

Molecules and Populations: A Revitalization

Evolution at the Molecular Level. ROBERT K. SELANDER, ANDREW G. CLARK, and THOMAS S. WHITTAM, Eds. Sinauer, Sunderland, MA, 1991. xiv, 350 pp., illus. \$55; paper, \$28.95. From a symposium, University Park, PA, June 1989.

The impetus given to evolutionary biology by the great neo-Darwinians of the mid-20th century was due largely to an implicit promise, that population genetic models would be sufficient to explain the empirical data collected from laboratory and natural populations. For a while this seemed to be the case; measurable selection coefficients were associated with the clines and seasonal fluctuations of the inversions found in many *Drosophila* species, and lethal or otherwise deleterious chromosomes (in homozygous condition) could be maintained at reasonably high frequencies in natural populations by overdominance. As is well known, however, in the 1960s nondenaturing gel electrophoresis made it possible for evolutionary biologists to measure the frequencies of individual genes, in contrast to the larger chromosomal regions previously analyzed. Very quickly, the relationship between empirical data and theory became uneasy, then frantic, and finally schizoid as the failure of neo-Darwinian population genetics to explain the patterns of allozymes in most species led, in large part, to the development of Kimura's neutral theory. The resulting polemics between selectionists and neutralists did little to restore confidence that population genetics could make evolutionary biology a truly predictive science. Evolution was in danger of becoming a collection of "just so" stories.

In the meantime, however, DNA sequence information was being accumulated through the efforts of many molecular biologists (who were quite unconcerned about the state of evolutionary biology) and a smaller cadre of population geneticists wearing molecular biological hats. Some of this latter cadre have summarized their efforts in the chapters of this book, which are loosely arranged around four major foci: bacteria and viruses, organelles, "selfish" genetic elements, and, finally, several nuclear multigene families. One emerges from this book with a strong sense that the essential interplay between theory and data in molecular evolutionary biology has been rejuvenated. Indeed, in some cases, important new theo-

retical advances allow us to discern the role of natural selection at the molecular level. Several chapters stand out in this regard. For example, C.-I. Wu and M. Hammer effectively relate the behavior of the segregation distorter system of *Drosophila melanogaster*, a paradigm of an ultraselfish gene, to models developed earlier by B. Charlesworth and D. Hartl. In the chapters dealing with the mammalian major histocompatibility (MHC) locus by M. Nei and A. L. Hughes and by P. Hedrick *et al.* the effects of selection are illuminated in the patterns of nucleotide substitution and in the linkage disequilibria within and between the tandemly linked loci. Here both classical and newer population genetic models are sufficient to explain the observations. Thus, Nei shows convincingly that the MHC polymorphisms are due to overdominance, and Hedrick, with a more recently developed disequilibrium pattern analysis, separates the effects of selection on certain haplotypes from gene flow and genetic drift. W. Birky points out in his chapter how, despite their special features and our ignorance of many parameters, certain facets of the behavior of organellar genes within individuals and populations can be explained by neutral theory.

The above-mentioned chapters do much to restore confidence that molecular evolution has a robust theoretical base centered on established population genetic models. Other chapters in the book are perhaps even more satisfying because they exemplify how DNA sequence data have generated important new theoretical and experimental approaches. M. Kreitman elegantly shows how coalescent models can be used to detect the historical effects of selection on DNA based polymorphisms. Unlike ultraselfish genes and loci like MHC that have large effects on fitness, the selection coefficients that have been associated with these polymorphisms can be small if selection has acted over long periods of time. Similarly, B. Charlesworth and C. Langley utilize models developed in the 1980s to show that the inherent increase in the copy numbers of most transposable elements in *Drosophila melanogaster* must be balanced by directional selection against their carriers. It is intriguing that the loss of these elements occurs predominantly in chromosomal regions where crossing-over is highest. This implies that over long periods

of evolutionary time, a genome may become partitioned into gene-rich and gene-poor regions. Indeed, the isochores that differentiate mammalian chromosomes may represent a stage in such a process. Finally, R. F. Dubose and D. Hartl demonstrate in a more experimental way that molecular evolution need not be purely retrospective. Their analysis of the naturally occurring polymorphism in the alkaline phosphatase gene of *Escherichia coli* allowed them to target certain amino acid residues in the protein for site-directed mutagenesis. Importantly, not all of the mutations generated to date in evolutionarily conserved positions have obviously deleterious effects on enzyme activity. It will be extremely interesting to ascertain the fates of the potentially neutral mutants in chemostat populations.

In this review I have focused on those chapters in which molecular data and population genetics are particularly well meshed. But there is much more in this book. One can also find excellent reviews of the evolution of the tryptophan genes and their regulation (I. P. Crawford and R. Milkman), the AIDS virus and its relationship to other retroviruses (S. Yokoyama), chloroplast genes and their use in molecular systematics (M. Clegg), and the globin gene clusters (R. Hardison). In addition, the book contains information on certain features of the genus *Salmonella* (R. Selander *et al.*) and a retrospective chapter demonstrating how ribosomal RNA sequences were used to revolutionize our understanding of the deepest branches in the phylogenetic tree of extant living forms (C. Woese). Clearly, this volume helps establish molecular evolution as a major component of evolutionary biology, a component where pattern and process will come together to break rich new ground in the next century.

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Earthquake Assessment

Earthquake Hazard Analysis. Issues and Insights. LEON REITER. Columbia University Press, New York, 1991. xii, 254 pp., illus. \$65.

Earthquakes are no longer the mystery they once were. Enough is now known about the physics of the rupture process and the propagation of seismic waves to permit quite successful modeling of ground motion effects of specific earthquakes. The predictive value of this type of calculation is lim-