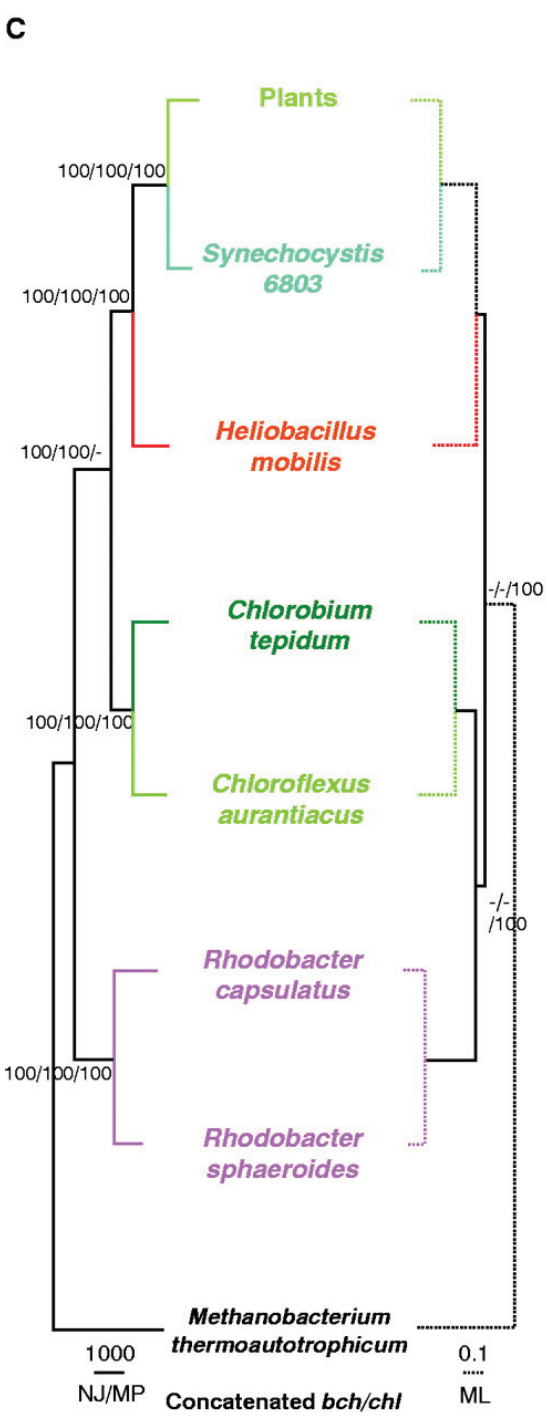
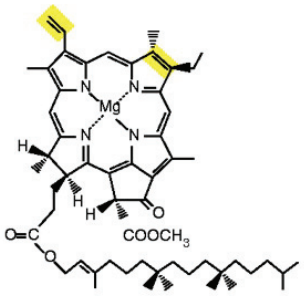
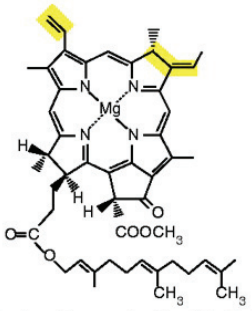
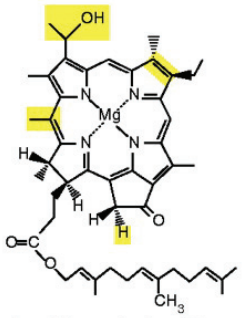




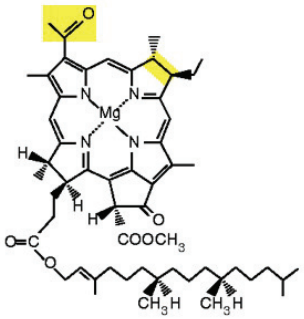
Chlorophyll a (Plants/Cyanobacteria)



Bacteriochlorophyll g (Heliobacteria)



Bacteriochlorophyll c (Green bacteria)



Bacteriochlorophyll a
(Purple bacteria/green bacteria)

Photosynthesis SC/BIOL 4160

LIGHT and CHLOROPHYLL

PHOTOSYNTHETIC DIVERSITY

Photosynthesis occurs in both prokaryotes and eukaryotes.

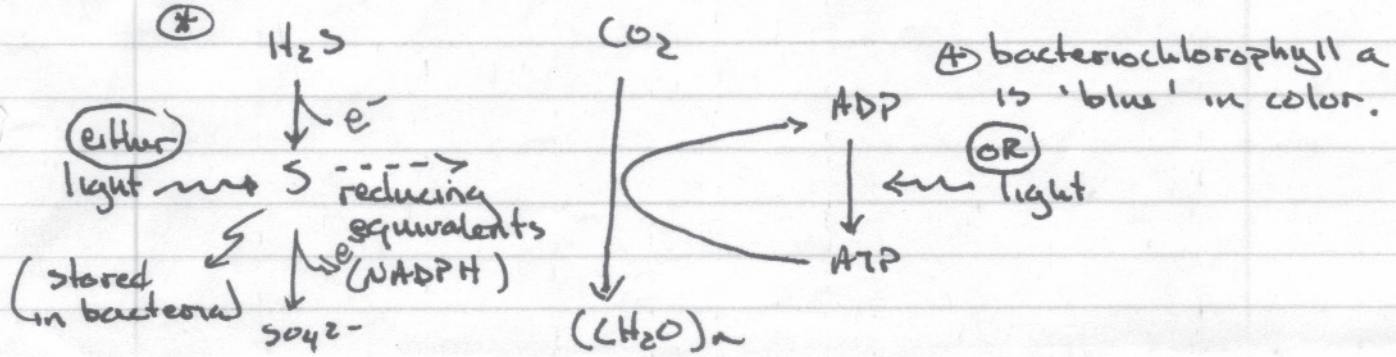
The prokaryotes are simple in structure, but tend to be biochemically diverse. Many of the major photosynthetic prokaryotes are ✱ posses anoxygenic photosynthesis ✱

PURPLE BACTERIA

The purple bacteria (proteobacteria) group includes a number of non-photosynthetic genera (Escherichia coli, Salmonella & Yersinia are examples).

The phototrophs are "delightfully colored" in a range of pink to greens.
They are subdivided into purple nonsulfur phototrophs & purple sulfur phototrophs
although this is not categorical, simply an indicator of relative abilities to use reduced sulfur compounds such as H_2S (the "non-sulfurs" are sensitive to high H_2S but can use it at lower concentrations.)

The pigments they use include bacteriochlorophyll a ⊕ and carotenoids.



⊕ bacteriochlorophyll a is 'blue' in color.

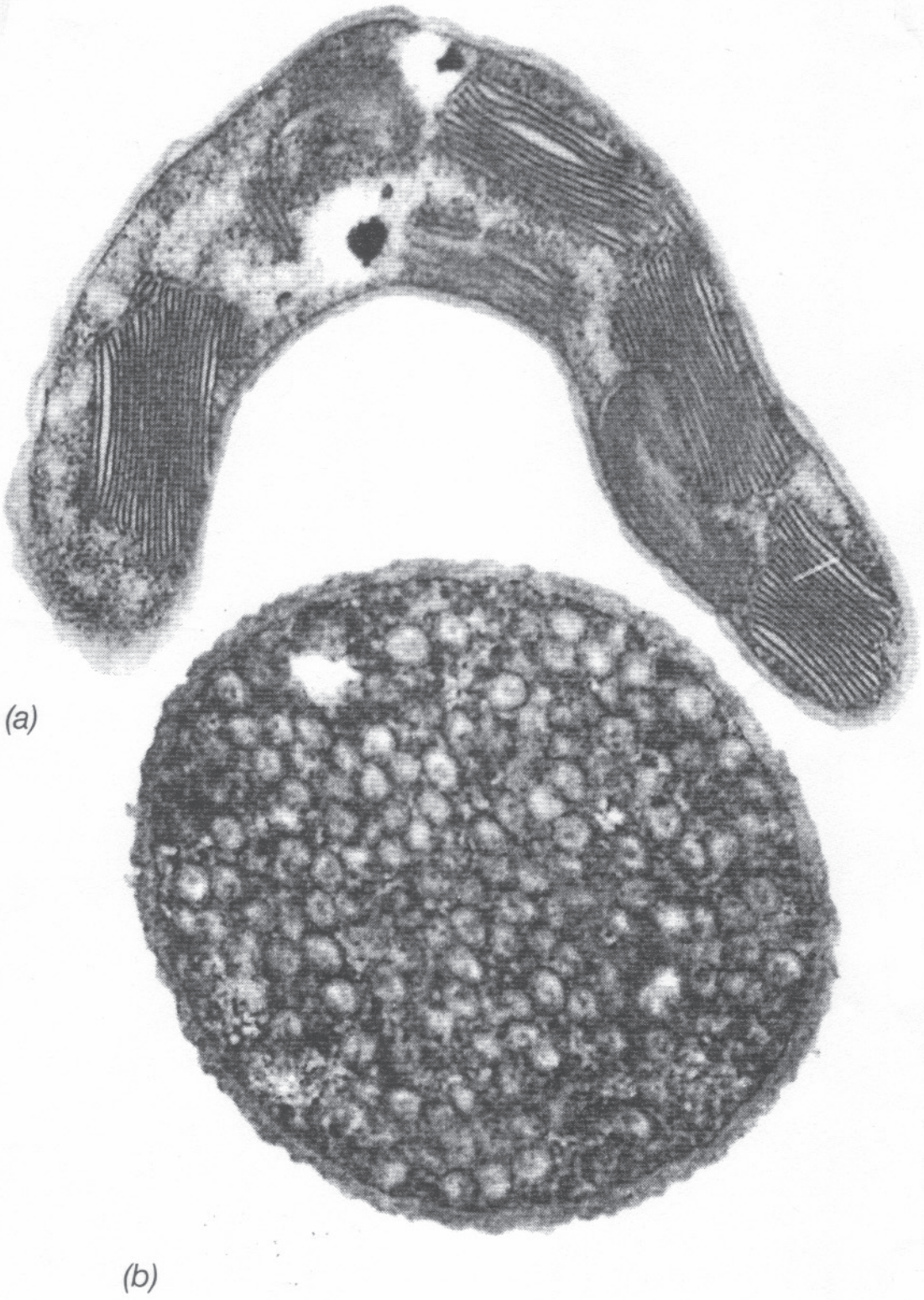


Figure 12.3 Membrane systems of phototrophic purple bacteria as revealed by the electron microscope. (a) Purple phototrophic bacterium, *Ectothiorhodospira mobilis*, showing the photosynthetic membranes in flat sheets (lamellae). (b) *Allochromatium vinosum*, another purple phototrophic bacterium, showing the membranes as individual, spherical-shaped vesicles.

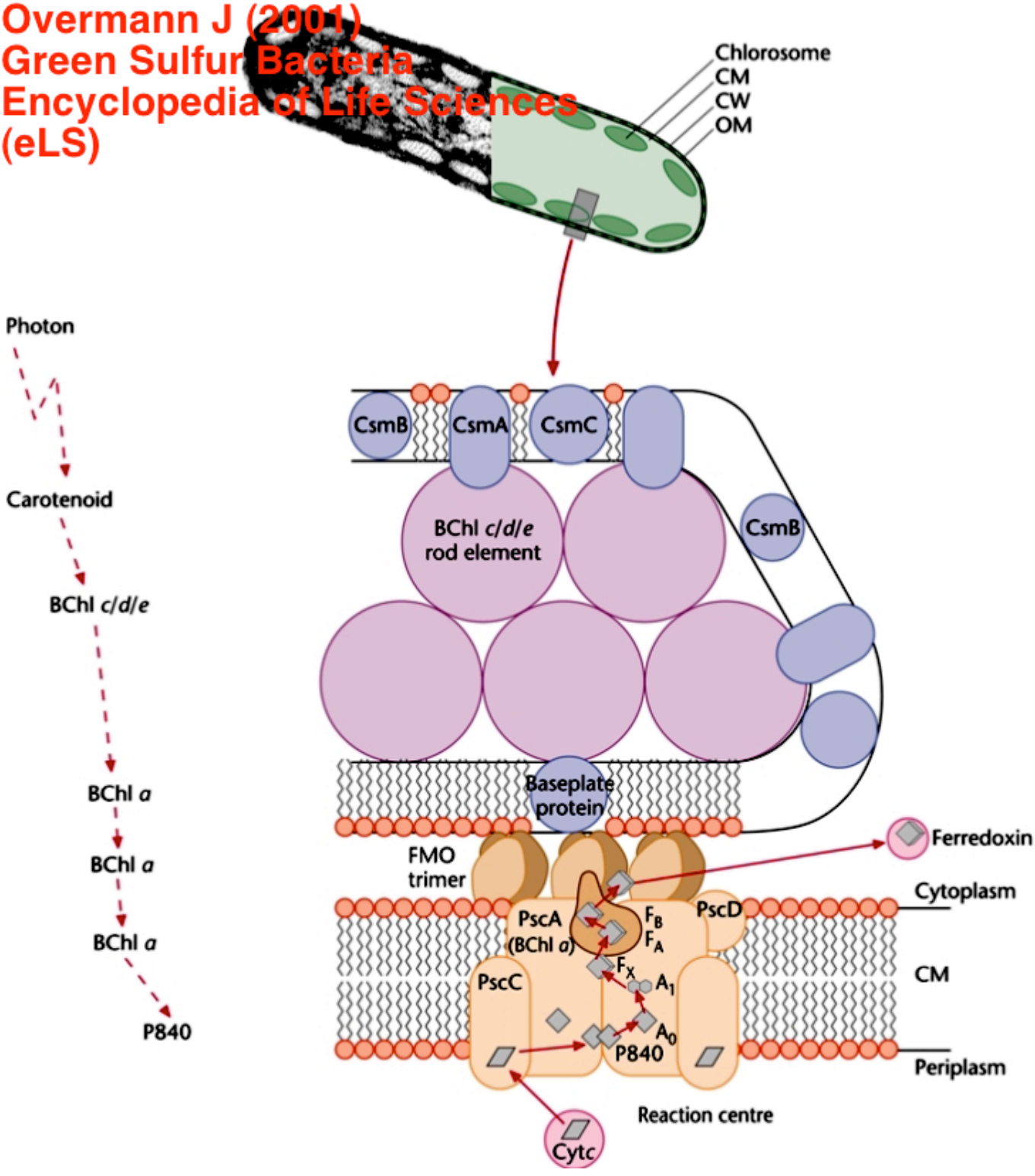
Characteristic genera of the phototrophic purple bacteria include Rhodobacter (sphaeroides) & Rhodospirilum (rubrum).

They have internal membrane systems, analogous to thylakoid membranes.

The purple sulfur bacteria are found in anoxic illuminated aquatic environs. Sulfur springs is one example. Another is stratified lakes in which sulfide is produced in the sediments and diffuses upward into the anoxic bottom waters.

The purple non sulfur bacteria can utilize $CO_2 + H_2$ or CO_2 + low levels of H_2S, or use light to produce energy and organic compounds as the carbon source (photoheterotrophy)

Overmann J (2001)
Green Sulfur Bacteria
Encyclopedia of Life Sciences
(eLS)



GREEN SULFUR BACTERIA.

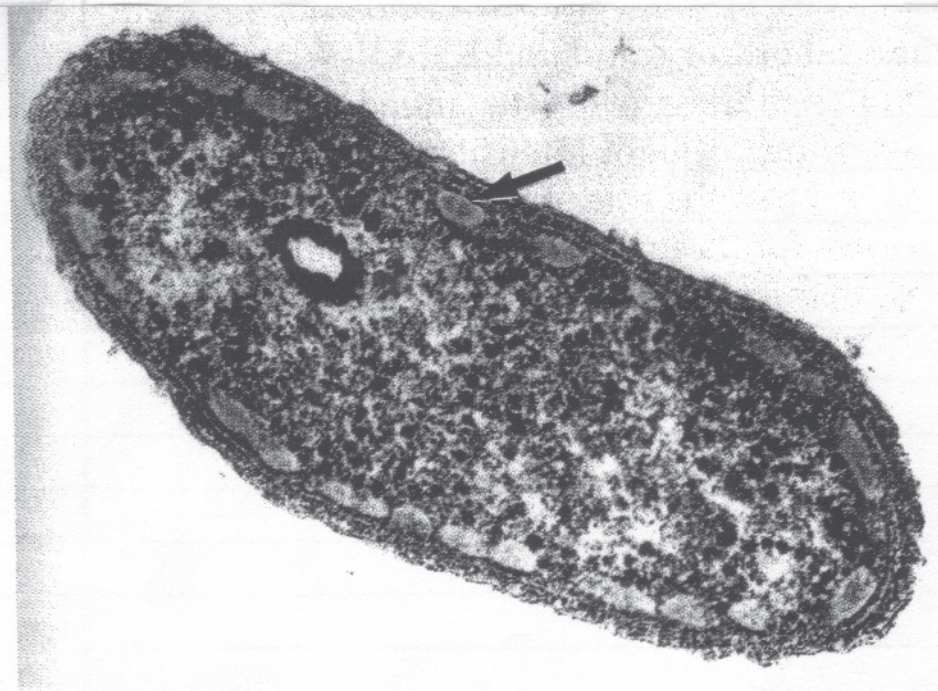
The pigments include bacteriochlorophyll a and either bacteriochlorophylls c, d, or e which function in light-harvesting.

electrons are obtained from sulfur:

$$H_2S \xrightarrow{e^-} S \xrightarrow{e^-} SO_4^{2-}$$

CO_2 fixation occurs by reversal of steps in the Krebs cycle, rather than the Calvin cycle.

The bacteria have a structure called the chlorosome which are oblong bacteriochlorophyll-rich bodies bounded by a membrane and attached to the cytoplasmic membrane in the periphery of the cell



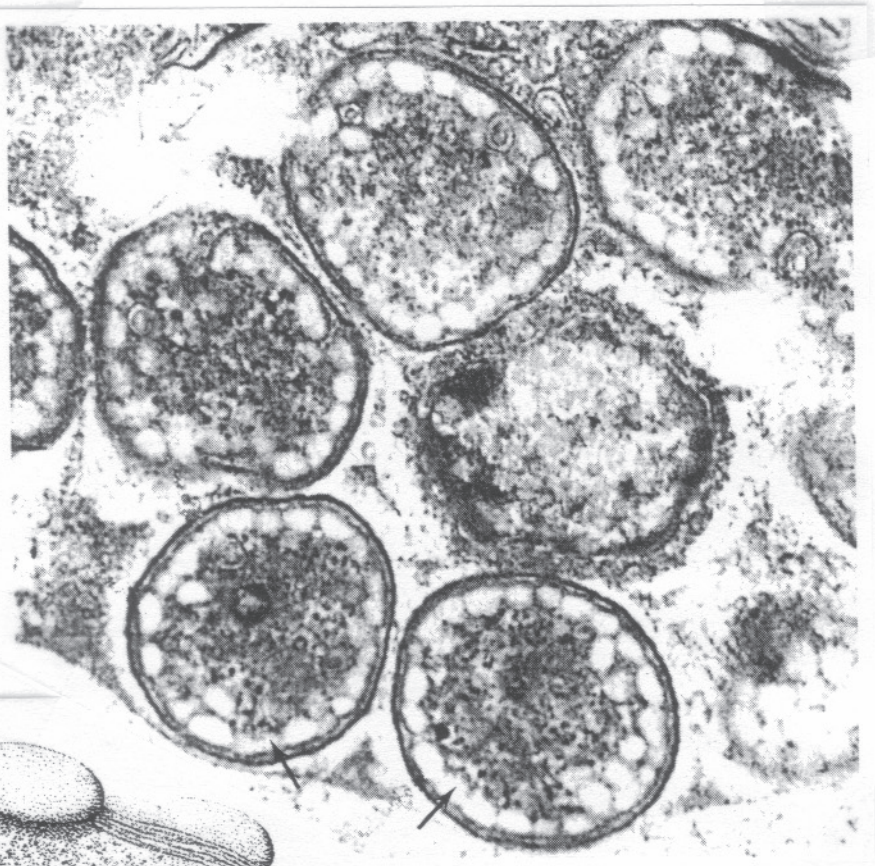
F. Rudy Turner and Michael T. Madigan

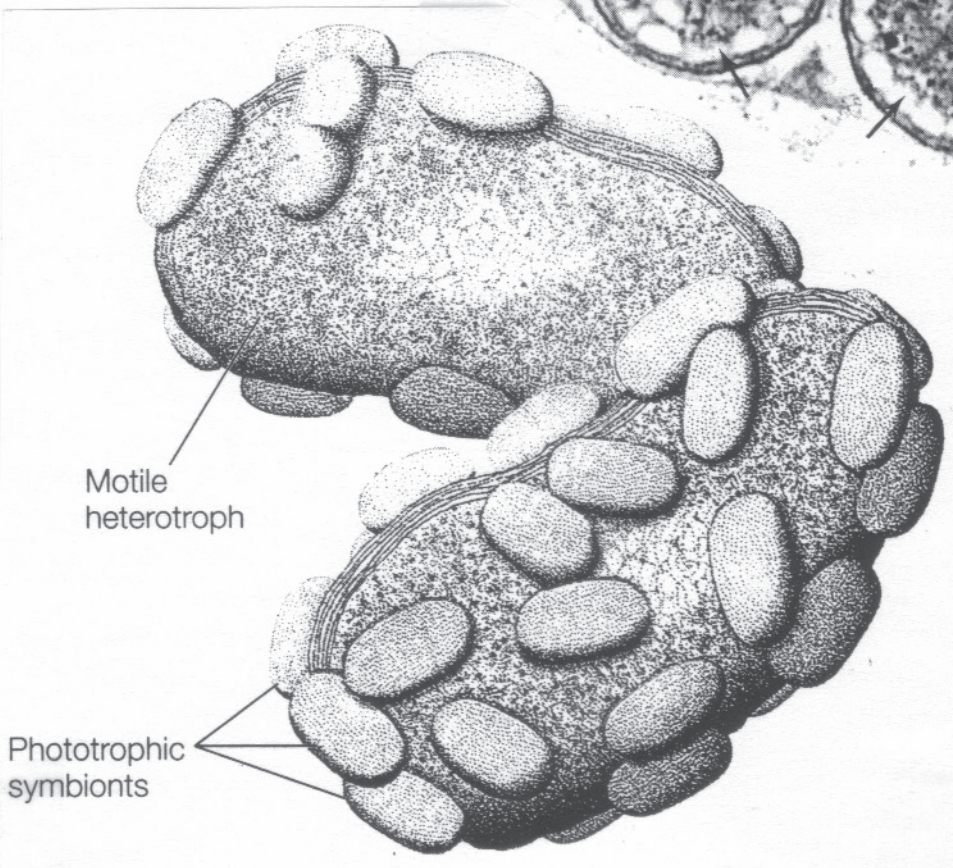
Figure 12.92 Thin section electron micrograph of a cell of the green sulfur bacterium *Chlorobium tepidum*. Note chlorosomes (arrow) in the cell periphery. A cell is about 0.7 μm wide.

They also exist in multi-cellular consortia of photo-trophic cells surrounding and in close contact with a central heterotrophic cell.

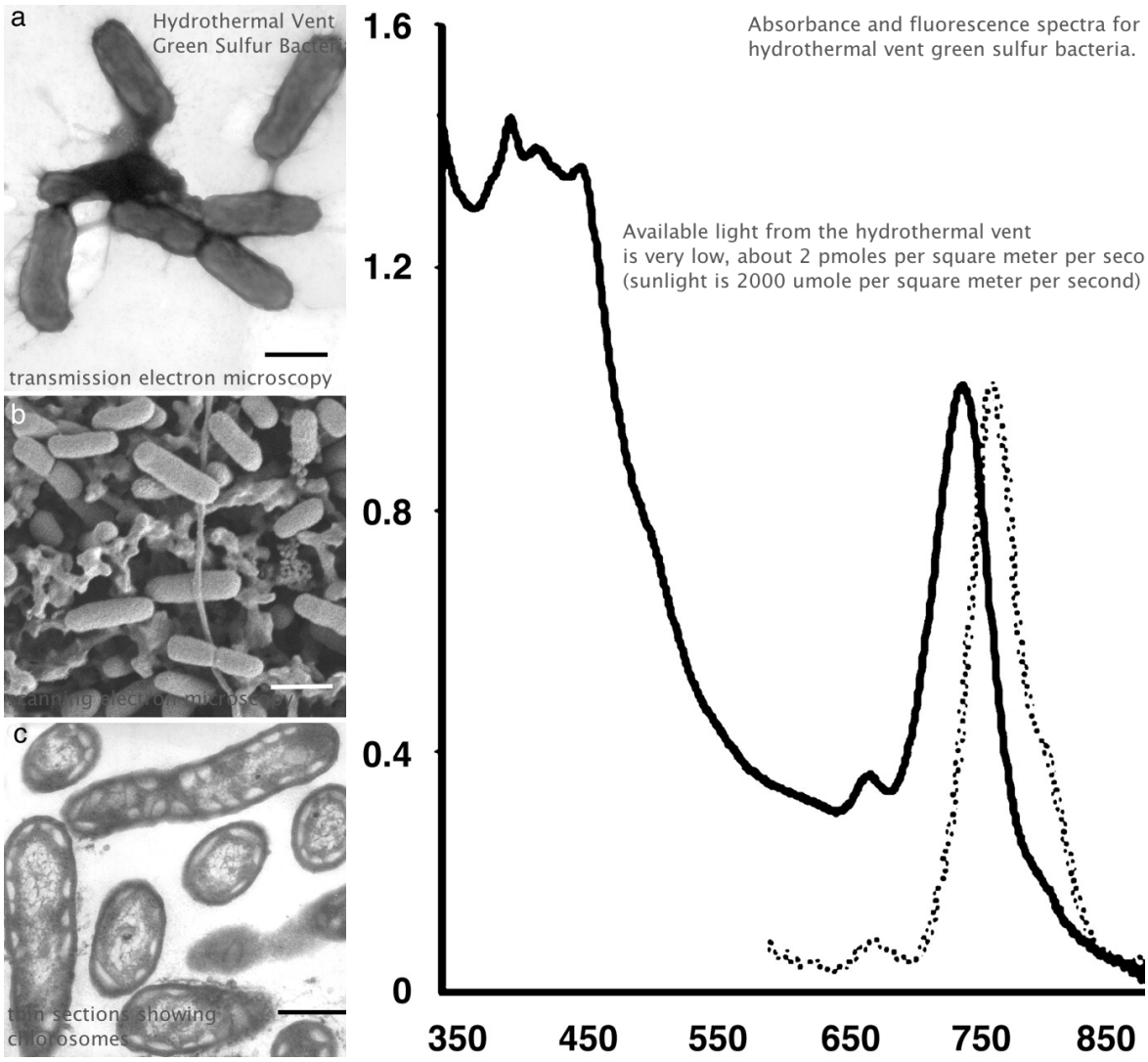
source: Brock Biology of Micro-organisms.

Green Sulfur Bacteria Consortia.





Sources:
MT Madigan, JM Martinko and J Parker 2003. Brock Biology of Microorganisms. 10th edition. Prentice Hall
L Margulis and KV Schwartz 1998. Five Kingdoms. 3d edition. WH Freeman.



Hydrothermal Vent Green Sulfur Bacteria. The bacteria do perform photosynthesis, but where does it get its light from? The only light source is the hydrothermal vent itself. Light availability is measured in pmoles (10^{-12}) compared to mmoles (10^{-3}) m^{-2} s^{-1} for full sunlight. The doubling time of the bacteria is expected to be about 2 years. Green sulfur bacteria uniquely contain a light-harvesting protein called the Fenna-Matthews-Olson (FMO) protein (of quantum entanglement fame).

Source: Beatty JT, Overmann J, Lince MT, Manske AK, Lang AS, Blankenship RE, Van Dover CL, Martinson TA, Plumley FG (2005) An obligately photosynthetic bacterial anaerobe from a deep-sea hydrothermal vent. PNAS 102:9306-9310.

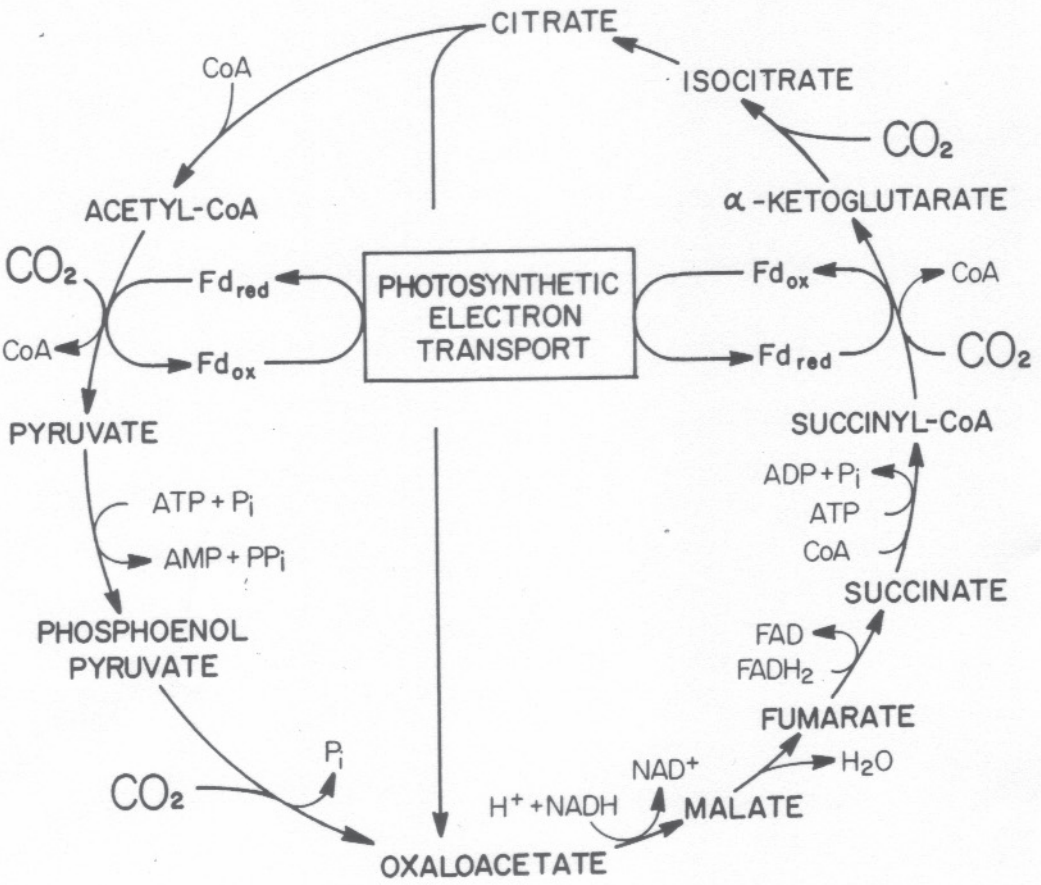


FIG. 5.12. The reductive carboxylic acid cycle in *Clostridium thiosulfatophilum*, an anaerobic organism that uses H_2S as a source of electrons for photosynthesis rather than H_2O. One turn of the cycle results in the incorporation of four molecules of CO_2. The cycle is in essence the reverse of the oxidative tricarboxylic acid cycle in aerobic organisms. In this photosynthetic bacterium, reduced ferredoxin, generated by photosynthetic electron transport, provides a strong reductant to drive the operation of the cycle in the direction of CO_2 incorporation. Intermediates of the cycle can be removed by transamination reactions with pyruvate to alanine, oxaloacetate to aspartate, and α-ketoglutarate to glutamate for other biosynthetic processes. (Adapted from Evans *et al.*, 1966.)

HOOBER, JK
CHLOROPLASTS
1984

GREEN NON-SULFUR BACTERIA

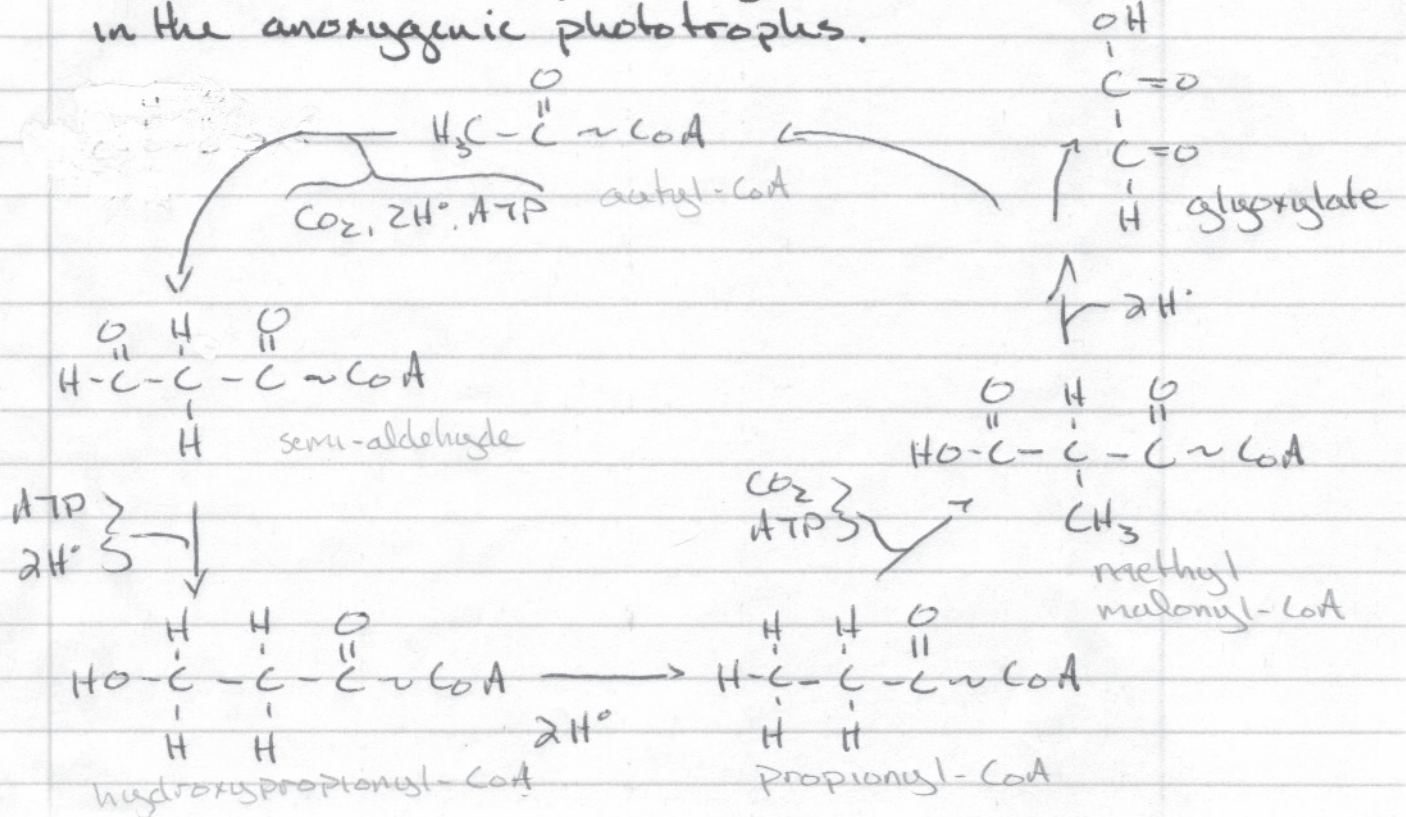
Similarly to the green sulfur bacteria, the green non-sulfur bacteria have bacteriochlorophyll a and often c, and may have chlorosomes.
Often found in hot springs or nonthermal marine microbial mats.
They can use either H_2S or H_2 as an electron donor in photosynthesis

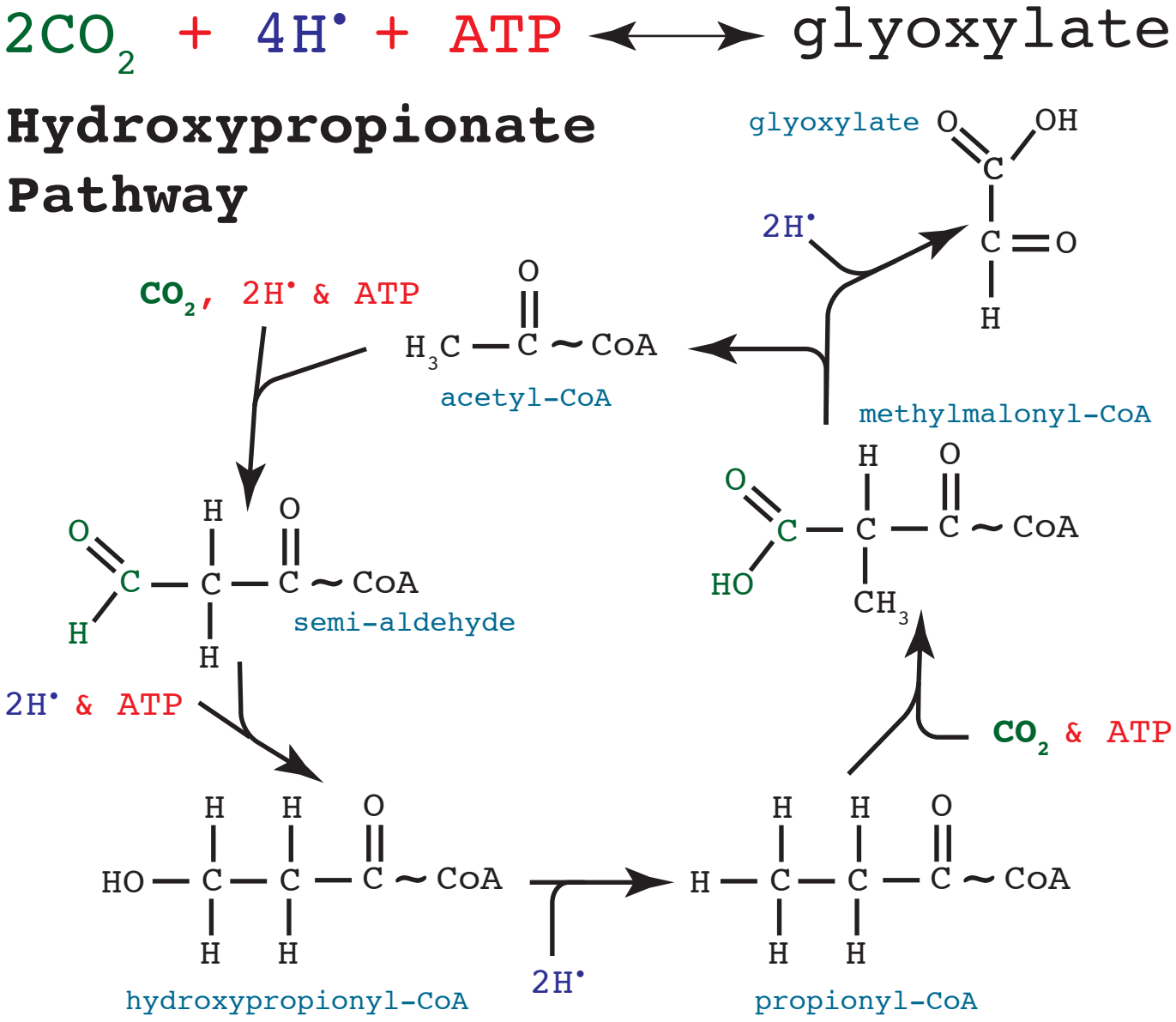
Carbon fixation occurs by the unique hydroxypropionate pathway in which

acetyl CoA is carboxylated twice to yield methylmalonyl-CoA which is then cleaved to form acetyl-CoA and glyoxylate:

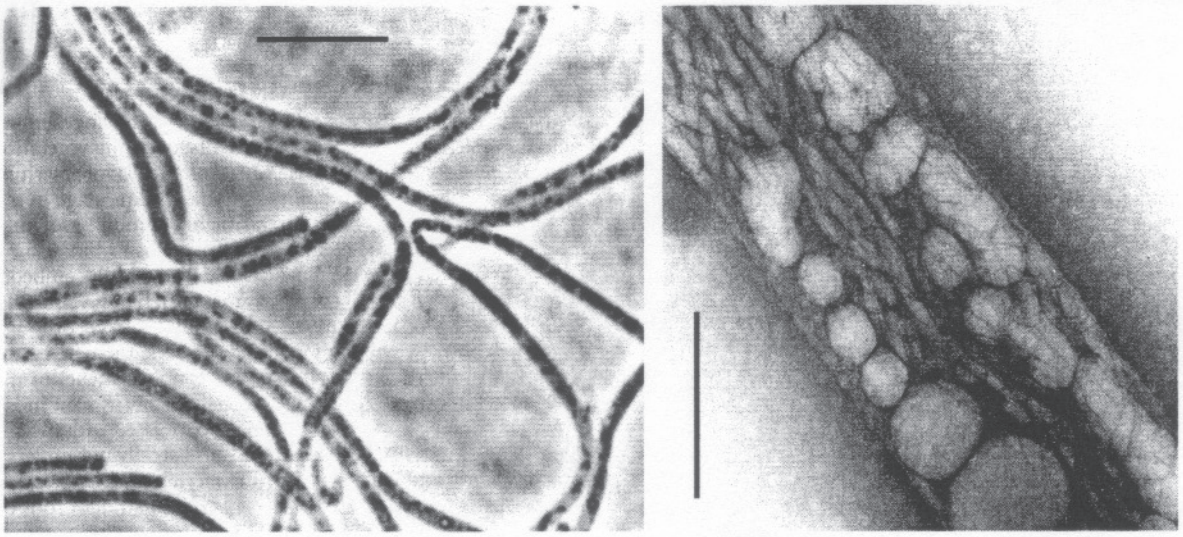
$$2\,CO_2 + 4H^+ + 3\,ATP \longrightarrow \text{glyoxylate}.$$

This is only found in Chloroflexus, and may be the ancestral pathway of autotrophism in the anoxygenic phototrophs.

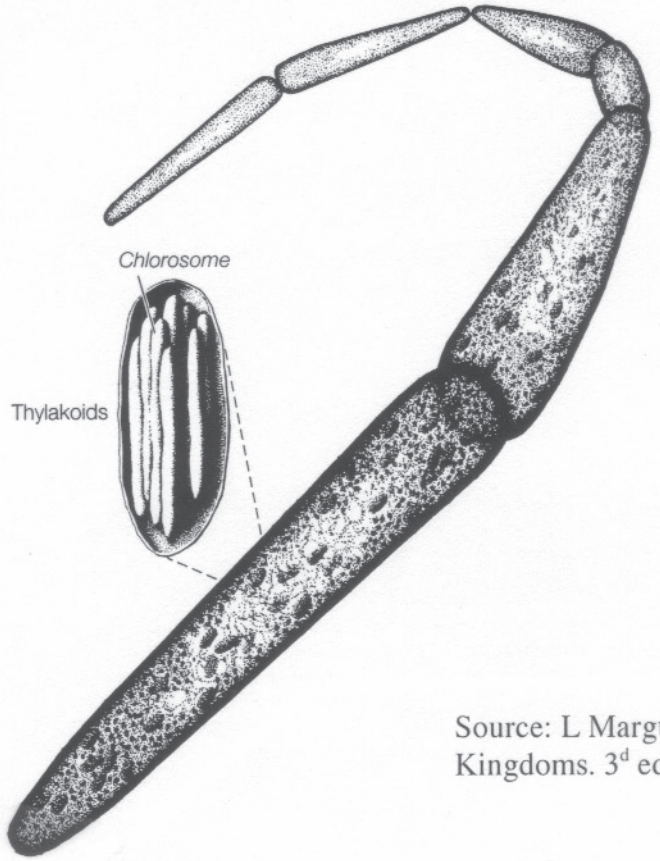



2CO2 + 4H• + ATP ⟷ glyoxylate
Hydroxypropionate Pathway
glyoxylate
2H•
CO2, 2H• & ATP
acetyl-CoA
methylmalonyl-CoA
semi-aldehyde
2H• & ATP
CO2 & ATP
2H•
hydroxypropionyl-CoA
propionyl-CoA

Chloroflexa (Green non-sulfur phototrophs)



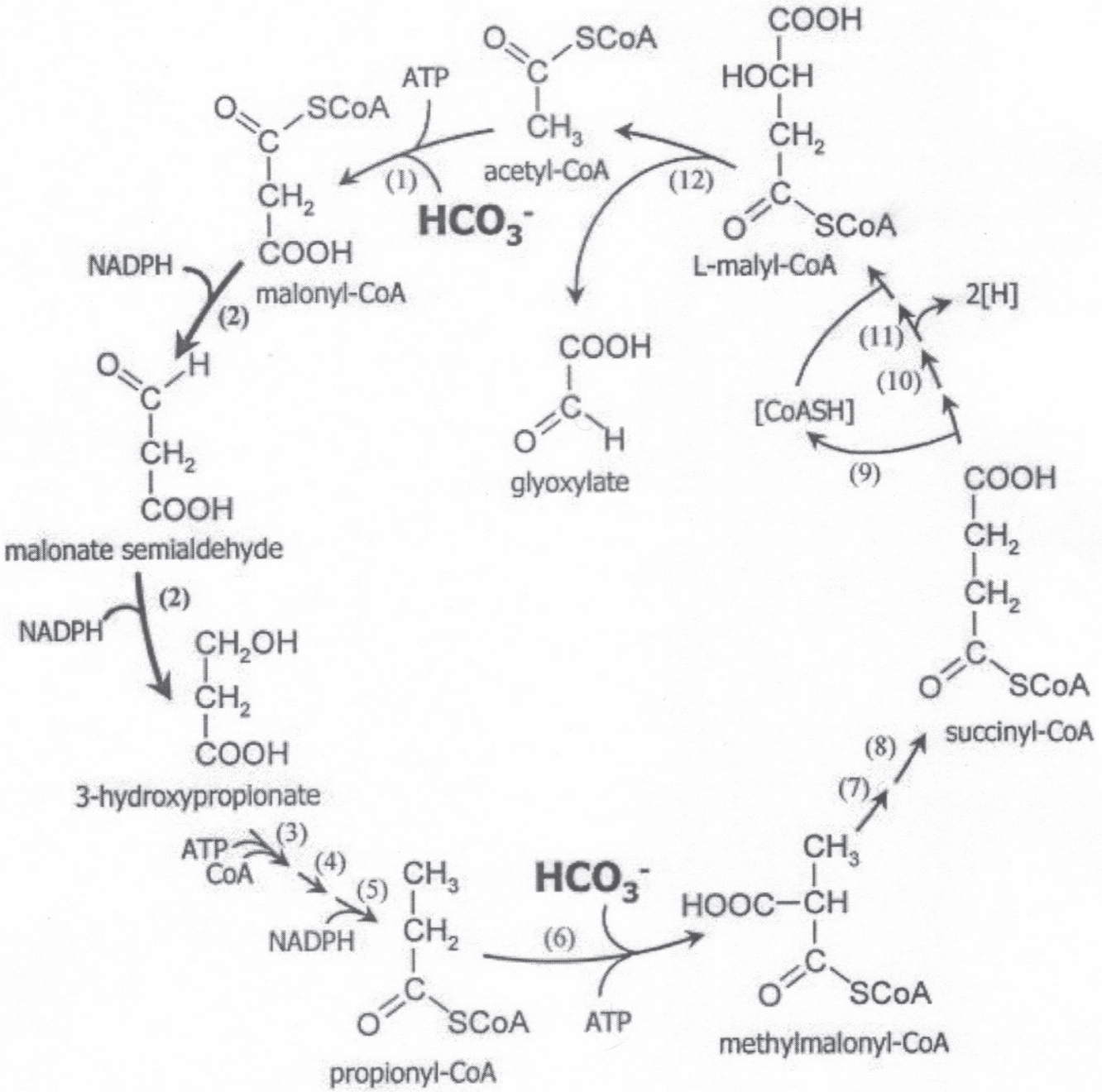
A (Left) Live photosynthetic gliding filamentous cells, 1 μm in diameter, of *Chloroflexus* from hot springs at Kahneeta, Oregon. LM (phase contrast), bar = 5 μm. [Courtesy of B. Pierson and R. Castenholz. *Arch. Microbiol.* 100:5–24 (1975).] (Right) Magnified view showing the typical membranous phototrophic vesicles that contain the enzymes and pigments for photosynthesis. EM (negative stain), bar = 1 μm. [Courtesy of R. Castenholz.]



B *Chloroflexus aurantiacus.* Filamentous, thin photosynthesizers showing distribution of their chlorosomes as seen by light microscopy. (Inset) The entire chlorosome as reconstructed from electron micrographs. The membranous plates are the sites of the bacterial chlorophylls and their bound proteins. [Drawings by C. Lyons.]

Source: L Margulis and KV Schwartz 1998. Five Kingdoms. 3^{d} edition. WH Freeman.

FIG. 1. Proposed 3-hydroxypropionate cycle of autotrophic CO2 fixation in the phototrophic green nonsulfur bacterium *Chlorflexus aurantiacus*, illustrating the role of malonyl-CoA reductase. Enzyme activities: 1, acetyl-CoA carboxylase; 2, malonyl-CoA reductase (NADPH), the enzyme studied in this work, catalyzing both malonyl-CoA and malonate semialdehyde reduction; 3, 3-hydroxypropionyl-CoA synthetase; 4, 3-hydroxypropionyl-CoA dehydratase; 5, acryloyl-CoA reductase (NADPH); 6, propionyl-CoA carboxylase; 7, methylmalonyl-CoA epimerase; 8, methylmalonyl-CoA mutase; 9, succinyl-CoA:l-malate CoA transferase; 10, succinate dehydrogenase, electron acceptor unknown; 11, fumarate hydratase; 12, l-malyl-CoA lyase. Note that the different enzyme activities indicated above do not necessarily mean that all these reactions are catalyzed by different enzymes. For instance, as shown here, malonyl-CoA reductase catalyzes two reactions. [CoASH], transferred coenzyme A.



Source: J Bacteriol. 2002 May; 184(9): 2404–2410.

HELIOBACTERIA

Heliobacteria are the only Gram-positive anoxygenic photosynthesis bacteria. They contain the unique bacteriochlorophyll g.

They are allied with an endospore-forming, low GC. Gram-positive group (the Endospora) which includes Bacillus and Clostridium.

They are commonly found in wet soils and are important N_2-fixers.

Table 1. Major groups of phototrophic prokaryotes[1].

Type of photo-synthesis	Phototrophic group	Pigment of photosynthetic reaction center	Primary products of energy conversion	Photosynthetic electron donors	Carbon source
Anoxygenic	Halobacteria	Bacteriorhodopsin	ATP	Not applicable	Organic
Anoxygenic	Filamentous green bacteria	Bchl a	ATP	Organic, S_2^-,$S_2O_0^{2-}$	Organic, CO_2
Anoxygenic	Green sulfur bacteria	Bchl a	ATP + NADH	H_0, S_2^-, S^0,$S_2O_3^{2-}$	CO_2
Anoxygenic	Purple bacteria	Bchl a or b	ATP	H_0, S_2^-, S^0,$S_2O_3^{2-}$, organic	CO_2 and/or organic
Anoxygenic	Heliobacteria	Bchl g	ATP + NADH	Organic	Organic
Oxygenic	Cyanobacteria	Chl a	ATP + NADH	H_2O	CO_2

[1]Source: http://141.150.157.117:8080/prokPUB/chaphtm/013/02_00.htm
The Prokaryotes. An Evolving Electronic Resource for the Microbiological Community

at 3 km. The $\delta^{18}O$ record for *G. ruber* is very similar to the previously published record for *G. sacculifer* from 806B, as well as other piston cores from the OJP, but our sampling resolution is twice that of the previous study of Hole 806B. We slightly modified the existing age model using our *G. ruber* $\delta^{18}O$ record, generated at twice the resolution, correlated to the standard SPECMAP chronology. We also corrected the core-top age to the typical radiocarbon age of core-tops from this region and depth (*34*). The average sedimentation rate is about 2 cm/ky.

34. W. S. Broecker, E. Clark, D. C. McCorkle, I. Hajdas, G. Bonani, *Paleoceanography* **14**, 13 (1999).
35. N. J. Shackleton, J. Le, A. Mix, M. A. Hall, *Quat. Sci. Rev.* **11**, 387 (1992).
36. Spectral analysis of Hole 806B data indicates that the overall cross correlation between Mg/Ca and $\delta^{18}O$ is $r = -0.73$, with Mg/Ca leading by 3 ky. The 100-, 41-, and 23-ky orbital periods in the $\delta^{18}O$ and Mg/Ca records are all coherent at the 95% CI.
37. We determined $\delta^{18}O$ and Mg/Ca in *G. sacculifer* shells from the top 150 cm of Hole 806B. As is observed for TR163-19, the Mg/Ca values for *G. sacculifer* are systematically lower than for *G. ruber* and the $\delta^{18}O$ values are systematically more positive. The *G. sacculifer* Mg/Ca change over termination I is 2.8 to 3.6 mmol/mol, equivalent to a 2.8°C increase in SST and essentially identical to the SST change calculated from the *G. ruber* data.
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44. D. J. Andreasen and A. C. Ravelo, *Paleoceanography* **12**, 395 (1997).
45. We used a low-light paleotemperature equation derived for *Orbulina universa* (*46*): $\delta^{18}O_w = (T - 16.5 + 4.8*\delta^{18}O_{calcite})/4.8 + 0.27$. Because the slopes of $\delta^{18}O$ change versus temperature are similar (0.20 to 0.23‰ per °C), the choice of paleotemperature equations does not have a large impact on the calculations. The estimated uncertainty of the $\delta^{18}O_w$ values is ±0.18‰, calculated from the uncertainty in the paleotemperature equation, the standard error of the Mg/Ca-SST calibration, and the reproducibility of $\delta^{18}O$ and Mg/Ca in a typical interval.
46. B. E. Bemis, H. J. Spero, J. Bijma, D. W. Lea, *Paleoceanography* **13**, 150 (1998).
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48. R. G. Fairbanks *et al.*, *Coral Reefs* **16**, S93 (1997).
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55. We thank J. Kennett and D. McCorkle for samples; T. Crowley, E. Bard, H. Elderfield, N. Pisias, and P. Martin for comments on earlier drafts; M. Kashgarian and T. Guilderson for radiocarbon dating; P. Howell for time-series software and advice on its use; I. Winograd for the suggestion to compare to the Devils Hole record; Q. Xie, G. Paradis, and H. Berg for mass spectrometer operation and maintenance; D. Gates, A. Schilla, P. Dekens, A. Davé, P. von Langen, L. Juranek, and M. Thomas for sample preparation; and E. Christian for clerical assistance. This research was funded by the NSF.

29 March 2000; accepted 13 July 2000

Molecular Evidence for the Early Evolution of Photosynthesis

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The origin and evolution of photosynthesis have long remained enigmatic due to a lack of sequence information of photosynthesis genes across the entire photosynthetic domain. To probe early evolutionary history of photosynthesis, we obtained new sequence information of a number of photosynthesis genes from the green sulfur bacterium *Chlorobium tepidum* and the green nonsulfur bacterium *Chloroflexus aurantiacus*. A total of 31 open reading frames that encode enzymes involved in bacteriochlorophyll/porphyrin biosynthesis, carotenoid biosynthesis, and photosynthetic electron transfer were identified in about 100 kilobase pairs of genomic sequence. Phylogenetic analyses of multiple magnesium-tetrapyrrole biosynthesis genes using a combination of distance, maximum parsimony, and maximum likelihood methods indicate that heliobacteria are closest to the last common ancestor of all oxygenic photosynthetic lineages and that green sulfur bacteria and green nonsulfur bacteria are each other's closest relatives. Parsimony and distance analyses further identify purple bacteria as the earliest emerging photosynthetic lineage. These results challenge previous conclusions based on 16*S* ribosomal RNA and Hsp60/Hsp70 analyses that green nonsulfur bacteria or heliobacteria are the earliest phototrophs. The overall consensus of our phylogenetic analysis, that bacteriochlorophyll biosynthesis evolved before chlorophyll biosynthesis, also argues against the long-held Granick hypothesis.

The advent of photosynthesis is one of the central events in the early development of life on Earth. The origin and evolution of photosynthesis, however, have long remained unresolved. Studies have demonstrated that photosynthetic eukaryotes acquired photosynthetic properties from endosymbiosis with cyanobacteria (*1*). This observation, coupled with the fact that no Mg-tetrapyrrole–based photosynthesis has been found in Archaea, supports the notion that photosynthesis is a bacterially derived process (*2*). To obtain insight into the early evolution of photosynthesis, it is essential to conduct detailed phylogenetic analysis of many photosynthesis genes from each of the five known photosynthetic bacterial lineages. However, a paucity of photosynthesis gene sequences across the entire spectrum of photosynthetic bacteria has required that previous analyses rely on the use of nonphotosynthesis genes, which have given conflicting results for the evolution of photosynthesis and of photosynthetic organisms. For example, phylogenetic analysis of small-subunit rRNA suggests that green nonsulfur bacteria are the earliest evolving photosynthetic lineage (*3*). In contrast, using portions of the Hsp60 and Hsp70 heat shock proteins as markers, Gupta *et al.* (*4*) concluded that heliobacteria are the earliest evolving photosynthetic lineage and that this lineage subsequently diverged to green nonsulfur bacteria, cyanobacteria, green sulfur bacteria, and purple bacteria, in that order. The conflicting trees derived from such studies indicate that extrapolating the evolution of photosynthesis from nonphotosynthesis gene trees may be invalid.

Another problem arises when only a single set of photosynthesis genes is used for phylogeny. Previous attempts to analyze the evolution of photosynthesis using photosynthetic reaction center apoproteins failed to construct a phylogeny that includes all five photosynthetic bacterial lineages, because anoxygenic photosynthetic bacteria contain only one type of photosynthetic reaction center (type I or type II), whereas cyanobacteria contain both types of reaction center. Though the two types of reaction centers share significant structural similarities (*5*), their sequences have diverged to such an extent that it is virtually impossible to perform a statistically

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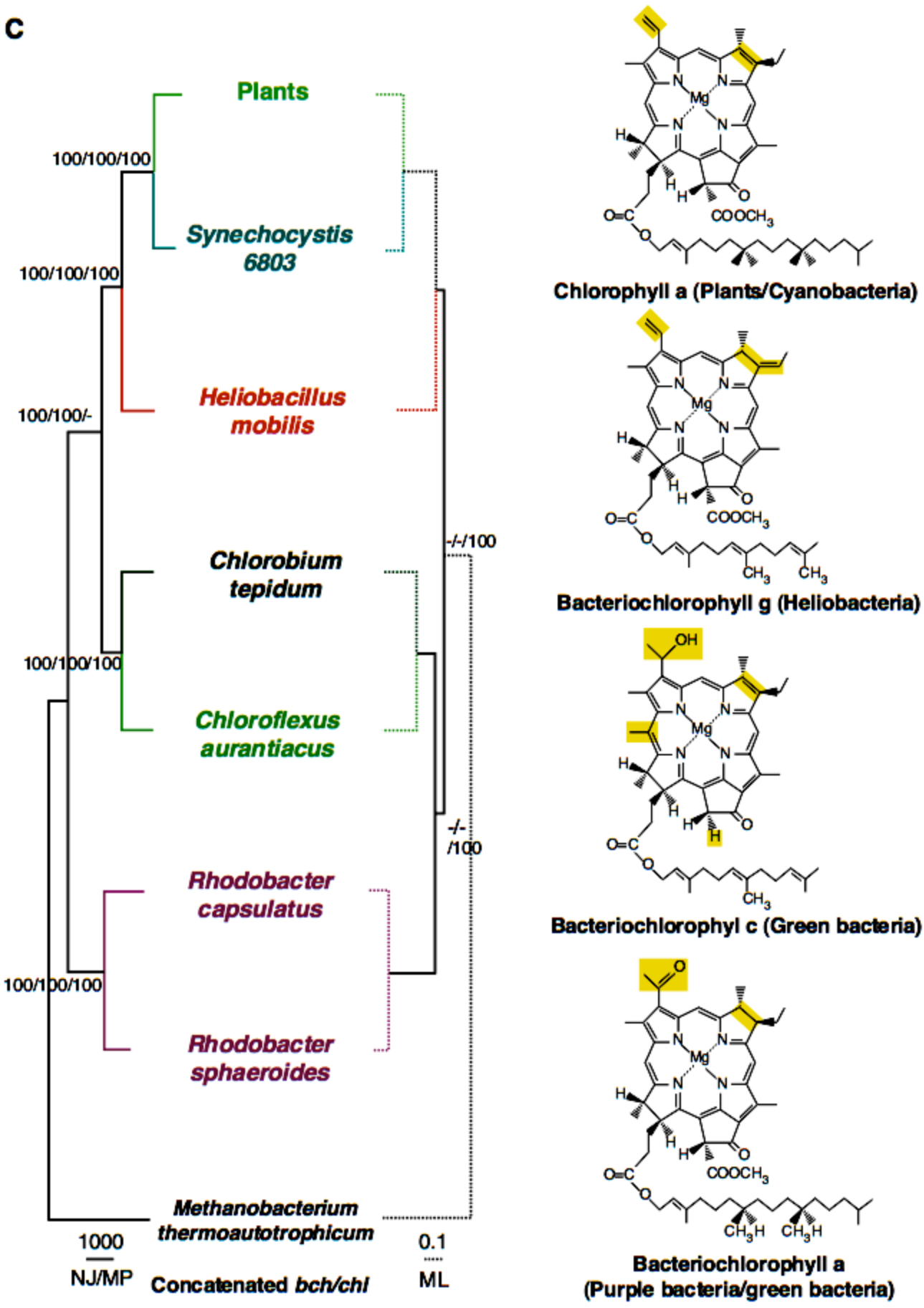
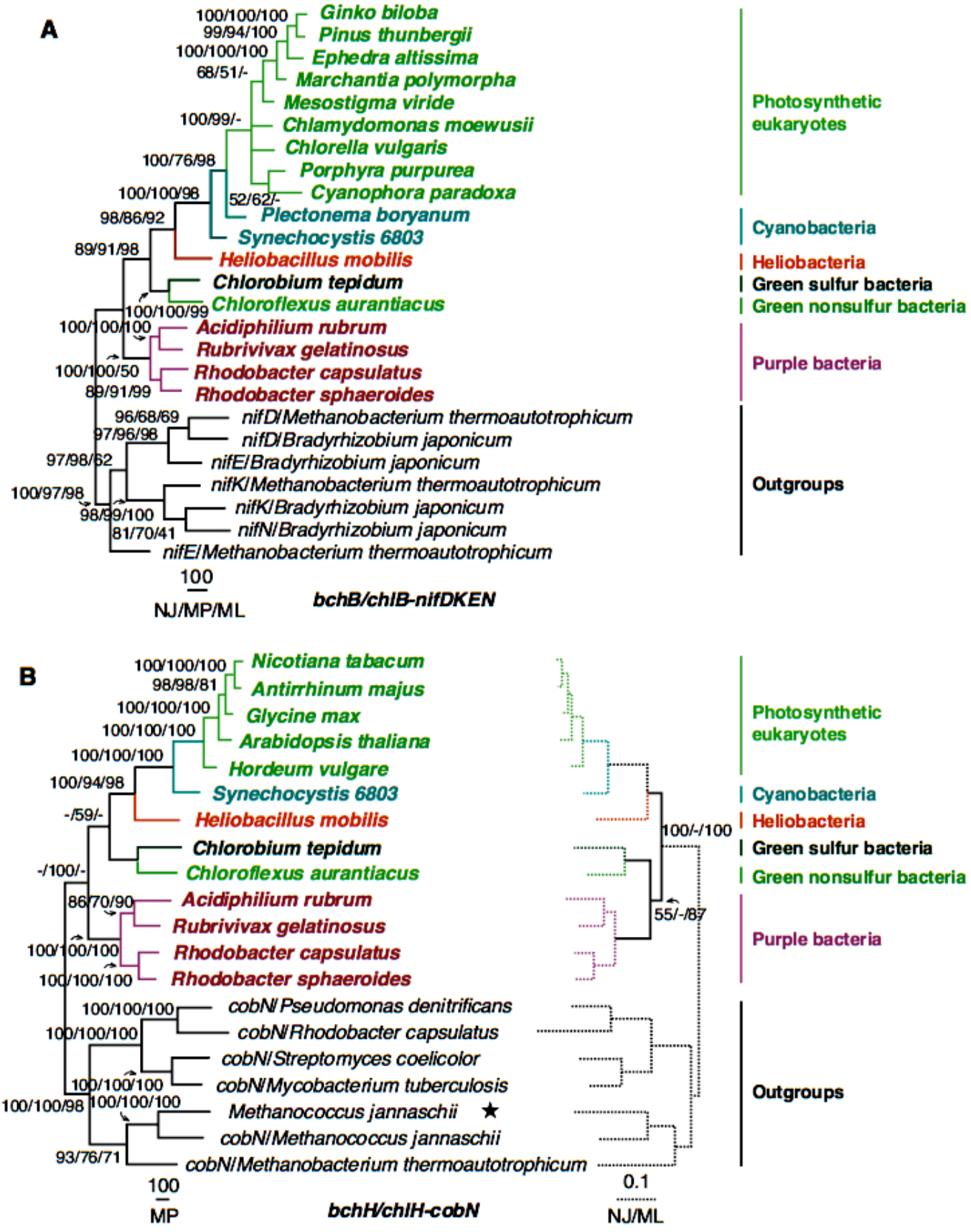

c
Plants
Synechocystis 6803
Heliobacillus mobilis
Chlorobium tepidum
Chloroflexus aurantiacus
Rhodobacter capsulatus
Rhodobacter sphaeroides
Methanobacterium thermoautotrophicum
100/100/100
100/100/100
100/100/-
100/100/100
100/100/100
-/-/100
-/-
/100
1000
NJ/MP
0.1
ML
Concatenated bch/chl
Chlorophyll a (Plants/Cyanobacteria)
Bacteriochlorophyll g (Heliobacteria)
Bacteriochlorophyl c (Green bacteria)
Bacteriochlorophyll a
(Purple bacteria/green bacteria)


A
100/100/100
Ginko biloba
99/94/100
Pinus thunbergii
100/100/100
Ephedra altissima
68/51/-
Marchantia polymorpha
Mesostigma viride
100/99/-
Chlamydomonas moewusii
Chlorella vulgaris
100/76/98
Porphyra purpurea
100/100/98
52/62/-
Cyanophora paradoxa
98/86/92
Plectonema boryanum
Synechocystis 6803
89/91/98
Heliobacillus mobilis
Chlorobium tepidum
100/100/99
Chloroflexus aurantiacus
100/100/100
Acidiphilium rubrum
Rubrivivax gelatinosus
100/100/50
Rhodobacter capsulatus
89/91/99
Rhodobacter sphaeroides
96/68/69
nifD/Methanobacterium thermoautotrophicum
97/96/98
nifD/Bradyrhizobium japonicum
97/98/62
nifE/Bradyrhizobium japonicum
nifK/Methanobacterium thermoautotrophicum
100/97/98
98/99/100
nifK/Bradyrhizobium japonicum
81/70/41
nifN/Bradyrhizobium japonicum
nifE/Methanobacterium thermoautotrophicum
100
NJ/MP/ML
bchB/chlB-nifDKEN
Photosynthetic eukaryotes
Cyanobacteria
Heliobacteria
Green sulfur bacteria
Green nonsulfur bacteria
Purple bacteria
Outgroups
B
100/100/100
Nicotiana tabacum
98/98/81
Antirrhinum majus
100/100/100
Glycine max
100/100/100
Arabidopsis thaliana
100/100/100
Hordeum vulgare
100/94/98
Synechocystis 6803
-/59/-
Heliobacillus mobilis
Chlorobium tepidum
-/100/-
Chloroflexus aurantiacus
86/70/90
Acidiphilium rubrum
Rubrivivax gelatinosus
100/100/100
Rhodobacter capsulatus
100/100/100
Rhodobacter sphaeroides
100/100/100
cobN/Pseudomonas denitrificans
100/100/100
cobN/Rhodobacter capsulatus
cobN/Streptomyces coelicolor
100/100/100
cobN/Mycobacterium tuberculosis
100/100/98
100/100/100
Methanococcus jannaschii ★
cobN/Methanococcus jannaschii
93/76/71
cobN/Methanobacterium thermoautotrophicum
100
MP
bchH/chlH-cobN
100/-/100
55/-/87
0.1
NJ/ML
Photosynthetic eukaryotes
Cyanobacteria
Heliobacteria
Green sulfur bacteria
Green nonsulfur bacteria
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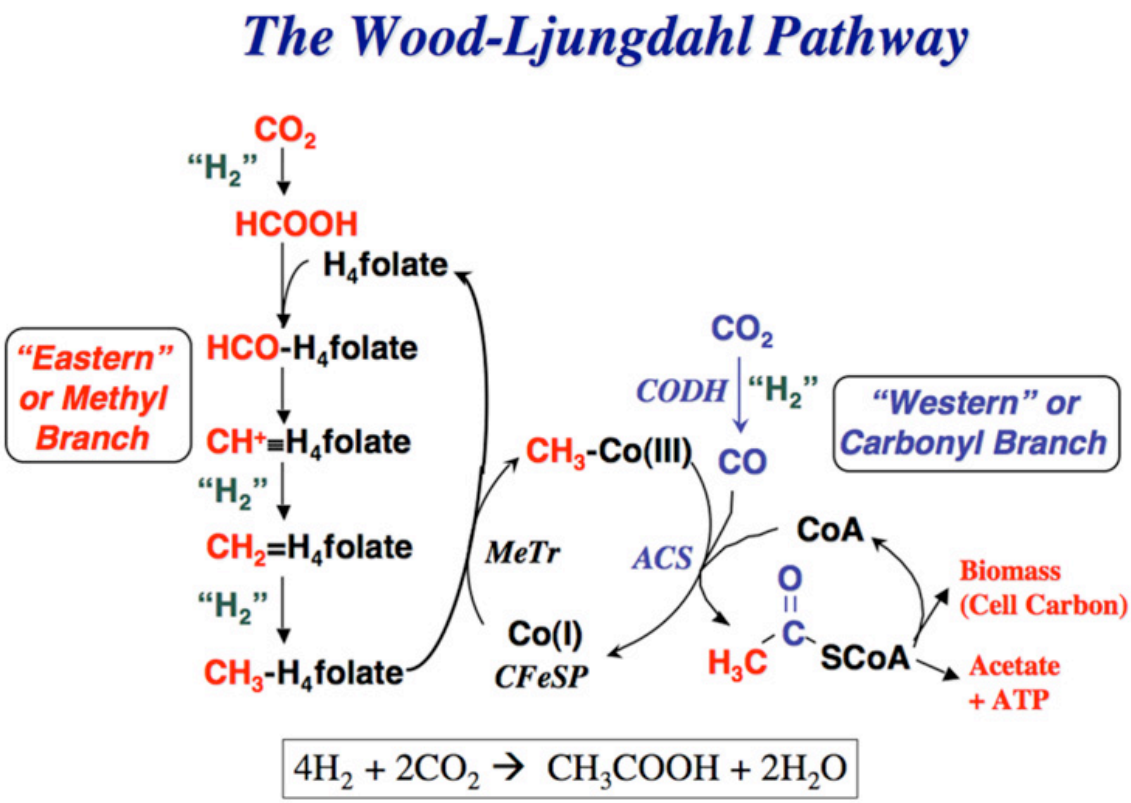
Outgroups



The Wood-Ljungdahl pathway. "H_2" is used in a very general sense to designate the requirement for two electrons and two protons in the reaction.

Nota bene. This is not a photosynthetic pathway in the usual sense. Instead, it is a mechanism to fix (or release) carbon dioxide that can progress in either a reductive (CO_2 fixation) or oxidative (CO_2 release) direction. It is found in acetogens and methanogens, a diverse set of prokaryotes that embrace multiple phylogenetic lineages and are found in numerous environments (anaerobic).

Stephen W. Ragsdale and Elizabeth Pierce (2008) Acetogenesis and the Wood-Ljungdahl pathway of CO_2 fixation. Biochim Biophys Acta. 1784:1873–1898.