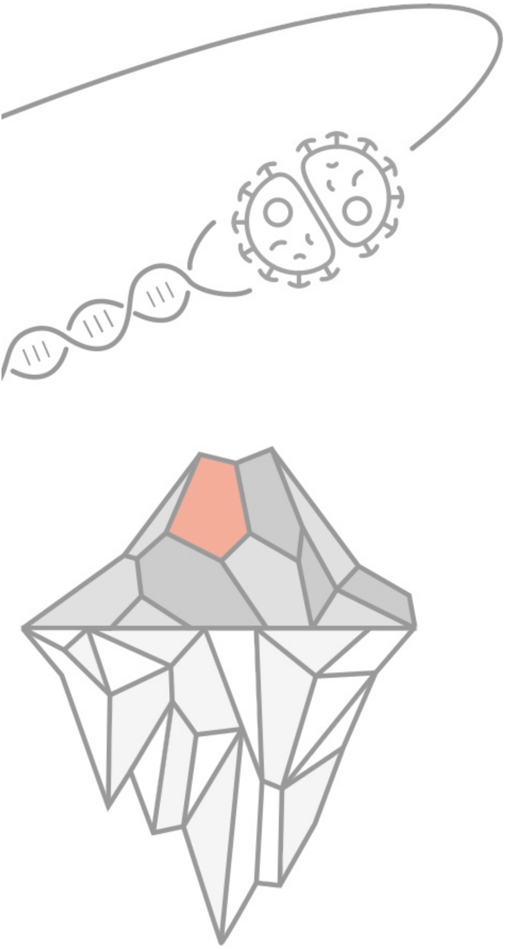

MICROBIAL ENERGETIC METABOLIC DIVERSITY

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BIOLOGY OF EXTREME ENVIRONMENTS

DIPARTIMENTO DI BIOLOGIA

Aerobic and Anaerobic Respiration

- *Respiration is the process of using an inorganic terminal electron acceptor in the electron transport chain*
- *Aerobic respiration is the dominant process in the extant biosphere*
- *Because the O_2/H_2O couple is very electropositive, more energy is available when O_2 is used as a terminal electron acceptor than when most other acceptor is used*
- *Other electron acceptors involved in anaerobic respiration are manganic ion (Mn_4^{+}), ferric iron (Fe_3^{+}), nitrate (NO_3^{-}), and nitrite (NO_2^{-}), sulfate (SO_4^{2-}), elemental sulfur (S^0), and carbon dioxide (CO_2) among others*
- *Prokaryotes performing aerobic and anaerobic respiration can be both* ***heterotrophs*** *and* ***autotrophs***

Assimilative and Dissimilative Reductions

- *Inorganic compounds (e.g. NO3−, SO42−, CO2) are reduced by many organisms as sources of cellular nitrogen, sulfur, and carbon (e.g. amino groups, sulfhydryl groups, organic carbon). This is* **assimilative** *reduction because the group is assimilated into biomass*
- *This is different from respiration, which is the reduction of inorganic compound for energy conserving reason. This is also known as* **dissimilative** *reduction, and often the product are excreted from the cell*
- *Most organisms carry out an assortment of assimilative metabolisms, whereas a more restricted group catalyze dissimilative metabolisms*
- *The list of possible inorganic and organic electron donors and acceptors includes geological, biological, and anthropogenic compounds*

Carbon Metabolism

Carbon in energy metabolism

Besides providing building block for anabolism (through carbon fixation pathways) Carbon is also used in energy conserving reactions either as an electron donor or acepetor

Can be used in these roles both in its inorganic (CO2, CO, HCO3-) and organic forms

Organic carbon utilization is very complex and requires a variety of specialized enzymes to break down organic molecules. Many of these enzymes are secreted extracellularly at great metabolic cost

Besides the catabolic complexities, the central pathways of organic carbon utilization are well conserved across the tree of life. Inorganic carbon pathways appears to be more divers

Heterotrophy

Heterotrophy (chemoorganotrophy) is the use of organic carbon sources for anabolic purposes. In heterotrophy carbon can and is also generally used as energy source

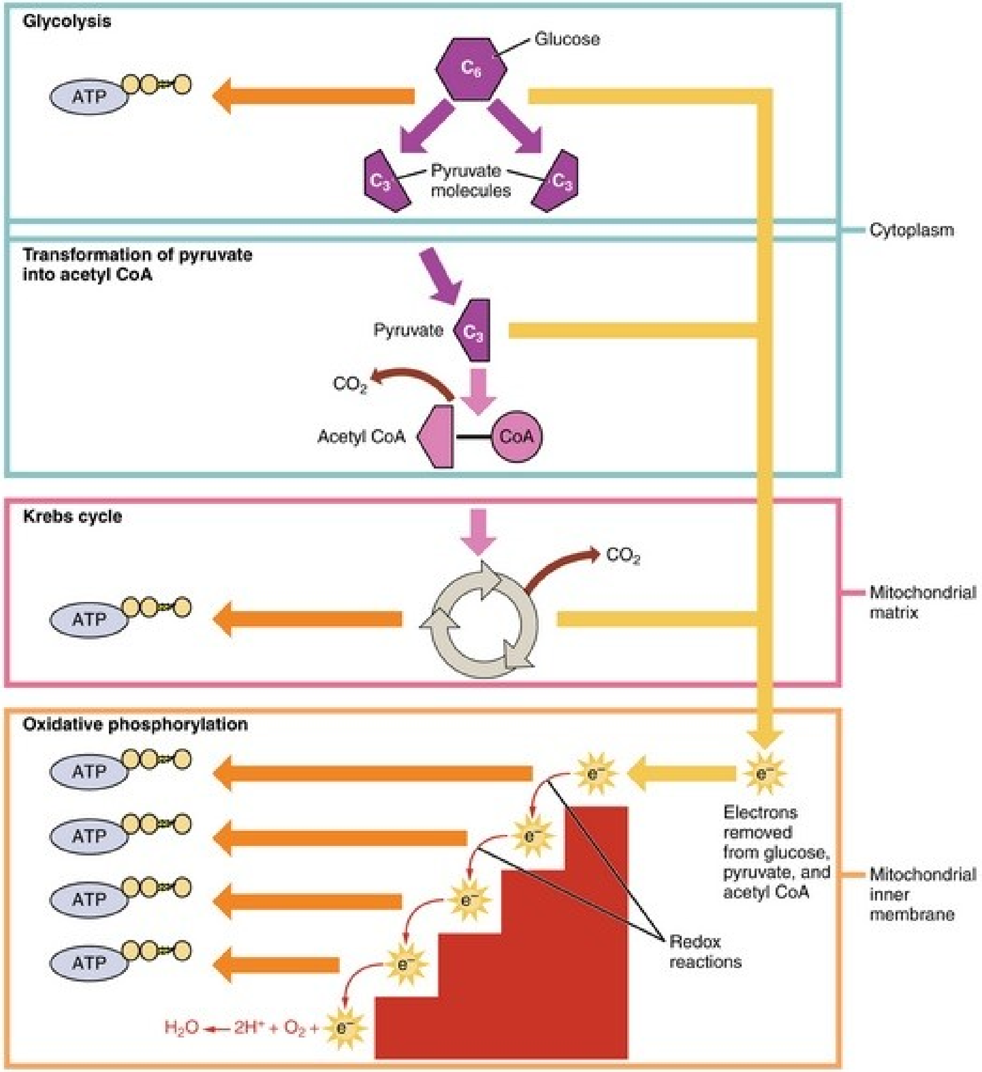
Major pathways involved in heterotrophy are Glycolisys, the Tri-Carboxylic Acid cycle (TCA cycle) and the Pentose Phophate pathway

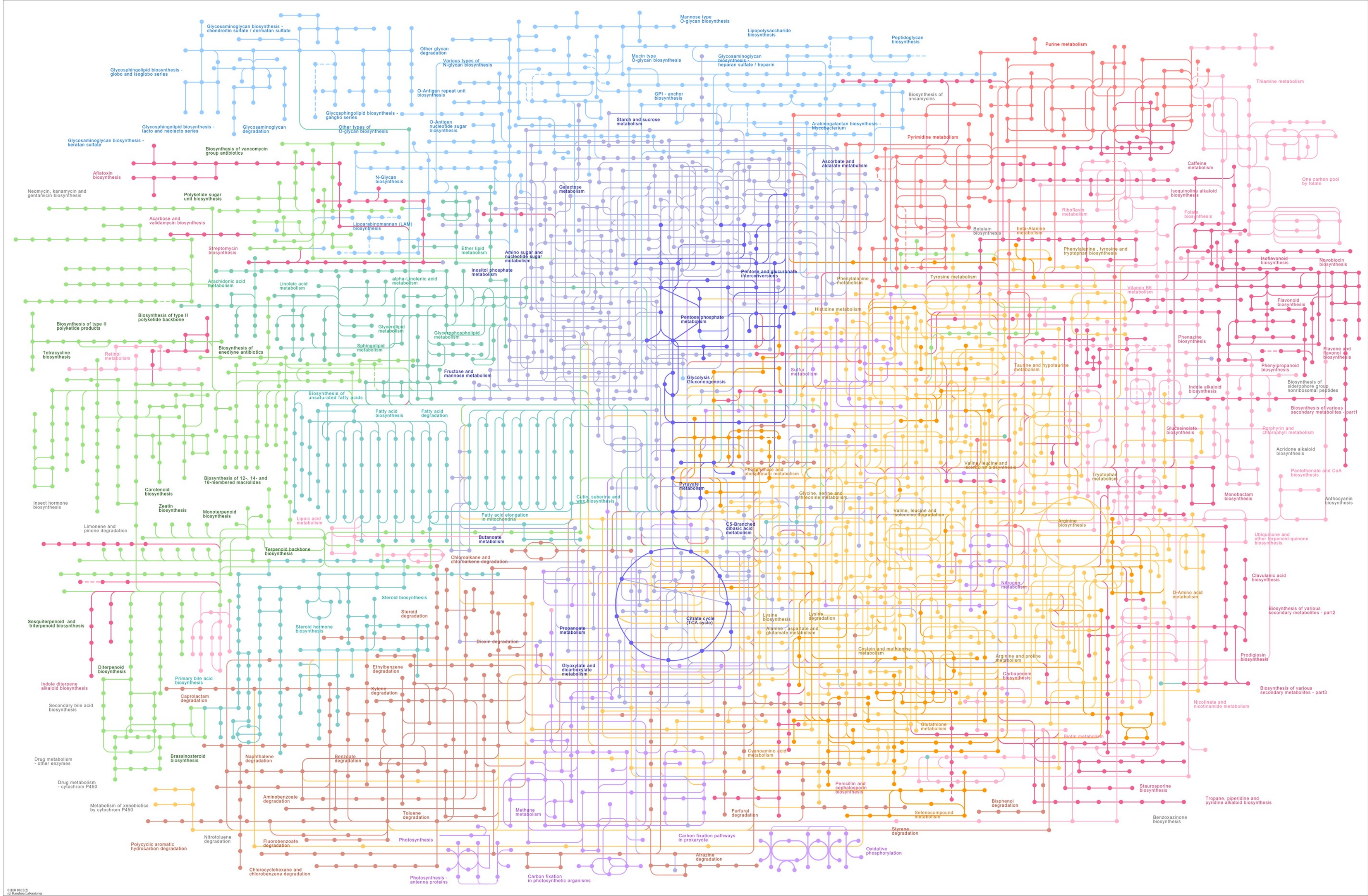
Can be coupled to aerobic or anaerobic respiration, with variable amounts of energy obtained

Aerobic chemorganoheterotrophy is a major sink of oxygen and responsible for a large fraction of organic carbon degradation globally

Many heterotrophic microorganisms have the "fermentation option"

Cellular Respiration





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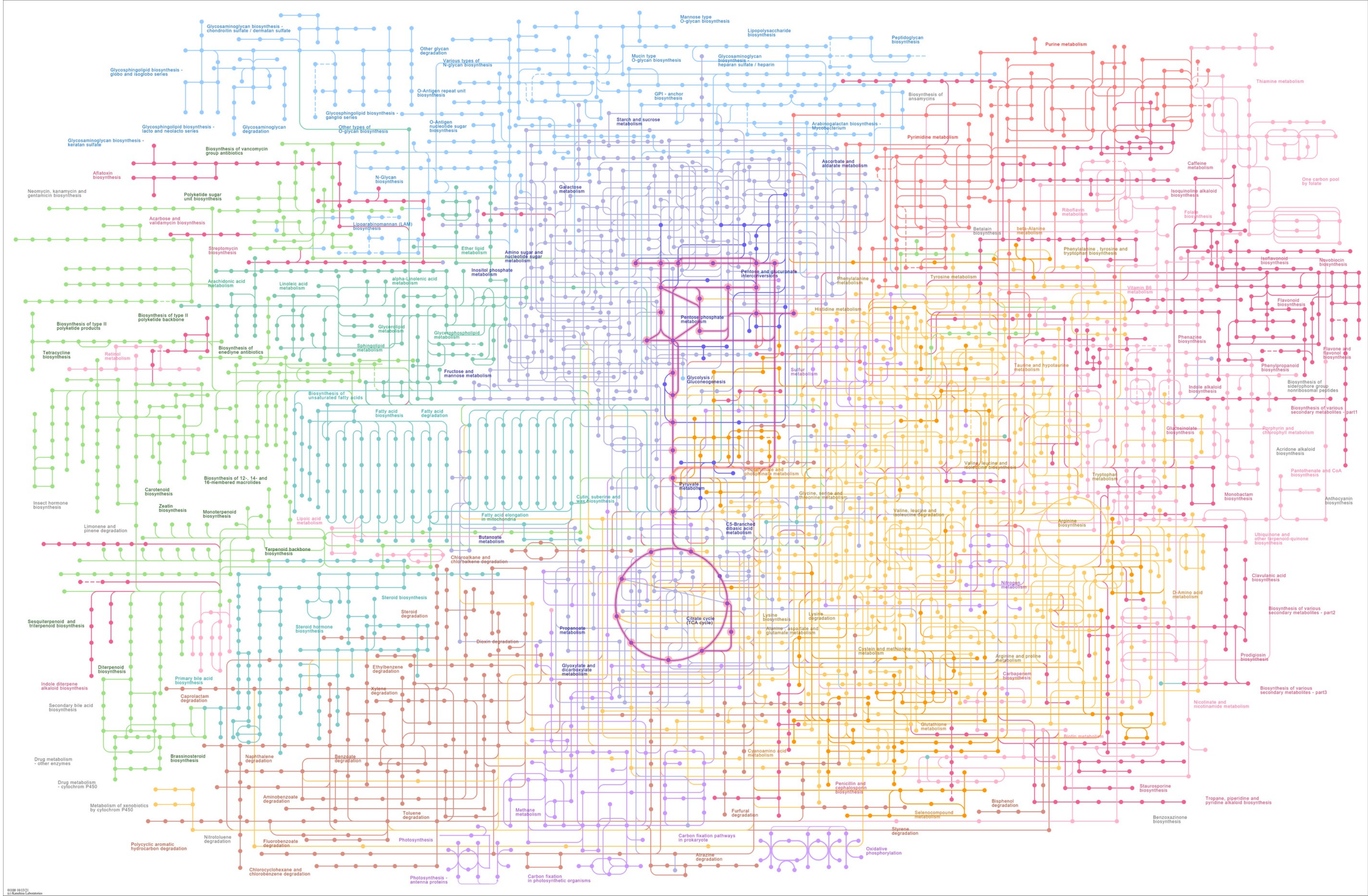
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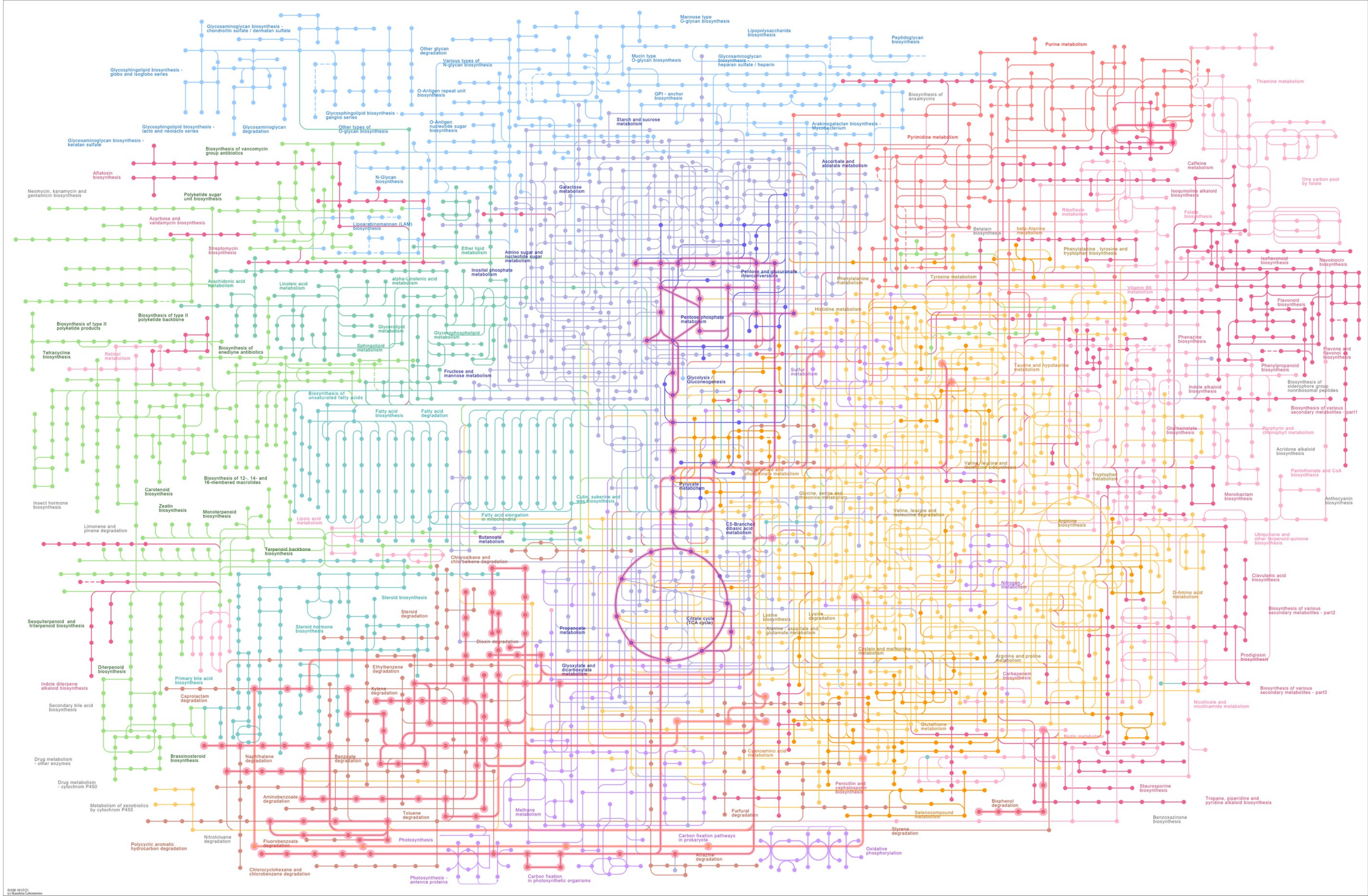

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Glycolysis and alternatives

Glycolysis (Embden–Meyerhof–Parnas pathway) is well known in mitochondria, and represents one of several pathways by which bacteria can catabolically attack glucose, converts glucose, into pyruvate

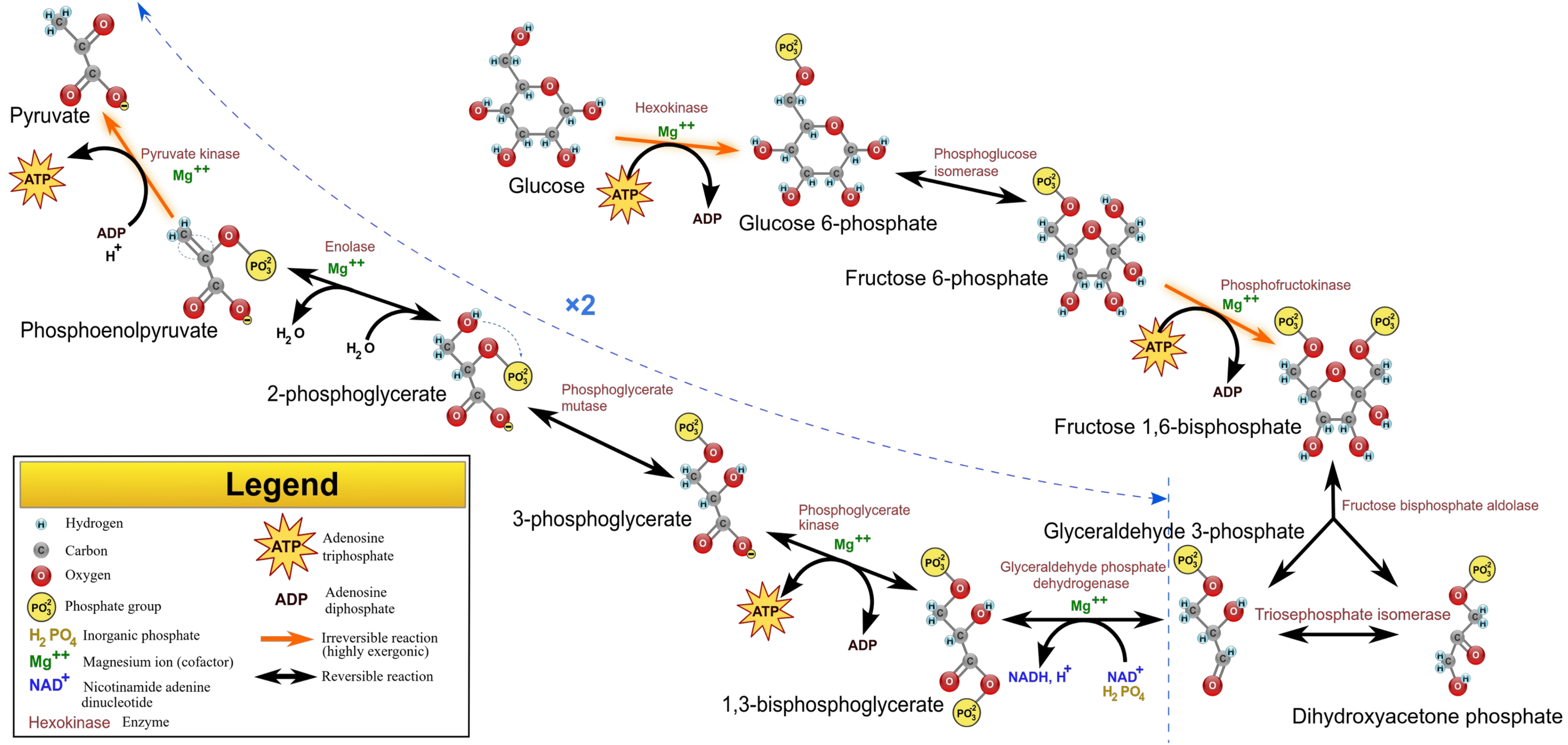
The free energy released in this process is used to form the high-energy compounds ATP (adenosine triphosphate) and NADH (reduced nicotinamide adenine dinucleotide). Most bacteria use glycolysis and the pentose phosphate pathway. One of the key enzyme to distinguish the variants is phosphofructokinase-1

Its reductive (anabolic) counterpart is called Gluconeogenesis

The Entner–Doudoroff pathway is an alternative pathway of glucose assimilation to glycolysis found especially in Archaea. Distinct features of the Entner–Doudoroff pathway are that it occurs only in prokaryotes and it uses 6-phosphogluconate dehydratase and 2-keto-3-deoxyphosphogluconate aldolase to create pyruvate from glucose.

Glycolysis yields 2 ATP and 2 NADH per glucose. The Entner–Doudoroff pathway yields 1 ATP and 1 NADH and 1 NADPH per glucose

Glycolysis


Pyruvate
Pyruvate kinase
Mg++
ATP
ADP
H+
Phosphoenolpyruvate
Enolase
Mg++
H2O
H2O
2-phosphoglycerate
×2
Phosphoglycerate mutase
3-phosphoglycerate
Glucose
Hexokinase
Mg++
ATP
ADP
Glucose 6-phosphate
Phosphoglucose isomerase
Fructose 6-phosphate
Phosphofructokinase
Mg++
ATP
ADP
Fructose 1,6-bisphosphate
Fructose bisphosphate aldolase
Glyceraldehyde 3-phosphate
Triosephosphate isomerase
Dihydroxyacetone phosphate
Glyceraldehyde phosphate dehydrogenase
Mg++
NADH, H+
NAD+
H2PO4
Phosphoglycerate kinase
Mg++
ATP
ADP
1,3-bisphosphoglycerate
Legend
Hydrogen
Carbon
Oxygen
Phosphate group
H2PO4 Inorganic phosphate
Mg++ Magnesium ion (cofactor)
NAD+ Nicotinamide adenine dinucleotide
Hexokinase Enzyme
ATP Adenosine triphosphate
ADP Adenosine diphosphate
Irreversible reaction (highly exergonic)
Reversible reaction

Krebbs Cycle

The Krebs cycle (Tri-Carboxylic Acid cycle, Citric Acid Cycle) is a series of chemical reactions used by all aerobic organisms to generate energy through the oxidization of acetate into carbon dioxide.

Intermediates can enter from the degradation of several different carbon sources

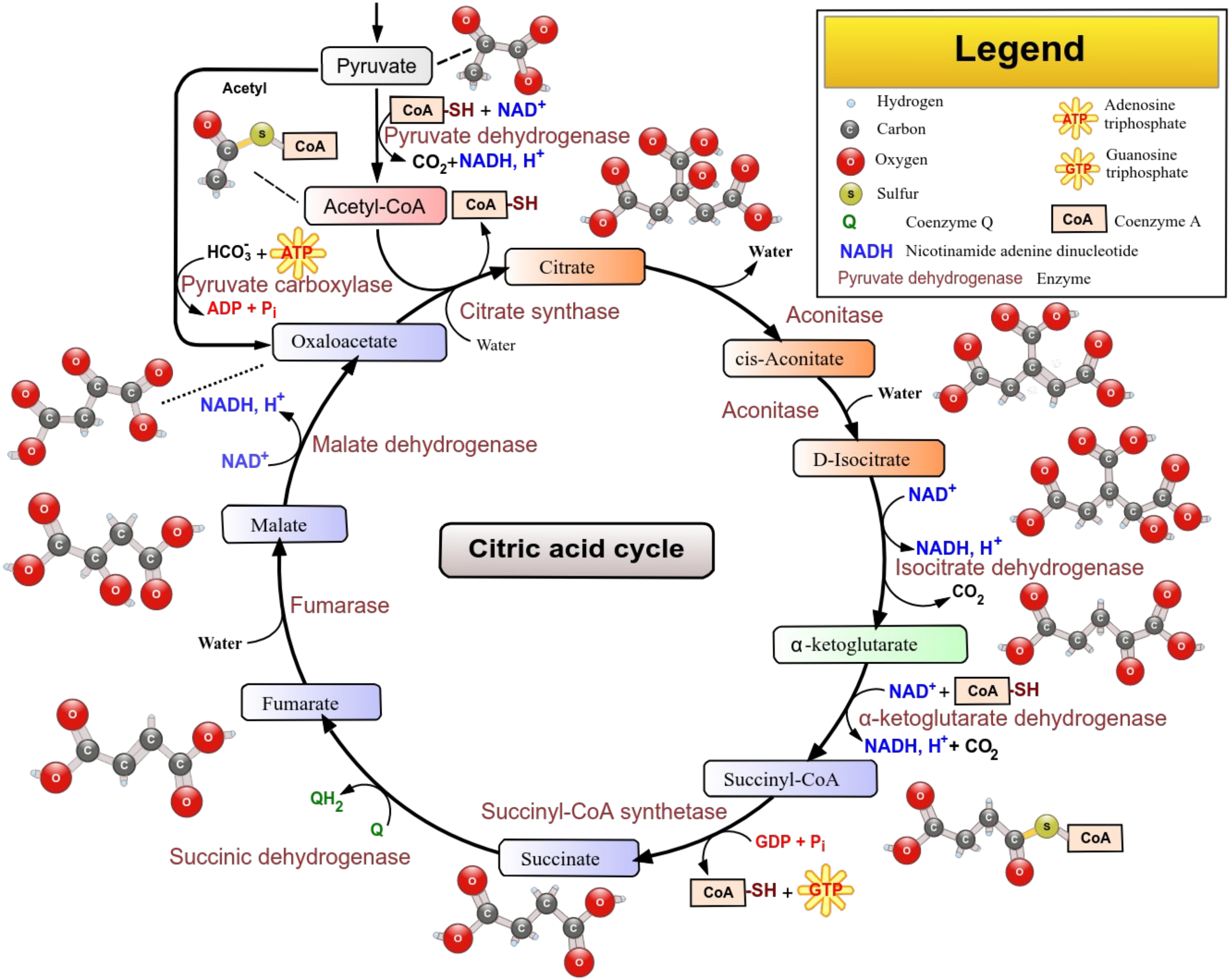
While the TCA cycle is present in most heterotrophs, portions have been identified in various other type of microorganisms (incomplete TCA cycles, variants, etc...)

Its reductive (anabolic) counterpart is called rTCA cycle (Arnon-Buchanan cycle)

The pathway is central to the catabolic and anaboilic metabolism of most organisms, and it is believed to have originated very early during evolution

The eight steps of the cycle are a series of redox, dehydration, hydration, and decarboxylation reactions that produce two carbon dioxide molecules, one GTP/ATP, and reduced forms of NADH and FADH2 per Actetyl-CoA

Krebbs Cycle



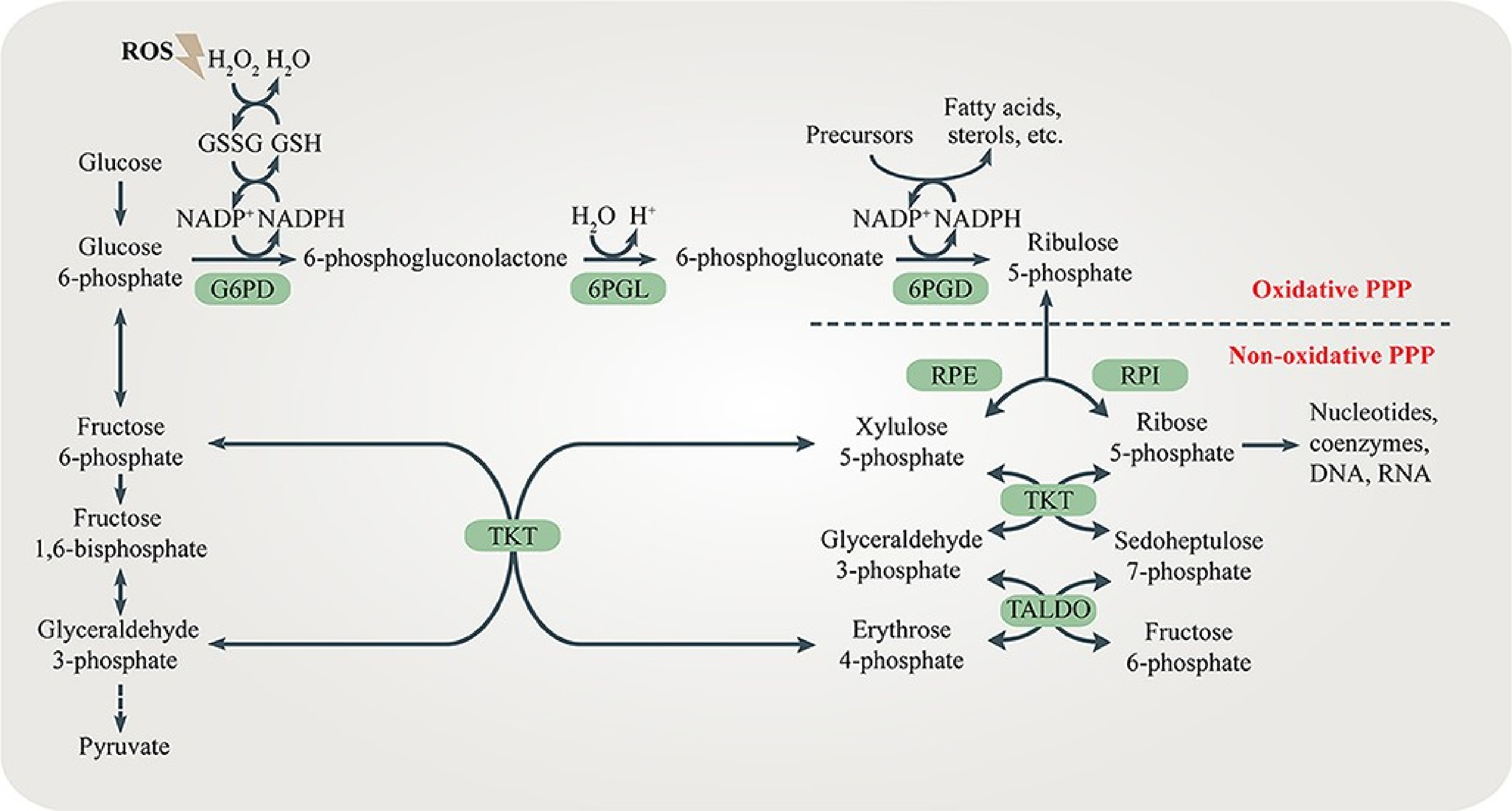
Phentose Phosphate pathway

The pentose phosphate pathway (PPP, aka hexose monophosphate shunt, HMP Shunt) is a metabolic pathway parallel to glycolysis with important role in replenishing intermediates for anabolic reactions

It is divided in two branches, oxidative and non-oxidative, which might not be present in every organisms. The oxidative PPP is widespread in Bacteria and Eukarya, and alternative to the pathway have been reported in Archaea, and a a complete non-oxidative PPP appears to be rare

Glucose flux through the oxidative branch produces NADPH. The non-oxidative branch generates the five-carbon sugar Ribose-5P (R-5P) that can be redirected to glycolytic intermediates such as glyceraldehyde 3P (GA-3P) and Fructose-6P (F-6P)

Phentose Phosphate pathway



Assimilating one carbon (C1) compounds

Several pathway for assimilating one carbon (C1) compounds (methane, methanol, formate, formaldehyde, etc...) have been described, and all go through he key intermediate formaldehyde

Ribulose monophate (RuMP) pathway *(present in methanotrophs), begins with 3 molecules of ribulose-5-phosphate condensed with 3 formaldehyde molecules to make 3 molecules of 3-hexulose 6-phosphate, of which 1 is used for biomass*

Serine cycle *uses carboxylic acids and amino acids as intermediates instead of carbohydrates. 2 molecules of formaldehyde are added to 2 molecules of the amino acid glycine, producing serine, converted to 2-phosphoglycerate. The regeneration of glycine requires a molecule of CO2, making the Serine pathway anaplerotic as well*

Dihydroxyacteone *(DHA) cycle is found exclusively in yeast.This pathway assimilates three molecules of formaldehyde into 1 molecule of DHAP using 3 molecules of xylulose 5-phosphate as the key intermediate*

Methylotroph *are also C1 oxidizers capable of using methanol suing some of the above pathways*

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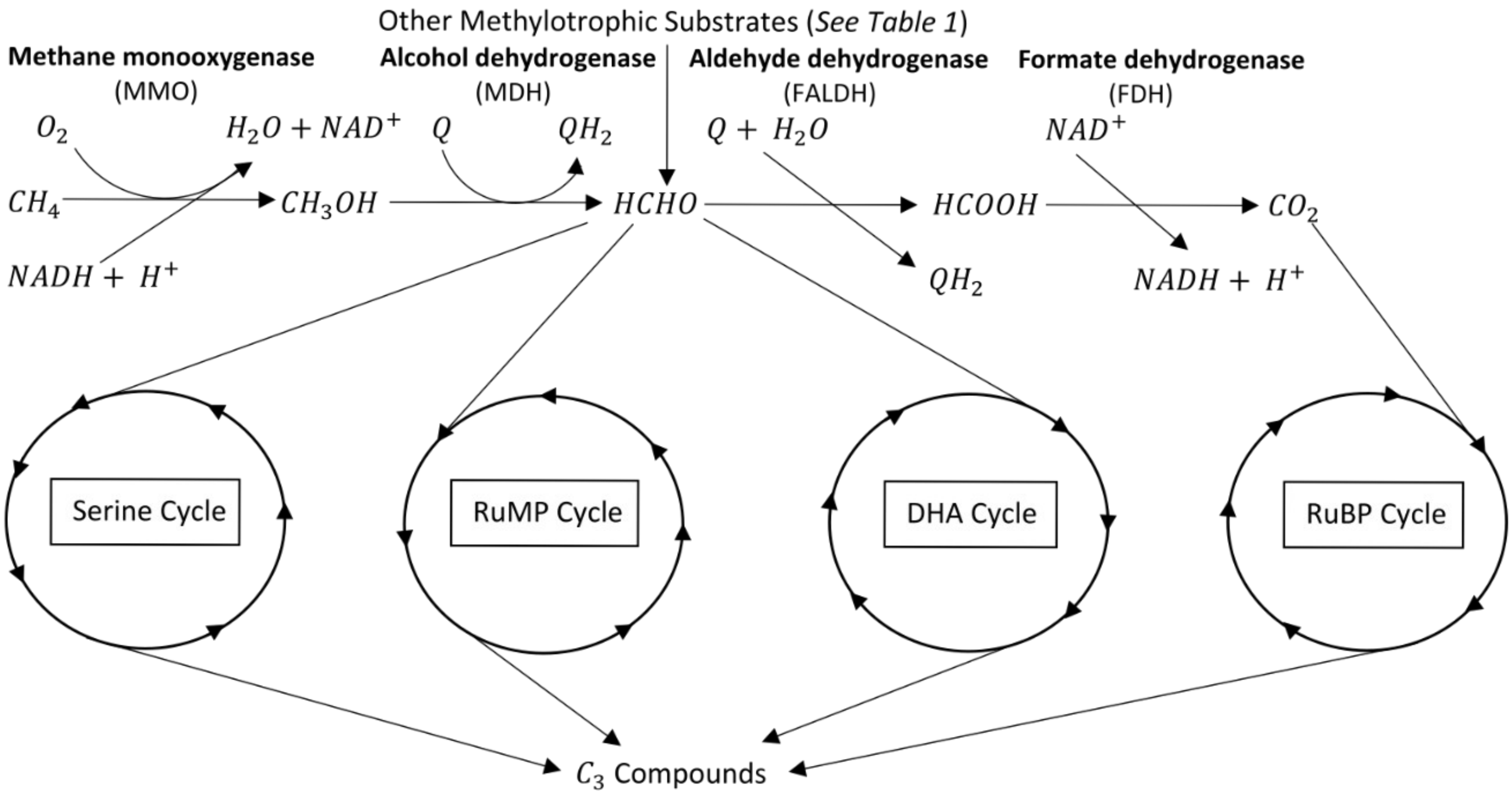


General steps of methylotrophic metabolism. Methane monooxygenase (MMO), Formate dehydrogenase (FDH), Methanol dehydrogenase (MDH) and Formaldehyde dehydrogenase (FALDH)

Compounds known to support methylotrophic metabolism[7][8][9][10][11]

Single Carbon Compounds	Chemical Formula	Multi-Carbon Compounds	Chemical Formula
Carbon monoxide	CO	Dimethyl ether	$(CH_3)_2O$
Formaldehyde	CH_2O	Dimethylamine	$(CH_3)_2NH$
Formamide	$HCONH_2$	Dimethyl sulfide	$(CH_3)_2S$
Formic acid	$HCOOH$	Tetramethylammonium	$(CH_3)_4N^+$
Methane	CH_4	Trimethylamine	$(CH_3)_3N$
Methanol	CH_3OH	Trimethylamine *N*-oxide	$(CH_3)_3NO$
Methylamine	CH_3NH_2	Trimethylsuphonium	$(CH_3)_3S^+$
Methyl halide	CH_3X		

C1 metabolism: Methane Oxidation

Methane oxidation is a special case of methylotrophy. Can be either aerobic (AMO) or anaerobic (AOM). It is a major global sink of methane, a strong greenhouse gas

Aerobic Methane Oxidizers generally work alone in oxidizing methane, while ANME generally require a bacterial partner to carry out ANaerobic Methane Oxidation

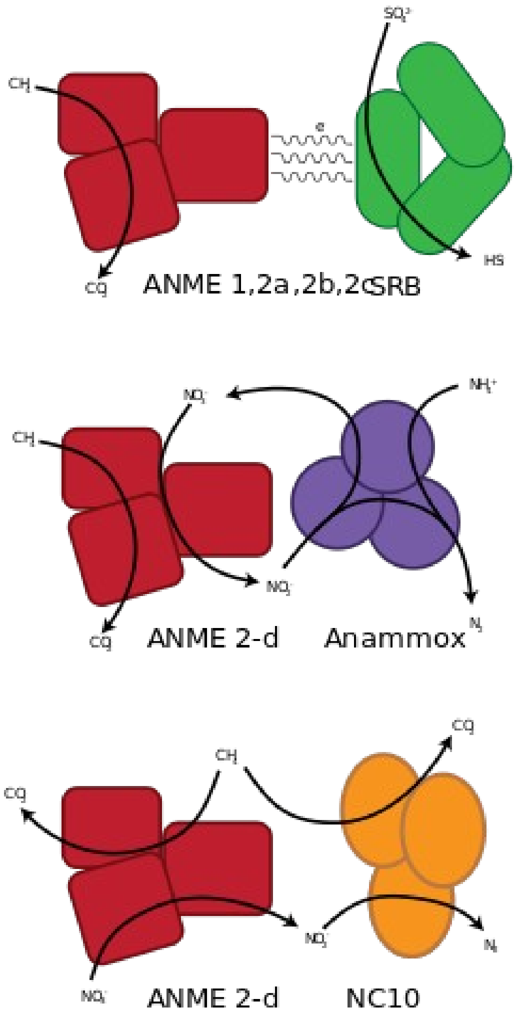
Diverse members of the Bacteria carry out the AMO (Proteobacteria, Verrucomicrobia) while AOM is carried out by a polyphyletic ogroup f Archaea (ANME group) and Bacteria (NC10 candidate division)

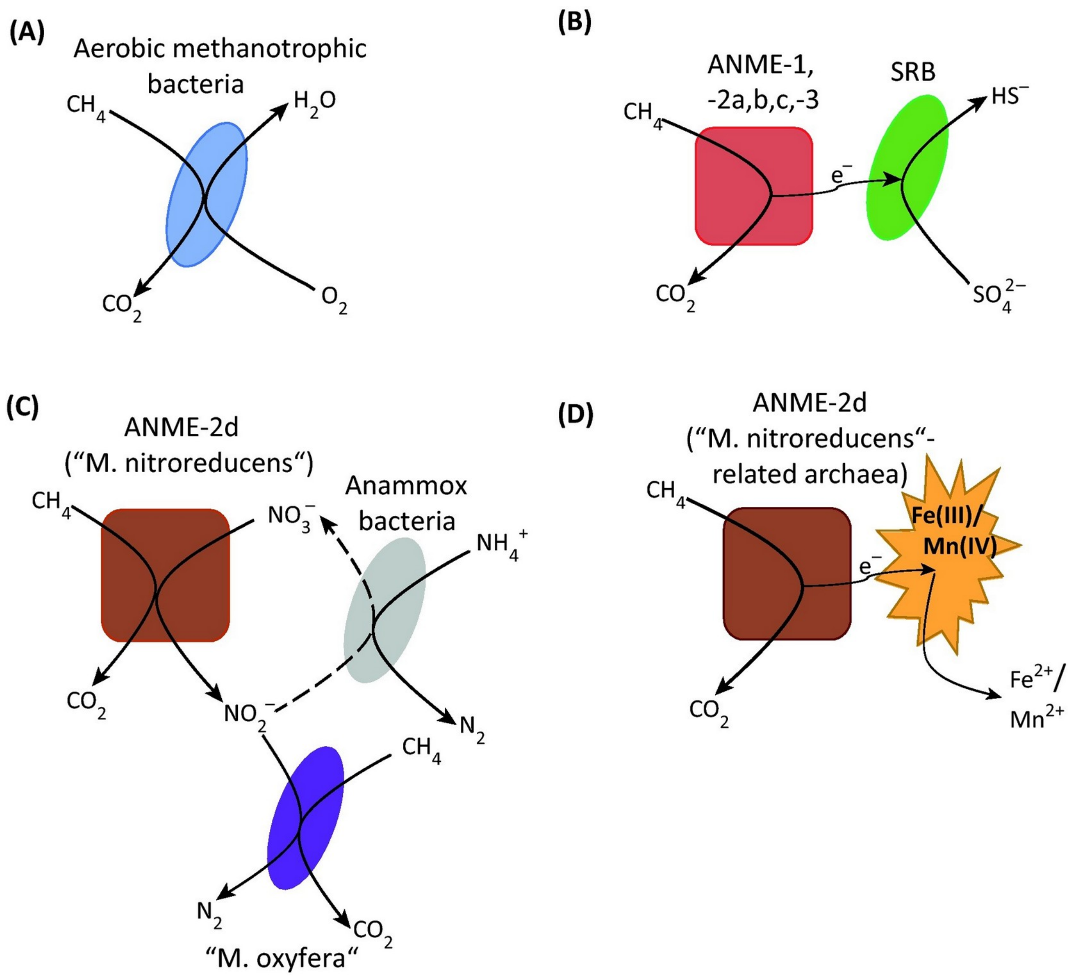
Aerobic Methane Oxidizers oxidize methane by first initiating reduction of an oxygen atom to H2O2 and transformation of methane to Methanol using methane monooxygenases (MMOs)

AOM happens in anoxic sediments, and it has been reported in worldwide sediments. AOM is driven by the yet uncultured anaerobic methanotrophic archaea group (ANME), usually syntrophically coupled to sulfate-reducing bacteria (SRB)

Recently (2010!!!) a new intra-aerobic metabolism has been discovered, coupling anaerobic methane oxidation to nitrate reduction (n-damo)

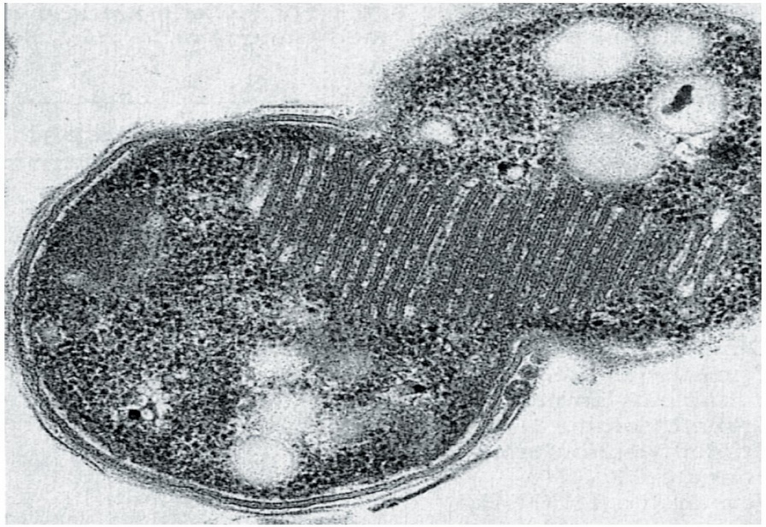
Methane Oxidation





Trends in Microbiology

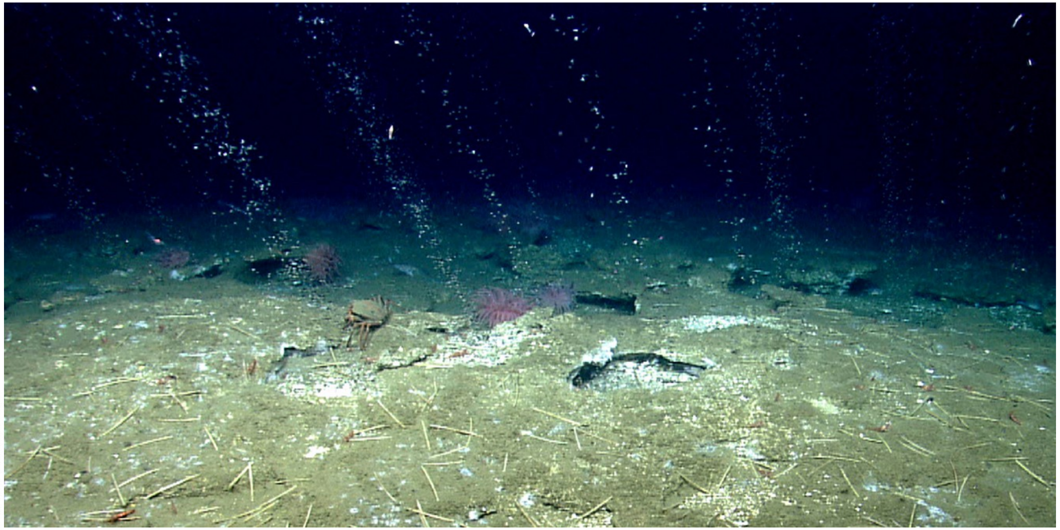
Aerobic Oxidation of Methane



D.W. Ribbons

Figure 12-15b Brock Biology of Microorganisms 11/e

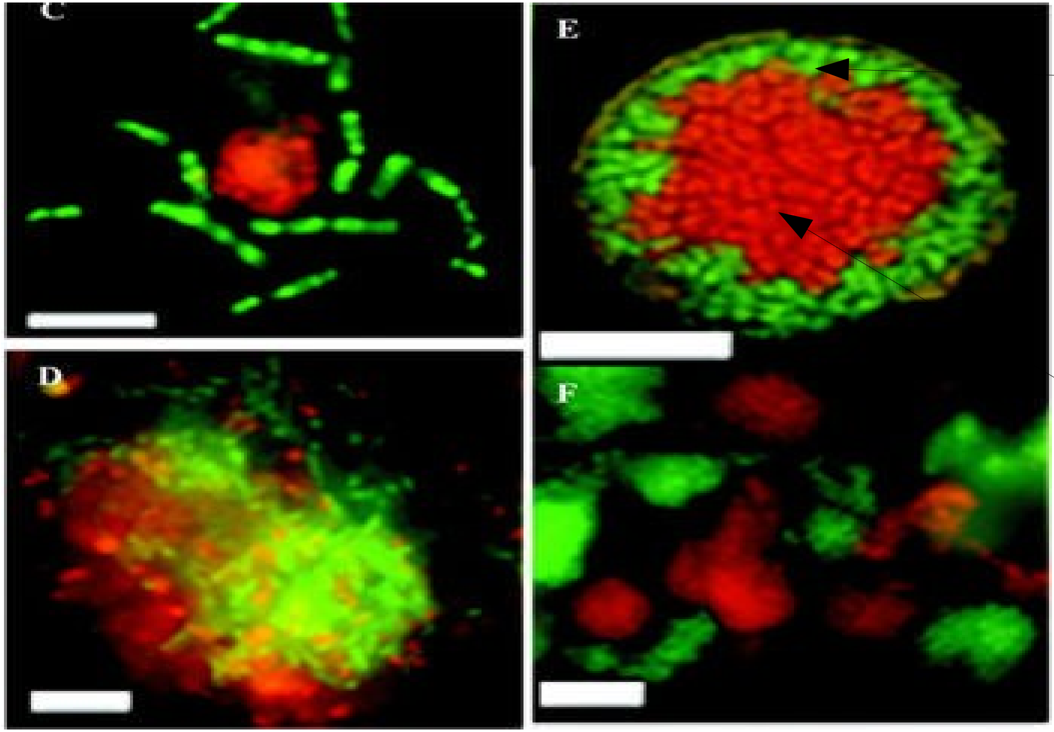
Note stacked membranes



Cold seeps: bubbling methane

$$CH_4 + 2O_2 = CO_2 + 2H_2O$$

Anaerobic Methane Oxidation: ANME1+SRB



ANME-1

Desulfosarcina spp.
SBR Bacteria

$$CH_4 + 2SO_2 = HCO_3^- + 2HS^- + H_2O$$

Assimilation of complex organics, aliphatics and aromatics

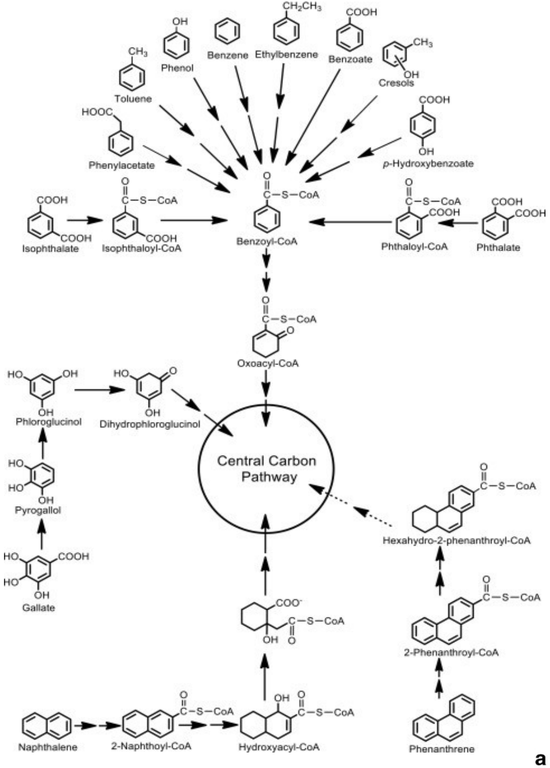
Prokaryotes are capable of assimilation a large number of organic compound for their metabolism, including the use of aliphatics and aromatics of different kinds

Common substrates used are Benzene, Toluene, Ethylbenzne, Xylene, Phenol, Poly-chlorobiphenyls, alknanes, alkenes and aromatics of different complexities

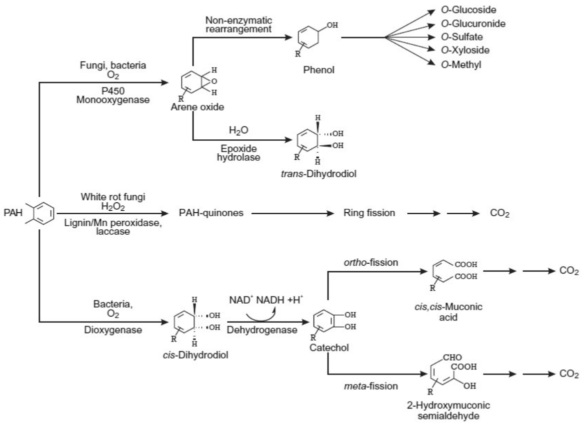
Some microorganisms are know to be completely dependent on those compounds. For example the Obligate Hydrocarbonoclastic Bacteria Alcanivorax borkumensis

Several different pathways for organic degradation have been described, all feeding intermediates to the central metabolism

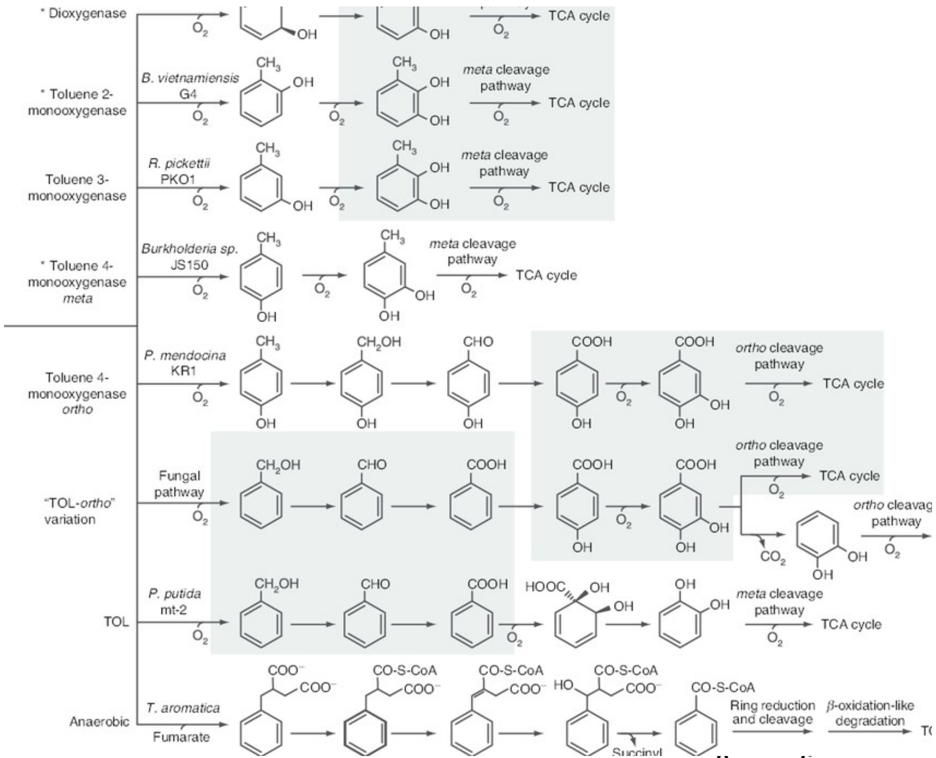
Degradation of these compounds can be coupled both to aerobic and anaerobic respiration



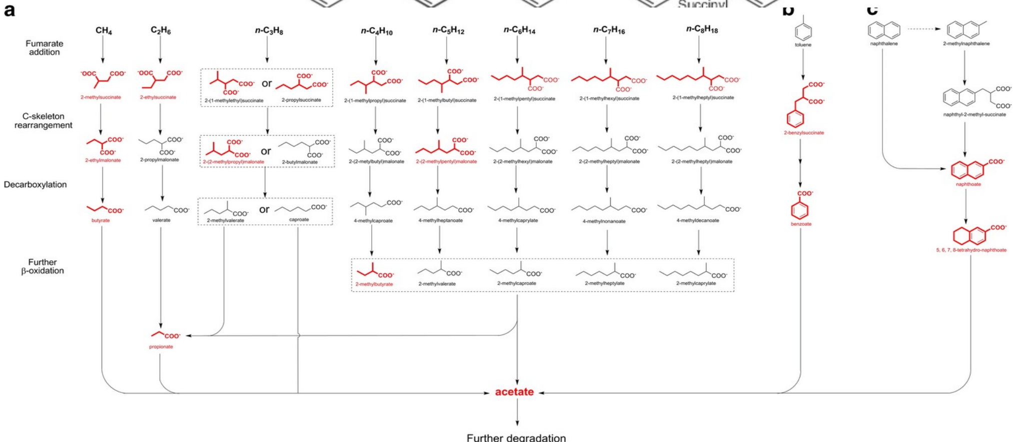
Toluene
Phenol
Benzene
Ethylbenzene
Benzoate
Cresols
Phenylacetate
p-Hydroxybenzoate
Isophthalate
Isophthaloyl-CoA
Benzoyl-CoA
Phthaloyl-CoA
Phthalate
Oxoacyl-CoA
Phloroglucinol
Dihydrophloroglucinol
Pyrogallol
Gallate
Central Carbon Pathway
Hexahydro-2-phenanthroyl-CoA
2-Phenanthroyl-CoA
Naphthalene
2-Naphthoyl-CoA
Hydroxyacyl-CoA
Phenanthrene



Non-enzymatic rearrangement
Phenol
O-Glucoside
O-Glucuronide
O-Sulfate
O-Xyloside
O-Methyl
Fungi, bacteria
P450 Monooxygenase
Arene oxide
Epoxide hydrolase
trans-Dihydrodiol
PAH
White rot fungi
Lignin/Mn peroxidase, laccase
PAH-quinones
Ring fission
ortho-fission
cis,cis-Muconic acid
Bacteria,
Dioxygenase
cis-Dihydrodiol
Dehydrogenase
Catechol
meta-fission
2-Hydroxymuconic semialdehyde



* Dioxygenase
TCA cycle
B. vietnamiensis G4
* Toluene 2-monooxygenase
meta cleavage pathway
R. pickettii PKO1
Toluene 3-monooxygenase
Burkholderia sp. JS150
* Toluene 4-monooxygenase meta
P. mendocina KR1
Toluene 4-monooxygenase ortho
ortho cleavage pathway
Fungal pathway
"TOL-ortho" variation
P. putida mt-2
TOL
T. aromatica
Anaerobic
Fumarate
Ring reduction and cleavage
β-oxidation-like degradation



a
b
c
Fumarate addition
C-skeleton rearrangement
Decarboxylation
Further β-oxidation
acetate
Further degradation

Fermentation

Fermentation is a major metabolism in absence of inorganic electron acceptors. Fermenting organisms can be obligate or facultative

In fermentation redox balance is achieved by having the substrate serve as both electron donor and electron acceptor and that ATP is synthesized by substrate-level phosphorylation. PMF is not involved

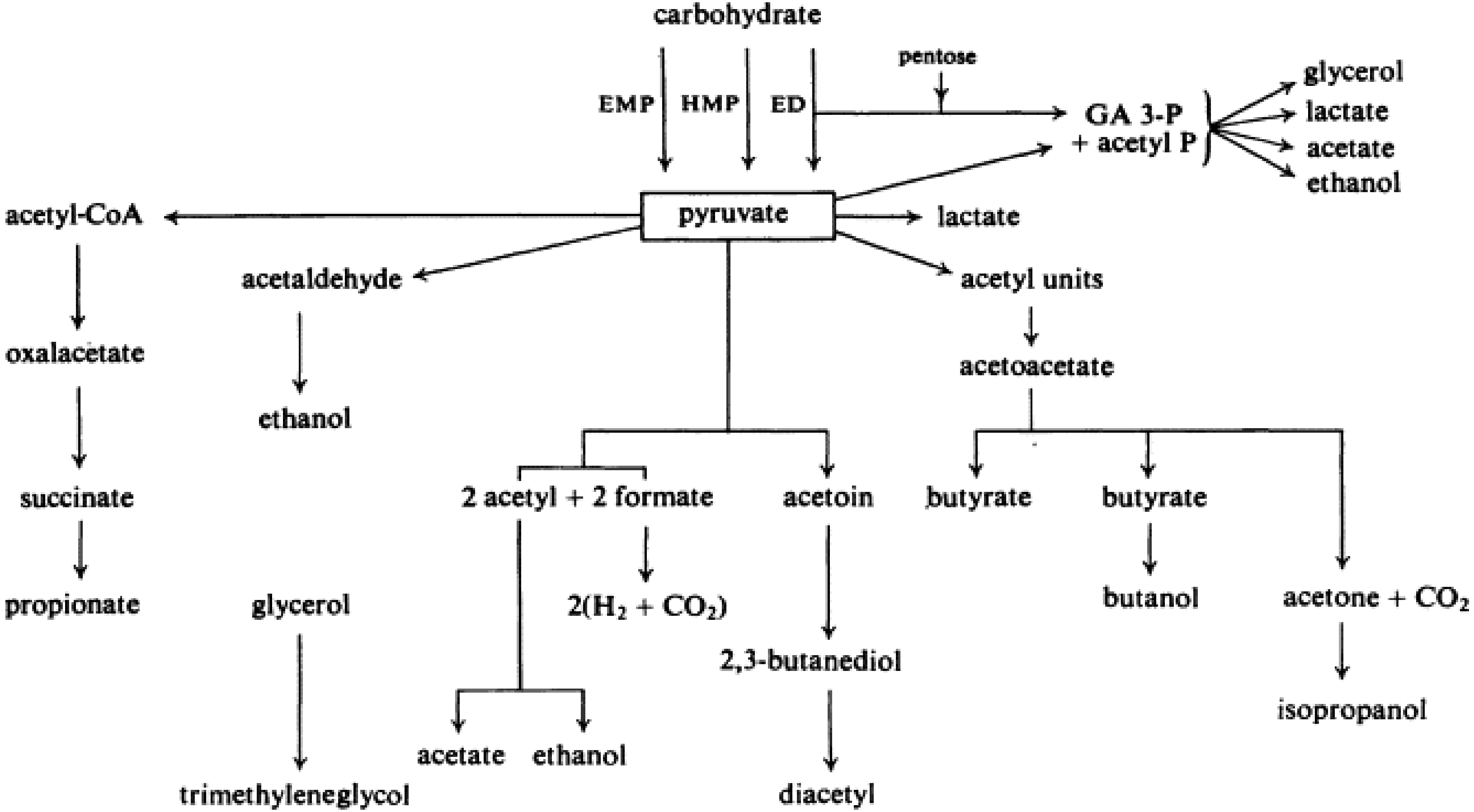
Energy obtained from fermentation are generally more than 1 order of magnitude less than with respiration

Redox balance is achieved in fermentations by the excretion from the cell of fermentation products, reduced substances such as acids or alcohols that are produced as end products of the catabolism of the original fermentable substance

Fermentations are classified by either the substrate fermented or the products formed. A diverse array of products can be produced. Hydrogen can be produced as well as by product

Fermentation is a major sink of organic carbon in electron acceptor depleted anaerobic environments

Fermentation



CO2 as terminal electron acceptor

CO_2, being the oxidized state of carbon, can be used as terminal electron acceptor. The reduction of CO_2 by H_2 to form methane or acetic acid is a form of anaerobic respiration in which CO_2 is the electron acceptor AND carbon source. Other organic electron donors are used by some groups

Methanogenesis is carried out by a strictly anaerobic group of Archaea. Recently (2021!) the possibility for aerobic methanogenesis has been described

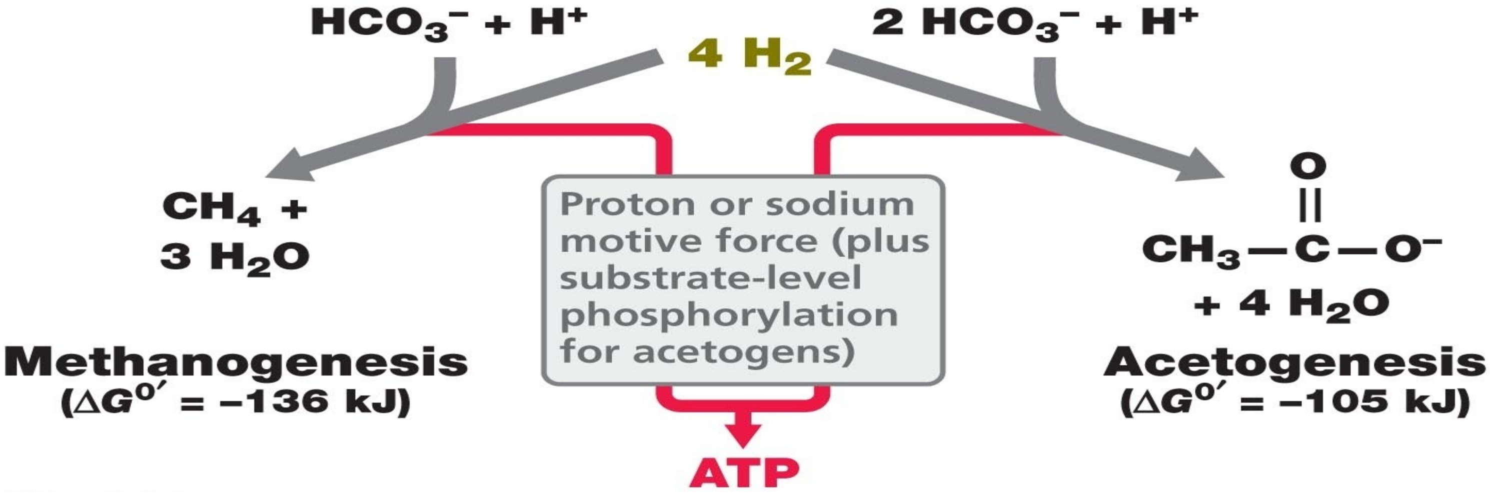
Acetogenesis is carried out prevalently by gram positive Bacteria (especially members of the genera Clostridium or Acetobacterium)

Energy conservation in acetogenesis results from both substrate-level phosphorylation and PMF

Methanogens play a big impact in roganic matter degradation and climate stability. The role of acetogens is less clear

The key enzyme fro methanogenesis is the Methyl coenzyme M reductase (McrA) gene

CO2 as TEA: Methanogens and Acetogens



CO as electron donor (and carbon source)

CO (Carbon monoxide) can be used by prokaryotes as both energy surce and cerbon source. Organisms using CO as energy source are known as Carboxydotrophs, such as Carboxydothermus hydrogenoformans

As carbon source, CO can be used by several microbes using the Wood-Ljungdahl pathway since CO is the activated product of one of the pathway key enzyme, the bifunctional codh/acs

As energy source, CO requires a number of related enzymes used for CO sensing and CO-respiration. CODH-I (energy conserving), CODH-II (energy conserving?), CODH-III (carbon fixation), CODH-IV (oxidative stress response) and CODH-V (unknown function)

In several environments, carboxydotrophy is dominated by the hydrogenogens, which are anaerobic, thermophilic bacteria or archaea that carry out CO oxidation using water as an electron acceptor and produce H2 as by product

Hydrogen Metabolism

Hydrogen in energy metabolism

Hydrogen is used in energy metabolism as electron donor (H2). These microorganisms are known as hydrogenotrophs or hydrogen oxidizing

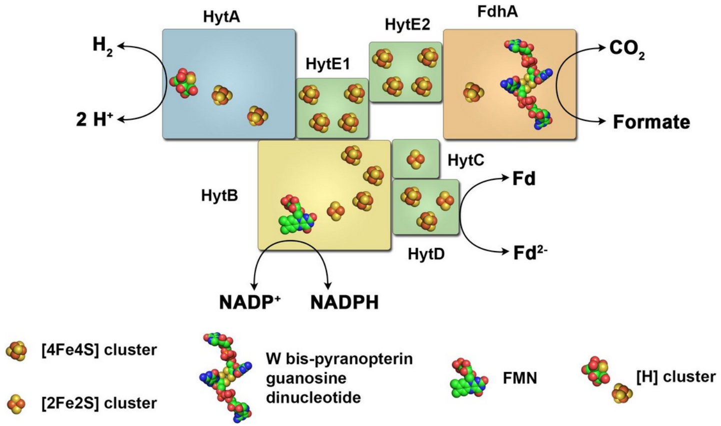
In a few metabolisms H2 is instead produced either using H2O as electron donor or organic substrates from which H2 is released (hydrogenogens)

Enzymes that use hydrogen are called Hydrogenases, and are generally multi subunit oxidorectutases that use either NiFe, FeFe or Fe as key metal center

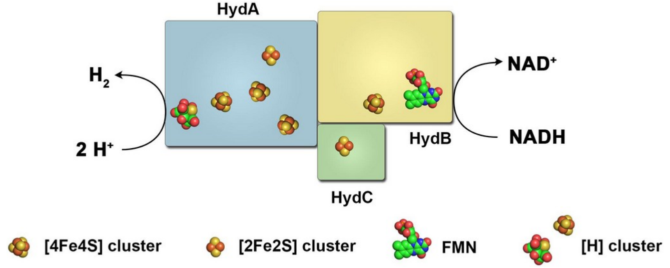
The diversity of Hydrogenases is enormous, and hydrogenotrophic microbes are phylogenetically different, and present in all three domain of life

Aerobic hydrogenotrophs are known as knallgas bacteria, and produce water as byproduct. Anaerobic chemolithotrophs couple the oxidation of hydrogen to a large number of acceptors

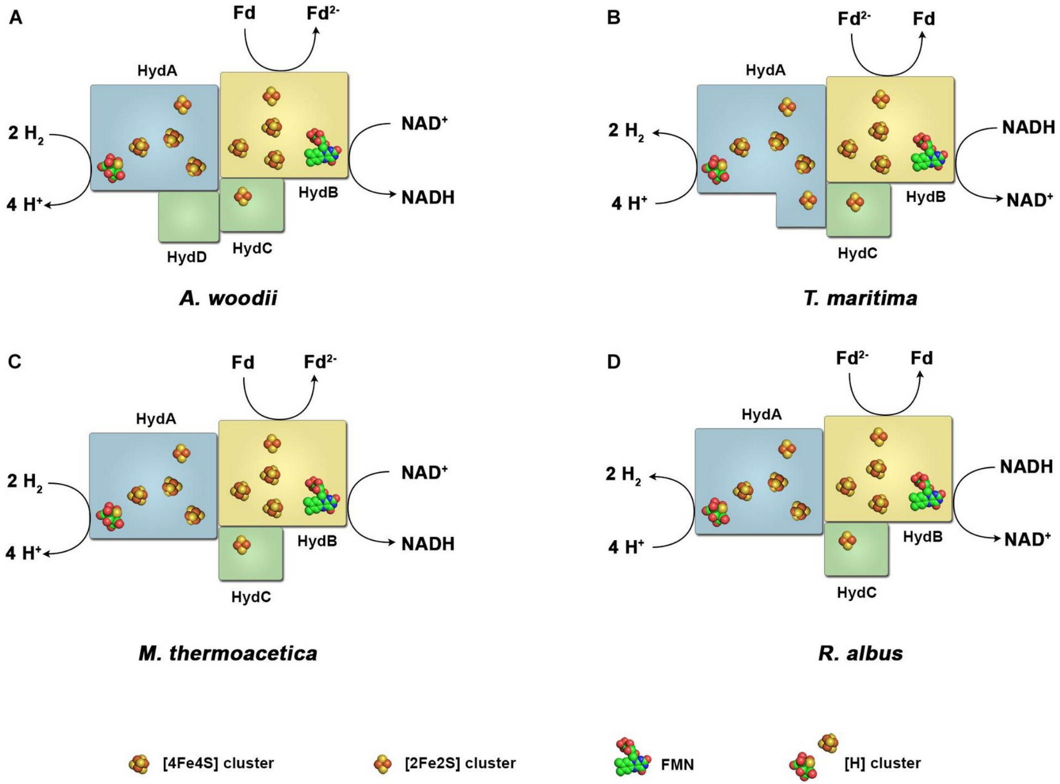
H2 is considered the energetic exchange currency among prokaryotes



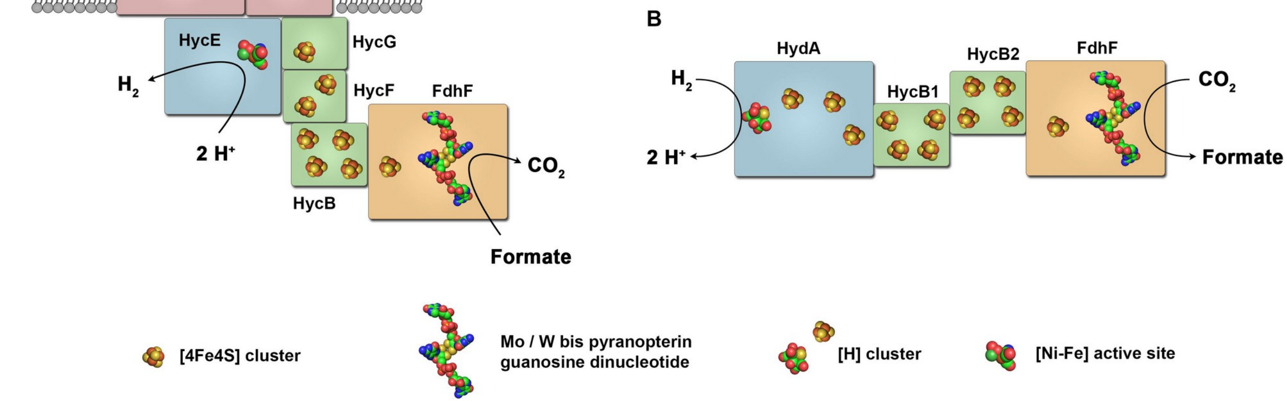
HytA
HytE2
FdhA
HytE1
H_2
$2 H^+$
CO_2
Formate
HytB
HytC
HytD
Fd
Fd^{2-}
$NADP^+$
NADPH
[4Fe4S] cluster
[2Fe2S] cluster
W bis-pyranopterin guanosine dinucleotide
FMN
[H] cluster



HydA
H_2
$2 H^+$
HydB
HydC
NAD^+
NADH
[4Fe4S] cluster
[2Fe2S] cluster
FMN
[H] cluster

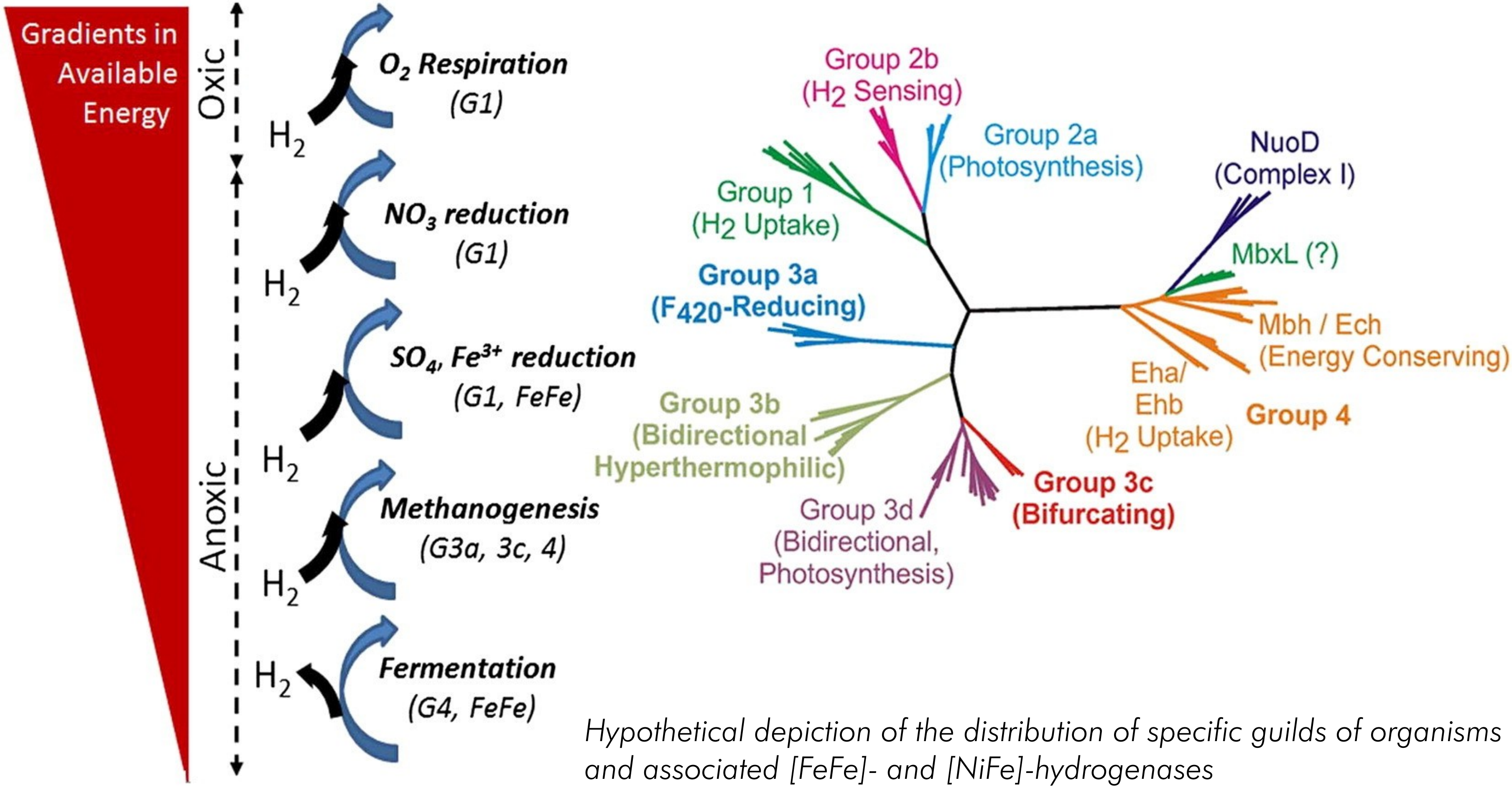


A
Fd
Fd^{2-}
HydA
$2 H_2$
$4 H^+$
NAD^+
NADH
HydB
HydC
HydD
A. woodii
B
Fd^{2-}
Fd
HydA
$2 H_2$
$4 H^+$
NADH
NAD^+
HydB
HydC
T. maritima
C
Fd
Fd^{2-}
HydA
$2 H_2$
$4 H^+$
NAD^+
NADH
HydB
HydC
M. thermoacetica
D
Fd^{2-}
Fd
HydA
$2 H_2$
$4 H^+$
NADH
NAD^+
HydB
HydC
R. albus
[4Fe4S] cluster
[2Fe2S] cluster
FMN
[H] cluster



A
HycD
HycC
HycE
HycG
HycF
FdhF
HycB
H_2
$2 H^+$
CO_2
Formate
B
HydA
HycB1
HycB2
FdhF
H_2
$2 H^+$
CO_2
Formate
[4Fe4S] cluster
Mo / W bis pyranopterin guanosine dinucleotide
[H] cluster
[Ni-Fe] active site

Hydrogenases diversity



Hypothetical depiction of the distribution of specific guilds of organisms and associated [FeFe]- and [NiFe]-hydrogenases

Hydrogen oxidation (aerobic)

Figure 12-14 Brock Biology of Microorganisms 11/e

Ralstonia eutropha

$H_2 + 1/2O_2 + H_2O$ $\Delta G^{0'} = -237kJ$

$6H_2 + 2O_2 + CO_2 + (CH_2O) + 5H_2O$

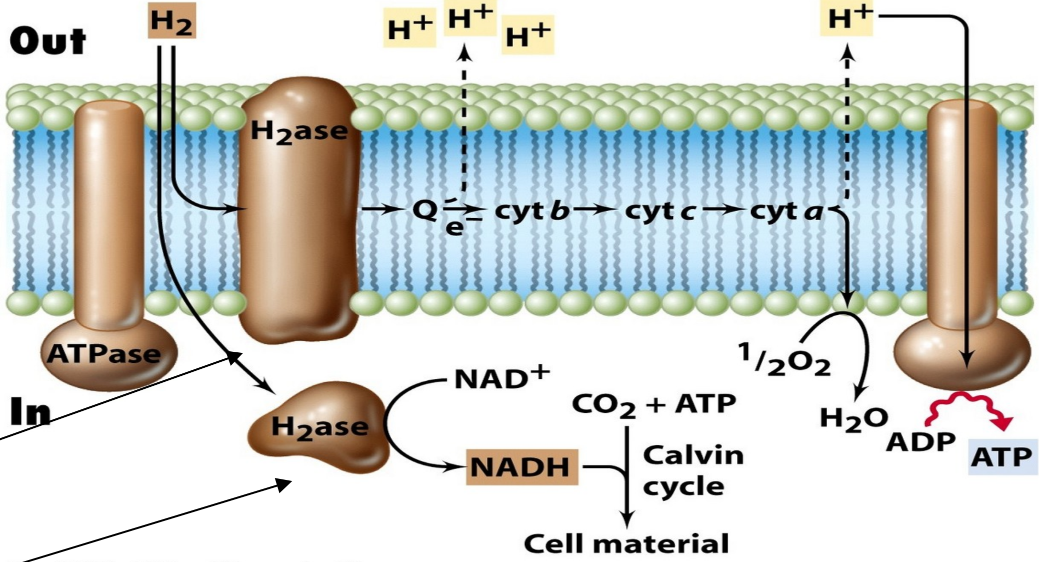


Figure 17-25 Brock Biology of Microorganisms 11/e

***Two hydrogenases** are present: the membrane-bound is involved in energetics (PMF), while the cytoplasmic (assimilatory) makes NADH for Carbon Fixation*

Nitrogen Metabolism

Nitrogen in energy metabolism

Nitrogen is widely used by prokaryotes as electron acceptor and energy source. Owing to its multi valence state, can be used in a complex series of reactions

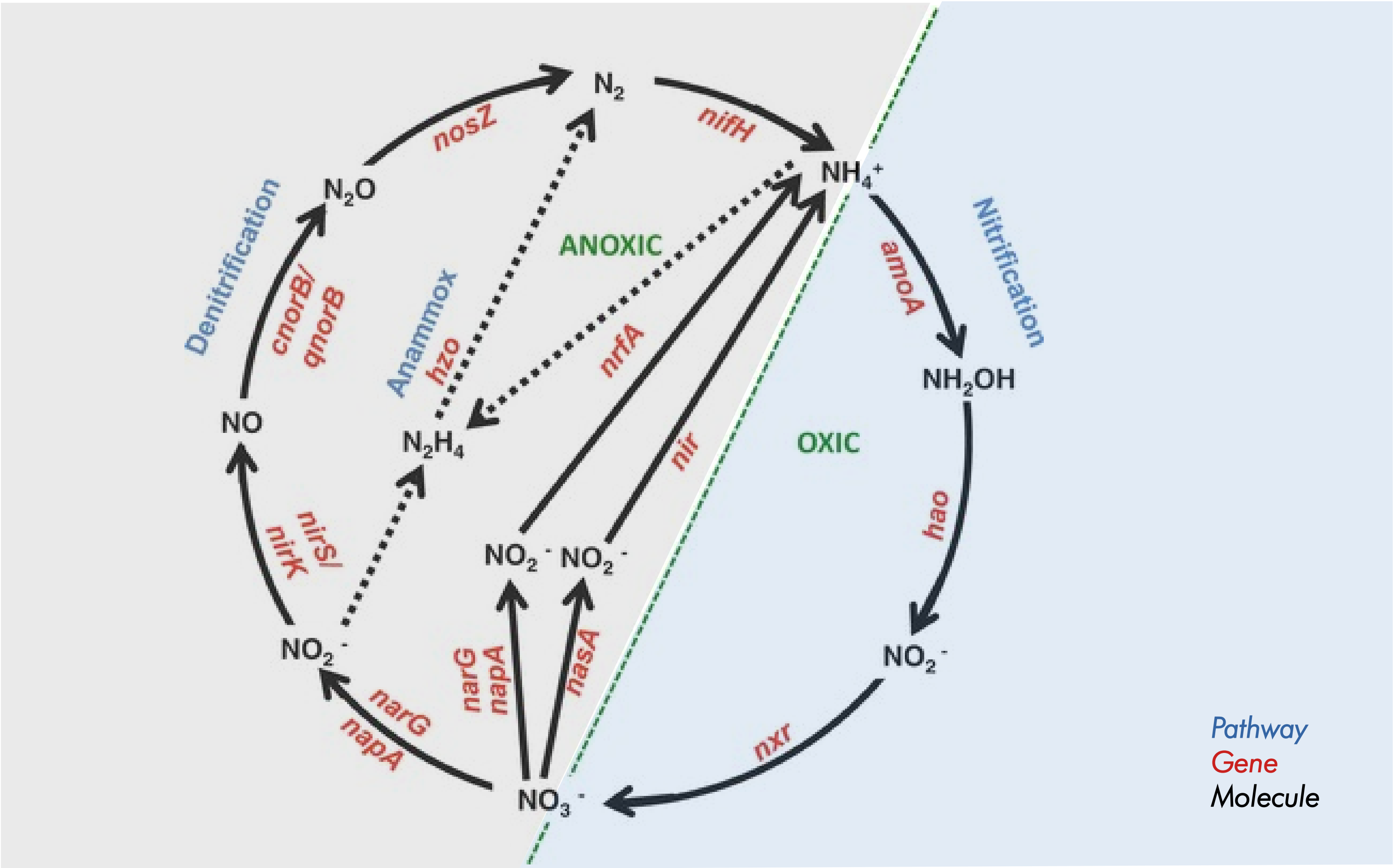
Oxidized nitrogen species, with NO3- being the chief molecule, dominate anaerobic respiration in many ecosystems and are responsible for the degradation of a significant portion of organic carbon

Of the possibly biological reactions with nitrogen, numerous abiotic reaction have rates that are too slow (or activation energies that are too high) to give any meaningful quantitative contribution

All this makes the nitrogen biogeochemical cycles being a biology dominated cycle, with strong anthropogenic influences

Energy reactions with nitrogen in prokaryotes often require multi-enzyme complexes and are highly modular

Nitrogen energy metabolism



Nitrogen Fixation

Nitrogen fixation, converting atmospheric N2 to ammonia, is a key process in the N cycle and fundamental to access the large pool of atm N otherwise unavailable for anabolism

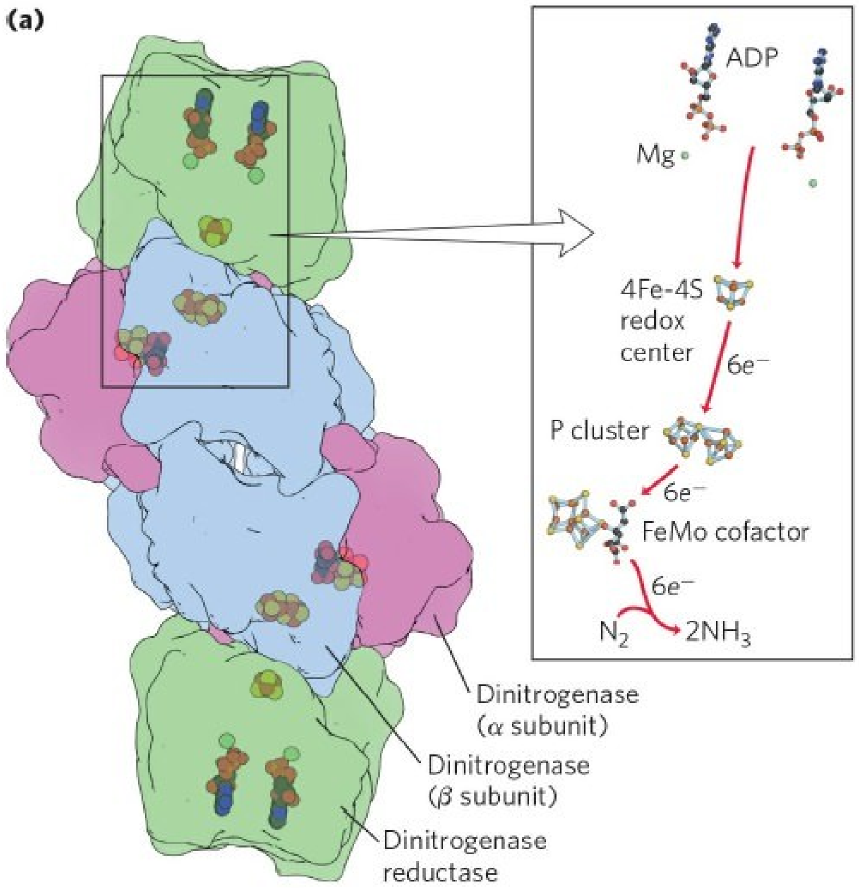
Only certain prokaryotes can fix nitrogen, called diazotrophs. Some nitrogen fixers are free living and others are symbiotic. They are widely distributed in the Tree of Life

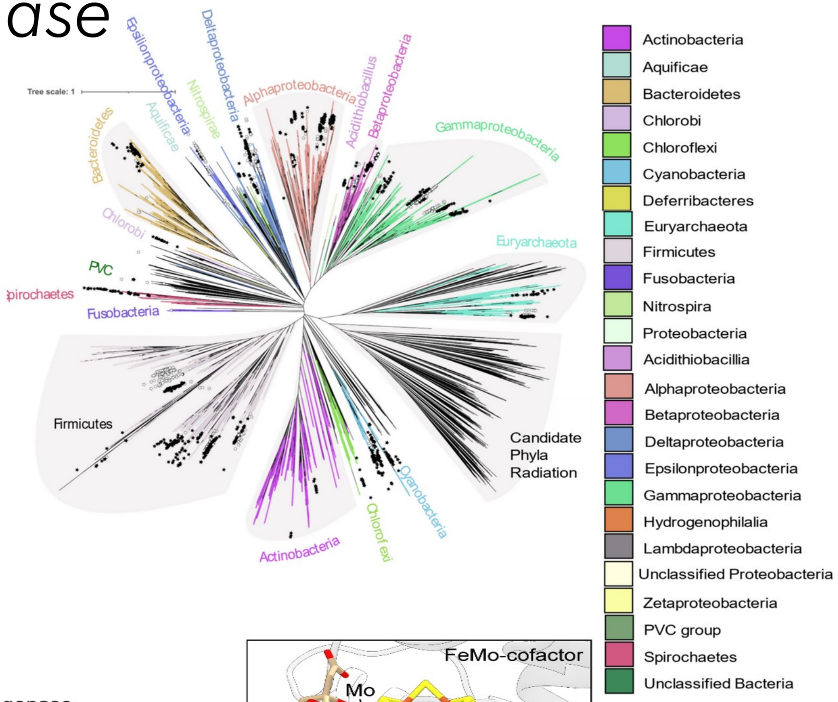
Breaking down the N2 triple bond is highly energy demanding (8e$^-$ and 21-25 ATPs)

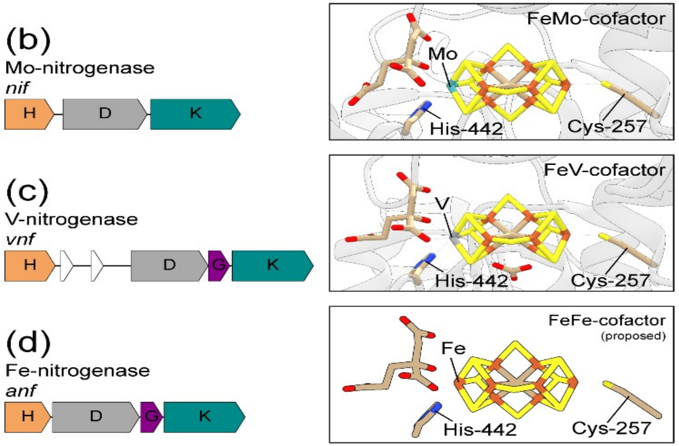
Reaction is catalyzed by nitrogenase (Nif), sensitive to the presence of oxygen, and buffer proteins (like Leghemoglobin) are used to buffer oxygen in the cell. A wide variety of nitrogenases use different metal cofactors (MoFe, V, and FeS)

Nitrogenases are promiscuos enzymes. They catalyze a high number of side reactions (e.g. cyanide, cyanate, acetylene, azide, hydrogen, thiocyanate, carbonyl sulfide)

Nitrogenase







Oxidized Nitrogen Species Reduction

Inorganic oxidized nitrogen compounds are some of the most common electron acceptors in anaerobic respiration. Can be linked to autotrophy and heterotrphy

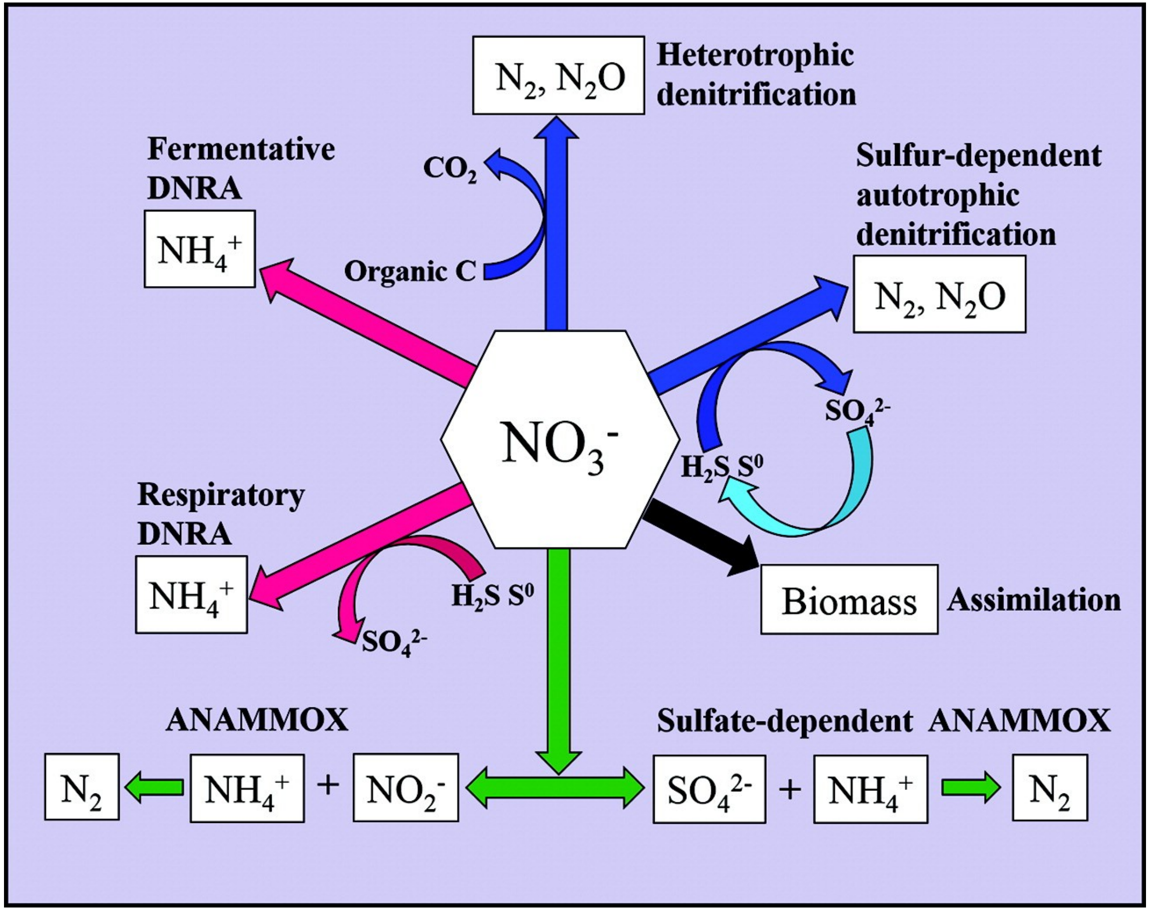
One of the most common alternative electron acceptors for dissimilative purposes is nitrate. It can be reduced with two electrons to nitrite, or reduced further to nitric oxide, nitrous oxide, and dinitrogen gas. The process of reducing an oxidized nitrogen species is known as Denitrification

Nitrate can also be reduced all the way to ammonia, a special case of denitrification, is known as Dissimilatory Nitrate Reduction to Ammonia (DNRA)

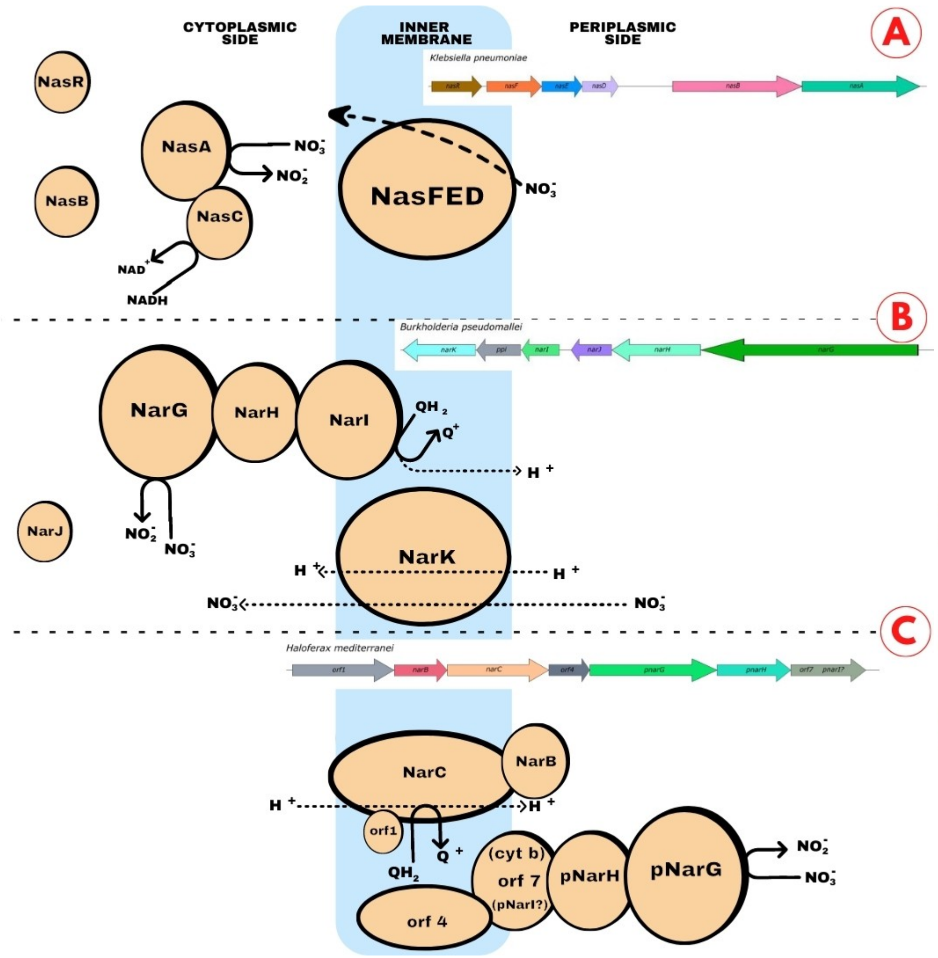
Denitrification is composed of multiple steps that can be accomplished by a single organism or multiple organisms. Multiple enzymes are involved

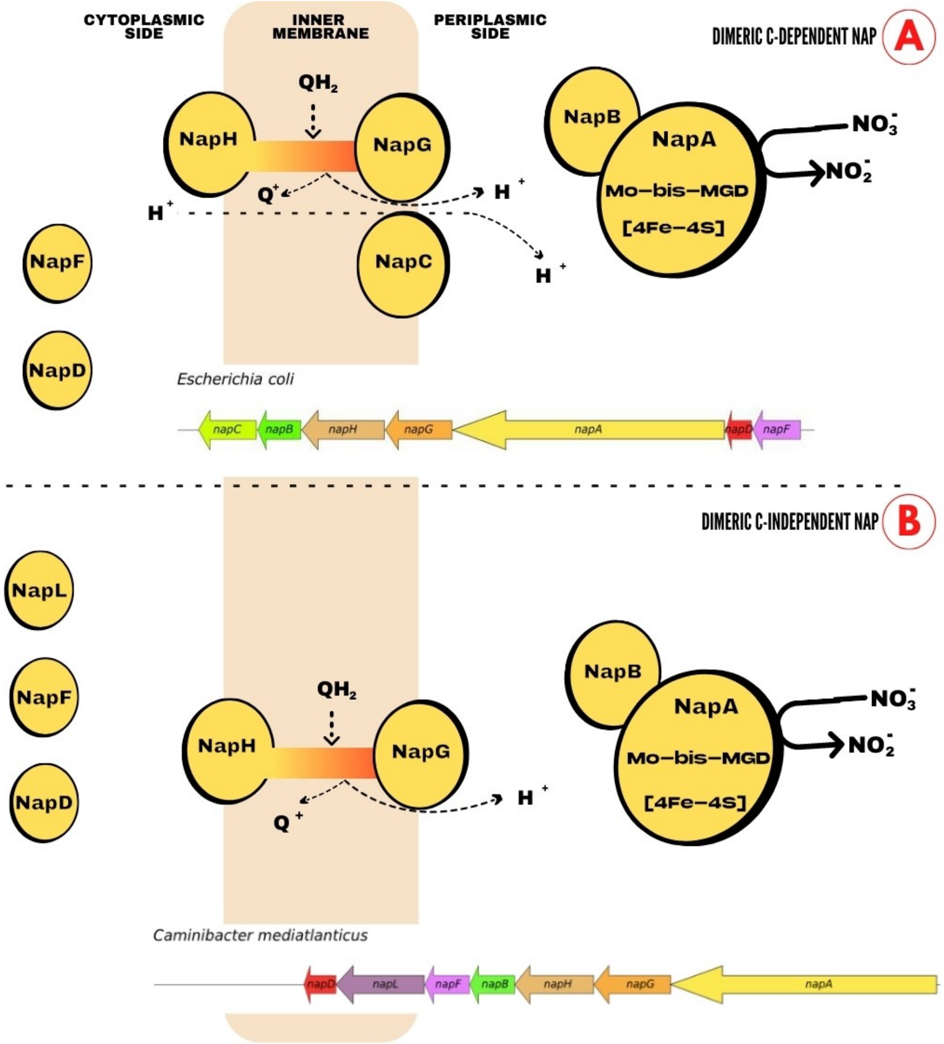
Three different enzymes can catalyze the first step of nitrate reduction (nitrate to nitrite): assimilatory nitrate reductase (Nas), membrane bound nitrate reductase (Nar) and the periplasmic nitrate reductase (Nap). These enzymes are widely distributed in the Tree of Life

Nitrate as a key electron acceptor

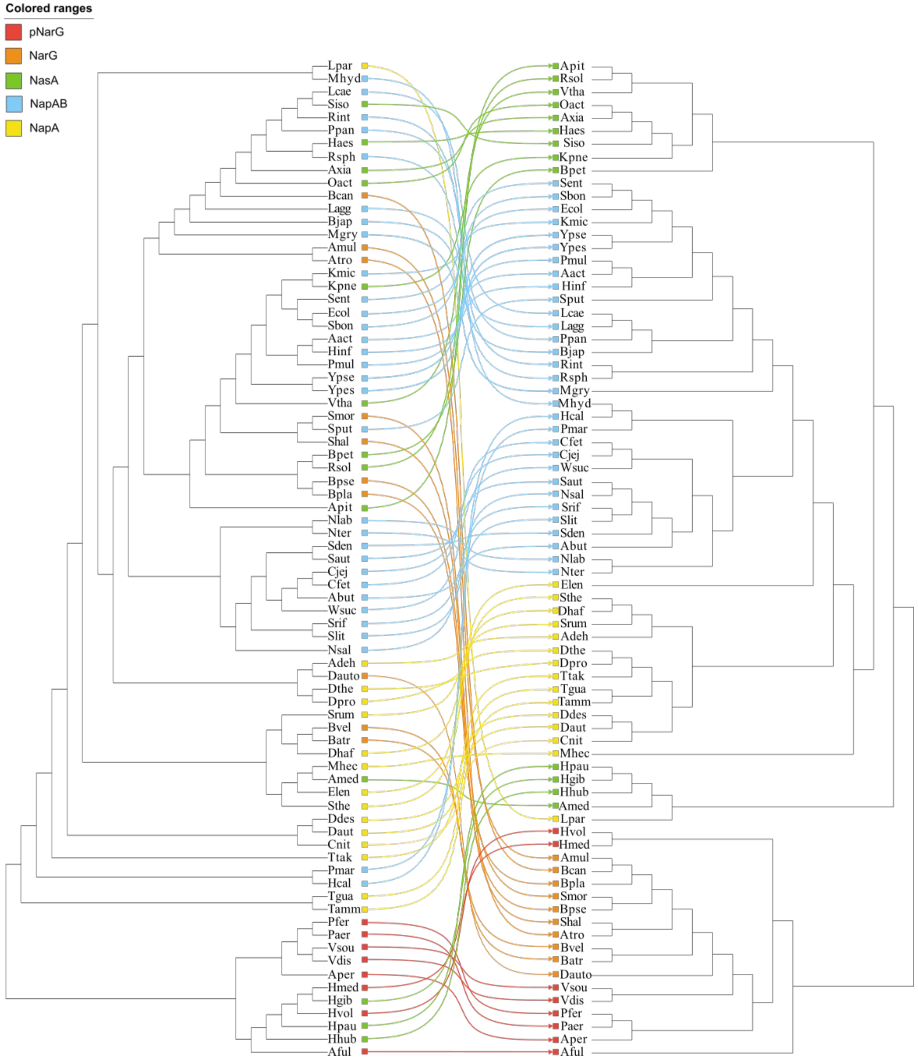


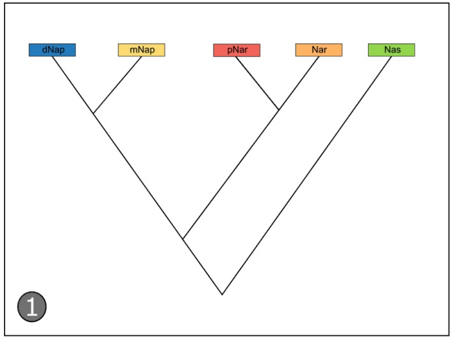
Nitrate Reductase diversity

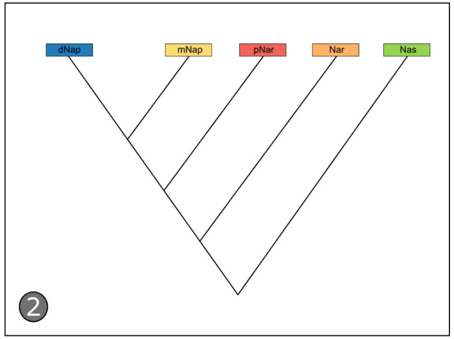


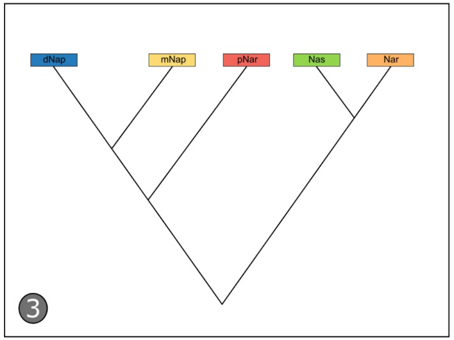


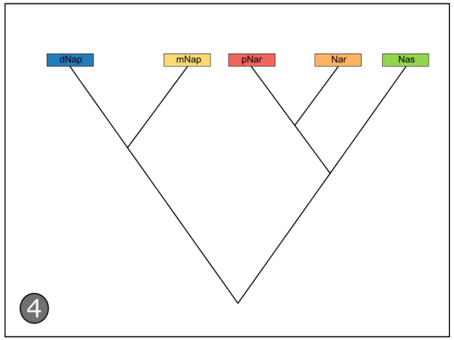
Nitrate Reductase diversity











Reduced Nitrogen Species Oxidation

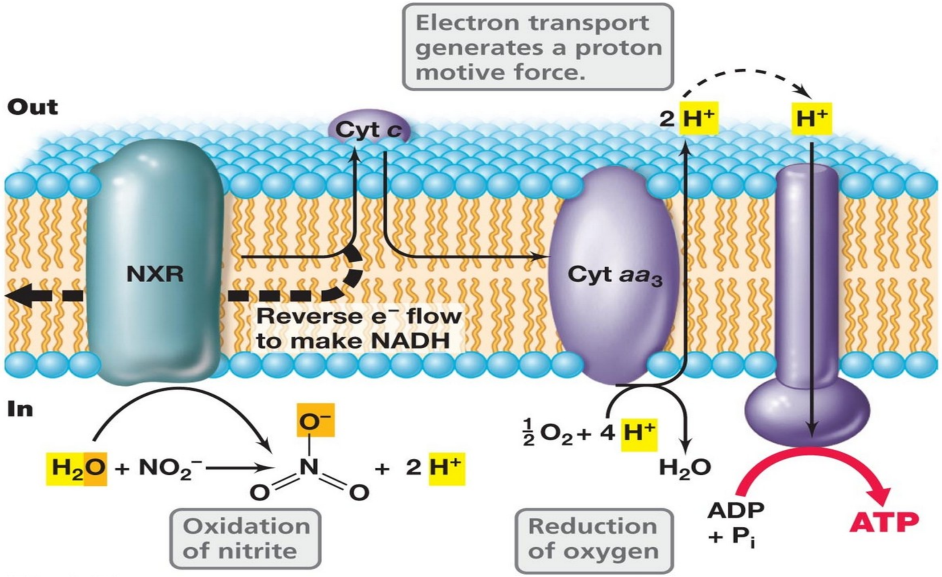
NH3, NO2- and their intermediate can also be used as energy sources and they are oxidized by nitrifying prokaryotes during the process of nitrification. Nitrifying prokaryotes are generally autotrophs

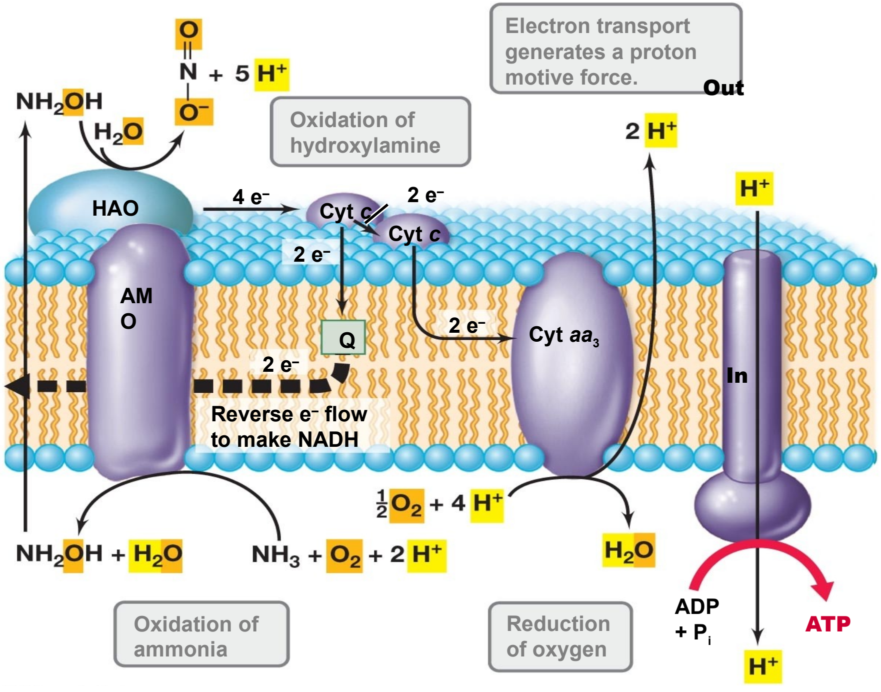
A few groups are well known for their nitrification metabolisms: Nitrospirae and selected genera of the Proteobacteria (Nitrosomonas, Nitrosospira, Nitrosococcus, Nitrosolobus ,and Nitrobacter, Nitrospina, Nitrococcus) in the Bacteria and one group of Archaea withing the Creanachaeota responsible for ammonia oxidation (Thaumarchaeota)

Key enzymes in nitrification are ammonia monooxygenase, hydroxylamine oxidoreductase, and nitrite oxidoreductase. The oxidation of nitrogen species is generally coupled to O2, but can be coupled to other compounds as well (SO4, NO2, etc...)

Only small energy yields from these reaction. Despite this Ammonia Oxidizing Bacteria (AOB) and Ammonia Oxidizing Archaea (AOA) are key player in many environments and control a large portion of the non-photosynthetic primary productivity in the Oceans

Nitrite Oxidation and Ammonia Oxidation





Anaerobic Ammonia Oxidation

Anerobic ammonia oxidation, known as ANAMMOX is a key process in the anaerobic side of the nitrogen cycle. It was predicted thermodynamically in 1977 and only discovered in 1999 in a waste-water sludge

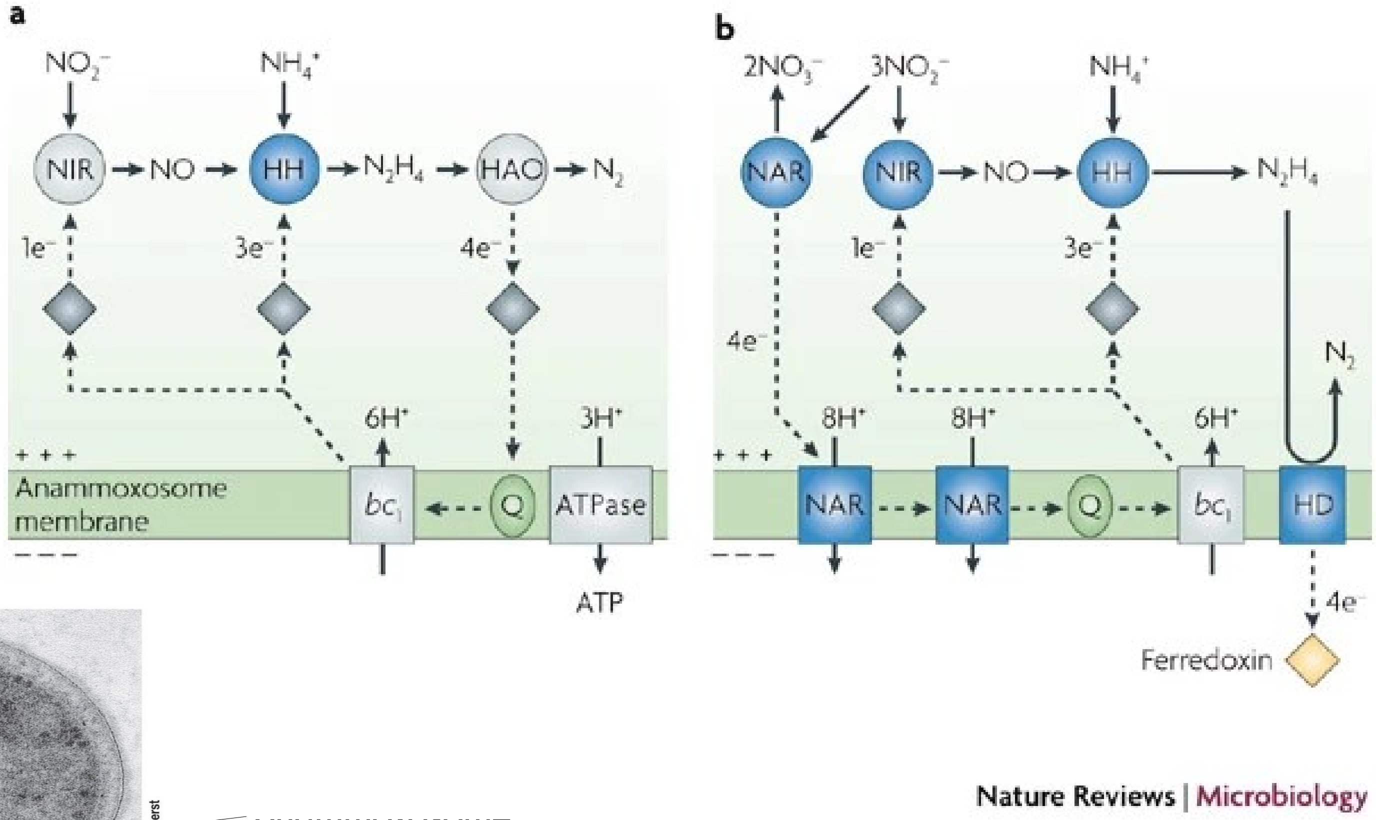
ANAMMOX is a comproportionation of of Ammonia and nitrite to N2 gas. It competes with primary productivity and might be responsible for 30-50% of the N2 gas produced in the oceans

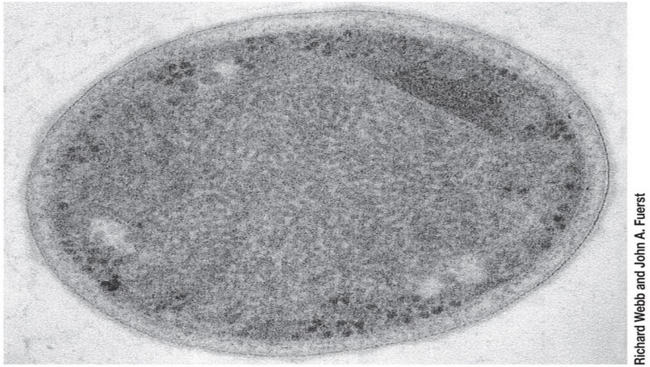
$$NH_4^+ + NO_2^- \rightarrow N_2 + 2\ H_2O$$

Performed by unusual group of obligate anaerobes (Planctomycetes, order Brocadiales).

Anammoxosome is a membrane-enclosed compartment where anammox reactions occur since its key intermediate, hydrazine (H2N=NH2) is a very strong reductant. Lipids that make up the anammoxsome are not the typical lipids of Bacteria

The hydroxylamine oxidoreductase (HAO) enzyme is considered a key enzyme in the pathway





(b)

Anammoxosome

Kuenen 2008 Nat Rev Microbiol

Sulfur Metabolism

Sulfur in energy metabolism

Sulfur is widely used by prokaryotes as electron acceptor and energy source and has a very similar role to nitrogen with respect to its multi valence state

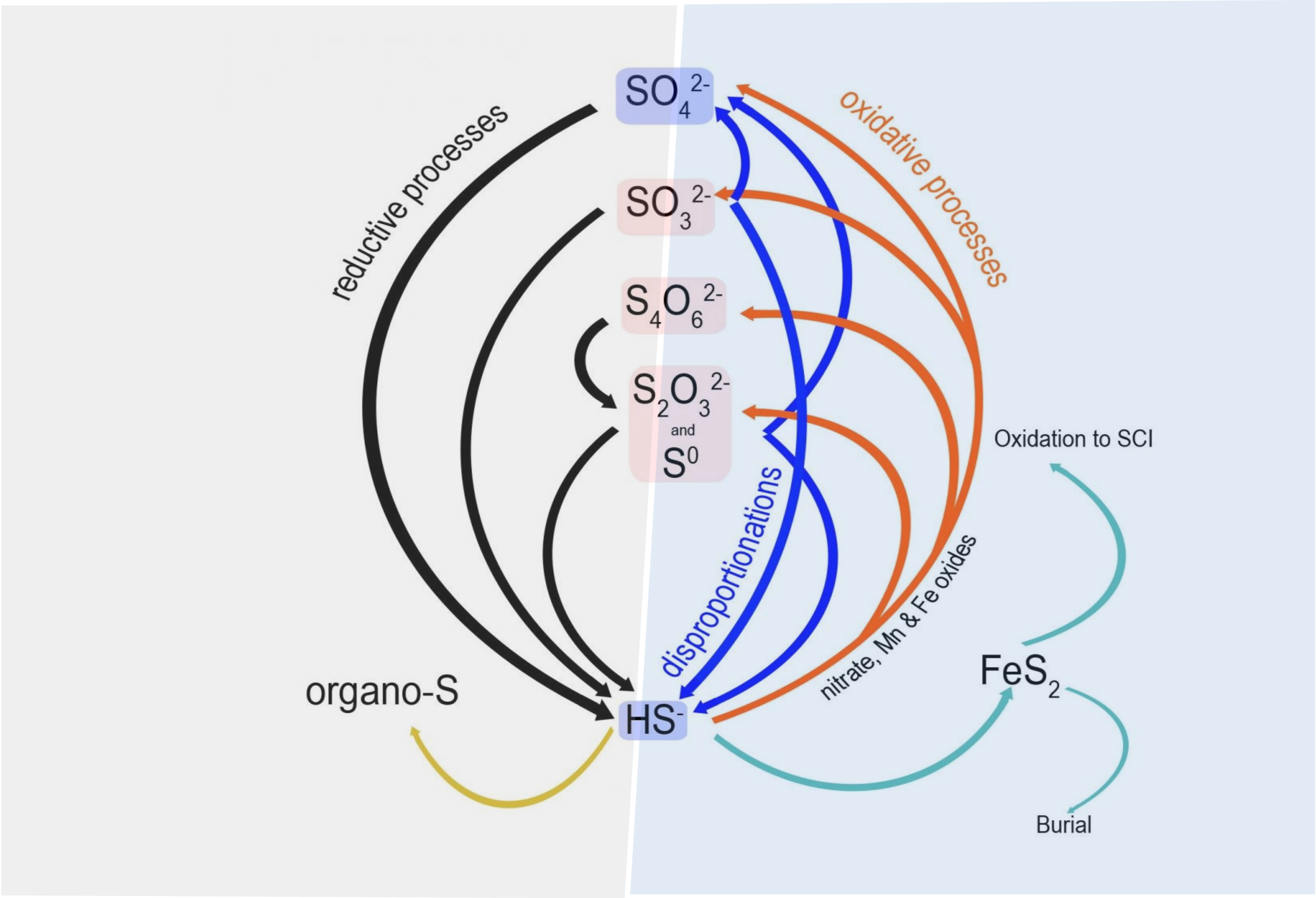
Oxidized sulfur species, with SO42- (sulfate) being the chief molecule, dominate anaerobic respiration in many ecosystems and are responsible for the degradation of a significant portion of organic carbon

Of the possibly biological reactions with Sulfur, numerous abiotic reaction have rates that comparable or faster than biotic rates, with abiotic rates comprising a large portion of total reaction in certain conditions

Energy reactions with Sulfur in prokaryotes often require multi-enzyme complexes and are highly modular

Sulfur energy might have been very important at the emergence of life and has played a key role during our planet evolution

Sulfur energy metabolism



Oxidized Sulfur Species Reduction

Oxidized sulfur species are used as electron acceptor by a variety of different prokaryotes. Among these Sulfate (SO42-) is one of the most important electron acceptor, followed by the disproportionation of Thiosulfate (S2O32-). They might be organotrophic or lithotrophic, and either heterotrophs or autotrophs

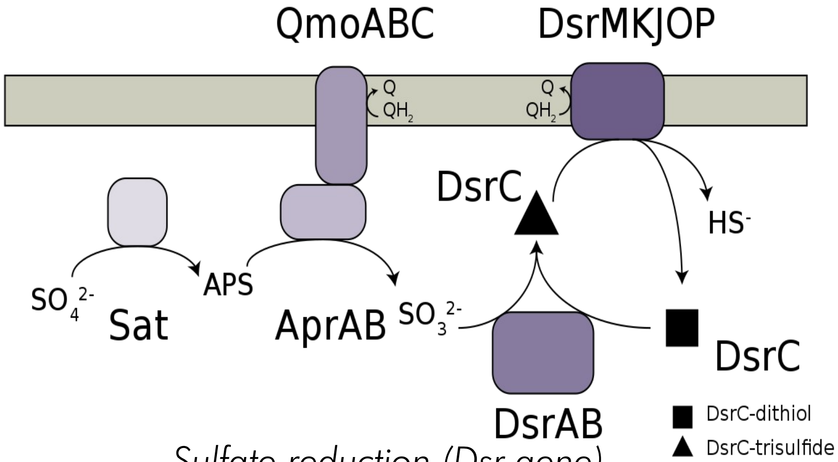
Sulfate is reduced by the sulfate-reducing bacteria (SBR), a highly diverse group of obligately anaerobic bacteria widely distributed in nature. A number of environmentally important SRB are Deltaproteobacteria. Sulfate reduction is also present in the Archaea

The end product of sulfate reduction is hydrogen sulfide (H2S), an important natural product that participates in many biogeochemical processes

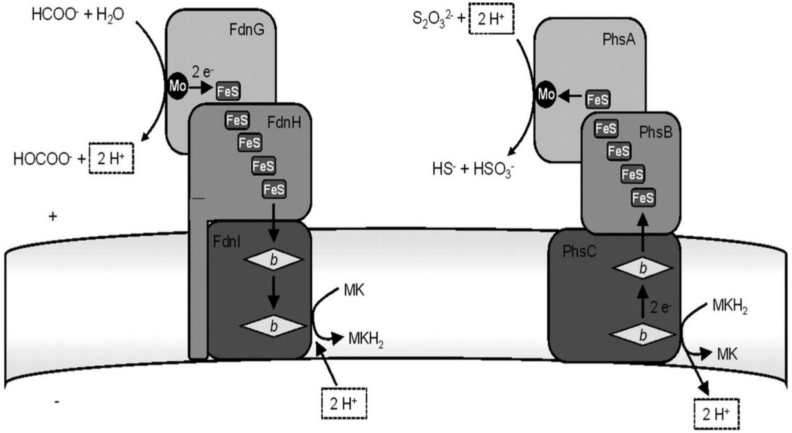
Sulfate reduction is a widespread and important pathway of organic matter degradation in anaerobic sediments. Sulfate reducers can be autotrophic or heterotrophic

A diverse suite of enzymes can be used for Oxidized Sulfur Species reduction

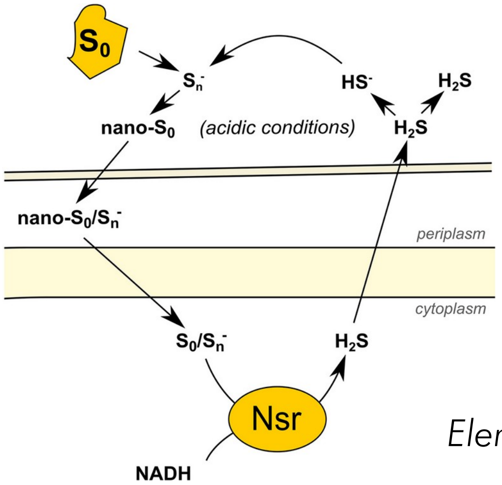
Oxidized Sulfur Species Reduction



Sulfate reduction (Dsr gene)



Thiosulfate reduction (Tsr gene)



Elemental Sulfur reduction (Nsr gene)

Reduced Sulfur Species Oxidation

Reduced sulfur species are used as electron donor by an incredible variety of different prokaryotes, including anoxigenic phototrophs. Among these Sulfide (H2S) is one of the most important electron donor in anaerobic system

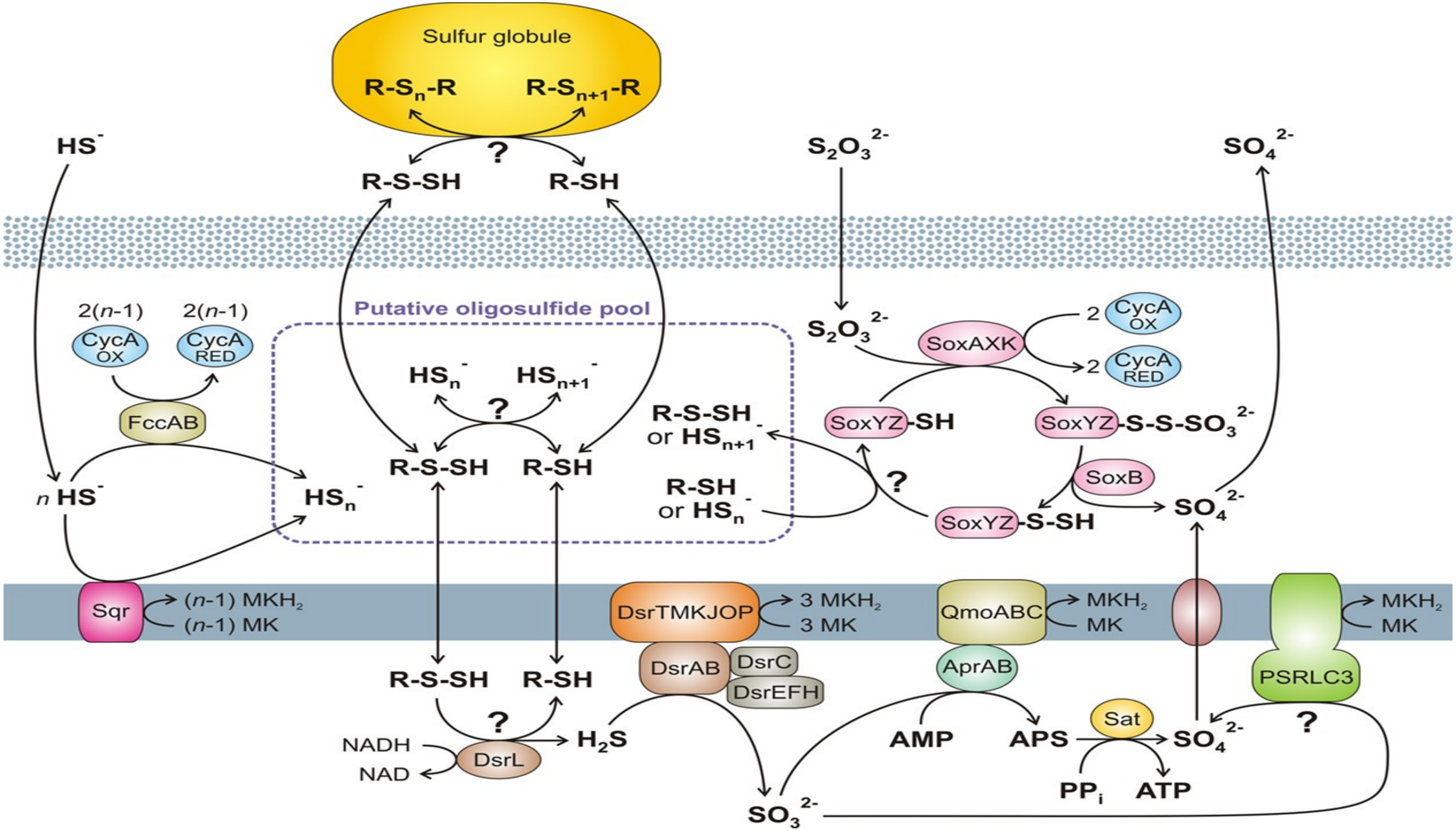
Sulfide, Polysulfide, Elemental Sulfur and Thiosulfate are oxidized by a large number of Bacteria and Archaea. These microbes are usually versatile and

The end product of sulfate reduction is hydrogen sulfide (H2S), an important natural product that participates in many biogeochemical processes, and interacts with other oxidants abiotically forming a number of intermediate species

Sulfur oxidizing microbes are key players in a number of extreme environments, and are often control primary productivity in these systems

A diverse suite of enzymes can be used for reducing oxidized Sulfur, and the system is highly modular

Reduced Sulfur Species Oxidation



Iron Metabolism

Iron energy metabolism

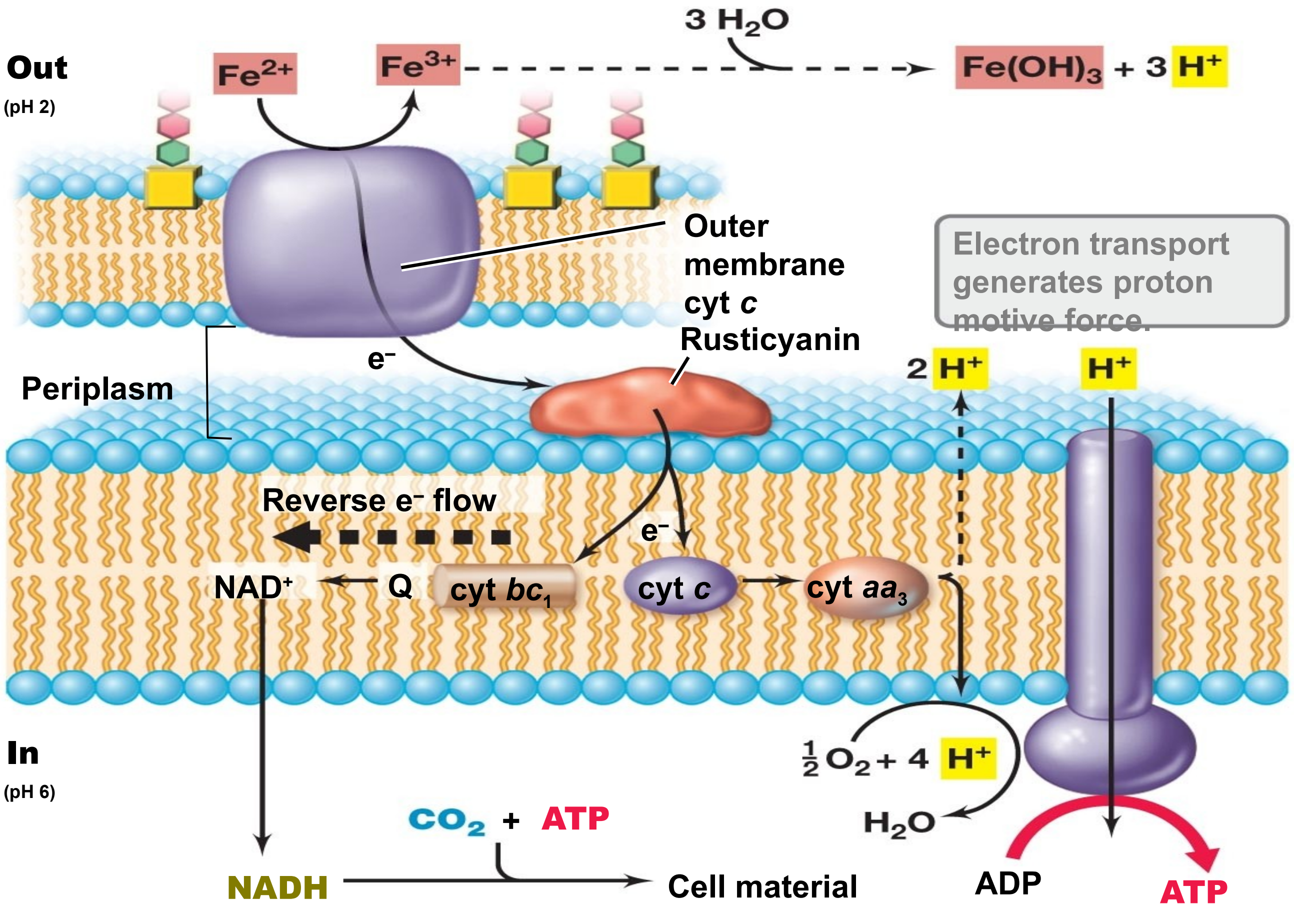
Iron is an important electron acceptor and donor in active redox environments. It is carried out by a diverse group of microbes that include anoxygenic phototrophs

Due to its limited number of oxidation states (Fe^{2+} and Fe^{3+}) its cycle is relatively simple. Despite this the large amount of iron mineral that can be used either directly or indirectly as donor/acceptor by microorganisms complicates the cycle

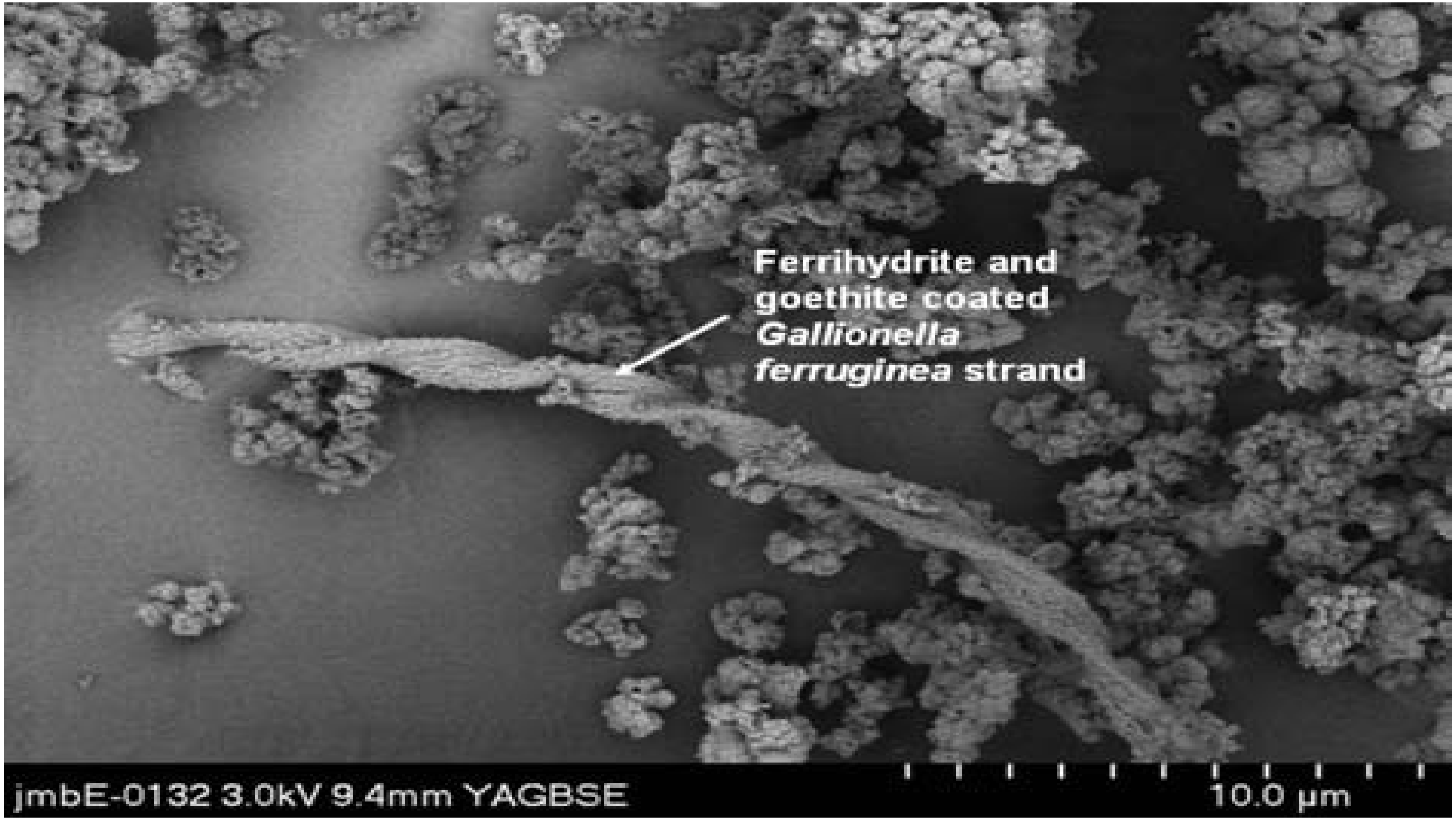
Iron reduction is an important pathway of organic matter degradation. Iron oxidation might be important in primary productivity in several ecosystems

Iron oxidizers often produce characteristic biominerals of Iron hydroxide, called twisted stalks that can be useful in identify the metabolism in the sediment record

Iron Oxidation



Twisted Iron Stalks



Other Elements Metabolism

Other element energy metabolism

A number of other elements can be used as electron donor and acceptor by microorganism, including Arsenic, Manganese, Selenium, Tellurium, Uranium and others

While their contribution can be locally and globally important, we have comparatively small information for these reactions, and often the metabolic pathways are not completely elucidated

Additionally several of these reactions might be carried out under specific condition by other promiscuous oxidoreductases

Future work will be needed to elucidate the global biogechemical and energetic impact of these elements

This lecture reads

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