

## The Seliger – Moscow hybrid zone between chromosome races of common shrews – an initial description

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**ABSTRACT.** We provide the first description of a hybrid zone between chromosome races of *Sorex araneus* in Central European Russia. In the area near Lake Seliger (Upper Volga), the locally-distributed Seliger race (diagnostic chromosomes *hn, ik, mq, pr, g, o*) meets and hybridises with the more widespread Moscow race (*gm, hi, kr, no, pq*). This hybrid zone appears to be narrow and constrained to the inter-lake isthmus between Lake Seliger and the River Volga system. The hybrid zone may be centred on a minor road. Hybrids occur between the two races but at low frequency. There were three F<sub>1</sub> hybrids out of a total of 87 specimens. These were expected to form the maximally long meiotic chain that can be found in the common shrew: a chain-of-eleven (CXI). Such a configuration was observed in meiotic preparations from one adult male F<sub>1</sub>. Two other complex heterozygote karyotypes were found. The existence of these backcross individuals reflects Robertsonian polymorphism for certain race-specific chromosomes. It is presumed that these various hybrids have reduced fertility, consistent with the narrowness of the hybrid zone and bimodal structure. This is likely to be a “strong” hybrid zone with a greater probability of reduced gene flow and evolution of reproductive isolation than other hybrid zones in the common shrew.

**KEY WORDS:** chromosome race, hybrid zone, Robertsonian fusion, *Sorex araneus*.

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## Гибридная зона между хромосомными расами Селигер и Москва обыкновенной бурозубки – вводное описание

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**РЕЗЮМЕ.** Впервые описана гибридная зона двух хромосомных рас обыкновенной бурозубки в Европейской России. В окрестностях оз. Селигер (Верхняя Волга) локальная хромосомная раса Селигер (диагностические хромосомы *hn, ik, mq, pr, g, o*) контактирует с образованием гибридов с распространенной далее на восток расой Москва (*gm, hi, kr, no, pq*). Эта гибридная зона узкая и ограничена перешейком между озерами в верховьях Волги. Центр гибридной зоны сосредоточен вдоль шоссе местного значения. Гибриды между двумя расами очень редки. Найдены три гибридных особи F<sub>1</sub> из общего числа проанализированных кариологически 87 экземпляров. У таких гибридов возможно образование максимальной для вида мейотической цепочки из одиннадцати элементов (CXI). Подобная конфигурация действительно наблюдалась на мейотических препаратах у единственного из изученных гибридных особей половозрелого самца. Найдены также два рекомбинантных кариотипа, которые могли возникнуть вследствие Робертсоновского полиморфизма в некоторых диагностических метацентриках обеих рас. У гибридов предполагается ограничение плодовитости, что согласуется с узостью гибридной зоны и ее бимодальной структурой. Это пример «сильной» гибридной зоны, поскольку вероятность ограничения генного потока и эволюции изолирующих механизмов в данном случае больше, чем в других гибридных зонах обыкновенной бурозубки.

**КЛЮЧЕВЫЕ СЛОВА:** хромосомная раса, гибридная зона, Робертсоновское слияние, *Sorex araneus*.

### Introduction

The common shrew (*Sorex araneus* Linnaeus, 1758) is one of the most remarkable mammals from the viewpoint of chromosomal variation. Approximately 70 chromosome races have so far been found over the wide, Eurasian range of this species (Wójcik *et al.*, 2003). The ancestral condition in this species consisted largely

of acrocentric chromosomes, but through the action of Robertsonian fusions and whole-arm reciprocal translocations (WARTs) different combinations of metacentrics have been generated in each race (Searle & Wójcik, 1998; Wójcik *et al.*, 2002). According to the standard nomenclature, each ancestral acrocentric is labelled by a letter of the alphabet (Searle *et al.*, 1991). It is the autosomal acrocentrics *g, h, i, k, m-r* which combine together into various metacentrics in the different chromosome races (Wójcik *et al.*, 2003), and which there-

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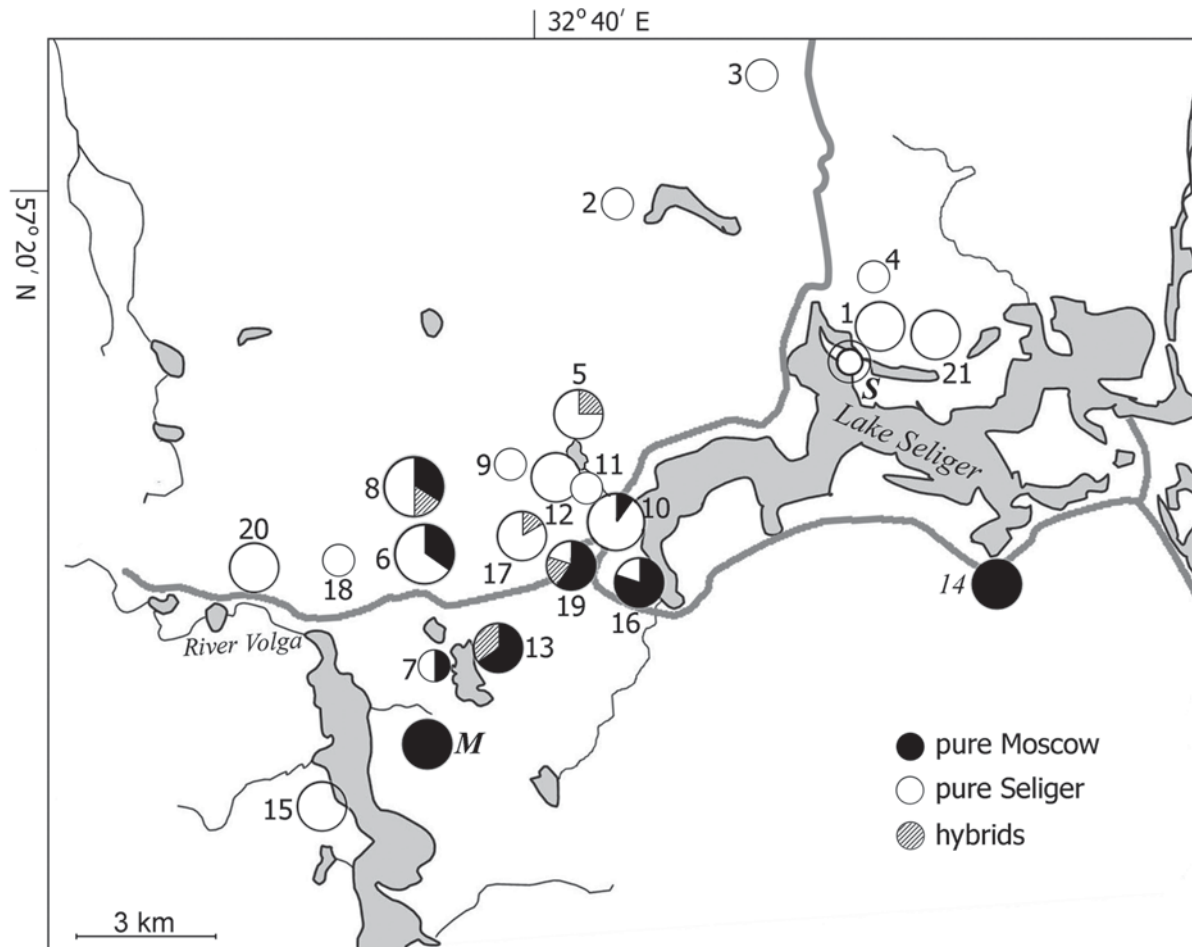


Figure 1. A schematic map of the hybrid zone between the Moscow and Seliger races of the common shrew showing the trapping localities and frequencies of the pure races and hybrids. The localities are numbered as in Tab. 1 which provides full details of all karyotypes. The size of each circle reflects the sample size. Double circle (S) — the type locality of Seliger race. M — first locality for the Moscow race in the vicinity of the zone (see text). Lakes are shown with shading, thin black lines show rivers and thick grey lines indicate roads.

fore constitute chromosome arms of the race-specific metacentrics (e.g. *hi*).

These chromosome races of the common shrew come into contact with each other, and hybridise. Such areas where hybrids occur are known as hybrid zones (Harrison, 1993) and are of great interest because they may be sites of reduced gene exchange and even speciation. Fourteen examples of the best studied chromosomal hybrid zones in the common shrew have been singled out by Searle & Wójcik (1998) and Wójcik *et al.* (2002), which form the basis for comparison with any newly discovered zone. In contrast to the situation in central and western Europe where 13 hybrid zones were included in these reviews (from Britain, Switzerland, Sweden, Poland and the Czech Republic), only one zone from Russia was sufficiently well-described: the Novosibirsk-Tomsk hybrid zone (Aniskin & Lukianova, 1989; Polyakov *et al.*, 1996).

The present paper describes the first hybrid zone recognised in European Russia between two chromo-

some races of common shrews, that involving the Moscow (Mo) and Seliger (Sl) races. These two races are different in all variable chromosome arms, generating five metacentrics in the Moscow race (*gm, hi, kr, no, pq*) and four metacentrics and two acrocentrics in the Seliger race (*hn, ik, mq, pr, g, o*). The Moscow race was first defined by Aniskin & Lukianova (1989) and the Seliger race was found about 10 years ago by the authors of the present work during international studies under the INTAS project No. 93-1463 (Bulatova *et al.*, 2000).

This publication presents the initial stages of a multidisciplinary study of the Moscow-Seliger hybrid zone, defining its basic chromosomal characteristics.

### Material and methods

Bulatova *et al.* (2000) demonstrated that the Moscow and Seliger races occurred within 15 km of each other in the vicinity of the source of the River Volga in the Tver Region of European Russia. In view of these findings,

Table 1. Chromosomal characteristics of each locality sampled in the vicinity of the Seliger-Moscow hybrid zone.

Locality number	Date of collection	Coordinates	Number of specimens	Number of individuals				
				Seliger	Seliger variants	Moscow	Moscow variants	Hybrids
<i>M</i>	Jul 1997	N 57°12', E 32°37'	5			5		
<i>S</i>	Jul 1997	N 57°17', E 32°47'	2	1	1 ( <i>m/g</i> )			
1	Jun 2001	N 57°17', E 32°49'	5	5				
2	Jun 2001	N 57°19', E 32°44'	1	1				
3	Jun 2001	N 57°22', E 32°46'	1	1				
4	Jun 2001	N 57°18', E 32°48'	2	1	1 ( <i>p/r</i> )			
5	Jun 2001	N 57°16', E 32°41'	4	1	1 ( <i>j/l</i> ) 1 ( <i>p/r</i> )			1 BX1
6	Sep 2001	N 57°14', E 32°37'	6	4		2		
7	Sep 2001	N 57°13', E 32°37'	2	1		1		
8	Sep 2001	N 57°16', E 32°41'	6	3		2		1 F <sub>1</sub>
9	Sep 2001	N 57°16', E 32°39'	2	2				
10	Sep 2001	N 57°15', E 32°41'	8	6	1 ( <i>p/r</i> )	1		
11	Sep 2001	N 57°16', E 32°41'	2	2				
12	Sep 2001	N 57°16', E 32°40'	5	4	1 ( <i>j/l</i> )			
13	Jun 2002	N 57°13', E 32°38'	3			2		1 F <sub>1</sub> ( <i>j/l</i> )
14	Jun 2002	N 57°15', E 32°51'	4			4		
15	Jun 2002	N 57°12', E 32°34'	5	4	1 ( <i>p/r</i> )			
16	Nov 2004	N 57°14', E 32°42'	5	1		4		
17	Nov 2004	N 57°14', E 32°39'	6	5				1 F <sub>1</sub>
18	Nov 2004	N 57°14', E 32°34'	2	2				
19	Sep 2005	N 57°14', E 32°39'	5	1		2	1 ( <i>g/m</i> )	1 BX2
20	Sep 2005	N 57°14', E 32°29'	3	3				
21	May 2005	N 57°17', E 32°50'	3	3				
Totals (23 localities)			87	51	7	23	1	5

*M* and *S* indicate localities sampled by Bulatova *et al.* (2000). For the Moscow and Seliger variants, the polymorphic chromosomes are indicated. Three categories of hybrid karyotype are classified as F<sub>1</sub>, BX1 and BX2. See Tab. 2 for further details.

the presence of a hybrid zone was expected in this area, and further specimens were collected and karyotyped. New samples were obtained from 21 localities between July 2001 and September 2005 in the geographical area defined by the following coordinates: N 57°12' – 57°22' and E 32°29' – 32°51'. A total of 87 specimens were examined including two samples collected by Bulatova *et al.* (2000) which are labelled here by letters *S* (Seliger, type locality) and *M* (Moscow, Lake Sterzh) (Fig. 1 and Tab. 1). The geographical coordinates for all localities were obtained via a GPS (the previous map-based coordinates for *M* and *S* have been corrected).

Shrews were collected around the western bay of Lake Seliger and further westwards across the inter-lake isthmus towards the source of the River Volga (Fig. 1). All this area is situated in the Valdai Heights (maximum height 343 m a.s.l.), and forms the southern part of the natural taiga zone. Forests (mainly coniferous or mixed)

cover the area under study. Grasslands only occur in small areas along the banks of the numerous lakes in this region and at the sites of abandoned settlements within the forested area. Live traps described by Shchipanov *et al.* (2000) were arranged in lines 375 m long consisting of 50 traps. All lines except locality 10 (see below) represent all types of habitats in approximately similar proportion. Each line was regarded as a single locality. Contrary to the trapping protocol described elsewhere in this volume (Shchipanov, 2007), the traps in each locality were only operative until the first set of captures (usually 1.5 – 3 h) and so the results of this trapping could not be used to calculate population density. In total 23 localities were examined. The shrews from locality 10 were caught in the garden (ca. 100 m in length) of a private house on the shore of Lake Seliger, adjacent to a reedbed. Twenty traps were operative here for three days along a fence overgrown with grass.

Specimens were processed in a field laboratory. Chromosome preparations of spleen and bone marrow were treated with colchicine *in vivo* or *in vitro* followed the methodology of Král & Radjabli (1974). G-banding was used for chromosome identification. Descriptions of karyotypes follow Searle *et al.* (1991).

## Results

Tab. 1 presents details of all karyotypes found in the contact area between the Seliger and Moscow races. Samples from localities *M* and 14 consisted solely of the Moscow race and those from localities *S*, 1–4, 9, 11, 12, 15, 18, 20 and 21 included Seliger race individuals only. However, there were also samples which consisted of both Moscow and Seliger race individuals (localities 6–8, 10, 16, 19). Finally, hybrid individuals with chromosomes derived from both races have been found in several localities (5, 8, 13, 17, 19). So, we have established the presence of a new hybrid zone in the common shrew: that between the Seliger and Moscow races.

Fig. 1 shows the distribution of samples with each of these characteristics. Moscow samples were collected in the south-east of the study area and the Seliger samples were found in the north and west. Samples consisting of both races and/or including hybrids were localised in a rectangular area of 4 km by 6 km and pure race Seliger and Moscow samples were detected within 4 km of each other. This suggests that the Seliger – Moscow hybrid zone is very narrow (i.e. with a standardised width of a few kilometres rather than tens of kilometres; see Searle & Wójcik, 1998). However, further samples are clearly needed to define the zone properly.

The Moscow and Seliger shrews in the mixed samples 6–8, 10, 16 and 19 were caught in the same habitats in neighbouring traps or even in the same trap (when the trap line was checked two or more times). The two races were found together alongside the road that crosses the inter-lake isthmus between Lake Seliger and the River Volga system (Fig. 1). There are no clear indications of any other geographical or habitat feature that may separate the races: there is the same mix of taiga habitats on either side of the road.

All the individual karyotypes found in the Seliger – Moscow hybrid zone and its vicinity are listed in Tab. 2, and their distribution can be determined from Tab. 1 and Fig. 1. In addition to the fully metacentric Moscow race karyotype (*gm, hi, kr, no, pq*), one individual was found to be heterozygous for *gm* (i.e. a simple heterozygote). Among variants of the Seliger race karyotype (*hn, ik, mq, pr, g, o*), there were individuals separately heterozygous for *jl, mq* and *pr* (i.e. simple heterozygotes). These variants have implications with regards the types of hybrids that may be detected (with the exception of the *jl* heterozygotes, because the metacentric *jl* characterises both races).

Homozygotes for the fully metacentric Moscow and Seliger karyotypes are expected to produce complex heterozygous hybrids with the following karyotype: *g/gm/mq/qp/pr/rk/ki/ih/hn/no/o*, i.e. individuals that should produce a chain-of-eleven configuration (CXI) at meiosis I. This  $F_1$  karyotype has been found in three individuals. A meiotic preparation of one of these males (locality 13) was made using the technique of Williams *et al.* (1971). This demonstrated the presence of a CXI in seven cells examined at diakinesis / metaphase I. This individual was also a simple heterozygote for *jl*, and a trivalent was also observed in the meiotic spreads.

In a system consisting purely of fully metacentric Seliger and Moscow race individuals, the only karyotypes expected in the hybrid zone are the pure races and the  $F_1$ . The balanced gametes from individuals with the  $F_1$  karyotype are the haploid set of Seliger and Moscow chromosomes, respectively. So, interbreeding of the  $F_1$ , Seliger and Moscow karyotypes in any combination can only generate further individuals with an  $F_1$ , Seliger and Moscow karyotype. Therefore, it is not possible to tell whether an  $F_1$  is a true  $F_1$  or a backcross.

However, because variants of the Seliger and Moscow karyotypes are present, backcross individuals can be detected. These are the individuals labelled BX1 and BX2 in Tabs 1 and 2. Thus, at locality 19 the BX2 individual has a karyotype *gm, q/qp/pr/rk/ki/ih/hn/no/o*. This individual is a backcross product between an  $F_1$  variant and a Moscow race homozygote. The  $F_1$  variant would itself have been the product of a Seliger race

Table 2. Karyotypes of common shrews observed in the Seliger – Moscow hybrid zone.

Karyotype	<i>jl</i> status	Diagnostic chromosomes	2NA	Number of specimens
Moscow	<i>jl</i>	<i>gm, hi, kr, no, pq</i>	18	23
Moscow variant ( <i>g/m</i> )	<i>jl</i>	<i>g/m, hi, kr, no, pq</i>	19	1
Seliger	<i>jl</i>	<i>hn, ik, mq, pr, g, o</i>	20	51
Seliger variant ( <i>j/l</i> )	<i>j/l</i>	<i>hn, ik, mq, pr, g, o</i>	21	2
Seliger variant ( <i>p/r</i> )	<i>jl</i>	<i>hn, ik, mq, p/r, g, o</i>	21	4
Seliger variant ( <i>m/q</i> )	<i>jl</i>	<i>hn, ik, m/q, pr, g, o</i>	21	1
Hybrid $F_1$	<i>jl</i>	<i>g/gm/mq/qp/pr/rk/ki/ih/hn/no/o</i>	19	2
Hybrid $F_1$ ( <i>j/l</i> )	<i>j/l</i>	<i>g/gm/mq/qp/pr/rk/ki/ih/hn/no/o</i>	20	1
Hybrid BX1	<i>jl</i>	<i>hn, ik, o, g/gm/mq/qp/pr/r</i>	20	1
Hybrid BX2	<i>jl</i>	<i>gm, q/qp/pr/rk/ki/ih/hn/no/o</i>	19	1

variant heterozygous for *mq* and a Moscow race homozygote.

Another backcross individual was detected at locality 5 (the BX1 karyotype in Tabs 1 and 2). This animal was the product of an F<sub>1</sub> variant and a Seliger race homozygote. In this case, the F<sub>1</sub> variant would have been the product of a Moscow race individual heterozygous for *kr* and a Seliger race homozygote.

Overall, 66.7% of the individuals so far sampled in the vicinity of the Moscow – Seliger hybrid zone have been Seliger race homozygotes or Seliger variants, 27.6% have been Moscow race homozygotes or Moscow variants and 5.7% have been hybrids.

## Discussion

The hybrid zone between the Moscow and the Seliger races involves the two most karyotypically distinct races in European Russia. The Moscow chromosome race shares two metacentrics, *gm* and *hi*, with many European races described as the West European Karyotypic Group, or WEKG (Searle, 1984; Hausser *et al.*, 1994). All five diagnostic metacentrics of this race (*gm*, *hi*, *kr*, *no*, *pq*) show monobrachial homology with diagnostic metacentrics and acrocentrics of the Seliger race (*hn*, *ik*, *mq*, *pr*, *g*, *o*). The affiliation of the Seliger race is not as clear as the Moscow race. Bulatova *et al.* (2000) have pointed out that although its karyotype includes the widespread East European metacentric *hn* and the unfused arms of another eastern metacentric *go* (acrocentrics *g* and *o*), this race is also characterised by the rare metacentric *ik* known in three geographically disjunct races — Istranca from the Balkans, Białowieża from Poland and Novosibirsk from West Siberia (Wójcik *et al.*, 2003).

Hybrids between the Moscow and Seliger races should form the longest meiotic chain possible in the common shrew, namely a chain-of-eleven (CXI). This is because all the variable chromosomes in the common shrews (*g*, *h*, *i*, *k*, *m-r*) contribute to the differences between the Moscow and Seliger races.

It is not certain whether the CXI-forming Seliger-Moscow F<sub>1</sub> hybrids can produce progeny or not. Any products of these individuals would be either further F<sub>1</sub> hybrids or pure race individuals, exactly the same as could be produced by Seliger or Moscow homozygotes. So, our chromosome survey does not provide direct data on the production of progeny by F<sub>1</sub> hybrids. We did catch one adult male F<sub>1</sub> hybrid in which we observed the CXI in diakinesis – metaphase I cells. The slides from this individual, which was also heterozygous for *jl*, displayed abundant mature sperm. There is a likelihood therefore that F<sub>1</sub> hybrids in the Seliger – Moscow zone may be fertile. Previous studies have already shown that in the common shrew interracial hybrids with long meiotic chains may be fertile (e.g. CVII hybrids: Mercer *et al.*, 1992).

However, the narrowness of the hybrid zone suggests a degree of infertility associated with the F<sub>1</sub> hybrids. The width of a hybrid zone maintained by hybrid unfitness (i.e. a “tension zone”) relates to the degree of unfitness, such that zones with highly unfit hybrids are narrower than those with moderately unfit hybrids (Bar-

ton & Hewitt, 1985). In the case of hybrid zones between chromosome races, the unfitness is expected to be in the form of reduced fertility. A narrow zone is also found in other cases where the F<sub>1</sub> hybrid produces a long meiotic chain (for review see: Searle & Wójcik, 1998). In particular, narrow zones were found between the Novosibirsk / Tomsk and the Białowieża / Drnholec chromosome races with 9- and 10-element meiotic chain configurations in hybrids, respectively. There are further karyotypic similarities with the Seliger – Moscow hybrid zone: while the Białowieża and Novosibirsk races carry metacentric *ik* like the Seliger race, the Drnholec and Tomsk races are characterised by metacentric *hi* like the Moscow race. However, the proportion of hybrids produced in the three hybrid zones differs substantially: 4% for the Novosibirsk – Tomsk (Aniskin & Lukianova, 1989) and 6% for the Seliger-Moscow (this paper), but 20% for the Białowieża – Drnholec (Szałaj *et al.*, 1996). In this latter zone, there was a particularly large range of hybrids: 14 out of possible 16 hybrid karyotypes were found. This reflects Robertsonian polymorphism of some of the race-specific chromosomes, such that they may be present as both metacentrics and twin acrocentrics. Such polymorphism also occurs in the Seliger – Moscow zone, but not to the same degree as in the Białowieża – Drnholec. Heterozygotes were found for chromosomes *mq* and *pr* (Seliger race) and *gm* (Moscow race). The Seliger race polymorphism for *pr* has not previously been reported (Bulatova *et al.*, 2000). A further new polymorphism (*kr* in the Moscow race) can be inferred from the backcross karyotype BX1. The backcross karyotypes BX1 and BX2 arose from crosses between F<sub>1</sub> variants and pure race homozygotes. The F<sub>1</sub> variants concerned would have formed two CVI configurations (*k/ki/ih/hn/no/o* and *g/gm/mq/qp/pr/r*) and one CIX configuration (*q/qp/pr/rk/ki/ih/hn/no/o*), respectively. Therefore, we can say that individuals with long chain configurations in the Seliger – Moscow hybrid zone can, at least occasionally, be fertile.

Another way to examine fertility in the Seliger – Moscow hybrid zone is through molecular studies, to see if gene flow can be detected. A first attempt has been carried out through the analysis of inter-SINE-PCR DNA polymorphism. Bannikova *et al.* (2003) revealed possible genetic exchange between the Seliger and Moscow races. Some shared band patterns with the Seliger race (specimens of localities 1–5, 8, 9, 12 in Tab. 1) were detected in MIR-fingerprints of two specimens of the Moscow race from locality 6 compared to samples of this race from geographically distant points. The BX1 individual used in this molecular analysis was indistinguishable from Seliger race individuals when analysed with MIR-PCR. Likewise, later inter-SINE PCR studies by Bannikova *et al.* (2006) showed that two of the F<sub>1</sub> hybrid specimens gave similar results to Moscow race individuals.

These issues of fertility and gene flow within the Seliger – Moscow hybrid zone are important. In the terminology of Jiggins & Mallet (2000) this hybrid zone is “bimodal”, i.e. dominated by pure race individuals with few hybrids. Such zones can be viewed as “strong”,

i.e. zones which may be expected to suffer reduced gene flow and which may be the sites of speciation. Given that the  $F_1$  hybrids within this zone are expected to form the longest meiotic chain configuration possible given the set of variable chromosomes in the common shrew, then the Seliger-Moscow hybrid zone can be considered one of the "strongest" in the species. Further work on fertility and gene flow in this hybrid zone will be very interesting, especially in comparison with the detailed studies that have been carried on hybridisation between *S. araneus* and *S. antinorii* in Switzerland, where there is clear evidence for an interruption to gene flow between chromosomally differentiated shrews (Brünner *et al.*, 2002).

Further studies are also needed to provide a precise localisation of the Seliger – Moscow hybrid zone. The races meet in the isthmus between Lake Seliger and the River Volga lake system (Fig. 1). If the Seliger race colonised the area from the north and the Moscow races colonised from the south, this may be the area that they would be expected to meet. The lakes clearly act as boundaries between the races and the isthmus is the point where the races would be forced to meet. There is no geographic barrier within the isthmus, so the exact position of the hybrid zone may be rather labile. However, the current sampling suggests that the hybrid zone may be centred on the road that crosses the isthmus (Fig. 1). Even though this road, which is unmetalled and narrow, would certainly not be an absolute barrier to common shrews, it may reduce dispersal sufficiently that it now acts as the centre to the hybrid zone. If so, it would follow another example of a hybrid zone centred on a man-made feature: Szałaj *et al.* (1996) demonstrated that the Białowieża – Drnholec zone is centred on a railway embankment.

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