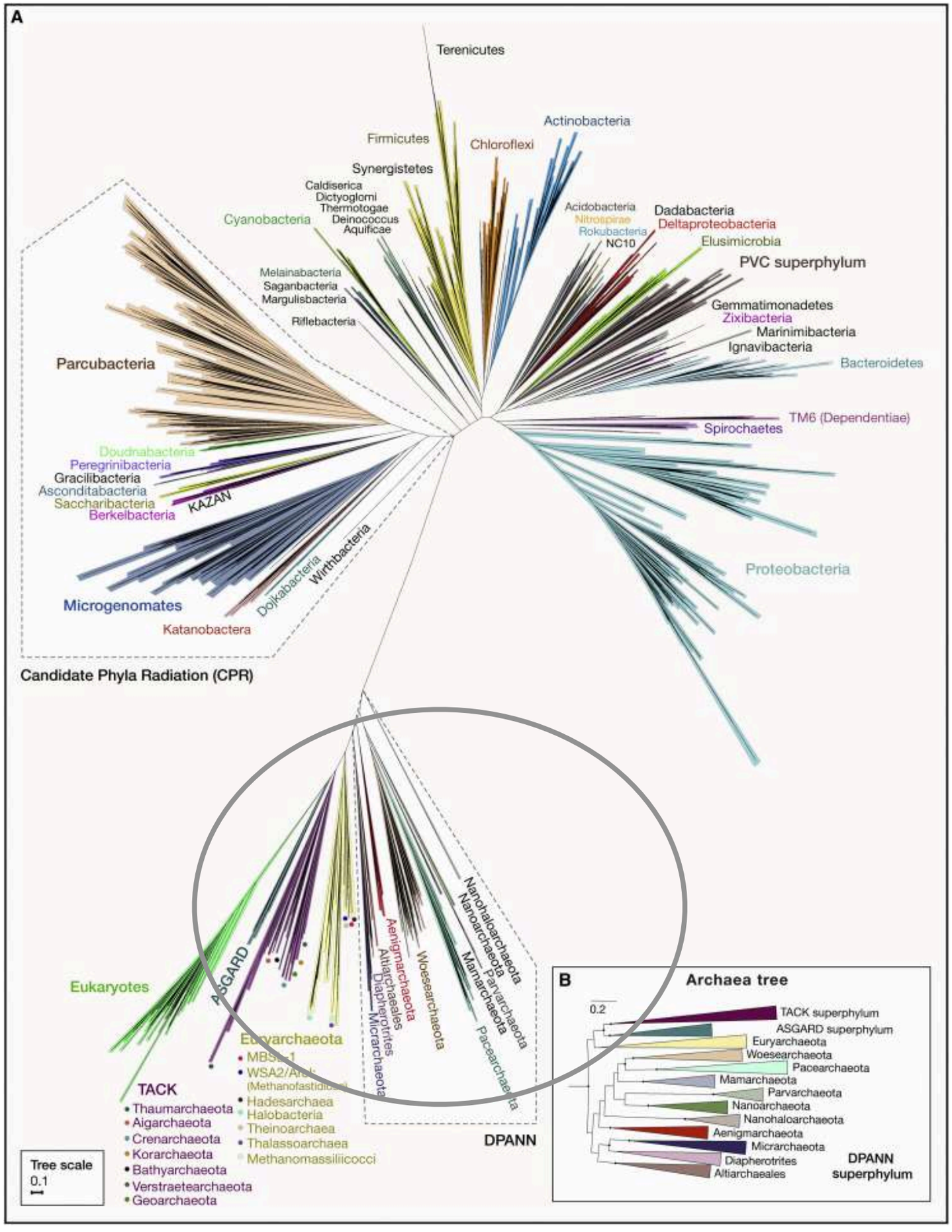
L03b: Diversity of Marine Bacteria, Archaea, Eukarya and Viruses

Archaea

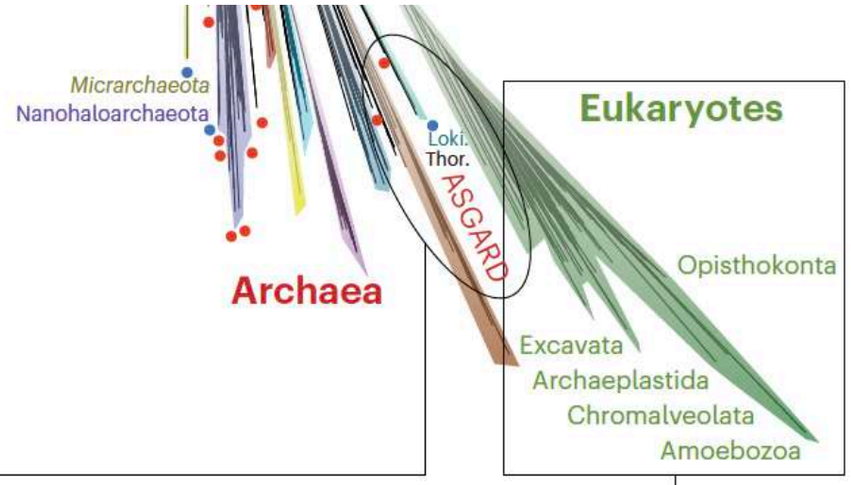


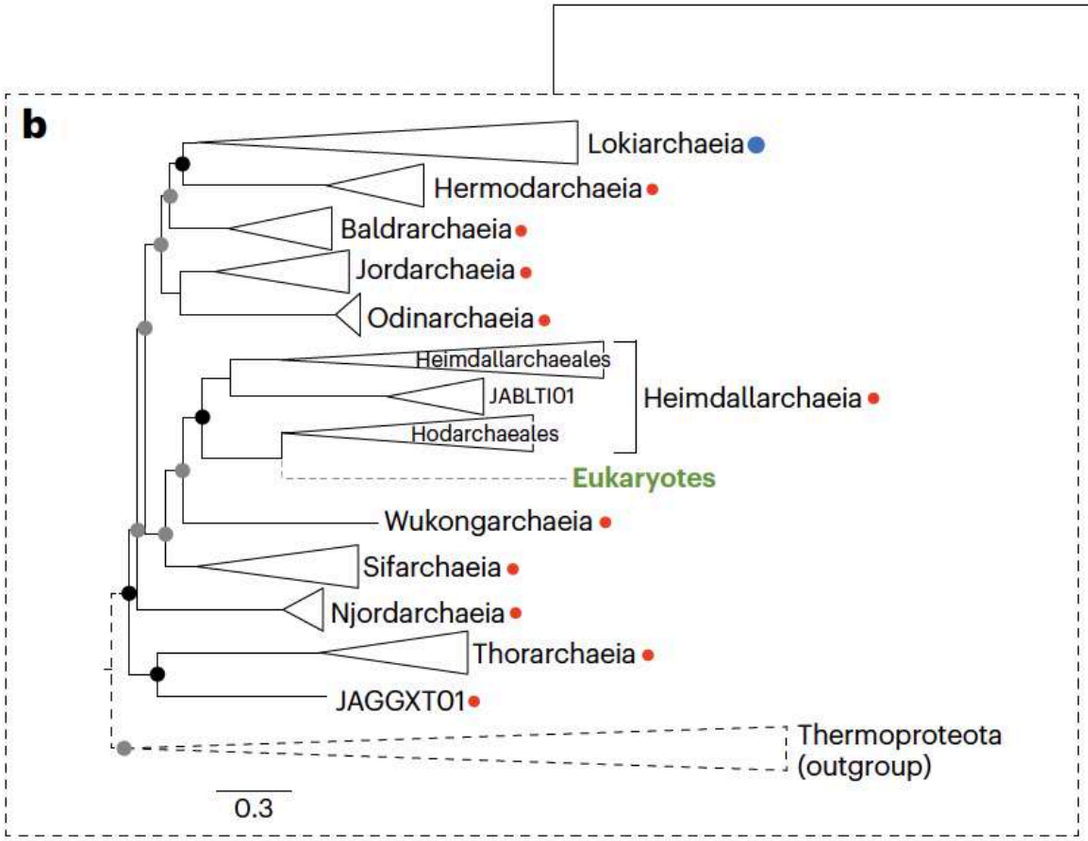
Castelle & Banfield, 2018

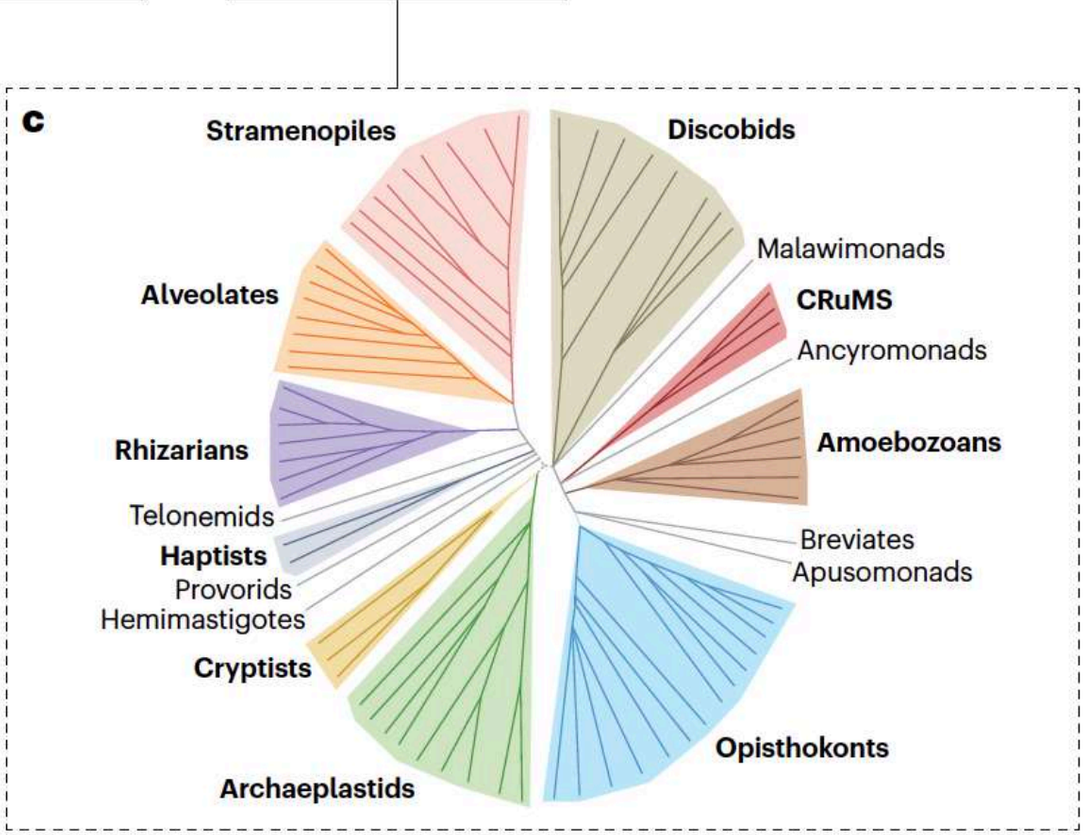


Archaea and Eukaryotes

A two-domain tree with Eukarya branching from within the Archaea, sister to the Asgardarchaeota







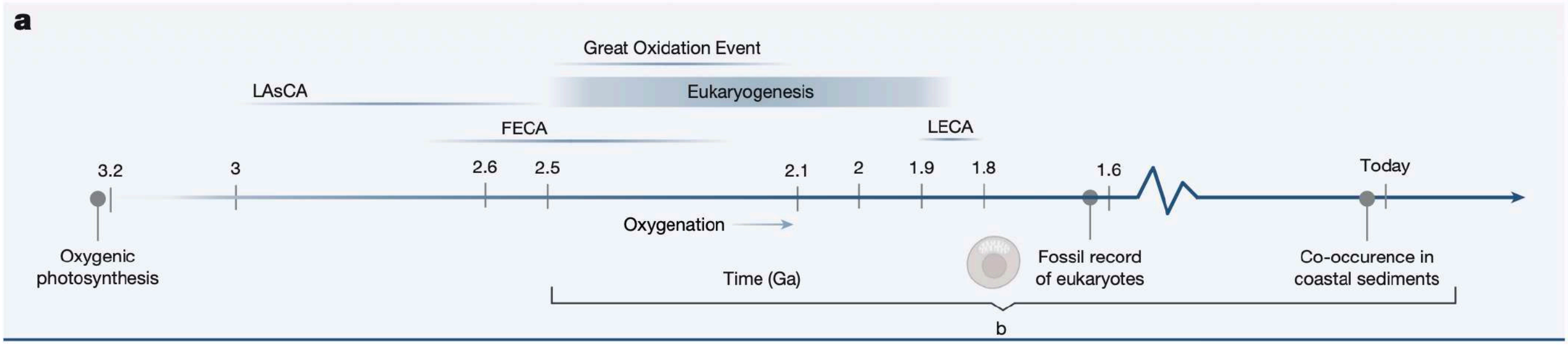
Hug et al., 2016; Hug, 2024

Timeline spanning from before the Last Asgard archaea Common Ancestor (LAsCA)

Asgard archaea were pivotal in the origin of complex cellular life

Heimdallarchaeia (a class within the phylum Asgardarchaeota) are inferred to be the closest relatives of eukaryotes

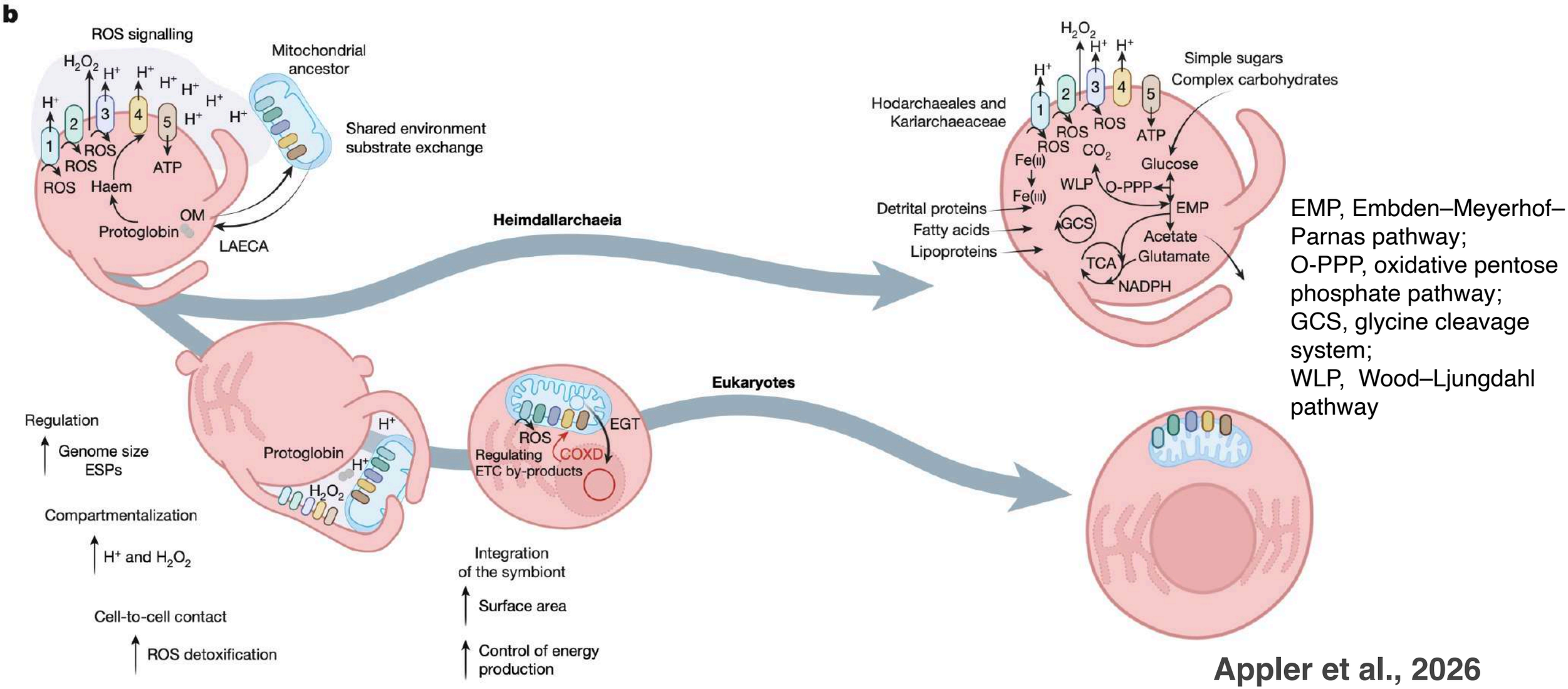
Many models of eukaryogenesis—including the hydrogen hypothesis, syntrophy hypothesis, entangle–engulf–endogenize (E3) model and reverse flow model—predict the host was an anaerobic archaeon that conserved energy via substrate-level phosphorylation through fermentation of organic compounds to acetate, typically coupled with hydrogen exchange with a bacterial partner, consistent with interactions observed in enrichment cultures



Appler et al., 2026

Eukaryogenesis

Predicted to be **aerobic chemoheterotrophs or facultative anaerobes, and co-occur with Alphaproteobacteria in oxic coastal sediments**



EMP, Embden–Meyerhof–Parnas pathway;
O-PPP, oxidative pentose phosphate pathway;
GCS, glycine cleavage system;
WLP, Wood–Ljungdahl pathway

Appler et al., 2026

Metabolite exchanges and response to rising oxygen levels may have increased cell-to-cell contact between partners, enabling initial compartmentalization or microscale spatial segregation in matrices via predicted lokiactin protrusions.
The host could have used protoglobin to bind oxygen, a potential terminal electron acceptor.
By the LECA, endosymbiotic gene transfer (EGT) relocated mitochondrial-encoded ETC subunits to the nuclear genome (red ring). The red highlights potential regulation of ETC by-products (ROS and ATP) by CoxD.

Phylum Euryarchaeota, I

- **MESO- TO THERMOPHILIC OBLIGATE ANAEROBES**
  - **Anoxic sediment, symbiont of anoxic protists**
  - **Hydrothermal vents**
  - **Production of methane as a final step of anaerobic degradation of organic material**
  - **Some fast grow 1h generation time at 110ºC**

- **ANME, ANAEROBIC METHANOTROPHIC ARCHAEA**
  - **Anaerobic oxidation of methane (AOM)**
  - **In consortia with sulfate-reducing bacteria, reverse metanogenesis and provide N**
  - **Diverse clades: anoxic sediment and mud volcanos**
  - **Soluble cytochrome and nanowires to exchange electrons**

- **HYPERTHERMOPHILES**
  - **Thermococci**
  - **Biotechnological interest for heat-resistant enzymes**
  - **Hydrothermal vents and subsurface rocks**

Phylum Euryarchaeota, II

- **EXTREME THERMOPHILES**
  - **Strictly anaerobes**
  - **Archaeglobus and Ferroglobus**
  - **Archaeglobus: reduction of sulfate with oxidation of H_2 to produce H_2S —> "souring" crude oil**
  - **Ferroglobus: iron-oxidizing and nitrate reducing chemolithoautotrophs**

- **EXTREME HALOPHILES**
  - **Extreme halophiles > 9% or saturated solution of NaCl**
  - **Haobacteriaceae**
  - **Chemoorganotrophs**
  - **Cell lyse without enough NaCl**
  - **Pigmented —> produce ATP using light with bacteriophotorodopsin**

- **UNCULTIVATED MARINE GROUP II, III, IV**
  - **Particle associated**
  - **MG-II, up to 4-20% of total microbial community in surface waters**

Phylum Crenarchaeota

- **GROWING AT HIGH TEMPERATURE**
- **Terrestrial hot springs and hydrothermal vents**
- **Chemororganotrophic or chemoheterotrophic, chemolithoautotrophic (—> very important source of organic carbon)**
- **Most obligate anaerobes**
- **Decomposers organic matter**
- ***Igniococcus* is the host of an archaeon parasite (Nanoarchaeum equitans) —> blebbing periplasmic space with secretory functions. Anaerobic and CO_2 fixation via sulfur reduction with molecular hydrogen**

Phylum Thaumarchaeota

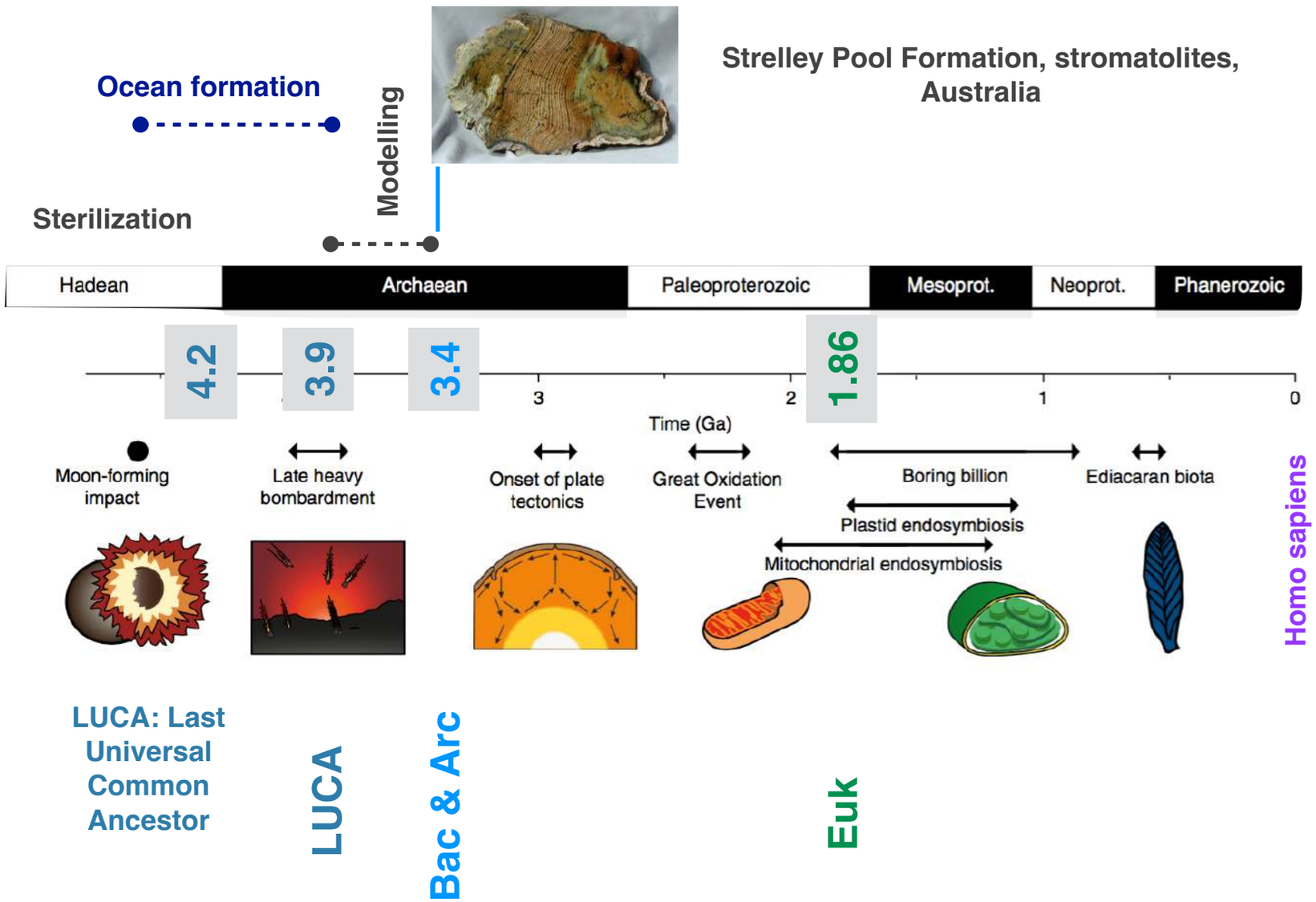
- **WATER COLUMN COLD AND POLAR WATERS**
- **Symbionts of cold-water sponges —> ammonia oxidation**
- **Marine Group I, MG-I, very abundant —> chemolihotrophic autotrophs—> ammonia oxidation —> nitrification and carbon fixation in deep cold ocean**

Phylum Nanoarchaeota

- **Cytoplasmatic PARASITE**
- **Hyperthermophile**
- **Small size and genome reduction**

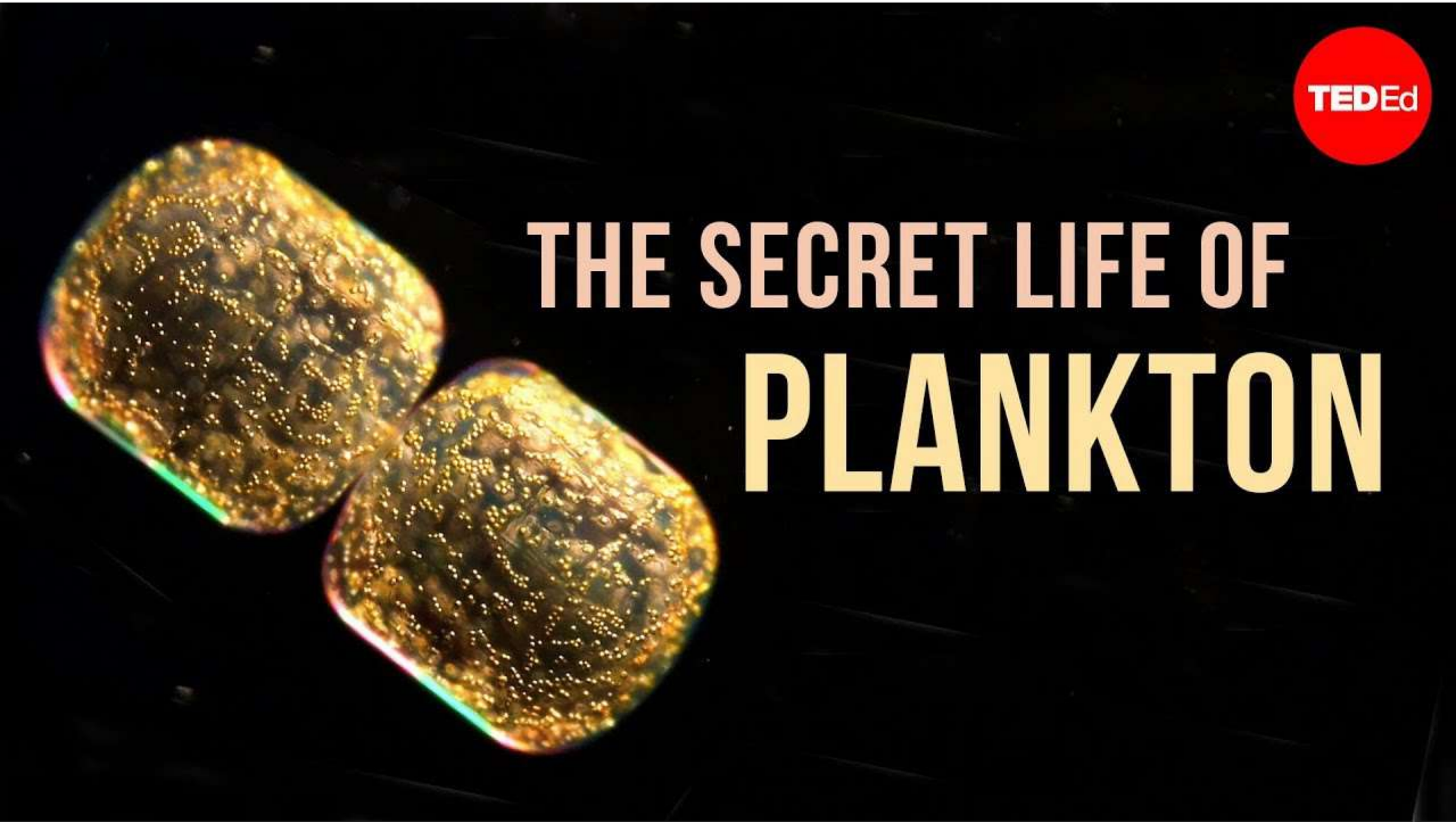
Origin of the EUKARYA

- From Archaeon (nucleus) and H_2-producing bacterium (mitochondria)
- Chloroplasts arisen on several occasions



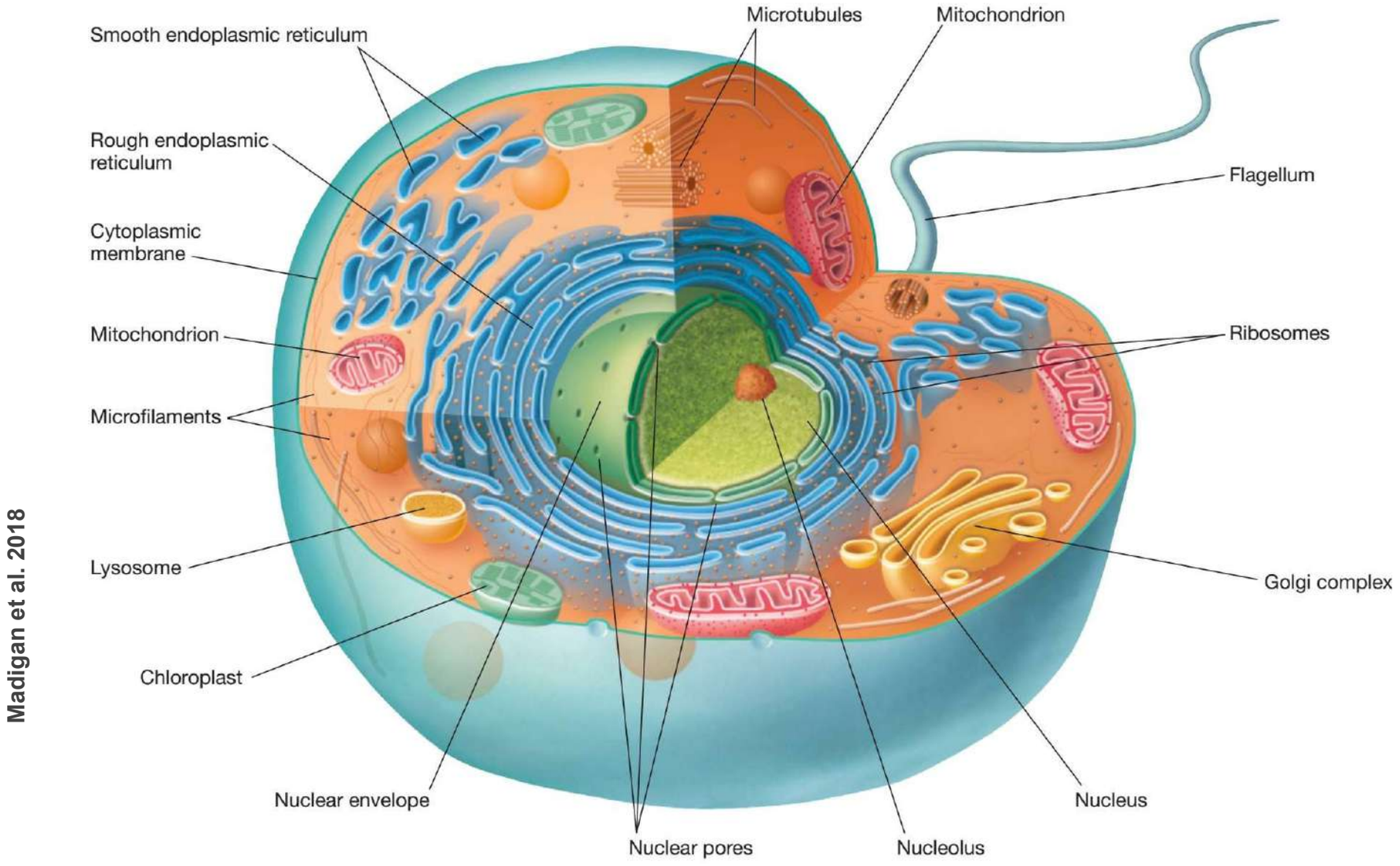
Betts et al., 2018
Moody et al., 2024


Tara Oceans
new results


TEDEd
THE SECRET LIFE OF
PLANKTON


FEEDING THE SEA
Phytoplankton Fuel Ocean Life

Eukaryotes

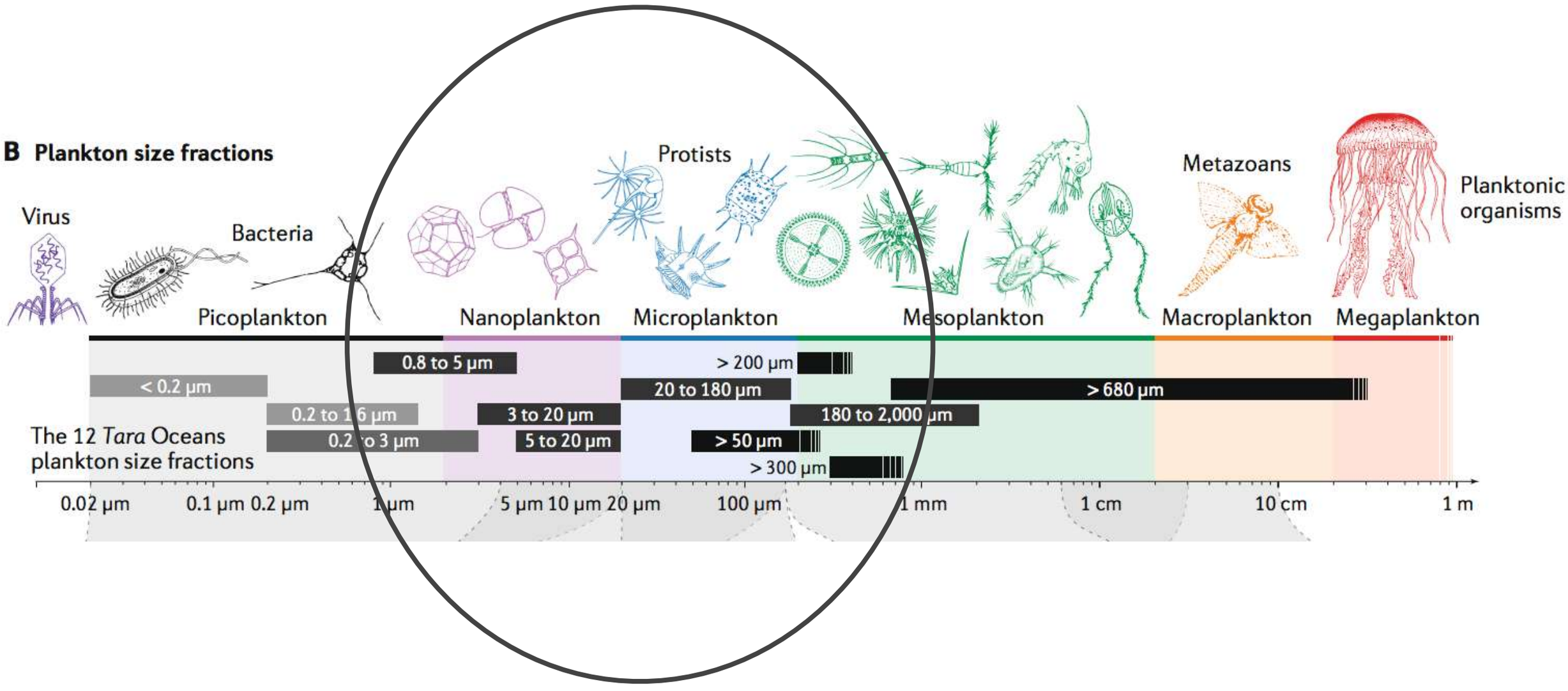


Madigan et al. 2018

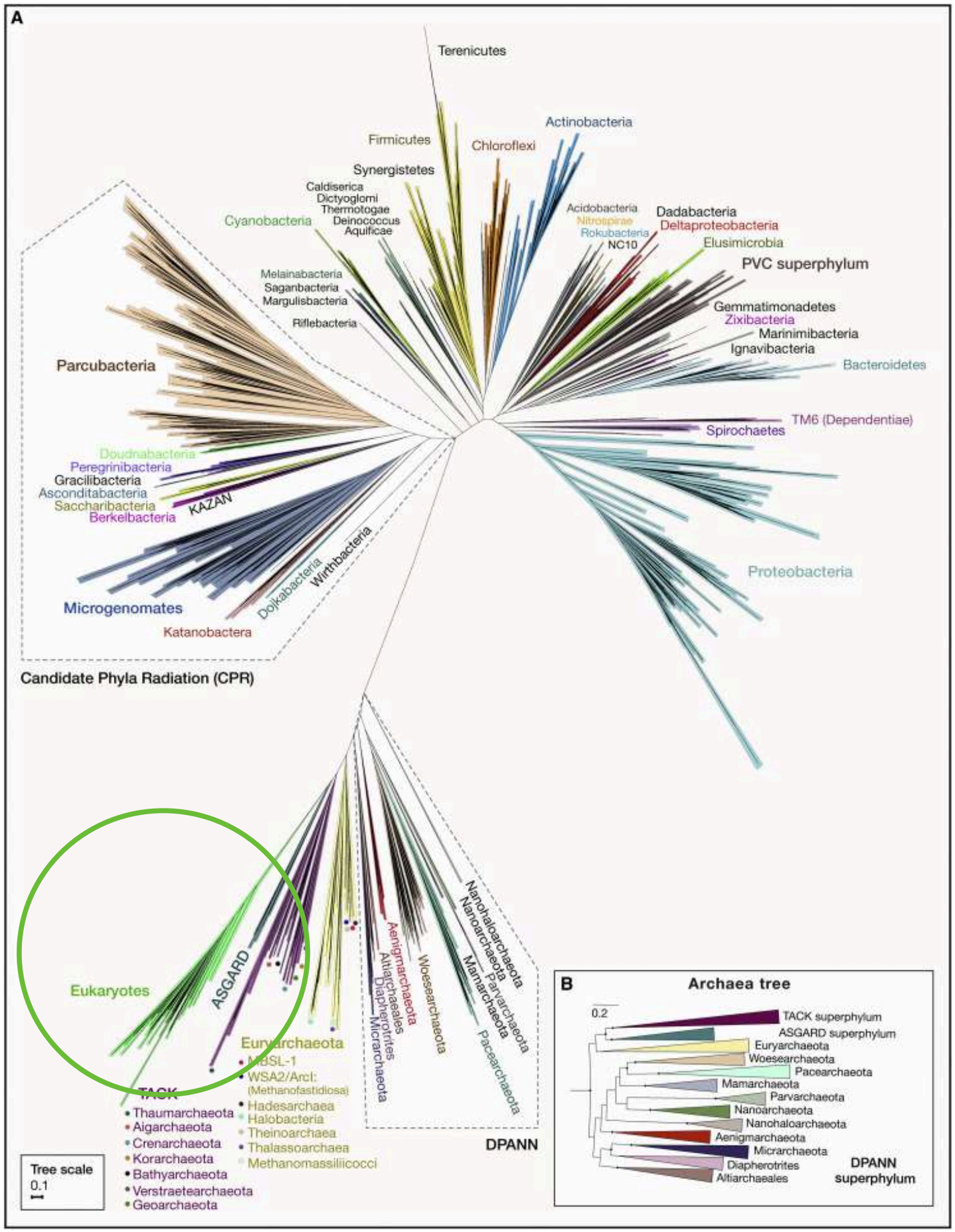
Eukaryote:

Defined **nucleus** with nuclear membrane genomes structured in chromosomes-bodies containing the hereditary material) Organelles: **mitochondria** (cellular energy, oxidation); **hydrogenosomes** (fermenative metabolism); **Golgi apparatus** (secretory device); an **endoplasmic reticulum** (a canal-like system of membranes within the cell for protein, lipid synthesis); **lysosomes** (digestive apparatus within many cell types); **chloroplast** (glucose and ATP production and O_2 in plants); **cytoskeleton** (3D structural architecture); **flagella** and **cilia**

Size-range of marine EUK-microbes

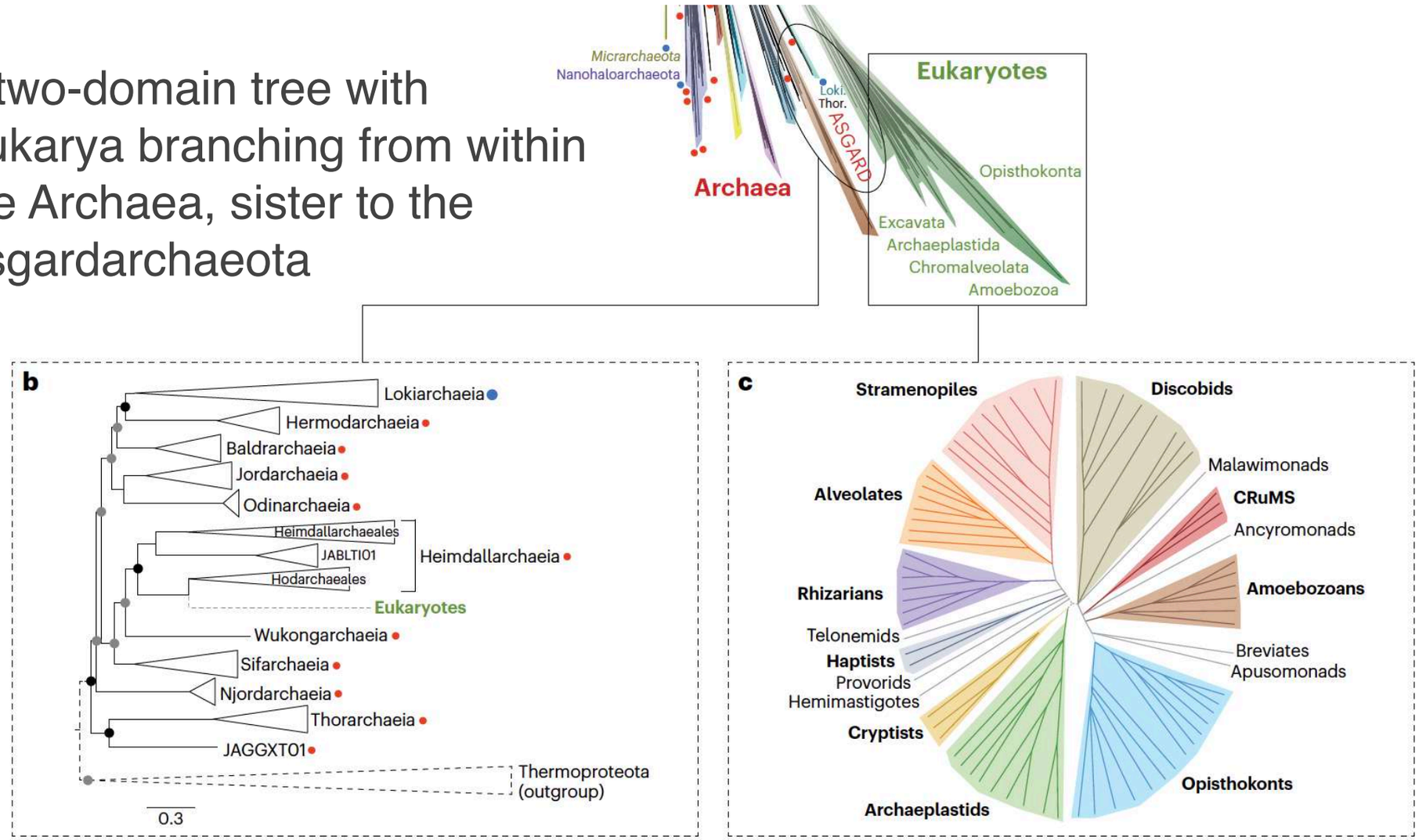


Sunagawa et al., 2020


A
Terenicutes
Actinobacteria
Firmicutes
Chloroflexi
Synergistetes
Caldiserica
Dictyoglomi
Thermotogae
Deinococcus
Aquificae
Cyanobacteria
Acidobacteria
Nitrospirae
Rokubacteria
NC10
Dadabacteria
Deltaproteobacteria
Elusimicrobia
PVC superphylum
Melainabacteria
Saganbacteria
Margulisbacteria
Riflebacteria
Gemmatimonadetes
Zixibacteria
Marinimibacteria
Ignavibacteria
Bacteroidetes
Parcubacteria
TM6 (Dependentiae)
Spirochaetes
Doudnabacteria
Peregrinibacteria
Gracilibacteria
Asconditabacteria
Saccharibacteria
Berkelbacteria
KAZAN
Proteobacteria
Microgenomates
Dojkabacteria
Wirthbacteria
Katanobacteria
Candidate Phyla Radiation (CPR)
Nanohaloarchaeota
Nanoarchaeota
Parvarchaeota
Aenigmarchaeota
Altiarchaeales
Diapherotrites
Micrarchaeota
Woesearchaeota
Mamarchaeota
Pacearchaeota
ASGARD
Eukaryotes
Euryarchaeota
• MBSL-1
• WSA2/ArcI: (Methanofastidiosa)
• Hadesarchaea
• Halobacteria
• Theinoarchaea
• Thalassoarchaea
• Methanomassiliicocci
TACK
• Thaumarchaeota
• Aigarchaeota
• Crenarchaeota
• Korarchaeota
• Bathyarchaeota
• Verstraetearchaeota
• Geoarchaeota
DPANN
Tree scale
0.1
B
Archaea tree
0.2
TACK superphylum
ASGARD superphylum
Euryarchaeota
Woesearchaeota
Pacearchaeota
Mamarchaeota
Parvarchaeota
Nanoarchaeota
Nanohaloarchaeota
Aenigmarchaeota
Micrarchaeota
Diapherotrites
Altiarchaeales
DPANN superphylum

Archaea and Eukaryotes

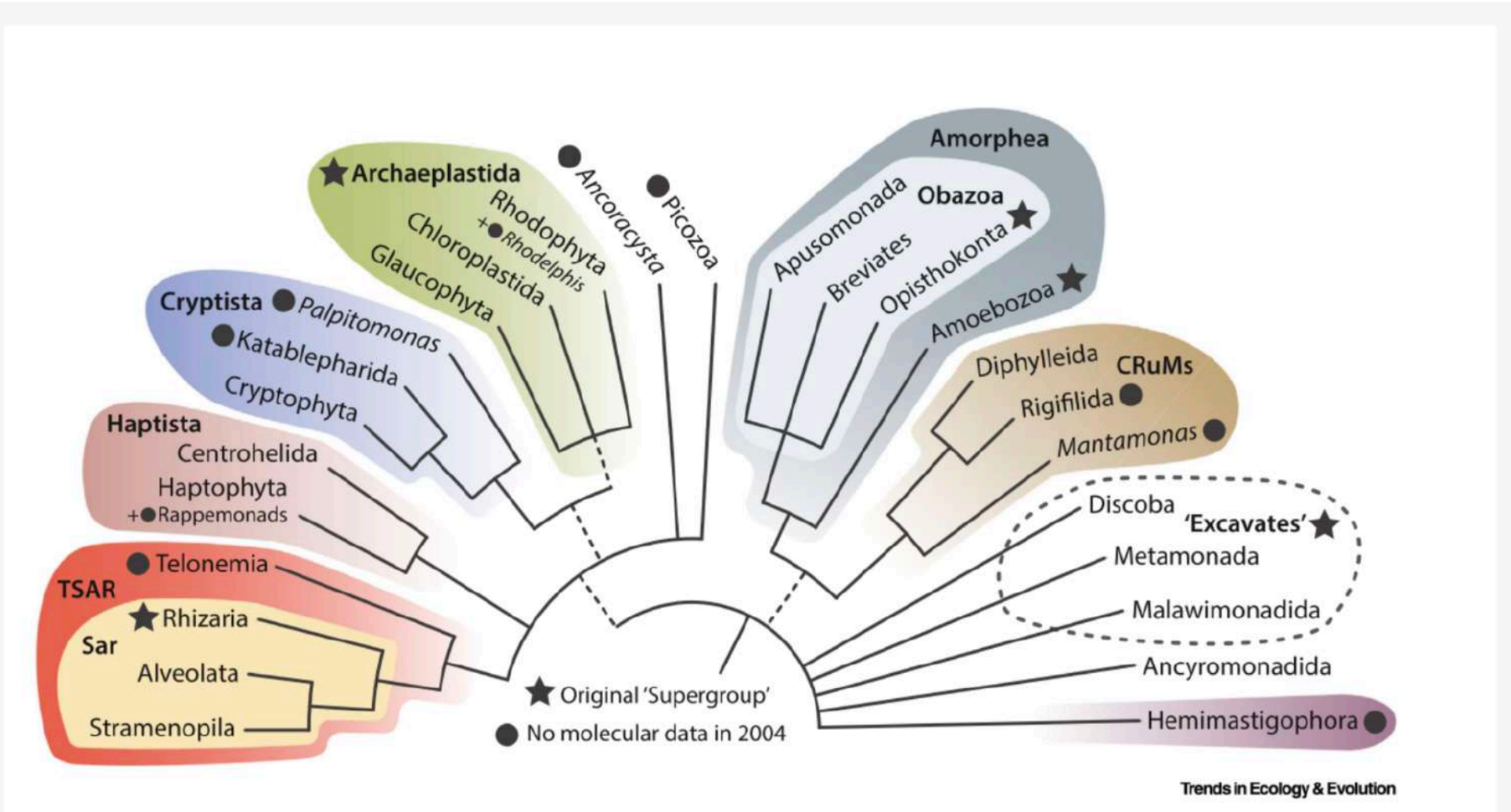
A two-domain tree with Eukarya branching from within the Archaea, sister to the Asgardarchaeota



Hug et al., 2016; Hug, 2024

Protists

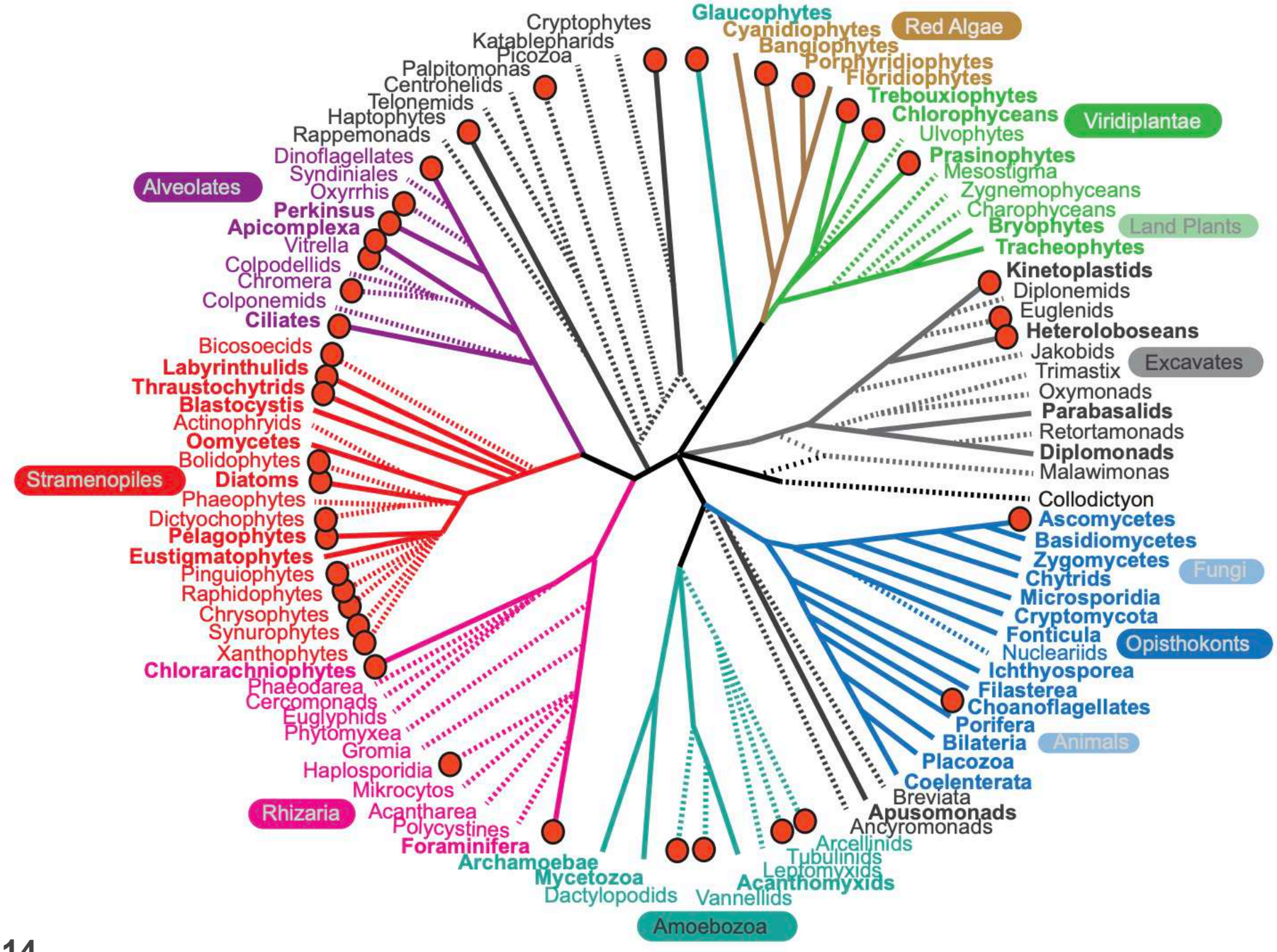
- Unicellular eukaryotic microbes
- Photosynthetic, heterotrophic and mixotrophic life style
- 1- 200 µm size
- Haeckel first classification of HMS Challenger expeditions
- 18S rRNA gene



The eukaryotic tree. From Burki et al. 2019. The New Tree of Eukaryotes. Trends in Ecology & Evolution. DOI: 10.1016/j.tree.2019.08.008.

https://pr2-database.org/

Major lineages in the eukaryotic tree of life



Keeling et al. 2014

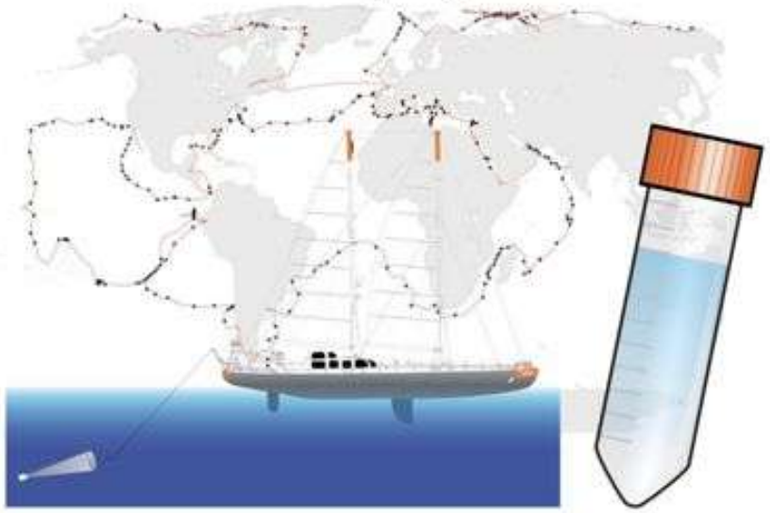
Picture is worth a thousand words…especially in the microbial world!

Sampling

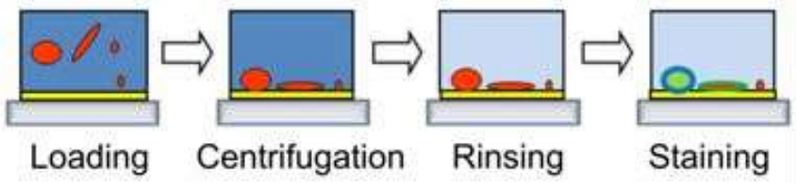
https://planktonchronicles.org/en/the-project/

a

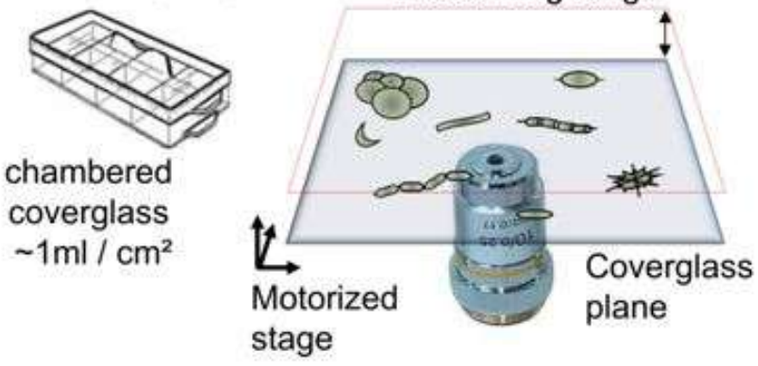
1. Plankton sampling



2. Sample preparation



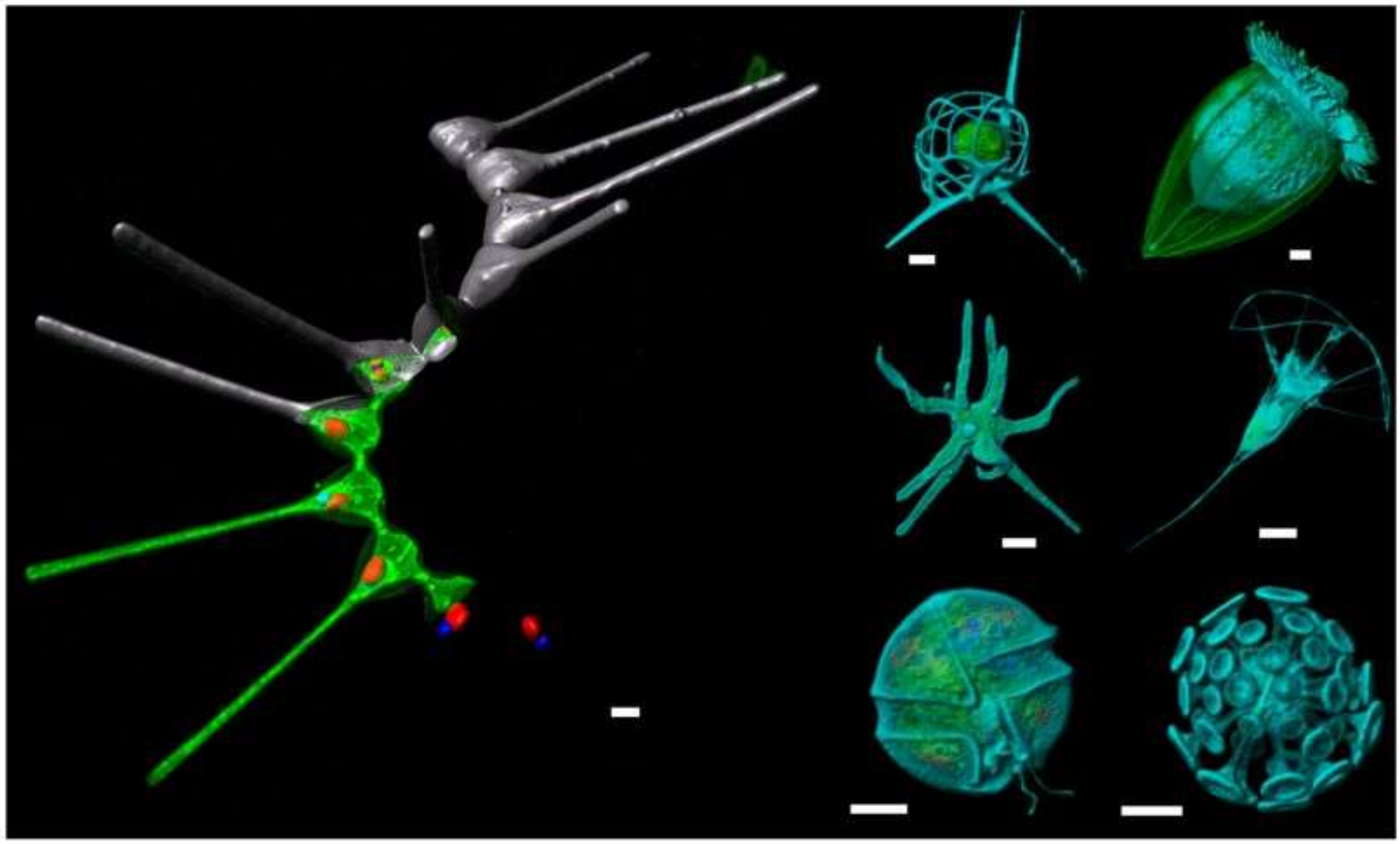
3. Imaging



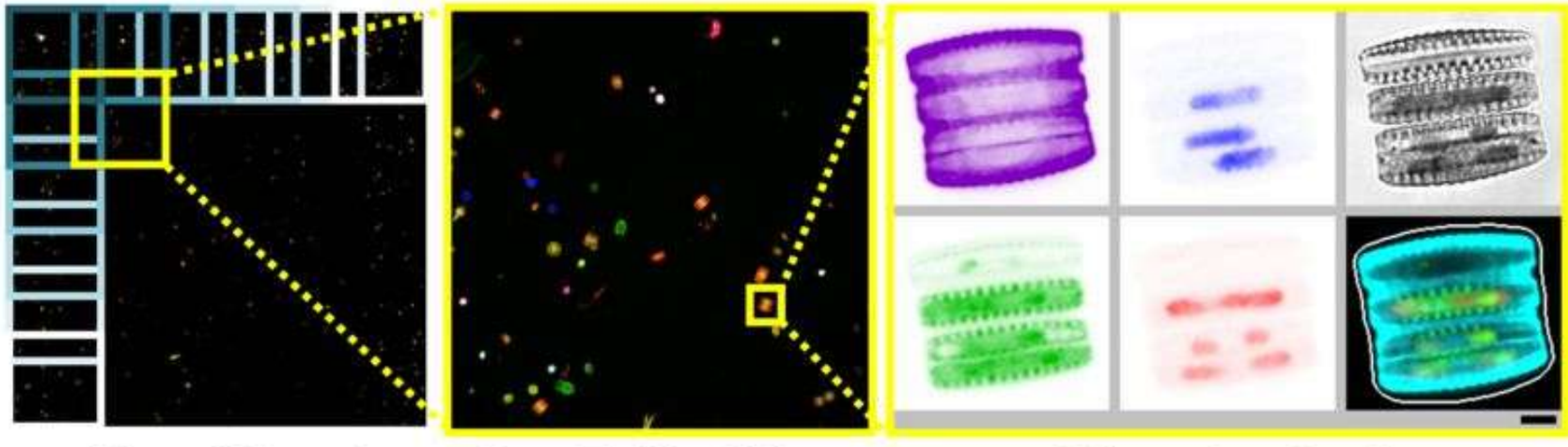
4. Image processing

5. Automated identification

b

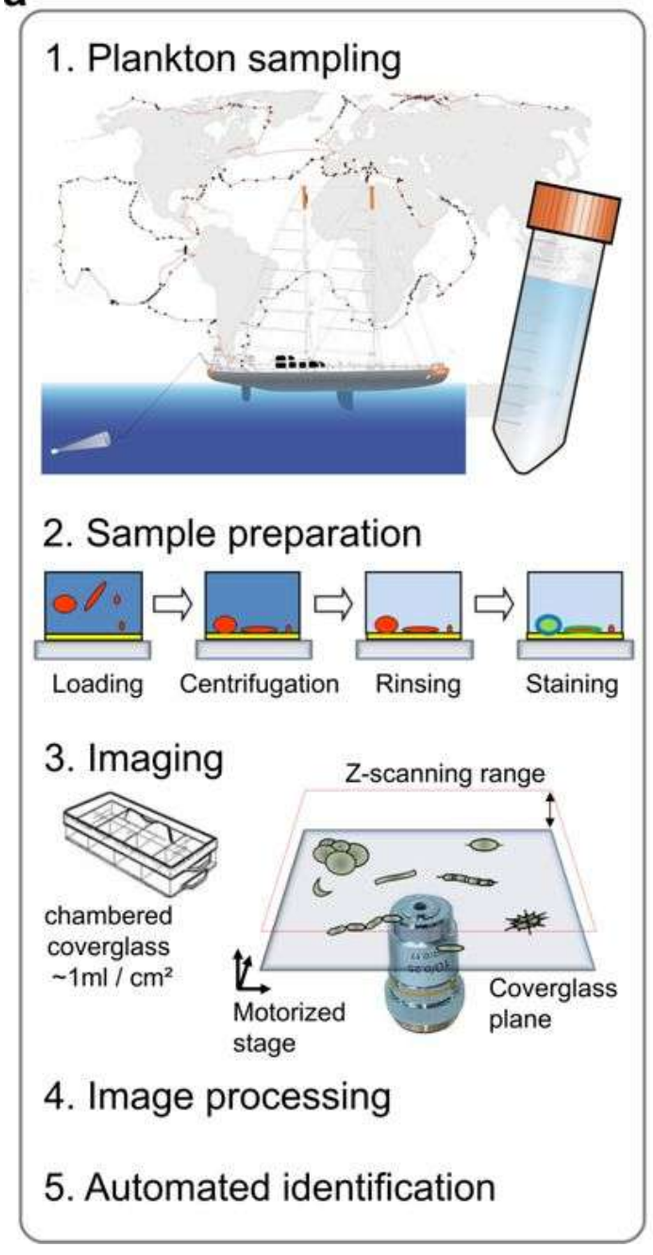


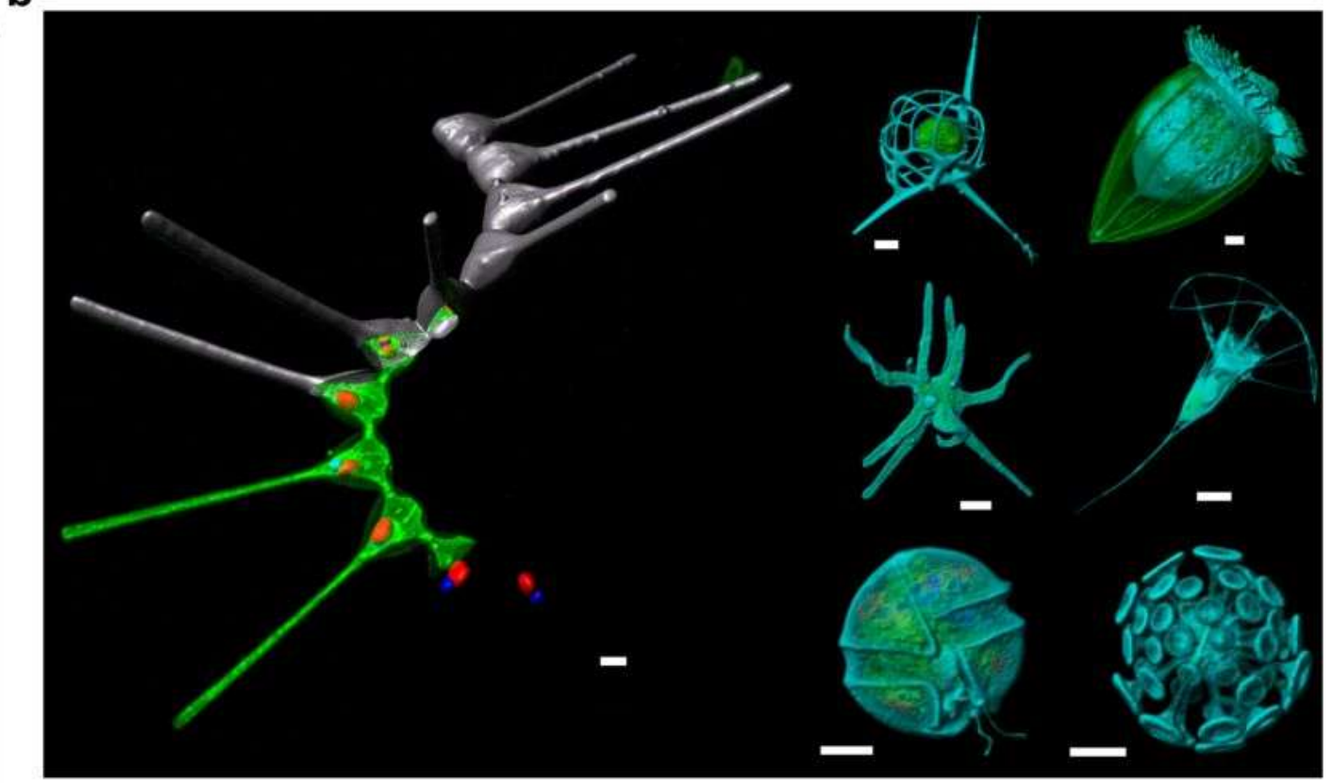
c



Colin et al., 2021

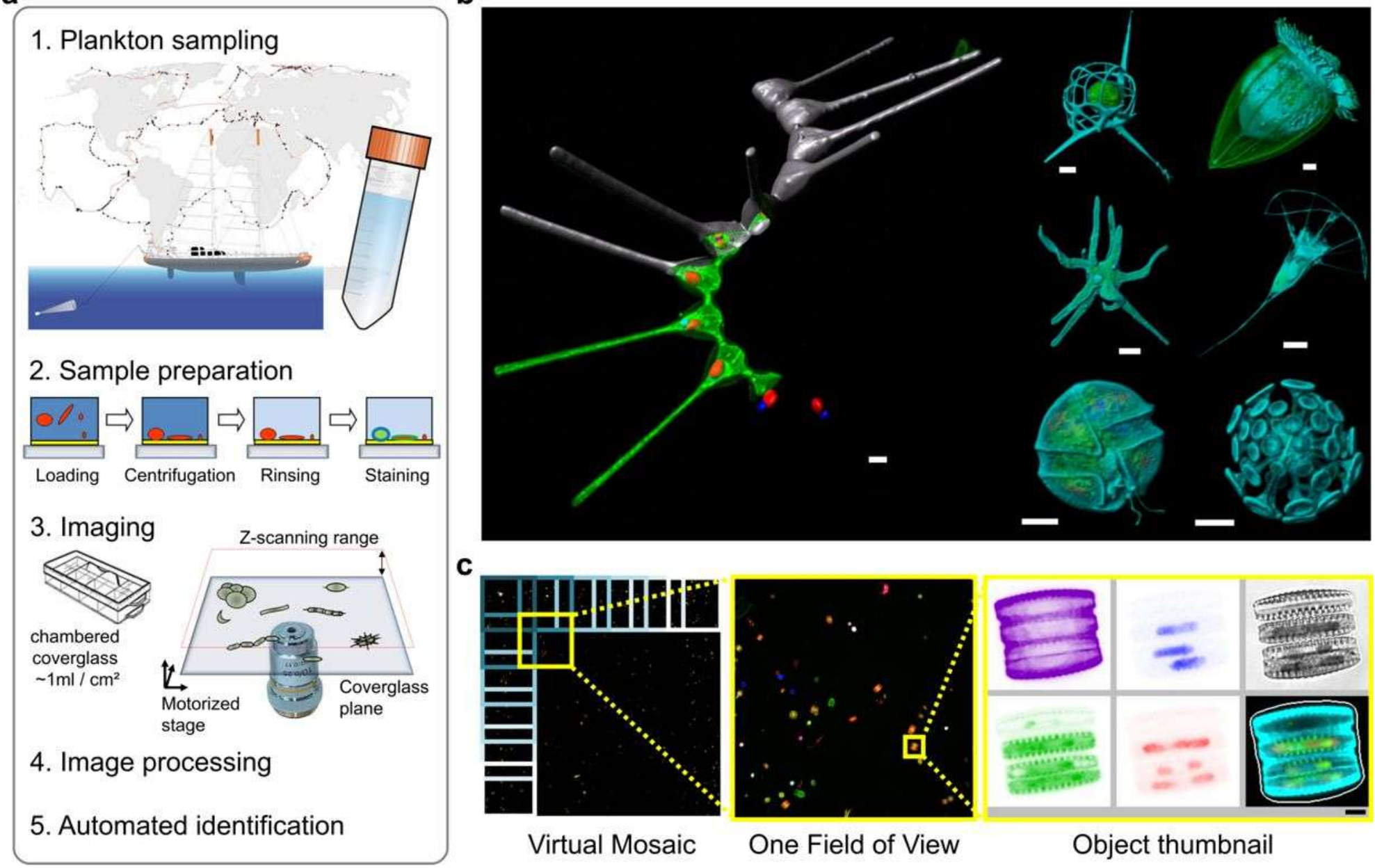
Colin et al., 2021



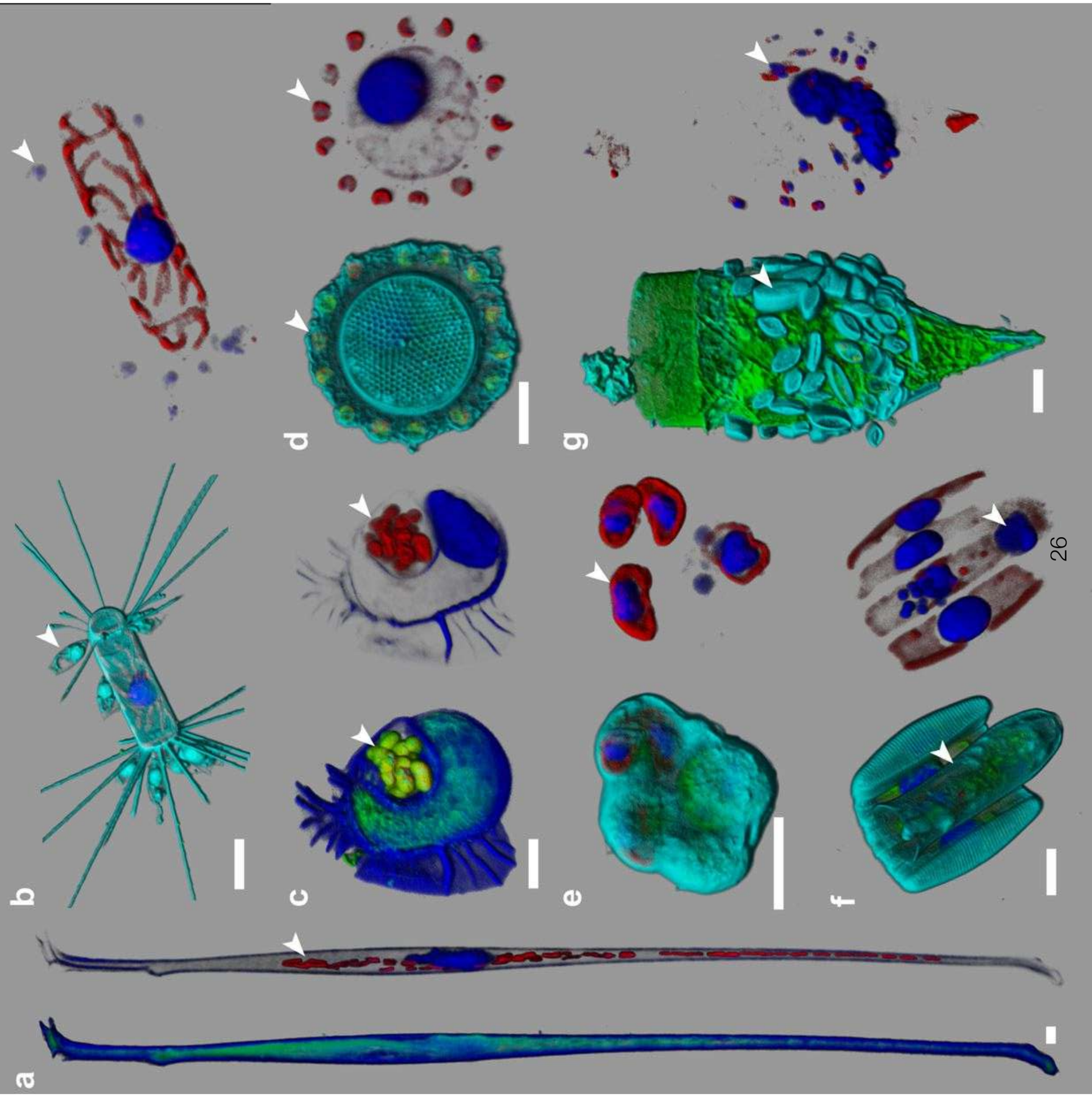


Left panel: a chain of **diatoms** (*Asterionellopsis* sp., Heterokonta); right panel, top left to bottom right: **radiolarian** (Rhizaria), **ciliate** (Alveolata), **amoeba** (Amoebozoa), **choanoflagellate** (Opisthokonta), **dinoflagellate** (Alveolata), **coccolithophore** (Haptophyta)

Colin et al., 2021

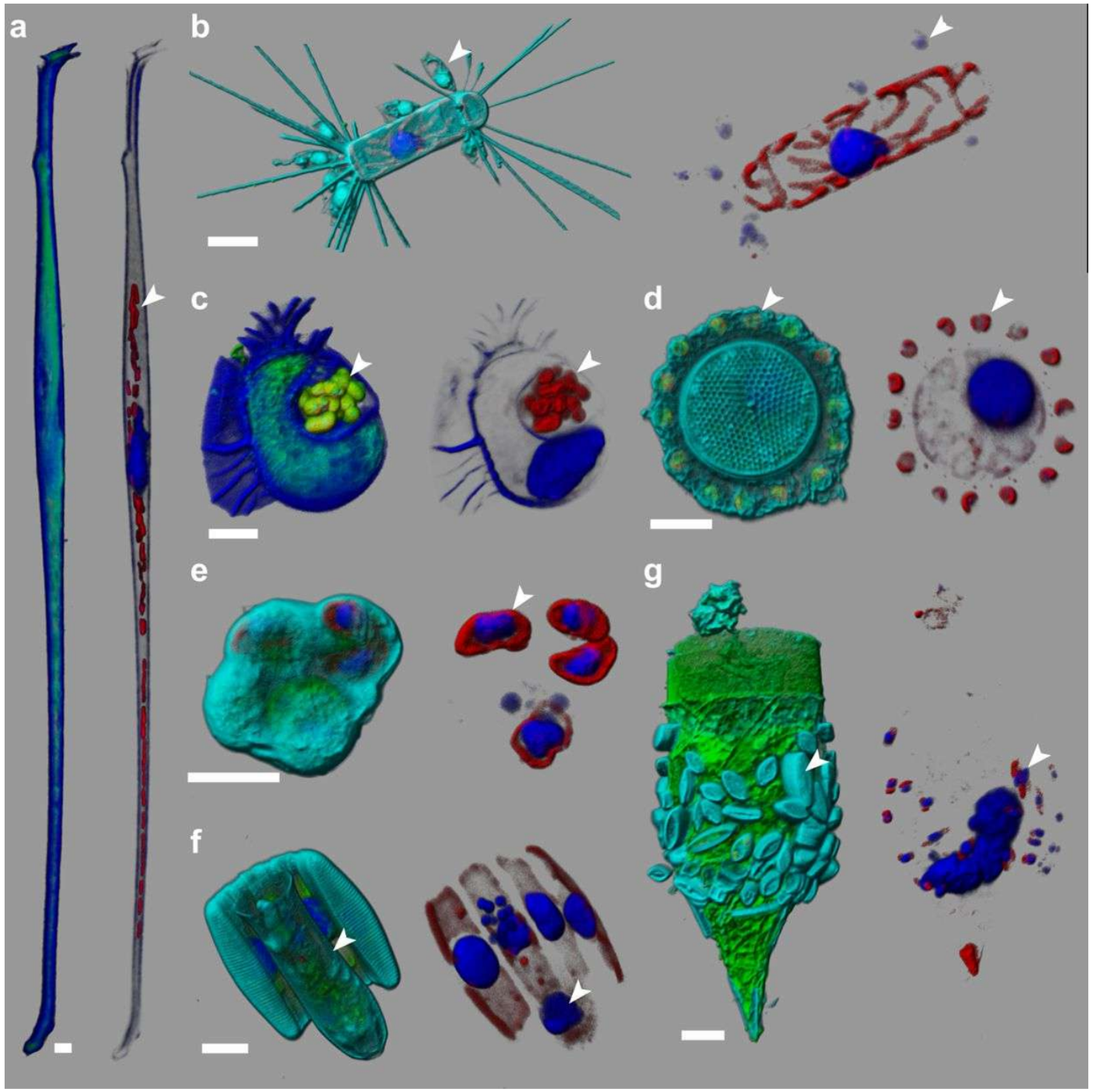


Key cellular features are labelled with various dyes: DNA/nuclei (blue, Hoechst33342); (intra)cellular membranes (green, DiOC6(3)); cell covers and extensions (cyan, PLL-AF546, a home-made conjugation between α-poly-L-lysine (PLL) and Alexa Fluor 546 (AF546)); chloroplasts (red, chlorophyll autofluorescence).



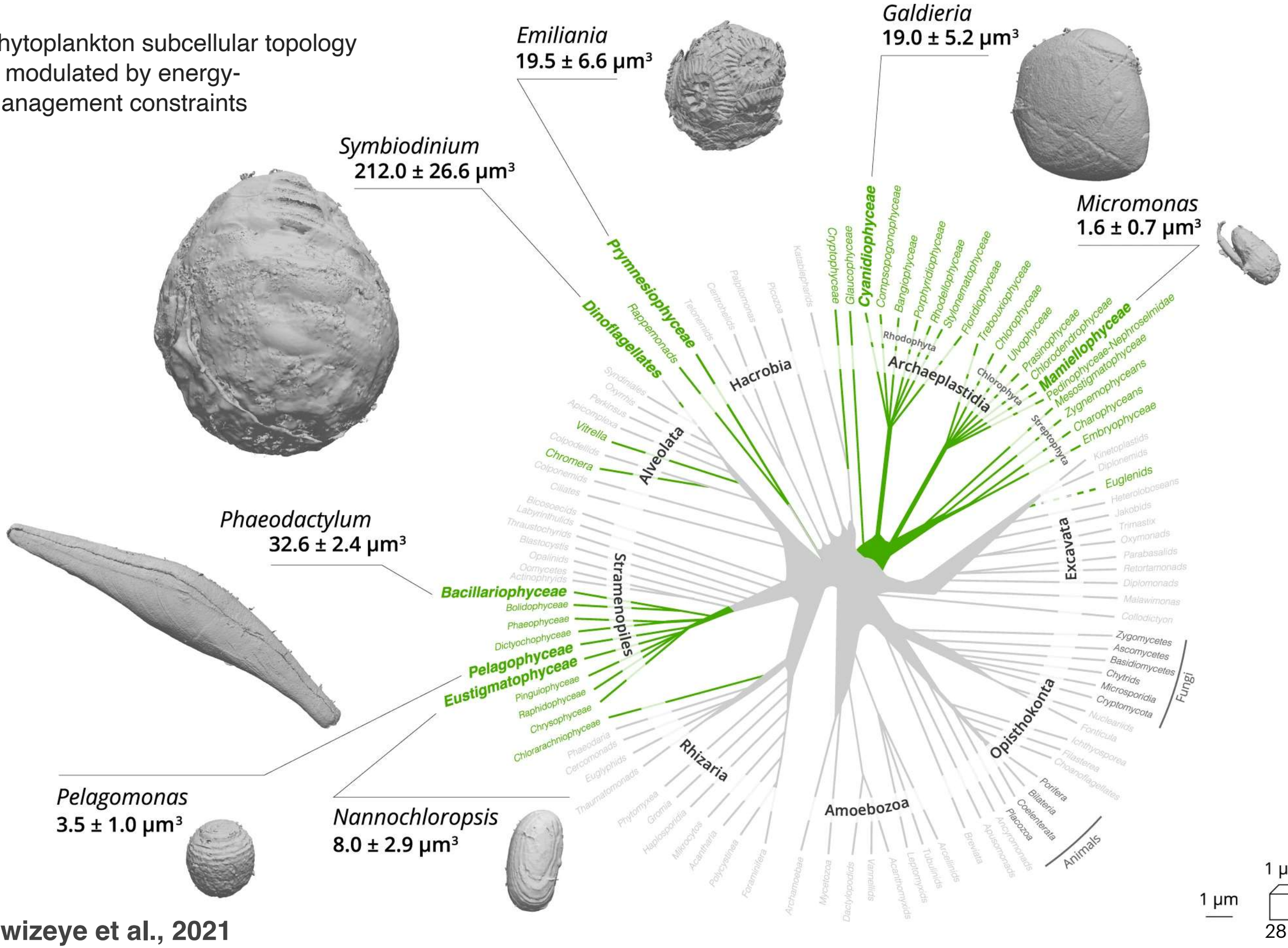
Colin et al., 2021

Colin et al., 2021

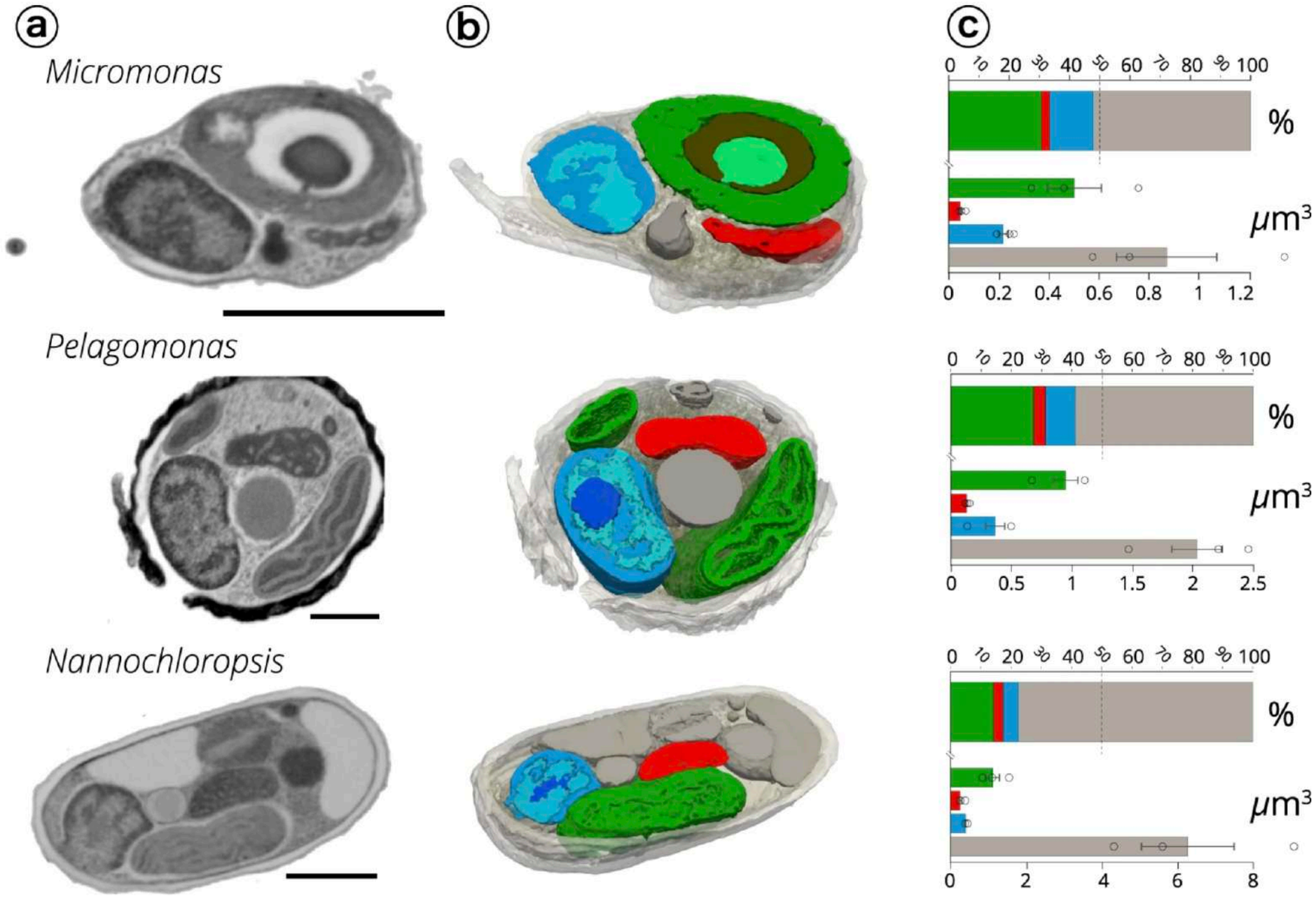


Four fluorescent channels were recorded: (i) Green: cellular membranes (DiOC6(3)) indicate the core cell bodies; it also stains loricas of tintinnid ciliates (g); (ii) Blue: DNA (Hoechst) identifies nuclei; it also stains the cell-wall of thecate dinoflagellate (**a, c**); (iii) Red: chlorophyll autofluorescence resolves chloroplasts; (iv) Cyan: PLL-A546 is a generic counterstain for visualizing eukaryotic cells' surface

Phytoplankton subcellular topology is modulated by energy-management constraints

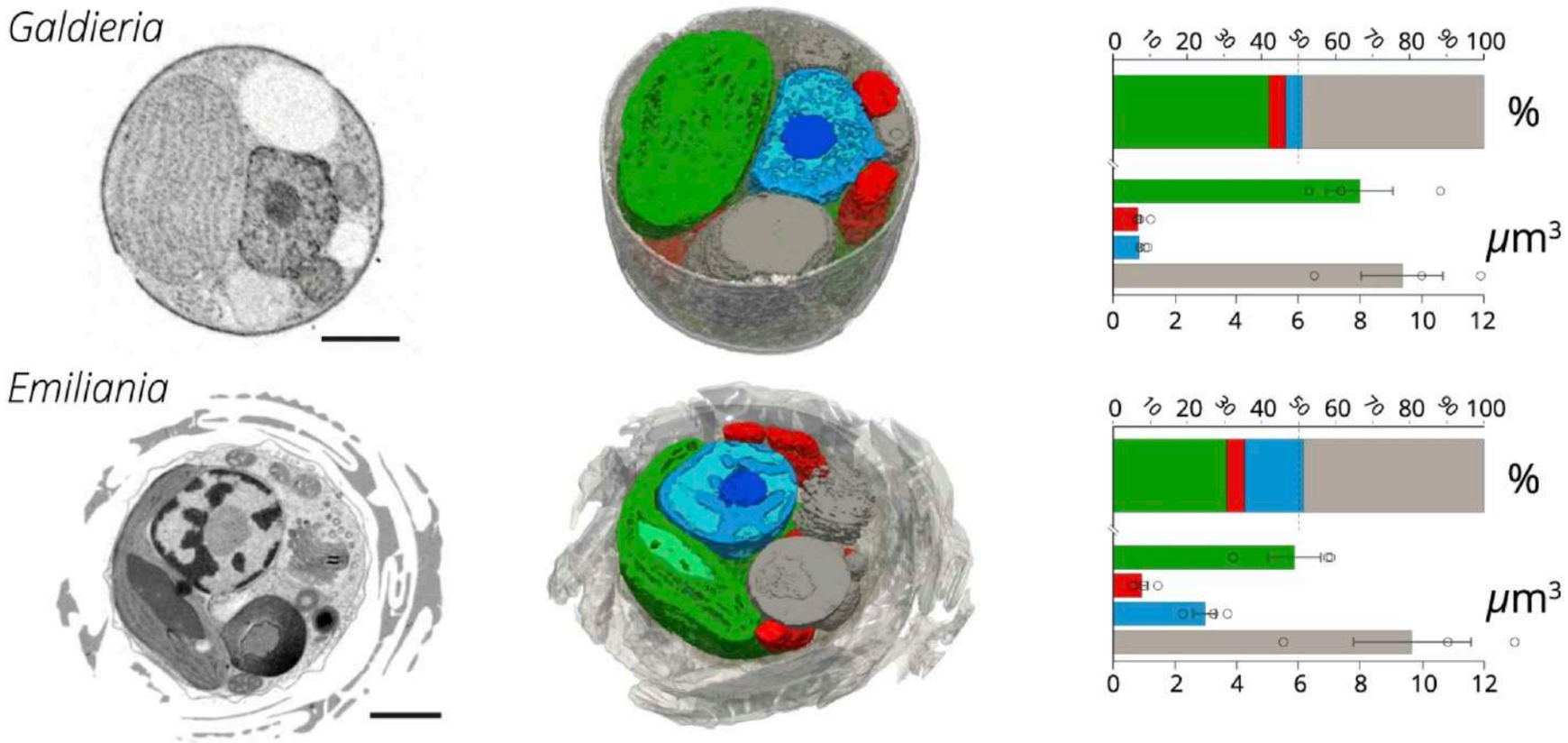


Uwizeye et al., 2021



Green: plastids (containing thylakoids and pyrenoids—light green—in some cell types); red: mitochondria; blue: nuclei (with different intensities of staining possibly corresponding to euchromatin—light blue—heterochromatin—blue and the nucleolus—dark blue); grey: other compartments
Volume occupancy by the different subcellular compartments in different microalgal cells. Top plot: % of cell-volume occupation; bottom plot: absolute volume sizes. Data refer to three cells ± s.d. for every species

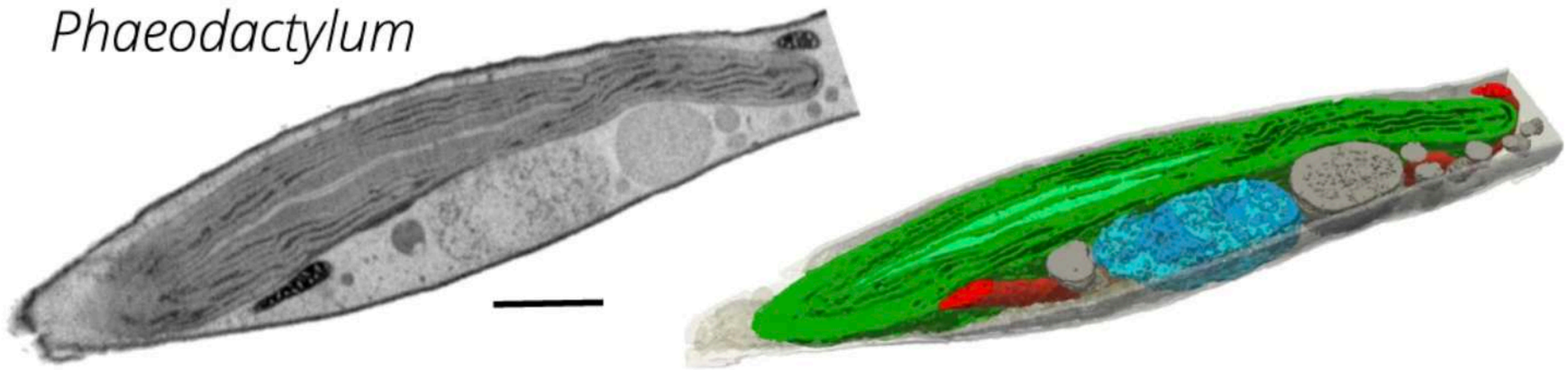
Uwizeye et al., 2021

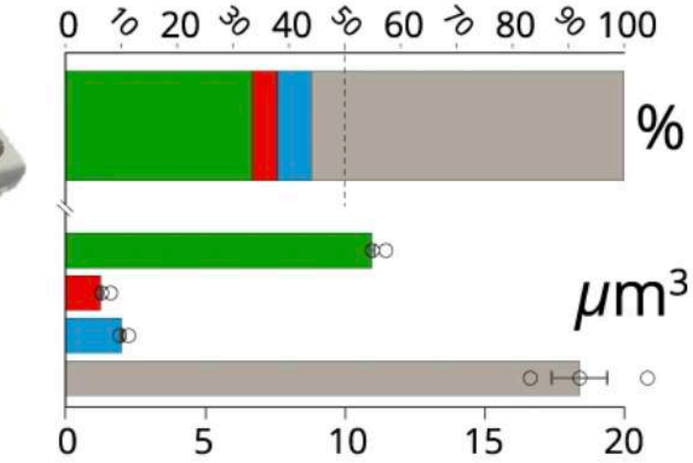


Green: plastids (containing thylakoids and pyrenoids—light green—in some cell types); red: mitochondria; blue: nuclei (with different intensities of staining possibly corresponding to euchromatin—light blue—heterochromatin—blue and the nucleolus—dark blue); grey: other compartments
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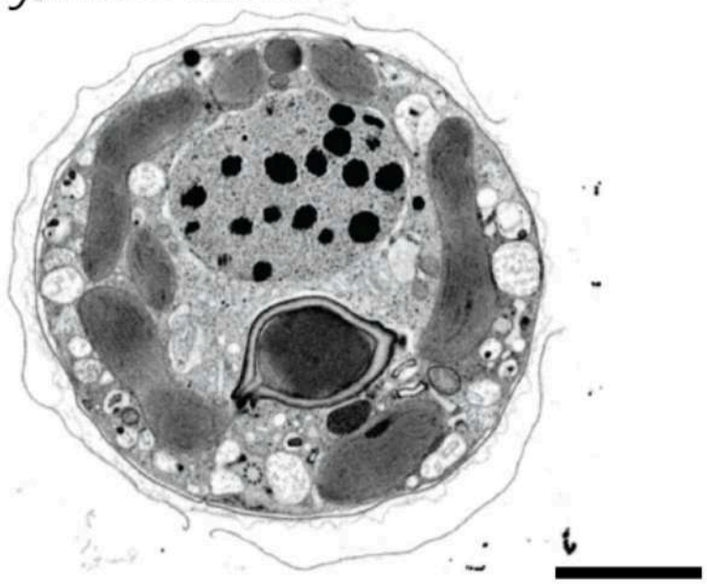
Uwizeye et al., 2021

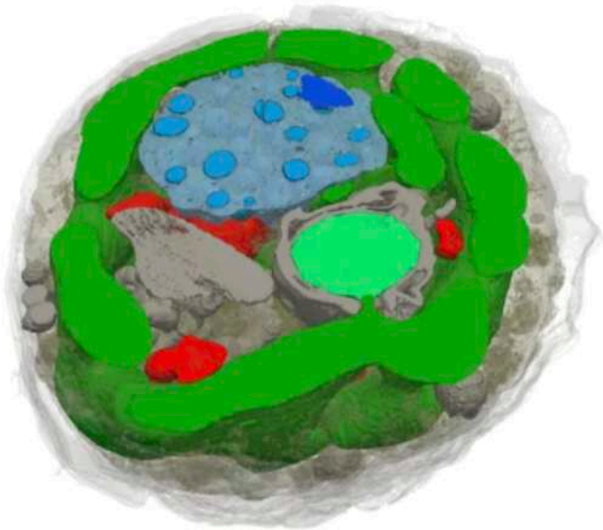
Phaeodactylum

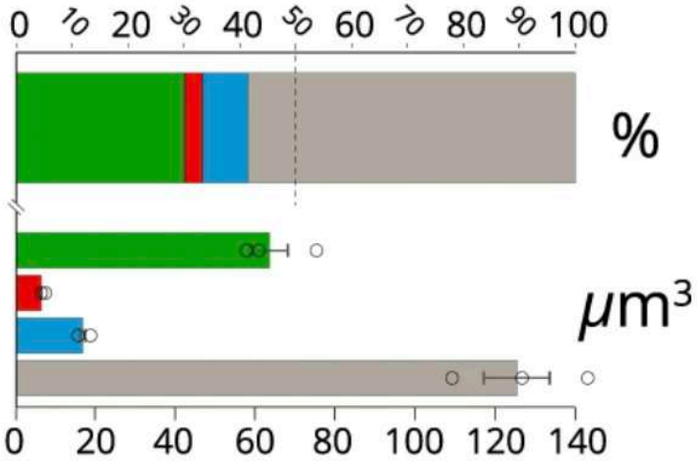




Symbiodinium







Plastid Mitochondria Nucleus Other

Green: plastids (containing thylakoids and pyrenoids—light green—in some cell types); red: mitochondria; blue: nuclei (with different intensities of staining possibly corresponding to euchromatin—light blue—heterochromatin—blue and the nucleolus—dark blue); grey: other compartments
Volume occupancy by the different subcellular compartments in different microalgal cells. Top plot: % of cell-volume occupation; bottom plot: absolute volume sizes. Data refer to three cells ± s.d. for every species

Uwizeye et al., 2021

Picoeukaryotes

- Photoautotrophs, osmotrophic heterotrophs, grazing predators, parasites
- 1-3 µm cell diameter
- In surface waters, 10^4 cells/mL
- *Ostreococcus, Prasinophytes*
  - Chl a, primary producer
  - Up to 80% of primary production with *Prochlorococcus* and *Synechococcus* in subtropical ocean
  - 13.9 Mb, with 7932 predicted genes
  - C4 photosynthesis beside C3
- *Micromonas pusilla, Prasinophytes*
  - Open and coastal ocean
  - Summer bloom terminated by viruses
  - Autotrophic and phagotrophic (=bacterivor in Artic Ocean)
  - 21.9 Mb, with 10242 predicted genes

Heterotrophic flagellated protists

- One or more flagella for feeding and movement
- Important bacteria grazers in water column and sediment, sea ice, intestinal habitat
- Flagella structure is important to identify them
- Preying on bacteria they are then consumed by ciliates and dinoflagellates, that are then consumed by copepods
- Strong top-down control on bacteria population
- 10^5 cells/mL
- Discard up to 30% of indigested food via vacuoles that becomes DOM and POM pool
- Produce pico-fecal pellets that funnel C export into the deep ocean
- Mixotrophic with chloroplasts that can be kept after ingesting prey

Heterotrophic flagellated protists

- HNF: heterotrophic nanoflagellates 3-10 µm
  - Prey on Bacteria and Archaea
  - Prey difference
  - Suspension feeder, creating feeding currents that concentrate pray
  - Genome > than PicoEuk
  - *Bodo, Cafeteria*
- HMF heterotrophic microflagellates > 20 µm
  - Channel C to higher trophic levels
  - In deep ocean up to 30% carbon to higher trophic levels

Choanoflagellates

- Similar to feeding cells in sponges
- 3-10 µm cell diameter
- Single flagellum with microvilli around the mouth part
- Some have a basket-like shell (lorica) in silica
- Genome > than HNF

Dinoflagellates

- Traverse flagellum —> spinning motion
- Armor made by cellulose
- Important bacteria grazers in water column and sediment, sea ice, intestinal habitat
- Genome > than HNF and Choanoflagellates, Diatoms
- Huge genome: 1.2-272 Gb (*e.g.* humans 3.2 Gb), large region of repeated and interspersed non coding DNA, intensive HGT
- Benthic community, corals, sediment, seaweeds, on surface and water column
- Chl a, c and carotenoids and xanthophylls
- Important primary producers coastal in high latitudes
- Spring bloom of dinoflagellates and diatom
- Symbionts in corals: Symbiodiniaceae
- Endosymbionts in protists, ciliates, foraminiferans and colonial radiolarians
- Predators of bacteria, phytoplankton and zooplankton eggs
- Predated by copepods
- Vertical migrations during the night —> circadian rhythm
- Bioluminescence: *Gonyaulax* and *Lingulodinium*
- Toxin producers, *Dynophysis*

Cilliates

- Voracious grazers
- Covered by cilia to create feeding currents and to move
- 15-80 µm - 200 µm
- Tintinnids lorica, house made of protein and carbohydrates and particles collected from water
- 1- 150 ciliates/ mL, >> number in marine snow, benthic sediment and microbial mats
- Prey bacteria and smaller protists —> larger protists and zooplankton
- Some are photosynthetic
- Two nuclei: one with genes and mRNA, the second is diploid for sexual reproduction

Haptophytes (Primnesiophytes)

- Important primary producers
- Complex life style: motile and not-motile, naked or with coccoliths
- Accessory pigments diadinoxanthin and fucoxanthin
- Calcification depend on inorganic calcium carbonate
- Coccoliths are calcifying in the Golgi apparatus
- Calcification enhance photosynthetic efficiency by lowering cellular pH thus increasing CO_2 concentration for RuBisCO
- Coccoliths: grazing protection and photodamage protection
- At 3000 m, due to high pressure calcite dissolved
- Important carbon export, preyed by zooplankton
- Visible from satellite
- Evolved 290 MYA

Haptophytes (Primnesiophytes)

- ***Emiliana huxleyi*** **167.7 Mb with 38544 predicted genes**
  - **4-5 µm cell diameter**
  - **Haploid stage non calcified scales and motile**
  - **Diploid stage calcified and non motile**
  - **Bloom in temperate and subtemperate waters and coastal and oligotrophic waters**
- ***Chrysochromulina*** **and** ***Phaeocystis*** **forms mucilage, DMS and foam**

Diatoms

- Stramenopiles, Bacillariophyceae
- Important primary producers in coastal water
- Two valves, of hydrated silica, like a box
- 2 - 200 µm
- Asexual reproduction until the cells becomes too small (*i.e.* 1/3 of regular size) than sexual reproduction
- Ge can be take-up instead of Si —> valves become fragile
- A dark period, synchronise the population in lab culture
- 76.2 MB genome size with 18246 predicted genes
- Free-living or benthic

Diatoms II and Raphidophytes

- Some are heterotrophs
- Chl a, c, carotenoid fucoxanthin
- ~40% of total primary productivity
- On ice important primary producers, spring bloom in temperate waters and in upwelling areas
- Silica is limiting nutrients
- Silica is precipitated due to protein, silaffins that create a low pH environment —> silica dissolve at seater pH without protein protection
    - Diatoms form the diatomaceous ooze in sediment at seawater pH
    - Formation of petroleum hydrocarbon —> biofuel production
    - Toxin production
- Raphidophytes (Stramenopile)
    - 50-100 µm, no cell wall, two flagella
    - Red tides, *Heterosigma akashiwo*
    - Toxin production
    - Good food in aquaculture: *Nannochloropsis,* brown tide former

Thraustochytrids and Labyrinthulids

- Stramenopile
- Slime/mucus net producers
- Look like Fungi
- 1-100 cell/mL
- Coastal water, parassite on mollusks, associated on macro algae
- Osmothrophy of DOM
- Extracellular enzyme in slime able to degrade large polymers
- Digest refractory material, including mangrove detritus
- Predate by Ciliates and Amoebae
- Produce high level of PUFA, omega-3-polyunsaturated fatty acid —> important for Crustacea such as copepods (i.e. zooplankton)

Amebozoa

- Grazers of particle associated bacteria
- Crawling with pseudopodia
- More abundant than Ciliate
- Coastal waters and estuaries

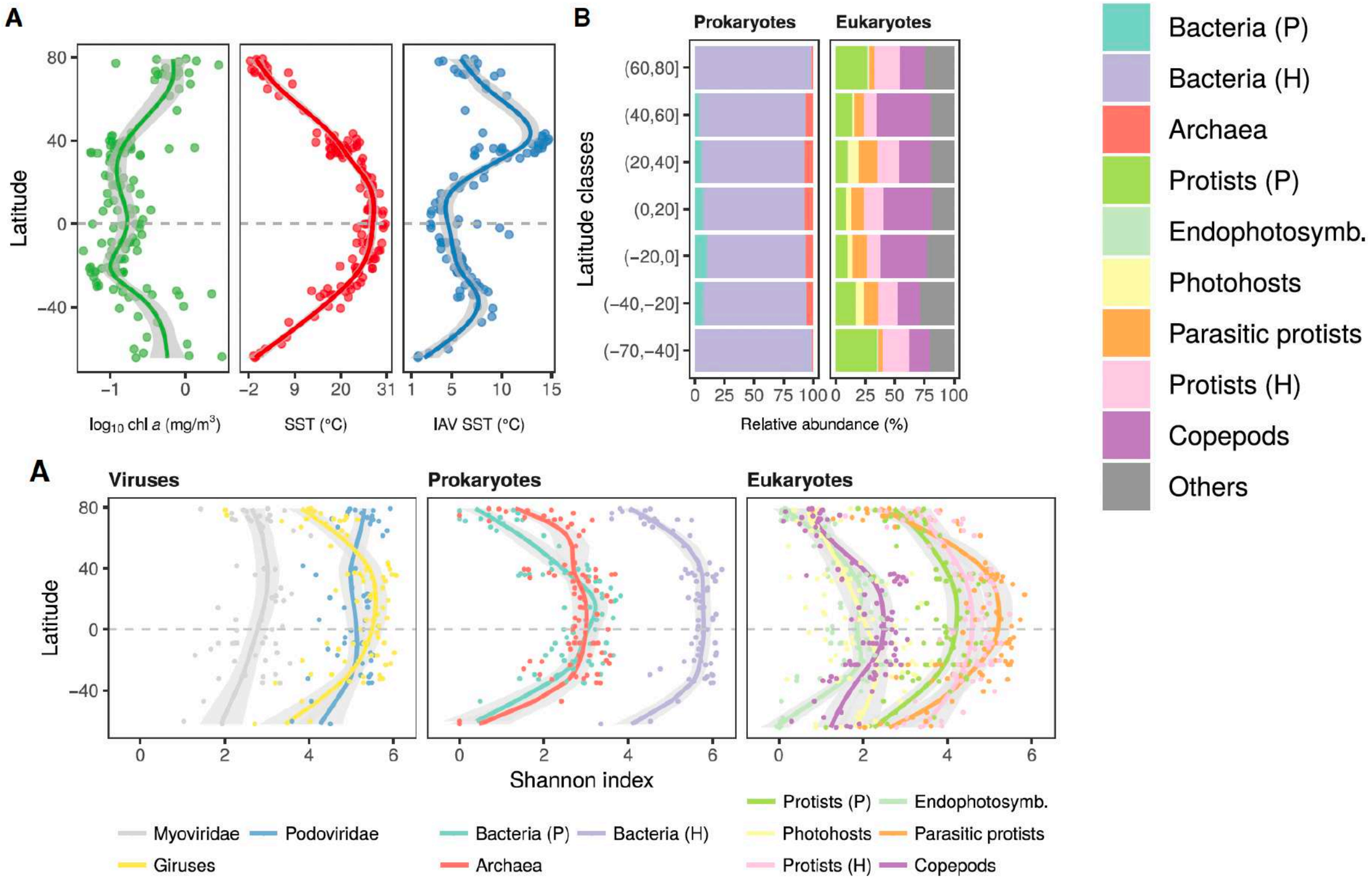
Radiolarians & Foraminifera

- Rhizaria
  - Radiolarians
  - 0.1-0.2 mm, stiff needle-like pseudopodia in radial symmetry and internal silica skeleton (some have strontium)
  - 10^4 cells/cm^3 in subtropical ocean
  - Preying protists and small zooplankton
- Foraminifera
  - Multichambered organisms, with pseudopodia
  - Deep ocean, productive waters
  - Predators of bacteria, phytoplankton and small metazoan animals
  - Many fossils, globigerine ooze

Marine Fungi

- Monophyletic group
- Opistokonta
- ~1.5 BYA diverged from animals
- Ascomycota
- Basidiomycota
- Chytridiomycota
- Heterotrophic osmotrophs
- Secretion of extracellular enzymes —> degrading recalcitrant compounds, hydrocarbons and xenocompounds and plastics
- Parassites of algae, other protists and animals and plants
- Cell-wall composed by N-acetyl-glucosamine polymer: chitin
- Spores can travel —> sea foam
- Source of natural products
- Bioremediation
- Surface of coastal ocean waters, deep waters subsurface sediments from polar to tropical regions

Tara: surface ocean across a latitudinal gradient 0-1000 m



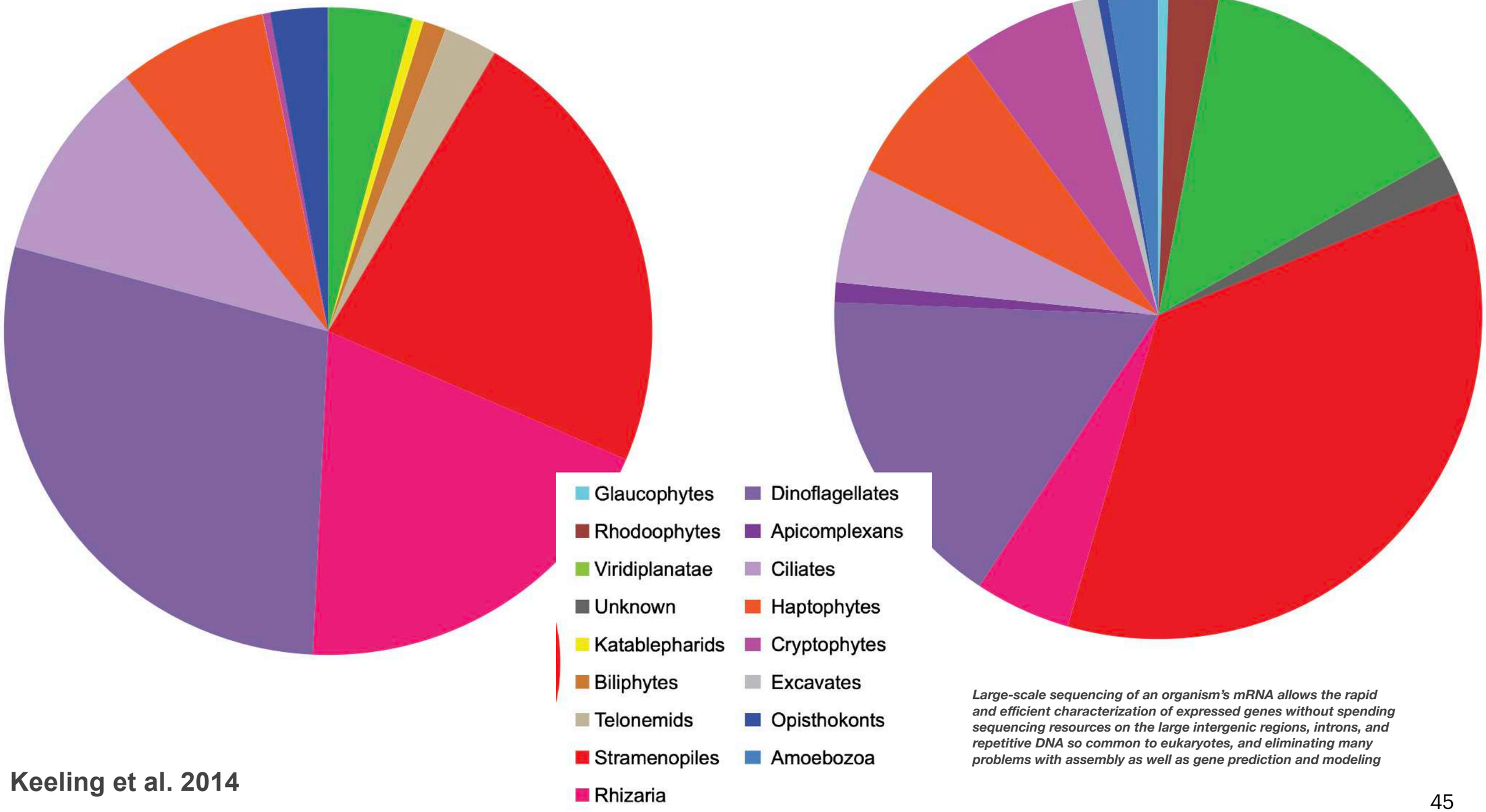
Ibarbalz et al., 2019

- **Temperature is an important driver in shaping microbial community**
- **Drop in diversity at the Tropics-Poles**

From 18S rRNA genes to mRNAs

(A) Unicellular taxa in a marine sample based on environmental 18S rRNA genes

(C) MMETSP transcriptomes



Large-scale sequencing of an organism's mRNA allows the rapid and efficient characterization of expressed genes without spending sequencing resources on the large intergenic regions, introns, and repetitive DNA so common to eukaryotes, and eliminating many problems with assembly as well as gene prediction and modeling

Keeling et al. 2014