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Astrobiology (Overview)

Sean McMahon^{1,2}

¹ UK Centre for Astrobiology, School of Physics and Astronomy, James Clerk Maxwell Building, Peter Guthrie Tait Road, University of Edinburgh, EH9 3FD, UK.

² School of Geosciences, Grant Institute, University of Edinburgh, EH9 3FE, UK.

Article summary

Astrobiology seeks to understand the origin, evolution, distribution and future of life in the universe and thus to integrate biology with planetary science, astronomy, cosmology, and the other physical sciences. The discipline emerged in the late twentieth century, partly in response to the development of space exploration programmes in the USA, Russia, and elsewhere. Many astrobiologists are now involved in the search for life on Mars, Europa, Enceladus, and beyond. However, research in astrobiology does not presume the existence of extraterrestrial life, for which there is no compelling evidence; indeed, it includes the study of life on Earth in its astronomical and cosmic context. Moreover, the absence of observed life from all other planetary bodies requires a scientific explanation, and suggests several hypotheses amenable to further observational, theoretical, and experimental investigation under the aegis of astrobiology. Despite the apparent uniqueness of Earth's biosphere — the “n=1 problem” — astrobiology is increasingly driven by large quantities of data. Such data have been provided by the robotic exploration of the solar system, the first observations of extrasolar planets, laboratory experiments

into prebiotic chemistry, spectroscopic measurements of organic molecules in extraterrestrial environments, analytical advances in the biogeochemistry and palaeobiology of very ancient rocks, surveys of Earth's microbial diversity and ecology, and experiments to delimit the capacity of organisms to survive and thrive in extreme conditions.

Keywords: Astrobiology, exobiology, origin of life, habitability, biosignatures, life detection, extraterrestrial life, life on Mars, bioastronomy, SETI

1. What is astrobiology?

Astrobiology is organised around a core of fundamental questions: When, where, and how did life arise on Earth? Has it arisen anywhere else? What physicochemical conditions are required to generate life and to sustain it? How do planetary, stellar, and cosmic processes — and the activity of life itself — shape the distribution of these conditions across time and space? What can be said about the likely characteristics of extraterrestrial life, and what, therefore, are the optimal strategies for finding it? Thoughtful people have pondered these questions since ancient times, but it was not until the dawn of the Space Age that they seemed scientifically promising enough to call for a new discipline. The first known use of the word “astrobiology” was made by astronautics expert Ary J. Sternfeld in a French popular science magazine in 1935. His article claimed that progress in astronomy and natural science had “led to the birth of a new science whose main objective is to assess the habitability of other worlds” (Sternfeld, 1935; Briot, 2012). “Astrobiology” was also the title of a book published in 1953 by the Soviet scientist Gavrill Tikhov, which

discussed the possibility of life on other planets and suggested that spectroscopy might be used to detect it (Tikhov, 1953; Cockell, 2001). American Nobel Laureate Joshua Lederberg sought to promote the new field of “exobiology” in a 1960 paper in *Science*, but confined its scope to “the evolution of life beyond our own planet” (Lederberg, 1960). The Life Sciences Division of the US National Aeronautics and Space Administration (NASA) launched the NASA Exobiology Program the same year and has funded a broad range of research into the origin, evolution, and distribution of life — including life on Earth — ever since. This profoundly interdisciplinary science is now more widely referred to as “astrobiology” than “exobiology” but the two terms are synonymous and remain equally valid (Cockell, 2001).

The first two decades of the twenty-first century have seen a major global expansion in astrobiological teaching and research. An important catalyst was the controversial 1996 discovery of purported martian nanofossils in meteorite ALH84001 (McKay et al., 1996). Today, after decades of debate, these minute structures and their associated mineralogical features are not widely accepted as *bona fide* martian biosignatures. Nevertheless, excitement and controversy over the original findings triggered a rapid succession of NASA and White House initiatives to increase understanding of the origin and evolution of life in a planetary and astronomical context. These initiatives, dovetailing with longer-running efforts by some NASA scientists to accelerate progress in the field, culminated in the establishment in 1998 of NASA’s Astrobiology Institute (NAI), a distributed “virtual” research network which ran until 2018 and involved hundreds of investigators across the US as well as numerous international partners. New journals, national and international conferences, societies,

and university courses soon followed, and there are now hundreds of active astrobiology research groups around the world. The field is now well established and continues to attract contributions from geologists, chemists, microbiologists, physicists and astronomers (many of whom describe themselves as “astrobiologists” or “exobiologists”), as well as historians of science, philosophers, and social scientists.

2. Habitability and the limits of life

What is life?

Biology is a part of nature and not an exotic form of matter. There is no satisfying definition of “life” that applies to all organisms in all contexts and excludes everything else, and it is debated whether such a definition is necessary or even possible. The famous “working definition” of life as “a self-sustaining chemical system capable of undergoing Darwinian evolution” promulgated by a 1994 NASA workshop has well known limitations (e.g., Cleland and Chyba, 2002). “Self-sustaining” is meant to imply not only that life self-replicates but that it does not need looking after by some other agency — but many living organisms, populations and even species palpably do require such interventions (and some abiotic chemical systems, such as flames and crystals, do not). The capacity for Darwinian evolution is a property of populations, not of individual organisms, some of which are unable even to reproduce (e.g., worker bees) but are nonetheless fully alive. Evidently, life manifests different properties and behaviours when viewed at different levels of the hierarchy: cells, organisms, populations, communities, and the biosphere as a whole.

Nevertheless, any unambiguous instance of life must, when studied at the correct levels in the hierarchy, at the right spatiotemporal scales, and under the right conditions, display a certain set of core attributes. Firstly, it must harness energy from redox reactions (chemotrophy), sunlight (phototrophy), or other sources, and use it to assemble and maintain complex, ordered structures (while entropy increases in the environment overall). Secondly, these structures must be encapsulated within selectively permeable boundaries that permit the maintenance of relatively stable internal physical and chemical conditions (homeostasis). Thirdly, it must self-replicate according to a genetic code subject to evolution by natural selection. Life on Earth can be regarded as one among many diverse self-organised dissipative phenomena produced by the internal dynamics of far-from-equilibrium systems; other examples include convection cells, oscillatory chemical reactions, flames, stars, and rivers. What sets life apart from these is its capacity for stability over time and for evolution by natural selection.

Life, but not as we know it?

It is difficult to generalise further about the essential nature of life because of the “n=1 problem”, i.e., the fact that all known organisms share a single common ancestor and thus represent only one instance of life. There is considerable speculation in science fiction and a small technical literature about exotic forms of life that may have arisen from non-Earth-like conditions. For all we know, evolving organisms might originate from self-organisation within stellar plasma, molecular clouds, liquid hydrogen, etc., although the details of such imaginative proposals can often be challenged on technical grounds (Schulze-Makuch and Irwin, 2018a). Less radically, it is often

asked whether a viable form of life could diverge from the familiar “carbon-based” composition. Biomass on Earth is built primarily from assimilated compounds of the CHNOPS elements (carbon, hydrogen, nitrogen, oxygen, phosphorus, sulfur), which form an extraordinary variety of stable macromolecules and polymers organised around covalently bonded chains and rings of carbon atoms with various functional groups attached. These compounds form higher-order structures via ionic interactions, hydrogen bonding, disulfide bridges, van der Waals forces, and hydrophobicity. It is unknown whether a similarly rich “alternative biochemistry” might be possible in which, for example, silicon plays a structural role analogous to carbon, or arsenic replaces phosphorus. CHNOPS elements are among the most abundant in the universe and are produced by nucleosynthesis in main sequence stars, so their availability may not greatly limit life’s cosmic distribution.

Since liquid water is not available on many planets and moons, some astrobiologists have considered whether alternative biochemistries could rely on other liquid solvents (e.g., McKay and Smith, 2005; Schulze-Makuch and Irwin, 2018b). Water molecules are polar: the electrons in the H–O bond are drawn towards the oxygen, and the mutual repulsion of the two remaining electron pairs on one side of the oxygen atom forces the two hydrogen atoms closer together on the other side (**Figure 1**). Because of this polar structure and the tendency of water to form hydrogen bonds, water readily dissolves other polar compounds such as carbohydrates, amino acids, nucleic acids, proteins and salts, which can then react in aqueous solution inside cells. The hydrophobicity of non-polar compounds or functional groups is also important for biology, for instance in favouring the formation of lipid membranes. Water is also critical to sundry other biological functions, and exhibits physical properties — such

as UV absorption, high surface tension, and the ability to form low-density ice-I — that may have helped life to emerge on Earth (Ball, 2017; Schulze-Makuch and Irwin, 2018a). Whether polar solvents other than water (e.g., ammonia) could play a fully analogous role in sustaining alternative, non-aqueous biochemistries on other worlds is still debated. In any case, water is an extremely abundant compound both in this solar system and others.

Even carbon- and water-based alternative biospheres may not share the dependence of all known organisms upon left-handed (“L”) amino acids and right-handed (“D”) carbohydrates rather than their mirror-image stereoisomers, a phenomenon known as “homochirality” (**Figure 2**). Prebiotic organic matter on the early Earth was probably of nearly even handedness, although there is evidence for excesses of L-amines and L-amino acids in meteorites (Pizzarello and Yarnes, 2016). Homochirality may have been favoured by natural selection; polypeptides condensed from homochiral amino acids differ in folding (and hence function) from those condensed from heterochiral amino acids. Nevertheless, there may be no adaptive reason why biology should have opted for one set of stereoisomers in the first place rather than its opposite. A “mirror biosphere” thus seems quite possible.

Habitability and extremophiles

The physical and chemical limits outside of which no conceivable form of life could persist are unknown. Astrobiologists have, however, searched for the limits of life “as we know it” on Earth, while acknowledging that these limits may not be shared by [alternative forms of life](#). Thus, “habitability” has been defined as “the ability of an

environment to support the activity of at least one *known* organism” (Cockell et al., 2016; emphasis added), where “activity” means the survival, maintenance and reproduction of living cells. Habitability requires liquid water of sufficient thermodynamic activity, bioavailable carbon and other nutrients, the availability of an energy source (e.g., redox couples), and values of pH, temperature, pressure, ionizing radiation flux, and other chemical and physical stresses within known physiological limits. “Extreme environments”, where such parameters are close to the limits of habitability, typically sustain low productivity, low diversity ecosystems in which the energy cost of homeostasis leaves only a small margin for growth and reproduction. For example, microbial chemotrophs inhabiting deeply buried rocks and sediments (the “deep biosphere”) endure high temperatures, high salinities, and a meagre supply of energy, and accordingly reproduce very slowly (Kieft, 2016). Such examples suggest that the concept of “extreme” is not overly anthropocentric, although the particular limits of life on Earth may reflect local evolutionary and developmental constraints that would not apply to extraterrestrial biospheres. No environment in the universe can support life unless it provides energy quantitatively sufficient to meet the challenges of sustaining biochemistry (of whatever local flavour) in that environment (e.g., Hoehler, 2007).

Extremophiles are organisms that grow optimally in extreme conditions. *Mesophiles* grow optimally in non-extreme conditions; *extremotolerant* mesophiles can survive extreme conditions. Extremophiles define the physicochemical limits of known life and hence the empirical boundary between “habitable” and “uninhabitable” environments. As such, studies of extremophiles using microbiological, molecular biological and biophysical approaches have made important contributions to

astrobiology ever since the American microbiologist Thomas Brock isolated heat-loving (*thermophilic*) bacteria from hot springs at Yellowstone National Park (Brock, 1967). Thermophiles have now been discovered around volcanic fumaroles, seafloor hydrothermal vents, and hot springs around the world. A microbe isolated from seafloor hydrothermal vent fluid has been observed to divide at 122 °C (Takai et al., 2008). This organism, in common with many other thermophiles, was not a bacterium but an archaeon, i.e., a member of a separate, similarly ancient group of single-celled microorganisms (archaea).

Heat unfolds proteins, damages DNA, and makes cell membranes more fluid.

(Hyper)thermophile adaptations compensate in part by producing more thermostable biomolecules, e.g., more compactly folded proteins (Berezovsky and Shakhnovich, 2005; Wang et al., 2015). At the other end of the temperature scale, cold-loving *psychrophiles* in (sub)glacial habitats are valuable model organisms for understanding how life might adapt to cold worlds such Europa, Enceladus, and Mars. The most extreme psychrophiles known are bacteria isolated from Arctic marine sediment, which remain motile at –10 °C, reproduce at –12 °C, and maintain some level of enzyme activity at –20 °C (Youle et al., 2012). Many psychrophilic adaptations are functionally the reverse of those seen in thermophiles — e.g., more flexible and labile proteins, and the incorporation of unsaturated fatty acids to increase lipid membrane fluidity. Some psychrophiles also produce “antifreeze proteins” that prevent the nucleation and growth of disruptive ice crystals, effectively lowering the freezing point of cytoplasm. Although freezing arrests metabolic activity, diverse organisms can be resuscitated after long periods in a frozen, dormant state (*cryobiosis*). Viable bacteria have been found in ice at least $\sim 10^4$ years old and possibly up to $\sim 10^6$ years

old (Bidle et al., 2007). It is still uncertain for how long organisms can survive in stasis, a question of key interest in relation to [lithopanspermia](#) and environments with intermittent habitability.

Cellular and evolutionary responses to extreme pressures have received less attention than those of extreme temperatures. Although not sterilizing, ultra-low pressures are incompatible with the presence of liquid water and hence cannot support microbial growth. High pressure, like low temperature, lessens the fluidity of lipid membranes and is countered by pressure-loving organisms (*barophiles* or *piezophiles*) in much the same way as *psychrophiles*: by introducing unsaturated fatty acids. The effects of high pressure partially compensate the effects of high temperature; thus, the most extreme hyperthermophile known is also a piezophile and cannot grow at ambient pressures (Takai et al., 2008).

Life requires aqueous fluids with pH ~0–13 and with sufficiently high “water activity” (a_w , the mole fraction of water in the fluid multiplied by its activity coefficient). Water activity decreases when liquid water is removed from the fluid (e.g., by evaporation or ice crystallization), diluted by salts or other solutes, or sequestered into molecular hydration shells. Biotic responses to low water availability are of particular interest in the study of the habitability of Mars, whose surface is desiccated and whose subsurface waters may be highly saline (e.g., Orosei et al., 2018). Most organisms require water activities > 0.9 , but exceptions (*xerophiles*) are very diverse; some can reproduce at water activities as low as 0.605 (Stevenson et al., 2015). Prolonged dehydration impairs the normal mechanisms that protect proteins and nucleic acids from the damaging effects of reactive oxygen species (ROS

— hydrogen peroxide and oxygen radicals). Thus, many xerophiles produce strong antioxidants that scavenge ROS. Some organisms can survive periods of dehydration in a dormant state by replacing intracellular water with small organic molecules that stabilize proteins and lipids and vitrify when dry. This process has been observed in diverse bacteria, fungi, plants and micro-animals including the famously resilient tardigrade (“water bear”), a micro-invertebrate.

Water retention is important both for xerophiles and for *halophiles*, i.e., organisms that grow in fluids with at least 15% NaCl_(aq). Many obligate halophiles pump extra potassium ions into the cell, bringing the internal osmolarity into balance with the environment to prevent water loss by osmosis; others accumulate small soluble organic molecules within the cell that are more compatible than potassium ions with normal cellular metabolism. Salts can also debilitate organisms for several reasons other than simple osmotic stress or reduction in water activity; charged ions interfere directly with biomolecules and disrupt the network of hydrogen-bonded water molecules in the cell (Fox-Powell et al., 2016). Perchlorate salts like those occurring on Mars are especially damaging.

It is interesting to note that some of the harmful effects of desiccation — particularly DNA damage and the accumulation of ROS — are also induced by ionizing radiation. Evolutionary adaptations to tolerate dehydration may thus improve survival under irradiation. This may explain why some terrestrial organisms, such as the well-known xerophile bacterium *Deinococcus radiodurans*, can withstand far higher radiation doses than they or their ancestors are likely to have encountered at any time on Earth, whose atmosphere and magnetic field attenuate and deflect harmful cosmic and solar

irradiation. Indeed, adaptation to one stress factor commonly confers resistance to others, and many extremophiles are *polyextremophiles* for this reason. Some generic stress responses are shared by very diverse organisms — mesophiles and extremophiles alike. One example is the rapid production of protective *heat shock proteins* by all living cells in response not only to heat but also to many other stresses; another is the formation of robust, highly stress-resistant resting spores or “cysts” seen in many algae, fungi, and bacteria.

Planetary habitability

Planetary habitability is partly a function of stellar insolation: an environment cannot be habitable if it is too hot or too cold for liquid water. The range of orbital distances where the surface temperature of an Earth-like planet would fall between these limits has become known somewhat misleadingly as the *habitable zone* (HZ). Kasting et al. (1993) provided the classic treatment of habitable zones for rocky planets with carbonate-silicate weathering feedbacks like Earth’s, which expand both the inner and the outer edges. Briefly, atmospheric CO₂ dissolved into rainwater and humidity forms carbonic acid, which weathers silicate minerals at a temperature-dependent rate to produce silica and carbonate minerals that are ultimately sequestered into the mantle by subduction. Any externally forced increase in surface temperature is partly compensated by an intensification of this process, which draws down CO₂ and so diminishes the atmospheric greenhouse, limiting the temperature increase. Conversely, any decrease in Earth’s temperature is partly compensated by a strengthening of the atmospheric greenhouse. The limits of these feedbacks define the HZ edges. At the inner edge, the atmosphere is saturated with water vapour and can

no longer compensate for further increases in temperature; moreover, water is photodissociated and lost to space at the top of the atmosphere, allowing carbon dioxide to accumulate. The consequence is runaway global warming. At the outer edge, the atmosphere is CO₂-saturated and cannot dampen any further decrease in temperature; runaway cooling ensues. By representing these feedback processes in a relatively simple model of Earth's surface temperature, Kasting et al. showed that a habitable zone can be drawn around a star of any luminosity.

Dozens of later papers have refined and modified this model in various ways, for instance by updating the atmospheric thermal physics (Kopparapu et al., 2013), by accounting for the effect of clouds on albedo (Selsis et al., 2007) and by showing how the HZ edges migrate through time as a consequence of stellar evolution (Rushby et al., 2013). Nevertheless, the habitable zone as it is usually conceived today only predicts the habitability (in a loose sense) of planets whose albedos, atmospheres, and climatic/tectonic feedbacks strongly resemble the Earth. Many planets observed within conventional HZs are gas giants to which the HZ model is thus fundamentally inapplicable. Rocky planets are common in HZs, but most of these are in close orbits around cool M-dwarf stars, which inundate them with intense X-ray and ultraviolet irradiation exacerbated by frequent solar flares. These conditions may drive the loss of water/hydrogen to space and could force some of these worlds into a highly oxidizing, desiccated state, limiting their habitability (Shields et al., 2016). Even rocky planets orbiting within the habitable zones of sun-like stars may be too hot for surface water if their particular tectonic regime results in less efficient drawdown of CO₂ than occurs on Earth, or for myriad other reasons (Foley, 2015). Planetary mass also influences global habitability, not least because small planets such as Mars are

less able to retain thick atmospheres (e.g., Tian et al., 2009; Kopparapu et al., 2014). Thus, it cannot be inferred that a rocky planet is habitable, or even that it can sustain surface water, merely from its presence in the HZ.

Equally, many planets outside the habitable zone may be habitable. In this solar system, [Mars](#) straddles the outer edge of the conventional HZ while the icy moons Europa and Enceladus are far beyond it, yet geothermally heated water may still permit subsurface life on these worlds. In the Earth's subsurface "deep biosphere" (which harboured the majority of the planet's biomass for billions of years; McMahon and Parnell, 2018), many organisms obtain carbon from CO₂ and energy from water–rock reactions that should occur on any rocky planet or moon with sufficient interior heat. If the conventional habitable zone were expanded to include rocky worlds with frozen surfaces but liquid water at 10 km depth or less, its outer edge would be further out than Saturn (McMahon et al., 2013). Indeed, even a "rogue" rocky planet drifting through interstellar space could support oceans of water beneath an ice crust (Abbot and Switzer, 2011). Life might also occur in water-rich atmospheres of [Venus](#)-like worlds closer to their stars than the HZ inner edge (Cockell, 1999).

Planetary habitability may be improved or degraded by the activity of life itself. Metabolising cells tend to exhaust the nutrients available to them, poison their own environment with exported toxins, and diminish the chemical disequilibrium on which they depend. Biological contributions to weathering, albedo, and the carbon and oxygen cycles can regulate global temperatures and thus influence the planet's habitability over the long-term (e.g., Lenton, 2002). It is still debated whether there is any fundamental reason why biological feedbacks should necessarily stabilize rather

than destabilize climate, as suggested by British environmental chemist James Lovelock and American microbiologist Lynn Margulis (the “Gaia Hypothesis”; Margulis and Lovelock, 1974).

3. Biosignatures

A biosignature has been defined as an “object, substance, and/or pattern whose origin specifically requires a biological agent” (Des Marais et al., 2008). Biosignatures are thus taken to be fingerprints of past or present biological activity; ideally, they are phenomena whose probability of arising abiotically is negligible. Examples include molecules of DNA, absorption bands attributed to chlorophyll in Earth’s reflectance spectrum, and the silicified cellular structure observed in petrified wood.

Astrobiologists seek biosignatures in a wide variety of materials from the early Earth, from space, and on other worlds, and also strive to extrapolate beyond the particular products of life on Earth to the biosignatures that might result from [alternative biochemistries](#) (e.g., Seager et al., 2016; Cronin, 2017; Johnson et al., 2018). Indeed, it may be possible to search for “agnostic” or “universal” biosignatures common to all conceivable biochemistries. Potential examples include complex molecules whose assembly requires many steps, or whose aperiodic structure suggests an “informational”, nucleic-acid-like function (Marshall et al., 2017; National Academies of Science, Engineering and Medicine, 2019).

To identify biosignatures robustly, astrobiologists must evaluate the risk of false-positive detections related to abiotic natural phenomena, sample preparation artefacts, and contamination by organisms exogenous to the sample of interest. In nature,

abiotic “pseudobiosignatures” commonly arise from nonequilibrium processes; examples include kinetic isotope fractionations in hydrothermal systems, ramifying growth-structures produced by simple gravitational particle deposition, and an excess of O₂ occurring in a planetary atmosphere where water vapour is photodissociated and hydrogen lost to space. Awareness of these problems has motivated some authors to use the term “potential biosignature” for phenomena that seem lifelike but may, with non-negligible probability, have arisen abiotically (e.g., Des Marais et al., 2008).

On Earth, numerous field and laboratory methods, some of which can be adapted to space missions, are used to verify the presence and activity of currently living organisms. Cell division and motility can be observed microscopically; fluorescent stains can be applied in order to confirm the presence of DNA and proteins within cells. Innumerable biomolecules can be detected using standard methods of chemical analysis. Nutrient uptake and waste production can be quantified directly. Metabolic activity can also be monitored in solids, liquids and gases through the study of isotopic biosignatures using mass spectrometers (and in some instances optical spectrometers). Carbon, sulfur, nitrogen, and many other elements are isotopically fractionated by enzymes such that metabolic products are enriched in the lighter isotopes while residual feedstocks are depleted in them. This results from the fact that bonds between lighter isotopes break at lower activation energy than those between heavier isotopes. In consequence, to give one example, photosynthesis fixes carbon-12 slightly more readily into biomass than carbon-13. Isotopic compositions of natural materials are now routinely measured to a precision of at least parts-per-thousand (“permil”) with appropriately calibrated mass spectrometers. The interpretation of isotope compositions as biosignatures depends critically upon the

environmental context, since non-biological processes can induce similarly strong isotope fractionations under some conditions (e.g., in carbon [McCollom and Seewald, 2006] and sulfur [Machel, 2001]).

Geological biosignatures (“fossils”)

Rocks, minerals, and fluids can preserve evidence of life on billion-year timescales; geochemical processes can transform and preserve biomolecules, cells, tissues, organisms, metabolic waste, biogenic isotope anomalies, and even the trails and burrows made by motile organisms in viscous substrates. Even a mouldic fossil retaining no chemical traces of life can be a strong biosignature if its morphology is sufficiently complex, functionally adaptive and highly organised; the shape of a dinosaur skeleton cannot be explained by any conceivable abiotic process. However, simpler morphologies like those of bacteria are ambiguous indicators of biogenicity because they can be mimicked by non-biological processes of self-organization (García-Ruiz et al., 2002; McMahon, 2019). Stringent “biogenicity criteria” have therefore been proposed for candidate fossil microbes in very ancient or extraterrestrial materials; these include consistent microbe-like morphology and spatial distribution in a habitable palaeoenvironment, a CHNOPS-rich composition, and isotopic evidence for metabolic processes. The remains of ancient biomolecules, known as “molecular fossils” or “biomarkers”, can be extracted from some clay- and silica-rich ancient rocks and sediments. Complex biopolymers degrade over time and under the influence of heat, pressure, and radiation, losing non-carbon elements and converging on the composition and structure of graphite (Alleon and Summons, 2019). However, some biogenic lipids are exceptionally resilient and have a fossil

record reaching back at least 1.7 Ga (Vinnichenko et al., 2020).

Spectroscopic biosignatures

The presence of life on Earth can be verified from afar using spectroscopic methods. In 1990, the Galileo probe obtained near infra-red reflectance spectra from the Earth showing absorption features due to O₂, CH₄ and N₂O, products of oxygenic photosynthesis, microbial methanogenesis, and microbial denitrification respectively (Sagan et al., 1993). Absorption by O₃ (ozone), the photochemical product of O₂, was observed at both near-infrared and ultraviolet wavelengths. These four gases have become paradigmatic examples of atmospheric biosignatures. All of them have abiotic sources: O₂ is liberated by the photolysis of water vapour; CH₄ is produced by several geochemical pathways including the breakdown of abiotic organic matter and the abiotic reduction of CO and CO₂; N₂O is produced by lightning. Nevertheless, any potentially habitable exoplanet with high atmospheric concentrations of these gases would deserve further investigation. The sustained co-occurrence of CH₄ and O₂/O₃ implies continual replenishment since these gases are strongly out of equilibrium with each other, although thermodynamic disequilibrium is not necessarily a biosignature since it can arise from impact events, volcanism, and other dynamic abiotic processes (Sagan et al., 1993; Seager and Bains, 2015). Seasonal variation in gas concentrations could potentially offer further evidence of biological processes (Olson et al., 2018). Methyl chloride (CH₃Cl) and dimethyl (di)sulfide (CH₃SCH₃ and CH₃S₂CH₃) have both been proposed as alternative biosignature gases with a lower risk of false-positive signals, although they are so photosensitive that they could only accumulate to measurable concentrations around stars with lower UV fluxes than the Sun's

(Segura et al., 2005; Domagal-Goldman et al., 2011). Seager et al. (2016) document numerous similarly stable and detectable gaseous molecules that might be produced in similar amounts by [alternative biochemistries](#).

In addition to these biosignature gases, some features of Earth's reflectance spectrum are due to the spatial extent of biomass on the planet's surface. Among these, the best known is the "vegetation red edge", a sharp increase in reflectance with increasing wavelength from 680 to 730 nm. This feature (which was also observed by the Galileo probe) is due to the strong absorption of red light, and reflectance of near infra-red light, by chlorophyll. Other photosynthetic pigments with different spectral properties — including fluorescence as well as absorbance and reflectance — are known on Earth and may feature much more prominently in the spectral features of inhabited worlds orbiting M or F stars, or in binary star systems (O'Malley-James et al., 2012; O'Malley-James and Kaltenegger, 2018). It has been proposed that purple pigments found in certain bacteria may have been identifiable in Earth's reflectance spectrum in the Archaean (>2.5 Ga ago), before modern photosynthesizers rose to dominance (DasSarma and Schwieterman, 2018).

4. The origin and evolution of life

The origin of life on Earth and the critical turning points in its evolutionary trajectory are central areas of research for astrobiology with far-reaching implications. The distribution of life in the universe is limited not only by the availability of habitable environments but by the occurrence of conditions and processes through which life can begin *de novo* and, having arisen, survive for long spans of time. Speculation

about the possible nature of life elsewhere must also take account of the relative importance of evolutionary convergence, planetary and stellar environments, and blind chance in shaping the diversity of life over billions of years. Reconstruction of biospheric influences on Earth's spectral characteristics in deep time can also suggest search images for the detection of life on remote exoplanets (e.g., Krissansen-Totton et al., 2018).

Earth before life

Our sun ignited ~4.6 Ga ago in the spinning nebular disc formed by the gravitational collapse of a molecular cloud. Cooling of the disc produced solid metallic particles at least ~4.57 Ga ago (Bouvier and Wadhwa, 2010). Compared to metals and silicates, compounds with lower condensation temperatures (“volatiles” such as water and CO₂) condensed in cooler, more distal regions of the disc — beyond the *snow line*. Agglomeration and accretion produced ever larger solid bodies in the disc; a complex dynamical process that is still poorly understood. Kilometer-scale *planetesimals* formed within a few million years; these continued to collide, melt, and fuse into larger bodies. The heat produced by mineral radioactivity, collisions, and gravitational compression melted larger planetesimals including the proto-Earth, and initiated a density-driven process of internal differentiation that endowed these bodies with iron-rich cores and lighter, silicate mantles and crusts. The moon formed within ~100 million years of these events (Jacobson et al., 2014), almost certainly via the condensation and accretion of rock vapour produced when the proto-Earth collided with a Mars-sized planetary body. Earth's mantle and surface would have remained molten for a few millions years after the impact (Sleep, 2010). Outgassing from this

“magma ocean” produced a 100-bar CO₂–H₂O greenhouse atmosphere, which maintained surface temperatures of ~250 °C and pressurized liquid water oceans (Sleep, 2010). Projectiles from beyond the snow line may have added a late veneer of volatile-rich material but this was probably a minor contribution to Earth’s water budget (Wu et al., 2018).

Earth’s surface probably became technically habitable as soon as temperatures declined below the upper limit for life. This required large quantities of CO₂ to be removed from the primitive atmosphere as carbonate minerals and then subducted into the mantle. High mantle temperatures would have precluded modern-style plate tectonics, but numerical models show that asteroid/planetesimal bombardment likely drove an alternative form of subduction capable of delivering carbon to the mantle (Hansen, 2007; O’Neill et al., 2017). There are no well preserved rocks older than about 4 Ga, when the Hadean Eon ended and the Archaean Eon (4.0–2.5 Ga) began. However, 4.4–4.0 Ga-old detrital zircon (zirconium silicate) crystals incorporated into younger rocks contain oxygen-isotopic evidence of abundant surface water, and temperatures below 200 °C (Valley et al., 2002). Thus, it appears that the Hadean Eon was more clement than previously thought and not as “hellish” as its name suggests.

The Archaean oceans were salty, mildly acidic, and habitable (Sleep, 2010; Halevy and Bachan, 2017). Seawater and surface temperatures must have varied considerably through the Archaean — a span of 1.5 Ga — but are still poorly constrained, with unresolved conflicts between different geochemical and isotopic palaeotemperature proxies. Glacial deposits record several cool intervals, but average surface temperatures were probably warmer than today for most of the aeon. Since the sun

was ~30% dimmer at 4.0 Ga than today, these conditions imply a CO₂-rich greenhouse atmosphere, although its overall composition is still debated. The inner planets experienced intense, slowly declining asteroid infall in the Hadean and Archaean, which may or may not have included a discrete pulse of massive impactors around ~3.9 Ga historically referred to as the “Late Heavy Bombardment” (Chapman et al., 2007; Bottke and Norman, 2017; Mojzsis et al., 2019). These impacts would have created both challenges and opportunities for the earliest development and diversification of life (Abramov and Mojzsis, 2009).

The origin of life and its precursors

The earliest [fossil and geochemical records](#) of life on Earth are heavily disputed; rocks of the appropriate age are scarce and poorly preserved, with no intact organic molecular biomarkers. A slew of somewhat equivocal geochemical candidate biosignatures have been reported from 4.1–3.5 Ga. The oldest convincing morphological fossils are microbial cells and laterally extensive microbial communities (“microbial mats”) ~3.5 Ga old (Westall et al., 2006; Wacey et al., 2011; Baumgartner et al., 2019;). Measurements of the genetic disparity between distantly related organisms can be combined with assumptions about evolutionary rates and temporal calibration points from the fossil record to yield “molecular clock” estimates placing the origin of life close to 4.0 Ga (e.g., Wolfe and Fournier, 2018; Betts et al., 2018). Taken together, the available evidence suggests that Earth became an inhabited planet within its first billion years; possibly the first half-billion.

Modern work on the origin of life builds on ideas developed independently by the

Soviet biochemist A. I. Oparin (1894–1980) and the polymathic British evolutionary biologist J. B. S. Haldane (1892–1964). The “Oparin–Haldane hypothesis” proposes that life began in an organic-rich, hot, chemically reducing ocean, which Haldane compared to a “dilute soup”. In this somewhat simplistic model, lightning and/or UV irradiation activated the polymerization of small organic precursors in the oceans and atmosphere to form proteins and other prebiotic molecules, which then selectively integrated with self-assembled lipid droplets or vesicles to form replicating protocells capable of Darwinian evolution. In 1952, American chemists Stanley Miller (1930–1970) and Harold Urey (1893–1981) famously tested the Oparin–Haldane hypothesis in the laboratory (Miller, 1953). The “Miller–Urey experiments” produced amino acids (among other interesting compounds) from an *in vitro* simulation of the early Earth, which included a heated aqueous “ocean” and a gaseous “atmosphere” of water vapour, methane, ammonia, and hydrogen, through which electrical sparks passed between electrodes. Although the early atmosphere is now thought to be less reducing than Miller and Urey assumed, appropriately modified experiments continue to support the possibility of abiotic amino acid synthesis mediated by spark discharges in the primitive atmosphere (Cleaves et al., 2008).

The theoretical and experimental study of prebiotic chemistry on the early Earth (and beyond) has broadened since Urey–Miller to encompass a wide variety of physical and chemical conditions, precursor compounds, sources of energy, and mineral catalysts. Indeed, it is hard to think of any Hadean or Archaean macro- or micro-environmental setting that has not been invoked by at least a few studies for its possible significance in the origin of life. Early Earth as a whole has been considered a “global chemical reactor” within which many local settings and material transport

mechanisms had roles to play (Stüeken et al., 2013). It is also apparent that many prebiotically important compounds were generated in the protoplanetary disk (and planetesimals and protoplanets within it) and delivered to Earth exogenously by asteroids, interplanetary dust particles, comets, and multiple compositional classes of meteorites (Chyba and Sagan, 1992). Analyses of recent, uncontaminated meteoritic infall reveal abundant insoluble polyaromatic compounds, carboxylic acids, amino acids, and other hydrocarbons as well as phosphides, nitrides, and carbides (Pasek and Lauretta, 2008). Small amounts of ribose and other carbohydrates have also been detected in meteorites (Furukawa et al., 2019). Aromatic macromolecules are surprisingly common even in the interstellar medium.

Atmospheric photo- and electrochemistry, perhaps enhanced by mineral catalysis near Earth's surface, were probably essential in contributing formaldehyde and hydrogen cyanide, feedstocks for the production of amino acids, sugars, and nucleobases (Cleaves et al., 2008; Rimmer and Rugheimer, 2019). However, the focus of contemporary debates about prebiotic chemistry has largely shifted from the atmosphere and open oceans to hydrothermal systems, particularly since the discovery of deep marine vents in the 1970s. High-temperature water–rock reactions facilitate a rich ensemble of prebiotically interesting reaction pathways, including the abiotic synthesis of amino acids from simple carbon and nitrogen sources (e.g., McCollom, 2013; Simoneit, 2004). “Hydrothermal conditions” can also generate lipids via “Fischer-Tropsch-type” synthesis, whereby metal or mineral surfaces catalyse the reduction of CO and CO₂ with H₂; products include fatty acids found in the lipid bilayers of living cells (McCollom et al., 1999). Such lipids readily self-assemble into bilayers and cell-like vesicles under a wide range of aqueous

conditions, including warm, saline, alkaline fluids characteristic of marine hydrothermal settings (Jordan et al., 2019). The formation of the first proteins via peptide bonding of amino acids is more difficult to envisage in aqueous environments, where it is not energetically favourable. Nevertheless, it is suggested that layered double hydroxide minerals in hydrothermal systems might have concentrated amino acids and templated their polymerization (Erastova et al., 2017).

A gulf of complexity separates organic polymers from even the simplest known organisms. One possible intermediate state is described by the well-known “RNA world” hypothesis formulated in the 1960s, which posits that the catalytic functions of proteins and the genetic functions of DNA were originally both carried out by RNA (which still provides the genetic material of many viruses). This hypothesis was greatly buoyed by the Nobel prize-winning discovery of ribozymes, RNA molecules with enzyme-like catalytic functions (Kruger et al., 1982). Detractors of the RNA world hypothesis emphasize the difficulty of assembling RNA prebiotically given the complexity and instability of RNA molecules, especially those large enough to be catalytically useful (Bernhardt, 2012). Important steps in this process have now been demonstrated under experimental conditions analogous to the early Earth (e.g., Powner et al., 2009). However, the overall synthesis may be difficult to achieve in nature, requiring different conditions at each step (Powner et al., 2009; Neveu et al., 2013). It may be that RNA synthesis itself arose through natural selection in some more primitive evolving system (Cronin, 2017). In any case, once formed, RNA can catalyse its own synthesis from oligonucleotide units (Lincoln and Joyce, 2009), creating the potential for natural selection between competing RNA sequences. RNA replication could plausibly have become coupled to the reproduction of an

encapsulating, protective lipid vesicle in a kind of “minimal cell” (Oberholzer et al., 1995; Dzieciol and Mann, 2011). Advocates of alkaline hydrothermal vents as crucibles for the origin of life have proposed that lipid membranes were preceded by inorganic mineral compartments occurring in these vents, which can support trans-membrane proton gradients similar to those sustaining ATP synthesis in living cells today (e.g., Martin and Russell, 2003).

Future progress in understanding the origin of life may result both from increasingly sophisticated and geochemically realistic laboratory experiments and from new computational approaches to the simulation of large, diverse populations of organic molecules in dynamic, far-from-equilibrium conditions (Coveney et al., 2012; Preiner et al., 2020). If it turns out that multiple substantially different routes to the origin of life are plausible under early-Earth conditions, it may not be possible to say definitively which of these routes gave rise to Earth’s biosphere. However, every possible route to life increases the potential number and diversity of inhabited planets in the universe.

Panspermia and the transfer of life between worlds

The *panspermia* hypothesis proposes that micro-organisms are widely distributed throughout the universe including interstellar space, and that life on Earth springs from this extraterrestrial source rather than indigenous abiogenesis. Versions of this idea date back to ancient Greece and were promulgated in the early twentieth century by the Swedish physicist, Arrhenius, who envisaged that “seeds” of life were propelled through space by stellar radiation pressure. Such a view is not widely

supported today and there is no particular evidence in its favour. Viable organisms have been sampled by stratospheric balloons but their reported characteristics are consistent with a terrestrial origin (Wainwright et al., 2004).

In an alternative scenario known as *lithopanspermia* or *transpermia*, microbes protected within porous rock fragments could have been transferred between Earth, [Mars](#), and perhaps [Venus](#) in the early history of the solar system, when these worlds frequently exchanged material excavated from their surfaces by impact events. Organisms within this material would have faced a succession of ordeals, beginning with heat, shock pressure, and acceleration due to the initial impact event (Clark, 2001). Interplanetary transfers would usually take >10,000 years, during which exposure to ionizing radiation would kill most organisms. On arrival at the second planet, any survivors would be heated during atmospheric entry and subject to impact shock once again. Finally, favourable conditions for growth and dispersal would be needed to enable colonization. Lithopanspermia might have occurred in spite of these obstacles if the interplanetary traffic in meteorites was sufficiently great. Experiments have shown that cyanobacteria, lichens, and fungi can survive for at least 1.5 years on the outside of the International Space Station (de la Torre et al., 2010; Onofri et al., 2012). Bacteria placed within chips of rock mounted onto the heat shield of a Russian spacecraft did not survive atmospheric re-entry, but might have done so if insulated by a greater thickness of rock and protected from flames; large meteorites remain cool in their interiors (Cockell et al., 2007; Foucher et al., 2010). Lithopanspermia would receive strong support from any future discovery of organisms on [Mars](#) genetically related to life on Earth. Neither panspermia nor lithopanspermia explains [how life originated](#) in the first place.

Biosphere transformations and the “rare Earth” hypothesis

Astrobiological interest in palaeobiology has tended to focus on major evolutionary innovations that have increased organismal and ecological complexity, transforming the character of the biosphere and hence its remotely detectable signatures. Examples include the rise of oxygenic photosynthesis, the origin of eukaryotes (the lineage of organisms with nuclei and organelles, including all animals, plants, and fungi), the origin of multicellularity, the origin of animals, and the origin of human intelligence (e.g., Watson, 2008). If each of these transitions resulted from highly improbable and contingent events, complex Earth-like biospheres may be vanishingly rare in the universe, a proposal described as the “rare Earth hypothesis” (Ward and Brownlee, 2000). On the other hand, very little is known about how *other* improbable and contingent events might have acted to ratchet up the complexity of alien but Earth-like biospheres. Thus, the best way to test the rare Earth hypothesis is actually to search for extraterrestrial life. Study of Earth’s evolutionary history informs this task by suggesting how different [biosignatures](#) may be distributed through time on an Earth-like planet.

Once established, Earth’s biosphere quickly became highly productive, recycling enough carbon to form black shales by 3.8 Ga ago (Rosing and Frei, 2004) and possibly producing enough methane to warm the planet (Wolfe and Fournier, 2018). Early Archaean fossil and geochemical records are cryptic and controversial, providing relatively weak constraints on the origin of major metabolic pathways and groups of microorganisms (e.g., Wacey et al., 2011; Westall et al., 2011).

Nevertheless, it is clear that life was already highly metabolically and genetically diverse by the end of the eon and included bacterial phototrophs and chemotrophs capable of cycling iron, sulfur, nitrogen, and phosphorus, as well as methanogens and other archaea (Javaux, 2019; Hickman-Lewis et al., 2020).

The rise of oxygen was a gradual, non-monotonic, and stepwise process modulated by global biogeochemical feedbacks (e.g., Alcott et al., 2019). Isotopic evidence of anoxic photochemical sulfur cycling recorded by Archaean minerals indicates atmospheric oxygen concentrations $<10^{-5}$ PAL (present atmospheric level; Johnston, 2011; Reinhard et al., 2017). The disappearance of this signature at ~ 2.4 Ga ago marks the onset of the so-called “great oxidation event” (GOE). Bacteria were almost certainly producing abundant oxygen long before the GOE, but it could not accumulate in the atmosphere until reducing sinks were overwhelmed (Planavsky et al., 2014; Wolfe and Fournier, 2018). Oxygen levels were probably in the range 10^{-3} – 10^{-1} PAL for a billion years after the GOE, and did not reach modern levels until ~ 0.4 Ga (Krause et al., 2018). One astrobiological implication is that even the most Earth-like inhabited exoplanets may not have detectable O_2/O_3 [spectroscopic biosignature](#) for several billion years after the origin of life (Reinhard et al., 2017). Nevertheless, atmospheric spectra acquired from exoplanets with typical Archaean-like biospheres might still reveal a biogenic disequilibrium mixture of N_2 , CH_4 , CO_2 and H_2O (Krissansen-Totton et al., 2018).

Oxygen availability may have been necessary for the origin of eukaryotes (*eukaryogenesis*), which ultimately facilitated a dramatic increase in the organismal and ecological complexity of life on Earth. But it was not sufficient: eukaryogenesis

occurred <1.8 Ga ago, and only once — not independently within multiple lineages as one might expect from the release of a purely external brake (Lane, 2017; Betts et al., 2018). The American evolutionary biologist Lynn Margulis overhauled understanding of eukaryogenesis in the 1970s with her *endosymbiotic* theory, which (in its modern form) interprets eukaryotes as chimaeras resulting from the engulfment of an aerobic alphaproteobacterium by an archaeon. Eukaryogenesis may have involved an exceedingly unlikely chain of events, implying that any extraterrestrial life may be dominantly microbial. Earth’s animals did not evolve until ~0.6 Ga ago; rising atmospheric oxygen may again have played some role, although this is debated (Mills and Canfield, 2014). Land plants (embryophytes) probably evolved later, becoming highly abundant and diverse only ~0.4 Ga ago (Kenrick et al., 2012).

The fossil record shows that Earth’s biodiversity has fluctuated over time along with the rates of speciation and extinction. However, the “Big Five” most impressive and widely studied mass extinctions in the fossil record — including the Permian-Triassic and Cretaceous-Palaeogene boundary events — appear to have affected the diversity of animals far more severely than that of plants, and probably had very little effect on prokaryotes (e.g., McElwain & Punyasena, 2007; Louca et al., 2018).

Astronomical factors in Earth’s history

Astronomical bodies, events, and processes have influenced Earth’s biosphere throughout its history. Some of these influences are now fairly well understood, such as the climatic oscillations induced by periodic variations in Earth’s orbital parameters (named “Milanković cycles” after the Serbian astronomer who discovered

them, Milutin Milanković); others are murkier. It is not yet understood, for example, whether or how Earth's moon has contributed to Earth's habitability (Waltham, 2006). Nor is it clear from the available evidence whether gamma-ray bursts have caused major extinctions on Earth (Bond and Grasby, 2017).

Impacts with comets and asteroids have undoubtedly altered the course of evolutionary history. There is now very strong evidence that the global mass extinction ~66 million years ago was triggered by an impactor >10 km across, which formed the Chicxulub crater in Mexico's Yucatan Peninsula (e.g., Hull et al., 2020). Earthquakes, tsunamis, and global wildfires would have followed within hours of the impact event (Robertson et al., 2004). The impact ejected >50,000 km³ of rock as well as hundreds of gigatonnes of CO₂, water vapour, and other volatiles including sulfur aerosols. In the ensuing cold, dark "impact winter", the diminishment of photosynthetic primary production caused marine and terrestrial ecosystems to fail (Schulte et al., 2010; Vellekoop et al., 2013). A role for impacts in several smaller extinctions in Earth history has been conjectured but not firmly demonstrated (e.g., Bond and Grasby, 2017). In addition, asteroid break-up events in space may have transiently increased the influx of extraterrestrial dust on multiple occasions in Earth's history, which would have stimulated primary productivity in iron-limited regions of the ocean (Reiners and Turchyn, 2019).

4. Prospects for life on other worlds

Life on Venus

Venus may once have been more Earth-like, but is today an extreme greenhouse world whose surface temperature is ~ 470 °C. It has been suggested that airborne bacteria-sized organisms might be able to survive in the Venusian cloud layers, where conditions are cooler and CHNOPS elements may be available (Cockell, 1999; Grinspoon and Bullock, 2007). However, clouds at the relevant altitudes on Venus consist of highly concentrated sulphuric acid, with water activity < 0.1 and a pH well below the tolerance of Earth's hardest acidophiles; these conditions are empirically uninhabitable (Zhang et al., 2012). This implies that any phosphine (PH_3) present in the clouds of Venus — a matter of dispute — cannot be considered a probable biosignature on the basis of a simple analogy with Earth; some bacteria on Earth produce this gas but none could survive on Venus (Greaves et al., 2020). A complete determination of the potential for life on Venus awaits detailed characterization of the structure and composition of the cloud layers by future missions.

Life on Mars

Numerous lander, rover, and orbiter missions have confirmed that the martian surface is inhospitable if not absolutely uninhabitable. Surface temperatures average -60 °C, similar to Antarctica. The thin CO_2 atmosphere exerts an average pressure of 6 mbar at the surface, affording little protection against ionizing solar and cosmic radiation, and permitting extreme diurnal temperature variations. Liquid water is unstable under these conditions and appears only as transient films on hygroscopic salts, although water ice is widespread in clouds and in the upper metre of soil, particularly at high latitudes (Lasue et al., 2019). Any organic molecules in the soil would be degraded by the combined effect of ionizing radiation and strong oxidants

such as perchlorates (Wadsworth and Cockell, 2017). In the 1970s, NASA's Viking landers conducted three experiments designed to test for the presence of viable organisms in surface materials at two localities on Mars. The results were negative, with the possible exception of one experiment whose implications are still debated (e.g., Navarro-González et al., 2010; Levin and Straat, 2016).

Life on Mars may still be possible within pores and fractures deep underground, where harmful radiation is attenuated by overlying rock and liquid water may be sustained geothermally. Deep basaltic aquifers on Earth host diverse chemotrophic microbes including methanogens, which obtain energy and produce methane from the reaction of CO₂ with H₂. H₂ is a product of water–rock reactions (serpentinization) known to have occurred on Mars, and can also be provided by radiolysis and fracture-driven mechanisms (Blair et al., 2007; McMahon et al., 2016). It has been estimated that basaltic Martian crust could support habitable aquifers >5 km beneath the surface, (Clifford et al., 2010). These depths are inaccessible to radar instruments aboard existing Mars orbiters. Radio-reflective surfaces interpreted as subglacial lakes have been detected by the European Space Agency (ESA) Mars Express Orbiter at only ~1.5 km depth within the icy southern polar layered deposits (Orosei et al., 2018; Lauro et al., 2020), but the salinity necessary to prevent freezing at this shallow depth may be too high for life. Methane has also been detected on multiple occasions in the martian atmosphere at parts-per-billion levels using Earth-based telescopes, Mars orbiters, and NASA's *Curiosity* rover (e.g., Formisano et al., 2004; Mumma et al., 2009, Webster et al., 2015). Numerous abiotic sources have been conjectured, but it remains possible that this gas is biogenic. ESA's ExoMars Trace Gas Orbiter (TGO) is capable of determining the hydrogen- and carbon-isotopic composition of this gas

and detecting any co-released organic compounds, which would help to constrain the methane's biogenicity. However, methane was found to be absent (or present below detection limits) in the period for which suitable TGO data have been analysed (Korablev et al., 2019).

The search for life on Mars extends to the deep past as well as the deep subsurface. A rough chronology has been established by crater counting, and was corroborated by in-situ radiometric dating performed by *Curiosity* (Farley et al., 2014). The early shutdown of Mars' core magnetic dynamo exposed the atmosphere to sputtering by solar radiation and allowed charged particles to escape along solar magnetic field lines (Chassefière et al., 2007). The bulk of the atmosphere was thus lost over time, causing surface pressure, temperature and habitability to decline ~4–3 Ga ago (Jakosky et al., 2017). Later hydrological activity was dominantly glacial; water that had not already been sequestered by hydrated minerals was mostly frozen into the cryosphere or lost to space. However, there is extensive evidence that surface conditions were warmer, wetter, and broadly habitable around 4 Ga ago, roughly coincident with the [origin of life on Earth](#). Rivers draining ~10³ km² incised valleys into the landscape that remain perfectly preserved along with sedimentary lake deposits, deltas, and possibly the shorelines of ancient oceans. At Gale Crater, *Curiosity* has explored the ~3.7 Ga-old sedimentary record of a mildly saline, circumneutral lake that endured, at least intermittently, for perhaps ~10⁵–10⁶ years, and may have sustained a vertical redox gradient conducive to microbial chemotrophy (Grotzinger et al., 2014; Hurowitz et al., 2017). Ancient organic matter of indeterminate (probably meteoritic) origin was preserved in these rocks and only recently exposed to radiation by erosion (Freissinet et al., 2015). Future missions,

notably the ESA-Roscosmos *Rosalind Franklin* rover and NASA's *Perseverance* rover will both be equipped to analyse organic matter and detect potential [geological biosignatures](#) analogous to those produced by early life on Earth. *Rosalind Franklin* will drill to extract rock samples from ~2 m below the surface, where any ancient organic molecules would have escaped significant radiation damage. *Perseverance* will gather promising rock samples for subsequent return to Earth by a follow-on NASA-ESA mission.

Life in the outer solar system

Most of the liquid water in this solar system resides in dark oceans within dwarf planets and the larger moons of the gas giants. These icy bodies differ greatly in size, density, and surface composition, and accordingly in their potential to harbour life. Communication between the surface, the ocean, and the rocky seafloor increases the potential for redox disequilibrium and hence habitability. Among the most promising icy bodies from this point of view is Jupiter's moon Europa, whose slightly eccentric orbit induces tidal forces strong enough to deform the ice shell and melt the interior (Sotin et al., 2009). The resulting ocean is ~100 km deep and salty enough to possess an induced magnetic field, which was detected by the Galileo spacecraft (Khurana et al., 1998). The thickness of Europa's ice has long been debated; the brittle outer shell may be <5 km thick but the amount of ductile ice undergirding it is still poorly constrained (Billings and Kattenhorn, 2005). The ice shell turns over on timescales of 10^6 – 10^8 years through tectonic "subduction" and cryovolcanic repaving (Zahnle et al., 2008; Kattenhorn and Prockter, 2014). Such dynamism is clear from the blocky mosaic of cracks and ridges scarring the surface, and possibly also from disputed

evidence of plumes of water vapour/ice venting into space (Jia et al., 2018; Hand et al., 2020). Oxidants produced by photolysis and radiolysis of water and salts at the surface include O_2 , H_2O_2 , CO_2 , SO_2 and SO_4^{2-} , which are estimated to reach the interior ocean at a rate equivalent to $\sim 10^8$ – 10^{11} mol O_2 yr⁻¹ (Vance et al., 2016). This oxidizing power is counterbalanced at depth by a supply of reductants from water–rock reactions including serpentinization, equivalent to $\sim 10^9$ – 10^{11} mol H_2 yr⁻¹ (Vance et al., 2016). Thus, Europa’s ocean may provide redox disequilibrium sufficient to support life. Salinity, pH, and the supply of CHNOPS elements also appear to be within habitable limits (Hand and Chyba, 2007; Hand et al., 2009).

Tidal heating also enables Saturn’s small moon Enceladus (~500 km across) to maintain a global subsurface ocean 10s of km deep, which may be habitable (Thomas et al., 2016). The overlying ice crust is thinnest and youngest in the southern polar region, where a thermal anomaly has produced sub-parallel linear fissures > 100 km in length, known as “tiger stripes”. Geysers distributed along these stripes vent plumes of water into space, contributing to Saturn’s e-ring (Dougherty et al., 2006; Postberg et al., 2009). Mass spectrometers aboard the Cassini spacecraft have detected sodium salts, silica particles, H_2 and CH_4 within this material, signatures of hydrothermal water–rock reactions at the base of a mildly alkaline, moderately saline ocean (Hsu et al., 2015; Waite et al., 2017). Diverse organic compounds bearing oxygen, nitrogen, and aromatic rings have also been discovered in the plumes (Khawaja et al., 2019). These observations suggest that the Enceladean ocean may be habitable (although highly alkaline and oxidant-poor; Hand et al., 2020) and perhaps even favourable for [abiogenesis](#).

Internal oceans in some larger bodies, including Jupiter's moons, Ganymede and Callisto, and Saturn's moon, Titan, are probably cut off from the interior rocky mantles by interlayers of high-pressure ices. These oceans may therefore lack a sustained source of chemical disequilibrium to sustain life. Titan is nevertheless of special interest because of its organic-rich atmosphere and surface environments, replete with ethane and methane lakes. It has been speculated that Titan's cold (~94 K) surface could support exotic forms of life that use liquid methane as a solvent instead of water, and might extract energy from the reaction of H₂ with acetylene and ethane (McKay and Smith, 2005). The low abundance of acetylene detected on the surface may be consistent with such a biotic sink, although abiotic explanations are being explored (McKay, 2016; Lunine et al., 2020). It has also been pointed out that Titan's temperature and other environmental conditions were likely far more Earth-like ~4.0 Ga ago when life began on Earth and could have facilitated [abiogenesis](#) independently (Schulze-Makuch and Grinspoon, 2005).

Forthcoming missions aim to provide further insights into the habitability of icy moons in the outer solar system, including ESA's Jupiter Icy Moons Explorer ("JUICE", which will target Europa, Callisto, and Ganymede) and NASA's Europa Clipper. These missions will deploy ice-penetrating radar, gravimeters and magnetometers to constrain these bodies' interior structures, and will use spectrometers and cameras to characterize their surface materials. Europa Clipper will characterize and attempt to sample Europa's plume ejecta to determine the habitability and organic chemistry of its source fluid. NASA's *Dragonfly* mission aims to deploy a rotorcraft lander to characterise surface and atmospheric chemistry on Titan, which may reveal new aspects of prebiotic organic chemistry (Lorenz et al.,

2018).

Life on extrasolar planets

Thousands of exoplanets have been detected; it seems there are at least as many planets in the galaxy as stars (Cassan et al., 2012). Many detections were made in the period 2009–2018 by NASA’s Kepler Space Telescope using the transit method, whereby planets orbiting in a plane inclined towards the Earth partially eclipse their host star. The resulting dip in brightness reveals the radius of the planet, its orbital period (if repeated), and hence its orbital distance (from Kepler’s Third Law); an equilibrium surface temperature can then be estimated given the luminosity of the star. The radial velocity method deployed by other instruments detects the Doppler shift caused by the slight movement of a star about the gravitational centre of its system, and thereby constrains the mass of orbiting planets. Combining both methods can yield a planet’s bulk density and thus reveal whether it is likely to be rocky or gaseous. Where transits are not observed, the radial velocity method provides only a minimum mass. These methods have revealed an extraordinary diversity of planets, many of which are quite unlike those in this own solar system and defy easy classification. Some planets of near Earth-size have been detected within their star’s [habitable zone](#) and may be rocky, although it is doubtful whether any of these are truly “Earth-like”. Most planets so far detected are intermediate in size between Earth and Neptune (“super-Earths” and “mini-Neptunes”). Many others are gas giants orbiting very close to their host stars, implying that they migrated inwards from beyond the snow line.

Discoveries of exoplanets have also inspired theoretical studies of the habitability of planetary systems unlike this one. For instance, astrobiologists have discussed the prospects for life on tidally locked planets, planets orbiting multiple stars, and planets drifting through interstellar space (Edson et al., 2012; O'Malley-James et al., 2012; Abbot and Switzer, 2011). The overriding goal of much of this work is to determine which exoplanets should be prioritised for future observations. The James Webb Space Telescope, developed by NASA, ESA and the Canadian Space Agency and scheduled for launch in 2021, is expected to characterize the absorption spectra of transiting exoplanets and may be capable of detecting [atmospheric biosignatures](#) on nearby worlds (Lustig-Yaeger et al., 2019). Ground-based telescopes such as the European Southern Observatory's Extremely Large Telescope in Chile offer higher angular resolution and will enable direct imaging and spectroscopy of non-transiting exoplanets (Kasper et al., 2010).

6. SETI and the future of life

The discovery of extraterrestrial organisms cognitively similar to ourselves would be a profound and historic achievement. Since "intelligence" (a rather fraught concept) is not an astronomical observable, the "search for extraterrestrial intelligence" (SETI) seeks instead the electromagnetic signatures or astronomical artefacts produced by technological civilizations. Radio telescopes have been used since the 1960s to survey the sky for transmissions originating outside this solar system. Some observational programmes have also sought to detect laser pulses beamed in Earth's direction. There have been no unambiguous positive detections in any of these research programmes; arguments for their continuation appeal to the extremely high scientific

pay-off should they ever succeed. Various other detectable signatures of alien technology (“technosignatures”) have been envisaged including artificial megastructures build to encircle stars and capture their energy (“Dyson spheres”; Dyson, 1960), and the anomalous destruction of planets (Stevens et al., 2016). Such phenomena are also undetected as yet.

The lack of evidence for extraterrestrial intelligence — the “Great Silence” — has attracted considerable commentary. Habitable planets existed billions of years before the Earth. If only a small fraction of these planets produced technological civilizations with the ability and desire to broadcast signals through space, or to propagate themselves through space by colonizing suitable star systems or dispatching probes, humanity should have encountered them by now (depending on one’s assumptions; Prantzos, 2013). This problem is known as the Fermi Paradox after the Italian-American physicist Enrico Fermi, who is supposed to have asked “Where are they?”. However, there are many possible reasons why alien civilizations might be non-existent, rare, non-colonizing, or undetectable. The “Drake equation”, devised as an aid to thought by the American SETI astronomer Frank Drake in 1961, provides one well known formulation of the relevant parameters:

$$N = R_{*} \cdot f_{p} \cdot n_{e} \cdot f_{l} \cdot F_{i} \cdot F_{c} \cdot L$$

Where N = the number of detectable planetary civilizations in the galaxy, R_{*} = the mean rate of star formation; f_{p} = the fraction of stars that host planets; n_{e} = the average number of habitable planets per planetary system; f_{l} = the fraction of habitable planets that develops life; F_{i} = the fraction of inhabited planets that develops the cognitive capacity for civilization; F_{c} = the fraction of these civilizations that produces signatures detectable from Earth; and L = the average length of time for which these

signatures continue to be detectable. Of these parameters, only the first two are now reasonably well constrained. n_e is unknown; the number of Earth-like planets within the [habitable zones](#) of sun-like stars can be estimated with data from the Kepler mission (e.g., Petigura et al. 2013) but not all of these worlds are in fact habitable. f_i , F_i , F_c , and L are completely unconstrained; the solution to Fermi's Paradox may lie in a low value for any or all of them. The parameter L is of anthropological interest since it is partly a reflection of the longevity of technologically advanced civilizations.

Earth will remain habitable for the next ~2.8 billion years even without geoengineering (O'Malley James et al., 2013). Nevertheless, reflection on the ultimate fate of human civilization prompts some authors to advocate an expansionist ethic for humanity. For example, it has been argued that Mars and perhaps ultimately other planets should be "terraformed" to create Earth-like conditions allowing us to "back up" the biosphere, including *Homo sapiens*. This proposal is debated by social scientists and philosophers as well as astrobiologists. The threat that terraforming would pose to the scientific search for indigenous [life on Mars](#) is one motive for caution (McKay and Marinova, 2001).

7. Conclusion

The science of astrobiology has forged a strong and coherent identity since the martian meteorite controversy of 1996. Progress on fundamental questions has been impressive since that time, although much of it has taken place within more traditional disciplinary frameworks. Thus, microbiologists and molecular biologists have probed the limits of life on Earth and discovered that living organisms are far

more pervasive and resilient than previously thought. Synthetic chemists have reached “the end of the beginning” in the struggle to understand the [origin of life](#) (Sutherland, 2017). Geologists have retraced the co-evolution of Earth’s biosphere, lithosphere and atmosphere over four billion years. Astronomers have catalogued thousands of exoplanets, and planetary scientists have revealed that [Mars](#) and the [icy moons](#) of the outer solar system are geologically dynamic and potentially habitable. Astrochemists have detected ever more complex “building blocks” of life in space. It is the unique task of astrobiology to synthesize these insights and draw out their implications for the origin, nature, evolution, distribution, and future of life across the universe.

Astrobiologists have also developed special expertise in the study of field and experimental “analogues” to extraterrestrial and early-Earth environments. For example, the dry valleys of Antarctica and the intensely UV-irradiated Atacama Desert have served to elucidate the habitability of Mars-like extreme environments and to inform strategies for detecting biosignatures under Martian conditions (e.g., Wierzchos, et al., 2006; Musilova et al., 2015). Analogue studies have placed forthcoming life-detection missions on a much surer footing than the (arguably) unsuccessful Viking experiments. However, the future of astrobiology surely lies in ever more sophisticated space exploration missions and methods of astronomical observation. Rovers (or even astronauts) may eventually find traces of life on Mars, probes may identify biosignatures in the plumes of Europa and Enceladus, and the next generation of space- and ground-based telescopes may confirm the detection of habitable exoplanets or perhaps even alien civilizations. If any of these or other forthcoming life-detection missions yield positive results, astrobiology will enter an exciting new chapter. Negative results may be perceived as disappointing, but will

nevertheless make an important contribution to human understanding of the possible distribution of life in the universe.

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Figure 1

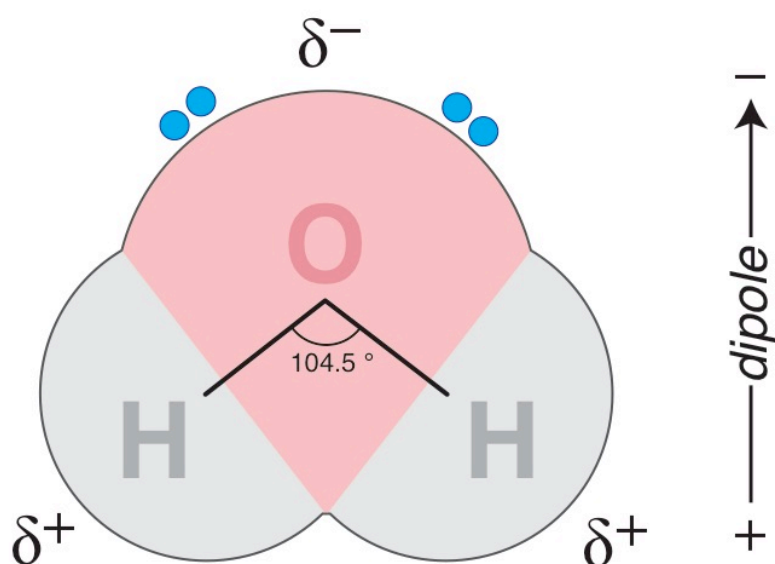


Figure 1: Water molecules are polar: the electrons in the O–H bond are drawn towards the oxygen atom, giving it a partial negative charge (δ^-) and leaving the two hydrogen atoms with partial positive charges (δ^+). The four electron pairs repel each other, pushing the hydrogen atoms together and resulting in a net dipole. The angle between the O–H bonds is further decreased because the mutual repulsion of oxygen’s two lone pairs (blue) slightly exceeds the mutual repulsion of the O–H bond pairs.

Figure 2

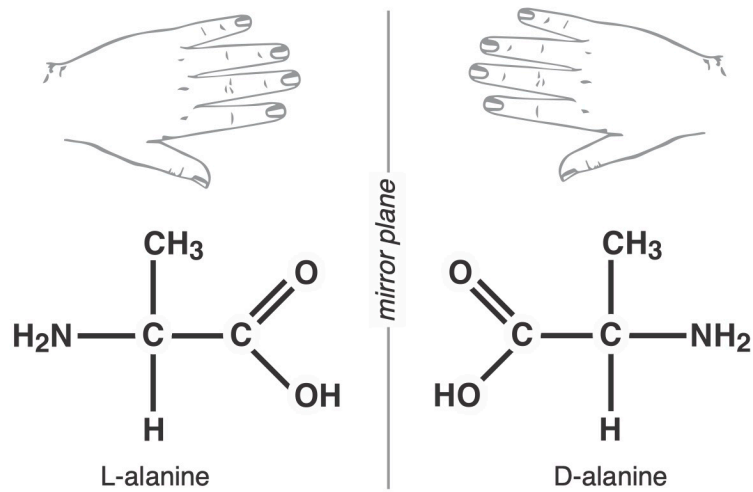


Figure 2: “Chiral” organic molecules can be constructed in left- and right-handed forms (enantiomers), which, like a pair of hands, are mirror images of each other and cannot be superimposed. Life on Earth synthesizes proteins from left-handed (“L-“) amino acids, and prefers right-handed (“D-“) carbohydrates. Shown here are L- and D-alanine, an amino acid.