

Review

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THE CENTURY OF THE GENE.

By Evelyn Fox Keller. Cambridge (Massachusetts): Harvard University Press. \$22.95. vi + 186 p; ill.; index. ISBN: 0-674-00372-1. 2000.

This is exciting reading. With her background in mathematics, physics, history, and philosophy, the author has ranged widely and assembled a great deal of material not familiar to most biologists. She gives readers something to ponder on every page. I say this excitedly, despite my generally contrary view—that of a jaded, unreconstructed, bean-bag simplifier.

Keller believes that the gene, despite its glorious history, has lost its relevance. Furthermore, DNA has been excessively hyped, especially with the Human Genome Project. There is too much simplified genetic determinism in the air. In its simplicity the gene concept may actually have become a hindrance to progress. The process of development is so complicated and interconnected that traditional genetic analysis is misleading; different paradigms and different words are needed. She argues for a “distributed program” in which DNA, RNA, and protein function both as instructions and data.

In the ultimate gene-centered view, an organism is a “Quine”—computer jargon for a program that generates its own source code, named after the late logician, W F Quine. Useful as this has been for evolutionary thinking, it clearly falls far short as a developmental program. An elephant does much more interesting things than improving the fidelity of DNA transcription. But Keller goes further. In her holistic view, the developmental program extends well beyond the genome and may be no less than the organism itself. The robustness of embryogeny is developmental stability, not genetic. She also envisions a future in which the genetic approach will lessen its hold on the popular mind and new concepts, yet to be specified, will lead to more realistic public policy.

While pondering what this brave new developmental world might be, I decided to take another look at Keller’s excellent earlier book, *A Feeling for the Organism: The Life and Work of Barbara McClintock* (1983. San Francisco (CA): W. H. Freeman)—the story of McClintock and her dynamic whole-organism view. Indeed, some of McClintock’s phenomena did seem mysterious in 1983. But the mysteries have largely succumbed to the reductionist onslaught of molecular genetics. Double-strand breaks, transposase, methylation, and other familiar mechanisms seem sufficient. Does this mean that, in the next few decades, the forest of organismic properties that Keller is so impressed by will fall under myriad axes chopping away at individual details? I suspect so, but we will have to wait and see.

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EVOLUTIONARY GENETICS: FROM MOLECULES TO MORPHOLOGY.

Edited by R S Singh and C B Krimbas. Cambridge and New York: Cambridge University Press. \$95.00. xvii + 702 p; ill.; index. ISBN: 0-521-57123-5. 2000.

The past 35 years have witnessed a revolution in evolutionary genetics that, like the proverbial *The Little Engine that Could* going over the mountain pass, shows no signs of slowing, much less stopping. To a considerable extent, we owe much to one person, Richard Lewontin, for getting this little train over the hump and conducting it while the masses have shoveled coal into the boiler. Indeed, few have had such a substantive and pervasive impact on evolutionary biology in general, and so this edited volume is a welcome and well-deserved tribute to the powerful and varied influence of Lewontin on the fast-growing, important discipline of evolutionary genetics.

Among other major contributions, Lewontin pioneered the use of electrophoresis to detect genetic variation, which profoundly influenced the field. He has also been remarkably prolific in training outstanding students and postdoctoral researchers, and has played a crucial role in critiquing science and its relationship to society. Still, it is my feeling that his greatest, most longstanding impact ultimately will be his emphasis on the inextricable relationship between genotype and environment. Sadly this is a lesson that few, if any, of those involved in genome sequencing projects have yet to recognize or embrace in their great rush to promote the value of their work to politicians, granting agencies, and the public. Lewontin says it best in his homage to the phenotype: “Gene sequences do not mate, they do not migrate, they do not live or die differentially, except as a consequence of the physiology and the metabolism of the organismic carriers in interaction with the physical and biotic environment” (p 10).

This volume contains 32 chapters by an all-star cast of Lewontin’s colleagues. The articles are separated into eight sections that revolve around areas in which Lewontin has had a seminal impact: problems, foundations, and historical perspectives in population genetics; molecular variation and evolution; selection and genetic polymorphism; linkage, breeding systems, and evolution; quantitative genetics and phenotypic evolution; gene flow, population structure, and evolution; population genetics and speciation; and behavior, ecology, and evolution.

But are these chapters, and the lengthy book as a whole, worth reading? With few exceptions, my answer is a resounding “yes.” Let me briefly mention some of the many highlights. Ewens (Chapter 2) offers fresh, insightful thoughts on the historical and practical roles of mathematics in evolutionary theory. I also enjoyed Kreitman and Antezana’s em-

pirically-oriented contribution (Chapter 5) on synonymous substitutions. It is my sense, however, that our understanding of codon bias would be greatly improved by at least two additional approaches: adopt a more explicitly phylogenetic, comparative framework (e.g., use well-defined series of outgroups with a phylogenetic tree structure) and recognize that not all identical amino acids within a gene are equally free selectively to vary (e.g., freedom to vary might depend on the impact of a given amino acid on the secondary structure of the gene). We must strive to increase our level of sophistication in models of molecular evolution. Berry and Barbadilla (Chapter 6) nicely and provocatively illustrate the underappreciated role of gene conversion in contributing to intralocus genetic diversity (*contra* crossing over, which is more important in generating interlocus genetic diversity). Gene conversion is surely important in many ways; still, predictions of models of gene conversion can be improved by incorporating back (compensatory) mutation, which is increasingly recognized as a significant factor in different evolutionary models.

Other highlights include Levin's (Chapter 12) engrossingly written essay on antibiotic resistance, Slatkin's (Chapter 21) revealing and insightful description of issues involving gene flow, and Maynard Smith's (Chapter 30) entertaining and illuminating (and often personal) discussion of historical aspects of animal behavior, particularly sexual selection, as they coevolved with evolutionary theory in the past 100 years. There are many other great chapters too, but I would be deeply remiss not to mention Felsenstein's (Chapter 29) delightful recounting of and reflection on the maturation of population genetics over the past 35 years. I eagerly consumed nuggets of testable ideas that were liberally sprinkled throughout. For example, I was intrigued by Felsenstein's speculations on disentangling the roles of selection and drift in causing between-population differentiation in a trait of interest by appealing to the rapidly growing Quantitative Trait Loci (QTL) database. I also enjoyed his take on other crucial issues, including the growing use of Bayesian methods in evolutionary genetics, and the need to forge stronger links between molecular evolutionary data and ecological models.

The editors are to be applauded for assembling such a stellar cast of evolutionary geneticists, an unintentional although highly appropriate example of the brilliance of the Lewontin coalescent. One particularly nice touch was a list of Lewontin's publications, from his first (a book review in 1952) to nearly ten in 1999 (including books, chapters, commentaries, and peer-reviewed articles in the primary literature). In line with the theme of this celebratory book, an insightful addition would have included a list of students and postdoctoral re-

searchers who have trained under Lewontin. Still, considering the length of the book, many of the chapters are intense, and the price is rather high. I hope that these obstacles are not insurmountable for students and practitioners of this field because the effort is worth it.

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ADAPTIVE GENETIC VARIATION IN THE WILD.

Edited by Timothy A Mousseau, Barry Sinervo, and John A Endler. Oxford and New York: Oxford University Press. \$60.00. x + 265 p; ill.; index. ISBN: 0-19-512183-X. 2000.

This superb collection of 11 chapters focuses on biological function and ecological process as the basis for natural selection, and the role of genetic architecture (e.g., number of loci and alleles, gene expression, and interactions among loci) in molding the evolutionary response to selection. In addition to gathering information on microevolution in several important model systems, the chapters illustrate diverse methods to study natural selection and the genetics of adaptive traits in natural populations, and highlight the value of exploiting unusual properties of model organisms (e.g., cross-fostering in wild birds) to gain otherwise unattainable insights.

Six chapters summarize specific model systems, with three on birds and one each on a lizard, an insect, and a flowering plant. Generally, one or more closely related species and traits are considered in depth. Another chapter compares postglacial freshwater fish groups to infer patterns of adaptive genetic divergence. Two chapters emphasize methodology: one concerns use of molecular markers to estimate relationships and phenotypic similarities among relatives to estimate inheritance in natural populations, and the other compares heritabilities estimated using laboratory and natural populations of *Drosophila*. Mousseau's chapter reviews analyses using several unrelated species and diverse methods. Endler does a good job of tying together the chapters, addressing infrequent errors in previous chapters, and listing goals for future research.

The cohesiveness of this collection of papers, combined with the diversity of methods and organisms discussed, make it an excellent textbook for graduate seminars. It will also be invaluable to investigators as a source of research methods. On average, the quality of the papers is variable, but high. Some of the model systems reviewed are better developed than others, and there are occasional lapses of presentation. The final two chapters help integrate the book, and an index facilitates location of topics within different chapters. This volume will