Origin of Mitochondria

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Introduction

- Mitochondria are essential double-membrane bound subcellular compartments that are best known as the 'powerhouses' that supply eukaryotes with energy in the form of ATP to serve their cellular needs.
- We are taught in introductory biology courses that mitochondria are the site of aerobic respiration, a complex biochemical process by which pyruvate is oxidized to CO_2, generating reduced cofactors that drive the electron transport chain (ETC) to chemiosmotically fuel ATP synthesis.
- The final electron acceptor for this process is oxygen, which is why the majority of eukaryotes require oxygen to survive.

Mitochondria is the results of endosymbiosis

- ✓Mitochondria arose through a fateful endosymbiosis more than 1.45 billion years ago.
- ✓Many mitochondria make ATP without the help of oxygen.
- ✓Four main mitochondrial types can be distinguished on the basis of functional criteria concerning how or whether ATP is produced.
- ✓These functional types do not correspond to natural groups, because they occur in an interleaved manner across the tree of eukaryotic life. Instead they correspond to ecological specializations.

The theories about the origin of mitochondria

- There are currently two main, competing theories about the origin of mitochondria.
- They differ with regard to their assumptions concerning the nature of the host, the physiological capabilities of the mitochondrial endosymbiont, and the kinds of ecological interactions that led to physical association of the two partners at the onset of symbiosis.

Traditional view endosymbiosis

- The traditional view posits that the host that acquired the mitochondrion was an anaerobic nucleus-bearing cell, a full-fledged eukaryote that was able to engulf the mitochondrion actively via phagocytosis.
- This view is linked to the ideas that the mitochondrial endosymbiont was an **obligate aerobe**, perhaps similar in physiology and lifestyle to modern ***Rickettsia* species**; and that the initial benefit of the symbiosis might have been the endosymbiont's ability to detoxify oxygen for the anaerobe host.

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- Because this theory presumes the host to have been a eukaryote already, it does not directly account for the ubiquity of mitochondria.
- That is, it entails a corollary assumption (an add-on to the theory that brings it into agreement with available observations) that all descendants of the initial host lineage, except the one that acquired mitochondria, went extinct.
- The oxygen detoxification aspect is problematic, because the forms of oxygen that are toxic to anaerobes are reactive oxygen species (ROS) like the superoxide radical, O_2^{-}. In eukaryotes, ROS are produced in mitochondria because of the interaction of O_2 with the mitochondrial electron transport chain.
- In that sense, mitochondria do not solve the ROS problem but rather create it; hence, protection from O_2 is an unlikely symbiotic benefit.
- This traditional view also does not directly account for anaerobic mitochondria or hydrogenosomes, and additional corollaries must be tacked on to explain why anaerobically functioning mitochondria are found in so many different lineages and how they arose from oxygen-dependent forebears.

An alternative theory endosymbiosis

- **An alternative theory** posits that the host that acquired the mitochondrion was a prokaryote, an archaebacterium outright.
- This view is linked to the idea that the ancestral mitochondrion was a metabolically versatile, **facultative anaerobe** (able to live with or without oxygen), perhaps similar in physiology and lifestyle to **modern Rhodobacteriales**.
- The initial benefit of the symbiosis could have been the production of H_2 by the endosymbiont as a source of energy and electrons for the archaebacterial host, which is posited to have been H_2 dependent.
- This kind of physiological interaction (H_2 transfer or anaerobic syntrophy) is commonly observed in modern microbial communities.
- The mechanism by which the endosymbiont came to reside within the host is unspecified in this view, but in some known examples in nature prokaryotes live as endosymbionts within other prokaryotes. In this view, various aerobic and anaerobic forms of mitochondria are seen as independent, lineage-specific ecological specializations, all stemming from a facultatively anaerobic ancestral state.
- Because it posits that eukaryotes evolved from the mitochondrial endosymbiosis in a prokaryotic host, this theory directly accounts for the ubiquity of mitochondria among all eukaryotic lineages.

Mitochondrial gene transfer to nucleus during course of evolution

- Eukaryotes are genetic chimeras. They possess genes that they inherited vertically from their archaebacterially related host.
- Genes for cytosolic ribosomes in eukaryotes, for example, reflect that origin. But eukaryotes also possess genes that they inherited vertically from the endosymbiont - for example, mitochondrially encoded genes for mitochondrial ribosomes.
- During the course of mitochondrial genesis, many genes were transferred from the genome of the mitochondrial endosymbiont to the genome of the host.
- This kind of endosymbiotic gene transfer is nothing unusual; endosymbiosis very often entails gene transfers from the endosymbiont to the host.
- It happened during the origin of plastids too, and it is still ongoing in our own genome: Mitochondrial DNA constantly escapes from the organelle and becomes integrated as copies into nuclear DNA.
- The vast majority of mitochondrial proteins are encoded by nuclear genes, and many of these are endosymbiotic acquisitions from the mitochondrial ancestor.

Geochemical views of mitochondrial origin

- The oldest undisputedly eukaryotic microfossils go back 1.45 billion years in the fossil record.
- Given the coincidence of mitochondria with the eukaryotic state, this can also be seen as a minimum age for mitochondria and a rough best-guess starting date for eukaryotic evolution.
- According to newer geochemical views, this date of origin corresponds to a protracted phase in Earth history when the oceans were mostly anoxic — from 1.8 billion years ago until about 580 million years ago — because of the workings of marine, H_2S-producing bacteria.
- Eukaryotes thus arose and diversified in an environment where anoxia was commonplace.
- Accordingly it is hardly surprising that many independent eukaryotic lineages have preserved anaerobic energy-producing pathways in their mitochondria.

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- Like eukaryotes themselves, mitochondria appear to have arisen only once in all of evolution. The best evidence for the single origin of mitochondria comes from a conserved set of clearly homologous and commonly inherited genes preserved in the mitochondrial DNA across all known eukaryotic groups.
- In the case of hydrogenosomes (which usually lack DNA) and mitosomes (which so far always lack DNA), the strongest evidence for their common ancestry with mitochondria is twofold.
- First, aspects and components of the mitochondrial protein import process are conserved in hydrogenosomes and mitosomes, arguing strongly for common ancestry with mitochondria.
- Second, all known lineages of eukaryotes that possess hydrogenosomes or mitosomes branch as sisters to mitochondrion-bearing lineages.

Summary

- Mitochondria arose once in evolution, and their origin entailed an endosymbiosis accompanied by gene transfers from the endosymbiont to the host.
- Anaerobic mitochondria pose a puzzle for traditional views on mitochondrial origins but fit nicely in newer theories on mitochondrial evolution that were formulated specifically to take the common ancestry of mitochondria and hydrogenosomes into account.
- The presence of mitochondria in the eukaryote common ancestor continues to change the way we look at eukaryote origins, with endosymbiosis playing a more central role in considerations on the matter now than it did twenty years ago.
- The integral part that mitochondria play in many aspects of eukaryote biology might well reflect their role in the origin of eukaryotes themselves.

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