

## Endosymbiosis

### History of the theory of endosymbiosis

- AFW Schimper, 1883, noted that plastids of plant cells, which divided by binary fission independently of the surrounding plant cell, bore an uncanny resemblance to free-living cyanobacteria.

Schimper, 1883. Über die Entwicklung der Chlorophyllkörner und Farbkörper. Bot. Zeitung, 41:105-162

### History of the theory of endosymbiosis

- Mereschkowsky (1905, 1910)  
Proposed reticulated tree of endosymbiosis for origin of algal plastids  
Called them "little green slaves"  
Remarkable insights, given technology of the time (light microscopy)

### History of the theory of endosymbiosis

- Not much for 50 years (and certainly no broad acceptance).
- Klein and Cronquist derisively remarked: "this bad penny has been circulating for a long time" (1967)

From fringe hypothesis to widely accepted theory...

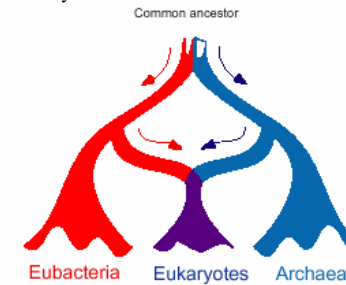
- In 1959 Stocking and Gifford discovered DNA in plastids of green algae (*Spirogyra*).
- **Persuasive writings and synthesis of Linn Margulis, 1970s,**
- Carl Woese (1977): "the case is a clear cut one, and it has now been proven"
- Norm Pace (1986): "beyond reasonable doubt"
- Gray (1991): "it seems pointless to consider seriously alternative explanations"
- Taylor (1987): arguments against endosymbiosis theory are "flogging a dead horse"

### Endosymbiosis and The Origin of Eukaryotes

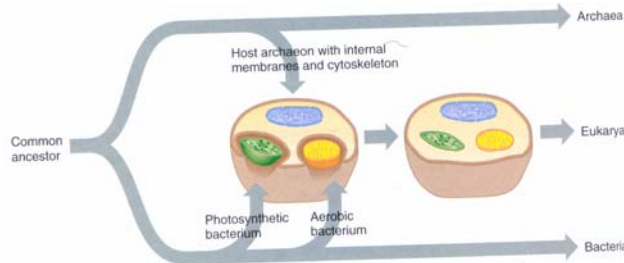
rRNA sequences place Eukarya closer to Archaea than Bacteria

other evidence suggests Eukarya closer to Bacteria than Archaea

Endosymbiotic theory combines these – suggests Eukarya evolved from symbioses between Archaea and Bacteria



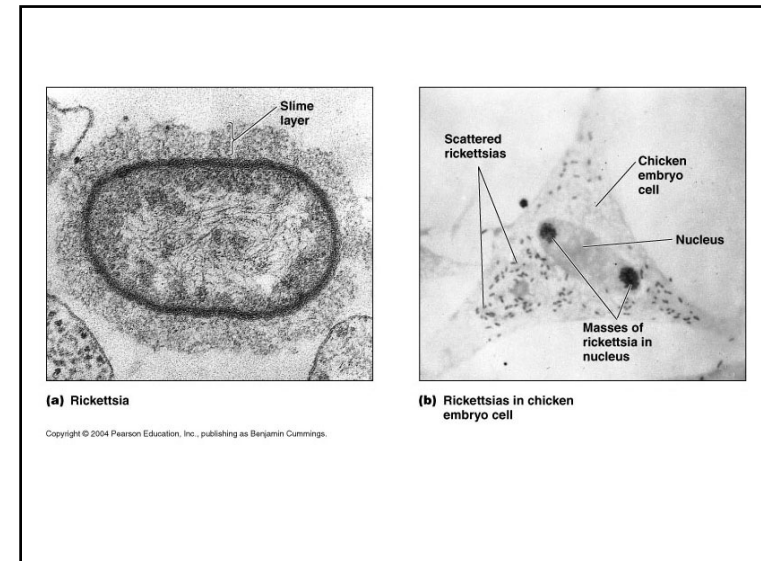
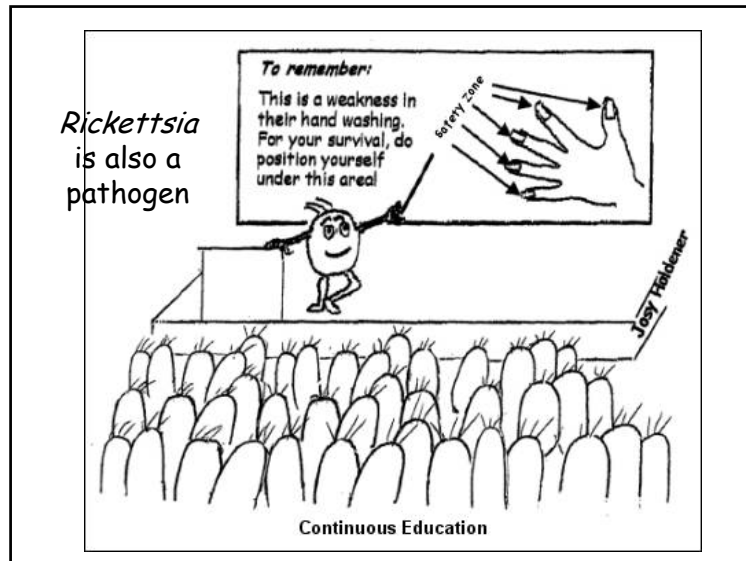
The **mitochondria** of eukaryotes evolved from endosymbiotic prokaryotes (living within their host cell). Because of the similarities of their genomes, rickettsias may be the closest relatives to the ancestors of mitochondria.



The **chloroplasts** of eukaryotes evolved from endosymbiotic **cyanobacteria** (autotrophic prokaryotes), and from other algae (multiple origins of plastids).

- Because of the similarities of their genomes, rickettsias may be the closest relatives to the ancestors of mitochondria.
- **Rickettsias** are Bacteria, too small to be clearly seen under the light microscope. Almost all are obligate intracellular parasites. This means that they can only grow and reproduce while within the living cells of their host - certain arthropods (ticks, mites, lice, fleas) and mammals.





## II. The evidence for mitochondria and chloroplasts

- 1) mitochondria and chloroplasts arise only from preexisting mitochondria and chloroplasts.
  - cannot be formed in a cell that lacks them because nuclear genes encode only some of the proteins of which they are made.
  - divide by simple fission, splitting in two just as bacterial cells do.
- 2) mitochondria and chloroplasts have their own genome
  - resembles that of prokaryotes, not that of the nuclear genome.
  - replicate and partition their DNA in much the same way as bacteria.
  - both genomes consist of a single circular molecule of DNA
  - no histones associated with the DNA

3) mitochondria and chloroplasts have their own protein-synthesizing machinery, and it resembles that of prokaryotes not that found in the cytoplasm of eukaryotes.

- a) **rRNA** and ribosomes resemble those of prokaryotes
- b) first amino acid of their transcripts is always **fMet** as it is in bacteria (not methionine [Met] as in eukaryotic proteins).
- c) antibiotics (e.g., **streptomycin**) that act by blocking protein synthesis in bacteria (but not eukarya) also block protein synthesis in mitochondria and chloroplasts.
- d) inhibitors (e.g., **diphtheria toxin**) of protein synthesis by eukaryotic ribosomes affect neither bacterial nor mitochondrial and chloroplast protein synthesis
- e) The antibiotic **rifampicin**, which inhibits the RNA polymerase of bacteria, also inhibits the RNA polymerase within mitochondria, but not the RNA polymerase within the eukaryotic nucleus.

4) Both mitochondria and chloroplasts are surrounded by two membranes: inner probably from the engulfed bacterium, the outer probably from the plasma membrane or endoplasmic reticulum of the host cell.



5) Mitochondria and chloroplasts contain ribosomes that are similar in size and structure to bacterial ribosomes.

### III. Chloroplasts – multiple origins

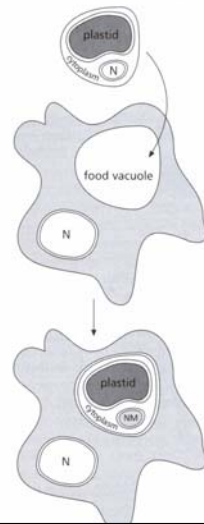
A. Primary endosymbiosis: when bacterium engulfs bacterium and engulfed becomes organelle

1) Example: Glaucophytes: freshwater microalgae

- i. blue-green plastid called cyanelles, very similar to cyanobacteria
- ii. plastid wall is made of peptidoglycan, biochemically different from that of other algal plastids
- iii. external coating of lipopolysaccharides, very similar to gram negative eubacteria
- iv. inner membrane very similar to plasma membrane of cyanobacteria

B. Secondary endosymbiosis: incorporation of eukaryotic endosymbiont having plastids derived from primary endosymbiosis

1) Secondary endosymbiosis is the current model for the origins of the plastids of euglenoids, cryptomonads, chlorarachniophytes, dinoflagellates (all these are different groups of algae)



2) Evidence for secondary endosymbiosis, and examples:

a) more than two membranes around plastids of these algae; outermost of the extra membranes likely a remnant of the secondary hosts' phagocytotic vesicle (i.e., food vacuole)

some groups have 4 membranes, others only 3  
all mitochondria have only 2 - not thought to have arisen by secondary endosymbiosis

b) occurrence of structures that look like very small nuclei and eukaryotic-sized ribosomes located between the two pairs of membranes surrounding plastids of cryptomonads  
'nucleomorphs' are bounded by a porous membrane, divide by pinching into two equal halves - highly reduced nucleus?

c) nucleomorphs contain DNA, arranged in tiny chromosomes, encoding genes necessary for the maintenance of the nucleomorph itself, several of which are expressed (to make ribosomes, proteases)

d) comparisons of DNA sequences, host nuclei and plastids suggest independent origins of the plastids of various algal groups

i. phagotrophic amoeba engulfed a green alga to give rise to the chlorarachniophytes

ii. flagellate engulfed a red alga to give rise to the cryptomonads

#### IV. Modern Endosymbionts

1) New endosymbiotic consortia are being described all the time, and appear to be the rule rather than the exception, particularly between certain protozoa and algae or bacteria.

The endosymbiotic theory for the origin of eukaryotic organelles gains much support from the ease with which protozoa can be seen to enter into symbiotic relationships with bacteria. With the transfer of genes from the symbiont's nucleus to that of the host, the relationship becomes obligate and the symbiont becomes an organelle - no longer capable of independent existence.

#### 2) Examples of modern endosymbionts:

##### A. Ciliate symbionts

Sand-dwelling ciliate "farms" sulphur bacteria on its surface, consuming what it needs, thus treating its symbionts as a portable kitchen garden.

Many anaerobic ciliates have methanogens in their cytoplasm.  
- lack mitochondria but have organelles called hydrogenosomes which, like mitochondria, can oxidise pyruvate  
- hydrogen is removed by the symbiotic methanogens which use it to obtain energy from the reduction of  $CO_2$  to methane.

- Such ciliates are believed to be important in production of methane (a greenhouse gas) in municipal landfill sites

Similar associations also occur between ciliates and methanogens in the rumen.

### B. Symbionts of heterotrophic protozoa

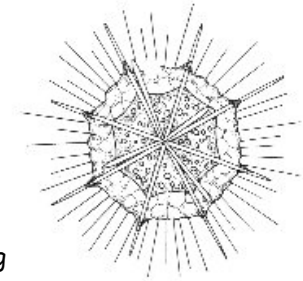
Heterotrophic free-living protozoa frequently incorporate photosynthetic organisms (bacteria, unicellular "algae" including phytoflagellates) as symbionts.

The photosynthesising symbiont hands on some of the products of carbon dioxide fixation to its host organisms, the host in turn passes on its  $CO_2$  and nitrogenous wastes to the symbionts for utilisation in growth. The symbionts divide in pace with the host cell.

### C. Marine protozoan symbionts

The possession of photosynthesising symbionts by marine protozoa may make them important primary producers as well as being consumers.

Thus the radiolarian protozoa, which lives suspended in the euphotic zone of warm seas, "farm" photosynthetic dinoflagellates as symbionts in their cytoplasm while also feeding phagotrophically on other planktonic organisms.



radiolarian protozoan

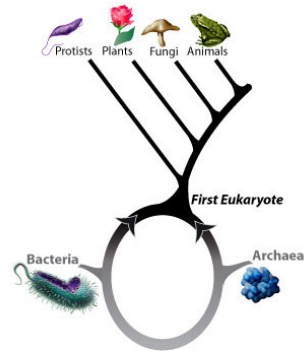
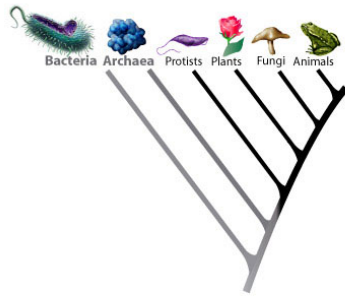
### D. Protozoa - algae Paramecium and Chlorella

alga provides fixed carbon and  $O_2$   
protozoan provides protection,  $CO_2$ , and growth factors  
relationship can persist in anaerobic habitats

E. All aphids have "mycetomes" - cell clusters that house bacteria  
when eliminated with antibiotics (prokaryote-specific), the aphid dies, suggesting dependence on the bacteria

### New Frontiers in endosymbiosis...

- Rivera and Lake, 2004 – origin of nuclear genome in eukaryotes?
- Analyzed complete genome data for 30 eukarya, archaea, and bacteria



One of science's most popular metaphors, the "tree of life," (left) with its evolutionary branches and roots, turns out to be a misnomer and is instead a ring (right), according to UCLA molecular biologist, James Lake.

Credit: *National Science Foundation.*

- "At least 2 billion years ago, ancestors of these two diverse prokaryotic groups fused their genomes to form the first eukaryote, and in the process two different branches of the tree of life were fused to form the ring of life," Jim Lake, UCLA.