

Endosymbiotic theory the modern or organelle biology essay



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Endosymbiosis; a theory that proposes the evolution of the eukaryotic cell or yet is it another biological theory that is complete garbage? This is what this essay has been investigating, whether the evidence gathered over the last fifty years is good enough to support the endosymbiotic theory and to change the views of millions of biologists who still do not agree with it. The theory was first postulated in 1905 by a Russian biologist, Konstantin Mereschkowsky but was more popularised in the 1960s by Lynn Margulis. According to this hypothesis, about two billion years ago, a prokaryotic organism consumed a chemo-organotrophic bacteria giving rise to the eukaryotic cell and its organelles such as the mitochondrion. Later on this eukaryotic cell then consumed a cyanobacterium, giving rise to the chloroplast (plastid) through a secondary endosymbiosis event. Despite it being one of the most controversial and laughable theories when first hypothesised, the endosymbiotic model is now immensely respected by many biologists and many aspects have been confirmed spectacularly by ongoing evidence including phylogenetic analysis, genome analysis and comparisons of organelles to prokaryotic organisms. With the theory never going to be a hundred percent proven the strong evidence gathered has made it one of the strongest contenders for the evolution of the eukaryotic cell.

Introduction

The three major domains of life including the archaea, bacteria (prokaryotes) and eukarya were first established by Carl Woese using ribosomal RNA (rRNA) for phylogenetic analysis. The original divergence of lineage gave rise to bacteria and archaea about 3.5 billion years ago (bya), but not

eukaryotes, these diverged about billions of years later. However, major changes took place in the Earth's biosphere as consequence of the diversification of microorganisms from bacteria and archaea, such as the generation of an oxygenated atmosphere. Bacteria took advantage of this oxygen and developed the ability to respire oxygen, with the oxidation of organic compounds they were able to obtain more energy leading to the development of larger cell populations including the eukaryotic cell. Eukaryotic organisms contain several interrelated characteristics that distinguish them between prokaryotes. Table 1 below, shows the unique differences between prokaryotic and eukaryotic organisms, despite there being vast differences between the two organisms, the endosymbiotic theory still states that there huge significance between the two[1].

Characteristic

Eukaryotes

Prokaryotes

Membrane Enclosed Organelles

Yes

No

Ribosomes mass

80S

70S

Plasmids

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Rarely

Yes

Cell Wall component

Cellulose (in plants), Chitin (fungi)

Peptidoglycan, muramic acid

Histone proteins

Yes

No

DNA Structure

Contained in the nucleus and forms structures called chromosomes.

Circular and covalently closed. It is naked and lies free in the cytoplasm.

Genes arranged in operons

No

Yes

Nucleus present

Yes

No

Table 1: The differences of certain characteristics of eukaryotic and prokaryotic organisms

This got scientists probing the origin of eukarya, asking how this third domain of life which including a membrane enclosed nucleus and organelles, emerged. Many hypotheses have been proposed on the origin of the eukaryotic cell, the most supported is the endosymbiotic theory. Symbiosis is defined as an association between two or more different species. This definition clearly excludes associations between individuals of the same species. A major event in which symbiosis supposedly played a beneficial role was in the evolution of the eukaryotic cell and its organelles (i. e. chloroplast, mitochondria) through associations involving different species of prokaryotic cells. In this manner, the eukaryotes acquired the metabolic machinery of cellular respiration and photosynthesis from the endosymbionts, an endosymbiont being any organism that lives within the body or cell of another organism[2].

Figure 1[3]- The different symbiotic associations - Organisms that are involved in this process can either benefit, be harmed or not be affected by this association. In parasitism one of the species benefit, the degree of harm to the host is very severe and it depends on the host for food e. g. fungi, viruses and worms. In commensalism, one of the species benefit while the other one remains unaffected, e. g. remora suckerfish attach to the shark to gain food. In mutualism both organisms benefit from the symbiosis event.

The endosymbiotic theory claims that the eukaryotic cell is not a single entity but rather a combination of different prokaryote cells that evolved to live together in a mutually beneficial way. The endosymbiosis theory is best

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explained in the origins of the organelles of the mitochondria and the chloroplast. It was thought about two billion years ago, in which only prokaryotes inhabited the Earth, successive symbiosis occurred between different prokaryotic species as figure 1 on the page below illustrates and explains.

Figure 2[4]- Endosymbiotic theory - Chloroplasts and mitochondria may have descended from a small cyanobacteria and aerobic bacteria respectively that were engulfed by another larger prokaryote. A large prokaryotic organism engulfed a chemo-organotrophic organism, but did not digest it and it became the eukaryotic cell with the common organelle known as the mitochondria (A). This eukaryotic cell, then similarly took up a species of cyanobacteria by a similar engulfing event (B). The cyanobacteria evolved into a chloroplast, enabling the eukaryotic cell to become photosynthetic (C). This process also involves the extensive loss of DNA from the bacteria symbiont as well as transfer of genes to the nucleus of the eukaryotic host.

As stated above, the key step that the endosymbiotic theory supposedly played a role in was the evolution of the two key organelles, the chloroplast and the mitochondria. Both the organelles are very similar in terms in both structure and function, but most importantly both of these evolved in a very similar fashion. The mitochondria (figure 2) are the key players in aerobic respiration, they facilitate the process of oxidative phosphorylation in which the flow of electrons is energetically favourable enough to produce a gradient of protons, which is finally used to synthesise ATP - arguably one of the most important molecules ever to have existed on Earth.

Figure 3[5]- Mitochondria structure - Mitochondria are surrounded by two membranes. The outer membrane is quite permeable and is composed of proteins and lipids, the inner membrane is rich in proteins and is less permeable to ions and small organic molecules. The cristae are a series of folded internal membrane that has attached the stalked particles for the influx of protons and the enzyme ATP synthase that together catalyze the synthesis of ATP via oxidative phosphorylation. The matrix possesses the enzymes needed for the link reaction and Krebs cycle, the reactions that proceed before oxidative phosphorylation.

The chloroplast is the site of photosynthesis in plants, one of the most important organelles in the plant behind the nucleus. In this two step process, light captured from the sun is used to excite electrons in chlorophyll molecules and produce a proton gradient just like of the mitochondrion to produce ATP (Photophosphorylation), and then carbon dioxide is fixed to produce glucose and other sugars which are vital for the plants survival (Calvin Cycle).

Figure 4[6]- Chloroplast structure - Chloroplast are surrounded by a double membrane, a permeable outer membrane and a less permeable membrane like that of the mitochondria. The stroma is a fluid filled matrix which houses the Calvin Cycle and also contains storage structures such as starch grains. The grana are stacks of disc like structures called thylakoids which contain the chloroplast pigments. They are arranged in complexes called photosystems which is very important in capturing light and producing ATP.

The endosymbiotic theory is strongly supported by findings from structural, molecular and biochemical studies of the eukaryotic cell. Circumstantial evidence commonly used to support the theory of endosymbiosis is the similarity of the organelles of the mitochondria and chloroplast compared to the bacteria. However more rigorous evidence to support this theory comes from the examination of evolutionary relationships of the mitochondria and chloroplast genomes via phylogenetic analysis.

Kwang Jeon's surprise discovery

In 1966, a discovery was made by microbiologist Kwang Jeon that supported the hypothesis of endosymbiosis; that bacteria can evolve into organelles. Jeon was studying a single cell protist species *Amoeba proteus* which is mostly aquatic living in fresh water ponds and moves by extending a finger of protoplasm called pseudopodium. But accidentally one of his cultures containing the organism became contaminated and infected by a bacterium. Jeon was intrigued that not all of the infected amoebas died straight away as some continued to grow, so he maintained those infected cultures for further analysis. About five years later, the descendant amoebas were host to many bacterial cells, yet they were still healthy and alive. When those amoebas received antibiotics that usually do not harm amoeba, they died. This unintentional experiment confirmed that those amoebas had come to rely on the bacteria that had infected them originally. Through transplanting experimentation, Jeon found out that the nucleus of the amoebas could not live without the once pathogenic bacteria. Studies had showed the infected amoebas had lost the ability to make an essential enzyme and depended on the bacteria to make them. The bacterial cells had become vital

endosymbionts and Jeon's accidental discovery proved that it was possible for an organism to become dependent on and a functional part of invading organisms[7]. " Rather than eliminating competitors, evolution eliminated competition itself on the basis of symbiotic relationships[8].

Symbiosis between present day photosynthetic organisms and non-photosynthetic organisms also support the endosymbiotic hypothesis of the formation of the eukaryote. For instance, *Cyanophora paradoxa*, a biflagellate protist, engulfed an endosymbiotic cyanobacterium (known as a cyanelle), which once taken up functions as a chloroplast and supplied the host cell with photosynthetically reduced carbon[9]. These discoveries basically proved that the theory of endosymbiosis does actually exist, and it could have led to the formation of the eukaryotic cells and its organelles.

Genetic Evidence

Supporting the symbiotic origin of the mitochondria and chloroplast is both the organelles possess their own genetic material, DNA which is distinctly different from the nuclear DNA of eukaryotic cells. The architecture of most the mitochondria and all of the chloroplast DNA is evidentially prokaryotic, being circular and having a single origin of replication, as figure 4 below clearly indicates. The genes of the mitochondria are also arranged in operons which are " one or more genes transcribed into a single mRNA and under the control of a single regulatory site[10]" which also reflects prokaryotic ancestry, with similar arrangement of genes. Lactose uptake is controlled by an operon in prokaryotic organisms, with the binding of RNA polymerase blocked by a repressor protein, but is not in eukaryotic organisms. This organization of genes is with stark contrast compared to that of the <https://assignbuster.com/endosymbiotic-theory-the-modern-or-organelle-biology-essay/>

eukaryotic nucleus which has multiple, linear chromosomes and individual genes, each with its own regulatory elements[11].

Figure 5[12]- Map of the human mitochondrial genome - The circular genome contains over 15, 000 base pairs. The genome encodes the 16S and 12S rRNA, which correspond to the prokaryotic 23S and 16S rRNAs.

Furthermore, evidence suggests over evolutionary time, these organelles lost many genes that were unnecessary for life as an organelle inside the new host cell, and many genes were transferred to the nucleus (Lake and Rivera 1996, Martin 1996). Thus, non-phototrophic eukaryotic cells are genetic contain DNA from two different sources, the first from the endosymbiont and the second the host cell nucleus. Photosynthetic eukaryotic contain three sources of DNA, the mitochondrial and chloroplast endosymbionts and the nucleus. In the mitochondria of a freshwater protozoan *Reclinomona*, it bears the largest collection of mitochondrial genes coding for 97 genes and contains 69, 034 base pairs. However as table 2 (page 6) illustrates, the human mitochondria genome is less than a quarter of this size meaning the base pairs missing were almost certainly genes coding prokaryotic characteristics from its bacterial ancestors that were not required. According to Anderson and co-workers in 1998 many genes remaining in *Reclinomonas* mitochondria are strikingly similar to that of the obligate intracellular parasite, *Rickettsia prowazekii* the unicell causing typhoid disease[13]. Therefore this provides supportive evidence that some mitochondria in some present day eukaryotic organisms still contain genes that caused them to become a prokaryote, and hence shows their bacterial past just as the endosymbiotic theory proposes.

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Figure 6[14]– Comparison of the genomes of *Reclinomonas americana* and *Rickettsia prowazekii* – The S10, spc and $\hat{I}\pm$ -operons are organized similarly in these two genomes indicating that *R. prowazekii* may have been one of the endosymbionts of the mitochondria in the evolution of the eukaryotic cell. The genes *rplKAJL* and *rpoBC* are also identically organized in *R. prowazekii* and the mitochondrial genome of *R. americana*.

Name and Symbol

Homo sapiens

Reclinomonas americana

Ribosomal RNA

Small rRNA

Larger rRNA

5S RNA

1

1

0

1

1

1

Transfer RNAs

22

26

NADH dehydrogenase (subunits ND1-ND4L)

7

12

ATP Synthase

(subunits 6, 8, others)

Total protein coding genes

13

62

Total genes

37

92

Size of DNA (kbp)

15. 596

69

Table 2[15]: A comparison of the mitochondrial genes of the Homo sapiens and Reclinomonas americana. As it clearly indicates above R. Americana contains many more genes than Homo sapiens in their mitochondria, demonstrating that it did not transfer the genes it did not require to the nucleus like the human mitochondria, and it is these genes that have not been transferred that are very similar to R. prowazekii.

Most DNA is stored in the nucleus, protected from the nucleus by the double nuclear envelope. The DNA of chloroplasts and mitochondria are protected from enzymes found in the cytosol by being located within the organelles themselves. However, one distinct difference from the nucleus is that the DNA in chloroplast and mitochondria is histone free. Histone proteins cause the linear DNA molecules that make up the eukaryotic chromosomes, to wound around these proteins to form specialised structures called nucleosomes. With no histones, the mitochondria is prone to free radicals and oxygen reactive species attacking the organelles and causing damage and mutations, no histone proteins therefore account for the high mutation rate in the mitochondria. Histone free DNA is a characteristic of prokaryotic organisms, indicating that there was a high chance that mitochondrial and chloroplast endosymbionts are indeed prokaryotic.

Comparisons of both the order and sequences for subunits of ATP synthase from chloroplasts and Synechococcus; a unicellular cyanobacterium, are consistent with the hypothesis that the chloroplast genome is part of the cyanobacterium. ATP synthase is an enzyme that catalyses the production of ATP via ADP and inorganic phosphate in oxidative phosphorylation. The genes for the ATP synthase of Synechococcus are arranged in two clusters, <https://assignbuster.com/endosymbiotic-theory-the-modern-or-organelle-biology-essay/>

this arrangement resembles those found in chloroplasts of eukaryotic cells, differing only in the absence of the \hat{I}^3 and s genes.

Binary Fission

Mitochondria and chloroplast reproduce identically to bacterial cells do; by binary fission, this process is explained by figure 6 below. Chloroplasts also contain traces of ftsZ, a protein which is required in the early stages of cell separation in binary fission. The chloroplast ftsZ is phylogenetically very close to ftsZ of Cyanobacteria, the assumed bacteria endosymbiont of chloroplast. This evidence is further enhanced by the fact that eukaryotic cells divide by mitosis, signifying these organelles must have come from a prokaryotic origin since they used the prokaryotic way to reproduce rather than the eukaryotic way of mitosis.

Figure 7[16]- The sequence of cell division in Binary Fission - The mitochondria begins by replicating a copy of its DNA to create two duplicate sets, the mitochondria then starts to elongate and increase in size (1). The two replicated DNA's migrate to the poles of the cell, cell division begins as the plasma membrane grows inwards (2). The plasma membrane grows inwards completely, and a complete cell wall is produced for both daughter cells (3 and 4).

Image

Figure 8[17]- Similarities between (a) eukaryote chloroplasts and (b) cyanobacteria noted by Schimper. Dividing chloroplasts (indicated by arrows on a) are very similar to those of dividing cyanobacteria (indicated by

arrows on b), both of them carry out the same replication process to reproduce; binary fission.

Antibiotic Resistance

It is astonishing to find many remarkable similarities in the structure and chemical mechanisms both employed by the mitochondria and chloroplasts compared to prokaryotes. One particular similarity is the response to specific antibiotics, which the mitochondria and chloroplasts share with prokaryotic, but do not share with the nucleus and the remainder of the organelles in the eukaryotic cell. Experimental tests on mitochondria and chloroplasts reveal that these organelles are susceptible to antibiotics such as tetracycline similar to that of prokaryotes however eukaryotic cytoplasm remains unaffected by these drugs. Tetracycline is a large family of antibiotics that inhibits almost all gram positive and gram negative bacteria and they work by inhibiting protein synthesis by binding to the small ribosomal subunits which prevent aminoacyl transfer RNA from entering the acceptor sites on the ribosome, so the amino acids can't be added to the growing peptide chain. The fact that mitochondria and chloroplasts are sensitive to tetracycline, indicates they contain their own protein synthesising machinery and it provides major evidence that these organelles contained bacterial endosymbionts.

Ribosomal Structure

The mitochondria and chloroplast contain their own 70S type ribosomes which are very similar to the type in prokaryotic organisms, and are unlike the 80S type ribosomes typical of the cytoplasm of the eukaryotic cell.

Ribosomes are organelles that catalyze the translation of mRNA into an
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amino acid sequence, it contains two subunits the 30S subunit which match the anticodon from the tRNA to the codon of the mRNA and a larger 50S subunit that catalyses the formation of a peptide bond that links the amino acids together.

Another difference between the mitochondria and chloroplast compared to prokaryotes is that translation is initiated by the same codon. Translation is the ribosome and tRNA mediated process by which a protein is produced whose amino acid sequence is derived from the codon sequence of an mRNA molecule. The initiator codon in translation for both bacteria and these two organelles is N-formylmethionine, and not with methionine as in the eukaryotic cell. The fact that mitochondria and chloroplasts start the process of translation with the same initiator codon as bacteria, indicate they are likely to be endosymbionts.

Phylogenetic Analysis

Phylogenetic analyses based on ribosomal RNA (rRNA) sequences are one of the standard methods of inferring relationships among diverse organisms. Although no single molecule can define an evolutionary lineage once gene transfer between organisms has occurred, but rRNA is the molecule of choice for inferring evolutionary relationships since its present in both eukaryotic and prokaryotic cells and is functionally conservative, evolving very slowly. In phylogenetic analysis sequences of relatively preserved genes from mitochondria and chloroplasts genomes of representative organisms of the three domains (bacteria, archaea and eukarya) are aligned, and a phylogenetic tree is constructed. If the mitochondria and chloroplasts

originated endosymbiotically from bacteria, their genes should branch from <https://assignbuster.com/endosymbiotic-theory-the-modern-or-organelle-biology-essay/>

the domain bacteria in the phylogenetic tree. More importantly, persuasive evidence in support of the endosymbiotic origin of the plastid and mitochondria has also been provided from similar analyses based on rRNA sequences.

The study was based on the small 16S rRNA, which is a small size class of rRNA characteristic of both prokaryotes and mitochondria and chloroplasts of eukaryotic organisms. “ As early as the late 1960s Carl Woese began to assemble catalogs of oligonucleotide sequences released by the in vivo digestion of rRNA isolated from living prokaryotes and eukaryotes”[18]. Using the data derived from the experiment, Woese constructed a phyletic hypothesis for the origins of the eukaryotes and the phyletic relationship among the prokaryotes. The rRNA data received indicated that both the plastid and mitochondria descended from very different prokaryotic organisms. More specifically, the 16S rRNA sequences of the plastid closely aligned with those from certain cyanobacteria. Whilst mitochondria share homologous sequences with the purple bacteria (proteobacteria) and their relatives, this is a big indication that these bacteria were the symbionts of these key organelles. As figure 3 on the page below clearly indicates cyanobacteria and plastids share sequence homology in the protein Elongation Factor Tu (the area in the red box showing this).

Figure 8[19]- Comparison of the amino acid sequences of Elongation Factor - Tu in cyanobacteria, plastids and proteobacteria - The box in red on figure 8 above shows a protein signature sequence that is similar from both plastids and cyanobacteria indicating that cyanobacteria could have been a possible bacteria endosymbiont of the plastid. Many other proteins containing similar <https://assignbuster.com/endosymbiotic-theory-the-modern-or-organelle-biology-essay/>

protein signatures between plastids and cyanobacteria include polymerase 1, sigma factor and ribosome S1 protein.

One importantly intriguing question yet to be answered is whether mitochondria and plastids are monophyletic or polyphyletic? In other words, are the chloroplasts of all living eukaryotic organisms descended from a single engulfed cyanobacterium (monophyletic) or are they descendants of several independent engulfed cyanobacteria (polyphyletic). Most studies based on partial 16SrRNA sequences from chloroplasts and cyanobacteria strongly supported a monophyletic origin of plastids, these include, Giovannoni et al. 1988; Douglas and Turner 1991; Maid and Zetsche 1991.

Barnabas and his co-workers performed a phylogenetic analysis that took both nucleotide sequences from 5S rRNA and amino acid sequences from Ferredoxin and c type cytochromes into account. Since ferredoxin is an iron sulfur containing protein which is used in a number of oxidative - reductive pathways including oxidative phosphorylation, the doubling event that occurred early in its evolution provided a baseline for the production of the phylogenetic tree. Organisms whose ferredoxins most resemble the sequences from the chloroplast were cyanobacteria, indicating the chloroplast had a prokaryotic ancestor.

The cytochromes c analysis that Barnabas and his co-workers used showed a phylogeny in which the eukaryotic cytochromes sequences were similar to that of the cytochromes c2 sequences of purple photosynthetic bacteria. Since cytochromes functions exclusively in the mitochondria, it is very likely that the organelle derives from these bacteria. The evidence of strong

homologies between cyanobacteria and plant chloroplasts for their cytochromes and ferredoxin sequences indicate that eukaryotic plant cells must have incorporated a chloroplast organelle that may at one time have been a prokaryotic cyanobacterium[20].

Nuclei

The nucleus also has evidence suggesting it was formed by endosymbiosis, since the nucleus was absent in prokaryotes, and was first seen only in eukaryotes. In 1994 Lake and Rivera suggested that the nuclear membranes were formed from a captured prokaryotic organism that provided genetic material. This was backed up accordingly by Gupta and his co-workers in 1994, when they found vast similarities in among endoplasmic reticular genes in the eukaryote *Giardia* and in genes of gram negative bacteria.

Alternative Hypothesis

The endosymbiotic theory has not always gained acceptance by some biologists, and many other hypotheses exist in the biological world on the evolution of the eukaryotic cell. The autogenous theory states that the organelles evolved within the cell by progressive compartmentalization and this led to the formation of other cell structures such as vacuoles, endoplasmic rectilum and lysosomes. The endosymbiotic theory was criticised in 1998 by Martin and Muller stating that the need for energy exchange in ATP drove the establishment of mitochondrial endosymbionts, this was known as the Hydrogen Hypothesis.

Conclusion

Many lines of evidence support the endosymbiotic theory in the formation of the eukaryotic cell in which cyanobacterium and chemoorganotrophic bacterium was incorporated into a prokaryotic cell. Most of the telling evidence is based on molecular and genetic studies of prokaryotic and eukaryotic organisms. Many phylogenetic analyses that were based on 5S rRNA sequences showed amino acid sequences similar in the mitochondria and plastid to many purple and cyano-bacteria respectively. Mitochondria and plastids share many similar characteristics including antibiotic sensitivity, cell division by binary fission, circular DNA and 70S ribosomes. But despite the theory being laughable when first proposed, it has now gained the acceptance from many top biologists including Doolittle and Brown in 1994 who stated “ the endosymbiont hypothesis for the origin of the mitochondria and chloroplasts is as firmly established as any fact in biology”[21].