Origin of Life Part 1: Organization of the biosphere

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Outline of 3 lectures

- Levels of organization of the biosphere, biochemistry, and bioenergetics
- Core carbon synthesis as the first step in the emergence of life?
- The emergence of hierarchy, cross-level constraints, and the directions of information flow

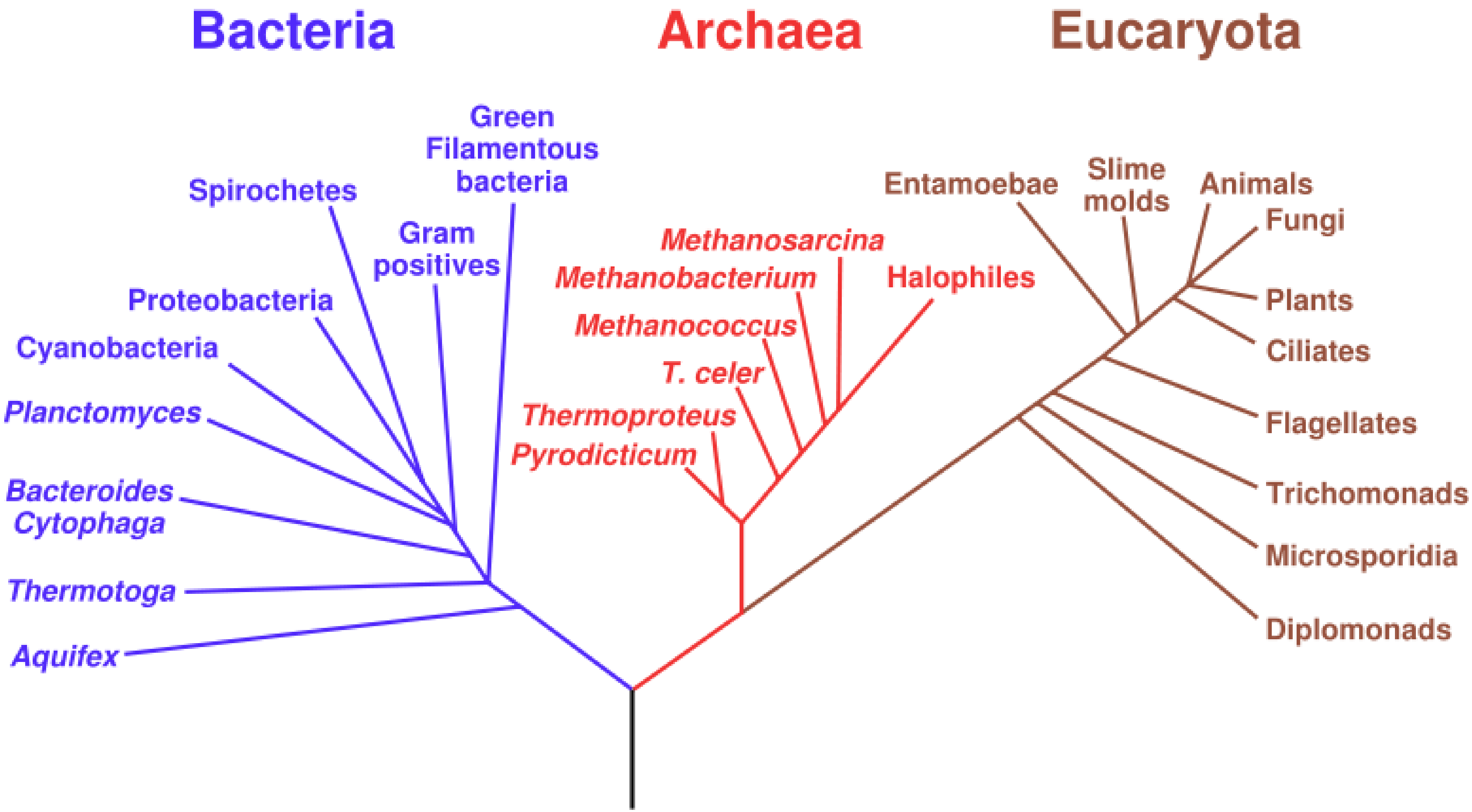
Outline for this lecture

- Genetic versus typological views of the organization of life
- Universal features of biochemistry and physiological organization
- Bioenergetics and the relation of biochemistry to geochemistry

Historical thinking in relation to typological thinking about life

- Darawinian thinking: history and process
- Ecology versus individuality
- Chance and necessity in species and metabolism

Accidents help reconstruct past from present
Reconstructions can tell about causation

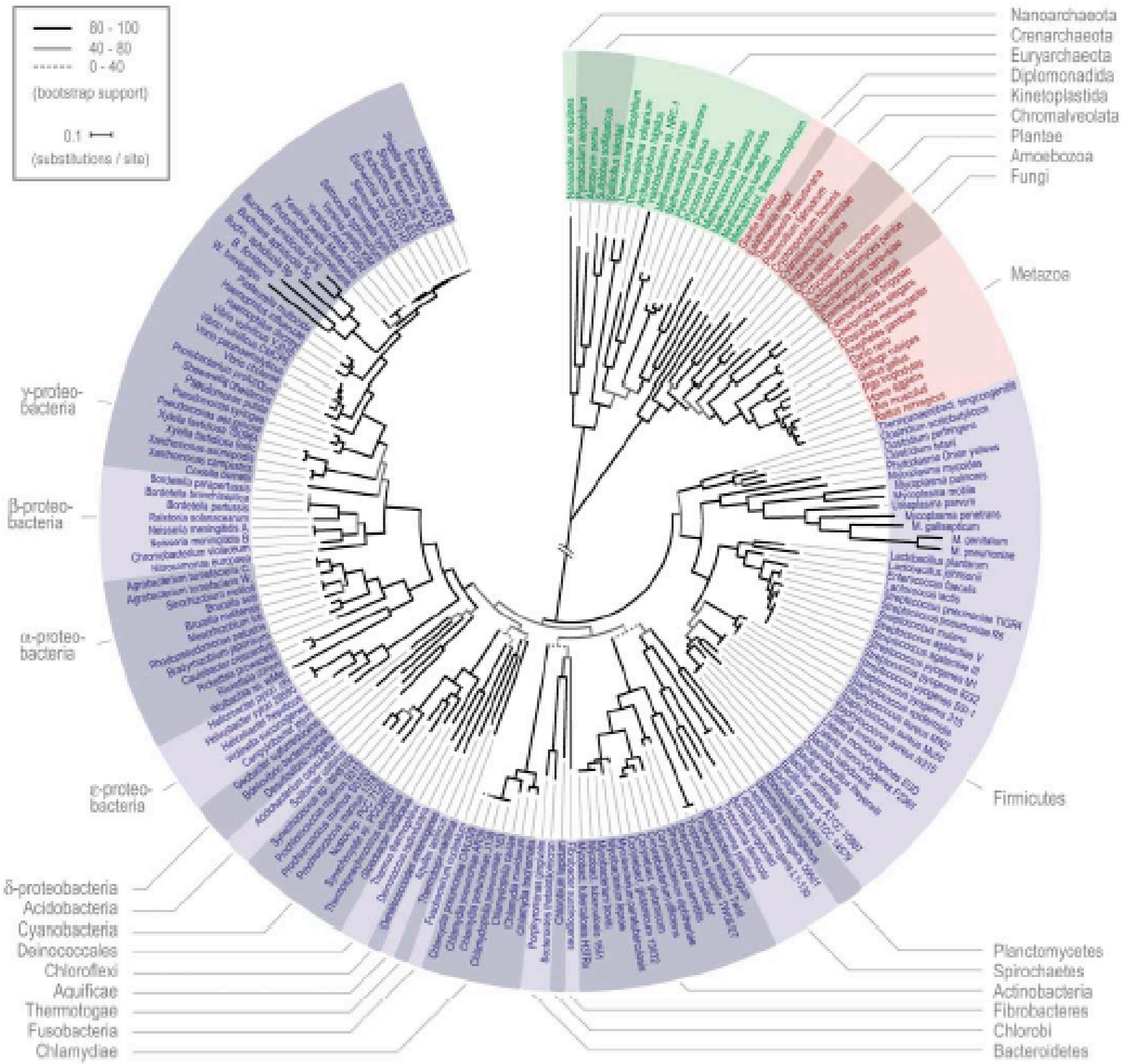


Deep branches suggest old forms and conditions

Widely preserved features in groups having deep common ancestors may be ancient

Thermophily and chemotrophy are good candidates for ancient traits

Cyanobacteria *per se* do not look like an old group



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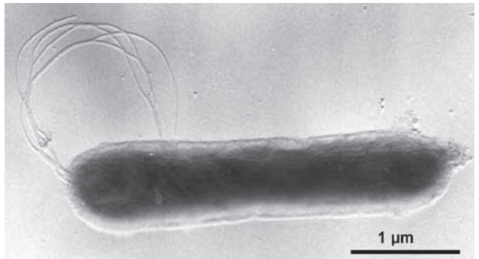
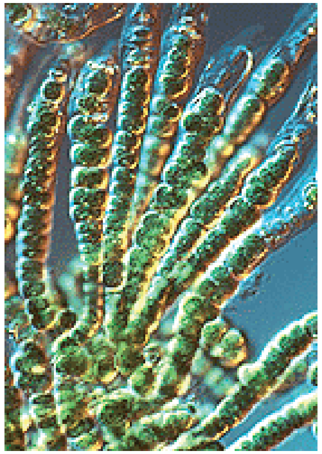
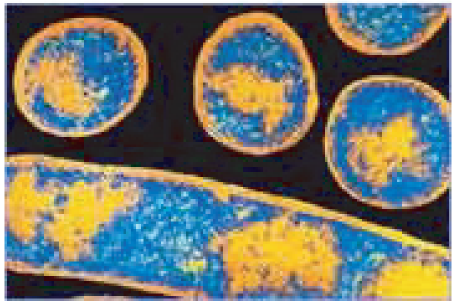
Two typological distinctions categorize metabolisms at the ecological and individual level

- Energy source: oxidation or reduction
- Biosynthesis: complete in individuals or shared across the ecology?

	Reductive metabolisms	Oxidative metabolisms
Autotrophs		
Heterotrophs		

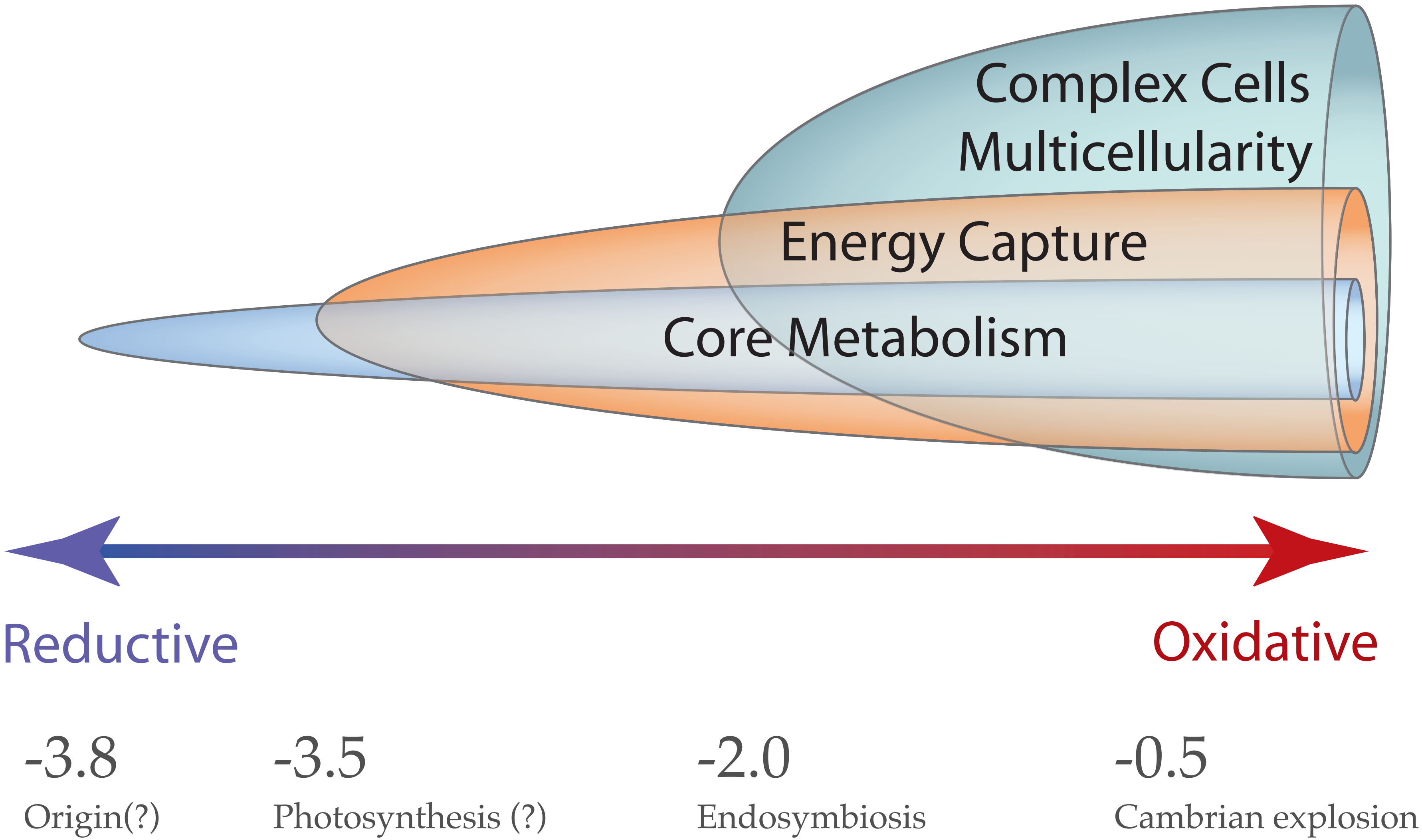
Whole-ecosystem metabolism is simpler and more universal than species metabolism

Reductive ecologies

Oxidative ecologies

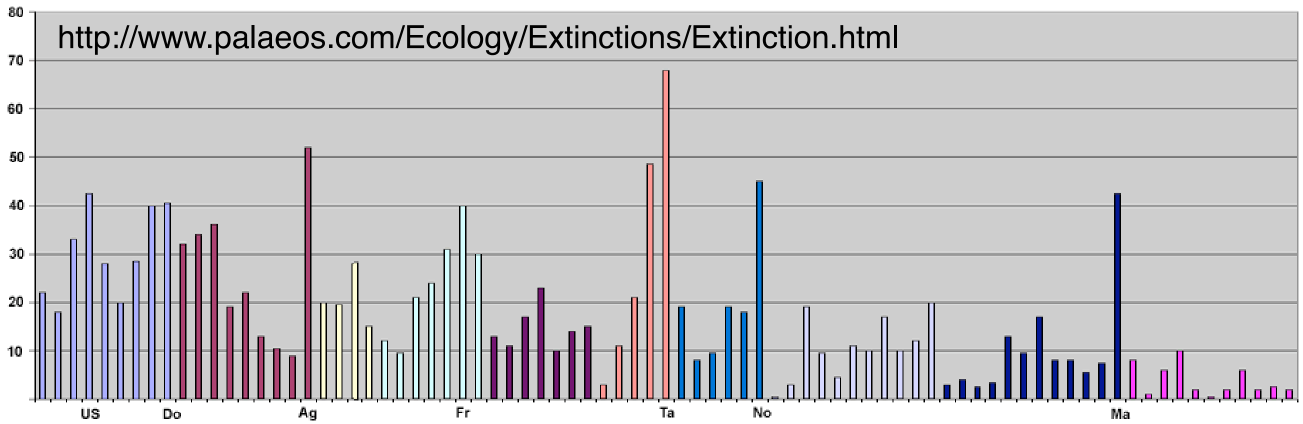
(Ecosystems are more fundamental than organisms)

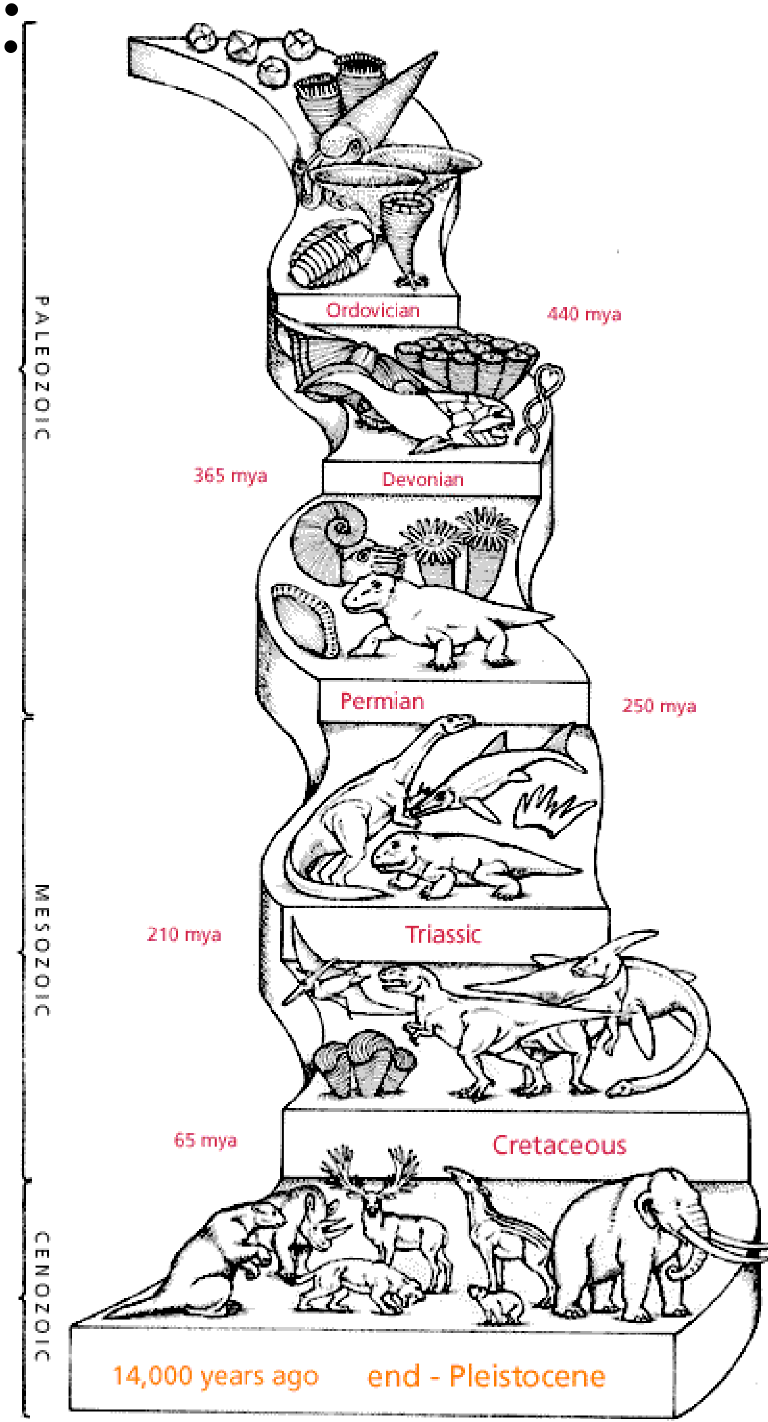
Technologies of life have emerged jointly with *geosphere modifications*



(The major transitions in evolution were chemical)

Species punctuated equilibrium: constancy in metabolism

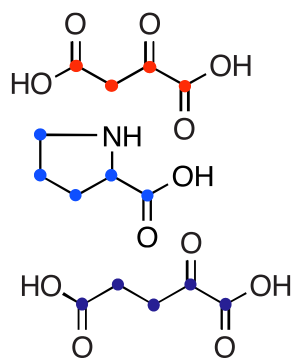


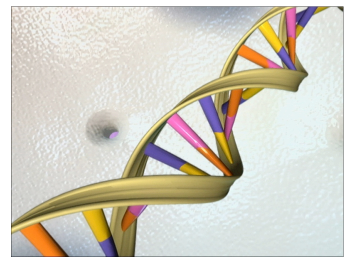


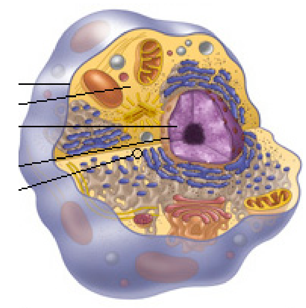
- Genus-level extinction has happened constantly
- Yet core biochemistry has persisted with little loss and only occasional innovation

http://www.amnh.org/science/biodiversity/extinction/Intro/OngoingProcess.html

Chance and necessity: life spans a continuum from thermodynamics to individuality







Necessity	Chance
Universal	Variable
Steady	Fluctuating
Predictable	Contingent

Ecological order is the natural bridge between geochemistry and life

General comments about ecology versus individuality in relation to origins thinking

- The deepest metabolic properties are most universal and constant at the ecosystem level
- It is not clear that individuality or Darwinian species dynamics are important to explaining this
- There does seem to be a level of "phenotypic necessity" that has constrained evolution so far

Organization and universal features of life that any theory of its origin should explain

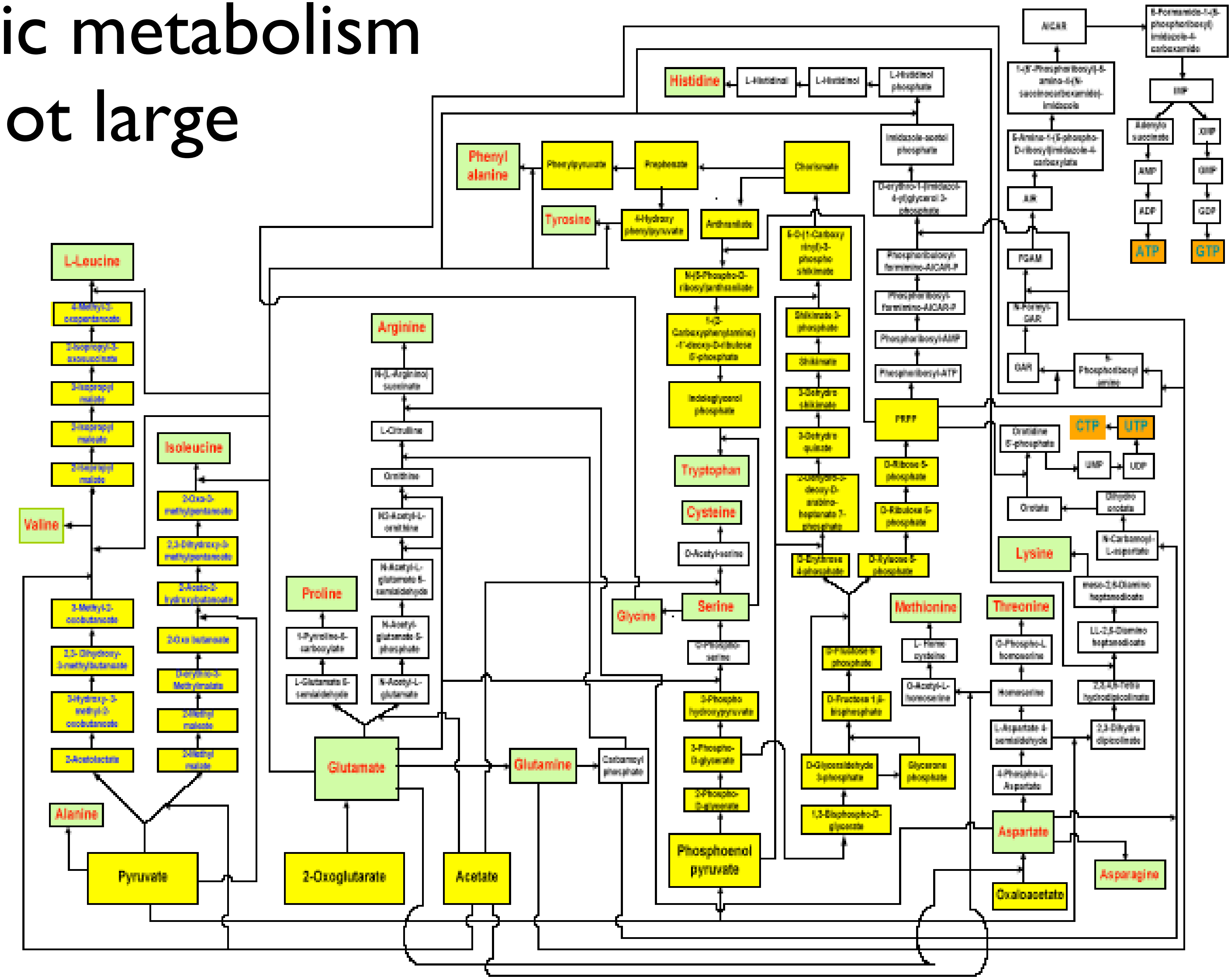
- Basic organization of biochemistry and physiology
- Kinetic control: catalysis and physical structures

The small-molecule metabolic substrate is organized into four major molecule classes

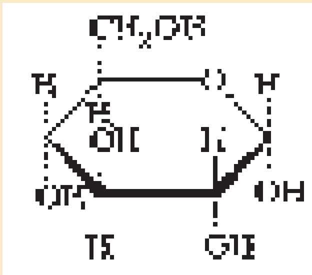
- Fatty acids (compartments, polar environments)
- Sugars (structure, signaling, energy storage)
- Amino acids (catalysis, structure)
- Nucleic acids (heredity, catalysis)

The necessary basic metabolism is not large

V. Srinivasan and H. J. Morowitz, Biol. Bulletin (to appear)



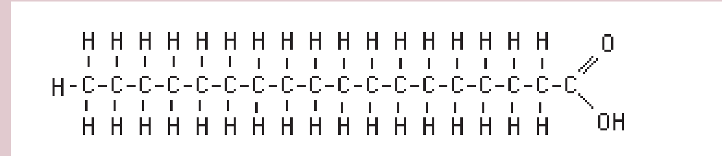
Function is tied to chemical form and synthesis



10s

sugars

Major Energy Carrier
Structure in cell walls

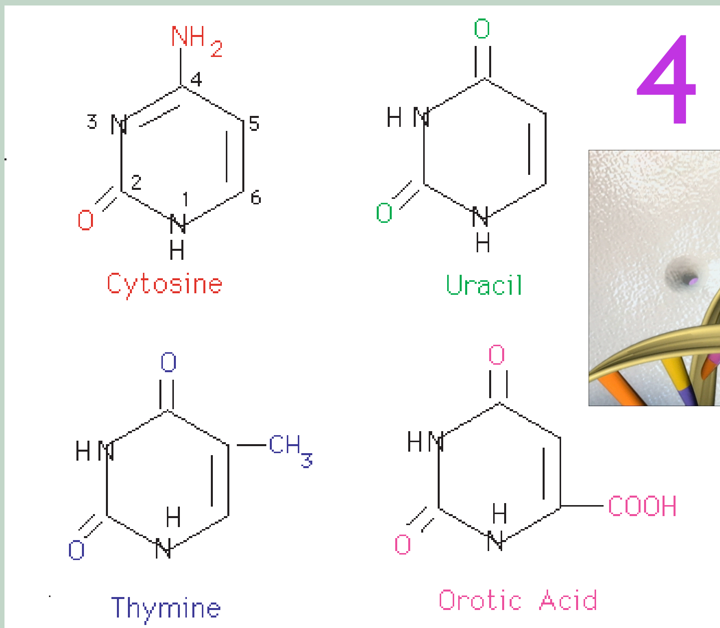


lipids

Compartments, proton semiconductors

10s

Nucleic acids



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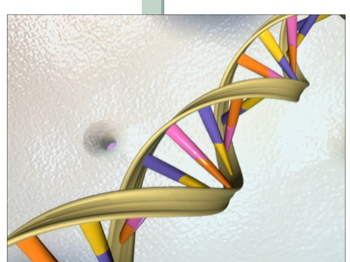
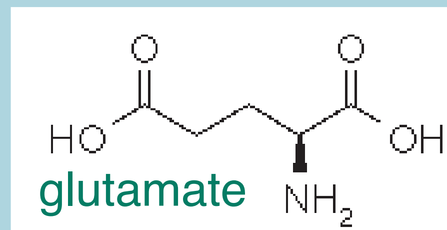
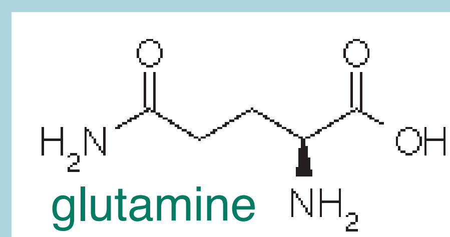


Structure, catalysis, heredity





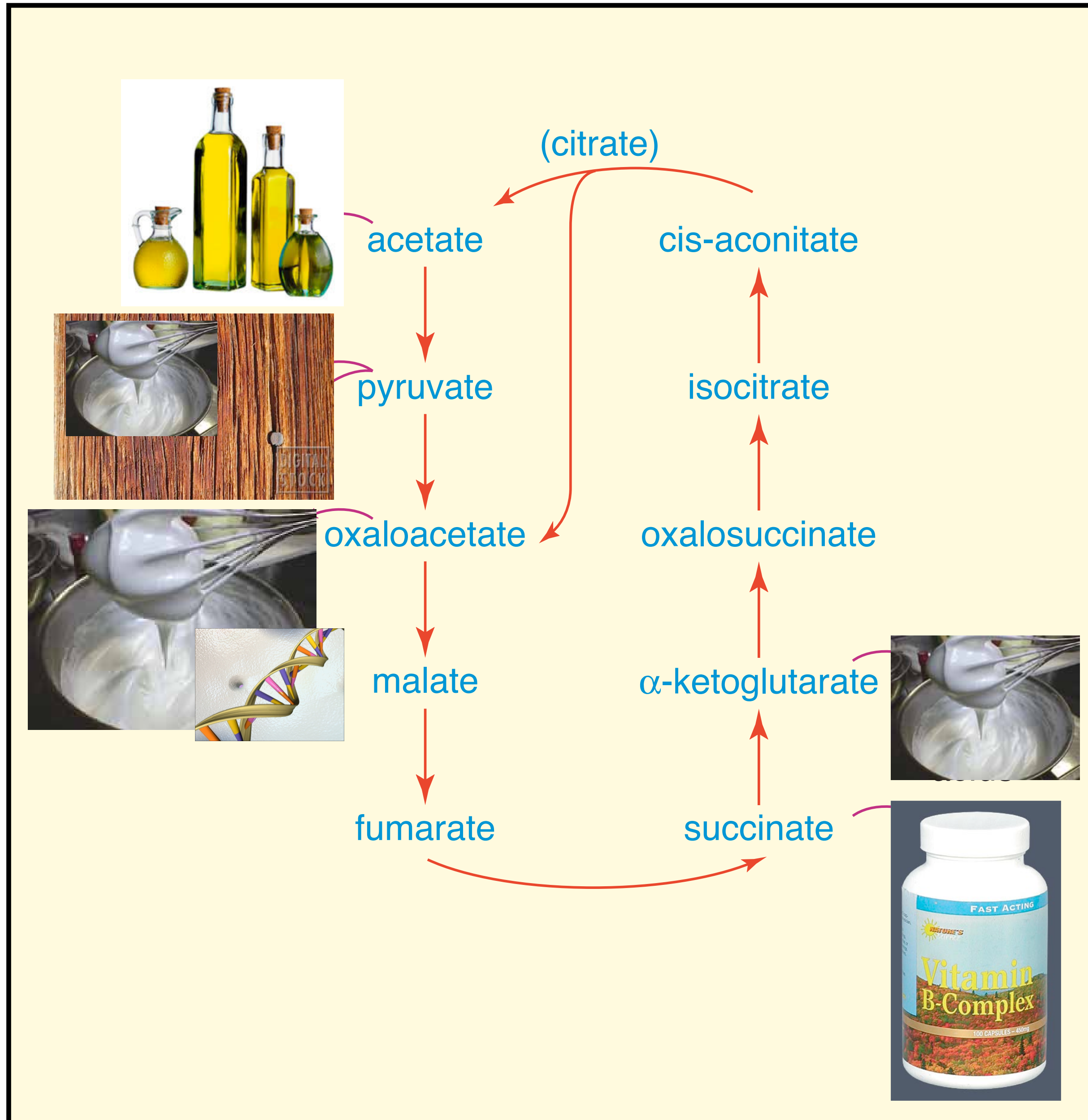
Amino acids

Catalysis/structure/motors

20

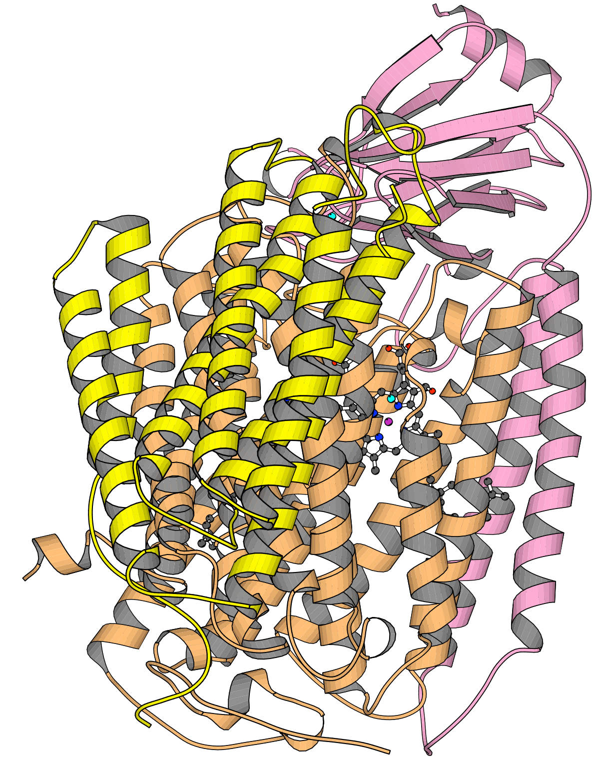
Biosynthesis has a simple core

- Krebs (TCA) cycle makes precursors to all five classes of biomolecules
- Eleven simple acids (<6 Carbon)
- Exists in oxidative and reductive organisms
- Extremely ancient and absolutely conserved



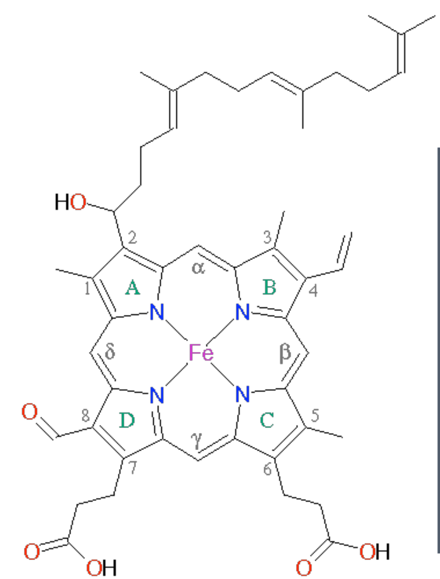
Polymerization assembles organic monomers into structures giving *kinetic control*

- Organic chemistry mostly ends, and phosphate-driven polymerization takes over, at ~C_{20}
- Polymers are divided between small hetero-polymers (mostly cofactors) and large oligomers (three classes)
- RNA/DNA mostly serve memory and regulation
- Most proteins and cofactors control reaction rates through catalysis or transport
- Other proteins and most sugars provide physical structure



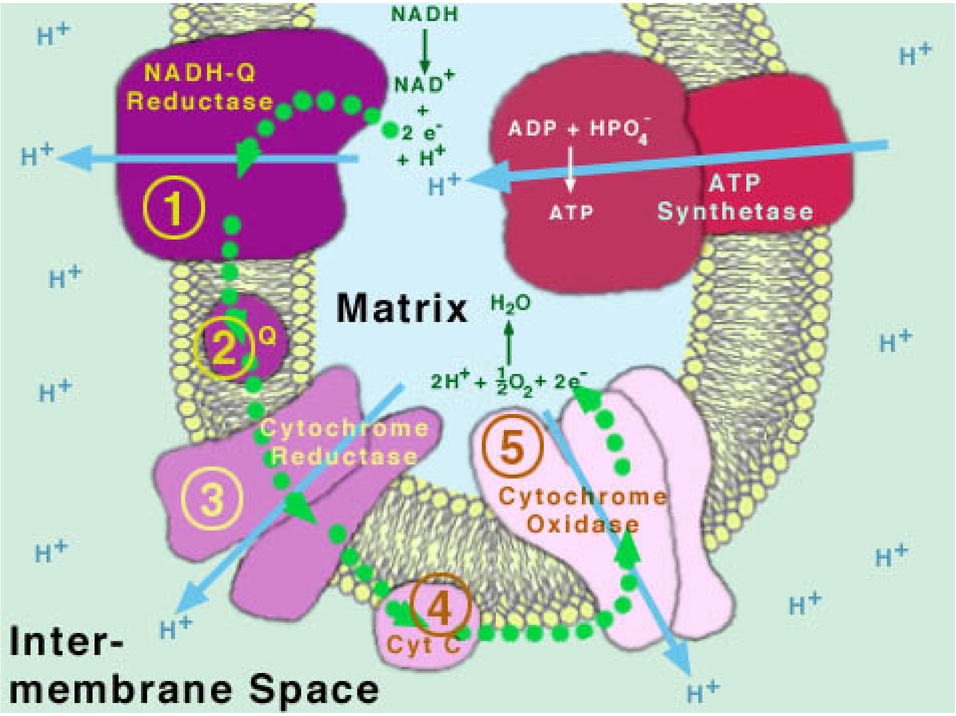
1OCC

http://metallo.scripps.edu/PROMISE/1OCC.html



Physical structures control chemistry and energetics

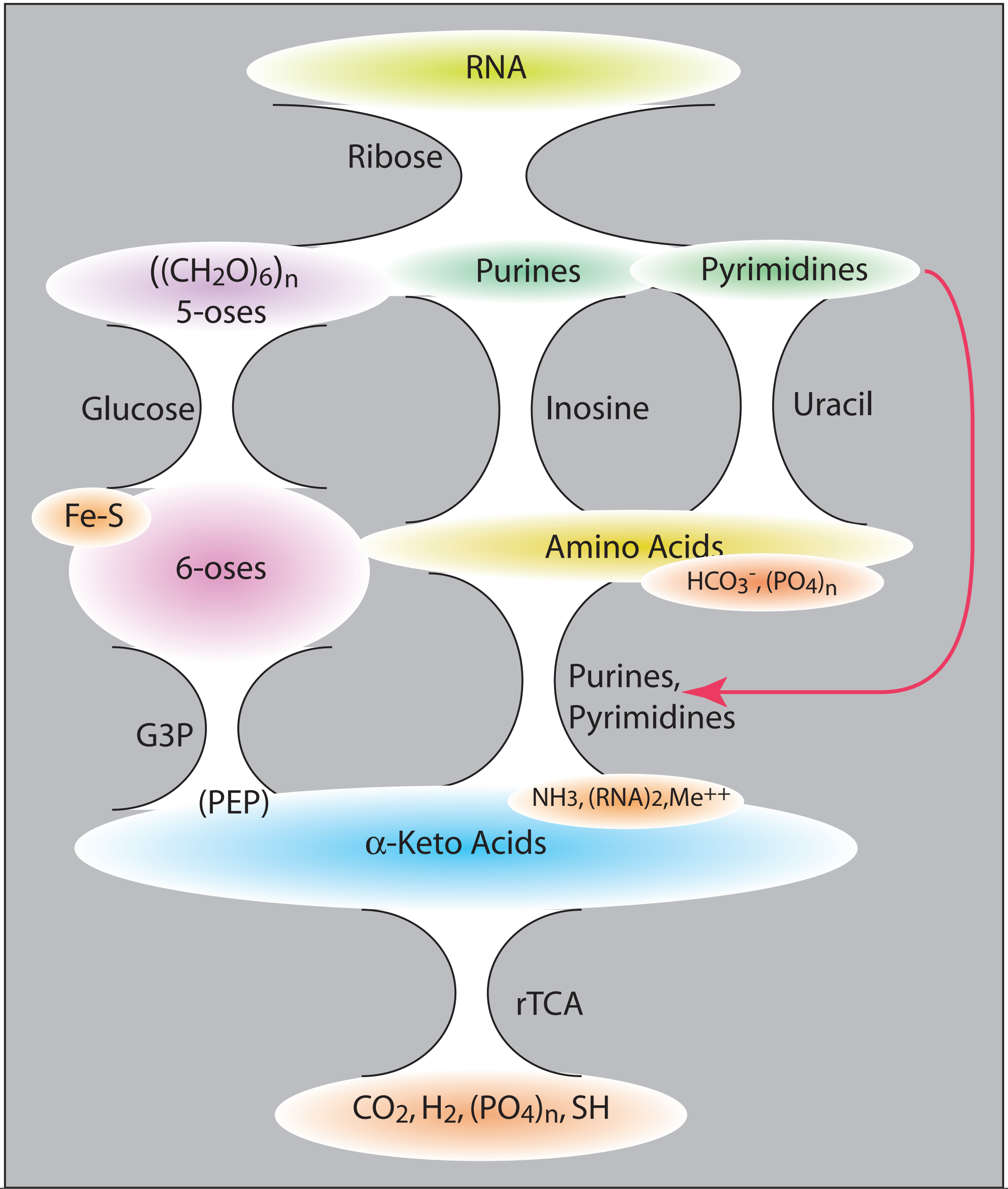
- Include membranes, ribosomes, pores, pumps, motors, walls, cytoskeleton
- Topology, geometry, and physical chemistry of membranes are all used
  - Topology concentrates reactants, excludes toxins, and creates pH and voltage differences
  - Geometry creates continuous *energy currency*
  - Oily membranes in a water medium are *proton semiconductors*



http://www.chemistry.wustl.edu/~edudev/LabTutorials/Cytochromes/cytochromes.html

The architecture of metabolism is significantly a hierarchy of "clouds" and "gateways"

- Combination of network topology catalytic diversity, and energetics creates modular architecture
- "Gateway" molecules or pathways are unique points of connection between molecule classes
- Within classes, synthesis often resembles thermodynamic ensembles

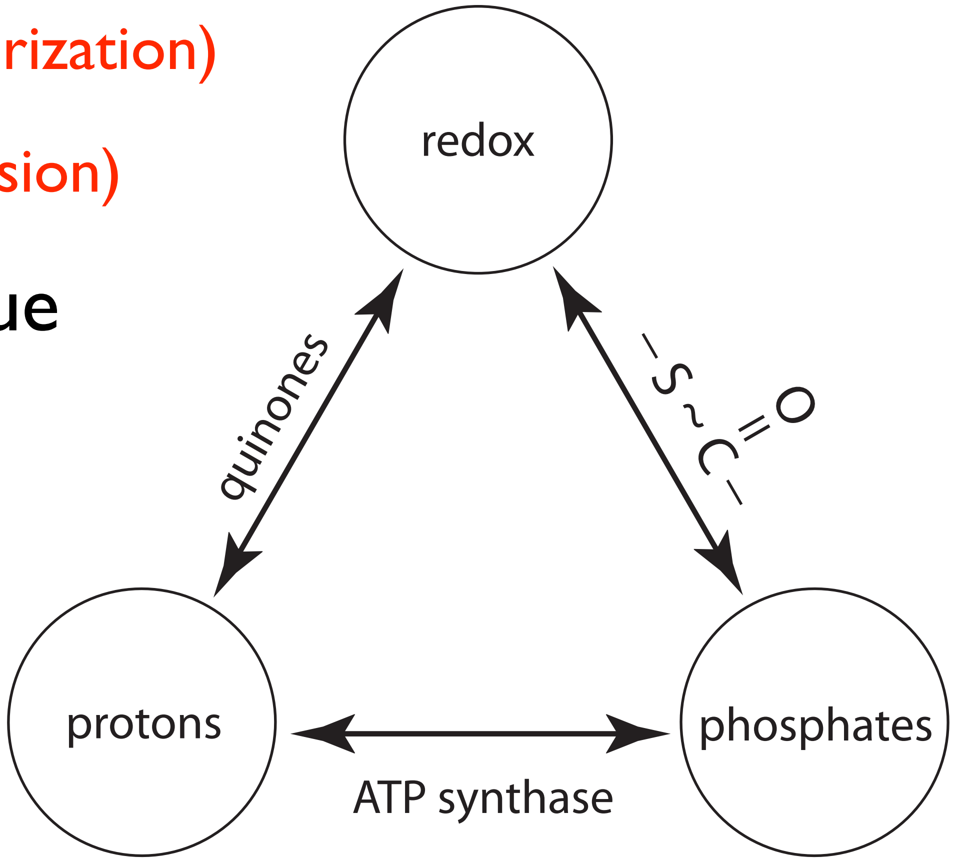


Bioenergetics in relation to biochemistry and geochemistry

- Biological energy systems and their roles
- Relations to metabolic and physiological organization
- Environmental sources of

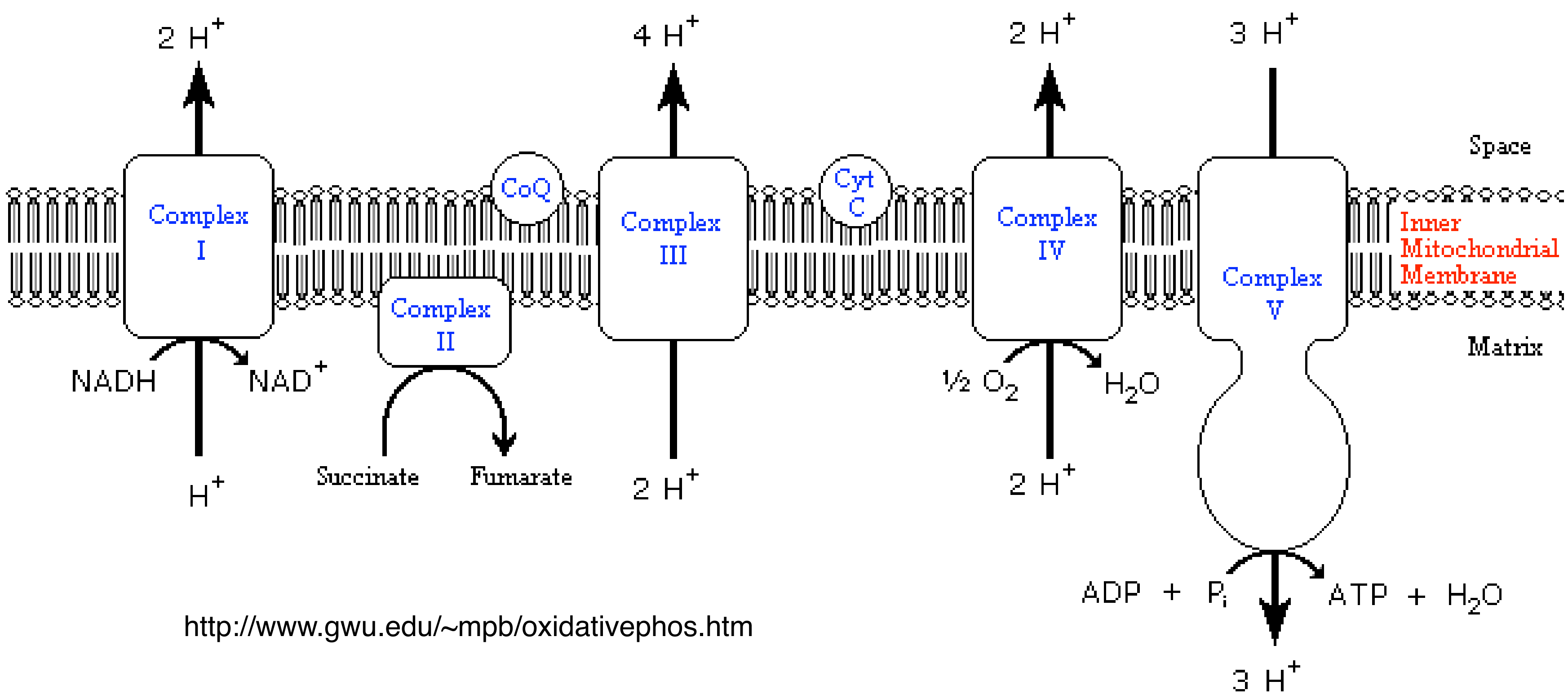
Biochemical processes are mediated by three coupled energy systems

- Electron transfer (oxidation-reduction)
- Phosphate group transfer (polymerization)
- Proton transport (motors, conversion)
- Each system supports unique functions
- Modern cells couple these, largely at membranes
- Ox-phos supplements / supersedes substrate-level phosphorylation



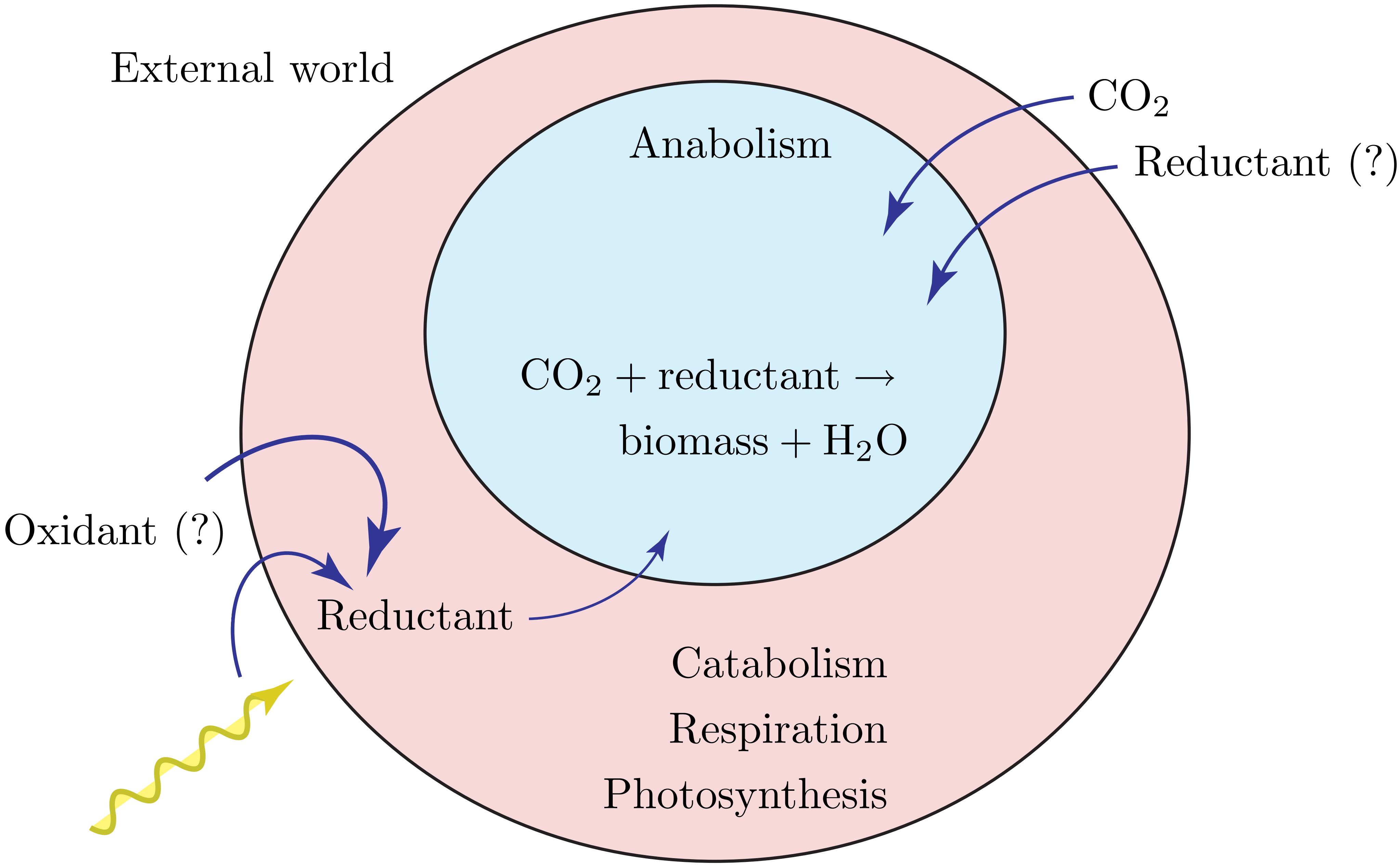
Membrane energetics couples, recycles, and buffers phosphates, protons, and electrons

- Lipid-soluble cofactors couple electron transfer to proton pumping
- Proton return recycles ATP from ADP and P_i

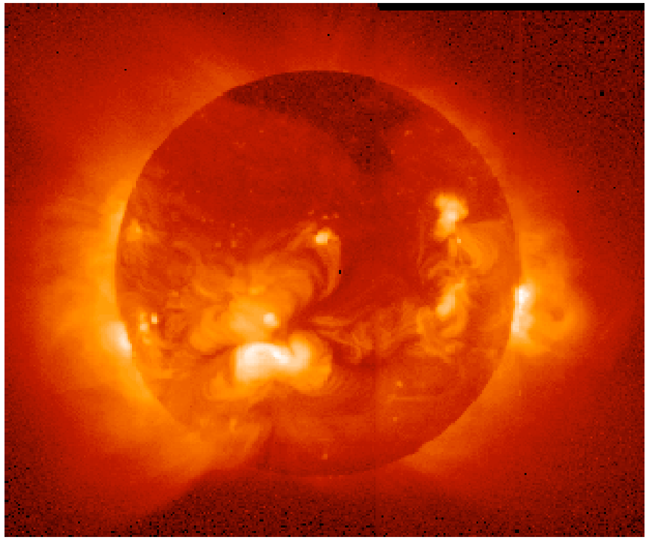


http://www.gwu.edu/~mpb/oxidativephos.htm

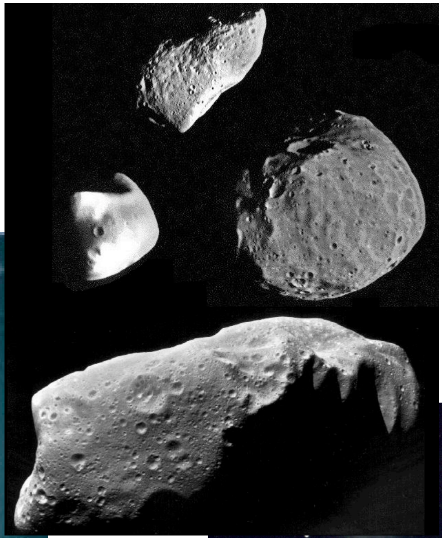
Biochemical and bioenergetic organization of oxidative and reductive organisms

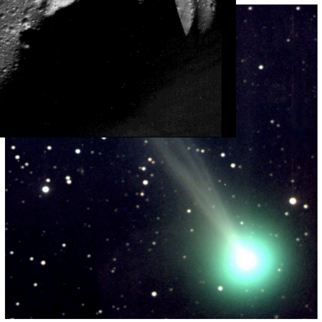


The energy source for oxidative life is nuclear fusion



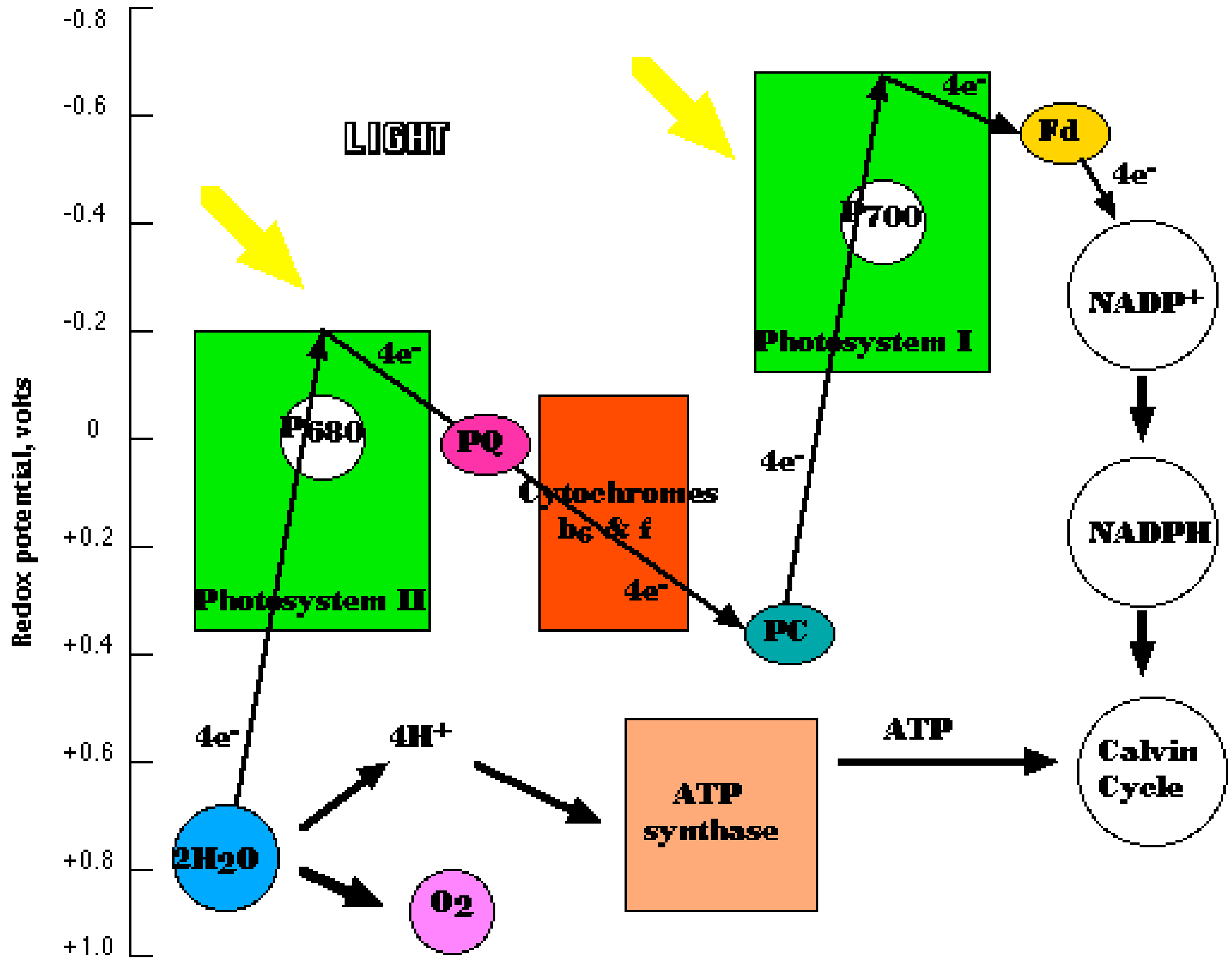
- Stellar radiation can directly excite chemical bonds
  - Very high-potential energy source
  - Hard to capture without photo-dissociation
- Secondary reactions in comets and asteroids create organics
- Atmospheric electro-chemistry of gas-phase free radicals creates rich species





The very complex function of photosynthesis is to convert light energy to reductant

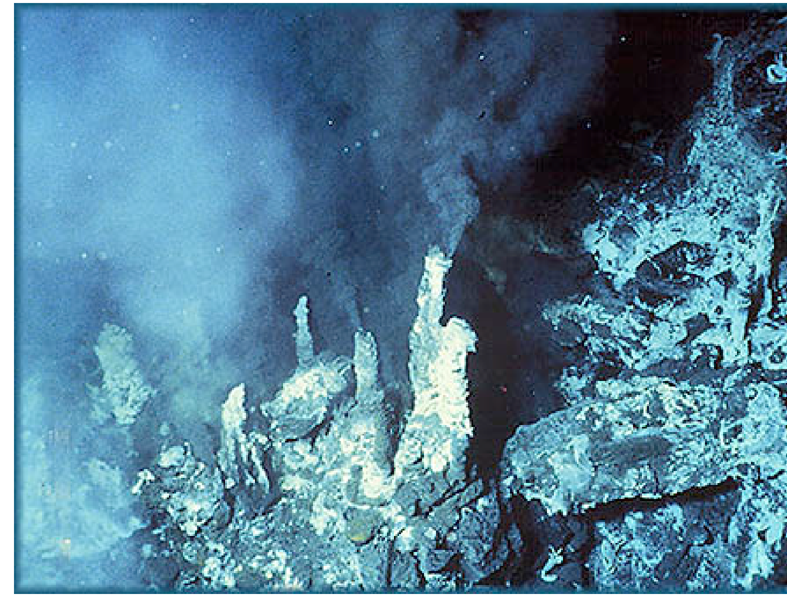
- Electrons are progressively raised in redox potential, then donated to $NADP^+$, to make NADPH, a powerful reductant used in anabolism
- Protons pumped directly can also be used to recycle phosphates

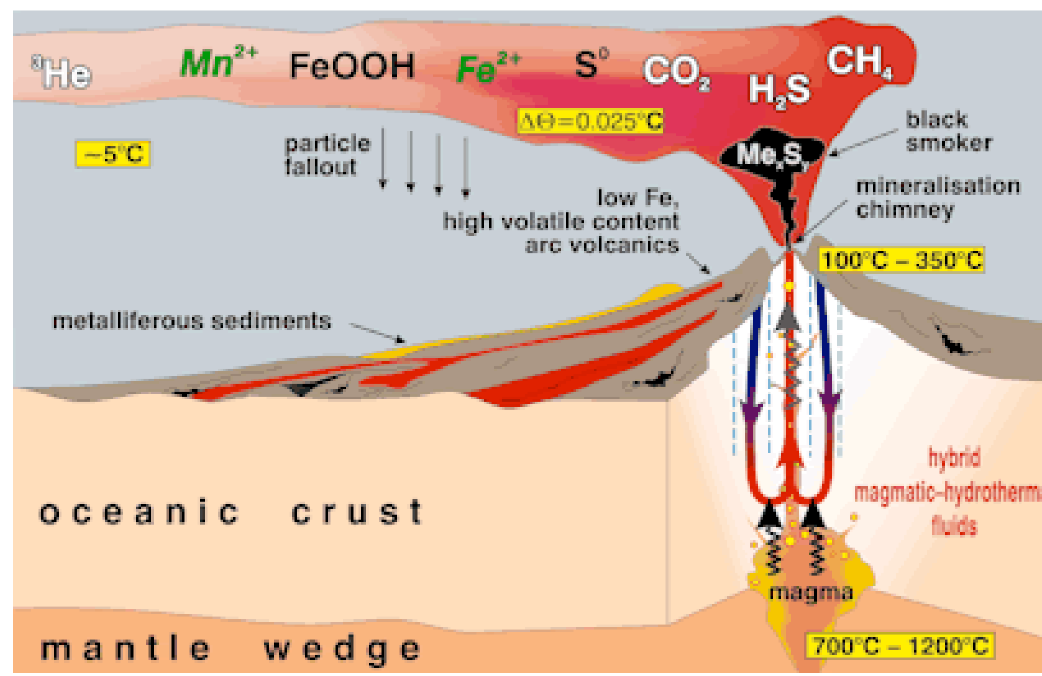


http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/L/LightReactions.html

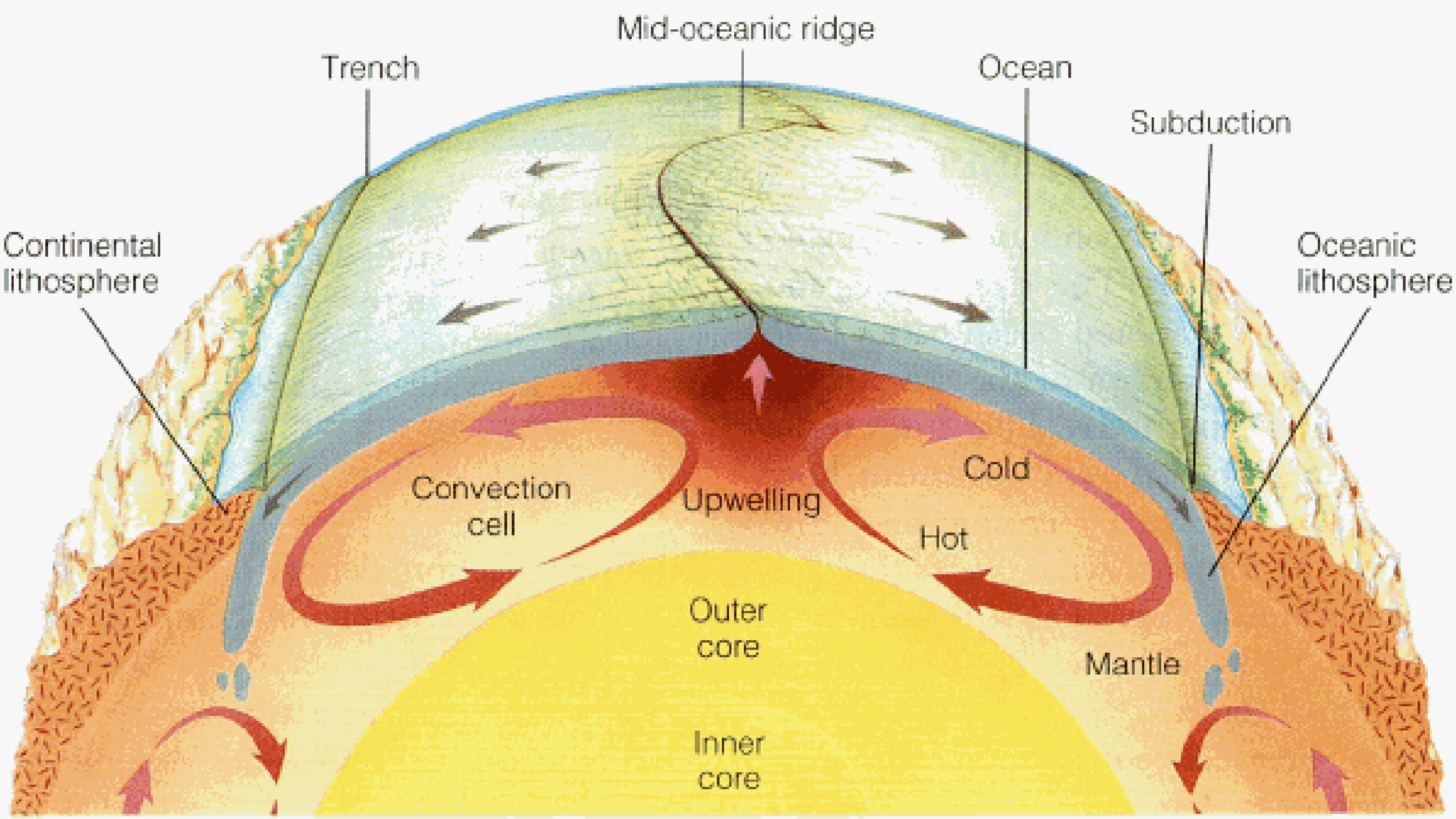
Geological processes originating in fission can produce reductant directly

- Mantle convection (powered by heat transfer) trades gravitational for chemical energy
- Reduced metals in contact with seawater generate reductant (H), carbon sources and reduced metals
- Mechanisms and chemicals produced often resemble those of biochemistry





The heat-gravity-chemistry transducer



http://bprc.osu.edu/education/rr/plate_tectonics/mantle_convection_cell.gif

- Serpentinization

$$(Mg,Fe)_2SiO_4 + H_2O + C \rightarrow Mg_3SiO_5(OH)_4 + Mg(OH)_2 + Fe_3O_4 + H_2 + CH_4 + C_2{-}C_5$$

Martin et al. Nature Reviews Microbiology

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- Basalt fracture and phosphates

Metals and light molecules in vents drive redox chem.

Table 1 | **Anaerobic and aerobic microbial metabolic reactions and potential energy yields in hydrothermal vent environments**

Metabolism	Reaction	$\Delta G^{0\prime}$ (kJ per mole)*	Examples in vent environments
Anaerobic			
Methanogenesis	$4\,H_2 + CO_2 \rightarrow CH_4 + 2\,H_2O$ $CH_3CO_2^- + H_2O \rightarrow CH_4 + HCO_3^-$ $4\,HCOO^- + H^+ \rightarrow 3\,HCO_3^- + CH_4$	–131 –36 –106	*Methanococcus* spp. common in magma-hosted vents; Methanosarcinales at Lost City
S° reduction	$S^0 + H_2 \rightarrow H_2S$	–45	Lithotrophic and heterotrophic; hyperthermophilic archaea
Anaerobic CH_4 oxidation	$CH_4 + SO_4^{2-} \rightarrow HS^- + HCO_3^- + H_2O$	–21	*Methanosarcina* spp. and epsilonproteobacteria at mud volcanoes and methane seeps
Sulfate reduction	$SO_4^{2-} + H^+ + 4\,H_2 \rightarrow HS^- + 4\,H_20$	–170	Deltaproteobacteria
Fe reduction	$8\,Fe^{3+} + CH_3CO_2^- + 4\,H_2O \rightarrow 2\,HCO_3^- + 8\,Fe^{2+} + 9\,H^+$	Not calculated‡	Epsilonproteobacteria, thermophilic bacteria and hyperthermophilic Crenarchaeota
Fermentation	$C_6H_{12}O_6 \rightarrow 2\,C_2H_6O + 2\,CO_2$	–300	Many genera of bacteria and archaea
Aerobic			
Sulfide oxidation§	$HS^- + 2\,O_2 \rightarrow SO_4^{2-} + H^+$	–750	Many genera of bacteria; common vent animal symbionts
CH_4 oxidation	$CH_4 + 2\,O_2 \rightarrow HCO_3^- + H^+ + H_2O$	–750	Common in hydrothermal systems; vent animal symbionts
H_2 oxidation	$H_2 + 0.5\,O_2 \rightarrow H_2O$	–230	Common in hydrothermal systems; vent animal symbionts
Fe oxidation	$Fe^{2+} + 0.5\,O_2 + H^+ \rightarrow Fe^{3+} + 0.5\,H_20$	–65	Common in low-temperature vent fluids; rock-hosted microbial mats
Mn oxidation	$Mn^{2+} + 0.5\,O_2 + H_2O \rightarrow MnO_2 + 2\,H^+$	–50	Common in low-temperature vent fluids; rock-hosted microbial mats; hydrothermal plumes
Respiration	$C_6H_{12}O_6 + 6\,O_2 \rightarrow 6\,CO_2 + 6\,H_2O$	–2,870	Many genera of bacteria

*From REFS 73,103 and W.J. Brazelton (personal communication). ‡Some hyperthermophiles from the Archaea and Bacteria domains can couple the reduction of Fe with the oxidation of H_2 (REFS 104,105). §Some epsilonproteobacteria from subsea-floor hydrothermal vents, including newly erupted vents, can oxidize H_2S to S° (REF. 106).

William Martin, John Baross‡, Deborah Kelley‡ and Michael J. Russell§*

Hydrothermal systems are ubiquitous, and were moreso on the hot early earth

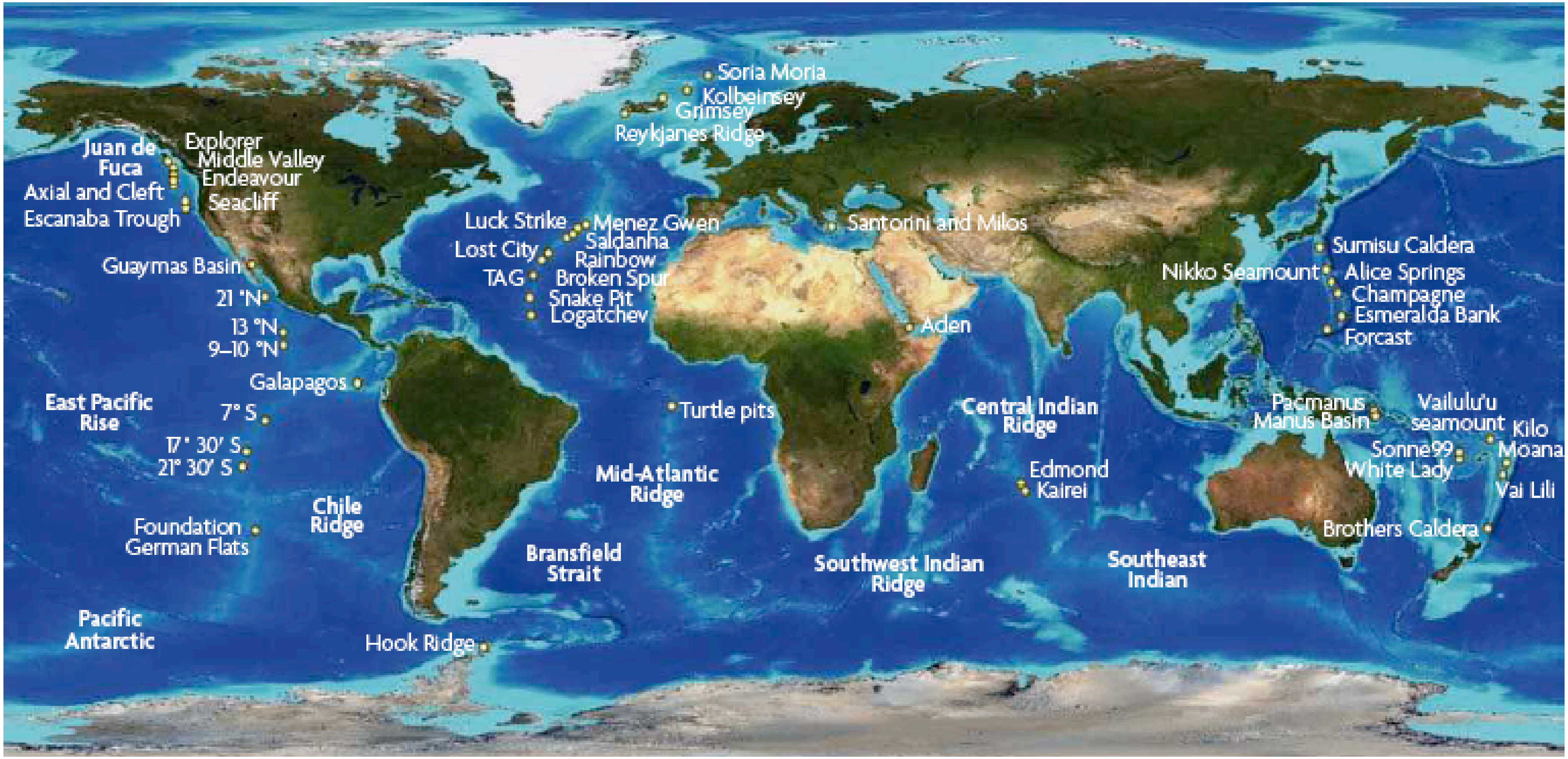

Figure 1 | **Global distribution of known hydrothermal vents.** Temperature and chemical anomalies hint that many more sites exist throughout the world's oceans. Data courtesy of D. Fornari and T. Shank, Woods Hole Oceanographic Institute, Massachusetts, USA.

William Martin, John Baross‡, Deborah Kelley‡ and Michael J. Russell§*

Interpretations of the relation of bioenergetics to biochemistry and geochemistry

- Historical inference suggests no oxygen and possibly high temperature environments
- Biochemical and ecosystem organization suggest that reductive metabolism were first
- Reductive metabolic chemistry has many resemblances to geochemistry
- Sites where geochemistry most resembles biochemistry are anoxic and hot

Next two lectures

- Chemistry of core carbon biosynthesis, and suggestions that this arose through geochemical self-organization
- The emergence of hierarchies of structure and control, and the relation of organization to stabilization of the biosphere

Further reading

- Stryer, Lubert **Biochemistry** New York : W.H. Freeman, 1995 4th ed
- Voet, Donald and Judith G. **Biochemistry** New York : J. Wiley & Sons, 1995 2nd ed
- Metzler, David E **Biochemistry : the chemical reactions of living cells** New York : Academic Press, 1977
- Morowitz, Harold J **Beginnings of cellular life : metabolism recapitulates biogenesis** New Haven : Yale University Press, 1992
- Lowry, Thomas H and Richardson, Kathleen Schueller **Mechanism and theory in organic chemistry** New York, N.Y. : Harper & Row, 1981 2nd ed
- William Martin, John Baross, Deborah Kelley, and Michael J. Russell Hydrothermal vents and the origin of life**,** *Nature Reviews Microbiology* **6**:805, 2008