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The distributions of telomeric and ribosomal DNA on the chromosomes of two closely related species, *Sorex araneus* and *Sorex granarius* (Soricidae, Eulipotyphla)

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ABSTRACT. It is widely believed that Robertsonian rearrangements have played a key role in the chromosome evolution of species of the *Sorex araneus* group. We present FISH data relating to the distribution of telomeric repeats and 18S rDNA on the chromosomes of *Sorex araneus* and *Sorex granarius*, which have karyotypes with almost identical chromosome arms. All chromosomes in *S. araneus* (Novosibirsk race) are metacentrics, whereas *S. granarius* has an acrocentric karyotype with two metacentric exceptions. In FISH experiments we revealed telomeric repeats at the ends of all *S. araneus* chromosomes but only on the short arms of *S. granarius* acrocentrics, which, as we have shown earlier, amount up to 300 kb in length. FISH signals of the (TTAGGG)n probe and the probe derived by microdissection of the pericentric regions of *S. granarius* acrocentrics *a* and *b* were co-localised or sequentially localised on distinct chromatin fibres of *S. granarius*. 18S rDNA clusters were found at the ends of short arms of 12 out of 16 *S. granarius* acrocentric pairs. In *S. araneus* primary cell culture fibroblasts rDNA was found at the ends of the *q*, *t* and *u* arms. However, after long cultivation of these cells an additional FISH signal of rDNA was found at the distal end of the *o* arm of chromosome *go*. In some regions the FISH signal of rDNA coincided with the signal of the telomeric probe. We suppose that rapid concerted evolution of telomeric and rDNA led to the repatterning of these repetitive DNA fractions in the sibling species *S. araneus* and *S. granarius* as well as the formation of "large" telomeres with unusual structure at the ends of the *S. granarius* chromosomes.

KEY WORDS: Shrew chromosomes, FISH, large telomeres, ribosomal DNA.

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Распределение теломерной и рибосомальной ДНК на хромосомах двух близкородственных видов, *Sorex araneus* и *Sorex granarius* (Soricidae, Eulipotyphla)

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РЕЗЮМЕ. Полагают, что Робертсоновские перестройки играли важную роль в эволюции кариотипов видов группы *S. araneus*. В этой связи проанализированы данные о распределении теломерных повторов и 18S рибосомальной ДНК в хромосомах двух видов-двойников, *Sorex araneus* и *Sorex granarius*, чьи кариотипы составлены из практически идентичных плеч. Все хромосомы *Sorex araneus* (Новосибирская раса) являются метацентриками, тогда как кариотип *Sorex granarius* является полностью акроцентрическим, за исключением двух пар метацентриков. Теломерные повторы были выявлены на концах всех хромосом *S. araneus*, а в хромосомах *S. granarius* только на концах коротких плеч акроцентриков, где они достигают размера 300 т.п.н. Используя пробу к теломерным повторам и микродиссекционную пробу к перицентромерным районам хромосом *a* и *b S. granarius,* мы выявили ко-локализацию и последовательную локализацию сигналов этих ДНК проб на хроматиновых фибриллах *S. granarius*. Кластеры 18S рДНК были обнаружены в коротких плечах 12 из 16 пар акроцентриков *S. granarius* и на концах длинных плеч *q*, *t* и *u* у *S. araneu*s. Однако при длительном культивировании фибробластов одной из особей *S. araneus* дополнительные кластеры 18S рДНК были выявлены в дистальной части плеча *o* хромосомы *go*. На некоторых хромосомах сигналы FISH теломерной и рДНК совпадали. По-видимому, быстрая амплификация и перераспределение теломерной и рДНК в хромосомах *S. araneus* и *S. granarius*, а также формирование «длинных» теломер с необычной структурой в коротких плечах акроцентриков *S. granarius* является следствием совместной эволюции этих типов повторов в ходе недавней реорганизации кариотипов землероек.

КЛЮЧЕВЫЕ СЛОВА: хромосомы землеройки, FISH, длинные теломеры, рибосомная ДНК.

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Introduction

Numerous data show that repetitive sequences including telomeric and ribosomal DNA can be involved in the evolution of mammalian chromosomes. The size of telomeric and rDNA clusters is, to a large extent, genetically determined (Zhu *et al*., 1998; Manning *et al*., 2002). (TTAGGG)n repeats are located mainly at the chromosome termini in so called telomeres and preserve the integrity of the cell genome, while telomere shortening or erosion leads to chromosomal instability and rearrangements. As well as telomeres, (TTAGGG)n have been found at interstitial chromosome sites (ITs) (Meyne *et al*., 1990). ITs can be the remnants of ancestral chromosome fusions (Azzalin *et al*., 2001; Ruiz-Herrera *et al*., 2002; Hartmann & Scherthan, 2004) and can increase chromosomal instability where they occur (Mondello *et al*., 2000; Kilburn *et al*., 2001; Rivero *et al*., 2004). The presence of telomeric repeats can probably lead to chromosome rearrangements in both directions: fusions and fissions. rDNA is also often involved in chromosome reorganization. Closely related species and even chromosome races of the same species differ in number and location of rDNA clusters (Dobigny *et al*., 2003). Nevertheless, only scanty information is available on the role and mechanisms underlying the redistribution of telomeric and rDNA during chromosomal evolution.

The fusion of acrocentrics (Robertsonian fusion) and the reverse process (Robertsonian fission) are among the most common rearrangements which took place during karyotypic evolution in mammals. Thus in the *Sorex araneus* group they played an especially important role (Wójcik & Searle, 1988; Searle, 1993). The study of repetitive DNA in the vicinity of evolutionary breakpoints may elucidate the mechanisms of Robertsonian (Rb) rearrangements.

Here we present data on the distribution of telomeric repeats and rDNA on chromosomes of two closely related species: *Sorex araneus* (Novosibirsk race) and *Sorex granarius* that diverged a few hundred thousands years ago (Taberlet *et al*., 1994). Their karyotypes have almost identical chromosome arms, differing only in the number of metacentrics (Wójcik & Searle, 1988). The comparative study of *S araneus* and *S. granarius* chromosomes provides an opportunity to clarify the role of repetitive DNA in karyotype evolution of mammals.

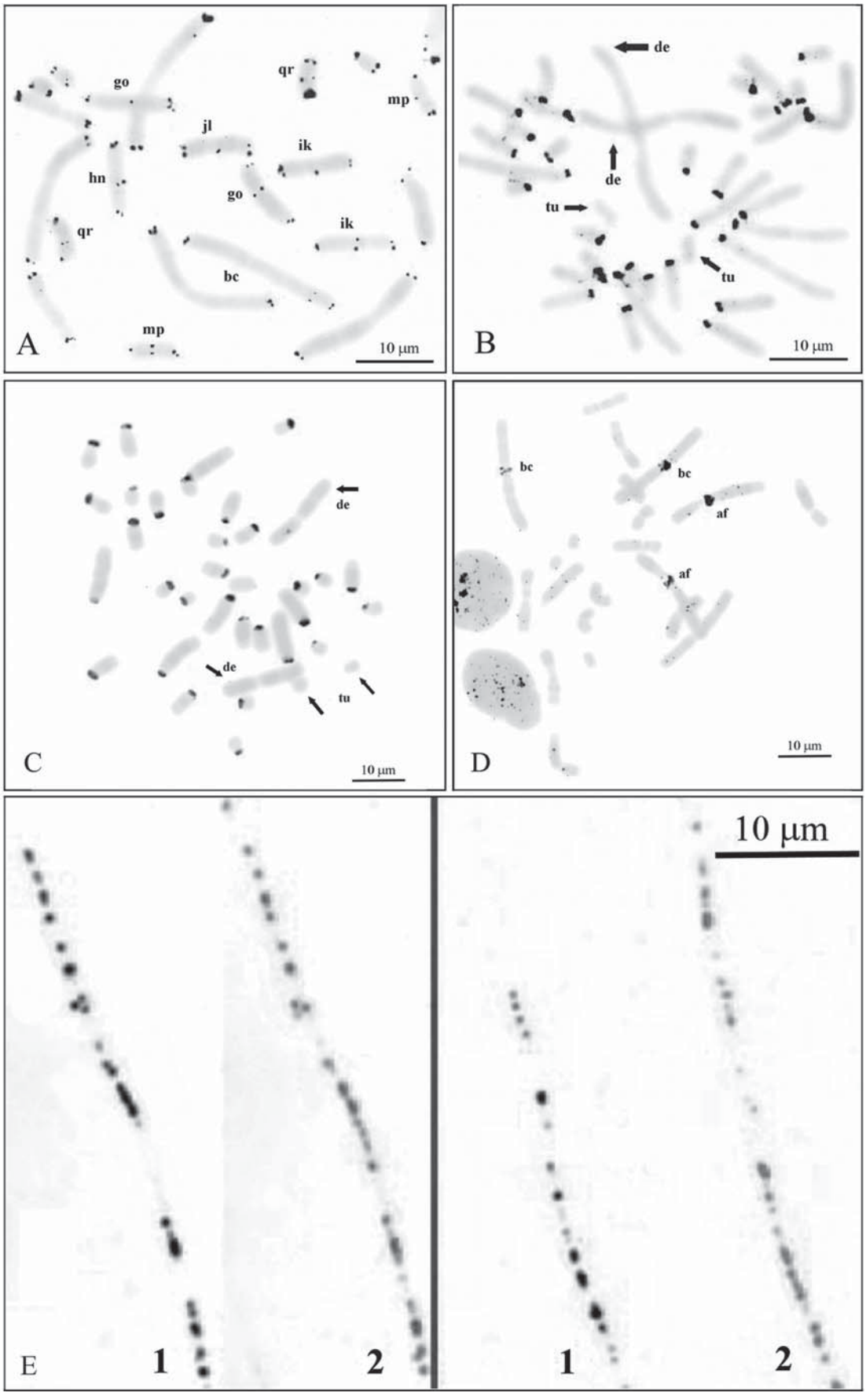
This paper summarises and extends upon the findings of a previously published work by Zhdanova *et al*. (2005).

Material and methods

The *S. araneus* and *S. granarius* primary fibroblast cell cultures were obtained from pieces of intercostal muscles. Metaphase chromosomes and distinct chromatin fibres for FISH and chromosome microdissection were prepared by standard techniques. A microdissected DNA probe was generated by DOP-PCR with the MW6 primer, and subsequent DNA labelling with biotin-16-dUTP or digoxigenin-11-dUTP was performed over additional PCR cycles (Rubtsov *et al*., 1996). The DNA probe used for detection of 18S rDNA (rDNA probe) was a 3.2-kb fragment of human 18S rDNA in pHr13 (Malygin *et al*., 1992). It was labelled with biotin-16-dUTP by nick translation. To visualize clusters of telomeric repeats the (TTAGGG)n probe labelled with biotin-11-dUTP (Ijdo *et al*., 1991) was used. FISH was performed according to a standard protocol with salmon sperm DNA as a carrier DNA. Biotin- and digoxigenin labelled probes were visualized with avidin-FITC and mouse antidigoxigenin antibodies conjugated to Cy3, respectively. Two-colour FISH with telomeric and microdissected DNA probes on distinct chromatin fibres was performed with suppression of dispersed repeats with shrew Cot1 DNA. Metaphase chromosomes and distinct fibres were counterstained with 4',6-diamidino-2-phenylindole (DAPI) and analyzed using an Axioskop 2 Plus microscope (Zeiss, Germany) equipped with a CCD camera (CV M300, JAI Corporation, Japan), CHROMA filter sets, and the ISIS4 image-processing package of Metasystems GmbH in the Microscopic Centre of the Institute of Cytology and Genetics SB RAS, Novosibirsk.

According to the nomenclature for *S. araneus* and *S. granarius*, the karyotypes in these species consist of chromosome arms named *a – u* in decreasing order of size (Searle *et al*., 1991). Thus, in biarmed chromosomes the first letter denotes the long arm and the second corresponds to the short arm. Arm *e* is the homologue of the original mammalian X chromosome. The females are XX (*de, de*) and the males are XY_1Y_2. The Y_1 is the true Y chromosome, whereas the Y_2 is autosomal arm *d* (Pack *et al*., 1993). The Novosibirsk race of *S. araneus* shows metacentrics: *af*, *bc*, *go*, *hn*, *ik*, *jl*, *mp*, *qr* and *tu* (Wójcik *et al*., 2003). In *S. granar-*

Figure 1. FISH on *S. araneus* (A) and *S. granarius* (B) chromosomes using a biotinylated telomeric probe generated by PCR. Chromosomes counterstained with DAPI. The *S. araneus* chromosomes on which ITs were detected are indicated. Metacentric chromosomes of *S. granarius* on which telomeric signals were not detected are indicated by arrows. FISH on *S. granarius* (C) and *S. araneus* (D) chromosomes, using a microdissected probe derived from the pericentric regions of six copies of the *S. granarius* chromosomes *a* and *b*. Chromosomes counterstained with DAPI. The *S. araneus* chromosomes on which signals were detected and metacentric chromosomes of *S. granarius* on which no signals were detected are indicated. Two-colour FISH (E) on *S. granarius* distinct chromatin fibres. The same fibres painted by biotinylated telomeric probe generated by PCR (1) and digoxigenin-11-dUTP labelled microdissected probe generated from the pericentric regions of six copies of *S. granarius* chromosomes *a* and *b* (2).


A
go
qr
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jl
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10 µm
B
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C
de
de
tu
10 µm
D
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bc
af
af
10 µm
E
1
2
10 µm
1
2

ius, only two pairs are metacentrics: *de* and *tu*. Other chromosomes are acrocentrics. The GTG-banding patterns of the chromosome arms of the two species are nearly identical (Wójcik & Searle, 1988; Volobouev & Dutrillaux, 1991).

Results and discussion

Distribution of telomeric repeats on chromosomes of *S. araneus* and *S. granarius*

FISH with the telomeric DNA probe gave distinct signals at all telomeres of the chromosomes of *S. araneus*. Signals corresponding to ITs were observed mostly at the pericentric regions of metacentrics *go*, *hn*, *ik*, *jl*, *mp* and *qr*. The frequencies of FISH signals at ITs varied from 29% for chromosome *jl* to 81% for chromosome *mp*. However, in pericentric regions of metacentrics *af*, *bc*, *de* and *tu*, the frequencies of signals did not exceed 10%. In addition, signals were also detected on arms *a* and *b* of chromosomes *af* and *bc* with frequencies of 19% and 12%, respectively (Fig. 1A).

Sorex araneus displays a surprising degree of chromosomal variation due to Robertsonian fusions. Only metacentrics *af*, *bc*, *de* and *tu* were present in the common ancestor of all races of *S. araneus.* These metacentrics were formed before race formation (Wójcik *et al*., 2003). The FISH experiments showed that the number of TTAGGG repeat copies at pericentric regions of these "old" metacentrics is lower than those of other biarmed chromosomes *go*, *hn*, *ik*, *jl*, *mp* and *qr* (see also Zhdanova *et al*., 2005). The latter are "younger". They originated from acrocentrics during chromosomal race formation. Metacentric *jl* is "younger" than *af*, *bc*, *de*, and *tu*, but "older" than *go*, *hn*, *ik*, *mp* and *qr*, since it is found in all races of *S. araneus* but absent in other species of the *S. araneus* group. The chromosome *jl* has more copies of telomeric repeats at the pericentric region than "old" metacentrics but less than chromosomes *go*, *hn*, *ik*, *mp* and *qr.* The data obtained are most easily explained by the retention of (TTAGGG)n repeats after Robertsonian fusion in *S. araneus,* and by the loss or modification of telomeric repeats with time. It has been shown that in some mammalian species telomeric DNA is directly involved in Rb translocations (Metcalfe *et al*., 1998; Slijepcevic, 1998; Castiglia *et al*., 2002). Contrary to that, in the house mouse breakpoints associated with Rb translocation are localized within subtelomeric regions containing sat-DNA (Garagna *et al*., 2002). Probably Rb fusions can be the result of nonhomologous crossing over within telomeric or subtelomeric chromosomal regions enriched with repetitive DNA.

In *S. granarius* FISH with a telomeric probe showed strong signals only on the short arms of acrocentrics (Fig. 1B). Earlier we showed that the short arms of acrocentrics contain telomeric repeats up to 300 kb in length (213 kb on average), while the other telomeres were on average 3.8 kb in length (Zhdanova *et al*., 2005). To our knowledge, telomeres about 300 kb in size have not hitherto been described in mammals. The longest telomeres previously detected (up to 150 kb) were found in some strains of laboratory mice. However, the size of telomeres in wild mice (*M. musculus* and *M. spretus*) does not exceed 25 kb and 5–15 kb, respectively. It is believed that inbreeding can result in the elongation of mouse telomeres by means of an unknown mechanism (Zijlmans *et al*., 1997; Zhu *et al*., 1998, Manning *et al*., 2002). Small differences in telomere lengths between the long and short arms of mammalian chromosomes have been described previously, and longer telomeres are usually located on the long arms of chromosomes (Zijlmans *et al*., 1997; Slijepcevic, 1998). Trying to explain this phenomenon, Slijepcevic (1998: 136–140) suggested that the difference in telomere size is caused by competitive telomere/centromere relations at the "bouquet" stage of meiosis. At this stage high tension and breakages in regions between telomeres and centromeres can be generated when long telomeres are located in short arms. The telomere organization in *S. granarius* does not agree with this hypothesis.

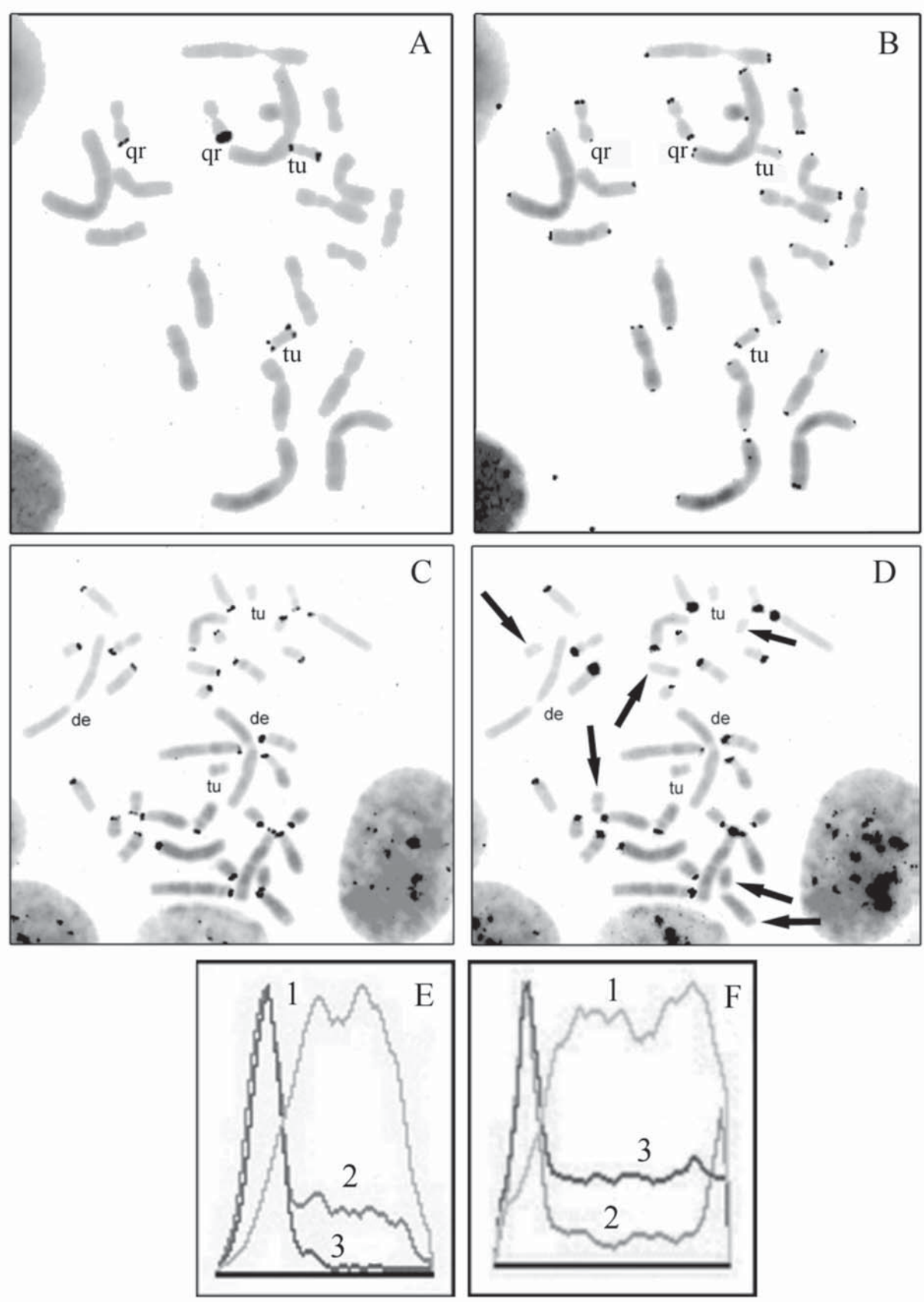
FISH on metaphase chromosomes and distinct chromatin fibres using telomeric and microdissected DNA probes

A microdissected probe was generated from 6 copies of the pericentric regions of *S. granarius* chromosomes *a* and *b*. In *S. granarius* it painted the regions which were also detected by the telomeric DNA probe (Fig. 1C) whereas in *S. araneus* chromosomes it only painted the pericentric regions of arms *a* and *b* of *af* and *bc* (Fig. 1D). Two-colour FISH on distinct chromatin fibres of *S. granarius* revealed regions painted either with telomeric and microdissected probes or only with one of them (Fig. 1E).

Distribution of 18S rDNA sequences on *S. araneus* and *S. granarius* chromosomes

In *S. araneus* fibroblasts from primary cell cultures, 18S rDNA was revealed at the ends of the *q*, *t* and *u* arms of chromosomes *qr* and *tu* (Fig. 2A). However, additional clusters of rDNA at the ends of the *o* arms

Figure 2. Two-colour FISH on *S. araneus* (A, B) and *S. granarius* (C, D) chromosomes, using biotinylated probe of 18S rDNA (A, D) and digoxigenin-11-dUTP labelled telomeric probe (B, C). Typical profiles of relative signal intensities along acrocentric *m* chromosome of *S. granarius* (E) and *qr* chromosomes *S. araneus* (F) from the proximal telomere (left) to the distal telomere (right). The maximum signal in the analysed image is given as 100%. 1 — DAPI staining of chromosome; 2 — profile of 18S rDNA probe; 3 — profile of telomeric probe.


A
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were revealed after long (about one year) cultivation of these cells. Previously, Ag-positive material was found at the ends of the *q*, *t*, *o* and *u* arms of several races of *S. araneus* (Olert & Schmid, 1978; Halkka & Söderlund, 1987). It is known there is a polymorphism for the size of NOR regions between animals belonging to the same species. It seems that the block of 18S rDNA on the *o* arm of the Novosibirsk race karyotype of *S. araneus* is too small to be revealed by FISH with the rDNA probe used. However, long cultivation of cells led to amplification of rDNA and increased the number of rDNA copies revealed by FISH.

In contrast, 18S rDNA in *S. granarius* was revealed on the short arms of 12 acrocentric pairs, and no FISH signals for the rDNA probe were observed on chromosomes *de*, *tu*, *p*, *o*, *q* and *r* (Fig. 2D). In some chromosomes rDNA was localized in the same regions as clusters of telomeric repeats, while in the others rDNA and clusters of telomeric repeats were ordered one after another (Fig. 2 E–F). An intermediate pattern in their distribution was also found.

Coming back to the results obtained in the study of *S. granarius* "large" telomeres using the microdissected DNA probe, it should be noticed that according to the probe preparation it could contain various DNA sequences including telomeric, rDNA and other repeats. However, FISH with this probe gave no signal in telomeric- and 18S rDNA positive sites on *S. araneus* chromosomes. This means that the telomeric and rDNA are only a minor fraction of the microdissected DNA probe. It seems that pericentric regions of *S. granarius* acrocentrics are enriched not only with telomeric repeats and rDNA but also with other repetitive sequences.

Based on comparative chromosome analysis it has been suggested that the *S. granarius* karyotype is similar to that ancestral for the *S. araneus* group (Wójcik & Searle, 1988; Volobouev & Dutrillaux, 1991). However, reexamination of the phylogenetic relationships within the Soricidae, using methods of molecular phylogeny, revealed that *S. granarius* is the nearest relative to *S. araneus* among the species of the *S. araneus* group (Taberlet *et al*., 1994). These results allowed us to define more exactly the ancestral karyotype for species of the *S. araneus* group and to suggest that it includes at least four metacentric chromosomes *af*, *bc*, *de*, and *tu*. In this case, acrocentrics *a*, *b, c* and *f* in the *S. granarius* karyotype should be the result of fissions of ancestral metacentrics (Taberlet *et al*., 1994). The fissions apparently resulted in the formation of new telomeres on "newborn" acrocentrics, global reorganization of chromosomal termini and spatial nuclear organization. Telomeric repeats and rDNA should have played an important role in this process.

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