

Open questions in the origin of eukaryotes

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1. Facts

2. Models

3. Testing the models

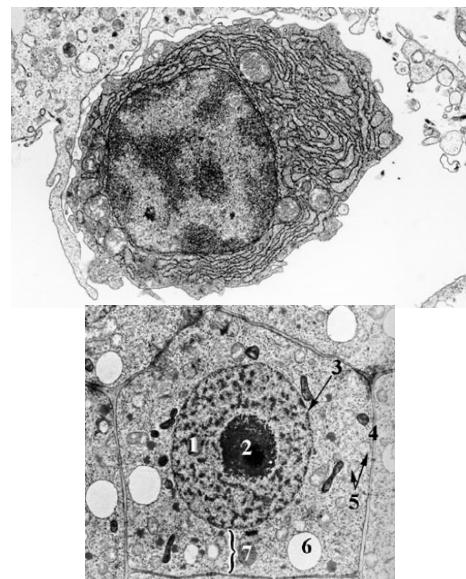
4. Open questions

The prokaryote - eukaryote dichotomy



Edouard Chatton (1925 and 1937)

Terms Prokaryote & Eukaryote
(autotrophic flagellated protozoa)

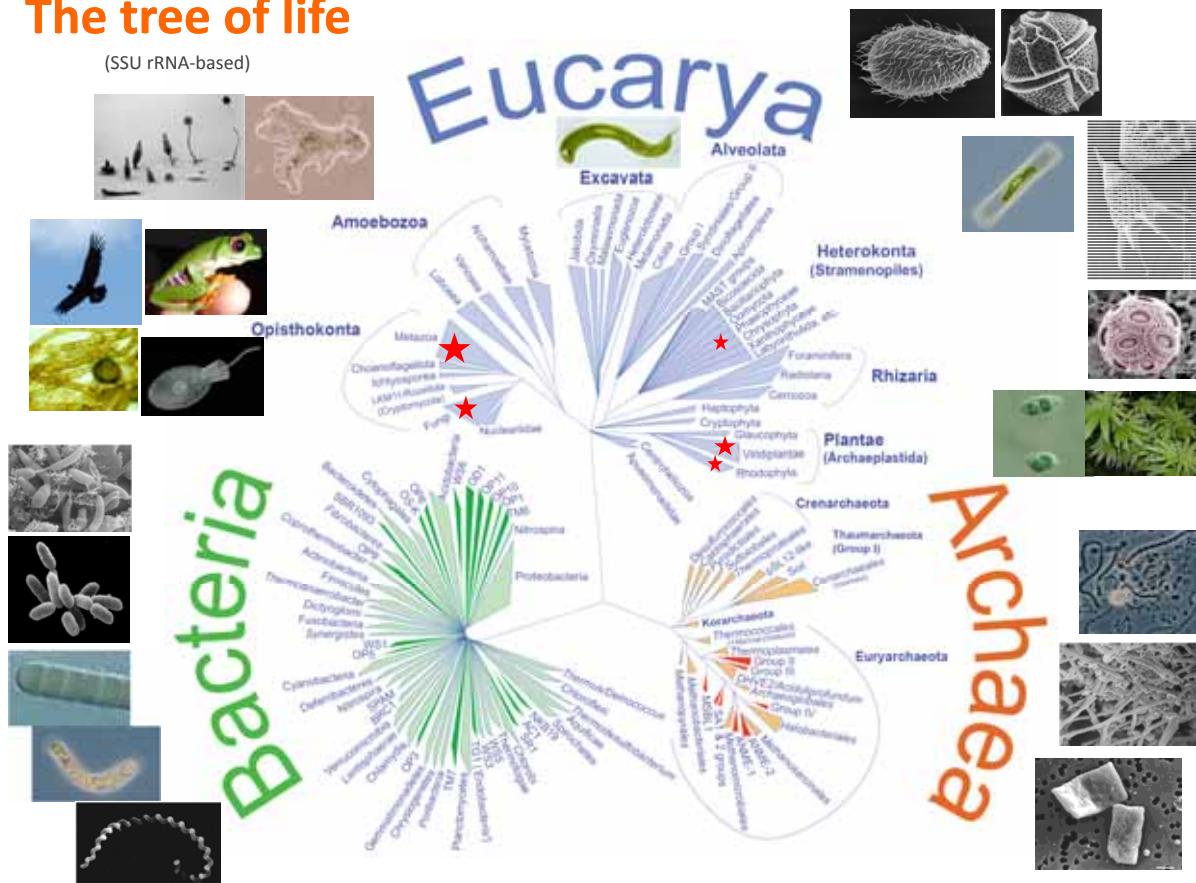


Stanier & van Niel, 1962

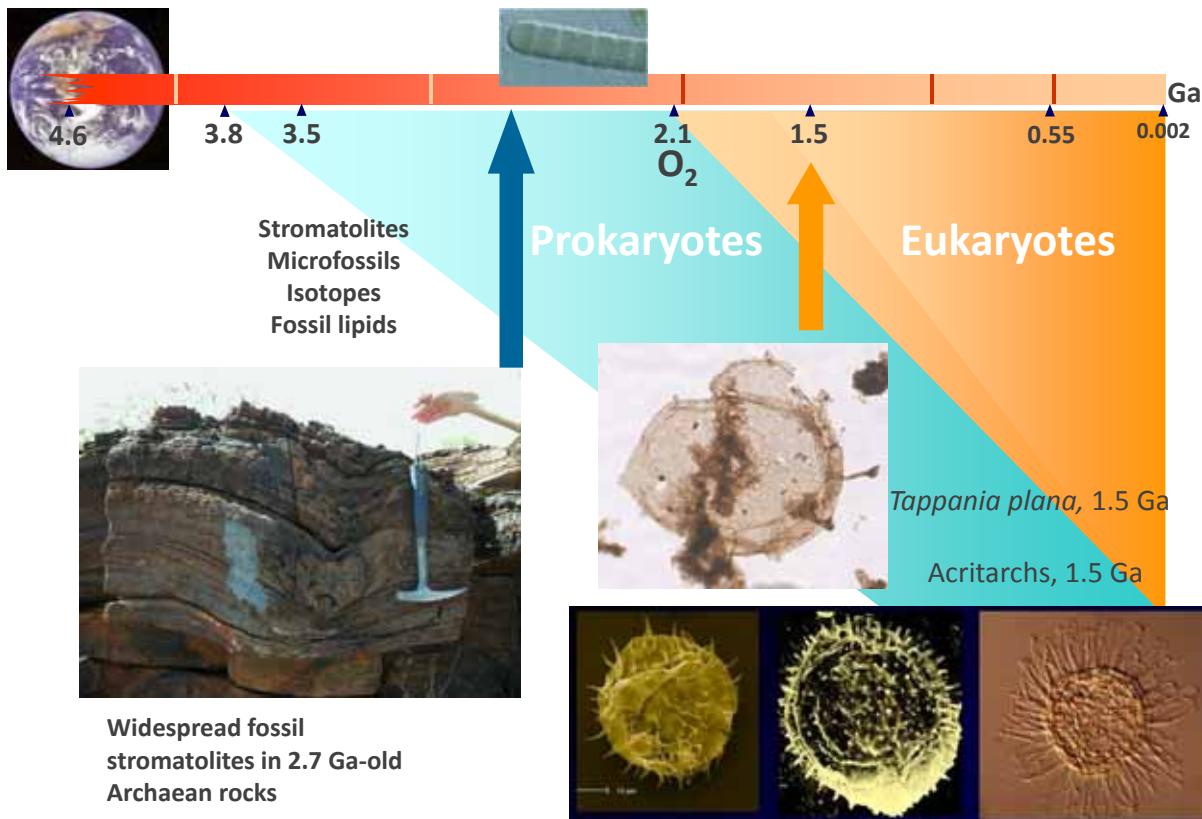
The concept of a bacterium
(modern meaning)

The tree of life

(SSU rRNA-based)

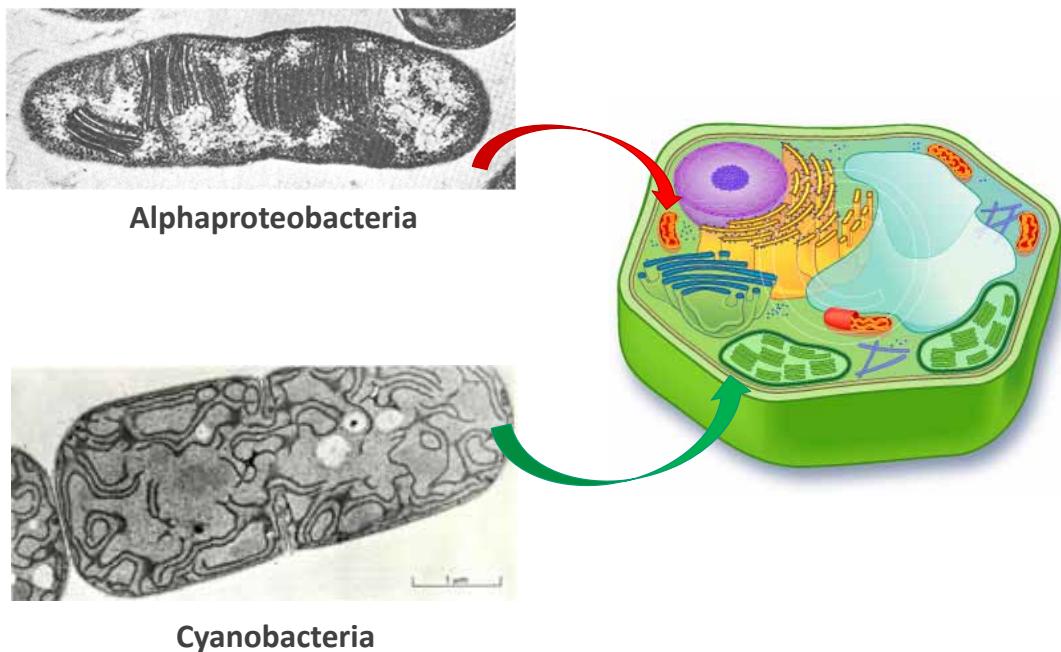


Prokaryotes predate eukaryotes: fossil evidence



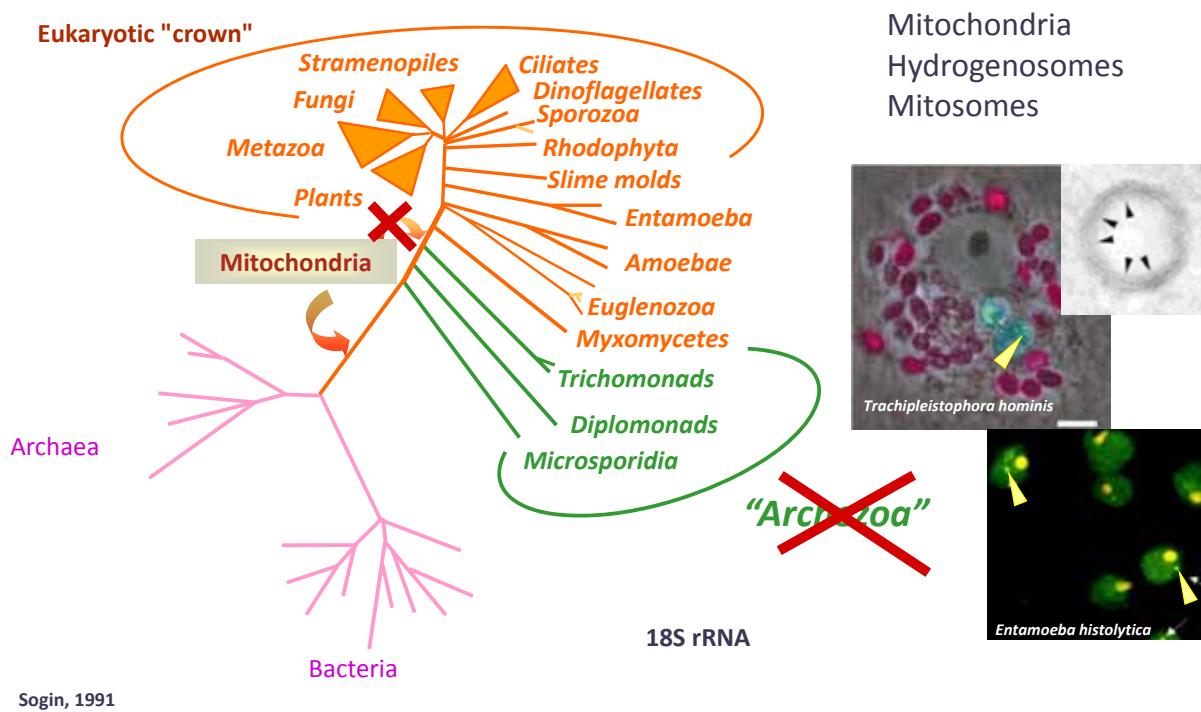
Prokaryotes predate eukaryotes: mitochondria

1) Mitochondria derive from endosymbiotic alphaproteobacteria



Prokaryotes predate eukaryotes : mitochondria

2) The last common ancestor of extant eukaryotes had mitochondria



Energy & Carbon

metabolism

Membrane lipids

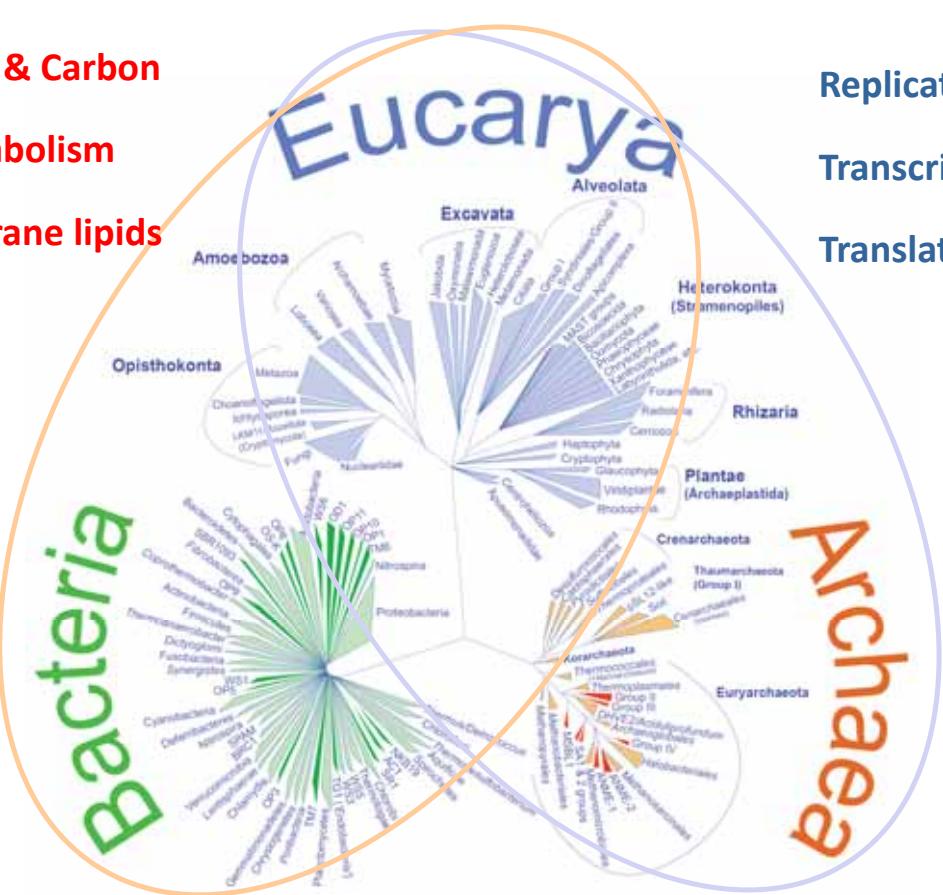
Bacteria

Eucarya

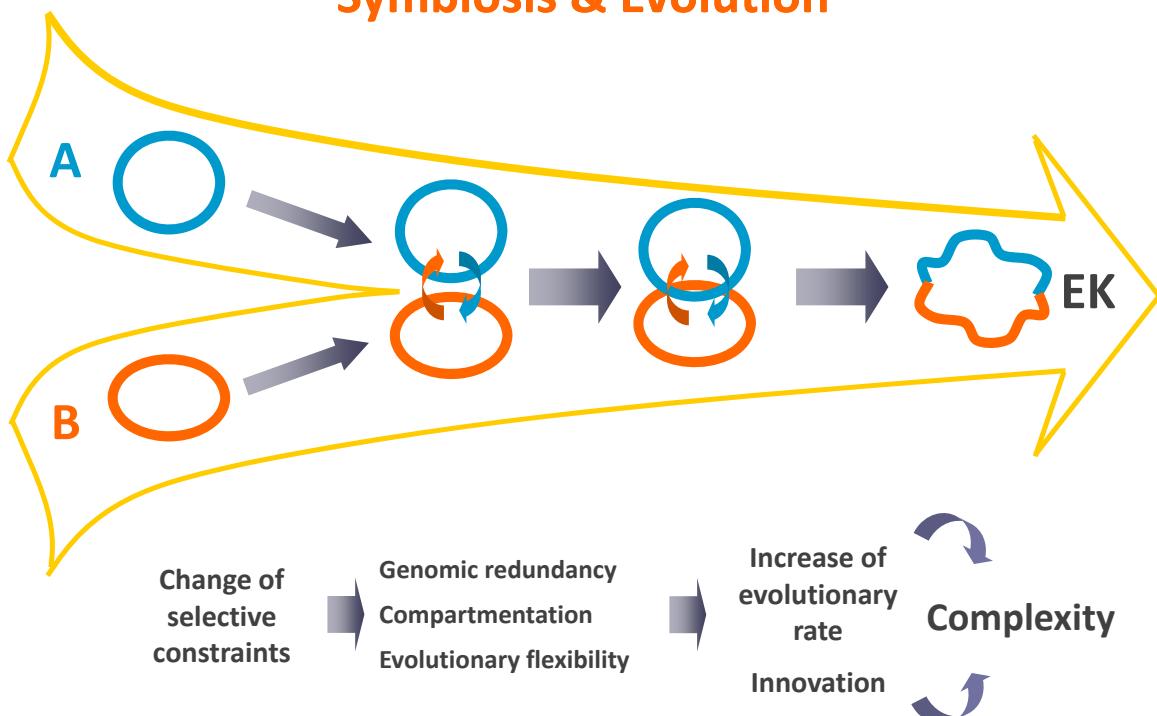
Replication

Transcription

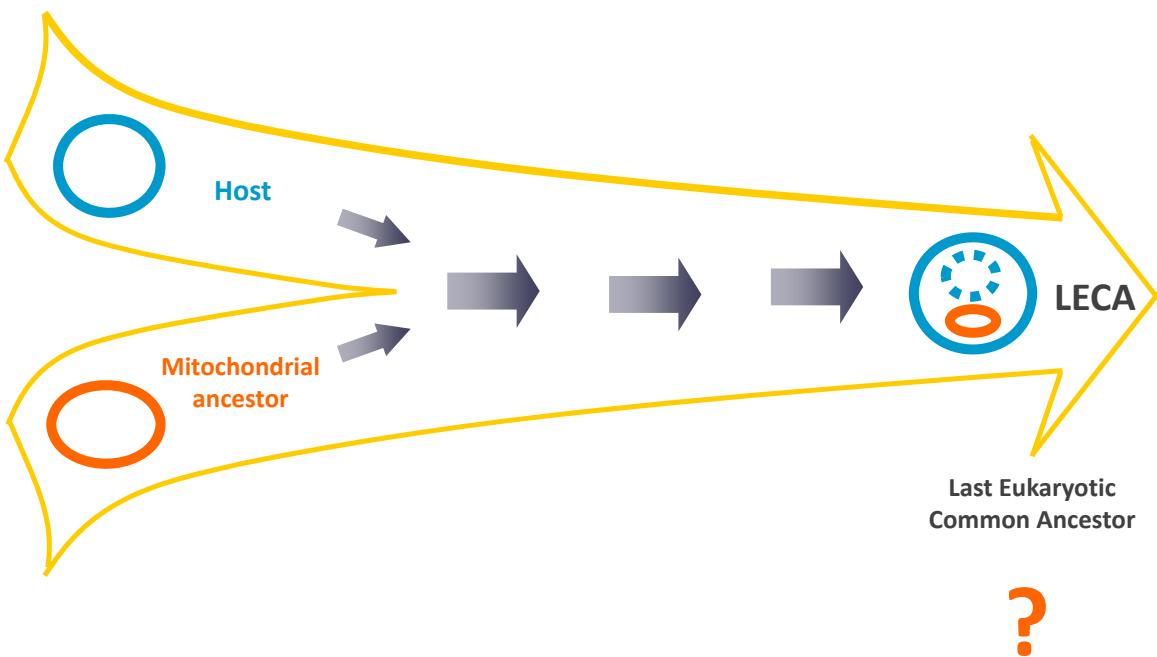
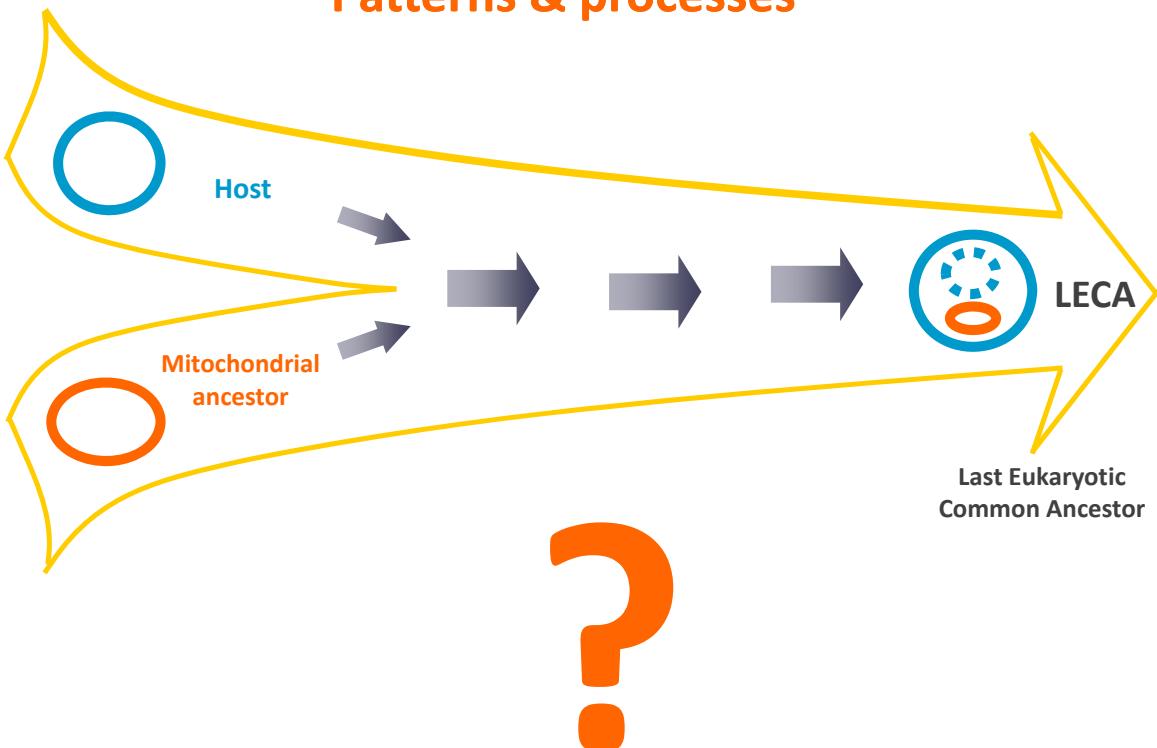
Translation



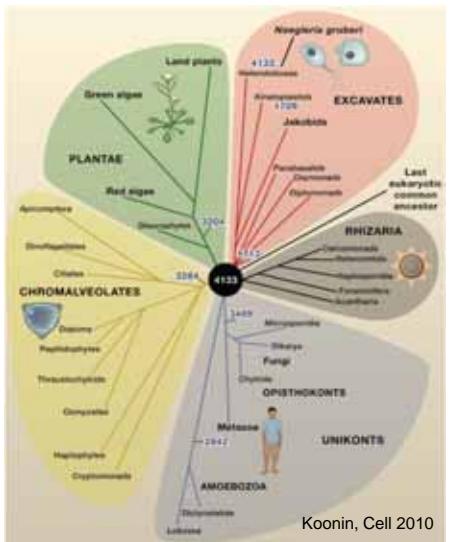
Symbiosis & Evolution



Patterns & processes



LECA, a complex ancestor



High metabolic flexibility & complexity

Cytoskeleton

Nucleus & nuclear pore complex

Endocytic & exocytic pathways

Complex trafficking network (Golgi, lysosomes/endosomes)

Eukaryotic flagellum

Proteasome

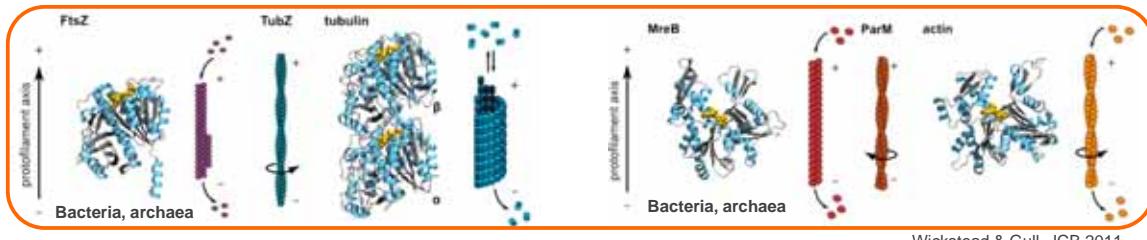
Ubiquitin signaling

Splicing

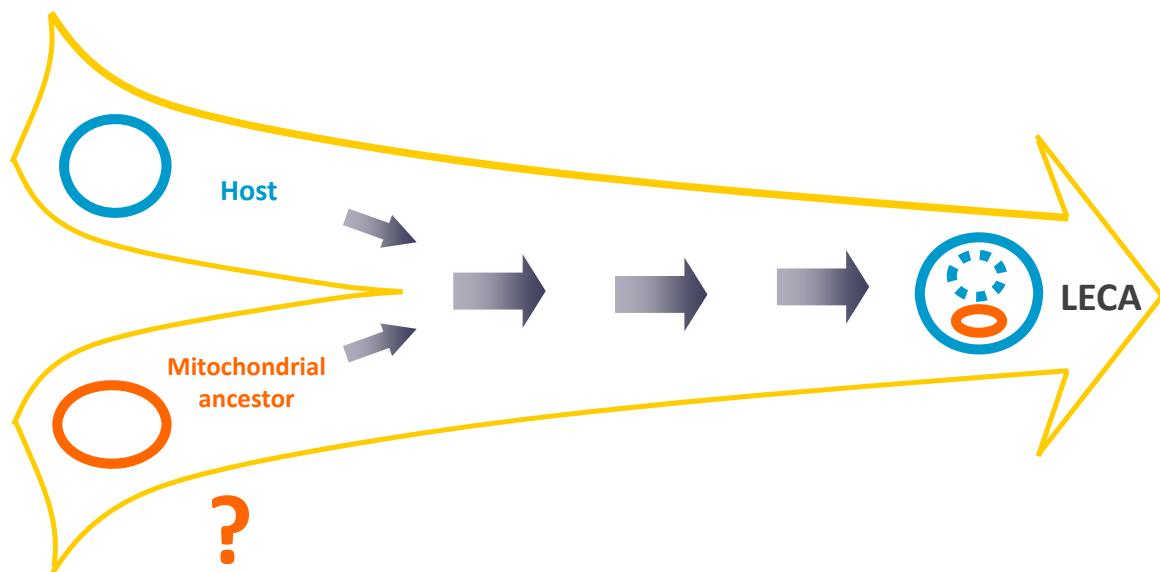
Mitosis & cytokinesis

Most likely sex (meiosis)

RNA interference



Wickstead & Gull, JCB 2011

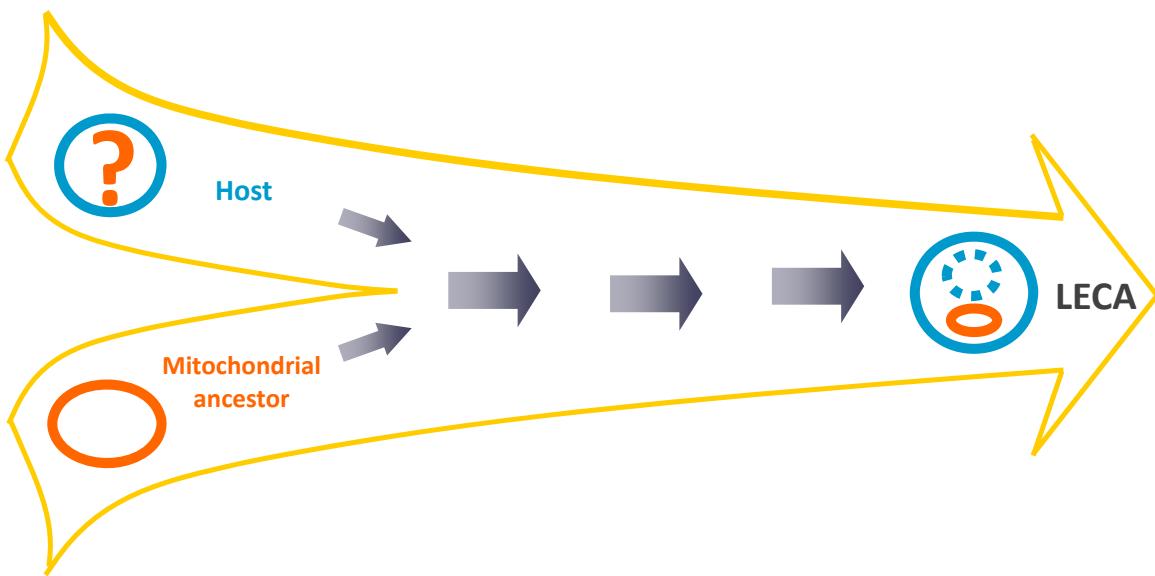


- What kind of alphaproteobacterium?

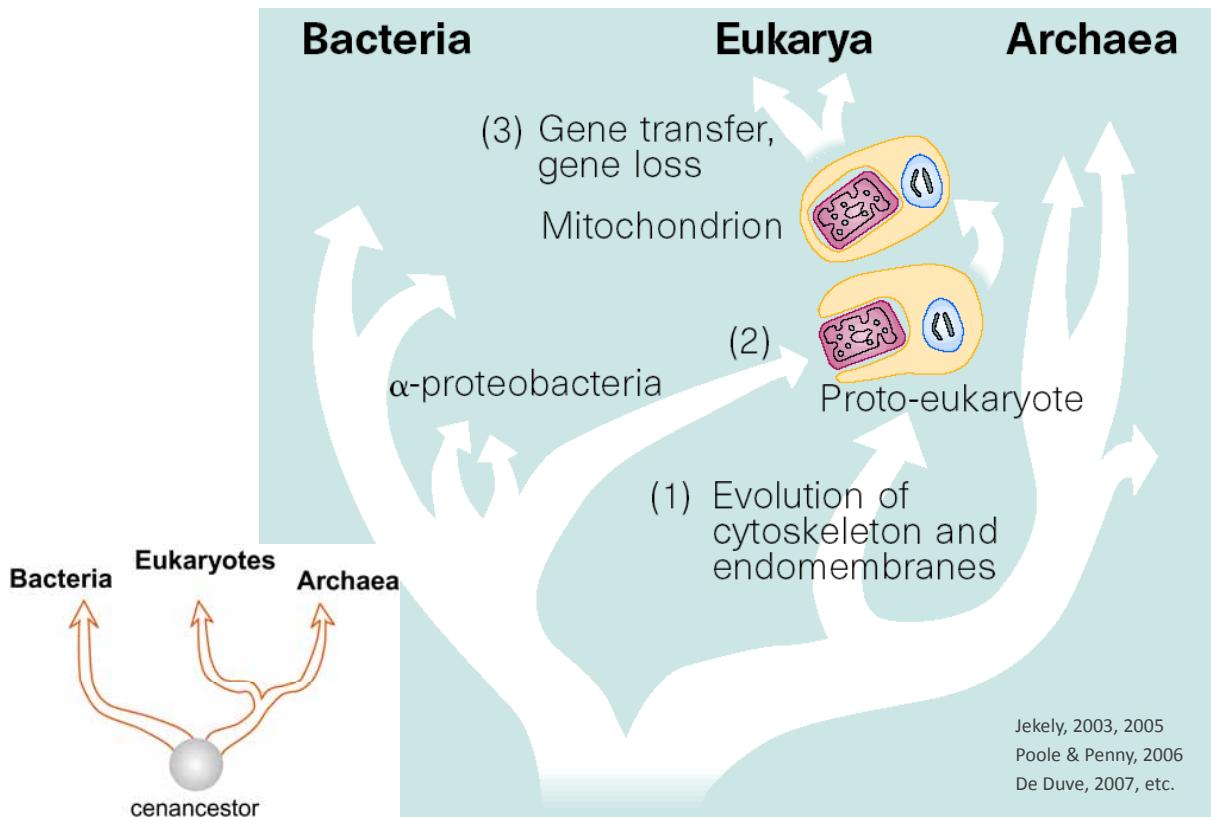
Rickettsia or *Pelagibacter* proposed affinities questioned

- Was it a facultative anaerobe?

Many mitochondria scattered in the phylogenetic tree ferment (as hydrogenosomes do) or use electron acceptors other than O₂ (nitrate, nitrite, fumarate) - ancestral or HGT?

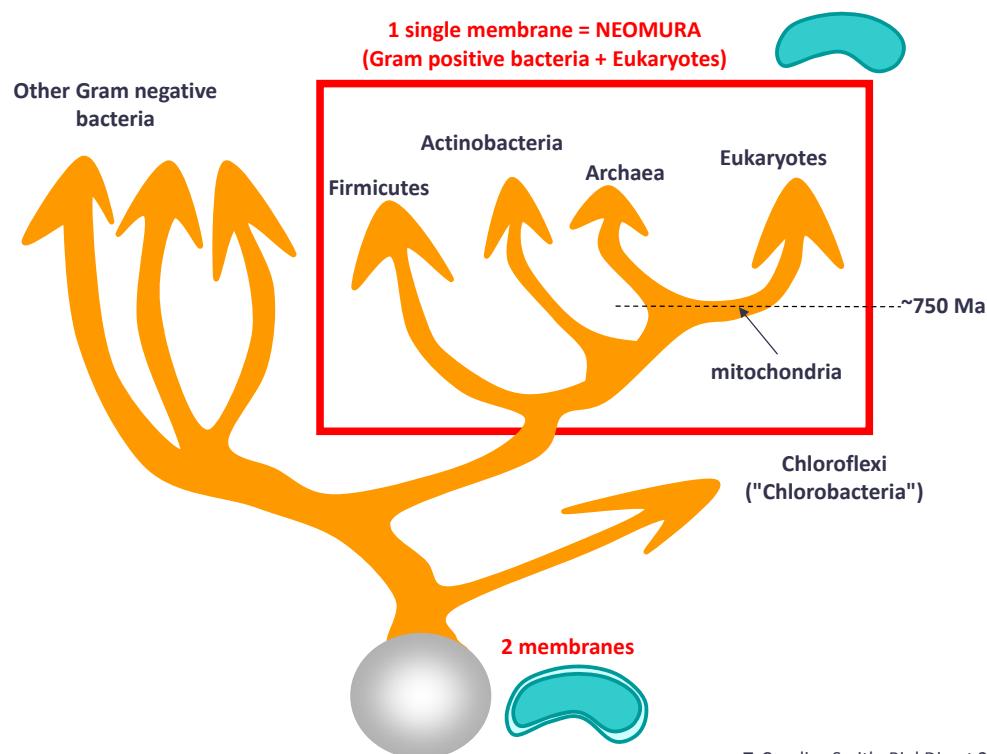


The "proto-eukaryote" or "tree of life" model

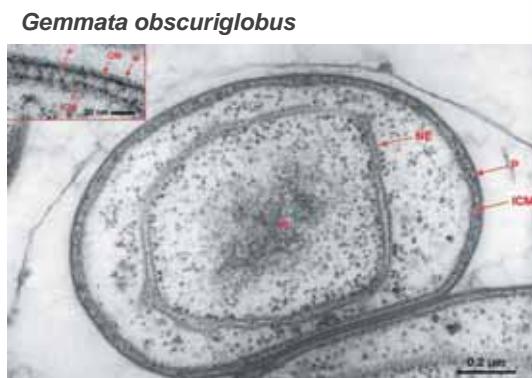


The Neomuran hypothesis

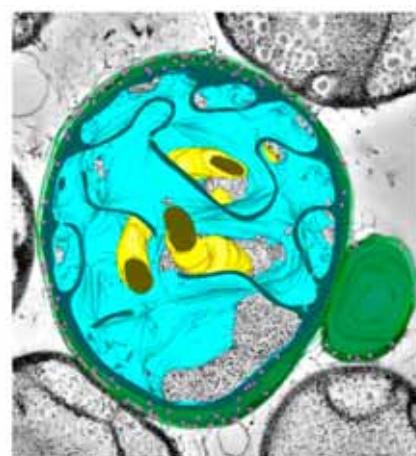
Tom Cavalier-Smith



Endomembrane system in Planctomycetes

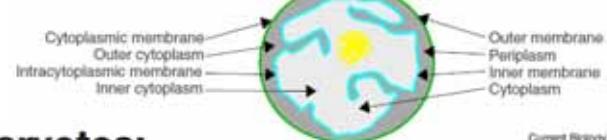


- Nucleus-like structure (ribosomes on both sides)
- Simple form of endocytosis



PVC super-phylum

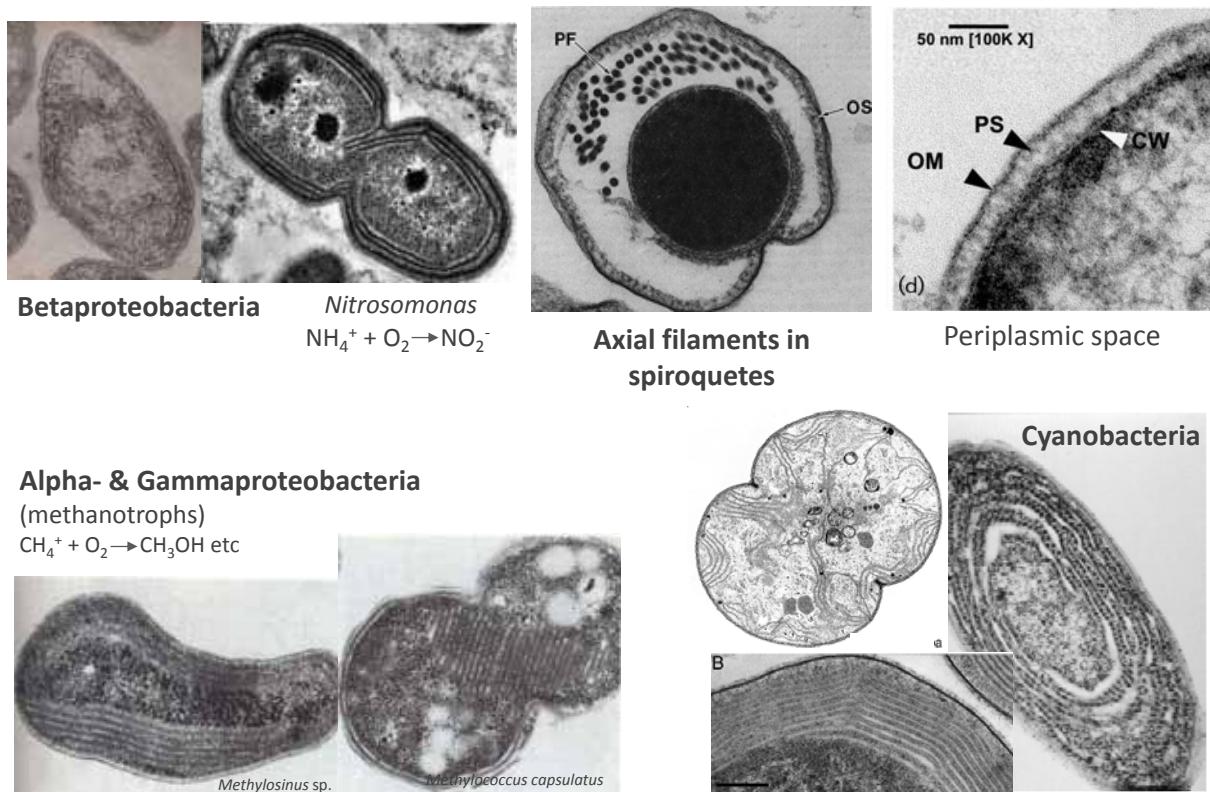
Planctomycetes-Verrucomicrobia-Chlamydia



Planctomycetes and eukaryotes: A case of analogy not homology

McInerney et al, BioEssays 2011

Endomembrane systems in bacteria

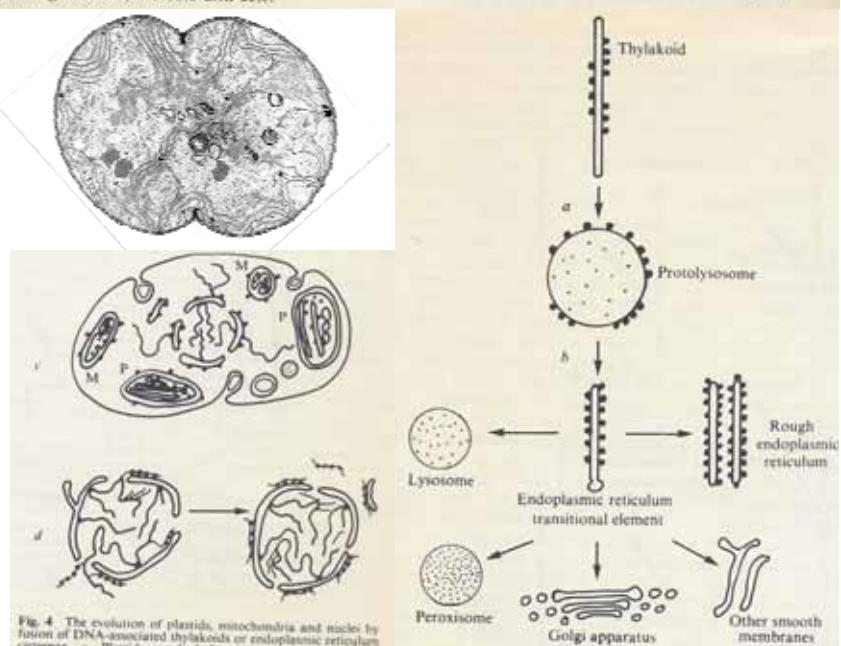


The origin of nuclei and of eukaryotic cells

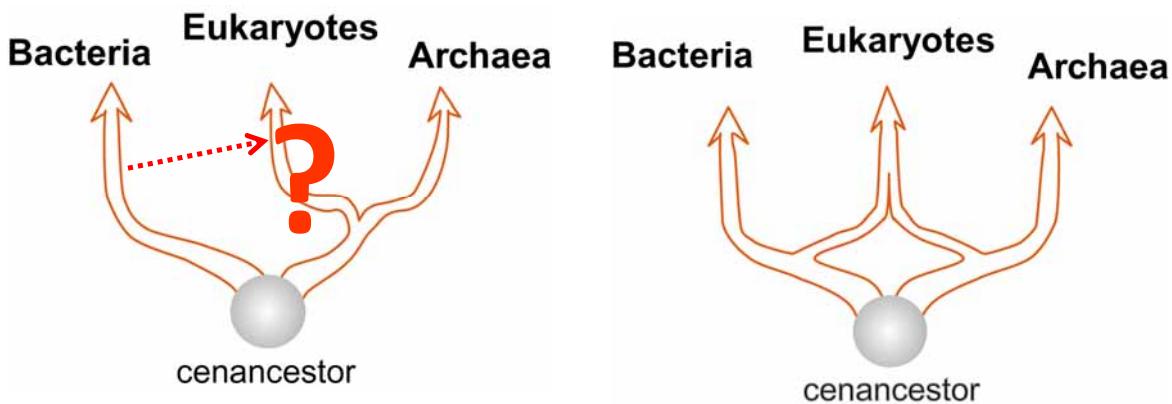
T. Cavalier-Smith*

Nature, Vol. 256, No. 5517, pp. 463–468, August 7, 1975.

A new theory not involving symbiosis is proposed for the origin of eukaryotic cells. It explains how the evolution of phagocytosis by a wall-free blue-green alga would have created selection pressures leading directly to the formation of all characteristic eukaryote organelles and cell properties including mitosis, meiosis and sex.



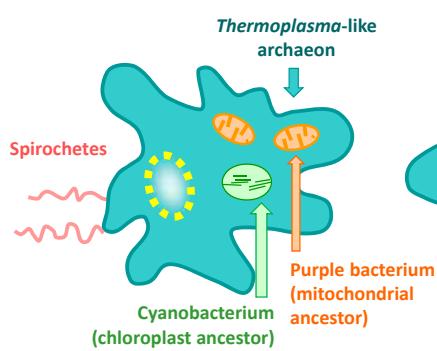
Symbiosis-based chimeric models



Sybiogenetic models...

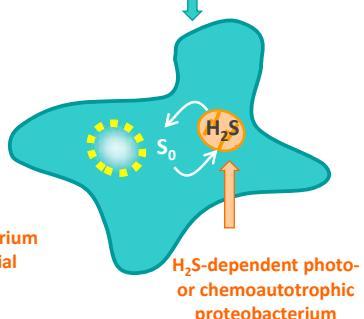
Serial Endosymbiotic Theory

Margulis 1970, 1993, 2000



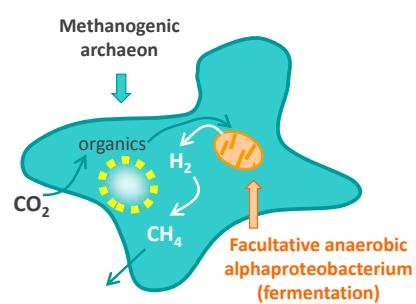
D. Searcy, 1992

Thermoplasma-like archaeon

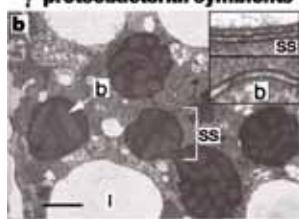


The hydrogen hypothesis

Martin & Müller, 1998



Mealybug β-proteobacterial endosymbionts contain γ-proteobacterial symbionts



von Dohlen et al, Nature, 2001
DOI:10.1038/35095093

Endosymbiotic bacteria even within mitochondria!

Alphaproteobacteria belonging to the Rickettsiales

Ixodes ricinus (tick)



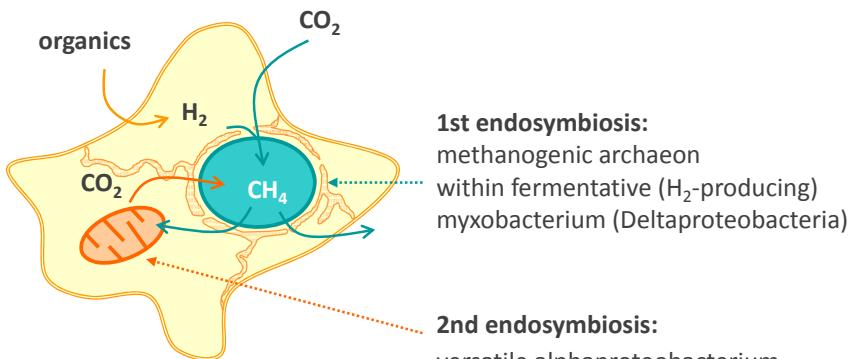
Sassera et al, 2006
DOI:10.1038/nature04730

Martin & Koonin, 2006

Endosymbiotic origin of the nucleus: 3 symbionts

Syntrophy hypothesis

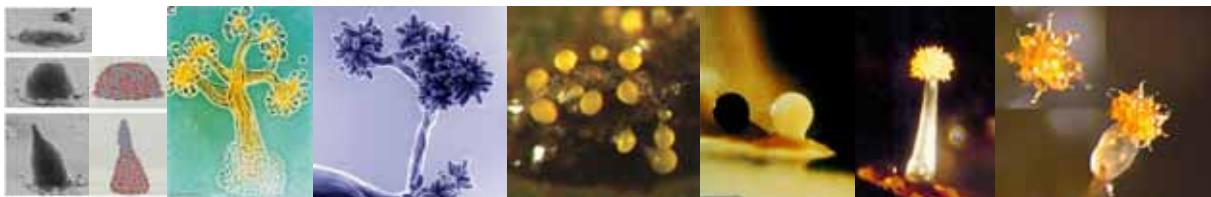
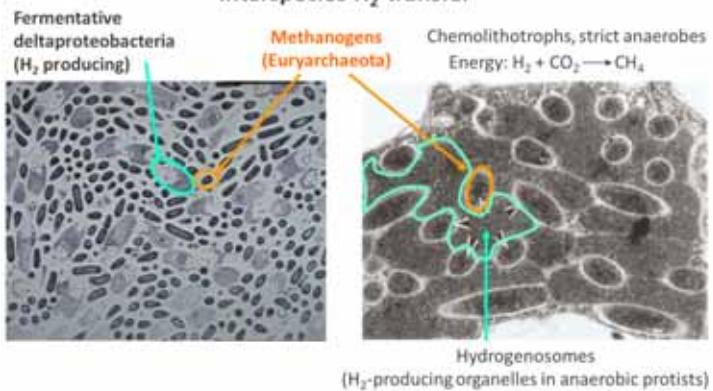
Moreira & López-García 1998
López-García & Moreira 2006



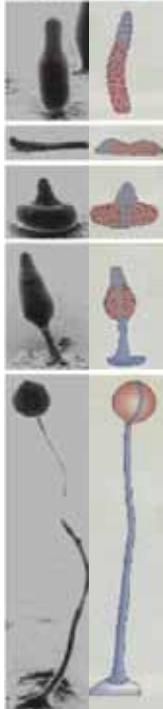
2nd endosymbiosis:

versatile alphaproteobacterium
facultative aerobe, methanotroph

Interspecies H_2 -transfer



Eukaryotic-like traits in myxobacteria



Specific proteins:

- Serine-threonine & tyrosine kinases
- Calmodulin-type morphogenesis protein
- 17 b-hydroxysteroid dehydrogenase
- Ras/Rab/Rho-type small GTPases
- High mobility group (Y-type) proteins
- Reverse transcriptase (and retrons elements)

Phylogenomics: at least some genes were ancestrally transferred from myxobacteria to eukaryotes: fatty acid β oxidation pathway

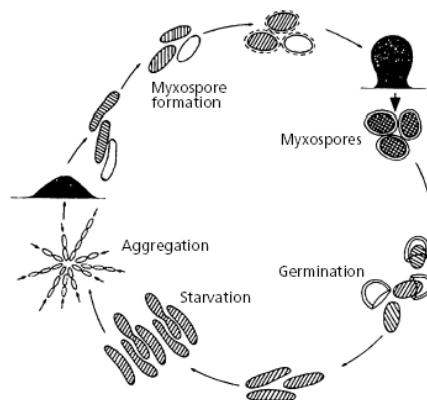
Schluter, Ruiz-Trillo & Pujol, 2011

General processes:

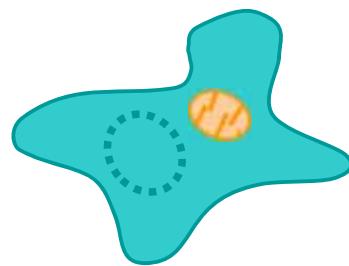
- Synthesis of sterols
- Phosphatidyl-inositol cycle
- Participation of G-proteins in signal transduction
- Synthesis of antibiotics (many against eukaryotes)
- Synthesis of melanin
- Predation: protein-digesting machineries (periplasm)

Large genomes, e.g. *Myxococcus xanthus* (9.14 Mb):

- >1500 selective specific duplications:
 - cell-cell signaling
 - small molecule signaling
 - integrative transcription control



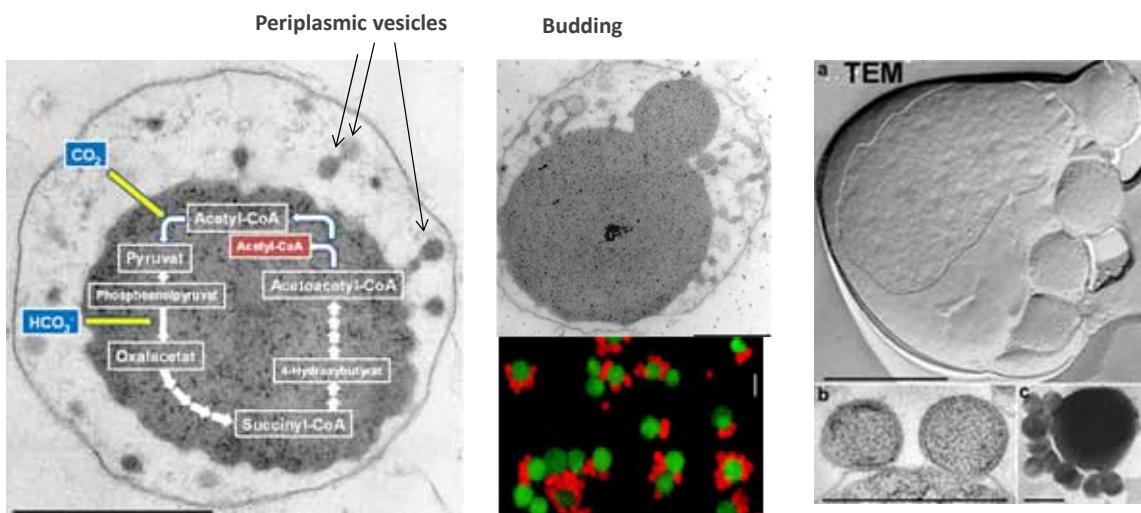
Origin of mitochondria ≈ origin of eukaryotes 2 symbionts



Various subsequent models to hydrogen hypothesis:

- In general, no clear metabolic or other driving force advanced (idem for nucleus)
- Based on protein/gene content & phylogenetic analyses
- Based on cell biology: potential to develop endomembranes

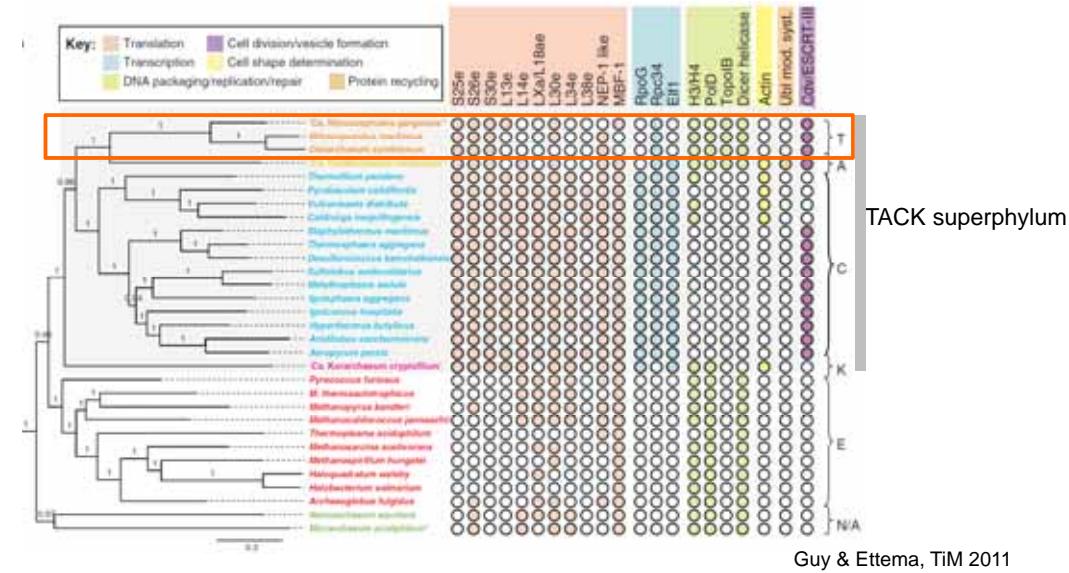
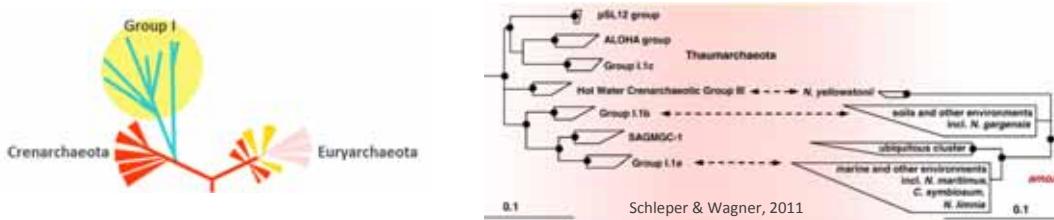
Membrane remodeling in archaea



Ignicoccus hospitalis and its symbiont (parasite?) *Nanoarchaeum equitans*

Chemolithoautotroph reducing S° to H₂S
T opt ~90°C

Thaumarchaeota as archaeal ancestor?



A stem archaeal ancestor as host?

Cell division & vesicle formation in archaea

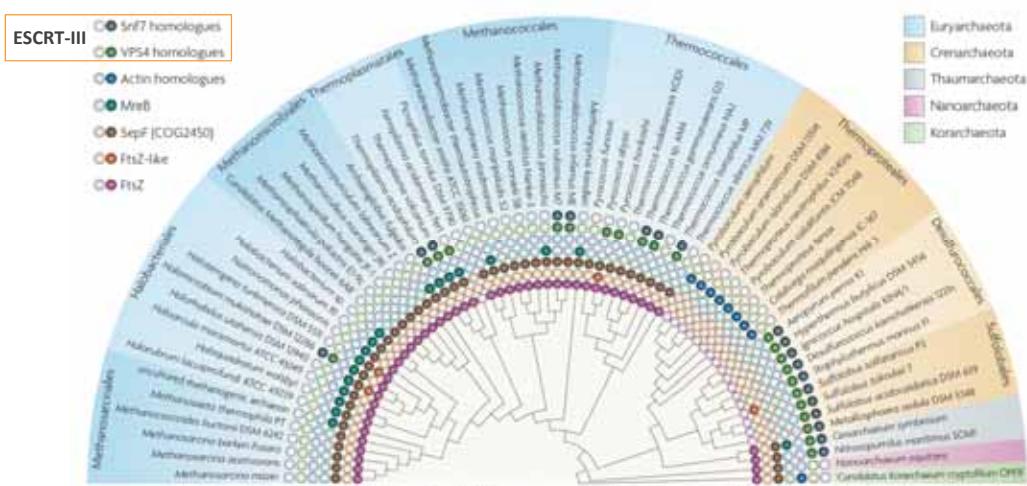
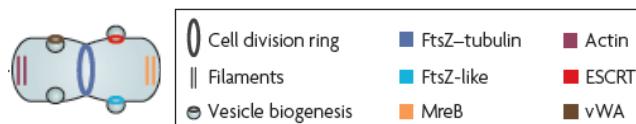
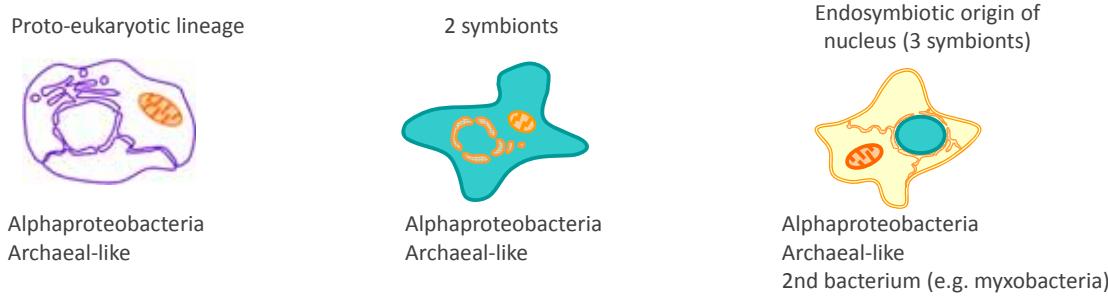


Figure 2 | The distribution of the key components of membrane manipulation systems among the Archaea.



Can we test these models?



Phylogenomics: difficulties

- Mitochondrial and chloroplast ancestry easily retrieved because:
 - More recent
 - Conservation of function
- Symbiotic ancestors of mitochondrial host difficult (impossible?) to identify because:
 - Ancient event: maybe no (discriminating) phylogenetic signal kept
 - (Drastic) change of function & innovations
 - Acceleration of evolutionary rate

Conflicting results, phylogenomic impasse?

Table 1 | Summary of seven recent large-scale phylogenomic analyses

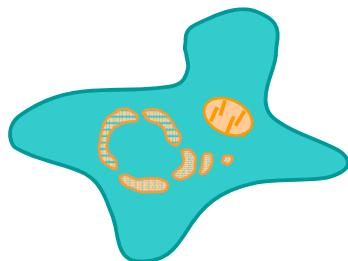
Publication	Number of markers used to infer relationships among the three domains	Taxonomic sampling	Number of amino acid positions used	Method	Model supported
Harris et al. ³¹	50	25 bacteria 1 crenarchaeote 7 euryarchaeotes 3 eukaryotes	Variable, depending on the gene	Single-gene analysis Maximum likelihood Maximum parsimony ENSEMBLE	2D
Ciccarelli et al. ³⁰	31	150 bacteria 4 crenarchaeotes 14 euryarchaeotes 23 eukaryotes	8,090	Single-gene analysis Maximum likelihood Maximum parsimony ENSEMBLE	2D
Yutin et al. ²⁸	136	Variable, depending on the gene	Variable, depending on the gene	Single-gene analysis Maximum likelihood	3D
Rivera & Lake ²⁵	Complete genome	Archaea Bacteria Eukarya	~100,000,000	Genome content (conditioned reconstruction)	2D (the Eukarya sister of the Crenarchaeota)
Pisani et al. ²²	22	10 bacteria 1 crenarchaeote 11 euryarchaeotes 17 eukaryotes	Variable depending on gene	Supertree	2D (the Eukarya sister of the Thermoplasmatales)
Cox et al. ²³	22	10 bacteria 3 crenarchaeotes 11 euryarchaeotes 16 eukaryotes	5,521	Concatenation Bayesian Maximum likelihood Maximum parsimony	2D (the Eukarya sister of the Crenarchaeota)
Foster et al. ²⁴	41	8 bacteria 8 crenarchaeotes 2 thaumarchaeotes 6 euryarchaeotes 11 eukaryotes	5,222	Concatenation Bayesian Maximum likelihood Maximum parsimony	2D (the Eukarya sister of a group comprising the Crenarchaeota and the Thaumarchaeota)

2D, 'two primary domains' scenario; 3D, 'three primary domains' scenario.

Current favoured model

The hydrogen hypothesis & alike

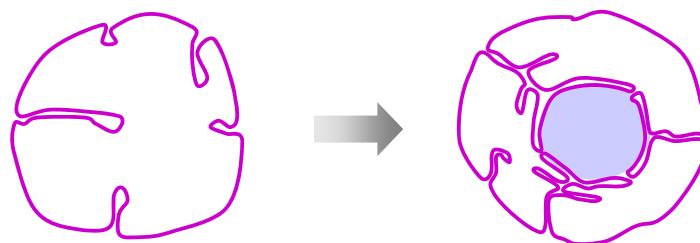
Archaeal host establishes symbiosis with the alphaproteobacterial ancestor of mitochondria



Need for detailed mechanistic process

... the devil is in the details!

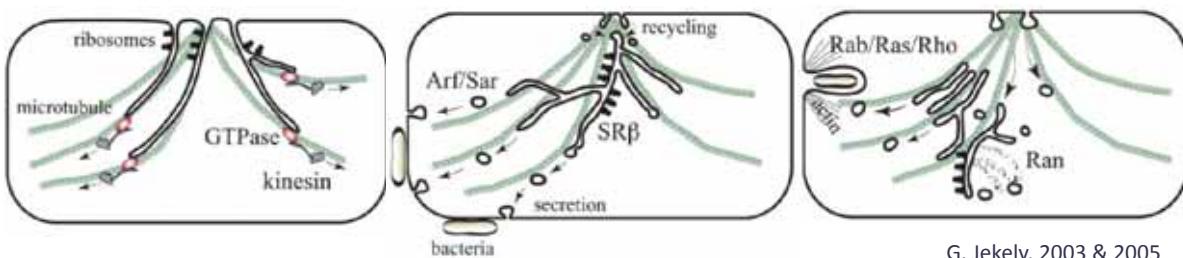
How did the nucleus evolve?



Selective forces proposed for the emergence of the nucleus in 3D models:

- T. Cavalier-Smith (1987): to prevent chromosome shearing by cytoskeletal movements
- G. Jékely (2008): to prevent the formation of chimeric ribosomes in a proto-eukaryote devoid of nucleus after engulfment of mitochondria

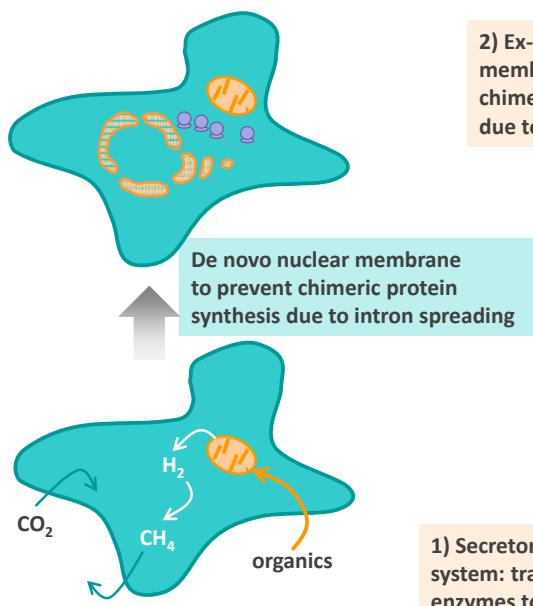
Primary secretory role of endomembrane system - Small GTPases: Sar1, Arf, SRB, Ran, Rab, Ras, Rho



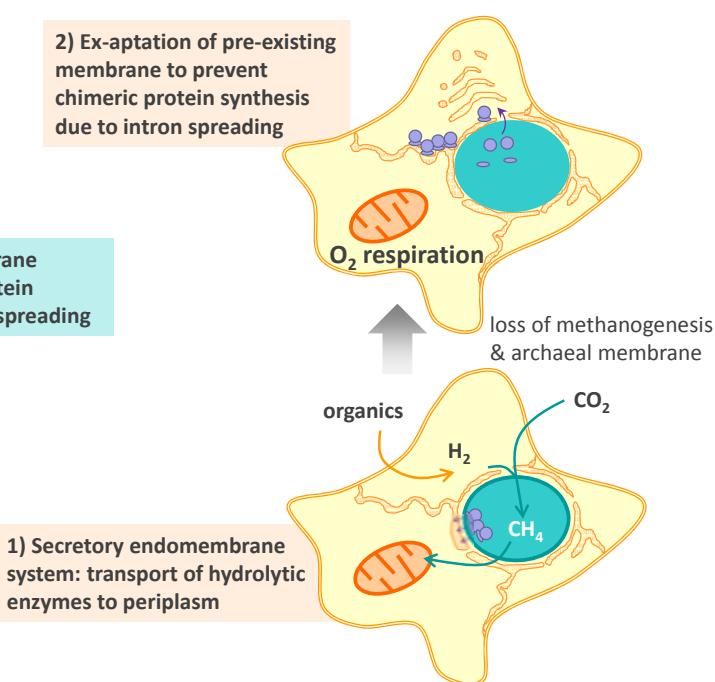
G. Jékely, 2003 & 2005

Selective forces for the origin of the nucleus

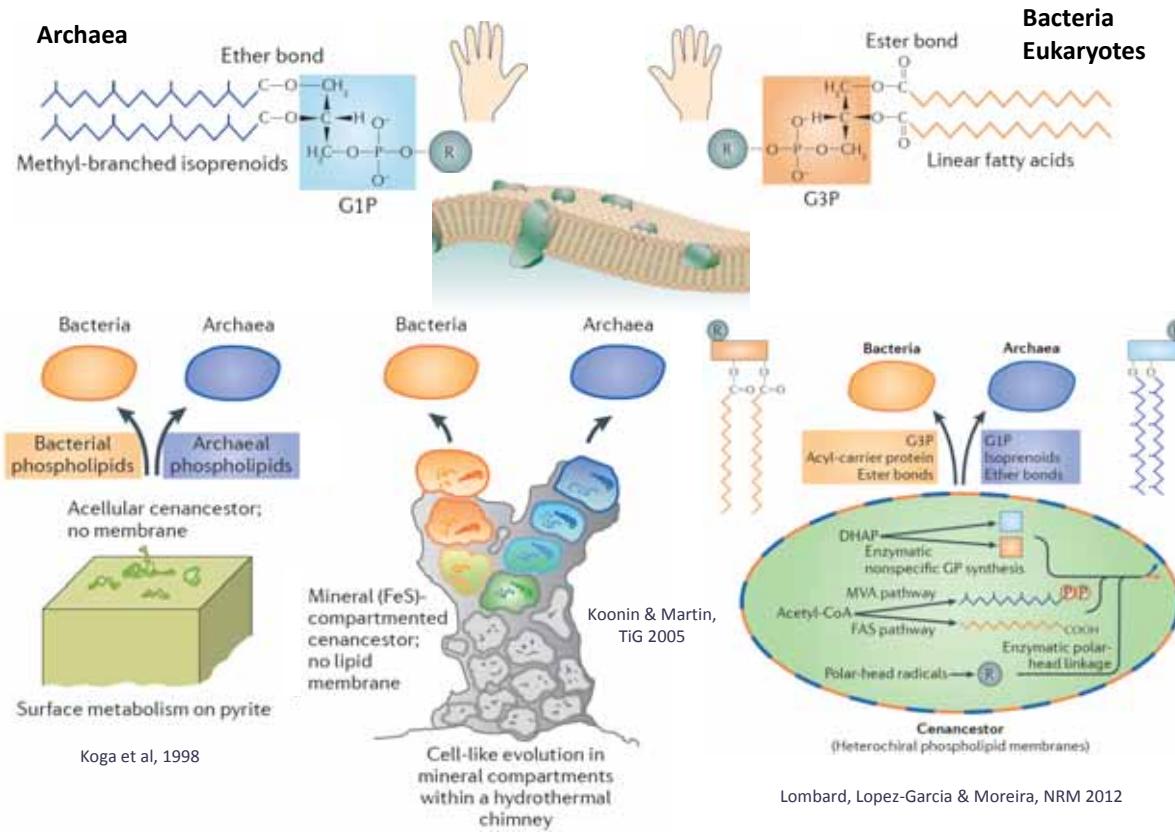
Hydrogen hypothesis



Syntropy hypothesis



The problem of the membranes



The problem of the membranes

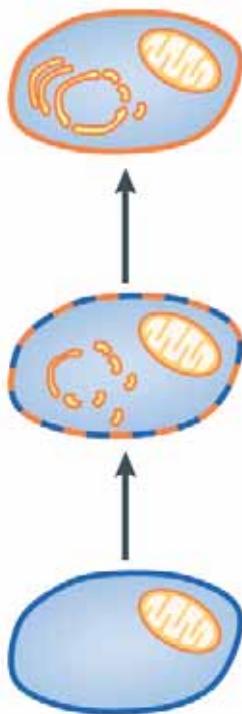
Hydrogen hypothesis

(& other H₀ where archaeon = host)

Formation of a nuclear membrane from nucleus-encoded bacterial phospholipid vesicles

Progressive replacement of archaeal membrane by bacterial phospholipids

Endosymbiosis of an alphaproteobacterium within an archaeal host



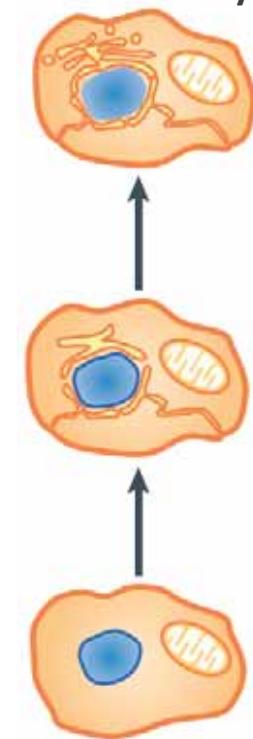
Syntropy hypothesis

(& other H₀ where archaeon = endosymbiont)

Loss of archaeal membrane

Formation of a secretory endomembrane system by invagination of bacterial membrane

Endosymbiosis of an archaeon within a myxobacterial host
Secondary endosymbiosis of an alphaproteobacterium



Conclusions

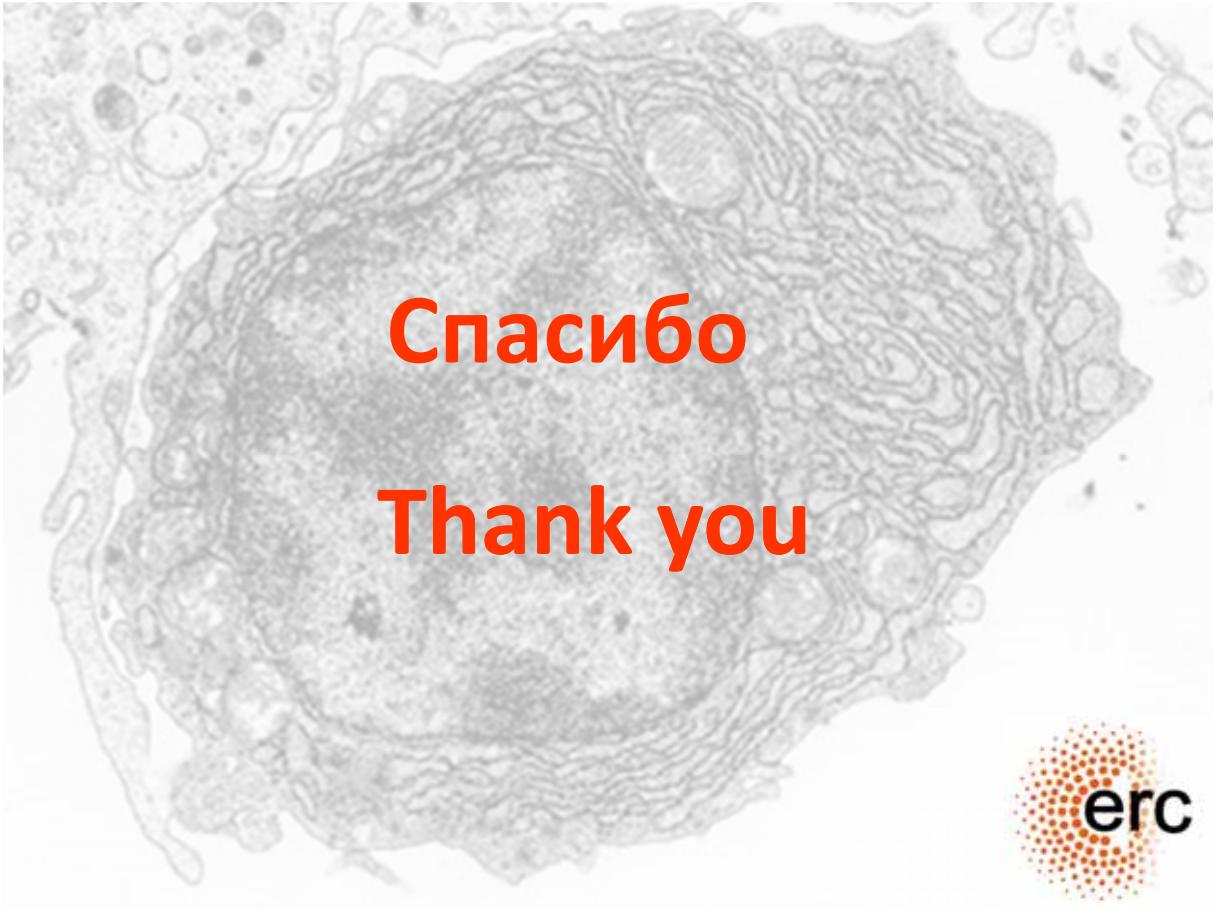
- Models on the origin of eukaryotes: we need the details!
plausible processes to account for observed phylogenetic patterns

Major problems:

- Origin of the **nucleus** unresolved (no clear selective forces)
- Nature of **membranes** unexplained in currently favoured endosymbiotic models (archaeon engulfs mitochondrial ancestor)
[the possibility of an endosymbiotic origin of the nucleus needs to be considered]

- Phylogenomic analyses might help to discriminate between/formulate new plausible models
 - Better eukaryotic (protist) sampling: LECA portrait
 - Better prokaryotic (B/A) sampling
- Perhaps we will never know: contingent event

More genomes...
& explore NATURE!



Спасибо

Thank you

