Book Reviews

Four Billion Years: An Essay on the Evolution of Genes and Organisms. By William F. Loomis. Sunderland, Mass.: Sinauer Associates, 1988. Pp. x + 286. \$22.95 (paper); \$39.95 (cloth).

From Empedocles of Acragas to the modern era, the origin of life has remained one of the most fascinating and, at the same time, one of the most frustrating areas of scientific inquiry. The field has been plagued by farfetched speculations, which, in the absence of hard data and consistent methodology, have left no lasting mark on the mainstream study of evolution. Too often, treatments of the subject start with a rehash of old thermodynamic and probabilistic arguments against the origin of life from natural processes and develop into highly esoteric mathematical or cosmological treatises. In some instances, extraterrestrials, cometary dust, and God pop up toward the end (e.g., in the work of Hoyle and Wickramasinghe). Consequently, most respectable textbooks of evolution deal with the origin of life as with a compulsory ritual that must be disposed of quickly, usually in the form of a series of open questions that the serious student is well advised never to address. Chronologically, at least, this avoidance constitutes an anomaly, since the term "origin of life" covers about two-thirds of the biological history of planet Earth, while "evolution" as traditionally taught deals with a mere 600 Myr.

William Loomis has set out to write an essay on evolution that "is weighted to the time of events rather than to the amount of available data," such that "only 10% of it is concerned with what went on in the last 100 million years." Surprisingly, he succeeds in this nearly impossible task. His "essay" is honest in that it delivers what it promises, and it does so by using rigorous scientific methodology, careful writing, and a wealth of data. Four Billion Years is essentially a narrative of a historical process, a scenario of how evolution might have happened. There is no escape from speculation, but the author goes to great pains to provide factual support for each claim, theory, or possibility.

The first part describes a plausible sequence of events leading from inorganic chemistry to "stable hereditary systems." Each step is substantiated by much geological, chemical, and biophysical evidence. There are, unavoidably, gaps. For instance, the scenario does not come near to producing the "fifty vital sequences," which, according to the author, is the minimum number needed "for bare survival." But in the absence of facts, the author lets these gaps stand, without submitting to the temptation of smearing purple prose over ignorance. Interestingly, this part also contains some rudimentary elements of what might become the Drake formulas of prebiotic evolution. Just as Frank Drake calculated the chances that extraterrestrial life exists as a product of a series of independent probabilities, so Loomis presents quantitative data from which he calculates equilibrium concentrations of the various compounds needed to generate the molecules in each step of his scenario. To the best of my knowledge, this is the first time such quantities have been compiled in a systematic fashion. We learn, for instance, how many moles of hydrogen cyanide were generated each year under prebiotic conditions, how many alanines, glycines, and purine residues were likely to have been formed as a consequence, and so on. Whenever a proposed pathway proves

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improbable, the author comes with an alternative that better withstands the probability test.

Part 2 describes the evolution of cells out of self-replicating droplets. Topics such as translation and metabolic pathways are discussed, and one finds an enlightening discussion on the evolution of primitive photosynthetic systems. By incorporating recent findings from molecular biology, such as exon shuffling, self-splicing introns, and feedback mechanisms of DNA repair, part 3 continues the saga up to the appearance of photosynthetic bacteria. The author shows both how each component within living systems could have started as a very inefficient process and how improvements on the prototype could have accumulated. One interesting observation is that, while living systems are constantly being improved on, the efficiency of biological processes remains generally low. Throughout the book, there are repeated attempts to infer the primary structures of ancient metabolic enzymes from those of extant ones. It is a matter of opinion whether these attempts lead us any closer to the truth, given the scarcity of data and the methodological hurdles. Sadly, no constructive alternative exists at the present time.

Part 4 deals with the emergence of eukaryotes and related problems in developmental biology, genetics, and ecology. This is without doubt the best and most original part. Drawing heavily on molecular biology, Loomis discusses such diverse topics as the evolution of sex, the packaging of chromatin, and multicellularity. It is interesting to note the casual ease with which Loomis accepts the fact that most DNA in eukaryotes is useless. Since there is room in the nucleus for vast excesses of DNA, and since the process of accumulating genomic junk affects neither the economy of the cell nor the kinetics of cell division, there is "nothing keeping a eukaryotic organism from accumulating a lot of useless DNA." I wish that more students of evolution would accept with such grace the fact that many biological phenomena are simple outcomes of known mechanisms, instead of feeling compelled to account for every phenomenon by means of adaptionist models.

Part 5, dealing with "classical" evolution, is predictably disappointing. The author's self-imposed limitations mean that most of what we *know* must be condensed to demeaning dimensions. Trying to cover speciation, the evolution of genes and gene families, selection, drift and adaptation, gene regulation, development and morphogenes, somatic mutations, and genomic rearrangements, not to mention demography, ecology, and species diversity, all in 44 pages including tables, figures, and DNA sequences can only result in the raising of an eyebrow or two. One notes, however, that the examples illustrating each of these topics are well chosen and, with rare exceptions, up to date. The book ends with an inventory of "distant planets" that, on the basis of "the constraints on biological and cellular processes," might sustain life.

I wish the author had chosen a more modern bibliographical system instead of the insufferable hazing inflicted on the reader by the archaic use of footnotes, which no publisher can afford to print at the foot of the page and which are thus relegated to unlisted places dispersed seemingly at random throughout the text. Such practices can only result, as in the present case, in a fragmented and repetitive bibliography that is virtually impossible to use.

Students of evolution should read *Four Billion Years* not for its long-lasting truths or all-encompassing theories but because it shows that the study of prebiotic and early biological evolution need not be a competition among just-so stories but a down-to-earth enterprise rooted in fact, consistent in logic, and refutable by observation.

Molecules and Morphology in Evolution: Conflict or Compromise? Colin Patterson, ed. Cambridge: Cambridge University Press, 1987. Pp. 229. \$49.50 (cloth); \$15.95 (paper).

To a casual observer, molecular biology and paleontology could be the ends of the spectrum of biology. Evolution is a unifying theme in biology, and many important advances in science occur when new techniques, data, and/or ideas break down old barriers and lead to a more powerful science. In the present case the book marks an end of an era of an apparent conflict between molecules and morphology in reconstructing evolutionary trees.

The book is the result of a symposium at the last International Conference on Systematic and Evolutionary Biology (ICSEB) which was held at the University of Sussex. The symposium was originally titled "Molecules versus Morphology," and it was clear that some conference participants expected fireworks. However, once the symposium started, it became apparent that there was more agreement than disagreement, and several authors suggested that a new title would be required for the book.

It is unfortunate that the chosen title is misleading, as it implies a broad coverage of evolutionary theory. The book is about phylogeny rather than about evolution in general. There is little on variations in rate (molecular or punctuated equilibria) or on the mechanism of evolution, or on methods of testing reliability of trees. Within this more limited scope, the book succeeds in giving a picture of a rapidly evolving field.

Colin Patterson introduces the book with an overview of problems and methodology. This succeeds in the difficult task in being a good introduction for nonspecialists as well as providing useful insight for specialists. The first contributed chapter, by Andrews, is on the human-ape relationships. Andrews contends that molecules and morphology both lead to the conclusion that humans, chimps, and gorillas form a natural group with orangutans as their nearest outgroup, but the ((human, chimp), gorilla) and ((chimp, gorilla), human) alternatives are not yet in agreement. Andrews has recently extended the comparison of morphology and molecular evidence to early divergences with the human species (*Science* 239:194, 1988).

McKenna treats the major groupings of mammals on the basis of a consideration of fossils, morphology, and protein sequences. He finds many areas of reasonable agreement—e.g., the early divergence of the edentates and the naturalness, and possible early divergence, of the paenungulates (elephant, hyrax, and manatees). I particularly liked his comment that "one should follow a computer only up to the edge of an intellectual cliff." This work (as well as that of Novacek) is a useful source that allows molecular biologists to compare their trees with those derived from morphological features of the mammals.

The approaches of Bishop and Friday, together with that of Goodman's group, form an interesting contrast to the study of earlier divergences within the vertebrates. Goodman uses the simpler parsimony method, which employs less of the information in the data but can handle a larger number of taxa. Bishop and Friday use a maximum likelihood method that is better statistically but only handles six taxa. The different results for the relationship of mammals and birds to the rest of the reptilian groups is worth reading to see the uncertainty that exists in the trees produced. How is it that so often authors' confidence in their trees is inversely proportional to their understanding of potential errors in their methods?

The book is strongest in zoology. The only paper not on animals, by Woese, is on his work on bacterial evolution (where there is little morphological data). It is

unfortunate that the one area where there are still major disagreements between molecules and morphology—namely, the realm of higher plants—is not covered.

Overall, the book marks the end of the idea that molecules and morphology are in any major conflict over animal phylogeny. Results from the two approaches are not always identical but are sufficiently similar to give confidence that more data and/or better analysis will give a single result. This is the strength of the book.

The main problems with the book are the lack of quantitative comparisons of results and the error estimates on the trees. It is now essential to get on with the more difficult stage of understanding the reliability of the results. There must, of course, be more data collection, and the taxa should be more carefully selected to maximize the value of the data. But for more data to help there must be an understanding of the strengths and weaknesses of methods, as well as of ways of evaluating the reliability of particular results. Are the assumptions of a particular method realistic for a given data set? How confident can we be of the resulting tree? Would doubling the length of sequences settle the problem? These questions are part of the next phase of study.

What, then, is the market for the book? It will be an important book for those with a general zoological background who need to stay up to date with new developments. The book shows that it is no longer reasonable for molecules to be neglected in any general zoology course. It will be useful for molecular evolutionists as a source for comparing molecular and morphological studies. The book can also be recommended to those with a general interest in evolution.

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