

# Origin and Evolution of Life on Terrestrial Planets

A. Brack,<sup>1</sup> G. Horneck,<sup>2</sup> C.S. Cockell,<sup>3</sup> A. Bérces,<sup>4</sup> N.K. Belisheva,<sup>5</sup> Carlos Eiroa,<sup>6</sup> Thomas Henning,<sup>7</sup> Tom Herbst,<sup>7</sup> Lisa Kaltenegger,<sup>8</sup> Alain Léger,<sup>9</sup> Réne Liseau,<sup>10</sup> Helmut Lammer,<sup>11</sup> Franck Selsis,<sup>12</sup> Charles Beichman,<sup>13</sup> William Danchi,<sup>14</sup> Malcolm Fridlund,<sup>15</sup> Jonathan Lunine,<sup>16</sup> Francesco Paresce,<sup>17</sup> Alan Penny,<sup>18</sup> Andreas Quirrenbach,<sup>19</sup> Huub Röttgering,<sup>20</sup> Jean Schneider,<sup>21</sup> Daphne Stam,<sup>22</sup> Giovanna Tinetti,<sup>23</sup> and Glenn J. White<sup>18,24</sup>

## Abstract

The ultimate goal of terrestrial planet-finding missions is not only to discover terrestrial exoplanets inside the habitable zone (HZ) of their host stars but also to address the major question as to whether life may have evolved on a habitable Earth-like exoplanet outside our Solar System. We note that the chemical evolution that finally led to the origin of life on Earth must be studied if we hope to understand the principles of how life might evolve on other terrestrial planets in the Universe. This is not just an anthropocentric point of view: the basic ingredients of terrestrial life, that is, reduced carbon-based molecules and liquid H<sub>2</sub>O, have very specific properties. We discuss the origin of life from the chemical evolution of its precursors to the earliest life-forms and the biological implications of the stellar radiation and energetic particle environments. Likewise, the study of the biological evolution that has generated the various life-forms on Earth provides clues toward the understanding of the interconnectedness of life with its environment. Key Words: Organic molecules—Origin of life—Astrobiology—Radiation. *Astrobiology* 10, 69–76.

## 1. The Precursors of Life

### 1.1. Chemical evolution of the precursors of life

**B**Y ANALOGY WITH CONTEMPORARY LIFE, it is generally believed that primitive life-forms developed from the processing of reduced organic molecules by liquid water.

Generally, liquid water is considered to be one of the prerequisites for life in that it would have to be present on a terrestrial planet for life to occur. Life is autocatalytic in essence and must have the capacity to evolve. To evolve, that is, improve the efficiency of self-reproduction and increase its diversity, the molecules that bear hereditary memory must be

<sup>1</sup>Centre National de la Recherche Scientifique, Centre de Biophysique Moléculaire, Orléans, France.

<sup>2</sup>DLR, Institute of Aerospace Medicine, Cologne, Germany.

<sup>3</sup>Geochemical Research Group, Open University, Milton Keynes, UK.

<sup>4</sup>MTA-SE Research Group for Biophysics, Hungarian Academy of Sciences, Budapest, Hungary.

<sup>5</sup>Polar-Alpine Botanical Garden-Institute, Kola Scientific Centre, Russian Academy of Sciences, Apatity, Russian Federation.

<sup>6</sup>Universidad Autonoma de Madrid, Madrid, Spain.

<sup>7</sup>Max-Planck Institut für Astronomie, Heidelberg, Germany.

<sup>8</sup>Harvard-Smithsonian Center for Astrophysics, Cambridge, Massachusetts, USA.

<sup>9</sup>Institut d'Astrophysique Spatiale, Université Paris-Sud, Orsay, France.

<sup>10</sup>Department of Radio and Space Science, Chalmers University of Technology, Onsala, Sweden.

<sup>11</sup>Space Research Institute, Austrian Academy of Sciences, Graz, Austria.

<sup>12</sup>University of Bordeaux 1, Bordeaux, France.

<sup>13</sup>NASA Exoplanet Science Institute, California Institute of Technology and Jet Propulsion Laboratory, Pasadena, California, USA.

<sup>14</sup>NASA Goddard Space Flight Center, Greenbelt, Maryland, USA.

<sup>15</sup>Research and Scientific Support Department, ESA, European Space Research and Technology Centre, Noordwijk, the Netherlands.

<sup>16</sup>Lunar and Planetary Laboratory, Tucson, Arizona, USA.

<sup>17</sup>Istituto Nazionale di Astrofisica, Rome, Italy.

<sup>18</sup>Space Science & Technology Department, CCLRC Rutherford Appleton Laboratory, Oxfordshire, UK.

<sup>19</sup>Landessternwarte, Heidelberg, Germany.

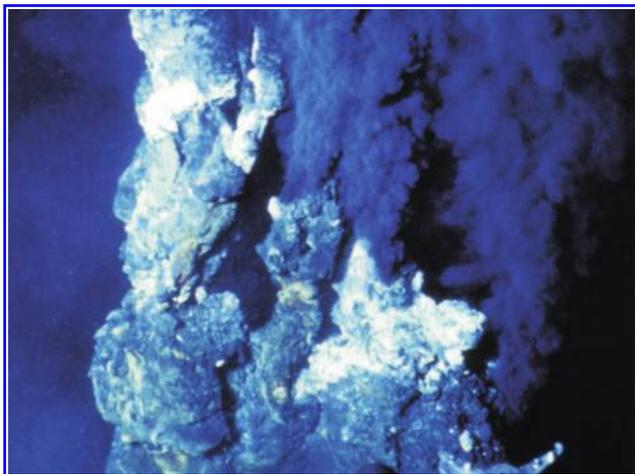
<sup>20</sup>Leiden Observatory, Leiden, the Netherlands.

<sup>21</sup>Observatoire de Paris-Meudon, Laboratoire de l'Univers et ses Théories, Meudon, France.

<sup>22</sup>SRON, Netherlands Institute for Space Research, Utrecht, the Netherlands.

<sup>23</sup>Department of Physics and Astronomy, University College London, London, UK.

<sup>24</sup>The Open University, Milton Keynes, UK.



**FIG. 1.** Some of the most primitive life-forms on Earth live in underwater hydrothermal vents. Color images available online at [www.liebertonline.com/ast](http://www.liebertonline.com/ast).

able to reach a certain degree of complexity. This can be best achieved with a scaffolding of polyvalent atoms. In chemists' hands, carbon chemistry is very productive in this respect. Another clue in favor of carbon is provided by radio astronomers: about 110 carbon-containing molecules, up to  $\text{HC}_{10}\text{CN}$ , have been identified in the interstellar medium, while only 11 silicon-based molecules, up to  $\text{SiH}_4$ , have been detected ([http://en.wikipedia.org/wiki/List\\_of\\_molecules\\_in\\_interstellar\\_space](http://en.wikipedia.org/wiki/List_of_molecules_in_interstellar_space)).

The simplest sources of carbon susceptible to build up the prebiotic organic molecules are gaseous, that is, carbon dioxide and carbon monoxide for the oxidized forms and methane for the reduced ones. Stanley Miller (1953) exposed a mixture of methane, ammonia, hydrogen, and water to spark discharge and silent electric discharge and obtained 3 of the 20 naturally occurring amino acids via the intermediary formation of hydrogen cyanide and aldehydes. Miller's laboratory synthesis of amino acids occurs efficiently when a reducing gas mixture containing significant amounts of hydrogen is used.

However, the dominant view is that the primitive atmospheres consisted mainly of  $\text{CO}_2$ ,  $\text{N}_2$ , and  $\text{H}_2\text{O}$ , along with small amounts of  $\text{CO}$  and  $\text{H}_2$  (Catling and Kasting, 2007; Lammer *et al.*, 2009). Only small yields of amino acids are formed in such a mixture, even though the amounts of these molecules have been shown to increase substantially when oxidation inhibitors, such as ferrous iron, are added to the system (Cleaves *et al.*, 2008).

Deep-sea hydrothermal systems as shown in Fig. 1 may also represent likely environments for the synthesis of prebiotic organic molecules and even for primitive life (Holm, 1992). Amino acids have been obtained, though in low yields, under conditions simulating hydrothermal vents. Hydrothermal vents are often disqualified as efficient reactors for the synthesis of bioorganic molecules because of the high temperature. However, the products that are synthesized in hot vents are rapidly quenched in the surrounding cold water, which may preserve the organics formed, at least on a timescale of 1 Myr or less.

- Since deep-sea hydrothermal systems are related to plate tectonics, the question arises as to whether such

processes can also occur in hypothetical oceans of tidally locked planets, where plate tectonics may be reduced due to slow rotation periods.

According to Wächtershäuser (1998), the carbon source for life on early Earth was carbon dioxide. The energy source required to reduce carbon dioxide was provided by the oxidative formation of pyrite from iron sulfide and hydrogen sulfide. Pyrite has positive surface charges and binds the products of carbon dioxide reduction, giving rise to a two-dimensional reaction system, a surface metabolism. Laboratory experiments by Heinen and Lauwers (1996) and Huber and Wächtershäuser (1997) supported this hypothesis.

It is now clear that a large fraction of organic matter on primitive Earth was of extraterrestrial origin, as evidenced by the presence of carbonaceous components in meteorites and micrometeorites. This is supported by estimates of micrometeorite flux from Antarctica, which suggest that about  $2.5 \times 10^{19}$  kg in the form of kerogen was delivered to primitive Earth over 200 million years (Maurette and Brack, 2006). The life cycle of interstellar amino acids, from their formation in the interstellar medium to their landing on Earth in meteorites, has been tested, both in the laboratory and in space (Boillot *et al.*, 2002; Muñoz Caro *et al.*, 2002; Bertrand *et al.*, 2008).

### 1.2. Organic matter in the interstellar medium and comets

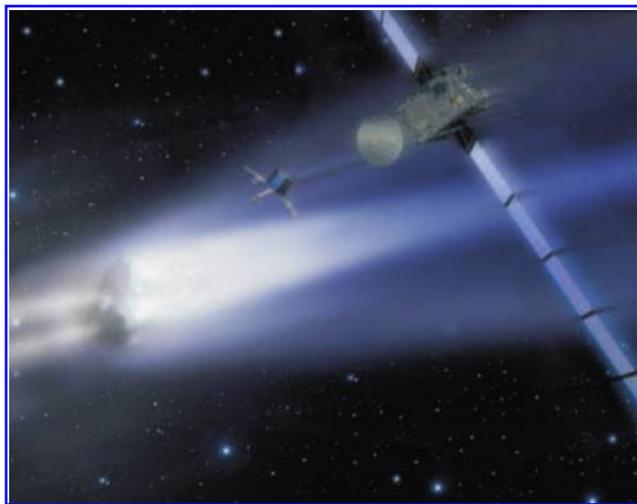
The Infrared Space Observatory, launched in November 1995, has provided extraordinary results concerning the nature of cosmic dust particles. Besides hydrogen and helium, 114 interstellar and circumstellar gaseous molecules have, to date, been identified in the interstellar medium (Cesarsky and Salama, 2005).

- Ultraviolet irradiation of dust grains may result in the formation of complex organic molecules or possible total carbonization of the sample, which forms—according to local environmental conditions—carbonaceous matter such as amorphous carbon, hydrogenated amorphous carbon, or coal- and kerogen-like material.

Kerogen is a complex organic macromolecule produced from the debris of biological matter. Apart from ultraviolet irradiation, cosmic rays and thermal processing are the most important processes which modify interstellar dust by collisions, sputtering, and grain growth.

The incorporation of interstellar matter in meteorites and comets in the pre-solar nebula (as evidenced by isotopic measurements) provides the basis of the cosmic dust connection. Polycyclic aromatic hydrocarbons, fullerenes, and complex aromatic networks have a strong common link, and their evolutionary cycle is dominated by ultraviolet irradiation, as shown by simulation experiments (Li and Greenberg, 1997).

The Infrared Space Observatory measured the composition of interstellar ices, thermal processing in the protostellar vicinity, and gas-grain chemistry (Ehrenfreund and Charnley, 2000). A comparison of interstellar and cometary ices with the use of recent Infrared Space Observatory data has revealed important similarities between interstellar ices and volatiles measured in the coma of some comets.



**FIG. 2.** Illustration of the Rosetta spacecraft and landing maneuver of the lander on comet Churyumov-Gerasimenko (ESA). Color images available online at [www.liebertonline.com/ast](http://www.liebertonline.com/ast).

- The striking identification of forsterite around some young stars and in comet Hale-Bopp indicates that the disks around such stars should also contain comets.

The link between processes in dark embedded clouds and comets seems to be evident, and studies on the connection between interstellar, cometary, and meteoritic dust have provided important constraints on the formation of the Solar System and early evolution on Earth. On average, dust particles ejected from the Comet Halley nucleus contained 14% organic carbon by mass.

Results to be obtained in the near future by *in situ* laboratory analysis of dust from Comet Wild taken by Stardust (NASA) and studies carried out on comets by missions like Deep Impact (NASA) and Rosetta (ESA) (see Fig. 2) will give us more insights as to how important cometary grains might have been a source of organic molecules delivered to primitive Earth.

### 1.3. The RNA world and RNA ancestors

By analogy with contemporary living systems, some believe that primitive life emerged as a cell-like organized system, while others feel that the development of the cell occurred at a subsequent step in the evolutionary process. A cell-like system would require, at least, information molecules that are capable of storing and transferring the information needed for reproduction (RNA), catalytic molecules that provide the basic chemical work of the cell (enzymes), and boundary molecules with the capacity to isolate the system from the aqueous environment (membranes).

Some RNA, the ribozymes, are able to act as catalytic molecules. Since RNA was shown to be able to act simultaneously as an information and catalytic molecule, RNA is often considered to be the first living system on primitive Earth (Jaeger, 1997). However, the synthesis of RNA under prebiotic conditions remains an unsolved challenge, and the direct formation of RNA is not a generally accepted model for the origin of life. This is because some of the steps in the

proposed prebiotic synthesis of the activated monomers of RNA are not convincing.

- Because the structural units that make up RNA are quite complicated, it has been proposed that the first life contained simpler RNA analogues or surrogates that evolved to RNA.

Many modified nucleic acid backbones have been synthesized as antisense DNA for gene therapeutics. Peptide nucleic acids (PNA) first synthesized by Nielsen and co-workers (Nielsen *et al.*, 1991) consisted of a backbone of achiral poly-2-aminoethyl glycine (polyethylenediamine monoacetic acid), with the bases being attached through an acetate linker. PNA forms very stable double helical structures with complementary strands of PNA (PNA-PNA), with DNA (PNA-DNA), and with RNA (PNA-RNA), and even forms stable PNA<sub>2</sub>-DNA triple helices.

It has been suggested that PNA might be a candidate as a prebiotic polymer and potentially the first genetic material that preceded the RNA world. PNA is attractive as primitive genetic material because it avoids some of the RNA difficulties:

- there is no asymmetric center in the starting building block (2-aminoethyl glycine), which is rather stable to decomposition, and the N-acetic acid derivatives of the bases are likely to be stable.

However, the fact that, first, activated PNA monomers have a strong tendency to cyclize, which thus makes the formation of oligomers very difficult under prebiotic conditions and, second, PNA hydrolyzes rather rapidly, restricts the chances of PNA to have ever accumulated in the primitive oceans.

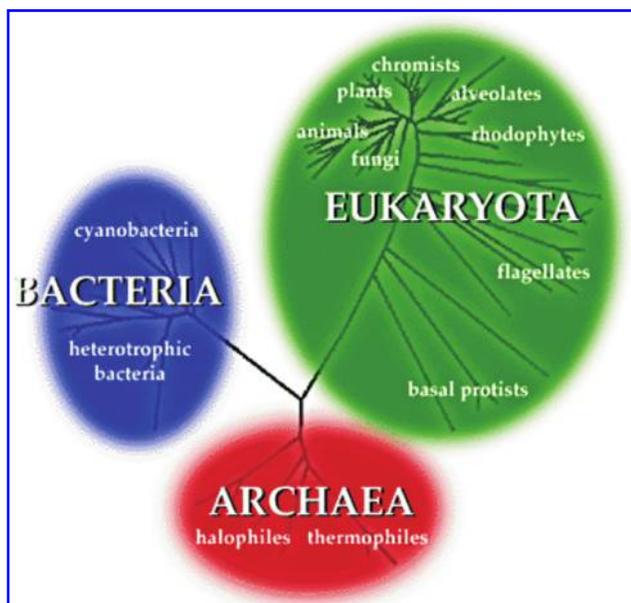
Chemists are also tempted to consider that primitive replicating systems must have used simpler informational molecules than biological nucleic acids or their analogues. They are looking for simple self-sustaining chemical systems capable of self-replication, mutation, and selection. Different templates have been tested, and simple molecules unrelated to nucleotides have been modeled to undergo exponentially replicating autocatalysis (Bachmann *et al.*, 1992; Terfort and von Kiedrowski, 1992).

A new hypothesis for a combination of monomolecular surface organization initiated by inorganic crystals interacting with nucleic acid bases may also provide an answer to the enigmatic origins of the information system necessary to promote the complexity of even microbial life (Sowerby *et al.*, 2001).

### 1.4. Phylogenetic tree of life

To investigate the phylogenetic relationship of living organisms, molecular techniques have provided clues to trace back the history of biological evolution to its roots. On the base of the 16S rRNA molecule, a phylogenetic tree illustrated in Fig. 3 was constructed that exhibits a division in three domains, the Bacteria, Archaea, and Eukarya (Woese *et al.*, 1990).

- The molecular record derived from 16S rRNA comparison allows also for inferences on the metabolic characteristics of the common ancestor.



**FIG. 3.** The phylogenetic tree of life on Earth. Color images available online at [www.liebertonline.com/ast](http://www.liebertonline.com/ast).

- Observations support the assumption of a chemolithoautotrophic hyperthermophilic nature of the last universal common ancestor (Kandler, 1994).

Thermophilic and hyperthermophilic microorganisms occur in numerous phylogenetic highly divergent lineages and could therefore represent an ancient phenotype. In the phylogenetic tree derived from 16S rRNA sequence comparison, hyperthermophiles are among members of both domains, Archaea and Bacteria, that form the deepest branchings (Stetter, 2001). They grow either chemolithoautotrophically and employ the redox couples  $H_2/S^0$ ,  $H_2/CO_2$ ,  $H_2/O_2$ ,  $H_2S/O_2$ , or  $H_2/SO_4$  as energy sources, or organotrophically by sulfur respiration (Seeger *et al.*, 1993).

This organism would have depended solely on planetary energy. It is interesting to note that photoautotrophic growth is completely absent among the thermophiles, which makes photoautotrophy a very unlikely feature of the common ancestor. This very hot (between 80°C and 112°C) origin of life hypothesis has been convincingly disputed (Forterre *et al.*, 1995). Phylogenetic trees reconstructed on the basis of RNA polymerases as a molecular marker place the bacterial lineage of hyperthermophiles far away from the root of this domain (Klenk and Zillig, 1994).

- An attractive hypothesis is that life appeared in a moderately thermophilic environment that was hot enough to boost catalytic reactions but cold enough to avoid the problem of macromolecule thermal degradation.

## 2. Appearance of Life: Terrestrial Life as a Reference for Habitable Exoplanets

### 2.1. Oldest fossil record

There are only three places on Earth with sedimentary rocks older than 3.3 Gyr:

- the greenstone belts of Isua in southwest Greenland,
- The Barberton area east of South Africa,
- The Pilbara area of northwest Australia.

Archean morphological fossils that occur in 3.4–3.3 Gyr rocks from South Africa have been recently described (Westall *et al.*, 2001). The isotopic signatures of the organic carbon of the Greenland metasediments bring indirect evidence that life may be about 3.9 Gyr old. The carbon atom has two stable isotopes,  $^{12}C$  and  $^{13}C$ . The  $^{12}C/^{13}C$  ratio in abiotic mineral compounds is 89. In biological material, photosynthesis raises the ratio to about 92, which indicates that living matter is enriched in  $^{12}C$ . The carbon isotopic composition of over 1600 samples of fossil kerogen has been compared with carbonates in the same sedimentary rocks (Schidlowski, 1987).

Those data showed that biosynthesis by autotrophic organisms was involved in all the sediments studied. In fact, this offset is now taken to be one of the most powerful indications that life on Earth was active nearly 3.9 Gyr ago, because the sample suite encompasses specimens right across the geological timescale. Although the origins of life were probably geothermal and chemosynthetic, derivatives of photosynthetic and UV-protective pigments have been found in ancient sediments up to 3.8–3.5 Gyr (Huseby and Ocampo, 1997). Some organic matter in ancient sediments has been measured as being enriched in the light isotope of carbon above even 92, which would suggest involvement of methane-utilizing organisms.

- By applying these results from Earth to terrestrial exoplanets, one may conclude that life may need at least a few 100 Myr ( $\leq 700$  Myr) in a moderate thermophilic wet environment after the planet formed inside the habitable zone (HZ), which covers the period from the organization of complex organic molecules to the appearance of self-replicating primitive life-forms.

### 2.2. The role of radiation and particle-induced stress on the evolution of life

A further question regarding the evolution of life on planetary surfaces is whether different UV radiation qualities can be responsible for evolutionary processes, like on early Earth, when an oxygen- and ozone-free atmosphere was transparent for UV radiation at wavelengths  $>200$  nm. This energetic UVC-range (200–280 nm), which is efficiently absorbed by a multitude of organic molecules, may have affected the earliest stages of prebiotic evolution and thereby led to organic complexity. Some products may have had prebiological significance (*e.g.*, Sagan and Khare, 1971; Mulikdjanian *et al.*, 2003; Fekete *et al.*, 2004; Rontó *et al.*, 2004).

Once biochemical scaffolding began to emerge from the more random building blocks of chemistry, most macromolecules would have had well-defined structure-function relationships. Disruption of structure by radiation invariably results in a critical disruption of function in any well-defined biochemical scaffolding.

Higher UV fluxes than on Earth, such as those experienced on planets of F-type stars (Kasting *et al.*, 1997; Cockell, 1999; Segura *et al.*, 2003), may have the potential

- to drive higher rates of mutation and thus
- produce a faster tempo of evolution.

Given the potential damage caused by UV radiation, however, it is clear that the overwhelming selection pressure is

probably more toward protecting from UV radiation to avoid increased rates of mutation.

- A key event in the origin of life on Earth has been the formation of self-replicating RNA-type molecules, which were complex enough to undergo a Darwinian-type evolution.

However, so far there has been no explanation as to how the first RNA-like biopolymers could originate and survive on primordial Earth. The condensation of sugar phosphates and nitrogenous bases is thermodynamically unfavorable. Also, even if these compounds did form, they probably would have undergone rapid hydrolysis (Mulikidjanian *et al.*, 2003).

Thus, formation of oligonucleotide-like structures could have happened only if, and when, these structures had some selective advantage over simpler compounds. It is well known that nitrogenous bases are powerful quenchers of UV quanta and effectively protect the pentose-phosphate backbones of RNA and DNA from UV cleavage. To determine whether such a protection could play a role in abiogenic evolution on the anoxic primordial Earth, Monte Carlo simulations of the formation of the first oligonucleotides under continuous UV illumination confirmed that

- UV irradiation could have operated as a selective factor that led to a relative enrichment of the system in longer sugar-phosphate polymers carrying nitrogenous bases as UV protectors (Mulikidjanian *et al.*, 2003).

Partial funneling of the UV energy into the condensation reactions could provide a further boost for the oligomerization. Thus, as for early Earth, it is not necessarily clear that varying UV fluxes on exoplanets would have a role to play in the rate of evolution of life on planetary surfaces.

- Terrestrial planet-finding missions like Darwin will give us knowledge about the composition of the atmospheres of detected terrestrial exoplanets so that we will be better able to define the UV radiation fluxes at their surfaces accurately.

However, greater fluxes of cosmic and gamma rays on planets in more energetic galactic environments (Dar *et al.*, 1998; Gonzalez *et al.*, 2001; Lineweaver *et al.*, 2004), or during the active flaring periods of their young host stars, may also cause biochemical damage or influence the nature of biological evolution (Dar *et al.*, 1998; Smith *et al.*, 2004; Griefsmeier *et al.*, 2005, 2009).

Galactic cosmic rays and solar/stellar cosmic radiation, which are manifested by the solar/stellar wind [electrons, protons, a few HZE (nuclei with high atomic number,  $Z$ , and energy,  $E$ )] and high energetic solar/stellar particle events (mostly electrons, protons) (Bieber *et al.*, 1999), expose a planet to a highly energetic radiation environment.

- Space- and ground-based observations have revealed that, during highly energetic solar particle events, the radiation exposure into Earth's atmosphere can be increased up to a factor of 1000 (Reeves *et al.*, 1992).

A planetary magnetic field like the Earth's magnetosphere separates the particle fluxes according to their energy spectrum, so that living systems on the surface are protected from

highly energetic primary cosmic rays, where the exposure of highly energetic particles would frustrate or even eradicate life on the planet's surface (Dar *et al.*, 1998).

Due to the geomagnetic cutoff associated with the structure of the magnetosphere, the less energetic part of the cosmic ray spectrum is deflected. Upon reaching the top of the atmosphere of a terrestrial planet, the residual part of higher energies is absorbed by the molecules of the atmosphere. If the planetary atmosphere is dense enough, the cosmic radiation cannot penetrate to the surface.

Primary cosmic ray particles interact with the atmosphere and generate secondary energetic particles, some of which can reach the surface of terrestrial planets with Earth-like surface pressure values (*e.g.*, Shea and Smart, 1995). The shielding of Earth's atmosphere amounts to  $1000 \text{ g cm}^{-2}$ , whereas that of Mars does not exceed  $16 \text{ g cm}^{-2}$ .

Smaller magnetic moments of tidally locked terrestrial planets inside the HZ of low-mass M and K stars more weakly protect the planetary surface against highly energetic cosmic rays (Griefsmeier *et al.*, 2005, 2009). Those planets will therefore experience more ground-level enhancements of the cosmic ray intensity associated with stellar flares and possible associated biological effects on their surface than an Earth-like planet orbiting a Sun-like G-type star at an orbital distance of about 1 AU.

- In such cases, secondary radiation produced due to particle showers in an Earth-like atmosphere may have global effects on life-forms on the surface and can enhance mutation rates. They may even sterilize the planet's surface (Belisheva *et al.*, 1994; Belisheva and Popov, 1995; Belisheva and Emelin, 1998; Dar *et al.*, 1998; Belisheva and Gak, 2002; Smith *et al.*, 2004; Griefsmeier *et al.*, 2005, 2009).

However, the effects on biological systems due to high energetic particles would be reduced or negligible if the atmosphere of a terrestrial planet is dense enough, as is the case for Venus, with a surface pressure of 100 bar (10 MPa) so that high energetic particles cannot reach the surface.

### 3. Environmental Limits to Extreme Life-Forms

Life on Earth is based on the chemistry of carbon in water. The temperature limits compatible with the existence of life are thus imposed by the intrinsic properties of chemical bonds involved in this type of chemistry at different temperatures. Microorganisms have invented several strategies to cope with, or specifically adapt to, environments, generally called extremes with regard to temperature, water activity, pressure, atmospheric composition, or radiation.

- Again, liquid H<sub>2</sub>O seems to be a necessary prerequisite for life.

At the boiling point of water, for example, at high hydrostatic pressure, the deep-sea archaea *Pyrolobus fumarii* grows at temperatures as high as 113°C and can tolerate 121°C for an hour (Stetter, 1998).

- An important factor that prevents life at temperatures well above 110°C is the thermal instability of some chemical bonds involved in biological molecules and membrane permeability.

Life is extremely diverse in the ocean at temperatures of 2°C. Living organisms, especially microorganisms, are also present in permafrost areas of arctic and alpine environments (Vorobyova *et al.*, 1997; Vishnivetskaya *et al.*, 2006; Gilichinsky *et al.*, 2007). Antarctica has a wide range of extreme habitats, yet microbial ecosystems adapt and colonize such extreme environments, for example, dry valley rocks (Wynn-Williams and Edwards, 2000a). These extreme cold desert habitats are valuable analogues for postulated former habitats on Mars (Wynn-Williams and Edwards, 2000b).

- The lower limit for bacterial metabolism of about −20°C is comparable to the temperature at which intracellular ice is formed (Rivkina *et al.*, 2000).

To achieve such low habitat temperatures in nature, high concentrations of salts must also accumulate to achieve water in a liquid state. Salt-loving organisms, known as extreme halophiles, are well known in cold desert habitats and salt deposits such as salterns and salt mines (Grant *et al.*, 1998, McGenity *et al.*, 2000). They tolerate a wide range of salt concentrations (1–20% NaCl), and some prokaryotes are so dependent on such high salt concentrations that they cannot grow at concentrations below 10% NaCl (McGenity *et al.*, 2000).

The chemistry of life on Earth is optimized for neutral pH, but some microorganisms have been able to adapt to extreme pH conditions. These microorganisms live in environmental conditions from extremely acidic at pH 0 (Schäfer *et al.*, 1999) to extremely alkaline at pH 12.5 (Keller *et al.*, 1995), albeit maintaining their intracellular pH between 4 and 9.

As with temperature, the intracellular machinery cannot escape the influence of pressure. However, there are organisms in the deepest parts of the ocean at pressure values of about 1100 bar (1.1×100 MPa) (Liesack *et al.*, 1991).

- The extreme pressure limit for life on Earth is unknown—environments of above 1100 bar (1.1×100 MPa) have not been explored.

For a long time, it was believed that deep subterranean environments were sterile, but

- it has now been recognized that bacteria actually thrive in the terrestrial crust.

These organisms live completely independent from Earth's surface (*e.g.*, Gold, 1992; Krumholz *et al.*, 1997; Zierenberg *et al.*, 2000) and extract their energy from chemical sources due to fluids that migrate upward from deeper levels in the Earth. In terms of mass and volume, these organisms may even be comparable with all surface life.

Subterranean microorganisms are usually detected in subterranean oil fields or in the course of drilling experiments. For example, recent research has demonstrated that prokaryotes are present much deeper in marine sediments than was previously thought possible, extending to at least 750 m below the seafloor and probably much deeper (Parkes *et al.*, 1994). At depths of at least 432 m, microorganisms have been found in volcanic glasses.

These data provide a preliminary and probably conservative estimate of the biomass in such deep subsurface ecosystems to be about 10% of the surface biosphere. These discoveries have radically changed our perception of marine sediments and indicate the presence of a largely unexplored

deep bacterial biosphere that may even rival Earth's surface biosphere in size and diversity. For some activities, such as methanogenesis, anaerobic methane oxidation, and acetate metabolism, potential rates in the subsurface are greater than those near the sediment surface (Parkes *et al.*, 2000).

#### 4. Discussion

The emergence of life on Earth may have occurred almost immediately after the formation of a stable hydrosphere. It can be assumed that there are many terrestrial exoplanets in the Universe, which may not differ from early Earth in their evolution. It therefore seems reasonable to assume that life could have started on such planets. Even if the geodynamical processes on such extraterrestrial planets failed during evolution, there should have been enough active volcanoes, probably volcanoes under water as well, to provide local conditions comparable to those of black smokers. The crucial question is: how long do these conditions prevail before a planet evolves to be either too dry or too hot? If life has had enough time to evolve into sufficient complexity so that it could evolve in different habitats by utilizing various energy sources, it would be very hard to eliminate it completely.

#### Abbreviations

HZ, habitable zone; PNA, peptide nucleic acids.

#### References

- Bachmann, P.A., Luisi, P.L., and Lang, J. (1992) Autocatalytic self-replicating micelles as models for prebiotic structures. *Nature* 357:57–59.
- Belisheva, N.K. and Emelin, C.E. (1998) Self-organisation of living systems under geocosmical agents impact. *Nauchnoe priboroostroenie RAS* 7:35–37.
- Belisheva, N.K. and Gak, E. Z. (2002) Significance of cosmic ray variations for biosystem functions. In *Proceedings of the VII International Conference on Ecology and Development of North-West Russia*, Saint Petersburg, pp 118–120.
- Belisheva, N.K. and Popov, A.N. (1995) Dynamics of the morphofunctional state of cell cultures with variation in the geomagnetic field in high latitudes. *Biophysics* 40:737–745.
- Belisheva, N.K., Popov, A.N., and Poniavin, D.I. (1994) Biological effects in cell cultures and geomagnetic field variations. In *Charge and Field Effects in Biosystems*, edited by M.J. Allen, S.F. Cleary, and A.E. Sowers, World Scientific Publishing Co. Pte. Ltd., Singapore, pp 159–173.
- Bertrand, M., Westall, F., van der Gaast, S., Vilas, F., Hörz, F., Barnes, G., Chabin, A., and Bracket, A. (2008) Amino acid degradation after meteoritic impact simulation [abstract 1749]. In *39<sup>th</sup> Lunar and Planetary Science Conference*, Lunar and Planetary Institute, Houston.
- Bieber, J.W., Cane, H., Evenson, P., Pyle, R., and Richardson, I. (1999) Energetic particle flow near CME shocks and ejecta. In *Solar Wind Nine: Proceedings of the 9<sup>th</sup> International Solar Wind Conference*, AIP Conference Proceedings 471, edited by S.R. Habbal, R. Esser, and J.V. Hollweg, American Institute of Physics, Melville, NY, pp 137–140.
- Boillot, F., Chabin, A., Buré, C., Venet, M., Belsky, R., Bertrand-Urbaniak, M., Delmas, A., Brack, A., and Barbier, B. (2002) The Perseus exobiology mission on MIR: behaviour of amino acids and peptides in Earth orbit. *Orig. Life Evol. Biosph.* 32:359–385.
- Catling, D. and Kasting, J.F. (2007) Planetary atmospheres and life. In *Planets and Life*, edited by W.T. Sullivan III and J.A.

- Baross, Cambridge University Press, Cambridge, UK, pp 91–116.
- Cesarsky, C. and Salama, A. (2005) ISO science legacy—a compact review of ISO major achievements. *Space Sci. Rev.* 119: 1–4.
- Cleaves, H.J., Chalmers, J.H., Lazcano, A., Miller, S., and Bada, J.L. (2008) A reassessment of prebiotic organic synthesis in neutral planetary atmospheres. *Orig. Life Evol. Biosph.* 38:105–115.
- Cockell, C. (1999) Carbon biochemistry and the ultraviolet radiation environments of F, G, and K main sequence stars. *Icarus* 141:399–407.
- Dar, A., Laor, A., and Shaviv, N.J. (1998) Life extinctions by cosmic ray jets. *Phys. Rev. Lett.* 80:5813–5816.
- Ehrenfreund, P. and Charnley, S.B. (2000) Organic molecules in the interstellar medium, comets and meteorites. *Annu. Rev. Astron. Astrophys.* 38:427–483.
- Fekete, A., Rontó, Gy., Hegedüs, M., Módos, K., Bérces, A., Kovács, G., Lammer, H., and Panitz, C. (2004) Simulation experiments of the effect of space environment on bacteriophage and DNA thin films. *Adv. Space Res.* 33:1306–1310.
- Forterre, P., Confalonieri, F., Charbonnier, F., and Duguet, M. (1995) Speculations on the origin of life and thermophylie: review of available information on reverse gyrase suggests that hyperthermophilic procaryotes are not so primitive. *Orig. Life Evol. Biosph.* 25:235–249.
- Gilichinsky, D.A., Wilson, G.S., Friedmann, E.I., McKay, C.P., Sletten, R.S., Rivkina, E.M., Vishnivetskaya, T.A., Erokhina, L.G., Ivanushkina, N.E., Kochkina, G.A., Shcherbakova, V.A., Soina, V.S., Spirina, E.V., Vorobyova, E.A., Fyodorov-Davydov, D.G., Hallet, B., Ozerskaya, S.M., Sorokovikov, V.A., Laurinavichyus, K.S., Shatilovich, A.V., Chanton, J.P., Ostroumov, V.E., and Tiedje, J.M. (2007) Microbial populations in Antarctic permafrost: biodiversity, state, age, and implication for astrobiology. *Astrobiology* 7:275–311.
- Gold T. (1992) The deep, hot biosphere. *Proc. Natl. Acad. Sci. U.S.A.* 89:6045–6049.
- Gonzalez, G., Brownlee, D., and Ward, P. (2001) The galactic habitable zone: galactic chemical evolution. *Icarus* 152:185–200.
- Grant, W.D., Gemmill, R.T., and McGenity, T.J. (1998) Halobacteria—the evidence for longevity. *Extremophiles* 2:279–288.
- Griessmeier, J.-M., Stadelmann, A., Motschmann, U., Belisheva, N.K., Lammer, H., and Biernat, H.K. (2005) Cosmic ray impact on extrasolar terrestrial planets. *Astrobiology* 5:587–603.
- Griessmeier, J.-M., Stadelmann, A., Grenfell, J.L., Lammer, H., and Motschmann, U. (2009) On the protection of extrasolar Earth-like planets around K/M stars against galactic cosmic rays. *Icarus* 199:526–535.
- Heinen, W. and Lauwers, A.M. (1996) Sulfur compounds resulting from the interaction of iron sulfide, hydrogen sulfide and carbon dioxide in an anaerobic aqueous environment. *Orig. Life Evol. Biosph.* 26:131–150.
- Holm, N.G. (1992) Marine hydrothermal systems and the origins of life. *Orig. Life Evol. Biosph.* 22:181–242.
- Huber, C. and Wächtershäuser, G. (1997) Activated acetic acid by carbon fixation on (Fe, Ni)S under primordial conditions. *Science* 276:245–247.
- Huseby, B. and Ocampo, R. (1997) Evidence for porphyrins bound, via ester bonds, to the Messel oil shale kerogen by selective chemical degradation experiments. *Geochim. Cosmochim. Acta* 61:3951–3955.
- Jaeger, L. (1997) The new world of ribozymes. *Curr. Opin. Struct. Biol.* 7:324–335.
- Kandler, O. (1994) The early diversification of life. In *Early Life on Earth*, edited by H. Baltscheffsky, S. Bengtson, J. Bergström, G. Vidal, and A. Knoll, Columbia University Press, New York, pp 152–160.
- Kasting, J.F., Whittet, D.C.B., and Sheldon, W.R. (1997) Ultraviolet radiation from F and K stars and implications for planetary habitability. *Orig. Life Evol. Biosph.* 27:413–420.
- Keller, M., Braun, F.-J., Dirmeier, R., Hafenbradl, D., Burggraf, S., Rachel R., and Stetter, K.O. (1995) *Thermococcus alcaliphilus* sp. nov., a new hyperthermophilic archaeum growing on polysulfide at alkaline pH. *Arch. Microbiol.* 164: 390–395.
- Klenk, H.P. and Zillig, W. (1994) DNA-dependent RNA-polymerase subunit B as a tool for phylogenetic reconstructions: branching topology of Archaeal domain. *J. Mol. Evol.* 38:420–432.
- Krumholz, L.R., McKinley, J.P., Ulrich, G.A., and Suflita, J.M. (1997) Confined subsurface microbial communities in Cretaceous rock. *Nature* 386:64–66.
- Lammer, H., Bredehöft, J.H., Coustenis, A., Khodachenko, M.L., Kaltenecker, L., Grasset, O., Prieur, D., Raulin, F., Ehrenfreund, P., Yamauchi, M., Wahlund, J.-E., Griessmeier, J.-M., Stangl, G., Cockell, C.S., Kulikov, Yu.N., Grenfell, J.L., and Rauer, H. (2009) What makes a planet habitable? *Astronomy & Astrophysics Review* 17:181–249.
- Li, A. and Greenberg, J.M. (1997) A unified model of interstellar dust. *Astron. Astrophys.* 323:566–584.
- Liesack, W., Weyland, H., and Stackebrandt, E. (1991) Potential risks of gene amplification by PCR as determined by 16S rDNA analysis of a mixed-culture of strict barophilic bacteria. *Microb. Ecol.* 21:191–198.
- Lineweaver, C.H., Fenner, Y., and Gibson, B.K. (2004) The galactic habitable zone and the distribution of complex life in the Milky Way. *Science* 303:59–62.
- Maurette, M. and Brack, A. (2006) Cometary petroleum in Hadean time? *Meteorit. Planet. Sci.* 41:5247.
- McGenity, T.J., Gemmill, R.T., Grant, W.D., and Stan-Lotter, H. (2000) Origins of halophilic microorganisms in ancient salt deposits. *Environ. Microbiol.* 2:243–250.
- Miller, S.L. (1953) The production of amino acids under possible primitive Earth conditions. *Science* 117:528–529.
- Mulkidjanian, A.Y., Cherepanov, D.A., and Galperin, M.Y. (2003) Survival of the fittest before the beginning of life: selection of the first oligonucleotide-like polymers by UV light. *BMC Evol. Biol.* 3, doi:10.1186/1471-2148-3-12.
- Muñoz Caro, G.M., Meierhenrich, U.J., Schutte, W.A., Barbier, B., Arcones Segovia, A., Rosenbauer, H., Thiemann, W.H.P., Brack, A., and Greenberg, J.M. (2002) Amino acids from ultraviolet irradiation of interstellar ice analogues. *Nature* 416:403–406.
- Nielsen, P.E., Egholm, M., Berg, R.H., and Buchardt, O. (1991) Sequence-selective recognition of DNA by strand displacement with a thymine-substituted polyamide. *Science* 254:1497–1500.
- Parkes, R.J., Cragg, B.A., Bale, S.K., Getliff, J.M., Goodman, K., Rochelle, P.A., Fry, J.C., Weightman, A.J., and Harvey, S.M. (1994) Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371:410–413.
- Parkes, R.J., Cragg, B.A., and Wellsbury, P. (2000) Recent studies on bacterial populations and processes in seafloor sediments: a review. *Hydrogeology Journal* 8:11–28.

- Reeves, G.D., Cayton, T.E., Gary, S.P., and Belian, R.D. (1992) The great solar energetic particle events of 1989 observed from geosynchronous orbit. *J. Geophys. Res.* 97:6219–6226.
- Rivkina, E., Friedmann, E.I., McKay, C., and Gilichinsky, D. (2000) Microbial activity of permafrost bacteria down to  $-20^{\circ}\text{C}$ . *Appl. Environ. Microbiol.* 66:3230–3233.
- Rontó, Gy., Bérces, A., Fekete, A., Kovács, G., Grof, P., and Lammer, H. (2004) Biological UV dosimeters in simulated space conditions. *Adv. Space Res.* 33:1302–1305.
- Sagan, C. and Khare, B.N. (1971) Long-wavelength ultraviolet photoproduction of amino acids on the primitive Earth. *Science* 173:417–420.
- Schäfer, G., Kruklwich, T.A., Poole, R.K., Padan, E., Konings, W.N., Skulachev, V., Fillingame, R.H., Matin, A., Dimroth, P., Booth, I.R., Bogachev, A., Cook, G.M., Dilworth, M.J., and Epstein W. (1999) How can archaea cope with extreme acidity? In *Bacterial Response to pH*, edited by R.K. Poole, John Wiley & Sons, Chichester, UK, pp 131–151.
- Schidlowski, M. (1987) Application of stable carbon isotopes to early biochemical evolution on Earth. *Annu. Rev. Earth Planet. Sci.* 15:47–72.
- Segerer, A.H., Burggraf, S., Fiala, G., Huber, G., Huber, R., Pley, U., and Stetter, K.O. (1993) Life in hot springs and hydrothermal vents. *Orig. Life Evol. Biosph.* 23:77–90.
- Segura, A., Krelove, K., Kasting, J.F., Sommerlatt, D., Meadows, V., Crisp, D., Cohen, M., and Mlawer, E. (2003) Ozone concentrations and ultraviolet fluxes on Earth-like planets around other stars. *Astrobiology* 3:689–708.
- Shea, M.F. and Smart, D.F. (1995) History of solar proton event observations. *Nuclear Physics B—Proceedings Supplements* 39:16–25.
- Smith, D.S., Scalo, J., and Wheeler, J.C. (2004) Transport of ionising radiation in terrestrial-like exoplanet atmospheres. *Icarus* 171:229–253.
- Sowerby, S.J., Cohn, C.A., Heckl, W.M., and Holm, N.G. (2001) Differential adsorption of nucleic acid bases: relevance to the origin of life. *Proc. Natl. Acad. Sci. U.S.A.* 98:820–822.
- Stetter, K.O. (1998) Hyperthermophiles and their possible role as ancestors of modern life. In *The Molecular Origins of Life: Assembling Pieces of the Puzzle*, edited by A. Brack, Cambridge University Press, Cambridge, UK, pp 315–335.
- Stetter, K.O. (2001) Hyperthermophilic microorganisms. In *Astrobiology—The Quest for the Conditions of Life*, edited by G. Horneck and Ch. Baumstark-Khan, Springer Verlag, Heidelberg, pp 169–184.
- Terfort, A. and von Kiedrowski, G. (1992) Self-replication by condensation of 3-aminobenzamidines and 2-formylphenoxyacetic acids. *Angew. Chem. Int. Ed. Engl.* 31:654–656.
- Vishnivetskaya, T.A., Petrova, M.A., Urbance, J., Ponder, M., Moyer, C.L., Gilichinsky, D.A., and Tiedje, J.M. (2006) Bacterial community in ancient Siberian permafrost as characterized by culture and culture-independent methods. *Astrobiology* 6:400–414
- Vorobyova, E., Soina, V., Gorlenko, M., Minkovskaya, N., Zalinova, N., Mamukelashvili, A., Gilichinsky, D., Rivkina, E., and Vishnivetskaya, T. (1997) The deep cold biosphere: facts and hypothesis. *FEMS Microbiol. Rev.* 20:277–290.
- Wächtershäuser, G. (1998) Origin of life in an iron-sulfur world. In *The Molecular Origins of Life: Assembling Pieces of the Puzzle*, edited by A. Brack, Cambridge University Press, Cambridge, UK, pp 206–218.
- Westall, F., De Witt, M.J., Dann, J., Van der Gaast, S., De Ronde, C., and Gerneke, D. (2001) Early Archean fossil bacteria and biofilms in hydrothermally influenced, shallow water sediments, Barberton greenstone belt, South Africa. *Precambrian Res.* 106:93–116.
- Woese, C.R., Kandler, O., and Wheelis M.L. (1990) Towards a natural system of organisms: proposal for the domains Archaea, Bacteria and Eucarya. *Proc. Natl. Acad. Sci. U.S.A.* 87:4576–4579.
- Wynn-Williams, D.D. and Edwards, H.G.M. (2000a) Proximal analysis of regolith habitats and protective biomolecules *in situ* by laser Raman spectroscopy: overview of terrestrial Antarctic habitats and Mars analogs. *Icarus* 144:486–503.
- Wynn-Williams, D.D. and Edwards, H.G.M. (2000b) Antarctic ecosystems as models for extraterrestrial surface habitats. *Planet. Space Sci.* 48:1065–1075.
- Zierenberg, R.A., Adams, M.W.W., and Arp, A.-J. (2000) Life in extreme environments: hydrothermal vents. *Proc. Natl. Acad. Sci. U.S.A.* 97:12961–12962.

Address correspondence to:

André Brack  
Centre de Biophysique Moléculaire, CNRS  
Rue Charles Sadron 45071  
Orleans cedex 2  
France

E-mail: brack@cnrs-orleans.fr

This article has been cited by:

1. G.R. Osinski, C.S. Cockell, A. Pontefract, H.M. Sapers. 2020. The Role of Meteorite Impacts in the Origin of Life. *Astrobiology* 20:9, 1121-1149. [[Abstract](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
2. M. J. Way, Anthony D. Del Genio. 2020. Venusian Habitable Climate Scenarios: Modeling Venus Through Time and Applications to Slowly Rotating Venus-Like Exoplanets. *Journal of Geophysical Research: Planets* 125:5. . [[Crossref](#)]
3. Lammer Helmut, Sproß Laurenz, Grenfell John Lee, Scherf Manuel, Fossati Luca, Lendl Monika, Cubillos Patricio E.. 2019. The Role of N<sub>2</sub> as a Geo-Biosignature for the Detection and Characterization of Earth-like Habitats. *Astrobiology* 19:7, 927-950. [[Abstract](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
4. Helmut Lammer, Aubrey L. Zerkle, Stefanie Gebauer, Nicola Tosi, Lena Noack, Manuel Scherf, Elke Pilat-Lohinger, Manuel Güdel, John Lee Grenfell, Mareike Godolt, Athanasia Nikolaou. 2018. Origin and evolution of the atmospheres of early Venus, Earth and Mars. *The Astronomy and Astrophysics Review* 26:1. . [[Crossref](#)]
5. Michael Perryman. The Exoplanet Handbook 51, . [[Crossref](#)]
6. Marisa R. Myers, Gary M. King. 2017. Perchlorate-Coupled Carbon Monoxide (CO) Oxidation: Evidence for a Plausible Microbe-Mediated Reaction in Martian Brines. *Frontiers in Microbiology* 8. . [[Crossref](#)]
7. Frédéric Foucher, Keyron Hickman-Lewis, Frances Westall, André Brack. 2017. A Statistical Approach to Illustrate the Challenge of Astrobiology for Public Outreach. *Life* 7:4, 40. [[Crossref](#)]
8. Lisa Kaltenegger. 2017. How to Characterize Habitable Worlds and Signs of Life. *Annual Review of Astronomy and Astrophysics* 55:1, 433-485. [[Crossref](#)]
9. S. P. Schwenzer, J. C. Bridges, R. C. Wiens, P. G. Conrad, S. P. Kelley, R. Leveille, N. Mangold, J. Martín-Torres, A. McAdam, H. Newsom, M. P. Zorzano, W. Rapin, J. Spray, A. H. Treiman, F. Westall, A. G. Fairén, P.-Y. Meslin. 2016. Fluids during diagenesis and sulfate vein formation in sediments at Gale crater, Mars. *Meteoritics & Planetary Science* 51:11, 2175-2202. [[Crossref](#)]
10. Teresa Wong, Viatcheslav S. Solomatov. 2016. Constraints on plate tectonics initiation from scaling laws for single-cell convection. *Physics of the Earth and Planetary Interiors* 257, 128-136. [[Crossref](#)]
11. M. Safonova, J. Murthy, Yu. A. Shchekinov. 2016. Age aspects of habitability. *International Journal of Astrobiology* 15:2, 93-105. [[Crossref](#)]
12. Barbara Cavalazzi, Roberto Barbieri. Emergence and Evolution of Early Life in the Geological Environment 3-13. [[Crossref](#)]
13. Gary M. King. 2015. Carbon monoxide as a metabolic energy source for extremely halophilic microbes: Implications for microbial activity in Mars regolith. *Proceedings of the National Academy of Sciences* 112:14, 4465-4470. [[Crossref](#)]
14. Cady Lawrence P., Brack André, Bueno Prieto Jorge E., Cockell Charles, Horneck Gerda, Kasting James F., Lineweaver Charles H., Raulin François, Schopf J. William, Sleep Norman, von Bloh Werner, Westall Frances, Deamer David, Lehman Niles, Pérez-Mercader Juan. 2014. Where Do We Go from Here? Astrobiology Editorial Board Opinions. *Astrobiology* 14:8, 629-644. [[Citation](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
15. Kepa Ruiz-Mirazo, Carlos Briones, Andrés de la Escosura. 2014. Prebiotic Systems Chemistry: New Perspectives for the Origins of Life. *Chemical Reviews* 114:1, 285-366. [[Crossref](#)]
16. Martin Schmieder, Fred Jourdan. 2013. The Lappajärvi impact structure (Finland): Age, duration of crater cooling, and implications for early life. *Geochimica et Cosmochimica Acta* 112, 321-339. [[Crossref](#)]
17. Jan Spitzer. 2013. Emergence of Life from Multicomponent Mixtures of Chemicals: The Case for Experiments with Cycling Physicochemical Gradients. *Astrobiology* 13:4, 404-413. [[Abstract](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
18. J.C. Bridges, S.P. Schwenzer. 2012. The nakhlite hydrothermal brine on Mars. *Earth and Planetary Science Letters* 359-360, 117-123. [[Crossref](#)]
19. Joseph Kula, Suzanne L. Baldwin. 2012. On hematite as a target for dating aqueous conditions on Mars. *Planetary and Space Science* 67:1, 101-108. [[Crossref](#)]
20. H. Lammer, V. Eybl, K. G. Kislyakova, J. Weingrill, M. Holmström, M. L. Khodachenko, Yu. N. Kulikov, A. Reiners, M. Leitzinger, P. Odert, M. Xiang Grüß, B. Dorner, M. Güdel, A. Hanslmeier. 2011. UV transit observations of EUV-heated expanded thermospheres of Earth-like exoplanets around M-stars: testing atmosphere evolution scenarios. *Astrophysics and Space Science* 335:1, 39-50. [[Crossref](#)]
21. Lewis R. Dartnell. 2011. Ionizing Radiation and Life. *Astrobiology* 11:6, 551-582. [[Abstract](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
22. Marc Tissera. 2011. Origin of Evolution versus Origin of Life: A Shift of Paradigm. *International Journal of Molecular Sciences* 12:6, 3445-3458. [[Crossref](#)]

23. André Brack. 2011. From the Love of Peptides to the Search for Life on Mars, an Astrobiology Itinerary. *Astrobiology* 11:4, 275-279. [[Citation](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
24. John N. Maina. Accretion and Shifts of the Levels of O<sub>2</sub> and CO<sub>2</sub> in the Biosphere 1-29. [[Crossref](#)]
25. John N. Maina. Functional Designs of the Gas Exchangers 141-221. [[Crossref](#)]
26. H. Lammer, V. Eybl, K. G. Kislyakova, J. Weingrill, M. Holmström, M. L. Khodachenko, Yu. N. Kulikov, A. Reiners, M. Leitzinger, P. Odert, M. Xiang Größ, B. Dorner, M. Güdel, A. Hanslmeier. UV transit observations of EUV-heated expanded thermospheres of Earth-like exoplanets around M-stars: testing atmosphere evolution scenarios 39-50. [[Crossref](#)]
27. Karl-Heinz Glassmeier, Joachim Vogt. 2010. Magnetic Polarity Transitions and Biospheric Effects. *Space Science Reviews* 155:1-4, 387-410. [[Crossref](#)]
28. Malcolm Fridlund, Helmut Lammer. 2010. The Astrobiology Habitability Primer. *Astrobiology* 10:1, 1-4. [[Citation](#)] [[Full Text](#)] [[PDF](#)] [[PDF Plus](#)]
29. Karl-Heinz Glassmeier, Joachim Vogt. Magnetic Polarity Transitions and Biospheric Effects 387-410. [[Crossref](#)]