Bound [Oxford University Press, 1988]) the non-expert might find his account of the science skimpy and hard to follow. But he does convey the excitement and passion that characterize creative work in this frontier area of science.

Pais knew everyone, including Einstein, Dirac, Bohr, Feynman, von Neumann, Kramers, Pauli, Oppenheimer, Uhlenbeck, Sakharov, and non-scientists such as Chaim Weizmann, George Kennan, Erwin Panofsky, Pablo Casals, Theodore Reik, Lillian Hellman, and many others. He is a marvelous raconteur. The book teems with anecdotes and stories of the great men and women he encountered, wonderful stories that often capture the personalities of these historic figures in a single paragraph. For the scores of thumbnail portraits alone the book is worth the price.

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Vignettes: Fateful Metal

Copper was indeed queen of the Nile until about 3000 B.C., when some no goodnick in Iran added a pinch of a white metal called tin to the liquid copper. . . . Faster than priority mail, copper had a partner and the Bronze Age was upon us.

—*Ron L. Morton, in Music of the Earth: Volcanoes, Earthquakes, and Other Geological Wonders* (Plenum)

It might be thought that the politico-economic-social structure of Europe in the early 19th century was determined by the military alignments in Europe of the period. This is another misapprehension. It was, perhaps surprisingly, determined by the allotropy of tin. This shiny familiar metal turns below 13°C into a yellow powder. . . . The buttons on the uniforms of the soldiers of Napoleon's armies were largely composed of tin and in the long drawn out campaign against the Russians, the buttons turned to powder and fell off the soldiers' uniforms. This made them more concerned with wrapping their uniforms round them in the hostile climate than pointing their rifles at the Russians. The retreat from Moscow . . . was the result.

—*Charles J. M. Stirling, in The Future of Science Has Begun: The Communication of Science to the Public, Science and The Media* (Fondazione Carlo Erba)

Evolution Step by Step

Selection. The Mechanism of Evolution. GRAHAM BELL. Chapman and Hall, New York, 1996. xxvi, 699 pp., illus. $75 or £55. ISBN 0-412-05521-x.

The Basics of Selection. GRAHAM BELL. Chapman and Hall, New York, 1996. xxii, 378 pp., illus. Paper, $37.50 or £24.99. ISBN 0-412-05531-7. Briefer edition of *Selection: The Mechanism of Evolution.*

The goal of evolutionary biology is to explain the complex and intricate organization of living things, and this is done by identifying mechanisms that cause evolution and by demonstrating their consequences. Bell's two books are about the main mechanism, natural selection. Mechanisms such as genetic drift can cause heritable changes in populations and species (one definition of evolution), and mechanisms such as mutation and migration can hinder evolution, but only selection can cause evolution of complex structures. *Selection: The Mechanism of Evolution* is a detailed and erudite monograph on the topic, and *Basics of Selection* is a summary of the major points found in *Selection*. The focus of the books is on how selection can work and its consequences, rather than on adaptation or how selection has worked.

Bell begins with an outstanding introduction to the process of natural selection. He proposes 10 principles: (i) Heritable variation in replication rate causes evolution. (ii) Heritable variation arises as random alterations of genes; it does not in itself direct the course of evolution. (iii) Replication rate is the only attribute that is selected directly. (iv) Characters that cause changes in replication rate will be selected indirectly and may evolve as a consequence. (v) Adaptation caused by selection in given conditions is likely to be associated with loss of adaptation in others. (vi) Selection proceeds by sequential substitution of superior variants, not exclusively by sorting pre-existing variation. (vii) A given character state can evolve from a prior state only if the two states are connected by a continuous series of modifications, each being advantageous. (viii) Selection causes the modification of prior states of organization but cannot abruptly give rise to wholly novel states; its course is contingent on the fortuitous occurrence of particular variants. (ix) Selection tends to improve performance in given conditions but does not necessarily optimize performance; improvements will vary geographically. (x) Because selection is caused by differences in replication rates, its outcome will often depend upon the kinds of competitors present, not just physical conditions of growth. These processes will be modulated by developmental, physiological, genetic, and ecological circumstances in which they operate. The rest of the books discuss these principles and their consequences.

Bell makes frequent use of selection experiments, mostly from the rich microbial evolution literature, which might otherwise be unknown to more ecologically oriented readers, and they successfully illustrate and test the validity of the broad general principles.

Bell distinguishes between selection and sorting. Sorting is the population geneticist's version of selection, in which some existing alleles spread at the expense of others, and does not include the origin of new variants. Selection includes the origin of new alleles, with consequences having to do with chance, contingency, and cumulation. (Some would quibble that what Bell means by selection is in fact evolution by natural selection.) Sorting takes place on shorter time scales and is predictable, whereas cumulation of mutations takes place on longer time scales and is affected by chance and contingency. Sorting is well understood, but there has been confusion about the influence of chance, contingency, and cumulation.

One usually thinks of chance affecting selection only as the variance around the mean trajectory expected from standard population genetics theory. However, this applies only to sorting. The result of long-term selection has three phases, as shown by most artificial selection experiments: sorting of variation expressed in base population, that is, selection of existing genes and blocks of linked genes; sorting of the variation that is newly expressed every generation as a result of recombination; and sorting of newly arisen variants (mutants). Population size will affect the timing of the phases, and the latter two Bell calls cumulation. Not much is known about the second phase and even less is known about the third. Cumulation may not occur if the selective environment changes too rapidly. Cumulation is affected by contingency; which variants actually appear will profoundly affect the subsequent response to selection.

Characters evolve through their effect on differential survival and reproduction, and in any population there are a large number of potential mutations that can affect fitness. This favors divergence among populations subject to identical selection because different populations will experience different mutations by chance, each population represents only a sample of all possible allele combinations, effects of a gene may depend upon the alleles present at other loci, and each episode of selection modifies the composition of the population. Any divergence of lines predisposes future selection in each to favor different mutations. Different lineages will accumulate different working combinations so that the effects of subsequent mutations on fitness will be different. The differences will continue to cumulate, with each line evolving higher fitness by different gene combinations. Thus the cumulation of different gene combinations is contingent upon history; long-term selection is Bayesian.

The Bayesian approach helps to avoid a misunderstanding exhibited by many non-evolutionists (including creationists) who argue that complex adaptations are "unlikely." Consider a cultured RNA gene sequence of length 218. There are 4^{218} or about 10^{128} different sequences of length 218. How long would we have to wait for a functional sequence to show up? A culture tube contains about 10^{16} molecules. The world's ocean could fill about 10^{22} culture tubes, containing altogether 10^{38} molecules. If we could change the sequence of every molecule every second, never allowing any sequence to be repeated, we would have tried out every possible sequence and found our best adapted molecule in $10^{128}/10^{38} = 10^{72}$ years, or about 10^{62} times the age of the universe. This is the non-evolutionist's version and overlooks two major considerations: only alterations that give rise to functional improvements are favored by selection, and new improvements build upon past improvements. We know that highly adapted molecules of RNA can evolve in culture within a week, insufficient time for something to turn up all at once. Components turn up sequentially; better ones replace the inferior ones, and then additional variants show up. Each altered sequence forms the basis for further improvement. This can proceed very rapidly, of the order of the single-position substitution rate, not the product of the probabilities of changing all sites at once. It is conditional rather than absolute probabilities that are important in evolution, just as we must work with relative rather than absolute fitnesses.

The cumulative nature of evolution places severe constraints on the kinds of organisms and adaptations that can evolve. The degree to and ways in which adaptedness can be improved depend upon the connectance of the genotypic space through which the population could travel. If it is very connected, then evolution can proceed rapidly, otherwise it will be slow or stagnate. But the contingent nature of the paths taken also explains the diversity of effects of selection on different populations in the same selective environment.

Although populations starting from a single base population diverge even under identical selection, selection lines starting from different base populations will become more similar through time if subject to the same selection. This is not a contradiction. First, there is convergence at the level of fitness and the trait function (phenotype) undergoing selection, but not at the level of physiology, development, and genetics. Second, there are just phases of selection; divergence occurs under sorting, but the lines will eventually converge in phenotype when enough mutations have occurred. The point here is that there are multiple genetic solutions to the same environmental challenge. Owing to cumulation and contingency of the evolutionary paths taken, evolutionary reversals may be unlikely at the genotypic level, even if likely at the phenotypic level.

Bell's literature survey suggests that populations of all kinds of organisms at all scales are kept in flux by continual change in the intensity and direction of selection. It is doubtful whether natural environments are uniform with respect to selection at any scale of time or space. Bell discusses many consequences of temporal and spatial heterogeneity, and they are especially interesting for multiple traits. Although particular combinations of traits are favored in one environment, different combinations may be newly superior if the environment changes, and response is limited by the strength of the genetic correlation between the traits. Adaptation to novel environments is hindered by existing genetic covariance structure. In contrast, in a constant environment adaptation is hindered by a lack of genetic covariance. The strengths of genetic covariances can evolve and may reflect the scale of temporal and spatial variance.

In addition to offering new views and taking up topics that have not heretofore been put in a genetic context, Bell discusses most of the active topics in the selection-oriented part of evolutionary biology, including the evolution of life cycles, life history, sex, gametes, recombination, epistasis, genetic variance, plasticity, specialization, and parasitism. In most cases he gives clear and interesting summaries, with excellent examples and questions to ponder. I recommend the books to anyone interested in almost any aspect of natural selection and its importance in evolution.

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Charging Ahead. The Business of Renewable Energy and What It Means for America. John J. Berger. John Macrae (Henry Holt), New York, 1997. xvi, 399 pp., illus. $30 or $C41.95. ISBN 0-8050-3771-3.

The Chemokine FactsBook. Krishna Vaddi, Margaret Keller, and Robert C. Newton. Academic Press, San Diego, 1997. xii, 205 pp., illus. Paper, $42 or £24.95. ISBN 0-12-7099905-0.

Classical Mechanics. Transformations, Flows, Integrable and Chaotic Dynamics. Joseph L. McCauley. Cambridge University Press, New York, 1997. xviii, 469 pp., illus. $85, ISBN 0-521-48132-5; paper, $39.95, ISBN 0-521-57882-5.

Combinatorial Chemistry. Synthesis and Application. Stephen R. Wilson and Anthony W. Czarnik, Eds. Wiley-Interscience, New York, 1997. xii, 269 pp., illus. $69.95. ISBN 0-471-12687-x.

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Euclidean Quantum Gravity on Manifolds with Boundary. Giampiero Esposito, Alexander Yu. Kamenshchik, and Giuseppe Pollifrone. Kluwer, Norwell, MA, 1997. xiv, 319 pp. $154 or £94 or Dfl. 240. Fundamental Theories of Physics, vol. 85.

The Evolution of Social Behavior in Insects and Arachnids. Jae C. Choe and Bernard J. Crespi, Eds. Cambridge University Press, New York, 1997. xiv, 541 pp., illus. $105, ISBN 0-521-58028-5; paper, $47.95, ISBN 0-521-58977-0.