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On the Origin and Evolution of Life: An Introduction

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Fundamental to a deeper understanding of complex biological functions are ideas about how life originated and evolved. They include questions about how the first compounds, essential to life, appeared on Earth; how the first replicating molecules came into being; how RNA and DNA were formed; how prokaryotes and the earliest eukaryotes emerged; how different species, with traits like susceptibility, sentience, perception, cognition, and self-consciousness, and with various patterns of behaviour, evolved; and how, with these developments, the environment and the ecological systems changed. These questions differ in some sense from other problems of natural science. The study of the origin and evolution of different forms of life is both a matter of trying to reconstruct the past, and of studying present structures and processes. Conclusions about how things might have happened are drawn from evidence such as that obtained from fossils, theories based upon knowledge about present biological processes, models based on knowledge about chemical reactions and assumptions about various conditions on the early Earth. The analysis involves a great number of widely differing disciplines, such as chemistry, geology, biology, physics, computer science and philosophy (e.g. Darwin, 1859; Wallace, 1891; Oparin, 1924; Haldane, 1929; Schrödinger, 1944; Urey, 1952; Goudge, 1961; Woese, 1967; Miller & Orgel, 1974; Varela *et al*., 1974; Gánti, 1979; Crick, 1982, 1994; Mayr, 1982; Cairns-Smith, 1986; Delbrück, 1986; Orgel 1987; Eccles, 1989; Edelman, 1991; Rosen, 1991; Shopf & Klein, 1992; Eschenmoser, 1993; Kasting, 1993; de Duve, 1995; Kauffmann, 1995; Maynard Smith & Szathmáry, 1995; Murphy & O'Neill, 1995).

The articles of this special issue focus mainly on certain selected stages in the origin and evolution of life. The papers are organised in four groups: the first discussing the general aspects of the origin and evolution of life; the second the development leading from minerals and early molecules to the evolution of metabolism; the third the origin of organisational aspects of life; and the fourth the evolution of cognition and consciousness. A majority of the papers were developed from a series of lectures on theoretical biology and molecular evolution held since 1991 at the Karolinska Institute, the Royal Institute of Technology, and Stockholm University.

General Aspects of the Origin and Evolution of Life

In the first three articles, Richard D. Keynes, Michael Ruse, and Günther Wächtershäuser discuss historical, philosophical, and methodological aspects of the study of the origin and evolution of life.

Although the speculations about how life on Earth began have a long history—possibly as long as the history of mankind—the currently widely accepted hypothesis that life originated from chemical processes is comparatively recent. The hypothesis can be said to largely derive from the Russian biochemist Alexander I. Oparin (1924, translated to English, 1938). Another prominent figure in the early

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development of the modern theories of the origin of life was the Scottish physiologist, biochemist and geneticist J. B. S. Haldane (1929). The history and philosophical basis of Oparin's and Haldane's works are discussed by Ruse. He also discusses why Charles Darwin in his published works downplayed the issue of the origin of life. Ruse concludes that history suggests that the studies of the origin of life have to a large extent been philosophical and metaphysical, and perhaps more so in this area than in many other fields of science.

Keynes focuses on the early stages of Darwin's development of his fundamentally new way of thinking about life on Earth; especially, how he arrived at the theory of common descent and that of natural selection. Keynes bases his discussion partly on Darwin's unpublished notes from his voyage as geologist on H.M.S. Beagle. Keynes calls attention to the possible influence of Erasmus Darwin, grandfather of Charles, regarding the theory of common descent. Keynes also discusses the possibility that Charles Darwin's reading, in 1838, of Malthus' *An Essay on the Principle of Population* (1798) simply "triggered the surfacing of an idea [of natural selection] already dormant in Darwin's mind, though not hitherto consciously expressed; and afterwards it seemed very obvious". Keynes concludes by pointing out that Darwin, contrary to what he claims in his *Autobiography* (published in Barlow, 1958), did not work in what was considered a Baconian fashion, trying to collect data without any theory, but that "there are ingenious speculations on every page of his notebooks", and that he in fact believed that without speculation there is no good and original observation.

Wächtershäuser discusses from a methodological point of view the historical development of the study of the origin and evolution and life. He calls attention to Immanuel Kant's argument that the natural sciences should replace teleological judgements by mechanistic explanations, and he points out that Charles Darwin and Alfred Russell Wallace only partly succeed in achieving this goal in their accounts of the mechanisms of evolution. Wächtershäuser also emphasises the significance of Karl Popper's introduction of the problem-solution relation into evolution theory. Wächtershäuser traces the history of a mechanistic theory of the origin of life back to the works of the German botanist Matthias Jacob Schleiden, and discusses the development up to the most recent theories. The analysis leads into a discussion of how Popper's situational logic of problem-solution relations may serve as a heuristic guide to generate a mechanistic theory of the origin of life, and how such a theory may be evaluated and tested. Based on central tenets of his theory of the chemo-autotrophic origin of life—such as his proposals of a two-dimensional surface metabolism and the origin of membrane lipids, of a chemiosmosis on pyrite surfaces and of the origin of the genetic machinery, among other examples given—Wächtershäuser discusses the early evolution of life as a process that begins with chemical necessity and winds up in genetic chance. Some of these proposals have recently been intensely debated (see, e.g. de Duve & Miller, 1991; Wächtershäuser, 1994; and also Popper, 1990; Hill *et al*., 1994).

From Minerals and Early Molecules to the Molecular Evolution of Metabolism

The papers by Herrick Baltscheffsky, Gustaf Arrhenius *et al*., Alan W. Schwartz, Thorsten Friedrich and Hanns Weiss mainly discuss molecular aspects of the processes leading up to the early and current metabolic systems.

The detailed hypothesis of Wächtershäuser (1992) concerning chemiosmosis on pyrite surfaces involves his "iron-sulphur world", which is one of three currently discussed alternatives for prebiological energy conversion at the prenucleotide level. The two others are the "thioester world" (de Duve, 1991) and the "inorganic pyrophosphate world" or "PPi world" (Baltscheffsky, 1993). Plausible molecular links between these three worlds have been suggested (Baltscheffsky, 1996). The view that the PPi world may directly have preceded the "ATP world" is based on biological, chemical and geological facts. They include the observation that inorganic pyrophosphate (PPi) operates as an alternative carrier and donor of biologically useful chemical energy, with a "business" or "working" structure essentially identical with that of the more complex adenosine triphosphate (ATP) molecule.

The old Greek word *anastrophe*, which may be interpreted as "to turn back" or "to turn in the opposite direction" (from anastrephein, *αναστρεφειν*, where ana = back and strephein = to turn) has been introduced by Baltscheffsky as a logical and practical term for describing sudden and/or drastic changes in the constructive direction of biological evolution. Compare: anabolism for metabolic build up and catabolism for metabolic breakdown, and catastrophe for sudden and/or drastic destruction. With the anastrophe concept Baltscheffsky discusses the origin and early evolution of biological energy conversion, covering the time period from before the origin of life to the emergence in photosynthetic prokaryotes of light induced splitting of water and production of molecular oxygen, i. e. from perhaps 4 to perhaps 3.5 or 3 Ga ago. The start of the cellular use of the hydrogen from water as a biological reductant was an evolutionary event of major anastrophic significance. Recently, Prigogine (1996) has presented a detailed background for his view supporting constructivity as the normal or main direction of the cosmic evolutionary process, and destructivity as what goes in "the opposite direction".

The remarkably central role of phosphate compounds—both inorganic and organic—in all living cells, is brought into an early geophysical and geochemical perspective in the paper by Arrhenius *et al*., with particular emphasis on the significance of the trivalent, anionic property of inorganic orthophosphate. This charge is well known to play a crucial role in the characteristics of phosphate compounds such as oligophosphate ions and charged phosphate esters in their reactions with, for example, cationic crystal surfaces and in living organisms. On the basis of model experiments, Arrhenius *et al*. examine in detail the question of how concentration of dilute phosphate in nature could have occurred at the time of the earliest processes of biopoiesis.

Arrhenius *et al*. discuss charge and entropy in evolution on the basis of the properties of phosphates and their reactions. Both selective concentration and activation leading to oligomerisation on crystal surfaces are treated incisively. Upon heating of phosphate minerals, such as brushite, newberyite and whitlockite, P-O-P bonds are formed, with PPi dominating among the resulting oligomers. These results, as well as those of Yamagata *et al*. (1991), seem to strongly indicate that there was continuous production, over extended periods of time, of energy-rich phosphate compounds in numerous locations on the primitive, abiotic Earth.

The possibility that RNA might have been preceded in evolution by a related molecule, perhaps more amenable to prebiotic synthesis than RNA, is discussed by Schwartz. He points out that there does not exist any convincing demonstration of prebiotic synthesis of RNA building blocks and that at least two synthetic analogues of nucleic acids have been described with properties remarkably similar to those of RNA. These are the "peptide nucleic acid" (PNA) and the "pyranosyl-RNA" (p-RNA), which have extremely favourable "nucleic acid-like" properties and which form even more stable complementary structures than do DNA and RNA. Both systems are of interest in the context of the origins of life, although questions about potentially prebiotic synthesis still remain. Plausible prebiotic synthesis of phosphonic acids was investigated in the laboratory of Schwartz as a consequence of the earlier described presence of methyl and ethyl phosphonic acids in water extracts of the Murchison meteorite and of the possibility that phosphonic acids were very early prebiotic compounds. Based on his recent results and on theoretical considerations he proposes further investigation of the possibility that phosphonic acid derivatives, rather than derivatives of phosphate, may have been among the precursors of RNA. The "RNA world" concept (Gilbert, 1986) may be considered in this context. This notion has been increasingly well established since the discovery of the ribozymic capability of this molecule, and has recently become actualized by the findings that DNA can act as an enzyme (Breaker & Joyce, 1994) and that peptides can self-replicate (Lee *et al*., 1996).

The proton-pumping NADH:ubiquinone oxidoreductase (Complex I) is one of the major redox complexes providing in biomembranes the proton motive force required for the synthesis of ATP. This multi-subunit enzyme, which is found in purple bacteria and in mitochondria, contains different functional modules. Homologues of its polypeptides and modules are found in cyanobacteria and chloroplasts as well as in various bacterial electron transfer and ion transport proteins. The modular evolution of the complex and the possible origin of its modules are discussed in the paper of Friedrich & Weiss.

The authors examine the relationships between the mitochondrial complex I (42 subunits in bovine, 27 in *Neurospora crassa* complex I), the 14 subunit purple bacterial complex, the homologous, 11 subunit cyanobacterial and chloroplast complex (which lacks the three genes encoding the NADH dehydrogenase part of the complex present in the respiratory electron transfer chain) and other bacterial electron transfer enzymes such as, for example, a formate hydrogen lyase and sugar permeases. From sequence homologies in different, related complexes, the authors date back the origin of complex I to five different proteins. This common ancestor of complex I and of formate hydrogen lyase then acquired new subunits to form the common ancestor of complex I of photosynthetic and respiratory electron transfer chains, which later diverged to give, after additional acquisitions, their respective complexes I. With this contribution Friedrich & Weiss illuminate current possibilities to trace evolutionary pathways of even the most complicated multi-subunit complexes of living cells.

Origin of Organisation

In the next group of papers, Clas Blomberg, Eörs Szathmáry, John Maynard Smith, Massimo Di Giulio, and Tibor Gánti discuss the steps from the first replicating units, possibly in an RNA world, to the first cell, including the appearance of the genetic translational apparatus. During that development, the intricate machinery of today's cells was to be organised. At the present state of science, it should be clear what processes had to appear at these stages, but it is not as clear in which order things occurred and how some steps really developed.

There is still the old discussion, whether the first stages towards life were of a metabolic or a genetic kind. Proponents of the metabolic start emphasise that the first stages of the origin of life were of a metabolic character and that the genetic system was introduced at a late stage, produced by the metabolic system. Recent support of that idea has been given by Kauffmann (1995). Yet, most of the recent work has put the emphasis on the genetic system, for the obvious reason that it is the only known system that can evolve. Even though, in that view, some metabolism was necessary, the appearance of replicating macromolecules is the true start of the path to life. Sometimes, one sees claims of a direct development from a first "naked gene" into the complete organisms governed by the general laws of evolution. A genetic view has been proposed, for example, by Eigen, Schuster and their co-workers (Eigen, 1971; Eigen & Schuster, 1979).

The concept of an RNA world is very relevant for the "genetic start". This means a stage with self-replicating, catalytic molecules. This must have been an important achievement in the path to life; a major transition or an anastrophe, to use some of the metaphors in this special issue. Still, the prerequisites are obscure, and the steps from such a stage to the first stage of life are far from clear. See, for instance, the article by Schwartz about the early synthesis of template molecules.

Such difficulties have provoked alternative views. Wächtershäuser argues for the relevance of a first, two-dimensional *metabolic start* with autocatalysis, and with some lifelike features, such as membrane-building. From this, the template system would arise by a kind of natural development. In that picture, there is a true metabolic, autotrophic start. The article by Arrhenius *et al*. presents the prerequisites for such a scenario.

The view of the papers by Blomberg and by Szathmáry and Maynard Smith is that such a metabolic system only had a limited capacity of replication (heredity). For the evolutionary path to life, the virtually unlimited possibilities of a template system were necessary. Both these papers discuss difficulties with a catalysing, self-replicating system, in particular due to selfish mutations (parasites). Szathmáry & Maynard Smith discuss some explicit models that can cope with such problems. Blomberg deals with these problems primarily by spatial models.

A big question, which has for a long time been an obstacle for the theoretical framework, is to understand the origin of the translation apparatus and the genetic code (Crick, 1968; Crick *et al*. 1976; Woese, 1967). What in particular has been puzzling about the genetic code is that, while there are some clear relations between triplet codons and amino acids and also some logic that appears important for reducing the effect of errors, there are also features that look arbitrary. Various ideas to understand these features are discussed by Di Giulio. He argues against stereochemical ideas which imply steric fits between nucleotide sequences and amino acids (or small peptides), and is rather in favour of the coevolution theory, first suggested by Wong (1975). According to that theory, the genetic code has evolved simultaneously with the biosynthetic pathways of the amino acids. This is illustrated by relations between the code structure and the pathways.

Blomberg, Szathmáry and Maynard Smith discuss some alternative scenarios. Szathmáry & Maynard Smith suggest that the relations between amino acids and nucleic acid sequences were established before the translation apparatus, serving as improved catalysts in an RNA world. Blomberg claims that the only way to get a stable translation mechanism is by a feedback between the code and proteins that were synthesized by the mechanism which they controlled. Such a view leads to the conclusion that important features of the genetic code are due to a frozen accident: the possibility to get feedback. (Crick, 1968).

Blomberg, as well as Szathmáry & Maynard Smith, discuss the Eigen dilemma: accuracy is needed to get long molecules with proper function, and long molecules with proper function are needed to provide a satisfactory accuracy.

This leads to the question about the organisation of the "living" systems, the proper biogenesis, which is brought up in the paper by Gánti. A problem here is where to draw a line between non-life and life. Many authors want to call an RNA world a first stage of life, and Wächtershäuser refers to his ideas of rather primitive entities on mineral surfaces as "two-dimensional life". The views in the papers of this group are more restrictive and claim that any world without spatially confined functioning units, and without any proper reproduction is not to be called life. The concept and the relevance of reproduction is discussed in detail by Szathmáry & Maynard Smith.

The requirements for the first organisms are not much discussed in the literature, and there are few other serious attempts besides Gánti (1979) and Maturana & Varela (Varela *et al*., 1974; Maturana & Varela, 1992). An important question here is to define a "minimum" requirement of a living organism. Gánti's proposal is based on his "chemoton" model which is a closed system of a kind he calls a programme-controlled, self-reproducing fluid automaton. It has three essential subsystems: a genetic system, a functioning unit synthesizing the components, and a membrane part. Gánti also discusses how such a system may have originated.

Evolution of Cognition and Consciousness

In the last three papers, Sverre Sjölander, Peter Århem, Hans Liljenström and Ingemar Lindahl focus on the origin of cognition and consciousness, transitions at much later stages in evolution than those discussed in the other contributions of this special issue. Being related to the mind-brain problem, they are often seen as principally different from and more problematic than the earlier stages in the evolutionary process. The problems of the origin of cognition and consciousness have therefore been much neglected [for a discussion see Eccles, (1989)]. However, as pointed out in a previous special issue of this journal (Blomberg *et al*., 1994), these problems ought to be analysed in an evolutionary perspective. The origin of cognition and of consciousness are fundamental biological problems in the evolution of life.

The evolutionary perspective leads the authors to treat the problems of cognition and consciousness in a less anthropocentric way than traditionally done. Sjölander emphasises that primitive cognition is not so primitive as usually taken for granted; Århem and Liljenström argue that knowledge and problem solving in a wide sense are as old as life itself; and Lindahl calls attention to the evolution of different forms of consciousness. No attempt to determine a point in time and space for the origin of consciousness is made in the papers. On the contrary, the difficulty in determining such a point is stressed both by Århem and Liljenström and by Lindahl. As Mayr (1982) points out, this is largely a matter of taste. If defined in terms of adaptation to environmental stimuli, there does not seem to be any lower limit (Mayr, 1982; Delbrück, 1986).

Sjölander draws attention to the adaptive character of cognition. Drawing on results from ethology, he discusses how the surrounding reality is depicted by the mind in different species. In the spirit of Lorenz (1973), and before him Kant (1790), Sjölander argues that mind does not depict reality faithfully. Depending on the adaptive value of the construct of the reality, there are species-specific reality representations. A special case described is the stepwise evolution in different species regarding the ability to construct integrated representations that are multimodally governed. For instance, reptiles cannot form a common representation from different sensory channels, but keep them separate. The multimodal mind with a central representation of reality seems to have originated with mammals.

Århem and Liljenström emphasise the principal difference between cognition and consciousness. This difference is not always recognized in the debate on the mind-brain problem and has caused confusion. Cognition is not necessarily conscious cognition, and is not necessarily identical with knowledge processing. This means that the evolution of the three phenomena, knowledge, cognition and consciousness, do not show congruent time courses. This has important consequences for more philosophical problems of knowledge. It suggests, for instance, that the dominant empiristic view of today, that all knowledge come through our senses, is a mistake.

A further point discussed is the view that cognition—conscious or non-conscious—is primarily an active process. Traditionally, the active role of the conscious mind in the biological evolution is not emphasised. Instead, the external selection pressure is understood to be the active force of evolution. However, as pointed out by Popper (1992), and further commented on by Lindahl, the conscious mind may be seen to play a more active role in evolution. In fact it may be argued that this is a more plausible interpretation of biological evolution. According to this view, knowledge is seen as mainly created by the organism, and not merely as information passively received from the environment.

An extension of this view is that consciousness also plays an active role in evolution when it comes to generating behaviour. The idea, that the preservation and development of consciousness in the biological evolution seem to indicate that consciousness is efficacious, and has a survival value, appears to have been first developed by James (1879), and has later been discussed by Broad (1925), Beloff (1965), Popper & Eccles (1977) and Edelman (1991). The consequences of this idea are described by Århem and Liljenström and in more detail by Lindahl. The relevance of Darwin's theory of natural selection to the explanation of how conscious mental processes are related to neural processes is critically examined by Lindahl. He, as well as Århem and Liljenström, conclude that in an evolutionary perspective an interactionistic theory appears to be the most promising solution to the mind-brain problem.

These last three papers of this special issue clearly demonstrate the explanatory value of an evolutionary approach to the problems of the nature and function of mental processes.

Concluding Remarks

The multi-faceted collection of papers in this special issue illustrates the wide range of subjects and fields of research involved in the study of the origin and evolution of life. Here, we have chosen to emphasize certain areas, not always in focus that we find essential for the further development of the field. These areas comprise main hypotheses about the prebiotic world, the development of the genetic code, the early organization of living systems and the evolution of cognition and consciousness.

It is clear that studies of the molecular characteristics of biological systems have provided the natural background for the success of physics and chemistry in unravelling various problems concerning the origin and evolution of life. Also evident is the additional value of computational and philosophical analysis in the investigation of the complex systems and functions of the evolutionary process. Although science still has a long way to go in this field, it seems a valid enterprise to try to disclose the essentially anastrophic transitions leading from the early mineral reactions to the organisation of the early living cells, and up to the emergence of consciousness.

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