BOOK REVIEW

An inordinate fondness for bacteria

Origin and Early Evolution of Life

T Fenchel

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Reviewed by DC Krakauer

In the autobiography of Henry Adams, Adams wrote of himself that 'He still felt he might get the best part of Darwinism from the easier study of geology; a science well suited to idle minds as well though it were history'. And as in history, where ambiguity licenses more than a century of interpretations for the Napoleonic campaigns and an equal number of theories for the decline of Rome, the Origin of Life has spawned its own industry of explication from spontaneous generation, Panspermia through to the prebiotic soup. As natural scientists we find this disconcerting, after all the philosophers have told us that our vocation is distinct from the humanities and the 'Sciences of society', in that we have the demarcation criterion of refutability, the empirical advantage of the laboratory and conceptual precision from mathematics. Geology, the first of the sciences to deal with the 'history of nature rather than its order' (Gillespie, 1951), upset this boundary, and called for a histiography of the earth, rather than a mechanistic model of a directly observable process.

In considering studies of the origin of life, we need to be aware that the temporal distance to the event in question creates a degree of uncertainty unfamiliar to many of today's mechanistically oriented sciences. However, great breakthroughs in our ability to recreate conditions resembling those of the early earth, better techniques for extracting information from the planet and advances in our models and theories have transformed the study of the origin of life into a serious scientific endeavor and one that is truly interdisciplinary – as the questions it poses sit on the boundaries of physics, chemistry, biology and geology. It is in part the rigorously interdisciplinary nature of the topic, that makes for its difficulty, as few are qualified to comment comprehensively on its progress.

For this reason, the publication of a short book (around 150pp) that aims to place the many facts in order, spans chemistry, biology and geology, and nowhere tries to present a new theory, comes as a welcome addition to an ever-expanding literature. Tom Fenchel, a microbial ecologist at the University of Copenhagen, and author or editor of five previous books on bacterial and mineral cycling, evolution in anoxic worlds and bacterial biogeochemistry, has written the 'Origin & early evolution of life' as a short review of our current understanding of the field. In the introduction, by way of a disclaimer, he writes, 'I run the risk of disclosing a lack of authoritative grip on some topics' aware as he is of the magnitude of the task.

The book is arranged in 15 chapters, the first five of which review ideas about life and its origins, followed by chapters on the RNA world, the evolution of metabolism, the eucaryotic cell and multicellularity. Then in no apparent order are further chapters on sex and speciation, our anaerobic inheritance, the molecular tree of life, geology and evolutionary transitions. Many of these are based on examples from bacteria. Chapters vary in length from under 5pp long to 25pp long. Chapters also vary in quality with some, particularly those on metabolism and geology informative, whereas those on multicellularity and speciation are weaker.

Before discussing the scientific content of the book, I need to register some editorial objections. The book has no references, and few of the studies described in the text name authors or provide citations. This means that statements made by the author cannot be checked for accuracy (very difficult for a reviewer) and neither can the book be used as the basis for a more detailed exploration of ideas in the primary literature. As compensation, the book offers a Further reading list, which we are told, is sufficient for readers to find 'the original literature on which this book is based'. Of the total 27 references provided, over 20 of them are books. I do not see how a publisher of a monograph aimed at undergraduates could fail to provide a bibliography, often a very useful function of a short text. A particularly serious omission in this case, as no single chapter has sufficient depth or detail to act as the basis of an essay or report. Fenchel himself commends one of the books in the 'Further reading' section on the grounds that 'the reference list is comprehensive and up to date'. I have come to suspect that the publisher is at fault, as the book is riddled with typographic errors and solecisms. On just one page (p. 158) of the 'Further reading' section, we find 'The tropic is also treated' and 'is a recommend account'. In each chapter I have found similar errors, from 'antikodon' to 'inverse transcription'. I am happy to observe that these are all easily corrected faults, and I would hope for a full reference list and a more thorough editing at the next printing.

Chapters one through to six offer summary accounts of the geological time frame, a historical review of theories on the origins of life, a discussion of thermodynamics and replication and a short section on the origins of the genetic code. There is much recent work in these areas that had it been included or cited, would have enriched these chapters, and avoided a few mistakes.

In chapter four, Fenchel points out that that one of the truly amazing things about life is that it spans up to 20 orders of magnitude of size variation, from bacteria measuring 0.5 µm to large whales on the order of tens of meters. He subsequently discusses limits to individual cell size based on diffusion and thermodynamic considerations of significance to living systems. Over the last 5 years, a number of theories based on a combination of selection and thermodynamics, have given us the clearest picture yet of why animal sizes scale according to peculiar allometric laws (see Brown and West, 2000).

It is a remarkable fact of biology that the scaling relationships for mass, M , are power laws, $y \propto M^b$, with exponents, b , which closely approximate simple

multiples of $1/4$ (eg $1/4$, $3/4$, $3/8$). For mass dependence, West and Brown have postulated three generic principles, which can be viewed as a derivative from natural selection: (i) networks must be space-filling in order to service all local biologically active regions in an organism; (ii) their terminal units, which interface with the resource environment (eg capillaries, petioles, mitochondria, cytochrome oxidase molecules, etc), are invariant in size; and (iii) organisms have evolved so that the energy required to distribute resources and sustain them is minimized. Building upon these assumptions, it can be shown how 15 orders of magnitude of variation in b across highly diverse phylogenetic groups can be reduced to a factor of 20 in M .

One of the more significant consequences of this work for evolutionary biology is that it shows to what extent thermodynamic considerations have a direct impact on macroscopic observables, and the degree to which size variation reflects energetic considerations, rather than other selective pressures. All of life obeys the $1/4$ power laws, and any new form hitherto not observed is expected to appear somewhere on these curves. The evolution of life was only free to evolve within the limits circumscribed by efficient energy transport.

When discussing the origin of the code (p 56), Fenchel states that the code is arbitrary and that there is 'no relationship between the code and the chemical structure of the amino acids'. In recent years, great progress has been made in our understanding of the origins of the code, with three compatible explanations all receiving some empirical support. These explanations have been termed 'adaptive', 'chemical' and 'historical' (Knight *et al*, 1999). Fenshel shows some familiarity with adaptive theories when he points out that codon assignments are such that replication errors are minimized. This is a partial explanation as equally important are errors in translation. A more significant omission is those cases where dissimilar amino acids synthesized from related biosynthetic pathways share similar codons. A particularly striking example is that first position bases of a codon connecting amino acids from the same biosynthetic pathway (Taylor and Coates, 1989). Support for the role of chemistry is gleaned from the fact that the amino-acid 'polar requirement' can be predicted by the second position bases. Those interested in further examples are directed to Knight *et al* (1999).

An erroneous statement made in chapter six is that 'viruses have only a couple of genes' (p54). Viruses show three orders of magnitude variation in gene content (1–100s) and range from the smallest virus, *Arabis mosaic virus satellite*, with 300 base pairs to one of the largest, *Lectocarpus siliculosus*, with 335 593 base pairs. The latter is almost as large as a small bacterium, *Mycoplasma genitalium* (580 073 base pairs). Furthermore, Fenshel uses Eigen's term 'Quasispecies' to refer to individual strains throughout the book. Quasispecies refer to the cloud of interconverting mutants surrounding a master sequence, and thus is a description of a population of strains in mutation-selection balance, not a single sequence (see Krakauer and Nowak, 2002 for an introduction to the concept). It is also rather surprising that Eigen's error threshold theory is never named or adequately explained, apart from a rather short arithmetic example for mutation load (p48), whereas Eigen and Shuster's Hypercycle theory

(described as Eigen's theory) warrants a page of explanation.

Many of these topics are covered in greater detail in Maynard Smith's and Szathmary (1995) book 'The Major Transitions in Evolution' (1995), which appears in the same series published by Oxford University Press. Given the short and sometimes confused treatment that this book gives to these topics, I would rather recommend that book.

Chapter seven is on the evolution of metabolism, and one has the sense that this is a topic with which the author is very familiar. Having said that, the chapter is almost exclusively concerned with bacteria. The chapter does a nice job of explaining the basics of electron transport through coupled redox reactions. Fenshel stresses the highly conserved nature of proteins associated with electron transport, spending some time explaining the structure of porphyrin. In this chapter, the fundamental types of energy metabolism are also reviewed, including phototrophy, photosynthesis and chemotrophy. The early evolution of metabolism is explored through a simple model assuming only a membrane (across which an electrochemical gradient can form), iron sulfide as an electron acceptor, a quinone and a porphyrin molecular capable of photoactivation. The reductive citric acid cycle is briefly discussed, but a more complete treatment is given by Morowitz (1992).

Chapter eight is on the eucaryotic cell and is little more than a description of the differences between eucaryotes and procaryotes, with a short review of evidence bearing on the symbiotic origin of cellular organelles (mitochondria and chloroplasts). Chapter nine is 5pp long and is on multicellularity. It introduces colonial species, cell differentiation and senescence. Given the enormous importance of multicellularity in the evolution of life, and the many evolutionary problems that it raises (not least the origin of the germ line, and the evolution of development), this chapter is disappointing. I appreciate that the author was aiming for a short volume to cover some fundamental problems. However, this chapter falls short of this modest objective, as it does not even explain why multicellularity represents a problem for natural selection, and why life had to wait for over a billion years for multicellularity to arise from unicellular lineages.

There is then a chapter on sex and species concepts. Why this appears in a book on the origin of life is not made clear. Most of it is rather basic and covered in greater depth in standard textbooks of evolution, such as Futuyma and Ridley. Over half of the chapter is dedicated to the old question as to what constitutes a species for an asexual lineage. Fenchel points out that molecular evidence does not help too much as it is in essence a modern form of phenetics, albeit with the advantage of avoiding paraphyly. I have always found these discussions somewhat confusing. The essence of the biological species concept (defined in terms of sexual reproduction) is that either through drift or reinforcement, barriers to genetic compatibility evolve. These barriers are often advantageous to genotypes, as they minimize the production of dysgenic hybrids. Species then represent clusters of reciprocally incompatible genomes, in much the same way that languages say, are defined as mutually incomprehensible sign systems. There is no reason why this concept should not apply to asexuals. The probable reasons that we do not see clear

asexual species are twofold: (a) because the number of genes exchanged is relatively small in comparison with sexual reproduction, and (b) the unicellular environments are sufficiently variable to make sustained reinforcement on incompatibility weak. While there are doubtless other interesting explanations, there really is no great mystery here.

There are further chapters on the reconstruction of the tree of all living species, considering mainly the relationships between bacterial groups and a short chapter on the ubiquity of oxygen as the terminal electron acceptor in respiration, stressing our common anaerobic inheritance.

The second best chapter is a late chapter on geology. I am surprised how often treatments of the origin of life ignore geology and geochemistry altogether. Here tectonics is discussed, as are the geological contributions to nutrient cycles essential to life. Precambrian glaciations are discussed in relation to the snowball earth hypothesis. The snowball earth hypothesis was put forward by Paul Hoffman and (my sometime Santa Fe Institute Colleague) Daniel Schrag, as an explanation for the fact that the earth appears to have been ice covered for long stretches of time 600–700 million years ago and that this ended under extreme greenhouse conditions. The theory picks up on a two-dimensional energy balance model by the Russian geophysicist, Mykhail Budyko. Hoffman and Schrag describe the following chain of events. The Earth's climate is controlled by the way that solar radiation interacts with the Earth's surface and atmosphere. The earth receives around 343 W/m² of radiation from the Sun. Some of this is reflected back to space by clouds and by the Earth's surface, but approximately two-thirds is absorbed by the Earth's surface and atmosphere, increasing the average temperature. The Earth's surface emits radiation at longer wavelengths (infrared), balancing the energy of the radiation that has been absorbed. If more of the solar radiation were reflected back to space, then less radiation would be absorbed at the surface and the Earth's temperature would decrease. Budyko showed using his mathematical model that if the Earth's climate were to cool, and ice were to form at lower and lower latitudes, the planetary reflection would rise at a faster and faster

rate because there is more surface area per degree of latitude as one approaches the Equator. In his model, once ice formed beyond a critical latitude (around 30° North or South, equivalent to half the Earth's surface area), the positive feedback became so strong that temperatures of the surface plummeted, yielding a completely frozen planet. The earth thaws as a result of tectonic activity, whereby volcanic out-gassing replenishes atmospheric CO₂, creating a greenhouse effect, melting the ice and reversing the process. It is shortly after this freeze and thaw that multicellular life appeared on the surface of the earth.

Reading back over my review, I feel that I have been rather negative about this book. I recognize the amount of time and energy that goes into writing and how destructive a review can be. However, as a reviewer my primary responsibility is to the students and researchers who need to make judicious decisions about how to spend their time and their money. I believe that a short book on the origin of life is needed. I feel that this is an author, who given the time, effort and editing, could have written such a book. This is not that book.

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