Chromosomal evolution
and phylogenetic relationships
of the *Sorex araneus-arcticus* species group

BY

V. VOLOBOUEV and B. DUTRILLAUX[1]

Summary.–VOLOBOUEV V. and DUTRILLAUX B., 1991. Chromosomal evolution and phylogenetic relationships of the *Sorex araneus-arcticus* species group. *In*: J. HAUSSER, ed. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat. 19.1*: 131-139.

Comparative chromosome banding data for six species of the *araneus-arcticus* group (Insectivora, Soricidae) are considered in the context of available biochemical, molecular, paleontological and biogeographical set of data. A new hypothesis about their origin and phylogenetic relationships is put forward.

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Les données du marquage chromosomique de six espèces du complexe *araneus-arcticus* (Insectivora, Soricidae) sont considérées dans le contexte des données biochimiques, moléculaires, paléontologiques et biogéographiques. Une nouvelle hypothèse sur leur origine et leurs relations phylogénétiques est proposée.

Among the shrews of the genus *Sorex*, 8 species at least possess a pecular sex chromosome complement in the male: XY_1Y_2. This formula, which results from a X-autosome translocation, was first described in *Sorex araneus* (SHARMAN 1956). These species are now known under the name of *araneus-arcticus*, or *Sorex araneus* species group or XY_1Y_2 group (FEDYK and IVANITSKAYA 1972, KRAL and IVANITSKAYA 1973, MEYLAN and HAUSSER 1973).

[1]C.N.R.S.-U.R.A. 620, Structure et Mutagenèse chromosomiques, Section de Biologie, Institut Curie, 26 rue d'Ulm, F-75231 Paris Cédex 05, France··

Since the rearrangement leading to the XY_1Y_2 formula is presumed of a very rare occurrence, a common origin of all these species is strongly suspected. This interpretation was confirmed by further cytogenetic, biochemical and molecular data (GEORGE 1984, CATZEFLIS 1984, 1987, VOLOBOUEV and CATZEFLIS 1989, VOLOBOUEV 1989), which all indicate a monophyletic origin of the Sorex araneus species complex. However, our knowledge about phylogenetic relationships within this group remains rather limited.

The only complete hypothesis on the general pattern of speciation and dispersal of araneus-arcticus species group was put forward in the absence of any biochemical and chromosomal data (HOFFMANN and PETERSON 1967). According to this hypothesis, shrews ancestral to the araneus-arcticus group appeared in Eurasia around the early or mid Pliestocene. In the Mindel period (400,000-500,000 b.p.) these shrews colonized North America via Beringian bridge where, being isolated, they evolved into typical S. arcticus whose fossils are known from Irwingtonian and Rancholabrean sites (KURTÉN and ANDERSON 1980 cited by JUNGE et al. 1983). During the Riss (Illinoian) period (110,000-250,000 b.p.), one population of S. arcticus inhabited the Beringian tundra refugium, giving rise to the North American and Siberian subspecies of S. tundrensis. As for the Euroasian lineage of this ancestral shrew, it evolved into S. araneus during the Riss-Würm period.

After a revision of available chromosomal, biochemical, paleontological and biogeographical data for the araneus-arcticus species group, a new hypothesis about their origin and phylogenetic relationships is put forward.

CHROMOSOMAL DATA

At present 6 out 8 species of the Sorex araneus group were studied with at least one chromosome banding technique (R- or G-). Due to the correspondance between these two different types of banding established for S. araneus (VOLOBOUEV and CATZEFLIS 1989) and taking into account the homologous banding patterns found between S. araneus and other species of the group (VOLOBOUEV 1983, 1989, ZIMA 1991), all these data could be compared and summarized in Table 1.

Comparative analysis of banded chromosomes in 6 species of araneus-arcticus group revealed a high level of homoeology. In most cases, the differences between species could be attributed to Robertsonian translocations. Other differences were interpreted as either telomere-centromere translocations, centromeric shifts or pericentric inversions. The reconstruction of the chromosomal phylogeny is not univocal for several reasons. Firstly, this group of species has not yet been compared to more distantly related species or genera among Insectivora. This makes impossible to know which chromosomes can be regarded as ancestral. Secondly, the Sorex group possesses chromosomes or chromosome arms which are not shared by other Mammals. This situation is quite different from that of Primates, Lagomorpha, Carnivora and Rodentia, for which it is possible to select

Table 1.–Comparison of chromosomes and chromosome arms of six species of the *Sorex araneus* group.

SGR	SAR[1]	SCO	SDA[2]	SAM	STU[3]
1	2q (*a*)	1q	1q	2	3pq
2	1q (*b*)⁻	3pq	2q	prx 1q	11q;1q
3	1p (*c*)⁺	2q	3q	5	11p;10p;2q
4	2p (*f*)	1p	1p	prx 3q	9p;8pq
5	4q(*g*)	4q	3p	dis 4	7pq
6	3p (*h*)	9pq	2p	6	14;4q
7	3q (*i*)	2p	6	7	1p
8	5q (*j*)	5q	5	8	2p
9	6p (*k*)	7q	7	9	5q
10	5p (*l*)	6q	4q	10	6q
11	4p (*m*)	8q	4p	11	4p
12	7q (*n*)	6p	8	dis 1q	5p
13	7p (*o*)	5q	12pq	dis 3q	9q
14	8 (*p*)	4p	9	12	13
15	8 (*q*)	7p	13pq	13	6p
16	6p (*r*)	8p	10pq	prx 4	10q
17p	9p (*u*)	10p	11p	3p	12p
17q	9q (*t*)	10q	11q	1p	12q

[1] In brackets: letter nomenclature of the chromosomes of *S. araneus*

[2] Data from ZIMA (1991)

[3] Data from VOLOBOUEV (1983)

species with very similar chromosomes (DUTRILLAUX *et al.* 1982), and thus reconstruct common ancestral chromosomes. This probably indicates that shrews possess chromosomes which have undergone a very complex evolution. Thirdly, the comparison of the chromosomes of the 6 species of *Sorex* leads to the reconstruction of various phylogenies among which 2 are about equiprobable.

The first reconstruction based on the fact that *S. granarius* possesses many acrocentric chromosomes which correspond to chromosome arms in other species. Thus, a first possibility is that *S. granarius* has retained an ancestral karyotype. Then, using the parsimomy principle, the phylogenetic relationships exhibited in Figure 1 can be proposed. In this scheme, 43 chromosomal rearrangements at least are necessary, all but one being proper to a single species. A common trunk for *S. araneus*, *S. coronatus* and *S. daphaenodon* is determined by a common Robertsonian translocation.

A second possibility is that no living species has conserved the ancestral karyotype, which would have been composed of more chromosomes (46 versus 36) than the karyotype of *S. granarius*. The first diverging branch would lead to *S. tundrensis*, which would have accumulated 8 Robertsonian translocations (Fig. 2). Then, a common trunk for other species would have existed, after which *Sorex arcticus maritimensis* would have first diverged, followed by *S. granarius* and lastly, the trifurcation of the 3 other species.

This scheme requires 42 chromosomal rearrangements, a number very close to that of Figure 1.
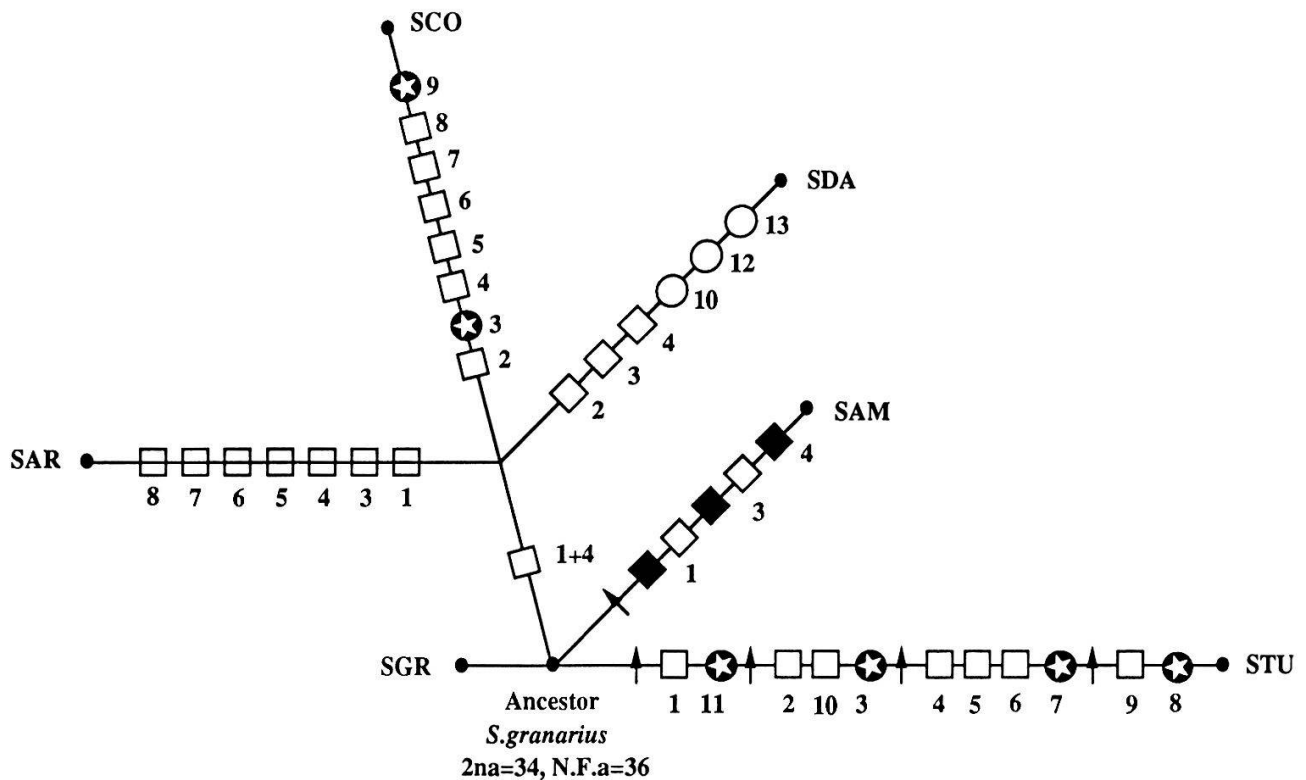
Figure 1.–Scheme of chromosomal evolution of the species of *araneus-arcticus* group in the hypothesis that the karyotype of *S. granarius* is ancestral and characterized by 2Na = 34 and NFa = 36. STU = *S. tundrensis*, SAM = *S. arcticus maritimensis*, SGR = *S. granarius*, SAR = *S. araneus*, SCO = *S. coronatus*, SDA = *S. daphaenodon*. Open squares, Robertsonian translocations; closed squares, tandem translocations; stars within closed circles, centromeric shifts; open circles, pericentric inversions; arrows, fissions. The numbers on the common trunks correspond to chromosomes of *S. granarius*.
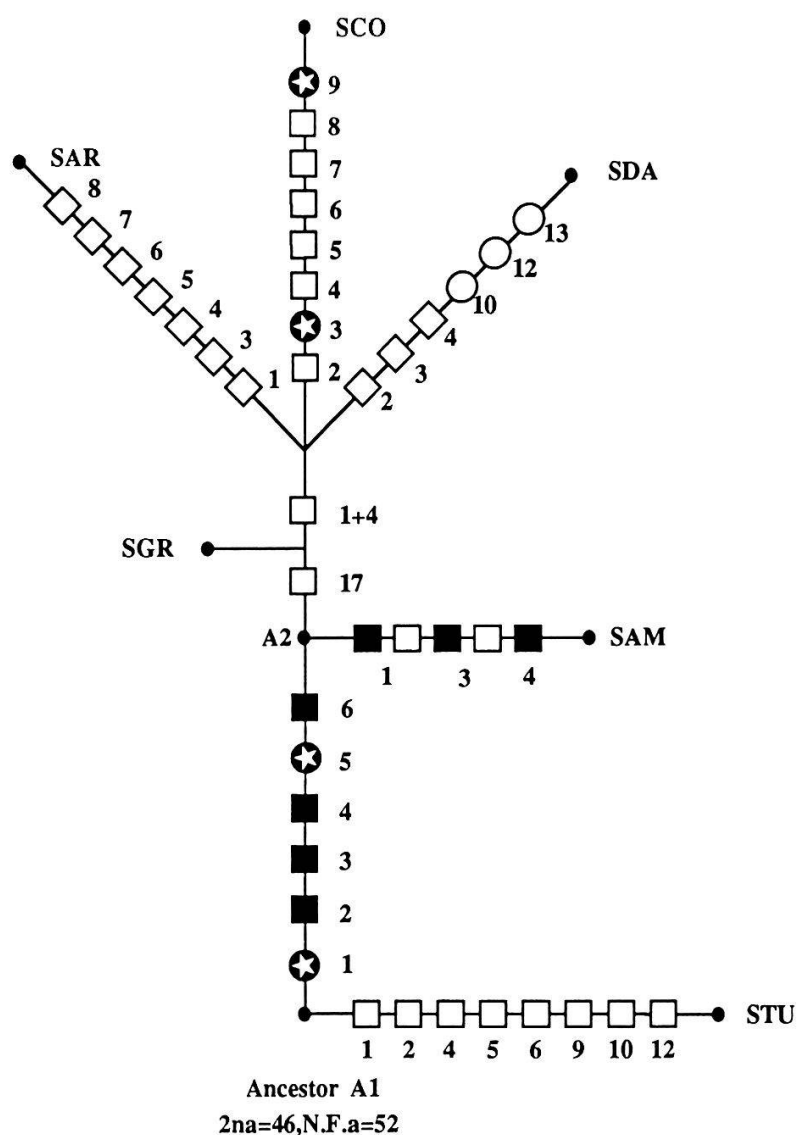
Figure 2.–Scheme of chromosomal evolution of the species of *araneus-arcticus* group in the hypothesis of a "*tundrensis*"-like ancestor characterised by 2na = 46 and NF.a = 52. The symbols are the same in Fig. 1. The numbers on the common trunk correspond to chromosomes of *S. granarius*.

Finally, the choice between the 2 schemes is quite difficult, although indirect arguments suggest that the second one is most likely:

–the chromosomal rearrangements are, on the average, simpler in scheme 2 than in scheme 1, being almost limited to Robertsonian and end-to-end translocations.

–the chromosome number of the presumed ancestral *Sorex* karyotype is closer to that of other mammals (about 60, RUMPLER and DUTRILLAUX 1986) in scheme 2 (46) than in scheme 1 (36).

–the hypothesis that the ancestral karyotype remained strictly unchanged in a given species, such as *S. granarius*, is not very likely.

As we shall see, this interpretation of chromosome data is supported by other available data.

BIOCHEMICAL AND MOLECULAR DATA

Biochemical and molecular data are available for five species of the *Sorex araneus* group. The study of electrophorectic variation of 22 loci encoding for enzymes in 11 populations belonging to 6 european shrew species, among which, *S. araneus*, *S. coronatus*, and *S. granarius* revealed that they are genetically very uniform. The genetic distances within this group are of the same order than that generally observed in mammals at intermediate stage of speciation process (CATZEFLIS *et al.* 1982, CATZEFLIS 1984). Further DNA-DNA hybridization experiments revealed that the nuclear genomes of *S. araneus* and *S. coronatus* are more than 99 % identical (CATZEFLIS 1987). Thus, these very close relationships between european species of the *S. araneus* group implies that their speciation is a recent phenomenon.

The study of GEORGE (1984) is of special interest because among 26 Soricid species studied there were two Nearctic (*S. arcticus* and *S. tundrensis*) and one Palearctic (*S. araneus*) species belonging to *araneus-arcticus* group. This author proposed a cladogram separating most Nearctic from Palearctic species. All Palearctic species share a common trunk together with 2 Nearctic species *S. tundrensis* and *S. arcticus*. These two last species in turn form a separate clade with *S. araneus*, and afterwards underwent a trichotomy. This interpretation favoured a monophyletic origin of Palearctic and Nearctic species of *araneus-arcticus* group.

PALEONTOLOGICAL DATA

Despite the relatively frequent occurrence of Soricid fossil records their interpretation must be taken into account cautiously, especially for *Sorex araneus* species group whose morphological analysis remains very difficult because overlaping characters.

HOFFMAN and PETERSON (1967) related the origin of a shrew ancestral to the *araneus-arcticus* group with *S. cf. praearaneus* from the early Pleistocene of Europe (KOWALSKI 1959). However, according to ZEUNER (1959) the ancestral shrew evolved into modern *S. araneus* much more recently, during the late Pleistocene (Riss-Würm), thus not earlier than 110,000 b.p. Undoubtedly dated fossil records are available for two species of the group. *S. arcticus* known from Pleistocene deposits dating back to the Illinoian, i.e. ca 250,000 b.p. (HIBBARD 1963) and *S. tundrensis* whose relict population from Maneron island is known from the early Pleistocene, not later than 700,000 b.p. (KAPITSA 1963, MASAO *et al.* 1968 cited by OKHOTINA 1983).

BIOGEOGRAPHICAL DATA

By their geographical distribution the species of the *araneus-arcticus* group are very different. Some of them, namely *S. granarius* and *S. coronatus*, are characterized by a West European distribution. *S. araneus* is spread over all Europe up to Siberia but the triangular configuration of its distribution area (with a base at the West Europe and a summit in Siberia) suggests that this species is also typical western Palearctic with a relatively recent eastward expansion which now is going (YUDIN 1989). At contrast with these three species *S. daphaenodon* is a typical eastern Palearctic species whose western limit of distribution passes by Ural mountains (YUDIN 1989).

The tundra shrew *S. tundrensis* is one of the few mammalian species characterized by Holarctic distribution although its Nearctic part is limited by Alaska and Yukon territory (VAN ZYLL DE JONG 1983). The arctic shrew *S. arcticus* is a purely Nearctic species.

HYPOTHETICAL SPECIATION AND DISPERSAL PATTERN OF THE *ARANEUS–ARCTICUS* SPECIES GROUP

Taking into consideration the chromosomal, biochemical and paleontological data presented here, a scheme of phylogenetic relationships within the *araneus-arcticus* group different from that proposed by HOFFMANN and PETERSON (1967) may be put forward. The karyotype of Palearctic *S. tundrensis* seems fairly close to that of the presumed ancestral karyotype A1 (Fig. 2) and the branch leading to the tundra shrew apparently separated first from the ancestral stock of the *araneus-arcticus* group. This conclusion is in good agreement with paleontological data. As for Nearctic part of tundra shrew distribution area, we propose that *S. tundrensis* penetrated into North America later, apparently over one of the last Beringian land bridges. Its limited Nearctic distribution (VAN ZYLL DE YONG 1983) and its morphological (OKHOTINA 1983) and karyotypic (MEYLAN and HAUSSER 1991) resemblance with Palearctic populations suggest a recent arrival into North America.

The other karyotypic lineage arising from the presumed ancestor A1 led to a form with a karyotype intermediate to that of A1 and the five species of the group (Fig. 2). This ancestral form A2 (*"granarius"*-like from karyological point of view) hypothetically spread over the whole Palearctic before the Riss (Illinoian) period. One population with a northeastern Asian distribution was the first form of *araneus-arcticus* group that crossed the Beringian land bridge and came into North America. There, with the beginning of the Illinoian period, this form was pushed southward during the glacial period, as documentated by paleontological data. At the end of the Pleistocene glaciations, the range of *S. arcticus* moved northward and attained its modern

distribution. During colonization of ice-free territories, the distribution of two subspecies, *S. arcticus arcticus* and *S. arcticus maritimensis*, may have been continuous, as suggested by from subsequent morphological (VAN ZYLL DE JONG 1983) and chromosomal studies (VOLOBOUEV and VAN ZYLL DE JONG 1988).

As for the Eurasian lineage of the "*granarius*"-like ancestral form, it spread over the whole Palearctic region to the west as far as the Iberian peninsulae. Apparently in one of its populations with a central European distribution, the first fusion, *1+4*, occurred and then spread over most of Europe. The Riss glaciation cut off the Iberian peninsulae where, together with the *granarius*-like ancestor, a population of shrews with an *1+4* karyotype was isolated, whereas the central European populations retreated to more easterly Mediterranean regions. The subsequent evolution of these populations was independent: the *granarius*-like shrews became *S. granarius* without change of karyotype. The Iberian population of shrews with *1+4* karyotype acquired eight further chromosome rearrangements and became *S. coronatus*. In the more eastern European populations a further Robertsonian fusion occurred, giving rise to the form that spread over central and eastern Europe between Riss and Würm. At the beginning of the Würm, the distributional area of this latter form broke into at least three separate groups, which subsequently gave rise to all known modern races of *S. araneus*, whose postglacial evolution is considered in detail elsewhere (SEARLE 1984, CATZEFLIS 1984).

Although we place *S. daphaenodon* together with *S. araneus* and *S. coronatus* (Fig. 2) because of sharing of the same Robertsonian translocation (*1+4*) and, thus, relate its origin with Central Europe, it might be noted that in the light of biogeographical data independent origin of *1+4* translocation in *S. daphaenodon* cannot be excluded. Further biochemical and/or molecular studies will allow to precise phylogenetic relations of *S. daphaenodon* with other species of *araneus-arcticus* group.

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