

## The diversity of chromosome races in *Sorex araneus* from European Russia

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Over recent years there has been a particular effort to identify the main chromosome races of the common shrew *Sorex araneus* Linnaeus, 1758 in the European part of Russia. We report here on the karyotypes of 40 shrews from 18 widely distributed sites in European Russia. Three new chromosome races were described: the Manturovo (*go, hi, j/l, kq, mn, pr*), the Neroosa (*g/o, hi, j/l, k/r, mn, p/q*) and the Seliger (*g, hn, ik, j/l, m/q, o, pr*). In addition, a single individual from Belarus, was from a new race: the Lepel (*g/m, hk, i/p, j/l, n/q, o/r*), which has been further characterised by Mishta *et al.* (2000). Considering European Russia alone, there are now described eleven distinct chromosome races of the common shrew. Some of these races appear to belong to a Finnish-Ural Mts-West Siberian lineage, others have an affinity with the West European Karyotypic Group: European Russia appears to be a particularly interesting area, from the viewpoint of the colonization history of the common shrew. In terms of chromosome mutations, it appears that whole-arm reciprocal translocations have had an important role in the chromosome evolution of European Russian shrews.

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### Introduction

It is now twenty-five years since the first description of a chromosome race in the common shrew *Sorex araneus* Linnaeus, 1758 using banding techniques (Halkka *et al.* 1974). Over that period it has become clear that this species is subdivided into numerous such forms, with ranges that vary from a few tens of square kilometres to many hundreds of thousands of square kilometres (Zima *et al.* 1996, Searle and Wójcik 1998). Each of these races differ in their complement of metacentric and acrocentric chromosomes, with chromosome arms *g-r* distributed

in a very wide variety of ways. It is believed that these chromosome arms existed ancestrally as single-armed (acrocentric) chromosomes, but that in different parts of the species range different combinations of them have fused at the centromere (ie Robertsonian fusion) to form biarmed (metacentric) chromosomes. On the basis of accumulating evidence (eg Halkka *et al.* 1987, 1994, Polyakov *et al.* 1997), it is believed that further evolution of metacentrics has occurred by the swapping of arms between metacentrics or between metacentrics and acrocentrics, mutations known as whole-arm reciprocal translocations (WARTs) (Searle *et al.* 1990, Hauffe and Piálek 1997).

The study of chromosome variation in common shrews from European Russia (ie the area of the Russian Federation west of the Ural Mts) has a history that predates the first chromosome banding analysis in the species. In the late 1960's and early 1970's it was shown that *Sorex araneus* displays Robertsonian variation in European Russia and that, as elsewhere in its range, chromosome studies can help distinguish *S. araneus* from other morphologically similar species of shrews (Orlov and Alenin 1968, Orlov and Kozlovsky 1969, Kozlovsky 1972, 1973). Despite these early investigations, it is only over the last 5 years that systematic geographical sampling of common shrews coupled with G-banding of chromosomes has been carried out in European Russia. This study was initiated as part of a project funded by the 'International Association for the promotion of cooperation with scientists from the New Independent States of the former Soviet Union' (INTAS) to analyse chromosome variation in the common shrew over the whole of the former USSR.

Previous publications have reported our first results within the INTAS and related projects (Orlov *et al.* 1996, Bulatova *et al.* 1999, Zaitsev and Bulatova 1999, Kozlovsky *et al.* 2000). In the present paper, we will review this published work on chromosomal variation in European Russia, taking the opportunity to make a few minor corrections. We will also present new data on 40 shrews from 18 widely-distributed sites. As well as the work initiated in Moscow and Penza, we will include data collected just to the west of the Urals by the Siberian team of the INTAS project (Polyakov *et al.* 2000), in order to complete the coverage of European Russia. Taking together all available information, the knowledge of chromosomal variation in European Russia is now comparable with that in other parts of the species range.

In addition to the data that we collected in European Russia, we made one field trip into Belarus that led to the discovery of a new race. Although the formal description of this form is given in the present paper, the race is considered in more detail by Mishta *et al.* (2000), who have carried out a systematic study of chromosome variation in Belarus, Ukraine, Lithuania, Latvia and Estonia, as part of the INTAS project. Likewise, Mishta *et al.* (2000) discuss our published chromosomal data (Orlov *et al.* 1996) on shrews from the Kaliningrad Region (a small isolate of European Russia located between Lithuania and Poland).

## Material and methods

Animals were collected between summer 1995 and autumn 1999 during a number of field trips. Individuals were captured alive with traps designed by Shchipanov (1986). They were usually processed in the field. Air-dried chromosome preparations were made from bone marrow and spleen after *in vivo* or *in vitro* treatment with colchicine. Subsequently, the chromosomes were G-banded under laboratory conditions. Karyotypes and chromosome races are described according to the current rules of nomenclature (Searle *et al.* 1991, Hausser *et al.* 1994).

## Results and discussion

### Chromosome races

The new race discovered in Belarus is as follows:

#### Lepel race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af*, *bc*, *g/m*, *hk*, *i/p*, *jl*, *n/q*, *o/r*, *tu*

An individual of this race was collected at Lepel (54°40'N, 28°30'E). Its karyotype is shown in Fig. 1 and includes one heterozygous chromosome pair (*or*). Other variable chromosomes have been found in another site by Mishta *et al.* (2000).

The full details of the individuals that have been karyotyped in European Russia using G-banding are given in Table 1. Altogether there are data on 109 individuals from 38 sites in European Russia. All collection localities and their racial characteristics are shown in Fig. 2. Table 1 lists sites generally in order north to south, with an emphasis on keeping together sites of the same race. For simplicity, we will consider each race in the same order as it appears in Table 1. As is standard

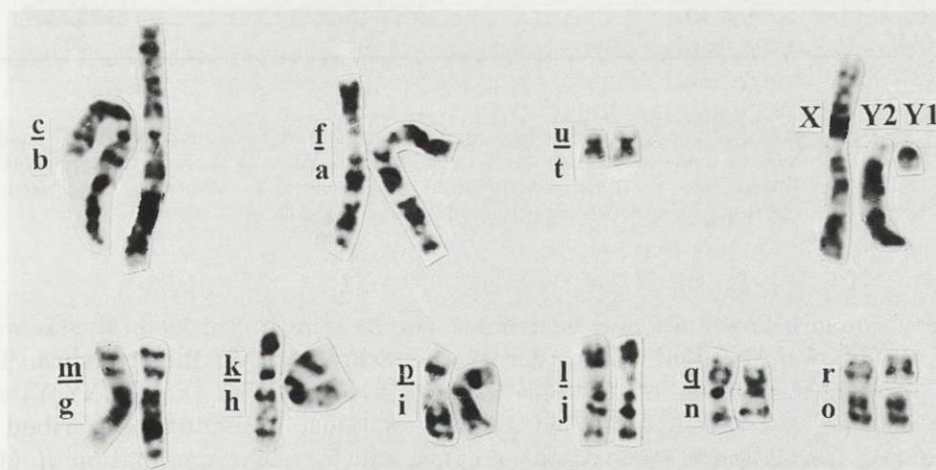


Fig. 1. The karyotype of an individual of the Lepel chromosome race (male, type site, Lepel, Belarus).

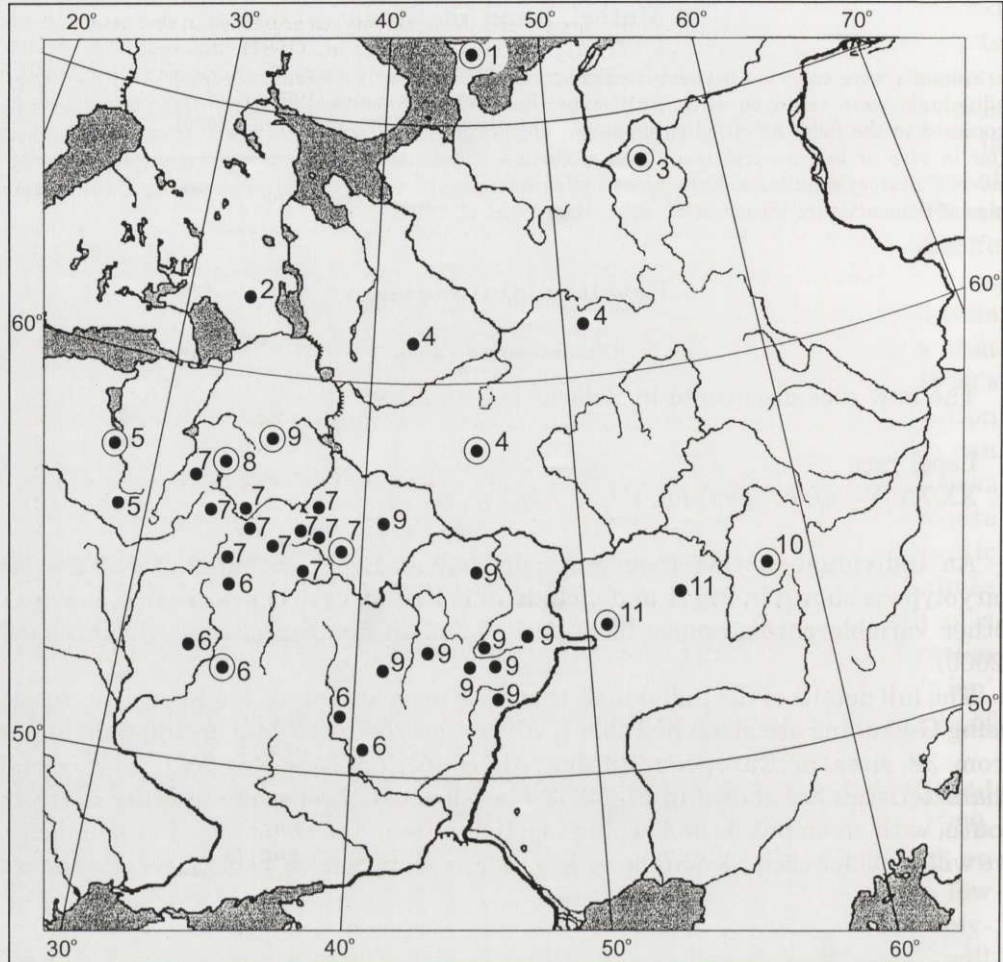


Fig. 2. Collection sites in European Russia where common shrews have been analyzed with G-banding (solid dots). Each number refers to a separate race (in the same order as in Table 1); the type sites are indicated by circled solid dots. 1 – Kanin, 2 – Ilomantsi, 3 – Petchora, 4 – Manturovo, 5 – Pskov, 6 – Neroosa, 7 – Moscow, 8 – Seliger, 9 – Mologa, 10 – Yuryuzan, 11 – Sok.

for the common shrew, the only variable autosome arms in European Russia were  $g-r$ , which were present as acrocentrics or paired within metacentrics. The autosomal metacentrics  $af$ ,  $bc$  and  $tu$  were invariant and the  $XX/XY_1Y_2$  sex chromosome system characterised all shrews. Most individuals described in European Russia were homozygous metacentric for arm combination  $jl$  (104 individuals, 95% of the total), the remainder were heterozygotes for this arm combination. No other variation involving chromosome arms  $j$  and  $l$  was detected.

Table 1. The karyotypes of common shrews from European Russia. This table only includes G-band data. The type sites for each chromosome race (\*) and those karyotypes presented in this article (†) are indicated. The description of each karyotype follows Searle *et al.* (1991), but only the variable chromosome arms *g-r* are included. 1 – Fredga (1996), 2 – Present study, 3 – Kozlovsky *et al.* (2000), 4 – Recorded incorrectly in Orlov *et al.* (1996), 5 – Zaitsev and Bulatova (1999), 6 – Orlov *et al.* (1996), 7 – Aniskin and Lukianova (1989), 8 – Bulatova *et al.* (1999), 9 – Polyakov *et al.* (2000).

Site name	Latitude/Longitude	No. of shrews	2na	Karyotype	Race	Ref.
1	2	3	4	5	6	7
Yamalo-Nenets Autonomous District						
Kanin Peninsula*	68°20'N, 45°13'E	1	18	<i>gp, hi, jl, kq, mn, or</i>	Kanin	1
Karelia Republic						
Pertozero	61°45'N, 34°25'E	1	20	<i>g, hn, ip, jl, kr, mq, o</i>	Ilomantsi	2
		1	22	<i>g, hn, i/p, jl, k/r, mq, o</i>		2
		1	22	<i>g, hn, i/p, jl, kr, m/q, o</i>		2
		1	23	<i>g, hn, i/p, jl, k/r, m/q, o</i>		2
		1	23	<i>g, hn, i/p, j/l, kr, m/q, o</i>		2
Komi Republic						
Petchora*	65°30'N, 57°00'E	2	18	<i>gi, hn, jl, kq, mo, pr</i>	Petchora	3
Syctyvkar	61°30'N, 51°00'E	2	18	<i>go, hi, jl, kq, mn, pr</i>	Manturovo	3
Arkhangelsk Region						
Velsk	61°00'N, 42°00'E	6	18	<i>go, hi, jl, kq, mn, pr</i>		3
		1	19	<i>go, hi, j/l, kq, mn, pr</i>		3
Kostroma Region						
Manturovo*	58°30'N, 45°00'E	1	18	<i>go, hi, jl, kq, mn, pr†</i>		2, 4
		1	19	<i>go, hi, j/l, kq, mn, pr</i>		2, 4
Pskov Region						
Izborsk*	57°45'N, 27°50'E	1	18	<i>gm, hk, ip, jl, nr, oq</i>	Pskov	5
Sebezh	56°20'N, 28°50'E	2	18	<i>gm, hk, ip, jl, nr, oq</i>		5
Bryansk Region						
River Neroosa*	52°20'N, 34°10'E	2	18	<i>go, hi, jl, kr, mn, pq†</i>	Neroosa	2
Novozybkov	52°30'N, 32°20'E	1	21	<i>go, hi, jl, k/r, mn, p, q</i>		2
		1	23	<i>g, hi, jl, k/r, mn, o, p, q</i>		2
		1	24	<i>g, hi, jl, k, mn, o, p, q, r</i>		2
Kaluga Region						
Spas-Demensk	54°20'N, 34°10'E	6	18	<i>go, hi, jl, kr, mn, pq</i>		2
Voronezh Region						
Talovaya	51°05'N, 40°55'E	1	18	<i>go, hi, jl, kr, mn, pq</i>		3
		1	19	<i>go, hi, j/l, kr, mn, pq</i>		3
		4	19	<i>g/o, hi, jl, kr, mn, pq</i>		3
		3	20	<i>g, hi, jl, kr, mn, o, pq</i>		3
Voronezh	51°30'N, 39°00'E	1	18	<i>go, hi, jl, kr, mn, pq</i>		2, 4

Table 1 – continued.

1	2	3	4	5	6	7
Moscow Region						
Sergiev Posad	56°20'N, 38°00'E	2	18	<i>gm, hi, jl, kr, no, pq</i>	Moscow	6
Chernogolovka*	55°55'N, 38°30'E	3	18	<i>gm, hi, jl, kr, no, pq</i>		7
Zvenigorod	55°45'N, 36°50'E	2	18	<i>gm, hi, jl, kr, no, pq</i>		3
Moscow (Strogino)	55°40'N, 37°00'E	1	18	<i>gm, hi, jl, kr, no, pq</i>		2
Moscow (Ismailovo)	55°30'N, 37°30'E	1	18	<i>gm, hi, jl, kr, no, pq</i>		6
Serpukhov	54°50'N, 37°20'E	1	18	<i>gm, hi, jl, kr, no, pq</i>		2
Smolensk Region						
Izdeshkovo	55°10'N, 33°50'E	3	18	<i>gm, hi, jl, kr, no, pq</i>		3
Tver Region						
Lake Sterzh	57°15'N, 32°40'E	5	18	<i>gm, hi, jl, kr, no, pq</i>		8
Lake Seliger (Upper Volga)	56°35'N, 33°30'E	1	19	<i>g/m, hi, jl, kr, no, pq</i>		8
Rzhev (l bank Upper Volga)	56°11'N, 34°40'E	2	18	<i>gm, hi, jl, kr, no, pq</i>		2
Rzhev (r bank Upper Volga)	56°10'N, 34°30'E	10	18	<i>gm, hi, jl, kr, no, pq</i>		2, 6
Lake Seliger (NW shore)*	57°10'N, 33°30'E	1	20	<i>g, hn, ik, jl, mq, o, pr†</i>	Seliger	2
River Mologa*	58°20'N, 36°00'E	1	21	<i>g, hn, ik, jl, m/q, o, pr</i>		2
		1	18	<i>gm, hn, io, jl, kr, pq</i>	Mologa	6
		1	19	<i>g/m, hn, io, jl, kr, pq</i>		2
		1	19	<i>gm, hn, io, jl, kr, pq</i>		3
		1	19	<i>gm, hn, io, jl, kr, p/q</i>		6
		1	20	<i>gm, hn, io, jl, kr, p/q</i>		6
		1	20	<i>gm, hn, i, jl, kr, o, pq</i>		6
Vladimir Region						
Kovrov	56°20'N, 41°25'E	1	18	<i>gm, hn, io, jl, kr, pq</i>		2
Chuvash Republic						
Alatyr	55°00'N, 46°40'E	2	18	<i>gm, hn, io, jl, kr, pq</i>		2
Penza Region						
Zemetchino	53°20'N, 42°40'E	3	18	<i>gm, hn, io, jl, kr, pq</i>		2, 8
		1	19	<i>gm, hn, io, jl, kr, pq</i>		2
		1	19	<i>gm, hn, io, jl, kr, p/q</i>		8
Gorodishche	53°05'N, 45°44'E	2	18	<i>gm, hn, io, jl, kr, pq</i>		2
Kondol	52°54'N, 45°54'E	1	18	<i>gm, hn, io, jl, kr, pq</i>		2
		2	19	<i>gm, hn, io, jl, kr, pq</i>		2
Shemysheika	52°58'N, 45°22'E	1	18	<i>gm, hn, io, jl, kr, pq</i>		2
		1	20	<i>gm, hn, io, jl, kr, pq</i>		2
Ulyanovsk Region						
Nikolayevka	53°10'N, 47°20'E	1	18	<i>gm, hn, io, jl, kr, pq</i>		8
Tambov Region						
Tambov	52°40'N, 41°30'E	3	18	<i>gm, hn, io, jl, kr, pq</i>		3

Table 1 – concluded.

1	2	3	4	5	6	7
Saratov Region						
Tatishchevo	51°40'N, 45°30'E	1	20	<i>gm, hn, i/o, jl, kr, p/q</i>	Mologa	8
		1	20	<i>gm, hn, i, jl, kr, o, pq</i>		8
Chelyabinsk Region						
Yuryuzan**	54°50'N, 58°20'E	2	18	<i>go, hn, ip, jl, kr, mq</i>	Yuryuzan	9
Samara Region						
Sok*	53°35'N, 50°30'E	2	18	<i>go, hn, ip, jl, kq, mr</i>	Sok	9
Bashkiria Republic						
Usen'	54°30'N, 54°00'E	2	18	<i>go, hn, ip, jl, kq, mr</i>		9

## Kanin race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, gp, hi, jl, kq, mn, or, tu*

This race is defined on the basis of a single individual from the extreme north of European Russia (Fredga 1996). This race has a unique metacentric for the common shrew: *gp*. Of the other metacentrics *hi* is of particular interest, as it is found in several other Russian races (Manturovo, Neroosa, Moscow), as well as being one of the metacentrics that defines the West European Karyotypic Group (WEKG) that occurs over much of central and western Europe (Searle 1984, Searle and Wójcik 1998).

## Ilomantsi race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, g/o, hn, i/p, j/l, k/r, m/q, tu*

This race was described by Halkka *et al.* (1987, 1994) in the extreme east of Finland and has metacentrics *go, hn* and *ip* which are found in several of the Finnish chromosome races. Given where the race is found in Finland, it is not surprising to find it over the border in northern European Russia (Fig. 2). The individuals karyotyped in Pertozero (near Lake Onega) were homozygous metacentric or heterozygous for *ip, kr* and *mq* but homozygous acrocentric for *g* and *o* (Table 1).

## Petchora race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, gi, hn, jl, kq, mo, pr, tu*

This chromosome race was found in one site in north-eastern European Russia (Kozlovsky *et al.* 2000). Again there is an unusual metacentric including chromo-

some arm *g*, in this case *gi*, which has only previously been described in the Valais race, which is found in Italy and southern Switzerland and is genetically very distinctive from all other chromosome races in the common shrew (Hausser *et al.* 1985, Br unner and Hausser 1996, Lugon Moulin *et al.* 1996). Metacentric *hn* is also worthy of note as a metacentric frequently found in races of eastern and northern Europe (Searle 1984, Searle and W ojcik 1998)

#### Manturovo race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, go, hi, j/l, kq, mn, pr, tu*

This is a new chromosome race for the common shrew. It was discovered on reanalysis of chromosome preparations of individuals from Kostroma (River Unzha, relabelled as Manturovo) which were previously thought to be of the Moscow race (Orlov *et al.* 1996). The race was also found by Kozlovsky *et al.* (2000) in Syctyvkar and Velsk, well to the north of Manturovo (Fig. 2), suggesting that it may have at least a moderately large range. At all sites the only polymorphism detected involved *jl*; the karyotype of a fully metacentric individual is shown in Fig. 3.

The karyotype includes metacentric *go* which is found both in the vicinity of the southern Ural Mts (eg Yuryuzan and Sok races) and Finland (eg Ilomantsi race), as well as *hi* that is characteristic of the WEKG.

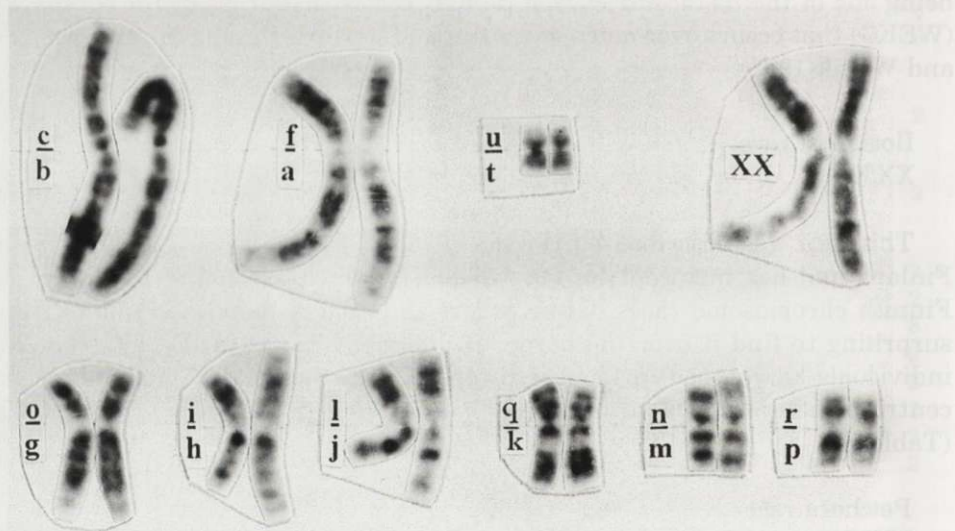


Fig. 3. The karyotype of an individual of the Manturovo chromosome race (female, type site, Manturovo, Kostroma Region).



## Pskov race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, gm, hk, ip, jl, nr, oq, tu*

Zaitsev and Bulatova (1999) described this race from north-western European Russia in two closely located sites. It has also been found in a geographically close site in Estonia (Mishta *et al.* 2000). This race is of interest because its karyotype includes metacentrics characteristic of wide, but different geographical areas: *gm*, characteristic of the WEKG (Searle 1984), *hk*, which is widespread in the Baltic States and neighbouring areas (Mishta *et al.* 2000) and, *ip*, found throughout Finland and in the vicinity of the southern Ural Mts (Halkka *et al.* 1974, 1987, 1994, Polyakov *et al.* 2000).

## Neroosa race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, g/o, hi, j/l, k/r, mn, p/q, tu*

This is a new chromosome race for the common shrew. Although first identified in Neroosa, it was subsequently realised that individuals of this race had been karyotyped previously at Voronezh by Orlov *et al.* (1996), but that the shrews were erroneously identified as belonging to the Moscow race (Table 1). This is a widespread race. Not only does it occur in the Bryansk, Kaluga and Voronezh Regions of Russia, it occupies the eastern half of Ukraine (Mishta *et al.* 2000). Fig. 4 shows the fully metacentric karyotype but some populations in both European Russia and Ukraine are polymorphic. Like the Manturovo race, the Neroosa race is characterised by the widespread metacentrics *go* and *hi*.

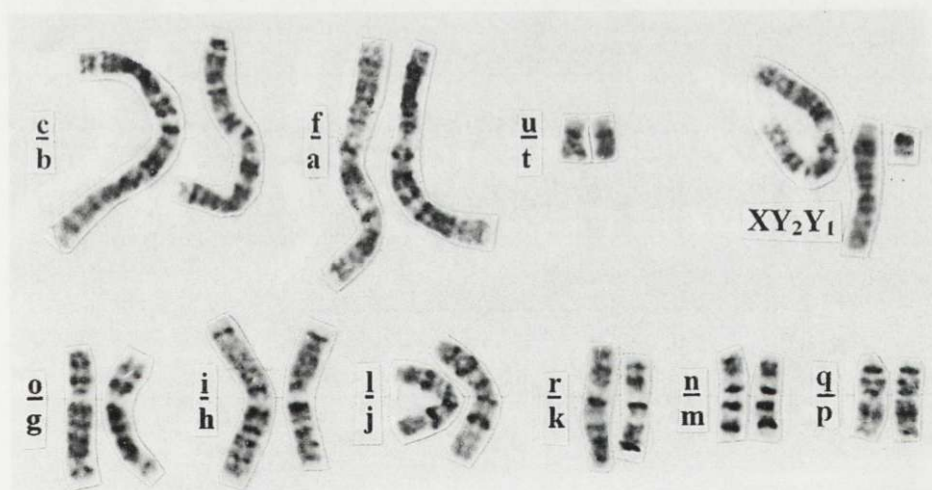


Fig. 4. The karyotype of an individual of the Neroosa chromosome race (male, type site, River Neroosa, Bryansk Region).

## Moscow race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, gm, hi, jl, kr, no, pq, tu*

The Moscow race, despite its geographical location in the heart of eastern Europe, carries the two metacentrics that define the West European Karyotypic Group: *gm* and *hi*. In our previous paper (Orlov *et al.* 1996) we considered it to be a very widespread form. It is now clear that this perception was wrong, because of misidentification of individuals at two sites (see Table 1 and above). The Neroosa and Mologa races appear to have larger ranges than the Moscow race (Fig. 2).

## Seliger race

XX/XY<sub>1</sub>Y<sub>2</sub>, *af, bc, g, hn, ik, jl, m/q, o, pr, tu*

This is a new chromosome race for the common shrew. A karyotype of a homozygous individual is given in Fig. 5. So far, the race is only known from one site. The karyotype includes the widespread east-European metacentric *hn*, and it is likely that there is a polymorphism for another eastern arm combination, *go* (although the two individuals karyotyped were homozygous acrocentric for *g* and *o*). The race is also characterised by metacentric *ik* that is found in several races in eastern Poland and in the Novosibirsk race of western Siberia.

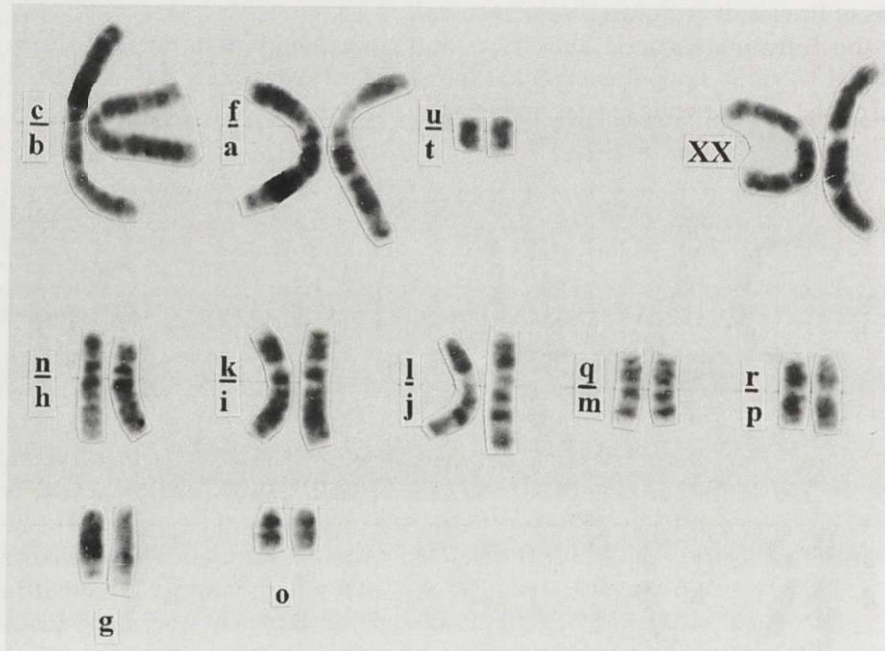


Fig. 5. The karyotype of an individual of the Seliger chromosome race (female, type site, Lake Seliger, Tver Region).

## Mologa race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, g/m, hn, i/o, jl, kr, p/q, tu*

The Mologa race was first described in Tver Region (Orlov *et al.* 1996). However, Bulatova *et al.* (1999) also found the race in localities much further to the south. In this paper we add data from five new sites. This is certainly a widespread race extending in longitude from 36–47°E and in latitude from 51–58°N (Fig. 2) although it is not certain that this distribution is continuous. As described earlier, metacentrics *gm* and *hn* are widespread in western and eastern Europe, respectively.

## Yuryuzan race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, go, hn, ip, jl, kr, mq, tu*

## Sok race

XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, go, hn, ip, jl, kq, mr, tu*

These two races were described by Polyakov *et al.* (2000) in the vicinity of the southern Ural Mts who noted that they have exactly the same metacentrics as two races in Finland (Ilomantsi and Kuhmo).

#### Relationships between races and patterns of chromosomal evolution

Ten out of the eleven races that have been found in European Russia were first described there. The eleventh race, Ilomantsi, was first found at one site in Finland near the border with European Russia (Halkka *et al.* 1987) and reasonably close to Pertozero, the only locality where we found the race (Table 1). The Pskov and Neroosa races, while first described in European Russia, have also been found in neighbouring countries, in Estonia and Ukraine, respectively (Mishta *et al.* 2000).

In addition to these cases, there are also some examples of races limited to European Russia that are chromosomally very similar to races in neighbouring areas. As has already been noted by Polyakov *et al.* (2000), the Yuryuzan and Sok races can be viewed as two of a series of four related races that occur in the vicinity of the Ural Mts. The others are the Serov race (XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, go, hn, ip, jl, km, qr, tu*), on the eastern side of the mountain range, and the Novosibirsk race (XX/X<sub>1</sub>Y<sub>2</sub>, *af, bc, g/o, hn, ik, jl, m/p, q/r, tu*) which has a very large range over western Siberia (Polyakov *et al.* 1996). Polyakov *et al.* (2000) suggest that the southern Ural Mts may have acted as a refugium for the common shrew during the last glaciation, with range expansion from that source both eastwards and westwards. The expansion westwards may have extended well beyond the current range of the Yuryuzan and Sok races. Two races in Finland (the Ilomantsi and Kuhmo) have the same karyotypes as the Yuryuzan and Sok races, indicating that shrews with these chromosomes may have spread many hundreds of kilometers north-westwards from a southern Ural refugium (Polyakov *et al.* 2000). If this model is correct, there is not currently a continuous link between the Yuryuzan and Ilomantsi races or between the Sok and Kuhmo races. The Manturovo race occupies intervening territory (Fig. 2). However, the Manturovo race may represent a

derivative of the Sok race that formed during or after the proposed north-westward expansion from the southern Ural Mts. Comparison of karyotypes shows that the Manturovo race can be derived from the Sok race by two WARTs (metacentrics *hi*, *mn* and *pr* deriving from *hn*, *ip* and *mr*). Furthermore, the Manturovo race may itself have spread northwards and generated another race; the Kanin race can be derived from it by only a single WART (metacentrics *gp* and *or* deriving from *go* and *pr*).

The new Seliger race is also of interest with regards the possible expansion of races from a southern Ural glacial refugium north-westwards. It occurs in north-western European Russia and has a karyotype that is similar to the Novosibirsk race.

While some of the races in European Russia have similarities to eastern (Siberian) races, others are more similar to western (west European) races. In particular, the Moscow race, by virtue of inclusion of *gm* and *hi* in its karyotype, can be defined as a member of the WEKG (Searle 1984). In the past it was thought possible that the WEKG formed a continuous block between Britain in the west and European Russia (represented by the Moscow race) in the east (Orlov *et al.* 1996, Searle and Wójcik 1998). However, the data that we report here (Fig. 2) and that presented by Mishta *et al.* (2000) show that the Moscow race is not such a widespread form in European Russia as previously thought, and is separated by the Neroosa race from the nearest race that carries *gm* and *hi*: the Kiev race of Ukraine.

Once again evolution of one race into another by WARTs represents a possible explanation for the discontinuity in the range of the WEKG. The Neroosa race can be derived from the Moscow race by a single WART (metacentrics *go* and *mn* deriving from *gm* and *no*). The Mologa race which also neighbours the Moscow race can likewise be derived from that race by a single WART (metacentrics *hn* and *io* deriving from *hi* and *no*). Together the Moscow, Neroosa and Mologa races cover a huge south-western sector of European Russia (Fig. 2). It is possible that all these races derive from an eastwards expansion of the WEKG, but with modification of the standard WEKG complement of metacentrics *gm* and *hi* by occurrence of WARTs in part of the European Russia range (to generate the Neroosa and Mologa races). This expansion of the WEKG may have been at the end of the last glaciation; possible refugial areas for the WEKG include the Balkan and Carpathian Mts (Searle 1984, Bilton *et al.* 1998). Further consideration of the colonization history of the common shrew in European Russia and neighbouring areas will be made in a forthcoming paper that will make use of a full phylogeny of all the chromosome races in the former USSR and new data on mtDNA variation.

It should be noted that certain 'important' metacentrics (that define large lineages) are generated by the WARTs that have been proposed above, eg *go* of the Finnish-Ural Mts-West Siberian lineage and *hi* of the WEKG. Clearly, WARTs have the potential to generate such important metacentrics for the first time, but more often they are likely to generate secondarily a metacentric that already exists.

While chromosome mutations (Robertsonian fusions, WARTs) may be the primary force in generating the chromosome races of *S. araneus*, reticulate evolution may also be important. The Pskov race is most striking in this regard. This race is

characterised by metacentrics *gm* (of the WEKG), *ip* (of the Finnish-Ural Mts-West Siberian lineage) and *hk* (which is found in shrews in the Baltic States). It is found in north-western European Russia at an intersection of all these lineages, just as would be expected if the race has derived its metacentric complement from them.

Clearly, the pattern of chromosomal evolution in European Russia is complex and detailed analysis is needed to help decide between the range of possible explanations for the pattern. A full explanation of chromosomal evolution in the common shrews of European Russia will go a long way towards providing a complete understanding of the chromosome variation throughout this remarkable species.

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