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MITOPLASTIDE GENOME AND ORIGIN OF MITOCHONDRIA AND CHLOROPLAST IN PLANTS

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ABSTRACT

All extant photosynthetic organisms descend from a primeval photosynthetic operon of the single evolutionary line of cells. This hypothesis proposed existence of mitoplastide genome in the aerobic oxygen non-producing proto-eukaryot. This genome is composed of whole mitochondrial replicon and photosynthetic gene cluster surrounded by membrane. Development of water spliting-PSII superoperon in plants, is a results of mitoplastide genome duplication and gene's function replacement. After both events, mitoplastide genome contain two functionaly polarized replicons (mitochondrial and plastid's). The origin of mitochondrion and chloroplast occured in three steps. First, a replication fork pauses and collapsed, generating a break in the mitoplastide genome. Second, the double-strand break was repaired by complementary strands invasion. Third, this duplicated genome was segregated into two compartments by reciprocal genetic

recombination. Simultaneous, with genetic recombination, fission of the mitoplastide membrane formed two compartments, mitochondrial and plastid's.

Keywords: origin of mitochondrion and chloroplast in plants.

Introduction

Thrty-six Eubacterial lineages have been identified, of which only five are capable of using chlorophyll-based energy conversion to create a protonmotive force to drive ATP synthesis and reduce CO_2 to sugars. Out of five bacterial groups capable of photoautotrophic photosynthetic growth, four perform photosynthesis under anaerobic conditions and do not oxidized water to molecular oxygen via the oxygen evolving complex (OEC) (anoxygenic photosynthesis). The cyanobacteria are the only group of bacteria that have incorporated the OEC necessary for spliting water as a source of electrons. The only eubacteria to use the OEC in oxygenic photosynthesis utilize phycobilisomes. It can be that, regarding the evolution of photosyntehsis in eubacteria, the first phototrophs were anaerobic ancestor of cyanobacteria, procyanobacteria (or even "pro-protocyanobacteria" GREEN 2003), that conducted anoxygenic photosinthesis using a photosystem I-like reaction center (MULKIDJANIAN et al. 2006). Cyanobacterial photosynthetic machinery is far greater complex to considering it as a lineage in which photosynthesis could have emerged.

Some of the strong conclusions concerning the early evolution of photopigments include: (1) the requirement for distinguishing the evolution of modern photopigments and photosynthetic systems from the earliest light-driven reactions; (2) the theory that respiration preceeded photosynthesis, evidence by appearance of hems and cytochromes prior to chlorophyll; (3) the theory that UV radiation was the driving force in the development of the first organisms to use light-driven reactions; and (4) the evolution of primitive pigments appearing after the evolution of the redox-active hems taking advantage of pigments which evolved initially to protect against UVR.

Physical conditions in the prebiotic world conduct inevitable outset and kind of semi-

cellular form of life (WACHTERSHAUSER 1988). 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 (walvelength from the Sun and temperature of the mineral support). In accordance with those four elements, following deffinition of the origin of life can be established: "Aquatic polymerization of the essential tricarbonate molecules on the mineral support at 100 ℃, a ~ 20m 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. "20m beneath the ocean" – because biochemical reaction in Fe-S world, (with a pyrite as a mineral support) leading to the origin of life are performed at 100 ℃ and pressure of 0,2 MPa (WACHTERSHAUSER 2000). In the harmony with these four principal elements that guided the origin of life and maxim: "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) and C) DNA sequences for carbohydrate metabolisms. According to the existence of ORFs with unknown functions, spreading all around completely sequenced genomes, and its similarity with the genes from the group B in the first DNA replicon (BLANKENSHIP 2001), it is possible that there are some of the unknown metabolic process that existed in the ancient cellular form of life or even in contemporary cells.

In the context of 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 family divergences. The major driving forces in gene modeling and functional replacements in photosynthetic genes replicon are diameter of the Earth and brightness of the Sun at the time when life originated. The earth is expanding at a rate of 0,01cm a year, this expansion is quicker than it was 3.8 billion of years (By) ago (when recA, kaiC, dnaG ... common ancestor multifunctional sequences originated, i.e. gene of the first DNA replicon under A) which effects the length of the day. 800 million of years ago day was only 18 hours long and separation of the recA from kaiC DNA sequences that happened about 3.0 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 colour in the visible spectrum was not, probably, equal as it was at the time of appearance of the chlorophylle based photosynthesis and water oxidation evolving complex (~2,8 By ago), effecting the divergences of the common ancestor multifunctional 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, but cooler lines being more redshifted. The light is absorbed by the pigments, chlorophyll which absorbs red and blue light (and appear green) and carotenoids which absorb in the blue (and appear yellow). By this way, change in the brightness of the Sun is responsible for coulor evolutionary shift, and at the same time for transition from carotenoide to the chlorophylle based photosynthesis, i.e. evolutionary shift of the photosyntetic genes.

This theory propose existence of a single evolutionary line of cells, as a genetic backbone across three groups of living organisms, and autogenous origin of plastids starting from mitoplastide genome of archaebacterial originated proto-eukaryot. There are two ways for evolution of photosynthesis, cyanobacterial and plants.

ORIGIN OF PLASTIDS

"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. Genetic evolution of the photosynthesis comprised:

1. evolution of photosynthetic gene operon,

2. evolution of photosynthetic gene cluster (superoperon), and

3. evolution of photosynthetic gene replicon, in the mitoplastide genome.

Genetic promotion of photosynthesis

One of the prominent example 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, CASTRESANA 1994) are 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 (ESPOSITI 1985). On the other hand, Cyt b562, less efficient at corresponding wavelenght, are present in archaea and plants (IWASAKI 1995).

Photosynthetic reaction centers have originated, after gene duplication, from cytochrome b (this is a link between respiration and photosynthesis) subunit of cytochrome bc1 complex (XIONG and BAUER 2002). Second example of gene duplication is found with the genes of PS I - like RC core polypeptide, where psa A (P700 chlorophyll a) and psa B are derived from an ancient gene duplication from cytochrome b and are conserved with the cofactor ligands in psa A/ psh A – like ancestor. Regarding core antena 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 of the PSI-type RC polypeptide. This double duplication events precede the divergences of all oxygenic lineages and may have occurred well before speciation of the photosynthesis. Phylogenomic analysis of the complete genome sequence of *Chlorobium tepidum* (green-sulfur obligate anaerobic photolitotrophs bacterium utilized homodimeric type I reaction center) reveals likely duplications of genes involved in biosynthetic pathways for photosynthesis and the metabolism of sulfur and nitrogen as well as *strong similarities between metabolic processes of many archaeal species* (EISEN 2002).

The OEC extrinsic proteins (PsbO, P, Q, U, V) do not ligate to the (Mn)4 cluster but rather provide a molecular environment to stabilize it and to maintain optimal levels of Ca and Cl ions required as essential cofactors for the water oxidation reaction (DEBUS, 1992). Results indicates that Ca and Cl ions can be replaced (by Br, I, NO3) but with slower kinetics (WINCENCJUSZ 1999). Before the evolution of water oxidase activity, there must be precursor of currently known extrinsic OEC proteins, as a cytochrome c in archaea (RIVAS 2004). The extrinsic proteins of the

OEC differ between plants on the one hand and cyanobacteria on the other (RIVAS, 2004). Mechanisms generating a high potential for water oxidation by PSII can be measured by redox potential of the primary electron acceptor pheophytin. New research points out the presence of the eukaryotic type chlorophyll a and pheophytin a in archaea (MAITENA et al 2011). This Chl a could catalyze light-driven proton transfer across archaeal membrane. Evolutionary, is better to say that eukaryotes posses archaebacterial type of chlorophyll a and pheophytin a. Attempt of this paper is to explain that there are two independent branches of the evolution of photosyntesis (i) cyanobacterial, and (ii) eukaryotic.

Reflection

All contemporary genes stem from pre-existing ancestral genes by serial duplication, gene chimerization, and that the ancestry of modern genes goes back through trillions of successive replication. After duplication, only the minority of gene pairs will adopt a new function, quickly enough to escape disabling mutations that would lead to their eradication; rampant gene loss rapidly erases this signal of genome duplication (DEHAL, 2005). First whole-genome duplication, leaded to the mitochondrial and nuclear compartmentalization (STUPAR 2006). Second duplication events required duplication of the whole mitoplastide genome leading to the transition of photosynthetic gene cluster to the photosynthetic gene replicon (Fig. 1).

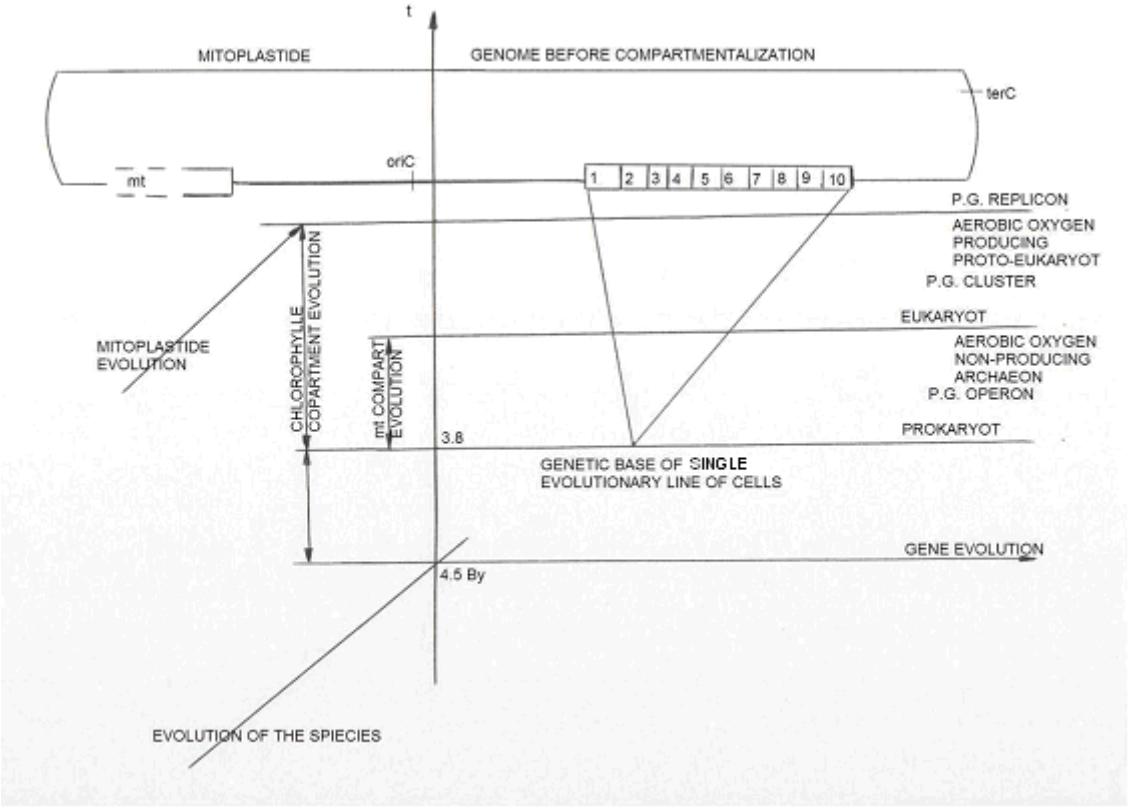

Fig. 1. Global evolution of photosynthetic gene replicon in the mitoplastide genome of a proto-eukaryot; 1-fdx, 2-cyt/rieske, 3-kai, 4-hem, 5- beta-car, 6-chl, 7-PSI, 8-PSII, 9-slr, 10-wox. P.G. = photosynthetic gene, t = time in By, mt 0 mitochondrial replicon, oriC = origin of replication, terC = end of replication.

Chlorophyll biosynthesis is one of the intermediate steps in bacteriochlorophyll a biosynthesis, this means that chlorophyll- containing oxygenic photosynthetic organisms predate bacteriochlorophyll-containing anoxygenic organisms. But, molecular phylogeny

clearly indicates that bacteriochlorophyll a is indeed more ancient pigment. So, chlorophyll a/containing cyanobacterial reaction centar are a more recent evolutionary product and that the evolution of pigment biosyntehsis from bacteriochlorophyll to chlorophyll may have involved gene loss and shortening of the pathway. The putative archaeal bchG (ar-bchG) from archaeon *Ignicoccous* was cloned and expressed in *E. coli* (MENG et al. 2009). The protein was found to be capable of synthesizing bacteriochlorophyll a by esterification of bacteriochloroohyllide a with phytyl diphosphate or geranylgeranyl diphosphate. Phylogenetic analysis clearly indicates that the ar-bchG diverges before the bacterial bchG. The discovery of a functional enzyme involved in

Bchl biosynthesis in archaea raise the significant possibility that the origin of photosynthesis predates the divergence of bacteria and archaea. It would be possible that Ar-BchG has other function than in photosynthesis, such as synthesis of membrane lipids in these archaeon.

Nitrogen fixation and photosynthesis

The nifH, nifD, nifK, nifE, nifN genes are universal in nitrogen fixing organisms, found within highly conserved operon in Archaea (CHIEN and ZINDER 1996). NifH and NifD homologs are not known to be involved with fixing nitrogen. The pigment biosynthesis complex protochlorophyllide reductase and chlorophyllide reductase are not only homologous but are functionally analogous to nitrogenase. As with nitrogenase, electron flow from a NifH-like ATPase (BchL and BchX) to a NifD-like putative heterotetramer where the tetrapyrrole is bound (Bch NB and BchYZ). These two enzymes catalyze late steps in chlorophylle and bacteriochlorophylle biosynthesis. Based on sequence similarity, the Bch LNB and Bch XYZ complexes appear to have originated from a duplicated common ancestor that was less substrate specific and able to catalyze both ring reductions, albeid less efficiently. Both complexes are found together only in anoxygenic photosynthetic prokaryots, only one (Bch or Chl LNB) is found in modern cyanobacteria. This fortuitous change, likely prompted by the loss of Bch XYZ complex in the last common ancestor of cyanobacteria and archaeal ancestor of photosynthetic proto-eukaryots, resulted in a blue shift (P 680 to P 700) in primary pigment absorption wavelenght, increasing redox potential of the photosynthetic reaction center.

Recent studies have shown ubiquitous existence of cytochrome b and Rieske-iron-sulfur proteins, essential components of the cyt bc complexes and photosynthesis in archaea, eubacteria and eukarya (SCHUTZ 2000, SCHMIDT 1995). There are also indication that many respiratory components including cytochrome bc complex and cytochrome c oxidase existed in the last common ancestor of Archaea and Eubacteria. Mg-tetrapyrrole-based photosystem are found in Eubacteria only, inclusive of the chloroplast lineage, and are therefore less likely to have appeared after the advent of respiratory metabolism . But, photochemical reaction centers may have evolved by integration into an existing respiratory electron transport chain. The evidence for the existence of respiratory components prior to photosynthetic ones, is contrary to the common believe that oxygenic photosynthesis must precede respiration because respiratory process

requires oxygen as a substrate. The primitive form of cytochrome bc complex may have perform either an anaerobic type of respiration or, an aerobic type of respiration in the presence of an extremely low level of oxygen.

Nitrogen fixation is unknown in plastids and may involve toxicity. The corresponding homologs in the PChloride reductase of Chl-synthesizing organisms are chlL (frxC), chlN (gidA), and chlB. Archaeal nif H gene sequence shows significant homology to that of frx C (chl L), i.e. protochlorophyllide reductase (FUJUTA et al. 1992. BURKE et. al. 1993.); chl P-geranylgeranyl reductase is already widespread among Archaea. The genes responsible for the reductive conversion of a geranylgeranyl group into a phytyl group have been identified in plants and bacteria. The chl P genes encode multifunctional geranylgeranyl reductase are involved in the biosynthesis of chlorophyll. In archaea, homologues of GGR are engaged into production of fully saturated heptaprenyl side chain (HEMMI 2005). The initial reaction of tetrapyrrole formation, precursor molecule for the biosynthesis of chlorophylls, in archaea as well as in plants is catalized 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 chlorophylle precursor in the same way.

Very important event in evolution of PG replicon is nitrogen fixation genes function replacement and integration in PG cluster, by mitoplastide genome duplication. Function replacement is one of the significant processes in evolution of the photosynthesis in plants. During archaebacterial 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 glutamat-semialdehid aminomutase gene, contributed to the later chlorophylle biosynthesis in plant's precursor. 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 which encode two Mg-chelatase subunits necessary for chlorophylle biosynthesis, suggesting that ancient gene duplication might have occurred well before photosynthetic speciation event. Burke et al. (1993.) have concluded that duplication of nitrogenase iron protein gave rise to the ancestral chlorophyll iron protein, and that ancient duplication of nifH gene preceded the divergence of eubacteria and methanogenic archaea. Recent discovery of chlorophyll a and pheophytin a gene in

archaebacteria, identical to those from plant, could reconsider the implication of archaea in the establishment of photosynthesis on earth (MAITENA et. al. 2011).

Mg⁻ and Mn⁻ complexes

Three proposals have been put forward regarding compounds which may have served as precursor to the manganese complex: formate (OLSON 1970), hydrogen peroxide (BLANKENSHIP and HARTMAN 1998, LIANG et al. 2006) and bicarbonate (dasGUPTA et al. 2004). Hydrogen peroxide might be an important oxidant of the early anoxic Earth (LIANG et al. 2006). Binuclear manganese protein catalyzes reaction: 2H2O2 to 2H2O + O2, whereas tetranuclear manganese protein (water oxidation protein) drive water hydrolysis: 2H2O to 4H+ + 4e- + O2. The additional evidence supporting hydrogen peroxide use is following: - To dissipated the excess of energy (in the case when excited chlorophyll molecules improperly transfer their energy state to oxygen), the water-water cycle channels electrons obtained from the splitting of water molecule at PSII through the photosynthetic apparatus. These electrons are transferred to oxygen by PSI and result in the formation of superoxide radicals. A membrane-attached copper/zinc superoxide dismutase converts those radicals into hydrogen peroxide and a chloroplast membrane-bound ascorbate peroxidase (thylakoid-APX) converts the hydrogen peroxide back into water. So that hydrogen peroxide serves as the precursor to the manganese complex and as a chloroplast protector from the superoxide radicals.

Existence of manganese in Hem F/ Hem N has been proved (MALITZ 2002). 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 (SOFIA et al. 2001).

Porphyrins, for example heme and chlorophyll, are vital to the biological processes such as respiration and photosyntehsis. Both cofactors are synthesized through a common pathway to protoporphyrin IX (PPIX) which than branches: Fe 2+ chelation into the macrocycle by ferrochelatase results in heme formation; by contrast, Mg2+ addition by Mg-chelatase commits the porphyrin to bacterio(chlorophyll) synthesis. It was discovered (JASCHKE 2010), that Mg2+ can be replaced by Zn2+; Zn-BChl biosynthetic pathway is a new way to make BChl. This discovery allows refinement of electron transfer rules within pigment-protein complexes by

showing that the coordination state and conformation of cofactors in RC2, can have equally important role as the protein. Which correlates with observation of the role of gene (protein) functions replacements.

Genome sequence of archaeon *Picrophilus torridus* (FUTTERER 2004), reveald the presence of the two genes homologous to Mg-chelatase subunits chl I and chl D flanking the cob N gene. It has recently been suggested that Chl I and Chl D may take over the funxction of Cob S and Cob T (RODIONOV 2003).

Modeling of the genes participating in Mn-proteins biochemical pathways, having in mind his incorporation in PSII and atmospheric conditions before 2,7 By, would be as following:

1. 2HO2 (super oxide) – Mn-superoxid dismutase (mononuclear Mn-centrum) = H2O2 + O2

2. H2O2 – catalase (binuclear Mn-centrum) = 2H2O + O2

3. H2O – wox (tetranuclear Mn-centrum) = 4H+ + 4e- + O2

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 and plastide 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 (HIROKAZU 2003), 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.

CONCLUSION

It can be deduced that evolution of the plant's pigments biosynthetic pathway started in Archaea and terminated in Mg-tetrapyrrole biosynthetic enzyme encoded by mitoplastide

genome of an aerobic proto-eukaryot arose after division of archaeal whole-genome duplication, and resolved by genetic recombination. 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 oxygene non-producing proto-eukaryote. This way of thinking can be supported by finding that an orthologous of slr 2013 gene, whose product is engaged in functional assembly of photosystem II, are found in Archaea (KUFRYK and VERMAAS 2003). Cyanobacterial rubredoxin gene (rub A), whose product is engaged in assembly of photosystem I has a 50 amino-acids domain with very high similarity with archaeal rubredoxin. So, archaeal and cyanobacterial genes engaged in PSI and PSII assembly and stability, have common ancestry!!!

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* (BALIGA et al. 2005), 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 favourable environment, by genetic mutation(s), influenced by above mentioned driving forces, all archaeal photosynthetic-like genes can evolve in the plant's photosynthetic ones. This type of genetic evolution connected with genes duplication can make possible evolutionary shift from archaeal non-oxygen producing to the plants oxygen producing organisms. It seems that eubacteria and archaebacteria, regarding biochemical pathways used are "twins in mirror" (SODERBERG 2005).

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.

When 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 (STUPAR 2008). It is obvious that both, integration of water oxidation complex or mitoplastide whole-genome duplication can provide a new DNA sequence, but certainly genome duplication complete the photosynthetic gene replicon and cause mitoplastide fission by genetic recombination (Fig. 2), as it is the case of the fission of mitochondrial from nuclear gene compartment.

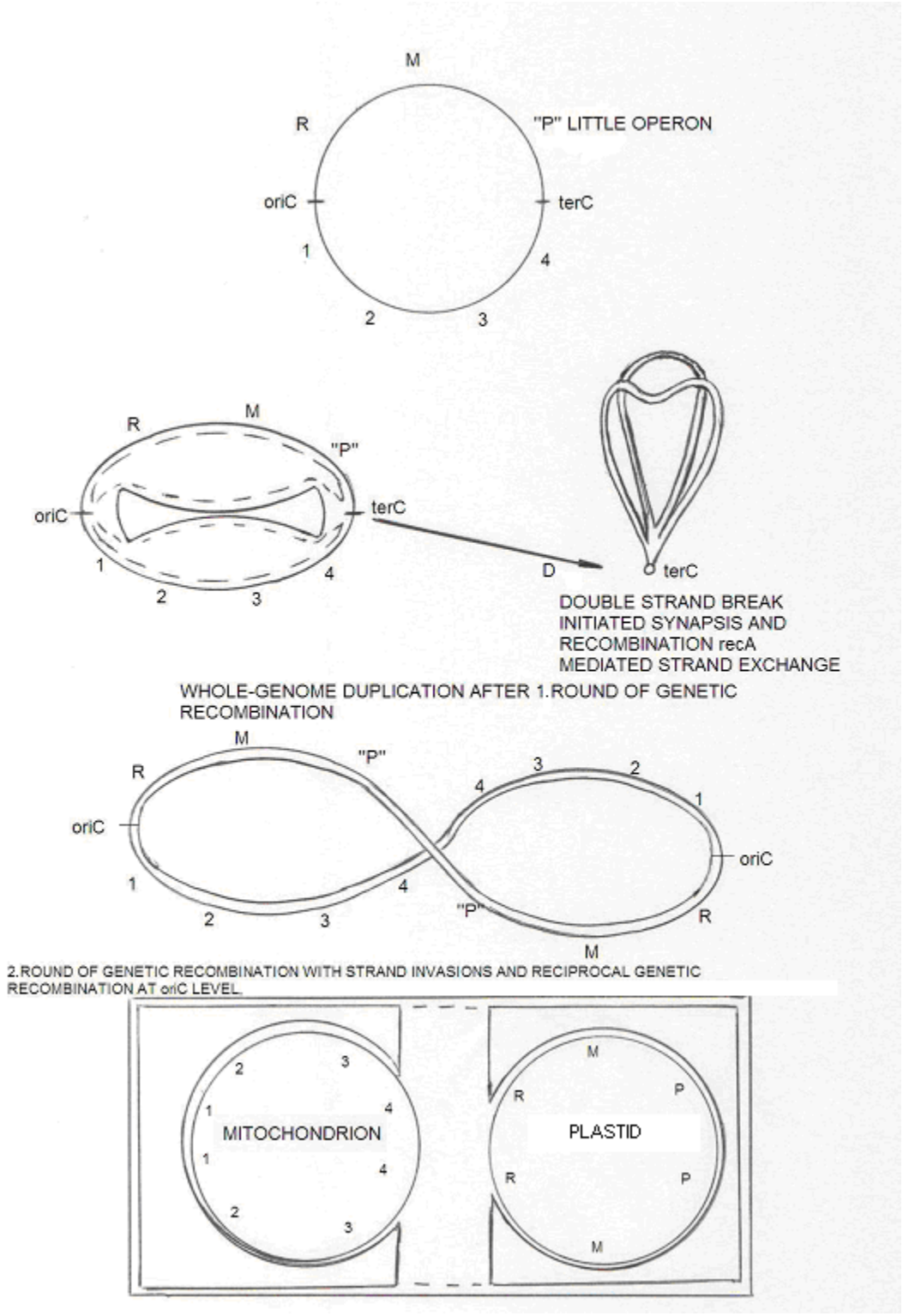

Fig.2. Set of the subsequent steps leading to the fission of the proto-eukaryotic mitoplastide genome into mitochondrial and plastid compartment. 1, 2, 3, 4-different operons in the

mitochondrial replicon, R,M,P-different oprons in photosynthetic replicon, "P"-little primeval photosynthetic operon.

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