Exosymbiogenetic (Coevolutionary) Model of Eukaryogenesis (hypothesis)

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Introduction

According to the now popular endosymbiogenetic theory, eukaryotes evolved from a fusion of archaeal and bacterial cells. The resulting superorganism became the first eukaryocyte 1, 2.

Various pairs of symbionts have been proposed (3, 4, 5, 6,7). Genomic data confirm that most eukaryotic proteins are of either archaeal or bacterial origin. These proteins have few common characteristics, most importantly, a single source has not been found for them. Rather, they come stem from many different bacteria through the transfer of individual groups of genes, rather than through endosymbiosis and fusion of whole cells. To date, only a variant of the endosymbiotic hypothesis is being considered, in which the third partner might be a large virus 1, 2.

There is no doubt about the viral origin of the individual components of the eukaryotic cell. Thus, the enzyme telomerase, which completes the protective terminal structures of chromosomal DNA (telomeres), comes from the reverse transcriptase of retroviruses. Part of the genetic apparatus of mitochondria — DNA polymerase, RNA polymerase, and primase — is inherited from the tailed bacteriophage. Viral origin has a transcription initiation factor. Presumably, at first, the Archean methanogen, suffering from oxygen, was able to switch to a completely different metabolism: fermentation. Then it entered into symbiosis with the ancestors of mitochondria 1.

There is an invaginative (1), reductionist theory of the origin of the nucleus (8)

The newest theory of the Baums assumes the origin of the nucleus from the body of the archaeal cell itself and the endoplasmic reticulum from its flagella by the gradual expansion of the latter 1.

The existence of so many theories indicates the inferiority of the existing ones. The problem is so serious that some consider eukaryogenesis a unique accident, comparing it to the origin of life in the universe, which does not have a strictly scientific explanation 1, 9.

Here we propose an exobiogenetic model of eukaryogenesis that explains the origin of the nucleus, endoplasmic reticulum, and all other eukaryocyte organelles. In contrast to existing theories, we have assumed that eukaryogenesis is not a consequence of endosymbiogenesis, but of exosymbiogenesis of ectoparasitic microbes.

When creating this hypothesis, we proceeded from the concept that progressive evolutionary changes are caused by damaging, pathogenic factors that totally entail diseases within phyla. Adaptation of descendants of ancestral phyla to new realities - evolutionary sanogenesis occurs through natural selection of progressive morphological and physiological changes. Pathogenic factors could be both abiotic and biotic (panzootic, panphytotic) 10, 11, 12, 13.

In microbial communities, before the emergence of eukaryocytes, there was a close, relationship between archaea and bacteria (1). This consortium was a fairly strong structure with numerous intercellular connections, carried out with the help of villi, flagella, pili of various types and syncytial bridges. Under such conditions, horizontal transfer of genes and even entire genomes, infection with viruses and cell parasites easily occurred. In addition to endoparasites, significant damage to cells was caused by ectoparasites (ectobionts). For example, endoparasites do not actually occur in archaea, with the exception of viruses, although they have many ectoparasites in the form of archaea and bacteria (1).

We believe that the starting event in eukaryogenesis was the infection of a prokaryotic host with a virus (presumably a giant virus). In order to get rid of the virus, the host cells used nuclear-like pores, portal machines through which the viral genome enters and exits the virus nucleocapsid (14).

Similar molecular motors are present in archaea and bacteria in archellum, villi, pili in the form of type 4 excretion system (T4SS). As is known, type IV pili are involved in the interaction of bacteria with the cells of infected organisms, they can help them get inside the cells. They also include conjugation pili, through which bacteria exchange genetic information, ensure the sexual process. Finally, with the help of type IV pili, bacteria can move. In addition, type IV pili are necessary for the formation of biofilms and are receptors for bacteriophages (15, 16, 17). The nuclear pores of eukaryotes (NPC) share an evolutionary origin with these endomembrane and intraflagellar transport system complexes. The modern NPC was fully established by the time of the last common ancestor of eukaryotes (LECA) and therefore before the diversification of eukaryotes (18).

It is likely that virus-infected host cells have learned to get rid of viruses by exporting DNA and RNA into the intercellular space of the prokaryote consortium using these nuclear-like portals. The membranes of the capsid of the virus in some places could merge with the portals of the host cells. Through nuclear-like pores, cells have established the export of ribosomal RNA, tRNA, mRNA, and other macromolecules to the extracellular space.

From this moment, a new round of the arms race between prokaryotic hosts and viruses begins. Viruses forced into the extracellular space transferred the translation of their RNA into the intercellular space of the consortium. With the assistance of viruses, eukaryotic-type ribosomes were created, which were exported through nuclear-like pores to the noncellular space. Of viral origin, it has the translation initiation factor eIF4E, a necessary protein for mRNA association with the 40S subunit of ribosomes (1). With the help of this protein, only capped RNAs are translated on ribosomes. Eukaryocyte-type ribosomes colonized the outer surface of the ectobionts membrane. They started translating viral RNA.

Archaea possessed the most perfect genetic programs among prokaryotes. A more advanced molecular computing system provided control over genetic processes and antiviral protection, including an RNA quality control mechanism, a ubiquitination system, and antiviral RNA interference (1, 2, 9). Bacte-

ria were able to use archaea in the fight against infection, giving them metabolic and other advantages in return.

Indeed, we see that eukaryotic cells inherited from archaea the central information systems of the cell (protein synthesis, DNA copying, and repair), the rudiments of the cytoskeleton, the rudiments of membrane control systems, and the ubiquitin protein labeling system. Bacteria gave rise to enzymes that metabolize sugars, lipids, and partly sterols, oxygen-protecting systems, as well as all kinds of signaling and regulatory proteins (1, 2).

These events coincided with the outbreak of the intron invasion (9). It became necessary to create a spliceosomal apparatus, spatial separation of transcription from translation. Nuclear pores and extracellular translation made this possible. The imported genes posed a potential hazard to the host cells. For the latter, it was beneficial to transfer the translation of not only viral RNA but also newly acquired genes outside the cell into the intercellular space.

In the new realities, it was beneficial for bacteria to transfer control of genetic processes to smarter cells. The genomes of ectobionts were gradually transferred to the archaea. After their translation into the intercellular space of the archaean-bacterial chimera, the synthesized complex proteins and macromolecules returned back inside the ectobiont cells with the help of membrane transport. This stimulated the development of the membrane transport system. With the acquisition of phagocytosis, vacuoles, lysosomes and other organelles had involved in the transport of substances (19).

Subsequently, the host cell used this method of getting rid of alien and invalid genetic information in relation to the ectobionts genes that were transferred in them and gradually completely transferred the translation of all genes into the interectobiont space using nuclear-like pores. Such a redistribution of functions was safer for the host and ectobionts; they were not directly affected by the waste products of neighboring cells. This stimulated the emergence of a single supercell with a consolidated genome, a single common outer membrane, and a biochemical apparatus.

The dynamics of exosymbiogenesis looked like this: ectoparasitism - commensalism - symbiosis. On this path, the first task was to minimize and then completely neutralize the negative consequences of cooperation between the host cell and ectobionts. To do this, the host archaea used the ubiquitination system they already had, RNA interference and DNA interference. Pathogenic proteins and RNA that came from ectobionts into the host cell underwent ubiquitination and RNA interference, which ensured the elimination of harmful factors (20, 21). The same systems provided ectobionts with similar protection against viruses and the negative consequences of cohabitation with archaea. This forced host cells to develop complex systems for ubiquitination and RNA quality control (22, 23, 24, 25). Consequently, in the process of natural selection, genetic and metabolic mutual adaptation the conformation of host cells and ectobionts took place. Genetic information has become useful for the entire cellular community of host archaea and ectobiont bacteria.

Gradually, all the DNA of viruses and ectobionts consolidated in the archaea cell. Bacteria have lost their DNA, from which the membranes of ectobiont cell symplasts remain in the form of deflated vesicles and cisterns, where biochemical reactions have moved. Thus, the cell nucleus surrounded by a nuclear membrane has gradually formed from the archaeal host cell, and the endoplasmic reticulum from enucleated cells free of DNA - symplasts of bacterial and archaeal ectobionts. The intercellular space was transformed into the cytoplasm of eukaryocytes.

Whole genomes of ectobionts could ended up in the host cell. It was the prototype of sexual reproduction and hybridization. Onced in the host archaea, the genetic information was anaiased and then either integrated into the host genome or continued to function separately as an independent chromosome 13, 14, 15, 16.

The size of prokaryocytes is approximately 10 times smaller than that of eukaryocytes. This means that the latter's volume is three orders of magnitude larger. Consequently, dozens of different ectobiont cells could simultaneously parasitize archaeal cells, from which the hosts could adopt various innovations. In modern bacterial communities, there are examples of close cohabitation of archaea with bacteria. For example, in areas of black smokers, methane-oxidizing archaea and sulfate-reducing bacteria live in close symbiosis, and electrons are exchanged between them using iron compounds. So the archaeal ancestor of eukaryotes could also live in close symbiosis with some bacteria. According to the most popular version, it was a methanogen [1], and the anaerobic fermenters methanotrophs, which populated the surface of the host archaea, could become a symbiont.

The vast majority of methanotrophs are immobile cocci or spherical microbes [26]. These are unique protein factories with a very high yield. They made up the first layer, the inner sphere of the cell complex, where the center of the complex was the archaea methanogen. Obviously, after the microbes were deflated, cocci and spherical microbes took the form of deflated vesicles and cisterns.

At the next stage of eukaryogenesis, the second layer of the cell complex, the outer sphere, was occupied by microbes with a more efficient energy system, anaerobic respiration, and various biochemical systems. Comparative genomic analysis indicates that all eukaryotic glycolysis enzymes are most similar to proteins of fermenting bacteria of the genus Clostridium. Hopanoids - sterols of bacterial origin - from the bacteria Streptomyces or actinomycetes, and tubulins are borrowed from Thaumarchaeot or Prosthecobfcteria.

Actinomycetes have the ability to form branching mycelium. In the affected tissues (tissue form), actinomycetes form clusters of intertwined threads with flask-shaped thickenings at the ends [26].

With the exception of C. perfringens, Clostridium species have peritrichous flagella that allow organisms to move. [26]. It has been shown that Geobacter sulfurreducens can synthesize various hopanols under severely anaerobic conditions [27]. Geobacter sulfurreducens is a gram-negative metal- and sulfur-reducing proteobacterium. Rod-shaped, obligately anaerobic, non-fermenting microbe, has a type IV flagellum and fimbria, a close relative of Geobacter metallireducens.

Tubulins, which are components of microtubules, have long been thought to be exclusive to eukaryotes. However, it has recently been shown that Prosthecobacter, a representative of proteobacteria, has tubulin-like genes [28].

Most bacteria have a homologous FtsZ structure. An exception is Prosthecobacter, which contains genes that have higher sequence homology to eukaryotic tubulin than FtsZ. These genes are called bacterial tubulin a (BtubA) and bacterial tubulin b (BtubB).

Prosthecobacter fusiformis is morphologically similar to caulobacteria. The results of the phylogenetic analysis placed spindle-shaped caulobacteria in a subdivision of bacteria that are closely related to the Planctomyces-Chlamydia group [29]. The morphology of prostecobacteria is filamentous or spiny. Prostecobacteria have superficial outgrowths. In some species they are long, and have a tubular shape, in others they are short. Some species have flagella or filament bundles [30]. Sometimes cells with appendages are combined into so-called rosettes due to the adhesion of their stalks.

As can be seen, all ectocells of the second layer of the bacterial complex had branched, tubular structures - flagella, micelles, fimbriae, pili, secretion systems, prosthecae (appendages). The similar tubular, branched morphology suggests that the smooth endoplasmic reticulum is a descendant of these bacteria.

After the elimination of the genome and the transfer of protein translation into the intercellular space, the spherical microbes that make up the first layer of the cell consortium took the form of deflated vesicles and cisterns and created a rough EPR, and pili fimbriae, prosthecae and other tubular structures that microbes had in the outer sphere turned into a smooth EPR. Here one can see the connection between bacterial secretory systems and the secretory function of the smooth ER of many eukaryotic cells.

At the third stage, alpha proteobacteria from which eubacteria acquired mitochondria and a way of aerobic respiration joined in. They occupied the third orbit of the complex.

Intron infection contributed to the formation of eukaryocytes. Under these conditions, representatives of all layers of the complex were forced to transfer their genomic apparatus to the smarter archaean cell, which by that time already had a spliceosomal apparatus and extracellular translation of proteins.

All of the above can be visually conveyed with the help of drawings. The cell consortium consists of the host archaea, a complex-forming center, around which cells are located - "ligands", presented in the form of bacteria and archaea (Fig. 1),

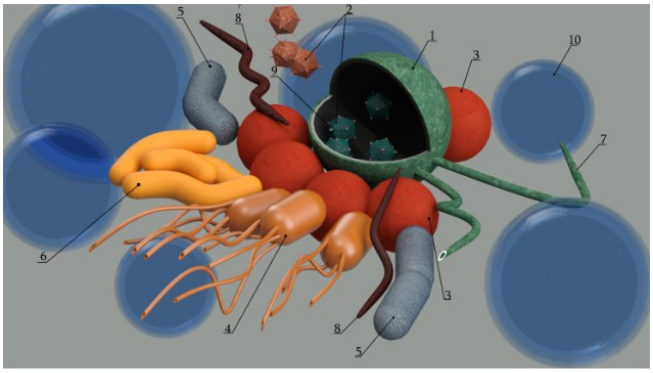

Fig. 1

Fig. 1 depicts the microbial consortium before eukaryogenesis: 1. Archaeon 2. Gigant viruses 3. Microbes of the spheroid and ovoid form 4. Lophotrichous bacteria (Prosthecobacteria, Clostridia) 5. Alphaproteobacteria 6. Sulfur bacteria 7. Archaella 8. Spirilla and spirochetes 9. Nuclear-like pores of viruses 10. Bacteria and archaea are located at the outermost periphery of the microbial consortium.

some of which had flagella (lophotrichous, peritrichous) or pili, fimbriae, prosthecae. The next row is alpha-proteobacteria. Bacteria and archaea are located on the extreme orbit, which, as it were, limit the outer perimeter of the consortium. (Picture 1). The entire structure was reinforced with outgrowths, cilia, and flagella of the archaeal hosts and other members of the consortium.

Subsequently, through evolutionary transformations, a single cell arose from a consortium of cells - a eukaryocyte. The central cell transformed into the nucleus of the cell, and the exocells lost their genome, deflated and turned into a rough endoplasmic reticulum. The smooth network arose from flagella or fimbriae, prosthecae of bacteria and spirilla (spirochetes) by expanding the lumen of the flagella. Cells located on the edge of the consortium, which had flagella after mutual fusion (or incomplete division) have created a single space that limited the outer perimeter of a single supercell, pierced by intracellular tubules. A complex of the nucleus, enucleated exocells and descendants of alpha-proteobacteria plunged into this space. The emerging space turned into hyaloplasm (Fig. 2).

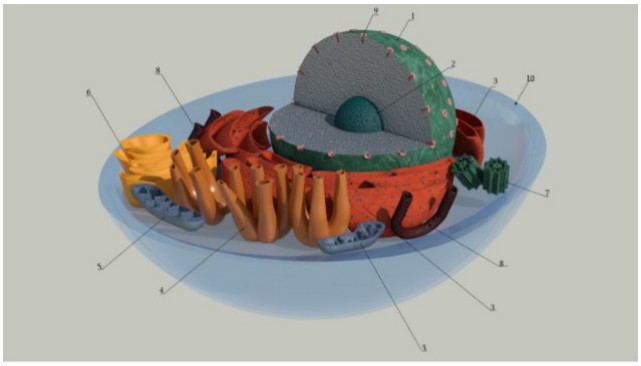

Fig. 2

Fig. 2 depicts a microbial consortium transformed into one unitary cell as a result of eukaryogenesis: 1. Nucleus - transformed host archaeon 2. Nucleolus 3. Rough endoplasmic reticulum after spheroidal bacteria deflated 4. Smooth reticulum formed by transformation of bacterial flagella, prosthecs, pilli 5. Mitochondria 6. Golgi apparatus - deflated sulfur bacteria 7. Centrioles - transformed archaella 8. Smooth reticulum formed by transformation of spirilla and spirochetes 9. Nuclear pores formed from nuclear-like pores of viruses and the bacterial secretion systems 10. Hyaloplasm - the former intercellular space.

Thus, the nucleus and endoplasmic reticulum arose from archaean-bacterial chimeras. Compartmentalization of eukaryotic cells is a consequence of exosymbiosis rather than endosymbiosis. According to this scenario, it is possible to restore the origin of individual eukaryocyte organelles:

Golgi apparatus (GA) - its main functions are sulfation of carbohydrate and protein components of glycoproteins and glycolipids, as well as protein proteolysis. It can be assumed that the precursors of GA were sulfur bacteria, chemosynthetic bacteria that live near black smokers. Before the advent of GA, sulfur bacteria coexisted in archaea-bacterial chimeras as ectobionts. During eukaryogenesis, the sulfur bacteria genome was transferred into the host archaea cell. Symplasts of sulfur bacteria that lost their genome had taken the form of cisterns and vacuoles. They have started specific biochemical reactions.

Centrioles and centromeres - centrioles are similar in structure to flagella and, apparently, are rudiments of the host cell archellum. Since there are two centrioles, the host archaea must also have had two archellum. As can be seen, the hosts of archaea used flagella not only for locomotion, obtaining food, or escaping from predators and toxic environments, but also for separating two daughter cells. Separation of two host cells inhabited by ectobionts and cellular symplasts would be difficult without the mechanical assistance of flagella. In eukaryogenesis, the archaeal cell membrane evolved into a nuclear membrane, and the flagella evolved into centrioles.

Mitosis - In eukaryogenesis, the amount of genetic information had progressively increased. The number of chromosomes had increased. At first, the chromosomes could remain circular, attached to the inner surface of the cell membrane of the archaeal hosts. Subsequently, after the transformation of host cells into the nucleus of eukaryocytes, the sites of attachment of chromosomes to the archaeal membrane turned into centromeres. Each centromere was attached to its own segment of the cell membrane. Subsequently, the membrane segments had been reduced into filaments of the mitotic spindle. Like the division of prokaryotes, when the flagella pull their half of the cell membrane towards themselves, so the centrioles - the rudiments of the flagella perform the same function through the mitotic spindle. However, the exact separation of genetic information under conditions of plurality of chromosomes by the previous method was impossible. The cyclic shape of chromosomes made it difficult to accurately and unhindered division of genetic information using mitotic threads. During mitosis, circular chromosomes and threads could intertwine with each other. Therefore, the chro-

mosomes acquired a linear shape.

Pseudogenes that do not code for repetitive genetic elements: Whole genomes of ectobionts had entered the host cell. It was the prototype of sexual reproduction. Obviously, most of the non-coding DNA is remnants, "fragments" of the genomes of former ectobionts. Given that most of the genome is made up of non-coding DNA, it is clear that effective validation of DNA needs successful correction of foreign DNA. The essence of this mechanism is not yet clear. If individual NPR compartments are vestiges of former exocells, and noncoding DNAs are their former genomes that ended up in the host cell, then the function of noncoding DNAs may be to regulate compartment-specific transport and translation.

Mitochondria: considered as later acquisitions. They were acquired after the creation of the nuclear-reticular complex and were exoparasites. They ended up inside the cell before the completion of the construction of the outer membrane of the eukaryocyte, after the latter acquired phagocytosis.

Compartmentalization of eukaryotic cells is a consequence of ectoparasitism rather than endosymbiosis. Cellular infection has played a critical role in eukaryogenesis.

Progressive evolution is a long process of adaptation of living organisms to new, often harmful, conditions of existence 10, 11, 12, 13. In the process of natural selection, pathomorphological changes acquire an expedient, adaptive character due to the complication of the structure, increasing the organizational level of organisms. In fact, the ultimate goal of progressive evolution is the adaptation of newly formed phyla to new conditions of existence by evolutionary sanogenesis. 10, 11, 12, 13.

The exobiogenetic model, in addition to helping to better understand the structure and details of the biochemistry of eukaryocytes, leads to a number of important conclusions: 1. Like eukaryogenesis, exobiogenesis (ectoparasitism) must play an important role in the origin and evolution of multicellular organisms. 2. Confirms the important role of pathology in the progressive evolution of living forms.

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