

# Evolution of Eukaryotes

*Course Project in CL 717, Chemical Department, IITB*

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## Introduction

The origin of Eukaryotes was a major singular step in evolution. The origin of life on earth goes back to around 4 billion year and life forms were morphologically similar for ~2 billion years. This change in structure and complexity happens with the sudden evolution of Eukaryotic cells. Very less is known about the intermediate steps in the course of evolution. Eukaryotic cells are fundamentally different from those of bacteria and archaea at almost every level of organization, starting with their physical size. The earliest common Eukaryotic ancestor already has most of the modern Eukaryotic features as a nucleus and other endomembrane system organelles.

The most widely accepted hypothesis is of Endosymbiosis, in which a bacteria is engulfed by an Archaea. They formed a symbiotic relationship in which host Archaea provide a stable environment and food for bacteria while bacteria provides energy to the symbiotic system. It later evolved into a eukaryotic cell where bacteria assumes the role of mitochondria and Archaea becomes the cell. This transition from a symbiotic relation to complete eukaryotic cell happened in a series of evolutionary steps. Since there are no intermediates or fossils, which suggests this transition had happened very quickly in evolutionary timescale.

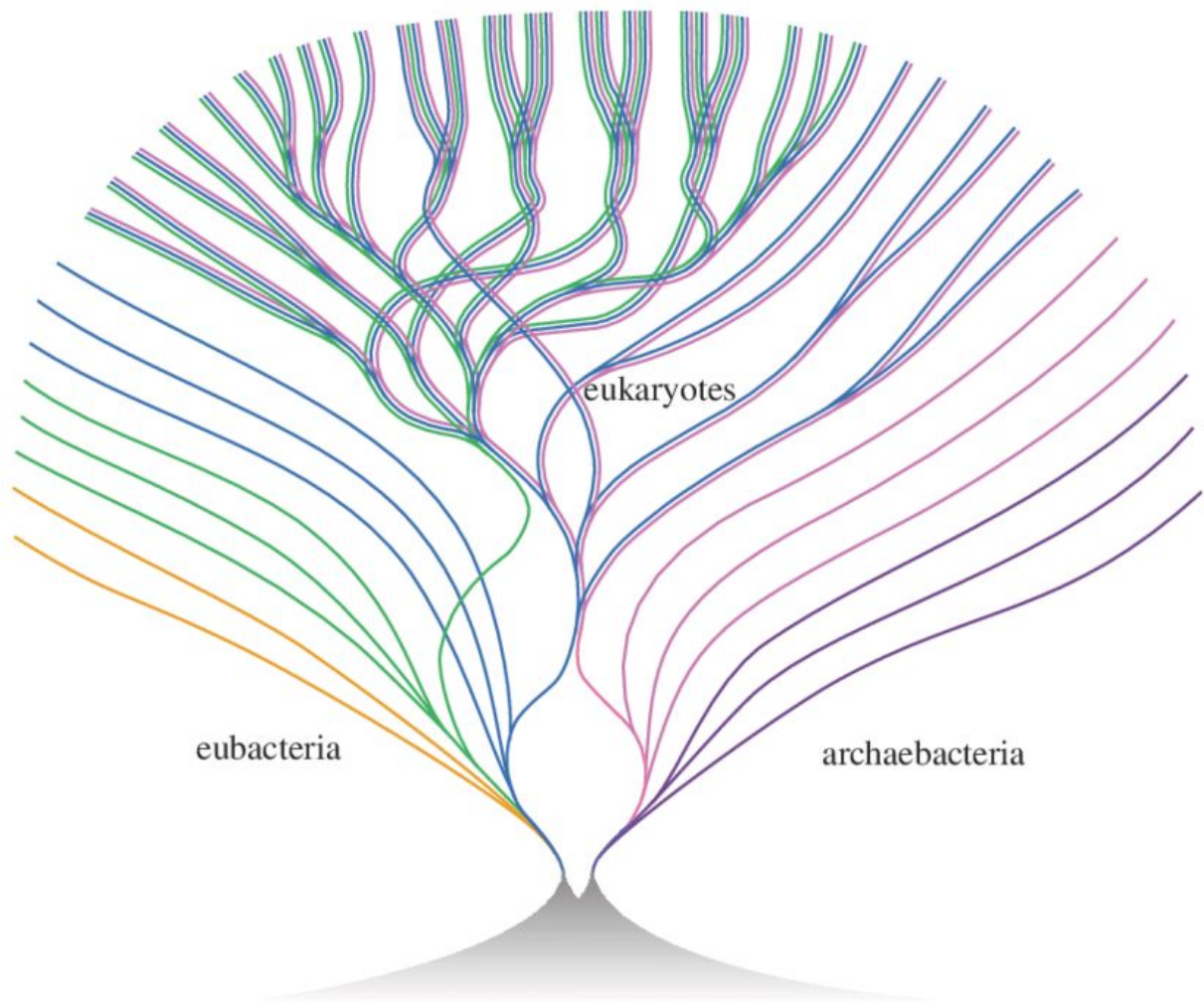
## Steps Involved

This project will look at the time interval elapsed between the engulfment of bacteria and the formation of Nucleus inside the cell.

1. Archaea engulfing a bacteria
2. Number of bacteria grows inside the archaea host
3. Bacteria started to shed its genes to host genome.
4. Parasitic genes from Bacteria bombarded the host genome
5. Formation of split genes and spliceosome
6. Development of nucleus

## STEP 1. Archaea engulfing a bacteria

Modern eukaryotic cell has proteins which are present in both Archaea and bacteria exclusively which suggest a chimeric origin of Eukaryote. It could be explained with the symbiotic relationship between bacteria inside an Archaeal host.



**Figure.** A tree of life drawn by Bill Martin in 1998, reflecting whole genomes. The tree shows the chimeric origin of eukaryotes, in which an archaeal host cell acquired bacterial endosymbionts that evolved into mitochondria; and the later acquisition of chloroplasts in Plantae.

## STEP 2. The number of bacteria grows inside the Archaeal host cell:

Since the bacteria found itself in a relatively stable environment the number of bacterial cell per host began to increase rapidly which is only stopped by the amount of food material archaea could supply to the bacteria.

## STEP 3. Bacteria started to shed its genes

Since the bacteria have a relatively stable environment now it could easily discard many genes which are no longer needed into the cytoplasm of the host.

Many of these genes would be picked by the host genome and the size of genome began to increase.

Further many of the common genes which are not needed for the urgent operation of the bacterial cell were also incorporated to the host genome and the size of the host genome continues to grow while the genetic size of bacteria continues to decrease.

The bacteria started to rely upon the host proteins and machinery for most of its function.

## STEP 3. Bacteria started to shed its genes

The parasitic DNA molecules from the bacteria started to incorporate itself in host genome in multiple copies which increase the genetic load of the host cells. But this load of coping more genetic material can be balanced due to extra energy generated by individual bacterial cells which now has more energy per gene.

## STEP 4. The Parasitic DNA attacks the host genome:

The bombardment of parasitic DNA resulted into the formation of split genes which require spliceosome to form the correct mRNA and form correct protein.

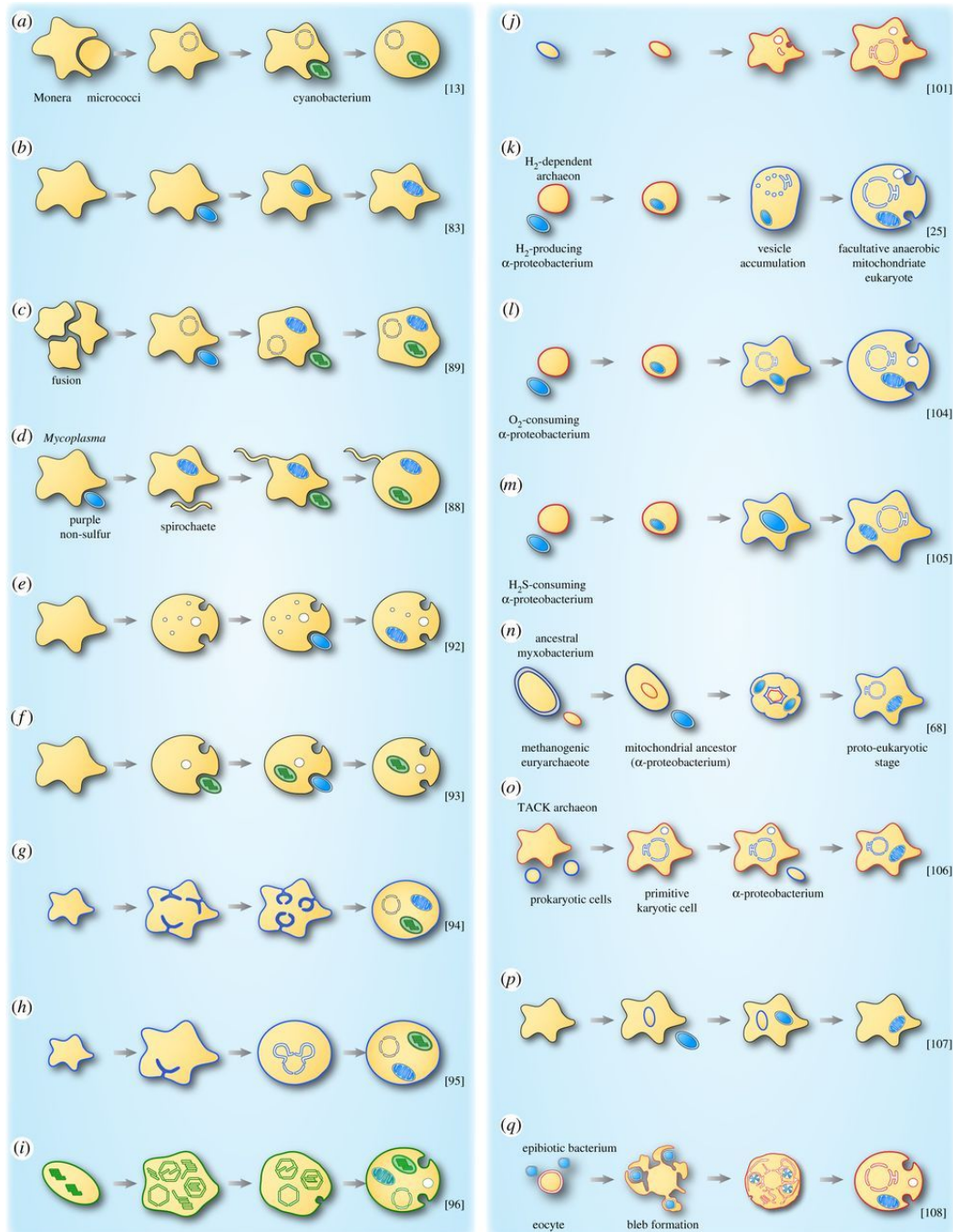
## STEP 6. Formation of nucleus

The speed of spliceosome to cut and paste the RNA is much slower than the speed of translation by ribosomes hence there is a need for the separate compartmentalization inside the cell where splicing of a mRNA could be done in absence of Ribosomes. Hence

it provided a path for the formation of the nucleus, which separated the mRNA from the cytoplasm.

## Modelling endosymbiosis

There are many hypotheses which try to explain the origin of mitochondria inside the cell which is a crucial stage in the evolution of Eukaryotes.



**Fig.** Models describing the origin of mitochondria and/or chloroplasts in eukaryotes. (a–q) Schematic of various models accounting for the origin of mitochondria and/or chloroplasts. Archaeal cells/membranes are represented with red, while blue indicates eubacterial cells/membranes. Black membranes are used when the identity of the cell is not clear and green is used for cyanobacterial derived cells/membranes

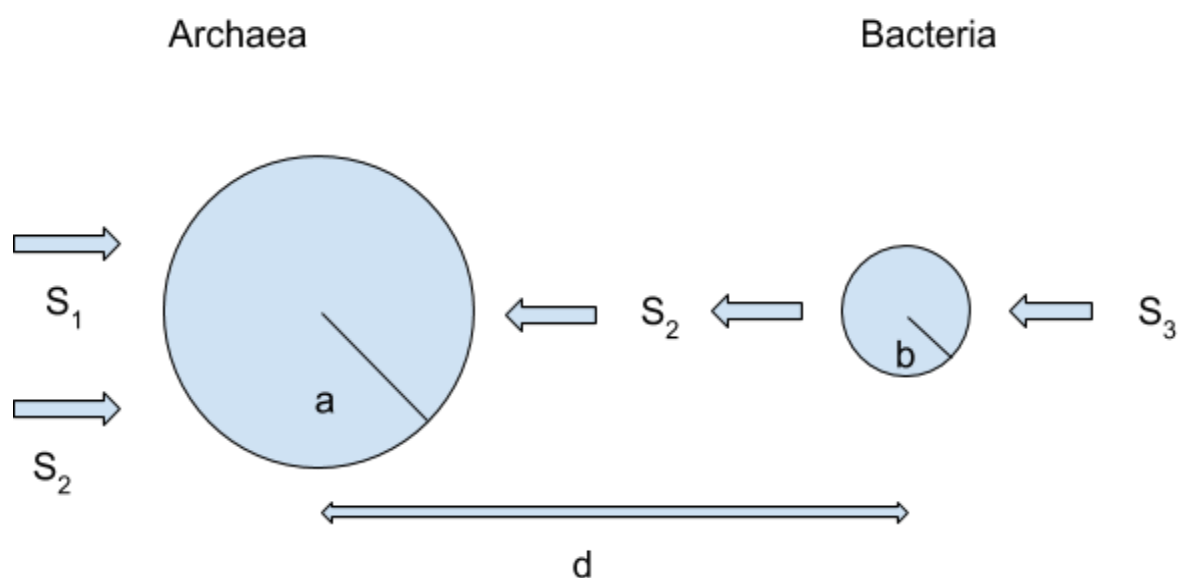
Of these hypotheses, the most popular for endosymbiosis is **Hydrogen hypothesis**. It was proposed by **William F. Martin and Miklós Müller in 1998**.

According to this theory:

1. A host that acquired the mitochondria was a hydrogen dependent archaeon, similar to modern methanogens and which uses carbon dioxide and methane as a byproduct.
2. The modern mitochondria are once a facultative anaerobic bacteria which produces carbon dioxide and hydrogen as the byproduct for the anaerobic respiration.
3. There was a symbiotic relationship between the host and the symbiont based on the need of the host for hydrogen. (anaerobic syntrophy).

The syntrophy was a crucial step in the development of endosymbiosis since it explains the evolutionary pressure for a close association between the host and endosymbiosis. And since it doesn't require phagocytosis, which is not compatible with the membrane which an archean cell have, it is more acceptable.

## Model





Assumptions:

- 1) Both bacterial and archaeal cells are assumed to be spherical in shape
- 2) The archaea require two different substrates  $S_1$  and  $S_2$  while the bacteria requires one substrate  $S_3$  and produces  $S_2$
- 3) The concentration of  $S_1$  and  $S_3$  are assumed to be constant in the surrounding while the concentration of  $S_2$  is mediated by the production by bacteria since it is assumed that evolutionary pressure for the symbiosis will only appear in  $S_2$  limiting conditions.
- 4) The influx of material from the environment is directly proportional to the concentration in the environment.

### 1. For Archaea:

Influxes:

$$IF_{S_1} = k_1 [S_1]$$

IF - Influx

$$IF_{S_2} = k_2 [S_2]$$

### 2. For Bacteria:

$$IF_{S_3} = k_3 [S_3]$$

OF = Outflux

$$[S_2] = \frac{K_2' [OF_{S_2}] A_b}{\frac{4}{3} \pi d^3}$$

$A_b$  = Area of bacterial cell

$$[S_2] = \frac{K_2'' [OF_{S_2}] A_b}{d^3}$$

$\beta$  = Fraction of  $S_3$  turned into  $S_2$  and released into the environment

$$OF_{S_2} = \beta [IF_{S_3}] = \beta k_3 [S_3]$$

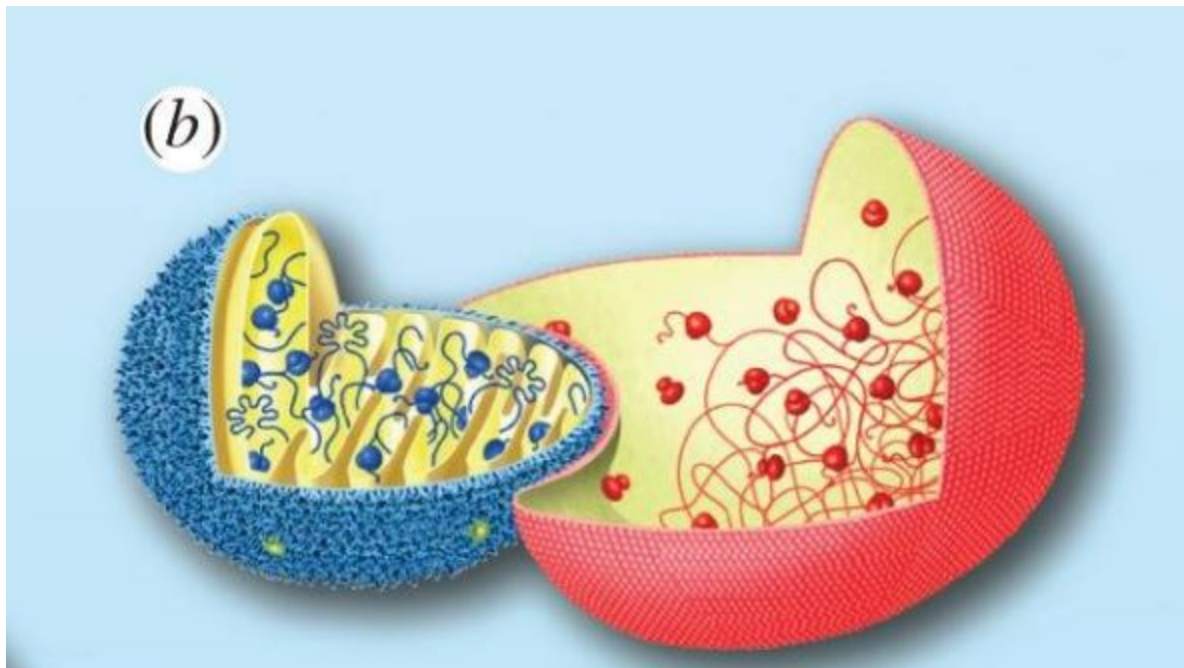
$$[S_2] = \frac{K_2'' A_b \beta k_3 [S_3]}{d^3}$$

Now the total inflow of  $S_2$  inside the archaeal cell is given by:

$$\frac{\left( K_2'' K_2 K_3 \beta \right) A_b A_a [S_3]}{d^3}$$

The benefit to the archaeal cell is assumed to be proportional the amount to  $S_2$  and  $S_1$  is could take inside the cell. Since the concentration of  $S_1$  is assumed to be constant in the environment hence benefit will only depend upon the total inflow of  $S_2$ , which is inversely proportional to the cube of distance. Hence to maximise the benefits the archaeal cell will try to minimise the distance between itself and the bacterial cell. Closest the archeal cell could get is when bacteria resides at its surface.

**When Archaea tries to morph and increase its surface area with the bacterial cell :**



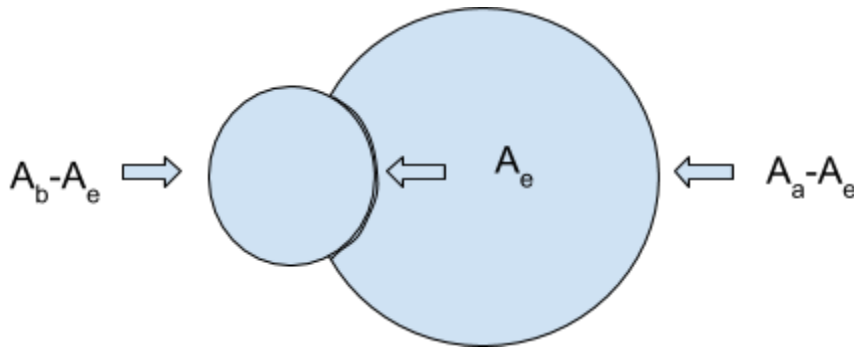


Suppose  $A_e$  is the area of engulfment.

The area exposed to the environment then is

For archaea =  $A_a - A_e$

For bacteria =  $A_b - A_e$



The influx of nutrients from the environment could only happen through the area exposed to the environment.

$$\text{Total inflow of } S_1 = K_1[S_1](A_a - A_e)$$

$$\text{Total inflow of } S_2 = K_2[S_2](A_a - A_e) + (OF_{S_2})A_e$$

$$(OF_{S_2})A_b = \beta(IF_{S_3})(A_b - A_e) \quad IF_{S_3} = K_3[S_3]$$

$$[S_2] = \frac{K_2''(OF_{S_2})(A_b - A_e)}{(a + b)^3}$$

$$IF_{S_2} = \frac{\beta K_3[S_3](A_b - A_e)}{A_b} \left\{ \frac{K_2 K_2''}{(a + b)^3} (A_b - A_e)(A_a - A_e) + A_e \right\}$$

Slight correction: At the last equation it is not  $IF_{S_2}$  but the total inflow of  $S_2$ .

Now since the benefit to the archaea depends upon the amount of nutrient inflow, we could quantify (total inflow of  $S_2$ )\*(total inflow of  $S_1$ ) as the representative benefit function  $B(A_e)$ .

Now for maximum Benefit differentiate  $\frac{d(B(A_e))}{d(A_e)} = 0$ .

So applying this condition we could arrive at the optimum value of  $A_e$ .

If the value to  $A_e > 0$  then the evolution of Eukaryotes must have followed this path.

Now if  $A_e > 0$  then it is the critical Area of engulfment above which archaea cannot further engulf the bacterial without losing benefit since bacterial cell need some of its surface to be exposed to the environment for the influx of  $S_3$  for producing  $S_2$ , hence  $(A_e)_{\max} < A_b$ .

Unless there is some other mechanism to transfer the  $S_3$  to the bacterial cell endosymbiosis couldn't happen. This problem is solved by developing  $S_3$  transporters in the Archaeal cell surface, which then could transfer this to bacterial cell and in return get larger amount of  $S_2$ . This could help the critical  $A_e$  to increase and we could say that endosymbiosis had happened when critical  $A_e \geq A_b$ .

Now the transporters at the archaeal surface could develop as a result of gene transfer from the bacteria to archaea.

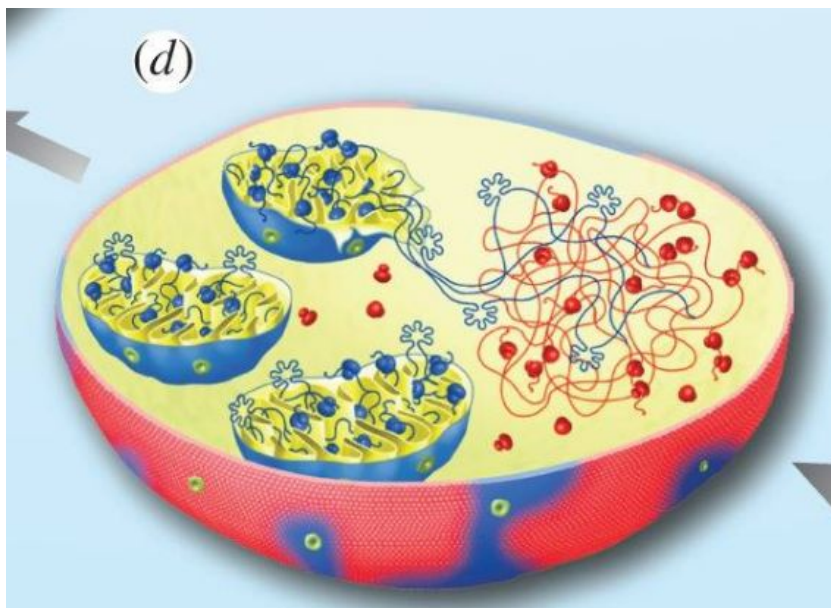
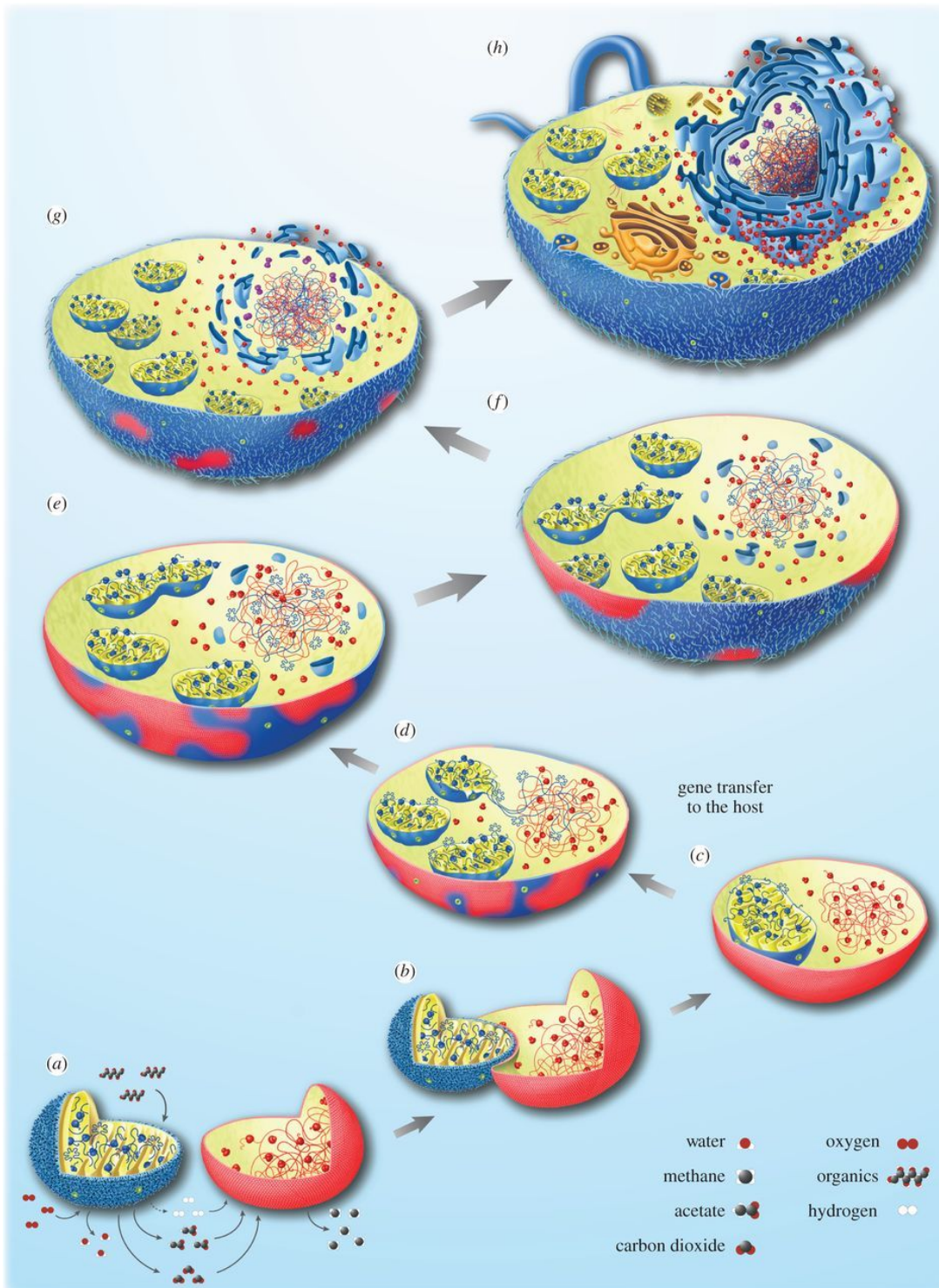


Fig: Lysis of a bacterial cell and mixing of its genome in archaeal cytoplasm.

However the model predicts this transfer (atleast genes for transfer) has to happen much before the complete engulfment of bacteria.



**Fig.** Mitochondrial origin in a prokaryotic host. (a–h) Illustrations for various stages depicting the transition of an H<sub>2</sub>-dependent archaeal host (in red) and a facultatively anaerobic α-proteobacterium (in blue) to a eukaryote

Showing various stages of development and formation of mitochondria inside the cell.

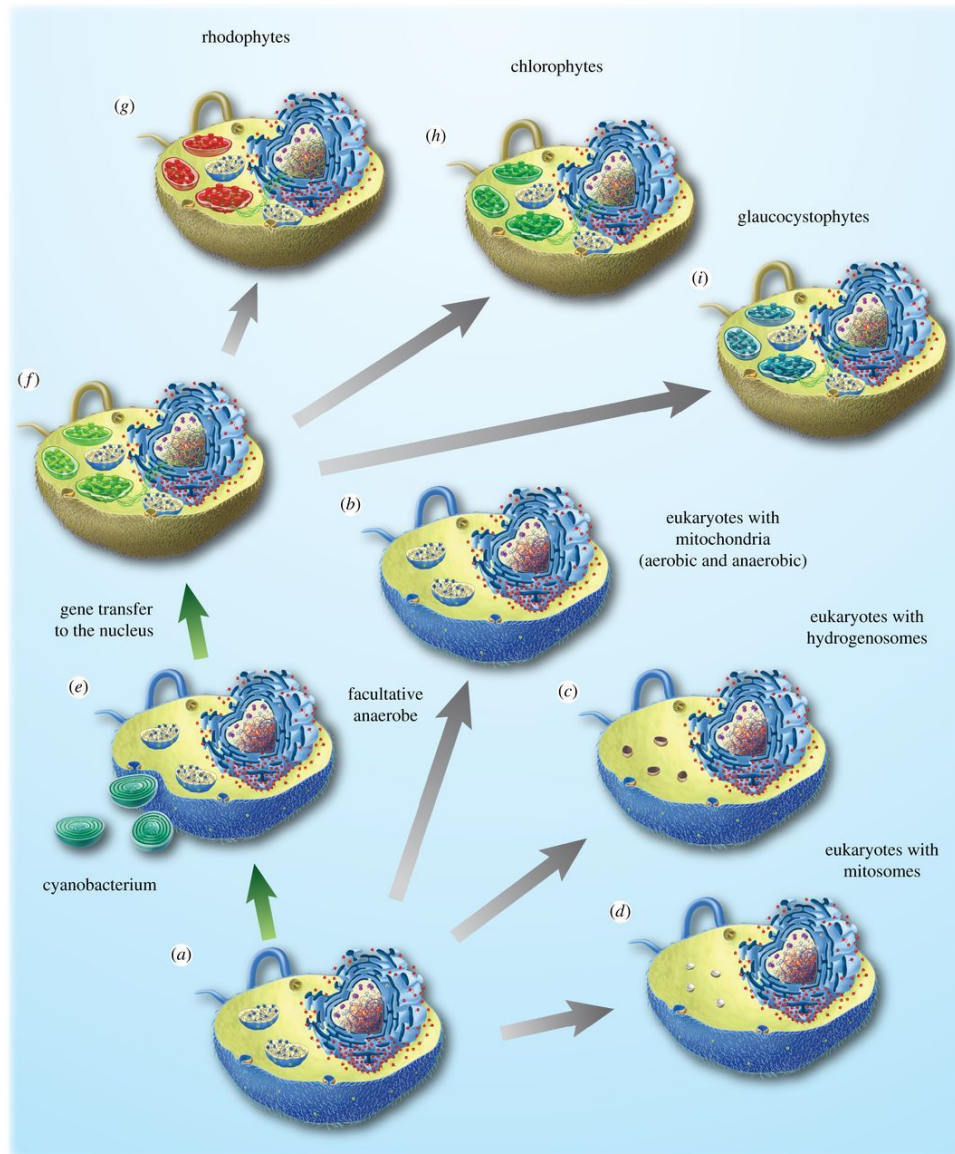


Fig. Evolution of anaerobes and the plastid. (a–d) Diversification of the mitochondria-containing ancestor to eukaryotes containing specialized forms of the organelle, hydrogenosomes, mitosomes and anaerobic mitochondria. (e,f) Primary symbiotic origin of a plastid involving a cyanobacterium in a facultative anaerobic host followed by gene transfer to the nucleus resulting in a plastid-bearing ancestor.. (g–i) Diversification of the plastid-bearing ancestor to glaucocystophytes, chlorophytes and rhodophytes..

Showing diversification of Eukaryotes.

## References

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