Evolutionary Origins of Compartmentalized Cells

The prokaryote-to-eukaryote transition

The energetics of genome complexity

Bangalore 2012

10 µm

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A well-nourished human makes ~60 kg ATP per day (~500 tonnes per generation).

Origin of compartmentation in eukaryotes, there are a lot of models

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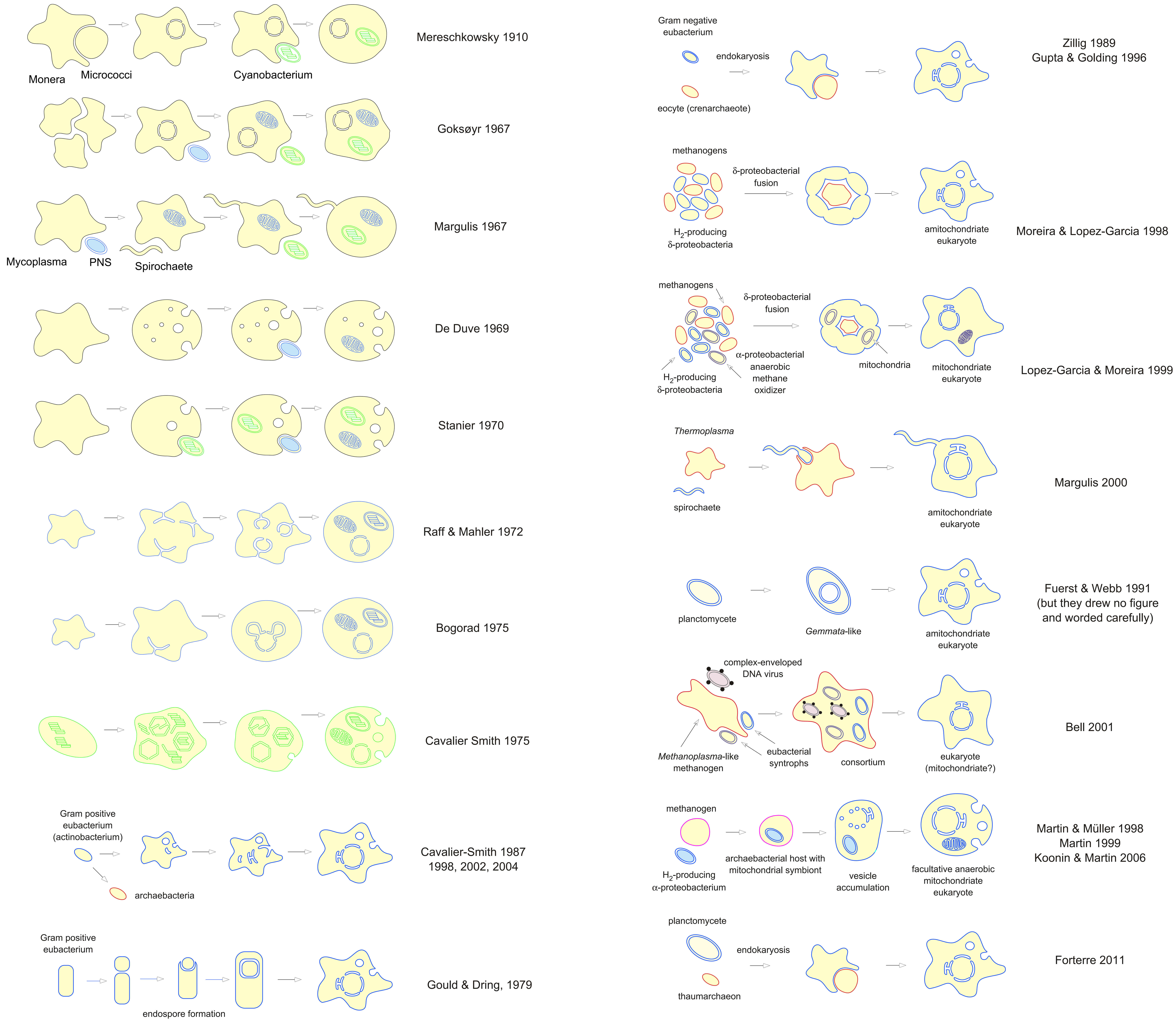
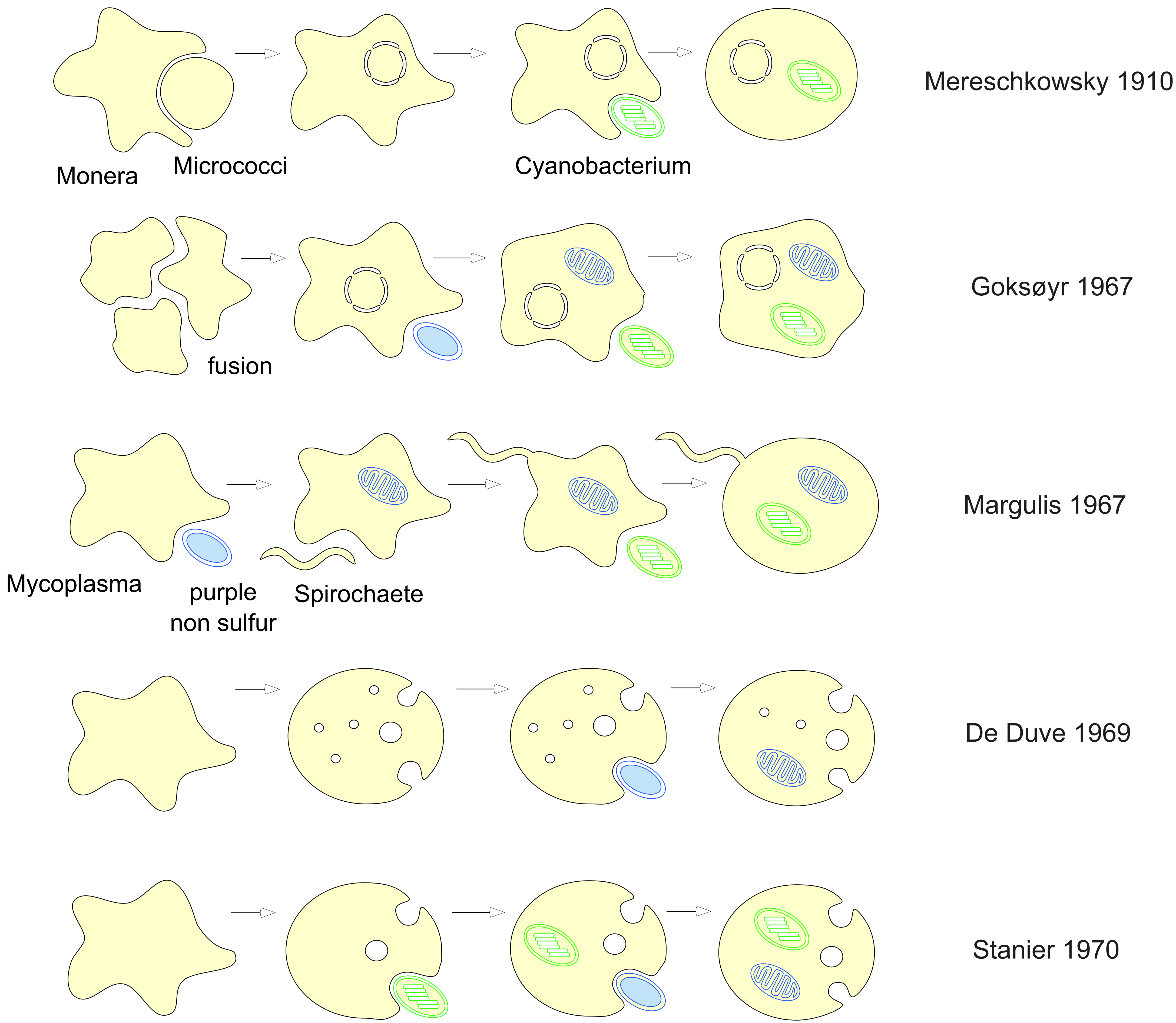
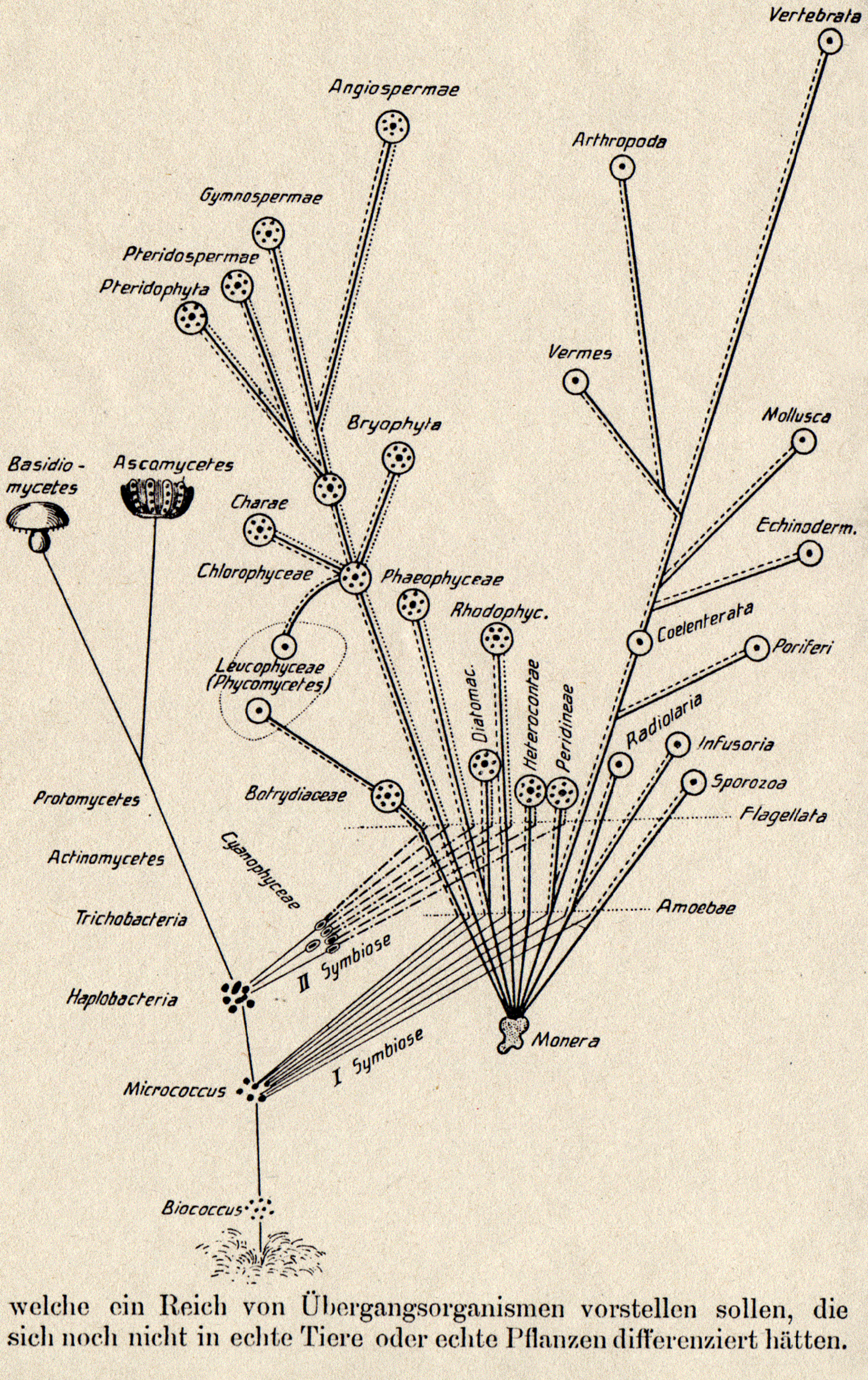




Monera
Micrococci
Cyanobacterium
Mereschkowsky 1910
fusion
Goksøyr 1967
Mycoplasma
purple
non sulfur
Spirochaete
Margulis 1967
De Duve 1969
Stanier 1970

Noch eine Schlussfolgerung meiner Theorie ist die Aufhebung des Reiches der Protisten — dieser Zoophyten des 19. Jahrhunderts,



welche ein Reich von Übergangsorganismen vorstellen sollen, die sich noch nicht in echte Tiere oder echte Pflanzen differenziert hätten.

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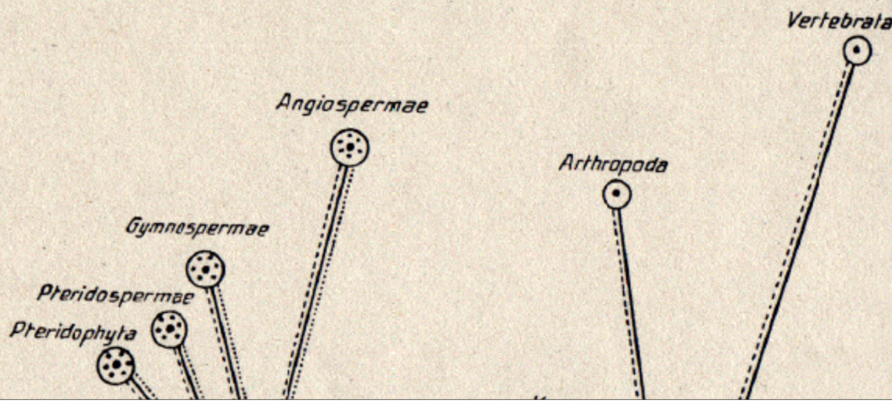
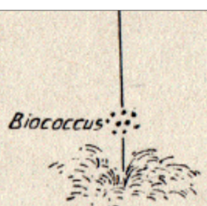


"Such an hypothesis [endosymbiosis] is of course unverifiable, and for this reason will to many appear worthless. …. To many no doubt, such speculations may seem too fantastic for mention in polite biological society; nevertheless it is within the range of possibility that they may someday call for more serious consideration." (1926)

THE CELL IN DEVELOPMENT AND HEREDITY

Edmund B. Wilson



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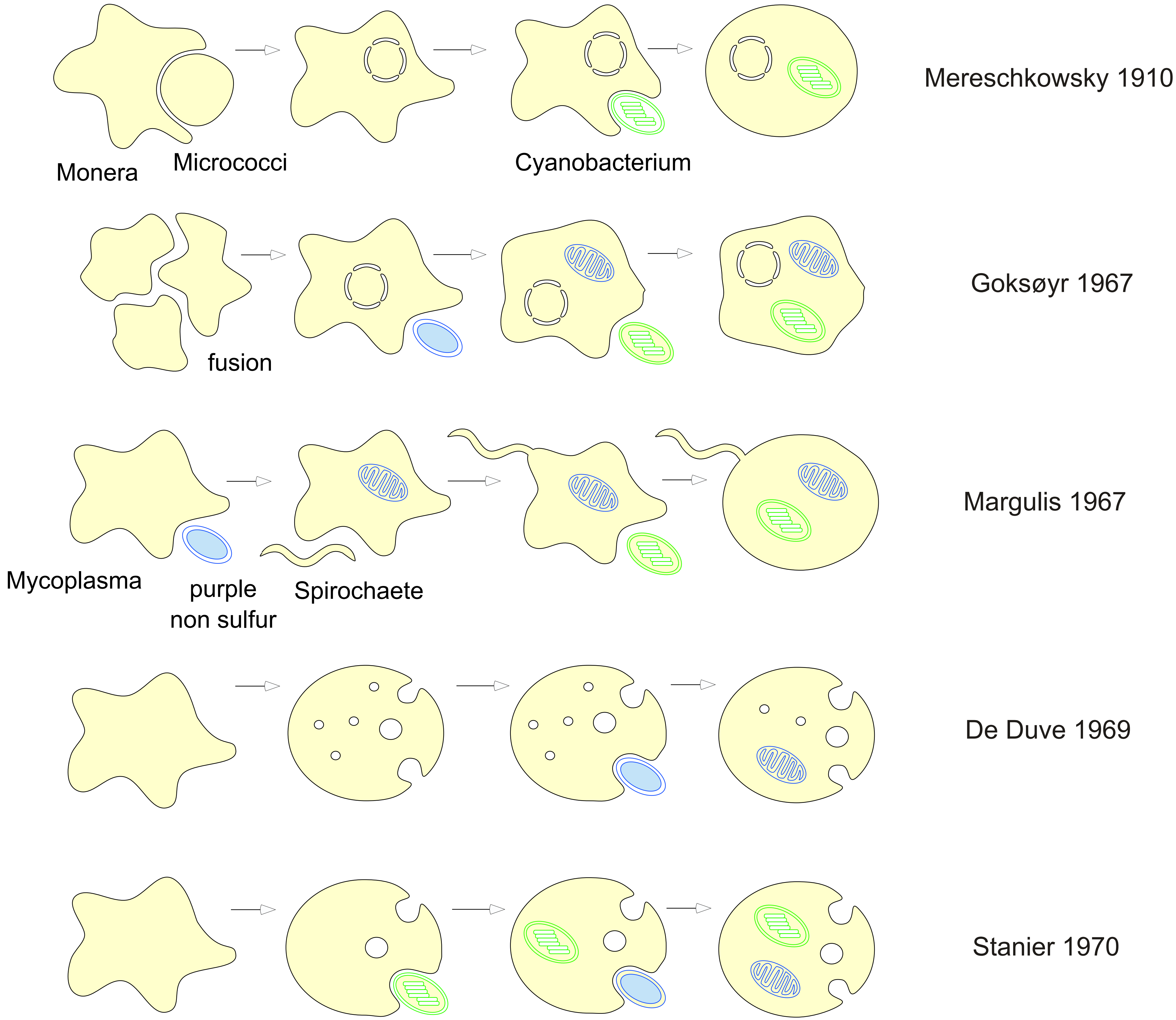
Mereschkowsky 1910
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Goksøyr 1967
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purple
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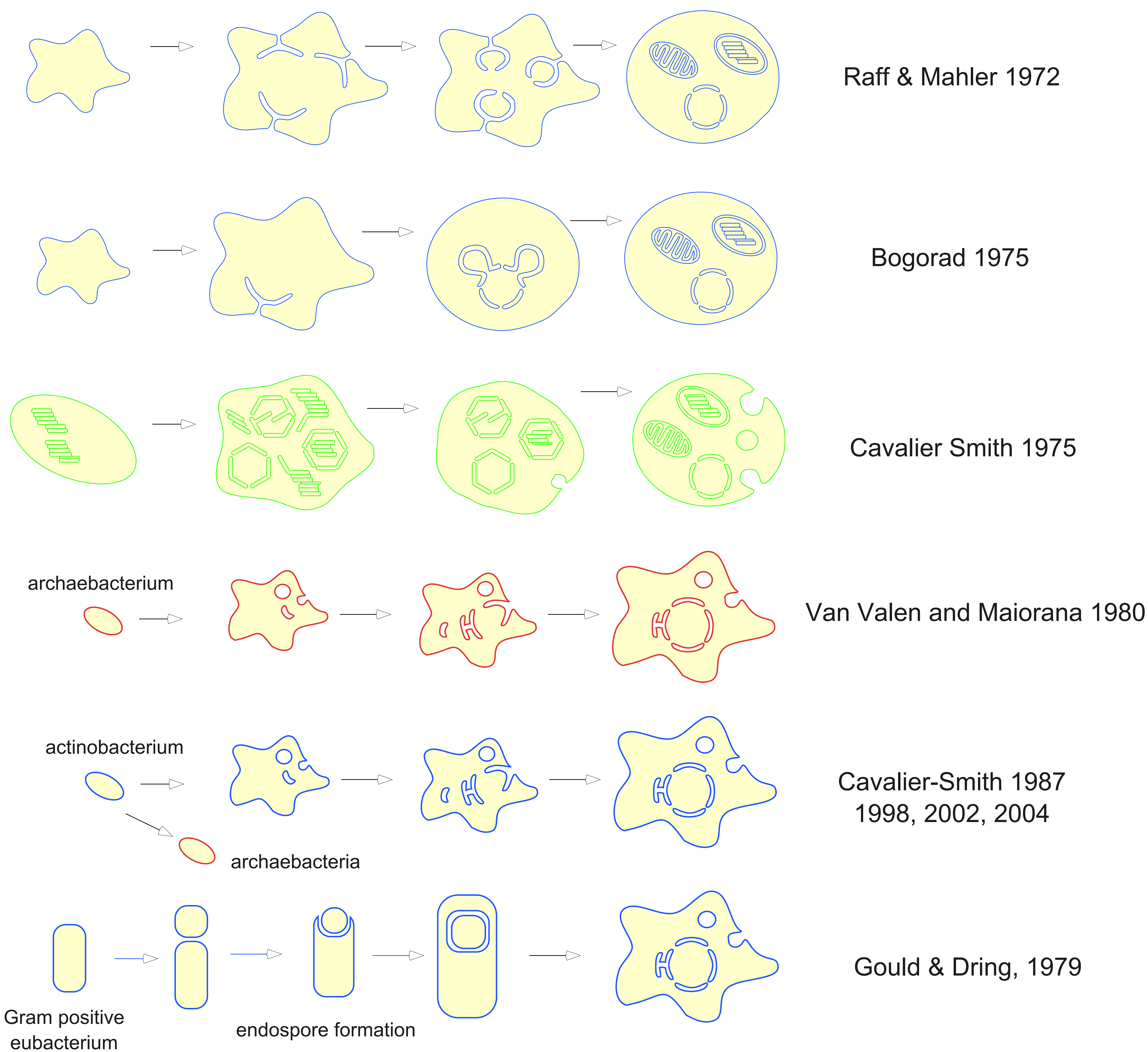
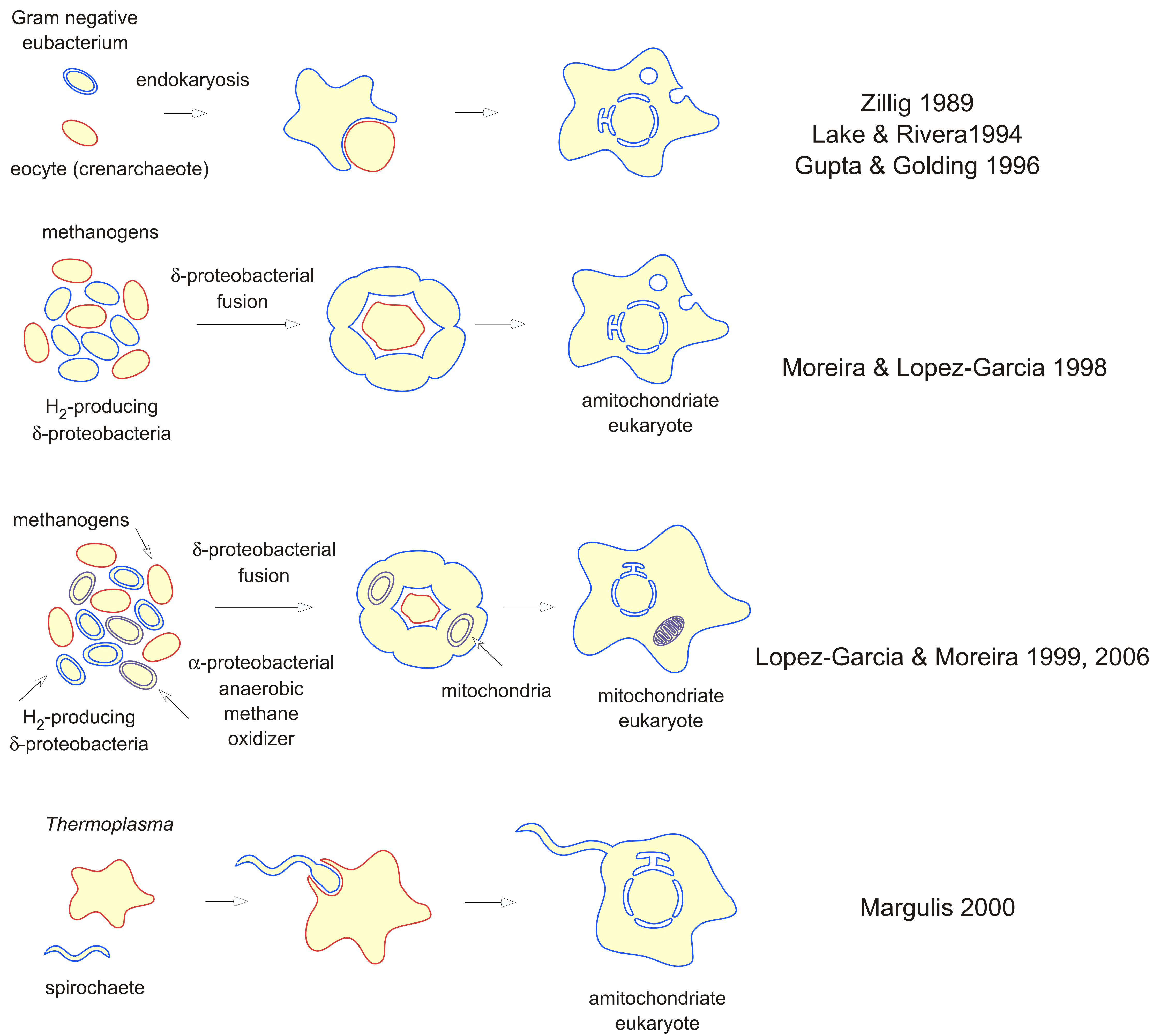
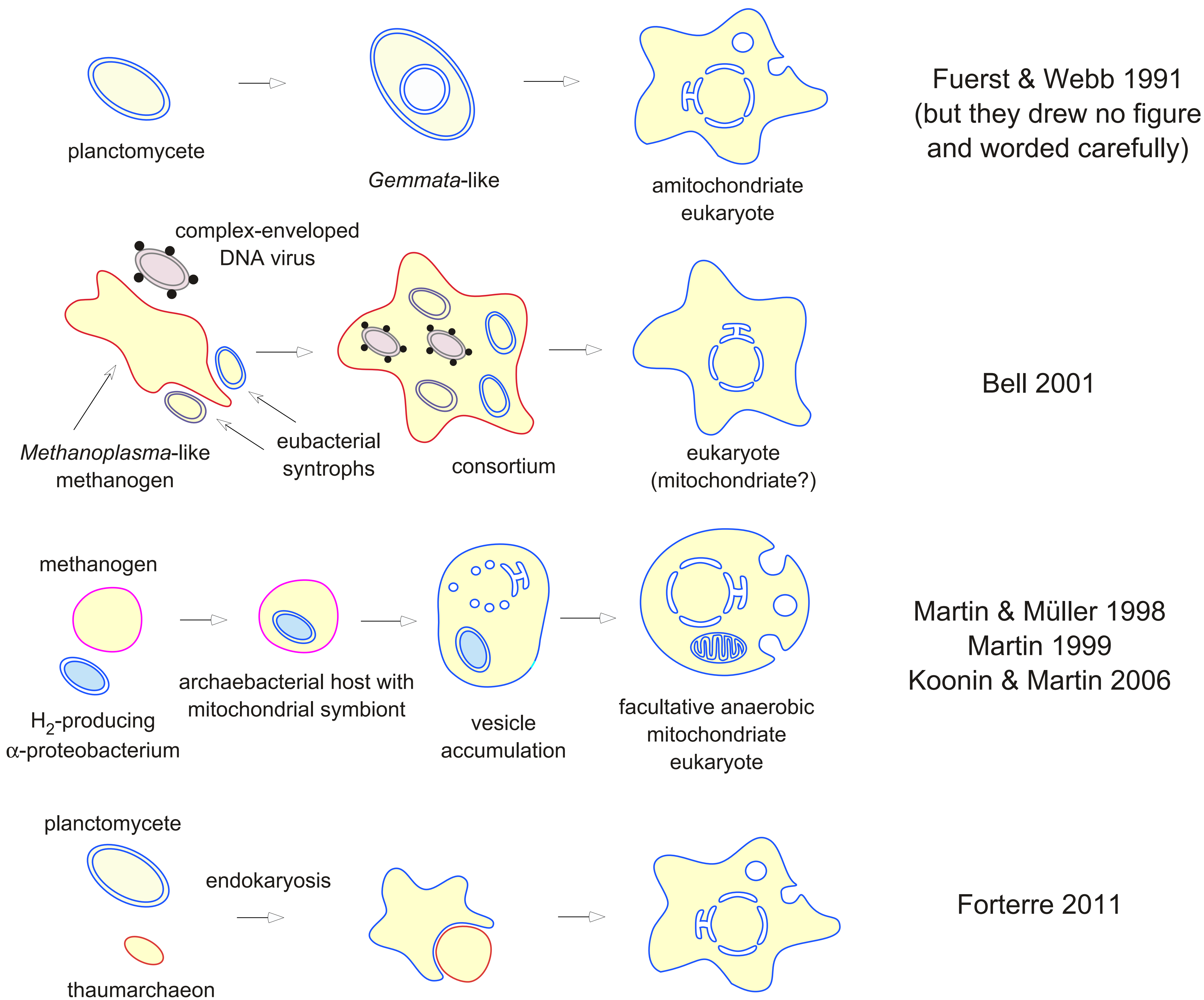
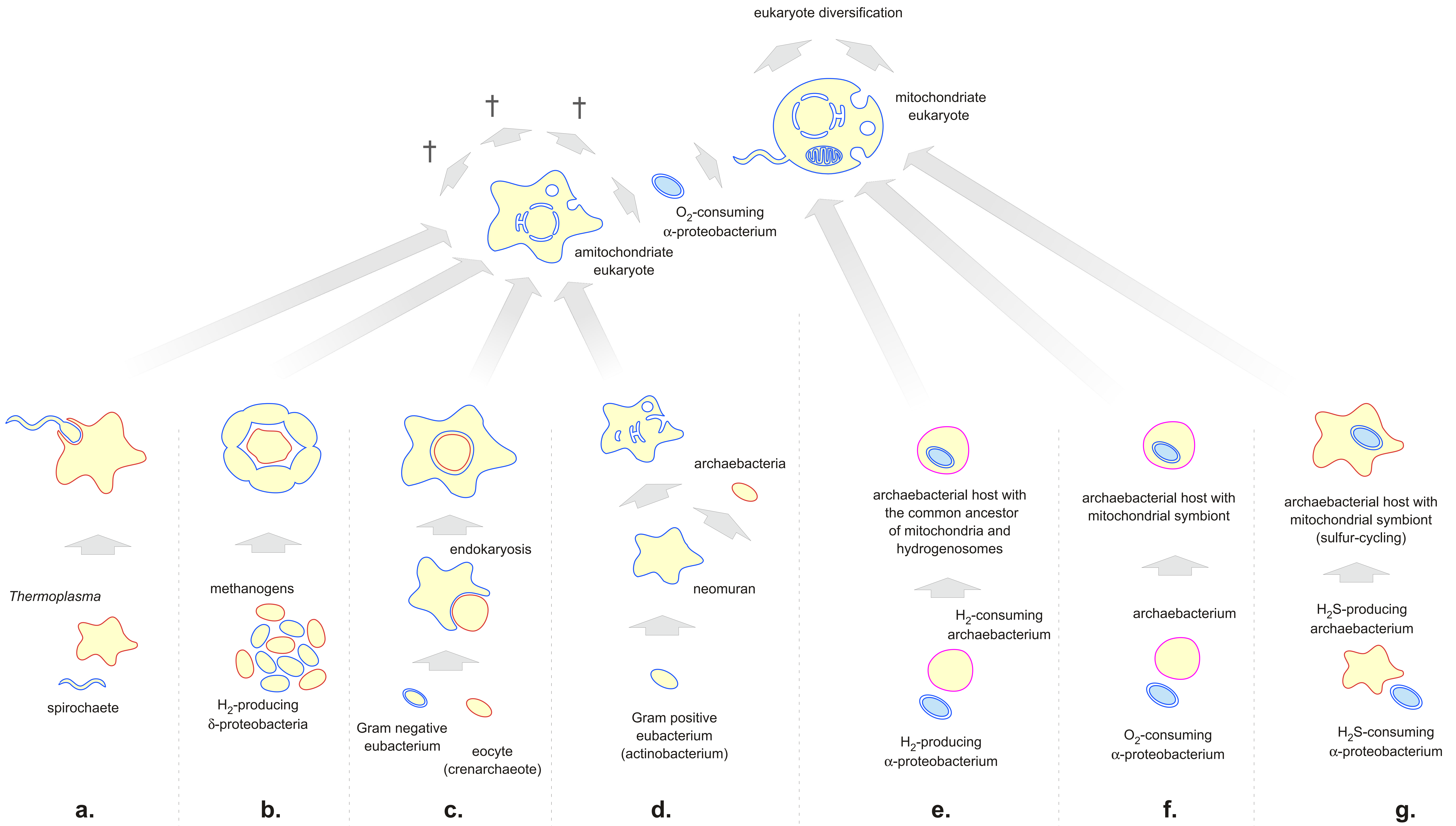

Raff & Mahler 1972
Bogorad 1975
Cavalier Smith 1975
archaebacterium
Van Valen and Maiorana 1980
actinobacterium
archaebacteria
Cavalier-Smith 1987
1998, 2002, 2004
Gram positive
eubacterium
endospore formation
Gould & Dring, 1979



Gram negative
eubacterium
endokaryosis
eocyte (crenarchaeote)
Zillig 1989
Lake & Rivera1994
Gupta & Golding 1996
methanogens
δ-proteobacterial
fusion
H_2-producing
δ-proteobacteria
amitochondriate
eukaryote
Moreira & Lopez-Garcia 1998
methanogens
δ-proteobacterial
fusion
α-proteobacterial
anaerobic
methane
oxidizer
H_2-producing
δ-proteobacteria
mitochondria
mitochondriate
eukaryote
Lopez-Garcia & Moreira 1999, 2006
Thermoplasma
spirochaete
amitochondriate
eukaryote
Margulis 2000

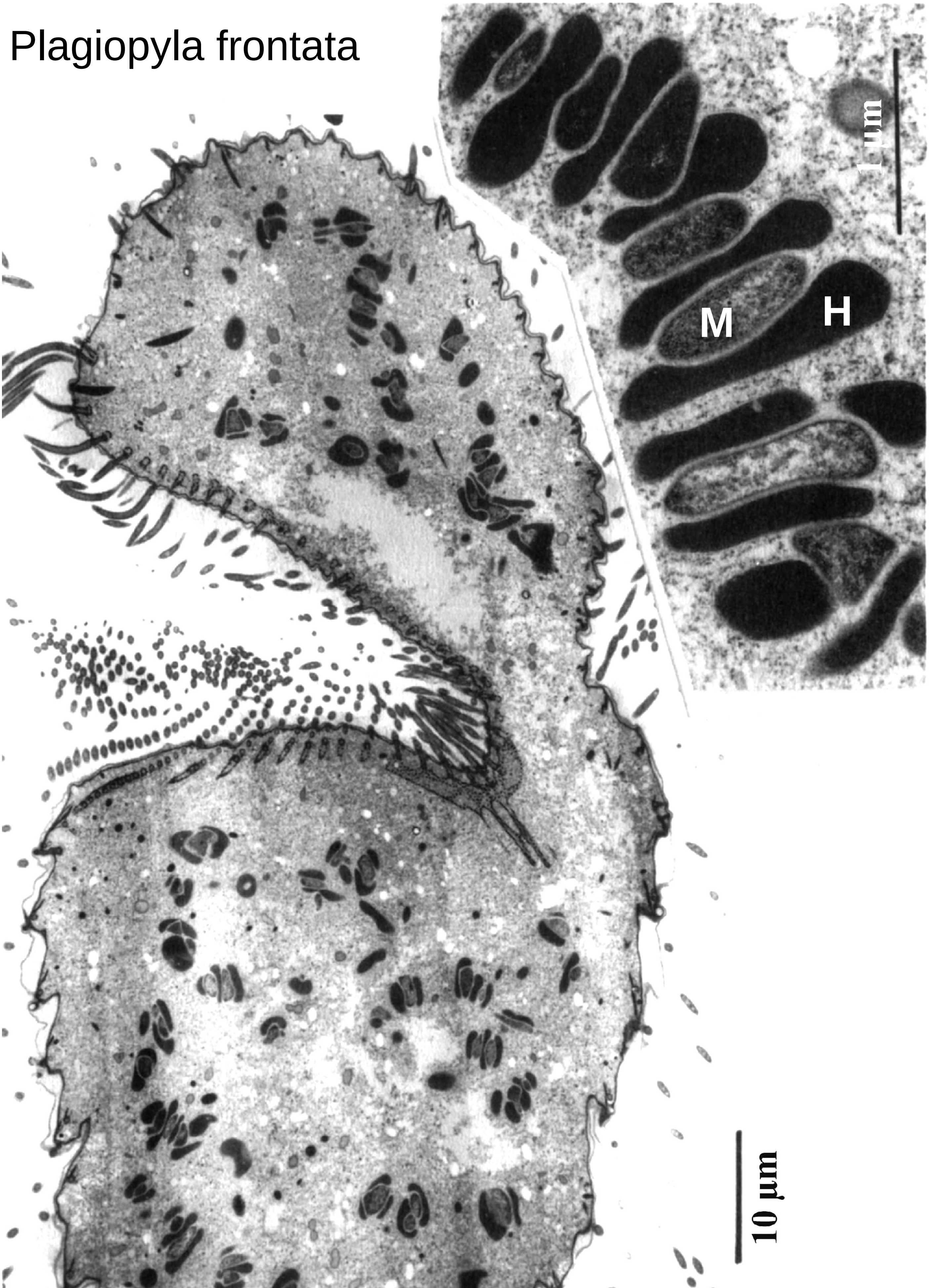


Martin et al. (2001) An overview of endosymbiotic models... Biol. Chem. 382:1521–1539
Martin (2005) Archaebacteria (Archaea) and the origin of the eukaryotic nucleus. Curr Opin Microbiol. 8:630-637.

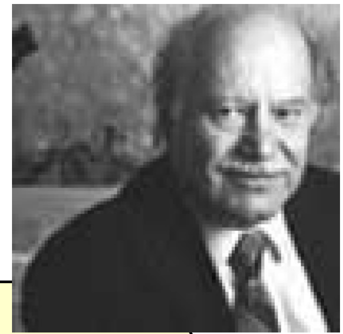


Embley & Martin. Eukaryotic evolution, changes and challenges *Nature* 2006

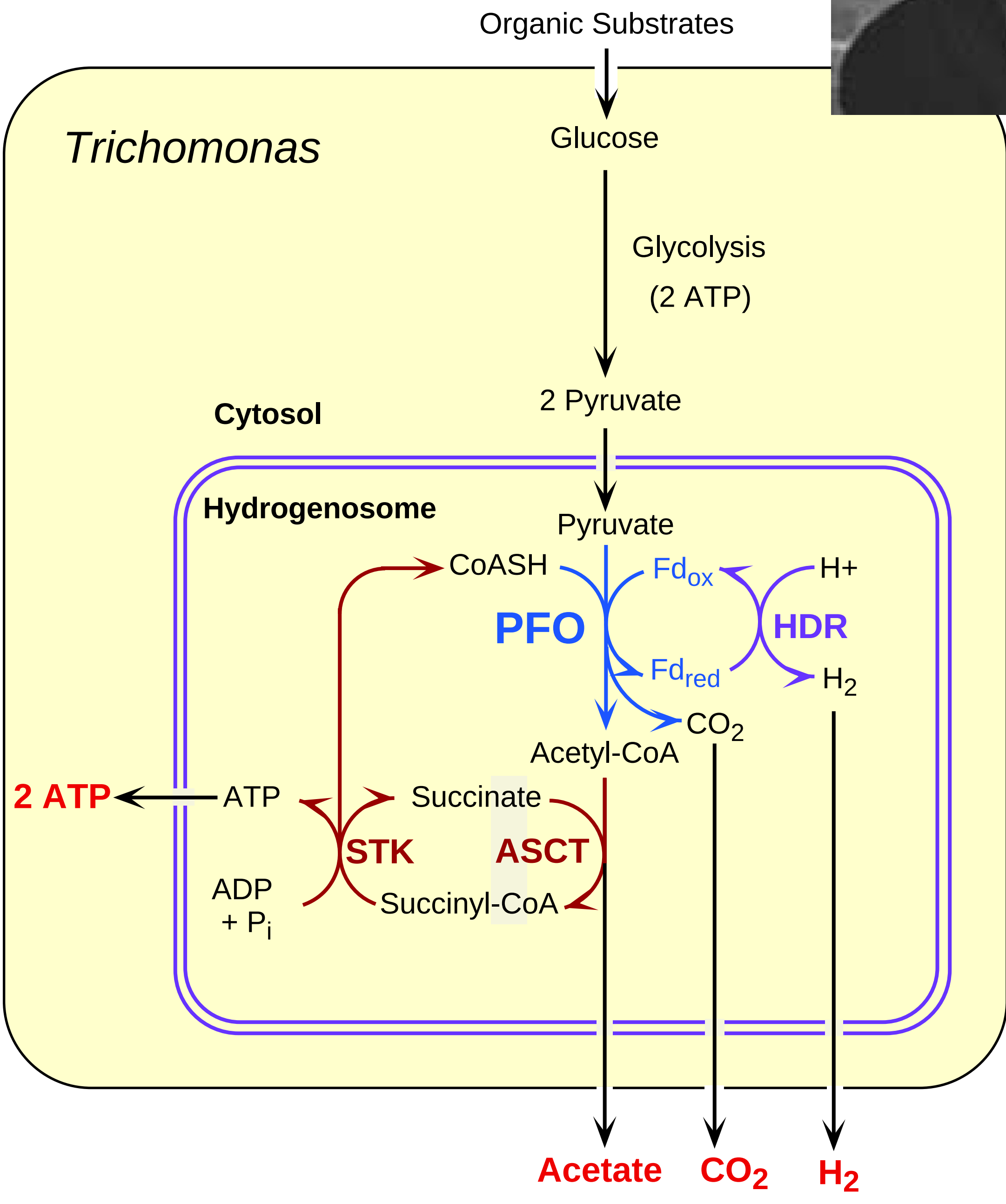
Plagiopyla frontata



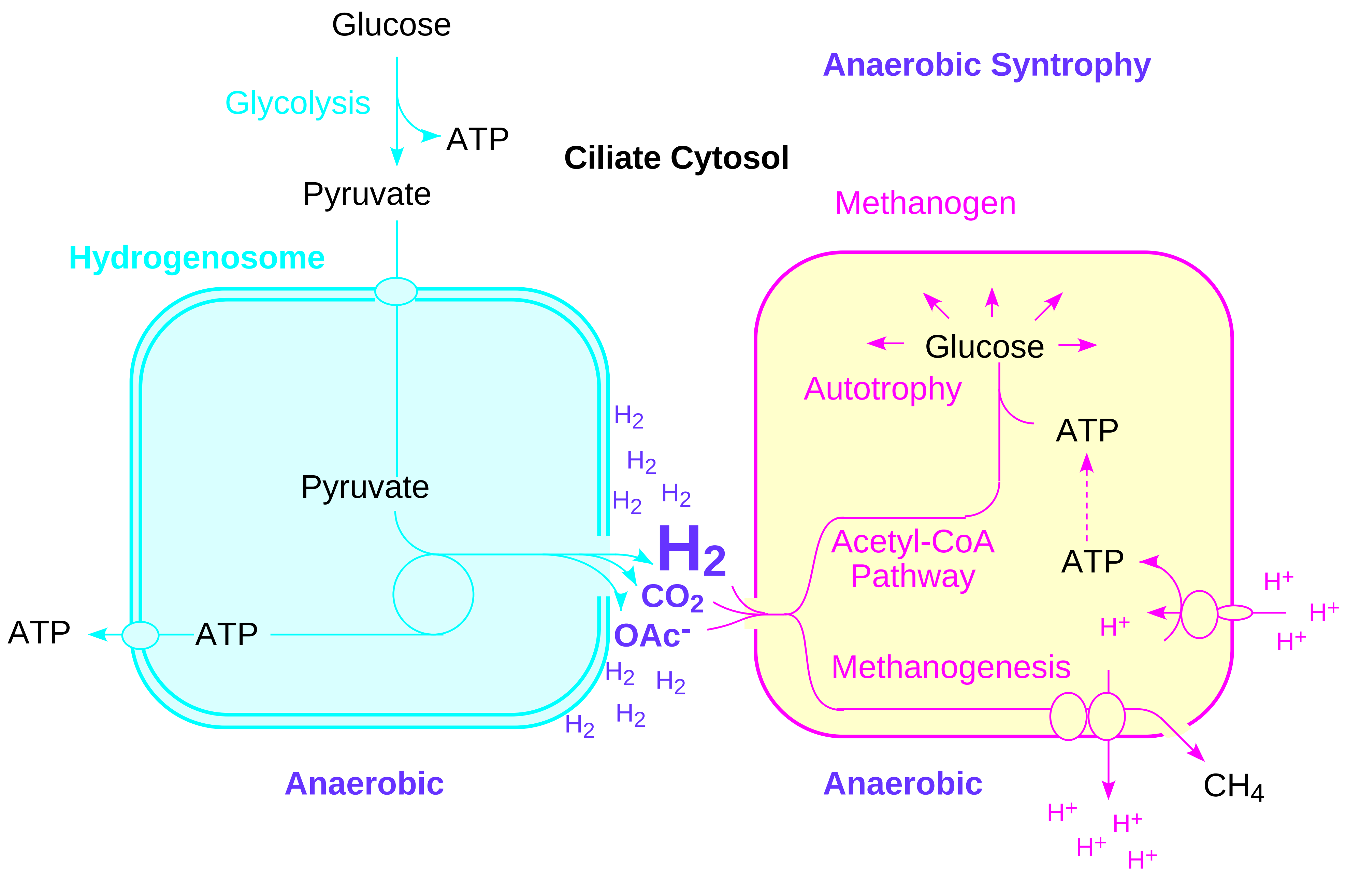
Miklos Müller, The Rockefeller University



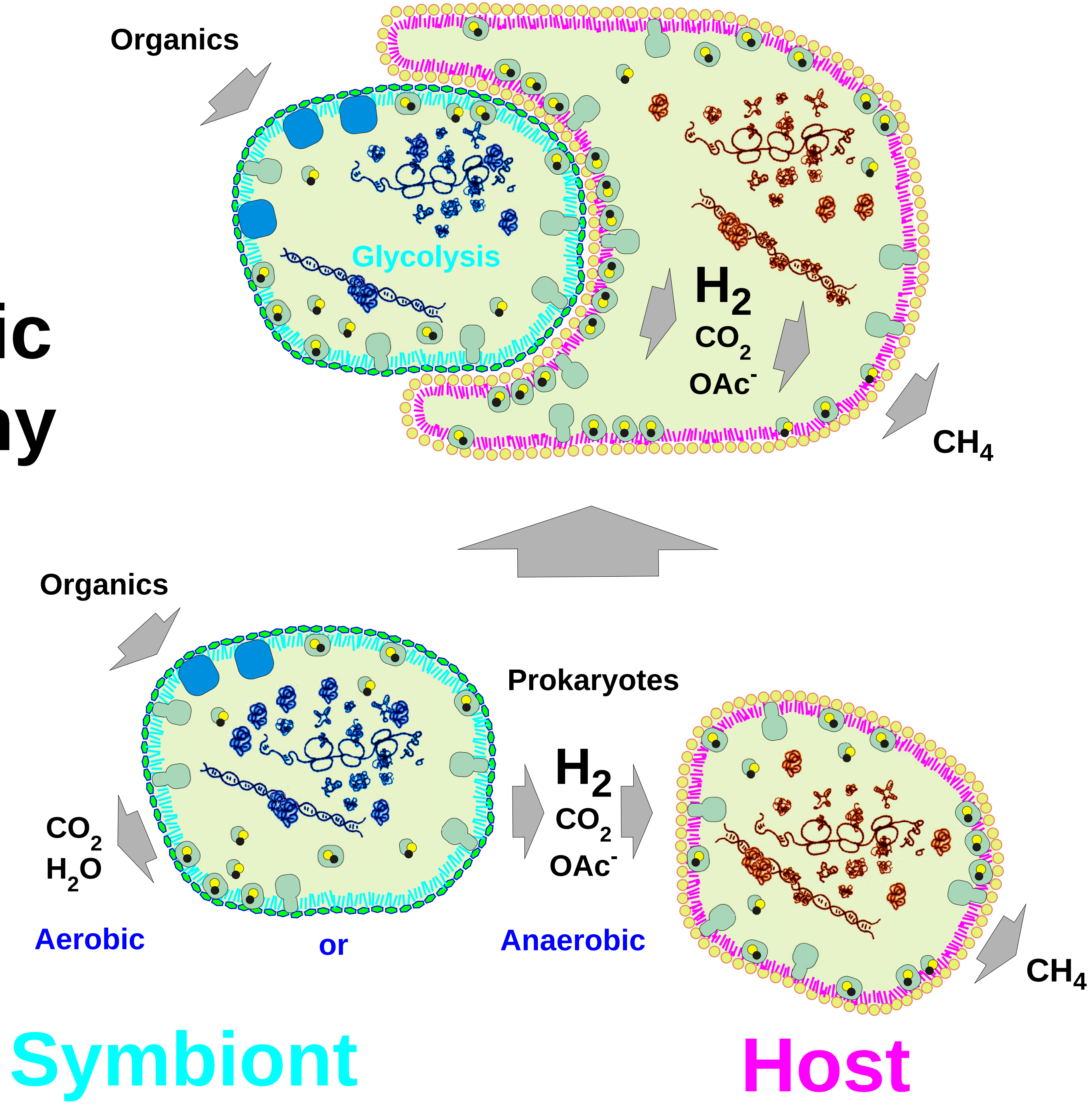
Eukaryotes with Hydrogenosomes



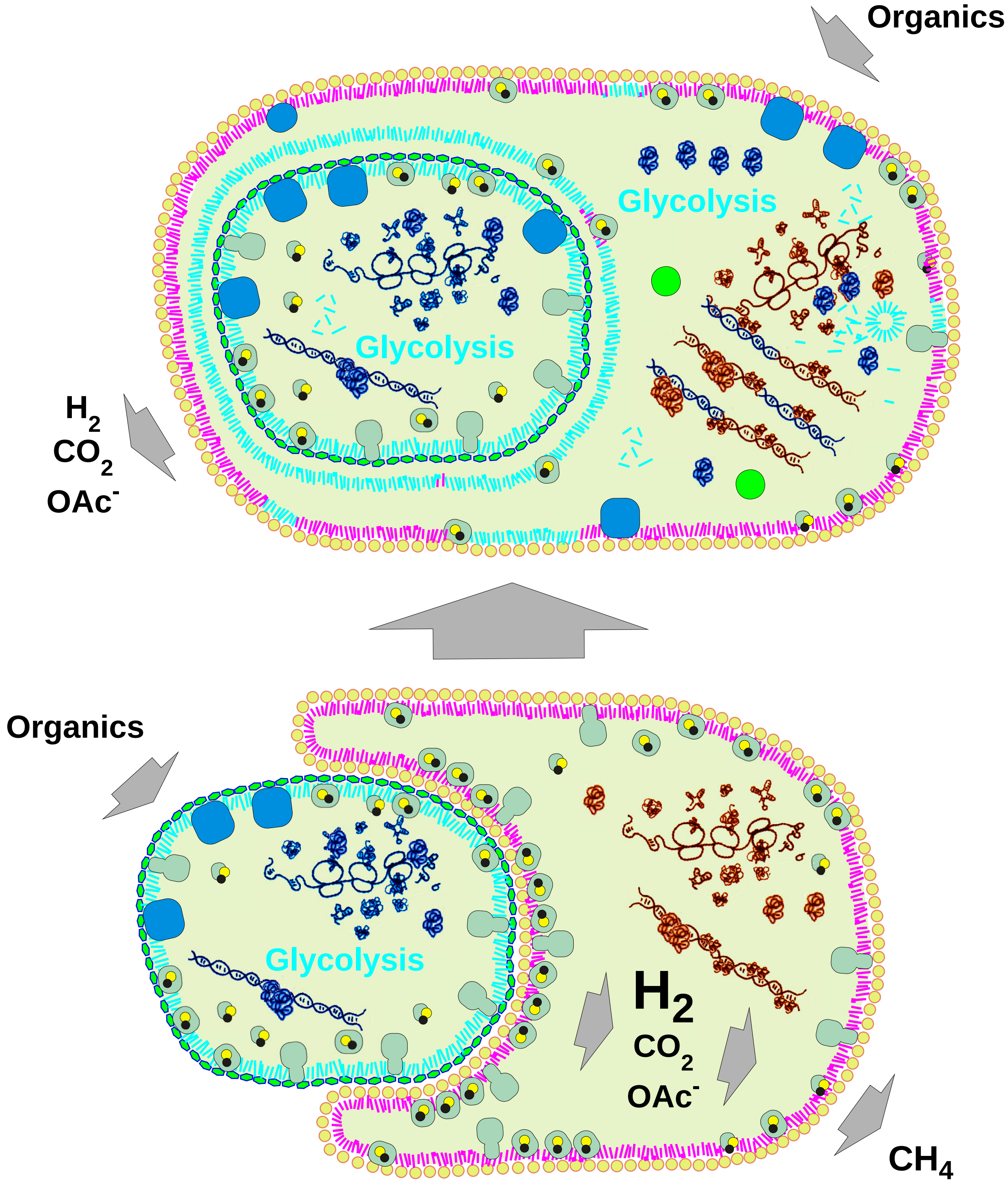
Hydrogenosomal Enzyme		Occurence in Mitochondria of:
HDR	Hydrogenase [Fe]	*Nyctotherus*
ASCT	Acetate:Succinate CoA-Transferase	*Trypanosoma* (many)
STK	Succinate Thiokinase	
PFO	Pyruvate:Ferredoxin Oxidoreductase	*Euglena* (as a Fusion)


Glucose
Glycolysis
ATP
Pyruvate
Ciliate Cytosol
Anaerobic Syntrophy
Methanogen
Hydrogenosome
Pyruvate
ATP
ATP
H2
CO2
OAc-
Glucose
Autotrophy
ATP
Acetyl-CoA Pathway
ATP
H+
Methanogenesis
CH4
Anaerobic
Anaerobic

Anaerobic Syntrophy

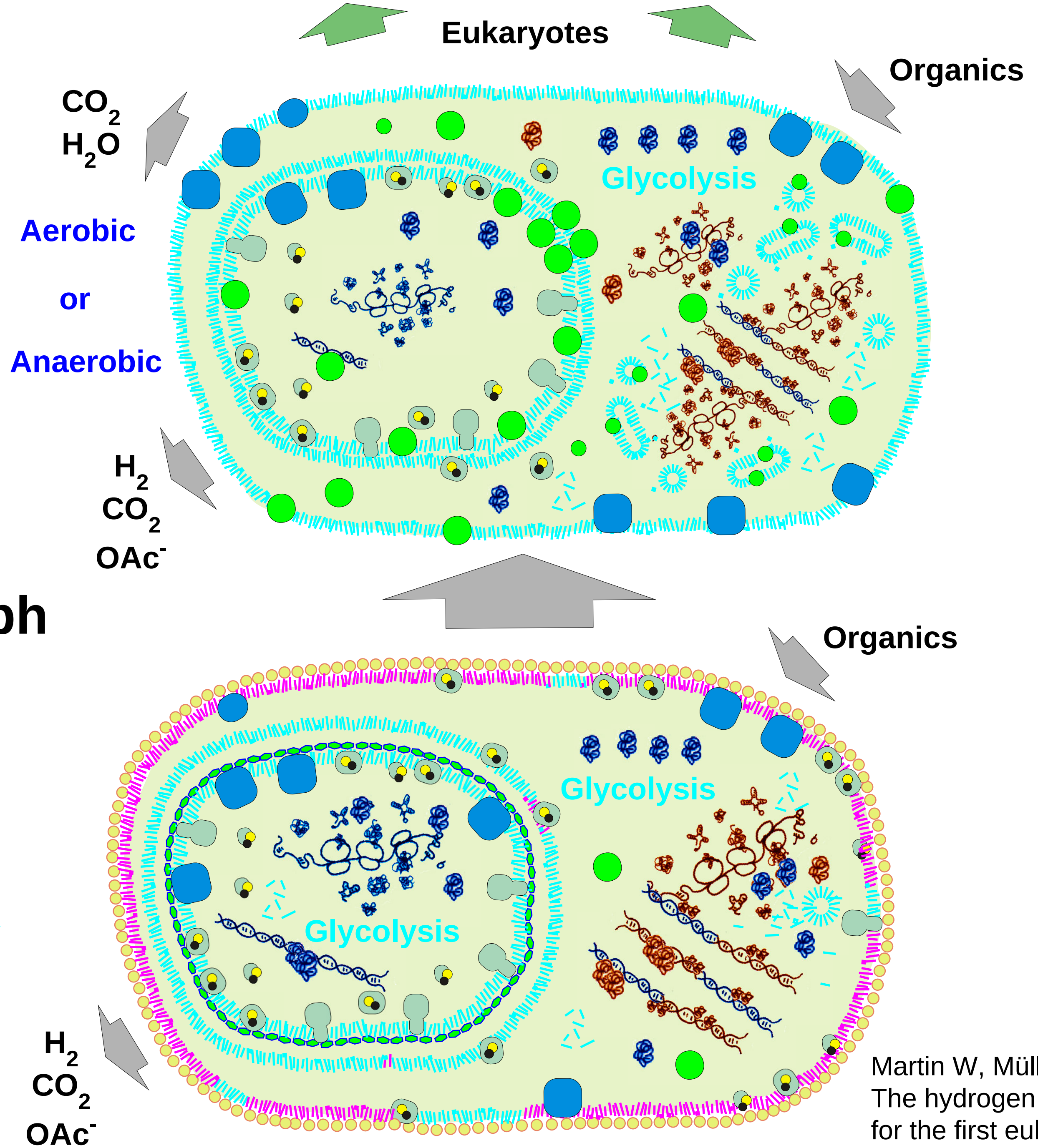


Gene transfer from Symbiont to Host



Invention of eukaryotic novelties

A bipartite, facultatively anaerobic heterotroph with an archaebacterial genetic apparatus and eubacterial energy metabolism



Martin W, Müller M (1998)
The hydrogen hypothesis
for the first eukaryote.
Nature 392:37–41

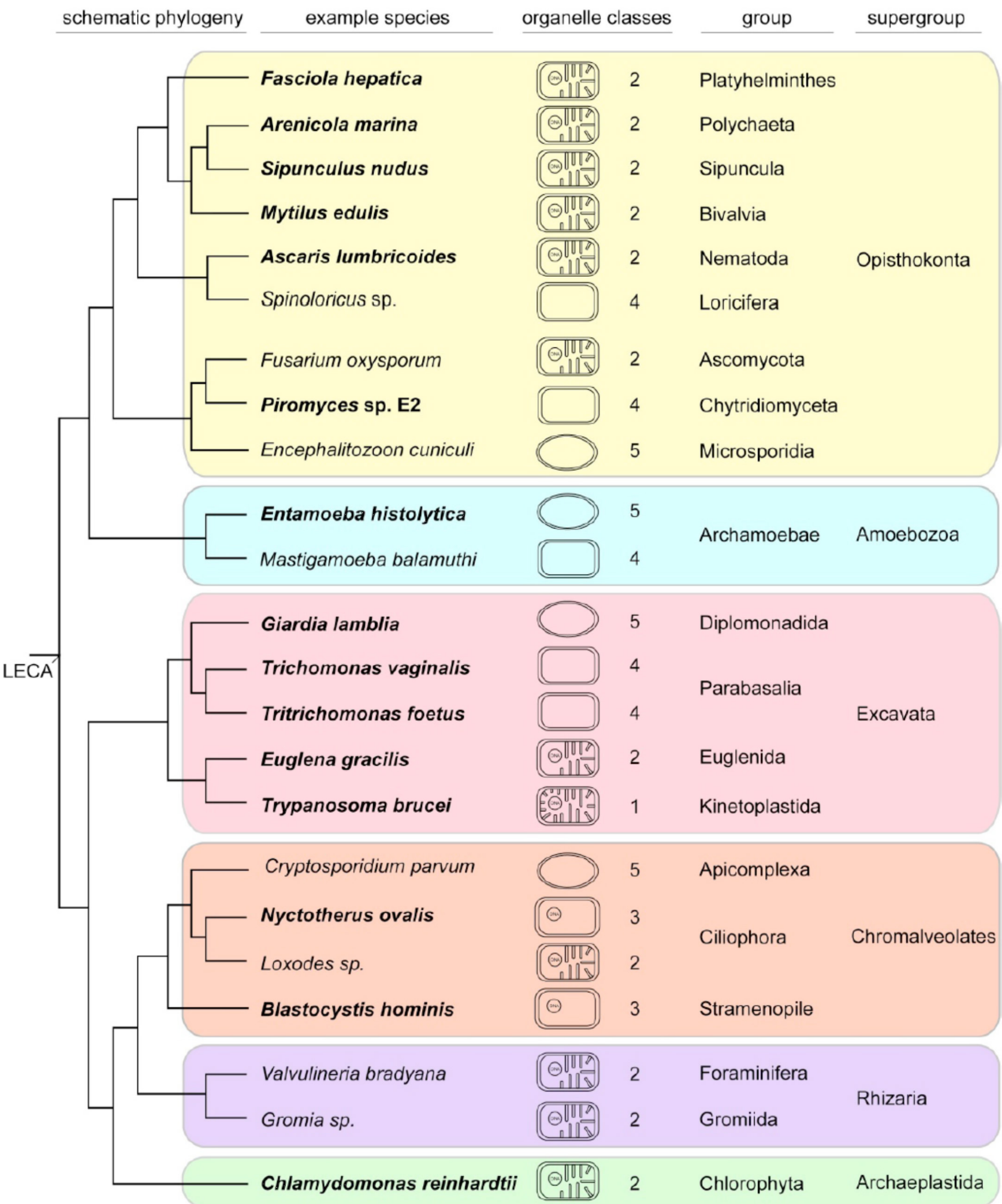
Reality Check (Testable Predictions)

	Hydrogen hypothesis	Neomuran theory et al.
Are hydrogenosomes *really* mitochondria?	yes	no comment
Do primitively amitochondriate eukaryotes exist?	**no**	**yes**
Eukaryotic aerobes and anaerobes in phylogeny	interleave	anaerobes basal
Genomically, eukaryotes should be chimaeras	yes[1]	well, it depends[2]

1. archaebacterial genetic apparatus (euryarchaeotes)
   eubacterial energy metabolism (proteobacteria)
   plus lineage specific inventions (and allowing for LGT)

2. Eukaryotes should be genomically
   Actinobacteria (TCS)
   Planctomycetes...
   Clostridia... etc. one must be explicit here, otherwise the theory is not testable with gene data, hence not science.

Mentel & Martin Energy metabolism in eukaryotic anaerobes Phil Trans 2008



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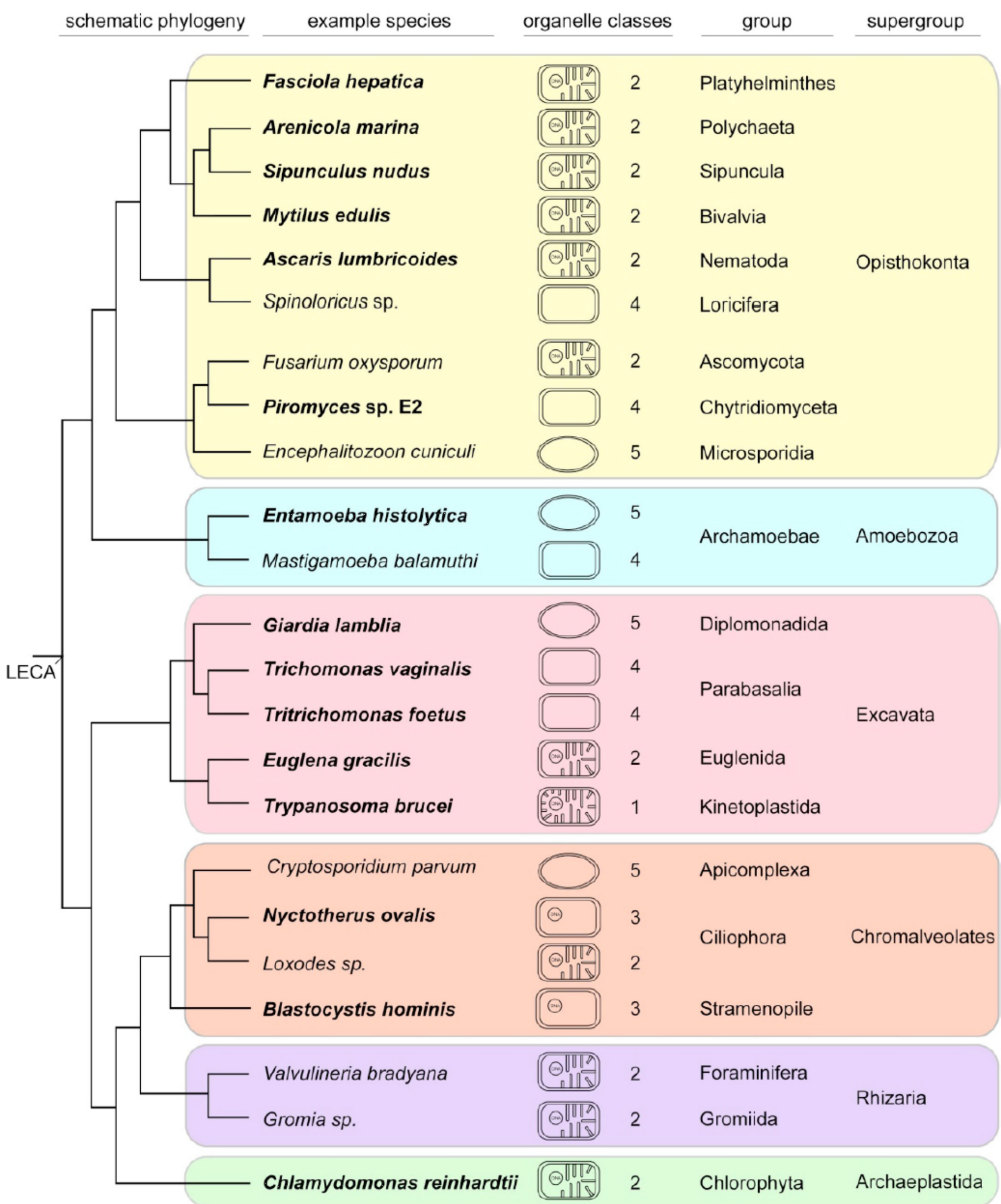
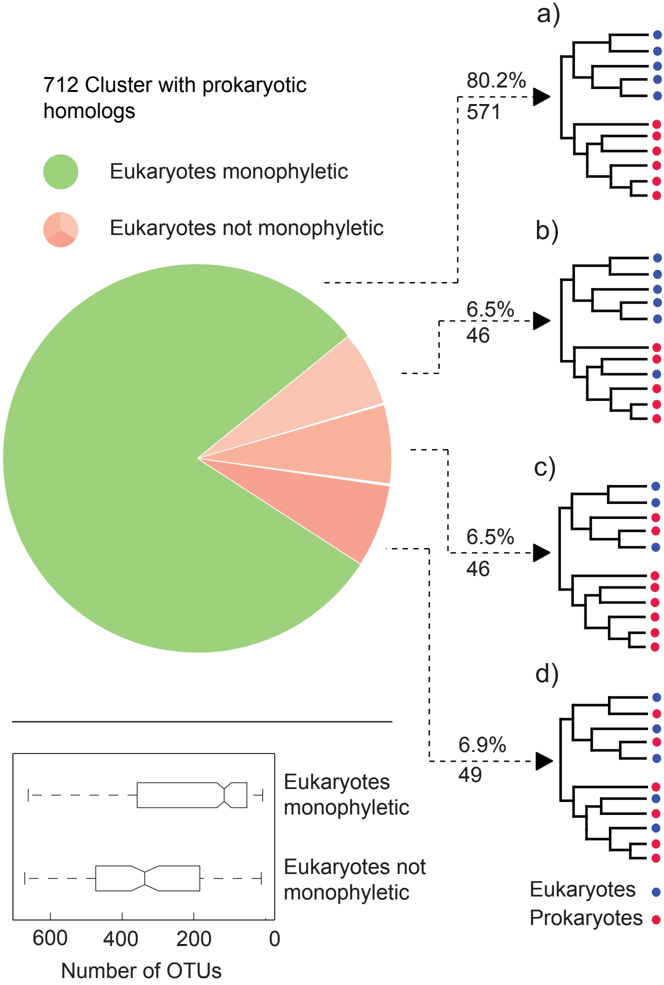
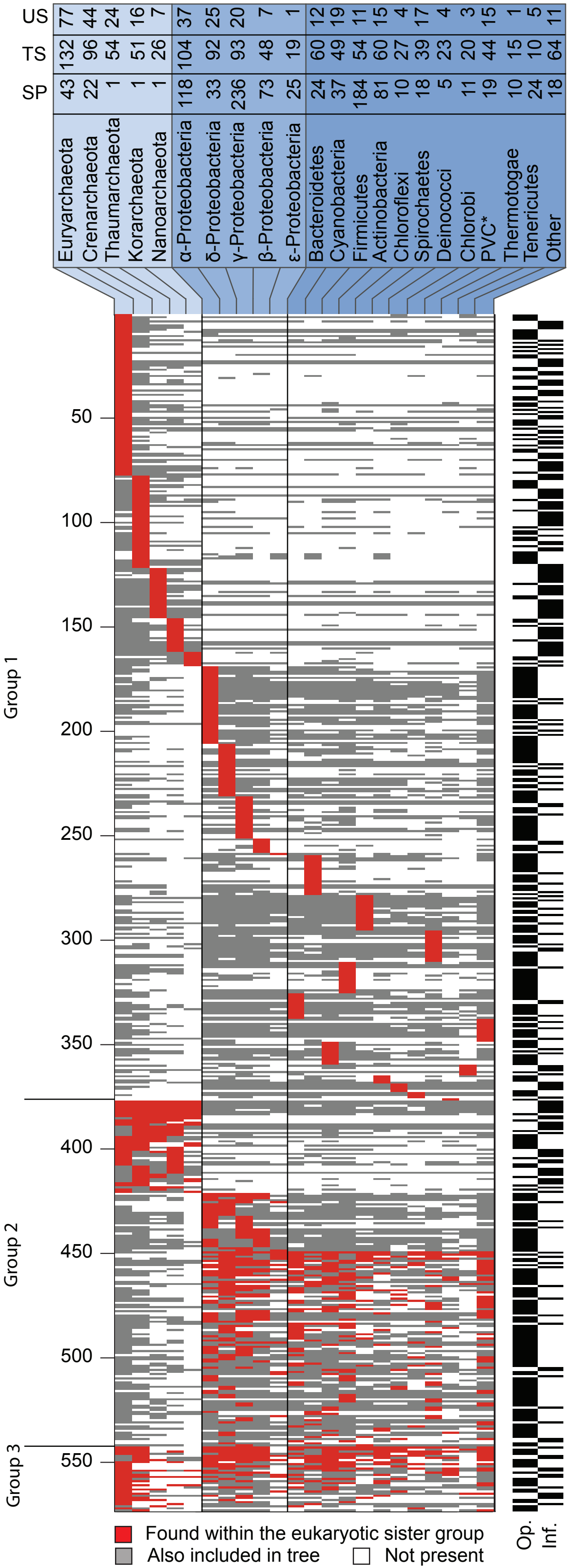
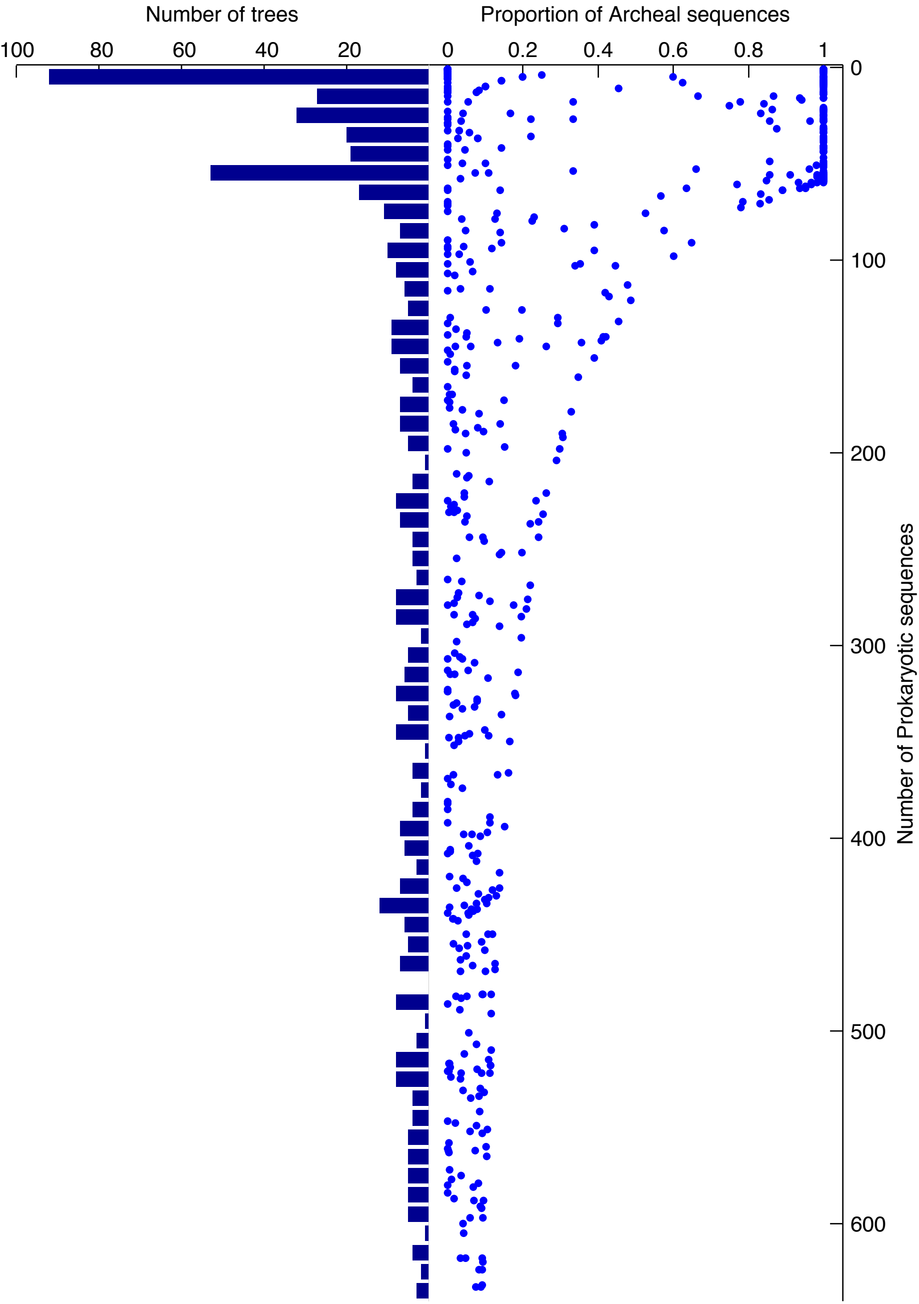


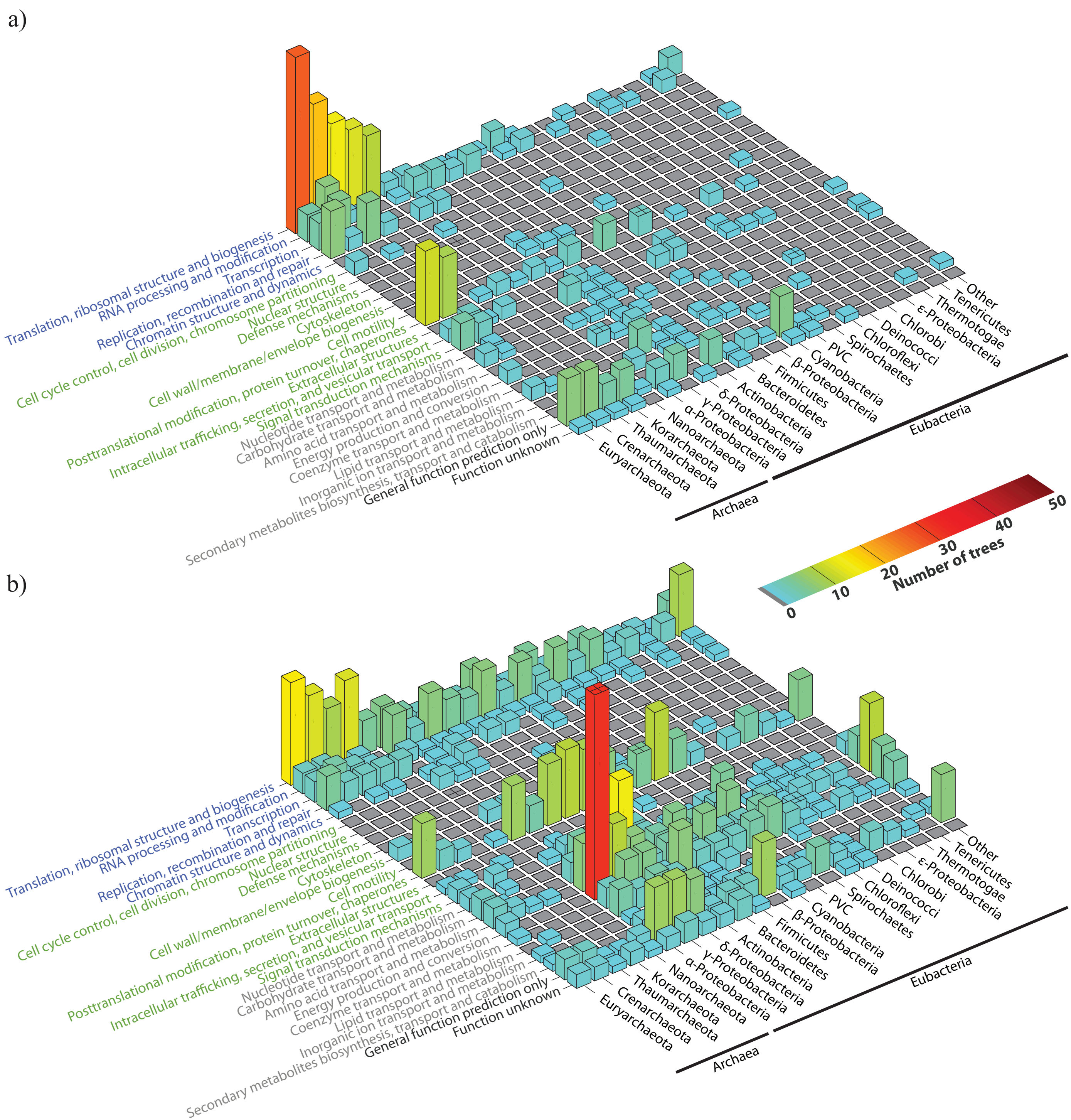
Thiergart et al. (2012) An evolutionary network of genes present in the eukaryote common ancestor... Genome Biol Evol

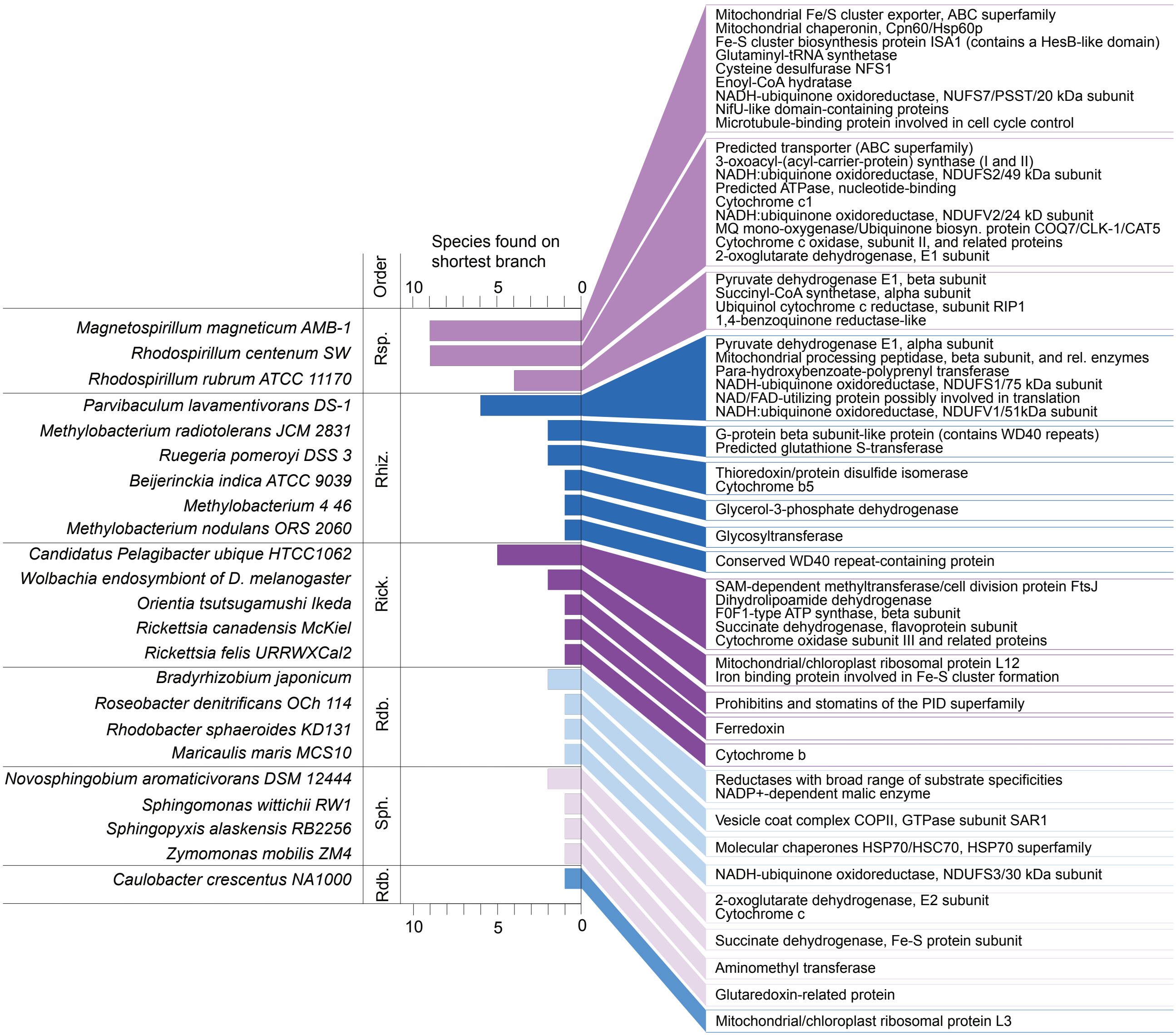

712 Cluster with prokaryotic homologs
Eukaryotes monophyletic
Eukaryotes not monophyletic
a)
80.2%
571
b)
6.5%
46
c)
6.5%
46
d)
6.9%
49
Eukaryotes
Prokaryotes
Eukaryotes monophyletic
Eukaryotes not monophyletic
600
400
200
0
Number of OTUs


US
TS
SP
Euryarchaeota 77 132 43
Crenarchaeota 44 96 22
Thaumarchaeota 24 54 1
Korarchaeota 16 51 1
Nanoarchaeota 7 26 1
α-Proteobacteria 37 104 118
δ-Proteobacteria 25 92 33
γ-Proteobacteria 20 93 236
β-Proteobacteria 7 48 73
ε-Proteobacteria 1 19 25
Bacteroidetes 12 60 24
Cyanobacteria 19 49 37
Firmicutes 11 54 184
Actinobacteria 15 60 81
Chloroflexi 4 27 10
Spirochaetes 17 39 18
Deinococci 4 23 5
Chlorobi 3 20 11
PVC* 15 44 19
Thermotogae 1 15 10
Tenericutes 5 10 24
Other 11 64 18
50
100
150
200
250
300
350
400
450
500
550
Group 1
Group 2
Group 3
Op.
Inf.
Found within the eukaryotic sister group
Also included in tree
Not present

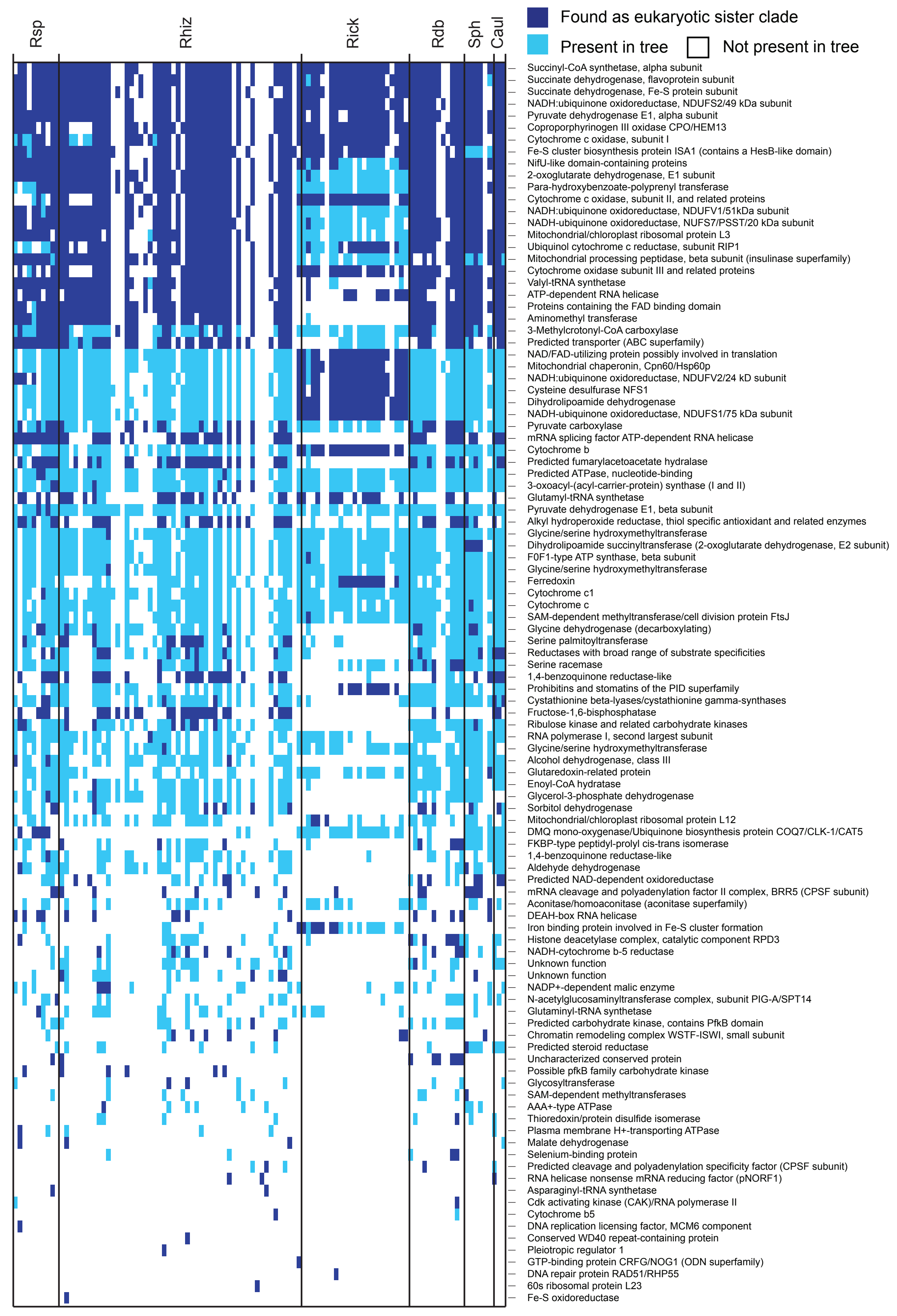


Number of trees
100
80
60
40
20
Proportion of Archeal sequences
0
0.2
0.4
0.6
0.8
1
Number of Prokaryotic sequences
0
100
200
300
400
500
600

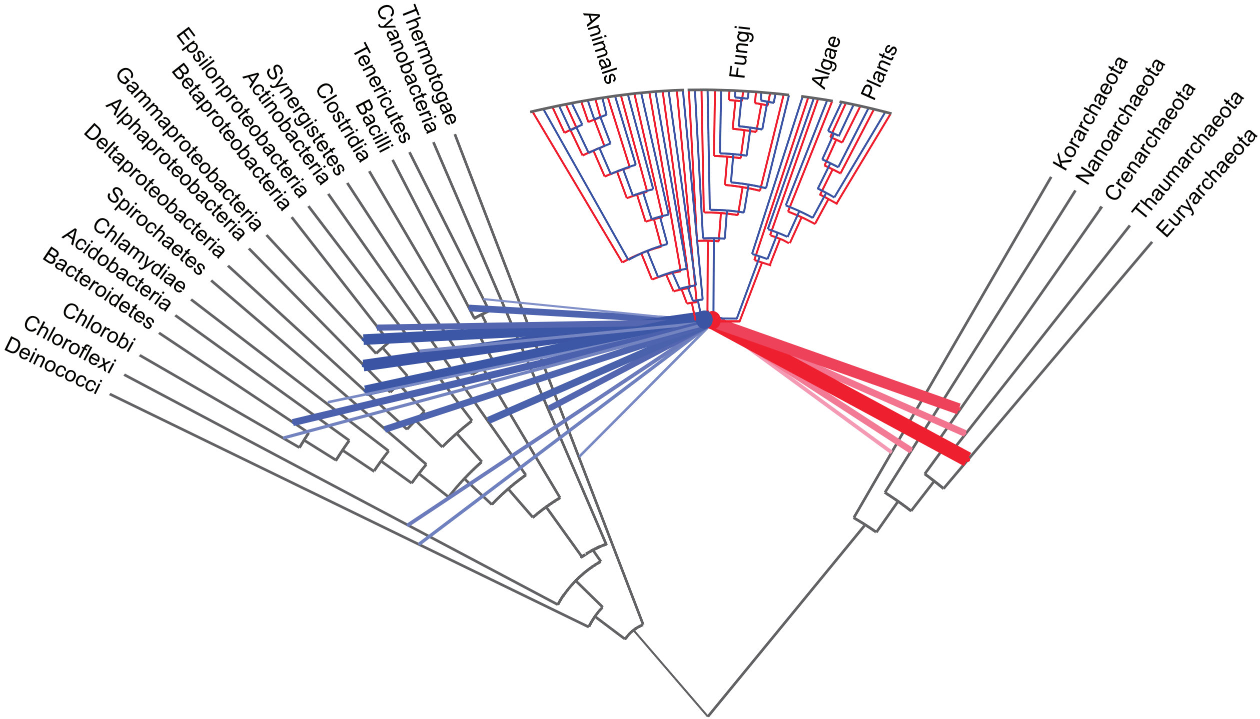

a)
b)
Translation, ribosomal structure and biogenesis
RNA processing and modification
Transcription
Replication, recombination and repair
Chromatin structure and dynamics
Cell cycle control, cell division, chromosome partitioning
Nuclear structure
Defense mechanisms
Cytoskeleton
Cell wall/membrane/envelope biogenesis
Cell motility
Posttranslational modification, protein turnover, chaperones
Extracellular structures
Intracellular trafficking, secretion, and vesicular transport
Signal transduction mechanisms
Nucleotide transport and metabolism
Carbohydrate transport and metabolism
Amino acid transport and metabolism
Energy production and conversion
Coenzyme transport and metabolism
Lipid transport and metabolism
Inorganic ion transport and metabolism
Secondary metabolites biosynthesis, transport and catabolism
General function prediction only
Function unknown
Euryarchaeota
Crenarchaeota
Thaumarchaeota
Korarchaeota
Nanoarchaeota
α-Proteobacteria
γ-Proteobacteria
δ-Proteobacteria
Actinobacteria
Bacteroidetes
Firmicutes
β-Proteobacteria
Cyanobacteria
PVC
Spirochaetes
Chloroflexi
Deinococci
Chlorobi
ε-Proteobacteria
Thermotogae
Tenericutes
Other
Archaea
Eubacteria
Number of trees
0
10
20
30
40
50

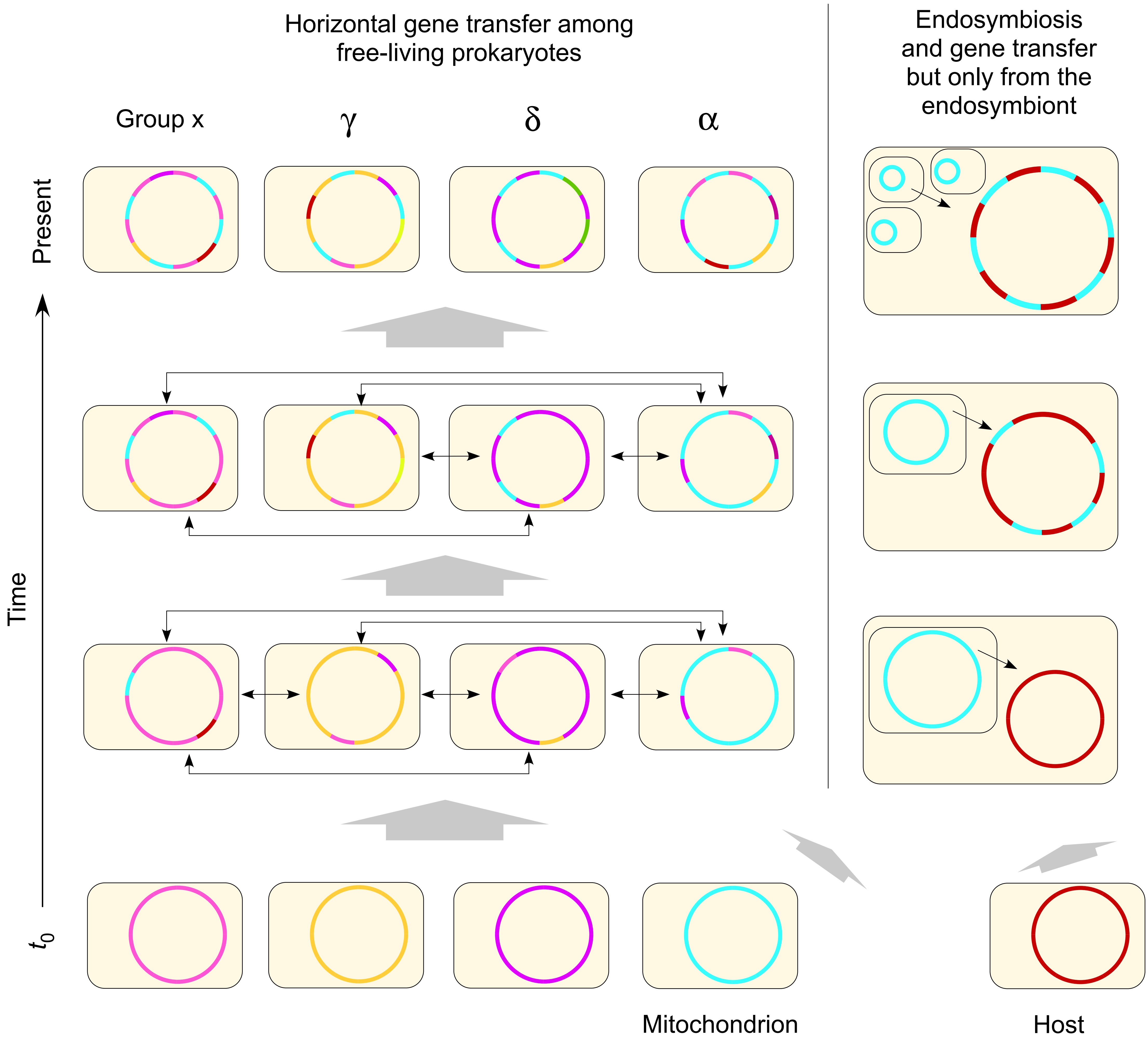


Species found on shortest branch
Order
10
5
0
Magnetospirillum magneticum AMB-1
Rhodospirillum centenum SW
Rhodospirillum rubrum ATCC 11170
Rsp.
Parvibaculum lavamentivorans DS-1
Methylobacterium radiotolerans JCM 2831
Ruegeria pomeroyi DSS 3
Beijerinckia indica ATCC 9039
Methylobacterium 4 46
Methylobacterium nodulans ORS 2060
Rhiz.
Candidatus Pelagibacter ubique HTCC1062
Wolbachia endosymbiont of D. melanogaster
Orientia tsutsugamushi Ikeda
Rickettsia canadensis McKiel
Rickettsia felis URRWXCal2
Rick.
Bradyrhizobium japonicum
Roseobacter denitrificans OCh 114
Rhodobacter sphaeroides KD131
Maricaulis maris MCS10
Rdb.
Novosphingobium aromaticivorans DSM 12444
Sphingomonas wittichii RW1
Sphingopyxis alaskensis RB2256
Zymomonas mobilis ZM4
Sph.
Caulobacter crescentus NA1000
Rdb.
Mitochondrial Fe/S cluster exporter, ABC superfamily
Mitochondrial chaperonin, Cpn60/Hsp60p
Fe-S cluster biosynthesis protein ISA1 (contains a HesB-like domain)
Glutaminyl-tRNA synthetase
Cysteine desulfurase NFS1
Enoyl-CoA hydratase
NADH-ubiquinone oxidoreductase, NUFS7/PSST/20 kDa subunit
NifU-like domain-containing proteins
Microtubule-binding protein involved in cell cycle control
Predicted transporter (ABC superfamily)
3-oxoacyl-(acyl-carrier-protein) synthase (I and II)
NADH:ubiquinone oxidoreductase, NDUFS2/49 kDa subunit
Predicted ATPase, nucleotide-binding
Cytochrome c1
NADH:ubiquinone oxidoreductase, NDUFV2/24 kD subunit
MQ mono-oxygenase/Ubiquinone biosyn. protein COQ7/CLK-1/CAT5
Cytochrome c oxidase, subunit II, and related proteins
2-oxoglutarate dehydrogenase, E1 subunit
Pyruvate dehydrogenase E1, beta subunit
Succinyl-CoA synthetase, alpha subunit
Ubiquinol cytochrome c reductase, subunit RIP1
1,4-benzoquinone reductase-like
Pyruvate dehydrogenase E1, alpha subunit
Mitochondrial processing peptidase, beta subunit, and rel. enzymes
Para-hydroxybenzoate-polyprenyl transferase
NADH-ubiquinone oxidoreductase, NDUFS1/75 kDa subunit
NAD/FAD-utilizing protein possibly involved in translation
NADH:ubiquinone oxidoreductase, NDUFV1/51kDa subunit
G-protein beta subunit-like protein (contains WD40 repeats)
Predicted glutathione S-transferase
Thioredoxin/protein disulfide isomerase
Cytochrome b5
Glycerol-3-phosphate dehydrogenase
Glycosyltransferase
Conserved WD40 repeat-containing protein
SAM-dependent methyltransferase/cell division protein FtsJ
Dihydrolipoamide dehydrogenase
F0F1-type ATP synthase, beta subunit
Succinate dehydrogenase, flavoprotein subunit
Cytochrome oxidase subunit III and related proteins
Mitochondrial/chloroplast ribosomal protein L12
Iron binding protein involved in Fe-S cluster formation
Prohibitins and stomatins of the PID superfamily
Ferredoxin
Cytochrome b
Reductases with broad range of substrate specificities
NADP+-dependent malic enzyme
Vesicle coat complex COPII, GTPase subunit SAR1
Molecular chaperones HSP70/HSC70, HSP70 superfamily
NADH-ubiquinone oxidoreductase, NDUFS3/30 kDa subunit
2-oxoglutarate dehydrogenase, E2 subunit
Cytochrome c
Succinate dehydrogenase, Fe-S protein subunit
Aminomethyl transferase
Glutaredoxin-related protein
Mitochondrial/chloroplast ribosomal protein L3



Found as eukaryotic sister clade
Present in tree
Not present in tree
Rsp
Rhiz
Rick
Rdb
Sph
Caul
Succinyl-CoA synthetase, alpha subunit
Succinate dehydrogenase, flavoprotein subunit
Succinate dehydrogenase, Fe-S protein subunit
NADH:ubiquinone oxidoreductase, NDUFS2/49 kDa subunit
Pyruvate dehydrogenase E1, alpha subunit
Coproporphyrinogen III oxidase CPO/HEM13
Cytochrome c oxidase, subunit I
Fe-S cluster biosynthesis protein ISA1 (contains a HesB-like domain)
NifU-like domain-containing proteins
2-oxoglutarate dehydrogenase, E1 subunit
Para-hydroxybenzoate-polyprenyl transferase
Cytochrome c oxidase, subunit II, and related proteins
NADH:ubiquinone oxidoreductase, NDUFV1/51kDa subunit
NADH-ubiquinone oxidoreductase, NUFS7/PSST/20 kDa subunit
Mitochondrial/chloroplast ribosomal protein L3
Ubiquinol cytochrome c reductase, subunit RIP1
Mitochondrial processing peptidase, beta subunit (insulinase superfamily)
Cytochrome oxidase subunit III and related proteins
Valyl-tRNA synthetase
ATP-dependent RNA helicase
Proteins containing the FAD binding domain
Aminomethyl transferase
3-Methylcrotonyl-CoA carboxylase
Predicted transporter (ABC superfamily)
NAD/FAD-utilizing protein possibly involved in translation
Mitochondrial chaperonin, Cpn60/Hsp60p
NADH:ubiquinone oxidoreductase, NDUFV2/24 kD subunit
Cysteine desulfurase NFS1
Dihydrolipoamide dehydrogenase
NADH-ubiquinone oxidoreductase, NDUFS1/75 kDa subunit
Pyruvate carboxylase
mRNA splicing factor ATP-dependent RNA helicase
Cytochrome b
Predicted fumarylacetoacetate hydralase
Predicted ATPase, nucleotide-binding
3-oxoacyl-(acyl-carrier-protein) synthase (I and II)
Glutamyl-tRNA synthetase
Pyruvate dehydrogenase E1, beta subunit
Alkyl hydroperoxide reductase, thiol specific antioxidant and related enzymes
Glycine/serine hydroxymethyltransferase
Dihydrolipoamide succinyltransferase (2-oxoglutarate dehydrogenase, E2 subunit)
F0F1-type ATP synthase, beta subunit
Glycine/serine hydroxymethyltransferase
Ferredoxin
Cytochrome c1
Cytochrome c
SAM-dependent methyltransferase/cell division protein FtsJ
Glycine dehydrogenase (decarboxylating)
Serine palmitoyltransferase
Reductases with broad range of substrate specificities
Serine racemase
1,4-benzoquinone reductase-like
Prohibitins and stomatins of the PID superfamily
Cystathionine beta-lyases/cystathionine gamma-synthases
Fructose-1,6-bisphosphatase
Ribulose kinase and related carbohydrate kinases
RNA polymerase I, second largest subunit
Glycine/serine hydroxymethyltransferase
Alcohol dehydrogenase, class III
Glutaredoxin-related protein
Enoyl-CoA hydratase
Glycerol-3-phosphate dehydrogenase
Sorbitol dehydrogenase
Mitochondrial/chloroplast ribosomal protein L12
DMQ mono-oxygenase/Ubiquinone biosynthesis protein COQ7/CLK-1/CAT5
FKBP-type peptidyl-prolyl cis-trans isomerase
1,4-benzoquinone reductase-like
Aldehyde dehydrogenase
Predicted NAD-dependent oxidoreductase
mRNA cleavage and polyadenylation factor II complex, BRR5 (CPSF subunit)
Aconitase/homoaconitase (aconitase superfamily)
DEAH-box RNA helicase
Iron binding protein involved in Fe-S cluster formation
Histone deacetylase complex, catalytic component RPD3
NADH-cytochrome b-5 reductase
Unknown function
Unknown function
NADP+-dependent malic enzyme
N-acetylglucosaminyltransferase complex, subunit PIG-A/SPT14
Glutaminyl-tRNA synthetase
Predicted carbohydrate kinase, contains PfkB domain
Chromatin remodeling complex WSTF-ISWI, small subunit
Predicted steroid reductase
Uncharacterized conserved protein
Possible pfkB family carbohydrate kinase
Glycosyltransferase
SAM-dependent methyltransferases
AAA+-type ATPase
Thioredoxin/protein disulfide isomerase
Plasma membrane H+-transporting ATPase
Malate dehydrogenase
Selenium-binding protein
Predicted cleavage and polyadenylation specificity factor (CPSF subunit)
RNA helicase nonsense mRNA reducing factor (pNORF1)
Asparaginyl-tRNA synthetase
Cdk activating kinase (CAK)/RNA polymerase II
Cytochrome b5
DNA replication licensing factor, MCM6 component
Conserved WD40 repeat-containing protein
Pleiotropic regulator 1
GTP-binding protein CRFG/NOG1 (ODN superfamily)
DNA repair protein RAD51/RHP55
60s ribosomal protein L23
Fe-S oxidoreductase


Deinococci
Chloroflexi
Chlorobi
Bacteroidetes
Acidobacteria
Chlamydiae
Spirochaetes
Deltaproteobacteria
Alphaproteobacteria
Gammaproteobacteria
Betaproteobacteria
Epsilonproteobacteria
Actinobacteria
Synergistetes
Clostridia
Bacilli
Tenericutes
Cyanobacteria
Thermotogae
Animals
Fungi
Algae
Plants
Korarchaeota
Nanoarchaeota
Crenarchaeota
Thaumarchaeota
Euryarchaeota



Horizontal gene transfer among free-living prokaryotes
Endosymbiosis and gene transfer but only from the endosymbiont
Group x
γ
δ
α
Present
Time
t_0
Mitochondrion
Host

So, along with

- a cell cycle,
- meiosis,
- mitosis,
- introns,
- spliceosomes,
- centrioles (including their fuzz),
- nucleus,
- ER,
- Golgi,
- full blown membrane traffic,
- flagellae,
- a eukaryotic cytoskeleton,
- ca. 2000 novel gene families underpinning those massive evolutionary innovations,
- and >500 gene families with clear prokaryotic homologues (maybe “yawn” for cell biologists but crucial for evolutionary biologists probing this major evolutionary transition because they track our provenance)

mitochondria were present in the eukaryote common ancestor.

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mitochondria were present in the eukaryote common ancestor.

Why?

The energetics of genome complexity

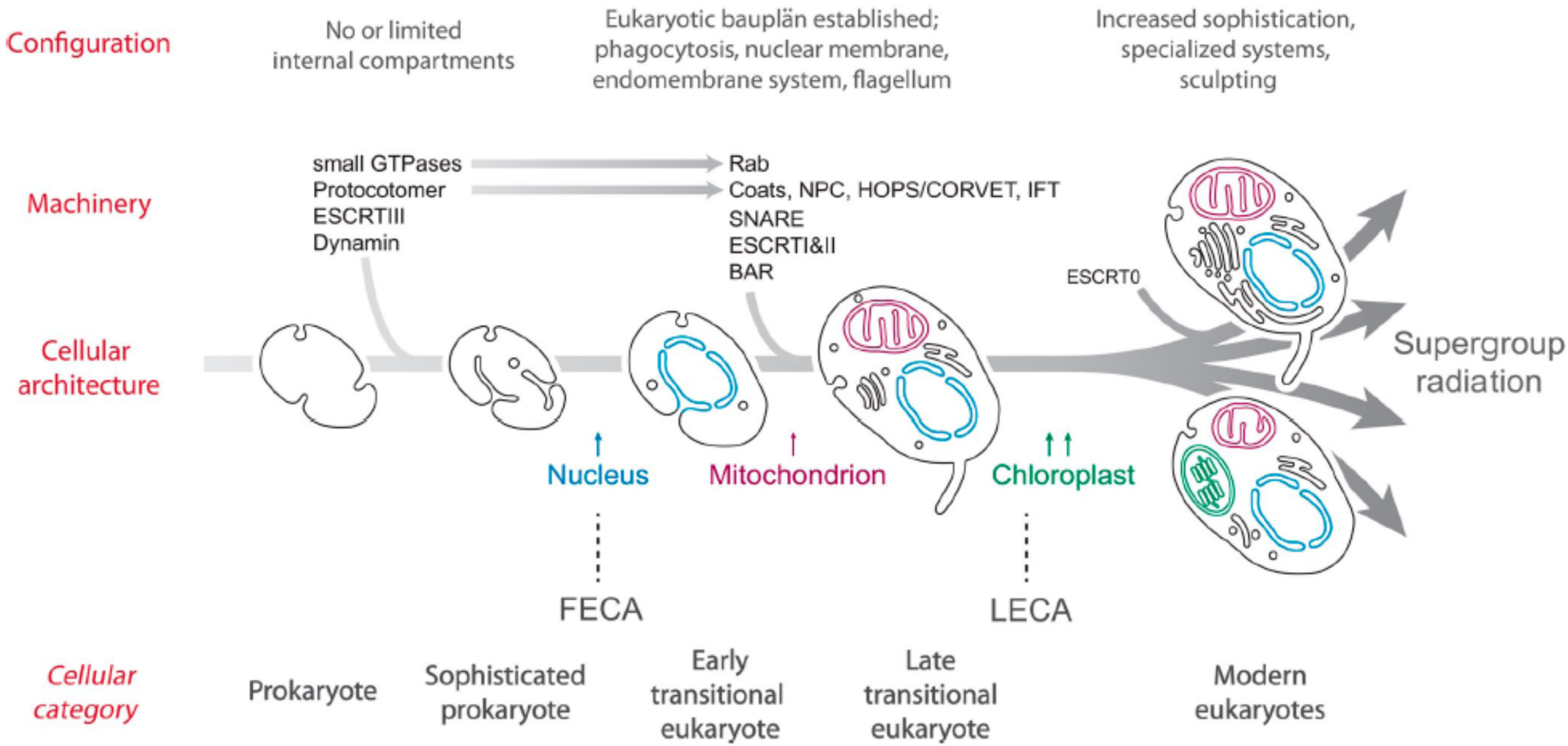
Nick Lane[1] & William Martin[2]

All complex life is composed of eukaryotic (nucleated) cells. The eukaryotic cell arose from prokaryotes just once in four billion years, and otherwise prokaryotes show no tendency to evolve greater complexity. Why not? Prokaryotic genome size is constrained by bioenergetics. The endosymbiosis that gave rise to mitochondria restructured the distribution of DNA in relation to bioenergetic membranes, permitting a remarkable 200,000-fold expansion in the number of genes expressed. This vast leap in genomic capacity was strictly dependent on mitochondrial power, and prerequisite to eukaryote complexity: the key innovation en route to multicellular life.

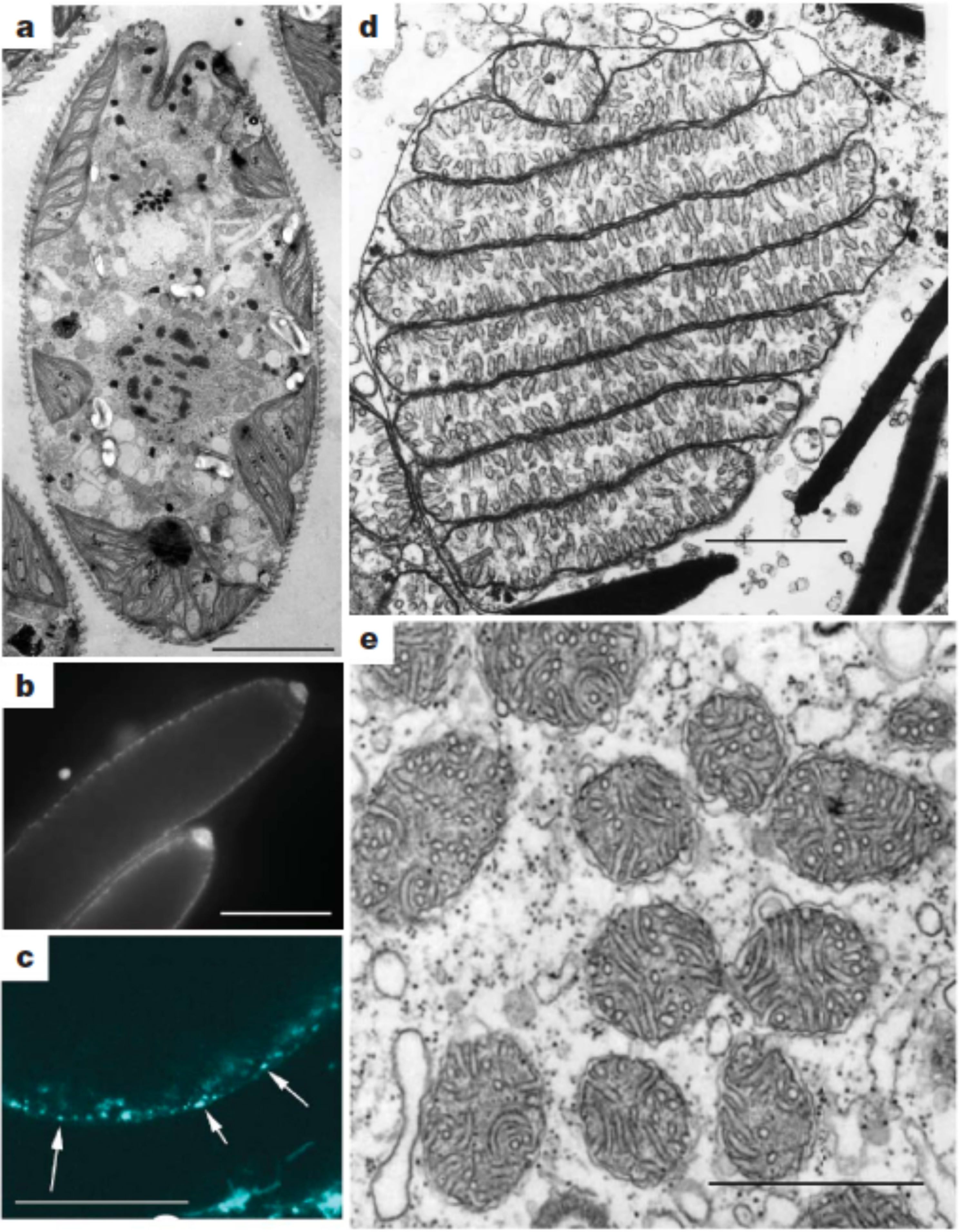
Table 1 | Energetics of bacteria and eukaryotes by cell and genome size

	Prokaryotes					Eukaryotes				
Parameter	Mean	S	M	L	XL	Mean	S	M	L	XL
Weight of cell ($\times 10^{-12}$ g)	2.6	0.2	1.2	4	1×10^6	40,100	250	7,000	33,000	1×10^6
Power ($W g^{-1}$)	0.19	0.07	0.3	0.11	0.0005	0.06	0.09	0.03	0.05	0.01
Power per cell (pW)	0.49	0.014	0.36	0.44	500	2,286	21.5	224	1,782	10,000
Ploidy level	4	1	6	4	10,000	2	2	2	100	3
Haploid genome size (Mb)	6	1.9	4.6	9	7.5	3,000	300	3,000	100	11,000
Power per haploid Mb (pW)	0.02	0.01	0.01	0.01	0.01	0.38	0.04	0.04	0.18	0.3
No. of haploid genes $\times 10^3$	5	2	4.4	6	6	20	12	20	25	15
Power per gene (fW)	0.03	0.01	0.01	0.02	0.01	57.15	0.90	5.6	0.71	222.2
Power per genome (fW)	0.12	0.01	0.06	0.11	0.05	1,143	10.75	112	17.8	3,333

rokaryotes, the mean is from 55 values given in ref. 32; specific examples are derived from ref. 32, Supplementary data. For eukaryotes, the mean is from 12 values re-calculated independently from ref. 3 fic examples from data given in Table 1, ref. 33. We have converted from nl O_2 per cell per hour to watts using the same conversion factor as Makarieva *et al.*[31] (complete aerobic oxidation of endogenou trates yields 20 J per ml O_2). Metabolic rate for *Thiomargarita namibiensis* is from ref. 73. The standard deviations in metabolic rate per gram (given in main text) are not transformed further here, but th nce of around twice the mean falls significantly short of the differences calculated. There is an appreciable range of uncertainty in measurement for both cell mass and metabolic rates for microbes: valu ing by one or two orders of magnitude might not be meaningfully different. Nonetheless, differences of four to six orders of magnitude, as calculated, certainly are. Power per gene depends partly on ploid high ploidy, as in *Thiomargarita* (Schulz-Vogt, personal communication) and to a lesser extent *Bresslaua insidiatrix*[74], lowers energy per gene. Genome sizes are from the Joint Genome Institute (http:// gi.doe.gov/cgi-bin/pub/main.cgi). For prokaryotes: S, small (*Streptococcus pyogenes*); M, medium-sized (*Escherichia coli*); L, large (*Azospirillum lipoferum*); XL, very large (*Thiomargarita namibiensis*). For ryotes: S, small (*Ochromonas sp.*); M, medium-sized (*Euglena gracilis*); L, large (*B. insidiatrix*); XL, very large (*Amoeba proteus*). Power per genome is power per haploid gene times haploid gene number.



Field et al. 2011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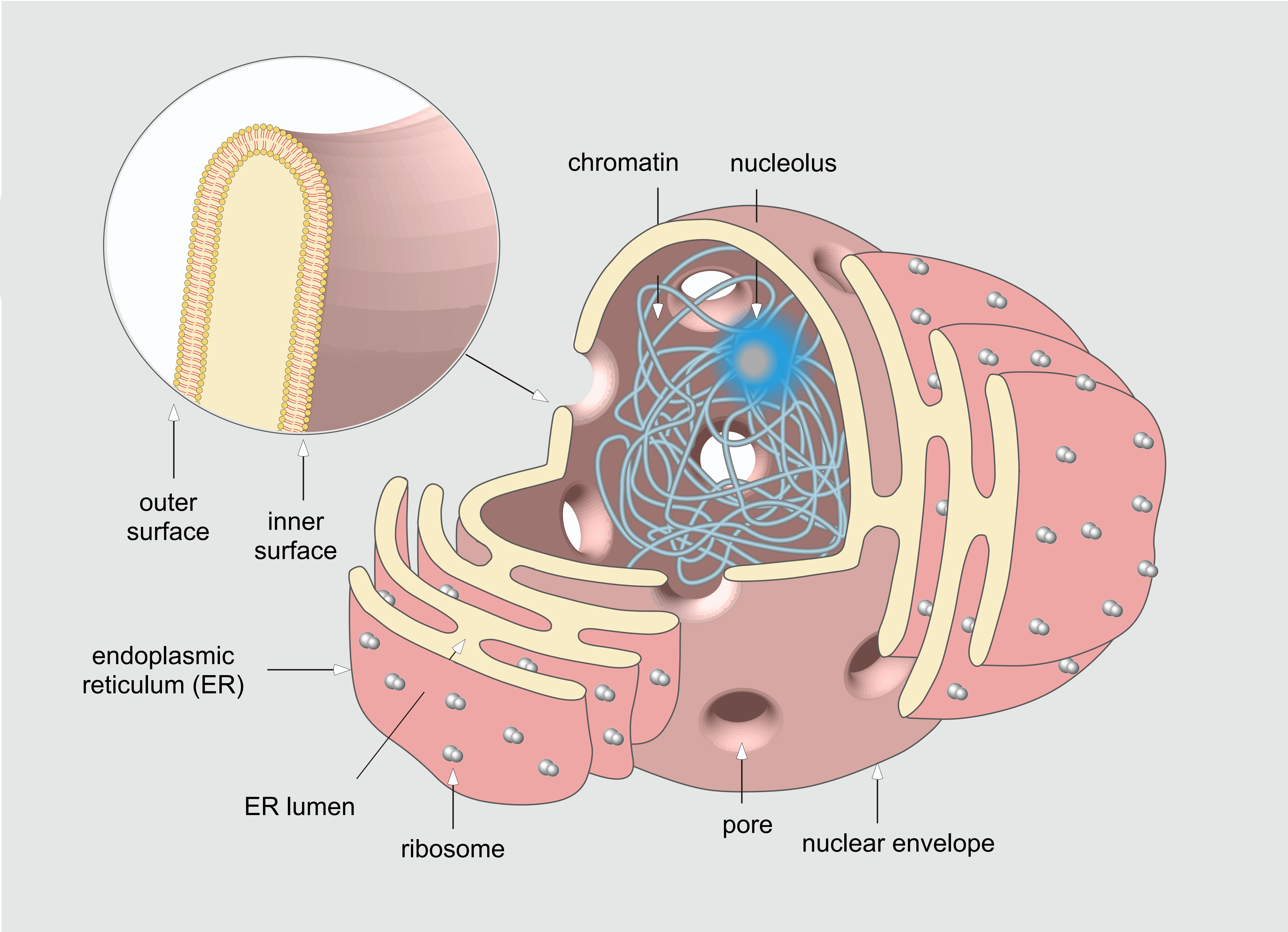


chromatin
nucleolus
outer surface
inner surface
endoplasmic reticulum (ER)
ER lumen
ribosome
pore
nuclear envelope

Introns in eukaryotic genes:

- interrupt the mRNA, removed by spliceosomes in the nucleus.

- Ca. 30% might be as old as eukaryotes themselves, because they share positional homology (conserved positions) across distant groups.

- the experts think that both spliceosomal RNAs and their cognate substrates originate from group II introns, that likely entered entered the eukaryotic lineage via the mitochondrion

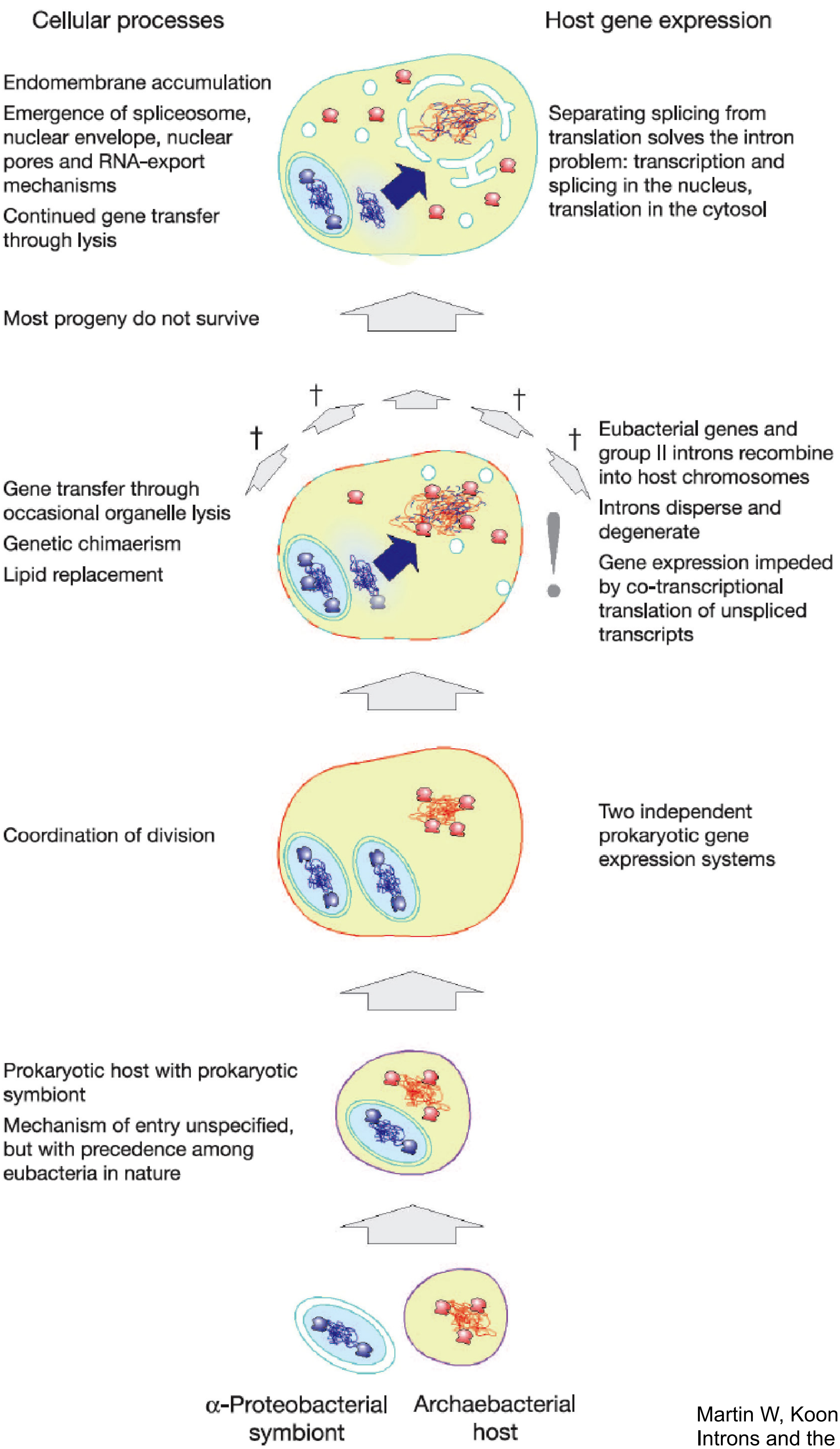
- indeed α-proteobakteria, antecedants of mitochondria, have the highest group II intron density among prokaryotes (>30 in *Sinorhizobium*)

- prokaryotes do not possess spliceosomes

- the “intron transition” thus took place in eukaryotic chromosomes

- but---spliceosomes are slow (ca. 1-7 min. per intron). while ribosomes are fast (ca. 10 AA per sec.).

....what happens if...?



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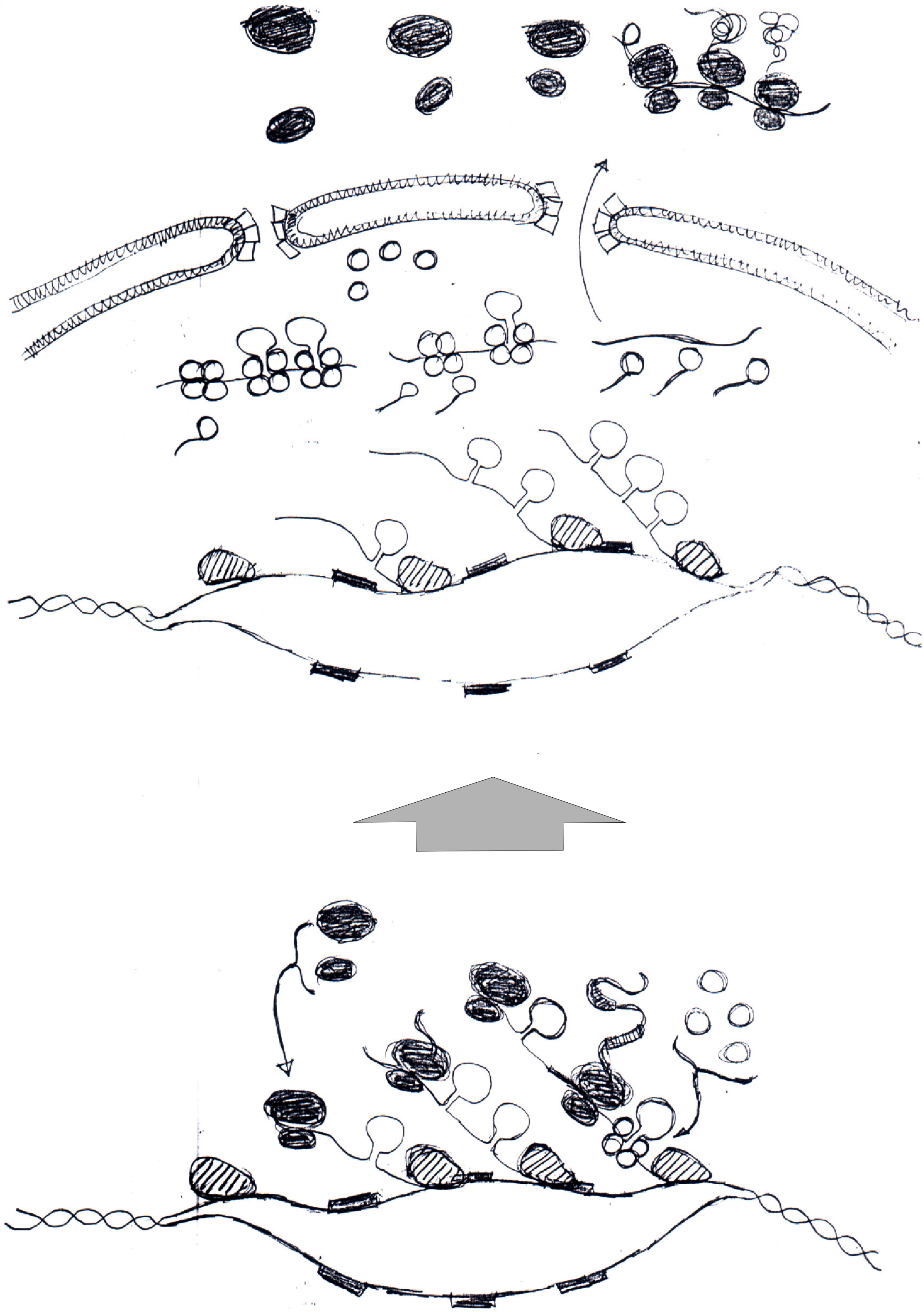
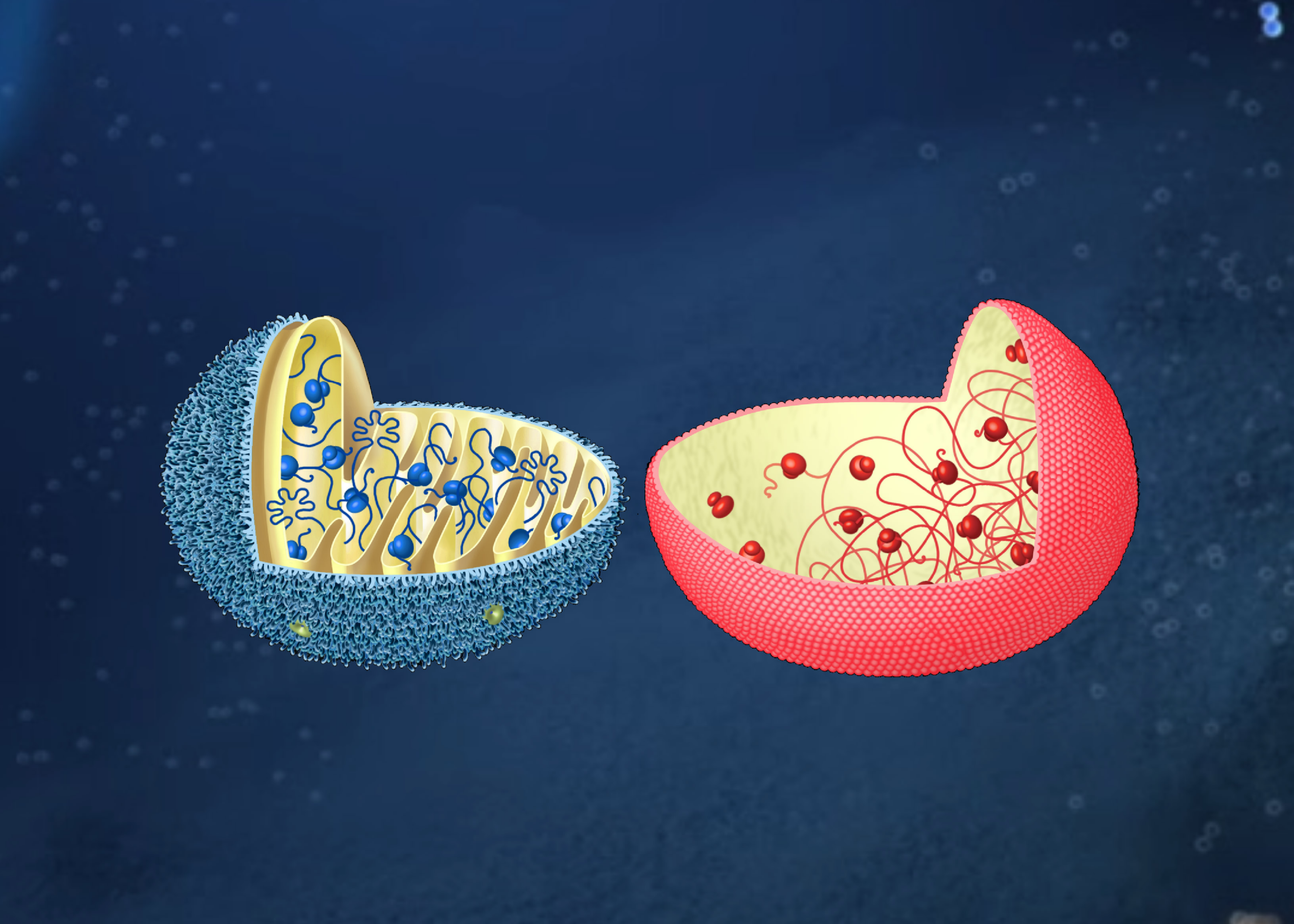
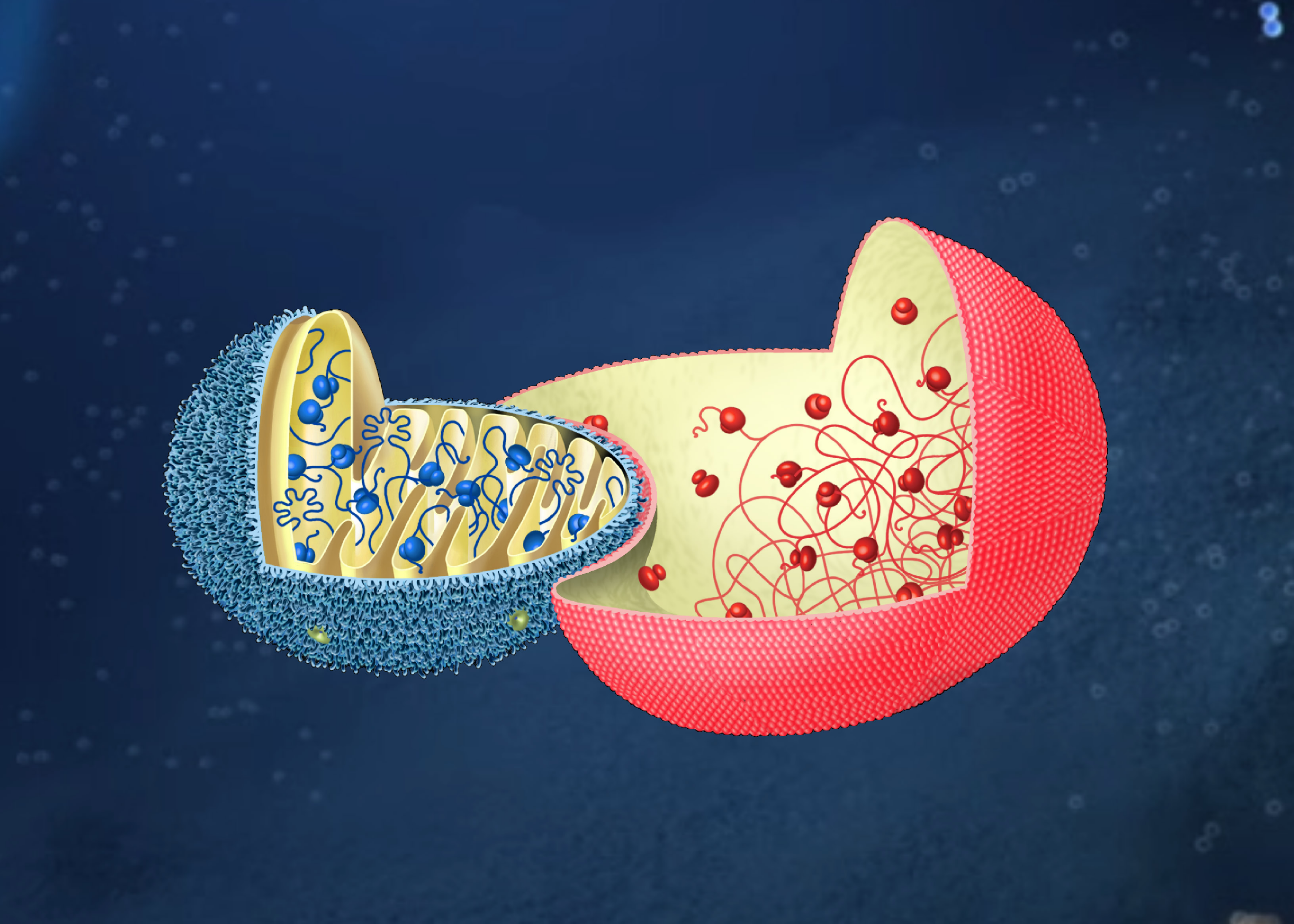
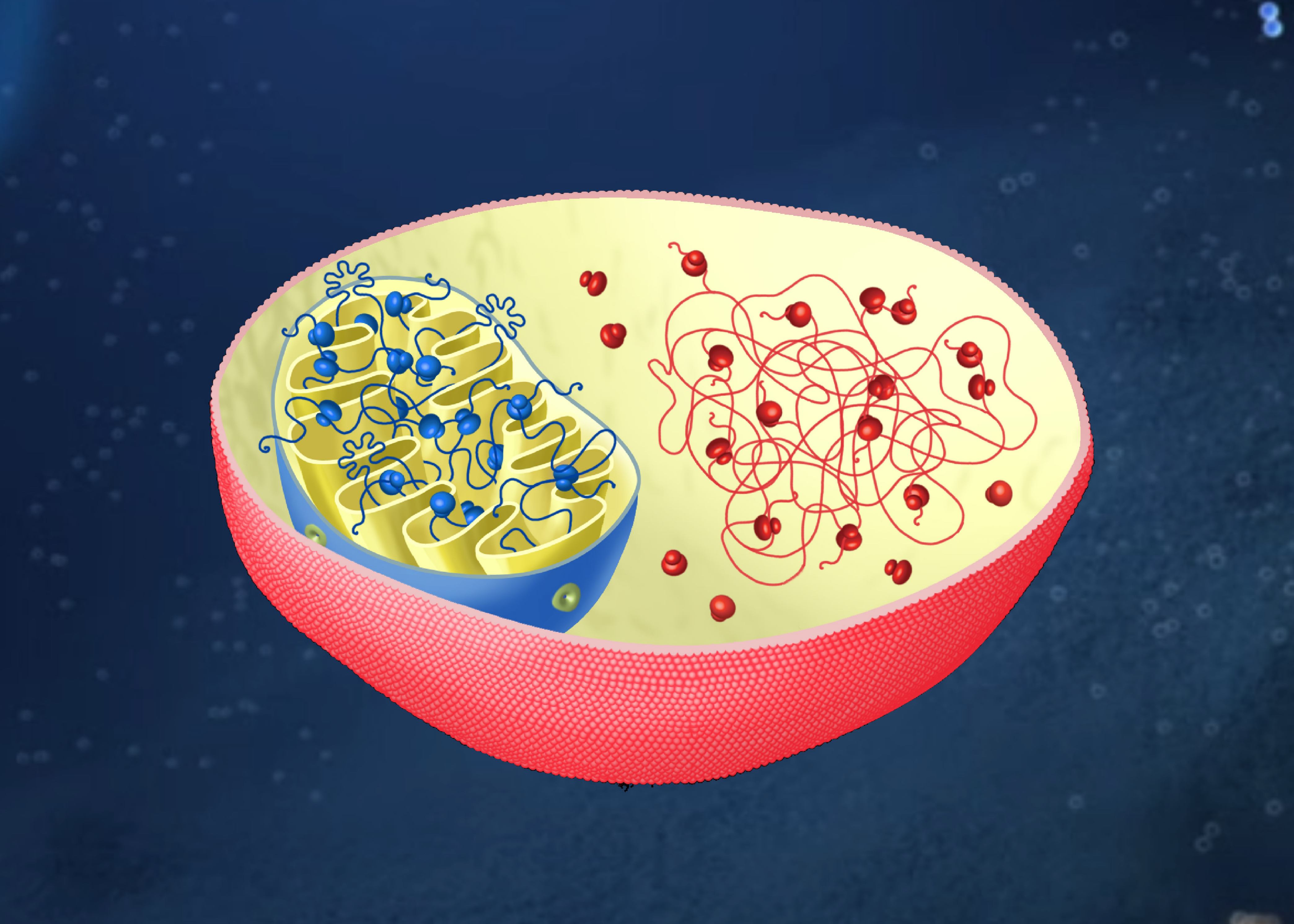
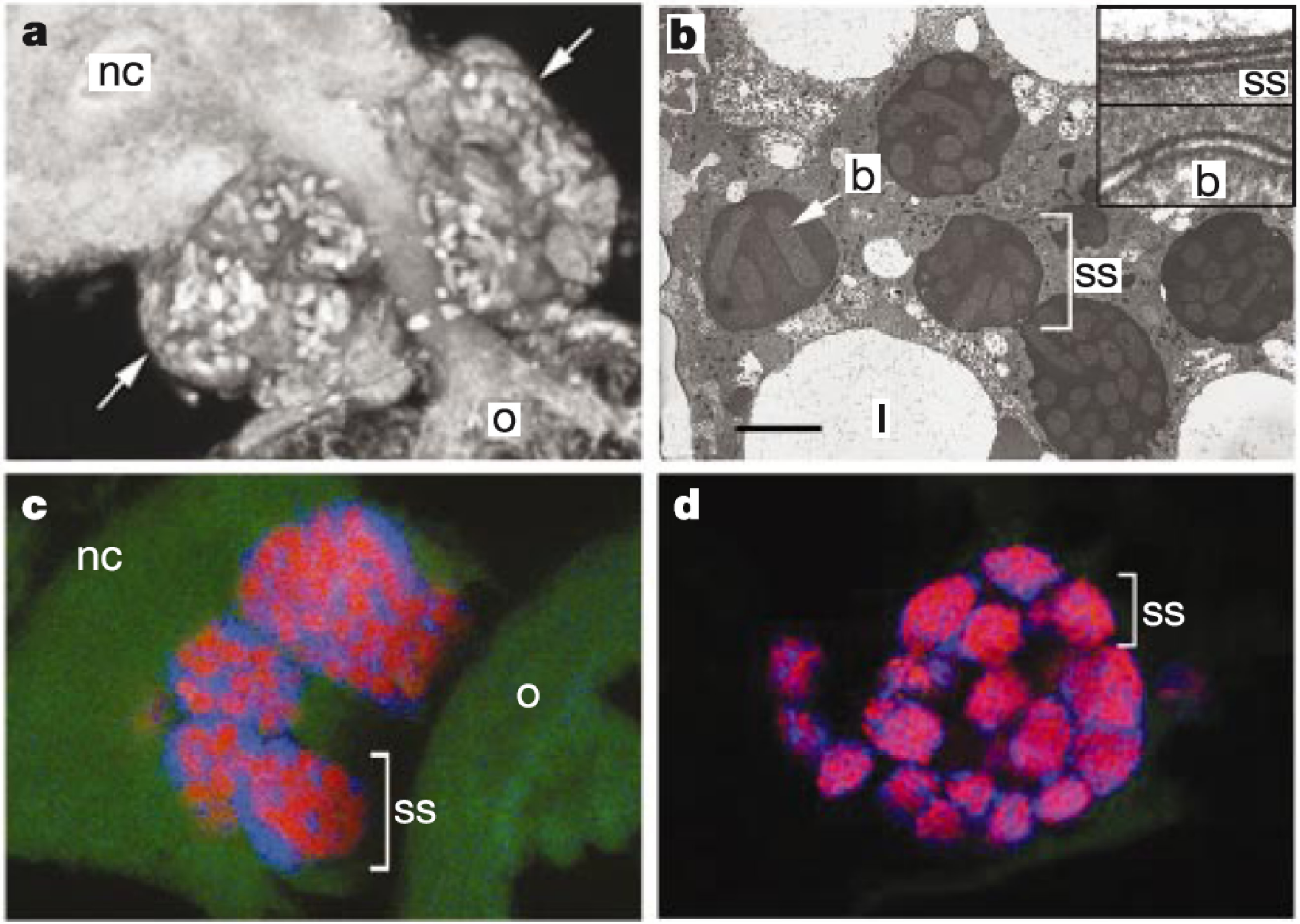
Introns and the origin of
nucleus-cytosol compartmentation.
Nature 440:41–45.



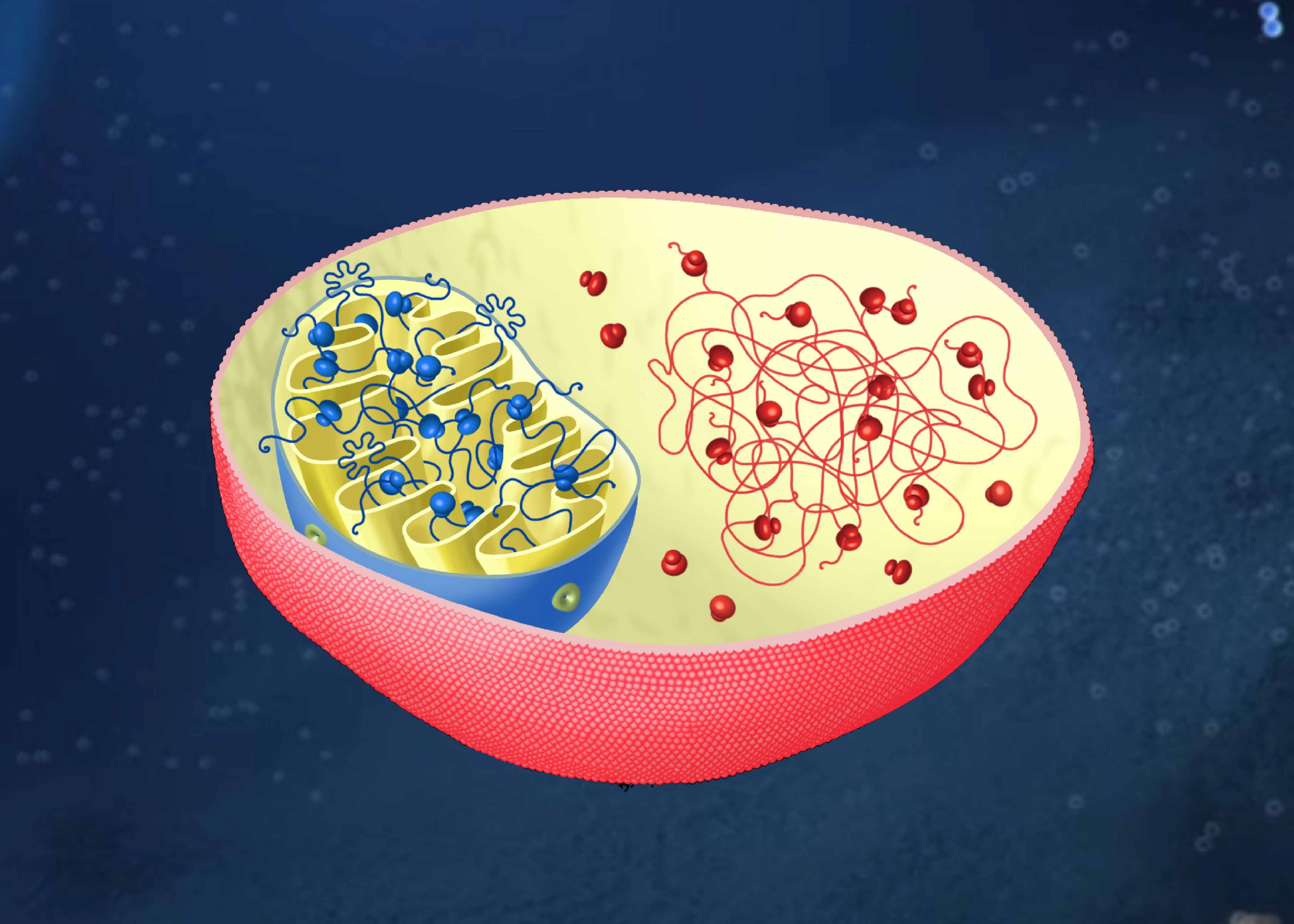


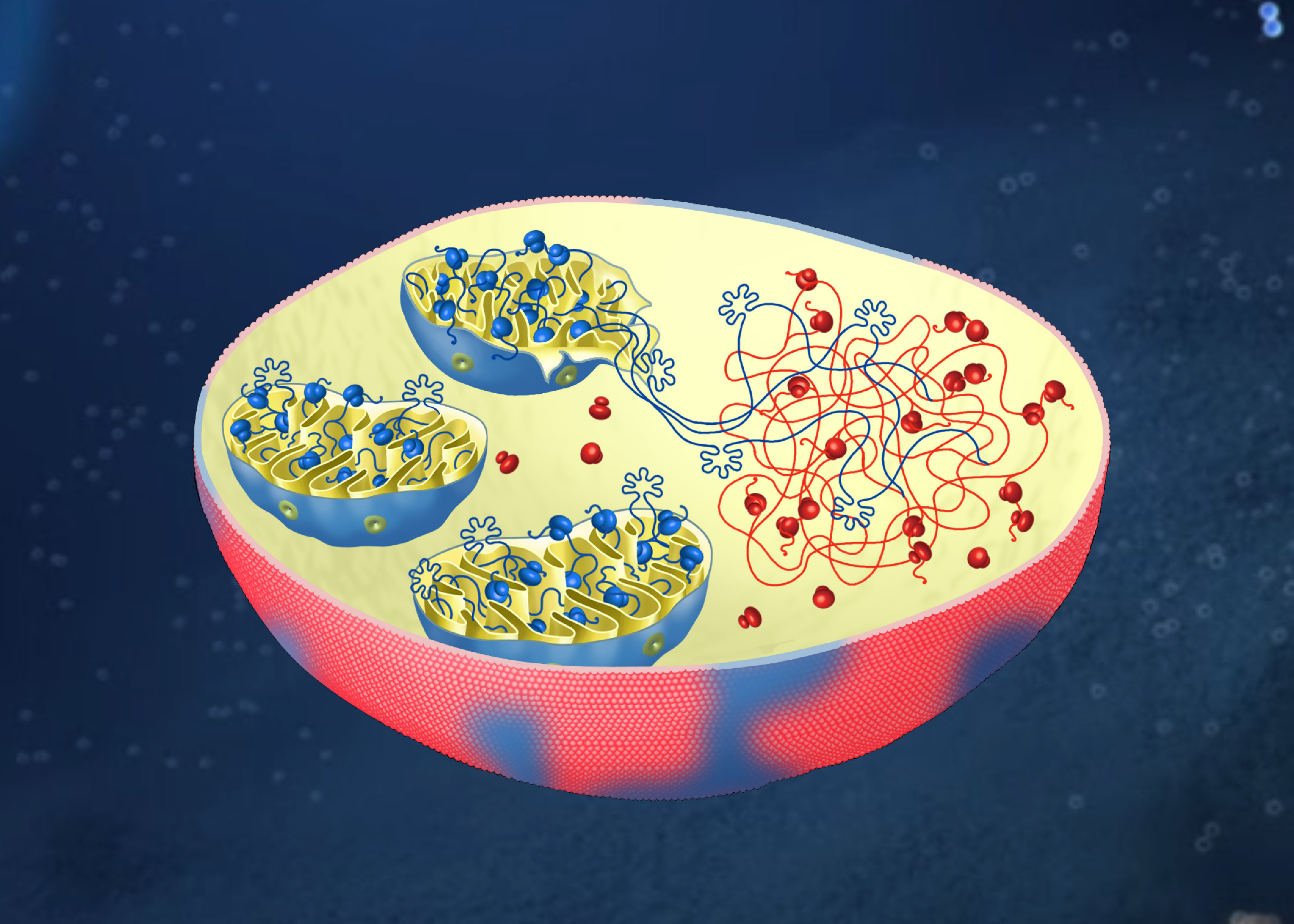


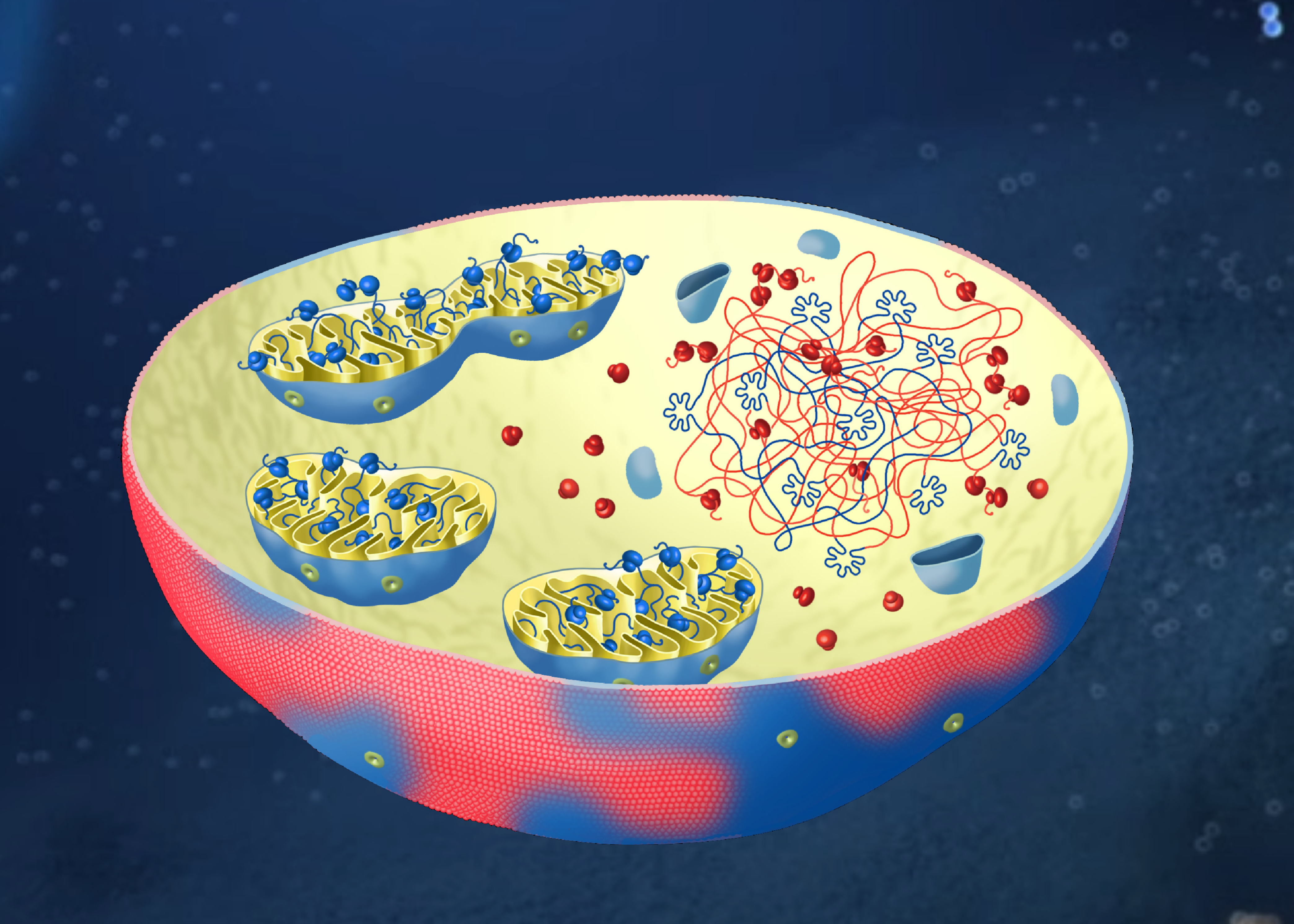


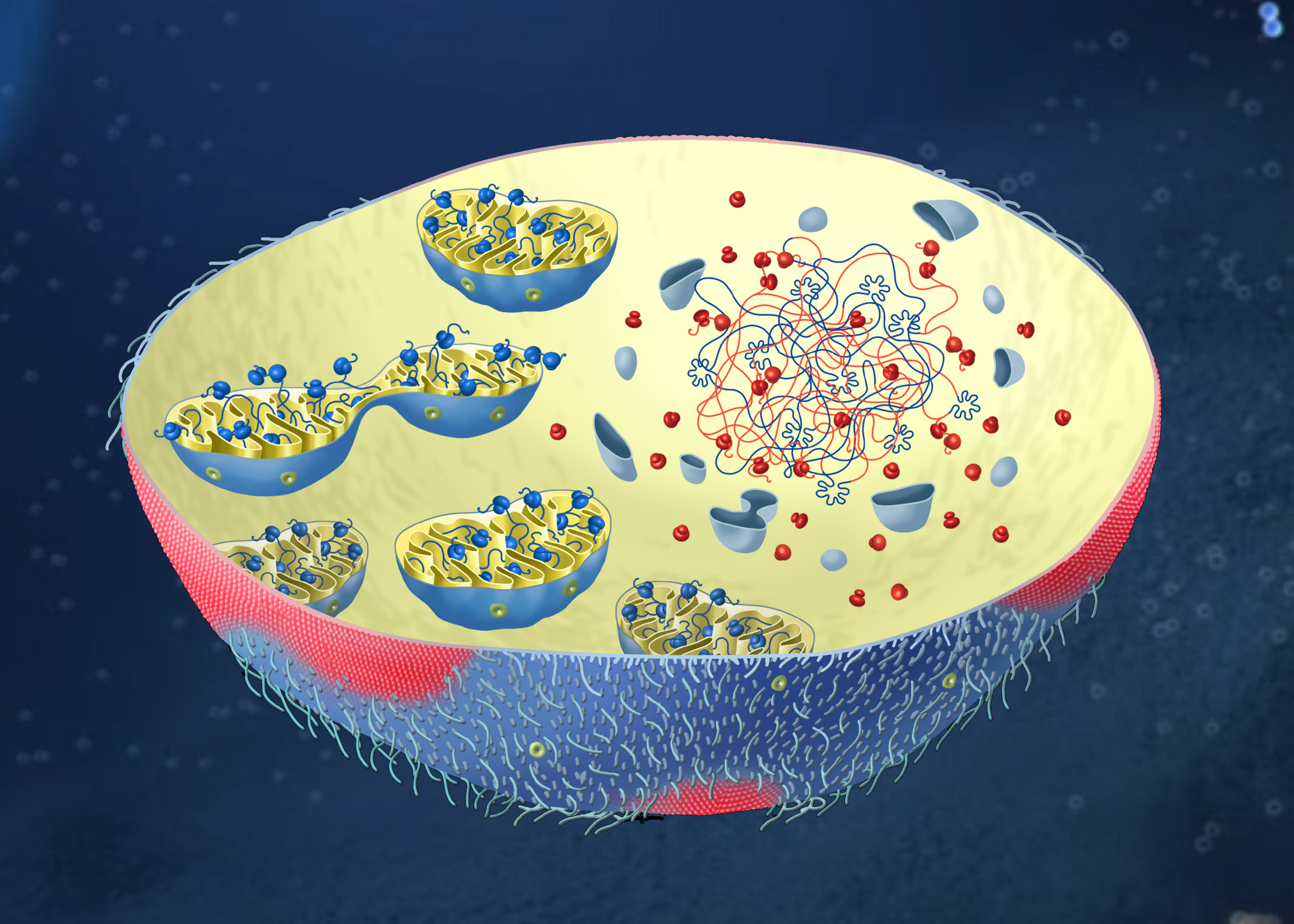


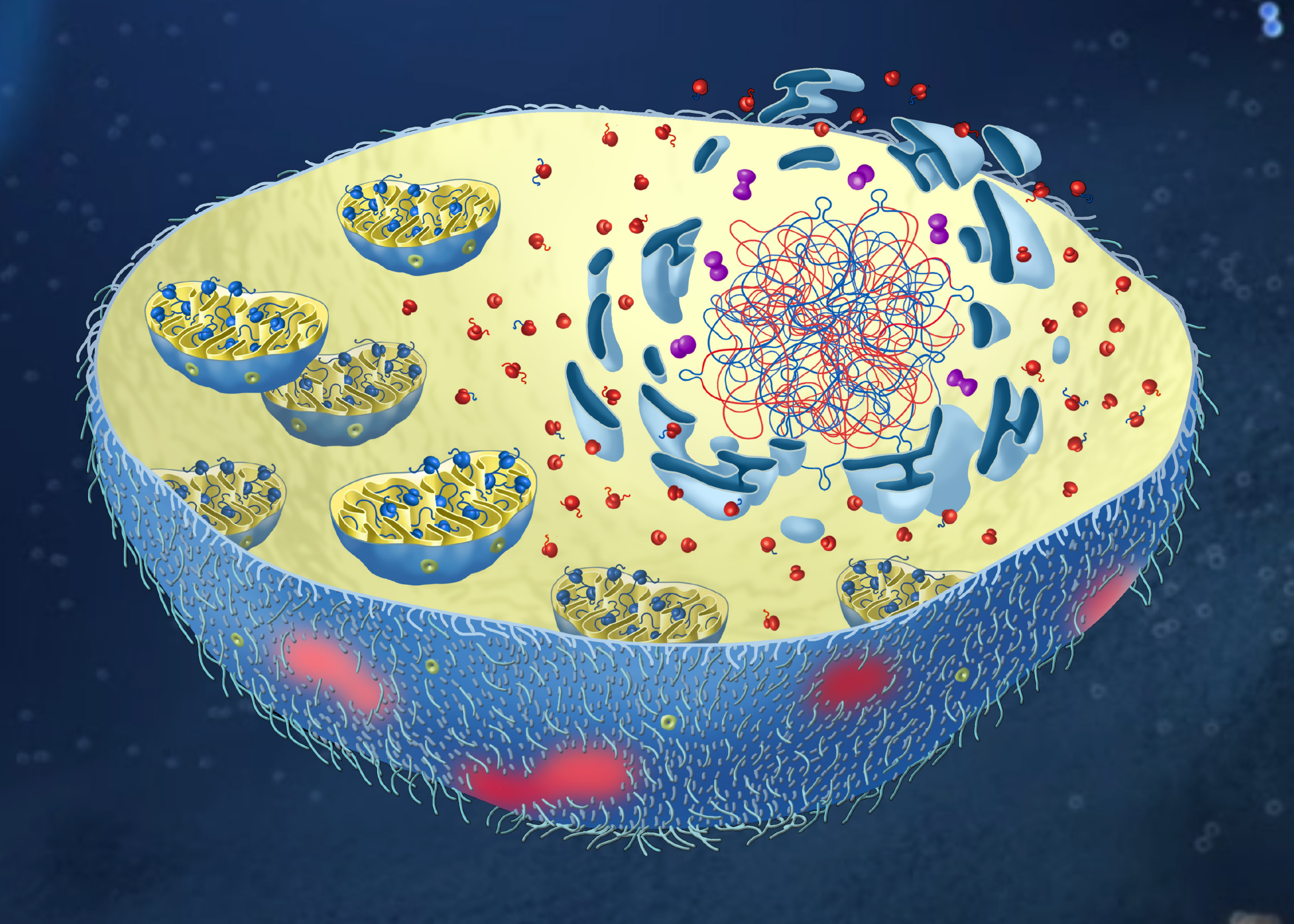
von Dohlen, C.D., Kohler, S., Alsop, S.T., and McManus, W.R. (2001) Mealybug β-proteobacterial endosymbionts contain γ-proteobacterial symbionts. *Nature* **412:** 433-436.

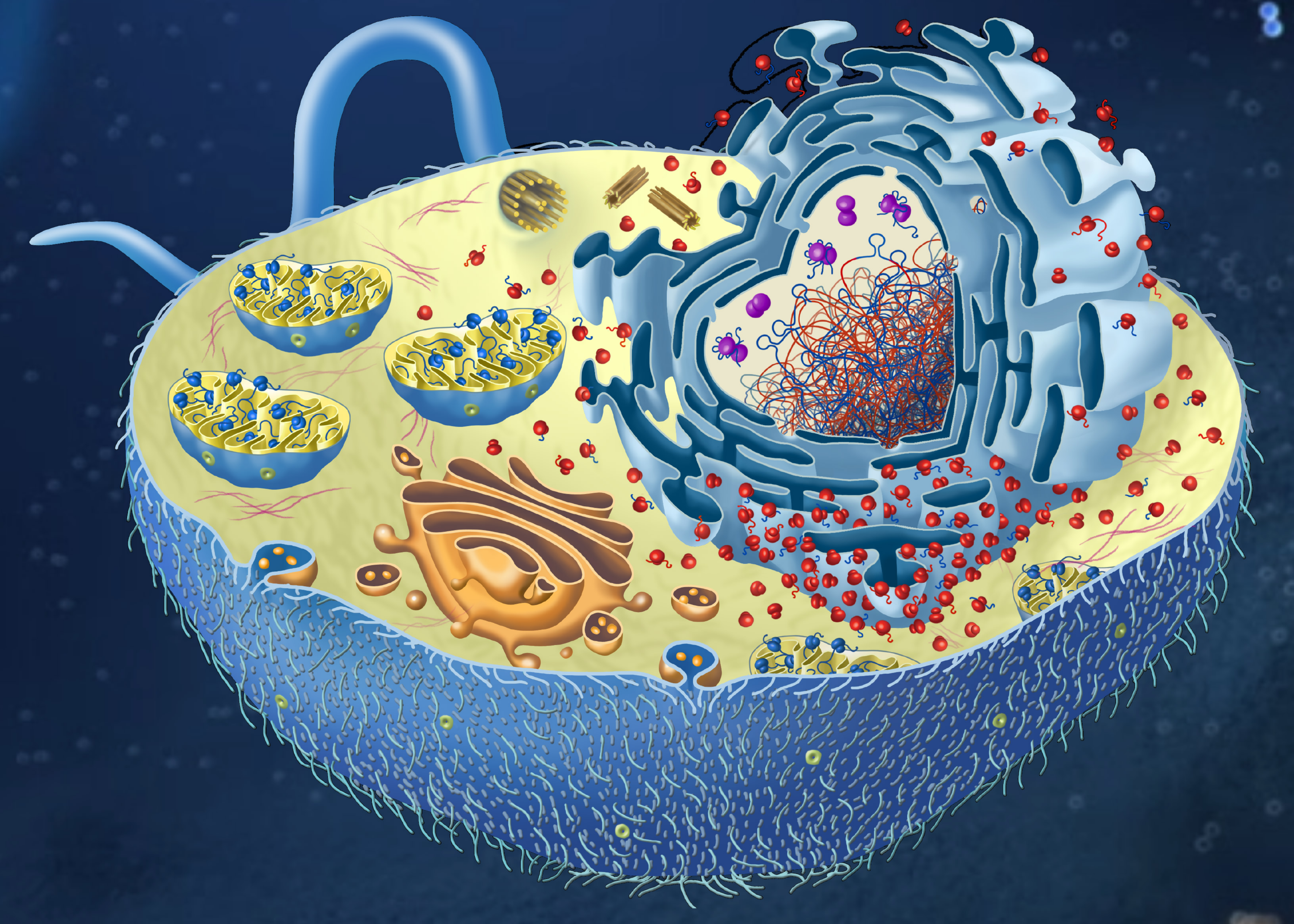












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