

## Endosymbiosis Theory

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Most eukaryotic cells contains a variety of organelles, including mitochondria, chloroplasts for plants and algae, nucleus, and et al. The bulk of genome if an eukaryotic organism is contained in the chromosomes in the cell nucleus while a much smaller portion is located in the mitochondria and chloroplasts.

Non-photosynthetic eukarya do not have chloroplasts. Some early-branching eukarya, such as *Giardia lamblia*, have neither mitochondria nor chloroplasts. They are all anaerobic. These facts suggest that mitochondria and chloroplasts do not appear to be intrinsic components of eukarya cells. Rather, they could be integrated into the cells of eukarya at a later evolutionary stage. In addition, mitochondria and chloroplasts resemble simple bacteria from their appearances to the circular forms of their DNA. Therefore, a hypothesis concerning the origin of mitochondria and chloroplasts was raised that eukaryotic organelles such as mitochondria and chloroplasts were of bacterial origins. This hypothesis, known as endosymbiosis theory, can be best tested by molecular phlogenetics.

The idea is as follows. The sequences of a relatively conserved gene from nuclear, mitochondrial and chloroplast genomes of representative organisms of bacteria, archaea and eukarya are aligned and a universal phylogenetic tree is constructed. If the mitochondria and chloroplasts are originated from bacteria, their genes should branch from within the bacteria domain. If the mitochondria and chloroplasts are originated independently within the eukarya domain, then their genes should branch from within the eukarya domain.

As examples, the phylogenetic trees of small-subunit rRNA, cytochrome c, cytochrome c553 and ferredoxin were built (Figures 1, 2, 3 and 4, respectively).

Figure 1 (Taken from Evolutionary Analysis, 2001, Freeman & Herron) shows that both *Zea Mays* mitochondrial small subunit rRNA and chloroplast small subunit rRNA are branched from within the bacterial domain, with mitochondria being proteobacteria (purple bacteria) and chloroplasts being cyanobacteria. This phylogeny confirms that mitochondria and chloroplasts are descended from free-living bacteria, with mitochondria closely related to  $\alpha$ -proteobacteria and chloroplasts closely related to cyanobacteria.

Figure 2 shows the mitochondrial cytochrome c and bacterial cytochrome c2 phylogenetic tree. First, it shows the close relation between mitochondrial cytochrome c and bacterial cytochrome c2. Second, the cytochrome c2 from *Rhodospseudomonas viridis* intervenes between the mitochondrial cytochrome c from *Tetrahymena pyriformis* and those from other species, suggesting the existence of two divisions for mitochondrial cytochrome c. Indeed, there are two major divisions of mitochondria, one with tubular cristae and one with lamellar cristae.

Figure 3 shows the eukaryotic algal and cyanobacterial cytochrome c6 (or c553) phylogeny. From the phylogenetic tree, one can conclude that the chloroplasts of yellow-green algae, red algae and brown algae are more closely related to cyanobacteria than the chloroplasts of green algae and Euglena. Figure 4 shows the plant, algal and cyanobacterial ferredoxin phylogeny. Again, ferredoxin sequences also tend to support the close relationship between the chloroplast and the cyanobacteria.

An interesting observation is that some eukaryotic chloroplast is related to another eukaryote. As an example, *Cryptomonas F* is an alga whose chloroplasts have two pairs of envelope membranes. Besides the normal circular chloroplast chromosome inside the inner membrane pair, it also has a nucleomorph, a small nucleus-like organelle, between the inner and outer membrane pairs. The small subunit rRNAs of nucleomorph are of eukaryotic origin but having nothing to do with nuclear small subunit rRNAs. This example implicates that the outer chloroplast membrane pair and the nucleomorph of *Cryptomonas F* are likely from an eukaryotic ancestor with a chloroplast itself.

So far our data support the hypothesis of endosymbiosis theory. Now the question is when the event of endosymbiosis occurred for eukaryotic mitochondria, before or after the nucleus formed. First of all, phylogenetic evidence (Figure 5) supports that all mitochondrial genomes are descended from a common protomitochondrial ancestor. In another word, mitochondria originated only once in evolution. Second, what was the host organism? The existence of a group of eukaryotes (named Archezoa) lacking both mitochondria and early diverging promoted the popular serial endosymbiosis model, which assumes that the host provided the nuclear genome of the resultant combination, with subsequent mitochondrion-to-nucleus gene transfer. This is to say, the mitochondria evolved after the formation of nucleus. However, recently, several observations started to challenge this view. One of the most important observation is that some of the genes encoding typical mitochondrial proteins are found in the nuclear genomes of the amitochondriate eukaryotes, such as Archezoa. An alternative endosymbiosis model was therefore raised (Figure 6), in which a simultaneous origin of the ancestor of eukaryotic cells (in particular nucleus) and its mitochondria was allowed.

#### References:

1. Freeman S. and Herron J. (2001) Evolutionary Analysis. 2<sup>nd</sup> ed. Prentice Hall. Upper Saddle River, NJ.
2. Gray et al. (1999) Mitochondrial Evolution. Science. Vol. 283, p1476-81.
3. Moore G. and Pettigrew G. (1990) Cytochromes c: evolutionary, structural and physicochemical aspects. Springer-Verlag. Berlin, New York.

Fig.1. Small sub-unit rRNA phylogeny. (Taken from Evolutionary Analysis, 2001, Freeman & Herron)

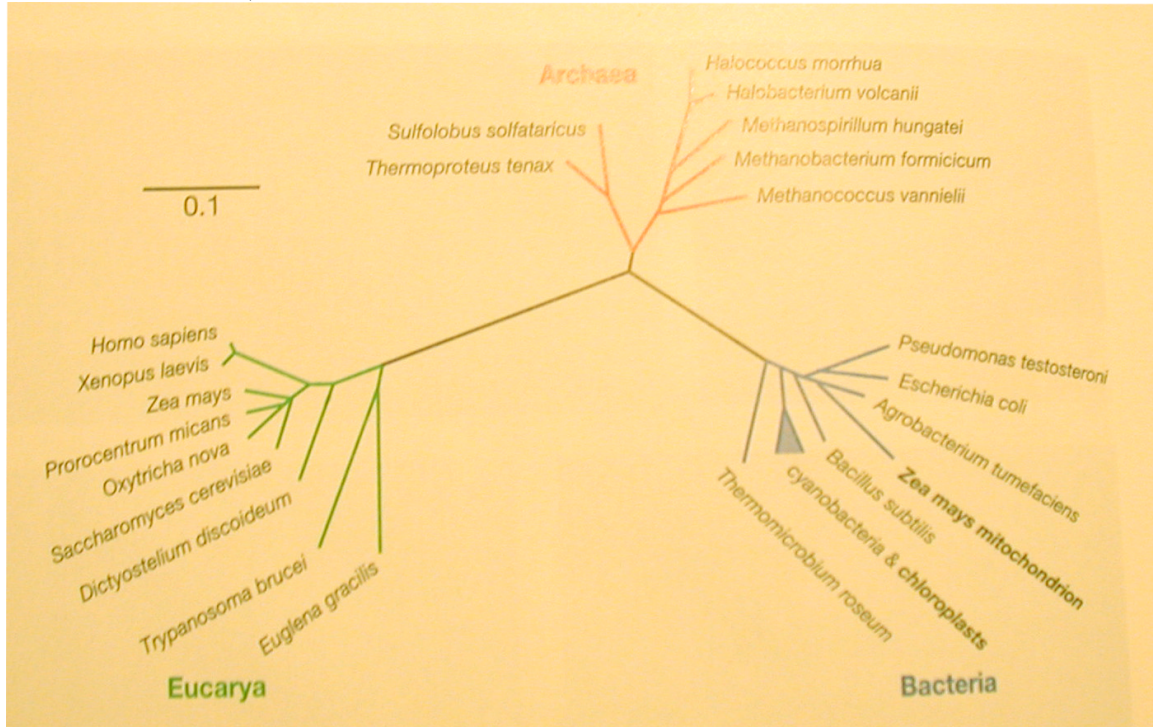


Fig.2. Mitochondria cytochrome c and bacterial cytochrome c2 phylogeny.

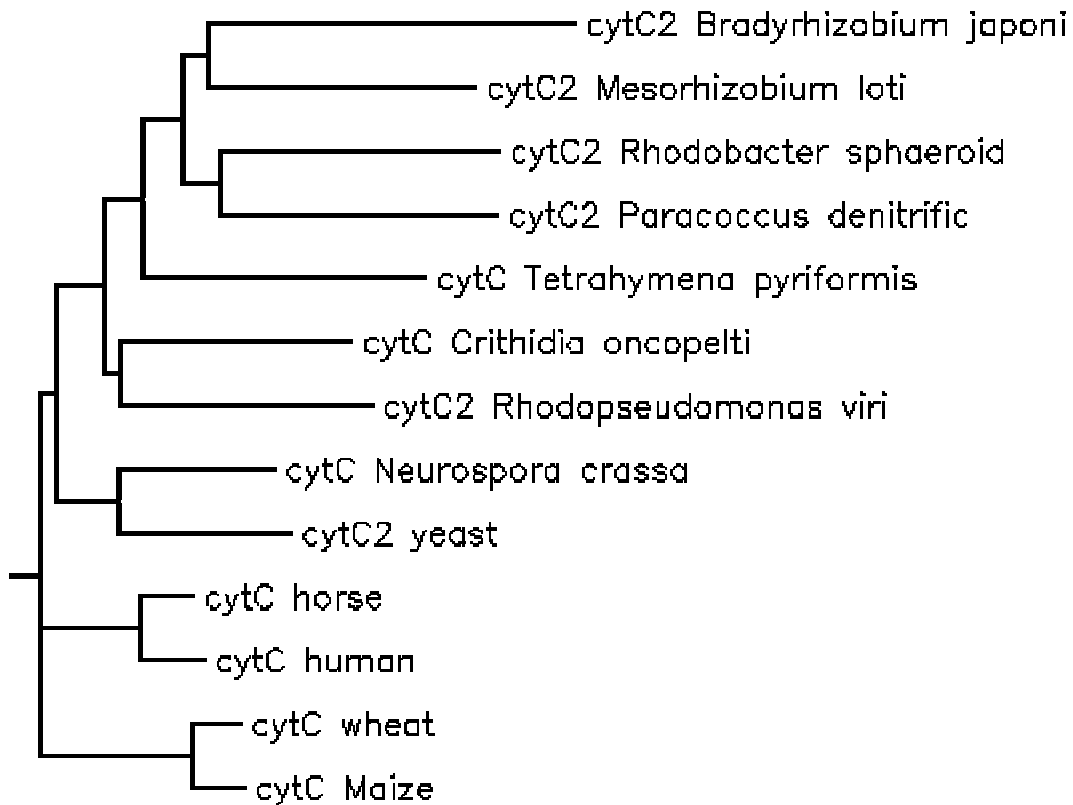


Figure 3 shows the eukaryotic algal and cyanobacterial cytochrome  $c_6$  (or  $c_{553}$ ) phylogeny.

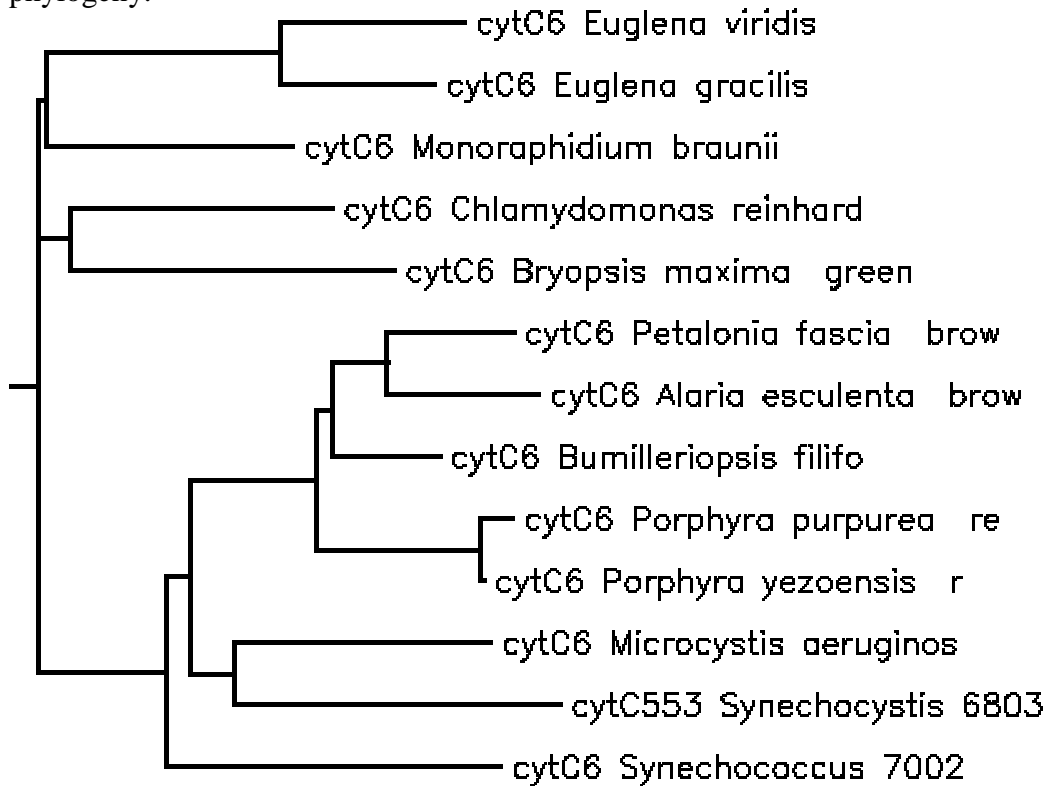


Fig.4. Chloroplast and cyanobacterial ferredoxin phylogeny.

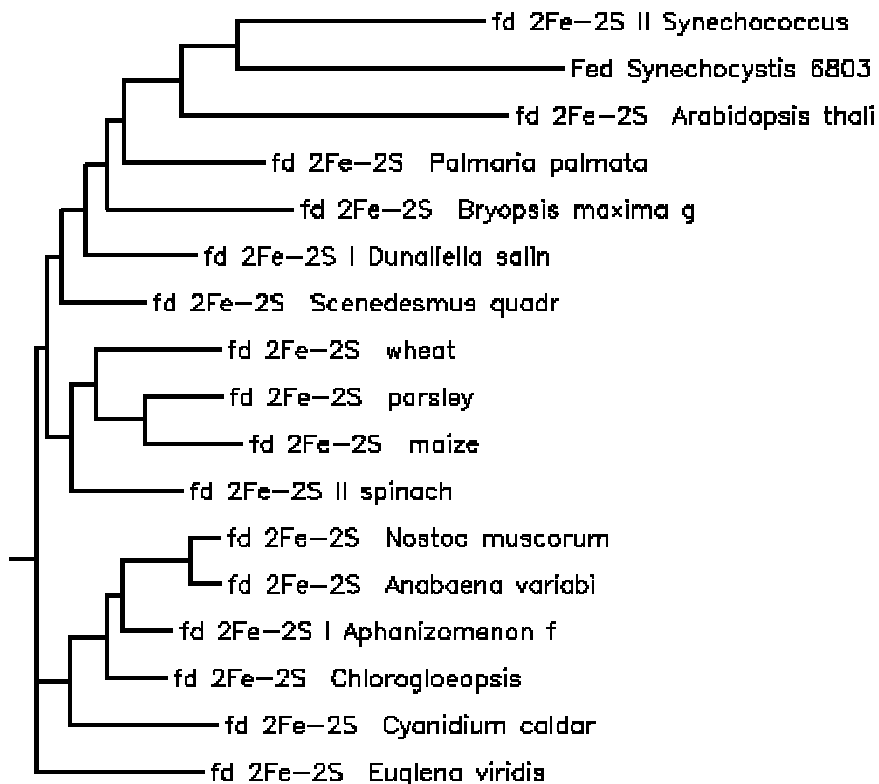


Figure 5. (Take from Gray et al. 1999)

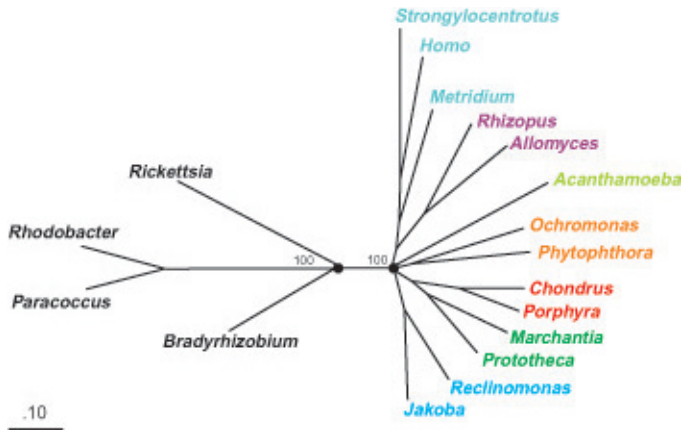


Figure 6. (Take from Gray et al. 1999)

**Fig. 3.** Alternative hypotheses describing the origin of eukaryotic cell. Lavender arrows, simultaneous creation of the eukaryotic nucleus (gray) and mitochondrion (orange) by fusion of a hydrogen-requiring, methanogenic Archaeobacterium (host) with a hydrogen-producing  $\alpha$ -Proteobacterium (symbiont) (58). Magenta arrows, two-step scenario, initially involving formation of an amitochondriate eukaryote by fusion of an Archaeobacterium and a Proteobacterium (46) followed by acquisition of the mitochondrion through endosymbiosis with an  $\alpha$ -Proteobacterium. Bacterial and mitochondrial genomes are blue.

