# Unravelling complexity: Exploring the evolution of microbial eukaryotes through phylogenomics and phylogenetics

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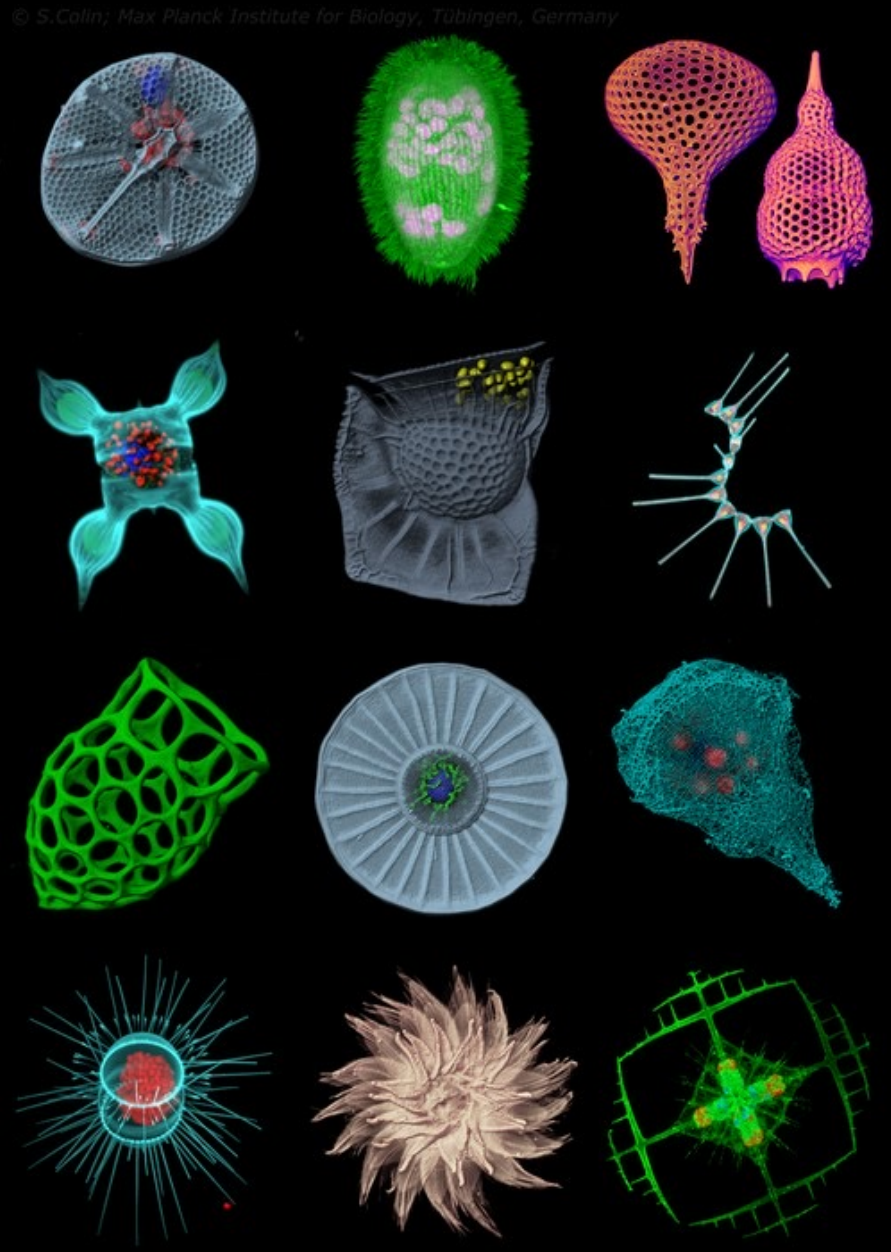
Institute of Evolutionary Biology




Courtesy of Sebastien Colin

# about me

**Phd**
2011

**post-doc**
2013

**post-doc**
2016

**PI**
2017

**sabbatical**
2022

UNIVERSITY OF WARSAW

CHARLES UNIVERSITY IN PRAGUE

UBC

UNIVERSITY OF WARSAW

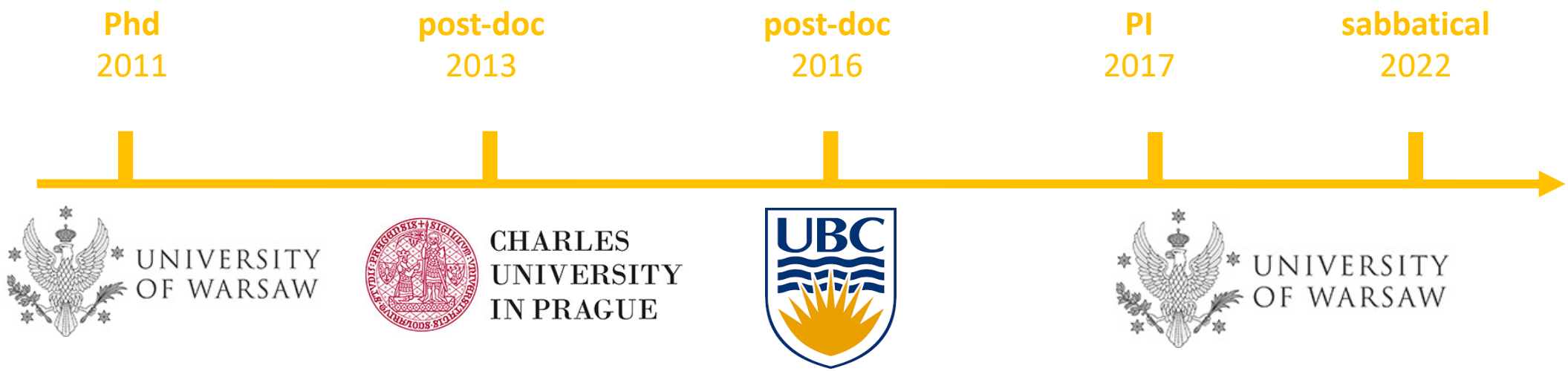
INSTITUT de BIOLOGIA EVOLUTIVA iBe CSIC upf.





# about me

- Taxonomy & Phylogenetics of Euglenophyta



# My first (published) tree ever in 2005!

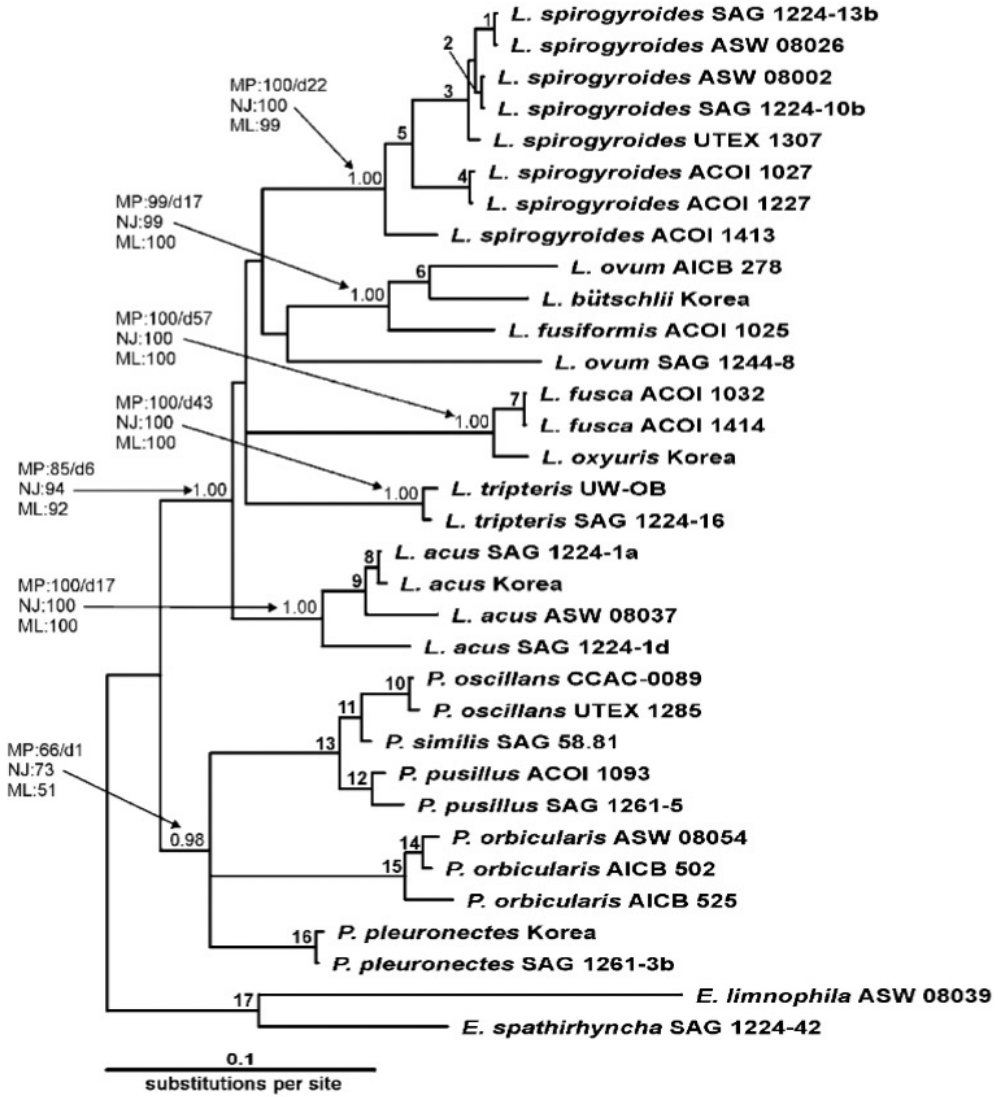



FIG. 2. The phylogenetic tree of the 18S rDNA sequence obtained by Bayesian inference (model GTR + G + I). Numbers at the essential nodes show posterior probabilities of the tree bipartitions as well as the bootstrap values/decay indices obtained for the main clades by MP analysis and bootstrap values obtained by NJ and ML analysis (model GTR + I + G). The support for the remaining nodes (numbered) is listed in Table 5. Branches leading to nodes with support of less than 50% are collapsed, and those without substantial support (pp < 0.95, bs < 0.75) are not listed.

# about me

- Taxonomy & Phylogenetics of Euglenophyta

- Evolution of mitochondria
- Reductive evolution
- Eukaryotic cell evolution
- Phylogenomics & comparative genomics of microbial euks.

- Evolution of organelles
- Eukaryotic cell evolution
- Reductive evolution
- Eukaryotic rhodopsins diversity & evolution
- Freshwater protists diversity and interactions
- Phylogenomics & comparative genomics

**Phd** 2011 — **post-doc** 2013 — **post-doc** 2016 — **PI** 2017 — **sabbatical** 2022




UNIVERSITY OF WARSAW

FACULTY OF BIOLOGY · UNIVERSITY OF WARSAW

Centrum Nauk Biologiczno-Chemicznych Uniwersytetu Warszawskiego

Institute of Evolutionary Biology

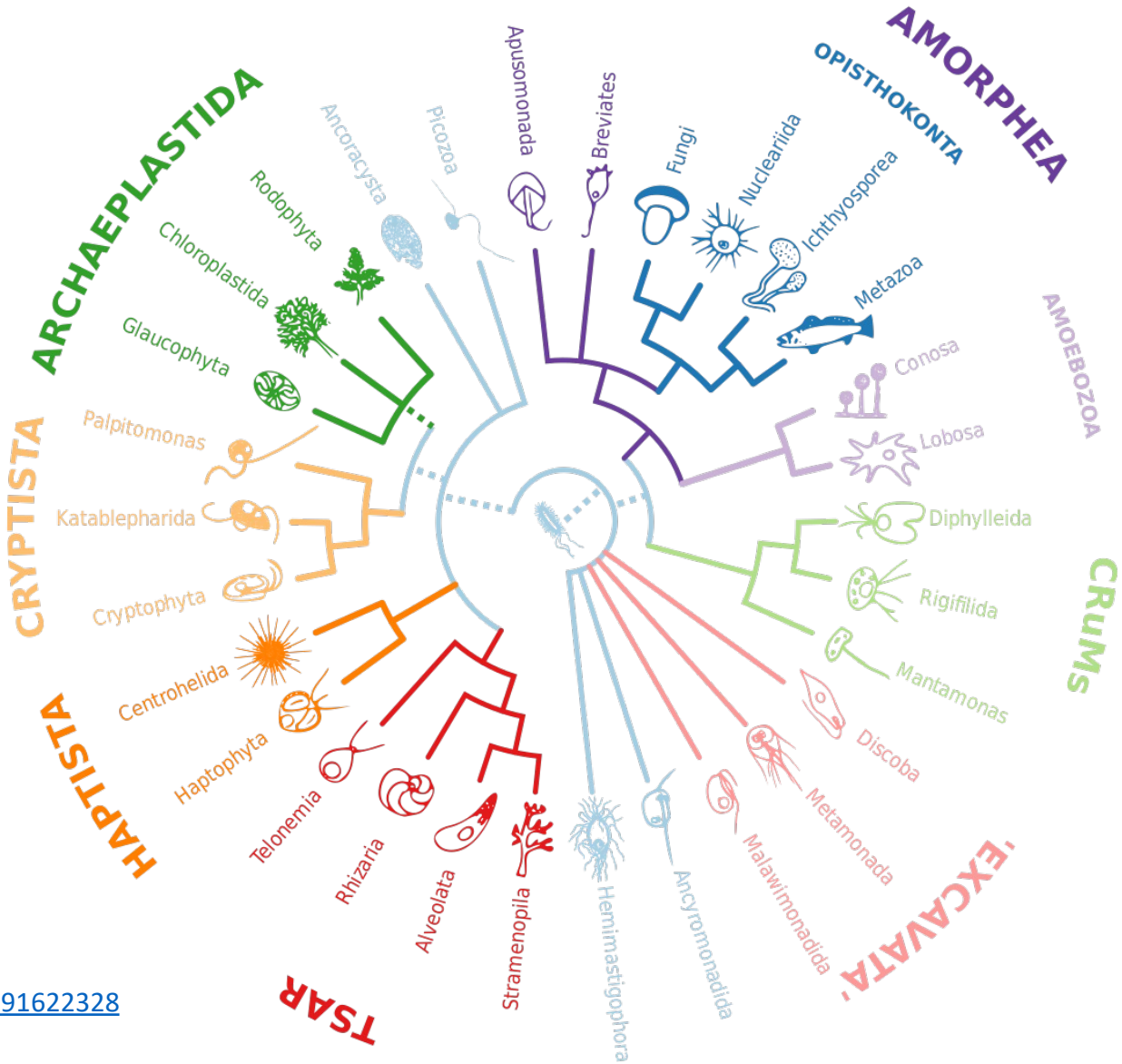
# Evolution & genomics of microbial eukaryotes

EMBO

National Science Centre Poland

EXCELLENCE INITIATIVE RESEARCH UNIVERSITY

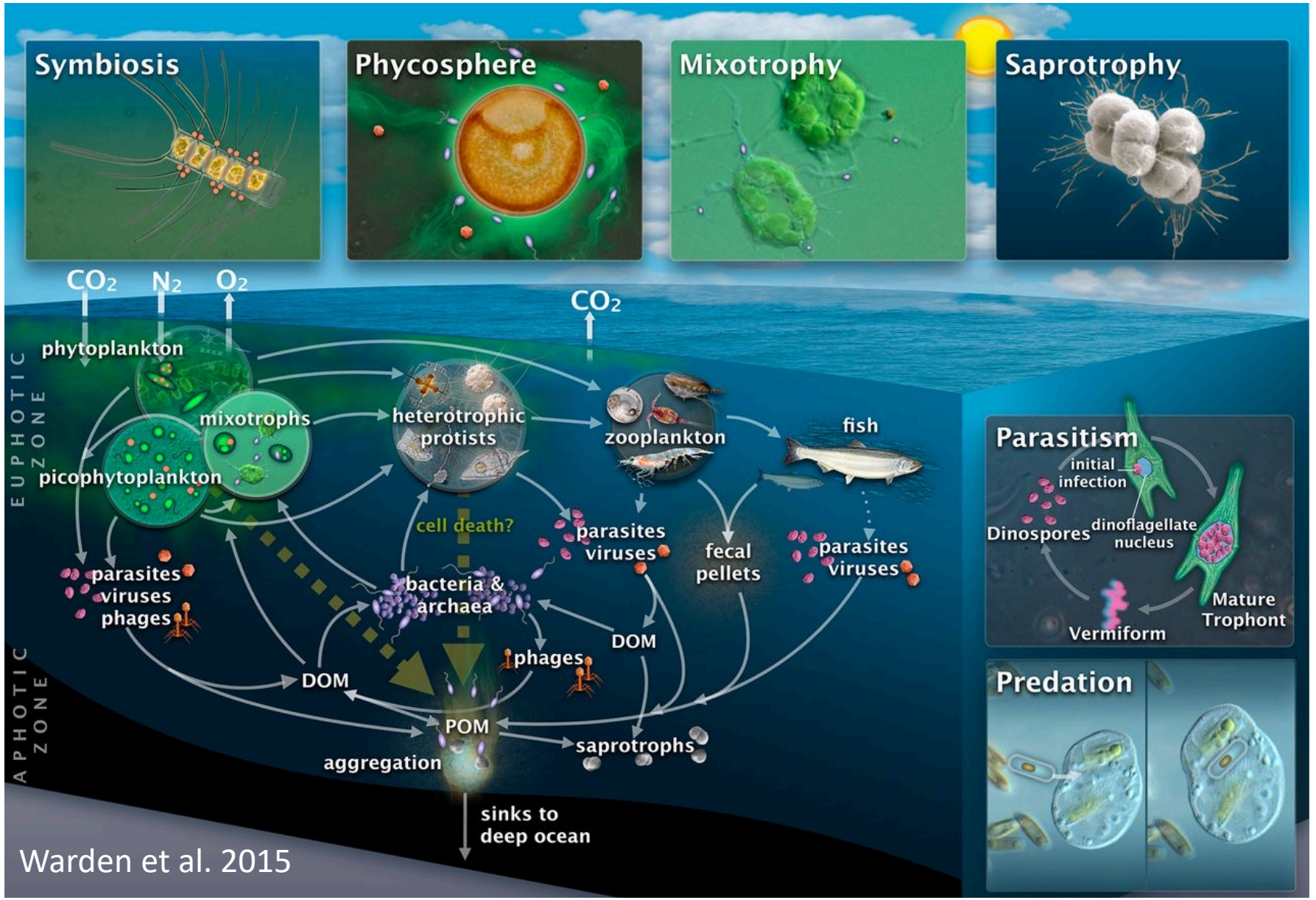
# microbial eukaryotes (protists) constitute majority of lineages on the eukaryotic tree of life




By Tricholome - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=91622328
Burki et al. 2020

# morphological diversity of protist

# functional diversity of microbial eukaryotes

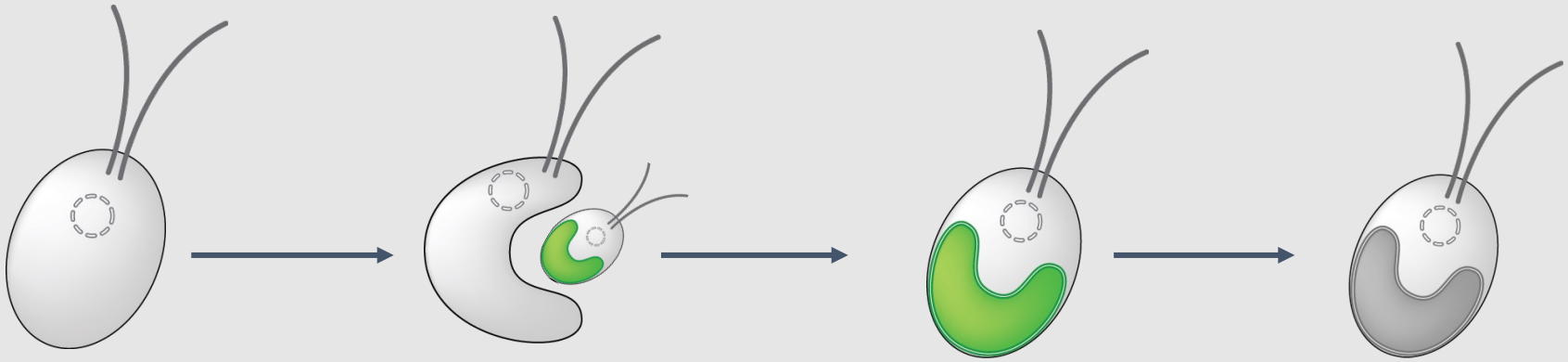



Warden et al. 2015

How the eukaryotic **cell complexity** evolved?
What drives **diversification of eukaryotes**?

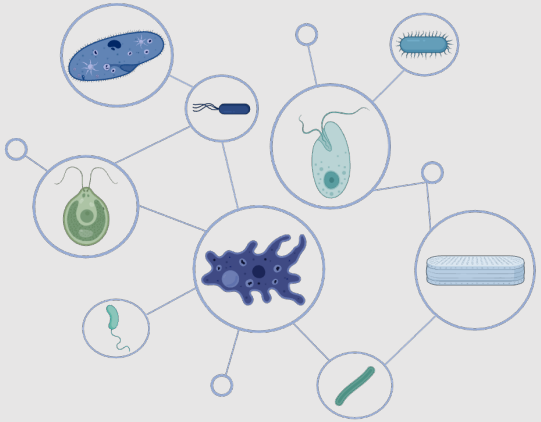
# Endosymbiosis

## Origin, evolution and fate of endosymbiotic organelles

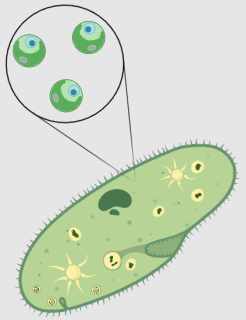


## Interactions of microbial eukaryotes in the changing environment

interactions

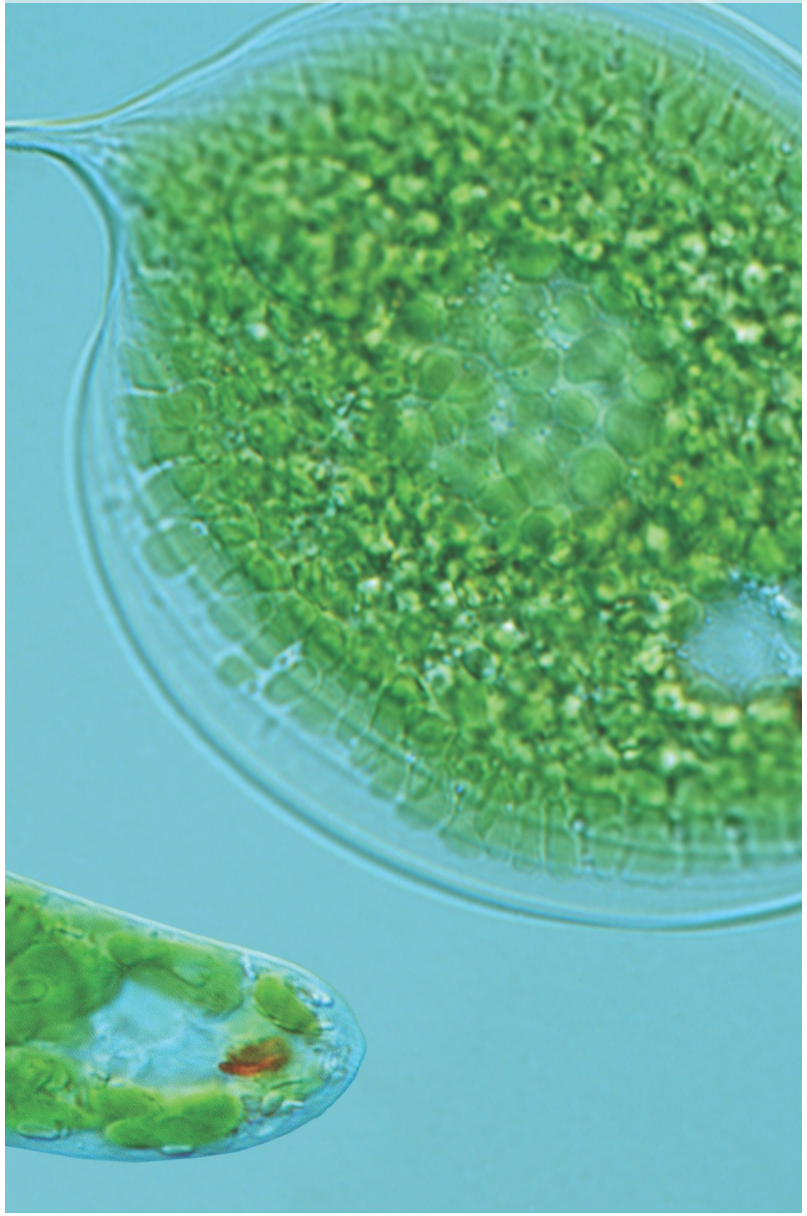


endosymbionts

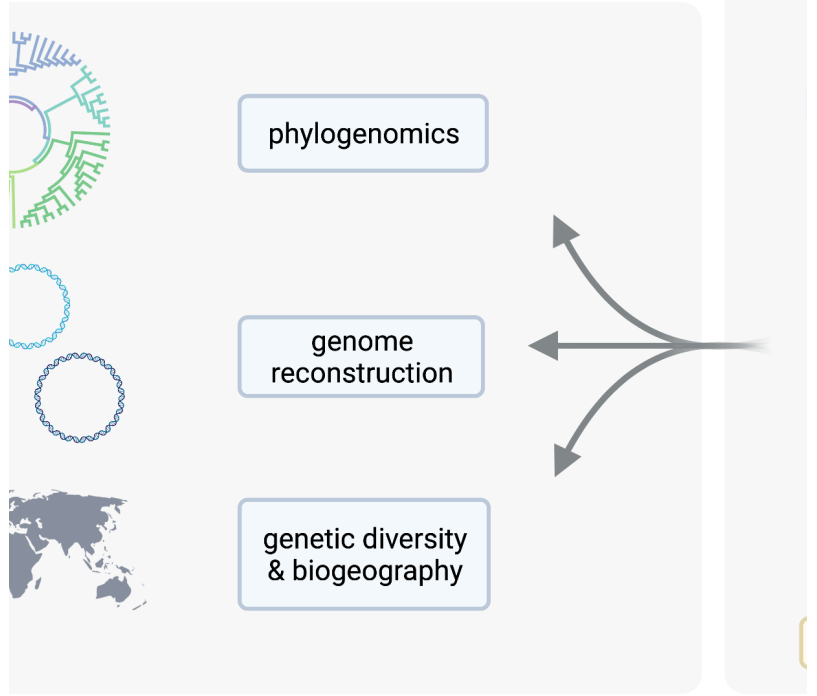


## SAMPLING

## EXPERIMENTS

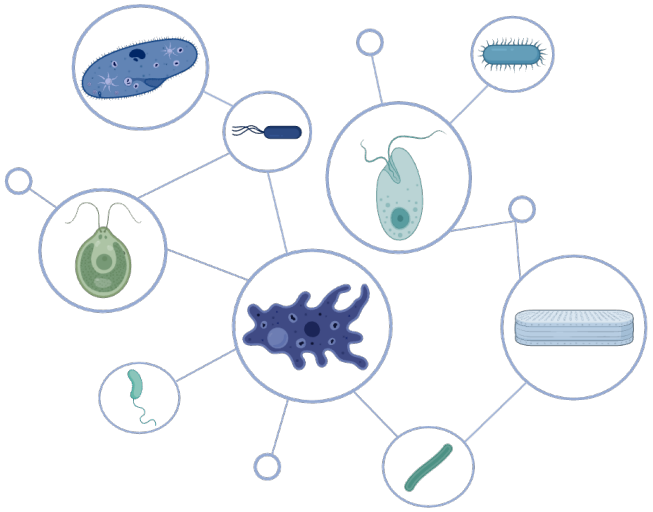


## BIOINFORMATICS

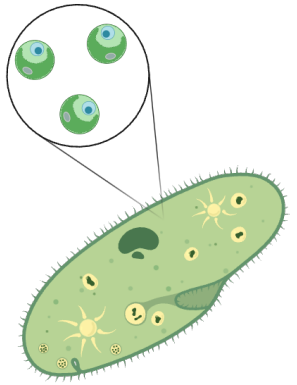


# Diversity & interactions of microbial eukaryotes

interactions



endosymbionts



Who is there? What are the interactions?
Which environmental factors influence interactions?
Do all cells of the same species have the same (endo)symbionts?

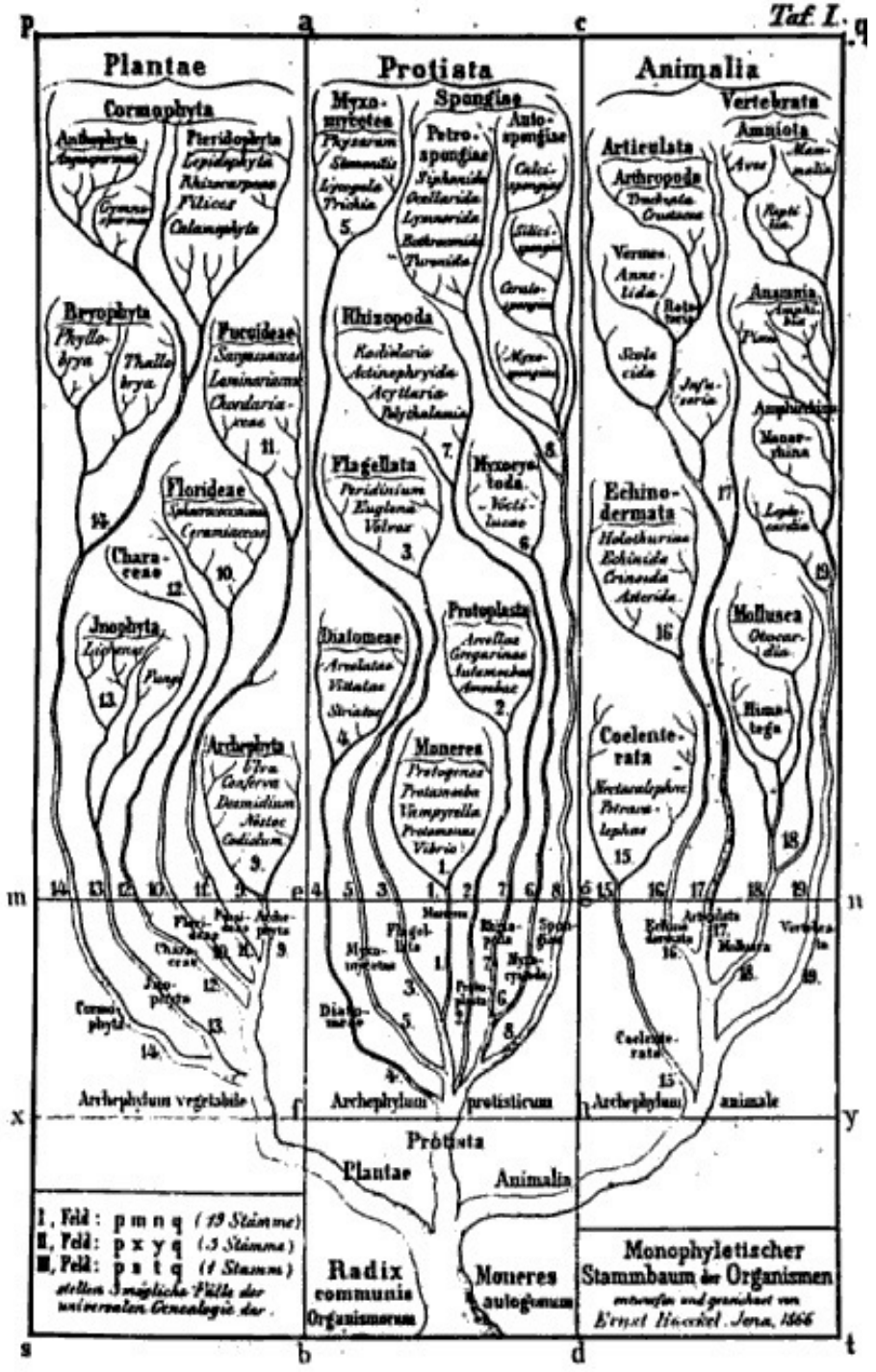
# Overview

- Tree of eukaryotes – history
- Phylogenomics and the tree of eukaryotes
- Why do we need to resolve the tree of euakryotes?
- Origin of eukaryotes
- Metagenomics in phylogenomics

- Phylogenomics as a tool to address (my) evolutionary questions

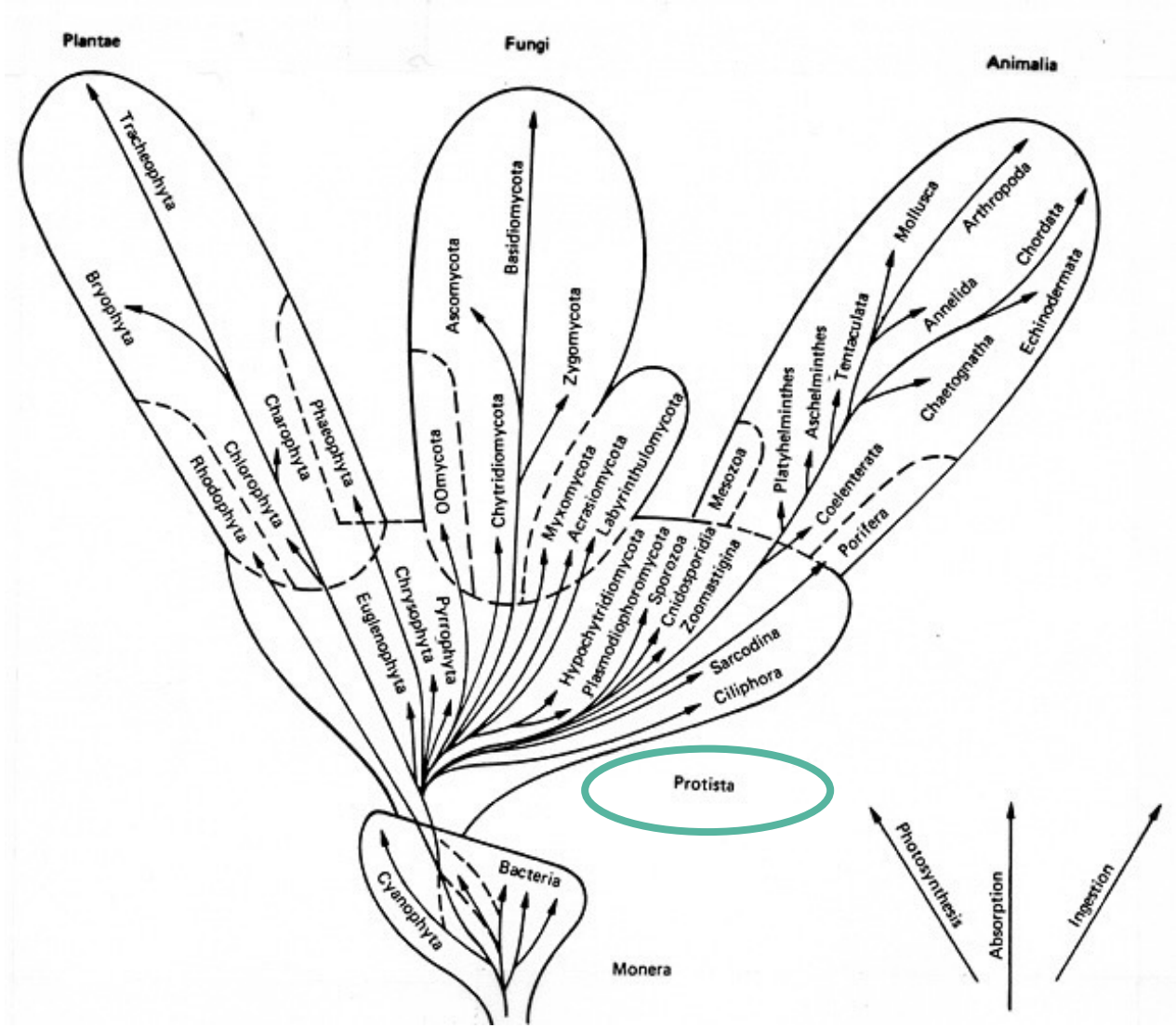
# First tree of eukaryotes with a kingdom Protista

Ernst Heckl - 1866



# New kingdom of Fungi

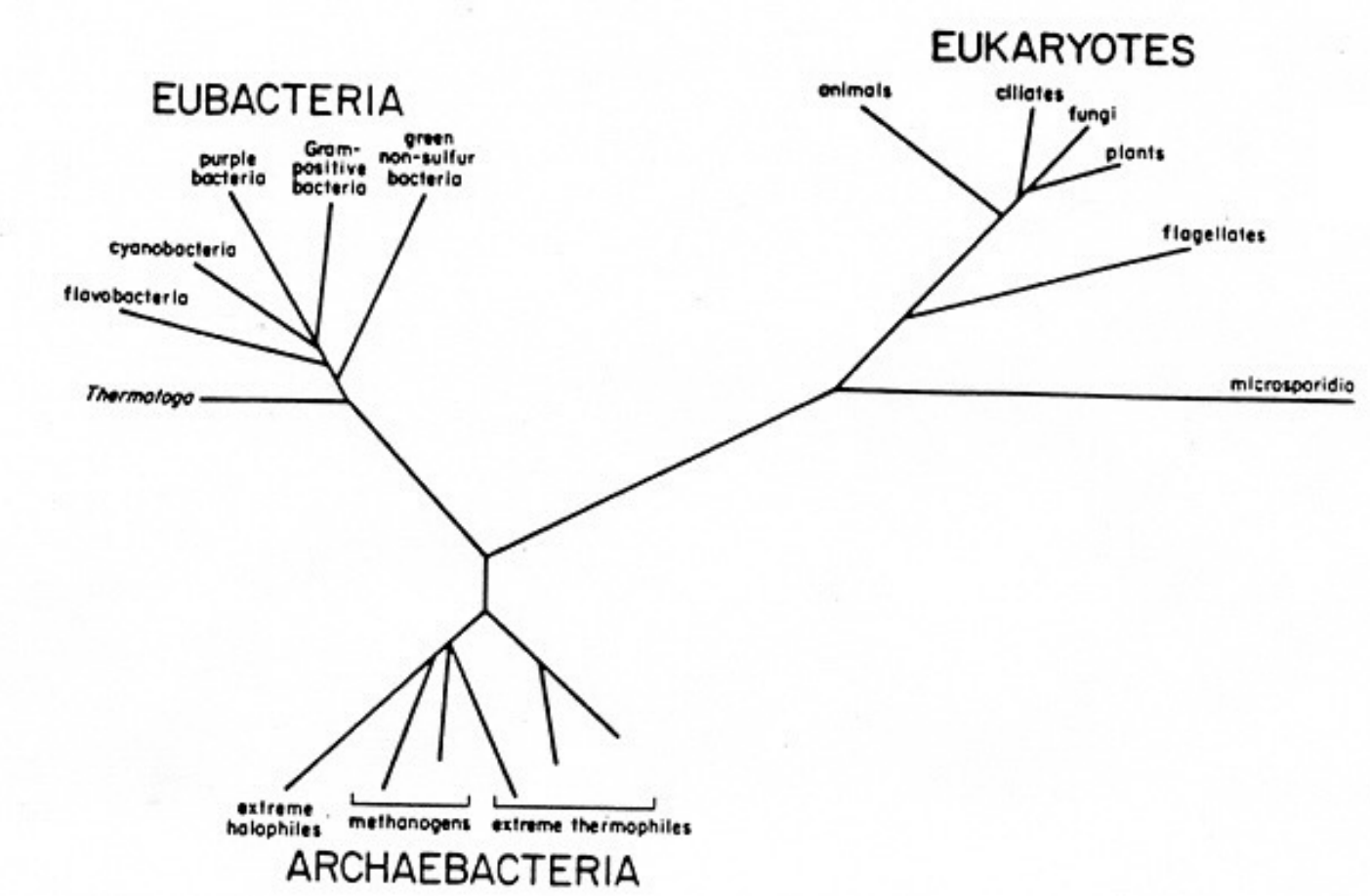
## Whittaker 1967



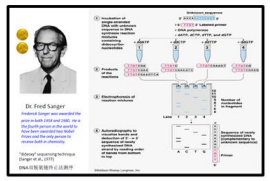
# Molecular phylogeny

Carl Woese 1988

- only one phylogenetic marker - rDNA
- three domains of life
- new relationships have been detected

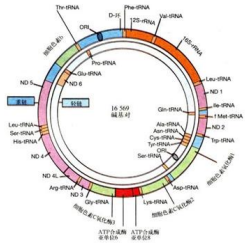


# The Next Generation Sequencing Revolution



1977 **Sanger method**

1981 **Human mitochondrial genome sequence**



1990 **Human Genome Project**

1995 **Complete cell genome**

1996 **Complete eukaryotic genome**

2001 **Complete the Human Genome Project**

2005 **Second generation sequencer： 454 GS20**

2007 **Second generation sequencer： Genetic Analyzer 2**

2008 **Research Human Microbiome Project**

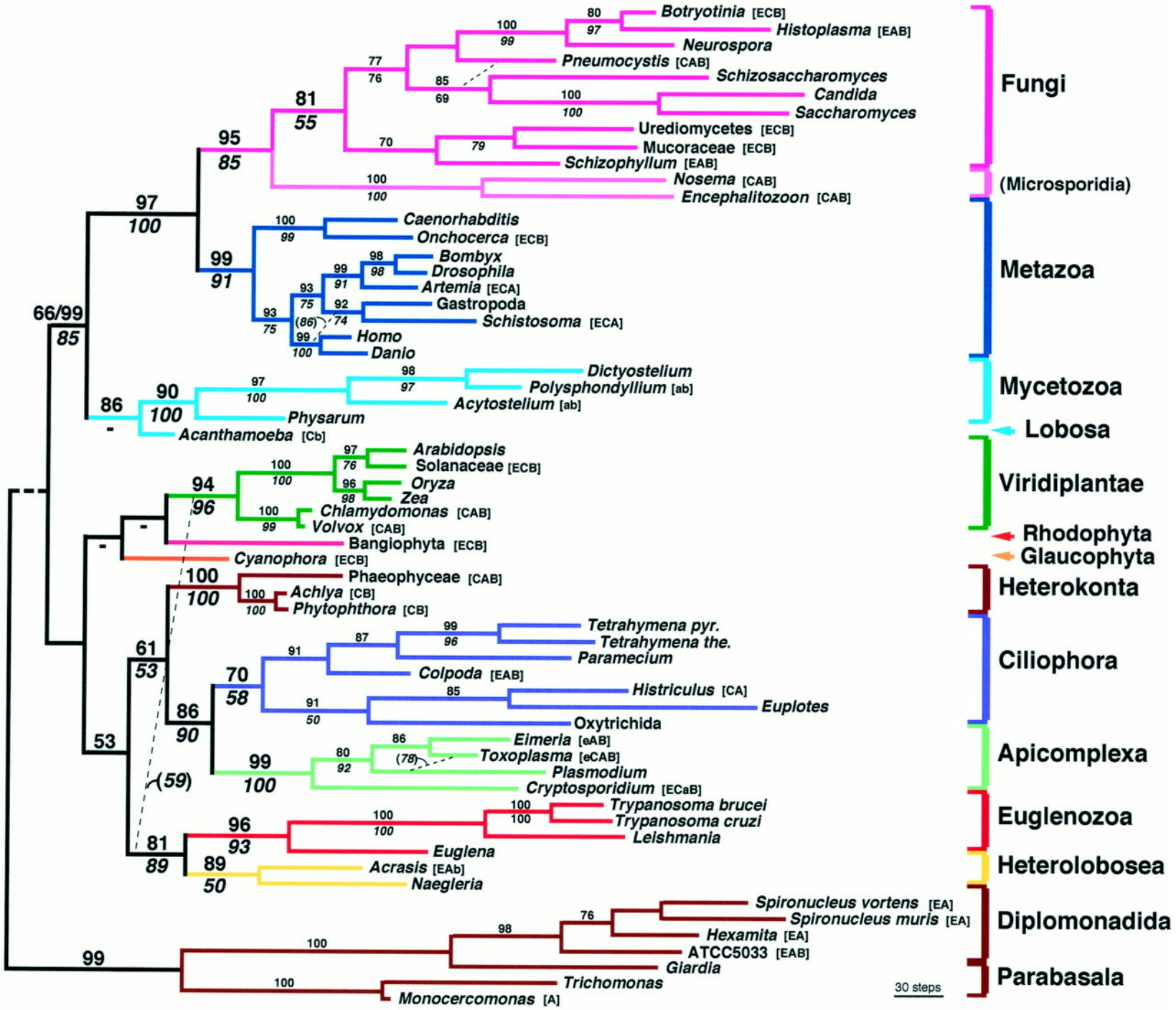
2011 **Third generation sequencer： PacBio RS**

2014 **Nanospace sequencing**

2019 **The third stage Human microbiome project**

# More molecular data

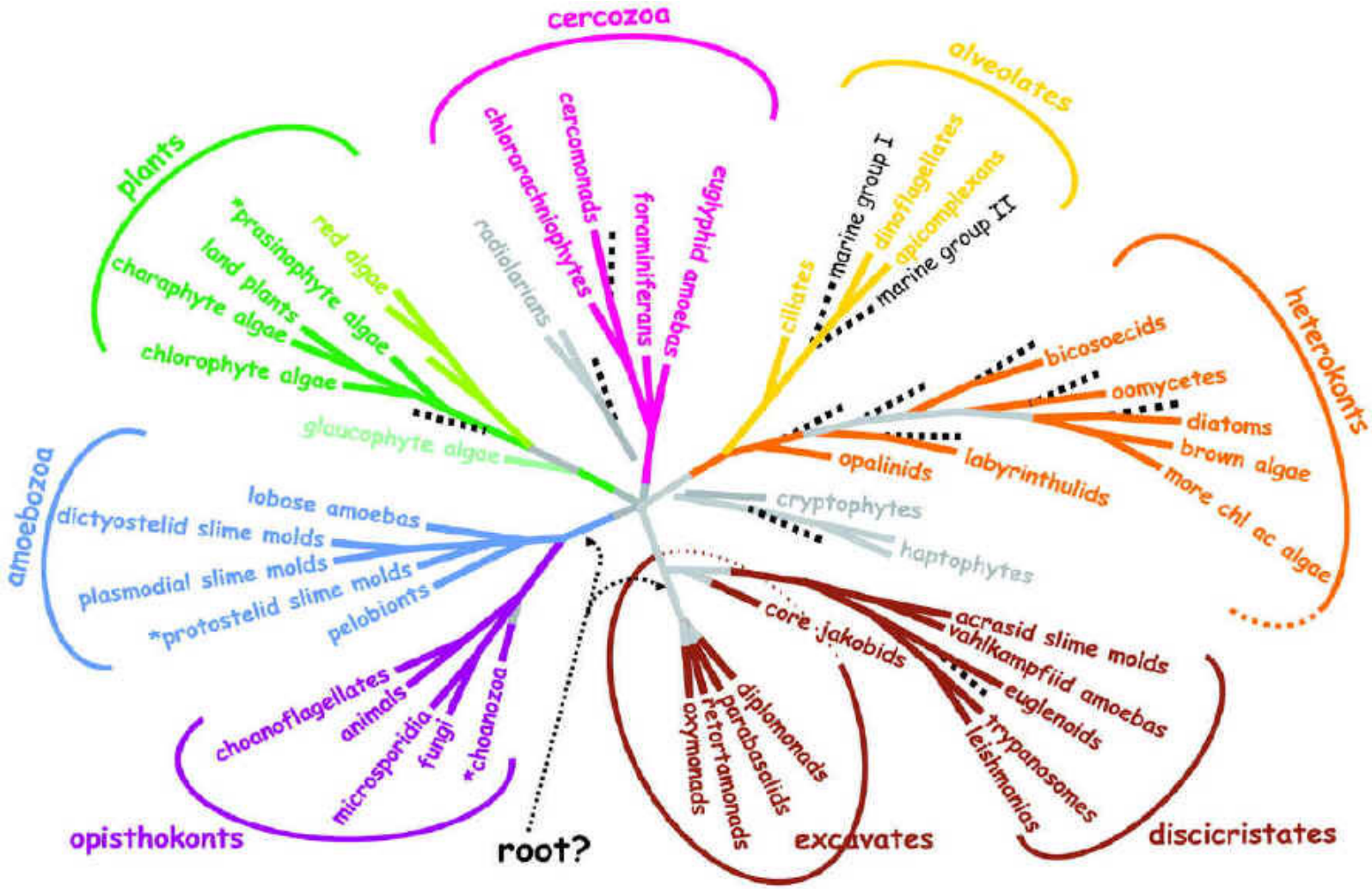
The tree shown is one of two shortest trees found by parsimony analysis of concatenated four protein-encoding genes EF-1α, actin, α-tubulin, and β-tubulin amino acid sequence



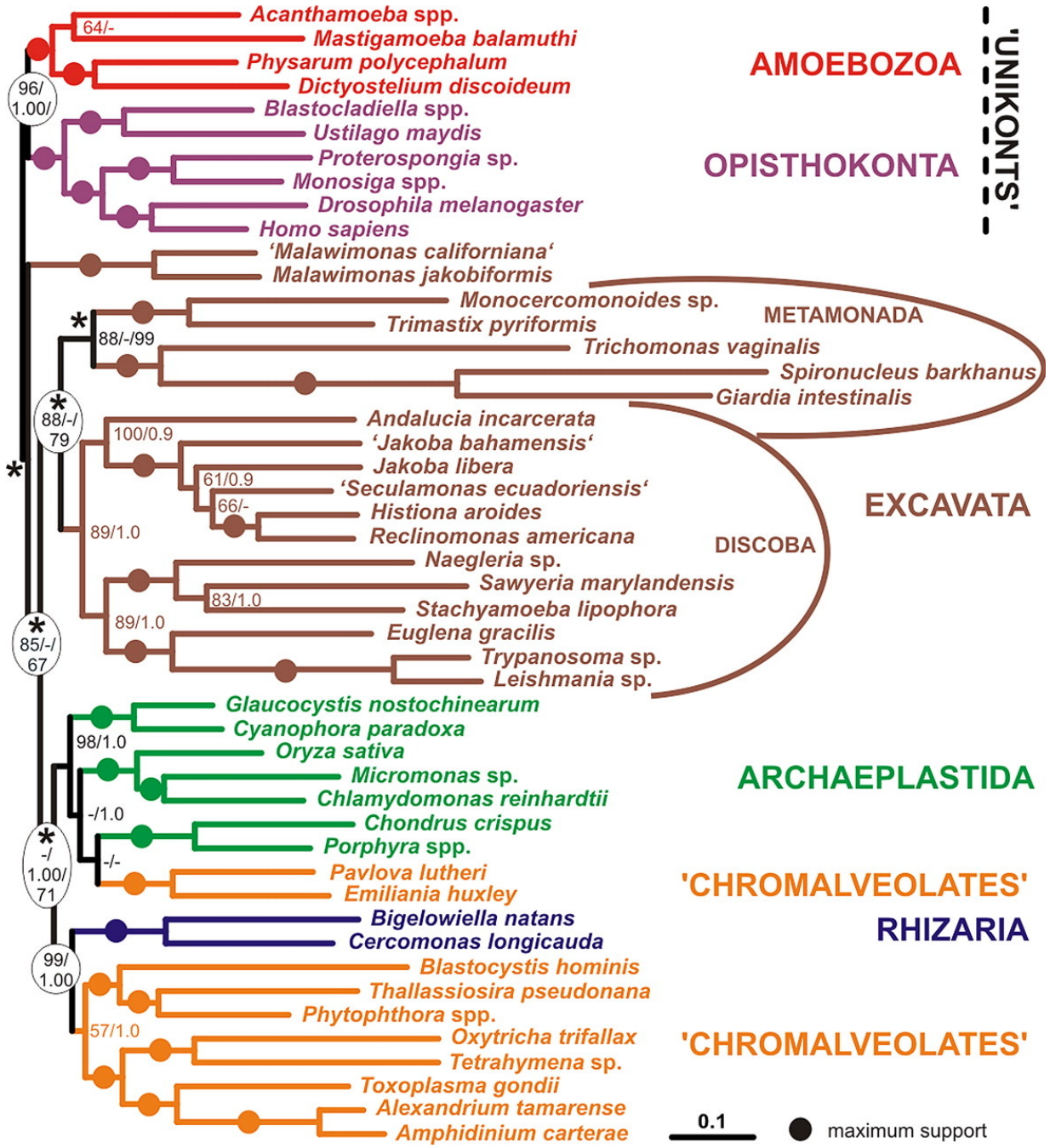

Baldauf et al. 2000, Science

# More molecular data

Eukaryotes subdivided into supergroups



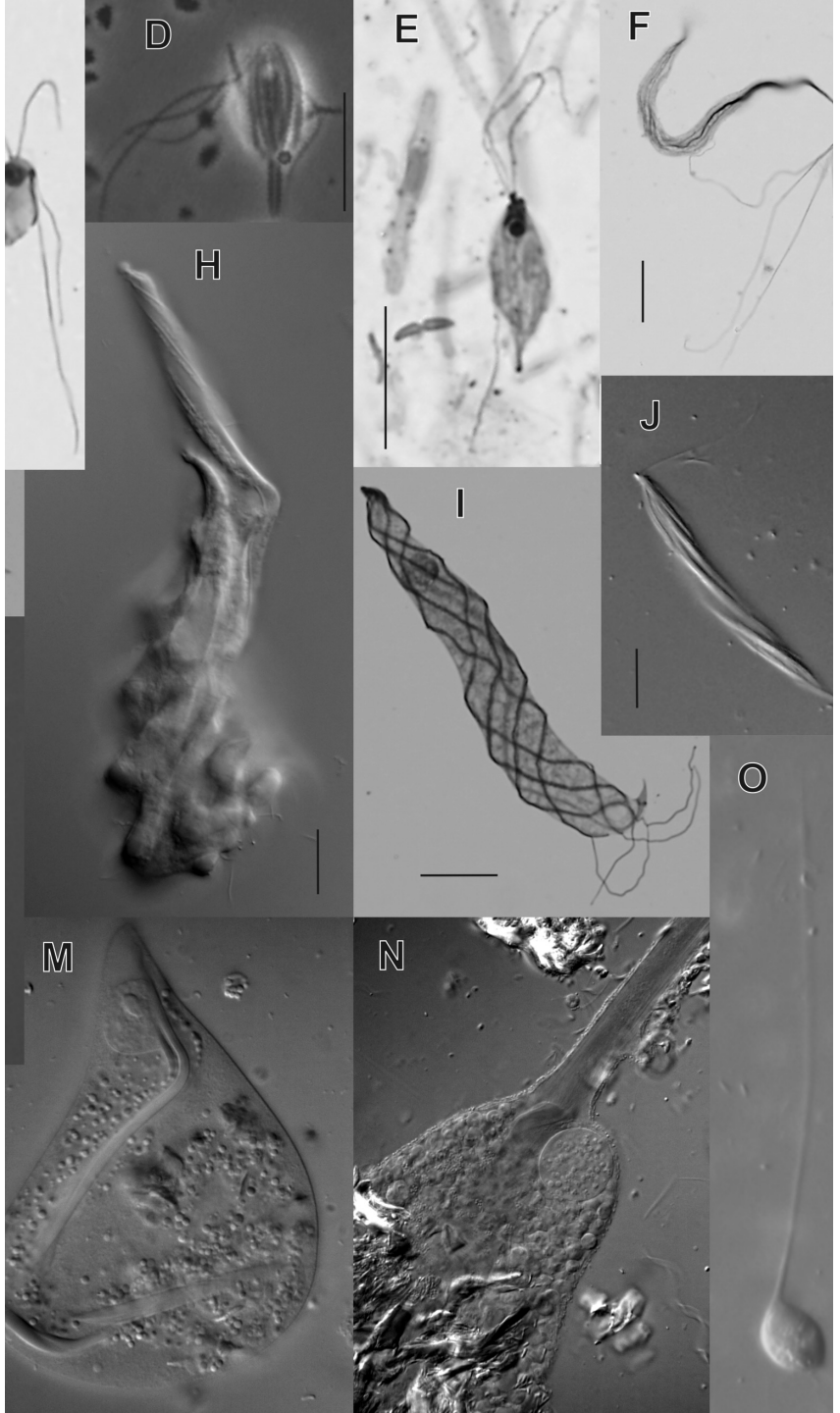

Baldauf 2003




# Holy Grail of "Excavata"

- 143 gene sumermatrix
- maximum likelihood method, using RAxML under WAG+ Γ model
- Bayesian analyses, implemented in PhyloBayes version 2.1c employing the CAT+ Γ model

Hampl et al. 2009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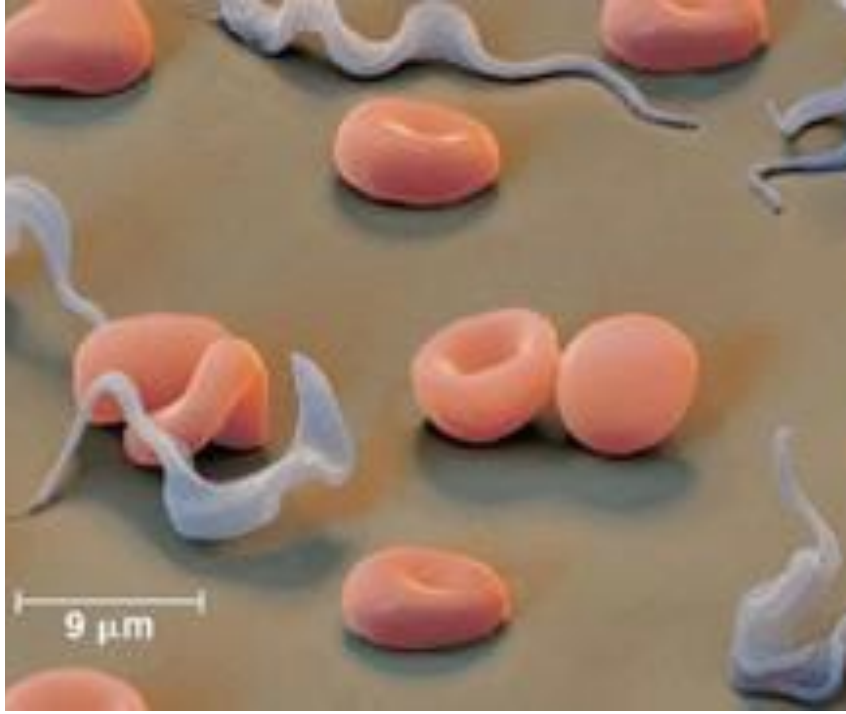
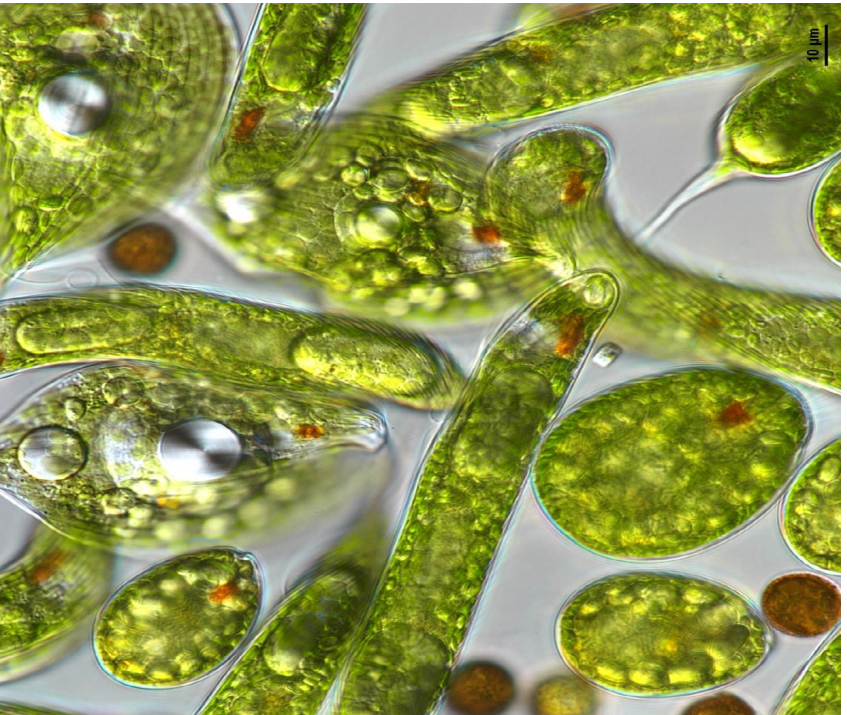
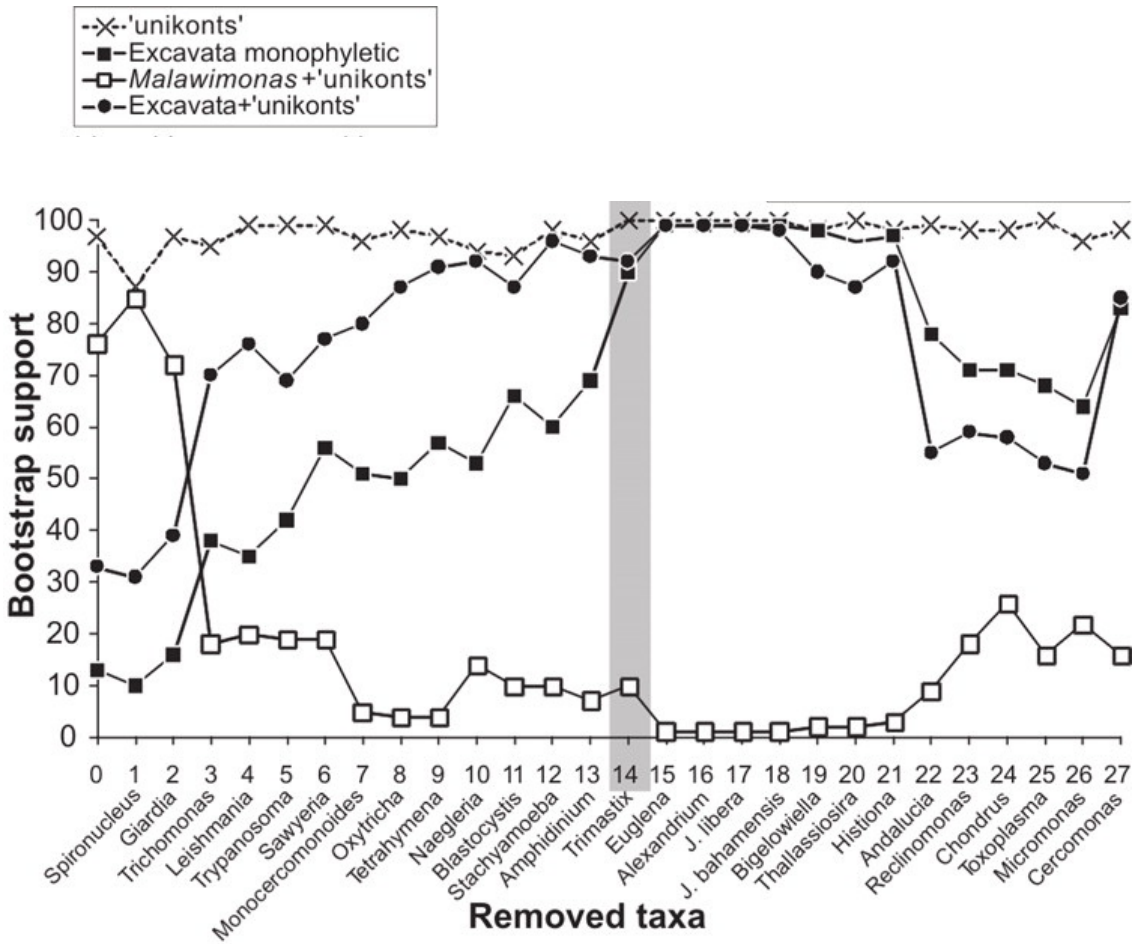
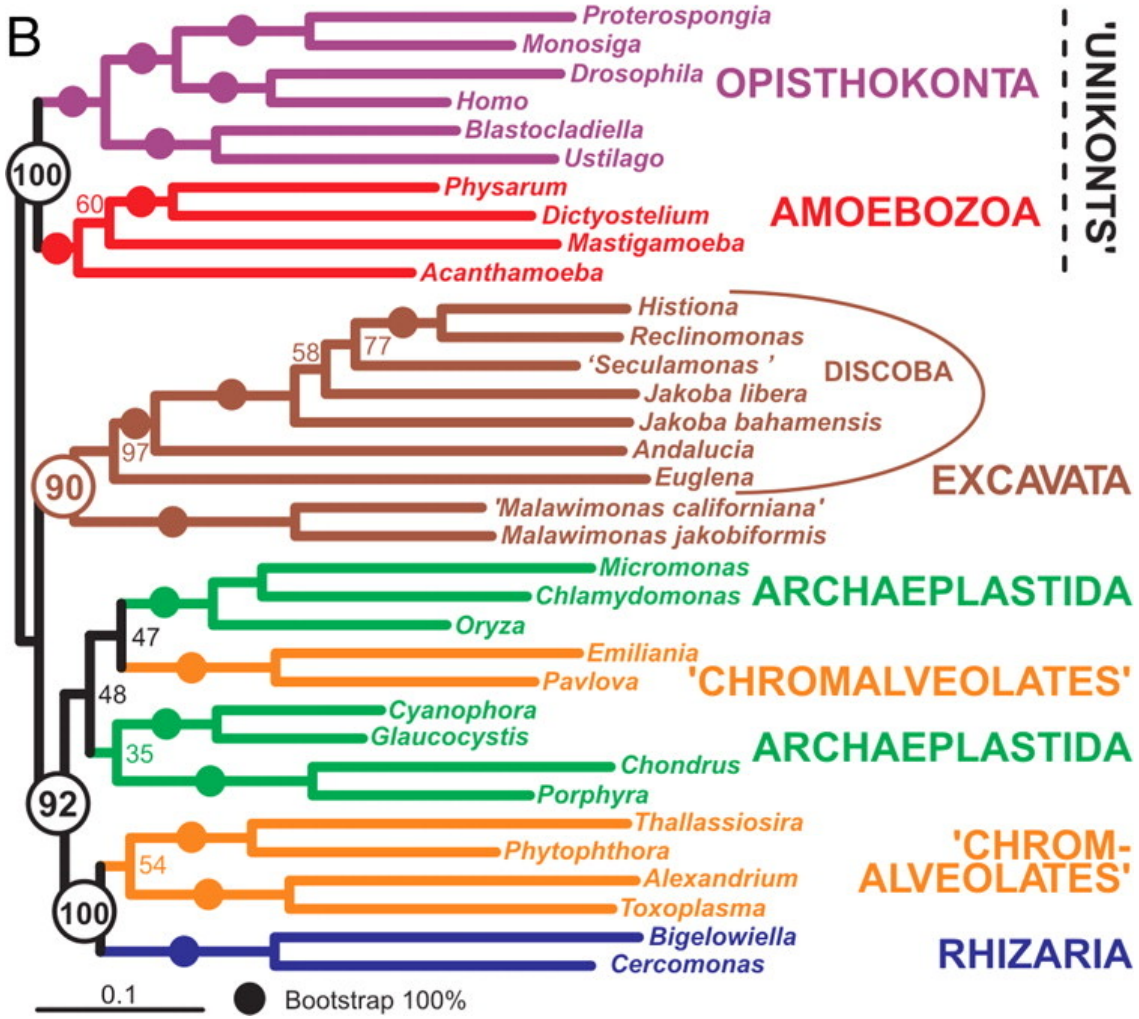

9 µm


10 µm

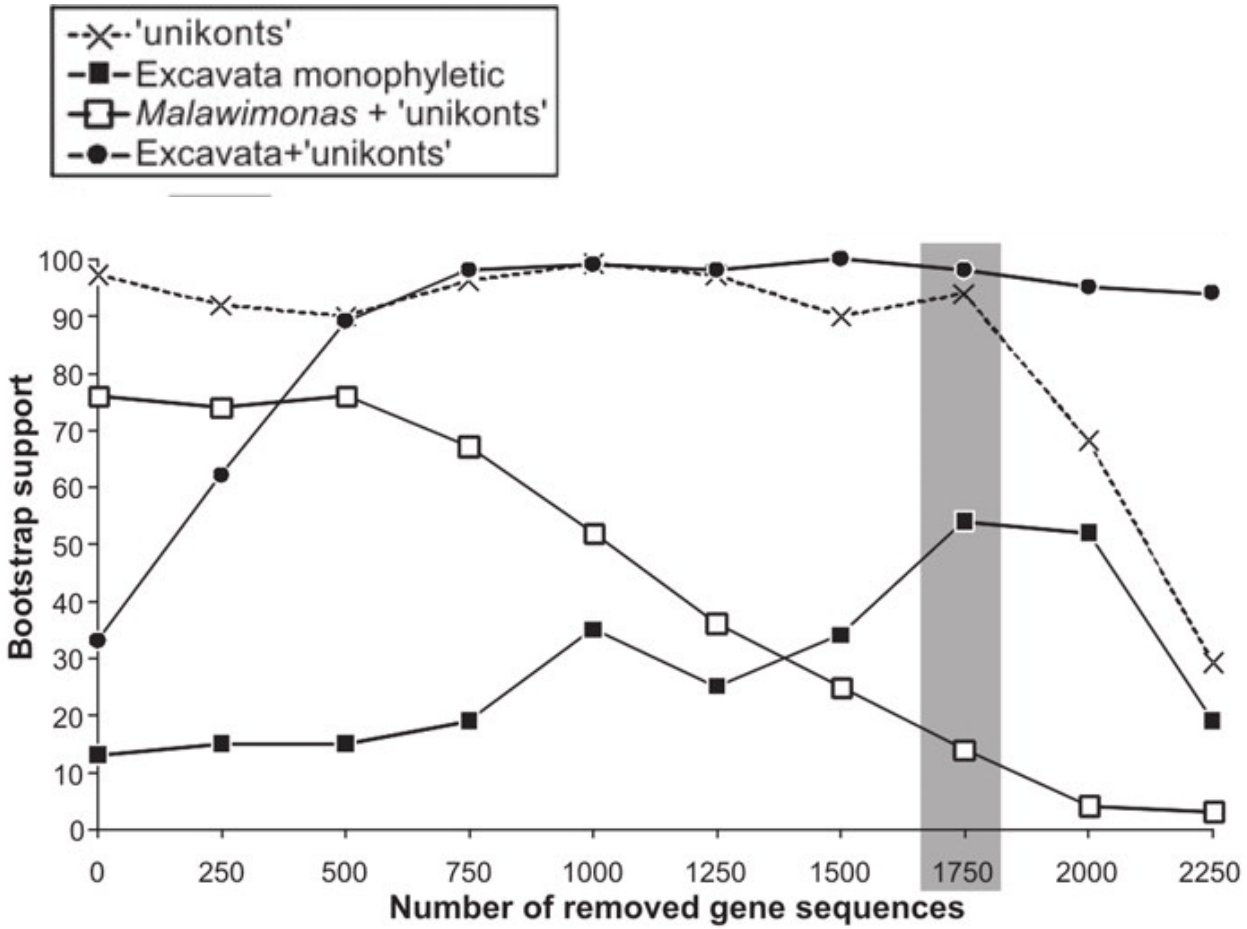
# Removal of long-branch taxa

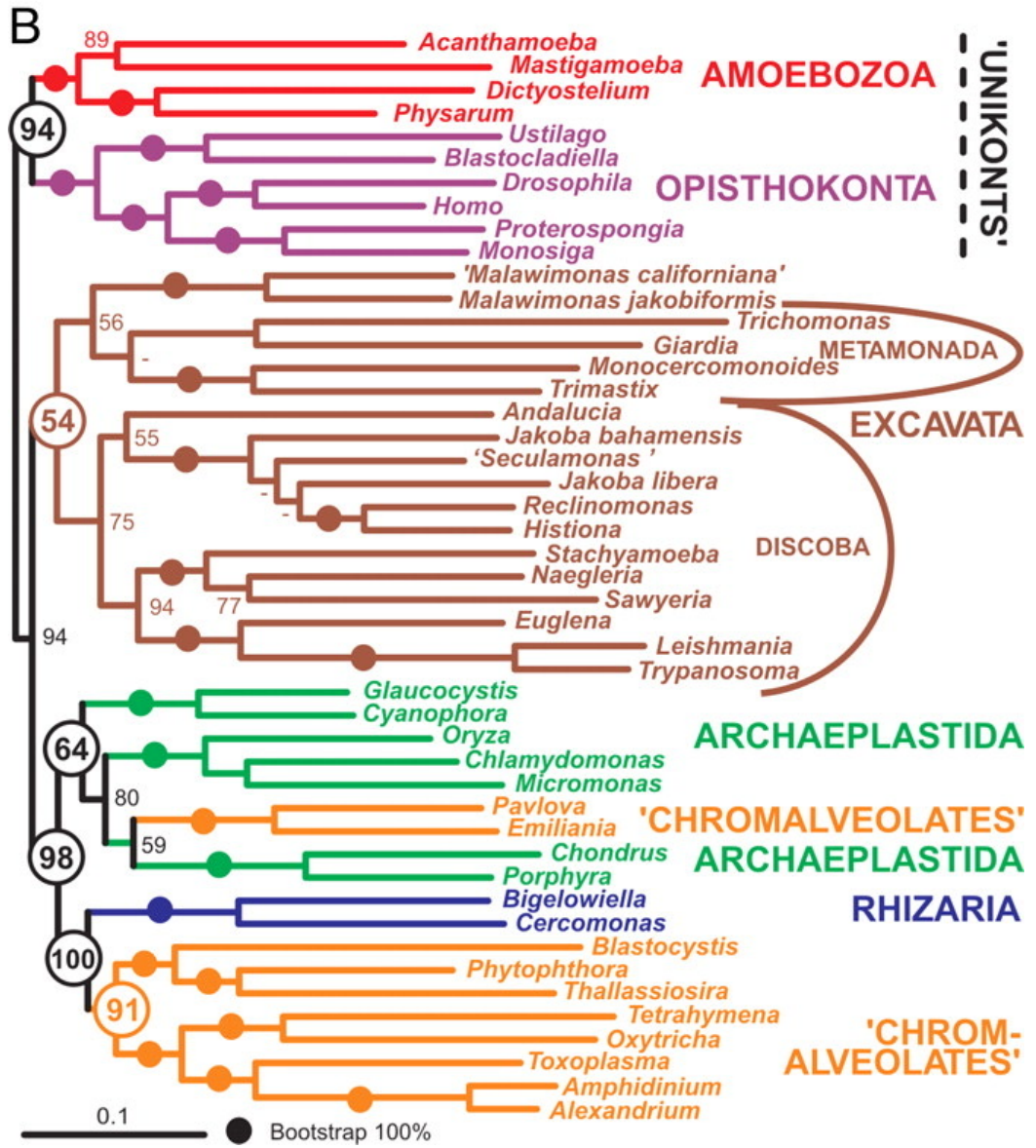



Hampl et al. 2009

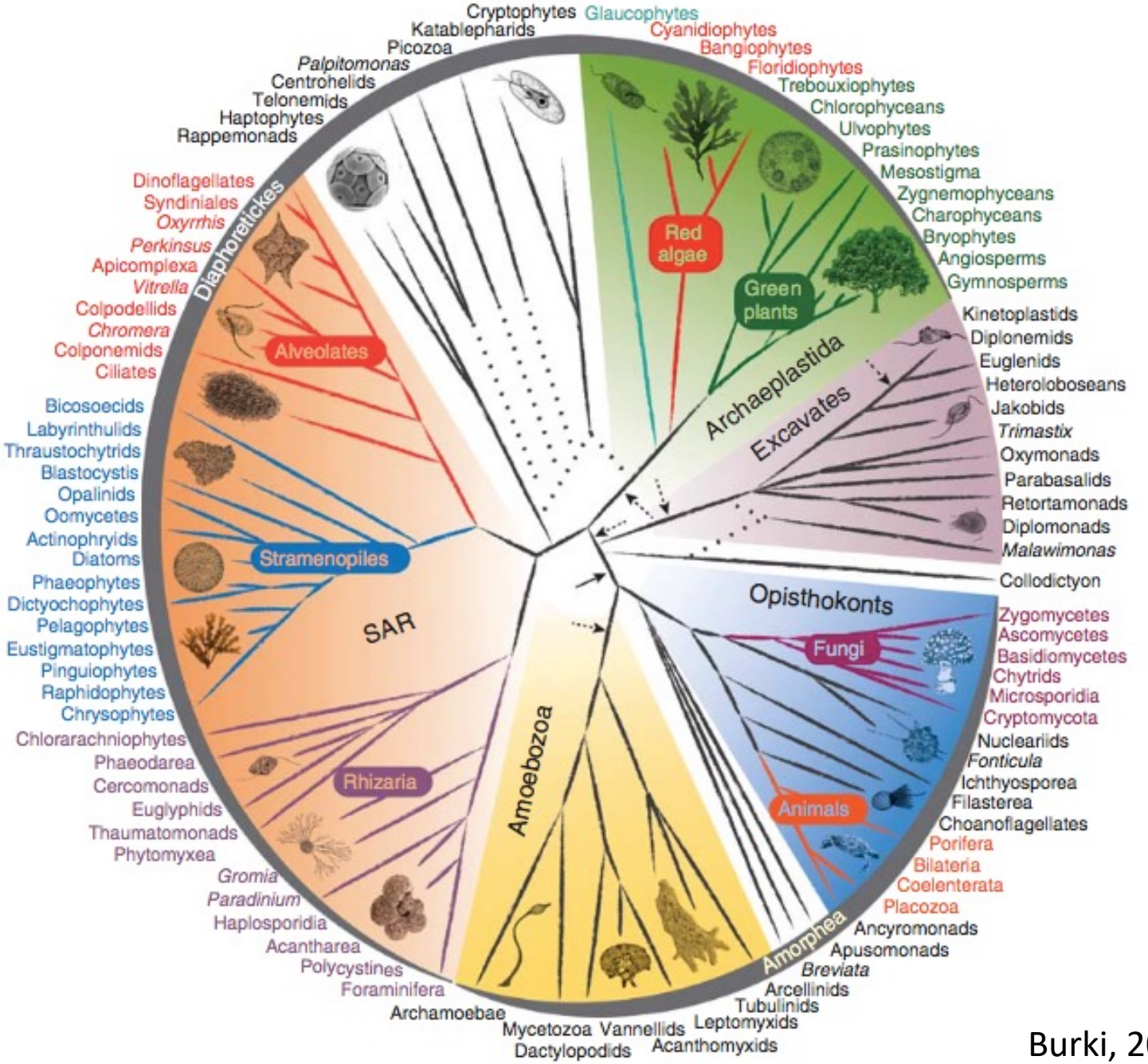
# Removal of long-branch gene sequences




Hampl et al. 2009

- Many of the general biases that apply to single-gene phylogenetics are exacerbated in a phylogenomic context
- The goal of a phylogenetic inference is to minimize the noise and maximize the true phylogenetic signal




Burki, 2014

# More data & errors

- Saturated positions in the data set (stochastic errors) - arise when the number of positions in an alignment is small and the random background noise will have a neutralizing effect on the positions that contain the phylogenetic signal.

More data should have more phylogenetic signal

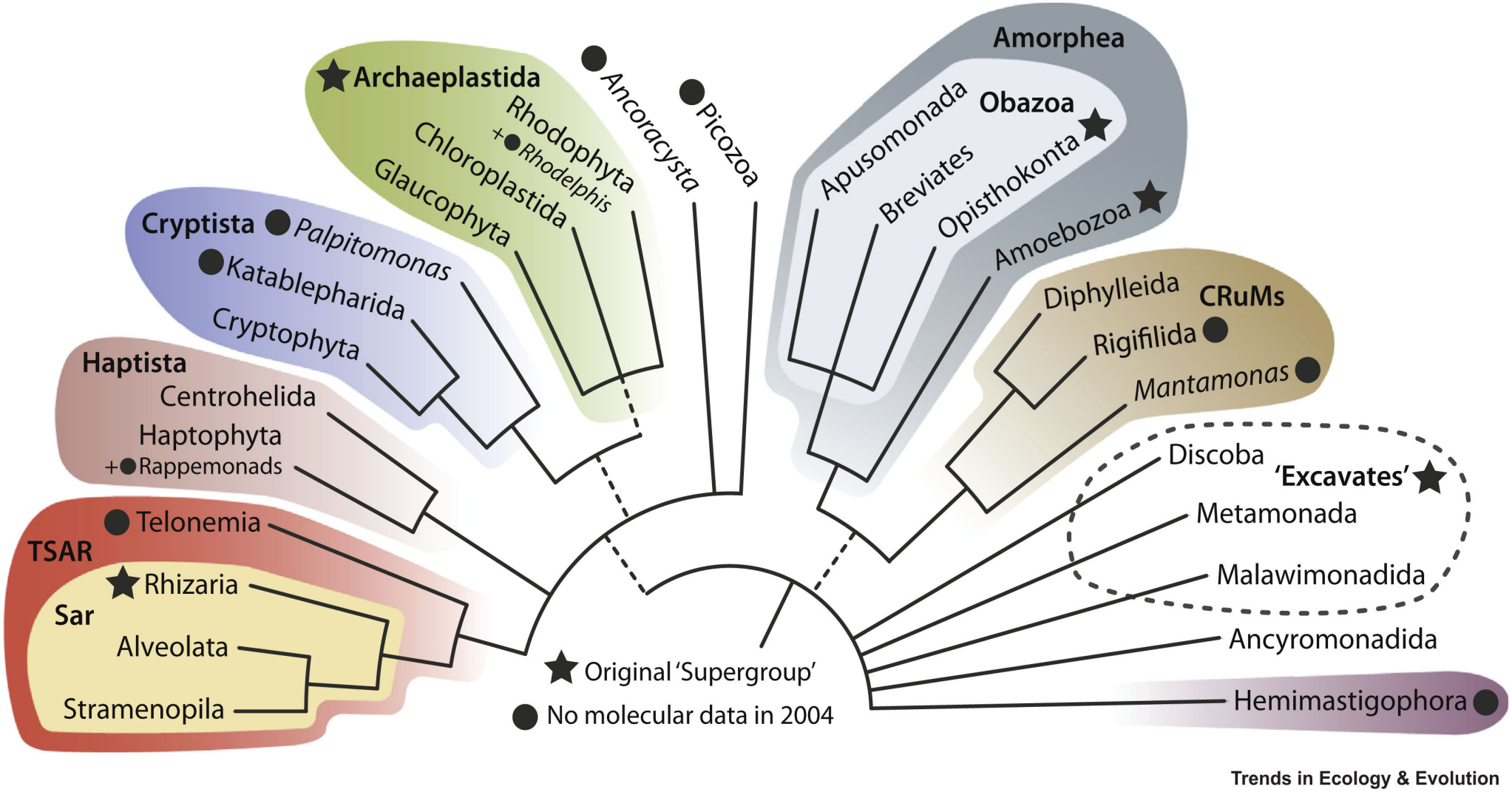
- Model misspecifications (systematic errors) - heterogeneity of nucleotide or amino acid composition, which tends to incorrectly cluster together species sharing the same composition, or the heterogeneity of the evolutionary rates, which can result in the LBA artefact.

More data do not solve systematic errors , yet since more data are available strategies to diminish the known sources of systematic errors can be applied

With more data there is a risk of amplification of errors!

Burki, 2014 & 2020

# Eukaryotic phylogeny based on genomic and transcriptomic data



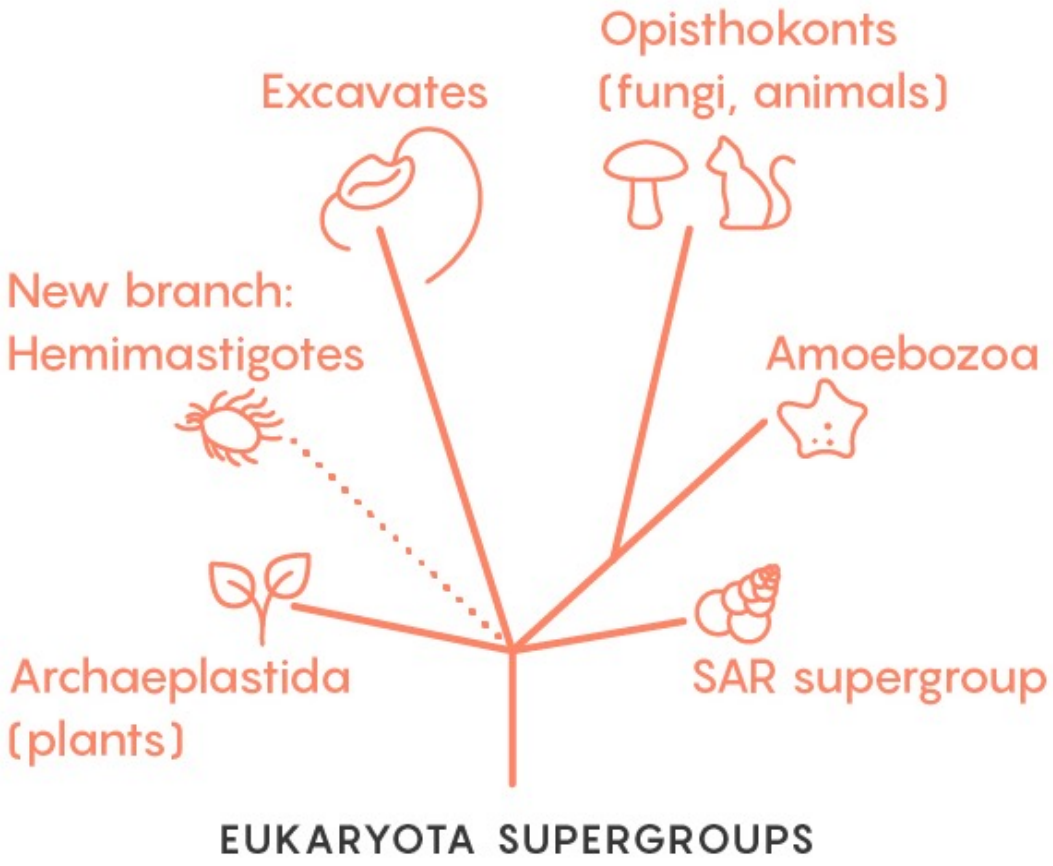

*Trends in Ecology & Evolution* 2020 3543-55DOI: (10.1016/j.tree.2019.08.008)

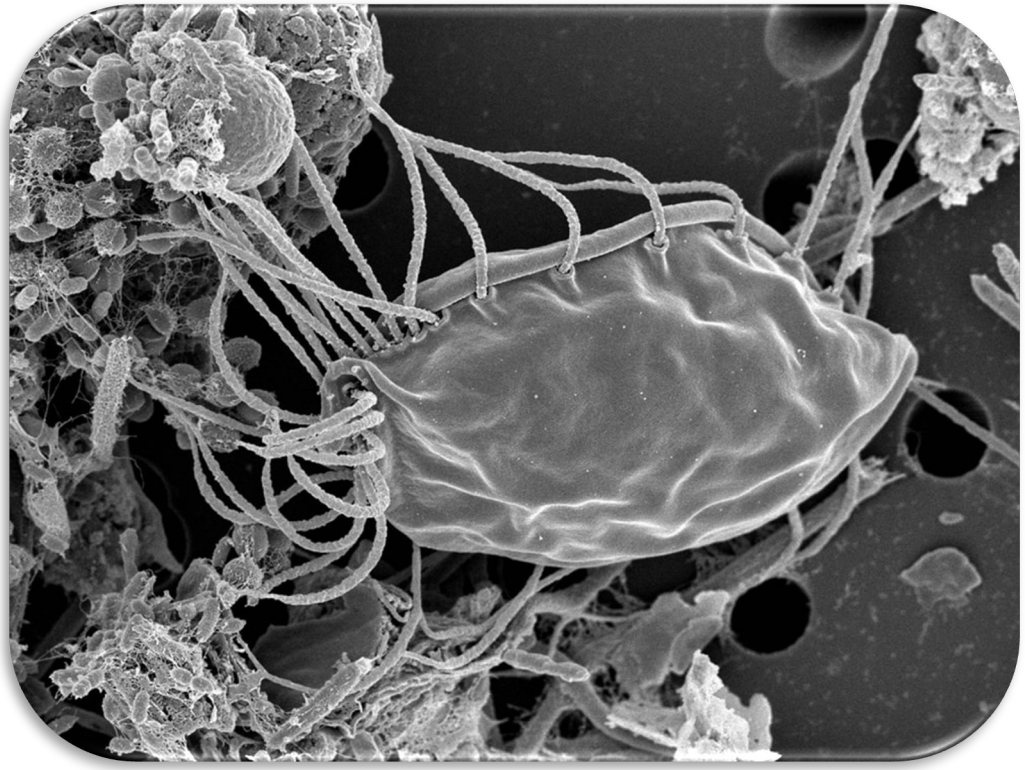
# Typical pipeline

1. Inferred amino acid sequences of proteins retrieved from genomic or transcriptomic data
2. Adding sequences from new taxa to the well-curated sets of orthologous genes
3. Single-gene trees analysis to identify lateral gene transfers, incorrect paralog selections, and various contaminants (still mainly manual).
4. A subset of taxa is selected for the actual analysis to evenly cover the relevant phylogenetic breadth while excluding problematic species (e.g., those with limited data, extreme evolutionary rates in many genes, etc.).
5. Genes are concatenated into a phylogenomic 'supermatrix'.
6. Usually, both ML and Bayesian analyses are conducted. Various evolutionary models are employed (site-heterogeneous models), with choice often constrained by computational logistics.
7. Testing whether results are robust to perturbations of the data, especially excluding data most likely to foster incorrect phylogenetic inference (e.g., the fastest-evolving species, sites, or genes).

Burki et al. 2020

# Discoveries of new evolutionary lineages



*Hemimastix kukwesjijk*

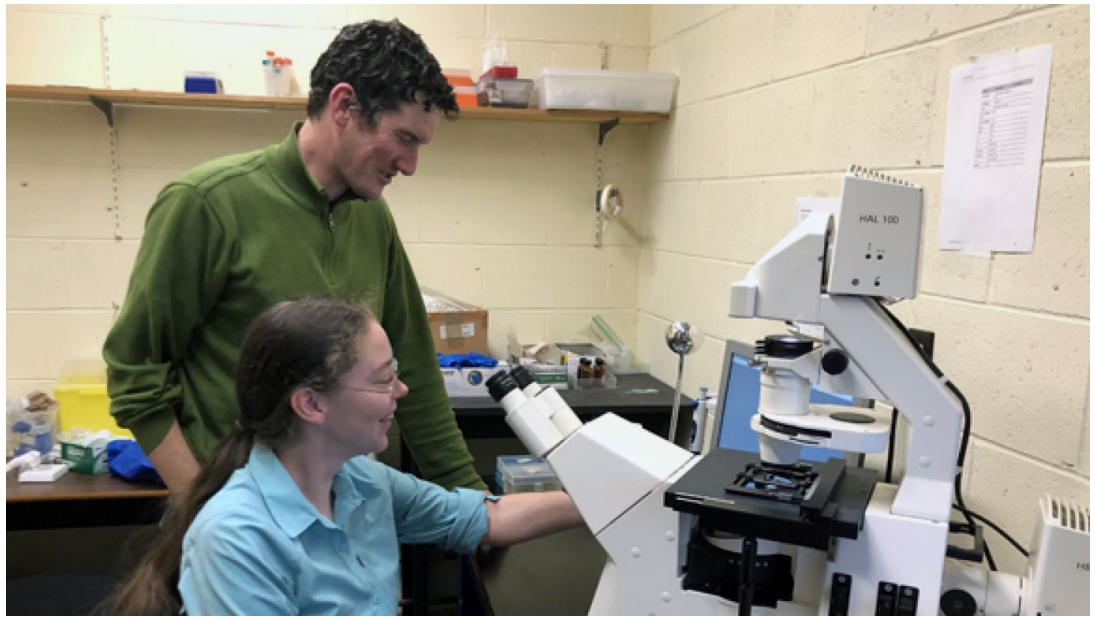
Lax et al. Nature, 2018

# Hemimastigophora is a novel supra-kingdom-level lineage of eukaryotes

Gordon Lax, Yana Eglit, Laura Eme, Erin M. Bertrand, Andrew J. Roger & Alastair G. B. Simpson

*Nature* **564**, 410–414 (2018) | Cite this article

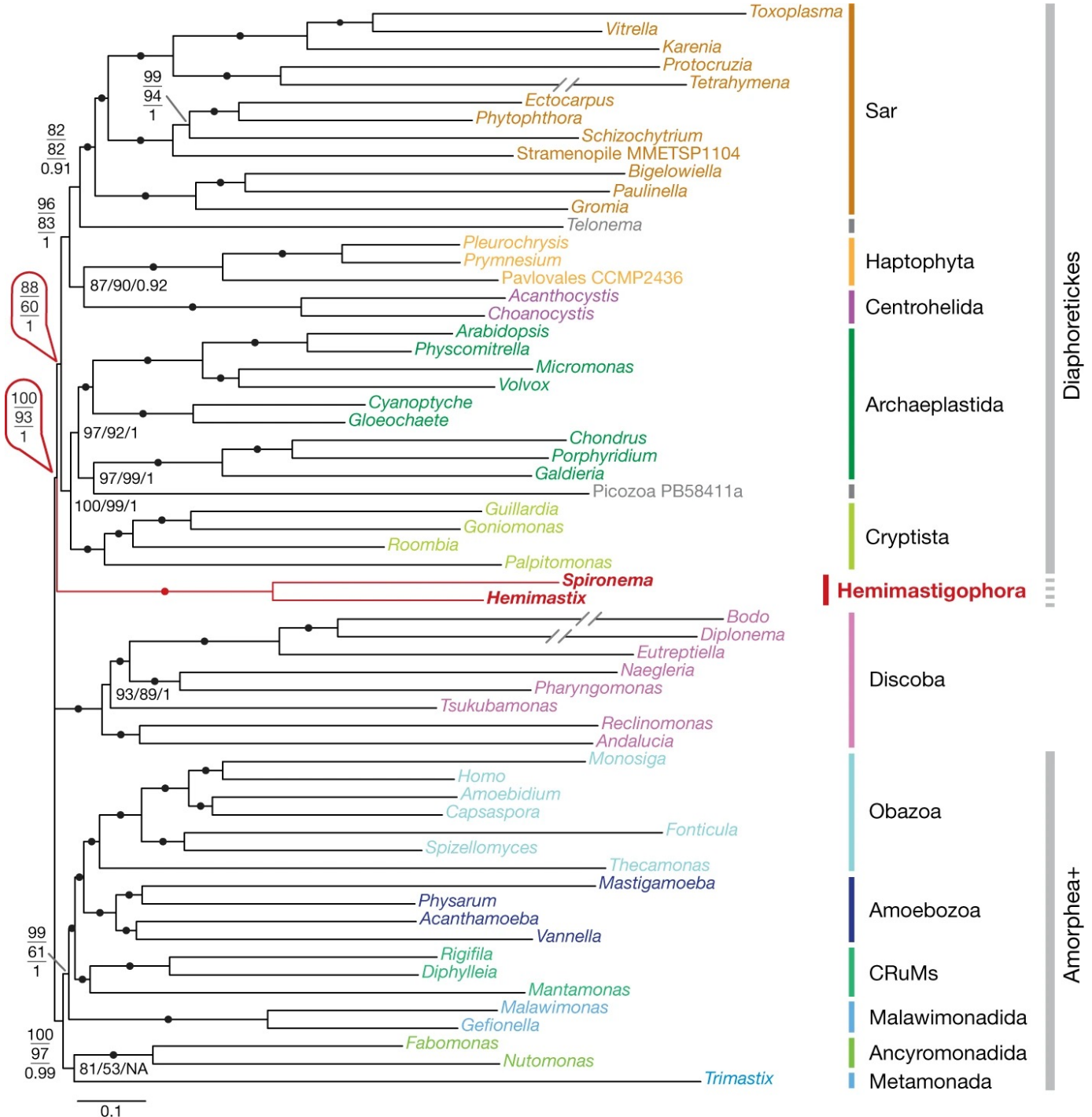
*It was a cold April day on a local trail in Nova Scotia during a hike.* ***Sporadic sampling is a known professional hazard in protistology****, since all we really need for an explosion of interesting things to look at is a few millilitres of water or dirt.*



*Yana soaked the soil in distilled water for about a month, periodically observing what was living there'. One evening, small, ~20 µm long,* ***lanceolate cells showed up that behaved not quite like any 'common' flagellate.***

# Hemimastigophora is placed outside of all established eukaryote supergroups

Unrooted phylogeny inferred from 351 genes and 61 taxa. Most of data comes from transcriptomes, *Hemimastix* and *Spironema* data from single cells!

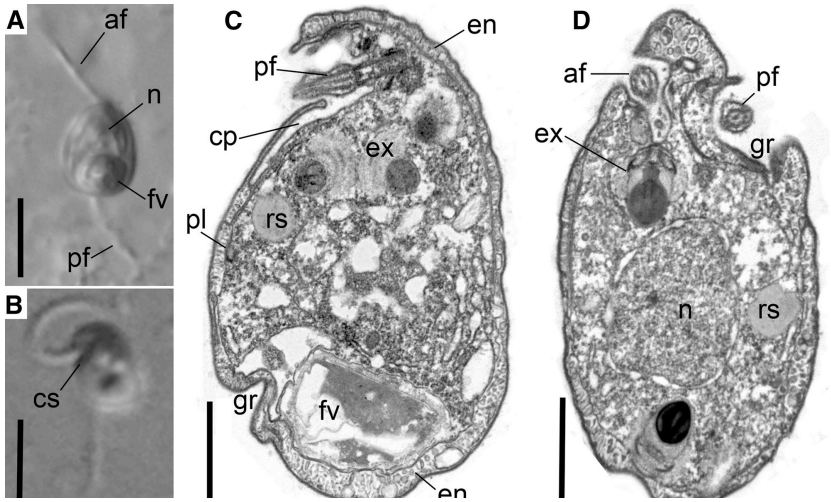


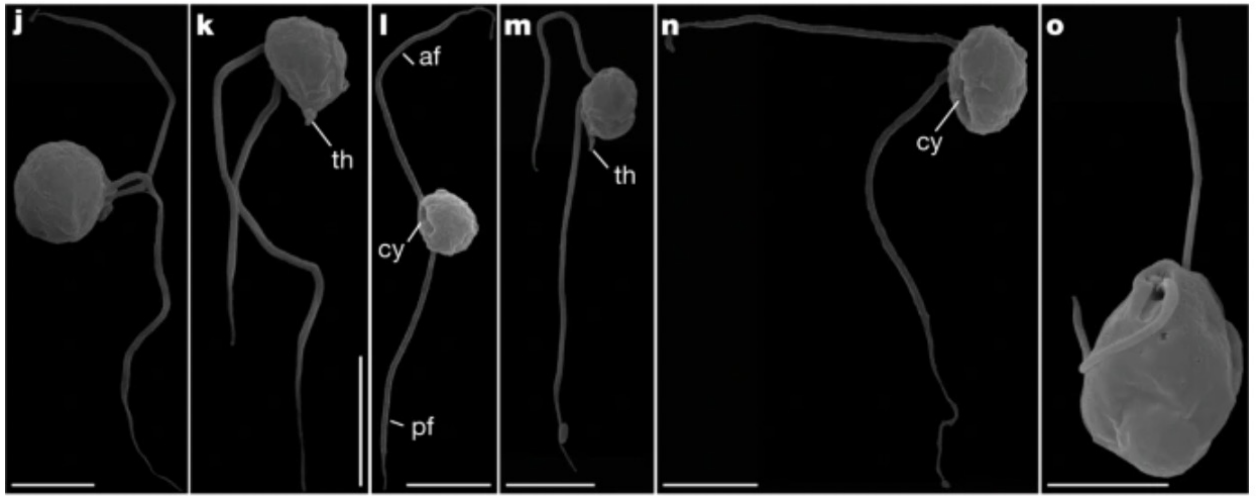

Lax et al. Nature, 2018

# Microbial predators form a new supergroup of eukaryotes

Denis V. Tikhonenkov ✉, Kirill V. Mikhailov, Ryan M. R. Gawryluk, Artem O. Belyaev, Varsha Mathur, Sergey A. Karpov, Dmitry G. Zagumyonnyi, Anastasia S. Borodina, Kristina I. Prokina, Alexander P. Mylnikov, Vladimir V. Aleoshin & Patrick J. Keeling

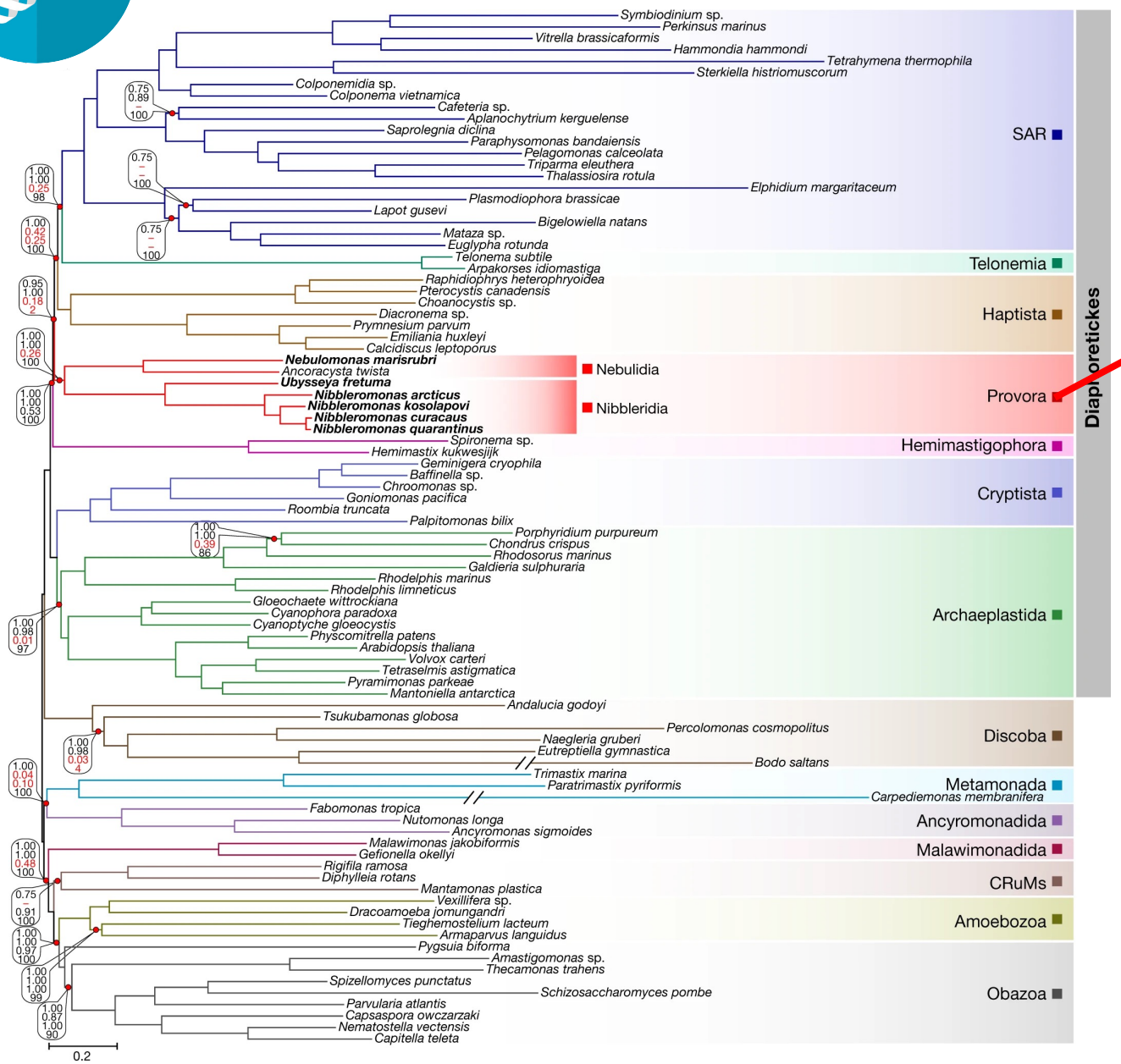
*Nature* **612**, 714–719 (2022) | Cite this article

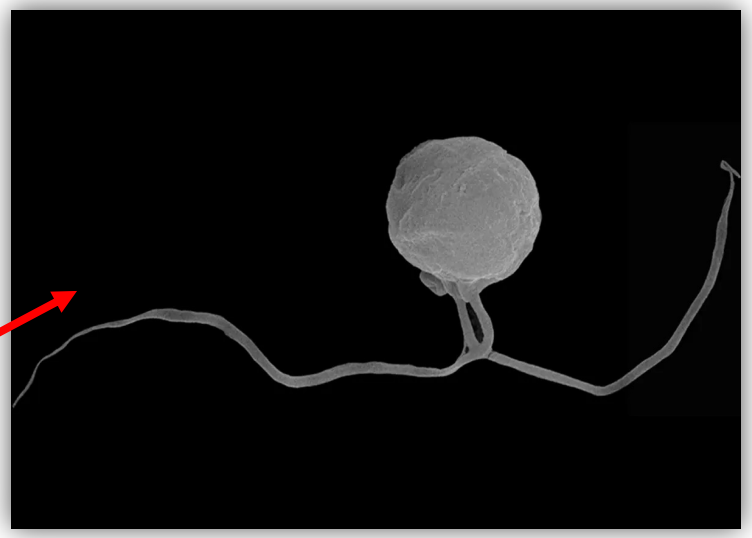




*"They have different behaviours. One group eats its prey. It literally just swallows cells whole. The other has a tooth — they'll gang up in a swarm and nibble it to death" – I prefer to call them nibblers and lions*

# Provora at the tree of eukaryotes



320 orthologous gene groups for 69 species

Bayesian inference approach implemented in PhyloBayes and the maximum-likelihood approach of IQ-TREE.

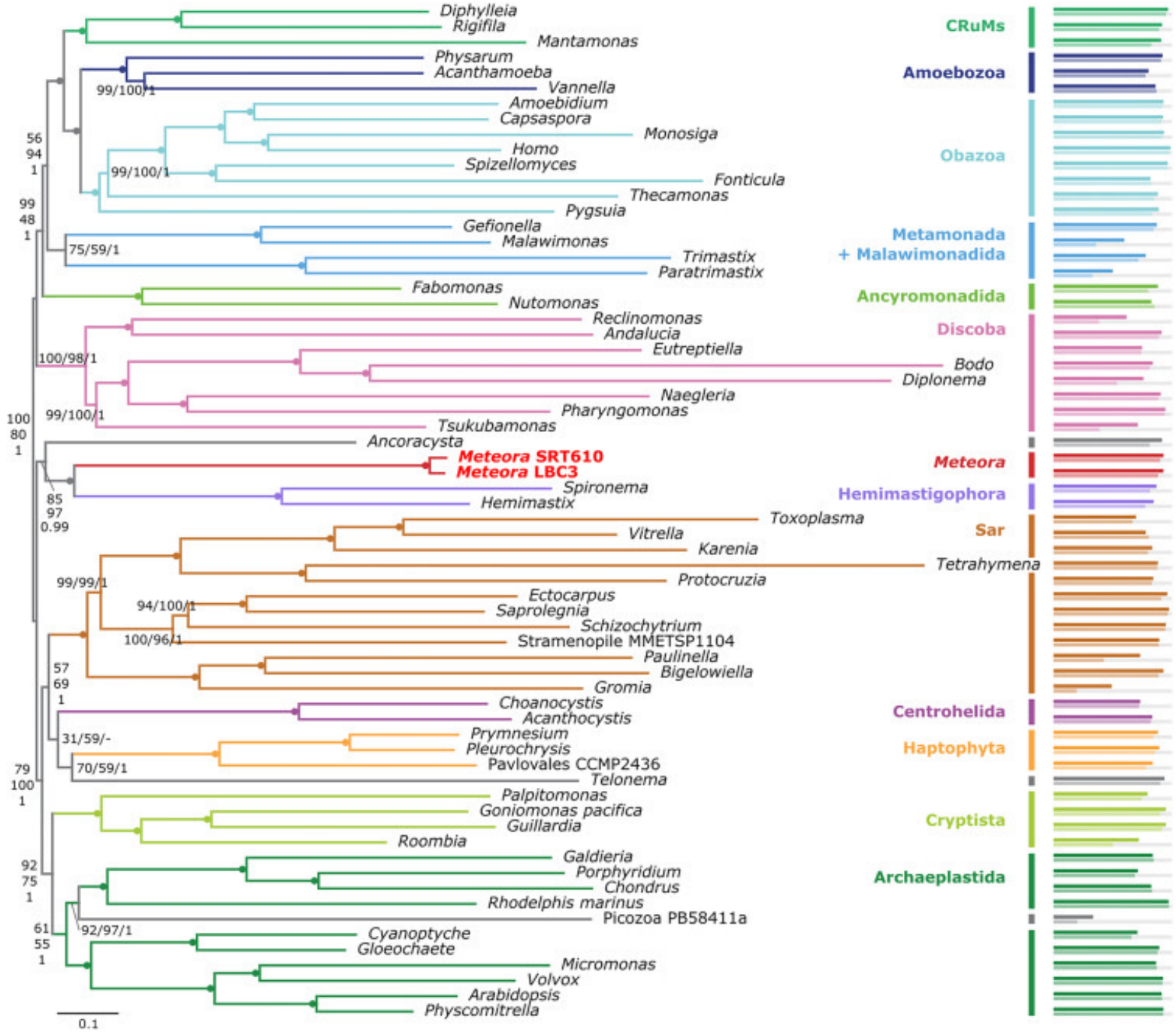
Tikhonenkov et al. 2022

# Anything new in 2024?

## Meteora!

Maximum likelihood phylogeny
70,471 sites across 254 genes over 66 taxa LG + MAM60 + Γ model

Bars on the right indicate % coverage by gene (above) and by site (below).



# Anything new in 2024?

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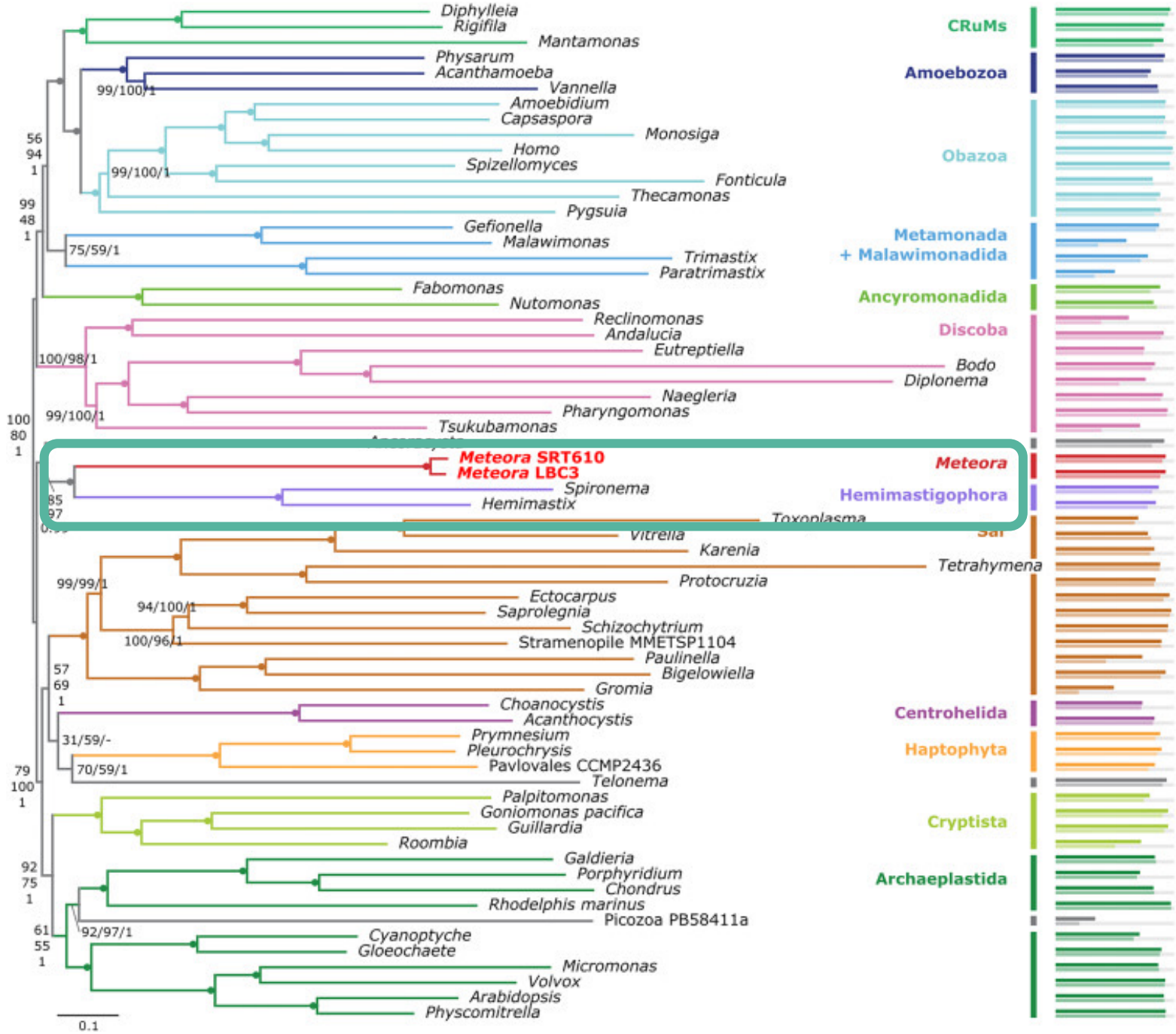
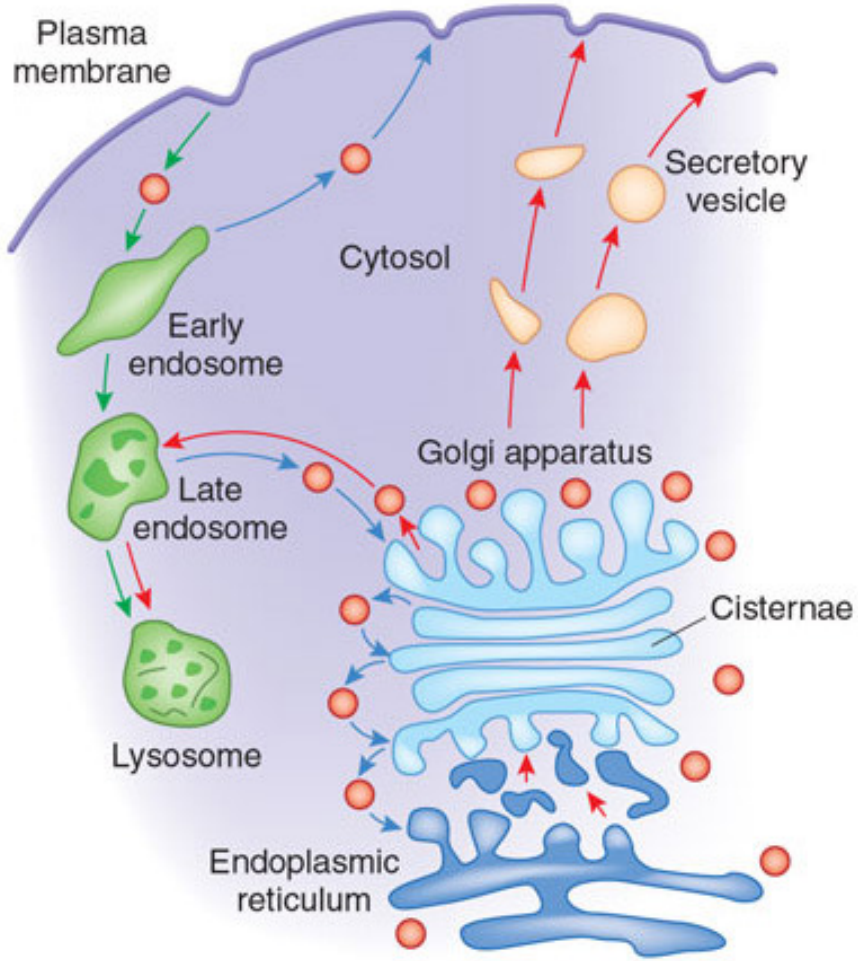


# Validating robustness of the *Meteora* + Hemimastigophora clade

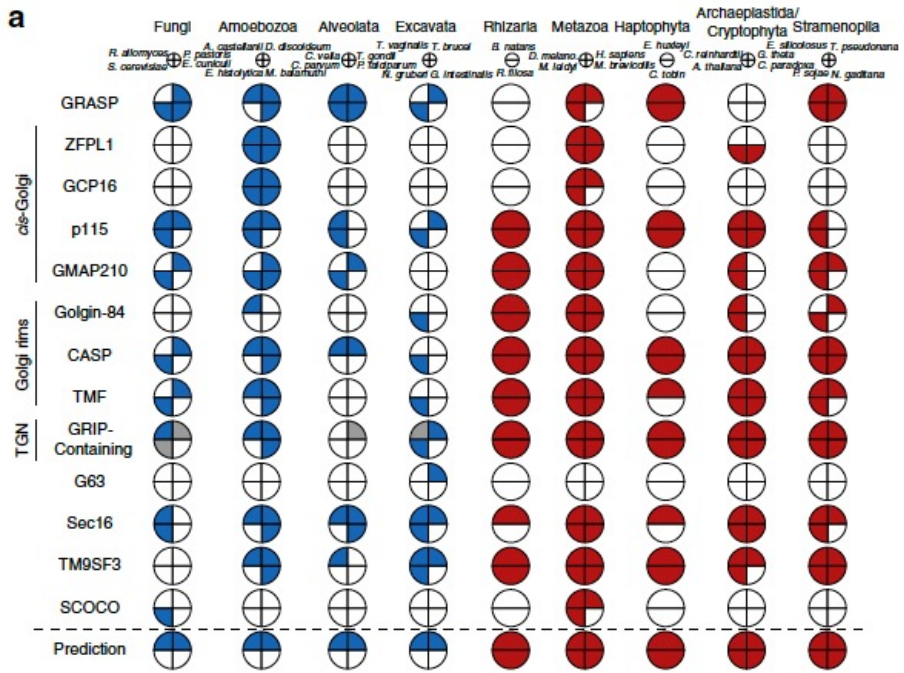
1. An analysis that excluded three taxa identified as long-branching outliers -> maximal support for the *Meteora* + Hemimastigophora clade
2. Recoding the amino acid data into a reduced alphabet of 4 classes -> robustly supported *Meteora* + Hemimastigophora
3. Removal of the fastest evolving sites in 10% increments (fast-site removal analysis) -> *Meteora* + Hemimastigophora as maximally supported until 30% sites remaining
4. Random subsampling of 50% of the genes -> robust support for *Meteora* + Hemimastigophora. The phylogenetic signal for the *Meteora* + Hemimastigophora relationship is broadly distributed across genes.

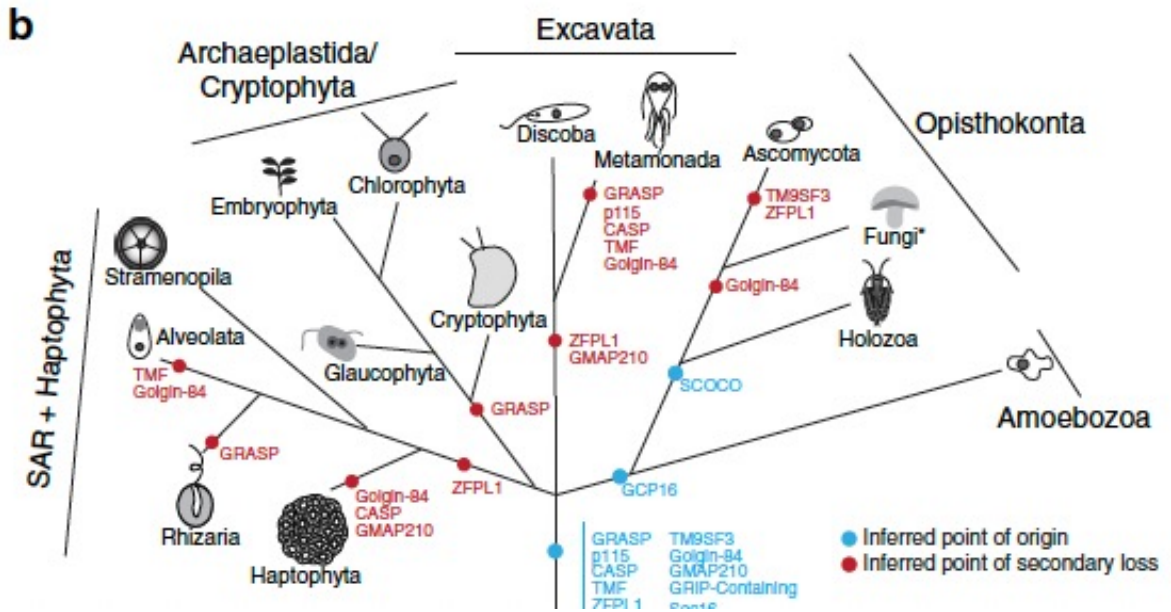
Why do we need well resolved  tree of eukaryotes?

# Evolution of cellular systems
# Intracellular transport



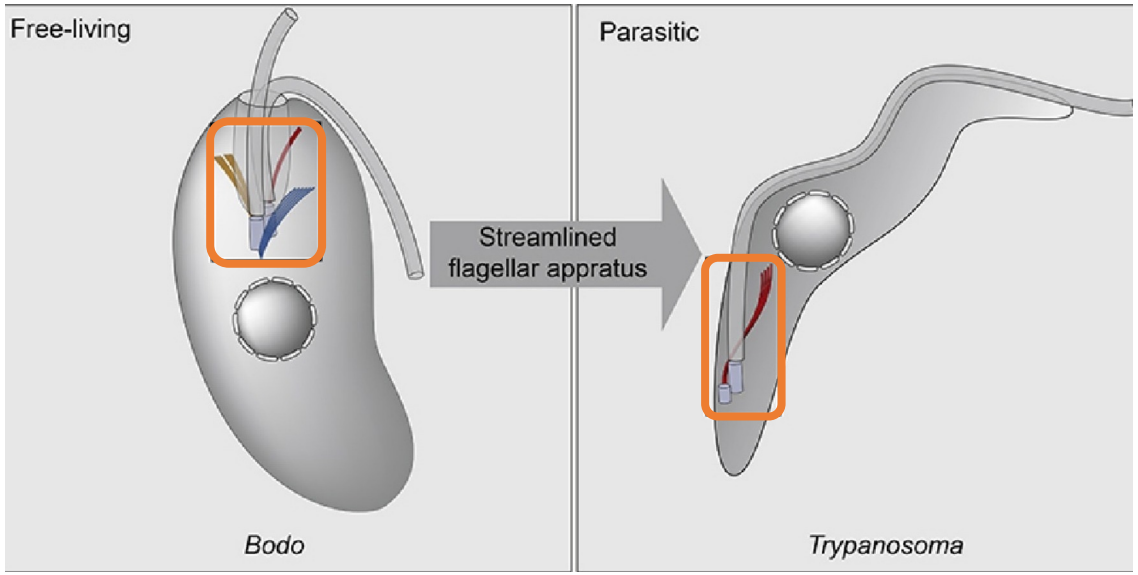

https://www.nature.com/scitable/topicpage/how-do-proteins-move-through-the-golgi-14397318/

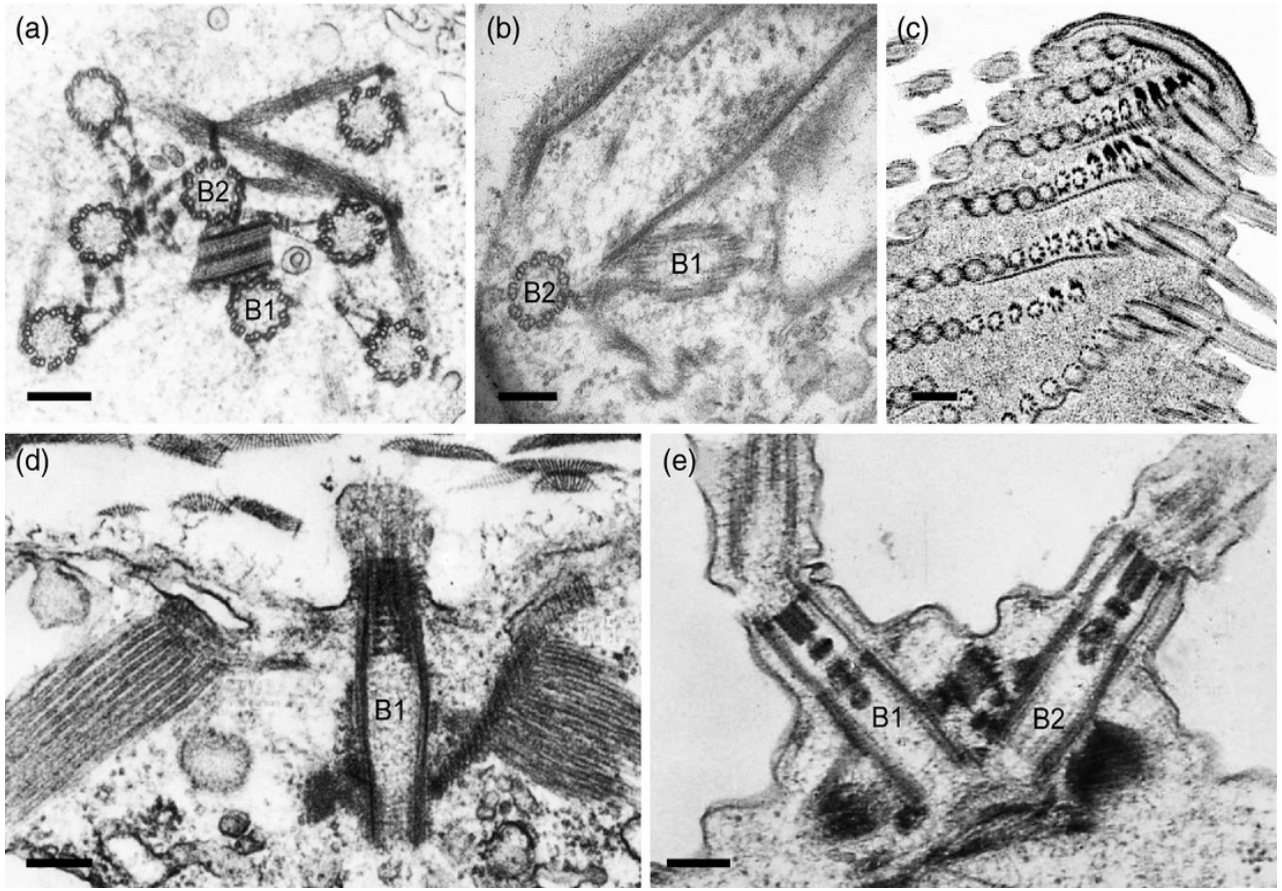



Barlow et al. 2018

# Flagellar aparatus

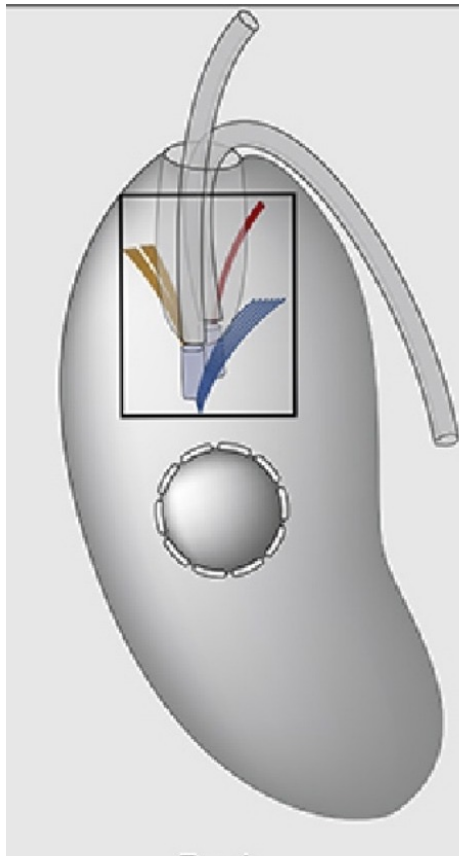


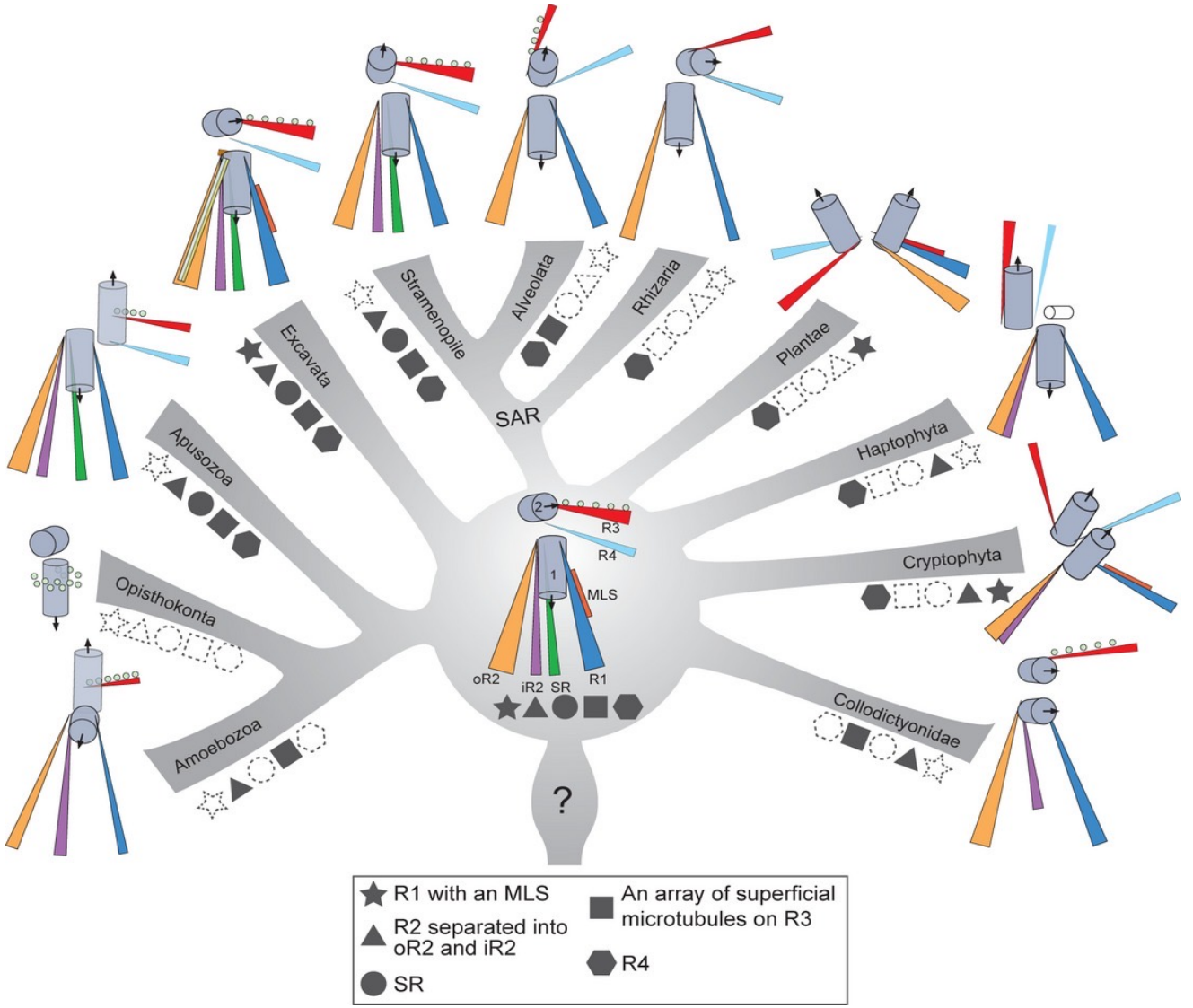




Transmission electron microscope micrograph

Yubuki & Leander, 2013

# Reconstruction of the cytoskeleton supporting the flagellar apparatus

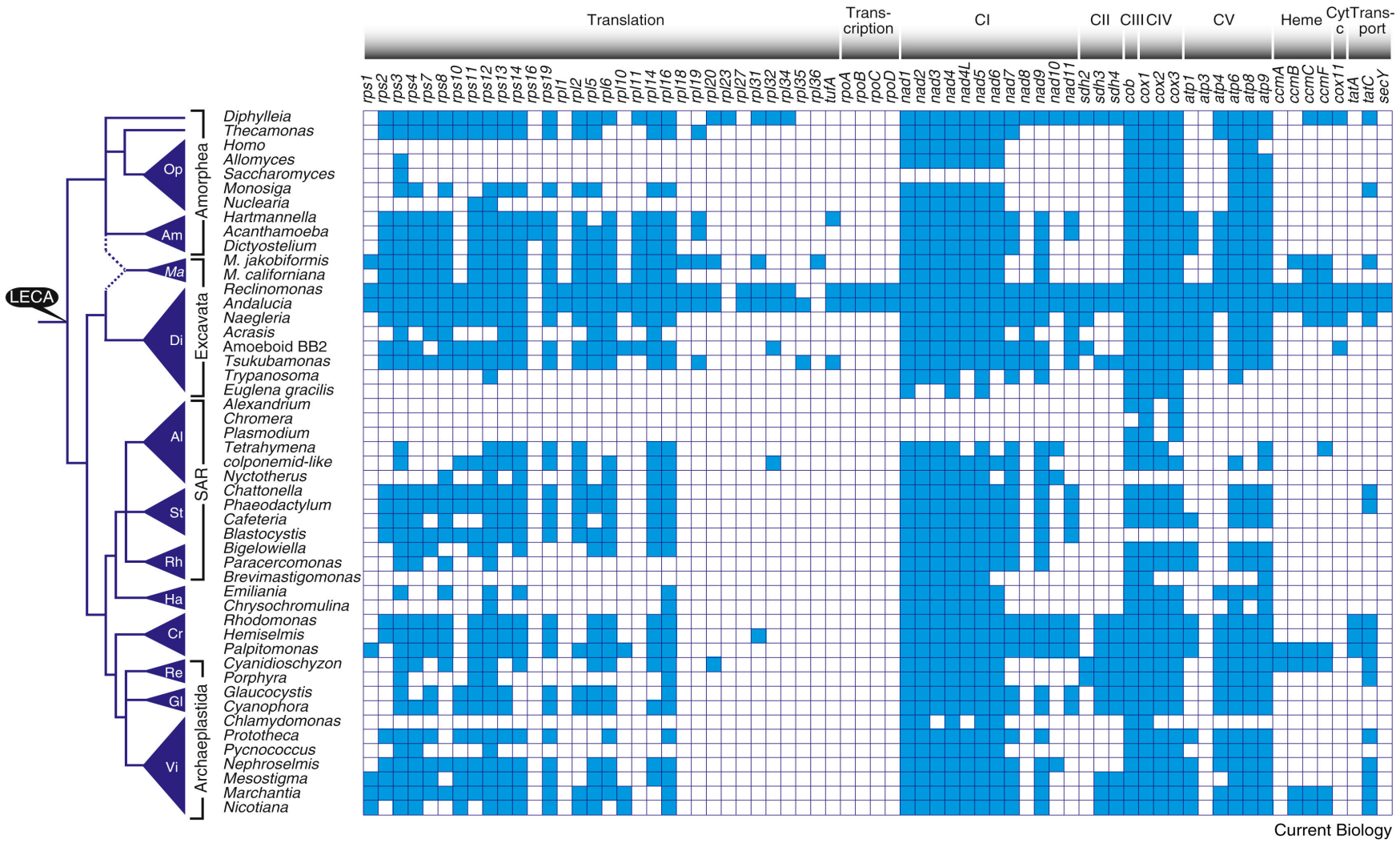





Yubuki & Leander, 2013

# Evolution of orgenelles

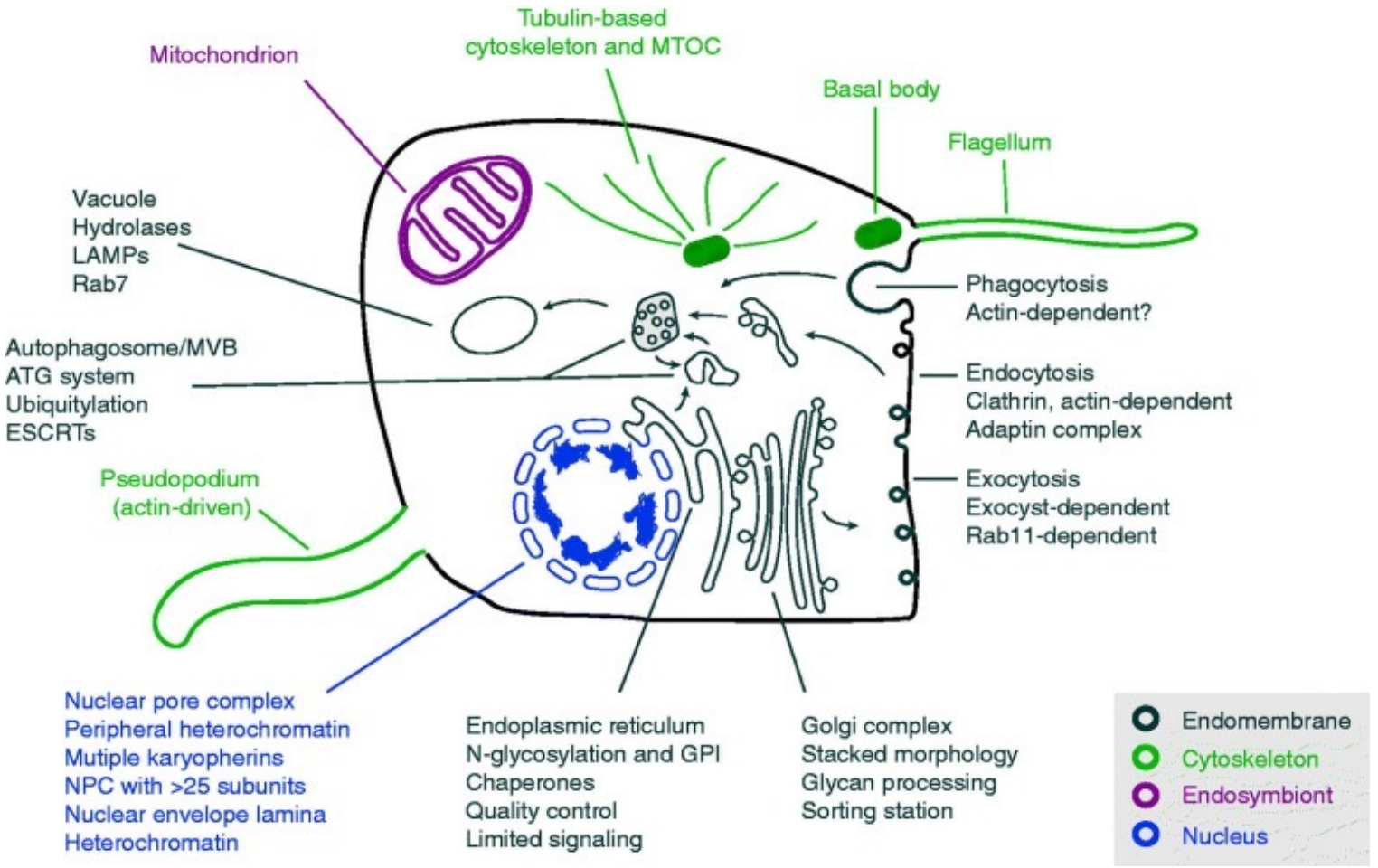
## gene content of mitochondial genome




Presence or absence of genes in mitochondrial genomes of various eukaryotes is shown by closed and open boxes, respectively.

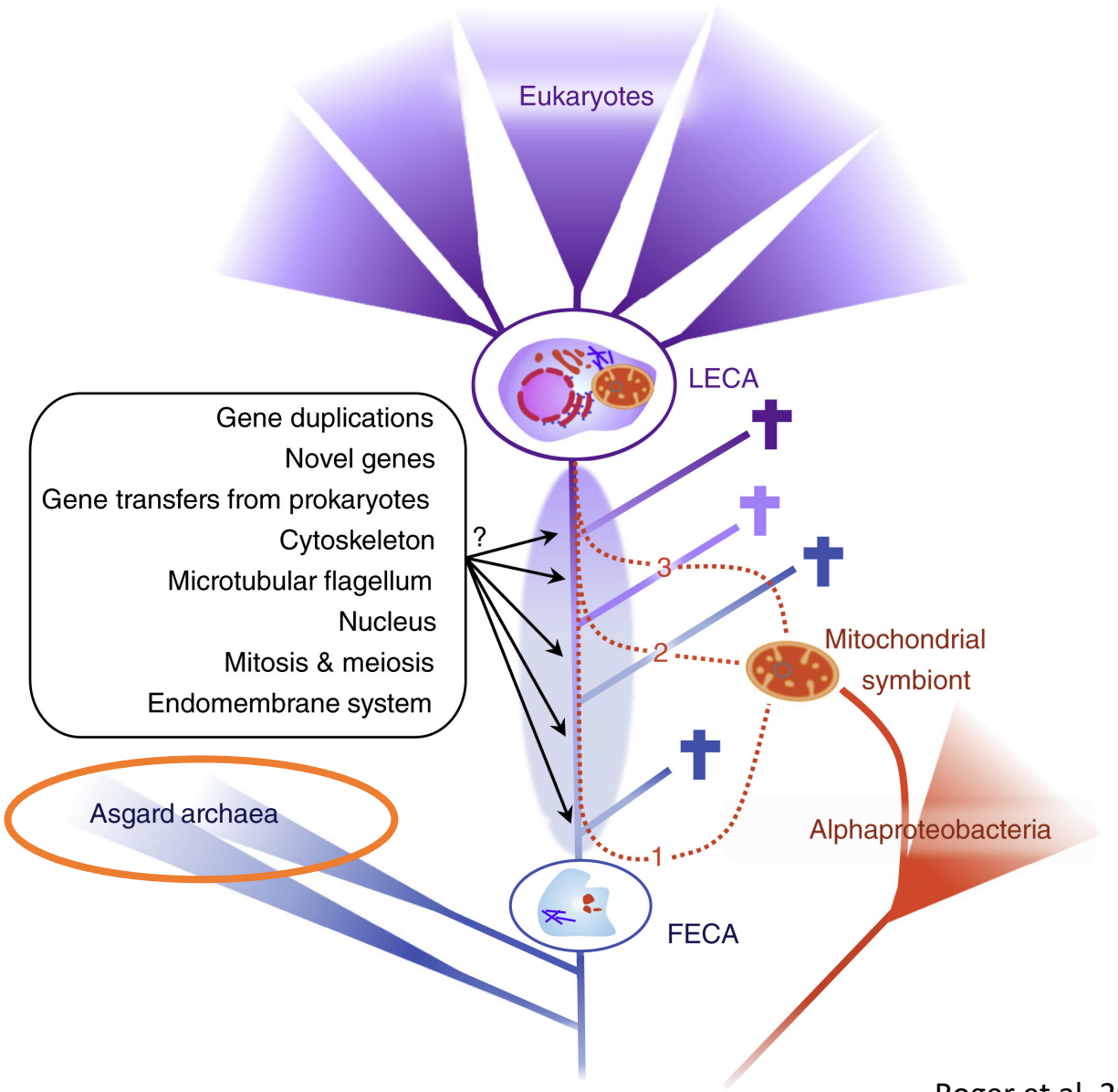
Roger et al. 2017

# With more data and well resolved tree of eukaryotes we've learned that the last common ancestor was complex eukaryotic cell

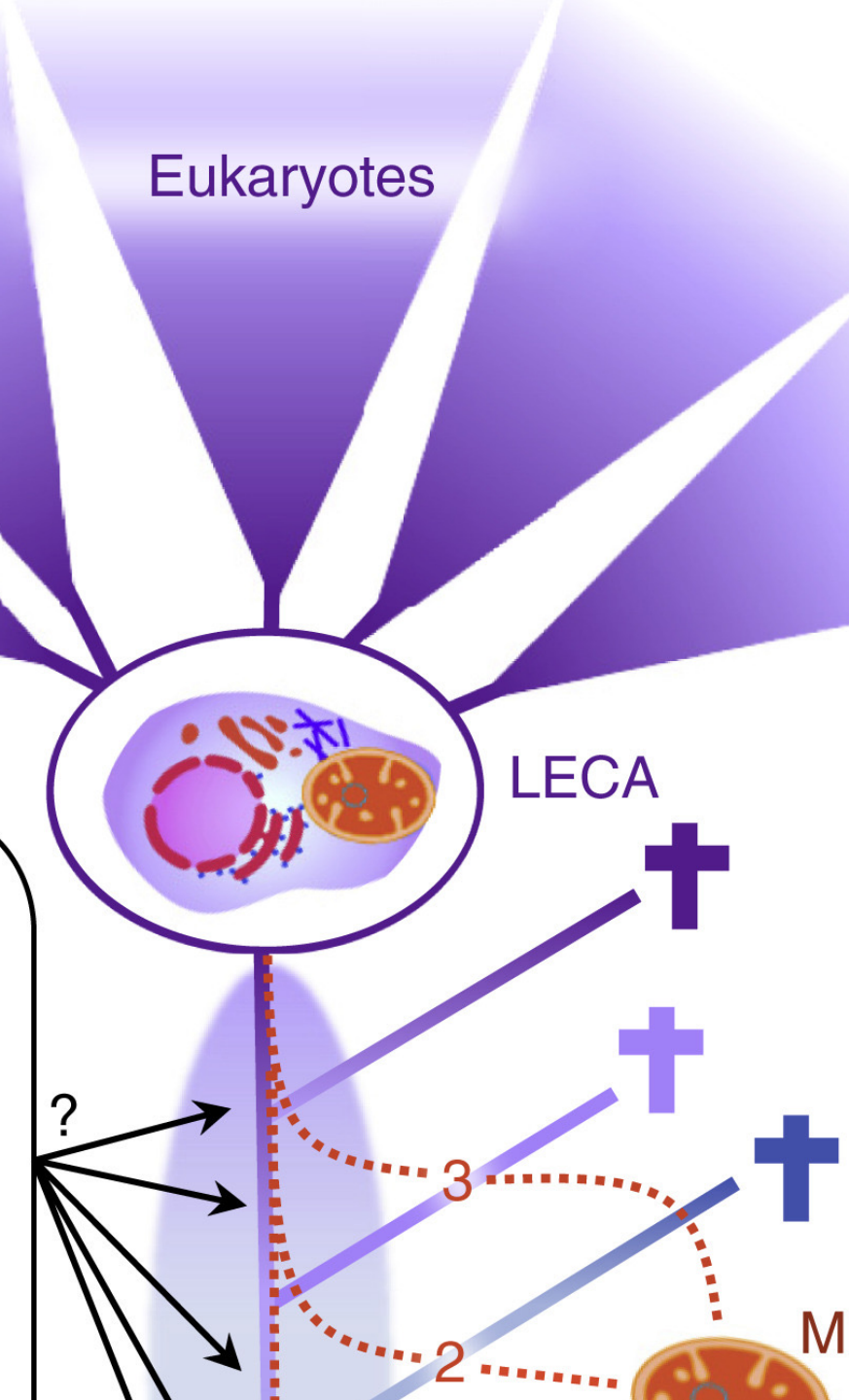



Komandou et al. 2013

# The long march of eukaryotes



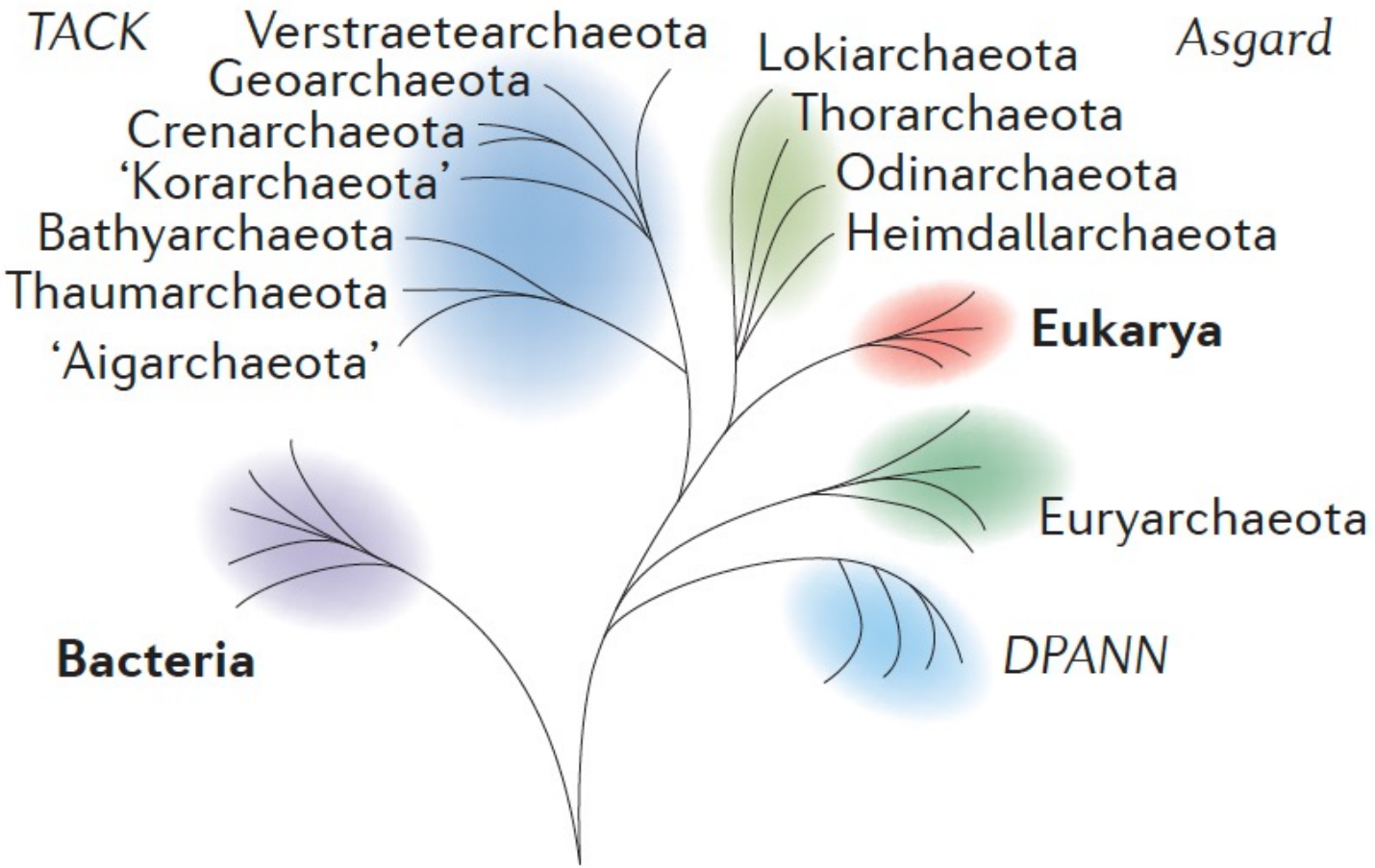

Roger et al. 2021




- Comparative genomic analyses have reconstructed a complex last eukaryotic common ancestor.
- But how and in which order these complex eukaryotic features evolved in an Asgard archaea?

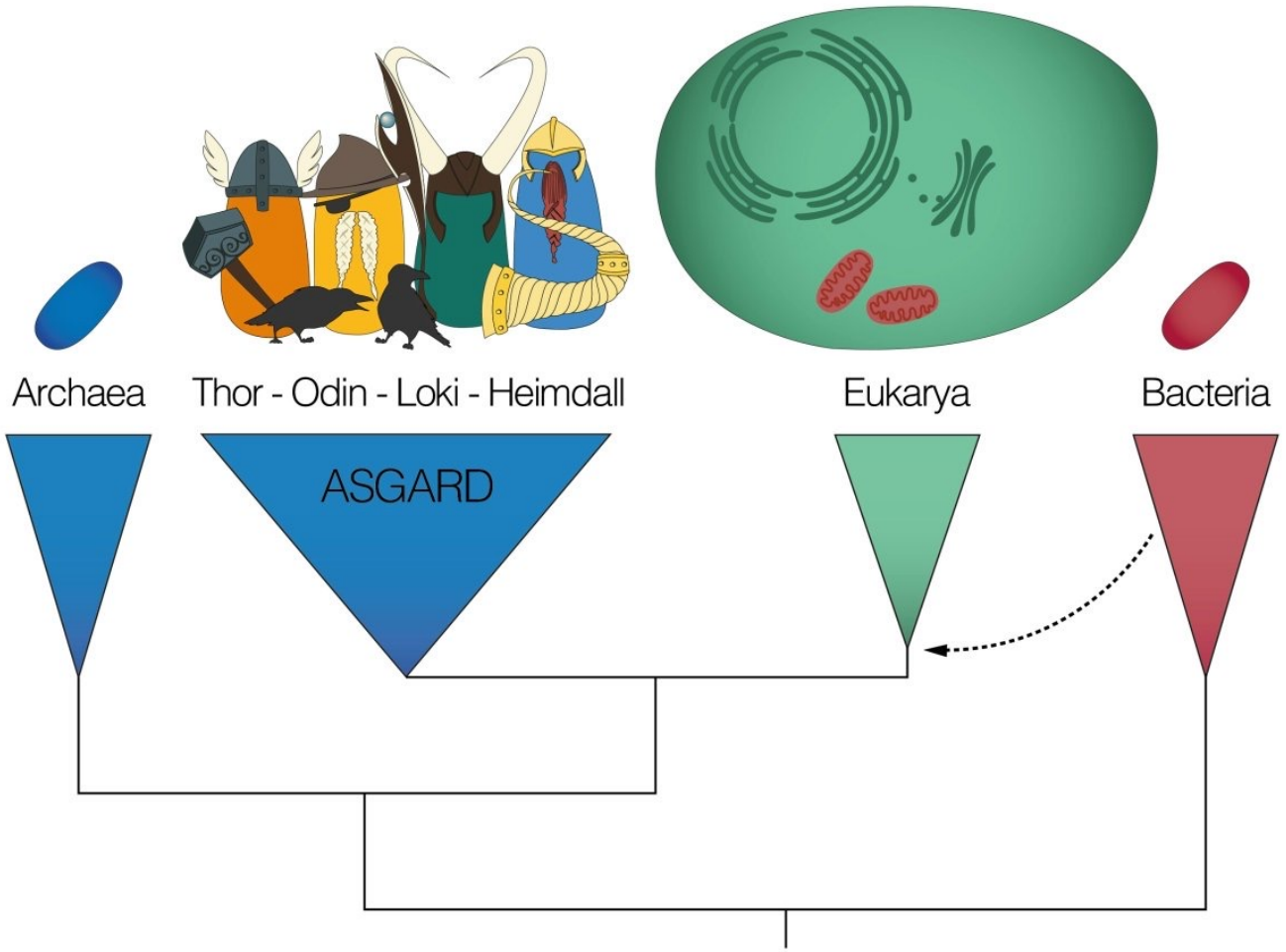
Roger et al. 2021

Metagenomics has revealed the vast diversity of Archaea, including the recently described Asgard superphylum



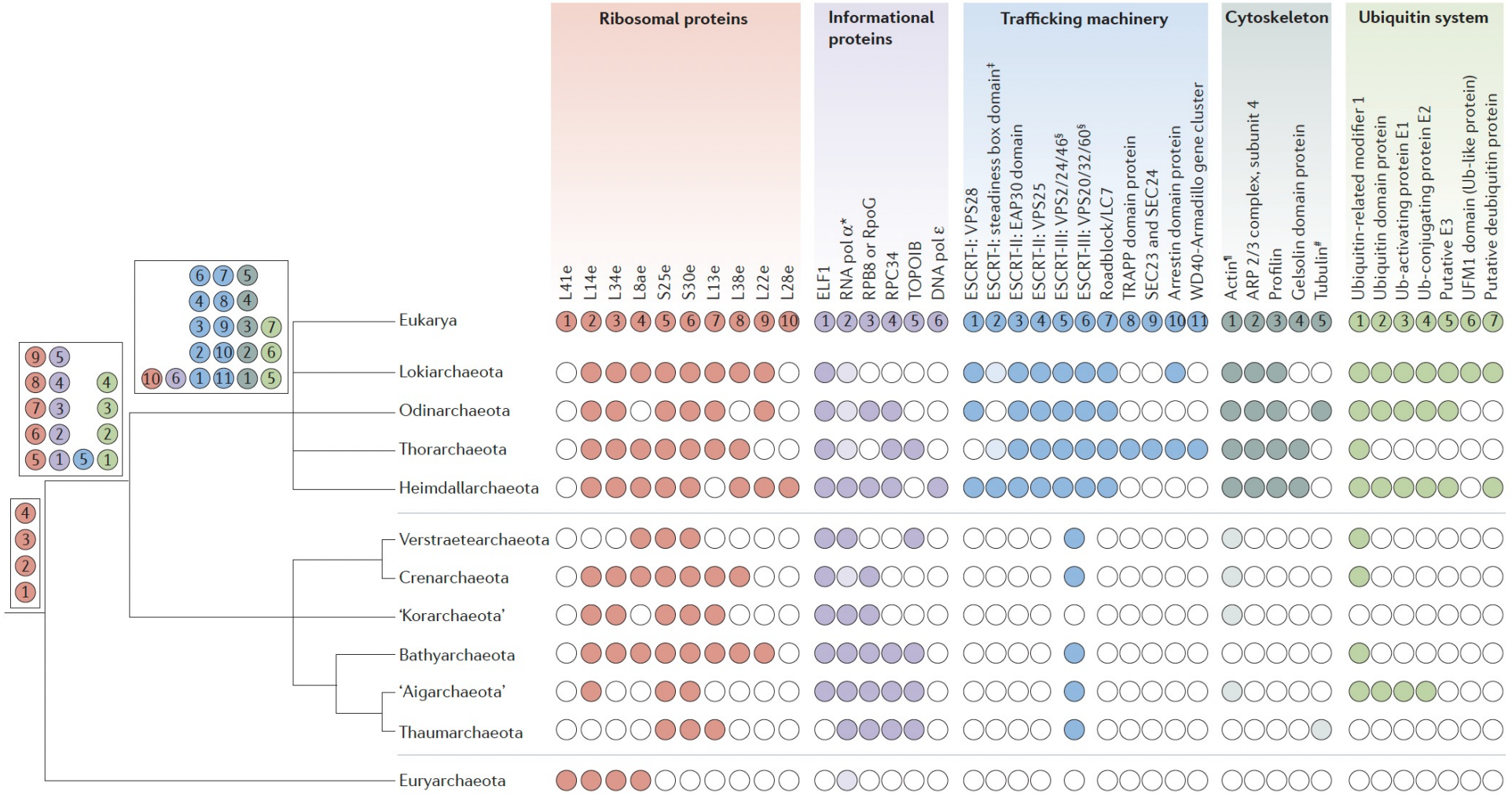

Eme et al. 2017

# Phylogenomic analyses have placed the Asgard archaea as the closest prokaryotic relatives of eukaryotes



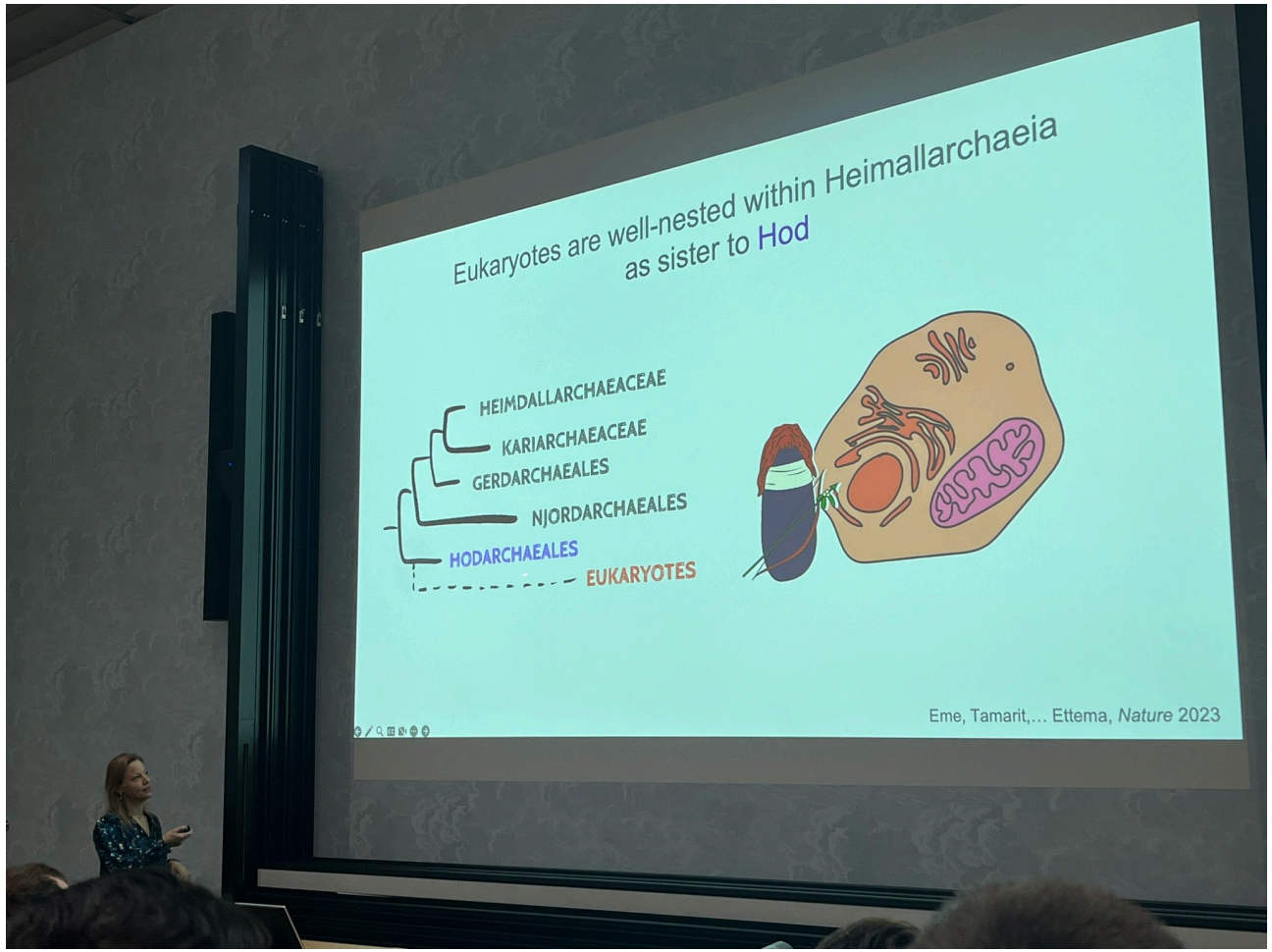

Zaremba-Niedźwiedzka, 2017

# Genomic investigation of Asgard archaea showed that they carry several genes believed to be eukaryotic specific




Eme et al. 2017

# Inference and reconstruction of the heimdallarchaeial ancestry of eukaryotes




Hod in Norse mythology, is a blind god, associated with night and darkness.

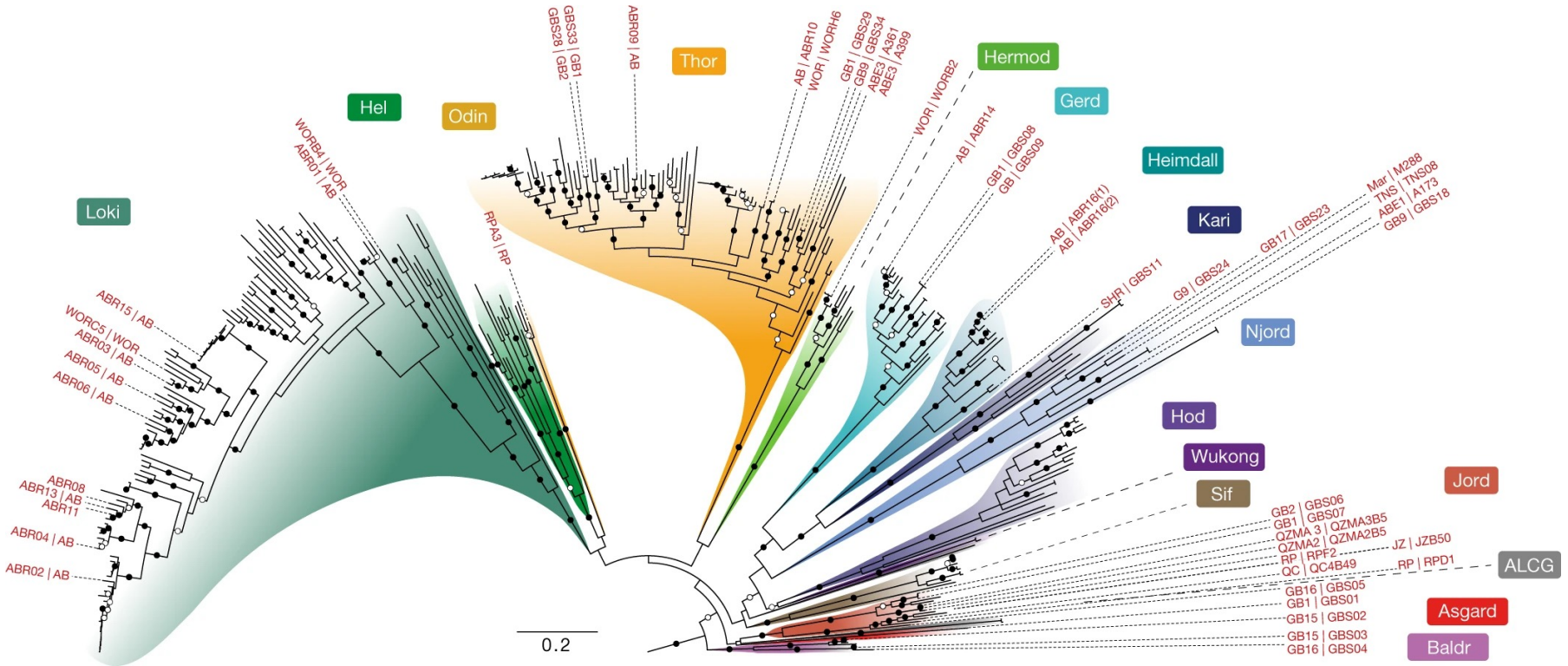
**Received: 23 April 2021**

**Accepted: 10 May 2023**

Eme et al. 2023

# Expandind genomic diversity of Asgard archaea with metagenomics

63 new Asgard archaeal metagenome-assembled genomes (MAGs) from samples obtained from 11 locations around the world



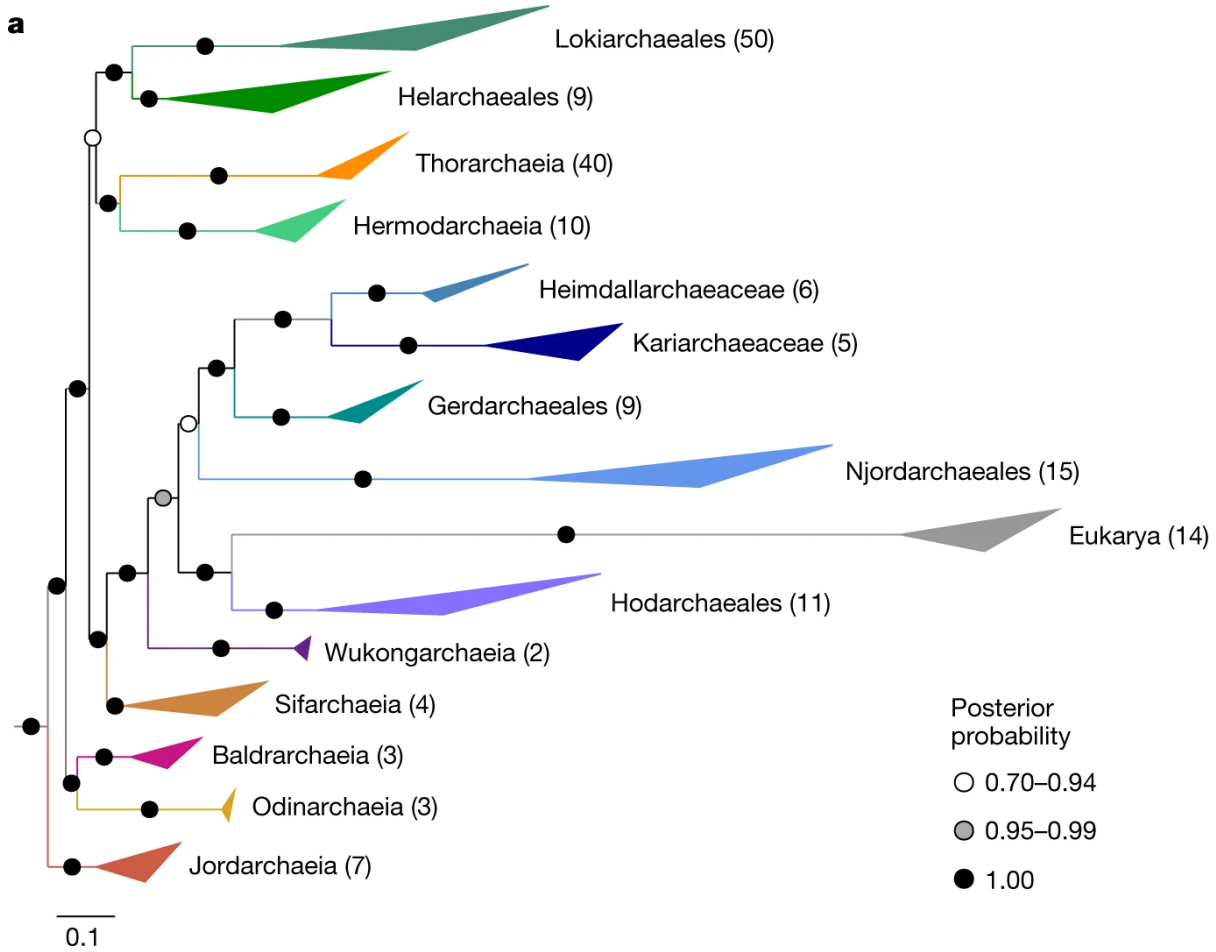

Eme et al. 2023

# Exploring new phylogenomic markers

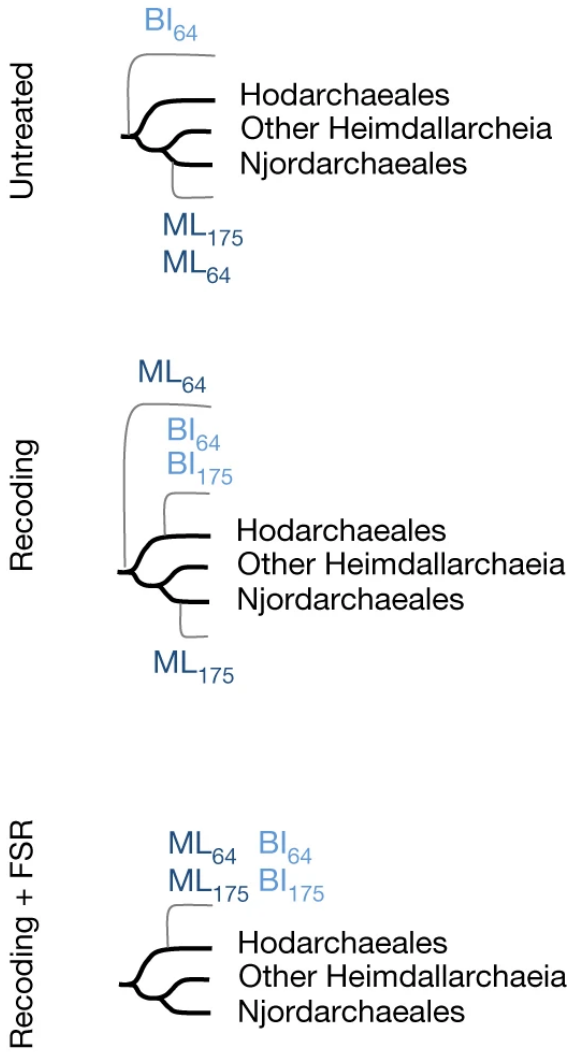
- typically ribosomal proteins have been used in phylogenomic analyses of archaea and eukaryotes (RP56), however they might co-evolve and therefore might contribute to phylogenetic artefacts
- independent new marker dataset comprising 57 proteins of archaeal origin in eukaryotes
- the NM57 proteins are mostly involved in informational, metabolic and cellular processes, but do not include ribosomal proteins
- they are longer and therefore putatively more phylogenetically informative compared with the RP56 markers
- broader functional distribution of NM57 markers is less likely to cause phylogenetic reconstruction artefacts

Eme et al. 2023

# Eukarya as sister to Hod




BI based on 278 archaeal taxa, 15,733 AA positions
The concatenation was SR4-recoded and analysed using the CAT+GTR model



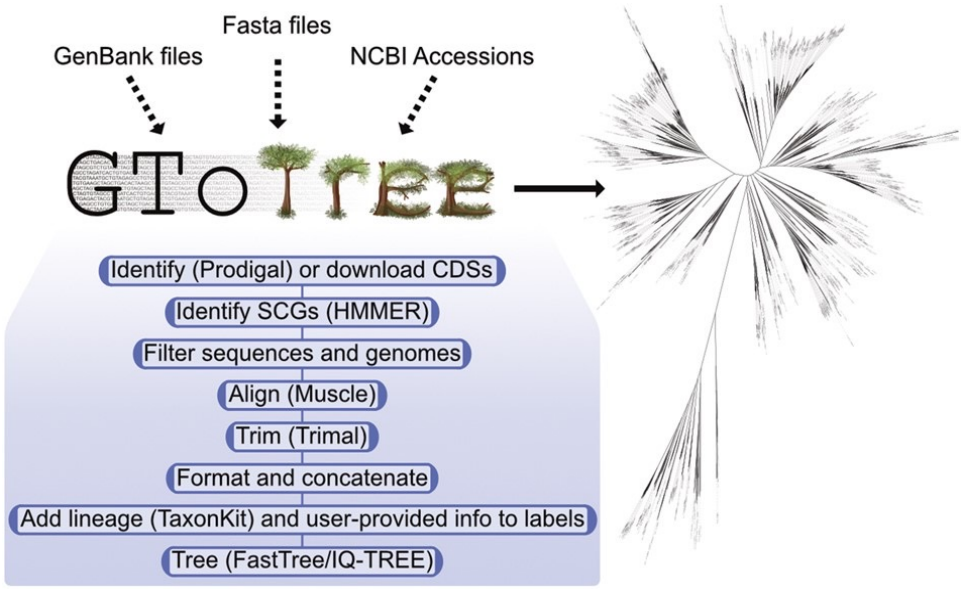

The indices 175 and 64 refer to phylogenomic datasets containing 175 and 64 Asgard archaea, respectively.

Schematic representation of the shift in the position of eukaryotes (grey branches) in ML and BI analyses under different treatments

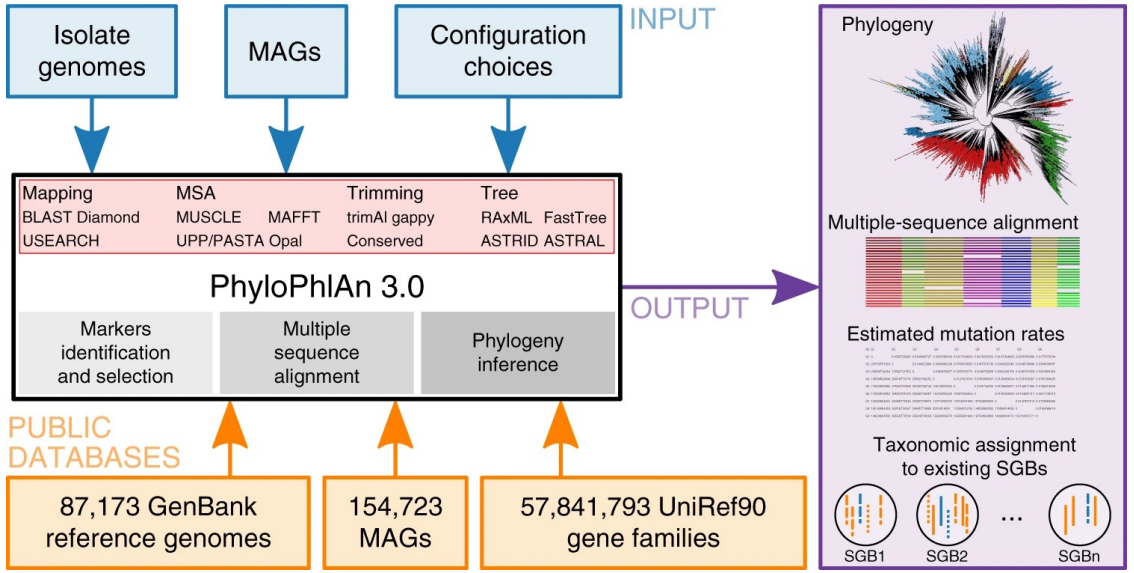
Eme et al. 2023

# Metagenomic data to the rescue

If MAGs can be recovered from metagenomic data, they can be used as a source of data for phylogenomics in a similar manner as genomes (with higher risk of contamination)

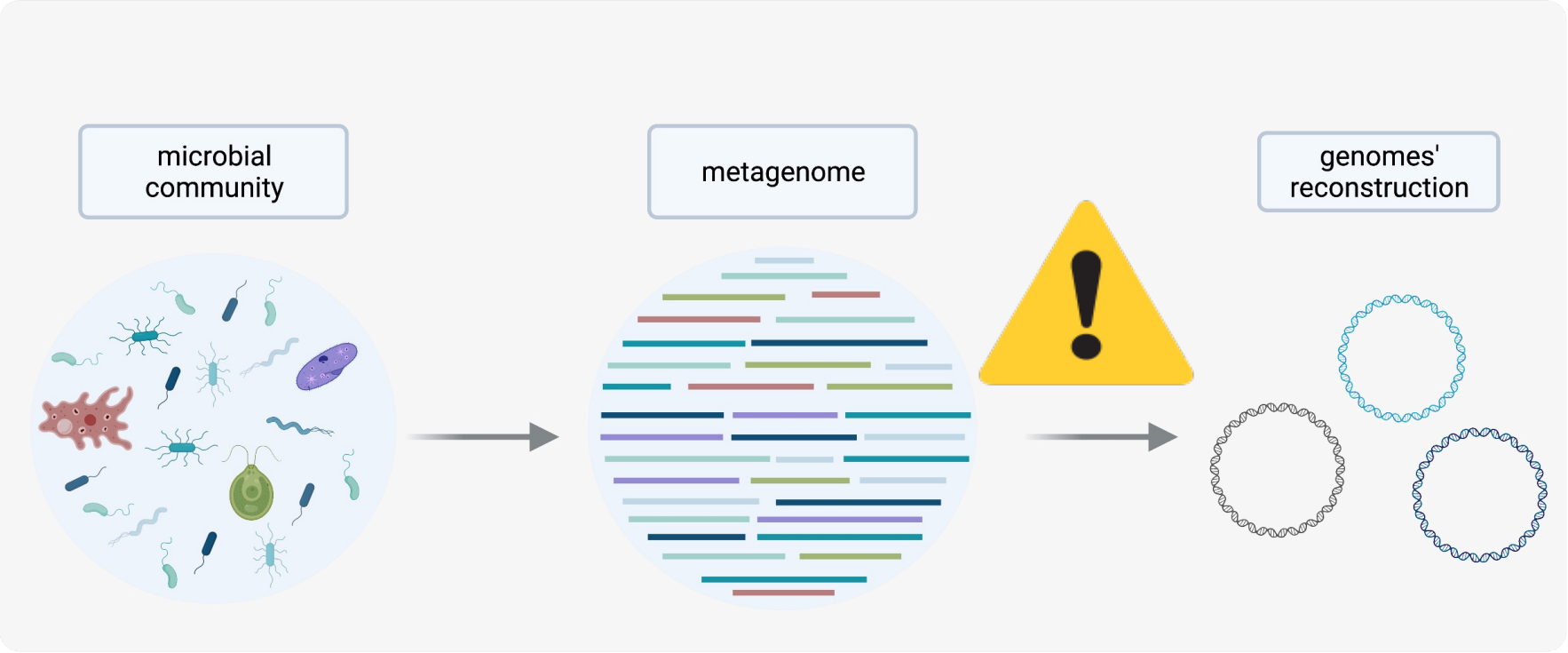



Lee 2019



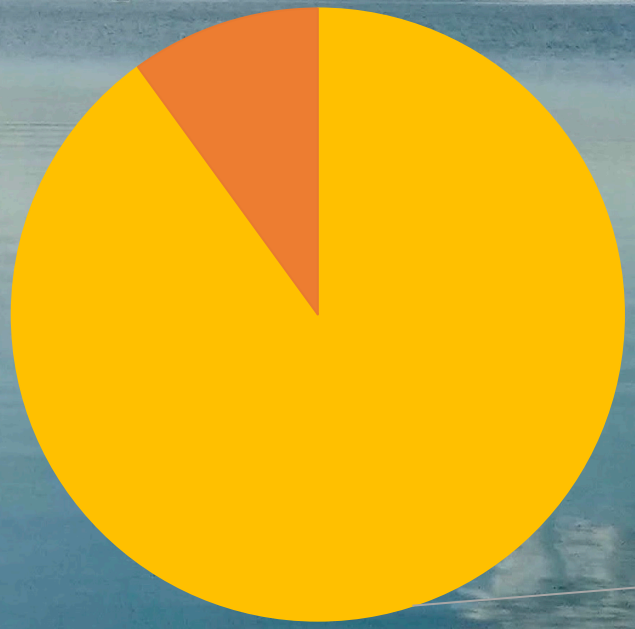

Asnicar et al. 2020

# Metagenomics

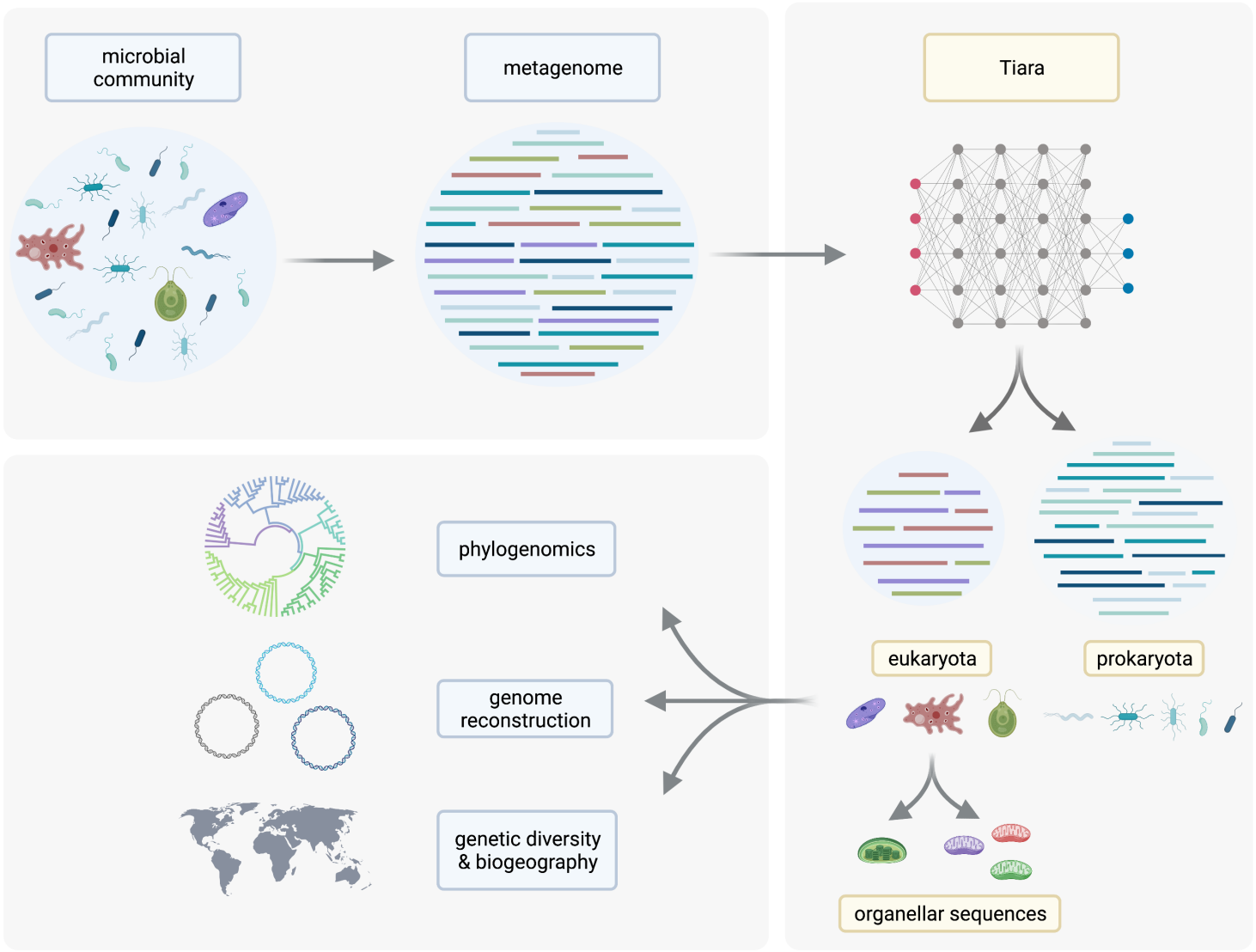



The genomic analysis of microbial communities by extraction and sequencing of their DNA, which allows studying organsims directly in their natural environment

# Metagenome of lake



# How to obtain eukaryotic genomes from metagenomes?




**tiara**

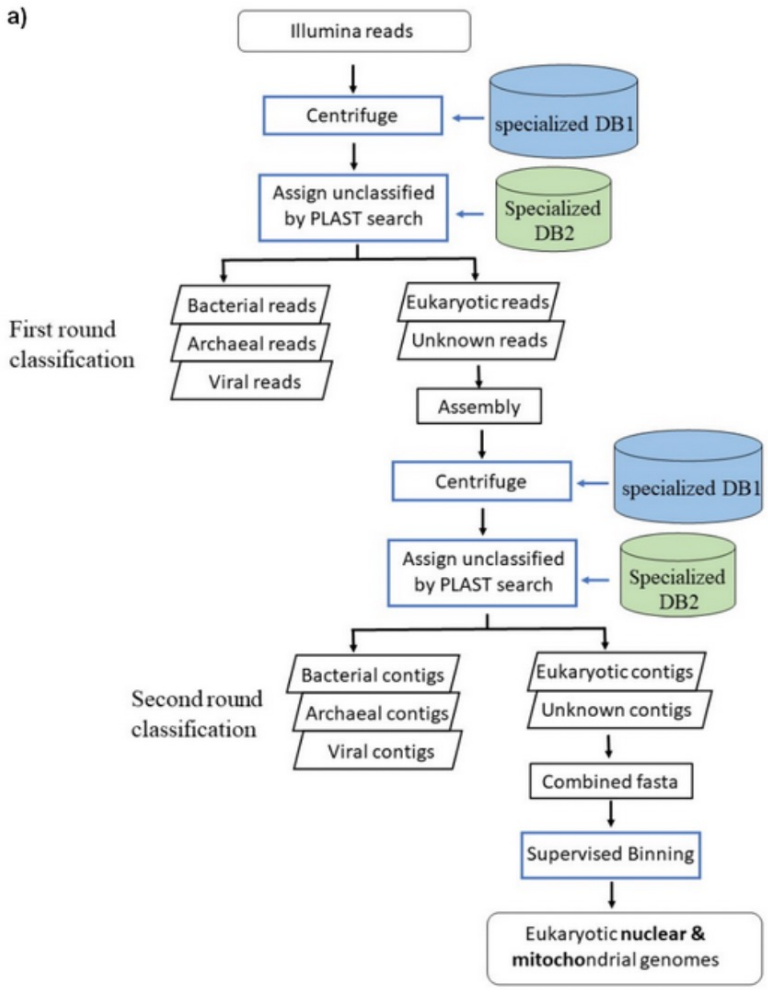
tiara – a tool for DNA sequence classification

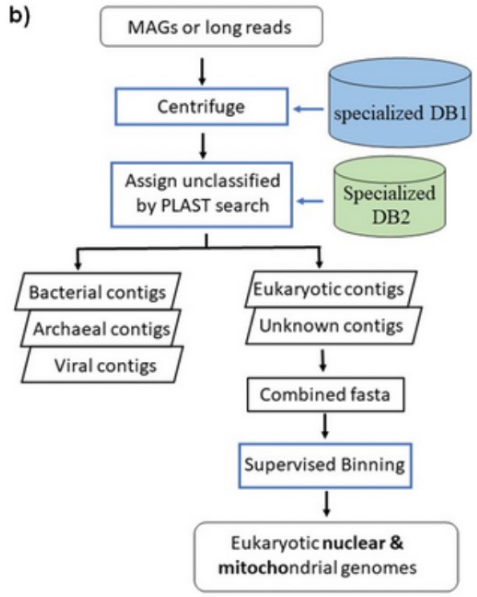
View on GitHub

Karlicki et al. *Bioinformatics*, 2022

# Other tools - Eukfinder

*With sufficient reads, Eukfinder efficiently assembles high-quality near-complete nuclear and mitochondrial genomes from diverse Blastocystis subtypes from metagenomic data without the aid of a reference genome.*



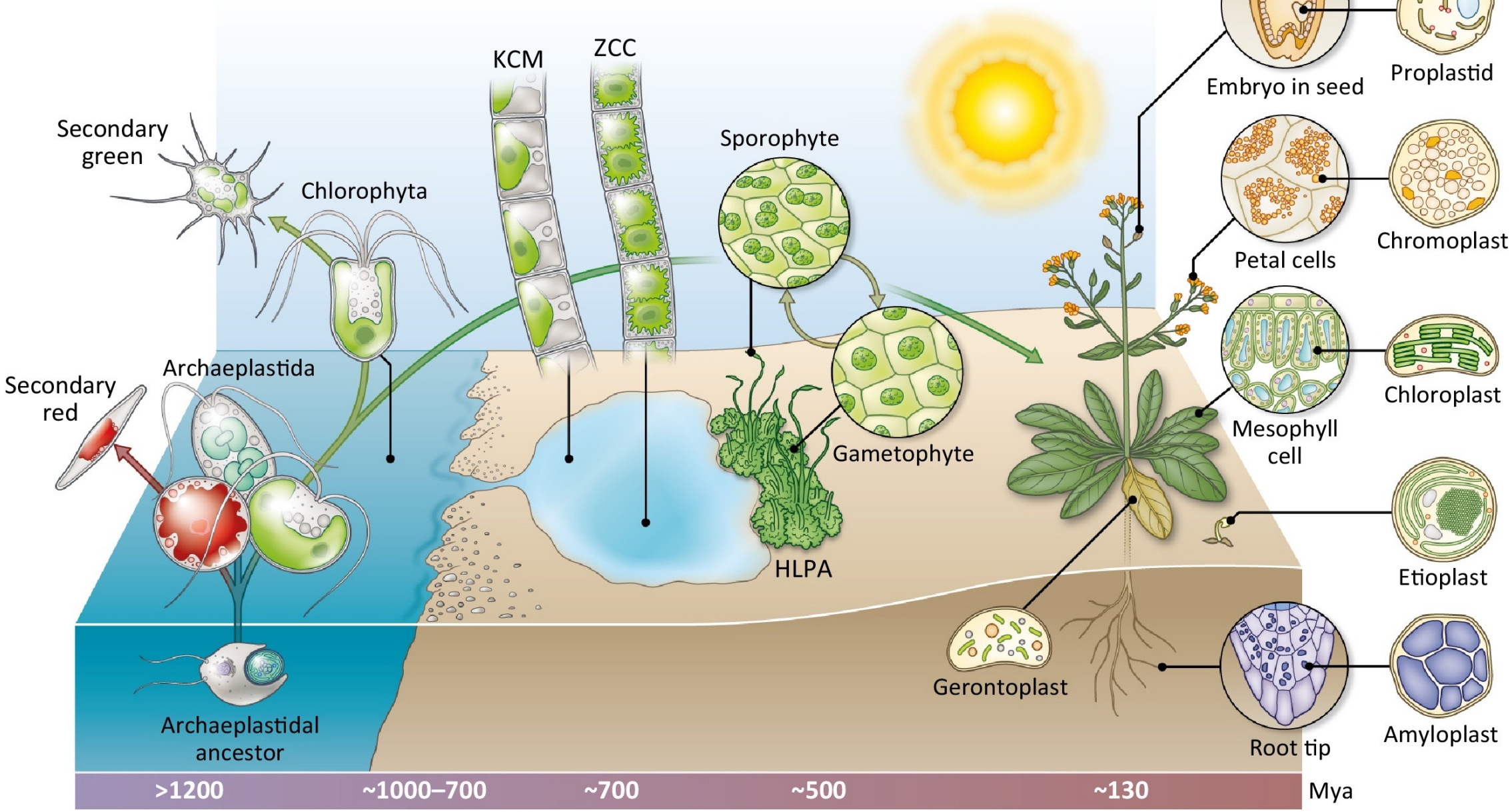




Zhao et al. 2023 BiorXiv

How the eukaryotic **cell complexity** evolved?
What drives **diversification of eukaryotes**?

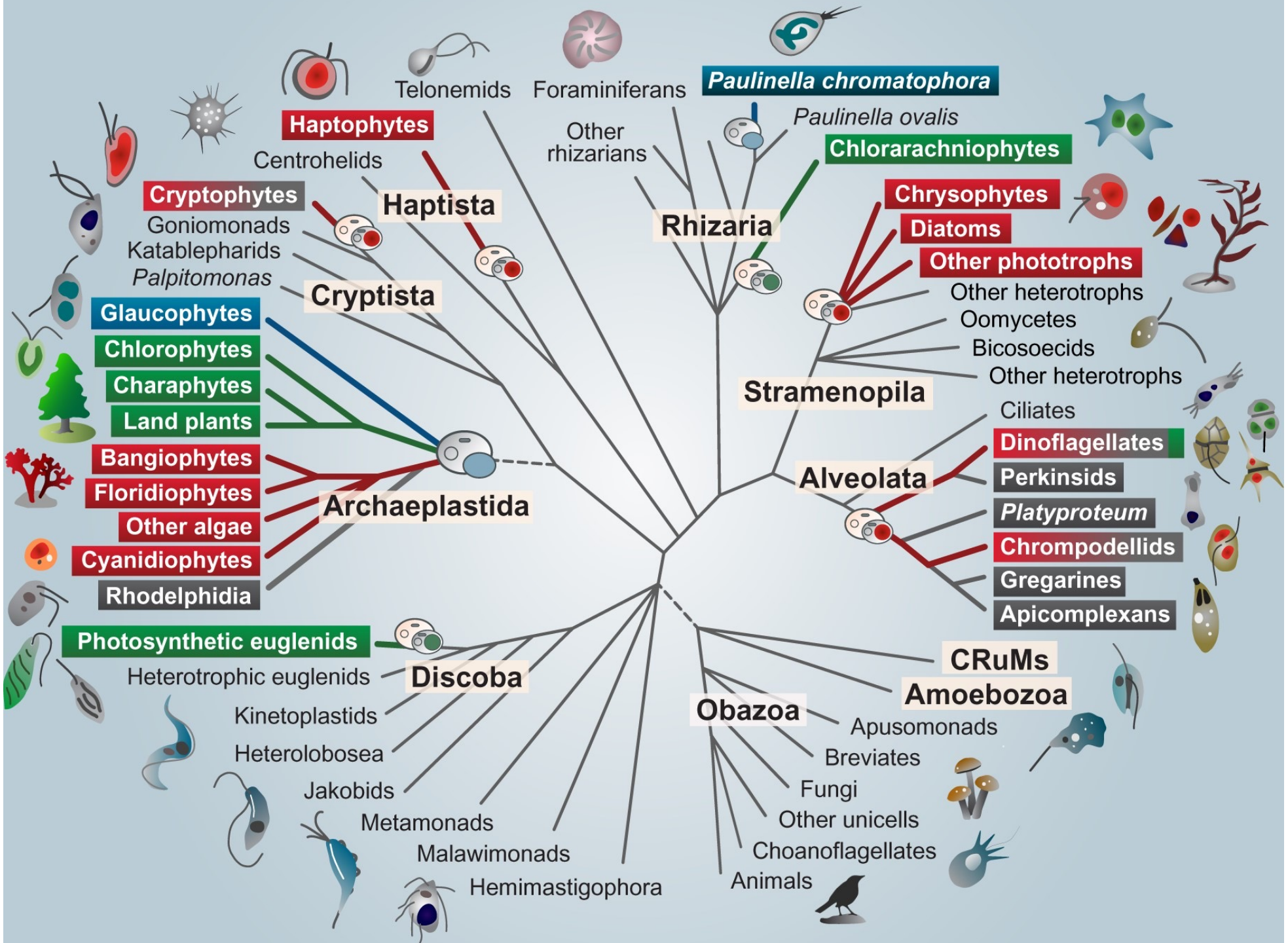
# Endosymbiosis

# plastids' evolution

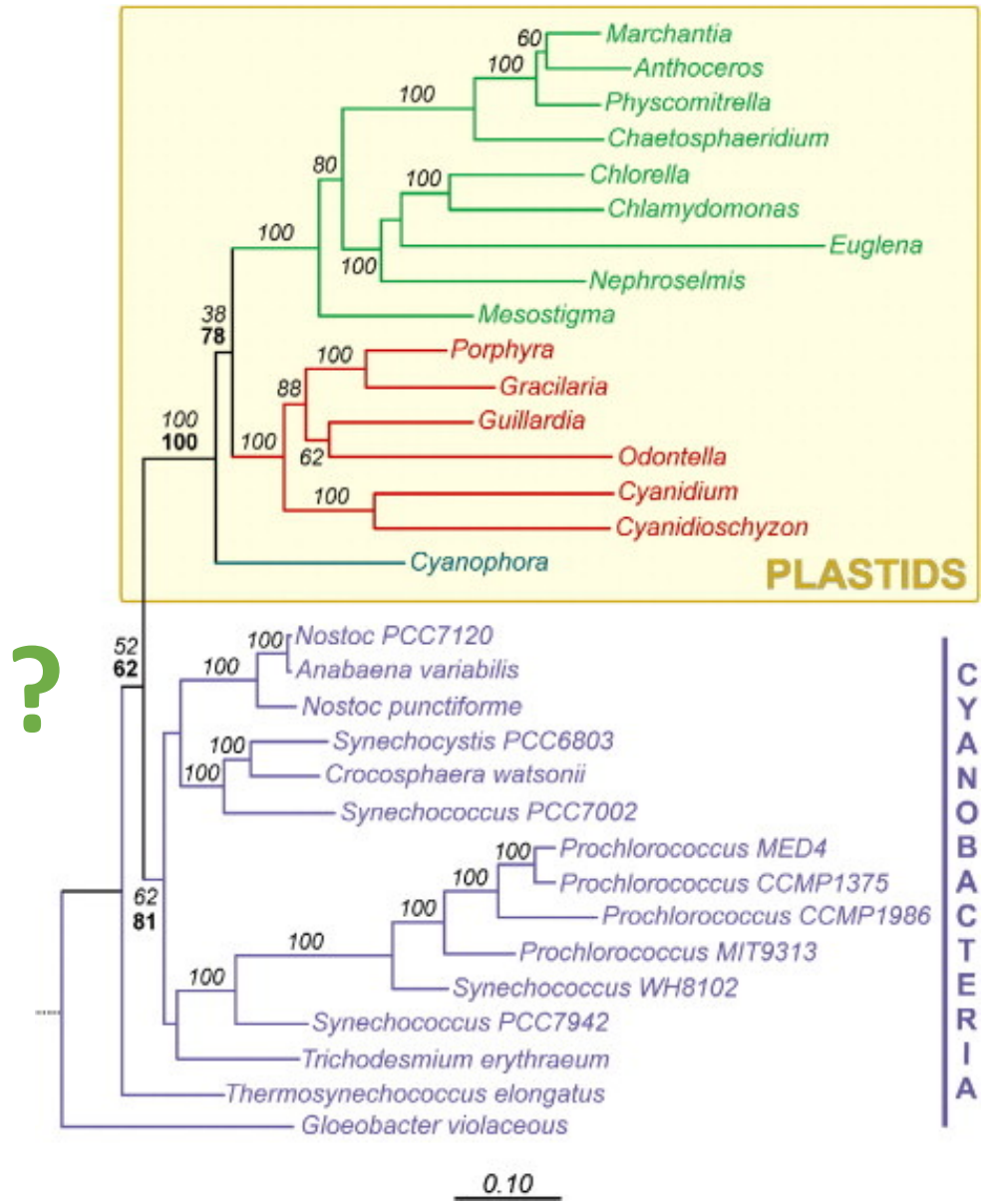



De Vries et al. 2016

Trends in Plant Science




McGrath 2020

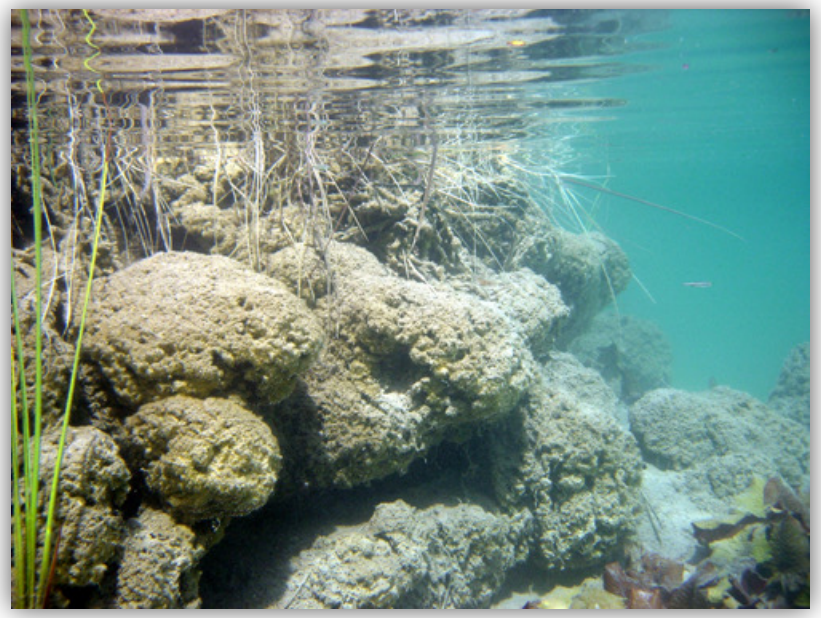


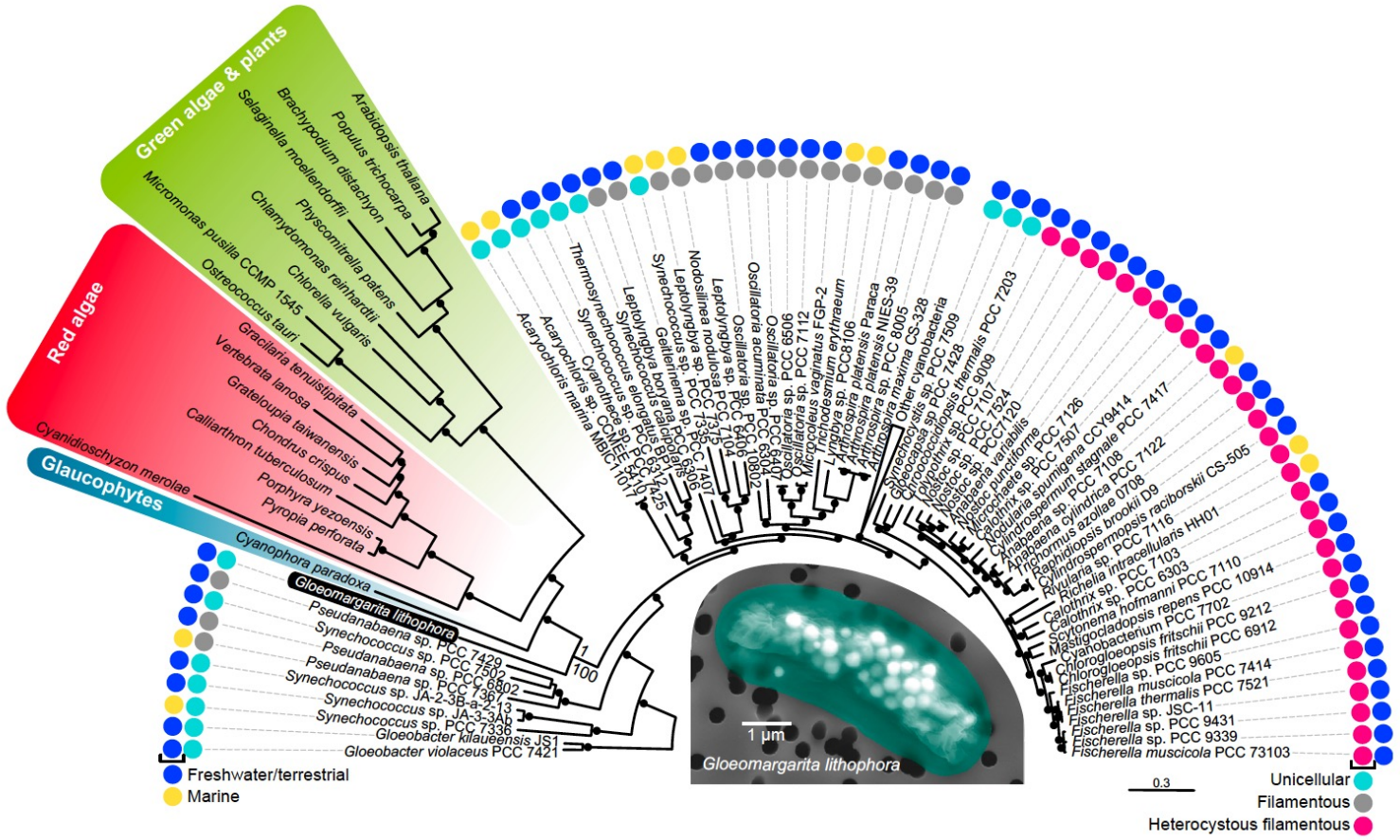

Plastids and cyanobacteria have been recovered repeatedly as a monophyletic group pointing to the cyanobacterial origin of primary plastids

**Rodriguez-Ezpeleta** et al. (2005) Curr Biol

# Cyanobacteria which became a chloroplast

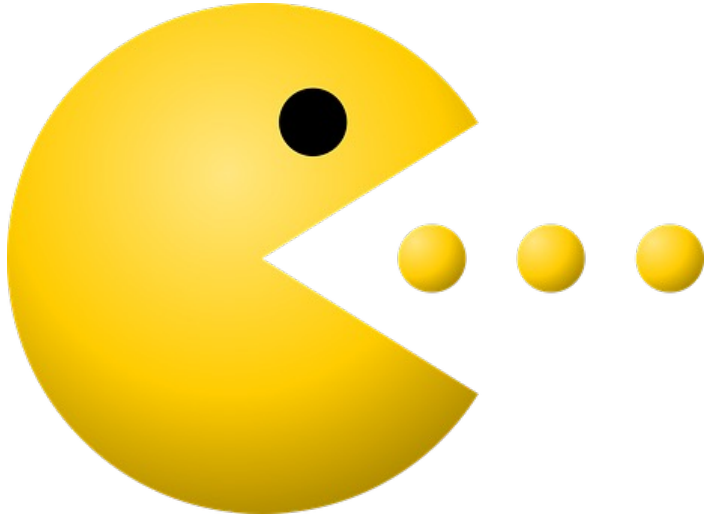
- *Gloeomargarita lithophora* is the closest extant cyanobacteria to plastids
- old cyanobacterial lineage
- freshwater cyanobacteria (!)

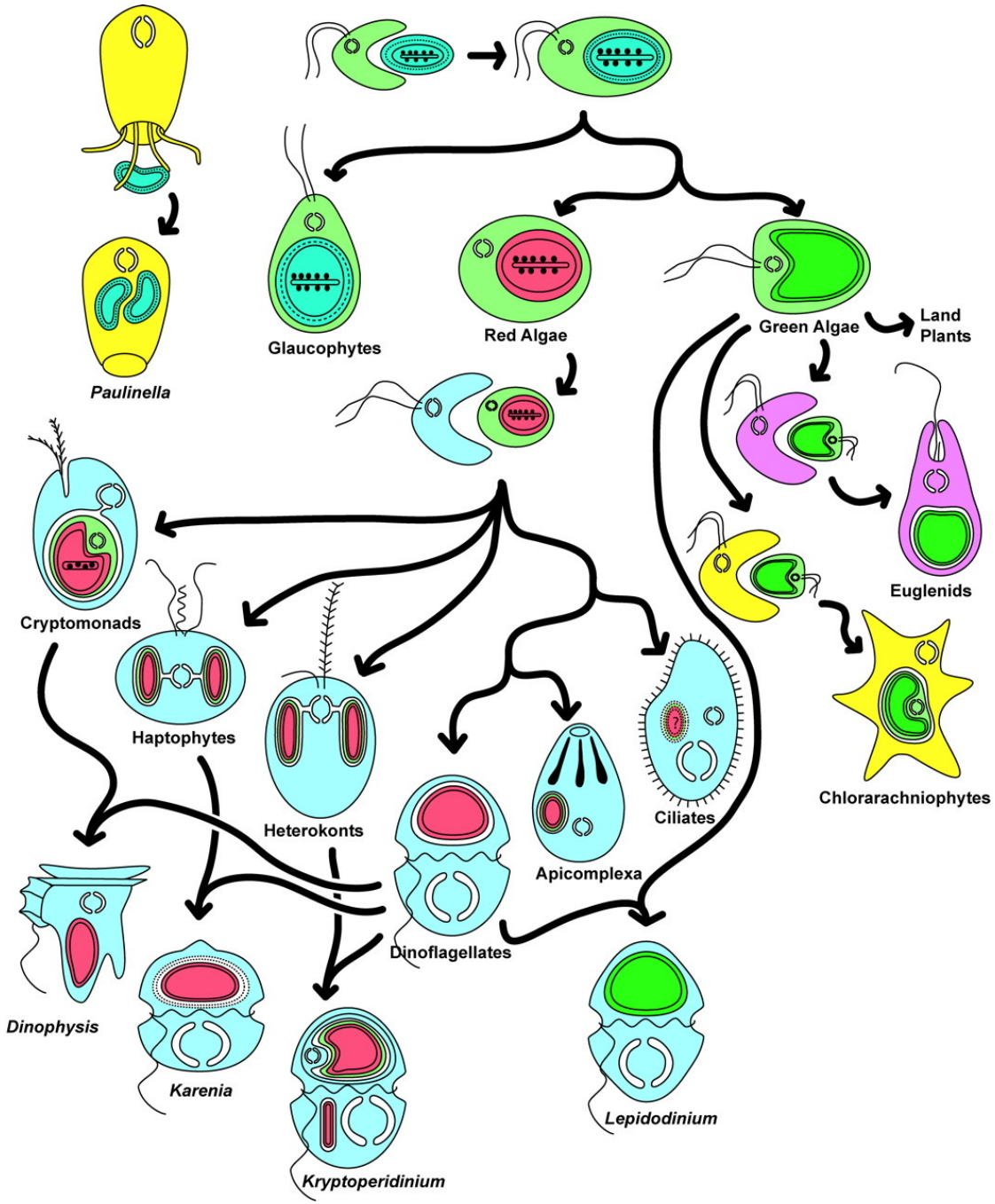





Ponce-Toledo et al., 2017

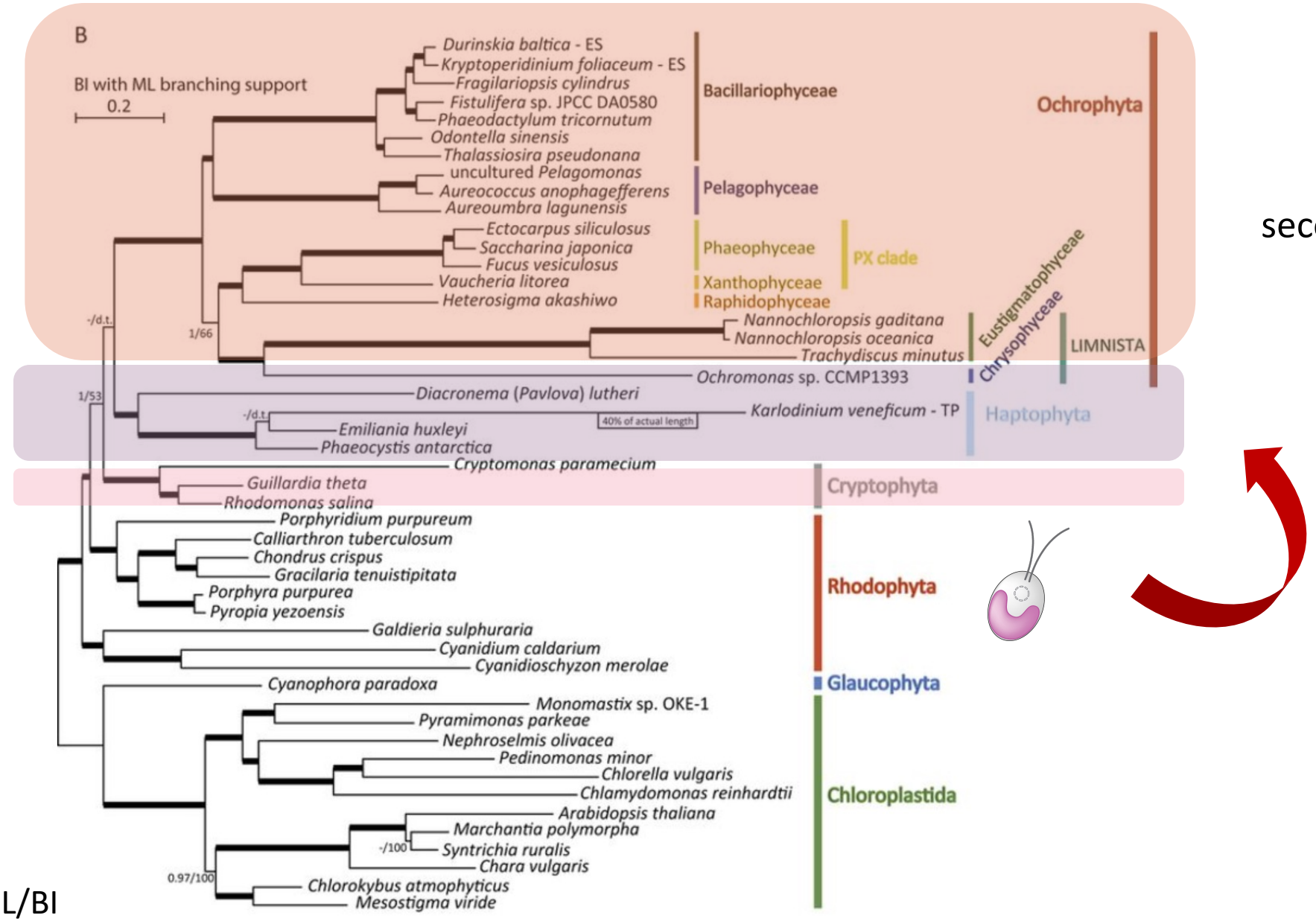
# Secondary endosymbioses in several lineages of microbial eukaryotes






Keeling (2004) Am J Bot

# Phylogenomics of plastids



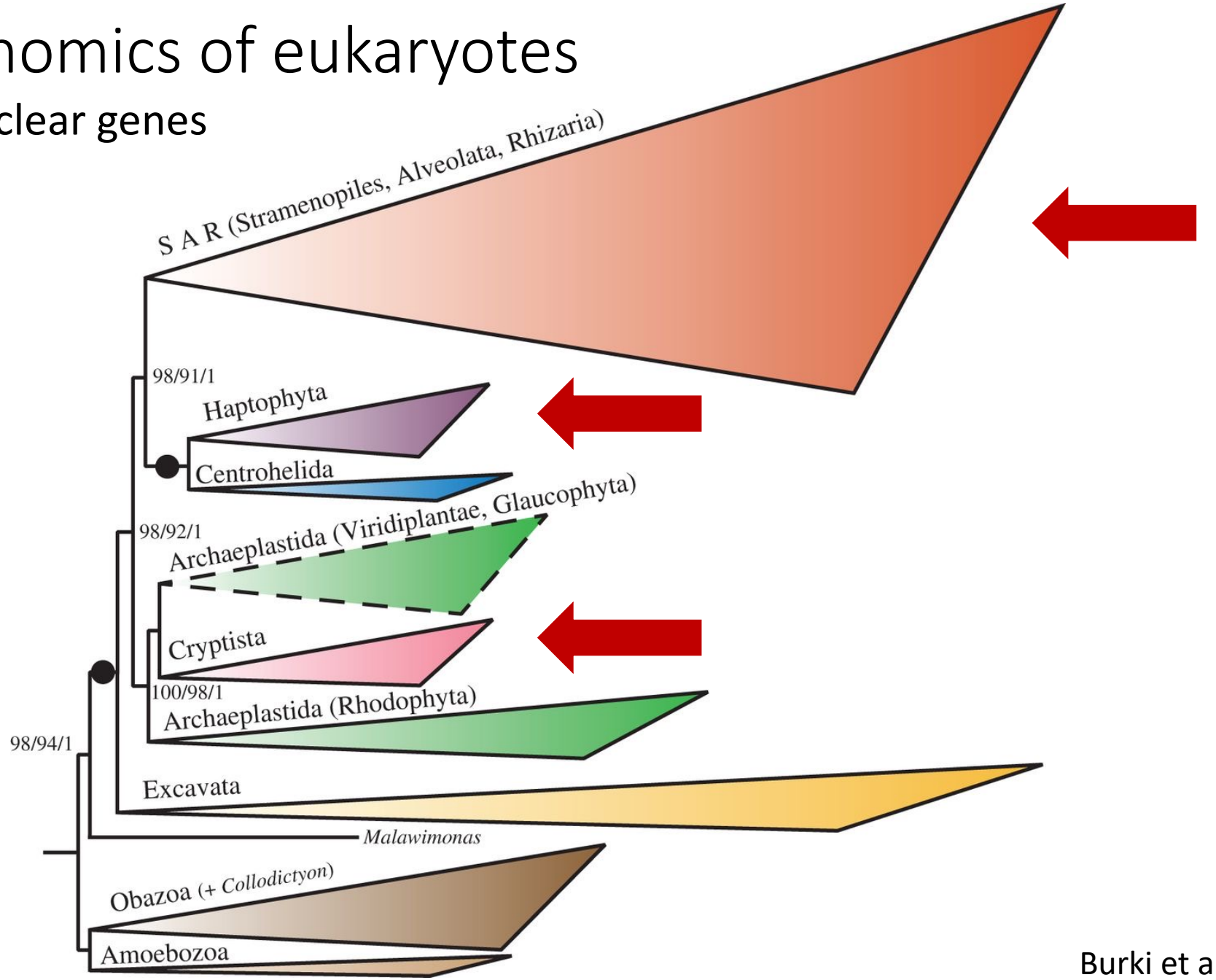

secondary „red” endosymbionts

ML/BI

Sevcikova et al. 2015

# Phylogenomics of eukaryotes

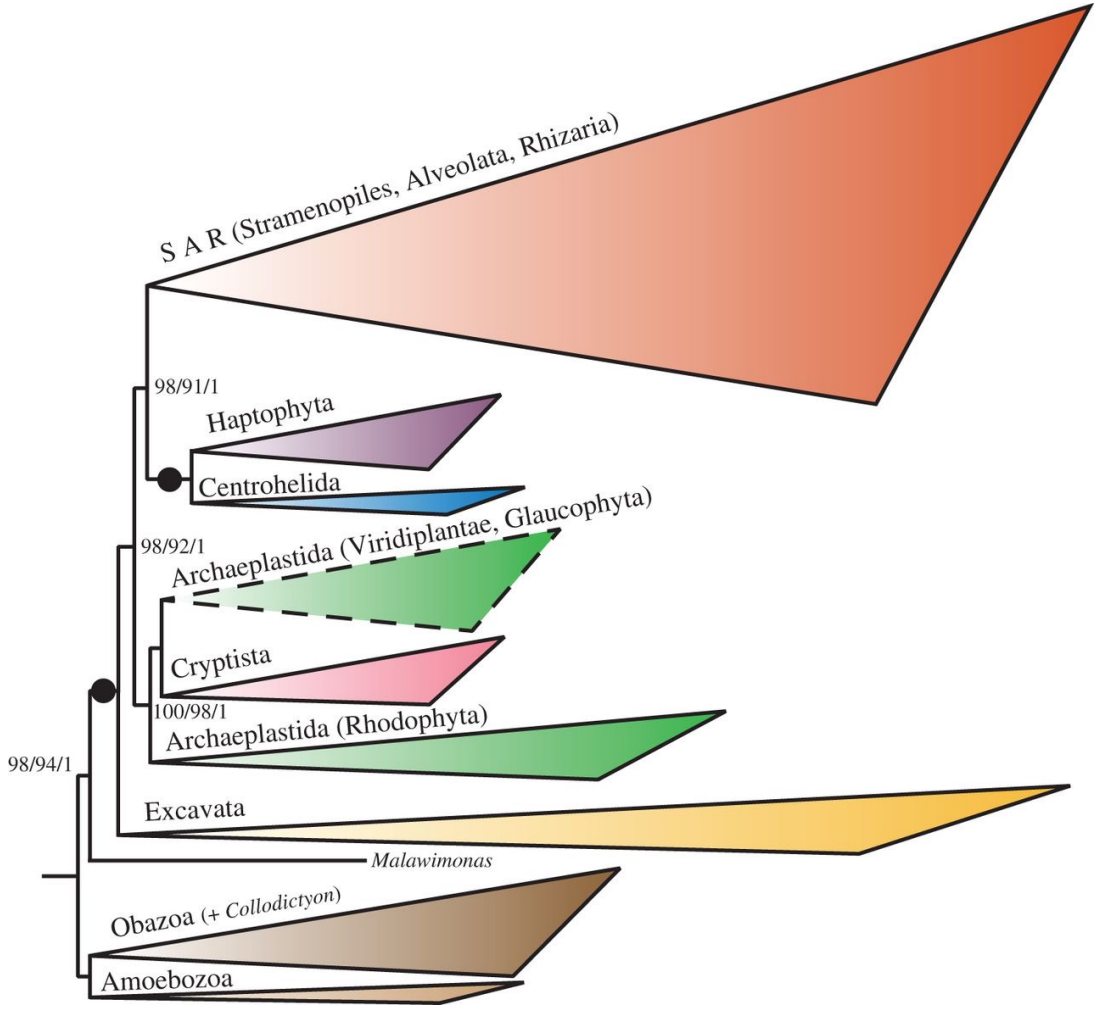
## based on nuclear genes

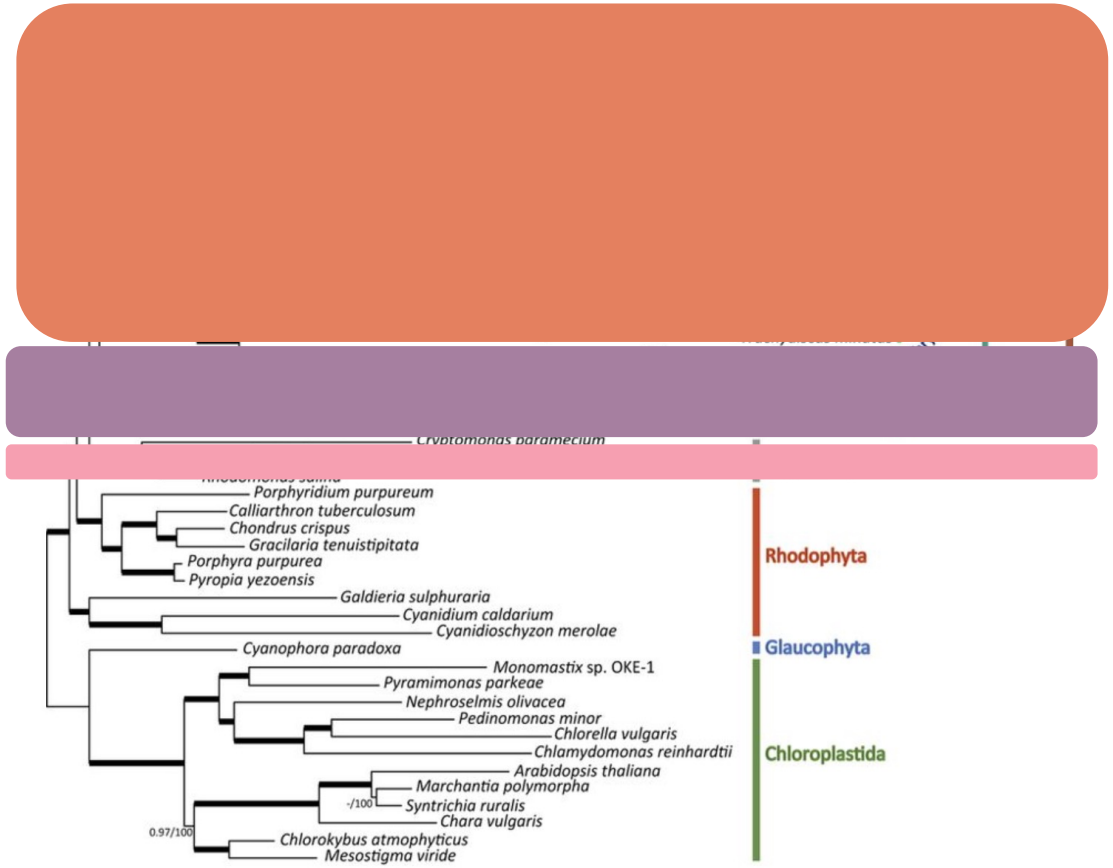



ML/BI 250 genes

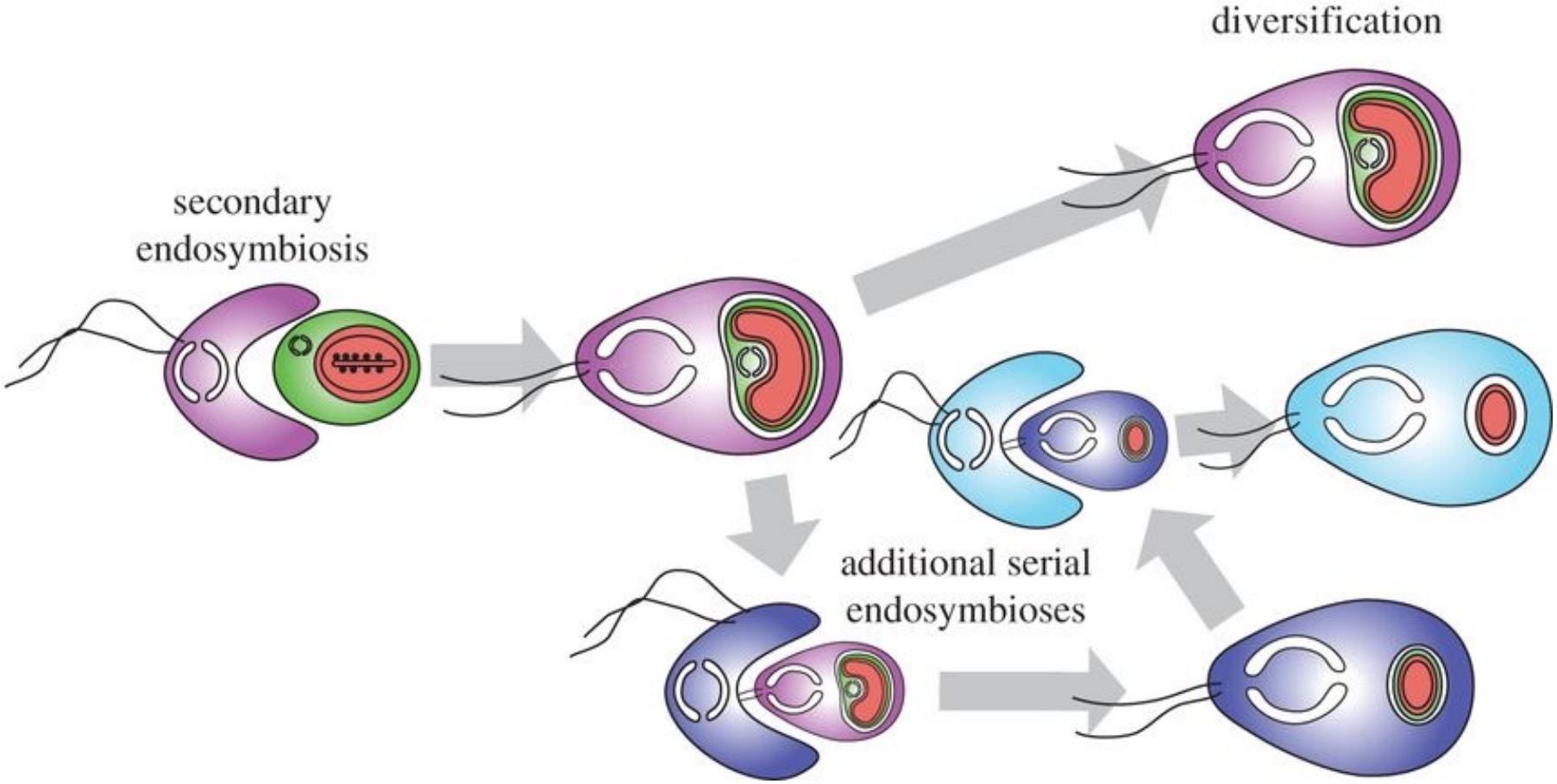
Burki et al. 2016

# Nuclear-encoded genes vs plastid-encoded genes



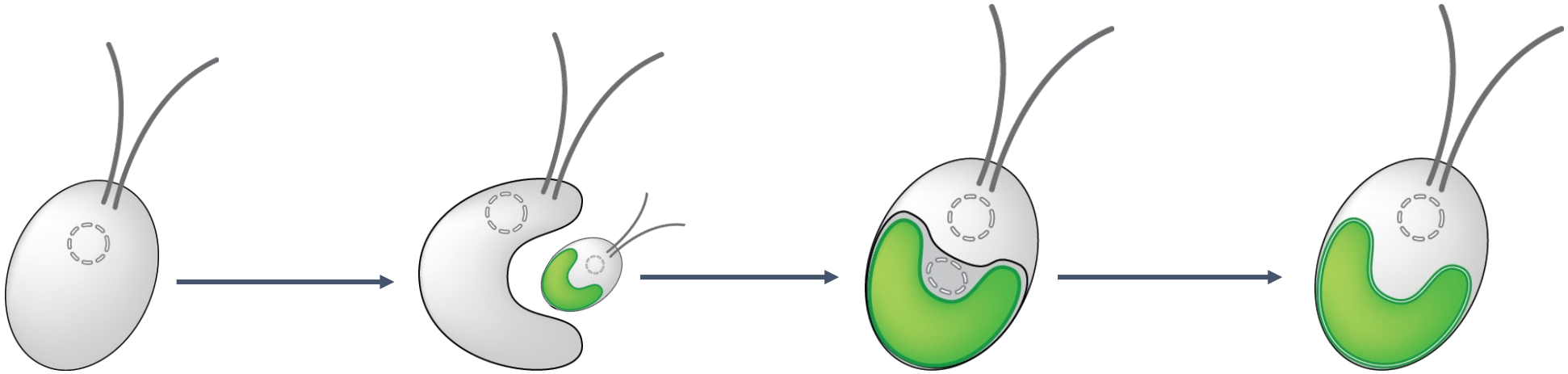



# Cryptic serial endosybiosis




Burki et al. 2016

# Plastid endosymbiosis

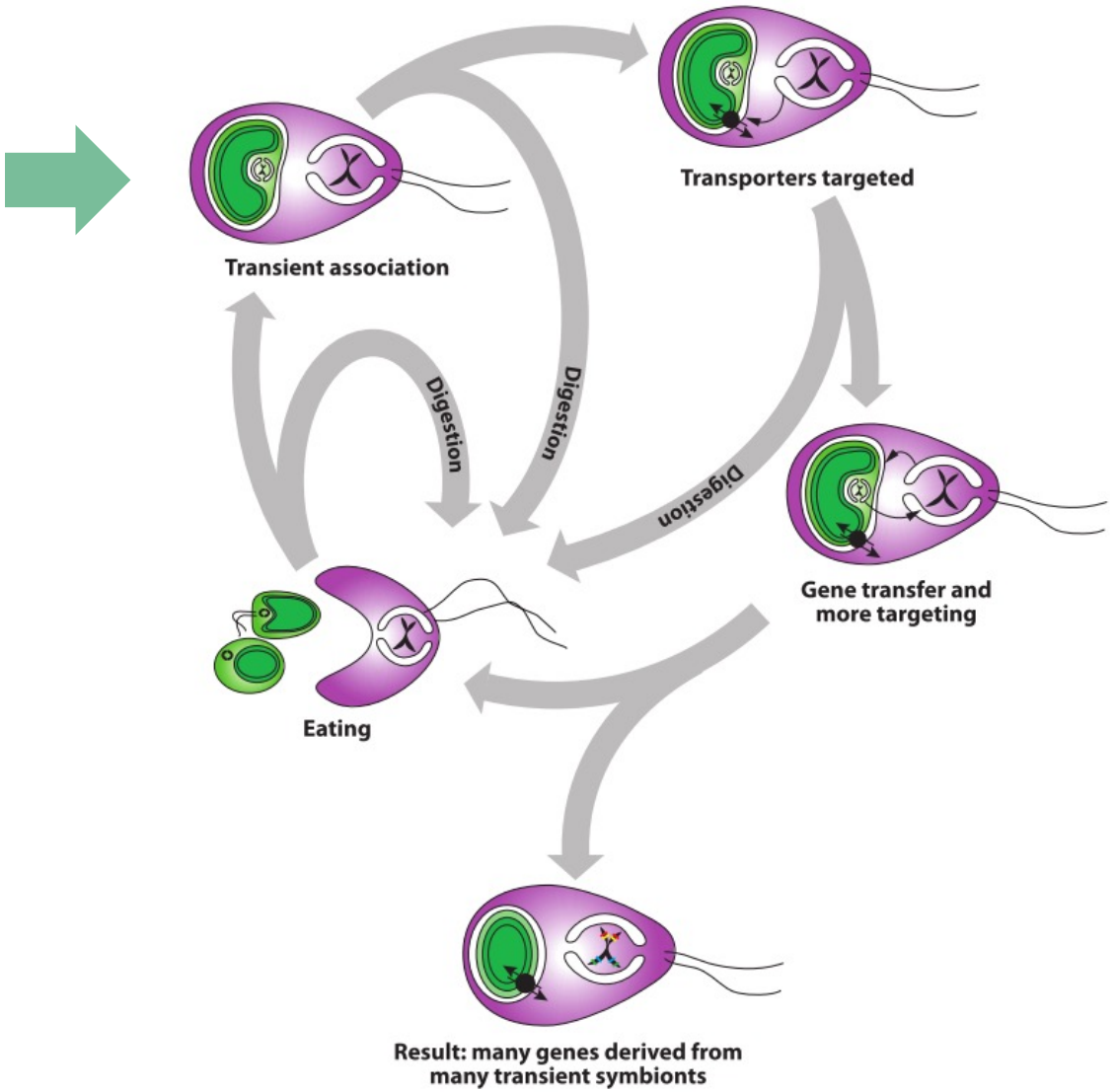


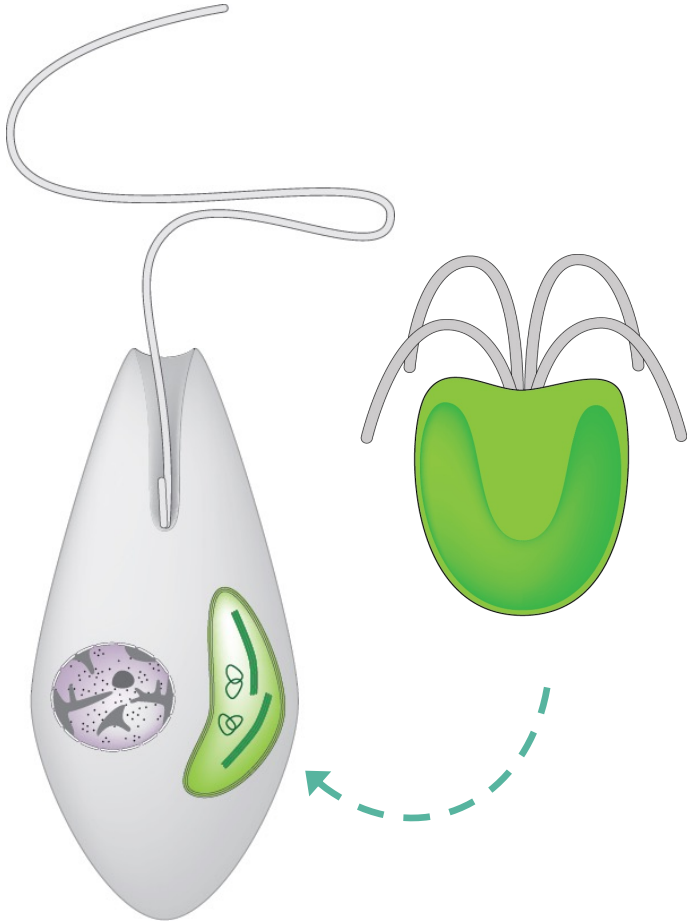
What are the initial steps of endosymbiosis?

What are the steps in the transition from endosymbiont to organelle?

# Which comes first, gene transfer or cellular fixation?

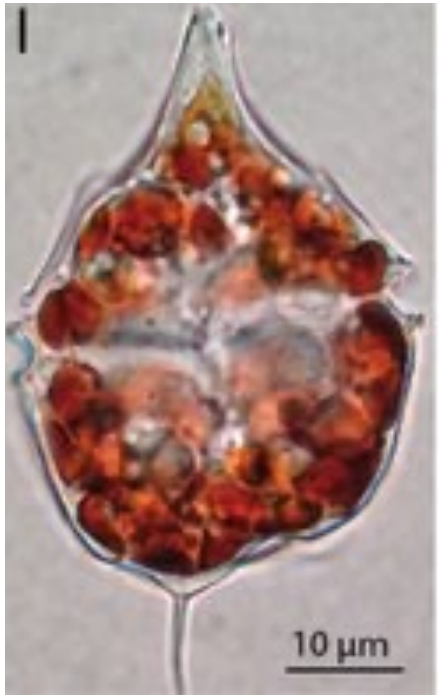
A targeting-ratchet model for the endosymbiotic origin of plastids
Keeling, 2013



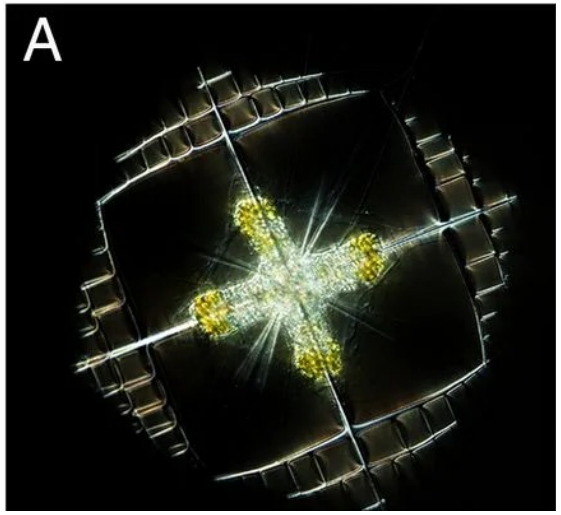


## kleptoplasty

transient association between host and endosymbiont, which might resemble the initial steps of the establishing endosymbiosis



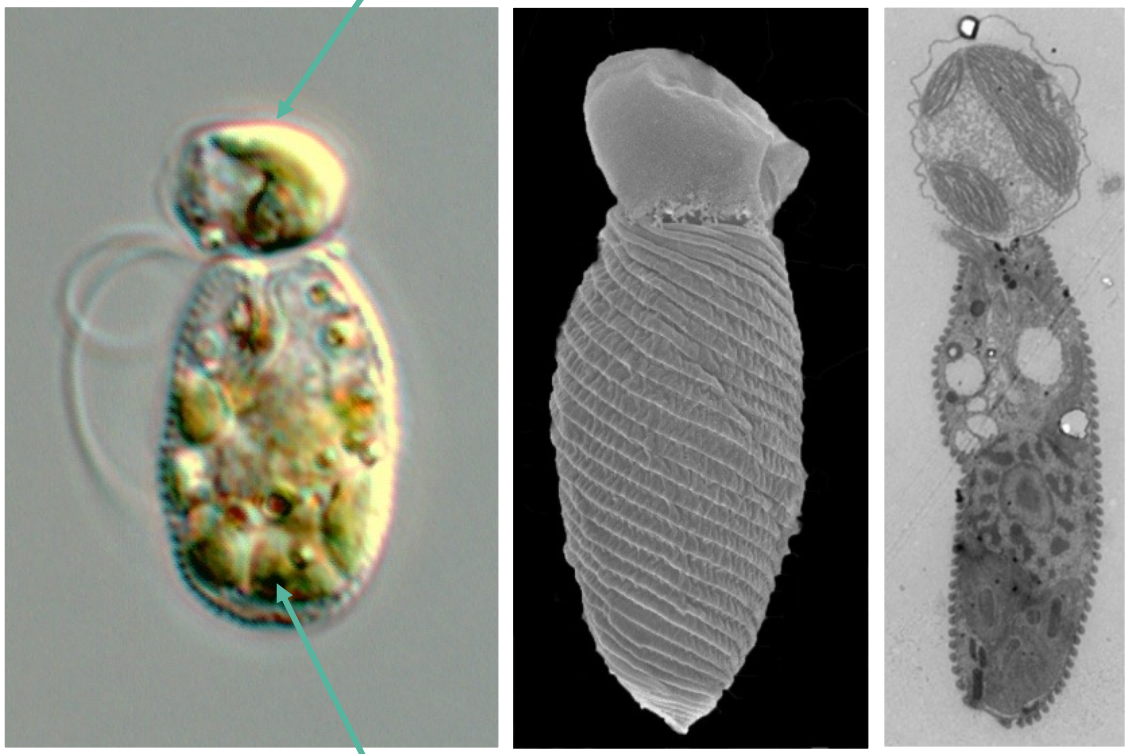




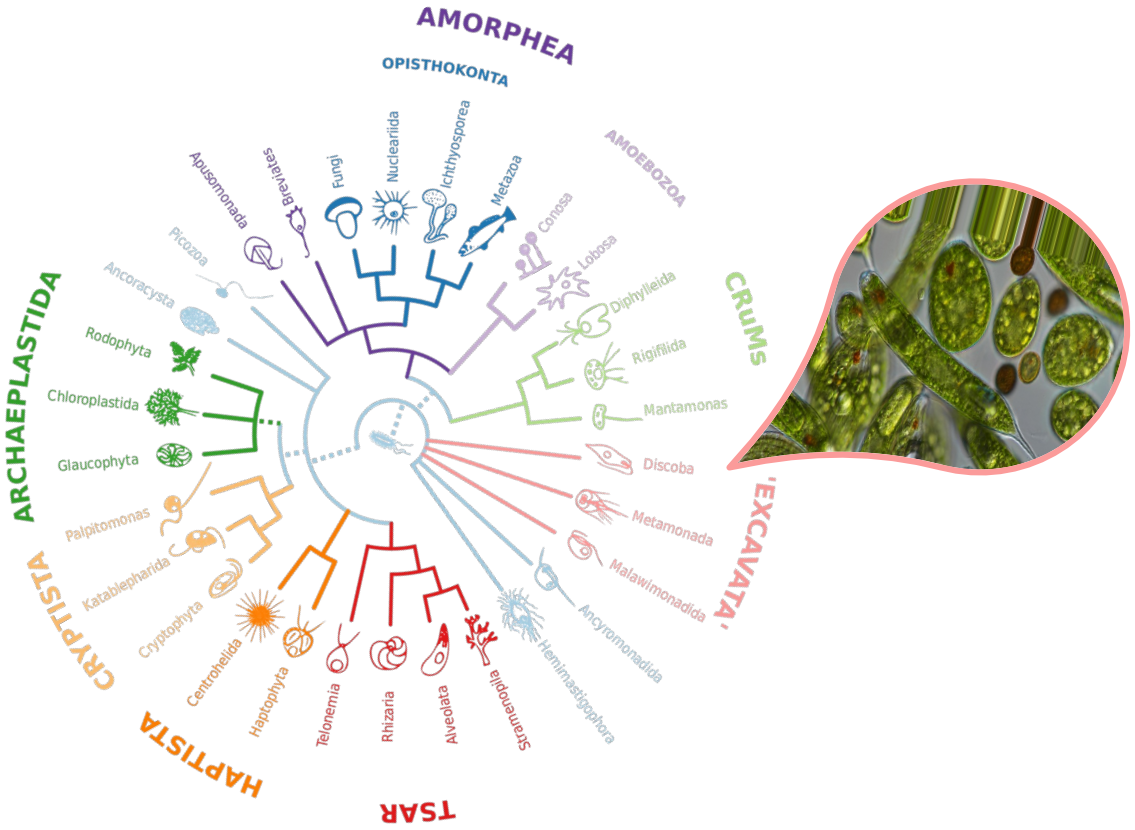

Kleptoplasty is widespread among eukaryotes

# *Rapaza viridis* – mixotrophic euglenid

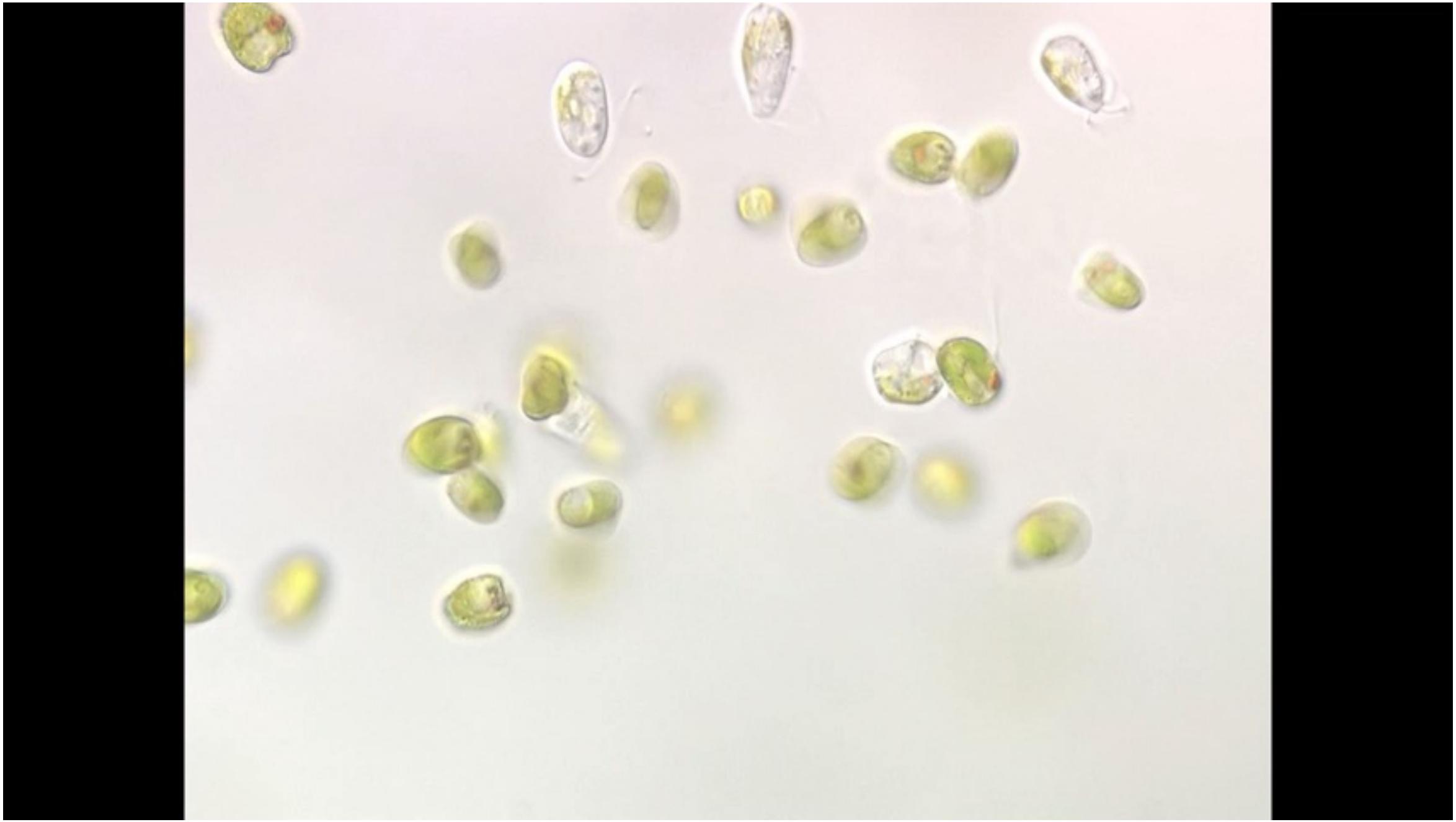
feeds on a specific strain of green algae, *Tetraselmis* sp.



*Rapaza viridis*

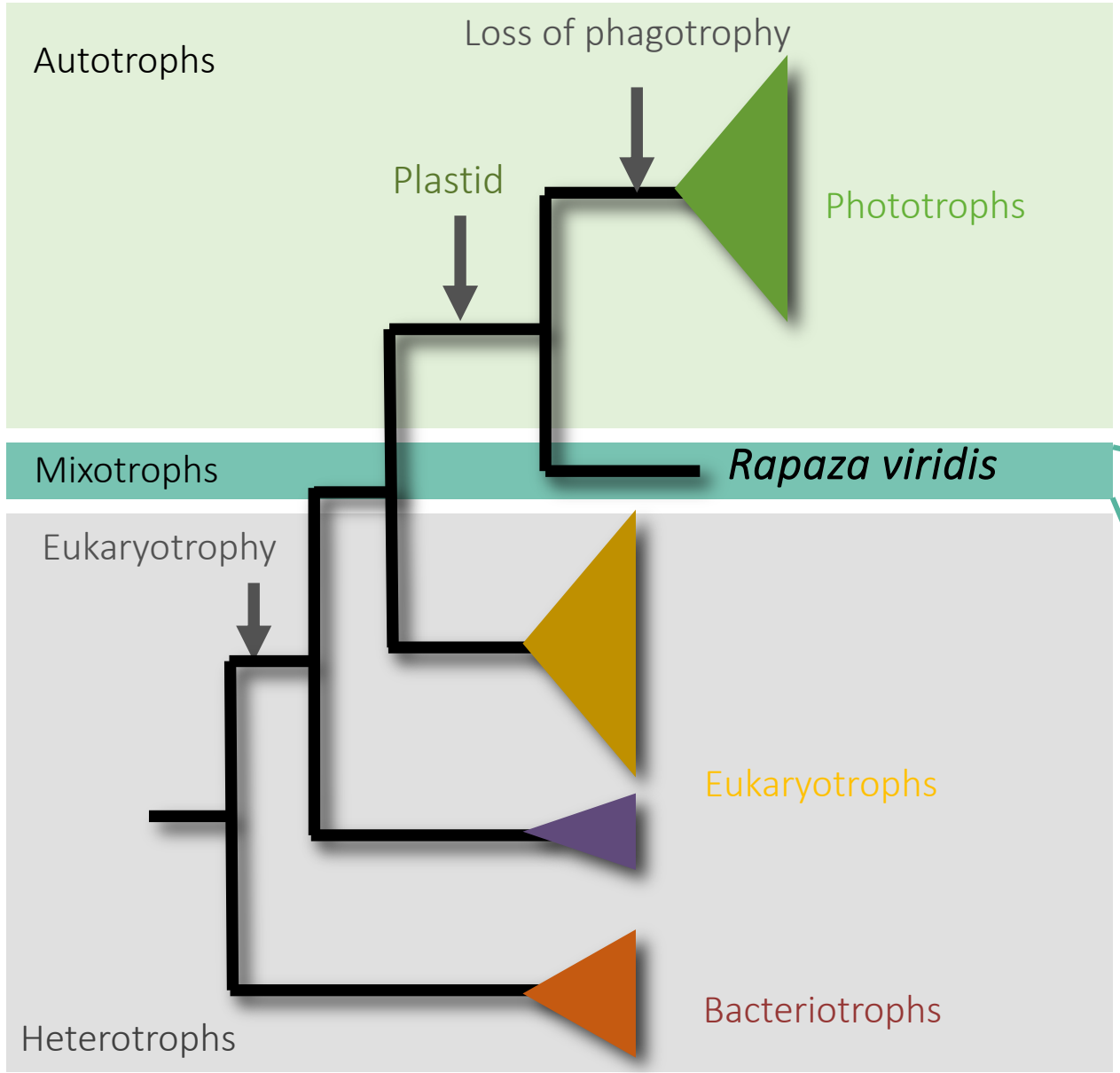


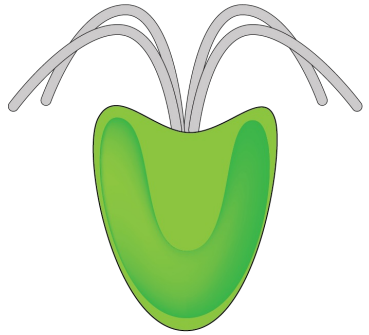

Yamaguchi, Yubuki & Leander (2013)



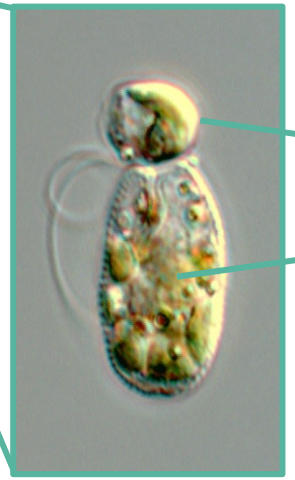
Karnkowska et al. 2023

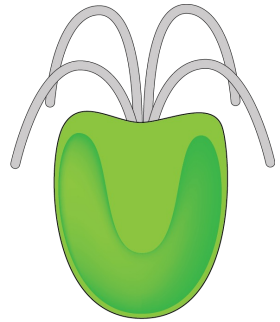
# *Rapaza viridis* phylogeny



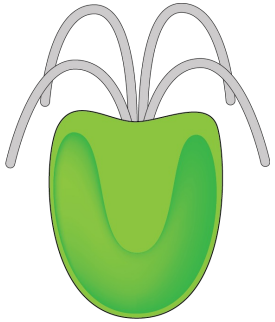



*Pyramimonas*
Prasinophytes

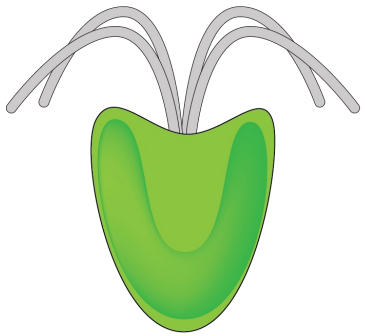




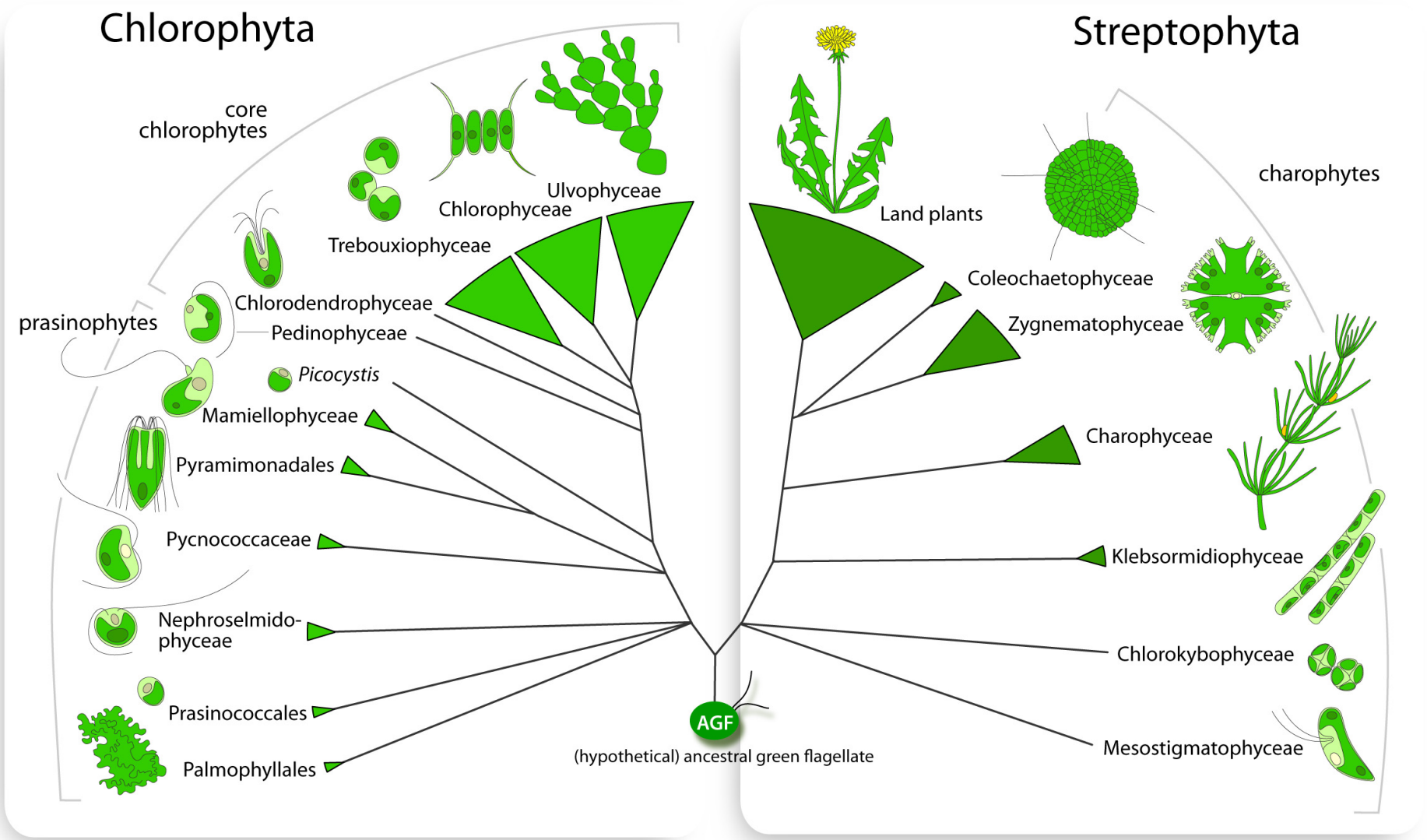
*Tetraselmis*
'core' chlorophytes



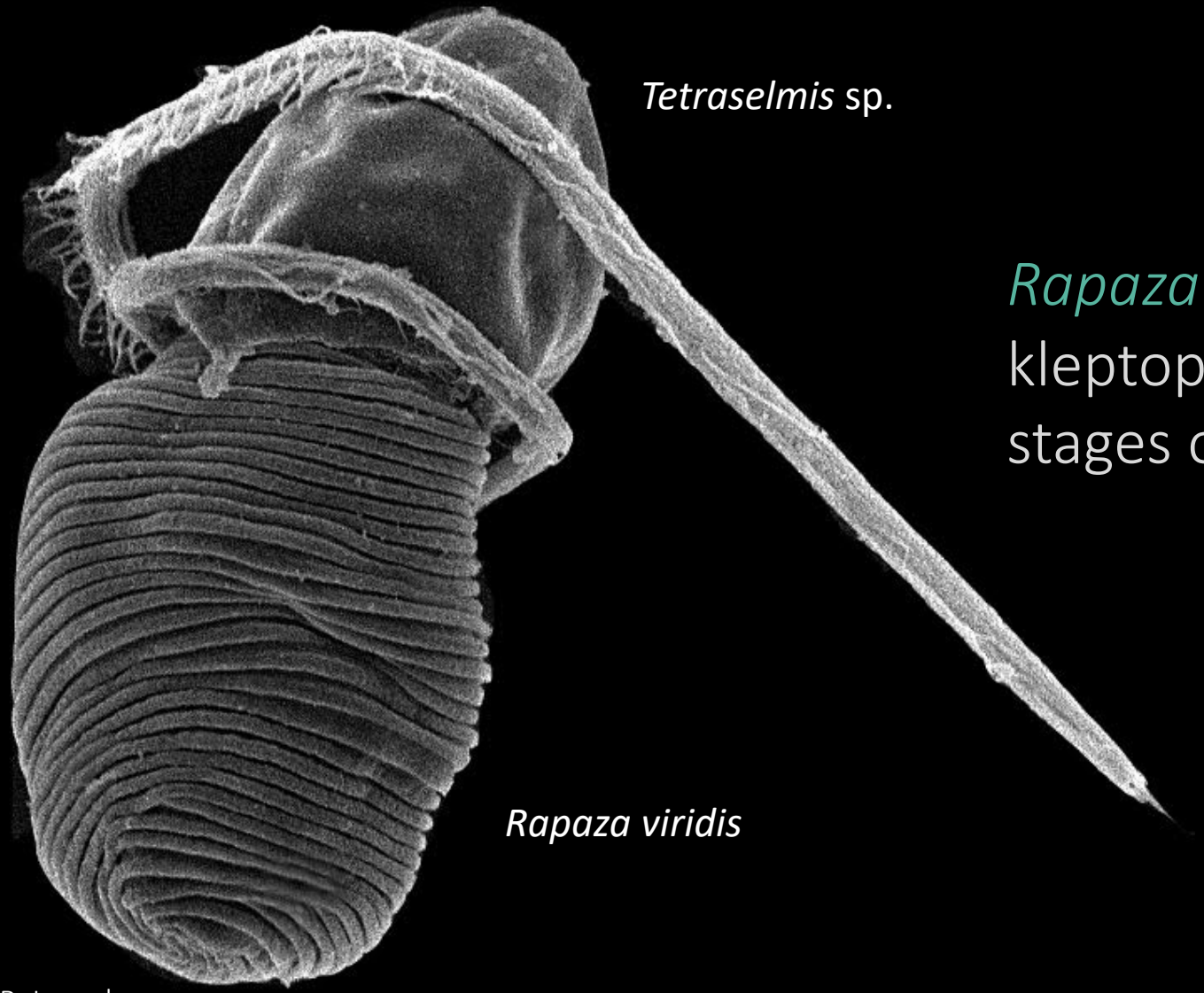
*Tetraselmis*
'core' chlorophytes



*Pyramimonas*
Prasinophytes



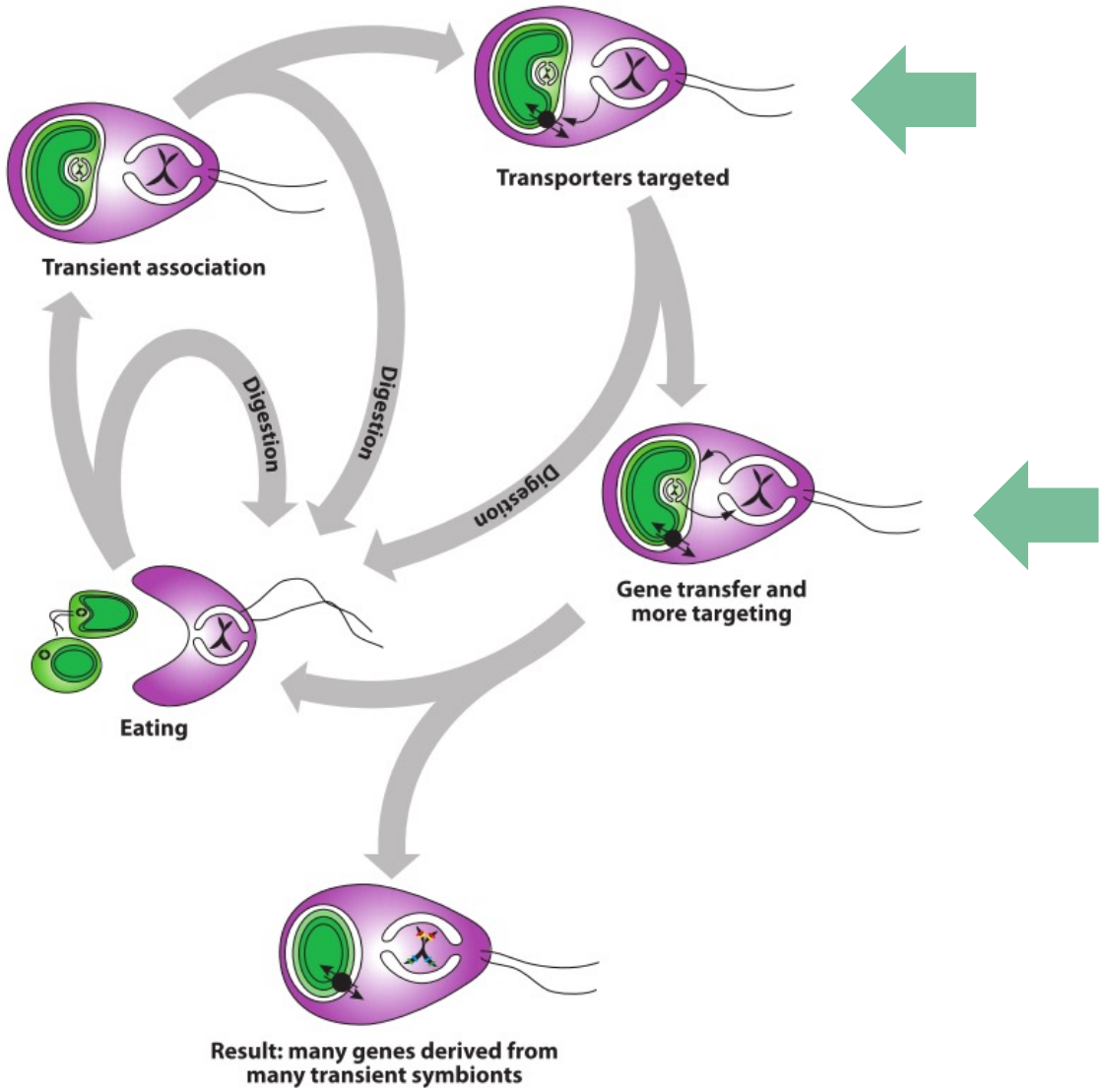

Modified from Leliaert *et al.*, *Crit. Rev. Plant Sci.* 31:1-46 (2012)
updated 25 Oct 2013




# *Rapaza viridis* (Euglenophyceae) and its kleptoplast as a model for studying early stages of endosymbiosis

B. Leander

# Which comes first, gene transfer or cellular fixation?

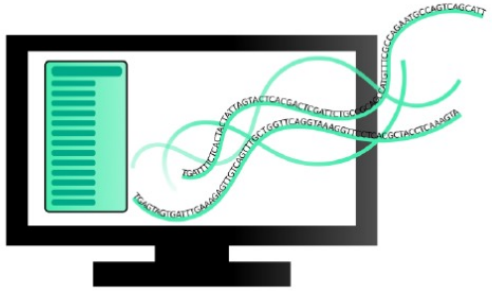



Genes encoding chloroplast proteins are transferred to nuclear genome via endosymbiotic gene transfer (EGT).

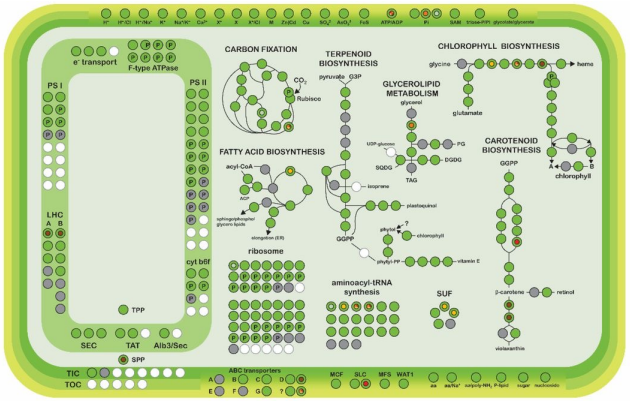
Plastid proteins encoded in nuclear genome are targeted to the plastids.

# Searching for plastid-targeted proteins in *Rapaza* transcriptome

## Sequencing and RNAseq analysis

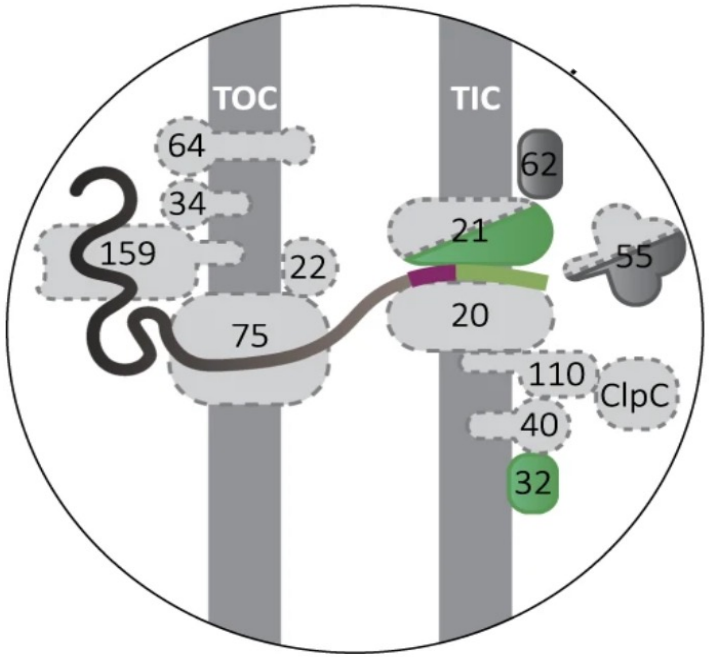


## Plastid proteins identification




274 proteins

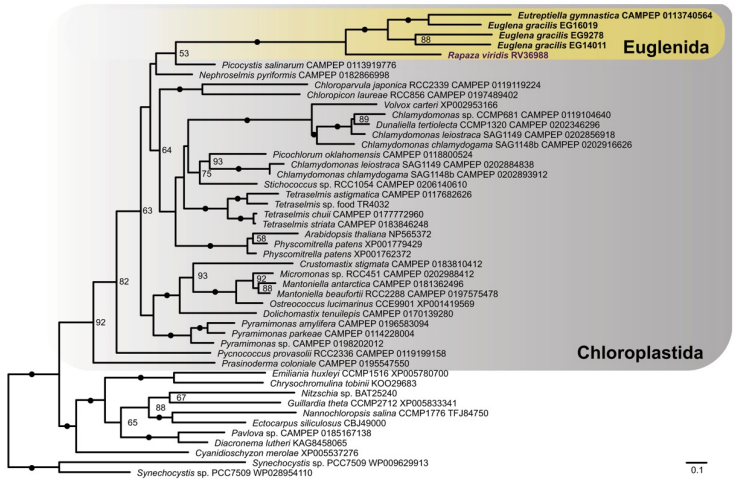
## Searching for translocon components



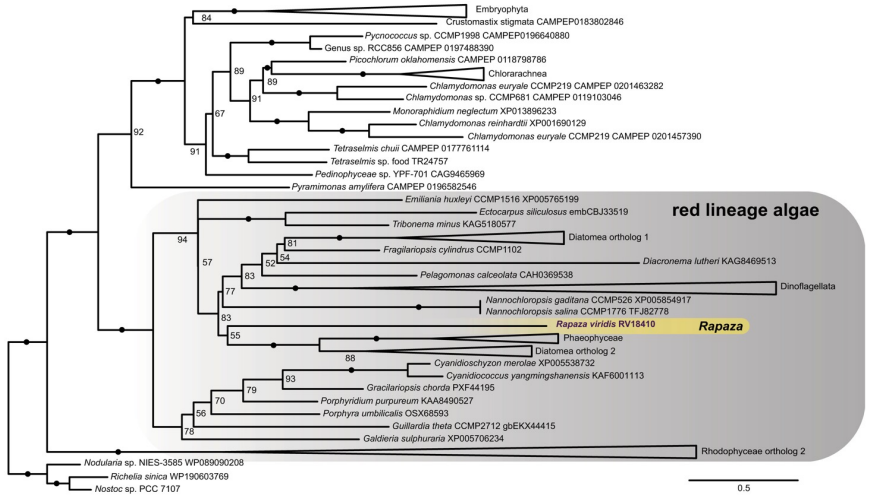

*Euglena* translocon components
Zahonova et al. 2018

# Translocon components of *R. viridis*

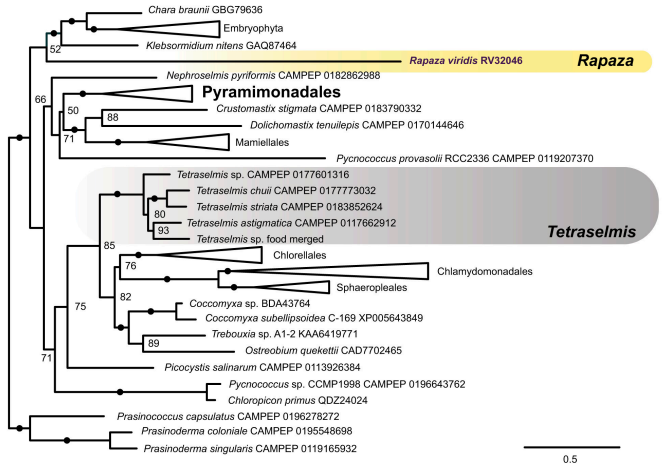
## Tic21

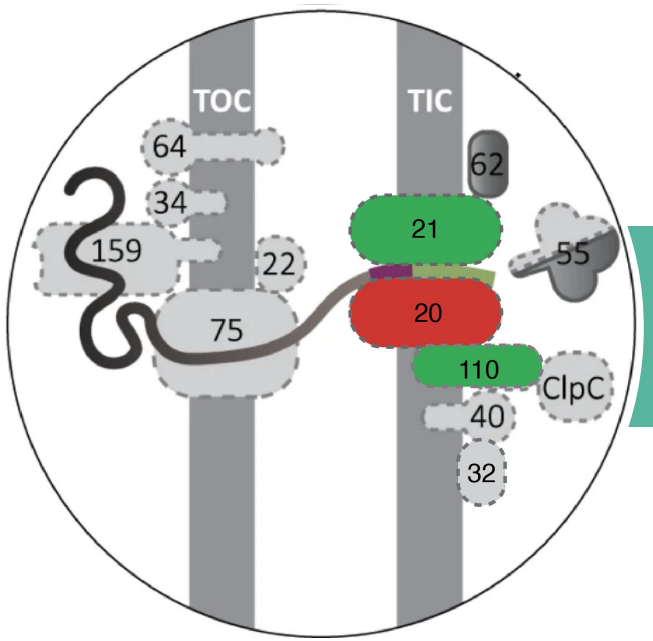



## Tic20




## Tic110



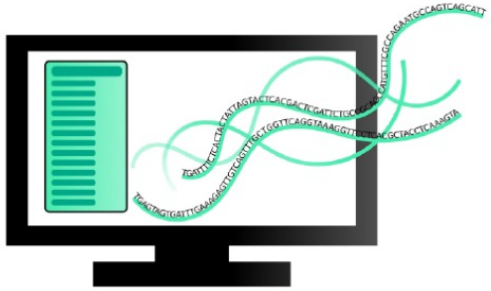

More components of translocon than in core Euglenophytes
Diverse origin of genes encoding translocon components

Karnkowska et al. (2023)

Are there any plastid proteins encoded in nuclear genome of *Rapaza* targeted to kleptoplasts?

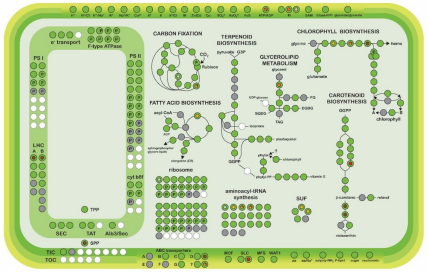
# Searching for plastid-targeted proteins in *Rapaza* transcriptome

## Sequencing and RNAseq analysis



## Plastid proteins identification

274 proteins



## Targeting signal prediction

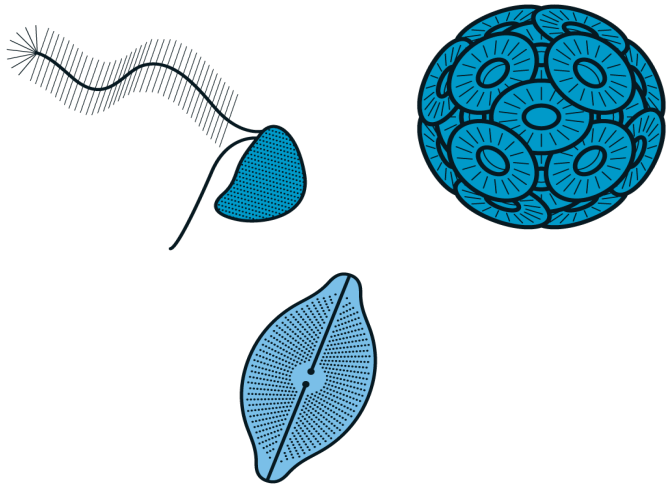
Yes!


## Phylogenetic analyses of candidate proteins

# Searching for plastid-targeted proteins in *Rapaza* transcriptome

Phylogenetic analyses of candidate proteins

60% originated from green algae



40% from other evolutionary lineages

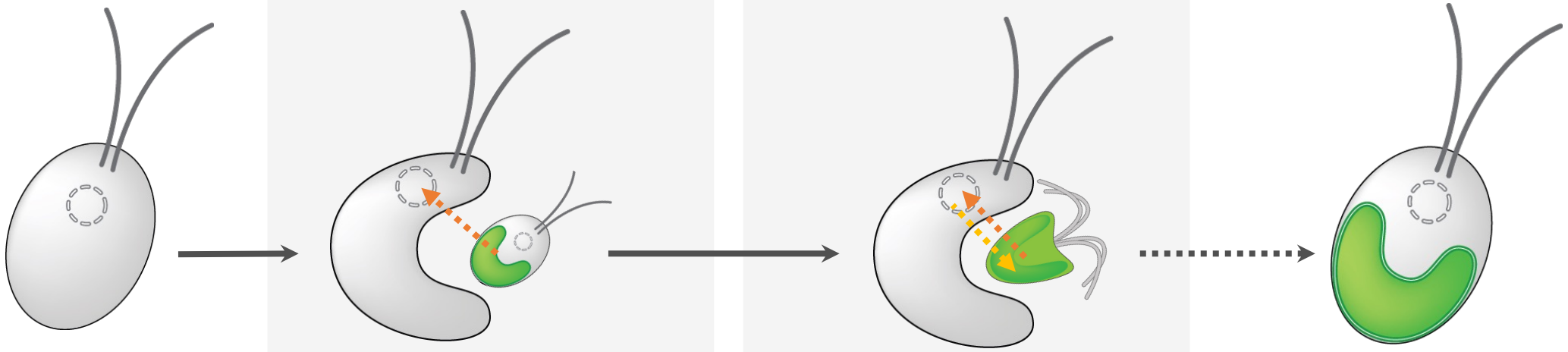
proteins derived from different lineages as the kleptoplast indicate that transfer of genes preceded establishment of the endosymbiont

# origin of plastids via kleptoplasty

## gene transfer comes before cellular fixation

transfer of genes encoding plastid proteins to the nuclear genome

targeting of plastid proteins to the kleptoplast



heterotrophic euglenid

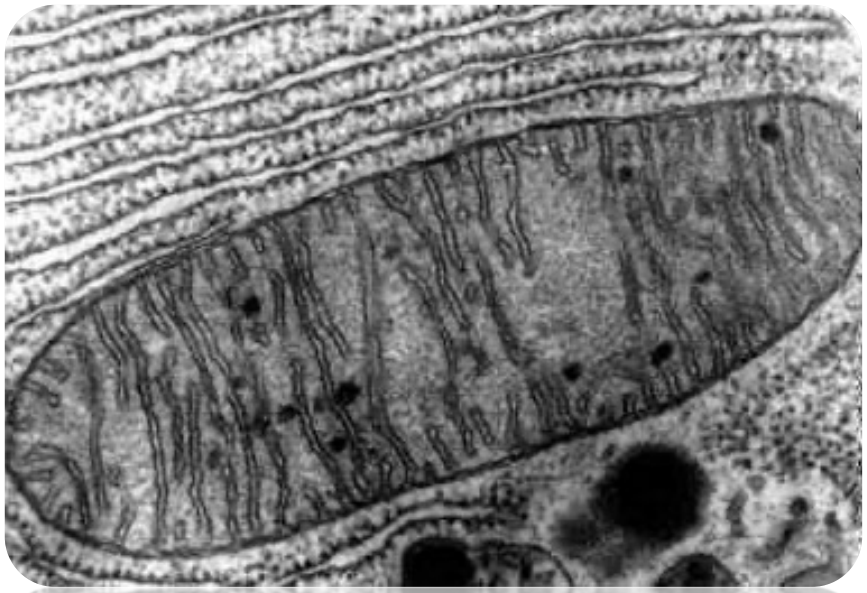
feeding on various algae

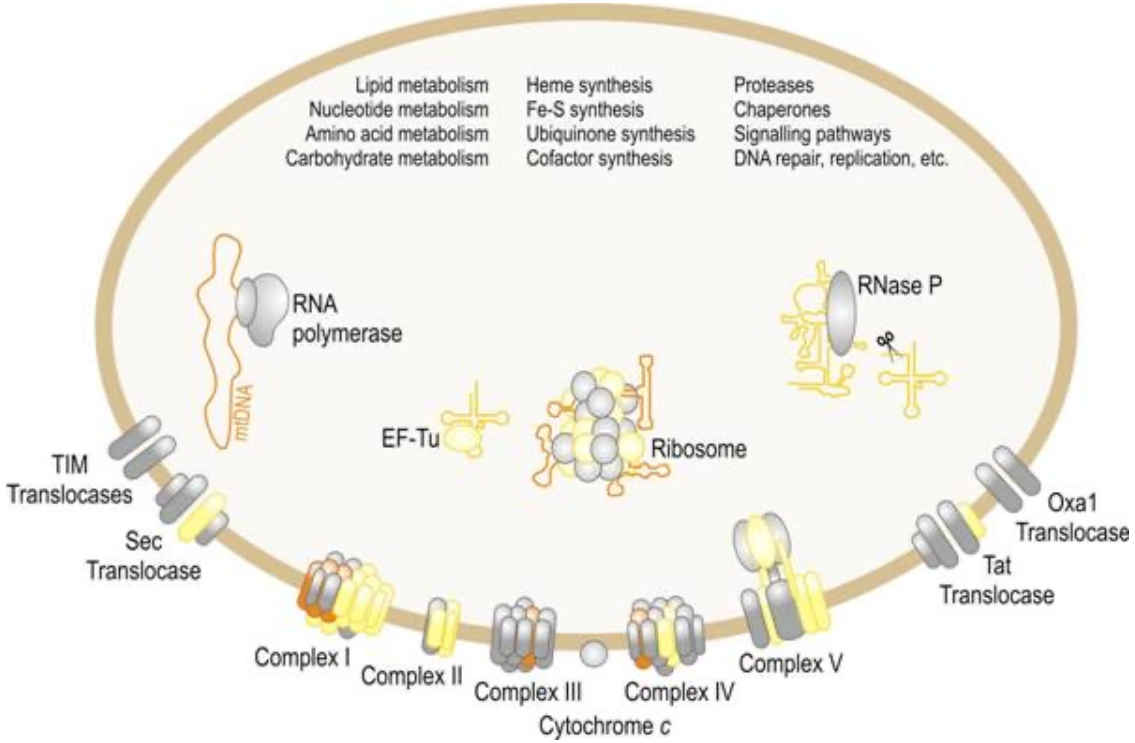
mixotrophic euglenid

phototrophic euglenid

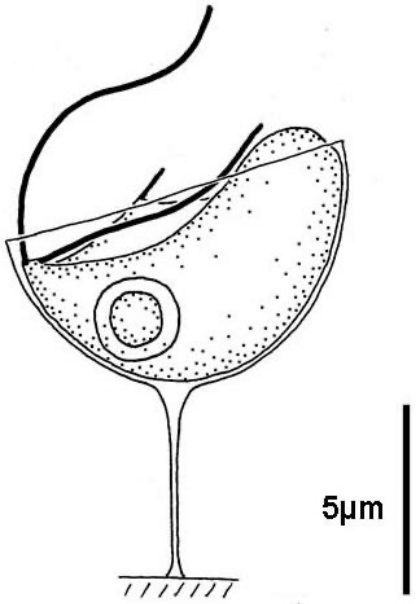
Karnkowska et al. (2023)

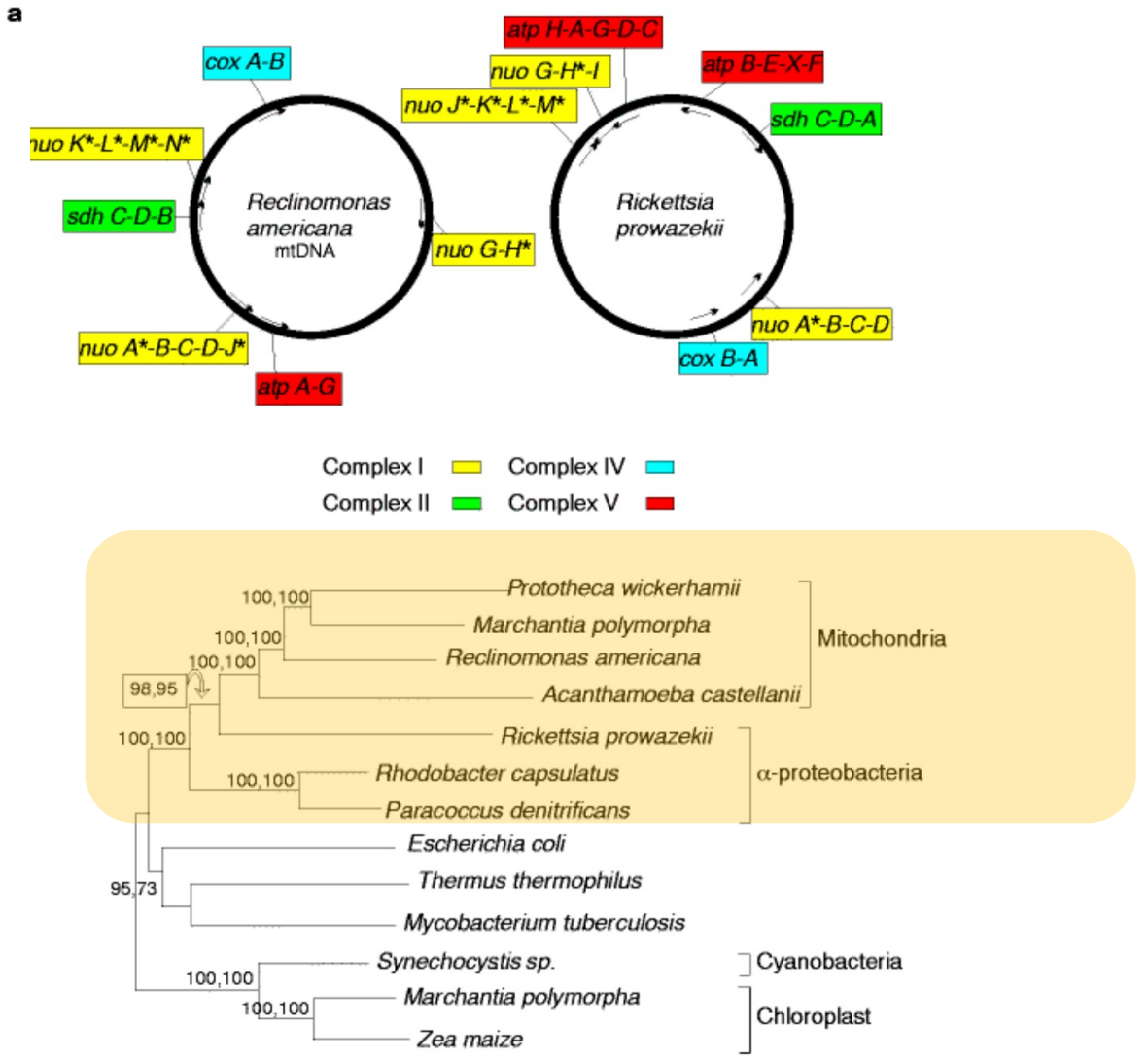
# mitochondria





# The genome sequence of *Rickettsia prowazekii* and the origin of mitochondria

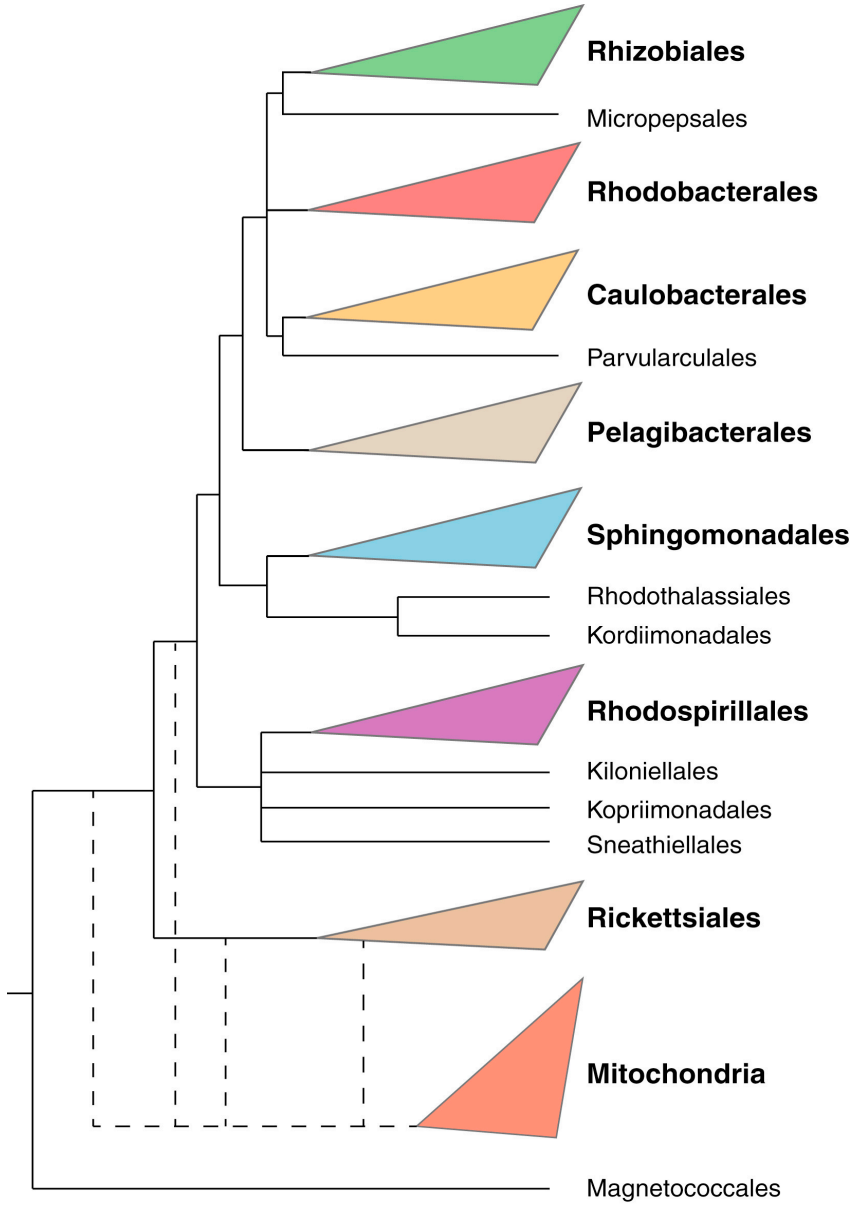



Andersson (1998), Nature

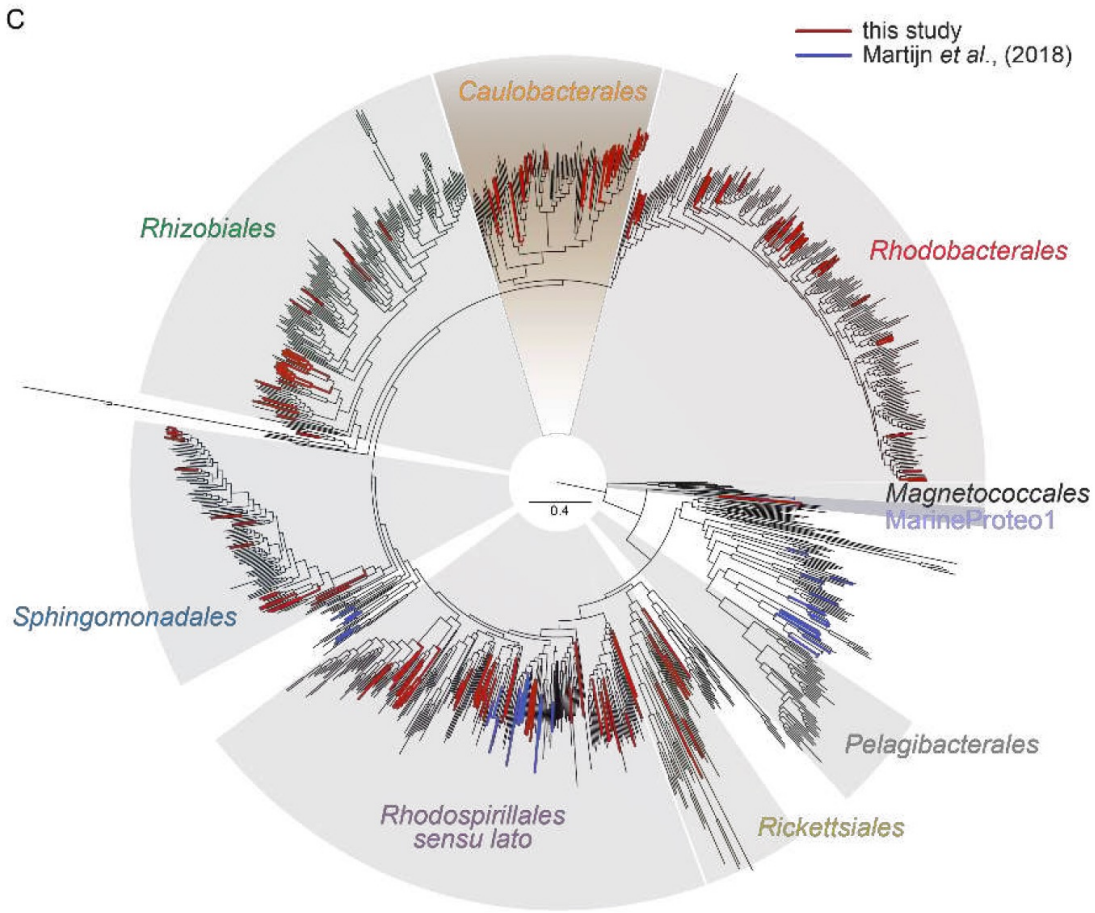
# Alphaproteobacterial phylogenomics and origin of mitochondria

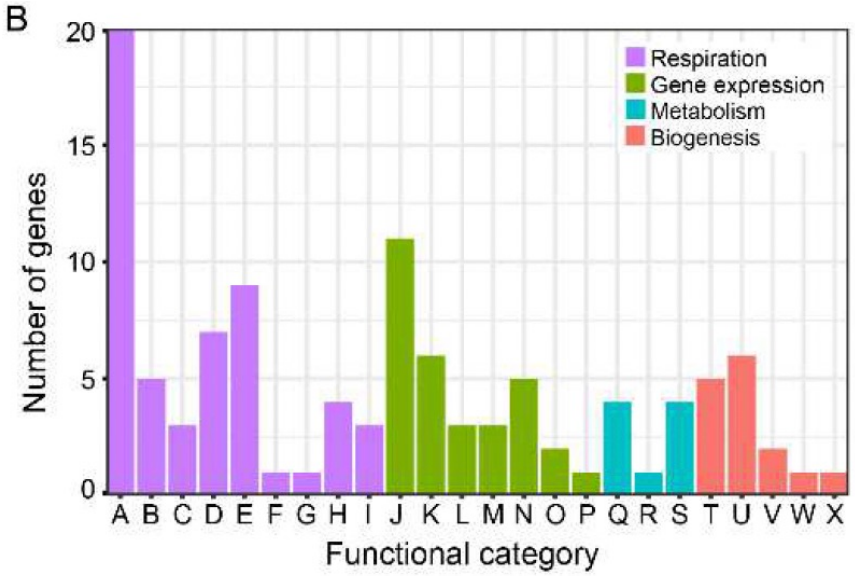
- The tree of alphaproteobacteria is not resolved
- Number of genes of alphaproteobacterial origin in mitochondrial genomes is limited (not much phylogenetic signal)

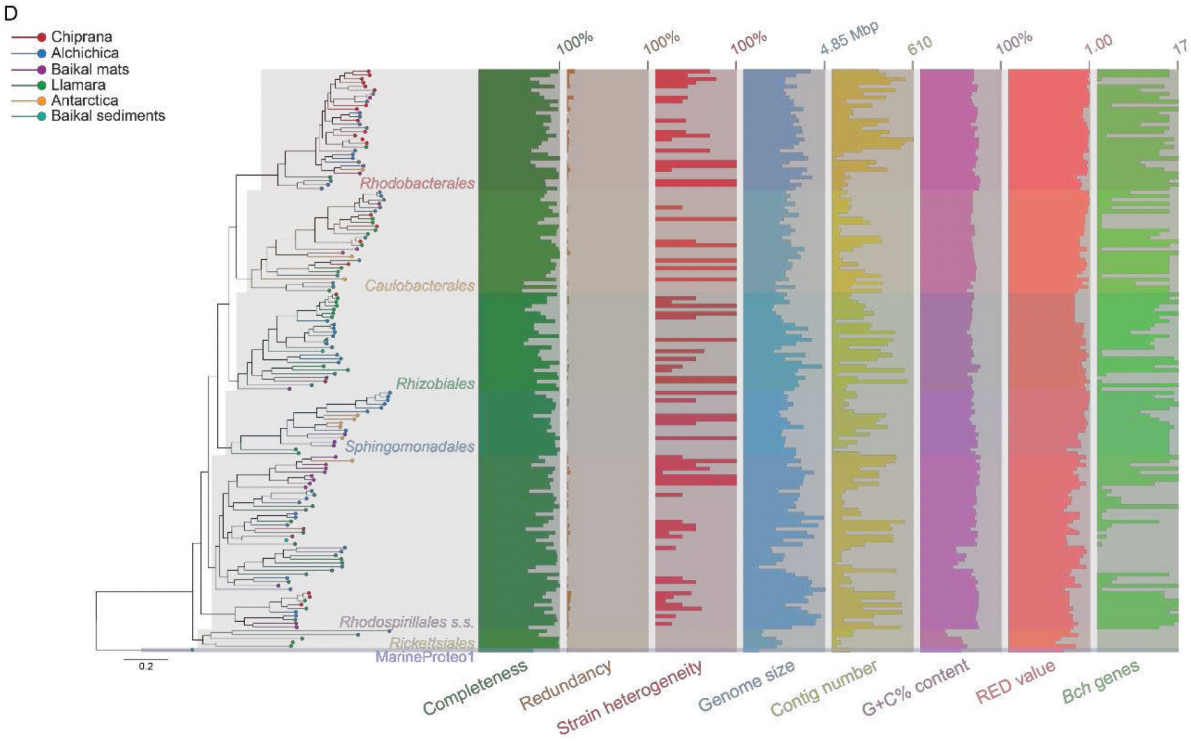



Roger et al. 2017

# Environmental MAGs allow to expand the taxa sampling

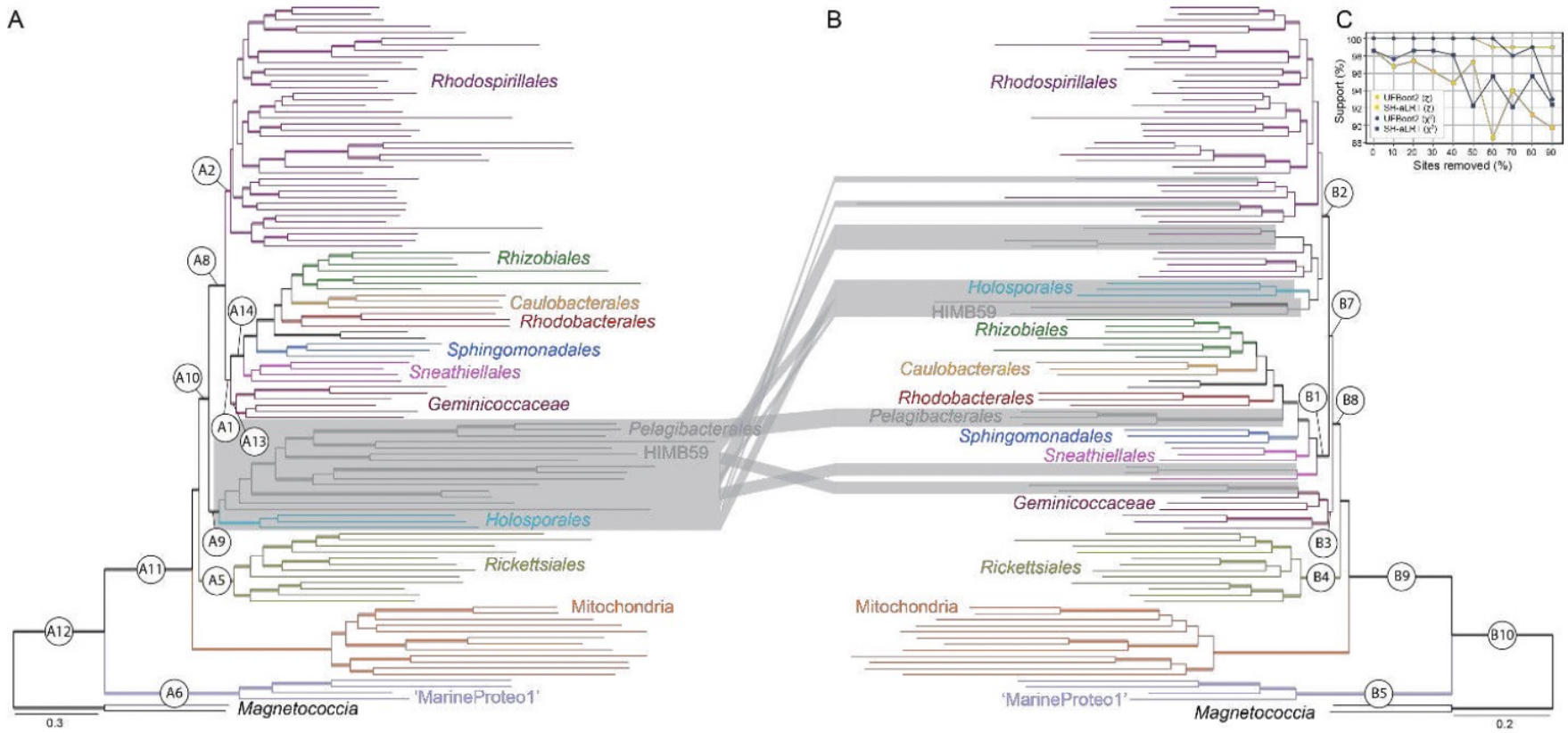



Munoz-Gomez et al. 2022

# Expanded dataset favour mitochondria as sister to known Alphaproteobacteria




(A) Phylogenetic tree for the *Alphaproteobacteria* and mitochondria derived from a site-heterogeneous analyses of an untreated dataset.

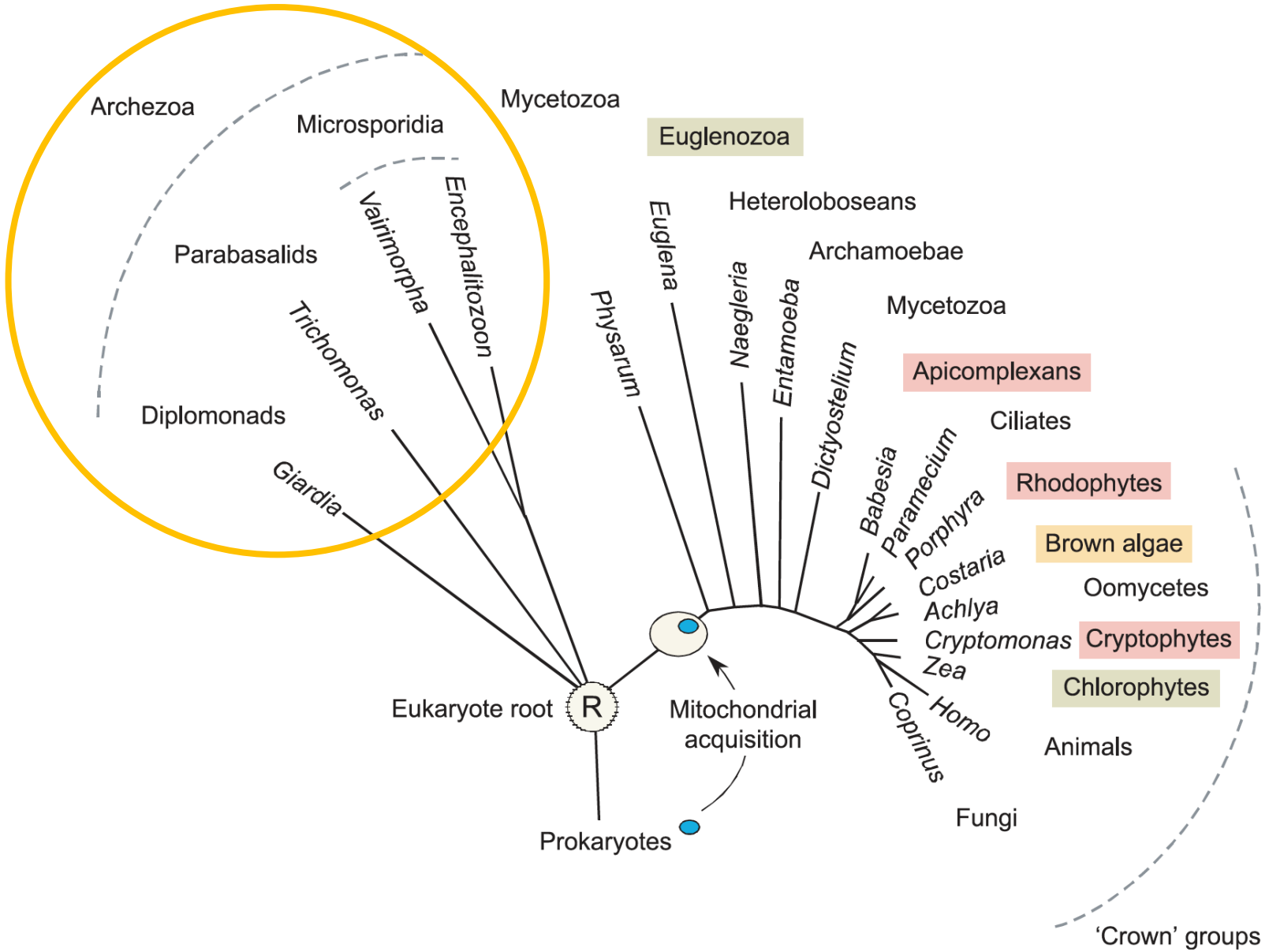
(B) Phylogenetic tree for the *Alphaproteobacteria* and mitochondria derived from a site-heterogeneous analysis of a dataset from which 50% of the most compositionally heterogeneous sites had been removed.

Munoz-Gomez et al. 2022

Which came first nucleus or mitochondrion?

# Archezoa hypothesis

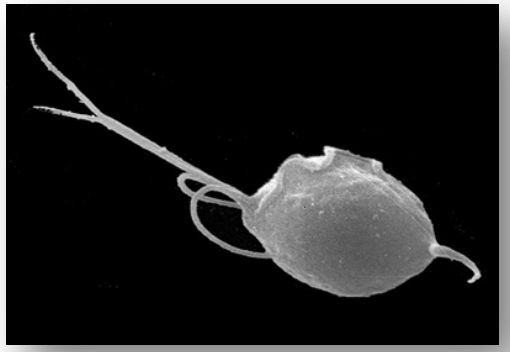
Thomas Cavalier-Smith, 1989



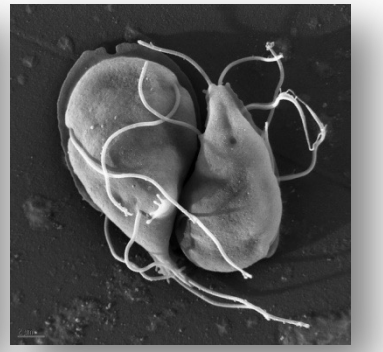

Embley and Martin (2006) Nature

# Archezoa

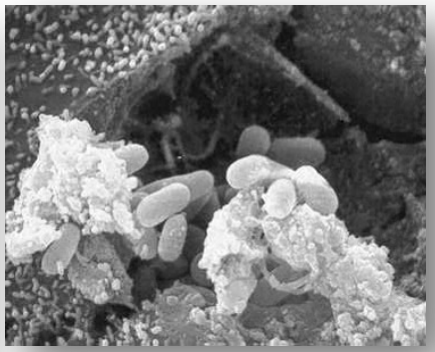
- early branching eukaryotes
- lack of introns
- no sexual reproduction
- lack of peroxisomes
- lack of Golgi apparatus
- lack of mitochondria



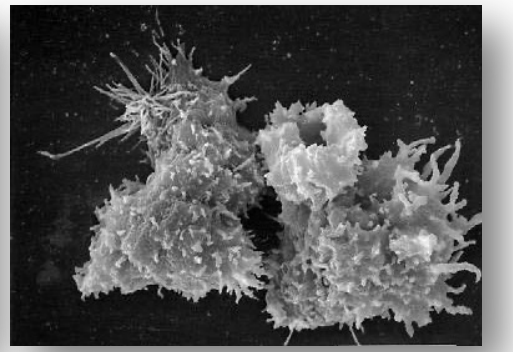
*Trichomonas*



*Giardia*



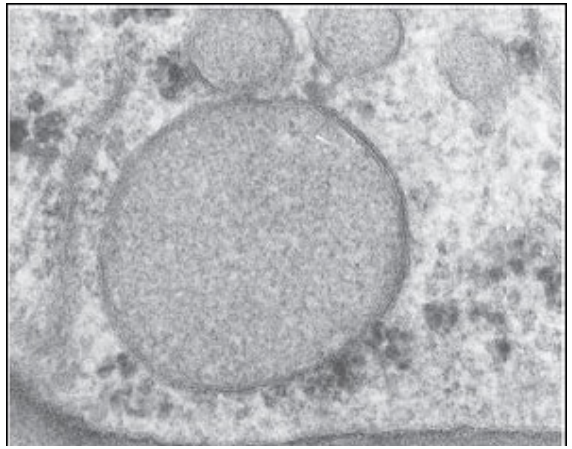
Microsporidia



Archamoebae

# Archezoa posses mitochondria related organelles (MROs)

mitochondrion



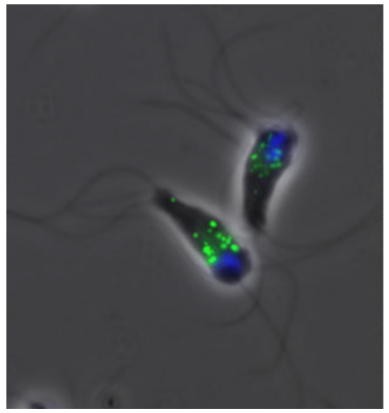
hydrogenosome

mitosomes

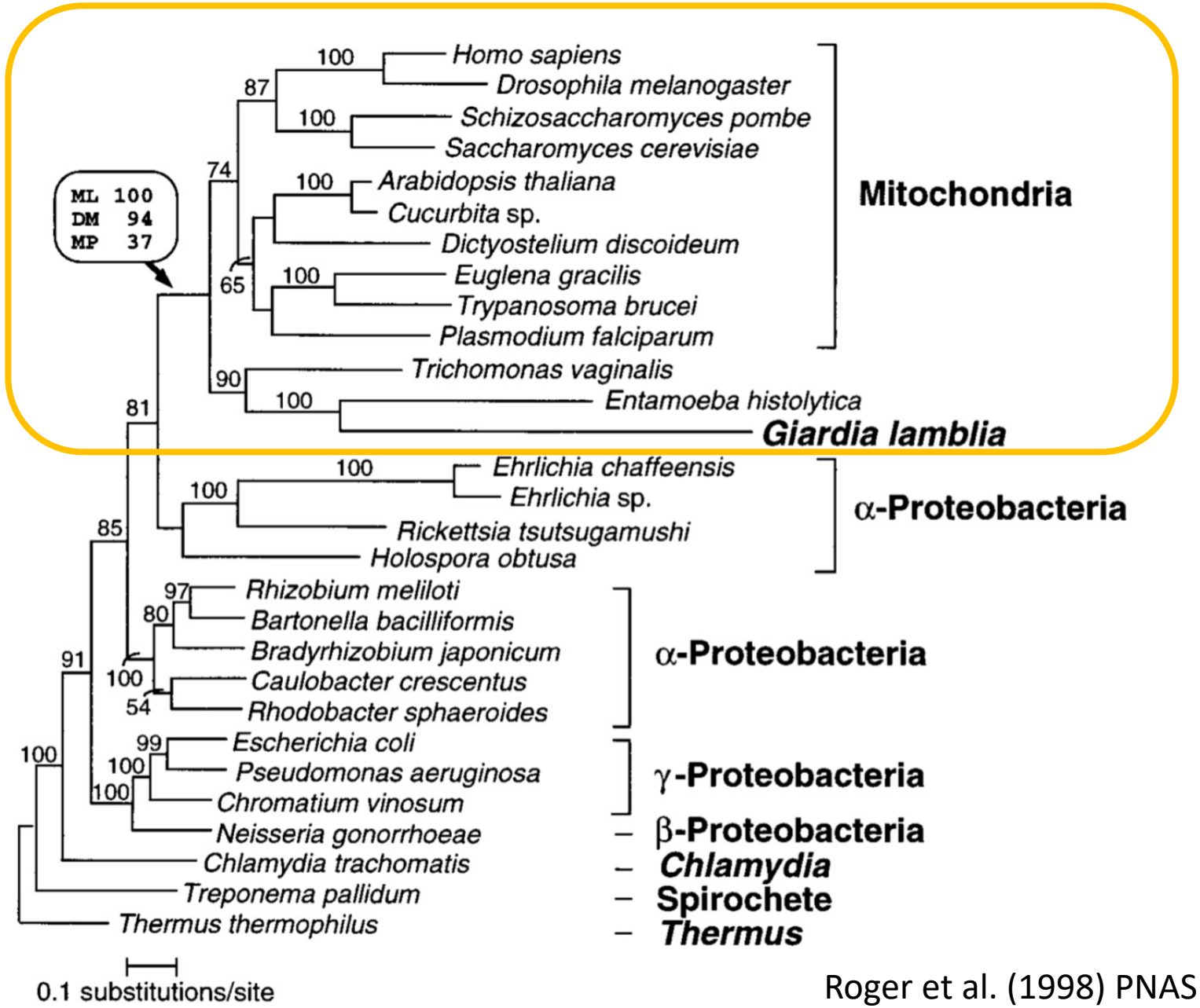
# Common origin of mitochondria and MROs

**Cpn60 chaperonin**

- mitochondrial chaperonins
- ATP transporters
- mitochondrial membrane transport proteins
- Fe-S cluster assembly proteins



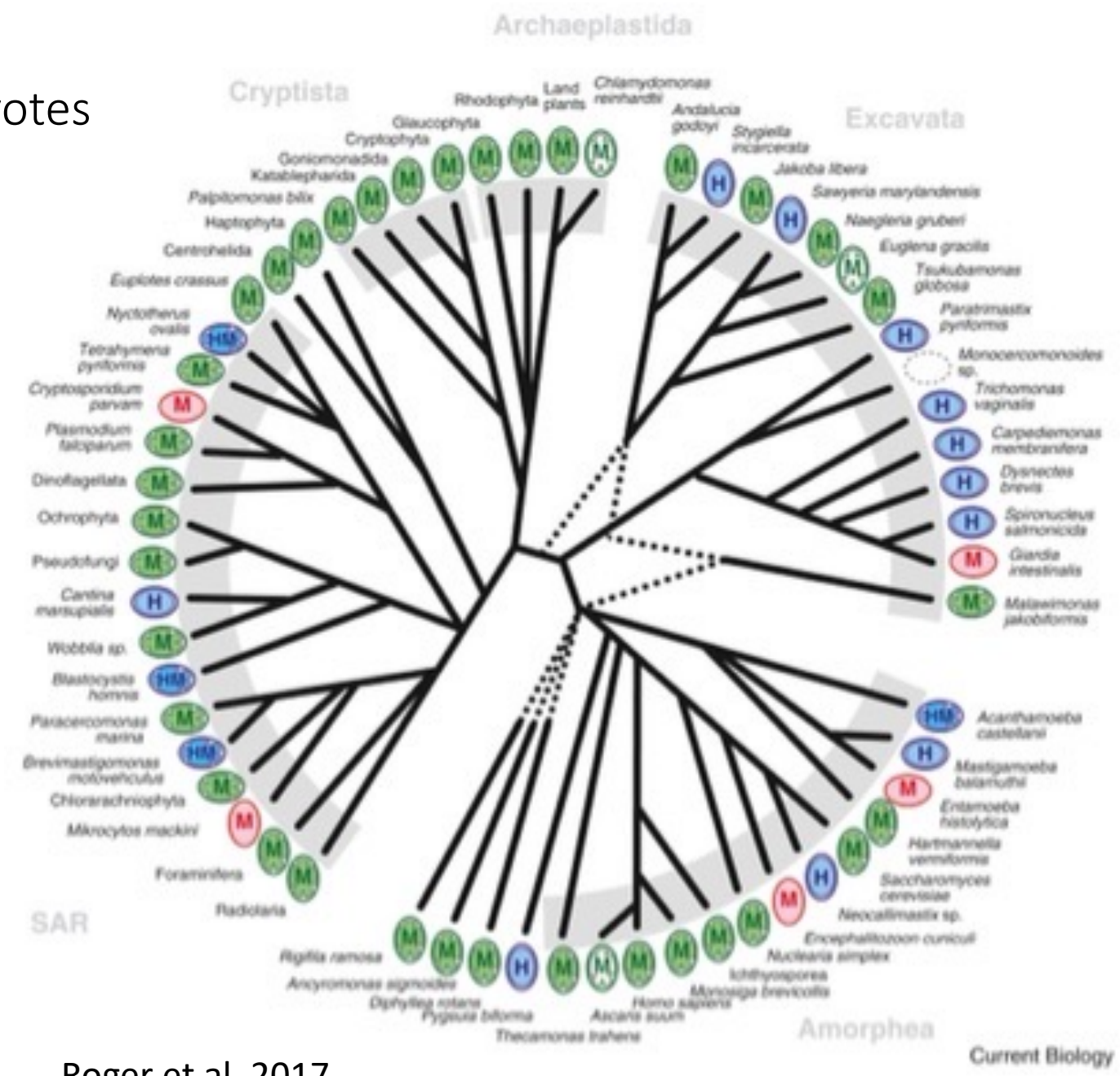
cpn60 localization
Jerlström-Hultqvist et al. 2013




Roger et al. (1998) PNAS

# Evolution of mitochondria

MROs are widespread at the tree of eukaryotes



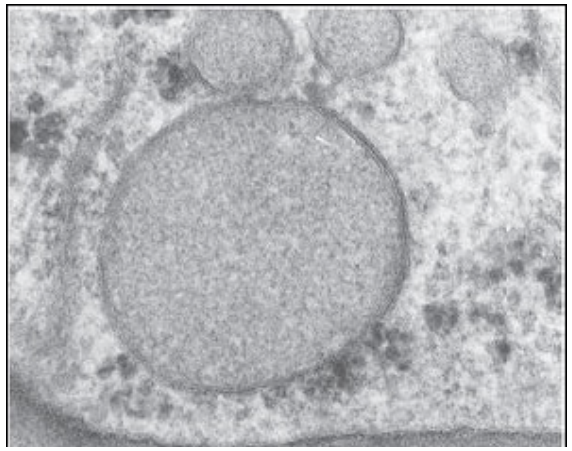

Roger et al. 2017

# Archezoa hypothesis rejected

• All “archezoa” possess:
- mitochondrial genes in nuclear genomes
- degenerate derivatives of mitochondria
- they do not group together on the modern tree of life

Common ancestor of all eukaryotes possessed mitochondria

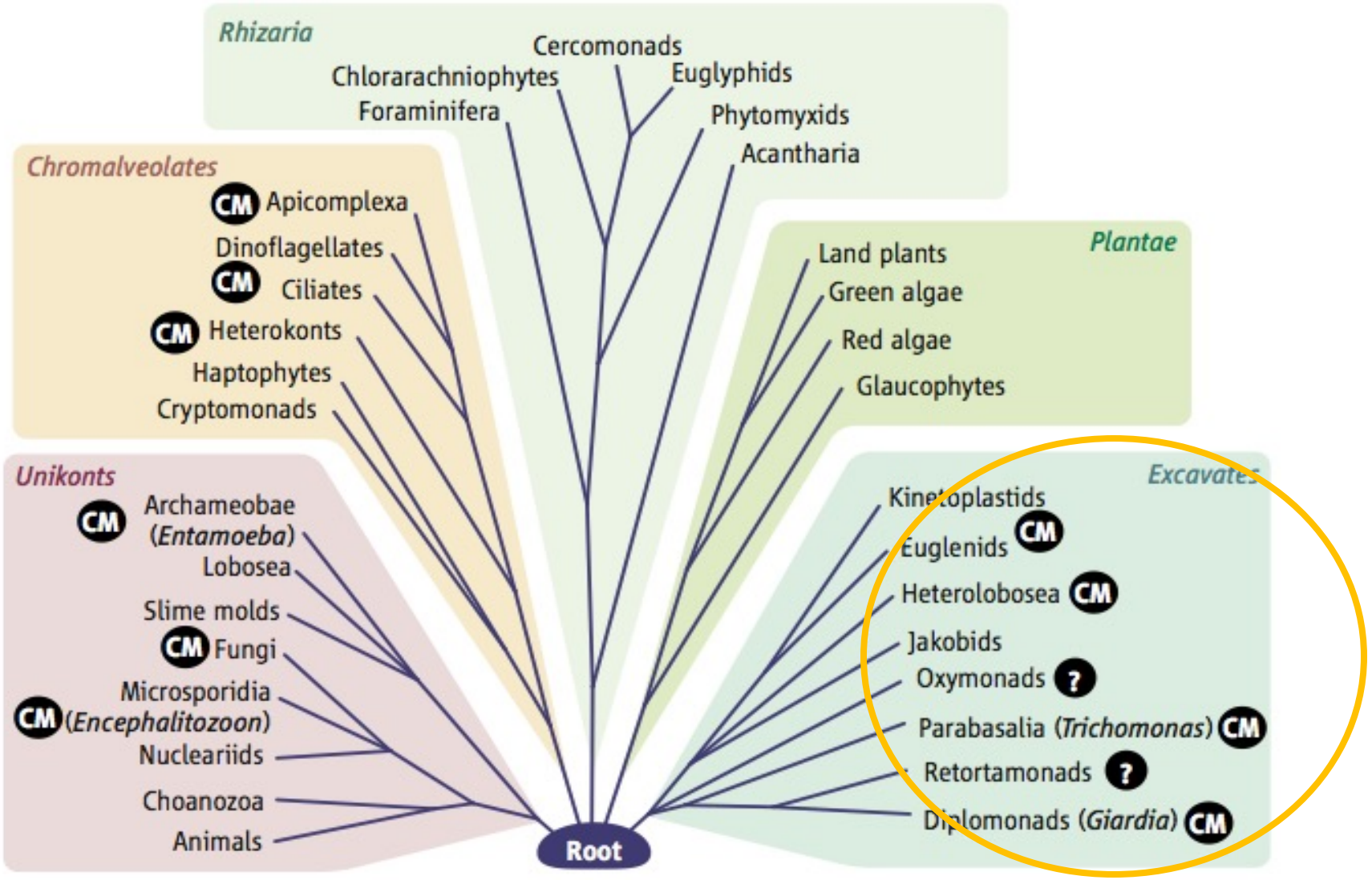
mitochondrion



hydrogenosome

mitosomes

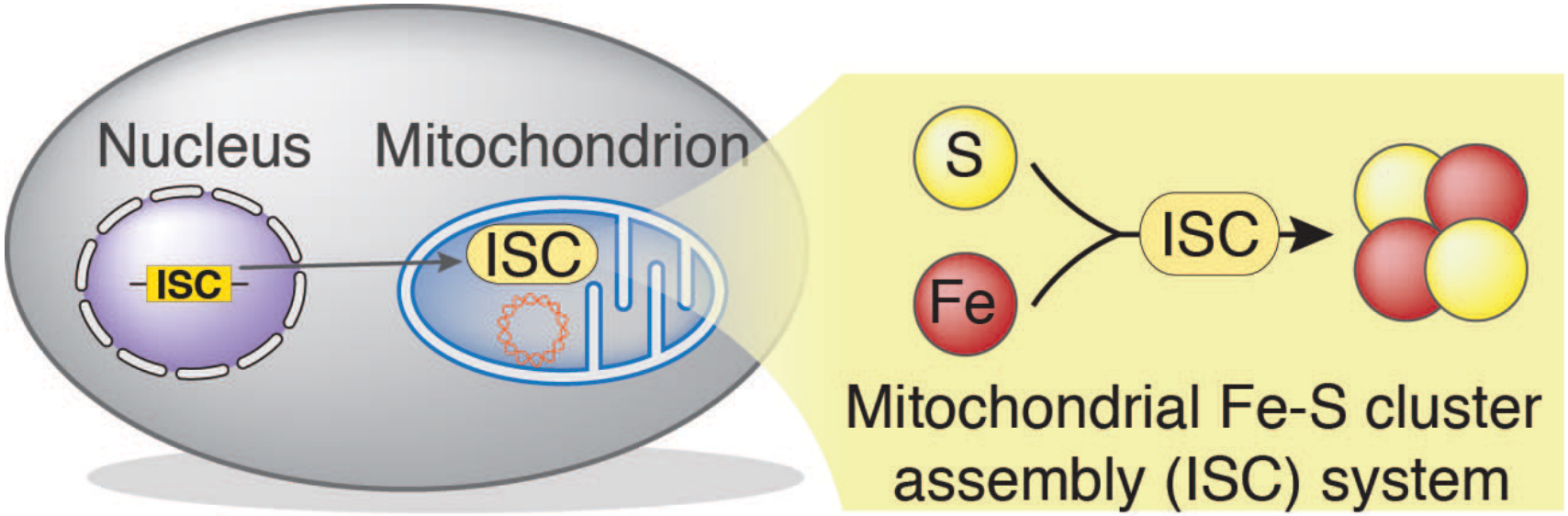
Does amitochondriate eukaryote exist?




CM cryptic mitochondria

Keeling, 2007

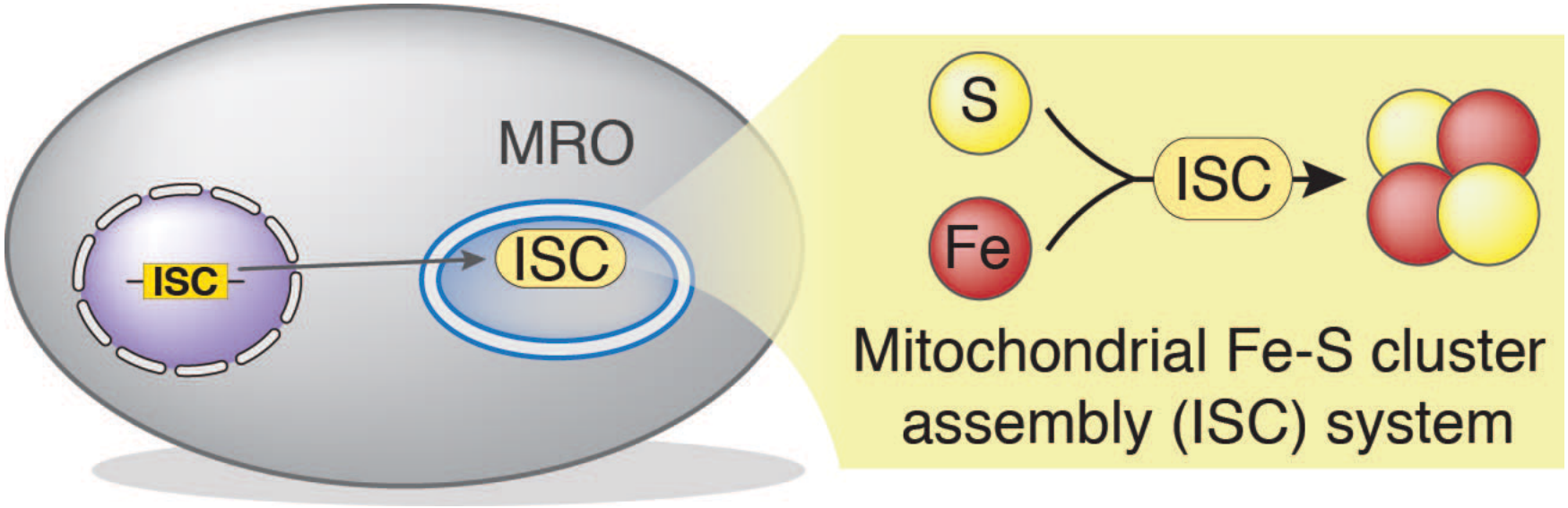
# A eukaryotic cell with typical mitochondria

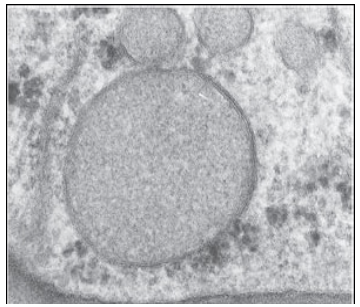



Oxidatvie phosphorylation, and other essential process such as Fe-S cluster formation takes part in mitochondria

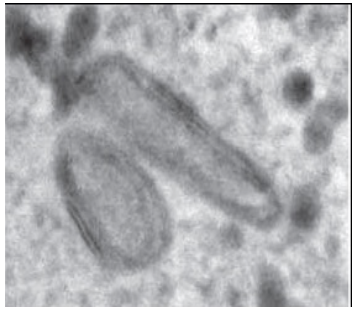
**Fe-S clusters are cofactors of essential enzymes**

# An anaerobic eukaryote with mitochondrion related organelles (MROs)



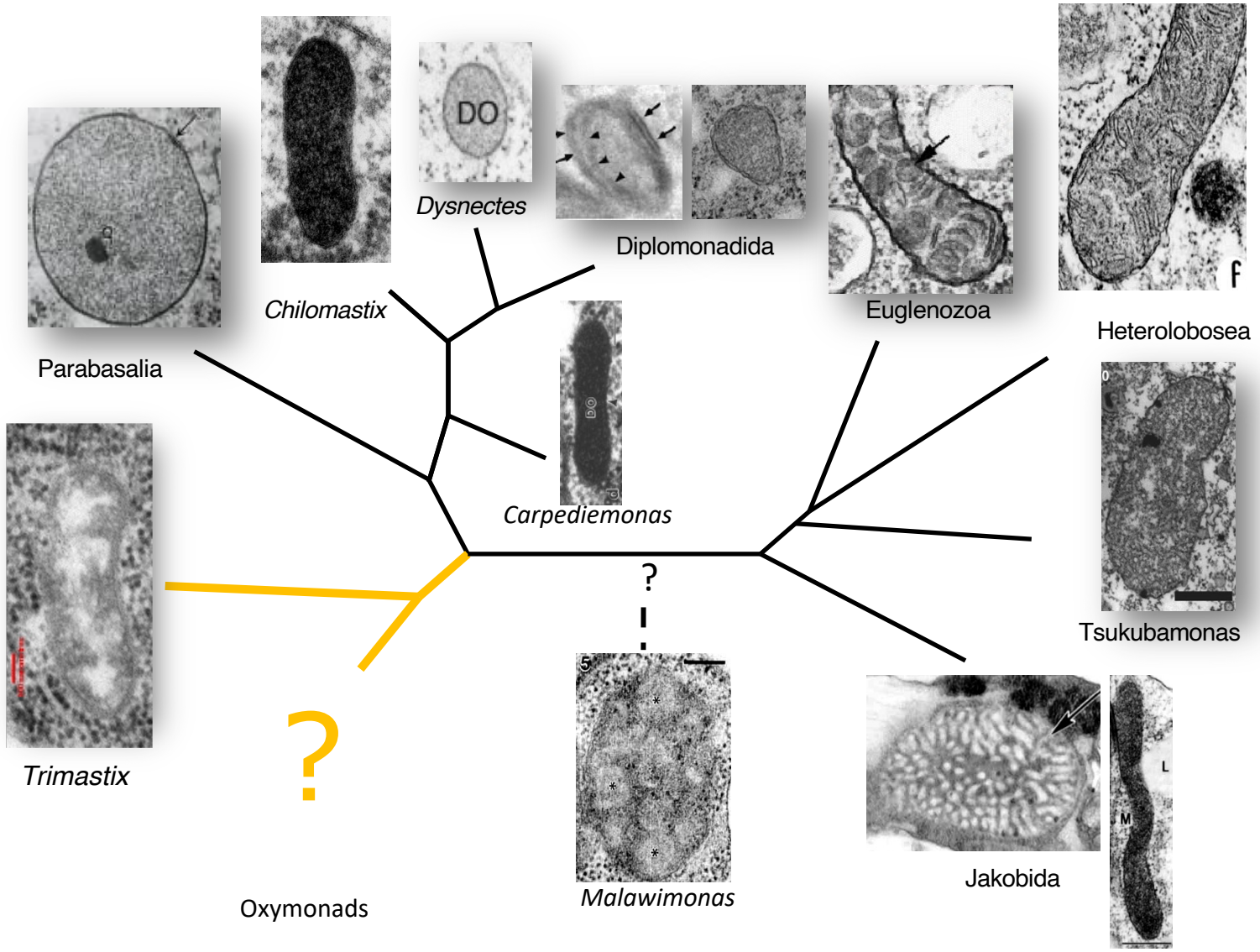
hydrogenosome

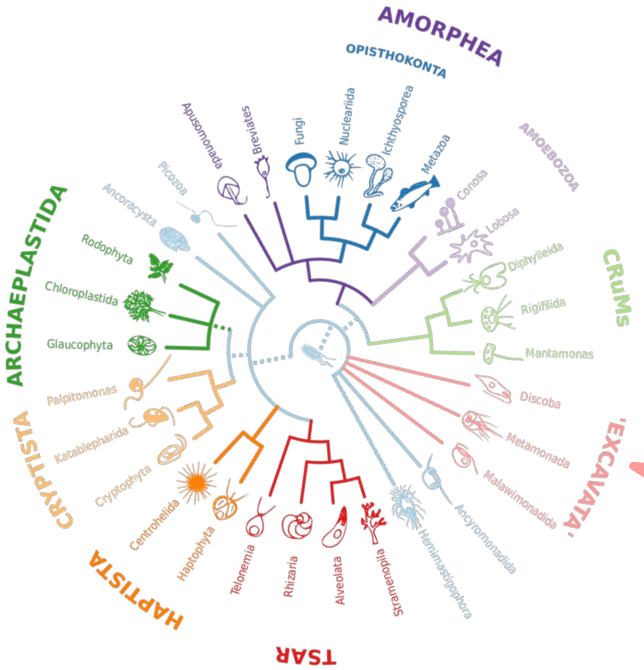


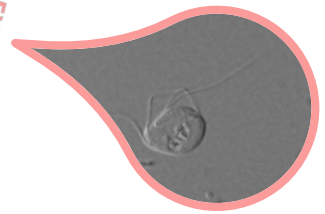
mitosome

**Loss of oxidative phosphorylation** in anaerobic eykaryotes

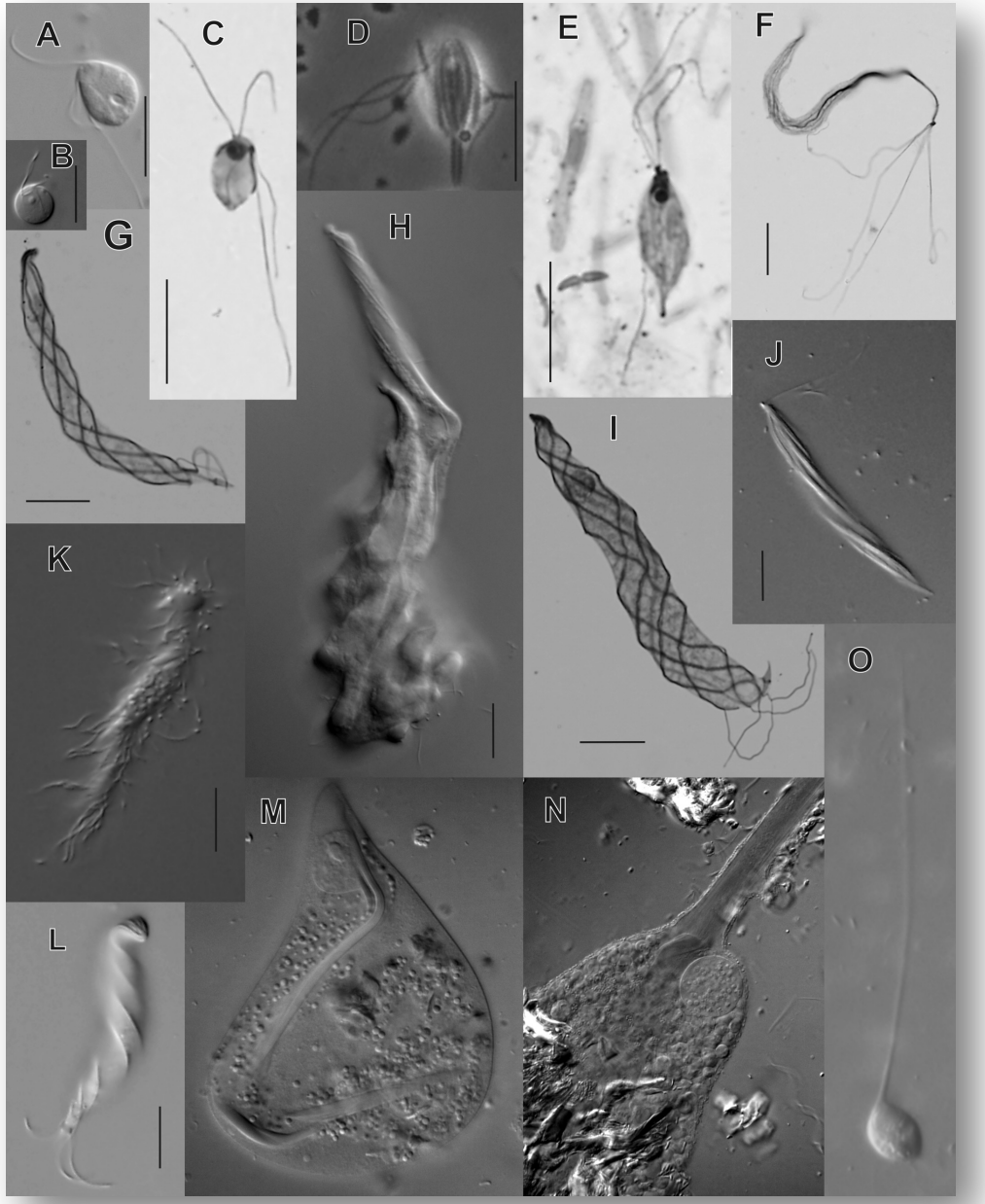
# mitochondria in ‘Excavata’





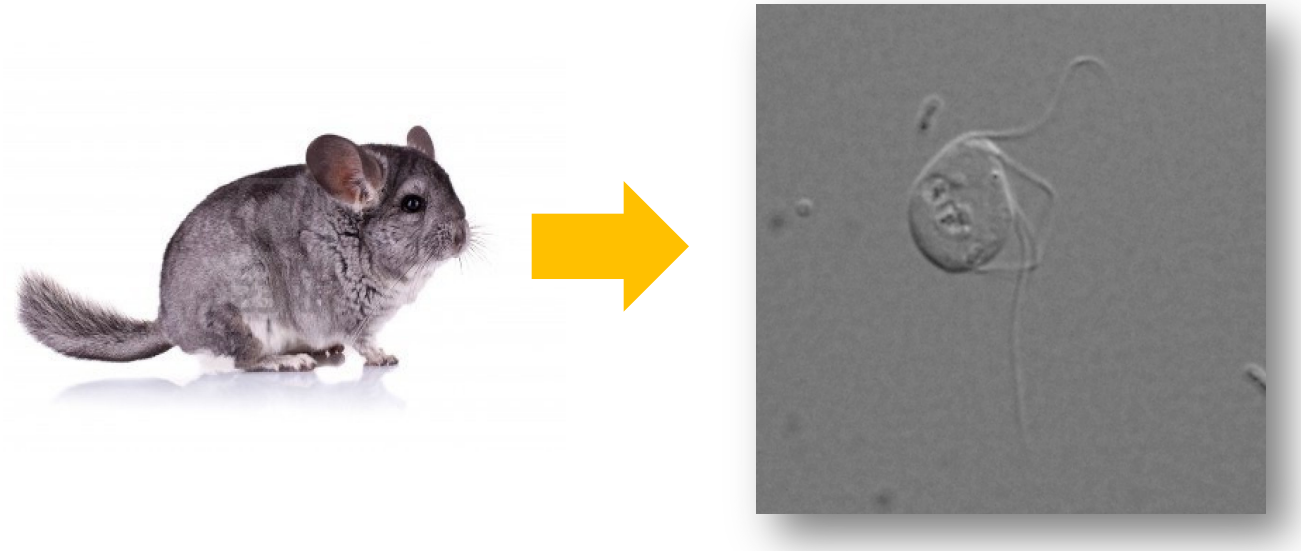



Metamonada
- Parabasalia (*Trichomonas*)
- Fornicata (*Giardia*)
- Preaxostyla
  - Trimastix
  - oxymonads




- found in the intestinal tracts of animals
- sexual reproduction debatable
- no peroxisomes
- no Golgi apparatus
- no mitochondria

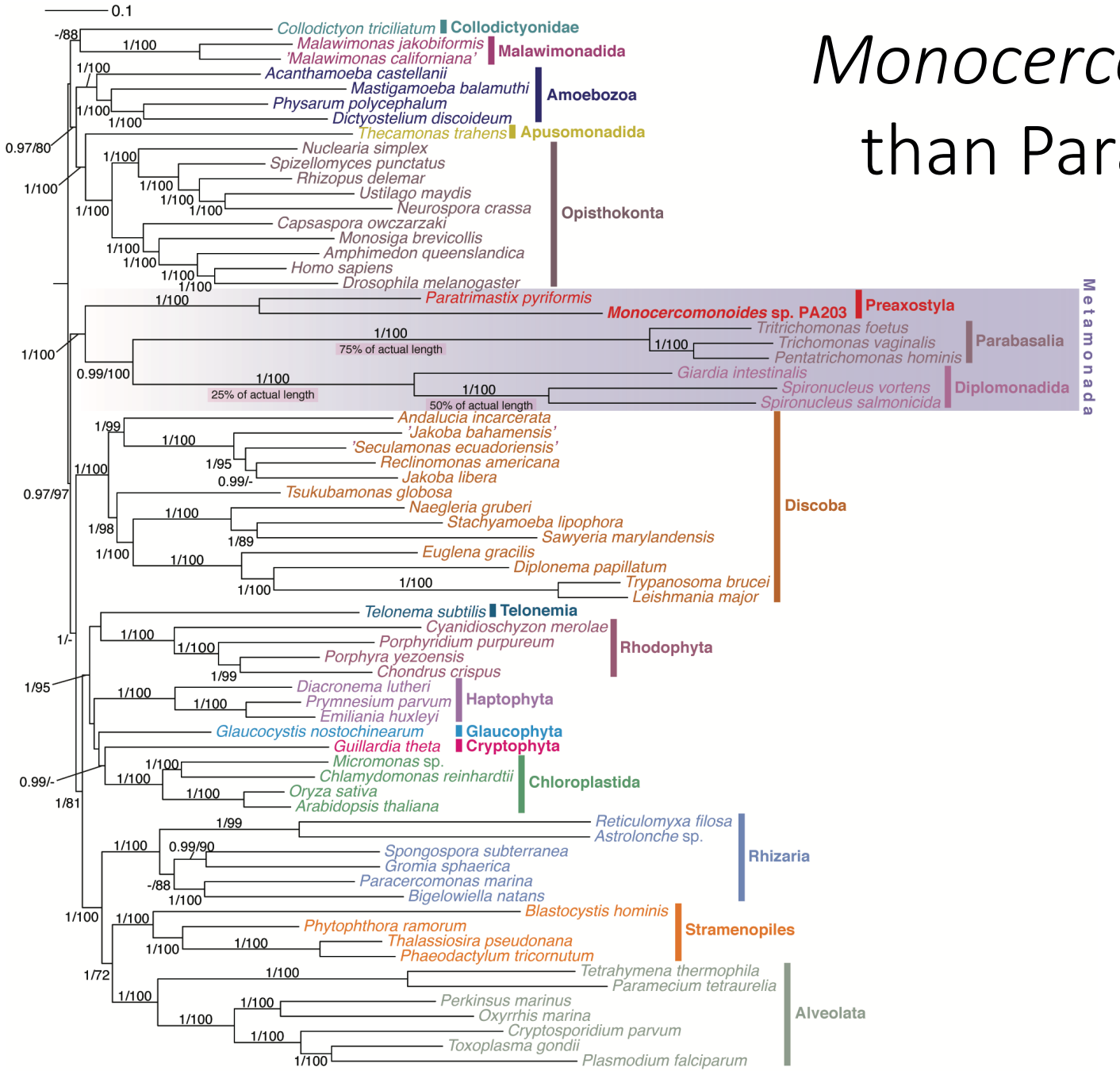
# *Monocercomonoides* - microaerophilic, commensal of animals



lack of mitochondria in *Monocercomonoides* under the microscope

genome analysis of *Monocercomonoides*

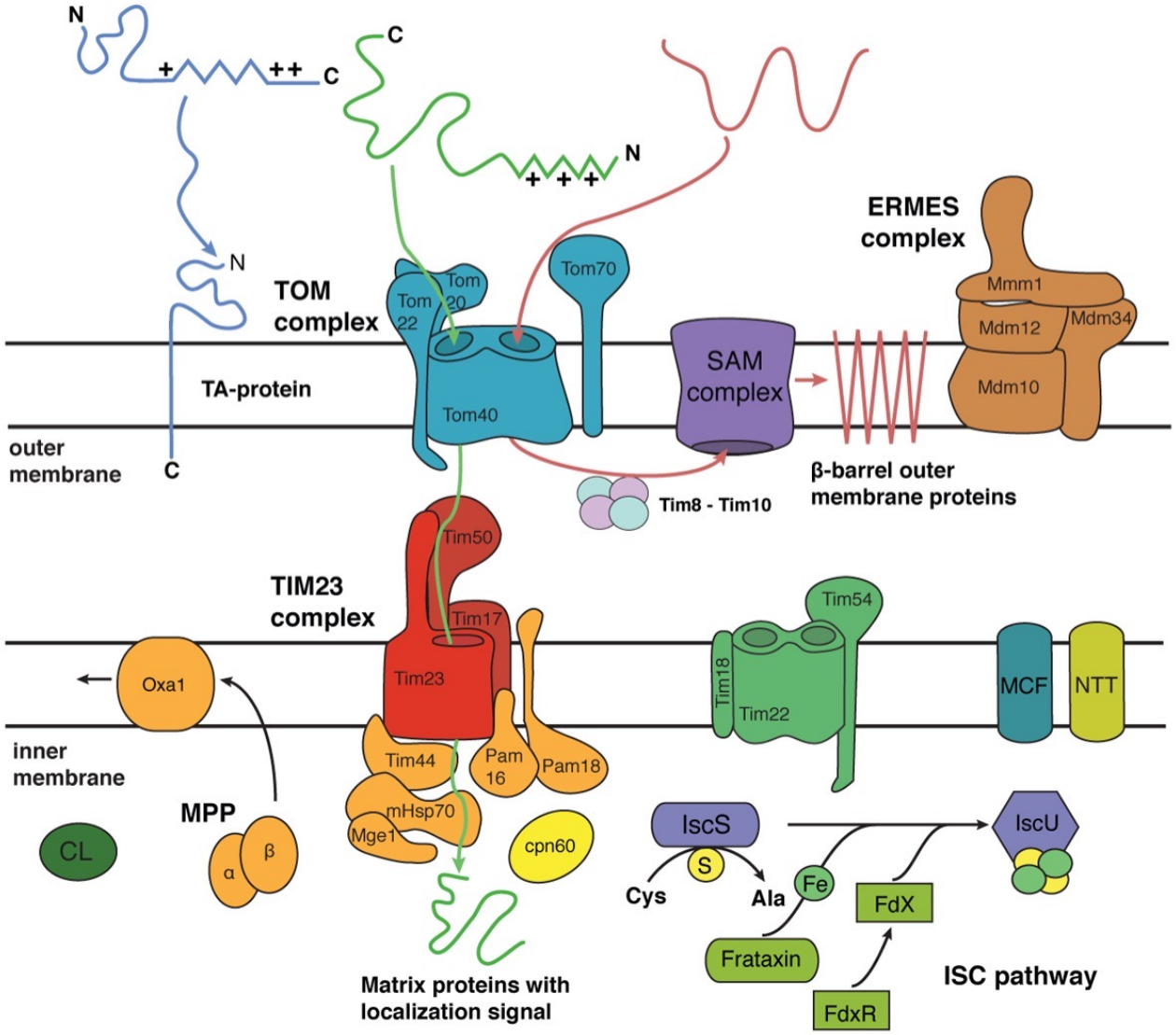
# *Monocercomonoides* is less divergent than Parabasalids and Diplomonads




Karnkowska et al. (2016)

# Searching for mitochondrial proteins

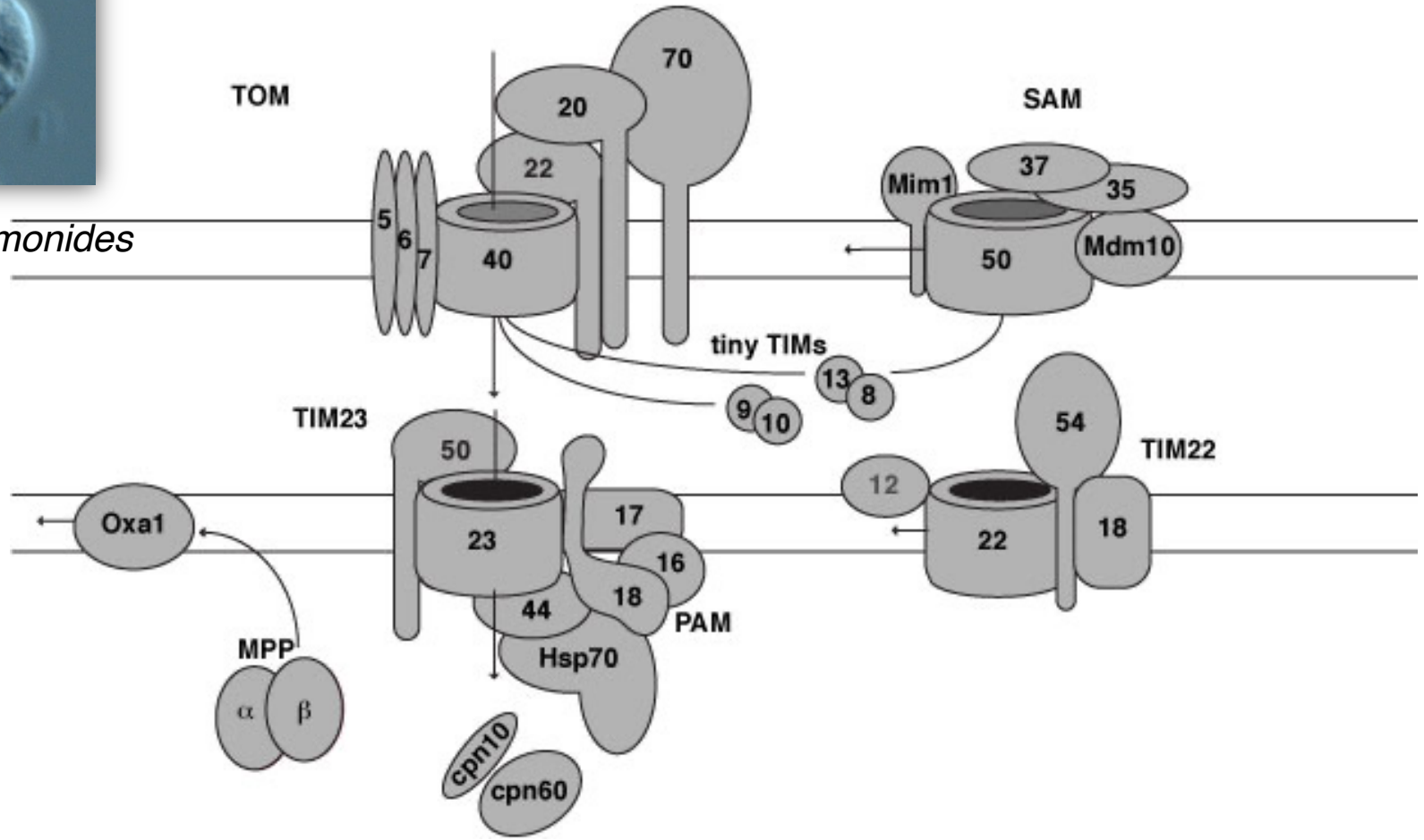
Mitochondrial outer membrane targeted proteins (TA)
Proteins with mitochondrial localization signal
β-barrel mitochondrial outer membrane proteins



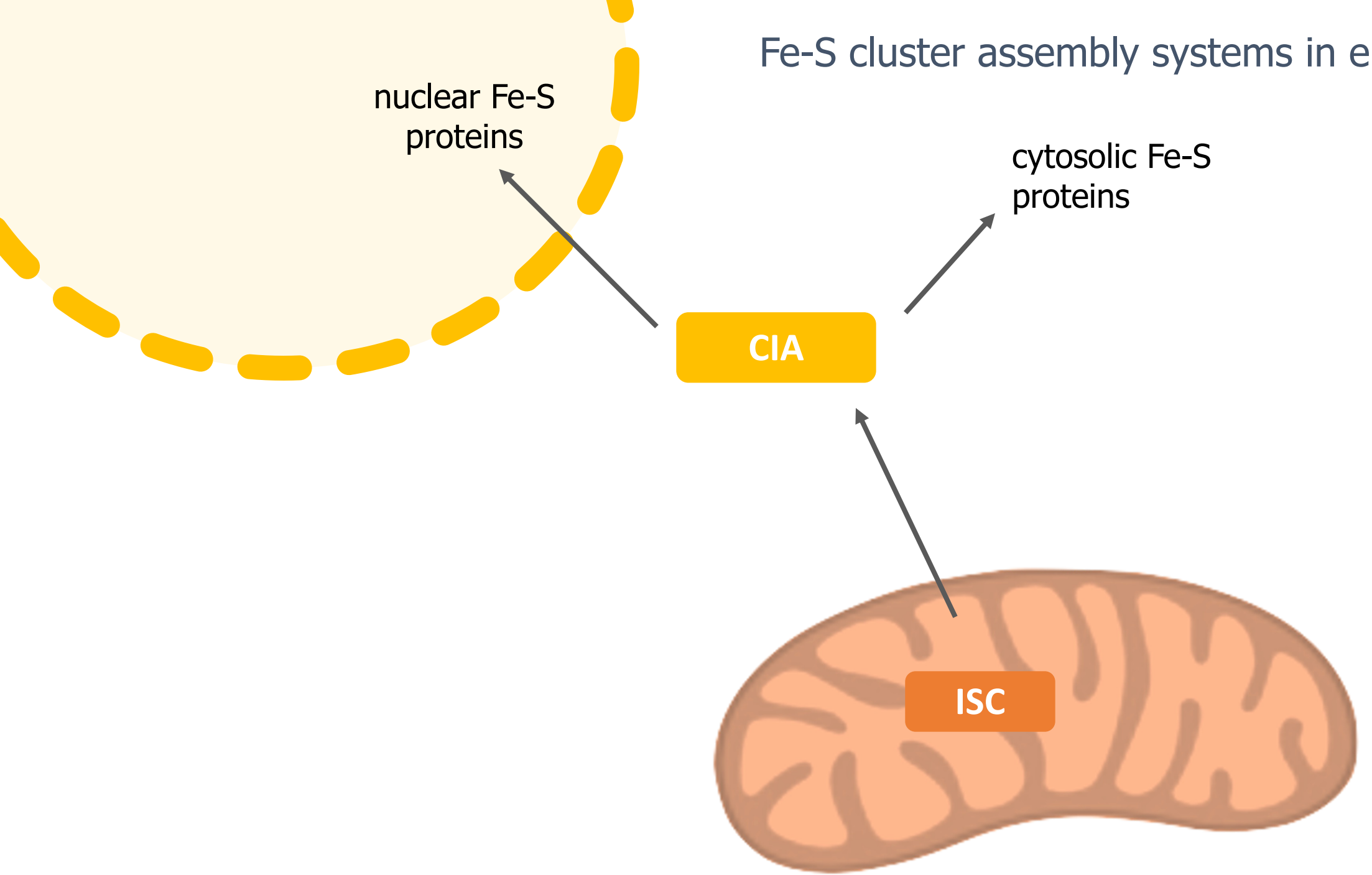

Karnkowska et al. (2016)

# mitochondrial membrane transport proteins

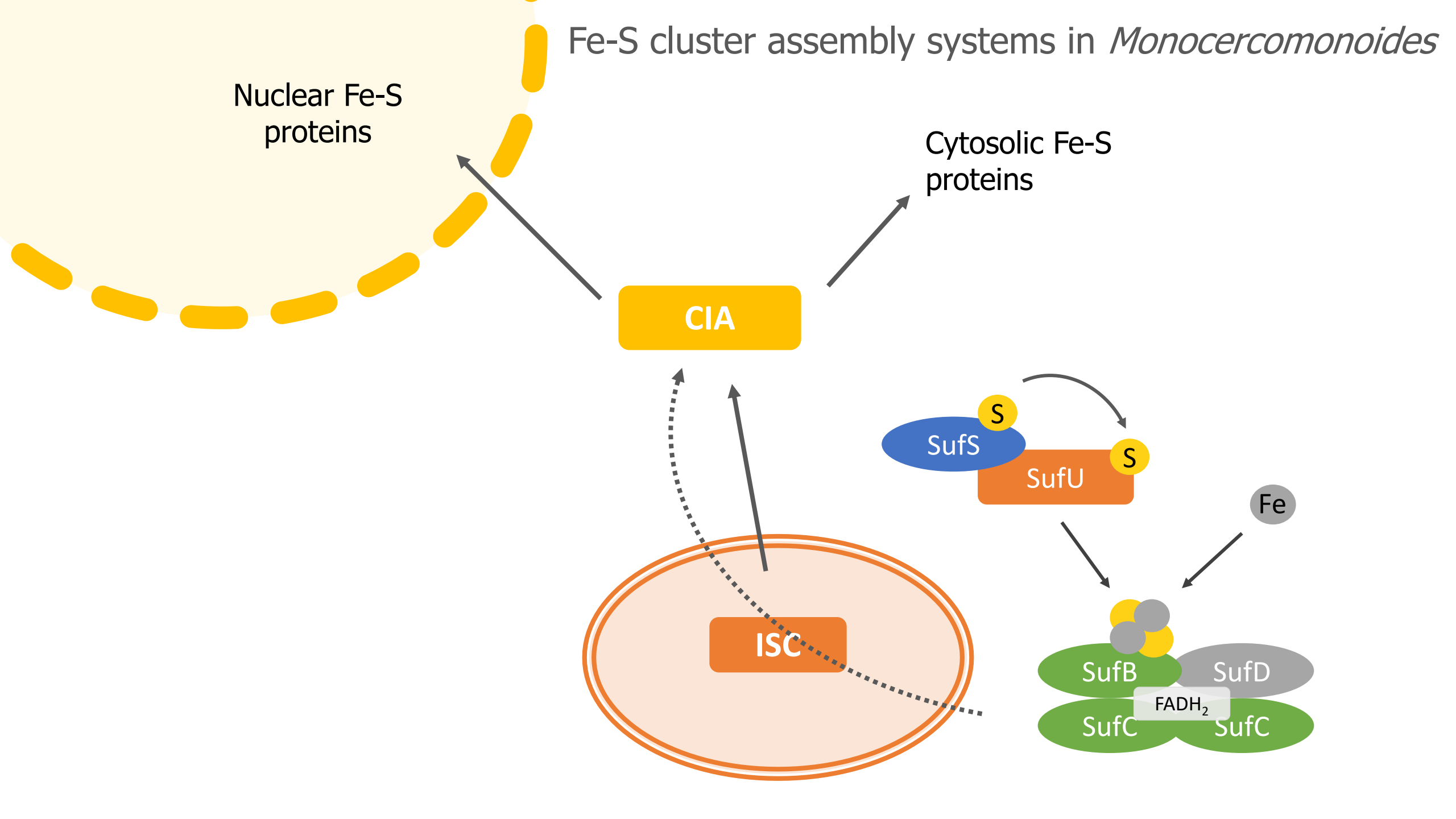

*Monocercomonides*



# Fe-S cluster assembly systems in eukaryotes



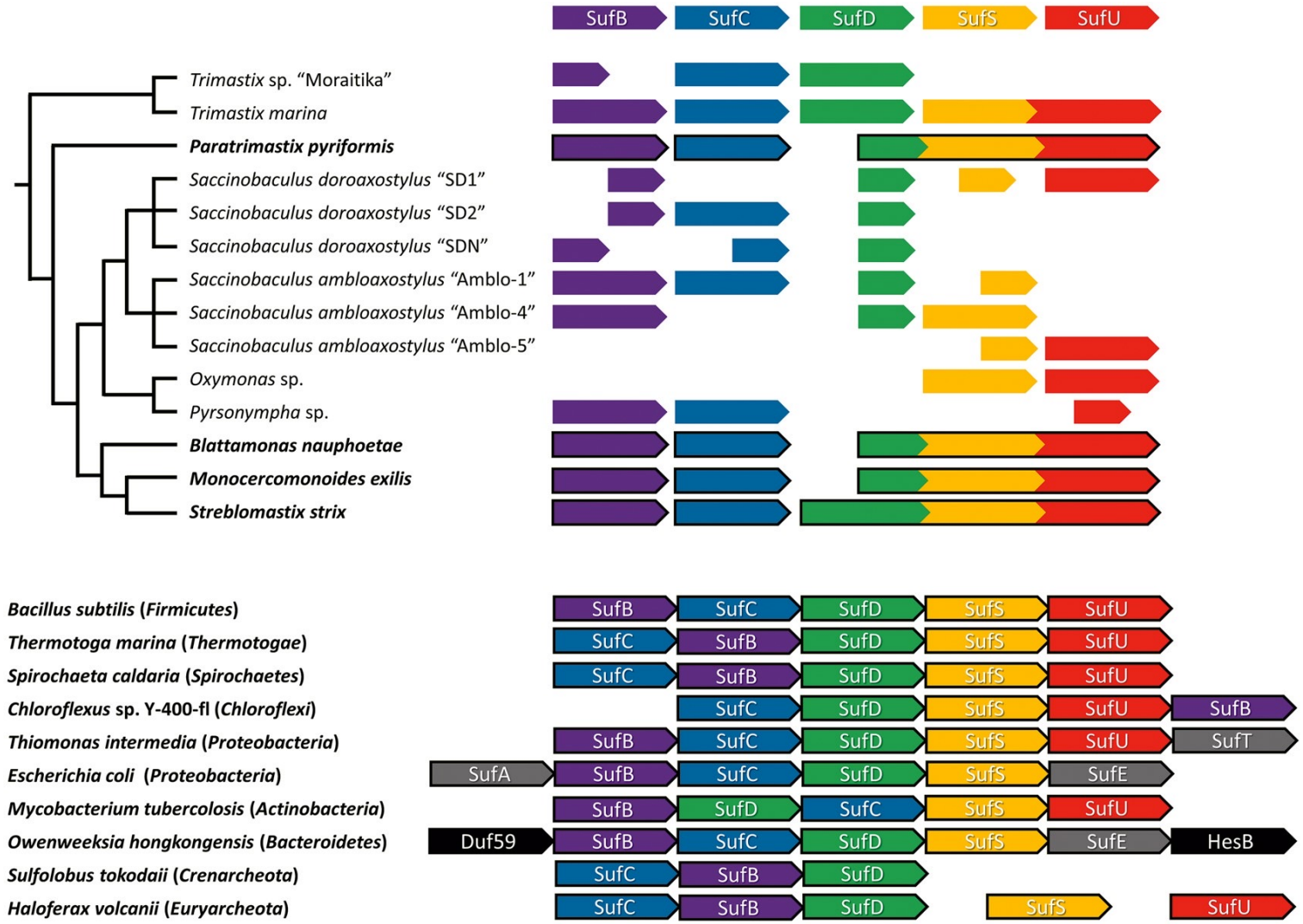
# Fe-S cluster assembly systems in *Monocercomonoides*



# Lateral gene transfer (LGT) of SUF system

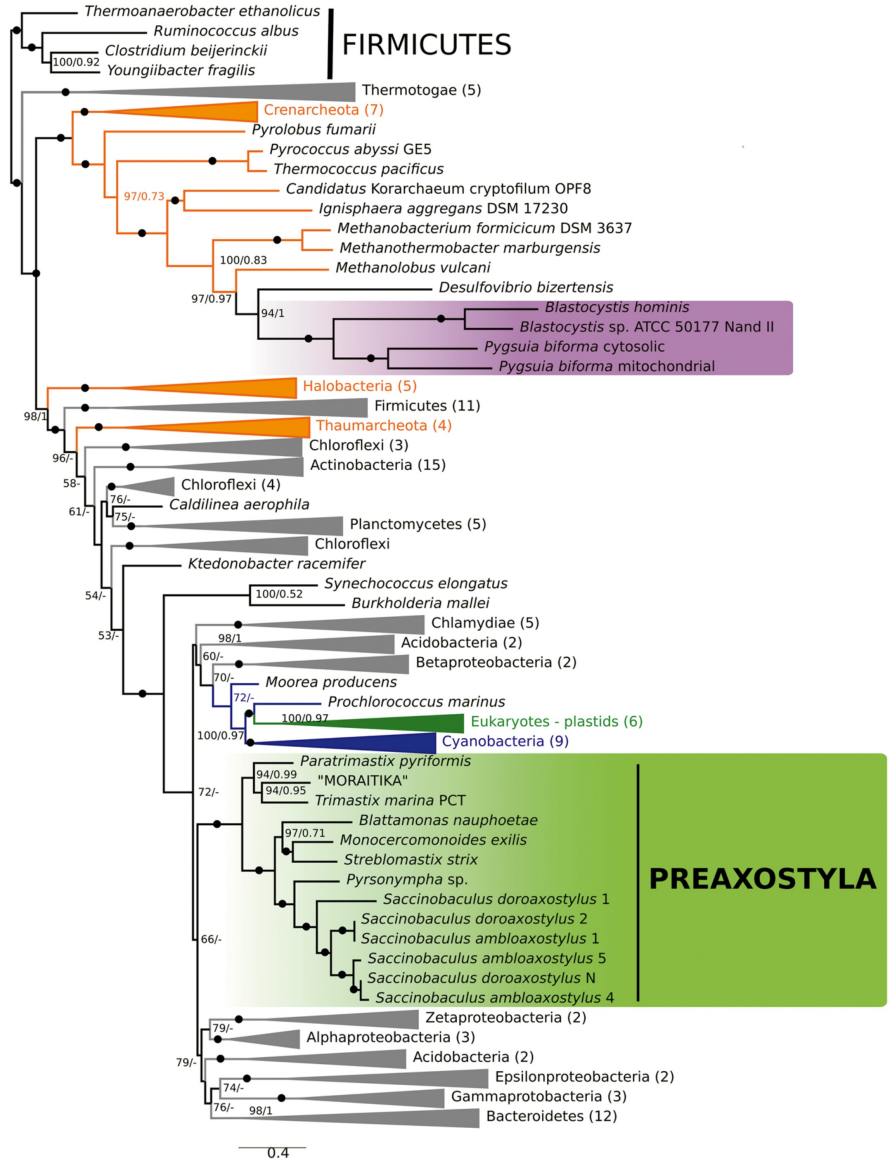

Karnkowska et al. Curr Biol (2016)

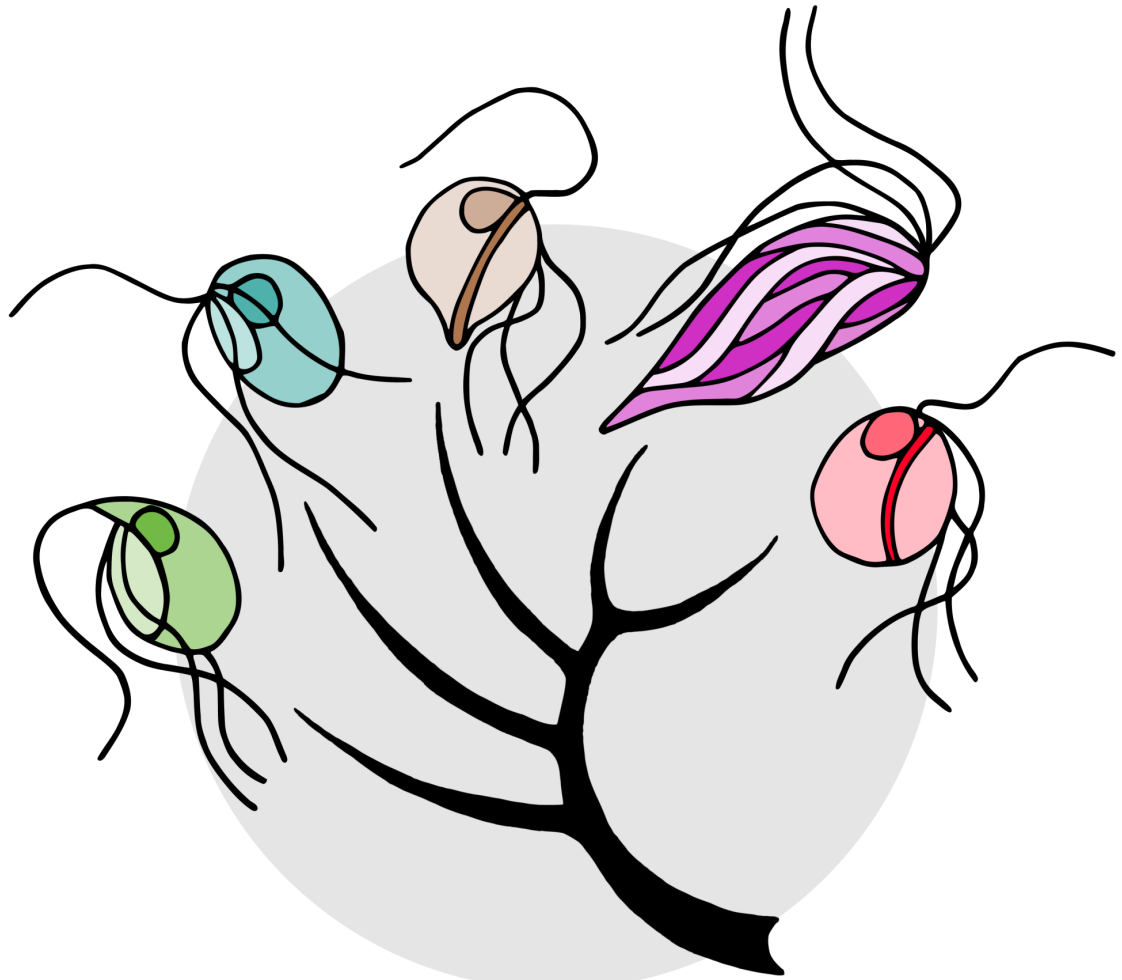
# SUF proteins in Preaxostyla and representatives of bacteria




Vacek et al. 2018

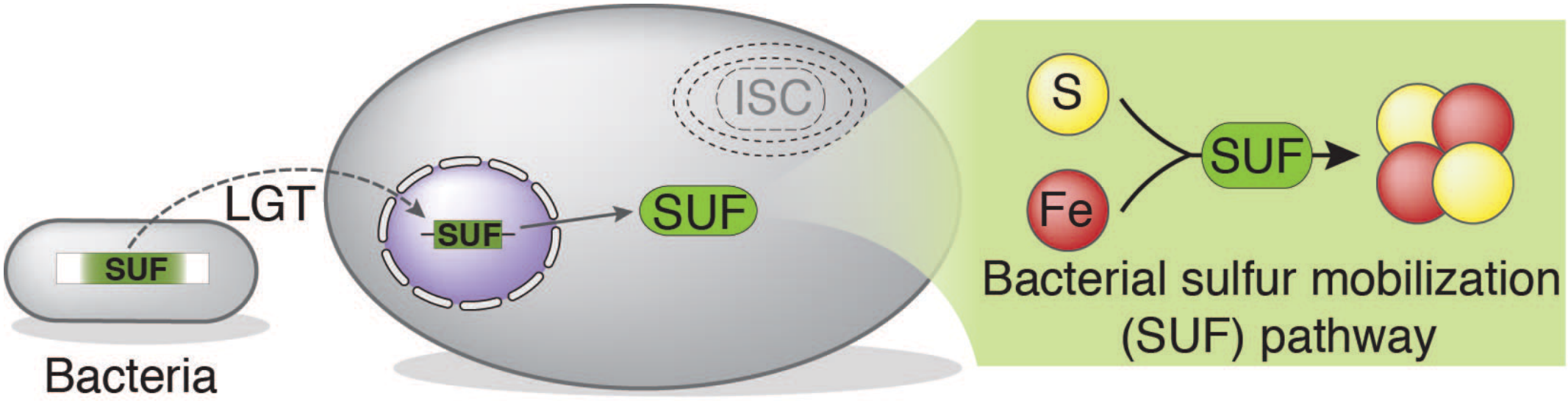
# SUF system is widespread in Preaxostyla



Vacek et al. 2018

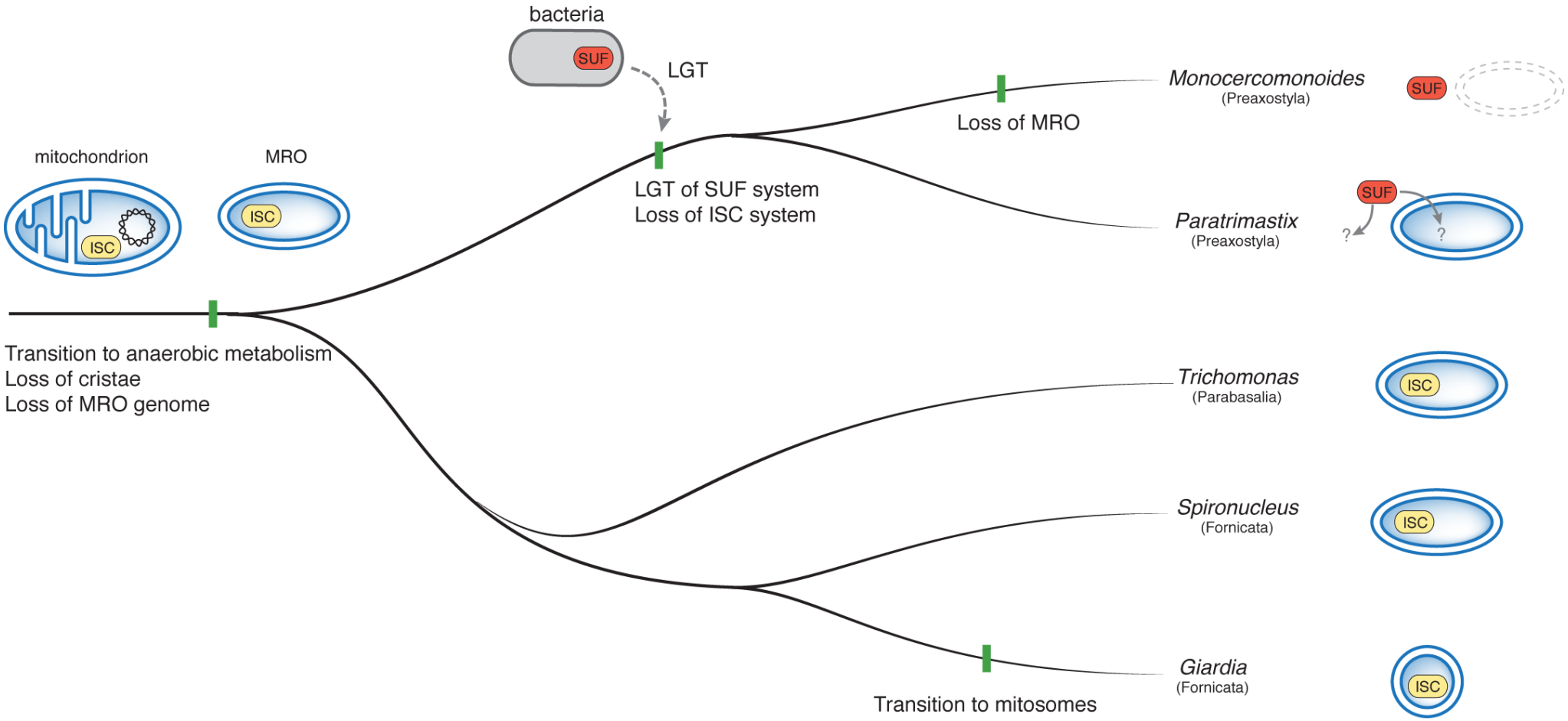
# *Monocercomonoides* an **amitochondriate** eukaryote




Lateral gene transfer (LGT) of bacterial genes encoding sulfur mobilization pathway (SUF) and loss of reduced mitochondrion

# Loss of a mitochondrial organelle

LGT of SUF system resulted in relocation of the pathway to the cytosol




Endosymbiosis can be undone!

Karnkowska et al. (2016)