Chapter 4
Lessons from the History of Life on Earth

The discussion of life on other worlds is inevitably qualified by the phrase, "life as we know it." This customary and appropriate caution among scientists serves to (1) admit that all our speculations and extrapolations are based on a known sample size of only one, and (2) imply that the one form of life we know may be peculiar to the physical conditions under which it exists. While these constraints do place boundaries on the scientific latitude we should allow ourselves in speculating about unknown forms of life, the sample with which we are familiar does constitute a specific and robust example that has persisted through numerous crises in variable, changing, and often extreme environments. Assuming that the laws of physics and chemistry are universally operative, then life elsewhere might be expected to follow the same evolutionary and ecological principles that have characterized its history on Earth. Thus, rather than thinking of "life as we know it" in terms of constraints, this chapter explores the insights to be gained by regarding the one life we know as a harbinger and example of the life we can reasonably expect to exist on other worlds.

4.1 A Brief History of Life on Earth

The Earth is presumed to have formed about 4.56 billion years ago by accretion, the gradual accumulation of submeter-sized objects (Levison et al. 2015). Like all concentrations of matter in the Universe, it formed through gravitational collapse and consequent rotation (Cassen and Woolum 1999). Recurrent bombardment continued for at least 0.5 billion years, during which the Earth's interior differentiated, the first islands formed (Burnham and Berry 2017), and the atmosphere stabilized in composition, with N_2 and CO_2 as major constituents.

Based on dating of the earliest fossils, the first life on Earth appeared rather quickly (Schopf 1999; Dodd et al. 2017). While evidence for the ultimate ancestry of life on Earth is controversial at this time (Brasier et al. 2002; Mojzsis et al. 1996; Westall et al. 2001), few experts doubt that life was present by 3.5 billion years ago,

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and some believe it is likely closer to 4.0 billion years old (Lazcano and Miller 1994), or even older (Bell et al. 2015; Dodd et al. 2017).

The earliest life was unicellular, microscopic, and anaerobic (Schopf 1993) and this type of life still persists today. Though far more complex than any non-living particle of comparable size, its internal structure was relatively undifferentiated, lacking internal membranes or extensive subcellular segregation of function. Once the simple architecture of the prokaryotic cell emerged, it remained relatively unchanged for 2 billion years, or half of the history of life.

Based on fossil evidence, photosynthesis arose fairly early to harvest the abundant source of energy from the Sun (Cowen 1995; Margulis and Sagan 1995; Cardona 2016). Once oxygen began to be produced by photosynthesis, it was first consumed by the oxidation of minerals, then gradually began to increase in the atmosphere. At least a billion years of photosynthesis took place before the oxygen content of the atmosphere reached 10% of its current level (Walker 1977).

Gradually, subcellular specialization developed in concert with the availability of more efficient oxidative metabolism, enabling the enlargement of cells to the size of eukaryotes (Han and Runnegar 1992; Margulis and Sagan 1995). Life persisted, however, exclusively as unicellular and water-borne for perhaps another half billion years, and unicellular descendants of early microbial life thrive to the present day.

After the mineral capacity of the Earth to absorb oxygen became saturated, and free O_2 began to accumulate in the atmosphere, oxidative metabolism became sufficiently available to support multicellular and macroscopic structures. These forms of life remained small and probably sluggish for close to a billion years (Cowen 1995). Widespread glaciation about 600 million years ago was followed by a warming trend that coincided with an explosive diversification of structural forms and lifestyles about 541 million years ago, usually referred to as the Cambrian explosion (Cowen 1995). The diversification of animal morphology occurred quite sharply at the end of that glaciation. Peterson et al. (2004) points to the diversification of the bilaterian phyla as the signature event of the Cambrian explosion. Based on a molecular clock analysis using seven different amino acid sequences, the last common ancestor of bilaterians was estimated to have existed somewhere between 573 and 656 million years ago (the earliest unequivocally bilaterian fossils are about 555 million years old). Lowenstein (2006) argued that the rising oxygen concentrations at the end of the Precambrian period promoted macroorganisms, which fed on stromatolites. This led to a decreasing ability of stromatolites to fix Ca^{2+} from the ocean water. As the Ca^{2+} concentrations further increased, the ocean became toxic, which in turn led to evolutionary innovation in the form of shell producing organisms that represent the fossil record of the Cambrian explosion. The Cambrian explosion was the result of an interplay between changing ecological conditions (including the rise in oxygen levels and Ca^{2+} concentration), the innovative bilaterian developmental system, and an increase in complex ecological interactions (Marshall 2006). The vast breadth of biological diversity was not maintained for long, however, as many of life's new experimental forms did not survive an environmental crisis 488 million years ago. Most of the extant higher order taxa of plants and animals were fixed at that time and have remained essentially unchanged to the present.

Larger life forms conquered land habitats less than 500 Ma ago (Margulis and Sagan 1995). Those organisms that did so, however, quickly radiated into a variety of forms that occupied niches above, on, and beneath the terrestrial surface, which affords a higher degree of environmental heterogeneity.

Life has been recurrently inventive, with a tendency toward increasing complexity in a minority of forms over time (de Duve 1995). Most of the diversions from basic forms and strategies have become extinct relatively quickly. A few innovations have proven highly adaptive, and have persisted with little modification once they became established (Eldredge 1985). The general rule for biomass as a whole, however, has been to remain simple.

The subsurface of the ocean, and subterranean habitats even more so, provide much more stable environments than the air or the surface of the water and earth. Much if not most of the Earth's biomass has evolved to occupy these niches, where it remains relatively simple, microscopic, and unchanged in basic form and function from the early days of life on Earth.

4.2 Lessons from the History of Life on Earth

A number of generalizations are suggested by a consideration of the history of life on Earth, as outlined above. While we lack evidence at the present time that any of these generalizations apply to life on other worlds, if that life is subjected to the same physical and chemical principles that apply on Earth, there is no reason to assume that the same patterns and principles would not apply to the trajectory of life wherever it occurs. Those generalizations and their implications are elaborated below.

4.2.1 Life Arises Relatively Quickly Under Conducive Conditions

The fact that life arose or took hold relatively soon after the recurrent heavy bombardment had subsided suggests that it is not a highly improbable phenomenon in relation to the time available for it to occur. Whether life originated on Earth or was transported here from another point of origin, the one example that we have shows the origin or colonization of life to be achievable within a few 100 million years of the opportunity for it to happen (de Duve 1995; Lahav 1999; Bell et al. 2015), and some have argued that as little as a few 1000 years may be required (Lazcano and Miller 1994).

It follows that if life could take hold on Earth within tens to hundreds of millions of years, it could do so anywhere under comparable circumstances in the Universe. Comparable circumstances (cessation of constant bombardment, presence of a liquid solvent, and reduced compounds or other forms of energy) probably existed on other planetary bodies in our Solar System at one time, and surely have existed abundantly throughout the Universe over the 12 billion years or more since the first galaxies formed. Life itself may well have originated or existed for some time on other bodies in the Solar System, and almost surely is part of the extended fabric of the Universe as a whole.

The criticism can be raised that the relatively sudden establishment of life on Earth is exceptional, rather than indicative of an intrinsic tendency. However, assuming the window of opportunity extended from 25 to 600 million years, Lineweaver and Davis (2002) calculated a probability of 0.13 at the 95% level of confidence for the origin or establishment of life on any suitable body with an age of at least 1 billion years. This amounts to saying that 13 out of every 100 suitable planetary bodies with an age of at least 1 billion years has a significant probability of harboring life. While the number of "suitable bodies" in the Universe is not known, it has to be very large, even if only a small fraction of the trillions of stars in the Universe contain such planetary bodies. While statistical probability cannot prove the actuality of specific events, it does provide a quantitative argument for the plausibility of the widespread existence of life in the Cosmos. Specialists in the theory of complexity, in fact, suggest that given the proper materials, appropriate physical conditions, and a flow of energy, that matter will form itself inevitably into complex, self-organizing systems (Goodwin 1994; Kauffman 1995; Morowitz 1968). Once these systems become self-propagating, the basic criteria for life have been met.

4.2.2 Life Tends to Stay Small and Simple

Size and complexity are, of course, relative terms, but in relation to the size and complexity into which some forms of life have evolved, the vast majority of the biomass on Earth, even today, is microscopically small and no more complex than the solitary eukaryotic cell.

Physiology favors simplicity, and simplicity is aided by small size. The ratio of surface to volume decreases inversely as size increases. The simplest living functions (physiological processes) depend critically on exchange of materials across the boundaries of the system (external membrane). Not only does the high surface to volume ratio of small compartments favor exchange of materials, the ability of those materials to migrate to and from the center of the cell by diffusion, the simplest mode possible, depends on having a cell radius small enough for diffusion to be a practical mechanism for movement.

Ultimately, some advantages are gained by increased complexity. Multicellular organisms can achieve greater mobility and enhanced capacity to deal with a specific range of environmental fluctuations, but multicellularity requires specializations for distribution of materials, ingestion and excretion, and coordination of different body parts. This requires greater hereditary information for coding development and physiological coordination, consumes more energy, requires more space, and draws more resources from the environment. The density of such organisms is thereby reduced. Also, while advantages accrue for adaptation to specific niches, flexibility is diminished so that overall fitness to a broad range of changing conditions over time remain with the simpler structures and functions that require less coding, smaller size, and less elaborate cellular engineering.

It is not apparent whether life intrinsically requires 2 billion years to evolve into multicellular complexity, or if conditions on Earth simply precluded it from happening sooner. The lack of oxidative metabolic capacity has been cited as one characteristic that possibly was limiting. The constancy of the oceans, chemically and thermally, over the prolonged dawn of the history of life may have been another. Whatever the reason, there is no reason to assume that the tendency for life to remain simple and small on Earth would not be true of life on other worlds where conditions have long remained constant.

Also, we do not know how multicellularity started during Earth's history. There are some tantalizing hints of evolutionary convergence toward multicellularity. Examples are multicellular aggregates of magnetotactic bacteria (Keim et al. 2004) and microbialite structures that hint toward an analogue for the construction of a proto-macroorganism from loosely affiliated microbial cells (Schulze-Makuch et al. 2012a; António and Schulze-Makuch 2012).

4.2.3 Most Organisms Remain Relatively Unchanged over Their Evolutionary Life Spans

While life may arise or take hold fairly quickly, it has little propensity to evolve very fast in general. It is perhaps surprising, in fact, that given the rapid pace of which evolution is sometimes capable, that little evolution at the macroscopic level took place for over half of the entire history of life on Earth. And when life did achieve multicellularity, it took many millions of years additionally for any of it to abandon the aquatic cradle of its birth and earliest nourishment (Margulis and Sagan 1995).

Every major group of organisms consists of some members whose lineage is easily traceable to a point early in the appearance of the taxon. Salamanders, turtles, crocodiles, armadillos, sturgeons, and sharks are vertebrate examples. Clams, lobsters, cockroaches, and jellyfish are just a fraction of the invertebrate examples. Within individual species, constancy is the rule, and extinction is much more common than gradual change (Eldredge 1985; Gould 1981).

In theoretical terms, we understand the tendency for living systems to retain their basic form and function for long periods of time in the context of *stabilizing selection* (Campbell 1996, p. 431). Under constant conditions, the mutations, genetic

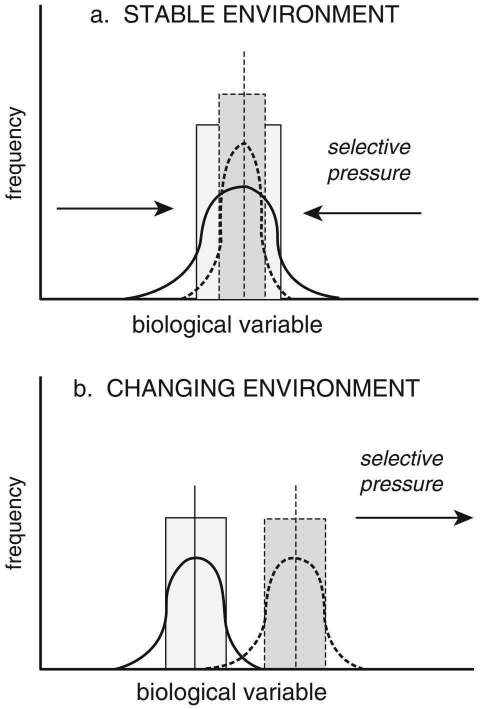

Fig. 4.1 Effect of selective pressure on biological characteristics, illustrated by changes in the frequency distribution of a quantitative biological trait in response to different forms of selective pressure. (**a**) In stable environments, stabilizing selection promotes elimination of peripheral values in the original population, reducing the range in the descendent population (dashed rectangle) without altering the mean value (dashed vertical line). (**b**) In changing environments, natural selection favors change in the direction that better adapts the organism to the new environment. The range for the majority of organisms from the original population (solid rectangle) and their mean value (solid vertical line) shift toward a different mean (dashed vertical line) without changing the range of the variable in the new population (dashed rectangle)

recombinations, and genetic drift that lead to deviations from the optimum phenotype are less adaptive and tend to be selected against. Those traits that are nearest the optimum are favored most strongly. So long as the environment remains stable, the optimal adaptations to it will remain the same. Outlying phenotypes will be selected against, and phenotypes conforming most closely to the optimum will be selected for, over time. The frequency distribution of traits will narrow and stabilize around the optimal, providing the highest proportion of organisms with the greatest adaptive advantage (Fig. 4.1a). Thus well adapted, the organisms will remain static as long as the environment does so.

Most of the planets and satellites in the Solar System have been static for long periods of time (Buratti 1999). It seems likely that all the planets except for Venus, Earth, and Mars assumed their current form and characteristics soon after their accretion. Of the sizeable satellites, only the Moon, Io, and possibly Titan have not been ice covered for most of their existence. The barren surface of Mercury, the swirl of dense atmospheres on the gas giants, and the frozen worlds of the gas giant satellites all provide environments that have been constant for billions of years. Since the interiors of the "snowball" satellites are insulated by ice layers from the radiation, vacuum, and cold of outer space, whatever life may have gained a foothold there would be subjected to stabilizing selection in the extreme, unless changes in the flow of energy from the interior would have altered the course of physical conditions below the surface of those bodies, as might have occurred on the smaller satellites after their radiant cores expended their capacity for nuclear decay. On Venus and Mars, where irreversible changes have apparently transformed ocean bearing planets like Earth to an oppressive greenhouse on the one hand, and to a frigid desert on the other, stable environments may still be found beneath the surface of both, and possibly in the dense cloud layers of the lower atmosphere on Venus (Schulze-Makuch et al. 2013b). In short, the dynamic nature of the Earth's biosphere appears to be exceptional in the Solar System. The role of the diurnal and annual cycles might have been important as they at least require storage of energy over shorter and longer periods of time. Most of the worlds close at hand provide environments of enduring constancy. If life on those worlds has followed the trajectory of life under constant conditions on Earth, we can expect that life on those bodies has been relatively unchanged from the ancient forms that characterized its beginnings.

Combining this point with the previous one above, whatever life exists on other worlds in our Solar System is likely to be microscopic, relatively simple, and basically unchanged from its earliest forms. Possibly Europa, and conceivably Titan and Triton could harbor exceptions, under circumstances to be argued later. The special histories of Venus and Mars may likewise raise alternative possibilities. But to the extent that our Solar System is typical of others throughout the Universe, most life on other worlds is likely to be small, simple, and persistent in form and function from its early origins. Thus, while the possibility of some exceptions will be argued in subsequent sections, we concur in general with the view of Ward and Brownlee (2000) that most of the living fabric of the Universe belongs in the province of microbiology.

4.2.4 Evolution Is Accelerated by Environmental Changes

While the normal pace of evolution under stabilizing selection is negligible, changes in either the biotic or abiotic environment can alter the pace and direction of evolution relatively rapidly (Reznick and Ghalambor 2001). The macroevolutionary examples of greatest note include the major extinctions, followed by introduction of novel forms, at times of major environmental crisis, such as the end of the Cambrian, the Permian-Triassic boundary, and the Cretaceous-Tertiary boundary (Eldredge 1985). On a microevolutionary scale, industrial melanism is often cited as the definitive example. Cryptic coloration of moths changed over a few years in concert with changes in the color of tree trunks associated with increased soot production at the onset of the industrial revolution in England (Raven and Johnson 1999, p. 409). But very rapid evolution has been induced in the lab for a number of systems as well (Elena and Lenski 2003). Rapid evolutionary change illustrates the principle of *directional selection* (Campbell 1996, p. 432). When an environmental feature shifts in a particular direction (say the average habitat temperature gets colder), the optimum for the phenotype that is adapted to that feature (say thickness of fur) shifts to accommodate the change, so that formerly favorable phenotypes (short fur) become maladaptive and are selected against, while formerly maladaptive traits (thicker fur) become more favorable and are selected for. The frequency distribution for the phenotype, and its underlying genetic basis, shifts accordingly (Fig. 4.1b).

The more drastic and sudden the environmental change is, the quicker the evolutionary response needs to be in order for the organism to avoid extinction. In fact, extinction is more often the case, so the ones that survive are changed more radically in a briefer period of time. Over geological time spans, the fossil record thus appears to be discontinuous, with new forms arising relatively suddenly. This is the basis for the theory of "punctuated equilibrium" (Eldredge and Gould 1972).

4.2.5 Complexity Inevitably Increases but as the Exception Rather than the Rule

Since geological and climatic changes are very slow in relation to the life span of all organisms, from one generation to the next, stabilizing selection is the more pervasive influence, and tends to favor constancy of biological form and function. Since, as argued above, simplicity is favored over complexity by the evolutionary process, most life remains stable, and the majority of biomass remains simple. But occasional episodes of directional selection and genetic drift inevitably give rise to some forms better adapted by adopting a greater level of complexity.

To a degree, increased complexity equates with increased size. Thus, the evolution of the more complicated eukaryotic cell from its simpler prokaryotic ancestor was the first great leap in size and complexity in the history of life (Margulis and Sagan 1995; Schulze-Makuch and Bains 2017). The evolution of multicellular organisms from unicellular ancestors was another quantum leap in complexity (Cowen 1995). Within a given size range, however, the rule of preference for maintaining the status quo continues to hold. Only a small minority of mollusks developed complex nervous systems (the cephalopods). Only a minority of vertebrates developed the complex physiological regulatory mechanisms required for homeothermy. And only a small minority of mammals developed the refined sensorimotor coordination required for manual dexterity (primates) and eventually, complex language (humans).

But those levels of complexity did arise, and complexity theory argues in general that such complexity will arise eventually and inevitably (Gel-Mann 1994; Goodwin

1994; Kauffman 1995). This is because complexity enables specialization, and specialization sooner or later confers adaptive advantages under specialized circumstances. But specialization is difficult to reverse, as a host of interrelated organismic attributes become adapted to the specialized conditions. Once homeothermy evolves, as an example, other metabolic reactions adapt to narrow to optimal temperatures, and cease to function if the organism loses its ability to maintain the narrow thermal optimum. Thus the loss of thermal homeostasis would lead to extinction, so the specialization of homeothermy is retained as long as it provides an adaptive advantage.

Evolutionary biologists use the metaphor of a hilly landscape, where the altitude of a hill represents the degree to which its occupants are well adapted, or fit, to their particular biological niche (Dobzhansky 1951, adapted from Wright 1932). Complexity arises inevitably as time favors the "occupation" of higher points on the fitness landscape, but descent from the peaks of higher fitness is penalized by natural selection. While the overall landscape consists of fitness plains and valleys populated by less complex organisms with a broader range of general adaptations, the average level of complexity undergoes a net increase over time.

4.2.6 Biodiversity Is Promoted by Heterogeneous Environments

Habitats can be relatively uniform over a large area (such as a desert) or volume (such as the interior of the ocean). The number of different varieties of organisms that occupy such environments is smaller than the number that occupy more diverse habitats, such as coral reefs or tropical forests (Brooks and McLennan 1991; Cowen 1995). This is because heterogeneous environments provide more niches to which different forms of life can become optimally adapted. The greater variety of living forms in turn creates more complex food webs and ecosystems. Thus, biodiversity, as measured by the overall variety of life and degree of interaction among components of the ecosystem, is greater where the habitat itself is more diverse.

By supporting a richer diversity of organisms, heterogeneous environments provide a more bountiful supply of progenitors for future evolution. Habitat fractionation thus becomes a spur to further evolution. With gradual changes in heterogeneous environments, biodiversity tends to increase even more. With sudden cataclysmic changes in such environments, biodiversity is reduced but survival of more forms is favored because of the numerical probability that more of them will be pre-adapted to persist through the cataclysm or thrive under the new environmental conditions. Thus, environmental heterogeneity not only promotes biodiversity but favors the persistence of life through challenging environmental changes.

These theoretical assumptions are well supported by the empirical evidence of life on Earth. The number of different species that occupy terrestrial habitats, which are inherently more complex than marine environments, is far greater than the number of marine species. On land, tropical rainforests provide the greatest habitat fractionation and support the greatest biodiversity. In the ocean a much greater diversity of species is found on the continental shelves, than in the deep ocean, and in the former, biodiversity is greater in coral reefs than in subtidal waters with smooth, sandy floors. The exception that proves the rule in the deep ocean is the proliferation of biodiversity around hydrothermal vents, such as "black smokers" or alkaline vents, where heated sulfur-rich effluents create fragmented microhabitats with radical chemical and thermal gradients (Campbell 1996; Stetter 1985).

It follows that those other worlds in which the physical environment is heterogeneous, and complex are likely to evolve a richer diversity of living forms than on those with more homogeneous habitats.

4.2.7 Individuals Are Fragile, But Life Is Hardy

Once life evolved on Earth, it proved to be extraordinarily resilient. Despite numerous global catastrophes and recurrent environmental crises—several of which wiped out a large proportion of the species in existence—life has persisted to occupy every suitable habitat on the planet. The widespread extinctions that accompany global catastrophes (Cowen 1995; Eldredge 1985; Bond and Grasby 2017) illustrate that individual organisms lack the capacity to survive radical changes. However, at the population, species, and higher taxonomic level, the capacity for survival is more robust, because the group has a wider range of survival mechanisms than the individual.

Macroevolutionary theory is based on the view that the large-scale patterns of evolution derive from differential survival of species (Gould 1981). The ability of the group to survive despite the fragility of the individual is attributed to the concept of inclusive fitness (Raven and Johnson 1999). Contributing mechanisms include altruistic behavior, spore formation, cannibalism, fluctuating sex ratios, and adjustable reproductive strategies. At the microbial level, spores and other dormant states such as the cryptogenic state in cold environments are of special relevance, because they allow organisms to stay dormant through harsh conditions until the environment becomes suitable for survival again. An especially intriguing example is provided by *Bacillus subtilis*, a common soil bacterium. Not only can it form spores, but under starvation conditions some of the cells resist sporulation by killing sister cells, enabling them to feed on the released nutrients for survival (González-Pastor et al. 2003).

4.3 Adaptations to Extreme Environments

Microbial life has proliferated into almost every environmental niche imaginable on Earth. These include extreme temperature, pressure, and pH environments, habitats exhibiting low nutrient and oxygen availability, and high salinity and radiation environments. From the human perspective, most of these environments are considered extreme, and the organisms living in them are considered extremophiles. This, however, is an anthropocentric characterization, as pointed out by Rothschild and Macinelli (2001). A more suitable set of criteria might be based on certain conditions that destroy biomolecules, such as desiccation, radiation, and oxidation. From this perspective, all aerobic organisms including humans could be considered extremophiles, since oxygen forms reactive oxygen species which cause oxidative damage to nucleic acids, proteins, and lipids (Newcomb and Loeb 1998; Tyrell 1991). Regardless of which organisms are regarded as the extremophiles, the basic point is that life on Earth has adapted to the far edges of the range of niches available, and therefore could be expected to adapt to very different conditions on other worlds. Most renowned for their adaptation to extreme environments on Earth are the archaea, but extremophiles occur in all domains including multicellular organisms and vertebrates (Islam and Schulze-Makuch 2007). A classification with examples of extremophiles is provided in Table 4.1.

4.3.1 Temperature Extremes

Temperature is a fundamental physical parameter that affects all life processes. First and foremost, it determines the liquidity of water. Secondary effects of temperature include its impact on the structure of biological macromolecules (e.g. proteins) and its constraints on cellular processes, such as the fluidity of membranes (Charlier and Droogmans 2005). As temperatures increase, proteins denature, resulting in the loss of quarternary, tertiary, and even secondary structures, thereby eliminating all uses related to conformation (Rothschild 2007). Variations in temperature affect the optimum activity for enzymes, and when enzymes denature they loose their catalytic activity completely. DNA usually melts well below 100 °C, and chlorophyll degrades above 75 °C. Nevertheless, some bacteria appear to be able to grow above 100 °C (Kashefi and Lovley, 2003), though, no eukaryotic organism appears to be able to complete its life cycle above 60 °C, and most not above 40 °C (Clarke 2014). An additional challenge is that the solubility of gases in water goes down as temperature goes up, creating problems at high temperatures for aquatic organisms requiring oxygen or carbon dioxide. At temperatures below the freezing point of water, membranes become dehydrated and rupture, and solute concentrations in un-frozen inclusions can create high osmotic pressures and possibly reach toxic levels. On a macroscopic level, ice crystals form and pierce cellular membranes.

Table 4.1 Known environmental limits for extremophiles for growth or tolerance

Environmental parameter	Bacteria and archaeans	Eukaryotes	Example environments
Temperature	122 °C, *Methanopyrus kandleri, for growth,* 130 °C, *Geogemma barossii*, for survival Bacterial growth at least down to ~ −18 °C	~105 °C Pompeii worm, Himalayan midge and the yeast *Rhodotorula glutinis* at −18 °C	Submarine hydrothermal systems, geothermal hot springs, brine pockets in sea ice at about −30 °C
pH	~pH 0, acidophilic archaeans such as *Ferroplasma sp.*; pH 13, *Plectonema*, pH 10.5 *Natrobacterium*	pH 0, fungi such as *Cephalosporium*; pH 10, many species of protists and rotifers	Acid mine drainage, geothermal sulfurous sites (e.g. Yellowstone) Soda lakes, peridotite-hosted hydrothermal systems (e.g. Lost City vent)
Water activity	0.611, halophilic bacteria and archaea	0.605, xerophilic fungi such as *Xeromyces bisporus*	Deep-sea brines, soda lakes, evaporate ponds, dry soils and rocks, food with high solute content
Low O_2 content	Any anaerobic bacteria or archaea such as methanogens	Some fungi (chytrids), loricifera?; high tolerance to low O_2 also in some turtles and the Crucian carp	Anoxic marine or lacustrine sediments, intestinal organs, early Earth environments
Pressure	High diversity of bacteria and archaeans in deep ocean trenches including piezophiles and barophiles	High diversity of invertebrates and fishes in ocean trenches	Deep oceanic trenches such as the 11,100 m deep Marianas Trench
Radiation	At least 10,000–11,000 Gy (gamma radiation), *Deinococcus radiodurans*	Cockroach *Blatella germanica* can survive exposure to radiation above 1000 Gy	No natural source of radiation on Earth at levels tolerated *by Deinococcus radiodurans*
Chemical extremes	Cd 2–5 mM, bacteria and archaea; Ni 2.5 mM, Co 20 mM, Zn 12 mM, Cd 2.5 mM, *Ralstonia eutrophus*	Algae, e.g. *Euglena* and *Chlorella* can grow in Cd, Zn, and Co at mM concentrations	Submarine hydrothermal vent fluids and sulfides; some high-metal containing lakes

4.3.1.1 Psychrophily

Low temperature environments are common on Earth. They include microenvironments within ice, cold terrestrial environments, the deep sea, and the troposphere. Ice environments include snow, glaciers, frozen lakes, sea ice, and permafrost. Examples of cold terrestrial environments include the Dry Valleys of Antarctica and Arctic polar deserts. Temperatures in the oceanic abysses are about 2 °C at a maximum hydrostatic pressure of 110 MPa (1100 bars or 10,660 m) in the Mariana Trench (Yayanos 1995). Temperatures in the troposphere can drop to −50 °C, but life in cloud droplets, claimed to independently grow and reproduce (Sattler et al. 2001), may only extend to temperatures slightly lower than 0 °C. There are a number of reports in recent years that have demonstrated that some microbes can metabolize, albeit slowly, at temperatures in the range from −15 °C to −20 °C (Junge et al. 2001, 2004, 2006; Rivkina et al. 2000; Mykytczuk et al. 2013). These reports also include observations about active photosynthesis in Antarctic cryptoendolithic organisms at temperatures as low as −20 °C (Friedmann and Sun 2005). These organisms include bacteria, lichens (a symbiotic association of algae and fungi), and fungi (yeasts). For example, the yeast *Rhodotorula glutinis* and the lichen *Umbilicaria* have been shown to grow in that temperature range (De Maayer et al. 2014). Metabolic activity in glacial ice has been inferred from anomalous concentrations of gases at temperatures as low as −40 °C (Campen et al. 2003; Sowers 2001). Further, there is some evidence for the transfer of electrons and enzyme activity in a marine psychrophilic bacterium at a temperature of −80 °C (Junge et al. 2006). Enzyme activity has been measured to occur in a mixture of methanol, ethylene glycol, and water at temperatures as low as −100 °C (Bragger et al. 2000). Price and Sowers (2004) argued that there is no evidence of a minimum temperature for metabolism (growth, maintenance, or survival), though the metabolic turnover of the entire carbon of a cell would take 100 million years at −40 °C. Active metabolism becomes much more challenging at very low temperatures, which is also due to the decrease in available water (see Sect. 4.3.3 about water activity). An especially intriguing example of metabolic activity in ice was reported by Rohde and Price (2007), who found evidence of microorganisms in glacial ice metabolizing dissolved small molecules such as CO_2, CO, O_2, N_2, and CH_4 through diffusion into the ice lattice. They detected proteins associated with high concentrations of microbial organisms and determined via modeling the minimum amount of metabolism that has to occur to ensure survival of the organism as 1900 molecules per cell per year. This metabolic rate is about six orders of magnitude lower than that necessary for exponential growth and mobility. Nevertheless, Rohde and Price (2007) claim that an adequate supply of dissolved gases would meet the needs of this very slow metabolism rate for at least 10,000 years. A more recent estimate of the limit for life at a low temperature was provided by Clarke et al. (2013) who predicted that the limit for growth is approximately −26 °C for microbes and −50 °C for multicellular organisms with advanced abilities for thermoregulation. There is no principle lower limit for survival, as being in the frozen state can be equivalent to being dormant (Schulze-Makuch et al. 2017). That is clearly demonstrated by the survival of some species of tardigrades which extends down to nearly absolute zero (Jönsson et al. 2008).

As the fluidity of membranes decreases with decreasing temperatures, organisms can maintain fluidity by increasing the ratio of unsaturated to saturated fatty acids (Rothschild and Macinelli 2001). Organisms adapt to temperatures below freezing by deploying mechanisms for either freezing avoidance or freezing tolerance. Freezing avoidance is often utilized by insects. For example, the super cooling point of the larvae of *Dendroides canadensis* decreases from a summer maximum of −2 °C to −7 °C to a winter minimum of −20 °C or lower via the removal of highly active hemolymph and gut fluid ice nucleators along with the inhibition of residual nucleators by antifreeze protein (Olsen and Duman 1997). Freeze tolerance usually involves cryobiosis, a state in which all of the water within the cells of an organism freezes and the organism becomes dormant (no measurable metabolic activity) until warmer conditions reappear. The longer an organism remains in cryobiosis, the longer it takes for the organism to come out of that state (Keilin 1959). Another strategy often used in mammals is hibernation, which only involves a reduction of metabolic activity [see Islam and Schulze-Makuch (2007) for more details].

4.3.1.2 Thermophily

Microbes have been identified with temperature tolerances above 100 °C in various environments such as submarine hydrothermal vents, the subterranean deep biosphere, and terrestrial hot springs (Marion et al. 2003). Microbes have been isolated from terrestrial hot springs that can tolerate temperatures up to 103 °C (Stetter 1999). The highest temperature tolerances are found in microbes from marine hydrothermal vents and the subterranean deep biosphere; high pressures prevent these waters from boiling at 100 °C, the normal boiling point of water at 1 atm (10^5 Pa, 1.01 bar) pressure. Kashefi and Lovley (2003) reported culturing microorganisms in the laboratory at a temperature of 121 °C, and an even higher survival range of at least 130 °C (Table 4.1). Hyperthermophilic organisms have an amazing versatility of biochemical adaptations to high temperatures. Nevertheless, the molecular building blocks disintegrate at temperatures above 150 °C (e.g., DNA in water), which is likely the uppermost limit for life as we know it (White 1984; Madigan and Oren 1999). At the time of this writing the current record holder is *Methanopyrus kandleri*, which still can grow at 122 °C (Takai et al. 2008). In principle, alternative biochemical building blocks could be used to achieve even higher temperatures, but the energetic costs for doing so would become increasingly prohibitive (Schulze-Makuch et al. 2017). Hyperthermophilic organisms (microorganisms that grow best at temperatures above 80 °C) are either bacteria or archaea. Most eukaryotes have an upper temperature range of ~50–60 °C, vascular plants of about 48 °C, and fish of about 40 °C, possibly a function of the low solubility of oxygen at high temperatures (Madigan and Marrs 1997; Nealson 1997; Rothschild and Macinelli 2001).

Hyperthermophilic microbes have fundamental changes in their macromolecular structures which compensate for the increased mobility and fluidity at high temperature (Charlier and Droogmans 2005). Protein structures are stabilized at high temperature through amino acid substitutions and the increased use of disulfide bonds (Beeby et al. 2005). Heat stable, ether-linked lipids are universal in hyperthermophilic archaea and in some hyperthermophilic bacteria, and all hyperthermophiles studied have a reverse gyrase that positively supercoils DNA—the DNA of all other organisms being negatively supercoiled (Baross et al. 2007).

Supercoiling with cationic proteins increases the thermal stability of DNA (Daniel et al. 2004b). Proteins of thermophilic organisms have evolved to cope with high temperatures by increasing ion-pair content, forming higher-order oligomers, and by utilizing monovalent and divalent salts enhancing the stability of nucleic acids (Rothschild and Macinelli 2001). Also, external factors such as high pressure appears to increase the thermal stability near the known upper temperatures of life (Holden and Baross 1995). Microbes are not the only thermophilic organisms. The most thermophilic metazoan is the Pompeii worm capable of withstanding temperatures as high as 105 °C (Chevaldonne et al. 1992). The worm uses both physical means (e.g., circulation of cold water over its exterior) and biochemical means to achieve this feat. One biochemical adaptation is the use of the most thermostable fibrillar collagen known (collagens are extracellular proteins with triple-helical domains). While the interstitial collagen of coastal polychaete worms (e.g., *Arenicola marina*) is denatured at 28 °C, the collagen of the Pompeii worm remains stable at 45 °C (Gaill et al. 1995). Its collagen is adapted to the hydrothermal vent environment by its stability at higher temperatures, high pressures, and associated enzymatic processes, which appear to be optimized under anoxic conditions. Thermophilically-inclined terrestrial organisms also include the desert snail *Sphicterochila boisseri*, which can survive in the desert at temperatures of up to 50 °C (Schmidt-Nielsen et al. 1971) and the desert ant *Proformica longiseta*, which forages on sand surfaces when temperatures reach as high as 60 °C (Wehner 1989).

4.3.2 Extreme pH-Conditions

Acidity is typically quantified using the pH scale:

$$\mathrm{pH} = -\log_{10}(a_{\mathrm{H}+}) \tag{4.1}$$

where $a_{\mathrm{H}+}$ is the hydrogen ion activity. Bacteria, archaea, fungi, and algae have all been demonstrated to tolerate pH values ≤ 1.0 (Bachofen 1986; Schleper et al. 1995; Huber and Stetter 1998; Schrenk et al. 1998; Edwards et al. 2000; Robbins et al. 2000). For example, the red alga, *Cyanidium caldarium* can live at a pH ~0 (Gross 1999) and *Ferroplasma acidarmanus*, which was isolated from acid mine drainage, can grow at a pH of 0 (Edwards et al. 2000). Natural highly acidic environments include sulfur-rich hydrothermal pools such as those in Yellowstone National Park (USA). The archaea *Picrophilus oshimae* and *P. torridus* can grow at a pH of -0.06 (Schleper et al. 1995). *P. oshimae* is a polyextremophile tolerating a pH of 0 and temperatures up to 65 °C (Fütterer et al. 2004). There are fewer studies of high alkalinities (pH $>$ 10) than of extreme acidities (pH $<$ 1.0), probably because high alkalinity environments (e.g., soda lakes) are rarer in nature. The challenge for organisms living at a high pH is that they must either pump protons to maintain an intracellular pH close to neutrality or use an alternative genetic structure different from standard DNA. Also, the hydroxide anion, arising from water at high pH, is a powerful nucleophile and destroys many molecules which are essential parts in metabolic reactions (Baross et al. 2007). Nevertheless, there are reports of organisms tolerating pH values >11, and even as high as 13.2 (Bachofen 1986; Duckworth et al. 1996; Tiago et al. 2004; Roadcap et al. 2006). A diversity of organisms, from bacteria to cyanobacteria and rotifers have been reported to live at pH 10.5 (Martins et al. 2001) and microbial communities have been reported to live at pH 12.9 in the soda lakes of Maqarin, Jordan (Pedersen et al. 2004). Kelley et al. (2005) reported about a marine environment (Lost City hydrothermal field) with a pH of up to 11 and temperatures of up to 90 °C that was teeming with microorganisms. Preiss et al. (2015) also found microbes growing at alkaline hydrothermal vents and at continental serpentinization sites. At one spring a beta-proteobacterium with the proposed name S*erpentinomonas* was identified, which grew fastest at a pH of 11 (Robinson and Mikucki 2016). The Vinegar eelworm (*Turbatrix aceti*) is probably the most pH-tolerant multicellular organism. It can grow at a pH range of 3.5–9, and tolerate a range of 1.6–11 (Wharton 2002).

Low pH-values are challenging for organisms, because a surplus of hydrogen ions can enter the cell and disrupt its internal biochemistry. For example, proteins denature under very acidic conditions. On the other hand, a high pH is challenging for organisms due to a lack of hydrogen ions which are needed for the proton pumps in the cell. Most organisms living at moderately extreme pH-values maintain a near neutral pH in their cytoplasm. In general, acidophiles evolved efficient proton pumps and low proton permeabilities, and alkaliphiles evolved an efficient proton transport system (Rothschild 2007). Active mechanisms to achieve this adaptation may also involve secondary proton uptake mediated by membrane-associated antiporters (Rothschild and Macinelli 2001). Other mechanisms include specially adapted bioenergetics and permeability properties, surface charges, high internal buffer capacity, overexpression of proton export enzymes and unique transporters for acidophilic organisms (Pick 1999), and negatively charged cell-wall polymers in alkaliphilic organisms (Krulwich et al. 1998).

4.3.3 Low Availability of Water

Life processes on Earth are mediated in water as a solvent. The availability of water is referred to as water activity and is defined as the vapor pressure of water divided by that of pure water at the same temperature. Pure water has a water activity of exactly one. A higher water activity in the medium tends to support more microorganisms. The lowest water activity at which halophilic bacteria and archaea can metabolize, confirmed from measurements in the laboratory and a natural environment, is 0.611 (Stevenson et al. 2015a). However, that value appears to be higher in chaotropic solutions as no microbial reproduction could be demonstrated in Dead Sea brine dominated by $CaCl_2$ and $MgCl_2$ (Special Regions Science Analysis Group 2007), which has a water activity of about 0.67 (Kis-Papo et al. 2003). The record holder as of this writing for metabolism at low water activity are xerophilic fungi that can still metabolize in a saturated sugar solution at a water activity of 0.605 (Williams and Hallsworth 2009). Values for liquid water activity in equilibrium with ice decrease with temperature. Ice has a water activity of 0.82 at −20 °C, and a water activity of 0.67 at −40 °C, respectively. Thus, the lack of available water at low temperatures will greatly affect the survival ability of psychrophilic microorganisms (Sect. 4.3.1.1).

In a dormant state, without biological activity occurring, some organisms can survive a 99% loss of water and about 0 water activity (Mazur 1980). A drop in water activity or desiccation causes DNA to break, lipids to undergo permanent phase changes, and proteins to crystallize, denature, and undergo condensation reactions (Potts 1994). One strategy of organisms to survive in an environment with low water activity is to match their internal water activity with that of the surrounding environment. Microbes can accomplish this feat by accumulating compatible solutes such as potassium ions or low molecular weight soluble organic compounds that do not interfere with the normal physiological functions of the cell (Mueller et al. 2005). Some microbes employ a different adaptation strategy and go dormant, for example forming spores or cysts, while others such as the bacterium *Deinococcus radiodurans* employ mechanisms to repair their DNA (Cox and Battista 2005).

A very powerful adaptation to desiccation is anhydrobiosis, which allows organisms to survive up to 99% of water loss. It is defined as the state of an organism in which there are no visible signs of life and metabolic activity is unmeasurably low or non-existent. Anhydrobiosis is exhibited by many forms of life ranging from unicellular organisms such as yeast, bacteria, protozoans, and fungal spores, to nematodes, rotifers, tardigrades, springtails, cysts of primitive crustaceans, and resurrection plants. Anhydrobiosis is commonly identified by morphological changes such as the coiling of the body observed in tardigrades. Trehalose, the disaccharide of glucose, plays a major role in protecting anhydrobiotic unicellular organisms, invertebrates, and resurrection plants, while other disaccharides, mainly sucrose, are present in seeds and pollen of higher plants (Crowe et al. 1992). In addition to trehalose, heat shock proteins and the so-called LEA (late embryogenesis abundant) proteins appear to be involved in conveying protection to organisms in the anhydrobiotic state. A summary of anhydrobiosis and its biochemical changes is provided in Islam and Schulze-Makuch (2007).

If salt concentrations become too high, organisms have to cope with a lack of water availability and high osmotic stress. The higher the salinity, the more energy an organism has to expend to maintain a favorable osmotic balance (Marion and Schulze-Makuch 2006). Measures of salinity include salt %, molality, or the thermodynamic activity of water. Seawater has a water activity of 0.98, but most bacteria and fungi can tolerate much higher salinities than sea water. Organisms best adapted to high salt conditions are usually archaea. However, cyanobacteria and the green alga *Dunaliella salina* are also able to withstand periods in saturated sodium chloride solutions (Rothschild and Macinelli 2001). Microbes tend to respond to increases in osmolarity by accumulating osmotica (compounds used to attain an osmotic balance) in their cytosol to protect them from cytoplasmic dehydration and desiccation (Yancey et al. 1982). Halobacteriaceae use K^+ as their osmoticum (Larsen 1967), while glycine betaine is the most effective osmoticum in most other prokaryotes (Le Rudulier and Boillard 1983). However, there is evidence that environments that have $MgCl_2$ at concentrations greater than 2.3 M may inhibit life due to the ability of $MgCl_2$ to denature biological macromolecules (Baross et al. 2007). Brine shrimps (*Artemia*) are the best known multicellular organisms to withstand high salt concentrations in their natural habitat of terminal inland salt lakes and coastal salterns. Adaptation to high salt conditions can involve a cessation of metabolism as observed in the nematode *Steinernema feltia* (Chen et al. 2005), and is referred to as osmobiosis. Encysted embryos of the primitive crustacean *Artemia franciscana* appear to be most resistant to high salt concentrations. *Artemia's* survival abilities are enhanced by a protective cyst wall, the accumulation of trehalose and glycerol, the protein artemin, and the involvement of heat-stress proteins, which act as molecular chaperons.

4.3.4 Low Oxygen Availability

It could be argued that all aerobic organisms are extremophiles, because oxygen forms reactive oxygen species which cause oxidative damage to nucleic acids, proteins, and lipids (Rothschild and Macinelli 2001). In fact, with the advent of the cyanobacteria and the production of oxygen more than 2.5 billion years ago, oxygen concentration increased in Earth's atmosphere sharply (Kasting 2006). This must have resulted in the largest mass extinction in Earth's history, as oxygen and oxygen species are potent toxins for the then anaerobic organisms of the earlier Earth. However, given that Earth's atmosphere has been oxygen-rich for at least 1.5 billion years (albeit not at levels as high as those at the start of the Cambrian), and that aerobic respiration is the metabolic pathway of highest energy yield and the one to which Earth's fauna has fully adapted, it is informative to explore how aerobic organisms on Earth have adapted to a lack or temporal unavailability of oxygen.

Oxygen has become essential for any life based on aerobic respiration. Anaerobic energy sources can supply the requisite ATP to maintain cellular functions for a limited time only, before substrate depletion, energy shortfall, or end-product poisoning threaten the survival of the organism (Islam and Schulze-Makuch 2007). Tolerance to anoxia is on the order of minutes for many vertebrates, because of the immediate dependence of the heart, central nervous system, and brain on a continuous supply of oxygen. A particularly effective way for an organism to withstand oxygen deficiency is the state of anoxybiosis, during which metabolism comes to a standstill. For example, brine shrimps have been stored in anoxic conditions for 4 years and then hatched successfully without using any of their food reserves, such as trehalose, glycogen, or glycerol (Wharton 2002). Research indicates that the protein p26 and Gp4G molecules are associated with biochemical changes during the anoxybiotic state (Clegg 2001).

An especially remarkable example of adaptation to a lack of oxygen is exhibited in the Crucian carp (*Carassius carassius*). It is known that some turtles can survive without oxygen for a long period of time by inactivity at low temperatures. The carp, however, remains active during anoxic conditions. When water temperatures are dropping in its habitat in Northern Europe, the carp begins to store vast amounts of glycogen in the brain, which enables the carp to make the switch to anaerobic metabolism. Stored glycogen in the body of the carp is then broken down into glucose and ethanol providing sufficient energy to survive (Vornanen and Paajanen 2006). Its survival is very temperature dependent though. The Crucian carp can survive anoxia for several months at 0 °C during the winter when the small lakes and ponds in which it thrives become oxygen depleted, but it can survive only a few days without oxygen at room temperatures (Nilsson and Lutz 2004).

A special case in this regard is the phylum Loricifera, consisting of small animals with a protective outer case dwelling in marine sediments. Danovaro et al. (2010) suggested that their complete life cycle takes place in an anoxic environment, though it has generally been assumed that all animals require oxygen (Canfield et al. 2007).

4.3.5 Pressure

Pressure affects living processes by determining the liquidity ranges of water, and by forcing changes in volume. Pressure compresses the packing of lipids, resulting in decreased membrane fluidity (Bartlett and Bidle 1999), and alters gene expression (Nakasone et al. 1998). Most chemical reactions produce increases in volume, and pressure counteracts this increase (Rothschild and Macinelli 2001).

High pressures occur in both deep-earth and deep-sea environments, but there are some fundamental differences between these two habitats. In the deep sea, hydrostatic pressures on organisms are strictly a function of depth. For example, 1 atm = 1.01325; bars = 0.101325; MPa = 9.816 m (Yayanos 1995). Deep in the terrestrial subsurface, the confining pressure could be atmospheric with organisms growing in air pockets or, in contrast, very high as in brine pockets, where the organisms may be subjected to both hydrostatic and lithostatic pressures (Marion and Schulze-Makuch 2006). Another significant difference between the two habitats is that temperatures underground increase with depth, but deep-sea environments decrease in temperature with increasing depth. Microorganisms have been recovered from the Mariana Trench in the Pacific (10,660 m depth) where pressures reach 110 MPa (Abe et al. 1999; Kato et al. 1998; Yayanos 1995) and temperatures are about 2 °C. Two bacteria similar to *Moritella* and *Shewanella* are apparently obligately barophilic; they grow optimally at 70 MPa and do not grow at all below 50 MPa (Kato et al. 1998). There are some archaea associated with deep-sea hydrothermal vents that can survive at pressures as high as 890 bars (Pledger et al. 1994). The high pressure at hydrothermal vents appears to have a compensatory effect that allows stabilization of molecules at high temperatures (Marion and Schulze-Makuch 2006). Piezophilic bacteria have been obtained from the Marianas Trench, which can grow at 70–80 MPa, but not below 50 MPa (Bartlett 2002). Using a diamond anvil cell in the laboratory, it was demonstrated that *Shewanella* *oneidensis* and *Escherichia coli* strains remain physiologically and metabolically active at pressures of 68–1680 MPa for up to 30 h (Sharma et al. 2002). At pressures of 1200–1600 MPa, living bacteria resided in fluid inclusions in Ice VI crystals (Fig. 7.2) and continued to be viable when pressure returned to 1 bar—1% of the total population survived (Sharma et al. 2002). The rate of change in pressure may be significant in that experiment as organisms are extremely sensitive to sudden pressure changes. Nevertheless, it demonstrates that pressure may not be much of an impediment for some forms of life.

Organisms may be more sensitive to low pressures, since low pressure leads to rapid desiccation. It is difficult to envision how an organism would hold on to its environmental substrate on a planet with no or only a thin atmosphere. It has been shown that for terrestrial organisms under Martian surface conditions, the low pressure is at least as much of an environmental obstacle as UV irradiation (Diaz and Schulze-Makuch 2006). Nevertheless, when Schuerger and Nicholson (2016) exposed different microorganisms to pressures existing on the surface of Mars (about 0.6 kPa), many of them survived, and not just species adapted to low pressures.

4.3.6 Radiation

The types of radiation that have a detrimental effect on life include high-energy electromagnetic radiation (ultraviolet, x-ray, and gamma radiation) and high-energy alpha and beta particles. Ultraviolet radiation is the most abundant form of damaging radiation on the Earth's surface and probably also the most common natural mutagen. Ultraviolet light can also kill cells as a result of dimerization of thymidine residues in the DNA, preventing replication (Baross et al. 2007). Ionizing radiation, including x-rays, gamma rays, alpha and beta particles, and also part of the UV spectrum is detrimental to cells because it causes multiple breaks in the double-stranded DNA (Obe et al. 2001). Direct damage to DNA or indirect damage due to the production of reactive oxygen species creates modified bases and single and double-strand breaks (Rothschild and Macinelli 2001). While the major source of UV irradiation is the Sun, sources of ionizing radiation include cosmic rays, x-rays, and radioactive decay. Most organisms have mechanisms for protection from damaging radiation such as radiation-absorbing pigments and DNA repair mechanisms, but resistance to one form of radiation does not necessarily convey protection from other forms (Marion and Schulze-Makuch 2006).

Deinococcus radiodurans is the most well-known organism for radiation resistance. This resistance is thought to have evolved initially as an adaptation to desiccation (Mattimore and Battista 1996). The mechanism for conveying this resistance is thought to be attributable to the ability of *D. radiodurans* to quickly repair DNA damage with high fidelity (Bachofen 1986; Kushner 1981; Smith 1982; Zahradka et al. 2006). However, hyperthermophilic archaeans recovered from a submarine hydrothermal vent environment were found to also withstand radiation levels of up to 8000 Gy (Jolivet et al. 2004). There are also some multicellular organisms that are quite resistant. For example, the tardigrade in its desiccation-resistant "tun" state can survive high levels of UV radiation (Horikawa et al. 2013); and the cockroach *Blatella germanica* can withstand ionizing radiation levels of up to 1000 Gy (Schulze-Makuch and Seckbach 2013). Microbial mechanisms to limit radiation damage include photorepair, excision repair, and homologous recombinational repair, avoidance behavior, and the production of antioxidants and detoxifying enzymes (Petit and Sancar 1999; Rothschild 1999; Smith 2004; Yasui and McCready 1998). Mechanisms to protect organisms from UV radiation also include the development of iron-enriched silica crusts (Phoenix et al. 2001), habitation beneath protective layers of soil or water (Pierson et al. 1987; Wynn-Williams and Edwards 2000), specialized organic pigments such as carotenoids and scytonemin (Wynn-Williams et al. 2002), self-shading (Smith 1982), and shielding by organic compounds derived from dead cells (Marchant et al. 1991).

4.3.7 Low Nutrient Availability and Chemical Extremes

Life on Earth requires or interacts with 70 elements (Wackett et al. 2004), and 16 of these are considered essential for life. These essential elements are carbon, oxygen, hydrogen, nitrogen, potassium, calcium, phosphorus, magnesium, sulfur, iron, chlorine, copper, manganese, zinc, molybdenum, and boron (Marion and Schulze-Makuch 2006). The first nine elements (carbon to sulfur) are macronutrients because they are needed in large amounts (on a percentage basis), while the last seven elements are micronutrients (iron to boron) that are needed in trace amounts, in a ppm range (Raven and Johnson 1999). Any one of these nutrients may limit life. The macronutrients are likely the more limiting nutrients in any environment because they are needed in larger amounts than micronutrients. Nitrogen, phosphorus, and potassium are usually the most critical elements in this regard, hence their inclusion in fertilizers for agricultural purposes.

There are many toxic elements that can limit life including mercury (Hg), lead (Pb), cadmium (Cd), and arsenic (As). On Earth, high toxic element concentrations are often associated with high acidities because strong acids are very effective in dissolving primary minerals and releasing heavy metals into the environment (Fernandez-Remolar et al. 2003; Lopez-Archilla et al. 2001; Robbins et al. 2000). Thus, organisms that tolerate strong acidity usually also tolerate high levels of heavy metals. However, several of the toxic elements are also essential nutrients (Marion et al. 2003). There is often a delicate balance between adequate nutrients and excess toxins. Interestingly, some of the elements that are generally toxic, such as arsenic and selenium, are used by some bacteria in their metabolic pathways as a source of energy (Stolz and Oremland 1999).

4.4 Questions Unanswered by the History of Life on Earth

While a great deal of insight can be harvested by studying historical evolution and the adaptation of Earth's organisms to extreme environments, there are some questions critical to anticipating the nature and history of life on other worlds that the history of the one life we know cannot answer.

Though life arose relatively quickly on Earth, it isn't certain that it would inevitably arise as quickly, even under the same conditions as on Earth. All we know for certain is that it *can* arise endogenously, or take hold following importation, within a half billion years of the appearance of a suitable environment.

There are no theoretical reasons or empirical observations compelling us to think that the biochemistry of life on Earth, at the molecular genetic or metabolic level, is based on the same or even similar biomolecules as on other worlds. While it could be that some or all of the nucleotides, sugars, amino acids, and other metabolic intermediates that have evolved with life on Earth are so favored by physicochemical and thermodynamic selection that the same molecular configurations will inevitably evolve elsewhere, this by no means is apparent. In fact, the existence of alternative amino acids in meteorites that are not found commonly in living organisms (Cronin et al. 1988), argues against such a premise. Life on Earth shows us one form of molecular architecture that is possible, but does not rule out alternatives.

The duration of evolutionary episodes cannot be predicted from a sample size of one. While it may have taken 2 billion years for eukaryotes to evolve from prokaryotes, and a billion years for macrofauna to evolve from microscopic multicellular forms, were these lengths of time necessary? The one sample we know cannot tell us whether these qualitative changes in the nature of life inherently require such long periods of time, or simply took that long for reasons that were either fortuitous, or peculiar to conditions on Earth.

The details of form and function that a different history of life would take cannot be predicted. Will taxa with calcified exteriors, such as the shells of bivalve mollusks, inevitably arise in marine environments? Will photosensitive receptors such as eyes inevitably arise if light is available? Will metabolic mechanisms for detoxifying, then utilizing oxygen for energy production, inevitably arise in the presence of oxygen? The fact that systems such as these have evolved independently under appropriate circumstances on Earth suggests the possibility that they would or at least could do so elsewhere (Bains and Schulze-Makuch 2017), but such an extrapolation is not warranted by the observation of a single case.

We have pointed out numerous examples of astonishing adaptations to extreme environments. Indeed, there is virtually no habitat anywhere near the surface of the planet, however extreme the temperature, pressure, dryness, salinity, or pH, that hasn't been found to harbor life. Thus, the one case of life in the Universe provided by the example on Earth gives very little evidence of limiting conditions that have been reached.

We are left with the conclusion that life *could* arise quickly on other worlds, *possibly* using similar molecular and metabolic machinery to our own; that it *might* take as long to undergo revolutionary changes in form, size and complexity as it did on our planet, that it *conceivably* could follow macroevolutionary trajectories that mimic the history of life on Earth, and that it *might not* be limited by any physical or chemical conditions, short of those that lead to molecular destruction. That any of these things is true cannot be ascertained from the one limiting case we have before us. It is tempting, however, to speculate that given the number of other worlds in the Universe, a fraction of them could be like Earth, and that a fraction of those could have harbored life with a history similar to our own. For the vast majority of other worlds, which are dissimilar to Earth, other forms of life are clearly possible, as subsequent chapters argue. Whether similar to life as we know it on Earth or not, life as we do know it provides a suite of expectations about the nature of life throughout the Universe, and there is no reason to doubt the validity of these general expectations.

4.5 Chapter Summary

Life arose relatively quickly on Earth, suggesting that it could do so elsewhere under appropriate conditions. Without defining (since we don't know) precisely what those conditions are, the vast number of worlds in the Universe makes it virtually certain that conditions suitable for life exist on a large number of them. Therefore, life is almost surely highly redundant throughout the Universe, well adapted to its environment, and as diverse as the habitats that it occupies—as the one example from Earth demonstrates. Given the harshness and volatility of conditions at most planetary and satellite surfaces, more stable environments are to be found beneath their surfaces where the constancy of conditions favors simplicity, and stabilizing selection favors stasis of form and function. The majority of the biomass across the Universe is likely, therefore, to be microscopic, simple, subsurface, and similar to its early forms. However, the range of physical and chemical conditions over which those forms of life could survive is great. Where the physical history of the planetary body has been complex, or where the physical environment is relatively heterogeneous with a variety of boundary conditions, life can be expected to have evolved into more complex forms, especially if the planet hosting that life has stayed habitable long enough. This would be particularly true on worlds where environments are extremely variable. In proportion to the total number of worlds harboring life, however, these are likely to constitute a distinct minority.