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On the Origin of the Eukaryotic Cell

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Abstract—The eukaryotic cell appeared 2.7 Ga or earlier as a result of coevolution of prokaryotic components of Archean microbial communities. The crisis events at the Archean–Proterozoic boundary, which partially destroyed the Archean prokaryotic biota, may have played an important role in the development of the first eukaryotes. The separation of the nucleus from the cytosol and the presence of heterogeneous genomes within the same cell provided the prerequisites for more efficient regulatory mechanisms of gene expression and genetic recombination, which, in turn, could have become the basis for modification variability, composite life cycles, sexual process, and, eventually, multicellular organization. The more efficient mechanisms for regulation and modification, which increased their ecological tolerance, probably gave eukaryotes an advantage during crises. The new mechanisms supporting and controlling genetic variation associated with the sexual process (copulation of gametes, meiosis) gave rise to new types of biological systems—endogamous populations and species, which stimulated intense biodiversification. The emergence of eukaryotes (as well as other higher taxa) should be regarded as being the result of coevolution of ecosystems, the biosphere, and even the Earth as a whole.

INTRODUCTION

The origin of the eukaryotic cell can be reasonably regarded as the second most significant event of the biological evolution (Martin and Russell, 2003). No direct evidence is known as to where, when, how, why, and in what conditions such aromorphosis happened, while the available indirect data allow a wide range of hypotheses, which are mostly controversial. Direct evidence is only provided by specific biomarkers, remains of steroid compounds specific to eukaryotic cell membranes, which were found in deposits dated 2.7 Ga (Brocks *et al.*, 1999).

It seems expedient to begin the discussion with the basic characters of eukaryotes, which provided their evolutionary–ecological advantages.

THE ORIGIN OF EUKARYOTES AS THE MOST SIGNIFICANT AROMORPHIC EVENT: ADVANTAGES OF THE EUKARYOTIC CELL

The separation of the nucleus (storage of genetic information) from cytosol (a zone of active metabolism) was a manifestation of a global evolutionary tendency, i.e., the separation of the soma from the germ. This tendency was best characterized by Rautian (2001): "The division of organisms into the soma and the germ stems primarily from the fundamentally different requirements of storing genetic information and of organismal functioning… the maintenance of the soma requires dynamics, while the preservation of the germ with its genetic information requires stability. A compromise between these opposite requirements has been achieved through the spatial separation of the soma from the germ inside the organism."

However, this cannot entirely explain the biological essence of nucleus separation. The principal distinguishing feature of eukaryotes from prokaryotes was their more complex and more efficient genome regulation. The nucleus is not only storage, but also the area of transcription and replication of DNA and, most importantly, the zone of active *regulation* of transcription and posttranscriptional modifications of RNA. The appearance of a double nuclear membrane between the hereditary material and the cytosol subjected to intense biochemical processes provided a progressive evolution of gene regulation, which, in its turn, gave rise to effective mechanisms for modification variability. Eukaryotes became capable not only of biochemical but also of morphological modifications (e.g., they can transform from ameboid to flagellate form and conversely), with their genome being unaltered. This has provided a higher level of adaptation potential. Note that the increasing adaptability (and, consequently, stability) of living systems is one of the basic trends in biological evolution; for example, it manifests itself in the increase in the average life-span of genera (Markov, 2002).

It was owing to the capability for morphological and functional modifications, depending on the environment (with the genome being unchanged due to more delicate regulation), that unicellular eukaryotes could later develop, first composite life cycles and sexual reproduction and, subsequently, multicellular organization. In both a protozoan with a composite life cycle and a multicellular organism, the same genome provides the development of essentially different cell types in different conditions. The ability of prokaryotes for such modifications is one order weaker.

The nucleus separation promoted the development of a better system of DNA protection and repair (although this system might be initiated by archaebacteria in extreme conditions, see below). This resulted in less frequent mutations in eukaryotes than in prokaryotes and provided them with an important advantage at low concentrations of atmospheric oxygen, because, in ozone-deficient environments, strong ultraviolet radiation might bring about very intensive mutagenesis of surface water organisms. Thus, the effective repair system might noticeably enlarge a potential adaptive zone of the earliest eukaryotes, so that they could survive in better illuminated water layers. However, there is abundant evidence of considerable atmospheric oxygen concentration as early as the Archean Time (see below).

The lower mutation rate and the development of mechanisms restricting genetic exchange (horizontal gene transfer) were undoubtedly combined with more effective and controlled mechanisms of genetic recombination (copulation of gametes, crossing-over). The sexual process must have provided eukaryotes (as well as the biota as a whole) with essential advantages and produced a complex of important consequences: reproductive isolation, endogamous species and populations, di- and polyploidy (for details, see below). It should be mentioned that the earliest eukaryotes were probably devoid of a sexual process. Many of the eukaryotic advantages manifested themselves later, in the course of evolution. Of most significance for the earliest eukaryotes was probably their increasing ability to adapt to environmental changes through modification variability based on more effective genome regulation.

ON POSSIBLE RELATION OF THE ONSET OF EUKARYOTE EXPANSION TO THE CRISIS EVENTS AT THE ARCHEAN–PROTEROZOIC BOUNDARY

All the above suggests that eukaryotes emerged in the period of biosphere history when conditions were especially unstable and unpredictable, when the prokaryotic adaptation strategy (a high mutation rate, horizontal gene transfer, and selection of resistant clones) appeared to be excessively wasteful and, hence, inefficient. Under these conditions, a more universal and economical adaptation strategy based on a more adequate (expedient) modification variability might have gained a great advantage.

This supposition is indirectly confirmed by paleontological and geological records. The earliest certain signs of eukaryotes (hydrocarbon biomarkers, i.e., cholestane, its C_{28} and C_{30} analogues) were found in rocks dated 2.7 Ga, i.e., in the Upper Archean (Brocks *et al.*, 1999).

At present, there are different interpretations of events occurring in the lithosphere, hydrosphere, and atmosphere of the Earth at the Archean–Proterozoic boundary; however, the fact that these events were rather significant is beyond doubt. Some researchers think that they involved lowering of atmospheric carbon dioxide concentration, essential fluctuations of seawater temperature and pH, intensive tectonic processes, formation of the first integral supercontinent of the Earth (Monogea), and others (Sorokhtin and Ushakov, 2002).

Whatever the nature of the changes was, they might have promoted the appearance and expansion of eukaryotes in two ways. First, the rapid and unpredictable environmental changes should have favored organisms with more efficient and universal adaptive mechanisms. The complicated and fine regulation system of environmentally dependent gene expression and post-transcription RNA modifications should have given eukaryotes a selective advantage. Second, sharp climatic changes at the Archean–Proterozoic boundary might have destroyed some local prokaryotic communities of the Archean. Particularly, the supposed cooling and subsequent Huronian glaciation should have greatly affect warm-water cyanobacterial communities. Carbon dioxide deficiency may have been equally unfavorable for photosynthesizing organisms. In fact, within the interval of 2.5–2.3 Ga, stromatolitic structures were sharply reduced in number (Semikhatov *et al.*, 1999). The destroyed Archean cyanobacterial communities were replaced by new (as usual, more complex and more perfect) communities, where eukaryotes were an indispensable component. The first eukaryotes might have appeared long before the terminal Archean, but they started to constitute a considerable portion of the biota near the Archean–Proterozoic boundary. Their records have been known since 2.7 Ga. Similarly, the appearance of mammals and birds may be recorded beginning from the Early Cenozoic, when they became dominating components of communities, although they had appeared a long time before.

THE THEORY OF SYMBIOGENESIS

At present, the symbiogenetic theory of the eukaryotic cell is best substantiated and commonly accepted (although some researchers argue against it; see, e.g., Cavalier-Smith, 2002). Mitochondria and plastids were convincingly proved to have been originated from symbiotic eubacteria (alphaproteobacteria and cyanobacteria, respectively). Regretfully, no other facts are available. The nature of the host cell, the emergence of the cytosol and the nucleus are subjects of controversy. An archaebacterial cell is commonly supposed to have served as the host cell (Margulis and Bermudes, 1985; Vellai and Vida, 1999). This was inferred from the similarity of archaebacteria and eukaryotes in genome structure (in particular, the exon–intron organization), replication, repair, transcription, and translation as well as other molecular data (Slesarev *et al.*, 1998; Cavalier-Smith, 2002).

The symbiotic organism had a chimerical (archaebacterial–eubacterial) genome, with many components duplicated in function (Gupta, 1997). Subsequently, excessive elements were reduced or performed different functions (Martin and Schnarrenberger, 1997). In particular, the development of membranes follows only one of two fashions, namely, that characteristic of eubacteria (in the archaebacteria, the basis of membranes is composed of isoprenoid esters, whereas in eubacteria, they are composed of esters of fatty acids). According to one hypothesis, the nuclear membrane was formed as a by-product of expression of eubacterial genes responsible for the membrane synthesis in the archaebacterial genetic environment (Martin and Russell, 2003). There are many other hypotheses, including very extravagant ones, such as the origin of nucleus of the archaebacterial cell through virus infection (Takemura, 2001).

A point of concern is that prokaryotes are devoid of analogues of characteristic eukaryotic cytoskeleton composed of microtubules (mitotic spindle, flagella, etc.), and related ability for phagocytosis. A hypothesis for the origin of organisms with a microtubular cytoskeleton (in combination with the nuclear membrane) from symbiosis of an archaebacterium and a mobile eubacterium is also worthy of attention. Though not commonly accepted, it is still attractive (Dolan *et al.*, 2002). Another hypothesis suggests the existence in the past of a peculiar group of prokaryotes, so-called chronocytes, related to neither bacteria nor archaeans. Chronocytes had a cytoskeleton and were capable of phagocytosis; they swallowed different bacteria and archaeans and gave rise to eukaryotes (Hartman and Fedorov, 2002).

Probably, eukaryotes are a monophyletic group, i.e., the successful fusion of archaebacteria and eubacteria into single organisms, which gave rise to all kinds of eukaryotes, was a unique event in the Earth's history (Gupta, 1997). Analysis of mitochondrial genomes also indicated the monophyletic origin of the mitochondria of all extant eukaryotes (Litoshenko, 2002).

The symbiotic nature of eukaryotes made some researchers realize that symbiogenesis is of greater evolutionary significance than was previously thought. The emergence of eukaryotes, lichens, and reef-building corals with zooxanthellae are neither oddities nor exceptions but probably an apparent manifestation of an universal law governing many other macroevolutionary events, although not evidently (Margulis and Bermudes, 1985).

A HYPOTHETICAL PROKARYOTIC COMMUNITY AS A “COLLECTIVE ANCESTOR” OF THE EUKARYOTIC CELL

It would be incorrect to consider the earliest eukaryotes to have evolved from several prokaryotic species united into a symbiotic organism. Following the system view of life and biological evolution, it would be more exact, although paradoxical, to state that eukaryotes were derived from a prokaryotic community including at least three components: (1) anaerobic heterotrophs (most likely, archaebacteria with the exon–intron genome design), which obtained energy through anoxic carbohydrate fermentation; (2) aerobic heterotrophs (eubacteria) obtaining energy mostly through the oxidation of low-molecular carbohydrates (particularly, pyruvate, lactic acid, ethanol, or acetate, which were final products of energy metabolism of the first component); and (3) anaerobic autotrophs, i.e., photosynthesizing organisms (cyanobacteria), which provided the first component with high-molecular carbohydrates and the second one with oxygen.

Advantages of such triple symbiosis are evident: each component benefited from coexistence with two others. Cyanobacteria and archaebacteria got rid of excessive toxic oxygen and products of anoxic metabolism; archaebacteria and aerobic eubacteria had organic food, and eubacteria obtained oxygen to successfully utilize organic compounds.

A surface 1-mm-thick layer of cyanobacterial mats, which were widespread as early as the Archean, contained oxygen concentration sufficient for aerobic organisms to exist even in an oxygen-deficient atmosphere (Rozanov and Fedonkin, 1994). Zavarzin (1993) emphasized that, within a microbial community, oxygenic photosynthesis yielded immediately high O_2 concentration and, hence, aerobic organisms might emerge long before atmospheric oxygenation. It is to be noted that the common opinion on relatively late atmospheric oxygenation is the subject of criticism at present; many facts indicate a high concentration of atmospheric oxygen as early as the Archean (Ikemi *et al.*, 2002; Watanabe and Ohmoto, 2002; Rozanov, 2003).

Oxygen, a by-product of photosynthesis, was primarily toxic for cyanobacteria. In the course of evolution, they developed some biochemical protections against this aggressive metabolite (Paerl, 1996). One of them was probably aerobic respiration. It is interesting that the most important part of cellular breathing—the electron transfer chain—appeared as a result of modification of an enzymatic system of photosynthesis (Nakamura and Hase, 1991). Modern cyanobacteria prefer to be associated with oxygen-absorbing microorganisms, the rates of oxygen liberation and absorption being strictly balanced (Paerl, 1996). Most likely, the surface layer of cyanobacterial mats containing high concentrations of high molecular weight carbohydrates and oxygen was a “cradle” where communities of, at first, heterotrophic (aerobic and anaerobic) prokaryotes and, subsequently, eukaryotes emerged (Rozanov and Fedonkin, 1994).

The hypothetical bacterial community, including the three components described above, had great advantages over a pure cyanobacterial mat, even without components being united under a common cellular membrane, i.e., without the formation of the eukaryotic cell.

Most likely, the appearance of the eukaryotic cell was preceded by a long coevolution of the components, whose increasing interaction led to the transformation of a bacterial biocenosis into a single quasi-organism.

Microorganism communities can demonstrate a very high level of integration. Owing to horizontal gene transfer, which is widespread among the prokaryotes, microbial biocenoses composed of various bacterial species are similar to the populations of higher organisms. The stable existence and functioning of a microbial community is maintained by well-balanced trophic connections, in particular, the optimal ratio and spatial distribution of producers and destructors. Occasionally, trophic connections may be so rigid that an organism cannot develop without its excretions being utilized immediately by the next component of the trophic chain (Zavarsin, 1993). Of other mechanisms of prokaryotic integration, the systems of chemical signals for behavior coordination (i.e., phenotypic expression) are worth mentioning. Some eukaryotes have learnt to imitate such signals in order to control prokaryotic activity in the community (Rice *et al.*, 1999). The mechanism for programmed cell death was also developed in a bacterial culture (Endelberg-Kulka and Glaser, 1999); the ability of individuals to be sacrificed for the sake of the entire community seems to be a sign of a high integrity of (individualized) microbial communities.

Logically, many mechanisms (first of all, signal transduction and regulation cascades) providing integrity and coordination of parts of the eukaryotic cell have been developed long before these parts were united under a single cell membrane. The horizontal gene transfer might be an important preadaptation that afforded a subsequent transfer of most of mitochondrial and plastid genes into the nucleus (Shestakov, 2003).

Members of modern microbial communities demonstrate remarkable readiness to form symbioses. Up to the present day, unicellular eukaryotes retain the capability of acquiring various (both prokaryotic and eukaryotic) endosymbionts with different metabolic strategies (Duval and Margulis, 1995; Bernhard *et al.*, 2000). However, modern prokaryotes cannot acquire intracellular symbionts, being incapable for phagocytosis. As mentioned above, this is considered to be a weak point of the theory of symbiogenesis. However, carnivorous and parasitic bacterial species, such as *Daptobacter*, are known to be able to penetrate the cytosol of other prokaryotes. Thus, even being devoid of a phagocytosis mechanism, prokaryotes can acquire intracellular parasites and symbionts (Guerrero *et al.*, 1986).

The hypothetical ancestral community of eukaryotes was probably a kind of improved cyanobacterial mat, including heterotrophic anaerobic archaebacteria and heterotrophic aerobic eubacteria as symbionts. In distinction to a pure cyanobacterial culture, such a community should have a more balanced composition of various substances: excessive oxygen, which was toxic to cyanobacteria, was removed; some amount of carbon dioxide necessary for photosynthesis was produced (especially valuable because of its presumed low concentration in the Early Proterozoic atmosphere); excessive organic matter was utilized; the population of cyanobacteria was probably controlled to some degree by carnivorous organisms; etc. These factors made such communities more stable and promoted their expansion during the crisis under consideration. Some modern associations of various (auto- and heterotrophic, anaerobic and aerobic) bacteria can be considered to be analogous to ancestral communities of eukaryotes. These bacterial mats occur in various extreme environments, show high ecological tolerance and high integrity, in particular, complicated spatial distribution controlled by gradation of oxygen content, pH, and other essential parameters (Zavarzin, 1993, 1994; Paerl *et al.*, 2000).[1]

Microbial communities should become even more stable when they included various true eukaryotes. The appearance of such communities probably stimulated a new outburst of development of stromatolitic formations after the minimum of 2.5–2.3 Ga (Semikhatov *et al.*, 1999).

An evident advantage of the eukaryotic cell over an association of its free components is primarily the centralized genetic regulation of all symbionts. In fact, the eukaryotic cell is a small compact community with biochemically complementary components under central control. As said above, eukaryotes had developed a better system for maintaining DNA stability and repair, which resulted in a lower mutation rate. Such systems might be characteristic of archaebacteria that occurred in extreme environments (Grogan, 1998), e.g., hyperthermophiles or residents of surface water layer subjected to strong ultraviolet radiation, which caused intense mutagenesis. The endocellular symbiosis enabled genomes of eubacteria (eventually, plastids and mitochondria) to be protected by the repair system of the archaebacterial cell-host. It was the need of protection that might have stimulated a rapid transfer of most of the mitochondrial and plastid genes into a nucleus.

The early formation of systems for regulation, stabilization, and protection of eukaryotic (and partly archaebacterial) genome suggests that ancestral microbial communities as well as the earliest mixed prokaryotic–eukaryotic associations occurred in environments unfavorable for usual Archean cyanobacterial mats, probably, in unstable shallow-water zones with more intense ultraviolet radiation. In these environments, microorganisms with a more efficient system of

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[1] All these gradients are highly variable (particularly, due to daily changes in illumination and photosynthesis intensity) in cyanobacterial mats (Pierson, 1988; Zavarzin, 1994). This might induce development of organs of active locomotion (flagella and cilia). To move actively flagellae needed additional energy, which they obtained from mitochondrial symbionts. According to some hypotheses, the flagellum and nucleus emerged simultaneously through a symbiosis of an archaebacterium as a host and a mobile eubacterium (Dolan *et al.*, 2002).

genome protection and regulation might have a selective advantage. This contradicts a hypothesis of a deep-water origin of eukaryotes (Bernhard *et al.*, 2000), which proceeded from the assumption that to live in areas exposed to high-energy ultraviolet radiation was difficult. The supposition of unfavorable environments in the ancestral biotope is supported by some authors, who think that archaebacteria, the basic components of symbiotic organism, were acidothermophiles (Dolan *et al.*, 2002). However, it is unlikely that the earliest eukaryotes were thermophiles (see below). Modern cyanobacterial mats that include various kinds of heterotrophic symbionts and occur mostly in extreme environments (Paerl *et al.*, 2000) can be regarded to be analogues of the ancestral eukaryotic community in terms of ecology and structure.

ECOLOGICAL TOLERANCE AND ANCESTRAL BIOTOPE OF EUKARYOTES

A set of environmental changes, including many vital ones, occurred around the Archean–Proterozoic boundary. The nature and scale of these changes have not yet been established. Therefore, it is hardly possible to reveal a single chief cause and conditions (water temperature, salinity, pH, composition) of the eukaryotic emergence. Modern protists (unicellular eukaryotes), especially primitive groups, can inhabit a very wide range of environments. They show only slightly lower ecological tolerance than prokaryotes. In particular, they can produce a large biomass under conditions close to those of the Archean, i.e., at high heavy metal salt content and very low pH values (down to 0.5); moreover, unicellular eukaryotes occasionally exceed prokaryotes in abundance and diversity in such hostile environments (Edwards *et al.*, 1999; Zettler *et al.*, 2002).

Unicellular eukaryotes can endure wide salinity fluctuations. Thus, the ameba *Platyamoeba pseudovannellida* grows at salinity from 0 to 138‰ (!) and easily adapts to very rapid salinity variations by changing pseudopodium shape (Hauer *et al.*, 2001). Eukaryotes survive in both the ice-cold Antarctic lakes almost lacking biogenic elements (Laybourn-Parry, 2002) and hot salt-rich water of marine hydrothermal vents. For example, the thermophilic infusorian *Trimyema minutum* is capable for reproduction at temperature up to +52°C (optimum +48°C) (Baumgartner *et al.*, 2002). Deep underground waters contain yeast cells growing at pH ranging from 4 to 10, temperature from 4 to 30°C, and salinity from 0 to 70‰ (Ekendahl *et al.*, 2003).

The most probable constraint is extremely high temperature conditions where informational RNA molecules become unstable. In hyperthermophilic bacteria, iRNA exists for a short time (from transcription to translation), whereas the eukaryotic cell must have a long period of iRNA stability (needed for RNA molecule transportation from nucleus, place of synthesis, to cytosol for translation) (Forterre, 1995).

As rare exceptions, some fungi and green algae survive at temperature of 60–70°C (Izhboldina and Galkin, 1999); however, in general, eukaryotes are much less adaptable to high temperature than prokaryotes (particularly, cyanobacteria). Therefore, water temperature of the ancestral eukaryotic biotope was unlikely over 40–50°C. This is in disagreement with some reconstructions of average Late Archean temperature as 60°C and higher.

Summarizing all the above, we conclude that characteristics of the ancestral biotope of eukaryotes might have been as follows:

(1) Unstable conditions, which are typical of shallow-water environments. Sharp unpredictable variations of vital parameters (pH, salinity, concentrations of biogenic elements, heavy metal salts, and others). The conditions must have been tolerable for cyanobacteria, but far from optimal;

(2) Illumination sufficient for cyanobacteria to exist;

(3) Oxygen concentration sufficient for the existence of aerobic bacteria and eukaryotes (as it was at the surface of cyanobacterial mats even in oxygen-deficient atmosphere);

(4) Temperature not higher than 40–50°C.

EARLY STAGES OF EUKARYOTIC EVOLUTION

There are no proved paleontological records of the initial stages of eukaryotic evolution. Therefore, we can judge them by only indirect evidence.

1. Was the acquisition of mitochondria a basic aromorphosis? Contrary to previous suppositions on the relatively late appearance of eukaryotic mitochondria, there are strong grounds to believe that aerobic endosymbionts (mitochondria) were acquired earlier than the nucleus. Possibly, the acquisition of mitochondria rather than the nucleus was the turning point in the eukaryotic emergence (Vellai *et al.*, 1998; Vellai and Vida, 1999). Coexistence of two different genomes within the same cell required a perfect system of their composite regulation and coordination to be developed. Thus, the acquisition of endocellular symbionts might be an essential stimulus for emergence of nucleus and gene regulation systems. The supposition that the earliest eukaryotes possessed efficient signal transduction and regulatory systems of a eukaryotic type was confirmed by molecular data (Janssens, 1988). This agrees with the above assumption that the nucleus was formed to provide perfect regulatory mechanisms. In addition, the transport of substances, in particular, proteins, through the double mitochondrial membrane should be acquired at the very early stage of symbiosis. The development of this transport system combined with the appearance of double-membrane organelles might serve as an important prerequisite of nucleus formation.

Molecular data confirm the acquisition of mitochondria at the early eukaryotic evolution. Modern mitochondrion-less protozoans apparently evolved from organisms having mitochondria (their nuclear DNA contains mitochondrial genes). It was interesting to find nuclear genes of eukaryotes that encode cytosol proteins and show nucleotide sequences similar to the genes of protebacteria (presumed ancestors of mitochondria). This indicates that mitochondrial symbionts could have had greater significance in the development of the entire genetic and biochemical structure of the eukaryotic cell than was previously thought (Roger, 1999).

2. Dispersal from the ancestral biotope. Until the partial pressure of atmospheric oxygen increased to 10^{-3} of the modern level, aerobic organisms, including eukaryotes, must have been intimately connected with the surface layer of the cyanobacterial mats. Only after this point could they leave their "cradle" to occupy different ecological niches. According to some hypotheses, this happened about 2.0 Ga, because at that time termination of mass iron ore deposition of the Early Proterozoic enabled a rapid increase in the atmospheric oxygen concentration (Sorokhtin and Ushakov, 2002). At that time, there was a burst of diversification of microfossils, some of which might be eukaryotes (Semikhatov *et al.*, 1999).

3. Development of the sexual process is of prime significance for genetic recombination. As discussed above, there are many records of oxidization of the Earth's atmosphere as early as the Archean. In this case, the diversification burst at 2.0 Ga could have been induced by other factors, for instance, by the development of the sexual process. Although this principal evolutionary event is difficult to date, it must have been a powerful stimulus for biodiversity increase and acceleration of progressive evolution.

Horizontal gene transfer of eukaryotes proceeds in an essentially different way than that of prokaryotes. Prokaryotes usually undergo an irregular exchange of DNA fragments, including that between different, unallied taxa (Shestakov, 2003). Interspecific gene exchange is retained by eukaryotes, especially primitive forms. Horizontal transfer was established between all three superkingdoms: Archaea, Bacteria, and Eukaryota (Paul, 1999; Andersson *et al.*, 2003; Koonin *et al.*, 2003). However, this mechanism of variability and adaptation apparently plays a less significant role in eukaryotes than in prokaryotes. Instead of and in parallel to it, eukaryotes developed the sexual process as a more efficient, more controlled mechanism of intraspecific gene exchange. Remarkably, according to some hypothesis, the sexual process evolved through alterations in transposons, transposable or mobile dispersed elements (Hickey, 1992). This cardinal change in the method of biotic genetic integration had far-reaching evolutionary implications, and affected the structure and dynamics of biodiversification. The eukaryotic biota first gave rise to new classes of organized biosystems, that are, *relatively endogamous populations and species.* The prokaryotic biota is not composed of true endogamous biological species; in some senses, it can be considered as a single, vast polymorphic quasi-species. The morphophysiological discontinuity of prokaryotic taxa is in general supported only by the discontinuity of ecological niches or biochemical functions. Apparently, uncontrolled horizontal transfer slowed down the evolution of the prokaryotic biosphere (Rudi *et al.*, 1998). The interspecific reproductive isolation of eukaryotes had first become the main factor regulating the biodiversity and providing its rapid increase. The increased rate of diversification might have greatly contributed to the higher stability of communities and the biosphere (Ponomarenko and Dmitriev, 1993).

The development of sexual process (copulation, cell fusion) inevitably led to the diploid stage in the life cycle and meiosis, which brought about new, more perfect mechanisms for maintaining genotypic variability at necessary level. It became possible to increase cryptic genotypic variability through the accumulation of recessive alleles in the heterozygous state. On the one hand, this innovation brought the threat of the growth of genetic load of harmful mutations, but, on the other hand, some alleles harmful in present conditions were preserved and could have become useful in different environments. The meiosis probably brought about linear (noncircular) chromosomes and crossing-over, an effective means of developing and maintaining recombinant variability. In general, eukaryotes have more effective and regulated mechanisms of polymorphism control than prokaryotes (intense mutation process and irregular horizontal transfer). This, along with modification variability, should have provided higher adaptability and stability of eukaryotes and their communities. The sexual process, as it is, emerged as a means of surviving in changeable environments (Krassilov, 1986), as confirmed by many modern primitive eukaryotes: in favorable conditions they exercise asexual reproduction (descendants being precise copies of parents), but as conditions deteriorate copulation takes place. A zygote with a double reserve of nutrients and frequently under a dense cover has better chances of survival in unfavorable conditions; owing to recombinant variability, cells produced by meiotic division differ from their parental cells. This can be interpreted as a way of increasing variability in emergency situations, which is more efficient and less wasteful than the chaotic genome alteration of prokaryotes.

Thus, the origin of eukaryotes and the development of the sexual process made the variability and diversity structure more discrete and regulated, which must have increased the rate of diversification, as well as evolutionary plasticity and ecological tolerance of species, communities, and the biota as a whole.

CONCLUSIONS

The origin of the eukaryotic cell can be regarded as a standard aromorphosis. This event is a brilliant manifestation of the general progressive trend of biological evolution, which is exhibited not only in the organizational complexity, expansion of the adaptive zone, increase in biomass, abundance, and autonomy of organisms, etc. but also, more importantly, in the greater stability of living systems (Krassilov, 1986).

The origin of eukaryotes was a result of natural integration processes within the Archean prokaryotic biota. In their turn, these processes were determined by the entire preceding evolution of our planet and its outer geospheres. Eukaryotes provide an excellent example that the appearance of new life form, including new large taxa, should not be interpreted as a result of evolution of individual phylogenetic lineages or clades but a regular and inevitable effect of the development of communities, the biosphere, and, probably, the planet as a whole.

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