The Emergence of Life on Earth

BY MITCHELL SCHULTE

AMONG THE MOST enduring and perplexing questions pondered by humankind are why, how, and when life began on Earth, and whether life exists elsewhere in the solar system or the universe. Attempts to answer these questions have fallen under the purview of a number of areas of inquiry, including philosophy, religion, and, more recently, dedicated scientific inquiry. Scientific study of life's beginnings necessarily draws from a wide variety of disciplines. Because of the complexity of the problem, geologists, chemists, biologists, and physicists, as well as engineers and mathematicians, have all been involved in origin-of-life research.

Geologic evidence indicative of biological processes dates back to around 3.8–3.5 billion years ago. Features that resemble modern microorganisms are present as microfossils in 3.5-billion-year-old rocks in Australia and are thought by some to show that life was well developed by that time. Carbon found in metamorphosed rocks from Akilia Island, Greenland, is isotopically light, thought by many to demonstrate that organisms were fractionating carbon isotopes 3.8 billion years ago. Much of the fossil and chemical evidence once thought with certainty to be products of biological activity has been questioned recently, however, and a definitive time frame for life's beginnings remains controversial (Chyba and Hand, 2005). Regardless of exactly when life first appeared, Earth was very different at the time than it is at present. The early Earth was a violent place, with remnants of the solar system's formation colliding with its surface frequently until around 3.8 billion years ago. Many of the collisions would have been of sufficient force to heat the oceans to temperatures above 100°C, and even to vaporize them on occasion[1]. In fact, the oceans are thought to have maintained temperatures as high as 70–100°C for much of Earth's early history (Robert and Chaussidon, 2006), due in part to the atmospheric composition. The atmosphere contained no oxygen (oxygenic photosynthesis had yet to develop), and could have contained up to 10–100 bars of carbon dioxide, which would have warmed Earth's surface and caused the oceans to be acidic (Nisbet and Sleep, 2001; Russell et al., 2005). Earth's interior was hotter than at present due to friction from collisions, higher radioactive decay, and remnant frictional heat from its formation. Because of the high heat flow, volcanic and hydrothermal activity on the early Earth would have been greater than at present. It was under these geological conditions that life made its debut.

[1] The collision of the earth with a particularly large body, roughly the size of Mars, ~ 4.4 billion years ago resulted in melting of the earth and the formation of the moon.

LIFE IN EXTREME ENVIRONMENTS

The discovery in 1977 of hydrothermal systems at a seafloor spreading center near the Galápagos Islands provided new direction and revolutionized "origin-of-life" studies (Corliss et al., 1979). The abundance and diversity of animals and microorganisms found in the dark depths of the seafloor near the hydrothermal vents, far removed from the direct influence of the sun's energy (although the animals at hydrothermal vents do require oxygen, originally produced through photosynthesis and extracted from seawater), naturally attracted a great number of researchers to study the nature of the life in such a seemingly inhospitable environment. While the animals include unique but somewhat familiar forms, the microorganisms inhabiting seafloor hydrothermal systems are unusual and demonstrate a remarkable ability not only to tolerate such challenging environments, but to thrive in, and in fact require, these conditions. These organisms, dubbed "extremophiles" for their ability to tolerate extremes in environmental conditions, exhibit a vast diversity of metabolisms and inhabit niches that were once considered unsuitable for life. Our current understanding of extreme habitats extends to conditions of extreme pH (< 2 and > 10), pressure (from surviving the vacuum of space to the deepest submarine trenches), metal content, salinity, alkalinity, radiation, and low water activity. Nonetheless, organisms living at high temperatures, like those found at deep-sea hydrothermal black smoker chimneys (see article by Fisher et al., this issue), are some of the most extraordinary examples. The current record holder for high-temperature life is a microorganism known as Strain 121 (tentatively named *Geogemma barossii*) for its ability to grow at a temperature of 121°C[2] (Kashefi and Lovley, 2001; Lovley et al., 2004). Strain 121 was isolated from a hydrothermal vent chimney recovered from the Endeavour Segment of the Juan de Fuca mid-ocean ridge, ~ 2200 m below sea level off the Pacific northwest coast of North America. Ongoing research in extreme environments continues to broaden our view of habitability on the early Earth and throughout the solar system.

What can these modern organisms tell us about how life began, and the nature of early life on Earth? According to comparisons of sequences of the 16S rRNA gene (Figure 1), prokaryotic organisms (single-celled Bacteria and Archaea that lack a nuclear membrane) exhibiting the most primitive characteristics are all thermophilic (heat-loving), with optimal growth temperatures above 60°C. This observation suggests that the "last common ancestor" to all life currently on Earth was an organism (or community of organisms) that lived at high temperature. This result, coupled to the fact that volcanic and hydrothermal activity were greater on the early Earth has led to the widely accepted hypothesis that life began under hydrothermal conditions. Other researchers disagree, however, and contend that thermophily may simply represent an adaptation to survive the violent nature of the early Earth (Forterre, 1998; Galtier et al., 1999; Miller, 1998).

Other clues from the convergence of biology and hydrothermal geochemistry support a hydrothermal origin of life. First, there are structural and compositional resemblances between iron-sulfur minerals that form routinely during hydrothermal processes and the iron-sulfur centers of electron transfer proteins that are part of the core metabolism of many organisms (ferrodoxins) (Russell et al., 2005). Second, the abundance of sulfur-bearing minerals in hydrothermal systems could have supported sulfur-based metabolisms that are common energy sources for primitive chemolithotrophic microorganisms (i.e., those that use inorganic chemicals as an energy source). The connection between early life and sulfur chemistry is reinforced by the reliance of biology on a variety of sulfur-bearing organic compounds, including essential enzymes, amino acids, and proteins (Schulte and Rogers, 2004). Finally, hydrothermal systems have very likely operated continuously on Earth since the establishment of its oceans. Their existence beneath the ocean's surface would have provided safe haven for incipient life, protecting it from changing solar, atmospheric, and surface conditions as Earth evolved. Thus, these systems would have been a reliable source of geochemical energy for over four billion years (Shock et al., 1998). In addition, they provide a natural mechanism for concentrating energy and chemicals,

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[2] Strain 121 has been shown to tolerate temperatures as high as 130°C, but is not capable of growth at that temperature.

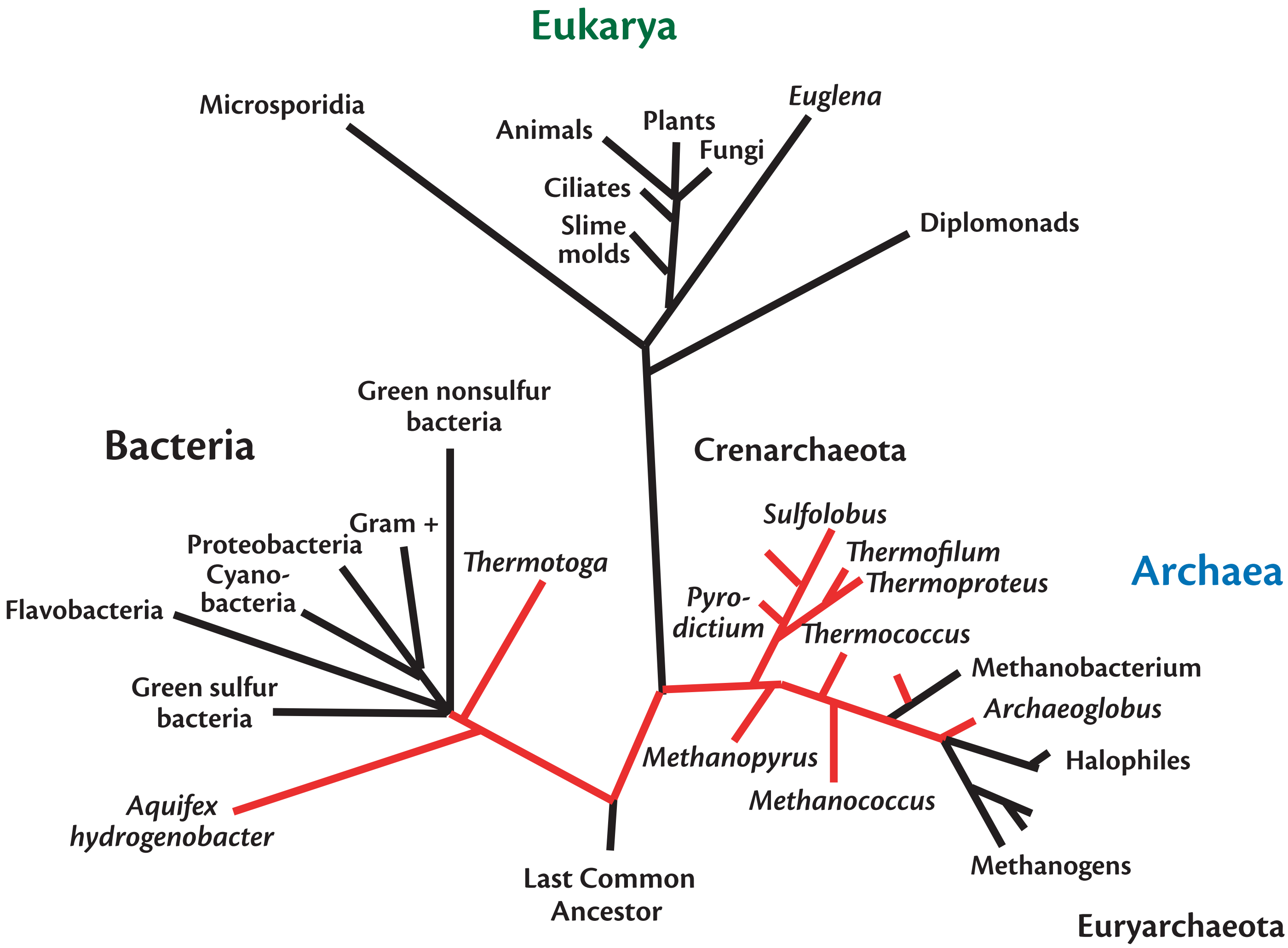

Figure 1. The universal tree of life, showing the three domains, based on comparison of the ribosomal RNA gene. The lengths of individual line segments indicate the evolutionary distance in terms of the number of changes in the genetic sequence from one organism to another. The segments in red indicate thermophilic organisms; note that they cluster near the base of the tree, implying that the last common ancestor of extant life was thermophilic. *After Woese et al. (1990)*

especially trace metals (e.g., molybdenum, zinc, tungsten, cobalt) that are essential for proper enzyme function, including those found in thermophiles.

Whatever the nature of the conditions under which life began, it is clear that it was necessary to have a source of metabolic energy, which requires both electron donors (such as hydrogen and hydrogen sulfide) and electron acceptors (reasonable candidates for the early Earth include carbon dioxide and oxidized forms of iron that may have been generated photochemically). Many of the organisms with "primitive characteristics" are lithotrophs that metabolize the inorganic chemicals found in abundance in volcanic and hydrothermal environments (such as hydrogen and hydrogen sulfide). Most are also autotrophs, meaning that they are able to synthesize their own organic matter starting with carbon dioxide, one of the most abundant volcanic gases, as their source of carbon. Indeed, shortly after the first discovery of deep-sea hydrothermal vent fields, Corliss et al. (1981) and Baross and Hoffman (1985) suggested that the constant supply of energy from geochemical reactions on the early Earth might have provided the perfect circumstances for life to develop.

ABIOTIC SOURCES OF ORGANIC COMPOUNDS

Because life on Earth is primarily carbon-based, identifying sources of prebiotic organic compounds on the early Earth is a key element to understanding the emergence of life. The famous Miller-Urey experiment (Miller, 1953, 1955; Miller and Urey, 1959) demonstrated for the first time that organic molecules essential for life could be generated from strictly abiotic constituents. In their experiments, Miller and Urey started with methane and ammonia gases. Energy in the form of electrical sparks, representing lightning discharges, facilitated chemical reactions to generate a variety of organic compounds, including amino acids, in a tarry matrix. As amino acids are the primary components of proteins, the most versatile and essential biological macromolecules, many scientists thought it would be a simple step to decipher the origin of living systems through polymerization of these smaller molecules. However, despite this early success, the processes through which life developed from simple organic molecules into systems that use encapsulating membranes and pass information to succeeding generations remains to be solved. In addition, the relevance of the starting materials used by Miller and Urey in their experiment has been called into question. At the time, Miller and Urey thought, by extrapolation from the composition of Jupiter's presumably primitive atmosphere, that methane and ammonia represented major constituents of Earth's early atmosphere. While the nature of the early Earth's atmosphere is not certain, geological evidence suggests that it was not strongly reducing (i.e., composed of large concentrations of methane and ammonia), but instead consisted of a mixture of substantial amounts of carbon dioxide and dinitrogen gases. Attempts to repeat the Miller-Urey experiment with these gases have yielded little, if any, "interesting" organic compounds (Chyba and Hand, 2005).

Suggestions for other sources of organic material that may have been available to incipient life include carbonaceous chondrite meteorites and comets. Carbonaceous chondrites contain up to 10 wt.% carbon, primarily in a complex aromatic structure. Up to 600 ppm of carbon are found in the form of soluble organic compounds such as carboxylic acids, ketones, alcohols, and even amino acids (Cronin, 1998). Studies show that these materials frequently survive the journey through Earth's atmosphere and are delivered intact to the surface. Whether they could then be concentrated and react to form more complex molecules remains an open question. However, meteorites and comets would have been a significant source of raw materials, like carbon and nitrogen.

Hydrothermal systems have also been proposed as locations where organic compounds could have been synthesized on the early Earth. Experimental work has demonstrated that organic compounds like amino and carboxylic acids can be formed under hydrothermal conditions. In some of these experiments, reactions on the surfaces of sulfur-bearing minerals involving inorganic forms of sulfur and carbon provide the energy to convert carbon dioxide or carbon monoxide into organic matter (Cody et al., 2000; Heinen and Lauwers, 1996; Hennet et al., 1992; Wächtershäuser, 1988). Some claim that these environments are simply too hot for organic molecules to survive (Miller and Bada, 1988; Miller and Lazcano, 1995; White, 1984). These arguments are countered by theoretical (Shock and Schulte, 1998) and experimental (Seewald, 1994; Seewald et al., 2006) evidence that demonstrates the formation and stability of organic compounds at relatively high temperatures given the right geochemical conditions. Measurements of deep-sea hydrothermal fluids also show that methane and other light hydrocarbons have a probable abiotic origin (Holm and Charlou, 2001). Other abiotically produced organic compounds in these fluids are predicted to occur, but have not been studied to date.

Among the organic compounds predicted to form during fluid mixing of hydrothermal vent fluids and seawater are long-chained carboxylic acids (Shock and Schulte, 1998). Aggregates of these molecules can develop into spherical structures called micelles. Micelles have an outer surface that is composed of the nonpolar, hydrophobic portion of long-chained carboxylic acids, which excludes aqueous fluids and chemicals from the interior. The polar, hydrophilic ends of these molecules point toward the interiors of the micelles, forming a charged surface that can attract ionic species. This structure can maintain a separation of charge and a redox gradient, similar to the way modern organisms' cells operate and could have been the primitive membranes that allowed life to develop.

Alternatively, Michael Russell and his colleagues at the University of Glasgow (Russell et al., 2005) speculate that iron-sulfur minerals that form hollow, spherical structures may have served as templates for the first cells. These structures were shown to develop during experiments in which alkaline hydrothermal fluids are mixed with acidic solutions thought to represent the early oceans. Similar structures are seen in more modern sulfide deposits that form as mounds during hydrothermal generation of ore bodies. Russell et al. (2005) speculate that these hydrothermally produced sulfide mounds formed in abundance on the early Earth due to disequilibrium between the oceans and the hydrothermal fluid. The sulfide minerals served as catalytic surfaces where carbon dioxide would be reduced to organic acids and other organic compounds. In this view, the inorganic protomembranes thus formed were gradually replaced by the organic material being continually generated through hydrothermal circulation.

IS THERE LIFE BEYOND EARTH?

Because geology seems to be intricately linked with life on this planet, the question arises about whether there are other Earth-like planets in the universe that may have developed life. In addition, the planetary history of other planets and moons in our own solar system is similar to that of Earth, leading to questions about the best possibilities for finding extraterrestrial life close to home. Because life as we know it requires liquid water, most of the effort has focused on those planetary bodies displaying evidence of liquid water, either at present or at some time in the past. Most of the attention recently has focused on Mars, where NASA has a vigorous research program; Europa, one of the moons of Jupiter; and Titan, one of the moons of Saturn.

Mars has long commanded attention as a possible site for extraterrestrial life. Tales of martians invading Earth aside, factors that make Mars a plausible site for life include its compositional similarity to Earth and abundant evidence for liquid water at its surface some time in its early history. No evidence of life has yet been found at the surface of Mars. It could be that we have simply not looked in the right place. The other possibility is that any extinct or extant martian life must be contained in the subsurface. Such life would likely be similar to chemotrophic life on Earth that feeds on geochemical rather than photosynthetic energy.

The discovery of the Lost City hydrothermal vent field near the Mid-Atlantic Ridge may provide a glimpse into the nature of life on Mars, if it exists (or ever existed). In the Lost City hydrothermal vent field, chemical reactions between the reduced ultramafic (high in magnesium and iron) rocks and seawater produce very alkaline hydrothermal fluids (Kelley, 2005). These fluids react with seawater to form carbonate chimneys as well as abundant hydrogen and methane, which serve as very useful energy sources for in situ microbial communities. While there are a number of types of hydrothermal systems present on Earth, early in Earth's history these would likely have been dominated by ultramafic rocks reacting with acidic fluids (Russell et al., 2005). Similar systems also might have been present early in the history of Mars, especially in the subsurface, the most likely location for martian life (Russell and Hall, 1999). Recent observations of the martian atmosphere indeed indicate modest amounts of methane that appear to correspond with outcrops of the mineral olivine, consistent with Lost City-type chemistry. Because methane would be quickly photooxidized by ultraviolet light from the sun, finding even these concentrations of methane means that it is being actively generated. On Mars, the observed methane could be coming from reactions between subsurface fluids and ultramafic minerals (Schulte et al., 2006). Alternatively, it is possible that the methane is being produced by methanogenic (methane-producing) microorganisms living in the subsurface.

Europa, one of the Galilean satellites of Jupiter, has recently become another very attractive target for researchers interested in the possibility of life outside Earth. Beneath a thick ice layer, Europa has a 100-km-thick liquid water ocean that most likely covers a rocky mantle (Figure 2). The tidal pull of Jupiter provides enough frictional heat to keep the water liquid below the ice layer, and may also provide enough heat to melt at least some portion of the rocky mantle. This heat availability could result in a situation analogous to Earth's hydrothermal systems, in which molten rock induces hydrothermal circulation through the crust, leading to water-rock interactions that produce hydrothermal vent fluids. On Earth, the resulting fluids are out of chemical and thermal equilibrium with the original seawater, providing energy sources for a great diversity of chemosynthetic microorganisms. Will we find similarly strange communities of microorganisms and animals in the depths of Europa's ocean? Geochemical modeling suggests that there is chemical energy available to support a microbial community (McCollom, 1999), but only continued exploration will allow us to answer this question.

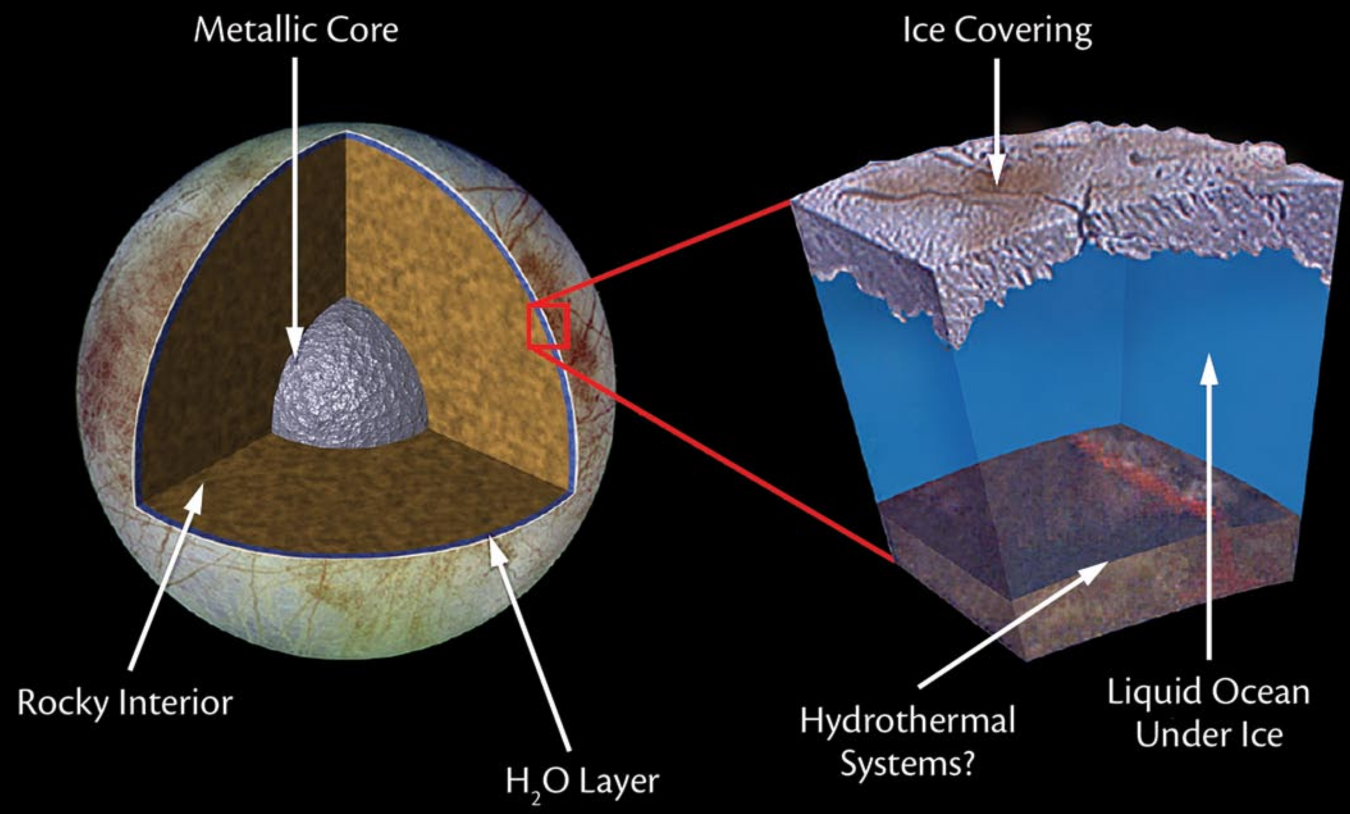

Figure 2. Europa, one of Jupiter's moons, has a liquid water ocean beneath its exterior ice shell, and a rocky mantle. Hydrothermal systems are postulated to exist at the interface between the ocean and mantle. *Modified from a NASA illustration*

SUMMARY

Despite a great deal of advancement in origin-of-life research, the steps that led from chemistry to life remain elusive. Some of the outstanding issues that are poorly understood include the selectivity of molecules (why does life use only 22 protein-forming amino acids out of over 70 amino acids?), the origin of chirality (why does biology use only "left-handed" amino acids but primarily "right-handed" sugars?), the role of mineral surfaces in adsorbing organic molecules and serving as templates for further reaction, the formation of the first membranes and encapsulation of chemical reactions into cells, and the development of genetic information molecules (RNA and DNA).

Origin-of-life research takes essentially two approaches to these issues. One, called the "bottom-up" approach (building life), addresses the formation of life starting with abiotic chemistry and trying to understand the chemical evolution that led to life. Recent research along these lines has led to progress in addressing a number of these issues. For example, common rock-forming mineral surfaces appear to absorb certain organic molecules selectively, including amino acids, and to absorb biological molecules of a particular handedness (Hazen, 2004). Minerals may thus have provided a template for organizing life.

The other approach is called "top down" (breaking down life). The idea is to use what we know about modern forms of life to trace back the genetic and metabolic nature of the first life. As an example, researchers have shown that RNA is capable of catalyzing reactions and storing genetic information. This observation led to the idea of an RNA world, in which RNA served both roles, rather than the current situation in which DNA and proteins share these duties (Orgel, 2004). However, the chemistry that led to the development of RNA remains unexplained. In addition, molecular biology studies are unraveling the differences in genetic sequences of modern organisms that live in extreme environments, helping us decipher the way these organisms are able to use geochemical energy and therefore how they are related to Earth's first life.

Ultimately, both approaches are useful and necessary. Perhaps the combined efforts of all those studying the origins of life will result in a more comprehensive understanding of the processes that led to the emergence of life on Earth, and will help us explore the solar system and beyond for evidence that we are not alone. While continuing advances have furthered our understanding of how biology relates to abiotic processes, far more research will be needed to understand the transition from chemical processes to life.

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