THE SOCIAL INSECTS

The Social Insects, Vol. I, edited by Henry R. Hermann. Academic Press, New York, 1979, 437 p., illus., $36.00 (78-4871).

This is the first of three volumes intended to collate investigations of insect sociality. It contains eight chapters by nine authors, on topics ranging from origin, antiquity, and evolution of eusociality to territoriality, caste differentiation, genetics, larvae of Hymenoptera, and the significance of symbionts. The remaining two volumes, whose contents and authors are already established, will deal with communication, defense, reproductive behavior, systematics, and the individual groups of social insects.

Overall, the volume reads like an annual review of social insects. Its chapters are uneven in quality, length, and usefulness, and they have not been organized into a coherent treatise. There is some overlap with materials already published elsewhere (e.g., Crozier, Kistner, the Wheelers), and two chapters (Starr, Crozier) overlap one another considerably. Nevertheless, this is a rich concentration of information from diverse approaches to the study of social insects, in which specialists and newcomers alike are almost certain to find something interesting and new to them.

In the opening chapter, Hermann points up the lack of resolution among phylogenetic, genetic, and comparative behavioral efforts to model and reconstruct the origins of eusociality. He introduces an array of topics relevant to this problem to be dealt with in depth in later chapters: dominance, aggregation, territoriality, group defense, group foraging, inquilinism, fungus cultivation. Starr and Crozier (in chapters 2 and 6, respectively) address the question directly. Both provide valuable historical treatment and clear explanations, key concepts such as altruism, inclusive fitness, reciprocity, and measures of genetic relatedness. Both indicate the importance of considering the termites (whose sociality parallels that of the Hymenoptera so closely) in constructing models of the evolution of eusociality. Crozier discusses the impact of haplodiploidy on the social evolution of the Hymenoptera and upon various issues in population genetics. He, unfortunately, follows Wilson (1975) in classifying kin selection as a form of group selection (see Dawkins 1979). Brian's encyclopedic chapter on caste differentiation and division of labor, and that of Kistner on social insect symbionts, are especially informative and present significant new data. The Wheelers' chapter on larvae of the Hymenoptera is an informative, mainly morphological treatment.

Other reviewers have questioned whether volumes such as this are appropriate so soon after Wilson's (1971) classic. The problem is not that there isn't enough new to be said; instead, it is one of timing. The rapid development of theory and accumulation of information since 1976, when this volume was completed, practically ensure that much of the book would be out of date before it appeared. For example, Hermann's summary of phylogenetic efforts to reconstruct the evolution of eusociality does not include recent papers by West Eberhard (1978) and Hamilton (1979), which apply current genetic models to proposed phylogenies. Carpenter and Hermann's brief treatment of the antiquity of eusociality has been superceded by Burnham's major review in *Psyche* (1978).

The two chapters dealing with evolutionary theory, excellent in their reviews of the field up to 1976, suffer the most from dating. Thus, Starr and Crozier both discuss Trivers and Hare's (1976) analysis of sex ratios of parental investment in social insects, but were unable to include Alexander and Sherman's (1977) critique of that paper or several recent estimates of actual investment ratios. Similarly, both discuss parental manipulation in detail, but could not include the numerous analyses of this topic since 1976. Starr repeats Alexander's (1974) error, since discussed by numerous authors, that selfish tendencies in offspring that reduce the parent's reproduction cannot spread. This conclusion is perhaps attributable to a failure to ask what would happen to alleles with certain effects, as opposed to asking what would happen to the fitness of individuals without considering that conflicts of interest may exist among genes that occur

ELECTROPHORETIC APPROACHES TO ANIMAL SYSTEMATICS

Biochemical Systematics and Evolution, by Andrew Ferguson. Halsted Press, John Wiley & Sons, New York, 1980, 194 p., illus., $42.95 (79-20298).

This text would have been more appropriately entitled "Introduction to Electrophoretic Approaches to Animal Systematics and Evolution," or some such. In his preface, the author acknowledges that "the greater part of this book is devoted to the application of gel electrophoresis" and "that most examples concern animals." Indeed, nearly all of the text is preoccupied with that approach and that kingdom. There are 14 pages of bibliographic citations, only a few of which contain botanical references. With 6 pages devoted to a topic index, we have a text of 194 pages containing about 70 illustrations. Most of the latter are histograms, electrophoregrams, dendrograms, or other line drawings designed to portray the presentation of electrophoretic data.

Practically all of the published work discussed or reported upon is from the zoological literature. Only 4 of the 170 pages of text and only 12 references (from among ca. 286 citations) are devoted to the botanical literature, most of this relating to polyploidy and its detection by electrophoresis.

One searches in vain among the references for such well-established botanical chemosystematic workers as Alston, Fairbrothers, Harborne, Hegnaur, Mabry, McNair, Mirov, and Swain, to name but a few. Surprisingly, Boulter's extensive comparative work on cytochrome *c* is omitted, although this is portrayed in a diagram from some other reference. Even the section entitled "History of the Biochemical Approach" neglects the botanical side, ignoring completely the historical roots that clearly began, at least in principle, with DeCandolle in the early 1800s and, at least in practice, by lichenologists (using secondary compounds) during that same century. Ferguson erroneously states (p. 13) that "the term *chemosystematics* is sometimes used synonymously with *biochemical systematics*, although the former tends to be favoured by botanists and the latter by zoologists. In part this stems from the use by botanists, in the past, of low-molecular-weight chemicals—the study of which is the realm of the chemist—while zoologists have concentrated on proteins and nucleic acids—the concern of the biochemist." In fact, I fancy that he coined the term *chemosystematics* (perhaps along with several others) in the 1950s, intended as an abbreviation of biochemical systematics. After all, micromolecules, both plant and animal, are biochemicals, much as are macromolecules.

According to its author, the book is designed primarily for "the advanced undergraduate" student but "the postgraduate and research worker should find parts of interest and benefit." In my opinion, this is so because the author has organized his material well and communicates clearly and concisely. He does not attempt to overload the reader with "such-and-such have found this-and-that, *however*. . . ." Rather, the text is a simple telling of the contribution, both real and potential, of electrophoretic methods for systematic purposes, albeit animal. He covers that field admirably, weaving in, when appropriate peripheral but germaine accounts of polymorphism, selectionism vs neutralism, Hardy-Weinberg expectations, parthenogenesis, hybridization, genetic distance and identity, DNA hybridization, amino-acid sequence studies, and molecular clocks. But as a botanical worker, I can't help but believe that the text could have lived up to its title had the author taken the time to digest the rich field of literature in botanical chemosystematics, both micromolecular and macromolecular.

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in the same genomes. (Crozier illustrates this point using a two-allele, one-locus model.) It is probably unfortunate that this particular aspect of parental manipulation has received so much attention, for it detracts from the obvious fact that parents do manipulate their offspring, and that, as Starr concludes, parental care does evolve to contribute to the parent's inclusive fitness.

This series should attract a wide readership because the social insects have figured so importantly in the development of modern evolutionary theory. While the first volume contributes essentially no new theories, ideas, or insightful general observations (as Wilson did so well in *The Insect Societies*), it draws together and presents clearly much specialized information from scattered sources. Workers in the field of insect sociality, evolution, and behavior will find it a valuable resource.

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BASIS FOR MOLECULAR BIOLOGY

The Hypercycle: A Principle of Natural Self-Organization, by M. Eigen and P. Schuster. Springer-Verlag, New York, 1979, 92 p., illus., $9.80 (paper).

In his "Conclusion" to *The Origin of Species*, Charles Darwin wrote: "Therefore, on the principle of natural selection with divergence of character, it does not seem incredible that, from such low and intermediate form, both animals and plants may have been developed; and, if we admit this, we must likewise admit that all the organic beings which have ever lived on this earth may be descended from one primordial form." The subject of the development of "primordial form" is the subject of prebiotic or molecular evolution, an area which has received considerable experimental attention since the pioneering efforts of Stanley Miller in the 1950s. Since then, several laboratories have determined that some of the precursor molecules of proteins and polynucleotides can be produced by various nonbiological means, either by random or nonenzymatic catalytic chemical means. However, an understanding of the possible mechanisms for prebiotic evolution requires more than a knowledge of the underlying organochemical possibilities. It requires a quantitative description of the synthesis, self-reproduction, and organization of biological macromolecules.

In the present work, Eigen and Schuster have elaborated in detail theoretical arguments aimed at investigating how far Darwin's principle of natural selection can be extended to molecular events using quantitative physical-chemical theory. They show that there are inherent quantitative limitations in information content, which result from applying the Darwinian mechanism of natural selection to molecular systems, and that a new principle of self-organization is required to understand prebiotic evolution. The authors have developed a novel class of nonlinear reaction networks, called *hypercycles*, which exhibit unique properties. They present a comprehensive mathematical treatment of these networks, which leads to a detailed kinetic description of a new principle of self-organization. Whereas Darwinian selection is based upon a linear selection of random events, hypercycle organization is based upon cyclic (second or higher order) autocatalysis, which the authors show is necessary (but probably not sufficient at the molecular level) in order to have stable, restricted-length polynucleotide self-replication.

This short book is divided into three sections. The first introduces a quantitative representation of the Darwinian behavior of macromolecular systems with examples from molecular genetics. The concept of "quasispecies" is lucidly introduced as the molecular analog of the "wild type" in an organismal population. This careful definition is later shown to be both physically meaningful and mathematically tractable by well-known methods. The authors conclude that the first self-reproductive macromolecules with stable information content were probably transfer-RNA-like structures. However, the information content of such structures is insufficient by at least one order of magnitude to provide reproducible translation. Something else is needed to increase the reliability of information transfer.

An analysis of RNA-phage replication shows that this information requirement is satisfied by replicases, which themselves could not have evolved without a highly perfected translation mechanism. Thus, RNA viruses, as they now exist, must be late products of evolution. This barrier to the molecular evolution of nucleic acids at the tRNA-like level of structure thus requires a new kind of mechanism (non-Darwinian, i.e., nonlinear autocatalytic) in order to expand information content. The mechanism by which molecular evolution advanced was integration of several linear self-reproducing units to give rise to a cooperative system. The mechanism for this integration is postulated to be described by the cyclic linkage of reactions called hypercycles.

The second part of this sonata-form monograph is a detailed mathematical development of the properties of hypercycles, which also presents logical arguments directly accessible to nonmathematically inclined readers. Familiarity with differential equations and matrix algebra is sufficient to follow the theoretical development of the properties of hypercycles. The imprint of Eigen's development of relaxation-kinetics theory to analyze elementary-step chemical reactions is clearly seen throughout this section.

The third section deals with the application of hypercycle theory to protein synthesis, the origin of the genetic code, and the origin of hypercyclic reaction coupling. The section ends with a discussion of 10 fundamental questions of molecular evolution that serve as a recapitulation of the central ideas in this brilliant work.

This volume is highly recommended for its clarity and conciseness of expression. The central conclusions can be understood without working through the mathematical presentations, thus making the content accessible to readers from various disciplines. By analyzing the basic questions in molecular evolution with fundamental physical-chemical theory, the authors have pointed the way to the development of a conceptual basis for the whole of molecular biology.

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