Molecular evolution in bacteria

J.T. Trevors
Laboratory of Microbial Technology, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Received 30 September 1994; accepted 13 February 1995

Key words: bacteria, ecology, evolution, metabolism, microbiology, molecular biology

Abstract

Recent advances in microbiology and molecular biology have a unifying influence on our understanding of genetic diversity/similarity and evolutionary relationships in microorganisms. This article attempts to unify information from diverse areas such as microbiology, molecular biology, microbial physiology, clay crystal genes, metal-microbe-clay interactions and bacterial DNA restriction-modification systems (R-M) as they may apply to molecular evolution of bacteria. The possibility is discussed that the first informational molecules may have been catalytic RNA (micro-assembler) not DNA (now the master copy) and these first micro-assemblers may have been precursors of ribosomes.

The Earth is estimated to be about $4.6 \times 10^9$ years old (Ehrlich 1990). One view is that life began on Earth and an alternative view is that life travelled to Earth as protected spores (Ehrlich 1990). Spores encapsulated in a matrix 0.9 $\mu$m in thickness, with a refractive index of 0.5 would be protected from ultraviolet light and could possibly survive for 4.5 to 45 million years in outer space, thus allowing time to travel to Earth (Weber & Greenburg 1985). The origin of the spores and their entry into outer space could have been due to a collision between a planet on which life existed and a meteorite (Ehrlich 1990). In the remainder of this manuscript, information from several areas of science will be used to unify aspects of evolution with an emphasis on bacteria.

Pyrite formation as an initial energy source for life

Wächtershäuser (1988a) hypothesized pyrite formation from hydrogen sulfide and ferrous ions may have been the first energy source for life. Subsequently, energy flows are biochemical derivatives of this initial process. During early evolution, inorganic compounds such as carbon dioxide, phosphates and ammonia on surfaces of positively charged (anionic) iron pyrite were used as chemical building blocks (Wächtershäuser 1988b). Polymerizations of surface bound molecules are also thermodynamically favourable compared to the same reactions in an organic soup, where water would favour hydrolytic cleavage not polymerization or assembly. Membranes composed of isoprenoid lipids could then encapsulate or enclose autocatalytic 2-dimensional surface metabolists (primitive cells) (Wächtershäuser 1988b). Surfaces of minerals may still be present in the primitive cells until at some time in the future evolution had progressed to a stage where metabolists detached from mineral surfaces and became functional in a primitive cytoplasm. The involvement of a mineral surface as a support, scaffold, or part of a micro-assembler is supported by the clay crystal gene theory of Cairns-Smith (Cairns-Smith 1985) discussed in section 1. It is also possible there was an overlapping period of both chemical and biological evolution occurring at the same time. However, initially chemical evolution would be necessary to provide chemical components required for biological/biochemical/molecular evolution.
Reducing power for metabolism may have originated from the chemical reaction of Fe$^{2+} + 2\text{H}_2\text{S}$ yielding FeS$_2 + 4\text{H}^+ + 2\text{e}$ (Wächtershäuser 1988a). This is possible given that both hydrogen sulfide and Fe(II) would have been abundant on the early Earth and most archaea bacteria require hydrogen sulfide and some enzymes contain iron-sulfur reaction centres (Wächtershäuser 1988a).

In the chemical soup model, the first cells were postulated to be anaerobic heterotrophs (Ehrlich 1990) with evolution to possibly chemosynthetic autotrophs such as methanogens, capable of reducing carbon dioxide to methane and water. Strict methanogen anaerobes exist today under thermophilic conditions similar to that of the Earth’s past. The methanogens belong to the archaea bacteria, a group of bacteria distinct from the true bacteria or eubacteria (Woese 1982). The archaea bacteria, eubacteria and some aspects of eukaryotic cells represent distinct lines of evolution (Woese 1982). In a manuscript by Kandler (1994), it was reported that of the three domains, bacteria are characterized by the presence of a single murein cell-wall polymer. The archaea bacteria do not contain a rigid murein component, but instead a proteinaceous surface layer consisting of subunits in regular patterns (Kandler 1994). This S-layer is mostly composed of glycoprotein.

Since bacterial evolution is fundamentally molecular and biochemical and closely linked to geochemical processes, information on evolution of archaea bacteria which are distinct from other prokaryotes may provide insights into bacterial evolution. According to Woese (1987), the ancestral Archaeabacterium would be a thermophilic anaerobe that could obtain energy from reducing sulfur. Another possibility may be photosynthetic prokaryotes as the initial autotrophs (Ehrlich 1990) such as the purple and green anaerobic, photosynthetic bacteria capable of photosynthesis without evolving oxygen (Ehrlich 1990). Oxygen producing cyanobacteria would then evolve from these non-oxygen producing photosynthetic organisms.

ATP (adenosine triphosphate)

Microorganisms use chemical energy to do work (Peusner 1974). ATP plays a central role in energy storage and utilization as it can be hydrolysed to yield ADP (adenosine diphosphate) with a free-energy change of 7000 cal/mole at 25°C and pH 7 (Peusner 1974). Hydrolysis of ATP proceeds with a decrease in free energy sufficient to drive other reactions and couple to other reactions by transferring the phosphate group (Peusner 1974). However, phosphate molecules of many compounds can not enter or leave cells as they can not pass freely through the cell membrane.

Adenine may have been a common component in the chemical construction kit that preceded molecular biological evolution. For example, adenine is a component of DNA, RNA, ATP, ADP and AMP (adenosine monophosphate). Adenine is also a component of the key biochemicals, NAD (nicotinamide adenine dinucleotide) and FAD (flavin adenine dinucleotide). Ribose (and the closely related compound deoxyribose in DNA) are also components of RNA, and ATP, ADP and AMP. Phosphate is a component of ATP, DNA and RNA. Possibly, evolution of nucleic acids, ATP and NAD, FAD shared some linkages in the evolutionary past. These examples of common biochemical components are used to provide some insight into common components of present day biochemicals.

First organisms, bacteria, water, clays, metals and gene transfer

The investigation of evolution can be divided into geophysical, chemical and biological or molecular biological evolution (Dyson 1985) with the level of organization proceeding from atom to molecule to polymer to cell (Calvin 1969). The biological role of hereditary material is a template for self-replication and the biochemicals for cellular growth and genetic exchange or transfer (Glass 1982). During bacterial evolution, the capability to direct replication to establish a process for transmission of genetic information was necessary. The objective of this article is not to review literature on nucleic acids per se (Adams et al. 1986; Watson & Crick 1953) and evolution (Fox & Dose 1977; Seleander et al. 1991), but to add to and unify information on molecular evolution in bacteria by using information from soil science, microbial ecology, physiology/biochemistry, genetics and molecular biology. The reader is also referred to a recent excellent manuscript by Koch (1994) which deals with development and diversification of the last universal ancestor. Koch (1994) presents information on major categories of early evolutionary development and the monophyletic epoch, defined as the interval between generation of the first living cell and generation of initial stable diversity. This period would be the interval when major biological processes developed (Koch...