Water Transport Mechanisms

Water Movement Through Lipid Bilayers, Pores, and Plasma Membranes. Theory and Reality. ALAN FINKELSTEIN. Wiley-Interscience, New York, 1987. xii, 228 pp., illus. $39.95. Distinguished Lecture Series of the Society of General Physiologists, vol. 4.

Water transport, or "osmosis," is one of the most venerable problems in biology. Superficially, the phenomenon seems quite simple: water moves in response to gradients of hydrostatic and osmotic pressure. However, inquiry into the mechanistic details of this process often leaves one with the uneasy feeling that it may never be possible to understand why water moves in one direction or another. *Water Movement Through Lipid Bilayers, Pores, and Plasma Membranes: Theory and Reality*, by Alan Finkelstein, may not eliminate this chronic uneasiness, but it is sure to bring the underlying causes into sharp focus.

The book is divided into three parts. The first outlines the fundamental physical principles that pertain to water movement by diffusion and bulk flow. Part 2 reviews the water-transport properties exhibited by lipid bilayers in the presence and in the absence of the well-characterized, pore-forming antibiotics Nystatin and gramicidin A. The final section considers the results and implications of water-transport measurements on red blood cells and epithelial sheets. Each of these sections would have been a valuable contribution alone. Together they provide an enormous resource that enables the reader to examine the application of basic principles in model systems as well as in biological membranes.

Part 1, the theory section, is important for several reasons. First, it is the only source known to this reviewer that presents a systematic development of the physical laws governing water flow. More important, however, the author keeps the discussion firmly rooted in physical reality by exploring the fundamental physics of water flow in terms of two limiting cases: the "oil" membrane, through which water and solute must permeate by simple solubility and diffusion, each interacting only with the substance of the membrane, and the "porous" membrane, in which the dominant transport route consists of water-filled pores within which water-water and water-solute interactions are important. A central feature of this section is an analysis of the driving force for bulk water flow in a pore due to a transmembrane osmotic gradient. The author develops the concept that an applied osmotic gradient results in a pressure gradient within the pore despite the absence of a net difference in hydrostatic pressure across the membrane. Although this is not a new idea, its implications have never been so fully explored.

The development of the physics of water flow proceeds inexorably from the basic notion of solubility and diffusion in an "oil" membrane to the final conflict: the analysis of volume flow in a porous membrane that is also permeable to solute. A central character in this drama is the reflection coefficient, σ, a phenomenological parameter derived from a purely thermodynamic analysis of fluid flow which has been widely used to "correct" the driving force for osmotic volume flow in the case of a permeant solute. The goal is to penetrate beyond equations to the physical underpinnings of the process, and the author pits the physical-intuitive view of water flow in leaky membranes against that derived from the phenomenological theories of irreversible thermodynamics. The battleground is the well-known "uphill water flow" experiment of Meschia and Setnikar, in which water is induced to move in a direction *opposite* to the orientation of its chemical potential gradient by bathing the opposite sides of a porous membrane with solutions containing a permeant solute (urea) and an impermeant solute (dextran). Several related experimental situations are discussed for which the underlying physics appears transparent, whereas the "explanation" derived from a thermodynamic analysis seems hopelessly muddled. The author argues convincingly that the irreversible thermodynamic approach, because of its tendency to cast thermodynamic potentials in the role of mechanical driving forces, can suggest an interpretation of osmotic flow that "completely distorts reality." There will doubtless be those who are offended by Finkelstein's somewhat irreverent treatment of irreversible thermodynamics, but even devotees of the theories will be forced to admit that this book represents a long overdue attempt at a critical analysis of our collective thinking about the concepts of solute and water flow embodied in the reflection coefficient.

The material in the second section comes largely from the author's laboratory, in which the relatively simple planar bilayer, with or without added pore-forming molecules, has been used as a proving ground for the analytical approaches to water transport described in part 1. Part 2 highlights the invaluable role that such studies play in providing a sound conceptual basis for an attack on the more formidable problems posed by the complexities of biological membranes. A prime example is the concept of single-file water flow and the effect of this flow mechanism on the ratio of osmotic to diffusional water permeability.

The final section reviews two biological situations for which most of the data on water transport have been obtained, the red cell and ADH-sensitive epithelia, with emphasis on the identification of the major pathways for water transport.

Finkelstein's clarity of exposition and his dedication to revealing the physical basis of biological transport phenomena make this a monograph that can be read with profit by a wide audience, including beginning students as well as experienced practitioners. It is such a genuinely satisfying book that I have considered not only giving it to my friends but simply leaving it where it can be discovered by others who might benefit from it.

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Control of Development

Developmental Genetics of Higher Organisms. A Primer in Developmental Biology. GEORGE M. MALACINSKI, Ed. Macmillan, New York, 1988. xxxvi, 503 pp., illus. $74.95. Primers in Developmental Biology, vol. 3.

The ultimate goals of developmental genetics are to elucidate the logic of the "genetic program" specifying development and to reduce the complexities of development to problems in cell and molecular biology. Current research is aimed either at identifying by classical genetic analysis those genes that control development or at understanding the role played during development by genes that have been identified by other means (for example, oncogenes or tissue-specific cDNAs). The essence of modern developmental genetics can be extracted from this volume, but not without some work by the reader. As the editor admits in his introduction, some of the main issues in developmental genetics are addressed only indirectly. Moreover, the order of the 20 chapters does not directly reflect the four main themes of the book.

One theme is that the intense application of classical genetic analysis to the fruitfly and the nematode, organisms with simple genetics, has identified a large number of developmental control genes. The methods and logic of the genetic analysis of *Caenorhabditis elegans*, for example the determination of null phenotypes and the construction of genetic pathways from tests of epistasis, are clearly described by Kimble and Schedl for genes controlling sex determination. The genetic analysis of early embryogenesis, fo-