, M. B chromosomes and developmental homeostasis in the yellow-necked mouse, *Apodemus flavicollis* (Rodentia, Mammalia): Effects on nonmetric traits. *Heredity (Edinb)* **2004**, *93*, 249–254. [CrossRef] [PubMed]

222. Adnađević, T.; Jovanović, V.M.; Blagojević, J.; Budinski, I.; Čabrilo, B.; Bjelić-Čabrilo, O.; Vujošević, M. Possible influence of B chromosomes on genes included in immune response and parasite burden in *Apodemus flavicollis*. *PLoS ONE* **2014**, *9*, e112260. [CrossRef] [PubMed]

223. Jovanović, V.M.; Čabrilo, B.; Budinski, I.; Bjelić-Čabrilo, O.; Adnađević, T.; Blagojević, J.; Vujošević, M. Host B chromosomes as potential sex ratio distorters of intestinal nematode infrapopulations in the yellow-necked mouse (*Apodemus flavicollis*). *J. Helminthol.* **2018**. [CrossRef] [PubMed]

224. Belayev, D.K.; Volobouev, V.T.; Radjabli, S.I.; Trut, L.N. Investigation of the nature and role of additional chromosomes in silver fox II. Additional chromosomes and breeding of animals for behaviour. *Genetika* **1974**, *X*, 83–91.

225. Volobuev, V.T.; Radjabli, S.I. Investigation of the nature and the role of additional chromosomes in silver fox. I. Comparative analysis of additional chromosomes in different tissues and types of preparations and at different seasons. *Genetika* **1974**, *X*, 77–82.

226. Volobujev, V.T.; Radzabli, S.I.; Belajeva, E.S. Investigation of the nature and the role of additional chromosomes in silver foxes. III. Replication pattern in additional chromosomes. *Genetika* **1976**, *XII*, 30–34.

227. Östergren, G. Parasitic nature of extra fragment chromosomes. *Bot. Not.* **1945**, *2*, 157–163.

228. White, M.J.D. *Animal Cytology and Evolution*, 3rd ed.; Cambridge University Press: Cambridge, UK, 1973; ISBN 0-521-07071-6.

229. Camacho, J.P.M.; Shaw, M.W.; López–León, M.D.; Pardo, M.C.; Cabrero, J. Population dynamics of a selfish B chromosome neutralized by the standard genome in the grasshopper *Eyprepocnemis plorans*. *Am. Nat.* **1997**, *149*, 1030–1050. [CrossRef] [PubMed]

230. Vujošević, M. B-chromosome polymorphism in *Apodemus flavicollis* (Rodentia, Mammalia) during five years. *Caryologia* **1992**, *45*, 347–352. [CrossRef]

231. Blagojević, J.; Vujošević, M. The role of B chromosomes in the population dynamics of yellow-necked wood mice *Apodemus flavicollis* (Rodentia, Mammalia). *Genome* **1995**, *38*, 472–478. [CrossRef] [PubMed]

232. Vujošević, M.; Blagojević, J. Seasonal changes of B-chromosome frequencies within the population of *Apodemus flavicollis* (Rodentia) on Cer mountain in Yugoslavia. *Acta Theriol. (Warsz)* **1995**, *40*, 131–137. [CrossRef]

233. Borisov, Y.M.; Sheftel, B.I.; Safronova, L.D.; Aleksandrov, D.Y. Stability of the Population Variants of the B-Chromosome System in the East-Asian Mouse *Apodemus peninsulae* from the Baikal Region and Northern Mongolia. *Russ. J. Genet.* **2012**, *48*, 1020–1028. [CrossRef]

234. Blagojević, J.; Stamenković, G.; Jojić Šipetić, V.; Bugarski-Stanojević, V.; Adnađević, T.; Vujošević, M. B chromosomes in populations of yellow-necked mice—Stowaways or contributing genetic elements? *Ital. J. Zool.* **2009**, *76*, 250–257. [CrossRef]

235. Adnađević, T.; Bugarski-Stanojević, V.; Blagojević, J.; Stamenković, G.; Vujošević, M. Genetic differentiation in populations of the yellow-necked mouse, *Apodemus flavicollis*, harbouring B chromosomes in different frequencies. *Popul. Ecol.* **2012**, *54*, 537–548. [CrossRef]