Annu. Rev. Ecol. Syst. 1999. 30:397–420
Copyright © 1999 by Annual Reviews. All rights reserved

ASTROBIOLOGY: Exploring the Origins, Evolution, and Distribution of Life in the Universe

D. J. Des Marais
Ames Research Center, NASA, Moffett Field, California 94035-1000;
e-mail: ddesmarais@mail.arc.nasa.gov

M. R. Walter
School of Earth Sciences, Macquarie University, North Ryde, N.S.W., Australia;
e-mail: gc_walter@hope.ocs.mq.edu.au

Key Words microorganisms, Precambrian, biospheres, solar system, planets, origin of life

■ **Abstract** The search for the origins of life and its presence beyond Earth is strengthened by new technology and by evidence that life tolerates extreme conditions and that planets are widespread. Astrobiologists learn how planets develop and maintain habitable conditions. They combine biological and information sciences to decipher the origins of life. They examine how biota, particularly microorganisms, evolve, at scales from the molecular to the biosphere level, including interactions with long-term planetary changes. Astrobiologists learn how to recognize the morphological, chemical, and spectroscopic signatures of life in order to explore both extraterrestrial samples and electromagnetic spectra reflected from extrasolar planets.

INTRODUCTION

Humanity has long been fascinated with the possibility that life exists beyond Earth. Recently, the discipline of astrobiology has been created to study the origin, evolution, and distribution of life in the Universe, including the prospects for Earth-based life to move beyond its planet of origin. Astrobiology is broadly interdisciplinary because, in its quest to understand the origins and evolution of habitable planets and biospheres, its agenda integrates investigations across the biological, chemical, geological, and space sciences.

So what is novel about astrobiology? What does it offer beyond, for example, earlier programs in exobiology that addressed the origin and early evolution of life and searched for extraterrestrial life? Perhaps the major differences between astrobiology and previous efforts are a more concerted attempt to incorporate related

disciplines into a more tightly integrated program, and the substantial involvement of new communication and information sciences and technologies to achieve this integration. The motivation to move forward now has been triggered by the remarkable array of key recent discoveries. For example, a resonance is developing between studies of the origin of life, molecular biology, and bioengineering. Laboratory demonstrations of self-replication and evolution of biological macromolecules (48), now an integral part of the search for new pharmaceutical products, are being employed to explore the origins of molecular replication. Computational simulations of membrane function that have provided insights into mechanisms of drug activity (76) also explore the roles played by membranes in the earliest cells (protocells). The rapidly developing field of information sciences includes, among its many applications, a mandate to define the properties that emerge from complex systems having many interacting components. Such systems might include regional electrical power grids, spacecraft, or, for that matter, ecosystems and the molecular machinery of cells. Life is an information-rich entity, and its origins are a prime candidate for study.

Recent Discoveries Create a Mandate

New tools for molecular analyses now permit exploration of the enormous diversity of microbial life, and this search has expanded the known range of environments in which microorganisms can thrive. These discoveries also expand the range of habitable conditions within which we might expect to find life beyond the Earth. Life may have started soon after Earth became habitable (82, 84, 70), which encourages the thought that it could also have arisen rapidly elsewhere. Liquid water may have persisted for perhaps hundreds of millions of years in other planets of our own solar system (Mars: 15, Europa? 77). Earth's subsurface harbors habitable environments and an extensive biota (30) based upon nonphotosynthetic sources of energy and perhaps persisting to depths where it encounters its thermal limit (33). Accordingly, Mars (12) and Europa (77) may still have subsurface habitable conditions. Because habitable environments might have developed beyond the Earth and persisted sufficiently long for life to begin, we are encouraged to search for those environments as a prelude to our search for other biospheres.

Astrobiology's mandate arises from discoveries of potential habitats beyond our own solar system. Models for solar system formation indicate that planets probably accompany billions of other stars (99). Such models have been supported by recent discoveries of extrasolar planets (65a). While these newly found planets may not be habitable, they indicate that a broad diversity exists among planetary systems. New methods for finding smaller, more habitable planets are being developed (7), and so we shall soon chart the frequency of habitable planets within that diversity of solar systems.

Astrobiology will lead inevitably to a deeper understanding of life itself. Current definitions of life focus upon its key properties (71) and tend to reflect the

particular perspectives of their authors. For example, molecular and cell biologists cite the ability of cells to harvest energy and metabolize, to replicate and to evolve. Those with an ecological perspective emphasize that ecosystems are fundamental units of life. Advocates of the Gaia Hypothesis mandate that nothing less than the entire biosphere-Earth system is the most fundamental unit of life (63). Our search for life beyond Earth clearly compels a scrutiny of our definition of life, as that definition establishes the criteria by which life might be identified elsewhere. If extraterrestrial life is indeed discovered, the diversity of known life-forms will increase. For example, life as we know it utilizes only a small fraction of the possible organic compounds. It seems likely that alien life forms will have explored alternative possibilities.

Key Components of the Discipline

Operationally, astrobiology integrates key research disciplines into a program that combines technology development, remote observation (space missions), model building, and the extensive involvement of educators and the public. This agenda addresses the following three canonical questions: How does life begin and develop? Does life exist elsewhere in the Universe? What is the future of life on Earth and in space? This review emphasizes the first two questions, although the three are interdependent. For example, an improved understanding of the morphological, chemical, and isotopic traces of early life on Earth (first question) prepares us to analyze samples returned from Mars and elsewhere (second question). Studies of habitable environments and the potential for life beyond Earth (second question) help us chart our future (third question). The search for past and present habitable environments on Mars will locate the resources necessary to sustain future human exploration. The size and scope of this agenda necessarily make it an international endeavor. The requisite scientific and technical expertise spans international borders, and multigovernmental support will be essential for the long-term exploration of the full range of extreme environments on Earth and beyond.

Astrobiology recognizes that students and the public are essential ongoing participants. The search for the origins and distribution of life in the Universe has great religious and philosophical significance. The universal human imperative to explore will both strengthen and shape the effort. Our stewardship of the planetary environments we explore will reflect the ethics of our global society. Public health concerns will arise during, for example, the return of samples from Mars, mandating a plan of exploration and research that reflects public input.

Astrobiology is fundamentally important for education. It motivates students to acquire scientific and technical skills that create a broad array of economically important careers. Astrobiology strengthens linkages between science, technology, and the humanities, creating an integrated view of our world that will be beneficial for helping to define the roles that future generations will play as stewards of our global environment and its resources.

Life in the Universe: The Basic Issues

Astrobiology depends critically upon our understanding of the processes that control the origin and evolution of both habitable environments and life. The range of relevant issues are succinctly highlighted by the Drake Equation (80), which assesses the distribution of intelligent, communicative civilizations in our galaxy, as follows:

$$N_C = R_S f_P n f_L f_I f_C L, \quad 1.$$

where N_C is the number of civilizations in our galaxy with whom we might communicate, R_S is the rate of formation of stars in the galaxy, f_P is the fraction of stars that have planetary systems, n is the average number of habitable planets within a solar system, f_L is the fraction of habitable planets on which life arises, f_I is the fraction of biospheres that developed intelligent species, f_C is the fraction of intelligent species that are interested in communicating with other civilizations, and L is the average lifetime of a civilization.

If this assessment is broadened to include all biospheres in our galaxy, a "Biosphere Equation" might take the following form:

$$N_B = R_S f_P n f_L L_B, \quad 2.$$

where N_B is the number of biospheres in our galaxy, and L_B is the average lifetime of a biosphere. Clearly all of these terms are important for a comprehensive assessment of life's cosmic distribution; however, astrobiological research focuses particularly upon the latter terms of these equations (from the term "n" on to the right), as these directly address planetary habitability and life. The sections that follow summarize how our current understanding of these factors might shape the research agenda.

RESEARCH AND EXPLORATION

Formation and Distribution of Habitable Planets

Abundance of Planetary Systems

The view that planetary systems are abundant has been strengthened recently by discoveries of several protoplanetary nebular disks in star-forming regions (11). Perhaps one quarter to one half of very young stars have disks similar to the one from which our own solar system formed. The term "f_P" in the above equations might possibly be as large as 0.2 to 0.5. Extrasolar planets are now being discovered at a rapid rate (see 65a), although these are not Earth-like and habitable. This is because the currently most successful detection method identifies planet-induced oscillatory shifts in the star's spectra and thus is most sensitive to closely orbiting planets that are about Jupiter-size or larger, probably gas-rich, and thus not habitable. Although the apparent multitude of solar nebulae indicates that Earth-like planets might be widespread, the most immediate benefit of their discovery is

that we can now study diverse examples of the planet-forming process. Someday we will understand in detail the context for the formation of planets, including Earth-like ones, and thus quantify the "f_P" and "n" terms in the above Drake and Biosphere Equations. Such an endeavor is a key focus of NASA's new Origins Program (7).

Controls on the Habitability of Planetary Surfaces

A rigorous search for life should include a strategy for locating, describing, and modeling habitable planetary environments and their evolution. The life-enabling commodities that most sharply distinguish Earth from other planets in our solar system are liquid water and the climates that maintain it (66). We have not yet located *any* liquid water beyond Earth, although it is anticipated. Mars and Europa are exploration targets in part because liquid water apparently once existed at or near their surfaces. A planetary habitat also must provide biologically useful sources of energy (46, 95), chemical nutrients, and a degree of environmental stability that allows life to arise and evolve at a rate sufficient to survive environmental changes that do occur.

Planetary habitability depends upon several factors. One is the amount of sunlight received by a planet; this has been used to delineate the habitable zone (43), namely, that region around a star within which planetary surfaces are habitable. Because the luminosity of main-sequence stars slowly increases, such a habitable zone will uniformly migrate away from the star. The region that sustains a habitable zone continuously during the history of the solar system is called the continuously habitable zone (40).

Planetary processes also influence the habitable zone. Planetary surface temperatures reflect the energy balance of the atmosphere, which is influenced strongly by greenhouse gases (40, 55). Water vapor achieves most of the greenhouse warming on Earth today. However, CO_2 also contributes substantial greenhouse warming, and it also has played a long-term role in stabilizing Earth's climate and surface temperature (50). Earth's interior thermal activity (volcanism and tectonics) adds CO_2 to the oceans and atmosphere, and CO_2 is removed via aqueous rock weathering, water transport, and burial in sediments as organic matter and carbonates. Climate regulation is achieved because the processes that remove CO_2 are temperature-dependent. Temperature increases are offset by greater rates of removal of this greenhouse gas from the atmosphere. As temperatures decline, slower removal rates allow Earth's thermal sources of CO_2 to increase atmospheric levels of CO_2 and thus enhance greenhouse warming.

Greenhouse gases have strongly influenced the extent and the evolution of the habitable zone (55). Because the ancient sun was less luminous, Venus might have once enjoyed a habitable surface environment. However, CO_2-water–mediated climate regulation eventually failed on Venus because increased solar heating allowed water vapor to invade the Venusian stratosphere and then escape to space (54). With the loss of aqueous processes for removing CO_2, "runaway greenhouse" conditions forever trapped Venus in an uninhabitably hot environment. Mars also

illustrates the role of planetary processes. Mars' surface environment is now uninhabitable (19), owing principally to low temperatures and the absence of liquid water. Because the ancient sun was less luminous, it would follow that Mars' early surface environment was even colder than it is today. However, evidence of elevated erosion rates, rivers, and standing water on early Mars indicates that its early environment was apparently wetter and at least somewhat warmer (15, 39). This is possible if, early in Mars' history, thermal processes added CO_2 more rapidly to the surface environment than they do today. As the interiors of rocky planets cooled because radioactivity-based heating declined, volcanism and other thermal processes delivered less CO_2 to the surface environment (23). The surfaces of both Venus and Mars once might have been habitable; thus, planetary processes might have sustained a habitable zone in our early solar system that was wider than it is today.

For astrobiology, a more rigorous assessment of the habitability of Mars' surface environment over time is necessary to define better the evolution of our solar system's habitable zone and continuously habitable zone. The physical and chemical composition of Mars' ancient crustal materials must be assessed (68). This characterization is a major objective of NASA's Mars Surveyor Program, which has been chartered to assess Mars' climate history, its past and present potential to support life, and its resources for future human exploration (68). All of these objectives require that the abundance and physical state of water be assessed. This program combines orbital mapping (1), surface reconnaissance, and a series of sample returns.

Extrasolar Habitable Zones and Planets

As we explore habitable zones around other stars, we must consider the range of stellar sizes as well as multiple star systems. Larger stars burn much more brightly and evolve more quickly through their main sequence phase, and therefore their habitable zones are shorter lived (55). For example, a star 0.5 times as massive as our sun (0.5 M_S) dwells on the main sequence for much longer than ten billion years; a star 1.5 times as massive as our sun (1.5 M_S) dwells there for less than two billion years. Perhaps two thirds or more of the stars within the size range 0.5 M_S to 1.5 M_S occur in binary and multiple star systems (27). It was once believed that planetary orbits would be unstable in such systems. However, stable planetary orbits can exist either at radii that are more than five times the distance between binary stars (external binary: planet orbits the center of mass of both stars), or at radii that are less than 20% of the distance between binary stars (internal binary: planet orbits only one star) (75). Perhaps 5% of external and 50% of internal binary systems, respectively, might support a habitable zone (55). Because stars in the mass range 0.5 M_S to 1.5 M_S are so abundant, circumstellar habitable zones may be widespread.

We can apply to extrasolar planets the same factors affecting climates in our solar system. The distance between a star and its habitable zone increases with stellar size and luminosity. The habitable zones of a 0.5 M_S and a 1.5 M_S star are

centered at 0.3 A.U. (one astronomical unit is the distance from Earth to our sun) and 2.5 A.U., respectively (55). Current models predict that terrestrial-like planets indeed develop frequently between 0.3 A.U. to several A.U. (99).

Giant planets can significantly affect the habitable zone. Recent discoveries of Jupiter-sized planets having very small orbits (65) indicate that gas giants, which form farther out in the nebular disk, can migrate inward (61), perhaps sweeping up terrestrial-like planets in their path. We cannot yet determine the relative abundances of more stable solar systems like our own, versus those where gas giant planets have spiraled inward. Giant planets also can significantly affect the delivery of planetesimals to the inner solar system. For example, a Jupiter-like planet greatly reduces the flux of comets (98). In simulations where Jupiter and Saturn were replaced by Neptune-class bodies, the comet flux from the Kuiper belt (the region beyond the planet Pluto) increased by roughly three orders of magnitude! Large Jupiter-sized planets shield inner habitable planets from a rain of environmentally disruptive impactors. Are such shepherd planets necessary for biospheres to begin and develop? If so, then the need for a shepherd planet might lower our estimates of the total number of continuously habitable solar systems.

Astrobiologists will benefit from the efforts of astronomers to map the distribution of various types of solar systems. Soon, even Earth-sized planets will be found using the photometric method for detecting the reduction in starlight that accompanies the transit of planets in front of their stars. Interferometric astronomical techniques that greatly reduce the light from the star might capture family portraits of extrasolar planetary systems within the next decade or two (7). Evidence of atmospheric CO_2 and abundant water vapor, hence habitability (24), seems obtainable from the infrared spectra of Earth-like planets. The first detection of an extrasolar habitable planet will be a major step toward discovering the first extrasolar biosphere.

Subsurface Habitable Environments

Earth's subsurface environments (aquifers, oil fields, and hydrothermal systems) harbor an extensive biota that can be partially or totally independent of photosynthetically derived energy (30). Life might persist to depths where it encounters its thermal limit, and subsurface biomass might equal or even exceed the biomass at Earth's surface (33, 34). Abundant subsurface life is significant for astrobiology because it implicates additional planets and environments that previously had not been considered seriously as sites for life.

For example, the surface of Mars is currently uninhabitable (19); therefore strategies to search for life once focused principally upon a search for fossil evidence in ancient terrains (66). However, because life can pursue a subsurface chemosynthetic life style (12) and because subsurface martian aquifers might be sustained by geothermal heat (20) or by residual heat from impacts (73), life may have persisted after the surface environment became hostile. Have subsurface habitable environments survived until today? One approach is to examine all martian meteorites for additional evidence of hydrothermal activity (60). Inactive

thermal spring sites should be explored as part of the Mars Surveyor Program. Hydrothermal mineral deposits might reveal when these springs were active, what the conditions were, and whether life existed there (95). A third approach is to search directly for subsurface aquifers. In the Mars Surveyor mission scheduled for launch in 2003, an Italian geophysical sounder may search at crustal depths of hundreds of meters to kilometers.

Liquid water might exist within planetary satellites such as Jupiter's moon Europa (77), owing to the deposition of energy by tidal stresses. Europa's sparsely cratered landscape indicates that its surface remains active. Satellites in the Jovian system fall completely outside the habitable zone defined according to the availability of solar energy (43). An orbiter has been proposed to search for evidence of a subsurface "ocean" using geophysical methods (18). Subsurface chemical processes might be revealed by, among other things, the variably colored deposits decorating the linear fracture systems that criss-cross Europa's surface.

Can subsurface Europa-like biospheres be discovered in extrasolar planets? Such a search seems extraordinarily difficult, given the great distances to these planets, the subtlety of evidence for subsurface habitability, and the extreme difficulty in imaging Europa-like planetary satellites next to planets as large as Jupiter. One perspective on this challenge is offered by comparing biospheres driven by photosynthesis with those driven only by energy sources for chemosynthesis. Detecting even extrasolar biospheres sustained by photosynthesis will be extraordinarily challenging, especially if these biospheres are not accompanied by an abundant atmospheric inventory of O_2 (7, 24). If Earth's biosphere depended only upon chemical energy derived from hydrothermal activity and weathering, global productivity levels would be less than one percent of the levels supported by photosynthesis (26). Detecting an extrasolar biosphere that lacks photosynthesis seems impossible in the forseeable future.

The Origins of Life

How Does Life Begin?

Phrasing this question in the present tense reflects the hypothesis that the origin of life is a deterministic process, that life might begin wherever and whenever the necessary environmental conditions occur (71). Thus, the origin of life might be an ongoing process in the Universe; indeed, perhaps someday it will be an ongoing process in research laboratories engaged in assembling model protocells. Historically, origin of life research has focused upon synthesizing organic monomers in reducing atmospheres and examining their assembly into structures ("proteinoids") and macromolecules (i.e. peptides and polynucleotides) whose roles embody life's most diagnostic properties, namely, its ability to replicate and to evolve (69). Following naturally from the traditional theory that life arose within a reducing organic-rich aqueous broth, the earliest cells were assumed to have been fermentative heterotrophs (69). A long-standing paradox has been that the functions performed by the nucleic acid–protein translation apparatus were

assumed to be essential for life to begin; yet this apparatus seems too complex to have arisen in the prebiotic milieu. The discovery of "ribozymes" (16) offers one potential solution to this paradox because both information storage and catalysis might have been achieved by a single class of compounds early in life's history. Even so, it seems extraordinarily difficult for ribozymes to have been synthesized in the absence of cellular life.

Current research explores in more detail the potential roles played by environmental conditions in prebiotic evolution and the origin of life. Some studies have recognized that prebiotic chemical processes required sustained energy sources that were actually available in the environment. For example, Wächtershäuser (93) developed a model whereby prebiotic evolutionary biochemistry was driven by oxidation/reduction reactions involving iron and sulfur species. Such energy-rich species occur abundantly in hydrothermal systems within planetary crusts. Amphiphilic compounds (lipids) assemble spontaneously into vesicles that resemble cellular membranes and that create chemical microenvironments favorable for the development of "protometabolism" (21). Similar amphiphilic compounds have been identified in meteorites. The increase in complexity of these molecular systems imparts emergent properties (structures, specific molecular interactions) that probably led to life's origin but that require specific attention by theorists and experimentalists. This relationship between theories of complexity and the origin of life has been explored (56).

Origin of Life Within a Planetary Context

Astrobiology contributes to research on the origin of life by addressing both theoretical and experimental approaches in the context of those planetary environments, be they on Earth or elsewhere, that favored the origin of life. For example, extraterrestrial organic matter from cosmic dust and ice rained down on the early Earth (17). If this external supply was abundant only early in a solar system's history yet was essential for life to begin, it imposes a key constraint on life's distribution in the cosmos. Perhaps planetary processes also created prebiotic organic matter. A mildly reducing early atmosphere, sustained by thermal processes acting upon a more reduced crust and upper mantle, might have sustained prebiotic organic synthesis (53). Hydrothermal systems may have hosted prebiotic organic synthesis (78, 87). A cold early surface environment would have allowed prebiotically important species to survive and accumulate (3). It therefore becomes important to define the nature of early habitable planetary environments on Earth and elsewhere (45, 79). Assessing the relative importance of various organic sources should at least partially constrain the range of plausible prebiotic scenarios.

The Value of a Second Example of Life

There is a spectrum of opinion as to whether the origins of complex living systems was a directed (deterministic) process or was more random (driven by contingency). For example, perhaps chance plays a role, but only within limits set by the physical and chemical properties of life (22). Evolution looks random when the

whole range of species is viewed, but trim the tree of life "of this outer diversity and you are left with a stark trunk delineated by a relatively small number of major forks...." While there is plenty of scope for evolution on another planet to have taken different pathways, "certain directions may carry such decisive selective advantages as to have a high probability of occurring elsewhere as well..." (22). In contrast, the process of evolution may be based upon an infinite number of contingent events (35). That is, each new species evolves when a local environmental opportunity exists, and others become extinct for any one of many causes. Thus, if we were able to "rewind the tape of life and replay it," we would get a different result every time. One major barrier to resolving these contrasting views is that we know only one example of a tree of life. If we had other examples, we would not have to argue in the abstract; we could directly analyze the degrees of similarity between them and from that begin to discern general principles of evolution, including the role of pure chance. This circumstance creates a powerful scientific argument for looking for life elsewhere.

Accordingly, we must broaden the agenda beyond attempting to recreate precisely the events leading up to the origin of life on Earth. To the extent that the earliest phase of our existence was driven by contingency, including the destruction of the earliest fossil record, we are unlikely ever to know the exact history of our own origins. Furthermore, laboratory studies on a diverse array of molecules might reveal principles of molecular evolution that are otherwise too subtle to discern through studies restricted to our own biomolecules. An effective search for life elsewhere also demands a broader approach. If life beyond Earth obeys similar principles but uses different molecules, we must devise more flexible strategies to detect it.

Even with the need for a diversity of studies, a focus upon understanding how the first protocellular structures were assembled remains a centrally important goal. The spontaneous self-assembly of amphiphilic molecules into vesicles may have been an important part of this process (21), as it perhaps created favorable chemical gradients as well as microenvironments. However, the processes leading to the first energy-harvesting metabolism (71, 93) and the mechanisms for self-replication also merit attention. The development of such systems leads to dramatic increases in complexity and information content, increases that were made possible by inputs of chemical energy. Theoretical and experimental models for the coupling of such energy to the emergence of molecular complexity lie at the heart of this effort. Also, laboratory-based molecular systems that are capable of self-replication and evolution are excellent testbeds for exploring prebiotic evolution.

Evolution on Molecular, Organism, Ecosystem, and Biosphere Levels

Microorganisms deserve particular attention in astrobiology because our biosphere was exclusively microbial for more than three quarters of its history (82) and because microorganisms continue to dominate our biosphere. Still, only a small

percentage of all molecular biologists and paleontologists are specialists in microbial evolution. However, new methods for identifying, manipulating, and analyzing biomolecules and fossiliferous rocks allow microbial life to be explored from molecular to global scales. Our knowledge of the diversity of the microbial world is still very incomplete (74). An objective search and analysis of natural microbial ecosystems will identify the environmental and biological drivers of evolution and reveal how life diversified and adapted to extreme conditions. If the full range of Earth's habitable conditions can be precisely defined, it will help to identify more fully the range of environments to be explored beyond Earth.

The early record of our biosphere exists in two forms. One is the living record of life preserved within the structure and function of its biopolymers and metabolic pathways. For example, the sequences of monomers in highly conserved biopolymers reflect their descent from their molecular ancestors (100, 101). The second record is the remnants within rocks of fossilized cells, ecosystems, and chemical and isotopic compositions that reflect biological activity.

The Living Record of Early Life

The increasing ease of sequencing macromolecules and the rapid growth of sequence databases are creating unprecedented opportunities for evolutionary studies. However, these databases have been developed principally for their biotechnological applications; therefore, many microorganisms having great potential value for evolutionary research still await study. Furthermore, evolutionary interpretations of sequence data require specialized software and groups of investigators, both currently in short supply. Such teams could examine how genes and gene families are created (via gene duplication), rearranged within genomes, and transferred between organisms.

Studies of molecular phylogeny should be extended to include additional key biomolecules, particularly those enzyme systems that exerted profound impacts upon the environment. For example, enzymes for CO_2 assimilation arose early in evolution and very likely played key biogeochemical roles on the early Earth (32, 97). Accordingly, the phylogeny of ribulose bisphosphate carboxylase-oxygenase (RUBISCO) has been studied extensively. However, several other CO_2-assimilating enzymes merit comparable attention, for example, those associated with the reverse-TCA cycle, acetyl coenzyme-A pathway, etc. Genetic analyses might identify key "nodes" within the phylogenetic trees of these enzyme systems, for example, a radiation of enzyme lineages. It is important to identify the factors that contributed to such evolutionary events. Perhaps environmental changes played a role in many cases.

Understanding how microbial life adapts to environmental gradients and extremes is essential not only for understanding evolution, but also for defining the limits of habitable conditions to be sought beyond Earth. Environmental parameters include temperature, availability of chemical and/or light energy, water potential, solute composition (pH, nutrients, toxins, etc), and environmental variability. Adaptation to environmental gradients and variability has contributed

at least in part to diversity. For example, "guilds" of thermophilic cyanobacteria apparently have diversified along thermal gradients in hot spring streams (96). Thermophilic microorganisms have stabilized their molecular machinery against the challenges of high temperatures (10, 91), but the details of these adaptations by various cellular "subsystems" are still poorly known.

Modern microbial ecosystems can help us interpret both the living and rock records of our biosphere. Many types of fossils (morphological, chemical, isotopic) are emergent properties of ecosystems. For example, stromatolites, which are macroscopic laminated forms built by trapping and binding of sediment by microbial mat (biofilm) communities, are the most ancient and widespread morphological evidence of pre-Phanerozoic life (94). Stromatolite morphology probably arises from complex interactions that occur between microbial mats and their environment (38, 94). The microenvironments within microbial mats reflect the structure and function of these ecosystems, for example, the sharing of wavelengths of light (47) and the exchange of metabolic substrates (14). Mat microenvironments can differ markedly from their surroundings and thereby shape both the adaptation and the evolution of the microorganisms as well as the nature of the microbial remains that become incorporated into the fossil record (88).

The Geologic Record of Early Life

Our biosphere has altered the global environment by influencing the chemistry of those elements that are important for life–carbon, nitrogen, sulfur, oxygen, phosphorus, and transition metals such as iron and manganese. Such interactions can be viewed as part of a system of "biogeochemical cycles." Such cycles are networks consisting of elemental reservoirs (within the biosphere, atmosphere, oceans, crust, and mantle) that are linked by geological, biological, and other environmental processes (36).

For example, the coupling of oxygenic photosynthesis with the burial in sediments of photosynthetic organic matter has increased the oxidation state of the oceans and atmosphere and also created highly reduced conditions within sedimentary rocks that have extensively affected the chemistry of other elements (31). Nonbiological processes have also influenced the course of biological evolution. For example, the decline of volcanism during Earth's history has decreased the flux of reduced chemical species that reacted with photosynthetically produced O_2 (51, 58). Therefore, atmospheric O_2 levels were destined to increase. To the extent that the development of modern aerobic bacteria, algae, and multicellular life has certain minimum O_2 requirements, the long-term net accumulation of photosynthetic O_2 via biogeochemical processes has influenced our atmosphere and biosphere profoundly (58).

Microorganisms have also affected the precipitation of minerals (5), thereby altering Earth's crust and creating a record of microbial activities in ancient sediments. For example, the precipitation of carbonate in the marine environment has apparently come under stronger biological control over the past two to three billion years (37). One important aspect of mineral formation lies in the tendency

for patterns of precipitation that develop at the molecular or microscopic level to be propagated to macroscopic scales (millimeters to centimeters or larger; 44). Perhaps the macroscopic morphologies of some carbonate stromatolites originated as microscopic phenomena whose biological control is uncertain (38). To the extent that sulfidic ores form as a consequence of the accumulation of sedimentary organic matter and biogenic sulfides, processes operating at the microscale can create sulfide ore bodies that can attain kilometer-scale dimensions. Understanding such mineralogical effects is important, not only for understanding the evolution of our own biosphere, but also for locating and interpreting fossil evidence of life on Earth and elsewhere.

Interactions between the long-term evolution of the biosphere and its environment can be explored by focusing upon time intervals that witnessed profound environmental changes. For example, atmospheric O_2 levels apparently rose dramatically between 2.2 and 2.0 billion years ago (42). Can the biological consequences of this event be identified in the living molecular biological record? Major glaciations in the late Proterozoic (800 to 600 million years ago) appear to be correlated with major excursions in the diversity of eukaryotic plankton (41, 92). Can a cause-and-effect relationship be demonstrated?

Our own biosphere would share one important circumstance with other biospheres. Silicate-rich planets (Venus, Earth, and Mars) experience evolutionary trends that are most similar early in their history. For example, the inner planets of our solar system all experienced an early heavy meteoritic bombardment, similar styles of formation and chemical evolution of the early crust, a long-term decline in volcanic activity, and a long-term increase in solar luminosity (see summary in 26). To the extent that similar geological processes have affected the evolution of all habitable planets, those aspects of our own biosphere's history should assist our search for extraterrestrial life.

Recognizing Signatures of Life Beyond Earth

The Challenge

How will we recognize life elsewhere? The discovery of habitable environments beyond Earth would indeed set the stage for learning whether we are truly alone in the Universe. However, habitable environments are geologically and climatologically active places. How can we distinguish between this nonbiological activity and life? We can start with the following basic definition of life: One, life maintains metabolism, that is, a network of chemical reactions that harvest energy for the biosynthesis and maintenance of cellular components; two, life is capable of self-replication; and three, life is capable of Darwinian evolution. This definition lists a few key properties of life, more specifically, its key processes. Such a definition aids our search for life principally to the extent that we can directly observe biological processes. Accordingly, the Viking life-detection experiment was designed to establish life's presence on Mars specifically by observing processes of metabolism and growth (reproduction) (57). However, most astrobiologists

agree that the Viking mission did not deliver the final verdict about the history of life on Mars. Our approach cannot be restricted only to observing biological processes directly. The discussion that follows summarizes additional approaches for broadening the search for life on Mars and beyond.

A more effective search for evidence of life addresses the following circumstances that make a Viking-like approach inconclusive and/or impossible:

1. It is possible to detect certain chemical consequences of a biosphere's activity, but it is not possible to observe organisms directly. One hypothetical example is a martian biosphere that resides several kilometers beneath the surface and is currently inaccessible but that alters the trace gas composition of the atmosphere. A second example is a biosphere on a distant extrasolar planet detectable only through its effect upon the composition of its atmosphere (59).
2. Extraterrestrial life might differ substantially from life on Earth. If living organisms existed on the martian surface but simply did not respond to the particular incubation experiments deployed by Viking, they clearly could have escaped detection (57). The nondetection of organic compounds by the Viking mass spectrometer did set upper limits on the quantity of organisms present, but scenarios can be envisioned in which even traces of Earth-like life might have escaped detection (8a). Because biological diversity in the Universe probably exceeds the diversity on Earth, our search strategy must be appropriately broadened.
3. Life has become extinct, or it was once active in a sample or landing site and has since retreated elsewhere. This circumstance compels us to become paleontologists because we must search for fossil evidence of life. A recent example of this approach has been the examination of the martian meteorite ALH84001 (67) and the claim that an array of morphological, chemical, and mineralogical features collectively indicate the presence of life on early Mars.

The Universal Properties of Life Guide Our Search

It is useful to consider those attributes that are universal for life on Earth and thus potentially form the basis for recognizing biological indicators of life ("biomarkers") elsewhere. In his book *Beginnings of Cellular Life*, Morowitz delineated the following 15 universal features of life (71):

1, 2. "*All life is cellular in nature. There is a universal type of membrane structure used in all biological systems.* A cell is the most elementary unit that can sustain life. The chemical reactions that produce the molecules of living organisms take place in cells. Every cell is surrounded by a selectively permeable membrane barrier that keeps it separate from other cells and from the environment." Because cellular forms can be preserved upon burial in sedimentary rocks and yield diagnostic microfossils, the cellular habit has created a key category of biomarker for detecting life's former presence (85).

3. "*The water content of functioning living forms varies from 50% to over 95%.* The chemistry of life is carried out in aqueous solutions or at water interfaces." Cells can survive the removal and restoration of cellular water, but water is essential to cellular function. This attribute reiterates the necessity of liquid water for ensuring life's long-term survival; therefore we should search the cosmos for evidence of liquid water.

4. "*The major atomic components in the covalently bonded portions of all functioning biological systems are carbon, hydrogen, nitrogen, oxygen, phosphorus and sulfur.*" Accordingly, enrichments of phosphorus or organic carbon and nitrogen in terrestrial geological deposits have been interpreted to be strong indicators of biological activity. Certain sulfide ore deposits might also owe their origin to biogenic organic matter.

2, 5, 6, 7, 8, 9, 11. "*There is a universal set of small organic molecules that constitutes a large portion of the total mass of all cellular systems. There exists a universal network of intermediate reactions such that the metabolic chart of any extant species is a subset of the universal chart. Most of the nonaqueous portion of functioning biological systems consists of proteins, lipids, carbohydrates and nucleic acids. The flow of energy in the biosphere is accompanied by the formation and hydrolysis of phosphate bonds. Every replicating cell has a genome made of deoxyribonucleic acid.... All growing cells have ribosomes.... The translation of information from nucleotides [to proteins] takes place through specific activating enzymes and transfer RNAs. There is a universal type of membrane structure used in all biological systems.*" In contrast to the enormous diversity of organisms, the variety of biochemical pathways, metabolic intermediates, and classes of macromolecules and membrane lipids universally employed by life is remarkably small. Perhaps for purposes of functional efficiency, life has restricted itself to a very small subset of the near-infinite array of organic compounds that might exist. Therefore, the "unusually" high relative abundance of specific organic compounds in an environmental sample might by itself be highly diagnostic evidence of a biogenic origin of those compounds.

12. "*Biological information is structural.*" If some organisms are chilled to near-absolute zero or are desiccated in a way that preserves the structural integrity of their membranes and macromolecules, they can revive upon returning to normal conditions. This observation indicates that life on other planets might survive periodic freezing and/or desiccation; therefore we should broaden our search for life to include environments that are only periodically habitable.

13. "*Those reactions that proceed at appreciable rates in living cells are catalyzed by enzymes.*" One of life's hallmarks is its ability to accelerate organic chemical reactions, which, in the absence of life, are typically quite sluggish. Accordingly, for example, life can accelerate a variety of oxidation-reduction reactions in nature in order to harvest chemical energy. Biologically mediated interactions between organic and inorganic compounds can affect the deposition of minerals (carbonates and transition metal oxides and sulfides) in ways that create mineralogical evidence of life (5). Characteristic isotopic patterns among carbon

and sulfur species reflect the enzymatic acceleration at ambient temperatures (0 to 30°C) of oxidation-reduction reactions that, in the absence of life, would proceed at significant rates only above 200°C (25). Such "biogenic" isotopic patterns have been preserved in ancient sedimentary rocks.

14. "*Sustained life is a property of an ecological system rather than a single organism or species.*" More than one species are necessary for primary production and organic degradation and nutrient regeneration. Such cycling of chemical constituents often seems required to maintain the flow-through of energy at the rate needed to sustain the ecosystem. Communities of organisms (biofilms) can create chemical products (minerals) and physical features (sedimentary structures) that are much larger than individual cells and/or that persist long after biological activity has ceased. For example, iron oxides and sulfides can indicate previous biological activity (29). Sedimentary microfabrics such as laminae and larger structures such as stromatolites can indicate the former presence of biofilms (94).

15. "*All populations of replicating biological systems give rise to altered phenotypes that are the result of mutated genotypes*. This is the empirical generalization that is a sine qua non for the process of evolution as well as the science of genetics." Progressive changes in fossil biomarkers (fossil morphology) over time can record aspects of the processes of biological evolution.

Biomarkers An effective search for extraterrestrial life must create more effective means for recognizing and interpreting the full range of biomarkers, as mentioned above. Summarizing the foregoing discussion, categories of biomarkers that can survive in geological deposits, or else be detected remotely, include the following:

1. Cellular remains
2. Textural fabrics in sediments that record structure and/or function of biological communities (e.g. stromatolites; 94)
3. Biogenic organic matter, including hydrocarbons
4. Minerals whose deposition has been affected by biological processes
5. Stable isotopic patterns that reflect biological activity
6. Atmospheric constituents whose concentrations require a biological source.

Precambrian paleontology offers a rich legacy of experience in the study of microbial biomarkers, including the effects of biological processes upon the atmosphere (42, 83, 85).

Other Biospheres in Our Solar System?

Mars

The debate surrounding the study of martian meteorite ALH84001 offers a recent example of the issues regarding the effective use of biomarkers to search for

evidence of life beyond Earth. Citing an array of significant observations of ALH84001, a martian meteorite recovered from Antarctica, McKay et al (67) proposed that martian life existed, at least at the time that the carbonate formed in the meteorite. A brief summary of the ensuing debate follows.

Establishing Whether Habitable Conditions Existed The meteorite ALH84001 is an igneous rock; therefore, it formed at temperatures that were too high for life. However, it contains disc-shaped carbonates that subsequently developed along fractures and that contain the features cited as evidence for life (67). Did these carbonates form under habitable conditions—namely, with liquid water and cooler temperatures (known organisms on Earth are restricted to $<113^{\circ}$C; 10)? Unfortunately, estimates of the temperatures of formation of these carbonates are poorly constrained, in part because the meteorite had a complex history (90) that included multiple heating events due to meteorite impacts. Thus, it is uncertain whether geochemical estimates of temperature reflect the original conditions of carbonate formation or some later event. Also, not enough is known about the broader geological context of the environment in which these carbonates formed. For example, because the composition of the fluids that deposited the carbonate (60) is uncertain, one can propose either low temperatures of formation assuming one fluid composition or high temperatures ($>200^{\circ}$C) assuming another composition. A key objective for astrobiology is to ensure that future missions to Mars acquire samples that provide firmer constraints for early, potentially habitable conditions.

Cell-Shaped Objects Perhaps the most visually compelling life-like features in ALH84001 are the submicron cell-shaped objects that resemble microorganisms. However, the sizes of many of these objects seem too small to accommodate the biochemical machinery required for free-living microorganisms (64, 72). Some cell-shaped objects may be minerals oriented crystallographically along carbonate substrates (13). Cell-shaped objects have been reported in lunar meteorites found in Antarctica (86), even though these rocks never experienced habitable conditions on the Moon. These observations highlight the challenge to avoid terrestrial contamination in samples returned to Earth and, furthermore, to develop diagnostic criteria (internal morphology and composition of cell-shaped objects) that provide definitive interpretations of the origins of cell-shaped objects.

Organic Matter The observation of polycyclic aromatic hydrocarbons (PAH) in ALH84001 (67) raised two issues: Did these compounds come from Mars, and are they biogenic? The absence of PAH from the external fusion (melt) crust of the meteorite indicates that they were not acquired on Earth (67), whereas their close association with the carbonate globules and rims indicates that they once resided on Mars (28). However, PAH also occur in interplanetary dust particles and in chondritic meteorites (8), meteorites that were probably delivered to the martian surface in the past. It is not possible to interpret from their structures

whether these PAH were derived from biogenic matter. However, other organic compounds in ALH84001 are clearly terrestrial contaminants (4, 49). The challenge for astrobiology, therefore, is to avoid organic contamination by terrestrial organic matter and also to devise criteria for determining the mechanisms for the synthesis of extraterrestrial organic matter (biological or abiotic?).

Minerals The structure and/or composition of some minerals can be influenced by biological activity; therefore, they can become indicators of life (6). Multiple populations of magnetite (Fe_3O_4) have been reported in the carbonate globules of ALH8400l (89), and these might reflect multiple mechanisms of formation. For example, some have clearly grown simultaneously with the surrounding carbonate (13, 9) and therefore could not have developed inside a microorganism. Others, upon their removal from the carbonate for analysis, revealed shapes otherwise reported only from bacteria (89). Minerals have the potential to reveal life's former presence in samples that have lost other evidence. However, the relationships between the processes of formation and the composition and shapes of potentially biogenic minerals requires much further study.

The Geological Context The ALH84001 debate illustrates the need to develop further the basis for interpreting potential biomarker features in extraterrestrial materials. It also indicates that, during our campaigns to return samples from Mars and elsewhere for astrobiological study, we must constrain as much as possible our interpretation about the geological context of those samples. The remarkable preservation of minerals and morphology at the nanometer scale in ALH84001 indicates that the martian crust has indeed retained, at least at some localities, a rich storehouse of information about the history of its earliest environments, environments that might have witnessed a second example of life in our solar system. The now-international Mars Surveyor Program is challenged to continue the exploration of that storehouse (68), through a series of missions to conduct global surveillance, rover-based exploration of the surface, and sample return.

Europa

Many of the considerations outlined for Mars exploration are relevant also to a search for evidence of life on Europa, the satellite of Jupiter. Materials (ice, etc) that might have experienced a habitable subsurface Europa "ocean" should be examined for evidence of life. A search for evidence of life within Europa might be conducted in several ways. An orbiting IR spectrometer could analyze surface ices for evidence of organic components that emerged from within the planet. A lander might examine surface ices locally and in more detail. A flyby orbiter could, as it approaches, release an impacting projectile and then, after it orbits Europa, it could sample ejected materials for return to Earth. As with Mars, we are challenged to distinguish between the formation of minerals and organic components by nonbiological versus biological processes.

Biospheres in Other Solar Systems?

Direct Observations are Challenging but Essential

Although a planet's presence can be inferred by indirect means (discussed above), the remote search for evidence of life requires direct observation of photons from a planet. Viewed from distances of several light-years, a habitable planet would appear quite faint in the visible wavelength range (10^{-10} times as bright as its star), yet extremely close (about 0.1 second of arc) to the star (59). Such a planet appears relatively brighter in the mid-infrared (MIR) range (10^{-7} to 10^{-6} times as bright); however, a MIR telescope must be located above Earth's atmosphere in order to avoid interferences from H_2O in Earth's atmosphere. Optical interferometry can image the planet by filtering out direct starlight (2, 7). Within the next two decades, space-based interferometric telescopes might obtain low-resolution MIR (6 to 18 μm) spectra of the atmospheres of habitable planets located within 20 parsecs (light-years) (7).

Spectroscopic Indicators of Life

The challenge to detect an extrasolar biosphere is therefore to identify, within MIR spectra of extrasolar planetary atmospheres, absorption features whose presence requires a biological source (59, 24). Ideally, atmospheric "biomarker" compounds would be well-known biological products, and they would create an overall atmospheric composition that is out of thermodynamic equilibrium with the planet's crustal composition (62). For example, evidence of life on Earth was "confirmed," using data from the Galileo spacecraft's near-IR mapping spectrometer, by detecting the presence of both oxidized and reduced biogenic gases in the atmosphere (O_2, CH_4, and N_2O) (81). It will not soon be possible to explore the near-IR region in the faint light from extrasolar planets. However, it should be possible to search for O_2 because its abundance is closely related to that of O_3, which exhibits a strong MIR band at 9.6 μm (59). Atmospheric O_2 can accumulate solely by nonbiological processes under certain conditions. For example, a Venus-like planet with a runaway greenhouse climate, which can attain several hundred degrees Celsius, can lose H to space as atmospheric H_2O is photodissociated, thus allowing O_2 to accumulate in the atmosphere (54). However, a runaway greenhouse can be independently inferred if the planet lies inside the habitable zone, as does Venus. High temperatures can also be indicated independently by the IR spectra of CO_2 and H_2O.

If a habitable, Earth-like planet lacked a biosphere, its atmospheric O_2 levels would be very low because the small amount of O_2 from photodissociation of H_2O would be rapidly consumed by reduced volcanic chemical species (51). Thus, a planet that is both habitable at its surface and has abundant atmospheric O_2 is indeed inhabited. However, a habitable planet lacking abundant O_2 is not necessarily uninhabited. Earth's fossil record extends back at least 3.5 billion years (85); however, atmospheric O_2 levels probably became substantial only about 2.1 billion years ago (42). How might we detect an early-Earth-like biosphere around

another star? Atmospheric methane from methanogenic bacteria might be one indicator, but nonbiological sources of methane might be substantial on young habitable planets (53). Anaerobic bacteria produce other reduced gases that might be more diagnostic of life (24); however, very little modeling has been done of trace gas compositions in Earth's early anoxic atmosphere. An astrobiology research program that addresses the biological, geological, and photochemical aspects of anoxic atmospheres will benefit studies of our early biosphere as well as our search for extrasolar biospheres.

ASTROBIOLOGY: The Whole Exceeds the Sum of Its Parts

Just as life is an emergent property of highly complex and coordinated molecular systems, astrobiology must emerge as a highly coordinated program of research, exploration, and education, a program sustained by biological, chemical, earth, and space scientists, engineers, and educators. The natural universe works as a unified whole, and so we must unify our efforts in order to learn its deepest and most valuable secrets. Foremost among those secrets is an understanding of the origin, evolution, and distribution of life in the universe.

Visit the Annual Reviews home page at http://www.AnnualReviews.org

LITERATURE CITED

1. Albee AL, Pallueoni FD, Arvidson RE. 1998. Mars Global Surveyor Mission: overview and status. *Science* 279:1671–72
2. Angel JRP, Woolf NJ. 1996. Searching for life on other planets. *Sci. Am.* 274:60–66
3. Bada JL, Bigham C, Miller SL. 1994. Impact melting of frozen oceans on the early Earth: implications for the origin of life. *Proc. Natl. Acad. Sci. USA* 91:1248–50
4. Bada JL, Glavin DP, McDonald GD, Becker L. 1998. A search for endogenous amino acids in Martian meteorite ALH84001. *Science* 279:362–65
5. Banfield J, Nealson K, eds. 1997. *Geomicrobiology.* Washington, DC: Mineralogical Soc. Am.
6. Bazylinski DA, Moskowitz BM. 1997. Microbial biomineralization of magnetic iron minerals: microbiology, magnetism and environmental significance. In *Geomicrobiology: Interactions Between Microbes and Minerals,* ed. JF Banfield, KH Nealson. 35:181–223, Washington, DC: Mineralogical Soc. Am.
7. Beichman CA. 1996. *A road map for the exploration of neighboring planetary systems. Jet Propulsion Lab. Pub. #96-22*
8. Bell JF. 1996. Evaluating the evidence for past life on Mars. *Science* 274:2121–22

8a. Benner SA. 1999. The missing organic molecules of Mars, alternative interpretation of experiments from the Viking 1976 lander. *Proc. Natl. Acad. Sci. USA.* In press

9. Blake D, Treiman A, Cady S, Nelson C, Krishman K. 1998. Characterization of magnetite within carbonate in ALH84001. In *Lunar and Planetary Science, XXIX, abstract #1347,* CD-ROM. Houston: Lunar & Planetary Inst.

10. Blochl E, Rachel R, Burggraf S, Hafenbradl D, Jannasch HW, et al. 1997. *Pyrolobus fumarii,* gen. and sp. nov., represents a novel group of archaea, extending the upper temperature limit for life to 113 degrees C. *Extremophiles* 1:14–21
11. Boss AP. 1998. The origin of protoplanetary disks. In *Origins, Astron. Soc. Pac. Conf. Ser.,* ed. CE Woodward, JM Shull, HA Thronsen, 148:314–26. San Francisco:
12. Boston PJ, Ivanov MV, McKay CP. 1992. On the possibility of chemosynthetic ecosystems in subsurface habitats on Mars. *Icarus* 95:300–8
13. Bradley J, McSween HY, Harvey RP. 1998. Epitaxial growth of nanophase magnetite in Martian meteorite Allan Hills 84001: implications for biogenic mineralization. *Meteor. Planet. Sci.* 33:765–73
14. Canfield DE, Des Marais DJ. 1993. Biogeochemical cycles of carbon, sulfur, and free oxygen in a microbial mat. *Geochim. Cosmochim. Acta* 57:3971–84
15. Carr MH. 1996. Water erosion on Mars and its biologic implications. *Endeavour* 20:56–60
16. Cech TR. 1989. RNA as an enzyme. *Biochem. Int.* 18:7–14
17. Chyba C, Sagan C. 1992. Endogenous production, exogenous delivery and impact-shock synthesis of organic molecules: an inventory for the origins of life. *Nature* 355:125–32
18. Chyba CF. 1998. Radar detectability of a subsurface ocean on Europa. *Icarus* 134:292–302
19. Clark B. 1998. Surviving the limits of life at the surface of Mars. *J. Geophys. Res.* 103:28,545–55
20. Clifford SM. 1993. A model for the hydrologic and climatic behavior of water on Mars. *J. Geophys. Res.* 98:10973–11016
21. Deamer DW, Oro J. 1980. Role of lipids in prebiotic structures. *BioSystems* 12:167–75
22. DeDuve C. 1995. *Vital Dust*. New York: Basic Books. 362 pp.
23. Des Marais DJ. 1985. Carbon exchange between the mantle and crust and its effect upon the atmosphere: today compared to Archean time. In *The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present,* ed. ET Sundquist, WS Broecker, 32:602–11. Washington, DC: Am. Geophys. Union
24. Des Marais DJ. 1996. The Blue Dot workshop: spectroscopic search for life on extrasolar planets. *NASA Conf. Publ. 10154,* Ames Res. Cent., Moffett Field, CA
25. Des Marais DJ. 1996. Stable light isotope biogeochemistry of hydrothermal systems. In *Evolution of Hydrothermal Ecosystems on Earth (and Mars?),* ed. GR Bock, JA Goode. *Ciba Found. Symp.* 202:83–98. Chichester, UK: Wiley
26. Des Marais DJ. 1997. Long-term evolution of the biogeochemical carbon cycle. In *Geomicrobiology,* ed. J Banfield, K Nealson, 35:429–45. Washington, DC: Mineralogical Soc. Am.
27. Duquennoy A, Mayor M. 1991. Multiplicity among solar-type stars in the solar neighborhood. II. Distribution of the orbital elements in an unbiased sample. *Astron. Astrophys.* 248:485–524
28. Flynn GJ, Keller LP, Miller MA, Jacobsen C, Wirrick S. 1998. Organic compounds associated with carbonate globules and rims in the ALH84001 meteorite. In *Lunar and Planetary Science, XXIX, abstract #1156,* CD-ROM. Houston: Lunar & Planetary Inst.
29. Fortin D, Ferries FG, Beveridge TJ. 1997. Surface-mediated mineral development by bacteria. In *Geomicrobiology: Interactions Between Microbes and Minerals,* ed. JF Banfield, KH Nealson, 35:161–77. Washington, DC: Mineralogical Soc. Am.
30. Fredrickson JK, Onstott TC. 1996. Microbes deep inside the Earth. *Sci. Am.* 275:68–73
31. Garrels RM, Perry EA Jr. 1974. Cycling of carbon, sulfur, and oxygen through

geologic time. In *The Sea*, ed. ED Goldberg, 5:303–36. New York: Wiley
32. Gogarten JP. 1998. Origin and early evolution of life: deciphering the molecular record. In *Origins*, ed. CE Woodward, JM Shull, HAJ Thronson. San Francisco: Astronom. Soc. Pacific Conf. Ser. 148.
33. Gold T. 1992. The deep, hot biosphere. *Proc. Natl. Acad. Sci. USA* 89:6045–49
34. Gold T. 1999. *The Deep Hot Biosphere.* New York: Copernicus
35. Gould SJ. 1996. *Full House.* New York: Three Rivers
36. Gregor CB, Garrels RM, MacKenzie FT, Maynard JB. 1988. *Chemical Cycles in the Evolution of the Earth.* New York: Wiley
37. Grotzinger JP, Kasting JF. 1993. New constraints on Precambrian ocean composition. *J. Geol.* 101:235–43
38. Grotzinger JP, Rothman DH. 1996. An abiotic model for stromatolite morphogenesis. *Nature* 383:423–25
39. Haberle RM. 1998. Early Mars climate models. *J. Geophys. Res.* 103:28467–80
40. Hart NH. 1978. The evolution of the atmosphere of the Earth. *Icarus* 33:23–39
41. Hoffman PF, Kaufman AJ, Halverson GP, Schrag DP. 1998. A neoproterozoic snowball Earth. *Science* 281:1342–46
42. Holland HD. 1992. Distribution and paleoenvironmental interpretation of Proterozoic paleosols. In *The Proterozoic Biosphere: a Multidisciplinary Study*, ed. JW Schopf, C Klein, pp. 153–55. New York/Cambridge, UK: Cambridge Univ. Press
43. Huang AS. 1959. Occurrence of life in the Universe. *Am. Sci.* 47:397–402
44. Hyde ST, Andersson S, Blum Z, Lidin S, Larsson K, et al. 1997. *The Language of Shape.* Amsterdam: Elsevier Sci. B.V.
45. Jakosky B. 1998. *The Search for Life on Other Planets.* Cambridge, UK: Cambridge Univ. Press
46. Jakosky BM, Skock EL. 1998. The biological potential of Mars, the early Earth, and Europa. *J. Geophys. Res.* 103:19359–64
47. Jørgensen BB, Des Marais DJ. 1988. Optical properties of benthic photosynthetic communities: fiber optic studies of cyanobacterial mats. *Limnol. Oceanogr.* 33:99–113
48. Joyce GF. 1992. Directed molecular evolution. *Sci. Am.* 267:90–97
49. Jull AJT, Courtney C, Jeffrey DA, Beck JW. 1998. Isotopic evidence for a terrestrial source of organic compounds found in Martian meteorites Allan Hills 84001 and Elephant Moraine 79001. *Science* 279:366–69
50. Kasting JF. 1993. Earth's early atmosphere. *Science* 259:920–26
51. Kasting JF. 1997. Habitable zones around low mass stars and the search for extraterrestrial life. *Orig. Life* 27:291–307
52. Deleted in proof
53. Kasting JF, Brown LL. 1999. Setting the stage: the early atmosphere as a source of biogenic compounds. In *The Molecular Origins of Life: Assembling the Pieces of the Puzzle*, ed. A Brack, pp. 35–96. New York: Cambridge Univ. Press
54. Kasting JF, Pollack JB, Ackerman TP. 1984. Response of Earth's atmosphere to increases in solar flux and implications for loss of water from Venus. *Icarus* 57:335–55
55. Kasting JF, Whitmire DP, Reynolds RT. 1993. Habitable zones around main sequence stars. *Icarus* 101:108–28
56. Kauffman S. 1995. *At Home in the Universe.* New York: Oxford Univ. Press. 321 pp.
57. Klein H. 1998. The search for life on Mars: What we learned from Viking. *J. Geophys. Res.* 103:28,463–28,466
58. Knoll AH, Holland HD. 1995. Oxygen and Proterozoic evolution: an update. In *Effects of Past Global Change on Life*, ed. S Stanley, pp. 21–33. Washington, DC: Natl. Acad. Press
59. Leger A, Pirre M, Marceau FJ. 1993. Search for primitive life on a distant planet: relevance of O_2 and O_3 detections. *Astron. Astrophys.* 277:309–13

60. Leshin LA, Epstein S, Stolper EM. 1996. Hydrogen isotope geochemistry of SNC meteorites. *Geochim. Cosmochim. Acta* 60:2635–50
61. Lin DNC, Bodenheimer P, Richardson DC. 1996. Orbital migration of the planetary companion of 51 Pegasi to its present location. *Nature* 380:606–7
62. Lovelock JE. 1965. A physical basis for life detection experiments. *Nature* 207:568–70
63. Lovelock JE. 1979. *Gaia: a New Look at Life on Earth.* Oxford, UK: Oxford Univ. Press
64. Maniloff J, Nealson KH, Psenner R, Loferer M, Folk RL. 1997. Nanobacteria: size limits and evidence. *Science* 176:1773–76
65. Marcy GW, Butler RP. 1996. A planetary companion to 70 Virginis. *Astrophys. J.* 464:L147–51
65a. Marcy GW, Butler RP. 1998. Detection of extrasolar giant planets. *Annu. Rev. Astron. Astrophys.* 36:57–97
66. McKay CP, Stoker CR. 1989. The early environment and its evolution on Mars: implications for life. *Rev. Geophys.* 27: l89–2l4
67. McKay DS, Gibson EK Jr., Thomas-Keprta KL, Vali H, Romanek CS, et al. 1996. Search for past life on Mars: possible relic biogenic activity in Martian meterorite ALH84001. *Science* 273:924–30
68. Meyer MC, Kerridge JF. 1995. *An exobiological strategy for Mars exploration, NASA Spec. Publ. 530*
69. Miller S, Orgel LE. 1974. *The Origins of Life on the Earth.* New York: Prentice Hall
70. Mojzsis SJ, Arrhenius G, McKeegan KD, Harrison TM, Nutman AP, et al. 1996. Evidence for life on Earth before 3,800 million years ago. *Nature* 384:55–59
71. Morowitz HJ. 1992. *Beginning of Cellular Life.* New Haven, CT: Yale Univ. Press
72. Nealson K. 1997. The limits of life on Earth and searching for life on Mars. *J. Geophys. Res.* 102:23,675–86
73. Newsom HE, Brittelle GE, Hibbitts CA, Crossey LJ, Kudo AM. 1996. Impact crater lakes on Mars. *J. Geophys. Res. Planets* 101:14951–55
74. Pace NR. 1997. A molecular view of microbial diversity and the biosphere. *Science* 276:734–40
75. Pendleton YJ, Black DC. 1983. Further studies on criteria for the onset of dynamical instability in general three body systems. *Astron. J.* 88:1415–19
76. Pohorille A, New MH, Schweighofer K, Wilson A. 1999. Insights from computer simulations into the interactions of small molecules with lipid bilayers. In *Membrane Permeability: 100 Years Since Ernst Overton*, ed. D Deamer, pp. 49–76. San Diego, CA: Academic Press
77. Reynolds RT, Squyres SW, Colburn DS, McKay CP. 1983. On the habitability of Europa. *Icarus* 56:246–54
78. Russell MJ, Hall AJ. 1997. The emergence of life from iron monosulfide bubbles at a submarine hydrothermal redox and pH front. *J. Geol. Soc. London* 154:377–402
79. Sagan C. 1994. The search for extraterrestrial life. *Sci. Am.* Oct. 1994:92–99
80. Sagan C, Drake F. 1975. The search for extraterrestrial intelligence. *Sci. Am.* 232:80–89
81. Sagan C, Thompson WR, Carlson R, Gurnett D, Hord C. 1993. A search for life on Earth from the Galileo spacecraft. *Nature* 365:715–21
82. Schopf JW. 1983. *Earth's Earliest Biosphere.* Princeton, NJ: Princeton Univ. Press. 543 pp.
83. Schopf JW, Klein C, eds. 1992. *The Proterozoic Biosphere: a Multidisciplinary Study.* New York: Cambridge Univ. Press
84. Schopf JW, Packer BM. 1987. Early Archean (3.3 billion to 3.5 billion-year-old) microfossils from the Warrawoona

Group, Western Australia. *Science* 237: 70–73
85. Schopf JW, Walter MR. 1983. Archean microfossils: new evidence of ancient microbes. In *Earth's Earliest Biosphere, Its Origin and Evolution,* ed. JW Schopf, pp. 214–38. Princeton, NJ: Princeton Univ. Press
86. Sears DWG, Kral TA. 1998. Martian "microfossils" in lunar meteorites? *Meteor. Planet. Sci.* 33:791–94
87. Shock EL, Schulte MD. 1998. Organic synthesis during fluid mixing in hydrothermal systems. *J. Geophys. Res.* 103:28,513–28,527
88. Stal LJ, Caumette P. 1994. *Microbial mats: structure, development and environmental significance. Series G. Ecological Sciences.* Heidelberg: Springer Verlag
89. Thomas-Keprta KL, Bazlinski DA, Wentworth SJ, McKay DS, Golden DC, et al. 1998. *Mineral biomarkers in Martian meteorite Allan Hills 84001? Martian meteorites: Where do we stand and where are we going? In LPI, Contribution #956, 51-3* Houston, TX: Lunar Planetary Inst.
90. Treiman A. 1998. The history of Allan Hills 84001 revised: multiple shock events. *Meteor. Planet. Sci.* 33:753–64
91. Trent JD. 1996. A review of acquired thermotolerance, heat-shock proteins, and molecular chaperones in archaea. *FEMS Microbiol. Rev.* 18:249–58
92. Vidal G, Knoll AH. 1982. Radiations and extinctions of plankton in the late Precambrian and early Cambrian. *Nature* 197:57–60
93. Wächtershäuser G. 1992. Groundwork for an evolutionary biochemistry: the iron-sulphur world. *Prog. Biophys. Molec. Biol.* 58:85–201
94. Walter MR, ed. 1976. *Stromatolites.* Amsterdam: Elsevier
95. Walter MR, Des Marais DJ. 1993. Preservation of biological information in thermal spring deposits: developing a strategy for the search for fossil life on Mars. *Icarus* 101:129–43
96. Ward DM, Ferris MJ, Nold SC, Bateson MM. 1999. Microbial biodiversity within hot spring cyanobacterial mat communities: an evolutionary ecology view. *Microbial Mol. Biol. Rev.* In press
97. Watson GMF, Yu JP, Tabita R. 1999. Unusual ribulose 1,5-bisphosphate carboxylase/oxygenase of anoxic Archaea. *J. Bacteriol.* 181:1569–75
98. Wetherill GW. 1994. Provenance of the terrestrial planets. *Geochim. Cosmochim. Acta* 58:4513–20
99. Wetherill GW. 1996. The formation and habitability of extra-solar planets. *Icarus* 119:219–38
100. Woese CR. 1998. The universal ancestor. *Proc. Natl. Acad. Sci. USA* 95:6854–59
101. Woese CR, Fox GE. 1977. Phylogenetic structure of the prokaryotic domain: the primary kingdoms. *Proc. Natl. Acad. Sci. USA* 74:5088–90