



Review: Chromosomal Speciation

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BOOK REVIEWS

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CHROMOSOMAL SPECIATION¹

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Species Evolution: The Role of Chromosome Change by Max King, is an update of the argument made by the late M. J. D. White (1978) for the primacy of chromosomal rearrangements in speciation via the fixation of underdominant rearrangements and their contribution to postmating isolation in hybrid zones. The author pulls no punches about his own position, stating clearly at the outset that “This book is written about the two most common forms of speciation in bisexual plants and animals, the non-chromosomal forms of allopatric speciation and the processes of chromosomal speciation” (p. xvi). King covers this subject matter in 11 chapters, and summarizes information from 540 references dating from 1857 through 1991. Because the book has already been briefly reviewed by Butlin (1993) and Coyne (1993), I focus most of my comments on the specifics not dealt with by those authors.

Chapter 1 outlines King’s views of what has transpired in evolutionary theory since White’s (1978) book was published and summarizes the organization of his own book. King stresses that there has been an overemphasis on allopatric speciation at the expense of the vast amount of new data supporting one or more chromosomal speciation hypotheses. The tone of writing evident in this chapter resurfaces periodically throughout the rest of the book; King states that many of the data presented in his book had been previously downgraded or ignored by other workers (particularly in North America) in favor of other speciation mechanisms. A more accurate assessment would have been to acknowledge a number of post-1978 reviews (Futuyma and Mayer 1980; several papers in Atchley and Woodruff 1981; and others in Barigozzi 1982; Hall 1980, 1983; Patton and Sherwood 1983; Barton and Hewitt 1985; De Boer 1986; King 1987; Sites and Moritz 1987; some papers in Daniel 1988), and papers dealing with selected conceptual points (cited in recent papers by Barton and Rouhani 1991; Barton 1992; Fontdevila 1992; King 1992; Spirito 1992; Michalakis and Olivieri 1993; Searle 1993; and Sites and Reed 1994), and then state unequivocally what the unresolved issues are. Many of these papers are considered in later parts of the book, but the slant of this chapter wrongly implies that few others have thought much about these issues since 1978.

Chapters 2, 3, and 4 review species concepts, and several interrelated issues of genetic variability, allopatric divergence, and founder effects. Because King is arguing for a major role for chromosomal rearrangements in establishing profound reproductive isolation between hybridizing populations (pp. 29–30), his case is based on selection for repro-

ductive isolation and is thus best served by the biological species concept. He nevertheless reviews recognition, cohesion, ecological, evolutionary, and phylogenetic species concepts, and is especially critical of the PSC (p. 26), because the hierarchical level at which species are diagnosed may be a function of the characters used. Here his argument would have been strengthened by reference to the “concordance principles” proposed by Avise and Ball (1990), which call for the use of multiple data sets and establish conservative guidelines to define species boundaries. Concordance principles capitalize on the strengths of both biological and phylogenetic species concepts (see also Kluge 1990) and offer an operational way out of the problem of defining “unknown future potential” in cases of ongoing hybridization and for the PSC (O’Hara 1993).

Some of the arguments made in chapters 3 and 4 are based on dated literature and are therefore misleading or incomplete, and others seem internally contradictory. For example, King is critical of the need for a sympatry test to establish the certainty of biological species in nature, but seems to endorse a definition by Key (1981) that requires a “parapatry test” to determine whether or not two populations will hybridize (p. 33). The entire section on genic variation (pp. 34–37) relies heavily on dated literature (with few exceptions) and could have benefited from a more recent review (Murphy et al. 1990) of the strengths and limitations of allozyme data in estimating divergence between populations and species. The statement that “In eukaryotes, most of the gene systems that are responsible for major reproductive functions consist of multigene families which act in concert to produce an integrated end-product in the final phenotype” (p. 46) needs documentation. King calls into question the utility of allozyme data as a valid test for past population bottlenecks (pp. 69–71) but fails to cite several important papers showing that estimates of different aspects of nuclear genetic variability (e.g., heterozygosity vs. mean number of alleles per locus) behave differently during and after bottlenecks. Under certain demographic conditions, these estimators may retain the signal of a population bottleneck (Nei et al. 1975; Chakraborty and Nei 1977; Sirkkoma 1983; Maruyama and Fuerst 1985). A more serious omission is the failure to mention the increased sensitivity of mtDNA markers for such tests, because of reduced effective population sizes associated with matrilineal inheritance (Birky et al. 1983, 1989).

Chapter 5 presents a thorough overview of what kinds of chromosomal rearrangements act as postmating isolating mechanisms, and under what conditions and by what mechanisms these operate. There are few generalities because the same kind of rearrangement may segregate in a balanced manner in one species and yet be strongly underdominant in

¹ *Species Evolution: The Role of Chromosome Change*. Max King. Cambridge University Press, New York. 1993. xxi + 336 pp. \$59.95 cloth.

another (e.g., Coyne et al. 1991). For this and other reasons, King seems to think that the theoretical studies published to date (through 1991) are “wasted effort” because they used a faulty data base and have not focused on “particular types of rearrangements in isolation” (p. 91). I found this overly pessimistic; analytical or simulation studies must make assumptions about such things as selection, drift, gene flow, and meiotic drive, and these then permit modeling of demographic or genetic parameters that show conditions under which strongly underdominant rearrangements may be fixed, spread, and contribute to postmating isolation. Although always oversimplified, the models frequently have corollaries (i.e., the permissible population structure or mating system for a given outcome) that can be tested in nature. As in any other discipline, models can be improved upon with larger empirical data bases, but this by itself does not detract from the heuristic exercise of model building.

In chapter 6, King summarizes data relevant to the issues of the origin and fixation of chromosomal rearrangements in natural populations. Here substantial progress has been made since White (1978) proposed that random arrays of rearrangements were produced by mutation, and only a subset of these later become fixed. Molecular studies have revealed immense complexity in the structure of the eukaryote genome, and this structure may constrain the types of chromosomal mutations possible (King gives several examples [pp. 97–101]; see review by Holmquist and Filipowski 1994). King also correctly points out that several mechanisms, including recurrent origin of the same rearrangement(s) and meiotic drive, would offer a way around the constraints required by models assuming strong underdominance and requiring fixation to occur primarily by drift. This has been shown earlier in a number of theoretical treatments (e.g., Hedrick 1981), but King argues strongly that stochastic processes have been overemphasized and that sufficient evidence has accumulated in favor of meiotic drive that it must now be considered as an alternative. King describes several examples of segregation distortion for chromosomal polymorphisms, but as pointed out by Coyne (1993), few of these distinguish meiotic drive from viability effects, and King fails to cite the one experimental test of this possibility, which gave negative results (Coyne 1989). Meiotic drive also requires the co-occurrence of uncommon events; the origin of a chromosomal rearrangement linked to the origin of a meiotic-drive mutation. Contra King’s claim “that meiotic drive is a significant evolutionary mechanism which can no longer be ignored” (p. 116), this alternative to selection and drift remains unsubstantiated as a factor of major importance (Coyne and Orr 1993).

Chapter 7—the impact of structural hybridity on fertility and viability—deals with a central issue of the chromosomal speciation debate; do rearrangements contribute significantly to fitness loss (by any of a number of mechanisms) in heterozygous karyotypes in hybrid zones? King first provides a review of a number of well-known systems in which meiotic behavior and fitness effects of specific rearrangements are well documented, including several in which nondisjunction and gametogenic impairment is high in hybrid crosses. Much of this type of evidence, however, comes from crossing either distinct lab lines of *Mus*, or crossing taxa that appear not to

hybridize in nature. Although not irrelevant to the speciation issue, it is difficult to determine in these cases how much of the postzygotic isolation was actually associated with speciation (or at least allopatric divergence) and how much has accumulated since then (e.g., in *Equus*, pp. 151–153).

Much is made of minimum allozyme differences between populations as evidence for little or no divergence in “genic” backgrounds, but given the very tiny portion of the nuclear genome sampled by this method, and the myriad of other ways that genomes may differ from each other in the absence of allozyme divergence, genetic distances can serve as no more than crude indicators of total genome divergence. I think few would fully endorse King’s statement that “The elimination of the genic component in organisms such as *Rattus* and *Mus* (since the chromosome races are genically indistinguishable in terms of electrophoretic, mtDNA, or immunogenetic differences), leaves nothing but a chromosomal mechanism that can be associated with induced sterility” (p. 168). Later in the book, for example, King describes a well-known case in which ethological and physiological differences have been established between hybridizing chromosomal races, despite the absence of “genic” change (the *Spalax ehrenbergi* complex, p. 183).

Although allozyme identity between parents of chromosomal hybrids certainly strengthens the case for major chromosomal contributions to fertility loss (whether this alone will lead to speciation is a separate issue, see below), there are other examples of fertility loss in hybrids between closely related, chromosomally indistinguishable taxa (e.g., *Bos*, p. 166), which must result from other genomic differences. The larger issue here is, in cases of continued natural hybridization between chromosomally differentiated populations, is gene flow severely restricted across the zone, and is selection against hybrid genotypes strong enough to favor the evolution of premating isolation? Recent reviews of hybrid zones (Barton and Hewitt 1985; Harrison 1990) show that a large range of possible outcomes have been documented in nature, suggesting that generalizations about the influence on hybrid fitness of both chromosomal rearrangements and genetic background are elusive.

In chapter 8, King addresses the genic change issue head on and states that “If it can be consistently demonstrated that chromosome races which are distinguished by fixed chromosome differences are established before genic or morphological changes have reached fixation, then it follows that chromosome change is the primary and causative factor in speciation and other changes are secondary” (pp. 171–172). He then gives two assumptions critical to the assessment of genetic diversity between chromosomally differentiated populations (or species), both based on the use of genetic distances to infer relationships and relative ages of the chromosome races under consideration. Besides being based on dated opinions about the validity of protein-based molecular clocks (for a recent review, see Gillespie 1992), King’s approach reflects a lack of appreciation for the power of phylogenetic methods to provide independent tests of many of the assumptions of character evolution (i.e., the direction of chromosome change) in many of the case studies he describes. For example, King argues that the order of derivation of chromosome races in the *Sceloporus grammicus* complex

was nearly linear, as originally suggested by Hall (1980, 1983). Yet a study of phylogenetic relationships of the members of this complex, on the basis of mtDNA sequences, showed a much more complex pattern of chromosome evolution that requires independent origins of some races and of several polymorphisms within races.

The remainder of this chapter describes numerous examples of chromosomal polytypism in several groups of rodents (*Acomys*, *Gerbillus*, *Peromyscus*, *Proechimys*, *Rattus*, *Spalax*, and *Thomomys*), bats (*Rhogeessa*), shrews (*Sorex*), and lizards (*Gehyra*, *Phyllodactylus*, and *Sceloporus*). Many of these groups do appear to have "speciation potential" based on chromosomal rearrangements, but in most descriptions, extremely complex systems are unavoidably presented in condensed summaries that do not do justice to any of the taxa. As one example, King presents some sweeping generalizations about my own work on the *Sceloporus grammicus* complex that are not supported by critical examinations of the data. Porter and Sites (1987) showed that levels of meiotic malassortment in chromosomal heterozygotes in some hybrid (F₁-like) animals were no higher than those for chromosomal homozygotes, or nonhybrid animals segregating similar rearrangements as within-population polymorphisms. Sites and Davis (1989) presented a molecular phylogenetic hypothesis for the derivation of chromosome races that contradicted the strictly linear sequence by Hall (1980) and presented some evidence for mtDNA introgression across boundaries of chromosome races. Although based on limited samples in some cases, no objective review of the evidence would support King's claim that "Most recent evidence supports the model of speciation presented by Hall and Selander (1973)" (p. 189). More detailed phylogenetic and hybrid-zone studies (Sites et al. 1995) of this complex (1) have verified earlier conclusions of a nonlinear sequence of derivation of the races (Arévalo et al. 1994) and absence of meiotic effects in hybrid zones for the rearrangements diagnostic of most races (Reed et al. 1995a); (2) have shown that fitness in females is a function of both karyotype and position in the hybrid zone (Reed and Sites 1995); and (3) have shown that one example of a single complex rearrangement may contribute significantly to fitness reduction because of meiotic malassortment in males (Reed et al. 1995b). I use this system simply as an example of the kinds of data that can be brought to bear on the issue of chromosomal evolution and speciation and of the difficulty of unambiguously assigning a major role to structural rearrangements alone.

In the "Concluding Remarks" section of this chapter, King summarizes the three major assumptions made about the primacy of chromosome change during speciation, and then the eight salient features of the complexes reviewed as case studies (p. 205). Most of these center on characteristics of parent and daughter chromosome races and imply that the direction of karyotypic evolution is known. Here again the need for phylogenetic testing stands out as an unknown piece of the puzzle for most of the examples described in this chapter. On page 206, King argues that studies interpreting genetic similarity between hybridizing taxa (based on assessment of allozyme frequencies), as a possible consequence of gene flow, are fatuous because such studies cannot provide any evidence for gene flow. Such a statement should be qualified

in the context of several recently developed methods for estimating gene flow from either geographic variation in allele frequencies or their cladistic structure (reviewed in Slatkin 1994a, 1994b). These kinds of omissions permit sweeping generalizations that, in my opinion, are not warranted for most of the examples presented in this chapter.

Chapter 9 summarizes the major chromosomal speciation hypotheses, which can be divided into those requiring the origin of a novel form within the distribution of its ancestor versus those in which a new race is postulated to originate outside of the ancestor's range. King reviews the relevant models within each of these, and concludes that most evidence supports the "external" modes. These require fixation of negatively heterotic chromosomal differences in founding populations, which subsequently make contact with the parental species to form a "hybrid zone which is an impermeable barrier to gene flow" (p. 244). The major weakness in King's development of this theme is his failure to integrate the ideas into the broader contexts of hybrid-zone and speciation theory (see chapters in Harrison [1993] and Otte and Endler [1989], respectively), which is essential to making a complete case for speciation by any of the mechanisms described.

Chapter 10 is a useful review of several molecular mechanisms that drive or influence chromosomal evolution, particularly with regard to mutation rates and the production of novel rearrangements.

Chapter 11 synthesizes the data and arguments presented throughout the book and repeats the same omissions described above: failure to integrate observations or assertions into a phylogenetic framework or to synthesize the same observations into the broader context of hybrid-zone or speciation theory. A possible reason for the exclusion of detailed consideration of hybrid-zone literature is evident in King's statement that "It is my perception that the study of hybrid zones is not the key to our understanding of speciation processes" (p. 285), despite his claim on page 244 that hybrid zones must function as impermeable barriers to gene flow to effect chromosomal speciation. At the very least, some consideration of reinforcement processes should be given somewhere in chapter 9 or here (reviewed by Howard 1993). In the few cases where use of indirect methods to estimate gene flow is discussed, as with the plethodontid salamanders (original paper by Larson et al. 1984), King concludes that species do not generally comprise units connected by gene flow. Here, however, most of the allozymically distinct units within complexes of salamanders of similar morphologies are considered cryptic species (Larson 1989), so that extensive gene flow between these is not expected.

In my opinion, a more inclusive view of the evolutionary literature suggests that, to make a really strong case for speciation based on chromosomal rearrangements, one must at minimum demonstrate three facts. (1) Organisms heterozygous for one or more rearrangements suffer significant fitness reduction in a natural hybrid zone entirely or mostly because of structural heterozygosity (this could be by any number of well-known mechanisms; for a review, see Searle 1993). (2) These rearrangements were established simultaneously with, or before, any other genetic, ecological, or behavioral differences that might also contribute to partial reproductive isolation (this will require a phylogenetic hypothesis for in-

ferring the order of appearance of other divergent traits; Brooks and McLennan 1991; but see Frumhoff and Reeve 1994). (3) Selection against the structural heterozygotes in the hybrid zone is strong enough to initiate a reinforcement process that could lead to speciation (reviewed by Howard 1993). This last condition alone has its own set of minimum requirements, most notably that reproductive character displacement has occurred and that it did so as a consequence of selection against hybrids, and not for other (ecological) reasons (Howard 1993). King does not appear to appreciate the kinds of inferences that can be drawn from multidisciplinary studies of hybrid zones (Harrison 1990, 1993; M. Arnold 1992; J. Arnold 1993), and there are no unambiguous cases presented in this book that meet all of these criteria.

King seems to reverse himself on the importance of studying hybrid-zone dynamics, stating first that they are unimportant to understanding speciation (see quote above from p. 285), but later saying "However, the key to our understanding of chromosomal speciation still lies in the analysis of hybridization and the coupling of this to sophisticated cytogenetic and molecular techniques which can break down the components responsible for the formation of reproductive isolating mechanisms between species" (p. 290). No mention is made of the value of studying heritabilities of morphological, behavioral, or vocal (where relevant) characters, which would provide insight into what characters are capable of responding to selection, or of placing all of this in an ecological context. King's disdain for the use of phylogenetic methods overtly manifests itself in this chapter: "The born-again cladists who have not only constructed their own language, think their own logic, and are obsessed with phylogenetic relationships to the exclusion of all else, now require their own species definitions" (p. 289). There is room for disagreement on views of species and many other things in contemporary phylogenetic systematics, but such writing is guaranteed to isolate, rather than integrate, the subdisciplines that should be complementary parts of speciation investigations.

In summary, I share Butlin's (1993) view that, despite his claim to provide a "broad and integrated view of the concept of chromosomal speciation" (p. 3), King has failed to integrate the specifics of chromosomal polytypy into a larger evolutionary perspective. His book summarizes a lot of new observations, but no synthesis has been achieved.

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HYBRID ZONES¹

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Hybrid zones entered the evolutionary literature through systematics, because of the challenge they presented to those who would have liked their species to be clearly demarcated. The patterns of variation in hybrid zones were among the important factors that led systematists with an interest in evolutionary processes to articulate the biological species concept and to develop arguments for the ubiquity of allopatric speciation, the coadaptation of species' gene pools, and the origin and nature of reproductive isolation (Mayr 1963). More recently, hybrid zones have served as "windows on evolutionary process" (Harrison 1990), providing opportunities for studying the effects of gene flow, linkage, and several forms of selection on genetic dynamics.

¹ *Hybrid Zones and the Evolutionary Process*. Richard G. Harrison, ed. x + 364 pp.; ill.; index. Oxford University Press, New York and Oxford. 1993.

What should we hope to learn from studying hybrid zones? We might expect insight into some traditional questions about speciation: whether it occurs not only by allopatric divergence but also by any of several parapatric processes; whether prezygotic reproductive barriers evolve in response to selection for isolation; what the nature of genetic differences among species is, and why differences evolve; what the outcomes may be of contact between species *in statu nascendi*. We might use them to learn about epistasis, and the factors that cause population divergence. And there are questions about hybrid zones in their own right: Do they move? Are they the locus of novel genetic variation? Does hybridization transfer adaptations among species, give rise to new adaptations, or give rise to new species?

These are among the questions posed by the authors of the twelve chapters of this book, of which four review conceptual issues and eight describe case studies. As the editor, Richard