

Speciation by monobrachial centric fusions

(chromosomes/reproductive isolation/cryptic species/population genetics)

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ABSTRACT Fixation of centric fusions in natural populations often encounters minimal meiotic problems due to the ability of trivalents to segregate normally; therefore, little sterility barrier is achieved between a founder population and the parental stock. However, a strong sterility barrier can develop between different founder populations fixed for centric fusions that are monobrachially homologous in the resulting biarmed chromosomes (one arm is homologous but the other is nonhomologous). Hybridization through secondary contact then results in complex multivalents, which encounter problems in segregation and produce unbalanced gametes. Speciation mediated by centric fusions is a peripatric speciation model that does not postulate populational phenomena atypical of those characteristic of most mammals. The model appears applicable to a diversity of mammalian taxa such as bats of the *Rhogeessa tumida-parvula* complex, shrews of the *Sorex araneus* complex, and rodents of the *Mus musculus* and *Rattus rattus* complexes.

The role of chromosomes in speciation has been controversial. On the one hand, there have been advocates of the view that a restructuring of the karyotype is a sine qua non of speciation, but this clearly was refuted by the demonstration of homosequential species (1). Yet the fact that so many closely related and obviously very similar species differ in their karyotype is rather strong evidence that at least in some and perhaps the majority of speciation events, a restructuring of the chromosomes is involved.

Two primary areas of controversy are (i) the role of geography in chromosomal changes associated with speciation (2–11) and (ii) the dilemma of how any chromosomal mutation that causes sufficient loss of fitness in a heterozygote to be an effective isolating mechanism can become established in a population. The solution to this dilemma is addressed below in detail relative to the proposed model. Geographic aspects need to be established at this point as a foundation for the remainder of the model.

Two major models of the geographic situation of chromosomally mediated speciation have been considered in the past (below we propose a third one). White (2) proposed a sympatric model (stasipatric speciation), in which a new chromosomal mutation occurs within the continuous range of a species. Even though the heterozygotes between the old and new karyotypes are postulated to be inferior (e.g., owing to difficulties in meiosis), eventually homozygotes for the new karyotypes are formed and they are superior and outcompete individuals of the parental karyotype, giving rise to a new species. White's sympatric model, or variants thereof (2, 4, 12), have been discussed extensively in the literature and two points are critical to this discussion. First, the determined attempt to put all chromosomal speciation under a sympatric model [as reflected by White's (5) position,

“is speciation geographic or chromosomal?”] is misleading (3), and second, as Mayr (3) and Key (11) have shown, the situations ascribed to the sympatric models do not conform to the postulated sequence of events observed in natural populations.

The second geographic alternative postulates chromosomal speciation to occur only in small-sized founder populations in the course of a peripatric speciation event. The logic for such a conclusion comes from the fact that such models of chromosomal speciation rely on a measure of selection against the heterozygote as a direct indication of the effectiveness of a rearrangement in producing reproductive isolation. Thus, chromosomal rearrangements responsible for speciation infer a high level of sterility (negative heterosis) upon the heterozygote. A problem with such an assumption is that the probability of a rearrangement being established in a population is inversely related to its effectiveness as an isolating mechanism. This dilemma has led some authors to conclude that chromosomal speciation occurs only in species that have demes (breeding populations) with small effective population sizes. The fixation of a rearrangement with sufficient negative heterosis to be an effective isolation mechanism has a finite probability of occurring only in extremely small geographically isolated demes (13–17). Consequently, Futuyma and Mayer (18), Templeton (19), and Nei *et al.* (20) regarded chromosomal speciation as being virtually impossible under current population genetics theory. Regardless of the validity of the above models, there exists a set of circumstances under which chromosomal rearrangements can be the mechanism of reproductive isolation during speciation.

THE MODEL

This model requires extrinsically isolated subpopulations and best fits the conditions associated with a peripatric founder population or some other small extrinsically isolated population. The model requires fixation of different chromosomal rearrangements in two independent populations. However, as centric fusions cause little or no loss of fertility in heterozygotes, extreme populational bottlenecks are not required.

This model is concerned with a single type of chromosomal rearrangement—centric fusion. The model is not applicable to other types of chromosomal rearrangements. Centric fusions result when two acrocentric chromosomes are combined at their centromeric region into a single biarmed chromosome (Fig. 1a). Cytogenetic theory leads to the prediction that centric fusion would be among the most common types of chromosomal rearrangement incorporated in evolution. Centric fusions have minimal impact on the euchromatic genome and do not generally cause severe problems in the production of balanced gametes in a heterozygote.

In this model, separate isolated populations independently become fixed for different chromosomal centric fusions, with

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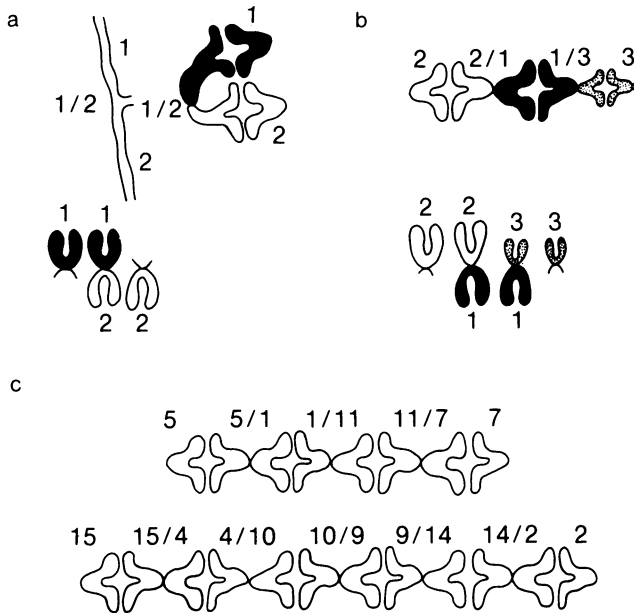


FIG. 1. Pairing of chromosomes in the first meiotic division of hypothetical hybrids or heterozygotes for Robertsonian fusions. (a) A heterozygote for the fusion of acrocentric chromosomes 1 and 2. Mitotic chromosomes are shown below. (Upper Left) Pachytene pairing with cis conformation; (Upper Right) subsequent metaphase I configuration with acrocentrics oriented to one pole and the metacentric to the other pole. (b) A hybrid with two monobrachially homologous chromosomes including arms 1, 2, and 3. Mitotic chromosomes are shown below. (Upper) Quadrivalent present in metaphase I. (Lower) Seven chromosomes. (c) Metaphase I configuration, including multivalents of five (Upper) and seven chromosomes (Lower), of a hypothetical hybrid between the 32N and 32B chromosomal forms of *R. tumida* (21). Not shown are 10 bivalents, including the sex chromosomes.

each population encountering minimal meiotic problems. Nevertheless, if these two populations hybridize, when combined in a heterozygote the same centric fusions that became fixed with minimal meiotic problems produce reproductive isolation through a greater level of meiotic impairment. All aspects of this model are developed from a synthesis of empirical studies on mammals, and the model appears to be applicable to a diversity of mammalian taxa.

As outlined in Fig. 2, the model relies on the establishment in separate founder populations of different biarmed chromosomes with monobrachial homology (2). Monobrachially homologous biarmed chromosomes result from the independent fusion of homologous acrocentric chromosomes to different nonhomologous acrocentrics (Fig. 2). The resulting biarmed chromosomes have only one arm that is homologous. In meiosis of individuals heterozygous for monobrachially homologous biarmed chromosomes, quadrivalents or more complex multivalents are formed that usually do not segregate normally and result in severely reduced fertility (Fig. 1b). On the other hand, heterozygotes for a simple centric fusion form trivalents in meiosis (Fig. 1a) that often segregate normally and produce minimal meiotic problems.

The criticisms (refs. 18–20; see Introduction) derived from population genetics theory that normally cast doubt on the probability of chromosomally mediated speciation are not relevant to speciation by fixation of monobrachially homologous chromosomes. This is because the fixation of metacentric chromosomes initially results in only a low level of sterility (Fig. 1a), while providing essentially complete reproductive isolation between different derived populations because interpopulational hybrids have a high degree of sterility (Fig. 1b).

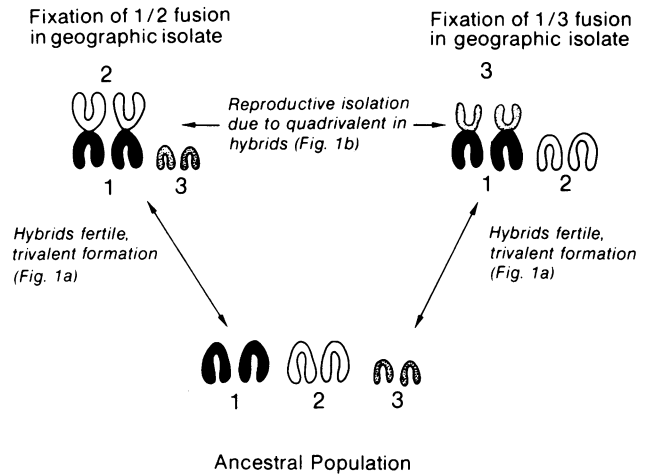


FIG. 2. Hypothetical speciation event in which acrocentric chromosomes 1, 2, and 3 are fused in different combinations in separate geographically isolated populations. The production of trivalents in animals heterozygous for a single fusion, such as hybrids between the ancestral and derived populations and in the heterozygous founders of the derived populations, fails to result in sterility. However, hybrids between the derived populations are sterile because of quadrivalent formation, and thus they represent reproductively isolated species. The disappearance of populations with the ancestral karyotype, as in the case in *Rhogeessa* (21), removes any chance for gene flow between the species.

It is not critical to our model whether selection or stochastic processes drive the centric fusions to fixation within a population, although this is often a most important issue in other models (4, 22). It is only critical that centric fusions commonly become fixed under natural conditions.

EMPIRICAL DATA

Empirical studies on various mammalian taxa document that the frequency of centric fusions for a given taxon range from zero to many. Critical to the model is the fact that centric fusions are often the most common type of rearrangement for certain mammalian taxa. For example, in a G- and C-band analysis of 78 species of bats, centric fusions were more than twice as common as all other types of identifiable rearrangements (23). Capanna *et al.* (24) indicated that individuals of *Mus musculus* heterozygous for a centric fusion have a fertility impaired at the order of 5–18%. Even in individuals of *Mus* that were heterozygous for three centric fusions, <25% of the gametes were aneuploid [had either too many or too few chromosomal arms (25)]. Heterozygotes for centric fusion that have occurred spontaneously in laboratory stocks of mice produced few imbalanced gametes (26), and the mice did not appear to suffer reduction in fitness relative to chromosomal homozygotes (27). Empirical evidence suggests centric fusions are tolerated well in natural populations because they are found as populational polymorphisms in a wide variety of mammalian species (28–31). Indeed, in a sample of 10 rice rats (genus *Oryzomys*) from a natural population, two were homozygous with no fusions, two were heterozygous for one, two were heterozygous for two, one was heterozygous for three and four each, and two were heterozygous for five fusions. A total of nine different fusions were polymorphic in the sample (31).

In contrast to the low level of meiotic problems associated with heterozygosity for centric fusion, heterozygotes for a single monobrachial fusion can develop a much greater impairment of meiosis during gamete production (Fig. 1b). Gropp *et al.* (32) demonstrated 58% aneuploidy in a male heterozygous for a monobrachial fusion. This clearly is in

excess of the necessary selection deficit for heterozygotes (>0.3) proposed as minimal for speciation (33–35). Capanna (21) illustrated the meiotic configurations associated with these two conditions, and Baker *et al.* (36) calculated expected reductions in fertility for the rearrangements observed in the bat genus *Rhogeessa*.

The species complexes of *Rhogeessa tumida* (36, 37), *M. musculus* (21, 32), *Rattus rattus* (38–40), and *Sorex araneus* (41, 42) contain examples of populations distinguished by monobrachial fusions. Furthermore, in the model, the effectiveness of reproductive isolation becomes greater as the number of monobrachial fusions that distinguish species (21, 32, 36–41) increases. In *Rhogeessa* (37, 38), *Mus* (21, 32, 36), and *Sorex* (42, 43), species isolated by monobrachial fusions are usually distinguished by more than one such fusion and some species are distinguished by as many as nine different monobrachial fusions. The types of complex meiotic formations that must develop if pairing is normal for two such species of *Rhogeessa* (37) are diagrammed in Fig. 1c. As noted by Capanna (21), the balanced gametes made by monobrachial hybrids either reconstruct the hybrid state or rebound to a parental state. Hence, unlike many barriers that tend to weaken or introgress under recurrent hybridization, this model does not.

The above mentioned taxa of mammals in which this type of speciation appears to have occurred are all locally common and broadly distributed. They are representative of the three largest orders of mammals (Rodentia, Chiroptera, Insectivora).

DISCUSSION

Speciation by monobrachial centric fusion is a special case and not applicable to most mammalian speciation. Nonetheless, for the above examples the taxonomic diversity (21, 32, 36–41) and the breadth of biological parameters (demography, litter size, longevity, etc.) (21, 36–41) that are characteristic of these taxa imply that speciation by monobrachial centric fusions can be expected to be phylogenetically widespread within the class Mammalia.

The time constraints for the development of reproductive isolation of populations through the fixation of monobrachially homologous centric fusions are a function of the time required to fix centric fusions in separate populations. Capanna (21) concluded that 22 different centric fusions have been fixed in *Mus* populations during the past 6000 years. Under such circumstances as found in *Mus* (21) and *Oryzomys* (31), the potential for relatively rapid speciation is apparent.

The model of speciation by monobrachial centric fusions is not a specialized example of White's (2) stasipatric speciation. First, in stasipatric speciation the effectiveness of a chromosomal rearrangement in producing a fertility barrier was the same during its establishment in a population and later as a postmating reproductive isolating mechanism. White did not recognize the potential of synergistic effects for the production of a fertility barrier by different chromosomal rearrangements becoming established in separate populations.

Second, White claimed that in the stasipatric model the chromosomal change was primary (required no geographic isolation of populations) and that any geographic isolation was secondary. We agree with Mayr (3) and Key (11) that geographic isolation is primary and that a contact zone between the populations containing monobrachially homologous centric fusions would be the results of secondary contact (as shown in Fig. 2).

The model proposed herein is based in part on the studies of *Mus*. Two other models, Capanna's emblematic model (21) and White's chain process (4), have been based entirely on

the empirical data from *M. musculus*. In Capanna's emblematic model (21), the effectiveness of monobrachial homology in reproductive isolation is clearly defined. [The idea of differential fitness in *Mus* due to monobrachial homology was introduced by Gropp *et al.* (32).] However, Capanna (21) perceived speciation in *Mus* as resulting from the unique commensal relationship with humans, which facilitated the initial fixation of centric fusions through inbreeding and drift in microdemes. Capanna (21) interpreted the conditions associated with *Mus* as being so unique that his model has limited applicability to chromosomal speciation in general. The emblematic model as outlined by Capanna (21) clearly encompasses explanations of the situation associated with *Mus* that are not relevant to some other species that we think have speciated by monobrachial centric fusions. It is not our intent to explain all the aspects associated with a single organism, as did Capanna in his excellent papers on *Mus* (21, 36), but rather to propose a model that has broad applicability to any species group that undergoes chromosomal evolution involving monobrachial centric fusions being established in separate populations.

White's chain process of speciation (4) envisioned reproductive isolation being established through the successive fixation of numerous chromosomal rearrangements (not restricted to centric fusions) in an area effect population. White's chain process was a modification of the stasipatric model and involved sympatric speciation. White did not envision the difference in degree of reproductive isolation provided by monobrachial homology as compared to trivalent formation for centric fusions.

One of the interesting aspects of speciation by monobrachial centric fusions is that reproductive isolation can be achieved between two or more populations that possess derived karyotypes while these incipient species maintain reproductive compatibility with populations possessing the primitive acrocentric karyotype. A spectrum of possibilities exists regarding the fate of such incipient species. In *Rhogeessa*, no population has been identified as possessing the assumed primitive acrocentric karyotype, and each of the chromosomally derived species appears to be reproductively isolated (37). In *Mus*, at least some of the derived populations appear to have maintained compatibility with the primitive acrocentric form, which is broadly distributed (21).

The model of speciation by monobrachial centric fusions is uniquely concordant with a growing body of empirical data from mammalian populations. Probably more than any other model of speciation, the situation associated with speciation by monobrachially homologous centric fusions lends itself to experimentation with the scientific method. It is easy to identify which populations are distinguished by monobrachially homologous fusions and to design tests on the degree of sterility, genetic and morphological differentiation, compatibility with other populations, gene flow, differential fitness, etc. If the quality and types of studies that have been conducted on populations of *Mus* with monobrachial fusions (21, 32, 36, 44, 45) are any indication, our understanding of population aspects of the speciation process will profit significantly.

This model is dedicated to the memory of Professor Robert Matthey, who in describing a "Robertsonian Fan" (46) based on nondifferentially stained karyotypes in *Mus (Leggada)* probably uncovered the first example of speciation by monobrachial centric fusions. We thank Ernst Mayr, Alan Templeton, Craig Moritz, Rodney Honeycutt, John Patton, Karen McBee, Craig Hood, Mazin Qumsiyeh, Ron Chesser, Robert Owen, J. Knox Jones, Jr., Steve Carr, and Gordon Jarrell for critically reading earlier drafts of this paper. This work was supported by National Science Foundation Grants PCM-8202794 and DEB-8107039.

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