Mitochondrial Evolution

Introduction

The mitochondrion is normally referred to as the "powerhouse of the cell" and for good reason. Mitochondria are a pervasive and diverse group of organelles. They are composed of a phospholipid bilayer double membrane. The inner membrane is composed of cristae while the outer membrane is smooth. The inner membrane separates the intermembrane space from the mitochondrial matrix- where different enzymes used in cellular respiration as well as mitochondrial DNA reside (1).

There are four different categories of mitochondria found within different organisms. The first category is probably the most familiar and is typical to mammalian cells. These mitochondria respire diatomic oxygen (O_2) during ATP synthesis and pyruvate breakdown in which carbon dioxide and water are produced as end-products. Approximately 36 moles of ATP per mole of glucose is generated during the Kreb's cycle and by the electron transport chain that is found within the inner lining of the mitochondria. This particular group of mitochondria are found in organisms that rely solely on oxygen for biochemical processes including vertebrates, plants, and some protists. However, mitochondria found within invertebrates do not use O_2 as the terminal acceptor during certain phases of their life cycle. Only 5 moles of ATP per mole of glucose are produced by these anaerobic mitochondria. There are other mitochondria found in certain unicellular eukaryotes that produce only 4 moles of ATP per mole of glucose. An electron transport chain is completely absent in these kind of mitochondria; ATP is instead synthesized from pyruvate breakdown via simple fermentations. These mitochondria are often referred to as hydrogenosomes. The final category of mitochondria are often called mitosomes. Mitosomes are not involved with ATP synthesis whatsoever. Eukaryotes that have these organelles instead synthesize ATP within the cytosol using enzymes that are typically found in hydrogenosomes. This process generates approximately 2-4 moles of ATP per mole of glucose (2). Mitosomes and hydrogenosomes are often referred to as mitochondrion -related organelles since their genome is so reduced.

Origin and Evolution

At present the endosymbiotic hypothesis is the dominant and recognized dogma when it comes to mitochondrial origin and evolution. The endosymbiotic hypothesis states that an early ancestor of eukaryotes engulfed a prokaryotic cell that was aerobic but non-photosynthetic. The engulfed prokaryotic cell eventually formed a symbiotic relationship with the eukaryotic cell and became dependent on it as a host cell. As evolutionary time passed, what was once two individual organisms (a prokaryotic cell and a eukaryotic cell) fused into a single organism- a eukaryotic cell with a mitochondrion.

Evidence for the Endosymbiotic Hypothesis

Mitochondria are bound by a double membrane rather than just a single membrane. This is evidence that a prokaryotic cell was engulfed and eventually gave rise to mitochondria. Mitochondria also contain ribosomes and multiple circular DNA molecules within their matrix that are similar to those found in prokaryotic cells. These organelles are also autonomous meaning they grow and reproduce within the cell itself (1). In order to test the endosymbiotic theory, scientists have looked specifically at the rRNA within the mitochondrial genome. Phylogenetic data from these specific sequences have revealed that rRNA within mitochondrial genomes is more closely related to Bacteria rather than Archaea or Eucarya. Analysis showed that the specific bacterial lineage from which mitochondria originated was most likely the α-class of Proteobacteria (*Alphaproteobacteria*). Further research has confirmed this statement and has provided evidence that close relatives of the mitochondria belong to an order within *Alphaproteobacteria*- the Rickettsiales. This order is comprised of obligate parasites including: *Anaplasma*, *Ehrlichia*, and *Rickettsia* (3).

The argument for the endosymbiotic theory has been further reinforced by the sequencing of the mitochondrial genome of a protist called *Reclinomonas americana*. Sequencing revealed that *Reclinomonas americana*'s mitochondrial genome is comprised of bacterial characteristics unlike anything seen in other mitochondrial genomes. It contained Shine-Dalgarno sequences upstream of protein-coding genes, rRNA and tRNA secondary structures that were strongly bacteria-like, and operon-like cluster genes. This particular genome is considered to be a miniature eubacterial genome (3). Another factor that points to a bacterial origin is the fact that mitochondria use an N-formylmethionyl-tRNA for the initiation of protein synthesis (4).

Analysis of DNA sequences within the two groups of mitochondrial-related organelles- mitosomes and hydrogenosomes- have shown that these groups are evolutionary derivatives of the mitochondrion. Both mitosomes and hydrogenosomes contain proteins that are found within mitochondrial genomes. Mitosomes genomes are more highly reduced than the genomes of hydrogenosomes. It is thought that these mitochondrial-related organelles have evolved independently multiple times (3). Hydrogenosomes are found in the protist group of parabasalids and are able to generate ATP. Mitosomes are found within the protist group of diplomonads and did not retain ATP-generating capacity. These organelles are reduced to a greater extent than other classes.

Mitochondrial Genome

Mitochondria that are found in mammalian cells and produce ATP through respiration using diatomic oxygen contain their own DNA which is referred to as mtDNA. Reduced mitochondria, hydrogenosomes and mitosomes, do not contain this DNA. Replication, translation, and transcription within the mitochondrial genome is somewhat divergent to that of the nuclear genome. The replisome consists of: polymerase γ, a mitochondrial single-stranded binding protein, and an enzyme called Twinkle which has 5'-3' DNA helicase activity. These proteins along with mitochondrial transcription factor A associate with mtDNA to form nucleoids. Nucleoids are structures that scientists believe act as the mtDNA's units of inheritance and transmission. MtDNA is replicated by this complex either by a strand displacement model or the more conventional leading-lagging strand model. Transcription can occur on both strands and initiation is induced by mitochondrial RNA polymerase and mitochondrial transcription factors B1 or B2. Mitochondria contain their own ribosomes which are then used to translate proteins similar to the mechanisms observed within the nuclear genome (5).

MtDNA is unique in mammals due to the fact that it can only be passed through the maternal line- not the paternal line. MtDNA allows scientists to determine when and where certain mutations within the mitochondrial genome occurred. These mutations can be used to track human migration patterns (4). Normally mtDNA in animals is composed of singular, circular chromosomes. However, some organisms including the box jellyfish have fragmented, linear chromosomes that make up their mitochondrial DNA (6). This divergence in genome structure demonstrates the continued evolution of the mitochondria.

No Need for a Mitochondria?

It seems that a mitochondrion is a staple factor to eukaryotic organisms. There are, however, eukaryotic organisms that do not have mitochondria. *Monocercomonoides* is a eukaryotic organism that completely lacks a mitochondrion. It does not contain any of the hallmark mitochondrial proteins. Most eukaryotes rely on a mitochondrial iron-sulfur cluster assembly pathway, but *Monocercomonoides* relies instead on a cytosolic sulfur mobilization system. Scientists concluded that this organism was not always lacking a mitochondrion but had instead lost the organelle secondarily. This recent discovery has demonstrated to the world of science that eukaryotes do not need a mitochondrion to survive- it is possible for alternate pathways to arise in evolutionary time and then be utilized (7).

Conclusion

Mitochondria are organelles that are now vital to sustaining most eukaryotic life. A substantial amount of research points in the direction that these organelles originated from prokaryotic organisms far back in evolutionary time. What were once free living cells have now become endosymbionts within nearly every extant organism's cells although it has recently been discovered that eukaryotes can utilize other biochemical pathways in order to sustain life.

Highly reduced mitochondria have arisen multiple times throughout evolutionary time as well. As species continue to evolve, it will be interesting to see how mitochondria are affected by the steady march of evolutionary time.

References

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