Nucleogenesis and origin of organelles

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SUMMARY

Division of the ancestral prokaryotic pragenome into two circular double-stranded DNA molecules by genetic recombination is a base for the future separate evolution of the nuclear and mitochondrial gene compartment. This suggests monophyletic origin of both mitochondrion and nucleus. Presumed organism which genome undergoes genetic recombination has to be searched among an aerobic, oxygen non-producing archaeon with no rigid cell wall, but a plasma membrane. Plastids evolve from an aerobic, oxygen producing proto-eukaryot, after mitoplastide genome duplication and subsequent functional segregation. In this proposal, origin of eukaryots occurs by a three-step mechanism. First, replication fork pauses and collapses generating a breakage in the genome of archaeal ancestor of eukaryots. Second, the double-strand break can be repaired intergenomically by complementary strands invasion. Third, this duplicated genome can be fissioned into two compartments by reciprocal genetic recombination. Scenario is accomplished by aberrant fission of the inner membrane surrounding separately those two compartments.

Key words: *Recombination, Genetic; Gene Duplication; Eukaryotic Cells; DNA, Archaeal; DNA, Mitochondrial; Plastids; Archaea*

INTRODUCTION

Physical conditions in the prebiotic world conduct inevitable outset and kind of semi-cellular form of life (semi-cellular form of life is a long living autocatalytic set of biotic molecules without genetic material which, involved in cell division, contribute to the cell death). On/in the vicinity of the Earth, there are four principal elements driving biogenesis: (1) land (Fe, S, Ni, Mg, Mn...); (2) water (*particularity*, temperature, pressure); (3) air (N, C, H, O...) and 4. fire (wavelength from the Sun and temperature of the mineral support). In accordance with those four elements, following definition of the origin of life can be established: "aquatic polymerization of the essential tricarbonate molecules on the mineral support at 100°C, 20 m beneath the ocean and light-driven membrane protection assembly".“Light driven membrane protection assembly" – because the primeval photosynthetic sequence are used to code for the membrane lipids biosynthesis. Twenty meters beneath the ocean – because biochemical reaction in Fe-S world leading to the origin of life are performed at 100°C and pressure of 0.2 MPa (25).In harmony with four principal elements that lead the origin of life and diction "when gene for biochemical process exist, that means that coding pathway is in advance stage", first DNA replicon can be established. Genes of the first DNA replicon has to code for the : (A) DNA replication (including common ancestor sequence for archaeal primase, cdc6, recA, dnaG, kaiC); (B) Fe-S proteins assembly and functions (common ancestor sequence for respiration, photosynthesis, membrane lipids biosynthesis, nitrogen fixation); (C) for carbohydrate metabolisms. According to the existence of ORFs with unknown functions and its sequence similarity with the genes from the group B in the first DNA replicon, it is possible that there are some of the unknown metabolic process that exist in the ancient cellular form of life or even in contemporary cells.

This theory proposes existence of a single evolutionary line of cells, as a genetic backbone across three groups of living organisms and archaebacterial origin of eukaryots. In the biogenesis, i.e. in the development of single evolutionary line of cells, two very important physical parameters have not been taken in account, but both are strongly engaged in gene modeling and common ancestor gene/genes divergences. Those are diameter of the Earth and brightness of the Sun at the time when life originated. The earth is expanding at a rate of 10cm a year (as a result of absorption of the neutrino`s energy), this expansion is quicker than it was 3.8 billion of years (By) ago (when recA, kaiC, dnaG ... common ancestor gene originated, i.e. gene of the first DNA replicon under A and effects the length of the day. Eight hundred million of years ago day was only 18 hours long and separation of the recA from kaiC DNA sequences that happened 3.5 By ago, is due to the increasing of the length of the day. From the other side, 4.5 By ago Sun was only 70% as bright as it is today. Intensity of the different color in the visible spectrum was not, probably, equal as it was at the time of appearance of the chlorophyll based photosynthesis and water oxidation evolving complex (3.3 By ago), affecting the divergences of the common ancestor sequence for cytochromes, nitrogen fixation, photosynthetic reaction centre, i.e. genes of the first DNA replicon under B. The intensity of each wavelength depends upon the brightness of the Sun and, interestingly for us, correlation between blueshifts and redshifts depends also on the brightness of the Sun, above 30.000K there are blueshift and cooler lines being more redshifted. The light is absorbed by the pigments, chlorophyll that absorbs red and blue light (and appears green) and carotenoids, which absorb in the blue (and appear yellow). By this way, brightness of the Sun is responsible for color evolutionary shifts and at the same time for the impact on transition from carotenoide to the chlorophyll based photosynthesis, i.e. evolutionary shift of the photosynthetic genes.

The motivation for this kind of thinking is an old dreams and DNA "figure eight." In this dreams, mathematical symbol for eternity has been repeated few times. The message from these dreams becomes clear 40 years later, and this is its story.

Archaebacterial ancestor of eukaryots

Archaea, one of three major evolutionary lineages of life, are a fascinating and divers group of organisms with deep roots overcapping those of eukaryots. So, it is intelligent to search for the origin od eukaryots within those group of microorganisms. Gene duplication plays a major role in the gene modeling. The duplication of DNA and faithful segregation of newly replicated chromosomes at cell division is frequently dependent on recombinational processes. The fact that replication, recombination, chromosome segregation and cell

division are linked together, tell us that once upon a time existed unique DNA sequence that code for all those processes. Evolutionary modeling of those sequence are the basis for functional separation of those four processes. Archaea (archaebacteria) is one of the three groups of living organisms. There is opinion that they have an ancestor in common with eukaryots, which has been shown by a phylogenetic analysis based upon nucleotide and amino acid sequences comparison (26). Archaebacteria and eukaryots have many common characters, notably obligate co-translation secretion of N-linked glycoproteins, signal recognition particle with 7S RNA and translation-arrested domain, eight-subunit chaperonin, protein-spliced tRNA introns, core histons, small nucleolar ribonucleo-proteins, exosomes and similar replication, repair, transcription and translation processing. In order to come near each other, eukaryotic lineage and its prokaryotic sister group have to overcome transition from the archaeal candidate eukaryotic ancestor towards first proto-eukaryot, this is possible only by genetic rearrangement, i.e. genetic recombination and gene/genome duplication. According to the gene origin, two functionally energy-metabolic pathways can be distinguished: (I) nitrogen fixation, respiration, and photosynthesis and (II) carbohydrate metabolism: glycolisis (hexose), pentose-phosphate cycle, and tricarboxylic cycle (triose). It is hard to imagine free-living archaeal ancestor of the first proto-eukaryot without both groups of metabolisms.

Recent discoveries in the molecular biology and new DNA sequencing data has been show that Archaea possesses a genetic apparatus for multiple types of energetic activity. Genes for the glycolitic (Embden-Meyerhof-Parnas) pathway (18), reductive tricarboxylic acic cycle (1), reductive pentose phosphate cycle (20), Entner-Doudoroff pathway (3), Fe-hydrogenase catalytic H2 production (14), the sulphate assimilation (24), nitrogen fixation (6), are widely distributed among Archaea and they are often considered a central to the origin of metabolisms. Gene for cytochrome oxidase, which presence indicates that aerobic metabolism is possible in an environment with a low level of oxygen, was present in common ancestor of archaea and eubacteria (4). This means that aerobic respiration was a monophyletic and ancient enzymatic system before oxygenic photosynthesis. Ribulose bisphosphate carboxylase, central enzyme in carbon fixation, is present in archaeal genomes (20). Genetic apparatus of the electron transport chain (complex I-V), which are responsible for oxidative phosphorylation, are examined in archaeon *Natromonas pharaonic* (9). Genes for NADH-dehydrogenase type II, succinate dehydrogenase, terminal oxidase, ATP synthase and equivalent for cytochrome-C reductase, have been identified. Experimental studies provide the existence of a functional respiratory chain in these archaeon. And finally, archaea can perform oxygen non-producing carotinoide based photosynthesis, so they possess a primeval photosynthetic operon, which is the basis for the future photosynthetic replicon and plant's photosynthesis (Figure 1).

Whole-genome sequencing has revealed several cases where prokaryotic genomes have more than one large replicon. When second largest replicon approaches the size of the largest replicon, a chromosome splits to form a secondary chromosome. Genome of the archaeal ancestor of eukaryots (AAE) might be organized up of two replicons. Presence of two replicons in AAE correlates with the distribution of the majority of housekeeping functions in its chromosome. At the level of compact genome organization, recombination/repair, replication, and cell division were brought together functionally and physically, because they evolved from a single gene with multiple functions (ancestor sequence of the recA, kaiC, dnaB...). Recombination evolved in prokaryots not only as a means to exchange genetic information but also as a DNA repair process. Recombinational DNA repair is associated with replication, every time bidirectional replication is initiated at oriC, there is a chance that fork encountered a situation requiring recombinational repair. Common ancestor gene for herA, dnm-like gene, ftsZ, ftsK, cdc6 from one side and dnaG, recA, resT, from the other side, where encoded by a single operon sequence with dual function: (dnaG +recA + resT) + (ftsZ + herA + cdc6). In the presumed archaeal ancestor of the first proto-eukaryot (AAE), this operon is placed at the level of oriC. To allo functional polarization, genes participated in energy production and ribosomal operon with elongation factors, are encoded by the "mitochondrial" replicon and others, luxury genes, by "nuclear" replicon (Figure 1), something like in the *Nitrosomonas europea* (5), for example. It may be that bilateral inverse symmetry is a vestige of kinship between chromosomal halves, where one half of the genome begat the other via an ancient whole-genome inverse duplication event (19).

Bidirectional replication from an internal origin forms a circular head-to-head, tail-to-tail dimer with two DNA monomers covalently linked at the terC. During AAE's whole-genome duplication it can be that replication fork pauses and collapses causing double-strand break, after bidirectional replication is terminated, to promote compartmentalization, there is no generation of two daughter genomes. Resolution in terC continued, after strand break, by strands invasions and homologous recombination. Such type of duplication from oriC to terC, could explain compartmentalization of the functionally polarized AAE's genome by subsequent reciprocal genetic recombination at the level of oriC (23).

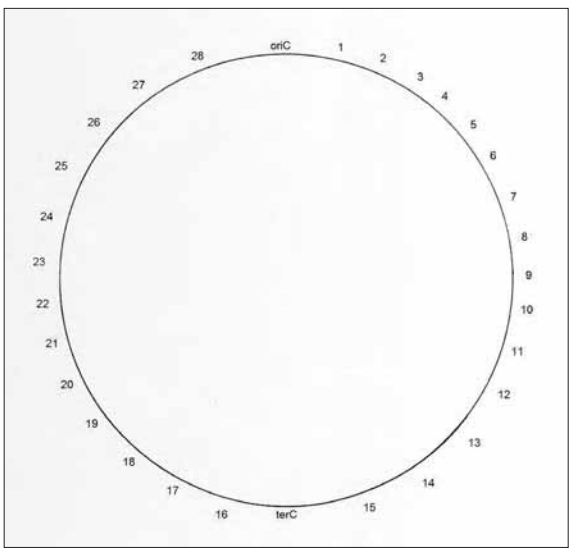

Figure 1. According to the possibility that all genes are derived from common ancestor sequence and compact genome organization of the single evolutionary line of cells, this is a roughly prediction of its genes composition; where pbs is a connection between energy production and biomembrane's lipids biosynthesis and transfer; ATP-grasp enzymes as a connection of energy production and amino-acids synthesis with mptN – cofF as a common ancestor genes for ribosomal proteins. 1-hydrogenase, 2-cytochrome, 3-ferredoxin, 4-isc, 5-nif, 6-oxa1, 7-carotenoides, 8-hem, 9-chlP, 10-pbs, 11-rubisco, 12-ATP-grasp enzymes, 13-amino-acids ligase common sequence, 14-mptN-cofF, 15-ssrA, 16-EF (Tu), 17-tRNA genes common sequences, 18-cobN, 19-recA with small ancestor sequences for further SOS regulon, 20-kaiC, 21-cdc sequences, 22-dnaG, 23-resT, 24-ftsZ, 25-herA, 26-different chelatase genes, 27-replication/repair cell division operon with nucleotide synthesis or nucleotide exogenous capture and introduction, 28-heat shock genes,uvr...

Mitochondrial origin

In prokaryots, cell division occurs through binary fission and it is driven by the formation of the septum. Septum formation structurally altered envelope, so that inner membrane is connected closely to the cell wall and outer membrane layer (22). A network of proteins interactions must be carefully tuned, both in time and in space, in order to allow the correct and timely generation of two identical daughter cells. Genetic rearrangement, and mutation or change of time and level of expression of the genes participating in septum formation, could cause separated inner and outer membrane fission. ftsZ and dnm1-like genes did not necessary tune when both are recruited to constriction site, indicating that inner and outer dividing machineries are not in tight association during the late stage of cell division (7). Surely, addition of new DNA sequences, either in "mitochondrial," either in "nuclear" replicon, can cause this dramatic event, i.e. fission of two replicons. Dynamin regulates membrane squeezing and peroxisomal (organelle surrounded by one membrane) fission (10). In that way, AAE's inner membrane becomes proto-nuclear and proto-mitochondrial outer unique membrane of the resulting proto-eukaryot (for the time before evolution of endomembranes and endosceleton of mature eukaryot).

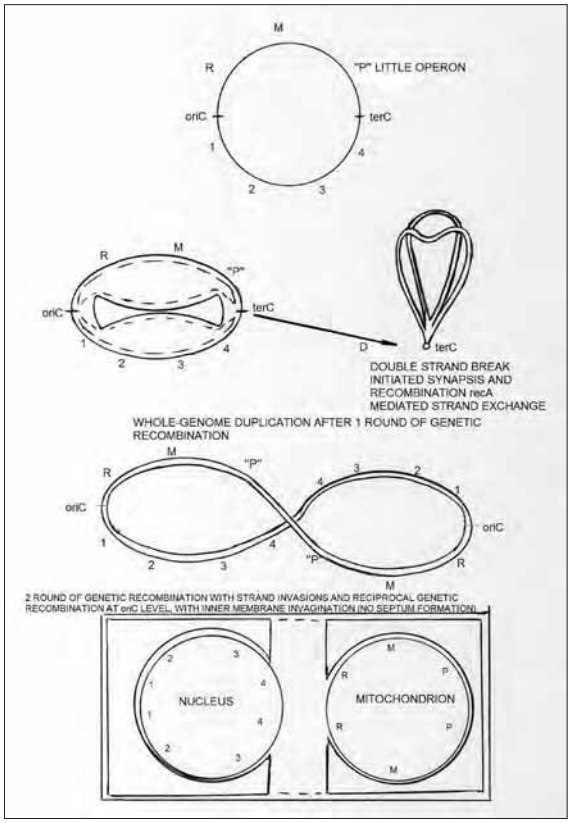

Figure 2. Set of the subsequent steps leading to the fission of the eukaryotic common ancestor genome into nuclear and mitochondrial compartment and origin of the eukaryots. 1, 2, 3, 4 –different operons in the nucleus; M and R – different operons in mitochondrion, P – primeval photosynthetic operon

The scenario reaches culminating point: on one side there is an AAE's whole-genome duplication (with homologous strands invasions and reciprocal recombination) and on the other side, partial cell fission, including only inner membrane invagination and squeezing. Resolution in terC, by strains invasion, was followed by the resolution in oriC, still attached to the inner membrane probably at the mesosome level; two oriC pairs at the corresponding repeated sequence, probably mt-telomere like [div-sequence (23)], allowing a reciprocal genetic recombination to generate two duplicated, functionally separated genomes. Invagination of the inner membrane continued, after genome fission, and then envelops each of the replicon separately, in that way it give rise a two new compartments (Figure 2).

DNA duplication take place early in the evolution, after evolution by nucleotide acquisition was terminated. DNA duplication has an ancient and continuing process during evolution. The types of sequences at the break points as well as their superposition with the replication map suggest that spontaneous duplication result from replication accidents and repair of this replication-dependent double-strand break in AAE's genome could be the origin of eukaryots, which correlate with existence of *div* sequences (23). Mitochondrial telomeres play essentially the same biological roles as their nuclear counterparts (ensure the complete replication, mask the ends from DNA repair machinery and protect them from exonucleolytic degradation and/or end-to-end fusions) because they have same origin and results from same molecule and processing.

What is the reason for such radical exchange? There are two possible answers: (1) Biologically: the growing photosynthetic gene cluster was enriched with additional sequences in the smallest mitoplastide replicon, which, approaching the size of the largest mitochondrial replicon might cause mitoplastide genome (chromosome) split. In this "step-wise" model for the evolution of oxygenic photosynthesis, all steps are performed within genome of the single evolutionary line of cells; and (2) cosmologically: in the ribosomal genes traveling, and formation of the fourth, ribosomal compartment. In the human mitochondrial genome there are two ribosomal genes, coding for 12S and 16S rRNA, still encoded after hundreds millions of years ribosomal DNA travelling from mitochondria to the nucleus. Transferred to the nucleus, they can cause origin of the new organelle – ribosomal compartment, infrastructural formerly defined by nucleolar organizers and nucleolus (engaged in ribosomal protein assembly and telomerase action). If transfer of two ribosomal genes took place at the sexual chromosomes, than nucleolar organizers from sexual chromosomes transferred to the nucleolus can cause qualitative jump-on in human evolution. In this case, human race can evolve versus open field of intelligence (development of the hemisphere right...), long living (just it is a case with semi-cellular form of life) and ... sterility.

Plastide origin

"There are some tantalizing homologies between mitochondrial and chloroplast genome"

Lewin B., 2000. Genes VII.

This hypothesis proposed existence of mitoplastide genome in the aerobic oxygen non- producing proto-eukaryote. This genome is composed, at the very beginning, of the whole mitochondrial replicon and photosynthetic gene cluster. All extant photosynthetic cells descend from a primeval photosynthetic operon. In genetic evolution of the photosynthesis, following steps can be recognized:

1) evolution of photosynthetic gene operon,
2) evolution of photosynthetic gene cluster, and

3) evolution of photosynthetic gene replicon

One of the prominent examples of the univerzalization in Biology is cytochrome bc1 complex in mitochondria and cytochrome b6f in chloroplasts. These two quinol oxidoreductase in respiration ("reverse photosynthesis") and in photosynthesis are closely related, and appear to share common ancestor. Many respiratory components including cytochrome bc and cytochrome C oxidase (an enzyme older than atmospheric oxygen) are also present in archaea. While cyanobacterial PSII most probably derived from an ancestral type II reaction center of purple bacteria, homologues of Cyt b559 are absent from purple bacteria. It can implies that Cyt b559 might be less critical to the photochemical function of PSII. On the other hand, Cyt b562, less efficient at corresponding wavelength, are present in archaea and plants.

Photosynthetic reaction centers have originated, after gene duplication, from cytochrome b subunit of cytochrome bc1 complex (27). Three of the four ligands in cytochrome b are conserved with the cofactor ligands in the reaction centre (RC) polypeptides, including the chlorophyll Z ligand for oxygenic reaction centre only (27). Second example of gene duplication is found with the genes of PS I - like RC core polypeptide, where psa A and psa B are derived from ancient gene duplication from cytochrome b and are conserved with the cofactor ligands in psa A/ psh A – like ancestor. Regarding core antenna polypeptides of PS II, phylogenetic analysis indicates that psb B (coding for CP47) and psb C (coding for CP43) genes arose after psh A duplication of psh A – like common ancestor, i.e. from gene fragmentation and subsequent duplication from a common ancestor to the PSI-type RC polypeptide. This double duplication event precedes the divergences of all oxygenic lineages and may have occurred well before speciation of the photosynthesis.

First gene duplication event, happened after whole-genome duplication, leaded into the mitochondrial and nuclear compartmentalization. Second duplication events required duplication of the whole mitoplastide genome leading to the transition of photosynthetic gene cluster to the photosynthetic gene replicon (Figure 3). Final evolution of the photosynthetic gene (PG) replicon implies integration of the oxygen evolving complex in PG cluster. The first photochemical RC was integrated in an existing respiratory electron transport chain. Purified protein - pigment complex from *Rhodopseudomonas* is capable to carry on light - driven electron transport in concert with mitochondrial membrane electron carriers.

Very important event in evolution of PG replicon is nitrogen fixation genes function replacement and integration in PG cluster. Function replacement is one of the significant processes in evolution of the photosynthesis in plants. Bch L and bch D, which may be subunits of a Ni-chelatase for the biosynthesis of the Ni-containing coenzyme F430 in Archaea, share a significant similarity with bch I and bch D that encode two Mg-chelatase subunits necessary for chlorophyll biosynthesis, suggesting that ancient gene duplication might have occurred well before photosynthetic speciation event. During AAE's whole-genome duplication the function of the bch I and bch D, which are already present in Archaea, can be replaced and, in concert with archaeal's hem A and glutamate-semialdehyde aminomutase gene, contributed to the later chlorophyll biosynthesis in plant's precursor. Nitrogen fixation is unknown in plastids and may involve toxicity. Archaeal nif H gene sequence shows significant homology to that of frx C (chl L), i.e. protochlorophyllide reductase (11); chl P-geranylgeranyl reductase is already widespread among Archaea. The initial reaction of tetrapyrrol formation, precursor molecule for the biosynthesis of chlorophylls, in archaea as well as in plants is catalyzed by hem A gene product glutamyl-tRNA reductase. 5-aminolevulinic acid (ALA) is the general precursor molecule for the synthesis of tetrapyrroles form ALA, in the same way in plants as in archaea i.e. in a two-step reaction from the skeleton of glutamate bound to glutamyl-tRNA. So, plants and archaea form chlorophyll precursor in the same way. Three proposals have been put forward regarding compounds, which may have served as precursor to the manganese complex: formate (17), hydrogen peroxide (2,16), and bicarbonate (12). Hydrogen peroxide might be an important oxidant of the early anoxic Earth (16). Binuclear manganese protein catalyzes reaction: 2H2O2 to 2H2O + O2, whereas tetranuclear manganese protein (water oxidation protein) drive water hydrolysis: 2H2O to 4H+ + 4e- + O2. Existence of manganese in Hem F/ Hem N has been proved (8). Hem F/ Hem N is coproporphyrinogen III oxidase, converting coproporphyrinogen III in protoporphyrinogen IX, an antepenultimate step in chlorophyll biosynthesis. Sequences of the archaeal nif B gene show significant homology with that of hem N (21). It can be concluded that functional replacement and integration of the nif B gene in PG cluster were a final drop to the PG replicon evolution. In this way, evolution of the polarized mitoplastide genome was terminated, harvesting mitochondrial replicon and plastid replicon. Traces of the existence of mitoplastide genome are visible in plant mitochondrial genome, where plastide-like sequence exists, i.e. non-functional pieces of psa, ndh, rbc, rpo, psb D ... genes (13), as well as intensive exchange between these two organelles. Speculating about genesis of the thylakoid membranes and according to this way of thinking, they should originated from mitoplastide inner membranes. Over time, oxygen-dependent enzymes, will gradually replace the anaerobic version, so that the present list of anaerobic enzymes may be only a small fraction of the number that once existed on the anaerobic Earth.

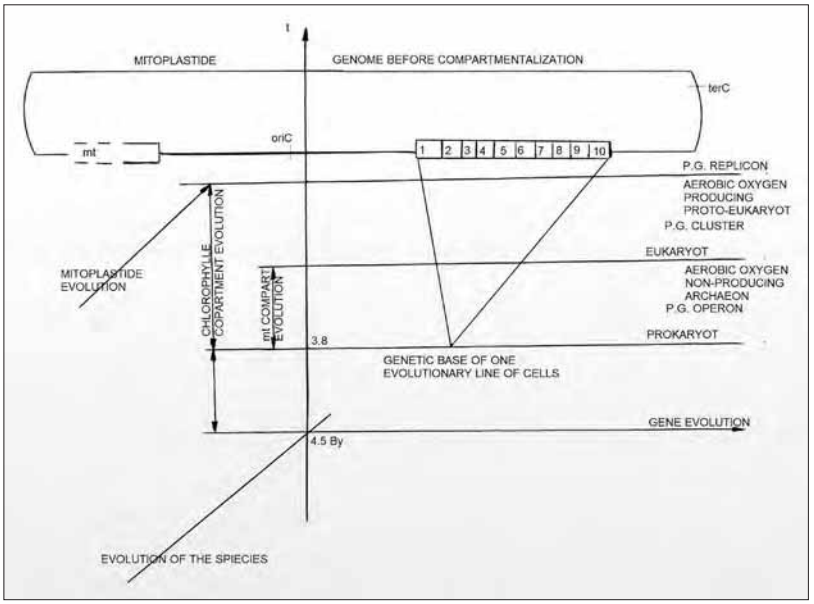

Figure 3. Global evolution of photosyntetic gene replicon in the mitoplastide genome of an proto-eukaryot: 1 – fdx, 2 – cyt /rieske, 3 – kai, 4 – hem, 5 – beta-car, 6 – chl, 7 – PSI, 8 – PSII, 9 – slr, 10 – wox

It can be deduced that evolution of the plant's pigments biosynthetic pathway started in Archaea and terminated in Mg-tetrapyrrol biosynthetic enzyme encoded by mitoplastide genome of an aerobic proto-eukaryot arose after division of archaeal whole-genome duplication resolved by genetic recom-

bination. Evolution of the plant's reaction center apoproteins (PS I and PS II gene spectrum), begins from archaeal cytochrome b protein, first by duplication event and subsequent archaeal nif genes family function replacement and integration (as an active component or regulatory proteins) in the PG cluster of the above mentioned aerobic oxygen non-producing proto-eukaryote. This way of thinking can be supported by finding that an apparent form of slr 2013 gene, whose product is engaged in functional assembly of photosystem II, are found in Archaea (15). Light harvesting chlorophyll complexes, phycobilisomes, and chlorosomes make up the principal types of light harvesting systems for organisms to use the oxygen evolving complex in oxygenic photosynthesis. In the archaeon *Haloarcula marismorti* (1), nine plastocyanin precursor-like proteins were identified, as well as phycocyanobilins, which are major components of the phycobilisomes. *H. marismorti* has at least 29 unique proteins containing a light-response domain motif found in plants and cyanobacterial phytochromes. In the favorable environment, by point mutation(s) all archaeal photosynthetic-like genes can evolve in photosynthetic ones. This type of genetic evolution connected with genes duplication can make possible evolutionary shift from archaea to eukaryotes .Once, mitoplastide genome was organized in that way, containing two functionally polarized replicons (mitochondrial and plastid's), it can undergo the same process which divided that of mitochondrial from the nuclear replicon. It is obvious that both, integration of water oxidation complex or mitoplastide whole-genome duplication can provide a new DNA sequence, but surely genome duplication complete the photosynthetic gene replicon and cause mitoplastide fission.

Conflict of interest

We declare no conflicts of interest.

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