grated into the chromosome of the bacterium and is propagated passively until the lysis-lysogeny decision is reversed.

After introducing the basic underpinnings of gene expression (transcription of DNA into RNA and the concept of regulation via DNA-binding proteins), Ptashne proceeds to describe the components of the system (operators, repressors, promoters, and RNA polymerase) and explain how they interact to form an on-off switch. The successes of recent x-ray diffraction studies of the two repressor molecules (CI and Cro) pave the way for a detailed description of how proteins recognize and bind to specific DNA sequences (the so-called "strong forces" of the switch). Likewise, the clarity of existing descriptions of how the CI repressor interacts with itself, and with the host-encoded RNA polymerase, leads to a smooth exposition on the importance of specific protein-protein interactions ("weak forces") in the construction and modulation of the switch. These are crisp, clear illustrations of science at its best.

Ptashne completes his description of the lysis-lysogeny switch with a chapter outlining the events that surround its actual setting. The influences of the CII and CIII regulatory proteins are described clearly, although perhaps from a somewhat limited perspective. Along with the protease-sensitive domain that connects the amino- and carboxyl-terminal domains of the CI repressor, CII and CIII are the "sensors" that λ uses to evaluate the physiological state of its host. Though the modes and consequences of interaction of these regulatory proteins are not fully understood (particularly, in the case of CIII), they may be a more fundamental component of the switch than is suggested by this chapter. The passage describing the events that follow activation of the switch is a lucid synopsis of a remarkable series of accomplishments in the fields of bacterial genetics and molecular biology. One comes away from this section with awe for the exquisitely logical manner in which λ marshals the physical forces of its environment to form and follow either of its orderly pathways of existence.

Our understanding of how the lysis-lysogeny switch is constructed, modulated, and interpreted is sufficiently complete that the processes can be described in simple terms. Ptashne succeeds in this effort by writing in a direct and economical style and by utilizing an effective series of schematic drawings. This is an excellent book that offers a splendid opportunity for the uninitiated scientist to appreciate the logic of genetic regulation.

Biologists have long regarded the organization of living systems as resulting from differential gene expression. It is satisfying that a quarter of a century of genetic and biochemical dissection of bacteriophage λ has led to a sharp focus on the virtues of an on-off switch. As Ptashne suggests, hierarchies of binary switches could be used to regulate the more complicated developmental programs of multicellular organisms. That a bacterial virus has evolved such a switch is a fact ripe for appreciation by all scientists.

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A Cellular Structure

The Cytoskeleton. An Introductory Survey. M. SCHLIWA. Springer-Verlag, New York, 1986. xii, 326 pp., illus. $78. Cell Biology Monographs, vol. 13.

In *The Cytoskeleton*, Manfred Schliwa has produced a readable and comprehensive review of the filamentous networks that provide the structural framework of the cytoplasm of eukaryotic cells. Schliwa begins with an introduction to the characteristics of each of the three main cytoskeletal structures (actin-myosin filaments, microtubules, and intermediate filaments), including lucid accounts of the known biochemistry of each major filament subunit and associated components. After a brief description of filament assembly dynamics, he then confronts the larger questions of cytoplasmic organization: How are the cytoskeletal polymers arranged three-dimensionally? What are the interactions between the major cytoskeletal components? How do these internal cytoplasmic structures interact with membranes and extracellular components? And in light of the foregoing considerations, what is the cytoplasm really like?

Discussion of each question is accompanied by extensive citation of the original literature. Indeed, the book ends with a 79-page list of references that will itself be of great value to both the novice and the specialist. In addition, the presentation is enhanced by 88 beautifully reproduced and well-chosen micrographs.

Moreover, with reviews of the relevant literature Schliwa has combined valuable critical judgments concerning individual experimental contributions and interpretations. For example, though acknowledging that universal acceptance has not been achieved for the concept of a microtrabecular matrix encompassing not only the known filament proteins but also a large repertoire of biochemically undefined subunits, Schliwa explains why he believes it to be correct in substance if not detail. Similarly, considering Lazarides's hypothesis that intermediate filaments are mechanical integrators of space, he concludes that this is much too general a description.

In some regards the volume is at both its best and its weakest when the larger questions are confronted. This reviewer found the sections that attempted such confrontation all too brief. Just how fluid and crowded is the cytoplasm? Are cytoplasmic components such as ribosomes really attached to a skeletal substructure? These issues deserve treatment at greater depth.

It is also disappointing that topics that have seen explosive growth since early 1985 are not included. Dynamic instability of microtubules and how it can establish cell-cycle–dependent changes in microtubule function are barely mentioned. In the section on membrane-cytoskeletal interactions, the now well-documented movement of vesicles along microtubules in axons is not considered at all.

For what audience is this book appropriate? It will serve as a reference source for anyone (specialist or novice) with an interest in the cytoskeleton and the organization of the cytoplasm. Moreover, in conjunction with a standard cell biology textbook to fill the occasional gap and original literature to provide the most recent results, it could form an excellent core reference for a graduate course on cytoplasmic structure. In both of these regards, it currently has no rival.

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Sex Ratio Theory

Theoretical Studies in Sex Ratio Evolution. SAMUEL KARLIN and SABIN LESSARD. Princeton University Press, Princeton, NJ, 1986. xvi, 314 pp., illus. $47.50; paper, $14.95. Monographs in Population Biology, 22.

The main result of sex ratio theory is that, under population-wide random mating and other simplifying assumptions, the primary sex ratio (the proportion of males at birth) should be 1/2. If this were not so, a newly conceived member of the rare sex would, on average, have more offspring than one of the common sex, since each offspring has one mother and one father; thus there is frequency-dependent selection in favor of parents producing the rare sex. This argument was partially formulated by Darwin in the first edition of his book on sexual selection

(1871), but he retracted it in the second edition (1874), and it was left to Fisher in 1930 to develop the theory in its general form.

Despite the wide applicability of Fisher's principle, recent work has concentrated on situations where it breaks down, such as the effect of population structure and local mate competition, the consequences of the fitness of the two sexes varying differentially with environmental conditions, and the evolution of sequential hermaphroditism (sex reversal). A previous monograph in this series (*The Theory of Sex Allocation* by E. L. Charnov) gave a fine synthesis of theoretical and empirical work in this area.

The book under review has a different aim. It is written by two mathematicians who are dissatisfied with the theory underpinning the subject. They observe that there are two approaches to sex ratio theory, a more heuristic approach focusing on optimality principles and adaptive functions of sex allocation (including the evolutionarily stable strategy—ESS—concept), and a more rigorous approach based on the full analysis of a population genetic model. The authors' program is to explore in detail the implications of the latter approach, which has been avoided in most studies because of its complexity.

The authors bring highly developed mathematical skills to this task, and the techniques they use deserve close study by anyone involved in this type of modeling. The results are presented in rather an abstract form, and it may be helpful to consider two specific examples.

Suppose that the sex of a zygote is determined by a single locus with two alleles, the three genotypes having different probabilities of being male. If the two homozygote probabilities straddle both the heterozygote probability and 1/2, the population sex ratio at equilibrium will be 1/2, in accordance with Fisher's principle, but otherwise this may not be true. For example, if both homozygote probabilities are 0.1 and the heterozygote probability is 0.75, the population sex ratio at equilibrium is not 0.5 but 0.425. This might seem to contradict Fisher's principle, but it does not really do so. With so much overdominance, additive genetic variability is not available to produce the Fisherian sex ratio, but a third allele leading to an even sex ratio can always invade the system. On the other hand, a system with an even sex ratio at equilibrium cannot be invaded by a new allele leading to a departure from the Fisherian value.

Another example supposes that the sex of a zygote is determined by two loci with two alleles, double heterozygotes being male and all other genotypes female. The equilibrium sex ratio under this system is 1/4, provided the recombination fraction exceeds 1/6. The reason is clear under free recombination, since every possible cross produces a sex ratio of 1/4 and there is no genetic variability on which selection can operate. As before, the system is structurally unstable, in the sense that it can be invaded by alternative alleles or loci which lead to an even sex ratio.

The authors extend their analysis to multifactorial sex determination models involving many factors of small effect. This chapter is flawed by their use of an ad hoc model of multifactorial inheritance that does not adequately reflect its Mendelian basis.

The conclusion I draw from these studies is that sex ratio models (whether single or multilocus) that do not give an even sex ratio under the usual simplifying assumptions are likely to be structurally unstable and thus of little evolutionary importance. The authors would dispute this conclusion with respect to multilocus and multifactorial models.

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