karyotic diversity in a 100-cm^3 soil sample can be compared to the regional diversity of macroorganisms (γ diversity) (*20*).

Despite a growing knowledge of the magnitude of prokaryote diversity, most of the prokaryotes seen in natural environments are uncultivated, and their functional roles and diversity are unknown. The realization that genes for harvesting of light energy occur widely in marine prokaryotic genomes (*21*) is a striking demonstration of the need to know more about prokaryotic diversity in order to understand how they contribute to the ecological and biogeochemical functioning of our ecosystems.

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VIEWPOINT

Life and the Evolution of Earth's Atmosphere

James F. Kasting[1*] and Janet L. Siefert[2]

Harvesting light to produce energy and oxygen (photosynthesis) is the signature of all land plants. This ability was co-opted from a precocious and ancient form of life known as cyanobacteria. Today these bacteria, as well as microscopic algae, supply oxygen to the atmosphere and churn out fixed nitrogen in Earth's vast oceans. Microorganisms may also have played a major role in atmosphere evolution before the rise of oxygen. Under the more dim light of a young sun cooler than today's, certain groups of anaerobic bacteria may have been pumping out large amounts of methane, thereby keeping the early climate warm and inviting. The evolution of Earth's atmosphere is linked tightly to the evolution of its biota.

Microorganisms are important for many reasons, not the least of which is their responsibility, direct or indirect, for the production of nearly all of the oxygen we breathe. Oxygen is produced during photosynthesis by a reaction that can be written as $CO_2 + H_2O \rightarrow CH_2O + O_2$. Here, "$CH_2O$" is a geochemist's shorthand for more complex forms of organic matter. Most photosynthesis on land is carried out by higher plants, not microorganisms; but terrestrial photosynthesis has little effect on atmospheric O_2 because it is nearly balanced by the reverse processes of respiration and decay. By contrast, marine photosynthesis is a net source of O_2 because a small fraction (~0.1%) of the organic matter synthesized in the oceans is buried in sediments. This small leak in the marine organic carbon cycle is responsible for most of our atmospheric O_2.

Although higher plants (e.g., kelp) are found in the oceans, most marine photosynthesis is performed by single-celled organisms. The most abundant of these are eukaryotic algae, such as diatoms and coccolithophorids (Fig. 1). Roughly 99% of primary production can be attributed to such organisms (*1*). Prokaryotic bacteria are also important for another reason. Though they make up only ~1% of marine biomass, cyanobacteria (or blue-green algae) are the main organisms responsible for fixing nitrogen (*1*). This capability is quite remarkable because the enzyme responsible for reducing N_2, nitrogenase, is poisoned by O_2. Thus, cyanobacteria have had to evolve complex mechanisms for protecting their nitrogenase. Some, such as the filamentous *Anabaena* spp., do so by fixing nitrogen only in specialized cells called heterocysts. Other cyanobacteria fix nitrogen at night and photosynthesize by day. Still others, such as *Trichodesmium* spp. (very abundant in tropical waters), fix nitrogen in the morning and photosynthesize in the afternoon (*2*). Such specificity shows that these are highly evolved pieces of biological machinery.

In some sense, when it comes to producing oxygen, cyanobacteria are the entire story. Because cyanobacteria can live anaerobically and aerobically, they are universally believed to have been responsible for the initial rise of atmospheric O_2 around 2.3 billion years ago (Ga) (*3*, *4*). Comparison of ribosomal RNA from cyanobacteria with portions of the DNA inside chloroplasts implies that all eukaryotes, including algae and higher plants, derived their photosynthetic capabilities from cyanobacteria by way of endosymbiosis (*5*). The *Prochlorococcus* spp., an important component of today's marine ecosystem, may be the living ancestor of the cyanobacterium involved in this event (*6*). It appears that oxygenic photosynthesis—an extremely complex biochemical process—was "invented" only once, and a primitive cyanobacterium was the organism responsible.

Though the production of O_2 is the most notable effect of organisms on the atmosphere, it is by no means their only one. Our modern atmosphere contains numerous trace gases (e.g., CH_4, N_2O, CH_3Cl, COS, dimethyl sulfide) whose sources are almost entirely biological. Some of these gases influence climate today by contributing to the atmospheric greenhouse effect. Concentrations of CH_4 (methane) and N_2O (nitrous oxide) have been increasing in recent

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years as a consequence of agricultural activities, and this is of some concern with respect to the problem of human-induced global warming.

More interesting from a long-term perspective, however, is the effect that such reduced biogenic gases might have had before the rise of O_2. Some of them, like N_2O, should have been rapidly photolyzed in the absence of an ozone shield (*7*), but others—CH_4 in particular—could have been quite abundant in an anoxic atmosphere. CH_4 has only a 10-year residence time today because it reacts with the hydroxyl radical, OH. In an anoxic atmosphere, OH would have been much less abundant and CH_4 would have been destroyed mainly by photolysis at Ly α wavelengths (121.6 nm). Under such conditions, its residence time should have been more like 10,000 years (*8*). A biogenic CH_4 source comparable to the modern flux of 535 Tg CH_4/year (*9*), which produces an atmospheric CH_4 concentration of 1.6 ppm (parts per million) today, could have generated over 1000 ppm of CH_4 in the distant past. This is enough to have had a major warming effect on climate (*10*). The Sun was considerably dimmer at that time, so the added greenhouse effect of CH_4 was precisely what was needed to keep the Archean Earth from freezing. The rise in atmospheric O_2 corresponds precisely with Earth's first well-documented glaciation (*11*), suggesting that the glaciation was triggered by the accompanying decrease in atmospheric CH_4.

Methane is of such potential importance on the primitive Earth that we should say more about the organisms that produce it. The methanogenic bacteria, or methanogens, are members of the Euryarchaeota branch of the Archaea, one of the three major kingdoms of life identified by sequencing ribosomal RNA. They have several characteristics, including a strictly anaerobic lifestyle and a tendency toward thermophily, that suggest they are evolutionarily ancient (*12*, *13*). Today, methanogens are confined to restricted, oxygen-free environments such as the intestines of cows and the soils beneath flooded rice paddies. They make their metabolic living by converting the by-products of fermentation (e.g., formate, acetate, lactate) into methane. The overall reaction (fermentation plus methanogenesis) can be written as: $2CH_2O \rightarrow CO_2 + CH_4$. This process would have assumed greater importance on the early Earth (*14*) because low concentrations of dissolved O_2 and sulfate (*15*) would have meant less recycling of organic matter by aerobic respiration or biological sulfate reduction.

On the anoxic primitive Earth, methanogens may also have been primary producers of organic matter. All methanogens can use hydrogen as a substrate, described by the reaction $CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$. Predicted H_2 concentrations in an anoxic early atmosphere are of the order of 1000 ppm (*16*), which is well above the threshold for methanogenesis, even at today's relatively low CO_2 level (*17*). H_2 concentrations would have dropped once methanogens proliferated (*18*, *19*); however, other gases, such as CO (carbon monoxide), could have served as biological substrates as well. CO hydrolyzes to $HCOO^-$ (formate ion), which in turn converts to hydrogen via the reaction $HCOO^- + H_2O \rightarrow HCO_3^- + H_2$. This latter reaction is catalyzed by enzymes released by methanogens (*20*).

All of this suggests that, before the rise of O_2, CH_4 could have been produced at rates that exceeded today's rate by factors of 10 to 100. But this leads to a conundrum: the modern solar Ly α flux is only $\sim 5 \times 10^{11}$ photons cm^{-2} s^{-1}, which corresponds to a methane destruction rate of 2140 Tg CH_4/year, or about fourfold the modern methane flux. Even if the solar EUV (extreme ultraviolet) flux was several times higher back then (*21*), it appears that CH_4 should have accumulated to very high concentrations in the atmosphere. The factor that limited the CH_4 abundance was likely the production of organic haze, which is predicted to form when the atmospheric CH_4/CO_2 ratio exceeds unity (*8*). This haze would have created an "anti–greenhouse effect," which would have lowered surface temperatures and made life less comfortable for the predominately thermophilic methanogens (*22*).

Thus, microorganisms have probably determined the basic composition of Earth's atmosphere since the origin of life. During the first half of Earth's history, this may have resulted in a planet that looked much like Saturn's moon Titan (Fig. 2).[2] During the latter half of Earth's history, microorganisms created the breathable, O_2-rich air and clear blue skies that we enjoy today. Atmospheric evolution on an inhabited planet is determined largely by its microbial populations.

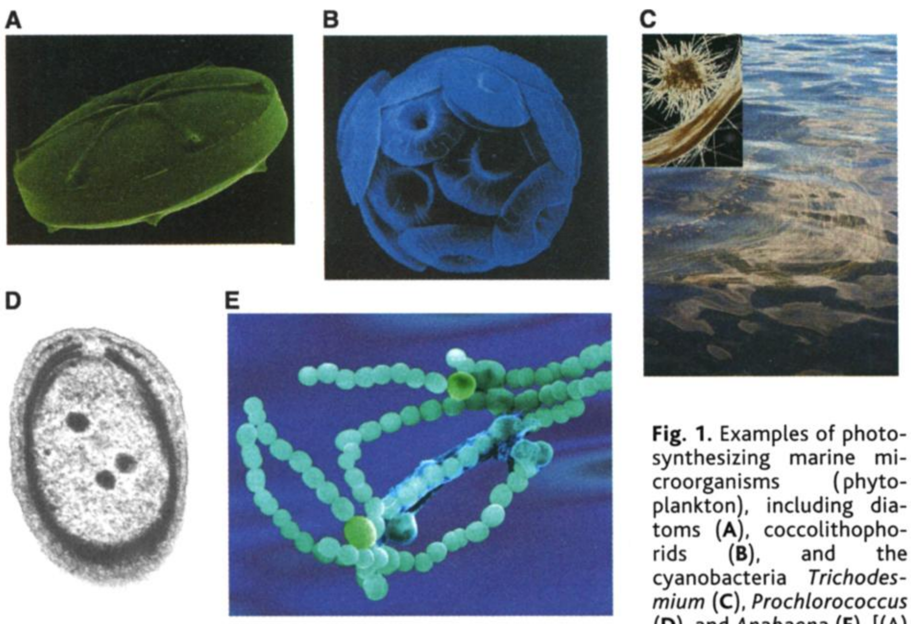

Fig. 1. Examples of photosynthesizing marine microorganisms (phytoplankton), including diatoms (**A**), coccolithophorids (**B**), and the cyanobacteria *Trichodesmium* (**C**), *Prochlorococcus* (**D**), and *Anabaena* (**E**). [(A) and (B) from (*23*), (C) from (*2*), (D) courtesy of S. Chisholm and C. Ting, and (E) copyright Dennis Kunkle Microscopy, Inc.]

Fig. 2. This photograph of Saturn's moon, Titan, shows the orange-tinted haze that is thought to be formed by photolysis and charged-particle bombardment of methane in Titan's upper atmosphere. The Cassini mission, now on its way to Saturn, will test this model by dropping a probe into Titan's atmosphere. [Photo courtesy of NASA: http://photojournal.jpl.nasa.gov/]

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REVIEW

Microbial Behavior in a Heterogeneous World

Tom Fenchel

Most microorganisms are motile during at least part of their life cycle, because they need to find optimal conditions in a patchy world. The sheer volume of microorganisms in the biosphere means that their motile sensory behavior also contributes to the global transformation and cycling of matter. How microorganisms move and how they orient themselves using environmental cues are integral to understanding the complex structure and function of microbial communities, but although motility in response to external stimuli was first described more than 120 years ago, understanding of the cellular and molecular mechanisms involved has only been achieved more recently.

All motile species of microorganism respond to different kinds of chemical stimuli. Many also respond to light intensity and to mechanical stimuli, and a few even orient themselves in magnetic fields or in relation to the force of gravity (*1–5*).

Microorganisms swim using flagella and move on surfaces by gliding or by amoeboid movement. They may respond directly to ambient conditions or, more frequently, to temporal changes in stimulus intensity. Although microorganisms are too small to sense the direction of a chemical gradient directly, they can sense a change in intensity or concentration over time, because they have a short term "memory" with a time constant of 0.5 to 1 s (*6*). Cells respond to temporal changes in stimulus intensity by changing swimming direction or velocity. If, for example, changes in swimming direction are more frequent when an organism moves away from an attractant than when it swims toward it, the result is a biased random walk leading the organism toward the source of the attractant (*6*). Larger eukaryotic microorganisms can use greater precision in swimming to approach the source of a chemical attractant more directly, but essentially their orientation is also based on temporal gradient sensing (*7*). The small size and low swimming velocities of microorganisms mean that they live at low Reynolds numbers; that is, under conditions in which viscous forces dominate and molecular diffusion of solutes is often more important than advective transport (*8*).

The adaptive significance of particular types of sensory motile behaviors appears obvious in many cases. Nevertheless, the role of such behavior in natural habitats is only now being elucidated in detail, with the recognition that microbial communities are spatially and temporally complex. Moreover, in natural habitats, different physiological types of microorganisms closely interact, hence the insights derived from the behavior of pure cultures are often of limited relevance. Microorganisms respond to microscopic spatial and temporal heterogeneity, while simultaneously creating spatial heterogeneity resulting from the output of their own metabolic activities.

Recent progress in describing natural microbial communities stems from methodological developments, including the use of microsensors that can map chemical heterogeneity at a fine spatial scale, improvements in microscopy, in situ fluorescent treatment that labels particular microbial species or discloses their physiological state, and theoretical modeling. Together, these efforts have revealed microbial communities that may be as complex and intriguing as coral reefs and rainforests.

Chemotaxis in the Turbulent Water Column

Suspended motile organotrophic bacteria respond rapidly to point sources of dissolved low-molecular-weight organic matter (Fig. 1). These point sources may arise when protozoan or algal cells lyse as a result of viral attack or predation. Concentration gradients of dissolved organic molecules form around the lysed cell, and bacteria located in the surrounding few microliters accumulate within minutes. Because the dissolved substances eventually disappear by diffusion or are consumed by the bacteria, such patches of organic matter are short-lived (5 to 10 min), and eventually the bacteria redistribute. Such events can be modeled theoretically, using known values for diffusion coefficients and parameters for bacterial motile behavior.

Intuitively, it seems that concentration gradients could not develop in an oceanic water column that is exposed to turbulent mixing; however, the effect of turbulence vanishes at the small spatial scales at which these gradients develop. Thus, below the Kolmogorov minimum length scale, turbulence is replaced by linear shear caused by viscous forces. Depending on the rate of wind-driven energy dissipation, the range of the Kolmogorov minimum scale is between 0.6 and 3.5 cm, corresponding to rough and calm seas, respectively, and the shear strength ranges from 0.5 to 0.005 s^{-1} (*9*). In steady continuous shear, an initially spherical solute distribution (such as that arising from a point source) will be drawn into ellipsoid or disc-shaped distributions. The distortion caused

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