Book Reviews

The Origin of Sex

Sex and Evolution. GEORGE C. WILLIAMS. Princeton University Press, Princeton, N.J., 1975. x, 202 pp., illus. Cloth, $13.50; paper, $4.95. Monographs in Population Biology, 8.

The most interesting question about sex is not how but why. Why has such an elaborate and expensive process evolved? Sexual reproduction is in every way a consuming biological activity. Reproductive organs tend to be elaborate in structure, courtship activities lengthy and energetically expensive, and genetic mechanisms of sex determination finely tuned and easily wrecked. But more important, a female that elects to reproduce by sex cuts her genetic contribution to each gamete by one-half, without, in the vast majority of species, receiving any material aid from the male. If an egg develops parthenogenetically without meiosis—the simplest way to proceed—all of the genes in the resulting offspring will be identical to those of the mother. In sexual reproduction, which entails reduction division during meiosis, only half are identical. The female, in other words, has thrown away half of her investment. If current evolutionary theory is correct, sexual reproduction must therefore confer at least a twofold selective advantage in order to overcome the 50 percent deficit. Such powerful selection should be one of the most pervasive and obvious forces at work in evolution—yet biologists have not been able to demonstrate it to general satisfaction.

This is the paradox to which G. C. Williams addresses his new book, *Sex and Evolution*. Before considering the author's attempted solution, the reader should be aware of the controversy that has arisen from the theory. There is first the "long-term explanation," which began in the writings of August Weismann and has been successively refined by H. J. Muller, J. F. Crow, Motoo Kimura, Tomoko Ohta, and John Maynard Smith. In essence this theory states that entire populations evolve faster when they reproduce by sex, and as a consequence they usually prevail over otherwise comparable asexual populations. In sexual populations, favorable mutations can be joined more quickly by the processes of meiosis and recombination. While the asexual population waits for the mutations to occur one after the other in the same lineage, the sexual population can combine the best mutations through matings among its many diverse members. The competing "short-term explanation" has been most effectively championed by G. C. Williams. According to this hypothesis, sexual reproduction evolves because it permits each parent to diversify its own offspring and thus overcome unpredictable changes in the environment encountered from one generation to the next.

The long-term and short-term explanations are not incompatible, but their relative weights in particular groups of organisms remain to be measured. In *Sex and Evolution*, Williams has produced some strong new arguments and supporting evidence that favor the short-term explanation for most kinds of lineages. In so doing he has transcended the basic controversy and made significant contributions to several other areas of evolutionary theory. This book impressed on me the fact that there are two ways to create first-class theory. The first is to start with existing assumptions and to build new or at least superior models, usually mathematical in form, to solve the key problems. This approach is exemplified by R. M. May's *Stability and Complexity in Model Ecosystems*, an earlier number of the Princeton Monographs in Population Biology series. The second way, illustrated by *Sex and Evolution*, is to enrich the assumptions. Williams has not been satisfied with arguing from the narrow base of premises that limited earlier formal theory. In searching for the missing 50 percent advantage, he has systematically reexamined features in the environment and life cycle that affect fitness. His main argument can be summarized in three steps as follows. First, as is generally accepted, sexual progeny vary in fitness more than asexual progeny. But in addition the intensity of selection is far greater than we had intuitively believed, so that usually only a few individuals possessing certain extreme traits survive in each cycle from zygote to zygote. Those individuals lucky enough to acquire the very highest "fitness dosage" are found predominantly among the sexual progeny. Hence genes inducing sexual reproduction will be consistently favored.

The core of the book is a series of models, with accompanying documentation, of ways in which selection can be sufficiently intensified. The models lead into an exploration of some hitherto neglected areas, and they suggest new correlates in the size of organisms, fertility, dispersal ability, steepness of environmental gradients, and other major parameters. Williams correctly points out that population geneticists have been overly preoccupied by low-fertility organisms such as *Drosophila*, man, and a few higher plants. When species with high fertility are examined, a different picture emerges; the generation-by-generation reinforcement of sexual evolution becomes much more plausible. Williams further suggests that fitness is lognormally distributed owing to the multiplicative interactions of contributing factors, a circumstance that would distinguish the winning class of genotypes still more sharply. He proposes the general occurrence of "sisyphean" fitness: congeries of genes assembled in the extremely fit fraction of the population are disassembled by the sexual process each generation, rendered less fit by subtle changes in the environment, or both. The sisyphean quality intensifies the selective process favoring genetic diversity in progeny, and hence sustains genes favoring sexual reproduction indefinitely. Overall, Williams does make a convincing case for the short-term hypothesis in a wide variety of organisms, and by so doing he lays the foundation for a more systematic and interesting study of life cycles.

The principal flaw in *Sex and Evolution* is its lack of balance. Having examined the origin of sexuality in the first ten chapters, Williams conducts an excursion into the equally important subjects of sexual selection and division of labor. His presentation is sound but short and sketchy, so that the reader will not be left with a sense of the full scope of problems remaining for evolutionary analysis. Even less adequate is the treatment of group selection. The evolution of traits by

the differential extinction and reproduction of populations is a process uncongenial to Williams's world view, and he attacks it with the same vigor that characterized his earlier book *Adaptation and Natural Selection* in 1966. But the situation has changed greatly since 1966. At that time there was an urgent need to rebut V. C. Wynne-Edwards's *Animal Dispersion in Relation to Social Behaviour*, a task Williams performed with distinction. In the past several years a real theory of interpopulation selection has begun to be forged, with both enriched premises and rigorous model building. This part of the subject Williams ignores. He is still convinced, on intuitive grounds and in apparent puritanical devotion to the principle of parsimony, that interpopulation selection cannot be important in nature. His guess may or may not prove right—organic evolution is *not* parsimonious. But that is really beside the point. The possibility of evolution by interpopulation selection must be fully explored with an open mind. Insofar as the new theory considers the results of counteraction between group and individual selection, it will produce complex, nonobvious results that constitute testable alternatives to the hypotheses of individual selection. My own intuitive feeling is that interpopulation selection is important in special cases, and that its investigation will make evolutionary biology a much more interesting and challenging discipline in the future. At the very least the subject must be systematically developed. To deny that much would be to misconstrue the true nature of theory and evidence.

These faults are nevertheless secondary to the important accomplishments of a really excellent book. *Sex and Evolution* ranks among the best general works on evolutionary biology in recent years. The author also deserves to be saluted for his sense of the real and important, his crystalline prose, and his frank and modest style. He correctly observes that "the contest of ideas on these fundamental problems has only just begun. History has afforded a rare opportunity to ardent participants and alert spectators in the years ahead." *Sex and Evolution* will serve as the invitation and the guide to this contest.

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Biochemistry of DNA

DNA Synthesis. ARTHUR KORNBERG. Freeman, San Francisco, 1974. x, 400 pp., illus. $18.

DNA Synthesis is a clearly written and interesting presentation of the subject as viewed through the eyes of the durable patriarch in the field. The format of the book makes it easily readable, and it is well illustrated. In addition, it includes numerous tables compiling data that were previously widely scattered. Examples are the tables comparing properties of *Escherichia coli* DNA polymerases I, II, and III and listing mechanisms of degradation by exonucleases and mechanisms of inhibition in replication and transcription. The book is written at such a level that it will be useful for researchers in DNA replication as well as for persons interested in supplementing their general biochemical knowledge of the subject.

The first two chapters of the book deal with the structure and function of DNA and the biosynthesis of DNA precursors. These chapters help make the book complete and perhaps will be useful to the novice, but the elementary presentation of this material seems out of step with the sophisticated presentation in the remaining chapters.

The next two chapters describe many aspects of the *E. coli* DNA polymerase I including isolation, types of reactions catalyzed, proteolytic cleavage, properties of the DNA product, and physiological role. The work embodied in this discussion represents a primary research interest of the Kornberg laboratory during the last ten years; hence most of the account tends to be complete in its detail and the material is logically and clearly presented. However, little emphasis is placed on the substantial contributions of the geneticists. Several years ago a variety of mutants of genes affecting DNA synthesis were characterized. Biochemical and genetic studies with these mutants have provided new insights into this complex process and promise to be even more revealing in the future.

The extensive documentation of the properties of the *E. coli* DNA polymerase is followed by two chapters giving a rather cursory account of bacterial, phage-induced, and eukaryotic cell DNA polymerases. Minimal coverage is given to DNA polymerase II and the alternate forms of polymerase III from *E. coli*, the polymerases from *Bacillus subtilis* and *Micrococcus luteus*, and the polymerases induced by T-even, T-odd, and *B. subtilis* phages. Likewise, eukaryotic cell DNA polymerases are covered only spottily despite the fact that they have been a subject of enormous research interest in the past several years. An example of the sparse coverage is the two-page treatment of terminal nucleotidyl transferase, an enzyme known for more than ten years and widely used in a variety of laboratories in several different contexts.

The chapter on the replication of DNA viruses is one of the most outstanding presentations in the book, in my judgment. It is based on the use of small, well-characterized DNA viruses as tools to study DNA replication events. The structure of the viruses, their mechanisms of infection and replication, and genetic studies are presented. The viruses include M13, ϕX174, T7, T4, λ, certain plasmids, and SV40 and polyoma. The easily readable comparison of the features of these viruses is unique to this book.

A chapter on RNA polymerase is included near the end of the book. The chapter provides a useful overview of the subject for the elementary reader; however, since many excellent and complete reviews on this subject exist, it adds little in the way of usefulness to researchers in the field. The last chapter of the book briefly cites some of the achievements of chemical and enzymatic synthesis of polynucleotides.

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Molecular Genetics

Gene Expression. BENJAMIN LEWIN. Two volumes. Vol. 1, Bacterial Genomes. xviii, 642 pp., illus. $29.50. Vol. 2, Eucaryotic Chromosomes. xvi, 468 pp., illus. $23.50. Wiley-Interscience, New York, 1974.

Benjamin Lewin has put together for the first time an advanced, comprehensive, and exacting account of our knowledge of gene expression in both prokaryotic and eukaryotic organisms. The presentation is well organized, documentation is extensive, and facts are separated from opinions. Of particular value are the large number of figures depicting current models of various aspects of gene expression. These two volumes should prove extremely useful