Thinking About Evolution

Historical, Philosophical, and Political Perspectives

This is the second of two volumes published by Cambridge University Press in honor of Richard Lewontin. The first volume, *Evolutionary Genetics from Molecules to Morphology*, honors Lewontin's more technical contributions to genetics and evolutionary biology. In this second volume of essays, philosophical, historical, and political dimensions of his work are honored.

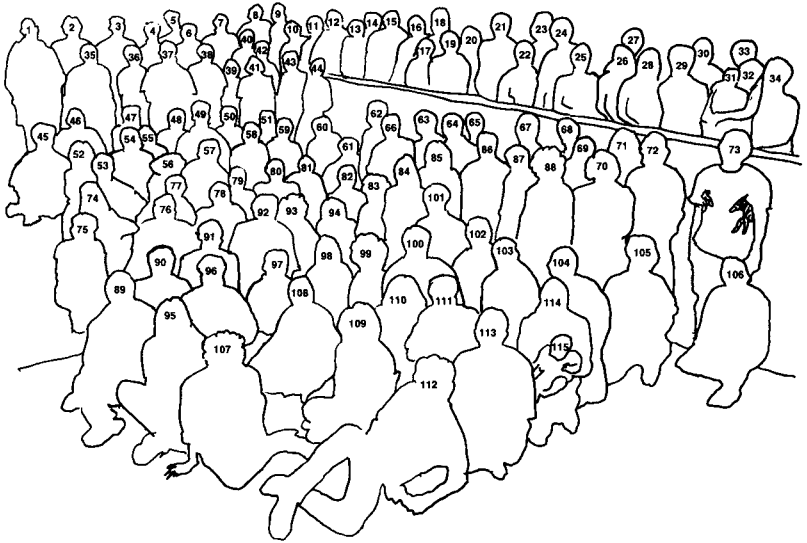
Given the range of Lewontin's own contributions, it is fitting that the volume covers such a wide range of perspectives on modern biology. He is not only a very successful practitioner of evolutionary genetics but also a rigorous critic of the practices of genetics and evolutionary biology, and an articulate analyst of the social, political, and economic contexts and consequences of genetic and evolutionary research. The volume begins with an essay by Lewontin titled "Natural History and Formalism in Evolutionary Genetics." Chapter 2 is an extended interview with Lewontin covering the history of evolutionary genetics as seen from his perspective and as exemplified by his career. The remaining chapters, contributed by former students, postdoctoral fellows, colleagues, and collaborators, cover issues ranging from the history and conceptual foundations of evolutionary biology and genetics, to the implications of human genetic diversity, to the political economy of agriculture and public health.

Rama S. Singh is Professor in the Department of Biology at McMaster University.

Costas B. Krimbas is Professor of Philosophy and History of Science at the University of Athens.

Diane B. Paul is Professor of Political Science at the University of Massachusetts at Boston.

John Beatty is Professor of Ecology, Evolution, and Behavior at the University of Minnesota.



1. Tim Prout
2. Chris Dick
3. Mark Siegal
4. Mike Dietrich
5. Dmitri Petrov
6. Michael Bradie
7. Joe Felsenstein
8. Will Provine
9. Norman Johnson
10. Jeff Dole
11. Marcos Antezana
12. Lloyd Demetrius
13. Christian Biemont
14. Bill Piel
15. Dan Hartl
16. Jean David
17. Naomi Pierce
18. Elliott Sober
19. Julio Rozas
20. Yvonne Parsons
21. David Rand
22. Lisa Lloyd
23. Michael Cummings
24. Dan Weinreich
25. Carmen Segarra
26. Suzanne Kaplan
27. Michael Hammer
28. Rachel Nasca
29. Manyuan Long
30. David Glaser
31. Michele Zimmerman
32. Susan Albert
33. Lenard Diggins
34. Amanda Benson
35. Janet Collett
36. Diane Paul
37. John Beatty
38. Antonio Barbadilla
39. Teresa Sebastiá
40. Donal Hickey
41. Montsé Aguadé
42. Richard Kliman
43. Rasmus Nielsen
44. Kristin Ardlie
45. Toshinori Endo
46. Monty Slatkin
47. Diddahally Govindaraju
48. Rob Kulathinal
49. Rob Dorit
50. Hiroshi Akashi
51. Tomoko Steen
52. Hongping Tian
53. Weber Amaral
54. Ken Weber
55. Richard Morton
56. Tracy McLellan
57. Dave Parker
58. Einar Arnason
59. John Ramshaw
60. Marty Kreitman
61. Peter Haas
62. Dan Dykhuizen
63. John Gillespie
64. Curtis Strobeck
65. Fred Cohan
66. Dick Lewontin
67. Jeff Powell
68. Mark Kirkpatrick
69. Lisa Brooks
70. Maryellen Ruvolo
71. Gisella Caccone
72. Richard Burian
73. Russ Lande
74. Dana Campbell
75. Belinda Chang
76. Alex Felton
77. Antonia Monteiro
78. John Wakeley
79. Tim Keith
80. Walt Eanes
81. Steven Irwin
82. Jerry Coyne
83. William Wimsatt
84. Marcy Uyenoyama
85. Adriana Briscoe
86. Rama Singh
87. Costas Krimbas
88. Laura Landweber
89. Peter Godfrey-Smith
90. Eleutherios Zouros
91. Bob Berwick
92. Michel Veuille
93. Michael Turelli
94. Peg Riley
95. Simon Frost
96. Peter Goss
97. Sally Otto
98. Maria Pompeiano
99. Evan Balaban
100. Carlos Bustamante
101. Chuck Taylor
102. Geoff Morse
103. Jean-Pierre Berlan
104. Doug Futuyma
105. Yaneer Bar-Yam
106. William Brown
107. Cay Craig
108. Cathy Laurie
109. Soojin Yi
110. Anna Haynes
111. Jeff Townsend
112. Andrew Berry
113. Dennis Cullinane
114. Lynn King
115. William Clark King

Photo taken at the Harvard Museum of Comparative Zoology, September 6, 1998 by Liza Green, Harvard Medical School Media Services.

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VOLUME TWO

Edited by

RAMA S. SINGH
McMaster University

COSTAS B. KRIMBAS
University of Athens

DIANE B. PAUL
University of Massachusetts at Boston

JOHN BEATTY
University of Minnesota

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UNIVERSITY PRESS

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Contents

Section B: Philosophy of Evolutionary Biology

Section C: The Politics of Evolutionary Biology

List of Contributors

BALABAN, E., The Neurosciences Institute, San Diego, California 92121

BEATTY, J., Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108

BERLAN, J.-P., Economie et Sociologie Rurales, Institut National de la-Recherche Agronomique, 34060 Montpellier, France

BRANDON, R. N., Departments of Philosophy and Zoology, Duke University, Durham, NC 27708

FALK, R., Department of Genetics, The Hebrew University, 91904 Jerusalem, Israel

GAYON, J., Université Paris 7-Denis Diderot, UFR GHSS, cc7001, 75251 Paris, France

GODFREY-SMITH, P., Philosophy Department, Stanford University, Stanford, CA 94305-2155

GOULD, S. J., Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

GRAY, R. D., Department of Psychology, University of Auckland, Auckland 92019, New Zealand

HAYNES, R. H., Department of Biology, York University, Toronto, Ontario, M3J 1P3, Canada

HUBBARD, R., Department of Biology, Harvard University, Cambridge, MA 02138

KITCHER, P., Department of Philosophy, Columbia University, New York, NY 10027

KRIMBAS, C. B., Department of Philosophy and History of Science, The National University of Athens, Greece

LEWONTIN, R. C., Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

LEVINS, R., Department of Population Sciences, Harvard University, Boston, MA 02115

LLOYD, E. A., Department of History and Philosophy of Science, Indiana University, Bloomington, IN 47405

PAUL, D. B., Department of Political Science, University of Massachusetts Boston, Boston, MA 02125

PIATTELLI-PALMARINI, M., Cognitive Sciences Program, University of Arizona, Tucson, AZ 85721–0025

PROCTOR, R. N., Department of History, Pennsylvania State University, University Park, PA 16802

ROSE, S. P. R., Brain and Behavioral Research Group, The Open University, Milton Keynes, MK7 6AA UK

RUVOLO, M., Department of Anthropology, Harvard University, Peabody Museum, Cambridge, MA, 02138

SARKAR, S., Faculty of Philosophy, University of Texas at Austin, Austin, TX 78712-1180

SCHANK, J. C., Department of Psychology, University of California, Davis, CA 95616

SEIELSTAD, M., Program for Population Genetics, Harvard School of Public Health, Boston, MA 02115

SINGH, R. S., Department of Biology, McMaster University, Hamilton, Ontario, Canada, L8S 4K1

SOBER, E., Department of Philosophy, University of Wisconsin, Madison, WI 53706

SPENCER, H. G., Department of Zoology, University of Otago, Dunedin, New Zealand

TAYLOR, P. J., Program on Critical and Creative Thinking, Graduate College of Education, University of Massachusetts Boston, Boston, MA 02125

VANDERMEER, J., Department of Biology, University of Michigan, Ann Arbor, MI 48109

VEUILLE, M., Ecole Pratique des Hautes Etudes, Laboratoire d'Ecologie, cc237, Université Pierre et Marie Curie, 75252 Paris cedex 05, France

WIMSATT, W. C., Department of Philosophy, Committee on Evolutionary Biology, The University of Chicago, Chicago, IL 60637

Preface

Scientists earn their reputation by making special contributions in a variety of ways. Some become known for a discovery that revolutionizes their science. Others are respected as intellectual leaders for significant contributions leading to sustained progress in their field. Still others become known for providing guidance, opportunity, and uniquely inspiring rapport to a large number of graduate students, writers, and research colleagues. A rare few do all the above and remarkably enough still find time to deal with the broader issues of epistemology, philosophy, history, and sociology of science. Richard Lewontin is one of these rare scientists.

If we are to attach a major discovery or a conceptual breakthrough to Lewontin's name (such as Haldane's cost of natural selection, Fisher's fundamental theorem of natural selection, Wright's shifting balance theory, or Maynard Smith's game theory applications) then the successful completion of the genetic variation research program of the Chetverikov–Dobzhansky School will be known as the outstanding highlight of Lewontin's career. Dobzhansky and his students and collaborators pursued the twin problems of the amount and the adaptive role of genetic variation for nearly 25 years without a satisfactory solution. All estimates of genetic variation were indirect or inadequate, for there was no reductionist research program that could allow the study of genetic variation at the level of the gene. Lewontin's pioneering success in the application of protein electrophoresis to the problem of genetic variation changed the scene radically. The estimation of electrophoretic variation was direct and more useful than any one had expected. The technique also removed the experimental limitations imposed by genetic incompatibility between species and allowed reliable comparisons of genetic variation between populations and species without any need to make genetic crosses. The impact and the anticipation of the avalanche of future results from the use of electrophoresis were discussed in his well-known book *The Genetic Basis of Evolutionary Change* (1974). This book sets out the problem of population genetics in a rationally constructed historical context and is required reading for all aspiring population geneticists.

Evolutionary research requires broad interest and versatility in modeling, experimental design, statistics, field biology, and much more. Such breadth

allowed Lewontin to be successful, time and again, in designing new experimental systems or suggesting key concepts to answer old questions or pursue new ones. Lewontin became interested in the uniqueness of the phenotype and genotype–environment interactions inspired mainly by the Russian biologist I. Schmalhausen's book *Factors of Evolution.* Lewontin's doctoral thesis studied fitness as a function of genotype frequency and density and showed that "viability of a genotype is a function of the other genotypes which coexist with it, the result of any particular combination not being predictable on the basis of the viabilities of the coexisting genotypes when tested in isolation." This was followed by studies of interlocus epistatic interactions in fitnesses and the evolution of naturally occurring inversion polymorphism in *Drosophila.* His mathematical work on linkage disequilibrium provided a new direction for research, and results from a series of papers on multilocus fitness effects anticipated discussion on the units of selection. His experimental work on norms of reaction in *Drosophila* was exemplary in exposing the problem of genetic determination and led to a new appreciation of genotype–environment interaction and phenotypic plasticity. He pointed out the importance of developmental time in fitness, which is something usually forgotten when describing fitness components. His 1972 article on the "Apportionment of Human Diversity" pointing out that any genetic differences between races has to be compared with genetic variation within population and races, is a landmark in human genetics and evolution. More recently, his laboratory has been a major center for studies of DNA sequence variation. Lewontin has provided training and guidance to a large number of graduate students and postdoctoral fellows. The number is well over one hundred! Many more have worked in Lewontin's laboratory but have not necessarily coauthored publications with him.

But what makes Lewontin known more in the wider circle of evolutionary biology and in science in general is his role as a critic of how science is done on the one hand and his passionate engagements with the issues of science and society on the other. He has made important contributions and has influenced research workers in the history and philosophy of science and in the areas of science and society such as agriculture, social health problems, bioethics, and genetics and IQ. If you drop Lewontin's name in any group of biologists, an animated discussion is sure to follow! These discussions are not about science but about its relevance and applications to human affairs. His concern about social issues springs directly from his unique perspective of evolutionary biology. Lewontin's research program may be reductionist, but he is not. He has encouraged and challenged evolutionary biologists to find the most desirable combination of Platonic and Aristotelian traditions in studying nature. Accordingly, the mathematical rigor of early population biology must be extended to accommodate interactive, hierarchical, probabilistic, and historical factors as learned empirically in the field. To him, "*context and interaction are of the essence*" (Lewontin 1974, p. 318) whether one is talking about interactions between hierarchical levels, between organisms and the environment, or between causes and effects. A reductionist approach to science does not necessitate a

reductionist view of the world. No level of analysis is specially privileged for a general understanding of causality. Genetic and environmental effects are interdependent, and the phenotypic variance cannot be partitioned into fixed components. Organisms do not fit in preexisting ecological niches but create their own niches. History and contingencies are so important in evolution that looking for adaptive explanations for all organismic traits undermines the role of natural history. These ideas essentially follow from his belief that relationships between organisms and their environments, and likewise, those between groups and hierarchical levels, are governed by forces so weak that the outcomes are neither fixed nor predetermined.

John Maynard Smith has written (first volume, pages 628–640) that "Richard Lewontin has contributed to science not only by his own work on evolution theory and molecular variation, and by his influence on the many young scientists who have worked with him but also by asking us to think about the relationships between the science we do and the world we do it in." Although one may not agree with Lewontin on all issues (he would be surprised if you did!), one thing is sure – Lewontin has been a colorful personality who has made evolutionary biology rigorous and interesting at the same time. We affectionately dedicate this volume to him.

This volume has been long in preparation, and we thank the authors for their patience. We are extremely grateful to many colleagues who provided help as reviewers. At the Cambridge University Press we express our sincere thanks to Robin Smith for his early enthusiasm and help in the preparation of this book, and to Ellen Carlin for supervising its completion. Eleanor Umali and her associates at Techbooks have done a superb job of production. Finally we would like to thank Kathy McIntosh of McMaster University for her enthusiasm and the enormous amount of work that she has put in, from communication with authors to preparation of final manuscripts of this book.

Rama Singh
Hamilton, Ontario, Canada

Costas Krimbas
Athens, Greece