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Is the trend toward low 2Na numbers inescapable for *Sorex araneus* populations ?

BY

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Summary.—ZIMA J., 1991. Is the trend toward low 2Na numbers inescapable for *Sorex araneus* populations ? 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: 63-71.

The trend toward low 2Na numbers via fusions of acrocentric chromosomes is apparently the prevailing characteristic of the Robertsonian process in the common shrew. This opinion is supported by interspecific karyotype comparisons, existence of several karyotype races possessing different arm combinations in Rb metacentrics, as well as by the composite features of the sex chromosomes.

Meiotic drive operating in favour of metacentric chromosomes seems to be the most adequate mechanism of enhanced fusion fixation rate. The causal reasons for the fusion preference should be looked for in selective advantages at the population and species levels. The permanent trend toward lowering 2Na numbers can be considered a species adaptive tool inhibiting an undesirable rise of information entropy. It is suggested that karyotype changes do play a role in divergence processes in *Sorex araneus*, and that the speciation represents a response to increased information entropy caused by accumulated karyotypic variation. Similar speciation scenarios may be proposed for evolutionary divergence of the ancestral forms of the *Sorex araneus* species complex and recent karyotypic races of the common shrew.

Résumé.—ZIMA J., 1991. La tendance à la diminution du 2Na dans les populations de *Sorex araneus* est-elle inévitable ? 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: 63-71.

La tendance à la diminution du 2Na par la fusion de chromosomes acrocentriques paraît être la caractéristique dominante des processus Robertsoniens observés chez la musaraigne carrelet. Cette opinion est confortée par la comparaison des caryotypes au niveau interspécifique, l'existence de nombreuses races chromosomiques présentant des métacentriques Robertsoniens formés par la combinaison de bras chromosomiques différents, ainsi que par les caractéristiques composites des chromosomes sexuels.

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Le mécanisme le plus adéquat pour expliquer la tendance à la fixation de ces fusions semble être le "meiotic drive" en faveur des métacentriques. Les causes d'une préférence pour les fusions doivent être cherchées dans un avantage sélectif aux niveaux des populations et des espèces. La tendance permanente vers un abaissement du $2Na$ peut être considérée comme un outil adaptatif contrebalançant un accroissement indésirable de l'entropie génétique. On suggère que les changements chromosomiques jouent un rôle dans le processus de diversification de *Sorex araneus* et que la spéciation représente une réponse à l'accroissement de l'entropie génétique causée par l'accumulation des variations chromosomiques. Des scénarios de spéciations similaires peuvent être proposés tant pour la divergence des formes ancestrales du complexe *araneus* que pour celle des races chromosomiques récentes de la musaraigne carrelet.

INTRODUCTION

An exceptional and fascinating karyotype variation pattern observed in the common shrew, *Sorex araneus*, evokes plenty of questions, hypotheses, and models. The empirical evidence from natural populations of the common shrew has been evaluated in conclusions dealing with various general problems of karyotype evolution. One of the important problems is a trend toward low $2Na$ numbers mediated by fusions of acrocentric chromosomes. Does this trend represent a real phenomenon in the common shrew populations, and what are the causal forces and mechanisms enabling it? In searching for answers to these questions, the problem of inter- and intrapopulation chromosomal differentiation, evolution in hybrid zones, and interspecific relations in the *Sorex araneus* species group should be considered.

CENTRIC FUSION VS. FISSION HYPOTHESES OF KARYOTYPE EVOLUTION

The Robertsonian rearrangement represents one of the major changes contributing to karyotype evolution in mammals. The Robertsonian rearrangement implies two opposite chromosome alterations, centric fusion and fission, and different views have been published evaluating the relative importance of both changes in karyotype evolution. Some cytogeneticists have supported a significant role for fusions (e.g. CAPANNA 1982, BAKER and BICKHAM 1986), other for fissions (e.g. TODD 1970, IMAI 1978, IMAI and CROZIER 1980), and there is also a modal hypothesis evaluating both types of rearrangement as equally important (MATTHEY 1973). IMAI (1978) suggested a cyclical model of chromosome change, involving centric fission as a chief element. Under this model mammalian karyotypes have an overall tendency to evolve higher numbers of chromosomes, and IMAI and CROZIER (1980) have concluded that various cases of fusion represent local "back eddies" in the mainstream of mammalian karyotype evolution.

The empirical data obtained in the common shrew do not agree with the fissionist's predictions. There are several reasons to believe that the prevailing mode of karyotype evolution in *Sorex araneus* is the fusion. The origin of the

composite sex chromosome constitution can be explained solely on the basis of a fusion event, indicating thus the general direction of karyotype change. Different arm combinations in metacentric autosomes have been found in karyotypic races of the common shrew, as well as in individual species of the *Sorex araneus* group. Hence, centric fusions rather than fissions appear to be the main cause of chromosomal divergence in *Sorex araneus* and related species. High-resolution chromosome analysis of the *Sorex araneus* species complex indicates that the karyotype evolution has proceeded in the direction from high to low 2N numbers by means of fusions of both a Robertsonian and a tandem type (VOLOBOUEV 1989). Does the karyotype differentiation process in the common shrew represent a "back eddy" in mammalian karyotype evolution, and/or is there something wrong in the fission hypothesis ?

MODES OF FUSION FIXATION

There can be little doubt that centric fissions do occur in the common shrew karyotype evolution, but it is still doubtful if they influence the prevailing trend toward low 2Na number. The occurrence of fissions in the common shrew populations may be insinuated from data gathered in hybrid zones (FREDGA 1982, SEARLE 1986a, FEDYK and LENIEC 1987) or findings in related species (OLERT 1973). The different frequency of occurrence of fusions vs. fissions could result from different raw mutation rates or different final fixation rates. There is practically no information on the raw occurrence rate of fusions or fissions, and no grounds to consider it highly differential. The difference in the final fixation rate between fusions and fissions appears to be the more plausible explanation. The causes of the preferential fusion fixation may be stochastic or selective. The stochastic change is mediated by genetic drift, inbreeding, and social structuring of populations. The exclusive determination of the trend toward low 2Na numbers by these mechanisms would require high rates of occurrence of fusions, and seems to be improbable, but a participation of stochastic processes (namely population density fluctuations) in *Sorex araneus* karyotype evolution should be seriously considered (see Fig. 1). Selective forces enhancing the fusion fixation rate can be non-adaptive (meiotic drive, selection at haplophase), or adaptive (selection at organismal, populational or species level). The adaptive role of chromosome rearrangements at the organismal level remains the subject of debate (BICKHAM and BAKER 1979, SITES and MORITZ 1987), and there are no data from the common shrew supporting this view. Direct adaptive differences between alternative homozygotes for different autosomal fusions should lead to preferential occurrence of particular karyotypes in specific habitats, and this phenomenon has been observed only exceptionally in the common shrew (WÓJCIK 1991). Strong indications of segregation distortion in favour of the metacentric chromosome type was found by SEARLE (1986b), and the meiotic drive seems to be the most adequate explanation of enhanced fusion fixation rate. Nevertheless, the meiotic drive premise can account only a mechanism and not a causality for the fusion trend. The adaptive

significance of this phenomenon should be looked for in indirect advantages at the populational or specific level. The protection of coadapted gene complexes can serve in local habitats as a mechanism for the fixation of fusions (WHITE 1978). I shall attempt to evaluate another hypothetical causal mechanism operating at specific level.

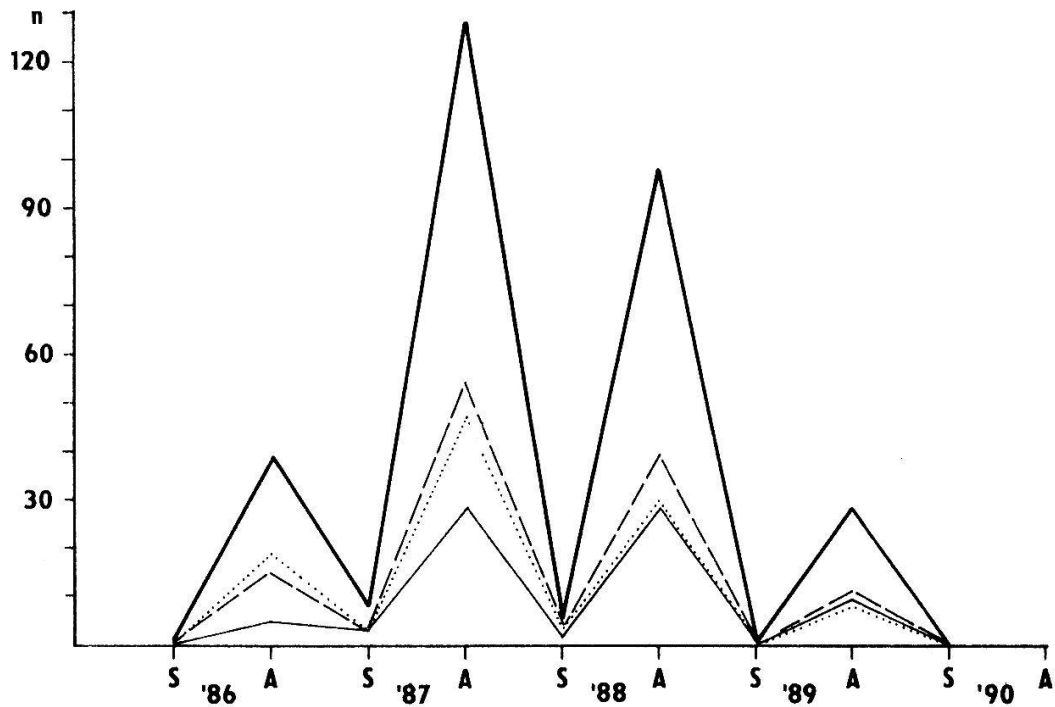


Fig. 1.—An example of seasonal density fluctuation in the common shrew. The data were obtained on three 1 ha plots in northern Bohemia. The solid line represents cumulative fluctuation in all three plots. Ordinate: number of shrews trapped. Abscissa: successive seasons and years. S: Spring, A: Autumn.

KARYOTYPIC VARIATION AND INFORMATION THEORY

In 1982, WILEY and BROOKS published their paper dealing with a nonequilibrium approach to evolution. In spite of much criticism evoked by that unconventional interpretation of evolutionary processes, I should like to borrow from it certain terms and ideas, and use them in speculations on *Sorex araneus* karyotype variation and differentiation.

WILEY and BROOKS (1982) stated that evolution is best explained as an irreversible nonequilibrium phenomenon determined by the second law of thermodynamics. Three aspects of populations and species are considered in this approach: “information” specifying successful growth and ontogeny, “cohesion” resulting from mating bonds between parts of species, and “energy flow”. “Canalized information” is that information responsible for the sequence of ontogenetic events of organism, “non-canalized information”

is derived from structural gene loci, and is used to produce structural products. "Stored information" is that information expressed at one or several times during the life of the individual. "Potential information" is information that is present but not expressed. Speciation is a process which results in differential consolidation of potential canalized information in an ancestral species into two or more canalized stored information system in descendants. Any change in the information system of a species must result in increased complexity and higher entropy state. The species has become more complex because of new potential information, and if this new potential information is converted into stored information, the species will exhibit a decrease of its entropy level. All modes of speciation may be described by a summary equation which charts the changes of entropy states of information and cohesion over time.

I suggest that karyotype structure and variation can be described in terms of information theory as a kind of canalized information (e.g. by Shannon-like functions). The origin of new karyotypic variants produces new potential information resulting in an increase in entropy in a species. The information entropy level of a karyotypically variable species is strongly connected with the species cohesion, defined as a measure of the overall reproductive losses determined by cytogenetical incompatibility. The increase of information entropy above a critical threshold would lead to a collapse of cohesion and consequently to the extinction of the species. This development could be prevented by suppression of karyotype variability and by evolving a monomorphic situation. The trend toward low 2Na numbers in *Sorex araneus* populations may be evaluated as a mechanism operating namely in this direction. The number of theoretically possible karyotypic variants in the common shrew is considerably high, but only a small portion of this imaginable diversity has actually been found in natural populations (ZIMA *et al.* 1988). If the fusion as well as fission fixation rates were equal and dependant solely on stochastic factors, the extent of the overall karyotype variation would be substantially higher than actually observed. Every realized fusion event, with insignificant probability of a reversal, will considerably reduce the number of consequently arising new variants and tend to limit the entropy rise (Table 1). The permanent trend toward lowering of diploid autosomal numbers can thus be considered a species adaptive tool inhibiting an undesirable rise of entropy states of information.

Table 1.—The decrease of combination possibilities as a function of a reducing number of free acrocentrics. Upper row: Number of free acrocentric autosomal pairs in karyotype. Lower row: Theoretical number of all-metacentric karyotypes with different arm combinations composed of the available acrocentric pairs.

| | | | | | |
|-------|-----|-----|----|---|---|
| 12 | 10 | 8 | 6 | 4 | 2 |
| 10395 | 945 | 105 | 15 | 3 | 1 |

A MODEL OF KARYOTYPE EVOLUTION IN *SOREX ARANEUS*

The tendency to Robertsonian change in *Sorex araneus*, its relatives and ancestors, has probably been favoured by evolving certain molecular characteristics of pericentromeric (and telomeric) heterochromatin (e.g. high repetitiveness of the DNA involved, the presence of the same major type of satellite DNA over acrocentric chromosomes as suggested by REDI *et al.* 1986, REDI and CAPANNA 1988). As soon as these basic pre-requisites for the Robertsonian process and mechanisms favouring fusion fixation did originate, the karyotype differentiation could begin. The time and space pattern of the karyotype differentiation in the common shrew has undoubtedly been influenced by geographical isolation of populations, which must be expected particularly in periods of glaciation. Certain paleontological findings from Central Europe (HORÁČEK *in litt.*) indicate that many small isolated refuges of *araneus*-like shrews existed during the last glacial episode rather than few large refuges situated solely in Southern Europe. The fixation of different autosomal fusions supported by meiotic drive and drift appeared in the separated glacial refuges, and new karyotype variants and races originated (HAUSSER *et al.* 1986). This development was followed by rising information entropy. In the postglacial period, shrews spread from refuges, and karyotypically different populations became in contact. Hybridization of different karyotypic races resulted in cohesion disturbances and reproductive losses. This unfavourable state could be resolved either by coalescence of both karyotypic races and evolving of an uniform population, or by complete reproductive isolation, i.e. speciation (Fig. 2). The strategy adopted is apparently dependent on the ratio of population numbers, size of the distribution areas of both races, and magnitude of karyotype differences

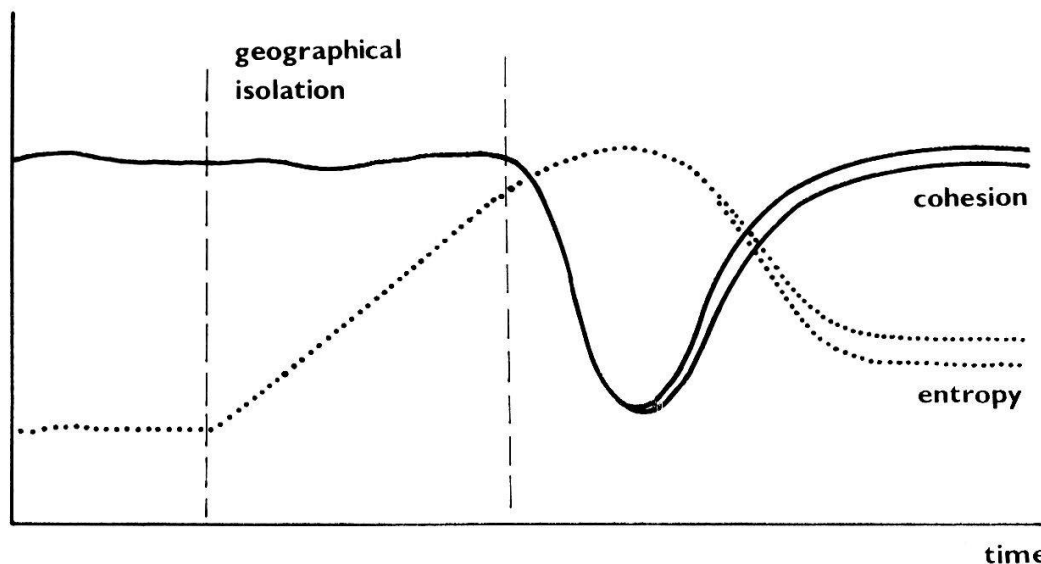


Fig. 2.—Hypothetical course of entropy and cohesion changes during differentiation of two large races. Cohesion level represents only overall reproductive losses. Changes due to geographical isolation are not considered.

between them. If the difference in number of individuals and size of distribution ranges between two encountering populations was large, and their karyotypic difference was small, then the smaller population should probably be encompassed and gradually assimilated by the larger one. The assimilation might be facilitated by a temporary selective advantage for fissions in the hybrid zone. Large karyotype races could successively absorb small populations and races, and extend their areas of distribution.

A different situation can be anticipated after contact of two large races of numerous populations distributed over an extensive area. The assimilation of one race by the other cannot be excluded even in this case, but a different strategy to avoid reproductive losses ought to be expected. The contact between two large karyotypic races could hardly be established at once and at all points of the present hybridization line. On the contrary, rather broad and mosaic hybridization zone should evolve at the beginning of the geographical contact (Fig. 3). Regarding the recent history of these events, the different character of distribution of allelic frequencies and karyotypic variants over a hybridization zone becomes comprehensible. Isolated pioneer populations belonging to a particular race could fall inside the range of the other race during the formation of the hybridization zone, and they could be rapidly assimilated as consequence of their low density. In this way, race-specific alleles were transferred into another race. This past development can evoke an impression of current genetic mixing between races (BENGTSSON and FRYKMAN 1990).

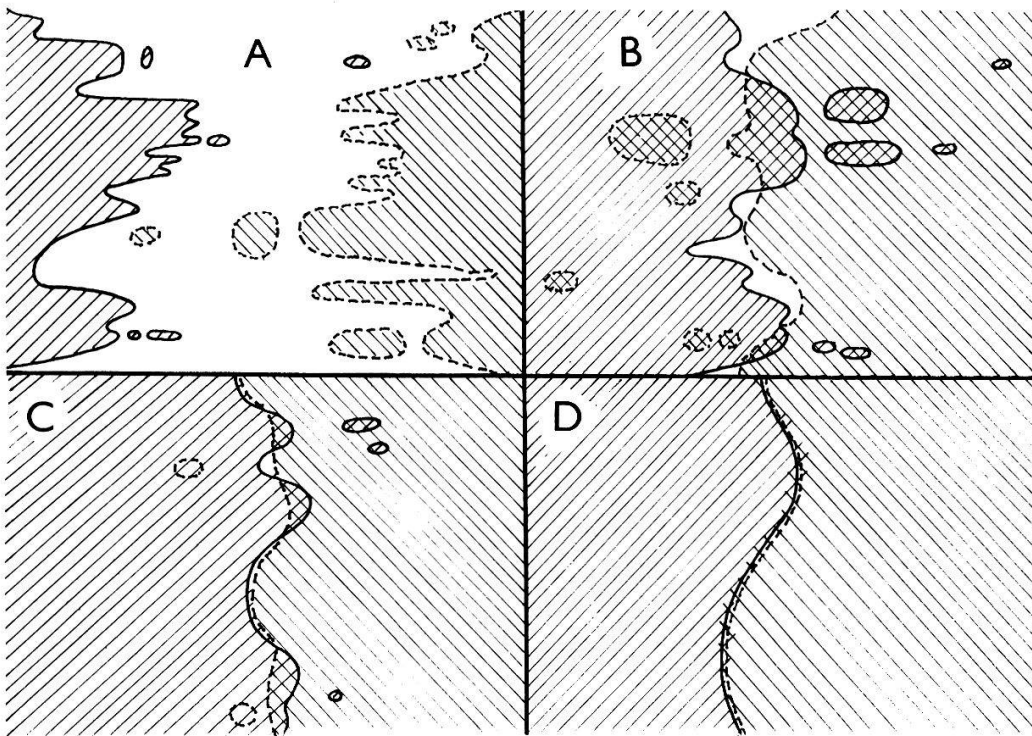


Fig. 3.—Presumptive course in the establishment of contact between two karyotypic races.

Therefore, I suggest that chromosome changes do play a role in speciation processes in *Sorex araneus*, and that the speciation represents a response to increased information entropy caused by accumulated karyotype variation. The detailed karyotype comparison made by VOLOBOUEV (1989) has shown that chromosomal differences between well-differentiated species of the XY₁Y₂ group are apparently caused by the same types of chromosome rearrangements as those between karyotype races of the common shrew. Similar speciation scenarios may be proposed for evolutionary divergence between the ancestral forms of *Sorex araneus* complex and recent karyotypic races of the common shrew. The phylogenetic history of this group can be evaluated as one continuous process.

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