Shrews, Chromosomes and Speciation

The chromosome complement (karyotype) often differs between related mammalian species (including humans versus chimpanzees), such that evolutionary biologists muse whether chromosomal difference is a cause or a consequence of speciation. The common shrew is an excellent model to investigate this problem because of its many geographical races (potential species) differing chromosomally, and its several sibling species (recently speciated forms) that are also chromosomally different. This system is an exceptional opportunity to investigate the role of chromosomes in speciation and this volume reflects detailed research following these approaches. Highlights include the demonstration that chromosomal rearrangements can be associated with complete loss of gene flow and thus speciation, and that selection within species hybrid zones may lead to de-speciation rather than speciation. This book represents an extraordinarily detailed consideration of the role of chromosomes in speciation in one astonishing species, providing insights to those interested in mammalian diversity, chromosomal evolution and speciation.

Jeremy B. Searle is Professor of Evolutionary Biology at Cornell University, Ithaca, NY. He has studied the evolutionary biology of small mammals, including research into colonisation history, speciation and chromosomal evolution. His PhD was on the chromosomes of the common shrew and he founded a series of triennial international meetings that continued for 21 years and stimulated much of the work in this book.

P. David Polly is a vertebrate palaeontologist at Indiana University in Bloomington. He studies the evolution of mammals and other vertebrates in the fossil record, including trait-based studies of community response to environmental change, geometric morphometric analysis of evolution and morphology, phylogenetics, biogeography, and speciation on regional and continental geographic scales.

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Preface

From the earliest studies of chromosome complements (karyotypes) of animals and plants, it has been found repeatedly that closely related taxa differ in numbers of chromosomes and the morphologies of those chromosomes. Even early researchers realised that this need not be a coincidence, and that karyotypes could be implicated in speciation. Case studies and mechanisms were argued in a variety of seminal papers, such as Winge (1917; The chromosomes: their numbers and general importance), Müntzing (1930; Outlines to a genetic monograph of the genus *Galeopsis*), Painter and Stone (1935; Chromosome fusion and speciation in Drosophilae) and Wright (1941; On the probability of fixation of reciprocal translocations). Cytotaxonomic studies continued and come the 1970s a remarkable set of books synthesised the considerable knowledge that had accrued by that time: *Chromosomal Evolution in Higher Plants* (Stebbins, 1971), *Plant Speciation* (Grant, 1971), *Animal Cytology and Evolution* (White, 1973), *Cytotaxonomy and Vertebrate Evolution* (Chiarelli and Capanna, 1973), *Mammalian Karyosystematics* (Orlov, 1974) and *Modes of Speciation* (White, 1978). These books influenced the whole field of evolutionary biology, and really are the bedrock of our understanding of chromosomal evolution and the role of chromosomes in speciation. Methodical approaches to mammalian cytology were more complicated compared with plants and other animals (particularly *Drosophila*), but once they took off in the 1950s, mammals provided some of the iconic examples of extreme rapid karyotype evolution of the sort that may have a relevance to speciation, such as the Indian muntjac (Wurster and Benirschke, 1970; Indian muntjac, *Muntiacus muntjak*: a deer with low diploid chromosome number) and the Poschiavo mouse [Gropp *et al*., 1969; Chromosomenuntersuchungenbei der Tabakmaus (*M. poschiavinus*) und bei Tabakmaus-Hybriden]. It is interesting that it was in the same period of frenetic activity of cytotaxonomy that the one existing monograph about the chromosomes of one species of mammal was published: T. H. Yosida's (1980) *Cytogenetics of the Black Rat: Karyotype Evolution and Species Differentiation*.

Now, nearly 40 years later, we have produced the second such monograph, on another small mammal, the common shrew *Sorex araneus*. Without belittling what Yosida achieved, which was considerable, comparing his volume with ours is like comparing night and day. Evolutionary biology has moved on so much

since 1980. Chromosome variation can now be evaluated in the rich context of speciation theory that has developed since Yosida, including a detailed understanding of the processes that occur within hybrid zones and radical new perspectives on the roles that chromosomes may play in speciation (e.g. Rieseberg, 2001; Chromosomal rearrangements and speciation). The range of genetic markers available to study gene flow and colonisation history is hugely expanded. The study of phenotypes that may be influenced by such gene flow and colonisation history has also moved on, with the new field of geometric morphometrics. The cytological methods to study chromosomal structures and phases of meiosis are massively more sophisticated than they used to be. And so on. All these improvements have been applied to the common shrew. Furthermore, the understanding synthesised in this book reflects the dedication of many researchers, not just one. We are reviewing substantial sets of data accumulated by many individuals over the course of more than four decades. This book thus represents a major update on the state-of-the-art developments since Yosida concerning the role of chromosomal variation in differentiation within a species and in speciation. It provides up-to-date, considered reviews of the best studied wild mammal in terms of chromosomal variation and its consequences. Evolutionary biology has thrived due to detailed studies of single species or groups of closely related species, and we believe that our book will be of interest to the large community of evolutionary biologists working on speciation and the racial subdivision of species and hybrid zones, and as a resource for those teaching these subjects at the university level. Also, cytogeneticists of all persuasions will find this system a fascinating example of the impact that chromosomal rearrangements can have in the natural world. And for mammal biologists, shrews are not high on the charisma scale, but they should be!

The researchers who, through enormous dedication over recent years, have done the bulk of the work on chromosomal variation in the common shrew, have been an extraordinarily close-knit community and this has benefitted the production of this book. Over a 21-year period there were eight regularly spaced meetings of shrew chromosome researchers, which moulded our understanding of chromosome variation in shrews – not through competitive interactions, but through many, many cooperative ventures and friendships where everybody encouraged and fostered everybody else. It was at the last of those shrew chromosome meetings in 2008 in York, UK, that the idea of a book was suggested. Now, 10 years on, and after much scholarly work, the book is completed and published. We are first and foremost grateful to the authors for this effort, and the way that they have made their chapters as comprehensive, balanced and interesting as possible. We are grateful for their patience and their continued dedication to the project at all times. Taking all the chapters together,

the book covers a very large amount of ground and provides an extraordinarily detailed picture of the consequences of chromosomal variation in the common shrew, and its role in speciation. As well as writing their own chapters, the authors have advised on other people's chapters, and that service has been much appreciated. Nina Bulatova, Svetlana Pavlova and Jacques Hausser have been particularly supportive and encouraging throughout, and Jacques deserves special thanks for his wonderfully witty and apposite cartoons throughout the book. As well as thanking the authors, we are very grateful to the staff at Cambridge University Press for their patience and friendly help at all times. They have been a superb support. Finally, we would like to express our sadness that Gregg Gunnell (series editor) and Włodzimierz Chętnicki and Natalia Moraleva (authors) are not able to see the published version of the book, because they died before its completion – we miss them.