

tants in heterozygous state and the influence of genetic background and to recent revolutionary changes in the concept of genetic load. The subject of genetically effective population size is particularly well presented, but a revised edition may include major changes in this section, for genetic drift and effective population size are currently being viewed in new ways by Kimura and others in relation to problems of the maintenance of protein polymorphisms in populations. Some "non-Darwinian" evolutionists may feel that their contributions have been slighted, yet I think the major arguments of the proponents of evolution by "random walk" are satisfactorily outlined. The Cavalli-Sforza-Edwards "phylogenetic tree" of human racial evolution is presented without critical comment, and several pages are devoted to phylogenies based on amino acid substitutions in cytochrome c and hemoglobin and to the concept of evolutionary clocks. Dobzhansky's treatment makes it clear that not all the arguments advanced by the neutralists have been effectively countered by those who would attribute most or all protein polymorphism and evolution to selection. Chapters 9 through 11, dealing with types and patterns of variation in populations, methods of reproductive isolation between species, and patterns of species formation, contain relatively little new material of major consequence, and these subjects have been covered in greater detail in Mayr's recent books. In the final chapter, Dobzhansky, touching upon such widely divergent topics as the mysticism of Teilhard de Chardin and the "eccentric" genetic system of *Oenothera*, sketches out major areas of knowledge and ignorance of evolutionary patterns and processes.

One of the dominant themes of the work is the "balance model" of genetic population structure, which "envisages a greater or lesser proportion of the gene loci being in the heterozygous state, frequently though not invariably for pairs of interacting alleles that give heterosis." The recent demonstration of extensive allelic variation at structural gene loci clearly supports this model (finally sinking the "classical" model, which assumes that there exists a "normal," largely homozygous type of each species or population). But the new discoveries do not, of course, necessarily support the "balance model" insofar as it envisages the variation's being maintained largely by heterosis

or other forms of balancing selection.

I think that Dobzhansky has to a remarkable degree accomplished his aims of picturing evolutionary genetics as a field in an exciting period of development and of showing how current discoveries are upsetting "some classical theories that have acquired a status almost of dogmata." The book will serve as a text, a critical review for workers in evolutionary genetics, and an authoritative source of information for those biochemists, molecular biologists, ecologists, and others whose work leads them to considerations of the evolutionary process. In performing these functions it may well prove to be as important a contribution as *Genetics and the Origin of Species*. The next major development that lies ahead in evolutionary biology will be the integration of the growing body of data from biochemistry and molecular biology with that from population genetics, systematics, and ecology. Meanwhile, we have in Dobzhansky's book a superb evaluation of the present state of affairs from a master of the field.

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Mathematics as Metaphor

Dynamical System Theory in Biology. Vol. 1, Stability Theory and Its Applications. ROBERT ROSEN. Wiley-Interscience, New York, 1970. xiv, 302 pp., illus. \$17.95. Series on Biomedical Engineering.

Everybody likes to discover general and unifying principles in biology. Unfortunately, the grammatical form of principles that claim generality does not tell how useful those principles are in particular experiences. To show that the modern theory of evolution and the fundamental models of molecular biology are widely useful in detail has required the imagination and hard work of naturalists and biochemists. The division of scientific labor may make it economical for some people to concentrate on empirical foundations, others on conceptual interpretation, unification, and development. But either without the other yields the sound of one hand clapping.

Because the elaboration of language is, for some people, much easier than the labor of establishing concordance or tension between general principles and experience, there is an enormous tempta-

tion to spin out language that has the sound and syntax of general principles and to declare it scientifically satisfying without scrupulous regard to its relations to reality. Rosen's newest book is not the only recent work on theoretical biology that succumbs to this temptation.

A "dynamical metaphor," according to Rosen, is a system of ordinary differential equations of specified form the qualitative behavior of which in some way resembles the qualitative behavior of a class of biological phenomena. Rosen proposes that dynamical metaphors be accepted as explanations of phenomena they resemble.

For example, a Rashevsky-Turing construction, as presented here, is a finite set of first-order, linear, autonomous, homogeneous ordinary differential equations. The coefficients of these equations are chosen so that (i) the variables can be identified with concentrations in an open chemical system, (ii) the unique critical point of the system is asymptotically stable, (iii) the location of the critical point depends on the coefficients (interpreted as rate constants), and (iv) "overshoots" in adjusting to perturbations can occur.

Rosen says,

Now these four properties of open systems, as opposed to closed systems, are in a qualitative sense highly reminiscent of morphogenesis, and other characteristic features of metabolizing organisms. . . . many of the dynamical properties of organisms can be explained simply by knowing that the organism is in fact an open chemical system, and without knowing anything further about the specifics of its dynamics [pp. 194-95].

What we really mean, then, when we say that the Rashevsky-Turing constructions can explain the phenomena of morphogenesis is the following: *Any particular morphogenetic system, with its own definite physicochemical structure, can be considered as a realization of some Rashevsky-Turing system, by the proper identification of observables of the morphogenetic system with the state variables of the corresponding Rashevsky-Turing system. . . . [Though] clearly radically different from the more conventional explanations and descriptions built out of specific physicochemical models, . . . explanations of this kind are at least equally valid as those based on specific model-building, and must be explicitly accepted scientifically on an equal footing* [pp. 189-90].

No single instance of any particular morphogenetic system is shown in this book to behave in detail like the state variables of any Rashevsky-Turing system. But all real morphogenetic systems must behave so for the same trivial rea-

son that Rosen (p. 260) objects to the Hodgkin-Huxley equations for nerve excitation: as long as the variables corresponding to observable quantities are few relative to the total number of state variables assumed, equations involving the unobservable or "intervening" variables can be arranged to yield an arbitrary behavior for the observables. The Rashevsky-Turing constructions impose no limitations on the numbers of variables that may be assumed to explain a given observation.

This treatment of morphogenesis fills the first of the three chapters at the end of the book that involve the language of biology. The second of these three chapters explores the properties and possible realizations of networks of "two-factor elements." In such an element, one unidentified state variable corresponds to excitation, the other to inhibition. Fact cited: some cellular metabolites and some parts of the nervous system seem to turn other metabolites and parts on and off.

On the basis of these analogies, the entire well-developed theory of networks in the central nervous system can be carried over intact to the study of differentiation phenomena based on the interaction of operon units, and conversely. This is a startling and unexpected illustration of the way in which dynamical analogies can formally unite two apparently totally dissimilar areas, and thus conceptually enrich the whole of biology. It is a manifestation in biology of the same kind of reasoning used in physics, in which apparently quite unrelated areas can be conceptually unified through formally analogous action principles [p. 247].

Physics-envy is the curse of biology. When somebody else has done the dirty, tedious work of showing that a mathematically formulated physical principle leads to predictions correct to a specified number of decimal places in the boring world of Euclidean 3-space with Cartesian coordinates, theoreticians and textbook writers can axiomatize, generalize, and dazzle your eyes with the most coordinate-free, cosmically invariant representations you please. The areas of learning Rosen has united by these formal analogies are provinces of Atlantis, and the deed and lot numbers of the foundations on which his analogies rest are recorded nowhere.

The final chapter of these three, and the final chapter of the book, describes attempts to force the size-12 feet of ecological communities, cellular biochemistry, and neural networks into the glassy size-4 slippers of the formalism of statistical mechanics. Here, in a singular

moment of lucidity, Rosen observes that "contortions are necessary to force an underlying dynamical system to have a conservative character, so that present techniques can be employed" (p. 293). But he still fondles the shoehorn of stability theory, his hip-pocket mathematical enforcer.

The first six chapters of the book present the elementary qualitative theory of ordinary differential equations with the same attention to detail as the last three chapters on applications. In these first 179 pages, a single reading revealed 123 mistakes. Notwithstanding Rosen's prefatory commitment "to tell the reader no lies," the solutions to ordinary differential equations stated on pages 12, 82, and 122 are false, as is the illustration accompanying the last. A mistake in sign in finding a constant of the motion of the Volterra equations on page 44 leads to a faulty stability argument on page 127. Biologists should command the material covered here well enough to explore the stability properties of their more mundane structural mathematical models; but many other less confusing sources present stability theory with greater care and at a lower price.

According to its author, this book "is the only species of its genus; its nearest living relative is Lotka's classic work, *Elements of Physical Biology*" (p. v). The stunning immodesty of this claim matters less than the extent to which it is misleading. Lotka took the trouble to graph the growth of American railways, to tabulate the average yearly gains in weight of steers, and to relate these data to his models; Lotka respected reality, and the odor of that respect rises from his still living pages.

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The Colonization Hypothesis

Origin of Eukaryotic Cells. Evidence and Research Implications for a Theory of the Origin and Evolution of Microbial, Plant, and Animal Cells on the Precambrian Earth. LYNN MARGULIS. Yale University Press, New Haven, Conn., 1970. xxii, 350 pp., illus. \$15.

The last billion years of life have been the easiest to explain in terms of evolution. Before they began, two major events occurred which are difficult to understand, yet important for the subsequent evolution of life as we know

it. The first cell originated and evolved into organisms very similar to bacteria and blue-green algae (prokaryotes). Within this group of organisms considerable biochemical evolution has occurred, but in spite of their biochemical virtuosity the world would have remained a dull place if no further evolution in cell type had occurred. There would have been no birds, or mosses, or trees, or even book reviewers. All these organisms are composed of aggregates of a cell type, the eukaryotic, which differs significantly from that of the bacteria or the blue-green algae. The prokaryotes exhibit only modest attempts at differentiation and the development of multicellular organisms.

Strong evidence has been produced by biochemistry and molecular biology for the fundamental unity of all life, but much evidence is also arising for the uniqueness of the biochemical and structural properties of each of the two fundamental kinds of cells. The apparent complexity of the eukaryotic cell increases with increasing amounts of evidence that at least some of the organelles of this type of cell are partially autonomous genetically and, in addition, resemble prokaryotes in their biochemical properties.

This book begins with a discussion of the chemical evolution which must have preceded the origin of life and then very briefly considers the origin of the first cell. Margulis spends more time discussing the possible courses of the biochemical evolution of the first cells and particularly considers the profound effects of the origin of photosynthesis on the primitive world. After thus setting the stage she begins the central argument of the book—that the eukaryotic cell is the result of a series of intracellular symbioses between prokaryotic colonizers and a primitive cell. Invasion or ingestion of bacteria and of blue-green algae produced mitochondria and chloroplasts, respectively. Thus the eukaryotes are the results of the fusion of two or more lines of cellular evolution. This thesis has been offered before, as Margulis notes. The first clear statement of it (not, however, mentioned by Margulis) was given by Richard Altmann in *Die Elementarorganismen und ihre Beziehungen zu den Zellen*, published in 1894:

Cells are not elementary organisms but colonies of such with strange laws of colonization; the cells originate not through the assembly of granules [that is, organelles] but they have originated in that way in former historical periods; which