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Whole-arm rearrangements in the common shrew in a wider context[1]

BY

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Summary.–GARAGNA S., SEARLE J.B. and REDI C.A., 1991. Whole-arm rearrangements in the common shrew in a wider context. *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*: 45-49.

The common shrew has one of the most variable karyotypes of any mammal. Recent karyotypic evolution in this species has predominantly involved rearrangements which result in changes in the disposition of chromosome arms without changes within the arms. A chromosome arm may be present as an acrocentric chromosome or as a part of a variety of different metacentric chromosomes. While Robertsonian (centric) fusions are apparently the predominant form of rearrangement, other mechanisms like fissions or whole-arm reciprocal translocations should not be excluded.

The analogous chromosomal variation encountered in the house mouse can be explained by the presence of very homogeneous highly repetitive (satellite) DNA in the centromeric region. Recent data indicate the presence of heterochromatin near the centromeres of the common shrew, except for the evolutionary oldest metacentrics. Preliminary results of *in situ* hybridisation with the highly conserved (TTAGGG)n telomeric sequence suggests a loss of telomeric sequences during or after fusions.

Résumé.–GARAGNA S., SEARLE J.B. et REDI C.A., 1991. Réarrangements des bras chromosomiques de la musaraigne carrelet considérés dans un contexte plus général. *In*: J. HAUSSER, dir. 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*: 45-49.

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La musaraigne carrelet présente le caryotype le plus variable de tous les mammifères. L'évolution récente du caryotype de cette espèce implique surtout des réarrangements qui changent les relations entre les bras chromosomiques, sans changer la structure des bras eux-mêmes. Un bras chromosomique peut être présent sous forme de chromosome acrocentrique ou participer à différents chromosomes métacentriques. Si les fusions Robertsoniennes (ou centriques) constituent vraisemblablement le mécanisme prédominant dans ces réarrangements, d'autres modifications comme les fissions ou les translocations réciproques ne peuvent pas être exclues.
La situation analogue rencontrée chez la souris domestique peut être expliquée par la présence d'ADN hautement répétitif (ADN satellite) très homogène à proximité des centromères. Des données récentes indiquent également la présence d'hétérochromatine près des centromères chez la musaraigne carrelet, sauf pour les métacentriques évolutivement les plus anciens. Les résultats préliminaires d'hybridations *in situ* avec une séquence télomérique très conservée (TTAGGG)n suggèrent une perte du DNA télomérique pendant ou après le processus de fusion.

In the common shrew (*Sorex araneus*), an extremely large number of chromosomal rearrangements have been described due primarily to centric (Robertsonian: Rb) fusion of the ancestral acrocentric chromosomes giving rise to metacentrics. As a consequence of these frequent rearrangements, there are many karyotypic races of the common shrew all over Europe, making it one of the most interesting mammals for studies of karyotypic evolution.

The role of structural chromosome rearrangements in the speciation process has long been debated (WHITE 1968, 1978, BUSH *et al.* 1977, BUSH 1981, CAPANNA 1982, BAKER and BICKHAM 1986) and a number of hypotheses have been proposed based mainly on the general assumption that karyotypic heterozygosity can perturb the meiotic process, with gene flow between populations prevented by the consequent subfertility or sterility of the hybrids. However, BENGTSSON and FRYKMAN (1990) have argued that simple chromosomal rearrangements do not play a special role in speciation in the common shrew. They cite evidence that gene flow occurs between different shrew populations in contact zones (FRYKMAN 1984, FRYKMAN and BENGTSSON 1984), despite likely heterozygote disadvantage (SEARLE 1988). In addition, an increase of acrocentric chromosomes (a sort of "return" to the ancestral karyotype) has been found in the karyotypes of individuals caught in several shrew hybrid zones (FEDYK and LENIEC 1987, FREDGA 1982, SEARLE 1986) which may further ease flow of genetic information across the zones. The situation found in Britain where new karyotypic races are apparently being formed as a result of modification of hybrid zones, reinforces the idea that speciation, through chromosomal rearrangements, is unlikely to occur in the common shrew (review in SEARLE *et al.* 1990).

Thus, we have some appreciation of the relevance of chromosomal rearrangements to the present-day genetic architecture of the common shrew. However, it remains difficult to understand how such rearrangements become established in this species and, crucially in this regard, what are the molecular processes involved in the structural change of the karyotype. At this point, it must be underlined that although Rb fusions are likely to have been the predominant form of chromosomal rearrangement in the recent karyotypic

evolution of *Sorex araneus* (VOLOBOUEV 1989), we may also have to envisage molecular mechanisms for the following additional categories of rearrangement: Rb fissions (OLERT 1973, HALKKA *et al.* 1987, SEARLE *et al.* 1990), whole-arm reciprocal translocations (WÓJCIK 1986, HALKKA *et al.* 1987) and centromeric shifts (VOLOBOUEV 1989).

To help predict the molecular processes important in the karyotypic evolution of the common shrew, we will digress to a much better studied system: the house mouse, *Mus musculus*. As is well known, a very high frequency of Rb fusions have occurred in *M. musculus domesticus* (CAPANNA *et al.* 1976, GROPP *et al.* 1982, WINKING *et al.* 1988, review in REDI and CAPANNA 1988). The study of the molecular constitution of the pericentromeric region in this species is crucial to our understanding of these chromosomal rearrangements (REDI *et al.* 1990c). We have found that the highly repetitive (satellite) DNA, which is located near the centromeres of all chromosomes except the Y (PARDUE and GALL 1970), is particularly homogeneous and arranged in very long tandem repeats in *M. musculus domesticus* (REDI *et al.* 1990b). This pericentromeric constitution could favour a high frequency of Rb rearrangement through mispairing of homologous sequences of satellite DNA of nonhomologous acrocentrics (REDI *et al.* 1990a). Interestingly, in *M. musculus musculus*, in which the satellite DNA is less homogeneous, only one Rb chromosome has been detected (ZIMA and MACHOLAN 1989).

Even though a wider array of chromosomal rearrangements may occur in the common shrew than in the house mouse, a molecular analysis of the pericentromeric region of autosomes is again of pre-eminent importance for our understanding of the mechanism of chromosomal mutation in this species. Until now, efforts to isolate the satellite DNA from the shrew genome have failed (WORSMAN 1981). However, some preliminary data on the pericentromeric constitution of shrew chromosomes are available. Heterochromatin has been found located around the centromeres of all autosomes except the three pairs of evolutionary-old metacentrics (SEARLE 1983), indicating the presence of highly repetitive DNA. Highly repetitive DNA has also been detected after DNA digestion with restriction enzymes (WORSMAN 1981). Recently, we analysed the pericentromeric regions of Rb chromosomes in the common shrew by *in situ* hybridization with synthetic oligonucleotides that have the highly conserved vertebrate telomeric sequence (TTAGGG)n (MEYNE *et al.* 1989). Our preliminary data suggest that there is loss of these telomeric sequences during or after fusion.

In addition to satellite DNA, it is probable that other factors, such as transposons (HALKKA *et al.* 1987) or elements able to increase the recombination frequency like minisat-DNAs (WAHLS *et al.* 1990), could be active in the karyotypic evolution of the common shrew at the molecular level.

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