Chromosomal rearrangements, speciation and reproductive isolation: The example of two karyotypic species of the genus Sorex

Cornelis R. Neet and Jacques Hausser

Institut de Zoologie et d’Ecologie Animale, Université de Lausanne, Bâtiment de Biologie, CH-1015 Lausanne, Switzerland

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Introduction

During the last twenty years, growing evidence appeared in favour of the role of chromosome rearrangements as a factor that may promote speciation (White, 1978). Several theoretical models have been proposed (Sites and Moritz, 1987), many of which are based on empirical data from various taxa, including, among others, the genus Drosophila (Wallace, 1953), grasshoppers (Shaw, 1981), lizards (King, 1981) and mice (Capanna, 1982). However, Sites and Moritz (1987) still find this evidence for a chromosomal involvement in speciation too fragmentary. Moreover, chromosomal speciation models are often taken as sympatric speciation models and thus assume that when pre-mating barriers have evolved to reduce the production of unfit hybrids, this should have occurred by reinforcement of characters increasing assortative mating, a process that still lacks good theoretical and empirical support (Butlin, 1987; Coyne and Barton, 1988). One further problem is that, in many natural cases, hybrid zones are found between karyotypic races, sometimes with appreciable stability and persistence that does not necessarily suggest current speciation (Barton and Hewitt, 1985). For example, a study on British karyotypic races of the shrews of the Sorex araneus complex has shown that between some races, each characterized by different sets of metacentric chromosomes, natural hybridization may occur without any evidence for strong pre- or post-mating barriers. On the contrary, in the hybrid zone, a karyotype with a higher number of acrocentric chromosomes and that may hybridize with other karyotypes appears to be favourably selected (Searle, 1984a, 1986).

In this paper, we present results obtained by biochemical and karyological analyses of two other taxa of the Sorex araneus complex, Sorex coronatus and the Vaud race of Sorex araneus (Hausser et al., 1986). These taxa are considered to be
two karyotypic species, and are more differentiated than the British karyotypic races. They are distinguishable by subtle morphological characters and a few biochemical characters (Hausser et al., 1985), and their distributional ranges are parapatric, with a few narrow contact zones where syntopic populations are found (Hausser 1978; Hausser et al., 1985). On the basis of karyotype, hybrids between these species would have a high probability of being sterile (Olert and Schmid, 1978), but almost nothing is known of their reproductive isolation in nature. The individuals we studied were all taken from syntopic populations that have coexisted over periods of at least two years and which both reproduced (within taxa) in the contact zone (Neet and Hausser, 1989). The populations also exhibit interspecific territoriality, and, during the mating period, interspecific contacts between males and females were frequent (Neet, 1989). Thus, in these contact zones, we may expect to find evidence either for hybridization or for complete reproductive isolation. Since it has previously been hypothesized that S. coronatus and S. araneus have been separated in the recent past by a chromosomal speciation process (Hausser et al., 1985), it is of great interest to evaluate whether reproductive isolation without hybridization, i.e. pre-mating isolation, has evolved between them since. If such was the case, this example would provide corroborative evidence for the hypothesis that chromosomal rearrangements were involved in the process of speciation.

Materials and methods

Shrews were trapped in two contact zones, one in the heights of Bassins, in the Swiss Jura mountains, the other on the coast of the Lake of Neuchâtel, between Yverdon and Yvonand (Switzerland). For karyological analyses the shrews were taken to the laboratory where direct, air-dried, mitotic chromosome preparations were made from bone marrow. The preparations were either Gimsa stained or G-banded. For electrophoretic analyses, a blood sample of about 2 µl was taken, in the field, from the tail. The blood samples were diluted in a buffer solution and run on a disc-polyacrylamide gel system (Hausser and Zuber, 1983) to compare serum albumin patterns of both species. Each species has a characteristic pattern that permits precise identifications (see below). The technique has, so far, given 100% correct identifications when tested with about 50 individuals of S. coronatus and 70 individuals of the Vaud race of S. araneus by karyology.

Results

No hybrid karyotypes were found in the sample (Table 1). The electrophoretic results are best understood after considering the serum albumin patterns (Fig. 1). S. coronatus is characterised by a slow double banded albumin pattern (C2) and the S. araneus Vaud race by a faster double band (A2). In some samples, the upper one of the two bands is less visible and may even be unnoticed on gel photographs (C1
Table 1. Numbers of individuals identified by karyology and electrophoresis of serum albumins. The individuals were taken from contact zones between the karyotypic species S. coronatus and the Vaud race of S. araneus.

<table>
<thead>
<tr>
<th></th>
<th>S. coronatus</th>
<th>S. araneus Vaud race</th>
<th>Presumable hybrids</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Karyology:</td>
<td>22</td>
<td>50</td>
<td>0</td>
<td>72</td>
</tr>
<tr>
<td>Serum albumin</td>
<td>103</td>
<td>224</td>
<td>4*</td>
<td>331</td>
</tr>
</tbody>
</table>
electrophoresis:      |             |                      |       |       |

* Only one of these individuals was karyotyped. It had a typical S. araneus karyotype.

...and A1). However, a careful inspection of the gels shows that the double banded pattern is always present. Although the intensity of both bands varies with sample concentration (the blood sample is taken in the field and cannot always be exactly dosed at 2 µl), we have noticed that the upper band is more variable in intensity than the lower band. Attempts were made to find the reason for this variability, e.g. by controlling for sample storage time or the age of the individuals from which samples were taken, but the source of this variability remains unclear. Nevertheless, the interspecific difference is always clearcut, the lower band being always very distinct.

As shown on Table 1, on four occasions a triple band pattern was observed (H3 in Fig. 1). Such a pattern may be interpreted as a hybrid since it combines the two double band patterns into a triple band pattern. A similar pattern, but with the
middle band being more intense, was actually obtained by mixing blood samples of S. araneus (A2) and S. coronatus (C2). However, in the case of the H3 individuals, the triple band pattern was not an artifact as it was obtained in different electrophoretic migrations and with various neighboring samples. Actually, the only H3 individual for which G-banded karyological preparations were obtained shows a typical S. araneus Vaud race karyotype, with no indication of hybridization. Therefore, we should not consider this triple band pattern to be a clear indication of hybridization. Having, on the other hand, no reason to doubt that a possible hybrid would have this pattern, we must infer that hybrids between S. coronatus and S. araneus Vaud race, if any, are rare and do not represent more than 1% of the syntopic individuals.

Discussion

The very low frequency of hybridization, if any, in the contact zones between these two karyotypic species suggests reproductive isolation. Most current definitions of reproductive isolation (Häuser, 1987) only require extensive hybrid sterility, while in this example hybrids are almost absent. As shown by Searle (1988), fitness reduction in Robertsonian heterozygotes is, as far as we know, almost only due to losses of fertility rather than reduced viability. It is therefore reasonable to assume that if F1 hybrids were, in fact, regularly produced, we would have found some. Thus, our results strongly suggest the existence of a pre-mating isolation mechanism between the species. According to Templeton (1981), such mechanisms are far more likely to evolve before secondary contact than after. In other words, it may seem likely that S. coronatus and the Vaud race of S. araneus have been separated by a geographic barrier in the past, and that speciation occurred by geographical isolation. The actual distribution of these species suggests that this barrier should have been the Pyrenees, during the last glacial periods (Searle 1984b; Hausser et al., 1985).

This view has the drawback that, during the Pleistocene, the Iberian Peninsula has never been completely isolated from the rest of the continent (Nilsson, 1983). Moreover, the genetic distances within the Sorex araneus complex are rather homogeneous, i.e., there is no clearcut difference between S. coronatus and the numerous karyotypic races of S. araneus (Catzeflis, 1984). Thus, with respect to genetical differentiation, there is no clear support for a long temporal separation between S. coronatus and the different races of S. araneus. For these two reasons, other speciation models that may produce pre-mating barriers without geographical isolation (e.g., Endler, 1977; Rosenzweig, 1978; Templeton, 1981) may apply equally well to this case.

Our results show that these two karyotypic species of the Sorex araneus complex are not only separated by a very low probability of hybrid fertility (Olert and Schmid, 1978), but also by a pre-mating barrier. Since the evidence for a long geographical isolation is at least weak, our results support the notion that the pre-mating barrier could well have appeared after Robertsonian chromosomal rearrangements had cut the gene flow between S. araneus and S. coronatus.
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