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Origin of biochemical organization

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Abstract

The problems of the origin of life and biochemical evolution are analyzed in the context of the biochemical organization concept proposed earlier by the authors. The traditional view according to which the evolution of biological systems occurred from lower levels to systems of higher levels is criticized. It is suggested that the formation of the cell and biological systems of lower levels (subcellular structures, supramolecular structures, biomacromolecules) occurred in a coordinated manner. The liposome and inorganic hypotheses of the origin of life are discussed. Regosome model based on ideas of Nussinov and Mekler which combines advantages of the liposome and inorganic hypotheses has been adopted and modernized. It is suggested that the initial metabolism of protocells based itself on C_2-C_3-compounds. Autodevelopment of catalytic systems of protocells is discussed. © 1997 Elsevier Science Ireland Ltd.

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1. Introduction

It is generally accepted that living organisms are highly organized systems. Indeed, organization is one of the main characteristic features of life. So the problem of the origin of life to a considerable degree is the problem of the origin of biological organization. What is biological organization? There is no single point of view. Recently we have suggested the concept of biochemical organization (Kurganov and Lyubarev, 1991, 1992; Kurganov, 1993) which enables us to reconsider the problem of the origin of biological organization and the wider problem of the origin of life.

2. The concept of biochemical organization

We propose that the notion of organization in biology is not exhausted by the notion of structure. Biological systems are functionally active structures and are characterized by a definite arrangement of their components and the interaction between them, which impart a biological function to the structure. Besides, this interaction is impossible without effective regulatory mechanisms. Therefore, we should view the biological organization as the unity of structure, function and regulation.

Biological systems are multilevel hierarchical systems. On the one hand, the principle of hier-

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archy asserts that a biological system with any degree of complexity is always included as an element in a system of a higher rank. On the other hand, it is a set of elements or subsystems of a lower rank. The transition from any level to the higher one means not only the emergence of a more complex system, but also the appearance of a new, more complicated function and a new regulatory mechanism occupying a higher hierarchical position relative to regulatory mechanisms realized at lower levels. Thus, the hierarchy of structural levels predetermines the existence of the functional hierarchy and the hierarchy of regulatory mechanisms.

The cell is the fundamental unit of living matter. Intracellular levels are the subjects of investigation of some interrelated biological sciences which may be called biochemistry in a wide sense. Therefore, we consider the cell, subcellular structures (organelles), supramolecular complexes, biomacromolecular and low-molecular-weight compounds as biochemical levels. In line with this notion, we have defined the biochemical organization as a combination of principles of the structural organization, function and regulation at the biochemical level.

3. Evolutionary problems in the context of the concept of biochemical organisation

In terms of the concept of biochemical organization, a theory of biochemical evolution should answer two principal questions. First, it is necessary to understand how the evolution of structures correlates with the evolution of functions and control mechanisms. The second problem is the interrelation between the origin and evolution of different levels. As applied to biochemical systems, the problem is formulated as follows. In what sequence did such levels as biomacromolecules, supramolecular complexes, subcellular structures and cells emerge and evolve?

It is most widely believed that structural levels were formed in succession 'from simple to complex' in the course of biochemical evolution: initially low-molecular-weight organic compounds emerged, then biopolymers formed, further supramolecular structures (micelles, coacervates, microspheres, etc.) arose, and, finally, protocells appeared. It is precisely this scheme which is stated in most of reviews on the problem of the origin of life (Oparin, 1968; Fox and Dose, 1977; Folsome, 1979; Gladilin, 1991; Oró, 1995). Besides, Bernal (1967) supposed that one more stage, namely the stage of separate organelle formation, had to exist.

This 'standard' scenario cannot explain the origin of biological functions. Indeed, the function of a biological system of a certain level should be realized as the role of this system in the system of the higher level (Kurganov and Lyubarev, 1992). Therefore the evolution of a function is impossible while the corresponding structure evolves separately.

Similar considerations can be applied to the evolution of control mechanisms. The concept of biochemical organization suggests two kinds of control: autoregulation directed to the maintenance of a constant level of key parameters of the system, and 'tracing' signals from the higher levels (Kurganov and Lyubarev, 1991, 1992; Kurganov, 1993). It is clear that mechanisms of 'tracing' cannot appear while the system evolves in isolation. It should be emphasized that it is mechanisms of 'tracing' which provide the functioning of the given system in a system of a higher level. Thus, these mechanisms are a significant system-forming factor. Therefore, it is hard to imagine the appearance of a new level in the absence of regulatory links with lower levels.

To overcome this obstacle Oparin (1978) proposed that 'at first, there could appear only the protein-like and nucleic acid-like polymers, whose intramolecular structure had no biological purposiveness. Only when these polymers were combined in multimolecular phase-separated systems, their interactions brought to a mutual adjustment of their molecular structure and biological functions as a result of natural selection of the whole open systems'.

Besides, the scheme 'from simple to complex' is not confirmed by model experiments on chemical evolution.

4. Chemical evolution in model experiments

The first success in modelling chemical evolution was achieved by Miller (1953). He used a mixture of methane, water, and ammonia. However, it became clear later that the early Earth atmosphere consisted mainly of carbon dioxide and nitrogen (Pollack and Yung, 1980; Levine, 1982; Kasting, 1993).

Therefore, the problem of the origin of organic matter on the Earth remains unsolved.

Some authors supposed that organics could be delivered to the Earth by cometary impact (Oró, 1961, 1995; Maurette et al., 1994). The other investigators attempt to find a way of CO_2 reduction under primitive Earth conditions (Wächtershäuser, 1990; Erokhin, 1994; Kritsky et al., 1996). The third group of authors believe that the primitive Earth atmosphere or hydrosphere contained some portion of reduced carbon compounds (Miller, 1986; Navarro-González et al., 1996).

Nevertheless, in any cases it is clear that the 'thick soup' of organics was not present on the primitive Earth. Abiogenic synthesis of some compounds, e.g. sugars (Choughuley, 1984; Shapiro, 1988), is especially doubtful. It is evident that the appearance of simple compounds such as glycine, alanine and some other amino acids, as well as formic and acetic acids, was the most probable.

Thus, the possibility of formation of biologically significant low-molecular-weight organic compounds is not quite confirmed by experiments. The next stage of the 'standard' scenario is even more doubtful. Numerous attempts to simulate a prebiotic synthesis of polymers similar to biological ones have failed (Mekler, 1980; Cairns-Smith, 1982; Oró et al., 1990; Gladilin, 1991). The main difficulties were the low rate of polymerization and formation of links atypical for biopolymers.

5. Liposome hypothesis of the origin of life

Thus, we believe that the scheme 'from simple to complex' is invalid. On the other hand, the supposition that the formation of biochemical systems occurred 'from complex to simple' is even more absurd, because higher systems consist of systems of lower levels. Therefore, we consider as the most acceptable the notion about the simultaneous and coordinated formation and development of the structures of biochemical levels.

This approach assumes that precursors of protocells had emerged before biopolymers appeared. Thus, it is proposed that protocells were formed from non-polymeric material.

Deamer and co-workers suggested a concept that lipid bilayer membranes arose before the accumulation of proteins, polynucleotides, and other complex molecules (Hargreaves et al., 1977; Deamer and Oró, 1980; Morowitz et al., 1988, 1991). Such liposome-like structures demonstrate barrier functions, but they should include some peptide and nucleotide molecules to provide transport and catalytic functions, as well evolution process (Deamer and Oró, 1980; Koch, 1985).

Baltscheffsky and Jurka (1984) discussed the possibility of the simultaneous, stepwise emergence of interacting oligopeptides, oligonucleotides, and protomembranes. These authors, however, did not propose concrete mechanisms for the interaction and evolution. Morowitz et al. (1988) suggested a model of membrane vesicles including primitive pigment molecules asymmetrically oriented in the bilayer. These vesicles could capture light energy in the form of an electrochemical ion gradient and use it for the synthesis of new lipid molecules and biopolymers, thereby providing their growth and evolution. Norris and Raine (1997) (also Norris and Madsen, 1995) suggested a model including the formation of domains in the liposome membrane, the catalytic formation of polymers on the membrane surface and the evolutionary dynamics of the protocell population driven by fusion and fission.

A disadvantage of the liposome hypothesis is that the inner space of the protocell is considered as a structureless bulk. However, the inner medium of contemporary cells have a strict organization. This organization includes cytoskeleton, organelles, and other intracellular membrane structures which divide the cell into numerous

compartments and, simultaneously, create the united structure within the cell. A significant role is played by microcompartmentation achieved by the spatial organization of enzymes in the cell: binding of enzymes by cell structures and formation of enzyme clusters (Friedrich, 1984; Clegg and Wheatley, 1991; Lyubarev and Kurganov, 1996a). Therefore, a model taking these facts into consideration is required.

6. Inorganic hypothesis of the origin of life

Some authors suppose that protocells emerged on a mineral base. This idea can be illustrated by the following example. As Cairns-Smith (1985) noted, a cooperative system (e.g. an arch) can be gradually constructed, if it is built on some support. Mineral particles could be such a support providing protocell formation.

A significant role for clay minerals in the origin of life was postulated by Bernal. Clay surface could adsorb and concentrate organic substances (Bernal, 1967), it could also catalyze polymerization and other reactions (Rao et al., 1980; Ponnamperuma et al., 1982; Negron-Mendoza et al., 1996). Besides, Cairns-Smith (1966, 1982, 1985) supposed that clay crystals could function as the earliest genetic information storing material, thus he considered clay crystals as the first organisms. Hartman (1975, 1992) postulated the significant role of iron-rich clay in the origin of the photosynthetic organisms.

Woese (1979) supposed that life emerged not in the ocean but in salt water droplets in the early Earth's atmosphere. He considered these droplets as precursors to cells.

Several authors suggested a significant role of iron-sulphur minerals in the origin of life. Wächtershäuser (1988) advanced a hypothesis that metabolism had originated at pyrite surfaces prior to the origin of the first cells. He considered surface-bonded constituents of the surface metabolism as a 'surface organism'.

Russel et al. (1994) proposed that life emerged from iron sulphide bubbles formed by the contact of sulphidic spring water and iron-bearing ocean water. These 'sulphide membranes' inserted abiogenic organic molecules and evolved into cells. Analogous model of sulphide vesicle was proposed by Erokhin (1994). These vesicles could be formed from liposomes with iron-rich inner contents as a result of diffusion of H_2S.

7. Regosome model

It is reasonable to suppose that protocells had to possess the basic attributes of real cells. In respect to cellular organization the significant property of mineral particles is porosity. Pores are compartments providing separate proceedings for various processes. Kuhn and Waser (1982) assumed that pores of different sizes in rocks provided the necessary compartments in which the earliest translation machinery could be assembled.

Nussinov and Vekhov (1978) supposed that up to the appearance of liquid water the Earth surface was covered by clay-like dust grains called regolith grains by the authors by analogy with the Moon's ground. Unlike the Moon's regolith the Earth's one had to possess considerable porosity. They were lighter than water and could float. Nussinov and Vekhov supposed that regolith grains could serve as platforms for the origin of life.

Mekler (1980) advanced a hypothesis that floating regolith grains adsorbed lipids located on the water surface and became covered with a lipid shell. A similar supposition was further made by Nussinov and Maron (1989) as well. The regolith grains covered by a lipid layer adsorbed and concentrated various organic compounds synthesized in small quantities in the ocean.

Mekler called such particles 'reinforced liposomes'. We have suggested a new term regosomes for them (Lyubarev and Kurganov, 1995).

The advantages of the regosome model are as follows. On the one hand, the lipid shell provides the barrier function and hydrophobic environment for synthetic processes. In regolith pores a hydrophobicity of different degrees could be achieved. On the other hand, regolith support not only could stabilize the lipid shell but could provide a great surface, reveal the catalytic activity and concentrate K^+ ions (Goldfeld and Goncharova, 1989).

The main advantage of regosomes, in contrast to the other models, is that they provide microcompartmentation. Besides, the regosome, as with the cell, is a multilevel hierarchical system including precursors of the structures of biochemical levels of organization.

8. Metabolism of protocells

Contemporary metabolism is divided on two branches, namely, catabolic and anabolic branches. They are connected via amphibolic pathways: the Krebs tricarboxylic acid cycle, the dicarboxylic acid cycle and the glyoxylate cycle. C_2- and C_3-compounds, namely, acetyl-CoA, glyoxylate and pyruvate, are the end products of catabolic pathways and, simultaneously, the initial substrates for anabolic pathways. This circumstance indicates that C_2- and C_3-compounds could be initial substrates for a primitive metabolism of protocells.

It was mentioned above that C_1- and C_3-compounds were the most probable products of chemical evolution. Therefore, we have proposed a scheme of initial metabolism of the protocell (Lyubarev and Kurganov, 1996b) based on glyoxylate, pyruvate and acetyl-thioester (precursor of acetyl-CoA). We suppose that the glyoxylate cycle was the main amphibolic pathway of the protocell providing (without carboxylation) succinate, glutamate (via isocitrate), aspartate (via oxaloacetate) and other compounds necessary for biosynthetic processes. The important role was played by the glycerate pathway in which two molecules of glyoxylate are transformed to glycerate. The latter could be a precursor for carbohydrate biosynthesis.

We propose that protocells could use for biosynthetic processes the same energy sources as those which provided abiogenic syntheses (or some of them). For example, if protocells floated on the ocean surface, they could use the UV-light of the Sun. The mechanism of UV-light energy utilization had to differ essentially from contemporary photosynthesis. Apparently, protocells used inorganic photocatalysts (Krasnovsky, 1974; Telegina and Pavlovskaya, 1995).

Erokhin (1994) suggested that the photocatalytic oxidation of hydrogen sulphide by Fe^{2+}/Fe^{3+} might be the main source of energy in the initial period of prebiotic evolution. A hydrated electron is one of the products of the reaction. The energy of this highly reactive particle could be used for chemical syntheses. For example, its interaction with hydrogen sulphide can lead to the formation of atomic hydrogen or an anion-radical of sulphur (Hart and Anbar, 1970). The latter can interact with organic compounds to form thiols. The interaction of a hydrated electron with a carboxylic acid leads to the formation of an acyl radical (Hart and Anbar, 1970) which can react with thiols to form a macroergic bond. Thus, owing to the above reactions the energy of light could be used for the synthesis of macroergic compounds.

9. Autodevelopment of metabolic systems

The initial catalysts were metal ions and their complexes with simple organic molecules. As a result of biosynthetic processes, substances promoting some reactions (oligopeptides, coenzymes or their precursors) were accumulated. The catalysts could become more complex, for example, by elongation of the peptide chain. The more active catalysts were preferred and better preserved in the course of natural selection. A significant role in the selection of catalysts was played by substrates (De Duve, 1987; Erokhin, 1994; Bar-Nun et al., 1994; Kochavi et al., 1996).

Inorganic catalysts usually have a low specificity. The same metal ions could accelerate different reactions. During autocomplication catalytic systems became more specific. Initially their set and distribution within the protocell were accidental. However, in the course of natural selection the protocells whose catalysts were suited to each other with the formation of a united metabolic network became preferred. These protocells could successfully evolve, they synthesized more organic compounds, and thereby increased the activity of their own catalysts.

The regolith pores were compartments where catalysts of reactions of a common metabolic pathway could be in proximity. This has some kinetic advantage and could be kept in the course of selection. During autodevelopment of catalysts and their transformation to polypeptide structures catalysts-enzymes of neighboring reactions had to acquire complementary sites allowing them to form complexes. Thus, multienzyme complexes and metabolons could arise, these playing an important role in metabolic systems of contemporary cells (Friedrich, 1984; Srere, 1987; Lyubarev and Kurganov, 1996a).

10. Conclusion

Thus, according to the regosome model, precursors of protocells had appeared before biomacromolecules, supramolecular complexes and cellular organelles were formed. Nevertheless, there were precursors to the structures of all the above-mentioned levels in the regosome. Indeed, oligopeptides and oligonucleotides are precursors to biomacromolecules, and complexes of oligopeptides and oligopeptides with oligonucleotides are precursors to supramolecular structures. As to cellular organelles, regolith pores may be considered as their precursors. Thus, the biochemical levels from biomacromolecules to the cell could evolve simultaneously.

The main problem is the origin of the genetic code and reproductive mechanisms. There are a lot of hypotheses on this subject (Woese, 1972; Mekler, 1980; Cairns-Smith, 1982; Altshtein, 1987; Prieur, 1994; Davydov, 1995; Otroshchenko and Kritsky, 1995) but a discussion of this problem is outside the framework of this paper. We believe that protocells emerged and biosynthesis of all necessary monomers evolved before the appearance of reproductive mechanisms. Evolution of mechanisms of transcription and translation occurred simultaneously with the development of biopolymer structures. Further biopolymers replaced and ousted the inorganic framework. From that moment on, we may speak of the appearance of real cells.

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