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Membrane heredity composed by symbiogenesis

Javeed Hussain, Guangxiao Yang, Guangyuan He

College of Life Science and Technology, Huazhong University of Science and Technology (HUST), Wuhan, China

Email address:
javed_choudary@msn.com (J. Hussain), ygx@hust.edu.cn (Guangxiao Yang), hegy@hust.edu.cn (Guangyuan He)

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Abstract: Symbiogenesis overshadows the importance of other eukaryogenetic processes. By working on the endosymbiotic cellular heredity in its entirety, it transformed the eukaryotic world. This mini-review strived to produce a concise account of symbiogenetic heredity of membranes in eukaryotes. Symbiogenesis integrated the endosymbiotic alpha-proteobacterium and cyanobacterium with the host, by utilising almost all the major prokaryotic components of membranes and protein translocation machinery along with a lot of eukaryotic inventions. It beautifully compartmentalized the eukaryotic cell by putting the prokaryotic membranes in continuity with the eukaryotic membranes and produced a whole spectrum of membrane topologies. Topogenesis of symbiogenetic hereditary membranes produced cell organelles with a diversity of metabolic capabilities. Development of protein translocation system manifests real ingenuity of symbiogenetic processes which integrates the working of entire compliment of cellular organelles. Protein translocation systems are also chimera of prokaryotic and eukaryotic components.

Keywords: Membrane Heredity, Symbiogenesis of Mitochondria, Symbiogenesis of Plastids, Membrane Chimera, Membrane Topology, Protein Import, Protein Translocation, Endosymbiosis

1. From Prokaryotes to Eukaryotes to Symbiosis

The living world produced two major kinds of cells: bacteria and eukaryotes. Bacteria appear on the evolutionary timescale around 3.5 billion years ago. The evolutionary timescale shows the birth of eukaryotes near to 1 billion years old [1]. Around 60 major innovations qualified the bacteria to enter into the eukaryotic world. These innovations supported three major realms of change: (1) the eukaryotic cell materialised the cytoskeleton and endomembrane system in coordination with the evolution of phagotrophy; (2) DNA-membrane attachments when internalised through phagocytosis, disrupted bacterial division; which resulted in the evolution of nucleus and mitotic cell division; (3) perfection of phagotrophy opened the doors for another important biological process 'symbiogenesis' [1].

The prokaryotic world does not support the intracellular symbiosis [2, 3]. On the evolutionary timescale, it emerged with the materialisation of phagocytosis by radically remodelling a bacterium. When radically transformed, that remodelled bacterium possessed complex internal cell membranes, endoplasmic reticulum (ER), endosomes, and lysosomes [1,4-6]. This architecture was required to support phagotrophy in the ancestral eukaryotes. Phagotrophy created possibilities of symbiosis between ancestral eukaryotic cells and prokaryotic world.

Symbiogenetic processes selected only few of symbiotic consortia and transformed the eukaryotic world. It also set the stage for the evolution of intracellular digestion of the prey, which actually expanded the adaptive zone for the organisms. The evolution of phagotrophic complement 'actomyosin motility system' provided enough support to the intracellular digestion to materialise the ingestion of whole prey [1]. In the eukaryotic evolution, this strip of timescale produced the most wide-ranging innovations in protein molecular machineries [1,2,5,7].

2. Symbiosis to Symbiogenesis

In context of phagocytosis, there are few unprecedented developments on the evolutionary timescale. First is the emergence of intracellular symbiosis between ancestral phagotrophic eukaryotes and the prokaryotic world, in spite of the presence of an operational intracellular digestion of the prokaryotic prey. Second development is the transformation of symbiosis into symbiogenesis. Symbiogenetic processes worked on few stable symbiotic consortia of ancestral eukaryotes and prokaryotic

symbionts and produced stunning diversity of eukaryotic life on Earth.

Symbiogenetic processes orchestrated the cellular heredity in its entirety. It produced stable mergers of the DNA, membranes, ribosomes etc. from two distinct cellular worlds. This mini-review focuses on one aspect of symbiogenetic inheritance: membrane heredity.

3. Symbiogenesis of Two Major Symbiotic Consortia

Symbiogenetic evolutionary timescale shows major activity on a symbiogenetic consortium between an α-proteobacterium and phagotrophic ancestral eukaryote [8-10]. Here symbiogenesis integrated the bacterial respiration with the eukaryotic cell. It converted the endosymbiont into an operational organelle: mitochondria. This integration involved grand but heritable changes in the components of membranes and DNA compliment.

Around 500 million years later, another important symbiogenesis is spotted on the evolutionary timescale. Here symbiogenetic processes worked on a symbiotic consortium between a mitochondriate host and cyanobacterial symbiont [11-13]. Photosynthetic symbiont was permanently integrated with the heterotrophic host as plastid.

There are innumerable interesting aspects of symbiogenesis. To name a few for instance: transfer of some of the genome of endosymbionts into the host nucleus and loss of most of the remaining genome; reconfiguration of endosymbiont membranes to retarget the nuclear encoded proteins; invention of the protein translocation machinery to transport the proteins across the membranes of endosymbiont.

Therefore symbiogenesis is a grand process which deals with not just the addition of an extra foreign genome to a pre-existing cell, but it also integrates and establishes the inheritance of host and endosymbiont membranes. Along with it, it also materialised operational protein-targeting systems for the endosymbionts turned organelles [14,15]. This mini-review gives a concise account of symbiogenetic membrane topogenesis and heredity with only necessary details of symbiogenetic accomplishments in protein translocation.

4. Cellular Hereditary Matrix and Symbiogenesis

Life cycle of a eukaryotic cell passes through a complex matrix of independent hereditary processes which sustain a dynamic molecular cellular architecture within the fluidity of molecular world. This hereditary matrix operates the gene heredity in conformity with the membrane heredity. It manufactures molecular components of membranes and inserts them into continuously pre-existing supramolecular structures [16]. Each genetic membrane type has a distinct composition of molecular components which include the proteins and lipids, which is marvellously maintained during growth.

Membrane heredity is associated with DNA heredity up to the extent that the properties of receptors and targeted proteins are encoded by genes. Although this is essential but it is not sufficient without the preformed cell structures [16,17]. Membrane operations require distinct membrane topology with unique receptors in the correct polarity [15,18,19], which a cell cannot create de novo in spite of possessing all the respective genes [20].

Symbiogenetic processes not only preserved the hereditary wealth of prokaryotic genetics in its entirety but also recombined and augmented it. Symbiogenesis constructed endomembrane system from the components borrowed from prokaryotic inheritance and some eukaryotic inventions [14,15,18]. Symbiogenetic processes conserved prokaryotic membrane constructs for over hundreds of millions of years. Membranes of thylakoids are genetic membranes and also possess distinct topology. Thylakoids in plastids and cyanobacteria mostly contain glycolipids and sulpholipids, not phospholipids [16]. They actually evolved directly from those of a cyanobacterium, and symbiogenetic processes did not change their topology, chemistry, or function [21]. Retention of membrane heredity for hundreds of millions of years, even after the loss or relocation of genes from the respective organelles emphasizes the immense stability of membrane heredity [16].

Cellular world cannot produce two supramolecular structures membranes and chromosomes *de novo* from their constituent components. They are always constructed by division and growth or fusion of pre-existing membranes. Interestingly, all the diverse membranes of the millions of living species are actually lineal descendants of those of the first bacterial cell [18-20].

There are numerous distinct types of membranes in a eukaryotic cell. DNA replication proceeds on the pre-existing DNA template. Likewise, membrane growth (polarity of molecular assemblies, their location in the supramolecular matrix etc.) depends entirely on the pre-existing membranes [16]. Purely genetic membranes, like the nuclear envelope/RER membranes or mitochondrial inner or outer membranes, always arise by growth and division of already existing membranes [18]. Some membranes, for example, lysosomal membranes do not possess this genetic continuity. Like DNA genomes, genetic membranes are also a part of an organism's germ line [16].

5. Membranes Orchestrated the Protein Code at the Early Stages of Evolution

It is argued that at early stages of evolution, membranes had been orchestrating important functions. If we look at the level of complexity of protein synthesis machinery, then it seems impossible that it evolved before membranes. Most of the scientists think that this function had been performed by the membranes, replicators, and catalysts, in a symbiotic consortium. This symbiotic consortium set the stage for the origin of code and thereby mediated the

transition from molecular world of independent replicators to a nucleic acid/protein/lipid world of reproducing organisms [22].

Membranes initially worked as functional supramolecular bases. Evolutionary processes selected this supramolecular structure as a grand reproductive unit or the proto-organism. It is argued that what proteins now accomplish as enzymes, it had been achieved primarily through their structures while held within the membranes. Membranes as biological supramolecular structures contained amphipathic peptidyl-tRNAs and prebiotic mixed lipids. Biological membranes accomplished the respective work from the peptidyl-tRNAs by bringing their polarity and affinity for water in a specific range. Peptidyl-tRNAs worked as genetically-specified lipid analogues [22].

Here proteins were also engaged in coupling the flow of energy with the phosphorylation of genes and peptide precursors, through the kinases anchored in the membrane. All these processes actually operated on the outer surface of an 'inside out-cell', which materialised a hydrophobic code with four prebiotic amino acids and proline. It actualised initiation by isoleucine anticodon CAU. Supramolecular membrane structures anchored all the necessary proteins and nucleozymes. Working on four amino acids code slowly upgraded to ten-acid doublet code by evolving hydrophobic substrate binding and addition of catalytic domains and signal peptides. It also improved replication, translation, and lithophosphorylations. It also set the stage for this supramolecular setup to go for parasitism, and predation [22].

At this stage on the evolutionary timescale, Cavalier-Smith [22] proposes the fusion of two 'inside out-cell', actually produced a protocell, which consisted of double envelope, protocytosol, internal genome and ribosomes, and periplasm. It contained a concentrated autocatalytic internal cytosolic soup, which could support an intermediary metabolism. These conditions yielded 12 new amino acid assignments, termination, rapid freezing of the 22-acid code, and consequently recruitment of anticodons. Here we see the materialisation of photoreduction, CO_2 fixation, and lipid synthesis prior to photophosphorylation.

Here this fusion infused the evolution of signal recognition particles, chaperones, compartmented proteases, and peptidoglycan before transforming into a complex autotrophic, anaerobic photosynthetic bacterium [22]. Prokaryotic world actualised photosynthesis at this stage on the evolutionary timescale. All this work strictly depended on the attributes of membranes like molecular composition, localisation, and polarity. Symbiogenetic processes preserved these attributes and set the cell-division processes in such a way as to ensure the inheritance of membranes in the entirety of their functions.

6. Translocation

One of the important aspects of membranes is convening the molecular traffic across the cellular compartments. Complexity of translocation machinery depends on the complexity of respective membrane topology. Plasma membrane in all eukaryotic cells is single. However, α-proteobacteria (ancestors of mitochondria) and cyanobacteria (plastid ancestors) have a cell envelope which consists of an inner cytoplasmic membrane (CM) and an outer membrane (OM) [7]. The CM and OM are distinct in both architecture and chemistry. In both organelles (plastid and mitochondrium), symbiogenetic processes converted the prokaryotic CM and OM into double envelopes while the phagosomal membranes were removed [23,24].

Symbiogenesis re-situated a lot of endosymbionts' genes into the host nucleus, but no big change in working location of proteins and lipids [25]. Organelles have to import thousands of nuclear encoded proteins from cytosol [26,27], which is materialised with the help of symbiogenetic protein translocation systems [28]. Symbiogenetic configuration of mitochondria and plastids produced numerous morphologies with diverse metabolic abilities [29]. It materialised non-photosynthetic potentials in some plastids, for instance, isoprenoid synthesis, fatty acid synthesis, and heme synthesis [30,31].

Protein import mechanisms and membrane topology divide plastids into three major groups [32]: (i) Plastids in biliphytes and Viridaeplantae [32] are situated in the cytosol and covered with a double-membraned envelope. These plastids originated directly from a cyanobacterium [23] and import of nuclear encoded proteins requires only transit sequences [33-35]; (ii) Secondary chromist plastids are situated in the lumen of rough endoplasmic reticulum (RER). To materialise the transportation of proteins both signal and transit sequences are needed [15,36,37]; (iii) Symbiogenesis materialised the most complex topogenesis in chlorarachnean plastids. These plastids are surrounded by two additional smooth membranes.

Ancestral chlorarachnean acquired six distinct genetic membranes directly from a green alga. The sixth genetic membrane was actually produced by modification of the host phagosomal membrane [16]. Secondary plastids in chromists also consist of four membranes [14,15,37]. Primary plastids reside in the cytoplasm, whereas secondary plastids are situated within the lumen of the endomembrane system [38]. Here, installing and/or reconfiguring the protein import apparatus across four membranes was even more difficult [39-41]. But symbiogenetic processes succeeded in establishing the transport of nuclear encoded proteins in these plastids [42-48] by orchestrating a chimera of host and symbiont protein components [49-51].

Symbiogenesis bestowed a great push to the eukaryotic evolution. Incorporation of plastid with the cellular metabolism produced three eukaryotic lineages of plants. Plants that diverged from these lineages, at around 400 to 475 million years ago on the evolutionary timescale [52], consequently settled on the terrestrial environment. It paved the way for animals to populate the terrestrial lands.

6.1. Eukaryotic Protein Translocation Processes

Deeper study of the important eukaryotic protein translocation machineries reveals the real ingenuity of symbiogenetic processes. It either directly employed prokaryotic inventions or combined them with some eukaryotic traits and produced chimera of molecular assemblies [53-55]. There are three important eukaryotic protein translocation molecular assemblies in eukaryotes: (i) the ER-associated degradation (ERAD) transport machinery of the endoplasmic reticulum, (ii) the peroxisomal importomer and (iii) SELMA, the pre-protein translocator of complex plastids. Outwardly, they appear quite different. But in the mechanism of their operations, they actually show close similarity, which indicates a common ancestor. Phylogenetic analyses also support their common ancestry. It shows that evolutionary forces effectively recycled the pre-existing components [41,56,57].

Materialisation of these translocation machineries actually supported the compartmentalisation in the eukaryotic cells, which allowed the separation of complex metabolic processes [58]. Symbiogenetic processes played the most important role in assembling, and situating operational molecular translocation assemblies and subsequently compartmentalising the eukaryotic cell [7,30,58-60].

ERAD translocation molecular assembly exports misfolded proteins from the ER lumen into the cytosol, where they are degraded by the proteasome [61,62]. All essential components of this system have been found to be the chimera of the host and red algal endosymbiont [57,63-65].

Peroxisomes are present in most eukaryotes and involved in various oxidative reactions [66]. Transport across the peroxisomal membrane into the matrix is facilitated by the so-called peroxisomal importomer [67-69]. SELMA is pre-protein translocation molecular assembly which is present in secondary plastids and involved in the translocation of nucleus-encoded plastid proteins across the second outermost membrane of complex plastids in cryptophytes, haptophytes, heterokontophytes, and some apicomplexans [36,57,58,70-72].

The above three protein translocation machineries share some interesting similarities at the level of mechanism. Each involves ubiquitination of transport intermediates by specific enzymes and subsequent extraction by AAA-ATPases. Their proteins also share a conserved domain structure. These evidences suggest a common origin for all three translocation molecular systems [58]. Phylogenetic analyses also support it [65,69,73]. In knitting together the transport infrastructure and processes for the compartments of eukaryotic cell, symbiogenesis not only recycled the pre-existing components of transport systems but also it employed the prokaryotic mechanisms [58]. Translocation apparatus also triggered rearrangement in the DNA hereditary archives i.e. the transfer of symbiotic genes into the host nucleus [23].

7. Conclusions

It is argued that life stepped into the real cellular world by the fusion of two cup shaped ‘inside out ancestral cells’ which produced a protocell. In the initial stages of cellular evolution, membrane played important role in hosting the symbiosis among the biomolecules in this protocell. Here membrane materialised supramolecular assemblies of biomolecules which could perform important functions for the cell. Evolutionary forces selected the inheritance of important formations of membranes. Membrane heredity actually precedes the DNA heredity [22,74,75].

Complex molecular assemblies of biomolecules in the membrane engaged in evolution of efficient digestive processes in the protocells. Perfection in the inheritance of membranes and efficient metabolic processes gave rise to the prokaryotic world. With the rearrangement and inventions of proteins, prokaryotic world materialised the machinery for photosynthesis. Photosynthesis emerges on the evolutionary timescale at around 2.5 billion years ago [30,76].

Radical changes in a bacterium set the course for the evolution of eukaryotes. Perfection in phagotrophy amplified the pace of eukaryogenesis. Phagocytosis opened the possibilities for symbiosis. Symbiosis opened the doors for symbiogenesis. Evolutionary timescale highlights the working of symbiogenesis of mitochondria from a stable endosymbiotic consortium of an alpha-proteobacterium and phagotrophic ancestral eukaryote around 1.5-2 billion years ago. It materialised an efficient aerobic metabolism in the autotrophic eukaryotic world [77].

Around half a billion years later, another symbiogenesis selected an endosymbiotic consortium between endosymbiotic cyanobacterium and a mitochondriate host. Here the eukaryotic world stepped into autotrophic realm. One interesting feature of symbiogenesis is that it preserved cellular heredity in its entirety. This mini-review focused on some salient features of symbiogenetic heredity of membranes in the eukaryotic world. It provided the eukaryotic world with around 13 kinds of genetic membranes [25].

Eukaryotic cell could not sustain this diversity of genetic membranes without the symbiogenetic apparatus for protein import. This translocation machinery is also chimeric from the level of components of molecular assemblies to entire molecular assemblies. Symbiogenesis therefore exquisitely compartmentalised the eukaryotic cell.

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