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Authors: Shchipanov, Nikolay A., and vlova, Svetlana V. Pa

Source: Folia Zoologica, 62(1) : 24-35

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/fozo.v62.i1.a4.2013>

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Contact zones and ranges of chromosomal races of the common shrew, *Sorex araneus*, in north-eastern European Russia

Nikolay A. SHCHIPANOV and Svetlana V. PAVLOVA*

A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninskiy pr., 119071 Moscow, Russia; e-mail: swpavlova@mail.ru, shchipa@mail.ru

Received 24 May 2012; Accepted 14 June 2012

Abstract. The common shrew is a major evolutionary model for understanding the factors that lead to chromosomal subdivision; it is one of the most chromosomally variable species. We karyotyped 106 common shrews (*Sorex araneus*) from 24 localities in north-eastern European Russia which we showed to belong to five chromosomal races: Kirillov, Manturovo, Petchora, Serov and Sok. These new data were combined with published results on 146 individuals from 55 localities (with three additional races: Kanin, Yagry and Yuryuzan) to provide a substantive analysis of chromosomal variation in this region. The ranges of the eight races were mapped, the areas of contacts between neighbouring races were determined and new interracial hybrid zones were localised. In total, F₁ hybrid karyotypes were found in 22 individuals from 11 localities; including our demonstration of Manturovo-Petchora, Manturovo-Sok, Petchora-Serov, Petchora-Sok and Serov-Sok F₁ hybrid karyotypes for the first time. These hybrids would be expected to produce ring-of-four, ring-of-six or ring-of-eight meiotic configurations. The distribution of the races could not readily be related to environmental or geographic features, and in particular major rivers did not appear important in separation of races. This represents one of the most detailed studies of chromosomal variation in the common shrews at a regional geographic scale and is of especial significance because north-eastern European Russia has been little affected by human activity, and therefore the results are likely to represent fully natural processes.

Key words: distribution, environmental barriers, hybrid zone, parapatry, Robertsonian fusion

Introduction

Due to its extremely high karyotypic variability, the common shrew *Sorex araneus* is an extraordinary model for evolutionary studies (Searle & Wójcik 1998). It is a small insectivorous mammal (order Eulipotyphla, family Soricidae) subdivided into at least 72 parapatric chromosomal races, each characterised by a unique set of metacentric chromosomes formed by Robertsonian fusions and/or whole-arm reciprocal translocations (WARTs; Hausser et al. 1994, Wójcik et al. 2003, White et al. 2010). Among mammals this degree of within-species chromosomal subdivision is only matched by the house mouse *Mus musculus* (Piálek et al. 2005), a species whose chromosomal variation is tied to a colonisation history linked to humans (Gabriel et al. 2010). There is a need to understand why the common shrew should be chromosomally variable in such a dramatic way.

The common shrew is distributed over an area ranging from the British Isles and the Pyrenees in the west to Central Siberia in the east. The northern

part of the European range is of especial interest in terms of the origin of new karyotypic forms (Halkka et al. 1987, 1994, Fredga 1996, 2007, Pavlova 2010), and the pattern of postglacial recolonisation (Hewitt 2000, Polyakov et al. 2001, Orlov et al. 2007), due to both diversity of chromosomal races and complex glacial history of the region. The chromosomal races in this area can be attributed to an origin in glacial refugia in southern parts of Europe (Hewitt 1999, Polyakov et al. 2001), and subsequent long-distance spread northwards; *in situ* or nearby origin in northern glacial refugia (Bilton et al. 1998, Orlov & Kozlovsky 2002, Orlov et al. 2007); or postglacial origin *in situ* or nearby (Wójcik 1993). Anthropogenic alterations to the natural landscape may also contribute to the current distribution of the races and their interactions. For example, the narrow hybrid zone between the Białowieża and Drnholec races in Poland is located at a railway embankment (Szałaj et al. 1996) and anthropogenic changes to landscape structure might promote genetic differentiation among hybridising

* Corresponding Author

Table 1. New karyotypic data on common shrews from north-eastern European Russia. Only the race-specific chromosomes are listed and karyotypic categories include: a) individuals with a homozygous Kirillov (Kr), Petchora (Pt), Sok (So), Manturovo (Ma) and Serov (Se) karyotype; b) simple heterozygotes (denoted as Kr //, etc.); and c) complex heterozygotes (e.g. Kr-Pt hybrid, i.e. F₁ hybrid between Kirillov and Petchora races). Expected meiotic configurations for simple and complex heterozygotes are indicated as CIII (chain-of-three), RIV (ring-of-four), RVI (ring-of-six) and RVIII (ring-of-eight). The interracial karyotypes described for the first time are marked in bold. For some localities there were previous data; karyotypes of individuals published in Pavlova & Bulatova (2010) are indicated by one asterisk, and those published in Shchipanov et al. (2008) by two asterisks.

Map reference	Site name	Latitude/ Longitude	Number of specimens	2NA	Karyotypic category	Karyotype	Meiotic configurations
Arkhangelsk Region							
5	Koynas (left bank of the River Mezen)	N 64°45' E 47°38'	2	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	
8	Kyssa (right bank of the River Mezen)	N 64°38' E 47°52'	6	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	
			1	19	Kr <i>j/l</i>	<i>gm, hi, j/l, kq, no, pr</i>	CIII
			12	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
			5	18	Kr-Pt hybrid	<i>gm/gi/hi/hn/no/mo, jl, kq, pr</i>	RVI
			1	19	Kr-Pt hybrid <i>k/q</i>	<i>gm/gi/hi/hn/no/mo, jl, k/q, pr</i>	RVI + CIII
			1*	18	Kr-Pt WART hybrid or Pt race with WART	<i>gm/gi/io/mo, hn, jl, kq, pr</i>	RIV
9	Kyssa (left bank of the River Mezen)	N 64°38' E 47°51'	8+1**	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	
10	Kyssa, island in the River Mezen	N 64°38' E 47°51'	1	18	Kr-Pt hybrid	<i>gm/gi/hi/hn/no/mo, jl, kq, pr</i>	RVI
			3	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	
			1*	18	Kr-Pt WART hybrid or Pt race with WART	<i>gm/gi/io/mo, hn, jl, kq, pr</i>	RIV
11	Vozhgora (left bank of the River Mezen)	N 64°31' E 48°26'	1+1**	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	
12	Vozhgora (right bank of the River Mezen)	N 64°32' E 48°27'	3	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
			2	18	Kr-Pt hybrid	<i>gm/gi/hi/hn/no/mo, jl, kq, pr</i>	RVI
13	Malaya Pyssa (right bank of the River Mezen)	N 64°09' E 48°50'	2	18	Kr-Pt hybrid	<i>gm/gi/hi/hn/no/mo, jl, kq, pr</i>	RVI
17	Verkhnesensensk	N 64°09' E 49°32'	1	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
			1	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	
			2	18	Ma-Pt hybrid	<i>go/gi/hi/hn/mn/mo, jl, kq, pr</i>	RVI
			1	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
			1	19	Pt <i>j/l</i>	<i>gi, hn, j/l, kq, mo, pr</i>	CIII
			1	18	Pt-Se hybrid	<i>gi/go/mo/km/kq/qr/pr/ip, hn, jl</i>	RVIII
19	10 km S of Dutovo (left bank of the River Pechora)	N 63°41' E 56°34'	1	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
20	15 km N of Lenavozh (left bank of the River Vel'u)	N 63°37' E 55°38'	4	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
21	Ukhta (western outskirts)	N 63°34' E 53°38'	2	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	
22	Sosnogorsk	N 63°36' E 53°53'	1	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	

23	Ukhta (eastern outskirts)	N 63°33' E 53°48'	4 2	18 18	Pt Pt-So hybrid im	<i>gi, hn, jl, kq, mo, pr</i> <i>go/gi/im/mo, hn, jl, kq, pr</i>	RIV
24	Sed'u	N 63°33' E 53°48'	2 1 1	18 19 18	Pt Pt <i>j/l</i> Pt-So hybrid	<i>gi, hn, jl, kq, mo, pr</i> <i>gi, hn, j/l, kq, mo, pr</i> <i>gi/go/mo/mr/pr/ip, hn, jl, kq</i>	CIII RVI
27	15 km N of Komsomol'sk-na-Pechore	N 62°17' E 56°36'	2 1	18 18	So So-Se hybrid	<i>go, hn, ip, jl, kq, mr</i> <i>go, hn, ip, jl, km/mr/qr/kq</i>	RIV
Mary-El Republic							
44	Starozhilsk	N 56°38' E 47°16'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	
Kirov Region							
48	20 km S of Kirov (left bank of the River Viatka)	N 58°39' E 49°00'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	
Komi Republic							
54	Verkhnyaya Omra	N 62°48' E 55°25'	3 1	18 19	So So <i>j/l</i>	<i>go, hn, ip, jl, kq, mr</i> <i>go, hn, ip, j/l, kq, mr</i>	CIII
55	Troitsko-Pechorsk	N 62°42' E 56°11'	2	18	So	<i>go, hn, ip, jl, kq, mr</i>	
56	Puzla	N 62°26' E 54°39'	6	18	So	<i>go, hn, ip, jl, kq, mr</i>	
62	Ezhva (left bank of the River Vychegda)	N 61°47' E 50°44'	1 1	18 18	Ma Ma-So hybrid	<i>go, hi, jl, kq, mn, pr</i> <i>go, jl, kq, hn/hi/ip/pr/mr/nm</i>	RVI
63	Mikun	N 62°21' E 50°04'	3	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	
72	20 km W of Koslan (right bank of the River Mezen)	N 63°31' E 48°53'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	

shrew populations in the Łęgucki Młyn-Guzowy Młyn hybrid zone (Ratkiewicz et al. 2003).

Part of the northern European range of the common shrew that has received particular attention in recent years for study of chromosomal races and their contact areas/hybrid zones is north-eastern European Russia (Orlov & Kozlovsky 2002, Shchipanov et al. 2005a, 2008, 2009a, Bystrakova et al. 2007, Orlov et al. 2007). Here we extend that analysis to generate a coverage that is one of the most detailed for a geographic area of this size in the common shrew and incorporating a substantial number of races. This region is of particular interest because it is still covered by virgin forests, unique for Europe (Taskaev 2006), and consequently, the species distribution should have been impacted barely at all by humans. This makes north-eastern Russia ideal for an understanding of the natural processes involved in creating the current distribution of chromosomal races of common shrews.

Material and Methods

Study area

The focus of the study was the region of European Russia on the left bank of the River Volga; in particular, the south-eastern part of Arkhangelsk Region, and the central and south-western part of Komi Republic (N

56°38'-64°45' and E 47°16'-56°39') (Table 1). The eastern part of this area (from the southern slope of the Timan Ridge to the Ural Mountains) is covered by forests with a large component of Siberian vegetation. The area is divided into two taiga subzones: mid taiga and northern taiga. The northern taiga biome occupies an area northward from the lower reaches of the River North Dvina, middle parts of the Mezen and Pechora rivers and the upper catchment of the River Ilych. The northern forest limit extends between the estuary of the River Mezen, the lower reaches of the River Pechora and the upper catchment of the River Usa before descending several hundred kilometres southward following the hills of the northern Ural Mountains (Taskaev 2006).

Specimens and chromosome analysis

A total of 106 common shrews were collected at 24 new localities in July 2007 and in September-October 2008-2009 (Table 1) using home-made live traps (Shchipanov 1986) and a specific protocol for sampling red-toothed shrews (Shchipanov et al. 2005b), which greatly facilitated the sampling over such a vast area. Standard mitotic chromosome preparations of each animal were made in the field from the bone marrow and/or spleen after colchicine treatment *in*

Table 2. Previously published karyotype data for common shrews from north-eastern European Russia (only race-specific chromosomes indicated) with karyotypic categories as in Table 1 (with the Kanin /Kn/, Yagry /Ya/ and Yuryuzan /Yu/ races in addition). The type locality of each race is marked by an asterisk.

References: 1 – Polyakov et al. 1997; 2 – Bulatova et al. 2000; 3 – Kozlovsky et al. 2000; 4 – Polyakov et al. 2000; 5 – Polyakov et al. 2001; 6 – Orlov & Kozlovsky 2002; 7 – Shchipanov et al. 2002; 8 – Bystrakova et al. 2003; 9 – Orlov et al. 2004; 10 – Wójcik et al. 2003; 11 – Shchipanov et al. 2005a; 12 – Pavlova et al. 2006; 13 – Bystrakova et al. 2007; 14 – Orlov et al. 2007; 15 – Shchipanov et al. 2008; 16 – Shchipanov et al. 2009a; 17 – Shchipanov et al. 2009b; 18 – Pavlova & Bulatova 2010; 19 – Fredga 1996.

Map reference	Site name	Latitude/ Longitude	Number of specimens	2NA	Karyotypic category	Karyotype	Reference
Kn	Kanin peninsula*	N 68°20' E 45°13'	1	18	Kn	<i>gp, hi, jl, kq, mn, or</i>	19
Ya	Yagry Island*	N 64°35' E 40°00'	3	18	Ya	<i>go, hi, jl, kq, mp, nr</i>	14
1	Arkhangelsk Region, Kirillov*	N 59°50' E 38°25'	3	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	6
2	Arkhangelsk Region, 15 km S of Onega	N 63°50' E 38°15'	1 2 1 1	18 19 20 20	Kr Kr <i>k/q</i> Kr <i>g/m</i> Kr <i>g, m, k/q</i>	<i>gm, hi, jl, kq, no, pr</i> <i>gm, hi, jl, k/q, no, pr</i> <i>g/m, hi, jl, k/q, no, pr</i> <i>g, m, hi, jl, k/q, no, pr</i>	9
3	Arkhangelsk Region, 20 km S of Severodvinsk	N 64°20' E 40°00'	3	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	6
4	Kostroma	N 57°55' E 41°00'	1 1 1	18 18 18	Kr Ma Kr-Ma hybrid	<i>gm, hi, jl, kq, no, pr</i> <i>go, hi, jl, kq, mn, pr</i> <i>go/gm/mn/no, hi, jl, kq, pr</i>	6, 14
6	Arkhangelsk Region, Petuchovo (right bank of the River Mezen)	N 64°39' E 47°51'	2	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	15
7	Arkhangelsk Region, Podgorelaya (left bank of the River Mezen)	N 64°36' E 47°47'	4	18	Kr	<i>gm, hi, jl, kq, no, pr</i>	15
14	Komi Republic, Ulyashevo*	N 65°25' E 57°01'	2	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	3
15	Arkhangelsk Region, Kyssa (right bank of the River Mezen)	N 64°38' E 47°52'	5 2 2	18 18 18	Pt Kr-Pt hybrid Kr	<i>gi, hn, jl, kq, mo, pr</i> <i>gm/gi/hi/hn/no/mo, jl, kq, pr</i> <i>gm, hi, jl, kq, no, pr</i>	15
16	Arkhangelsk Region, Kobylskaya	N 64°48' E 49°13'	5	18	Pt	<i>gi, hn, jl, kq, mo, pr</i>	15
25	Sverdlovsk Region, Serov*	N 59°50' E 60°22'	5	18	Se	<i>go, hn, ip, jl, km, qr</i>	1
26	Komi Republic, 42 km S of Ukhta	N 63°14' E 54°21'	2	18	Se	<i>go, hn, ip, jl, km, qr</i>	11, 13
28	Komi Republic, the River Berezovka	N 61°41' E 56°31'	2	18	Se	<i>go, hn, ip, jl, km, qr</i>	11
29	Komi Republic, the River Nem	N 61°40' E 56°14'	2	18	Se	<i>go, hn, ip, jl, km, qr</i>	11
30	Komi Republic, the River Volosnitsa	N 61°42' E 56°44'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	11
	Yaksha	N 61°49' E 56°50'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	
31	Komi Republic, the River Pechora in foothills of Ural Mts.	N 62°03' E 58°25'	4	18	Se	<i>go, hn, ip, jl, km, qr</i>	11
32	Komi Republic, the River Pechora in Ural Mts.	N 62°05' E 59°05'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	11
33	Komi Republic, the River Ilych in foothills of Ural Mts.	N 63°03' E 58°36'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	13

34	Komi Republic, the River Ilych in foothills of Ural Mts.	N 62°38' E 58°55'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	13
35	Komi Republic, the River Ilych in foothills of Ural Mts.	N 62°28' E 58°58'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	13
36	Chelyabinsk Region, Techa	N 55°59' E 61°15'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	1, 4, 5
37	Chelyabinsk Region, Miass	N 55°15' E 61°50'	7	18	Se	<i>go, hn, ip, jl, km, qr</i>	4
37a	Kurgan, right bank of the River Tobol	N 55°30' E 65°20'	4	18	Se-No hybrid	<i>go, hn, jl, ik/ip/mp/km, qr</i>	4
38	Orenburg Region, Kvarkeno	N 52°10' E 60°01'	1	18	Se	<i>go, hn, ip, jl, km, qr</i>	12
39	Yekaterinburg	N 56°50' E 60°35'	1	18	Se-Yu hybrid	<i>go, hn, ip, jl, rk/km/mq/qr</i>	17
40	Samara Region, the River Sok *	N 53°35' E 50°30'	2	18	So	<i>go, hn, ip, jl, kq, mr</i>	2, 4
41	Saratov Region, Diakovka Forest	N 50°46' E 46°42'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	7
42	Orenburg Region, the River Shagan	N 51°40' E 51°29'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	8
43	Mary-El Republic, Zvenigovo	N 56°02' E 48°28'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	8
45	Kirov Region, Tuzha	N 53°38' E 47°56'	3	18	So	<i>go, hn, ip, jl, kq, mr</i>	8
46	Kirov Region, Kotel'nich	N 58°01' E 48°27'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	8
47	Kirov Region, Yur'a	N 59°02' E 49°14'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	8
49	Bashkiria Republic, the River Usen'	N 54°30' E 54°00'	2	18	So	<i>go, hn, ip, jl, kq, mr</i>	2, 4
50	Orenburg Region, Kuvandyk	N 51°04' E 57°17'	2	18	Yu	<i>go, hn, ip, jl, kr, mq</i>	8, 10
51	Bashkiria Republic, Zilair	N 52°17' E 57°33'	2	18	Yu	<i>go, hn, ip, jl, kr, mq</i>	8, 10
52	Bashkiria Republic, Beloretsk, Southern Ural Nature Reserve	N 54°30' E 54°00'	1	19	Yu j/l	<i>go, hn, ip, j/l, kr, mq</i>	13
53	Chelyabinsk Region, Yuryuzan*	N 54°50' E 58°20'	2	18	Yu	<i>go, hn, ip, jl, kr, mq</i>	4, 5
57	Komi Republic, the River Roptcha	N 63°00' E 52°19'	2	18	So	<i>go, hn, ip, jl, kq, mr</i>	13, 15
58	Komi Republic, Malaya Sluda (right bank of the River Vychegda)	N 62°00' E 50°35'	3	18	So	<i>go, hn, ip, jl, kq, mr</i>	15
59	Komi Republic, Priozerniy (right bank of the River Vychegda)	N 61°47' E 51°49'	5	18	So	<i>go, hn, ip, jl, kq, mr</i>	15
60	Komi Republic, Storozhevsk (right bank of the River Vychegda)	N 61°57' E 52°20'	5	18	So	<i>go, hn, ip, jl, kq, mr</i>	15
61	Komi Republic, Ust'-Nem (right bank of the River Vychegda)	N 61°40' E 54°53'	1	18	So	<i>go, hn, ip, jl, kq, mr</i>	13, 15
64	Kostroma Region, Manturovo*	N 58°30' E 45°00'	2	19	Ma j/l	<i>go, hi, j/l, kq, mn, pr</i>	2
65	Nizhny Novgorod Region, Gorodets	N 56°33' E 43°53'	2	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	8

66	Arkhangelsk Region, Velsk	N 61°00' E 42°00'	6 1	18 19	Ma Ma <i>j/l</i>	<i>go, hi, jl, kq, mn, pr</i> <i>go, hi, j/l, kq, mn, pr</i>	2
67	Arkhangelsk region, Krasnoborsk	N 61°42' E 46°41'	1	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	8
68	Komi Republic, 50 km downstream from Verkhnevezensk (left bank of the River Mezen)	N 63°49' E 49°13'	1	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	16
69	Komi Republic, Borovo (right bank of the River Mezen)	N 63°32' E 49°28'	1	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	16
70	Komi Republic, Glotovo (right bank of the River Mezen)	N 63°28' E 49°28'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	16
71	Komi Republic, Koslan (right bank of the River Mezen)	N 63°27' E 48°52'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	16
73	Komi Republic, Usogorsk (left bank of the River Mezen)	N 63°26' E 48°44'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	15
74	Komi Republic, Syktyvkar	N 61°30' E 51°00'	2	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	2
75	Komi Republic, Danj (River Lokchim, left tributary of the River Vychegda)	N 61°23' E 51°48'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	15
76	Kostroma Region, Buj	N 58°30' E 41°30'	4	18	Ma	<i>go, hi, jl, kq, mn, pr</i>	14

vivo following Ford & Hamerton (1956) with some modifications (Bulatova et al. 2009). The trypsin – Giemsa staining technique of Král & Radjabli (1974) was used for identification of each chromosome arm by G-bands. The racial status of each individual was determined according to the standard nomenclature for the karyotype of the common shrew (Searle et al. 1991) and described in terms of the metacentrics and free acrocentrics comprising the autosomal arms *g-r* (Searle & Wójcik 1998). The metacentrics are described by two letters (e.g. *gi*) and acrocentrics by a single letter (e.g. *j*). Heterozygotes are indicated as simple heterozygotes (e.g. *j/l* for an individual with metacentric *jl* and two acrocentrics *j* and *l*) and complex heterozygotes (e.g. *km/mr/qr/kq* for an individual with metacentrics *kq, km, mr* and *qr*) following the definition in Searle (1993).

Capture locations were determined using a GPS (Garmin) personal navigation system and then imported to ArcView. The samples of karyotyped shrews in localities previously surveyed within the study area and published elsewhere are summarised in Table 2.

Results

Twenty four new localities, adding to the list of 55 previously known, provided new details on the distribution of the Kirillov, Manturovo, Petchora,

Serov, and Sok chromosomal races (Fig. 1). We localised areas of hybridisation between the Kirillov and Manturovo, Manturovo and Petchora, Manturovo and Sok, Petchora and Serov, Petchora and Sok, and Serov and Sok races. The details are described below and in Table 1.

Kirillov race (Kr)

We found this race on the left bank of the River Mezen (site 5), and on both banks near the villages of Kyssa (nos. 7-10) and Vozhgora (sites 11-12) (Fig. 2). Locality 13 near the village of Malaya Pyssa, where the Kirillov race meets and hybridises with both the Manturovo and Petchora races, is the most easterly record for this race. Kirillov-Petchora F_1 hybrids were found on both banks of the River Mezen (sites 8-9, 12) and on a river island (site 10). The karyotype of the Kirillov race differs by two pairs of metacentrics from the Manturovo race and by three pairs of metacentrics from the Petchora race such that their F_1 hybrids would be expected to form ring-of-four (RIV: *gm/go/no/mn*) and ring-of-six (RVI: *gm/gi/hi/hn/no/mo*) configurations at meiosis I, respectively.

Petchora race (Pt)

We found that the Petchora race crosses the River Mezen, and meets and hybridises with the Manturovo

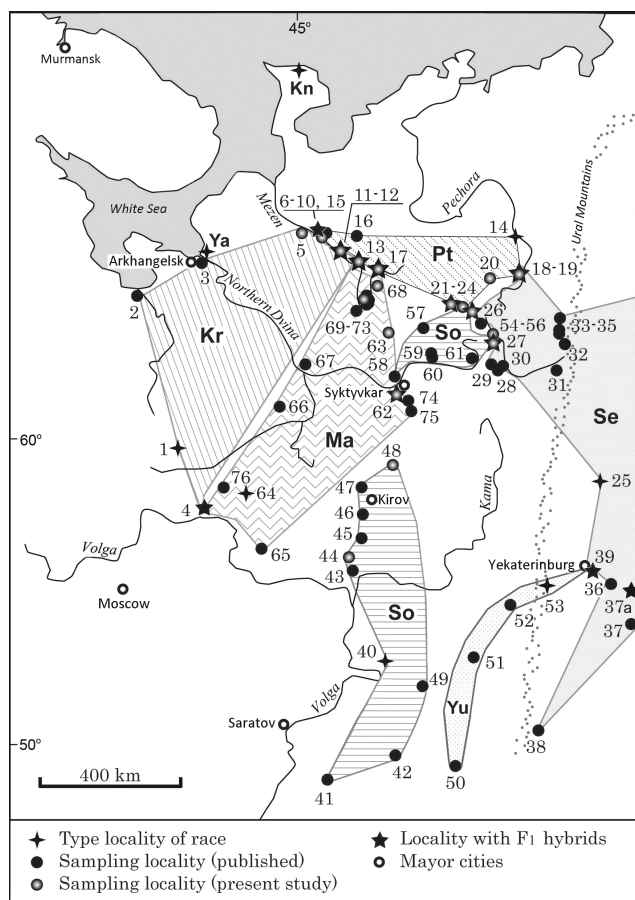


Fig. 1. Map of the chromosomal races in north-eastern European Russia: Kanin (Kn), Yagry (Ya), Kirillov (Kr), Petchora (Pt), Sok (So), Manturovo (Ma), Serov (Se), Yuryuzan (Yu). Ranges were constructed around the outermost localities where each racial karyotype has been recorded. Numbers refer to the listing of sampling localities in Table 1 and 2.

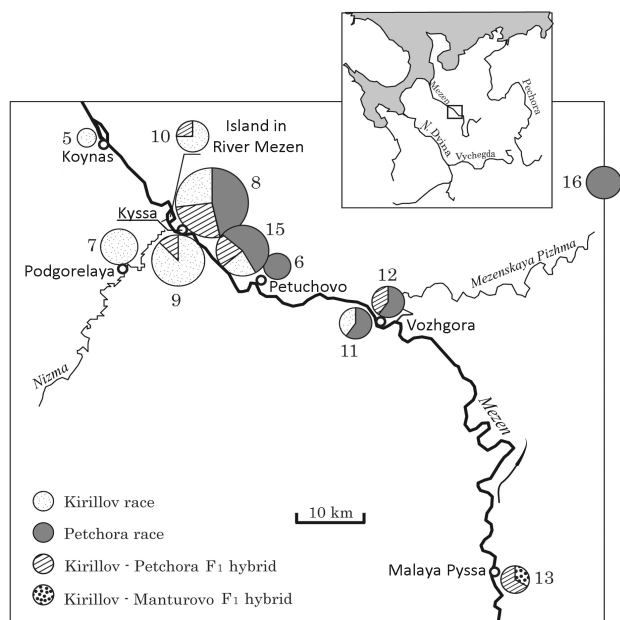


Fig. 2. Distribution of common shrews of different chromosomal races and interracial hybrids around the middle part of the River Mezen. The area of each circle is proportional to sample size. See Table 1 and 2 for further details.

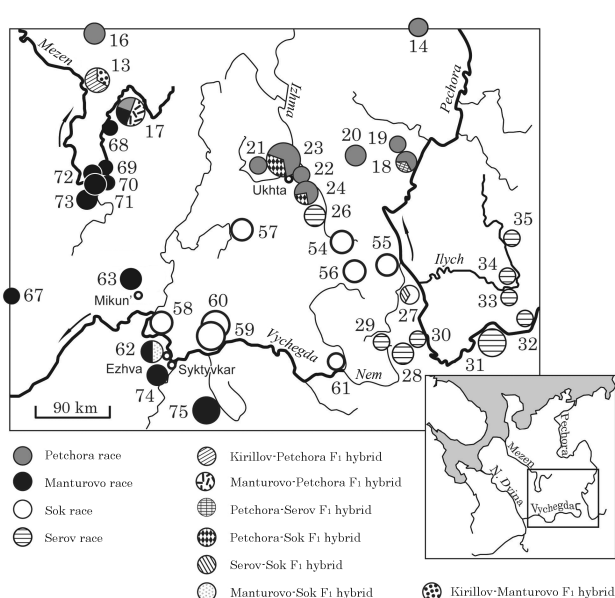


Fig. 3. Distribution of individual chromosomal races and interracial hybrids in the upper catchment area of the Mezen, Vychegda, and Pechora rivers. The area of each circle is proportional to sample size. See Table 1 and 2 for further details.

race on the left bank near Verkhnemezensk (site 17). An F_1 hybrid between these races would be expected to produce an RVI configuration at meiosis I, but with a different chromosomal combination (*go/gi/hi/hn/mn/mo*) from the Kirillov-Petchora F_1 hybrid. Locality 18, where the Petchora race hybridises with the Serov race, indicates the southern limit of the Petchora race range (Fig. 3). The karyotype of the Petchora-Serov F_1 hybrid is shown in Fig. 4A and includes chromosomes *gi, hn, kq, mo, pr* of the Petchora race and *go, hn, km, ip, rq* of the Serov race. Individuals with such a karyotype would form a RVIII configuration at meiosis I – *gi/go/mo/km/kq/qr/pr/ip* – which is the longest ring meiotic configuration anticipated from any hybrid karyotype of the common shrew.

Individuals with a pure Petchora race karyotype were found to the north and east of the Petchora-Serov hybrid locality (in localities 19 and 20). The Petchora race meets the Sok race close to the towns of Ukhta (site 21) and Sosnogorsk (site 22); both pure race and Petchora-Sok F_1 hybrid individuals were found in the nearby localities 23 and 24. A Petchora-Sok F_1 hybrid karyotypes would be expected to produce a meiotic RIV (*go/gi/im/mo*) and RVI (*gi/go/mo/mr/pr/ip*) configurations, respectively (Table 1).

Serov race (Se)

We did not find pure Serov race individuals but did collect an F_1 Serov-Sok hybrid together with pure Sok

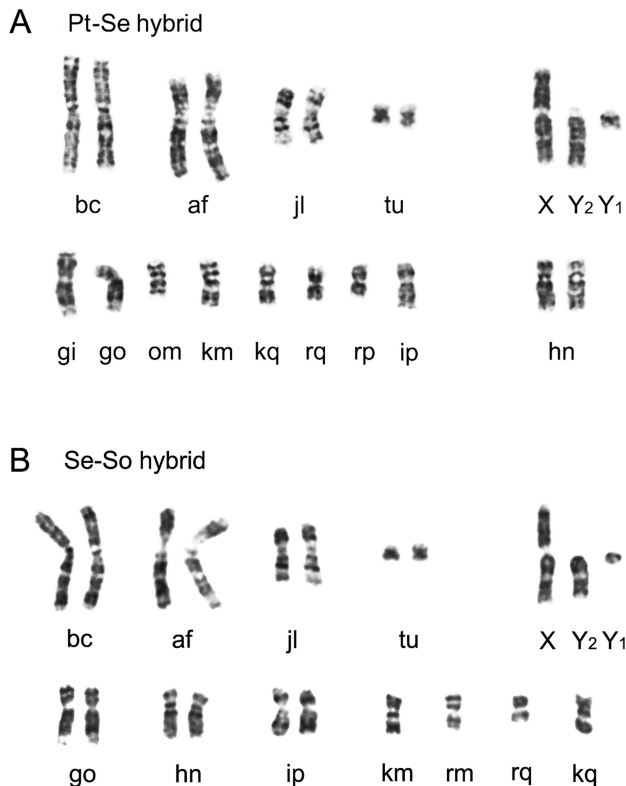


Fig. 4. G-banded karyotypes of F₁ hybrids: A – between the Petchora and Serov races, B – between the Serov and Sok races. The top row of each karyotype displays the autosomes found in all common shrews (bc, af, jl, tu) and the male sex chromosomes (XY₂Y₁). The bottom row shows the remaining autosomes which define the hybrid karyotypes.

race individuals in locality 27, within homogeneous plain forest habitat (Figs. 1, 3). The Serov-Sok hybrid karyotype should be associated with a RIV meiotic configuration – *km/mr/rq/kq* (Fig. 4B).

Sok race (So)

In the north-east of the region sampled we found three new Sok race localities along the road to Troitsko-Pechorsk (sites 54-56) and one more locality (27) where the Sok race meets and hybridises with the Serov race (see above). We also found an F₁ hybrid between the Sok and Manturovo races, expected to form a RVI meiotic configuration (*hn/hi/ip/pr/mr/mn*).

Manturovo race (Ma)

Pure Manturovo race individuals were recorded at the town of Mikun' (site 63). Further north, in middle parts of the River Mezen, the Manturovo race makes contact with the Kirillov and Petchora races. At this location, the River Mezen forms a big loop and we found the Manturovo race inside the loop at localities 68-73 (Fig. 3, Table 1). Moreover, at the start of the loop (site 17), we recorded both the Manturovo and Petchora pure races, as well as their hybrids, and at the

end of the loop (site 13) we found both Manturovo-Kirillov and Kirillov-Petchora hybrids (Fig. 3, Table 1).

Discussion

In total, we found five of the eight chromosomal races previously reported to occur in north-eastern European Russia. We did not collect individuals of the Kanin and Yagry races, which have been described from single localities (Fig. 1) from the Kanin peninsula (Fredga 1996) and Yagry Island in the North Dvina river delta (Orlov et al. 2007), respectively. The nearest locality to these type sites that we surveyed was locality 5, situated 420 km south of Kanin and 270 km east of Yagry (Fig. 1). Thus, the areas between the estuary of North Dvina, the lower reaches of the River Mezen and the lower reaches of the River Pechora, together with the southern part of the Kanin peninsula, still remain unsurveyed. Among the shrews that we karyotyped we also did not find the Yuryuzan race.

Among hybrid zones, previously only the Kirillov-Petchora zone was known within the region under study (Shchipanov et al. 2008), and only 17 hybrid zones have been described in the common shrew overall (Searle & Wójcik 1998, Orlov et al. 2007, Bulatova et al. 2007, 2011, Polyakov et al. 2011, Orlov et al. 2012).

Here we provide a much more detailed appreciation of the ranges of the five races that we find, and describe further six hybrid zones, based on the discovery and description of F₁ hybrids. These F₁ hybrids are expected to produce three types of meiotic configuration: RIV configurations in Kirillov-Manturovo and Serov-Sok hybrids, RVI configurations in Kirillov-Petchora, Manturovo-Petchora, Manturovo-Sok and Petchora-Sok hybrids and RVIII configurations in Petchora-Serov hybrids. Previous studies have shown hybrids that are expected to form RIV and RVI configurations (Narain & Fredga 1997, Searle & Wójcik 1998, Banaszek et al. 2000, Orlov et al. 2012). Here for the first time we show hybrids that are expected to form RVIII configurations. Hybrids with small to medium ring configurations would not be expected to be as unfit as those that form long chain configurations (e.g. CIX-forming and CXI-forming hybrids recently described by Polyakov et al. 2011 and Bulatova et al. 2011), but nevertheless would be expected to suffer reduced hybrid fitness (Searle 1993). However, no substantial barriers to the gene flow were recorded in hybrid zones between certain chromosomal races of the common shrew (Horn et al. 2012).

The occurrence of the hybrids clearly represents some of the boundaries of the five races under consideration.

We describe our total appreciation of the distributions of each of these races below.

Locality 1 is the type locality of the Kirillov race (Orlov & Kozlovsky 2002), which has also been reported from localities 2-4 (Orlov et al. 2004, Fig. 1 and Table 2).

The type locality of the Petchora race (Fig. 1) is situated near the village of Ulyashevo (site 14) on the left bank of the River Pechora (Kozlovsky et al. 2000). This race is further known from localities 8, 12, and 15 on the right bank of the River Mezen, where it hybridises with the Kirillov race, and from localities 6 and 16 in the middle of the Timan Ridge (Shchipanov et al. 2008) (Fig. 2).

The Serov race was first described from locality 25, to the east of the Ural Mountains, and was considered Asian in distribution (Polyakov et al. 1997). But later the Serov race was recorded on the European side of the mountains, from the valleys of the River Berezovka of the Kama basin (site 28) and the River Nem of the Vychegda basin (site 29), on both banks of the River Pechora (site 30), on the European slope of the Ural Mountains (sites 31 and 32) and alongside the River Ilych from localities 33-35 (Shchipanov et al. 2008) (Figs. 1, 3 and Table 2). Locality 26 indicates the western limit of known distribution of the race at present (Shchipanov et al. 2005a, Bystrakova et al. 2007). The eastern border of the Serov race range is situated in Siberia, in Tyumen Region (Polyakov et al. 2000). This race and Serov-Novosibirsk F_1 hybrids are also known from other localities in the Ural Mountains (sites 36, 37 and 37a) (Polyakov et al. 1997, 2000) and from locality 38 in the Orenburg region (Pavlova et al. 2006), which is the southern limit of the known range. A Serov-Yuryuzan F_1 hybrid has been described from locality 39 in a city park of Yekaterinburg (Shchipanov et al. 2009b) (Fig. 1, Table 2).

Locality 40 on the left bank of the River Volga is the type locality of the Sok race (Polyakov et al. 2000). The most southern localities for the race (41 and 42) are known from the Saratov and Orenburg regions (Shchipanov et al. 2002, Bystrakova et al. 2003). The range of the race follows the left bank of the River Volga and crosses the River Kama (sites 43-48). The eastern locality for the Sok race (site 49) is known from the Bashkiria Republic (Polyakov et al. 2000). Localities of the neighbouring Yuryuzan race (sites 50-53) mark the possible south-eastern border of the Sok race. A large gap in chromosomal studies remains between the southern and the northern segments of the area of the Sok race (Fig. 1, Table 2). In the

northern part of the range of the Sok race (Fig. 3), the most western record is from near the village of Ropcha (site 57) and near the village of Malaya Sluda (site 58) on the right bank of the River Vychegda. From here the race follows upstream along the right bank of the River Vychegda to the place where the River Nem flows into the River Vychegda (sites 59-61) (Shchipanov et al. 2008) (Table 2), except for the town of Ezhva where we found a Manturovo-Sok F_1 hybrid on the left bank (site 62) (Figs. 1, 3 and Table 1).

The type site of the Manturovo race is at locality 64 in the south-western part of its subsequently described range (Bulatova et al. 2000). The distribution of the race in the south is known to be bounded by the left bank of the River Volga (site 65) (Fig. 1; Bystrakova et al. 2003). Locality 4, where individuals of both pure races, as well as Kirillov-Manturovo hybrids, occur together, marks the south-western limit of distribution of the Manturovo race (Orlov et al. 2007). The pure race is found in a north-eastern direction in localities 76 (Orlov et al. 2007), 66 and 67 (Bulatova et al. 2000, Bystrakova et al. 2003). The eastern border of the range of the race reaches the town of Syktyvkar (site 74) (Bulatova et al. 2000) and the village of Dan' (site 75) (Shchipanov et al. 2008) (Fig. 1, Table 2). Barriers such as rivers (Mercer & Searle 1991), wet riverine meadow habitats (Fedyk et al. 1993), lakes (Bulatova et al. 2011), highlands (Jones & Searle 2003) or transitions between different habitats (Polyakov et al. 2000, 2003, 2011) have previously been described as the boundaries between chromosomal races of the common shrew, including hybrid zones. However, in north-eastern Russia, wetlands are patchily distributed and, therefore, can hardly form a continual barrier to the distribution of common shrews. Almost all the area under the study constitutes the mid-taiga biome, and only the Ural Mountains represent a significant elevation within the area, and then as the eastern border to the area under study. Rivers could potentially limit the distribution of the races. However, water may not be an absolute barrier to common shrews given that Hanski and colleagues demonstrated that immatures can migrate to small islets across a lake swimming 40-820 m (Hanski 1986, Hanski & Peltonen 1988, Peltonen & Hanski 1991, Hanski et al. 1991 and others). We did not find evidence that even the biggest rivers in north-eastern European Russia (over 500 m in width) limit the dispersal of populations. In particular, the Kirillov race crosses the River North Dvina (width 500-1300 m), the Manturovo race must have crossed either the

North Dvina (900 m) or the Vychegda rivers (600 m) to achieve the northern parts of its range, and the Sok race crossed the River Kama, which is over 1000 m wide in its lower reaches (Fig. 1).

Moreover, in our study most contacts between the races in north-eastern Russia, either observed or expected, occur when races move alongside the rivers to meet each other. Thus, the majority of our localisations of hybrid individuals cannot be attributed to the barrier effect of riverine systems *per se*, though we usually found them next to rivers due to the local transport facilities. For example, at locality 17 the races meet each other moving along the same left bank of the River Mezen up (the Manturovo race) and down (the Petchora race) (Fig. 3). In fact, a riverine barrier obviously contributes to the occurrence of hybrids between the Kirillov and Petchora races, i.e. in all the three localities where hybrids were found, the pure races inhabited the opposite banks of the river (Fig. 2). Apparently, the record of the Manturovo-Sok hybrid (site 62) may represent an additional case of this kind, considering the fact that in this part of the River Vychegda, the Sok race was found only on the right bank and the Manturovo race on the left (Fig. 3). Only those four sites out of the 11 localities with the hybrid individuals could be attributed to the riverine barrier effect.

Contacts between the Kirillov and Manturovo, Manturovo and Sok, Sok and Yuryuzan, and Serov and Yuryuzan races may be expected in areas lacking distinct environmental barriers (Fig. 1). The Manturovo and Petchora races should meet each other somewhere within a loop of the River Mezen in its upper parts. This area is covered by homogeneous taiga free of significant altitudinal changes; there are no rivers and the terrain is featureless without any

potential barriers for migration. The area between the southern localities of the Petchora race and the northern localities of the Sok race is also homogeneous (Fig. 3).

North-eastern Russia is a natural area of colonisation of the common shrew. The chromosomal races there may represent expansions from populations in glacial refugia, or populations of postglacial origin (Wójcik 1993, Polyakov et al. 2001, Orlov et al. 2007). These races are found in the area despite an absence of high elevations to act as geographic barriers. Major rivers may have been expected to separate the races, but our results indicate that they do not have a major role. Nor, given the homogeneity of habitat are there habitat transitions that may explain the boundaries of chromosomal races. It is clear that it is not possible to have a simplistic explanation of major environmental barriers to explain the manner in which chromosomal races form their natural limits. We plan to carry out further fine-scale studies to understand more fully the determinants of race distribution in north-eastern European Russia, which we believe to be a particularly fruitful area for such studies.

Acknowledgements

We thank Drs. A.V. Bobretsov, I.F. Kuprianova, A.A. Kalinin, A.V. Kouptsov, T.B. Demidova, and O.N. Batova for their assistance in collecting shrews. We are thankful to Dr. Nina Bulatova for her valuable consultations in karyology. We appreciate the assistance of Prof. Joseph Merritt in preparing the first English version of manuscript. We thank Dr. Andrey Tchabovsky for his comprehensive and fruitful discussion on the structure of the manuscript and the English. We would like to thank also Prof. Jan Zima for his helpful advices on the manuscript. We are especially grateful to Prof. Jeremy Searle for valuable comments on this manuscript and the English. This work was supported by RFBR (08-04-00553, 12-04-00937, 12-04-31200) and President Grant for Russian Distinguished Young Scientists MK-2500.2011.4 (to S. Pavlova).

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