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Symbiogenesis of mitochondria and plastids

The endosymbiotic theory, which holds that eukaryotic mitochondria and plastids arose from the engulfment and integration of a bacterium by another cell, has long been a matter of controversial debate, but growing evidence over time has led to the substantiation and universal acceptance of the theory. Recent genetic and biochemical analyses have provided detailed insights into the fundamental events that happened more than a billion years ago.

Konstantin Sergejewitsch Mereschkowsky (1855-1921)

In 1905, Konstantin Mereschkowsky, a prominent Russian biologist, published his piece of work in "The nature and origins of chromatophores in the plant kingdom" where he proposed that the photosynthetic organelles of plants (plastids, chromatophores) originate from unicellular algae that live in a symbiotic relationship with their host cells.

Plastids are symbionts rather than cell organelles

Mereschkowsky was a leading lichenologist and his theory was inspired by his work on lichens where he had shown that lichens are symbiotic organisms composed of fungi and algae. Four years later in 1909, Mereschkowsky presented his theory of symbiogenesis according to which higher, i.e. more complex cells evolve from the symbiotic relationship between less complex ones. He came up with some astonishing conclusions: "Chlorophyll bodies (i.e. plastids) can grow and divide independently of the nucleus, and produce substances synthetically; in short they do not behave like organs at all, but like independent organisms and must therefore either be regarded as such or as symbionts."

Mereschkowsky based his theory on the symbiogenesis of the plastids of green plant cells

Electron microscope picture showing the division of chloroplasts. The prominent smooth structures surrounded by hollow space are starch grains.
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(chloroplasts) on the work of the German botanist Andreas Schimper (1856-1901) who had previously observed that chlorophyll bodies in plant cells do not develop de novo, but reproduce by dividing (in the same way as yeast cells) and are distributed to the daughter cells when the plant cell divides. The power of observation, patience and perspicacity of the 19th century cell researchers is without a doubt highly admirable, and led them to discoveries that were only confirmed much later before being considered self-evident by many people. The 19th century researchers used rather primitive devices with a resolution that was much less effective than a light microscope. This makes their findings even more admirable. Mereschkowsky's and Schimper's research and interpretation was initially dismissed and ignored and over the years fell virtually into oblivion.

Endosymbiotic theory becomes universally accepted

The theory of symbiogenesis was somehow "rediscovered" in the 1960s by the American researcher Lynn Margulis who was apparently unaware of Mereschkowsky's and Schimper's work. Margulis based her findings mainly on investigations involving electron microscopes. A lot of additional evidence from other disciplines – biochemistry, genetics, pharmacology, evolutionary research and ecology – has eventually led to the theory of symbiogenesis being universally accepted. However, plant plastids did not develop from algae but from cyanobacteria (which were previously erroneously named blue-green algae).
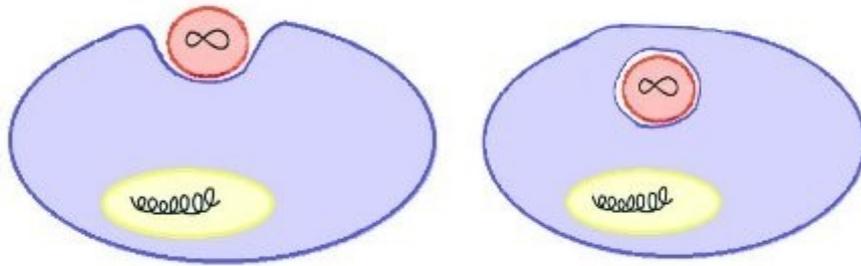
Schematic representation of how mitochondria enter eukaryotic cells via endocytosis.
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According to the endosymbiotic theory, organelles such as plastids and mitochondria (mitochondria generate most of a plant or animal (eukaryotic) cell's energy) were taken up by another cell by way of endocytosis. Seen under an electron microscope, both cell organelles are surrounded by two membranes. Biochemical analyses carried out by numerous scientists, including the author of this article, have shown that the outer membrane is similar in composition to the plasma membrane of a eukaryote; the innermost, strongly folded membrane, is of a different chemical composition than the other membranes of a cell. The inner mitochondrial membrane contains, amongst other things, the components of the respiratory chain, including cytochrome b and c, the cytochrome oxidase enzyme and a special lipid known as cardiolipin, which is otherwise only found in a small number of bacterial species. The photosynthesis machinery, including lipid-like electron carriers such as tocopherol and carotinoids (which are also found in cyanobacteria), is located on the inner membrane stacks of the chloroplasts. These findings can easily be explained by the "endosymbiotic theory of cell evolution" which is another name for the theory of symbiogenesis according to which mitochondria and plastids originated as free-living bacteria that were ingested by another prokaryotic cell.

The endosymbiotic theory has been substantiated by a wealth of data and its main features are now taken for granted by many. Lynn Margulis also argued that typical eukaryotic cell properties such as flagella, cilia and basal bodies developed from endosymbiotic spirochaetes (long helically coiled cells). This idea was almost unanimously refuted. Lynn Margulis, who was a rather controversial scientist due to her fondness for radical new concepts (including James Lovelock's Gaia hypothesis which is quite popular among New Agers), died in November 2011; her provocative ideas resulted in the fact that her valuable work on the endosymbiotic theory has hardly been recognized in the literature, especially in Germany.

Broad evidence supports endosymbiotic theory

There is broad evidence to show that mitochondria and plastids arose from bacteria and one of the strongest arguments to support the endosymbiotic theory is that both mitochondria and plastids contain DNA that is different from that of the cell nucleus and that they have their own protein biosynthesis machinery. The DNA of mitochondria and plasmids is similar to that of bacteria: it is in the form of plasmids, a circular double-stranded DNA. It is not bound to histones. In addition, many features of the RNAs and the ribosomes in the mitochondria of eukaryotic cells resemble those in bacteria. However, the DNA of plastids and mitochondria has a much lower number of genes than nuclear DNA; the majority of the mitochondrial and plastid proteins are encoded by nuclear genes. The DNA ring (cpDNA) of the chloroplasts of green plant cells is up to 200,000 base pairs long and is present in around 20 to 40 copies. As green plant cells contain numerous chloroplasts, this corresponds to around 1,000 or more cpDNA copies per cell. Mitochondrial DNA (mtDNA) of animal

cells is considerably smaller. It is between 14,000 to 19,000 base pairs long and is present in 5 to 10 copies per mitochondrion. However, every cell contains more than 1,000 mitochondria, so the mtDNA accounts for around one per cent of a cell's entire DNA.

Dr. Peer Bork, Senior Group Leader and Joint Coordinator of the Structural and Computational Biology Unit, EMBL, Heidelberg
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The endosymbiotic theory achieved its greatest success so far when it became technically possible to sequence the cpDNAs and mtDNAs of plants and animals and compare them with the sequences of a broad range of different microorganisms. Dr. Peer Bork's team at the European Molecular Biology Laboratory in Heidelberg has made a considerable contribution to these achievements. In order to derive sensible information from the huge amount of sequence data, information needs to be filtered and assessed using specific bioinformatic tools that reduce the background noise and exclude genes (e.g. genes that have arisen as a result of horizontal gene transfer) that impede the deduction of information on their descent (see article entitled Genome analysis leads to a new tree of life).

The astounding thing is that such bioinformatic tools enable phylogenetic relationships that go back to common ancestors that lived more than a billion years ago to be deduced. Phylogenetic analyses suggest that mitochondria derive from bacterial lines related to alpha-proteobacteria. This is a major group of bacteria, which also includes a wide variety of pathogens, including Rickettsia bacteria, tiny Gram-negative microbes that can cause diseases such as typhus. The sequence comparison of plastids of algae and higher plants shows that all plastids have a cyanobacterial origin. However, the data do not provide information on whether plastid symbiogenesis occurred only once or whether it occurred several times during evolution. Many experts believe that there were two symbiogenetic events, one for green and one for red algae: the plastids of all other photosynthetic eukaryotic organisms are derived from either green or red algae. It can therefore be safely assumed that all photosynthetically produced oxygen on earth goes back to cyanobacteria – either as free-living microorganisms or as "domesticated" plastids that were taken up as endosymbionts.

Symbiogenesis models

There are many modern organisms that can be used as model systems for the symbiogenesis of

mitochondria and plastids. The primitive fungus Geosiphon occasionally forms structures (bladders) that enable it to phagocytose certain cyanobacteria (Nostoc punctiforme) that then take over the function of chloroplasts and cover the fungus' energy requirements for fixing nitrogen from the atmosphere. Many organisms, including unicellular Paramecium bursaria, corals and giant saltwater clams (Tridacna), take up chloroplast-containing algae that then carry out photosynthesis for the host organism. However, the two organisms do not live in obligatory symbiosis, they can also subsist on their own. This is in contrast to mitochondria and plastids, which have long ago lost their autonomy and underlie the control of the cell nucleus of their host cell.

The study of such symbiogenesis models has also contributed to clarifying the somewhat confusing relationships between the different algal groups: the plastids of red and green algae, including ones in higher plants that descended from red and green algae, are the result of a primary endosymbiotic event (such as described above) between a cyanobacterium and another free-living cell. All other algae have plastids that are surrounded by more than two, i.e. three or even four membranes, and some of them even contain nuclear material. These plastids have arisen through secondary (or tertiary) endosymbiosis, in which a eukaryote already possessing plastids (green or red algae) is engulfed by a second eukaryote.

Dinoflagellates have evolved by way of tertiary endosymbiosis involving the engulfment of a secondary endosymbiont, a situation reminiscent of Russian Matrjoschka dolls: a flagellate cell engulfed a haptophytic alga which itself arose from a red alga being engulfed by a unicellular organism while the red alga arose from a (presumably eukaryotic) host cell that had taken up cyanobacteria and turned them into its plastids.

It appears that the symbiogenesis of mitochondria occurred before the primary endosymbiosis of cyanobacteria. Mitochondria are genetically more strongly integrated into the host cell than plastids; and all plastid-containing cells also have mitochondria. So the question arises as to when did the steps that were crucial to the evolution of higher life occur? Molecular clocks, which are based on the mutation rates of gene sequences, are not reliable enough for estimating the timescale of events that happened such a long time ago and for which no reference systems are available; estimates range between 850 million and 2 billion years ago. Over the last few years, a growing number of microfossils has been found in Precambrian rock. These fossils are far from easy to interpret. State-of-the-art knowledge suggests that cyanobacteria existed as many as 2.7 billion years ago. Multicellular fossils (e.g. Bangiomorpha pubescens) have been found in rock dating back 1.2 billion years, and these fossils closely resemble the modern red algae Bangia. To date, this is the oldest fossil eukaryote known. It can therefore be safely assumed that the symbiogenetic events that gave rise to mitochondria and plastids, which are key steps in the evolution of higher life, took place before then.

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