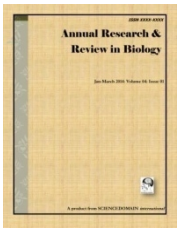

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Symbiogenesis Driven Biogenesis

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Authors' contributions

Collaboration between all authors produced this work. Authors GH and GY conceived the study and author JH wrote the manuscript with significant contribution from other two authors. All authors read and approved the final manuscript.

Review Article

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ABSTRACT

Only seven major endosymbiotic consortia, between the phagotrophic host and respiratory or photosynthetic bacteria, have been identified which were chosen by the processes of symbiogenesis. Symbiogenesis exploited every bit of these consortia and consequently produced a stunning diversity and complexity of eukaryotic life on this planet. Based on an extensive synthesis of literature, this study contemplates the working of symbiogenesis, spanning a time period of around 2 billion years, and its fruits for the eukaryotic world. Endosymbiosis effectively started with perfection in phagotrophy in the ancestors of eukaryotic cells. Phagotrophic internalisation of bacteria produced the chances of endosymbiosis. The rest of the work was accomplished by symbiogenesis. To sustain the respective form of symbiosis, it shuffled, rearranged, and invented new molecular assemblies and remarkably established import and export of proteins across the membranes. This transformation in protein import convened transfer of hereditary information from the symbiont into the host nucleus. Another important role which this process played in the eukaryotic cells is enrichment of cellular heredity in context of membranes. It integrated together the membrane compliments from both members of the endosymbiotic consortia.

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1. INTRODUCTION

One of the major drivers of biodiversity on this planet is the process of symbiogenesis. It transformed the eukaryotic world by working on the entire compliment of endosymbiotic elements, producing complex chimera of molecular assemblies, which we now call cellular organelles including mitochondria and plastids. Symbiogenesis, which worked for more than two billion years on the endosymbiotic consortia [1-3], produced remarkable diversity of life on earth.

One string of symbiogenesis is tied with evolution of mitochondria. It is connected with the endosymbiotic event in which an ancestrally phagotrophic host cell, which already had a nucleus, endomembranes, and endoskeleton [4], incorporated an α-proteobacterium around 1.5-2 billion years ago, close to the time when the nucleus itself originated [5]. Around 500 million years later there was a second significant development: an endosymbiotic relationship between a cyanobacterium, capable of photosynthesis, and a heterotrophic eukaryote [6]. Under the processes of symbiogenesis, these endosymbiotic guests co-evolved with their hosts, lost much of their own identity, and were transformed into organelles: plastids and mitochondria [7,8].

Symbiogenesis simulated grand changes in endosymbiotic consortia. It brought about a large-scale reduction in genomes of symbionts, owing to losses of all the dispensable functions [9] and massive translocation of the hereditary information to the host nucleus [3,7,9-11]. Hundreds of endosymbiont-derived genes are present in the nuclear genomes of endosymbiotic hosts. Organelle genes which changed their compartments not only encode organelle-targeted proteins but others that have evolved non-organelle, host-associated functions [3,10,12].

Organelles are still running the same biochemistry which is supported by several thousand different proteins [13] encoded by the nuclear genome [14]. Respective proteins are translated on cytoplasmic ribosomes and transported to the organelles post-translationally by an outstanding protein import apparatus [15]. Eukaryotic cell owes the invention of this protein-import apparatus to the ingenuity of symbiogenetic processes.

Based on an extensive synthesis of literature, this article strives to highlight the role of symbiogenesis in the biogenesis of unprecedented diversity of the eukaryotic world. When abridged in the form of events, it consists of seven major endosymbiotic events. It has been knitting together the molecular bits from eukaryotic and prokaryotic sources into seamless wholes. This remarkable process has been changing the entire molecular, structural, and compartmental complement of the eukaryotic cell. It has been working on every bit of the endosymbiotic consortia.

2. SYMBIOGENESIS

Symbiogenesis brought about radical changes in the endosymbiotic mergers of two organisms [16]. It changed not only the membranes of the symbionts, but entire protein complexes are converted into the chimeras of host and symbiont polypeptides. In fact, mitochondria and chloroplasts are not bacteria enslaved in eukaryotes, but novel, chimeric

organelles arising from intimate mergers at all scales of two fundamentally different organisms. Symbiogenetic integration involved inserting numerous host molecular assemblies, transferring symbiotic genes into the nucleus, and losing numerous redundant pieces of genetic information from both genomes.

All the above mentioned changes were carried out by evolving a generalized mechanism for inserting proteins made in the host cytosol into and across the organelle envelope [16]. The complexity and corresponding evolutionary difficulty of organelle protein-import in symbiogenesis is entirely unlike intracellular symbiosis, which, after phagocytosis evolved, could evolve extremely easily in eukaryotic cells, yielding ecological innovations like lichens [16].

2.1 Seven Important Endosymbiotic Consortia

Three endosymbiotic consortia are exceptionally important: intracellular enslavement by an early eukaryote of an α-proteobacterium resulting in mitochondria through the processes of symbiogenesis; later symbiogenetic conversion of a cyanobacterium into the first plastid, resulting in the establishment of kingdom Plantae; and secondary endosymbiotic enslavement of a red alga produced more complex membrane topology in the phagophototrophic kingdom Chromista. Two other episodes involved independent acquisition of green-algal plastids by ancestrally phagotrophic lines, producing chlorarachnean algae and euglenophyte algae. Less radically, plastid replacement occurred within dinoflagellate Chromista by two episodes of symbiogeneses: they replaced ancestral peridinin-containing plastids by green algal or haptophyte plastids.

Governed by symbiogenetic processes, these seven mergers were all mediated by the evolution of novel modes of transmembrane protein import into the symbiont. It also simulated massive gene transfer from enslaved cell into the host nuclear genomes [16]. All extant eukaryotes owe their existence to the symbiogenetic incorporation of mitochondria [4,17,18]. Six other symbiogenetic accomplishments made plastids (thus, the plant kingdom) or transferred plastids between distant lines of plants to make diverse algae of amazingly different cell structures [19-21].

3. SYMBIOGENESIS OF MITOCHONDRIA

Mitochondria appear to be the direct descendants of a bacterial endosymbiont that became established in a eukaryotic host cell, approximately 1.5-2 billion years ago [4-6]. Biochemical proof specified resemblance of mitochondria with the α-proteobacteria even before the availability of sequence data. Studies on the molecular SSU rRNA data also suggest a monophyletic source of the mitochondrion that originated from an α-proteobacterial ancestor [22].

Contemporary α-proteobacterium Mesorhizobium loti possesses 7 Mb of DNA. M. loti's chondriome transcribes more than 6,700 proteins [3]. Sequenced mitochondrial genomes transcribe from 3 to 67 proteins [16,23-25]. In some plants e.g. angiosperms, exchange of DNA between the nuclear and mitochondrial genomes occurs relatively frequently [26,27]. Larger chondriomes retain conventional bacterial circularity and genetic codes, whereas smaller ones became linear and DNA minicircles with mild changes in the genetic code [16].

In context of mitochondria, work of symbiogenetic processes for more than 1.5 billion years produced diverse morphologies as well as metabolic capabilities in mitochondria [28]. But in spite of all these genetic, morphological, and functional differences among mitochondria and mitochondria-derived organelles, they share some common attributes. For instance, all of these organelles consist of double membranes and a huge part of their proteome is acquired from the cytosol [29].

Symbiogenesis of mitochondria produced a rich variety of derived organelles. However, it did not incline towards horizontal evolution. It is also not characterised with dead-ends. Ten major groups in eukaryotes from Protozoa, Chromista, Fungi, and animals evolved lineages that became anaerobic or microaerophilic [30,31]. In these organisms, the proteins which were no more useful were lost including the respiratory chain and its IM proteins. They also lost the mitochondrial genomes and ribosomes. But they still keep both the inner and outer membranes and their protein-import apparatus. It shows that mitochondria had acquired functions other than respiration. They are actually still keeping the membrane inherited from the symbiont. Some eukaryotes modified their mitochondria in such a way as they are a mix of aerobic and anaerobic functions [32,33]. In protists genomeless anaerobic mitochondria either work as large hydrogenosomes [34] or tiny mitosomes [35].

4. SYMBIOGENESIS OF PLASTIDS

Assimilation of oxygen in the atmosphere that started approximately 2.7 billion years ago coincides with the coming into being of cyanobacteria. They could use electrons from the water molecule with the help of two photosystems [15,36]. With the evolution of phagocytosis in eukaryotes, around one billion years later an endosymbiotic association between a photosynthetic cyanobacterium and a heterotrophic eukaryote [4,6], set the stage for the evolution of plastid. When this endosymbiont was gradually put to the processes of symbiogenesis, it evolved to become a bona-fide organelle. It lost most of the cyanobacterial genes which were not important for the maintenance and division of the symbiont [37].

Multiple episodes of eukaryote-eukaryote endosymbioses in combination with the processes of symbiogenesis produced a tangled web of plastid-bearing lineages [19]. Symbiogenesis driven biogenesis produced three eukaryotic lineages: the Chloroplastida (green algae and land-plants), the Rhodophyceae, and the Glaucophyta [38]. Plants, that probably departed from their green algal lines around 400 to 475 million years ago [39], consequently inhabited the terrestrial environments. Plants' occupation of terrestrial lands also paved the way for the arrival of terrestrial animals on land.

4.1Symbiogenesis of Secondary Plastids

Many algal lines obtained their plastids through secondary endosymbiosis. This episode starts with the uptake and retention of an algal cell, containing primary plastid, by another eukaryotic lineage [15,40,41]. The algal cells were probably internalised through phagocytosis, by other non-photosynthetic eukaryotes. Secondary episode of endosymbiosis, when passed through the processes of symbiogenesis, produced a rich diversity of secondary endosymbiosis lines with derived plastids [42]. All plastids produced by this episode are surrounded by more than two membranes. Altogether, this secondary spread of plastids had a major impression on the entire eukaryotic world in context of variety, evolution, and global ecology [37].

Belonging to the non-photosynthetic group Rhizaria, chlorarachniophytes still keep the nucleus of the enslaved alga which is also called as nucleomorph [43]. The nucleomorph genome from one of the chlorarachniophytes (Bigellowiella natans) has been sequenced [44]. The nucleomorph genome retains a different set of genes, obviously associated with the nuclear genes of green algae, which affirms the involvement of a different secondary endosymbiosis [38].

4.1.1 Chromist secondary plastids

Most chromist lineages did not evolve cell walls and retained phagotrophy. In all chromist plastids except dinoflagellates, the stroma is separated from the cytosol by four chemically distinct membranes [45]. This extremely complex membrane topology is associated with the endosymbiotic event, when a biciliate host bearing cortical alveoli endosybiotically enslaved a unicellular red alga [46-50]. It converted the algal plasma membrane into the periplasmic membrane (PPM) by inserting duplicates of endoplasmic reticulum (ER) proteins that originally established the protein-extrusion machinery [ER-associated protein degradation (ERAD)]. This duplicated protein-extrusion machinery (ERAD), when relocated to the periplasmic membrane, it started working as novel protein-import channels and receptors. It established the export of chloroplast proteins from the ER lumen across the PPM [51-53].

Once evolved through the processes of symbiogenesis, PPM-ERAD could differentiate plastid-destined proteins from secretory ones. Closely related ERAD-PPM importers are found in all four major groups of photosynthetic chromists (Myzozoa, Ochrophyta, Haptophyta, Cryptophyceae) [54,55]. It supports the assumption that all chromist plastids evolved from one symbiogenetic enslavement of a red alga.

4.1.2. Multiple secondary endosymbioses

Multiple episodes of secondary endosymbioses occurred because there is evidence for both green and red algal enslavement [43,56,57]. In the case of green algal symbionts, two lineages with green secondary plastids (euglenids and the chlorarachniophytes) acquired secondary plastids independently [58]. Phylogenetic trees based on whole plastomes also show that they are not specifically related within the green algae [59]. Hosts are also phylogenetically distant [60,61].

Cryptomonads, haptophytes, stramenopiles, and dinoflagellates contain the secondary plastids which originated from red alga. Plastids in these four lineages are also characterized by the unique presence of chlorophyll c [47,62]. Plastids in cryptomonads, haptophytes, and stramenopiles share a common structure with four membranes [21,48]. However, dinoflagellate plastids are bounded by three membranes [63]. The last group which contains a red algal plastid is the apicomplexans. They are obligate intracellular parasites [58].

The cryptomonads and the haptophytes share the presence of a horizontally transferred rpl36 in their plastids. It supports their common ancestry [64-68]. Phylogenetic trees based on whole plastomes have generally put cryptomonads, haptophytes, and stramenopiles together [59, 66, 69]. But alveolates (dinoflagellates and apicomplexans) do not fit into this tree [70-72]. A recent phylogenetic analysis of two dinoflagellate symbionts proves that they are the deep-branching relatives of apicomplexans [73,74]. It puts the alveolate and stramenopile plastids together but fails to unite the chromalveolates as a whole [66]. Computational analyses including rhizarian representatives show a strong relationship with the alveolates and stramenopiles [68,75-79].

4.2 Symbiogenesis of Tertiary and Serial Secondary Plastids

The tertiary episode of endosymbiosis started with the taking up of an alga originated through the secondary endosymbiosis by a eukaryote. Serial secondary endosymbiosis is the substitution of an original complex plastid with a new alga originated through primary endosymbiosis. Dinoflagellates involved in both tertiary and serial secondary endosymbioses. Some of them have a 'tertiary' plastid [43,58,80], and some possess serial secondary plastids [40].

Unambiguous tertiary endosymbiosis is only really known in dinoflagellates lineages, represented by the genera Karenia and Karlodinium. Their ancestor lost its ancestral plastid and acquired a new one from a haptophyte [81]. Dinoflagellates Kryptoperidinium and Durinskia have acquired a plastid from diatoms [82]. Plastids in both lineages are permanent and completely integrated with the host cell cycle, but in this case the diatom still retains its own nucleus and even intact mitochondria [83].

Only one event of serial secondary endosymbiosis is generally recognised in the dinoflagellate genus Lepidodinium. It replaced its ancestral red algal secondary plastid with a green algal one [84]. Lepidodinium's plastome confirms its ancestry from a chlorophyte. Analysis of its nuclear-encoded plastid-targeted proteins reveals that it acquired genes from a variety of sources [85].

Plastid replacement by serial secondary symbiogenesis in meta-algae was mechanistically easier as compared with the secondary plastid acquisition by heterotrophic hosts. It is easier because both host and symbiont already had nuclear genes for import machinery across multiple membranes and nuclear-encoded plastid proteins with suitable topogenic sequences [86-89].

Endosybiogenesis at the level of tertiary plastids also offers two practical advantages. First, because the associations are relatively recent on the evolutionary timescale, therefore fewer clues would have been erased by time. In this context the symbiogenetic processes of integration can also provide invaluable insights [58]. Second, the phylogenetic identities of both hosts and endosymbionts can be easily established [81,82,90].

Evolution of plastid also resulted in an equally rich variety of organelles, but the movement of plastids across the host lineages on several occasions has added other strata of complexity [43]. A broad number of lineages individually reduced their plastids. In these lineages plastids, which also include the parasitic plants and apicomplexan parasites, have lost their photosynthetic competence [20]. Several other protists also abridged their plastids (e.g., the euglenid Astasia and the dinoflagellate Crypthecodinium) [91], and have put them to use in other essential functions for the host cells–for example, isoprenoid synthesis, fatty acid synthesis, and heme synthesis [92].

5. MOLECULAR MACHINERY WHICH ACTUALISED THE SYMBIOGENESIS

The origin of symbiogenetic processes traces back to the evolution of phagocytosis during the origin of eukaryotes by radically modifying a bacterium Fig. 1. Eukaryotes, in fact, were ancestrally phagotrophs. Phagotrophy in eukaryotes was supported by complex internal cell membranes, ER, endosomes, and lysosomes [18,93-95]. The inventions of membrane

budding and fusion actually set the foundations for phagotrophy and the origin of eukaryotic endomembrane systems [93].

All these eukaryotic attributes owe their existence to the extensive concerted innovations in protein domains and molecular machinery since the first bacterial cell took its course to be converted into eukaryotes [93, 95, 96]. In collaboration with the processes of symbiogenesis, phagotrophy makes the foundations of eukaryotic complexity. With the establishment of endomembranes, endoskeleton, and mitosis, it actually revolutionized nuclear genetics Fig. 1 [93,95].

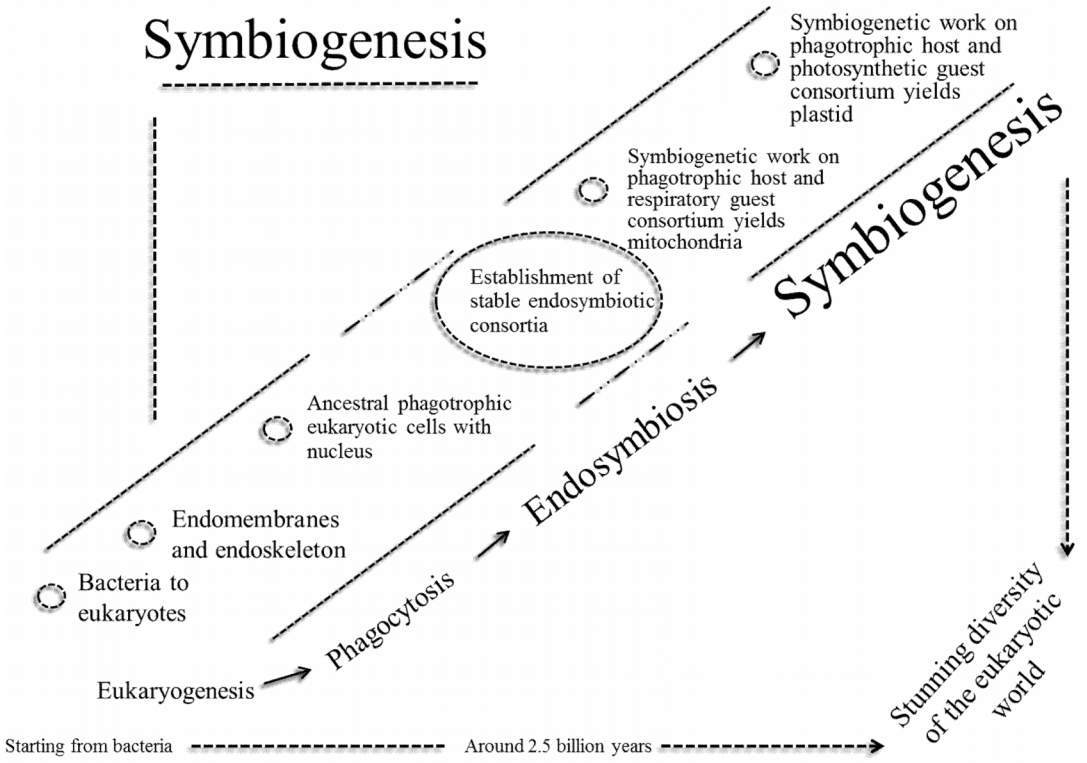

Fig. 1. From phagocytosis to symbiogenesis

Evolution of plastids goes back to the enslavement a cyanobacterium by a phagotrophic biciliate host. The cyanobacterium possessed phycobilisomes on the surface of unstacked thylakoids [46,49]. Here comes into action what the symbiogenetic processes have already produced. The host inserted inner membrane (IM) carriers of likely mitochondrial origin to tap the photosynthesate of symbiotic guest for host use. Through the symbiogenetic processes, the host also evolved chimeric translocator of the outer chloroplast membrane (TOC) protein import machinery. Chimeric in the sense that this protein translocator has an outer membrane (OM) Toc75 protein channel, descended from cyanobacterial Omp85 (a16-strand β-barrel) and a Toc34 transit-peptide receptor of host origin.

In plastids, the inner membrane Tic110 protein channel is host derived [97]. TOC evolution allowed massive transfer of cyanobacterial DNA to the host nucleus. Chloroplasts and thylakoid-bearing cyanobacteria also have extra protein-insertion processes for transporting

proteins into or across thylakoid membranes which are not found in mitochondria and typical negibacteria with only two membranes [98].

6. MEMBRANE HEREDITY AND SYMBIOGENESIS

Symbiogenesis not only adds foreign genomes but also foreign membranes. It makes cells radically more complex by integrating more than one distinct kind of membranes, genomes, and ribosomes in one cell. All these changes increase complexity of the three-dimensional architecture of cell [16]. In symbiogenesis, the heredity of novel membranes arises only from pre-existing membranes. During normal development of an individual organism, genetic membranes grow only from membranes of the same kind. Nevertheless, specific genetic membranes differ from other kinds of genetic membranes in directly inherited composition, polarity, and topology of other cell structures. Specific genetic membranes with all these attributes are inherited directly by preformed cell structures, to a large extent independently of parallel DNA replication [16].

6.1 Symbiogenetic Membrane Chimera and Establishment of Re-import

Cylindrical β-barrel porins perforate the OMs of cyanobacteria and α-proteobacteria. Porins are manufactured in the cytosol and transported across the cytoplasmic membrane (CM) by the signal mechanism. Their insertion into the OM is mediated by Omp85 family proteins. Omp85 have Sam50 homologs in mitochondrial OMs [99]. In bacteria, Omp85 is inserted from within, crossing the CM SecYE channel, then Omp85 which are already there help it into the OM. But after gene transfer to the nucleus, Toc75 which is a chloroplast homolog of Omp85 was inserted from the cytosol, thus inverting its polarity [100]. Sam50 retains its ancestral orientation, nevertheless most of its bacterial accessory periplasmic proteins were replaced by eukaryotic ones on the cytosolic face of the OM [16]. Thus we see that the symbiogenetic processes adapted the similar protein import apparatus in contrasting ways in chloroplasts and mitochondria [101].

Organelle OMs are originally negibacterial and contained β-barrel proteins. By adding the host α-helical proteins, the processes of symbiogenesis made them genuinely chimeric membranes. Symbiogenetic processes also selected lipids from both sources [102]. Over time, insertion of new Omp85s by old Omp85s in every generation has maintained OM identity distinct from the CM for 3.5 billion years [103].

The processes of symbiogenesis wonderfully integrated the pre-formed cell structure (e.g., membrane topology and location of pre-existing elements of the membrane which determine its identity) into the eukaryotic cells. Tremendous increase in the complexity of eukaryotes is the result of eukaryogenesis [93,95,104] and the work of symbiogenetic processes on the successive episodes of endosymbiosis Fig. 1. [4,21,50,96,104].

In primary plastids proteins are usually targeted to 6 regions within the plastids: three membranes as well as three soluble compartments [91]. Symbiogenesis assisted evolution of protein-sorting machinery to identify and transfer nuclear-encoded polypeptides into the organelles actualised this transportation feat [5,7,13,29]. These protein-sorting systems include the Toc and Tic (translocator of the inner chloroplast membrane) protein translocons in present-day plastids [105,106], and the sorting and assembly machinery (SAM), the Tom and Tim23 translocons, the solute carrier Tim22 insertase etc. in present-day organelles [13,14,29,107,108].

The IM of mitochondria is furnished by a family of ~18 carrier proteins [e.g. ATP/ADP carrier (AAC)] for exchanging metabolites with the cytosol [16]. It is asserted that these carriers arose by multiple gene duplications of a single ancestral carrier, probably derived from peroxisomes [93]. A lot of 6-helix carriers in plastids, probably arose from retargeted duplicates of mitochondrial carriers. Currently, these carriers are encoded by the nuclear genome in both organelles [16].

In higher plants, presequences of AAC and animal phosphate and citrate carriers were actually added to boost import efficiency long after these groups departed from other eukaryotes [109]. Some Euglenozoa have only one TIM complex with combined functions of neokaryote Tim22 and Tim23. It also has fewer accessory proteins, and probably represents the ancestral condition [110]. After the ancestral neokaryote diverged from Euglenozoa, it evolved separate Tim8 and Tim13 as well as Tim22 and Tim23 by gene duplications [110]. Recruitment of extra Tom proteins in the import complexes actually increased the efficiency of TOM by easily recognizing the imported proteins through their N-terminal presequences.

Symbiogenetic addition of host proteins to the α-proteobacterial structural core protein import apparatus created integrated chimera [16]. Therefore, symbiogenetic processes set a wonderful precedence of recycling of pre-existing protein trafficking machinery [111]. It takes us to another insight that processes of symbiogenesis do not depend entirely on intracellular gene transfer and gene control [16]. Symbiogenesis actually worked equally well with all the elements of prokaryotic and eukaryotic origin to build chimera of molecular assemblies and processes.

7. COURSE OF PLASTID SYMBIOGENESIS

The above mentioned order of events went through complex processes of symbiogenesis. The processes have been going through innumerable subtle changes and courses. Here, we are going to consider the implications of establishing protein targeting systems before the endosymbiont is permanently integrated with the host [58]. Consider for example that a grazing heterotroph starts to transiently keep the photosynthetic prey before putting them to digestion [112-114]. Over time, with the development of control over the signalling degradation in the host, the retention period might have increased. Symbiogenetic processes indeed played a key role in this context. Symbiogenetic ingenuity produced the chimera of transporters and located them in the prey. It helped the host to extract energy and nutrients from the transient symbiont without digesting it [58].

Establishment of chimeric transporters and their location in the prey also helped to set up a powerful evolutionary ratchet which actualised the acquisition of additional genes from transient symbionts. In other words, targeting protein transporters actually ratcheted the system towards fixation. This cycle would have continued with transient symbionts remaining in the cytoplasm for increasing periods of time before being digested. Over time, the host-encoded genes for symbiont-targeted proteins grew in the nucleus. These symbiogenetic processes ultimately integrated some prey cell with host in such a way that it was never digested and became the bona-fide organelle.

If the symbiogenetic processes, especially in case of plastids, followed this course then it is possible that the genes for plastid-targeted proteins within the nuclear genome of a single cell need not all be derived from the same lineages as the organelles to which they are targeted [115,116]. This is actually the case in most secondary algal lineages [87,117,118].

8. CONCLUSION

Strings of symbiogenesis are tied with seven major endosymbiotic consortia which had been established over the last 2 billion years. It starts with the endosymbiotic enslavement of an α-proteobacterium around 1.5-2 billion years ago by a phagotrophic host Fig. 1. Symbiogenesis produced the chimera of molecular assemblies by taking elements from the host and the endosymbiont and converted the endosymbiotic guest into mitochondria. Unicellular eukaryotes from this line have been phagotrophically engulfing cyanobacteria. These consortia also passed through the work of symbiogenetic processes and ultimately yielded plastid. With the biogenesis of mitochondria and plastids, an extraordinary diversity of life flared up in the eukaryotic world.

All episodes of endosymbioses were actually materialized after the establishment of phagotrophy in the ancestral eukaryotes. And the establishment of protein-import machinery in the endosymbiotic consortia is the real ingenuity of symbiogenetic processes. Symbiogenesis driven evolutionary processes actualised the generalized mechanisms for inserting proteins made in the host cytosol into and across the organelle envelope. Once put into work, this transmembrane protein import system convened a massive gene transfer from enslaved cell into the host nuclear genomes.

Another remarkable feature which the eukaryotic world borrowed from symbiogenesis is the inheritance of foreign membranes and ribosomes. Thus working on every bit of endosymbiotic consortia, symbiogenesis changed the entire molecular, structural, and compartmental complement of the eukaryotic cell. This scale of change in the eukaryotic world would have been impossible by DNA mutation alone.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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