

From Protoplanets to Protolife: The Emergence and Maintenance of Life

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Despite great advances in our understanding of the formation of the solar system, the evolution of Earth, and the chemical basis for life, we are not much closer than the ancient Greeks to an answer of whether life has arisen and persisted on any other planet. The origin of life as a planetary phenomenon will probably resist successful explanation as long as we lack an early record of its evolution and additional examples. Plausible but meagerly investigated scenarios for the origin of important prebiotic molecules and their polymers on Earth involving atmospheric chemistry, meteorites, deep-sea hot springs, and tidal flat sediments have been developed. Our view of the diversity of extant life, from which properties of a last universal common ancestor (LUCA) can be inferred, has also improved in scope and resolution. It is widely thought that the geologic record shows that life emerged quickly after the end of prolonged bombardment of Earth. New data and simulations contradict that view and suggest that more than half a billion years of unrecorded Earth history may have elapsed between the origin of life and LUCA. The impact-driven exchange of material between the inner planets may have allowed earliest life to be more cosmopolitan. Indeed, terrestrial life may not have originated on Earth, or even on any planet. Smaller bodies, e.g., the parent bodies of primitive meteorites, in which organic carbon molecules and catalytic transition metals were abundant, and in which hydrothermal circulation persisted for millions of years, offer alternative environments for the origin of life in the solar system. However, only planet-sized bodies offer the stable physiochemical conditions necessary for the persistence of life. The search for past or present life on Mars is an obvious path to greater enlightenment. The absence of intense geologic activity on Mars, which contributes to its inhospitable state today, has also preserved its ancient history. If life did emerge on Mars or was transferred from Earth, the lack of sterilizing impacts (due to a low gravity and no oceans) means that a more diverse biota may have thrived than is represented by extant life on Earth. On the other hand, a habitable but still lifeless early Mars would be strong evidence against efficient transfer of life between planets. The subsurface oceans of some icy satellites of the outer planets represent the best locales to search for an independent origin of life in the solar system because of the high dynamical barriers for transfer, intense radiation at their surfaces, and thick ice crusts. These also present equally formidable barriers to our technology. The “ultimate” answer to the abundance of life in the cosmos will remain the domain of speculation until we develop observatories capable of detecting habitable planets — and signs of life — around the nearest million or so stars.

1. INTRODUCTION

This contribution's place as the final chapter in *Proto-stars and Planets V* may betray a subtle conceit in how we view our place in a cosmic order that runs from the interstellar medium to planetary bodies. (Read in reverse order, the chapters would suggest a more humble search for our origins among wisps of interstellar gas and dust.) Nevertheless, this sequence makes sense, both in a temporal and also a physical order: It describes a gradation in phenomena in which physical and chemical inevitability (the laws of gravity, classical and quantum mechanics, and electromagnetism) that govern the collapse of the interstellar medium and the formation of stars are replaced by more stochastic proc-

esses such as accretion during planet formation and evolution. For example, it may be inevitable that a cooling molecular cloud collapses, a disk forms, and that runaway growth of planetesimals occurs in that disk, but the final masses, orbits, and surface environments of planets may not be predictable in more than a statistical sense. Ultimately it is no longer sufficient to describe what could happen; one must also describe what *did* happen. Whereas stars can be described by a relatively small number of variables (age, rotation, and heavy element abundance, for example), planets, particularly terrestrial planets, cannot. In that context, the origin and survival of life might be the ultimate contingency.

On the other hand, what little we know about the origin of life seems to suggest some element of inevitability. The

primary constituents of life (C, H, N, and O) are four of the five most abundant elements in the universe. Some of the monomeric molecules of life (amino acids, sugars, etc.) are found everywhere. Laboratory experiments have suggested possible pathways along which those monomers might become polymers, make copies of themselves, and interact in complex ways on which Darwinian selection can act. Evidence for life appears in Earth's rock record as soon as there is any geologic record at all.

The dichotomy between chemical inevitability and historical contingency infuses studies of the origin and propensity of life in the universe (not to mention the question of what life is), and it has spawned numerous popular books on the subject. We leave resolution of that problem to scientists-*cum*-philosophers. In this review we concentrate on those lines of inquiry that have experienced especially fruitful development since the review of this subject by *Chyba et al.* (2000) for *Protostars and Planets IV*, including new age constraints on the appearance of clement environments and life on Earth, a reassessment of predictions for the chemistry of the prebiotic atmosphere and oceans, the formulation of a dynamical scenario for a "late" cataclysmic bombardment that may have profoundly influenced the emergence of life, and the development of new theories for the origin of Earth's water. Because science knows so little about the origin of life on Earth and the potential environments for its origin elsewhere, we feel it is important to be open-minded — and even provocative — in the scenarios that we consider. Our review is structured as follows: We consider the timing and environment of the origin of terrestrial life (section 2) and our understanding of the combination of factors that permit Earth-like life to persist on a planet for an astronomically interesting period of time (section 3). Finally, we address how the search for life elsewhere in the solar system, and particularly for life-bearing planets around other stars, promises to ultimately inform us about the evolution of our own habitable planet and the possibility of other origins elsewhere in the cosmos (section 4). Other relevant reviews since that of *Chyba et al.* (2000) include *Shock et al.* (2000), *Kasting and Catling* (2003), *Gaidos et al.* (2005), and *Chyba and Hand* (2005).

2. WHEN AND WHERE DID LIFE EMERGE?

2.1. Origin of a Theory of Origin

Recorded speculation on the setting of the origin of life goes back at least to ancient Greek civilization. Thales of Miletus (640–546 BCE) presciently suggested that all life, including humans, arose from the single "element" water — i.e., the sea. His student Anaximander (611–545 BCE) slightly modified his master's idea, substituting mud for water and thus proposing the first primordial "soup" hypothesis. Empedocles (490–435 BCE) further elaborated (or obfuscated) the theory, proposing that life emerged in a random fashion from a combination of the four classic Greek "elements." The concept of "spontaneous generation" of life from nonliving matter relied on unsupported anecdote

and uncontrolled experiment for two full millenia, but was doomed by the invention of the compound microscope ca. 1590, the discovery of ubiquitous microorganisms by Antonie von Leeuwenhoek a century later, and the *coup de grace* delivered by Louis Pasteur's irrefutable 1864 demonstration of microbial contamination in all previous origin-of-life experiments. Modern inquiry into the origin of life began once science had discovered aspects of the chemical basis for life, described the theory of evolution by natural selection, and appreciated the age of Earth: In the 1920s Oparin and Haldane independently described a new theory in which life emerged from "prebiotic" chemistry driven by electricity or solar ultraviolet radiation in a reducing atmosphere of the early Earth.

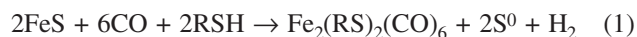
By necessity, tests of such theories have been limited to demonstrations of plausibility by laboratory experiments. This is because the same geologic activity (volcanism, plate tectonics, and metamorphism) that sustains geochemical cycles and life on Earth today has destroyed nearly all of the earliest record of surface conditions and possible life that could be used to test such theories. Earth formed 4.56 b.y. ago (Ga) but the paltry record of the first 600 m.y. consists of a handful of zircon crystals as old as 4.4 Ga (*Wilde et al.*, 2001) and a single outcrop of heavily metamorphosed gneiss dated at 4.0 Ga (*Bowring and Williams*, 1999). The oldest putative evidence for life on Earth is isotopically fractionated C in 3.85 Ga rocks from Akila Island and the 3.8–3.7 Ga Isua formation in Greenland (*Schidlowski*, 1988; *Mojzsis et al.*, 1996; *Rosing*, 1999). However, some of this evidence has recently been challenged (*van Zuilen et al.*, 2002; *Fedo and Whitehouse*, 2002; *Mojzsis et al.*, 2002). Likewise, the origin and provenance of the oldest (3.46-Ga) putative microfossils, from the Apex chert in Australia (*Schopf and Packer*, 1987), have been disputed (*Brazier et al.*, 2002, 2004). The biological nature of even the 3.5–3.4 Ga fossil stromatolites, laminated microbial mats, in Australia and South Africa (*Walter et al.*, 1980) has been questioned (*Grotzinger and Rothman*, 1996). Despite the controversy, it seems likely that at least some of the evidence for life by 3.5 Ga will withstand scrutiny and new kinds of evidence may emerge (*Furnes et al.*, 2004). However, the geologic record of the origin and evolution of earlier, more primitive life seems irretrievably lost.

Any successful theory of biogenesis must provide a prebiotic source of the organic monomers (e.g., amino acids and nucleotides) as a starting point, and one or more mechanisms of chemical condensation of these monomers into polymers and more complex molecules. The Oparin-Haldane conjecture of an atmospheric source assumed a reducing primordial atmosphere containing abundant CH₄, NH₃, and H₂. This mechanism was brilliantly supported by Stanley Miller's experiment (*Miller*, 1953). However, this scenario fell into disfavor upon the development of models predicting that planetary core formation was contemporaneous with homogeneous accretion (*Stevenson*, 1980), leaving the mantle depleted of metallic Fe, and volcanic gases relatively oxidized (N₂, CO₂, and H₂O). Discharge experiments with such gas mixtures fail to produce significant

quantities of organic molecules and underscore the particular importance of CH₄ and H₂ (Miller and Schlesinger, 1983; Sleep et al., 2004).

New models of Earth's earliest atmosphere predict chemically significant concentrations of H₂ and CH₄: Although most of the Fe in Earth would have been sequestered into the core, degassing during impact of material with a carbonaceous chondrite composition would have created a reducing atmosphere composed of CH₄, N₂, NH₃, H₂, and H₂O (Schaefer and Fegley, 2005). The isotopic and elemental abundances of rare gases suggest that this primordial atmosphere was lost: Massive H escape was probably complete by 4.47 Ga (Podeseck and Ozima, 2000) and the atmosphere was closed to all elements except H and He by 4.3 Ga (Tolstikhin and O'Nions, 1994). However, this still leaves a period of between 30 and 200 m.y. after core formation in which a Urey-Miller atmosphere could have existed, perhaps plenty of time for biogenesis to occur. Furthermore, H outgassing later from volcanos may have been more strongly retained by an anoxic atmosphere where the upper atmosphere did not contain singlet O that absorbs extreme ultraviolet radiation from the Sun (Tian et al., 2005), although this is not conclusive (Catling, 2006). Nevertheless, alternative sources of organic monomers are available: One appeared serendipitously in the form of a meteorite that fell near the town of Murchison, Australia, in 1969. The archetype CM meteorite was found to contain a suite of organic molecules including many of the biotic amino acids (see review by Ehrenfreund and Charnley, 2000). Both meteorites and comets might have provided organics to the early Earth (Chyba et al., 1990).

A decade after the Murchison meteorite fell, the first deep-sea hot spring chemotrophic ecosystem supported by the mixing of sulfidic hydrothermal fluids with oxygenated seawater was discovered (Corliss et al., 1979). The appreciation that microorganisms could have colonized such high-temperature settings and exploited chemical energy sources before the advent of photosynthesis led to interest in their potential role in the origin and early evolution of life. Currently, the hypothesis of a hydrothermal origin of life draws support from three observations: First, hydrothermal systems are sites where organic synthesis is thermodynamically favored (Shock and Schulte, 1988; Shock et al., 2000). Second, these environments contain abundant Fe and Ni sulfides that may catalyze reactions of potential prebiotic importance (Huber and Wächtershäuser, 1997) and are present as co-factors in many enzymes (Johnson et al., 2005). Cody et al. (2001) showed that reaction of iron sulfide (FeS) with alkyl thiols (RSH), where R is an alkane group, produces carbonylated Fe-S compounds via



which they suggest to be responsible for catalysis, in lieu of mineral surfaces themselves. [The possible role of metal sulfides in prebiotic chemistry and subsequent incorporation into central metabolic pathways has been recently reviewed by Cody (2004). Holm and Andersson (2005) dis-

cuss the challenges of conducting hydrothermal chemistry under geologically relevant conditions.] Third, many thermophilic and hyperthermophilic archaea and bacteria are located near the root of phylogenetic trees constructed from small subunit ribosomal RNA gene sequences. This has been taken to suggest that a primitive character of the last universal common ancestor of all life was adaptation to high temperature, as originally suggested by Woese (1987), an inference widely, but not completely, accepted (Galtier et al., 1999; Brochier and Philippe, 2002; Di Giulio, 2003). (See the next section for an alternative explanation of thermophily.)

Another successful conjecture in origin of life studies is the idea of an "RNA world" in which ribonucleic acid (RNA) played the role of both DNA and protein in primitive organisms by carrying information and catalyzing chemistry (Orgel, 1968; Crick, 1968; Gilbert, 1986). This conjecture is supported by the appearance of RNA in ubiquitous and highly conserved — and thus evolutionarily ancient — parts of the cellular machinery such as the ribosome, the demonstration that ribonucleotides are catalytically active (Cech, 1986), and by the success of evolving catalytically active RNA molecules in the laboratory (Joyce, 2004). In contrast to the hypothetical high-temperature origin of life described above, the phosphodiester backbone of RNA and the nucleobases themselves are unstable under high-temperature aqueous conditions (e.g., Levy and Miller, 1998). One scenario is for an RNA world to evolve under near-freezing conditions, perhaps in pockets of eutectic brine within ice where components were cyclically frozen and rehydrated (Orgel, 2004; Vlassov et al., 2005). Brines have also been suggested as the site of prebiotic purine and pyrimidine synthesis and polymerization (Bada et al., 1994; Miyakawa et al., 2002a,b).

Recently, investigators have turned to wet-dry cyclic chemistry at clement temperatures, perhaps driven in the sediments of intertidal flats. Commeyras et al. (2004) describe a mechanism of prebiotic polypeptide synthesis through cyclic condensation of N-carbonyl amino acids under alternating pH conditions in the presence of significant N oxides in the atmosphere. [See also Lathe (2004) for a speculative scenario based on salt concentrations.] Alternatively, a more stable predecessor to RNA such as a peptidal molecule has been posited. Russell and Arndt (2005) argue for biogenesis at low-temperature, alkaline submarine seeps. These seeps form mounds containing precipitated Fe-Ni sulfides through which strong chemical gradients are maintained between the H₂-rich, reducing fluids and more oxidizing oceans, driving the reduction of CO₂ or HCO₃ to acetate (COOH).

If core metabolism reflects a hydrothermal environment, and RNA evolved before protein, then the thermal instability of RNA suggests that it in turn was preceded by an unknown protobiotic world that functioned at higher temperatures, and therefore the thermophilic character of a LUCA is unrelated to a high-temperature origin of metabolism. Alternatively, RNA and the core metabolism of extant organisms appeared in different lineages. These considerations suggest

a substantial evolutionary history preceding LUCA. Such a history may have involved the extensive chimerism of lineages that evolved from different environments. An analogous history is recorded in the complex organelle structure of eukaryotic microalgae that have experienced engulfment and endosymbiosis of independent unicellular lineages (*McFadden, 2001*). *Woese (2000)* has suggested that the earliest history of RNA/DNA-based life was marked by the rampant “horizontal” transfer of genes between organisms, absence of distinct lineages, and communal evolution of the gene pool. Less efficient and redundant components would have been discarded (e.g., the information-carrying molecules in the high-temperature contributor, the metabolic machinery in the low-temperature contributor), leaving an organism whose chemical ancestry derives from very different environments.

Furthermore, the environment(s) in which the origin of life took place need not resemble any environment on the modern Earth, and indeed may not be habitable by the standards of modern organisms. The evolution of life may have involved “frozen accidents” in which universal biological attributes selected for in an archaic environment are retained, even in the face of maladaptation in a new environment, because any changes in them would be too costly to the fitness of organisms. For example, while the eukaryotic cell may have arisen from a chimeric fusion of representatives of the Bacteria and Archaea, both domains of life that contain species that thrive at temperatures near 100°C, no eukaryote has been found that grows at temperatures above ~60°C, probably because the incorporation of membrane-surrounded organelles such as the nucleus requires permeability that renders the membrane susceptible to destruction at high temperatures. It is conceivable that life arose at temperature exceeding 120°C, but that the universal use of lipid membranes for structure and triphosphates for energy has rendered those environments forever inaccessible to life.

Darwin’s proposal that all life on Earth shares a common ancestry is supported by vast amounts of molecular work. Yet, much of the microscopic world is classified only by molecular techniques such as the polymerase chain reaction (PCR) and it is conceivable that completely “alien” organisms based on different molecules flourish undetected under our feet (*Davies and Lineweaver, 2005*). If all Earthly life does have a single origin this might mean that the origin of life is sufficiently infrequent that the probability of it happening more than once on the same planet is low. Alternatively, it might mean that sometime in Earth history all other forms of life went extinct. Although it may be chauvinistically satisfying to think that other forms of life were out-competed by our common ancestor, nature tolerates the competitive or noncompetitive coexistence of countless forms of life, often within the same ecological niche (e.g., there are 300,000 known species of plants). Although there is no evidence that independent forms of life ever existed, it is difficult to exclude them from the first billion years of history in the absence of morphological fossils, and impossible to exclude them from the first 600 m.y.

as there is no record at all. Such a loss in diversity would not be the first to be inferred in the history of life. For example, the diversity of animal body plans recorded in fossil deposits of exceptional preservation such as the Burgess Shale is thought to greatly exceed later body plan diversity. Instead of competition, perhaps a uniquely catastrophic event extinguished all but a few, related forms of life that occupied some refuge.

2.2. Impacts, Bottlenecks, and Frozen Accidents

Giant impacts capable of vaporizing the oceans may have provided such an extinction event. A “late” (3.9-Ga) episode of impacts is recorded on the Moon and in the martian meteorite ALH 84001 (*Turner et al., 1997*). Sterilizing impacts may have limited the emergence of life (*Maher and Stevenson, 1988*) and imposed a high-temperature “bottleneck” through which only adapted organisms could have passed, thus explaining the inference that LUCA was a thermophile (*Sleep and Zahnle, 1998; Nisbet and Sleep, 2001*). Giant impacts may also have contributed to the destruction of the rock record itself. One model for this “late heavy bombardment” involves the decay of a long-lived reservoir of impactors somewhere in the outer solar system (*Fernández and Ip, 1983*). However, searches for geochemical evidence for an extraterrestrial input to the Earth system at 3.8–3.7 Ga have yielded ambiguous results (*Anbar et al., 2001; Schoenberg et al., 2002; Frei and Rosing, 2005*). A null result from such searches supports an alternative scenario in which the impacts occurred in a single cataclysm ca. 3.9 Ga (*Dalrymple and Ryder, 1993; Cohen et al., 2000*). Such an event can be produced by a 1:2 mean-motion resonance crossing of Jupiter and Saturn (*Tsiganis et al., 2005*) during an early period of giant planet migration driven by planetesimal scattering (*Hahn and Malhotra, 1999*). This scenario is consistent with evidence for an asteroidal origin of the impacts (*Strom et al., 2005*).

Previously, the earliest evidence for life in the rock record, apparently at the tail end of a continuous period of sterilizing giant impacts, was taken to suggest that the origin of life was geologically instantaneous and would occur just as quickly on other planets were conditions correct (e.g., *Lineweaver and Davis, 2002*). If the scenario of a “brief” cataclysm is correct, life may have emerged during the previous 600-m.y. period that followed a magma ocean (*Boyett and Carlson, 2005*) and Moon-forming impact (*Lee et al., 2002*) at around 4.5 Ga. During that time the impact rate may have been permissible for life, and considerable prebiotic and biological evolution could have taken place of which we have no record. Or do we? Assuming that life emerged prior to 3.9 Ga and survived the impact bottleneck in deep refugia, the genetic information carried in the LUCA(s) might tell us something about that early environment. For example, molecular oxygen in a pre-3.9-Ga atmosphere would explain the paradox of the presence of cytochrome *c* terminal oxidases in many species of both bacteria and archaea, and thus presumably in a LUCA, and before the origin of oxygenic photosynthetic cyanobac-

teria (Castresana *et al.*, 1994). A giant ocean-vaporizing impact would extinguish photosynthetic life, but perhaps not deeper-living organisms that had profited from that O₂ (such as those that exist in modern vent systems). A narrow bottleneck would be a convenient explanation for why only one form of life exists on modern Earth. The requirement of giant planets near a resonance suggests that such cataclysms may not occur (or may occur at a different time) in extrasolar planetary systems with different giant planet architectures.

Impacts also provide a mechanism by which life might be transferred from one planet to another. Interest in the interplanetary transfer of life (“lithopanspermia”; related to, but to be distinguished from conjectures of cosmological “panspermia”) was catalyzed by the discovery of meteorites from Mars, the elaboration of the spallation mechanism of impact ejection (Melosh, 1984), and dynamical simulations showing small but finite probabilities that such ejecta could be transferred between the inner planets on timescales of thousands of years or less (Gladman and Burns, 1996). Magnetic constraints on the thermal history of the ALH 84001 meteorite during its ~17-m.y. transit (Goswami *et al.*, 1997) are permissive of life (Weiss *et al.*, 2000a). Laboratory experiments indicate that bacteria and their spores can survive the shock pressures and acceleration associated with impact ejection (Mastrapa *et al.*, 2001; Burchell *et al.*, 2001, 2003, 2004) and can find sufficient protection from radiation within rock fragments a few centimeters in size (Horneck *et al.*, 2001).

Transfer between the inner planets may have been a ubiquitous process. Simulations by Gladman *et al.* (2005) show that 1%, 0.1%, and 0.001% of ejecta from Earth reach Earth, Venus, and Mars in 30,000 years. In the first case, this suggests that ejecta may have been a refugia for microorganisms during a giant impact event in which sterilizing conditions existed for thousands of years (Wells *et al.*, 2003). Alternatively, ejecta on “express” trajectories (a few years) could have reseeded planets after giant impact extinction events, provided there was a second, life-bearing planet. Climate models suggest that Venus, if it started out with an Earth-like inventory of water, could have experienced clement surface temperatures (Kasting *et al.*, 1993) and there is geomorphological evidence for a very early warm, wet Mars (Jakosky and Phillips, 2001). Even if a sterilizing impact was inevitable on each planet, the probability of simultaneous events (within a few thousand years) on the two planets would be vanishingly small. This could mean a novel requirement for planetary habitability, that of a second habitable planet.

If life can be transferred between planets then it is not too great a leap of logic to suppose that it arose on another planet and was later transferred to Earth. [Although it appears unlikely that meteorites could be exchanged between planetary systems (Melosh, 2003; Wallis and Wickramasinghe, 2004) it was more likely for stars (possibly like the Sun) formed in a dense cluster (Adams and Spergel, 2005).] Mars is *a priori* the favorite alternate planet of origin because of its lower escape velocity and because there is evidence for

at least episodic Earth-like conditions in the past — although the exact conditions are controversial (Carr, 1999; Craddock and Howard, 2002; Bhattacharya *et al.*, 2005). There is no such evidence (one way or another) for Venus and it has a deeper gravity well. Sleep and Zahnle (1998) have also found that any organisms on Mars would have been more likely to survive giant impacts in the past, again because the kinetic energy of the impact is smaller, and because of the absence of the latent heat of fusion of a vaporized global ocean that would delay cooling (assuming Mars had no such ocean). However speculative such theories may seem, the absence of any record of early life on Earth suggests that we keep an open mind on such matters.

2.3. Life First, Planets Second?

Indeed, planetary bodies much smaller than Mars represent a potential site for the origin (but not maintenance) of Earth life. Many carbonaceous chondrite meteorites record geochemical alteration by liquid water, and it is presumed that they originate from parent bodies a few tens of kilometers across, i.e., large enough to have maintained temperatures above the freezing point of water for millions of years, but too small to have experienced differentiation and high-temperature metamorphism (Keil, 2000). The main asteroid belt presently contains more than 300 asteroids with diameters larger than 50 km and the primordial belt may have contained 10³–10⁴ times as many (Weidenschilling, 1977). A scenario for the origin of life in a primitive planetesimal and its subsequent transfer to Earth would involve biogenesis while liquid water was present, transfer of protoorganisms to Earth after the Moon-forming impact approximately 30 m.y. into solar system history (Jacobsen, 2005), and preservation of the organisms during any intervening period. This scenario is distinct from the survivability of organisms in asteroids to the present day, which Clark *et al.* (1999) have dismissed based on thermal, radiation, and energetic arguments.

Carbonaceous chondrite meteorites contain abundant (up to a few weight percent) water. Masses of several main-belt asteroids determined by the orbits of satellites give low densities suggestive of high water ice content and/or high void space (Marchis *et al.*, 2005) and consistent with a picture of an asteroid as an icy “rubble pile” (Weidenschilling, 1981). Highly permeable, water-rich asteroids would have been sites of hydrothermal circulation early in their history. Water in the interior of parent bodies would be liquefied and mobilized by the heat from decaying ²⁶Al and ⁶⁰Fe while protected by an ice-filled impermeable crust a few kilometers thick. Additional internal heat may come from exothermic serpentinization reactions (see the chapter by Jewitt *et al.*) and possibly impacts. Detailed three-dimensional simulations of hydrothermal convection in a 40-km body show interior temperatures remain well above the freezing point for millions of years (Travis and Schubert, 2005).

Carbonaceous chondrites (and by inference their parent bodies) also contain organic molecules, including amino acids (Kvenvolden *et al.*, 1970) and polyhydroxylated com-

pounds (e.g., sugars) (Cooper *et al.*, 2001), and their possible role as a source of important biotic precursor molecules has long been scrutinized. The stable isotopes of C and N in this organic matter suggests an origin in the interstellar medium (Alexander *et al.*, 1998), but significant processing could have occurred in the solar nebula and in meteorite parent bodies. Although aqueous alteration in many parent bodies involved relatively oxidizing conditions and thus led to loss of organic material (e.g., conversion to CO₂ and carbonates) (Naraoka *et al.*, 2004), a few meteorites, particularly CM meteorites like Murchison, seemed to have been altered by reducing fluids (Browning and Bourcier, 1996). Moreover, Shock and Schulte (1990) make thermodynamic arguments for amino acid synthesis by aqueous alteration of polycyclic aromatic hydrocarbons (PAHs), a common organic in the interstellar medium and primitive meteorites, and Strecker synthesis by reaction of ketones or aldehydes with HCN and NH₃ (Schulte and Shock, 1992).

Clark *et al.* (1999) argue that the emergence of endogenous organisms is *a priori* less likely in an asteroid than on a planet because the former are smaller, and because they supposedly comprise less diverse environments. However, the macroscopic scale of an environment is unlikely to affect its potential to host microscopic prebiotic chemistry. First-order chemical kinetics depends on the *concentration* of reactants rather than the total molar quantity and high concentrations of reactants (a “soup”) are more plausibly produced in small environments (“puddles”) than in large ones. If the first steps in the origin of life consist of prebiotic chemistry, it is chemical diversity rather than physical or geologic diversity that is important. Melting and high-temperature metamorphism associated with the accretion and differentiation of planetary embryos and planets results in chemical equilibrium and the destruction of chemical diversity. Besides many of the important terrestrial minerals such as olivines, pyroxenes, and clays, meteorites contain a diverse suite of minerals that have not been found on Earth, including various metal sulfides and phosphates (Table 1). Carbonaceous chondrite meteorites also contain abundant metallic Fe-Ni grains, in contrast to the surface of Earth where such metal alloys are extremely rare and found only associated with ophiolites (preserved pieces of oceanic crust that have been heavily altered by the reducing fluids associated with serpentinization). As discussed above, metal sulfides and metals may have played an important catalytic role in prebiotic chemistry.

Although these parent bodies were small, they were extremely numerous and diverse. Each of these bodies would have differed because of chemical gradients in the solar nebula, their precise accretion history, and their final size. The simulations of Travis and Schubert (2005) also show that within a single (undifferentiated) body there is a diversity of hydraulic histories and presumably, degrees of chemical alteration. Individual impacts at speeds low enough to be nonsterilizing would induce additional heterogeneity in physiochemical conditions. Essentially, each of these bodies would represent a different “experiment” in low-temperature

TABLE 1. Uniquely extraterrestrial minerals.

Name	Chemical Formula
barringerite	Fe _{2-x} Ni _x P
brezinaite	Cr ₃ S ₄
brianite	Na ₂ CaMg(PO ₄) ₂
carlsbergite	CrN
daubreelite	FeCr ₂ S ₄
farringtonite	Mg ₃ (PO ₄) ₂
gentnerite	Cu ₈ Fe ₃ Cr ₁ S ₁₈
haxonite	Fe ₂₀ Ni ₃ C ₆
heideite	(Fe,Cr) _{1+x} (Ti,Fe) ₂ S ₄
krinovite	NaMg ₂ CrSi ₃ O ₁₀
lawrencite	(Fe,Ni)Cl ₂
majorite	Mg ₃ (Fe,Al,Si) ₂ (SiO ₄) ₃
merrihueite	(K,Na) ₂ (Fe,Mg) ₅ Si ₁₂ O ₃₀

inorganic and organic chemistry. Many or most of these experiments would be cut short by accretion onto large embryos where melting and differentiation would occur. However enough bodies might have survived the 30 m.y. during which accretion of Earth was completed. Disruption of these bodies by mutual collisions induced by the gravitational perturbations of Jupiter might have produced frozen fragments containing protolife that successfully transited the thick atmosphere of an abiotic Earth to thaw on and colonize its surface.

Could some form of protolife have emerged in a primordial asteroid and then persisted long enough (perhaps in a frozen state) to await collisional disruption of the body into fragments small enough for a relatively gentle arrival on Earth? Such a scenario requires that (1) life evolved “very quickly” (within a few to tens of millions of years); (2) it was preserved in the parent body or fragments of the parent body during the period of the formation and cooling of the terrestrial planets (perhaps 30–100 m.y.), (3) it was successfully transferred to Earth (or Mars) intact, perhaps in a small fragment; and (4) it arrived in an environment in which it could thrive.

The unsuccessful (or overly successful) search for fossil life in meteorites has been well documented (e.g., Anders *et al.*, 1964). If life did emerge in the interior of primitive planetesimals, why has it or evidence for biological activity not been found in a collected primitive meteorite? One possibility is that any organisms or biomarkers have been degraded by radiation or impacts over the intervening 4.5 b.y. since these bodies were warm. Furthermore, only the small fraction of organics that are soluble have been thoroughly studied. The remainder is thought to be dominated by complex (poly)aromatic hydrocarbons (Cody *et al.*, 2002; Sephton *et al.*, 2003). There are controversial measurements of L-excess chirality of meteoritic amino acids (Engel and Nagy, 1982; Pizzarello and Cronin, 2000). Another explanation is that the world’s meteorite collection probably samples only ~100 parent bodies in the present asteroid belt. Finally, the population of bodies that could have seeded

Earth within a few tens of millions of years has been completely depleted over the age of the solar system. In other words, if terrestrial life did emerge in a planetesimal, then we do not find it in our meteorites because that body or its fragments already arrived long ago, and we, and all life on Earth, are the result.

The scenario that life arose in the interior of an undifferentiated, primitive body and subsequently found a permanent home on a differentiated planet requires a population of small bodies with a dynamical lifetime longer than (but not much longer than) the accretion timescale of a potentially habitable planet. Terrestrial planet formation is a relatively efficient process, i.e., most planetesimals are accreted into large embryos (which differentiate and melt) rather than small bodies; nevertheless, final clearing may take well over 100 m.y. (Goldreich *et al.*, 2004). In addition, the gravitational perturbation of a gas giant planet such as Jupiter inhibits planet formation and scatters bodies at large distances. Thus, the formation of a giant planet and the equivalent of an asteroid belt may be a prerequisite for the emergence of life in a planetary system.

3. ELEMENTS OF HABITABILITY

3.1. The Habitable Zone

Once life is established on a planet, and assuming it survives catastrophes such as giant impacts, what factors are important to its persistence over a significant (i.e., observable) period of time? The range of orbital semimajor axes for which the surface temperatures on Earth-like planets would permit liquid water describes a “habitable zone” around a star (Huang, 1959). This will change with stellar luminosity evolution (Hart, 1979) and will depend on the concentration of greenhouse gases in the atmosphere and therefore on geochemical feedbacks (Kasting *et al.*, 1993) and rates of geologic activity such as volcanism (Franck *et al.*, 2000). That region of space in which a planet on a stable orbit will remain in the habitable zone over an extended period of time is known as the continuously habitable zone. Earth’s orbit is relatively stable against the perturbations of the other planets over billion-year timescales (Laskar, 1994). It will remain in the habitable zone for another 1–2 b.y. before experiencing a runaway greenhouse (Caldeira and Kasting, 1992).

However, the known systems of extrasolar planets have giant planet configurations quite unlike that of our solar system. Yet unseen terrestrial planets in the habitable zones of these stars may have orbits that are dynamically unstable against gravitational perturbation by the detected giant planets. The criterion of dynamical habitability has motivated a host of publications that explore the stability of small (i.e., massless) planets within known giant planet systems (Érdi *et al.*, 2004; Asghari *et al.*, 2004; Ji *et al.*, 2005; Jones *et al.*, 2005, see also references in Gaidos *et al.*, 2005). These show that small planets could persist in the habitable zone of some, but not all these systems for the duration of the

simulations (which tend to be limited to millions of years). The kinematics of hypothetical extrasolar planets and the implications for habitability have been less explored: In the presence of at least two other planets, planets may experience chaotic obliquity fluctuations. The presence of oceans would moderate surface temperatures, however, making them habitable at least for simple life (Williams and Pollard, 2003). A similar conclusion is reached for planets on eccentric orbits (Williams and Pollard, 2002). Planets in the close-in habitable zones around much fainter M stars will be subject to tidal locking; however, even in this case, sufficient convective heat transport to the dark side can maintain atmospheres against collapse (Joshi *et al.*, 1997). Although we may have a quantitative understanding of the allowed ranges of orbital and rotation necessary for the habitability of an Earth twin, many other factors determine whether a planet can support life (Taylor, 1999). Some of these, including the frequency of supernovae and giant impacts, have been explored by Gonzalez *et al.* (2001).

3.2. Planetary Water

Water is an indisputably indispensable commodity of planetary habitability and a defining constituent of Earth’s surface. Any model of terrestrial planet habitability must include a component that addresses the abundance of water, and any such component must satisfactorily explain the origin of Earth’s water. The inner regions (~1 AU) of model primordial solar nebulae are devoid of water, as a consequence of diffusion of water vapor outward along a thermal gradient and condensation at a “snow line,” and in apparent agreement with the correlation between the water content and the orbital distance of asteroids (assumed to be their formation distance). It is also thought that retention of water against loss to space is efficient only when a planet had grown to a certain mass. Compared to the abundance of water in primitive materials such as CI chondrites (1–10%), the bulk Earth is indeed dry; roughly 0.023% by weight for the oceans and an uncertain but probably similar amount for the water in the hydrous mantle (Lécuyer, 1998). Rare gas isotopic and elemental abundances also indicate the loss of copious H to space (Pepin, 1991) and since water is the major reservoir of H (at least on the modern Earth), this must be accounted for as well (see below).

The accretion of a late “veneer” of water-rich material has been postulated as the source of Earth’s water. Water-rich carbonaceous chondrite meteorites were early suspects (Boato, 1954). Observations and models of the solar nebula suggest that bodies beyond 2.5 AU may be water rich and the source of carbonaceous chondrites. The relative abundance of D to H of H₂O in these meteorites spans the value of seawater (1.53×10^{-4}). (In these discussion, it should be kept in mind that the material that was the source of Earth’s water may not have any representatives in our meteorite collections or indeed in the solar system; terrestrial planet accretion is a relatively efficient process!) A major contribution by comets (Chyba, 1987), is not consistent with the

D/H values nor the abundances of rare gases (*Dauphas and Marty, 2002*) and is dynamically difficult. Another mechanism of inward water transport is the condensation of ice grains beyond the “snow lines” where temperatures are below 160 K, inward migration by gas drag, and sublimation (*Cyr et al., 1998; Cuzzi and Zahnle, 2004; Mousis and Alibert, 2005*).

New developments in isotopic geochemistry and numerical dynamics calculations have added substance to investigations of the source and timescales of delivery of Earth’s water. Investigators have sought to use the abundance of siderophilic elements (Ni, Co, Ge, and the platinum group elements) in Earth’s crust as a constraint on any “late” (post-core-formation) accretion of primitive material onto Earth (*Chyba et al., 1990*). *Righter and Drake (1997)* has proposed that the high abundances are instead controlled by equilibration with metallic Fe at the base of an early magma ocean. New results illuminate, but do not resolve, this controversy; Nd-isotopic data support the existence of a magma ocean (*Boyet and Carlson, 2005*) but new high-pressure experiments for some elements have not supported *Righter’s* explanation for crustal siderophile abundances (*Holzheid et al., 2000; Righter, 2003; Kegler et al., 2005*). Based on analysis of the Hf-W and Sm-Nd isotope systems, the bulk of Earth is now thought to have accreted in about 10 m.y., and was essentially complete at 30 m.y. (*Jacobsen, 2005; Boyet and Carlson, 2005*). Rapid accretion of Earth makes the delivery of siderophilic elements more dynamically plausible since complete clearing of planetesimals may have taken as long as 300 m.y. (*Goldreich et al., 2004*). This implies that dehydrated but undifferentiated material near Earth’s orbit supplied the siderophilic elements — but no water. (Of course, those same simulations fail to produce Earth in the required 30 m.y.!)

Numerical simulations have been employed to investigate mechanisms by which water-bearing material beyond 2.5 AU might be transported inward to the orbit of Earth. The late impactor cataclysm scenario described in *Gomes et al. (2005)* is not a contender as the event occurs long after the earliest evidence for water on the planet, i.e., the isotopic composition of O in 4.4–4.3-Ga zircons (*Mojzsis et al., 2001*). [Zircons are abundant in granitic rocks produced by partial melting in the presence of water, but zircons have also been found in lunar igneous rocks (*Meyer et al., 1996*)]. Also, the estimated total accreted mass is too low to supply the water. An alternative mechanism is that self-scattering of planetary embryos (and their water) in the late stages of planetary accretion moved water inward (*Morbidelli et al., 2000*). N-body simulations (*Chambers and Wetherill, 1998; Chambers, 2001*) suggest that Earth is the result of the fusion of tens of individual planetary embryos that formed within a broad range of orbital distances. Some of them may originate from regions at or beyond 2.5 AU where hydrated minerals or even ices were stable. Only a small number of these volatile-rich embryos are expected to contribute to the formation of an Earth at 1 AU, but a single Moon-sized embryo formed at 3 AU and made of 10% water by mass

would give Earth the equivalent of five modern oceans. In this scenario, the delivery of water to the telluric planets by “wet” embryos from more distant parts of the primordial solar system is a stochastic process relying on a small number of collisions. As a consequence, the water content of terrestrial planets is expected to be variable, even within a single planetary system. *Raymond et al. (2004)* carried out simulations of embryo scattering and accretion terrestrial planet formation with different nebular solid densities, position of the “snow line,” and orbit of an outer giant planet. The vast majority of planets that formed in the “habitable zone” (0.8–1.5 AU) had water inventories equal to or greater than that of Earth. They found that the terrestrial planets in their simulations ended with an average water abundance about that of Earth, as long as the giant planet configuration was not too different from the one in the solar system. They showed that dry planets and extremely water-rich planets can also be expected.

This mechanism of water delivery can explain the difference in the water inventories of Earth and Mars: At the orbital distance of Mars, planetary formation is less efficient because of the influence of Jupiter, and Mars can be a remaining dry embryo (or the result of a very small number of dry embryos) formed locally and to which water was only brought by the late bombardment (*Lunine et al., 2003*). However, some discrepancies between N-body simulations and observations still need to be explained. *Wiechert et al. (2001)* pointed out that the identical isotope fractionation of O on Earth and the Moon implies a similar composition of the Moon-forming impactor “Theia” and the proto-Earth. Oxygen-isotopic fractionation is a signature of the heliocentric distance of formation. Even if Earth and Theia formed at the same distance from the Sun (*Belbruno and Gott, 2005*) it is difficult to explain how Theia and the proto-Earth could have shared the same isotopic signature. Although O isotopes might have been homogenized in the circumterrestrial disk in the aftermath of the giant impact (*Pahlevan and Stevenson, 2005*), this would not explain its terrestrial-like superchondritic $^{142}\text{Nd}/^{144}\text{Nd}$ (*Boyet and Carlson, 2005*).

Another potential issue with the delivery of water by embryos is its escape from the embryos themselves. “Wet” embryos formed from kilometer-sized objects in $\sim 10^4$ yr but were unable to radiate away the energy of accretion ($>3GM^2/5R$) in this period because the required cooling rate exceeds (by orders of magnitude) the $\sim 300 \text{ W m}^{-2}$ runaway greenhouse limit. This created a “magma ocean” phase, during which a dense steam atmosphere equilibrated with a molten rocky surface (*Zahnle, 1998*). For embryos with masses between 0.01 and 0.1 M_{\oplus} , this phase lasted 0.5 to 4 m.y., which is comparable to the typical lifetime for protoplanetary gas disks (*Lyo et al., 2003; Armitage et al., 2003*). While the disk was present, its opacity screened the embryos from intense UV radiation from the young star (*Ribas et al., 2005*). Once the disk is absent, however, this radiation can drive photolysis of water in the upper atmospheres of water and escape of H to space. Furthermore, if core formation in these embryos is incomplete, water reacts

with Fe in the mantle, releasing large amounts of molecular H (Zahnle, 1998). Escape to space of H from the relatively low gravitational potential of lunar-sized embryos would be efficient. The history of water may be very different in the inner regions of planetary systems that hosted different-sized embryos (due to a different mass surface density and isolation mass, for example) or had a different disk lifetime than that of our solar system.

How much water is “enough,” and where does it end up? Matsui and Abe (1986) showed that the amount of water at Earth’s surface is roughly what would be expected were it controlled by the solubility of water in silicate melt, i.e., an early magma ocean. Besides the reservoir of the global ocean, a significant amount of water may be sequestered in the mantle. The concentration of water in Earth’s mantle is a subject of active research (Tarits *et al.*, 2004) but it may be the equivalent of several oceans (Litasov *et al.*, 2003). A significant amount of water could have been lost as the hydrous silicates reacted with metallic Fe during core formation to form Fe hydrides (FeH_x) that would be sequestered into core. The residual O then reacted with ferrous Fe in the mantle. Hiraio *et al.* (2004) estimates that the core could contain H that is the equivalent of 8–24 oceans of water. Water may also have been lost by erosion of the atmosphere by giant impacts, and (as H) by continued hydrodynamic escape from the growing planet (Pepin, 1991). Chen and Ahrens (1997) estimated that such impacts produce ground velocities above the escape velocity, resulting in the escape of almost all the atmosphere. However, the question was revisited by Genda and Abe (2003): They found that, even in a collision the size of the Moon-forming impact, less than 30% of the atmosphere of both bodies is lost to space. Therefore, giant impacts can actually result in a net delivery of water to the growing protoplanet.

There may be other, important mechanisms for the removal of volatiles, including water from the surfaces of otherwise “habitable” planets. The habitable zone of M stars is very close to the star. Because M stars tend to have a higher ratio of X-ray and ultraviolet to bolometric luminosity, radiation and stellar wind-driven escape of planetary atmospheres may be important. Exospheric temperatures between 10,000 and 30,000 K are expected. It is within this range of temperature that Jeans (thermal) escape of the atmosphere is significant. Figure 1 shows the mass loss from a terrestrial planet for O (solid), N (dotted), and C (dashed) for a CO_2 -rich atmosphere with 10% of N, as a function of the planetary mass. (Planets with high CO_2 levels are attractive in this context because the diurnal temperature difference on the tidally locked planet is damped.) The mass loss is given in units of mass of Earth atmosphere per billion year. Thin lines are for $T_{\text{exo}} = 10,000$ K and thick lines for 30,000 K. At these temperatures, H loss is of course diffusion-limited.

But around G stars, terrestrial planets may have water abundances much larger than that of the Earth. Kuchner (2003) described another mechanism of forming water-rich worlds; migration of entire icy planets inward by interaction with a gas or planetesimal disk. Such “ocean planets” have

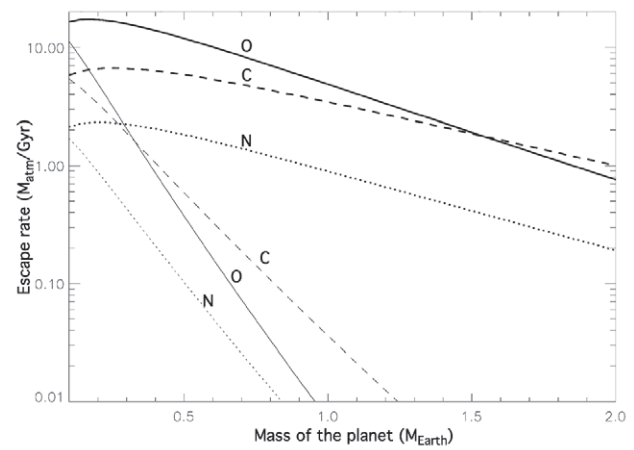


Fig. 1. Mass loss from a terrestrial planet in the habitable zone of an M star for O (solid), N (dotted), and C (dashed) for a CO_2 -rich atmosphere with 10% N, as a function of the planetary mass. The mass loss is given in units of Earth’s present atmosphere per billion years. Thin lines are for an exosphere temperature of 10,000 K and thick lines are for 30,000 K. At these temperatures, H loss is diffusion limited (Kulikov *et al.*, 2006).

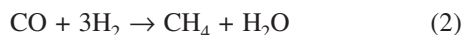
also been described by Léger *et al.* (2004). The abundance of water in a planet-forming nebula may have other secondary but potentially important implications for habitability, namely the presence of a giant planet and its dynamical effects. For example, the leading theory for the formation of Jupiter (and some of the habitability properties that it may confer to Earth) involves the rapid accretion of a core before depletion of nebular gas, an accretion accelerated by condensation of water beyond the “snow line” (Stevenson and Lunine, 1988). Nebulae with varying water abundances would presumably be more or less likely to form gas-accreting cores.

3.3. Planetary Composition and Diversity

As proposed by Kuchner (2003) and Léger *et al.* (2004), Earth-sized planets around other stars may have very different bulk compositions than that of our planet. Even seemingly minor differences in planetary composition could affect — perhaps dramatically — geologic activity and geochemical cycles at the planet’s surface. Just as distance from the Sun, accretion history, and incorporation of varying amounts of nebular gas have produced a diversity of planets in our solar system, we should expect no less diversity, or probably much more, among a collection of planetary systems with different cosmochemical inheritances and formation histories. For example, two abundant planet-forming elements are Si and Fe. Silicon is an α -chain element and produced in massive stars, whereas Fe is produced primarily in type I SN from intermediate stars. As a consequence the ratio Fe/Si has increased with time. This will influence the size of planetary cores relative to the mantle as well as the

abundance of radiogenic ^{60}Fe , an important heat source in the early nebula. Even the relative abundances of the major silicate mineral-forming elements (which controls such properties as melting temperature) vary more from star to star than they do within the solar system (Fig. 2). Some potential relationships between cosmochemistry, planetary composition, and habitability have been discussed by *Gonzalez et al.* (2001) and *Gaidos et al.* (2005). Gaidos (in preparation) calculated the relative rates of geologic activity on an Earth whose bulk mantle composition was that of CI chondrites (perhaps not far from the actual Earth) and a planet of identical size whose composition was that of enstatite EH chondrite after the metal has been removed. The latter has a significantly higher concentration of the long-lived radioisotopes ^{40}K , ^{232}Th , ^{235}U , and ^{238}U (*Anders and Grevesse, 1989; Newsom, 1995*) and such a body would have significantly enhanced rates of geologic activity, and would remain active for a longer period of time.

A major parameter that controls the composition of planets is the ratio of C to O (C/O) in the primordial nebula. Carbon and O are the two most abundant elements in the interstellar medium after H and He; their predominant form in the interstellar medium is thermodynamically stable CO molecules. Collapse of molecular cloud gas leads to higher pressures that favor the formation of water and methane



However, this reaction is kinetically inhibited on formation timescales (millions of years) and requires a catalyst such

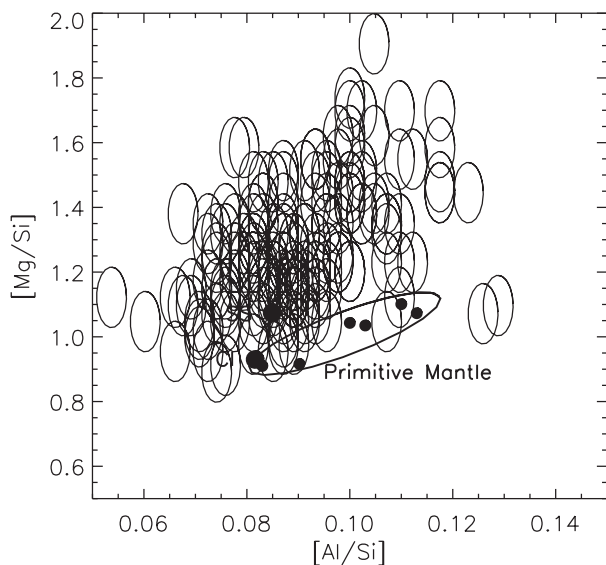


Fig. 2. Plot of Mg/Si vs. Al/Si on hypothetical planet-forming nebula based on the solar-type star photosphere data of *Edvardsson et al.* (1993). Circles represent the approximate range due to measurement errors. Edvardsson et al. measurements are compared with solar system (SS), chondritic (CI), and several primitive terrestrial mantle models. From Gaidos, in preparation.

as free Fe (*Lewis and Prinn, 1980*). If O is more abundant than C, then nearly all C is bound in CO and remaining O is available for the formation of H_2O . Conversely, excess C results in all O being bound in CO, absence of H_2O , and the formation of graphite and organic molecules.

The solar photosphere has a C/O of 0.5 ± 0.07 (*Allendo Prieto et al., 2002*), and presumably the primordial nebula was oxidizing and water-rich. Measurements of C and O abundances in nearby solar-type stars both with and without planets suggest a significant scatter in C/O (Gaidos, in preparation) with the Sun occupying a relatively C-poor, “water-rich” region of the distribution and some stars with $\text{C/O} > 1$. Solar-mass stars do not themselves produce significant C or O, and therefore these abundances reflect that of the gas and dust (ISM and molecular clouds) from which the stars formed. Stellar nucleosynthesis theory predicts that the relative production and ejection of C and O from massive stars (in winds and supernova ejecta) depend on stellar mass, metallicity, and the amount of “dredge-up” from the C-rich interior (*Woosley and Weaver, 1995*). About 57% of the C returned to the ISM from a solar-metallicity stellar population is via the winds of massive stars: 33% is produced in intermediate-mass stars and the remainder in high-mass star ejecta. Oxygen is almost entirely (87%) derived from supernovae and the rest is from their winds. Molecular clouds and their offspring can have different C/O because of local supernovae. Thus stars and disks that form from the chemically heterogeneous and evolving interstellar medium will start with different C/O ratios. The mean C/O of stellar ejecta increases with galactic radius such that the older bulge should be more O-rich than the younger disk. As the galaxy ages, the C/O ratio of the ISM and the stars that form from it increases (Fig. 3). This picture is consistent with observations of dwarf galaxies (*Garnett et al., 1995*).

Within a single star-forming region, the C/O can vary because of condensation and sedimentation of grains (*Lattanzio, 1984*) or contamination by very massive, short-lived stars within the same generation. In fact, the primordial chemistry of the solar system may have been influenced by mass loss from nearby massive stars. *Olive and Schramm* (1982), among others, have suggested that anomalous Al-, Pd-, and O-isotopic ratios in the solar system can be explained if the primordial nebula was contaminated with ejected from supernovae, possibly from short-lived massive stars formed in association with the Sun. Local C/O in a planet-forming disk will also be altered by diffusion of water outward along the thermal gradient (*Cyr et al., 1999*) and pile-up of C-rich interstellar dust in the inner regions of a disk.

The condensation sequence in a nebula with $\text{C/O} \sim 1$ will be markedly different than that proposed for solar conditions, namely carbides will replace silicates and C will precipitate as graphite (*Larimer, 1975; Sharp, 1990*). *Gaidos* (2000) suggested that terrestrial planets would be composed of SiC, a ceramic with melting temperatures exceeding 3000 K, as well as other carbides. *Kuchner and Seager* (2006) discuss the properties of potential $\text{C/O} \gg 1$ planets and cal-

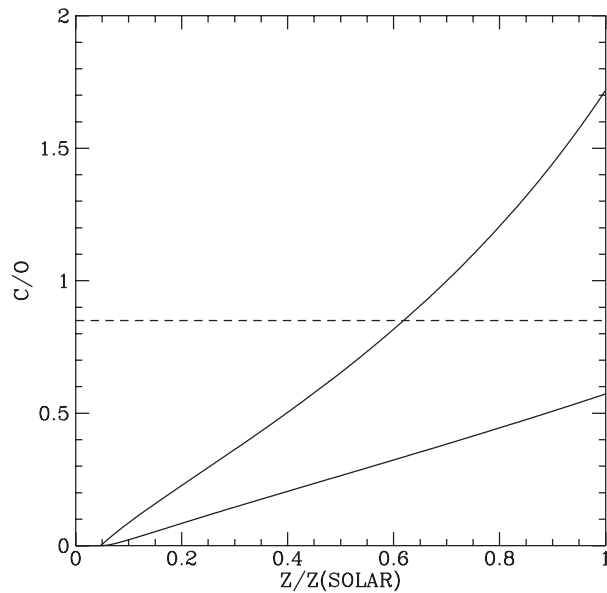


Fig. 3. Calculated evolution of the C/O of stellar wind and supernova ejecta (top line) and the average interstellar medium (bottom line) in the disk as a function of the abundance of heavy elements normalized to the solar value. The dashed line is the approximate threshold above which reducing, rather than oxidizing, conditions are expected. The solar photosphere has C/O of 0.5. From Gaidos, in preparation.

culated an atmospheric spectrum. They proposed that the surface of these planets will be covered with organics. A “ceramic planet” will have a Fe-Ni core containing 5–7% of dissolved C. Because of the high melting temperature of SiC, the planet will heat up by a corresponding amount until mantle convection can remove the heat produced by radiogenic elements. The core will be entirely molten and this may mean that such a planet will lack a magnetic field (Gaidos, in preparation). Excess C in the mantle will exist as either graphite, diamond, or liquid C, depending on conditions. The last will be extremely buoyant and may erupt to the surface. Because of the high thermal conductivity of SiC (2–3 times that of silicates), a thick, rigid lithosphere will develop and plate tectonics will be less likely. This example shows that future searches for other Earths may find instead rather exotic planets. There is really only one way to find out.

4. EXTRASOLAR EARTHS AND OTHER ORIGINS

4.1. Prospects in the Solar System

It is difficult to test theories of the origin of life when we are limited to a single example and when all of the early record of that life is lost. Thus searches for a second origin of life outside the Earth are paramount to understanding our own origins. Historically, Mars has been the favorite target

in the solar system; it is the nearest planet with an accessible surface, and has an atmosphere and evidence for past geological processes and water. Initial disappointment that the Viking missions did not turn up unambiguous evidence for even simple life forms and that the surface proved chemically inhospitable directed subsequent searches for habitable conditions (i.e., liquid water) into Mars’ past (or most recently with the MARSIS radar, deep beneath its surface). Geomorphological evidence from orbit in the form of outflow channels, valley networks, and possible playa lakes has now been complemented by more direct geological evidence in the form of aqueous alteration and evaporite deposition (Squyres *et al.*, 2004; Herkenhoff *et al.*, 2004; Klingelhöfer *et al.*, 2004; Rieder *et al.*, 2004; Haskin *et al.*, 2005; Hynek, 2004). A picture is emerging of a very early period (of uncertain duration, but perhaps a few hundred million years) of a warm, wet Mars, and a cold Mars in the intervening time (Jakosky and Phillips, 2001; Gaidos and Marion, 2003; Solomon *et al.*, 2005). A very exciting possibility is that, due to a cold climate regime and the absence of plate tectonics, Mars has preserved information about early prebiotic conditions that has been lost on Earth. The oldest rock on Earth is a meteorite from Mars (4.5 Ga).

Recent discoveries have also rejuvenated the possibility of habitable environments on current Mars, albeit at isolated locations in the subsurface. These include the presence of abundant regolith ice, the discovery of “young” gully-like formations, and the detection of atmospheric methane (Mumma *et al.*, 2004; Krasnopolsky *et al.*, 2004; Formisano *et al.*, 2004). Methane can be produced from the high-temperature reduction of CO₂ by H₂ during hydrothermal serpentinization of mafic rock (Oze and Sharma, 2005; Lyons *et al.*, 2005). While the possibility of biogenic methane cannot yet be ruled out, the estimated atmospheric concentration of a few tens of parts per billion and the lifetime in the atmosphere (~300 yr) suggest a source flux much weaker than the estimated abiogenic flux of methane on Earth. If reports of latitudinal variation in methane abundance are correct (M. Mumma, personal communication), the lifetime must be much shorter (~1 yr) and the flux commensurately higher. Combined with an upper limit for SO₂ (Krasnopolsky, 2005) this might disfavor an abiotic seepage source. However, martian geochemistry might be more reducing, thereby favoring a higher CH₄/SO₂ ratio, and SO₂ disproportionates in water to sulfate (which is soluble) and hydrogen sulfide (which will rapidly oxidize to sulfuric acid in the Mars atmosphere). Regardless, Mars CH₄ gives future astrobiological investigations a focus, e.g., measurement of the ratio of stable C isotopes to search for biogenic fractionation. If life is found on Mars, one possibility is that it will be unexpectedly familiar. Efficient ejection and transfer of material between the planets may have produced a common ancestry between the planets. However, if Mars was once habitable and no evidence for past or present life is found, this constrains models of lithopanspermia.

Beyond Mars, there are prospects for habitable environments in the water-rich interiors of the icy satellites of Ju-

Jupiter, including Europa and Callisto, and the satellites of Saturn, Titan and Enceladus. The debate on the suitability of these objects to support life centers around the potential energy sources available; while plausible energy sources are many orders of magnitude lower than the potential energy from sunlight on Earth (Gaidos *et al.*, 1999), there are several mechanisms by which very low energy fluxes might be generated in the form of a redox gradient between the atmosphere and the surface, or between the crust and an interior ocean (Gaidos *et al.*, 1999; Chyba and Phillips, 2002). At the minimum, these bodies offer examples of possible prebiotic chemistries in the solar system that might be literally frozen in time. However, the same dynamical barriers, radiation environment, and thick crust that have isolated these bodies from contamination by interplanetary transfer of Earth material also challenge the technologies of humans that choose to investigate these intriguing environments.

4.2. Extrasolar Planets

Because the objects in our solar system are likely to represent a meager sample of the cosmic diversity of possible habitats for life, a more complete understanding of the potential abundance and distribution of life depends on the successful exploration of other planetary systems. The Kepler (Borucki *et al.*, 2003) and Corot (Bordé *et al.*, 2003) observatories will be capable of detecting Earth-sized planets as they transit the parent star and will foreshadow the eventual deployment of far more advanced telescopes that can directly detect the emitted or reflected light from such planets. As spatial resolution of such planets is beyond foreseeable technology and sources of funding, such characterization will rely on spectroscopy of their surfaces and atmosphere. Life manifests itself by *biosignatures*, in this case spectral features of the surface or atmosphere that reflect its biogeochemical activity and cannot be found in the absence of life. However, it is possible that abiotic mechanisms that are not known in the solar system might reproduce what was thought to be a reliable biomarker. In fact, many features once claimed to be biosignatures now have convincing abiotic explanations, e.g., martian vegetation (Sinton, 1957) and “nanobacteria” in the ALH 84001 meteorite (McKay *et al.*, 1996). The reliability of a biosignature depends strongly on contextual information. For instance, the detection of an O₂-containing atmosphere does not have the same implications on the icy moon of a giant planet compared to a terrestrial planet in the habitable zone of its star (Selsis *et al.*, 2002). This is because on the latter the weathering of minerals will consume O₂ and the only source of comparable intensity is oxygenic photosynthesis. Conversely, the detection of O₂ or O₃ is certainly a better biomarker when associated with a reducing compound such as CH₄ or NH₃ (Lovelock, 1975).

Moreover, the absence of a biosignature may not be evidence that a planet is lifeless, just that a particular metabolism is not present, that the activity is below detectable limits, or that differences in the planet’s abiotic chemistry mask

the biological effect. Let us consider that a metabolism M (for instance, oxygenic photosynthesis) produces a biogenic species S (O₂) that, upon accumulation in the atmosphere, can result in a spectral signature B (the 760-nm band of O₂ or the 9.6 μm of O₃). The nondetection of B could have multiple explanations: (1) Life forms based on M do not exist on this planet. (2) Life forms based on M do exist but S does not reach detectable concentrations. This was probably the case on Earth between the emergence of O₂ producers and the rise of O₂, a period that could have lasted 500–1500 m.y. (Catling and Claire, 2005). (3) S reaches levels that would be detectable alone but B is masked by other spectral features; e.g., the 9.6-μm O₃ band would be masked by the high CO₂ level required for greenhouse warming in most of the habitable zone (Selsis *et al.*, 2002). The Lovelock example is another case in point. The thermodynamic disequilibrium that Lovelock advocated as a biosignature is a result of photosynthesis and the conversion of electromagnetic energy into potential chemical energy in the atmosphere. In the absence of photosynthesis, one biosignature might be the *absence* of such a disequilibrium, as this represents an unused source of energy for microorganisms (Weiss *et al.*, 2000b).

The spectrum of Earth exhibits biosignatures, including the presence of O₂ (and O₃) simultaneously with CH₄, that are detectable from space (Sagan *et al.*, 1993). Table 2 gives some groups of atmospheric molecular bands that could serve as biosignatures for future missions. Any biomarker should include the signature of H₂O, water being considered as a requisite for life as we know it. Some of the listed features are not observable in the spectrum of present Earth but may have been present in the past. Some other biogenic compounds, such as N₂O, were probably never observable in a low-resolution spectrum of Earth but would be at slightly higher concentrations. In addition to atmospheric molecules, the vegetation “red edge” (the increase of plant reflectivity between 700 and 800 nm) may be another promising way to detect complex extraterrestrial life (Arnold *et al.*, 2002; Seager *et al.*, 2005). However, the red edge results from photosynthetic pigments like chlorophyll that are much more complex than simple gases such as O₂. A life form able to use H₂O as an electron donor to reduce CO₂ will produce O₂ whatever the pigments or the energy source. On the other hand, evolution could select other pigments, characterized by different radiative properties. Moreover, detecting the red-edge on a distant Earth replica requires a level of resolution and sensitivity that will not be reached by the next generation of telescopes. There may be other, more readily obtainable pieces of information contained in the time-variability of emitted or reflected radiation from a planet about its ability to support life, e.g., period of rotation and the presence of an ocean or thick atmosphere (Ford *et al.*, 2001; Gaidos and Williams, 2004; Williams and Gaidos, 2005).

Our ignorance of when and where life emerged in our solar system, as well as the complexities associated with the maintenance of life on planetary bodies, means that this area of scientific inquiry will be driven by observations into the

TABLE 2. Atmospheric biomarkers: Molecular bands detectable by future space observatories at infrared (6–20 μm) and optical (0.5–0.8 μm) wavelengths with plausible spectral resolution.

λ (μm)	IR ($\lambda/\Delta\lambda = 25$)						Visible ($\lambda/\Delta\lambda = 70$)			
	H ₂ O	CO ₂	O ₃	CH ₄	N ₂ O	NX	H ₂ O	O ₂	O ₃	CH ₄
	<8	15	9.6	7.5	7.8	*	0.72	0.76	0.6	0.73
	>18				17			0.82	± 0.1	0.79
Level [†]	<1	<1	<10	‡	>10	>100	≤ 1	<10	≥ 1	>50
	IR alone						Visible alone			
	•	•	•				◦	◦	(◦)	§
	•		•	•			•	•	(•)	§
	•				•					
	•		•							
	•			•						
	◦					◦				
	Examples of Biosignatures Requiring both IR and Visible									
	(◦)	◦					◦	◦	(◦)	¶
	•	(•)	•				•			**

A planet exhibits a biosignature if all the marked bands from a same line are detected in its spectrum. Bands in parentheses are conditional. Empty circles indicate an unlikely but known possible abiotic origin (Owen, 1980; Léger et al., 1993, 1999; Léger, 2000; Des Marais et al., 2002; Selsis et al., 2002; Segura et al., 2003; Kasting and Catling, 2003; Selsis et al., 2005).

*NX = NO, NO₂, or NH — See Selsis et al. (2005) for wavelengths and required abundance.

† Levels in present atmospheric level (PAL) required for detection at the expected resolution.

‡ 1 PAL without H₂O, >20 PAL with H₂O.

§ O₃ conditional: tracer of O₂.

¶ Dense CO₂ atmosphere: the IR band of O₃ is hidden.

** O₂ and O₃ too low for visible but O₃ detected in IR, CH₄ hidden by H₂O in IR.

foreseeable future. As a consequence, the first planet-characterizing missions must be designed for broader objectives than the search for a specific biomarker. Perhaps the best approach is to “expect the unexpected” and to design instruments not on the basis of a specific biosignature, but to maximize the potential for characterization of the physical and chemical properties of the planet. Inference of biological activity on a planet could emerge from a more general understanding of its spectrum, even if none of the expected biosignatures are found. For the foreseeable future, a working definition for the biosignatures of remote, inaccessible planetary life might remain *chemical phenomena that cannot be explained by all known abiotic chemistry*. This is ultimately an unsatisfactory state of affairs but we should not despair too quickly: Not quite four centuries have elapsed since Galileo turned his telescope to the other planets in our solar system, and it has been a mere decade since the discovery of the first extrasolar planet around a main-sequence star. Should our species desist from threatening the life and habitability of this world, our progeny will have the fullness of time to answer the question of whether other planets host living beings and whether any of them also ponder the same questions.

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REFERENCES

- Adams F. C. and Spiegel D. N. (2005) *Astrobiol.*, 5, 497–514.
- Alexander C. M. O’D., Russell S. S., Arden J. W., Ash R. D., Grady M. M., and Pillinger C. T. (1998) *Meteoritics & Planet. Sci.*, 33, 603–622.
- Allende-Prieto C., Lambert D. L., and Asplund M. (2002) *Astrophys. J.*, 573, L137–L140.
- Anbar A. D., Zahnle K. J., Arnold G. L., and Mojzsis S. J. (2001) *J. Geophys. Res.*, 106, 3219–3236.
- Anders E. and Grevesse N. (1989) *Geochim. Cosmochim. Acta*, 53, 197–214.
- Anders E., DuFresne A., Fitch F. W., Cavaillé A., Dufresne E. R., and Hayatsu R. (1964) *Science*, 146, 1157–1161.
- Armitage P. J., Clarke C. J., and Palla F. (2003) *Mon. Not. R. Astron. Soc.*, 342, 1139–1146.
- Arnold L., Gillet S., Lardié O., Riaud P., and Schneider J. (2002) *Astron. Astrophys.*, 392, 231–237.
- Ashgari N., Broeg C., Carone L., Casa-Miranda R., Castro Palacio J. C., et al. (2004) *Astron. Astrophys.*, 426, 353–365.

- Bada J. L., Bigham C., and Miller S. L. (1994) *Proc. Natl. Acad. Sci. USA*, *91*, 1248–1250.
- Belbruno E. and Gott J. R. III (2005) *Astron. J.*, *129*, 1724–1745.
- Bhattacharya J. P., Payenberg T. H. D., Lang S. C., and Bourke M. (2005) *Geophys. Res. Lett.*, *32*, L10201.
- Boato G. (1954) *Geochim. Cosmochim. Acta*, *6*, 209–220.
- Bordé P., Rouan D., and Léger A. (2003) *Astron. Astrophys.*, *405*, 1137–1144.
- Borucki W. J., Koch D. G., Lissauer J. J., Basri G. B., Caldwell J. F., et al. (2003) *Proc. SPIE Conf.*, *4854*, 129–140.
- Bowring S. A. and Williams I. S. (1999) *Contrib. Mineral. Petrol.*, *134*, 3–16.
- Boyet M. and Carlson R. W. (2005) *Science*, *309*, 576–581.
- Brasier M. D., Green O. R., Jephcoat A. P., Kleppe A. K., van Krenedonk M. J., et al. (2002) *Nature*, *416*, 76–81.
- Brasier M., Green O., Lindsay J., and Steele A. (2004) *Orig. Life Evol. Biosph.*, *34*, 257–269.
- Brochier C. and Philippe H. (2002) *Nature*, *417*, 244.
- Browning L. and Bourcier W. (1996) *Meteoritics & Planet. Sci.*, *31*, A22.
- Burchell M. J., Shrine N. R. G., Mann J., Bunch A. W., Brandão P., et al. (2001) *Adv. Space Res.*, *28*, 707–712.
- Burchell M. J., Galloway J. A., Bunch A. W., and Brandão P. F. B. (2003) *Orig. Life Evol. Biosph.*, *33*, 53–74.
- Burchell M. J., Mann J. R., and Bunch A. W. (2004) *Mon. Not. R. Astron. Soc.*, *352*, 1273–1278.
- Caldeira K. and Kasting J. F. (1992) *Nature*, *360*, 721–723.
- Carr M. H. (1999) *J. Geophys. Res.*, *104*, 21897–21910.
- Castresana J., Lübben M., Saraste M., and Higgins D. G. (1994) *EMBO J.*, *13*, 2516–2525.
- Catling D. C. (2006) *Science*, *311*, 38a.
- Catling D. C. and Claire M. W. (2005) *Earth Planet. Sci. Lett.*, *237*, 1–20.
- Cech T. R. (1986) *Cell*, *44*, 207–210.
- Chambers J. E. (2001) *Icarus*, *152*, 205–224.
- Chambers J. E. and Wetherill G. W. (1998) *Icarus*, *136*, 304–327.
- Chen G. Q. and Ahrens T. J. (1997) *Phys. Earth Planet. Inter.*, *100*, 21–26.
- Chyba C. F. (1987) *Nature*, *330*, 632–635.
- Chyba C. F. and Hand K. P. (2005) *Ann. Rev. Astron. Astrophys.*, *43*, 31–74.
- Chyba C. F. and Phillips C. B. (2002) *Origins Life Evol. Biosph.*, *32*, 47–67.
- Chyba C. F., Thomas P. J., Brookshaw L., and Sagan C. (1990) *Science*, *249*, 366–373.
- Chyba C. F., Whitmire D. P., and Reynolds R. (2000) In *Protostars and Planets IV* (V. Mannings et al., eds.), pp. 1365–1393, Univ. of Arizona, Tucson.
- Clark B. C., Baker A. L., Cheng A. F., Clement S. J., McKay D., et al. (1999) *Orig. Life Evol. Biosph.*, *29*, 521–545.
- Cody G. D. (2004) *Ann. Rev. Earth Planet. Sci.*, *32*, 569–599.
- Cody G. D., Boctor N., Filley T. R., Hazen R. M., Scott J. H., Sharma A., and Yoder H. S. Jr. (2001) *Science*, *289*, 1337–1340.
- Cody G. D., Alexander C. M. O., and Tera F. (2002) *Geochim. Cosmochim. Acta*, *66*, 1851–1865.
- Cohen B. A., Swindle T. D., and Kring D. A. (2000) *Science*, *290*, 1754–1755.
- Commeyras A., Taillades J., Collet H., Boiteau L., Vandenbeeke-Trambouze O., et al. (2004) *Orig. Life Evol. Biosph.*, *34*, 35–55.
- Cooper G., Kimmich N., Bellsle W., Sarinana J., Brabham K., and Garrel L. (2001) *Nature*, *414*, 879–883.
- Corliss J. B., Dynmond J., Gordon L. I., Edmont J. M., von Herzen R. P., et al. (1979) *Science*, *203*, 1073–1083.
- Craddock R. A. and Howard A. D. (2002) *J. Geophys. Res.*, *107*, 5111.
- Crick F. H. C. (1968) *J. Mol. Biol.*, *38*, 367–379.
- Cuzzi J. N. and Zahnle K. J. (2004) *Astrophys. J.*, *614*, 490–496.
- Cyr K. E., Sears W. D., and Lunine J. I. (1998) *Icarus*, *135*, 537–548.
- Cyr K. E., Sharp C. M., and Lunine J. I. (1999) *J. Geophys. Res.*, *104*, 19,003–19,014.
- Dalrymple G. B. and Ryder G. (1993) *J. Geophys. Res.*, *98*, 13,085–13,095.
- Dauphas N. and Marty B. (2002) *J. Geophys. Res.*, *107*, 5129, doi:10.1029/2001JE001617.
- Davies P. C. W. and Lineweaver C. H. (2005) *Astrobiol.*, *5*, 154–163.
- Des Marais D. J., Harwit M. O., Jucks K. W., Kasting J. F., Lin D. N. C., et al. (2002) *Astrobiol.*, *2*, 153–181.
- Di Giulio M. (2003) *J. Mol. Evol.*, *57*, 721–730.
- Edvardsson B., Andersen J., Gustafsson B., Lambert D. L., Nissen P. E., and Tomkin J. (1993) *Astron. Astrophys.*, *275*, 101–152.
- Ehrenfreund P. and Charnley S. B. (2000) *Ann. Rev. Earth Planet. Sci.*, *38*, 427–483.
- Engel M. H. and Nagy B. (1982) *Nature*, *296*, 837–840.
- Érdi B., Dvorak R., Sándor Z., Pilat-Lohinger E., and Funk B. (2004) *Mon. Not. R. Astron. Soc.*, *351*, 1043–1048.
- Fedo C. M. and Whitehouse M. J. (2002) *Science*, *296*, 1448–1452.
- Fernández J. A. and Ip W. H. (1983) *Icarus*, *54*, 377.
- Ford E. B., Seager S., and Turner E. L. (2001) *Nature*, *412*, 885–887.
- Formisano V., Atreya S., Encrenaz T., Ignatiev N., and Giuranna M. (2004) *Science*, *306*, 1758–1761.
- Franck S., Block A., von Bloh W., Bounama C., Schellnhuber H.-J., and Svirezhev Y. (2000) *Planet. Space Sci.*, *48*, 1099–1105.
- Frei R. and Rosing M. T. (2005) *Earth Planet. Sci. Lett.*, *236*, 28–40.
- Furnes H., Banerjee N. R., Muehlenbachs K., Staudigel H., and de Wit M. (2004) *Science*, *304*, 578–581.
- Gaidos E. J. (2000) *Icarus*, *145*, 637–640.
- Gaidos E. J. and Marion G. (2003) *J. Geophys. Res.*, *108*, doi:10.1029/2002JE002000.
- Gaidos E. and Williams D. M. (2004) *New Astron.*, *10*, 67–77.
- Gaidos E. J., Nealon K. H., and Kirschvink J. L. (1999) *Science*, *284*, 1631–1633.
- Gaidos E., Deschenes B., Dundon L., Fagan K., McNaughton C., Menviel-Hessler L., Moskovitz N., and Workman M. (2005) *Astrobiol.*, *5*, 100–126.
- Galtier N., Tourasse N., and Gouy M. (1999) *Science*, *283*, 220–221.
- Garnett D. R., Skillman E. D., Dufour R. J., Peimbert M., Torres-Peimbert S., et al. (1995) *Astrophys. J.*, *443*, 64–76.
- Genda H. and Abe Y. (2003) *Icarus*, *165*, 149–162.
- Gilbert W. (1986) *Nature*, *319*, 618.
- Gladman B. and Burns J. A. (1996) *Science*, *274*, 161–162.
- Gladman B., Dones L., Levison H. F., and Burns J. A. (2005) *Astrobiol.*, *5*, 483–496.
- Goldreich P., Lithwick Y., and Sari R. (2004) *Astrophys. J.*, *614*, 497–507.
- Gomes R., Levison H. F., Tsiganis K., and Morbidelli A. (2005) *Nature*, *435*, 466–469.
- Gonzalez G., Brownlee D., and Ward P. (2001) *Icarus*, *152*, 185–200.
- Goswami J. N., Sinha N., Murty S. V. S., Mohapatra R. K., and Clement C. J. (1997) *Meteoritics & Planet. Sci.*, *32*, 91–96.
- Grotzinger J. P. and Rothman D. H. (1996) *Nature*, *383*, 423–425.
- Hahn J. M. and Malhotra R. (1999) *Astron. J.*, *117*, 3041–3053.
- Hart M. H. (1979) *Icarus*, *37*, 351–357.
- Haskin L. A., Wang A., Jolliff B. L., McSween H. Y., Clark B. C., et al. (2005) *Nature*, *436*, 66–69.
- Herkenhoff K. E., Squyres S. W., Arvidson R., Bass D. S., Bell J. F. III, et al. (2004) *Science*, *306*, 1727–1730.
- Hirao N., Kondo T., Ohtani E., Takemura K., and Kikegawa T. (2004) *Geophys. Res. Lett.*, *31*, L06616.
- Holm N. G. and Andersson E. (2005) *Astrobiol.*, *5*, 444–460.
- Holzheid A., Sylvester P., O'Neill H. S. C., Rubie D. C., and Palme H. (2000) *Nature*, *406*, 396–399.
- Horneck G., Rettberg P., Reitz G., Wehner J., Eschweiler U., et al. (2001) *Orig. Life Evol. Biosph.*, *31*, 527–546.
- Huang S.-S. (1959) *Am. Sci.*, *47*, 392–402.
- Huber C. and Wächtershäuser G. (1997) *Science*, *276*, 245–247.
- Hynek B. M. (2004) *Nature*, *431*, 156–159.
- Jacobsen S. B. (2005) *Ann. Rev. Earth Planet. Sci.*, *33*, 531–570.
- Jakosky B. M. and Phillips R. (2001) *Nature*, *412*, 237–244.
- Ji J., Liu L., Kinoshita H., and Li G. (2005) *Astrophys. J.*, *631*, 1191–1197.

- Johnson D. C., Dean D. R., Smith A. D., and Johnson M. K. (2005) *Ann. Rev. Biochem.*, *74*, 247–281.
- Jones B. W., Underwood D. R., and Sleep P. N. (2005) *Astrophys. J.*, *622*, 1091–1101.
- Joshi M. M., Haberle R. M., and Reynolds R. T. (1997) *Icarus*, *129*, 450–465.
- Joyce G. (2004) *Ann. Rev. Biochem.*, *73*, 791–836.
- Kasting J. F. and Catling D. (2003) *Ann. Rev. Astron. Astrophys.*, *41*, 429–463.
- Kasting J. F., Whitmire D. P., and Reynolds R. T. (1993) *Icarus*, *101*, 108–128.
- Kegler P., Holzheid A., Rubie D. C., Frost D., and Palme H. (2005) In *Lunar Planet. Sci. Conf. XXXVI*, Abstract #2030.
- Keil K. (2000) *Planet. Space Sci.*, *48*, 887–903.
- Klingelhöfer G., Morris R. V., Bernhardt B., Schröder C., Rodionov D. S., et al. (2004) *Science*, *306*, 1740–1745.
- Krasnopolsky V. A. (2005) *Icarus*, *178*, 487–492.
- Krasnopolsky V. A., Maillard J. P., and Owen T. C. (2004) *Icarus*, *172*, 537–547.
- Kuchner M. J. (2003) *Astrophys. J.*, *596*, L105–L108.
- Kuchner M. J. and Seager S. (2006) *Astrophys. J.*, in press.
- Kulikov Y. N., Lammer H., Lichtenegger H. I. M., Terada N., Ribas I., et al. (2006) *Icarus*, in press.
- Kvavonidze K., Lawless J., Pering K., Peterson E., Flores J., et al. (1970) *Nature*, *228*, 923–926.
- Larimer J. W. (1975) *Geochim. Cosmochim. Acta*, *39*, 389–392.
- Laskar J. (1994) *Astron. Astrophys.*, *287*, L9–L12.
- Lathe R. (2004) *Icarus*, *168*, 18–22.
- Lattanzio J. C. (1984) *Mon. Not. R. Astron. Soc.*, *207*, 309–322.
- Lécuyer C. (1998) *Chem. Geol.*, *145*, 249–261.
- Lee D.-C., Halliday A. N., Leya I., Wieler R., and Wiechert U. (2002) *Earth Planet. Sci. Lett.*, *198*, 267–274.
- Léger A. (2000) *Adv. Space Res.*, *25*, 2209–2223.
- Léger A., Pirre M., and Marceau F. J. (1993) *Astron. Astrophys.*, *277*, 309–313.
- Léger A., Ollivier M., Altwegg K., and Woolf N. J. (1999) *Astron. Astrophys.*, *341*, 304–311.
- Léger A., Selsis F., Sotin C., Guillot T., Despois D., Mawet D., Ollivier M., Labèque A., Valette C., Brachet F., Chazelas B., and Lammer H. (2004) *Icarus*, *169*, 499–504.
- Levy M. and Miller S. L. (1998) *Proc. Natl. Acad. Sci. USA*, *95*, 7933–7938.
- Lewis J. S. and Prinn R. G. (1980) *Astrophys. J.*, *238*, 357–364.
- Lineweaver C. H. and Davis T. (2002) *Astrobiol.*, *2*, 293–304.
- Litasov K., Ohtani E., Langenhorst F., Yurimoto H., Kubo T., and Kondo T. (2003) *Earth Planet. Sci. Lett.*, *211*, 189–203.
- Lovelock J. E. (1975) *Proc. R. Soc. London*, *B189*, 167–180.
- Lunine J., Chambers J., Morbidelli A., and Leshin L. (2003) *Icarus*, *165*, 1–8.
- Lyo A.-R., Lawson W. A., Mamajek E. E., Feigelson E. D., Sung E.-C., and Crause L. A. (2003) *Mon. Not. R. Astron. Soc.*, *338*, 616–622.
- Lyons J. R., Manning C., and Nimmo F. (2005) *Geophys. Res. Lett.*, *32*, L13201.
- Maher K. A. and Stevenson D. J. (1988) *Nature*, *331*, 612–614.
- Marchis F., Descamps P., Hestroffer D., Berthier J., and de Pater I. (2005) *Bull. Am. Astron. Soc.*, *36*, Abstract #46.02.
- Mastrapa R. M. E., Glanzberg H., Head J. N., Melosh H. J., and Nicholson W. L. (2001) *Earth Planet. Sci. Lett.*, *189*, 1–8.
- Matsui T. and Abe Y. (1986) *Nature*, *322*, 526–528.
- McFadden G. I. (2001) *J. Physiol.*, *37*, 951–959.
- McKay D. S., Gibson E. K. Jr., Thomas-Keprta K. L., Hojatollah V., Romanek C. S., et al. (1996) *Science*, *273*, 924–930.
- Melosh H. J. (1984) *Icarus*, *59*, 234–260.
- Melosh H. J. (2003) *Astrobiol.*, *3*, 207–215.
- Meyer C., Williams I. S., and Compston W. (1996) *Meteoritics & Planet. Sci.*, *31*, 370–387.
- Miller S. L. (1953) *Science*, *117*, 528–529.
- Miller S. L. and Schlesinger G. (1983) *Adv. Space Res.*, *3*, 47–53.
- Miyakawa S., Cleaves H. J., and Miller S. L. (2002a) *Orig. Life Evol. Biosph.*, *32*, 195–208.
- Miyakawa S., Cleaves H. J., and Miller S. L. (2002b) *Orig. Life Evol. Biosph.*, *32*, 209–218.
- Mojzsis S. J., Arrhenius G., McKeegan K. D., Harrison T. M., Nutman A. P., and Friend C. R. L. (1996) *Nature*, *384*, 55–59.
- Mojzsis S. J., Harrison T. M., and Pidgeon R. T. (2001) *Nature*, *409*, 178–181.
- Mojzsis S. J., Harrison T. M., Friend C. R. L., Nutman A. P., Bennett V. C., Fedo C. M., and Whitehouse M. J. (2002) *Science*, *298*, 917a.
- Morbidelli A., Chambers J., Lunine J. I., Petit J. M., Robert F., Valsecchi G. B., and Cyr K. E. (2000) *Meteoritics & Planet. Sci.*, *35*, 1309–1320.
- Mousis O. and Alibert Y. (2005) *Mon. Not. R. Astron. Soc.*, *358*, 188–192.
- Mumma M. J., Novak R. E., DiSanti M. A., Bonev B. P., and Dello Russo N. (2004) *Bull. Am. Astron. Soc.*, *36*, 26.02.
- Naraoka H., Mita H., Komiya M., Yoneda S., Kojima H., and Shimoyama A. (2004) *Meteoritics & Planet. Sci.*, *39*, 401–406.
- Newsom H. E. (1995) In *Global Earth Physics: A Handbook of Physical Constants* (T. J. Ahrens, ed.), pp. 159–189. AGU, Washington, DC.
- Nisbet E. G. and Sleep N. H. (2001) *Nature*, *409*, 1083–1091.
- Olive K. A. and Schramm D. N. (1982) *Astrophys. J.*, *257*, 276–282.
- Orgel L. E. (1968) *J. Mol. Biol.*, *38*, 381–393.
- Orgel L. E. (2004) *Orig. Life Evol. Biosph.*, *34*, 361–369.
- Owen T. (1980) In *Strategies for the Search for Life in the Universe* (M. Papagiannis, ed.), pp. 177–188. Reidel, Dordrecht.
- Oze C. and Sharama M. (2005) *Geophys. Res. Lett.*, *32*, L10203.
- Pahlevan K. and Stevenson D. J. (2005) In *Lunar Planet. Sci. Conf. XXXVI*, Abstract #2382.
- Pepin R. O. (1991) *Icarus*, *92*, 2–79.
- Pizzarello S. and Cronin J. R. (2000) *Geochim. Cosmochim. Acta*, *64*, 329–338.
- Podesek F. A. and Ozima M. (2000) In *Origin of the Earth and Moon* (R. M. Canup and K. Righter, eds.), pp. 63–72. Univ. of Arizona, Tucson.
- Raymond S. N., Quinn T., and Lunine J. I. (2004) *Icarus*, *168*, 1–17.
- Ribas I., Guinan E. F., Güdel M., and Audard M. (2005) *Astrophys. J.*, *622*, 680–694.
- Rieder R., Gellert R., Anderson R. C., Brückner J., Clark B. C., et al. (2004) *Science*, *306*, 1746–1749.
- Righter K. (2003) *Ann. Rev. Earth Planet. Sci.*, *31*, 135–174.
- Righter K. and Drake M. J. (1997) *Earth Planet. Sci. Lett.*, *146*, 541–553.
- Rosing M. T. (1999) *Science*, *283*, 674–676.
- Russell M. J. and Arndt N. T. (2005) *Biogeosci.*, *2*, 97–111.
- Sagan C., Thompson W. R., Carlson R., Gurnett D., and Hord C. (1993) *Nature*, *365*, 715–721.
- Schidowski M. A. (1988) *Nature*, *333*, 313–318.
- Schaefer L. and Fegley B. Jr. (2005) *Bull. Am. Astron. Soc.*, *37*, 29.15.
- Schoenberg R., Kamber B. S., Collerson K. D., and Eugster O. (2002) *Geochim. Cosmochim. Acta*, *66*, 3151–3160.
- Schopf J. W. and Packer B. M. (1987) *Science*, *237*, 70–73.
- Schulte M. D. and Shock E. L. (1992) *Meteoritics*, *27*, 286.
- Seager S., Turner E. L., Schaefer J. and Ford E. B. (2005) *Astrobiol.*, *5*, 372–390.
- Segura A., Krelove K., Kasting J. F., Sommerlatt D., Meadows V., et al. (2003) *Astrobiol.*, *3*, 689–708.
- Selsis F. (2002) In *The Evolving Sun and Its Influence on Planetary Environments* (B. Montesinos et al., eds.), pp. 273–281. ASP Conf. Series 269, San Francisco.
- Selsis F. and Ollivier M. (2005) In *Lectures in Astrobiology, Vol. 1* (M. Gargaud et al., eds.), pp. 385–419. Springer, Berlin.
- Selsis F., Despois D., and Parisot J.-P. (2002) *Astron. Astrophys.*, *388*, 985–1003.
- Septon M. A., Verchovsky A. B., Bland P. A., Gilmour I., Grady M. M., and Wright I. P. (2003) *Geochim. Cosmochim. Acta*, *67*, 2093–2108.
- Sharp C. M. (1990) *Astrophys. Space Sci.*, *171*, 185–188.

- Shock E. L. and Schulte M. D. (1998) *J. Geophys.*, *103*, 28513–28528.
- Shock E. L. and Schulte M. D. (1990) *Nature*, *343*, 728–731.
- Shock E. L., Amend J. P., and Zolotov M. Y. (2000) In *The Origin of the Earth and Moon* (R. Canup and K. Righter, eds.), pp. 527–543. Univ. of Arizona, Tucson.
- Sinton W. (1957) *Astrophys. J.*, *126*, 231–239.
- Sleep N. H. and Zahnle K. (1998) *J. Geophys. Res.*, *103*, 28529–28544.
- Sleep N. H., Meibom A., Fridriksson Th., Coleman R. G., and Bird D. K. (2004) *Proc. Natl. Acad. Sci. USA*, *101*, 12,818–12,823.
- Solomon S. C., Aharonson O., Aurnou J. M., Banerdt W. B., Carr M. H., et al. (2005) *Science*, *307*, 1214–1220.
- Squyres S. W., Arvidson R. E., Bell J. F. III, Brückner J., Cabrol N. A., et al. (2004) *Science*, *306*, 1709–1714.
- Stevenson D. J. (1980) In *Lunar Planet. Sci. Conf. XI*, pp. 1088–1090.
- Stevenson D. J. and Lunine J. I. (1988) *Icarus*, *75*, 146–155.
- Strom R. G., Malhotra R., Ito T., Yoshida F., and Kring D. A. (2005) *Science*, *309*, 1847–1850.
- Tarits P., Hautot P., and Perrier F. (2004) *Geophys. Res. Lett.*, *31*, L06612.
- Taylor S. R. (1999) *Meteoritics & Planet. Sci.*, *34*, 317–239.
- Tian F., Toon O. B., Pavlov A. A., and De Sterck H. (2005) *Science*, *538*, 1014–1017.
- Tolstikhin I. N. and O’Nions R. K. (1994) *Chem. Geol.*, *115*, 1–6.
- Travis B. J. and Schubert G. (2005) *Earth Planet. Sci. Lett.*, *240*, 234–250.
- Tsiganis K., Gomes R., Morbidelli A., and Levison H. G. (2005) *Nature*, *435*, 459–461.
- Turner G., Knott S. F., Ash R. D., and Gilmour J. D. (1997) *Geochim. Cosmochim. Acta*, *61*, 3835–3850.
- van Zuilen M. A., Lepland A., and Arrhenius G. (2002) *Nature*, *418*, 627–630.
- Vlassov A. V., Kazakov S. A., Johnston B. H., and Landweber L. F. (2005) *J. Mol. Evol.*, *61*, 264–273.
- Wallis M. K. and Wickramasinghe N. C. (2004) *Mon. Not. R. Astron. Soc.*, *348*, 52–61.
- Walter M. R., Buick R., and Dunlop J. S. R. (1980) *Nature*, *284*, 443–445.
- Weidenschilling S. J. (1977) *Astrophys. Space Sci.*, *51*, 153–158.
- Weidenschilling S. J. (1981) *Icarus*, *46*, 124–126.
- Weiss B. P., Kirschvink J. L., Baudenbacher F. J., Vali H., Peters N., Macdonald F. A., and Wikswo J. P. (2000a) *Science*, *290*, 791–795.
- Weiss B. P., Yung Y. L., and Neelson K. H. (2000b) *Proc. Natl. Acad. Sci. USA*, *97*, 1395–1399.
- Wells L. E., Armstrong J. C., and Gonzalez G. (2003) *Icarus*, *162*, 38–46.
- Wiechert U., Halliday A. N., Lee D.-C., Snyder G. A., Taylor L. A., and Rumble D. (2001) *Science*, *294*, 345–348.
- Wilde S. A., Valley J. W., Peck W. H., and Graham C. M. (2001) *Nature*, *409*, 175–178.
- Williams D. M. and Gaidos E. (2005) *Bull. Am. Astron. Soc.*, *37*, 31.13.
- Williams D. M. and Pollard D. (2002) *Intl. J. Astrobiol.*, *1*, 61–69.
- Williams D. M. and Pollard D. (2003) *Intl. J. Astrobiol.*, *2*, 1–19.
- Woese C. R. (1987) *Microbiol. Rev.*, *51*, 221–271.
- Woese C. R. (2000) *Proc. Natl. Acad. Sci. USA*, *97*, 8392–8396.
- Woosley S. E. and Weaver T. A. (1995) *Astrophys. J. Suppl.*, *101*, 181–234.
- Zahnle K. (1998) In *Origins* (C. E. Woodward et al., eds.), pp. 364–391. ASP Conf. Series 148, San Francisco.