Chapter 8 (Strickberger 4th ed.) Origins of Cells and the First Organisms

Early organisms required energy to carry out life's functions. However this need for energy could only be satisfied once a system was in place to harness the potential energy present in early compounds.

How did early organisms harness this energy?

Remember, Earth's atmosphere was devoid of oxygen until about one billion years following the appearance of the first life forms.

Aerobic metabolism as we know it was not possible… Was this a problem?

The progression of metabolism (What we think thus far…)

1. Simple **anaerobic** systems arose that were dependent on simple, early energy sources.
2. **Autotrophic** systems evolved that were capable of generating energy from sunlight.
3. **Aerobic** systems evolved that gained energy by transferring electrons to oxygen.

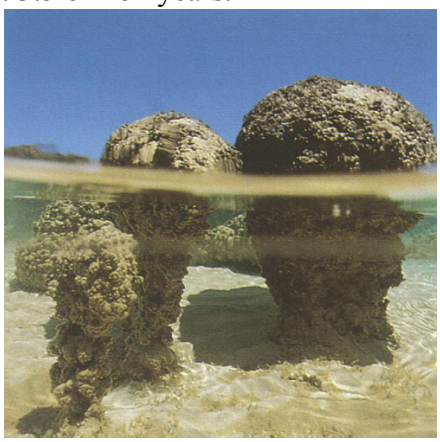
All of these are still around today.

Some of the best evidence for this progression comes from analyses of **stromatolites**.

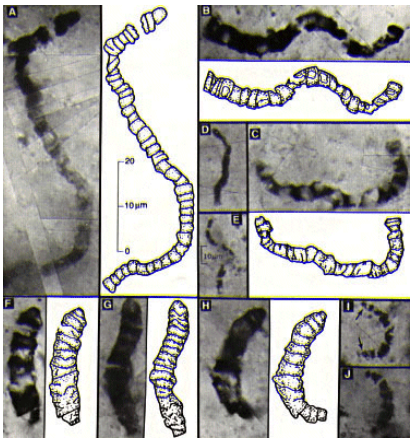
Mats of microorganisms cemented together by sediments.

Some are 3.5 billion years old.

Stratification in stromatolites reveals layers of chemical and biological evidence suggesting that the progression of anaerobic to aerobic metabolism took place over the past 3.5 billion years.



Unique view of a living stromatolite in Australia.



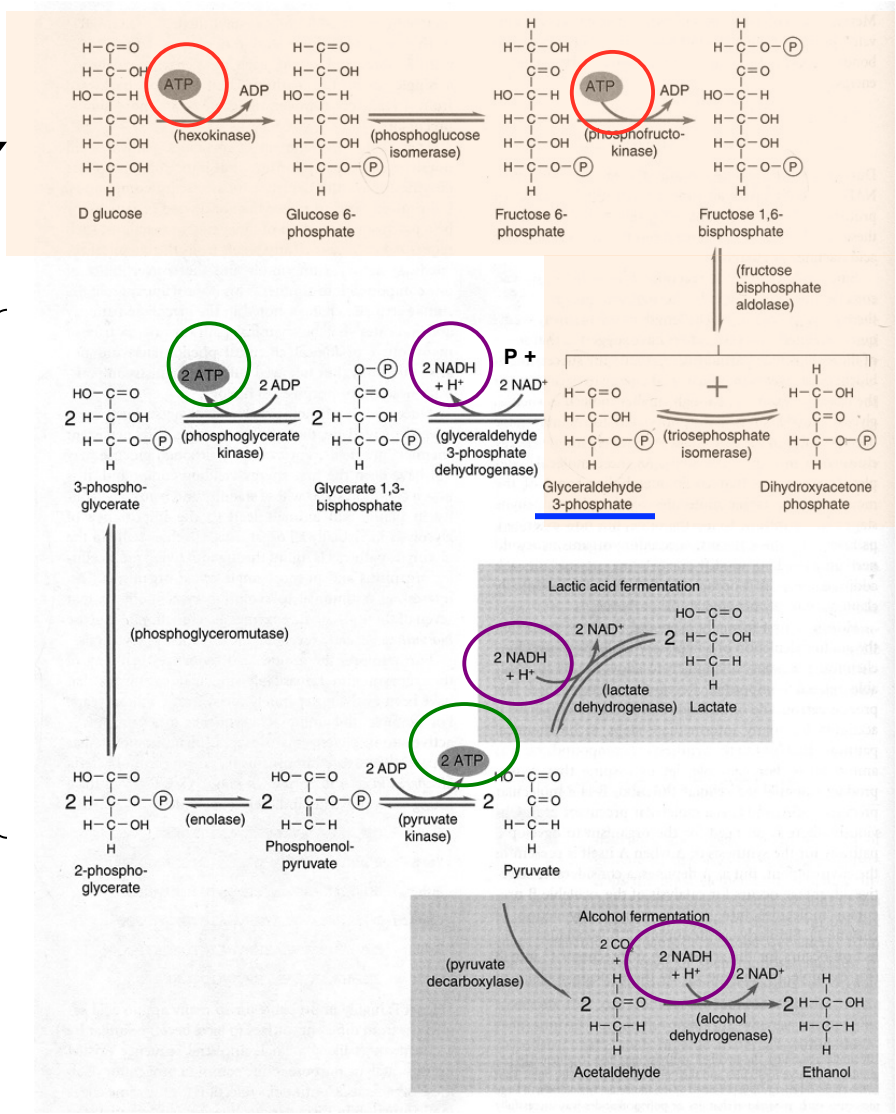
Microfossils from 3.5 BYBP (Australia) that resemble filamentous cyanobacteria.

ANAEROBIC METABOLISM

Anaerobic glycolysis – breakdown of glucose (sugar) in the absence of oxygen (organotrophic nutrition). e.g. Embden-Meyerhof glycolytic pathway

Preparatory steps

Energy steps



Yields free energy = 2 ATP

All living organisms today share <u>at least</u> a portion of this pathway. What might this tell you about this pathway?

The anaerobic glycolysis pathway can begin with a variety of molecules, <u>as long as</u> they can be converted to glucose.

Sugars, fats, amino acids can all be converted.

Glucose breakdown yields **two pyruvate molecules** and **two ATP**.

Complex pathway in which only **two steps yield energy**. Efficient or inefficient?

Therefore, the other steps can be considered preparatory.

Is this efficient enough for early organisms that possessed broad, nonspecific metabolic capacity??

Think about this:

A person needs (burns) 50 calories to walk for 15 min.

Each molecule of glucose provides about 10^{-21} calories of energy…so, $50/10^{-21} = 5x10^{22}$ molecules of glucose are needed to walk for 15 min.

Each molecule of glucose provides 38 ATP, so 38 ATP x $5x10^{22} = 2x10^{24}$ ATP needed to walk for 15 min.

Glycolysis nets two ATPs. Efficient?

Question: If selection should theoretically "streamline" such a metabolic process, then why is this pathway so complex? (It is complex even today)

Early organisms metabolized much simpler compounds as compared to today's organisms.

e.g. glyceraldehydes (underlined in figure above)

Energy production probably occurred in just a few steps.

But what happens when these molecules become depleted?

The pathway must be able to convert other, more complex compounds into energy.

Therefore, organisms had to expand the pathway backwards, one step at a time, to accommodate increasingly complex compounds.

This is called "retrograde" or "backwards" evolution.
Accounts for many of the intermediate steps in today's biochemical pathways.

Example: **A** is a product essential for cellular function.
B is a precursor of **A**.
C is a precursor of **B**.

An organism does not need to develop a pathway to produce **A** if **A** is already present.

If **A** becomes depleted, then the ability to convert **B** to **A** is selected for.

If **B** becomes depleted, then the ability to convert **C** to **B** is selected for.

As a result: **C → B → A** pathway is developed.

Each step actually extends the pathway backwards from a relatively simple molecule (**A**) to more complex precursors (**B and C**).

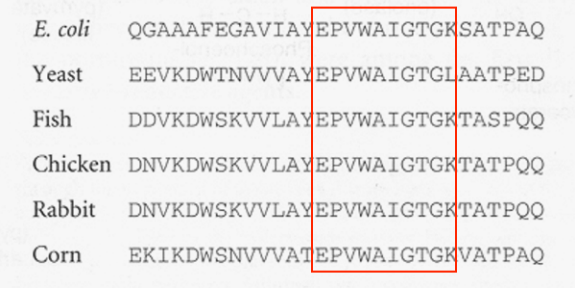
Stepwise, organized changes in metabolized compounds implies non-random pathway development.

How do we know that these pathways are "historic"?

Survival of certain metabolic pathways is evident in the similarity of catalytic enzymes in very different organisms.

The amino acid sequence of the active site of the enzyme **triosephosphate isomerase** (necessary in the glycolytic pathway) is highly conserved.

Features amino acid sequence **homology** in organisms ranging from *E. coli* to corn plants.



Improbable that such similarity arose randomly.

A single ancestor likely held the "original" sequence.

So why was the sequence conserved?

LITHOTROPHIC NUTRITION

Anaerobic nutrition (using of sequentially reduced carbon compounds or "organic" carbon) probably led to the depletion of those reduced organic compounds.

Lithotrophic nutrition allowed the use of simpler, more readily available carbon sources such as CO_2 (inorganic carbon source).

Provided an evolutionary advantage for organisms that could do it. Why?

H_2, H_2S, FeS, S and primitive enzyme catalysts were available to generate early energy.

$H_2S \rightarrow 2H^+ + 2e' + S$, via hydrogenase and FeS.

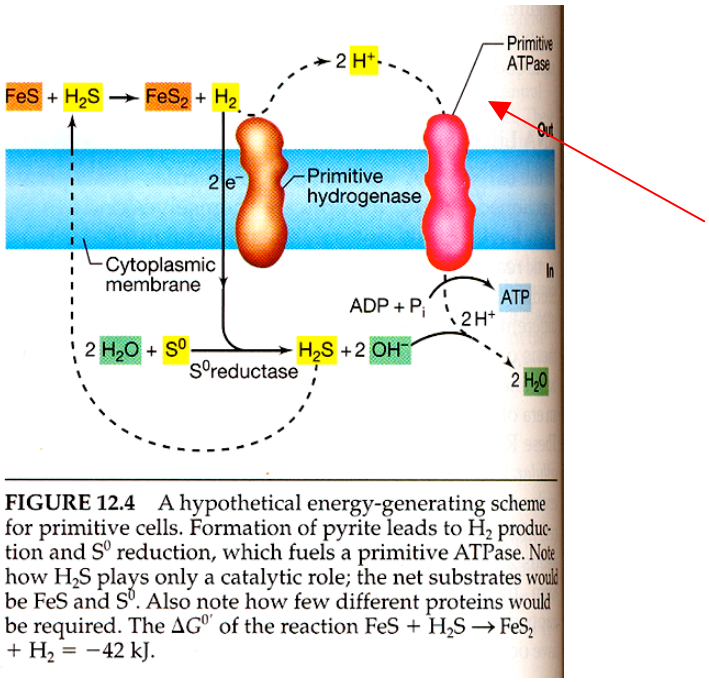


FIGURE 12.4 A hypothetical energy-generating scheme for primitive cells. Formation of pyrite leads to H_2 production and S^0 reduction, which fuels a primitive ATPase. Note how H_2S plays only a catalytic role; the net substrates would be FeS and S^0. Also note how few different proteins would be required. The $\Delta G^{0'}$ of the reaction $FeS + H_2S \rightarrow FeS_2 + H_2 = -42$ kJ.

Electrons from this reaction were used to aid in **energy production**.

Important: electrons can't simply flow alone from molecule to molecule.

They must be transferred via an **electron carrier** (e.g. an enzyme like hydrogenase).

Hydrogenase transfers electrons from an electron donor (H_2) to an electron acceptor (S^0).

Facilitates reduction-oxidation reactions.

During electron transfer, released energy forces protons (H^+) into extracellular spaces.

As this continues, a "proton gradient" is created.

Accumulation of H^+ outside of the cell membrane is **potential** energy.

Energy is liberated when H^+ diffuses back through an ATPase in the cellular membrane

Energy is used to power the phosphorylation of ADP to ATP.

Is ATP useful?

This reaction ($H_2S \rightarrow 2H^+ + 2e' + S$) is evolutionarily feasible. **How?**

1. Required few proteins (3)
2. Almost limitless, as H_2, S, FeS and H_2S were abundant.
3. This reaction is still carried out today by hyperthermophilic archaea.

This energy production is great, but how does this help organisms grow?

The production of energy was achieved relatively easily using simple metabolic pathways, but where did **structural** compounds come from?

Two possibilities

1. From pre-biotic synthesis reactions

   Oparin-Haldane process, thermal protenoids, microspheres, coacervates, etc.

… and then later…

2. From early autotrophy

   CO_2 (abundant in early atmosphere) gets "fixed" into biomass, i.e. it gets reduced.

AUTOTROPHY

$CO_2 + 2H_2O + energy \rightarrow CH_2O + O_2 + H_2O$ … this process consumes energy.

Requires inorganic carbon source (CO_2), H, electrons, and seemingly complex genetic machinery.

Once thought unlikely to occur on early Earth...too complex for simple organisms,

But…microbial genome sequencing has shown that some of today's "primitive-looking" organisms do have this ability

Therefore, it is thought that some early organisms might have possessed autotrophic capacity.

Aquifex spp. – hypothermophilic autotroph located close to the root of the **tree of life**.

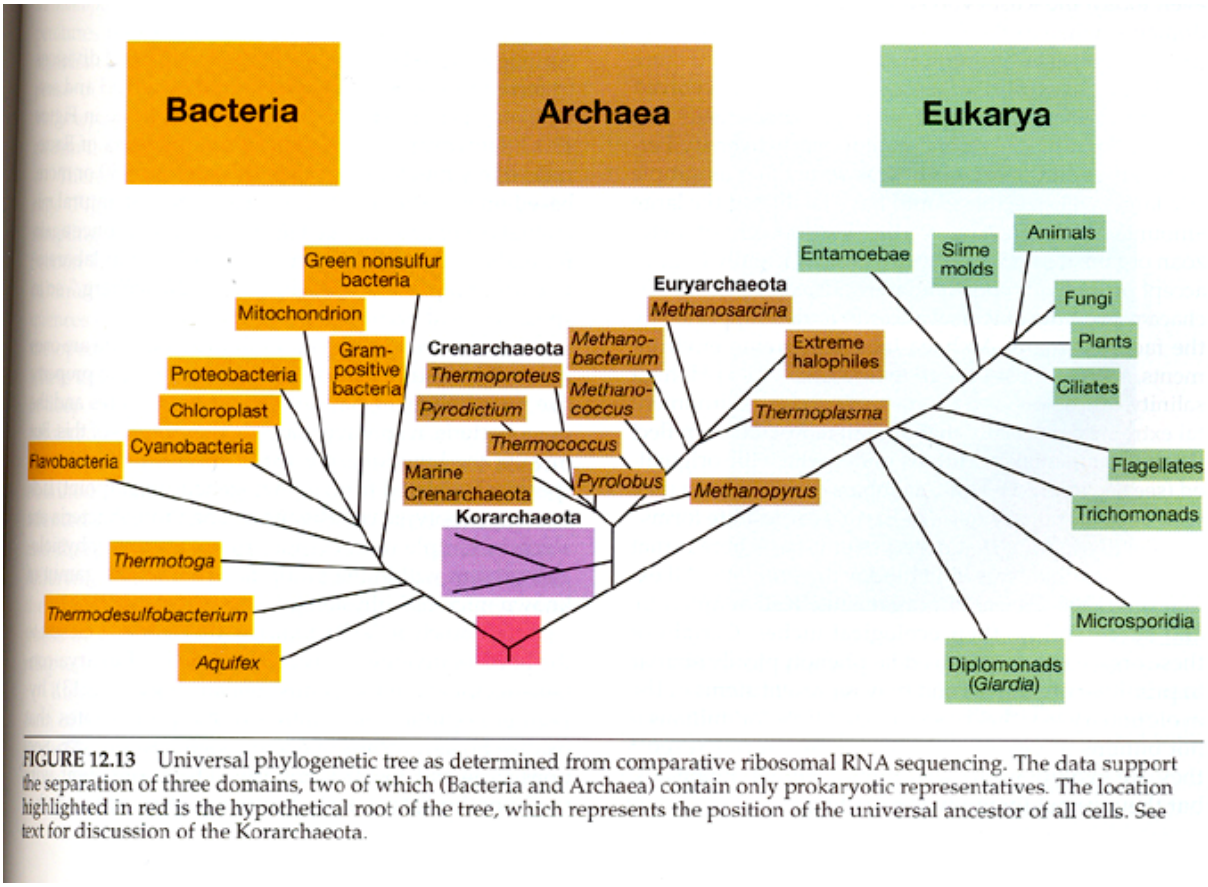


FIGURE 12.13 Universal phylogenetic tree as determined from comparative ribosomal RNA sequencing. The data support the separation of three domains, two of which (Bacteria and Archaea) contain only prokaryotic representatives. The location highlighted in red is the hypothetical root of the tree, which represents the position of the universal ancestor of all cells. See text for discussion of the Korarchaeota.

From an evolutionary standpoint, why is the **root** of the tree important?

What do we know about the niches inhabited by today's organisms "at the root"?

Aquifex spp. contain a very small genome (1500 kb vs 5500 kb in *E. coli*) **yet** is autotrophic…seems contradictory based on the complexity of autotrophic machinery???

So… it *is* possible that a relatively "simple" organism could carry out such a complex process.

No oxygen around until 2.5 bybp: the first autotrophy was <u>anoxygenic</u> photosynthesis

Although energy was produced via simple metabolic pathways, it could only be done in the presence of the appropriate organic or inorganic compounds serving as electron donors.

The development of the first electron transport systems was valuable but at the same time restrictive and somewhat inefficient.

What do you think made them restrictive?

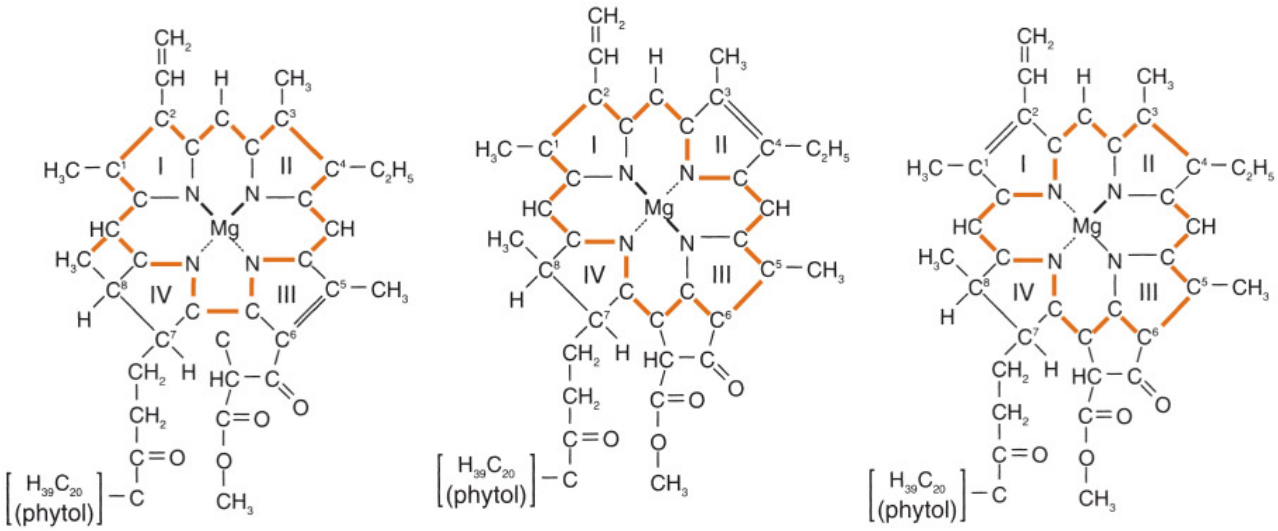
A significant advance: The development of early **photosynthesis** allowed **light** to be used as energy to drive H^+ ions across membranes to form a proton gradient and via ATPases, phosphorylate ADP to ATP (*compare with lithotrophic energy generation*).

Dependent on chlorophyll in early organisms, as in today's organisms.

Support: Several major (diverse) bacteria groups include members that are photosynthetic and rely on chlorophyll. These likely derived from a common ancient ancestor.

Why chlorophyll?

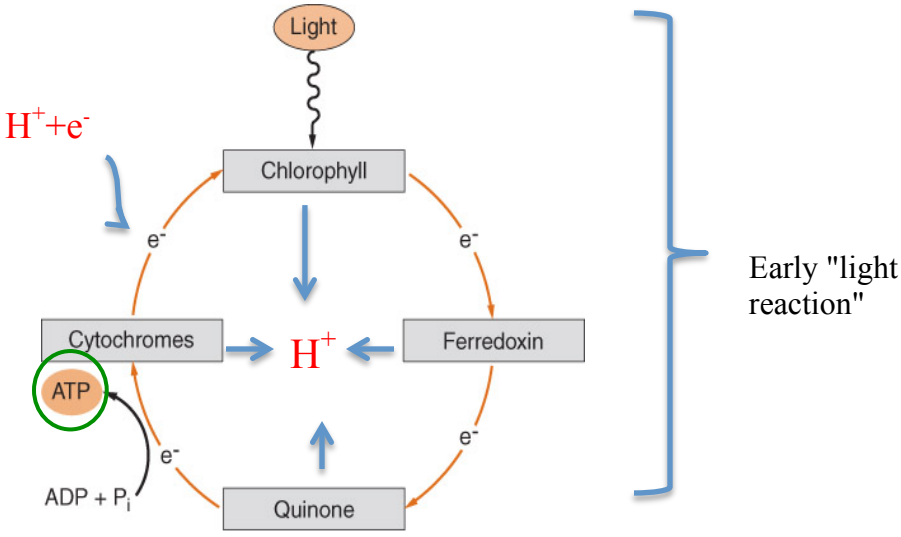
Chlorophyll exhibits a number of **resonance** forms.



Double and single bonds shift although the molecule remains stable.

It can receive light-energy, maintain it, and eventually transfer it.

An early anoxygenic photosynthetic pathway was called **cyclic photosynthesis.** It was used to generate energy to power the fixation of C from CO_2.

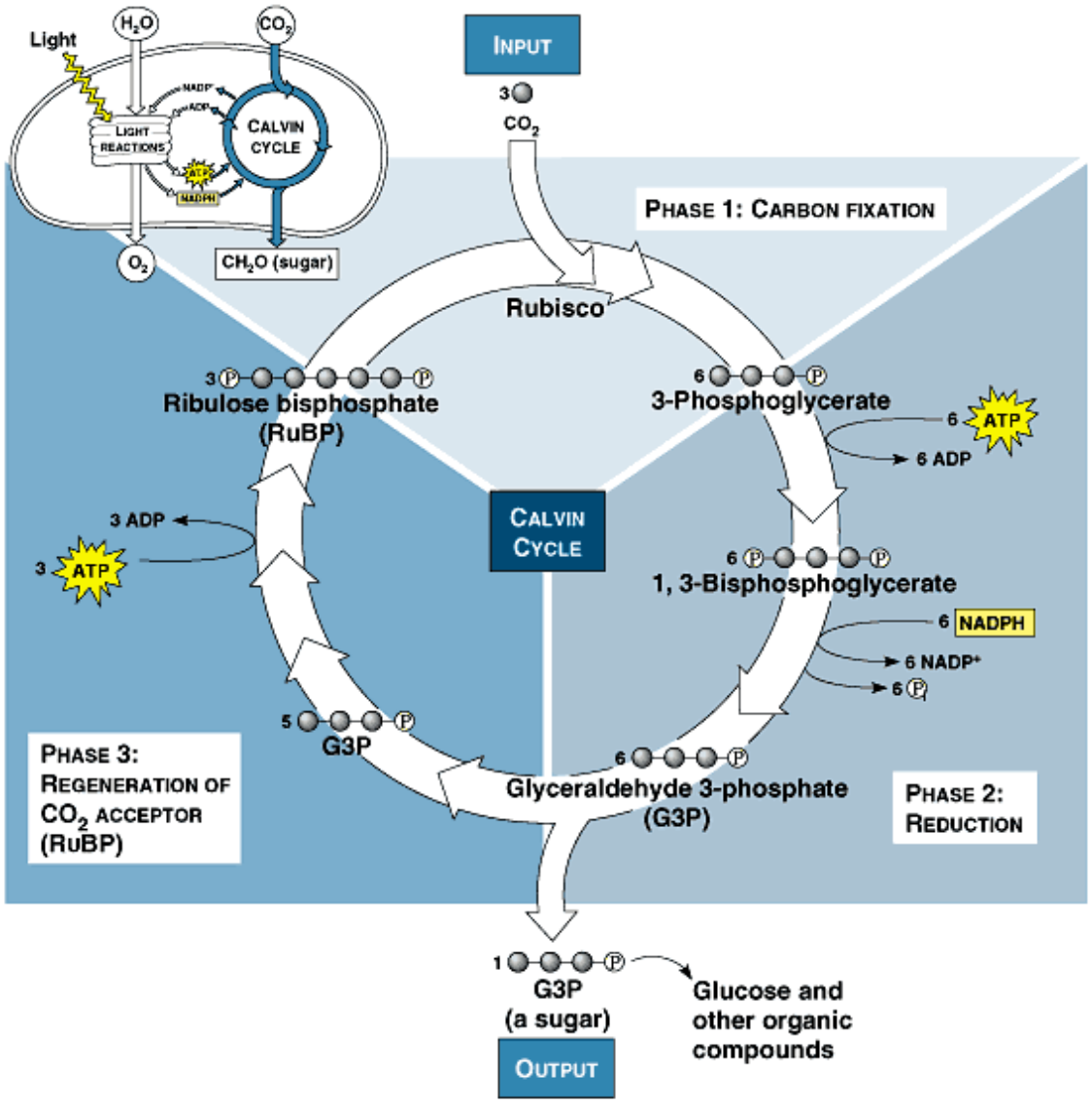


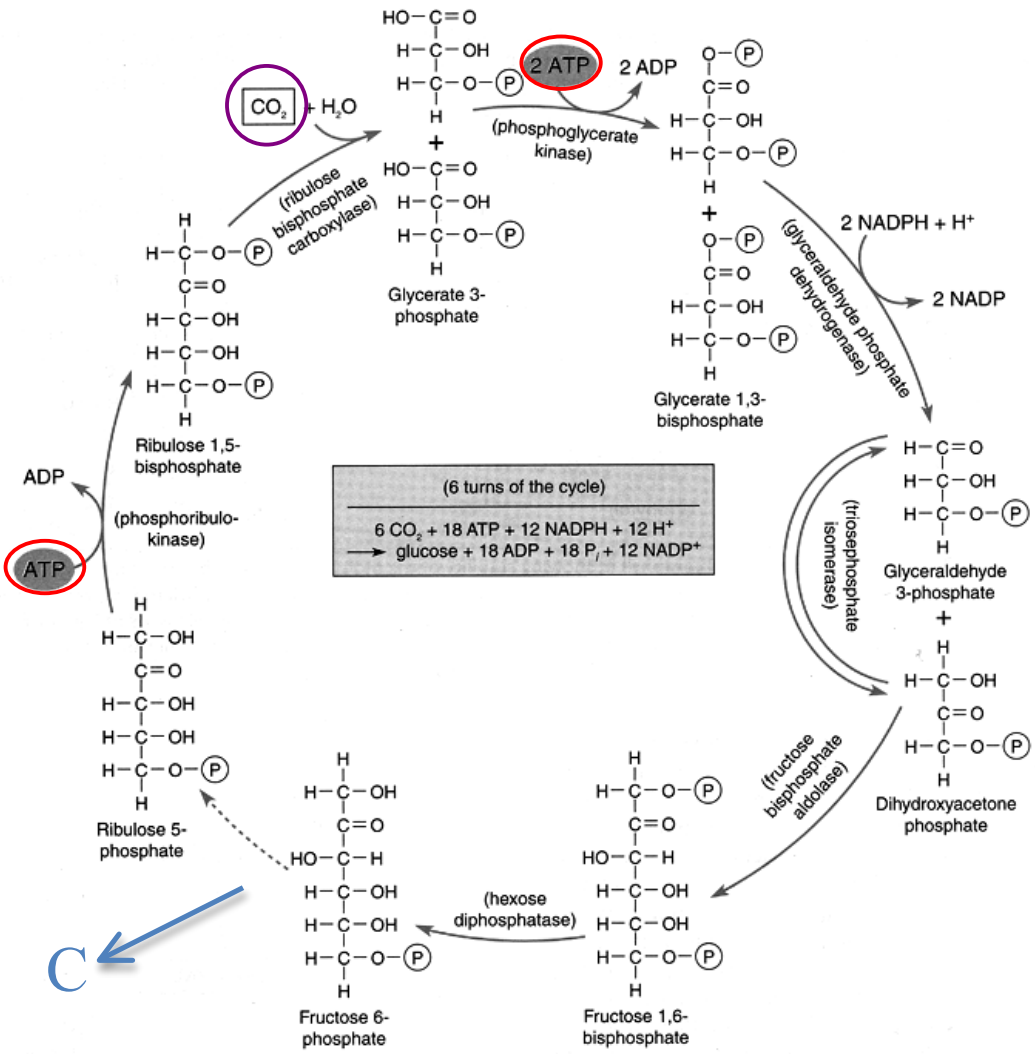
This pathway must have been coupled to a membrane phosphorylation system to stabilize the cycle.

Energy could be produced, but how could CO_2 be used to generate **structural carbon?**

Where in a growing cell might structural carbon be necessary?

Carbon was fixed from CO_2 through the Calvin cycle.





The calvin cycle (or some derivation) is observed in almost all photosynthetic organisms.

Each turn of the cycle generates one "fixed" carbon from ribulose bisphosphate and CO_2.

Six turns (six CO_2s) are necessary to generate one glucose (a six–C compound).

This system allowed organisms the ability to use light for energy and CO_2 as a carbon source, but metabolism of compounds such as H_2S (lithotrophic nutrition) were still necessary for an electron and H^++ e^- source.

This could have limited the distribution of photosynthetic organisms.

What has evolved as the H^++ e^- source today?

OXYGEN

Oxygenic photosynthesis

Evolutionary advances eventually allowed for the use of **water** as an electron and H^+ source (instead of, for example, H_2S).

When the electron and H^+ source is water… $2\ H_20 \rightarrow 4e' + 4H^+ + \underline{O_2}$

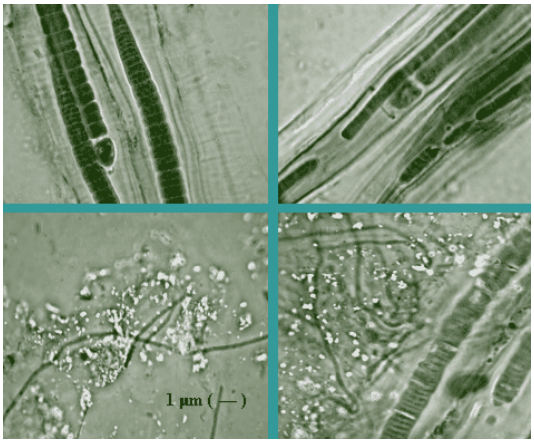
An important consequence of using water as an electron and hydrogen donor was the **liberation of oxygen**.

Created an **aerobic** environment

Driven early by cyanobacteria-like bacteria capable of oxygenic photosynthesis.

Fossil evidence is present in 2.5 in stromatolites (2.5 billion tears old). How old is the Earth?

Stromatolites in a historic tidal plain



Cyanobacteria isolated from a stromatolite.

Oxygen concentrations were approximately 1% of today's concentration (21%) for 1-2 b.y., and then increased as photosynthetic organisms became competitive.

Why did it take so long for oxygen to accumulate?

Early atmosphere was highly reducing.

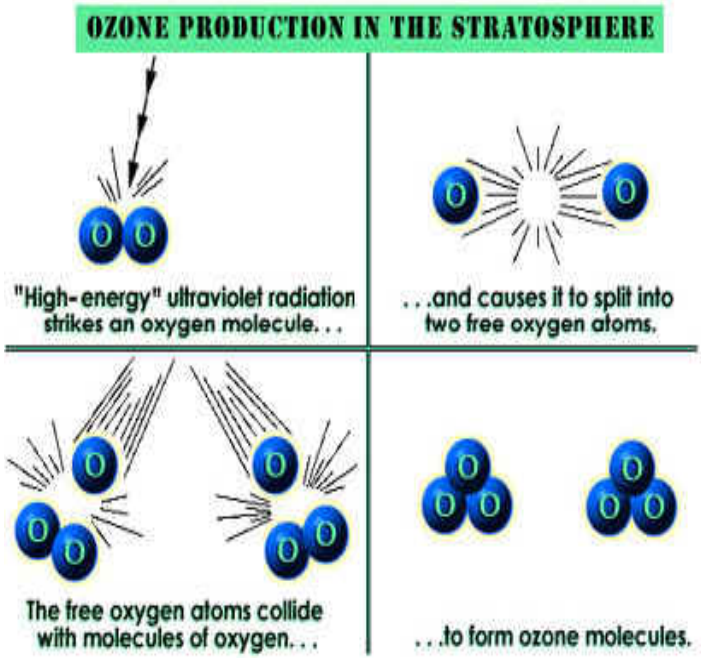
H_2S, and CH_4 reacted with liberated O_2 to produce water (and other compounds), effectively consuming the O_2.

The impact of atmospheric O_2 was extensive.

1. **O_3 shield** – provided a barrier that prevented sunlight (uv radiation) from reaching Earth's surface.

   uv light actually drove its own attenuation.

   uv light + O_2 → O_3



   Without the O_3 shield, DNA-damaging uv light would preclude evolution in all but the most sheltered environments.

   e.g. oceans and subsurface (perhaps this is one reason why these two environments contained the first organisms??? No DNA damage there prior to atmospheric O_2.)

2. O_2 could be used as an **electron acceptor** – aerobic metabolism

   More efficient energy conservation

   Evolution of aerobic organisms and new metabolic strategies.

   Increased population densities and diversity

AEROBIC METABOLISM

With the presence of O_2 in the atmosphere, new enzyme systems could develop that could help produce much more energy than their anaerobic predecessors.

More energy could be extracted from a compound by donating electrons to O_2 vs. previously used electron acceptors.

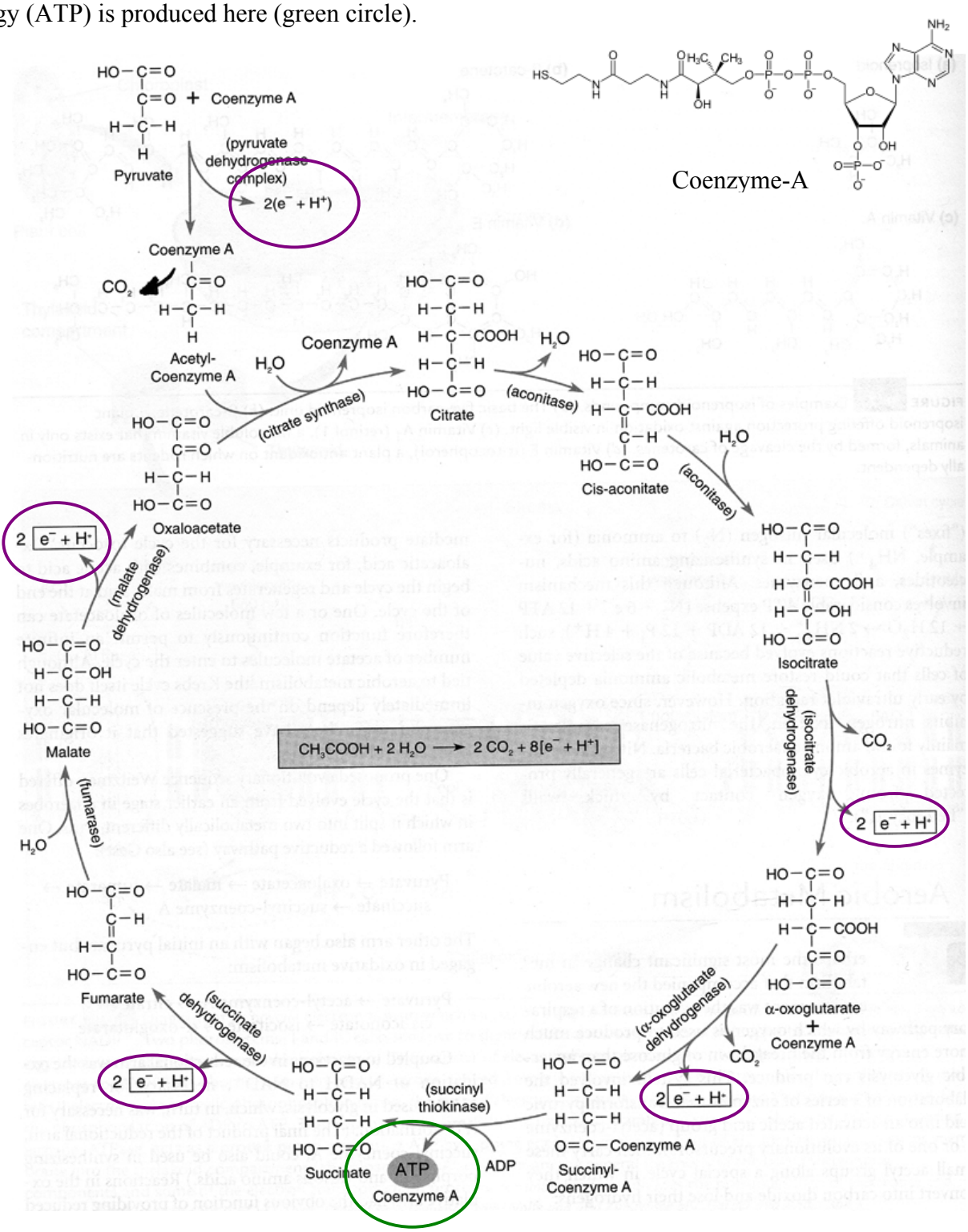
Remember from above that pyruvate (the end product of anaerobic glycolysis) could be used to produce either **lactate** or **ethanol**.

These were dead-end metabolites in terms of generating energy, but…

An aerobic system could utilize enzymes that transformed pyruvate (remember, this was a product of anaerobic glycolysis) into an activated acetic acid group (acetyl coenzyme-A) by releasing CO_2 (respiration) and $H^+ + e^-$ couples, which could be used for energy generation in subsequent steps.

Acetyl coenzyme-A could then enter the **Krebs cycle** (or "tricarboxylic acid cycle")…

Energy (ATP) is produced here (green circle).



The Krebs cycle is self-catalytic – it continuously generates the intermediates needed for subsequent "turns" of the cycle.

e.g. oxaloacetate combines with acetyl coenzyme-A to begin the cycle and is regenerated from malate at the end of the cycle.

Therefore, one or a few oxaloacetate molecules can sustain the processing of an infinite number of acetyl coenzyme-A molecules – **as long as** a steady supply of pyruvate is present (from where?).

How is ATP generated in the cycle?

A series of enzymes catalyze transformations of intermediates to produce:

1. **One ATP** from within the cycle (succinyl coenzyme-A – to – succinate).

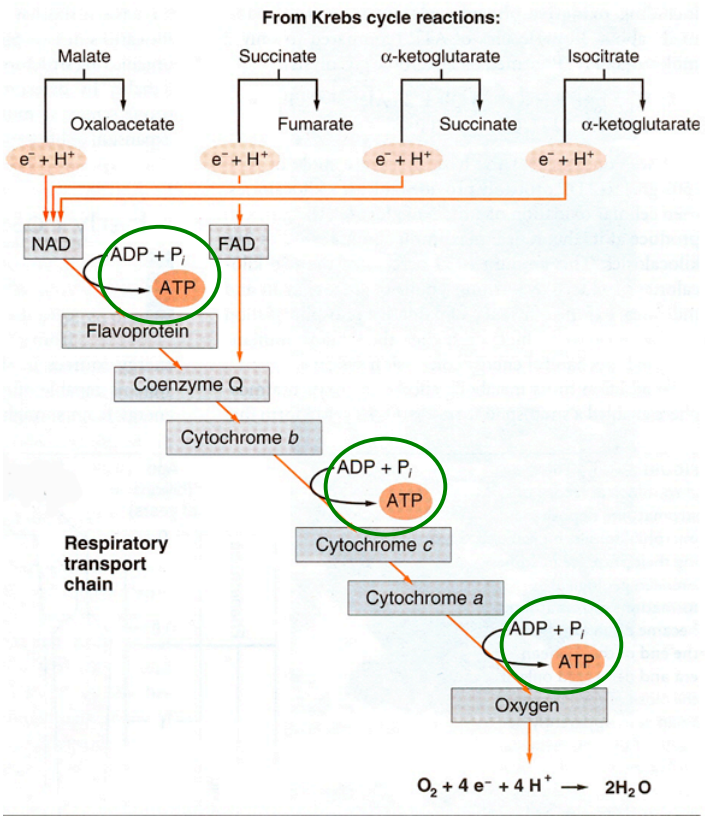
2. **Eight electron-H^+ couples**

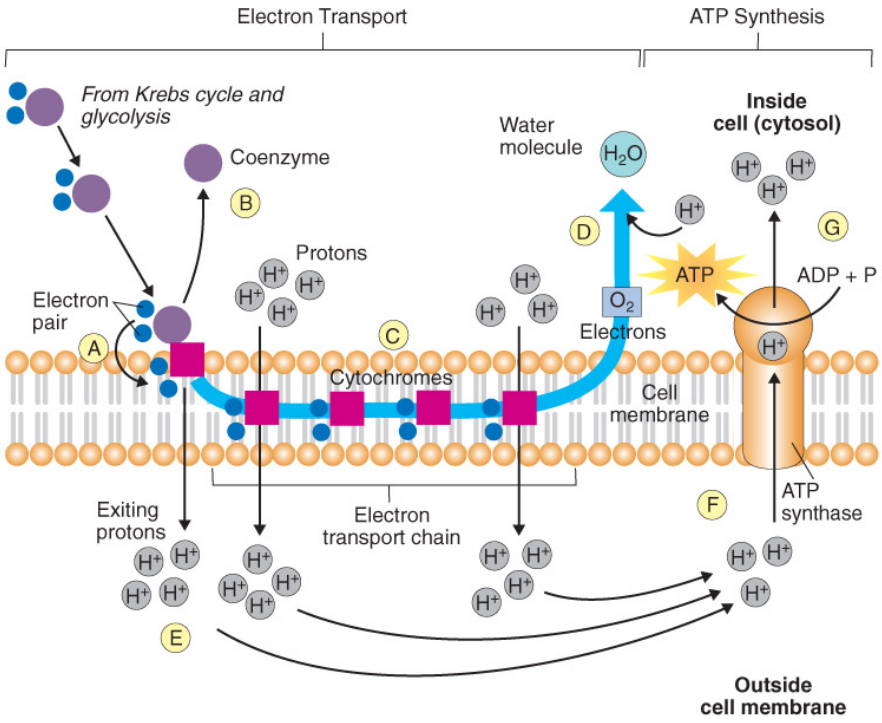
These couples are collected by coenzymes called:

1. nicotinamide adenine dinucleotide (NAD^+)

2. flavin adenine dinucleotide (FAD^+)

…and then shuttled to the electron (respiratory) transport chain.





Protons (H^+) are pumped across the cell membrane to create proton gradients that drive ATP synthesis.

Did aerobic metabolism really facilitate more efficient energy production?

Remember, *anaerobic* glycolysis produced **2 ATPs**

Complete *oxidation* of one molecule of glucose can produce up to **38 ATPs**

2 ATPs directly from glycolysis

2 ATPs (actually GTP) from the Krebs cycle (one for each turn of the cycle…remember glycolysis yields 2 molecules of pyruvate)

Succinyl coenzyme-A → succinate step

But, remember all of the NADH and FADH (H+ - e' couples)…

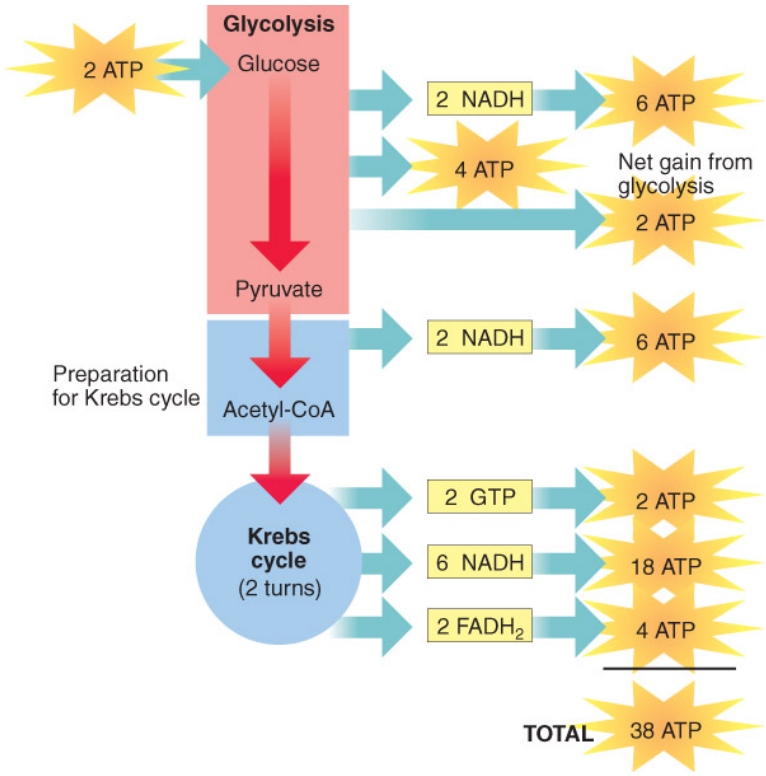
34 ATPs from electron transport

6 ATPs from NAD-based electron transport (3 ATP per NADH from glycolysis)

6 ATP from decarboxylation of pyruvate (3 ATP per NADH in preparation for the Krebs cycle)

18 ATPs from NAD-based electron transport (3 ATP per NADH from Krebs cycle)

4 ATPs from FAD-based electron transport (2 ATP per FADH from Krebs cycle)



DIVERSIFICATION: PROKARYOTES AND EUKARYOTES

One of the most significant biological changes to take place was the division between prokaryotes and eukaryotes.

Prokaryotes

Bacteria and *Archaea* – two phylogenetically distinct groups
No organelles
Divide by binary fission

Eukaryotes

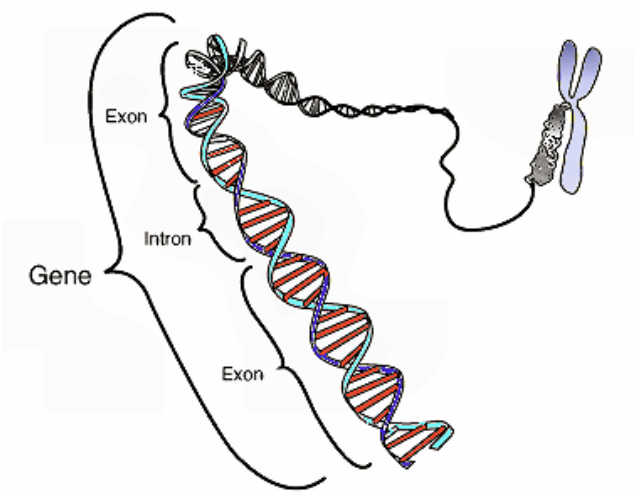
Multicellular organisms (including single-celled protists such as algae and protozoa)
Contained organelles
Divide by mitotic mechanisms

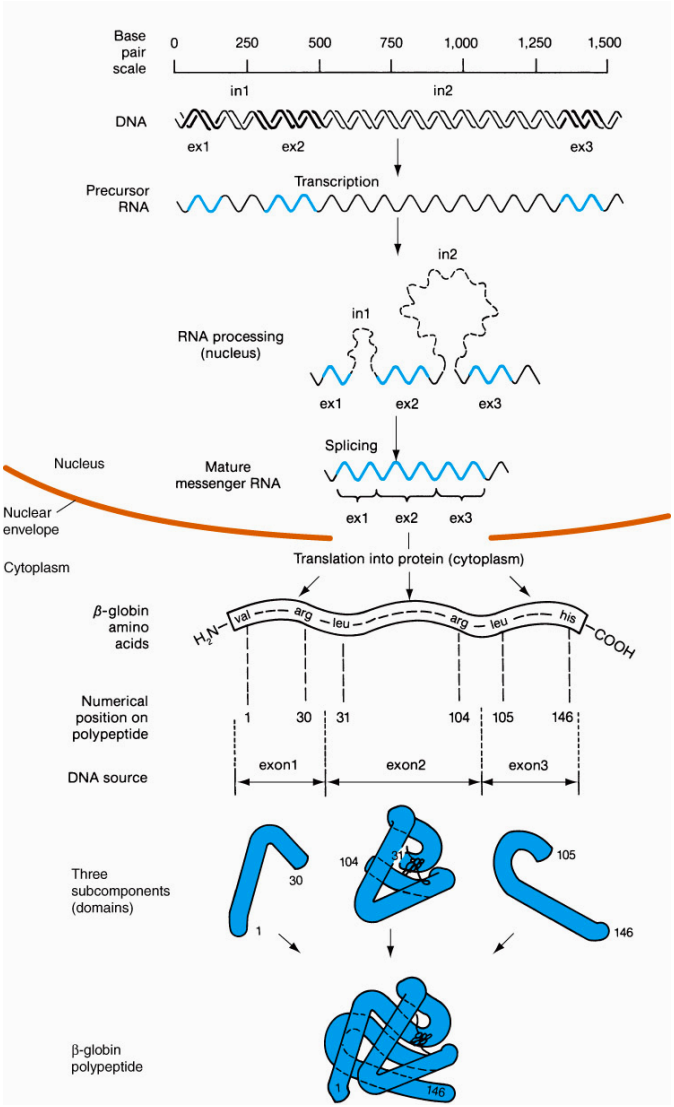
In addition to these differences, **gene structure** differentiated prokaryotes from eukaryotes.

Split genes are present in eukaryotes **but not in prokaryotes**.

The nucleotide sequence (DNA) that encodes for a single gene is commonly divided up by stretches of potentially hundreds of nucleotide bases.

When the mRNA is transcribed, the intervening sequence (introns) is excised and the expressed, information-encoding sequences (exons) are joined in a final mRNA product.





Why?

The intron-exon system must be advantageous, but strong evidence why has not been presented.

Theory 1: Translation of several different exons represented first attempts at combining proteins for complex metabolic functions.

Various combinations of exons could facilitate the formation of optimally functional polypeptides.

Perhaps resources were conserved when a discrete number of short protogenes could be arranged/rearranged to form functional proteins.

Theory 2: Each exon might have originally encoded a discrete polypeptide domain (gene) that had a certain function.

Evidence: The average exon size (coding 20 to 80 amino acids) of early protein-encoding sequences correlated with the shortest polypeptide sequence that could fold into a stable structure (20 to 40 amino acids).

Introns might be "mobile" DNA sequences that have the ability to splice themselves into and out of target sites.

Encoded useful functions at some point in time (like today's antibiotic resistance).

The inclusion of these sequences would certainly impact the mRNA sequence by adding additional nucleotides to the message.

But, would a cell want to deal with this **extra information**?

Two hypotheses surrounding the evolution of introns.

1. "**introns early**" – originally, both eukaryotes and prokaryotes featured introns **and** exon sequences.

   What problem might this have caused early, simple organisms?

   Introns were abandoned in prokaryotic lines likely due to the selection of increased streamlining of DNA replication and transcription efficiency.

   In other words, it was too expensive for an organism already at its limit.

2. "**introns late**" – introns were inserted into eukaryotic genomes after the lineage split from prokaryotes.

   Support: - several introns are of recent origin in some eukaryotes.

   Another question: Why might all of this unneeded information be conserved throughout evolution?

   Possibly to promote genetic recombination.

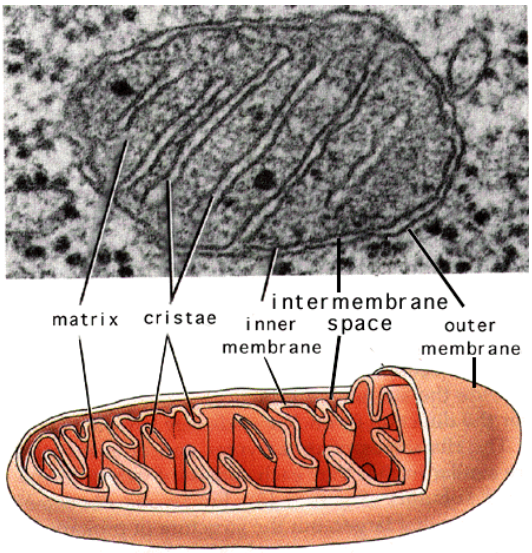
   Long introns would oppose linkage and promote splitting of contiguous gene segments.

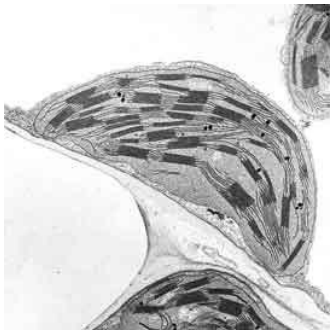
So, which theory is correct….probably a combination of both occurred. Nevertheless, within the 26,564 annotated genes in the human genome, ~234,000 exons and 207,000 introns exist.

EVOLUTION OF ORGANELLES: MITOCHONDRIA AND CHLOROPLASTS

Both organelles are found only in **eukaryotic** organisms.

Membranous structures, distinct from the cytoplasm.





Plant Cell Chloroplast Structure

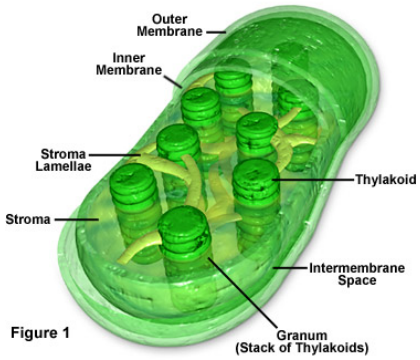


Figure 1

What is the general function of these organelles?

One early theory stated that these structures were simply the result of an invagination of the cell membrane that detached to form a separate structure within the cell. However…

1. Mitochondria and chloroplasts have their **own DNA.**

2. Both contain **independent ribosomes** and are most like ribosomes of **prokaryotes**.

   Size, sensitivity to antibiotics, nucleotide sequence of RNA component.

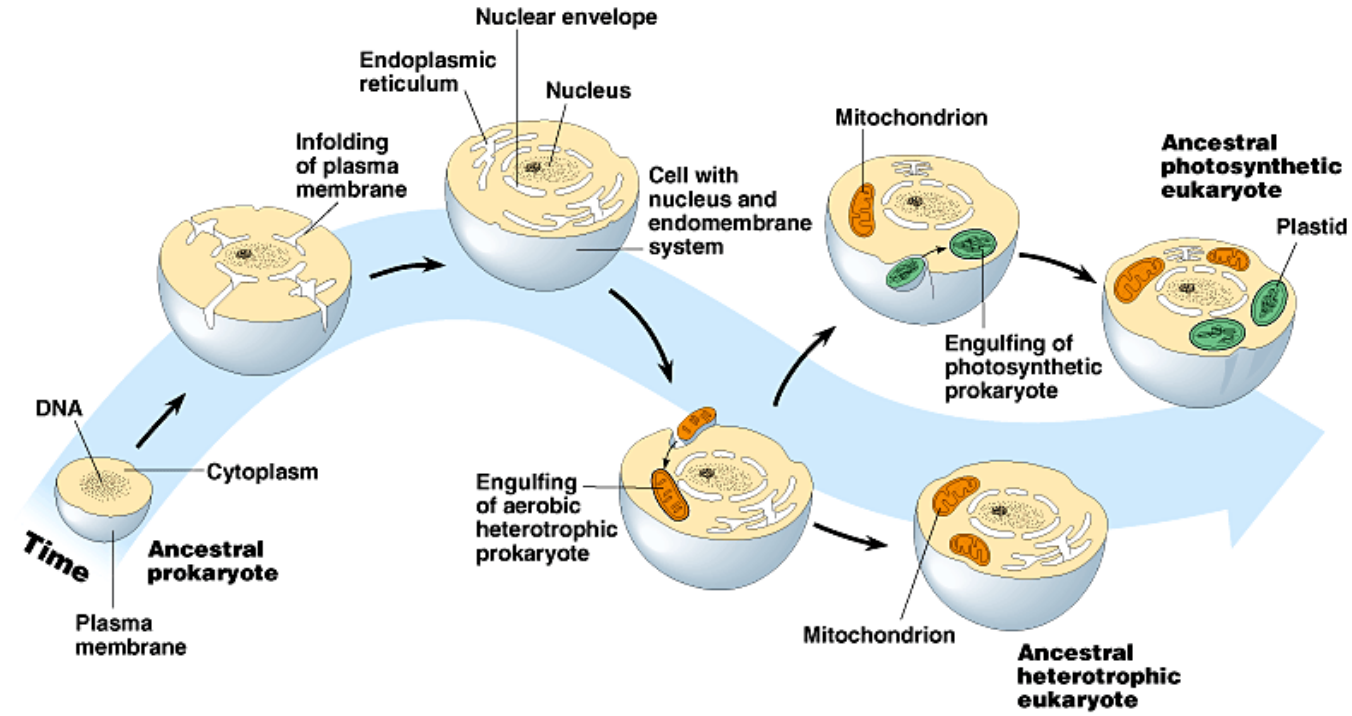
3. Neither structure is synthesized ***de-novo,*** each divides by fission during eukaryotic cell division.

The invagination theory could explain the presence of a nucleus, but not the mitochondrion or organelles.

How can we explain the presence of these organelles?

Endosymbiotic theory (~1.5 b.y.a.) what also occurred about 1.5 b.y.a.?

Theory states that eukaryotic cells evolved by incorporating prokaryotic organisms into their cytoplasm.



At some point, ingested photosynthetic and heterotrophic bacteria developed a symbiotic relationship with the host.

If this new symbiont was a heterotrophic bacterium…

The bacterium gained safe residency while the eukaryote benefited from energy generated by the bacterium.

The organelle represented a primitive **mitochondrion**.

What if the eukaryotic cells developed a similar relationship with photosynthetic bacteria?

Resulted in a photosynthetic eukaryote, independent from the need for organic materials as a source of carbon and electrons.

The organelle represented a primitive **chloroplast**.

Endosymbiosis represented a significant advance in evolution, as now the selection for algae, plants and higher eukaryotes was possible.

A question: why didn't the advancements in metabolic efficiency and increased complexity of eukaryotes spell the end for prokaryotes?

Prokaryotes maintained key features that the eukaryotes abandoned:

1. Haploid genome – much simpler genetic requirements.

2. Rapid reproduction – worked the increased likelihood for mutations to their advantage in the form of adaptation potential.

   Competitive advantage, as well.

3. Structural simplicity – allowed for colonization of physically inaccessible niches.

4. "Extreme" tolerance – habitats included environments where eukaryotes could not survive.

These features are still important today to the success of prokaryotes.