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Karyology of the Bats from the Russian Far East

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Additional information is available at the end of the chapter

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Abstract

Recent studies based on morphologic and molecular genetic data have revealed quite a serious variety in the trans-Palearctic species, which brought about taxonomic status changes in 14 of 18 Russian Far Eastern bat species. Far Eastern bat status revisions resulted in species growth whose chromosome characteristics have been described either under other names or have not been studied at all. This paper has inventoried bat chromosome research in the Russian Far East and neighboring regions and has improved the accuracy of chromosome characteristics for 17 of 18 valid species today. For the first time, the karyotypes and their variation type for the valid bat species in the Russian Far East have been described.

Keywords: Chiroptera, karyotype, chromosome, nucleolar organizer regions, heterochromatic material

1. Introduction

Till the middle of the twentieth century, most of the Russian bats were considered to belong to widespread Palearctic species. Since the mid-1960s, a gradual transition from the “wide” polytypic species concept appears to be replaced by the “narrow” monotypic one [1]. This is largely due to the improved morphological data processing methods [2–4] and the use of the molecular genetic [5, 6] and the karyological [7–9] methods in bat systematics. Many of the Far Eastern bat taxa were treated formerly as eastern subspecies within polytypical trans-Palearctic species. Recently, most of the Far Eastern subspecies have been elevated to a species rank, which resulted in taxonomic status changes of 14 Far Eastern bat species [5, 6, 10–21]. However, the taxonomic status of certain forms needs to be clarified [22]. Most of these species are restricted to Northeast Asia, with the western species distribution bordering the Trans-Baikal and the Altai regions [22, 23].

Karyotype features are essential diagnostic characteristics of many mammalian species [24, 25]. Even species with similar diploid number ($2n$) and chromosome morphology have been shown to differ significantly in distributional patterns of nucleolar organizer regions (NOR) [26–29] and the amount and location of heterochromatic material on chromosomes [30–34].

Bats are characterized by high level of karyotype stability at the genus and low intraspecific chromosomal variability, e.g., in *Myotis* Kaup, 1929; *Eptesicus* Rafinesque, 1820; *Vespertilio* Linnaeus, 1758; *Barbastella* Gray, 1821; *Plecotus* Gray, 1866 [7, 35–39].

The so-called *Myotis*-type karyotype with $2n = 44$ and fundamental number (N_{Fa}) being 50 is accepted to be the ancestral karyotype of family Vespertilionidae Gray, 1821 [37]. The chromosomal arms are usually numbered using Bickham's scheme, in which ordinal numbers have been assigned to all the autosomal arms based on GTG-banding patterns [40].

The position and number of the nucleolus organizer regions (NORs) and the amount and location of heterochromatic material (C-band) on chromosomes of many vespertilionid species have been shown to represent species-specific characteristics. The sequential staining methods (G-band; NOR; C-band) revealed karyological differences in species of the same karyotype [7, 8, 39, 41–45].

Chromosomal studies of the Far Eastern bats were initiated by N.N. Vorontsov [35] and continued by his colleagues and students [46–49]. The conventional staining of 10 bat species karyotypes was described. Differential staining (NOR and C-band) was reported for two species, *Plecotus ognevi* Kishida, 1927 and *Eptesicus nilssonii* Keyserling & Blasius, 1839.

Species composition revision of the Far Eastern bats caused an increase in the number of species, whose chromosomal characteristics were reported either under the wrong species names or were not studied at all.

The paper presents an inventory of available karyological data on bats from the Russian Far East and neighboring regions. It provides revision of specified chromosomal characteristics of 18 valid bat species from the Russian Far East. The karyotype descriptions of valid Far Eastern bat species and their chromosomal variability are given for the first time.

2. Karyotypes of Far Eastern bat

Table 1 shows valid Russian Far Eastern bat species. The columns represent species belonging to geographically various regions. The last one gives the species names describing the karyotypes. The table demonstrates the level of karyological knowledge available of certain bat species in every region studied. European and Northeastern Asian karyotype species have been studied to the fullest extent possible. Less data have been obtained regarding karyotype species in Siberia and the Russian Far East.

To illustrate the intrageneric and intraspecific variability of the Russian Far Eastern bat karyotypes based on data available, **Table 2** is drawn, which made it possible to compare chromosome characteristics of a similar Far Eastern bat species from different geographic

Valid species						Formerly named in sources		
Europe		Siberia		Russian Far East		Northeast Asia		
<i>Myotis nattereri</i>	E	<i>Myotis bombinus</i>	No	<i>Myotis bombinus</i>	No	<i>Myotis bombinus</i>	J	<i>Myotis nattereri</i>
–		<i>Myotis ikonnikovi</i>	No	<i>Myotis ikonnikovi</i>	FE	<i>Myotis ikonnikovi</i>	J	<i>Myotis ikonnikovi</i>
–		<i>Myotis longicaudatus</i>	No	<i>Myotis longicaudatus</i>	No	<i>Myotis longicaudatus</i>	J	<i>Myotis frater</i>
<i>Myotis capaccinii</i>	E	–		<i>Myotis macrodactylus</i>	FE	<i>Myotis macrodactylus</i>	J K	<i>Myotis capaccinii</i>
<i>Myotis daubentonii</i>	E	<i>Myotis daubentonii</i>	No	<i>Myotis petax</i>	FE	<i>Myotis petax</i>	K	<i>Myotis daubentonii</i>
		<i>Myotis petax</i>	No					
<i>Myotis brandtii</i>	E	<i>Myotis brandtii</i>	No	<i>Myotis gracilis</i>	No	<i>Myotis gracilis</i>	K	<i>Myotis brandtii</i>
		<i>Myotis sibirica</i>	S	<i>Myotis sibirica</i>	FE			
<i>Plecotus auritus</i>	E	<i>Plecotus ognevi</i>	S	<i>Plecotus ognevi</i>	FE	<i>Plecotus sacrimontis</i>	J	<i>Plecotus auritus</i>
		<i>Plecotus auritus</i>	No	<i>Plecotus sacrimontis</i>	No			
–		–		<i>Barbastella darjelingensis</i>	No	<i>Barbastella darjelingensis</i>	J	<i>Barbastella leucomelas</i>
–		–		<i>Pipistrellus abramus</i>	No	<i>Pipistrellus abramus</i>	J C K	<i>Pipistrellus abramus</i>
<i>Vespertilio murinus</i>	E	<i>Vespertilio murinus</i>	S	<i>Vespertilio murinus</i>	FE	<i>Vespertilio murinus</i>	no	<i>Vespertilio murinus</i>
–		<i>Vespertilio sinensis</i>	No	<i>Vespertilio sinensis</i>	FE	<i>Vespertilio sinensis</i>	J	<i>Vespertilio orientalis</i>
<i>Hypsugo savii</i>	E	–		<i>Hypsugo alashanicus</i>	FE	<i>Hypsugo alashanicus</i>	K	<i>Pipistrellus savii</i>
<i>Eptesicus nilssonii</i>	E	<i>Eptesicus nilssonii</i>	No	<i>Eptesicus nilssonii</i>	FE	<i>Eptesicus nilssonii</i>	J	<i>Eptesicus nilssonii</i>
–		–		<i>Murina ussuriensis</i>	No	<i>Murina ussuriensis</i>	J	<i>Murina aurata</i>
–		<i>Murina hilgendorfi</i>	S	<i>Murina hilgendorfi</i>	FE	<i>Murina hilgendorfi</i>	J	<i>Murina leucogaster</i>
<i>Miniopterus schreibersii</i>	E	–		<i>Miniopterus fuliginosus</i>	No	<i>Miniopterus fuliginosus</i>	J C T M	<i>Miniopterus schreibersii</i>

Notes: The geographical regions with the names abbreviated karyotypes investigated: E—Europe, S—Siberia, FE—Far East, J—Japan, C—China, K—Korea, T—Thailand, M—Malaysia.

Sources for species of Europe: [7, 39, 42, 44, 50], of Siberia: [47, 51], of the Far East—see **Table 2**. “no” — unknown.

Table 1. Valid species of the Far Eastern bats and their karyological studies.

Valid species	Species named in sources	Reg	2n	NFa	M-SM (large + medium + small)	ST	A	X	Y	NOR	Diff. stain.	N	Ref.
Vespertilionidae Gray 1821 – common bats													
<i>Myotis bombinus</i>	<i>M. nattereri</i>	J	44	50	3 + 0 + 1	–	17	SM	–	–	C	1f	[41]
	<i>M. n. bombinus</i>	J	44	50	3 + 0 + 1	–	17	M	A	11 cmc	C, G	1m	[43]
<i>Myotis ikonnikovi</i>	<i>M. hosonoi</i>	J	44	52	5 + 0 + 0	–	16	SM	A	–	–	1m	[52]
	<i>M. hosonoi</i>	J	44	52	3 + 0 + 2	–	16	SM	A	–	–	2m 1f	[53]
	<i>M. hosonoi</i>	J	44	50	3 + 0 + 1	–	17	SM	A	–	C, G	10m 14f	[41]
	<i>M. hosonoi</i>	J	44	50	3 + 0 + 1	–	17	M-SM	–	–	C, G, Q	5m 3f	[54]
	<i>M. ikonnikovi</i>	FE	44	50	3 + 0 + 1	–	17	SM	–	–	–	1f	[47]
<i>Myotis longicaudatus</i>	<i>M. hosonoi</i>	J	44	52	3 + 0 + 2	–	16	M	A	5 cmc	G	2m 1f	[43]
	<i>M. frater kaguyae</i>	J	44	50	3 + 0 + 2	–	16	SM	A	–	C, G	6m	[41]
	<i>M. frater</i>	J	44*	50	–	–	–	M-SM	SM	–	C	–	[55]
	<i>M. frater</i>	J	44	50	3 + 0 + 1	–	17	M-SM	–	–	C, G, Q	3m 4f	[54]
	<i>M. frater</i>	J	44	52	3 + 0 + 2	–	16	M	ST	13 cmc	C, G	3m 4f	[43]
<i>Myotis macrodactylus</i>	<i>M. capaccinii</i>	FE	44	50	3 + 0 + 1	–	17	M	A	–	–	1m	[46]
	<i>M. macrodactylus</i>	J	44	52	3 + 0 + 2	–	16	SM	A	–	–	2m 2f	[53]
	<i>M. macrodactylus</i>	J	44 + B	52	3 + 0 + 2	–	16	SM	A	–	–	5m 5f	[56]
	<i>M. macrodactylus</i>	K	44	50	3 + 0 + 1	–	17	SM	A	–	–	2m 3f	[57]
	<i>M. macrodactylus</i>	J	44	52	3 + 0 + 2	–	16	SM	A	–	C, G	4m 6f	[41]
	<i>M. macrodactylus</i>	J	44	50	3 + 0 + 1	–	17	M-SM	–	–	C, G, Q	8m 2f	[55]
	<i>M. macrodactylus</i>	J	44	52	3 + 0 + 2	–	16	M-SM	SM	–	C	–	[54]
	<i>M. macrodactylus</i>	K	44	52	3 + 0 + 2	–	16	M-SM	M-SM	–	–	5m	[58]
	<i>M. macrodactylus</i>	J	44	52	3 + 0 + 2	–	16	M	A	6 cmc	G	7m 5f	[43]
	<i>M. macrodactylus</i>	J	44	52	3 + 0 + 2	–	16	M	A	6 cmc	G	7m 5f	[43]

Valid species	Species named in sources	Reg	2n	NFa	M-SM (large + medium + small)	ST	A	X	Y	NOR	Diff. stain.	N	Ref.
<i>Myotis petax</i>	<i>M. daubentonii</i>	FE	44*	50	3 + 0 + 1	–	17	M	A	–	–	1m 2f	[47]
	<i>M. daubentonii</i>	K	44	52	3 + 0 + 2	–	16	M	A	–	–	2m	[58]
<i>Myotis sibirica</i>	<i>M. brandtii</i>	S	44*	50	3 + 0 + 1	–	17	M	A	–	–	2m	[47]
	<i>M. brandtii</i>	FE	44*	50	3 + 1 + 0	–	17	M	A	–	–	1m 1f	[48]
<i>Myotis gracilis</i>	<i>Myotis mystacinus gracilis</i>	K	44	50	3 + 0 + 1	–	17	M-SM	A	–	–	2m	[58]
<i>Plecotus ognevi</i>	<i>P. auritus</i>	FE	32	50	9 + 0 + 1	–	5	SM	–	4	C	1f	[47]
	<i>P. auritus</i>	S	32	50	9 + 0 + 1	–	5	SM	A	–	G, Q, FISH	1m	[51]
	<i>P. ognevi</i>	FE	32	50	9 + 0 + 1	–	5	SM	A	–	–	1m	[49]
<i>Plecotus sacrimontis</i>	<i>P. auritus sacrimontis</i>	J	32	50	9 + 0 + 1	–	5	SM	A	–	–	2f	[53]
	<i>P. a. sacrimontis</i>	J	32*	–	–	–	–	–	–	–	–	1m 1f	[59]
	<i>P. a. sacrimontis</i>	J	32	50	9 + 0 + 1	–	5	M	A	4 cmc	G	1m 3f	[43]
<i>Barbastella darjelingensis</i>	<i>B. leucomelas</i>	J	32	50	10	–	5	SM	A	–	–	1m	[60]
	<i>B. leucomelas</i>	J	32	50	10	–	5	SM	A	–	–	–	[61]
	<i>B. l. darjelingensis</i>	J	32	50	9 + 0 + 1	–	5	M	A	5 cmc	G	2m 1f	[43]
<i>Pipistrellus abramus</i>	<i>P. abramus</i>	J	26	44	6 + 4 + 0	–	2	A	M	–	–	2m	[52]
	<i>P. abramus</i>	J	26	44	6 + 4 + 0	–	2	A	A	–	–	3f	[53]
	<i>P. abramus</i>	J	26	44	6 + 4 + 0	–	2	A	A	–	G	4m 3f	[62]
	<i>P. abramus</i>	J	26*	–	–	–	–	–	–	–	–	1m 1f	[59]
	<i>P. abramus</i>	J	26	44	10 + 0 + 0	–	2	A	A	–	C	–	[55]
	<i>P. abramus</i>	J	26	44	6 + 4 + 0	–	2	ST	–	–	C, G, Q	3m 7f	[54]
	<i>P. abramus</i>	K	26	44	8 + 0 + 0	2	2	A	A	–	–	1m	[58]
	<i>P. abramus</i>	J	26	44	10 + 0 + 0	–	2	A	A	1 int	C, G	7m 3f	[43]
	<i>P. abramus</i>	C	26	44	10 + 0 + 0	–	2	A	A	–	C, G	9m 6f	[63]
	<i>P. abramus</i>	C	26	44	10 + 0 + 0	–	2	A	A	–	–	2m 2f	[64]
	<i>P. abramus</i>	C	26	44	10 + 0 + 0	–	2	A	A	–	C, G	1m 7f	[65]

Valid species	Species named in sources	Reg	2n	NFa	M-SM (large + medium + small)	ST	A	X	Y	NOR	Diff. stain.	N	Ref.
<i>Vespertilio murinus</i>	<i>V. murinus</i>	S	38	50	6 + 0 + 1	–	11	M	A	–	–	2m	[35]
	<i>V. murinus</i>	E	38	50	6 + 0 + 1	–	11	M	–	–	G, Q	1m 1f	[66]
	<i>V. murinus</i>	E	38*	50	–	–	–	–	–	2 int	–	1m	[42]
	<i>V. murinus</i>	FE	38*	50	6 + 0 + 1	–	11	M	–	–	–	1f	[47]
	<i>V. murinus</i>	S	38	50	6 + 0 + 1	–	11	M	A	–	G, Q, FISH	1m	[51]
	<i>V. murinus</i>	FE	38	50	6 + 0 + 1	–	11	M	A	–	–	1m 1f	[49]
<i>Vespertilio sinensis</i>	<i>V. superans</i>	FE	38	50	6 + 0 + 1	–	11	M	A	–	–	3m 2f	[35]
	<i>V. orientalis</i>	J	38	50	6 + 0 + 1	–	11	SM	A	–	–	–	[61]
	<i>V. orientalis</i>	J	38	50	6 + 0 + 1	–	11	SM	A	–	C	3m 7f	[67]
	<i>V. superans</i>	J	38	50	6 + 0 + 1	–	11	M-SM	A	–	C	–	[55]
	<i>V. superans</i>	J	38	54	6 + 0 + 3	–	9	SM	Dot	–	C, G	5m 5f	[68]
	<i>V. orientalis</i>											3m 5f	
	<i>V. superans</i>	FE	38*	50	6 + 0 + 1	–	11	M	A	–	–	2m 2f	[47]
	<i>V. superans</i>	J	38	50	6 + 0 + 1	–	11	M	A	2 int	G	3m 5f	[43]
	<i>V. superans</i>	J	38	50	6 + 0 + 1	–	11	M	A	–	C, T, Q, FISH	1m	[69]
<i>Hypsugo alashanicus</i>	<i>P. savii koreensis</i>	K	44	50	3 + 0 + 1	–	17	M	–	–	–	2f	[57]
	<i>P. savii</i>	FE	44*	50	3 + 0 + 1	–	17	M	–	–	–	1f	[47]
	<i>P. koreensis</i>	K	44	50	3 + 0 + 1	–	17	M-SM	A	–	–	3m	[58]

Valid species	Species named in sources	Reg	2n	NFa	M-SM (large + medium + small)	ST	A	X	Y	NOR	Diff. stain.	N	Ref.
<i>Eptesicus nilssonii</i>	<i>E. parvus</i>	J	50	48	–	–	–	–	–	–	–	1f	[59]
	<i>E. nilssonii</i>	E	50*	48	–	–	24	–	–	–	–	–	[70]
	<i>E. nilssonii</i>	FE	50	48	–	–	24	M	–	1 int	C	2f	[47]
	<i>E. nilssonii</i>	J	50	48	–	–	–	–	–	–	–	–	[71]
	<i>E. n. parvus</i>	J	50	50	–	1	23	M-SM	A	–	T, Q, FISH	2m 1f	[69]
	<i>E. nilssonii</i>	FE	50*	48	–	–	24	M	A	–	–	1m 1f	[48]
	<i>E. nilssonii</i>	E	50	48	–	–	24	M-SM	–	1 int	G	1f	[44]
<i>Murina hilgendorfi</i>	<i>M. leucogaster hilgendorfi</i>	J	44	50	3 + 0 + 1	–	17	M	A	–	–	1m	[53]
	<i>M. leucogaster</i>	J	44	58	3 + 0 + 1	4	13	SM	A	–	–	–	[60]
	<i>M. l. hilgendorfi</i>	J	44	56	3 + 0 + 1	3	14	SM	A	–	C, G	2m	[72]
	<i>M. leucogaster</i>	FE	44	50	2 + 1 + 1	–	17	SM	A	–	–	1m	[47]
	<i>M. hilgendorfi</i>	S	44	56	3 + 0 + 1	3	14	SM	A	–	G, Q, FISH	1m	[51]
<i>Murina ussuriensis</i>	<i>M. aurata</i>	J	44	60	3 + 0 + 2	4	12	SM	A	–	–	–	[61]
	<i>Murinus auratus ussuriensis</i>	J	44	50	3 + 0 + 1	–	17	M	A	–	–	1m	[59]
	<i>M. aurata ussuriensis</i>	J	44	56	3 + 0 + 1	3	14	SM	A	–	C, G	1m 1f	[72]
	<i>M. sylvatica</i>	J	44	56	3 + 0 + 1	3	14	–	–	num. cmc	–	1m 2f	[43]

Valid species	Species named in sources	Reg	2n	NFa	M-SM (large + medium + small)	ST	A	X	Y	NOR	Diff. stain.	N	Ref.
Miniopteridae Dobson 1835—Bent-winged Bats													
<i>Miniopterus fuliginosus</i>	<i>M. schreibersii fuliginosus</i>	J	46	52	2 + 1 + 1	—	18	SM	A	—	—	3m 1f	[73]
	<i>M. s. fuliginosus</i>	J	46	52	2 + 1 + 1	—	18	SM	A	—	—	8m 6f	[53]
	<i>M. schreibersii</i>	M	46	50	2 + 0 + 1	—	19	SM	A	—	—	1m 1f	[74]
	<i>M. s. haradai</i>	T	46	52	2 + 1 + 0	1	18	SM	A	—	—	2m	[70]
	<i>M. s. fuliginosus</i>	J	46	50	2 + 0 + 1	—	19	M	A	1cmc 1int	G	1m 1f	[43]
	<i>M. schreibersii</i>	T	46	50	2 + 0 + 1	—	19	SM	A	—	—	1f	[75]
	<i>M. fuliginosus</i>	C	46	50	2 + 0 + 1	—	19	SM	A	—	G, FISH	—	[76]
	<i>M. fuliginosus</i>	C	46	50	2 + 1 + 0	—	19	SM	—	—	C, G	1f	[77]
	<i>M. schreibersii</i>	C	46	50	2 + 1 + 0	—	19	SM	A	—	—	1m	[65]

*The chromosome image is not shown at the sources; "—", no data.

Columns: reg.—geographical regions, M-SM—number of biarmed chromosome pairs (size: large + medium + small); Diff. stain.—differential staining of chromosome (G, C, etc.); NOR—AgNOR-banding (cmc—centromere-cap NORs, int—interstitial NORs); N—number of specimens examined (f—female, m—male); Ref.—literature sources.

Morphology of chromosomes: M—metacentric, SM—submetacentric, M-SM—biarmed, ST—subtelocentric, A—acrocentric, dot—dot-like chromosome.

Geographical regions abbreviations: E—Europe, S—Siberia, FE—Far East, J—Japan, C—China, K—Korea, T—Thailand, M—Malaysia.

Table 2. Far Eastern bats karyological data.

regions for the first time and to reveal availability or lack of this variability. For simplicity sake, three size groups have been introduced to analyze size variability of two-arm (M-SM) chromosomes: large, medium-sized, and small ones, with their respective karyotype numbers assigned. This allowed us to show the karyotype variability based on this feature. Besides, **Table 2** also shows the previous study of the species by using different sequential staining methods for the chromosomes, thus making it possible to differentiate species with a similar chromosome formula.

Integrated data on the karyotypes, extent of their studies, and chromosome variability of the Russian Far Eastern bats are provided below.

2.1. Family Vespertilionidae Gray, 1821: common bats

2.1.1. Genus *Myotis* Kaup, 1829: mouse-eared bats

All *Myotis* species have similar karyotypes: $2n = 44$ [7, 35, 39, 42, 46]. The fundamental arms number varied from 50 to 52 in different studies. This is due to the fact that some authors accounted for short euchromatic arms on the seven autosomal pairs [7, 39], while the others described this one as an acrocentric [41, 43, 46–48, 54–57]. For some authors, NFA also covered the additional heterochromatic short arms on 24 or 25 pairs of acrocentrics [41, 43, 52, 53, 55, 57]. The species of genus *Myotis* showed the centromere-cap NORs (cmcNORs), with the distributional pattern of NORs in *Myotis* karyotype being species-specific [7, 39, 42].

The amount and location of C-band in Eurasian *Myotis* chromosomes varies intra- and inter-specifically [39, 41, 43, 54, 55]. Eurasian *Myotis* species proved to have small heterochromatic segments close to the centromere on most of the chromosomal arms. Certain *Myotis* species show a distinct intercalary heterochromatic segments found in the proximal part of chromosome 15, in the vicinity of the centromere on chromosomal arm 16, and in the short arm of the X-chromosome adjacent to the centromere [39]. The size and morphology of Y-chromosome were species-specific and depended on amount of heterochromatic material in chromosome [39]. Asian bat species karyotypes have a distinctly pronounced totally heterochromatic short arm on one of the dot-like chromosomes 24 and 25. There might be a tiny second arm in several species or a large heterochromatic secondary arm of the same size as the euchromatic arm [39, 41, 43].

The genus *Myotis* is the most frequently found bats genus in the Russian Far East, with seven recorded species. Of these, six species are also spread in Northeast Asia and five species are common in Siberia. Karyotype of one species was reported found in Siberia. The karyotypes of four *Myotis* species studied are common for the Russian Far East. The karyotypes of five *Myotis* species were described from Northeast Asia.

***M. bombinus* Thomas, 1906.** The karyotypes were described from Japan species. The cmcNORs were shown to be located in 11 autosomal pairs: from 7 to 15, 19, and 22. The heterochromatic short arms on chromosome 25 of *M. bombinus* were tiny or absent at all [41].

***M. ikonnikovi* Ognev, 1912.** The karyotypes were reported from Japan and the Russian Far East. It was shown that the cmcNORs were located in 7, 13, 14, 22, and 23 autosomal pairs.

Intraspecific variability is likely to exist here regarding the large heterochromatic short arms on the 25 autosomal pairs [41].

***M. longicaudatus* Ognev, 1927.** The karyotype was studied using the Japan species. The cmcNORs were located on 13 autosomal pairs: from 8 to 11, from 13 to 15, and from 18 to 23. The morphology of Y-chromosome seems to vary from acrocentric [41] and subtelocentric [43] to submetacentric [55]. The morphology of chromosome 25 appears to vary from acrocentric to submetacentric due to the presence or absence of heterochromatic short arms [41, 43].

***M. macrodactylus* (Temminck, 1840).** The karyotype was described using Northeast Asia and the Russian Far East specimens (**Figure 1**). The cmcNORs were located on 18–23 autosomal pairs. The morphology of chromosome 25 seems to vary from acrocentric chromosome in *M. macrodactylus* from the Russian Far East [46], Korea [58], and Japan [54] to metacentric chromosome in other Japanese *M. macrodactylus* [41, 43, 53, 55, 56]. The presence of one B-chromosome for *M. macrodactylus* from Japan has been showed [56].

***M. petax* Hollister, 1912.** The conventionally stained karyotype of *M. petax* was studied from Korea and the Russian Far East. The Korean and Far Eastern *M. petax* appeared to differ by a number of small biarmed chromosomal pairs.

***M. sibirica* Kaschenko, 1905.** The routinely staining karyotype was described from Siberia and the Russian Far East. No pronounced differences in the karyotypes of Siberian and Far Eastern *M. sibirica* have been found.

***M. gracilis* Ognev, 1927.** The conventionally stained karyotype of *M. gracilis* was studied from Korea.

So, out of seven Far Eastern species, *Myotis* karyotype has been studied for all of them. Although all *Myotis* species have similar karyotypes with $2n = 44$, the distributional pattern of NORs and the amount and location of heterochromatic material in the karyotype are the

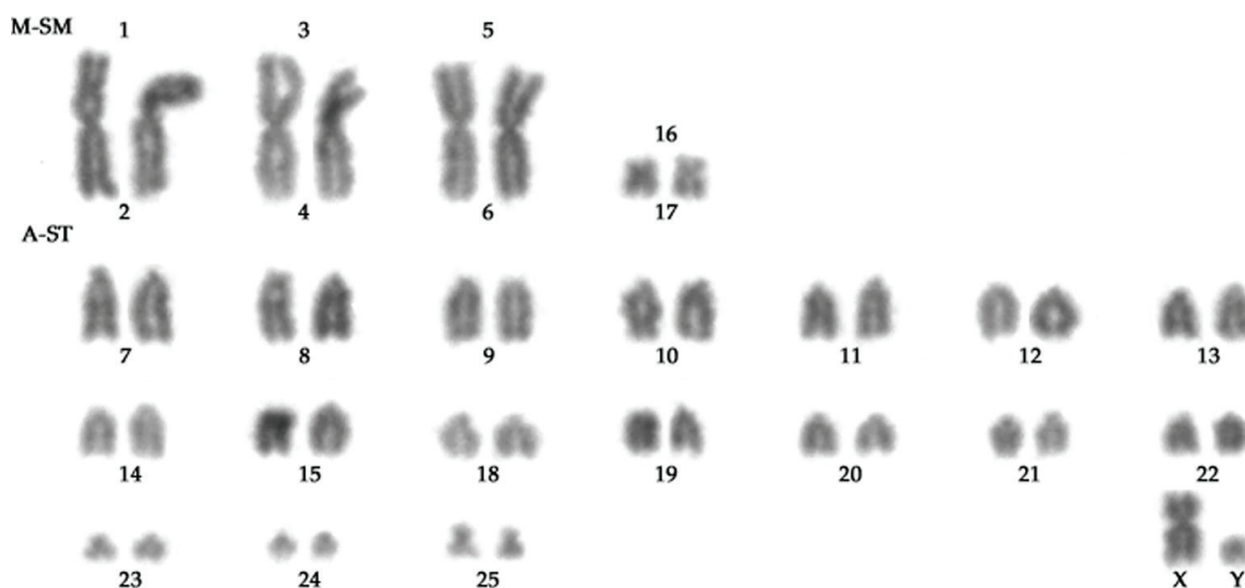


Figure 1. Karyotype of *Myotis macrodactylus* from the Russian Far East [our data].

most important differentiating characteristics for the *Myotis* species. Various levels of the data studied for differently staining *Myotis* chromosomes from various Northeastern regions make it impossible to do species comparative analysis based on the above features.

2.1.2. Genus *Plecotus* Gray, 1866: Old World long-eared bats

The species of genus *Plecotus* are characterized by a karyotype with $2n = 32$, $NFa = 50$ [43, 47, 49, 66]. The distributional pattern of NORs is a centromere-cap NOR (cmcNORs) [42, 43, 47].

There are two species of *Plecotus* in the Russian Far East: *P. ognevi* and *P. sacrimontis*.

***P. ognevi* Kishida, 1927.** The karyotype of *P. ognevi* was described from the Russian Far East (Figure 2). Four NORs were found belong to acrocentric chromosomes of *P. ognevi*; but it was impossible to determine the numbering of these chromosomal arms according to *Myotis*-type karyotype because of G-banding failure [47]. The distributional patterns of heterochromatic material in karyotype were shown: large heterochromatic segments were found in all biarmed autosomal pairs, while small C-band emerged in the most acrocentric chromosomes except the first pair [47].

G-staining, Q-banding, and Zoo-FISH of Siberian *P. ognevi* karyotypes were studied. A pericentric inversion or centromere shift on the smallest metacentric *P. ognevi* chromosome 16/17 using the HSA 16 probe was revealed, which accounted for the differences between G-banding patterns and the homologous *Myotis* species chromosome [51].

***P. sacrimontis* G. Allen, 1908.** Karyotype of *P. sacrimontis* was reported from Northeast Asia. NORs were located on chromosomes 20, 22, 23, and 24 [43], while the European species *P. auritus* Linnaeus, 1758 showed NORs on 20, 22, 24, and 25 autosomal pairs [42].

So, all *Plecotus* species have similar karyotypes with $2n = 32$, $NFa = 50$. *P. auritus* and *P. sacrimontis* had different NORs distribution on chromosomes. For *P. ognevi*, it was impossible to determine the numbering and NOR location on chromosomal arms. Heterochromatic distribution pattern in karyotype was studied only for *P. ognevi* from the Russian Far East, thus making it impossible to compare data from various species and regions.

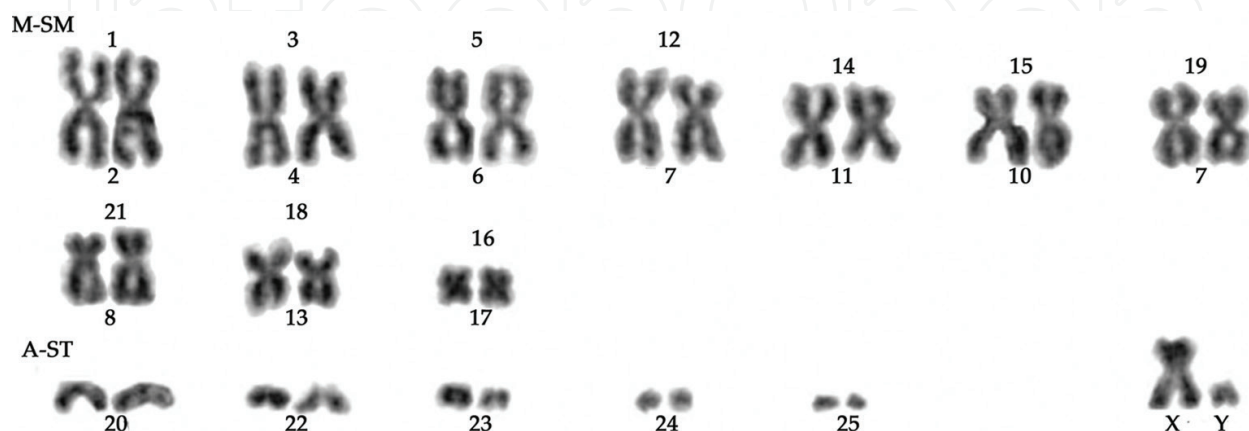


Figure 2. Karyotype of *Plecotus ognevi* from the Russian Far East. The figure was previously published in our paper, see [49].

2.1.3. Genus *Barbastella* Gray, 1821: *barbastelles*

Karyotype of *Barbastella* is similar to that of the *Plecotus* karyotype: $2n = 32$, $NFa = 50$. The distributional pattern of NORs is cmcNORs [43].

There is only one species of genus *Barbastella* in the Russian Far East—*B. darjelingensis* **Hodgson, 1855**. It can be found exclusively on the island of Kunashir [23, 78]. The chromosomal set was reported only from *B. darjelingensis* from Northeast Asia. Five NORs were found on 21–25 autosomal pairs of standard *Myotis-type* karyotype [43].

2.1.4. Genus *Pipistrellus* Kaup, 1829: *pipistrelles*

The genus *Pipistrellus* is characterized by considerable variability of $2n$ and NFa [35].

There is one pipistrelles species inhabiting the Russian Far East, i.e., *P. abramus* **Temminck, 1840**. Karyotype of *P. abramus* was described from Northeast Asia. Unlike other pipistrelles, *P. abramus* has low number $2n$ and NFa ($2n = 26$, $NFa = 44$) due to centric fusions. Chromosome rearrangements complexity makes it impossible to identify the chromosomal arms by G-banding that were involved in composition of 5 out of 10 banded pairs of *P. abramus* karyotype. Therefore, the numbering of *P. abramus* chromosomes differs from *Myotis-type* karyotype [43, 54, 63, 65].

The distributional pattern of NORs is interstitial (intNORs). The large NOR was located in secondary constriction (SC) of five metacentric pairs consisting of 14 and 7 autosomal pairs of *Myotis-type* karyotype [43].

The intraspecific variations of sex chromosomes in karyotype of especially *P. abramus* were likely to be found. Many researchers identified X chromosome morphology as a medium-sized acrocentric, while the X chromosome of the *P. abramus* from Fukuoka prefecture (Japan) was described as subtelocentric [54]. The Y chromosome of *P. abramus* was usually characterized as the smallest acrocentric, while the Y chromosome of the same species from Gunma prefecture (Japan) was described as a small metacentric [52].

High intraspecific variability of heterochromatic material seems to be specific of the *P. abramus* karyotype. This variability for *P. abramus* from Northeast Asia is presented in **Table 3**.

The *P. abramus* karyotype is described only from Northeastern Asia specimens, which can be possibly accounted for by existing intraspecific variability based on morphology of sex chromosomes, number and localization of structural heterochromatin in karyotype.

2.1.5. Genus *Vespertilio* Linnaeus, 1758: *particolored bats*

All specimens of genus *Vespertilio* showed the karyotypes with $2n = 38$, $NFa = 50$ [35, 44, 79]. All *Vespertilio* species showed location of two large intNORs in the SC of 15 and 23 autosomal pairs [42, 43]. There are two *Vespertilio* species in the Russian Far East—*V. murinus* and *V. sinensis*.

V. murinus Linnaeus, 1758 is the trans-Palearctic bat species, whose karyotype was described from Europe, Siberia, and the Russian Far East. The NOR distributional pattern was reported from Europe [42]. The chromosome characteristics show stability across the entire area of its distribution (Figure 3).

V. sinensis Peters, 1880 belongs to the East Asian bat species. The karyotype was described from Northeast Asia and the Russian Far East. NFa = 54 was shown to characterize some specimens from Japan, probably due to the fact that certain researchers included small heterochromatic secondary arms on the two smallest acrocentric in NFa [68]. The distributional pattern of NORs was reported from Northeast Asia [43]. The significant intraspecific polymorphism seems to exist in regard to amount and location of heterochromatic material in karyotype of Japanese *V. sinensis* (Table 4).

2n	NFa	No. chromosomal arms														Reg.	Ref.
		1	2	3	4	5	6	7	8	9	10	11	12	X	Y		
26	44	+	+	+	+	+	+	+	o	o	o	+	o	+	•	J	[55]
26	44	+	+	+	+	+	o	o	o	o	+	+	o	+	–	J	[54]
26	44	+	+	+	+	o	o	o	o	o	o	o	o	o	–	J	[43]
26	44	+	+	+	+	+	o	+	o	+	+	+	+	+	•	C	[63]
26	44	+	+	+	+	o	o	o	o	o	+	+	o	+	–	C	[65]

Note: o—totally euchromatic chromosomes; +—heterochromatic band in vicinity of the centromere; •—totally heterochromatic chromosomes.

Geographical regions abbreviations: J—Japan, C—China.

Table 3. Intraspecific variations of heterochromatic material in karyotypes of *Pipistrellus abramus*.

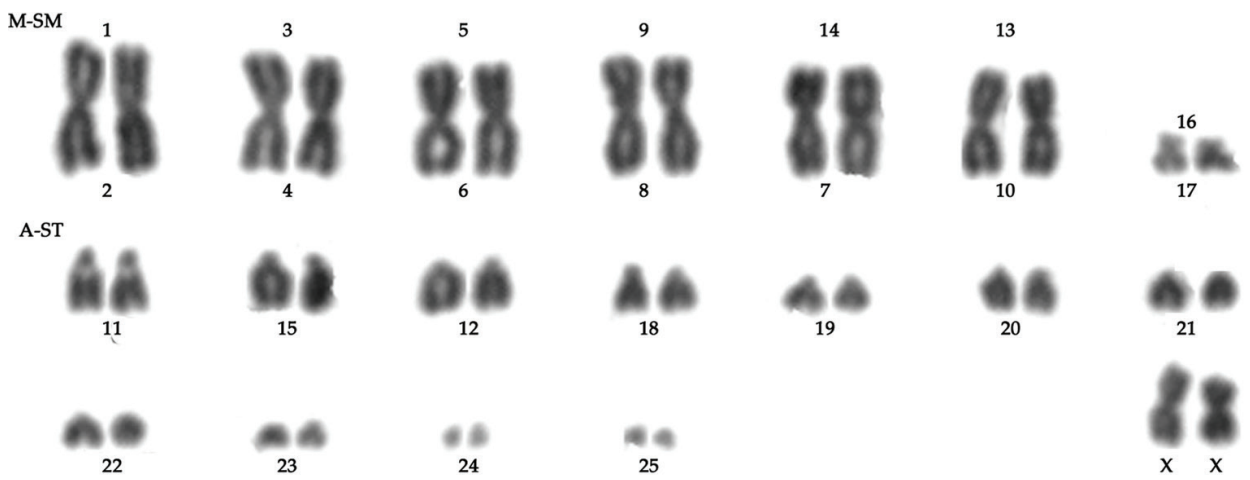


Figure 3. Karyotype of *Vespertilio murinus* from the Russian Far East. The figure previously was published in our paper, see [49].

2n	NFa	No. chromosomal arms																				Ref.
		1/2	3/4	5/6	13/7	11/8	9/ 10	16/ 17	12	14	*15	18	19	20	21	22	*23	24	25	X	Y	
38	50	○	○	○	○	○	○	○	○	○	int	+	+	+	+	+	+	●	●	+	●	[67]
38	50	○	○	+	○	+	○	+	+	+	+	○	+	+	+	+	+	●	●	+	●	[55]
38	54	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	●	●	+	●	[68]
		int		int							int											
38	50	+	+	+	+	int	+	+	+	+	○	+	+	+	+	+	+	●	●	+	●	[69]
				int							int											

Note: ○—totally euchromatic chromosomes; +—heterochromatic band in vicinity of the centromere; ●—totally heterochromatic chromosomes; *—secondary construction on the chromosome.

Table 4. Intraspecific variations of heterochromatic material in karyotypes of Japanese *Vespertilio sinensis*.

The localization of telomeric sequences (TTAGGG)_n was described by FISH for *V. sinensis* from Japan. Hybridization signals were observed at both ends of all *V. sinensis* chromosomes along with very faint and small-sized interstitial signals that were also present at centromeric sites of all seven biarmed chromosomes. Large and intense hybridization signals revealed themselves at the centromeric regions in eight pairs of acrocentric autosomes (18–25) and the Y chromosome of *V. sinensis*. It is interesting to note that C-band of the smallest acrocentric pair 25 and of the Y chromosome displayed a complete hybridization, while interstitial C-band in 5/6, 7/13, and 15 autosomal pairs in *V. sinensis* exhibited no hybridization. Internal telomeric sequences were observed in the heterochromatic regions or satellite DNA on chromosomes that may indicate recent chromosomal rearrangements occurred in the evolution process [69].

While the chromosome characteristics of *V. murinus* show stability across the entire area of its distribution, the karyotype of *V. sinensis* seems to have a significant intraspecific polymorphism regarding the content of structural heterochromatin in the karyotype.

2.1.6. Genus *Hypsugo* Kolenati, 1856: *high pipistrelles*

The diploid number and fundamental number of genus *Hypsugo* chromosomes noticeably vary due to the centric fusions as well as inversions and centromere shift [44]. The *Hypsugo* species show both intNORs and cmcNORs. The *H. savii* Bonaparte, 1837 (2n = 44, NFa = 50) and *H. eisentrauti* (Hill, 1968) (2n = 42, NFa = 58) exhibit only one intNORs in SC of chromosome 15, while *H. crassulus* Thomas, 1904 (2n = 30, NFa = 56) possesses cmcNORs on chromosomes 3 and 19 and in proximal part of chromosome 15/25 [44].

There is only one *Hypsugo* species found in the Russian Far East—*H. alashanicus* Bobrinskoy, 1926. This karyotype was described from Northeast Asia and the Russian Far East 2n = 44, NFa = 50.

2.1.7. Genus *Eptesicus* Rafinesque, 1820: *serotines*

Karyotypes of all autosomes belonging to *Eptesicus* species can be characterized as acrocentric: 2n = 50, NFa = 48 [8, 36, 44].

There is only one *Eptesicus* species found in the Russian Far East—*E. nilssonii* Keyserling & Blasius, 1839. *E. nilssonii* species distribution is trans-Palearctic. The karyotype of *E. nilssonii* was reported from Europe, Northeast Asia, and the Russian Far East (**Figure 4**). $2n$ and NFa are the same for most of the studied *E. nilssonii* excepting this one from Hokkaido with one biarmed autosomal pair in karyotype [69]. The large intNORs is located on secondary constriction in chromosome 15 [44, 47].

The amount and location of heterochromatic material in karyotype was described for *E. nilssonii* from the Russian Far East. There were small C-bands on all chromosomes pairs, and the fourth largest pair showed a large interstitial heterochromatic segment. The SC on chromosome 15 showed C-band [47].

The chromosome characteristics of *E. nilssonii* including distributional pattern of NORs show stability across the entire area of its distribution. Structural heterochromatin distribution pattern was studied only for the Far Eastern *E. nilssonii*, which prevented us from evaluating variability of this feature.

2.1.8. Genus *Murina* Gray, 1842: tube-nosed bats

The karyotypes of tube-nosed bats do not differ from $2n = 44$ [72, 80, 81], while NFa varies from 50 to 60 probably due to subtelocentric pairs produced by the pericentric inversions [7, 71, 79]. The distributional pattern of NORs is cmcNORs [43, 80]. There are two *Murina* species in the Russian Far East, which are *M. hilgendorfi* and *M. ussuriensis*.

***M. ussuriensis* Ognev, 1914.** Karyotype of *M. ussuriensis* was described from Japan. With the known localization type, the localization of multiple cmcNORs on chromosomes has not been determined yet because G-banding has not been done [43].

The amount and location of heterochromatic material in *M. ussuriensis* karyotype were described from Japan. The autosomal pairs 5/6, 16/17, 20, 24 and X chromosome showed small centromeric C-bands, while the Y chromosome was totally heterochromatic. The interstitial faintly stained C-band was revealed in the distal part of X chromosome [72].

***M. hilgendorfi* Gray, 1842.** Karyotype of *M. hilgendorfi* was described from Siberia, Northeast Asia, and the Russian Far East region (**Table 2**).

Karyotype of one specimen from Primorsky Velican cave (the Russian Far East) was clearly different from other *M. hilgendorfi* ones by the number of large biarmed pairs: there were only two large metacentric pairs, one medium-sized submetacentric pair being approximately equal to a long arm of large metacentric pair and one small metacentric pair [47]. The same karyotype was previously described for a tube-nosed bat from Thailand [70]. It was originally reported as *M. leucogaster* Milne-Edwards, 1872, though later the bat was redefined as *M. harrisoni* Csorba & Bates, 2005 [82]. However, karyotypes of other specimens of *M. harrisoni* [81, 83] and *M. leucogaster* [84] exhibited karyotype with three large biarmed chromosomal pairs.

The amount and location of heterochromatic material in karyotype were shown for *M. hilgendorfi* from Japan. There were small C-band close to centromere on chromosomes 5/6, 16/17, 20, 24 and X chromosome with totally heterochromatic Y chromosome [72].

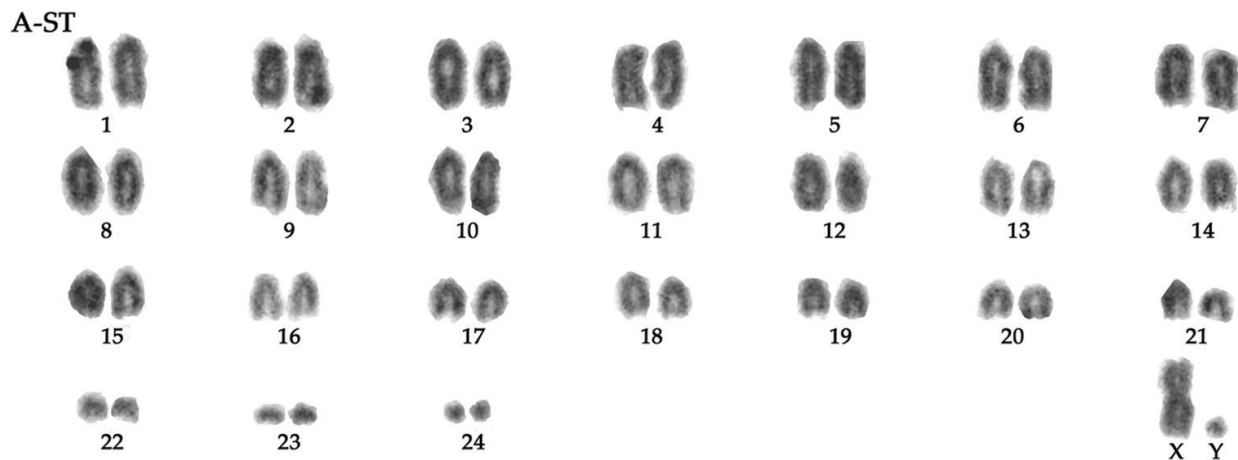


Figure 4. Karyotype of *Eptesicus nilssonii* from the Russian Far East. The figure previously was published in paper [48].

The location of structural heterochromatin of *M. ussuriensis* and *M. hilgendorfi* from Japan scarcely differs from each other. *M. hilgendorfi* karyotype with two large metacentric pairs, one medium-sized submetacentric pair and 1 small metacentric pair described from the Russian Far East, seemed to be either in error or an isolated case that requires verification.

2.2. Family Miniopteridae Dobson, 1875: bent-winged bats

2.2.1. Genus *Miniopterus* Bonaparte, 1837: bent-winged bats

Karyotypes of bent-winged bats are clearly different from standard *Myotis-type* karyotype due to chromosomal rearrangements. By using GTG-staining and FISH methods, the biarmed chromosome 3/4 of *Myotis-type* karyotype was shown to be similar to two acrocentric pairs of *Miniopterus*, due to centric fissions the metacentric pair 16/17 assumed the shape of an acrocentric, and the acrocentric pair 12 became biarmed due to pericentric inversions, with the G-banding pattern of 7 and 10 autosomal arms being different from standard *Myotis-type* karyotype [76].

There is one species of the monotypic family Miniopteridae found in the Russian Far East that is *M. fuliginosus* Hodgson, 1835. Karyotype ($2n = 46$, $NFa = 50-52$) was described from Northeast Asia.

The *M. fuliginosus* seems to exhibit intraspecific polymorphism by the number of biarmed autosomal pairs. Karyotype with two large and one small biarmed pairs is most common. *M. fuliginosus*, with its mostly encountered karyotype, was found in Malaysia, Thailand, China, and Japan [43, 74–76]. Karyotype with two large and one medium biarmed chromosomal pair was described from China [65, 77]. Karyotype of *M. fuliginosus* from Thailand was similar to the previous one with one exception: it had one subtelocentric pair [71]. Karyotype with two large, one medium, and one small biarmed pairs was described from Japan [53, 73].

One cmcNORs was shown to be located on 20 autosomal pair and one intNOR is located on chromosome 23 in the *M. fuliginosus* karyotype from Japan [43]. The small C-band close to centromere was described to be located on all chromosomal pairs of Chinese *M. fuliginosus* [77].

So, *M. fuliginosus* from Northeastern Asia seems to be characterized by intraspecific chromosome polymorphism based on the number of autosomal pairs.

3. Conclusion

For the first time, the references' analysis undertaken enabled us to demonstrate the extent of chromosome characteristics studied for bats from the Russian Far East. It also illustrated the nature of the intrageneric and intraspecific chromosome variability of the bats from the Russian Far East.

The data available enable us to suggest *Miniopterus fuliginosus*, *Murina hilgendorfi*, and some *Myotis* species to show intraspecies chromosome polymorphism regarding biarmed autosomal pairs. Intraspecies variability could be fairly assumed to exist as regards X,Y chromosomes in *P. abramus*, *M. longicaudatus* and *M. macrodactylus* karyotypes from Northeastern Asia. A significant intraspecies polymorphism regarding structural heterochromatin in a karyotype seems to be available in *V. sinensis*, *P. abramus*, and *Myotis* species. Such important characteristic as the amount and localization of cmcNORs on chromosomes has been very irregularly studied for the Far Eastern bat species, which restricts our ability to compare data from different regions. There is not enough data to compare *Barbastella* and *Hypsugo* species in terms of their karyotype chromosome characteristics.

Thus, one might make a conclusion that karyotypes of the majority bats from the Russian Far East and Siberia still remain to be studied. The bats from Northeastern Asia and Europe have their bats' chromosome characteristics somewhat more fully explored, though we still have considerable gaps in our knowledge of karyotypes for certain bats' species.

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References

- [1] Strelkov PP. The crisis of the polytypic species concept as illustrated by the genus *Plecotus*. *Plecotus et al.* 2006;**9**:3-7
- [2] Tiunov MP. Bats of the Russian Far East. Vladivostok: Dal'nauka Press; 1997. 134 pp

- [3] Kruskop SV. Towards the taxonomy of the Russian *Murina*. Russian Journal of Theriology. 2005;4(2):135-140. DOI: 10.15298/rusjtheriol.4.2.01
- [4] Bulkina TM, Kruskop SV. Search for morphological differences between genetically distinct brown long-eared bats (*Plecotus auritus* s. lato, Vespertilionidae). Plecotus et al. 2009;11-12:3-13
- [5] Matveev VA, Kruskop SV, Kramerov DA. Revalidation of *Myotis petax* Hollister, 1912 and its new status in connection with *M. daubentonii* (Kuhl, 1817) (Vespertilionidae, Chiroptera). Acta Chiropterologica. 2005;7(1):23-37. DOI: 10.3161/1733-5329(2005)7[23:ROMPHA] 2.0.CO;2
- [6] Spitzenberger F, Strelkov PP, Winkler H, Haring E. A preliminary revision of the genus *Plecotus* (Chiroptera, Vespertilionidae) based on genetic and morphological results. Zoologica Scripta. 2006;35(3):187-230. DOI: 10.1111/j.1463-6409.2006.00224.x
- [7] Volleth M, Heller KG. Phylogenetic relationships of vespertilionid genera (Mammalia: Chiroptera) as revealed by karyological analysis. Zeitschrift für Zoologische Systematik und Evolutionsforschung. 1994;32:11-34. DOI: 10.1111/j.1439-0469.1994.tb00467.x
- [8] Kearney TC, Volleth M, Contrafatto G, Taylor PG. Systematic implications of chromosome GTG-band and bacula morphology for southern African *Eptesicus* and *Pipistrellus* and several other species of Vespertilioninae (Chiroptera: Vespertilionidae). Acta Chiropterologica. 2002;4(1):55-76. DOI: 10.3161/001.004.0107
- [9] Volleth M, Son NT, Wu Y, Li Y, Yu W, Lin LK, Arai S, Trifonov V, Liehr T, Harada M. Comparative chromosomal studies in *Rhinolophus formosae* and *R. luctus* from China and Vietnam: Elevation of *R. l. lanosus* to species rank. Acta Chiropterologica. 2017;19(1):41-50. DOI: 10.3161/15081109ACC2017.19.1.003
- [10] Maeda K. Review on the classification of little tube-nosed bats, *Murina aurata*, group. Mammalia. 1980;44(4):531-551. DOI: 10.1515/mamm.1980.44.4.531
- [11] Horaček I, Hanak V. Comments on the systematics and phylogeny of *Myotis nattereri* (Kuhl, 1818). Myotis. 1984;21-22:20-29
- [12] Yoshiyuki M. A Systematic Study of the Japanese Chiroptera. Tokyo: National Science Museum; 1989. p. 242
- [13] Horaček I. Status of *Vesperus sinensis* Peters, 1880 and remarks on the genus *Vespertilio*. Vespertilio. 1997;2:59-72
- [14] Horaček I, Hanak V, Gaisler J. 2000. Bats of the Palearctic : A taxonomic and biogeographic review. In: Proceedings of the 8th European Bat Research Symposium (EBRS'00); January 2000; Krakow. Krakow: Institute of Systematics and Evolution of Animals PAS; 2000. pp. 11-157. DOI: 10.13140/2.1.4099.2643
- [15] Kawai K, Nikaido M, Harada M, Matsumura S, Lin LK, Wu Y, Hasegawa M, Okada N. The status of the Japanese and east Asian bats of the genus *Myotis* (Vespertilionidae) based on mitochondrial sequences. Molecular Phylogenetics and Evolution. 2003;28(2):297-307. DOI: 10.1016/S1055-7903(03)00121-0

- [16] Tian L, Liang B, Maeda K, Metzner W, Zhang S. Molecular studies on the classification of *Miniopterus schreibersii* (Chiroptera: Vespertilionidae) inferred from mitochondrial cytochrome b sequences. *Folia Zoologica*. 2004;**3**(53):303-311
- [17] Kawai K, Kondo N, Sasaki N, Fukui D, Dewa H, Satô M, Yamaga Y. Distinguishing between cryptic species *Myotis ikonnikovi* and *M. brandtii gracilis* in Hokkaido, Japan: Evaluation of a novel diagnostic morphological feature using molecular methods. *Acta Chiropterologica*. 2006;**8**(1):95-102. DOI: 10.3161/1733-5329(2006)8[95:DBCSMI]2.0.CO;2
- [18] Benda P, Dietz C, Andreas M, Hotovy J, Lucan RK, Maltby A, Meakin K, Truscott J, Vallo P. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 6. Bats of Sinai (Egypt) with some taxonomic, ecological and echolocation data on that fauna. *Acta Societatis Zoologicae Bohemicae*. 2008;**72**:3-103
- [19] Artyushin IV, Bannikova AA, Lebedev VS, Krusko SV. Mitochondrial DNA relationships among North Palaearctic *Eptesicus* (Vespertilionidae, Chiroptera) and past hybridization between Common Serotine and Northern Bat. *Zootaxa*. 2009;**2262**:40-52. DOI: 10.11646/zootaxa.2262.1.2
- [20] Krusko SV, Borisenko AV, Ivanova NV, Lim BK, Eger JL. Genetic diversity of northeastern Palaearctic bats as revealed by DNA barcodes. *Acta Chiropterologica*. 2012;**14**(1):1-14. DOI: 10.3161/150811012X654222
- [21] Ruedi M, Csorba G, Lin LK, Chou CH. Molecular phylogeny and morphological revision of *Myotis* bats (Chiroptera: Vespertilionidae) from Taiwan and adjacent China. *Zootaxa*. 2015;**3920**(1):301-342
- [22] Krusko SV. Order Chiroptera. In: Pavlinov IY, Lisovsky AA, editors. *The Mammals of Russia: A Taxonomic and Geographic Reference*. Moscow: KMK Sci. Press; 2012. 604 p
- [23] Tiunov MP. Distribution of the bats in Russian Far East (Problems and questions). In: *Proceedings of the Japan-Russia Cooperation Symposium on the Conservation of the Ecosystem*; 2011; Okhotsk. Sapporo. 2011. pp. 359-369
- [24] Vorontsov NN. The importance of chromosomal sets for mammalian taxonomy. *Bulletin of the Moscow Society of Naturalists*. 1958;**6**(2):5-36
- [25] Matthey R. The chromosome formulae of eutherian mammals. In: *Cytotaxonomy and Vertebrate Evolution*. London: Academic Press; 1973. pp. 531-616
- [26] Korablev VP. Localization of nucleolar organizer regions in mammals. In: *Questions of Evolutionary Zoology and Mammalian Genetics*. Vladivostok. 1987. pp. 37-44
- [27] Sánchez A, Burgos M, Jiménez R, Díaz de la Guardia R. Variable conservation of nucleolus organizer regions during karyotypic evolution in Microtidae. *Genome*. 1990;**33**(1): 119-122
- [28] Boeskorov GG, Kartavtseva IV, Zagorodnyuk IV, Belyanin AN, Lyapunova EA. Nucleolus organizer regions and B-chromosomes of wood mice (Mammalia, Rodentia, Apodemus). *Russian Journal of Genetics*. 1995;**31**(2):185-192

- [29] Kartavtseva IV. Karyosystematics of Wood and Field Mice (Rodentia: Muridae). Vladivostok: Dal'nauka Press; 2002. 144 p
- [30] Hsu TC, Arrighi FE. Distribution of constitutive heterochromatin in mammalian chromosomes. *Chromosoma*. 1971;**34**(3):243-253. DOI: 10.1007/BF00286150
- [31] White MJD. *Animal Cytology and Evolution*. 3rd ed. Cambridge: Cambridge University Press; 1973. 961 p
- [32] Prokofyeva-Belgovskaya AA. Heterochromatic regions of chromosomes: Structure and functions. *Biology Bulletin Reviews*. 1977;**38**(5):735-757
- [33] Prokofyeva-Belgovskaya AA. *Heterochromatic Regions of Chromosomes*. Moscow: Nauka; 1986. 431 p
- [34] Korobitsyna KV, Korablev VP. The intraspecific autosome polymorphism of *Meriones tristrami* Thomas, 1892 (Gerbillinae, Cricetidae, Rodentia). *Genetica*. 1980;**52-53**(1):209-221. DOI: 10.1007/BF00121829
- [35] Vorontsov NN, Radjabli SI, Volobuev VT. The comparative karyology of the vespertilionid bats, Vespertilionidae (Chiroptera). In: Vorontsov NN, editor. *The Mammals (Evolution, Karyology, Taxonomy, Fauna)*. Novosibirsk: Nauka Press; 1969. pp. 16-21
- [36] Baker RJ. Karyotypic trends in bats. In: *Biology of Bats*. Vol. 1. New York: Academic Press; 1970. pp. 65-95
- [37] Baker RJ, Bickham JW. Karyotypic evolution in bats: Evidence of extensive and conservative chromosomal evolution in closely related taxa. *Systematic Zoology*. 1980;**29**(3):239-253. DOI: 10.1093/sysbio/29.3.239
- [38] Baker RJ, Qumsiyeh MB, Hood CS. Role of chromosomal banding patterns in understanding mammalian evolution. In: Genoways HH, *Current Mammalogy*. Boston: Springer; 1987. pp. 67-96. DOI: 10.1007/978-1-4757-9909-5_2
- [39] Volleth M, Heller KG. Variations on a theme: Karyotype comparison in Eurasian *Myotis* species and implications for phylogeny. *Vespertilio*. 2012;**16**:329-350
- [40] Bickham JW. Banded karyotypes of 11 species of American bats (genus *Myotis*). *Cytologia*. 1979;**44**:789-797. DOI: 10.1508/cytologia.44.789
- [41] Harada M, Yoshida TH. Karyological study of four Japanese *Myotis* bats (Chiroptera, Mammalia). *Chromosoma (Berlin)*. 1978;**65**:283-291. DOI: 10.1007/BF00327623
- [42] Volleth M. Differences in the location of nucleolus organizer regions in European vespertilionid bats. *Cytogenetics and Cell Genetics*. 1987;**44**:186-197. DOI: 10.1159/000132371
- [43] Ono T, Obara Y. Karyotypes and Ag-NOR variations in Japanese vespertilionid bats (Mammalia: Chiroptera). *Zoological Science*. 1994;**11**(3):473-484
- [44] Volleth M, Bronner G, Gopfert MC, Heller KG, von Helversen O, Yong HS. Karyotype comparison and phylogenetic relationships of *Pipistrellus*-like bats (Vespertilionidae; Chiroptera; Mammalia). *Chromosome Research*. 2001;**9**:25-46. DOI: 10.1023/A:1026787515840

- [45] Volleth M, Heller KG, Fahr J. Phylogenetic relationships of three “Nycticeiini” genera (Vespertilionidae, Chiroptera, Mammalia) as revealed by karyological analysis. *Mammalian Biology—Zeitschrift für Säugetierkunde*. 2006;**71**(1):1-12. DOI: 10.1016/j.mambio.2005.09.001
- [46] Volobuev VT, Strelkov PP. The karyotypes identity in the genus *Myotis*. *Russian Journal of Zoology*. 1971;**4**(12):1892-1894
- [47] Korablev BP, Yakimenko LV, Tiunov MP. Karyotypes of bats in the Russian far east. In: Kryukov AP, Chelomina GN, Pavlenko MV, editors. *The Present-Day Approached to Studies of Variability: Collection of Scientific Papers*. Vol. 1989. Vladivostok: The Far Eastern Branch Academy of Sciences of the USSR; 1989. pp. 95-98
- [48] Kartavtseva IV, Dokuchayev NE. Studying chromosomes of two types of bats in Kamchatka. In: *Proceedings of the Biological Diversity of Siberian Animals*; 28-30 October 1998; Tomsk. Tomsk: Del'taplan; 1998. pp. 67-68
- [49] Kartavtseva IV, Gorobeiko UV, Tiunov MP. The current status of chromosomal investigations of bats (Chiroptera) from the Russian far east. *Russian Journal of Zoology*. 2014;**93**(7):887-900. DOI: 10.7868/S0044513414070083
- [50] Arslan A, Zima J. Karyotypes of the mammals of Turkey and neighbouring regions: A review. *Folia Zoologica -Praha-*. 2014;**63**(1):1-62. DOI: 10.25225/fozo.v63.i1.a1.2014
- [51] Kulemzina AI, Nie W, Trifonov VA, Staroselec Y, Vasenkov DA, Volleth M, Yang F, Graphodatsky AS. Comparative chromosome painting of four Siberian Vespertilionidae species with *Aselliscus stoliczkanus* and human probes. *Cytogenetic and Genome Research*. 2011;**134**:200-205. DOI: 10.1159/000328834
- [52] Tsuchiya K, Harada M, Yosida TH. Karyotypes of four species of bats collected in Japan. *Annual Report of National Institute of Genetics (Japan)*. 1972;**2**:50-51
- [53] Harada M. Chromosomes of nine chiropteran species in Japan. *La Kromosomo*. 1973;**91**:2885-2895
- [54] Ando K, Harada M, Uchida TA. A karyological study on five Japanese species of *Myotis* and *Pipistrellus*, with special attention to composition of their C-band materials. *Journal of the Mammalogical Society of Japan*. 1987;**12**(1-2):25-29
- [55] Ando K, Tagawa T, Uchida TA. The C-banding pattern of 6 Japanese species of vespertilionine bats (Mammalia: Chiroptera). *Experientia*. 1980;**36**:653-653. DOI: 10.1007/BF01970118
- [56] Obara Y, Tomiyasu T, Saitoh K. Chromosome studies in the Japanese vespertilionid bats: I. Karyotypic variation in *Myotis macrodactylus* Temminck. *Japanese Journal of Genetics*. 1976;**51**(3):201-206. DOI: 10.1266/jjg.51.201
- [57] Park SR, Won PO. Chromosomes of Korean bats. *Journal of the Mammalogical Society of Japan*. 1978;**7**:199-203. DOI: 10.11238/jmammsocjapan1952.7.199
- [58] Yoo DH, Yoon MH. A karyotypic study on six Korean vespertilionid bats. *Korean Journal of Zoology*. 1992;**35**(4):489-496

- [59] Tsuchiya K. A contribution to the chromosome study in Japanese mammals. Proceedings of the Japan Academy. 1979;**55B**(4):191-195. DOI: 10.2183/pjab.55.191
- [60] Uchida TA, Ando K. Karyotype analysis in Chiroptera (I): Karyotype of the eastern barbastelle, *Barbastella leucomelas darjelingensis* and comments on its phylogenetic position. Science Bulletin of the Faculty of Agriculture. Kyushu University. 1972;**26**(1/4):393-398. DOI: 10.15017/23098
- [61] Ando K, Tagawa T, Uchida TA. Considerations of karyotypic evolution within Vespertilionidae. Experientia. 1977;**33**:877-879. DOI: 10.1007/BF01951257
- [62] Obara Y, Tomiyasu T, Saitoh K. Chromosome studies in the Japanese vespertilionid bats: G-banding pattern of *Pipistrellus abramus* Temminck. Proceedings of the Japan Academy. 1976;**52**(7):383-386
- [63] Lin LK, Motokawa M, Harada M. Karyological study of the house bat *Pipistrellus abramus* (Mammalia: Chiroptera) from Taiwan with comments on its taxonomic status. The Raffles Bulletin of Zoology. 2002;**50**(2):507-510
- [64] Wu Y, Harada M, Li Y. Karyology of seven species bats from Sichuan, China. Acta Theriologica Sinica. 2004;**4**(1):30-35
- [65] Wu Y, Motokawa M, Li YC, Harada M, Chen Z, Lin LK. Karyology of eight species of bats (Mammalia: Chiroptera) from Hainan Island, China. International Journal of Biological Sciences. 2009;**5**:659-666. DOI: 10.7150/ijbs.5.659
- [66] Volleth M. Chromosomal homologies of the genera *Vespertilio*, *Plecotus* and *Barbastella* (Chiroptera: Vespertilionidae). Genetica. 1985;**66**:231-236. DOI: 10.1007/BF00128044
- [67] Obara Y, Saitoh K. Chromosome studies in the Japanese vespertilionid bats: IV. Karyotypes and C-banding pattern of *Vespertilio orientalis*. The Japanese Journal of Genetics. 1977;**52**(2):159-161. DOI: 10.1266/jjg.52.159
- [68] Harada M, Ando K, Uchida TA, Takada S. Karyotypic evolution of two Japanese *Vespertilio* species and its taxonomic implication (Chiroptera: Mammalia). Caryologia. 1987;**40**(3):175-184. DOI: 10.1080/00087114.1987.10797821
- [69] Ono T, Yoshida MC. Differences in the chromosomal distribution of telomeric (TTAGGG)_n sequences in two species of the vespertilionid bats. Chromosome Research. 1997;**5**:203-212. DOI: 10.1023/A:1018403215999
- [70] McBee K, Bickham JW, Yehbutra S, Nabhitabhata J, Schlitter DA. Standard karyology of nine species of vespertilionid bats (Chiroptera: Vespertilionidae) from Thailand. Annals of Carnegie Museum. 1986;**55**(5):95-116
- [71] Ono T, Yoshida MC. Banded karyotype of *Eptesicus nilssonii parvus* (Mammalia: Chiroptera). Chromosome Information Service. 1995;**59**:9-21
- [72] Harada M, Ando K, Uchida TA, Takada S. A karyological study on two Japanese species of *Murina* (Mammalia: Chiroptera). Journal of the Mammalogical Society of Japan. 1987;**1-2**:15-23. DOI: 10.11238/jmammsocjapan1987.12.15

- [73] Tsuchiya K. Chromosomes of two insectivorous bat species from Japan. *Journal of the Mammalogical Society of Japan*. 1971;**5**(3):114-116
- [74] Harada M, Kobayashi T. Studies on the small mammal fauna of Sabah, East Malaysia. II. Karyological analysis of some Sabahan mammals. *Contributions from the Biological Laboratory*. 1980;**26**:83-95
- [75] Lin LK, Motokawa M, Harada M. Karyology of ten vespertilionid bats (Chiroptera: Vespertilionidae) from Taiwan. *Zoological Studies*. 2002;**41**(4):347-354
- [76] Ao L, Gu X, Feng Q, Wang J, O'Brien PC, Fu B, Mao X, Su W, Wang Y, Volleth M, Yang F, Nie W. Karyotype relationships of six bat species (Chiroptera, Vespertilionidae) from China revealed by chromosome painting and G banding comparison. *Cytogenetic and Genome Research*. 2006;**115**(2):145-153. DOI: 10.1159/000095235
- [77] Li N, Ao L, He SY, Gu XM. G-bands and C-bands in 3 species of Vespertilionidae. *Chinese Journal of Zoology*. 2007;**42**(2):96-101
- [78] Selezneva TA, Tiunov MP. *Barbastella leucomelas* (Cretzschmar, 1826)—A new species for the fauna of the Russian Far East. In: *Proceedings of VIII Meeting of Theriological Society*; 31 January—2 February 2007; Moscow. Moscow: KMK Scientific Press Ltd; 2007. p. 443
- [79] Bickham J. Chromosomal variation and evolutionary relationships of vespertilionid bats. *Journal of Mammalogy*. 1979;**60**(2):350-363. DOI: 10.2307/1379807
- [80] Volleth M. Karyotype analysis of *Murina suilla* and *Phoniscus atrox* from Malaysia (Chiroptera: Murininae, Kerivoulinae). *Lynx (Praha)*. 2006;**37**:275-284
- [81] Son NT, Csorba G, Tu VT, Thong DV, Wu Y, Harada M, Oshida T, Endo H, Motokawa M. A new species of the genus *Murina* (Chiroptera: Vespertilionidae) from the Central Highlands of Vietnam with a review of the subfamily Murininae in Vietnam. *Acta Chiropterologica*. 2015;**17**(2):201-232. DOI: 10.3161/15081109ACC2015.17.2.001
- [82] Francis CM, Eger JL. A review of tube-nosed bats (*Murina*) from Laos with description of two new species. *Acta Chiropterologica*. 2012;**14**(1):15-38. DOI: 10.3161/150811012X654231
- [83] Wu Y, Motokawa M, Li YC, Harada M, Chen Z, Yu WH. Karyotype of Harrison's tube-nosed bat *Murina harrisoni* (Chiroptera: Vespertilionidae: Murininae) based on the second specimen recorded from Hainan Island, China. *Mammal Study*. 2010;**35**(4):277-279. DOI: 10.3106/041.035.0407
- [84] Gu XM. The karyotypes of six species of bats from Guizhou. *Chinese Journal of Zoology*. 2006;**41**(5):112-116

