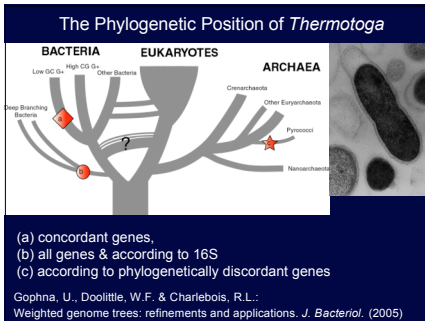
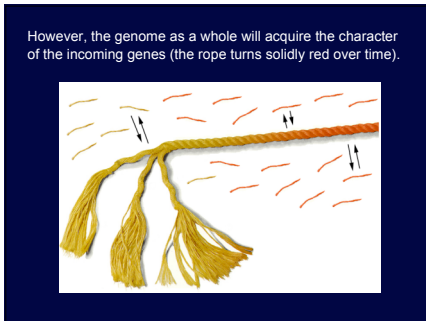
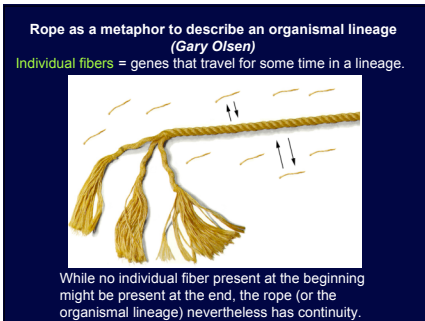
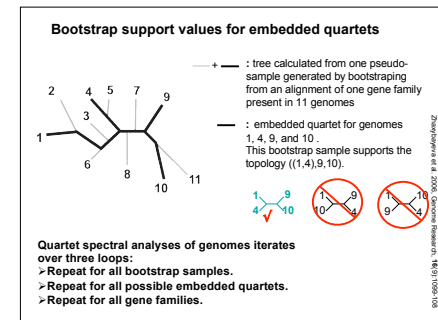
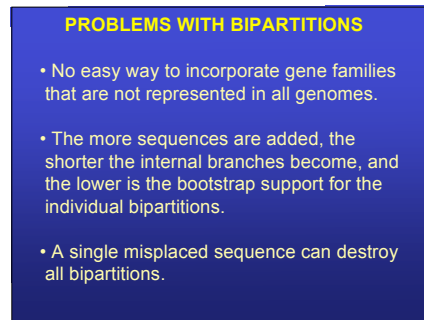
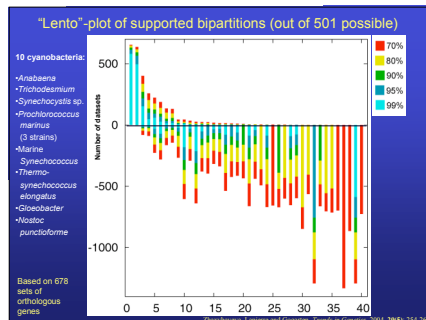
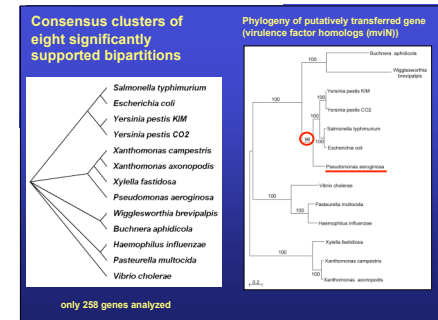
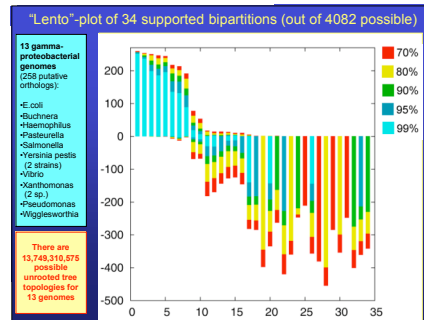
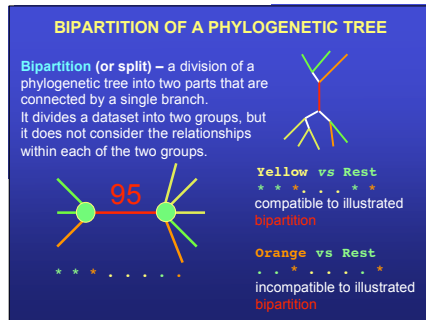
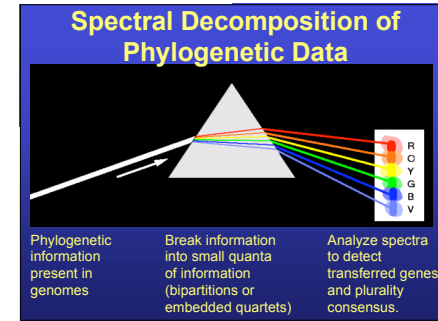
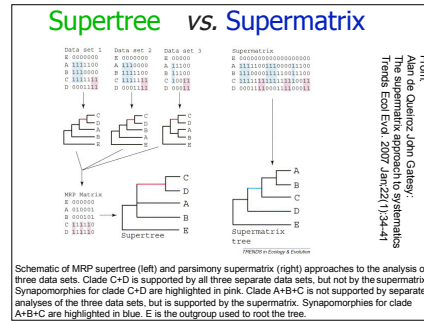
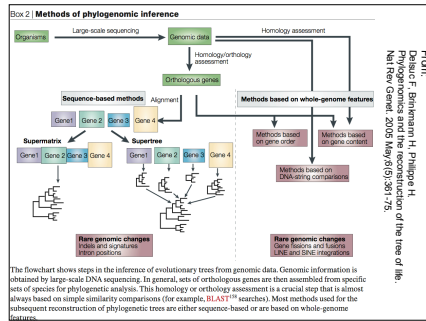
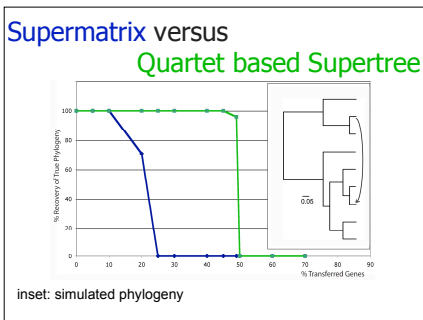
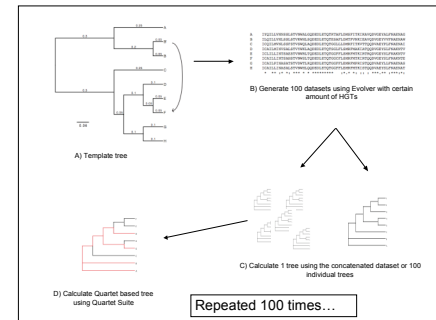
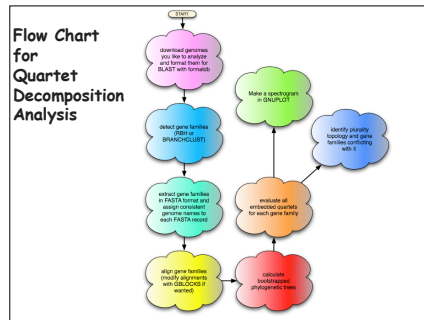
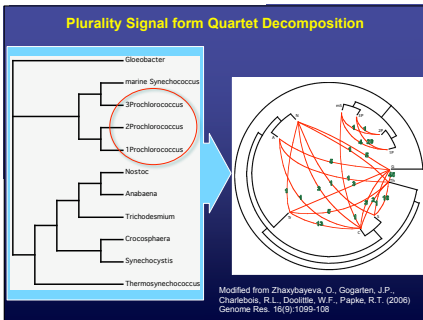
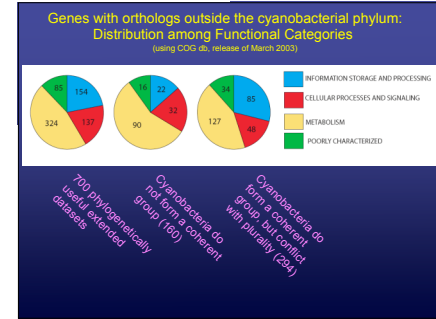
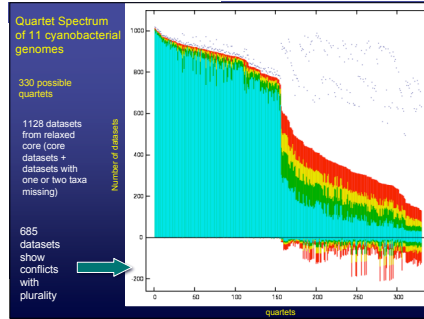
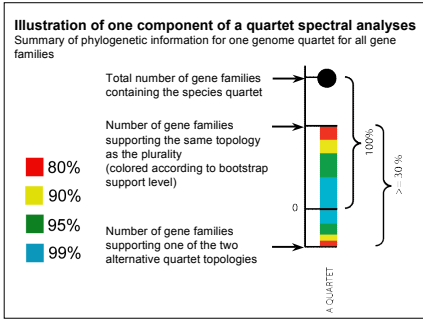


- Most transferred genes belong to the "accessory pool", are only under weak selection, and often found in genomic islands.
- All types of genes have been horizontally transferred, including ribosomal RNA operons and genes encoding ribosomal proteins.



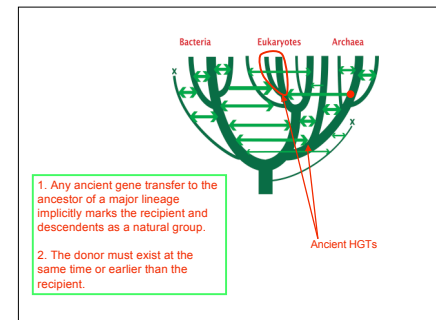


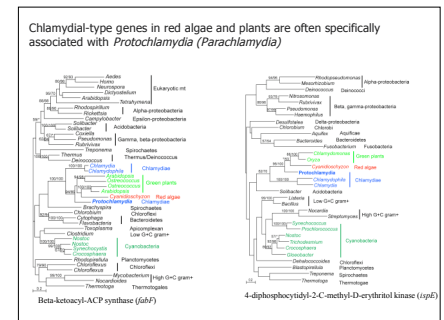
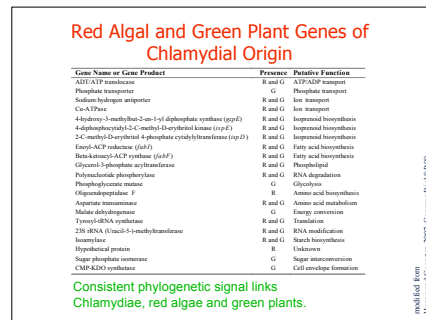
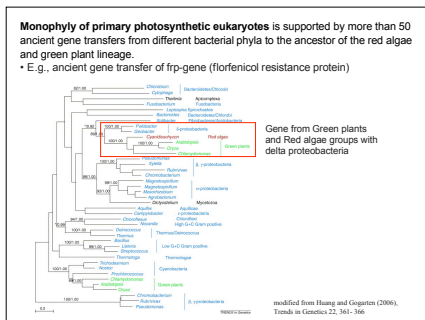
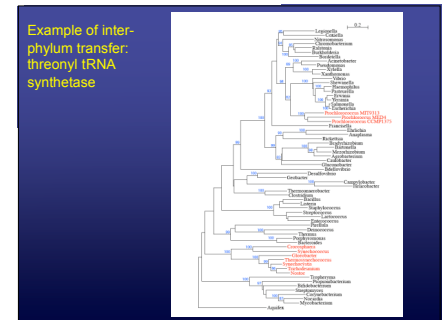
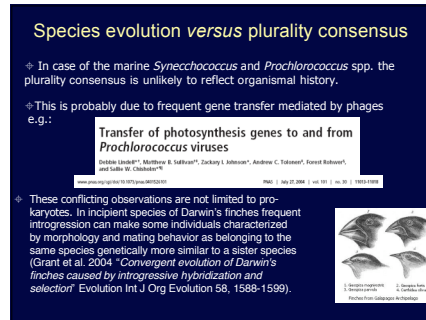
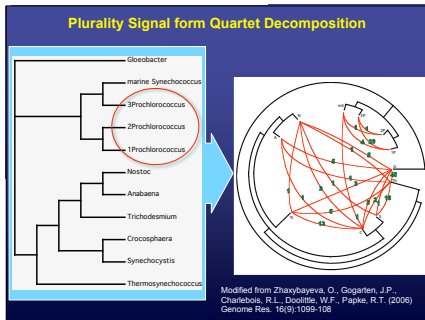
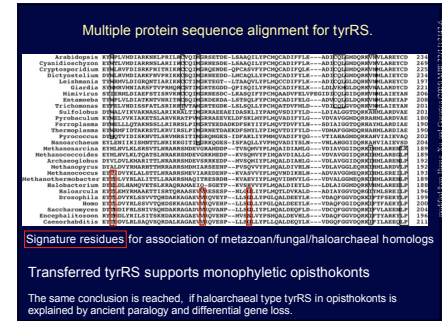
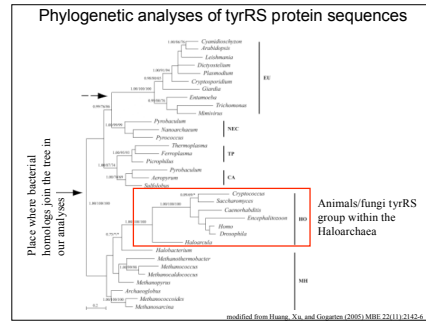
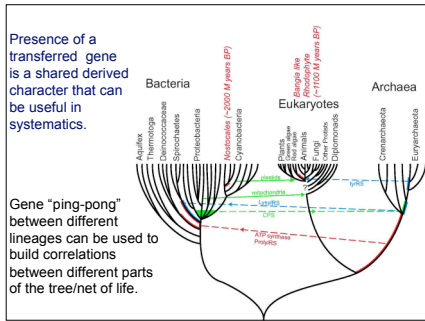


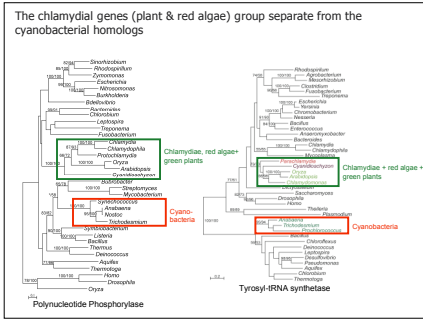
### Ancient Gene Transfer and Phylogenetic Reconstruction: Friends or Foes?

Popular view  
 Gene transfer is a disruptive force in phylogenetic reconstruction.

New view  
 Events of ancient gene transfer are valuable tools for reconstructing organismal phylogeny.







### Examining possible Hypotheses

- Plants acquired chlamydial genes via insect feeding activities (Everett et al. 2005).  
No. The ancestor of red algae and green plants is much older than insects.
- Chlamydiae acquired plant-like genes via Acanthamoeba hosts (Stephens et al. 1999; Wolf et al. 1999; Ortutay et al. 2003).  
No. All these genes are of bacterial origin. The direction of gene transfer is from bacteria to eukaryotes.
- Chlamydial and plant sequence similarities reflect an ancestral relationship between chlamydiae and cyanobacteria (Brinkmann et al. 2002; Horn et al. 2004).  
No. Genes of chloroplast ancestry should still be more similar to cyanobacterial than to chlamydial sequences. In many instances the cyanobacterial homologs form a clearly distinct, and separate clade.

### What do we learn from the data??

(Chlamydial genes in red algal and plant genomes)

Unless a stable physical association existed, it is highly unlikely for any single donor to transfer such a number of genes to a single recipient.

**Our Hypothesis:** An ancient, unappreciated symbiotic association existed between chlamydiae and the ancestor of red algae and green plants.

Genes from this chlamydial symbiont might have been crucial to establish communication between host and the cyanobacterial cytoplasm.

### Hypothesis: Chlamydiae and the primary plastids

A) The Host

Within:  $\alpha$ -proteobacterial (mitochondrial) symbiont

- Gene transfer to the nucleus
- Transport of nuclear encoded proteins to symbiont
- Direction of symbiotic benefit

### Hypothesis: Chlamydiae and the primary plastids

B) The Host invaded by a parasite

Yellow: parasitic chlamydial bacterium  
Green: cyanobacterium (as food)

- Gene transfer to the nucleus
- Transport of nuclear encoded proteins to symbiont
- Direction of symbiotic benefit

### Hypothesis: Chlamydiae and the primary plastids

C) The chlamydial symbiont becomes mutualistic

Genes might be transferred between the different symbionts

The machinery that provides benefits to the chlamydial parasite also begins to provide some benefits to the enslaved cyanobacterium

- Gene transfer from the symbionts to the nucleus
- Transport of nuclear encoded proteins to symbiont
- Direction of symbiotic benefit

### Hypothesis: Chlamydiae and the primary plastids

D) The cyanobacterium evolves into an organelle

Products from genes that were transported to the nucleus are targeted into the cyanobacterium

- Chlamydial and cyanobacterial type gene products are targeted to the plastid
- Gene transfer from the symbionts to the nucleus
- Direction of symbiotic benefit

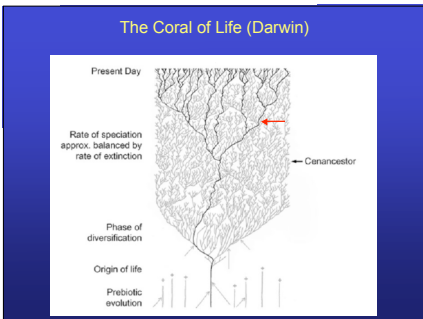
### Hypothesis: Chlamydiae and the primary plastids

D) Loss of chlamydial symbiont

With the help of genes contributed by the chlamydial parasite, the cyanobacterium has evolved into a photosynthetic organelle

The chlamydial symbiont is lost - possibly without trace, except for the genes that facilitated the integration of the metabolism of the host with that of a photoautotroph.

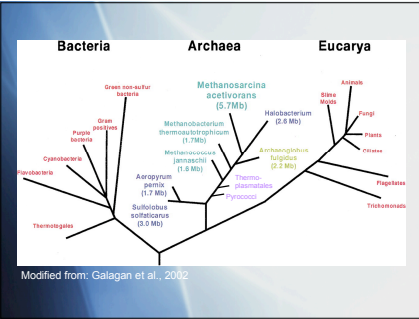
This hypothesis also explains why the evolution of an organelle from a primary endosymbiont is rare. A photoautotroph with a single compartment has few transporters available that would allow integration with the host metabolism. The simultaneous presence of an intracellular parasite allows for the integration of the two cytoplasm.



## Mapping Metabolic Pathways on the Tree of Life

Chris House, Bruce Runnegar, and Sorel Fitz-Gibbon conclude from their analyses of genome based phylogenetic trees (Geobiology 1, 15-26, 2003):

*"Our results suggest that the last common ancestor of Archaea was not a methanogen and that methanogenesis arose later during subsequent microbial evolution. This leaves sulphur reduction as the most geochemically plausible metabolism for the base of the archaeal crown group."*



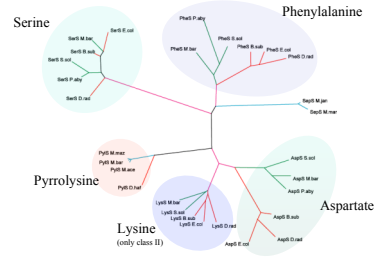
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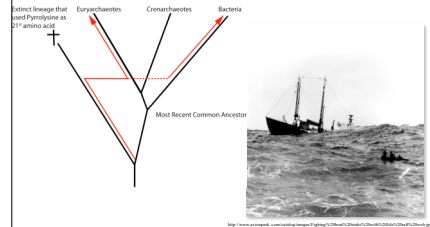
*"Our results suggest that the last common ancestor of Archaea was not a methanogen and that methanogenesis arose later during subsequent microbial evolution. This leaves sulphur reduction as the most geochemically plausible metabolism for the base of the archaeal crown group."*

This conclusion is at odds with the ancient origin of many of the enzymes specific to methanogens. Enzymes involved in methylamine reduction use pyrrolysine as a 21 amino acid. The enzyme that charges the pyrrolysine tRNA is as old as the genetic code.

## Class II aaRS Phylogeny

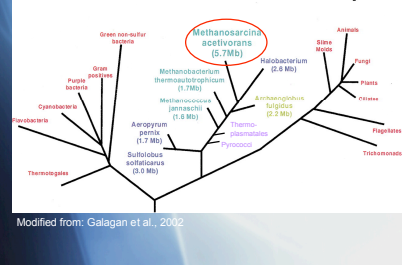


## Pyrrolysine as 21st amino acid: A genetic "life raft"?

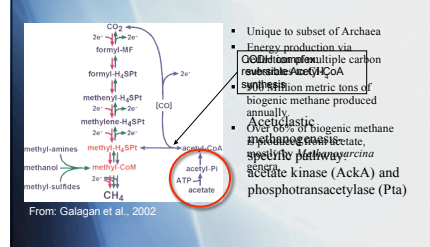


## Evolution of Aceticlastic Methanogenesis in Methanosarcinales via Horizontal Gene Transfer from Clostridia

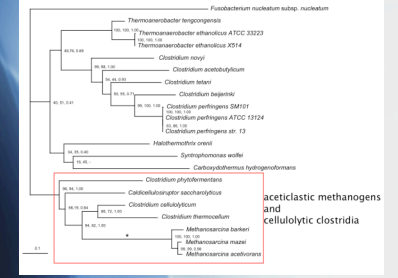
## Bacteria Archaea Eucarya



## Methanogenesis

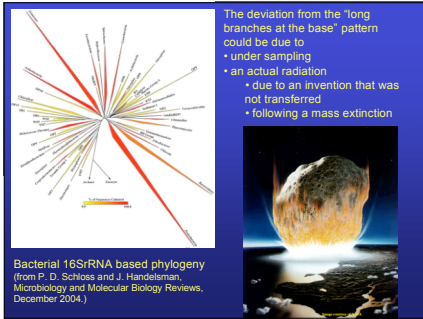


## Phosphotransacetylase (Pta)









## Conclusions

- Ancient gene transfers provide good cladistic markers, especially for relationships between phyla.
- Organismal evolution is only insufficiently described as a single furcating tree. Life is a "dance" (a network of interactions changing over time). Interactions between lineages are of different duration and can involve gene transfer.
- To unravel early evolution concepts of population genetics need to be applied also to higher taxonomic units of prokaryotic evolution.
- Individual gene trees coalesce to an MRCA, but these molecular MRCAs did not co-exist in the organismal MRCA.
- Tracing metabolic pathways through the net/web of life might provide hints to the order in which metabolic pathways evolved.
- Some pathways that dominate the extant biosphere appear of comparatively recent origin.

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NASA Exobiology & AISR Programs

## Signature Proteins

### The origin of the eukaryotic cell: A genomic investigation

Hyman Hartman<sup>1</sup> and Alexei Fedorov<sup>2</sup>

Table 1. List of 91 ESPs associated with cytoplasm and membrane systems

Category	Subcategories (ID)
Cytoskeleton	
****	
Vacuole	Vacuolar protein (Pep4) Retromer complex component 5 (p135) Vacuolar ATPase V <sub>0</sub> domain subunit c (Cup5) Vacuolar ATPase V <sub>0</sub> domain c' (Ppa1, Ttp2)

The Proteolipid is less conserved within Eukaryotes, and has diverged beyond ready recognition fir inter domain comparisons:

