

Marking the spot

Microsatellites: Evolution and Applications

edited by D.B. Goldstein
and C. Schlötterer

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Since their discovery less than two decades ago, microsatellites have revolutionized molecular biology, molecular evolution, functional genetics, quantitative genetics, population biology and evolutionary biology. Accordingly, the intention of *Microsatellites: Evolution and Applications* is to '... serve the interests of the widest possible range of biologists using microsatellite markers ...'. The diversity of topics covered in the book fits this aim and it contains much important information that researchers who use (or should use) microsatellites might otherwise not encounter. For example, Kashi and Soller give an overview of the diverse functional roles of microsatellites, and Eisen reviews mechanisms of microsatellite instability.

Key features contributing to the impact of microsatellites in biology are their hypervariability, their abundance and relative homogeneity through the genome, the fact that they yield frequency and genealogical information, and their assayability by polymerase chain reaction. Molecular evolution and the taxonomic and/or genomic occurrence of microsatellites is represented strongly in the book. The hypervariable nature of the markers makes them suitable for investigations at the fine-scale and/or the short-term end of the hierarchy of life. Accordingly, chapters deal with issues such as estimating the age of new mutations, population expansions, inbreeding, outbreeding, conservation biology, reconstruction of human population history, forensics, recent selective sweeps, human gene mapping and analysis of diseases. Nonetheless, because microsatellites are single-locus, codominant markers, they can be analysed as individual genes, arrays or entities with evolutionary trajectories and relationships. Useable variation at all three levels allows microsatellites to be informative over a broad range of spatial and temporal scales, even in a single study. This and other broader attributes of microsatellites are dealt with a little diffusely, which tends to work somewhat against Goldstein and Schlötterer's aim to '... serve as a resource not only for graduate students, but also for working scientists considering the

introduction of genetic markers in their areas of research'. It would have been better to have at least an introductory chapter to explain why microsatellites have become so important so quickly, to outline their diverse roles in biology and to guide readers around the book.

Important recent developments in microsatellite analysis include methods to use allelic distributions (e.g. frequency and size distributions), correlations among loci (e.g. linkage disequilibrium and likelihoods of genotypic arrays) and genealogical relationships among alleles. The book presents some recent and forward-looking developments in these areas. Estoup and Cornuet, and Beaumont and Bruford provide overviews of the field; and Pemberton *et al.* give worked examples of the recent use of microsatellite data to detect inbreeding and outbreeding (see also Luikart and England¹ who provide a list of computer programs in population genetic analysis, and Refs 2–4 for overviews of microsatellites in population biology).

In examining the relationship between microsatellite characteristics and demography, the apparently disparate fields of molecular evolution and genetic–demographic modelling work synergistically with previously unimaginable outcomes. Expectations about microsatellites under different demographic scenarios can be derived and genetic data can yield demographic inferences, or the converse.

Chapters are contributed by some of the most creative and prominent workers in these fields. Amos's chapter on comparative approaches to microsatellite evolution certainly falls within Goldstein and Schlötterer's aspiration '... to inspir(e) novelty in future projects'. Reich and Goldstein show how to estimate the age of mutations using linked markers, Chakraborty and Kimmel explore the relationship between microsatellite mutation rates and population expansions, and Donnelly's chapter on coalescence is very readable. Several chapters that focus on human populations contain important approaches that would also be applicable more generally (e.g. Balding on forensics, and Ruiz Linares, Stephens *et al.* and Karafet *et al.* on aspects of human population history). Similarly, other chapters with apparently specific remits (e.g. Carrington *et al.* on mapping complex diseases, Schlötterer and Wiehe on selective sweeps, and Shibata on cancer evolution) could provide ideas for researchers in diverse areas.

As with many edited volumes of broad theme, the book suffers from a certain lack of coherence. Chapters are general or specific, conflicting statements often are not acknowledged or resolved (e.g. there is considerable inconsistency about the data concerning mutation models), and many

broader messages have to be derived by the reader rather than being spelt out in synthetic chapters. That said, it is the most comprehensive volume on microsatellites and has contributions from many excellent researchers. I enjoyed, or at least learned a lot from, every chapter; I expect to refer to *Microsatellites: Evolution and Applications* frequently.

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Tracking biogeographic history

Panbiogeography: Tracking the History of Life

by R.C. Craw, J.R. Greham
and M.J. Heads

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The distribution of organisms has long been seen as related to taxic history. If we say that there are marsupials in Australia and South America, and this implies that these two areas have a biogeographic relationship, the accuracy of the statement hinges on conjecture about what a marsupial is and whether the groups in the two areas are related more closely to each other than to a taxon in a third area. Thus, biogeography and systematics are linked inextricably.

Understanding biogeography is, in many respects, a much more difficult problem than understanding taxic history. Not only does the former require the latter, but also

spatial patterns are complex in their own right (e.g. phenomena such as widespread taxa and redundant distributions), and areas themselves have ambiguous geological and ecological histories; all this serves to complicate the reconstruction of how taxa and areas have evolved over time.

Many methods of biogeographic analysis have been proposed and it is clear that no one approach is necessarily superior to another. Each has strengths and limitations in describing and explaining biogeographic patterns. However, this does not prevent advocates of a method seeing their approach as conceptually superior; few methods have had such strong adherents as panbiogeography.

Panbiogeography arose from the work of Leon Croizat in the 1950s and 1960s. Most of his voluminous writings were published privately in book form and have remained relatively inaccessible to mainstream biologists. Although Croizat's thinking has influenced several biogeographers, his persistent champions have been a band of New Zealand botanists and zoologists. In this book, three of these supporters have produced a concise monograph on panbiogeography, which finally summarizes this method for a larger audience. All biogeographers, and those interested in the inter-relationship between geological and biological history, should read *Panbiogeography: Tracking the History of Life*.

Panbiogeography seeks to describe biogeographic history by: drawing a line ('track') between the distributions of related organisms; searching for congruence in these tracks ('standard' or 'generalized' tracks); seeing where standard tracks intersect on a map ('nodes'); describing where the greatest taxonomic diversity is located ('main massings'); and noting correlations between generalized tracks that traverse a geographic or landscape feature ('baseline').

Most applications of the panbiogeography method tend towards the narrative rather than the analytical, at least in the sense observed in vicariance biogeography. In recent years, panbiogeographers have introduced the use of minimum spanning trees to draw tracks among disjunct distributions. Various biogeographers have criticized this approach, mainly for being phenetic and not cladistic in its resolution of patterns. Although this is the method proposed in this book, unfortunately the authors devote little space to it, do not answer their critics adequately and, in effect, opt out of introducing rigor into their discussion.

All three authors are phylogeneticists to one degree or another and they note, albeit too briefly, the importance of cladistic hypotheses. However, they strongly advocate using biogeographic distributions as evidence of phylogenetic relationships,

but their examples have preconceived notions of relationships built into them. This reinforces the reader's perception that panbiogeography, which started out in Croizat's writings as being antagonistic (or at least agnostic) towards cladistics, has still not come to terms with the role of phylogenetics in biogeography. The authors are strong supporters of the importance of systematics, but they are short on specific analytical procedures of how biogeography might be used to infer relationships. Their position, I believe, undercuts the use of systematics as an independent discovery method of area relationships.

A major weakness of their presentation and the method is the oversimplistic interpretation of generalized tracks and of the geological events that are assumed to cause them. For example, a track running from South America to Africa to Southeast Asia is typically interpreted as a Mesozoic vicariant event owing to the formation of the South Atlantic and Indian oceans. Too little attention is paid to whether taxa with seemingly congruent tracks actually have congruent phylogenetic patterns and are of the same age. Their solution to discovering the ages of taxa seems to be using a molecular clock rather than a rigorous assessment of congruent patterns of phylogenetic, and thus area, relationships. These concerns strike at a fundamental problem, which has not been fully addressed: generalized tracks are hypotheses about the shared geological history of individual tracks. However, what is the evidence and the test for individual tracks being a manifestation of cladistic patterns rather than phenetic similarity? The tests of cladistic and/or vicariance biogeography are hierarchies of shared phylogenetic relationships. In panbiogeography, it is not immediately obvious that a rigorous method exists – short of moving in the direction of cladistic biogeography – for teasing apart the histories of the elements of a generalized track.

There are many other points that could be raised, especially in the superficial attempt in the last chapter to link panbiogeography with conservation – a subject that calls for a more thoughtful analysis than it has received. Nevertheless, the book has much to recommend it. The authors forcefully raise the important point that earth history and biotic history are deeply interrelated and cannot be ignored. All biogeographers can agree that we have only just begun to appreciate and explore this fundamental concept.

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A brief history of the past three billion years

The Origins of Life:
From the Birth of Life to the
Origin of Language

by John Maynard Smith and
Eörs Szathmáry

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This remarkable little book seeks nothing less than to specify the major events in the evolution of life on earth and to explain them in a coherent theoretical framework, all in less than 200 pages and in prose understandable by an intelligent layperson. By 'major events' they do not refer to the origin or proliferation of taxonomic groups, such as land plants or mammals, but to evolutionary changes that resulted in an increase in the complexity of life – the appearance of interesting new things in the biosphere, such as bodies, animals, colonies and human societies. The framework is the approach to evolution that focuses on the 'selfish' replication of genes and that sees the fundamental property of genes as an ability to store and transmit information. This book is adapted from a more technical one, *The Major Transitions in Evolution*¹, and is designed to reach a wider, nonspecialist audience. Technical terms are minimized, a glossary is supplied, and the prose is dotted with irreverent asides and turns of phrase. The authors correctly worry that the book will still be hard for laypeople, but in these days of academic hyperspecialization it is enough of an achievement that it will be understandable by professors in a different field.

Maynard Smith and Szathmáry begin with the theory of natural selection and the two faces of living things: informational and metabolic. The first entity we would call 'living' would have to multiply, vary and pass on its traits; the authors discuss how such an entity could arise from autocatalytic cycles of simple compounds and a medium of digital information storage (which they see as crucial in maintaining complexity both in living and in human information-processing systems). Maynard Smith and Szathmáry note that the theory of selection by itself does not predict that organisms will become more complex, only better adapted to surviving and reproducing in their environment. This raises the puzzle of why, in so many lineages, living things have become more complex, often dramatically so. Their general answer is that information-carrying entities that once could replicate