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 theoretical 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 limited, however, since there can be huge variations in ground motion that depend on details of the specific rupture, details that can only be known after the fact. Alternatively, enough strong-motion data may now be available to permit empirical and statistical estimation of future ground motion if one can specify the probability of occurrence of earthquakes of various "sizes" and their expected distances from a site of interest. These two approaches, modeling and empiricism, illustrate a simplified way the deterministic and probabilistic strategies of specifying vibratory ground motion for design of structures in earthquake-prone regions. In either case, some information must be specified about the future occurrence of earthquakes. Reiter's book provides the technical background needed to fully appreciate what goes into seismic hazard analysis and thus to better understand the strengths and weaknesses of what can emerge from such analysis.

The past decade has seen significant advances in understanding the fundamental nature of the earthquake process as well as the characteristics of destructive ground motion. Each new earthquake provides lessons to be learned by the scientific and engineering communities. Often, the place where this new information on the earthquake process was first translated into policies and procedures has been in the arena of nuclear power plant licensing. The author has been active on the regulatory side of nuclear siting controversies for many years, and thus his emphasis is on the techniques used in high-visibility projects where public concern is greatest.

Seismic hazard analysis is the first part of an integrated scientific, engineering, societal, and legal process that tries to provide practical solutions for earthquake hazards at particular sites. This has to be done even when data are inadequate and the understanding of the earthquake process is imperfect. To make the problem even more difficult, the scientists, engineers, and lawyers who must work together to arrive at these solutions come from very different professional cultures. The author, with deep experience in these matters, crisply argues that the mix of these cultures and the painful process that ensues is in fact the best way to take into account all of society's needs.

Earthquakes are caused by faulting; on that there is little disagreement. Unfortunately, one cannot always identify specific faults well enough ahead of time to adequately define the earthquake hazard that they may represent. This circumstance has led to procedures, some might call them rituals, for defining *seismotectonic provinces* and *localizing structures* and to formal rules for measuring the capability of these features to produce future earthquakes. It is refreshing to see a balanced discussion of this matter, in which the author freely admits that there is some inherent unreality involved. He goes on to make a convincing case that, flawed though it may be, the current process seems to do a better job of capturing the information available and accounting for its uncertainty than does anything else that has yet been suggested.

An issue not raised, and one on which it would have been interesting to have the author's insight, involves how the system can best adapt to new data that may alter previous conclusions, particularly after a structure has already been built. No matter how extensive investigation for a particular site might be, the rapidly improving technology and evolving scientific understanding almost guarantee that there will be changes in the assessment of the earthquake hazard for it.

One of the strengths of this book is that earthquake phenomenology from the standpoint of seismologists and ground motion characterization as viewed by engineers are treated together in an integrated fashion. This has the effect of demonstrating how elements of our basic undertanding of the earthquake process are translated into seismic design. A central theme is the clarification of the different assumptions made in deterministic and probabilistic approaches to seismic hazard analysis and their implications. The concluding chapter lays out these differences and suggests ways in which the two different approaches might be integrated. In the final analysis, the approach taken must be tailored to suit the specific problem being addressed. The analysis appropriate to protect the public from radioactive release from an underground nuclear waste repository with a 10,000-year lifetime is quite different from that needed to prevent earthquake casualties during the 50-year lifetime of an office building.

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Geologic Fluid Mechanics

Flow and Reactions in Permeable Rocks. O. M. PHILLIPS. Cambridge University Press, New York, 1991. x, 285 pp., illus. $59.50.

The role of subsurface fluid flow in geologic processes is emerging as an important theme in the earth sciences. Water participates in fluid-assisted chemical reactions, and fluid flow is a dominant factor in the redistribution of solutes and heat that controls such processes as diagenesis and ore genesis. In this book Phillips presents a set of mathematical tools and models useful for understanding ground water flow and its influence on geochemical systems and thermal regimes within the uppermost region of the earth's crust. He provides a good introduction to those principles of fluid mechanics that are needed to describe how rates and patterns of fluid flow influence geologic systems. Indeed, the strength of this book is its linkage to the analysis of geologic processes; this is not a textbook concerned primarily with ground water flow theory.

Although the appearance of the term "reactions" in the title may suggest otherwise, this also is not a book on geochemical thermodynamics. The focus is clearly on fluid dynamics and how the effects of chemical reactions are introduced into the fluid-flow equations to form the link between patterns and rates of flow and reaction kinetics. Examples are developed to quantify isothermal reaction fronts, gradient reactions, the concept of mixing zones, and isotherm-following reactions. The book will be useful to geochemists who want an introduction to fluid flow and heat transfer in porous geologic media, presented from the perspective of how some simple geochemical and hydraulic models can be linked.

Three broad topic areas are covered: fluid flow and relationships between patterns of flow and geologic structure; fluid flow and patterns of geochemical reactions; and fluid instabilities arising from temperature or salinity gradients. Mathematical results are emphasized, especially the analytic treatment of simple geometries. Rather than provide a detailed examination of field applications, Phillips develops examples that illustrate the nature of the processes involved and how they may be quantified.

The book offers a good introduction to the techniques used to analyze interface stability and fluid instabilities caused by spatial gradients in fluid density that, in turn, arise from temperature or salinity variations. Hydrologists familiar with isothermal systems will find the discussions of fluid instability and thermal convection a useful bridge to the extensive coverage of these topics in the fluid mechanics literature. The next-to-last chapter describes selective aspects of pressure-driven flows in confined and unconfined aquifers, including analytic models of the disturbance of a conductive thermal regime by advective heat transfer. The last chapter describes thermally driven flows in which the hydraulic forcing terms are of minor or no importance. Coverage of both these topics illustrates the similarities and differences in ground water flow systems