Astron Astrophys Rev
DOI 10.1007/s00159-010-0030-4

REVIEW ARTICLE

Habitability: from stars to cells

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Received: 2 February 2008

Abstract To determine where to search for life in our solar system or in other extrasolar systems, the concept of habitability has been developed, based on the only sample we have of a biological planet—the Earth. Habitability can be defined as the set of the necessary conditions for an active life to exist, even if it does not exist. In astronomy, a habitable zone (HZ) is the zone defined around a sun/star, where the temperature conditions allow liquid water to exist on its surface. This habitability concept can be considered from different scientific perspectives and on different spatial and time scales. Characterizing habitability at these various scales requires interdisciplinary research. In this article, we have chosen to develop the geophysical, geological, and biological aspects and to insist on the need to integrate them, with a particular focus on our neighboring planets, Mars and Venus. Important geodynamic processes may affect the habitability conditions of a planet. The dynamic processes, e.g., internal dynamo, magnetic field, atmosphere, plate tectonics, mantle convection, volcanism, thermo-tectonic evolution, meteorite impacts, and erosion, modify the planetary surface, the possibility to have liquid water, the thermal state, the energy budget, and the availability of nutrients. They thus play a role in the persistence of life on a planet. Earth had a liquid water ocean and some continental crust in the Hadean between 4.4 and 4.0 Ga (Ga: billions years ago), and may have been habitable very early on. The origin of life is not understood yet; but the oldest putative traces of life are early Archean (∼3.5 Ga). Studies of early Earth habitats documented in the rock record

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hosting fossil life traces provide information about possible habitats suitable for life beyond Earth. The extreme values of environmental conditions in which life thrives today can also be used to characterize the "envelope" of the existence of life and the range of potential extraterrestrial habitats. The requirement of nutrients by life for biosynthesis of cellular constituents and for growth, reproduction, transport, and motility may suggest that a dynamic and rocky planet with hydrothermal activity and formation of relief, liquid water alteration, erosion, and runoff is required to replenish nutrients and to sustain life (as we know it). The concept of habitability is very Earth-centric, as we have only one biological planet to study. However, life elsewhere would most probably be based on organic chemistry and leave traces of its past or recent presence and metabolism by modifying microscopically or macroscopically the physico-chemical characteristics of its environment. The extent to which these modifications occur will determine our ability to detect them in astrobiological exploration. Looking at major steps in the evolution of life may help determining the probability of detecting life (as we know it) beyond Earth and the technology needed to detect its traces, be they morphological, chemical, isotopic, or spectral.

Keywords Habitability · Astrobiology · Geodynamics · Early Earth · Biosignatures · Extremophiles

1 Introduction: habitability and astrobiology

Astrobiology is the study of the origin, evolution, and distribution of life in the universe. Astrobiology brings a common, biological perspective to such diverse fields as astronomy, astrophysics, biochemistry, chemistry, ecology of extremophiles, geology, geophysics, microbiology, molecular biology, paleontology, physiology, planetary sciences, prebiotic chemistry, space exploration, and technology, without omitting law and philosophy. Recent and future exploration in the solar system and beyond offers new opportunities to investigate the possibility of life beyond Earth. To determine where to search for life in our solar system or in other extrasolar systems, the concept of habitability has been developed, based on the only sample we have of a biological planet—the Earth. This habitability concept can be considered from different scientific perspectives on different spatial and time scales.

Before developing this concept from different points of view, we must try to define what is life—at least life as we know it; what are the properties of life, its limits, and its potential habitats; and how to recognize its traces on early Earth, and beyond Earth. Defining life is not an easy task. Several attempts have been made (e.g., Lazcano 2008), focusing on various characteristics of life which, taken separately, may not be restricted to life (for example auto-replication, or exchange of energy and matter with the environment, or change through time). A wild fire reproduces and uses energy. So do crystals and various chemical reactions. A star changes through time. But none of these have embedded instructions in a genetic code. The only such instructions we know are DNA (Deoxyribonucleic acid) and RNA (Ribonucleic acid), but there may be other genetic systems possible in the universe. The minimum unit of life (as we know it) is the cell (if we exclude viruses which are not cellular and cannot live outside a host).

So what is life? Life can be defined as a suite of chemical processes enclosed in a compartment (the cell), exchanging energy and matter with the environment and transforming it (metabolism), reproducing by transfer of its information material (genes) to its descendants, and evolving by natural selection. Necessary ingredients for life include liquid water, chemical elements, energy sources, possibly on a geologically active planet. Although the conditions necessary for life to emerge on a planet might require more than simply mixing a few ingredients, it is possible that suitable conditions for life to appear and evolve exist or existed elsewhere in the universe, possibly even in our solar system. Extraterrestrial life would probably be based on organic chemistry in a water solvent (Pace 2001) although alternative biochemistries have been hypothesized (Bains 2004; Benner et al. 2004). Indeed, organic molecules (molecules composed of at least carbon and hydrogen) are common in the universe, in interstellar medium or in meteorites. Moreover, carbon (C) builds complex molecules with high information content. Carbon (C), hydrogen (H), oxygen (O), nitrogen (N), the building blocks of life, are among the first elements to form in stellar environments, and are ubiquitous in the universe. The origin of life on Earth is not constrained and although the necessary ingredients and conditions occurred on Earth, in principle, life could have appeared on another inner planet or even on smaller bodies, (e.g., the parent bodies of primitive meteorites) and been transported by meteorites (the so-called "panspermia" hypothesis). Considering the evolution of terrestrial life, the most probable form of life that could exist beyond Earth would be microbial (see Fig. 1). The search for intelligent (not only intelligent, but also technologically advanced) life (SETI[1]) will not be considered in this article. The discussion will focus on the habitability conditions necessary for the origin and persistence of microbial life; the earliest, most abundant, ecologically successful and metabolically diverse forms of life on Earth, driving the Earth's biogeochemical cycles.

For astronomers, the habitable zone (HZ) is the region in a stellar/sun-centered orbit where an Earth-like planet (with the same atmospheric pressure conditions) can maintain liquid water on its surface and Earth-like life (carbon-based life). It does of course depend on the temperature, which in turn depend on the distance from the mother star (Kasting et al. 1993). Figure 2 shows the HZ for different mass/luminosity of the mother star as well as for our own solar system (relative mass with respect to the Sun = 1).

Around our Sun, the HZ extends from after Venus to just before Mars, so the only planet within it is the Earth. Images from Mars' surface show that early Mars conditions may have been different, showing convincing evidence that liquid water once flowed on Mars as well. Moreover, Earth's Moon which is in the HZ is not habitable, whereas some icy moons beyond the HZ might include a liquid ocean under their icy crust, and might be habitable. So there must be more to whether a planet can sustain life than just its distance from the Sun, as discussions in this article will show. A common view of habitability conditions implies that planets can host a surface biosphere, where photosynthesis and efficient bio-productivity are possible (light and water simultaneously

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[1] Search for Extra-Terrestrial Intelligence (SETI) is the collective name for a number of activities people undertake to search for extraterrestrial life. SETI projects use scientific methods to search for electromagnetic transmissions from civilizations on distant planets.

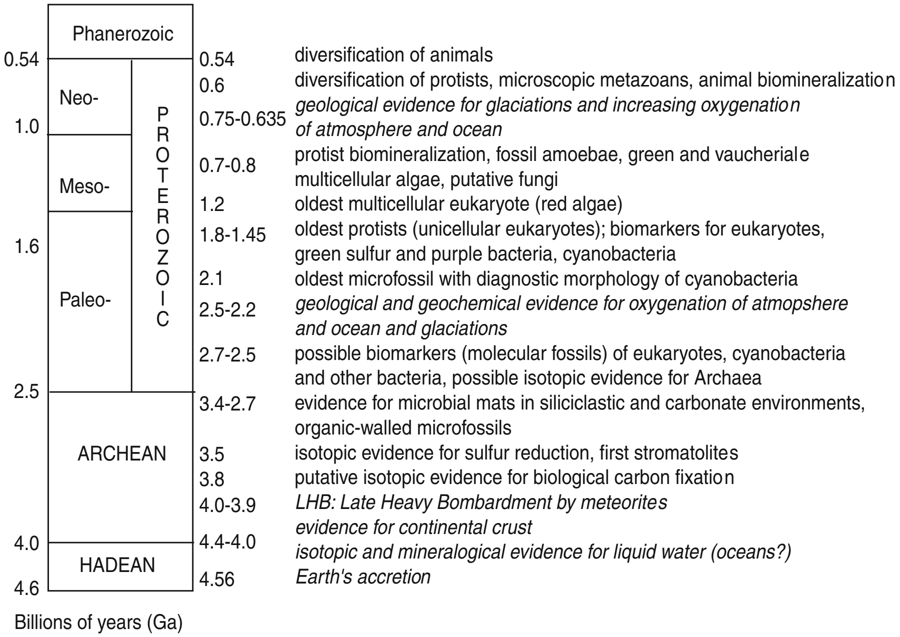

Fig. 1 Major biological and geological events in the Precambrian (modified from Javaux 2006)

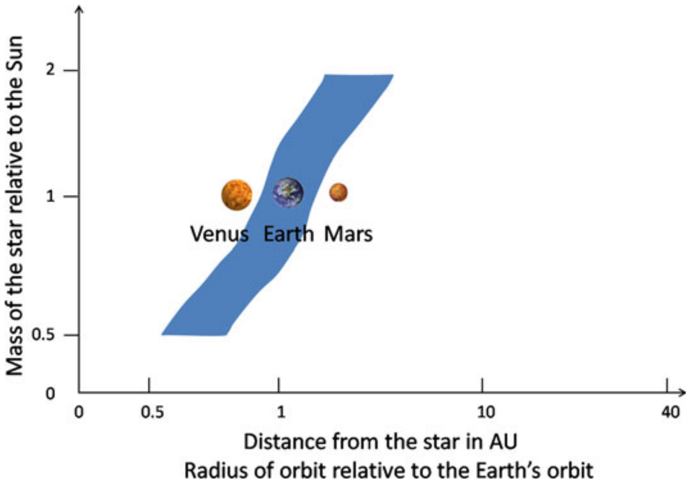

Fig. 2 Habitable zone (modified from Kasting et al. 1993)

available). This definition is very restrictive and limited by our detection technologies of spectroscopic biosignatures beyond the solar system. It does not reflect the habitability of Earth where life has spread also in subterranean and aquatic habitats and where many life forms do not depend on the solar energy for their metabolism. Moreover, photosynthesis is a complex metabolism and thus was probably not

Fig. 3 The Rio Tinto in southern Spain is an extremely acidic river (pH 1–3) where microorganisms (including eukaryotes) thrive. The red color of the water is due to the precipitation of iron oxides, which can preserve biological remains (filaments and cells) by mineral casting. This site is extensively studied by researchers from the Centro De Astrobiologia (Madrid) in collaboration with NASA, as a possible terrestrial analog to Terra Meridiani on Mars that the Mars Exploration Rover Opportunity has been exploring for a few years, and with ESA, in preparation for the 2018 ExoMars mission (photograph by Javaux)

primordial, although the occurrence of 3.46 Ga old stromatolites may suggest a very early origin of (anoxygenic-not releasing oxygen) photosynthesis in Earth history (Allwood et al. 2006, 2008) (Fig. 3). Processes in the biosphere, atmosphere, hydrosphere, the crust, and the deep planet interior interact to stabilize the greenhouse effect and provide the necessary conditions for liquid water and life to exist and for life to evolve. Terrestrial life, as we understand it, requires liquid water, implying the stability of liquid water on the surface of a planet. This criterion is used to define a HZ around a star: depending on the luminosity/energy of the star, the surface temperature is required to be slightly above the temperature of the triple point of water (where liquid, solid, and gaseous states exist). In this limited approach, the surface temperature and the presence of an atmosphere are the only geophysical processes considered. Other geophysical processes, such as those related to the planet interior, are usually disregarded. However, a planet could be habitable only during a fraction of its evolution. The planet Mars may have been habitable in its infancy, as geomorphology and mineralogy seem to suggest (Bibring et al. 2005, 2006), but very early on (about 4 Ga ago) it has lost its magnetosphere and most of its atmosphere, preventing the presence of liquid water at the surface. Earth is habitable (and inhabited) at present, but it will not be habitable once the Sun evolves to a red giant or even later to a black dwarf; it will no longer be in the "habitable zone." On the other hand, the Moon, which is in the HZ of the solar system, is not habitable, but the Jovian satellite Europa, located outside the HZ, may have a habitable ocean under its icy crust.

Fig. 4 Stromatolites from Shark Bay, Western Australia. These stromatolites are built today by trapping, binding and cementation of sedimentary particles and/or precipitation of carbonates by cyanobacteria and other microorganisms, along oxygenated hypersaline shorelines. These laminated structures occur in the rock record since about 3.5 Ga; however early Earth stromatolites occurred in similar habitats but in an ocean and atmosphere with little or no free oxygen. The biogenicity of some of the oldest examples is questioned, as they are difficult to differentiate from chemical precipitates prior to 2.7 Ga (photograph by Javaux)

Although the concept of habitability requires environmental conditions where liquid water occurs, we suggest that additional conditions, especially geophysical processes, are required to maintain habitable conditions, i.e., an environment that supports life and permits its evolution. In this context, coupling geophysics, geology, and biology is crucial to understand how the dynamics of the planetary interior and/or of its surface fluid reservoirs permit nutrients recycling, enabling life to reproduce, grow, adapt to varying environmental conditions, and to evolve. Defining the habitability of a planet also requires understanding the range of physico-chemical conditions in which life -as we know it- can exist, and the limits of life. In the last decades, biologists have discovered life in a wide range of Earth habitats, from the surface through the crust, from the deep ocean black smokers to the dry cold Antarctic rocks, from acidic rivers (Fig. 3) to hypersaline lagoons (Fig. 4), even to nuclear reactors. Life has developed a rich diversity of metabolisms to adapt to these "extreme conditions." Life actually originated and evolved from an "extreme" early Earth exposed to harsh UV, sometimes heavy meteoritic bombardments, with no or very little oxygen in the atmosphere and oceans, conditions that were extreme compared to the present ones. The search for life in potential habitats of a habitable planet (on Earth or beyond) requires the characterization of traces or indices of life (often called biosignatures) permitting its detection in ancient rocks (past life) or recent substrates (sediments, water, ice, rocks) (extant life). Habitats are also HZs in a sense, but at the smaller scale of a portion of the planet [e.g. deep ocean, intertidal zone (area of the seashore between the lowest and the highest tidal levels), desert, forest. . .] or even at the microscopic scale, micro-habitat (e.g., pores within rocks, layer within microbial mat, surface of a pyrite cube. . .).

Our understanding of the HZ around a star has recently improved with the discovery of planets outside the Solar System (Beaulieu et al. 2006; Udry et al. 2007, see also theoretical development in Boss [2006]), and in particular of a so-called "super-Earth," the COROT-Exo-7b, the smallest terrestrial planet detected so far, with a radius of about twice the Earth's radius (Léger et al. 2009). The astronomical, geophysical, and biological processes are now all recognized being important to consider. In particular, factors like evolution of atmospheres, radiation and particles fluxes and initial water inventories have been reviewed in a recent article of Lammer et al. [2009]. We will review here some of the geophysical and biological processes that may play an important role in habitability.

2 Habitability of planetary systems

2.1 Stellar conditions

The recent discovery of Earth-like exoplanets (Udry et al. 2007; Léger et al. 2009) triggers also a great interest from the scientific community as well as the general public. Since 1995, more than 300 new planetary systems have been discovered around nearby (and a few less nearby) stars (around M, K, G, F stars). Among the 404 exoplanets discovered so far (as of November 6th 2009, http://exoplanet.eu), 66 are in the HZ of a star as of November 6th 2009, (http://www.planetarybiology.com/hz_candidates/).

Super-Earths (with masses between 2 and 10 times the Earth's mass) have been discovered and other candidates are promising, suggesting that "one solar-like star out of three harbors planets less than 30 Earth masses" (http://www.eso.org/public/outreach/press-rel/pr-2008/pr-19-08.html).

Recently, the COROT (COnvection, ROtation, and planetary Transits) mission reported the finding of the smallest exoplanet COROT-Exo-7b with a measured diameter of 1.7 times that of the Earth (http://www.cnes.fr/web/CNES-fr/7496-corot-exo-7b-la-petite-planete-qui-peut-en-cacher-une-autre.php).

About 7% of the observed stars host at least 1 planet (this fraction increases with the stellar abundance in heavy elements). Instruments such as the HARPS spectrograph (High Accuracy Radial Velocity Planet Searcher, http://www.eso.org/sci/facilities/lasilla/instruments/harps/) at the ESO La Silla Observatory, present space missions such as COROT, (http://smsc.cnes.fr/COROT/) (launched in December 2006) and Kepler (http://kepler.nasa.gov/) (launched in March 2009), and future missions such as Gaia (launch 2011), JWST (launch 2013), and possibly Darwin (Cockell et al. 2009), have triggered a definite renewed interest in the field of exoplanets. However, although planets occur around several types of stars, the lifetime, size and evolution of the star will determine the planetary habitability through time. Moreover the presence of a planet in the so-defined habitability zone is certainly not the only condition for life to appear. "Habitable" is not equivalent to "inhabited"! The presence of an atmosphere over a certain period of time and its characteristics are important, as well as the interior of a planet, its evolution, its geodynamics, and its thermal state (see Sect. 2.2). Examining the building blocks of life, Lammer et al. [2009] have evaluated the cosmo-chemical aspects and in particular, the carbon chemistry in relation to interstellar clouds, as well as stellar activity, radiation and plasma environment of the main sequence stars. Along with the high and long lasting stellar XUV emissions and energetic particles fluxes, the stellar activity itself may also have potential strong effects on the planetary magnetospheres and thus on habitability as will be explained later on (see also Lammer et al. 2009). The notion of HZ has been extended further by Guillermo [2005] to the scales of the Galactic HZ or Cosmic Habitable Age. These notions detailed in the mentioned article are often treated as separate concepts and will not be discussed here. Lammer et al. [2009] proposed a classification of habitable bodies in four categories:

- Class I: bodies on which stellar and geophysical conditions allow Earth-analog planets to evolve so that complex multi-cellular life forms may originate;
- Class II: bodies on which life may evolve but due to stellar and geophysical conditions that are different from the class I habitats, the planets rather evolve toward Venus- or Mars-type worlds where complex life-forms may not develop;
- Class III: bodies where subsurface water oceans exist which interact directly with a silicate-rich core, like Europa;
- Class IV: bodies in which there are large liquid water layers between two ice layers, or liquids above ice (also called “super-Ganymeds” or “ocean planets”).

2.2 Planetary conditions

Habitability as defined above involves the existence of liquid water on an Earth-like planet and depends on the amplitude of emission from the mother star (related to type of the star, its magnitude and mass) and on the temperature as a function of the distance to the mother star. This was recognized centuries ago, but it was only in the last few decades, when exoplanets were discovered, that astronomers began to define HZs. The HZ concept applied to the space around a star is called the Circumstellar Habitable Zone (CHZ) or simply the Habitable Zone (HZ) (Guillermo 2005). The HZ concept is simple: when the planet is too close to its star, water evaporates and runs away, and when the planet is too far, water freezes. The zone boundaries also vary in time with the evolution of the emission of the mother star. As summarized in Franck et al. (2001, see also Lammer et al. 2009), the HZ concept was introduced by Huang [1959, 1960] as related to an Earth-like planet that would be moved closer to or further away from the Sun. This idea was extended by Dole [1964], Shklovskii and Sagan [1966], and Hart [1979] accounting for the planetary mass, rotation, obliquity, insulation variations, atmospheric dynamics (e.g., convection and clouds) and radiation transfer processes. As mentioned in Lammer et al. [2009], the classical HZ is defined for surface conditions only. Our understanding of habitability needs to integrate other aspects as the question of what makes a planet habitable is much more complex than having a planet located at the right distance from its host star. Lammer et al. [2009] have already examined some of these aspects such as the radiation and the host stars plasma environment. These authors have as well examined complementary geophysical and geodynamical aspects. We developed more the geophysical and geodynamical aspects relevant for understanding the habitability conditions and the persistence of life. While the article of Lammer et al. [2009] addresses more the chemical conditions for detection of life in the universe, our article aims at better evaluating the conditions that have led life to persist and develop.

Planetary rotation is highly relevant to habitability as it affects its day–night temperature variation and in some models, it impacts magnetic field generation (there is a minimum rotation required for magnetic field to exist). Another important factor is the mass/radius of the planet. Valencia et al. [2007] have demonstrated that, as planetary mass increases, the shear/yield stress available to overcome resistance to plate motion increases while the plate thickness decreases, thereby enhancing plate weakness. This model is however rather simple (one-dimension neglecting pressure effect). One also finds in the literature the opposite more realistic conclusion that increasing planetary radius acts to decrease the ratio between the driving forces and the resistive shear/yield strength, both through the formation of a lower-mantle stagnant lid (decrease of the convection pattern scale) and through increased resistance strength, and thereby increasing the plate thickness and forming a stagnant lid convection (O'Neill and Lenardic 2007). Planetary mass may thus only contribute favorably to the subduction of the lithosphere for Earth-sized planets, an essential component of plate tectonics. The surface gravity has also an important role. The low gravity of Mars results in a stretched depth-pressure scale for the solidus and liquidus of mantle rock (for the possible presence of partial melting in the mantle) and for the phase transitions (such as the transformation of the mineral olivine into perovskite and magnesiowustite) compared to Earth/Venus and therefore an increased likelihood and volume of melt production and outgassing.

The terrestrial planets provide a substrate on which life may develop but the persistence of life depends as well on the planetary evolution (Van Thienen et al. 2007). Earth, Mars, and Venus are quite similar in composition, and Earth and Venus also in size, but the geodynamics of these planets are quite different: plate tectonics on Earth, possible episodic resurfacing on Venus, and a multi-billion year stagnant lid on Mars. The role of volatiles, specifically H_2O and CO_2, is not yet well understood although they must play an important role in the exchange between the solid planet and its atmosphere/hydrosphere, through subduction of hydrated crust and volcanism. The absence or presence of plate tectonics must be considered as well among the habitability conditions. These processes are mentioned in the literature (Franck et al. 2000; Guillermo et al. 2001; Parnell 2004; Van Thienen et al. 2007; Valencia et al. 2007; Lammer et al. 2009; Gillmann et al. 2009) but are not yet fully understood.

The presence of an atmosphere and its characteristics are important for planetary habitability. The loss of the atmosphere on Mars is considered as the main factor for the low probability of the existence of extant life on Mars surface. The escape of the Martian atmosphere is probably a combination of thermal and non-thermal processes such as charge exchange, dissociative recombination, sputtering, and ionization (Lammer et al. 2003), as well as asteroid or comet impacts (Pham et al. 2009). The atmosphere is protected against these escape processes by the presence of a magnetic field. However, the magnetic field could be considered as a possible agent for enhancing the escape as well (see Barabash et al. 2007; Barabash 2009), but this is rather controversial. The greenhouse effect is important as well in the definition of the HZ, by increasing the atmosphere mean temperature (Kasting et al. 1993). Franck et al. [2001] have further accounted for a system based on an integrated Earth system analysis that relates the boundaries of the HZ to the limits of photosynthetic processes, considering the evolution of the atmosphere through geological time scales. Lammer et al. [2007b], Lundin et al. [2007], Dehant et al. [2007], and Lammer et al. [2009] have further studied the escape of the atmosphere and recognize the important influence of the existence of a strong magnetic field for the Earth that protects life from severe radiation from the Sun and shields the atmosphere against erosion by the solar wind. The later article provides full detail on the processes of particle loss, for ions or electrons or neutral particles in the atmosphere, and the relation with the presence of a magnetic field. The CO_2 cycle and its exchange between the interior of the planet and the atmosphere (degassing/erosion/weathering) is investigated by Spohn [2007, see also Gillmann et al. 2006, who take into account the effects of volcanic degassing focusing on CO_2]. High EUV at the beginning of the solar system history does also induce loss in some species of the atmosphere. The effect of these forcing terms is to ionize, to heat, to chemically modify, and to slowly erode the upper atmosphere throughout the lifetime of a planet (see Lammer et al. 2009). Volatile exchange between the mantle and the atmosphere is a very effective mechanism influencing the atmosphere's mass for planets with plate tectonics. In the case of a mono-plate system (where there is only one plate) such as the planet Mars, most models of the evolution of the Martian surface require removal of CO_2 from the atmosphere, in principle possible by carbonate precipitation. Carbon is indeed known to occur on Mars as CO_2 gas in the atmosphere and as CO_2 ice in the polar caps. The Tharsis volcanic province appeared in the early history of Mars and was accompanied by water and carbon dioxide in quantities possibly sufficient to induce a greenhouse effect and a warm climate (Phillips et al. 2001b; Solomon et al. 2005). If there was ever a period of standing water on Mars, then theory requires that carbonate rocks form, since the atmosphere was rich in carbon dioxide. However, this assumption has been challenged recently and the presence of other greenhouse gases such as methane has been suggested to explain the absence of Noachian carbonates on Mars (Catling 2007; Chevrier et al. 2007). Carbonates occur in the Martian meteorite ALH84001 (Corrigan and Harvey 2004) and have been recently detected by orbiter (by Mars Reconnaissance Orbiter (MRO) with CRISM (Compact Reconnaissance Imaging Spectrometer for Mars), Ehlmann et al. 2008) but in one limited area. Carbonates have been detected in the Martian soil by the Phoenix lander (Boynton et al. 2009). The occurrence of carbonates at the surface of Mars is however puzzling as carbonates dissolve quickly in acid. Therefore their survival until today on Mars challenges suggestions that an exclusively acidic environment later dominated that planet (Ehlmann et al. 2008). The study of the different carbon reservoirs on Mars would improve the understanding of Mars' carbon cycle (Wright et al. 1992; Grady et al. 2004). The scarcity of carbonates on the Martian surface, as seen from the "Observatoire pour la Minéralogie, l'Eau, les Glaces, et l'Activité" (OMEGA) onboard Mars Express (Bibring et al. 2005), is questioning the presence of water in the evolution of Mars. Recent modeling by Tian et al. [2009] suggest, contrary to the general hypothesis, a cold early Noachian period with an instable CO_2 atmosphere subjected to thermal escape. By mid to late Noachian (after 4.1 Ga), the solar EUV flux would have decreased enough to permit volcanic CO_2 to accumulate and form a thick atmosphere and liquid water to be stable at the surface for a few hundred Myrs. These calculations suggest that Mars and Earth were dissimilar in their early history, and underline the importance of the planet's mass to retain its atmosphere and to maintain habitability (Tian et al. 2009).

The Earth is the only planet in the solar system to have a substantial hydrosphere together with its atmosphere. The other inner planets may have possibly encountered a similar situation in their history but they have evolved quite differently. Oceans covered by ice shells may be considered as extreme examples of atmosphere–hydrosphere systems and exist in our solar system. The Galilean satellite Europa is a good example and could thus possibly be habitable. Its ocean should be in contact with the lithosphere and tidal heating may cause volcanic activity supplying energy and nutrients. Tides and in particular tidal heating is believed to play a significant role in planetary evolution (Jackson et al. 2008, 2009), together with radiogenic heating. It must be mentioned though that high pressure ice may exist below the water layer preventing the contact to the lithosphere. The examples of two moons of Saturn, Enceladus and Titan, are discussed in Lammer et al. [2009] in full detail, in addition to Europa.

Thus, the concept of habitability requires consideration of many more factors than simply the distance planet-star. These factors include the planetary rotation with consequences on the climate and magnetic field generation; the relationships between the planet mass and the atmosphere and plate tectonics; the role of volatiles in the hydrosphere, atmosphere and plate tectonics; the atmosphere evolution; and the co-occurrence of an atmosphere and hydrosphere. The geodynamic processes involved in these factors are examined in detail now. They comprise the internal dynamo, magnetic field, atmosphere, plate tectonics, mantle convection, volcanism, thermo-tectonic evolution, meteorite impacts, and erosion, modify the planetary surface and the energy budget. They thus have implications for life persistence and evolution. Obviously involving geodynamic processes in the notion of habitability is in its infancy and our understanding is far from complete. We will examine some of these processes and try to characterize their role in the habitability conditions.

2.2.1 Plate tectonics

The situation for a planet with and without plate tectonics is evaluated in Lammer et al. [2009]. No planetary body in the solar system other than the Earth seems to have developed a system with a lithosphere (continental or oceanic crust plus the solid upper part of the upper mantle) made of plates (tectonic plates), moving above a plastic asthenosphere (part of the upper mantle immediately below the lithosphere), and leading to continents building and subduction of oceanic crusts. Three stages occurred in the early geological history of the Earth: : after a magma ocean, a transition phase with heavy crust, super plumes and breaks in the crust, and since then the development of slow plate tectonics (Martin et al. 2006a, b; Lammer et al. 2009; see also Sect. 3.1). Plate tectonics regulates the composition of the terrestrial atmosphere by cycling the volatiles such as CO_2 and thus favoring greenhouse temperatures and the presence of surface liquid water. Thus plate tectonics seems crucial in maintaining habitable conditions over long geological time scales. The relationships between plate tectonics and other geodynamic processes are further examined in the following sections.

2.2.2 Mantle convection

Mantle convection, as presented in Breuer and Spohn [2003] for instance, may occur in three regimes: stagnant lid convection, intermittent convection, and mobile lid convection. The planet Mars has a stagnant lid regime, while the Earth has plate tectonics (i.e., mobile lid convection; the lithosphere is broken up into what are called tectonic plates.). Venus and Mars could have had plate tectonics in the past, which is surely no more the case for Mars. Plate tectonics is the most efficient way to cool the mantle. Earth mantle's cooling is therefore appreciable. The type of mantle convection mainly depends on the planet dimension and thermal evolution. The following parameters are most important in determining which regime is prevailing: the first parameter is the Rayleigh number, a dimensionless measure of planetary mantle size, interior heating rate, and viscosity. The second parameter is the viscosity contrast across the mantle, and the third describes the threshold between elastic and viscous deformation of the mantle. The temperature profiles are different from one regime to the other.

2.2.3 Surface–mantle interaction

The interior and the surface reservoirs interact through plate tectonics and the exchange of volatiles, mainly water and carbon dioxide. These volatiles induce deformability of the lithosphere, permitting subduction to occur, thereby enabling plate tectonics. The presence of water is thought to be crucial in the generation of plate tectonics (in addition to the planet size through weakening the lithosphere) and in the generation of mantle convection with low-degree geometry (condensing matter at only a few places in the mantle) (Regenauer-Lieb et al. 2001). Volatiles thus play an important role in the engine of plate tectonics. They enhance the convection and, therefore, the mantle cooling. In the absence of volatiles, volcanism and mantle convection cannot be maintained. Thus, plate tectonics associated with mantle convection may be required to provide minerals/nutrients for life to exist and persist.

Climate evolution and the planet interior are coupled through partial melting and mantle convection (e.g., Phillips et al. 2001b). A positive feedback process can operate by the release of water to the atmosphere via mantle melting, leading to an increase in atmospheric opacity and the radiative temperature gradient. The resulting amplification of the greenhouse surface temperature raises the mantle temperature leading to an increase of the partial melting rate.

2.2.4 Core motions

The origin of a magnetic field is generally related to the existence of strong motions within the core, with a particular geometry. These motions are related to all the accelerations undergone by the fluid in the core and thus can be related to a range of factors such as thermal effects, buoyancy/pressure effects, rotation effects, viscosity effects, advection effects, gravitational effects, core size, mantle size. Describing a dynamo necessitates to simplify the equations, therefore, ignoring some of these contributions. The role of the rotation and the dynamo without rotational influence are examined in Lammer et al. [2009]. Some authors have indeed estimated the magnetic moments of terrestrial planets with different core sizes, masses, and rotation periods (see Griessmeier et al. 2005); other authors have examined the thermal conditions for a dynamo to exist (see Christensen and Aubert 2006). These conditions will further be discussed in the next section as they depend on the mantle convection state and temperature.

2.2.5 Core–mantle interaction

Mantle cooling plays, in turn, an important role in the magnetic field generation, as it controls the temperature gradient between the core and the surface. A planet with a stagnant lid, such as Mercury or Mars, implies less volatile, thus less mantle convection. Thermal convection requires a gradient of temperature between the core and the mantle in order to be able to evacuate heat from the core. This only happens above a critical value of temperature gradient (a sufficiently large temperature gradient between the core and the mantle is required in order to drive thermal convection in the core; if it is too small then the core will be cooling by conduction); this corresponds to a “critical” heat flow out of the core. To produce motion in the core, a hot core and a large temperature gradient in the mantle are needed. Plate tectonics creates this gradient as the heat moves away from the mantle. For a super-heated core (when the ratio of the core heat on the mantle heat is high), the temperature gradient is large and a magnetic field is possible; then after only a few 100 million years just after the planet formation, the critical value is reached and the magnetic field disappears. It may last a little bit more in the case plate tectonics starts in the early history of the planet. Without super-heated core (when the ratio of core heat/mantle heat is low) just after the planet formation, building the heat in the core requires a little time to reach a temperature above the critical value (increase the ratio between the heat of the core and the heat of the mantle). But this only happens when plate tectonics is there to provide heat transfer out of the planet and decrease the heat in the mantle (See Breuer and Spohn 2006). The role of water and of plate tectonics in heat transfer is examined by Lammer et al. [2009] who indicate that the large amount of water and the related plate tectonics could have played a role in keeping a magnetic dynamo alive over geological time scales.

Composition buoyancy convection requires that the temperature in the core would be between the solidus and liquidus of the core alloy (iron or nickel with a small fraction of a light element such as sulfur). This temperature is very high for pure iron, implying that the solidification of the core is reached rapidly after its formation. The core of Mars (or any mono-plate planet) would be solid now if this would have been the case. But when there is a small amount of a light element, the temperature of solidification decreases, which allows keeping the core liquid longer in the history of Mars. The higher proportion there is of a light element, the longer it takes before having solidification (for the same mantle conditions). When the solidification begins, the liquid part of the core gets less iron and the relative percentage of the light element increases (if the composition is on the left side of the eutectic point, where the alloy crystallizes with a precipitation of the heavy element; the eutectic point being the melting point of a mixture of two or more solids (such as an alloy) where the crystallization is taking place without passing through a phase of precipitation; it depends on the relative proportions of its ingredients). This lowers the temperature of solidification. In order to keep this compositional convection resulting from iron precipitation in the solid part of the core—the inner core, a cooling of the planet is necessary.

The magnetic field then will exist at the beginning of the formation of a planet (high heat transfer): due to the high temperature gradient within the planet, there is thermal convection in the liquid core and, therefore, a magnetic field. After a certain time, as the temperature decreases, the strength of the magnetic field decreases as well. Again after a while, the temperature is low enough for the core to reach the solidus condition; the mixture of iron and a light element in the liquid core is such that the iron particles precipitate and participate in a chemical convection. This motion in the core induces a magnetic field while the solid inner core (the seed) is forming and the core is cooling. This is what presently happens for the Earth. The amplitude of the magnetic field is expected to be less than at the beginning of the planet's life. When this composition convection is on, it will stay on and be long standing, until the eutectic of the core alloy composition is reached.

2.2.6 General sketch

Thermal convection in the core is believed to be the first process to generate a magnetic field at the beginning of the planet formation. In the case of a mono-plate planet (e.g., Mars), thermal convection would not last long and the classical scenario of conductive cooling would take over. In the plate tectonic case, thermal convection is still believed to be the first process generating magnetic field at the beginning of the planet formation and may last longer than in the mono-plate case. The core and the mantle continue to cool and the temperature gradient is important, implying convection both in the core and the mantle, and most probably the generation of a magnetic field. Chemical convection related to the formation of the inner core would start early, and it is the process in place presently within the Earth, generating its present-day magnetic field.

The atmosphere is generated through outgassing by volcanism due to mantle convection and protected from solar wind erosion by the magnetic field (when the atmosphere does not extend above the magnetopause). Evaporation of the hydrosphere (and biogenic gases when there is a biosphere) also contributes to the atmospheric composition. Meteorite impacts may also play an important role in atmosphere loss and/or replenishment as shown by Pham et al. [2009]. Without a magnetic field or when the magnetopause is below the top of the atmosphere, atmospheric erosion is possible. Gravity and thus the mass and dimension of the planet may also play a role in preserving or not the volatiles; atmospheric losses will be more important for lower gravity. Consequently, transfer of volatile species like water and CO_2 between different reservoirs clearly occurs. The solar wind erosion is studied in particular in the case of the planet Mars. Mars had a magnetic field at the beginning of its existence from 4.6 to 4 Gyr ago. At small spatial scales the Martian crust shows remnant magnetism with high amplitude values (Connerney et al. 2004). Presently Mars lacks a detectable global magnetic field (Acuña et al. 1998, 2001). The explanations for these detections are discussed in the later articles and in Lammer et al. (2009). In parallel it is generally accepted as well that a late heavy bombardment (LHB) of meteorites and comets affected the inner planets of the solar system between ~4.1 and 3.9 Gyr ago (see also Sect. 3.1). In the Nice model (Morbidelli et al. 2007 see also Gomes et al.

2005; Tsiganis et al. 2005; Levison et al. 2008), the LHB is triggered by the dispersion of the planetesimal disk (for an opposite view see Hartmann 1975), and there was a very active period of volcanism around the same epoch. From 3.5 Gyr ago, Mars has become very dry while there are traces of water and related flooding events from 4.6 to 3.5 Gyr ago (Jakosky and Phillips 2001; Jaumann et al. 2005; Bibring et al. 2005). The role of volcanism in climate evolution or at least in the presence of water at the surface of Mars is a subject of debate. Some authors (e.g., Fassett and Head 2005, 2007) suggest that valleys might have formed via basal melting of summit snowpack rather than flowing surface water.

The absence or loss of the atmosphere (together with radioactive or EUV unprotected environment, and absence/loss of nutrients coming from tectonic/volcanic activity) may possibly lead to extinction of life after some time. The general hypothesis is that it would occur after the extinction of the magnetic field when the atmosphere would be eroded by the solar wind and be completely or almost completely lost. However, the protective role of a magnetic field has been recently challenged as the chemical species in the atmosphere and the solar condition may push the limit of the atmosphere above the magnetopause or may decrease the amount of loss in the atmosphere (Barabash et al. 2007; Lammer et al. 2007b, 2008, 2009). For example, Venus has kept a thick atmosphere despite the absence of a magnetic field, which is explained by Bullock and Grinspoon [1996] by volcanic outgassing, coupled with surface processes, in the massive Venus' atmosphere controlled by the presence of radiative processes.

This leads to important questions regarding planetary habitability: Is a magnetic field required? Is an atmosphere required? Is plate tectonics required? What is the role of the composition of the atmosphere? What is the importance of the atmospheric radiative–convective equilibrium with surface processes? All the possible actors entering into the habitability conditions are summarized in Fig. 5 (see also Fig. 7). Nutrient recycling seems essential for the persistence of life after it originated on a planet. These nutrients are in the minerals building rocks, so some geological activity (at least hydrothermalism, maybe plate tectonics) has to occur on geological time scale. This activity cools the planet interior, and produces volatiles such as CO_2 and water. The transfer of volatile species like water and CO_2 between different reservoirs is very important since both species are essential materials of life (nitrogen, phosphorus, and sulfur are other important basic raw materials; see point 3.3.2.), and also main constituents of the hydrosphere/cryosphere and atmosphere. As discussed above, depending on the amount of volatiles, the number of plates (0, 1, many), and the composition of the core, convection in the mantle and in the core will occur, enabling plate tectonics and the generation of a magnetic field. The presence of liquid water at a planetary surface requires an atmosphere ensuring sufficient pressure to maintain water in a liquid phase. If liquid water can persist in the subsurface for geological time scale, an atmosphere may not be needed. Is it conceivable to have a planet with a stagnant lid, with or without an atmosphere, with or without a magnetic field, but liquid water in the subsurface? Icy satellites with an ocean under an icy crust like Europa illustrate such cases. There again, replenishing nutrients is crucial and requires some geological activity at the rock/water interface. The occurrence of such activity, besides tidal heating (see Sect. 2.1), is unknown at the moment.

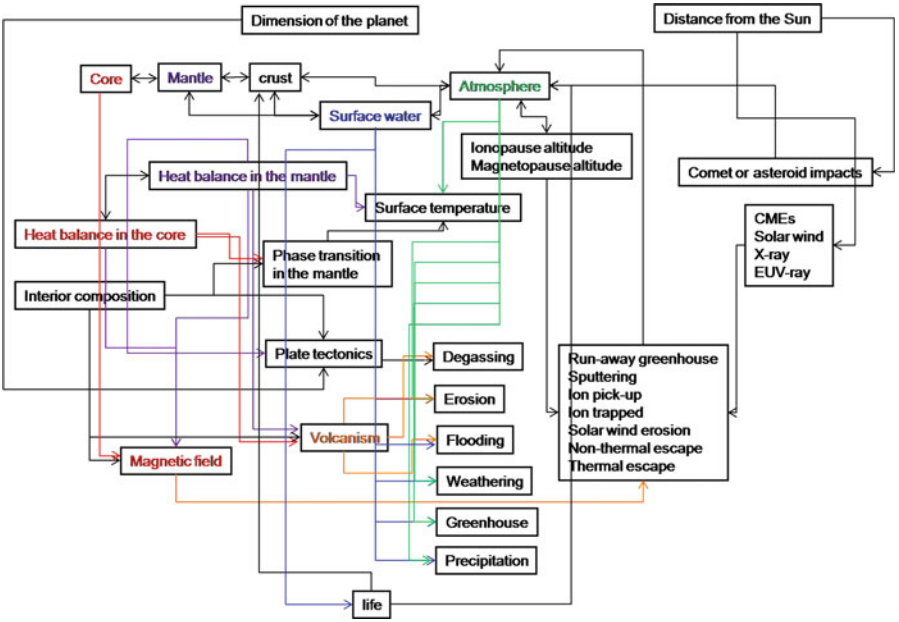

Fig. 5 All possible actors for the habitability. Life inhabits the hydrosphere, crust, and atmosphere of Earth, and uses material (metals, other elements see Table 2, molecules available as gas, organics or minerals) and (not all forms of life) solar energy. These material and energy are recycled through microbial biochemistry (see Falkowski et al. 2008a), but a fraction is lost through burial in sediments and to the atmosphere. The persistence of life requires regeneration of material (elements) by geological processes such as erosion of relief (and thus mountain building) and geothermal processes (see text for detailed explanations). These geodynamic processes are caused by the tectonic activity of the planet, directly linked to the heat transfer through a density-layered structure and thermal gradient, causing mantle convection. This situation itself requires a rocky planet with a sufficient mass (but not too large), at the right distance from a star. The atmosphere is stable, ensuring climate stability and enough pressure for the presence of surface liquid water on long geological time scales, thanks to its protection from solar erosion by the magnetosphere, and the heat transfer from the mother star. The magnetosphere itself results from convection (thermal or compositional convection) in the core, resulting also from the cooling of the planet through heat transfer to the mantle (in addition to the composition of the core). Are all these compartments and interactions needed for life not only to originate, but to persist on a planet? This question is at the heart of planetary habitability

From these speculations, it seems that geological activity is an important ingredient to add to the recipe of a habitable planet, next to liquid water, energy source, and chemical elements.

3 Habitability of planet Earth

3.1 When did Earth become habitable?

Earth formed 4.567 Ga ago, at the beginning of an eon[2] called the Hadean (See Fig. 1). The Hadean is followed by the Archean, the eon between 4 and 2.5 Ga. The eon

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[2] Eons are the longest subdivisions of the geological time scale. Earth history comprises four eons: the Hadean, the Archean, the Proterozoic, and the Phanerozoic. These slices of time are subdivided into eras, themselves subdivided into shorter periods.

Proterozoic ranges from 2.5 to 0.56 Ga and is subdivided into the Paleo-, Meso-, and Neoproterozoic (Fig. 1). Following its accretion, the planet Earth differentiated a core and a mantle by cooling. The upper mantle may have been first a magma ocean (∼4.56–∼4.45 Ga). The next steps included the formation of the Earth atmosphere, ocean, and continental crust as well as a magnetic field and later plate tectonics (Martin et al. 2006a). The only terrestrial geological record that we have from this time is an assemblage of detritic minerals, zircons, dated at ∼4.4 Ga, found in younger rocks from the Jack Hills area in Australia. These old minerals contain Rare Earth Elements, Hafnium isotope signatures, and mineral inclusions indicating their crystallization in granitoid rocks and, therefore, the presence of a continental crust (Martin et al. 2006a). Moreover, their oxygen isotope signature indicates interaction with liquid water (Mojzsis et al. 2001). Their zoned rims indicate melting and growth, implying reworking, thus erosion of the continental crust by water (Martin et al. 2006a).

The oldest rocks preserved on Earth are located in Greenland and Canada and provide evidence for volcanic and sedimentary processes, the latter demonstrating the presence of a hydrosphere (ocean) and emerged continents with weathering, erosion, and transport of sediments as old as 3.87 Ga. Zircons in the Canadian magmatic rocks indicate an Archean crust at ∼4.031 Ga. The oldest zircons mentioned above indicate an even earlier Hadean crust and ocean (Martin et al. 2006a). Thus Earth had a liquid water ocean and some (probably underwater) continental crust in the Hadean (geological eon, from 4.6 to 4.0 Ga), and might have been habitable very early on. The moon-forming event, a few tens of Ma after the solar system formed, probably resulted into a drastic degassing from the proto-mantle and loss of the primitive atmosphere. If water arrived early on Earth, the impact could have vaporized the early ocean and produced a thick H_2O–CO_2 rich atmosphere, that later condensed and precipitated on a molten proto-crust, forming a hot saline then cooler early ocean (165–400 Ma after solar system formation). Therefore, in addition to a solar nebula contribution whose remnant is found in the deep mantle, an external source of water was carried after the moon-forming impact to Earth by meteorites, as supported by D/H isotopic signatures, and accreting cosmic dust, and contributed to the mantle inventory of volatile elements (Martin et al. 2006a). At the age of the oldest zircons, habitable oceans were in place, 165 Ma after the solar system formation. However in the early Archean, the LHB might have vaporized the early ocean. The LHB is now clearly established all over the inner solar system but controversy remains regarding the magnitude and frequency of the collisions between 4.5 and 4 Ga (Martin et al. 2006a; see also Sect. 2.2.6.). Two opposite views propose either a slow progressive decrease, or a rapid decline followed by a cataclysmic peak between 4 and 3.9 Ga, the latter hypothesis being supported by the moon record.

Since the LHB, the Earth has known a relative stability, although there were periods of intense bombardments and glaciations through Earth history that probably impacted life's evolution. The internal heat production of the early Earth was several times greater than today, resulting in high geothermal flux that induced the genesis of particular rocks (such as komatiites and TTG suites) until 2.5 Ga and a particular style of plate tectonics, different from modern plate tectonics (Martin et al. 2006b). Plate tectonics recycle the dense oceanic crust by subduction (when a slab of crust slides into the mantle) every 60 Ma in average, the oldest oceanic crust being 180 Ma. The continental crust is lighter and cannot sink, and therefore can accumulate (the oldest rocks are about 4 Ga) and accrete to form continents. The continental crust has grown episodically due to mantle plume events until today. The presence of oceanic and continental crusts is probably important for life. Indeed the crusts provide a substrate at the water/rock interface and a source of nutrients through geothermal activity and through erosion of older rocks. In the Archean, modern style horizontal plate tectonics existed and horizontal structures resulting from collision between continental crusts occurred. Another style of plate tectonics, called sagduction (vertical tectonics) also occurred until 2.5 Ga, when high density rocks (such as komatiites, Banded Iron Formations) were emplaced onto lower density rocks (TTG), leading to the downward motion of the high density rocks and upward motion of the lighter TTG (Martin et al. 2006b). Since the Archean–Proterozoic boundary (2.7–2.5 Ga), the Earth has cooled enough and only horizontal plate tectonics occurs. A first supercontinent formed at that time around 2.7 Ga. Throughout Earth's history, supercontinents have formed and broken up, playing an important role in the evolution of life by controlling the surface areas of shallow seas along the continental margins and by limiting or enabling the genetic exchanges between populations. For example, in the Phanerozoic, a period of great diversification is linked to the breakup of the supercontinent Pangea.

Rocks at 3.4–3.45 Ga in South African Archean craton[3] record the fossilized signals of Earth's magnetic field, with strengths within 50–70% of the present-day value, indicating that a magnetosphere sheltered (at least partly) the early Earth's atmosphere from solar wind erosion (Tarduno et al. 2010).

3.2 When did life originate on Earth?

We still do not know when, where and how life did originate on our planet. The first steps, studied by prebiotic chemistry (bottom-up approach) or molecular biology (top-down approach), occurred in a warm little pond of unknown salinity dear to Charles Darwin or in a shallow or deep hydrothermal vent (review in Bada 2004; Lazcano and Miller 1996). The building blocks of life, some of which are formed abiotically in the interstellar medium, found in meteorites or easily produced in the laboratory (the Stanley-Miller experiments, e.g. Cleaves et al. 2008) gave rise to early cells with an early genetic code. As mentioned above, in principle, life could have also appeared on another inner planet or parent-body of chondritic meteorites, and then been delivered to the Earth (Gaidos and Selsis 2007; Selsis et al. 2007). However, this hypothesis does not improve our understanding of the origin of life. We will never find traces of these early Earth cells since there are no sedimentary rocks preserved older than about 3.87 Ga. It is remarkable that putative isotopic traces of life might have been found in these oldest metasediments (metamorphosed sediments), suggesting an earlier origin of life (Rosing 1999) (although much debated).

Life on Earth comprises three domains which have evolved from a common ancestor: Bacteria, Archaea, and Eucarya. The domains Bacteria and Archaea include

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[3] The Archean eon is a geological period between −4 and 2.5 Ga (billion years ago); it is one of the four principal eons of Earth history; the Earth of the early Archean may have supported a tectonic regime unlike that of the present. A craton is an old, large and relatively undeformed (stable) continental block.

microscopic cells with a prokaryotic organization: the cells have neither nucleus nor organelles, but they display a high diversity of metabolisms. They differ by the composition of their cell membrane and their genome. The domain Eucarya includes unicellular (protists) or multicellular organisms (such as plants, fungi, and animals) made of cells with a nucleus, membrane-bound organelles and a cytoskeleton (a proteinic network contained within the cytoplasm, useful for internal molecular transport and cell deformation during phagocytosis—when a cell engulfs another cell or particle—and locomotion).

Possibly in the Hadean, certainly in the Archean, life arose on a planet exposed to harsh UV radiation and without oxygen in its atmosphere and oceans (and thus no atmospheric ozone layer), but with surface liquid water, organic molecules (from endogenous formation and/or exogenous delivery), and (hydrothermal, solar, chemical) energy sources, although, when the Sun formed at 4.65 Ga, it was probably 30% less bright than today (Kasting and Catling 2003). These environmental conditions would have frozen the Earth without increased concentrations of greenhouse gases such as CO_2 and CH_4. Between 2.4 and 2.0 Ga, several geological evidences reveal a change from global anoxic (without free oxygen) to oxic (with free oxygen) atmospheric conditions, so-called "the Great Oxidation Event" (G.O.E.). The G.O.E. has been dated around 2.32 Ga based on sulfur isotopes data (Bekker et al. 2004) but some oxygen might have been produced earlier in the Paleoproterozoic (Anbar et al. 2007) or even in the Archean (see Holk et al. 2008; review in Martin et al. 2006b; Buick 2008). Indeed, the main source of oxygen is biological, resulting from oxygenic photosynthesis by cyanobacteria. The origin of these bacteria is still unknown; biomarkers (fossil lipids) suggest a minimum age of 2.77 Ga (Brocks et al. 2003; but see Rasmussen et al. 2008, for a reassessment), and microfossils with demonstrable cyanobacterial affinity are 2.1 Ga (review in Knoll 2003). However some earlier fossils in photic habitats (in water at a depth exposed to sufficient sunlight for photosynthesis to occur) could be cyanobacterial but their simple morphologies do not permit identification. The rise of oxygen producers would have resulted in oxidation of methane into carbon dioxide, decrease of anoxic conditions needed by methanogens, increase of CO_2 consumption by enhanced biological productivity, and consequently climate cooling, as evidenced by glacial deposits (Bekker et al. 2005). The oxygenation event(s) also modified the chemistry of early oceans, going from anoxic conditions, to anoxic and sulfidic (rich in H_2S) deep oceans topped by slightly oxygenated surface waters, to more oxygenated conditions (according to Canfield et al.'s model 2000). These changing redox conditions in early oceans impacted the patterns of life diversification, possibly by limiting trace element availability (see review in Anbar and Knoll 2002; Knoll 2003; Falkowski et al. 2008b).

Possible evidence for life in the early Archean includes microfossils, stromatolites (laminated carbonate sedimentary rocks, produced by trapping, binding, and cementation of sedimentary grains, and/or by mineral precipitation by microorganisms, Fig. 4), and isotopes of sedimentary carbon and sulfur (review in Buick 2001). The biogenicity (biological origin) of these possible traces of life is difficult to prove because of the high degree of metamorphism of the enclosing rocks, the difficulty to reconstruct the sedimentary conditions and thus the paleo-environment, or the possibility of younger contamination or abiotic origin (Brasier et al. 2006). Younger microfossils, biomarkers (molecular fossils) (if their endogenicity is confirmed), large stromatolites, and carbon isotopes at 2.8–2.65 Ga provide unambiguous traces of life and may indicate that the photic zone was inhabited by oxygen-producing cyanobacteria, aerobic heterotrophic (requiring organic carbon for metabolism) bacteria and eukaryotes of unknown physiology (review in Buick 2001). Recently, large (up to 300 μm) organic-walled microfossils were discovered in the 3.2 Ga photic zone of shallow-marine siliciclastic tidal deposits (Javaux et al. 2010). The transition zone between oxic and anoxic water was inhabited by microaerophilic (requiring low level of oxygen to survive) heterotrophic bacteria, possibly including methanotrophs (bacteria using methane for their metabolism). The low δ^{13}C content of organic matter in sedimentary rocks indirectly suggests activity of methanogenic (methane-producer) Archaea under anoxic conditions (Brocks et al. 2003). By the mid-proterozoic, green sulfur and purple Bacteria had evolved (Brocks et al. 2005).

These Archean traces possibly document life in various marine habitats: from deep hydrothermal vent (Rasmussen 2000), to open ocean water column (Brocks et al. 2003), to subseafloor sediments (Hashizume et al. 2006; Westall et al. 2000; Westall 1999; Schopf 1993) and volcanic basalts (Furnes and Staudigel 1999), to shallow water and intertidal normal marine or hypersaline lagoons or carbonate platform (Allwood et al. 2006, 2008; Westall et al. 2000; Shen and Schidlowski 2000; Sugitani et al. 2007), to shallow water siliciclastic (terrigeneous) marine environment (Noffke et al. 2003a, b, 2006; Javaux et al. 2010). So, a large diversity of microbes from the two prokaryotic domains Archaea and Bacteria flourished and still thrives without much change in their morphology, physiology, or habitat over 4 billion years. Early metabolisms included sulfur reduction ($>$3.5 Ga), possibly anoxygenic photosynthesis, oxygenic photosynthesis ($>$2.77–2.32 Ga), methanogenesis and methanotrophy ($>$2.8 Ga), and fermentation (Fig. 1; review in Brocks et al. 2003; Javaux 2006; Southam et al. 2007).

The oxygenation of oceans and atmosphere expanded possible niches for life to diversify. Well before the advent of animals at the end of the Proterozoic, cells may have synthesized eukaryotic sterols (lipid molecules) ($>$2.77 Ga). Eukaryotes diversified moderately around 1.8–1.3 Ga (Knoll et al. 2006), and evolved multicellularity, sexual reproduction, and photosynthesis through engulfment (endosymbiosis) of a cyanobacterial ancestor of the chloroplast by at least 1.2–1 Ga. The atmospheric oxygen level had to reach sufficient level for multicellular organisms to develop locomotion and thus has important implications on the evolution of animals including the evolution of intelligence. Thus, microorganisms have been cycling carbon, sulfur, and nitrogen on Earth possibly since the early Archean, first in various anoxic, photic and non-photic, shallow-water and below wave-base, marine and lacustrine environments, then diversifying in increasingly oxygenated niches.

3.3 Present terrestrial habitats and the “envelope” of life

3.3.1 The limits of life-as-we-know-it

Habitability on Earth can be defined by the limits of past and present physico-chemical conditions in which life as we know it can exist. Early Earth habitats documented in the rock record where life traces have been discovered provide information about possible habitats suitable for life beyond Earth. The extreme values of environmental conditions in which life thrives today can also be used to characterize the "envelope" of life and the range of potential extraterrestrial habitats. Extremophiles include organisms from the three domains of life-Archaea, Bacteria, and Eucarya, that grow optimally in extreme environmental conditions. (note that Eukaryotes do not tolerate hyperthermophilic conditions and high doses of radiation). Extremophiles not only survive in these conditions, they require these conditions. Extreme environments are characterized by physico-chemical conditions close to the limit values in which an organism can live. These extreme conditions can be physical (temperature, radiation, and pressure) or geochemical (desiccation, salinity, pH, oxygen tension, high concentrations of metals, and gases). Table 1 summarizes the limit conditions in which life on Earth can exist as well as examples of habitats characterized by extreme conditions (data from Rothschild and Mancinelli 2001; Lopez-Garcia et al. 2006). Most extreme environments are extreme in more than one parameter. Note that most of the limits of extant life summarized in Table 1 are also applicable to early Earth, with the exception of oxic conditions and conditions induced by human activities. Modern extreme environments are interesting to study in multiple aspects. They permit to increase our knowledge of the modern biodiversity, to study the mechanisms by which life has adapted to these conditions, and how traces of life can be preserved in various environments. This latter point is extremely important when tracing life in the past or beyond Earth. In Shark Bay, Western Australia, microbes precipitate laminated calcium carbonates, producing laminated macrostructures called stromatolites (Fig. 4). In the acidic Spanish river Rio Tinto (Fig. 3), microbial filaments and cells are preserved as cast of iron oxides (Fernandez-Remolar and Knoll 2008), whereas in the Yellowstone hot springs, they are silicified by silica-rich fluids (Konhauser et al. 2007). In Antarctica, endolithic microbes (microorganisms living inside rocks) may be silicified and give a special porous texture to the hosting sandstone (Wierzchos et al. 2005). The (paleo)geobiologist attempts to understand how traces of life can be preserved at various scales, in various physico-chemical conditions (studying preservational environments); how these conditions will alter or erase initial biological properties (taphonomy, i.e. the study of a decaying organism over time), and how to distinguish biological from non-biological features such as a structure, a molecule, an isotope fractionation (defining biogenicity) (see Botta et al. 2008; Javaux 2006).

3.3.2 The requirements of life-as-we-know-it

"A key feature of all living organisms is their ability to direct chemical reactions and organize molecules into specific structures" (Madigan et al. 2000). The fundamental unit of life as we know it is the cell (excluding viruses). A cell is composed mostly of macromolecules made of C, H, O, N, P, S (which are common in the universe, except for H) and water. Silicon (Si) is also common but commonly forms minerals on Earth, not life. Models have proposed a life based on silicon, or using another solvent than water, like liquid methane (Bains 2004; Benner et al. 2004). Benner et al. [2004] challenged the idea of a common chemical model for life in the universe and suggested that the only absolute requirements for life are a thermodynamic disequilibrium and

Table 1 The limits of life as we know it (data from Lopez-Garcia 2006; Rothschild and Mancinelli 2001)

Physico-chemical parameters	Limits	Type of organisms growing optimally at limit values	Examples of habitats
Temperature	$-17/-20$–121°C	Hyperthermophile ($>80°C$)	Hydrothermal vents, hot springs, deep continental and oceanic subsurface
		Psychrophile (<10–15°C)	Antarctic lake, permafrost, ice
pH	0–12	Acidophile (pH$<$2–3)	Acidic river and springs, acid mining drainage
		Alkaliphile (pH$>$9)	Alkaline hot springs, soda lakes
Salinity	? to ∼5 M NaCl	Halophile	Saline lake, sabkha, evaporites, salt mines
Pressure	? to ∼130 MPa	Barophile (Piezophile)	Deep sea, deep subsurface
Radiation	High doses of ionizing radiations, UV		Nuclear reactor, radioactive wastes, deserts, high mountains
Gravity	?Tolerate microgravity	Tolerated by some bacteria and humans	Microgravity experiments, ISS, moon exploration
Vacuum		Tolerated by tardigrades, insects, microbes, seeds	Vacuum experiments in space environment
Dessication	Reduced and episodic availability of liquid water	Xerophiles	Hot and cold desert crusts, endolithic (inside rock) habitats
Oxygen tension		Anaerobe (cannot tolerate O_2)	Inside Earth crust, anaerobic mud, deep sea sediments
		Microaerophile (tolerates some O_2)	Within microbial mats, . . .
		Aerobe (requires O_2)	Top layer of microbial mat, surface environnements
Metal concentration	High concentration of Cu, As, Cd, Zn, Co, Hg, Pb	Metallo-tolerant	Industry waste, metal contaminated aquifers, space ships

Extremophilic members of the three domains of life, Bacteria, Archaea and Eucarya thrive in the following extreme environments (except Eukaryotes which do not tolerate hyperthermophilic conditions and high doses of radiation)

temperatures consistent with chemical bonding. However, for life-as-we-know-it, it seems that carbon is the only element able to construct molecules with high information content, and making chemical bounds to other elements that are breakable for chemical reactions (Pace 2001), and liquid water has unique physico-chemical properties. Organic chemistry in a water solvent could however form carbon-based extraterrestrial life forms using other molecules than DNA and RNA for their genetic material. Davies et al. (2009) hypothesize that even on Earth, some “shadow biosphere” (“weird life” that is not discovered yet on our planet) could exist and, for example, be based only on RNA (Benner et al. 2004).

The highly informative macromolecules, such as RNA and DNA, include the instructions for the functioning, adaptation and reproduction of life. Understanding how such a complex system of information has appeared and evolved is one of the greatest challenges of science. These macromolecules are formed of complexes of sugars, amino acids, phosphates and nucleic bases. A particularity of life as we know it is the homochirality of these building molecules: most amino acids are left-handed and sugars are right-handed, and they infer the same chirality to the spiral secondary structures of proteins and nucleic acids. Molecules are chiral if they have two non-superposable mirror-image forms (called enantiomers): a left-handed and a right-handed form. Amino acids occur in greater diversity in meteorites, and they can show enantiomeric excess up to 15% for non-terrestrial amino acids. Enantiomeric excess lower than 100% (homochirality) would therefore not be an unambiguous indication of extraterrestrial life (Barron 2008). Moreover chirality is not chemically stable and tends to not be preserved over long time scales, so it could only be an index of extant or recently active life. The origin of homochirality is unknown although several mechanisms have been hypothesized, such as the differential solubility of one enantiomer, or its differential destruction by circular polarized light, or the enhancement of enantiomeric excess by a chiral mineral surface (e.g. Barron 2008; Breslow and Cheng 2009). Recent analyses of the amino acids alloisoleucine and isoleucine from a pristine Antarctic meteorite show that their likely precursor molecules, the aldehydes, which are abundant interstellar molecules, carried a molecular asymmetry up to 14% in the asteroidal parent body, suggesting that "chiral asymmetry could have been seeded in abiotic chemistry ahead of life" (Pizzarello et al. 2008).

Elements that are required by life in large amounts are called macronutrients and include C, H, O, N, P, S, and potassium (K), Magnesium (Mg), sodium (Na), calcium (Ca), and iron (Fe). Other elements are needed in trace amounts, the micronutrients, and include Cromium (Cr), Cobalt (Co), Copper (Cu), Manganese (Mn), Molybdynum (Mo), Nickel (Ni), Selenium (Se), Tungsten (W), Vanadium (V), and Zinc (Zn) (Madigan et al. 2000). Table 2 summarizes the use of these elements in various biological functions.

To grow and reproduce, a cell needs to synthesize new cell material (biosynthesis). A cell needs to obtain energy for biosynthesis and for other functions like transport (inside the cell) and mobility. This energy can come from light or from the oxidation (removal of electron from a substance) of chemical compounds. Oxidation–reduction reactions (called redox) involve the transfer of electron from one substance to another, yielding free energy (usable to do work). This chemical energy is conserved by the cell in the form of high energy phosphate compounds such as ATP (adenosine triphosphate). ATP is used by all living organisms for the biosynthesis of cellular components and for the functioning of the cell.

Prokaryotic microorganisms can use a wide diversity of metabolisms, that unable them to colonize every conceivable habitats on Earth. Microorganisms can use organic chemicals (they are called chemoorganotrophs) or inorganic chemicals (chemolithotrophs) as electron donors. Organisms that use light as energy source are called phototrophs. Oxygenic photosynthesizers like land plants, algae, and cyanobacteria use water as electron donor and produce O_2 as waste. This oxygen first produced by cyanobacteria has dramatically modified our planet, as seen above. Other phototrophs

Table 2 Minor and major elements needed for life as we know it (data from Madigan et al. 2000)

Nutrients	Used by the cell for	Sources	Forms of life
Carbon (C)	Major element in all types of macromolecules: nucleic acids (DNA, RNA), proteins, poly-saccharides, lipids, amino acids	CO_2, organic compounds, minerals	All
Hydrogen (H)	Macromolecules as above	H_2O, organic compounds	All
Oxygen (O)	Macromolecules as above	H_2O, O_2, organic compounds	All
Nitrogen (N)	Major elements in nucleic acids, proteins, ...	NH_3, NO_2, N_2, organic nitrogen compounds	All
Phosphorous (P)	Synthesis of nucleic acids (genetic material) and phospholipids (membrane constituents)	Inorganic and organic phosphates	All
Sulfur (S)	Some amino acids, several vitamins, coenzyme A	Inorganic sulfate (SO_4) or sulfide (HS)	All
Potassium (K)	Diverse enzymes involved in protein synthesis	In solution or in K-salts or in silicates	All
Magnesium (Mg)	Stabilization of ribosomes, cell membranes, nucleic acids, required for activity of many enzymes	In solution or in Mg-salts or in silicates	All
Calcium (Ca)	Stabilization of bacterial cell walls and for heat stability of endospores	In solution or $CaSO_4$ or Ca salts	Required by some
Sodium (Na)	For growth	NaCl in solution (seawater) or other Na salts	Required by marine and halophile life
Iron (Fe)	Major role in cellular respiration (cytochrome and iron-sulfur proteins involved in electron transport)	In insoluble inorganic iron compounds	All
Metals: micronutrients (Co, Cu, Mn, Mo, Ni, Se, W, V, Zn)	Critical to life in trace amounts, structural role in many enzymes		Not all required for all life, some only for specific microorganisms

can use other inorganic (H_2S, reduced sulfur compounds or reduced iron) or reduced organic substances as electron donors. Phototrophs and chemolithotrophs can often use carbon dioxide as carbon source (they are autotrophs). Others use organic carbon (heterotrophs). Mixotrophs use inorganic electron donors and organic carbon source. For detail, see Lopez-Garcia et al. (2006) and Madigan et al. [2000]. The macro- and micro-nutrients can be found in the Earth sediments, crust and mantle and delivered to water bodies through erosion of continental rocks and through hydrothermal activities.

The requirement of these nutrients may suggest that a dynamic and rocky planet with erosion of relief and transport of material to water bodies may be required to sustain life (as we know it) (Fig. 5; see also Falkowski et al. 2008a, and our discussion below related to Fig. 7).

4 Implications for the astrobiological exploration of the solar system and beyond

Characterizing habitability at various scales in time and space requires interdisciplinary research. In this article, we have chosen to develop some of the geophysical, geological, and biological aspects and to insist on the need to integrate one another. The concept of habitability is very Earth-centric, as we have only one biological planet to study. However, life elsewhere would probably be based on organic chemistry (Pace 2001) and leave traces of its past or recent presence and metabolism by modifying microscopically or macroscopically the physico-chemical characteristics of its environment. The extent to which these modifications occur will determine our ability to detect them in astrobiological exploration.

The discussions presented above illustrate how crucial the characterization of the geophysics and geology of a planet is to evaluate its habitability. Reconstructing the range of past and present environments, including the presence of liquid water, implies to study the geomorphology, sedimentology, mineralogy, atmosphere composition, and insolation of the planet, and to look for evidence of a magnetic field and tectonic activity, both depending on the characteristics of the internal structure and composition of the planet, the planet mass, and its cooling pattern. These studies are essential in order to understand the planet evolution and to determine where and when life might have appeared and might get preserved. Exploration by orbiters, rovers, or in situ robots is essential to get information at the macro- and microscopic scales and to further precise the areas to explore in detail. Looking for traces of life requires a good understanding of the potential past or present habitats of the planet, as well as the biosignatures (indices of life) to expect depending on the physico-chemical characteristics of these potential preservational environments. Geobiological research in the early Earth rock record and in present Earth extreme environments is crucial in this respect. Considering the evolution of life on Earth, the most probable forms of life that may exist beyond Earth would be microbial, and might not be detectable by remote sensing (for exoplanet) or by orbiters (Fig. 6). (For a recent review of possible strategies for life detection, see Botta et al. 2008). The spectral analysis of the early Earth atmosphere from space would not have revealed the presence of the flourishing biosphere before ~2.4 Ga when oxygen and ozone accumulated in detectable amount in the primitive atmosphere (as mentioned above, oxygen is produced by photosynthetic metabolism converting solar energy into chemical energy), thus more than 2 Ga after Earth's accretion, although it would pick the presence of water vapor and maybe of silicates (depending on the cloud cover). An orbiter might have shown the presence of continents and oceans, volcanic activity, a magnetic field, and even the localized concentration of macroscopic structures along the seashore since 3.5 Ga. Such information would be very promising and such a planet analog to early

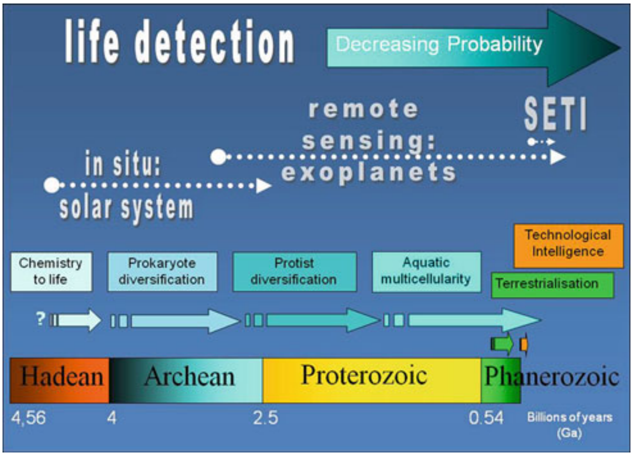

Fig. 6 Limitations of Astrobiological exploration based on the evolution of life as we know it (modified from Knoll and Bambach 2000). The probability of life detection decreases with increasing morphological complexity of life, but it does not decrease with metabolic complexity which is the greatest among prokaryotes (include two domains of microscopic life, Bacteria and Archaea, where cells have no nucleus nor membrane-bound organelles) and which appeared probably very early in Earth history. The most probable form of life to detect beyond Earth is microbial, but can be detected only in situ and thus in the solar system, considering our technological limitations. Until about 2.4 Ga, microbes produced gases that would not be distinguishable from abiotic gases in the atmosphere. (This does not mean that there was no life on Earth or another planet if oxygen or ozone and liquid water were not detected, but we will not be able to detect it). Only from 2.4 Ga, biologically produced oxygen accumulated in sufficient levels to alter significantly the atmosphere, hydrosphere, and geosphere. Such a planet could be detected by spectral analyses of exoplanetary atmosphere. But life elsewhere might not develop a metabolism that produces oxygen, like oxygenic photosynthesis. The least probable form of life, not only intelligent life but also technologically developed, can be ironically looked for in a wider portion of the universe around us

Earth would be considered habitable. However in situ exploration would be needed to interpret the structures as stromatolites or microbially induced laminated structures. Even then, their biogenicity would still be questioned unless detailed petrographic analyses of the rock show fossilized cells or organic matter with a microbial mat-like distribution (e.g. Allwood et al. 2009) and not in the form of trapped abiotic hydrothermal or meteoritic carbonaceous material. Interpreting the isotopic signatures of life beyond Earth would be difficult if the whole geochemical cycle of the considered element is not characterized on the planet (Van Zuilen 2008). Indeed, to determine the presence of biological fractionation (the preferential use of one isotope over others in biochemical pathways) of stable isotopes of the elements S, C, Fe or N, the presence of contemporary abiological reservoirs of these elements (in the form of rocks such as carbonates, phosphates, sulfates, . . .) has to occur to serve as isotopic standard. Moreover, abiological processes of fractionation exist and have to be well characterized before trying to interpret the measurements. More conclusive evidence for life might occur in micro-habitats preserved in sedimentary rocks such as mineralized cell colonies, filaments oriented toward light, complex organic molecules or vesicles preserved in fine-grained siliciclastic sediments or in silicified carbonates, but they require in situ micro-analyses of mineral and organics composition to be detected. Studies of the Earth geological record illustrate the difficulty to determine unambiguously the presence of fossil indices of life, and underline the necessity to use a multidisciplinary approach and a set of morphological and geochemical criteria within a well-characterized geological context (Botta et al. 2008; Javaux and Benzerara 2009). Exobiological missions require rovers equipped with miniaturized high-resolution instruments, similar to those developed for the ESA-NASA Exomars, NASA Mars Laboratory, and future exobiological missions. The recently discovered phyllosilicates in the early terrains of Mars (Bibring et al. 2005), if related to aqueous processes, offer an interesting target to look for fossilized organics, by analogy with their excellent preservation in the early Earth fine-grained siliciclastic rock record (e.g. Knoll 2003; Knoll et al. 2006; Javaux and Benzerara 2009; Javaux et al. 2010). These missions cannot be decoupled from a detailed study of the local geological context at the same sampling sites, from macro- to microscopic scales, otherwise compromising the interpretation of the analyses, their potential biological significance, and thus the success and meaning of the whole missions. Unfortunately in situ missions are not possible for other solar systems.

The detection of life beyond our solar system relies on detecting "changes in planetary atmospheres that arise from non-equilibrium metabolic processes" (Falkowski et al. 2008a). Atmospheric gases considered to be reliable "biosignatures" are the co-occurrence of H_2O and O_2/O_3 and CH_4 and/or CO_2 and/or NO_2 (Gaidos and Selsis 2007). Another biosignature called the "Vegetation Red Edge" or the specific spectrum of surface vegetation's reflectance (review in Arnold 2007; Tinetti et al. 2007) also implies the evolution of oxygenic photosynthesis, but by green plants (whose photosynthetic abilities came from the engulfment of cyanobacterial ancestors of the chloroplasts) covering a large part of the planet. However the detection of this signature requires technical improvement permitting imaging of planetary surfaces, but also a low cloud coverage and the evolution of extraterrestrial plants, a step occurring relatively late in Earth's history (although plants appeared probably in the Ordovician, extensive forest covering characterize the Carboniferous, only 360 Ma ago). By analogy with the Earth-like planets and the large icy satellites of the Solar System, and based on the composition of the stars, theoretical models are being developed to predict the internal structure of extrasolar planets and the possible presence of an ocean (e.g. Sotin et al. 2007). Thus in the case of exoplanets, since the definition of habitability is limited by technology, we can only detect if a planet is in the HZ around its star, and if it is inhabited by a biosphere that has evolved microbial (and much less probably eukaryotic) oxygenic photosynthesis. At our current state of knowledge, we do not know exactly when oxygenic photosynthesis appeared on Earth, but it affected the rock record (and the atmosphere) significantly only after 2 Ga of the Earth history (Fig. 1 and Fig. 6). Rosing et al. [2006] have suggested that the presence of granitic continents (granite is a magmatic rock that makes up most the Earth continents but has never been observed elsewhere in the solar system) on a silicate planet might be itself an evidence for the presence of life. With the advent of photosynthesis on Earth, life has learned to use light as a source of energy, leading to an increased production of organic matter and release of oxidants (such as free oxygen, ferric oxide, sulfate . . .), which would enhance basalt weathering by a range of inorganic and organic processes. If basalt (another type of magmatic rocks, resulting from partial melting of silicate minerals, common in the terrestrial planets of the solar system, the moon, and some asteroids) is altered by aqueous fluids, new hydrated minerals will be produced which can lead to the production of rocks granitic in composition (richer in silica, aluminum, and alkali metals than the original basalt). Basalt has a high density and forms oceanic crust that will eventually melt into the mantle, whereas granite is less dense and "floats" on the viscous solid mantle, leading to the building of continents (see Sect. 3.1.). In this hypothesis (Rosing et al. 2006), the biologically controlled increased alteration of basalt would lead to the stabilization of continental crusts since about 4 Ga, when the first possible traces of (possibly photosynthetic) life have been reported (but questioned) (Rosing 1999). However it is not clear that life elsewhere would evolve along a similar path and develop (oxygenic or anoxygenic) photosynthesis although light is a common possible source of energy in the universe for a planet at the right distance of its star. Whether or not granitic continental crusts are related to the presence of life, their occurrence on a planetary surface evidences geological activity (plate tectonics) and therefore, as discussed above, indicates the habitability of the planet. Such a global vision of a living Earth, where biological and geological/geodynamic processes are intertwined, and where microbes have planetary scale impacts (that might be detectable from space), is undergoing new developments since Lovelock "Gaia" hypothesis (1970) by scientists from diverse disciplines, often in a multidisciplinary enterprise (e.g. Rosing et al. 2006; Bertrand 2007; Falkowski et al. 2008b; Krumbein

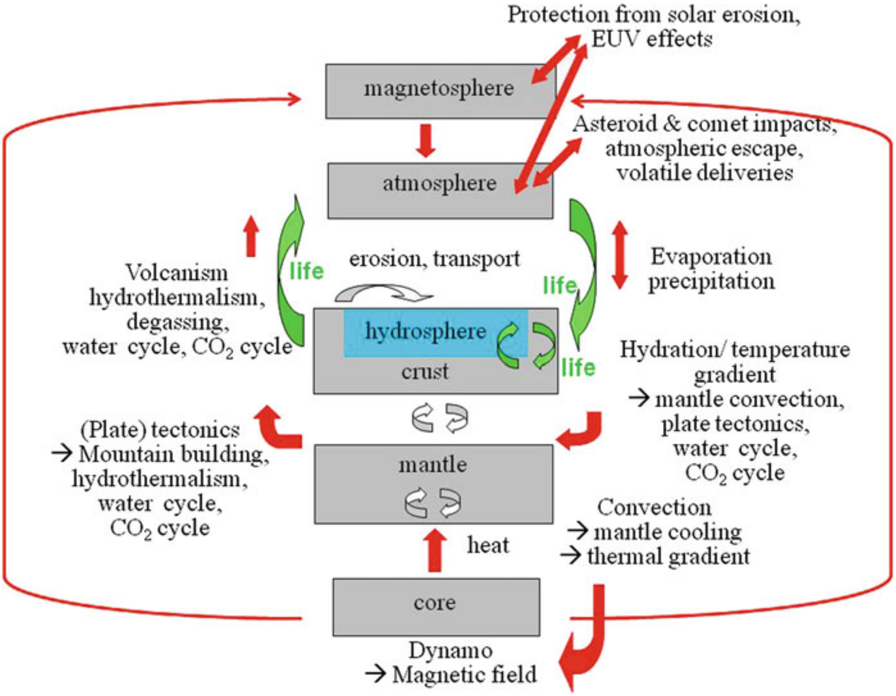

Fig. 7 Simplified scheme of Earth geodynamic processes (not to scale)

2008). Understanding the planetary impacts of microbial life is our only chance to define biosignatures that would be detectable in exoplanetary atmospheres.

Life on Earth has evolved and is evolving by natural selection. Although the size of the universe, the discovery of an increasing number of planetary systems, and the abundance of organic matter and water in the universe do not necessarily imply the existence of extraterrestrial microbial life, it is possible that life has appeared or will appear elsewhere where the necessary conditions are met. Astrobiology, by studying the origin, evolution, and distribution of life on Earth, attempts to understand these conditions, in order to determine the distribution of life in the universe. The necessary conditions may include geophysical processes, important for the persistence of life but also imprinted by life. Figures 5 and 7 present a (over)simplified summary of Earth geodynamic processes and interactions with—and implications for—the biosphere. Are all these compartments and interactions needed for life not only to originate, but to persist on a planet? This question is at the heart of planetary habitability, from stars to cells.

Acknowledgements The authors thank the editor Prof J. Surdej for his invitation to write this article following a session on Astrobiology at JENAM 2005. Support from the University of Liège and the Royal Observatory of Belgium is acknowledged. The material used for this review is coming from a large survey of the literature, and we acknowledge the different authors mentioned in these articles. Ö Karatekin and JC Plumier are thanked for their comments. Two anonymous reviewers allowed us to improve the first version of the manuscript. Athena Coustenis is also acknowledged for her careful second review.

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