Cyanobacteria

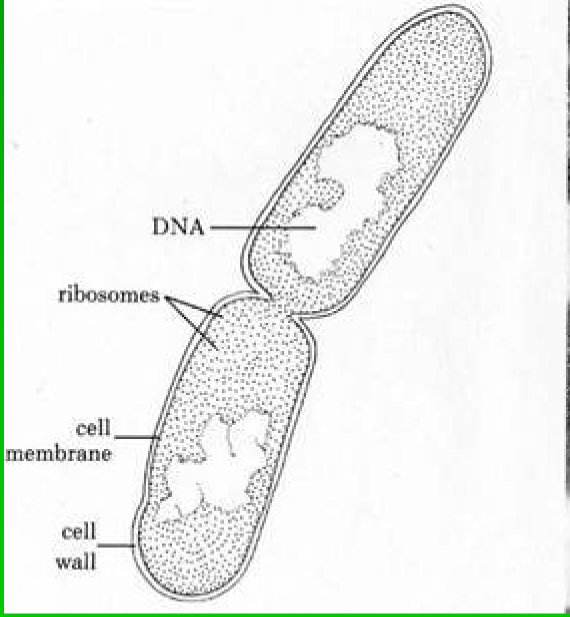
(syn. *Cyanophyta*, *Cyanoprokaryota*)

<u>Imperium</u>: Prokaryota (Prokarya)

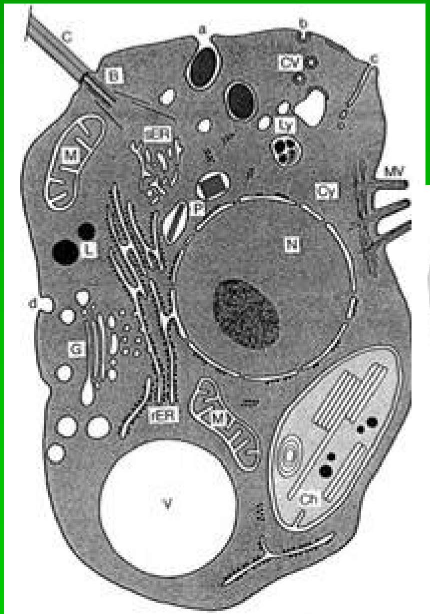
Bacteria

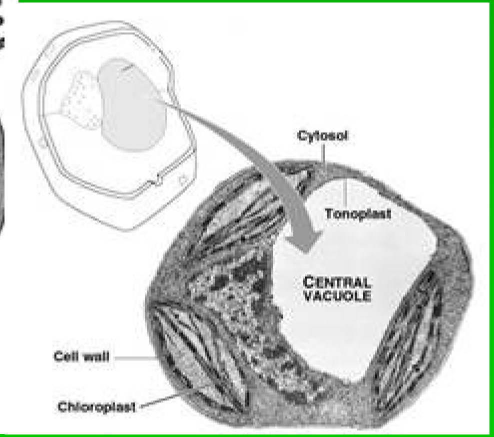
cyanos = bluegreen

bluegreen algae



prokaryotic cell

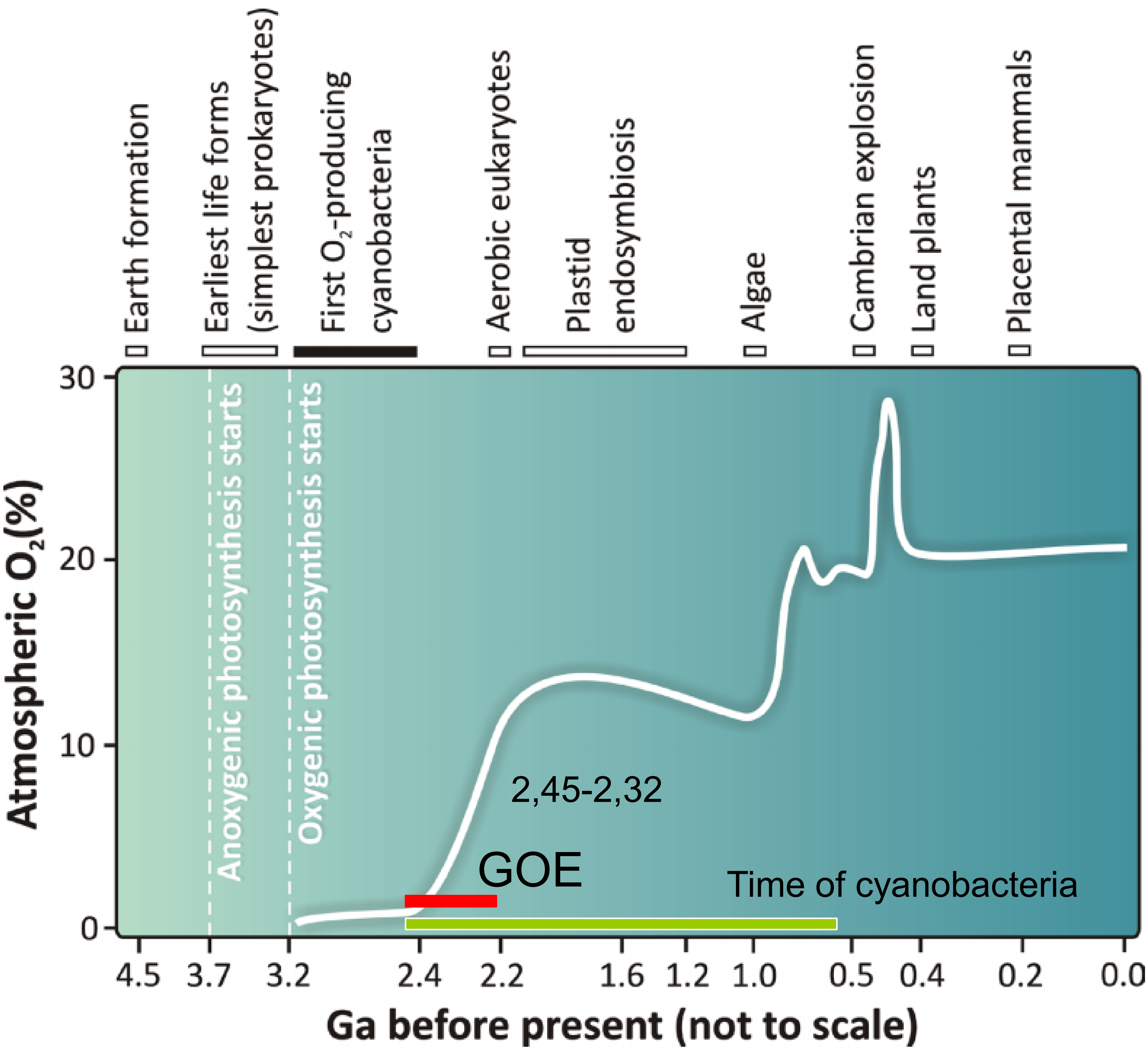




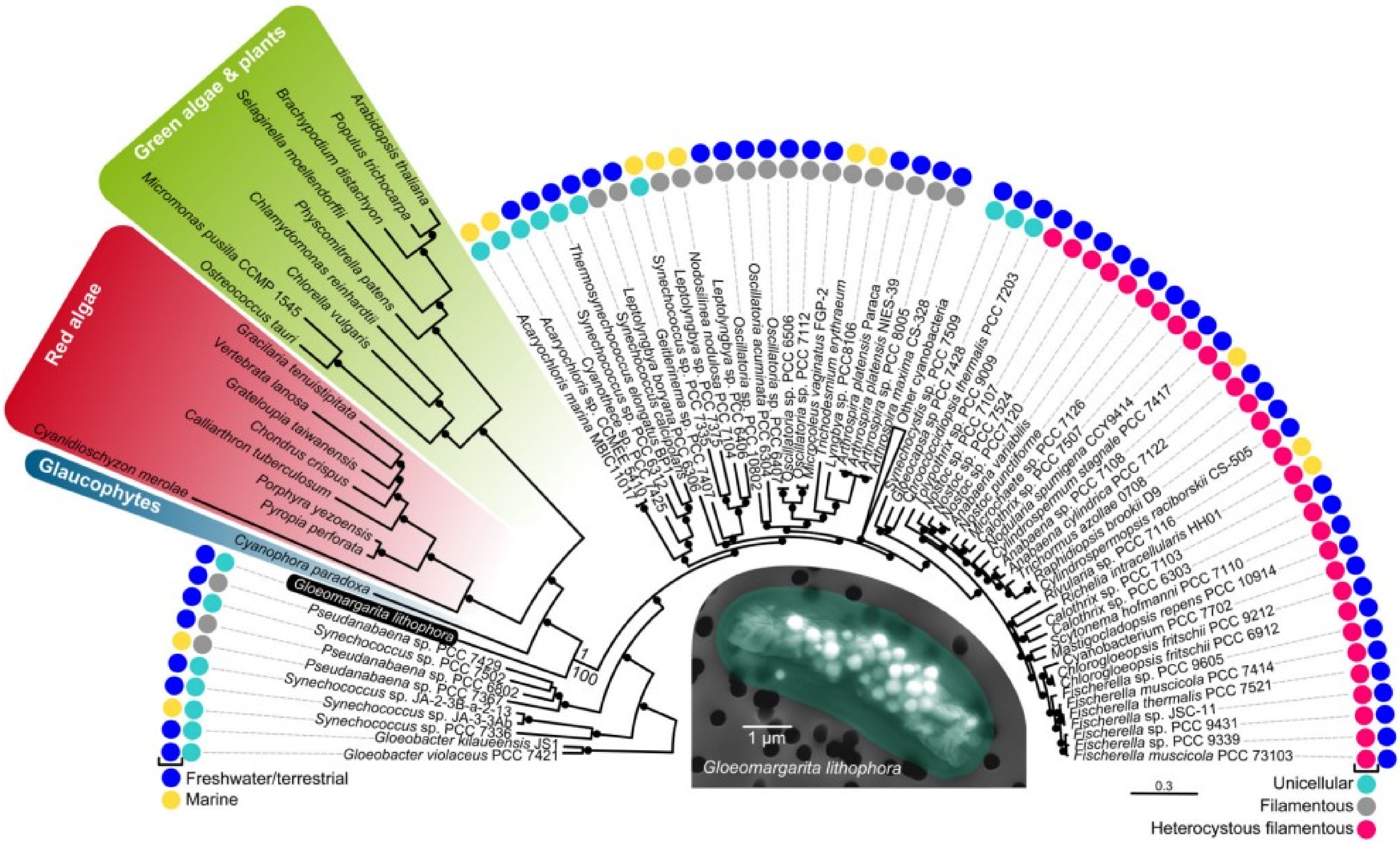
eukaryotic cell

Cyanobacteria

- cyanobacteria produced **Earth's first oxygen atmosphere** (water as the source of reducing power in photosynthesis - oxygen gas as a by-product
- cyanobacteria have **fostered the rise of eukaryotes** that benefit from aerobic respiration, ozone layer
- the first plastids arose from cyanobacteria, endosymbiotic partnerships with early protists - **diverse eukaryotic algal lineages and the land plants**
- for billions of years cyanobacteria have also generated massive underwater carbonate deposits that **sequester carbon** for geological time periods – reduction of atmospheric carbon dioxide levels and influence of global climate


Earth formation
Earliest life forms (simplest prokaryotes)
First O_2-producing cyanobacteria
Aerobic eukaryotes
Plastid endosymbiosis
Algae
Cambrian explosion
Land plants
Placental mammals
Anoxygenic photosynthesis starts
Oxygenic photosynthesis starts
2,45-2,32
GOE
Time of cyanobacteria
Atmospheric O_2(%)
30
20
10
0
4.5
3.7
3.2
2.4
2.2
1.6
1.2
1.0
0.5
0.4
0.2
0.0
Ga before present (not to scale)

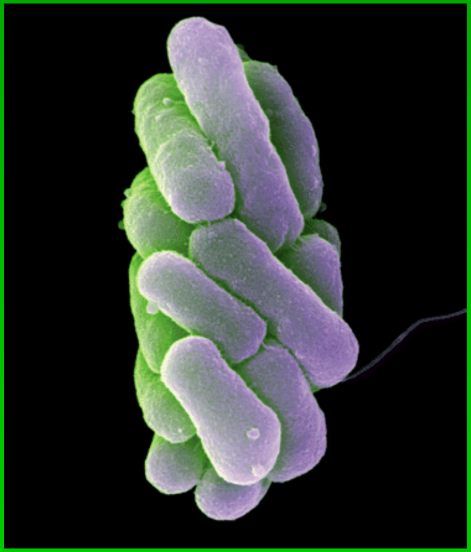
Gloeomargarita lithophora cyanobacterium; closest relative to endosymbiotic plastids, fresh water

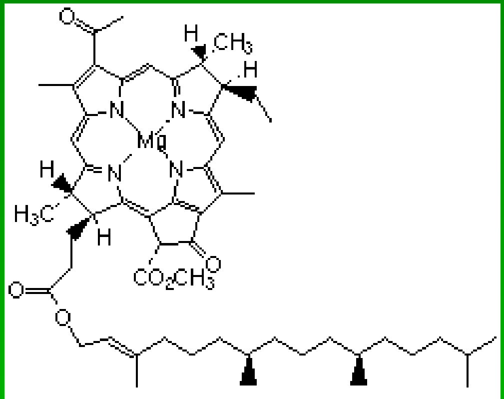


Green sulhur bacteria and cyanobacteria had probably a common ancester

„procyanobacteria“

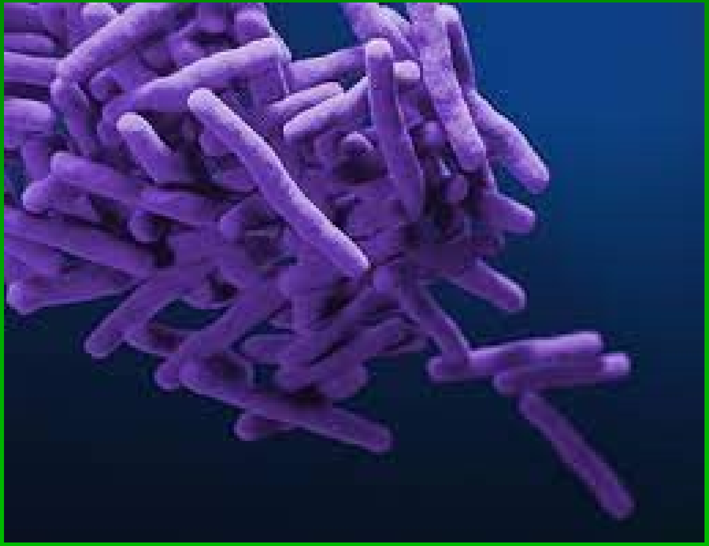
reaction center similar to PSI





Bacteriochlorophyll a

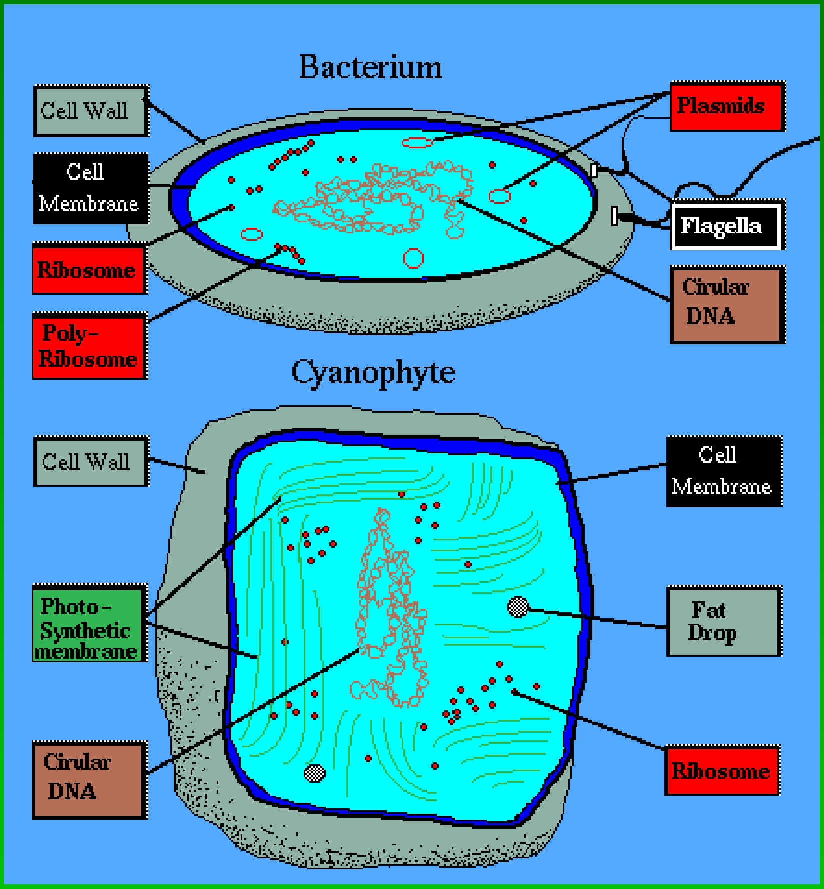
bacteriochlorophyl a

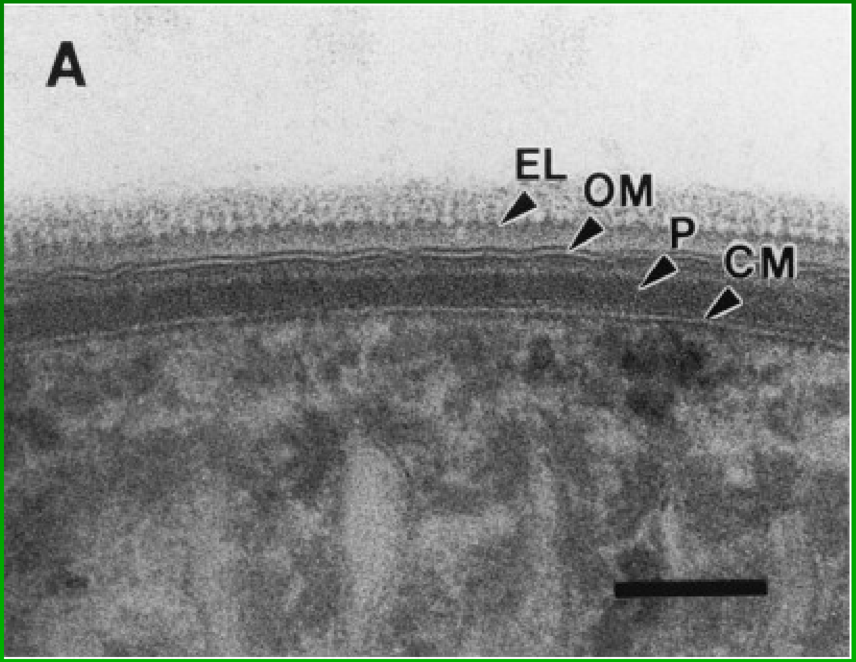


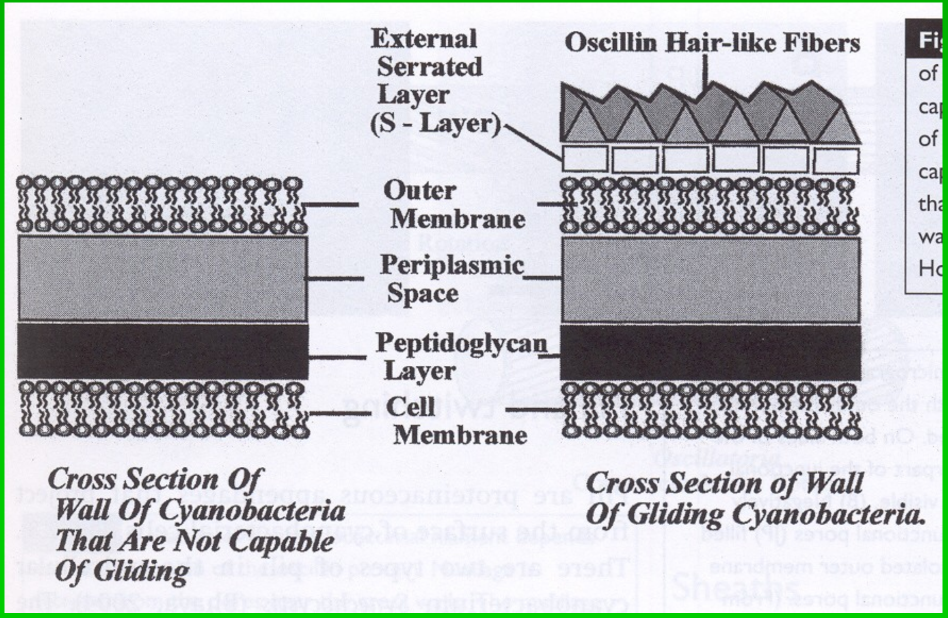
gain and coupling of the PS II (from purple b.) – horizontal gene transfer?

or the ancester had both photosystems

Cyanobacteria = G^{-} bakteria



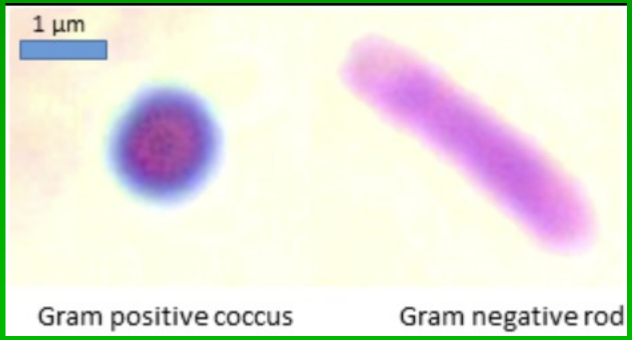


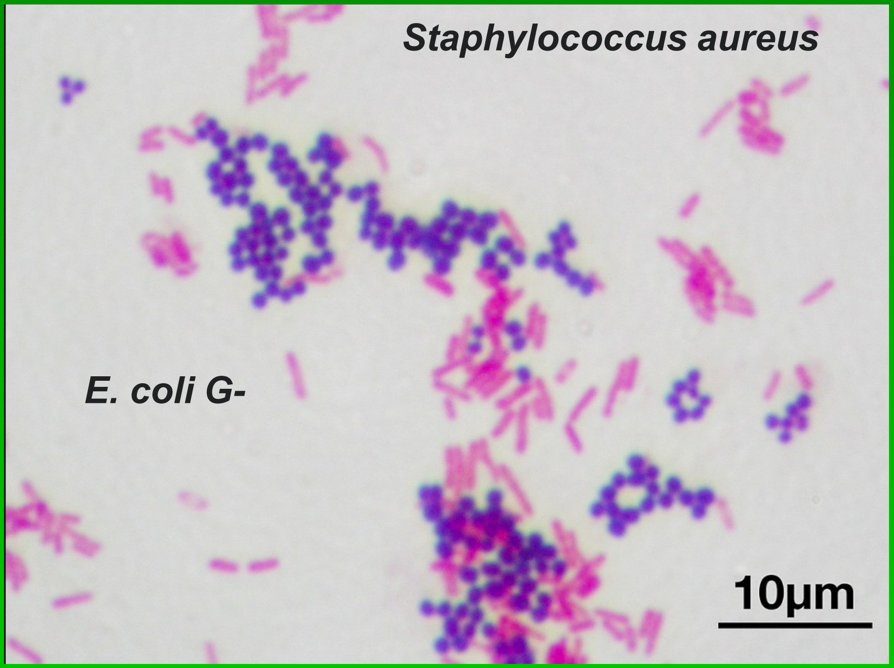


Cell wall structure

Gram staining, is a method of staining used to classify bacterial species into two large groups: gram-positive bacteria and gram-negative bacteria

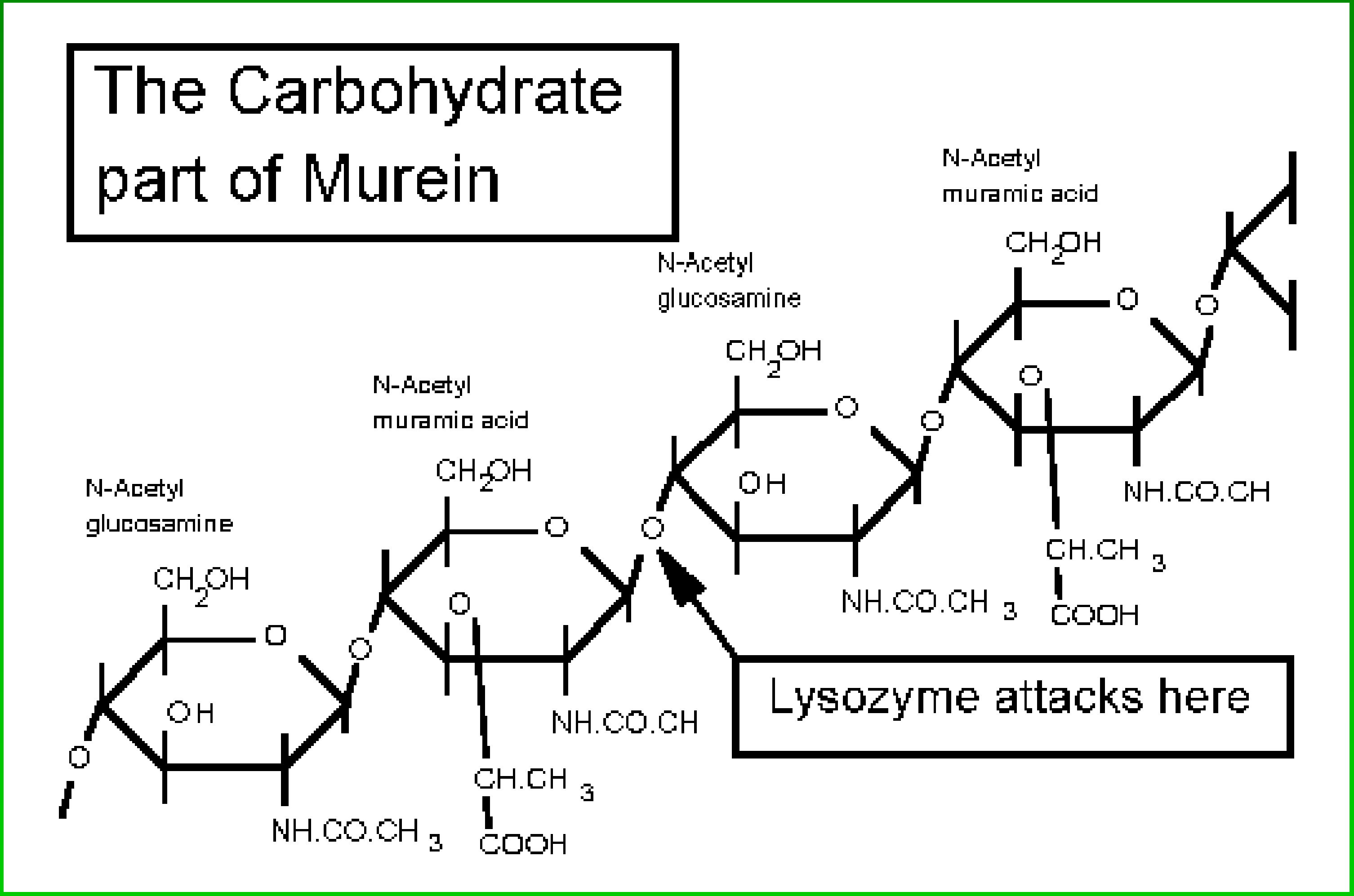
Danish bacteriologist Hans Christian Gram, who developed the technique in 1884





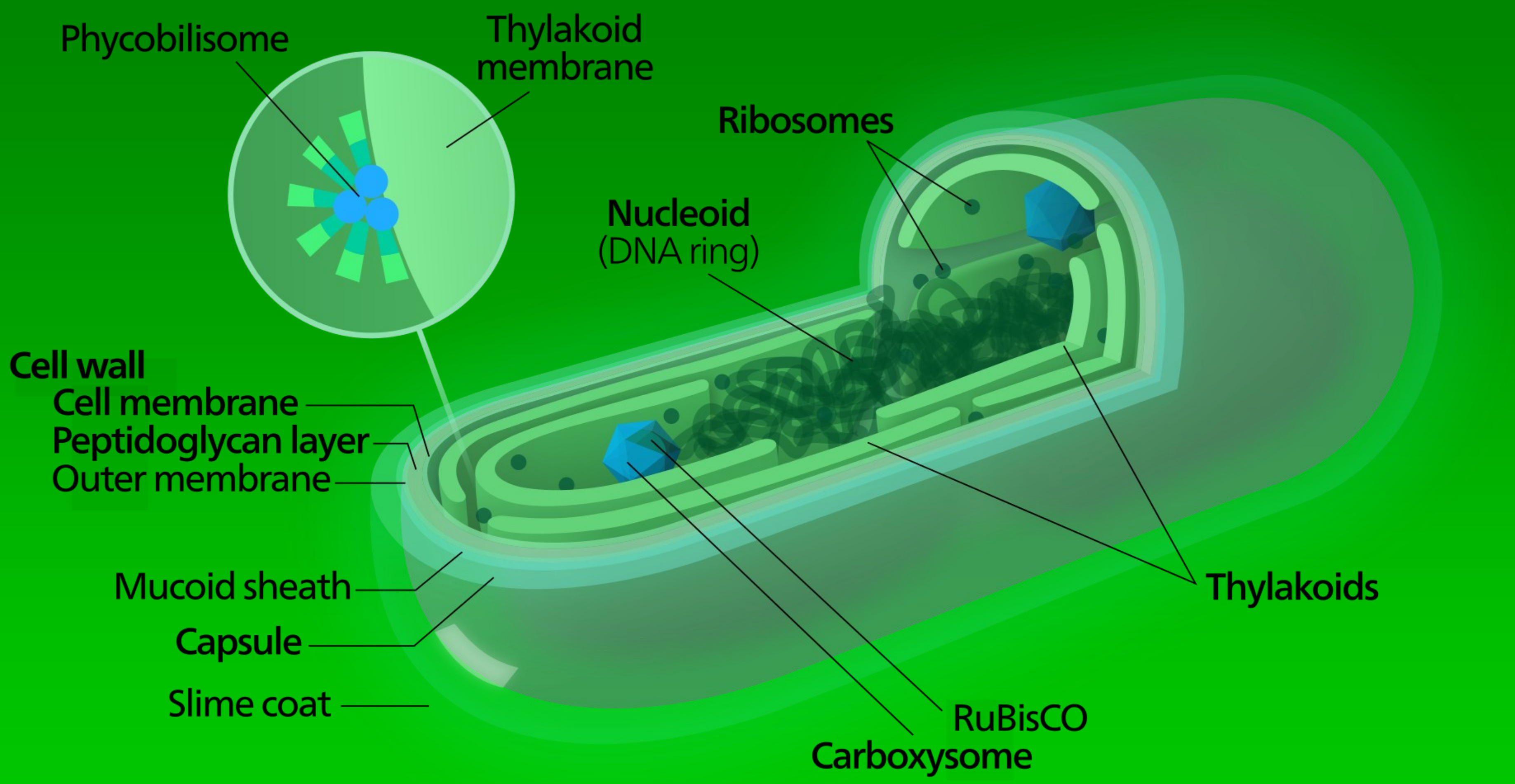
Gram+ a thick layer of peptidoglycan in the cell wall that retains the primary stain, crystal violet. Gram- have a thinner peptidoglycan layer that allows the crystal violet to wash out on addition of ethanol, counter-stained by safranin the cell wall composed of peptidoglycan (murein) similarly to the other G^- bacteria

CW cleaved by lysozyme, penicillin prevents CW synthesis



2 sugar derivatives

Cyanobacteria = G^- bacteria

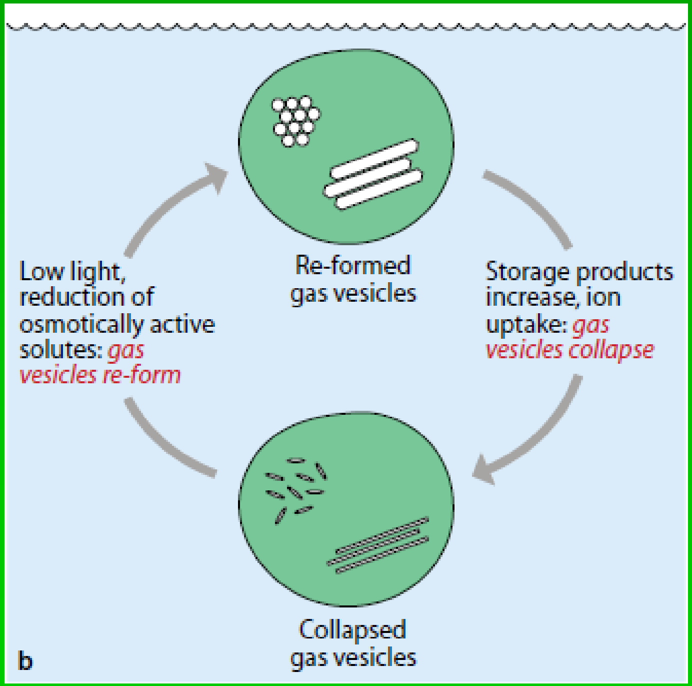


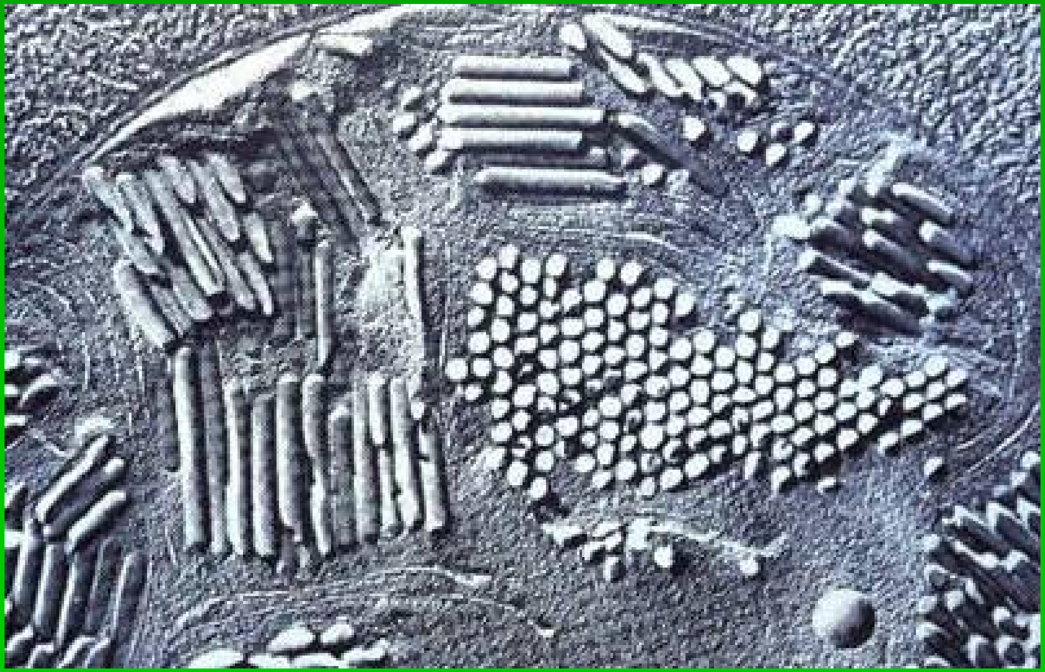
Aerotops (gas vesicles)

Gas vesicles are spindle-shaped structures provides buoancy to these cells by decreasing their overall cell density, glycoproteins (impermeable to water but permeable to most gasses)

- high light? increased PS → accumulation of polysaccharides → turgor increases → collaps of vesicles → the cell sinks out

- low light? decreased PS → metabolism of polysaccharides → turgor decreases → vesicle production → the cell rises up

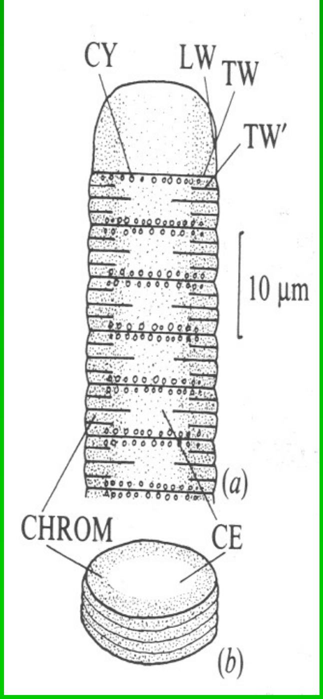


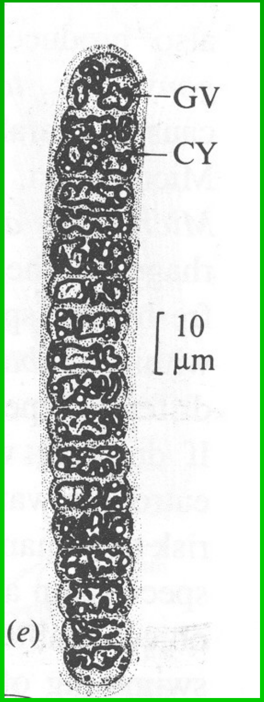


Tolypothrix, Calothrix – gas vesicules only in hormogonia – dispersal??

Reserve substances

- cyanophycean starch – small granules between thylakoids, α-1,4 linked glucan
- cyanophycin granules (fig. - CY) – polymers of Arg, Asp
- polyphosphate granules (volutin) – highly polymerized polyphosphate

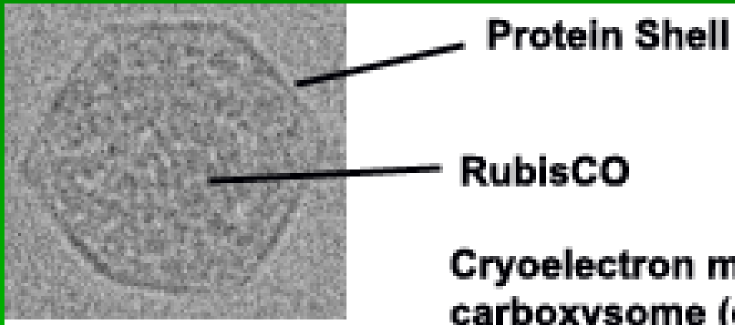




Oscillatoria - polyphosphate granules in the hormogonium

Carboxysomes

(polyhedral bodies) – Rubisco: $CO_2 \rightarrow$ polysaccharides



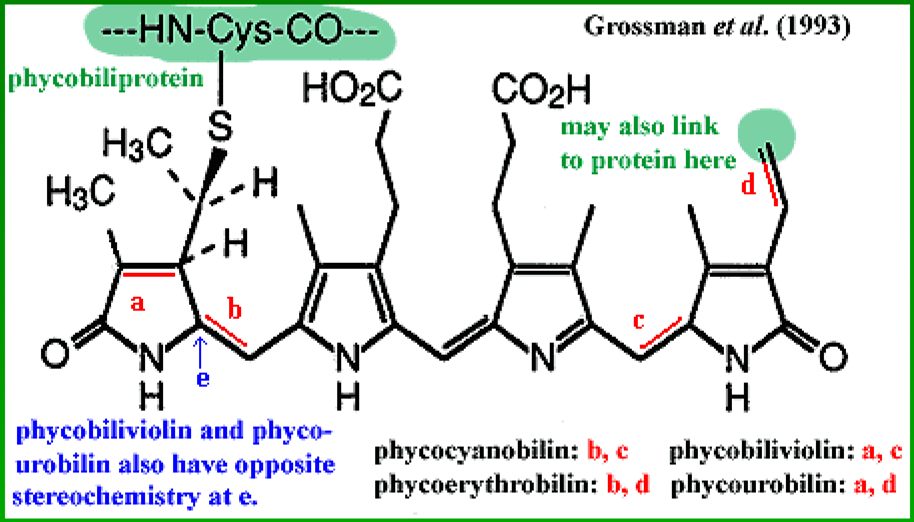
Cryoelectron micrograph of a carboxysome (diameter = 100 nm).

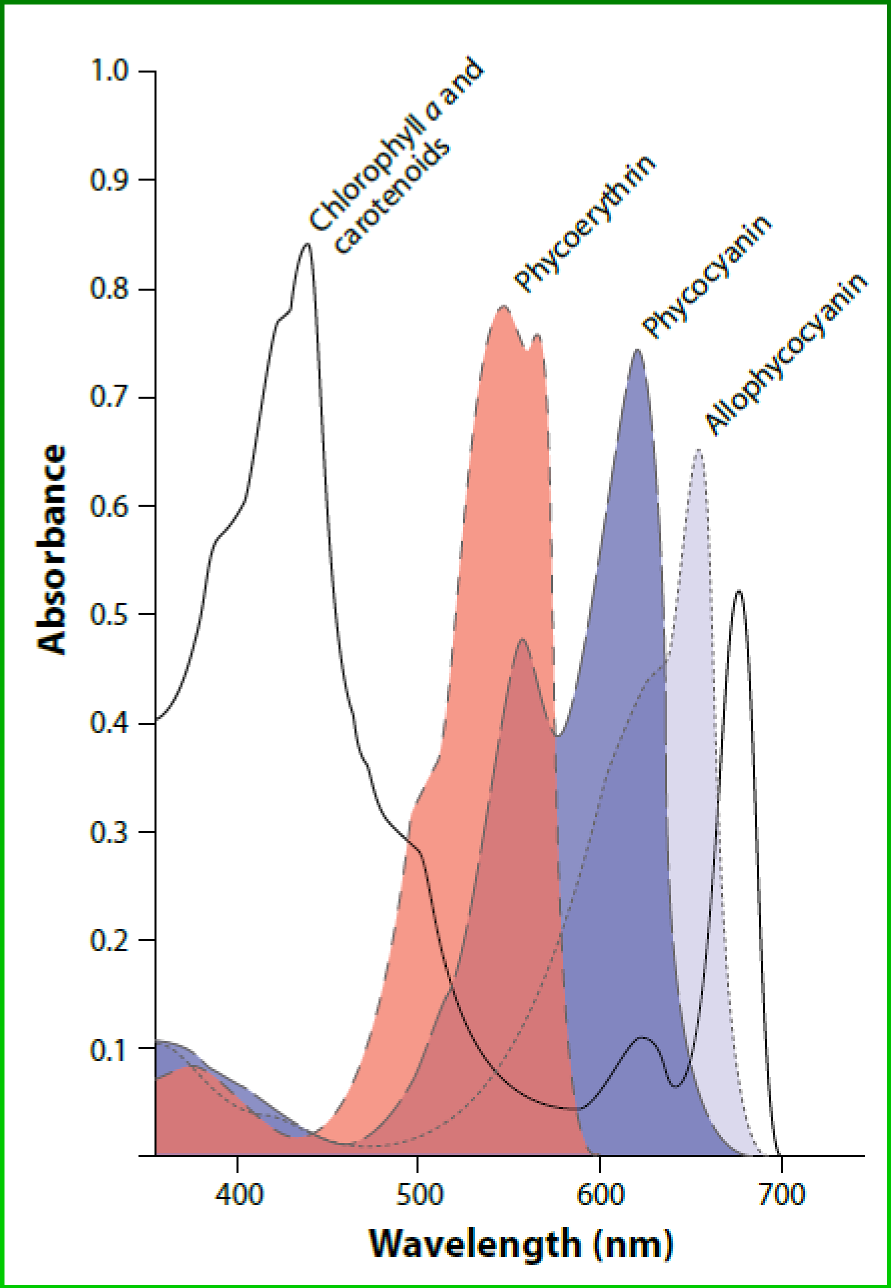
Enclosed in a proteinaceus cover, reserves of the enzymes RubisCO and carbonic anhydrase ($HCO_3^- \rightarrow CO_2$)

Proteinaceus cover of the carboxysome increases carboxylase activity of the RubisCO.

Hypothesis: the enzym enclosed in the carboxysome is forced to the conformation, that prefers CO_2 to O_2.

Pigments





phycobilines phycobiliproteins

open-chain tetrapyrrole structure

phycobiliproteins fill the „gap“ in the absorbance spectrum of chlorophylls and carotenoids

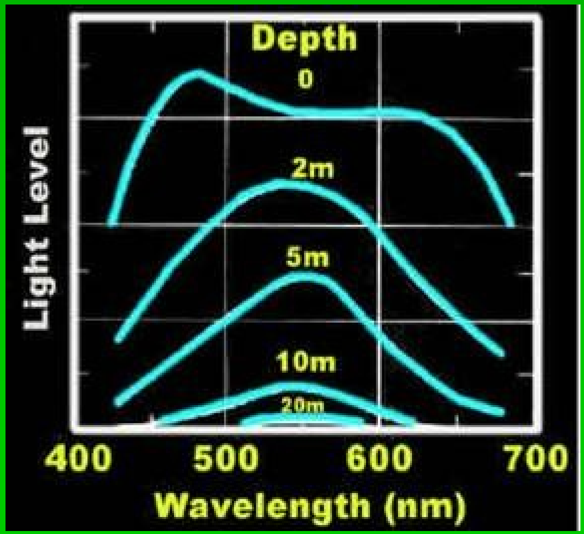
major pigments - Ch*a* and phycobiliproteins

Light absorption by phycobiliproteins

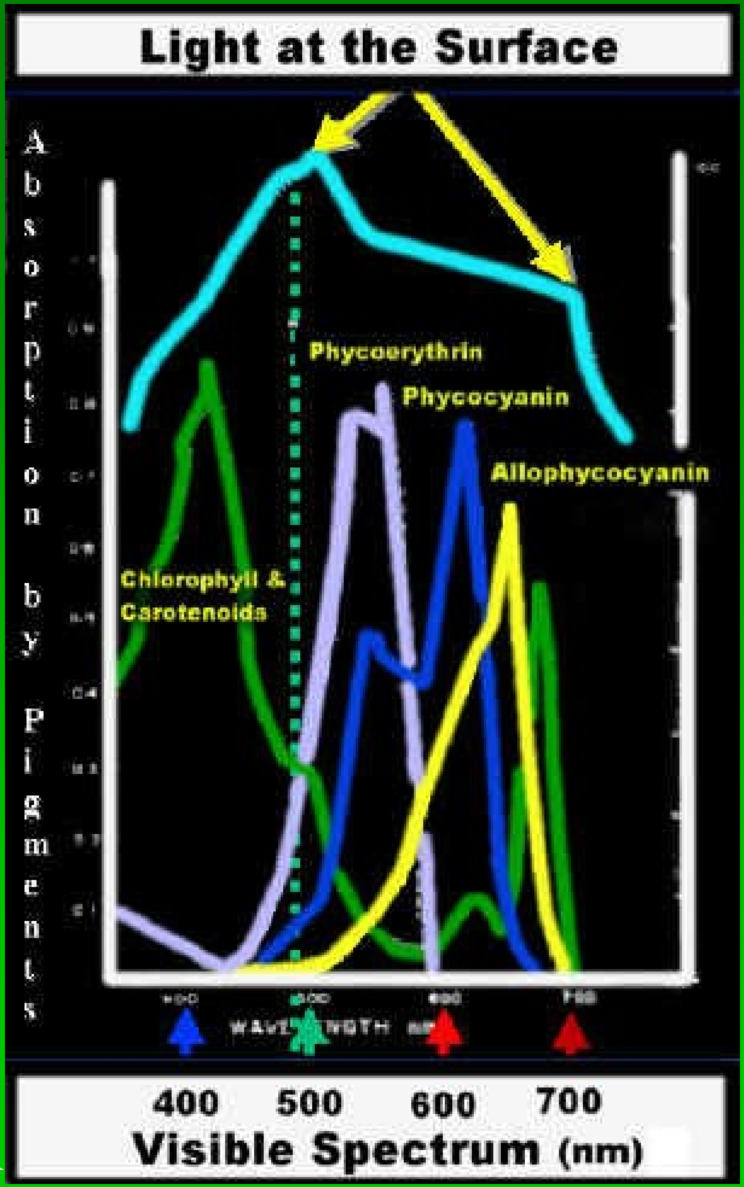
Blue, red: Chlorophyll *a, (b,d)*
β- caroten (much higher proportion than in euk. algae), echinenon, myxoxanthophyll

green (500-600 nm): C-phycoerythrin
green - yellow (550-650 nm): C-phycocyanin
orange - red (600-675 nm): allophycocyanin

→ combining of the pigments – absorption in the whole spectrum of visible light

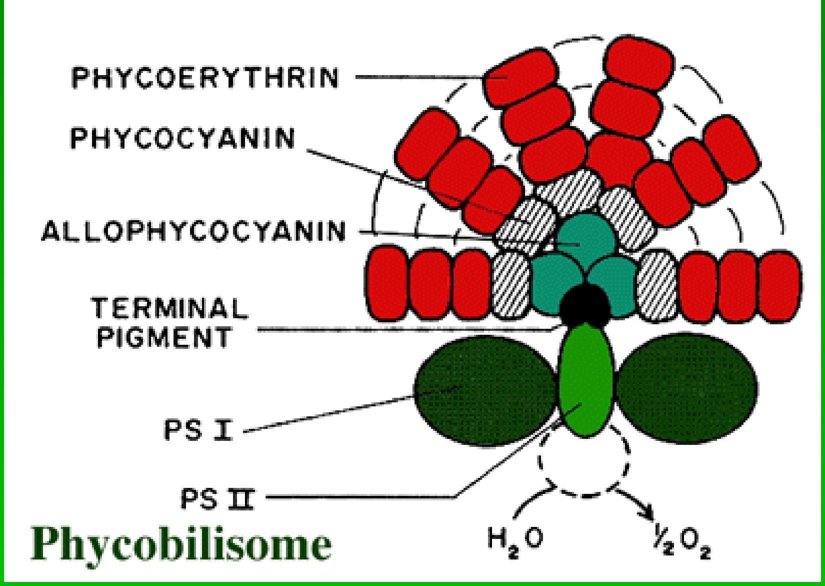


Absorption of light in a water column



Phycobilisome – light harvesting antenna

for photosystem II, I and nitrogen reserve



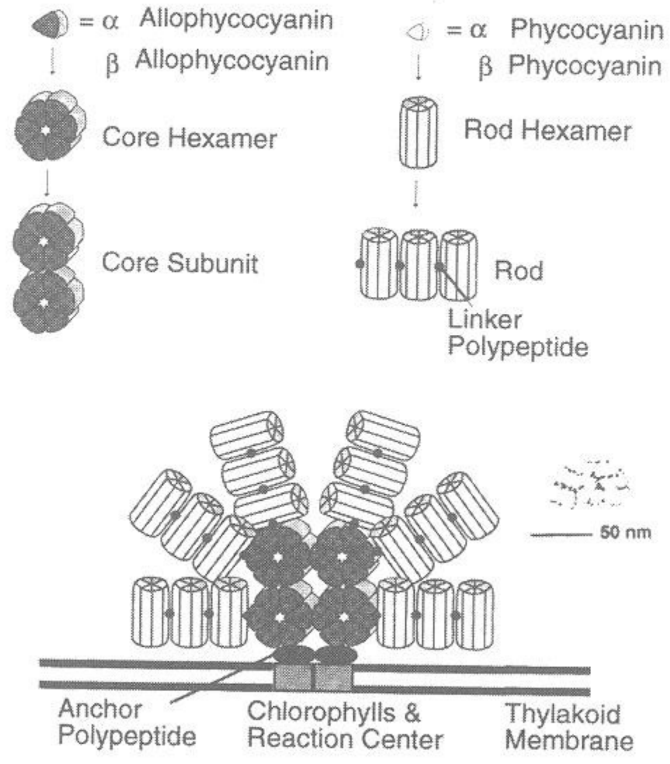


Fig. 1.23 Drawing of a phycobilisome from the cyanobacterium *Synechococcus*. (Adapted from Grossman et al., 1993.)

light harvesting in PSI-driven cyclic electron transport to facilitate nitrogen fixation and other reactions (Watanabe et al. 2014, PNAS)

Chromatic adaptation : the relative quantities of phycoerythrin and phycocyanin determines the color of the cell, λ dependent

green light ↑ phycoerythrin ↓phycocyanin

red light ↑ phycocyanin ↓phycoerythrin

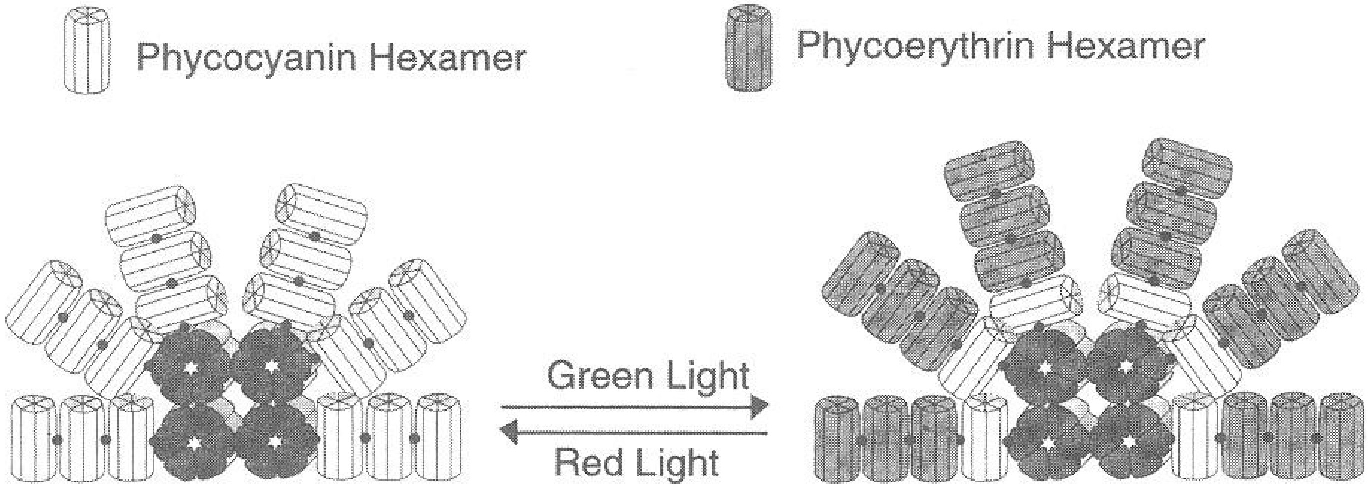


Fig. 1.24 Chromatic adaptation in a phycobilisome of a cyanobacterium.

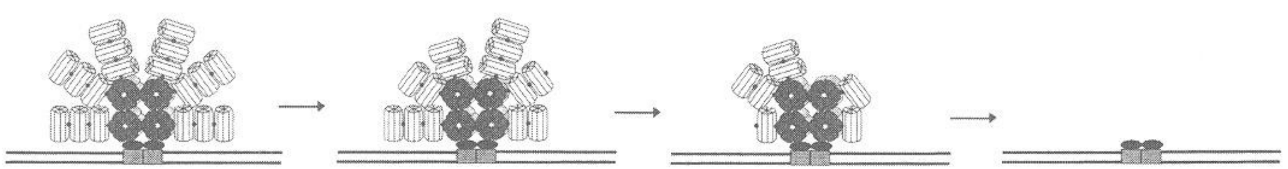
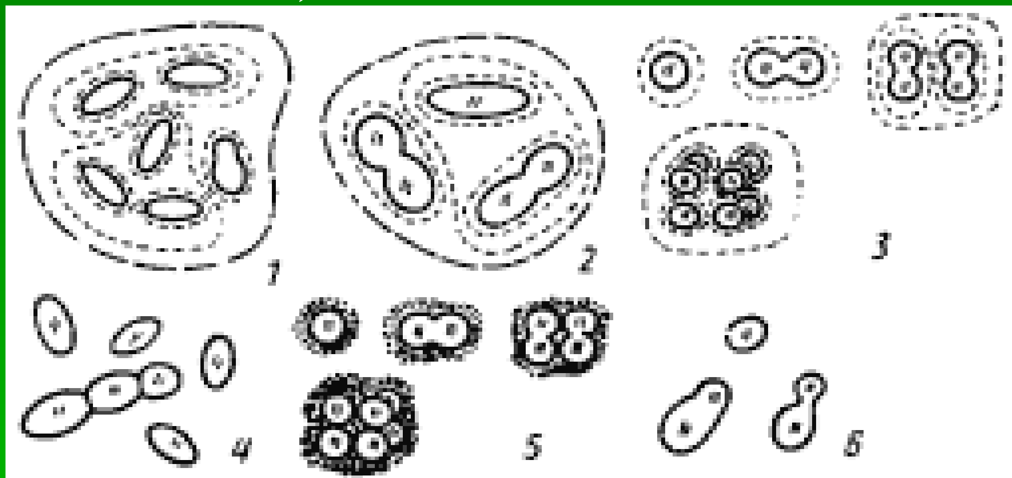
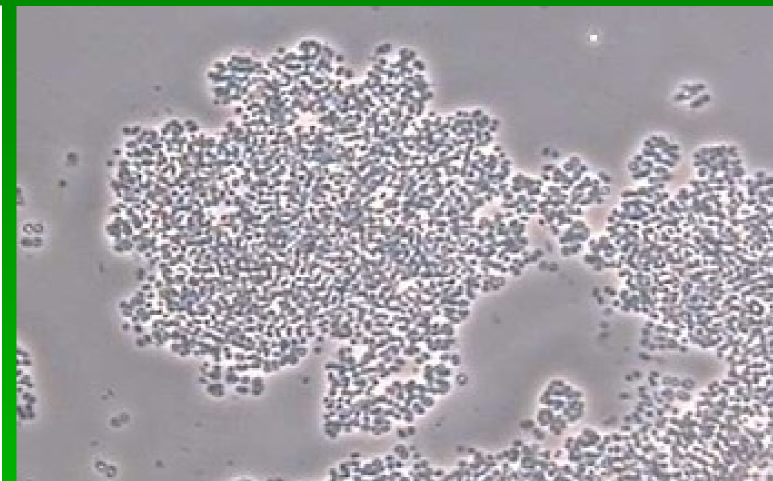


Fig. 1.25 Phycobilisome breakdown under conditions of nitrogen deprivation. (Adapted from Grossman et al., 1993.)

Different photosynt. apparatus

- ***Gloeobacter violaceus*** – primitive cyanobacteria, **no thylakoids** → phycobilisomes placed on plasmatic membrane (specialized domains), isolated from limestone, Switzerland

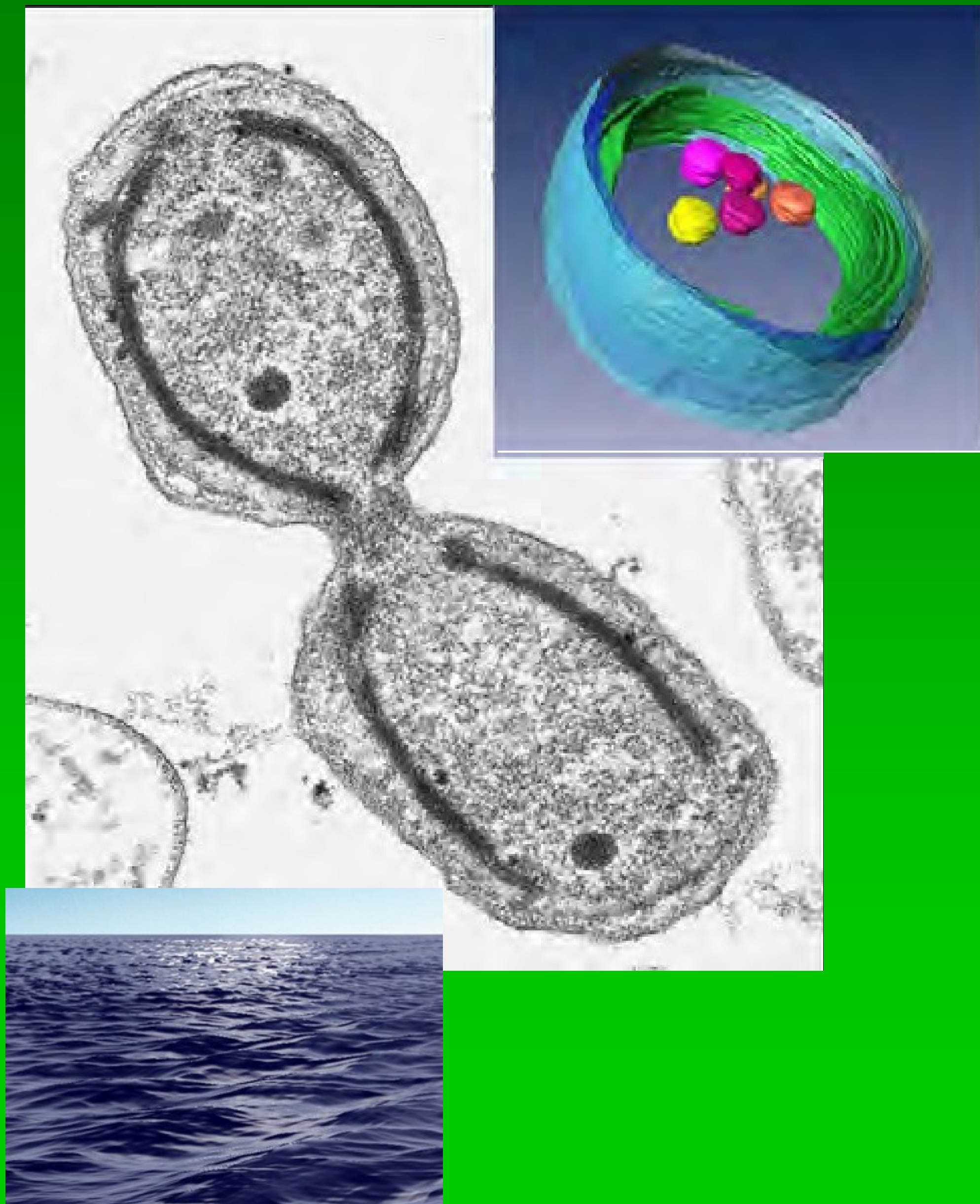




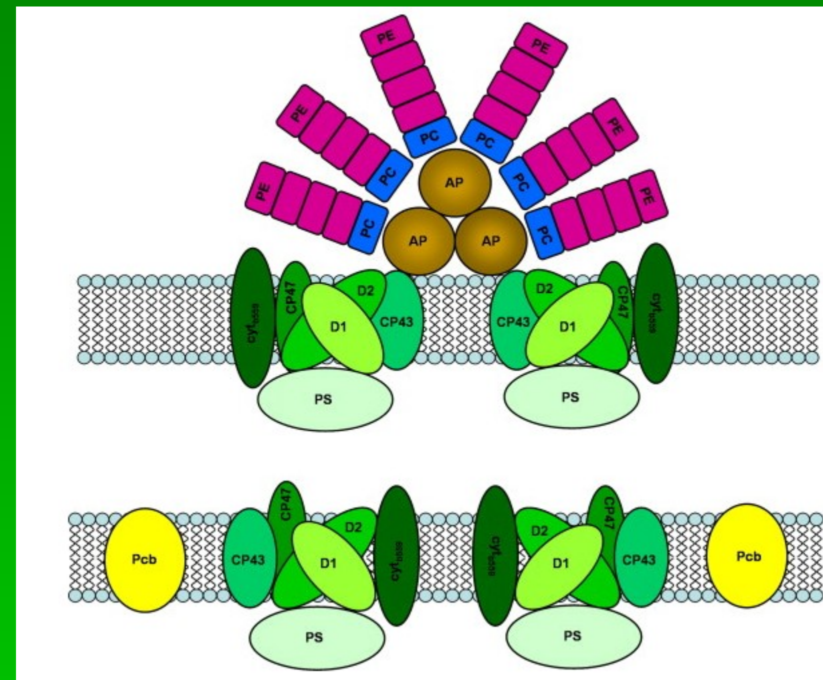
- former PROCHLOROPHYTES:

  posses additional pigments: chl. *b, c, d*; β - caroten, zeaxanthin
  thylakoids organized in lamelae, lack of cyanophycin granules

Prochlorophyta – polyphyletic group



cyonobacterium with
phycobilisom



Prochlorococcus – protein bounding chlorophyll b (yellow)

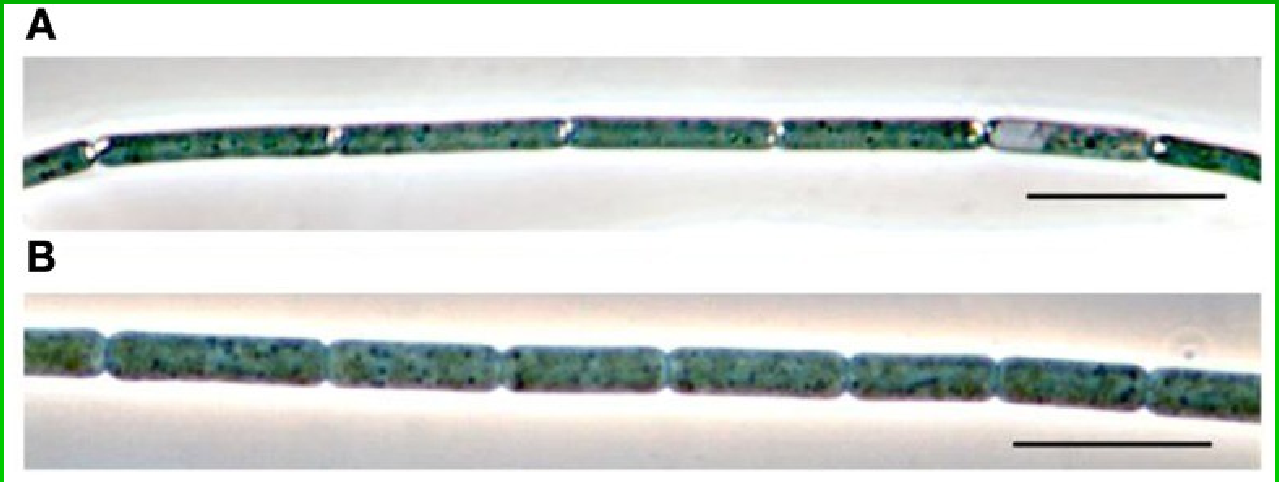
Prochlorophyta – polyphyletic group

Prochloron didemni - Prochlorons are distributed within the tissues of didemnid ascidians, mainly in the cloacal cavities under the upper tunic, Pacific ocean, chlorophyll *b*

Prochlorothrix hollandica – filamentous, in a brakish Lake Loosdrecht in Holand, masive mats

Prochlorococcus marinus – marine picoplankton, important primary producer, chlorophyll *a* and ***b***

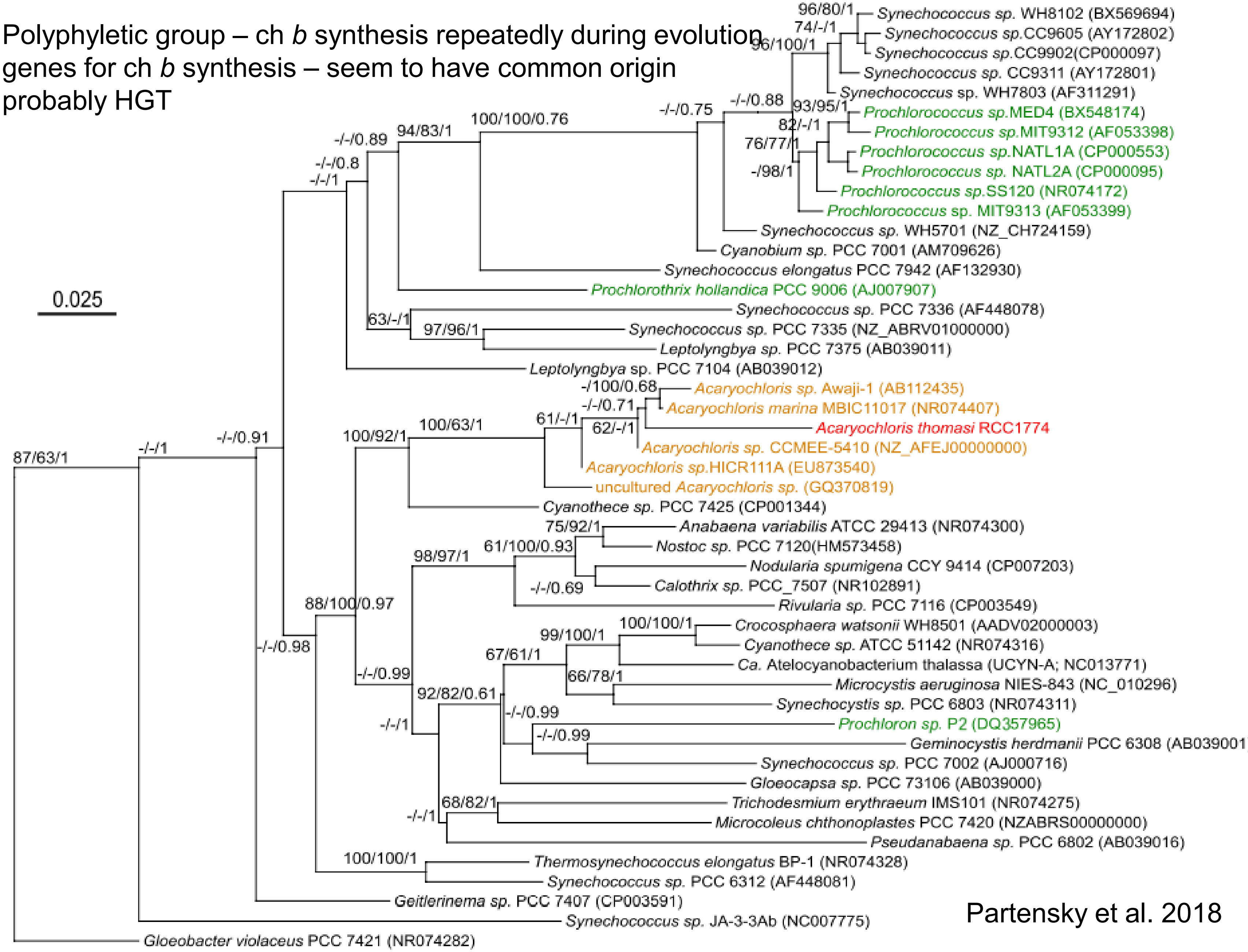
***Acaryochloris marina* – chlorophyll *d*,** reaction center



Prochloron

Prochlorothrix

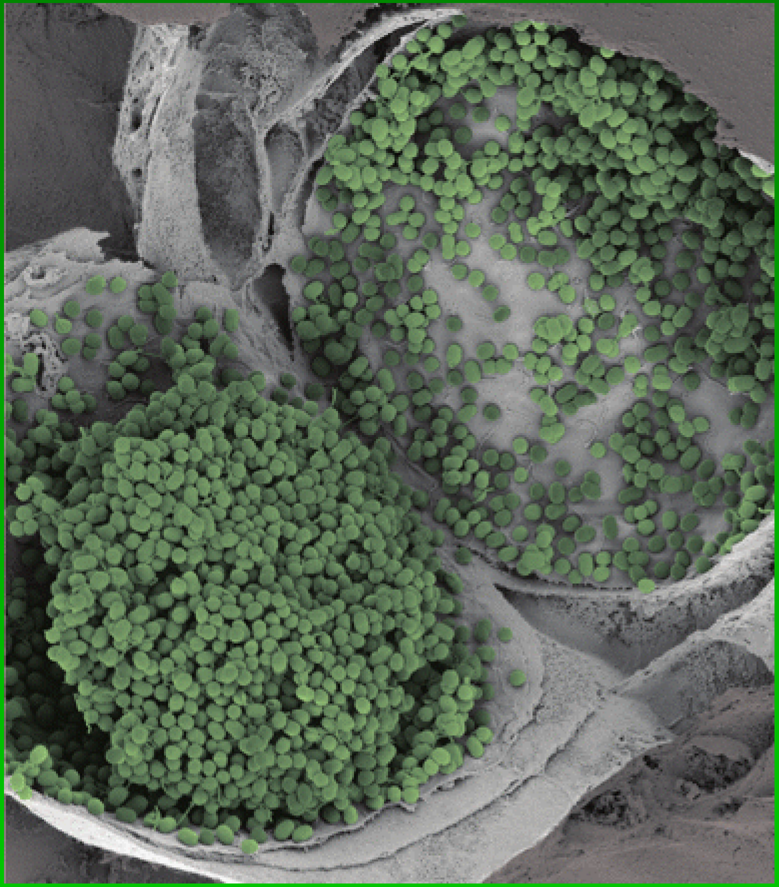
Polyphyletic group – ch *b* synthesis repeatedly during evolution, genes for ch *b* synthesis – seem to have common origin probably HGT



Partensky et al. 2018

Maximum likelihood phylogenetic tree based on the 16S rRNA gene showing the position of Prochlorophyta

Acaryochloris marina – chlorophyll *d*



Behrendt et. al 2012, Appl. Environ. Microbiol.

This unique cyanobacterium is the only known phototroph that has exchanged its Chl *a* for Chl *d*

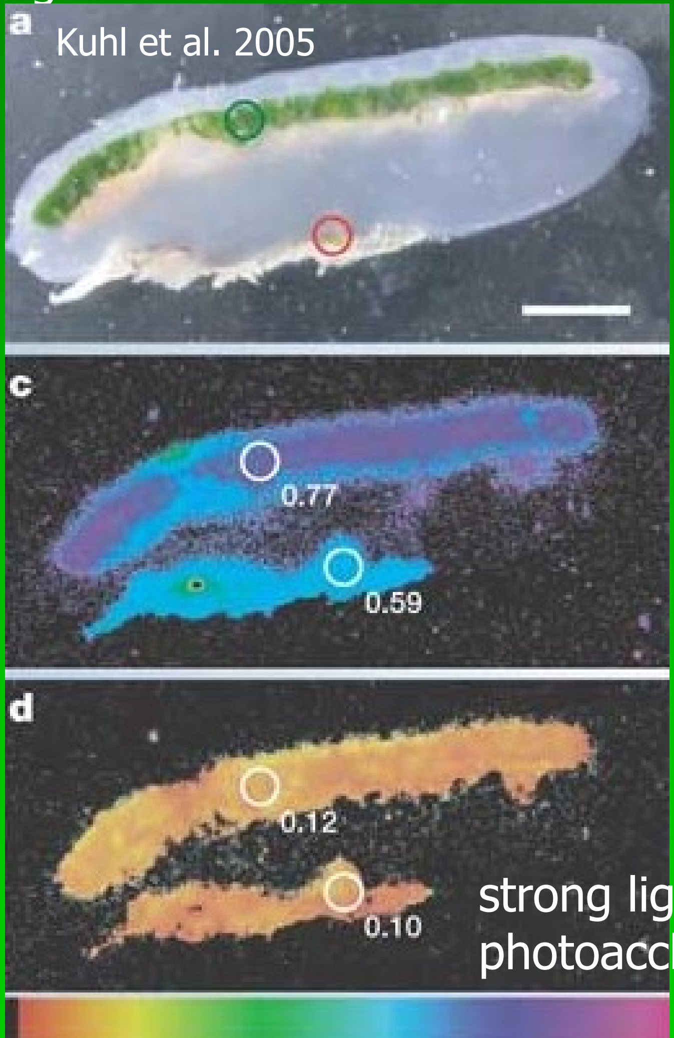
oxygenic photosynthesis using near-infrared radiation (NIR) 770 nm

In nature, *Acaryochloris* thrives in biofilms colonizing microniches experiencing strong depletion of visible light, while sufficient NIR prevails.

Chlorofyl *d* allowing it to use near-infrared light, at 770 nm wavelength.

Acaryochloris marina

associeted with didemnid ascidians or red algae



Prochloron

Acaryochloris

max. PSII quantum yealds in natural cond.

strong light photoacclimation

NASA: organisms that use chlorophyll d, rather than ch a, may be able to perform oxygenic photosynthesis on exoplanets orbiting red dwarf stars

Facultative phototrophic anaerobes

both photoaerobic and photoanaerobic habitats

electron donors?

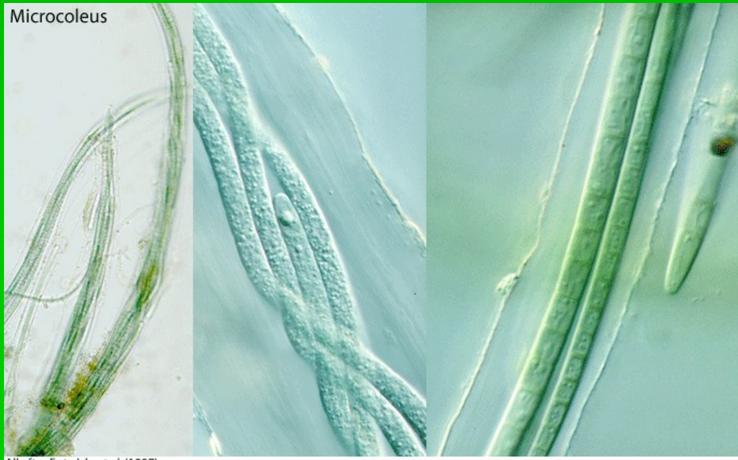
aerobic conditions e^- donor $\Rightarrow$ water (O_2 production)

$$\boxed{2\ H_2O + CO_2 \rightarrow [CH_2O] + O_2 + H_2O}$$

anaerobic conditions e^- donor $\Rightarrow$ hydrogen sulfide (no O_2 production)

$$\boxed{2\ H_2S + CO_2 \rightarrow [CH_2O] + 2S + H_2O}$$

only PS I involved



All after Entwisle et al. (1997)

fill an important ecological niche, fluctuation between aerobic and anaerobic conditions

Oscillatoria limnetica

Solar Lake – small hyper saline lake (eastern coast of the Sinai peninsula (Israel)

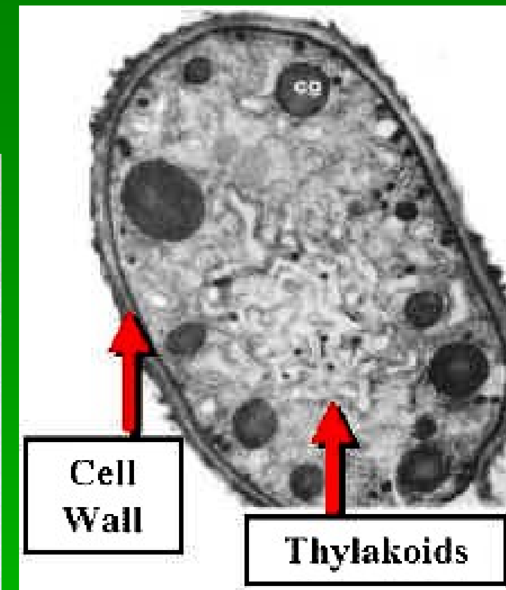
thermal stratification; winter – high concentrations of H_2S near the bottom

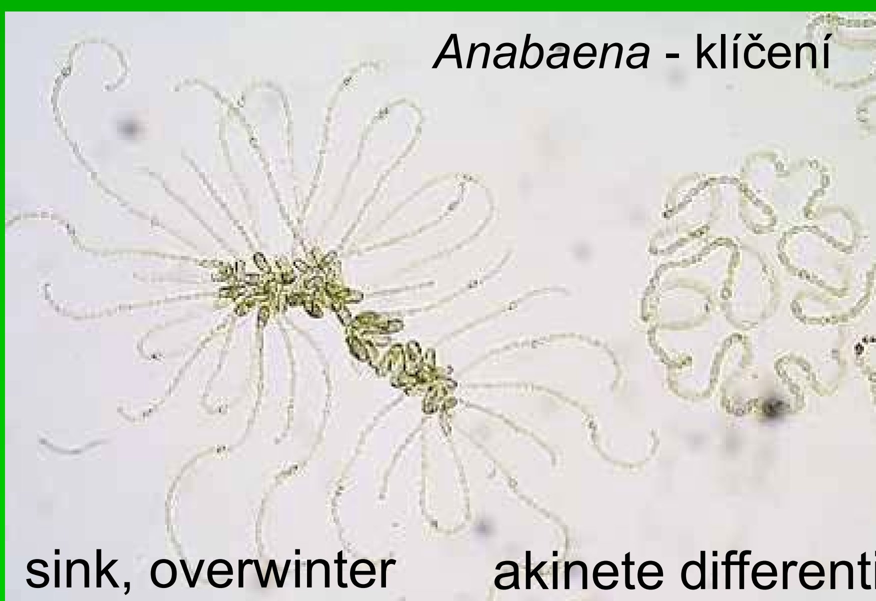
oxygenic vs. anoxygenic photosynthesis

Akinetes – resting stages

only in heterocyst forming cyanobacteria

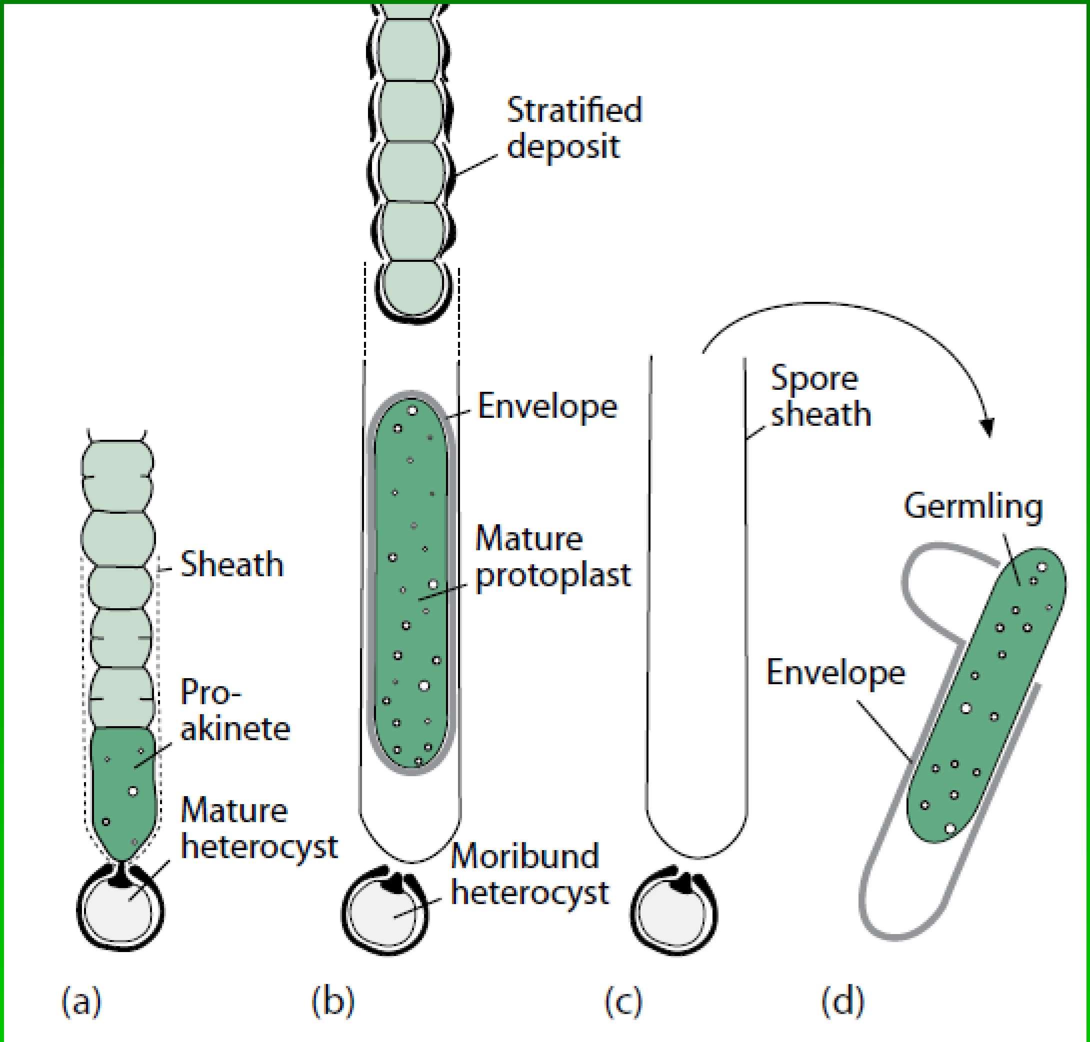
- they develope from vegetative cells
- thick-walled, full of reserve material
- may survive up to 86 years in the sediment





akinete differentiation stimulation

Development of the akinete of *Gloeotrichia echinulata*.



(a) Differentiation begins near a heterocyte. (b) Akinetes enlarge, develop thick walls, and (c) separate from subtending vegetative filaments and heterocytes, leaving an empty sheath. (d) Germination of akinetes. (After Cmiech et al. 1984.)

N_2 fixation

fixation = N_2 ($N \equiv N$) from atmosphere is fixed into ammonium (NH_4^+)

$$N_2 + 8\,H^+ + 16\,ATP \rightarrow 2\,NH_3 + H_2 + 16\,ADP + 16\,P$$

renewable energy source

N – limiting element in the sea water, amino-acid's synthesis

only cyanobacteria and bacteria are able to fix nitrogen; cyanobacteria also produce O_2 → **nitrogenase** is inactivated by O_2

spatial or temporal separation of both activities (except for *Trichodesmium*)

The most metabolically expensive process in biology!!

Spatial separation - heterocytes

Nostocales, Stigonematales

- thick wall, bigger than vegetative cells
- differentiation from vegetative cells
- in heterocysts PSII is lacking$\rightarrow$ nitrogenase protection from O2
- they do not fix C, C is transported in a form of disaccharides from veg. cells through the pore channel

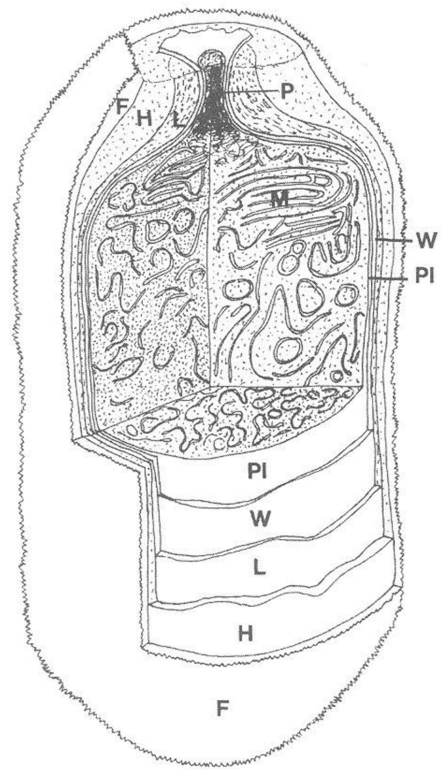
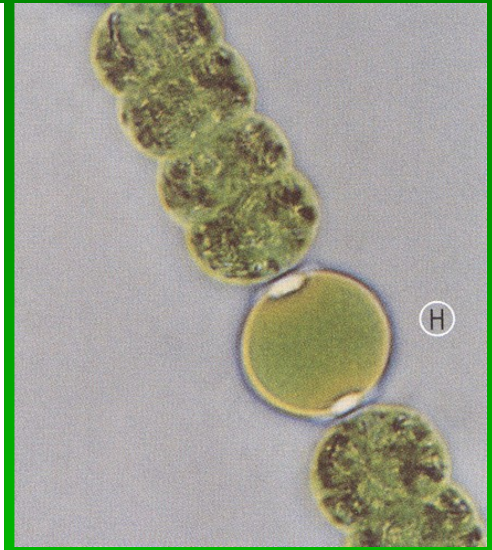
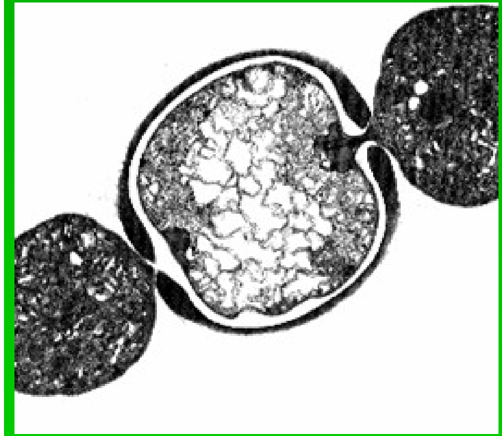


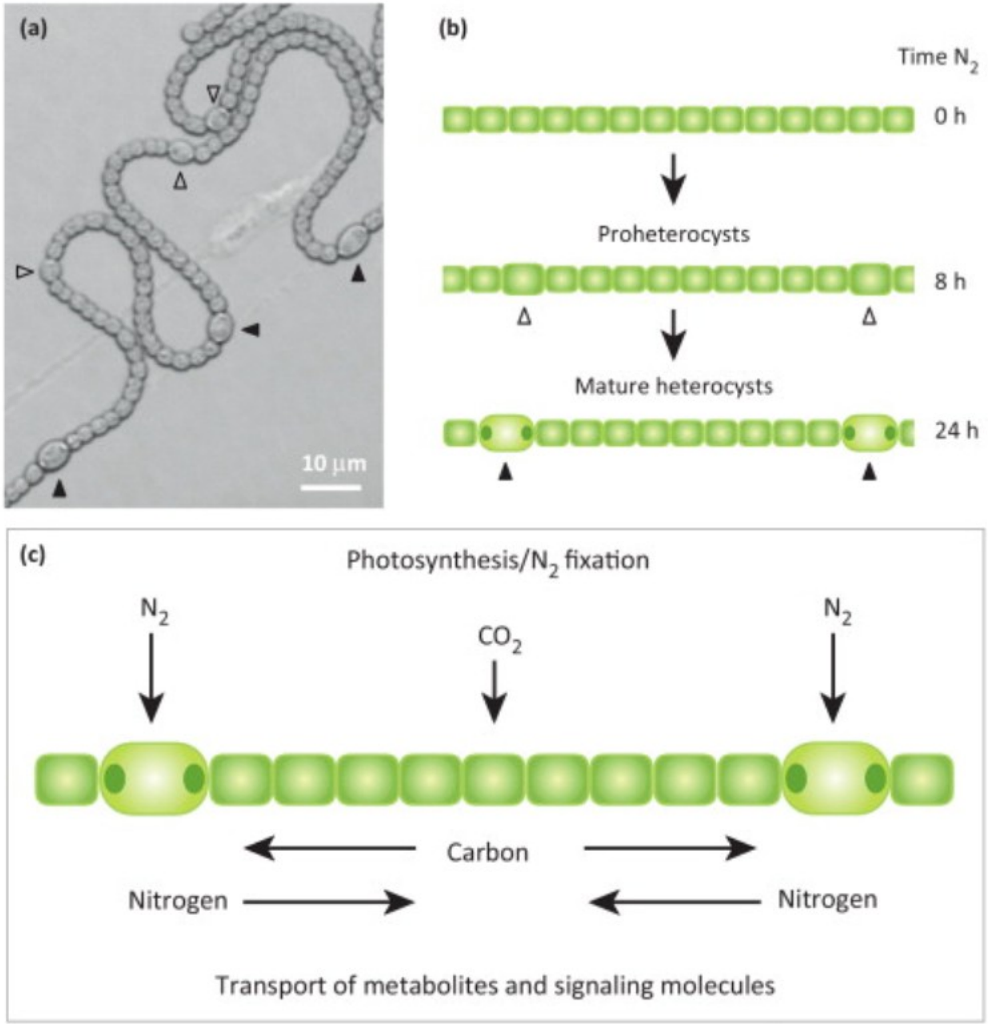
Fig. 2.25 Three-dimensional view of a heterocyst. The envelope has homogeneous (H), fibrous (F), and laminated (L) layers. (M) Membranes; (P) pore channel; (Pl) plasmalemma; (W) cell wall. (After Lang and Fay, 1971.)





heterocysts in distinctive patterns

differentiation of heterocysts, apoptosis



TRENDS in Microbiology

20–24 h to complete

Muro-Pastor et al. 2012

Heterocystous cyanobacteria evolution

Tomitani et al. 2006

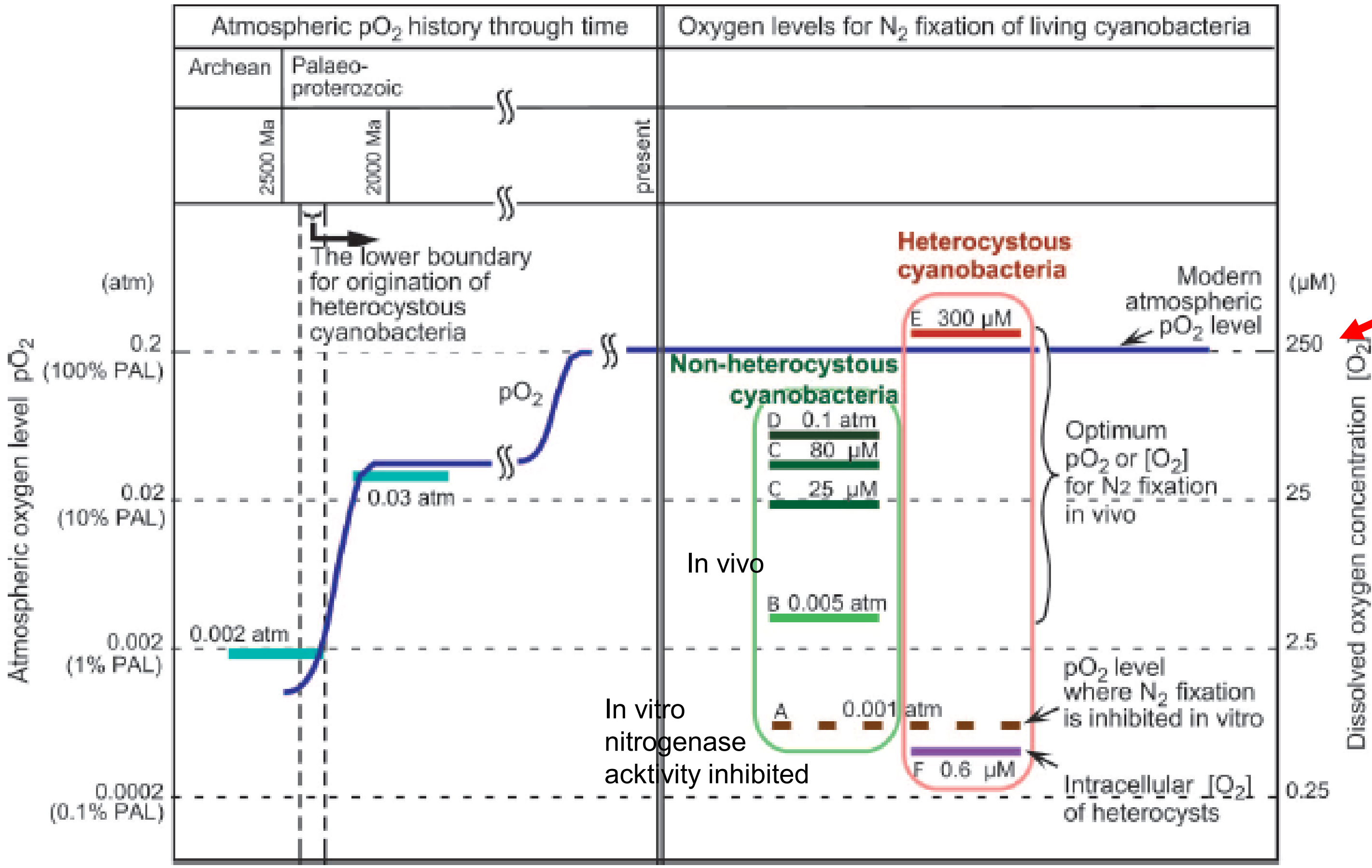


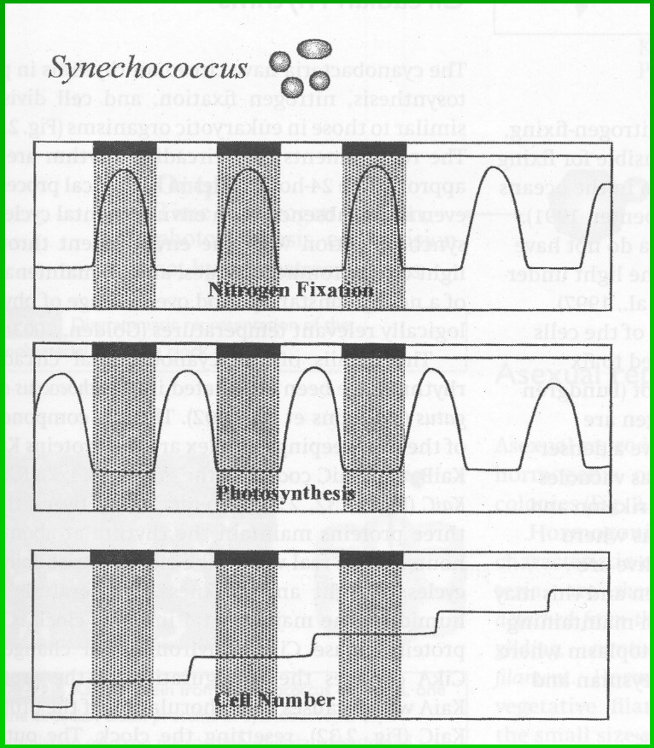
Fig. 3. The geochemical record of atmospheric oxygen as it relates to nitrogen fixation and the evolution of heterocystous cyanobacteria. The curve presents an estimate of atmospheric P_{O_2} through time, as constrained by paleosol (42) and S isotopic (43, 44, 46) data. Numbers in *Right* indicate the P_{O_2} level at which *in vitro* nitrogenase activity is inhibited in nonheterocystous *Plectonema* and heterocystous *Anabaena* (34) (A), and P_{O_2} or $[O_2]$ optima for *in vivo* nitrogenase activity of *Plectonema* (36) (B), nonheterocystous *Gloeothece* (37) (C), *Trichodesmium* (38) (D), and *Anabaena* (39) (E). F indicates the intracellular $[O_2]$ of *Anabaena* heterocysts. The $[O_2]$ (the left vertical axis) corresponds to P_{O_2} (right axis) when $[O_2]$ is 250 µM in air-saturated water. PAL, present atmospheric level.

Temporal separatoin

Fix N at night, fotosynthesis during the day

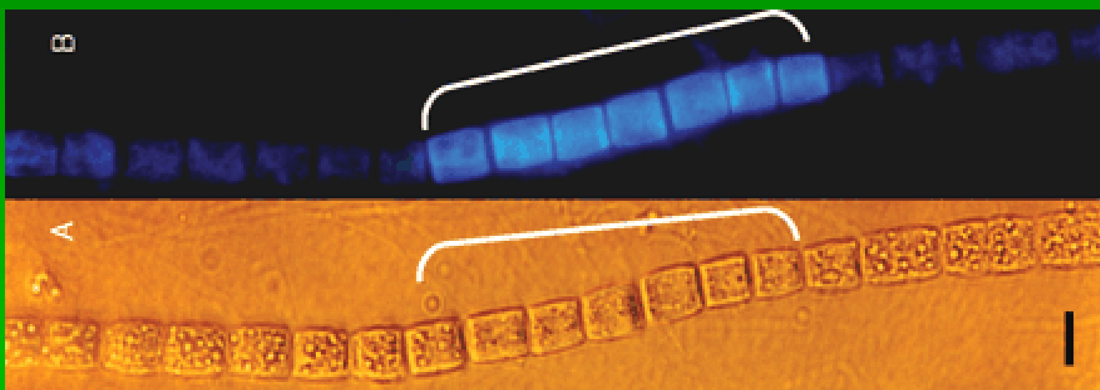
In the evening → phycobiliprotein's degradation → PSII switch off → O2 production stopped → fast nitrogenase synthesis → N2 fixation over night → nitrogenase synthesis stopped, the enzyme is disintegrated by oxygen, that penetrates to cells → resynthesis of phycobiliproteins → functional PSII → in the morning the photosynthesis may begin again.

Lyngbya aestuarii



Trichodesmium - diazocytes

Trichodesmium – sea water filamentous species, N2 fixation in the light under aerobic conditions – specialized cells – diazocytes (contain nitrogenase, adjacent to one another)



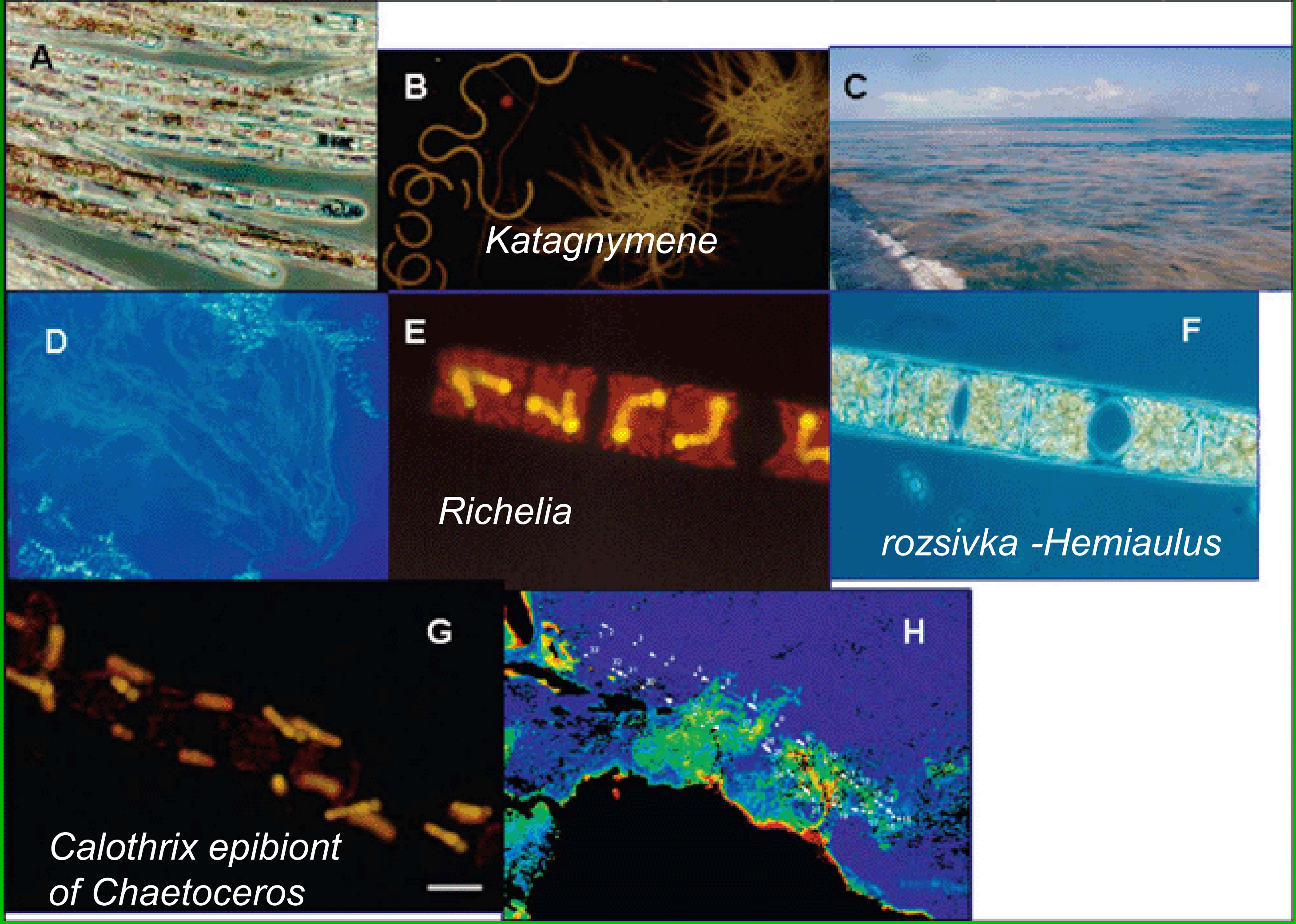
anti-nifH – přítomnost nitrogenázy ve fluorescenci

regulation of transcription of nif genes, daily de novo synthesis of the subunits

Katagnymene

oxygen-scavenging mechanisms – Mehler reaction

O_2 to H_2O_2



Examples of marine diazotrophs at various scales. (A) Photomicrograph of *Trichodesmium* trichomes. Cells are approximately 5 ìm in diameter. Photo courtesy of Kaori Ohki. (B) Blue excitation of *Katagnymene spiralis* (coiled), which clusters phylogenentically within the Trichodesmium radiation (16S, nifH, hetR), and bundles of *Trichodemium* sp. Photo courtesy of Rachel Foster. (C) Surface bloom of *Trichodesmium* in the Capricorn channel of the Great Barrier reef. Photo by D.G. Capone. (D) Photo from the space shuttle of the Capricorn channel of the Great Barrier reef. Horizontal span of photo is about 100 km. Photo courtesy of NASA. (E and F) Blue excitation epifluorescent and light micrographs of the diatom *Hemiaulus membranaceus* with its cyanobacterial endosymbiont, *Richelia intracellularis*, respectively. Photo courtesy of David Caron. (G) Epifluorescent micrograph of cyanobacterial epi-bionts (*Calothrix* spp.) of another diatom (*Chaetoceros* spp.). Photo courtesy of Rachel Foster. (H) Color chlorophyll image from the OCTs Satellite from Nov 1996. The elevated chlorophyll at the center right of the image was associated with a major bloom of the diatom *Hemiaulus hauckii*, which was concurrently sampled by an oceanographic cruise indicated by the cruise track.

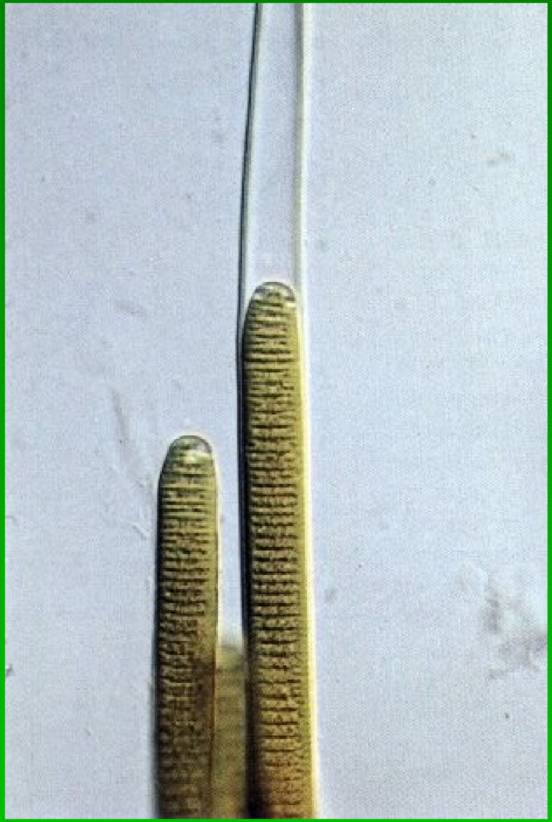
Morfology of cyanobacteria

• row of cells = trichom

• trichom in the slime sheath = filament

• the filament may be composed by more trichomes

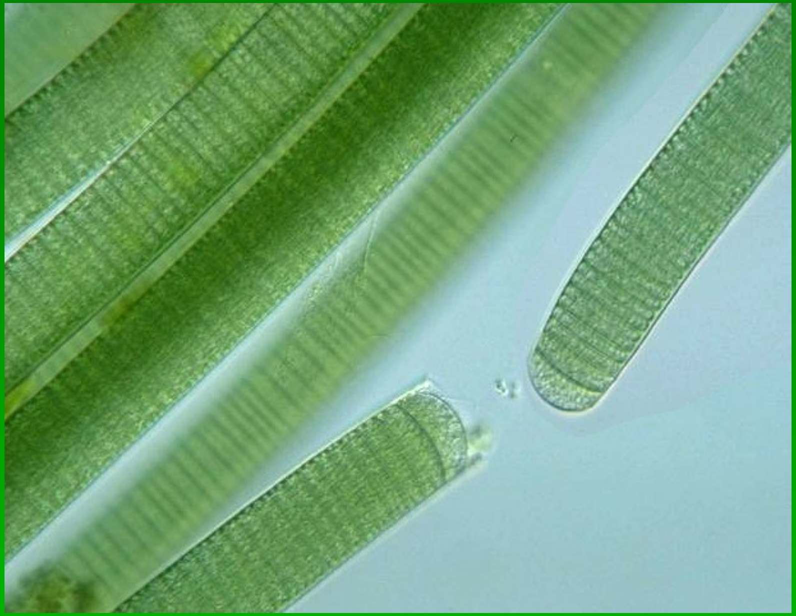
Microcoleus



Phormidium

• mucilage sheath - movement, UV protection, colony addition, capacity to capture micronutrients

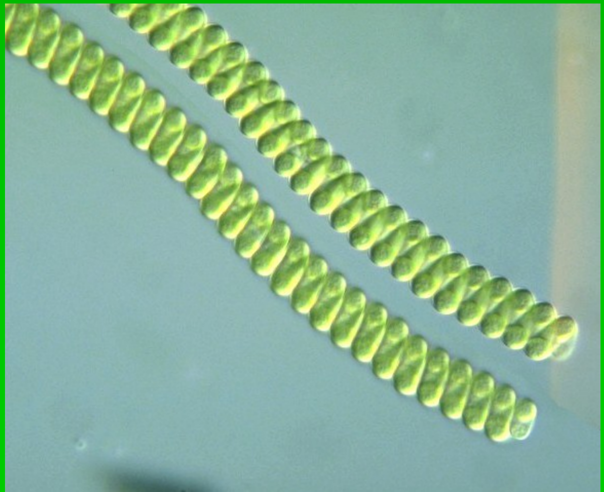
Movement



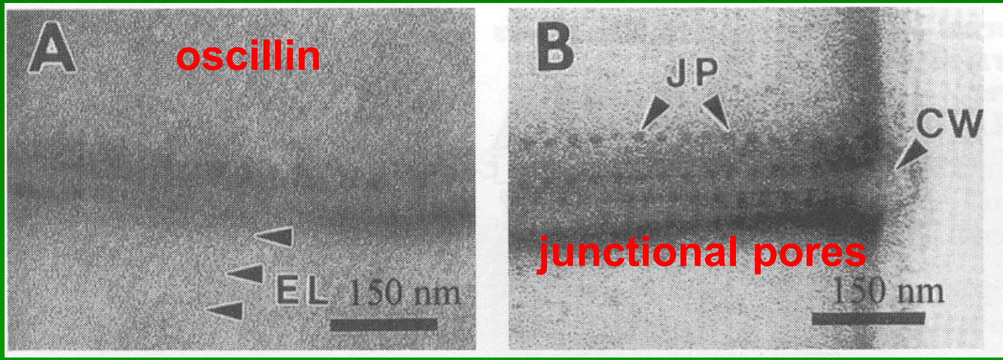

Oscillatoria *Cyanothece aeruginosa*

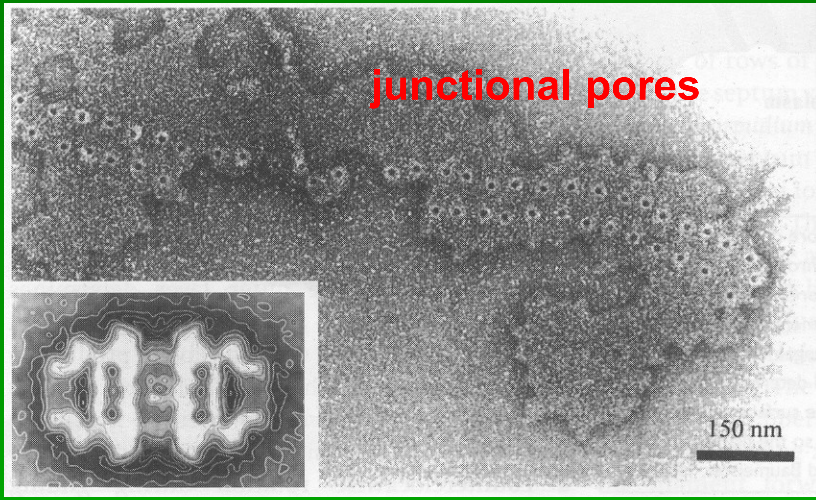
- gliding
- buoancy change – gas vesicles

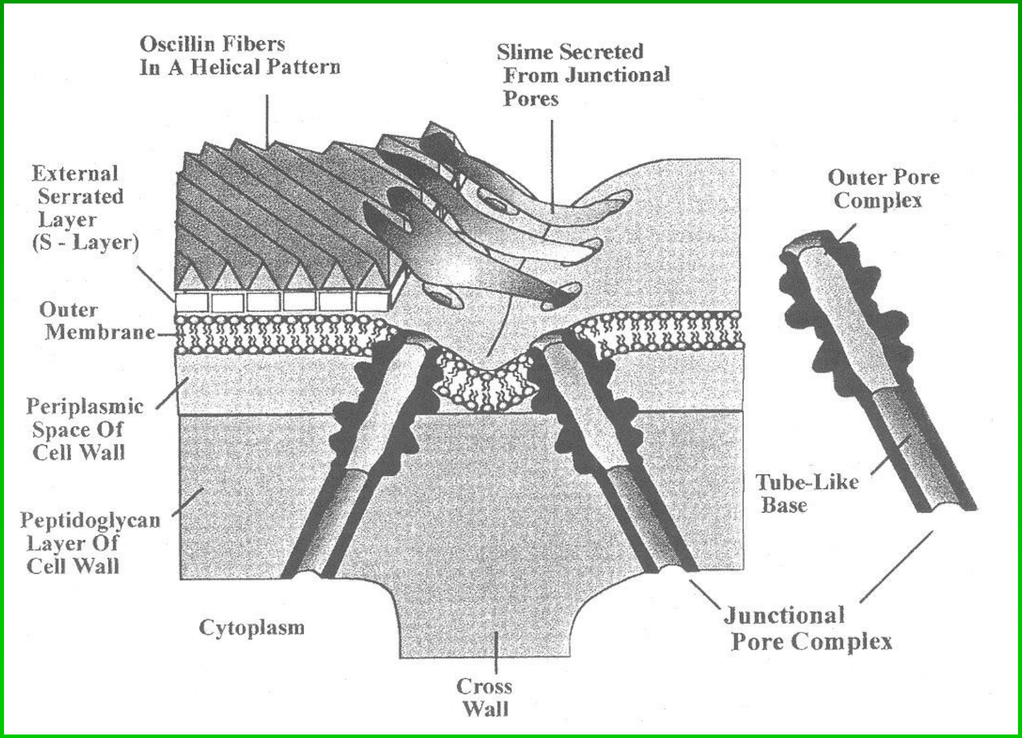
Merismopedia Waden See – migrate within the substrate

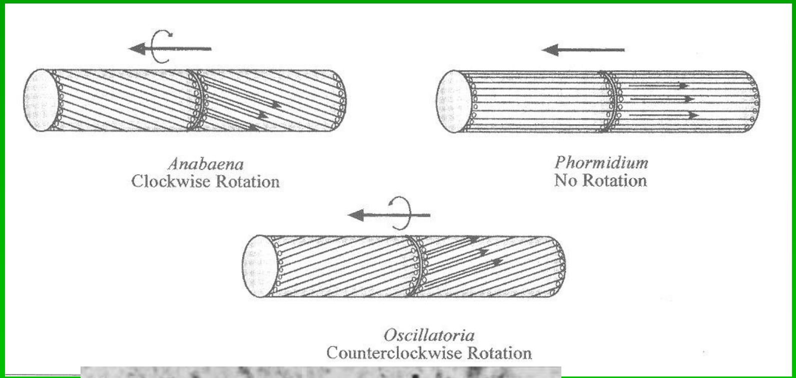


Gliding motion





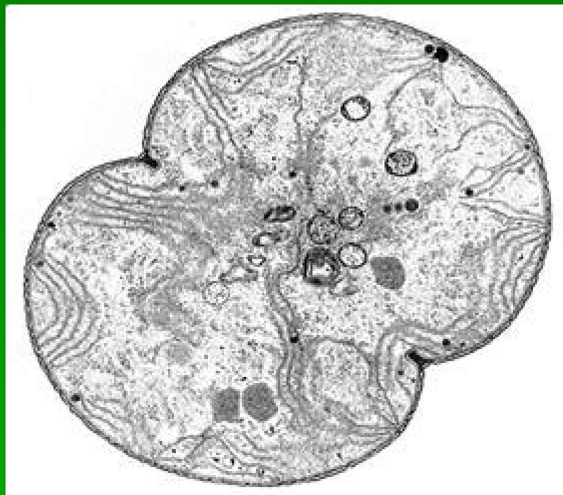


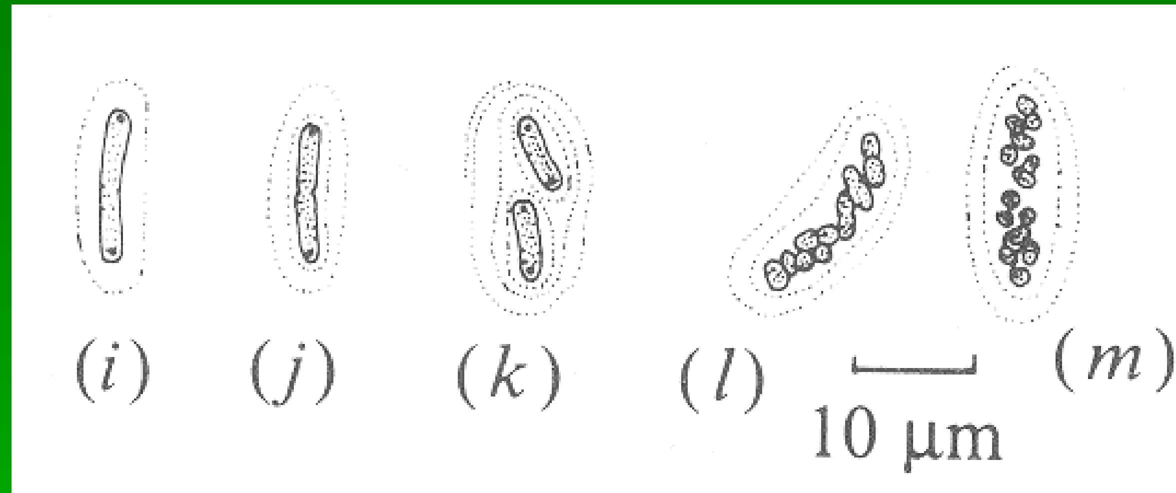


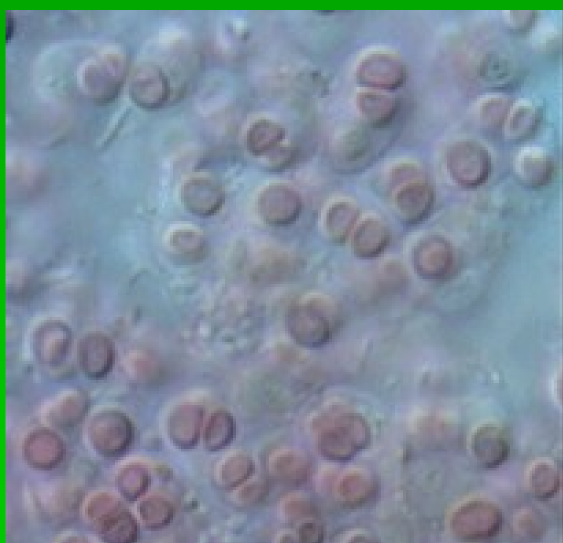
orientation of oscillin proteins reversal of gliding

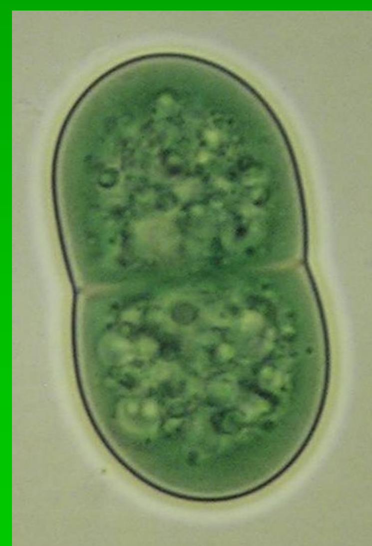
active movement on a solid substrate (up to 600 μm/sec.)

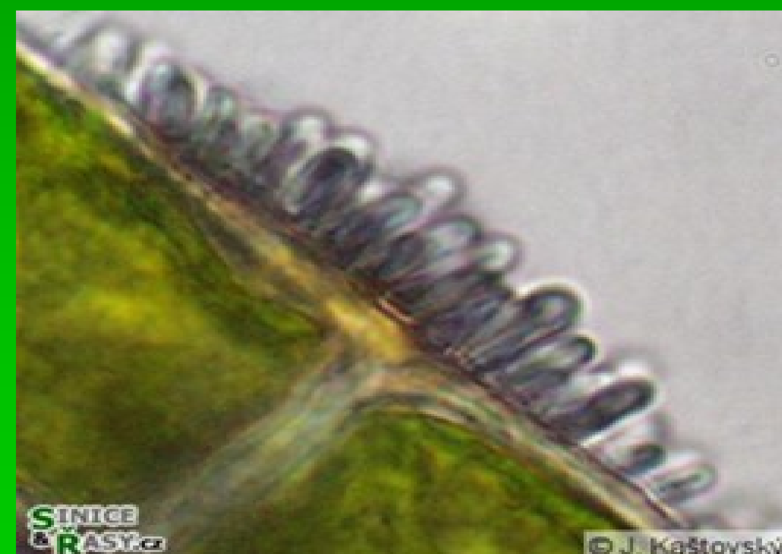
Morphology and cell division







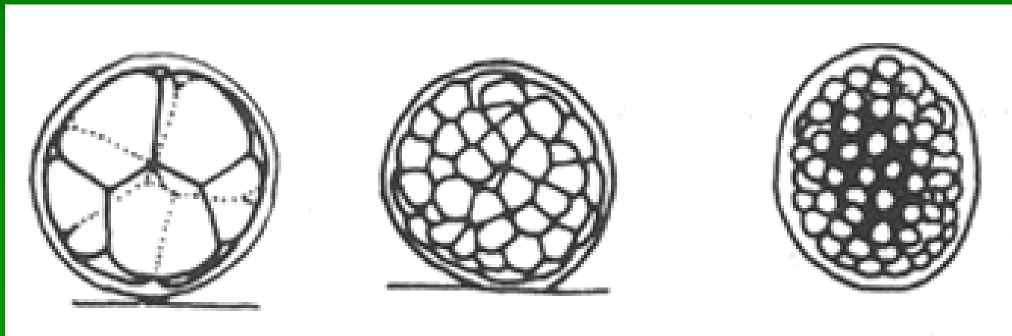


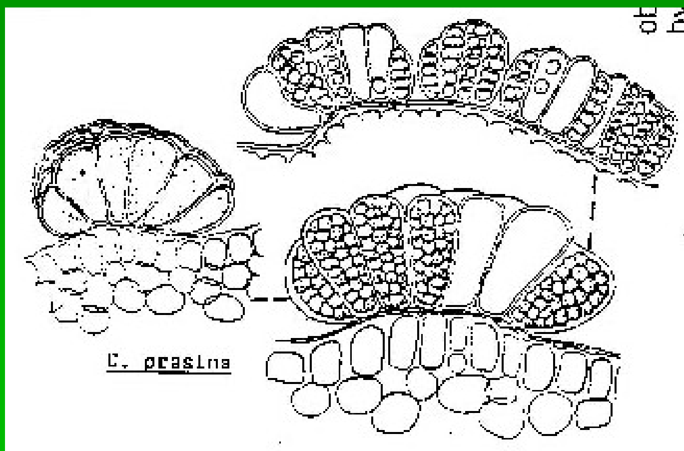


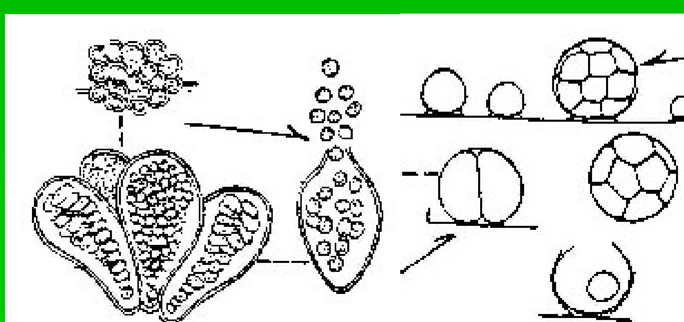
centripetal (*Synechoccocus, Cyanothece*)

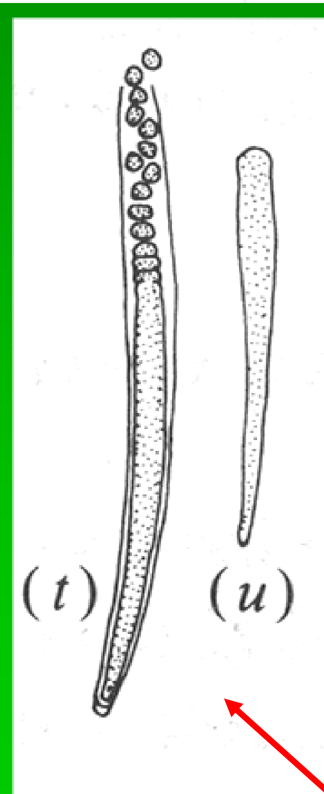
nanocytes (*Aphanothece*)

Morphology and cell division







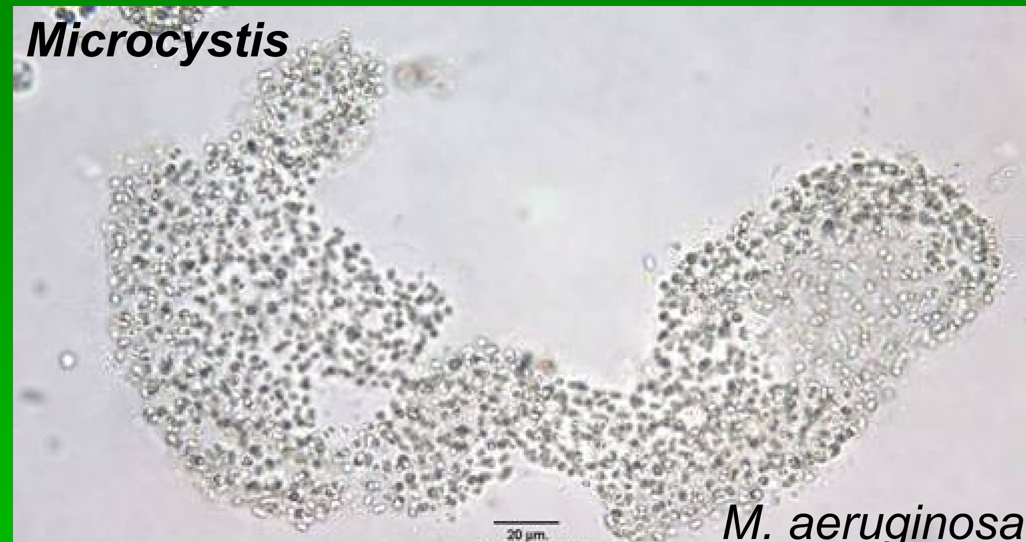


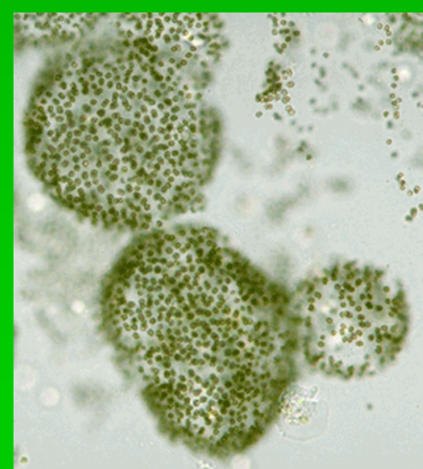
endospores-baeocytes (*Cyanocystis*)

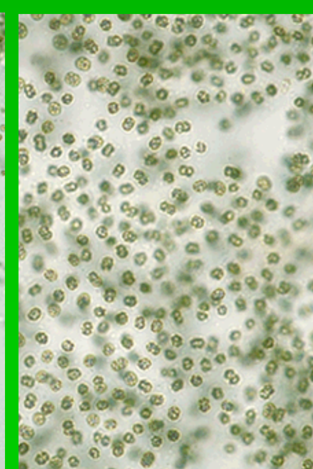
exocytes, exospores (*Chamaesiphon*)

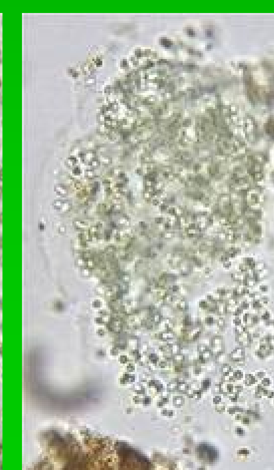
Morphology and cell division

- division in 2 or 3 directions → plate-like colonies *(Merismopedia)* or irregular colonies *(Microcystis)* embedded in a mucilage





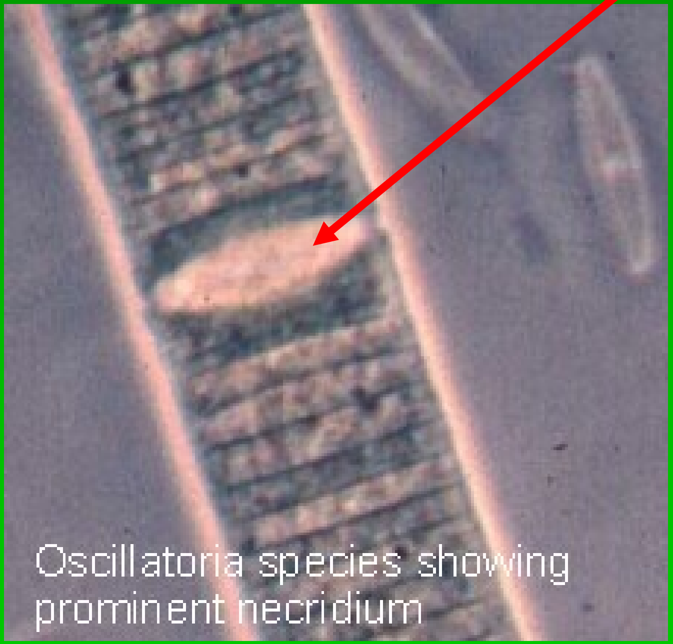


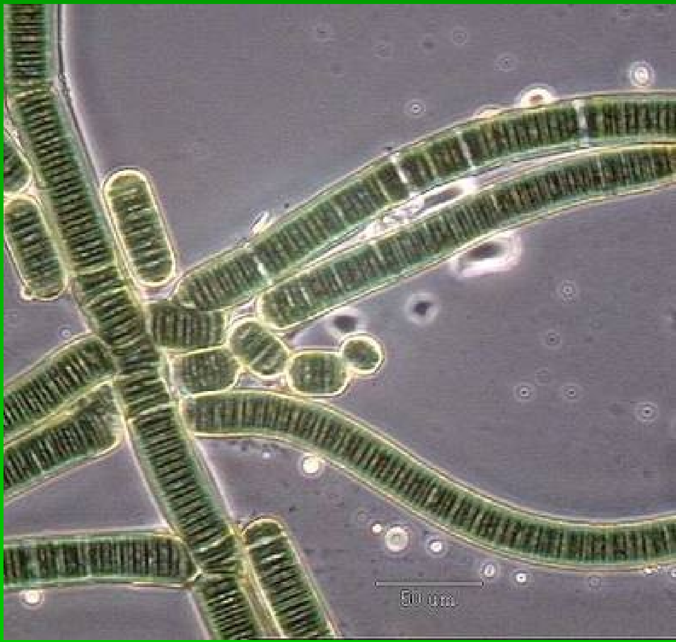


Morphology and cell division

- division of truly filamentous cyanobacteria (trichomes) –**hormogonia** = short pieces of trichomes, move away by gliding (trichomes fragmentation or necridia formation)

Lyngbya



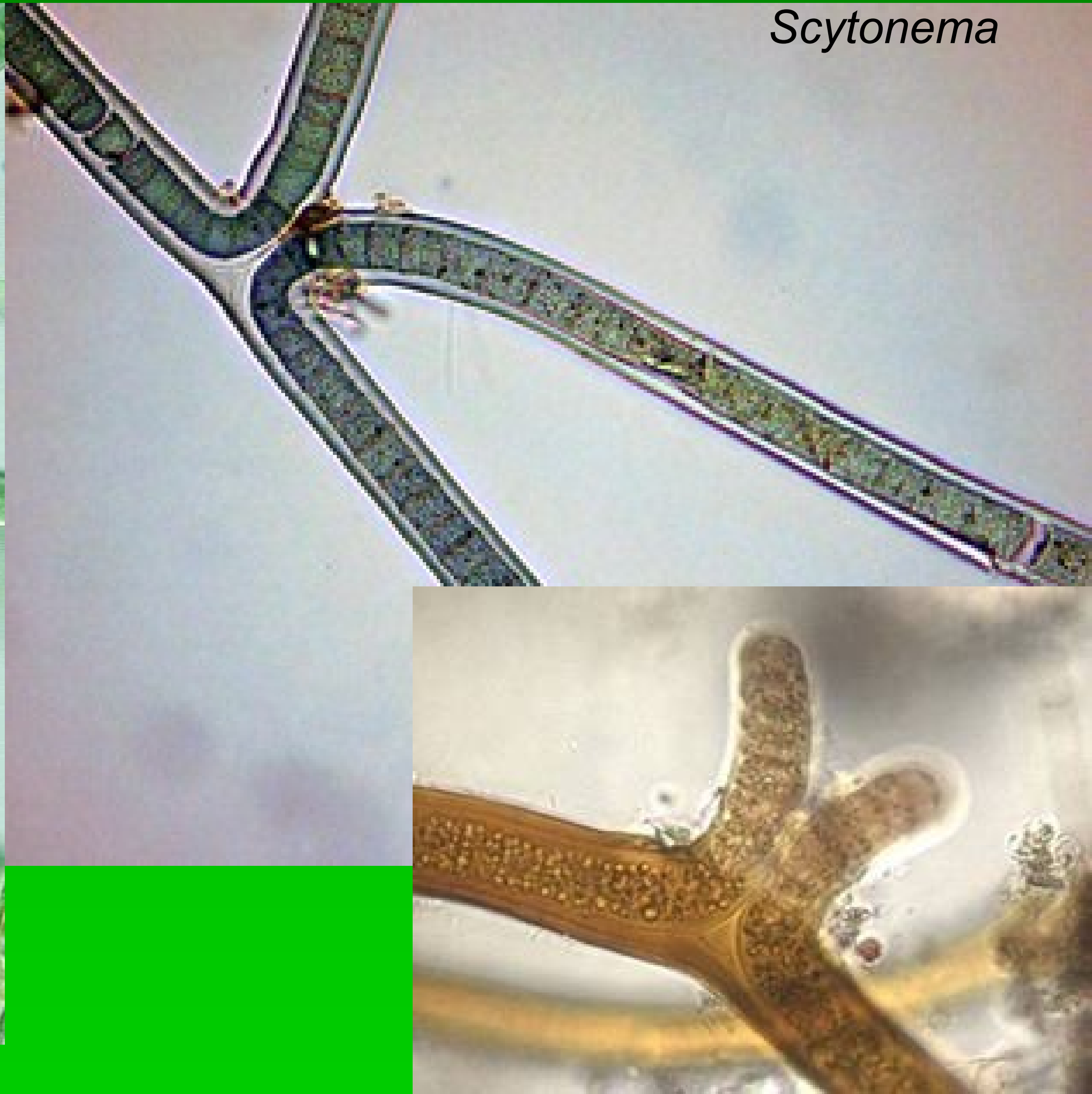


change in environmental parameters, gliding stage 36-48hrs, secretion of mucilage

Trichomes and branching

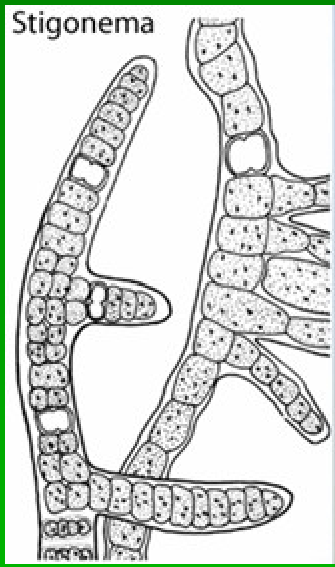
false branching = trichome breaks within the mucilage sheath

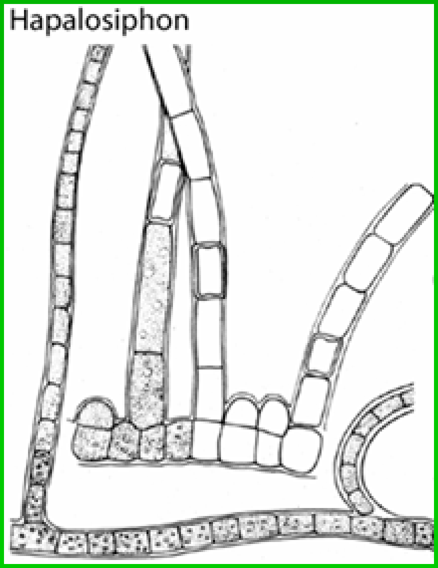
(*Scytonema, Tolypothrix*)



Trichomes and branching

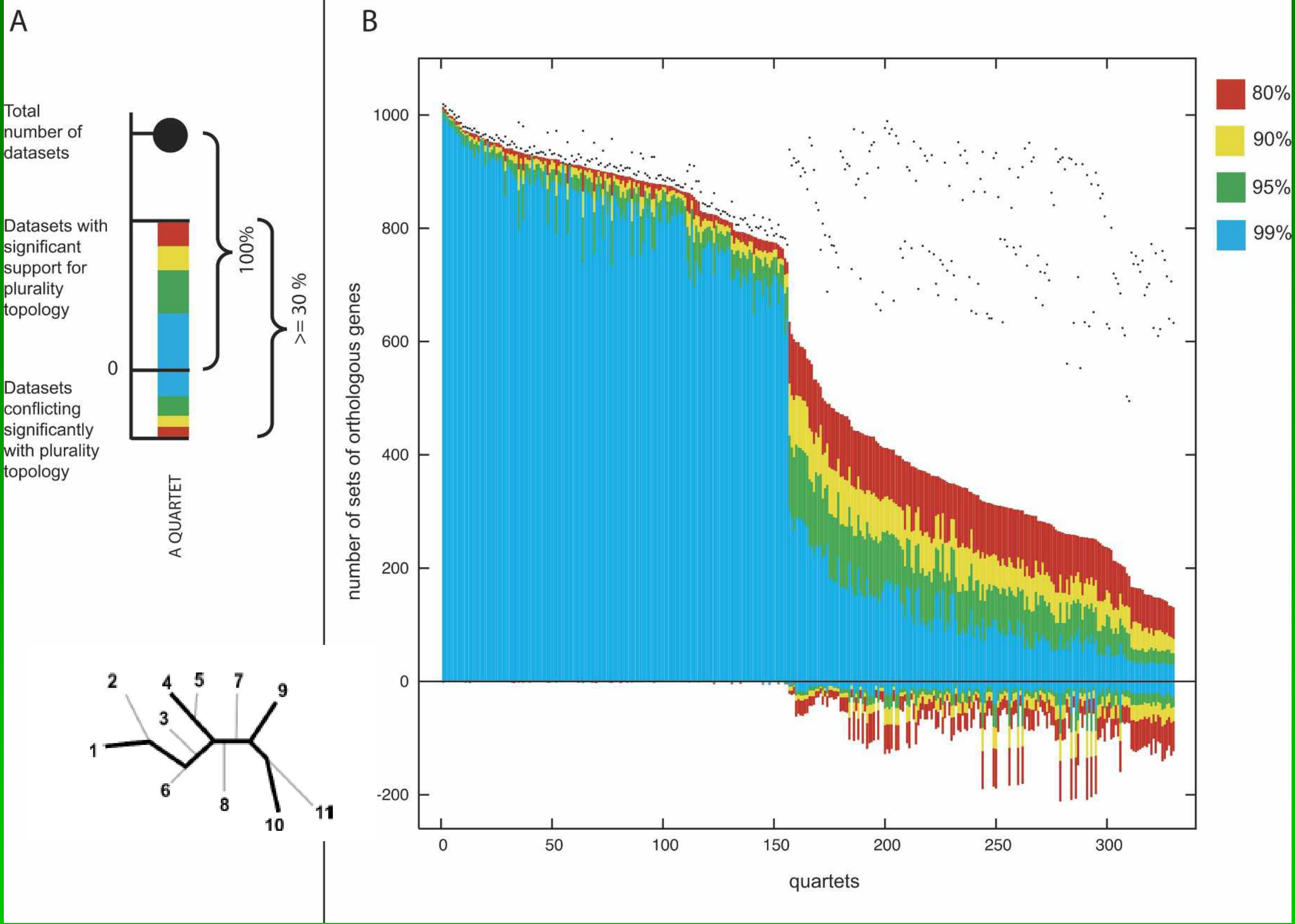
- **true branching** = change of the plain of the cell division (*Stigonema, Hapalosiphon*)



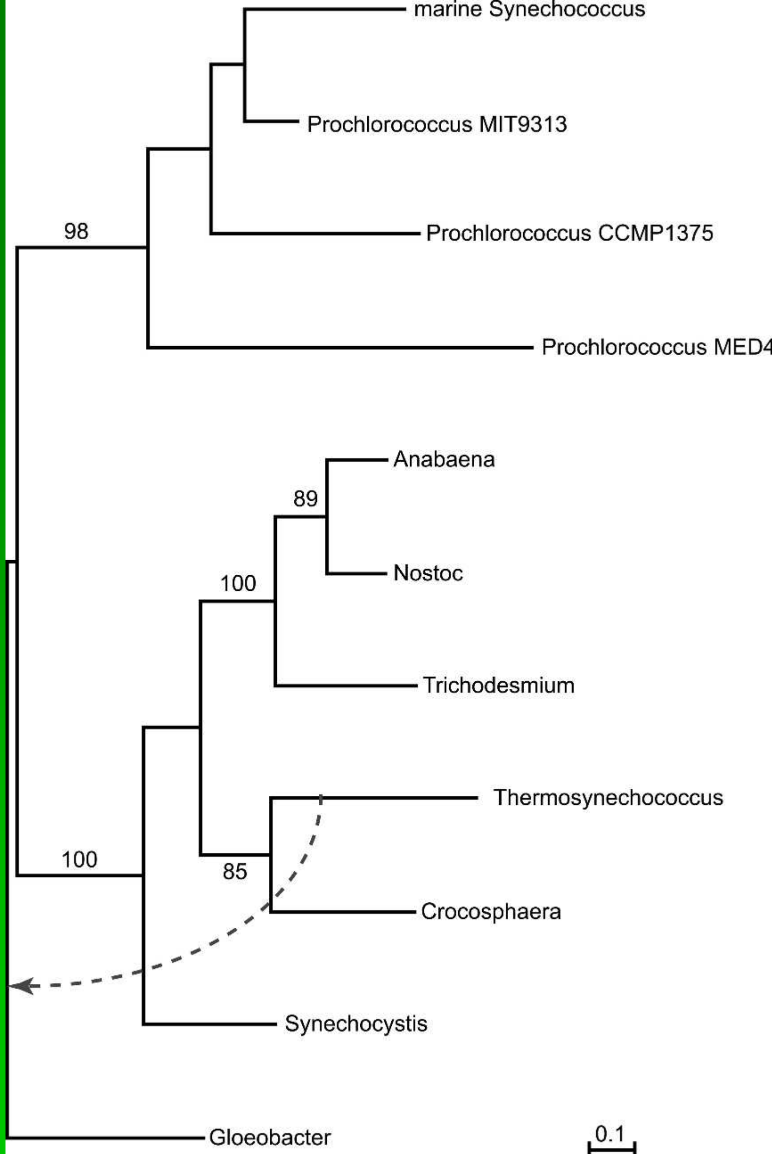


DNA transfer

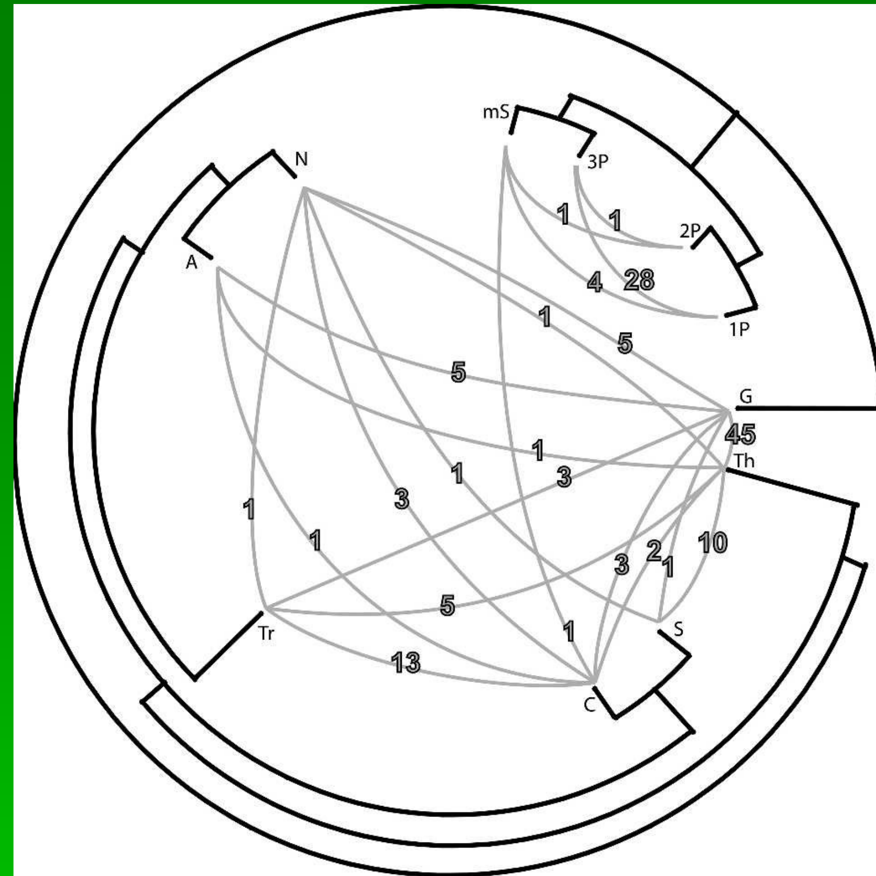
- horizontal gene transfer: ca 10-16% genes obtained by HGT by means of plasmids or viruses (cyanophages)
- conjugation not known
- cyanophages may serve as a „reservoir“ of genes for the host – enable the host to adapt to the changing environmental conditions
- Cyanobacteria and other prokaryotes are asexual but are subjected to episodic homologous recombination similar to sexual organisms, which is present in ca. 80% of prokaryotic species. Prokaryotic HR may lead to similar patterns of evolution as seen in sexual organisms if the rates of HR are higher than the mutation rate. Thus, cyanobacteria and other prokaryotes may be considered quasi-sexual.
- the frequency of horizontal gene transfer (HGT) and homologous recombination (HR) decreases with the genetic distance – there seem to be coherent evolutionary lineages, which might be called species.



analyzed 11 genomes of cyanobacteria, 1128 genes; left half – congruent topology (only one the most parsimony tree exists), right half -685 genes - 61% - conflict with majority signal



Example of intraphylum transfer: a hemolysin-like protein.



(A) *Anabaena sp.*; (Tr) *Trichodesmium erythraeum*; (S) *Synechocystis sp.*; (1P) *Prochlorococcus marinus*; (2P) *Prochlorococcus marinus*; (3P) *Prochlorococcus marinus*; (mS) marine *Synechococcus* ; (Th) *Thermosynechococcus elongatus*; (G) *Gloeobacter violaceus*; (N) *Nostoc punctiforme;* (C) *Crocosphaera watsonii*

Static evolution?? No!!

Castenholz (1992)

Why the precambric cyanobacteria look like present-day ones?

• long generation time and larger genome size compared to bacteria

• often polyploidy – mutation in a single allele will not be expressed (x haploid eukaryotes)

• reparation mechanisms are probably involved (shown in a chloroplast)

• low rate of spontaneous mutations (also under mutagenesis)

The same looking morphotypes developed repeatedly during evolution – great genetic diversity