

# Points of View

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## Reassessment of the Nature of Chromosomal Evolution in *Mus musculus*

It is well documented that rates of chromosomal evolution and the kinds of rearrangements involved vary markedly among taxa. This has led to the formulation of models that seek to identify biological factors that promote rapid chromosomal evolution. For the most part, these models focus on population genetic parameters under which a newly arisen chromosomal mutation would have a finite probability of becoming established. Most models assume that rearrangements of the chromosomes do not affect the function of genes and thus have no effect on the phenotype of the organism. They also assume that some degree of sterility is produced in the heterozygote due to an impairment of normal meiosis. Under these conditions, chromosomal evolution will be most rapid in species that possess small deme sizes because sampling errors due to stochastic events are what drive the rearrangement to fixation through the heterozygosity bottleneck. There is a finite probability of this occurring only in small demes. This may result not only in chromosomal evolution, but also in speciation (termed stasipatric speciation). We will collectively term these models the deme size model and note that they derive from the population genetics of Sewell Wright. Among the most important contributors to the development of the deme size model are M. J. D. White (1968, 1973, and 1978a), Bush (1975), Bush et al. (1977), Wilson et al. (1975), Arnason (1972), Hall (1973), and Lande (1979).

Still another model of chromosomal

evolution (White, 1978b) is based largely on work done by E. Capanna, A. Gropp, and their colleagues (see references in White, 1978b) on Italian and Swiss populations of mice of the *Mus musculus* complex. The model, termed "chain processes in chromosomal speciation," is an explanation of why some groups of animals have acquired numerous rearrangements, apparently during stasipatric speciation. Several populations of *Mus* are known to differ from the primitive  $2n = 40$  karyotype (all acrocentric autosomes) by as many as 9 and as few as 3 fusions. White considers this group of animals to exhibit a phenomenon known as area effects in which populations possess coadapted gene complexes that differ from other populations. Chromosomal rearrangements spread throughout the area effect population in spite of reducing the fertility of heterozygous individuals. Once the population has become fixed for the rearrangements, however, it will be more "fit" because its coadapted gene complex will be protected from the disruptive effects of introgression from neighboring populations.

This model is quite different from the deme size models mentioned above in that it considers populations with large numbers of demes, inbred to varying degrees but of essentially continuous distribution. It does not invoke founder effects, local extinctions, invasions, or phenotypic effects of the rearrangements. "It seems no longer necessary to assume . . . that the rearrangements that are adaptive in the homozygous state produce a

specific effect on the phenotype" (White, 1978b).

We see several problems with the model of White (1978b). 1) It invokes group selection rather than individual selection or genetic drift. "The effect of a structural chromosomal rearrangement in isolating a local population, or group of local colonies, from the disruptive effects of introgression, would operate partly through group selection rather than individual selection" (White, 1978b:294). As Williams (1966) pointed out, group selection is an unparsimonious explanation that should be invoked only when natural selection cannot explain a phenomenon. It should be emphasized that whether or not group selection ever occurs in nature is not at issue here. What is at issue is determining what is the most parsimonious explanation of the observed chromosomal evolution in *Mus*.

2) It is unclear to us how White envisions group selection to operate under this model. He states: "Near the boundary between the two main populations, those demes in which the fusion (or other rearrangement) has reacted [sic] fixation will be more successful than those in which it is present as a polymorphism" (White, 1978b:294). But he goes on to state that his model "does not invoke founder effects, local extinction of populations or invasions of occupied or unoccupied territories by individuals" (White, 1978b:295). However, group selection is a process which requires the frequent extinction of local populations, those populations that are best "fit" due to the presence of some altruistic trait have a greater likelihood of survival than populations that do not (Williams, 1966).

3) A third problem is that White's model is based on *Mus musculus*, a species complex that exhibits karyotypic orthoselection. White has argued that orthoselection is due to natural selection favoring identical rearrangements because they impart similar adaptive effects (White, 1975).

4) White assumes that chromosomal rearrangements reduce heterozygote fer-

tility, yet the *Mus* populations at Val Bregaglia and various populations in the Grisons and eastern Dolomites are polymorphic for various fusions. The Chiavenna population is polymorphic for fusions 1, 7, and 8 and may represent a hybrid population between Poschiavo and Mesolecina mice ( $2n = 26, 28$ ) with a  $2n = 40$  population. The rearrangements do not seem to be functioning according to White's model in this instance. Additionally, there are known populations of *Mus* that are reproductively isolated but karyotypically identical indicating that chromosomal rearrangements are not necessary for speciation in the group. Why then assume that they are the *de facto* cause of speciation when they may only represent an adaptive feature rather than a relatively ineffective isolating mechanism (see 5 below)?

5) For most cases of stasipatric speciation a single fusion (or fission) is enough to ensure speciation (White, 1978a) but in *Mus*, populations that differ by three such rearrangements freely interbreed. He states on p. 294 "the extent of introgression is diminished by the establishment of each successive fusion and it may take as many as nine to reduce it to a negligible state." From this, one might conclude that the low number of rearrangements (fissions or fusions) usually found between chromosomal races would be insufficient to cause speciation.

6) White says that the initial chromosomal rearrangement spreads out until it covers the area effect population but then stops (White, 1978b:294). If this is a continuous series of demes, as he says, what makes it stop? Presumably, if the chromosomes cannot continue to spread, neither can the genes and the coadapted gene complex is already protected by some behavioral or other type of reproductive isolation. Fixation of a new neutral chromosomal rearrangement cannot be explained in this instance by group selection but only by genetic drift. He further states that the next rearrangement will establish itself only if the first is insufficient to completely arrest introgression.

sion (p. 295). What regulatory mechanism exists that could perceive the presence or absence of introgression and then make the proper decision to favor or prevent the fixation of additional rearrangements?

7) White has not addressed the fact that, in general, species of *Mus* are karyotypically conservative (Hsu et al., 1978) with many species being homosequential. What is so unique about the *M. musculus* populations in Italy and Switzerland that they are undergoing such extensive chromosomal evolution while other populations of this species are not? It stands to reason that other species of *Mus* and other populations of *M. musculus* also have equally restricted vagility with small deme size and exhibit area effects. White suggests that the karyotypic evolution in these populations of *M. musculus* has occurred within the last 3,000 years due to changed conditions from agricultural practices. If this is true, then a model explaining karyotypic evolution as an adaptive process having been initiated by a change in relative fitness of individuals as a result of changing environmental conditions would seem more plausible.

We conclude that White has not made a convincing case for group selection in his "chain processes" model. It appears to us that, rather than group selection, there are four biological parameters which in concert or individually are more probable causes of the patterns of differential rates of chromosomal evolution in vertebrates: (1) variation in deme size and breeding structure (White, 1968; Arnason, 1972; Bush, 1975; Bush et al., 1977; Wilson et al., 1975; Lande, 1979), (2) variation in mutation rates (McClintock, 1978; Lande, 1979), (3) presence or absence of mechanisms which reduce meiotic malassortment in the heterozygote (White, 1973) and (4) chromosomal rearrangements which produce a positive phenotypic effect in both the heterozygote and new homozygote sufficient to outweigh the negative fitness resulting from meiotic problems in the het-

erozygote (Bengtsson and Bodmer, 1976; Bickham and Baker, 1979). However, the relative importance of these four parameters remains a question elucidated by little fact.

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JOHN W. BICKHAM

*Department of Wildlife and  
Fisheries Sciences  
Texas A&M University  
College Station, Texas 77843*

ROBERT J. BAKER

*Department of Biological Sciences and  
The Museum  
Texas Tech University  
Lubbock, Texas 79409*

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### Taxonomic Congruence: Rohlf and Sokal's Misunderstanding

Over much of its history, the phenetic position on the reasons for neglecting phylogenetic principles in classification has remained little changed. The same red herrings persist, such as: major groups "ought" to be separated by gaps; that phylogenies, being representable in pictorial form, need *ipso facto* not be represented in classification; or that grouping by raw similarity must logically be the best way to produce a stable, informative system. A striking feature of all this advocacy is that it has never possessed any objective force. Pheneticists' claims on stability and information content, though often recited, were never substantiated empirically. Recent work (Farris, 1977, 1979a, 1979b) has shown that pheneticists' claims for superior information content for their arrangements are false. My own research has had the same effect on claims of stability for phenetic arrangements. As Farris (1979b:518) summed up: "Advocacy of phenetic or syncretistic arrangements as the general reference system has never had any logical basis, but was grounded instead only in misunderstanding of the properties of methods of classification."

The major advocates of phenetics were notably silent as these new analyses were published. But, Rohlf and Sokal (1980) have at last decided to oppose these advances in understanding of the properties of methods, objecting on a variety of pre-

texts to my (1978) conclusions on taxonomic congruence. I was surprised—although, perhaps, I should not have been—to see that their arguments are much the same as have been customary among pheneticists. They dispute the meanings of words, and, while offering no empirical work express disbelief in previous results, rationalizing this, sometimes, with conjectures on the outcomes of conceivable investigations not yet undertaken. Acceptable as such reasoning may be among pheneticists, I am more interested in empirical and substantial issues than in choosing wording so as to bolster preconceived notions, and more intent on making progress on such issues than on hindering it. It can only invite confusion to leave the nature and implications of my work so obscured as Rohlf and Sokal would seemingly have them. Thus I aim to show here in detail how the discussion of Rohlf and Sokal reflects only "misunderstanding of the properties of methods of classification."

Much of the comment by Rohlf and Sokal (1980) is devoted to discussing the meaning of "stability." At first, they seem to express uncertainty on the use of the term, as it appears in *Taxonomic Congruence*, by commenting (p. 97): "Much of the discussion in the paper revolves around the concept of stability, nowhere explicitly defined." They then list what they consider to be the "types" of stabil-