

## PROKARYOTIC DIVERSITY

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### 1. Introduction

Prokaryotes possess an enormous diversity of morphological, nutritional, ecological and

genetic features. This diversity is reflected in the range of habitats, modes of energy generation, and life styles and life cycles of the bacteria. Early attempts at bacterial classification relied on many of these characteristics, and generated a bewildering array of possible taxonomic schemes, many of which were simply utilitarian and for specific application. One approach which allows the inclusion of all prokaryotes, is the classification based primarily on nutritional characteristics. Another is that based on morphological features. Clearly a combination of these would offer a general scheme for classification, and this was the approach taken to unify bacterial taxonomy. This is not the approach taken here. Bacterial structure and function, and growth and physiology are discussed elsewhere (see *Prokaryote Cell Structure and Function* and *Prokaryote Physiology in Anaerobic and Aerobic Atmospheres* respectively) and will not form the basis for this discussion of prokaryotic diversity.

Earth is estimated to be 4.6 billion years old. Fossilized remains of prokaryotes, dated to between 3.5 and 3.8 billion years BP, have been identified in stromatolites. Based on rRNA sequence data, the first major diversification occurred quite early in the evolutionary history. Figure 1 reflects the phylogenetic tree proposed by proponents of this view. The three domains indicate the early division of eubacteria and archaeobacteria, and the later development (about 1.4 billion years ago) of eukaryotes. Traditional kingdoms are distributed amongst the domains.

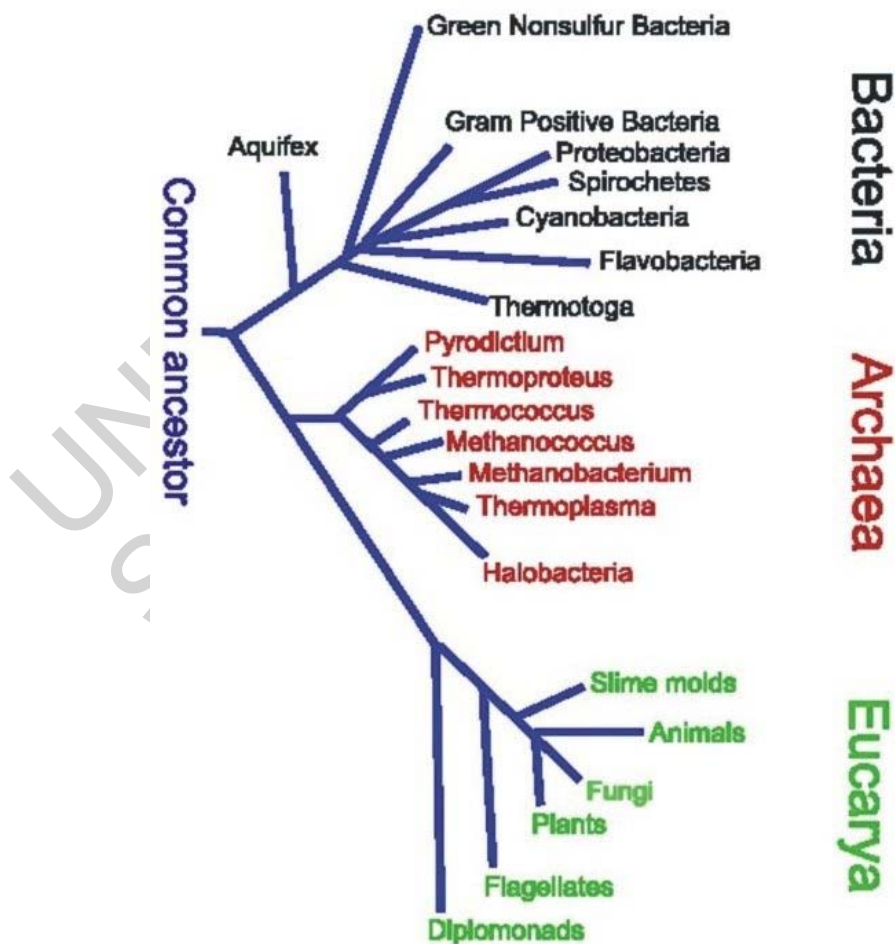


Figure 1. Universal phylogenetic tree as proposed by Olsen & Woese.

Although this view is the most widely accepted, alternatives do exist. Figure 2 depicts some of the more popular alternatives.

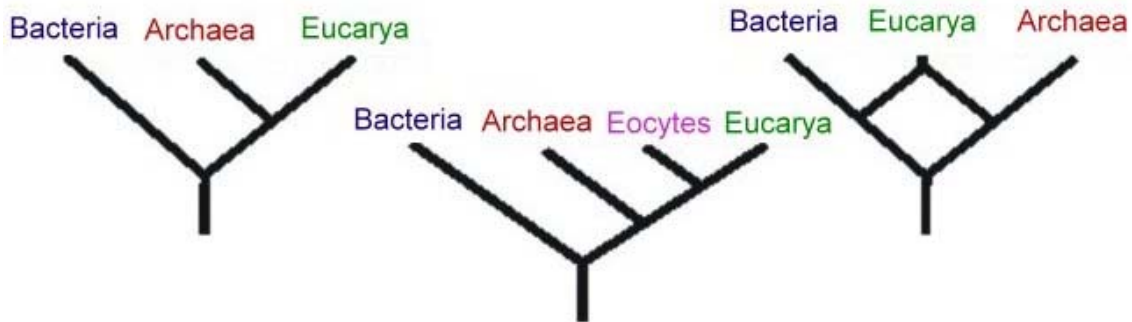


Figure 2. Alternative 'tree of life' designs.

Discussion of prokaryotic diversity could be based on any number of systematic systems including those derived from ecological, physiological, biochemical, evolutionary, morphological, pathological or industrial criteria. Bacterial systematics has traditionally relied almost exclusively on phenetic characterization, although the advent of, and rapid progress in molecular biology, is changing this. The major phenetic distinction of eubacteria is the nature of the cell wall as defined by gram staining.

This division is fundamental rather than arbitrary, since the division into gram-negatives, gram-positives and mycoplasmas (bacteria lacking a cell wall) also reflects differences in morphology, metabolism, reproduction, the presence of endospores and motility. In addition to gram-stain reaction, major distinctions are therefore made on the basis of cell morphology, oxygen relationships, motility, mode of energy production, endospore formation, and other physiological and metabolic characteristics. It is on the basis of these characteristics that the current edition of Bergey's Manual of Systematic Bacteriology was developed.

This definitive publication is divided into four volumes: 1) Gram-negative bacteria of general, medical or industrial importance, 2) gram-positive bacteria other than the actinomycetes, 3) gram-negative bacteria with distinctive properties, cyanobacteria and archaeobacteria, and 4) actinomycetes. The second edition of Bergey's Manual of Systematic Bacteriology is currently in production. This edition will consist of five volumes: 1) The Archaea, Cyanobacteria, Green phototrophs, and deeply branching genera, 2) The Proteobacteria, 3) the low G+C gram-positives, 4) The high G+C gram-positives, and 5) The Planctomycetes, Spirochaetes, Fibrobacter, Bacteroides and Fusobacteria, and therefore more closely reflects the phylogenetic relationships of these organisms.

This review of prokaryotic diversity will follow this taxonomic approach as far as is possible since the phylogenetic position and volume organization may change prior to publication, and use specific examples to illustrate group characteristics. Dendrograms presented below are based on sequence similarity of 16SrRNA. The algorithms used to generate such dendrograms, and even the similarity matrices, are beyond the scope of this document. The reader is referred to *Mathematical Biology – An Introduction to Modeling of Biological Phenomena and Processes* for a general explanation. Simply

stated, the distance of the representative organism from its nearest branch point reflects the evolutionary difference between it and other organisms emanating from the branch point.

## 2. The Archae, Cyanobacteria, Green phototrophs, and Deeply Branching Genera

Major differences between eubacteria and archaeobacteria are listed in Table 1. For more detailed discussion of structural differences the reader is referred to *Prokaryotic Structure and Function*.

Characteristic	Archaeobacteria	Eubacteria
Cell wall	Considerable variety. S-layer of protein, glycoprotein or pseudomurein, or complex polysaccharides and heteropolysaccharides.	Peptidoglycan and teichoic acids in Gram positives. Outer membrane in Gram negatives.
Membranes	Ether linked branched hydrocarbon chains. Sometimes tetraethers.	Ester linked fatty acids
tRNA	T $\psi$ C arm lacks thymine and contains pseudouridine or 1-methylpseudouridine. Initiator tRNA carries methionine	T $\psi$ C arm contains thymine. Initiator tRNA carries N-formyl-methionine
Ribosome	70S but sensitive to anisomycin and insensitive to chloramphenicol and kanamycin	Insensitive to anisomycin and sensitive to chloramphenicol and kanamycin
Histones	Many methanogens contain histone proteins	None
Metabolism	Methanogenic examples. No 6-phosphofructokinase and do not appear to utilize Embden-Meyerhof pathway	No methanogens. May use Embden-Meyerhof pathway

Table 1. Some major differentiating features of archaeobacteria and Eubacteria

Volume one of Bergey's Manual of Systematic Bacteriology is divided into sixteen sections, and encompasses a wide diversity of bacteria from two domains, including the archaeobacteria, green photosynthetic groups and phylogenetically distinct small groups. Each section will be discussed independently below.

The archaeobacteria, are divided into two kingdoms, the Crenarchaeota and the Euryarchaeota, as depicted in Figure 3. Sections I through V contain the archaeobacteria, with the Euryarchaeota in section II through V. Eubacteria are contained in sections VI to section XIV.

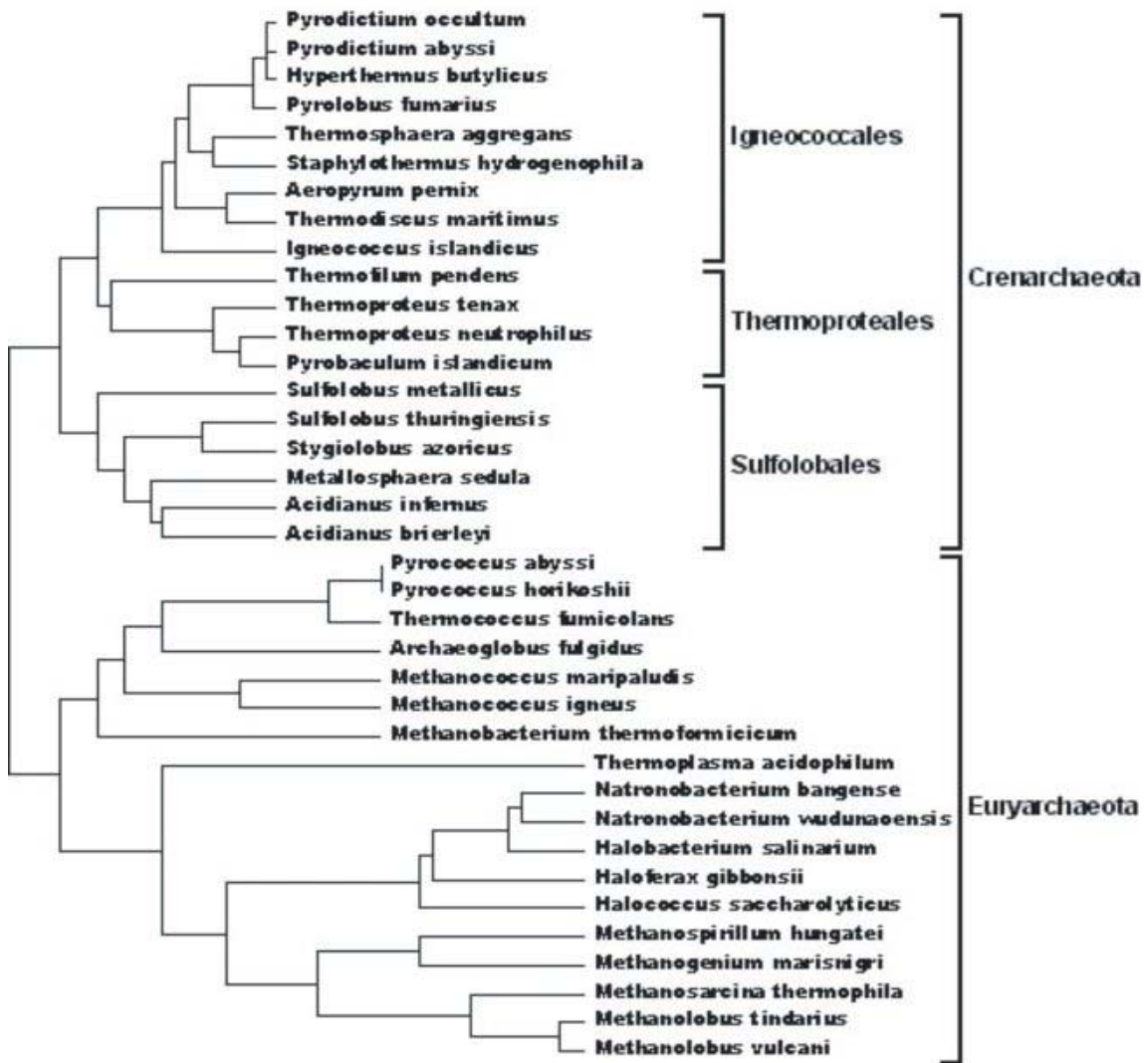


Figure 3. Phylogeny of the Archae based on 16SrRNA.

## 2.1. Thermoprotei, Sulfolobi and Barophiles

Section I contains the Crenarchaeota. Most Crenarchaeota are extremely thermophilic strict anaerobes. Many are acidophilic and sulfur dependant, and may be found in sulfur rich hot springs and areas surrounding submarine volcanic vents. They are divided into three orders, the Thermoproteales, the Sulfolobales and the Igneococcales ('Pyrodictiales'). The Thermoproteales consist of two families, the Thermoproteaceae and the Thermofilaceae, genera of which inhabit neutral to slightly acidic hot springs. *Thermoproteus* is the best-studied genus of the Thermoproteaceae, and is a long thin rod (0.5  $\mu\text{m}$  in diameter by up to 80  $\mu\text{m}$  long), which may be branched. The cell wall of this acidophilic (pH range between 2.5 and 6.5), thermophilic (temperature range between 70 and 97  $^{\circ}\text{C}$ ) archae is glycoprotein.

*Thermoproteus* can grow chemolithotrophically using  $\text{H}_2$  and  $\text{S}^0$ , with  $\text{CO}$  or  $\text{CO}_2$  as the sole carbon source, or organotrophically, oxidizing glucose, amino acids, alcohols and

organic acids with sulfur as the electron acceptor. *Thermofilum* are more slender (0.17 to 0.35  $\mu\text{m}$  wide) and longer (up to 100  $\mu\text{m}$  long), and are extremely oxygen sensitive. *Sulfolobus* is a representative of the Sulfolobales, and this thermoacidophile has temperature optima between 70 and 80  $^{\circ}\text{C}$  and pH optima between 2 and 3. Cells are spherical, but form distinct lobes. Cell walls contain lipoprotein and carbohydrate, and oxygen is the normal electron acceptor.  $\text{CO}_2$  is fixed and serves as the sole carbon source.

Lithotrophic growth relies on elemental sulfur or  $\text{H}_2\text{S}$ , which is oxidized to sulfuric acid. *Acidianus* is a facultative coccoid genus of the Sulfolobales which uses elemental sulfur both aerobically and anaerobically, either oxidizing it to sulfuric acid, or using the sulfur as an electron acceptor and producing  $\text{H}_2\text{S}$ . *Pyrodictium*, *Pyrobaculum* and *Pyrolobus* are members of the Ignococcales with temperature optima at or above 100  $^{\circ}\text{C}$ . *Pyrodictium* are irregularly disc-shaped cells which grow in a mycelium-like cell mass attached to sulfur crystals.

Growth is chemolithotrophically on  $\text{H}_2$  with sulfur as the electron acceptor, or chemo-organotrophically, with complex organic requirements. *Pyrolobus* is found in hydrothermal vent chimneys where it presumably plays a significant ecological role as a major autotroph, being an obligate chemolithotroph. This genus is of interest because it contains the organism with the highest known temperature maximum for growth (*P. fumarii* – 113 $^{\circ}\text{C}$ ). Cold-dwelling Crenarchaeotes have been identified in significant numbers in marine environments.

## 2.2. The Methanogens

Section II contains the relatively phylogenetically, structurally and morphologically diverse group, known as the methanogens. These Euryarchaeota are strict anaerobes that generate energy by the conversion of  $\text{CO}_2$ ,  $\text{H}_2$ , methanol, acetate, formate and other compounds into methane, or methane and  $\text{CO}_2$  (see *Prokaryote Physiology in Anaerobic and Aerobic Atmospheres*). Although few acetotrophic methanogens have been identified, about two thirds of the methane generated in methanogenic environments originates from acetate, suggesting a significant ecological role for this small group. Methanogenesis is exergonic and ATP is synthesized via normal chemiosmotic mechanisms. Methanogens may be found in anaerobic environments rich in organic matter, such as swamps and marshes, or the rumen or intestine of animals.

They are generally mesophilic although temperature and salinity extremophiles have been described. *Methanobacterium* is representative of the order Methanobacteriales. This genus contains species which are typically gram-positive (or gram-variable), non-motile long rods or filaments, with pseudomurein cell walls. *Methanococcus*, of the order Methanococcales are irregular cocci with protein cell walls.

The order Methanomicrobiales contains genera such as *Methanomicrobium* (short, curved, gram-negative rods), *Methanogenium* (irregular gram-negative cocci with protein or glycoprotein cell walls), *Methanospirillum* (spirilla or curved rods with protein cell walls), and *Methanosarcina* (gram-positive to variable cocci with heteropolysaccharide or protein cell walls).

### 2.3. The Halobacteria

The nine genera of extreme halophiles are currently grouped in one family, the Halobacteriaceae. These are non-motile (or motile by lophotrichous flagella) aerobic chemoheterotrophs with complex nutritional requirements and a respiratory metabolism. This group has an absolute requirement for NaCl levels in excess of 1.5 M, and a NaCl concentration growth optimum of 3 to 4 M, due to the relatively high levels of acidic amino acids in the glycoproteins of the cell wall.

In the absence of Na<sup>+</sup>, which shields the carboxyl groups, these repel each other, destabilizing the cell wall. For this reason they are found in specific habitats such as salt pans, but can also be involved in spoilage of salted food products. The bacteria are characteristically pigmented orange or red by carotenoids, primarily C<sub>50</sub> bacterioruberins. Undoubtedly, the best-studied member of this family is *Halobacterium salinarium*, an unusual organism in that it uses rhodopsins.

Bacteriorhodopsin, the component (up to 75%) of purple membranes of the *Halobacterium*, absorbs strongly at about 570 nm, and uses this light energy to generate ATP without chlorophylls, by pumping protons out of the cell. Amino acid uptake has also been shown to be light driven, in that the amino acid-Na<sup>+</sup> symport system depends on the light driven Na<sup>+</sup>/H<sup>+</sup> antiport system. Halorhodopsin is involved in chloride ion transport, and the remaining two rhodopsins are photoreceptors which regulate flagellar movement for optimum photopositioning.

### 2.4. The Thermoplasms

The order Thermoplasmatales currently contains only two genera that are placed in two separate families. Both genera are thermoacidophiles and lack cell walls. The genus *Thermoplasma* is found in iron pyrite rich coal mine refuse dumps where it oxidizes the FeS to sulfuric acid, thereby maintaining suitable growth conditions.

Cell membrane integrity is maintained by diglycerol tetraethers, lipopolysaccharides and glycoproteins. The cell's DNA is stabilized by histone-like proteins. The genus *Picrophilus* has irregular coccoid cells of about 1 to 1.5 μm in diameter, which have an S-layer. These organisms have temperature optima around 60 °C and a pH optimum of about 0.7, with a pH maximum of 3.5 and a pH minimum as close to 0 as possible.

### 2.5. The Thermococci

The order Thermococcales, one of the three in the thermophilic group, contains two genera, *Thermococcus* and *Pyrococcus* in one family. These strict anaerobes are motile by flagella and reduce sulfur to sulfide. The order *Archaeoglobales* has only one family and one genus, *Archaeoglobus*. Members of this genus are gram-negative irregular cocci, with glycoprotein sub-unit cell walls. Sulfate, sulfite and thiosulfate are reduced to sulfide, but not elemental sulfur. These organisms are found in marine hydrothermal vents. The remaining order, Methanopyrales, has a single, extremely thermophilic genus, *Methanopyrus* (*M. kendleri* 84-98-110 °C).

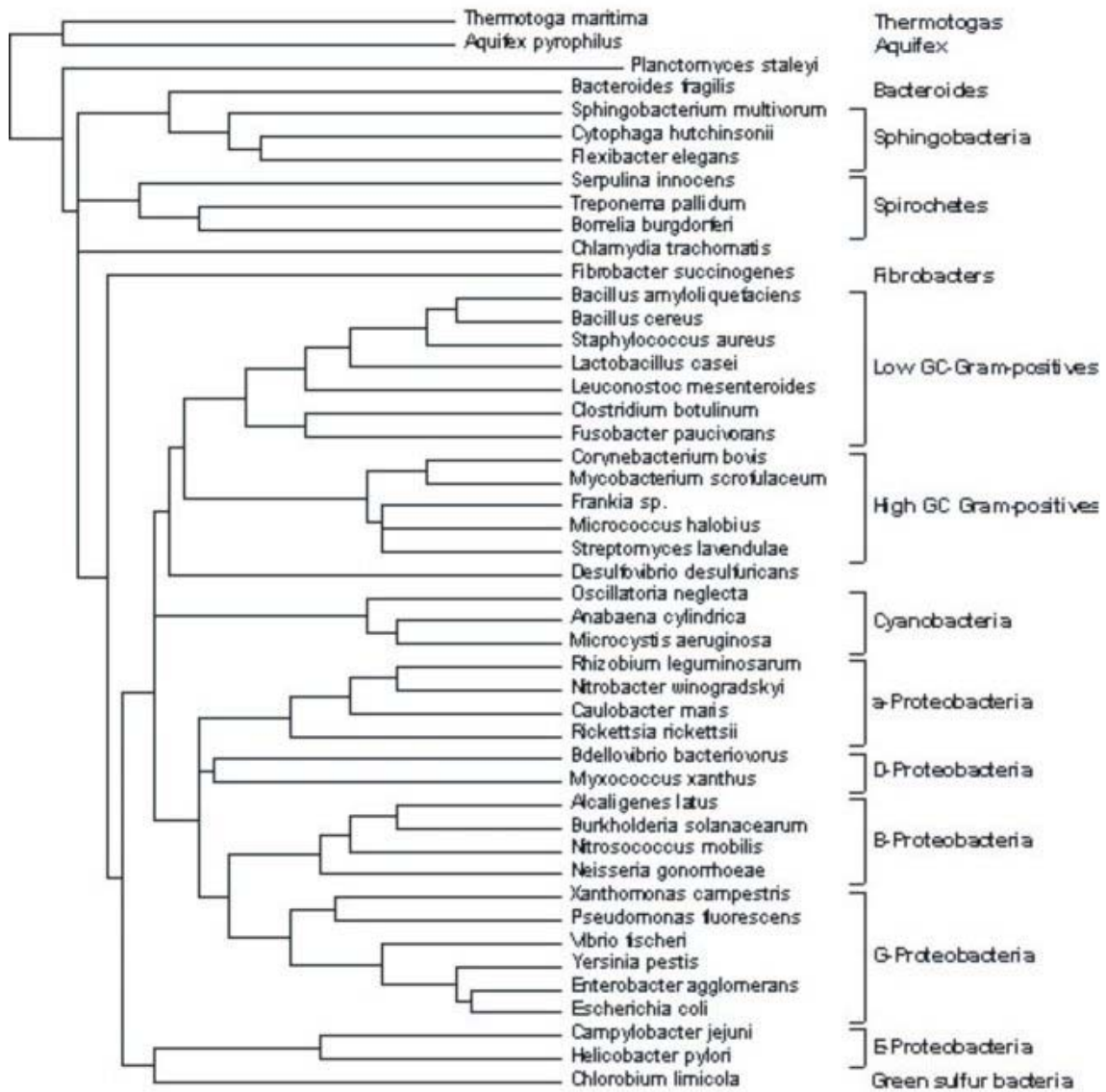


Figure 4. 16S rRNA phylogeny of the Eubacteria.

The remaining sections of Volume One of Bergey's Manual of Systematic Bacteriology cover the phototrophs and deeply branching Eubacteria. Figure 4 shows the relationship of these groups to the remaining Eubacteria.

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