

The Microbial World:

FOUNDATION OF THE BIOSPHERE

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a report from
The American Academy of Microbiology
Available on-line at <http://www.asmtusa.org/acasrc/aca1.html>

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Introduction¹

Although most microorganisms are too small to be seen, their importance cannot be ignored. Microorganisms are the foundation of the biosphere—both from an evolutionary and an ecological perspective. Microorganisms were the first organisms on Earth; they have lived on this planet for a period of at least 3.7 billion years of the 4.6 billion-year existence of the Earth. Microorganisms were living inhabitants for more than 3.0 billion years before the appearance of plants and animals. Not only did plants and animals evolve rather recently in Earth's history, but they evolved from microbial ancestors. A recent report of evidence for microbial life on Mars also is consistent with the concept that microorganisms preceded plants and animals on Earth.

The Earth's biosphere is largely shaped by geochemical activities of microorganisms that have provided conditions both for the evolution of plants and animals and for the continuation of all life on Earth. Many microorganisms carry out unique geochemical processes critical to the operation of the biosphere. Therefore, it is not surprising that the diversity of microorganisms—from genetic, metabolic, and physiological aspects—is far greater than that found in plants and animals.

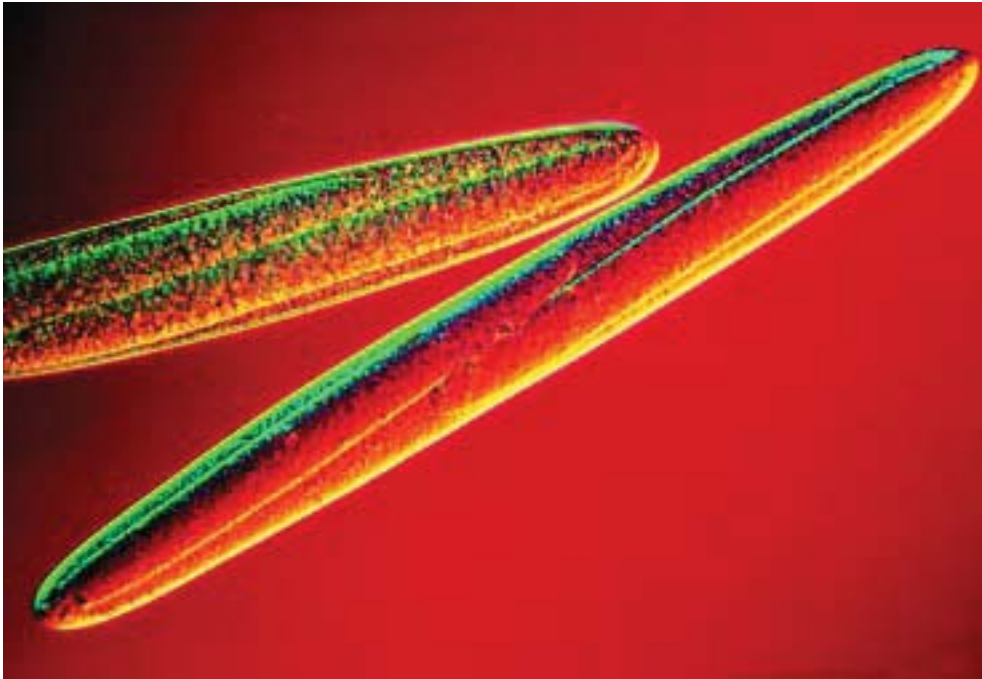
In contrast to plants and animals, the diversity of the microbial world is largely unknown (see Table 1), and, of that which is known, the diversity is spectacular. Some microorganisms live at boiling temperatures, or higher, in hot springs and deep sea thermal vents; others live at temperatures below

freezing in sea ice. Some produce sulfuric and nitric acids. Many grow without oxygen; the anaerobic activities of these microorganisms are necessary for carrying out the many essential processes in the environment that cannot be accomplished by plants and animals, including methane production and nitrogen fixation. Such familiar activities as leavening bread and production of yogurt, pickles, wine, beer, and cheeses rely on microorganisms carrying out the key processes.

Microorganisms also play other essential and beneficial functions for society. For example, we rely on them for production of antibiotics, antitumor agents, and a variety of biotechnology products (see Table 2). We use microorganisms to produce human insulin via genetic engineering and to provide enzymes for manufacturing. They are important in agriculture; their metabolic activities enhance soil fertility, especially in their often unique roles in the nitrogen, phosphorus, sulfur, and carbon cycles.

A new awareness of microbial diversity has developed in recent years. Advances in molecular biology have allowed biologists to compare all living organisms to one another on the basis of highly conserved genes. Initial studies focused on those genes that code for ribonucleic acid (RNA) of the ribosome, the cellular structure responsible for protein synthesis in all organisms. In particular, the sequence of the bases of the small subunit (16S or 18S) of ribosomal RNA (rRNA) has been used to map the relationship of all living organisms (see Figure 1). The phylogenetic tree shows the extraordinary diversity of microorganisms. Figure 1 also

¹ The colloquium held to develop this report was dedicated to Carl Woese for the role he has played in developing our understanding of the evolutionary tree of living organisms.



Two *Epulopiscium* cells. The cell in the center of the frame is about 600 microns in length.
(Courtesy of Esther Angert and Norman R. Pace, University of California, Berkeley)

illustrates that, like the plant and animal kingdoms, microbial groups also show equally deep branching, that is, an ancient evolutionary separation. Thus, there are approximately 12 phyla of Eubacteria (or true bacteria), three phyla of Archaea (previously called archaeobacteria), and several phyla of other microorganisms (fungi and protists).

It is now also known that many more forms of microbial life exist on Earth than previously expected. Indeed, most of the organisms from natural soil and aquatic communities have not yet been grown in culture and characterized. Thus, in contrast to plants and vertebrate animals in which 85 to 90% have been described, it is conservatively estimated that less than 1% of the bacterial species

and less than 5% of fungal species are currently known (see Table 1). The universal tree of life does not as yet include the latter. However, newly developed molecular techniques can be used to identify those microorganisms from the environment that cannot be cultivated. Furthermore, recent advances in the cultivation of microorganisms indicate that many of these organisms can be grown and compared to known microorganisms. Microbiologists can now use these new tools and procedures to explore and quantify the extent and variety of previously unrecognized life forms that exist on the planet, the last great frontier for biology on Earth.

Importance of Microorganisms to the Biosphere

Microorganisms are the foundation of the biosphere. Without them, other life forms would not have evolved and could not exist. Microorganisms established the geochemical conditions on Earth that enabled evolution of plants and animals. Plants and animals are descended from microorganisms, and their cells are now known to be composites of microorganisms. For example, the mitochondria of all plants and animals are derived from bacteria. Similarly, the photosynthetic organelle, the chloroplast, found in all plants and algae is descended from a group of photosynthetic bacteria, the cyanobacteria. Cyanobacteria are believed to be the first organisms on Earth to produce free oxygen gas and, concomitantly, the protective ozone layer around Earth, thereby providing conditions for evolution of land plants and animals.

Humans and other animals, as well as plants, are completely dependent on microorganisms for life. Like all animals, humans harbor billions of microorganisms in their digestive tracts, microorganisms necessary to digest food and provide nutrients, such as vitamins and amino acids, for growth and a source of energy. Plants also require microorganisms to provide nutrients for growth, an activity that takes place largely in root systems. There the organic materials in soil are broken down by bacteria and fungi to provide inorganic materials, such as nitrogen and phosphorus, the natural fertilizers made available by microorganisms and required by plants for growth and development.

Microorganisms exist everywhere physical conditions permit. Although lake water may appear transparent to the eye, a liter of the water can harbor a billion bacteria. A gram of soil can also contain over a billion bacteria. Many microorganisms have special dispersal cells that can be carried by winds across and between continents. In addition, birds and insects transport microorganisms as they fly. Thus, we live in a world teeming with

microbial life that carries out a myriad of activities essential for sustaining the biosphere of Earth.

Microorganisms are highly diverse genetically and metabolically, far more so than plants and animals. This should not seem surprising because microorganisms have existed on Earth for over 3.5 billion years, whereas multicellular plants and animals have existed only 600 million years. From analyses of molecular sequences of genes, such as 16S and 18S ribosomal RNA, approximately 20 separate, main phylogenetic groups of microbial life have been identified, comparable in depth and breadth to the animal and plant kingdoms (Figure 1; Woese 1994; Sogin 1994; Sogin et al. 1996a, 1996b; see also Table 5). Furthermore, microbiologists have discovered groups that represent new phyla, such as the Korarchaeota, not yet studied in pure culture (Barnes et al. 1996).

One of the most surprising characteristics of microorganisms is the range of physiological conditions under which they flourish. They grow across broad ranges of temperature, pH, salt concentration, and oxygen concentration (see Table 3). Some thrive at boiling temperatures in hot springs and at temperatures higher than 100°C in submarine vents. Others are found in sea ice off Antarctica and at the North Pole. Some produce sulfuric and nitric acids, and many microbial species live without oxygen. Others live in saturated salt brines, and some are resistant to high levels of radioactivity.

The variety of metabolic types of microorganisms is enormous. Some are photosynthetic and, like plants, produce oxygen in this process. In fact, this “biotechnology” first occurred in the cyanobacteria, which subsequently evolved endosymbiotically to form chloroplasts that enable algae and plants to conduct photosynthesis. Other bacterial groups carry out photosynthesis by different pathways and produce products such as sulfur. Microorganisms are the primary, if not sole, agents responsible for degradation of a great variety of organic compounds, including cellulose, hemi-

cellulose, lignin, and chitin (the most abundant organic matter on Earth). If it were not for microbial activities involved in natural decay, excessive amounts of organic matter would accumulate in forests and aquatic sediments. In addition, microorganisms are responsible for degradation of toxic chemicals derived from anthropogenic sources, such as PCBs (polychlorinated biphenyls), dioxins and other pesticides. Because microorganisms are so versatile, they are relied upon to digest wastes in sewage treatment plants, landfills, and toxic waste sites. It is in this regard that the field of bioremediation, encompassing all of these processes, is still in its infancy. Much needs to be learned before microbial breakdown processes can be controlled and enhanced *in situ*.

Microorganisms play important roles in geochemical processes. For example, the global nitrogen cycle in nature is dependent on microorganisms. Unique processes carried out by microorganisms include nitrogen fixation (the natural conversion of atmospheric dinitrogen gas to utilizable organic cell nitrogen), oxidation of ammonia and nitrite to nitrate, and nitrate reduction with formation of dinitrogen and nitrous oxide gases. Similar important and unique roles are played in other cycles, such as the sulfur and carbon cycles, as well as in the oxidation and reduction of metals. If it were not for microorganisms, substances such as cellulose and lignin would not be recycled; they would accumulate in the environment. Indeed, almost all organic substances are recycled via activities of bacteria, fungi, and protozoa.

The importance of microorganisms in agriculture is enormous and extends beyond geochemical cycles. Indeed, most of the fertility of soil is derived from microbial mineralization and in production of nitrogen for plant growth. These processes extend to lichen- and cyanobacterial-dominated soils which occupy a larger surface area on Earth than in tropical rain forests. Mycorrhizal fungi form important rhizosphere associations with almost all plants. Such associations are essential for optimum growth and, in fact, permit some plants to grow in areas they could not otherwise colonize. Recent

advances in agriculture stem from breakthroughs in the genetic engineering of plants; one of the most dramatic examples is that of the bacterium *Agrobacterium tumefaciens*. Normally the causative of crown gall disease in plants, this bacterium has been used to transfer favorable properties into an agriculturally important plant species, thereby providing a mechanism for introducing genes that provide resistance to plant diseases, insects or pesticides into plants. Microorganisms are important in recycling waste materials. Sewage (wastewater) treatment and the breakdown of garbage in landfills occur because of microorganisms. These microorganisms do this “for free” because, in most cases, they derive energy from the process.

A recent discovery indicates that microorganisms may influence weather. Some marine algae produce dimethyl sulfide (DMS). This compound is volatile and escapes into the atmosphere where it is photo-oxidized to form sulfate. The sulfate acts as a water nucleating agent and when enough sulfate is formed, clouds are produced; these clouds have three major impacts. First, they shade the ocean and, thereby, slow further algal growth and DMS production, eventually decreasing cloud formation. Second, the clouds lead to increased rainfall. And third, because clouds are reflective of incoming sunlight, the clouds reduce the amount of heat that reaches Earth, moderating global warming.

Microorganisms are at the core of biotechnology. Many antibiotics and anti-tumor agents are derived from microorganisms, including penicillin, streptomycin, and chloramphenicol. The emergence of multiple antibiotic-resistant pathogenic bacteria has necessitated the search for new antibiotics. Because there are so many types of microorganisms, they produce many unique products currently useful in biotechnology and offer great promise for exploitation in the future.

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