

ENVIRONMENTAL METAGENOMICS

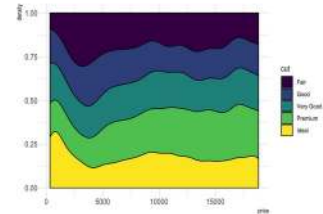
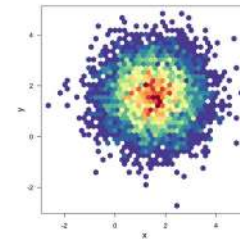
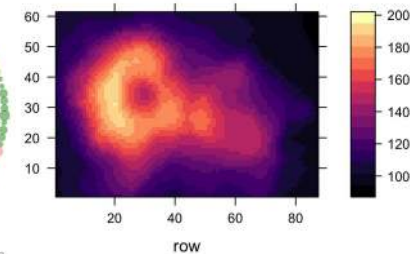
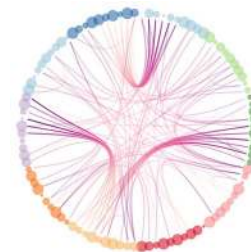
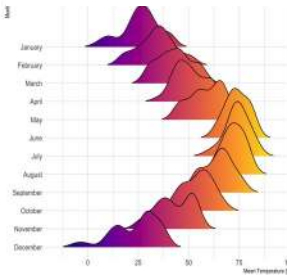
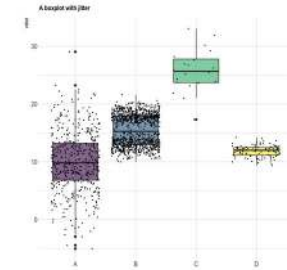
MICROBIAL METABOLISM AND NUTRITIONAL GROUPS

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Life uses energy in two forms, chemical and light. All life uses free energy released from one chemical reaction to drive another. More specifically, life catalyzes redox chemistry (i.e. electron transfer), capturing energy from the resulting flow of electrons to drive further reactions.

Life is based on RedOx reactions

Refresher:

An **oxidation-reduction** (redox) **reaction** is a type of chemical reaction that involves a **transfer of electrons** between two species. An oxidation-reduction reaction is any chemical reaction in which the oxidation number of a molecule, atom, or ion changes by gaining or losing an electron.



Life is Electric

Electron transfer (redox) reactions are most familiar as pairs of half-cell reactions, each half-reaction depicting an oxidized (electron poor) form of substrate having donated an electron, reversibly, to a reduced (electron rich) substrate (**Eq. 1**) or the reverse, (**Eq. 2**). Each half reaction has a given tendency to gain or lose electrons relative to a second half reaction.



$$E^\circ = A_E$$

Eq. 2. Oxidation half reaction: A is oxidized to A^+



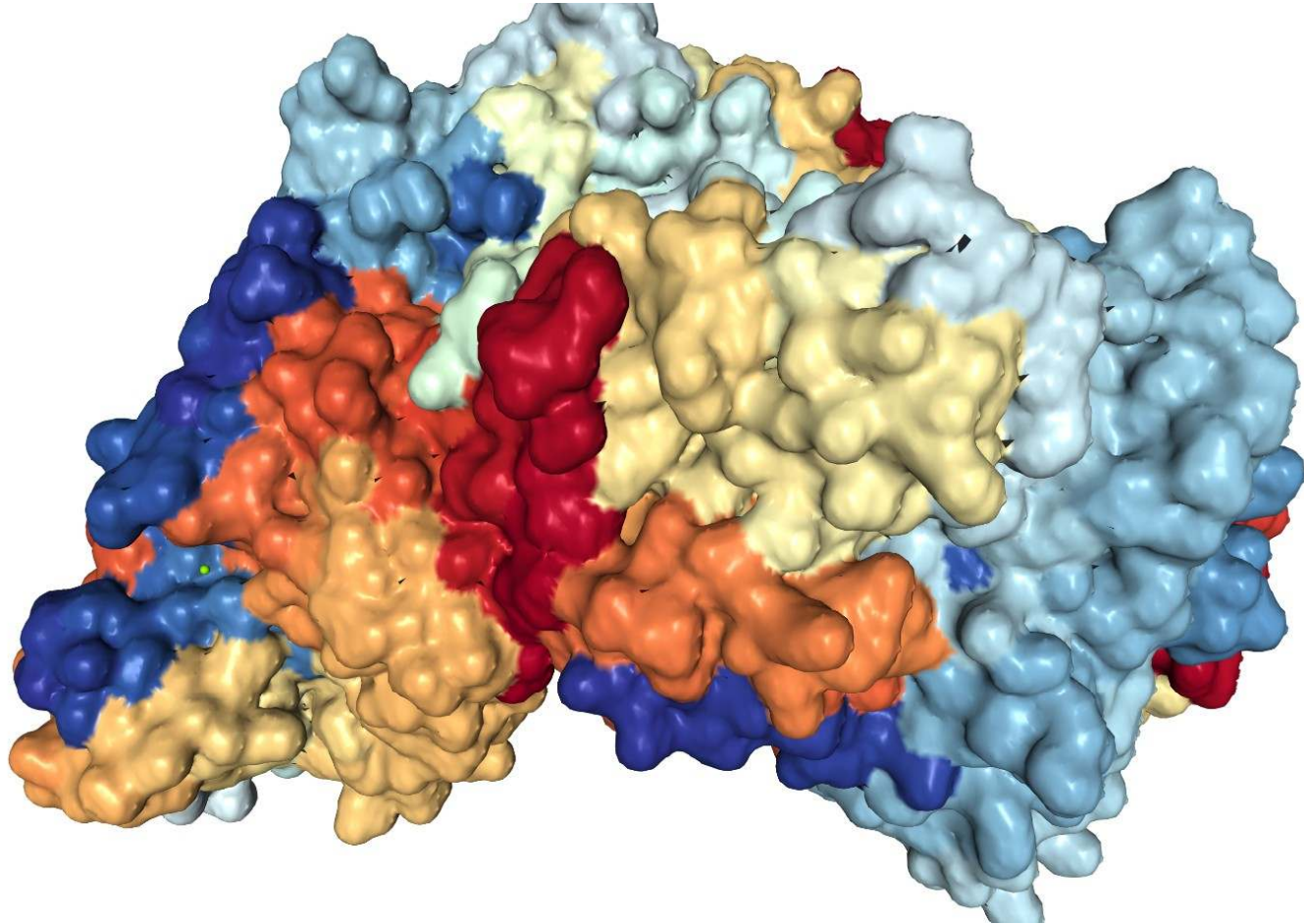
$$E^\circ = B_E$$

Eq. 3. Reduction half reaction: B^+ is reduced to B

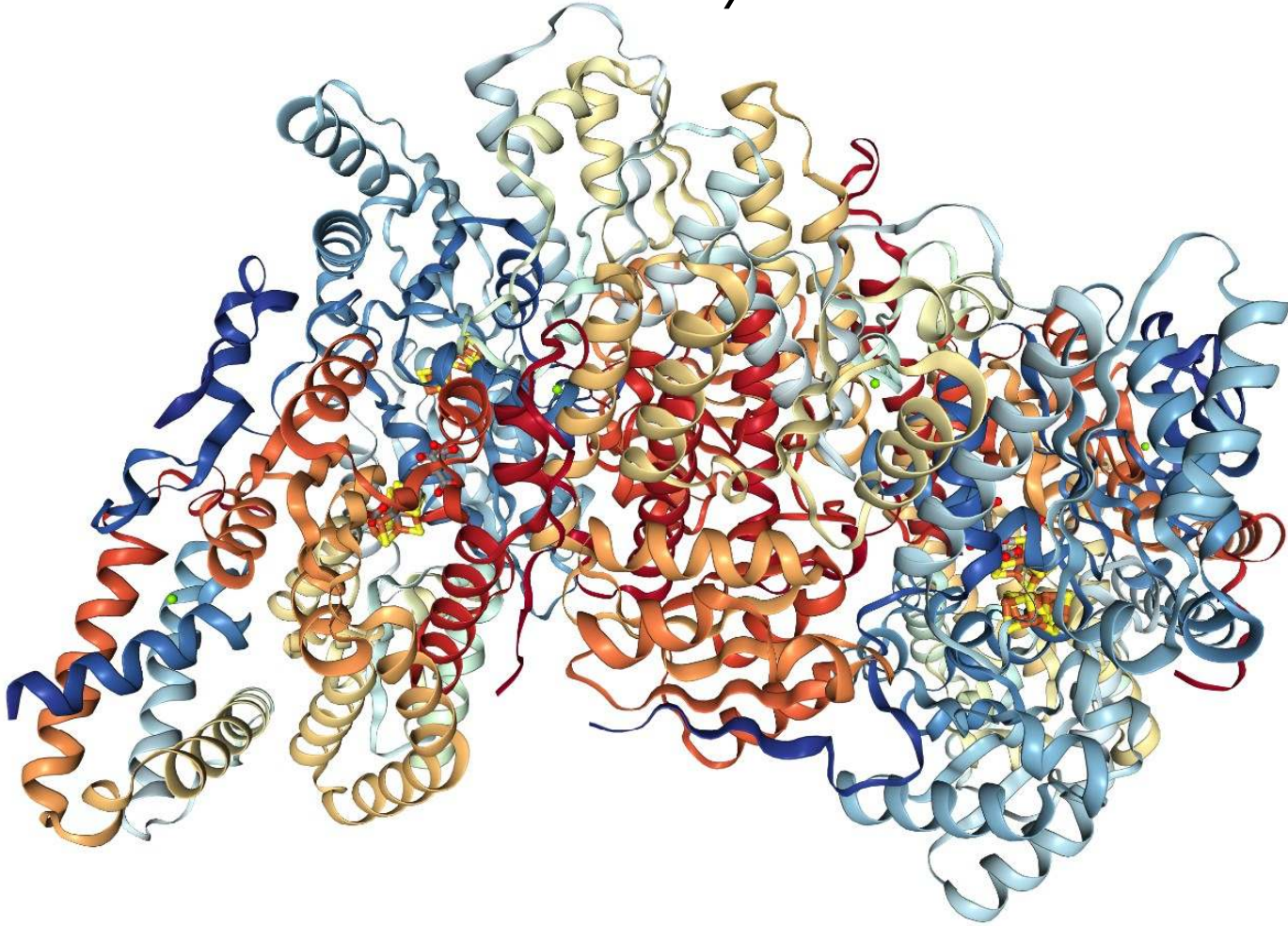
The standard reduction potential (E°), the potential (in Volts) to gain an electron under standard conditions, has been tabulated for a large number of half reactions, using the standard hydrogen electrode (SHE) as reference, with $E^\circ_{SHE} = 0$ V.

If the reduction potential is negative for a half reaction, it will donate electrons when coupled to the SHE, or to any other half reaction with a less negative reduction potential.

Life is literally electric



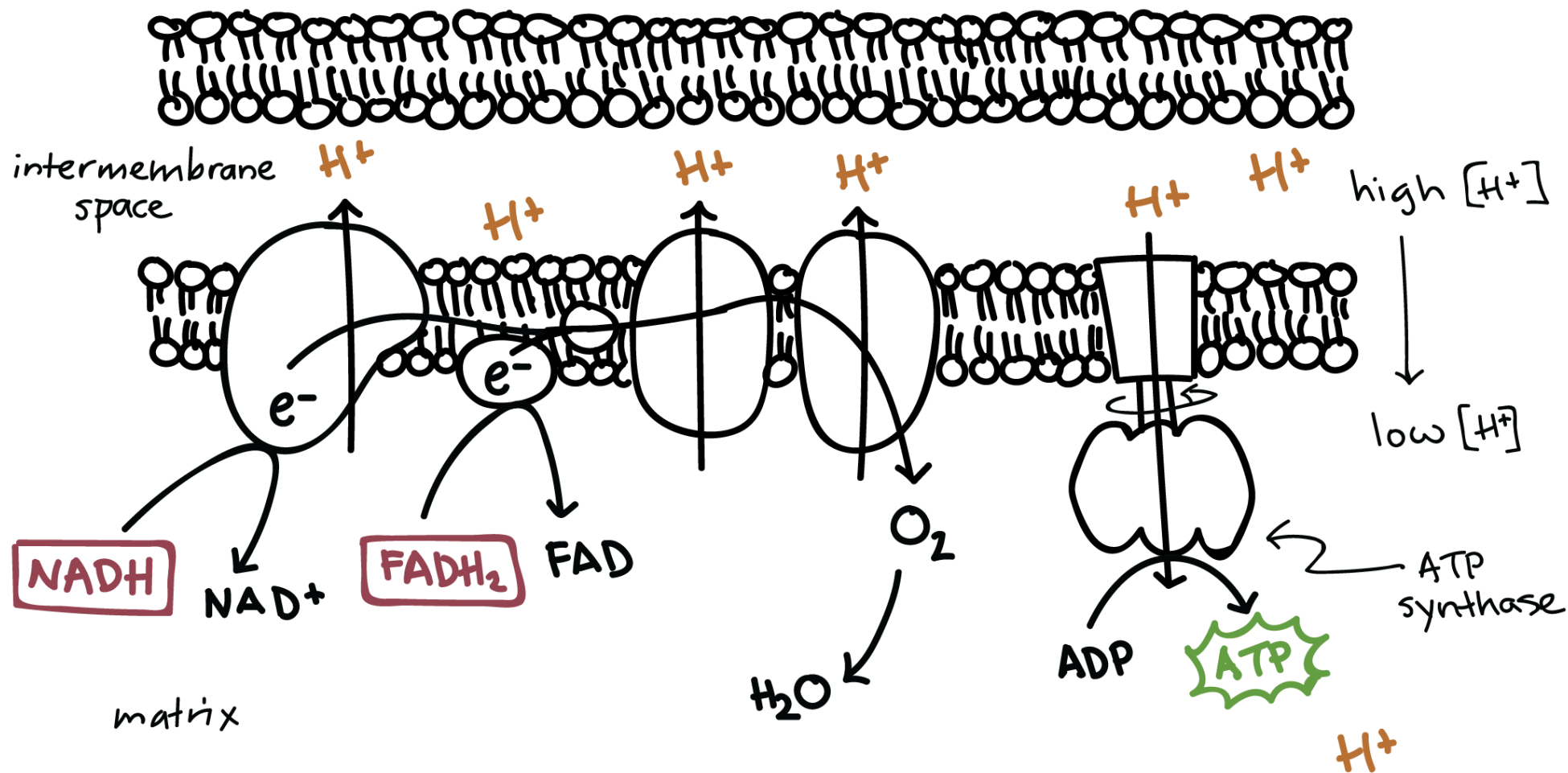
Life is literally electric



Life is literally electric



cytoplasm



Free Energy of Formation and Calculating ΔG^0

Table A1.1 Free energies of formation (G_f^0) for some substances (kJ/mol)^a

Carbon compound	Carbon compound	Metal	Nonmetal	Nitrogen compound
CO, -137.34	Glutamine, -529.7	Cu ⁺ , +50.28	H ₂ , 0	N ₂ , 0
CO ₂ , -394.4	Glyceraldehyde, -437.65	Cu ²⁺ , +64.94	H ⁺ , 0 at pH 0; -39.83 at pH 7 (-5.69 per pH unit)	NO, +86.57
CH ₄ , -50.75	Glycerate, -658.1	CuS, -49.02	O ₂ , 0	NO ₂ , +51.95
H ₂ CO ₃ , -623.16	Glycerol, -488.52	Fe ²⁺ , -78.87	OH ⁻ , -157.3 at pH 14; -198.76 at pH 7; -237.57 at pH 0	NO ₂ ⁻ , -37.2
HCO ₃ ⁻ , -586.85	Glycine, -314.96	Fe ³⁺ , -4.6	H ₂ O, -237.17	NO ₃ ⁻ , -111.34
CO ₃ ²⁻ , -527.90	Glycolate, -530.95	FeCO ₃ , -673.23	H ₂ O ₂ , -134.1	NH ₃ , -26.57
Acetaldehyde, -139.9	Glyoxalate, -468.6	FeS ₂ , -150.84	PO ₄ ³⁻ , -1026.55	NH ₄ ⁺ , -79.37
Acetate, -369.41	Guanine, +46.99	FeSO ₄ , -829.62	Se ⁰ , 0	N ₂ O, +104.18
Acetone, -161.17	α-Ketoglutarate, -797.55	PbS, -92.59	H ₂ Se, -77.09	N ₂ H ₄ , +128
Alanine, -371.54	Lactate, -517.81	Mn ²⁺ , -227.93	SeO ₄ ²⁻ , -439.95	
Arginine, -240.2	Lactose, -1515.24	Mn ³⁺ , -82.12	S ⁰ , 0	
Aspartate, -700.4	Malate, -845.08	MnO ₄ ⁻ , -506.57	SO ₃ ²⁻ , -486.6	
Benzene, +124.5	Mannitol, -942.61	MnO ₂ , -456.71	SeO ₄ ²⁻ , -744.6	
Benzoic acid, -245.6	Methanol, -175.39	MnSO ₄ , -955.32	S ₂ O ₃ ²⁻ , -513.4	
n-Butanol, -171.84	Methionine, -502.92	HgS, -49.02	H ₂ S, -27.87	
Butyrate, -352.63	Methylamine, -40.0	MoS ₂ , -225.42	HS ⁻ , +12.05	
Caproate, -335.96	Oxalate, -674.04	ZnS, -198.60	S ²⁻ , +85.8	
Citrate, -1168.34	Palmitic acid, -305			
o-Cresol, -37.1	Phenol, -47.6			
Crotonate, -277.4	n-Propanol, -175.81			
Cysteine, -339.8	Propionate, -361.08			
Dimethylamine, -3.3	Pyruvate, -474.63			
Ethanol, -181.75	Ribose, -757.3			
Formaldehyde, -130.54	Succinate, -690.23			
Formate, -351.04	Sucrose, -370.90			
Fructose, -951.38	Toluene, +114.22			
Fumarate, -604.21	Trimethylamine, -37.2			
Glucuronate, -1128.3	Tryptophan, -112.6			
Glucose, -917.22	Urea, -203.76			
Glutamate, -699.6	Valerate, -344.34			

^aValues for free energy of formation of various compounds can be found in Dean, J. A. 1973. *Lange's Handbook of Chemistry*, 11th edition. McGraw-Hill, New York; Garrels, R. M., and C. L. Christ. 1965. *Solutions, Minerals, and Equilibria*. Harper & Row, New York; Burton, K. 1957. In Krebs, H. A., and H. L. Kornberg. Energy transformation in living matter. *Ergebnisse der Physiologie* (appendix): Springer-Verlag, Berlin; and Thauer, R. K., K. Jungermann, and H. Decker. 1977. Energy conservation in anaerobic chemotrophic bacteria. *Bacteriol. Rev.* 41: 100-180.

Free Energy (G): defined as the energy released that is available to do useful work G_f^0 indicates the free energy of formation for a given compound, defined as the energy yielded or required for the formation of a given molecule from its constituent elements

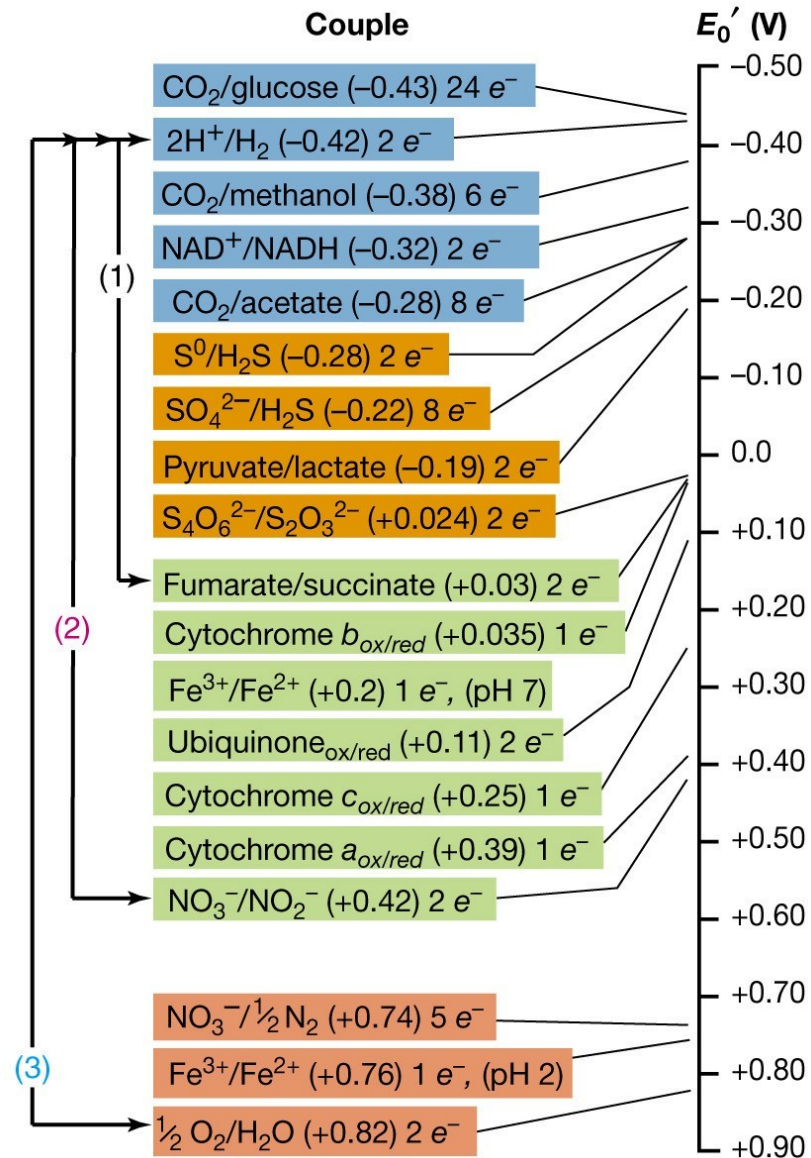
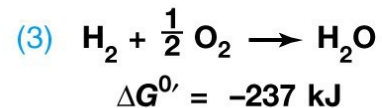
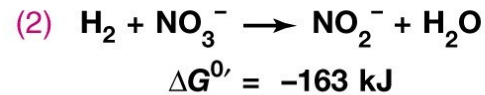
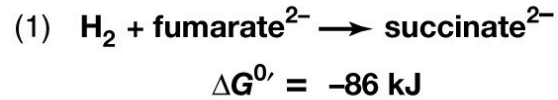
ΔG^0 is the change in free energy under standard conditions (pH 7, 25°C, 1 atm., [reactants] = 1 M)

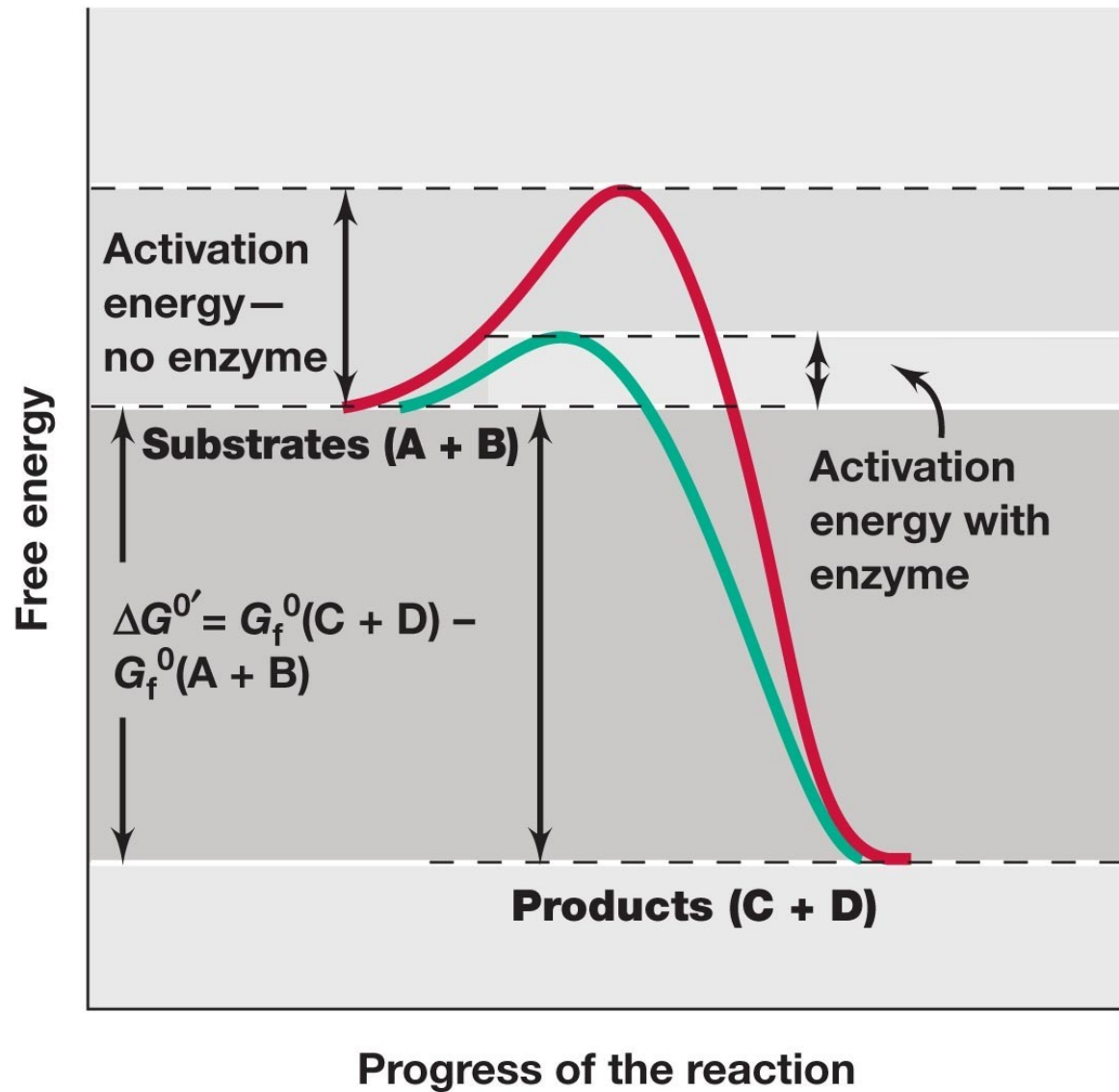
$$\Delta G^0 = \Delta G_f^0 (\text{products}) - \Delta G_f^0 (\text{reactants})$$

Neg. ΔG^0 / energy release / exergonic reaction

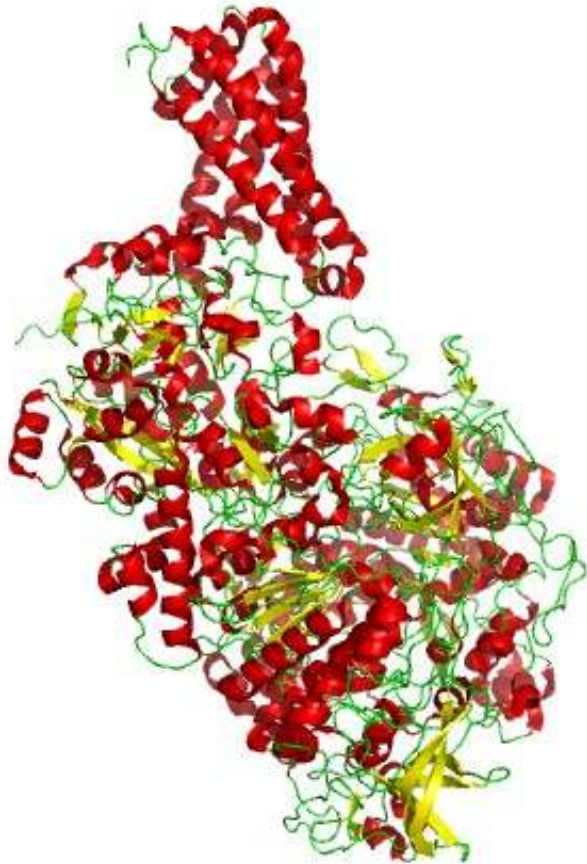
Pos. ΔG^0 / energy requirement / endergonic reaction

Examples of reactions
with H_2 as e^- donor

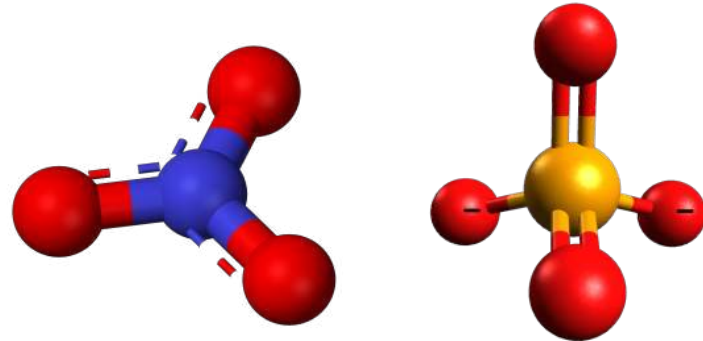




One more thing to keep in mind...



While working primarily on **Nitrate**, this reductase enzyme can also act on **Selenate**, thus being promiscuous with regard to the substrate

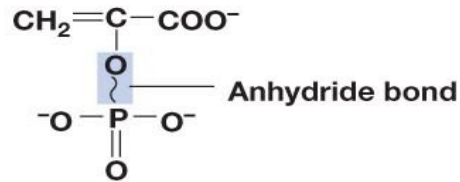


nitrite reductase enzyme $\text{NO}_3^- \rightarrow \text{NO}_2^-$

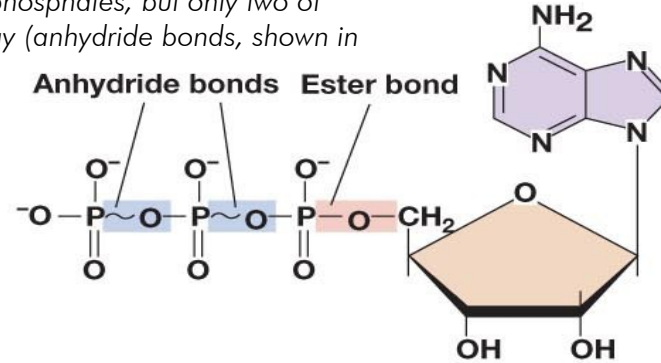
High-energy bonds

The energy released in redox reactions is conserved in the formation of certain compounds that contain energy-rich phosphate or sulfur bonds

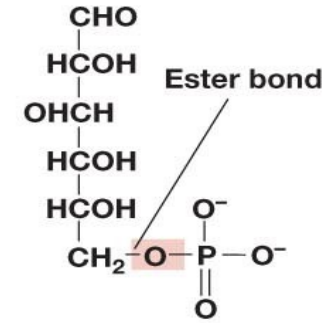
ATP contains three phosphates, but only two of them are high energy (anhydride bonds, shown in blue)



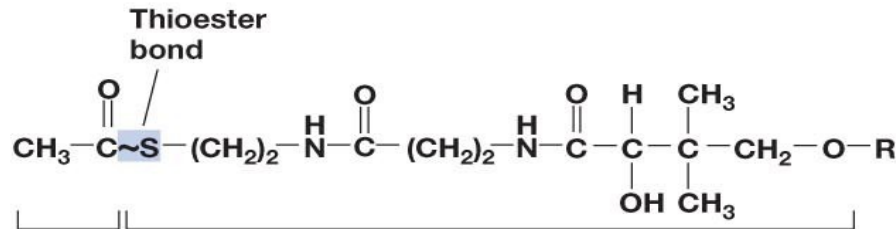
Phosphoenolpyruvate



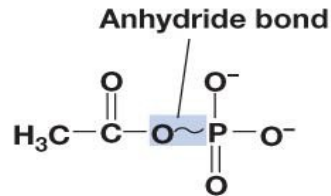
Adenosine triphosphate (ATP)



Glucose 6-phosphate

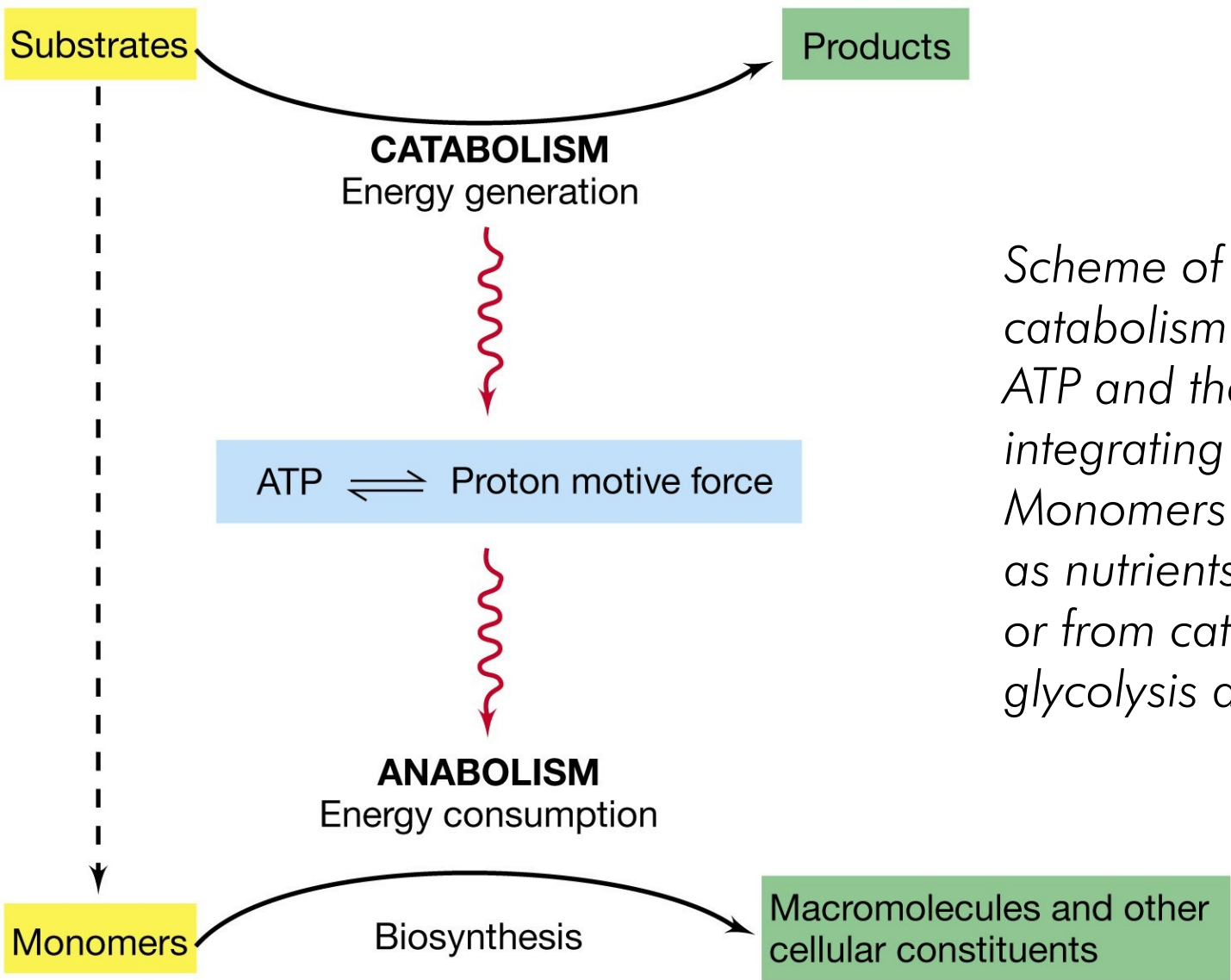


Acetyl-CoA



Acetyl phosphate

Compound	$G^{0'}$ kJ/mol
$\Delta G^{0'} > 30\text{kJ}$	
Phosphoenolpyruvate	-51.6
1,3-Bisphosphoglycerate	-52.0
Acetyl phosphate	-44.8
ATP	-31.8
ADP	-31.8
Acetyl-CoA	-35.7
$\Delta G^{0'} < 30\text{kJ}$	
AMP	-14.2
Glucose 6-phosphate	-13.8

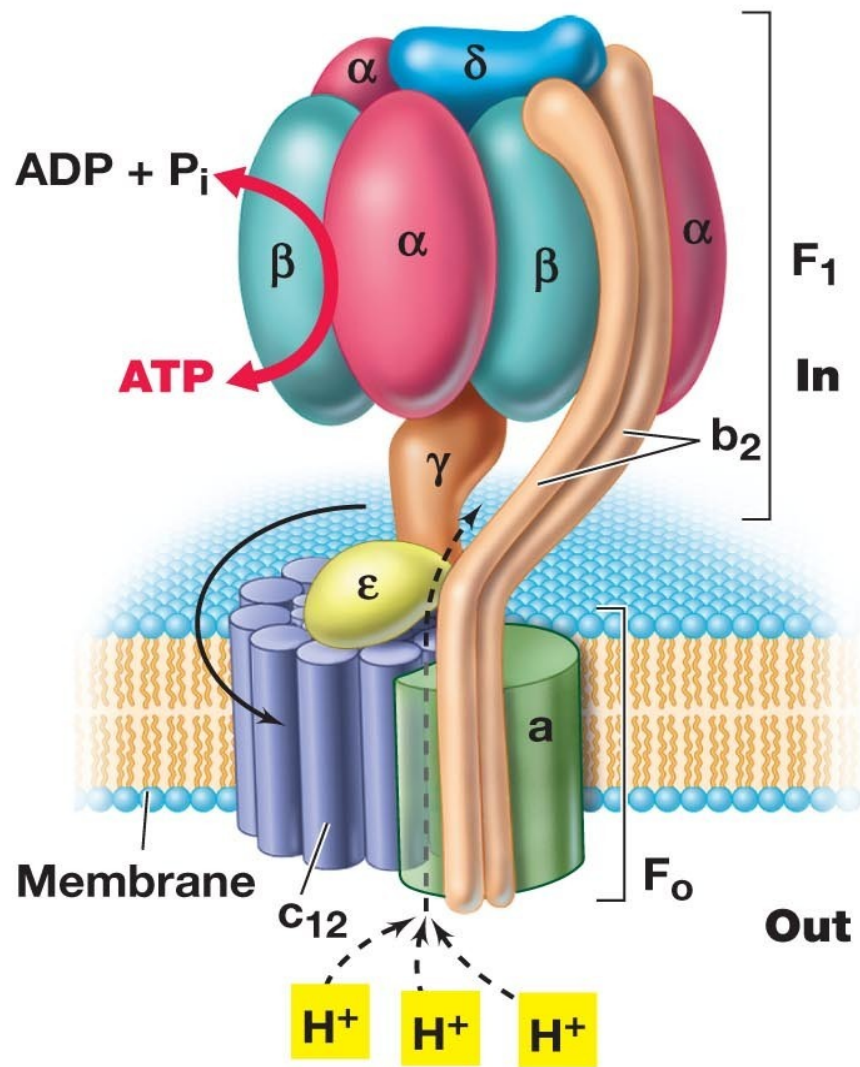


Scheme of anabolism and catabolism showing the key role of ATP and the proton motive force in integrating the processes. Monomers can come preformed as nutrients from the environment or from catabolic pathways like glycolysis and the citric acid cycle.

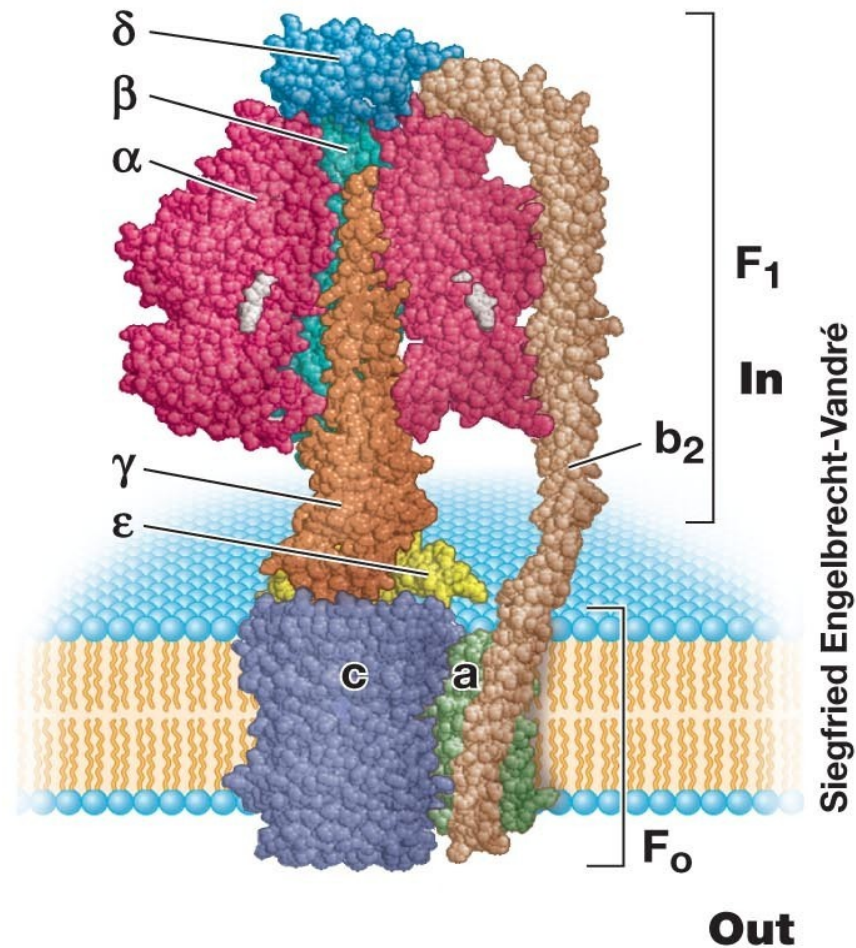
Proton Motive Force

With the exception of fermentation, in which substrate-level phosphorylation occurs, all other mechanisms for energy conservation employ the **proton motive force**. Whether electrons come from the oxidation of organic or inorganic chemicals or from light-driven processes, in all forms of respiration and photosynthesis, energy conservation is linked to the establishment of a PMF and its dissipation by ATPase to form ATP.

Respiration and anaerobic respiration can thus be viewed as variations on a theme of different electron acceptors. Likewise, **chemoorganotrophy**, **chemolithotrophy**, and **photosynthesis** are variations on a theme of different electron donors. Electron transport and the pmf link all of these processes, bringing these seemingly quite different forms of energy metabolism into a common focus.



(a)



(b)

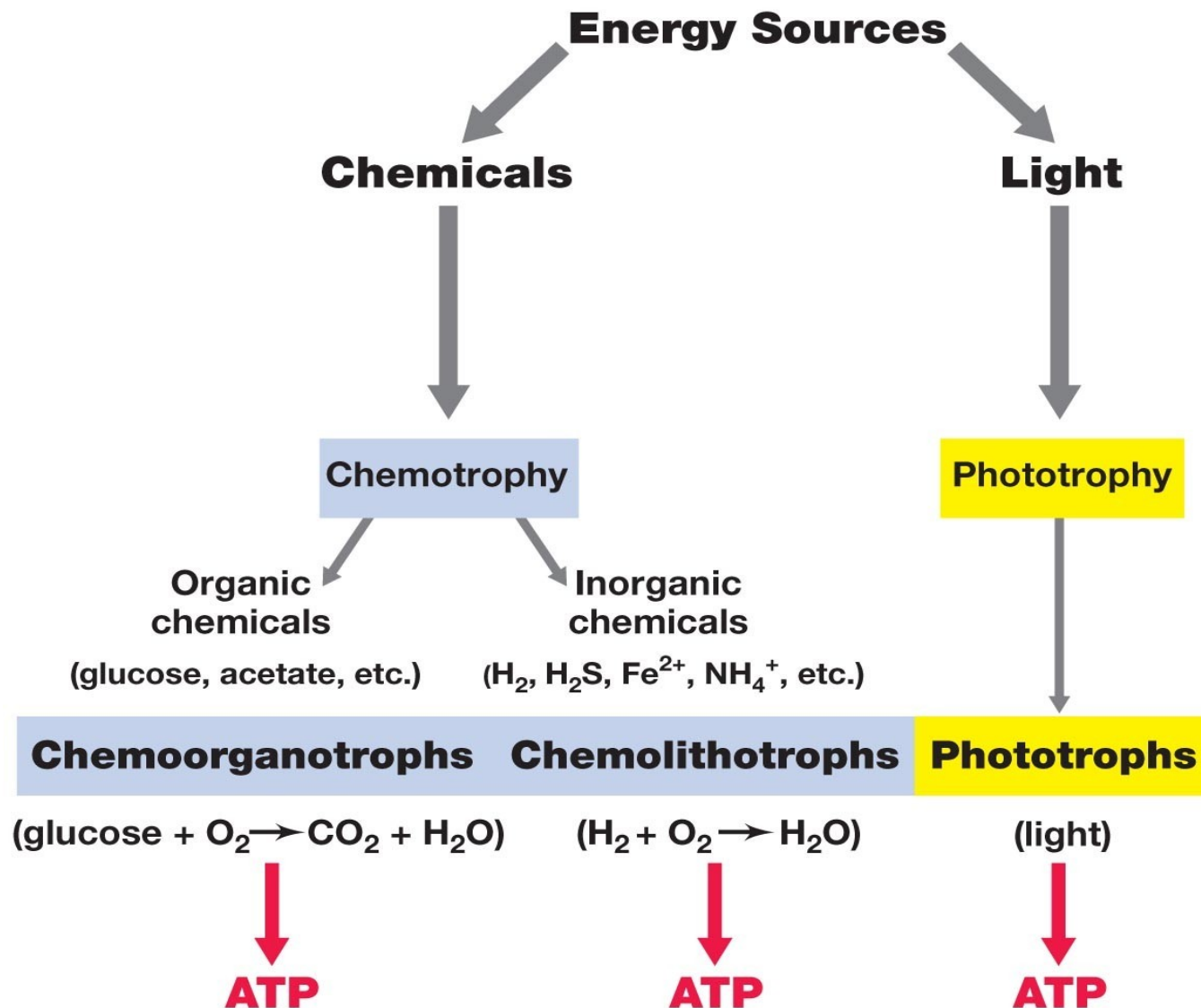
Basic Metabolism

An **electron donor** (also known as energy source)

A **carbon source** (for biosynthesis)

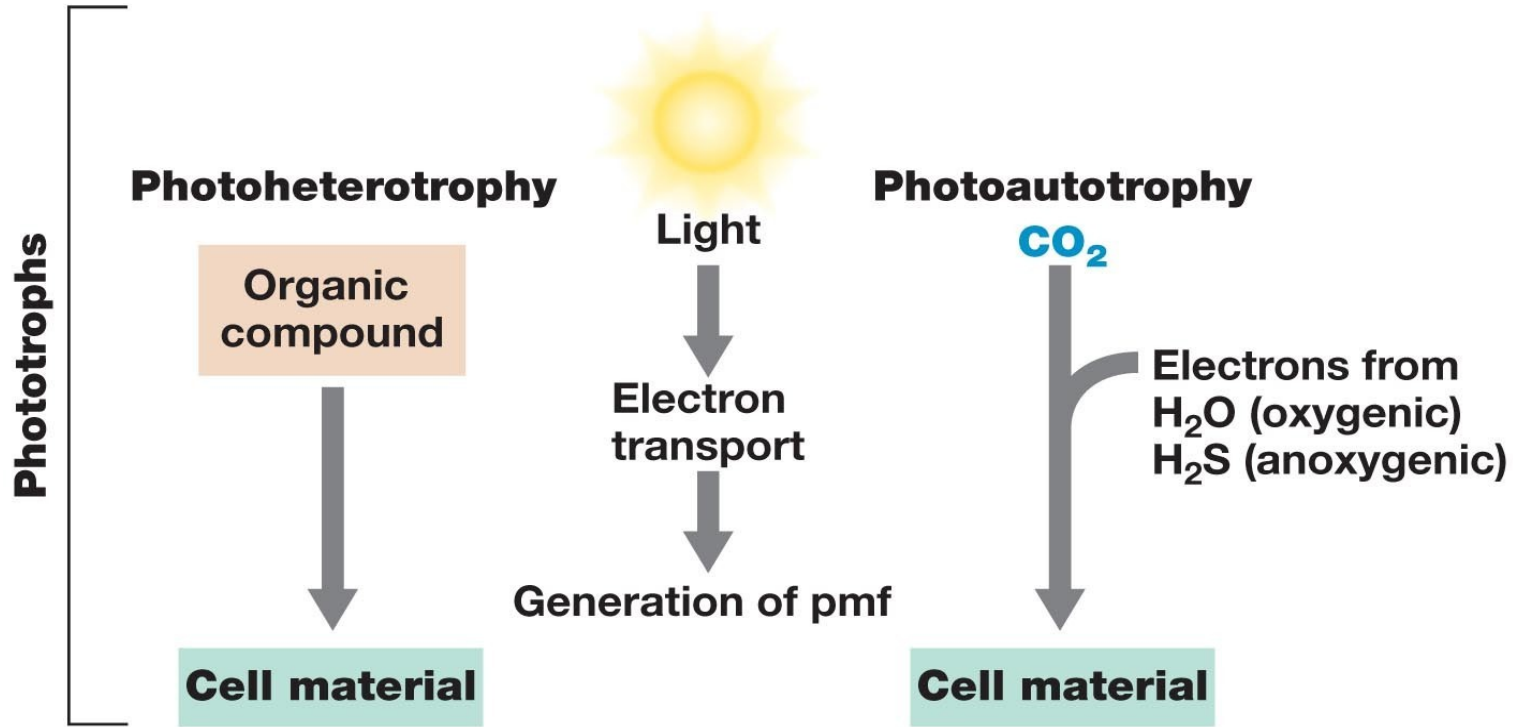
An **electron acceptor**

All type of metabolism, requires these three basic elements. An electron donor (the source of reducing power used to carry out redox reactions), a carbon source used as a donor of carbon for biosynthetic purposes, and an electron acceptor, used to dispose of excess reducing equivalents.



Phototrophy

Energy



(c) Phototrophy

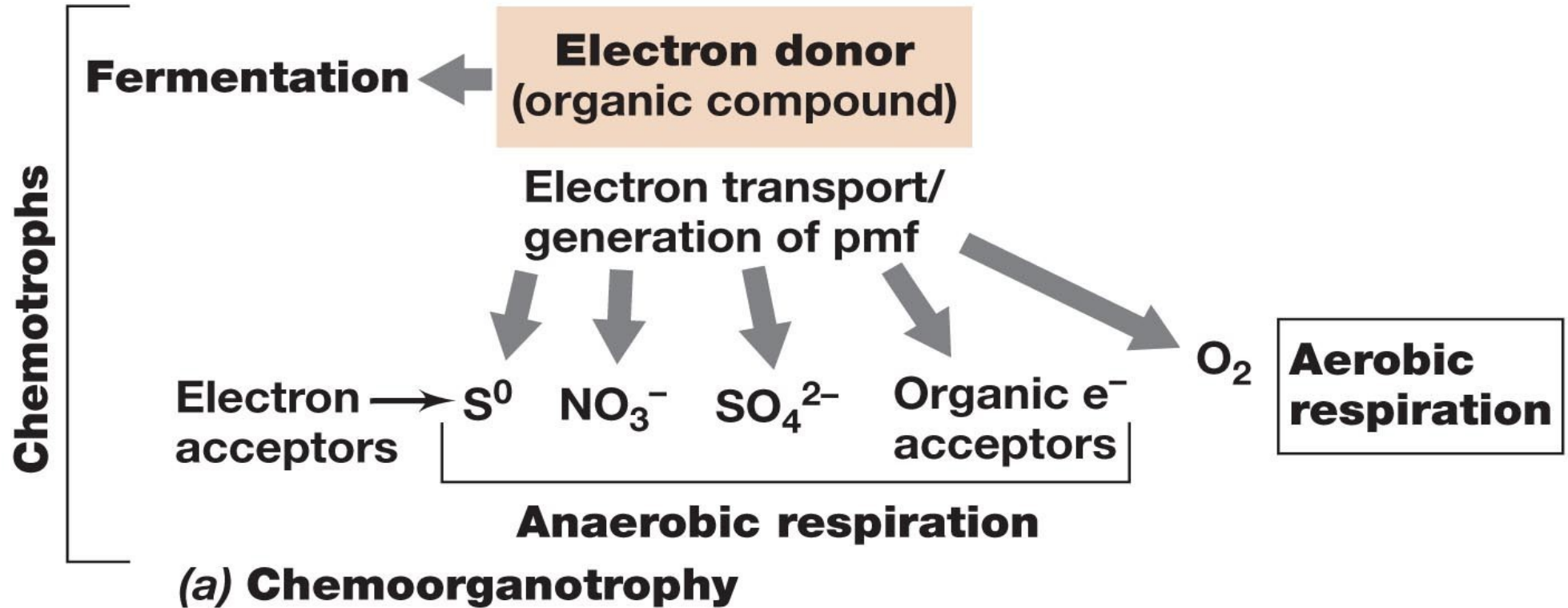
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Photoheterotrophs, Photoautotrophs: Anoxygenic photoautotrophs and Oxygenic photoauthotrophs

Chemoorganotrophy

Energy

Electrons



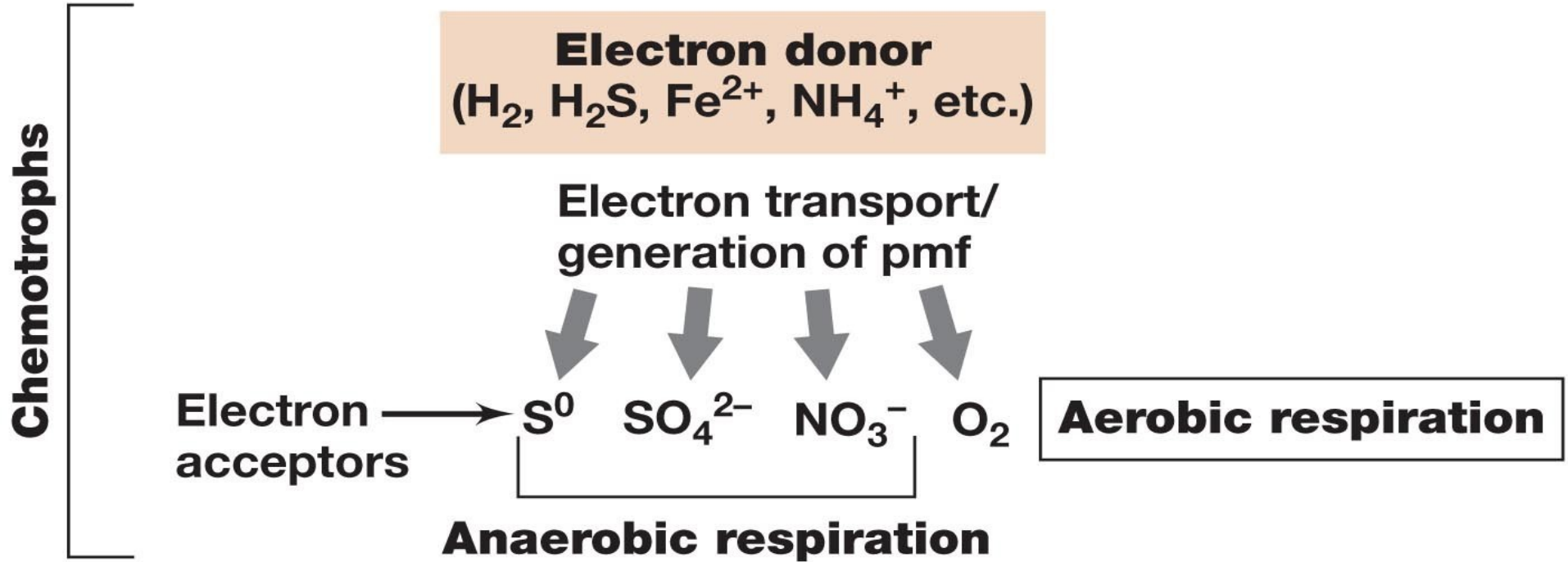
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Chemoorganotrophs can perform Aerobic Respiration, Anaerobic Respiration and Fermentation

Chemolithotrophy

Energy

Electrons



(b) Chemolithotrophy

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Chemolithotrophs can perform Aerobic Respiration and Anaerobic Respiration

Source of:

Energy Carbon Electrons

Photo-	auto-	litho-	
Chemo-	hetero-	organo-	trophy

Photo-litho-auto-trophic

Chemo-litho-auto-trophic

Chemo-litho-hetero-trophic

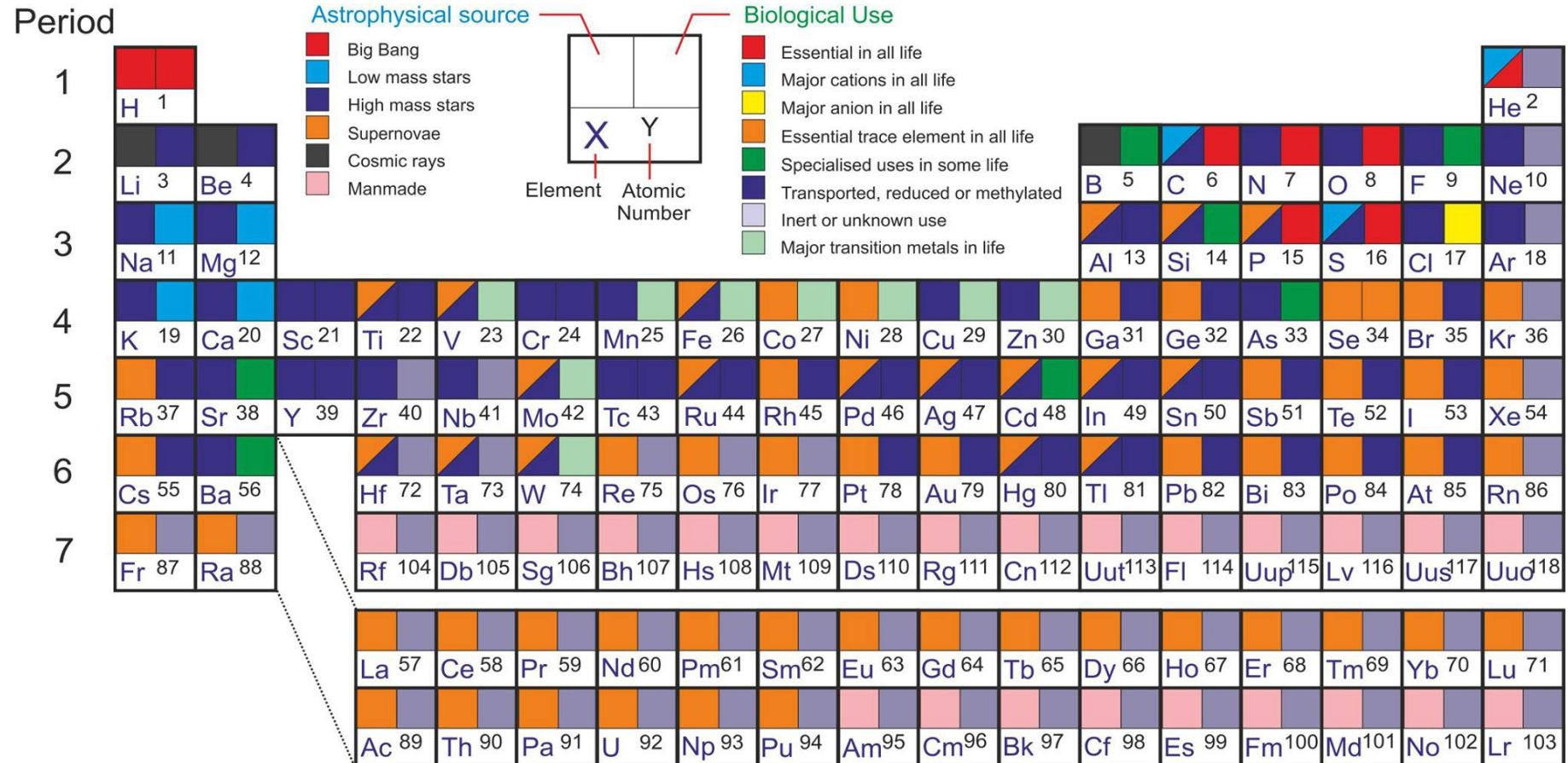
Special cases:

Methylo-trophic

Methanogenic

Syntrophic

Microbes interact with elements a lot



Basic Metabolisms

Photosynthesis

- *Phototrophs* are organisms that carry out photosynthesis
- *Most phototrophs are also autotrophs*
- Photosynthesis requires light-sensitive pigments called *chlorophyll*
- Photoautotrophy requires ATP production and CO_2 reduction
- Oxidation of H_2O produces O_2 (oxygenic photosynthesis)
- Oxygen not produced (anoxygenic photosynthesis), other electron donors used (H_2S , Fe^{2+} , H_2)
- *Oxygenic Photosynthesis* is the most important biological process on Earth

Oxygenic Photosynthesis:

Cyanobacteria (formerly known also as Cyanophyta or Blue-Green Bacteria)



Anoxic Photosynthesis:

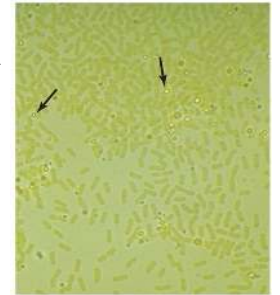
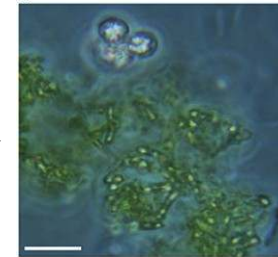
Purple Bacteria (Chromatiaceae and Rhodospirillaceae)



Green Sulfur Bacteria (Chlorobi)

Phototrophic Acidobacteria (Chloracidobacterium)

Green non-sulfur bacteria (Chloroflexi)



Photoheterotrophs:

Phototrophic Heliobacteria (Heliobacteriaceae)



Heterotrophy

- *Heterotrophy* is the use of *organic carbon sources* for anabolic purposes
- Major pathways are *Glycolisys* and *Tri-Carboxylic Acid cycle* (TCA cycle)
- Coupled to *aerobic or anaerobic respiration*. Aerobic chemorganoheterotrophy is a *major sink of oxygen*
- Many heterotrophic microorganisms have the “*fermentation option*”

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
- 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

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 $\text{O}_2/\text{H}_2\text{O}$ couple is most electropositive, more energy is available when O_2 is used as a terminal electron acceptor than when any 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. NO_3^- , SO_4^{2-} , CO_2) 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
- 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
- Several inorganic compounds can be both electron donor or electron acceptors (e.g. S^0) **depending on the redox couple** involved

The Energetics of Chemolithotrophy

- *Chemolithotrophs* are organisms that obtain energy from the oxidation of inorganic compounds
- Chemolithotrophs can tap into many natural sources of inorganic electron donors, including *geological, biological, and anthropogenic*
- *Mixotrophs* are chemolithotrophs that require organic carbon as a carbon source
- Many sources of reduced molecules exist in the environment
- The oxidation of different reduced compounds yields varying amounts of energy

Types of Chemolithotrophy

e^- donors

H_2 , NH_4^+ , H_2S , $S_{(n)}^-$, S^0 , $S_2O_3^{2-}$, S^{2-} , CH_4 , CO , Fe^{2+} , As^{3+} , etc...

e^- acceptors

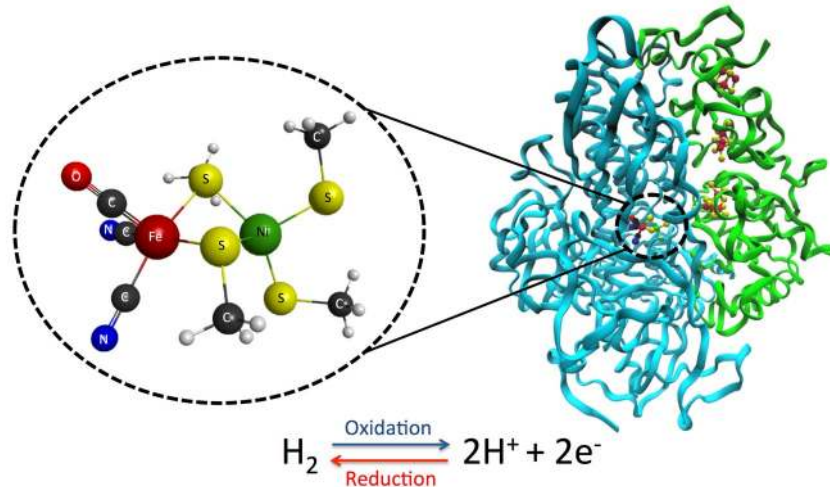
O_2 , NO_3^- , NO_2^- , N_2O , NO , SO_4^{2-} , SO_3^{2-} , S^0 , CO_2 , Fe^{3+} , Mn^{2+} , SeO_4^{2-} ,
 AsO_4^{3-} , UO_3^{2-} , TeO_4^{2-} , etc...

Hydrogen Oxidation

- **Hydrogen** (H_2) is a common product of microbial metabolism, especially of some fermentations, serpentinization and volcanic activity
- Hydrogen oxidizers obtain the most energy per two electrons oxidized
- A number of (phylogenetically different) **aerobic chemolithotrophs** can use hydrogen (known as **knallgas** bacteria), producing water as byproduct
- **Anaerobic chemolithotrophs** can also oxidize hydrogen at the expenses of other oxidized compounds (e.g. nitrate, sulfate, ferric iron, CO_2)

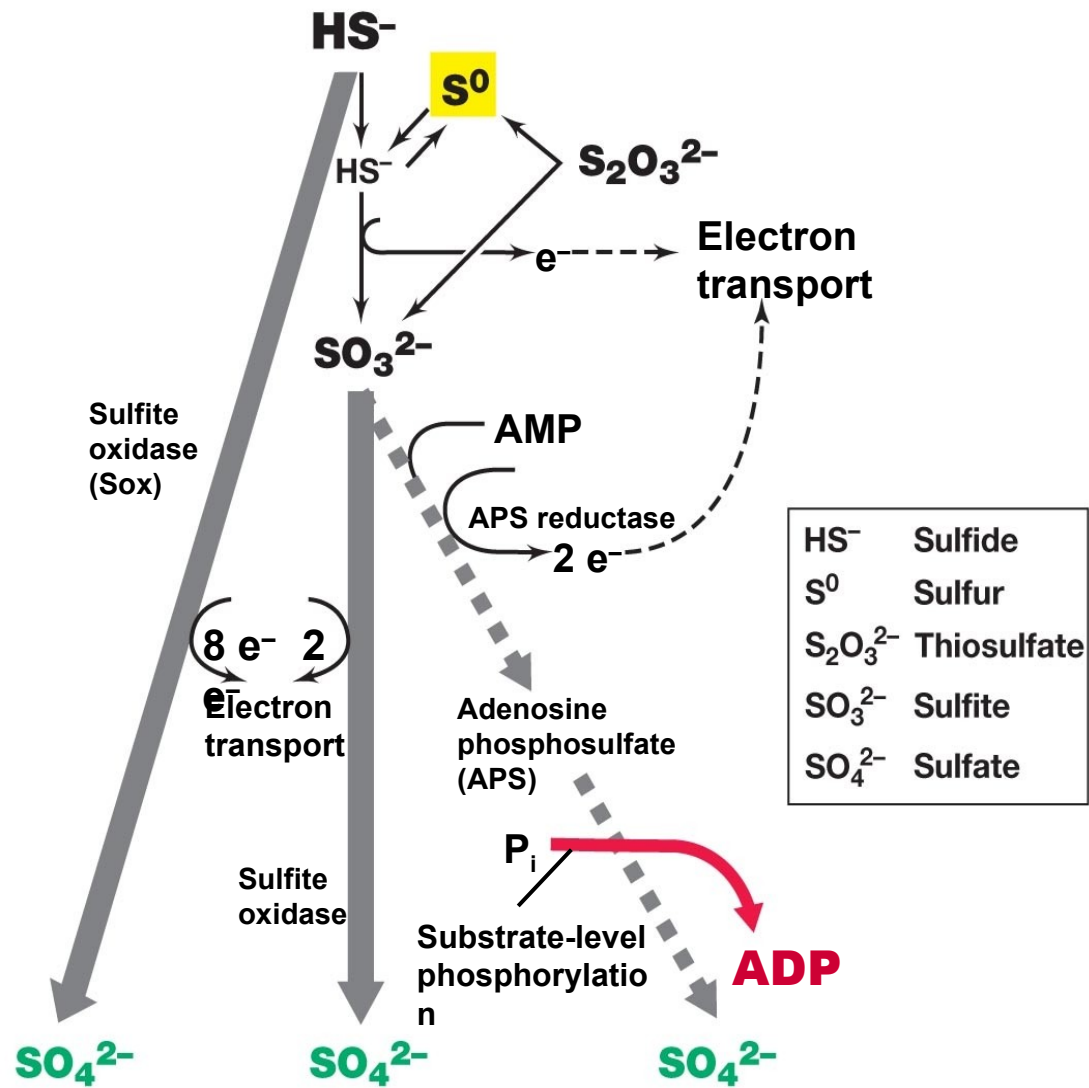
Hydrogen Oxidation

- *Hydrogenases* are the key enzymes in hydrogen oxidation
- The active site can be either a *[NiFe]*, *[FeFe]* or *[Fe]* center
- Hydrogenases are both *membrane bound, periplasmic or cytosolic*, and can be *respiratory, assimilatory or hydrogen producing*

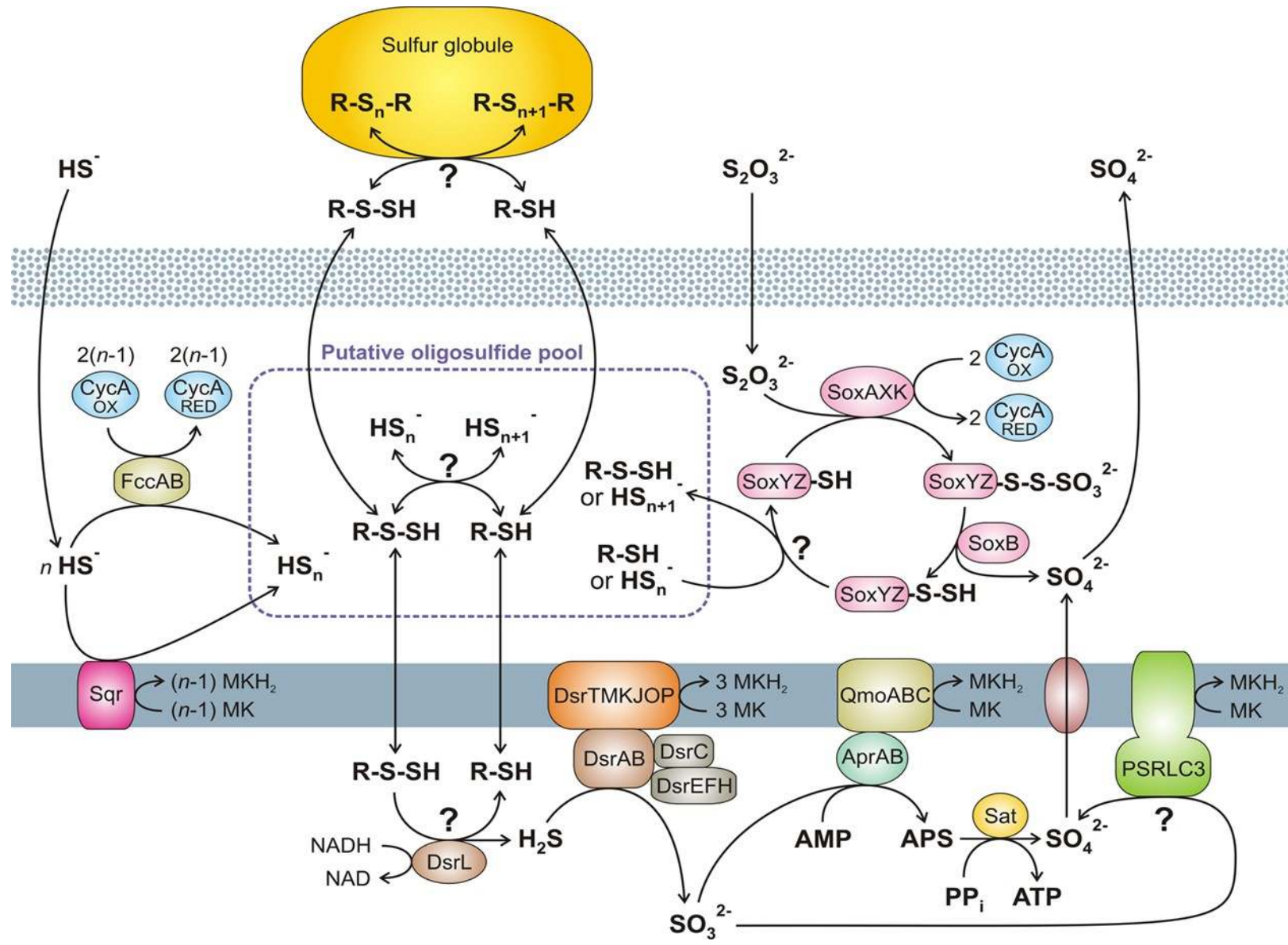


Oxidation of Reduced **Sulfur** Compounds

- Many reduced sulfur compounds are used as electron donors
- H_2S , S^0 , $S_2O_3^-$ are commonly used
- One product of sulfur oxidation is H^+ , which results in a lowering of the pH of its surroundings
- Several enzymes are involved in sulfur compound oxidation (e.g. Sox, Aps, Sulfite Oxidase)
- Sulfur Oxidizers are major player in numerous extreme environments
- Usually aerobic, but some organisms can use nitrate as an electron acceptor



(a)



Sulfate Reduction

- Sulfate (SO_4^{2-}) is reduced by the **sulfate-reducing bacteria (SBR)**, a highly diverse group of obligately anaerobic bacteria widely distributed in nature
- The end product of sulfate reduction is **hydrogen sulfide (H_2S)**, 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 number of sulfate reducers are member of the class **Deltaproteobacteria** of the phylum Proteobacteria
- **Hydrogen** and a number of **organic compounds and organic acids** (e.g. Acetate, Lactate, Propionate, Butyrate, Ethanol and other alcohols Long-chain fatty acids) are used as electron donors in sulfate reduction

Sulfur Reduction

- Besides sulfate, most sulfate-reducing bacteria can also conserve energy from the *reduction of elemental sulfur to sulfide*
- A variety of non-sulfate-reducing Bacteria and Archaea can also reduce sulfur in anaerobic respiration. These prokaryotes are phylogenetically diverse, and often can respire additional compounds (e.g. nitrate)
- *Sulfur reduction* has been proposed as a potentially ancestral metabolism

Nitrogen Fixation

- Only certain prokaryotes can fix nitrogen
- Nitrogen fixation is a **key process** in the N cycle
- Some nitrogen fixers are free living and others are symbiotic
- Reaction is catalyzed by **nitrogenase**, sensitive to the presence of oxygen
- A wide variety of nitrogenases use different metal cofactors (**MoFe, V, and FeS**)
- Nitrogenases are **promiscuous enzymes**. They catalyze a high number of side reactions (e.g. cyanide, cyanate, acetylene, azide, hydrogen, thiocyanate, carbonyl sulfide)

Oxidized **Nitrogen** Species Reduction

- Inorganic nitrogen compounds are some of the **most common electron acceptors in anaerobic respiration**
- 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. This process is known as **Denitrification**
- Nitrate can also be reduced all the way to ammonia, in this case the process is known as **Dissimilatory Nitrate Reduction to Ammonia (DNRA)**
- 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)**

Nitrification

- NH_3 and NO_2^- are oxidized by *nitrifying prokaryotes* during the process of *nitrification*; major player in the *N cycle*
- Two groups of bacteria Carry out ammonia or nitrite oxidation: *Nitrospirae* and selected genera of the *Proteobacteria* (*Nitrosomonas*, *Nitrosospira*, *Nitrosococcus*, *Nitrosolobus*, and *Nitrobacter*, *Nitrospina*, *Nitrococcus*)
- One group of archaea carries out ammonia oxidation (*Thaumarchaeota*)
- Key enzymes are *ammonia monooxygenase*, *hydroxylamine oxidoreductase*, and *nitrite oxidoreductase*
- Only small energy yields from this reaction

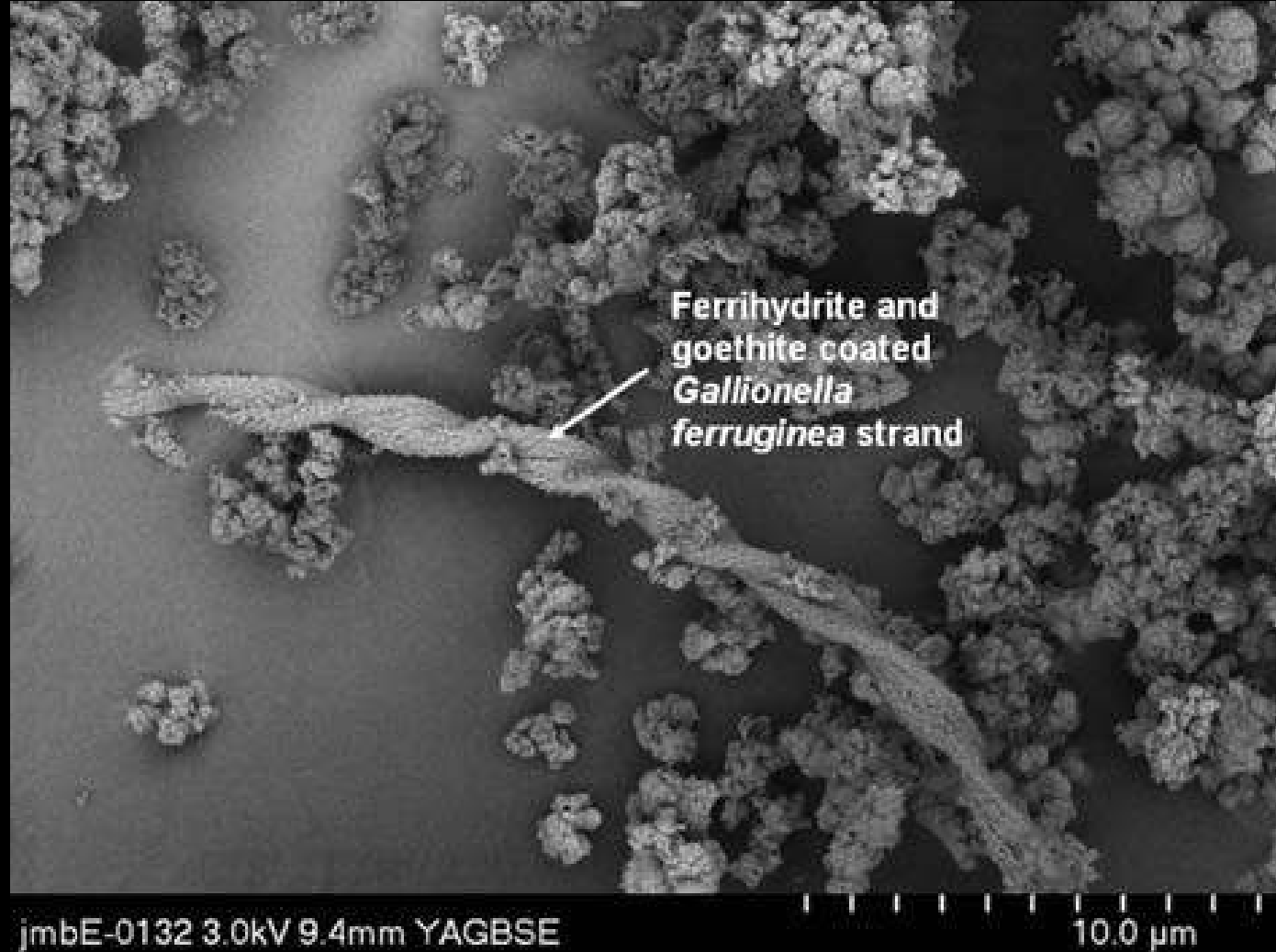
Anaerobic Ammonia Oxidation **Anammox**

- **Anammox**: anerobic ammonia oxidation (discovered 1999!)
 - $\text{NH}_4^+ + \text{NO}_2^- \rightarrow \text{N}_2 + 2 \text{H}_2\text{O}$
- Performed by unusual group of obligate **anaerobes** (*Planctomycetes*, order *Brocadiales*)
- **Anammoxosome** is a membrane-enclosed compartment where anammox reactions occur
 - Lipids that make up the anammoxosome are not the typical lipids of Bacteria
 - Protects cell from reactions occurring during anammox
 - **Hydrazine** ($\text{H}_2\text{N}=\text{NH}_2$), a very strong reductant, is an intermediate of anammox
- **Major sink for fixed nitrogen**. May be responsible for 30-50% of the N_2 gas produced in the oceans. It limits oceanic primary productivity

Iron Oxidation

- Ferrous iron (Fe^{2+}) oxidized to ferric iron (Fe^{3+})
- Ferric hydroxide precipitates in water
- Many Fe oxidizers are acidophiles (and can grow at pH < 1)
- Associated with mine drainage and geothermal emissions
- Both Bacteria and Archaea can oxidize iron
- Some anoxygenic phototrophs can oxidize Fe^{2+} anaerobically using Fe^{2+} as an electron donor for CO_2 reduction

Iron Hydroxide Twisted Stalks



Iron Reduction

- Ferric iron (Fe^{3+}) is reduced to ferrous iron (Fe^{2+})
- It is only possible in anaerobic conditions
- Iron III is a good electron acceptor in many anaerobic environments
- Electron donor can be organic matter (heterotrophy) or hydrogen and H_2S



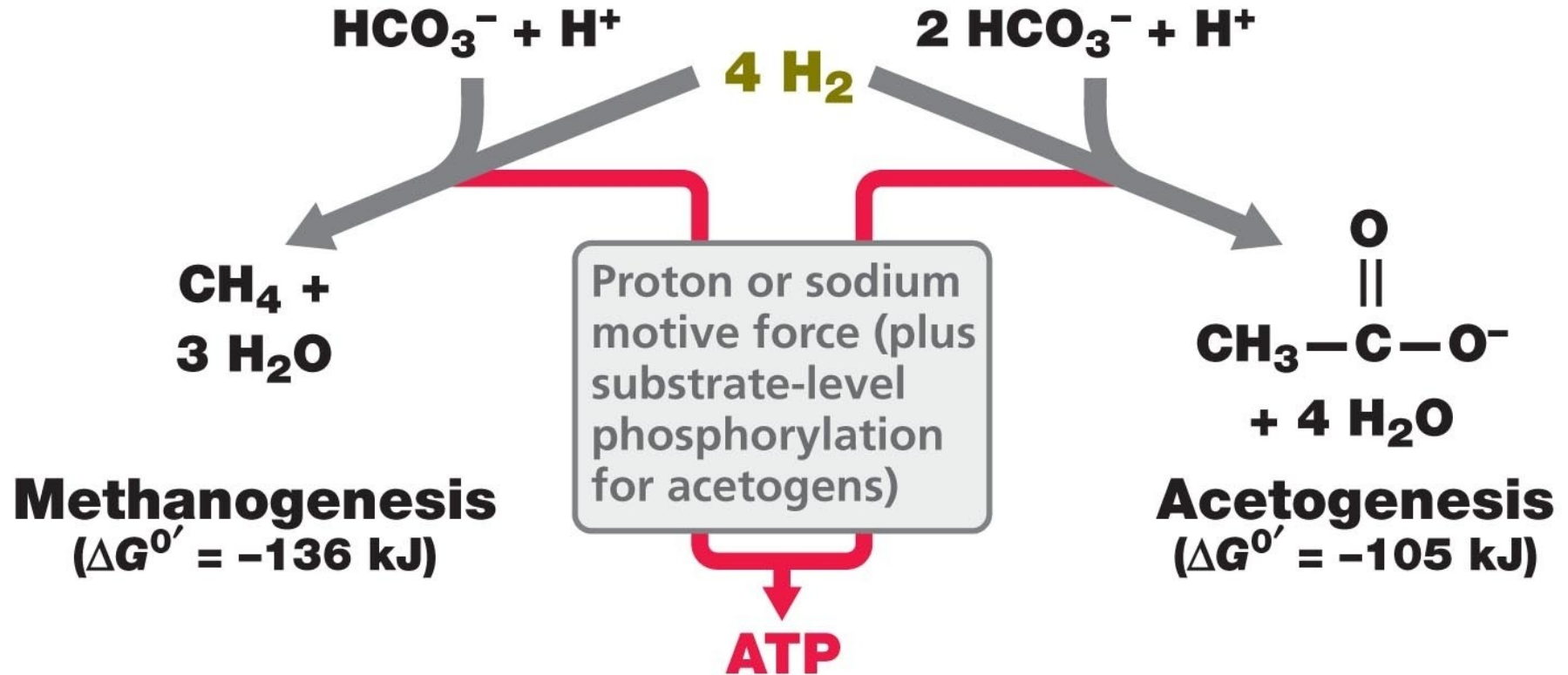
**- control
(no bacteria)**

**Iron-reducing
culture**

Methanogenesis and Acetogenesis

- The production of methane (*methanogenesis*) is carried out by a strictly anaerobic group of *Archaea*. *Acetogenesis* is carried out prevalently by *gram positive Bacteria* (especially members of the genera *Clostridium* or *Acetobacterium*)
- 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
- Energy conservation in acetogenesis results from both substrate-level phosphorylation and PMF. In methanogenesis substrate-level phosphorylation does not occur

Methanogenesis and Acetogenesis



Methane Oxidation

- Global sink of methane, a strong greenhouse gas
- Exists in two forms *Aerobic Methane Oxidation*, and *Anaerobic Methane Oxidation*
- Diverse members of the Bacteria carry out the former (*Proteobacteria*, *Verrucomicrobia*, while the latter is carried out by a polyphyletic of Archaea (*ANME group*) and Bacteria (*NC10 candidate division*)
- Aerobic Methane Oxidizers work alone in oxidizing methane, while ANME require a *bacterial partner* to carry out Anaerobic Methane Oxidation

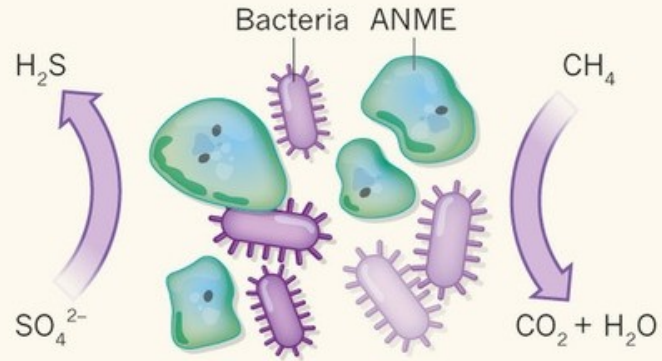
Aerobic **Methane** Oxidation

- Limited to areas to where methane reaches **oxic areas**
- **Methanotrophs** (organisms performing aerobic methane oxidation) are a special class of **Methylobacteria**
- Aerobic-methane oxidizers are exclusively Bacteria of the phyla **Proteobacteria (Alpha, Beta and Gamma classes)** and **Verrucomicrobia**
- Aerobic Methane Oxidizers oxidize methane by first initiating reduction of an oxygen atom to H_2O_2 and transformation of methane to CH_3OH using **methane monooxygenases (MMOs)**

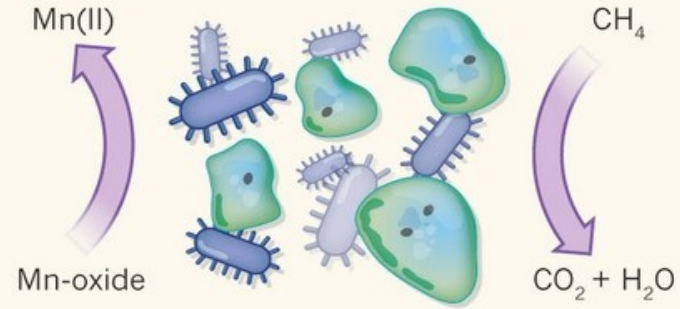
Anaerobic **Methane** Oxidation

- Anaerobic Oxidation of Methane – also known as AOM - is *the major sink* of methane worldwide
- It is responsible for the *removal of up to 90%* of the $85\text{-}300 \text{ Tg CH}_4 \text{ yr}^{-1}$ released from the seafloor
- AOM occurs in anoxic sediments, and it has been reported in the *methane-sulfate transition zone* (from few mm to 200 mbsf) 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)*

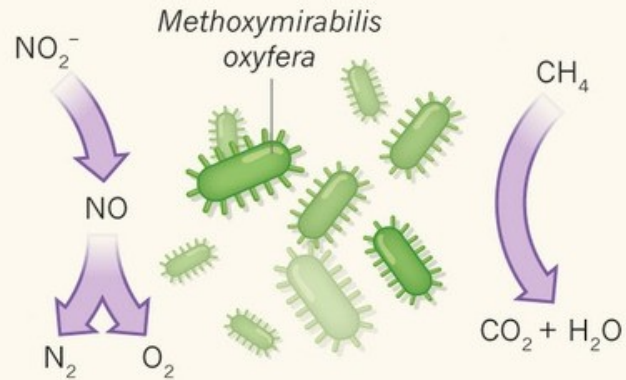
a AOM coupled to sulphate reduction



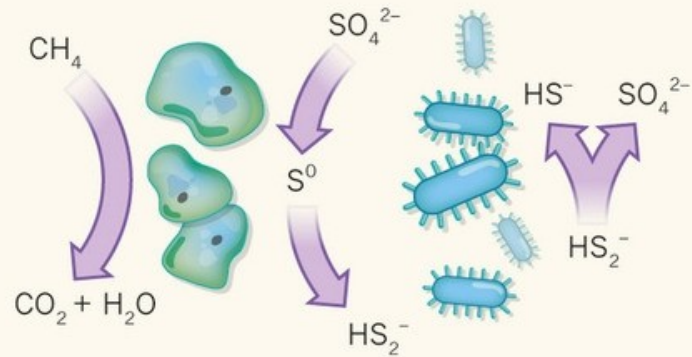
b AOM coupled to metal-oxide reduction



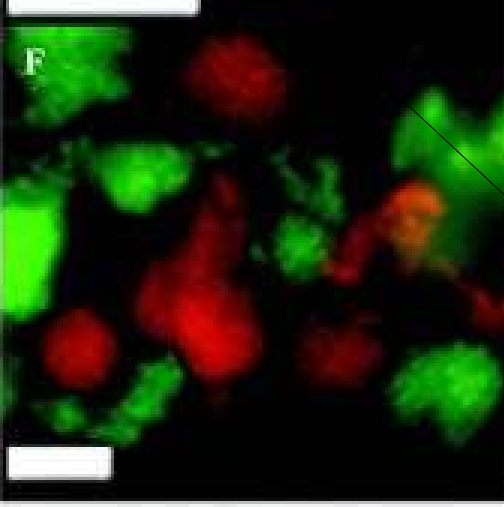
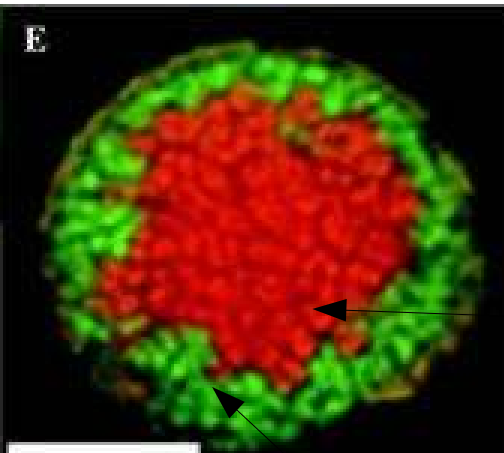
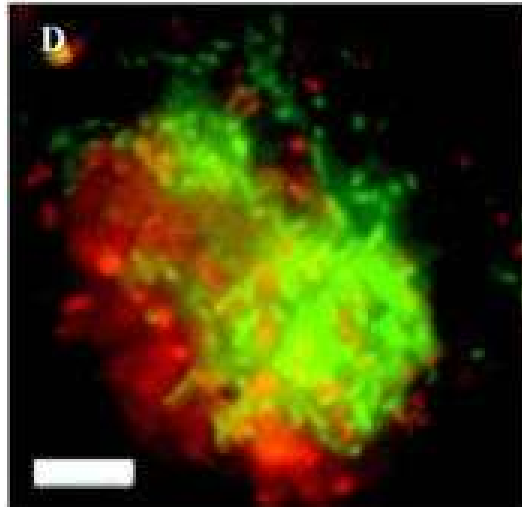
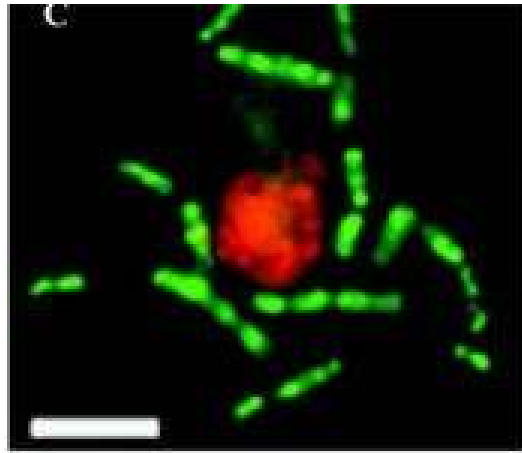
c AOM by nitrite dismutation



d AOM and disulphide disproportionation



ANME and SBR



ANME-1

Desulfosarcina spp.
SBR Bacteria

Autotrophy

- *Authotrophy* is the process of building biomass from *inorganic carbon sources* (e.g., CO_2 , CO)
- *Six different major pathways* of carbon fixation are known
- The *Calvin-Benson-Bassam* cycle is the major pathway in the extant biosphere, and is used by *oxygenic photoauthotrophs* and several *aerobic chemolithoautotrophs*
- *rTCA cycle* and *Wood–Ljungdahl pathway* are also widely distributed, although generally present in *microaerophiles* or *strict anaerobes*
- All six pathways partially overlap due to the centrality of certain metabolic intermediate

Types of Chemolithotrophy

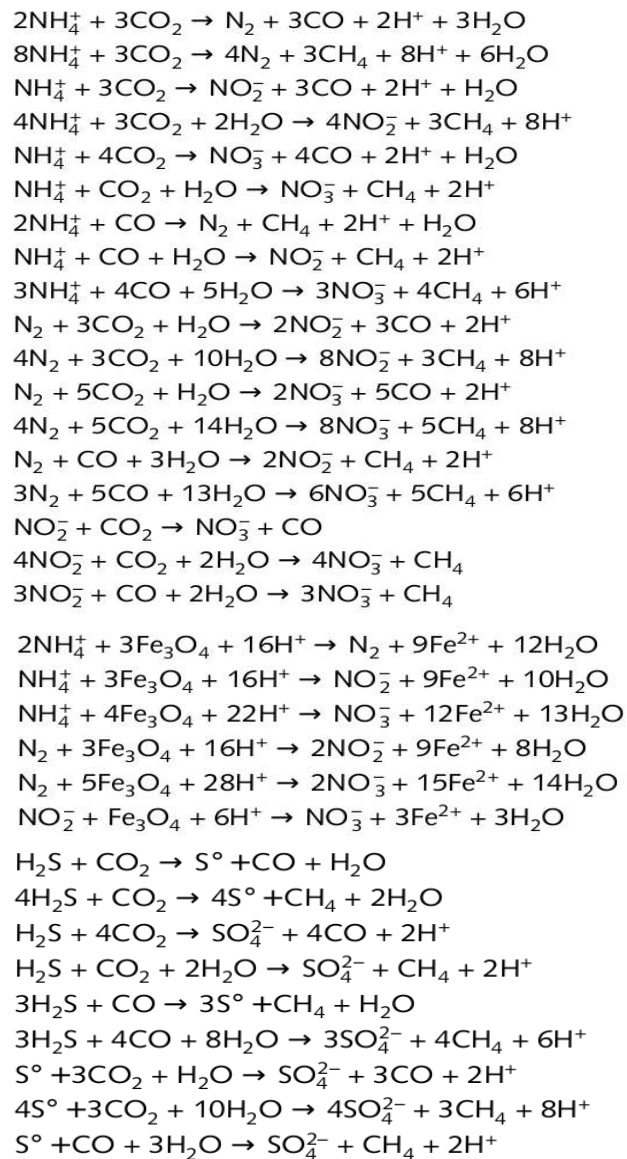
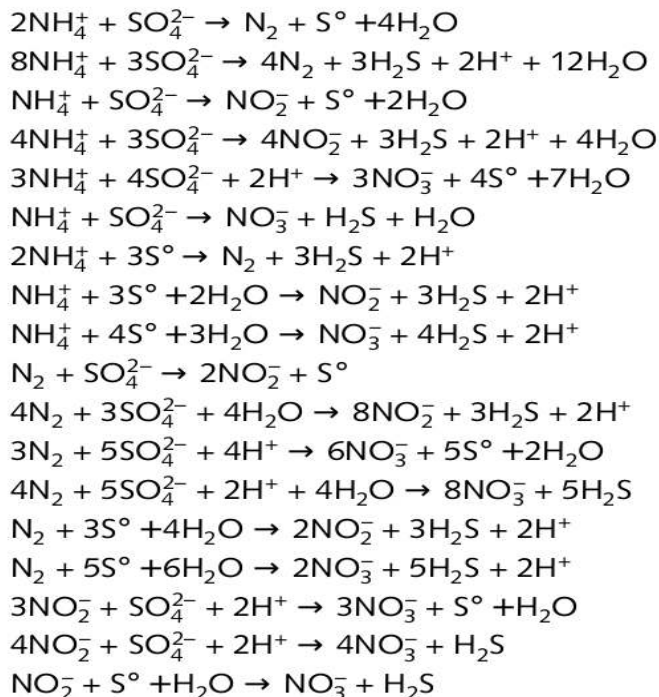
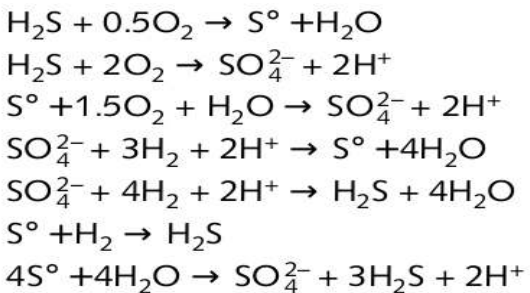
e^- donors

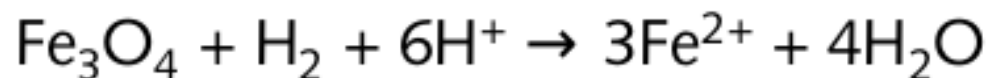
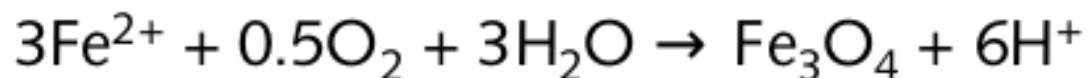
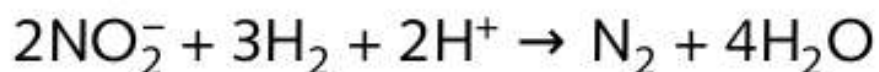
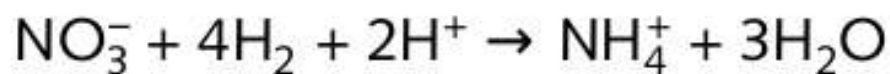
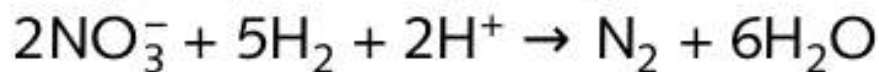
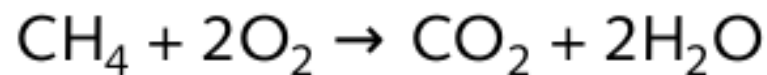
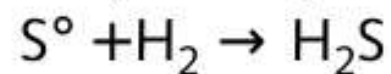
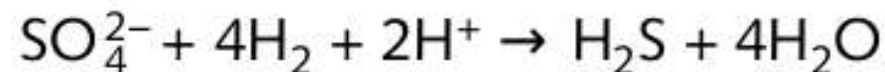
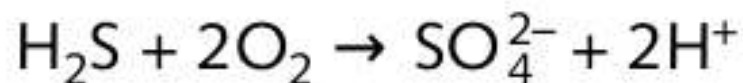
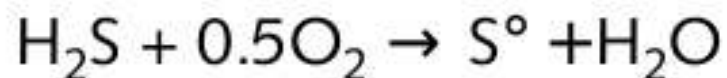
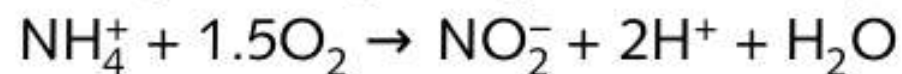
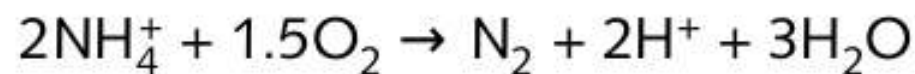
H_2 , NH_4^+ , H_2S , $S_{(n)}^-$, S^0 , $S_2O_3^{2-}$, S^{2-} , CH_4 , CO , Fe^{2+} , As^{3+} , etc...

e^- acceptors

O_2 , NO_3^- , NO_2^- , N_2O , NO , SO_4^{2-} , SO_3^{2-} , S^0 , CO_2 , Fe^{3+} , Mn^{2+} , SeO_4^{2-} ,
 AsO_4^{3-} , UO_3^{2-} , TeO_4^{2-} , etc...

Reaction
$2\text{NH}_4^+ + 1.5\text{O}_2 \rightarrow \text{N}_2 + 2\text{H}^+ + 3\text{H}_2\text{O}$ $\text{NH}_4^+ + 1.5\text{O}_2 \rightarrow \text{NO}_2^- + 2\text{H}^+ + \text{H}_2\text{O}$ $\text{NH}_4^+ + 2\text{O}_2 \rightarrow \text{NO}_3^- + 2\text{H}^+ + \text{H}_2\text{O}$ $\text{N}_2 + 1.5\text{O}_2 + \text{H}_2\text{O} \rightarrow 2\text{NO}_2^- + 2\text{H}^+$ $\text{N}_2 + 2.5\text{O}_2 + \text{H}_2\text{O} \rightarrow 2\text{NO}_3^- + 2\text{H}^+$ $\text{NO}_2^- + 0.5\text{O}_2 \rightarrow \text{NO}_3^-$ $\text{NO}_3^- + \text{H}_2 \rightarrow \text{NO}_2^- + \text{H}_2\text{O}$ $2\text{NO}_3^- + 5\text{H}_2 + 2\text{H}^+ \rightarrow \text{N}_2 + 6\text{H}_2\text{O}$ $\text{NO}_3^- + 4\text{H}_2 + 2\text{H}^+ \rightarrow \text{NH}_4^+ + 3\text{H}_2\text{O}$ $2\text{NO}_2^- + 3\text{H}_2 + 2\text{H}^+ \rightarrow \text{N}_2 + 4\text{H}_2\text{O}$ $\text{NO}_2^- + 3\text{H}_2 + 2\text{H}^+ \rightarrow \text{NH}_4^+ + 2\text{H}_2\text{O}$ $\text{N}_2 + 3\text{H}_2 + 2\text{H}^+ \rightarrow 2\text{NH}_4^+$ $4\text{N}_2 + 2\text{H}^+ + 9\text{H}_2\text{O} \rightarrow 3\text{NO}_3^- + 5\text{NH}_4^+$ $\text{N}_2 + 2\text{H}_2\text{O} \rightarrow \text{NO}_2^- + \text{NH}_4^+$ $4\text{NO}_2^- + 2\text{H}^+ + \text{H}_2\text{O} \rightarrow 3\text{NO}_3^- + \text{NH}_4^+$ $5\text{NO}_2^- + 2\text{H}^+ \rightarrow 3\text{NO}_3^- + \text{N}_2 + \text{H}_2\text{O}$
$\text{CH}_4 + 1.5\text{O}_2 \rightarrow \text{CO} + 2\text{H}_2\text{O}$ $\text{CH}_4 + 2\text{O}_2 \rightarrow \text{CO}_2 + 2\text{H}_2\text{O}$ $\text{CO} + 0.5\text{O}_2 \rightarrow \text{CO}_2$ $\text{CO}_2 + \text{H}_2 \rightarrow \text{CO} + \text{H}_2\text{O}$ $\text{CO}_2 + 4\text{H}_2 \rightarrow \text{CH}_4 + 2\text{H}_2\text{O}$ $\text{CO} + 3\text{H}_2 \rightarrow \text{CH}_4 + \text{H}_2\text{O}$ $4\text{CO} + 2\text{H}_2\text{O} \rightarrow 3\text{CO}_2 + \text{CH}_4$





This week reads

Jelen B, Giovannelli D, Falkowski PG . 2016. The Role of Microbial Electron Transfer in the Coevolution of the Geosphere and Biosphere. Annual Review of Microbiology, 70:45–62.

DOI: 10.1146/annurev-micro-102215-095521

Berg, I. A. (2011). Ecological Aspects of the Distribution of Different Autotrophic CO₂ Fixation Pathways. Appl. Environ. Microbiol. 77, 1925–1936. doi:10.1128/AEM.02473-10.