k28 The hydrogen hypothesis for the first eukaryote

< endo: within, symbiont: partner in a mutually beneficial relationship, ATP: “energy currency” >

> Whether true or false, it is the first new hypothesis about eukaryotic origins in 30 years to have been really thoroughly articulated at the biochemical, molecular, and cellular levels.
> —W. Ford Doolittle, 1998.[1]

Eubacteria, archaeabacteria, and eukaryotes (singular: eubacterium, archaeabacterium, and eukaryote) are three domains of life *if* no one of them evolved from the other. The same are referred to by Carl R. Woese, beginning in the 1970s, as bacteria, archaea, and eucarya (singular: bacterium, archaeon, and eucaryon).[2] The archaea are famous as extremophiles [3] (***Footnote k28.1***) as are some microbial eukaryotes: the cyanobacteria that photsynthesize even in the dim light under 6 feet of ice in frozen-across saline lakes of Antarctica,[4] and those discovered in Spain’s Rio Tinto (river of fire) water, which Sean Nee notes “is metal-contaminated and as acidic as your stomach.”[5] However:

> Evidence gathered in the years 1973 though 1995 has furthered an endosymbiont hypothesis which can be interpreted two ways. *Either* eukaryotes evolved from an archezoon (a hypothetical ancient eukaryote) that was a chimera of a eubacterium host and archaebacteria guests, as molecular phylogenetic data indicate *or* eukaryotes and archaebacteria diverged from common ancestral archezoon, as their similar interior fluids indicates. The “fusion” hypothesis, was proposed by Margulis in 1976 after the discovery of mitochondria genes found otherwise only in archaebacteria. The “divergence” hypothesis, was proposed by Tom Cavlier-Smith to explain the observation that mitochondria are not present in all lines of single-cell eukaryotes but of the archezoans of these, all known, even *Giardia*, have one by one, Jonathan Knight in 2004 reports, been found to contain mitochondria relicts such as mitosomes or hydrogenosomes. Archezoons become archezoans in both scenarios when they evolve a nucleus, a primitive cytoskeleton, and endocytosis.[6]

That mitochondria are endosymbionts (symbionts living inside a host) followed upon the observation that genes involved with their function, which are retained by them and are housed in the host nucleus, match those of archaeabacteria. The other genes in the host nucleus match those of eubacteria. Mitochondria retain the ability to reproduce independently of the nuclear DNA, which they do, in strenuously exercised muscle cells, to become more numerous.

The textbook endosymbiosis scenario is that the host cell was a fermenter producing ATP from sugar molecules without using oxygen, and the engulfed guest bacteria were respirers using oxygen to break down even more complex organic molecules and synthesize ATP. Endosymbiosis that turned them into mitochondria was win-win: an energy boost of sugars to the host cell in exchange for food. And protection for both. Physical protection for the guests and protection for the host that must venture for its guests where, for it, killing environmental oxygen enters unbidden by diffusion.

“Oxidative phosphorylation was entrained in the service of a new breed of life, and, in time, we came along,” writes Thomas B. L. Kirkwood.[7] The planet’s early dominant life form, namely photosynthetic bacteria, is the usual villain cited for excreting the “toxic” oxygen. But before this, defenses would long have been, suggests Nick Lane in *Oxygen: The Molecule that Made the World*, 2003, because water-splitting ultraviolet radiation on the ocean surface would, from the beginning, have pushed cells to evolve antioxidant enzymes, such as catalase.[8]

Since aerobic respiration generates ATP by an order of magnitude more efficiently than the alternative anaerobic pathway, some eukaryotes with mitochondria in environments that were becoming aerobic could cease being fermenters and so evolve into animals and plants. The evolutionary path that could guarantee this would be to obligate the mitochondria to stay by allowing them to relinquish to the host nucleus their functioning genes not needed onboard for their self-replication within the host cell when that divides. Neat, but not so, William Martin and Miklós Müller suggested in 1998. The scenario they propose is that eukaryotes evolved from a chimera of bacteria guests and an archaeon host. The bacteria were anaerobes but were also facultative aerobes (which can change their metabolism to use oxygen when that is present). In the evolution of the chimera to a eukaryote, the bacteria evolve to be obligate symbiotes that are either mitochondria if the eukaryote occupies aerobic environments or hydrogenosomes if the eukaryote occupies anaerobic environments. Hydrogenosomes are the power house (ATP producing) organelles that occur in some anaerobic eukaryotes in the place of mitochondria that have the power house (ATP producing) role in aerobic eukaryotes. Hydrogenosomes waste products are prodigious amounts of hydrogen and, lesser amounts of, carbon dioxide and acetate. The waste products of mitochondria are mostly carbon dioxide and water. As Martin tells it, a talk by Müller about hydrogenosomes included a slide that showed methogens (bacteria that feed on hydrogen, carbon dioxide and acetate) clustered against and feeding on the wastes of hydrogenosomes (in an anaerobic eukaryote, which they had invaded). This image would not leave him and mulling over it and imagining how the two might form a symbiotic relationship led to a collaboration with Müller that resulted in their "hydrogen hypothesis" (***Figure k28.1***) for the origin of heterotrophic (other eater, i.e. "animal-like") eukaryotes.[9]

As for the nucleus by which a so-called eukaryote cell is distinguished from no-nucleus bacteria and archaea cells, evidence, writes Roberta Freidman, from genomics is that the nucleus "is itself a donation from an ancestor of the microorganisms known as archaea."[10] ❑

Footnote ***k28.1*** In the Columbia plateau basalts, WA, reduced iron reacts slowly with aquifer water to release hydrogen that, to found depths of 1 km, chemoautotrophic archaea (those that are methanogens) oxidize (passing the freed electron to dissolved CO_2 to produce H_2O and methane).[11]

Figure ***k28.1*** [12] The 'hydrogen hypothesis' is that the organelles which produce ATP (adenosine 5'-triphosphate) in eukaryote are former bacteria. These have been stripped of genes that encode proteins to take in organic molecules and to produce from them pyruvate. Pyruvate is a carbohydrate that bacteria metabolize to ATP. These genes now removed to and held in the eukaryote nucleus obligate the 'power house' organelles to stay. In their former true state, the bacteria were anaerobes and facultative aerobes. Free living in an anaerobic environment, their metabolitic wastes, attracted methanogen archaea. The rest, as they say, is history.