Biology Syncretized

Evolution as Entropy. Toward a Unified Theory of Biology. DANIEL R. BROOKS and E. O. WILEY. University of Chicago Press, Chicago, 1986. xiv, 335 pp., illus. $25. Science and Its Conceptual Foundations.

Work directed to bridging the gulf between the physical and biological sciences cannot be judged by the same criteria as work in a single well-defined field. Perforce, in one or more of the fields they span, the authors will commit the errors of an amateur where the specialist would demand professionalism of others in the field. Continually as they write, the authors must visualize a potential readership and try to accommodate its probable ignorance of basic vocabulary and terminology in some of the topics. Brooks and Wiley have set themselves a fearful task, spanning evolutionary, developmental, and population biology and the possible relevance to these subjects of thermodynamics, chemical kinetics, information theory, and theory of languages. Their errors are legion, some of them quite serious. The reviewer must seek to determine wherein lies the real life of the enterprise and whether the various sins of omission and commission are mortal to it or only venial. And who should be the reviewer? Any scientist who has made a serious try at bridging the gulf might do. This one is a physical chemist, now with extensive experience in trying to put experiment and theory together in developmental biology, but a newcomer in the evolutionary field.

The book opens with a brief and therefore necessarily somewhat fragmentary survey of the history of evolutionary ideas, especially in relation to development. To my mind, the various views on recapitulation are somewhat overstressed, but the authors seem to think them important. Chapter 2, entitled "Why entropy?," opens a continuous line of reasoning that runs through the rest of the book. The progression is from classical thermodynamics of simple physical systems, via its extension into concepts of information theory, to ontogeny of the individual (chapter 3) and thence to populations and species (chapter 4), the ways to try to establish phylogenies (chapter 5), and finally the highest level of biological order, ecological associations (chapter 6). Chapter 7 is a brief summary.

The worst errors come early in chapter 2. The discussion of simple physical systems on pp. 26 to 29 is, to coin a word, teratothermodynamics. Closed systems are identified with isolated ones; and isolation, it seems, does not preclude $\Delta E < 0$. The spontaneity criterion $\Delta G < 0$, applicable only at constant temperature and pressure, is used when neither is constant. In a circuit of battery, wire, and light bulb almost every feature is catalogued as a source of irreversible behavior except the fact that the chemical system in the battery is out of equilibrium. These things will not endanger the beginner, because this is not a book from which the beginner would be expected to learn basics of any of its numerous topics. This is a work of philosophy, intended for scientists but surely not pretending to be exact science. It is provocative, not instructive. But the real trouble is that many physical scientists may read to p. 29 and go no further, having at that point lost confidence because of these gross errors, which should not have been published. For such potential readers, the book will have failed of its bridging purpose.

The rest of chapter 2 charts a course from thermodynamics to its metaphorical extensions in information theory, with emphasis on measures of order or the lack of it analogous to the statistical interpretation of thermodynamic entropy. Here and throughout the rest of the book, the authors seem in one respect to be trying to have their cake and eat it. They want to use these metaphorical ideas but still to retain the real driving force of the second law of thermodynamics, which is inapplicable once one goes from rigorously defined entropy in rigorously described systems to the partially analogous information concepts. Likewise, they repeatedly return to the topic of actual energy flow when it is irrelevant in anything except strict literal classical thermodynamics. The course is, however, well enough charted to let readers form their own opinions on this. The problem recurs in every subsequent chapter. To my mind, the question "why entropy?" is never satisfactorily answered. Nevertheless, one can get much out of this book without going along with what the authors probably see as the main thrust of their argument.

This is because it is really a thesis upon four propositions:

1) Natural selection, the shaping of life by environmental interaction, is not the be-all and end-all of evolutionary theory.

2) Evolution involves an intrinsic property of life which is also the main property involved in development: the power of self-organization.

3) The study of self-organization needs approaches from the physical (or physicochemical) sciences and mathematical language.

4) The appropriate physical science to this end is classical thermodynamics.

My position is that I agree with propositions 1, 2, and 3 but not 4. Brooks and Wiley passionately advocate proposition 4 when, it seems to me, their underlying motivation lies in 1, 2, and 3. Hence, when in chapter 3 they write of dynamics of ontogeny, they are despite our differences kind enough to take their account of reaction-diffusion largely from a review article of mine. They go on to Kauffman's computations on regulatory gene networks and in chapter 4 start with some dynamic modeling of their own (Brooks, LeBlond, and Cumming [1984]) on population genetics. To my mind, all this stands very well as dynamics, without the attempt to draw entropic morals from the story. It is clear, however, that Brooks and Wiley do not want this stuff to be chemical kinetics. They want it to be nonequilibrium thermodynamics. I find the language of the latter more cumbersome than that of the former for most of the purposes concerned. Even Prigogine slips into chemical kinetic language for most of his extensive accounts of how the Brusselator model works.

The concept of cohesion of a species (latter part of chapter 4) is, however, something that should be handled as a thermodynamic analogy. The authors miss the opportunity to point out that when a property is related to a variance its thermodynamic analogue is probably temperature. On p. 161, they make heavy weather of the fact that cohesion doesn't depend on system size; yet it is obviously an intensive property. Later, they relate cohesion to real energy flow, when the appropriate metaphorical analogue of energy flow would have something to do with flow of genetic information. This is mishandling of a promising topic; but they have shown the promise.

Chapters 5 and 6 are full of the diagrams that I call hay-rakes and Brooks and Wiley call cladograms. They write of a biological field in which they have solid reputations and extensive publications. I read as an outsider. When one is brought to a new country, or university, or family, it is difficult to grasp quickly the meaning of those internal squabbles that are part of its dynamic, and this field is full of them. To me, "evolutionary taxonomy" and "phylogenetic systematics" sound like rather precise synonyms, but they apparently designate groups who are at each other's throats. The authors here write with authority and command of detail. But about 26 pages of chapter 6 go by without the need for the entropy theme clearly emerging to me.

In claiming (chapter 7, p. 300) to have devised something comparable in significance to Einsteinian relativity, the authors indulge in hubris and bombast. The latter word reminds me, by the false etymology from his middle name, Bombastus, of Paracelsus. Brooks and Wiley have in their joint enterprise fabricated a modern similitude of his extraordinary character. Does the mixed-up medieval, initiator in his day of a fusion of chemistry and biology that was later completed in more orderly fashion by van Helmont, have the fitness to survive in the more highly evolved ecosystem of 20th-century science? Possibly, but he must take heed of his Achilles' heel, that great weakness in basics of classical thermodynamics, and do something about it.

Read this book, then as Paracelsian: muddled philosophy, to be read quickly, requiring disregard of obvious errors but with a genuine fire burning in it for provocation and stimulation.

LIONEL G. HARRISON
*Department of Chemistry,
University of British Columbia,
Vancouver, B.C., V6T 1Y6, Canada*

Muscle Contraction

Energetic Aspects of Muscle Contraction. ROGER C. WOLEDGE, NANCY A. CURTIN, and EARL HOMSHER. Academic Press, Orlando, FL, 1985. xiv, 360 pp., illus. $79.50. Monographs of the Physiological Society, no. 41.

The use of energetics as a framework for developing and testing hypotheses about muscle contraction, which began in earnest with the work of Fenn in the 1920's and continued with the publication of Huxley's crossbridge theory in 1957, diminished in the early '70's as recognition of thermodynamic constraints introduced complexities into energetics studies, causing many outside the immediate field to lose interest. The considerable progress made since then, presented in *Energetic Aspects of Muscle Contraction*, shows that the time has come for renewed attention to what energetics is telling us about muscle contraction.

Most of the book, which treats the energetics of vertebrate skeletal muscle, is contained in three chapters describing relevant studies of the mechanics of intact contractile systems, the biochemical kinetics of isolated contractile proteins, and heat production and chemical change measured in whole muscles. A short introductory chapter describes general properties of muscle, summarizes the crossbridge hypothesis, and presents a list of unanswered questions. The final chapter describes the 1957 theory and its recent variants and discusses them in the context of the experimental results presented in the book.

The organization of sections on biochemical kinetics and energy balance reflects the more rigorous hypothesis-testing characteristic of these relative newcomers among experimental approaches to muscle. The chapter on kinetics explains briefly how models of biochemical mechanisms are tested experimentally and summarizes some important issues concerning the mechanism of adenosine triphosphate hydrolysis by the isolated contractile proteins, all with commendable clarity. It is a palatable introduction to the subject and is especially recommended to those plagued by a high activation energy for learning about kinetics.

A section on energy balance contains the best lessons on energetics. The importance of studies on this subject and the progress made in recent years is readily appreciated by comparing the results of biochemical experiments by Kushmerick and Davies published in 1969 with those of very recent experiments by Homsher and colleagues in which both energy liberation and high-energy phosphate hydrolysis were measured. Kushmerick and Davies showed that although phosphate hydrolysis was adequate to account for the work done by active muscles it could not account for the heat production expected during rapid shortening, raising the possibility that heat is produced by a process unrelated to work production, which would call into question the relevance of Hill's heat measurements and thus compromise much of the predictive success of the 1957 theory. Homsher's experiments show that all the energy liberated by shortening muscles is explained by the quantity of phosphate hydrolyzed. The discrepancy appears because at high velocities phosphate hydrolysis lags behind energy liberation, and energy balance is achieved only after shortening ends. Although no existing model can accommodate this behavior, current crossbridge theories might be made to do so without drastic changes, and in the last chapter it is suggested that a branching physiological crossbridge pathway be explored.

The presence of so many facts and figures in one smallish volume makes it a handy reference. The book is also quite fun to read, for it provides the reader with many pieces of a large puzzle. One's sense of rediscovery in reading it is complemented by the style of presentation in sections on mechanics and on energy liberation. Sufficient information is included to make the uninitiated comfortable with concepts and methods, but the intellectual context of the experiments is not so well developed that it discourages the reader from rearranging the facts into novel hypotheses. An additional advantage is that many sections can be read individually.

The book contains minor flaws. The figure legends are too brief, and some information, such as the magnifications of several micrographs in chapter 1, is omitted altogether. On p. 16 we read "what is the nature of the binding between actin and myosin, covalent, electrostatic, . . . ?" and on p. 147 "actin binds, noncovalently but very tightly, to myosin." Some calculations are more obscure than they need be; for example, the work done by a crossbridge (p. 24) and the lifetime of an isometric crossbridge (p. 117) could have been clarified by more specific references to appropriate sections of later chapters. But the flaws are not serious, and chasing the numbers is rewarded by enhancement of insight into how facts, theories, and guesses can be blended most productively to stimulate better questions and experiments.

SUSAN H. GILBERT
*Department of Anatomical Sciences,
State University of New York,
Stony Brook, NY 11794*

Neuroanatomy

The Thalamus. EDWARD G. JONES. Plenum, New York, 1985. xx, 935 pp., illus. $135.

Seduction by passionate interest in the thalamus must have its hazards. Jones relates with charm an anecdote about Sir Wilfrid Le Gros Clark, one of his mentors, facing his fellow Oxford dons proclaiming expertise on the thalamus—a word endowed with a nuptial or bedchamber connotation in classical Greek. For all that, Jones has succumbed to a scholarly and research interest that has resulted in the production of a truly monumental contribution. There are few books of such enormous scope in modern times—perhaps Grant's *Anatomy* and Boyd's *Pathology* may serve as exemplars—and in neuroanatomy nothing of such magnitude since the extraordinary contribution of Ramón y Cajal.

One of the extraordinary and valuable features of the book is that it contains a large number of high-quality photomicrographs, a large proportion of the best of them derived from the author's own preparations. There are several series of sections in different species, mostly transverse and Nissl-stained and all of high technical quality. They are not quite sufficient to serve as atlases, but they do provide a good guide for comparative anatomy. There are a few con-