

Endosymbiotic theory in eukaryotic cells



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Endosymbiotic theory- the modern, or organelle- containing eukaryotic cell evolved in steps through the stable incorporation of chemoorganotrophic and phototrophic symbionts from the domain Bacteria.

The hypothesis of endosymbiosis is at present the most widely accepted theory on the evolution of the eukaryotic cell. This current theory states that the mitochondria and chloroplasts contained within the eukaryotic cell, are there due to the integration of free living bacteria which implement aerobic metabolism, chemoorganotrophic bacteria, and bacteria which implement oxygenic photosynthesis, cyanobacteria. It is thought that symbiosis, in addition to natural selection and mutations, is also a driving force in the evolution of the modern or organelle containing eukaryotic cell. This essay will describe in detail the endosymbiotic theory and its features, discuss the evidence which supports it and then discuss its major opposing theories, the hydrogen hypothesis and the syntrophy hypothesis.

Short history of the endosymbiotic theory

Many biologists have had a role in what is now known as the endosymbiotic theory. Firstly in 1883, Andreas Schimper proposed that particular organelles evolved from the symbiotic union of two different organisms, (this was while he was studying chloroplast division within green plants and observed a similarity between chloroplasts and free living cyanobacteria.), (Vargas-Parada, 2010). In 1905, Konstantin Merezhkovski devised the term, ‘ symbiogenesis’ , due to his work on lichens leading him to speculate that “ more complex cells evolved from a symbiotic relationship between less complex ones” (2006). Then in the 1920s, Ivan Wallin suggested that organelles such as mitochondria and chloroplasts began as symbiotic

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bacteria and that species creation could have occurred through endosymbiosis. Finally, much later in 1967 Lynn Margulis collected various microbiological observations which supported the hypothesis of endosymbiosis.

Evolution of the eukaryotic cell

The current evidence for the evolution of eukaryotic cells suggests that around 4 billion years ago ancestors of Bacteria and Archea arose. It is thought that in bacteria, around 3.2 billion years ago, phototrophy occurred, with the common ancestor of many bacteria thought to be an anaerobic phototroph. Then around 2.7 billion years ago oxygen-generating cyanobacteria developed, which over time caused an increase in the atmospheric oxygen levels. The atmosphere slowly changed from anoxic to oxic due to this rise in oxygen levels. At some point during this period eukaryotic microorganisms containing organelles evolved and the oxic environment drove their evolution.

Main distinguishable features of present day eukaryotes from prokaryotes

In many prokaryotic cells their DNA is arranged into a single loop, is circular and unlike eukaryotes, it is not associated with histones and is therefore termed naked. Prokaryotic cells reproduce by the process of binary fission, are mainly unicellular organisms and are usually smaller than eukaryotic cells. In the nucleus of the eukaryotic cell, the DNA is organised into chromosomes, which is surrounded by a membrane. Eukaryotic cells reproduce by the means of mitosis and meiosis, are usually larger than prokaryotic cells and are usually complex and multicellular. The main

distinguishing feature of eukaryotic cells is that they contain membrane bound organelles, with the most noteworthy being the mitochondria and chloroplasts.

The major organelles involved in the endosymbiotic theory

The endosymbiotic theory refers to the organelles mitochondria and plastids, (plastids refer to chloroplasts, chromoplasts, and gerontoplasts, to name a few), however mainly focuses on chloroplasts. The major reason for these two organelles being involved in the endosymbiotic theory is because they both contain a small genome. Moreover, both of these organelles contain the operating systems required for cellular functions such as protein synthesis, for example ribosomes and transfer RNA, and also the cellular constituents needed for translation.

Mitochondria

Mitochondria are the site of respiration and oxidative phosphorylation in eukaryotic cells. They are membrane bound organelles, with each cell containing thousands of them. Mitochondria show variations in their morphology, and can be rod-shaped or spherical. They are surrounded by two membranes, an outer membrane and an inner membrane. The outer membrane is made up of protein and lipid and contains channels which allow the diffusion of ions and small organic molecules. The inner membrane is less permeable and is invaginated to form cristae. Oxidative phosphorylation occurs on the inner membrane; with cristae allowing maximum surface area for ATP synthase molecules, which are involved in the synthesis of ATP (Adenosine Triphosphate), the final step of oxidative phosphorylation. It is for

this reason that they are considered to be the power generators of the cell. Mitochondria possess their own DNA which is independent of the cell's chromosomal DNA.

The mitochondrial genome mainly encodes proteins needed for oxidative phosphorylation and also encodes ribosomal RNAs, (rRNAs), transfer RNAs, (tRNAs) and proteins necessary for protein synthesis. Mitochondria use simplified genetic codes, which seem to have arisen from selection pressure for smaller genomes (Madigan, 2009 p. 351). Even though mitochondria possess their own genome they still require proteins encoded by nuclear genes.

Chloroplasts

Chloroplasts are membrane bound organelles found in phototrophic eukaryotic cells. These cells are found in plants algae and some protists. Chloroplasts contain chlorophyll which is the photosynthetic pigment present within them. Chloroplasts are usually larger than bacterial cells and can differ in size and shape. Chloroplasts again like mitochondria consist of two membranes and inner membrane and an outer membrane. Their outer membrane is permeable and the inner membrane is less permeable. The inner membrane surrounds the stroma, which houses the photosynthetic pigment, chlorophyll and other cellular components needed for the process of photosynthesis in thylakoids. Thylakoids stacked into the structural units, grana. The thylakoid membrane is not permeable to ions and other metabolites, due to the light reactions of photosynthesis needing the proton motive force which is necessary for the synthesis and release of ATP. The stroma of the chloroplast holds large amounts of the enzyme RubisCO, <https://assignbuster.com/endosymbiotic-theory-in-eukaryotic-cells/>

(ribulose biphosphate carboxylate), which catalyses the Calvin cycle or the dark reactions of photosynthesis. The Calvin cycle converts CO₂ into various organic compounds like glucose which are needed by cells.

Chloroplasts also contain their own DNA, which is also independent of the cell's chromosomal DNA.

The identified chloroplast genomes are all circular DNA molecules, with each chloroplast containing several matching copies of the genome (Madigan, 2009 p. 350). Genes contained within the chloroplast encode for proteins required for photosynthesis and autotrophy to occur and also rRNA and tRNA used for the processes of transcription and translation. Like mitochondria, chloroplasts have some proteins, which are encoded by nuclear genes and not just by the chloroplast genome.

Introduction to the endosymbiotic theory

The primary endosymbiotic theory implies that the mitochondrial ancestor was a free living facultatively aerobic alphaproteobacterium, attained by another cell and therefore giving rise to a eukaryotic cell. (Madigan, 2009 p. 520) A species of cyanobacterium is thought to be the ancestor of chloroplasts, obtained by a heterotrophic eukaryote, after eukaryotic cells had appeared around 1.5 billion years ago (Madigan, 2009 p. 520) and was obtained as an internal symbiont (Bruce Alberts, 2002).

Secondary endosymbiosis refers to the event where several non-phototrophic organisms attained chloroplasts, after the primary endosymbiosis event is said to have occurred. Secondary endosymbiosis is

said to have been an important factor in the evolution of eukaryotes, bringing the modern diversity of life into being (Macfadden, 2001).

Features of and molecular evidence for the primary endosymbiotic theory

The main point of the primary endosymbiotic theory, and which gives it its credibility, was that both mitochondria and chloroplasts both contain DNA, with rRNA, tRNA and proteins involved and needed for the respiratory chain in mitochondria and proteins needed for photosynthesis in chloroplasts, being encoded by these small genomes within mitochondria and chloroplasts. Non-phototrophic eukaryotic cells are genetic chimeras containing DNA from two different sources, the endosymbiont, which is the mitochondria, and the host cell nucleus (Madigan, 2009 p. 520). Eukaryotes which are phototrophic, for example algae and plants, have DNA from two endosymbionts, the mitochondria and the chloroplasts as well as the nuclear DNA. The majority of mitochondrial DNA and chloroplast DNA is similar to bacterial DNA in its shape, which is circular and size.

The second feature of primary endosymbiosis is that genes originating from bacteria are found in the nucleus of the eukaryotic cell. This has been proven by sequencing genomes, which have shown that nuclear genes encode properties unique to mitochondria and chloroplasts, (and also which closely resemble genes of bacteria), showing that during the evolution of the eukaryotic cell these genes were transferred to the nucleus of the eukaryotic cell, from the bacterial endosymbionts, during the development of the organelle from the engulfed cell (Madigan, 2009 p. 521).

The third feature of primary endosymbiosis is that the mitochondria and chloroplasts contain their own ribosomes. Ribosomes are present in eukaryotic cells and prokaryotic cells, with eukaryotic cells possessing the larger form, 80S, and prokaryotic cells containing the smaller, 70S, ribosomes. The mitochondria and chloroplast contain these 70S ribosomes.

The fourth feature is antibiotic specificity. Mitochondria and chloroplast are sensitive to antibiotics which kill bacteria or are bacterial inhibitors. Some for example streptomycin do this by specifically interfering with the functions of the 70S ribosomes, which occurs in the same way in mitochondria and chloroplasts (Madigan, 2009 p. 521). Rifampicin is an antibiotic which in bacteria affects the RNA polymerase. It does not have this effect on eukaryotic RNA polymerase however does inhibit mitochondrial RNA polymerase.

The fifth and final feature of primary endosymbiosis is that of molecular phylogeny. Phylogenetic studies comparing organelles and rRNA support the theory of mitochondria and chloroplasts deriving from bacteria.

There is also other evidence in addition to what is mentioned above. Both mitochondria and chloroplast are surrounded by two membranes. It is thought that the inner membrane is the original membrane which contained the prokaryotic cell and the outer membrane results from the process of endocytosis when the bacteria were taken into the eukaryotic cell. Protein synthesis in the endosymbionts begins with N- formyl methionine, the same amino acid that initiates protein synthesis in bacteria whilst in eukaryotic cells protein synthesis is initiated by methionine. Also the thylakoid

membrane and the protein complexes which it contains are like those that can be found in cyanobacteria (Pyke p. 5) , and chloroplasts can divide in a way which is similar to the process of binary fission which is carried out by bacteria.

This evidence all suggests that the host cell which obtained the mitochondrion by phagocytosis was an anaerobic eukaryotic cell, (which already contained a nucleus) and that the mitochondrial endosymbiont was an obligate anaerobe (Mentel, 2010). This event was later followed by the endosymbiosis of a cyanobacterium, allowing the eukaryotic cell to become photosynthetic. In this way the host eukaryotic cell attained permanent organelles which are suited to energy production. It was also mutually beneficial for the symbionts which obtained a constant and accommodating environment for their growth.

Secondary endosymbiosis

The primary endosymbiosis event in the common ancestor plants and in green and red algae is said to have created the modern day chloroplast. The secondary symbiotic event refers to non-phototrophic eukaryotes obtaining chloroplasts by the endocytosis of a green or red algal cell and consequently becoming phototrophic. It is thought that secondary and even further endosymbioses lead to the diversification of eukaryotes.

Problems with the endosymbiotic theory

To support the endosymbiotic theory in the 1980s, Tom Cavalier-Smith proposed that certain single-celled eukaryotes which are at present still living, bear a resemblance to earlier eukaryotes, were ‘ primitively

amitochondriate' (Lane, 2005 p. 42), (basically eukaryotes without any mitochondria), and Cavalier-Smith named them 'archezoa'. (He later abandoned this theory in 2002, (Cavalier-Smith, 2002)) These cells derived their energy via fermentation and prefer environments with little oxygen and were thought to be the bridge between early eukaryotic cells (as archezoa contain a nucleus) and prokaryotic cells, which would have supported the theory of a bacterial cell being phagocytised, but not digested, leading to the possession of a mitochondria in the early eukaryotic cell. It was then thought that as oxygen levels on earth started to rise, the mitochondria too, began to evolve, due to aerobic respiration being more resourceful than anaerobic respiration, which again supported that the phagocytosis of this bacterial cell was for the purpose of a more efficient way of generating energy. In March 2000, Jan and Siv Andersson proposed the Ox-Tox hypothesis to explain that aerobic respiration was the selective pressure leading to the gain of the mitochondria, originally selected for the removal of oxygen by the host cell (Andersson, 2000). This was due to research showing that the genome sequence of *Rickettsia prowazekii* had a strong phylogenetic relationship with mitochondrial proteins (Andersson, 2000).

However in the late 1990s these hypotheses were questioned due to the appearance of contradictory evidence. The genomes of archezoa were sequenced and genes were found which showed that the ancestors of archezoa once had mitochondria, even though there was no physical indication of them in the cell. Some 'archezoa' such as *Giardia* were found to have mitochondria but in the form of mitosomes, which still carried out mitochondrial processes (Lane, 2005 p. 47) again implying that these

eukaryotes once contained mitochondria within their cells. It was then suggested that the original host in the eukaryotic merger was a methanogen, due to the structure of eukaryotic and methanogenic histones and the 3D conformation of the DNA associated with the histones being closely related (Lane, 2005 p. 48).

Other problems with the endosymbiotic theory are that if a bacterium was phagocytised by a eukaryotic cell, it would definitely have been digested and neither mitochondria nor chloroplasts are able to survive independently outside of the eukaryotic cell.

Chloroplasts aren't the main focus when disproving the endosymbiotic theory as it's thought that when the phagocytosis of a phototrophic symbiont occurred, the host cell already contained mitochondria.

The alternative theories to the mainstream endosymbiotic theory

The hydrogen hypothesis

In 1998, William Martin and Miklós Müller proposed the hydrogen hypothesis. Unlike other hypotheses which suggested that the formation of eukaryotic cell was due to the rising oxygen levels, this hypothesis suggests that instead it was to do with hydrogen. They state that “ Eukaryotes are suggested to have arisen through symbiotic association of an anaerobic, strictly hydrogen dependent, strictly autotrophic archaeobacterium (the host) with a eubacterium (the symbiont) that was able to respire, but generated molecular hydrogen as a waste product of anaerobic heterotrophic metabolism.” (Müller, 1998). The hydrogen hypothesis is based on hydrogenosomes which are anaerobic mitochondria, that produce ATP and

with their waste products including hydrogen gas and carbon dioxide and which also are able to function in low oxygen environments. Martin and Müller suggested that there was a methanogenic ancestry of the host (Müller, 1998) due to methanogens needed the very products (hydrogen and carbon dioxide), which are released by hydrogenosomes and because hydrogenosomes survive in the same environment as methanogens. Due to the intimate association between the methanogen and the bacterium, the symbiosis becomes closer, due to the methanogen needing the products of respiration produced by the bacteria and it is gradually engulfed by the methanogen. By the process of lateral gene transfer from bacterium to methanogen, the methanogen is now able to carry out aerobic and anaerobic respiration (Lane, 2005).

There are known examples today of bacteria which live as endosymbionts within other prokaryotes (Mentel, 2010), which again helps support this hypothesis. Another point which gives the hydrogen hypothesis credibility is that all anaerobic and aerobic mitochondria all originated from a facultatively anaerobic ancestral state (Mentel, 2010). Also according to the hydrogen hypothesis, the host cell was not required to have possessed a nucleus (Müller, 1998). The formation of the nucleus is explained by genes for the synthesis of lipids being transferred to the host chromosome from the symbiont leading to the host synthesising these bacterial lipids and then resulting in the formation of the endoplasmic reticulum, an internal membrane system and origination of a eukaryotic nucleus (Madigan, 2009 p. 376).

The effects of the hydrogen hypothesis for chloroplasts have not been considered in much depth (Allen, 2003).

The syntrophy hypothesis

This hypothesis was proposed by Purificación López-García and David Moreira in 1999. This hypothesis is based on similar metabolic considerations as the hydrogen hypothesis proposed by Martin and Müller (Moreira, 1999). There are some similarities between the two hypotheses. Firstly, they both maintain that the metabolic nature of the original symbiotic event involved both hydrogen and syntrophy, secondly that the hydrogen dependent autotrophic archeon must have been a methanogen (Moreira, 1999) and finally that the mosaic nature of the eukaryotic genome can be explained by 'lateral gene transfer and replacement over a long symbiotic life' (Moreira, 1999). The difference between these hypotheses is that the syntrophy hypothesis states that the organisms involved were $\hat{\Gamma}$ -proteobacteria, which are ancestral sulphate reducing myxobacteria, and methanogenic archaea (Moreira, 1999). The hydrogen hypothesis states that an $\hat{\Gamma}$ -proteobacteria began the symbiosis, whereas in the syntrophy proposal it is thought that two eubacterial types were involved, a sulphate reducing $\hat{\Gamma}$ -proteobacteria, (which produced hydrogen for fermentation), and also an $\hat{\Gamma}$ -proteobacterial methanotroph became symbionts and used the methane which was generated by the methanogen to produce CO_2 . Both of these hypotheses agree that the ancestral mitochondria were of anaerobic origin (Moreira, 1999).

The chimeric nature of the eukaryotic cell

The hypotheses mentioned above, suggest that the modern eukaryotic cell is a chimera, which is a cell that is made up of features from both Bacteria and Archaea (Madigan, 2009 p. 376). Eukaryotes contain the same sort of lipids which are found in Bacteria and the tools they contain for transcription and translation are like those found in Archaea (Madigan, 2009 p. 376). “ The chimeric nature of nuclear genomes can be partially explained by the endosymbiont hypothesis of mitochondria” (Hua). At some stage in eukaryogenesis, cellular and genomic combination of the two different organisms (which vary for the hydrogen and syntrophy hypothesis) happened with gene transfer from bacteria to archaea and then subsequent replacement. The bacterial genome is then thought to have condensed down and could have also dematerialised as the cell underwent evolution, (as horizontal gene transfer, which includes the introduction and loss of genes, is often seen in symbionts (Madigan, 2009 p. 377)). The developing eukaryotic cell must have inherited some of the archaeal-DNA processing systems, whereas the cellular metabolism systems are thought to have come from bacterial organotrophy (Hua).

During its evolution the modern day eukaryotic cell has become ever more complicated and has led to the appearance of complex, multicellular life forms which are powered by mitochondria and chloroplasts in phototrophic eukaryotic cells. The progression of its evolution and how all the individual compartments of the cell occurred is expected to have taken an extensive amount of time. Variation and natural selection evidently occurred, perfecting the cell by the removal of mechanisms and cellular structures

which were deemed useless, leading to biological diversity. It is still undetermined which of these hypotheses mentioned accurately describe the origin of eukaryotes and is thought that the further sequencing of genomes and phylogenetic analyses of the prokaryotic and eukaryotic genomes will provide an improved elucidation of the origin and diversity of eukaryotes.