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A new perspective on the evolutionary history of western European *Sorex araneus* group revealed by paternal and maternal molecular markers

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Abstract

The species of the common shrew (*Sorex araneus*) group are morphologically very similar, but have undergone a spectacular chromosomal evolution. We investigate here the evolutionary history of the *Sorex araneus* group distributed in western Europe. In particular, we clarify the position of a difficult species, *S. granarius*, using sex-specific (mtDNA and Y-chromosome) markers. The karyotype of *S. granarius* is generally considered similar to the common ancestor of the restricted group considered here. The mtDNA data (1.4 kb) confirms the close relationship between *S. granarius* and *S. araneus sensu stricto* (hereafter *S. araneus s.s.*), but the Y-chromosome (3.4 kb) produces a quite different picture: *S. granarius* is closely related to another species, *S. coronatus*. Comparison of mtDNA and Y-chromosome phylogenies suggests that the genetic and chromosomal evolution in this group are disconnected processes. The evolutionary history of the south-western European populations of the *S. araneus* group can only be understood considering secondary contacts between taxa after their divergence, implying genetic exchanges by means of hybridization and/or introgression.

Keywords: Sex-specific loci; Y-chromosome; mtDNA; Common shrew; *Sorex araneus* group; Karyotypic structure; Introgression

1. Introduction

The shrews of the *Sorex araneus* group show one of the most spectacular patterns of chromosomal evolution observed in mammals. The species of this group are morphologically very similar but considerable chromosomal variation can be observed between and even within species. The males are characterized by a XY_1Y_2 sex chromosome complex (Sharman, 1956). Such chromosomal variability is mainly due to Robertsonian rearrangements accompanied by telomere–centromere tandem translocations, centromere shifts and pericentric inversions (Searle and Wójcik, 1998; Wójcik et al., 2002). It has therefore been proposed that the ancestral karyotype of the group most likely consisted of acrocentric chromosomes and was similar in karyotype to the Iberian shrew, *Sorex granarius* (Volobouev and Catzeflis, 1989; Volobouev and Dutrillaux, 1991; Wójcik and Searle, 1988). This species has each of its autosomal arms *a* to *r* (nomenclature according to Searle et al., 1991) in an acrocentric form, whereas the other European species of the group bear common (e.g. *af*, *tu*) or specific (e.g. *gm*, *go*) fusions. Populations sharing the same set of acro- and metacentric chromosomes common by descent are defined as a chromosome race (Hausser et al., 1994). In *Sorex araneus s.s.*, chromosomal polymorphism is both common within and between races. The chromosome number of this species varies between $2N = 20$ and $2N = 33$, but the fundamental number of chromosomal arms is always constant ($NF = 40$). At least 60 chromosomal races have been described in *S. araneus s.s.*, making this species one of the most chromosomally polymorphic mammals species (Wójcik et al., 2002).

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Although chromosomal differences do not seem to always affect gene flow between chromosome races of *S. araneus s.s.* (e.g. Andersson et al., 2004), gene flow seems arrested or very limited among the European species of the *S. araneus* group (Brünner et al., 2002b; Lugon-Moulin et al., 1999).

During the last Pleistocene glaciations, the Pyrenean and Alpine barriers played a major role in isolating the Iberian and Italian peninsulas from the rest of the continent. For numerous taxa, this geographical isolation led to genetic divergence, which later influenced the post-glacial recolonization of Europe (Taberlet et al., 1998). The shrews of the *S. araneus* group did not escape this pattern. Today, at least seven chromosomal races and species of the group meet in western Europe (Fig. 1). First, the common shrew (*Sorex araneus s.s.*) is widely distributed across the Palearctic regions. At least four closely related chromosomal races occur in south-western Europe: the races Cordon, Bretolet and Vaud in the western Alps and the race Carlit in the Pyrenees. Second, the Millet's shrew (*Sorex coronatus*) occurs in western Europe, from northern Spain to Germany. This species probably diverged in refugia situated in south-western France or Spain (Hausser and Jammot, 1974) and then colonized the European lowlands as well as some large Alpine valleys from the west. Third, the Valais shrew (*S. antinorii*) occurs in Italy, southern Switzerland, and south-eastern France. This species, which was formerly considered as a chromosome race of *S. araneus s.s.*, has recently been elevated to species status (Brünner et al., 2002a). It crossed different Alpine passes from its glacial refugia situated in the Italian peninsula to colonize the French and Swiss Alps (Brünner et al., 2002a,b). Finally, the Iberian shrew (*S. granarius*) is confined to the central and north-western parts of the Iberian Peninsula (López-Fuster et al., 1999).

Many efforts have been made to propose a global view of the evolutionary history of this group and to account for the large chromosomal variation (reviewed, in Searle and Wójcik, 1998), but the results based on karyotypic, biochemical or mitochondrial DNA data are often contradictory (Catzeflis et al., 1982; Ratkiewicz et al., 2002; Taberlet et al., 1994). In particular, the position of *S. granarius* within the *S. araneus* group varies according to the category of the marker analyzed. According to biochemical and mtDNA data, *S. granarius* seems closely related to *S. araneus s.s.* (Catzeflis et al., 1982; Fumagalli et al., 1999; Taberlet et al., 1994), but phylogenies based on karyotype indicate a basal position of this species to a group formed by *S. araneus s.s.*, *S. antinorii* and *S. coronatus*. This suggests that evolution of chromosomes and mtDNA are

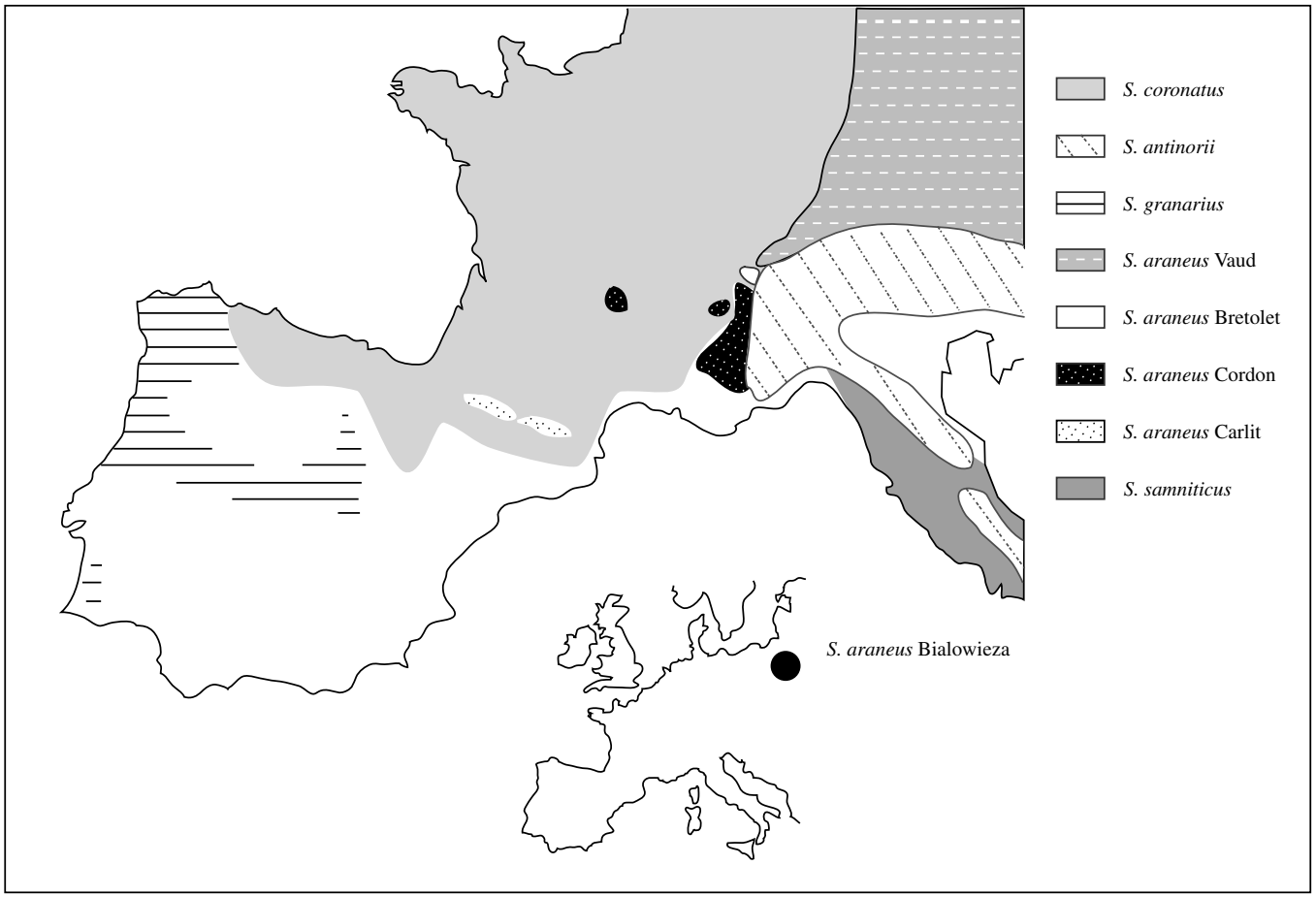

Fig. 1. The geographical distribution of the studied taxa.