

## The ISACC heritage

**Jeremy B. Searle\*, Jacques Hausser, Jan Zima, Karl Fredga, Jan M. Wójcik, Vitaly T. Volobouev, Nina S. Bulatova & Rena Nadjafova**

**ABSTRACT.** This article marks the coming of age of the meetings organised by the International *Sorex araneus* Cytogenetics Committee (ISACC). These meetings have continued every three years for 18 years. This paper complements the published proceedings for six of these meetings. It brings together in one place the contents lists of all those proceedings, the lists of delegates for all the meetings and all abstracts of posters and talks that were not published in the proceedings. Together with the proceedings this paper represents the heritage of ISACC.

**KEY WORDS:** common shrew, cytogenetics, history of science, *Sorex araneus*.

Jeremy B. Searle [jbs3@york.ac.uk], Department of Biology, University of York, York YO10 5YW, UK; Jacques Hausser [jacques.hausser@unil.ch], Department of Ecology and Evolution, Biology Building, University of Lausanne, CH-1015 Lausanne, Switzerland; Jan Zima [jzima@brno.cas.cz], Institute of Vertebrate Biology AS CR, Květná 8, CZ-60 365 Brno, Czech Republic; Karl Fredga [karl.fredga@ebc.uu.se], Department of Evolution, Genomics and Systematics, EBC, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden; Jan M. Wójcik [jwojcik@bison.zbs.bialowieza.pl], Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland; Vitaly T. Volobouev [vitaly@mnhn.fr], Laboratoire de Zoologie, Mammifères et Oiseaux, Muséum National d'Histoire Naturelle, 55 rue de Buffon, 75005 Paris Cedex 05, France; Nina S. Bulatova and Rena S. Nadjafova [admin@sevin.ru], A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia.

## Наследие Международного комитета по цитогенетическим исследованиям обыкновенной бурозубки (ISACC)

**Дж.Б. Сирл, Ж. Хойзер, Я. Зима, К. Фредга, Я.М. Вуйчик, В.Т. Волобуев, Н.Ш. Булатова, Р.С. Наджаfoва**

**РЕЗЮМЕ.** Настоящая публикация задумана в ознаменование совершеннолетия совещаний, организуемых Международным комитетом по цитогенетическим исследованиям обыкновенной бурозубки *Sorex araneus* (ISACC). На протяжении этих 18 лет такие встречи проходили регулярно каждые три года. Статья дополняет содержание опубликованных сборников трудов шести предшествующих совещаний. В ней приведены оглавления всех этих сборников, полные списки участников всех совещаний, а также тезисы стендовых сообщений и выступлений, которые в трудах не публиковались. Вместе со сборниками трудов эта статья очерчивает научное наследие ISACC.

**КЛЮЧЕВЫЕ СЛОВА:** обыкновенная бурозубка, цитогенетика, история науки, *Sorex araneus*.

### Introduction

On 30–31 August 1987, one of us (JBS) organised a meeting in Oxford that focussed on the chromosomal variation in the common shrew, *Sorex araneus*. It was attended by 23 delegates from Britain, Czechoslovakia (now Czech Republic), France, Italy, Poland, Sweden and Switzerland. The meeting was friendly and successful, and a grouping was formed to hold similar such meetings every three years (the 'International *Sorex araneus* Cytogenetics Committee': ISACC). Through these regular meetings the community of individuals working on chromosome variation in common shrews have been remarkably interactive

and collaborative. The work promoted and fostered by ISACC has helped make the common shrew one of the foremost mammalian models for the study of chromosome variation.

The most recent ISACC meeting, in St Petersburg on 28 August – 1 September 2005 was the seventh in the series and, with 47 delegates, was the best populated yet. Remarkably, the ISACC meetings have been continuing, in a regular fashion, for as long as 18 years. So, they have truly come of age! Furthermore, they have continued for a full cycle. The meeting has moved from country to country (Britain, Switzerland, Czech Republic, Sweden, Poland, France, Russia), jumping between the centres of shrew research. It has been agreed that the next meeting (in 2008) will return to Britain, thus starting, we hope, a second cycle!

\* Corresponding author

To mark the coming of age of the ISACC meetings, we decided to produce an article that documents the ISACC heritage. Much of the achievements of ISACC are laid out in the six volumes of conference proceedings. However, we felt it helpful to bring together the list of contents of these proceedings in one place. But we wanted to do more than that. In this paper we have also listed all the delegates of all the meetings, and have reproduced (after minor editing by JBS) all those abstracts of talks and posters that did not lead to publications in the proceedings. In particular, the first meeting did not have any proceedings and it is important to have some record of what was presented on that seminal occasion.

ISACC has achieved a lot and can be proud of its heritage. This article together with the previously published proceedings document nicely the history of cytogenetic and related research in the common shrew over the last 18 years. One of the reasons for the success of ISACC is that it has had a very stable membership, and a membership have all contributed to its success through commitment and hard-work. The first six authors of this paper all attended the founding meeting. They were also the people who organised the first six meetings. All these individuals are still members of ISACC and still interested in shrew cytogenetics!

Although we have emphasised the stability of the field of shrew cytogenetics, there have also been profound changes over the 18 years of the ISACC meetings. In particular, the centre of gravity of the field has moved eastwards. Everybody at the first meeting was based in western or central Europe. However, twenty-eight of the 47 delegates in the most recent meeting were from European and Siberian Russia. This is appropriate: the majority of the species range of the common shrew is in Russia and it is excellent that so much research should be conducted there (largely through the support of the INTAS funding agency). The seventh author of this paper (NSB) was the organiser of the most recent (St Petersburg) meeting, is a member of ISACC and a representative of the Russian component of shrew cytogenetic research. The final author (RN) was not a meeting organiser, but was the person who largely constructed this paper, working with JBS.

## DELEGATE LISTS

### OXFORD 1987 (23 delegates)

Barton, Nick  
Bengtsson, Bengt Olle  
Bosshard, Frédérique  
Dannelid, Erland  
Fedyk, Stanisław  
Ford, Charles  
Fredga, Karl  
Frykman, Ingrid  
Garagna, Silvia  
Hausser, Jacques  
King, Peter

Malmquist, Mats  
Mercer, Simon  
Mills, Walter  
Neet, Cornelis  
Redi, Carlo  
Searle, Jeremy (organiser)  
Szymura, Jacek  
Vogel, Peter  
Volobouev, Vitaly  
Wilkinson, Pernille  
Wójcik, Jan  
Zima, Jan

### LAUSANNE and ARZIER 1990 (22 delegates)

Capanna, Ernesto  
Fredga, Karl  
Fumagalli, Luca  
Garagna, Silvia  
Hausser, Jacques (organiser)  
Maddalena, Tiziano  
Mercer, Simon  
Meylan, André  
Neet, Cornelis  
Overgaard Jensen, Lisbeth  
Redi, Carlo  
Ruedi, Manuel  
Searle, Jeremy  
Sharman, Geoffrey  
Stopka, Pavel  
Stubbe, Anne  
Taberlet, Pierre  
Vogel, Peter  
Volobouev, Vitaly  
Wallace, Bridget  
Wójcik, Jan  
Zima, Jan

### BRNO and DOLNÍ VĚSTONICE 1993 (24 delegates)

Banaszek, Agata  
Brünner, Harald  
Dannelid, Erland  
Fredga, Karl  
Fumagalli, Luca  
Hausser, Jacques  
Horáček, Ivan  
Lukáčová, Lenka  
Macholán, Miloš  
Míroš, Patricia  
Mishta, Alina  
Narain, Yolanda  
Piálek, Jaroslav  
Pucek, Zdzisław  
Ratkiewicz, Mirosław  
Searle, Jeremy  
Sikorski, Michal  
Stopka, Pavel  
Volobouev, Vitaly

Wallace, Bridget  
 Wójcik, Jan  
 Wytttenbach, Andreas  
 Zagorodnyuk, Igor  
 Zima, Jan (organiser)

**NORR MALMA and UPPSALA 1996  
 (31 delegates)**

Bilton, David  
 Borodin, Pavel  
 Brünner, Harald  
 Bulatova, Nina  
 Chętnicki, Włodzimierz  
 Dannelid, Erland  
 Fredga, Karl (organiser)  
 Hausser, Jacques  
 Koroleva, Irina  
 Lugon Moulin, Nicolas  
 Lukáčová, Lenka  
 Macholán, Miloš  
 Malchenko, Sergey  
 Matyakhina, Ludmila  
 Mishta, Alina  
 Moraleva, Natalia  
 Narain, Yolanda  
 Oda, Sen-ichi  
 Orlov, Victor  
 Piálek, Jaroslav  
 Ratkiewicz, Mirosław  
 Rogatcheva, Margarita  
 Searle, Jeremy  
 Sheftel, Boris  
 Szałaj, Katarzyna  
 Volobouev, Vitaly  
 Wallace, Bridget  
 Wójcik, Anna  
 Wójcik, Jan  
 Wytttenbach, Andreas  
 Zima, Jan

**BIAŁOWIEŻA 1999 (33 delegates)**

Andersson, Anna-Carin  
 Balloux, François  
 Banaszek, Agata  
 Biltueva, Larisa  
 Bołtrusko, Joanna  
 Borodin, Pavel  
 Bulatova, Nina  
 Bystrakova, Natalia  
 Chętnicki, Włodzimierz  
 Fedyk, Stanisław  
 Hausser, Jacques  
 Larkin, Denis  
 Lugon Moulin, Nicolas  
 Mishta, Alina  
 Moska, Magdalena  
 Ochocińska, Dorota  
 Orlov, Victor

Perelman, Polina  
 Piálek, Jaroslav  
 Polyakov, Andrei  
 Pucek, Zdzisław  
 Ratkiewicz, Mirosław  
 Rogatcheva, Margarita  
 Ruczyński, Ireneusz  
 Rychlik, Leszek  
 Searle, Jeremy  
 Szałaj, Katarzyna  
 Szuma, Elwira  
 Turlejski, Krzysztof  
 Volobouev, Vitaly  
 Wójcik, Anna  
 Wójcik, Jan (organiser)  
 Zalewska, Hanna

**PARIS 2002 (31 delegates)**

Andersson, Anna-Carin  
 Aniskin, Vladimir  
 Banaszek, Agata  
 Bannikova, Anna  
 Basset, Patrick  
 Biltueva, Larisa  
 Borodin, Pavel  
 Bulatova, Nina  
 Bystrakova, Natalia  
 Chętnicki, Włodzimierz  
 Demidova, Tatiana  
 Fedyk, Stanisław  
 Fivaz, Fabien  
 Fredga, Karl  
 Hausser, Jacques  
 Jones, Ross  
 Lyapunova, Elena  
 Mishta, Alina  
 Nadjafova, Rena  
 Polly, David  
 Polyakov, Andrei  
 Ratkiewicz, Mirosław  
 Searle, Jeremy  
 Sheftel, Boris  
 Volobouev, Vitaly (organiser)  
 Wallace, Bridget  
 Wójcik, Anna  
 Wójcik, Jan  
 Yaskin, Vladimir  
 Zhdanova, Natalia  
 Zima, Jan

**ST PETERSBURG 2005 (47 delegates)**

Aleksandrov, Dmitry  
 Aleksandrova, Alina  
 Andersson, Anna-Carin  
 Balakirev, Alexander  
 Banaszek, Agata  
 Bannikova, Anna  
 Basset, Patrick

Belonogova, Nadezhda  
 Biltueva, Larisa  
 Bobretsov, Anatoly  
 Borodin, Pavel  
 Bukina, Marina  
 Bulatova, Nina (organiser)  
 Bystrakova, Natalia  
 Chang, Jean  
 Chętnicki, Włodzimierz  
 Demidova, Tatiana  
 Fedyk, Stanisław  
 Fredga, Karl  
 Hausser, Jacques  
 Ilyashenko, Vadim  
 Jadwiszczak, Katarzyna  
 Jones, Ross  
 Kalinin, Alexei  
 Kouptsov, Alexander  
 Kupriyanova, Inna  
 Lyapunova, Elena  
 Mishta, Alina  
 Nadjafova, Rena  
 Onitschenko, Sergei  
 Panov, Victor  
 Pavlova, Svetlana  
 Piálek, Jaroslav  
 Polly, David  
 Polyakov, Andrei  
 Poroshin, Eugene  
 Potapov, Sergei  
 Rubtsov, Nikolai  
 Searle, Jeremy  
 Shchipanov, Nikolai  
 Sheftel, Boris  
 White, Tom  
 Wójcik, Anna  
 Wójcik, Jan  
 Yannic, Glenn  
 Zhdanova, Natalia  
 Zima, Jan

## PUBLISHED PROCEEDINGS

### Mémoires de la Société vaudoise des Sciences naturelles: Vol. 19, Part 1, 1991: 1–151

The cytogenetics of the *Sorex araneus* group and related topics

Proceedings of ISACC's Second International Meeting, Lausanne and Arzier, Switzerland

12–16 September, 1990

Edited by J. Hausser

SHARMAN G.B. History of discovery and recognition of XY<sub>1</sub>Y<sub>2</sub> systems and chromosome polymorphism in mammals: pp. 7–12

SEARLE J.B., FEDYK S., FREDGA K., HAUSSER J., VOLOBOUEV V.T. Nomenclature for the chromosomes of the common shrew (*Sorex araneus*): pp. 13–22

WALLACE B.M.N., SEARLE J.B., GARAGNA S. Oogene-

sis in common shrews homozygous and heterozygous for Robertsonian rearrangements: pp. 23–31

MERCER S.J., SEARLE J.B., WALLACE B.M.N. Meiotic studies of karyotypically homozygous and heterozygous male common shrews: pp. 33–43

GARAGNA S., SEARLE J.B., REDI C.A. Whole-arm rearrangements in the common shrew in a wider context: pp. 45–49

WÓJCIK J.M. Chromosomal polymorphism in the common shrew *Sorex araneus* and its adaptative significance: pp. 51–62

ZIMA J. Is the trend toward low 2Na numbers inescapable for *Sorex araneus* populations?: pp. 63–71

MERCER S.J., SEARLE J.B. Preliminary analysis of a contact zone between karyotypic races of the common shrew (*Sorex araneus*) in Scotland: pp. 73–78

HAUSSER J., BOSSHARD F., TABERLET P., WÓJCIK J. Relationships between chromosomes races and species of *Sorex* of the *araneus* group in the western Alps: pp. 79–95

NEET C.R., HAUSSER J. Biochemical analysis and determination of living individuals of the Alpine karyotypic races and species of the *Sorex araneus* group: pp. 97–106

TABERLET P., FUMAGALLI L., HAUSSER J. mtDNA comparison of the Alpine chromosomal races and species of the *Sorex araneus* group: preliminary results: pp. 107–118

ZIMA J. Banded chromosomes of *Sorex daphaenodon*: A comparison with *S. araneus* (Mammalia, Insectivora): pp. 119–124

MEYLAN A., HAUSSER J. The karyotype of the North American *Sorex tundrensis* (Mammalia, Insectivora): pp. 125–129

VOLOBOUEV V., DUTRILLAUX B. Chromosomal evolution and phylogenetic relationships of the *Sorex araneus-arcticus* species group: pp. 131–139

CAPANNA E. Concluding remarks. *Mus domesticus* and *Sorex araneus* faced: two speciation models compared: pp. 141–151

### Folia Zoologica: Vol. 43, Suppl. 1, 1994: 1–116

The cytogenetics of the *Sorex araneus* group and related topics

Proceedings of ISACC's Third International Meeting, Brno and Dolní Věstonice, Czech Republic

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RATKIEWICZ M. A., BANASZEK A., LOBODZIŃSKA J. Isoenzyme variation in the common shrew (*Sorex araneus*) from the hybrid zone between the chromosomal

- races Družno and Łęgucki Młyn: Preliminary results: pp. 21–28  
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 ZAGORODNYUK, I., MISHTA, A. A geographical perspective on the karyotype evolution of *Sorex araneus*: p. 116
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- MALCHENKO S.N., KOROLEVA I.V., BRUSGAARD K., MATYAKHINA L.D., COLONIN M.G., PACK S.D., SEARLE J.B., BORODIN P.M., SEROV O.L., BENDIXEN C. Chromosome localization of the gene for growth hormone in the common shrew (*Sorex araneus*): pp. 243–245
- FREDGA K. A new chromosome race of *Sorex araneus* in the Kanin peninsula, NW Russia: pp. 247–248
- Acta Theriologica: Vol. 45, Suppl. 1, 2000: 1–190**  
Evolution in the *Sorex araneus* group: cytogenetic and molecular aspects  
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Edited by J.B. Searle, J.M. Wójcik
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- KOZLOVSKY A., ORLOV V., OKULOVA N., KOVALSKAYA J., SEARLE J.B. Chromosome studies on common shrews from northern and central parts of European Russia: pp. 27–31
- BULATOVA N., SEARLE J.B., BYSTRAKOVA N., NADJAFOVA R., SHCHIPANOV N., ORLOV V. The diversity of chromosome races in *Sorex araneus* from European Russia: pp. 33–46
- MISHTA A.V., SEARLE J.B., WÓJCIK J.M. Karyotypic variation of the common shrew *Sorex araneus* in Belarus, Estonia, Latvia, Lithuania and Ukraine: pp. 47–58
- FEDYK S., BANASZEK A., CHĘTNICKI W., CICHOMSKA A., SZALAŁAJ K.A. Reassessment of the range of the Drnholec race: studies on meiosis in *Sorex araneus* hybrids: pp. 59–67
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- BALLOUX F., LUGON-MOULIN N., HAUSSER J. Estimating gene flow across hybrid zones: how reliable are microsatellites?: pp. 93–101
- LUGON-MOULIN N., BALLOUX F., HAUSSER J. Genetic differentiation of common shrew *Sorex araneus* populations among different alpine valleys revealed by microsatellites: pp. 103–117
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- LARKIN D.M., SEROV O.L., BORODIN P.M., ZHDANOVA N.S., SEARLE J.B. Comparative genome mapping in mammals: the shrew map: pp. 131–141
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- WÓJCIK J.M., BOGDANOWICZ W., PUCEK Z., WÓJCIK A.M., ZALEWSKA H. Morphometric variation of the common shrew *Sorex araneus* in Poland, in relation to karyotype: pp. 161–172
- RYCHLIK L. Habitat preferences of four sympatric species of shrews: pp. 173–190
- Mammalia: Vol. 67, Part 2, 2003: 163–306**  
Evolution in the *Sorex araneus* group: cytogenetic and molecular aspects  
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## Abstracts of papers not published in proceedings

### First ISACC meeting, Oxford, 30–31 August 1987

#### Karyotype evolution — what we have learnt from shrews

B.O. Bengtsson & I. Frykman

*Department of Genetics, Sölvegatan 29, S-223 62 Lund, Sweden*

Karyotype differences are normally found between and not within species, and the role of chromosomal differentiation in speciation has been much discussed. The spread of a new chromosome mutation is also of great interest, since chromosome mutations are highly “non-additive” in their properties, i.e. with heterozygotes unlike an intermediary between the homozygotes. From the general discussion of chromosome mutations and evolution some questions have developed which we would like to pose for shrews:

- Are chromosomal heterozygotes always at a disadvantage?
- Is chromosome evolution explained by inbreeding?
- Do karyotype differences act as a barrier to gene flow?
- Will secondary selection strengthen a karyotypic hybrid zone?

To look for the answers to these questions information will be taken from our own work, from articles published by our colleagues and from data presented at the conference.

#### Patterns of chromosomal and biochemical differentiation of *Sorex* of the *araneus*-group in Switzerland

F. Bosshard

*Institut de Zoologie et d'Ecologie animale, Bâtiment de Biologie, Université de Lausanne CH-1015 Lausanne-Dorigny, Switzerland*

The distribution of the common shrew, *Sorex araneus*, in Switzerland is very fragmented because of the relief of the Alps and the presence of the sibling species, *Sorex coronatus*.

In Valais, we find a very interesting contact zone between different chromosomal races of *S. araneus*. Two races have already been described by Hausser *et al.* (1986). The Vaud race is characterised by the metacentrics *ih*, *lj*, *mg*, *rk* and *on* and is mainly situated to the north of the Alps. The Valais race is defined by the

metacentrics *ig*, *jh*, *nk* and *ol*. Its geographical distribution extends from southern Italy to Valais.

A population with all chromosome arms from *g* to *r* in acrocentric form (12 acrocentric pairs) has been discovered in France at Cordon, near Chamonix. Hausser considers this population as being the primitive race of *S. araneus*. It recolonised Switzerland after the last glaciation.

The presence of intermediate chromosomal forms between the acrocentric populations and the Vaud race can be explained by a previous geographical contact. The Vaud race, which at this time, did not possess all of the race-specific metacentric pairs, transmitted to the acrocentric populations its characteristic *lj*, *mg* and *rk* centric fusions. This contact was then disrupted by the arrival of *S. coronatus*. The Vaud race took refuge to the north of the Alps and differentiated chromosomally and biochemically from the intermediate populations.

On the other hand, the Valais race originating from Italy, crossed the Alps, its chromosomes invaded the acrocentric populations of the Valais and are now to be found as far as Chamonix in France.

There has probably never been any direct exchange between the Valais and the present Vaud race which are chromosomally well separated. Nevertheless, the biochemical results seem to support the hypothesis that gene flow was possible between the Valais race and the intermediate Vaud-acrocentric populations.

#### DNA studies on shrews

F. Catzefflis

*Inst. Sci. Evolution, L.A. 327 Univ. Montpellier II, Place Eugene Batallion, F-34080 Montpellier Cedex, France*

The unique-copy fraction of the nuclear DNA of *Sorex araneus* has been labelled and hybridised with the whole nuclear DNAs of: *S. araneus*, *S. coronatus*, *S. minutus*, *S. fumeus* and *S. cinereus* and all the experiments were repeated twice.

The percent nucleotide substitutions between these taxa were respectively  $0 \pm 0.5\%$  (n=10),  $0 \pm 0.5\%$  (n=10),  $4.0 \pm 0.8\%$  (n=9),  $13.3 \pm 0.5\%$  (n=12),  $13.8 \pm 0.5\%$  (n=5). It therefore appears that the nuclear genomes of *S. araneus* and *S. coronatus* are more than 99% identical, as far as DNA/DNA hybridisation can be informative in that way.

For comparison, there are from 1.0 to 4.5% nucleotide substitutions between chromosomal species of *Spalax ehrenbergi* (Catzefflis *et al.*, J. Mol. Evol., in



press) or less than 2.5% between the semi-species *Mus musculus* and *Mus domesticus*.

This, and other DNA data in the Soricidae, implies that speciation of the XY<sub>1</sub>Y<sub>2</sub> complex of species is a very recent phenomenon. Moreover, when compared to similar data in naturally hybridising pairs of mammals, the observed amounts of nuclear base replacements are fully compatible with hybridisation *in natura* between the different chromosomal races and species of the XY<sub>1</sub>Y<sub>2</sub> group, were it not for the fixed chromosomal differences.

### Hybrid origin of some local chromosome races of *Sorex araneus*

S. Fedyk

Laboratory of Genetics and Evolutionary Biology, University of Warsaw, Białystok Branch, Sosnowa 64, 15-887 Białystok

Two phylogenetic groups of European shrews (*S. araneus*) have come into contact with each other in Poland. In order to inspect the ranges of the Polish chromosome races, shrews have been caught systematically in NE Poland since 1984. Over 70 populations have been studied so far (Fig. 1).

There are five main types of autosome arm combinations in NE Poland. The western part of the area is occupied by populations belonging to the West European phylogenetic group (WEPG), the eastern part occupied by typical populations of the East European phylogenetic group (EEPG – nomenclature after Searle, 1984). In northern and central parts of the studied area local chromosome races occur (Fig. 2). Tab. 1 shows all autosome arm combinations found in NE Poland (compare Fig. 3).

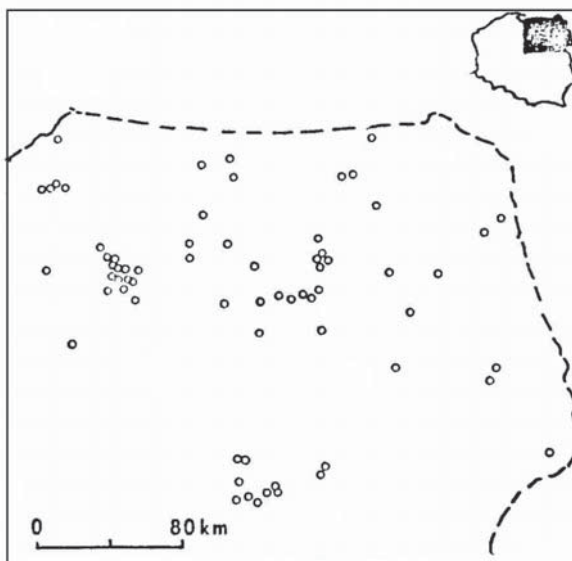


Figure 1.

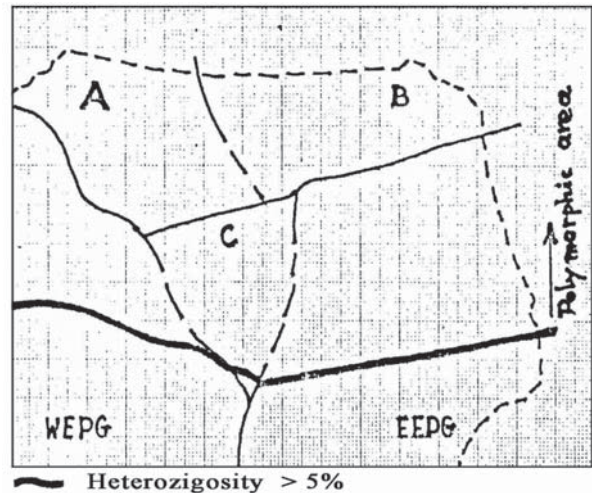


Figure 2.

Table 1. Chromosome arm composition.

WEPG	(1)	Northern part	<i>lj, ih, (ok)*</i>
	(2)	Central part	<i>lj, ih, ok, (mg)*, (np)*</i>
	(3)	Southern part	<i>lj, ih, ok, mg, np</i>
EEPG	(1)	North-west part	<i>lj, ki, rg</i>
	(2)	Central part	<i>lj, ki, rg, (nh)*, (mp)*</i>
	(3)	Southern part	<i>lj, ki, rg, nh, mp</i>
Local chromosome races	(A)		<i>lj, kh, oi, (rg)*, (mn)*</i>
	(B)	Northern part	<i>lj, kh, (rg)*, (mn)*</i>
		Southern part	<i>lj, kh, (rg)*</i>
(C)		<i>lj, (ki), (qh)*, rg, (mn)*</i>	

\*Explanation: (ok) – polymorphic pair “ok”

The whole studied area can be divided into two regions: (1) monomorphic – southern part, and (2) polymorphic – northern one. Hybrids (Fig. 4 and Tab. 2) were caught only in the zone of contact between the WEPG and the local race A. In other contact zones high frequencies of acrocentrics have been found (so-called “Buffer zones”) and hybrids occur rarely there.

What conclusion can be drawn from such a geographic distribution of the two phylogenetic groups and the local races in Poland?

(1) It can be supposed that homozygous shrews differing in four pairs of metacentrics came into contact in the south. Meiotic multivalents (Fig. 5) were formed, which was the cause of infertility of hybrids. Here, a very narrow hybrid zone was formed, existing up to the present day.

(2) In the north, on the other hand, shrews differing only in one or two metacentric pairs in a heterozygous state came into contact. Probably only slight disturbances in the meiosis of hybrids made it possible to



Figure 3.

form a large sympatric zone. In this zone, shrews with metacentrics *ih*, *ok* and *np* – of western, and with *ki* and *mp* – of eastern origin coexisted with each other. Three types of quadrivalents (Fig. 6) could be formed in the meiosis of hybrids. The close proximity of centromeres *m-n*, *k-h* and *o-i* made it possible to form fusions be-

tween these acrocentrics, which caused new (local) arm combinations to arise.

Table 3 presents the rule of formation (by hybridisation) of new fusions in the polymorphic region. Similar rules can be found also in Sweden and Southern Finland (see Tab. 3).



Figure 4.

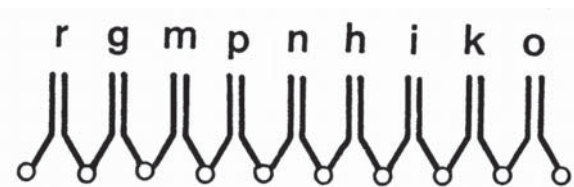


Figure 5.

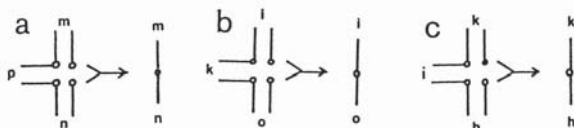


Figure 6.

Table 2. Hybrids (contact zone between WEPG and A).

- I Hybrids with integrated karyotypes
- (1)  $hi\ hi, ok\ ok$  (WEPG)  
 $rg\ rg, mn\ mn$  (A)
  - (2)  $hi\ hi, ok\ ok$  (WEPG)  
 $np\ np$  (WEPG)  
 $rg\ rg$  (A)
  - (3)  $np -$  (WEPG)  
 $kh\ kh, oi\ oi, rg -$  (A)
- II Hybrids with monobrachial homologies
- (1)  $hi\ hi, ok\ ok, rg -, mn/np$
  - (2)  $hi/kh, ok/oi, rg\ rg, mn\ mn$
  - (3)  $hi/kh, ok/oi, rg -, mn/np$
  - (4)  $hi/kh, ok/oi, rg/mg, --$

Table 3. North-eastern Poland (after Fedyk, 1987).

Races	I	II	III	IVa	IV	V	VI	VII
Autosome arm composition	$mg$	$mg$	$rg$	$rg$	-	$rg$	$rg$	$rg$
	$ok$	$ok$	$ok$	$oi$	$oi$	-	$ki$	$ki$
	$ih$	$ih$	$ih$	$kh$	$kh$	$kh$	$ki$	$ki$
	-	$np$	$mn$	$mn$	$mn$	$mn$	$mn$	$mp$
Origin of fusions	WEPG	Hybrid						EEPG

Sweden (after Fredga, 1982)

Races	Southern	Central	Northern
Arm composition	$ok$	$oq$	$kq$
Origin of fusions	WEPG	Hybrid	?

Southern Finland (after Halkka *et al.*, 1985)

Races	V	IV	III	II
Autosome arm composition	$ro$ $qm$ $ro$	$rm$ $qg$ $ok$	$mo$ - -	- $mg$ $rk$
Origin of fusions	?	Hybrid	?	

## The northern hybrid zone in Sweden

K. Fredga

*Inst. of Genetics, Uppsala University, Uppsala, Sweden*

At least six chromosome races of the common shrew, *Sorex araneus*, exist in Sweden and one in Denmark. Wide stretches of water separate the shrews of southern Sweden (S) from those of Denmark (Ox) and Öland (Ö). Thus there are four extensive zones of contact in Sweden.

Although only the northern (M<sup>N</sup>-N) zone has been studied in some detail, it seems fair to conclude that great differences exist between the zones with respect to frequency of single armed chromosomes. The S-S<sup>M</sup> zone of contact has not been localised. The S<sup>M</sup>-M zone is characterised by the presence of metacentric chromosomes and very little or no polymorphism.

The M-M<sup>N</sup> and M<sup>N</sup>-N zones are characterised by large numbers of telocentrics. Within this area (Fig. 1) 162 shrews from 15 localities have been studied so far. "True hybrids" (H) have been found at two localities, Bredbyn (n=27) and Kubbe (n=1). "Pseudo-hybrids" (psH) were found in four localities: Bredbyn, Ödsby, Långsele and Myckelgensjö, located 6, 8 and 15 km apart, respectively. "True hybrids" have arm combinations characteristic of both races, *hi* and *hn*. "Pseudo-hybrids" have *hi, h, i, n, p*.

The number of shrews of the various races and types was:

	N	M <sup>N</sup>	psH	H	Total
Bredbyn	15	3	2	7	27
Ödsby	0	9	5	0	14
Långsele	1	7	5	0	13
Myckelgensjö	1	10	3	0	14
	17	29	15	7	68

The number of telocentric chromosomes reaches its maximum in the hybrid zone. The frequency of telocentrics for each chromosome arm has been calculated.

The M<sup>N</sup>-M zone of contact deserves further study.

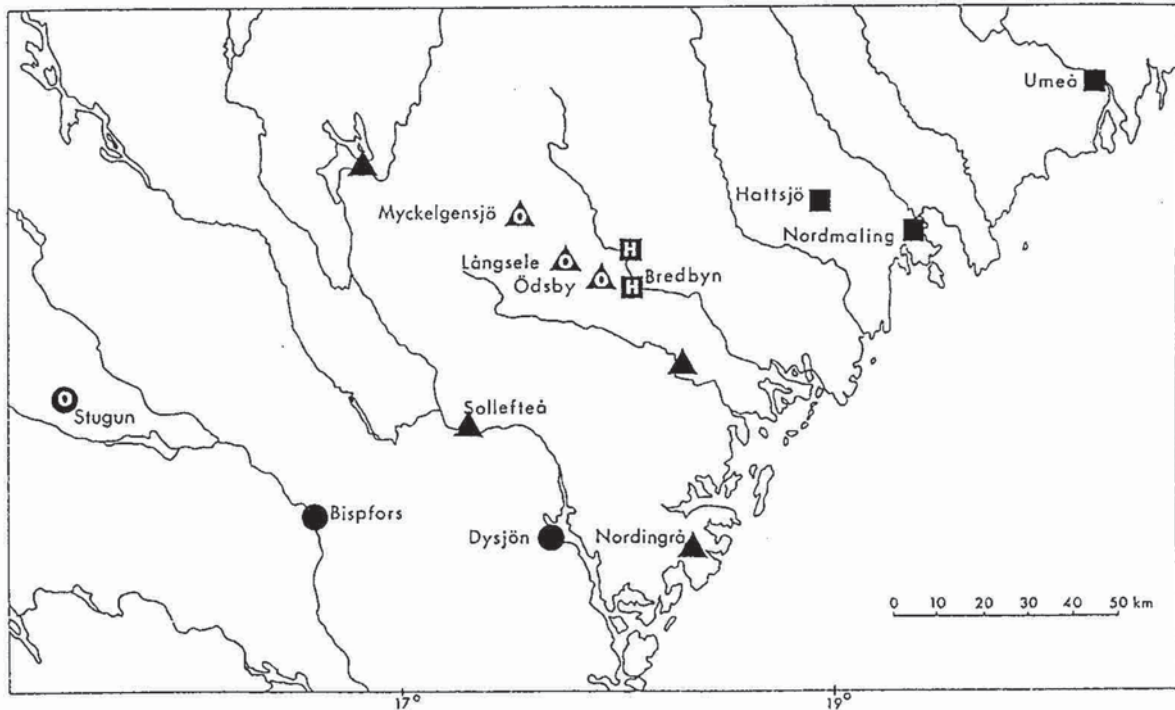


Figure 1.

### Distribution of chromosome races in Sweden and Denmark

K. Fredga

*Inst. of Genetics, Uppsala University, Uppsala, Sweden*

The karyotypes of more than 300 common shrews, *Sorex araneus*, were studied from over 60 localities in Sweden and the bordering parts of Norway. In addition, 18 specimens from one locality in Sjaelland and 15 specimens from one locality in Jutland in Denmark were analysed.

So far six chromosome races have been identified in Sweden and yet another race in Denmark, all characterised by their various combinations of telocentric chromosomes into metacentrics (Tab. 1). The distribution of the various races is shown in Fig 1. All but the northern race (N) belong to the West European phylogenetic group characterised by the arm combination *hi*.

Robertsonian polymorphism is common in the northern race and in a "hybrid" race ( $M^N$ ), located in a relatively narrow zone (about 50 km) between the northern and the central (M) races. Generally speaking the M race is characterised by few telocentrics and polymorphism occurs only in the pair *o/q*. The races  $S^M$  and S

(southern Sweden) are monomorphic, all autosomes being metacentric ( $2NA=18$ ). In the isle of Öland the arms *k*, *n*, *o*, *p*, *q* and *r* appear as telocentrics and only occasionally (19%) the arms *k* and *o* are fused ( $2NA=23-24$ ).

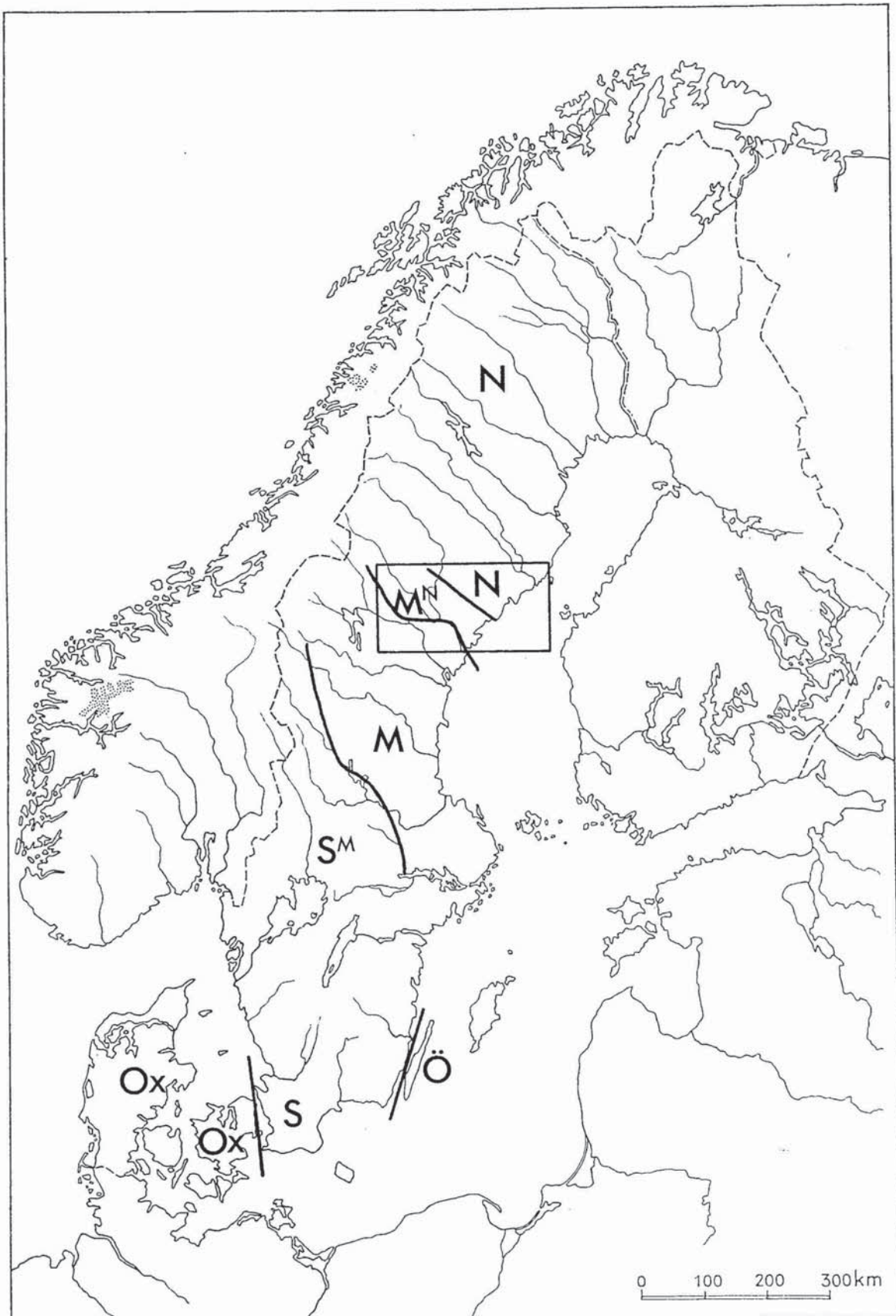
The Danish shrews belong to the Oxford race. The Sjaelland population is monomorphic,  $2NA=18$ . The Jutland population is also monomorphic but the arms *p* and *r* are not fused,  $2NA=20$ .

Table 1. Arm combinations of chromosomes 3-8 in *Sorex araneus* from Sweden and Denmark

Sweden	Abisko	N	hn	j/l	g/m	ip	k/q	o/r		
	Hattsjö	N	h/n	j/l	g/m	i/p	kq	o	r	
	Sidensjö	$M^N$	hi	jl	gm	k/q	n	r	o	p
	Stugun	M	hi	jl	gm	kp	nr	o/q		
	Hällefors	$S^M$	hi	jl	gm	ko	nr	pq		
	Åkarp	S	hi	jl	gm	ko	nq	pr		
	Öland	Ö	hi	jl	gm	k/o	n	p	q	r
Denmark	Sjaelland	Ox	hi	jl	gm	kq	no	pr		
	Jutland	Ox	hi	jl	gm	kq	no	p	r	

Figure 1.





## Sperm aneuploidy and its evaluation in some mammalian models of karyotypic variability

S. Garagna & C.A. Redi

*Dipartimento di Biologia Animale and Centro di Studio per l'Istochimica del CNR, Piazza Botta 10, 27100 Pavia, Italy*

The correct chromosome constitution is an essential prerequisite for the regular occurrence of spermatogenesis in mammals. The presence of structural heterozygosities such as whole arm translocations (Robertsonian translocations, Rb) can impair the gametogenic process to different extents:

1) segregational impairment, based on meiotic anaphase malsegregation and

2) breakdown of spermatogenesis that can vary from total arrest to a minimal disruption of the process.

In any case, germ cells can be lost at any stage of their development. Owing to the high frequency of Rb translocations, the house mouse represents a good model to study the influence of karyotype heterozygosity on the gametogenic process. Following the spermatogenesis of those karyotype constitutions known to be subfertile and sterile it was possible to determine the different levels at which heterozygosity acts. Looking at the cytological constitution of the seminiferous epithelium, three main steps seem to be particularly sensitive and can account for disruption of spermatogenesis:

1) a first step is at the premeiotic level, when the number of the proliferative Ao-A gonias is reduced;

2) a second step occurs at the meiotic level when most of the pachytene spermatocytes are unable to follow the normal cytodifferentiation pattern;

3) a third step is at the spermiogenesis level when spermatids undergo morphological and physiological changes. In subfertile animals, the spermatid reduction halves the population, but some spermatids can continue to differentiate until spermiation. In sterile animals, the few spermatids that arose degenerate soon after.

For the germ cells that are able to complete the spermatogenic process despite Rb heterozygosity, it is possible to determine the "ploidy" cytophotometrically, measuring the DNA content of the sperm making use of stoichiometric reactions for DNA like the Feulgen reaction. Sperm DNA content determinations have shown differences in the frequency of aneuploidy among different Rb heterozygous constitutions, and among different locations of the male germinal tracts: vas deferens aneuploid sperm are always fewer than those in the caput epididymis, probably partly related to the phagocytic activity of the epididymis.

Utilising cytophotometric methods it is also possible to follow the sperm cells along the passage through the female genital tracts; it was shown that no selection against unbalanced sperm took place during the female genital tract transit.

Analysis of the spermatogenic process was extended to other non-murine animals with karyotype variability such as *Akodon molinae*, *Sorex araneus* and *Spalax ehrenbergi*.

## Relationship between morphology, chromosomal status and geographic distribution of *Sorex* of the *araneus* group in Switzerland

J. Hausser

*Institut de Zoologie et d'Ecologie animale, Bâtiment de Biologie, Université de Lausanne CH-1015 Lausanne-Dorigny, Switzerland*

Western Switzerland and the French department of Haute Savoie is the contact area of four different forms of *Sorex* of the *araneus* group: *Sorex coronatus* and three main chromosomal forms of *Sorex araneus*, namely the "Valais" and the "Vaud" chromosomal races as well as a primitive form which retains all chromosome arms *g* to *r* as acrocentrics. Intermediates exist between "acrocentric" and "Vaud" forms as well as between "acrocentric" and "Valais" forms.

A morphological study was performed on the mandible of these forms. Thanks to substantial intergroup variance (38% of the total variance), a discriminant analysis allows perfect separation of these groups. The study of the Mahalanobis distances between groups reveals a pattern of relationships quite similar to the biochemical and chromosomal patterns.

Thus, in such a small area, morphological differences due to selection pressures by the habitat do not mask the genetic relationships between the studied taxa, as was the case in a similar study for four species of Southern Europe. But the shrews of Switzerland are of recent immigrant descent (Switzerland was entirely out of the species range during the last glaciation). Hence they could well be limited in their current geographical distribution by a set of adaptations selected in the habitat conditions of their native area.

The clear general morphological difference between the two main forms of *S. araneus* allowed an easy determination of chromosomally unknown individuals. Consequently, a general study of the potential distribution of the three main chromosomal forms in Switzerland was possible. It was computed by comparing the level of similarity of each square km of this country with the square kms where each form was actually observed; 39 ecological descriptors were used in this analysis.

The graphical output of this shows that a habitat differentiation exists at the species level (*araneus* versus *coronatus*), but is not obvious for the two main chromosomal forms of *S. araneus*, the distribution of which being due to historical factors above all. This suggests that *S. coronatus* was genetically isolated for a

long time in a mild, Atlantic environment, when the "Vaud" and "Valais" races either were submitted to a shorter isolation or were able to incorporate genes of the primitive acrocentric form during their progression.

In conclusion, both morphological distances and habitat differentiation confirm the results of chromosomal and biochemical studies.

### **The relationships between non-metric skeletal and karyotypic variation in *Sorex araneus***

**P. King**

*University College London, United Kingdom*

1627 shrews of the taxon *Sorex araneus sensu lato* were examined for 26 non-metric variants of the skull. These animals represent 51 localities. No significant differences were found between populations corresponding to variations of chromosomal race within the British Isles, and, in general, the differences between samples are small. However, the populations from most of the Inner Hebrides are extremely distinct from each other, and also from mainland Scottish populations; only Skye and Bute resembling the mainland closely. These differences are almost certainly unconnected with chromosomal variation, and can be attributed to founder effect with some degree of confidence. Populations of the sibling species *Sorex coronatus* from Jersey and France can be distinguished quite easily from British *Sorex araneus* on the basis of strong differences in frequency at two non-metric variants, and lesser differences at some others. Populations of *Sorex araneus* from North Norway, representing a distinct chromosomal race, are somewhat distinct from British shrews, though whether this is due to the chromosome race or to the extremely different environment and selective pressures under which they live must be a matter of doubt.

### **Vocalisation in Swedish karyotypic races of *Sorex araneus***

**M. Malmquist**

*Department of Zoology, Box 561, S-751 22 Uppsala, Sweden*

The karyotypic races of *S. araneus* have been studied with respect to variation in vocalisation. In confrontations between common shrews, typical sounds (confrontation screams) are emitted. Such sounds may also be generated by handling the shrews. Tape recordings of generated confrontation screams were made during the summers 1986 and 1987. Analyses of quantitative and qualitative features of these recordings have just started, and preliminary results, primarily from the Sidensjö race (for race definitions, see Fredga, K., abstract elsewhere in this communication) are presented.

The confrontation screams are characterised by pulses repeated at intervals of ca. 100 ms.

There are sound pressure peaks at frequencies which are more or less constant throughout the pulse (CF), but different degrees of frequency modulation (FM) occur.

Each pulse consists of a series of FM-peaks of short duration. It was found that the time interval between these peaks was shorter in the hybrid zone, compared with the Sidensjö and Stugun races, and in some cases, the pulse had a totally different structure. These shrews may be from the Hattsjö race (which dominates in this area) but unfortunately they died before their race status was determined. Moreover, a single hybrid (Sidensjö x Hattsjö) female emitted a certain sound which was different from any of the races studied.

I conclude that:

1. Larger samples from the hybrid zone and from the Hattsjö race (sampling is in progress) may tell whether the karyotypic races differ in terms of vocalisation.

2. If so, characters exist which are of potential use for avoiding hybridisation by means of positive assortative mating.

3. Vocalisation studies combined with field and laboratory experiments may be important in the study of evolutionary processes in the common shrew.

### **Niche and habitat of syntopic populations of two closely related species of the *Sorex araneus* group: *Sorex araneus* and *Sorex coronatus***

**C. Neet**

*Institut de Zoologie et d'Ecologie animale, Bâtiment de Biologie, Université de Lausanne CH-1015 Lausanne-Dorigny, Switzerland*

The European pattern of distribution and the morphological similarity of the two closely related species of the *Sorex araneus* group, *S. araneus* (Vaud race) and *S. coronatus*, suggest that interspecific competition is an important factor in the biogeographical process. In Switzerland, a dozen syntopic populations are known and two of them have been investigated in this study.

The trophic niches of the species were compared by measurements of niche overlap and several statistical tests on prey spectrum and prey size. Habitat was described by twelve variables on which a multivariate discriminant analysis was performed.

Preliminary results showed high niche overlap and no significant tendency for niche differentiation. On the other hand, there is evidence that microhabitat selection occurs. *S. araneus* appears to occupy damp microhabitats with a thick litter layer and loose soils. *S. coronatus* occupies relatively drier and denser soils.

Since the recorded population densities in the study sites were high, it is concluded that the two species



occupy the same niche, and that microhabitat selection is a consequence of interspecific competition. There is, thus, supportive evidence that a pattern of competitive exclusion between *S. araneus* and *S. coronatus* is occurring.

### A detailed survey of karyotypic variation in Britain

J. Searle

*School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

The three British races of common shrew (Oxford, Hermitage and Aberdeen) belong to the West European phylogenetic group of karyotypic races, which apparently was restricted to a refugium in south-eastern Europe during the last glaciation. The three British races were formed outside Britain. Their distributions suggest that they spread into Britain over the landbridge now occupied by the North Sea as waves of invasion, with each wave partially displacing the previous wave. Thus the first wave of invasion was the Aberdeen race (characterised by Robertsonian metacentrics *ko* and *np*) which now forms a 'Celtic fringe' to the west and north of Britain. The last wave of invasion was the Oxford race (characterised by *kq* and *no*) which now occurs over much of central and eastern Britain, while the Hermitage race (characterised by *ko* and *pr*) was the intermediate wave of invasion and has an intermediate present-day range.

Metacentrics *qr* (which occurs in part of the distribution of the Aberdeen race) and *pr* (which may be found in Oxford as well as Hermitage race individuals) may have arisen and spread once the races arrived in Britain.

The hybrid zones between these races follow geographic features to a certain degree. The factors maintaining these zones in their present locations will be discussed.

### Chromosome evolution of the European species of the *araneus-arcticus* complex (Insectivora, Soricidae) with special reference to the chromosomes of *Sorex granarius*

V.T. Volobouev

*UA 620 - C.N.R.S., Institut Curie, Section de Biologie, 26, rue d'Ulm, 75231 Paris Cédex 06, France*

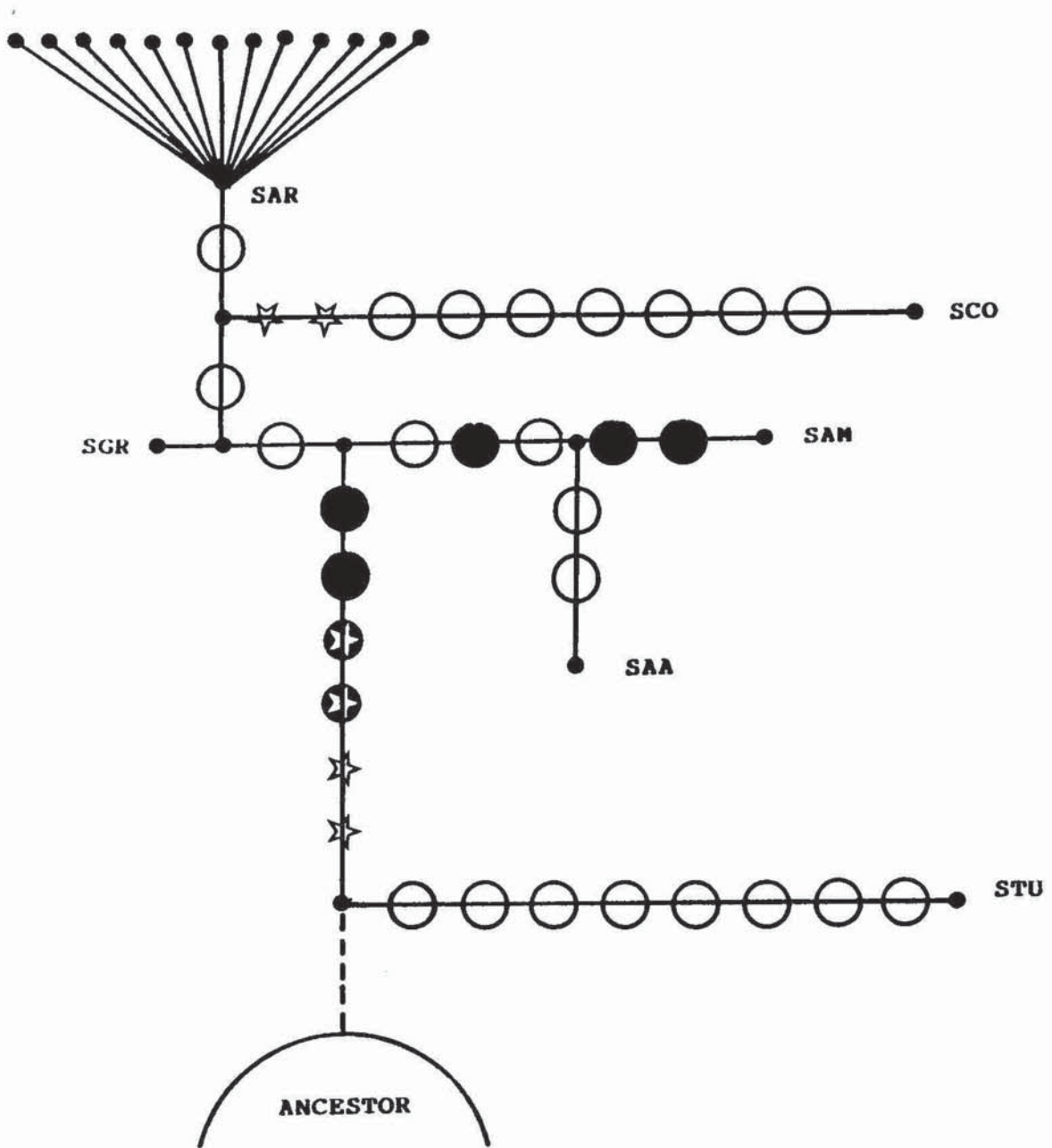
Comparative analyses of chromosome banding of five species of the *araneus-arcticus* complex, namely, *Sorex granarius*, *S. arcticus*, *S. coronatus*, *S. araneus* (present paper) and *S. tundrensis* (Volobouev, 1983) permitted analysis of chromosome evolution and to give a new insight into the phylogenetic relationships between the species of this complex (Fig. 1).

In accordance with this scheme, the karyotype of *S. tundrensis*, one of the most ancient species of the genus *Sorex* and the autochthon of North-East Asia, is the most close to that of the presumed ancestor of the *araneus-arcticus* complex (Volobouev, 1983). This common ancestor (C-ANC), characterised by a sex trivalent and  $2NA=44$  and  $NFa=52$ , appeared during the Pliocene. Not later than the end of the Pliocene this form gave rise to two lineages, one leading to *S. tundrensis*, which gave rise later to *S. asper* and presumably to *S. daphaenodon*, and another to the ancestral form (ANC-1) which gave rise to all the rest of the species of the complex. This ANC-1 with karyotype very close to that of modern *S. granarius*, spread over the Palearctic and into Beringia, where it passed into North America by one of the last Pliocene land bridges and spread over there, giving rise to *S. arcticus* at the beginning of the Pleistocene. As for the Palearctic branch of ANC-1 it split in two populations during the Mindel. One of these isolated populations gave rise to *S. granarius* and another to the ancestor (ANC-2) common to *S. coronatus*, *S. araneus* and presumably *S. caucasicus*. This last one was characterised by the first Robertsonian translocation, *a+f*. During the Riss glaciation and Moscow glaciation of the East European plane (Riss-II) in particular, only some isolated populations in South Europe survived. One of these isolates gave rise to *S. coronatus*, whereas another one acquired during this isolation a new Robertsonian translocation, *b+c*. Subsequently this last form spread over Europe and reached again West Siberia and gave rise to chromosome races of *S. araneus* during the last Pleistocene glaciation.

NB. Fig. 2 concerns suggestions for chromosome nomenclature of *S. araneus* discussed in the paper.

Figure 1. Scheme of chromosome evolution of the shrew species of *araneus-arcticus* complex (Insectivora, Soricidae). STU — *Sorex tundrensis*, SAA — *S. arcticus arcticus*, SAM — *S. arcticus maritimensis*, SGR — *S. granarius*, SCO — *S. coronatus*, SAR — *S. araneus* with its chromosome races.





- Robertsonian translocation
- Centromere-telomere translocation
- ⊛ Centromere-telomere translocation with subsequent centromere shift
- ☆ Centromere shift

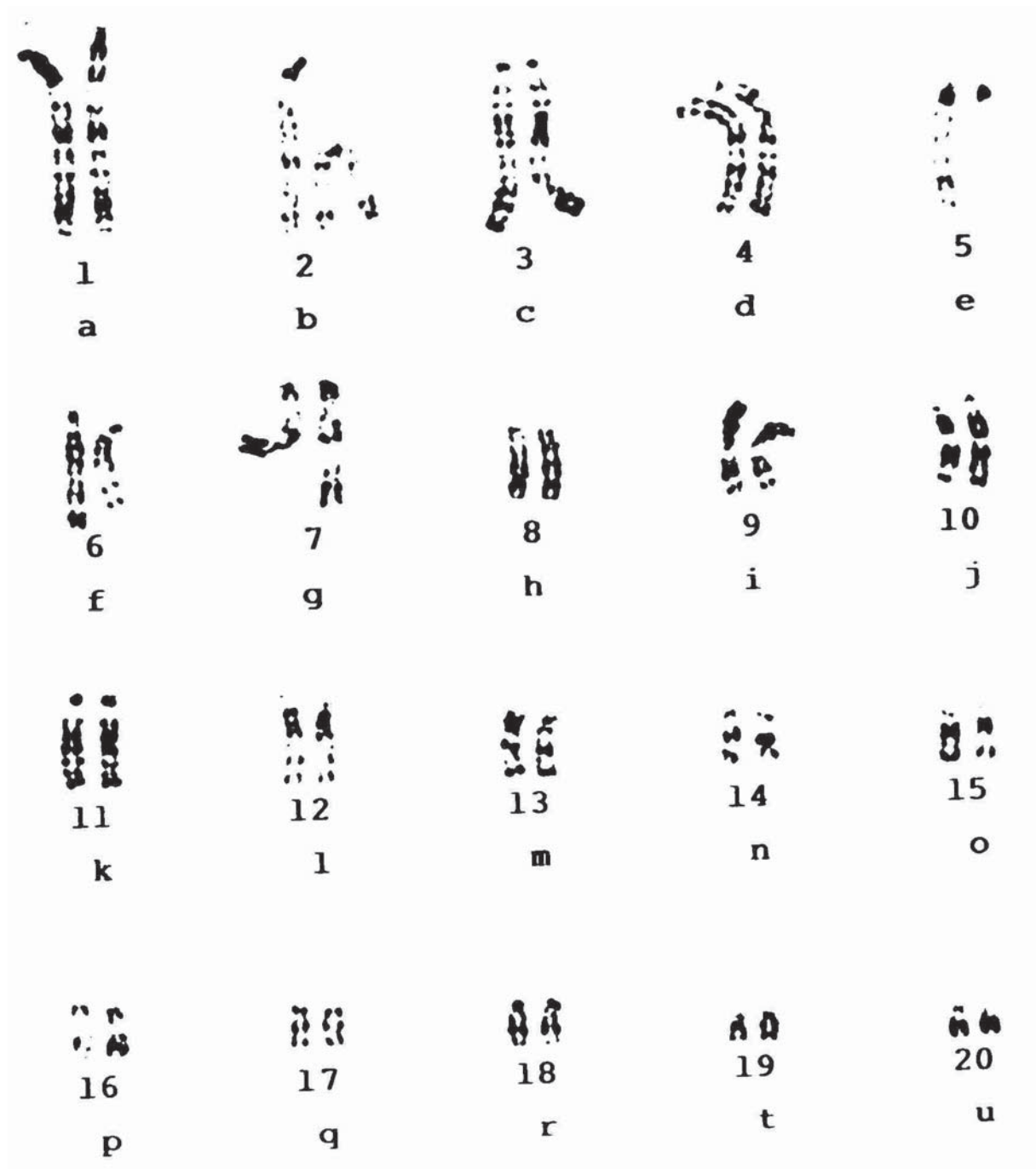


Figure 2. Chromosome arms of *Sorex araneus* from R-banded prometaphase obtained after synchronization by thymidine and 7-hours BrdU incorporation.

## Karyotypic races of common shrew from Poland

J. Wójcik

*Mammals Research Institute, 17-230 Białowieża, Poland*

The two karyotypic races of common shrew (*Sorex araneus*) from Poland are described. Western, northern, central, southern and south-eastern Poland are populated by the "Western race". This race is characterised by a maximum of eight pairs of metacentric autosomes. Four of these pairs are race-specific: *hi*, *gm*, *ko*, *np*; and *jl*, *gm*, *ko*, *np* display Robertsonian polymorphism. Within the Western race, populations differ with respect to autosome number. This is highest (2NA=25–26) in shrews from the extreme north of Poland (near Baltic Sea), and from south-eastern Poland (2NA=23–24). Shrews from central and western Poland are characterised by a lower autosome number (2NA=20–22).

The eastern part of Poland is populated by the "Eastern race" which has a maximum of eight pairs of metacentric autosomes; four pairs are race-specific: *ik*, *gr*, *hn*, *mp* and *jl*, *gr*, *hn*, *mp* display Robertsonian polymorphism. The autosome number varies between 20 and 22 in this race.

The secondary contact zone between the Western and Eastern races was mapped in eastern and south-eastern Poland. Inter-racial hybrids were found in one population from the south-east. It is suggested that the Western race colonised Poland from the south and west whereas the Eastern race came from the east.

## Nomenclature of karyotype races and forms of *Sorex araneus*

J. Zima<sup>1</sup> & J.M. Wójcik<sup>2</sup>

<sup>1</sup>*Institute of Systematical and Ecological Biology, Květná 8, CS 60365 Brno, Czechoslovakia;* <sup>2</sup>*Mammals Research Institute, 17-230 Białowieża, Poland*

At present about 2500 specimens of the common shrew have been examined karyologically and populations from more than 300 localities have been studied. The observed karyotype variation is determined by a Robertsonian system involving 12 acrocentric autosomal pairs (A) which can be combined by fusions to form different metacentrics. Theoretically, there may be:

$$(1) \binom{A}{2} = \binom{12}{2} = 66$$

metacentric morphs with a specific arm combination;

$$(2) \frac{A!}{2^{A/2} \cdot (A/2)!} = \frac{12!}{2^6 \cdot 6!} = 10\,395$$

different homozygous karyotypes containing only Robertsonian metacentrics;

$$(3) \sum_{m=0}^{A/2-1} \frac{A!}{(A-2m)! \cdot 2^m \cdot m!} = \sum_{m=0}^5 \frac{12!}{2! \cdot 2^5 \cdot 5!} = 88\,187$$

different homozygous karyotypes containing at least two acrocentric pairs.

The populations with unique arm combinations in Robertsonian metacentrics might be designated as races, and populations differing only in the diploid number as forms. Nomenclature and classification of these races and forms is extremely difficult, considering the possible extent of variation and the large number of theoretical combinations. Neither the traditional sub-specific nomenclature nor artificial systems based on alphabetic designation of races can be used properly. Various possibilities (phenetic, cladistic, evolutionary) of approaching this problem are discussed, with special reference to some paleontological data concerning phylogeny and Pleistocene glacial refugia of the species.

## Second ISACC meeting, Lausanne and Arzier, 12–16 September 1990

### The sex chromosomes during male meiosis in *Sorex araneus*

K. Fredga<sup>1</sup> & T. Ashley<sup>2</sup>

<sup>1</sup>Dept. of Genetics, Uppsala Univ., Box 7003, S-750 07 Uppsala, Sweden; <sup>2</sup>Dept. of Human Genetics, Yale Univ., School of Medicine, 333 Cedar St., New Haven, CT 06510, USA

*Sorex araneus* has XX/XY<sub>1</sub>Y<sub>2</sub> sex chromosomes. The X has arisen by a translocation between the original X and an autosome. One centromere is lost or inactivated. The homologue of the autosome is unchanged and is designated Y<sub>2</sub>. Y<sub>1</sub> is the original Y chromosome.

We have examined the meiotic behaviour of the sex chromosomes by light microscopy and by electron microscopy in microspread preparations of spermatocytes. Special attention was paid to the composition of the sex vesicle and to the association of the sex chromosomes during different stages of meiotic prophase. There is extensive synapsis between the X and Y<sub>1</sub> in zygotene and total synapsis in early pachytene. The synaptic behaviour of the sex chromosomes of the common shrew follows a pattern most similar to that of another insectivore, *Talpa occidentalis* (Jimenez *et al.*, 1990, Cytogenet. Cell Genet. 53: 97–103), rather than other species such as mouse and man. During the progression of pachytene the original X undergoes shortening and thickening, with development of progressively larger electron dense modules on the X axis. There is no evidence of desynapsis between X and Y<sub>1</sub> during late pachytene. The autosomal part of the X and Y<sub>2</sub> are completely synapsed by early pachytene in a way typical for autosomes in general, but are not included in the sex vesicle.

### Karyotypic variation in the common shrew (*Sorex araneus*) in Britain

S.J. Mercer & J.B. Searle

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

Since we last reported to this gathering in 1987, we have continued our extensive sampling programme to elucidate the pattern of karyotypic variation in the common shrew (*Sorex araneus*) in Britain. The general picture remains the same. There are three major karyotypic forms: the Aberdeen race (characterised by metacentrics *ko*, *np* and sometimes *qr*) found to the peripheral north, west and south of Britain, the Oxford race (metacentrics *kq*, *no* and sometimes *pr*) in central and eastern districts and the Hermitage race (metacentric *ko* and sometimes *pr*) that occurs between the Oxford and Aberdeen races in southern Britain. We have concentrated our recent studies on the following:

(a) the nature of the transition within the Oxford race between the area where metacentric *pr* occurs and the area where it is absent,

(b) the detailed course of the Oxford-Hermitage hybrid zone between the Thames estuary (to the east) and the Severn valley (to the west),

(c) the characteristics of the presumed zone of contact between the Oxford and Aberdeen races in Scotland.

Our detailed results will be presented and an appraisal made both of the factors which determine the gross pattern of distribution of karyotypic races in Britain and the precise location of individual chromosome clines.



## Fourth ISACC meeting, Norr Malma and Uppsala, 22–26/7 August 1996

### Historical biogeography of the pygmy shrew (*Sorex minutus*) revealed from mitochondrial sequences

D.T. Bilton

*Dept. of Biological Sciences, Univ. of Plymouth, Drake Circus, Plymouth PL48AA, UK*

Mitochondrial DNA sequences were used to reconstruct the phylogeography of Eurasian populations of the pygmy shrew, *Sorex minutus* L. 501 bp were sequenced from individuals obtained from throughout the Palaearctic range of the species, and the resulting phylogeny interpreted in the light of Pleistocene and Holocene events. Southern European populations in the Mediterranean peninsulae are in the main strongly differentiated from those further north, north European populations appearing in the same clades as those from northern Asia. This study suggests that the Mediterranean regions have been relatively unimportant as sources of Postglacial recolonists, and emphasises that in historical biogeographic terms Europe cannot be viewed in isolation.

### Chromosome geography of *Sorex araneus* from Ural to Baikal

P. Borodin

*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia*

Animals were collected during June–September 1994–6 in different sites of Siberia. Six field trips were carried out: from Ural to Baikal, from Novosibirsk to Hanty-Mansijsk, from Novosibirsk to Altai, from Krasnoyarsk to Nizhnyaya Tunguska.

The Novosibirsk race *go, jl/jl, ik, mp/m,p, qr/q,r* was found 1200 km to the west (hybrid zone with Serov race), 1100 km to the north and 400 km to the south of Novosibirsk. At 300 km to the east the hybrid zone with the Tomsk race was found. Our data demonstrate that the Novosibirsk population has maintained a stable polymorphism over a long period of time. Král & Radjabli (1974) found polymorphism for four chromosomes: *go, jl, mp* and *qr*. Twenty four years later we found the three of them (*jl, mp* and *qr*) remained polymorphic. In the localities of Serov, Chelyabinsk and Kedrovyy representatives of a new Serov race were found (*go, hn, ip, jl, km, qr*). This race differs from its easterly neighbour, the Novosibirsk race, by four arm combinations. The western, northern and southern borders of the Serov race have to be determined. The race certainly

differs from the Pechora race (*gi, hn, jl, kq, mo, pr*), described by Orlov *et al.* by six arm combinations and from the tentative South Ural race (Gabitova, 1991) (*gm, ho, in, jl, kp, qr*) by eight arm combinations. Samples taken from Eastern Siberia are under examination now.

### Karyotype and morphological differentiation of *Sorex araneus* in Ukraine

A. Mishta

*Institute of Zoology, Kiev 252601, Ukraine*

Chromosome studies of *Sorex araneus* in Ukraine allowed the distribution of four chromosome races to be localised. It was established that all *Sorex araneus* in Ukraine belong to the West European karyotypic group (WEKG): the Ulm race is distributed in Western Ukraine (Ukrainian Carpathians), the Moscow race in Eastern Ukraine, the Hermitage race in Central Ukraine (Kiev vicinity). Besides these known chromosome races, a new race of *Sorex araneus* was found in Central Ukraine (Kanev vicinity), with the following chromosome formula: *g/m, hi, jl, ko, nr, p/q*.

A multivariate analysis of cranial characters of *Sorex araneus* from 14 localities of Ukraine and some districts of Belorussia, Moldavia and Romania was used to establish the range of macromorphological variability. It was shown that geographical variability of cranial characters in *Sorex araneus* increase from north to south. Southern populations of *Sorex araneus* differ from northern ones by several characters. At the same time morphological differences between neighbouring populations in the northern part of the studied area are less obvious than in the southern one.

There was no correlation between the variability of chromosomal and cranial characters in the population studied. Morphological differentiation in *Sorex araneus* is perhaps determined by different ecogeographical conditions in the south. The greater differences between the southern populations is probably connected with a higher level of isolation due to the insular character of certain populations inhabiting wet biotopes of the steppe zone.

## Ethological differentiation in the speciation process of the *Sorex araneus* group

N.V. Moraleva<sup>1</sup>, B.I. Sheffel<sup>1</sup>, C.R. Neet<sup>2</sup>  
& J. Hausser<sup>3</sup>

<sup>1</sup>A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; <sup>2</sup>Wildlife and Nature Conservation Service, Canton Vaud, Switzerland; <sup>3</sup>Institute of Zoology and Animal Ecology, Biology Building, University of Lausanne, 1015 Lausanne-Dorigny, Switzerland

In this work the behavioural mechanisms able to support closely related forms of shrews in parapatric areas are discussed for *Sorex araneus* and *Sorex coronatus*, as well as for two chromosome forms of *Sorex araneus* – Vaud and Valais. Animals were taken from wild populations in contact zones and placed into a neutral arena of 80 cm<sup>2</sup> area. In over 300 experiments staged in November 1994 and November 1995 the level of activity and the character of contacts between individuals were recorded. In the experiments, non-adults, born in the year of observation, exclusively same-sex animals, were placed together.

It was discovered that the character of the behaviour both for the different species and the different chromosome forms essentially differs. The level of activity of the Vaud form of common shrew was less than in *Sorex coronatus* or in the Valais form. The amount of aggression when placing together conspecifics was at a maximum with *Sorex araneus* Vaud and at a minimum for *Sorex coronatus*. In addition, for *Sorex coronatus* conspecifics, we observed behavioural elements such as the subordination of one individual by another without a visible manifestation of aggression. In the experiments with *S. araneus* Vaud conspecifics this behavioural element was practically absent.

We made an attempt to evaluate the quantity of victories when placing non-conspecifics together. A victory was recorded if the animal initiating the contact succeeded to displace the rival and stay in its place. As a result we have noticed that in inter-species contacts *S. coronatus* won more frequently than *S. araneus*. The larger species, *S. araneus*, shows the same aggression both to conspecifics and to individuals of the other species. However, the more social *S. coronatus* is characterised by more frequent aggression to the other species than to conspecific forms. The same tendency was noticed in experiments both for *S. araneus* Vaud and *S. araneus* Valais.

## Analysis of allozyme variation and cytochrome *b* sequence (mtDNA) among chromosome races of *Sorex araneus* from Northern and Eastern Poland

M. Ratkiewicz<sup>1</sup> & P. Taberlet<sup>2</sup>

<sup>1</sup>Institute of Biology, Warsaw University in Białystok, ul. Świerkowa 20 B, PL 15-950 Białystok, Poland; <sup>2</sup>Laboratoire de Biologie des populations d'altitude, CNRS EP55, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France

Analysis of 30 protein loci in shrews from 6 chromosome races revealed low genic differentiation between WEKG and EEKG races. None of the alleles was diagnostic for a race and no clines of allele frequencies were found between the races. Differences in allele frequencies among the races were not considerably greater than within a race.

Analysis of a cytochrome *b* fragment 1002 bp long in 12 shrews from 6 chromosome races showed only a few nucleotide substitutions. Those slight differences found in *cyt b* sequence between individuals were not associated with their chromosomal characteristics. There were no differences between the races in amino-acid sequence after translation of the fragment studied, either.

The overall consistency of electrophoretic and mtDNA data which show no clear differences between shrew races belonging to WEKG and EEKG in Poland may indicate that these two groups are genetically very similar and the remarkable chromosomal difference between them is rather a recent phenomenon.

## Nomenclature of electrophoretically studied loci and allozymes in the common shrew (*Sorex araneus* L.)

M. Ratkiewicz<sup>1</sup>, J.M. Wójcik<sup>2</sup>, L. Lukáčová<sup>3</sup>  
& M. Macholán<sup>3</sup>

<sup>1</sup>Institute of Biology, Warsaw University in Białystok, ul. Świerkowa 20 B, PL 15-950 Białystok, Poland; <sup>2</sup>Mammal Research Institute, Polish Academy of Sciences, ul. Waszkiewiczza 1, PL 17-320 Białowieża, Poland; <sup>3</sup>Laboratory of Genetics and Experimental Embryology, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Veveří 97, CZ-602 00 Brno 2, Czech Republic

A nomenclature of loci and allozymes is proposed to standardise electrophoretic analyses of the common shrew in the future. This nomenclature is based on published papers which describe loci and allozymes most extensively. For unstudied or not well studied loci a new nomenclature is proposed. For common shrew samples migration of allozyme bands on gels is shown together with CBA or C57/BL mouse inbred strains to

make studies in all laboratories comparable. Allozyme patterns on starch and cellulose acetate gels are compared. Although there is a good agreement in zymograms on these gels, cellulose acetate is highly recommended for future studies, as it gives much better resolution of bands than starch gels.

### Chromosome variation in the house musk shrew, *Suncus murinus*

M. Rogatcheva

*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia*

A high-resolution G-banding technique was used for identification of the chromosomes of the house musk shrew and for characterising their individual G-banding pattern. In order to outline the main identifying characteristics of the individual chromosomes and make comparable the previously published karyotypes of races and individuals we include in our analysis a detailed study of G-banded chromosomes with different degrees of resolution at metaphase, prometaphase and prophase. On the basis of this study we have constructed an ideogram of prometaphase chromosomes and proposed a standard karyotype of *Suncus murinus*. A high-resolution G-banding technique was also used to identify chromosomes involved in five Robertsonian translocations characteristic of the chromosome race of *Suncus murinus* in Sri Lanka. Two of the translocations proved to be similar to those found in the Malaysian population of the house shrew. This finding provided strong support to the suggested hybrid origin of chromosome polymorphism in Malaysian shrews.

### Ecological differentiation in the speciation process of the *Sorex araneus* group

N.V. Moraleva<sup>1</sup>, B.I. Sheftel<sup>1</sup>,  
C.R. Neet<sup>2</sup> & J. Hausser<sup>3</sup>

<sup>1</sup>A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; <sup>2</sup>Wildlife and Nature Conservation Service, Canton Vaud, Switzerland; <sup>3</sup>Institute of Zoology and Animal Ecology, Biology Building, University of Lausanne, 1015 Lausanne-Dorigny, Switzerland

This study analyses the habitat distributions for parapatric species and chromosome forms of the *Sorex araneus* group in grids of 1 ha area located in contact zones. The contact zone under investigation between *S. araneus* and *S. coronatus* was situated on the southwest shore of Neuchatel Lake; the study of the contact zone between the Vaud and Valais chromosome forms of common shrew was carried out in the Haslital valley (Bern canton, Switzerland). Animals were marked in

November 1994 and November 1995. In addition to the species under study, all other small mammals and vegetation in the grids were recorded. Attention should be drawn to the fact that the centres of the contact zones were located in habitats that appeared in this region comparatively recently. On the shore of the Neuchatel Lake the hyperhumid habitat is associated with manipulation of water level at the beginning of the 20<sup>th</sup> century. The grid in Haslital was located in secondary alder-willow forest that appeared in place of beech-spruce forest destroyed by an avalanche twenty years ago.

The distribution of *S. araneus* and *S. coronatus* in both investigation years was identical. *S. araneus* confined itself to most humid areas, while *S. coronatus* preferred more drained habitats in the presence of oak. It should be noted that exactly the same distribution of species was detected by K. Need (1989), who studied the same area 10 years ago. Areas of habitats of the different species practically did not overlap. In the Haslital valley in 1995 the distribution of the habitat areas for the chromosome forms of Vaud and Valais was mostly identical to the distribution of *S. araneus* and *S. coronatus*. The Valais form preferred the most abundant habitats, while Vaud sticks to poorer quality habitat. The areas of distribution of the different forms did not overlap. But in 1994 the habitats of both chromosome forms were practically evenly distributed in the whole studied area. The reliable preference of certain habitats for the different forms was not revealed. The reason for the differentiation in distribution of these forms in different years is not clear yet, but it cannot be excluded that this is connected with changes in the structure of the small mammal community.

### Chromosome phylogeny of the *S. araneus* group revised after an *in situ* hybridisation study with a telomeric probe

V.T. Volobouev

*C.N.R.S. UMR 147 Institut Curie, Section de Biologie, 26 rue d'Ulm, 75231 Paris, France and Museum National d'Histoire Naturelle, Mammifères et Oiseaux, 55 rue de Buffon, 75005 Paris Cedex 05, France*

The previous attempts to reconstruct a chromosome phylogeny of the *S. araneus* species group were based on a hypothesis that the acrocentric state is primitive and that evolution goes towards formation of biarmed chromosomes mostly by means of Rb translocations. The observation that chromosome races in *S. araneus* are characterised by numerous non-homologous Rb fusions resulting in establishment of monobrachial homology has supported this hypothesis. The same tendency of karyotype evolution at the interspecific level is also consistent (Meylan & Hausser, 1973; Volobouev, 1989). In particular, all the schemes of chromosome



evolution are in agreement considering the karyotype of *S. granarius* as ancestral in relation to *S. araneus* and *S. coronatus* (Wójcik & Searle, 1988). However biochemical (Catzeflis *et al.*, 1982) and molecular (Taberlet *et al.*, 1994) data established that there is more genetic similarity between *S. granarius* and some chromosome races of *S. araneus* than between certain races of the latter. Together these two sets of data definitively cast doubts on the phylogenetic position of *S. granarius* established on the basis of chromosomal data.

To reconcile these approaches it is necessary to propose the occurrence of the fission of two Rb metacentrics (*af* and *bc*) in the lineage leading to *S. granarius* and one (*bc*) in that leading to *S. coronatus*. Consideration of the arguments for and against this possibility resulted in rejection of the hypothesis of double fission as «neither the most likely, nor the most parsimonious» (Taberlet *et al.*, 1994).

*In situ* hybridisation experiments with telomeric probes on the chromosomes of *S. granarius*, *S. coronatus* and three races of *S. araneus* have revealed a high level of amplification of the TTAGGG motif in pericentric regions of the two former species compared with the three chromosome races of *S. araneus*. Otherwise, the molecular composition of pericentric regions is different in these three species. I will consider how these data are consistent with the fission hypothesis.

### **Telomeric sequences before and after Robertsonian fusion: studies on *Sorex araneus* and two related species, *S. granarius* and *S. coronatus* (Insectivora, Soricidae)**

**V.T. Volobouev,<sup>1,3</sup> V. Vicherat,<sup>1</sup>  
J.B. Searle<sup>2</sup> & B. Dutrillaux<sup>1</sup>**

<sup>1</sup>C.N.R.S. UMR 147 Institut Curie, Section de Biologie, 26 rue d'Ulm, 75231 Paris Cedex 05, France; <sup>2</sup>Department of Biology, University of York, PO Box 373, York YO1 5YW, United Kingdom; <sup>3</sup>Museum National d'Histoire Naturelle, Mammifères et Oiseaux, 55 rue de Buffon, 75005 Paris Cedex 05, France

Data are presented on fluorescent *in situ* hybridisation (FISH) with the telomeric consensus sequences (TTAGGG)<sub>n</sub> onto metaphase chromosomes of *S. granarius*, *S. coronatus* and three chromosome races of *Sorex araneus*. These species and races, although morphologically very similar, have very different karyotypes, both with respect to numbers of metacentric and acrocentric chromosomes, and also the precise characteristics of the metacentrics. In all specimens of *S. araneus* studied hybridisation signals of moderate intensity (comparable with those usually detected on the human chromosomes) were detected on chromosome ends of both acrocentric and metacentric chromosomes but never at the primary constriction of the metacen-

trics. As each metacentric chromosome derives from two acrocentrics by the Robertsonian fusion process, it may be presumed that the large majority (all?) of the telomeric sequence proximal to the centromere is always lost from the acrocentrics on fusion. The difference between metacentrics and homologous acrocentrics is particularly clear in specimens heterozygous for Robertsonian fusions.

Under the same experimental conditions as those used for *S. araneus*, distal hybridisation signals in *S. granarius* and *S. coronatus* chromosomes were observed with difficulty, probably due to a reduced level of amplification of the TTAGGG motif. Often the telomeric sequences were only detected on one of the sister chromatids. In contrast, the centromeric regions of all acrocentrics in *S. granarius* and most of the metacentrics in *S. coronatus* showed hybridisation signals substantially amplified relative to *S. araneus*.

These findings raise questions about the universality of telomeric sequence loss during the Robertsonian fusion process and also shed some light on the possible role of telomeric sequences in the promotion or inhibition of centromeric fusions. Some possible implications of the data presented to our understanding of the general pathway of chromosome evolution in the *S. araneus* group are considered.

### **Review of shrews from the Crimea and southern border of the *Sorex araneus* range**

**I. Zagorodniuk**

*Institute of Zoology of NAS of Ukraine, Kiev, Ukraine*

The mammalian fauna of the Crimean peninsula is relatively poor and includes only a third of the total number of species of the Ukrainian fauna. Its main character is the absence of most woodland, wood-steppe and hydrobiontic species. From the geobotanical point of view, the mountain part of the Crimea is a wooden "island", which is mainly related to the northeastern Caucasus. The plain part of the peninsula seems to relate to the steppe zone of the Azov region.

Five shrew species are traditionally included in the Crimean fauna: one species of *Neomys* (*anomalous*), two of *Crocidura* (*suaveolens* and *leucodon*), and two of *Sorex* (*minutus* and *araneus*). An analysis of their taxonomic history, ranges and morphological variation suggest that the taxonomic status, as well as the systematic position of most taxa, remains uncertain. Museum collections of shrews from the Crimea were labelled as follows:

*C. suaveolens* (132), *S. minutus* (34), *C. leucodon* (15), *N. anomalous* (10) and *S. araneus* (1).

Re-investigation of the collections shows that traditional taxonomic views require essential amendments and comments.



Both *Crocidura* species are very abundant in the peninsula, particularly in the steppe part, and *suaveolens* is the shrew species which is easiest to trap. Crimean *Neomys* have often been designated as *N. fodiens*, but the latter is really absent, not only in the Crimea, but in the adjacent regions as well; the small *Neomys* from the Crimea is related to the pair *anomalous-schelkovnikovi*. Two *Sorex* species are known from the Crimea, but only *S. minutus* is actually present in zoological collections. Moreover, this small Crimean shrew is more similar to the Caucasian *S. volnuchini*, than to European *S. minutus*. The only specimen of “*araneus*” known from the Crimea was identified as *Neomys anomalous*. Another specimen signed as “*araneus*”, has a faulty confused label of *S. minutus* (from the town of Yalta). Thus, among these five species, only *Crocidura* has a clear status, and the others need further taxonomic revision. *Sorex araneus* is absent in the Crimea and the nearest findings to the peninsula are from the Lower Dnieper region.

Most reviewers specify a continuous distribution of the common shrew in Eastern Europe, The actual range of this species covers only wood and wood-steppe zones. In the south of Ukraine and in the northern Caucasus, that is in the steppe zone, *S. araneus* is absent. This fact is important for mapping and searching for geographically isolated populations and new chromosome races.

The southern border of the range of *S. araneus* passes through the Odessa (central), the Nikolaev, the Kherson (northern), the Dnepropetrovsk and the Kharkiv (southern) regions of Ukraine. The only isolated population known, is in the Kherson region in the Dnieper delta.

## Cladogenesis in the *Sorex araneus* group and its biogeographic interpretation

I. Zagorodniuk<sup>1</sup> & M. Khazan<sup>2</sup>

<sup>1</sup>*Institute of Zoology of NAS of Ukraine, Kiev, Ukraine;*

<sup>2</sup>*International Solomon University, Kiev, Ukraine*

The phylogenetic relationship of the nine shrew species that until recently were regarded as subspecies of *S. araneus* were examined. The data on their karyology were summarised using a first description of the *S. satunini* G-banded chromosomes. The cladistic analysis suggests a “comb”-shaped cladogram with the following taxonomic relations: *S. tundrensis* + *S. asper*? [*S. arcticus* [*S. granarius* [*S. daphaenodon* + *S. coronatus* [*S. satunini* + *S. “valaicus”* [*S. araneus* s. l. ]]]]]. The fusion *de* appears to be an apomorphy of the entire group. The steps of the main stem of the cladogram corresponding to the next apomorphic row are *de* -> [*ut* -> [*fa* -> [*cb* -> [*jl*]]]]. Fusions *bc*, *af*, *hg*, *ik*, *jn*, *lo* and *tu* and small elements that probably correspond to the arms *m*, *p*, *q* and *r* of *S. araneus* were identified in the *S. satunini* karyotype. Thus, the latter shows the most karyological similarity to *S. araneus* of all species of the group.

The evolutionary order of appearance of the taxa, as well as peculiarities of the geographic distribution of species and races, correspond to the main events of Pleistocene history of the group. The most ancient species and races are localised in the periphery of postglacial regions, while more advanced forms (the youngest races of *S. araneus*) occupy just the postglacial zone. The stepwise character of the main stem in the cladogram and the sequential manner of separation of taxa, shows the continuous nature of the cladogenesis within the group studied.

## Fifth ISACC meeting, Białowieża, 17–21 August 1999

### Chromosomal evolution of the genus *Crocidura* and *Suncus*

L.S. Biltueva<sup>1</sup>, M.B. Rogatcheva<sup>1</sup>,  
P.L. Perelman<sup>1</sup>, P.M. Borodin<sup>2</sup>, S. Oda<sup>3</sup>,  
K. Koyasu<sup>4</sup>, M. Harada<sup>5</sup>, J. Zima<sup>6,7</sup>  
& A.S. Graphodatsky<sup>1</sup>

<sup>1</sup>*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia;* <sup>2</sup>*Institute of Biology, Federal University of Rio de Janeiro, Brazil;* <sup>3</sup>*Laboratory of Animal Management, School of Agricultural Sciences, Nagoya University, Japan;* <sup>4</sup>*The Second Department of Anatomy, School of Dentistry, Aichi-Gakuin University, Nagoya, Japan;* <sup>5</sup>*Laboratory Animal Center, Osaka University Medical School, Japan;* <sup>6</sup>*Institute of Vertebrate Zoology, Academy of Sciences of the Czech Republic, Brno, Czech Republic;* <sup>7</sup>*Department of Zoology, Faculty of Science, Charles University, Praha, Czech Republic*

A high-resolution chromosome analysis of eight Palaearctic and Oriental species of white-toothed shrews revealed almost complete chromosomal homology between the karyotypes studied. Extensive chromosomal homology was demonstrated even between species of the genera *Crocidura* and *Suncus*. Robertsonian translocations, tandem fusions, fissions, reciprocal whole-arm translocations, centromeric shifts, heterochromatin additions, and a hypothetical ancestral karyotype with 44 chromosomes are proposed.

### Optimal sample size in chromosomal analysis of the common shrew populations

J. Boltruszko, S. Fedyk, M. Konarzewski,  
A. Banaszek, K. Szalaj & W. Chętnicki

*Institute of Biology, University of Białystok, Białystok, Poland*

We used 384 common shrews from eight populations situated in two hybrid zones: between Drnholec and Łęgucki Młyn and between Guzowy Młyn and Łęgucki Młyn karyotypic races. The races in both hybrid zones were characterised by five variable chromosome pairs. Thus, the karyotype of each individual can be assigned to one of five chromosomal variants. In effect about 20 chromosomal variants were distinguished in each population. For each population we created a table of karyotypes and chromosomal variants based on a 0/1 notation. Each column of the table corresponded to one chromosomal variant. The absence/presence of chromosomal variant in the shrew's karyotype was coded as 0/1. Each chromosomal variant was subjected to a computer simulation of random trapping of shrews.

The simulated chromosome frequencies were compared by Fisher's Exact Test. Only the chromosomal variants showing statistically significant deviations of chromosome frequencies were used for estimations of the optimal sample size. We conclude that optimal sample sizes range from 6 to 22 individuals and in most cases the collection of 15 shrews is sufficient.

### Studies on the molecular and cytogenetic variation in *Sorex araneus* over the former Soviet Union – A summary of the 1995–1998 INTAS project

S. Haynes<sup>1</sup>, N.S. Bulatova<sup>2</sup>, A.V. Mishta<sup>3</sup>,  
A.V. Polyakov<sup>4</sup>, A. Banaszek<sup>5</sup>, A.I. Kozlovsky<sup>2</sup>,  
P.M. Mirol<sup>1,8</sup>, R.S. Nadjafova<sup>2</sup>,  
E. Piontkovskaya<sup>3</sup>, J.M. Wójcik<sup>6</sup>, J. Zima<sup>7</sup>,  
P.M. Borodin<sup>4</sup>, V.N. Orlov<sup>2</sup> & J.B. Searle<sup>1</sup>

<sup>1</sup>*Department of Biology, University of York, York, UK;* <sup>2</sup>*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia;* <sup>3</sup>*Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine;* <sup>4</sup>*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia;* <sup>5</sup>*Institute of Biology, Warsaw University Białystok Branch, Białystok, Poland;* <sup>6</sup>*Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland;* <sup>7</sup>*Institute of Vertebrate Zoology, Academy of Sciences of the Czech Republic, Brno, Czech Republic and Department of Zoology, Faculty of Science, Charles University, Praha, Czech Republic;* <sup>8</sup>*Present address: CIGIBA, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, La Plata, Argentina*

From 1995–1998 we conducted an INTAS-funded project to study the molecular and chromosomal variation in the common shrew (*Sorex araneus*) over the Former Soviet Union (FSU). The fieldwork and chromosomal analysis was divided up among teams based in Novosibirsk (Siberia), Moscow (European Russia) and Kiev (Ukraine, Bialorussia and the Baltic States). The molecular work was carried out by the York team. At the outset of the project seven karyotypic races were known from the territory of the FSU; by its conclusion 25 such races had been described! From the phylogeny and distribution of the races, it is clear that race formation does not merely involve fixation of Robertsonian fusions. Whole-arm reciprocal translocations (WARTs) also appear to be important in the generation of new metacentric combinations and, once races have formed and expanded their ranges, they may hybridise with other races and generate new hybrid forms ('zonal racement'). There is remarkably little variation in cytochrome *b* sequence over the FSU suggesting recent

colonisation of the area from a single source area - but there is doubt as to how 'recent'. The chromosomal studies indicate substructure over the FSU, suggesting that the area was colonised from at least 3 (late?) Weichselian refugia: Altai Mts, Ural Mts and the Carpathian or Balkan Mts.

### **Do riverine barriers, history or introgression shape the genetic structuring of a common shrew (*Sorex araneus*) population?**

**N. Lugon-Moulin, H. Br nner, F. Balloux,  
J. Hausser & J. Goudet**

*Institut d'Ecologie, Laboratoire de Zoologie et Ecologie Animale, B timent de Biologie, Universit  de Lausanne, Lausanne-Dorigny, Switzerland*

The common shrew (*Sorex araneus*) is subdivided into numerous chromosome races. The Valais and Cordon chromosome races meet and hybridise at a mountain river in Les Houches (French Alps). Significant genetic structuring was recently reported among populations found on the Valais side of this hybrid zone. In this paper, a phylogenetic analysis and partial Mantel tests are used to investigate the patterns and causes of this structuring. A total of 185 shrews were trapped at 12 localities. All individuals were typed for nine microsatellite loci. Although several mountain rivers are found in the study area, riverine barriers do not have a significant influence on gene flow. Partial Mantel tests show that our result is caused by the influence of the hybrid zone with the Cordon race. The geographical patterns of this structuring are discussed in the context of the contact zone, which appears to extend up to a group of two rivers. The glacier they originate from is known to have cut the Arve valley as recently as 1818. The recent history of this glacier, its moraine and possibly rivers, may therefore be linked to the history of this hybrid zone.

### **A hybrid zone between the Gołdap and Popielno chromosome races of the common shrew (*Sorex araneus* L.) in Poland**

**M. Moska**

*Institute of Zoology, University of Wroclaw, Wroclaw, Poland*

The common shrew (*Sorex araneus* L., 1758) has one of the most variable karyotypes of any mammalian species. The variation of chromosomes occurs both within and between populations (polymorphism and polytypy) as the result of Robertsonian rearrangements, usually the Robertsonian centric fusion. Populations

(geographically contiguous or recently separated) that share the same set of metacentrics and acrocentrics by descent are considered to be a chromosome race. Fifty-two different karyotypic races of common shrew have been described, most of them from Europe. Karyotypic races that come into contact give rise to hybrid zones. Up to now several hybrid zones of the common shrew have been studied.

In the present paper I describe the location and preliminary results of my study of the contact zone between the Gołdap and the Popielno races. The Gołdap race (*gr, hk, jl, mn, o, p, q*) was first described by Fedyk (1986) and the Popielno race (*gr, hq, ik, jl, mn, o, p*) by Wójcik (1986). Both of them are from north-eastern Poland and belong to the East European karyotypic group. The Gołdap/Popielno contact zone is located in the area of Mazury near Krutynia river (near Ruciane-Nida town).

Up to now the shrews were collected from seven populations: Prawdowo, Lipowo, Lisunie/Kulinowo, Nowy Most, Zielony Lasek, Zakr t and Karwica. A total of 60 shrews were karyotyped. The shrews from Prawdowo, Lipowo, Lisunie/Kulinowo, Nowy Most all belong to the Gołdap race and shrews from Karwica belong to the Popielno race. The populations from Zakr t and Zielony Lasek belong to the hybrid zone Gołdap/Popielno. Among 18 individuals from Zakr t there were 12 shrews with the race Popielno karyotype, one shrew with the race Gołdap karyotype and five hybrids (complex heterozygotes). All of these hybrids formed at meiosis chain configurations that consist of four elements CHIV *i/ik/kh/h* (in two individuals), CHIV *k/ki/io/o* (in one individual) or five elements CHV *i/ik/kh/hq/q* (in two individuals). Because of the predominance of individuals with the Popielno race karyotype, the population from Zakr t probably marks the southern limit of the zone. Among seven individuals from Zielony Lasek there were four shrews with the Gołdap race karyotype, one shrew with the Popielno race karyotype, and two hybrids which formed a meiosis chain configuration that consists of five elements CHV *i/ik/kh/hq/q*. In the studied area, the Gołdap race is polymorphic in arm combinations *hk, jl, io, mn*, the Popielno race is polymorphic in arm combinations *jl, mn* and the hybrid populations in *ik, kh, jl, gr, hq, io, mn*.

### **Body size and Bergmann's rule in shrews: Geographical variation of body size in Palearctic *Sorex* species**

**D. Ochocińska & J.R.E. Taylor**

*Institute of Biology, University of Białystok, Białystok, Poland*

Bergmann's rule states that "races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates." The usual explanation is that larger animals have relatively smaller surface-to-volume ra-

tios, and therefore also lower costs of thermoregulation in the cold (northern) climates. The present study reviews the published data on body size in Palearctic species of shrews (genus *Sorex*) and analyses the intraspecific variation of body size in relation to climatic parameters and geographic location throughout the geographical ranges of these species.

The condylobasal length of the skull was used as a good indicator of the overall body size. Climatic variables included air temperature, precipitation, levels of evapotranspiration, their mean values, and various measures of climatic seasonality and among-year variability. The main finding is that body size in several species under study is negatively correlated with latitude and positively with ambient temperatures. The smallest shrews of a given species live, therefore, in the coldest climates. *Sorex* shrews follow the converse to Bergmann's rule. The results suggest that body size of shrews in cold climates may be limited by the amount of food available in winter. This hypothesis is reinforced by the fact that soricine shrews shrink their body size and drop body mass in winter (Dehnel's effect).

### **Dynamics of abundance in common shrew (*Sorex araneus* L.) populations in West Siberia**

V.V. Panov

*Institute of Systematics and Ecology of Animals, Russian Academy of Sciences, Novosibirsk, Russia*

Abundance dynamics of common shrew populations (eight localities populated by four different chromosome races) in West Siberia have been studied. The data sets comprise from 5 to 20 years for each locality. Differences in dominance, level of abundance, amplitude of fluctuation and the periods of cycles were detected between localities. However, the difference between chromosome races did not exceed the difference within races.

### **Comparative analysis of karyotypes of *Sorex araneus* and *Sorex minutus***

P.L. Perelman, L.S. Biltueva, N.B. Rubtsov,  
V.A. Trifonov, N.S. Zhdanova, I.A. Kumpyak  
& A.S. Graphodatsky

*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia*

This study of the karyotypes of *Sorex araneus* and *Sorex minutus* extends on the preliminary analysis made by Dannelid. Detailed cytogenetic analyses of GTG-banded karyotypes of *Sorex araneus* (Novosibirsk race) and *Sorex minutus* ( $2n=42$ ,  $NF=56$ ) were performed. The comparative analysis of the two karyotypes re-

vealed significant conservatism between the two chromosomal complements. Complete homeology of GTG-pattern was shown for 15 chromosomes of *Sorex minutus* with respect to the chromosomes of *Sorex araneus*. Some *Sorex minutus* chromosomes were present in the *Sorex araneus* complement in a fused state. However, homeology of five chromosomal regions of *Sorex minutus* is under question, due to the small size of these regions.

The region of homology for one of the most conservative chromosomes of the *Sorex araneus* complement - *tu* - was also not evident. To solve this task an additional molecular biological experiment was conducted. It has previously been shown, based on GTG-banding, that chromosome 17 of *Sorex granarius* is homologous to chromosome *tu* of the *Sorex araneus*. We proposed from GTG-pattern comparative analysis that chromosome *tu* is homologous to chromosome 17 of *Sorex minutus*. To prove it, FISH on metaphase chromosomes of *Sorex araneus*, *Sorex granarius* and *Sorex minutus* was conducted with a microdissected probe of chromosome 17 of *Sorex granarius*. This experiment completely confirmed our hypothesis.

Based on the data obtained we propose the probable ancestral complement for *Sorex araneus* and *Sorex minutus*.

### **Phylogeny of *Sorex araneus*: Old data in a new coat**

J. Piálek<sup>1</sup> & J. Zima<sup>2</sup>

<sup>1</sup>*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Studenec, Czech Republic;* <sup>2</sup>*Institute of Vertebrate Zoology, Academy of Sciences of the Czech Republic, Brno, Czech Republic and Department of Zoology, Faculty of Science, Charles University, Praha, Czech Republic*

The karyotype of the common shrew, *Sorex araneus*, is highly polymorphic due to centric fusions and fissions. Altogether over 50 chromosome races have recently been described based on chromosomal constitution of fused arms (Zima *et al.*, 1996, Searle & Wójcik, 1998). Starting in the eighties several attempts have been made to explain this variation on a phylogenetic basis. The majority of these attempts were based on an assumption that the acrocentric chromosomes are ancestral characters and that all recent karyotype variation stems from fusions to form different metacentrics. Parsimony criteria were employed to minimise tree length. The composition of metacentrics is more or less similar within a geographical area, hence, four karyotypic groups were defined.

Hauffe & Piálek (1997) used another mechanism able to generate chromosome variation – whole arm reciprocal translocations (WARTs) – to explain evolution of karyotype races of mice in northern Italy. They proved that employing WARTs resulted in a shortening of phylogenetic trees and more logical ordination of



geographically located races. Here we report a new model for the evolution of shrew races. The model adopts the assumption that the acrocentric chromosomes are ancestral, but in addition, it takes into account the effects of WARTs and zonal raiation. Both parsimony and geographic position of races were employed as criteria for tree optimisation.

Fifty races (sensu Zima *et al.*, 1996), four new races described recently and novel recombinant products confined only to hybrid zones were included into the model. Compared with the most recently published tree by Searle and Wójcik (1998), based on the process of fusions/fissions of a limited set of races, the resulting tree reflects a more plausible geographic arrangement of shrew karyotype races. We suggest that not only mechanisms of fusion and fission, but also WARTs and zonal hybridisation play a significant role in the evolution of common shrew races.

### Population structure of *Sorex araneus* from different chromosome races revealed by analysis of the cytochrome *b* gene

M. Ratkiewicz<sup>1</sup>, P. Taberlet<sup>2</sup>, S. Fedyk<sup>1</sup>, K. Szalaj<sup>1</sup>, A. Banaszek<sup>1</sup>, W. Chętnicki<sup>1</sup> & L. Gielly<sup>2</sup>

<sup>1</sup>*Institute of Biology, University of Białystok, Białystok, Poland;* <sup>2</sup>*Laboratoire de Biologie des Populations d'Altitude CNRS, Université Joseph Fourier, Grenoble, France*

DNA extraction from 28 individuals (12 populations, six chromosome races, West European and East European Karyotypic Groups), amplification of the cytochrome *b* gene with primers L14724 and H15915 via PCR and sequencing of a 1024 bp fragment revealed 35 variable positions, defining 25 distinct haplotypes. Unique mtDNA “fingerprints” provided for most shrews studied indicate very high long-term effective female population size (no recent population bottleneck). Present-day populations of *Sorex araneus* may consist of a mixture of several previously isolated populations (e.g. populations connected by postglacial zones of contact). Assuming a rate of 10% divergence per Myr, then the pairwise nucleotide divergence ( $p=0.99\%$ ) between the two most divergent haplotypes indicates that the common ancestor of all studied *Sorex araneus* haplotypes existed about 100,000 years ago. No haplotype divergence between WEKG and EEKG races of *Sorex araneus* indicates recent origin of these chromosomally different groups.

### Long-term chromosome and allozyme studies of a Białowieża race population of the common shrew

K. Szalaj, A. Banaszek, M. Ratkiewicz, S. Fedyk & W. Chętnicki

*Institute of Biology, University of Białystok, Białystok, Poland*

The Białowieża race of the common shrew is characterised by the diagnostic metacentrics *hn*, *ik*, *gr*, *mp*. The range of this race spreads through north-eastern Poland. We have been studying a population from the northern end of the range of the Białowieża race for 11 years. Data on chromosome and allozyme polymorphisms are presented.

### Anatomy of the shrew's brain: Is it conservative or evolved?

K. Turlejski

*Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland*

Enormous differences in the brain anatomy of various mammalian species must be created by modifications in some important genes and/or changes in the sequence of their induction. As a result of investigations in comparative neurobiology there has been postulated a hypothesis of the “initial mammalian brain”, the brain of the protoplast of mammals, which has been inherited without major changes by the first eutherians. Because insectivores, and especially shrews, are considered to be very close to the eutherian prototype, it is interesting if their brains resemble the hypothetical “initial brain”. Neocortex, the unique mammalian brain structure, constituted a low proportion of the “initial brain”, as in the extant shrews. Large olfactory and brainstem structures in shrews may also be considered a conservative trait. However, the external shape of the brain, that is compressed antero-posteriorly and dorso-ventrally, is a highly evolved trait in shrews, very different from the postulated elongated and conical prototype. Even more important are modifications of organs of senses and of the neocortical areas responding to particular modalities. The eyes of the majority of shrews seem to be highly reduced, and in the neocortex there exists only one small visual area, which is in contrast with other primitive mammals (opossums, tenrecs), which have at least two such areas. In spite of the good sense of hearing, there seems to be only one cortical auditory area. The sense of touch and especially the specialised sensory hairs (vibrissae) are a very important source of sensory information. In shrews there are two adjacent cortical somatosensory areas with large representations of vibrissae (in contrast to four in most primitive mammals). The topography of the sensory

areas in shrews is unique among mammals, as there is no associative areas separating them. This trait seems to be a regressive phenomenon (adaptation to the small size), rather than a preserved state. As sensory and motor areas occupy less than 50% of the neocortex, the remaining half must be occupied by limbic and frontal areas, that conduct evaluation of the emotional meaning of stimuli, guide execution of complex behavior and are involved in the memory storage and retrieval. This proportion is much higher than that postulated to exist in the "initial brain". Therefore, the anatomy of the brain in shrews is highly evolved as a result of the reduction of size of these mammals. This evolution depended on a mixture of both progressive and regressive changes.

**The necessity of creation of  
cryopreserved cell and tissue  
collections for chromosome races of  
*Sorex araneus***

**V.T. Volobouev**

*Museum National d'Histoire Naturelle, Laboratoire de Zoologie, Mammifères et Oiseaux, Paris Cedex, France*

Well developed cryobiological methods allow somatic cells to be stored in liquid nitrogen indefinitely

without alteration of their vital characteristics. Frozen then thawed, the cells retain their capacities to grow, to divide and to transmit their hereditary information. The  $10 \times 10^6$  cells easily obtainable after the third division of a primary cell culture are sufficient to perform various analyses such as cytogenetics, fluorescent *in situ* hybridisation (FISH), DNA/DNA hybridisation, protein electrophoresis, mini- and microsatellites, proteins, DNA or RNA sequencing, etc. and thereby to establish the complete genetic characteristics of any species. It follows that the cryopreservation under predetermined conditions of cell and tissue fragments of no more than  $0.3 \text{ cm}^3$  could prevent the irreversible loss of genetic information about a taxon and could serve as a universal and practically perpetual source of living material, useful in various research projects in the field of Molecular Systematics, Evolutionary Biology and Biotechnology. Cryopreserved cell and tissue collections (CC&TC) open large possibilities for effective and planned international co-operation and allow numerous studies in any taxon, from population genetics to phylogeny at various levels, from the unambiguous characterisation of any biological species to the global description of mammalian diversity. The common shrew *S. araneus* is a model of choice for the study of various aspects of evolution and speciation in mammals. The creation of CC&TC for chromosome races of *S. araneus* will open a new perspectives in the study of the milking cow of cytogenetics.

## Sixth ISACC meeting, Paris, 3–7 September 2002

### Robertsonian polymorphism in the common shrew (*Sorex araneus* L., 1758) – are there any differences between homozygotes and Rb heterozygotes?

A. Banaszek, J. Taylor, D. Ochocińska,  
W. Chętnicki & M. Ratkiewicz

*Institute of Biology, University of Białystok, Białystok, Poland*

Three general models – past hybridisation events, *de novo* mutation and natural selection – explain Rb polymorphisms in the common shrew external to hybrid zones. For the third model it has to be accepted that there are allelic differences between the twin acrocentric and metacentric morphs of a particular chromosome and that Rb heterozygotes are also genic heterozygotes. To test this hypothesis we compared several parameters between homozygotes and Rb heterozygotes collected in the Jurowce population in Poland (Białowieża race) during 1996–1999. We found no differences between two karyotypic classes in the following parameters:

- 1 – allozyme heterozygosity
- 2 – basal and maximum metabolic rate
- 3 – fluctuating asymmetry
- 4 – index of locomotor activity

Concluding, the hypothesis that Rb polymorphism in the common shrew could be maintained by heterozygous advantage of Rb heterozygotes cannot be supported.

### Comparative analysis of five *Sorex* species based on high-resolution GTG-banding and ZOO-FISH: preliminary data

L. Biltueva

*Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia*

Comparative analysis of the species *Sorex araneus*, *Sorex minutus*, *Sorex caecutiens* and *Sorex raddei* was performed using high-resolution chromosome banding and ZOO-FISH. Painting probes were generated from flow sorted chromosomes of *Sorex granarius*. They revealed 32 conservative autosomal segments. Different fusions of these segments have taken place in the chromosomal evolution of the species studied. This study represents an attempt to reconstruct the array of chromosomal rearrangements during the karyotypic divergence of these species.

Knowledge about the arrangement of conservative segments in species from two main karyotypic groups help us to understand the distinguishing features of chromosomal evolution of the genus *Sorex* as a whole.

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### Alps, genes and chromosomes: their role in the formation of species in the *Sorex araneus* group (Mammalia, Insectivora), as inferred from two hybrid zones

H. Brünner, N. Lugon-Moulin & J. Hausser

*Institut d'Ecologie, Laboratoire de Zoologie et d'Ecologie animale, Lausanne, Switzerland*

During the Pleistocene glaciations the Alps were an efficient barrier to gene flow between isolated populations often leading to allopatric speciation. Afterwards, they strongly influenced postglacial recolonisation of Europe and represent a major suture zone between differentiated populations. Two hybrid zones in the Swiss and French Alps between the genetically and karyotypically well differentiated Valais shrew, *Sorex antinorii*, and the common shrew, *S. araneus*, were studied using karyotypes and seven microsatellite loci. In the centre of the Haslital hybrid zone the two species co-occur over a distance of 900 m. Hybrid karyotypes, among them the most complex known from *Sorex* species, are rare. F-statistics calculated on microsatellite data revealed strong heterozygote deficit only in the centre of the zone, due to the sympatric distribution of the two species with little hybridisation. Structuring within species (both  $F_{IS}$  and  $F_{ST}$ ) was low. A hierarchical analysis showed high interspecific differentiation. Results were compared with those previously reported in another hybrid zone located at Les Houches (French Alps). Genetic structuring within and between species were comparable in both hybrid zones, although chromosomal incompatibilities are more important in Haslital where a linkage block of the race-specific chromosomes should additionally impede gene flow. Evidence for a more restricted gene flow in Haslital comes from the genetically intermediate hybrid karyotypes, whereas in Les Houches hybrid karyotypes are genetically identical to individuals of the pure karyotypic races. Genic and chromosomal introgression were observed in Les Houches but not in Haslital. The possible influence of a river, separating the two species at Les Houches, on gene flow is discussed.

## Phylogenetic associations among the karyotypes of the *ip*- and *hk*- lineages in *Sorex araneus* of Western Russia

N. Bulatova

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia*

During the three-year interval since the 5th ISACC meeting (Białowieża, Poland, 1999) several new chromosome races of *S. araneus* have been discovered in European Russia. Two of them are characterised by the two chromosome markers *ip*, *hk*. The St.-Petersburg (SPb) and West Dvina (WDv) races are found west of Moscow and are placed between the Moscow, Pskov, Seliger and Ilomantsi races. Although they carry the same metacentrics *ip* and *hk*, they differ in diagnostic arm combinations *g, o, mq, nr* (SPb) and *gm, no, qr* (WDv). Comparative chromosome analysis shows the hierarchy of phylogenetic associations in the karyotypes of shrews that might correspond to different phylogeographic complexes at lower intraspecific levels. The report should be dedicated to Liisa Halkka due to her pioneering works on races of the *ip*-lineage.

## Perspectives in studying a border zone between two chromosome races - Moscow and Seliger - of *S. araneus*

N. Bulatova<sup>1</sup>, N. Shchipanov<sup>1</sup>, A. Kalinin<sup>1</sup>,  
A. Aleksandrova<sup>2</sup> & D. Aleksandrov<sup>1</sup>

<sup>1</sup>*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia;* <sup>2</sup>*Moscow State University, Moscow, Russia*

Among 16 karyotypically identified races of the common shrew (*Sorex araneus* L.) known up to now in European Russia, two races have attracted our special attention since 1997.

The distributional ranges of the Moscow (*g/m, hi, jl, kr, no, pq*) and Seliger (*g, hn, ik, jl, m/q, o, pr*) races come into contact in the western vicinity of Lake Seliger which is situated at the location of the edge of the last glacial ice sheet. Among 27 animals caught in mixed race sites no hybrid specimens were found. However, a mixed karyotype was revealed in one case (*g/gm/mq/pq/pr/r, hn, ik, jl, o*). This suggests strongly restricted interracial hybridisation. Five years of data on chromosomal as well as population biology aspects of the border zone are discussed. The work is supported by the Russian Foundation for Basic Research, grants Nos. 01-04-48412, 00-04-48787.

## New type of recombined karyotype in a hybrid zone

S. Fedyk, U. Bajkowska, W. Chętnicki,  
A. Banaszek, & K. Jadwiszczak

*Institute of Biology, Białystok University, Białystok, Poland*

Two kinds of posthybridisation modifications minimising the low fertility of hybrids are known in hybrid zones between chromosomal races of the common shrew. The first of them is a peak of frequency of acrocentric chromosomes, which lowers the probability of production of complex heterozygotes. This type of modification occurs very often in *Sorex araneus* hybrid zones. Conversely, the second type of modification, that is the peak of frequency of recombinants which lowers the frequency of complex heterozygotes too, has been described only in the hybrid zone between the Drnholec and Łęgucki Młyn races in Poland.

The aim of the present study is the search for recombinants in another hybrid zone. We decided to investigate the hybrid zone between the Gołdap race (*hk, gr, mn*) and the Białowieża race (*ik, hn, gr, mp*). The hybrids theoretically should form the chain-VII meiotic complex *i/ik/kh/hn/nm/mp/p*. Robertsonian polymorphism causes a high frequency of *m, n, p* and a moderate frequency of *k, h* acrocentrics in the contact zone, and consequently we have very often observed chain complexes to be shortened to five (*i/ik/kh/hn/n*) or four (*i/ik/kh/h* or *k/kh/hn/n*) elements and the trivalent of *m/mp/p* excluded from the expected complex. In consequence shrews with the recombined karyotype (*hk, mp*) have arisen in the contact zone between the Gołdap and Białowieża races.

## Recent distribution of chromosome races of the common shrew (*Sorex araneus*) in Eastern Europe and possible routes of postglacial recolonisation in the region

A. Mishta

*Schmalhausen Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine*

Until the present time more than 60 chromosome races of the common shrew have been described. As fast as new information about distribution of chromosome races have appeared, there have been attempts to explain their origin.

Hypotheses on the evolution of *S. araneus* connect the origin of chromosome races with the period of the last glaciation (Searle, 1984; Wójcik, 1993; Polyakov *et al.*, 2001). It is accepted that in the ancestral karyotype of the common shrew all variable chromosomes were acrocentric. During the last glaciation the range of *S. araneus* was fragmented and reduced to a number of



refugial areas in southern parts of Europe, Ural and Siberia. As a result, in several small isolated populations Robertsonian fusions could occur and fix. Later on, after glacial retreat, the range of these populations could extend and neighbouring populations could come in contact producing in some cases new races with hybrid characteristics (Searle & Wójcik, 1998; Zima *et al.*, 1996). Alternative hypotheses suggests a cascade of successive whole-arm reciprocal translocations as in the case of common shrews inhabited Scandinavia (Halkka *et al.*, 1987, 1994).

When these hypotheses were being developed, information about distribution of chromosome races in *S. araneus* was lacking from the most part of Eastern Europe. By 1995, only three chromosome races of the common shrew were described from the European part of the territory of the Former Soviet Union (Ivanitskaja, 1986; Aniskin & Lukianova, 1989; Mishta, 1994). By now, intensive investigations (Bulatova *et al.*, 2000, 2002; Zaitsev & Bulatova, 1999; Mishta *et al.*, 2000; Kozlovsky *et al.*, 2000; Orlov *et al.*, 1996) have resulted in the description of more than 10 chromosome races and their distribution in the region.

On the basis of data analysis on paleoclimate, and the distribution of mammals and vegetation during and after the last glaciation and on the recent distribution of *S. araneus* chromosome races, a scheme of possible ways of recolonisation of the territory of Eastern Europe by the common shrew is proposed.

### The phenomenon of the inactivated “true” X-chromosome in male meiotic metaphases of *Sorex araneus*

R. Nadjafova

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia*

In spite of the absence of any prominent amount of C-banded heterochromatin in the chromosomes of *S. araneus*, the phenomenon of X-chromosome inactivation is demonstrated as a compaction of the short arm (“true” X) in the sex-autosome trivalent (XY<sub>1</sub>Y<sub>2</sub> system) shown in G-banded meiotic cells of males.

### Post-Pleistocene expansion of *Sorex araneus* in Poland revealed by mt cyt *b* gene sequences and implications for chromosomal evolution

M. Ratkiewicz<sup>1</sup>, S. Fedyk<sup>1</sup>, A. Banaszek<sup>1</sup>,  
L. Gielly<sup>2</sup>, W. Chętnicki<sup>1</sup>, K. Jadwiszczak<sup>1</sup>  
& P. Taberlet<sup>2</sup>

<sup>1</sup>University of Białystok, Institute of Biology, Białystok, Poland; <sup>2</sup>Laboratoire de Biologie des Populations d'Altitude, Université Joseph Fourier, CNRS, UMR 5553, BP 53 38 041 Grenoble, Cedex 9 France

Genetic variability of the common shrew (*Sorex araneus*) in Poland was assayed by sequencing a 1023 bp part of the cytochrome *b* gene (mtDNA) from 28 individuals.

Thirty four variable positions defined 21 distinct haplotypes with a maximum sequence divergence of 0.88%. Haplotype diversity estimates were high ( $h=0.800-0.928$ ), while nucleotide diversity estimates were low ( $\pi=0.0034-0.0053\%$ ). The distribution of pairwise nucleotide differences fits well with expectations of a “sudden expansion” model. No evidence was found for a recent bottleneck after the process of post-Pleistocene recolonisation of Poland by shrews. Thus, for *S. araneus* chromosome races in Poland, the data on the mt cyt *b* gene variability support the hypothesis that Robertsonian fusions spread into an ancestral acrocentric distribution.

### Population border. Is it reality?

N. Shchipanov<sup>1</sup>, A. Kalinin<sup>1</sup>, T. Demidova<sup>1</sup>,  
V. Oleinichenko<sup>2</sup>, A. Aleksandrova<sup>2</sup>,  
D. Aleksandrov<sup>1</sup>, A. Kouptsov<sup>1</sup> & N. Bulatova<sup>1</sup>

<sup>1</sup>A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; <sup>2</sup>Moscow State University, Moscow, Russia

Surveying *S. araneus* in Tver Province (Central European Russia) for 7 years we have found nonsynchronised population density fluctuations in two areas separated by 3 km distance. This may be affected by different movement activity of shrews in these areas. In studies of population structure, we noticed that different proportions of nonresidents are present in populations in different years. Thus, nonsynchronised density dynamics may result from preferential movement of nonresidents within the population area. And so, the population border may be treated as a zone of restricted trespassing. To check the hypothesis, we conducted a study of fungi carried on the fur of small mammals. This allowed us to reveal two areas where different fungal species were found on fur. The border as shown using this method coincides with the border between

different patterns of density dynamics. Finally, we studied the distribution of the Moscow and Seliger chromosome races. The analysis of 62 specimens revealed a narrow border zone, which could be considered in terms of nonresident inter-population trespassing. The study was supported by the Russian Foundation for Basic Research, grants Nos. 01-04-48412, 00-04-48787.

### Chromosome polymorphism of the Neroosa race (*Sorex araneus*) in the territory with radioactive pollution after the Chernobyl accident

B.I. Sheftel & E.Y. Krysanov

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia*

This work was conducted in the territory of No-vozybkov District of Bryansk Province (Russia). This territory was radioactively polluted after the catastrophe at Chernobyl NPP in 1986. The current level of radioactive pollution of the soil is 1480 kBq/m<sup>2</sup> (<sup>137</sup>Cs) (compared with a background level of radioactivity in non-polluted territories, which is 37 kBq/m<sup>2</sup>). Karyotypes of 77 animals were analysed. Shrew trapping was done in 1995–2001. The maximal distance between points of captures was 1 km. Diploid number of autosomes in the studied specimens (2NA) varied between 19–25. By G-banding analysis of seven animals with different chromosome numbers it was shown that they belong to the Neroosa race. The high level of chromosome polymorphism is typical for this race and was described earlier at different geographical points. It should be specially noticed, that we did not find animals with 2NA=18, which were described earlier as typical for representatives of Neroosa race in other geographical points. The animals with 2NA=22 or 25 have not been described before (according the literature). Most animals had 2NA=22 (23). Such chromosome polymorphism discovered in one place can be caused by a reaction of the population to radioactive pollution, but it can be a unique natural phenomenon as well.

Years	2NA							Total
	19	20	21	22	23	24	25	
1995			2	1	1	1		5
1996		2		1				3
1997			2	4		3		9
1998						3	1	4
1999	1		2	8	9	7	1	27
2000				5		2		7
2001	1	3	5	4	6	2		21
Total	2	5	11	23	16	18	2	77

### Phenotypic plasticity in spatial behaviour and brain structure in *Sorex araneus*

V.A. Yaskin

*Department of Vertebrate Zoology, Biology Faculty, Moscow State University, Moscow, Russia*

The hippocampus is involved in processing of spatial information in the environment, and its size is known to correlate positively with spatial ability (with size of home range in particular) among mammal species. Differences in space use predict differences in hippocampal size. The aim of my study was to find out if such a regularity is manifested also in ontogenesis and during the cyclic changes of spatial behaviour observed, for example, in some small mammals. Over an annual cycle, home ranges of *Sorex araneus* decrease in autumn and increase in spring. It is known that seasonal changes in the type of spatial behaviour of immature *S. araneus* transform from wide, active movements in summer to the restricted movements within the single home range in autumn. The decrease of the home range size reflects the end of the exploratory period and stabilisation of the home ranges. Comparison between the dynamics of the hippocampus formation size and data on the annual dynamics of the size of common shrew home ranges showed certain parallelism of the two parameters. A reduction in hippocampus size coincided with the shrinkage of the animals' home ranges. A morphometrical analysis showed that areas of sections of both the dentate gyrus and the hippocampus significantly declined from autumn to winter. Thereafter, however, another growth spurt occurred in the spring; it followed the winter decline. During a period of gain in brain mass in the spring, the rate of size increase was different in different brain structures. The most considerable increase was observed in the hippocampus (+33%;  $p < 0.001$ ). The highest relative mass increase (compared to the whole brain) during the winter-to-summer period was found in this brain region (+15%;  $p < 0.001$ ). Thus, the predicted growth processes in hippocampal formation of adult animals were found. Calculation of the number of nerve cells per mm<sup>2</sup> of sections of the dentate gyrus in the common shrew supports the existence of neurogenesis in this brain region. In contrast, the hippocampal volume decrease in winter might be particularly dependent upon apoptosis. The data obtained support a great seasonal morphological plasticity and protracted growth in behaviourally relevant brain regions. Seasonal dynamics of hippocampal size most precisely coincided with the dynamics of morphological development of the hypophysis and reproductive system. Seasonal modulation of the sex differences in the hippocampus size was also revealed. Sex dimorphism in both hippocampal volume and size of home ranges became distinct (favouring males) in the early

spring when sexual maturation of the shrews began. Since gonadal hormone levels also fluctuate among seasons in shrews, these data raise the possibility that sex differences in hippocampal volume may differ in close connection with both hormone levels and sexually dimorphic spatial ability. Both the behaviour and the

brain structure in adult animals may be phenotypically plastic in response to the seasonally changing demands of the environment. The study raises a new understanding of some mechanisms of Dehnel's phenomenon in *Sorex* species.

## Seventh ISACC meeting, St. Petersburg, 28 August – 1 September 2005

### Micromycetes on the fur of common shrews *Sorex araneus* L. as a natural marker for population studies

D.Y. Aleksandrov<sup>1</sup>, A.V. Aleksandrova<sup>2</sup>  
& N.A. Shchipanov<sup>1</sup>

<sup>1</sup>*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia;* <sup>2</sup>*Moscow State University, Moscow, Russia*

Studies were conducted on samples of the fur of common shrews (Moscow chromosomal race) and soil samples from Central Russia (South-east of Tverskaya area). Specimens of the fur and soil were placed on standard wort agar and Chapek mediums. Sporiferous stages of micromycetes were used for identification. Samples of the fur of 106 common shrews and 272 individuals of other small mammals (bank vole, masked shrew and pygmy shrew) were examined. The number of Petri dishes with presence of a micromycete species was considered as a positive test (PT) and was used for statistical analyses. In total, 107 micromycete species were found on the fur of common shrews (846 PT), 158 from the fur of all species studied (5726 PT) and 119 (1914 PT) from soil in the same habitats. Seventy-seven species of micromycetes were isolated exclusively from fur. Temporal monitoring of fungi on the fur showed that it changed significantly within a month. Correlations ( $r$ ) between subsequent months ranged from 0.53 to 0.60 while over a month correlations could be as low as 0.06 to 0.28. The fungal composition on the fur of common shrews was more closely correlated to that observed on bank voles ( $r=0.73$ ) than that observed on masked shrews (0.54) and pygmy shrews (0.47). It was found that micromycetes both on the fur and in the soil differed less in geographically close habitats compared to those in similar but remote habitats. In the common shrew the correlation of micromycetes diminished with distance between areas sampled. The correlation between the composition of fungal spores on the fur of common shrews sampled from pine and spruce habitats at 300-m distance in one forest site equalled 0.98, in another forest at 500-m distance = 0.52; between spruce and alder at 1 km distance = 0.08. This correlation abruptly became negative at the zone of contact of neighbouring populations, reflecting restricted mobility of individuals. In homogeneous alder habitat at a distance of about 200 m,  $r=-0.20$ .

The first results of this study suggests that: 1) common shrews (together with the other small mammals) play a rather important role in the ecosystem, greater than expected on the basis of its role in the food web; 2) the composition of fungal spores on the fur could be

used as a measure of temporal and geographical similarity of samples; 3) the composition of micromycete spores could be used to study ecological niches; 4) the composition of spores on the fur could be used as a natural marker for studying dispersal.

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### Fennoscandian phylogeography of the common shrew (*Sorex araneus*). Postglacial recolonisation – combining information from chromosomal variation with mitochondrial DNA data

A.-C. Andersson, C. Alström-Rapaport  
& H. Tegelström

*Program in Evolutionary Functional Genomics, Department of Evolution, Genomics and Systematics, EBC, Uppsala University, Uppsala, Sweden*

When the ice retreated after the Last Glacial Maximum, Fennoscandia was primarily recolonised by two routes, from the south via land bridges and from north-east through prehistoric Finland. In several mammal taxa the bi-directional recolonisation resulted in secondary contact between evolutionary differentiated lineages, in northern Sweden. The location of these zones coincides with a contact zone between two chromosome races of the common shrew, *Sorex araneus*. These races have very differentiated karyotypes, and belong to the North and West European karyotypic groups (NEKG and WEKG).

We found no mitochondrial DNA (mtDNA) variation between these two karyotypic groups in Sweden. MtDNA variation suggests that most haplotypes arose *in situ* and that the populations have undergone a rapid size expansion. Genetic variation is as large between populations within a race as between populations among the races or karyotypic groups. A noticeable exception is the Öland race, which shows higher mtDNA diversity compared to the other Swedish races. The high diversity of the Öland race is difficult to explain as cytochrome *b* variation suggests that the Öland race most likely evolved from mainland Swedish races. Furthermore, we also find significant mtDNA structure in Fennoscandia, but discordant with the chromosomal groupings. Common shrews from south Finland belong to a different evolutionary mtDNA lineage from other Fennoscandian shrews, thus the evolutionary history of south Finland might be different from remaining Fen-



noscandian regions which seem to share a common evolutionary history.

MtDNA variation suggests that the evolution of karyotypic groups appear to be more recent than previously proposed. However, by combining mtDNA data with existing karyotypic information we suggest that the Northern and Western groups recolonised Fennoscandia via the two different routes.

### **Effects of genetic drift and selection on the Drnholec/Białowieża hybrid zone of the common shrew: morphometric study**

**A. Banaszek, K.A. Jadwiszczak & M. Ratkiewicz**

*Institute of Biology, University of Białystok, 15-950 Białystok, Poland*

Morphometric differentiation of shrews from the Dn/Bi hybrid zone was examined by the use of 19 cranial and skeletal measurements described by Polyakov *et al.* (2002). Two sets of immature shrews were used for this study: 29 shrews of known karyotype – for morphometric analysis related to karyotype and 42 un-karyotyped shrews – for analysis related to habitat.

The shrews collected in different parts of the hybrid zone did not show any morphological differentiation in spite of habitat differences in the area studied. As the morphology of shrews is strongly influenced by habitat conditions, it suggests that populations in this hybrid zone are not stable, i.e. there is not enough time to diverge morphologically due to habitat conditions.

The shrews of three karyotypic classes – Białowieża race, Drnholec race and hybrids did not differ significantly in any single measurement. However, discriminant analysis revealed a rather clear grouping of the karyotypic classes.

The observed slight differentiation is similar to that acquired in other genetic studies in this hybrid zone and suggests the same conclusion. The races Bi and Dn were not differentiated except chromosomally when they met. However, from the time of contact the restricted gene flow in the hybrid zone has resulted in the accumulation of slight genetic differences including morphology.

### **Mitochondrial and nuclear DNA variability of the East European and Siberian chromosome races of the common shrew *Sorex araneus* L.**

**A. Bannikova<sup>1</sup>, N. Bulatova<sup>2</sup>, V. Lebedev<sup>2</sup> & D. Kramerov<sup>3</sup>**

*<sup>1</sup>Moscow State University, Moscow, Russia; <sup>2</sup>A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; <sup>3</sup>Enhelhardt Institute of Molecular Biology, Russian Academy of Sciences, Moscow, Russia*

Mitochondrial DNA and microsatellite studies initiated in response to the discovery of remarkable chromosome variation in the common shrew mainly deal with chromosome races of West Europe while the East European and Siberian parts of the range of the common shrew remain unexplored. The objective of this study was to examine the genetic differentiation among populations of common shrew of European Russia and Siberia using mitochondrial *cyt b* and nuclear DNA regions flanked by short interspersed elements (inter-SINE-PCR). For mtDNA data NJ and MP network analyses were performed. The IS-PCR data were analysed using UPGMA, NJ and multidimensional scaling (MDS). The analysis of the 16 haplotypes found by us for European Russia and Siberia and >15 haplotypes from Western Europe retrieved from GenBank revealed no well-supported groupings which could correspond to geographic populations or races. However, the specimens from Kemerovo region, the Yenisey valley, and the Baikal region showed some weak tendency for separation from the majority of shrews from West Europe and European Russia. The average level of divergence between haplotypes was relatively low being about 0.4% for intra- and 0.65 % for interpopulation comparisons. Such a pattern of *cyt b* variation based on haplotype data from most of the species range is consistent with the hypothesis postulating the existence of a single ancestral population surviving the last glacial cycle in a refugium in Europe and rapid recolonisation during the last 10-20 000 years. In this case most of the contemporary races must have originated in the Holocene. The division between common shrews of European Russia and Siberia may have occurred not earlier than in some late Würmian interstadial.

In contrast to the *cyt b* data, the IS-PCR fingerprints reveal some evident pattern of geographical variation. NJ and UPGMA analyses as well as the results of MDS clearly show the division of all examined common shrews of European Russia and Siberia into two main groups, the first one comprising specimens of the Moscow, Seliger and Manturovo races, the second consisting of the Yenisey and Kemerovo samples. The Neroosa race is closely related to the European group while Pechora specimens of the Serov chromosome race appear to be close to the Siberian group. The specimens of

the Sok race demonstrate no clear affinity to either of the large groups and, hence, might represent a separate cluster. The relationship between the Seliger and Moscow races is of particular interest due to a reduced observed level of hybridisation in the zone of sympatry. The cluster comprising the Moscow race specimens from the contact zone tend to join the Seliger race cluster rather than other Moscow race representatives. This pattern suggests the existence of gene flow between sympatric populations of the two races.

The work was supported in part by the Russian Foundation for Basic Research (05-04-49240a) and INTAS (03-51-4030).

### **Chromosomal rearrangements and gene flow in the *Sorex araneus* group**

**P. Basset, G. Yannic & J. Hausser**

*Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland*

The species and races of the *Sorex araneus* group of shrews exhibit a huge range of chromosome polymorphism. European species and chromosome races of this group are parapatric and exhibit contact or hybrid zones showing an extraordinary variety of situations, from absolute genetic isolation to almost free gene flow. This variety seems to depend for a large part on the chromosome composition of populations, which are primarily differentiated by various Robertsonian fusions of the same acrocentric chromosomes. Various data suggest that chromosomal rearrangements severely impede recombination in heterokaryotypes. In such circumstances, gene flow should be more restricted for markers housed on chromosomes involved in rearrangements than on chromosomes identical in both parent species.

In the present study we address the possibility of such a differentiated gene flow in the *Sorex araneus* group.

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### **Karyotypic versus genetic structure in the *Sorex araneus* group**

**P. Basset, G. Yannic & J. Hausser**

*Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland*

Identification of the morphologically very similar sibling species of the *Sorex araneus* group is of primary interest for the localisation of unknown hybrid zones. Different techniques based on karyotype, morphology, biochemistry and diagnostic genetic markers have been

developed to identify individuals from this group but all have drawbacks. Recently, numerous assignment methods based on assignment of individuals to a genetic sample have been developed and seemed especially effective. However, before using these techniques to allocate unknown samples to taxa, it is necessary to check the good agreement between genetic and taxonomic structure. This last point should not be underestimated in the *Sorex araneus* group as the genetic relations among taxa are not straightforward and no real trials have been done to link genetic and karyotypic structure at a larger scale than the hybrid zone. In this study, we explore this issue in the context of the species and chromosome races of the *Sorex araneus* group in western Alps.

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### **Pattern of meiotic recombination in interracial hybrids of the common shrew**

**N. Belonogova & T. Karamysheva**

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

The Novosibirsk and Tomsk chromosome races of common shrew display a narrow hybrid zone close to Novosibirsk. The hybrids are complex Robertsonian heterozygotes that form a chain-of-nine configuration at meiosis I. A simple Robertsonian polymorphism for *qr*, *mp*, and *go* chromosomes is also observed in this area. To estimate the gene flow between the races it is essential to assess how meiotic recombination is affected by these chromosomal rearrangements.

We analysed 260 pachytene cells from specimens of the Novosibirsk and Tomsk chromosome races and their hybrids. Using immunofluorescent detection of the recombination complex protein, MLH1, followed by FISH with arm specific DNA probes, we localised precisely the positions of crossover events on spread synaptonemal complexes. This allowed us to generate exchange distribution diagrams (recombination patterns) for all recognisable chromosomal arms including *m*, *o*, *p*, *q*, *r* that were present either as acrocentrics or metacentrics. The analysis revealed an increased exchange frequency near the centromeres in acrocentric chromosomes *o*, *p*, *q*, *r* when compared with the same arms involved in metacentrics *mp*, *qr* and *go*. The pattern of recombination in *q/r* trivalents was skewed towards the telomeres, but the overall recombination rate was higher than in *qr* metacentric bivalents. The results are discussed in view of the possible effect of the rearrangements on the divergence of chromosome races of the common shrew.

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## Chromosome evolution in the Insectivora

L. Biltueva, N. Vorobieva, P. Perelman  
& A.S. Graphodatsky

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

We used GTG-banding and comparative chromosome painting to identify regions of chromosomal homology in fourteen species from four genera: *Sorex*, *Crocidura*, *Suncus* and *Talpa*. Karyotypes with  $2n$  values within the limits from 20 to 64 were considered. The set of conservative segments and their rearrangements in the investigated karyotypes were revealed. This approach provides a basis for reconstructing the ancestral insectivoran karyotype.

Here we confirm that tandem and centric fusions play a fundamental role in the chromosome evolution of the order Insectivora. Different types of tandem fusions provide morphological distinction in karyotypes of closely related species such as *Sorex minutus* and *Sorex caecutiens* with the same value  $2n=42$ . According to our data, the putative ancestral insectivoran karyotype is composed of 33 conservative autosomal segments.

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## Craniological characteristics of *Sorex araneus* of two chromosomal races in Northeastern European Russia

A.V. Bobretsov, E.A. Poroshin  
& I.F. Kupriyanova

*Pechora-Ilychskii Nature Reserve, Institute of Biology of Komi Scientific Centre, Russia*

The morphometrics of common shrews of the Manturovo and Serov chromosomal races from six localities in Northeastern European Russia were studied using 27 craniological parameters (553 skulls of yearlings were measured). Three series of skulls from lowland ( $61.82^\circ$  N,  $56.83^\circ$  E), submountain ( $62.07^\circ$  N,  $58.46^\circ$  E) and highland ( $62.11^\circ$  N,  $59.08^\circ$  E) areas of the Pechora-Ilychskii Nature Reserve could be assigned to the Serov chromosomal race. Another three series have been collected in the Kotlas region of the Archangelsk Province ( $61.25^\circ$  N,  $46.96^\circ$  E), and in the Priluzskiy

( $60.64^\circ$  N,  $48.67^\circ$  E) and Kortekerosskiy ( $61.82^\circ$  N,  $51.85^\circ$  E) regions of the Komi Republic, which represent the Manturovo race. Cluster analysis on the basis of Mahalanobis distances revealed clear differences between these races. The most significant contribution in the discrimination can be attributed to the lower jaw length (LJL) and rostrum breadths (RB). Those were maximal in the Serov race. The LJL in the Serov races was  $10.29 \pm 0.01$  mm versus  $9.83 \pm 0.01$  mm for the Manturovo race. The representatives of a given race from various landscapes differed by condylobasal skull length (CSL) and by facial length (FL). Thus for example CSL in lowland populations of the Serov chromosomal race averaged  $19.71 \pm 0.03$  mm, and for highland populations it was  $19.99 \pm 0.03$  mm ( $p < 0.001$ ). The same differential was found for other skull characters: the height of the skull, interorbital breadth and RB. And so, highland populations of the Serov race possess morphological characteristics distinctive from lowland populations, whereas representatives of the Manturovo race differed to a lesser degree and formed a more compact group under cluster analyses.

## Molecular cytogenetics of chromosome pairing and recombination in the common shrew

P. Borodin, T. Karamysheva, N. Belonogova,  
M. Rodionova, A. Polyakov & N. Rubtsov

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

Chromosome pairing and recombination at meiosis involves scheduled formation and repair of double-strand breaks of DNA. There are two proteins that play a crucial role in these processes: Rad51 – the eukaryotic homologue of bacterial RecA protein, and MLH1, the protein involved in mismatch repair. Rad51 has been shown to bind double strand breaks. The distribution of MLH1 foci in human, mouse and chicken gonocytes has been shown to mark crossing-over events. The extended length of pachytene SCs, as compared to more condensed diplotene-metaphase I bivalents, makes mapping crossover events and interference distances using MLH1 foci more accurate than using chiasmata.

We used antibodies against these proteins and SCP3, the main component of the lateral elements of synaptonemal complex (SC), to examine the temporal and spatial distribution of Rad51 and MLH1 in the spermatocytes of the common shrew. SCs were identified by their relative size and arm ratio.

We found that hundreds of Rad51 foci appeared at leptotene. At the beginning of zygotene their close association with axial elements of meiotic chromosomes became apparent. From early to late zygotene the number of Rad51 foci gradually decreased. At pachytene we observed a very small number of foci.



These were distributed irregularly along the autosomal SCs. We detected a prevalence of Rad51 signals on arm *d* at early pachytene and on arm *e* at late pachytene.

The MLH1 foci in the common shrew were found to occur at early pachytene and remained visible until late pachytene. They showed a very regular distribution pattern along the arms of bivalents and multivalents, similar to the chiasma distribution at diakinesis-metaphase I. We assessed the general pattern of recombination in the common shrew (dependence of MLH1 focus number on SC length, interference between neighbouring foci within the same arm and across the centromere) and arm-specific patterns of MLH1 distribution. We compared these parameters in homozygous and heterozygous specimens of the Novosibirsk and Tomsk chromosome races and their hybrids and found significant differences between them. We discuss implications of these findings in relation to genetic exchange between the chromosome races.

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### **Analysis of hybrid fitness in the Tomsk and Novosibirsk chromosome races of the common shrew by means of chromosome *qr* variability**

**M. Bukina, P. Borodin & A. Polyakov**

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

The Novosibirsk and Tomsk chromosome races of the common shrew form a hybrid zone in West Siberia. In addition to the chromosomes that combine within a "chain of nine" at meiosis in hybrids (*go*, *hn*, *ik*, *mp* – Novosibirsk complement and *gk*, *hi*, *mn*, *o*, *p* – Tomsk complement) these two races are distinguished by chromosome *qr* that occurs as a metacentric morph in the Novosibirsk race and in a telocentric state in the Tomsk race. In comparison with the "chain of nine", the simple trivalent *qr/q*, *r* should hardly affect the fitness of hybrids. If this is true, the pattern of transmission of variants of chromosome *qr* through the hybrids may help to evaluate the level of hybrid unfitness. The karyotypes of 124 shrews from the area of the hybrid zone were studied for association of the *qr* or *q*, *r* variants with chromosomes of the Novosibirsk and/or Tomsk chain complex. It was found that the Novosibirsk chain chromosomes more frequently combine with the Novosibirsk variant of chromosome *qr* and likewise with the Tomsk chain chromosomes and Tomsk variant *q*, *r*. This observation suggests that transmission of chromosome *qr* through the hybrids is depressed. Mechanisms of this depression will be discussed from the point of view of hybrid fitness.

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### **Sequencing *Sorex araneus*: implications of a low coverage (2x) genome**

**J. Chang, S. Gnerre, C. Wade, M. Clamp & K. Lindblad-Toh**

*The Broad Institute of MIT and Harvard, 320 Charles Street, Cambridge, MA 02141, USA*

With the recent completion of a high-quality sequence of the human genome, the challenge is now to understand the functional elements that it encodes. Comparative genomic analysis offers a powerful approach for finding such elements by identifying sequences that have been highly conserved during evolution. We proposed an initial strategy for detecting such regions by generating low-redundancy sequence from a collection of 16 eutherian mammals, beyond the seven for which genome sequence data are already available. These 16 eutherian mammals were divided into two sets of eight mammals, with the first set receiving NHGRI funding last August. Sequence is now available for four of these mammals and all eight will be sequenced to two-fold redundancy by September of this year. We show that such sequence can be accurately aligned to the human genome and used to identify most of the highly conserved regions. While not a long-term substitute for generating high-quality genomic sequences from many mammalian species, this strategy represents a practical initial approach for rapidly annotating the most evolutionarily conserved sequences in the human genome, providing a key resource for the systematic study of human genome function.

The first set of mammals to be sequenced for this initiative, in chronological order, include: African savannah elephant, nine-banded armadillo, inbred New Zealand white rabbit, lesser hedgehog tenrec, inbred strain 2N guinea pig, common shrew, European hedgehog and domestic cat. Using the results from elephant and armadillo, we will discuss what to expect from the 2x common shrew assembly available later this year. While the goal of the sequencing is rather human-centric, a vast amount of information will be available about the common shrew, its gene content and relationship to other mammals as well as a significant resource of SNPs for phylogenetic analysis.

To optimise the properties of the genome assembly, we wished to select the best DNA donor available. Because one of the critical factors in whole genome assembly is the heterozygosity of the individual sequenced, we tested eight common shrews from five different Scottish islands to determine the heterozygos-



ity level within individual shrews. Heterozygosity testing results for *Sorex araneus* will be presented and the expectations and limitations of a low-coverage (2x) genome assembly will be discussed.

### Parental care in the common shrew, *Sorex araneus* L.

T. Demidova, V. Oleinichenko  
& N. Shchipanov

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia*

Time budgets, maternal behaviour and mating were studied in common shrews, using three over-wintered females and four over-wintered males. The females were caught pregnant in the wild and they produced their litters in enclosures. Females with litters were maintained in two-section outdoor enclosures, and males in one-section outdoor enclosures. The enclosures of males were linked to female enclosures through an additional one-section enclosure just after parturition. No copulation was observed. In the first two days after parturition, females spent almost all their time with their pups. On the 2<sup>nd</sup> day after parturition, females built their own separate nests and from that time periodically abandoned their litters for a long time. Overall, their activity included eating, moving around the enclosure, caring and feeding pups, and guarding an area. From the 10<sup>th</sup> day until the end of the experiment, the enclosures of the males were linked with those of the females and litters. The total time spent feeding was similar among females, but they differed in their periodicity of caring for pups. For example, one female visited her young frequently, another female much less so. The first female was more careful towards her pups but did not defend an area beyond several centimetres around the pup's nest. The second female was not a careful mother and she guarded the whole enclosure including the intermediate section and attacked males even in his section. Those attacks were so effective that we had to change the male. Pups were born blind, naked and with toes joined together. On the 11<sup>th</sup> day the toes separated, on the 18<sup>th</sup> day the eyes opened, and on the 26<sup>th</sup> day autonomous eating was observed. The first copulation of a yearling female was seen on the 40<sup>th</sup> day and after the 60<sup>th</sup> day all yearling females were found to be pregnant. Given that the litters were maintained in common enclosures, we can conclude that the maturation of yearling females was not suppressed by social interactions between mother and siblings.

This study was supported in part by grants of RFBR (05-04-49355) and INTAS 03-51-4030.

### Annual variability of the skeleton of the common shrew (*Sorex araneus*) from the hybrid zone between the Novosibirsk and Tomsk chromosome races

V.B. Ilyashenko & S.S. Onitschenko

*Department of Biology, Kemerovo State University, Kemerovo 650043, Russia*

A significant difference for a series of morphometric traits between shrews of the Tomsk and Novosibirsk chromosome races in the zone of their hybridisation has been described earlier (Polyakov *et al.*, 2002). In this report we analyse year by year variation of the same traits in the shrews from the hybrid zone and from pure race populations during 1998–2004. Altogether we examined more than 1500 skeletons of shrews from the Novosibirsk race (Akademgorodok), Tomsk race (Teletskoye Lake and the middle stream of the Tom River) and the hybrids of these two races. Patterns of year by year changes were found to be similar in populations of the same race but different between the races. Skeletons of hybrids were more variable in comparison with parental forms. In 2000 they revealed more similarity with the Novosibirsk race, while in 2004 – with the Tomsk race. The difference between shrews of the Novosibirsk and Tomsk races from the area of the hybrid zone was maximal in 1998–2000. Such dynamics can be explained by different reactions of shrews from different races to adverse climatic conditions.

In this analysis we have found that interracial difference was well preserved in this period and was not confounded by annual and/or seasonal variability.

The validity of using samples collected in different years for investigation of morphological divergence between shrews from different chromosome races will be discussed.

### Effects of genetic drift and selection in the Drnholec/Białowieża hybrid zone of the common shrew: molecular and morphological studies

K.A. Jadwiszczak, A. Banaszek  
& M. Ratkiewicz

*Institute of Biology, University of Białystok, 15-950 Białystok, Poland*

The Drnholec/Białowieża hybrid zone, localised in eastern Poland, is the most narrow described in the common shrew so far. Potential genetic differentiation between the Dn (specific metacentrics *hi*, *ko*, *gm*, *nr*) and Bi (*hn*, *ki*, *gr*, *mp*) races may result from differenti-

ation of these races in separate glacial refugia or it may be a consequence of reduced gene flow due to selection acting against hybrids forming 10-element chain configurations at meiosis I.

In order to give a detailed description of genetic differentiation between the Dn and Bi races we used both molecular markers (seven autosomal microsatellites, a Y-linked microsatellite and allozymes) and morphological measurements.

Analysis of molecular variance (AMOVA) showed little differentiation between the chromosome races for autosomal microsatellites ( $F_{CT}=0.00169$ ,  $p>0.05$ ), a Y-linked locus ( $F_{CT}=0.00000$ ,  $p>0.05$ ;  $R_{CT}=0.00698$ ,  $p>0.05$ ) and for allozymes ( $F_{CT}=0.01052$ ,  $p<0.05$ ). Nineteen cranial and skeletal measurements did not reveal significant differences between the Dn and Bi races, either. We suppose that a lack of molecular and morphological differentiation between the races results from a common glacial history.

Allozyme analysis showed that populations situated in the centre of the Dn/Bi hybrid zone were unstable and they were characterised by low  $N_c/N$  ratio (0.2–0.6). Next, analysis of microsatellites indicated that these populations experienced a bottleneck. Hence, it seems that any genetic differentiation between the Dn and Bi races resulting from a strong selection pressure against hybrids is obliterated by genetic drift caused by habitat instability.

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## The Oxford-Hermitage hybrid zone

R.M. Jones & J.B. Searle

*Department of Biology, University of York, PO Box 373, York YO10 5YW, UK*

There are several chromosome races of common shrew (*Sorex araneus*) in Britain characterised by different combinations of metacentrics and acrocentrics composed of the chromosome arms *k*, *n*, *o*, *p*, *q*, *r*. In this talk we define the Oxford race as characterised by metacentrics *kq* and *no* and the Hermitage race by metacentric *ko* and acrocentrics *n* and *q*. The chromosome arms *p* and *r* may occur in either a metacentric or acrocentric state. The Oxford and Hermitage races make contact in southern Britain and form a hybrid zone. Although this hybrid zone was already unknowingly described in the 1950s and was partially characterised in the 1980s, we present here the first description of the complete length of the hybrid zone, which runs 300 km from the Thames estuary westwards to the Severn estuary northwards to the Mersey estuary. A total of 1621 individuals from 210 sample localities have been karyotyped from the vicinity of this hybrid zone, making it one of the best characterised chromosomal hybrid zones. The hybrid zone can be described in terms of the clines

of frequency change in each of the metacentrics involved in the zone (*kq*, *no*, *ko*). The standardised cline widths for the Oxford race metacentrics *kq* and *no* are similar to each other (24 and 25 km) and greater than the cline width for *ko* (19 km). Along the whole length of the zone the Oxford race metacentrics have coincident clines which are staggered from the Hermitage race cline by 23 km on average. The cline centres of the metacentrics are in some cases localised at rivers or high ground. The roles of selection in generating these various characteristics of the Oxford-Hermitage hybrid zone are discussed.

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## Seasonal population dynamics in the common shrew *Sorex araneus* (Moscow race) in the southeast of the Tverskaya area

A. Kalinin, V. Oleinichenko, T. Demidova & N. Shchipanov

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia*

Data on 1181 *Sorex araneus* (4895 recaptures) obtained in the course of 10 years of monitoring are discussed. We distinguished three gradations of maximal population density: peak years =  $43.5 \pm 3.6$ , ordinary years =  $9.5 \pm 2.2$ , and  $2.1 \pm 0.7$  ind/ha under depression. The first young shrews were found on June 2. The numbers reached a maximum at the end of July in the years of peak numbers. In the years of ordinary numbers the maximum was observed at the end of August – early September. In the years of depression the maximum occurred at the end of September – October. The most substantial autumn decrease was found in the years of peak and ordinary population density. In all the years the numbers decreased in the late autumn to a value similar to the early spring numbers. The decrease in numbers through winter was low. Spring numbers was similar for all years while snow cover remained. The number of over-wintered individuals diminished substantially after the snow thawed, at a time when sexual maturation occurred simultaneously with moult. Maturation in females started a bit later and those individuals became mature only at the end of April. The number of adult females just after wintering in all the years was similar ( $3.4 \pm 1.3$  per 100 traps). In the peak years and in the years of regular population density the number of adult females in summer was almost identical ( $2.3 \pm 1.2$  versus  $2.3 \pm 0.8$  per 100 traps). Under depression this was lower ( $0.8 \pm 0.4$ ). A positive correlation of numbers in a given year and the summer numbers of over-wintered females ( $r=0.83$ ,  $p<0.05$ ) was found. First mature yearling females were found at the end of June. No mature males in their first calendar year

were found. Five percent of yearlings marked in June, 6% in July, and 8% from those marked in August were found in the next calendar year. The last pregnant females were found at the end of August. The longest life span for marked individuals was 14 months.

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### **Nonresident activity and dispersal in the common shrew, *Sorex araneus* L., with regard to the Moscow chromosome race**

**A.V. Kouptsov & N.A. Shchipanov**

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia*

Data on 1756 common shrews (Moscow race) marked in live-traps (7600 recaptures) and 353 individuals caught in pit-falls modified to be live-pits were obtained during long-term monitoring in the Southeastern corner of Tverskaya area. Patterns of nonresident activity such as pre-resident dispersal of yearlings, excursions, and nomadic activity in mature males were found. The incidence of these nonresident activities differed between years. It was found that in the same area at the same time nonresident individuals fall primarily into live-pits while residents regularly visited live-traps. The greatest proportion of nonresidents in the population was observed under population depression ( $2.1 \pm 0.7$  ind/ha) when it was 62.8%, while under ordinary population density ( $9.5 \pm 2.2$  ind/ha) the proportion of nonresidents equalled 41.7%, and under peak conditions ( $43.5 \pm 3.6$  ind/ha) nonresidence was 19.4%. The maximal capture rate of nonresidents as revealed in live-pits was found under ordinary density (22 ind/100 live-pits per day) with significantly lower values in years of population depression (18) and peak (16) density. Regarding the demography of dispersal, we found that on average 13.1% and 20.1% of over-wintered females and males, respectively, dispersed. The demography of nonresidents differed significantly ( $p < 0.01$ ) between years. In the years of peak population density the proportion of over-wintered females that dispersed was 3.7%, under ordinary density this proportion was 9.7% and under depression the proportion equalled 15.9%. The proportion of mature males that dispersed for those years was 22.2%, 16.8% and 21.4%, respectively. Social activity was tested for 114 shrews in 57 tests. Nonresidents displayed significantly less social activity compared to residents under conditions of population depression. Under peak population density nonresident individuals were more socially active. We regarded this as evidence of socially motivated dispersal under peak density.

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### **Climatic features of the modern area of *Sorex araneus* and the possibility for species survival in glacial refugia**

**V.N. Orlov, A.E. Balakirev & N.M. Okulova**

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia*

Common woodland rodents (*Clethrionomys glareolus* and *Microtus agrestis*) and *Sorex* sp. have been found in several regions of Eastern Europe and the Pre-Urals at the periphery of the glacial area at the maximum of the Late Valdai (Late Weichselian) glaciation (Markova *et al.*, 1995; Fadeeva, 2003). Conversely, such species have not been reported for the southern part of the Russian Plain (to the south of the Oka River) in that period.

These observations agree with available data on the natural processes during the Late Valdai glaciation. The annual precipitation in the extraglacial area decreased to 200 mm (as currently in modern semideserts!), while precipitation near the ice sheet boundary (West Dvina basin, Upper Volga basin, and south of the North Dvina basin) was higher.

In this communication, we consider the possibility of common shrew survival in glacial refugia. We made use of the method of "climatic fields" to analyse factors that limit the distribution of the common shrew. In East Europe and West Siberia the distribution area of the common shrew is exposed to an annual precipitation of 250-850 mm and annual mean temperature of  $-2.3^\circ\text{C}$  to  $+7.5^\circ\text{C}$ , but the microclimate depends on the relief. For example, in Mongolian mountainous forest steppe the annual precipitation and radiation may vary over wide limits according to relief.

It may be inferred from the data reviewed that the common shrew could inhabit some forest isolates at the periphery of the glacial area at the maximum of the Late Valdai glaciation.

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### **The annual cycle of the common shrew population in Western Siberia**

**V. Panov**

*Institute of Animal Systematics and Ecology, Russian Academy of Sciences, Novosibirsk 630091, Russia*

During 1991-2005 we examined abundance, reproduction, sex and age structure of a population of the common shrew (*Sorex araneus*) inhabiting a suburb of Novosibirsk city. Population number was assessed by capture efficiency of a series of trapping transects. Data



were plotted monthly. The reproductive season in shrews begins in the second half of April. Maturation of animals coincides with a rapid increase of body weight and size during a short period of time (10-15 days). A seasonal minimum in population number is observed in May, after the mating season but before the appearance of offspring. Then, population number grows continuously until the end of the summer. Overwintering females produce 2-3 and sometimes 4 litters. Some shrews born in spring and early summer take part in reproduction in the year of their birth. This group of animals makes a considerable contribution (about 30%) to population growth. The reproductive rate gradually decreases from the middle of August to the end of September. Population number is at a seasonal maximum at the end of August and then gradually decreases. The shrews that survived winter die first. We found none of them in October. The majority of animals which were born at the beginning of summer and took part in reproduction, die before November. After an abrupt decrease in population number in autumn, it remains at a relatively stable level during winter and only slightly decreases to spring. During the winter the population consists of young animals of small body mass (5-6 g), and size (60-64 mm).

### **Microscale analysis of the structure of the hybrid zone between the Novosibirsk and Tomsk chromosome races of the common shrew**

**A. Polyakov, M. Bukina & P. Borodin**

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

The hybrid zone between the Novosibirsk (*go, hn, ik, mp, qr*) and Tomsk (*gk, hi, mn, o, p, q, r*) chromosome races crosses the southern part of West Siberia. Earlier we reported that the position of this zone coincides with an altitude of 200 metres above sea level and that there is reduced gene flow between the races. In this report we are going to discuss the high resolution analysis of landscape structure within one of the sections of the hybrid zone under study. It seems that fragmentation of the forest habitat (where shrews live) by agricultural fields may decrease migration and thus generate narrow but important barriers to gene flow. Abrupt change in the frequencies of race specific chromosomes over distances of 300-400 metres supports the idea that local landscape structure may influence the structure of this hybrid zone.

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### **Effects of genetic drift and selection in the Drnholec/Białowieża hybrid zone of the common shrew: allozyme study**

**M. Ratkiewicz, K. Jadwiszczak & A. Banaszek**

*Institute of Biology, University of Białystok, 15-950 Białystok, Poland*

We investigated spatial and temporal aspects of population genetic structure in the Drnholec/Białowieża, or Dn/Bi hybrid zone in Poland.

About 450 individuals from nine populations were studied using allozyme electrophoresis. Significant changes in allele frequency data throughout time were recorded in the centre of the hybrid zone. Some hybrid populations were genetically unstable and were characterised by a low  $Ne/N$  ratio when compared to the other populations from the hybrid zone. Moreover, the spatial pattern of genetic variation differed among three temporal samples. We conclude that environmental instability in the centre of the hybrid zone is the most important factor responsible for changes in the genetic structure of the Dn/Bi hybrid zone. However, selection against hybrid individuals may also have an effect on the observed spatial and temporal patterns in this hybrid zone.

### **Chromosome microdissection, fluorescent *in situ* hybridisation and immunostaining in the cytogenetic study of the common shrew**

**N. Rubtsov & T. Karamysheva**

*Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk 630090, Russia*

For a long time chromosome studies on mammalian species have been performed with techniques developed for morphological analysis of mitotic and meiotic chromosomes, numerous types of banding, and the study of the synaptonemal complex. A drastic change in cytogenetics took place due to the development of new methods based on fluorescent *in situ* hybridisation (FISH), immunostaining, new types of fluorescence and confocal microscopy, and genetic engineering. Gene mapping, comparative chromosome analysis, studies on interphase, mitotic, and meiotic chromosomes and the architecture of the interphase nucleus as a whole, were performed as part of the new approach.

The power of new molecular cytogenetic techniques depends on the availability of DNA-probes, specific antibodies, cell cultures and general information on the genome of the species being studied. Numerous DNA-probes and specific antibodies have been obtained in



studies on human and mouse cells. Some of them appear to be suitable for shrew chromosome analysis. FISH with whole and partial human and mink DNA-probes were successfully used for detection of the homology between chromosomes of shrews and other mammals. Then the whole and partial chromosome paint probes of *Sorex araneus* and *Sorex granarius* were generated with metaphase chromosome microdissection followed by degenerate oligonucleotide-primed polymerase chain reaction (DOP-PCR). The sets of chromosome-specific paint probes of *Sorex araneus* and *Sorex granarius* were also obtained by DOP-PCR from flow-sorted chromosomes.

In spite of the special place in taxonomy provided by cytogenetical studies, investigation of mitotic and meiotic chromosomes in *Sorex araneus* and *Sorex granarius* plays an important role in modern cytogenetics. The karyotype of *Sorex araneus* is composed of almost identical chromosome arms but includes numerous chromosomal races that differ by the number and composition of banded chromosomes. As a result *Sorex araneus* provides unique possibilities for analysis of the influence of chromosome morphology on chromosome behaviour in meiosis and on nucleus architecture at interphase. Perspectives from the molecular cytogenetical studies of *Sorex araneus* and *Sorex granarius* are discussed.

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### **Ecological mechanisms of range formation for chromosome races of common shrews (*Sorex araneus* L.)**

**B.I. Sheftel**

*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia*

At the moment, about 70 different chromosome races of the common shrew (*Sorex araneus* L.) are known. We studied the spatial distribution of these races. It was shown that the size of their ranges varied substantially. We tried to analyse distinctions in distribution of chromosome races with different range sizes. We have shown that the races with a small range are situated most often in the central part of the total distribution of the common shrew, while races with a wide

range occupied the Southern and Eastern peripheries of the common shrew total distribution. We analyse the role of geographical barriers in the formation of borders between races. It was shown that large rivers (with width more than 800 m) practically always served as race borders. We analysed the ecological conditions of race borders in places where a visible geographical barrier was absent. The role of ecological factors in race border formation is especially important when hybridisation between races is limited. In such cases contact zones could only be formed in very rich habitats. The productivity of these areas should be higher than in neighbouring regions inhabited by only one race. This is the case with limited hybridisation because the races behave as two different species. For the sympatric co-existence of two very close species additional resources are necessary.

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### **Hybrid zone evolution in space and time: the case of the *S. antinorii* - *S. araneus* hybrid zone in the Swiss Alps**

**G. Yannic, P. Basset & J. Hausser**

*Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland*

After the Pleistocene glaciations, the Alps influenced the post-glacial recolonisation of Europe and represent a suture zone between differentiated populations or species. Such a suture zone is now well studied in the Swiss Alps where two species of the *Sorex araneus* group form a hybrid zone. Here we propose an analysis of the evolution of a hybrid zone in space and time, ten years after its initial study. By analysing the distribution of several microsatellites markers and by using the assignment method, we determine genetically the taxonomic status of each individual, the localisation of *S. antinorii*, *S. araneus* or sympatric populations, the hybrid zone centre and finally the level of introgression. Results are compared with those previously reported.

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