16

Astrobiology:
A Planetary Perspective on Life

At its root, the word "astrobiology" means "biology of the stars." It is the branch of science that concerns the origin and evolution of life on Earth – the only place that, at present, we are certain life exists – and the potential for life to be distributed across the Universe. In this chapter, we explore the evolutionary relationships of life on Earth and review the necessary ingredients and permissible environmental conditions for the origin and evolution of life. We also discuss the characteristics of early life on Earth, and the physical and geochemical evidence for life that might be used to target habitable environments – and potentially to detect evidence of life – elsewhere in the Universe.

16.1 The Diversity of Life

In 2003, the Hubble Space Telescope focused its lens at a single, dark and seemingly featureless spot in the Universe. At the end of 11 days, Hubble had gathered enough visible, near-infrared, and UV light to identify thousands of new galaxies, each containing billions of individual stars (Figure 16.1). This astounding image brings to mind an idea first articulated by Metrodorus in 400 BC, that "it is unnatural in a large field to have only one stalk of wheat, and in the infinite universe, only one living world." This astounding image brought new life to field of **astrobiology**.

Among the many challenges of astrobiology is finding a solution to the seemingly simple question of what is life? Typically, we consider life as a series of observable characteristics: life has an ordered structure (cells), built around a chemical blueprint (genetic material), that responds to its environment; life utilizes energy (metabolism) and shows growth; life is capable of reproduction. Although these characteristics are helpful in considering what to look for when investigating the potential for life in terrestrial and extraterrestrial environments, none of these characteristics are unique to life. Minerals, for example, have an ordered structure that is built around a chemical blueprint. Incorporation of trace elements into a crystal lattice reflects a mineral's capability to respond to its environment. A forest fire utilizes energy to grow, and can spawn new fires.

In order to define life uniquely, we must also consider the process that is most central to life on Earth – biologic evolution. The evolutionary process (also called "descent with modification") requires that the chemical coding of life (that is, our genetic material) is inherited by successive generations and is susceptible to modification by both random mutation and sexual recombination. Adaptation (also called "natural selection") then occurs when genetic characteristics that are favorable to survival within an environment increase in abundance within a population.

The central importance of evolution to our understanding of life on Earth also provides the opportunity for extraterrestrial life to potentially differ from life on Earth in significant ways, depending on the environments in which evolution occurs. With this in mind, the astrobiology community has coalesced around a popular working definition of life as a "self-sustaining chemical system capable of Darwinian evolution."

16.1.1 Reconstructing the Tree of Life

The acceptance of evolution as a driving mechanism for the diversity of life on Earth provides astrobiologists with a mechanism for deciphering how life might originate and evolve on another planet. To do this, we use our understanding of the process of evolution to look backward through time and to determine how evolution has modified the genetic blueprint of life on Earth. Organisms that have more of their genetic blueprint in common are determined to be more closely related, and by exploring
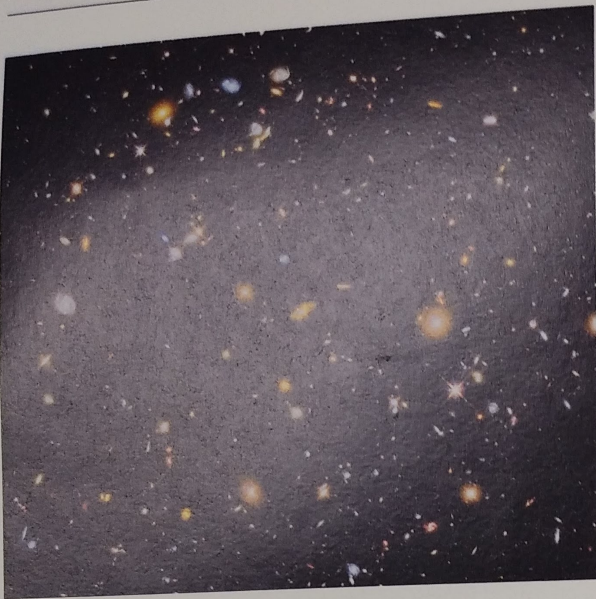
Figure 16.1 In 2014, NASA released this revised version of the 2003 Hubble Ultra Deep Field (HUDF) image. This image combines visible, near-infrared, and ultraviolet light to produce an image with the full range of colors visible to Hubble, and reveals approximately 10,000 galaxies that extend back to within a few hundred million years of the Big Bang. NASA image.

Figure 16.2 Phylogenetic tree of life, after Woese et al. (1990). The three primary domains of life include the Bacteria, the Archaea, and the Eukarya. Detailing the genetic activities of the most deeply branching organisms allows astrobiologists to infer the metabolic capabilities of the earliest life, and environments in which early life may have arisen.

the genetic similarity of all organisms, we can reconstruct what is commonly termed the **tree of life**.

The tree of life is a phylogeny, or a pattern of relationship, that utilizes similarity in genetic coding to define relationships (Gaucher et al., 2010). To construct a tree of life that deciphers relationships across a broad range of biological entities, scientists have focused on **ribosomal RNA** (rRNA). Ribosomal RNA is responsible for the production of ribosomes that catalyze amino acids into the proteins that carry out the most basic functions of biological cells, and therefore occurs in all known organisms. Certain portions of rRNA are also strongly conserved, meaning that rRNA undergoes evolutionary change very slowly. We use these portions to track evolutionary change over long periods of time and to compare diverse species. To build the tree of life, rRNA – specifically the subunits 16S and 18S of the rRNA molecule – is compared between organisms, and mapped to portray the closeness of relationships.

Figure 16.2 shows a basic phylogenetic tree of life (Woese et al., 1990), defined by three primary branches, or domains, of life. These include the Bacteria, the Archeae, and the Eukarya. **Bacteria** are a large and diverse group of single-celled organisms that have cell walls, but lack organelles and an organized nucleus. **Archeae** are similar to bacteria in their basic cell structure, in that they
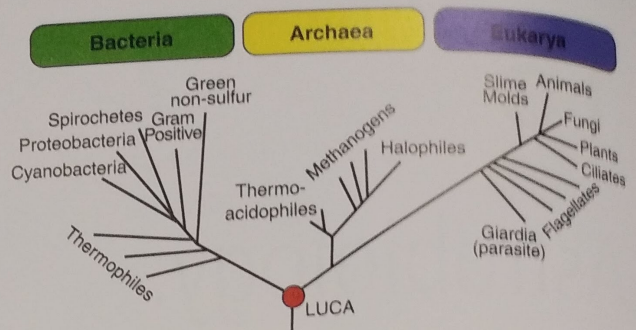
lack organelles and an organized nucleus, but are distinct in the structure of their cell membranes and their genetic coding. Archeae, like bacteria, also display a broad range of metabolisms (Table 16.1) which permit their dominance in a variety of extreme environments (Table 16.2). The third domain of life, the **Eukarya**, includes all organisms whose cells contain both a discrete nucleus and membrane-bound organelles. Although Eukarya make up only a small part of the diversity of life on Earth, they are commonly the most easily recognized because this group contains all larger, multicellular organisms.

From an astrobiological perspective, one of the most important aspects of the tree of life is the basic pattern of diversity. It is readily apparent that the greatest diversity of life on Earth occurs within the microbial (bacterial and archaeal) branches of the tree, which suggests that extraterrestrial life is most likely to be microbial. Astoundingly, however, we are only now beginning to understand the full range of genetic diversity of microbial life, and the capabilities that this genetic diversity grants to these organisms. In fact, less than 1 percent of microbial life has been successfully cultivated in the laboratory, so biologists have developed a wide range of techniques that focus on detecting the presence of different genes (metagenomics analysis) and the expression of these genes (metatranscriptomic and metaproteomic analysis) to decipher the true diversity represented by these domains (DeLong, 2009).

16.1.2 Complexities in the Tree of Life
In addition to helping us define the full range of diversity of life on Earth, analysis of the tree of life provides astrobiologists with a glimpse into the process of evolution of life on Earth. What we find is both complex and fascinating. We have learned, for example, that although

Table 16.1 Metabolic reactions carried out by bacteria and archaea

Process	Reactants	Products
Photosynthesis – metabolic reactions in which light is used as the source of energy for the synthesis of organic carbon molecules		
Photosynthesis (oxygenic)	Carbon dioxide, water	Organic carbon, oxygen
Photosynthesis (anoxygenic)	Hydrogen sulfide	Organic carbon, sulfate
Chemosynthesis – metabolic reactions in which energy for the synthesis of organic compounds is derived from the oxidation of inorganic compounds		
Sulfur oxidation	Hydrogen sulfide, oxygen	Organic carbon, sulfate
Ammonium oxidation	Ammonium, oxygen	Organic carbon, nitrite
Nitrite oxidation	Nitrite, oxygen	Organic carbon, nitrate
Iron oxidation	Iron (Fe^{2+}), oxygen	Organic carbon, iron (Fe^{3+})
Methane oxidation	Methane, oxygen	Organic carbon, carbon dioxide
Respiration – metabolic reactions in which organic carbon molecules are broken down to release energy for cellular processes		
Aerobic respiration	Organic matter, oxygen	Carbon dioxide, water
Sulfate reduction	Organic matter, sulfate	Hydrogen sulfide
Nitrate reduction	Organic matter, nitrate	Nitrogen
Iron reduction	Organic matter, iron (Fe^{3+})	Carbon dioxide, iron (Fe^{2+})
Methanogenesis	Organic matter, oxygen, hydrogen	Methane
Associated reactions – reactions that do not directly involve organic carbon, but which produce chemical products or energy necessary for metabolic reactions		
Nitrogen fixation	ATP, nitrogen	Ammonium
Anammox	Ammonium, nitrite	Nitrogen

Table 16.2 Extreme environments tolerated by bacteria and archea

Organism type	Environment	Consequences
Thermophiles	50–80 °C	Denaturing of proteins
Hyperthermophiles	>80 °C	Denaturing of pigments, nucleic acids
Psychrophiles	<15 °C	Loss of membrane fluidity, ice damage
Acidophiles	pH < 3	Denaturing of proteins
Alkaliphiles	pH > 9	Insufficient electrochemical energy
Halophiles	3–5 M NaCl	Osmotic stress, low water activity
Piezophiles	To 1000 atm	Loss of membrane fluidity
Radiophiles	To 5000 Gy	Direct damage to proteins, nucleic acids

genes involved in the most basic cellular processes, like protein synthesis and energy generation, produce similar phylogenetic trees, many other genes record distinct evolutionary histories. This provides evidence that the evolutionary process is more complex than a simple Darwinian model in which genetic information is transferred unidirectionally from parent and offspring, and likely contains aspects of either horizontal (or lateral) gene transfer or endosymbiosis.

Horizontal gene transfer is the direct movement of genetic material between extant organisms (McDaniel et al., 2010). Within the bacterial and archaeal domains, horizontal gene transfer can occur in three distinct ways. The first mechanism is transformation, which is the direct uptake of exogenous genetic material through the cell membrane. Although this process is not well understood, the ability for cell membranes to uptake exogenous material appears to be triggered by adverse environmental conditions. The second mechanism is conjugation, in which cells in direct contact with one another can transfer portions of their genetic material. The third mechanism of horizontal gene transport is conjunction, in which genetic material from a cell is incorporated into a virus, which then transmits this genetic material to a secondary host. Recent studies suggest that the degree of horizontal gene transfer is greater in extreme environments, where microbial populations are under stress, and that gene transfer can result in a large number of common genes between bacterial and archaeal domains that facilitate adaptation to such extreme environments (Fuchsman et al., 2017).

Endosymbiosis provides an additional mechanism for the wholesale horizontal transference of genetic material. Unlike horizontal gene transfer in microbial populations, endosymbiosis occurs in the eukaryotic domain when intact organisms are ingested and incorporated into the metabolic pathway of the cell (see, for example, Archibald and Keeling, 2002). Endosymbiosis is believed to be the primary mechanism by which Eukarya obtained their critical organelles, such as mitochondria used in energy utilization and chloroplasts used in photosynthesis.

Although the driving force behind endosymbiosis is not well understood, both horizontal gene transfer and endosymbiosis provide a means for organisms to rapidly adapt to inhospitable environments.

16.1.3 The Last Universal Common Ancestor

From an astrobiological perspective, the most important aspect of the tree of life may be in understanding the nature of the **Last Universal Common Ancestor** (**LUCA**). By definition, LUCA represents a population of organisms from which all modern life is derived. In most modern phylogenies (Figure 16.2), LUCA is placed at the division between the bacterial and archaeal domains. In light of studies indicating widespread transference of genes between Bacteria and Archaea, however, LUCA is unlikely to have been the only organismal population at this time. Rather, we should consider LUCA to represent a distinct population of cells that were well adapted to the environments of the early Earth and from which our current diversity of life originated.

Many of our efforts in understanding LUCA have therefore been focused on defining the environments in which the LUCA population thrived. These environments are derived by exploring the characteristics of organisms that comprise the earliest branches within the bacterial and archaeal domains. The most widely shared trait among these early branching organisms is genetic coding that is necessary to stabilize proteins at high temperatures, suggesting that LUCA may have thrived in thermophilic (50–80 °C) to hyperthermophilic (>80 °C) environments (Stetter, 1996). Similarly, analyses of discrete protein families suggest that LUCA likely inhabited a geochemically active, thermophilic environment that was rich in CO_2, H_2, and a variety of reduced metals (Weiss et al., 2016).

16.2 The Chemistry of Life

Whereas investigation into the character of LUCA has informed our understanding of the environments in which earliest life may have thrived, we must also consider the question of why such environments became the locus for emergence of life. Our first clues come from the chemical makeup of the primary biomolecules of life, which include nucleic acids, proteins, carbohydrates, and lipids.

Nucleic acids and proteins are both composed of **amino acids** (Figure 16.3), which consist of a carbon atom that is bonded with a carboxyl group (COOH), an amine (NH_2), and one of a variety of side chain groups. **Nucleic acids**, specifically deoxyribosenucleic acid (DNA) and ribonucleic acid (RNA), are complex
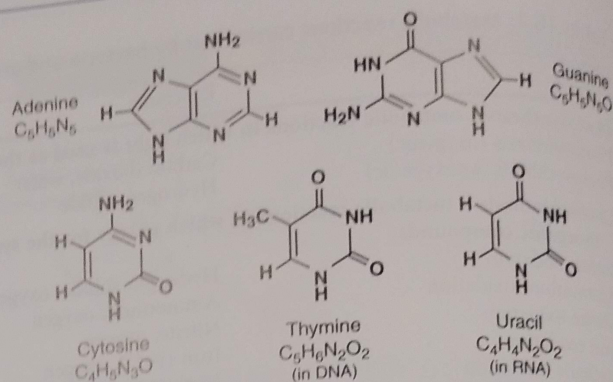

Figure 16.3 Amino acids are considered the building blocks of life, since they are the main component of both genetic material (DNA and RNA) and the proteins that carry out cellular functions. Here we see the structures of the amino acids that comprise genetic material: adenine, guanine, cytosine, thymine (in DNA only), and uracil (in RNA only).

macromolecules that provide the genetic coding to life; they are composed of amino acids bonded with a five-carbon sugar and a phosphate group. Similarly, **proteins** consist of chains of amino acids that coil or fold into three-dimensional shapes and that provide structural support for cells, aid in energy utilization (e.g., adenosine triphosphate, or ATP), and serve as enzymes to catalyze chemical reactions within the cell.

Although simpler in structure, carbohydrates and **lipids** are just as important to biology. **Carbohydrates** consist of simple chains of carbon bonded to a hydrogen (H^+) ion and a hydroxyl ion (OH^-). Short-chain carbohydrates are referred to as sugars, and are broken down in the cell to provide energy. More complex carbohydrates, such as starches, are used as energy storage within cells. By contrast, the basic structure of a **lipid** is a grouping of simple chains of carbon bonded to two hydrogen (H^+) ions attached to a glycerol ($C_3H_8O_3$) molecule. Lipids serve critical roles in energy storage and in the signaling of cellular functions, and, when augmented by a phosphate group (i.e., phospholipids), in the construction of cellular membranes.

16.2.1 CHNOPS and the Cosmos

The composition of the primary biomolecules of life shows that life on Earth is composed primarily of carbon, hydrogen, nitrogen, oxygen, and phosphorous. These five elements, along with sulfur, which occurs in several amino acids critical to protein formation, are together referred to as **CHNOPS**. In fact, these six elements can make up as much as 97 percent of cellular biomass (Wackett et al., 2004). These elements are also some of the most common elements in the Universe. Recall that hydrogen, the most abundant element in the Universe,
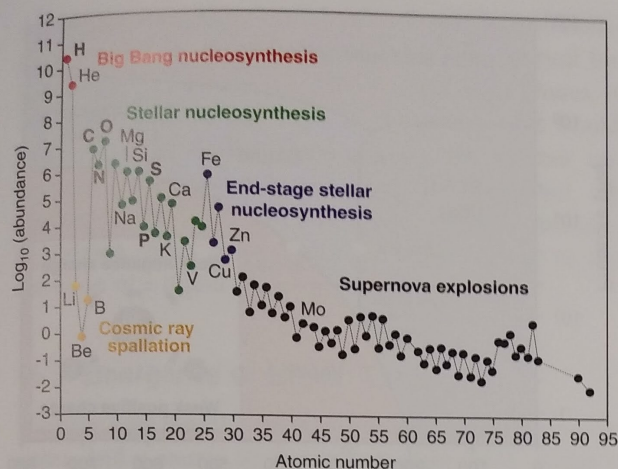
Figure 16.4 The elements that are most critical to life, CHNOPS, are also some of the most abundant elements in the Universe. Hydrogen, formed during the Big Bang, is the most abundant element, followed by oxygen (third), carbon (fourth), nitrogen (sixth), sulfur (ninth), and phosphorous (seventeenth), which are all produced during stellar nucleosynthesis. By contrast, many of the redox-sensitive metals that occur within biological enzymes, such as vanadium, iron, copper, zinc, and molybdenum, are produced only within end-stage nucleosynthesis and within supernova explosions.

was formed by nucleosynthesis during the Big Bang, and the rest of the CHNOPS sequence, as well as essential metals such as Ca, Mg, Na, and K, are the product of fusion reaction in stars (Section 4.2). By contrast, heavier metal ions that are critical components of many biological enzymes, such as V, Fe, Cu, Zn, are formed only in the final moments as stars transition into supernovae, while others, such as Mo, form only in supernova explosions (Figure 16.4, previously shown in Figure 4.9 but with different elements labeled).

Of these elements, carbon is the most critical for life (see Box 16.1). The importance of carbon results, in part, from its chemical versatility. The occurrence of four electrons in its outer electron shell allows carbon to host up to four covalent bonds. Carbon can form stable bonds with both itself and a broad range of other compounds. It can also utilize single, double, and triple bonds with another carbon atom to form a wide variety of stable two- and three-dimensional shapes. Perhaps most critically, the amounts of energy it takes to make (and break) bonds between carbon and CHNOPS are extraordinarily similar, which allows carbon-based compounds to readily exchange ions to drive the metabolic reactions of life.

The importance of carbon in the evolution of life is supported by abundant evidence that organic carbon molecules are common across the Universe. Spectroscopic analysis has detected organic molecules in a wide

BOX 16.1 SILICON AS A BASIS FOR LIFE?

In the original Star Trek series, on Star Date 3196.1, Federation miners of Janus IV began to be repeatedly attacked by a mysterious creature, known as the Horta. The Horta was a silicon-based life form, capable of tunneling through solid rock. The idea of extraterrestrial life based on silicon, rather than on carbon, has intrigued us ever since.

Silicon has many chemical properties similar to carbon. It is the eighth most abundant element in the Universe. Like carbon, silicon is tetravalent, and forms covalent bonds with both itself and other elements, including oxygen and hydrogen (Bains, 2004). Also, like carbon, silicon is capable of forming long-chain polymers and a variety of stable two- and three-dimensional topologies. But although some terrestrial organisms are known to use amorphous silica in making skeletal structures, there are no known instances of silicon–carbon bonding associated with life.

Researchers at Caltech, however, have recently coaxed the evolution of enzymes capable of driving Si–C bonding (Kan et al., 2016), and have suggested that if such evolution can occur in the laboratory, it may very well have occurred in nature. Yet, despite this discovery, there are substantial hurdles to the idea of silicon-based life. The first hurdle is in the behavior of silicon in water. Not only does silicon have a very low solubility in water with a pH less than 12, which restricts its availability, but silicon compounds are also generally unstable in water. Silicones (Si–O polymers) readily break down in water, and silanes (SiH_4 compounds) react explosively with water.

Perhaps the greatest hurdle to silicon-based life is the affinity between silicon and oxygen. Silicon readily oxidizes and forms an insoluble solid, silicon dioxide (SiO_2). The great energy it takes to break the SiO_2 bonds makes the silica tetrahedron a superb base for planetary minerals, such as pyroxenes, amphiboles, and feldspars, but an unlikely participant in life.

variety of planetary atmospheres, stellar envelopes, and in the interstellar medium (Ehrenfreund et al., 2011). These molecules are often termed **prebiotic compounds**, because they are the precursors from which biotic molecules are ultimately formed. While most of these organic carbon and associated molecules are relatively simple in their structure (e.g., CO, HCO, HCN, NH_3, and CH_4),
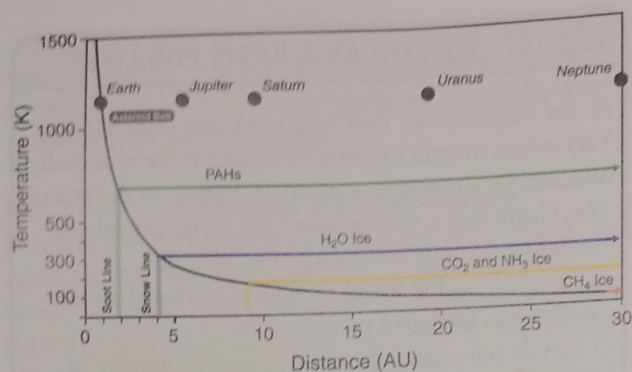
Figure 16.5 The "Soot Line" and the "Ice Line" mark the position in a planetary disk at which temperatures are low enough to retain complex organic matter – specifically polyaromatic hydrocarbons (PAHs) – and water, respectively, in the solid phase. Additional "ice lines" represent stability for other important planetary ices, including carbon dioxide (CO_2), ammonia (NH_3), and methane (CH_4).

more complex compounds including amines, long-chain hydrocarbons, and **polycyclic aromatic hydrocarbons (PAHs)** can also form via a series of gas-phase, carbon-insertion, and condensation reactions. In the colder regions of planet-forming accretion disks, these organic molecules condense, along with dust, water, carbon dioxide, ammonia, and methane (Figure 16.5) into icy bodies that are similar to those represented today by Kuiper belt objects and a variety of Main belt asteroids. Experimental evidence suggests that even in these inhospitable and frozen environments, ultraviolet radiation from stars can cause complex and stable organic molecules such as PAHs to transform into more complex organic species (Gudipati and Yang, 2012). Continuation of such chemical interactions may ultimately result in the formation of the most complex prebiotic molecules, such as amino acids, which have been recorded in chondritic meteorites delivered to Earth.

16.2.2 Water, the Elixir of Life

In addition to chemical nutrients (and the energy to drive chemical reactions), life also requires a stable medium in which these chemical reactions can occur. Given the importance of liquid water to all life on Earth (Mottl et al., 2007), most astrobiologists consider evidence for water to be key in our search for extraterrestrial habitability.

In many ways, water is the ideal medium for chemical reactions. The most important characteristic of water is its structure as a polar molecule (Figure 16.6, inset) that produces a slight positive charge on one end of the molecule and a slight negative charge on the other. This polarity produces a number of the key characteristics of
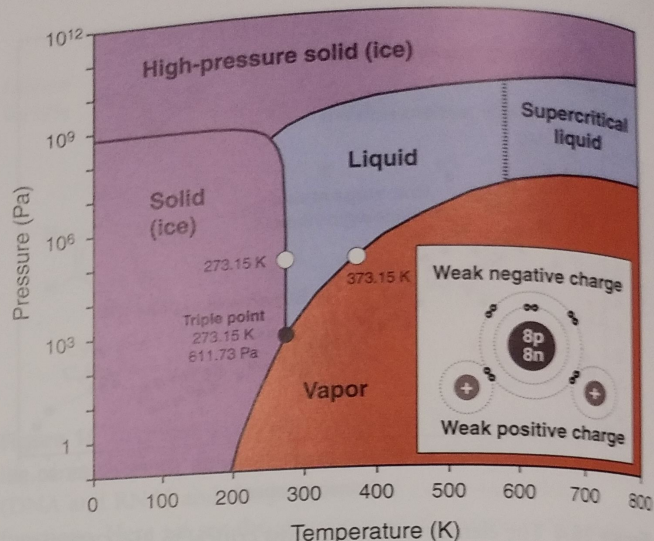

Figure 16.6 The polar structure of water (inset) imparts characteristics that are critical for its role in biological functions, including a broad range of temperature and pressure under which liquid water is stable, and the ability to dissolve a wide range of other chemical nutrients. The density difference between water in its liquid and solid forms may also be critical for the maintenance of habitable terrestrial and extraterrestrial environments. The black circle marks the solid–liquid–vapor triple point for water, at ~273 K and ~612 Pa; white circles mark the freezing point (273 K) and boiling point (373 K) for water at 1 atm.

water. First, water molecules have a propensity to bond to each other, which counteracts the relatively low molecular weight of water and results in a broad range of planetary temperatures and pressures under which water remains a stable liquid (Figure 16.6). Second, the polarity of water allows it to dissolve more substances than any other liquid, resulting in water being characterized as the universal solvent. For most polar substances, such as salts and small organic molecules, dissolved ions also distribute uniformly through the water. By contrast, other molecules, such as most lipids, are not readily soluble in water and remain as an immiscible component. However, some lipids, such as phospholipids associated with cell walls, contain an insoluble (hydrophobic) lipid chain attached to a soluble phosphate (hydrophilic) end, which allows them to form bilayer membranes that effectively encapsulate ambient fluids (see Section 16.3).

Another unusual property of water is that it (unlike other potential solvents like ammonia or methane) is less dense in its solid phase than in its liquid phase. This property results from the strength of the hydrogen bonding; in the liquid state, hydrogen bonds readily break and reform, allowing water molecules to freely flow past one another; in the solid state (ice), these hydrogen bonds are restricted in their movement, resulting in greater

spacing between adjacent molecules. From an astrobiological perspective, this difference in density is critical for habitability. If ice were the denser of the H_2O phases, it would immediately sink upon its formation. This would result in water bodies freezing from the bottom up, restricting the availability of a liquid component. By contrast, since ice is the less dense phase, it insulates underlying fluids from freezing, thereby aiding in the retention of a liquid component.

16.3 Emergence of Life on Earth

We have seen that the chemistry of life requires nutrients, water, and a source of energy (e.g., light, heat, chemical energy). These requirements would have been satisfied in a number of different environments of the early Earth. Volcanic degassing would have provided a suitable volatile inventory, including nitrogen, carbon dioxide, methane, sulfur dioxide, carbon monoxide, hydrogen, and water (Zhanle et al., 2010), and crustal weathering would have provided phosphorous. Water and organic compounds would also have been delivered from extraterrestrial sources by the continued accretion of asteroidal and cometary material (Chyba and Sagan, 1992).

There is no reason a priori to assume that the origin of life was a unique event, and the prebiotic Earth would have contained a variety of environments in which the chemical reactions of life could have occurred, including within surficial lakes, ponds, or oceans, or in association with surficial or deep-ocean hydrothermal vents. In fact, the tree of life tantalizingly suggests that LUCA may have been only one of a diverse population of early life forms (Delaye et al., 2005). But how did life actually emerge in these environments? Typically, we consider the emergence of life in three stages: the synthesis of complex prebiotic organic compounds, the origination of chemical reaction pathways, and the compartmentalization of these reactions within a cellular membrane.

The first stage in this process – the formation of complex prebiotic organic compounds – convincingly must have occurred in a warm, wet environment. Such a process was first described by Charles Darwin in 1871, when he envisioned "some warm little pond," infused with ions, in which the stuff of life (which we now know as nucleic acids, proteins, carbohydrates, and lipids), could result from simple chemical reactions. In 1953, Stanley Miller and Harold Urey brought this idea to life in an elegant experiment (Figure 16.7): They produced a synthetic "little pond" overlain by a reducing atmosphere containing methane, ammonia, hydrogen, and water vapor (with later experiments also including hydrogen sulfide). An electrical discharge within the atmosphere
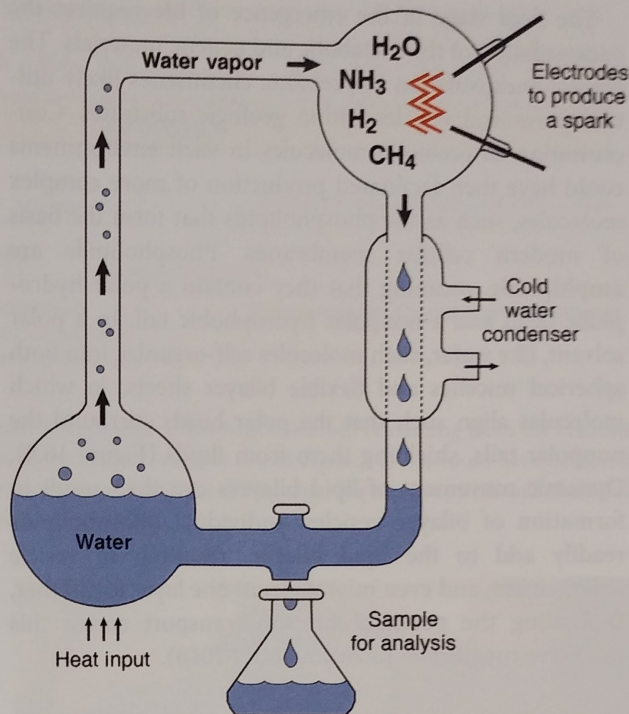

Figure 16.7 Schematic of the 1953 Miller–Urey experiment that showed the potential for formation of complex organic molecules, and specifically the formation of the amino acid building blocks of life, in any environment that contains water, chemical nutrients, and a source of energy.

provided a source of energy. The result was the formation of a wide range of organic compounds, notably a variety of amino acids.

The emergence of chemical reaction pathways is less well understood. Molecular phylogenies tell us that all life forms share basic cellular functions. In modern life, DNA provides the chemical blueprint for metabolism, and RNA acts as the messenger to translate this information to ribosomes and to transport amino acids to the ribosomes for protein synthesis. Proteins then carry out the cellular functions. It has been argued, however, that the complexity of DNA makes it an unlikely participant in the emergence of life. In the **RNA world** hypothesis (Gilbert, 1986), the much simpler nucleic acid RNA acts as both the blueprint for cellular functions and the driver for protein synthesis. Environments rich in prebiotic compounds would provide the necessary building blocks for the production of RNA and subsequent protein synthesis. An alternative hypothesis, based on the similarity between many metabolic reactions and metal-catalyzed chemical reactions (Cody, 2004), suggests that primitive metabolic pathways evolved first and reflected ambient geochemical conditions, and that RNA (and ultimately DNA) then evolved to perpetuate these reactions (Copley et al., 2007).

The final stage in the emergence of life requires the encapsulation of the metabolic and genetic materials. The earliest encapsulation of prebiotic chemistries likely utilized pores and vesicles within geologic substrates. Concentration of prebiotic molecules in such environments could have then facilitated production of more complex molecules, such as the phospholipids that form the basis of modern cellular membranes. Phospholipids are amphiphilic, meaning that they contain a polar hydrophilic head and a nonpolar hydrophobic tail. In a polar solvent, like water, such molecules self-organize into both spherical micelles and flexible bilayer sheets, in which molecules align such that the polar heads surround the nonpolar tails, shielding them from fluids (Figure 16.8). Dynamic movement of lipid bilayers can then result in formation of bilayer vesicles. Individual phospholipids readily add to the lipid bilayer, resulting in vesicle enlargement, and even migrate from one layer to another, facilitating the potential for ion transport across this primitive membrane (Schrum et al., 2010).
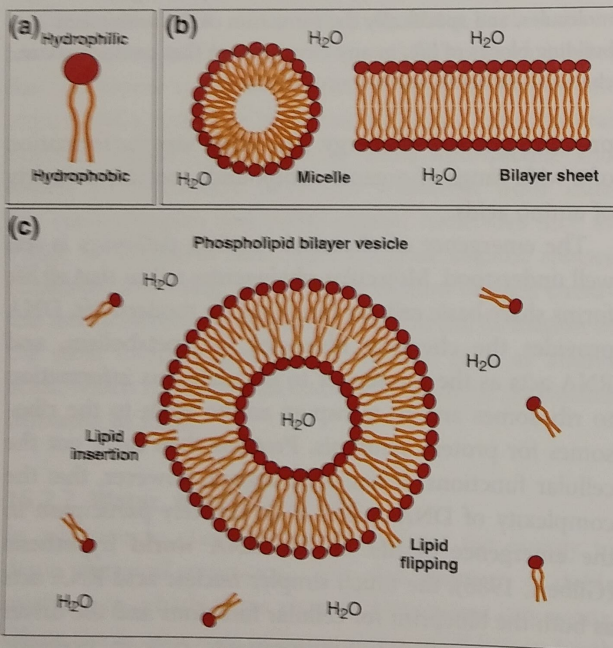

Figure 16.8 Membrane formation via amphiphilic fatty acids. (a) Phospholipids are amphiphilic molecules with a polar, hydrophilic head attached to two, nonpolar, hydrophobic lipid chain tails. (b) When concentrated in fluids, phospholipids self-organize into micelles and bilayer phospholipid sheets. (c) Dynamic movement of bilayer sheets forms vesicles and may represent the earliest cellular membranes. Addition of individual phospholipids can enlarge vesicles, and flipping of phospholipids provides a mechanism for transport of ions through the vesicle wall.

16.4 Earth's Early Biosphere

Relatively little is known about the Earth's biosphere in the Hadean, which spanned the Earth's first 500 million years. It would not have been until the Earth differentiated and cooled, about 100 million years after its formation, that a biosphere could begin to be established. By this point, a combination of volcanic degassing and the chemical weathering of the early crust would have provided the basic ingredients for life. This early biosphere, however, would have continued to experience the effects of extraterrestrial impacts until after the Late Heavy Bombardment (Section 5.6.2), which ended about 3.8 Ga. The largest of these impacts could have imparted enough energy to vaporize portions of the Earth's oceans, to heat the remaining surface fluids, and potentially to drive extinction within Earth's earliest life.

Within this dramatic and volatile environment, however, it is likely that biology gained its first foothold. Our only direct evidence of the Hadean Earth, however, comes from individual igneous mineral grains, zircons ($ZrSiO_4$). These zircons (Figure 16.9) originally crystallized 4.0–4.4 Ga, and were ultimately eroded and redeposited as detrital grains in Archean rocks of the Jack Hills, Western Australia. Analysis of the isotopic composition of these zircons suggests that the Hadean Earth may have retained relatively cool surface waters for extended periods of time between impact events (Wilde et al., 2001). As noted earlier, the tree of life suggests that LUCA was a biological population with the genetic capability of survival in elevated temperatures. Perhaps LUCA represents a population, then, that was capable of surviving heated fluids that derived from these early impact events.
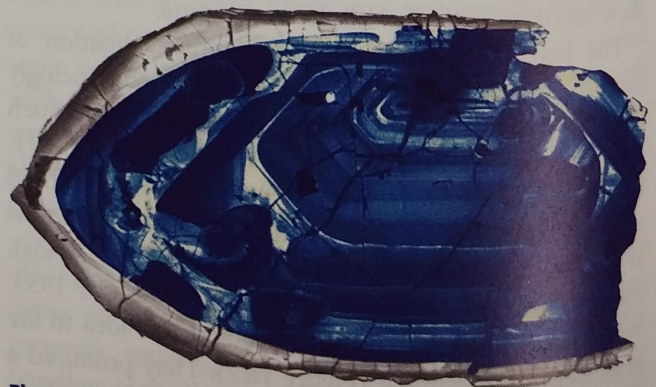

Figure 16.9 False-color image of a 4.4 billion-year-old zircon from Jack Hills, Australia. A small handful of similar zircons represent our only known materials remaining from the Hadean Earth. Image courtesy of J. Valley.
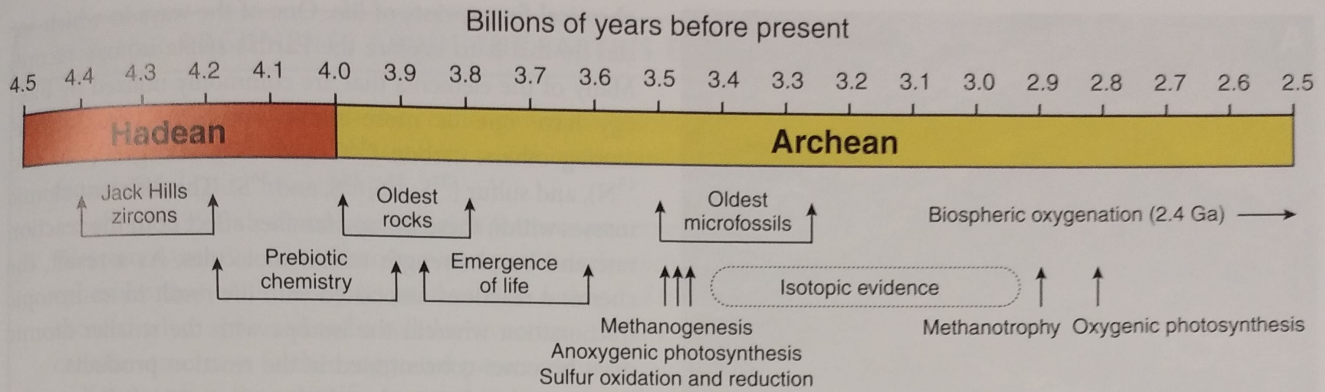
Billions of years before present

| 4.5 | 4.4 | 4.3 | 4.2 | 4.1 | 4.0 | 3.9 | 3.8 | 3.7 | 3.6 | 3.5 | 3.4 | 3.3 | 3.2 | 3.1 | 3.0 | 2.9 | 2.8 | 2.7 | 2.6 | 2.5 |

Hadean   Archean

Jack Hills zircons   Oldest rocks   Oldest microfossils   Biospheric oxygenation (2.4 Ga) ⟶

Prebiotic chemistry   Emergence of life   Isotopic evidence

Methanogenesis   Methanotrophy Oxygenic photosynthesis
Anoxygenic photosynthesis
Sulfur oxidation and reduction

Figure 16.10 Timeline of life on Earth in the Hadean and the Archean. The absence of geologic materials remaining from the Hadean does not allow clear delineation of environments and habitability that could address whether the emergence of life could have occurred prior to the Late Heavy Bombardment. Even with a potentially later emergence of life, the oldest unambiguous physical and chemical evidence for life does not appear for nearly 200 million years, between 3.4 and 3.5 Ga.

Another possibility is that Hadean life gained a foothold in deeper marine environments, such as hydrothermal vents, where disruption by impact events would have been lessened (Martin and Russell, 2007). At mid-ocean ridges, cold seawater circulates through the crust; hydrothermal vents occur where these fluids, now heated, emerge from the seafloor. Modification of these fluids in the subsurface results in strong gradients in both temperature and chemistry between emergent fluids and the surrounding seawater. Of particular interest to astrobiologists is the enrichment of metals in vent fluids, which catalyze the formation of organic molecules either directly or via mineral surfaces (e.g., iron–sulfur minerals).

16.4.1 Recognizing Early Life

A timeline of early Earth (Figure 16.10) highlights the difficulty of reconstructing the history of life on Earth. With the exception of the Jack Hills zircons, plate tectonics has destroyed the Hadean rock record. Even in the Archean (4.0–2.5 Ga), sedimentary rock successions that record environments of the Earth's surface are relatively scarce. Additionally, these sedimentary successions typically represent only shallow marine environments, which limits our potential to explore the breadth of Earth's early biosphere.

Direct evidence for life on the Archean Earth occurs as microbial structures preserved in silica (SiO_2). The precipitation of silica occurs primarily in evaporative, shallow marine environments, where increased silica saturation can overcome kinetic inhibition to precipitation (Manning-Berg and Kah, 2017). In these environments, silica-bearing fluids (or even a silica gel) can permeate the shallow substrate. Where the substrate is colonized by microbial mats, silica can bind to organic
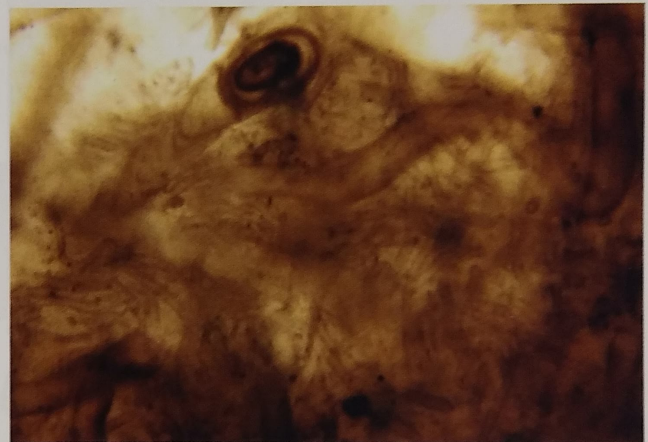

Figure 16.11 An example of a 1.1 billion-year-old microbial mat preserved in silica. Exquisite preservation of microbial morphology – here represented by two distinct sizes of microbial filaments and a coccoidal bacterium – results from binding of silica to organic molecules during mat growth. Image courtesy of L. C. Kah.

matter and effectively entomb the microbial community, resulting in spectacular preservation of microbial features (Figure 16.11). During recrystallization of the silica, however, much of the original morphological detail can be lost, resulting in a greater uncertainty regarding the biological character of preserved organic material (see Box 16.2).

More commonly, our evidence for early life comes from the interaction between microbes and the sedimentary environments in which they occur. Stromatolites, pictured in Figure 16.12, are laminated sedimentary structures that represent the modification of sedimentary substrates by microbial mat communities. Unfortunately, direct evidence for microbial communities is

Figure 16.12 Stromatolites represent the interaction between microbial communities and their sedimentary environment. (a) Irregular, centimeter-scale topographic relief resulting from microbial binding of the sedimentary substrate from the 2.9 Ga Pongola Supergroup, South Africa. (b) Well-laminated, decimeter-scale stromatolites from the 2.52 Ga Transvaal Supergroup, South Africa. Image courtesy of L. C. Kah.

typically lacking from stromatolites. Rather, microbial growth and decomposition are inferred to be reflected in millimeter-scale irregularities of lamina shape that are distinct from laminae formed by the physical transport of sediment. Accretion of successive laminae is similarly inferred to reflect either the trapping and binding of detrital sediment by microbes, or mineral precipitation induced by the microbial activity within mats (Grotzinger and Knoll, 1999). If we accept stromatolites as biological entities, we can confirm that microbial life inhabited shallow marine environments on Earth by at least 3.5 Ga, which agrees with evidence from permineralized microfossils.

16.4.2 The Chemical Record of Life

A more comprehensive understanding of the habitability of the early Earth has been gained from exploring the chemical fingerprints of life. One of the ways in which we can do this is to explore the Earth's stable isotope record. Many of the elements that are commonly utilized by biology have one or more stable isotopes. These include, among others, carbon (^{12}C and ^{13}C), nitrogen (^{14}N and ^{15}N), and sulfur (^{32}S, ^{33}S, ^{34}S, and ^{36}S). The different atomic masses within these isotope families affect both the reaction rate and bond strength within molecules. As a result, the chemical reactions associated with life result in an isotopic fractionation wherein the isotope with the smaller atomic mass becomes concentrated in the reaction products.

As noted earlier, carbon is the most critical element for life, so it should come as no surprise that the most commonly used stable isotope system to explore early life is that of carbon. When examining carbon's stable isotopes, we find that metabolic reactions that produce organic carbon from carbon dioxide in the oceans (Table 16.1) result in rather substantial isotopic fractionations. These fractionations are measured in "delta notation" which describes the ratio of ^{13}C to ^{12}C in a sample and a known standard, and expresses this ratio in parts per thousand (‰, or per mil). The fractionation between reduced carbon (organic matter) and oxidized carbon (carbon dioxide) phases in the oceans is approximately −25‰, meaning that the organic carbon is enriched in ^{12}C (or depleted in ^{13}C) by 25 parts per 1000 relative to the measured standard. Isotopic measurements since 3.5 Ga have shown a consistent fractionation between carbon dioxide in the ocean (as measured in marine carbonate minerals) and coeval organic matter (Figure 16.14), suggesting the continuous microbial occupation of the Earth's surface since this time. Similarly, sulfur isotope fractionation observed between oxidized and reduced phases at this same time suggests biological metabolisms capable of sulfur oxidation and reduction, as well (Figure 16.10).

In addition to measuring the isotopic composition of organic material, we can also explore molecular fossils, or biomarkers. **Biomarkers** are specific organic carbon structures, characterized by rings or chains, that represent the preserved components of biomolecules such as proteins and lipids (Newman et al., 2016). Lipids, in particular, can survive largely intact over billions of years and thus provide a unique glimpse into early life. One particularly important group of lipid biomarkers is the hopanoids – large molecules containing five carbon rings that serve as stabilizing compounds in bacterial cell walls. Hopanoids are widely distributed, but unique to bacteria. Modification of hopanoids, such as the addition of methyl groups, is less common and is hypothesized to be limited to specific bacterial groups, such as cyanobacterial (2β-methyl hopanes) or methanotrophic bacteria

BOX 16.2 ARGUMENTS ABOUT THE EARTH'S EARLIEST ECOSYSTEM

A single question highlights the challenges of astrobiological research: What is the oldest life on Earth? The answer to this question is critical both to our understanding of life's origins, and to determining the best targets for astrobiological investigation.

Schopf (1993) described carbon-rich features preserved in diagenetic silica within the ~3.5 Ga Apex Chert of Western Australia. This discovery was particularly exciting because preserved materials were not just simple spherules that could easily be attributed to a range of biotic and abiotic origins, but complex filaments that showed what appeared to be cellular structures (Figure 16.13). Differences in the size and shape of these cellular structures further suggested preservation of multiple different microbial taxa.

Yet not all in the scientific community agreed on the biogenicity of these microfossils – and even fewer now agree on biogenicity of some even older purported fossils. In 2002, after viewing some of the original material from the Apex Chert, Brasier et al. (2002) published an extensive petrographic and geochemical investigation of new material from the remote Australian site. Using advances in laser Raman spectroscopy (see also Schopf et al., 2002) and energy-dispersive X-ray spectroscopy, the "cellular structures" observed by Schopf were reinterpreted as carbon, synthesized abiotically within hydrothermal fluids, that had been deposited along the margins of mineral grains.

New technology, however, is continuing to advance the debate, and to turn the tables back toward a biogenic origin for structures preserved within the Apex Chert. For example, Schopf et al. (2018) released results of an investigation into the isotopic composition of carbon within the Apex Chert. Earlier work had revealed bulk isotopic compositions that were broadly consistent with production of organic carbon by photosynthetic microbes. The most recent study, which used secondary ion mass spectrometry (SIMS) to investigate the isotopic composition of individual preserved structures, reveals that isotopic compositions are specific to morphologic groups (Schopf et al., 2018). Together, the correlation between differences in isotopic composition and morphology of the structures suggests that, by ~3.5 Ga, the Earth not only had life, but potentially a complex ecosystem consisting of photosynthetic, methanogenic, and methanotrophic bacteria.
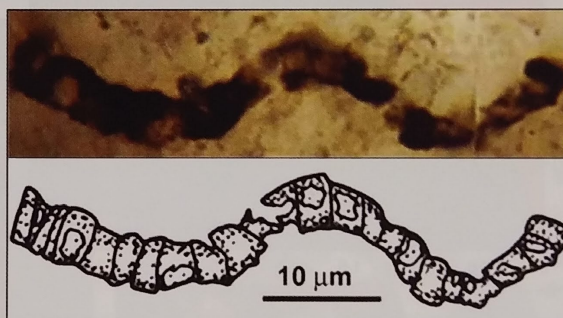

Figure 16.13 A segmented filament preserved within the 3.5 Ga Apex Chert, Western Australia. Purported microfossils from the Apex Chert have been the focus of more than 20 years of debate regarding whether these features represent Earth's earliest preserved life. Image courtesy of J. W. Schopf.

(3β-methyl hopanes). Other hopanoids, such as bis- and tris-norhopanes, have uncertain biologic origins but are strongly correlated to anoxic, sulfur-rich environments.

16.5 Life Beyond Earth

Frigid temperatures, low pressures, and elevated radiation make the survival of biological organisms in space unlikely (Olsson-Francis and Cockell, 2010), but are there habitable worlds beyond the Earth? We can begin to explore the potential for habitable extraterrestrial environments by returning to the key requirements of life: a source of energy, availability of chemical nutrients, and a stable medium in which to carry out biochemical reactions. With this approach, we readily find that sources of energy are abundant in the Universe, and nutrients occur in sufficient abundance to produce prebiotic organic molecules throughout the expanses of space (Ehrenfreund et al., 2011). This leaves a stable medium for chemical reactions as the key component in determining whether an environment may be habitable to life.

16.5.1 Habitable Zones

A **habitable zone** (Figure 16.15) is defined as the region around a star where liquid water is potentially stable on the surface of a planetary body with an atmosphere
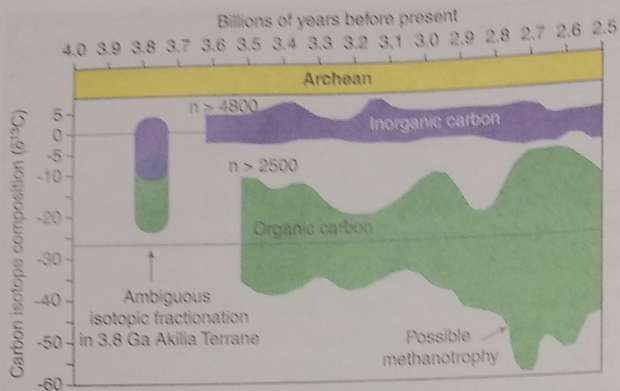
Figure 16.14 Carbon isotope record of life in the Archean. Persistent average fractionation of approximately –27‰ between inorganic carbon and organic carbon supports the biological origin of organic carbon. Isotopic fractionations greater than –50‰ in the late Archean likely result from the biological utilization of biologically formed methane.
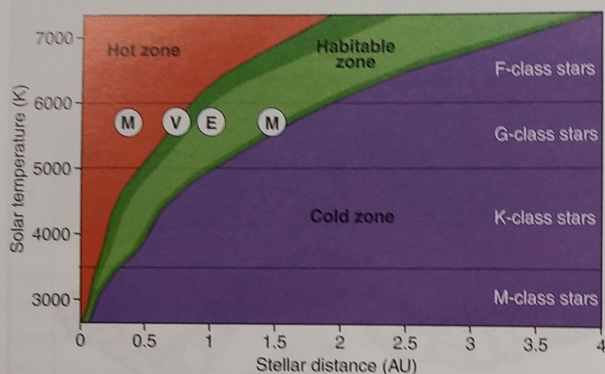

Figure 16.15 Proposed habitable zone around main sequence stars. The habitable zone marks the distance from a star in which liquid water may be present on the surface of a planetary body with an atmosphere. The position of the inner planets (Mercury, Venus, Earth, and Mars) are shown.

(Kasting et al., 1993). The idea of a habitable zone, however, is based primarily on the temperature and heat output of stars, and is therefore only a first-order guide to potential habitability. The stability of liquid water is also strongly dependent on other parameters that affect the surface temperature of a planetary body. These parameters include the composition and density of a planet's atmosphere, as well as the orbital dynamics of a planet, such as whether or not a planet always has the same side facing its parent star.

Our current definition of a habitable zone is also based on the presence of liquid water at the surface of a planetary body. However, even in our own Solar System, potential habitable worlds occur outside the traditional habitable zone. Liquid water, for example, has been proposed to occur, at least seasonally, in the subsurface of planets on the fringe of the habitable zone, such as Mars (McEwen et al., 2011). Icy moons that orbit gas giants and experience substantial tidal heating, such as Europa and Encedalus, also retain subsurface oceans (Section 12.4.3). The search for life is part of the motivation for the further exploration of these bodies by spacecraft. There is also the special case of Titan (Section 12.4.2). Titan possesses a thick nitrogen–methane atmosphere with a wide range of prebiotic organic molecules (Hörst et al., 2012). Although surface temperatures of Titan are too low to retain liquid water, it has been proposed that a substantial reservoir of liquid water could lie in the subsurface.

In addition to these potentially habitable worlds within our own Solar System, we have also identified thousands of exoplanets. Calculations suggest that there may be as many as 40 billion Earth-sized planets in our galaxy that occur within the habitable zone of their respective stars (Petigura et al., 2013). Exoplanets are described in the Epilogue at the end of this book. What a wonderful opportunity for future astrobiological studies!

16.5.2 Life in a Martian Meteorite?

Have we already found evidence for extraterrestrial life? McKay et al. (1996) stunned the world with their announcement of the discovery of potentially microbial fossils in a meteorite from Mars known as Allan Hills 84001 (ALH 84001). The following day, President Clinton stood outside the White House and commanded the scientific community to put these findings through a thorough peer-review process, and stated his own determination that the USA would put "its full intellectual power and technological prowess behind the search for further evidence of life on Mars."

The ALH 84001 meteorite was discovered in 1984 in Antarctica. Its identification as martian is inferred from the ratio of atmospheric gases trapped within the fusion crust, in conjunction with the oxygen isotope composition of minerals within the meteorite. Radiometric dating determined that ALH 84001 was ejected from Mars approximately 17,000 years ago, but the rock itself is nearly four billion years old, thus dating to a time when most scientists think the martian surface was much more Earth-like.

Preserved evidence of life within ALH 84001 was controversial from the start (McSween, 1997). Although the rock itself is igneous, various materials purported to be of biologic origin are contained in chemically zoned carbonate spherules (Figure 16.16a) precipitated from a
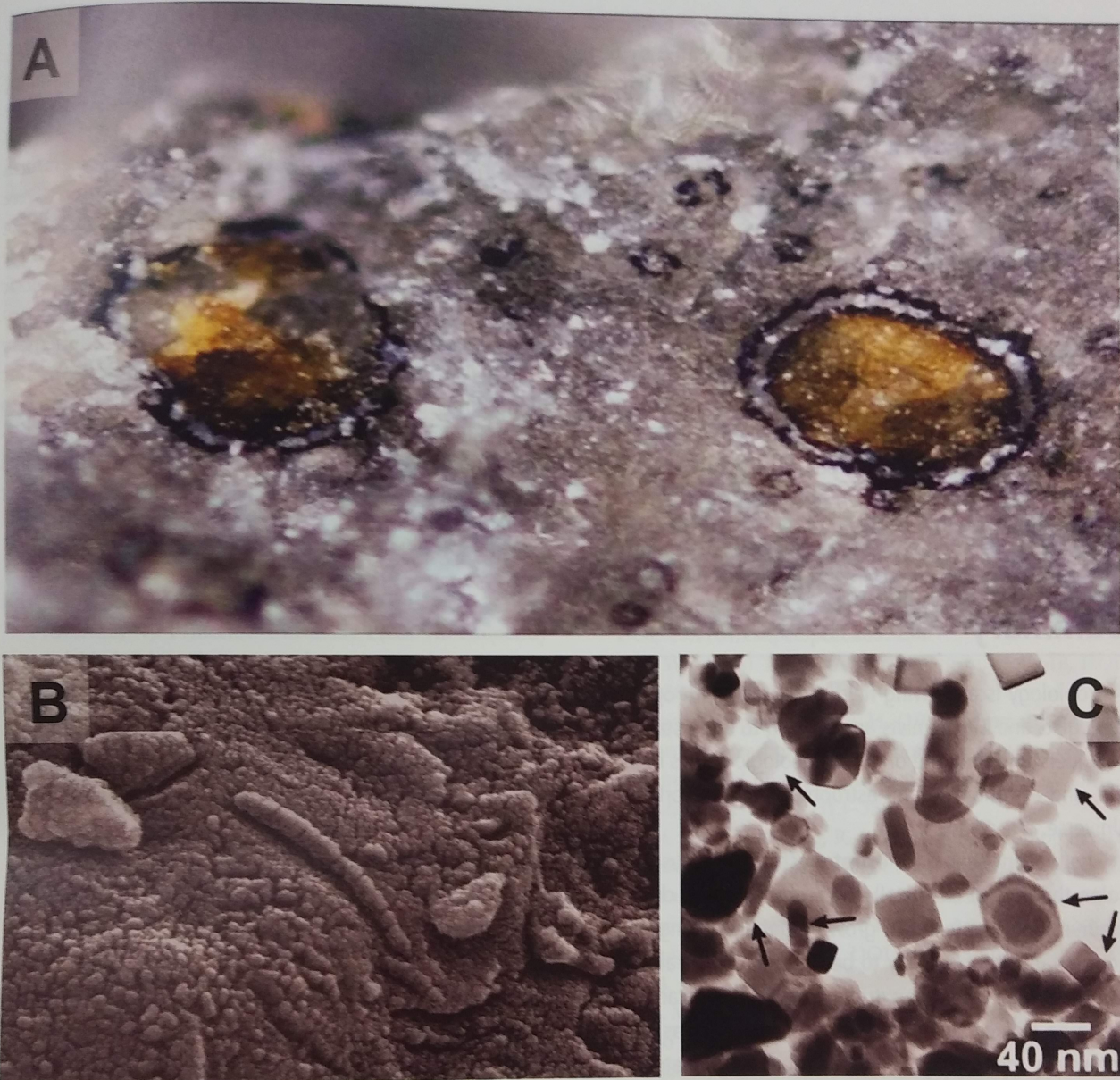
Figure 16.16 Purported evidence for life in Allan Hills 84001 martian meteorite. (a) Zoned carbonate spherules. (b) A segmented filament proposed to be a microfossil. (c) Tiny magnetite crystals proposed to be from magnetotactic bacteria. NASA images.

circulating fluid or evaporating brine. ALH 84001 was also found to contain complex organic molecules, specifically PAHs. PAHs are known from Earth as the combustion products of biological materials, but they also occur across the Universe as abiotic organic molecules; PAHs within ALH 84001 lack any of the side-chain components that would permit us to distinguish their true origin. The bacteria-shaped objects that caught the eye of researchers (Figure 16.16b) are reminiscent of filamentous bacteria, but are ten times smaller than size estimates for the smallest cells (Knoll, 1999). Similarly, tiny magnetite crystals found within ALH 84001 (Figure 16.16c) morphologically resemble the tiny crystals formed by magnetotactic bacteria. At the time, there was no other process understood to form such crystals. In the meteorite, however, these magnetite crystals do not occur in the alignment characteristic of magnetotactic bacteria. Research since the discovery of ALH 84001 suggests that magnetite results from shock decomposition of the iron carbonate, the microfossils may be surface features on shocked

carbonate, and the organic matter may be exogenic. Moreover, the meteorite was likely contaminated by terrestrial microorganisms while in the Antarctic environment. The "life in a martian meteorite" controversy thus illustrates how tricky it will be to make a definitive discovery, even once we have samples returned from another planet.

16.5.3 The Ongoing Search for Organic Matter on Mars

Although the controversy over potential biomarkers in ALH 84001 has mostly subsided, the search for potential evidence of life on Mars continues. In 2018, scientists working on the Curiosity rover reported finding a wide variety of organic compounds preserved in lacustrine mudstone of Gale crater (Eigenbrode et al., 2018). Organic compounds were released from powdered rock by **pyrolysis**, where they were converted into gas by stepwise heating.

These compounds included both simple aromatic (ringed) molecules, such as benzene (C_6H_6), methylbenzene (C_7H_7), and alylbenzene (C_8H_9), and a range of sulfur-containing compounds, such as thiophene (C_4H_4S), methylthiophene (C_5H_6S), and dimethylsulfide (C_2H_6S). Critically, many of the organic compounds evolved at high temperatures during pyrolysis, suggesting that these compounds were originally part of larger organic compounds that do not decompose readily. The diversity and composition of these compounds are consistent with the pyrolysis of abiotic organic material that occurs in both carbonaceous chondrites and decomposed organisms in terrestrial sedimentary materials. Although there is no certainty that these organic compounds are biotic in origin, this find is exciting to astrobiologists because these results show that organic molecules that could serve as a carbon source for microbial metabolism can survive the harsh radiation environment at the martian surface.

Summary

Astrobiology is a growing field of science, with opportunities for scientists from disparate scientific disciplines. As biologists and biochemists are working to understand the complex chemistry of life here on Earth, geologists are working to understand both the origins of geologic bodies in the Universe and how to read the geologic record of habitability and life, and astronomers and astrophysicists are working to identify the range of potentially habitable worlds across the Universe.

The present search for extraterrestrial life focuses on identifying the key components to life: a source of energy (e.g., solar, thermal, or chemical), the presence of key chemical nutrients (e.g., CHNOPS), and the availability of a stable liquid medium (e.g., water). Our growing understanding of the Universe suggests that it is the last of these, the presence of liquid water, that is likely to be the main constraint on the habitability of extraterrestrial worlds.

Still, in the search for extraterrestrial life, we cannot forget that the Earth is only a single model for life. LUCA, the Last Common Universal Ancestor of life on Earth, was likely only one population among several early life forms. With potentially more than 40 million habitable planets in the Universe, the geologic evolution of these individual planets could have driven the evolution of life in any number of different directions.

Review Questions

1. What is the Last Universal Common Ancestor (LUCA), and how can we use it to develop targets for astrobiological research?
2. Why is carbon important for life, and how widespread are carbon compounds in the Universe?
3. What difficulties are faced when determining a biologic origin for Earth's early life?
4. Why is the presence of organic matter not always an indication of the presence of life?
5. What lines of evidence can be used to argue for the astrobiological investigation of the moons Titan, Encedalus, and Europa?

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