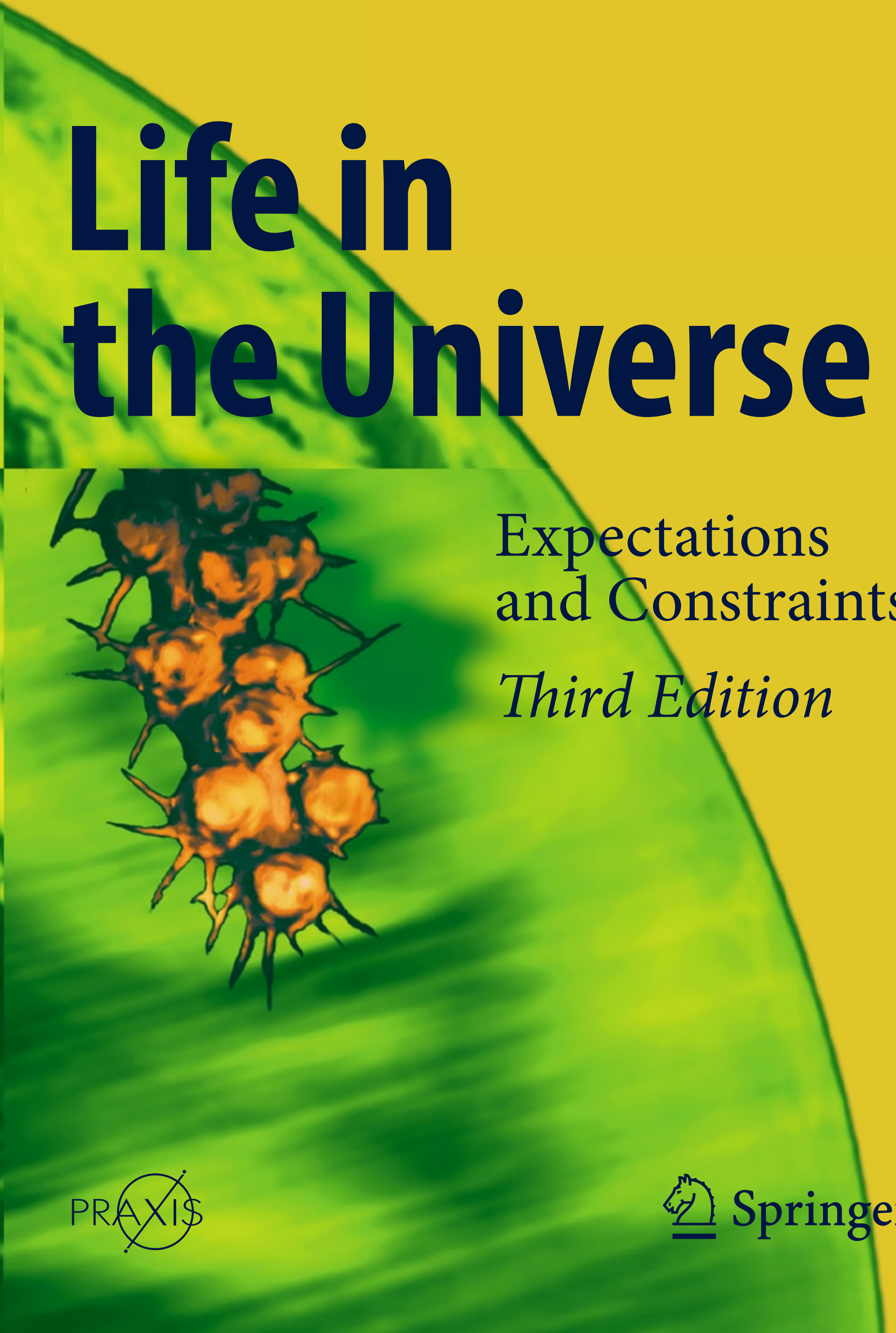
Dirk Schulze-Makuch
Louis N. Irwin

Life in the Universe

Expectations and Constraints

Third Edition



PRAXIS

Springer

Life in the Universe

Springer Praxis Books

Astronomy and Planetary Sciences

More information about this series at http://www.springer.com/series/4175

Dirk Schulze-Makuch • Louis N. Irwin

Life in the Universe

Expectations and Constraints

Third Edition

Springer

PRAXIS

Dirk Schulze-Makuch
Center for Astronomy and Astrophysics
Technical University Berlin
Berlin, Germany

Louis N. Irwin
University of Texas at El Paso
El Paso, TX, USA

Springer Praxis Books
ISSN 2366-0082 ISSN 2366-0090 (electronic)
Astronomy and Planetary Sciences
ISBN 978-3-319-97657-0 ISBN 978-3-319-97658-7 (eBook)
https://doi.org/10.1007/978-3-319-97658-7

Library of Congress Control Number: 2018955969

1st edition: © Springer-Verlag Berlin Heidelberg 2004
2nd edition: © Springer-Verlag Berlin Heidelberg 2008
© Springer Nature Switzerland AG 2018
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

As humans in the early years of civilization sailed beyond the isles of the eastern Mediterranean to learn about a larger planet, so the human species, still in its technological youth, now searches for life on other worlds.

To a species of life on a water-rich planet in
an otherwise unremarkable solar system at
an outlying part of the galaxy in an
unexceptional part of the Universe, just
beginning to explore the world beyond the
home on which it began to evolve about
4 billion years ago.

Preface

While grounded in the hard sciences of physics, chemistry, geology, and astronomy, as well as well-accepted principles in the life sciences, astrobiology remains the most speculative of all the sciences because it assumes a reality that has not been demonstrated conclusively: the presence of life on other planetary bodies. Until the discovery of a living organism from another world is confirmed, this part of astrobiology will continue to be a science in search of a factual base. We wrote the first edition of this book in 2004 to bring scientific rigor to that search.

However, astrobiology also includes investigations into the origin of life on Earth, life in extreme environments, and the future and fate of life on our planet, as a means of gaining insight into how life might emerge and play out wherever it exists. Those aspects of the field are backed up by robust (hence much less speculative) findings and increasingly insightful ideas. The second edition in 2008 was focused especially on those new developments.

In both editions, we set forth reasons for expecting that extraterrestrial life, if it were similar to life as we know it, is highly likely to be carbon based, using water as a solvent, and sunlight as its primary source of energy. This assumption has broad general agreement within the scientific community—so much so, that the search for alien life has driven the field to focus its enthusiasm, perhaps excessively, on worlds that look like our own. There is little doubt and growing evidence that such worlds do exist, but in solar systems other than our own.

Most exoplanets discovered to date, and all other planets and moons in our Solar System, are not at all like Earth. Therefore, the broader challenge for astrobiology is to look for life beyond where we are most likely to find—or at least recognize—it, and seek it wherever and in whatever form it might exist. This compels us to consider planetary environments where either (1) carbon-based organisms could exist in localized or global aqueous habitats considered extreme by terran standards or (2) exotic forms of life could be found in habitats unable to support life as we know it, but not incapable of supporting organisms with the generic properties of living systems.

The goal of the first two editions has thus been retained in this one: To define as precisely as possible what constitutes a living entity, to define the limiting parameters of its chemical composition, solvent requirements, and possible sources of energy, then systematically consider the possibilities for its distribution throughout the Universe in forms both known and unknown to us. In this third edition, we have retained the expanded consideration of both the origin and fate of living systems. We have also updated content and references extensively throughout to cover the vast number of experimental studies, discoveries, and conceptual advances that have occurred over the last decade.

As before, our definition of life (Chap. 2) sidesteps the abstract concept of life through time, in favor of a utilitarian view of what constitutes a living organism at a given point in time. Recent advances in various forms of "artificial life," from the reconstitution of living cells by insertion of genetic elements synthesized *de novo* ("synthetic life"), the tendency toward virtual and augmented reality ("virtual life"), and robotics ("mechanical life"), have compelled us to incorporate these developments into our discussion of what it means to be alive.

Our treatment of the origin of life (Chap. 3) has been updated with more recent research and references, including a more detailed discussion of the nature and implications of the genetic code.

The core chapters of the prior editions on energy (Chap. 5), chemical building blocks (Chap. 6), solvents (Chap. 7), habitats (Chap. 8), and signatures (Chap. 9) have been retained but significantly updated and more extensively documented.

The Viking Mission and alleged biomarkers in Martian meteorites are again described in detail (Chap. 10), as they still constitute the most serious claims to date of evidence for the existence of life on another world. The chapter now contains an updated repertoire of life detection instrumentation as well.

Whereas the expectations of and constraints on the possible distribution of life on other worlds in our Solar System were scattered among different sections in the previous editions, we have now concentrated the discussion into one place (Chap. 11), with detailed examination of the prospects for life in the light of newly obtained data from Mars, Ceres, Europa, Enceladus, Titan, and the Pluto-Charon system. We are even urging in this edition a closer look at the astrobiological potential of our own Moon.

The number of verified exoplanets has increased by an order of magnitude since the second edition, justifying an entirely new and complete discussion of exoplanets, exomoons, their means of discovery, and their taxonomy (Chap. 12).

The fate and future of life—a subject of concern but largely ignored in the astrobiological literature until recently—is again treated in a fact-based way, drawing on established evolutionary principles from the history of life on Earth (Chap. 14).

The search for extraterrestrial intelligence, which increasingly seems likely to include the search for extraterrestrial artifacts, has been described in a section of its own (Chap. 15). The controversy over the wisdom of trying to contact alien forms of life is described, and our thoughts on the so-called Fermi Paradox are offered in this chapter as well.

We conclude with a discussion of how the exploration of space can be optimized through the combination of both manned and robotic strategies (Chap. 16). We provide a detailed plan for establishing settlements on Mars, but consider the value of Venus, the Moon, Ceres, and the icy satellites of the outer Solar System as worthy targets for exploration also. Finally, we introduce the contentious topic of planetary protection which raises serious questions about missions that will land machines and/or humans on other worlds in the future.

Dirk Schulze-Makuch thanks his family, particularly his wife, Joanna, and his children, for their patience and understanding of his preoccupation with science even more than usual. He also thanks all his students and colleagues for their willingness to bounce around ideas.

Louis N. Irwin likewise appreciates the encouragement of his wife, Carol, and ongoing feedback from family members, friends, and former students who have commented kindly on the value of this work.

Berlin, Germany Dirk Schulze-Makuch
El Paso, TX, USA Louis N. Irwin

Contents

1 **Introduction** . . . 1

2 **Definition of Life** . . . 7
  2.1 Problems with Common Assumptions About the Nature of Life . . . 8
  2.2 Historical Views on the Definition of Life . . . 12
  2.3 Modern Definitions of Life . . . 13
  2.4 Thermodynamic Criteria . . . 14
  2.5 Reproducibility Criteria . . . 15
  2.6 Evolutionary Criteria . . . 16
  2.7 Life as a Global Entity . . . 17
  2.8 Artificial Life . . . 17
    2.8.1 Synthetic Life ("Wetware") . . . 18
    2.8.2 Virtual Life ("Software") . . . 18
    2.8.3 Mechanical Life ("Hardware") . . . 18
  2.9 A Utilitarian and Generic View . . . 19
    2.9.1 Self-Sustaining and Bounded Environments in Thermodynamic Disequilibrium . . . 19
    2.9.2 Transformation of Energy to Maintain a Low Entropy State, Adjust to Change, and Perform Work . . . 21
    2.9.3 Information Encoding and Transmission . . . 23
  2.10 Implications for the Remote Detection of Life . . . 24
  2.11 Chapter Summary . . . 25

3 **Origin of Life** . . . 27
  3.1 Scenarios for the Origin of Life . . . 27
    3.1.1 A Lukewarm Marine Origin of Life . . . 29
    3.1.2 A Benthic Thermophilic Origin of Life . . . 30
    3.1.3 An Ice Water Origin of Life . . . 31
    3.1.4 A Comprehensive Scenario for the Origin of Life . . . 32

3.2 Minimum Requirements for the Origin of Life 35
  3.2.1 Insights into the Origin of the First Cellular Membranes 36
  3.2.2 Insights into the Origin of the First Metabolism 37
  3.2.3 Insights into the Origin of the First Replication Mechanism 39
3.3 Other Insights and Inferences 41
  3.3.1 Size 41
  3.3.2 Environmental Conditions 42
  3.3.3 Medium 43
  3.3.4 Minerals and Substrates 44
  3.3.5 Implications for the Possibility of Life on Other Worlds 45
3.4 Synthetic Life 46
  3.4.1 The Standard Genetic Code 46
  3.4.2 The Flexibility of the Code and Non-canonical Amino Acids 48
  3.4.3 Bottom-Up and Top-Down Approaches to the Origin of Life 49
3.5 Chapter Summary 50

4 Lessons from the History of Life on Earth 51
4.1 A Brief History of Life on Earth 51
4.2 Lessons from the History of Life on Earth 53
  4.2.1 Life Arises Relatively Quickly Under Conducive Conditions 53
  4.2.2 Life Tends to Stay Small and Simple 54
  4.2.3 Most Organisms Remain Relatively Unchanged over Their Evolutionary Life Spans 55
  4.2.4 Evolution Is Accelerated by Environmental Changes . . . 57
  4.2.5 Complexity Inevitably Increases but as the Exception Rather than the Rule 58
  4.2.6 Biodiversity Is Promoted by Heterogeneous Environments 59
  4.2.7 Individuals Are Fragile, But Life Is Hardy 60
4.3 Adaptations to Extreme Environments 61
  4.3.1 Temperature Extremes 61
  4.3.2 Extreme pH-Conditions 65
  4.3.3 Low Availability of Water 66
  4.3.4 Low Oxygen Availability 68
  4.3.5 Pressure 69
  4.3.6 Radiation 70
  4.3.7 Low Nutrient Availability and Chemical Extremes . . . 71

4.4 Questions Unanswered by the History of Life on Earth 72
4.5 Chapter Summary 73

5 Energy Sources and Life 75
5.1 Life as We Know It 75
5.1.1 Oxidation-Reduction Chemistry as an Energy Source for Life 76
5.1.2 Light as an Energy Source for Life 79
5.2 Life as We Don't Know It 79
5.2.1 Electromagnetic Waves (Other than Visible Light) . . . 80
5.2.2 Thermal Energy 81
5.2.3 Kinetic Energy 84
5.2.4 Osmotic or Ionic Gradients 85
5.2.5 Magnetic Fields 88
5.2.6 Gravitational Forces 92
5.2.7 Tectonic Stress 93
5.2.8 Pressure Gradients 94
5.2.9 Spin Configurations 94
5.2.10 Radioactivity 96
5.3 The Question of Entropy, Uniformity, and Origin 97
5.4 Survey of Energy Sources in our Solar System 98
5.5 Chapter Summary 100

6 Building Blocks of Life 101
6.1 The Uniqueness of Carbon 101
6.2 An Alien Carbon Biochemistry? 105
6.3 Alternatives to Carbon as the Universal Building Block of Life 106
6.4 The Possibility of Silicon-Based Life 107
6.4.1 Physical Properties of Silicon 107
6.4.2 Role of Silicon for Life on Earth 110
6.4.3 Polymeric Chemistry of Silicon 112
6.4.4 Environmental Conditions for the Possibility of Silicon-Based Life 114
6.5 Other Alternatives as Building Blocks of Life 119
6.6 Chapter Summary 121

7 Life and the Need for a Solvent 123
7.1 Water as the Universal Solvent for Life on Earth 125
7.2 Inorganic Polar Solvents as Alternatives to Water 130
7.2.1 Ammonia 131
7.2.2 Hydrocyanic Acid 134
7.2.3 Hydrofluoric Acid 136
7.2.4 Hydrogen Sulfide, Sulfur Dioxide and Sulfuric Acid . . . 136
7.2.5 Hydrogen Peroxide 137
7.2.6 Hydrazine 139

7.3 Other Solvents as Alternatives to Water 139
  7.3.1 Inorganic Non-Polar Compounds 139
  7.3.2 Organic Polar Compounds 140
  7.3.3 Organic Non-Polar Compounds 141
  7.3.4 Supercritical Fluids: Carbon Dioxide 143
7.4 Quantitative Assessment of Solvent Candidates 144
7.5 Some Additional Thoughts 146
7.6 Chapter Summary 147

8 Habitats of Life 149
8.1 Life on the Surface 149
8.2 Life Beneath the Surface 150
8.3 Life in the Atmosphere 153
8.4 Life in the Space Environment 157
8.5 Cosmic Biogeography 159
8.6 Chapter Summary 163

9 Signatures of Life 165
9.1 Searching for Signatures of Life 166
  9.1.1 Atmospheric Composition of a Planetary Body 166
  9.1.2 Geological Evidence 168
  9.1.3 Fossil and Isotopic Evidence 169
  9.1.4 Macromolecules and Chirality 170
  9.1.5 Presence of Metabolic By-Products and End-Products 171
  9.1.6 Production of Biogenic Heat 172
  9.1.7 Signatures of More Advanced Life 173
9.2 Geoindicators of Life 173
  9.2.1 Presence of an Atmosphere or Ice Shield 174
  9.2.2 Internal Differentiation 175
  9.2.3 Polymeric Chemistry 175
  9.2.4 Energy Source 176
  9.2.5 Liquid Medium 178
9.3 Geoindicators for Life in our Solar System 179
9.4 Chapter Summary 181

10 Life Detection: Past and Present 183
10.1 The Viking Mission 183
  10.1.1 The Viking Landers 183
  10.1.2 Mission Preparation 185
  10.1.3 Mission Results 186
  10.1.4 Interpretation of Mission Results 188
10.2 Martian Meteorites and Evidence for Ancient Life 192
  10.2.1 The Claim of Fossilized Life in Martian Meteorite ALH84001 193
  10.2.2 A Cold Reception by the Scientific Community 195

10.2.3 Signs of Ancient Life in Another Martian Meteorite? 199
10.2.4 Conclusions Concerning Biomarkers in Martian Meteorites 199
10.3 Current Life Detection Instrumentation 200
10.4 Chapter Summary 202

11 Astrobiological Potential of Planetary Bodies Within the Solar System 203
11.1 Terrestrial Planets 203
11.1.1 Mercury 203
11.1.2 Venus 204
11.1.3 The Earth-Moon System 205
11.1.4 Mars 207
11.1.5 Ceres 209
11.2 Outer Solar System 210
11.2.1 Gas and Ice Giants 210
11.2.2 Io 212
11.2.3 Europa 212
11.2.4 Ganymede and Callisto 215
11.2.5 Enceladus 215
11.2.6 Titan 217
11.2.7 Triton 220
11.2.8 Dwarf Planets of the Outer Solar System 221
11.3 Small Bodies 223
11.3.1 Asteroids 223
11.3.2 Comets 224
11.4 Metrics for the Plausibility of Life in the Solar System 224
11.5 Chapter Summary 227

12 Exoplanets and Exomoons 229
12.1 Methods for Detecting Planetary Bodies Outside the Solar System 229
12.1.1 Radial Velocity 230
12.1.2 Transit Photometry 230
12.1.3 Astrometry 230
12.2 Detection Limits, or What We Know Now and What We Need to Learn 231
12.2.1 The One-Pixel Problem 231
12.2.2 Technologies Becoming Available in the Near Future 232
12.2.3 An Outlook of What Might Be Possible in the Next Decades 233
12.3 Taxonomy of Exoplanets 236
12.3.1 General Categorization of Exoplanets 236
12.3.2 Categorization of Earth-size Exoplanets 237

12.4 Examples of Some Intriguing Exoplanets 239
12.4.1 Proxima b 240
12.4.2 Kepler 452b 240
12.4.3 Kapteyn b 241
12.5 Extrasolar Moons 241
12.6 Habitability Metrics 242
12.6.1 Habitat Suitability Index 242
12.6.2 Earth Similarity Index (ESI) 243
12.6.3 Planetary Habitability Index (PHI) 244
12.6.4 Biological Complexity Index (BCI) 245
12.7 Chapter Summary 245

13 Ideas of Exotic Forms of Life 247
13.1 Life Based on Spin Configurations 247
13.2 Fred Hoyle's Black Cloud and Similar Ideas 249
13.3 Life on a Neutron Star 250
13.4 Life on a Brown Dwarf 250
13.5 Life on a Rogue Planet 251
13.6 Some Other Ideas on Forms of Exotic Life 252
13.7 Chapter Summary 252

14 The Future and Fate of Living Systems 255
14.1 Evolutionary Alternatives 255
14.1.1 Plateau 256
14.1.2 Collapse 257
14.1.3 Transition 258
14.2 Evolution of Intelligence 259
14.3 The Rise of Technological Competence and Its Fate 260
14.4 Application to the Possibility of Life on Other Worlds 262
14.5 Chapter Summary 263

15 The Search for Extraterrestrial Intelligent Life 265
15.1 Traditional SETI 265
15.2 Optical SETI 267
15.3 The Search for Extraterrestrial Artifacts (SETA) 268
15.4 False Positives, or How Do We Know a Signal Is Coming from ETI? 268
15.5 The Wow! Signal 269
15.6 Messaging to Extraterrestrial Intelligence (METI) 270
15.7 The Fermi Paradox 272
15.8 Chapter Summary 273

16 Optimizing Space Exploration 275
16.1 Mars 276
16.1.1 Robotic Missions to Mars 277
16.1.2 Human Missions to Mars 278
16.1.3 A Vision for Mars Exploration 279

16.2 The Moon 281
16.3 Venus 282
16.4 Other Exploration Targets 282
16.5 Planetary Protection Considerations 285
16.6 Chapter Summary 286

References 287

Index 333

Chapter 1
Introduction

Astrobiology studies the origin, evolution, distribution, and fate of life throughout the Universe, with no direct evidence that life exists anywhere in the Universe other than on Earth. But there are compelling reasons to assume that life exists pervasively throughout the cosmos. That assumption derives from empirical observations on the nature of the Universe and the natural laws that govern it, from analysis of the history and properties of the one case of life that we do know, and on a logical integration of fact and theory. The science of astrobiology is thus as strong, if not as revolutionary, as Darwin's theory of evolution before fossil humans were found to prove our animal origins; as firm, if not as precise, as the astronomical predictions that Neptune must exist before it was detected; and, in our view, as certain as the conclusion that the world was a sphere before Magellan sailed around it.

This book sets forth the argument that life occurs numerous times throughout the Universe. It further makes predictions about some likely characteristics of that life in most cases, explores the limits of diversity that might be found in forms of life on other worlds, and attempts to strain conventional thinking about the fundamental nature of living systems. At the same time, this book asks for no suspension of belief in or extension beyond the laws of chemistry and physics as we understand them now. It does not make predictions of a specific nature, where no basis for specificity exists. We offer our assessment about probabilities, but base those assessments on facts open to verification and a line of reasoning that invites the critical assessment of our fellow scientists. Like Darwin's arguments about the mechanism of evolution, we know that our vision of life in the Universe will change through subsequent insights and observations. As the predictable discovery of Neptune gave no indication of the altogether unpredictable planetoid Pluto yet to be discovered, we realize that surprises not anticipated by us will emerge when the reality of life on other worlds is confirmed. And finally, like Magellan, we fully expect some of our calculations about life in the Universe to miss their mark. But we do believe we have sketched a vision of cosmic biology that is tenable and therefore of predictive value in designing missions to search for and detect the life that is surely out there.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_1

The argument that life exists on other worlds is straightforward and simple. It begins with the definition of life as a self-perpetuating organization of complex chemistry that uses free energy to maintain disequilibrium with its environment. It continues with the observation that wherever chemical heterogeneity and a source of free energy are found, the capability for life exists. It notes that our own planet, which had an abundance of both energy and complex chemistry from its earliest age, gave rise to life (or was able to sustain life introduced from another place) almost as soon as the heavy bombardment of the planet receded. It assumes that the laws of chemistry and physics act in the same way throughout the Universe. It points to the vast numbers of stars in the Universe, and the possibility that the total number of planets will be even larger. The argument concludes: even if the probability on any given planetary body is low that an appropriate combination of energy and chemistry is available to enable the development of sufficient complexity for life to emerge, the enormous number of planetary bodies that must exist in the visible part of the Universe alone strongly suggests that life has arisen redundantly. Since the physical laws of nature pertain equally, we assume, over the entire extent of the Universe, wherever those laws allow the formation of life to occur, it will. Hence, life must be widespread as well as high in numerical frequency.

We should emphasize that we do not argue that life is common. The complexities of form and function that constitute the living state are highly improbable in a statistical sense, and probably arise only under a restricted set of circumstances. The second purpose of this treatise is to critically examine what those circumstances are. To the extent that our Solar System is exemplary (we cannot yet say that it is typical), the conditions that exist on Earth, where a large range of microscopic to macroscopic forms of life have diversified, appear to be very rare. We think, therefore, that the extent of biodiversity that we see on Earth is very seldom seen anywhere else. Among the organisms that thrive on our planet, however, are many microscopic forms that potentially could occupy a number of other sites in our Solar System, as carbon polymer and water-based life essentially as we know it. In addition, however, there are circumstances substantially unlike those with which we are familiar on Earth, under which life in forms unknown to us could arise and exist, in theory. Those circumstances are found within our Solar System, and are likely to be found beyond it in abundance. The circumstances that would allow for the origin and persistence of life are not unlimited, however. Much of this work is devoted to assessing what those limits might be.

Our analysis begins with four facets that are essential to life: energy, chemistry, solvent, and habitat. To provide the reader with an overview at the outset, a brief abstract of our analysis of the possibilities and limitations of each of these facets is given below.

Energy in many forms is abundant throughout the Universe. Electromagnetic energy at wavelengths visible to humans is a prominent product of the fusion reaction in all the visible stars. On Earth, a photosynthetic mechanism has evolved to capture that energy and transform it into chemical bonds with an efficiency that is difficult for any other form of energy to match. Where light is available, it thus provides an efficient, isothermal source of energy well matched to the needs of living systems. However, both inorganic and organic chemical bonds contain energy that is harvested by all non-photoautotrophs on Earth, so far as we are aware. As long as these sources of chemical energy remain available, either from cycling or a reserve not yet exhausted, they likewise provide an efficient basis for bioenergetics. Other forms of energy could in principle substitute to varying degrees light and chemical energy that support the forms of life with which we are familiar. Our theoretical calculations suggest that osmotic and ionic gradients, and the kinetic motion of convection currents, provide plausible alternatives. Thermal gradients are among the most widely available sources of energy flow, but the gradients are easily degraded and are thermodynamically inefficient. Magnetospheric energy, gravity, pressure, and other exotic forms of energy likewise could conceivably be harvested by living systems, but the amount of energy that they provide within our Solar System generally does not appear to make them competitive with light, chemistry, osmotic and ionic gradients, or convective currents as likely sources of free energy for the support of living systems.

All life as we know it resides in complex polymeric chemistry based on a covalently bonded carbon backbone. A systematic examination of carbon chemistry provides an impressive list of advantages that carbon has over any other compound, not only in forming the vast array of molecules required for complex systems, but by enabling the right combination of stability and flexibility for molecular transformations that underlie the dynamic complexity of life. In aqueous systems at temperatures common on Earth, carbon is so far superior to any other atom as a polymeric unit, that it has come to be the only basis for the structure of biomolecules essential for all basic metabolic processes. Silicon is the one other atom with properties similar to carbon, and its potential usefulness in living systems is shown by the fact that it too is an important constituent of many living cells. In most cases, it serves a rather passive structural role, as in the cell walls of plants, and the exoskeleton of diatoms and some other organisms. These examples could represent residual functions from a time in the history of life when silicon played a more central role, only to be replaced more effectively by carbon at a later stage. A detailed look at the chemistry of polymeric silicon reveals that it conceivably could have the combination of stability and lability exhibited by carbon, but under very different conditions, both at temperatures much higher and much lower, and in the presence of solvents other than water. Carbon bonds with oxygen and nitrogen to form parts of the polymeric chains of biomolecules, and mixed atomic backbones involving other compounds are a possibility. They already occur in some biomolecules of terrestrial life such as DNA but may be much more common elsewhere. A few other atoms have the capacity for the formation of covalent polymers, but they either occur in such low abundance, or have such inferior characteristics, that they seem a highly unlikely basis for an alternative living system.

Life as we know it requires a liquid medium. It can survive periods of dehydration, but appears to need a liquid for its dynamic transactions. We examine in some detail why life is much less likely to reside exclusively in a gaseous or solid medium. We also consider whether water is the only suitable solvent for a living system. Water does have some striking advantages, particularly with respect to carbon-based molecular interactions. At temperatures and pressures prevailing on Earth, and beneath the surfaces of numerous other planets and planetoids in our Solar System, water can exist in liquid form, and thereby provide the potential reservoir that carbon-based molecules need for their vast array of interactions. On the other hand, most of the Solar System, like most of the Universe, is very unlike Earth. For smaller planetary bodies distant from a star, temperatures are much colder than on Earth. This probably represents the vast majority of planetary bodies. At those sites, water cannot be liquid (absent a source of internal heat), but methane, ammonia, ethane, methyl alcohol, and related organic compounds might be. In principle, many of them are compatible with carbon-based polymeric chemistry, and thus should be considered as possible solvents capable of supporting life. On very large planetary bodies, or on those that are tectonically active or close to a central star, very high temperatures may prevail. Under those circumstances other compounds can exist in the liquid form. In some of those cases, silicon-based polymers appear more feasible. There is no question that water is an excellent solvent for living systems, but under conditions where it cannot exist as a liquid, a few other solvents can exist in that state, and could support living processes.

Habitats can be divided grossly into those that are constant and those that are variable. The surface of a planetary body under rare circumstances as on Earth may be quite variable, providing the opportunity for fragmentation of the environment into a great variety of subhabitats with specific but periodically changing characteristics. These variations and their changes over time represent selective pressures that generate through the evolutionary process a great variety of living forms. When, as on Earth, energy and appropriate chemical environments are abundant, life can assume macrobiotic forms of great complexity. The cost of this biodiversity and complexity, however, is frequent extinction, as changing conditions in variable habitats often render biological features that were advantageous under one set of circumstances, suddenly disadvantageous under others. The cycle of speciation followed by extinction generates the biodiversity and great deviation from primordial forms of life with which we are familiar. We must remind ourselves, however, that the primordial forms are still with us as well. They are sequestered primarily below the surface, where the constancy of conditions places a premium on stabilizing selection, or the retention of successful living processes that have experienced no pressure for change for a long time. Only now are we beginning to appreciate the vastness of this subterranean, unseen biosphere; but it probably represents the most favorable and most common habitat for life throughout the Universe as a whole. The consequences of subsurface life are two-fold: First, the minute size of the living spaces available restrict the size of living organisms to microscopic dimensions. Secondly, the long-term stability of the environment places a premium on stabilizing selection, which likely maintains life in an ancestral form. In those rare planetary bodies that have gaseous atmospheres, life may exist as well, but it likely is microscopic in that sphere also, though is much more likely to have deviated significantly from its ancestral form.

In the chapters that follow, we elaborate on these arguments in greater detail and discuss how life can be detected. We focus on previous attempts such as the Viking life-detection experiments and the controversy about possible fossilized life in the Martian meteorite ALH84001. The lessons from the past inform us on how we would attempt to detect life today and how reliable various geological and biological signatures of life are. We continue with an in-depth discussion of the astrobiological potential of the planetary bodies in our Solar System and selected planets outside of our Solar System. The discovery of over 3800 confirmed exoplanets to date has been one of the most exciting developments in the last decade and revealed some promising candidate planets that might be hosting life. On some of these planets life might even have advanced to a high degree of complexity, perhaps even to intelligent and technologically advanced organisms like us. However, no evidence so far exists for this conjecture, which is further discussed in the chapter on the search for extraterrestrial intelligence. Finally, we introduce our ideas to optimize space exploration, which involves both robotic and human missions.

Our vision of astrobiology is driven by our sense that life, like all of nature, is knowable in principle wherever it exists. We are strongly persuaded by scientific evidence and logic that it exists in profusion on other worlds. We believe it is likely that it exists elsewhere in our Solar System in at least a few instances, though probably in microbial form. We hope to see the day when this belief is confirmed by direct evidence. If we do not, we nonetheless are confident that a perceptive form of life somewhere, someday, will encounter life on a world other than its own. How similar or how different those forms of life will be is one of the most enticing questions of our age. This book is meant to explore the range of answers that might be offered.

Chapter 2
Definition of Life

The definition of life is a long-standing debate with no broadly accepted scientific consensus (Kolb 2007). The underlying problem in defining life is twofold. The first is that living systems use compounds that are abundant in the surrounding environment, and processes that are not intrinsically different from reactions that occur abiologically. There does not appear to exist a single characteristic property that is both intrinsic and unique to life. Rather we have to argue that life meets certain standards, or that it qualifies by the collective presence of a certain set of characteristics.

The second problem in defining life is linguistic. Life, grammatically, is a noun, which therefore calls for definition in terms of other nouns. Yet life is much more like a verb than a noun—more a process than an entity. Defining life is analogous to defining wind. Wind is air in motion, a state of being. The molecules of wind are the same as those of air, but their dynamic state is their defining characteristic.

Margulis and Sagan (1995), in their book whose title, *What is Life?*, honors the legacy of Schrödinger's (1944) earlier attempt to modernize the definition of life, resort to a multifaceted poetic characterization rather than a concise definition:

> Life is planetary exuberance, a solar phenomenon. It is the astronomically local transmutation of Earth's air, water, and sun into cells. It is an intricate pattern of growth and death, dispatch and retrenchment, transformation and decay. Life is the single expanding organization connected through Darwinian time to the first bacteria and through Vernadskian space to all citizens of the biosphere. Life . . . is a whirling nexus of growing, fusing, and dying beings. It is matter gone wild, capable of choosing its own direction in order to indefinitely forestall the inevitable moment of thermodynamic equilibrium—death.

While there is much truth and an admirable degree of esthetic appeal to the characterization of life embodied in the passage above, such a definition is too florid and imprecise to guide the search for life on other worlds. A pithier and more objective definition is needed, to make the recognition of the living state as unambiguous as possible whenever and wherever it may be encountered in the Universe.

Life can certainly be defined through a collection of properties, but the search for life wherever it occurs depends ultimately on an ability to recognize individual

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_2

entities with the properties of being alive, as distinct from their non-living surroundings. And, while life is like the wind in its pervasive distribution, it differs from wind in having finite boundaries. The challenge of defining life in the context of a cosmic biology, therefore, is to specify the defining characteristics of a dynamic process that occurs within discrete boundaries that set the process apart from its environment. While our everyday experience with life on Earth makes the distinction between the living and non-living for the most part unambiguous, a consideration of life on other worlds, where conditions may be different, and/or where life may have evolved from its inorganic precedents to a lesser degree, requires us to formulate a more formal and objective definition for life.

An added challenge to defining life is the rise of artificial intelligence in conjunction with the accelerating development of autonomous robots. Any comprehensive, generic definition of life must now incorporate the prospect of mechanical, or fabricated, forms of life that satisfy all the requirements of naturally evolved organisms. Henceforth in this book, we will occasionally be distinguishing between ***biological*** life, which consists of naturally evolved, self-replicating metabolic systems, and ***mechanical*** life, which is composed of self-propagating, fabricated structures that function through mechanical rather than metabolic manipulations. To the extent that either form meets the generic criteria for a “living entity,” they will be considered to be a form of life.

2.1 Problems with Common Assumptions About the Nature of Life

Historically, and still in popular usage, life has tended to be defined in terms of its dynamic features. Thus, the Random House dictionary (1987) defines life as a collection of characteristics and processes, such as metabolism, growth, reproduction and adaptation to the environment. This form of definition is generally followed by some biology textbooks (Campbell 1996; Raven and Johnson 1999), while others—tacitly admitting the difficulty of defining life—refer instead to its “unifying principles” (Curtis and Barnes 1986) or its “emergent properties” (Purves et al. 1998). The weakness in defining life as a collection of attributes is that any given attribute fails the exclusivity test—examples of entities that clearly are not alive can be found that exhibit one or more of these traits. The following examples will illustrate the point.

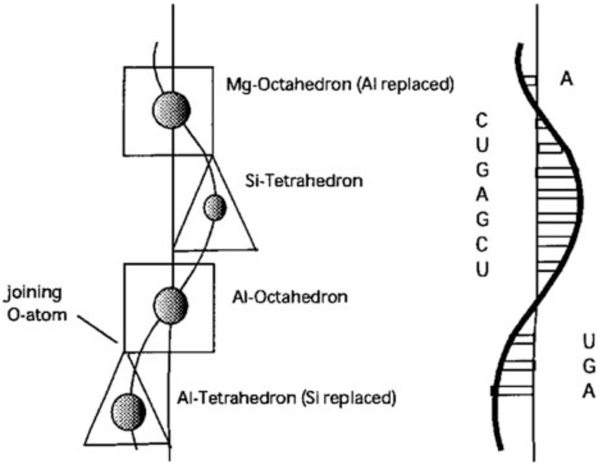
The consumption or transformation of energy is a central point in all traditional definitions of life. Energy metabolism in its most basic form consists of a collection of chemical reactions that yield energy by electron transfer. The central metabolism most often exploits the electrophilicity of carbon doubly bonded to nitrogen ($C=N$) or oxygen ($C=O$) or the electrophilicity of phosphorous doubly bonded to oxygen ($P=O$) (NRC 2007). Living organisms obtain energy from light by photosynthesis or by other electron transfer reactions associated with chemolithotrophy (extracting energy from non-biological molecules) or chemoorganotrophy (extracting energy from molecules synthesized by other living organisms). However, inorganic analogs of these processes are well known. Electrons can be lifted into higher energy levels by various forms of energy, such as heat or ultraviolet radiation. When the electrons fall back to their lower energy levels, the energy difference between these levels is released. When ions absorb energy and release it again in the form of light, this is known as luminescence. Phosphorescence and fluorescence are special cases of luminescence and describe the phenomenon of continued emission of light after irradiation is terminated. Common minerals with the property of luminescence include gypsum and calcite. Another possibility for storing energy in the form of heat is seen in clay minerals with interlayer sites. The interlayer water and OH-groups are suitable for storing heat energy due to their high heat capacity. Thus, nonliving substances can transfer external energy into energy-yielding transitions that under some circumstances can be maintained as potential energy, just as living organisms do (Schulze-Makuch 2002).

Another traditionally regarded property of life is growth. But just as cells grow in favorable environments with nutrients available, inorganic crystals can grow so long as ion sources and favorable surroundings are provided. Furthermore, just as the development of living organisms follows a regulated trajectory, so does the process of local surface reversibility regulate the course of silicate or metal oxide crystals that grow in aqueous solutions (Cairns-Smith 1982).

A third traditionally defined property of life is reproduction, which entails both multiplication of form and transmission of information. The visible consequence of reproduction in living organisms is the multiplication of individuals into offspring of like form and function. Mineral crystals do not reproduce in a biological sense, but when they reach a certain size they break apart along their cleavage planes. This is clearly a form of multiplication. The consequence of biological reproduction is also the transmission of information. Biological information is stored in the one-dimensional form of a linear code (DNA, RNA), that, at the functional level, is translated into the three-dimensional structure of proteins. Prior to multiplication, the one-dimensional genetic code is copied, and complete sets of the code are transmitted to each of the two daughter cells that originate from binary fission. An analogous process occurs in minerals, where information may be stored in the two-dimensional lattice of a crystal plane. If a mineral has a strong preference for cleaving across the direction of growth and in the plane in which the information is held (Cairns-Smith 1982), the information can be reproduced. Note that in contrast to living cells, information can be stored in multiple layers in a crystal. However, copying this type of three-dimensional information would be very challenging. Another important question is whether the stored information has actual meaning. We know that DNA has meaning because of the expressed segments of DNA (exons) that are read by the molecular machinery of the cell and translated into functional molecules. However, there is no obvious way of assessing whether any ion patterns in minerals have a meaning in terms of functional utility (Fig. 2.1).

Another hallmark of life is said to be adaptation to the environment. Short term adaptation can be achieved by an individual organism in a transient and reversible

Fig. 2.1 Spiral structure of (**a**) amesite-2H_2 and (**b**) RNA, two-dimensional and schematic. As the nucleotide sequence in RNA codes for information, so could in principle the cation order in amesite



way, such as enzyme induction, in which cells produce enzymes specific to a particular substrate only when that substrate is present. Other examples include the adjustment of microbial size to nutrient conditions, or the movement of a cell to a nutrient source or away from toxic substances. However, clay minerals can also adapt to their surroundings. The most common adaptation for clays with interlayer sites is their response to water availability. If the outside environment is dry, water is released from the interlayer to surroundings; if the outside environment is wet, water is adsorbed into the interlayer.

Long term adaptation is achieved by collective organisms through time by the essentially irreversible mechanism of natural selection. An analogous process occurs in clays, which over time can accommodate different ions at ion exchange sites that will affect the lattice structure during clay mineral formation. Also, where chemical weathering is prevalent, as in the tropics, clays can develop an outer, weather-resistant layer of aluminum oxide or silicate. Changes in mineralogy can also occur depending on the ion source and change in the environment. Dehydration reactions involving water molecules or hydroxyl ions lead in general to a structural change. In extreme cases, one clay mineral can transform into another. For example, gibbsite can transform into boehmite because of an alternation of dry and wet periods (Boulange et al. 1997).

As indicated above, good analogies can be found for each of the traditional criteria for living systems in the inorganic world, specifically for clay minerals and metal oxides. A summary is provided in Table 2.1. While we are not aware of any specific minerals that display all four characteristics, there is no reason conceptually to assume that a mineral fitting the sum of all the criteria cannot exist.

At the biological edge of the interface between the living and non-living world, viruses present a similar case in reverse. By the traditional definition viruses are not considered living entities because they cannot reproduce and grow by themselves and do not metabolize. Nevertheless, they possess a genetic code that enables them to reproduce and direct a limited amount of metabolism inside another living cell.

Table 2.1 Properties of biological organisms, comparing organic mechanisms with inorganic parallel

Property	Basic requirement	Organic mechanism	Inorganic parallel
Metabolism	Energy obtained from electron transfer	Various types of biochemical pathways including photosynthesis Energy storage as ATP or GTP	Energy uptake via heat or light, elevation of electrons to higher energy bands, where they absorb energy at specific frequencies. Energy storage by luminescence or at interlayers of clay minerals due to high heat capacity of water and OH-groups
Growth	Increase in size of single unit	Cell growth as long as nutrients are available and environmental conditions are favorable until reproduction occurs. Self-organizing as development proceeds, errors corrected by enzymes	Crystal growth as long as favorable environmental conditions prevail and a sufficient ion source is present. Local surface reversibility makes it possible to correct certain mistakes during the growth of silicate or metal oxide crystals from aqueous solution
Reproduction	Multiplication of information	Various mechanisms of reproduction (most commonly by binary fission). The genetic code is duplicated and preserved through successive generations.	Crystals commonly cleave during growth. If a mineral has a strong preference for cleaving across the direction of growth and in the plane in which the information is held, new “individuals” may form and each of the new “individuals” may expose the information on the new surface (Cairns-Smith 1982)
Adaptation to environment	Compensation for, reaction to, and development of new abilities in response to various types of environmental changes	Genetic adaptation over time through mutations, transposition of genetic material, transformation, conjugation, and transduction. Homeostatic adaptation within individuals: movement to nutrient source, cellular shrinkage or formation of spores in nutrient-poor environment, enzyme induction	Adaptation through changes in mineralogy due to changes in ion and environmental source (including transformation from one (clay) mineral to another in extreme cases). Adaptation within individuals: Adaptation to outside environment via water release or adsorption in interlayer (clay minerals), development of outer, weathering-resistant layers such as Al_2O_3 or silicate layers in tropical soils

Modified from Schulze-Makuch (2002)

They thus fulfill the traditional criteria only part of the time and under special circumstances. At best, by the traditional definition, they could be considered to be “reversibly alive.” Since viruses presumably evolved from bacteria that clearly are alive, do they represent a case in which a living entity has been transformed to a non-living state by natural selection? Alternatively, viruses might have been the evolutionary precursors of the three domains of life (Archaea, Bacteria, and Eukarya), as suggested by Forterre (2006), or they might have evolved from a plasmid that evaded a cell (Erdmann et al. 2017). Either way, where would we draw the line between life and non-life? If we accept the proposition that viruses are not alive, how would we consider parasitic organisms or bacterial spores? Parasites cannot grow by themselves either and spores remain in dormant stages with no dynamic biological attributes until they become active under favorable environmental conditions. Thus, if we consider parasites or bacterial spores to be alive, the logical consequence would be to consider viruses alive as well.

In summary, the traditional definition of life on close examination fails to distinguish consistently between the living and the non-living world (Table 2.1). Since biology and mineralogy have both been characterized extensively on Earth, the distinction between the two is not difficult to make on our home planet. Notwithstanding the semantic ambiguities, we generally know life (or non-life) when we see it. But the definition matters more when we leave the familiar context of Earth, and encounter more exotic conditions and environments where dynamic phenomena may exist with which we are unfamiliar. In that context, semantic ambiguities become conceptual stumbling blocks and observational obstructions. For that reason, we need a definition of life that more effectively and precisely captures the fundamental essence of the phenomenon for which we are searching.

2.2 Historical Views on the Definition of Life

From the earliest days of mechanistic thinking (the Greek philosophers, in the Western tradition), but particularly with the abandonment of vitalism in the nineteenth century, life increasingly became recognized as a state or process, in which otherwise non-living matter and energy acquire dynamic properties that generate a state of disequilibrium distinct from its non-living surroundings.

With scientific acceptance of the theory of evolution came the derivative notion of the origin of life from non-living precursors. As formal theories about this process were advanced (Haldane 1954; Oparin 1938), and evidence consistent with a plausible mechanism were reported (Miller 1953), the need became apparent for a definition that distinguishes between living and non-living states, since that boundary (at least in concept) had to be crossed at some point in the past. As the concepts of thermodynamics became formalized in the nineteenth century, the low entropy state of living entities came to be appreciated as one of their most fundamental characteristics. Because of the need to distinguish between a collection of molecules that is alive and a collection of the same molecules that is not, researchers have increasingly focused on the highly ordered state of the components of living systems, and of the energy flow required to maintain that order (Schrödinger 1944; Brillouin 1956; Morowitz 1968; Neubauer 2012; Chaisson 2013). The thermodynamic improbability of the living state has become one of its defining features.

The ability of living systems to reproduce themselves has always been one of the clearest distinctions between living and non-living systems. Up until the twentieth century, self-organization and reproduction remained as mysterious as they were distinctive. However, advances in genetics (Morgan 1915), biochemistry (Chargaff et al. 1951; Lwoff 1962), and molecular biology (Crick 1968; Watson and Crick 1953) elucidated the chemical basis of information storage and transfer in living systems, the extremely high information content of macromolecules, and the role they play in perpetuating the form and function of specific living systems. The encoding and transmission of information that enables self-assembly and reproduction have become collectively another indispensable feature of all contemporary definitions of life.

Two additional concepts have had a strong influence on modern definitions of life. The first is the contention that an essential criterion for life is the capacity for evolutionary change over extended periods of time. The second is that life is a global, as opposed to a local phenomenon.

2.3 Modern Definitions of Life

The modern attempt to redefine life in a more sophisticated way dates from Schrödinger's (1944) introduction of physical aspects such as energy states and entropy as the essence of what it means to be alive. A similar theme was developed later by Szent-Györgyi (1972). Moreno et al. (1990) focused on the autonomous nature of life by describing it as an autonomous system capable of self-reproduction and evolution. Maturana and Varela (1981) also emphasized the process of self-maintenance, or "autopoiesis", as the fundamental essence of life. Lwoff (1962) and Banathy (1998) emphasized the information processing properties of life, while Dyson (1999) in a similar vein defined life as a material system that can acquire, store, process, and use information to organize its activities.

Some authors have striven for a comprehensive definition that focuses more on the continuity of life through time. Monod (1971), for instance, combined the ecological, thermodynamic, and bioinformatic properties of life, but added the ambiguous concept of teleonomy (apparent purposefulness in living organisms). Another effort at comprehensiveness is the proposal of Koshland (2002) for seven pillars of life, which he designated as a program, improvisation, compartmentalization, energy, regeneration, adaptability, and seclusion.

Since all living forms operate within the constraints of environmental conditions and limitations, some authors have tried to incorporate an ecological perspective into their definitions. For instance, Feinberg and Shapiro (1980) proposed to redefine life as the fundamental activity of a biosphere—a highly ordered system of matter and energy characterized by complex cycles that maintain or gradually increase the order of the system through an exchange of energy with its environment.

These admirable attempts to include an ecological perspective illustrate one of the problems that has bedeviled historical attempts to define life: namely, the confusion between life as a process with a history, and the features of matter that constitute the state of being alive at a given moment in time. While almost all definitions of life refer in some way to reproduction as an essential feature, at a given moment an organism may be alive but not reproducing. Similarly, some authors insist that the capacity for Darwinian evolution is an essential feature of life, yet any single organism during its lifetime is clearly not undergoing evolution. Mix (2015) acknowledged the difficulty of finding a precise definition of life and suggested the use of provisional definitions such as *Darwin lif*e (exhibiting evolution by natural selection), *Haldane life* (exhibiting metabolism and maintenance), and *Woese life* (possessing small subunit rRNA). However, as previously outlined, clay minerals and crystals also fulfill a subset of the parameters usually attributed to life and thus may be mistakenly labeled as alive. Thus, the condition of "being alive" needs to be distinguished from the "properties of a living system." The distinction is more than a semantic technicality, if the search for life on other worlds depends on the definition of what is being searched for. While ultimately we must know that what we discover is a "living system" capable of self-perpetuation, at the moment when we first encounter it, we need more precise and practical criteria for judging whether or not it is "alive."

The current tendency is to focus on two essential characteristics of the living state: its consumption of energy to maintain thermodynamic disequilibrium, and its ability to replicate form and function indefinitely through time. More controversial but often incorporated into modern definitions is the capacity for evolution and the interdependent nature of living systems, extrapolated in the extreme to a global extent. Finally, the need to define life in a way that incorporates forms of mechanical life that meet the same criteria as biological organisms has become apparent. Each of these considerations will be evaluated in turn.

2.4 Thermodynamic Criteria

Once it is accepted that the living state maintains a high degree of order (low entropy) that persists in disequilibrium with its environment, thermodynamic considerations mandate that energy be provided to maintain that order. Nearly all modern definitions of life incorporate the assumption of a highly ordered state that degrades energy (consumes enthalpy) as a means of resisting the spontaneous tendency toward disorganization (increasing entropy) required by the 2nd Law of Thermodynamics.

Biological life on Earth has evolved in such a way that energy is drawn from complex molecules with high free energy content, through a series of reactions that capture the release of energy as the complex molecules are broken down to simpler compounds with lower free energy contents. Photoautotrophs and chemolithoautotrophs manufacture their own chemical fuel by using the energy from sunlight or reactions with inorganic chemicals found in the environment. Heterotrophs derive their chemical fuel and carbon by consuming autotrophs, other heterotrophs, or their organic products. The energy thus harvested is used not only to maintain the highly ordered state of the system, but to power any autonomous activity (work performed) by the system. Collectively, the repertoire of chemical reactions and interactions that carry out these processes constitute metabolism, so the capacity to carry out energy-consuming metabolism in order to maintain order and perform work is either explicitly or implicitly part of most definitions of the living state.

Now that any macromolecule whose precise chemical structure is known can in principle be synthesized in the laboratory, any metabolic reaction should be inducible by placing together the right constituents in appropriate concentrations under conducive conditions in a test tube. Would a minimal set of such metabolic processes carried out exclusively *in vitro* constitute a living system? Most would say not, unless that system could be shown to perpetuate itself indefinitely in a stable, autoregulated state with input only of simple constituents and energy. In the poetic words of Loren Eiseley (1946),

> . . . every bubble of the chemist's broth has left the secret of life as inscrutably remote as ever. The ingredients are known; they are to be had on any drug-store shelf. You can take them yourself and pour them and wait hopefully for the resulting slime to crawl. It will not. The beautiful pulse of streaming protoplasm, that unknown organization of an unstable chemistry which makes up the life process, will not begin. Carbon, nitrogen, hydrogen, and oxygen you have mixed, and the same dead chemicals they remain.

Thus chemistry alone, in the absence of organizing components, does not constitute the living state. But the day in which the biochemist and molecular biologist may indeed be able to brew a mixture with some elementary life-like functionality may not be far away. Theoretical models of self-sustaining metabolic systems have been in the design phase for some time (Cloney 2016; Luisi et al. 2006; Maturana and Varela 1981), and host cells infused with synthetic macromolecules are moving toward genomically engineered hybrids between natural and synthetic forms of life (Juhas 2016). These advances are described in greater detail in Chap. 3. Suffice it to say that definitions of life must include at a minimum the requirement of self-sustaining autoregulation, or autopoiesis (Luisi 2003a), powered by the controlled consumption of free energy.

2.5 Reproducibility Criteria

Metabolism in biological organisms is carried out in a directed, not a random, way because proteins (enzymes) catalyze specific reactions. The specificity of catalysis is due to the three dimensional structural uniqueness of the protein (Luisi 1979), and that in turn is a consequence of the one-dimensional (primary) structure conferred by the particular sequence of amino acids that make up the protein. The amino acid sequence of a given protein, with minor exceptions, is the same for that protein in every organism of the species, and to varying degrees in other species in which the protein catalyzes the same reaction. The ability to synthesize proteins of the same structure within organisms, and pass the instructions for synthesizing proteins of the same structure to succeeding generations, is based on a linear code of nucleic acid bases which can replicate themselves with high fidelity. This nucleic acid code determines not only the structure of protein catalysts, but controls many other structural and regulatory functions of the cell.

From the earliest observations of ancient people that organisms reproduce offspring as near-identical versions of their parents, the concept that information must be passed from parent to offspring has been self-evident. Thus the potential for reproduction is a vital part of any definition of life. Yet the failure of an individual organism to reproduce does not preclude it from being alive. Even if an individual organism does not duplicate itself in its entirety, it must continually replicate the macromolecular components that keep its metabolic disequilibrium operating. And for multicellular organisms, continual cellular turnover, requiring replication of all of a cell's constituents and capabilities, is the norm.

Two additional features of reproduction in biological organisms need to be specified to distinguish the living state from superficially similar processes in the inanimate world. The first is that living cells and multicellular organisms reproduce near-exact replicas of themselves, with regard to size and morphology. While mineral crystals grow by replicating precise molecular configurations, the resulting overall crystal is indefinite in size. While clouds multiply, they generate offspring of variable shapes and sizes. Indeed, it is this constancy of form through successive generations that enables the assignment of a living organism to a taxonomic category that extends through time and constitutes a unique and traceable biological history. The second unique feature of biological reproduction is that it constructs its descendants from raw materials, adding the informational specificity as well as the material composition to the offspring through the mere agency of its own intrinsic metabolism.

While biological organisms as they have evolved on Earth do reproduce near-exact replicas of themselves, it is less clear that mechanical entities would need to do so. To be considered alive, they certainly must be capable of autonomous fabrication from raw materials, but it is conceivable that a greater variety of structural and functional variations could be coded into the program that mechanical forms of life propagate through succeeding generations.

2.6 Evolutionary Criteria

Living entities reproduce themselves through an indefinite number of cycles, ensuring survival of the information content and metabolism for which it codes, despite the demise of predecessor carriers of the information. As a result, the living state at any point in time, in any single organism, has a history. Every species has a species history, marked by changes over time that have been introduced into its genetic code, resulting in alterations of form and function. Most (but not all) of these changes are assumed to be driven by natural selection— the mechanism for biological evolution first enunciated by Alfred Russell Wallace and, in greater depth, by Charles Darwin—resulting in the designation of this type of biological change over time as 'Darwinian evolution.' Some would argue that the ability to undergo Darwinian evolution is also a defining characteristic of living systems. It clearly is not, however, a property of an individual organism; so this criterion is not useful when evaluating whether a specific entity is alive at a given point in time (Fleischaker 1990). A nuanced version of this criterion is that the living state consists of materials that have been ordered as they are, through a sequence of historical contingencies (Luisi 2003b).

2.7 Life as a Global Entity

The notion that the Earth is alive as a whole is prevalent in ancestral cultures, and was famously promulgated in the late sixteenth century by Bruno, but generally fell out of favor as the Renaissance progressed and inanimate chemistry and physics matured as sciences. In the twentieth century, the concept was reborn in two different versions. Vernadsky (1997) argued that geology and biology are fundamentally indistinguishable - that biology is simply a particularly dynamic construction of the same material that constitutes the matter of all the Earth. Lovelock (1979, 1995) has argued that the Earth in its entirety operates as a living, self-regulating, homeostatic system whose properties derive from and define the nature of life itself (The Gaia Hypothesis). Both points of view have merit, and the Gaia Hypothesis, in particular, has some predictive value for the nature of biospheres on other worlds where living systems might be abundant (Lovelock 1965). They are not helpful, however, in assessing whether a specific entity is alive at a given point in time. Furthermore, if life exists in isolated local pockets of some other worlds, it seems unlikely that global indicators would reflect it. This is the fundamental flaw in Lovelock's (1965) *a priori* dismissal of the existence of life on Mars based solely on its atmospheric characteristics. At some semantic level it might always be argued that any world that harbors life at all is itself "alive," but acceptance of the argument does not have practical utility in finding and identifying local pockets of living systems.

2.8 Artificial Life

The rise of technological capability by the human species on Earth has raised the prospect that new forms of life could be created by *Homo sapiens.* Since such forms of life will have been brought into existence by means other than the natural process of evolution, they are referred to as **artificial life.** No such life has yet been created that matches all the criteria fulfilled by naturally evolved, organic life, but progress is being made in three areas, colloquially categorized as (1) "wetware," (2) "software," and (3) "hardware."

2.8.1 Synthetic Life ("Wetware")

Synthetic biology is a field of research in which the main objective is to create fully operational biological systems from the smallest constituent parts possible, including DNA, proteins, and other organic molecules (Rugnetta 2016). For our purposes, its greatest significance lies in the insights it can provide into the origin of life under natural circumstances. Accordingly, it is treated in more detail in the next chapter.

2.8.2 Virtual Life ("Software")

The computer revolution has brought forth the ability to create dynamic computer programs which have several functional similarities to biological forms of life, including the ability to execute dynamic actions, and to reproduce themselves and spread beyond their points of origin. But they are neither autonomous (absent a triggering event) nor do they exist in a material form that can carry out any actions outside a machine host. While artificial intelligence is dependent on such programmed information, and will play an increasingly critical role in developing intelligent, autonomous machines, the software itself does not have sufficient attributes to make it useful in the search for life elsewhere in the Universe. Therefore, it will not be considered further, apart from the role it plays in robotics.

2.8.3 Mechanical Life ("Hardware")

Once machines are fabricated which have significant intelligence and autonomy, to what extent will they qualify as being alive? A machine is a finite structure, clearly distinct from its surroundings. It is structurally complex, at an entropic level well below that of its ambient environment. It can, and ultimately will, fall apart if not maintained by an input of energy. It performs work by consuming free energy. Even the processing, evaluation, and storage of information (as in a computing machine) consumes some energy. So the thermodynamic criteria for being a living system can be met by any operable mechanical device.

On the other hand, machines at our current state of technology do not autonomously fabricate new machines from raw materials. They can, of course, be fabricated in unlimited numbers by other agents, including other machines. But they do not do this of their own accord, based on instructions derived from a predecessor, at their own initiative and under their sole control. Thus, they fail to meet the criterion of autonomous reproduction.

If and when a machine is built that can assemble from raw materials another machine (either like or different from itself) and pass along the instructions for the fabrication process so that the newly built machine can repeat the fabrication process through a succession of descendant machines with the same capability, then the reproducibility criterion will have been met. Any generic definition of a living system must take into account this eventuality.

It should be noted that even if fabricated entities do not meet all the requirements of being alive in themselves, they imply a "fabricator" that must be or have been alive. In that sense, they are bioindicators of living entities, even if the living entities are not themselves present where the fabricated entities are found.

2.9 A Utilitarian and Generic View

We see, therefore, that defining life is semantically ambiguous and operationally difficult. But a generic and objective definition is needed, to make the recognition of the living state as unambiguous as possible whenever and wherever it may be encountered in the Universe.

We propose to sidestep the semantic difficulties of defining "life," by focusing instead on defining a "living entity" – a finite collection of matter and energy for which search parameters can be devised and criteria for recognition can be specified. Our intent is to propose a definition that is both utilitarian but generic.

We propose, therefore, to define a "living entity" as a material system that (1) is a self-sustaining bounded local environment in disequilibrium with its surroundings, (2) consumes energy to maintain its high level of internal organization, carry out intrinsic activity, and adjust to its environment, and (3) is autonomously generated from or fabricated by antecedent (parental) entities that transmit information to the descendant (offspring) entities sufficient for the autonomous generation or fabrication of an indefinite succession of offspring.

The reader is referred to Chap. 9 for practical consequences of our definition of life and to Chap. 10 on how to use it to detect extraterrestrial life. In this section we expound on the theoretical basis for our definition.

2.9.1 Self-Sustaining and Bounded Environments in Thermodynamic Disequilibrium

A living entity is self-sustaining in that the processes necessary for its function and perpetuation arise from the particular collection of materials (molecules, for biological systems; fabricated components, for mechanical systems) that constitute the entity. A flow of energy through the system activates ordered processes, some of which produce distinctive structures. Components of a living system are constrained within space distinct from their surroundings because they constitute a more highly ordered state of matter than the environment, and physical constraint prevents rapid entropic decay. This requires a boundary which is finite and discontinuous between the non-living surroundings and living contents within the bounded space. The boundary is not absolute, since materials and energy have to be exchangeable between the entity and its surroundings, but it is sufficiently impervious to maintain a clear-cut distinction between the interior and exterior of the entity. Living entities are thus thermodynamically open but far from equilibrium.

A closed natural inorganic system, isolated from its surroundings, adheres to the 2nd Law of Thermodynamics and moves spontaneously toward a state of maximum entropy. It also moves toward a minimum amount of free energy with the Gibbs free energy between reactants and products being zero at equilibrium. Life, on the other hand, maintains a high free energy state. This enables it, first, to do work on its environment. Secondly, the entropy of living systems is low because they are highly organized compared to their environments (even though the 2nd Law of Thermodynamics remains valid, as it applies to the macrocosm as a whole). Minerals fall ambiguously between these two extremes. They are highly organized and therefore have low entropy (Fig. 2.2). But in a natural system they generally move spontaneously toward a lower state of free energy. However, as previously discussed, some luminescent minerals can absorb energy that temporarily elevates them to a higher free energy state than their external environment. Lacking a permanent storage mechanism, however, the energy gain is generally soon dissipated.

A major distinction between biological organisms and non-living systems is the presence of biomembranes. These establish boundaries that serve to (1) preserve the high free energy state of the system from dissipation, (2) encapsulate and confine a high concentration of interacting solutes and macromolecules, and (3) carry out complex functions such as selective solute permeation, light transduction and the development of chemiosmotic potentials that generate energy gradients and provide the basis for reversible states of excitation (Deamer and Pashley 1989).

Disequilibrium on a cellular scale is made possible by the cell membrane, which enables the establishment of different solute concentrations within and outside the cell. On a supracellular scale disequilibrium conditions are created most visibly by colony-forming organisms such as stromatolites and corals, which are multicellular aggregates on a local scale (see microenvironments below). On a planetary scale,

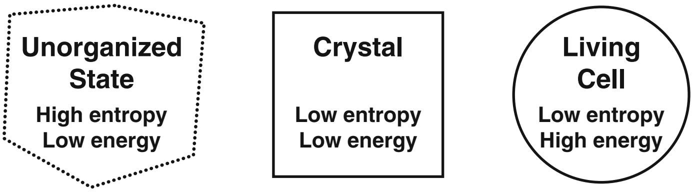


Fig. 2.2 Thermodynamic view of unorganized, crystalline and living state

disequilibrium conditions can be established by biological processes such as photosynthesis.

As we criticized the traditional definition before by comparing it to analogs in the mineral world, it is only fair to evaluate how our definition stands up to these kinds of comparisons. Minerals do not have a membrane composed of fatty acids or similar compounds that living systems use. However, macromolecules within clay minerals can be protected. Clay particles can be linked in face to edge contact that results in an open internal framework with very high porosity (Bennett and Hulbert 1986). In such a clay fabric compartment, macromolecules (or clay minerals themselves) can be protected from disturbances in the environment. This type of framework structure can even lead to selectivity of specific ions. Some surface-active solids such as double-layer metal hydroxide minerals are capable of transporting matter against concentration gradients.

Stable disequilibrium conditions are also possible in the inorganic world but only to a limited extent (by sudden volcanic activity or for the time a hydrothermal vent is active). In a completely inorganic world plutonic rocks with their volatile components would be expected eventually to reach equilibrium with sediments, the atmosphere and ocean water. Disequilibrium conditions or concentration gradients can be maintained within clay minerals for a period of time due to geometrical constraints and large energy barriers against ion exchange. Concentration gradients are most likely to form in the geometrically tight tetrahedral sites and to a lesser extent in the more spacious octahedral sites. However, lacking a distinctive boundary comparable to a biomembrane, clay minerals cannot maintain stable disequilibrium conditions at their reactive outer edges or in their reactive interlayer sites. Thus, like any inorganic system, this system would eventually reach equilibrium with its natural surroundings. Thus, while at any given instant, disequilibrium can be achieved by inorganic processes, this condition cannot be maintained indefinitely. By contrast, living systems are able to establish order within a chaotic world and perpetuate that order as long as energy is available for resisting the inexorable tendency toward increased entropy.

2.9.2 Transformation of Energy to Maintain a Low Entropy State, Adjust to Change, and Perform Work

Maintenance of the low entropy state of living systems requires the persistent infusion of energy (Morowitz 1968), first, to enable the system to maintain its complex organization and resist dissipation toward randomness. The second requirement for an input of energy derives from the fact that living processes adjust to their environments and perform work by growing and retracting, moving through the environment, emitting energy, counteracting concentration gradients, transforming materials, erecting and breaking down structures, and other endogenous activities.

While energy transformations are characteristic of all dynamic physical and chemical systems, energy flow in non-living systems tends to result in greater disorder among all elements of the system. Energy released through different stages of the rock and water cycles, for instance, generally erodes land and distributes water to increase the entropy of the total collection of water and land toward equilibrium (lower mountains, more dispersed water and soil). The energy transformations of living systems, on the other hand, serve primarily to harvest and store the levels of free energy necessary for maintaining the highly ordered structure of the organism and performing the work that living entities carry out. The net effect for living systems, in contrast to that for non-living systems, is to maintain and often increase order at local levels and on microscopic scales.

There are two consequences to the way in which life transforms energy. One is that much of the energy is used to create and sustain a level of complexity that supports emergent functions that in their totality exceed the sum of the parts of the system. A mountain may be structurally complex but its role in the rock cycle is not dependent on the detailed organization of its individual rocks and sediments. The mountain is in essence a simple conglomerate of its component parts. The function of a living organism, on the other hand, depends critically on precisely how it is put together. Its component parts function in a coordinated manner, to generate a complex array of emergent properties, both structurally and functionally. The generation and maintenance of this complexity is one of the primary uses of the energy that living systems transform.

A second consequence of biological energy transformations is to create one or more additional microenvironments within the natural environment. The Eh (redox-potential), pH, solute composition, and structural complexity of the living cell is maintained at levels different from the extracellular environment because of the autonomous functions carried out by the cell, but not in the abiotic environment surrounding the cell. New environments can also be created on a larger scale by colony forming organisms such as stromatolites and corals, which can alter the topography of large amounts of habitat. Life-induced changes can occur even on a planetary scale, such as the change in atmospheric oxygen composition brought about by oxygen producing microbes on Earth, beginning with the emergence of photosynthesis as a uniquely biological form of energy transformation (Knoll 1999; Schopf 1994). This innovation enabled life to become autotrophic (manufacturer of its own food from the simple and abundant molecule, CO_2) on a global scale. Thus, not only is the transformation of energy a characteristic of life, but so is the ability of life to alter conditions in the natural environment.

Note the dual requirement of living systems: to resist an increase in entropy, and to perform work. Both requirements are essential for the definition of a living entity. Any fabrication or machine is, for the time being, at a lower state of entropy than, and in disequilibrium with, its environment. Indeed, such objects are known to exist on other worlds: the lifeless Huygens lander rests on Titan, and the surfaces of Mars and the Moon are littered with man-made objects. They are not alive, however, in part because they perform no work and make no adjustments to changes in their environments. The rovers and orbiters on Mars that still are consuming energy and performing work are not alive because they fail the criterion in the next section.

2.9.3 Information Encoding and Transmission

Order is maintained within living systems despite the turnover of its individual components because information is contained within the system that directs replacement of the lost components, regulates their relative abundance, and controls their interactions. Furthermore, when the entity reproduces itself, all the information needed for reconstitution and function is passed intact to each successive entity. That information serves to constrain the structure and function of each reiterative, succeeding entity.

For biological organisms at the cellular level, this means that multiple descendent cells acquire the genetic information previously held by a single parental cell. At the level of the multicellular organism, it means that all the information for the organism’s development and function is replicated, then passed through reproductive cells to the offspring (next generation). When a cell or organism can no longer maintain steady disequilibrium conditions it approaches equilibrium with its environment and therefore dies. Despite the death of the parent organism, the informational blueprint for the organism's structure and function, which for life as we know it on Earth is based on a chemical code, survives to the descendent organism, and will be transmitted from generation to generation. Despite the demise of the individual organism that harbors the code in its cells during any single generation, the transmission of the code to a subsequent generation ensures that the instructions for life specific to that particular kind of organism will persist.

Genetic codes are meaningful because of the characteristics that they impart to the systems in which they reside. However, a code of information by itself is useless if there is no meaning or consequence associated with it. The distribution of atoms in mineral lattice may be understood as a code, in that the information content of the distribution pattern is greater than zero, but there is no apparent meaning associated with it since there is no functional consequence to the pattern. Another main difference that distinguishes living systems from the mineral world is a sharp difference between substance and information. Genetic information is chemically codified in separate units (nucleic acids) of the cell that are distinct from their physical manifestation, hence the functional consequences of the code. A segment of DNA codes for a protein that carries out a particular function. If the protein is broken down, the function ceases, but the DNA that coded for the protein persists through replication and the reproduction of successive generations indefinitely. A mineral, on the other hand, may be capable of rearranging atoms and molecules in response to environmental influences such as weathering; but even if it is supposed that this rearrangement has changed the nature of information encoded in the mineral, the altered information has no effect apart from the specific rock in which it is embedded. Therefore, the information persists only so long as the mineral itself remains intact. There is no obvious consequence to the information, and no expression of it distinct from itself.

A distinctive feature of a living entity, whether biological or mechanical, is that its construction requires only raw unorganized material from the environment, instructions provided by the informational code derived from a preceding entity, and energy. It differs from the manufacture of exact copies of inanimate objects in that the entity manufactures a copy of itself, the copy repeats the reproductive process, and this reiterative cycle of reproduction can continue indefinitely.

2.10 Implications for the Remote Detection of Life

If life conforms to the way we have defined it, our efforts will be maximized by focusing on the consequences of and requirements for the three components of our definition.

If living entities consist of bounded local environments in disequilibrium with their surroundings, we will be seeking to detect evidence of entities that stand out as collections of matter with discontinuous boundaries between themselves and their environment. Thus, any evidence of local chemical concentrations or physical properties distinct from their surroundings would be presumptive evidence for the possibility of life. In many cases, the living units may be small to microscopic, for reasons discussed in the next chapter, and therefore require high spatial resolution in the instruments sent to detect them. However, aggregates of those entities, analogous to stromatolite mats and coral reefs on Earth, may be large enough collectively for remote detection. The necessity for enclosure in a barrier, most likely and often in a liquid medium, leads us to look for particular types of molecules in particular environments—especially amphiphilic molecules.

Physical objects that are clearly distinguished from their surroundings as fabricated, technologically sophisticated objects, even if not living entities themselves, would indicate the involvement of living entities in their creation. While the host of robots and material residues from Earth that already litter the Moon, Mars, and Titan are not themselves alive, they indicate (and surely would be interpreted by alien intelligence as) products of technologically capable forms of life that put them there.

The nature of energy transformations—a nearly universal component of all definitions of life—depends on the nature of the energy gradients available. Since the easiest and most obvious way to detect biologically driven energy transformations is probably through either localized or global effects of the transformation, our instruments need to be attuned to the forms of energy available on the planetary object of our search. Energy sources other than light or chemical energy may be used by life elsewhere, as discussed in Chap. 5. And because of the simplicity of chemical conversions as a source of energy, disequilibrium chemistry in the atmosphere or global habitat is probably relevant anywhere. Finally, because energy is transformed in order to do work by living organisms, evidence of work, such as reactivity, growth, motion, repair, or maintenance of chemical, thermal, or other types of gradients is further presumptive evidence for the living state.

The third component of our definition—capacity for information encoding and transmission independent of the life span of the individual organism—will be difficult to confirm until actual samples of the candidate life forms are in hand.

The constraints applied by this part of the definition for remote detection strategies are thus limited. However, this part of the definition becomes critical once candidate samples are available, for only this third component will enable confirmation that the candidate structure in question is or was alive. The validity of this point is illustrated by the fact that all the lines of evidence in support of fossil organisms in the Martian meteorite ALH84001, including the pictures which could possibly be interpreted as nanomicrobial-like organisms (Chap. 10.2; McKay et al. 1996), are inconclusive, absent confirmation that the presumed fossil actually derived from an organism that did in fact replicate itself from a pre-existing organism. The same applies to the very early fossil record on Earth (Brasier et al. 2002; Schopf and Packer 1987; Schopf 1993; Dodd et al. 2017).

Our definition is geared toward the search for life on other planets and moons. The technical approaches needed for detecting life as we have defined it on other worlds is discussed in Chap. 10. However, the possibility of the existence, and hence detectability, of "alien" life on our home planet, has attracted some attention. Davies and Lineweaver (2005) computed probability scenarios of the origin of life and found that there is a significant likelihood that at least one more type of life has emerged on Earth and could have coexisted with known life. Cleland and Copley (2005) go even further to argue the possibility that the contemporary Earth contains a yet unrecognized alternative form of microbial life. Two counterarguments have been advanced. The first is that any "alien" life on Earth based on a different molecular architecture and biochemistry would be outcompeted very quickly. The second is that no tangible evidence of such organisms has been found in over a century and a half of microbiological study. Cleland and Copley (2005) responded by pointing to the complexity and diversity of microbial communities, and by emphasizing that microbial exploration relies heavily on detecting DNA and RNA, which may not be part of the "alien" forms of life.

2.11 Chapter Summary

Identifying the fundamental features of living entities is essential for identifying them on other worlds, particularly where they may exist in an unfamiliar form with novel features. There are several obstacles, however, to achieving a useful definition of life: (1) Living systems use compounds that are abundant in the surrounding environment and processes that are not intrinsically different from reactions that occur inorganically. (2) There does not appear to exist a single characteristic property that is both intrinsic and unique to life. (3) There was probably no sharp line but rather a gradual transition between a non-living and a living state of matter at the origin of life. (4) Finally, the condition of "being alive" has to be distinguished from the abstract concept of "life." We have chosen to sidestep the abstract concept in favor of defining "living entities" in a way that provides a practical guide for detecting instances of life in alien environments. We propose that living entities (1) are self-sustaining bounded local environments in disequilibrium with their surroundings, (2) consume energy to maintain their high level of internal organization, carry out intrinsic activity, and adjust to environmental changes, and (3) are autonomously generated from or fabricated by antecedent (parental) entities that transmit information to the descendant (offspring) entities sufficient for the autonomous generation or fabrication of an indefinite succession of offspring.

Our definition contains no components that are original with us, though our emphasis on physical boundaries, implying finite structures, has seldom been accorded the priority that we give it. We are consistent with most modern efforts to define life by emphasizing the three key features of low entropy, energy transformation, and replication. This definition anticipates that detection of life on other worlds must include three determinations. The putative life form must be shown to consist of a more highly organized state than its surroundings. It must be shown to transform free energy in a form available to it, to maintain its highly ordered state, adjust to its environment, and perform work at some level. And ultimately it must be shown to reproduce itself in a manner which preserves all the information necessary to perpetuate the living state through successive, individual replications of the entities from which they were replicated. Our definition excludes notions of evolution through time or globally distributed systems, not because these concepts are irrelevant, but because they are not useful in identifying living entities at a fixed point in time in a local habitat.

Chapter 3
Origin of Life

The origin of life is a large and active field of research, and one chapter in this book can hardly do it justice. Yet, if we are to make reasonable inferences about the probability of life on other worlds, we must be able to gauge the possibility that living systems could have arisen (or arrived) there in the first place. And that, in turn, depends on our understanding of what the possibilities are for the origin of life anywhere. In an effort to rescue those possibilities from the realm of total speculation, we consider first what we know or infer about the origin of life on Earth, hoping that this singular example can provide some insights into and boundaries upon our thinking about the generic origins of life, wherever they have occurred. Then we use our limited understanding of what may have happened at the dawn of life on Earth, in combination with our definition of life given in Chap. 2, to focus on inferences with regard to the first cellular membranes, the first metabolisms, and the first replication mechanisms. Finally, we will discuss the implications of these insights for the predictability of life elsewhere in the Universe.

3.1 Scenarios for the Origin of Life

The first living systems to persist on Earth are shrouded in mystery, and the first to persist may not have been the first to exist. Erwin Schrödinger predicted that quantum mechanics would solve the riddle of how life has started, but this has not been fulfilled (Davies 2005). Despite a century of speculation and a half-century of active experimentation, there is no consensus on a coherent sequence of events that brought life forth on our planet. There is, of course, the possibility that life was brought to Earth from another world. The spread of life by panspermia, at least among the inner rocky planets which may have shared a similar wet and warm surface in their early planetary histories, cannot be discounted. But life had to originate somewhere, and how that happened is what we would like to know if we are to understand whether it could happen on any other given body in the Universe,

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_3

including those so isolated that panspermia would be a most unlikely explanation for the genesis of life on their remote worlds. Therefore, for the purposes of this chapter, we will assume that life arose de novo on Earth, in order to see where that understanding takes us.

While we cannot say with anything close to certainty how living systems came into being, we are not totally lacking in plausible ideas. In fact, it is fair to say that consensus has crystallized around a basic outline of the major events in the origin of life, consisting approximately of the following, not necessarily in this exact order (Bada 2004): (1) Under conditions of an energy-rich neutral to reducing atmosphere, monomeric organic compounds were created from elementary molecules like H_2, N_2, CO_2, NH_3, HCN, and formaldehyde. To an unknown degree, the reservoir of monomers was probably supplemented by cometary bombardment (Chyba and Sagan 1992), which delivered organic compounds to the Earth's surface from an alien origin. (2) Monomers formed polymers and interchanged both atomic components and energy in a growing web of chemical interchange. (3) Films, micelles, or other protomembranous boundaries began to encapsulate the chemically interactive monomers and polymers, concentrating reactants and sequestering products. (4) A statistical recurrence of effective and efficient metabolites became prevalent, facilitated probably by inorganic catalysts like transition metals or heterogeneous surface minerals. (5) Reliably producible 'infopolymers' (Turian 2003) led to crude, and probably initially inexact, mechanisms of replication. (6) Refinement of replicative mechanisms enabled the emergence of ribonucleic acid (RNA) as a dominant macromolecular regulator of metabolism, with catalytic properties as well as the capacity to replicate itself. This inaugurated what has been termed the RNA world (Lazcano 1994; Orgel 1998)—though some newer studies dispute the existence of or need for an RNA world (e.g., Carter 2015). (7) Proteins assumed increasingly sophisticated structural and enzymatic properties, coincident with the emergence of RNA-directed protein synthesis. (8) Deoxyribonucleic acid (DNA) emerged as a stable repository for genetic information, rendering RNA an intermediate in the flow of information, as cellular life of constant form and function achieved the capacity to perpetuate itself indefinitely.

To be sure, there is a gulf of uncertainty about and between most of the steps above. How largely chaotic if not random interactions among simple organic monomers (step 2) could transition into reliably channeled metabolic pathways (step 4), for example, is an unresolved puzzle. One of the greatest "unknowns" is how the first RNA or oligonucleotide was formed. The link between the simplest early genetic codes (step 7) and the sophisticated steps of protein translation as it occurs in modern organisms (step 8) seems totally elusive. Furthermore, there is heated debate about the sequence itself (Pross 2004)—whether, for instance, sequestration and primitive metabolism (step 3) preceded or followed development of the capacity for replication (step 6). But most of the steps enumerated above have been at least convincingly modeled, and many have been demonstrated experimentally. While the steps individually, therefore, enjoy a broad degree of support, there is no consensus on the details or environments in which they unfolded during the early days of the Earth. For purposes of classification, three general scenarios can generally be recognized.

3.1.1 A Lukewarm Marine Origin of Life

The longest standing and still most influential scenario for the origin of life derives from the pioneering work of Oparin (1938) and Haldane (1954), who envisioned the synthesis of monomeric organic compounds from simple precursors prevalent in a reducing atmosphere, progressively concentrated in the early oceans to a point where critical interactions and assemblies could occur. Life emerged from this "primordial soup" (Lazcano and Miller 1994), probably at or near the surface where energy from lightning and electromagnetic radiation were readily available (Bada 2004). Dramatic support for this concept was first provided by Stanley Miller and Harold Urey, who generated amino acids by discharging electricity through a mixture of methane, ammonia, water, and hydrogen (Miller 1953). These "sparking" experiments have been reproduced countless times in many variations, with the outcome heavily dependent on the mix of starting gases and other conditions (Bada and Lazcano 2002a; Miller and Orgel 1974; Miller and Lazcano 1996). While there is considerable doubt that the early atmosphere was as reducing as assumed by Miller (Kasting and Brown 1998; Tajika and Matsui 1993; Walker 1977; Westall et al. 2001) even neutral atmospheres appropriately energized can give rise to larger organic molecules. When supplemented by cometary delivery of interstellar compounds such as HCN, formaldehyde, aldehydes, nitriles, and acetylenes (Oro et al. 1992; Chyba and McDonald 1995; Miller and Orgel 1974), there is little question that monomeric precursors for biotic molecules could have accumulated in Earth's early oceans (Keosian 1968).

Nor is there serious doubt that energy would have been readily available on the surface of the early Earth. The amount of energy from lightning and coronal discharges has been estimated to be substantial (Chyba and Sagan 1991). Lithoautotrophy would have been a potential energy source in the deep subsurface (McCollom 1999; Stevens and McKinley 1995). Impact shocks and ultraviolet light at the surface were probably substantial (Chyba and Sagan 1992). Fast tidal cycling (Lathe 2004), and even sound have also been advanced as energy sources for prebiotic evolution. Finally, thermal energy has been modeled as a primordial force for biogenesis, before it was rendered non-competitive by the evolution of photosynthesis (Muller 1985, 1993, 1995).

A major problem with the prebiotic soup scenario is that polymerization by condensation in water is difficult, and even optimistic estimates of the concentration of organic precursors leaves the prebiotic oceans relatively dilute in organic molecules. Hence, a concentration mechanism is generally assumed to have been necessary. Cyclic dessication, as produced by freeze-thaw cycles (Miller and Orgel 1974) or the periodic filling and dehydration of tidal pools (Irwin and Schulze-Makuch 2005), for example, could facilitate condensation reactions. While this scenario is generally presumed to proceed at moderate (Bada and Lazcano 2002b) if not cool (Miller and Orgel 1974) temperatures, Fox and Dose (1977) argued the importance of heat-driven desiccation as the mechanism for prebiotic organic condensation. For those reactions that are favored at low temperatures, sequestration in ice would also provide a means of concentration. A variation of this scenario is the origin of life in fresh-water ponds on land rather than marine waters (Monnard et al. 2004; Deamer and Damer 2017).

3.1.2 A Benthic Thermophilic Origin of Life

Interest in the possibility that life on Earth may have originated at ocean depths near hydrothermal vents has been spurred by the fact that the deepest rooted organisms in the tree of life include a number of thermophilic archaea (Stetter 1998; Woese 1979). Codon frequencies in barophilic (pressure-loving) organisms seem also to support a deep ocean origin for the genetic code (Di Giulio 2005). Yet, the strongest evidence supporting the hydrothermal vent scenario for the origin of life comes from an analysis of more than 6 million protein-encoding genes (Weiss et al. 2016) showing that 355 protein families were linked to the last universal common ancestor (LUCA). Based on the identified proteins, LUCA appeared to have obtained energy from hydrothermal vents by oxidizing hydrogen gas, and was not able to make amino acids itself—meaning it would have to have relied solely on amino acids formed naturally at hydrothermal vents.

This is consistent with a hypothesis developed by Wächtershäuser (1988, 2007) who proposed a chemo-autotrophic origin of life in a volcanic iron-sulfur world, in which underwater volcanic exhalations gave rise to pioneering organisms comprised of an organic superstructure built on a metallic core. Support is provided by the demonstration that peptide bonds can form by activation of amino acids with CO on (NiFe)S surfaces at high temperatures (Huber and Wächtershäuser 1998). Attractive features of this hypothesis include the incorporation of inorganic chemistry, which facilitates the transition from prebiotic to living processes, and the plausibility of forming peptide bonds which are otherwise difficult to assemble in weak aqueous solutions. The hypothesis was further expanded by pointing to several advantages for the origin of life that alkaline hydrothermal vents provide (Russell and Hall 1997; Branscomb and Russell 2012; Sojo et al. 2016). Not only could the iron sulfide mineral, mackinawite, have played an instrumental role when the first semipermeable membranes of life were formed, but a first mechanism for fixing carbon from the environment can also be envisioned (Russell et al. 2013). If the first organisms developed at these vent structures, they were probably initially confined to them and not able to survive away from them (Weiss et al. 2016). The alternative scenario of a fresh water origin on land offers the advantage of combining the heat and mineral contents of thermal pools with proximity to a solid substrate and access to sunlight and air (Deamer and Georgiou 2015; Deamer and Damer 2017). Schreiber et al. (2012) even envisioned the origin of life in deep subterranean fracture zones, assisted by supercritical carbon dioxide levels.

However, counterarguments to a hydrothermal origin contend that the variety of biomolecules that can be produced by the processes occurring at hydrothermal vents or even in hydrothermal ponds are much less than that which the sparking experiments can yield (Lazcano 2004). As for life originating at or close to the surface on land, the ability of the earliest organisms to survive the heavy meteorite bombardment that occurred in Earth's early history is questionable. The fact that the most ancient forms of life are thermophilic could simply represent the survivors of a hot-ocean bottleneck at the dawn of organic evolution (Nisbet and Sleep 2001).

3.1.3 An Ice Water Origin of Life

Sea ice provides some attractive features as a possible habitat for the origin of life. Its dynamic freeze-thaw cycles at the water-ice interface, and the formation of liquid inclusions within solid surroundings, alternately concentrates and dilutes sea water solutions, and provides substrates for catalytic actions. Trinks et al. (2005) proposed that sea ice may have provided the optimal conditions for early replication of nucleic acids, and supported the concept by using cyclic temperature fluctuations to produce polyadenylic acid from a polyuridylic acid template in artificial sea ice. They linked the sea ice environment to a reactor where UV light from the sky, partly circular polarized by the influence of the ice structure, provides a very active energy source at the surface (Trinks et al. 2005). A cubic meter of sea ice contains about 10^{14}–10^{15} compartments or a network of channels with a combined surface of 10^5–10^6 m^2. In these brine channels macromolecules are concentrated and have a chance to react. Peptides are relatively easy to synthesize under these conditions as they assemble under temperatures down to −20 °C (Liu and Orgel 1997). Stribling and Miller (1991) cooled down artificial sea water mixed with monomers to −18 °C and obtained complementary RNA oligomers with chain lengths of up to 12–15. Monnard et al. (2003) performed template-free poly(A) synthesis experiments at −18 °C and obtained oligo(A) with chain lengths of up to 17. Vlassov et al. (2004) observed complex RNA evolving at temperatures below the freezing point. They also found that RNA degradation slows down markedly at low temperatures preserving RNA molecules of significant complexity. Feller (2017) emphasized that the eutectic phase of ice would have provided great stability and confinement of RNA molecules, facilitating their interactions and replication. Some evidence pointing toward RNA self-replication (Attwater et al. 2013) makes the rise of the hypothesized RNA world more plausible. Price (2010) argued that a cold origin of life is more likely than a hot origin, because biomolecules in a cold environment are better stabilized against hydrolysis and can take advantage of higher encounter rates. Furthermore, even today's microorganisms still rely on the ions that comprise eutectic solutions in ice. While the notion of biogenesis at ice-cold temperatures may be counter-intuitive, the possibility that it could be so has great astrobiological relevance, in view of the large number of icy bodies that are likely pervasive throughout the Universe (Lipps and Schulze-Makuch 2008).

3.1.4 A Comprehensive Scenario for the Origin of Life

Regardless of the habitat, energy source, and chemical details of the earliest events in biogenesis, we think a scenario can now be constructed that contains the essential features common to most theories and consistent with most experimental evidence about the origin of life. We begin with the broadly held view that monomeric organic compounds, such as simple carbohydrates, amino acids, and nitrogen bases, formed by prebiotic chemical reactions driven by robust energy gradients and supplemented by delivery of organic constituents by meteorites (Chyba et al. 1990), became available on Earth by about 4 billion years ago. Assuming similar processes have occurred and may still be occurring throughout the Universe, a generic sequence of events for any planetary body can be envisioned, as follows.

Lacking consumer organisms or biocatabolic reactions, the planet or moon would accumulate these organic monomers to sizeable concentrations in primordial seas. In formative habitats, recurrent cycles of polymerization and depolymerization could occur. This is easiest to envision at a water-air interface in shallow reservoirs such as ephemeral tide pools driven by tidal cycles of desiccation and rehydration (Irwin and Schulze-Makuch 2005; Lathe 2004), with polymerization (by dehydration condensation) alternating with depolymerization (by hydrolysis) reactions (Fig. 3.1); but analogous processes could also take place in ice inclusions or at deep ocean vents (Burton et al. 1974; Chan et al. 1987; Lahav and Nir 1997; Orenberg et al. 1985; Sojo et al. 2016). Since all monomers would be capable of forming bonds through condensation reactions, the combinatorial possibilities initially are vast and virtually random, forming many permutations of bases + amino acids, bases + sugars, sugars +

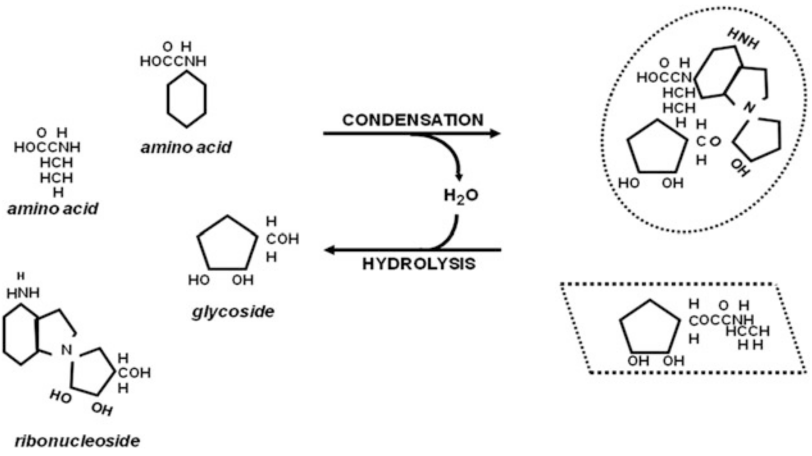


Fig. 3.1 Schematic effect of cyclic concentration and dilution in the formation of glyconucleopeptides. Organic monomers combine in various combinations when concentrated, often splitting upon dilution, and recombining perhaps differently in the next concentration cycle

amino acids, or all three. Collectively, these compounds could constitute a vast and ever-changing population of protopolymers.

Each concentration (or desiccation) cycle would destroy many protopolymers, but some would be more stable than others and survive to the next influx of monomers during the succeeding dilution cycle. Residual molecules from each concentration cycle provide a more concentrated and somewhat biased set of constituents for the next dilution-concentration (rehydration-dehydration) cycle. A succession of reconstitution and destruction cycles brings about continual change in the composition of local reservoirs, but integrated over a vast number of parallel reservoirs across the planet and extending through long periods of time, a progressive increase in complexity of constituents fills each pool. The contents are not the same across pools, but certain molecular motifs gradually emerge with higher frequency because of greater stability and/or favorable thermodynamic characteristics (Fig. 3.2). While the average complexity of the protobiomolecular pool would progressively increase under the scenario above, it would initially remain well below that of a living cell, primarily because directed replication would be absent. By definition, therefore, the system would not be alive (Lazcano 2004; Schulze-Makuch et al. 2002c). However, it would approximate replication of the overall capabilities of the system because of residual constituents carried over through each concentration-dilution cycle, and the bias that the residual contents would exert toward the reconstituted contents of the succeeding reservoir, achieving the “statistical chemistry” envisioned by Calvin (1969) and Dyson (1982) as important steps toward life.

Increased heterogeneity of reservoir contents enables a more complicated web of interactions. As protopolymers elongate, they acquire limited catalytic and autocatalytic functions, by virtue of assuming secondary and tertiary conformations. This in turn sustains an increasingly complex set of intermediary metabolic reactions. Consolidation of thermodynamically favorable interactions leads to reiterative

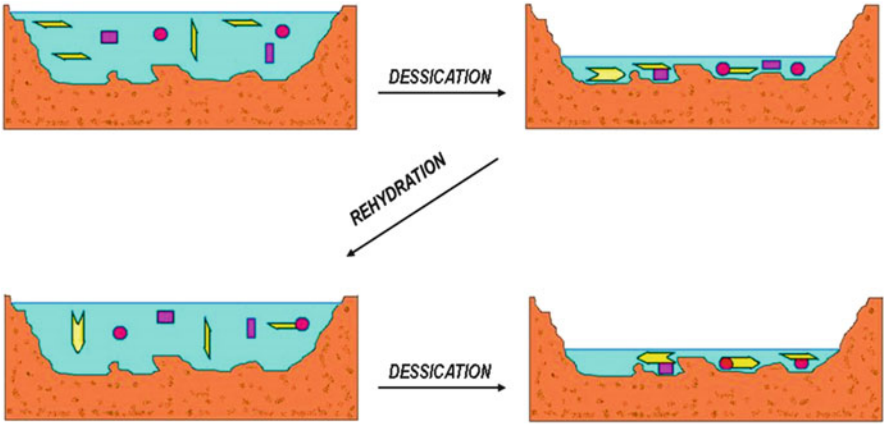


Fig. 3.2 Schematic representation of condensation, hydrolysis, and recondensation of protobiomolecules. Though basically undirected, interactions with a substrate could favor certain product combinations over many reiterations of dehydration-rehydration cycles

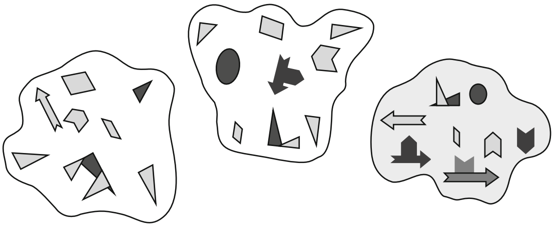


Fig. 3.3 Schematic representation of primordial pools of prebiotic reactants. Contents vary across pools, but certain molecular motifs gradually emerge with higher frequency because of greater stability and/or favorable thermodynamic characteristics

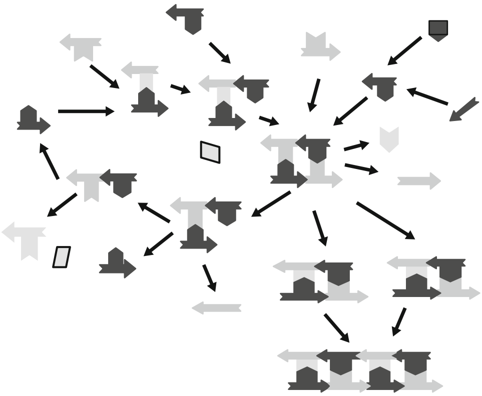


Fig. 3.4 Schematic view of a simple form of replication. Only four constituents with appropriate complimentarity could generate non-random polymeric sequences

sequences that represent the early stages of a primitive replication process, which is initially inexact but not random (Fig. 3.3).

Over a long succession of dissolution and reconstitution cycles, certain interactions will recur with greater frequency than others due to thermodynamically favorable biases, and the biased composition of the reactant pools. Systematic energy transfer reactions likewise become more standardized, as certain reactions—predisposed by survival of selective precursors and substrates from previous concentration cycles—form protometabolic pathways (Fig. 3.4).

Once high-energy bonds become readily produced by energy-harvesting reactions within the increasingly complex network of chemical interactions, endergonic as well as exergonic reactions occur. Encapsulation of these protometabolic events within lipid-bounded vesicles establishes a selective barrier between the internal and external environment, resulting in protocells. Now with the emergence of enclosed entities distinct from the environment, natural selection kicks in, promoting the survival of those with favored protometabolic pathways and progressively refining molecular processes and machinery leading to the RNA World. This, in turn, frees primeval and inexact replicative mechanisms from dependence on mineral or other structural substrates, all traces of which thereafter disappear (Cairns-Smith 1982). With the advent of both the coding and catalyzing capabilities of RNA, and the structural and catalytic properties of other macromolecules whose synthesis is directed by RNA, cellular life becomes totally distinct from the non-living environment, and evolves into the full-blown DNA-RNA-protein world that has persisted to the present day.

3.2 Minimum Requirements for the Origin of Life

There are three minimum requirements that any hypothesis for the origin of life has to address: (1) the origin of a semipermeable membrane to maintain a thermodynamic disequilibrium with the surrounding environment and regulate the exchange of nutrients and waste products; (2) the origin of metabolism and a cellular machinery that harvests the energy generated; and (3) the invention of a genetic code capable of transferring information from one generation to the next.

A major challenge in the view of some scientists is that all three events must occur at the same time, or at least close in time to each other, since the lack of any one event without the other would not result in anything resembling an organism. Schulze-Makuch and Bains (2017), for instance, have argued that since a semipermeable boundary (membrane), energy (metabolism), and information (genetic code) are all critical components, the lack of any one of them would preclude anything resembling a living organism. Assembly and concentration of interacting biomolecules without a bounding membrane would not be possible. Without harvesting and regulating the flow of energy, thermodynamic disequilibrium could not be maintained. And the lack of a replication mechanism would render reproduction impossible. Most research addresses only one of these three requirements at a time (because each is already challenging enough), but a notable exception is the hypothesis by Patel et al. (2015) who proposed a common origin for lipid precursors, proteins, and RNA from the interaction of UV light, hydrogen sulfide, and hydrogen cyanide and its precursors. While this approach is a major advance, the model does not take into account that the molecules involved in the proposed scheme also interact in other ways, so alternative reaction pathways could interfere with the proposed pathways leading to the biomolecules required for constituting a living organism. Thus, the proposed scheme is unlikely to occur in nature.

It is obviously true that all three elements must be present for a chemical system to be considered “alive.” It may be, however, that putative membranes, primordial energetic interactions, and primitive semi-replicative processes may go through their early evolutionary stages independently. We still seem to be far away from solving the riddle of the origin of life, but new insights are being gained all the time, so that we can at least offer informed speculations with regard to where life originates and what environmental parameters and resources are needed. Of particular interest is the question of whether there are multiple pathways to the origin of life and what if any bottlenecks leading to it exist (Scharf et al. 2015). Only when we are informed on this question, can we make reliable estimates on the frequency of life in the Universe. Below we detail what we know to date with regard to the origin of the first cellular membranes, the first metabolism, and the advent of reproduction.

3.2.1 Insights into the Origin of the First Cellular Membranes

The cells of all living organisms on Earth use a selectively permeable membrane to preserve the high free energy state of the system from dissipation, encapsulate and confine a high concentration of interacting solutes and macromolecules, and carry out complex functions such as selective solute permeation, substrate interaction, and energy transduction. The core of these membranes is made from amphiphilic lipids such as fatty acids and phospholipids, in which the hydrophilic ends of the molecules are oriented toward the outer aqueous environment, while the hydrophobic ends are pointed toward the inside of the membrane core.

Protocellular assemblies, generated by the catalyzed recruitment of diverse amphiphilic and hydrophobic compounds, might have constituted the first systems that eventually led to information storage, selection, and inheritance (Segre and Lancet 2000). The formation of vesicles from amphiphilic molecules appears to be relatively easy. Deamer and Pashley (1989) extracted organic material from meteorites that formed cell-like membranes. The spontaneous formation of vesicles appears to be characteristic of phospholipid compounds and similar materials. There are a variety of suggestions of how the first vesicles could have formed to become the precursor of the cell. Chang (1993) proposed bubble formation and breaking in the ocean-atmosphere interface as likely mechanisms for closing vesicles. Russell and Hall (1997) suggested the formation of iron sulfide membranes, precipitated as bubbles at submarine hydrothermal vents, as primordial cell membranes in a step leading to life. Deamer et al. (2002) pointed out that amphiphilic molecules having carbon chains lengths greater than six carbons form micelles as concentrations increase above a critical value. At chain lengths of eight carbons and higher, bilayers begin to appear in the form of membranous vesicles, which become the dominant structure as concentrations increase further (Fig. 3.5). Maurer et al. (2009) and Maurer and Nguyen (2016) found that the formation of vesicles depends much on the salt content of the medium. Deamer (2017) concluded that membrane assembly is most favored in low ionic strength solutions with a minimal content of salt and divalent cations, thus implying that fresh-water pools associated with volcanic islands would be more suitable for the origin of life than submarine hydrothermal vents. Further experimental and modeling work also included the successful simulation of the formation of daughter vesicles from parent vesicles (Segre et al. 2000; Andes-Koback and Keating 2011), and tests showed that multi-vesicle assemblies seem to outperform single compartment vesicles in both versatility and productivity (Hadorn and Eggenberger Hotz 2010).

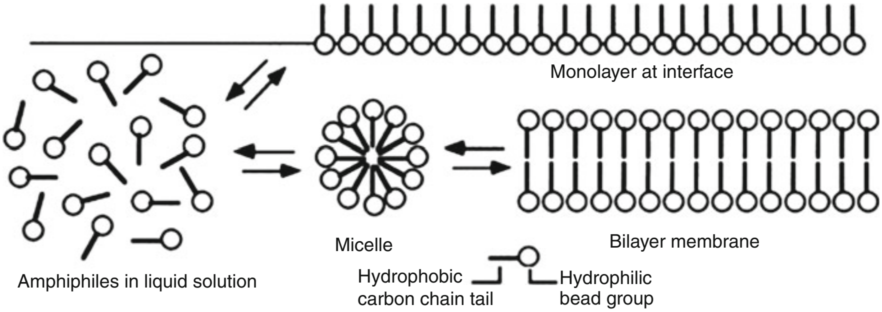


Fig. 3.5 Self-assembled structures of amphiphiles (from Deamer et al. 2002)

Phospholipids appear to be ideally suited as cell membrane constituents for life on Earth. That does not limit the possibilities though. In principal, many amphiphilic molecules could serve as a cellular boundary. Conditions different in temperature, pH and redox-potential of the liquid medium could favor amphiphilic compounds other than phospholipids. Amphiphilic compounds with outwardly oriented polar groups are well adapted for separating internal and external compartments submerged in a polar solvent. If the liquid environment were hydrophobic rather than hydrophilic, as likely on Titan, polar head groups at the surface of the membrane would be repelled by the hydrophobic solvent. How would a membrane be constructed in such an environment? Would molecules consisting of polar groups flanked by hydrophobic chains provide effective compartmental barriers in an organic milieu? Empirical studies are needed to answer this question. Since Titan may well represent a prototype of certain exotic environments found on other worlds, the search for membranes of a different composition from those known for terran organisms should be a priority for laboratory research in astrobiology.

3.2.2 *Insights into the Origin of the First Metabolism*

The chemical reaction that supported the first life on Earth must have been simple but very efficient. A reaction that appears to fit this description is the oxygenation of hydrogen to water. The oxidation can occur with oxygen or some other oxygenated compound:

$$H_2 + \tfrac{1}{2}O_2 \rightarrow H_2O \tag{3.1}$$

Reaction 3.1 yields an energy of 237.14 kJ/mol (or 2.6 eV) per reaction. There are various lines of evidence for why this reaction has such a central meaning: (1) hydrogen is the most common element in the Universe, and gaseous hydrogen molecules are supplied by volcanic outgassing and by the abiotic reaction of water with basaltic rocks (Stevens and McKinley 1995), so are readily available, (2) oxygen or oxygenated compounds are common in the Universe and also readily available for reaction, and (3) close relatives of the most ancient microbes on Earth use this reaction for metabolism. This oxidation of hydrogen was also proposed as a first type of metabolism by Weiss et al. (2016). On Earth, where volcanic activity, and with it carbon dioxide, are common, this reaction is often coupled to the reduction of CO_2 and called methanogenesis (Eq. 3.2).

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O \tag{3.2}$$

The reduction of CO_2 is energetically unfavorable but proceeds because of the net energy gain by the oxidation of 2 hydrogen molecules to water. The net energy gain of this reaction is 130.63 kJ/mol or 1.4 eV (474.28 kJ/mol of energy gained by the oxidation of two hydrogen molecules to water minus the 343.65 kJ/mol lost by the reduction of carbon dioxide to methane).

This kind of reaction can set the stage for a simple feedback process or pre-ecosystem. If the methane produced is exposed to oxygen-rich conditions, for example in some oceanic layer, it would be favorable to oxidize the methane back to carbon dioxide with an energy gain of 6.1 eV to close the loop for a nutrient cycle. However, the H_2 would not return to its molecular state, but most likely would be incorporated into some other chemical compound. Thus, the limiting compound in this feedback cycle is the supply of molecular hydrogen.

As an alternative, hydrogen may be oxidized in a simple but efficient reaction with the help of sulfur or iron as shown in Eqs. (3.3) and (3.4), respectively.

$$H_2 + S \rightarrow H_2S \tag{3.3}$$

$$H_2 + 2Fe(III) \rightarrow 2H^+ + 2Fe(II) \tag{3.4}$$

The energy yield from reaction 3.3 is 33.4 kJ/mol (0.36 eV per reaction) and 148.6 kJ/mol (1.6 eV per reaction) for Eq. 3.4. Both of these reactions provide sufficient energy to form energy-storing compounds (the terminal phosphate bond in ATP, a later development of high-energy storage efficiency, needs only about 0.3 eV per molecule to form). Iron and especially sulfur are readily available in volcanically active regions, thus the arguments made above for Eq. 3.1 can be made equally strong for reactions 3.3 and 3.4. The major advantage of oxidation of hydrogen via oxygen is its superior energy yield. However, on early Earth molecular oxygen was very rare. Also, in an early development state this reaction may have been too energy-rich, and the more benign oxidation of hydrogen to hydrogen sulfide may have been more controllable and suitable. A similar feedback mechanism as elaborated above for the oxidation of hydrogen via oxygen can be established for sulfur, iron and other compounds as well (Schulze-Makuch 2002). This indicates that the use of chemical energy, by itself or as a feedback cycle allowing microbial differentiation, should be fairly easy to establish. Photosynthesis on the other hand, is a much more complex mechanism with many intermediate steps, and because of its complexity probably evolved after chemoautotrophy. Also, photosynthesis requires the conversion from light energy back to chemical energy (to build energy storage compounds such as ATP, cellular components etc); which adds another layer of complexity. Hose et al. (2000) found that green sulfur bacteria that used photosynthesis outside of a cave oxidized hydrogen sulfide to elemental sulfur inside the lightless cave environment. This finding could support a hypothesis that Photosystem I (simplified in Eq. 3.5) may have developed from the chemotrophic oxidation of hydrogen sulfide, and that the observed green sulfur bacteria are capable of switching back to the older chemotrophic metabolic pathway when needed. Other opinions exist, however. Hartman (1998), for example, proposed photosynthesis as the key to the origin of life.

$$2H_2S + CO_2 + \text{light} \rightarrow CH_2O + H_2O + S_2 \tag{3.5}$$

Based on the previous discussion, it appears that the oxidation of hydrogen coupled to the reduction of some other compound is the most fundamental metabolic pathway for chemotrophic life. However, it does not mean that the first organisms were necessarily based on this type of metabolism. The oxidation of hydrogen does not occur under temperature and pressure conditions on Earth's surface without very good catalysis. Chemoautotrophic organisms have more complex internal requirements than for example heterotrophs feeding on organic macromolecules (McClendon 1999). Thus, heterotrophic organisms that gobbled up high-energy organic molecules present on the primordial Earth are a feasible scenario for the first cells on Earth. However, given the abundance of hydrogen and carbon in the Universe, and the pervasiveness of volcanic activity, at least in our Solar System, it seems reasonable to infer that life elsewhere, would also be based on chemoautotrophy; if not initially, then shortly after organic molecules become scarce (not being replenished at a high enough rate), and that chemoautotrophic life would probably oxidize hydrogen, possibly combined with the reduction of carbon dioxide. The coupling of the chemical reactions to metabolic "work" would have been accomplished either by (1) substrate-level phosphorylation, (2) charge-separation across a membrane with ion pumps, or (3) electron pair bifurcation (Scharf et al. 2015).

3.2.3 *Insights into the Origin of the First Replication Mechanism*

Replication is the ultimate challenge for origin of life researchers. The pre-evolutionary emergence of mechanisms for replication of genetic information are difficult to imagine, primarily because of the involvement of proteins whose structure presupposes a coding mechanism. Benner (2002) pointed out that a suitable biopolymer would have to be able to replicate, catalyze, and evolve without a loss of properties essential for replication, which is achieved in DNA and RNA by repeating charges. Since RNA has been shown to be capable of some catalytic activity (Cech

1985; Ferris 1993; Schwartz 1993), in principle it could have served as the first template and catalyst for its own replication (Lazcano 1994). The formation of RNA chains in water has been observed to occur at moderate temperatures of 40–90 °C (Costanzo et al. 2009). Ball and Brindley (2015) suggested that the oxidation of thiosulfate by hydrogen peroxide might have powered the RNA world, and that spontaneous pH cycling would have enabled the replication of longer RNA molecules. However, the RNA found in contemporary cells is quite labile to environmental degradation. If that was the case at the advent of life, before ribonuclease enzymes were common, RNA would not have been plausible as either the first replication template or agent. Furthermore, in order to be a suitable replicator under early terrestrial conditions, RNA molecules would have to have been very simple and capable of reproducing at a very low error rate. It is not clear whether RNA could have fulfilled this requirement. What was needed was a biopolymer that could be reproduced autocatalytically and undergo chemical evolution.

Lipids, peptide nucleic acids (PNA), threose nucleic acids (TNA), peptides, and proteins have also been considered as the basis for the origin of life on Earth (Bada and Lazcano 2002b; Chaput and Szostak 2003; Nielsen 1993; Orgel 1998; Schöning et al. 2000). In the view of many theorists, a prior stage in the evolution of life—an intermediate link long since lost in the evolutionary progression toward the current complicated mechanism—is needed to explain how replication was first achieved. Whatever the first nucleic acid was—whether RNA or some other compound—its polymerization may have been facilitated by intercalators, acting as "molecular midwives," which possibly also assisted in selecting the first base pairs, even if only trace amounts of suitable oligomers were present (Horowitz et al. 2010). In an alternative view, Dyson (1999) suggested that random populations of molecules evolved metabolic activities and that natural selection drove the evolution of cells toward greater complexity for a long time before the superior replication system based on nucleotides existed. In this view the first RNA would have been "parasitic" to these early cells and later evolved to the benefit of both entities, very similar to the process of the incorporation of mitochondria into eukaryotic cells.

The difficulty of identifying the first replicator led Bernal (1967) to propose the idea that clays or minerals were actively involved in the origin of life. This appears reasonable on the grounds that many properties of life can also be exhibited by minerals, especially clay minerals and metal hydroxides, as discussed before (Table 2.1). Cairns-Smith (1982, 1985, 1986) suggested catalytic clay surfaces as the first genetic mechanisms. A variety of biogenic compounds have been observed to interact with clays such as fatty acids, sugars, amino acids and proteins. Ferris (1993) even observed the formation of RNA oligomers on montmorillonite. The role of mineral templates in the ordering of proto-polynucleotides has been emphasized by Lahav and his colleagues (Chan et al. 1987; Lahav 1991; Lahav and Nir 1997; Lazard et al. 1987, 1988; Orenberg et al. 1985). Huber and Wächtershäuser (1998) have shown the synthesis of peptides on a (NiFe)S surface. Wächtershäuser (1994) and Huber and Wächtershäuser (1998) have proposed a sequence of mineral catalysts, which spontaneously form positive feedback synthesis involving both organic and inorganic compounds. It is interesting to note that adsorption and binding of

DNA on clay and sand particles protects the DNA against degradation by nucleases without inhibiting its transforming ability (Khanna and Stotzky 1992; Lorenz and Wackernagel 1987; Paget et al. 1992). RNA can establish an even stronger interaction with clay than DNA. Single stranded RNA, in fact, can interact with the clay substrate, not only by the formation of hydrogen bonds between the phosphate groups of the RNA and the silanol or octahedral Al(III) groups of the clay, but also through its nitrogen bases. The same would be much more difficult for a double stranded molecule such as DNA with its nitrogen bases inside the double helix (Franchi et al. 1999). This adds further circumstantial evidence that RNA came before DNA and that mineral surfaces are in some way involved in the first replication mechanism. DNA and RNA both use complimentary rather than identical components for replication. A replicator copying identical components seems to be more simplistic and the precursor of RNA and DNA may have functioned that way. It should be pointed out that chemical coding of information is not the only possibility. In principle, any type of stored information that can be replicated and transmitted from one generation to the next would be workable (for a proposed alternative mechanism on replication with magnetic orientations, see Fig. 13.1).

3.3 Other Insights and Inferences

3.3.1 Size

Although life can certainly be macroscopic (we are evidence of it), life's origin must have occurred microscopically. Bounded microenvironments must have a surface to volume ratio that allows diffusion throughout the cell in a brief period of time. Anything larger would slow the rate of essential metabolic reactions to a presumably non-viable level and require large amounts of energy to maintain the structural integrity of the cell. At the same time, a cell has to be large enough to host the molecular machinery required for carrying out its metabolic and reproductive functions. While eukaryotes developed internal specializations such as membrane bounded organelles to enable growth to larger sizes, the first organisms were surely simpler, un-differentiated, and correspondingly minute. While the revolutionary fusion of two or more prokaryotic cells apparently led to the subcellular specialization that enabled eukaryotes to assume an increase in cellular size by an order of magnitude (Margulis and Sagan 1995), the further revolutionary innovation of multicellularity was required to bring about the emergence of macroscopic organisms (Cowen 1995).

It has also been argued that there is a lower as well as upper limit to size. Schrödinger (1944) discussed why we observe organisms the size they are. The disordered activity of thermal motion is too prone to generate random deviation from the statistical determinism upon which a complex set of interactions depends, if the number of interacting components is not very large. A cell too small to contain a sufficient number of reactants would thus be subject to the risk of failure due to "sampling errors" in the normal course of its chemical and physical activities. However, convincing empirical confirmation of a definite lower limit for the size of a viable cell is not available, and evidence is accumulating on nano-sized bacteria about 100-fold smaller than common bacteria. For example, 100–200 nm large bacteria were identified in mammalian cells (Ciftçioglu and Kajander 1998; Kajander et al. 1997; Kajander et al. 2001) and 400 nm large hyperthermophilic archaea from a submarine hot vent (Huber et al. 2002). However, Schieber and Arnott (2003) interpreted nanobacteria as a by-product of enzyme-driven tissue decay. Support of the nanobacteria hypothesis, or at least of the existence of ultra-small microbial cells, was provided by Baker et al. (2006), who recovered an acidophilic archaea with DNA and RNA, which had a cell volume of less than 0.006 μm^3. Luef et al. (2015) also found diverse microbes in ground water with small cell sizes of 0.009 ± 0.002 cubic micrometers. These observations are particularly significant, in the light of claims that particles in the Martian meteorite ALH48001, which are much smaller than conventional terrestrial bacteria, could represent the remnants of life on Mars (see Sect. 10.2).

3.3.2 Environmental Conditions

Predictions of how life could have originated and on what planetary bodies life could be expected to exist would be greatly enhanced if the environmental conditions under which life can form were known. However, even on Earth we are uncertain of the conditions under which life originated. Many researchers (e.g., Kompanichenko 1996; Stetter 1998; Weiss et al. 2016) favor a hyperthermophilic origin of life based on the abundance of organisms discovered at hydrothermal vents on the ocean floors and the results from molecular biology, which appear to indicate that the universal tree of life is rooted in hyperthermophiles. However, high temperatures are generally detrimental to organic synthesis reactions, and the hyperthermophilic last common ancestor could have been simply a deep sea survivor from a near-sterilizing meteor impact. Others have proposed an origin for life on Earth by panspermia, the transport of living forms to Earth from an extraterrestrial source (Arrhenius 1903; Crick and Orgel 1973; Hoyle 1983). The exchange of viable microorganisms between planets in our Solar System appears to be possible via exchange of meteoritic material (Davies 1996; Horneck et al. 2008), however the exchange between stellar systems is statistically so unlikely, that the origin of life on Earth must be sought within the confines of our Solar System (Melosh 2003). Trace element composition in bacteria, fungi and higher organisms shows a strong correlation with the concentrations of these elements in sea water (Goldsmith and Owen 2003), which would support the origin of life in an aqueous environment on Earth. Deamer et al. (2002) and Deamer (2017) proposed a plausible scenario for the origin of life in an aqueous environment with a moderate temperature (<60 °C), low ionic strength, and pH values near neutrality (pH 5–8) with divalent cations at submillimolar concentrations. They based their conclusions on the following rationale: High salt concentration of the present oceans would exert a significant osmotic pressure on any closed membrane system, and divalent cations such as Ca^{2+} and Fe^{2+} (Fe^{2+} presence in the ocean because of the absence of atmospheric oxygen on early Earth) would have a strong tendency to bind to anionic head groups of amphiphilic molecules inhibiting them from forming stable membranes (Monnard et al. 2002). Other indicators, related to the stability and encounter rates of macromolecules, could even point to a cold origin of life (Price 2010; Feller 2017). Only a better understanding of the possible habitats for the earliest life and the processes operating on the early Earth can lead to better insights into which type of environment the first assembly of a living cell took place.

3.3.3 Medium

The presence of a liquid medium is usually assumed for the origin of life on Earth, and indeed the presence of a liquid medium is very favorable. A liquid can provide a suitable medium in which atoms and molecules can move around relatively freely, encounter their reaction partners, and undergo chemical reactions in a reasonable time frame. Atoms are essentially fixed in place in a solid medium, and each atom can only react with its immediate neighbors, limiting severely the possibilities of complex reactions. Densities of atoms and molecules are usually low in the gas phase, and time periods between collisions and interactions between various constituents are large. Thus, complex molecules are not created or transformed in a reasonable time frame (before their disintegration). A liquid has the additional advantage that molecules present in some liquids such as water dissolve into charged ionic species, enhancing reaction rates by orders of magnitude. A liquid medium also allows easy transport of nutrients and disposal of wastes, although some nutrients such as N_2 or CO_2 can also be assimilated from the atmosphere by Earth organisms. Thus, under conditions currently prevailing on Earth, a liquid medium is clearly essential for living processes (for a more comprehensive discussion, see Chap. 7). However, on other planetary bodies a gas can be compressed by gravity or other forces to a similar or higher density than a liquid, thus making up some of the disadvantage compared to a liquid medium. A different scenario can be envisioned in a gaseous atmosphere where no ozone shield is present to drastically reduce the penetration of UV radiation and/or where the atmosphere is relatively thin to allow more ionizing radiation to penetrate. In that case, ions, radicals and electrons are created that are highly reactive, producing versatile chemical species (to some extent this is the case in Titan’s atmosphere). Feinberg and Shapiro (1980) suggested that dense gases at high reaction-enhancing temperatures could be an equally convenient medium for chemically complex reactions and one which is much more common in the Universe than liquid media. Sagan and Salpeter (1976) went so far as to envision specifically adapted organisms living in Jupiter’s dense atmosphere. Evaluating the merit of these ideas is complicated by the fact that no distinct boundary exists between the liquid and gaseous medium at high temperatures and pressures. For example, water reaches the supercritical state at temperatures above 374 °C and pressures above 215 bar, at which conditions it cannot be described adequately as either liquid or gas. While empirical observations suggest that life tends to thrive at boundaries between states of matter, there appears to be no theoretical obstacle to the persistence of life in the absence of such boundaries.

3.3.4 Minerals and Substrates

Whether life could arise from prebiotic precursors in the absence of boundary conditions is another matter. At the very least, encapsulation would appear to be necessary, to keep reactants concentrated sufficiently for self-sustaining (autopoeitic) reactions to be maintained. Whether life first arose under cold, warm, or hot conditions, the ability to concentrate reactants is coincident with the presence of solid substrates in contact with aqueous solutions, whether they be basins of tidal pools, the walls of water droplet inclusions in ice, or the ocean floor. While the spontaneous formation of protomembranous structures that could surround a pool of reactants could also serve to concentrate them, it isn't clear that the protomembranes themselves could form in the absence of a substrate.

The catalytic potential of substrates is the second argument for their likely involvement in any origin of life scenario. Theorists and experimentalists alike have repeatedly turned to the likely role of a substrate in catalyzing reactions that otherwise proceed with great difficulty (Miller and Orgel 1974; Srivatsan 2004). Minerals, in particular, have received close scrutiny for their catalytic properties in the "iron-sulfur" world view of the origin of life (Huber and Wächtershäuser 1998; Wächtershäuser 1994, 2007; Russell and Hall 1997; Russell et al. 2013), where the chemistry of iron and sulfur are central to driving the formation of organic molecules, and coupling this to energy (Schulze-Makuch and Bains 2017).

Minerals that occur in meteorites might have a special relevance both to the catalysis and stabilization of organic compounds. Gull et al. (2015) found that the meteoritic mineral schreibersite promotes phosphorylation reactions of the nucleosides adenosine and uridine. Ruf et al. (2017) discovered new metallo-organic compounds in meteorites that might allow the stabilization of organic compounds on geological time scales. Citrates and other Krebs cycle intermediates discovered in a carbonaceous meteorite led Keller et al. (2017) to the insight that sulfate radicals can enable a non-enzymatic Krebs cycle precursor.

The capacity of minerals for structural regularity, combined with their ability to attract and bind specific organic monomers, makes them prime candidates for a role in the ordering of organic constituents that could have led to the earliest, simple coding mechanisms. This role has been argued most thoroughly and persuasively by Cairns-Smith and Hartman (1986), Lahav (1994), and Lazard et al. (1987, 1988). Even rocks might have played an instrumental role as substrates for the origin of life. Brasier et al. (2011) suggested pumice as possibly playing a critical role due to its remarkable properties including (1) the highest surface area to volume ratio of any rock type, (2) the only rock type that floats at the air-water interface and becomes beached in tidal zones for long periods of time, (3) exposure to various environmental changes including dehydration reactions, and (4) its ability to absorb many metals, organic compounds, phosphates, and even organic catalysts such as zeolites and titanium oxides.

3.3.5 Implications for the Possibility of Life on Other Worlds

A consideration of what we know about the origin of life on Earth provides a list of constraints that is frustratingly short. Indeed, plausible arguments have been made that life could have emerged on Earth in different habitats at the full range of planetary temperatures using a variety of energy sources. Schemes for protometabolism, minimal cells, and primeval coding mechanisms are numerous, with credible models and, in many cases, proof-of-concept data to back them up. Indeed, one is struck by the paucity of possible circumstances that can be ruled out at our current state of knowledge. The consequence of this is that, for now, the door to speculation on the conditions under which life could arise on other worlds needs to be kept open rather wide.

That said, there are virtually no proposals that life on Earth could have originated other than in water. This is natural enough, since Earth is a water world, and the organisms that comprise life on Earth are all aqueous systems at the cellular level. It does raise the question, however, of whether all life needs to originate in water. As we will argue in Chap. 7, while water is the most universal solvent, it is hardly the only one possible in which complex chemistry can occur. The more difficult question to answer is whether life can originate in any medium other than liquid. Wherever in the Universe where liquids exist, or existed at one time, therefore, would appear to provide in principle a candidate habitat for the origin of a living system of some sort.

Since the atmospheres of the gas giant planets grade into liquids at increasing depths, the question may be asked whether life could arise in such habitats—in the lower reaches of the cloud layers of Jupiter or Saturn, for example. That prompts the next issue—whether a solid substrate, or at least discontinuous phase transition, is a further requirement for the origin of life. A more extreme constraint would be to posit that solid mineral surfaces are the most likely substrates for the first formation of life. While there appears to be no absolute, theoretical necessity for solid substrates in biogenesis, many theoreticians and experimentalists have found their models and data to be reconciled much more easily if solid substrates can be invoked. If substrates turn out to be necessary for the generation of living systems, we may expect to find life much more likely on differentiated, heterogeneous worlds, where interfaces between atmospheres, oceans, and land are more common.

3.4 Synthetic Life

In lieu of finding life elsewhere in the Universe, efforts have been under way in recent decades to modify microorganisms in the laboratory with functions and capabilities that were previously unknown to exist. Synthetic approaches are less concerned with how life originated on Earth, but how to create the process de novo, either in the laboratory or in a simulation (Scharf et al. 2015). Thus, one of the eventual goals of some of these efforts is to create life that is markedly different from life as we know it. This has been attempted mostly through the use of biomolecules and their component materials that are usually not found in living organisms today, such as non-canonical amino acids, additional nucleotide bases, or extra codons. The ultimate goal is to design an artificial cell, but this has not yet been achieved. However, natural cells can be extensively modified, genetically engineered to degrade previously undegradable plastic polymers (Madison and Huisman 1999), fulfill medical applications (Saeidi et al. 2011), or even replicate an expanded genetic alphabet (Malyshev et al. 2014).

3.4.1 The Standard Genetic Code

Codons are nucleotide base triplets that specify which amino acid is added during protein synthesis. This genetic code is nearly universal, consisting of twenty amino acids assigned to 61 codons, with the remaining three serving as stop codons (Table 3.1). That arrangement is considered to be the standard genetic code, because of its (1) strict codon symmetry, (2) specification of a definite number of amino acids that serve as protein building blocks, and (3) redundancy of physicochemical properties, especially with regard to the hydrophobicity and hydrophilicity of the different amino acids (Ardell and Sella 2001). The twenty encoded amino acids are referred to as the standard or canonical amino acids. A subset of these amino acids can be grouped into positively charged, negatively charged, neutral hydrophilic, aliphatic hydrophobic, and aromatic hydrophobic chemical compounds. If any one of these amino acids would have to be replaced, another one with similar physicochemical properties would have to be included instead. This led Budisa (2005) to suggest that if the tape of life were to be rewound, or if life were to originate on another planetary body, about two-thirds of the basic building blocks would have to be of the same physicochemical nature as those on Earth. Several authors have suggested that some of the amino acids chosen by terran life might be universal to all life, while other amino acids were chosen later and are specific to life on Earth, perhaps as the result of early metabolic constraints or selective pressures under specific conditions (Higgs and Pudritz 2009; Philip and Freeland 2011; Rios and Tor 2012).

The code is also redundant, for example, all codons that start with GC code for the amino acid alanine. This has generally been interpreted as the consequence of a

Table 3.1 Codons and the related amino acids for protein synthesis

Base position			Amino acid	Base position			Amino acid
1	2	3		1	2	3	
G	G	G	Glycine	C	G	G	Arginine
		A	Glycine			A	Arginine
		C	Glycine			C	Arginine
		U	Glycine			U	Arginine
	A	G	Glutamic acid		A	G	Glutamine
		A	Glutamic acid			A	Glutamine
		C	Aspartic acid			C	Histidine
		U	Aspartic acid			U	Histidine
	C	G	Alanine		C	G	Proline
		A	Alanine			A	Proline
		C	Alanine			C	Proline
		U	Alanine			U	Proline
	U	G	Valine		U	G	Leucine
		A	Valine			A	Leucine
		C	Valine			C	Leucine
		U	Valine			U	Leucine
A	G	G	Arginine	U	G	G	Tryptophan
		A	Arginine			A	STOP
		C	Serine			C	Cytosine
		U	Serine			U	Cytosine
	A	G	Lysine		A	G	STOP
		A	Lysine			A	STOP
		C	Asparagine			C	Tyrosine
		U	Asparagine			U	Tyrosine
	C	G	Threonine		C	G	Serine
		A	Threonine			A	Serine
		C	Threonine			C	Serine
		U	Threonine			U	Serine
	U	G	Methionine		U	G	Leucine
		A	Isoleucine			A	Leucine
		C	Isoleucine			C	Phenylalanine
		U	Isoleucine			U	Phenylalanine

The codon assignments can generally be regarded as conserved and universal, through there are distinct exceptions. Twenty amino acids are assigned to 61 codons, and the remaining three are stop codons

G Guanosine, *A* Adenosine, *C* Cytidine, *U* Uridine

natural selection process imposed by the chemical environment at early stages of the origin of life, perhaps when fewer amino acids were employed and codons consisted of only two bases instead of three. New amino acids would have been brought into the code until no further significant improvements followed, at which time the conservation of the code took place—popularized as the “frozen accident” concept

(Crick 1968). However, as evidenced by recent research, remarkable flexibility has remained, as elaborated below.

3.4.2 The Flexibility of the Code and Non-canonical Amino Acids

While variations in the standard genetic code had been considered early on (Crick and Orgel 1973), the first confirmed variations were discovered in human mitochondrial genes (Barrell et al. 1979), and later also in other mammals, fungi, and invertebrates. Variations are relatively slight, such as the translation of the stop codon UGA as the amino acid tryptophan in *Mycoplasma* species (Yamao et al. 1985), the translation of CUG as the amino acid serine instead of leucine in *Candida* species (Santos and Tuite 1995), and the reassignment of the codon AGG that usually codes for the amino acid arginine (Table 3.1) as "stop" in the mitochondria of mammals, and as serine in the mitochondria of the fly *Drosophila*. Budisa (2005) suggested that variations in the translation of certain codons could be classified into two general categories: (1) reassignment of the standard termination codes UGA, AAA, and UAG to the amino acids tryptophan or glutamine in some bacteria, archaea, the mitochondria of many organisms, and even nuclear genes of some protozoa, and (2) translation alterations from methionine to isoleucine, lysine to asparagine, arginine to serine, leucine to threonine in mitochondria, and leucine to serine in the nuclear genes of *Candida*. Intriguingly, some viruses such as the totiviruses have adapted to the modified genetic code of their hosts by incorporating the same modifications into their own codes (Taylor et al. 2013).

In addition, recent studies have revealed that some organisms naturally encode for two additional amino acids: selenocysteine and pyrrolysine (Zhang et al. 2005). UGA can code for selenocysteine and UAG for pyrrolysine if the associated signal sequences are present in the mRNA. The amino acid repertoire can even be expanded under different growth conditions from 20 to 21 amino acids (to include pyrrolysine) as shown in the archaea *Acetohalobium arabaticum* (Prat et al. 2012).

While there is thus some variation and more flexibility in the code than thought just a few years ago, the fact remains that all organisms have three nucleotides in their codons and utilize tRNA and ribosomes to read the code in the same direction for translating into a specific sequence of amino acids. One interpretation of the observed variations is that the genetic code is still evolving, or at least still capable of evolving. This is also supported by experimental efforts to incorporate non-canonical amino acids into the genetic code, with varying degrees of success (Xie and Schultz 2005; Wang et al. 2009; Hoesl et al. 2015; Lin et al. 2017).

In principle, there are about 10^{84} genetic codes possible using the canonical amino acids and a triplet codon system. Natural selection would be expected to place a premium on reducing the frequency of translation errors, so the genetic code for terrestrial life must be highly optimized (Zamudio and José 2017). We would anticipate, however, that life on other worlds could use a different code with similar or perhaps even superior optimization to that on Earth. The genetic code for life on Earth is also optimized to water as a solvent, with its particular hydrophobic/hydrophilic character. If some other solvent is used for life elsewhere on a planetary body, then a different subset of amino acids with a different balance of hydrophobic and hydrophilic characteristics would be expected to be favored by natural selection, if proteins in those systems are composed of amino acids and function as they do in life on Earth.

3.4.3 Bottom-Up and Top-Down Approaches to the Origin of Life

There are two principle approaches to resolving the origin of life problem, both of which are based on the assumption that life increases in complexity with time. The bottom-up approach attempts to build life based on simple ingredients and first principles. An example would be the effort to yield synthetic life forms built from scratch with a genetic code having a novel arrangement and being based, for example, on different amino acids and nucleic acids. We are still far away from reaching this goal. Current research is still at the stage of analyzing what amino acids would, in principle, have to be included into a genetic code (Davila and McKay 2014), then replacing canonical with synthetic amino acids in microorganisms and evaluating their long-term survival (Hoesl et al. 2015). Another approach is to create artificial genetic systems, such as expanding the genetic code from, for example, four nucleotides to six nucleotides. Intriguingly, a synthetic genetic system tested with six nucleotides did further evolve as such without reverting back to a wholly natural system, indicating at least the possible viability of such a system (Yang et al. 2011). Another example of a bottom-up approach, in which information is also obtained about the general versatility of life, is the use of artificial protocells composed of fatty acids and proteins to study competition, including predatory behavior, between two protocell populations (Qiao et al. 2016).

The top-down approach has advanced a bit further. An example is the effort by the Craig Venter group to synthesize the microbe with the smallest genome known to date (Fraser et al. 1995; Hutchison et al. 2016). The starting point was a genome which was transplanted into the cell of a microorganism of the *Mycoplasma* group, a genus of parasitic bacteria without cell walls that already has a relatively small genome. After an arduous process of trial and error, a newly synthetic organism was achieved with only 531,000 base pairs of DNA. It is to date the record holder for the smallest genome (Hutchison et al. 2016). However, even this organism still has 149 genes with unknown biological functions, so the creation of a synthetic microorganism with an even smaller genome appears likely.

3.5 Chapter Summary

Despite huge gaps in our knowledge of how life actually began on Earth (or an alien world prior to its transport to Earth), a vague but plausible outline of how it happened can be postulated. There is good reason to assume that prebiotic organic precursors were able to accumulate in the primeval oceans, generated from simple precursors with the abundant energy at hand. Self-sustaining (autopoeitic) reactions could have begun, perhaps aided initially by inorganic structural features that could have provided catalytic functions and templates for regulating alignment of organic components. Eventually, stable and reproducible macromolecules could have arisen for directing metabolic pathways, once membranous boundaries semi-isolated the protobiotic systems from the ambient environment. Over time, the original inorganic catalysts and scaffolds that provided reproducibility would have disappeared, as fully organic means of replication took over.

Such a scenario, general though it is, has several implications for the generic origin of life anywhere. First, the most primitive organisms must be microbial in size. Remote detection from orbiters would therefore likely be restricted to visualizations of large aggregates of such organisms, while landers would need to be equipped with microscopes for a realistic view of individual organisms. Second, early forms of life probably derive their energy by the oxidation of hydrogen coupled to some other reaction. Thus, any other world with that potential would, in principle, be a candidate for the origin of life and its persistence to the present day. In fact, any world on which an energy gradient exists is potentially capable of supporting life. Finally, any genetic program for the encoding and transmission of information is based most likely on some form of macromolecular heterogeneity, possibly in concert with inanimate scaffolds such as clay or other minerals, prior to the transition to a wholly organic repository of information. Though the genetic code is nearly universal for life on Earth, some exceptions exist and experiments have shown that variations in the code are possible. Thus, life on other worlds—even if utilizing proteins constructed of amino acids—may use variations unknown to us.

While these inferences may be somewhat biased by the one case of life that we know on Earth, we would close this chapter by noting that the chemical composition of living matter resembles the composition of stars more closely than the chemical composition of our planet, so terran life may be more typical for life in the Universe than we think.

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,

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_4

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

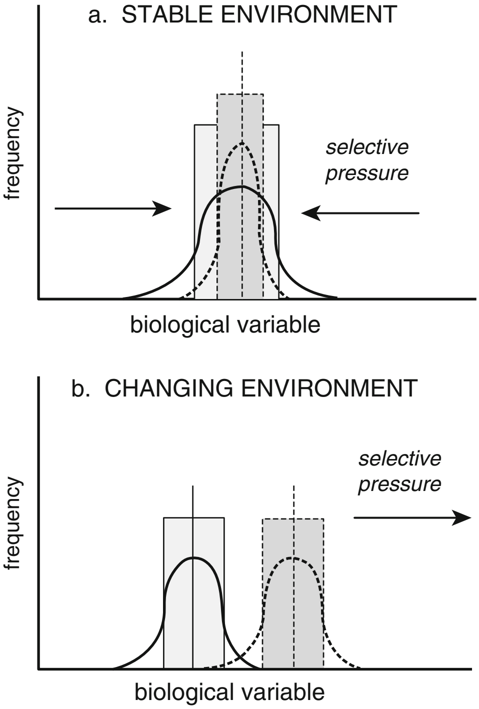


Fig. 4.1 Effect of selective pressure on biological characteristics, illustrated by changes in the frequency distribution of a quantitative biological trait in response to different forms of selective pressure. (**a**) In stable environments, stabilizing selection promotes elimination of peripheral values 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 ($\mathrm{pH} > 10$) than of extreme acidities ($\mathrm{pH} < 1.0$), 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.

Chapter 5
Energy Sources and Life

An external energy source is a necessary condition for life, because living systems require a flow of energy to organize materials and maintain a low state of entropy (Morowitz 1968). Energy is also needed to perform work. Life on Earth can be distinguished by the external energy source that it uses. Photoautotrophic life derives energy from sunlight and uses CO_2 as a carbon source. Chemolithotrophic life uses redox reactions involving abiological compounds and chemolithoautotrophic life uses CO_2 (or other small carbon compounds) as a carbon source. Chemoheterotrophic life uses high-energy organic molecules, produced in general by autotrophic life, as a source of energy and carbon. On other worlds, where other forms of energy may be more abundant, or where the primary sources for energy on Earth may be lacking, life may have evolved to depend on different forms of energy. In this chapter, we critically analyze the various forms of energy that are potentially available to living systems, consider other factors that bear on the evolution of energy harvesting mechanisms, and evaluate the apparent availability of different forms of energy at different sites in our Solar System.

5.1 Life as We Know It

The National Research Council (Baross et al. 2007) defined terran life as a form of life that (1) uses water as a solvent, (2) is built from cells and exploits a metabolism that focuses on the carbonyl group (C=O), (3) is thermodynamically dissipative, exploiting chemical-energy gradients, and (4) exploits a two-biopolymer architecture that uses nucleic acids to perform most genetic functions and proteins to perform most catalytic functions. Terran organisms store energy in two principle ways, either in a molecule that has a high free energy of reaction under the conditions that prevail inside the organism (e.g., ATP), or as a gradient of concentrations of chemical species across a physical structure (e.g., a biological membrane). The term "terran" was used to denote a particular set of biological and chemical characteristics that are

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_5

exhibited by all life on Earth. Thus, any alien life could be terran or nonterran depending on its characteristics. With regard to energy, terran life has evolved to use light, organic molecules, and oxidizable inorganic chemicals as abundant sources of energy on Earth, so living systems have evolved specialized adaptations to use these energy sources. As more organisms are discovered and described on our planet, the recognized "landscape" of terran life has expanded, and some theoretical possibilities previously considered only in science fiction have become reality. One example is the discovery of the first photosynthetic animal, a sea slug which has integrated a nuclear gene of oxygenic photosynthesis (*psb*O), derived from its algal food source, into its germ line (Rumpho et al. 2008). Another example is the discovery of the Loricifera, apparently actively metabolizing microscopic animals in the oxygen-free sediment on the bottom of the Mediterranean Sea (Danovaro et al. 2010), though whether they need no oxygen at all is still controversial.

5.1.1 Oxidation-Reduction Chemistry as an Energy Source for Life

Energetically favorable redox-reactions are the basis for life on Earth. The best known and most common types of metabolism are based on hydrogen oxidation and methanogenesis, sulfur reduction and oxidation, iron and manganese reduction, denitrification, and aerobic respiration. However, many other energy-yielding redox-reactions are known that involve the reduction or oxidation of relatively rare elements such as arsenic, selenium, copper, lead and uranium. Thus, there does not appear to be a basic limitation on which elements or redox-reactions can be used. Rather, the reactions that occur will likely be dictated by the abundance, availability and suitability of a specific element in a certain type of environment. The diversity of arsenic and selenium respiring bacteria thriving in playas (alkaline salt lakes) and mining tailings is a good example (Stolz and Oremland 1999). Another intriguing example is provided by co-cultured iron-reducing and iron-oxidizing bacteria that both use magnetite as a source medium. Magnetite contains both Fe(II) and Fe(III). Fe(II) was shown to be oxidized by *Rhodopseudomonas palustris TIE-1* using light energy, while the co-cultured bacterium *Geobacter sulfurreducens* reduced Fe(III) under anaerobic conditions, thus effectively using the mineral magnetite under varying environmental conditions as a naturally occurring battery (Byrne et al. 2015).

As pointed out in Chap. 3, the oxidation of hydrogen may be one of the most ancient and basic metabolic pathways for life on Earth, and possibly elsewhere. The oxidation of the most common element in the Universe yields an appreciable amount of energy, 2.5 eV per reaction (or 237.14 kJ/mole, 56.68 kcal/mole) assuming standard conditions (25 °C, 1 atm)

$$H_2 + \frac{1}{2}O_2 \rightarrow H_2O \tag{5.1}$$

The metabolic pathway is called methanogenesis if the oxidation of hydrogen is coupled with the reduction of carbon dioxide to methane.

$$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O \tag{5.2}$$

Methanogenesis as defined here does not imply that the hydrogen has to be supplied in molecular form, but it may also derive from an organic source. The reduction of carbon dioxide to methane requires the expenditure of energy, but due to the production of two water molecules the reaction is energy-yielding (1.4 eV energy yield at standard conditions, 474.28 kJ/mol). This reaction powers autotrophic life at hydrothermal vents and also some of the endolithic life present in the cracks and pores of the basaltic ocean floor. Seismogenic hydrogen gas, produced in rocks by brittle fracturing on fault planes, has also been suggested as a potential microbial energy source on Earth and Mars (McMahon et al. 2016). In addition to providing energy for metabolism, the methanogenesis pathway has the advantage of fixing carbon dioxide that can further be used for organic synthesis reactions. Another important redox reaction is the oxidation of molecular hydrogen coupled to the reduction of iron.

$$H_2 + 2Fe(III) \rightarrow 2H^+ + 2Fe(II) \tag{5.3}$$

The energy yield from this reaction is 1.6 eV (148.6 kJ/mol). Examples of terrestrial organisms that use this reaction are *Pseudomonas* sp. (Balashova and Zavarzin 1980) and *Shewanella putrefaciens* (Lovley et al. 1989). There are many other compounds that can be coupled to the oxidation of hydrogen. One intriguing example is the reaction of hydrogen peroxide (H_2O_2) with molecular hydrogen to water, which is performed by *Acetobacter peroxidans* (Doelle 1969; Tanenbaum 1956). This can serve as a model pathway for highly oxidized environments not commonly found on Earth.

Sulfur metabolism appears to be very ancient, as many terrestrial microbes are thermophilic and are associated with expressions of volcanic activity such as hot springs. One of the reasons that sulfur is so widely used is that it occurs in a wide variety of oxidation states including fractional nominal oxidation states. Oxidation states for sulfur of $+7, +5, +4, +3\frac{1}{3}, +3, +2.5, +2, -0.4, -0.5, -\frac{2}{3}, -1$ are known, leading to a complex inorganic sulfur cycle, much of which is mediated by microbes (Amend and Shock 2001). Sulfur reducing bacteria are quite commonly observed to populate anoxic sediments of bottom fresh waters, and marine and hypersaline aquatic environments including submarine hydrothermal vents. Many sulfate reducers prefer molecular hydrogen or hydrogen from an organic source such as acetate or lactate, which is used as an electron donor. Some of the sulfur reducing bacteria live symbiotically with green sulfur bacteria that photooxidize hydrogen sulfide to elemental sulfur (early photosystem). Other sulfur bacteria such as

Desulfobulbus are capable of organizing themselves into long, insulating cables made up of several thousand individual cells and connecting the bottom bacteria, living in low oxygen concentrations, to those in high oxygen concentrations, shuttling electrons from one to another (Pfeffer et al. 2012). Sulfur oxidizing microbes are common in oxygen-rich aquatic ecosystems and ground-water systems, often in close proximity to sulfur reducing microbes (Schulze-Makuch 2003). Sulfur oxidation may be coupled to the reduction of iron as in the case of *Thiobacillus thiooxidans* or the thermophilic microbe *Sulfolobus acidocaldarus* (Brock and Gustafson 1976; Lovley 1991).

$$S^{o} + 6\,\mathrm{Fe(III)} + 4\,H_2O \rightarrow HSO_4^{\,-} + 6\,\mathrm{Fe(II)} + 7H^{+} \tag{5.4}$$

This reaction yields a high amount of energy, 2.6 eV per reaction under standard conditions and occurs in acidic environments.

Iron and manganese reduction occur in those environments associated with hydrothermal vents in the oceanic basalt crust as well. Iron reduction is coupled to the oxidation of hydrogen (see Eq. 5.3) or the oxidation of organic sources such as glucose, lactate, formate and organic acids. Under oxygen-rich conditions the energetically favorable reaction is the oxidation of iron, which can already occur under slightly oxidizing conditions.

$$\mathrm{Fe(II)} + \frac{1}{4}O_2 + H^{+} \rightarrow \mathrm{Fe(III)} + \frac{1}{2}H_2O \tag{5.5}$$

This kind of reaction is performed on Earth, for example, by *Gallionella* and *Thiobacillus ferrooxidans* (note that *T. ferrooxidans* can grow by oxidizing sulfur as well as iron). The net gain of energy is 0.5 eV for each Fe^{2+} that is oxidized. While metal-oxidizing bacteria are difficult to study under conventional culture conditions, Summers et al. (2013) used an electrode as the sole energy source for a laboratory culture of the iron-oxidizing, lithotrophic bacterium, *Mariprofundus ferrooxydans PV-1*. Schulze-Makuch and Irwin (2002a) suggested an iron cycle between anaerobic ocean bottom water and oxidized upper ocean water for ice-covered planetary oceans (such as the one suspected on Europa) as a possibility for a primitive microbial ecosystem.

Denitrification and metabolism using molecular oxygen are metabolic pathways that likely developed later as the Earth's atmosphere became enriched in nitrogen and oxygen. Thus, they don't relate directly to the primordial stages of life. However, denitrification and metabolism using molecular oxygen are among the highest energy-yielding metabolic pathways, and thus are extremely important for the later evolution of life. Heterotrophic organisms that use pre-existing, energetically rich organic macromolecules are usually considered to have evolved later as well. However, speculation has long held that the very earliest organisms on Earth were heterotrophic rather than autotrophic (Fox and Dose 1977; Haldane 1929; Oparin 1938), based on the assumption that energetically rich organic macromolecules may have been supplied on the early Earth in abundance by prebiotic synthesis (Miller and Orgel 1974) and/or by comet delivery (Chyba et al. 1990).

5.1.2 Light as an Energy Source for Life

Probably one of the most important factors in the success of life on Earth is the use of a narrow band of electromagnetic radiation (visible light) emitted from the Sun at a high intensity. The evolution of photosynthesis allowed life to tap into a practically unlimited source of energy. Sometime early in the history of the Earth, photosynthesis developed as a favorable energy capture mechanism.

The free energy that can be provided by photoautotrophy can be calculated by multiplying the frequency (f) of the light that is used by Planck's constant (h).

$$\mathrm{W} = \mathrm{h}f \tag{5.6}$$

The frequency varies inversely with wavelength, and somewhat different wavelengths are used by different organisms. For example, bacterial chlorophyll uses a wavelength of 800–1000 nm, while carotenoids in plants absorb wavelengths ranging from 400 to 550 nm. The average energy gain across the visible spectrum is about 2 eV (190 kJ/mol, 45 kcal/mol). It is interesting to note that this value is very similar to the free energy provided by hydrogen-oxidizing prokaryotes thought to represent early chemoautotrophic organisms. Thus, from a purely energetic viewpoint, light energy and chemical energy are equally competitive.

5.2 Life as We Don't Know It

Light, organic molecules, and oxidizable inorganic chemicals are abundant sources of energy on Earth. Thus, living systems on our planet have evolved to use these forms of energy. However, living cells make biological use of other forms of energy as well. Organisms can sense heat (Viswanath et al. 2003), pressure, stretch, movement of air and fluids, gravity, and electric and magnetic fields (Blakemore 1982; Schmidt-Nielsen 1990). All these stimuli generate responses through membrane transductions, either by altering the gating of ions that change transmembrane potentials, or by initiating metabolic changes through secondary messenger systems. Thus, they indicate the capacity of living systems to use energy in a variety of forms to affect biological processes.

The accumulation of high-energy intermediates such as adenosine triphosphate (ATP) depends on the generation of proton gradients across membranes. Since the molecular machinery of cell membranes mediates most sensory transductions, it is reasonable to assume that natural selection could have favored the evolution of membrane mechanisms that transform heat, pressure, stress, magnetic fields, or kinetic energy into high-energy covalent bonds, either directly or indirectly by coupling to ion or proton pumps. Perhaps these mechanisms have failed to evolve in living systems on Earth only because of the lack of a need for them. On other worlds where light is unavailable, natural selection would be expected to favor the evolution of alternative energy harvesting mechanisms (Schulze-Makuch and Irwin 2002a).

How much energy is needed to power a living system? We do not know, but we can get a rough idea by calculating the amount of energy used by living organisms on Earth. First, as mentioned before, both light energy (in the visible spectrum) and chemical energy (hydrogen oxidation) provide about the same amount of energy (2 eV per photon or hydrogen molecule oxidized). Second, we know how much energy is required to assemble energy-storing compounds used on Earth. For example, an energy of about 7 kcal/mol or 0.304 eV per molecule (4.86×10^{-23} kJ or 1.16×10^{-23} kcal) is required to form the terminal phosphate bond in ATP. While the chemical storage form of energy used by another form of life would not necessarily be ATP or anything like it, the amounts of energy required for ATP phosphorylation on Earth provide a known benchmark. Given the required bonding energy of 0.304 eV, it follows that a photon of light or the oxidation of a molecule of hydrogen to water provides in theory sufficient energy to convert 6–8 molecules of ADP to ATP, if the conversion is close to 100% efficient. With this benchmark in mind, we can speculate whether other energy sources could be as efficient as chemical energy or light on Earth to provide sufficient energy for a living organism under a different set of environmental conditions.

5.2.1 Electromagnetic Waves (Other than Visible Light)

The wavelength of light used by phototrophic organisms lies in the visible and near-infrared spectrum. The fact that these specific frequencies are used may merely reflect adaptation by Earth organisms to the most prevalent wavelengths of electromagnetic radiation emitted from the Sun. These wavelengths are also transmitted through our atmosphere well, making them readily available to life on the surface of our planet. On other worlds the same may be true, even though many habitable worlds could be associated with other types of stars such as F, K or M dwarf stars. Kiang et al. (2007a, b) suggested that photosynthetic organisms on a planet surrounding an F2V star would likely exhibit peak absorbances in the blue, on a K2V star in the red-orange, and on an M star in the near infrared. Most atmospheres would absorb far less UV radiation, and absorb wavelengths below near-infrared to a great extent. However, in principle other wavelengths could be harvested. The problem with more energy-rich radiation such as that in the ultraviolet range, is its detrimental effect on many biogenic molecules such as proteins and DNA (Rettberg and Rothschild 2002). Thus, any organism using UV or more energy-rich radiation would need some kind of protection to harvest this type of electromagnetic wavelength, or would have to be based on a very different type of biochemistry. Alternatively, organisms may be able to take up a greater amount of less energy-rich radiation from near-infrared wavelengths. This radiation is plentiful in the Universe, as any body or substance above 0° K will radiate infrared light. A prime example is hydrothermal vents on the ocean floor of Earth that emanate infrared light at a depth where photons from the Sun cannot reach (Van Dover et al. 1994; White et al. 2002). Analysis of a green sulfur bacterium from a deep-sea hydrothermal vent indicated that geothermal radiation and associated reduced sulfur compounds are sufficient to at least enhance the survival of green sulfur bacteria in the otherwise dark oceanic depths (Beatty et al. 2005). This organism, which was not found to be present in the surrounding water, thus expands the range of possible environments that could harbor life dependent on electromagnetic energy to drive endergonic biochemical reactions. In a quantitative assessment for the potential of photosynthesis at hydrothermal vents, Perez et al. (2013) found that organisms could theoretically use infrared photons up to a wavelength of 1300 nm if a high efficiency is maintained. However, more photons of infrared radiation than of visible light would have to be harvested to obtain a comparable energy gain. Nevertheless, this may be an option for life at hydrothermal vents in subsurface oceans, as speculated to exist at the water-mantle boundary of Europa. Experimental evidence has also been provided by Gusev and Schulze-Makuch (2005) that microbes may be capable of converting radio waves into chemical energy to supplement their energy needs. They hypothesized that protons in liquid water could be excited at their natural resonance frequencies by the Sun's and Earth's natural magnetic field through Langmuir oscillations, generating enough kinetic energy to charge the transmembrane potential of a cell. Even less energy would be available from this source. The hypothesis is very controversial, however, and has not yet been independently confirmed by other research groups.

Terran life is dominated by oxygenic photosynthesis, which is used by all plants and some bacteria (e.g., cyanobacteria). The more ancient anoxygenic photosynthesis also uses chlorophyll to capture light energy and build biomass, but does not make free oxygen. It is used by some bacteria such as green sulfur bacteria and purple bacteria. Other types of photosynthesis have been suggested that are not known to occur on Earth. Houtkooper and Schulze-Makuch (2007) suggested a type of oxygenic photosynthesis with hydrogen peroxide rather than molecular oxygen as a product; and Bains et al. (2014) wondered about methane-based photosynthesis, which they thought might be common in hydrogen-dominated atmospheres. Haas (2010) proposed chlorinic photosynthesis, the phototolytic oxidation of aqueous Cl^- by hypothetical organisms to form dihalogen and halocarbon products, coupled with the assimilation of carbon dioxide. O'Malley-James et al. (2012) speculated that Earth-like planets in binary and multiple star systems could not only host photoautotrophs, but also allow for more exotic forms of photosynthetic life.

5.2.2 Thermal Energy

Radiogenic elements decay in planetary interiors and produce heat that drives all major processes in the interior of planetary bodies. Examples for Earth include keeping the outer core liquid, establishing a protective magnetic field, and driving plate tectonics. Tidal flexing can also cause heat to emanate as observed on Io, the volcanically most active planetary body in the Solar System. The tidal flexing is caused by the changes in gravitational attraction to Jupiter and to some minor degree to the other Galilean satellites. Heat released by tidal flexing is also observed in the Earth-Moon system, but to a lesser degree.

This geothermally produced heat results in thermal gradients on which thermotrophic organisms could feed. We have named these putative organisms "thermotrophs" by analogy with phototrophic and chemotrophic organisms that use light and chemical energy as basic energy sources, respectively (Schulze-Makuch and Irwin 2002a). A relatively straightforward possibility would be to harvest energy from the thermal gradients at hydrothermal vents. Thermotrophic life could harvest energy from the high heat capacity of water, which is about 4 kJ/kg K between 0 and 100 °C and 0 and 100 MPa pressure. If we assume a cell mass of 10^{-12} g comparable to that of microbes on Earth (Madigan et al. 2000), and further assume that one tenth of the cell mass is a vacuole of water from which the thermotrophic organism could extract energy, about 2.5×10^{6} eV would be obtained from cooling the vacuole by 1 °C. If a microbe were able to use the Carnot cycle, the organism could extract about 9000 eV of usable energy for a temperature change from 5 °C to 4 °C (Schulze-Makuch and Irwin 2002a); upon larger decreases the potential free energy gain would increase proportionally. High-energy metabolites within the organism could be produced via conformational changes if a temperature gradient between vacuole and cell plasma were present. For a cell as large as the giant pantropical alga, *Valonia macrophysa* (Shihira-Ishikawa and Nawata 1992), containing a water vacuole of approximately 10 g, the potential energy yield could be close to 1 J.

Thermal gradients could also be harvested directly. In a series of papers Muller (1985, 1993, 1995, 2003) and Muller and Schulze-Makuch (2006a) suggested thermosynthesis as a plausible metabolic pathway. Thermosynthesis, just as a steam engine, would make use of a phase transition (Muller and Schulze-Makuch 2006b). Membranes undergoing the thermotropic phase transition would increase the mobility of the molecules within the membrane (Muller and Schulze-Makuch 2006a). Due to a change in dipole potential, such a transition would quite plausibly result in a change in potential across the membrane (Muller 1993). Although this potential change has not been measured directly, similar potential changes that undergo the thermotropic phase transition have been measured across monolayers of lipids at the water/air interface. The changes can easily reach 100 mV—high enough to drive ATP synthesis (Muller and Schulze-Makuch 2006a). Electrogenic ATP synthases might be capable of converting the electrical energy gained by thermosynthesis into ATP if their activity and stoichiometry were properly regulated (Muller 1993). If correct, thermosynthesis could be a plausible basic pathway of metabolism for early organisms on Earth, possibly a progenitor of bacterial photosynthesis (Muller 1985, 1995, 2003), and an option for possible life on many other worlds.

A potential drawback to the use of thermal energy is its inefficiency. The most efficient thermodynamic system known—the Carnot engine—is very inefficient, especially for small temperature differences. Because of the low efficiency, most of the energy in a thermal gradient would be dissipated as heat without being captured by chemical bonds, and would readily degrade the thermal gradient itself. A possible solution to the problem would be a thermotrophic organism that could shuttle back and forth across fairly sharp environmental gradients, or a thermotrophic organism that possesses an elongated body and makes use of convection to dissipate the unusable entropy-related energy.

Based on these principles, Muller and Schulze-Makuch (2006a) visualized four different physiological versions of a possible thermotrophic organism (Fig. 5.1). In the first type, a water vacuole would be warmed when the thermotroph moved into the vicinity of a hydrothermal vent. It could then float into the colder ocean, using the buoyancy of the warm vacuole, and harvest the free energy released by heat flow down the internal thermal gradient between the vacuole and the surrounding cell.

The other three types of thermotrophs are envisioned as sessile, with one end remaining anchored to the surface of the hydrothermal vent. The second thermotroph is a filamentous-type of organism that spans the thermal gradient between the hot structure and the cold ocean. Near the structure it could take up hot water in a vacuole, and then gain free energy as the vacuole moves inside the cell to the cooler distal part. The third type of thermotroph would take up cold ocean water in a vacuole or cavity, and eject warm water from its base, not unlike the pattern of water flow seen in sponges, barnacles or mussels. While this process is used for filter feeding by these contemporary organisms, it may hint at an ancestral mechanism for the direct harvesting of energy from heat (Muller and Schulze-Makuch 2006a).

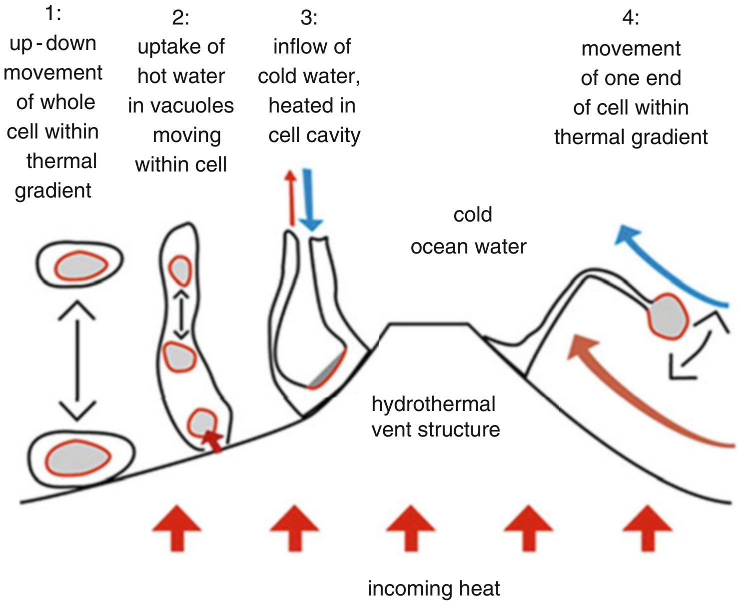


Fig. 5.1 Four types of thermotrophs that could be present near a hydrothermal vent. Areas within the organisms where the thermal gradient is tapped are marked in grey, hot water areas are red, and cold water areas are blue (modified from Muller and Schulze-Makuch 2006a)

Interestingly, mussels are still commonly found near vent structures today (Van Dover and Lutz 2004).

The fourth type of anchored thermotroph would have a distal end that moves freely in the cold ocean water, similar to the large sulfur bacteria (Gundersen et al. 1992) and giant tubeworms (Van Dover and Lutz 2004) present in the deep ocean environment today. Since the heat flux would vary on time scales as short as minutes (Tivey et al. 2002), water flow would be turbulent, and significant thermal fluctuations near the surface would therefore be expected, which could be harvested by the organisms, especially at summits of microscopic roughness that stick out above the boundary layer. Similar thermal fluctuations have been observed on top of bacterial mats in these environments (Gundersen et al. 1992). This type of thermotroph, can be compared to an organism that 'filters' temperature fluctuations from water, possibly sharing important characteristics of a direct progenitor of water filtering organisms such as the sessile protist ciliate *Vorticella*, with its long, quickly contractable stalk (Moriyama et al. 1998; Muller and Schulze-Makuch 2006a). It has to be emphasized that there are no known contemporary organisms that use thermal gradients as an energy source for metabolism, though such organisms conceivably could have existed on the early Earth, to be later outcompeted by phototrophic and chemotrophic organisms. But they could exist on an alien world. One possible example would be within the likely subsurface ocean of Europa, where light as an energy source is not readily available, but thermal gradients are likely to exist.

5.2.3 Kinetic Energy

The kinetic energy of convection cells or tidal currents could be harvested directly and used to sustain life. Organisms could contain pili or cilia much like ciliated bacteria or protozoa and adhere to a substrate at the ocean bottom or on the underside of an ice ceiling, where they are exposed to currents of moving water that cause the cilia to oscillate through bend and flex cycles that extract energy from the convection current (Fig. 5.2). The cells could enclose protein-like macromolecules that induce an electrical polarity across the membrane through a Donnan equilibrium. The hair cells could be surrounded by Na^+ channels whose permeability is proportional to the deflection of the hairs, with properties like those of sensory hair cells in the vestibular membrane of vertebrates or lateral line organs of fish (Fig. 5.3).

By bending the cilia, the convection currents could open the ion channels, allowing ions to flow into the cell passively down their concentration gradients. This thermodynamically favored process could be coupled to the direct formation of high-energy phosphate bonds or to a H^+ transporter across another internal membrane, by analogy with mitochondrial membranes (Schulze-Makuch and Irwin 2001). The ionic gradient would be maintained by extrusion of the ions via exocytosis. The ions could bind, for example, to intracellular macromolecules whose tendency to fuse with the external membrane and disgorge their ionic ligands is

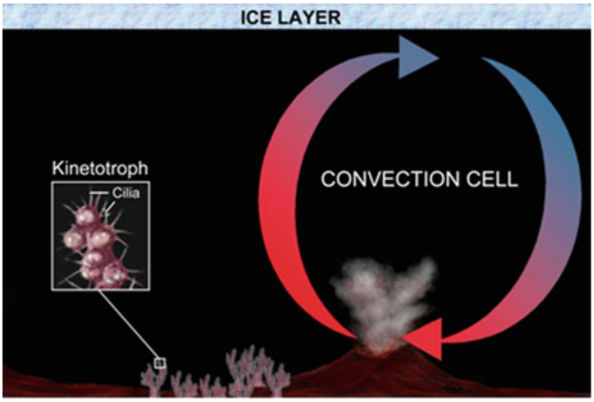


Fig. 5.2 Kinetotrophic organism in an oceanic environment, schematic. Convection currents can bend cilia leading to the opening of Na^+ channels, allowing Na^+ to flow into the cell passively down its concentration gradient. Art provided by Chris D'Arcy, Dragon Wine Illustrations, El Paso, Texas

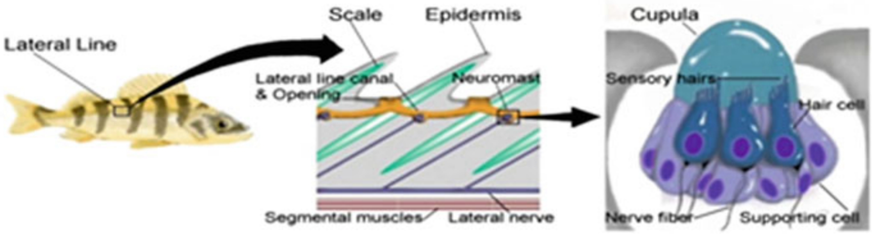


Fig. 5.3 Lateral line organ in fish, illustrating the role of cilia in transducing fluid movement into electrogenic signals. Cilia bend from the movement of fluid, allowing ions to move through the open channels. Art provided by Chris D'Arcy, Dragon Wine Illustrations, El Paso, Texas

thermodynamically favored, once the number of ions bound to the carrier reaches a concentration greater than the concentration of the ions outside the cell (Schulze-Makuch and Irwin 2002a). Alternatively, the ions could simply be precipitated as salts. A steady convection current with a velocity in the mm/s range would certainly be able to provide the requisite molecular distortion. Since this system works essentially like a battery that is charged over time, all that is needed is a minimal ionic gradient and enough time to charge the system high enough to form energy-storing chemical compounds.

5.2.4 Osmotic or Ionic Gradients

Osmotic gradients can be an enormously powerful source of energy. The osmotic pressure can be calculated by the van't Hoff formula.

$$\prod = c\,R\,T \tag{5.7}$$

where $\prod$ is osmotic pressure (atm), c is the molar solute concentration (mol/L), R is the universal gas constant (0.08206 L atm/mol K), and T is the absolute temperature (K). Some halophilic strains of cyanobacteria are known to tolerate salt concentrations of up to 2.7 M NaCl (Hagemann et al. 1999). Marine teleosts (bony fishes) retain a strong osmotic differential of roughly 0.7 osmoles between their intercellular fluids and their surrounding environment (Wilmer et al. 2000), where 1 osmole is 1 mole of osmotically active particles. Using this conservative figure as a first estimate at a temperature of 25° C (298 K), the osmotic pressure would be 16.9 atm (1.7×10^6 Pa). The force that acts on one water molecule along its concentration gradient is then

$$F = \prod A \tag{5.8}$$

where A is the cross-sectional area of one water molecule. This force is about 10^{-13} N. Further, assuming this force moves the water molecule through a membrane channel that couples the movement to the formation of a high-energy covalent bond, the energy available for bond formation is given by

$$W = F\,s \tag{5.9}$$

where s is the distance the water molecule moves down its density gradient (assumed to be 10^{-8} m for a biomembrane). Using the above figures, the calculated potential energy yield is 10^{-21} J, or 0.007 eV. Thus, one ATP could be phosphorylated from ADP for about every 45 water molecules entering the cell by osmosis. This is about two orders of magnitude below the energy yield for chemoautotrophs or photoautotrophs on Earth. The 0.007 eV may be a conservative estimate, because the osmotic differential calculated here is based on those of fish that have adapted from their freshwater origin to their marine environment rather than microbes adapted to use osmotic gradients. Halophilic microbes as described above, if adapted not only to tolerate but to use osmotic gradients, might easily be able to more than quadruple this energy yield.

The direct coupling of water movement to phosphorylation reactions is not known for living systems on Earth. However, evolution could have favored the origin of membranes in which water movement yields energy, where osmotic gradients were readily available and other forms of energy were not. A plausible mechanism would involve tertiary structural changes in a channel-associated protein that catalyzes formation of high energy bonds, much as ligand-induced conformational changes in membrane receptors lead to a series of steps culminating in the synthesis of high-energy cyclic AMP (Schulze-Makuch and Irwin 2002a). As in the case of thermal gradients, degradation of the osmotic gradient is a potential drawback to their use for generating free energy. The influx of many water molecules would either significantly increase the cell volume, or increase counteracting pressure in rigid cells that cannot expand in volume. This could be mitigated, however, by a compensatory loss of solutes, such as efflux of Na^+ (and Cl^- for electrical balance) powered by the rise in intracellular pressure. Either the extrusion of solutes, or the pressure itself, could be coupled to conformational changes that could catalyze high energy bond formation. Alternatively, cell volume could be reduced by reverse osmosis upon movement of the organism to a more hypertonic level of the liquid medium. The zone close to the ocean bottom would be expected to be high in total dissolved solids due to persistent dissolution of the mantle and a higher density of salt water compared to fresh water. Solute gradients would be present both at the ocean bottom and in higher regions, but in opposite directions if not much water circulation is occurring. For example, a membrane water channel could be coupled to a reaction that forms a high-energy bond inside the cell as the water moves inward from hypotonic surroundings, while a similar channel oriented in the opposite direction could harvest energy when water leaves the cell in hypertonic surroundings. The hypothetical organism could thus move between two layers of different salinity, using both to harvest energy (Fig. 5.4).

Ionic gradients and H^+ gradients conceivably could also provide energy. For a 100-fold ionic gradient between the cytoplasm of an organism and its external environment—a differential observed in halobacteria on Earth (Madigan et al. 2000)—the amount of potential energy can be calculated from the Nernst equation

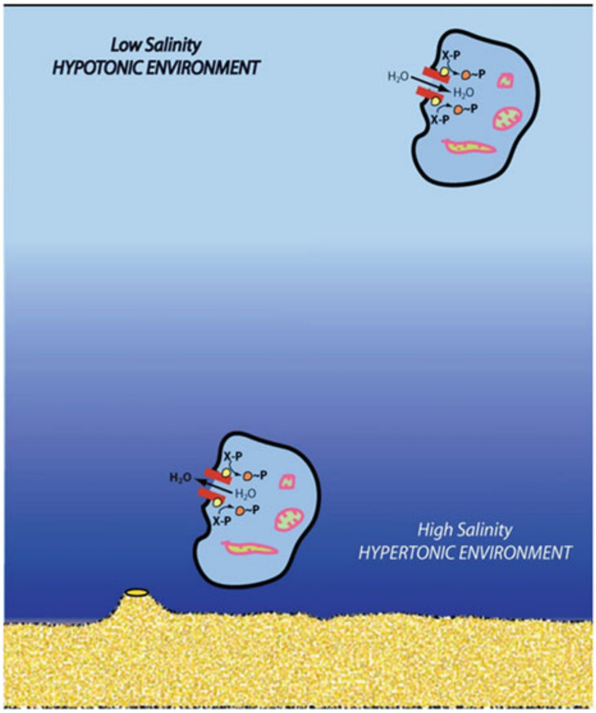


Fig. 5.4 A hypothetical osmotroph that harvests energy from osmotic gradients. Movement of water would be coupled to a reaction that forms a high-energy covalent bond through variants of a membrane molecular complex that are energized by the entrance or exit of water, depending on the direction of the osmotic gradient (P_i = inorganic phosphate, ATP formation is used as an example, not necessarily implying that ATP would be used by a hypothetical osmotroph). Redrawn from Schulze-Makuch and Irwin (2002a)

$$E = (RT/nF)\ln\left([\mathrm{ion}]_{\mathrm{ext}}/[\mathrm{ion}]_{\mathrm{int}}\right) \tag{5.10}$$

where n equals the number of charges transferred in the reaction, F the Faraday constant (J/mV mol) and R and T as above. The potential energy yield, $\Delta G = -nFE$, equals 0.12 eV, when $[\mathrm{ion}]_{\mathrm{ext}} = 100 \times [\mathrm{ion}]_{\mathrm{int}}$ at 298 K. This could drive the diffusion of about 3 ions, which could provide the energy for the phosphorylation of one ATP molecule. This might well be an underestimate of the potential energy yield since some bacteria achieve ionic distribution ratios as high as 10^6 across their membranes (Neidhardt et al. 1990).

Thus, the harvesting of osmotic or ionic gradients for bioenergetic purposes appears to be feasible in principle. Both types of gradients would often coexist, allowing for the possibility of reciprocal cycling between the two. On other planetary bodies where strong chemical concentration gradients are likely present, as in the putative liquid ocean on Europa (Kargel et al. 2000) and possibly other icy satellites, the use of osmotic or ionic gradients as bioenergetic sources must be considered a reasonable possibility, especially where other energy-yielding strategies may not be feasible. Irwin and Schulze-Makuch (2003) have modeled a putative multilevel ecosystem, based on the assumption of a hypertonic ocean bottom and a hypotonic ocean ceiling on Europa. Their calculations indicate that organisms the size of brine shrimp could be supported at a density of several hundred per cubic meter at the ocean bottom. While such an ecosystem is purely hypothetical at this point, their calculations point to the theoretical feasibility of an ecosystem in which the producer level is powered purely by osmotic or ionic gradients.

5.2.5 *Magnetic Fields*

Charge separation and extractable free energy can be generated from magnetic fields in theory. Magnetic fields can yield energy based on the Lorentz force, the movement of a charge within a magnetic field, or by induction from a periodically changing magnetic field. The Lorentz force can be expressed by

$$F_L = q(E + v \times B) \tag{5.11}$$

where E is the electric field acting on the charge (Newton/Coulomb; N/C), v is the velocity (m/s) of the charge in the magnetic field, and B (T) is the magnetic field strength. The cross product $v \times B$ is reduced to vB in the special case of a perpendicular movement of the charge with respect to the direction of the magnetic field B. If the movement of the charge occurs parallel to the direction of the magnetic field, the cross product is zero, and thus in the absence of an electric field no force acts on the charge q. A somewhat analogous directional dependence is observed for induction. In the absence of a magnetic field ($B = 0$), a charge is accelerated parallel to the electric field such that

$$F = qE \tag{5.12}$$

with E being the magnitude of the electrical field (N/C).

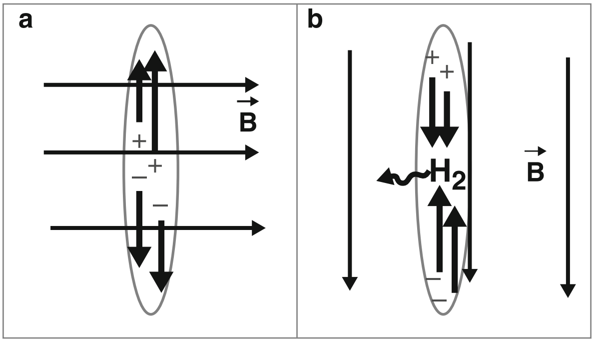
5.2.5.1 Possible Biogenic Use of the Lorentz Force

The amount of energy that can be extracted via the Lorentz force depends on the strength of the magnetic field of the particular planetary body. The strength of Earth's magnetic field at the surface is about 0.3 gauss, or 3×10^{-5} Tesla (T). There are planetary bodies that have a far larger magnetic field strength than Earth, such as Jupiter (4.3 gauss at the equator) and Saturn. Earth's magnetic field can be described in a first approximation as a magnetic dipole. Any charged particle moving in a conducting liquid at a direction perpendicular to the magnetic field line would experience the Lorentz force. Protons inside of organisms are charged and Earth's oceans consist of salt water, which is a conducting liquid. But would the Lorentz force be sufficiently strong to yield a significant amount of energy? Let us assume a hypothetical organism the size of an Earth microbe that is transported by the current of the convection cell at a rate of 1 m/s perpendicular to the magnetic field lines. Then the potential energy yield can be calculated from

$$W = F_L \ s \tag{5.13}$$

where W is the energy yield (J or eV), F_L is the Lorentz force as given above, and s is the distance where charge separation can occur. If it is assumed that the total length of the microbe (10^{-6} m) can be used for charge separation, then the Lorentz force that can act on a unit charge (electron or proton, $q = 1.6 \times 10^{-19}$ C) is about 5×10^{-24} N. This charge separation can be imposed if the magnetic field is perpendicular to the line of movement of the charge and released if the magnetic field is oriented parallel to the movement of the charge. It follows that the energy obtained from the Lorentz force is 3×10^{-11} eV, 11 orders of magnitude lower than the energy that could be obtained by chemoautotrophy (assuming hydrogen-oxidizing metabolism) or photoautotrophy. However, there is no conceptual reason why charge separation of only one electron or proton can be harvested at one time; several or thousands of reactions could occur in parallel. Also, the available energy yield could be increased by many orders of magnitude, if the microbe is an analog to hair cells on Earth with lengths in the millimeter or centimeter range instead of being ball- or pancake-shaped in the micrometer range. A plausible energy-harvesting mechanism could be that H^+-ions are driven across a one-way channel against their concentration gradient into an internal organelle, where they accumulate to a higher concentration gradient than on the outside of the organelle. Then, the H^+-ions can diffuse back out of the organelle through a different channel coupled to a phosphorylation reaction that produces a high-energy organic phosphate (similar to how mitochondria work). A more elaborate scheme would be if the Lorentz force is used to separate one electron and one

Fig. 5.5 Scheme for magnetotrophic organism to obtain energy, (**a**) Lorentz force separates protons and electrons, (**b**) magnetic field lines are oriented parallel to long axis of microbe, and protons and electrons form molecular hydrogen



proton from the center of the cell in opposite directions toward the respective ends of the hair cell. When the magnetic field lines are oriented parallel to the hair cell, the energy could be released and the proton and electron would move toward each other producing H_2 (Fig. 5.5). The efficiency of both types of model organisms could be increased if its cells would contain magnetite crystals orienting themselves to the external magnetic field to optimize the harvest of magnetic energy (Schulze-Makuch and Irwin 2001).

In addition to the model organisms discussed, there is another interesting possibility: charge separation would not necessarily have to occur within the microbial cell. Organisms of microbial dimensions could be envisioned that would cling to strips of inanimate conducting material and harvest energy from the magnetically induced electron flow in their substrates. That possibility would depend, in part, on whether a suitable mineral or aggregate of conducting matter would be present under the environmental conditions in question. Mineral assemblages including silicates, zeolites, albite, sphene, and illites, plus the iron minerals pyrite and hematite, have been identified at deep hydrothermal systems on Earth (Gonzalez-Partida et al. 2000) and could constitute suitable materials. Although not impossible, it would take a considerable effort to overcome a difference of 11 orders of magnitude in energy gain. Thus, it is not surprising that we don't encounter magnetotrophic life on Earth. However, sensitivity to magnetic fields, as in magnetotactic bacteria, is a well-established phenomenon (Blakemore 1982; Frankel et al. 1979), and there is strong evidence that some animals use magnetospheric orientation for navigation (Aekesson et al. 2001; Ioale et al. 2001). This implies the presence of cellular mechanisms for detecting magnetospheric energy. In the absence of more concentrated or effective sources of free energy, it seems plausible to assume that a cellular mechanism for transducing magnetospheric energy into a biologically useful form could evolve.

5.2.5.2 Possible Biogenic Use of Induction

The second physical option for harvesting energy from a magnetic field is by induction. The possibilities and problems associated with that option will be examined using Jupiter's moon Europa as an example (Schulze-Makuch and Irwin 2002a): It seems highly likely that Europa has a liquid subsurface ocean beneath its icy surface (Kivelson et al. 2000), which may be a suitable environment for microbial life. Jupiter's magnetospheric plasma corotates with Jupiter at a corotational velocity of 118 km/s at the orbit of Europa (Beatty and Chaikin 1990). Thus, Europa moves with respect to Jupiter's rotating field lines at a relative velocity of 102 km/s. However, the force exerted by this magnetic field cannot be used by an organism in the ocean. Europa's thick insulating layer of ice concentrates induced charges that produce an electric field that exactly cancels the Lorentz force. However, it was observed that Jupiter's magnetic field creates charge separation in a global conducting layer, which was interpreted as a shell of a salty ocean with a high electrical conductivity (Zimmer et al. 2000). Thus, the option remains that energy can be obtained from magnetic fields based on the induction from a periodically changing magnetic field (the Lorentz force, however, would still apply, as a charge can move perpendicular to the induced magnetic field, but it would be at a much lower magnitude). The alternating magnetic field that is experienced by Europa's ocean can be described as follows: Europa is subject to an oscillatory magnetic field

$$\mathrm{B} = \mathrm{B_o} \sin(\mathrm{w\,t}) \tag{5.14}$$

with an amplitude $\mathrm{B_o}$ of about 200 nT. Thus, the rate of change is

$$\mathrm{dB/dt} = \mathrm{w\,B_o} \cos(\mathrm{w\,t}) \tag{5.15}$$

with a maximum value of $2\pi\,\mathrm{B_o}/10$ h, which corresponds approximately to 2 nT/min (Khurana et al. 1998). The work W performed on a charge q (e.g. an electron or proton) is then given by

$$\mathrm{W} = \mathrm{U_{ind}\,q} \tag{5.16}$$

where $\mathrm{U_{ind}} = \mathrm{A\,(dB/dt)}$ with A being the microbial cross-sectional area (m^2), dB/dt the change of the magnetic field strength (T/s), W is work or energy (J), and q is a unit charge of 1.602×10^{-19} C per electron or proton.

Assuming a microbial diameter of 1 μm, and the above figure for a reasonable maximum temporal magnetic field change in Europa's ocean, the amount of energy per reaction that can be extracted via induction is about 4×10^{-42} J or 3×10^{-23} eV per electron, which is 23 orders of magnitude lower than the energy that can be harvested via chemosynthesis or photosynthesis on Earth. Even if many of those reactions would occur simultaneously, the energy gain is much too low. Thus, induction does not appear to be a feasible option for living systems to capture energy in Europa's ocean, and would only be very unlikely anywhere else.

5.2.5.3 Concluding Remarks on the Biogenic Use of Magnetic Energy

Life based on magnetic energy does not appear to be very promising in an Earth-type environment. However, magnetic field strengths much larger than on Earth would present certain possibilities. The gas giants Jupiter and Saturn have much larger magnetic field strengths, and neutron stars have magnetic field strengths millions of times stronger than the Sun or planets that surround a star like our Sun (Lattimer and Prakash 2004). Although life on gas giants or a neutron star itself would be very unlikely due to other considerations that are discussed in the following chapters, some moons that orbit the gas giants, and especially planets that orbit neutron stars, may provide an opportunity for organisms to harvest magnetic energy. For example, the neutron star SGR 1806-20, a magnetar, has been reported to have a magnetic field strength of about 10^{15} Gauss, or 10^9 T (Ibrahim et al. 2003). Energies from these huge fluctuating magnetic fields could become competitive for organisms on planets orbiting neutron stars, depending on the magnetic field strength of the particular star, distance of the planetary body from the neutron star, environmental conditions on the planet or moon, and the availability of suitable niches below the planetary surface for protection from radiation intensity, among other factors. Refined adaptive strategies by organisms that would have evolved in such an environment presumably would have increased the efficiency of magnetic energy to make it competitive with light and chemical energy, even under planetary conditions similar to our Solar System; but the strategies would have to be highly refined in a more efficient direction to make up for the generally low energy yield.

5.2.6 *Gravitational Forces*

Gravitational energy could be harvested in a direct fashion by the movement of protons or molecules through a gravitational field. The effects of gravity on a large scale are readily seen on Earth by the tidal amplitudes in the oceans caused by gravitational interactions between the Earth, Moon and Sun. Tidal flexing is more dramatic on Io, the volcanically most active planetary body in our Solar System, due to strong tidal interactions between Jupiter inside Io's orbit and the other three major moons beyond its orbit. But gravity is the weakest of the fundamental forces known in nature, and the free energy that it yields on a small scale is very slight. That value can be calculated by assuming a simple model in which a proton is moved a micrometer (assumed microbial diameter) against a defined gravitational attraction.

$$\mathrm{W} = \mathrm{m_H} + \mathrm{g\,h} \tag{5.17}$$

On Earth, the energy would be about 10^{-13} eV and thus much smaller than the energy than can be harvested via chemotrophy and phototrophy. If large macromolecules (~10^6 atomic mass units) instead of protons were moved, the energy yield could be as high as 10^{-7} eV. Even allowing for a planetary body the size of Jupiter, chemotrophy and phototrophy would still out-compete gravitational energy. Thus, gravitational forces seem unlikely as a useful direct basis for bioenergetics in our Solar System, because gravity is simply far too weak. However, the *indirect* effects of gravitational forces, such as convection currents in the oceans could be used to power living systems, as discussed before (see Sect. 5.2.3). It should also be pointed out that organisms are sensitive to gravity on Earth. Even single cell organisms can orient themselves in a gravitational field through the use of intracellular receptors located in the cell membrane (Bräucker et al. 2002).

5.2.7 Tectonic Stress

Meteorite impacts and fractures within a planetary crust release energy that could be used by organisms for obtaining energy. Meteorite impacts are common occurrences as can easily be observed on our Moon, Mercury and Mars. The meteorite's kinetic energy is converted upon impact into electrical potential, while the mechanical disruption of the impact causes the release of stress energy in the form of light, heat, electrical fields and magnetic fields (Borucki et al. 2002). While the impact only occurs in a short time period that can be measured in milliseconds, melted slurry pools under impact sites can persist for as much as a million years, depending on the size of the impact, as shown by Sagan et al. (1992) for Titan. Additional energy supplied from crustal stress to the subsurface regions after the impact could increase the lifetime of the melted impact zone and provide suitable conditions for microbial life. While the energy released from the immediate impact of the meteorite would dissipate relatively fast, energy provided by the piezoelectric effect could be provided for a very long time. Piezoelectric energy is a form of electricity generated when a pressure is applied to an ionic solid as a result of strain. A charge across the crystal is produced because a dipole moment is created by the deformation of the otherwise non-polar molecular structure. The polarization of the crystal faces parallel to the direction of strain converts the crystal into a capacitor, which temporarily stores an electrical charge. A good example for demonstrating this effect is a planar molecule of any ionic solid. Its structure has 3 electric dipoles at 120° to each other, which cancel and give a net dipole moment equal to 0. Applying a pressure or a voltage to this molecule will result in deformation of the molecule, and the generation of a dipole moment as a result of this deformation. The piezoelectric effect will immediately cease if the pressure or current is removed from the structure of the crystal. Piezoelectric energy, although somewhat "exotic," could thus provide a possible avenue for life. It could be associated not only with meteorite impacts but also with other geological events such as plate tectonics on Earth. However, it is restricted to 20 of the 32 crystal classes, ionic crystalline solids that lack a center of inversion such as quartz, perovskite, sodium chlorate, and Rochelle salt. Similar to the other alternative energy sources, no indication of its energetic use by microbial organisms has been observed on Earth. It is doubtful whether this process can provide a sufficient or sufficiently constant amount of energy. At the very least, it does not appear to be competitive with chemical or light energy.

5.2.8 *Pressure Gradients*

Life based on energy harvested from a pressure gradient is another theoretical possibility. There are three principal opportunities. Energy could be harvested from atmospheric, fluid or subterranian pressure gradients.

Pressure gradients exist in the vertical column of any atmosphere held by gravity. However, the capacity of such a pressure gradient to be used as an autotrophic energy source is questionable. Atmospheric pressure is the sum of the forces of all the molecules striking a surface area, and thus a measure of the linear momentum of the gas molecules. A pressure gradient is established if the molecules do not move randomly, but in a preferred direction. It is difficult to see how a microbial organism suspended in the atmosphere could utilize the pressure gradient. The organism would just be carried along with the wind, unable to maintain a consistent orientation within the pressure gradient, which in any event would be miniscule over the linear dimensions of the organism. This does not exclude the atmosphere of planets and large moons as habitable environments, but other metabolic strategies such as chemoautotrophy or photoautotrophy would have to be employed, as suggested originally for the Jovian atmosphere (Sagan and Salpeter 1976) and more recently for the Venusian atmosphere (Grinspoon 1997; Schulze-Makuch and Irwin 2002b).

Large pressure gradients can also exist in fluids. For an organism suspended in the fluid, the same problem would be faced as that of an organism suspended in an atmosphere. If the organism were attached to a fixed substrate, it could at least maintain a consistent orientation within a localized pressure gradient. Such localized pressure gradients exist, for example, at hydrothermal vents on the ocean floor. However, the wide fluctuations in pressure likely arising at the vents would represent a practical problem. Furthermore, how an organism could stay attached to a substrate at these pressures and at the same time harvest the pressure gradient is unclear.

Tremendous pressures are present in the vertical rock column of a planetary body's lithosphere. Since microbial organisms are known on Earth to live at considerable subterranean depths, there is precedence for assuming that life on other worlds would occupy this habitat. Although the absolute pressure is high, the pressure gradient is not, especially with respect to microbial dimensions. Thus, life based on pressure gradients in the subsurface does not appear likely.

5.2.9 *Spin Configurations*

Atoms in molecules can revolve and rotate in various ways. For example, the two atoms of hydrogen gas, H_2, perform a vibrational motion in the direction of the line

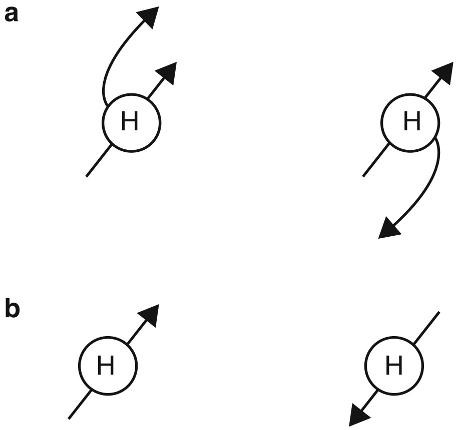


Fig. 5.6 Motions of o-hydrogen and p-hydrogen, (**a**) o-hydrogen atoms revolve around a common center, while their nuclei rotate around their own axis at the same time, (**b**) In the simplest version of p-hydrogen the atoms do not revolve and the nuclei rotate in opposite directions. Modified from Feinberg and Shapiro (1980)

joining the nuclei, and a rotational motion around a direction perpendicular to the molecular axis in addition to the translational motion. The vibrational and rotational motions are in quantum states resulting in two different modifications of hydrogen, parahydrogen molecules that have antiparallel nuclear spins and even rotational quantum numbers, and orthohydrogen molecules that have parallel nuclear spins and odd rotational quantum numbers (Fig. 5.6). The two sets of molecules do not easily convert into each other but can be considered as two gases differing from each other in certain optical and thermal properties (Farkas 1935). The o-hydrogen is the higher energetic state but is relatively stable kinetically. For example, although at 20 K equilibrium hydrogen consists practically of pure parahydrogen, simply cooling the hydrogen to this temperature or transitory liquefaction or solidification does not cause equilibrium to be established.

The two states of hydrogen could provide a source of energy in very cold environments with abundant hydrogen. For example, one could envision a mechanism to retrieve energy by having o-hydrogens on a cell boundary collide with o-hydrogen molecules in the environment. Both o-hydrogens would convert to p-hydrogen and a relative high energy yield of about 700 J/g would be obtained. P-hydrogens could then be converted back to o-hydrogens by allowing rotating p-hydrogens to collide with magnetic impurity molecules (such as oxygen), which would catalyze the formation of o-hydrogens. The potential of spin configurations as an energy source was first realized by Feinberg and Shapiro (1980), who suggested the possibility of life based on spin configurations on a very cold and dark planet, just a few 10s of degrees above absolute zero. Although energy based on spin configurations represents an intriguing idea, it is doubtful that at these low temperatures energy could be transferred into chemical energy usable to organisms at a high enough rate. Energy from spin configurations may rather present an interesting engineering opportunity and challenge to obtain energy for space probes on cold and dark planetary bodies.

5.2.10 Radioactivity

Radioactivity is one of the most basic processes in our Universe. Radioactive nuclei of atoms decay with time and release particles and electromagnetic radiation. Forms of high-energy radiation include alpha (helium nuclei) and beta particles (electrons or positrons), gamma rays (short wavelength, high-energy photons), X-rays, neutrons, and heavy ions. This type of radiation is very destructive to life as we know it because it destroys biologically important molecules, especially the sensitive machinery for molecular replication. Biological effects depend on the spatial density of ionizations produced per unit absorbed dose in the irradiated tissue. For example, particles with high atomic numbers and high energy (HZE particles) cause the greatest damage for a given dose (Baumstark-Khan and Facius 2002). Nuclear processes are the ultimate source of energy for life on Earth, since the Sun emits photons as a byproduct of the fusion of hydrogen into helium at its core. And heating produced by radioactive decay in the Earth's core could serve as the energy source for possible thermoautotrophic organisms. The question remains, however, whether radioactivity can be tapped directly by living organisms. This may be too destructive for organic synthesis and reproduction. Due to the presence of many radioactive isotopes with short half-lives, radioactive material was much more common on the early Earth, when life originated or first became established. Yet, today high-energy radiation does not serve as an energy source for any form of life as far as we know. Gamma radiation and X-rays may have been too rich in energy and too difficult to control. Or, was the visible light of our Sun simply more accessible and easier to use? How about the alpha and beta particles? They possess ample amounts of kinetic energy over the short distance of cellular dimensions. From an energetic viewpoint they would be a preferential energy source. Yet, they are not used as far as we know either. Again, the basic problem may be control, as well as insufficient frequency, and inconsistency. Radiation and particle emissions occur in a random fashion from a decaying atom. The frequency, direction, and precise level of energy are all unpredictable. It is difficult to envision how any organism could control the decay in a way to obtain energy on a consistent basis. On Earth, organisms have developed mechanisms to avoid, tolerate, and repair damage caused by ionizing radiation. A prime example is *Deinococcus radiodurans*, which possesses a high redundancy of repair genes to cope with ionizing radiation and organic pigments to cope with UV radiation. However, ionic radiation has not only deleterious effects on life, but can also have beneficial consequences (Dartnell 2011). Radiolytic compounds created within Europa's crust by radiation and impact gardening are one example. Based on estimated delivery rates to the subsurface ocean, Greenberg (2010) concluded that oxygen levels could be high enough to support a substantial macrofauna.

5.3 The Question of Entropy, Uniformity, and Origin

A qualitative and quantitative assessment of the various energy sources indicates the theoretical plausibility that several of them potentially could power living organisms on other worlds. From a purely energetic view, a thermotrophic organism appears to be most favored. Such an organism may have in fact developed on Earth, and may be the progenitor of the photoautotroph as suggested by Muller (1995). His proposed thermosynthesis scheme is certainly simpler than photosynthesis, and heat is a ubiquitous energy source. However, we do not observe the presence of thermotrophic life on Earth, even though it appears to be favored on the basis of theoretical energetic considerations. It may be present and yet undiscovered on Earth, but terran life definitely prefers chemical and light energy. What is the basic difference between thermal gradients on one hand, and chemical and light energy on the other hand that could account for this observation? Thermal energy has a high degree of entropy—it is highly disordered. Chemical and light energy are highly ordered forms of energy. According to the second Law of Thermodynamics, the degree of disorder in a system as a whole has to increase spontaneously with time. Any form of life is highly ordered and complex, and living processes increase the order of the system further. In order to maintain the highly ordered state of a living system, some free energy has to be expended to increase the degree of disorder, because the overall entropy of the system and its environment has to increase. In terran organisms this increase in entropy is achieved by giving off heat and waste products, which are highly disordered. Thus, using a highly disordered energy source to begin with is very inefficient. Much less of the total amount of energy obtained from a more highly ordered source has to be converted into the disorder required to obey the second Law of Thermodynamics. Clearly, then, entropy is a factor that needs to be considered when assessing whether alternative energy sources can be used to power an organism.

Another factor that needs to be considered is uniformity of intensity. An alternative energy source has to provide its energy in quanta suitable and manageable for the organism to use. High-energy particles as emitted from decaying atoms are inconsistent and unpredictable, for instance. It may be that living systems can evolve a capacity to harvest energy more easily when that energy comes in the specific and consistent quanta appropriate for the control of metabolic reactions in a reliable way.

One other factor that needs to be considered is the question of pre-biotic evolution. How difficult was it for the earliest organisms to develop a mechanism for harvesting a specific energy source? The molecular machinery that has survived in chemoautotrophs and photoautotrophs today is very complicated, hence highly unlikely to have been the earliest mechanism for energy extraction. At the origin of life, the mechanisms for harvesting energy must have been simpler, and quite possibly were dependent on sources other than those that are used today. Chemoautotrophy and photoautotrophy are now the dominant basis for life on Earth, presumably because of the abundance and efficiency of those sources of energy. However, there may have existed early bioenergetic mechanisms that possibly were outcompeted over evolutionary time by more efficient mechanisms.

5.4 Survey of Energy Sources in our Solar System

Energy sources are ubiquitous in our Solar System. Solar radiation providing light and thermal energy is one of the dominant energy sources for the interior terrestrial planets, and still significant for the Jovian and Saturnian systems. Heterogenous surface colorations such as on Venus and many of the icy outer satellites imply the presence of chemical energy. Geothermal energy is indicated by volcanism and a high-density interior that would imply radiogenic heating on planetary bodies such as Venus, Mars, Io, and Enceladus. Pressure is an energy source for planets with thick atmospheres such as the gas giants and Venus. Kinetic energy is a force on any planetary body with strong convection cells such as the gas giants, and possibly Europa. Tidal flexing is an energy source commonly found in the Solar System, for example at Io, Europa and Triton. Strong radiation and magnetic fields emanating from Jupiter and Saturn affect their satellites. Tectonic stress is definitely observable on Io, and osmotic gradients may be present on icy moons with a subsurface liquid ocean as proposed for Europa, Ganymede, and Titan. Observations indicating the presence of various energy sources on the major planetary bodies of our Solar System are listed in Table 5.1. This does not mean that the potentially available energy sources are actually used by putative organisms, but only that they are present based on our current knowledge. A discussion on the suitability of life on those planetary bodies based on energy sources plus other geoindicators is provided in Chap. 9.

Table 5.1 Energy sources in the Solar System that would be available in principle for other possible forms of life

Body	Observations	Energy source
Mercury	Thermal gradients pass through range for liquid water at slowly moving terminator. Possible water ice at poles. High density and electromagnetic field ⇒ metallic core	Solar radiation, geothermal
Venus	Extensive resurfacing ⇒ geological activity and chemical recycling. Very dense atmosphere ⇒ pressure gradients	Solar radiation geothermal, chemical, pressure
Moon	Extensive cratering ⇒ old surface. Evidence of past volcanism. High density ⇒ metallic core. Strong sunlight. Minor amount of frozen water at poles	Geothermal, solar radiation
Mars	Daily to seasonal temperature fluctuations above melting point of water at some latitudes, volcanoes. High density and weak electromagnetic field ⇒ metallic core. Surface erosion by flowing water. Likely aquifer beneath permafrost	Solar radiation, geothermal, chemical?
Jupiter, Saturn, Uranus, Neptune	Gas giants with indistinct high-pressure atmosphere/liquid transitions, extensive turbulence. Strong magnetospheres and radiation output	Pressure, convection, magnetism, radiation
Io	Volcanism, extensive resurfacing, large size, and density >3.5. Surface coloration ⇒ complex chemistry. Strong Jovian radiation. Weak intrinsic electromagnetic field	Geothermal, tidal flexing, chemical, stress (tectonic), magnetic
Europa	Extensive resurfacing, density >3. Surface coloration ⇒ complex chemistry and chemical recycling. Water ice surface, liquid subsurface water. Strong Jovian radiation. Projected high salt contents in subsurface liquids	Geothermal, tidal flexing, magnetic, chemical, convectional, radiation, osmotic gradients
Ganymede	Extensive resurfacing ⇒ geological activity, subsurface liquid water. Rippled surface, low density, weak magnetic field. Surface coloration ⇒ complex chemistry. Strong Jovian radiation	Geothermal, tidal flexing, chemical, radiation, magnetic
Callisto	Low density⇒ mostly water-ice. Strong Jovian radiation. Extensive cratering, lack of magnetic field ⇒ little internal energy	Magnetic, radiation
Enceladus	Very low density and high albedo ⇒ mostly water-ice. Strong Saturnian radiation. Heavily cratered but resurfaced in part, with evidence of a subsurface liquid water reservoir, ice geysers and volcanic activity ⇒ internal energy	Geothermal, tidal flexing, radiation, magnetic, convectional

(continued)

Table 5.1 (continued)

Body	Observations	Energy source
Iapetus	Low density and moderate albedo ⇒ mostly water-ice. Dark leading edge ⇒ possible hydrocarbon chemistry. Heavily cratered: Little internal energy	Chemical
Titan	Dense, colored atmosphere ⇒ complex chemistry. Density $\simeq 1.8$ ⇒ organic liquids and water-ice, with solid core. Atmospheric protection from radiation	Chemical, geothermal
Triton	Surface coloration ⇒ complex chemistry, unusual surface features ⇒ internal energy. Density $\simeq 2$ ⇒ rocky core. Elliptical, retrograde orbit ⇒ tidal flexing and seasonal temperature fluctuations; volcanism. Possible subsurface ocean	Chemical, geothermal, tidal flexing, stress (tectonic)
Pluto Charon	Density ~2.1 ⇒ rock/ice mixture. Mix of light and dark features⇒ complex chemistry	Tidal flexing, chemical

5.5 Chapter Summary

We have used relatively straightforward evaluations and calculations to show that life does not need to be restricted to energy from chemical bonds and light as a basis for bioenergetics, as it apparently is on Earth. While light and chemistry do indeed represent cosmically abundant and efficient sources of energy, on many worlds other sources of energy may be more practical. Thermal, ionic, and osmotic gradients, as well as the kinetic energy of fluids in motion, appear to be the most promising alternatives to light and chemistry on worlds where the latter energy sources are not available. But in specialized circumstances, other exotic forms of energy could be favored. Life evolving under those alternative conditions would be pressured by natural selection to make use of the forms of energy available. The numerous alternative options that are plausible within our own Solar System are shown in Table 5.1. Even though life on Earth may not use any energy source other than chemistry and light, the sensitivity of terran organisms to many other forms of energy provides a hint of other bioenergetic possibilities elsewhere in the Universe.

Chapter 6
Building Blocks of Life

Life is based on complex chemistry yet only a few of all the available elements participate in most life-supporting reactions on Earth: carbon, nitrogen, oxygen, hydrogen, phosphorous, and sulfur. Of these, the most characteristic element of biological systems is carbon. In this chapter we will discuss why carbon is so favored by life on Earth and whether other elements could replace carbon in its dominant role on other worlds.

6.1 The Uniqueness of Carbon

Carbon is the universal building block for life as we know it. Its ability to form complex, stable molecules with itself and other elements, particularly hydrogen, oxygen, and nitrogen is unique. Organic chemistry involves millions of compounds. The simplest are the alkanes, with the general formula C_nH_{2n+2} (for $n = 1$, the compound is CH_4, or methane). Alkanes are converted to other compounds by replacing a hydrogen atom with other functional groups. The most important substitutions for biochemistry are $-OH$ (alcohol), $-CHO$ (aldehyde), $-COO-R-$(ester, $R =$ alkyl group), $-COOH$ (carboxylic acid), $-PO_4$ (organic phosphate), and $-NH_2$ (amine). An organic acid with both amino (NH_2) and carboxyl ($COOH$) groups is an amino acid, and polycondensation of amino acids leads to proteins, whose virtually infinite variety of shapes provide a vast repertoire of macromolecular complexity. Carbon atoms can also be arranged in a ring, as in cycloalkanes and aromatic hydrocarbons, rather than a chain. The basic structure of the aromatic hydrocarbons is the benzene ring, a resonant ring held together by π-bonding. This structure forms the basis for cholesterol and steroids, which are vital biochemical compounds for many cellular structures (such as membranes) and functions (such as hormone signaling). Rings are also formed by -O-bridges between carbon atoms (Fig. 6.1). The stability of these structures accounts for the fact that sugars occur naturally in this form.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_6

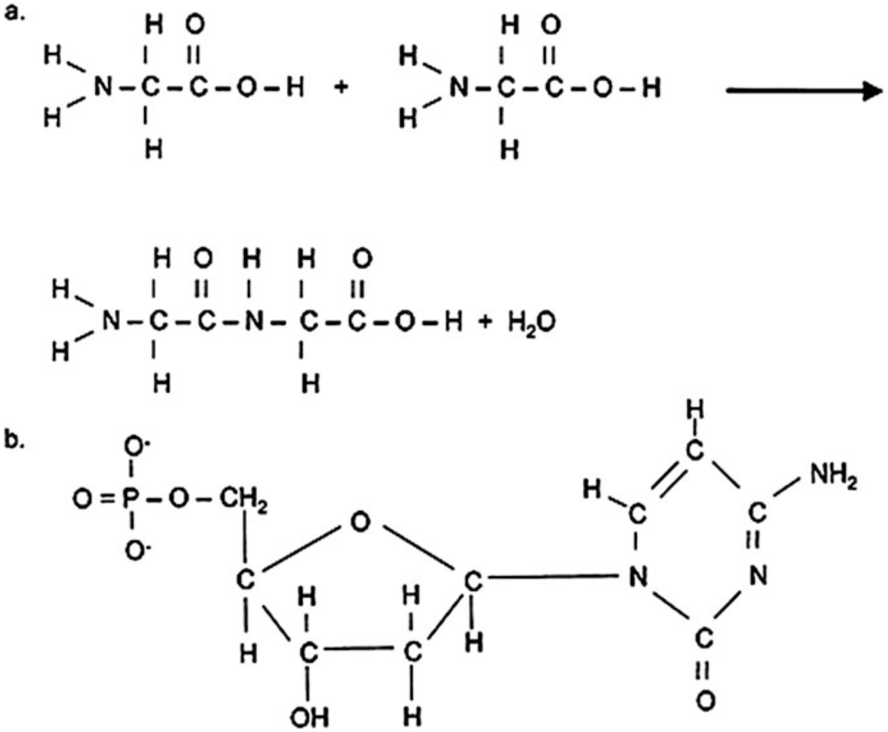


Fig. 6.1 Some selected important carbon molecules: (**a**) two glycine molecules (a simple amino acid) combine to form a peptide bond with the release of water as an important first step in the formation of proteins, (**b**) sugar (deoxyribose)—phosphate backbone and the base cytosine as one chain link of DNA (the next link of the chain would be the bonding of the upper oxygen of the phosphate group to the next sugar at the OH location)

The great variety of structures formed from carbon, from chains and rings to three-dimensional macromolecules, are mostly stable within a broad temperature range. The versatility of carbon is further enhanced by its ability to form double and triple bonds, which alters the chemistry and geometry of the molecule as well as its temperature-dependent fluidity. This ability of carbon to build an almost unlimited range of molecules can be attributed to various factors: (1) the stability of carbon macromolecules due to a carbon-carbon bond energy that is higher than that of any other non-metal, and is comparable to the strengths of carbon-hydrogen and carbon-oxygen bonds; (2) carbon's mid-range value of electronegativity that promotes the formation of primarily covalent bonds; and (3) high activation energies for substitution and bond cleavage reactions due to the absence of lone pairs or empty valence orbitals, thus enhancing the stability of hydrocarbons and halocarbons to water and oxygen (Sharma et al. 2002).

Chirality is an important property of life-supporting carbon compounds. With several exceptions, only right-handed carbohydrates and left-handed amino acids are used in Earth's organisms. Enzymes, which regulate a variety of biological processes, have the ability to recognize the desired chirality of a substrate. This further enhances the versatility of carbon (though chirality is not limited to carbon compounds and occurs in most macromolecules).

The ability of carbon to form the backbone of long-chain polymers is central to its contribution to the chemical complexity of living systems. The hydrocarbons that make up the long chain and cyclic skeleton of lipids consist exclusively of covalent carbon-carbon bonds. The backbones of proteins are repeating units of two carbon atoms followed by a nitrogen atom. These chains are made possible because of similar bond strengths between a carbon-carbon bond and a carbon-nitrogen bond (Table 6.1). The backbone of nucleic acids is formed by repeating units of three carbon atoms, one oxygen atom, one phosphorus atom and another oxygen atom (Fig. 6.1). The capacity for each of these backbones to exist in a myriad of sizes and shapes, and to be modified by the placement of a great variety of reactive functional side groups, while maintaining the stability of the skeletal framework, provides living systems with an almost endless repertoire of stable but variable and interchangeable molecular forms.

Energetically favorable redox-reactions are the basis for metabolism. Bains and Seager (2012) collected data for reactions pertaining to the core metabolism common to all terran life and found that 291 out of 787 of those reactions are redox reactions. Carbon can be converted fairly easily between its fully reduced state (methane, CH_4) with a valence of -4 and its fully oxidized state (carbon dioxide, CO_2) with a valence of $+4$, which makes it a favorable element for use in metabolism. It is a considerable advantage that both products are gases under a relatively broad temperature range including Earth environmental conditions (Table 6.2). These compounds are the end products of metabolic activity—carbon dioxide for aerobic respiration and methane for methanogenesis—and because they are gases they can be disposed of readily as metabolic end products. Furthermore, they continue to be available for reactions. CO_2 dissolves easily in water and dissociates when exposed to shortwave UV radiation, and methane reacts with oxygenated compounds in the Earth's atmosphere.

Carbon appears to fit ideally with water as a solvent. Of the common elements, carbon has the strongest bond enthalpy to hydrogen and also forms a strong bond to oxygen (Table 6.1)—the constituents of water. Further, many biochemical reactions

Table 6.1 Typical bond energies for carbon and silicon with some other elements, as enthalpy of bond formation (kJ/mol)

Atoms	With silicon	With carbon
Hydrogen	393	435
Oxygen	452	~360
Nitrogen	322	~305
Chloride	381	351
Carbon	360	368
Silicon	340	360

Note: Bond strengths are highly variable depending on which compounds are involved and on whether single, double or triple bonds formed. Data above indicate enthalpies of single bond formation, from Greenwood and Earnshaw (1984)

Table 6.2 Some physical properties of the fully reduced and fully oxidized forms of carbon and silicon

Property	CH_4	CO_2	SiH_4	SiO_2
Molecular weight	16.04	44.01	32.12	60.09
Melting point (°C)	-182.5	-56.6^a	-185	1713^c
Boiling point (°C)	-161.5	-75^b	-112	2950
Density (g/cm^3)	0.424 (at -164 °C)	1.03 (at -20 °C, 1.97 MPa)	0.68 (at -186 °C)	2.65 (solid)

Data from Greenwood and Earnshaw (1984), Christen (1984), CRC (2001), and Air Liquide (2003)

[a] At pressures above 5.1 bar

[b] Sublimation temperature at 1 bar

[c] SiO_2 as β-cristobalite

Table 6.3 Some elemental abundances in the Universe (as mass percent) and Earth

Atom	Sun	Earth	Earth's crust	Earth's atmosphere	Ocean	Microbe
Hydrogen	91	<0.1	0.14	<0.001	11	63
Oxygen	0.08	50	46	21	86	26
Carbon	0.03	<0.1	0.02	0.04	0.003	6.4
Nitrogen	0.010	<0.1	0.002	78	5×10^{-5}	1.4
Silicon	0.003	14	28	<0.001	2×10^{-4}	<0.1
Sulfur	0.002	1.6	0.035	<0.001	0.09	0.06
Phosphorus	3×10^{-5}	0.08	0.11	<0.001	6×10^{-6}	0.12

The elemental abundance of the Sun can be used as an approximate elemental abundance for the Universe

Data are from Goldsmith and Owen (2003) and CRC (2001)

Table 6.4 Some complex carbon compounds detected in the interstellar medium and meteorites

Number of atoms				
6	7	8	9	>9
C_5H, HCH_2OH	CH_3C_2H	CH_3OCHO	$(CH_3)_2O$	$(CH_3)_2CO$
NH_2CHO, CH_3CN	CH_3CHO	CH_3C_3N	CH_3CH_2OH	HC_9N
CH_3NC, CH_3SH	HC_5N, C_6H	C_7H, H_2C_6	CH_3CH_2CN	$HC_{11}N$
H_2C_4,HCC_2HO,	CH_3NH_2		HC_7N	C_6H_6,C^+_{60}
C_5H, C_5N, C_5O	CH_2CHCN		CH_3C_4H, C_8H	PAHs,
	C_2H_4O		CH_3C_4N	Glycine
				Aminocaproic acid

PAHs Polycyclic Aromatic Hydrocarbons

Based on data from Chièze (1994), Goldsmith and Owen (2003), Ehrenfreund and Menten (2002), Elsila et al. (2009), and http://www.spie.org/app/publications/magazines/oerarchive/july/jul97/extrater.html

involve the dissociation or production of water, such as photosynthesis and the polycondensation of sugars, lipids, nucleic acids, and proteins. Carbon is also a relatively abundant element in the Universe (Table 6.3), and thus no shortage of carbon as a universal building block of life should be expected in many types of planetary environments. Also, many complex carbon compounds have been found in the interstellar medium (Table 6.4) and meteorites, further strengthening the

Table 6.5 Some complex carbon compounds detected in the Murchison Meteorite

Compounds detected at concentrations of			
>1000 ppm	100–1000 ppm	10–100 ppm	1–10 ppm
Sulfonic acids	Carboxylic acids Polar hydrocarbons	Amino acids Dicarboxylic acids Hydroxy acids; Amides Alcohols; Aldehydes Ketones Aliphatic hydrocarbons Aromatic hydrocarbons	Phosphonic acids N-heterocycles Purines Pyrimidines Amines

ppm parts per million
Data from Cronin et al. (1988)

dominance of carbon as a building block for life. The Murchison meteorite contained an especially rich inventory of carbon compounds (Table 6.5) including adenine and guanine and their hydrolysis products, uracil, and ribitol and ribonic acids (the reduced and oxidized form of ribose), but not ribose itself (Cooper et al. 2001).

6.2 An Alien Carbon Biochemistry?

The ability of carbon to form the backbone of long-chain polymers is central to the chemical complexity of living systems on Earth. The carbon compounds that make up the long chain and cyclic skeleton of lipids consist exclusively of covalent carbon-carbon bonds. However, the make-up of the lipids is directly related to the solvent with which the lipids interact. Thus, a different make-up would be required for example in a non-polar solvent (Schulze-Makuch and Irwin 2006). The genetic code is also dependent on the solvent. For example, the solubility of DNA in water is beneficial to its stability (Westheimer 1987). However, even with water as solvent a variety of possibilities exist. Benner et al. (2004) pointed out the importance of phosphate linkages to molecular recognition in DNA and offered the following three hypotheses: (1) the repeating charges in the backbone force inter-strand interactions away from the backbone, causing the strands to contact at the edge of the heterocycles (without the polyanionic backbone, inter-strand contact could be anywhere (Steinbeck and Richert 1998), (2) the repeating monopoles in the backbone keep DNA strands from folding, and (3) the repeating backbone charges allow DNA to support Darwinian evolution by generating inexact copies, with the inexactness itself being replicable. The repeating element of RNA and DNA is a monopole (a charge) rather than a dipole. The backbone of DNA and RNA is formed from repeating units of three carbons, one oxygen, one phosphorus, and another oxygen. Benner et al. (2004) suggested that the polyanionic backbones dominate the physical properties of DNA, and that replacing a nucleobase by another would thus have only a second-order impact on the physical behavior of the molecule. Thus, different types of nucleotides could be expected in alien forms of life. Miller et al. (1981) and Reddy and Bruice (2003) suggested that a polycationic backbone may work as well as a polyanionic backbone. Benner (2017) generalized the requirement of a repeating backbone charge, pointing out that a genetic biopolymer must be a “polyelectrolyte,” and that we should search for such compounds in any type of extraterrestrial aqueous environment. Thus, the biochemistry of a genetic code in an alien organism may be quite different even though the same solvent (water) is used.

Proteins are essential to life on Earth. The backbones of proteins are repeating units of two carbon atoms and one nitrogen atom. These chains are made possible because of similar bond strengths between a carbon-carbon bond and a carbon-nitrogen bond (Table 6.1). Proteins are made up of amino acids connected by peptide bonds. Only 20 standard, or canonical, amino acids are found in living organisms (with a few exceptions, see Sect. 3.6.2). Experiments with non-canonical amino acids using the natural ribosome to incorporate them into proteins have expanded the amino acid repertoire of proteins for life (Bain et al. 1989; Hohsaka and Masahiko 2002; Noren et al. 1989; Wang et al. 2009b; Hoesl et al. 2015). Organisms transformed to use non-canonical amino acids are called synthetic life (Sect. 3.6), though Acevedo-Rocha and Schulze-Makuch (2015) have suggested they might also arise naturally. It is important to note that the functionality of proteins is based on their efficient catalytic properties, which is related to their folding capacity. The folding capacity requires dipolar repeating elements, so that the positive ends of one dipole can interact with the negative end of another dipole, inducing the tertiary structure of the protein. If that functionality is preserved, as found in polyamides, sulfonamides, or phosphoesters, there appears to be no reason why alternative sets of polypeptide chains and amino acids should be excluded from hypothetical proteins in putative alien forms of life (Benner et al. 2004).

6.3 Alternatives to Carbon as the Universal Building Block of Life

There has long been speculation about whether some other element could replace carbon as a universal building block for life (Reynolds 1906; Spencer 1940). Boron, nitrogen, silicon, phosphorus, and sulfur are other common elements that are known to form heat-resistant polymers. Macromolecules are required to address the essential needs of living entities as we have defined them in terms of biochemically based systems for compartmentalization, energy transduction, and information transmission (see Chap. 2: Definition of Life). Therefore, a key feature of the functional structure of biochemistry is the presence of highly specific non-repetitive macromolecules and their smaller components or interaction mediators (Bains 2004). Polymeric chemistry and macromolecules will still be required for life, even if it is based on building blocks unknown to us (Schulze-Makuch and Grinspoon 2005).

As a possible alternative to carbon as a building block, we will first discuss silicon, which has many properties similar to carbon and probably is the most promising substitute for carbon. Then we will discuss briefly other elements that form polymers, which could alone or with other elements together form the backbone for polymeric molecules. It will be hard for any other element to match the complexity and versatility of carbon, but we have to keep in mind that (1) the research on polymeric chemistry is carried out overwhelmingly under Earth environmental conditions and many polymers that are stable below the freezing point or above the boiling point of water are unknown, and (2) life may not in principle require any particular element to be as dominant as carbon is in terran biochemistry. Chains composed of just one element may not be necessary; chains of alternating atoms constructed from two or more different elements may work just as well (e.g. sequential units of B–N or Si–O). Proteins and nucleic acids already provide examples of structures that incorporate other elements into their backbones, as described above. Furthermore, in some other variety of carbon-based life, many of the carbon atoms could be replaced by silicon (Kan et al. 2016). The C–Si bond has about the same strength as the C–C bond (Table 6.1). Pure carbon-based and pure silicon-based forms of life may merely be the limiting cases, with a variety of transitional alternatives in between (Firsoff 1963). Some work on proteins and nucleic acids, where C atoms are replaced by Si atoms but functionality is attained, seem to support that assertion (Chen et al. 2001; Furusawa 1994).

6.4 The Possibility of Silicon-Based Life

6.4.1 Physical Properties of Silicon

Silicon is the most obvious potential substitute for carbon. It is also a p-block element of group IV (Group 14), just below carbon in the periodic table. With four electrons in its outer shell, it has somewhat similar physical properties to carbon (Table 6.6). Silicon and carbon are both small elements with small atomic weights and small atomic numbers, with carbon being the smaller of the two. Both elements have very high melting and boiling points, with carbon having the higher of the two (Table 6.6). Both elements are in the mid-range of electronegativities, but again carbon is higher. Both are solids at standard temperatures and pressures (STP) (298 K, 10^5 Pa) and both are semi-metallic. They both form sp^3 hybrid orbitals with tetrahedral structures in many of their compounds.

Silicon has a larger radius and therefore forms relatively weak bonds with the light elements that are abundant in the Universe (Tables 6.1 and 6.3). The electrons in carbon are closer to the nucleus, and thus form stronger bonds that can retain light elements much better. This increases carbon's chance of forming complex compounds. The Si–Si bond strength is lower than the C–C bond strength, thus carbon is much more likely to bond with itself than silicon. The smaller Si–Si bond energy is also reflected in silicon's lower energy of vaporization (Table 6.6). Silicon rarely forms any double or triple bonds, but double bonds and triple bonds are common and of great biological significance for carbon (Koerner and LeVay 2000). For example,

Table 6.6 Physical properties of carbon and silicon

Physical properties	Carbon	Silicon
Molecular Weight	12.011	28.086
Melting Point (in °C at 1 bar)	~3500	1414
Boiling Point (in °C at 1 bar)	~3900	3265
Density (g/cm^3 at 20 °C)	2.27[a]	2.34
Electronegativity	2.55	1.90
Single Bond Covalent Radius (pm)	77	118
Heat Capacity (J/g L at 25 °C)	0.709	0.705
Enthalpy of Fusion (kJ/mol)	0.00[b]	50.6
Enthalpy of Vaporization (kJ/mol)	394[c]	383

Data from Greenwood and Earnshaw (1984), Christen (1984); and CRC (2001)

[a] Measured as alpha-graphite

[b] Defined as standard state

[c] Enthalpy of combustion

amino acids, fatty acids, and nucleotides frequently have double bonds between carbon and oxygen. The fully oxidized form of silicon forms four single bonds with four oxygen atoms resulting in a relatively inert mineral. Carbon dioxide, the fully oxidized form of carbon, forms double bonds with two oxygen atoms, resulting in CO_2, a reactive gas. Double and triple bonds are also used by organisms to store varying amounts of energy.

The homogeneous bond length of silicon is 235 pm compared to 144 pm for carbon, due mostly to silicon's larger electron cloud, which provides a greater magnitude of shielding and results in weaker Si–Si bonds compared to C–C bonds (Linn 2001). The larger size of silicon results in larger bond angles than for carbon (Zeigler and Fearon 1989), which has a great effect on which compounds can bond with silicon. For example, silicon cannot duplicate carbon's π-bonding, which is necessary to stabilize the delocalized electrons in resonant ring structures like benzene (Linn 2001). Thus, there is no set of aromatic compounds for silicon as there is for carbon.

Due to silicon's strong bond enthalpy with oxygen, it will be oxidized if oxygen is present. The high abundance of silicates on many of the rocky planets is caused by the bonding of silicon with oxygen when the planets formed. When silicon is fully reduced, it forms silane, a compound analogous to methane in the carbon system. Silanes burn spontaneously when in contact with oxygen to form a silicate and molecular hydrogen. Silane decomposes in the presence of water vapor to SiO_2, which explains why no SiH_4 has been detected in the hydrogen-rich atmosphere of Jupiter (though H_2O, CH_4, NH_3, and PH_3 were detected), even though it has been detected in the interstellar medium (Goldsmith and Owen 2003). The much higher reactivity of silanes compared to the corresponding carbon compounds cannot be attributed only to lower bond strengths. Other factors include (1) the larger radius of silicon which is thought to facilitate attack by nucleophiles, (2) the great polarity of silicon bonds, and (3) the presence of low-lying d orbitals which permit the formation of 1:1 and 1:2 adducts (unbounded association of 2 or 3 molecules in which a molecule of one compound, is either wholly or partly locked within the crystal lattice of one or two molecules of the other compound), thereby lowering the activation energy of the reaction (Greenwood and Earnshaw 1984). The affinity of silicon to oxygen is so strong that if silicon is placed in water, it will form a silica shell, stripping the oxygen from the water (LeGrand 1998). Thus, water is not a compatible solvent for silicon-based compounds. Methane, ethane, or any compounds that contain methyl groups are more compatible solvents for a silicon-based system. Under surface conditions on Earth, the most stable silicon polymers are silicones, organic silicon polymers with a Si–O backbone. Silicon-silicon bonds are not stable under these conditions, but can be produced in the laboratory under conditions vastly different from those of the Earth's surface.

Silicon does occur with variable valences (4, 5, and 6), and forms stable covalent bonds with itself, carbon, germanium, nitrogen, phosphorus, oxygen, sulfur, halogens, and many metals (Muller et al. 1998; Walsh 1981). Some of the compounds that silicon can form include (1) stable tetra-, penta-, and hexa-coordinate compounds with N, C, and O bonds, with or without overall charge on the molecule (Bains 2004), (2) branched and unbranched chains, and ring systems such as cyclohexasilanes (Schulze-Makuch and Irwin 2006), (3) highly polarized systems where rapid, reversible chemistry occurs (Sharma and Pannell 1995), (4) cage systems such as silsesquioxanes that provide for complex core structures, which may be surrounded with other groups that are oriented precisely in space (Feher 2000; Harrison 1977) and may protect the core from degradation. Benner et al. (2004) pointed out that oligosilanes having up to 26 consecutive Si–Si bonds are known that can be (1) chiral, (2) support a variety of functionalized and non-functionalized side chains, (3) have alkyl side chains that are generally soluble in non-polar solvents, (4) carry carboxylic acid groups that are soluble in water, and (5) self-aggregate into amphiphilic structures in water, creating vesicles and micelles. Silanes cannot form a π-conjugated system, hence do not form aromatic compounds. However, silicon can form sigma conjugated polysilanes (Maxka et al. 1991) with electronic properties similar to those of the carbon containing π-conjugated system (Benner et al. 2004). When considering biochemical alternatives to carbon, the key is to look for functional rather than structural analogues. For example, Bains (2004) demonstrated this principle by elaborating on the possibility of photosynthesis in a silicon biochemistry. He pointed out that silicon's sp^2 structure is disfavored over carbon's sp^3 structure in its ability to delocalize charge over a large structure. However, sp^3 silicon can delocalize electrons via s-orbital overlap to a degree that carbon cannot, to the extent that polysilanes are semiconducting (Tokito and Okazaki 1998; West 2001). Electron delocalization could therefore occur readily in appropriate silicon compounds, and light-activated electronic effects (the basis of photosynthesis as observed on Earth) could also occur (Fujino 1987). Dahn et al. (1993) pointed out that layered silanes synthesized from calcium silicide of the general formula $(SiH)_n$ have a layered structure and are electroluminescent. A more thorough discussion of the polymeric chemistry of silicon and its possibilities for "exotic life" is provided in later sections of this chapter after we discuss the use of silicon by organisms on Earth.

6.4.2 Role of Silicon for Life on Earth

Silicon is not the basis for life on Earth, but it is still a very important component of living organisms. Without silicon, most of the plant and animal life on Earth would not exist as it does today. Plants use silicon as silica within the walls of the stems to provide rigidity so that the stem can remain erect, yet still remain flexible enough to not become brittle (Sangster and Parry 1981). Large amounts of silicon dioxide are used in the plant kingdom to form the rigid, defensive protrusions on plants. The silicon content of some plants such as the cucumber increases following fungal infection, and appears to exert a protective effect (Samuels and Glass 1991). Silicon, as silicic acid (0.1–0.6 mM), can be regarded as a plant nutrient (Birchall 1995; Epstein 1994). In the animal kingdom, silicic acid is a major constituent of the cells of the connective tissue where it is found in hair, nails, and the epidermis. Among vertebrates, silicon is essential for growth and bone development and for collagen and glycosaminoglycan synthesis (Carlisle 1981). When a bone is broken, high levels of silica are found around the break as it heals. The aorta, muscles, and tendons contain as much as 0.1% silicon, and the kidneys, heart, and liver contain about 0.05% silicon (Tacke and Wannagat 1979).

There is some evidence that silicon is an important nutrient for microbial life, and that it may even be used as a direct energy source for metabolism, or as a catalyst (Wainwright 1997). For example, Yoshino (1990) found that 100 μg/mL of silicon has a remarkable stimulatory effect on the growth of *Staphylococcus aureus*. Chakrabarty et al. (1988) and Das et al. (1992) showed that *Mycobacterium* and *Nocardia sp*. can grow in the absence of carbon, provided that silicon compounds are present. Similar observations were made by Tribe and Mabadje (1972) and Parkinson et al. (1989). They found that certain fungi grew in ultra-pure water only when silicon compounds were added. Wainwright et al. (1997) showed that silicic acid stimulates the growth of fungi, including *Penicillium* species, when growing in ultra-pure water as well as nutrient-rich media. A possible explanation for these observations was provided early in the twentieth century. Reynolds (1906) suggested that silicon takes the place of carbon in some types of microbial metabolisms, and Bastian (1914) suggested the existence of some form of silicon-based autotrophy, which, however, could not be confirmed. More recent research, though, has shown that heme proteins can catalyze the formation of organosilicon compounds in *Rhodothermus marinus*, an obligately aerobic and moderately halophilic, and thermophilic bacterium (Kan et al. 2016). Lauwers and Heinen (1974) proposed that a silicon cycle operates in the environment involving microbial transformations between insoluble and soluble forms, which may in part be based on an earlier finding by Henderson and Duff (1965) that a wide range of bacteria and fungi can solubilize insoluble silicates by producing mineral and organic acids, and chelating agents.

One of the best examples of silicon use by a carbon-based form of life is the presence of silicates in the diatom (Fig. 6.2). Diatoms may account for as much as one-fourth of the world's entire net primary production of biomass, and serve as the

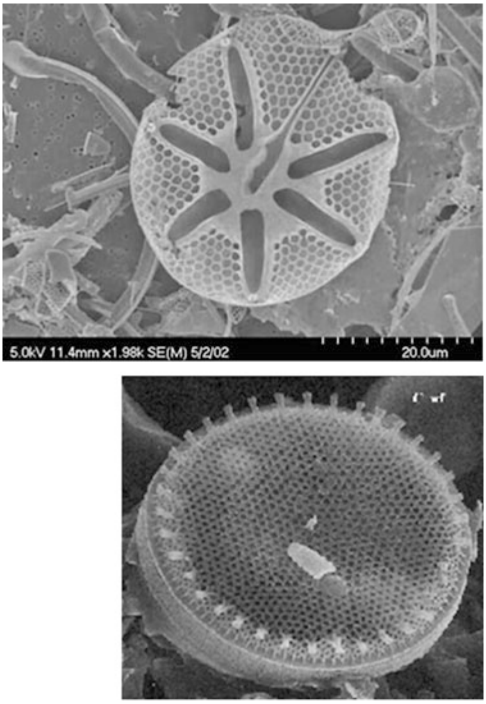


Fig. 6.2 Image of diatom *Asteromphalus hyalinus* provided by Tawnya Peterson, University of British Columbia (*top*), image of unknown diatom provided by Daniel Scheirer, Northeastern University (*bottom*)

basis for marine food webs. Although diatoms have a carbon-based energy metabolism, their shells are composed of silicon dioxide, and diatoms are absolutely dependent upon silicon for growth and development (Lewin 1954; Richter 1906). Diatoms require silicon in the form of $Si(OH)_4$ for their metabolism. Werner (1967) concluded that silicon affects (1) the citric acid cycle between acetyl-CoA and alpha-ketoglutarate, (2) the synthesis of special proteins, (3) the regulation of respiration, and (4) chlorophyll synthesis. Another example of the essential nature of silicon for diatoms is provided from an experiment conducted by Darley and Volcani (1969) in which DNA replication was stopped prior to mitosis by maintaining the newly divided cells of the diatom in a $Si(OH)_4$-free medium. The presence of silicon in the organelles of diatoms may indicate the possibility that it participates in the biochemistry of subcellular structures (e.g. Azam et al. 1974; Mehard et al. 1974).

Silaffins, a type of unique peptide, and long-chained polyamines are constituents of the biosilica of diatoms and can precipitate silica nanospheres (Kröger et al. 2002). The formation of the biosilica occurs within a membrane-bound compartment (silica deposition vehicle), which acts as a casting mold (Pickett-Heaps et al. 1990).

Thus, carbon compounds do interact with silicon compounds in diatoms to build a distinct organism. In diatoms the carbon compounds appear to act as a template for silicon structures. Cairns-Smith (1982, 1985) and Cairns-Smith and Hartman (1986) suggested that silicon compounds may have provided the first templates for carbon-based life, noting that the first carbon compounds may have received their initial handedness from clays or silicate minerals that also had handedness. For example, alpha-quartz, the thermodynamically most stable form of SiO_2 at Earth's surface conditions, forms tetrahedra that are interlinked to helical chains. Due to two slightly different Si–O distances of 159.7 pm and 161.7 pm and a Si–O–Si angle of 144°, the helices in any one crystal can be either right-handed or left-handed. A close association between minerals and the first forms of life is consistent with a variety of mineral characteristics (e.g. Table 2.1). Dessey (1998) suggested that silicon started the evolutionary process for carbon-based life on Earth. This is not impossible as conditions on Earth were quite different early in its history from today. Silicon could have played a vital role in the origin of life on Earth in its pre-biotic stage, but if so, its role was replaced by carbon relatively quickly as conditions became less harsh and more carbon friendly. If indeed silicon compounds were involved in molecular replication, this assembly alone must still have been far from the phenomenon that we call life, since this process meets only one of the characteristics of life as stated in Chap. 2.

6.4.3 *Polymeric Chemistry of Silicon*

Silicon hydrides or silanes have the generic chemical composition Si_nH_{2n+2} and occur both as branched and unbranched chains. They form direct analogs to hydrocarbons in the carbon-based world (Fig. 6.3). For example, a ring of six silicon atoms is called a cyclohexasilane, which has a direct analogy to a ring of six carbon atoms (Zeigler and Fearon 1989). However, because the silicon atom is larger than the carbon, it cannot duplicate carbon's π-bonding, which is essential for stabilizing the electron cloud in C_6H_6 and sustaining the benzene resonant ring structure. Thus, silanes do not form benzene analogs (siloxene has a ring of six silicon atoms but some of the Si–Si bonds are reinforced with oxygen bridges (Firsoff 1963), and thus are not an aromatic series analog). Because the bond energy between hydrogen and silicon is relatively weak compared to the bond energy to oxygen, silanes are much more reactive than their corresponding carbon compounds, and are readily oxidized into silicates in the presence of oxygen. The thermal stability of silanes decreases with increasing chain length. However, if hydrogen is replaced by organic groups, stable compounds are obtained. For example, polysilanes with molecular weights of above 10^6 have been synthesized (Sharma and Pannell 1995). Traces of alkali metals catalyze the hydrolysis of silanes, which is rapid and complete, to yield silicates and hydrogen molecules (Greenwood and Earnshaw 1984). Polysilanes are not stable at

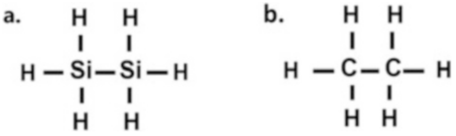


Fig. 6.3 Structural analogy between (**a**) disilane and (**b**) ethane

the temperature and pressure conditions of Earth's surface (with the exception of silane), but are fairly stable at low temperatures, especially at higher pressures.

Replacing the hydrogen in silane with organic groups produces an analogue to hydrocarbons that eventually leads to silicon polymers, possibly resembling a reaction pathway to very complex silicon compounds. Organosilicon compounds (silicones) have considerable thermal stability (many up to about 400 °C) and chemical inertness reflecting the strength of both the Si–O bond and the Si–C bond (comparable in strength to the C–C bond) in the polymer backbone. Silicone polymers are relatively stable to oxidation, repel water, have good dielectric properties, and show a prolonged resistance to ultraviolet radiation (Greenwood and Earnshaw 1984). Hydroorganosilanes, organic compounds with silicon and hydrogen, have bonds that are thermodynamically more stable than other silanes, but become unstable at temperatures over 25 °C. The organosilicon reactions, for the most part, form directly without radical formation, while carbon tends to form radicals in the intermediate stages. Organosilicon compounds also more readily undergo nucleophilic substitutions when compared with their carbon equivalents. Yet, even with silicon's ability to produce complex molecules and carbon analogs, to more readily undergo reactions without the formation of radicals, and to take more direct routes in the formation of organic compounds, silicon accounts for less than one percent of all known organic compounds. Furthermore, the organic compounds of silicon that are known have all been produced in the laboratory but have not been found in nature (Pawlenko 1986). And while a very large number of compounds have been synthesized that involve multiply bonded silicon (DeLeeuw et al. 1992; Sekiguchi et al. 2004; Stone and West 1994; West 1986, 1987), stable compounds containing double or triple silicon bonds are difficult to form because of the larger atomic size and bond angles required (Zeigler and Fearon 1989). Silicon forms stronger bonds to nitrogen and the halogens than carbon does, but forms weaker bonds to hydrogen, phosphorous, and sulfur. The strong Si–O bond can be avoided and the carbon scenario reproduced if oxygen is replaced by sulfur. Then the resulting ratio of bonding energies of Si–Si to Si–S is comparable to the ratio of the C–C to C–O bonding energies (Firsoff 1963). Also, silicon polymers have been obtained with nitrogen instead of oxygen, where nitrogen acts as an electron donor. In hydrogen-poor environments, hydrogen is often replaced by a halogen such as chloride, and long linear chains of silicon and chloride are formed. Large labile molecules based on a Si–O–Si or Si–NH–Si backbone, with halogens as side-groups, could provide a basis for complex chemical systems.

Due to the strength of the Si–O bond, silicon forms a silicon tetrahedron in the presence of oxygen with the silicon in the center and a single bond to each of the four oxygens (Fig. 6.4). The tetrahedra can combine into chains, double-chains, rings, sheets and three-dimensional structures depending on the mineral formed. Neso-silicates consist of discrete SiO_4 tetrahedrons, sorosilicates of discrete Si_2O_7 units with one oxygen atom shared, cyclo-silicates of closed ring structures with two oxygen atoms shared, ino-silicates of continuous chains or ribbons with two oxygen atoms shared, phyllo-silicates of continuous sheets with three oxygen atoms shared, and tecto-silicates consist of continuous three-dimensional frameworks with all four

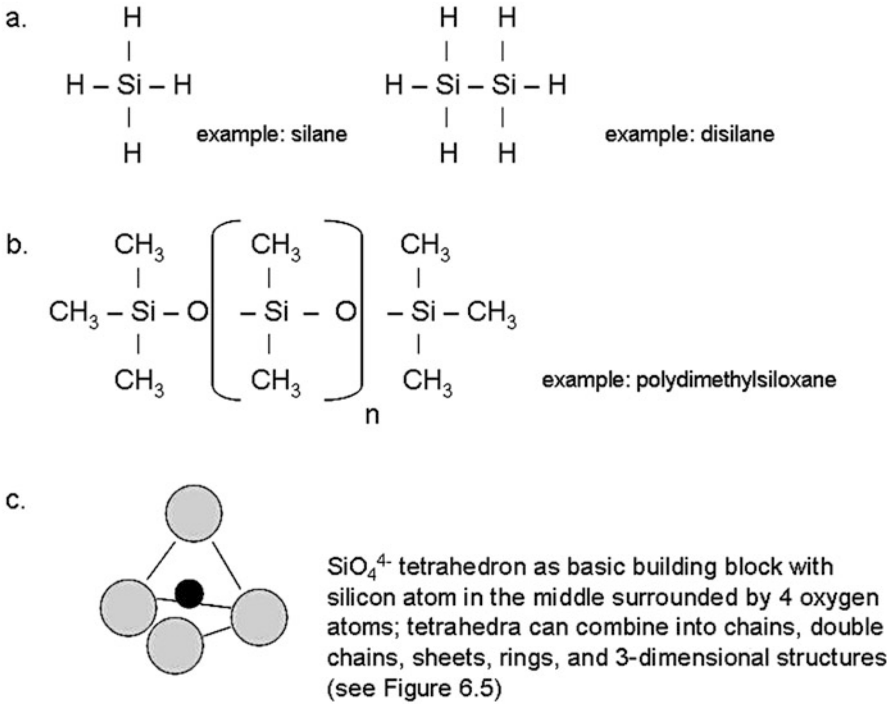


Fig. 6.4 Structure of (**a**) silanes, (**b**) silicones and (**c**) silicates

oxygen atoms shared (Fig. 6.5). All silicates have in common high melting points (e.g. SiO_2 (β-cristobalite) at 1713 °C) and are therefore a major constituent of Earth's crust. Aluminum can substitute for silicon in the silicate network. At the surface conditions of Earth silicon dioxide is a tough, unreactive polymer (Koerner and LeVay 2000). However, at temperatures above 1000 °C complex silicate structures become more labile, partially melt and react with each other.

6.4.4 Environmental Conditions for the Possibility of Silicon-Based Life

Based on the previous discussion, the prospect of silicon-based life under any conditions resembling those on Earth does not appear encouraging. Carbon can form a vast variety of complex compounds, not only from organic molecules on Earth, but also from material found in the heads of comets, inside meteorites, within the nebulae, and among the interstellar matter of the Universe (Fegley Jr. 1987; Gladstone et al. 1993; Hanon et al. 1996; Llorca 1998; Varela and Metrich 2000). While polymeric carbon compounds seem to be ubiquitous, polymeric silicon

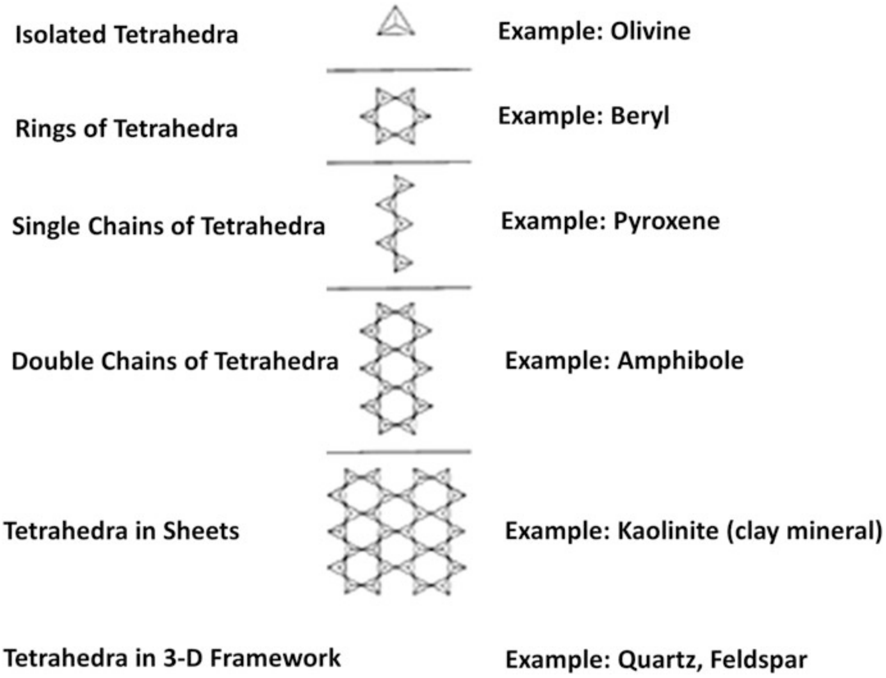


Fig. 6.5 Some silicate structures

compounds do not. Silicon, on the other hand, is found overwhelmingly as silicates making up the structure of the shell of the rocky planets, meteorites, and moons within our Solar System. A very dense polymorph of silica has been discovered in the Martian meteorite Shergotty (Sharp et al. 1999), but this polymorph could not support life and still raises the question of what compounds silicon can and cannot form when subjected to conditions other than the constraints of Earth's surface. Bains (2004), however, noted that in the protostellar disc W33A 1/250 to 1/40 of all infrared-visible silicon atoms seem to have a hydrogen directly bonded to them. Thus, there is a need to discuss the chemical pathways of possible silicon-based life and the environmental conditions that could make it possible. Our approach is to distinguish between silanes, silicones, and silicates on the basis of the different environmental conditions at which these polymers are reactive. We start with silanes, because they present the closest analog to hydrocarbons, which are so important to life processes as we know them on Earth.

6.4.4.1 Life Based on Silane?

Silicon forms a series of hydrides, the silanes, consisting of Si–H and Si–Si single bonds (Fig. 6.4a). If silanes could be a basis for life as hydrocarbons are for carbon-

Table 6.7 List of minimum conditions for silane-based life

1. Little or no atmospheric or lithospheric oxygen
2. Little or no water in liquid form
3. Low temperatures (at least below 0 °C) and/or high pressures
4. Solvent suitable for silane-based complex chemistry
5. Restricted abundance of carbon

based life, it would not be under the conditions found on present-day Earth, where silanes turn instantly into a silicate rock. A list of conditions can be derived that would have to be met as a minimum to make silane-based life a possibility (Table 6.7).

First, the atmosphere has to be reducing, with only minor amounts of oxygen available to avoid turning the silane polymers into silicate rocks. This kind of environment could exist if most of the original oxygen of a planetary body has been removed, for example by the precipitation of iron as iron oxides (as on early Earth). Oxygen could have also been lost to space due to fractionation during the early history of the formation of a planetary body and its atmosphere. Oxygen has a relatively high molecular weight of 32, but it dissociates to an atomic state in the outer atmosphere where the escape occurs. However, if the oxygen had escaped, then the much lighter hydrogen would also be expected to be severely depleted unless there was a specific mechanism to retain it. An oxygen-free atmosphere would allow the retention of free silicon instead of the formation of silicates.

Second, water, especially in the liquid state, is another compound that has to be scarce for silane-based life to form, because silicon is easily oxidized by water. Alkali-metals would likely be in solution catalyzing silane polymers into silicon dioxide and hydrogen gas. As for condition 1 (Table 6.7), the atmosphere would have had to undergo an extreme fractionation process to shed all lighter atmospheric gases with a molecular weight of up to 18 at least ($H_2O = 18$ g/mol), or alternatively temperatures on the planetary body would have to be much below the freezing point of water to immobilize nearly all the water in the frozen state.

Third, temperatures far below the freezing point of water would be needed to make the silane-reactions that are so volatile at surface conditions on Earth controllable and accessible for life processes. A high-pressure environment would slow the silane-reactions as well, and thus have a complementary effect.

Fourth, and very importantly, a suitable solvent would be essential to foster the chemical reactions essential for life. Methane would be a good solvent for a silane-based system, and would have the additional advantage that it stays liquid at fairly low temperatures. However, methane has a relatively low molecular weight (16 g/mol) and would be degassed if the atmospheric depletion of oxygen and possibly water is required (conditions 1 and 2; Table 6.7). Thus, in such an environment, heavier methyl-compounds such as methyl alcohol remain about the only alternative solvents.

Fifth, the availability of carbon should be restricted, because carbon may be able to outcompete silicon for building complex macromolecules due to its greater chemical versatility. Other opinions on this issue have been offered, however. For example, Feinberg and Shapiro (1980) argued that the great versatility of carbon could also be considered a disadvantage because life-supporting molecules would have a very difficult time finding each other during the origin-of-life phase. Either way, some carbon may be an asset to silane-based life due to the possible formation of silicon-carbon bonds, but too much carbon appears to be a disadvantage.

The conditions imposed on the availability of silane polymers that could lead to a living system thus are very restrictive: a non-oxidizing, nonhydrous, extremely cold, high-pressure world where carbon is not abundant. While some of these restrictions are mutually compatible and commonly found in the Universe, in their totality they are rarely found in our Solar System and are not likely to be common elsewhere in the Universe. The Saturnian moon Titan comes closest in our Solar System to meeting all the criteria, except for a low abundance of carbon, where the opposite is true. Still, there is some chance that under the extremely cold, reducing conditions on Titan, carbon would lose its competitive advantage over silicon. Processes and environments suggested by Bains (2004) for the creation of silanes include (1) serpentization reactions in a cryogenic environment, (2) meteorite impacts on cold planetary bodies, and (3) ice/silicate grains exposed to UV radiation and 1 MeV protons in a hydrogen atmosphere.

The conclusion that silane-based life, if it exists, is not common in the Universe is based on chemical reasoning, but is also supported by observational evidence. The apparent lack of silane polymers and the abundance of carbon polymers in meteorites would suggest that carbon-based life is much more probable than silicon-based life (Tables 6.4 and 6.5). There are significant variations in chemical abundances in our Galaxy and the Universe (e.g., in regard to metallicity), but no evidence seems to suggest that our Solar System is extraordinary. However, the possibility that life could exist in very exotic planetary environments based or partially based on silane-chemistry, as discussed above for Titan, should not be overlooked. The general failure to detect large amounts of silanes in space (the exception being the protostellar disc W33A), may just mean that silanes are very rapidly oxidized to silicates under the conditions of interstellar space.

6.4.4.2 Life Based on Silicone?

A silicone is an organo-silicon polymer with a silicon-oxygen framework. Its simplest fundamental unit is $(R_2SiO)_n$ (Fig. 6.4b). Carbon atoms can be included in the chain. Silicones are thermally stable at much higher temperatures than silane, even at temperatures where hydrocarbons are not stable. Silicones are also resistant to oxidation and prolonged exposure to UV radiation, thus are durable polymers under Earth's surface conditions and at higher temperatures. However, they repel water and would need a solvent such as methane or a methyl-compound to exhibit polymer activity. There is no suitable solvent for silicone in appreciable amounts on Earth, thus carbon with its excellent solvent partner—water—undoubtedly had the edge for the evolution of life on Earth. This holds true even though silicon and oxygen are the most common compounds in the Earth's crust (Table 6.3). The fact that silicone-based life did not develop on Earth—or was outcompeted very early in the origin-of-life phase—dims the prospects for silicone-based life elsewhere. However, the main problem for silicone-based life on Earth may have been the abundance of water and the lack of a suitable solvent in appreciable quantities. An Earth-type world with methane as a major solvent is certainly imaginable, but whether this scenario would result in a silicone-based life form is very uncertain. Other planetary conditions that would make silicone-based life more likely are high pressures, higher temperature (50–400 °C), higher abundances of silicon than carbon, and a reducing atmosphere. A niche could exist at the temperature range of 200–400 °C, because carbon-based macromolecules generally disintegrate at about 200 °C and would not be competitive. But a solvent that would be liquid at that temperature is difficult to envision. Complex chemistry in a semi-molten state that would resemble life is conceivable, but the structural stability required for the low entropy requirements of a living system under such conditions seems improbable. Thus, the chemical properties of silicones render a silicone-based evolutionary pathway to biology unlikely.

6.4.4.3 Life Based on Silicate?

Silicates are salts containing anions of silicon and oxygen with the silicon-oxygen tetrahedron being the basic building block (Fig. 6.4c). At the surface conditions of Earth, silicates are inert, very slowly reactive polymers; but some silicates melt at temperatures beyond 500 °C, and most melt above 1000 °C where they become reactive. Feinberg and Shapiro (1980) suggested the existence of lavobes, organisms that could exist in lava flows, and magmobes, organisms that could exploit thermal gradients or chemical energy sources within the molten rock. These proposed organisms could make use of the chemical complexity of silicate rocks in which aluminum could replace silicon in the tetrahedrons and cation exchange reactions could occur in interlayer sites between the tetrahedral and octahedral sheets. For this to occur, silicates would have to be in the form of sheets, such as the clay minerals smectite and montmorillonite. Information could be represented as irregularities in the crystal lattice of minerals. A particularly intriguing example is the clay mineral amesite, which has a helical structure. Information could be encoded by substitution of silicon with aluminum (Fig. 2.1).

It would be difficult to imagine how life could sustain itself at such high temperatures. Reactions at 1000 °C or above happen so fast that it would be difficult for an organism to control them. However, some silicates start to partially melt at much lower temperatures, such as zeolites. Organic-inorganic hybrid zeolite materials have been synthesized where siloxane bonds (Si–O–Si) have been replaced with methylene frameworks (Si–CH_2–Si) (Yamamoto et al. 2003). Zeolite minerals could provide a suitable silicate membrane, because they have been shown to act as semi-permeable membranes comparable to cell membranes, preferentially filtering some molecules but not others (Bowen et al. 2004). Thus, they possibly would be able to maintain disequilibrium conditions that are so crucial for life. They also may provide a durable enough membrane that would be needed as a boundary between the interior of the organism and the outside environment. Heron (1989) suggested that zeolites may also be used by silicon-based life as enzyme mimics. Still, the problem of a suitable solvent at these temperatures, as discussed for silicone, remains.

All inner planets of our Solar System have magmatic activity in their interiors, as do some of the moons of the gas giant planets. For example, Io is the planetary body with the most volcanic activity in our Solar System (Matson and Blaney 1999). All these bodies could present favorable environments for silicate-based organisms. However, given the environmental conditions of Earth's crust and its composition (46% oxygen, 28% silicon) with abundant silicate melts, Earth should be more favorable than most other planets and moons in our Solar System for such a form of life. Yet no fossilized remnants or structures consistent with such an organism have been found, even though outcrops of igneous and volcanic rocks are abundant. Thus, the existence of such organisms seems very unlikely.

6.5 Other Alternatives as Building Blocks of Life

A few other potential substitutes for carbon deserve consideration as candidates for polymer-based complex chemistry. In order to be a viable alternative to carbon, the element should be a non-metal and be able to form at least the alkane-equivalent to the hydrocarbons. The possible choices are boron from group III of the periodic table, nitrogen and phosphorous from group V, sulfur from group VI, and possibly germanium from group IV (in addition to silicon).

Boron, like carbon and silicon, has a marked propensity to form covalent, molecular compounds, but it has one less valence electron than the number of valence orbitals. Thus, it has somewhat different chemical properties from carbon (Greenwood and Earnshaw 1984). Boron forms many different structural varieties of hydrides, but the boron atoms are linked indirectly through hydrogen bridges and are therefore not direct analogs to hydrocarbons. Boron has a high affinity for ammonia rather than water. It forms bonds with nitrogen that resemble the carbon-carbon bond. Two electrons of the nitrogen are donated in addition to the covalent electron sharing (Fig. 6.6). Boron-nitrogen compounds reproduce the physical and chemical properties of alkanes and aromatic hydrocarbons to a great extent, but with higher melting and boiling points. Borazole especially bears a strong resemblance to ordinary benzene in both physical and chemical properties (Firsoff 1963; Fig. 6.6). Borazole and its derivatives have a higher reactivity than the corresponding benzene group and thus would fit with the lower temperature range at which ammonia is a liquid solvent. Reactions at this lower temperature range would be at a more controllable pace. Also, boron has an affinity for nitrogen and ammonia as solvents that would fit into a low-temperature biological scheme. Many B–N compounds, furthermore, exhibit high thermal stability. However, boron is an element of low abundance, with an average of about 10 ppm in Earth's continental crust (CRC

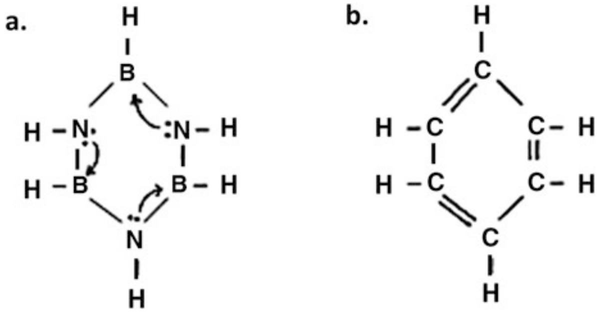


Fig. 6.6 Structure of (**a**) borazole and (**b**) benzene. The benzene ring is held together by π-bonding

2001), thus a biological scheme based on boron without a strong fractionation mechanism appears unlikely.

Nitrogen can form long chains at low temperatures with a liquid solvent such as ammonia or HCN. However, the major drawback of nitrogen as a backbone for large molecular structures is that the energy of the triple bond in N_2 is much greater than that of the single bond, thus nitrogen-nitrogen bonds tend to revert back to elemental nitrogen. However, nitrogen can form longer molecular structures with boron as described above as well as with carbon, phosphorous, and sulfur. Nitrogen can also form hydrides for which hydrazine is an example.

Phosphorus forms hydrides and has some merit as a potential building block with phosphine (PH_3) as a compatible solvent. While the abundance of phosphorus is relatively low, it is one of the most critical elements for terran life, because all major building blocks of life contain phosphate groups, including ATP, RNA, DNA, and cellular membranes. Gibard et al. (2017) showed that the phosphorylation reaction of prebiological substrates under aqueous conditions might have been a critical step in the origin of life, possibly being achieved by the compound diamidophosphate. Reactive phosphorus may have been supplied on early Earth by meteorites in the form of the iron–nickel phosphide mineral schreibersite, which reacts in water releasing soluble and reactive reduced phosphorus compounds, such as phosphite, that could then be readily incorporated into prebiotic molecules (Pasek et al. 2013). Wolfe-Simon et al. (2011) claimed that a bacterium isolated from Mono Lake, California, was able to substitute arsenic for phosphorus to sustain its growth, but that was heavily disputed and shown to be likely incorrect (Erb et al. 2012; Benner et al. 2013). Thus, we think that phosphorus retains its status as essential for life on Earth. In fact, it has a much higher enrichment factor than carbon when comparing its abundance in organisms with its occurrence in the natural environment (by a factor of about 100), so perhaps life on Earth should be called phosphorus-based life?

Sulfur forms hydrides as well, and could be of organic importance in a sulfur-rich environment with liquid solvents such as H_2S or H_2SO_4. Sulfur compounds with sulfur chains are known. However, given the poor variety of phosphorus and sulfur hydrides and the restricted environmental conditions, it is hard to imagine that either one of those elements would be a major building block of life. At best, they could form chains together with other elements such as carbon, silicon, or nitrogen. Sulfur, however, is unique in another way. It has more oxidation states than carbon, including fractional nominal states (e.g., +7, +5,+4, +3.33, +2.5, +2, −0.4, −0.5, −0.67, −1; Amend and Shock 2001), and thus can form a huge variety of different compounds. Germanium is not a suitable backbone element due to its large size, metallic character, and low abundance.

6.6 Chapter Summary

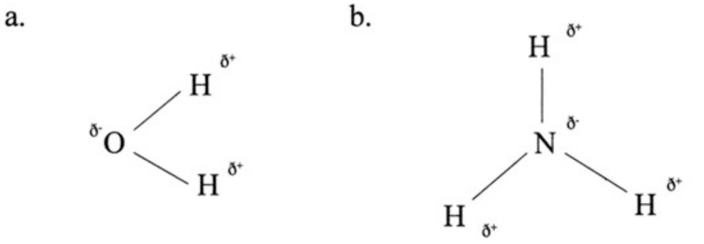
Carbon exhibits many characteristics that make it uniquely suited for life-supporting processes. Its usefulness for life derives primarily from (1) the versatility that enables it to form millions of complex polymers, including single-, double- and triple-bonded compounds, chiral compounds, and resonant ring structures, (2) the ease with which it changes from one valence state to another, thereby suiting it well for energy-transferring redox reactions, and (3) its compatibility with water (and ammonia) as a liquid solvent. The only other element that approaches the versatility of carbon and is common enough to be a universal building block is silicon. Silicon can form long chains as silanes, silicones, and silicates. Some of these compounds could present a possible alternative to carbon for the construction of polymers under very restricted environmental conditions. These are (1) little or no oxygen, (2) little or no liquid water, (3) temperatures above 493 K (silicones, silicates) or below 273 K (silanes), (4) pressures greater than on the surface of Earth, (5) presence of a solvent such as methane or methanol, and (6) relative lack of available carbon. Other elements would likely not be suitable as backbones for the building blocks of a living system, but might nonetheless be critical for life, like phosphorus is on Earth. However, it is not clear that polymeric skeletons have to be built from one element only. Polymers can also be assembled as chains of alternating elements such as Si–C, Si–O, and B–N. Alternation with carbon is used to some extent in terran organisms (such as C–C–N in proteins and C–C–C–O–P–O in nucleic acids), and silated compounds play important structural roles in the cells of many organisms on Earth. But no comprehensive bioenergetic metabolism is known to arise from non-carbon complex chemistry, despite the high abundance of oxygen and silicon on Earth, and the relative concentration of silicon on other terrestrial planets. Thus, if elements other than carbon constitute the building blocks for any living system on other worlds, they almost surely exist under conditions far different from those on Earth, including temperatures and pressures where water could not be the solvent. Titan provides the best natural laboratory in our Solar System for investigating this possibility.

Chapter 7
Life and the Need for a Solvent

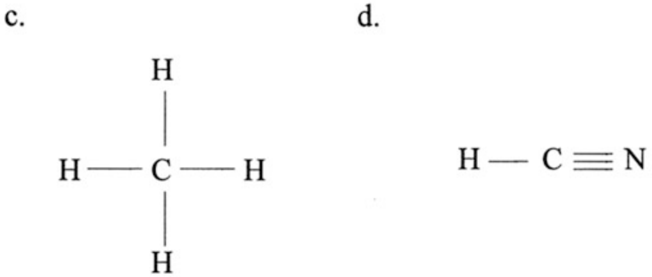
Life as we know it consists of chemical interactions that take place in the liquid state, yet the requirement that life be liquid-based is not normally part of anyone's definition of a living system. Thus, we cannot state categorically that life in either a solid or gaseous state is impossible. There are, however, compelling theoretical advantages for the complex chemical interactions that compose the living state to occur in a liquid medium. These include (1) an environment that allows for the stability of some chemical bonds to maintain macromolecular structure, while (2) promoting the dissolution of other chemical bonds with sufficient ease to enable frequent chemical interchange and energy transformations from one molecular state to another; (3) the ability to dissolve many solutes while enabling some macromolecules to resist dissolution, thereby providing boundaries, surfaces, interfaces, and stereochemical stability; (4) a density sufficient to maintain critical concentrations of reactants and constrain their dispersal; (5) a medium that provides both an upper and lower limit to the temperatures and pressures at which biochemical reactions operate, thereby funneling the evolution of metabolic pathways into a narrower range optimized for multiple interactions; and (6) a buffer against environmental fluctuations.

For a substance to be an effective solvent for living processes, its physical properties in the liquid state must be matched to those of the environment in which it occurs. Those relevant properties include the requirement that it be liquid at the prevailing temperatures and pressures on the planetary body in question. These properties include the melting and boiling point of the solvent, but also its critical temperature and pressure. The critical temperature of a compound is that temperature beyond which the liquid phase cannot exist, no matter how much pressure is applied to it. The critical pressure of a substance is the pressure required to liquefy a gas at its critical temperature. A suitable solvent must also have sufficient physical buffering capacity, which can be specified by its enthalpy of fusion (melting) and vaporization (kJ/mol) describing the amount of energy needed to change 1 mol of the substance from solid to liquid at its melting point and from liquid to gas at its boiling point, respectively. A large temperature range for the liquid state is favorable. For those reactions that depend on the making and breaking of ionic and hydrogen bonds, and

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_7



Bent , angle between Hs: 104.5°   Trigonal pyramidal, angles between Hs: 10°



Tetrahedral, angles between Hs: 109.5°   Linear, angles between C-H and C-N: 180°

Fig. 7.1 Structure of some molecules that are discussed here as a solvent; (**a**) water, (**b**) ammonia, (**c**) methane, and (**d**) hydrocyanic acid

for maintaining appropriate macromolecular configurations, a measure of the solvent's polarity is important. The common measure is the dipole moment in debye (D, 1 D = 3.335×10^{-30} cm), which describes the polarity of a molecule and is dependent on charge and distance. The more polar the compound the higher is its dipole moment, but if the geometry of the molecule is symmetrical (e.g. CH_4, Fig. 7.1c), the charges are balanced and the dipole moment equals zero. The maintenance of appropriate diffusion rates depends on both density and viscosity. Viscosity, the quantity that describes a fluid's resistance to flow, is very much dependent on temperature and is measured in poise (P, dyne s/cm^2) or pascal seconds (Pa s; 1 Pa s = 10 poise). To the extent that electrical conductivity is relevant to a particular living process, the dielectric constant is also pertinent. The dielectric constant (dimensionless) is the ratio of the permittivity of a substance to the permittivity of free space and describes the extent to which a material concentrates electric flux (permittivity is the proportionality constant between electric displacement and electric field intensity). The physical properties for a variety of inorganic candidate solvents are provided in Table 7.1.

First, we will discuss why water is such an excellent solvent for the environmental conditions of Earth. Then, we will discuss other possible solvents that could replace water under environmental conditions either similar to or vastly different from those existing on Earth. Finally, we will discuss how the nature of a solvent could

Table 7.1 Some physical properties of water and other polar compounds relevant to their solvent capabilities

Property	H_2O	NH_3	HCN	HF	H_2S	H_2SO_4	H_2O_2	N_2H_4
Molecular weight	18.02	17.03	27.02	20.01	34.08	98.08	34.01	32.05
Density (g/ml)	0.997	0.696	0.684	0.818	1.393	1.83	1.443	1.004
Melting point (°C at 1 bar)	0.00	−77.73	−13.3	−83.4	−85.5	10	−0.4	1.6
Boiling point (°C at 1 bar)	100.0	−33.33	26.0	20.0	−59.6	337	150.2	113.5
Liquid range (°C at 1 bar)	100	44.4	39.3	103.4	25.9	327	151	111
Critical temp. (°C)	374	132	184	188	100	NA	455	380
Critical pressure (bar)	215	111	54	64.8	88	NA	215	14.2
Enthalpy of fusion (kJ/mol)	6.0	5.7	8.4	4.6	2.4	10.7	12.50	12.7
Enthalpy of vaporization (kJ/mol)	40.7	23.3	25.2	30.3	18.7	NA	51.6	41.8
Dielectric constant (ε)	80.1	16.6	115	83.6	5.9	101	89(?)	51.7
Viscosity (10^{-3} P)	9.6	2.7 (at −34°C)	2.0	~4.3	4.3	260	11.4	9.8
Dipole moment (D)	1.85	1.47	2.99	1.83	0.98	2.7	2.01	1.9
Surface tension (10^{-3} J/m^2)	71.99	19.8	18.1	NA	NA	NA	79.7	66.39
Relative probability of occurrence[a]	1	0.25	0.14	NA	1.31	0.42	NA	0.26

Note: Data from CRC (2001), Firsoff (1963), Merck Research Labs (1996), Moeller (1957); http://www.trimen.pl/witek/ciecze/oldliquids.html and http://www.flexwareinc.com/gasprop.htm. NA = not available

[a] Relative probability of liquids on bodies >1000 km in diameter around any star in our stellar neighborhood as provided by Bains (2004)

determine the chemical characteristics of a living system, including the nature of its origin and evolution.

7.1 Water as the Universal Solvent for Life on Earth

Water is usually portrayed as the universal solvent for life as we know it, because of various properties that make it a very good solvent for the environmental conditions of Earth. Probably, the most important property of water is its polar structure (Fig. 7.1a). This polarity allows liquid water molecules to stick to each other via hydrogen bonding, providing it with polymer-like properties. The hydrogen bonding also raises the freezing and boiling point of water to much higher temperatures than would otherwise be expected from a molecule with a molecular weight as low as

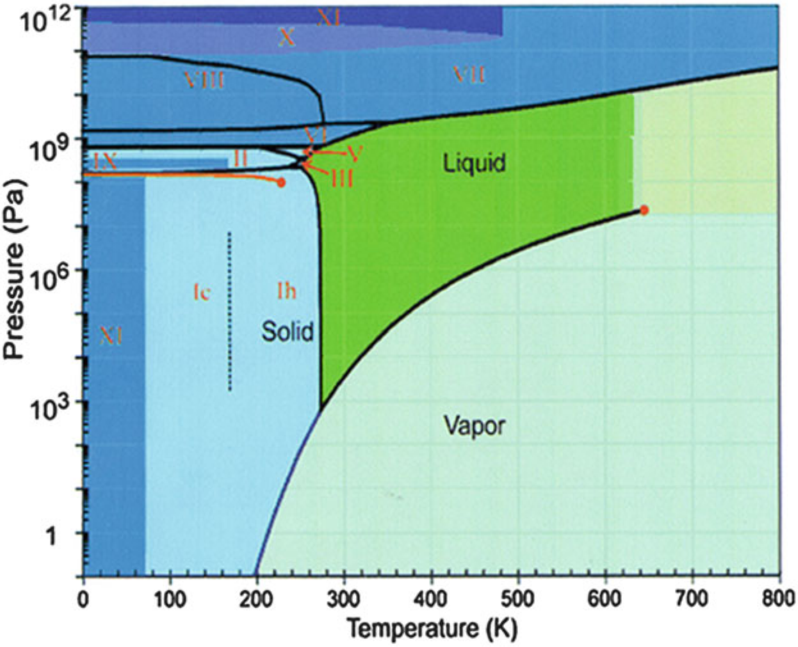


Fig. 7.2 Phase diagram for water. Stability fields for the solid, liquid, and gas phases as shown. All the different solid phases of ice involve hydrogen bonding of water molecules to four neighboring water molecules (from Chaplin 2003). Notice that the triple point is located very close to Earth's average temperature allowing all three phases to coexist under a wide variety of climatic conditions

18 g/mol. Water is a liquid in a temperature range of 0–100 °C (at 1 bar pressure). The triple point of water at which all three phases—solid, liquid, and gas—coexist is also located within this temperature range, very close to Earth's average temperature (Fig. 7.2). Thus, water in the liquid form allows for the wide variety of climatic conditions, differentiated habitats, and complex chemical and physical interactions found on Earth. And because life on Earth has evolved as a system that operates in liquid water, the temperature at which water is a liquid determines the range of temperatures at which living processes can proceed normally. The dynamic properties of life cease below the freezing point of aqueous solutions, and are destroyed at temperatures above their boiling point. This empirical fact lends credence to the supposition that life is fundamentally a liquid-based process. Some tardigrades (hydrophilous micrometazoans) have been recorded to survive temperatures below −250 °C and as high as 151 °C (Cavicchioli 2002), but this kind of survival occurs only in a dormant state.

The superiority of water as a good solvent for ionic and polar covalent bonds is a function of its high dipole moment (1.85 D), which quantifies the electric charges at its poles. Thus, water readily dissolves molecules such as salts that serve as co-factors for many metabolic reactions and mediate bioelectrical processes, as well as monomeric organic compounds with abundant polar groups such as sugars and amino acids that need to be capable of intracellular and transcellular mobility. On the other hand, water is not a good solvent for molecules with non-polar covalent bonds, such as those of hydrophobic organic molecules like lipids, which serve as the core of cellular membranes, and proteins embedded in the membrane core. Large biomolecules are thus able to maintain stable stereochemical configurations—a property essential for their biological activity—because of the stability of covalent carbonyl, peptide, glycosidic, phosphatidyl, and disulfide bonds in an aqueous solvent. Another advantage of water is that it offers organic non-polar compounds a way to be concentrated.

There are challenges, however. First, many organic synthesis reactions involve dehydration, which is inhibited in the presence of water, hence requiring energetically expensive and elaborately catalyzed reactions. Secondly, water is very reactive and therefore damaging to many biomolecules, including high-energy phosphatidyl compounds that break down easily, and many cellular macromolecules, particularly the nucleic acids (Feinberg and Shapiro 1980). Water does not support protein folding, because it disrupts the hydrogen bonds (Baross et al. 2007). Specific repair mechanisms have evolved to counter the damaging reactivity of water with DNA, and metabolic evolution has evolved generally under the limitations imposed by water on biochemical processes.

One of the most biologically favorable properties of water is its role as a thermal moderator. The reason is that (1) water's high heat capacity allows it to be available over a wide range of temperatures (from 0 °C to 100 °C at 1 bar pressure), and (2) water is a good heat insulator. For example, the heat of vaporization, the amount of energy required to change from the liquid into the vapor phase, requires 40.7 kJ/mol (at a pressure of 1 bar), compared to 23.3 kJ/mol for ammonia and 18.7 kJ/mol for H_2S (Table 7.1). This high heat of vaporization stabilizes an organism's intercellular temperatures and promotes consistent chemical reaction rates. This same property also accounts for the cooling capacity of water evaporated from the surface of animals living in air, a mechanism important in the dissipation of excess heat.

The property of water to act as a heat insulator can be quantified by its dielectric constant, which is relatively high compared to most other potential solvents (Tables 7.1 and 7.2). Taken together, the wide temperature range at which water stays liquid and its insulating properties allow organisms immersed in liquid water to be very well protected from temperature fluctuations. This property is readily observable in the tendency of the oceans of the Earth to maintain moderate temperatures and counteract extreme temperature climatic fluctuations (though the floating of water ice on top of liquid water is counterproductive). Water also provides stability against environmental fluctuations in a chemical sense. Water dissociates into a proton ($H+$), which is usually attached to a water molecule as a hydronium ion (H_3O^+), and an anion (OH^-), providing acid and base characteristics further increasing the solubility of compounds immersed in water. Drastic changes in pH, which could easily be detrimental to life, can be prevented by the presence of naturally and widespread occurring buffers such as carbonate and phosphate. The presence of acid and base possibilities also leads to neutralization reactions, in which the cation of the

Table 7.2 Comparison of physical properties for water, organic, and non-polar compounds relevant to their solvent capabilities

Property	H_2O	CH_4	C_2H_6	CH_3OH	$HCONH_2$	N_2
Molecular weight	18.015	16.04	30.07	32.04	45.04	28.01
Density (g/ml)	0.997	0.426 at −164°C	0.572 at −107°C	0.793	1.13	0.85
Melting point (°C at 1 bar)	0.00	−182	−172	−94	3	−210
Boiling point (°C at 1 bar) °	100.0	−161.5	−89	65	211	−196
Liquid range (° C at 1 bar) °	100	18	65	159	208	14
Critical temp. (°C)	374	−82.6	+32.3	240	NA	−147
Critical pressure (bar)	215	45.4	47.8	78	NA	33.3
Enthalpy of fusion (kJ/mol)	6.0	0.94	2.7	2.2	8.44	0.71
Enthalpy of vaporization (kJ/mol)	40.7	8.2	14.7	40.5	60.1 at 25°C	5.56
Dielectric constant (ε)	80.1	1.7	1.9	354 at 13°C	110	1.45
Viscosity (10^{-3} P)	9.6	0.009 at 20°C	0.011 at 20°C	5.9	33	2.04
Dipole moment (D)	1.85	0.0	0.0	1.6	3.4	0
Surface tension (10^{-3} J/m^2)	71.99	NA	NA	22.1	57.03	10.53
Relative probability of occurrence[a]	1	0.62	1.25	NA	NA	1.96

Notes: Data from CRC (2001), Goldsmith and Owen (2003), Firsoff (1963), Moeller (1957), Merck Research Labs (1996); http://www.trimen.pl/witek/ciecze/old liquids.html and http://www.flexwareinc.com/gasprop.htm

NA not available

[a] Relative probability of liquids on bodies >1000 km in diameter around any star in our stellar neighborhood as provided by Bains (2004)

base combines with the anion of the acid to form a salt, and the anion of the base combines with the cation of the acid to form a molecule of the solvent. Salts dissociate in their solvent, in this case water, into charged ions, increasing the reactivity of the solution as well as its conductivity. The usefulness of this electrolytic property is enhanced by the low viscosity of water. Ions can flow within and circulate efficiently through the solvent and participate in reactions within a reasonable time frame.

The role of water as a climatic stabilizer is an immensely important property for all organisms. Associated with that property is its unusual capacity to decrease in density as it freezes below its maximum density at 4 °C. This has obvious advantages for life in Earth's oceans and lakes, because the lighter water ice floats and acts as insulator for organisms beneath its surface and prevents the complete freezing of a body of water from the bottom to the top. This advantage is more important for multicellular forms of life than for microbial life, because microbes can more easily employ adaptive strategies against freezing such as surviving in a spore state. This peculiar property of water has a disadvantage as well, in that ice crystals pierce the cellular membranes due to the expansion of water as a solid. This is the basis for frost damage to plants, for example. However, this property is only valid for ice I (Fig. 7.2), while ice II or any other form of ice is denser than liquid water (Baross et al. 2007). Thus, on a planet much more massive than Earth, ice would sink in water. Another peculiar property of water is its high surface tension, which reflects the tendency of water to form droplets due to greater cohesion among adjacent water molecules than between water and the molecules of air with which it is in contact. The surface tension of water is very high with a value of 71.99 mN/m at 25 °C (CRC 2001), compared to most other liquids. The surface tension of other potential solvents at their respective temperature of liquidity is not very well known though. This property is not directly related to the solvent's ability to transport nutrients, but is likely to be relevant to the origin of life. Organic compounds may have been concentrated in small water droplets that enhanced the probability of a reaction sequence leading to prebiotic molecules (Gusev 2002).

The unusual properties of water have more recently been a focus of investigation. Morawietz et al. (2016) suggested that the 4 °C density maximum is caused by weak van der Waals forces that modulate the flexibility of the water´s hydrogen bond network. Wernet et al. (2004) and Nilsson and Pettersson (2015) hypothesized that many of the seemingly anomalous properties can be explained by water having two different types of structures: a tetrahedral geometry and a more random, disordered orientation of hydrogen bonds. According to that hypothesis, water at moderate temperatures would be a mix of both varieties, with the water molecules being more densely packed in the disordered structure. The discovery of high and low-density amorphous forms of water ice and their transition from one into the other appears to support the existence of two distinct liquid forms (Perakis et al. 2017). Many apparent anomalies of water, such as its high heat capacity, could be explained: when energy in the form of heat is applied to the low-density tetrahedral structures, many of them would be converted to the higher density disordered arrangement rather than increasing their kinetic energy (thus the temperature) of the water molecules. If this hypothesis is proven to be correct, observations for the existence of metastable bulk liquid water down to temperatures of about 227 K might be explainable as well (Sellberg et al. 2014).

One important environmental advantage of water is that in an Earth-type environment it is self-shielding against ultraviolet radiation. Ultraviolet photons dissociate water molecules, releasing oxygen and hydrogen into the atmosphere. If that happens, some of the oxygen atoms will form ozone molecules, which are an excellent absorber for UV radiation, thus shielding the planetary surface from this detrimental form of high energy.

Another important property for any candidate to be qualified as a vital solvent in a scheme of organic chemistry leading to biology is that it has to be related to that scheme (Firsoff 1963). A solvent may be as good as water in an Earth-type environment, but if it does not form any ions that could advantageously enter into biochemical reactions, it is of little interest. With respect to water, hydration and dehydration reactions are widespread in the biochemistry of Earth's organisms. Examples include the formation of peptide bonds between amino acids via dehydration synthesis reactions and the breakdown of complex sugars by hydration hydrolysis.

If life requires proteins, which are essential biomolecules for life on Earth, water is an ideal solvent. Proteins fold to a unique, globular conformation, which tightly packs over 80% of the peptide groups and non-polar side chains. This marginally higher stability of proteins in the folded state, which allows both stability and solubility, would be very difficult to reproduce in alternative solvents (Pace et al. 2004). However, Benner et al. (2004) pointed out that many organic molecules that are parts of a carbon-based metabolism display problematic reactivity with water, citing the difficulty with carbon dioxide cycling as an example. At a symposium on the biological importance of water, Daniel et al. (2004a) wondered about the biological functions of water at the molecular level and whether water is truly irreplaceable for the function of living systems. Terran organisms are very well adapted to water and other solvents are usually very toxic to them. The toxicity of these solvents is determined by their ability to permeate the cell membrane, which results in the leakage of macromolecules, including proteins and RNA (Isken and de Bont 1998). However, some bacteria tolerate other solvents at very high concentrations by membranes that limit the diffusion of solvents into the cell and by specialized efflux mechanisms that remove solvents that have diffused into the cell (Baross et al. 2007).

Perhaps the most important property of a life-sustaining solvent is that it has to occur in large quantities on the planetary surface or wherever the life-sustaining reactions are to occur. With oxygen the most common element on Earth, and hydrogen the most common element in the Universe, water would be expected to be common on Earth. Water is also known from spectral analysis to be a common molecule in the Universe, and thus may be the obvious choice as a solvent elsewhere as well. However, many properties that make water such a good solvent are directly linked to the environmental conditions existing on Earth as discussed above. Thus, considering environmental conditions unlike those on Earth may require the participation of some other types of solvents. This notion will be explored in the coming sections.

7.2 Inorganic Polar Solvents as Alternatives to Water

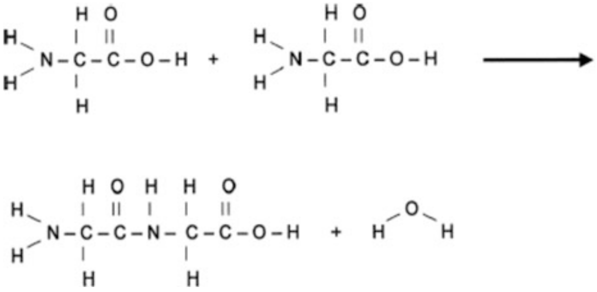
In their assessment of the limits of organic life in planetary systems, the National Research Council (Baross et al. 2007) found no compelling reason to limit the environment for life to water as a solvent, although terran life is constrained to use carbon as the scaffolding element for most of its biomolecules. Several potential candidates could replace water as a polar solvent on other worlds. For example, Benner (2002) suggested sulfuric acid (H_2SO_4) as a possibility for Venus, and ammonia (NH_3) as a possibility for Jupiter. Most of the potential solvent candidates are liquids at lower temperatures than water. Hydrazine, N_2H_4, which is a liquid from 2 °C to 114 °C at 1 bar pressure, is one of the few exceptions. There is, however, overlap with the thermal range of liquidity for water in some cases (e.g. HCN, HF). Chemical reactions occurring within these solvents would proceed at a much slower pace than on Earth, typically by a factor of 2 for every 10 °C decrease in temperature (Jakosky 1998). However, the key to developing a suitable chemistry at a given temperature lies in selecting chemical reactions suited to that temperature. For example, those reactions involving unstable and highly reactive free radicals have very low activation energies (Feinberg and Shapiro 1980) and would be suited for low temperature organisms. Also, lower temperatures and an abundance of nitrogen could open up new possibilities, such as polymeric chains of nitrogen atoms. Bonds of nitrogen to nitrogen are weaker than carbon to carbon bonds, and are less abundant on Earth. Some of them are very reactive under Earth conditions (e.g. hydrazine). At lower temperatures, however, these compounds would be more stable and may be suitable for the construction of complex molecules. Many planetary bodies within our Solar System have much colder surface temperatures than Earth, and planets and moons at these temperature ranges may be much more common than Earth-type bodies in the Universe.

In order to qualify as a suitable candidate for a polar solvent, the solvent has to be easily available and plentiful, as well as suitable for at least a hypothetical scheme that could lead to prebiotic chemisty. If not plentiful in the Universe, there has to be some kind of fractionation mechanism that could conceivably enrich the particular solvent on a planetary body. In the following we discuss the polar inorganic solvent candidates, which we rank according to the likelihood that they could replace water as the life-supporting solvent in certain types of environments. We further discuss methanol and formamide as the most promising polar organic compounds for alternative forms of life.

7.2.1 Ammonia

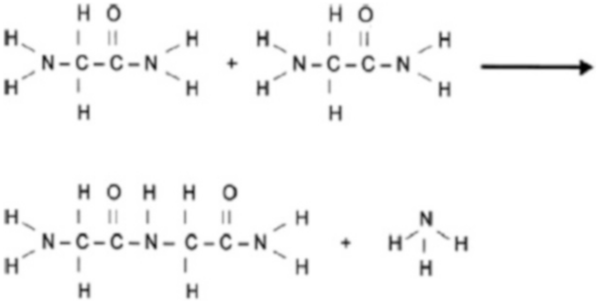
The idea of life based on ammonia as a solvent has received a considerable amount of attention. For example, Haldane (1954) pointed out ammonia analogues to water and suggested the possibility of building proteins, nucleic acids and polypeptides within a liquid ammonia solvent. Raulin et al. (1995) suggested that "ammono" analogues of terran biomolecules in which oxygen atoms are replaced by NH groups might yield an equally viable pseudo-biochemistry. Life on Earth exploits compounds containing the $C = O$ carbonyl unit. In ammonia, $C = O$ units would have to be replaced by $C = N$ units, but given this adjustment Benner et al. (2004) argued that metabolism in liquid ammonia is easily conceivable. Baross et al. (2007) argued that the $C = N$ bond would be equally satisfactory for supporting carbon-carbon bond forming reactions. Firsoff (1963) went into some detail showing similarities of synthesis reactions in water-based, ammonia-based and water-ammonia mixtures.

An especially interesting example provided by him is the synthesis of proteins from amino acids through a peptide bond. In a water system two glycine molecules combine with the release of water (Eq. 7.1):



(7.1)

If reaction (7.1) would take place in a water-ammonia mixture the COOH group would be replaced with a $CONH_2$ group and reaction (7.2) would be the result. In this reaction (7.2) the peptide bond is preserved and ammonia is released instead of water:



(7.2)

Firsoff (1963) speculated that the preservation of the peptide bond may be a relic of an ammono-organic scheme on Earth in the early stages of evolution.

In a pure ammonia solvent without the presence of oxygen, the carboxyl group could be replaced with a $–CH(NH_2)NH_2$ group and the peptide bond with a $–CH(NH_2)–NH–$ group. Similar analogues can be shown for the phosphate bonds in the nucleic acids (Firsoff 1963). A further parallel is that ammoniation reactions in ammonia as solvent are directly analogous to hydration reactions with water in which a salt and the solvent are produced. This leads to an important environmental consequence that minerals in a near-surface or subsurface "hydrosphere" would contain ammonia in their crystal structure just as Earth's rocks contain water. Although there appear to be chemical pathways leading from ammonia to prebiotic macromolecules, water is a more powerful solvent than ammonia based on its physical and chemical properties. Ammonia has a structure comparable to water (Fig. 7.1b) but a lower dipole moment and is thus less efficient at dissolving polarized compounds. Ammonia's heat of vaporization and heat of fusion are lower than that of water (although the heat of fusion is nearly equal, Table 7.1). Thus, ammonia is not as good at moderating temperature as water, but is still sufficient to have a stabilizing effect on climatic conditions. The surface tension of ammonia is only about one third of water; thus ammonia is not likely to concentrate organic macromolecules in microscopic interfaces as well as water. Ammonia dissociates into nitrogen and hydrogen, and does not afford any protection from UV light when compared to the dissociation of water. Thus any origin of life in ammonia would have to occur in some kind of protected environment. Ammonia, however, makes up for this disadvantage by its ability to dissolve alkali metals without reaction, which is of biological relevance because alkali metals can act as catalysts. Also, salt solutions in liquid ammonia have usually a greater electrical conductivity than an aqueous solution of the same salt (Mee 1934). Ammonia is about four times less viscous than water, thus dissolved particles and ions have a less difficult time to find and react with each other. Ammonia self-dissociates as water does but to a much lower degree (1.9×10^{-33} at −50 °C compared to 10^{-14} at 25 °C for water). Ammonia dissociates to NH_4^+ (equivalent to H_3O^+ of water) and the anion NH_2^-. It can further dissociate to form two more base anions, NH^{2-} and N^{3-}, thus acid-base reactions do occur in an ammonia system but to a much lower degree.

Ammonia is liquid at lower temperatures than water and has a smaller range in which it stays liquid, thus life would have to adapt to a smaller temperature window to survive on such a world. However, the temperature range over which ammonia is liquid for some relevant planetary surface pressures is greater than for water. For example, at a pressure of 60 bar ammonia is liquid from 196° to 371°K (Baross et al. 2007). Since solid ammonia is denser than liquid ammonia, there is no mechanism for preventing liquid ammonia from completely freezing during a cold spell. This is no problem for microbial life since it could have adapted to survive any cold spell or cyclic freezing in a spore state. However, survival of multicellular organisms in such an environment would be less likely. Further, chemical reactions would generally be expected to progress at a slower pace, lengthening life spans, and therefore decreasing the rate at which competition and adaptive radiation would drive evolution (Schulze-Makuch and Irwin 2006). Microbial life in ammonia might not be as differentiated or as well adapted compared to water-based life on Earth. Further, liquid ammonia cannot co-exist with free oxygen, thus aerobic metabolism would be inconsistent with ammonia as a solvent.

Liquid ammonia could, on the other hand, present an opportunity for microbial life on the more numerous colder bodies in the Solar System as well as for Jovian-size planets where the boiling point of ammonia could be as high as ammonia's critical temperatures of +132.4°C (given the extreme pressures). Ammonia and water are definitely related solvents, as indicated by the fact that life sustaining organic macromolecules such as proteins, amino acids and nucleic acids contain both OH and NH_2 functional groups in various combinations and proportions with which ammonia could easily interact. Aspinall et al. (2002) suggested that phosphate, a vital element for life on Earth, can be replaced by ammonophosphate analogues that are stable in water and ammonia, can lose protons to hold multiple negative charges, and can form stable amide-like bonds with carbon molecules.

Bains (2004) hypothesized that movement of electrons ("electricity") rather than protons ("proticity") would be a reasonable energy transaction for ammonium supported life. Different hydrocarbons become miscible with ammonia depending on temperature and pressure conditions. The formation of ammonia-philic and ammonia-phobic phases (analogous to hydrophilic and hydrophobic phases in water) is clearly conceivable in liquid ammonia at temperatures well below its boiling point at standard pressures (Baross et al. 2007).

Interestingly, several enzymes of terran organisms remain active down to temperatures of about −100°C (Bragger et al. 2000). In the likely subsurface oceans of the Galilean satellites, and possibly also at Titan and Triton, some ammonia dissolved in water may act as antifreeze, lowering the temperature at which water can stay liquid and thus possibly support life (Fortes 2000). Alternatively, any ammonia solvent in this type of environment should not be expected to be pure either. Water in the form of ice or icebergs would dissolve in liquid ammonia, thus the occurrence of water groups such as OH^- and O^{2-} should be expected within an ammonia solvent, if it indeed is capable of supporting life. Any ammonia-water mixture would be very basic, though. A 1.7% ammonia solution has a pH of 11.6 (Budavari et al. 1996) and it isn't clear how well life could adapt to this high basicity. On Earth, life is much more capable of withstanding and adapting to extreme acidities than basicities. However, there are not many natural environments on Earth with high pH-values (mostly soda lakes); thus there may have been no need for the evolution of organisms on Earth to develop this type of adaptation. Therefore, high pH may not be a fundamental obstacle for life. There is certainly enough ammonia in our Solar System, and in comets and the interstellar medium of the Universe in general, to sustain the possibility that living systems could thrive in a solvent of ammonia, or an ammonium-water mixture, within the appropriate thermal limits.

7.2.2 Hydrocyanic Acid

The structure of hydrocyanic acid, with a triple bond between the carbon and the nitrogen, is quite different from the structure of water, ammonia and methane (Fig. 7.1d). It is an excellent ionic solvent with a dipole moment of 2.8 D compared to 1.85 D for water and 1.47 D for ammonia. Also, as a thermal moderator it is about equal to water and superior to ammonia, with (1) a heat of fusion of 8.41 kJ/mol and heat of vaporization of 25.2 kJ/mol, and (2) a dielectric constant of 114.9. The range of temperature at which HCN remains a liquid is somewhat small, but it extends up to 26 °C allowing chemical reactions to proceed at a reasonable pace. Hydrocyanic acid dissociates into H^+ and CN^- with sulfuric and hydrochloric acids remaining acids in liquid HCN while cyanides are bases (Firsoff 1963). Cyan compounds are generally toxic to aqueous life in Earth's oceans and fresh water reservoirs.

However, the toxicity only indicates the occurrence of reactions that are competitive with water-based biochemistry and the ease with which water groups can be replaced by CN. CN bonds are of fundamental importance in proteins and other organic substances, and the substitution of CN for OH would yield HCN-analog compounds. Some compounds valuable for life such as metals are insoluble or only soluble to a small extent in HCN, while other compounds such as certain salts (e.g. potassium thiocyanite, permanganate) are highly soluble and give highly conductive solutions (Moeller 1957).

Hydrocyanic acid is not as abundant as water in the Universe but has been detected in comets and at planetary bodies such as Jupiter and Titan, and in the interstellar medium (Brown 1984; Lunine et al. 1999). Hydrocyanic acid not only offers protection from UV radiation, but can even combine with itself in alkaline solutions to form amino acids with the assistance of UV photons (7.3).

$$3HCN + 2H_2O + \text{UVlight} \rightarrow C_2H_5O_2N + CN_2H_2 \tag{7.3}$$

In addition to glycine, this reaction produces cyanamide (CN_2H_2), which can link amino acids together as the first step in the formation of proteins. Another promising pre-biotic pathway was offered by Matthews and Moser (1966), who suggested the direct synthesis of protein ancestors (heteropolypeptides) from hydrogen cyanide and water without the intervening formation of amino acids. Also of interest is that the important purine adenine ($C_5H_5N_5$) is a pentamer of HCN. A biochemistry based on hydrocyanic acid would likely be quite different from one based on either water or ammonia, and that is perhaps the primary reason why HCN did not receive much consideration as a solvent for life. HCN cannot interact as well with Earth-type organic macromolecules as ammonia. Its relatively small thermal window of liquidity, and its limited ability to dissolve some biologically important compounds are disadvantages for HCN as a solvent for living systems. However, it is intriguing that when dissolved in water HCN spontaneously reacts to form heterogeneous oligomers, which upon standing hydrolyze to release a variety of molecules of biological significance such as purines, pyrimidines, urea, and amino acids (Cleaves et al. 2008). To the extent that Earth provides a natural laboratory for comparing HCN with H_2O, with temperatures covering the range at which both compounds are liquid, HCN clearly is not competitive with water as a solvent, either because of its much lower abundance, or because the nature of biomolecules that would be stable and reactive in a hydrocyanic acid medium are not metabolically competitive with those that function in water. However, with its relatively high molecular weight of 27 g/mol, it could be the solvent of choice on a planetary body where most of the lighter molecules may have steamed off at some stage of atmospheric evolution. In such an atmosphere, cyanogen (C_2N_2) could be expected as an atmospheric constituent, which might provide energizing reactions analogous to oxidation in Earth's atmosphere (Firsoff 1963).

7.2.3 Hydrofluoric Acid

The solvent properties for hydrofluoric acid and water are very similar. The dipole moment and the dielectric constant are basically the same, while the heat of fusion and heat of vaporization of HF is only slightly lower (Table 7.1). Thus, hydrofluoric acid is an excellent temperature moderator and solvent. The temperature range at which HF remains liquid is a bit larger than for water and extends much lower (−83°C to + 20°C). Two hydrofluoric acid molecules dissociate into HF_2^- and H^+. Due to their non-polar nature most hydrocarbon compounds are insoluble in hydrofluoric acid, but many of them are polymerized, decomposed or lead to conducting solutions with complex cations, where the organic molecule bonds to the proton of HF (Firsoff 1963). Conceivably, F^- or HF_2^- could replace OH^-, and F_2^{2-} could replace O^{2-} in oxides. Fluorination could thus replace oxidation as the primary energy-yielding reaction, and would be more efficient due to the greater bonding energy of fluorine. As a result, free fluorine would be one of the atmospheric gases, and would likely have the same fate as oxygen had in the early Earth atmosphere (being such a very reactive element it would quickly be bound to surface rocks and removed from the atmosphere). The primary problem with hydrofluoric acid as a primary solvent is the low cosmic abundance of fluorine. Further, organofluorine compounds are extremely rare, at least in terran biochemistry (Budisa et al. 2014). The abundance of fluorine in the Solar System was estimated to be about 1000 times less than that of carbon, nitrogen or oxygen (Anders and Grevesse 1989). It is difficult to envision any fractionation mechanism that could enrich hydrofluoric acid to such a sufficient extent to become the primary solvent on a planetary body. One possibility is that all molecular oxygen could be used up in oxidation reactions on the planetary surface and that fluorine gas would be released from F-rich magmas later in the history of the planetary body. However, due to its low cosmic abundance and the unlikelihood of an efficient fractionation mechanism, we rank HF as an alternative solvent lower than ammonia and hydrocyanic acid in spite of the advantageous properties of the hydrofluoric acid molecule.

7.2.4 Hydrogen Sulfide, Sulfur Dioxide and Sulfuric Acid

Hydrogen sulfide remains a liquid at colder temperatures than any other candidate solvent introduced in Table 7.1, but its temperature range as a liquid is only 26 °C. Hydrogen sulfide does not moderate temperatures very well, given its low heat of fusion, heat of vaporization and dielectric constant. It is not particularly efficient as an ionic solvent, given its low dipole moment, but it does dissolve many substances, including many organic compounds. Similarly to water hydrogen sulfide dissociates into H^+ and SH^-. In a biochemical scheme with H_2S as solvent, the SH^- anion could simply replace the hydroxyl group in organic compounds. Hydrogen sulfide is a relatively common compound in the Universe, usually associated with volcanic activity on planetary bodies. H_2S could be a conceivable solvent on Io, the volcanically most active planetary body in the Solar System (Schulze-Makuch 2010; Irwin and Schulze-Makuch 2011). A subsurface layer of hydrogen sulfide could turn liquid when overhead lava warms the subsurface layer up to its range of liquidity (Table 7.1), then “spores” could become activated, reproduce, and perpetuate an exotic subsurface microbial ecosystem.

In this type of environment another sulfur solvent, sulfur dioxide, may compete with hydrogen sulfide. Sulfur dioxide is a solvent with a dipole moment of 1.6, remains a liquid at temperatures from −75 °C to −10 °C, and could be retained preferentially on massive planetary bodies due to its high molecular weight of 64 g/mol. However, due to the double bond in sulfur dioxide the development of a biochemical scheme would be more complicated for SO_2 than for H_2S, because rearrangements would be needed. Also, SO_2 is not a proton-based solvent. Proton-based solvents have the advantage that organic macromolecules such as nucleic acids are constructed via hydrogen bonds and are able to exchange materials with the solvent or change their formation for biological purposes without having to overcome a high-energy barrier. Interestingly, sulfates including sulfuric acid (H_2SO_4) are insoluble in sulfur dioxide, and would thus be rock material in a pool of sulfur dioxide.

Sulfuric acid has been suggested as a possible candidate for a life-supporting solvent within 1 AU (astronomical unit) of a star like our Sun (Fig. 7.3). Benner (2002) suggested sulfuric acid (H_2SO_4) as a possibility for Venus, where the atmosphere is rich in it. Sulfuric acid has a huge liquidity range, from 10°C to 337°C, a dielectric constant and dipole moment larger than water, and an extremely high viscosity (Table 7.1). The prospect of pure sulfuric acid as a life-sustaining solvent would require a biochemistry very different from the one with which we are familiar. The $C = C$ bond is reactive as a base in strong acids and could support metabolism as an analog to the $C = O$ unit (Baross et al. 2007), a reactivity shown to work in some terran biochemistry like that used by plants to synthesize fragrant molecules (Kreuzwieser et al. 1999). Sulfuric acid mixes well with water, and if life exists in the atmosphere of Venus (Sagan 1961; Grinspoon 1997; and Schulze-Makuch et al. 2002b, 2004), it would be expected to be adapted to a sulfuric-acid water mixture. This possibility is explored further in Sect. 8.3.

7.2.5 Hydrogen Peroxide

Hydrogen peroxide (H_2O_2) has a larger liquidity range than water (from −0.4 to 150.2°C), but mirrors water in many other properties (Table 7.1). As a pure compound, hydrogen peroxide does not qualify as a good solvent for life, because it is a strong oxidizer and would oxidize most carbon compounds rapidly to carbon dioxide. Thus, it is not compatible with biochemistry as we know it. However, mixtures of H_2O_2 and H_2O present an intriguing possibility, as suggested by Houtkooper and Schulze-Makuch (2007). Such a mixture would freeze at

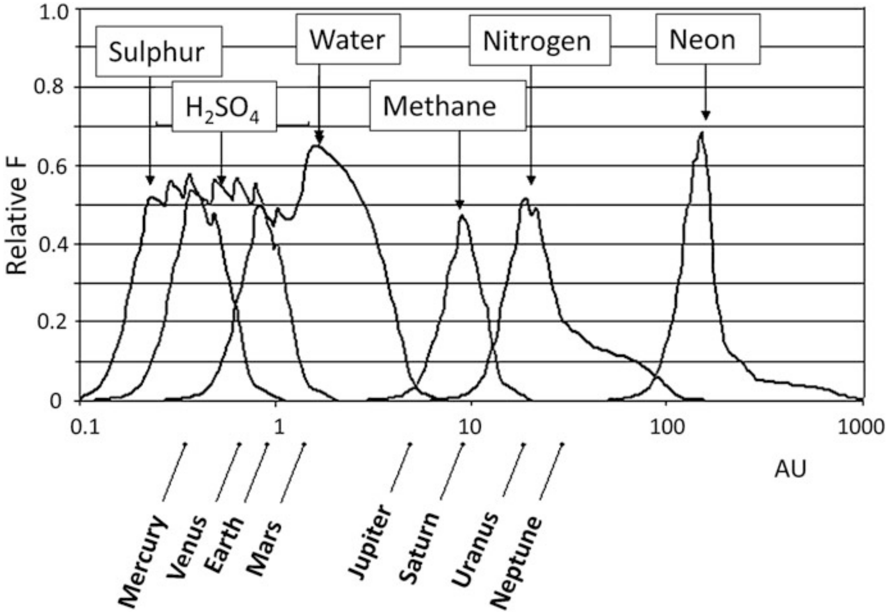


Fig. 7.3 Probability distribution for occurrence of different liquids as a function of distance from a Sun-like star. The x-axis represents distance and the y-axis represents the added probability of surface and subsurface liquid. Figure courtesy of William Bains, following the method described in Bains (2004)

temperatures significantly below the freezing point of water, because the lower eutectic point lies at −56.5 °C for a mixture with 61.2 weight % H_2O_2 (Foley and Giguère 1951). Also, mixtures with a high H_2O_2 concentration tend to supercool (Giguère and Secco 1954), and would thus not produce icy crystals that could pierce cellular membranes. H_2O_2–H_2O mixtures are slightly acidic, with a pH of 4.5 for the 60 weight % mixture. Because of the lower water vapor partial pressure in equilibrium with the liquid, H_2O_2–H_2O mixtures tend to be hygroscopic compared to water alone, which would offer the opportunity for an organism to scavenge water molecules from the atmosphere in an arid environment. Houtkooper and Schulze-Makuch (2007) hypothesized that organisms on Mars might use a H_2O_2–H_2O mixture as a mechanism of adaptation to Martian environmental conditions. They pointed out that such a biochemistry would explain the observations made during the Viking life detection experiments amazingly well (see also Sect. 10.1). There are various terrestrial analogs for the utilization of H_2O_2, including microbes that use H_2O_2 in their metabolic pathways, such as *Acetobacter peroxidans* (Tanenbaum 1956). Of course, the tendency for peroxides to form free radicals that are highly reactive would require the evolution of counteractive mechanisms for protecting cellular material in a peroxide-rich environment.

7.2.6 Hydrazine

Hydrazine (N_2H_4) is a liquid at a temperature range from 2 °C to 114 °C and thus one of the very few solvent candidates that has a larger temperature range and a larger absolute temperature at which it stays a liquid than water. Hydrazine is an excellent polar solvent with a dipole moment of 1.9 comparable to water. Its dielectric constant (51.7) and viscosity (9.8×10^{-3} P) are also very similar to water. Based on its physical properties it would be an excellent solvent candidate as an alternative to water. Hydrazine, however, is a very reactive molecule and decomposes extremely fast in the presence of oxygen, making it an ideal rocket fuel. This property suits it poorly to serve as a solvent in the presence of oxygen. Because of its high reactivity, it would be expected to make a better solvent at low temperatures in an anoxic environment, for driving biochemical reactions at a reasonable speed. However, at temperatures below 2 °C hydrazine is a solid and therefore not a suitable solvent. Furthermore, hydrazine is not an abundant molecule, and thus does not appear to be a promising solvent candidate despite its favorable physical properties.

7.3 Other Solvents as Alternatives to Water

Organic and non-polar compounds are usually not considered good candidates as alternative biological solvents. However, Carrea et al. (1995), Cabral (2001), and Klibanov (2001) have shown that terran enzymology can operate in a variety of non-aqueous solvents, and even in completely non-polar solvents such as benzene, diphenyl ether, or straight-chain hydrocarbons from heptane to hexadecane. Furthermore, the fungus *Fusarium alkanophilum* is known to be able to thrive in a hydrocarbon environment, extracting metabolic water from light hydrocarbons (Marcano et al. 2002). Also, many organic reactions fundamental to biochemistry can occur in nonaqueous solvents (Benner et al. 2004; Bragger et al. 2000). Table 7.2 provides some solvent-related physical properties of polar and non-polar hydrocarbons, and the non-polar compound dinitrogen. These compounds are relatively common in the Universe, and some of them are primary liquid compounds on at least one planetary body of our Solar System (e.g., methane and ethane on Titan, dinitrogen on Triton). Except for the notable exceptions of methanol (CH_3OH) and formamide ($HCONH_2$), which are discussed below in more detail, nearly all of these potential solvents are liquid at temperatures much lower than water (as most of the polar substitutes for water are).

7.3.1 Inorganic Non-Polar Compounds

Liquid nitrogen is probably the most promising non-polar inorganic compound. Liquid nitrogen boils at −196 °C and thus can occur in our Solar System in the liquid state only on the icy satellites of the outer Solar System (Fig. 7.3). Temperature and pressure conditions should be right for Triton to have liquid nitrogen in its subsurface. Even a liquid nitrogen ocean may be a possibility (Bains 2004). Though it is very abundant, dinitrogen does not have properties that would be considered as suitable for life from a terran perspective (Table 7.2). However, Bains (2004) hypothesized that silanols could dissolve in liquid nitrogen on very cold planetary bodies at concentrations sufficient to be precursors of life. Nitrogen may also occur in mixtures such as many of the other solvent candidates. While the surface liquids on Titan are a mixture of methane and ethane, substantial amounts of nitrogen from the atmosphere are thought to be dissolved into the hydrocarbon mixture, which would alter its properties significantly (Bains 2004; Lorenz and Lunine 1997; Thompson et al. 1992).

7.3.2 Organic Polar Compounds

Hydrocarbon compounds are generally non-polar but can be made into polar molecules by replacing H with an OH group in a hydrocarbon molecule. Two of them, methanol and formamide, have some potential as a suitable solvent for life in particular.

7.3.2.1 Methanol

Methyl alcohol or methanol (CH_3OH) is an excellent polar solvent with a dipole moment of 1.68 D compared to 1.85 D of water and 1.47 D of ammonia. It is also a better temperature moderator than water based on its extremely high dielectric constant and heat of vaporization (Table 7.1), and remains a liquid in the wide temperature range from -94 °C to $+65$ °C. It may also be a relatively common compound in the Universe as it has been found in the interstellar medium and in comets (Goldsmith and Owen 2003). Liquid hydrocarbon compounds are known to exist on Titan in large quantities, but methanol has not been found there. However, Tang et al. (2006) suggested the presence of pools or even oceans of methanol on early Mars. They pointed out that the gray hematite found on Mars could have been produced in a thermal system of organic compounds such as methanol that was generated from the photochemical oxidation of methane, since methane is thought to have been abundant in the early Martian atmosphere.

If methanol was present in reasonable quantities on the early Earth, it could have promoted organic synthesis such as the formation of sugars (Eisch et al. 2004). Methanol was delivered to the early Earth via comets, but visualizing an efficient production mechanism is challenging, because the oxidation of methane to methanol occurs at very low efficiencies due to the high C-H bond strength in methane. However, it could have occurred at much higher rates through iron or copper containing zeolites (Hammond et al. 2012). Methanol mixes well with water. The mixture has a eutectic temperature of 157 K. Thus, methanol could have been a valuable ingredient under early Earth conditions, and perhaps also in extraterrestrial locations, both as an antifreeze during cold spells and by promoting organic synthesis reactions (Schulze-Makuch and Houtkooper 2015).

7.3.2.2 Formamide

Another potential solvent is formamide ($HCONH_2$, Table 7.2). This compound has more than double the liquidity range of water and stays liquid at much higher temperatures. It is one of the few compounds with a peptide bond that has been found in the interstellar medium. It has a high surface tension to concentrate solutes, and a higher dipole moment and a larger dielectric constant than water. Benner et al. (2004) pointed out that many chemical species that are thermodynamically unstable in water with respect to hydrolysis, are spontaneously synthesized in formamide. This includes ATP from ADP and inorganic phosphate, peptides from amino acids, and even oligoribonucleotides (Schoffstall et al. 1982; Schoffstall and Liang 1985; Saladino et al. 2012). Formamide can be formed through electrical discharges in an atmosphere containing hydrogen, carbon, and nitrogen, and also through meteorite impacts (Ferus et al. 2015). Formamide itself is hydrolyzed by water and can thus only exist in a dry environment. However, desert environments have been proposed as potential sites for the prebiotic synthesis of ribose (Ricardo et al. 2004) and many synthesis reactions of organic macromolecules would be thermodynamically favorable in desert pools of formamide (Baross et al. 2007). Since desert environments are not thought to have been common on the early Earth, a Martian origin for terran life has been suggested (Benner and Kim 2015). However, though formamide is formed by the reaction of hydrogen cyanide and water, both of which are abundant, formamide itself does not appear to be abundant in the Solar System, nor probably elsewhere in the Universe.

7.3.3 Organic Non-Polar Compounds

Traditionally, it has been assumed that liquids other than water are unsuitable for the complex catalysis that is essential for biochemistry, especially non-polar organic compounds (Bains 2004). Membranes of terran organisms, which are submerged in the polar solvent, water, are amphiphilic with their polar (hydrophilic) heads exposed to the solvent and their non-polar (hydrophobic) tails oriented toward each other, away from the solvent. They interact with the polar solvent to take up nutrients, respond to intracellular signals, and discard wastes. If a non-polar solvent could support life, the chemical orientation of membranes would have to be fundamentally different. In this case, the heads immersed in the solvent would have to be non-polar in order to interact with the hydrocarbon solvent. However, broad empirical experience has demonstrated that organic reactivity in hydrocarbon solvents is no less versatile than in water, and many enzymes derived from organisms on Earth are believed to catalyze reactions by having an active site that is not hydrophilic (Benner et al. 2004). Also, a hydrocarbon solvent may actually improve chances for the origin of life, inasmuch as extensive experience with organic synthesis reactions has shown that the presence of water greatly diminishes the chance of constructing nucleic acids. Thus, the assemblage of organic macromolecules that could give rise to life appears to be much more straightforward in a hydrocarbon environment. A hydrocarbon solvent would also provide protection against UV radiation, as hydrocarbon smog emanating from the liquid solvent would absorb some of the UV radiation and thus offer a significant degree of protection. Hydrocarbons as the primary solvents on a planetary body are not beyond the realm of possibility. Saturn's moon Titan may provide a strong case in point. Spectroscopic results indicate the presence of methane rain on Titan (Lorenz 2000; Lunine et al. 1983) and the presence of liquid lakes on Titan's surface has been confirmed by the Cassini-Huygens mission (Stofan et al. 2007). In a non-polar hydrocarbon solvent such as methane or ethane, cellular membranes would likely be hydrophobic on the outside and hydrophilic at their cores. Thus, if a hydrocarbon liquid such as methane or ethane, or a mixture of both, could support life as a primary solvent, the resulting organisms would likely be quite different from those on Earth. In a solvent such as ethane a putative organism would be able to use hydrogen bonding more effectively, because the bonds would have the appropriate strengths for low temperatures.

Methanogenesis could be an energy-yielding strategy in this type of environment. For example, photochemically produced acetylene, which is a solid under Titan's surface conditions (Lorenz 2000), could be reduced with the help of hydrogen in the atmosphere to methane (Eq. 7.4)

$$C_2H_2 + 3H_2 \rightarrow 2CH_4 \tag{7.4}$$

In fact, methane is detected at a lighter isotopic fractionation than would be expected from Titan formation theory (Lunine et al. 1999), which could indicate activity of living organisms (Abbas and Schulze-Makuch 2002; Schulze-Makuch and Grinspoon 2005). Essential building blocks of life such as sugars, proteins and nucleic acids could exist in such organisms as well. However, given the vastly different environment from which that form of life would originate, it appears more likely that another solution to the make-up of life would have been found. Baross et al. (2007) suggested that the environment of Titan meets the absolute requirements for life, which include thermodynamic disequilibrium, abundant carbon containing molecules and heteroatoms, and a fluid environment—further concluding that "this makes inescapable the conclusion that if life is an intrinsic property of chemical reactivity, life should exist on Titan."

7.3.4 Supercritical Fluids: Carbon Dioxide

Supercritical fluids could also play a role as a life sustaining solvent on other worlds. The properties of supercritical fluids are usually quite different from those of regular fluids. Supercritical water, for example, is relatively non-polar and acidic. There are some advantages to supercritical fluids, especially for carbon dioxide and water, which include: (1) high solubility of gases within supercritical mixtures, (2) miscibility of gases such as O_2 and H_2 in supercritical fluids, (3) high diffusion rates and variable density, and (4) high dissolving power (Baross et al. 2007). Ikushima (1997) advanced the case for supercritical fluids as an appropriate medium for chemical and biochemical processes under certain conditions. One cited example was the synthesis of esters from acryl donors and terpene alcohols by lipase in *Candida cylindracea*, which in supercritical carbon dioxide caused drastic conformational changes that enabled active sites to catalyze stereoselective synthesis. Reactivity was found to be susceptible to small changes in pressure or temperature near the critical point of the supercritical fluid. Shkrob and Sauer (2001) showed that high-mobility CO_2-multimer anions in supercritical carbon dioxide form stable complexes with water, aliphatic alcohols, alkyl halides, and alkyl nitriles.

An example of how supercritical CO_2 might support living processes can be seen in the recent discovery of subsurface accumulations of liquid carbon dioxide under Earth's oceans (Inagaki et al. 2006). The low density liquid CO_2 has been found to be trapped by a surface pavement and subpavement cap of CO_2 hydrate ($CO_2 \times 6H_2O$). As the density of liquid CO_2 increases with depth, it becomes denser than sea water, opening up the possibility of many reservoirs of liquid carbon dioxide on the sea floor (House et al. 2006). Most amazing was the detection of 10^7 cells/ml at the liquid CO_2/CO_2-hydrate interface (Inagaki et al. 2006), which is quite remarkable given the potentially hostile nature of CO_2 (Nealson 2006). Carbon dioxide is usually described as a non-polar solvent, given the zero molecular dipole moment and its low dielectric constant. However, strong theoretical and recent experimental evidence indicates that CO_2 can participate in hydrogen-bonding interactions, and thus has polar attributes (Raveendran et al. 2005). Industrially, supercritical carbon dioxide is increasingly promoted as an environmentally benign alternative to conventional organic solvents (Raveendran et al. 2005) and is used in biotechnological applications to catalyze reactions that do not occur in water (Budisa and Schulze-Makuch 2014). Carbon dioxide is a very common compound on many planets, including our neighbors Venus and Mars. Supercritical carbon dioxide could occur in a number of these extraterrestrial locations, such as in the subsurface of Venus. It certainly deserves more attention as a potential life-sustaining solvent.

7.4 Quantitative Assessment of Solvent Candidates

In this section we will attempt to make a quantitative assessment regarding the suitability of a compound as an alternative solvent for life. There are some properties that are advantageous for life independently of the biochemistry of the living organism. Abundance is a definite advantage and may be the primary reason why life on Earth uses water as the universal solvent. Local abundance is most important for the solvent to be available for life processes, but overall cosmic abundance is relevant as well. If a compound is cosmically very rare a suitable fractionation mechanism has to be available to provide the compound in sufficient quantity. Aside from abundance, the most important property is being in a liquid state at the prevailing temperature of the local environment. The enthalpy of fusion and vaporization indicates how good a heat insulator the solvent is, and the dipole moment of the compound gives a general measure of its ability to dissolve other compounds (for life based on non-polar polymeric chemistry this criterion would be applied differently; for the present analysis that possibility will be disregarded).

A quantitative estimate of the feasibility that a given solvent could be effective in a particular planetary environment is shown in Table 7.3. The metric is obtained by assigning +1 to four favorable characteristics—cosmic abundance, local abundance, enthalpy of vaporization, and dipole moment; by assigning −1 for unfavorable instances of the same characteristics; and by assigning 0 to cases that fall between clearly favorable and unfavorable characteristics. A fifth property—liquid at prevailing local temperature—is of such obvious importance that +2 is assigned for favorable cases, −2 for cases in which the solvent cannot be liquid at the prevailing temperature, and 0 for intermediate or unknown situations. The range of temperatures at which a solvent candidate is in the liquid state (at a pressure of 1 bar) is given in Fig. 7.4. Adding the assigned points for each of the five characteristics yields a single composite value for each solvent on each planetary body shown in Table 7.4.

This estimate is obviously crude and speculative to a large degree, and we certainly have not considered all possible solvents. A more precise and systematic analysis may emerge from further research, a consideration of other relevant variables, and a more highly differentiated system of weighting the different factors. Nonetheless, some generalizations can be gleaned from even this preliminary analysis. These include the inference that water is the best solvent on warmer bodies, but methanol may be superior on some colder worlds; that ammonia or ammonia-water mixtures (with ammonia being the "antifreeze" for water) may be an important solvent on the colder worlds as well [also supported by Leliwa-Kopystyński et al. (2002)]; and that despite some favorable properties, hydrocyanic acid, hydrofluoric acid, and hydrogen sulfide do not appear particularly advantageous under any conditions.

With respect to specific planetary bodies, Table 7.4 suggests the following: (1) water is clearly the best solvent for Earth; (2) water is also the best solvent, perhaps in combination with ammonia and methanol, beneath the surface of the icy

Table 7.3 Feasibility of selected solvents for particular planetary environments

	Earth					Icy satellites					Gas giants				
Solvent	C	L	T	E	D	C	L	T	E	D	C	L	T	E	D
H_2O	+	+	++	+	0	+	+	0	+	0	+	–	0	+	0
NH_3	+	–	––	0	0	+	–	++	0	0	+	+	0	0	0
HCN	0	–	++	0	+	0	–	––	0	+	0	–	0	0	+
HF	–	–	0	0	0	–	–	++	0	0	–	–	0	0	0
H_2S	–	0	––	–	–	–	–	++	–	–	–	0	0	–	–
CH_3OH	0	–	++	0	+	0	–	++	0	+	0	–	0	0	+
C_2H_6	0	–	––	–	–	0	–	++	–	–	0	–	0	–	–
	Io (near subsurface)					Titan surface					Titan subsurface				
Solvent	C	L	T	E	D	C	L	T	E	D	C	L	T	E	D
H_2O	+	–	0	+	0	+	0	––	+	0	+	0	––	+	0
NH_3	+	–	0	0	0	+	0	––	0	0	+	+	++	0	0
HCN	0	–	––	0	+	0	0	––	0	+	0	0	––	0	+
HF	–	–	0	0	0	–	–	––	0	0	–	–	0	0	0
H_2S	–	+	++	–	–	–	0	––	–	–	–	0	++	–	–
CH_3OH	0	–	0	0	+	0	0	0	0	+	0	0	++	0	+
C_2H_6	0	–	0	–	–	0	+	++	–	–	0	+	++	–	–

Cosmic abundance (C): += major component on planetary bodies or in interstellar space; −= found only in trace amounts

Local abundance (L): += major constituent in local environment; −= trace amounts or less in local environment

Thermal range (T): ++= liquid at prevailing local temperature; −−= liquid outside of prevailing local temperature

Enthalpy of vaporization (E): $+ \geq 40$ kJ/mol; $- \leq 20$ kJ/mol

Dipole moment (D): $+ \geq 2$; $- \leq 1$

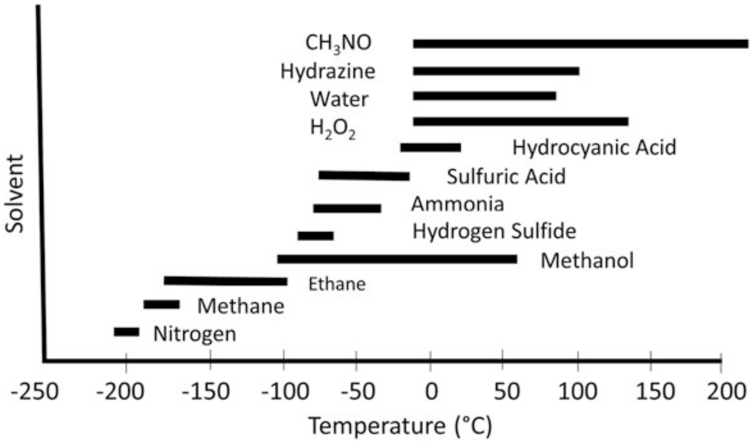


Fig. 7.4 Temperature ranges for selected solvent candidates to occur in the liquid state (at 1 bar)

Table 7.4 Summary assessment of selected solvent candidates for certain planetary environments

Solvent	Earth	Icy satellites	Gas giants	Io (near subsurface)	Titan surface	Titan subsurface
H_2O	+4	+3	+1	+1	+1	0
NH_3	−1	+1	+2	0	0	+3
HCN	+1	−1	0	−1	0	0
HF	−2	−1	0	−2	−3	0
H_2S	−4	−3	−3	0	−4	−2
CH_3OH	+1	+1	0	0	+1	+2
C_2H_6	−4	−2	−3	−3	0	0

satellites; (3) the gas giant planets do not favor any particular solvent except possibly water and ammonia within a particular thermal and pressure range; (4) the special circumstances of Io make it difficult for any solvent to function there, though some combination of water and H_2S might work beneath the surface; (5) Titan's surface is inhospitable for any other than organic solvents; while (6) the subsurface of Titan could function with a combination of organic solvents, ammonia, and water.

In conclusion, Table 7.4 suggests that other solvents may be more favorable under the many environmental conditions likely to be found on other worlds that differ from those on the Earth's surface. A good example is Titan, where water is in the solid state and ethane and methane are liquids, making them more suitable solvents. Over a large range of circumstances, however, it does appear that water is an adequate if not preferred solvent. Nevertheless, many more possibilities are worthy of investigation, such as the solvent dinitrogen, which would receive a favorable rating for Triton, a very cold icy satellite.

7.5 Some Additional Thoughts

Except for the fundamental thermodynamics of its constituent molecules, there is probably no property of a living system that is more important for determining its characteristics than the nature of the solvent in which the system originated and evolved. Since the solvent determines the thermal limits within which chemical reactions can take place, the type of molecules that dissolve and do not dissolve, and the nature of the chemical interactions that can occur, both among the molecules and between them and the solvent, it follows that the total chemical makeup of the living system is a consequence of the solvent in which it occurs.

If our Solar System is any indication, Earth-like planets are relatively rare, while planetary bodies that are either smaller and much colder, or larger and gaseous, are more frequently occurring. Both conditions render water useless as a solvent, but raise the prospects that an alternative solvent could be an effective medium for energy flow through chemically complex systems. Among the candidates are compounds that are not rare. Even those that are cosmically uncommon, like the sulfur-based solvents, may occur at critical densities under specialized circumstances (as on the volcanic planetoid, Io). In each case, however, the alternative solvent will almost surely foster a very different biochemistry from that which thrives in an aqueous environment. It is by no means apparent that exotic biochemical systems unfamiliar to us are less plausible under exotic conditions. As defined earlier, the essence of life has to do with complexity, energy flow, and information—none of which is limited in principle to the biochemical system with which we are familiar on Earth. In searching for life beyond Earth, we would therefore be well advised to expect the unusual.

The possibility does remain that the thermodynamic properties of any molecule that could undergo complex reactions and be assembled into stable macromolecular form is strictly constrained to conditions under which only water is an adequate solvent. Until research on complex chemical interactions in solvents other than water becomes more common, this possibility cannot be ruled out. If it should turn out that only water is an adequate solvent, the implication would be that life is likely to be restricted to water-abundant planetary bodies such as Earth, Mars and Europa. Even if this were the case, the astronomical number of planetary bodies that surely exist in the Universe, combined with the abundance of water throughout the Cosmos, makes it possible that life even as we do know it may be widespread. Our hunch, however, is that the nature of life is broader and more pervasive than most of us imagine.

7.6 Chapter Summary

Water is an ideal solvent for the complex chemical systems that constitute life on Earth, because of its broad thermal range of liquidity corresponding to Earth's average temperature and atmospheric pressure, and because of other characteristics that make it both an excellent physical buffer and advantageous medium for complex chemical interactions among the biomolecules that have evolved under the physicochemical conditions prevailing on Earth.

On other worlds where temperatures and pressures are different, other solvents are more likely to be found in the liquid state. Many of them have properties that make them adequate, if not advantageous, as solvents for complex chemical systems. This includes, in particular, polar solvents like ammonia, hydrocyanic acid, and methanol. Under specialized conditions, others such as hydrogen sulfide and sulfur dioxide, could serve as solvents as well. Likewise, non-polar solvents like methane and ethane can be stable liquids under some conditions. While each of these could in principle host complex biochemical interactions, the nature of the molecules that would thrive in a given solvent would be dependent on the nature of that solvent. On worlds where the physicochemical conditions require that a solvent other than water provide a liquid medium, the conditions for the origin of biomolecules and the evolution of their variations and transformations would be different, and likely would result in the elaboration of a biochemical system different from that known to us from the one example of life on Earth.

Chapter 8
Habitats of Life

There are four principal habitats in which life may exist—the surface of a planetary body, its subsurface, its atmosphere and space. From our own experience we know that life does exist on the surface of a planet, in its subsurface and transiently at least in the atmosphere. Where it is present, it exists in a surprising diversity and in a variety of microhabitats, from deep caverns (Hose et al. 2000; Melim et al. 2001) and water droplets (Meckenstock et al. 2014) to hydrothermal fluids and hot springs of various chemistries (Jannasch 1995; Rzonca and Schulze-Makuch 2002; Martin et al. 2008), to the frozen deserts of Antarctica (Friedmann 1982; Sun and Friedmann 1999; Goordial et al. 2016). In this chapter we will elaborate on the principle habitats, the constraints they impose on life, and the possibilities they provide.

8.1 Life on the Surface

We live on the surface of our planet, which makes us biased towards it being the common case. However, there are various factors that make life on the surface of a planetary body challenging. Life on the surface is much more exposed to environmental extremes of temperature, wind, radiation and humidity than, for example, life thriving in the subsurface protected by thick layers of soil and rock. A planet or moon with life on its surface requires an atmosphere to keep essential liquids on the surface from evaporating into the vacuum of space, to protect life on the surface from harmful cosmic and UV radiation (the degree of protection depending on the composition and thickness of the atmosphere), and to protect the surface to some degree from potentially devastating meteorite impacts. Smaller meteorites burn up in the atmosphere and the effect of larger ones is mitigated. However, meteorites still pose a grave threat to life on the surface of any planet. For example, the surface of our planet may have been sterilized several times early in Earth's history (Sleep and Zahnle 1999). In that case life could have only survived deep in the crust and then resettled the surface again after the effects of the impact were diminished with time.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_8

Life on the surface is also very susceptible to large-scale climatic fluctuations. Earth experienced several episodes of global freezing ("Snowball Earth") events (Hoffman et al. 1998; Kirschvink et al. 2000), when it substantially or perhaps completely froze over. Mars is currently a cold, arid planet with little or no liquid water on its surface, though it probably had oceans on its surface earlier in its history (Dohm et al. 2000; Head et al. 1998; Di Achille and Hynek 2010; Fairén 2010). Venus, probably wet and somewhat Earth-like early in its history, experienced a run-away greenhouse effect with current surface temperatures above 400 °C. If life as we know it ever existed on the surface of Venus, it does not anymore.

8.2 Life Beneath the Surface

Microbes, fungi, and small animals have lived in the upper layers of the soil since their first expansion from water onto the land. More recent evidence suggests that microbial life penetrates to great depths, beneath the surface of both the land and ocean bottom, deep into the crust (Johnson and Party 2003; Pedersen and Ekendahl 1990; Klein et al. 2015). Estimates indicate that the total amount of carbon in subsurface organisms may equal that of all terrestrial and marine plants (Table 8.1).

Microbial life appears to be abundant in various types of subsurface habitats such as the oceanic crust, and continental sedimentary and igneous rocks. While the overall number of organisms generally decreases with depth (Table 8.2), because of the huge amount of volume, the total subsurface biomass is enormous (Gold 1992).

However, life on the surface does provide two critical advantages: (1) the use of visible light as an energy source and (2) space to expand. Life on Earth without photosynthesis would be much more limited and may have remained in the microbial evolutionary stage. The biomass contribution via photosynthesis is immense; the total carbon content of plants is estimated to be 560 Pg (1 Pg = 10^{15} g) for terrestrial plants and 1.8 Pg for marine plants (Schlesinger 1997, Table 8.1). Space to expand may not be very important to microbial life, because most microbial life easily fits into the pore spaces of rocks. However, for complex multicellular life the surface does provide a challenging but suitable environment for growth and development to macroscopic forms. Thus, it is not a surprise that we as macroscopic organisms populate a planet in a climatically fairly stable environment with enormous amounts of liquid water. However, life remains very vulnerable on a planetary surface.

Table 8.1 Total carbon content in 10^{15} g of carbon

Ecosystem	Plants	Soil and aquatic prokaryotes	Subsurface prokaryotes
Terrestrial	560	26	22–215
Marine	1.8	2.2	303
Total	561.8	28.2	325–518

Note: Data from Whitman et al. (1998)

Table 8.2 Total number of prokaryotes in unconsolidated subsurface sediments

Depth interval (m)	Cells/cm^3, × 10^6	Deep oceans (no. of cells, × 10^{28})	Continental shelf and slope (no. of cells, × 10^{28})	Coastal plains (no. of cells, × 10^{28})
0.1–10	220	66.0	14.5	4.4
10–100	45.0	121.5	26.6	8.1
100–200	6.2	18.6	4.1	1.2
200–300	19.0	57.0	12.5	3.8
300–400	4.0	12.0	2.6	0.8
400–600	7.8	NA	10.1	3.2
600–1200	0.95	NA	3.7	1.2
1200–2000	0.61	NA	3.2	1.0
2000–3000	0.44	NA	2.6	0.9
3000–4000	0.34	NA	NA	0.7

Note: Data from Whitman et al. (1998); NA = not available

Threats include a large meteorite impact that could destabilize the climate or sterilize the surface of the planet, a cosmic disaster such as a nearby supernova-explosion that showers the surface with radiation, or exhaustion of fuel in the planet's central star, leading to the engulfment of the planet, similar to our Sun which will expand to become a red giant.

Some distinct advantages over life at the surface can readily be appreciated. Temperatures and vapor pressures are stable, and protection from damaging radiation is afforded. The obvious disadvantages are the unavailability of sunlight as an energy source, and limitations on organismic size. The latter restriction results from the fact that pore spaces that serve as habitats are generally small in size, and become smaller with increasing depth. Thus, life at any substantial depth is probably restricted to microscopic dimensions, but this allows for a great range of living systems, as evidenced by the variety of microbial life within the crust of the Earth. Microbes indigenous to crustal rocks have been isolated from a depth of 2800 m in continental sedimentary rocks (Onstott et al. 1999) and 5300 m in igneous rocks (Pedersen 2000). Temperature increases with depth and imposes an absolute limit on the temperature and pressure conditions under which water can remain in the liquid state. The amount of dissolved solids in the ground water also tends to increase with increasing temperature adding osmotic stress to any organism. Thus, there is an absolute limit to the depth at which organisms can thrive (Schulze-Makuch et al. 2017). The absolute limit of this depth, however, is very variable due to the heterogeneous conditions in the crust and variable geothermal gradients.

While sunlight is not available to provide energy in a subsurface environment, other sources of free energy are readily available. Chemical energy, both inorganic and organic, may be found in abundance, depending on the planetary body in question. Other energy sources such as those discussed in Chap. 5 may also be an option for certain subsurface environments. Availability of energy should not be a problem, if the planet or moon is large enough to have a metallic core and decaying radioactive elements as an energy source. In principal, energy in many forms can be transformed into biologically usable energy (Holm et al. 2015). If the availability of energy, then, is not an issue, and the living system is microscopic in size, the advantages of the subsurface habitat become overwhelmingly favorable for the persistence of life.

Although the subsurface clearly favors microbial life, there are a few niches and possibilities for macroscopic life. A bizarre example of a macroscopic subsurface organism is a fungus of the *Armillaria* family, which is pathogenic to trees (Armillaria root disease). These fungi are incredibly large, with one *Armillaria ostoyae* organism of genetic uniformity detected at a size of 9.65 km^2 (Ferguson et al. 2003). A subsurface niche particularly favorable for macroscopic forms is the cave environment, to which various types of animals on Earth are ideally adapted (Romero 2009). Caves do not occur only where karstic sedimentary rocks are present, but also commonly form in cooling lava flows. Thus, they can be expected to be common on other planetary bodies as well. Several locations have been suggested for Mars (Fig. 8.1). Due to the relatively low gravity on Mars, lava tube caves can be expected to be larger and more common than on Earth.

On all the terrestrial planets and all the larger satellites, subsurface strata probably exist where thermal stability and some solvent in liquid form can exist. Thus, the presence of at least microbial life at multiple sites beneath the surface of planets and some of their satellites throughout the Solar System is distinctly possible. The larger icy satellites that show evidence of tidal flexing or other energetic perturbations, such as Europa, Ganymede, Enceladus, Iapetus, Titania, and Triton, have at least the

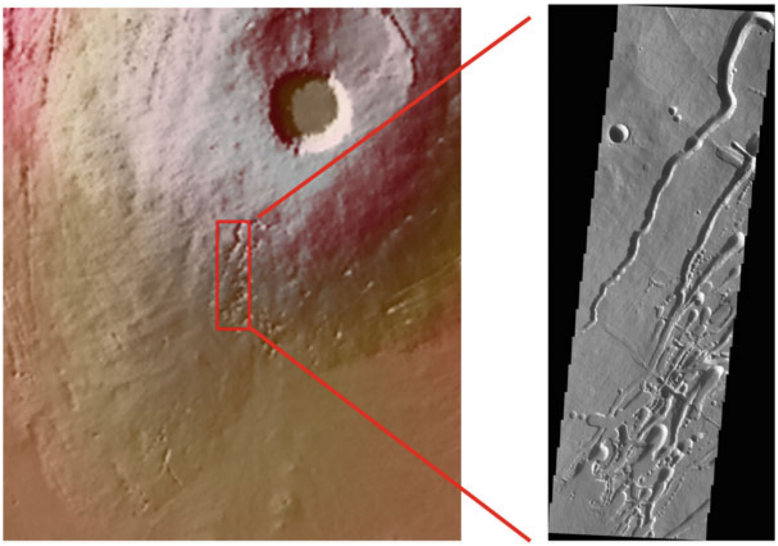


Fig. 8.1 Collapsed lava tubes on the side of Pavonis Mons. The linear features are believed to be lava tubes where the ceiling has collapsed into the free space below. *Credit: NASA/JPL-Caltech/ASU*

potential for liquid water beneath their icy crusts (Carr 1986; Chyba 1997; Coustenis and Lorenz 1999; Khurana et al. 1998; McKinnon and Kirk 1999; Irwin and Schulze-Makuch 2011). Evidence for a substantial amount of ground water within the upper crust of Mars is now compelling (Boynton et al. 2002; Carr 1996; Malin and Edgett 2000a, b; Schulze-Makuch et al. 2004). Thus, aquatic life approximately as we know it on Earth is even possible in those situations. While the surface of Io is normally frozen, periodic lava flows heat it from above, and tidal flexing heats this rocky planetoid from below. Titan is colder still, but as the second largest satellite in our Solar System, it is obviously large enough for radiogenic heating to possibly liquefy mixtures of ammonia, water, and organic compounds which may be sequestered beneath its surface (Coustenis and Lorenz 1999). Both of these satellites represent more unusual but certainly possible subsurface habitats for life. Even Mercury and the Moon, both of which show evidence of some polar ice (Showstack 1998; Slade 1992), and even Venus, where liquid silicates or water in a supercritical state could exist beneath the surface, cannot be completely ruled out as sites of possible subsurface life (Schulze-Makuch et al. 2002b). “Run-away” planets that were ejected from their Solar System and are now moving through empty space represent another theoretical possibility (Stevenson 1999; Strigari et al. 2012).

Stabilizing selection, which tends to narrow variation and optimize adaptive advantages (Chap. 4), is particularly effective in relatively constant habitats over long periods of time. Thus, life that has been optimized by stabilizing natural selection for a subsurface existence should be extremely durable and persistent. It also tends to be static, evolving little from the form and function that characterized it upon its introduction to the stabilized habitat. Subsurface environments may thus be repositories for early forms of life that have changed little since conditions made life on the surface untenable. On Earth, the microbes that are found at the greatest depths beneath the surface tend to be members of the evolutionarily ancient archaea, or eubacteria with ancestral forms of chemoautotrophic metabolism, and may include some types of extremely small microorganisms (Luef et al. 2015). It follows that life on other worlds is most likely to be found beneath the surface of those worlds, where it is probably microscopic and relatively unchanged from an ancestral state.

8.3 Life in the Atmosphere

The possibility that the gaseous envelope of planets and those satellites that hold an atmosphere could serve as a suitable environment for life is generally viewed with skepticism. This probably derives from our familiarity with the nature of the atmosphere and of life on Earth. We are aware of the diversity of terran life, both in the subsurface and on the surface of Earth, but no organism that spends its entire life cycle in the atmosphere has been documented. The lack of green clouds is visual evidence for the absence of concentrated airborne photosynthesis. And even the smallest organism has a higher density than air. Nevertheless, it has been recognized for some time that bacteria exist in cloud aerosols on Earth (Gislén 1948) and that rain and fog water rich in nutrients may provide a good substratum for microorganisms (Fuzzi 2002; Herlihy et al. 1987). While microbial taxa from every biological lineage have been detected in the upper atmosphere of Earth (Smith 2013), the claim that microbes independently grow and reproduce in Earth's atmosphere is controversial. Dimmick et al. (1979) reported the division of bacteria on airborn particles and Sattler et al. (2001) analyzed condensing clouds at the Sonnblick Observatory in Austria at an altitude of 3106 m, and suggested growth and reproduction of microbes in super-cooled cloud droplets.

However, in general the atmosphere of Earth is a poor analogy for atmospheric habitats where life would be more likely; namely that of planetary bodies or satellites where gases are denser, and liquids are found in larger aggregates with longer survival times. Also, any particles in the Earth's atmosphere have typically a short residence time in the range of several days only. Most atmospheres of other planetary bodies we know are dynamically much more stable in the vertical direction and particles do not precipitate out as frequently (e.g., Venus), thus particle residence times are much longer. On other planets various chemical compounds might serve as nutrient sources, such as H_2S in the case of Venus (Schulze-Makuch and Irwin 2002b) or complex carbon compounds in the case of gas giants like Jupiter (Boston and Stoker 1983; Stoker et al. 1990) or carbon-rich moons like Titan. The composition of some planetary atmospheres is provided in Table 8.3.

If, instead of the unstable and thin atmosphere of Earth, the denser atmospheres of Venus, Titan, and the gas giant planets are taken as a prototypical atmospheric habitat where life could exist, some positive advantages can be noted. For instance, many of the denser atmospheres are more stable and more richly endowed with organic molecules. Sunlight, especially in the ultraviolet frequencies, breaks apart simple organic molecules in the planetary atmosphere, producing ions, free radicals, and other highly reactive molecules that combine to form complex, energy-rich

Table 8.3 Composition of some planetary atmospheres (modified from Lewis 1995)

Planetary body	Major compounds	Minor compounds	Trace compounds
Venus	CO_2 (96.5%), N_2 (3.5%)	SO_2, Ar, CO, H_2O, He, Ne, H_2S	HCl, Kr, HF, COS
Earth	N_2 (78.1%), O_2 (20.9%), Ar (0.9%)	H_2O, CO_2, Ne, He, CH_4, Kr	H_2, N_2O, CO, Xe, O_3, NH_3, SO_2, H_2S, CH_2O, NO_2, NO, HCl,
Mars	CO_2 (95.3%), N_2 (2.7%), Ar (1.6%)	O_2, CO, H_2O, Ne,	Kr, Xe, O_3, CH_4
Jupiter	H_2 (82%), He (18%)	CH_4, H_2O, NH_3, C_2H_6, PH_3	H_2S, C_2H_2, CH_3D, HCN, CH_3NH_2, N_2H_4, GeH_4, CO
Saturn	H_2 (94%) He (6%)	CH_4, H_2O, NH_3, C_2H_6, PH_3	H_2S, CH_3NH_2, C_2H_2, CH_3D, HCN, N_2H_4, GeH_4,CO
Titan	N_2 (94%), CH_4 (6%)	Ar, H_2, CO, C_2H_6, C_3H_8, C_2H_2	C_2H_4, HCN, CH_3 CCH, HC_4H, HC_3N, NCCN, CO_2

Note: Major compounds are defined here as those compounds that have a mole fraction larger than 0.005 in the respective atmosphere, minor compounds as having a mole fraction between 0.005 and 10^{-6}, and trace compounds as having a mole fraction smaller than 10^{-6}

compounds. These heavier molecules sink until they reach a level where they are destroyed by temperature and pressure, as likely occurs on the gas giants, or they accumulate on the planetary surface, as on Titan. Sagan and Salpeter (1976) suggested that life could exist at a level of the Jovian atmosphere where descending organic molecules could be captured and used for energy. The organic rich atmosphere of Titan, with a density 50% greater than that of Earth, conceivably could support life in the same way.

Several challenges to life in an atmosphere must be met. A main problem is that the density of gas molecules in an atmosphere is much lower than on a planetary surface, so to achieve the level of interactions between molecules required for living processes, the density of the organism is inevitably going to exceed that of its surroundings, and buoyancy will be a problem. However, atmospheres can be very dense, achieving liquid-like states at sufficiently high pressures. And just as fishes evolved air bladders to give them buoyancy in water on Earth, an airborne microbe conceivably could evolve a gas-filled organelle that radically increases its volume to a point where its average density is sufficiently low to keep it afloat in the air. Another potential problem could be exposure to high radiation levels, thus conditions that would promote the survival of atmospheric organisms would favor the evolution of radiation protection mechanisms.

A critical problem for indefinite survival in the atmosphere is the question of a suitable solvent for the support of life-sustaining reactions. Both liquids and solids are generally present in an atmosphere, such as liquid water and aerosols in Earth's clouds. But their abundance in the atmosphere compared to the planetary surface is very low. To be effective solvents, the liquids need to be condensed into droplets of sufficient size and longevity to provide a transiently stable pool of airborne liquid. Such droplets do appear to exist in the upper atmosphere of Venus (Grinspoon 1997), and perhaps in other dense atmospheres elsewhere.

Another potential problem is the scarcity of a solid substratum. The interface of a liquid solvent with a solid surface is presumed to provide a much more likely circumstance for the development of complex chemistry, simply because the degrees of freedom for interacting components is reduced from three dimensions to two. Thus, the origin of life in particular, seems much more likely to come about at interfaces than in three-dimensional volumes of gasses or liquids. Once underway in its confined cellular compartments, life would have an easier time of surviving in three-dimensional volumes, as many organisms in water, and some forms in air, do on Earth. The plausibility of life in an atmosphere is thus higher on those planetary bodies where conditions at the surface were amenable for the origin or early cultivation of life on a solid substrate. This would mean that Venus and Titan, for example, would have experienced a greater chance for the origin of surface (or subsurface) life that eventually evolved adaptations for an airborne existence, than would the gas giant planets, where a solid substrate may never have existed under conditions appropriate for life to originate or take hold. For an alternative view, see Feinberg and Shapiro (1980) who consider that the absence of a surface might be an advantage, because it would allow free motion between different environments, making it possible for an organism to invent its own disequilibrium by moving from one condition to another.

Certainly, as summarized above, any form of life residing permanently in the atmosphere faces many challenges. However, the case has been made that atmospheres represent a viable target in the search for habitable zones on other worlds (Smith 2013). As an instructive example, we will consider the case of Venus in more detail. There is evidence for an early ocean on Venus while the early Sun was fainter than it is now. Life on Earth developed very fast once conditions became appropriate (Chap. 4). The same could have occurred on Venus. Alternatively, life may have been transplanted from Earth or Mars to Venus via meteorite impacts. Either way, life may have become established on Venus at an early point in its history. We know that conditions on the surface of Venus are now inhospitable to life as we know it, with temperatures around 733 K (~450 °C) and extreme desiccation. The change in planetary surface conditions was presumably caused by a run-away greenhouse effect as the Venusian atmosphere moved toward its present composition of 97% CO_2. If the environmental transformation occurred slowly enough, microbial life could have adapted to life in the clouds of Venus by directional selection (Schulze-Makuch et al. 2003, 2013a, b). More recent modeling supports the notion that relatively benign conditions could have prevailed on Venus for billions of years (Way et al. 2016).

Several factors would support such a life style in the atmosphere of Venus: (1) The lower atmosphere is thick, so under liquid-like conditions microbial transport between the surface and the cloud layer would be easier than in Earth's atmosphere. (2) The clouds of Venus are much larger, providing more continuous and stable environments than clouds on Earth. (3) Current conditions in the lower cloud layer of Venus are relatively benign at 300–350 K, 1 bar pressure and a pH of 0—conditions of temperature, pressure and pH under which thermoacidophilic microbes are known to thrive on Earth (these are also some of the oldest known forms of life on Earth!) (4) Cloud particles are projected to last for several months in the Venusian atmosphere compared to only days on Earth (Grinspoon 1997). (5) The Venusian atmosphere is super-rotating, thus cutting the nighttime significantly and thereby allowing for more photosynthesis. (6) Water vapor is reasonably dense in the lower cloud layers of Venus. (7) Oxygenated species such as SO_2 and O_2 coexist and are in thermodynamic disequilibrium with reducing species such as H_2S and H_2 in the Venusian atmosphere.

An ultraviolet absorber has been detected in the Venusian atmosphere that may be related to microbial UV protection and possible photosynthesis (Schulze-Makuch et al. 2004; Fig. 8.2), and the flux of ionizing radiation to which the Venusian atmosphere is exposed was shown likely not to pose a hazard to habitability in the zone ranging from an elevation of 51–62 km (Dartnell et al. 2015). These and other aspects of the possibility of life in the clouds of Venus have been raised by different authors over the years (Sagan 1961; Feinberg and Shapiro 1980; Grinspoon 1997; Schulze-Makuch et al. 2004, 2013a, b). They have also been discussed in the context of a proposed sample return mission to Venus (Schulze-Makuch and Irwin 2002a, b; Schulze-Makuch et al. 2003, 2005a). These authors concluded that Venus provides

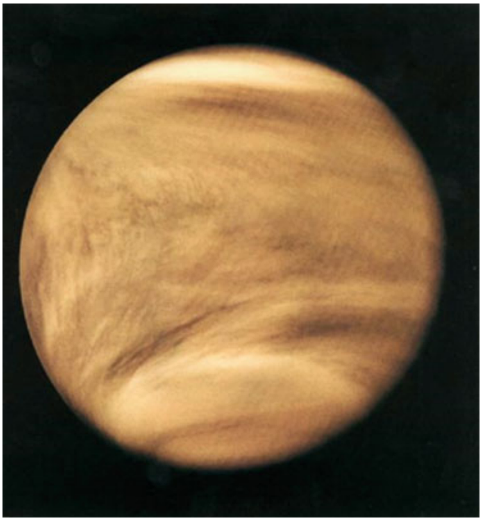


Fig. 8.2 Ultraviolet image of the clouds of Venus as seen by the Pioneer Venus Orbiter (5 February 1979). The dark streaks are produced by absorption of solar UV radiation. Source: NSSDC, http://nssdc.gsfc.nasa.gov/photo_gallery/photogallery_venus.html, image pvo_uv_790205

one of the best possibilities for harboring atmospheric life in the Solar System. Since it is also the most accessible planetary body beyond the Moon a sample return mission lies within the capabilities of existing technology.

Venus illustrates nicely the theoretical potential for atmospheric life. Nonetheless, the problems for persistence of living systems in an atmospheric habitat are formidable, so their existence warrants a lower probability than life on the surface, and much lower than life beneath the surface, on other worlds.

8.4 Life in the Space Environment

If the low density of matter would make life-supporting interactions between molecules in a gaseous atmosphere difficult to maintain, the problems are much more severe in space. The damaging potential of ultraviolet and particle radiation, the extremely low temperature and nonexistent vapor pressures, and the homogeneity of empty space further add up to such a hostile environment that outer space cannot be regarded as a likely habitat for life. However, the possibility that life could survive interplanetary travel through space in the protective sanctuary of meteorites or even dust particles cannot be discounted. There is increasing evidence that microbes, especially when in the dormant spore form, can survive space conditions fairly well (Horneck 1981; Koike et al. 1991; Nicholson et al. 2000; Horneck et al. 2008, 2012). This is especially the case if the microbe is surrounded by a thin layer of solid material that would shield it from cosmic and UV radiation. The effect of space vacuum is another constraint. Some space experiments have shown that up to 70% of bacterial and fungal spores survive 10 days exposure to space vacuum, even without any protection (Horneck 1993). Survival rates increased when *Bacillus subtilis* spores were embedded in salt crystals or if they were exposed in thick layers (e.g. 30% spore survival after nearly 6 years when embedded in salt crystals (Horneck et al. 1994). Spores from thermophilic bacteria are generally more resistant to heat than mesophilic spores (Ashton and Bernard 1992). Other studies showed that bacterial survival rates decreased by 2 to 4 orders of magnitude when exposed to space vacuum and short wavelength UV radiation (Saffary et al. 2002), but confirmed the protection provided by salt crystals (Mancinelli 1989). An intriguing example of microbial survival under space conditions was the reported recovery of living bacteria from the Surveyor 3 spacecraft after 3 years of exposure on the lunar surface (Mitchell and Ellis 1971), although this claim has been disputed. Nevertheless, microbes do apparently have the possibility to survive for extended periods in space. *Deinococcus radiodurans* appears to accomplish its resistance to radiation and desiccation by having multiple copies of DNA, large organelles, a large nucleus, a thick membrane, having the DNA in a ring-like structure (Levin-Zaidman et al. 2003), and by possessing a high redundancy of repair genes, but most microbes accomplish this feat by sporulation. During sporulation cytoplasm and genetic material is sealed off by the inner cell membrane. The DNA is then protected by thick layers of protective membranes (Fig. 8.3), which are only permeable to nutrients that the organism needs for germination.

Microbes can survive in this type of dormant phase for extremely long time. Cano and Borucki (1995) isolated a strain of *Bacillus sphaericus* from an extinct bee trapped in 25–30 million year old amber, while Vreeland et al. (2000) claimed to have isolated a 250 million year old halotolerant bacterium from a salt crystal.

Findings such as these lend new credibility to the idea of panspermia (Arrhenius 1903, 1908), the transfer of organisms between planetary bodies. However, any organism taking this type of journey would have to survive a series of hazards, including (1) survival of the meteorite impact that ejects the organism into space from the planet of its origin, (2) maintenance of viability for long durations of time inside the meteoritic material, (3) intense UV and cosmic radiation, cold, and

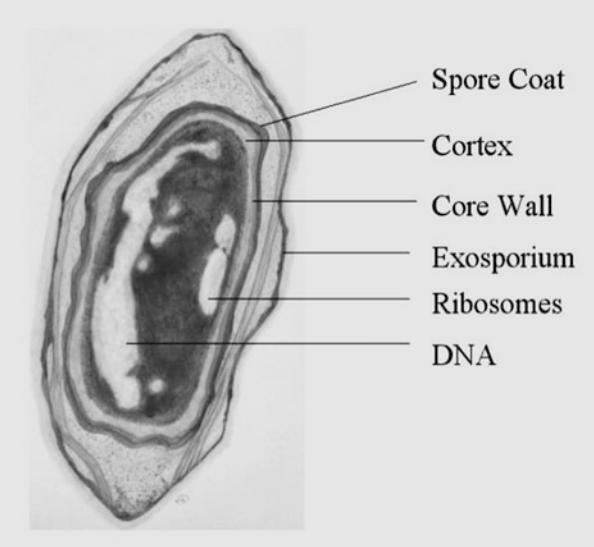


Fig. 8.3 *Bacillus subtilis* spore, schematic. The DNA is contained in the nucleoid (light regions) within the spore core. The core is surrounded by the protective cortex. The long axis of a *B. subtilis* spore is about 1.2 micrometers (Nicholson et al. 2000). Drawing provided by Chris D'Arcy, Dragon Wine Illustrations, El Paso, Texas

vacuum, and (4) the shock and heat of impact on the planetary body to which the organism is transferred. Mileikowsky et al. (2000) and Clark (2001) provided estimates on the likelihood of microbial survival for the different steps. Davies (1996) analyzed this scenario for the Mars-Earth case and concluded that it is a plausible scenario. A critical parameter is travel time, which can be as little as 2 months for microscopic particles from Mars to Earth (Moreno 1988). Boulder-size rocks, however, have been estimated to need a mean travel time of several hundred thousand to millions of years for the same distance (Melosh 1988). Nevertheless, interplanetary travel from one planetary body to another within a solar system is a definite possibility. The scenario is different for panspermia between different solar systems. Although the first interstellar asteroid, named Oumuamua, has recently been discovered (Keller et al. 2017), we rate chances for the transferal of dormant life from one solar system to another as slim, because the asteroid (1) would be exposed to cosmic radiation for a much longer time, effectively sterilizing the near surface of that planetary body and (2) would experience much more force upon impact due to the higher velocity of such an object compared with an asteroid originating from within the Solar System. Also, (3) the probability that an interstellar asteroid would strike a fairly small terrestrial planet, as opposed to the much larger gravity sink of the central star, or perhaps a gas giant, is very low.

It should be pointed out that viability in the space environment very likely involves only dormant forms of life. Active forms of life as speculated by Hoyle (1959; see Sect. 13.2) could not exist due to the harsh radiation environment, cold vacuum conditions and low density, plus the problem of origin. The idea that an ancestor of such an organism would have originated on a planetary surface and later adapted to life in space similar to marine animals and plants that conquered the land during Earth's history, seems unreasonable. There are many transitional habitats between land and sea, but not between a planetary atmosphere and space. Evolutionary pressure would have had to push certain types of organisms to adapt to life in the atmosphere, then pressed it to higher and higher levels of the atmosphere until finally the organism would have to be capable of living in space. Over Earth's history of immense evolutionary pressure during certain time periods, only a tiny fraction of terrestrial organisms adapted even to a life style involving the atmosphere. The major problem appears to be that chemical nutrients that are needed for growth in addition to light are not present in high enough concentrations in the higher atmosphere and certainly not in space.

8.5 Cosmic Biogeography

The possibility of worlds beyond our own has been appreciated since the speculations of the early Greeks. In 1584, Giordano Bruno asserted that there were "countless Suns and countless earths all rotating around their Suns," but confirmation of other Solar Systems with rotating, planar clouds of dust and gas that could lead to planet formation was not made until infrared observations were conducted of such a disk of dust surrounding the star Beta Pictoris, in the 1980s (Smith and Terrile 1984). Today we know of many extrasolar planets and even many star systems with multiple planets, but are they inhabited? Cockell et al. (2016) defined habitability as the ability of the environment to support the activity of at least one organism. But supporting life once it has formed is subject to fewer constraints than the origination of life and its persistence over time. Thus, a planetary body that is potentially habitable in theory is not necessarily occupied by a stable biosphere. In fact, most exoplanets may be devoid of life largely because of much stricter constrains on the origin of life than on its perpetuation (see also Chap. 3). As pointed out by Cockell and Westall (2004), the assessment of actual or past habitats on other planets poses a variety of problems for different reasons: (1) it is logistically difficult for scientists to visit extraterrestrial sites of interest, (2) data are limited and may have been acquired by just a few spacecrafts or by ground observations from Earth, (3) the data gathered may not have an astrobiological focus, because that might not have been the focus of the mission in the first place, and (4) environmental conditions on other planetary bodies are often very different from conditions known to support life on Earth, thus inhibiting any analog parallels that can be used to assess the possibility of life.

The traditional approach to habitability is to define a “Habitable Zone (HZ)”. The concept of the HZ of a star is based on equating the possibility of life with the existence of liquid water on the surface of a planet orbiting the star. This is motivated by the fact that liquid water is thought to be an important precondition for most, if not all forms of life (Bennett et al. 2003; Goldsmith and Owen 2003). The position and extent of the HZ depends on the stellar luminosity, even though the exact boundaries of circumstellar HZs vary from system to system because planets have different volatile inventories, albedos, and masses, which affect the rate of atmospheric escape of water near the inner edge and the rate of global refrigeration near the outer edge. The limits of the solar HZ often quoted are those of Kasting et al. (1993) obtained by a radiative-convective model for the Sun-Earth system. However, life may also be present outside of a traditionally defined HZ, such as in the putative subsurface ocean of Jupiter’s moon Europa (Figueredo et al. 2003; Schulze-Makuch and Irwin 2002a), or in the clouds of Venus (Schulze-Makuch et al. 2004). A life style between dormant and proliferative forms may expand the outer edge of the HZ, as it requires only periodic stability of liquid water on a planetary surface (Schulze-Makuch et al. 2005b). Also, life may be based on a novel biochemistry with different HZ requirements around a star.

The concept of the habitable zone as classically described thus is limited by its exclusion of the possibility of life in habitats more exotic than those found on Earth. With this limitation in mind, Lammer and his colleagues (2009) have proposed an expansion of the concept to include four different classes of habitats. Class I includes bodies on which stellar and geophysical conditions allow Earth-analog planets to evolve so that complex multi-cellular life forms may originate. Class II consists of bodies on which life may evolve but due to stellar and geophysical conditions evolve toward Venus- or Mars-type worlds. Class III habitats are planetary bodies where subsurface water oceans exist which interact directly with a silicate-rich core. Class IV habitats have liquid water layers between two ice layers, or liquids above ice.

However, following the traditional approach, the inner edge of the current HZ of our Solar System lies between 0.95 AU, where the Earth's stratosphere would become moist, and 0.84 AU, where the surface temperature would climb dramatically because of a positive feedback loop (Kasting et al. 1993). The outer edge of the HZ is determined by the formation of CO_2 clouds, which cool a planet's surface by increasing its albedo and by lowering the convective lapse rate. Thus, the outer edge of the HZ would be between 1.40 and 1.46 AU (or up to 2.0 AU for a larger planet than Mars), where clouds would snow out on to the ground causing atmospheric CO_2 levels and surface temperatures to decrease irreversibly (Forget and Pierrehumbert 1997; Williams and Kasting 1997). Work by Mischna et al. (2000) argues that the HZ of the Sun might extend up to 2.0 AU or more, allowing Mars at 1.52 AU to be well inside the HZ if it had a thick atmosphere with a strong greenhouse effect.

By analogy to the circumstellar habitable zone, the term of a Galactic Habitable Zone (GHZ) has been suggested as well (Gonzalez et al. 2001). The GHZ is defined as that region in the Milky Way where biogenic elements are available and where any life would be far enough away from the galactic center to not be exposed to disruptive gravitational forces or to too much radiation. The GHZ has been quantified by Lineweaver et al. (2004), who modeled the GHZ as an annular region between 7 and 9 kiloparsecs from the galactic center that widens with time and is composed of stars between 4 and 8 billion years old. Their assumptions for the presence of a GHZ were based on (1) the presence of a suitable host star, (2) enough heavy elements to form terrestrial planets, (3) sufficient time for biological evolution, and (4) an environment free of life-extinguishing supernovae. The concept of a GHZ has the same advantages and drawbacks as the concept of a circumstellar habitable zone. While these concepts are useful in prioritizing astrobiology targets, especially in a search for life as we know it, they do not take into account any life based on a different biochemistry, or life that simply utilizes adaptative mechanisms that don't require permanent liquid water on the planetary surface.

Much of the search for extrasolar planets (see Chap. 12) is motivated by the quest for terrestrial planets, for the common-sense reason that we are better qualified to recognize life as we know it, and therefore more likely to find it on smaller, rocky planets such as our own. It is important to consider, however—as we argue at numerous points in this book—that life in forms unfamiliar to us could flourish under conditions alien to the life with which we are familiar. There may thus be specialized niches for some forms of life on gas giants, or on their satellites, or on brown dwarfs or orphan planets, within radiation fields of high intensity, in liquids other than water, using metabolic systems and energy sources unlike anything we have ever seen. We have already been surprised to find, for example, that our closest star belongs to a triple star system (Alpha Centauri A, Alpha Centauri B and Proxima Centauri), and that one of them, Proxima Centauri is apparently orbited by a terrestrial planet (Anglada-Escudé et al. 2016), and we are just starting to explore other solar systems. The broader mandate for space and planetary science should therefore be to characterize the full range and variety of solar systems, and seek in the pattern of their distribution the clues that will lead us to consider how exotic our consideration of life on other worlds should remain.

The most extreme planetary body in our Solar System in this respect is Titan, being both extremely reducing (practically devoid of molecular oxygen and carbon dioxide) and extremely cold (surface temperature <100 K), with seas of liquid methane/ethane on its surface. However, due to Titan's potential to reveal alternative pathways for prebiotic chemistry and possibly even life, it has received much attention (Baross et al. 2007), and was even rated as the mission target of highest priority in our Solar System by Shapiro and Schulze-Makuch (2009). Could polymerized hydrocyanic acid with its structural and electronic variability push prebiotic chemistry to increased complexity on Titan (Rahm et al. 2016)? Could there even be exotic organisms that may use azotomes, compounds that contain polar nitrogen groups, to play the role of liposomes in terran biochemistry (Stevenson et al. 2015a, b)? The spectroscopic detection of vinyl cyanine (Palmer et al. 2017) provides a first support for such possibilities, but more is needed. And, could we possibly detect evidence of alien metabolism, which might be based on radical chemistry rather than redox chemistry in this type of cryogenic environment (Schulze-Makuch and Grinspoon 2005)? Might we even detect macromolecules with repeating backbone charges that act as a genetic polymer for life on Titan (Benner 2017). These are only a few of the questions we would like to be able to answer; and to achieve this we have to complete the step from fanciful speculations to predictions that can be tested by future missions to Titan. Such missions to Saturn´s largest moon should be of the highest priority if we truly want to understand the full "landscape" of life, not only on Earth, but universally.

Another example of where research should be expanded is the possibility of habitable planets around M stars rather than G stars like our Sun (Tarter et al. 2007). As of this writing there have now been detected several Earth-size planets, some of which might be habitable, and we are just at the cusp of detecting the first exomoon. M stars (also known as red dwarfs or dM stars) are the most common stars in the Universe and most of the discovered planetary bodies are and will be orbiting M stars. Based on their longevity and constant luminosities many of these are likely to be habitable (Guinan et al. 2007). Heath et al. (1999) even suggested higher plant habitability for red dwarf planets based on possible moderate climates and global water cycles on these bodies. They also pointed to the availability of photosynthetically active radiation in the sunlight of M stars. Some properties of red dwarf stars and their relationship to planetary habitability are listed in Table 8.4.

Finally, the notion of cosmic habitability could be expanded even further. Recent research efforts, especially into the cosmological idea of inflation, suggest the highly speculative possibility of many universes existing in parallel with ours, all with different values for the cosmological constants such as the Boltzmann constant, Newton's constant, the charge of the electron, electric permittivity, magnetic permeability, the speed of light, Fermi's constant, the Planck constant, etc. If that speculation is correct, many universes could exist which would be essentially unrecognizable to us, as, of course, would be any life existing within them. Another suggested alternative is that the fundamental constants have changed with time (Olive and Quian 2004), which, if true, would tie habitability in the Universe closely to time. At the core of this problem lies a version of the anthropic principle: our

Table 8.4 Properties of red dwarf (dM) stars and their relationship to planetary habitability (modified from Guinan et al. 2007)

M star property	Astrobiological assessment
Nearly constant luminosities over tens of billions of years	M star planets provide a stable environment for life to form and evolve within fixed habitable zones
M stars are ubiquitous, comprising >70% of stars	High chance for at least some habitable planets
Long life times (>50 Gyr)	Especially beneficial for evolution of complex/intelligent life, because of greater evolutionary time span (compared to 4.5 Gyr for evolution on Earth)
There are many old M stars (>5 Gyr)in our galaxy	Very old, metal poor, M stars would likely not be able to form rocky planets because of the paucity of metals. A low metal environment would also be problematic for the development of life
Theoretical studies by Boss (2006) indicate that "Super Earths" can easily form in the protoplanetary disks of M stars	Planets hosted by M stars should be at least as common as those hosted by solar-type stars. Even without much effort, several M stars have been found to host planets
HZ is located very close to the host star at <0.1–0.4 AU	The planet would easily become tidally locked, reducing likelihood of global habitability
Unlike solar-type stars, M stars have essentially no photospheric continua in the UV (<2500 Å), because of their low temperatures	While generally harmful to organisms, UV irradiation is a powerful force in evolutionary adaptation, and may also play a role in the origin of life
M stars have very efficient magnetic dynamos resulting in strong coronal X-ray, transition region FUV and chromospheric FUV-UV emissions	While generally harmful, these types of radiation are easily filtered out by planetary atmospheres and may be evolutionarily beneficial

Universe, however unique among all the possibilities, harbors a form of life that can see it because that life evolved under those same unique constraints. Whether our Universe is only a random chance event within an incredibly large number of other universes, a kind of bubble in a multiverse (Leslie 1996; Linde 1986; Rees 2001; Susskind 2005), and whether life can exist only in our type of universe, cannot currently be answered, and is perhaps not resolvable by the scientific method at all.

8.6 Chapter Summary

The human perspective of life as a planetary surface phenomenon is deceiving. The surface provides a heterogeneous environment conducive for the diversification of life over time as conditions change. It is just these circumstances, in all probability, that have given rise to macrobiological complexity on Earth. But the part of the biosphere that lies beneath the surface provides for a more stable and secure abode for life, and may even on Earth harbor a greater total biomass than is found above ground. Thus, life in the subsurface is much more likely to be the rule than the exception on other worlds. If this is so, there are compelling theoretical reasons for believing that in the vast majority of cases, such life is microscopic and relatively ancestral.

The gaseous atmosphere that surrounds planetary bodies is a much less favorable habitat for living systems. But at high densities with an appropriate mixture of chemicals and available free energy, atmospheres could harbor life. Like their subsurface counterparts they would probably be microscopic for reasons having to do with buoyancy, but because of the peculiar evolutionary trajectory that likely led to their adaptation to an aerial existence, they are more likely to be highly derived in form and function from their ancestors. Active life in space is highly improbable due to the harsh radiation environment, cold vacuum conditions and low density, relative homogeneity, and the problem of origin. However, organisms have developed protective mechanisms that allow them to travel passively through space for some time.

Habitable worlds might be widespread and would likely include planets that orbit other (e.g. M or K) stars. However, habitable does not mean inhabited, as there may be many uninhabited worlds that could potentially support life but that do not because the constraints for the origin of life on those planets are likely to be more stringent than for the persistence of life once it has originated. A first attempt to search for habitable planetary bodies would consist of defining habitable zones around stars and by quantifying galactic habitable zones within our own Galaxy. However, the traditional approach of the habitable zone concept is to consider only those planetary bodies as habitable that exhibit stable liquid water on their surfaces. This approach most likely omits many habitable worlds.

Chapter 9
Signatures of Life

In this chapter we will elaborate on how evidence for life on other worlds can be sought, and if present, possibly detected. The best evidence for extraterrestrial life, of course, would be recovery of actual specimens or their fossils. For the next one or two decades, the possibility of obtaining such direct evidence is almost surely restricted to samples from Mars and Venus, and possibly from some moons of the outer Solar System such as Europa and Enceladus. So detection of life beyond our nearest neighbors will be dependent for the near future on remote sensing. As technology of robotic exploration and remote sensing improves, the possibility of detecting extraterrestrial life will grow. While the size of individual organisms makes their detection at a distance virtually impossible, organisms in the aggregate alter their environments, generating signatures of their functional processes. These direct consequences of biological activity are referred to as "biosignatures". Other effects of the presence of living systems may be detected in global or geological features. These alterations of the geological environment due to life processes, we call "geosignatures". Even on worlds too remote, small, or difficult for whatever reason to monitor for the existence of explicit signatures of life, certain planetary characteristics can be detected that are more likely to be consistent with the presence of life than others. These we refer to as "geoindicators." They consist of parameters that are consistent with life as defined in Chap. 2, and the requirements for life as described in subsequent chapters, including a flow or gradient of energy, presence of an appropriate solvent, and availability of complex polymeric chemistry. While geoindicators point to the potential for supporting life, they do not confirm its existence. Most geoindicators can be detected by remote sensing methods with relative ease, however, and thus can be used in assessing the plausibility of the existence of life. At the end of the chapter, we apply our discussion of signatures and indicators of life to assess the relative plausibility for the existence of life on other bodies in our Solar System. How to detect and confirm living processes with life detection experiments will be discussed in Chap. 10.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_9

9.1 Searching for Signatures of Life

Examples of biosignatures and geosignatures of life are given in Table 9.1. None of these signatures are known to exist on any planetary body of our Solar System other than Earth. Thus, there is presently no available evidence for life as we know it elsewhere in the Solar System. Life could exist nonetheless, either in a form known or unknown to us, that does not give rise to any of the biosignatures or geosignatures indicated in Table 9.1, if it (1) occurs beneath an opaque surface, (2) is too small to cause environmental transformations extensive in magnitude or spatial extent, or (3) is insufficiently complex to generate complex phenomena, such as roads or radiowaves. Other difficulties are that extraterrestrial life may involve dynamic processes that occur on (1) a spatial scale too small to be detected by current remote technology, and (2) a time scale too prolonged to be sampled feasibly (Schulze-Makuch et al. 2002a). Also, there are many mineralogical features that look like biosignatures, but are entirely abiotic (e.g., Garcia-Ruiz et al. 2017). A recent discussion of the reliability of biosignatures has been provided by Fox and Strasdeit (2017).

Notwithstanding these reservations, several types of biosignatures may become relevant for the detection of life in the near future, either in our own or in another Solar System (Table 9.1)

9.1.1 Atmospheric Composition of a Planetary Body

An often cited geosignature of life is the presence of molecular oxygen and particularly the presence of ozone in an atmosphere. For example, Akasofu (1999) suggested the use of the green oxygen line at 557.7 nm from auroral emissions to

Table 9.1 Some examples of biosignatures and geosignatures of life

Observation	Signature
Organic macromolecules larger than 500 daltons	Biosignature
Atmospheric gas composition, such as O_2 and CH_4, resulting from biogenic processes	Geosignature
Rocks and sediments produced by biogenic processes such as the banded-iron formation (BIF) and stromatolite deposits of early Earth	Geosignature
Known biogenic substances such as chlorophyll not explicable by naturally occurring inorganic chemical processes	Biosignature
Rate and type of erosion consistent with biological processes	Geosignature
Structural complexity, such as geometric regularity (roads, canals) or unnatural local aggregates (cities) not explicable by natural geological processes	Geosignature
Distribution and magnitude of emitted heat inconsistent with an abiotic origin	Biosignature
Energetic emissions such as radiowaves, which are neither highly regular, as from a pulsar, or highly random, as in the universal background radiation	Biosignature

search for extraterrestrial life. Ozone was suggested to be more suitable than molecular oxygen because its abundance increases nonlinearly with the abundance of molecular oxygen (Leger et al. 1993) and ozone absorbs UV radiation known to be detrimental for terran life on extrasolar planets. Any such spectroscopic remote observation has two major technical challenges: the weak signal and the huge background from the parent star (Frey and Lummerzheim 2002). However, for the detection of the habitability of planets in other Solar Systems this may be the only reasonable approach for the near future. In our view, an oxygen atmosphere or ozone layer alone, in the absence of other abnormal concentrations of gases such as methane, should be regarded only as a geoindicator consistent with the presence of life, not as a geosignature. For example, Jupiter's moon Europa currently has a thin oxygen atmosphere from interactions of radiation with surface ice (Hall et al. 1995) and it can easily be envisioned that it had a much thicker oxygen atmosphere and possibly an ozone layer for part of its geological history. When the Solar System formed Europa most likely had oceans of water on its surface and a water vapor atmosphere. Given the high radiation environment of the Jovian system, water would have split into hydrogen and oxygen with the hydrogen escaping to space and the oxygen being retained for longer time periods because of its higher molecular weight. Thus, the presence of a high amount of molecular oxygen and even ozone for some time period is absolutely plausible based on physical means alone (Europa likely experienced global re-melting events for which the above scenario may be valid as well).

However, the atmospheric composition of Earth is a prime example of a signature of life (Table 9.1). Earth's atmosphere is the peculiar product of a particular biological process: photosynthesis. Oxygen by itself could not be considered a signature, as explained above. Further, it was shown that titanium (IV) oxide can produce abiotic oxygen from liquid water under near-ultraviolet light (NUV) on the surface of exoplanets (Narita et al. 2015). However, the high amounts of oxygen on Earth (about 21%) combined with the presence of hydrogen (H_2), methane (CH_4), ammonia (NH_3), methyl chloride (CH_3Cl), and methyl iodide (CH_3I), along with various sulfur gases can best be explained by the continuous metabolic production of these compounds faster than they can react with each other (Sagan 1994). These gases, highly reactive when mixed, would not coexist at such high concentrations unless their levels were being actively maintained. It is this type of disequilibrium, in combination with high amounts of oxygen that can be used as an indicator for oxygen producing photoautotrophs. These gases would be visible through their spectral signatures in the mid-IR and visible to near-IR wavelength ranges, thus providing not only valuable information regarding possible biosignatures but other planetary properties as well (Des Marais et al. 2002).

The spectral signature of photosynthesis on Earth has also been suggested as a signature for life on other planets. The reflectance spectra of most photosynthetic organisms exhibit a so-called red edge, although the exact spectrum varies quite a bit between different types of organisms (Kiang et al. 2007a, b). Photosynthesis can also be quite diverse, as exhibited by the two types of photosynthesis existing on Earth. Other types of light-driven metabolism have been suggested as well, such as chlorinic photosynthesis—the photolytic oxidation of aqueous Cl^- by organisms to form dihalogen or halocarbon products, coupled with the assimilation of carbon dioxide (Haas 2010). This hypothetical type of geochemically, physically, and energetically feasible metabolic pathway would result in a different type of spectrum.

A very thorough approach to listing possible gases in the atmosphere of exoplanets was taken by Seager et al. (2016). They showed that more than 600 gases from an initial list of about 14,000 molecules are known to be produced by life on Earth, and thus could serve in principle as potential biosignatures. A different approach was employed by Domagal-Goldman et al. (2011), who focused only on biogenic sulfur gases as remotely detectable biosignatures on anoxic planets. Currently, the ability to detect atmospheric biosignatures remotely is still in its infancy, demonstrated by the high likelihood of both false negatives (Reinhard et al. 2017) and false positives (Rein et al. 2014).

9.1.2 Geological Evidence

Particular signatures also exist for chemoautotrophic organisms. An example are the limestones and ironstones produced by biological activity on the early Earth. Both types of rocks can form from inorganic processes. The large quantities produced during Earth's early history, however, can hardly be explained by abiotic processes. For example, microbial life dominated the ecosystems of Precambrian shallow marine environments, and is likely to be implicated in widespread carbonate formation, and possibly also in the precipitation of other evaporates (Wrights and Oren 2005). The large amounts of deposited Banded Iron Formation (BIF) rocks are even less imaginable without microbial participation. Similar processes might be occurring on Mars. For example, Parro et al. (2005) described the development of technology to detect iron-powered chemosynthetic microbes. Chemosynthesis generates various chemical end-products depending on the exact metabolic process. Nevertheless, the chemical end-product may provide a useful marker, especially if produced in a large enough amount over an extended period of time to make it a signature of chemotrophic life. The biochemical end products often exhibit large-scale geomorphological characteristics such as stromatolite colonies and coral reefs, some of them large enough to be observed with the naked eye from the Moon such as the Great Barrier Reef.

Minerals themselves—particularly rare minerals—may serve as a biosignature as well. They may have played essential roles in the origin of life, or been formed, directly or indirectly, by biological processes (Hazen and Ausubel 2016). For example, Earth has many more minerals, and more rare minerals, than Mars due to a much larger diversity of environments. Thus, the distribution of rare minerals may constitute an important biosignature, reflecting the co-evolution of the geosphere and the biosphere.

The high rates of erosion and types of erosion observed on Earth due to biological and chemical weathering induced by living organisms provide another example of a geosignature. The biomass of fungus-lichen rock dwellers is estimated to be enormous, by one account 13×10^{13} tons (Margulis 1998). Thus, the effect of these rock dwellers on chemical weathering from metabolic by-products is immense. Rates and types of erosion can be inferred from the visible and microwave wavelengths of the electromagnetic spectrum (Schulze-Makuch et al. 2002a), but are traditionally not considered as a signature of life. Dietrich and Perron (2006) suggested the search for a topographic signature of life based on the quite apparent impact of life on rock weathering, soil formation and erosion, and slope stability and river dynamics, even over short time scales. But even for a topographical signature of life, high-resolution images are necessary to have confidence in the detection, and at present this type of resolution is only available for the inner planets of our Solar System. It would not be expected to be available for any extra-solar system planets, particularly not for any encased by an atmosphere.

9.1.3 Fossil and Isotopic Evidence

Fossil remnants and isotopic fractionation caused by biotic processes are other examples of biosignatures. One controversial example is the Martian meteorite ALH84001 in which McKay et al. (1996) claimed to have found evidence of fossilized microbes. However, these claims have come under intense scrutiny as have some of the oldest known records of life such as stromatolites and microfossils (Pasteris et al. 2002; see also Chap. 10). Biogenic textures have been described from oceanic crust and in pillow lavas from 3.4 billion year old rocks from the Barberton Greenstone Belt of South Africa (Fliegel et al. 2010), but the validity of these biosignatures has been disputed as well (Grosch and McLoughlin 2014). A similar skepticism has greeted claims that ancient sediment structures on Mars resemble macroscopic morphology and spatial and temporal relationships as observed in terran microbialites (Noffke 2015). Ruff and Farmer (2016) reported that opaline silica structures discovered on Mars by the Spirit rover are remarkably similar to active hot spring and geyser discharge channels at El Tatio in northern Chile, where complex sedimentary structures are produced by a combination of biotic and abiotic processes. Evaporite sediments such as gypsum seem to be especially suitable for preserving biosignatures, including microfossils (Schopf et al. 2012). Stüeken (2016) suggested that high nitrogen abundances in ancient muds can be considered a biosignature, and Nadeau et al. (2016) proposed microbial morphology and motility as possible biosignatures for outer planet missions.

The search for reliable biosignatures is currently a very active area of research, in part because it is extremely challenging to determine what a reliable biosignature is, and what type of life process it indicates (Fox and Strasdeit 2017). One approach to this challenge is to identify biosignatures that would be expected to be found in specific environments, created by the life processes occurring there. Lava tube caves are one example of such an environment (Boston et al. 2004).

Isotopic signatures of carbon, sulfur, nitrogen, hydrogen, iron and other elements are another form of fossil evidence (Schidlowski et al. 1983) that can also be interpreted as a biosignature. Observations from terran organisms show that chemically lighter isotopes are preferred resulting in a net fractionation of lighter isotopes. A carbon isotope fractionation, typical for biological processes, has been found in the geological record for the last 3.5–3.8 billion years of Earth's history (Schidlowski 1988). More recently Yeung et al. (2015) reported that biological factors influence the clumped isotope signature of oxygen produced during photosynthesis. They found that photosynthetic O_2 is depleted in $^{18}O^{18}O$ and $^{17}O^{18}O$ relative to a stochastic distribution of isotopes and speculated that similar biosignatures may be widespread in nature.

A robotic mission would be needed to detect these signatures of life unless a rare fortunate circumstance would bring a meteorite from that world to Earth where it can be analyzed by in-situ methods. However, microbial biofilms that become preserved on rock surfaces could possibly be identified with remote sensing methods if (1) spectroscopically identifiable compounds exist that display unique adsorption, diffraction, and reflection patterns characteristic of biogenerated organic compounds (e.g. chlorophylls, carotenes, melanins), (2) biogenic geomorphological features are exhibited (e.g. biopitting, biochipping, bioexfoliation), and (3) biominerals are detected that are produced in association with biofilms that occupy rock surfaces such as oxalates and certain types of carbonates and sulfides (Gorbushina et al. 2002).

9.1.4 Macromolecules and Chirality

Among the most powerful biosignatures are macromolecules that are directly linked to biogenic metabolism or other cellular functions. Chlorophyll is the prime example and can be identified by radiance spectra in the visible region (Gordon et al. 1980; Hovis et al. 1980) and by advanced very high-resolution radiometer (AVHRR) measurements (Gervin et al. 1985; Tucker et al. 1985). Methylhopanoids have also been suggested as biomarkers and have the additional advantage of distinguishing between cyanobacteria (2-methyl) and methanotrophic (3-methyl) bacteria (Farrimond et al. 2004). Proteins, polypeptides and phospholipids are other examples of macromolecules that are linked to life. Lipids have also been suggested as universal biosignatures of extraterrestrial life (Georgiou and Deamer 2014). In general, any macromolecule of a size larger than 500 daltons (protein-size) could be considered a possible biosignature (Table 9.1). Davila and McKay (2014) introduced the concept of necessity and chance: that some of these macromolecules or terran building blocks of life are an endowment of prebiotic processes and likely to be found also in extraterrestrial life, while others were introduced through the evolutionary process by chance, and thus are not likely to be shared with other forms of life from a different origin. An evolutionary approach was also taken by Dorn et al. (2011), who suggested that life leaves a distinct chemical signature in its environment, because it synthesizes only those molecules that maximize its fitness. In a lifeless environment, small, easily formed, low-formation-energy molecules prevail, while the measurement of chemical concentration ratios of monomers that would be contradictory to equilibrium thermodynamics or formation kinetics would indicate the likely presence of life. As examples they pointed to an apparent biotic bias toward even-numbered carbon chains in monocarboxylic acids and specific abundance patterns in amino acids.

Chirality, or non-racemic handedness, is a fundamental property of biogenic molecules on Earth and thus may be used as an indicator of possible extraterrestrial life detectable by remote sensing in the near future. Large macromolecules are not symmetrical and thus inevitably exhibit chirality. Plaxco and Allen (2002) pointed out that all terran life uses well-structured, chiral, stereo-chemically pure macromolecules of 500 or more atoms as their metabolic catalysts. Xu et al. (2003) argued that all life would employ these types of macromolecules irrespective of the specifics of their chemistry. They pointed out that these molecules strongly absorb at terahertz frequencies and exhibit significant circular dichroism, which they consider an unambiguous biosignature. Left- and right-handed circularly polarized light interacts differentially with chiral molecules, especially at blue-green and shorter wavelengths (Van Holde et al. 1998). Salzman et al. (1982) found that organisms also scatter circularly polarized light differentially, with angular and wavelength spectra somewhat characteristic of particular organisms or strains. Evidence presented by these authors and by Nicolini et al. (1991), Diaspro et al. (1991) and Lofftus et al. (1992) indicates that the configuration of DNA in organisms strongly affects their differential scattering.

Winebrenner (2008) developed an experimental system for the detection of biogenic molecules by means of circularly polarized light scattering with a polarization-dependent resonance at 436 nm. Sparks et al. (2009) reported on the detection of circular polarization in light scattered by photosynthetic microbes and proposed that circular polarization spectroscopy could provide a powerful biosignature for remote sensing searches for life. Creamer et al. (2017) described two capillary electrophoresis methods capable of resolving amino acid enantiomers down to a detection limit of 5 nM for the neutral amino acids and 500 nM for acidic amino acids, even with very little sample preparation. Once the collection of samples in situ can be achieved, the incredible sensitivity of today's technology, indicated by these examples, could provide a critical step toward the confirmation of biosignatures of life on other worlds.

9.1.5 Presence of Metabolic By-Products and End-Products

Metabolic by-products and end-products are well known for organisms on Earth. They include various biochemical compounds such as ATP and lipids, but also electron donor and acceptor pairs such as Fe^{3+}/Fe^{2+}, NH_3/N_2, and H_2S/S enriched in lighter isotopes. This isotope enrichment or fractionation occurs as part of the metabolic reactions for organisms on Earth and may also occur for life elsewhere. While biochemical macromolecules such as ATP are very specific signatures for certain biological processes, using isotopically light electron donors or acceptors as signatures for life is more challenging. An endless number of possible electron donor/acceptor pairs could potentially be used for energy-harvesting reactions on other worlds, and there are also numerous inorganic processes that lead to isotopic fractionation, many of them poorly understood. One promising approach might be the use of the oxygen isotopic ratio of phosphate, which was suggested as a means for detecting enzymatic activity since the exchange of oxygen isotopes between water and phosphate requires enzymatic catalysis at low temperatures (Blake et al. 2001). Also, the presence of gaseous electron acceptors and donors (e.g. H_2S, COS, CH_4) enriched in lighter isotopes may constitute a signature of life that can be screened readily by remote sensing methods. One example is the presence of CH_4 on Titan, which is isotopically lighter than would be expected from Titan formation theory (Lunine et al. 1999). However, any such interpretation is limited by our understanding of the physical and chemical processes occurring on a planetary body as foreign to us as Titan.

A related biosignature may be the metabolic multistep pathways that run close to equilibrium for some internal steps, but are coupled to a last step, which is energetically downhill, thus pulling the whole reaction to completion (Voet and Voet 2004). Baross et al. (2007) considered this feature as a possible universal biosignature as it exploits most economically a surrounding chemical disequilibrium.

9.1.6 Production of Biogenic Heat

Another possible signature of life is biogenic heat that may be detectable in the future by more advanced technologies. Living systems exist in thermodynamic disequilibrium by drawing energy from their environments. A consequence of the biochemical reactions that an organism needs to carry out to sustain itself is the production of “unorganized energy”, commonly in the form of heat. The production of heat follows as a consequence of the 2nd Law of Thermodynamics. Organisms by their very nature have to be structured and organized. However, in order to conform to the tendency of the physical world toward a state of greater disorder, any organism has to give up a portion of its energy in the form of heat or other type of disorganized energy. The distribution and magnitude of heat produced by living systems or colonies of living systems may be possible to detect by in-situ monitoring or remote sensing techniques in the near future, thereby serving as a biosignature if an abiotic origin can be ruled out.

9.1.7 Signatures of More Advanced Life

Signatures of life also include structural complexity produced by biogenic processes ranging from termite mounds to artificial constructions such as streets. Materials associated with our civilization, such as concrete, elemental aluminum, various plastic compounds, and radionuclides that change very little over geological time, would be examples of biosignatures for technologically advanced life (Waters et al. 2016). Evidence for a much further advanced civilization would be a Dyson Sphere—a spherical shell constructed around a star for absorbing most of its visible and shorter wavelength radiation (Dyson 1960; but see also Harrop and Schulze-Makuch 2010). Energetic emissions, such as radiowaves, which are neither highly regular, as from a pulsar, nor highly random, as in the universal background radiation, are currently used by SETI (Search for Extraterrestrial Intelligence) to scan the skies for signs of extraterrestrial intelligence. These kinds of signatures, of course, would be linked directly to the presence of more technologically advanced forms of life than microbes, but, if present, would also imply the presence of microbial life based on the presumption that more complex organisms would have to have evolved from simpler ancestors.

9.2 Geoindicators of Life

With the exception of our nearest Solar System bodies, the detection of life elsewhere in the Universe for the foreseeable future will likely focus on remote detection, given our current state of technology (Schulze-Makuch et al. 2002a). Retrieval of samples for direct analysis for years to come will be limited to meteorites, comet or asteroid material returned to Earth, and possibly collecting ejected material from Ceres or Enceladus. Retrieving samples from the atmosphere of Venus and the surface of Mars will be feasible technologically within the next decade or two. Yet, for the foreseeable future it is not feasible practically and economically to send robotic landers to each planetary body of our Solar System and beyond. Further, even on a planetary body with life the detection may be unsuccessful if (1) the site is unsuitable or sparsely populated, or (2) life detection experiments are not set up appropriately to detect life thriving in that particular environment.

Under these circumstances, the more sophisticated and abstract definitions of life alluded to in Chap. 2 may provide the basis for a set of parameters that could point to conditions favorable for generic forms of life, either known or unknown to us. Specifically, (1) the maintenance of disequilibrium from the environment requires the availability of energy flow (hence gradients of energy) for sustaining low entropy states; (2) the level of chemical complexity required to transform and store energy appears to require a fluid medium where concentrations can be high but molecular mobility can be maintained; and (3) the storage and transmission of information in organic forms of life appears to require polymeric chemistry that can involve the making and breaking of covalent bonds with relative ease. Parameters that indicate the presence of any of these conditions, and therefore imply that life could be present though not confirming its existence, are defined here as geoindicators. Based on the forgoing discussion primary geoindicators of life would include evidence of (a) an atmosphere or ice shield, (b) thermal gradients and chemical disequilibrium conditions, (c) internal differentiation of the planetary body, implying the capacity for radiogenic heating, (d) complex polymeric chemistry, (e) energy flow or gradients, and (f) a liquid medium as a solvent. The advantage of these geoindicators is that remote sensing can detect all of them readily in principle.

9.2.1 Presence of an Atmosphere or Ice Shield

It is difficult to envision the presence of life on the surface of any planetary body that is not shielded by an atmosphere. Without an atmosphere any liquid or gaseous compound will vaporize into the vacuum of space. Aside from the gas giants, relatively dense atmospheres exist only on Earth (1 bar), Venus (~90 bar) and Titan (~1.5 bar). However, for life to thrive at planetary surface temperatures on Venus (very hot) and Titan (very cold) would require a biochemistry with properties unfamiliar to life forms on Earth. The surface of both Venus and Titan is obscured from visual light penetration by a thick atmosphere. On Titan, organic compounds such as methane and ethane are present in the atmosphere (Coustenis and Lorenz 1999; Lorenz 1993), and Titan is also the only planetary body with a significant atmosphere other than Earth known to have nitrogen as the most abundant atmospheric gas. The high nitrogen content in Earth's atmosphere has been interpreted to result from biological processes (Lovelock 2000). Since Titan's atmosphere can only be penetrated by narrow frequency windows between bands for methane and radar with current remote sensing technology (Griffith et al. 1991; Lorenz and Lunine 1997), probes have to be sent to explore the physical conditions and chemistry of the surface (e.g. the Huygens probe which descended through Titan's atmosphere in January of 2005). On Titan a warmer subsurface could be a suitable habitat for microbial life. Venus, on the other hand, would provide very little hospitality for microbes in the subsurface habitat, unless they were able to use water that might possibly be present in a supercritical state. Instead, if life evolved on Venus, it may have retreated toward cooler conditions in the atmosphere (Schulze-Makuch and Irwin 2002b). Mars has a much thinner but still significant atmosphere dominated by CO_2. The Martian atmosphere would not provide much protection for any life on its surface, but life would be possible in protected niches such as caves or beneath the surface (Boston et al. 1992).

The Jovian moons Europa and Ganymede, and possibly Callisto, as well as Saturn's moon Enceladus and Neptune's moon Triton, do not have significant atmospheres, but suitable conditions for life in a subsurface ocean, if it exists, would be shielded by an ice crust. This ice crust would act as a shield preventing subsurface compounds from evaporating into space and would also provide a shield against cosmic rays. Planetary oceans capped by an ice shield may in fact be much more common in the Universe than “naked” or “near-naked” oceans as on Earth (Schulze-Makuch 2002).

9.2.2 *Internal Differentiation*

Life is easier to envision on any planetary body that is differentiated into a radioactive core, a mantle and a crust. Internal differentiation is a sign of endogenic activity that is powered by radioactive decay. The likelihood of internal differentiation, in turn, is directly related to global mass, and that can be deduced by a planetary body’s influence on orbiting or passing probes and by the gravitational attraction it exerts on other planetary bodies or light.

To the extent that the evolution of life on Earth is a typical example, plate tectonics, which are driven by the internal heat of Earth, or some other effective recycling mechanism for minerals and nutrients appears to be important for the persistence of living systems. Nutrients and minerals would otherwise be quickly exhausted and evolving life, especially when still in its infant stage and not well established, would not be able to meet its nutrient demands within a relatively short time frame (on a planetary time scale). On Earth and probably early Mars the recycling mechanism has been plate tectonics (Connerney et al. 1999; Sleep 1994). Plate tectonics on Earth have also constantly produced greenhouse gases that have acted as a global thermostat providing stability for the evolution of life (Ward and Brownlee 2000). The presence of plate tectonics can be identified with remote sensing methods based on measured magnetic properties of the rock, visible symmetry along a spreading axis, and specific patterns in fracture orientation and propagation.

9.2.3 *Polymeric Chemistry*

Chemical complexity is based at the molecular level on polymeric molecules joined by covalent bonds (Lwoff 1962). For reasons elaborated in Chap. 6, other life in the Universe, except under very exotic conditions, is likely to be based on polymers of carbon. Polymeric organic compounds are in general detected by their absorption spectra.

On an active planet, polymeric organic compounds will be subject to chemical cycling. This can be inferred from spectra and gradients in surface coloration, and it appears to be widespread in our Solar System. Io, Europa, Enceladus, Iapetus, and Triton, in addition to all the planets, provide examples. On Earth, chemical cycling occurs through oxidation-reduction reactions that are actively maintained by organisms, though they can occur inorganically as well.

9.2.4 Energy Source

A flow of energy is required to organize the material of the living state and to maintain its low entropic state (Morowitz 1968), thus an external energy source is a minimal requirement for life. Light and the oxidation of inorganic compounds provide the energy for the Earth's biosphere, so wherever light and a means for sustaining oxidation-reduction cycles can be demonstrated, the possibility for maintaining life is present. Light is a highly effective form of energy on Earth, and phototrophic organisms are responsible for the high oxygen content in the Earth's atmosphere. Light from the Sun could serve as the principle energy source for living systems on all the inner planets of our Solar System, and possibly as far as the Jovian and Saturnian systems. Light is directly measurable using remote sensing and thus a good indicator for the theoretical possibility of photosynthesis. In general, energy gradients can fairly well be detected by remote sensing as detailed in Table 9.2. On Earth, all these energy sources are present. However, the availability of certain energy sources, such as heat, motion or pressure, does not necessary imply that life relies on them, but merely that the planetary body in question is active and meets one of the prerequisites for life.

Table 9.2 Remote detection of energy gradients (modified from Schulze-Makuch et al. (2002a)

Type of energy	Examples within the Solar System	Examples of remote detection
Light	Mercury to Saturnian system	Directly measurable
Chemical Cycling	Io, Europa, Iapetus, Triton	Molecular absorption spectra, surface reflectance spectra, imaging spectroscopy, polarimetry, radar measurements, detection of alteration minerals, gradients in surface coloration
Thermal	Mercury, Titan, Jovian satellites, Triton	Gradients of infrared radiation, thermal radiometry, infrared to visible spectral imaging, distance to Sun, mass sufficient for internal differentiation of planetary body (gravitational measurements), microwave radiometry to detect geothermal heat flows
Motion	Venus, Mars, Enceladus, Jovian satellites, Triton, Titan	Doppler imaging, radar inter-ferometry, electromagnetic indications of a conducting liquid (e.g. Europa), thermal and infrared imaging (volcanic movement)
Gravitational Tides	Jovian and Saturnian satellites, Triton	Visible evidence of surface fragmentation and resurfacing, microwave radiometry
Pressure	Venus, Titan, Gas Giant planets	Visible clouds, changing atmospheric patterns (e.g. Red Spot on Jupiter), direct measurement by robotic probes
Electromagnetism	Jovian and Saturnian system	Measurement of electromagnetic field fluctuations, detection of energetic particles

Thermal gradients are commonly available energy sources throughout the inner Solar System, and also among some larger satellites as shown from gradients of infrared and thermal infrared radiation (e.g., Io and Titan). Thermal energy can be derived from solar emissions or from radioactive heating if the mass of a planetary body is sufficient for differentiation into a radioactive core, as in the major Jovian satellites, and in Titan and Triton. Multispectral remote sensing methods are suitable for detecting rocks altered by hydrothermal heat and solutions, because their reflectance spectra differ from those of unaltered host rock. Thermal radiometry has been used, for instance, to determine that night-time temperatures on Europa are colder at the equator than at mid-latitudes for some longitudes, apparently due to latitude-dependent thermal inertia (Spencer et al. 1999, 2001). Thermal radiometry has also been used extensively on Io (Spencer et al. 2000) and Mars (Christensen et al. 2003).

Kinetic energy is possible wherever gas or fluids exist. Atmospheric motion can be detected directly from visible clouds that move, such as those of Mars, Venus, the gas giant planets, and Titan from visible and reflected infrared images. Speed and direction of moving objects can be determined by Doppler imaging at various wavelengths in an atmosphere or on a planetary surface. Active faults on which earthquakes may occur can be identified by observation of topographical features from space using radar (Tapponnier and Molnier 1977). Changes in the shape of a volcano caused by an expanding or contracting magma chamber can be determined by radar interferometry. Increased emissions of gas and heat of volcanoes can be identified with thermal infrared images and movements of plumes by images in the visible or infrared wavelengths. Electromagnetic measurements with the magnetometer instrument on board the Galileo orbiter were used to infer a conducting liquid in Europa's interior (Khurana et al. 1998; Kivelson et al. 2000).

Gravitational tides are exhibited by planetary bodies and major satellites that are in periodic alignments such as the Earth-Moon system, the Neptune-Triton system, and Jupiter and its four major moons. Significant tidal fluctuations in these sufficiently massive bodies are visible by the evidence of surface fragmentation and resurfacing of the planetary or lunar surface. For example, arcuate lineaments of vast extension on Europa have been interpreted as surface expressions of these enormous tidal forces (Hoppa et al. 1999).

Pressure gradients in an atmosphere can be inferred from banded cloud patterns and measurements of their rotational velocities by large storm systems such as Jupiter's famous Red Spot and less dramatic but similar examples on the other gas giants. Also, stratification as measured at Jupiter is another indicator of pressure gradients. Osmotic pressure gradients may also exist in planetary oceans that could be conducive for the support of life (Schulze-Makuch et al. 2002a). Those gradients are difficult to confirm directly, but could be inferred by a subsurface probe analyzing ocean chemistry, or possibly by remote determination of the solute content of a liquid eruption to the surface.

Electromagnetism is another energy source that occurs wherever eletromagnetic fields are traversed or induced (Schulze-Makuch and Irwin 2001). Jupiter's magnetospheric plasma corotates with the planet at a velocity of 118 km/s, thereby creating a strong magnetic field (Beatty and Chaikin 1990). Energetic ion and electron intensities throughout the Jovian magnetosphere were measured by the Galileo orbiter using an energetic particle detector. Saturn generates a less massive but still large magnetosphere that will be mapped in detail by the Cassini orbiter. More benign electromagnetic fields and their fluctuations can be measured directly using a magnetometer.

9.2.5 Liquid Medium

Finally, a liquid medium appears to be favorable for living processes because macromolecules and nutrients can be concentrated within a bounded internal environment without immobilizing interacting constituents. This assumption is usually taken to mean an aqueous medium, though organic compounds and water mixtures with ammonia and other miscible molecules can exist in liquid form at temperatures well below the freezing point of water. The possibility that life could exist in dense atmospheres has also been suggested (Grinspoon 1997; Sagan and Salpeter 1976; Schulze-Makuch and Irwin 2002b). There is for example both experimental and observational evidence for organic synthesis in Jupiter's atmosphere (Guillemin 2000; Raulin and Bossard 1985; Sagan et al. 1967). However, it is difficult to envision how the boundary conditions necessary for compartmentalizing the flow of energy and restraining the population of interacting molecules could be established under such conditions. However, once originated in a liquid medium, life could adapt to thrive in a gaseous environment (Schulze-Makuch et al. 2002b, 2004).

Major amounts of liquid water are known for certain only on Earth, but very likely exist as subsurface water on Mars in underground aquifers (Carr 1996; Greeley 1987; Malin and Edgett 2000a, b; Malin et al. 2006), and on Europa and Ganymede, where subsurface oceans are inferred from electromagnetic measurements from the Galileo orbiter (Khurana et al. 1998; Showman and Malhotra 1999) and from the presence of hydrated salt minerals on the surface (Kargel et al. 2000). Mixtures of water-ammonia-organic compounds are another possibility on cold planetary bodies, since these mixtures are liquid at much lower temperatures than water (Jakosky 1998). Theoretical models indicate the presence of subsurface stores that are liquid at extremely cold temperatures on Titan (Coustenis and Lorenz 1999; Fortes 2000) and possibly some of the satellites of Uranus and Neptune. Liquid water at or close to the surface can easily be detected by radar, gamma-ray spectrometry, and the absorption spectrum of water, but not when it is present in the deep subsurface or shielded by a thick layer of ice.

Liquid ethane and methane are assumed to be present on Titan's surface (Lorenz et al. 2003), and could provide an alternative solvent for life (Schulze-Makuch and Grinspoon 2005). Liquid sulfur compounds are inferred to exist on Io (Kieffer et al. 2000), and sulfur dioxide or hydrogen sulfide could play a role as solvent as well. Liquid compounds on a planetary surface can most easily be identified by visible and radar images of the erosional features that they cause.

9.3 Geoindicators for Life in our Solar System

Neither biosignatures nor geosignatures have been identified unambiguously on any planetary body beyond Earth to date, though the search should continue as resolution improves. Mars, Venus, and perhaps Ceres are the only other planetary bodies where life as we know it could plausibly be discovered by direct sampling in the foreseeable future. Thus, missions to Mars should remain a priority as they are currently with NASA and ESA, particularly lander missions (e.g. Viking 1 and 2, Pathfinder, Spirit, Opportunity, Phoenix, Mars Science Laboratory, and ExoMars). In addition, the ease of reaching Venus and the possibility of an atmospheric habitat suitable for life there argue for an atmospheric sampling mission to Venus (Schulze-Makuch and Irwin 2002b; Schulze-Makuch et al. 2005a, b). In the meantime and for the coming decades, search for habitats suitable for life beyond the terrestrial inner planets of our Solar System should focus on geoindicators such as those listed above. The current emphasis on visualization of surface features by the Mars Global Surveyor, Mars Odyssey, Mars Express, Mars Reconnaissance Orbiter, and the visual data collected from the Jovian system by the Galileo orbiter and the Saturnian system by the Cassini orbiter, are compatible with this strategy. These missions have the ability to detect energy gradients, organic chemicals, and near-subsurface as well as surface water.

The Huygens probe, which landed on Titan in January 2005, added detailed knowledge of that body’s atmosphere, weather, and surface chemistry. Because of the apparent similarity of its atmosphere to that of the early Earth, and its abundance of organic constituents, Titan should remain a high-priority target for exploration. In fact, geoindicators discussed here point to Titan as a suitable environment for life (Table 9.3), thus Titan should be considered a priority target of astrobiological significance (Shapiro and Schulze-Makuch 2009).

Attention should also be given to some of the less known satellites. Organic constituents appear to be present on Triton and possibly Iapetus. Triton and Titania show evidence of resurfacing that would indicate the generation of internal energy. The Cassini orbiter detected water plumes on Enceladus (Porco et al. 2006), indicating geothermal activity on this moon of Saturn. Similar evidence has accumulated for the dwarf planet, Ceres. Geoindicators indicative of the possibility of habitable environments throughout the Solar System are given in Table 9.3. A full discussion of the plausibility that life could exist elsewhere in our Solar System is presented in Chap. 11.

Table 9.3 Geoindicators for the possibility of life on the planets and major satellites of our Solar System based on current knowledge (modified from Schulze-Makuch et al. (2002a))

Major planetary body	Atmosphere	Thermal gradients/ chemical disequilib	Internal differentiation	Polymeric chemistry	Energy source	Liquid solvent
Mercury	No	Yes	Yes	No	LH	None
Venus	Yes	Yes	Yes	Yes?	LCHP	H_2O, H_2SO_4
Earth	Yes	Yes	Yes	Yes	LCHKGPM	H_2O
Moon	No	No	Yes	No	LG	None
Mars	Yes	Yes	Yes	Yes?	LCH	H_2O
Jupiter	Yes	Yes	Yes	Yes	LCHKPM	?
Io	No	Yes?	Yes	Yes	CLHMG	H_2S?
Europa	Yes*	Unknown	Yes	Yes	CHKGOM	H_2O
Ganymede	Yes*	Unknown	Yes	Yes	CHKGOM	H_2O
Callisto	Yes*?	Unknown	Yes	Yes?	CHKGOM	H_2O
Saturn	Yes	Yes	Yes	Yes	CHKPM	None
Tethys	No	Unknown	No	Yes?	M	H_2O?
Dione	No	No	No	Yes?	M	H_2O?
Rhea	No	Unknown	No	Yes?	M	H_2O?
Enceladus	No	Yes	No?	Yes	CHKM	H_2O
Iapetus	No	Yes?	No	Yes	CM	H_2O?
Titan	Yes	Yes?	Yes	Yes	CHM	C_2H_6, CH_4, NH_3-H_2O?
Uranus	Yes	Yes?	Yes	Yes?	CHKPM	None
Titania	No	Yes?	Yes?	Yes?	CHG	H_2O?
Ariel	No	No?	No	No?	C?H?	None?
Miranda	No	No?	No	No?	C?H?	None?
Umbriel	No	No?	No	No?	C?H?	None?
Oberon	No	No?	No	No?	C?H?	None?
Neptune	Yes	Yes?	Yes	Yes?	CHKPM	None?
Triton	Yes*	Unknown	Yes?	Yes	CHGO	H_2O/ NH_3/ N_2?
Pluto/ Charon	Yes*	Yes?	Yes?	Yes?	CG	H_2O/ NH_3/ N_2?
Comets and Asteroids	No	No	Some	Some	L for some	None

Legend: L = light energy, C = chemical cycling, H = heat energy, K = kinetic energy (motion), G = gravitational energy (tides), P = pressure energy, O = osmotic gradients (in a possible high-salinity subsurface ocean), M = electromagnetic energy. Asterisks indicate a protective ice shield and trace atmosphere. Question marks indicate uncertainty, but with our estimate of probability in the indicated direction

9.4 Chapter Summary

The search for extraterrestrial life everywhere but on our planetary neighbors (Mars, Venus, and possibly Ceres) is limited for the foreseeable future by our inability to obtain physical samples. Therefore, information that can only be obtained by remote sensing and robotic probes will for now provide the only clues concerning the existence of life elsewhere. Biosignatures, which are reliable and clear indicators for specific life processes, are critical for identifying planets inhabited by ancient or current life. The search parameters we have proposed emphasize the importance of detecting the presence of physical and chemical gradients of all kinds, because of their potential for generating free energy. Other geoindicators that would enhance the prospects for life include evidence for polymeric chemistry in association with chemical cycling, the presence of an atmosphere or ice shield, sufficient mass for endogenic heating, and the availability of a liquid that may act as a solvent to enhance chemical reactions. Also, any unusual topographical features or surface patterns that cannot be easily explained by well understood geological and geochemical processes should be regarded as evidence for the possibility of environmental changes induced by living systems.

Chapter 10
Life Detection: Past and Present

In this chapter we go beyond the search for geoindicators and biosignatures that might *point to* the presence of life, with the specific aim of *detecting* and *confirming* the presence of life. First, we review the results and interpretations of the Viking mission—the only life detection experiment ever conducted on another planetary body to date. We also examine the claim of fossilized life in the Martian meteorite ALH84001, which is instructive for the problematic issue of what evidence constitutes a positive detection of extraterrestrial life. Finally, we will provide a brief overview on the development of current life detection methods and their likely implementation.

10.1 The Viking Mission

The Viking program, consisting of two orbiters with landers, Viking 1 and Viking 2, was the most ambitious mission ever sent to Mars. It was a major milestone in the exploration of our Solar System, following the human landings on the Moon, and is the best example to date of human attempts "to boldly go" in search for life on another world. Despite the unresolved controversy about the Viking life detection experiments, the mission was highly successful in providing an enormous amount of information about the environmental conditions on Mars.

10.1.1 The Viking Landers

Viking 1 was launched on 20 August 1975 atop a Titan III-E rocket with Centaur upper stages, followed two and a half weeks later by the launch of Viking 2. Inserting into orbit around Mars about 10 months later, the Viking orbiters functioned flawlessly to transport the landers, performed reconnaissance to locate and certify

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_10

landing sites, and conducted scientific investigations including imaging the surface, measuring atmospheric water vapor, and obtaining radio science data. About a month after arrival, on 20 July 1976, the Viking 1 lander disattached from its orbiter and touched down at 11:56:06 UT in the western Chryse Planitia region. Transmission of the first surface image began 25 seconds after landing. The Viking 2 lander followed a month and a half later, touching down about 200 kilometers west of the crater Mie in Utopia Panitia on 3 September 1976. The landers carried instruments to study the presumed biology, chemical compositions, meteorology, seismology, magnetic properties, and physical properties of the Martian surface and atmosphere. The team of scientists, selected by NASA in 1969 to plan and conduct investigations on the Viking spacecraft, included Wolf Vishniac, Harold ("Chuck") Klein, Joshua Lederberg, Alexander Rich, Norman Horowitz, Vance Oyama, and Gilbert Levin. The NASA team was aware that the Viking biology experiments could only detect certain types of life. However, the media heralded the Viking biology tests as experiments designed to prove whether life exists on Mars or not. Although the biology experiments were undoubtedly the crown jewel of the mission, the biology payload weighed only 15.5 kg, consisting of three separate experiments, with a Gas Chromatograph Mass Spectrometer (GC-MS) to detect organic molecules.

In the *Gas Exchange Experiment* Martian soil samples were carefully cleansed with helium, and then incubated with carbon dioxide, inert gases, and water. The instrument sampled the atmosphere of the incubation chamber periodically for concentration of several gases including carbon dioxide, oxygen, nitrogen, hydrogen, and methane. The mission scientists believed that metabolizing organisms would either consume or release at least one of the measured gases. The Gas Exchange Experiment was designed to be conducted in two different modes using the same equipment. In the humid mode, Martian surface samples were incubated in the presence of carbon dioxide and water vapor, based on the assumption that substrates might not be limiting on Mars, but that biological activity is dormant in these samples until enough water becomes available in the environment. The second (dry) mode assumed the presence of heterotrophic microbes on Mars that feed on organic molecules under dry conditions.

In the *Labeled Release Experiment* a sample of the Martian soil was inoculated with water and nutrient solution containing glucose with ^{14}C, a heavy, radioactive isotope of carbon. If any heterotrophic organisms feeding on simple organic compounds would be present, they would consume the nutrients and release ^{14}C containing carbon dioxide, which would easily be detected by a radioactivity counter. The ambient environment from which the soil was taken was anaerobic (oxygen-poor) and devoid of liquid water.

The *Pyrolytic Release Experiment* looked for evidence of photosynthesis by incubating Martian soil with light, water, and a carbon-containing atmosphere of either carbon monoxide or carbon dioxide. The gases were enriched with radioactive ^{14}C. If photosynthetic organisms were present on Mars resembling plants or cyanobacteria on Earth, then these organisms would incorporate some of the carbon as biomass by carbon fixation. After several days of incubation, the experiment removed the gases, heated the remaining soil to a sterilizing temperature of 650 °C,

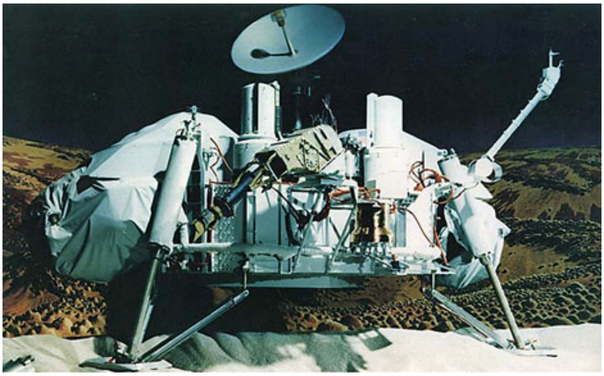


Fig. 10.1 Viking lander (image from NASA)

and collected the product to count radioactivity. If gaseous ^{14}C had been converted to biomass by carbon fixation, it would be vaporized during heating, and the radioactive counter would detect it.

The GC-MS in the Viking instrument load was designed to separate vapor components and to measure the molecular weights of chemicals. Thus, it could separate, identify, and quantify a large number of different chemicals, including organic compounds.

The operational life time of the Viking 1 lander was more than 6 years, from July 1976 to November 1982, while the Viking 2 lander operated for about 3 1/2 years. The Viking lander is shown in Fig. 10.1.

10.1.2 Mission Preparation

Counter to some arguments or perceptions, the Viking mission was well prepared even though budget cuts reduced its capabilities. A 4th planned biology experiment, the so-called "Wolf Trap", which was designed to monitor a vial of water for increasing turbidity after a soil sample was placed in it, was cancelled, mainly due to payload constraints.

Countless samples were tested before flight by the Viking instruments using a variety of microbial cultures, testing out the widest array of microbial populations that were available. Also, soil samples from widely differing geographic regions were obtained and tested, including samples from the Antarctic, the Gobi Desert, and Alaska. Large amounts of data were collected, analyzed, and interpreted. The principal investigators of the biology experiments agreed in advance how they would decide on a positive and negative outcome of the life detection experiments. Detectors, chromatograph columns, and other actual flight components were extensively tested for their scientific as well as their engineering characteristics. Both the Gas Exchange and Labeled Release Experiments were tested against a wide variety of terrestrial soils. The Viking team detected the presence of microbes in most samples when they were incubated under terrestrial conditions. When the soil samples were incubated under Martian environmental conditions similar responses were seen but with a prolonged lag period. The lag period, however, was not necessarily representative of possible Martian organisms, since it reflected the response of Earth organisms to the very different conditions on Mars. The Gas Exchange Experiment of the Viking mission was tested using sixteen different terrestrial soils (Oyama 1972). Fourteen of the sixteen soils showed positive gas exchanges related to microbial metabolisms, both under aerobic (oxygen-rich) and anaerobic (oxygen-poor) conditions. However, in retrospect, the two negative samples from extreme environments, including one from Antarctica, almost certainly contained organisms, but the Viking Gas Exchange Experiment was not able to detect it. There was another intriguing result from the test series as well. The team realized that false positives could occur when nutrient medium made contact with Martian soil. This was particularly evident if the elements calcium, cadmium, iron, lithium, magnesium, and zink were involved—some of which were expected to be common in Martian soil. Oyama (1972) concluded that these reactions would occur only early during the first cycle of the experiment and dissipate quickly during repeated rechargings. Especially, the production of hydrogen and methane gas accompanied by a relatively fast rate of carbon dioxide disappearance could be a nonbiological consequence of initial contact between Martian soil and the aqueous nutrient medium. This left open the possibility of other chemical and physical phenomena that could affect gas release rates. Thus, signs of potential trouble for the interpretation of the anticipated life detection results were present from the beginning.

10.1.3 Mission Results

The initial results from both landers were very exciting, but also very confusing. All three experiments observed changes that indicated the possible presence of life, although the expected signals were not always as large as expected, and often tapered off over time, casting doubt on a biological explanation:

First, the *Gas Exchange Experiment* was conducted in the humid mode. Results indicated that some carbon dioxide and nitrogen gas (N_2) was desorbed from the soil, and there was a surprising and rapid accumulation of oxygen after humidification. Oxygen release upon humidification had not been observed before with samples either from Earth or the Moon, and is still puzzling today. After the initial rapid gas release, later addition of water to the soil caused no further release of oxygen. In another experiment that was conducted in the humid mode at a sterilizing temperature of 145 °C, oxygen was again released from the sample, suggesting a chemical explanation for the observed phenomenon. The source of the N_2 is unclear. No nitrogen gas was added to the soil, but the nutrient contained nitrogen-containing compounds such as amino acids and nitrates.

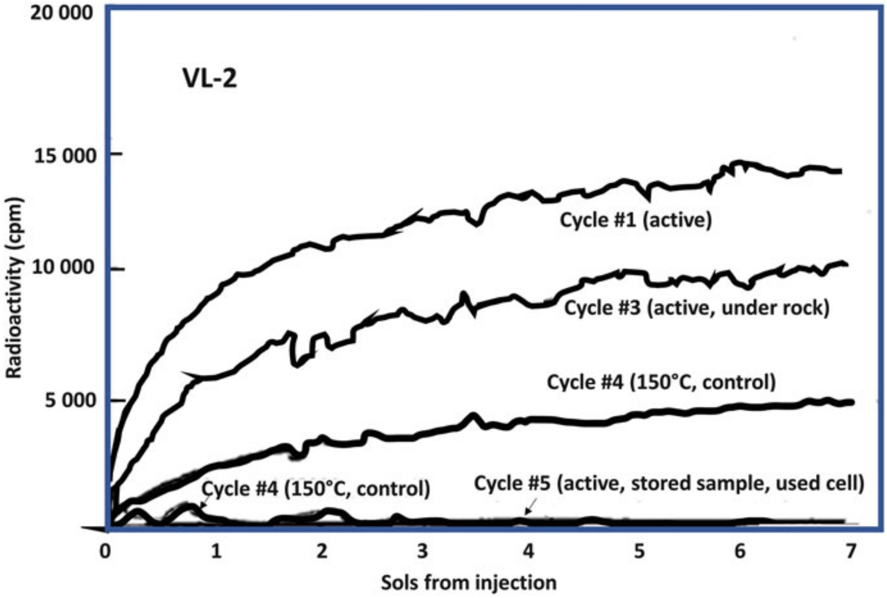


Fig. 10.2 Radioactivity evolved in the Labeled Release Experiment following the first injection of radioactive nutrient to each analysis cycle in the Viking 2 lander. A fresh sample was used for each cycle except cycle 5 which used a sample stored approximately 84 Sols (Martian days) at 7 °C prior to injection. The sample used in cycle 3 was obtained from under a rock. Cycles 1, 3, and 5 were active sequences, whereas cycles 2 and 4 were control sequences in which the samples were heated for 3 h at approximately 51.5 °C and 46 °C, respectively, prior to nutrient injection. All data have been corrected for background counts observed prior to injection (figure courtesy of Gilbert Levin, Spherix, Inc.)

In *the Labeled Release Experiment* the addition of an aqueous solution of dilute radioactive organic compounds to Martian samples resulted in a rapid release of labeled gas (Fig. 10.2). The process was virtually eliminated by prior heating of the samples at a sterilizing temperature of about 160 °C for 3 h, and was substantially reduced by heating to only 45–50 °C. As in the case of the Gas Exchange Experiment, upon prolonged incubations, there was a slow continued release of labeled gas after the initial rapid reaction was over. Also, each time additional liquid was added, about 30% of the labeled gas in the test cell went into solution. In contrast to the results obtained in the Gas Exchange Experiment, storage of the samples for 2–4 months essentially eliminated the agent responsible for the rapid decomposition of the nutrient in the Labeled Release Experiment.

In the *Pyrolytic Release Experiment* significant positive reactions were found at both Viking landing sites (Table 10.1). Prior heating of a sample at a sterilizing temperature of 175 °C for 3 h drastically cut down the reaction, while heating at 90 °C had no deleterious effects. The data also suggested that the observed reaction was proceeding better in light, but this conclusion was based on comparing reactions under “light” conditions on one lander site with “dark” conditions on the other.

Table 10.1 Data from the Pyrolytic Release Experiment (Horowitz et al. 1977). The Conditions Column indicates whether the lamp was on or off, whether or not water vapor was injected, and whether the soil sample was heat-sterilized (control is 175 °C for 3 h). The radioactivity of Peak 2 column represents organic matter synthesized from the labeled gases

Experiment	Conditions	Peak 2 (count/min)
Chryse 1	Light, dry, active	96 ± 1.15
Chryse 2	Light, dry, control	15 ± 1.29
Chryse 3	Light, dry, active	27 ± 0.98
Chryse 4	Light, dry, active	35 ± 1.6
Utopia 1	Dark, dry, active	23 ± 1.7
Utopia 2	Light, wet, active	2.8 ± 0.92
Utopia 3	Dark, dry, active	7.5 ± 2.5

Storage did not reduce the capacity of the Martian samples to yield statistically positive results. In one experiment the soil sample was first humidified for several hours, after which the test cell was heated and vented to dry out the sample. This treatment was intended to remove, or at least greatly decrease any major postulated oxidants such as superoxides and hydrogen peroxide. However, even after this treatment the Martian samples still yielded a positive result.

The GC-MS instrument on board the Viking landers did not detect conclusively any indigenous organics in any of the samples tested, at the levels down to what was thought parts per billion. A much later analysis indicated that the Viking GC-MS was much less sensitive than originally thought (Navarro-González et al. 2006).

As pointed out by Harold Klein, the lead scientist of the biology payload in 1977, the Viking experiments were predicated on the assumption of a widespread distribution of Martian biota that was reliably sampled at the two Viking landing sites. If, however, life were to exist on Mars in highly localized habitats, and perhaps constrained by unfamiliar metabolic limitations, the ambiguous results of the Viking experiments could well have been obtained, with inconclusive evidence for the presence of life on Mars.

10.1.4 Interpretation of Mission Results

After several months of receiving data from the Viking landers, controversy erupted within the Viking Program team. Harold Klein and most other participating scientists believed that the results from the experiments, taken all together, could best be explained by non-biological chemical reactions. Gilbert Levin, principal investigator of the Labeled Release Experiment, deviated from this opinion, arguing that the Labeled Release results were entirely consistent with a possible biological interpretation (Levin and Straat 1977) based on

1. the uniform production of gas from the Labeled Release nutrient when it was added to Martian soil at both lander sites;

2. a net loss of radioactive gas following the addition of more nutrient after the reactions had approached completion;
3. the lack of labeled release following direct exposure of the sample to visible or ultraviolet light on the Martian surface prior to placing it in the test cell (which would have been the case if oxidants produced by light were the reacting agent rather than a biological process); and
4. the reactant in the Martian soil being completely unreactive at the sterilizing temperature of 460 °C, whereas, in contrast, exposure to 18 °C for two Martian days did not inhibit the reaction.

Gilbert Levin also pointed out that the Labeled Release Experiment was the most sensitive test for the detection of life, and that by prior consensus only one experiment with a positive outcome would be needed to count as a positive sign of life. Nonetheless, scientific consensus shifted toward a non-biological explanation. The apparent inability of the GC-MS to detect significant amounts of organic molecules in the Martian soil was particularly difficult to explain if Martian microbial metabolism was responsible for the positive results seen by the Labeled Release, Pyrolytic Release, and Gas Exchange Experiments. Harold Klein, the lead scientist of the biology payload, acknowledged humbly that all of the Viking biology experiments deviated to some extent from ambient Martian conditions and stated that “while we have obtained significant and fascinating data in the Martian experiments, we may not have hit upon the proper conditions to elicit evidence of Martian metabolism” (Klein 1977). Various interpretations continued to be offered nonetheless. Klein (1978) compared the merits of various chemical and biological explanations for the detailed results of each experiment. He concluded that, while some of the results were consistent with a biological interpretation, most were not. Interestingly, the experiment that he deemed to be closest to a biological explanation was the Pyrolytic Release Experiment (Table 10.1). Most scientists, however, focused on the Gas Exchange Experiment and ignored somewhat the more challenging results from the Labeled Release and Pyrolytic Release Experiments.

A number of scientists proceeded to advance the idea that inorganic compounds were responsible for the observed behavior (Benner et al. 2000; Klein 1999; Mancinelli 1989; Quinn and Zent 1999; Yen et al. 2000), most of them championing some kind of very strong oxidant that would react with the added water to produce oxygen and hydrogen, and with the nutrients to produce carbon dioxide (Ballou et al. 1978; Klein 1978; Oyama et al. 1977). However, the oxidant would have to be a chemical unfamiliar on Earth, because the presence of humidity in Earth’s atmosphere would immediately destroy any oxidant strong enough to react with water. Unfortunately, none of the successful follow-on missions after Viking was equipped with a suitable sensor for the detection of oxidants. Another interesting suggestion was advanced by Nussinov et al. (1978) who argued that oxygen gas might physically be trapped in soil micropores. The trapped gas would have to be created by the direct interaction of solar UV radiation with the soil matrix, however, and the positive response in the Labeled Release Experiment on the sample from underneath a rock at the Viking 2 landing site is a problem for this hypothesis and similar ones (Cycle 3 in Fig. 10.2).

Zent and McKay (1994) pointed out the problems with oxidant reaction explanations under the environmental conditions on Mars. They concluded that none of the hypotheses in the literature is free of serious objections, many having to do with the instability of putative oxidants in the presence of heat, light, or atmospheric carbon dioxide. Or, the suggested hypotheses would require elaborate formation mechanisms for which there is no evidence. However, Zent and McKay (1994) also rejected the biological explanation, believing rather that the results obtained by Viking can best be explained by some kind of heterogeneous surface chemistry, yielding one or more types of oxidizing surfaces on the Martian regolith particles. Unfortunately, the Mars Oxidant Experiment on board the Russian Mars ’96 mission, which was to have tested the supposition of a reactive, oxidizing surface on Mars, was lost when the mission failed soon after launch in 1996.

In 2007 a new biological explanation for the Viking results was advanced by Houtkooper and Schulze-Makuch (2007). They suggested that Martian organisms, if they exist, might utilize a water-hydrogen peroxide (H_2O-H_2O_2) mixture rather than water as an intracellular liquid. This adaptation would have the particular advantages in the Martian environment of providing a low freezing point, a source of oxygen, and hygroscopicity, and would provide a logically consistent explanation to the Viking results (Table 10.2). Hygroscopicity would be an especially useful trait since it might allow the suggested organisms to scavenge water molecules directly from the Martian atmosphere. However, at the same time it would make them extremely vulnerable to abundant liquid water (as used in some of the Viking experiments).

H_2O_2-H_2O solutions are mostly known as disinfectants and sterilizing agents on Earth, but some microbial organisms (e.g., certain *Streptococcus* and *Lactobacillus* sp. (Eschenbach et al. 1989) and even human cells (e.g., macrophages, endothelial cells) produce hydrogen peroxide, while other microbes utilize H_2O_2 (e.g., *Neisseria sicca*, *Haemophilus segnis*; Ryan and Kleinberg 1995), and some others such as the microbe *Acetobacter peroxidans* use H_2O_2 in their metabolism (overall reaction $H_2O_2(aq) + H_2(aq) \leftrightarrow 2H_2O$; Tanenbaum 1956). Hydrogen peroxide is in fact widely used by organisms. H_2O_2 is included in many cells in nanomolar amounts and has an ancient relationship to metabolism, because many cells contain the enzyme hydrogen peroxide catalase.

Schulze-Makuch et al. (2008) simulated the experiments to be conducted by the TEGA instrument of the Phoenix lander to test the hydrogen peroxide-water hypothesis. They used differential scanning calorimetry to analyze phase transitions and thermodynamic properties of various compounds including pure water, various concentrations of hydrogen peroxide solution, Fe_2O_3, TiO_2, tetrasodium pyrophosphate ($Na_4P_2O_7$), phenacetin ($C_{10}H_{13}NO_2$), quartz sand, Martian regolith simulant soil, and combinations thereof. $Na_4P_2O_7$ and phenacetin are stabilizers of H_2O_2 and were included in the test set, because if the Martian H_2O_2 would be mostly of biogenic nature, a chemical stabilizer would have to be invoked to control the reactivity of the hydrogen peroxide. The addition of a chemical stabilizer in the tested H_2O_2 solutions was identified in the experimental thermograms and may serve as a biomarker for hydrogen peroxide-water supported life for the Phoenix and other future missions

Table 10.2 Comparison of chemical hypothesis and the biological H_2O_2-H_2O hypothesis based on Viking observations (modified from Houtkooper and Schulze-Makuch 2007)

Observation	Chemical explanation	H_2O_2-H_2O hypothesis
Lack of identified organic molecules	Organics were oxidized to non-volatile salts of benzenecarboxylic acids, and perhaps oxalic and acetic acid (Benner et al. 2000).	Upon death of organisms, organics were spontaneously oxidized by intracellularly bound H_2O_2 with little or no organic residue—a notion also supported by the release of 50–700 ppm of CO_2 as measured by the Viking GC-MS.
Lack of identified oxidant	An as yet unidentified mechanism on Mars produces H_2O_2 or other oxidants with no analog on Earth.	H_2O_2 in the H_2O_2-H_2O mixture is part of the biochemistry of putative Martian organisms.
Release and partial resorption of O_2, CO_2, and N_2 in Gas Exchange Experiment	Evolution of O_2 on humidification involved one or more reactive species such as ozonides, superoxides, and peroxides (Oyama and Berdahl 1977). CO_2 production in the wet mode could have been related to the oxidation of organic nutrients, with N_2 release related to initial N_2 desorption from soil by water vapor and subsequent resorption in liquid water (Oyama et al. 1977).	Release of O_2 (and possibly CO_2 to lesser degree) resulted from energy-producing metabolism. Also possibly produced by decomposition of dying Martian biota upon humidification. N_2 decrease could have been due to biological fixation exceeding the amount due to physical sorption.
Synthesis of organic material in Pyrolytic Release Experiment	Instrument malfunction, incorporation of ^{14}CO into carbon suboxide polymer preformed on the Martian surface, and reduction of ^{14}CO by H_2O_2 in the surface material (Horowitz et al. 1977).	Putative organisms were able to metabolize and synthesize organic compounds before they died from hyperhydration.
Results of Labeled Release Experiment	Inorganic process simulated by laboratory tests on Earth using inorganic oxidants and clay minerals, except for decrease of responses after storage at elevated temperatures (Klein 1999).	Limited metabolism (Levin and Straat 1977, 1981) before the organisms died due to hyperhydration, osmotic pressure, and/or heat shock.

(Schulze-Makuch et al. 2008). Unfortunately, the Phoenix mission did not provide a test of that hypothesis. Hopefully, it can be tested in a future mission.

The argument convincing most mission scientists at the time that the Viking life detection experiments yielded a negative result was the apparent failure of the GC-MS to find any indigenous Martian organic compounds (Biemann 1979). Only a very low amount of chlorinated organic compounds (chloromethane and dichloromethane) were detected, and these were interpreted as contamination (Navarro-Gonzalez et al. 2010). As Gerald Soffen, project scientist of the Viking program, put it starkly when trying to make sense of the incoming, contradictory

Viking results: “No bodies, no life!”; meaning if we don´t find organic compounds, then there can’t be life. However, today we know this interpretation and the resulting conclusions were most likely wrong. The Curiosity rover has also detected chlorinated organics on Mars, which most likely formed indigenously as the result of a reaction with strong oxidants (Freissinet et al. 2015). Perchlorates detected by the Phoenix mission (Hecht et al. 2009) and the Curiosity rover (Glavin et al. 2013) were likely involved in these reactions. Perchlorates have similar properties to hydrogen peroxide—specifically, a drastic lowering of the melting point of water. They are hygroscopic and energy-rich; so in principle, a water-perchlorate solution could serve instead of a water-hydrogen peroxide solution as a medium for life processes in the Martian environment (Houtkooper and Schulze-Makuch 2010). Perchlorates are also a constituent of recurrent slope lineae on Mars. These dark, wet-appearing features on steep Martian slopes (Ojha et al. 2015), are thus of high astrobiological interest. In retrospect, many scientists now interpret the chlorinated organic compounds detected by Viking’s GC-MS as a valid indication of indigenous Martian organics, and not contamination. Future samples should provide more certainty, because methods have been developed, based on stable isotope signatures of chloromethane, that enable a distinction between terrestrial contamination, meteoritic infall, and indigenous Martian sources (Keppler et al. 2014). One can easily imagine how the pendulum of scientific and public opinion might have swung in a different direction if these insights had been recognized at the time of Viking. Gil Levin, for that matter, is still convinced that the Labeled Release experiment of the Viking mission detected life, and continues to advocate for this interpretation of the results (Levin and Straat 2016).

Though widely perceived as a disappointment and the cause of a 20-year hiatus in the continued exploration of Mars, the Viking Mission in retrospect stands as a valiant testimony to the creativity and resourcefulness of the first human attempt to detect life on another world. Given the limitations of technology, distance, and lack of knowledge about the Martian environment at the time, the ambiguous results from the Viking landers are hardly surprising. Even today, the view that Viking may have provided the first evidence for life on Mars cannot be discounted.

10.2 Martian Meteorites and Evidence for Ancient Life

On an early August day in 1996 television lights illuminated the South Lawn of the White House. President Clinton, with NASA administrator Dan Goldin at his side, read a carefully crafted statement on the significance of the announcement to be made. An historic press conference had started, in which David McKay from the NASA Johnson Space Center and his colleagues announced to the world that they believed they had found evidence of ancient life in a Martian meteorite. The claim for ancient life on Mars from this potato sized meteorite, ALH84001, changed the field of astrobiology, and brought the discussion of possible extraterrestrial life back to the front burner of the public’s mind and the agenda for space science.

10.2.1 The Claim of Fossilized Life in Martian Meteorite ALH84001

The meteorite on which the claim of evidence for ancient life was based had been found in the Allen Hills of Antarctica in 1984 during a National Science Foundation search for meteorites in the Antarctic, hence the name, ALH (Allen Hills) 84 (1984) 001 (number 001). Visually the most unusual rock collected during the 1984–1985 field season, it was at first incorrectly classified as a rare achondritic meteorite and filed away. It took another 9 years before it was correctly identified as a member of the SNC (shergottite, nakhlite, chassignite) group of meteorites (Mittlefehldt 1994; Miura et al. 1995). The following picture appeared: ALH84001 is one of the oldest meteorites of the Solar System. It had formed a few kilometers deep within the congealing crust about 4.5 billion years ago, shortly after Mars itself had formed. Later, it was broken by the shock of one or more asteroid impacts on the surface about 3.6 billion years ago when Mars was warmer and wetter. Groundwater likely seeped through the fissures and fractures and filled them with carbonate material. Another huge asteroid must have struck Mars about 16 million years ago with such a tremendous force that it ejected parts of the Martian surface into space free of the gravitational pull of the planet. One of those pieces was ALH 84001. It remained in space until about 13,000 years ago when it was pulled in by Earth's gravity and fell onto Antarctica, where it was found in 1984. The dates are confirmed by a variety of radioactive isotope dating techniques. Although many thousands of meteorites have been recovered, only very few of them have been identified as Martian in origin (slightly over a hundred at the time of this writing). The link to Mars is made by mineral geochemistry of the meteorites, and particularly by the gas content trapped in tiny pockets (Mittlefehldt 1994; Miura et al. 1995). The Viking and later rover missions revealed a very distinct gas mix on Mars that differs from any known atmosphere elsewhere.

McKay et al. (1996) made their case for biology in ALH84001 based on (1) carbonate globules and features within the meteorite that resembled terrestrial biogenic carbonate structures, (2) magnetite and iron sulfide particles that could have resulted from oxidation and reduction reactions known to be important for microbial organisms on Earth, (3) the presence of complex organic compounds, specifically polycyclic aromatic hydrocarbons (PAHs), that were associated with the carbonate globules, and conceivably could represent breakdown products of organisms, and (4) ovoid and bean shaped structures that resemble fossilized ancient microbes (Fig. 10.3). They acknowledged that no single one of their observations was itself conclusive for the existence of past life on Mars, due to alternative possible explanations for each of the phenomena. However, they argued that the totality of their observations considered collectively, particularly in view of their spatial associations, constituted evidence for primitive life on early Mars.

There were several important implications regarding the organic material within ALH84001. First, the organic compounds provided proof that in fact organic material existed on Mars—one of the main arguments against a biological explanation for the Viking experiments. Second, the organic material was in the parts per million range, which is low, but much higher than the one part per billion range or lower for organic carbon detected in other meteorites found in Antarctica, or the parts per trillion range expected from contamination. Also, the fact that the organic carbon content increased towards the center of the meteorite was consistent with a fusion crust caused by an Earth atmospheric entry. Organic matter derived from contamination would have been more common near the outside than inside the meteorite. Thus, the organic compounds were presumed to be indigenous and therefore from Mars.

Details are important for this type of investigation. McKay et al. (1996) noted that the carbonate globules tended to be disc-shaped rather than spherical and were flattened parallel to the fracture surface indicating that the carbonates formed in the restricted width of a thin fracture by aqueous processes. The authors claimed that stable oxygen isotope data suggested that the carbonates formed at temperatures between 0° and 80 °C, compatible with a biogenic formation. They noted that the larger globules had calcium and manganese-rich cores, which were surrounded by alternating iron and magnesium-rich bands possibly containing iron sulfide—another observation consistent with biological processes. More importantly, they detected single-domain magnetite crystals in ALH84001 with no structural defects and without any detectable amounts of other elements. McKay et al. (1996) explained the co-existence of magnetite and iron sulfides within partially dissolved carbonate by biological processes, which are known to operate under extreme disequilibrium conditions. The importance here is that precipitation of iron sulfides and magnetite within individual bacterial cells is known to occur and that the magnetite particles in ALH84001 are chemically, structurally, and morphologically very similar to magnetite particles known to occur in some Earth organisms. This type of magnetite had also been found in ancient limestones on Earth, where it has been interpreted as biogenic in origin. Finally, and most controversially, was the claim that the jelly-bean shaped and threadlike structures in the images represent fossilized microbial organisms (Fig. 10.3). The researchers acknowledged that these structures were much smaller than typical microbes on Earth, and pointed to the more recent discovery of very small microbial organisms on Earth, named nanobacteria, by Bob Folk from the University of Texas and others, which have

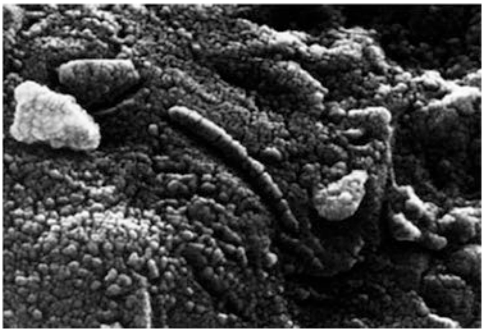


Fig. 10.3 The image that went around the world in 1996. Putative Martian microbe (segmented worm-like center structure) in meteorite ALH 84001. Image from NASA

about the same size as the structures in the meteorite. They pointed out that these objects were about 380 nanometers long and thus big enough to pack in all the cellular components needed for a typical terran microbe to function. Some of the other structures claimed to be of biological nature were much smaller, 20–170 nanometer inside, and interpreted to represent fragments or appendages, similar to the ones found in deep basalt samples near the Columbia River in Washington State (USA).

10.2.2 A Cold Reception by the Scientific Community

McKay et al. (1996) admitted that none of the lines of evidence provided a conclusive case for Martian life. Not surprisingly, therefore, each claim was soon met by a host of scientific critiques and counterclaims, ranging from disputes over the formation temperature of the meteorite, to the evidence for fossilized microbes and biogenically generated magnetite.

10.2.2.1 Formation Temperatures of ALH84001

The question of formation temperature is critical, because if the carbonate globules within ALH84001 formed above sterilization temperatures, the claim of ancient life in the Martian meteorite would be off the table. Several arguments were advanced in favor of a sterilizing formation temperature. These included the absence of water-rich minerals in the carbonates, an elemental composition indicating formation reactions most likely between hot (>650 °C) CO_2-rich fluid and host rock during an asteroid impact (Harvey and McSween 1996), the presence of whiskers and platelets consistent with vapor phase growth and a formation temperature of 500−800 °C (Bradley et al. 1996), and a formation model by Leshin et al. (1998), which indicated that the carbonates in ALH840001 formed either at temperatures of 125° to above 250 °C, or above 500 °C, both inconsistent with a biological explanation.

Their claims, however, were countered by other studies. Kirschvink et al. (1997) noted that heating can re-magnetize or erase previous magnetization, but mineral grains from the crushed zone of ALH84001 revealed a stable natural remnant magnetization indicating that the minerals had not been heated significantly since the formation of the internal crushed zone about 4 billion years ago. Since the carbonate globules formed later, they concluded that they must have formed at low temperatures. Valley et al. (1997) reported that the isotopic variations and mineral compositions of ALH84001 offered no evidence for high temperature (>650 °C) carbonate precipitation. Instead, they suggested non-equilibrium processes at low temperatures. Warren (1998) argued that the high-temperature models for the origin of carbonates in ALH84001 are implausible due to the absence of alterations in the mineral grains. He also dismissed the hydrothermal model, pointing to the lack of secondarily formed water-rich silicates in ALH84001. Instead, he suggested that the carbonates formed either as evaporate deposits from floodwaters that percolated through the fractures of the meteorite, or as a Martian form of calcrete, which forms as calcite is dissolved in groundwater and, under drying conditions, is precipitated when the water evaporates at the surface. Kent et al. (2001) used chemical diffusion rates of magnesium and calcium to suggest formation of carbonates in ALH84001 at low temperatures, most probably less than 200 °C. They also pointed out that carbonate zoning at formation temperatures in excess of 600 °C could only occur within the uppermost melt-rich portions of an impact structure.

The question appeared to be resolved when Eiler et al. (2002) reported that there were at least two distinct carbonate populations within ALH84001: one consisting of low-temperature water precipitates and the second produced by shock melting of the first due to asteroid impact. Romanek et al. (2002) confirmed the presence of at least two chemically distinct carbonates and claimed that the oxygen isotope composition of the carbonates indicated that they were precipitated from a low-temperature fluid in the Martian crust. One uncertainly during these heated discussions was the apparent lack of carbonate rocks on the surface of Mars. Their presence, however, was confirmed a few years later (Morris et al. 2010). In summary, none of the arguments either for or against a formation temperature consistent with the biogenic origin of carbonates is conclusive.

10.2.2.2 Fossil-like Structures in ALH84001

The argument for a fossil microbe in ALH84001 (Fig. 10.3) has always been tenuous. Recognizing fossil evidence is even an extremely contentious issue for early life on Earth (Brasier et al. 2002; Schopf 1993). The rod-like structure in ALH84001 clearly resembles a microorganism of some sort; but Bradley et al. (1997) claimed that these structures were just as likely to be laboratory artifacts from the deposition of conductive heavy-metal coating, a charge heavily disputed by the McKay group. One of the strongest initial arguments against the biological origin of these structures was their much smaller size than typical Earth organisms. However, as pointed out by McKay et al. (1996), recent discoveries have in fact revealed the existence of such very small organisms on Earth.

The term nanobacteria was first used by Folk (1993) to describe 10–200 nm sized objects observed in geological materials. Mineral forming nanobacteria have been isolated from human kidney stones, blood and blood products, among various other media (Ciftçioglu et al. 1999; Folk 1999; Kajander et al. 1997; Kajander and Ciftçioglu 1998; Kirkland et al. 1999; Schieber and Arnott 2003). Kajander et al. (1997) described coccoid cell-walled organisms with a size of 80–500 nm occurring in clusters and producing a biofilm containing carbonate and hydroxyl apatite. They found that the growth rate of the observed nanobacteria was about one hundredth of ordinary bacteria, that they contain DNA, and noted their high resistance to heat, gamma-radiation, and antibiotics. Their claim is highly controversial though, because most scientific groups were not able to reproduce their results, particularly of finding DNA associated with the nanobacteria. Since it is not clear what these nanobacteria represent, they are often referred to as calcifying nanoparticles. However, a more definite detection has been made of an acidophilic Archaea, which has a cell volume of less than 0.006 cubic micrometer (Baker et al. 2006) and is smaller than the minimum size expected on the basis of theoretical considerations for free-living cells. The organisms were discovered by community genomic analysis from acid mine drainage. Starvation of laboratory-cultured bacteria commonly leads to reduction in cell size. Thus small cells may be starved, miniaturized versions of culturable bacteria. Torrella and Morita (1981) reported that some microbes of small size respond to nutrient addition by increasing in cell number and size while others multiply but retain their small size. Thus, the counter argument based on size has weakened over time, but the possibility that the observed structures might be artifactual still cannot be discounted.

10.2.2.3 A Magnetite Biosignature?

Perhaps the most contentious discussions erupted around the magnetite grains in ALH84001, which were claimed by McKay et al. (1996) to represent a biomarker for life on Mars, due to their single-domain crystals, purity, and lack of structural defects. Bradley et al. (1996) disputed that point by reporting that their analysis of magnetite crystals in ALH84001 indicated the presence of whiskers and platelets that most likely formed in the temperature range of 500–800 °C by direct condensation from a vapor or precipitation from a supercritical fluid. In 2000 the McKay group, led on the magnetite issue by Kathie Thomas-Keprta, responded to clarify their argument. Thomas-Keprta et al. (2000) studied 594 magnetites from ALH84001 and grouped them into three populations based on morphology, and asserted six properties of biogenicity, which included narrow size range, restricted width to length ratios, chemical purity, few crystallographic defects, crystal morphology, and elongation along only one of the possible rotation axes of a regular octahedron. They emphasized that a potential seventh property, the presence of magnetite crystals aligned in chains would be even more revealing. Thomas-Keprta et al. (2000) claimed that about 25% of the magnetite crystals in ALH84001 conformed to these 6 properties. The elongated prisms were very similar to those of magnetotactic bacteria on Earth, particularly those from bacterial strain MV-1. Magnetotactic bacteria align to Earth's magnetic field and produce a single intracellular chain of about 12 well-ordered magnetite crystals, each encapsulated within a coating or membrane (Fig. 10.4). The chain of magnetite crystals acts very much like a compass needle to enable the passive alignment of the bacterium along the Earth's geomagnetic field lines. Thus, bacterial cells appear to exert strict physical and chemical controls on the formation of magnetite and this, the argument was, would produce a suitable biomarker for life within rocks. The association of biogenically produced magnetites with inorganically produced ones was not considered as surprising, because magnetites formed by bacteria from Earth are usually

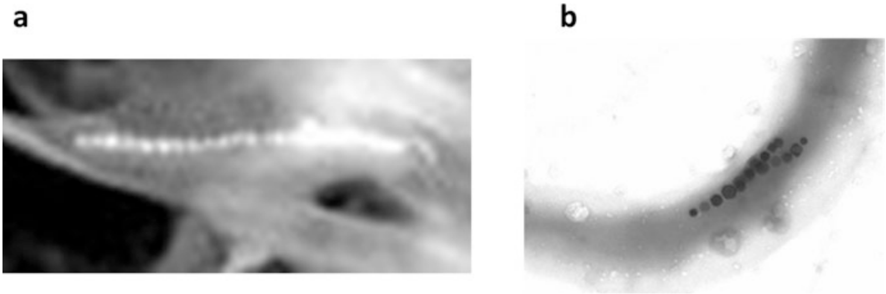


Fig. 10.4 Magnetite chain in a terran magnetotactic bacteria from Kelly Lake, Canada. Image is courtesy of Alfonso Davila from the NASA Ames Research Center

found in environments where inorganic magnetites are common. Shortly thereafter, Thomas-Keprta et al. (2001) extended their argument to a bolder claim that the magnetite crystals are in fact Martian "magnetofossils" and that these magnetites constitute evidence of the oldest life yet found. Independently, Friedmann et al. (2001) found magnetites aligned in chains in ALH84001 and argued that they would be nearly impossible to produce inorganically and were consistent with a biological origin.

These claims were vigorously disputed by arguments that an inorganic pathway could produce the carbonate globules that hosted the magnetites (Golden et al. 2001), or that magnetite alignment could be produced by solid-state diffusion as a result of carbonate decomposition during impact heating (Barber and Scott 2002). Thomas-Keprta et al. (2002) responded by arguing that the heat necessary to decompose iron carbonates and form magnetite was simply not present and would require homogenization of all magnetic dipoles. Instead, considerable heterogeneity was observed in the ALH84001 carbonates inconsistent with significant heating. A somewhat neutral perspective was provided by Weiss et al. (2004), who argued that magnetite crystals in the carbonate from ALH84001 have a composition and morphology indistinguishable from that of magnetotactic bacteria. They noted that the alignment of magnetites in chains was the strongest argument for a biogenic origin of the magnetite, even though no more than 10% of the magnetite in ALH84001 occurs in chains. They also pointed out that the magnetite is unusually pure and fine-grained, similar to terran magnetofossils, but that it would be difficult to conclusively prove the biogenic origin of the magnetites due to the low abundance of chains. Even in sediment deposits from Earth that have undergone diagenesis, typically more than half of the chain structures have been disrupted. Thus, like other aspects of the argument for biosignatures in ALH84001, the evidence from magnetite remains plausible but inconclusive.

10.2.3 Signs of Ancient Life in Another Martian Meteorite?

A new twist appeared in the discussions about life in the Martian meteorite ALH84001 when McKay et al. (2006) showed microscopic slides that revealed complex organic matter within microscopic veins in another Martian meteorite called Nakhla. These veins were similar to those observed in ALH 84001. At about the same time, Fisk et al. (2006) reported tunnel and borehole-like structures in basalts from Earth, the meteorite Nakhla, and one other meteorite (called Lafayette) related in origin to Nakhla. They pointed out that these tunnel structures tested positive for the presence of cellular material in the samples from Earth, and that the tunnel structures in the Martian meteorite Nakhla were indistinguishable in size, shape, and distribution from the Earth samples. Tunnel structures had previously been discovered in 3.5 billion year old rocks in the Barberton Greenstone Belt in South Africa (Furnes et al. 2004), providing evidence of submarine microbial activity during the very early history of Earth. Gibson et al. (2006) reported possible biogenic features in two additional Martian meteorites, Nakhla and Shergotty, which bore a strong resemblance to very similar structures discovered in Earth rocks that were almost surely biogenic in origin. The evidence remains in dispute, however. Fisk et al. (2006) pointed out that the biogenic-like features in Nakhla appear to be contemporary with hydrous alteration on Mars less than 1300 million years ago, which was a time when Mars was not wet and warm anymore, but likely experienced only intermittent events of liquid water. Further, meteorite Nakhla fell to Earth in Egypt in 1911 killing a dog and leaving plenty of time for Earth organisms to contaminate the meteorite in an environment more conducive than Antarctica. Furthermore, organic ingredients were used in the preparation and preservation of samples from Nakhla. A similar claim for biological structures was also made for the Mars meteorite, Tissint (Wallis et al. 2012). However, to conclude, the evidence for biomarkers in other Martian meteorites remains equivocal as well.

10.2.4 Conclusions Concerning Biomarkers in Martian Meteorites

McKay et al. (1996) argued from the beginning that the evidence for life on Mars deduced from ALH84001 consisted of a group of facts and observations, any one of which in isolation was not conclusive, but considered collectively added to a plausible argument for evidence of biogenic activity. The weakness of individual chains in the argument has elicited numerous and legitimate counter arguments, but the logic of the collective evidence remains persuasive. At a minimum, ALH84001, and to a lesser extent, the other Martian meteorites studied to date, provide circumstantial evidence justifying the continuation of a vigorous search for additional signs of past or present life on Mars.

10.3 Current Life Detection Instrumentation

It has been a long time, more than 30 years, since the only Life Detection Experiments ever attempted were conducted by the Viking landers. Improvements in technology, especially by making instruments smaller and lighter, have enhanced the prospects for success on new robotic space missions. The basic problem, however, still remains. What evidence is sufficient to provide an unequivocal case for life? The strategy of the Viking landers was largely based on presumed metabolic activities. Since the metabolic approach gave equivocal results, it has largely fallen out of favor with the scientific community. Instead, the focus has been to increase the capability and sensitivity of instruments to detect biosignatures, especially the so-called biomarkers of life.

Biomarkers are complex molecular fossils derived from biochemicals in once-living organisms (Peters et al. 2004) or evidence for currently existing life. For a more thorough discussion see Chap. 9; here we will focus on how biomarkers pertain to mission approaches. Examples include visible and near infrared spectrometric searches for chlorophyll (Wettergreen et al. 2005), the single molecule detector (SMD) approach as suggested by Ishii and Yanagida (2000) to screen for DNA, enzymes and proteins, and fluorescence imagers that use a dye, which only fluoresces if it binds to a target molecule such as a specific protein, nucleic acid or other biomolecule. Various instruments are sensitive to different biomarkers. While some research groups target relatively simple organic macromolecules such as amino acids (Glavin et al. 2001), others (e.g., Steele et al. 2001) focus on detecting more complex molecules. For example, the Micro-Capillary Electrophoresis Chip designed by Glavin et al. (2001) is an example of the targeted detection of amino acids with a sensitivity of about 10^{-18} mole! The Mars Organic Detector (MOD) has been developed for detecting amino acids, amines and polycyclic aromatic hydrocarbons (PAHs) on the Martian surface (Bada 2001). While PAHs have no known role in terran biochemistry, they can be a product of long-term degradation of biologically derived organic compounds (MacKenzie et al. 1982). Amino acids are readily destroyed on the Martian surface by UV irradiation (Stoker and Bullock 1997). However, amino acids can be preserved in the subsurface for billions of years, but a space probe has to drill deep enough to overcome the detrimental effects of gamma radiation in the near subsurface (1.5 to 2 m) to detect any amino acids from ancient life that may have been present 3 billion years ago (Kminek and Bada 2006). The upgraded Mars Organic Detector III is more versatile and is capable of detecting nucleobases, sugars, and organic acids and bases.

Even more ambitious is the Mars Immunoassay Life Detection Instrument (MILDI), which has the ability to look for three classes of biomarkers including biomarkers from extant life such as RNA, from extinct life such as hopanes, and from organic compounds not necessarily associated with life such as PAHs (Steele et al. 2001). The list of possible detections also includes lipopolysaccharides, exopolymeric substances, porphyrins including chlorophyll, specific amino acid and peptide sequences, RUBISCO, and flavin adenine dinucleotide (FAD) and nicotinamide adenine dinucleotide (NAD). The Life Marker Chip, which also utilizes an immunoassay approach to detect specific organic molecules or classes of molecules was considered for the ExoMars mission of the European Space Agency (Parnell et al. 2007). SOLID3 (Signs Of LIfe Detector, version 3), a further development of the immunoassay approach, is capable of detecting a broad range of molecular-sized compounds, which range from peptides and proteins to whole cells and spores, with sensitivities at 1–2 ng mL^{-1} for biomolecules and 10^4 to 10^3 spores per milliliter (Parro et al. 2011). While the list of possible organic molecules that can be detected with immunological approaches is impressive (Tang 2007), it warrants some concern for being overly focused on biochemistry as we know it on Earth. For example, the National Research Council elaborated on its concern that molecular methods would not likely find any life that is not related by common ancestry to the life we already know. A universal feature of chemical characteristics of living systems is believed to be chirality (Baross et al. 2007), the predominance of one enantiomer over the others. This approach was also proposed by Levin (1998) as a modification to the Labeled Release experiment of the Viking mission.

Another promising novel approach is the development of nanopore-gated optofluidic chips (e.g., Liu et al. 2014), which can detect biomolecules and single nanoparticles without assuming a certain biochemistry a priori. It was also included as part of a proposal for a life detection mission to Mars (Schulze-Makuch et al. 2012b). Advantages of nanopore-based analysis are their sensitivity (Vercoutere et al. 2001) and that they can characterize single polymer molecules with unmatched speed (micro to millisecond time scales—Storm et al. 2005). A special caveat is that this approach would allow the detection of monomers or fractions of polymers, because complete nucleic acids and proteins would not be expected to survive in extraterrestrial environments like those on the Martian surface.

Life detection methods are not based only on chemical or biochemical reactions, but also on spectroscopic approaches. An example is the Scanning for Extinct Astrobiological Residues and Current Habitats (SEARCH) method. SEARCH utilizes integrated spectroscopic sensing with a laser-diode array and photodetectors processed by a hyperspace data analysis algorithm (Dieter et al. 2005). Its spectrum includes UV, visible and near-IR wavelengths. The instrument can be mounted on a rover to scan ranges of up to 10 m. The reflectance data is processed for each illuminated point such that amino acids, carbohydrates, PAHs, and even organisms or fossils can be identified (Dieter et al. 2005). Also, Raman spectroscopy, a non-invasive method that provides a unique spectral “fingerprint” for any molecule depending on its vibrational state (Edwards and Newton 1999; Chen et al. 2008; Bowden et al. 2008; Böttger et al. 2012) has a great potential as a tool for life detection, especially if Raman spectrometers can be sufficiently miniaturized. The shift in wave number of the exciting radiation can be related to the structure, composition, and identification of the scattering molecules (Long 2002). Spectral methods, of course, are also used to scan planetary atmospheres for biomarkers such as the simultaneous detection of ozone or oxygen and methane. An example of improving technology in this area is the Multiple Instrument Distributed Aperture Sensor (MIDAS), which provides a large-aperture, wide-field, diffraction-limited telescope by integrating optical interferometry technologies into a mature multiple aperture array concept (Pitman et al. 2004).

A revival of the metabolic approach has occurred with the development and use of microbial detection arrays (Hoehn et al. 2007; Clark et al. 2017). These employ electrochemical sensors in two identical chambers, one sterilized and the other receiving an additional minute, non-sterilized inoculation sample. If it is assumed that the geological sample contained nutrients, organisms, and required water to initiate growth, the differential electrochemical measurements would then allow detection of metabolic activity. In addition, an electrochemical characterization of the soil samples in both chambers is achieved (Hoehn et al. 2007). A related effort, but under in-situ conditions, is the ecosynthesis approach, which relies on the principle of engineering local habitable hotspots on planetary surfaces to enhance the expression of their putative biological activity (Schulze-Makuch et al. 2013a), thereby revealing any subdued biosphere that may be present.

However, to succeed with an unequivocal detection of life, multiple approaches have to be pursued. This was a distinct outcome of a timely round table discussion hosted by the *Astrobiology Journal* (Schulze-Makuch et al. 2015b). Initially, a proper search strategy for life requires detailed orbital imaging and spectrometry to home in on potential habitable sites, and collection of surface data by spectrometric, biochemical, and microscopic instruments (Lipps et al. 2004). Once a planet or moon is concluded to be a possible host for life, a dedicated life detection mission should be launched which includes a variety of approaches from different disciplines.

10.4 Chapter Summary

The Viking Mission was a great success story, but it failed to provide a clear answer to the question of whether there is life on Mars. The claim for fossilized remnants of life in the Martian meteorite ALH84001 is a relatively persuasive collection of facts and observations consistent with biogenic origins, but individual links in the collective chain of evidence remain weak and controversial. Recent evidence for contemporary liquid water on Mars, and the detection of methane in the Martian atmosphere appears further to enhance the case for life on Mars, but what is needed is a new mission devoted to the detection of life. Thus, work should continue on in-situ life detection methods that can be tested on Mars and our other neighboring planets and moons in the near future. Screening methods and experiments should be designed with an open mind to allow the detection of life that may not utilize many, or any, of the biomolecules that are used by life on Earth.

Chapter 11
Astrobiological Potential of Planetary Bodies Within the Solar System

All the known planetary bodies and satellites in our Solar System are within reach of current technology for the detection of a number of the biosignatures and geosignatures that could indicate the possibility of harboring some form of life. In this chapter, we will review the strength of that possibility for each of the planets and the best studied dwarf planets and moons in our Solar System.

11.1 Terrestrial Planets

11.1.1 Mercury

The Solar System's innermost planet, Mercury, has little to commend it as a possible habitat for life. It is too small to hold an atmosphere, is the most heavily bombarded planetary body in the Solar System, has a very weak magnetic field, and no evidence of complex chemistry. It also appears no longer to be tectonically active, though volcanic activity may have continued on Mercury for longer than previously assumed, perhaps from the formation of the planet to about a billion years ago, based on data from the Messenger spacecraft (Goudge et al. 2014). Sunlight provides an abundance of energy, but the planet's proximity to the Sun and its lack of atmosphere results in temperature fluctuations between 430 °C in sunlight and −180 °C in darkness (Dinwiddie et al. 2008). The possibility of any kind of life on Mercury could be rated as negligible, but for two factors.

First, while its orbital period is 88 earth days, its period of rotation is 58.6 days, resulting in a slowly moving terminator (boundary between daytime and nighttime) where temperatures drop to an intermediate point between the extremes. Second, while most of the planet's surface appears to be totally desiccated, there is evidence that some ice exists in permanently obscured areas at the poles (Slade 1992). Thus, temperatures compatible with microbial life and the possibility of water-ice at the poles preclude total elimination of the prospect for life on Mercury.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_11

Yet, the odds are strongly against it. Even at the terminator, the temperature is estimated to be above 150 °C, so the surface must be totally dark by the time the temperature drops into a range tolerable for any known form on life on Earth, and there is no evidence of a liquid of any kind other than possibly at the poles, where there is virtually no light.

Even if some form of microbial life could have originated on Mercury or been delivered there, it seems most unlikely that it could ever have thrived there.

11.1.2 Venus

Venus has not always been the home of hellfire and brimstone that it is today. In *Cosmic Biology* (Irwin and Schulze-Makuch 2011) we detailed the argument that Venus in its early planetary history was a rocky water world, with conditions that would have made the evolution of an early biosphere as likely as the one we know occurred on Earth. As the temperature warmed, with increasing solar intensity and the heat-trapping effect of rising atmospheric humidity, evolution would likely have accelerated, possibly giving rise to a biodiversity exceeding that on Earth at the same time. Thermophilic autotrophs, nourished by abundant sunlight, may well have covered the planet in greater abundance and diversity than autotrophic life on Earth in the same time frame.

The contemporary reality, of course, has obliterated any plausibility that life exists on or near the surface of the planet today. As the Sun got brighter and greenhouse conditions worsened, abetted by catastrophic volcanic eruptions that persisted to less than 2.5 million years ago (Smrekar et al. 2010), water was driven from every reservoir and the planet's surface dried out and overheated (Kasting 1988). With a global temperature of 464 °C (Williams 2016) and no liquid at the surface today, Venus presents the most hostile habitat in the Solar System for life of almost any conceivable form. But that only applies to the surface and subsurface. Granted that this is where the search for life is naturally focused—given that Earth's biosphere is most dense and diversified at or near its surface. But the thick, multilayered clouds of the lower atmosphere of Venus differ drastically from its surface, and by their mass and global extent, they have attracted consideration as an alternative habitat for life.

Morowitz and Sagan (1967) long ago noted the presence of more benign conditions in the lower cloud layers, and suggested that "it is by no means difficult to imagine an indigenous biology in the clouds of Venus." We now understand the composition of the cloud layers in greater detail (Jenkins et al. 1994; Grinspoon 1997): A thick (~15 km), uppermost layer made up of tiny (0.1–0.2 micron) droplets of sulfuric acid with temperatures from −4 to −45 °C; a thin (~4 km) middle layer of larger (1.1–1.4 micron) droplets between 4° and 33 °C; and a lower layer from about 48 to 52 km above the surface, consisting of larger (~3.4 micron) droplets of water/sulfuric acid from 33° to 80 °C. The middle and lower layers are compatible with normophilic and thermophilic microbial life on Earth, respectively (Irwin and Schulze-Makuch 2011).

Grinspoon (1997, 2003), Morowitz (2011), and the authors of this book (Schulze-Makuch and Irwin 2002b, 2006; Schulze-Makuch et al. 2002b, 2004, 2013a) have been vocal advocates for the possibility of life in the clouds of Venus. We have even described chemically plausible scenarios for harvesting energy and sustaining a microbial metabolism in that environment (Schulze-Makuch et al. 2004; Irwin and Schulze-Makuch 2011). Similar ideas have been advanced by Limaye et al. (2018).

Missions to sample the cloud layers of Venus have been proposed (Schulze-Makuch and Irwin 2002a, b; Schulze-Makuch et al. 2002b, 2005b). Even though a sample return mission is technologically feasible and potentially easier than sample return missions from Mars or Europa (Schulze-Makuch et al. 2004), NASA has shown little interest in supporting such missions (Hand 2011), apparently based on devotion of limited funds to missions aimed at elucidating the formation of the Solar System, and a search for life as we know it on Earth. To be sure, survival of organisms in the confines of tiny droplets of liquid sulfuric acid with exposures to high levels of ultraviolet radiation would be a challenge by conventional Earth standards, but such extremophiles do exist, and microbial life up to high elevations in the atmosphere of Earth is abundant (Smith et al. 2012; Smith 2013).

In some ways, discovery of life on Venus would be more informative of the range of total possibilities for living systems, since directional selection on that planet would likely have driven the evolution of organisms with biochemistries substantially different from those known on Earth.

11.1.3 The Earth-Moon System

Even lacking an empirical observation of life on Earth, an alien observer at a level of technological development equivalent to ours within a distance of 10–15 light years would be highly likely to suspect the strong possibility of life on the third planet from the Sun in the Solar System.

At such a distance with instrumentation similar to ours, the alien scientist would probably be able to detect a strong signature for H_2O, H, N, O, S, C, and Si. Our observer might even be able to decipher the presence of an atmosphere rich in N_2 with about a fifth as much of O_2 and traces of CO_2, SO_2, H_2S, and methane. From infrared radiation, the temperature of the Earth could be deduced, and from the Sun's size and intensity, its age—hence the age of its orbiting planets and their moons as well—could be pegged at 4–6 billion years. Furthermore, radio signals emanating from the planet would likely be seen as an unnatural indicator of technological advancement.

The abundance of water and a global average temperature of about 15 °C would mean liquid water on the surface. The abundance of silicon would be consistent with a rocky planet, a fact confirmable by the planet's density if enough information were available to calculate that. The planet's relative proximity to the Sun would mean abundant sunlight. The presence of SO_2 and H_2S could reflect volcanic eruptions, indicating dynamic geological activity. The presence of both O_2 and methane would be a suspicious signature of biogenic processes. With all the elements necessary for carbon-based polymeric chemistry, with the abundance of liquid water quite likely interfacing with rocky continental masses, with chemical elements necessary for energy-yielding oxidation-reduction coupling reactions, not to mention the flood of sunlight and an atmosphere capable of protection against ultraviolet radiation and interplanetary debris, favorable conditions for the evolution of life would have to be assumed. Furthermore, as we know, a planetary history spanning four billion years is long enough for the evolution of life to a considerable degree of diversity.

The Earth's Moon is a different story. Despite formation in close proximity to the Earth—perhaps with material drawn from the early Earth itself (Mastrobuono-Battisti et al. 2015)—and at the same distance from the Sun, there is every indication that the Moon is totally lifeless. Not only is it lacking any geoindicators and bioindicators of life, no samples brought from the Moon back to Earth have contained anything resembling even complex biomolecules.

It seems likely that the Moon, along with the Earth, underwent a series of pulsatile bombardments up to around 3.8 Ga ago (Schmitt 2006). These early planetesimal collisions and bombardments by planetary formation debris could have delivered water to all the inner rocky planets and the Moon (Bottke et al. 2010), combined with magmatic outgassing, possibly even resulting in temporarily habitable conditions on the Moon (Schulze-Makuch and Crawford 2018). Organic chemicals could have been deposited in this manner as well. Whether because of its smaller mass, or other interplanetary dynamics, the Moon lost its atmosphere, probably early on, and that precluded its ability to hold any surface water. Whatever incipient organic chemistry may have been present was apparently lost, at least from the surface.

Whether more than the slightest trace of water exists in the Moon's interior is a subject of controversy (McCubbin et al. 2010; Sharp et al. 2010). First suggested by neutron flux data from both poles (Feldman et al. 1998), water-ice has been convincingly detected near the Moon's south pole (Clark 2009), amounting possibly to as much as 1% by volume and 6% by mass within the upper 1–2 m of the surface (Kerr 2009). However, at the Moon's extremely low surface temperature, water almost surely never exists there in the liquid state (Kerr 2010). The apparent absence of this fundamental requirement for life, combined with the total lack of any biogenic material in any sample returned from the Moon, leaves us to rate the likelihood of any form of life on the Moon as negligible.

However, in the earliest stages of its history, when the Moon and Earth were much closer and likely shared much of their material substance, including possibly even a conjoined atmosphere, they could have shared the same prebiotic environment. Thus, even if totally lifeless today, water-ice on the Moon could hold evidence of prebiotic chemistry of the Earth-Moon system from very early Solar System history (Armstrong et al. 2002; Baker et al. 2005). Sampling water-ice from the Moon could therefore be a mission well worth undertaking.

11.1.4 Mars

There is now widespread agreement that in their early planetary histories, Mars and Earth harbored similar habitats. Strong evidence favors a warmer, wetter Mars with long-lasting seas and lakes lasting into the Amazonian, <3.0 Ga ago (Fairén et al. 2009). By this point in time on Earth, microbial mat ecosystems (Noffke et al. 2013) and probably photosynthesis (Tice and Lowe 2006) were widespread on Earth. There is no reason to believe that the same could not have been true on Mars.

However, as Mars lost its atmosphere, it turned colder, leading to a prolonged phase of a colder but still wet planet (Fairén et al. 2003; Fairén 2010). While some climate models of an early Mars subjected to 20% less insolation from the young Sun (the faint Sun paradox) indicate a cold planet almost from its origin, greenhouse gases, meteorite impacts, and volcanism could still have generated long-standing bodies of liquid water (Wolf and Toon 2013; Wordsworth et al. 2013). In either event, with dropping temperatures and atmospheric pressures, retention of surface water diminished, until the cold dry habitat of today was reached, well over 1 Ga ago (Fairén et al. 2010).

The extensive stores of water that once covered much of Mars did not disappear entirely (Irwin and Schulze-Makuch 2011). The Mars Odyssey Orbiter revealed vast amounts of water-ice just below the surface over broad areas of the planet (Bandfield 2007). The visible topography of Mars shows strong evidence of flowing water (Carr 1996)—in large volumes carving massive channels, and in smaller spillways down steeply sloping terrain which seem in some cases to be very recent. Dark streaks currently observed on Martian slopes, called Recurrent Slope Lineae (RSL), may also have an origin that involves water—possibly brines consisting of chlorates and perchlorates (Ojha et al. 2015).

As Mars evolved from a warmer wetter, to a colder wetter, to a colder dryer surface with extensive stores of subsurface water-ice, life on Mars would have retreated to a psychrophilic lifestyle beneath the surface or to environmental niches near the surface, such as hydrothermal regions and caves (Schulze-Makuch et al. 2005a, b). Sequestered environments such as lava tube caves (Fig. 11.1) would have been particularly favorable due to the increase in destructive UV radiation at the surface as the atmosphere eroded. Strong directional selection could have pushed putative Martian life to evolve alternating cycles between active and dormant forms, as well as the innovation of new traits adapted to challenging near-surface conditions (Schulze-Makuch et al. 2013a). Equally plausible is the transition from widespread edaphic communities to localized lithic communities and finally to communities exclusively found in hygroscopic substrates, reflecting the need for organisms to maximize access to atmospheric sources of water (Davila and Schulze-Makuch 2016). All of these scenarios are consistent with the possibility of life on Mars until relatively recent times, perhaps even to the present (Houtkooper and Schulze-Makuch 2007; Schulze-Makuch et al. 2008; Irwin and Schulze-Makuch 2011).

Diverse organic compounds of endogenous origin have been found on Mars (Glavin et al. 2014; Freissinet et al. 2015; Eigenbrode et al. 2018) and the presence

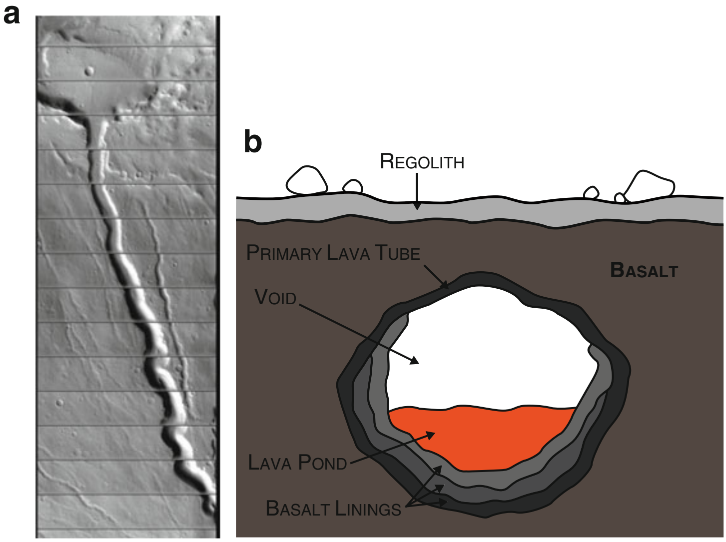


Fig. 11.1 Lava tubes on Mars. Under certain conditions, lava spills and flows can harden on top while magma continues to flow out, leaving a hollow tube which may (**a**) collapse, or (**b**) form caves that could sequester organisms, if life still exists on Mars. *Credit: (**a**) NASA/JPL-Caltech/ University of Arizona; (**b**) https://en.wikipedia.org/wiki/Martian_lava_tube, CC BY-SA 3.0*

of H_2O_2 (Clancy et al. 2004) and perchlorate (Webster and Cruz 2009) could serve as possible energy sources where sunlight is unavailable. While the traces of methane in the atmosphere of Mars could be produced abiotically, a biotic origin has not been ruled out (Krasnopolski et al. 2004).

Extremophilic microbes have been described on Earth that bolster the plausibility that such organisms could exist on Mars. Some bacteria living at the interface of ice and basalt on Earth can derive energy from Fe(II) in the igneous mineral olivine. These microbes can grow at temperatures as low as 5 °C using bicarbonate as a facultative source of carbon. This bacterium could thus live in near-surface, icy, volcanic environments on Mars (Popa et al. 2012). Wilhelm et al. (2012) have isolated a variety of psychrotolerant, halotolerant microbes capable of growing in ice wedges, in permanently cold, water-scarce, ice-rich environments. Species of *Carnobacterium* have been isolated from Siberian subsurface permafrost that grow in low temperature, low pressure, anoxic atmospheres (Nicholson et al. 2013); and 20 species of bacterial hypobarophiles capable of growth at 1–2 kPa have been recovered from arctic permafrost (Schuerger and Nicholson 2016).

In summary, the conditions for the origin or sustenance of life existed on Mars for at least a billion years early in its planetary history. Though conditions on Mars began to diverge dramatically about 3.5 Ga ago toward the cold and arid planet of today, directional selection should have promoted the evolution of organisms tolerant to cold and low pressure as conditions on the surface changed. With copious amounts of water-ice still permeating much of the Martian subsurface, as well as the presence of sinecures such as subterranean ice wedges, hydrothermal regions, and lava tube caves—living organisms, even including microbial mats and colonial aggregates in caves, may be present on Mars today. With the possible exception of subsurface oceans on some icy satellites, Mars seems the most likely planetary body in the Solar System other than Earth to have harbored life in the past, with the distinct possibility that a limited biosphere still exists there today.

11.1.5 Ceres

Ceres is the largest body in the asteroid belt between Mars and Jupiter. Because it resembles the rocky planets of the inner Solar System more than other bodies in the asteroid belt, it was classified as a dwarf planet in 2006. Its diameter of 952 km is slightly less than the width of the State of Texas. Its low density is consistent with a rocky core encased in a thick layer of water-ice, which could account for up to 25% of its volume (Fig. 11.2). This makes it comparable to many of the icy satellites in the outer Solar System.

Ceres is dominated by many small craters, with none greater than 280 km in diameter (Hiesinger et al. 2016). This, plus numerous indications of cryovolcanism and cryomagmatism (Buczkowski et al. 2016), suggests a geologically active body.

In 2014, scientists at the Herschel space observatory detected the expulsion of water vapor from the surface of Ceres (Küppers et al. 2014). Data collected by the *Dawn* spacecraft which arrived at Ceres in 2015 detected water-ice, probably of relatively recent origin, on the surface, as well as a variety of mineral hydrates indicative of formation in contact with water (Combe et al. 2016). Evidence of widespread clays on the surface of Ceres raises the intriguing possibility that the

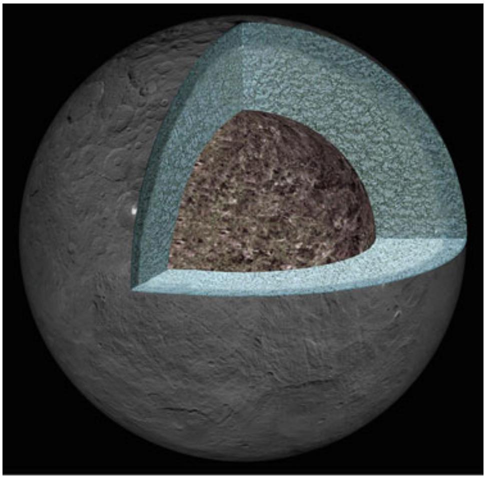


Fig. 11.2 Internal structure of Ceres. This artist's conception is based on gravimetric data collected by the *Dawn* spacecraft. Ceres appears to be differentiated into an internal core, probably of hydrated silicates, surrounded by a volatile-rich layer, encased in a crust of mixed material. *Credit: NASA/JPL-Caltech/UCLA/MPS/DLR/IDA*

subsurface ocean could be a very muddy reservoir of liquid water (De Sanctis et al. 2015). Eventually organic compounds were detected on the surface as well (De Sanctis et al. 2017). Thus, the ingredients for prebiotic chemistry are present on Ceres (Küppers 2017).

If a subsurface ocean lies beneath the outer crust (O'Brien et al. 2015), and if life had arisen on, or been delivered to, Ceres at an early stage of its planetary history, some forms of marine life could still exist beneath its surface. Such a possibility has long been suggested for Europa, and more recently for Enceladus, both of which are discussed below; and what applies to them could be the case for Ceres.

11.2 Outer Solar System

11.2.1 Gas and Ice Giants

The four giant planets of our Solar System—Jupiter, Saturn, Uranus, and Neptune—consist of planetary-sized cores enveloped by gases compressed by gravity into progressively denser and warmer layers, with no apparent sharp boundaries between gas, liquid, and solid or metallic plasma states.

Jupiter's mass is 2.5 times the mass of the other seven planets combined. Its atmosphere is 90% hydrogen, with helium and traces of methane and ammonia composing the other 10%. It has a very rapid period of rotation, making a complete revolution on its axis every 9.93 h. Beneath high, wispy clouds of ammonia race thick billowy clouds of various hydrocarbons. The temperature is about −145 °C at the top of the cloud layer, but reaches room temperature (~21 °C) at a depth where the pressure is ~10 bars. The warmer gasses deep in the atmosphere rise to the top, while the cooler gasses sink. This vertical movement, combined with the Coriolis Effect of the high rate of rotation, generates bands of strong winds circling the planet at up to 400 km/h (Irwin and Schulze-Makuch 2011).

Saturn's atmosphere is 96% hydrogen, with helium and trace compounds including ammonia and ammonium hydrosulfide making up the rest. It makes one revolution every 10.5 h, features clouds of different composition including methane and hydrocarbons at different levels. High winds blow at around 500 m/s (1800 km/h), and high altitude storms occur periodically (Dinwiddie et al. 2008). The equatorial temperature is about −188 °C at the top of the troposphere where the pressure is 100 mbars (Orton and Yanamandra-Fisher 2005).

The atmosphere of Uranus has a lower content of hydrogen (82.5%) and higher content of helium (15.2%) than the two larger gas giants. Methane, ammonia, water, and other trace compounds make up the remainder. Voyager 2 recorded a cloud top temperature of −214 °C. Beneath the placid surface, which appears smooth due to an ultraviolet light-induced haze of methane, dozens of discrete cloud features and banded zonal structures appear. Deeper into the atmosphere, a thick layer of water, methane, and ammonia ices is presumed to encase the rocky core. Beneath the gaseous layer, Uranus is thought to consist of a thick layer of water, methane, and ammonia ices (Dinwiddie et al. 2008). Wind velocities of 218 m/s (785 km/h) have been measured on Uranus (Hammel et al. 2005).

Neptune is the smallest, coldest, and windiest of the four giants. Cloud top temperatures are about −200 °C, and equatorial winds reach a staggering 600 m/s (2160 km/h). The atmosphere is 79% hydrogen, 18% helium, with methane and other trace gases making up the remainder (Dinwiddie et al. 2008). A thin methane cloud is found at 1.5 bars, and other clouds, probably of ammonia and other constituents, appear at 3 bars (Stone and Miner 1989). Like Uranus, the interior of Neptune is believed to be primarily composed of a fluid mixture of methane and water (Lee and Scandolo 2011), but at temperatures that make the stability of macromolecules unlikely (Baker et al. 2005).

More than 40 years ago, Carl Sagan and E. Saltpeter (1976) speculated that organisms in the form of thin gas-filled balloons could float at levels of atmospheric density great enough to support them. They envisioned an ecosystem consisting of autotrophic "sinkers" that would serve as food for a primary level of consumers, named "floaters," which in turn would supply nutrients for a secondary level of "hunters."

The availability of energy and abundance of building blocks for biomolecules, such as methane, ammonia, and sulfur compounds in the atmospheres of the giant planets, compel consideration of the possibility that some form of life could persist among them; and the fanciful idea of Sagan and Saltpeter seems as good a guess at the nature of that life as any. It is only at high enough altitudes for the atmosphere's constituents to be gasses that temperatures would be compatible with macromolecular structures and metabolism, so if life exists at all on the giant planets, it must be in the form of organisms that fly or float.

Opposing the theoretical possibility of life in the giants are three strong theoretical arguments against it, given in detail in our previous work (Irwin and Schulze-Makuch 2011). In summary, they are (1) lack of historical circumstance, (2) absence of solid substrates, and (3) atmospheric instability. By lack of historical circumstance, we mean that no clear path for the evolution of life can be envisioned in such an amorphous and unstable environment. The lack of solid substrates or sharp interfaces where constituents could be concentrated, and self-perpetuating metabolism could take hold is a severe apparent limitation. And even once formed, the survival of fragile organisms in such turbulent environments would be a challenge. Thus, we consider the existence of living organisms on any of the gas giants as extremely unlikely.

Besides the theoretical arguments against life on the gas giants is the total lack of any empirical evidence for the presence of any molecules of significant complexity within their atmospheres.

Notwithstanding the dilute concentration of precursors for biomolecules, it is not inconceivable that microscopic organisms able to survive in severely nutrient-depleted environments could have been delivered to the atmospheres of the giant planets by panspermia from a more benign point of origin. But all the giants are a long way from Earth, the only habitat for life known with certainty at this time. If life had taken hold on any of the nearby satellites of the gas giants, delivery from them is more likely. The possibility that life could have arisen and could exist on other planetary bodies in the outer Solar System will now be considered.

11.2.2 Io

The innermost and largest satellite of Jupiter, Io is the fourth largest moon in the Solar System. Stretched and compressed by the alternating alignment of the outer Galilean satellites (Europa, Ganymede, and Callisto) relative to the strong gravitational pull of Jupiter, frictional heating makes Io the most volcanically active planetary body in the Solar System (Matson and Blaney 1999). There is no lack of energy; and a rich mix of inorganic compounds—CO, CO_2, H_2S, SO_2, NH_3, with traces of H_2O and CH_3OH (Sandford and Allamandola 1993)—could in principle provide precursors for biomolecules.

Contrary to these potential advantages for the existence of life on Io is the stark hostility of the environment, which features temperatures as high as 2000 K (McEwen et al. 1998) in erupted lava and as low as 80 K (-193 °C) at the surface away from lava flows. The high temperatures are not compatible with macromolecular stability, and the low temperatures would make metabolism in a water-based medium impossible. Though a very small amount of water is found on Io (Salama et al. 1994), it could not exist in liquid form except as part of a mixed ice slurry of H_2S, SO_2, and H_2O at local warm spots (Salama et al. 1990). The surface and near subsurface of Io is subjected to wandering plumes of volcanic emissions and spreading lava fields which, at their edges, vaporize the SO_2 snow fields prevalent on the surface and probably liquefy the composites of H_2S, SO_2, H_2O, and whatever other compounds might be liquefiable (Kieffer et al. 2000).

We have previously speculated that local warming by moving boundaries of lava across the frozen surface of Io could liquefy pockets of H_2S, SO_2, NH_3, and H_2O, providing temporary habitats for the resurrection of dormant microorganisms (Schulze-Makuch 2010; Irwin and Schulze-Makuch 2011). This assumes that life could have arisen on or been transported to Io when conditions for the sustenance of life were more benign; though whether such conditions ever existed on a moon coalescing so close to the intense radiation and gravitational pull of Jupiter is a fair question. Our point here is simply that the possibility of life on Io cannot be summarily dismissed.

11.2.3 Europa

The next satellite out from Jupiter is Europa, the smallest of the Galilean moons, and a world hard to imagine more different from Io. The density of Europa can best be explained by a metallic core surrounded by a rock mantle, encased in an ice-salt water ocean 70–180 km deep (Fig. 11.3; Anderson et al. 1998; Carr et al. 1998). The

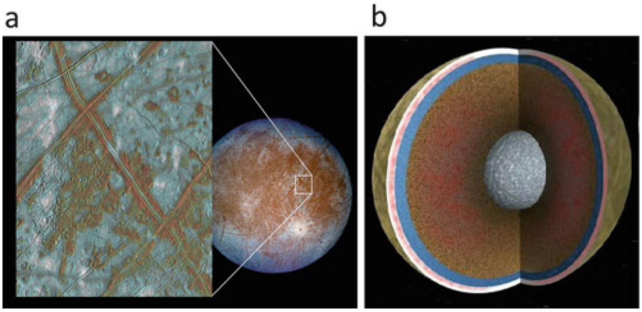


Fig. 11.3 Europa, surface and interior. Constant gravitational flexing has ground Europa's surface into the smoothest in the Solar System. (**a**) Close-up of surface showing criss-crossing lines and fractures reflecting dynamic forces that allow subsurface materials to erupt from the ocean below. The absence of craters indicates a young surface under constant reconstruction. (**b**) Artist's conception showing Europas's interior to consist of a metallic core, encased in a rocky mantle, surrounded by a global ocean frozen at the surface. *Credit: NASA/JPL/University of Arizona*

surface of the ocean is frozen solid to a depth thought to be at least 19 km (Schenk 2002), and possibly much more (Spohn and Schubert 2003). The ice may be much thinner in some areas, such as the Chaos region, where the surface appears heavily broken. The more recent detection of water plumes springing through the Europan crust (Roth et al. 2014) supports the notion that the crust may be quite thin in some regions. Many cracks, fissures (linnae), and separated blocks are evident (Sullivan et al. 1998; Figueredo et al. 2003), indicating translational forces presumably arising from tidal flexing between Europa's huge neighbors, Jupiter and Io, inside her orbit, and the significantly larger moons, Ganymede and Callisto, outside her orbit (Hoppa et al. 1999). Some surficial features on Europa are reminiscent of mid-ocean ridges and the process of subduction on Earth, hinting that some type of plate tectonics may also be occurring (Kattenhorn and Prockter 2014). Hydrated salt minerals such as magnesium sulfates and sodium carbonates have been detected in the optically darker areas of Europa, including the lineaments, and may represent evaporite deposits formed by water, rich in dissolved salts, reaching the surface from the ocean underlying the ice crust (McCord et al. 1998). Europa's surface is relatively devoid of craters, further suggesting a young age (Pappalardo et al. 1998).

Light cannot penetrate more than a few meters of the ice shell on Europa. Conceivably, some algae sequestered within liquified chambers in the ice near the surface could harvest sunlight for energy, perhaps as descendants of ancestral phototrophs that evolved before the ocean froze over. This one conceivable exception aside, if life exists on Europa, it must rely on forms of energy other than light.

Europa has a tenuous oxygen atmosphere, formed from oxygen dissociated by sputtering of ice by energetic particles from the Jovian magnetosphere (Hall et al. 1995; Sieger et al. 1998). Estimates of whether and how long it would take for oxygen to migrate through the ice to the ocean below have varied from a low probability and slow movement (Schenk 2002) to a high level of exchange between the atmosphere and the ocean (Greenberg 2010). The strong oxidant, hydrogen peroxide, has also been detected on Europa's surface (Carlson et al. 1999; Loeffler and Hudson 2015).

Europa is large enough to generate heat internally from radiolytic decay, so the prospect of thermal emissions at the rocky interface at the bottom of the ocean, analogous to hot spots on the floor of the oceans on Earth, is a tempting speculation. If, as on Earth, such hydrothermal emissions on Europa include H_2, energy might be obtained by reduction of the various sulfate salts known to be present in the ocean (Zolotov and Shock 2003), or by reduction of iron from Fe(III) to Fe(II). If CO_2 is present, energy could also be obtained by methanogenesis (McCollom 1999; Schulze-Makuch and Irwin 2002a). For chemical reactions to serve as a consistent and long-term energy source, reduced compounds have to be re-oxidized to maintain the oxidation-reduction cycle. Thus O_2 or H_2O_2 from the surface, or unknown oxidants at depth, have to be available to complete the cycle. As shown in Chap. 5, chemotrophy is a competitive alternative to phototrophy as an energy source for living systems, so the absence of light beneath the shell of ice that encases Europa is not a barrier to the evolution and persistence of life there. Other sources of energy that could be available in the subsurface ocean of Europa include thermal and ionic gradients, and the kinetic energy of ocean currents generated by tidal excursions (Schulze-Makuch and Irwin 2002a; Irwin and Schulze-Makuch 2011).

The attraction of Europa as a potential abode for life has long rested on three characteristics of the satellite: (1) The abundance of salty water containing an inventory of complex molecules, providing the possibility of redox chemistry; (2) the sequestration of the putative biosphere beneath a protective and insulating layer of thick ice; and (3) the availability of other forms of energy not including light. Most observers have tied speculation about the nature and extent of the putative biosphere to assumptions about the amount of energy that is actually available. We calculated a model ecosystem based on methanogenic producers (Irwin and Schulze-Makuch 2003). Making reasonable assumptions about the amounts of hydrogen and methane that could be available and using known efficiencies of energy transfer between trophic levels within ecosystems on Earth, we calculated that 1 g of biomass (about the size of a tadpole) could be found for every 32.5 cubic meters of ocean (about the volume of a small residential swimming pool). Using a similar strategy, Chyba and Phillips (2001) proposed an ecosystem based on oxidation of formaldehyde by radiolytically generated oxygen which yielded a global biomass nearly five times greater than our estimates, while Zolotov and Shock (2003) calculated a biomass over five orders of magnitude lower than ours for their ecosystem based on sulfate reduction. The large degree of uncertainty due to lack of actual data makes it impossible to gauge whether any of these models approaches reality, but they at least show that a biosphere of some magnitude could be supported in the ocean of Europa without making assumptions that are illogical or contrary to known facts.

We have provided the most detailed projection of what a biosphere on Europa could look like (Irwin and Schulze-Makuch 2011). We have envisioned a complex ecosystem based initially on chemoautotrophic producers (with descendants evolving to harvest energy from osmotic gradients, ionic gradients, and ocean currents) and three trophic levels of consumers—some of which inhabit the ice undersurface while others live on the ocean floor, along with benthic detrivores. Our guess is that the producers are largely stationary, and that motility is limited at all but the highest trophic levels, so that marine life on Europa would be more plant-like than animal-like. The availability of energy is the rate-limiting resource for motility. Until that information becomes available, the nature of life on Europa (if it exists) will remain largely guesswork.

11.2.4 Ganymede and Callisto

The two outermost and largest of the four Galilean satellites are larger versions of Europa, except that heavy cratering indicates older and more stable surfaces on both moons than on Europa. Tenuous atmospheres of O_2 have been detected on Ganymede, and of CO_2 on Callisto. Ganymede is well differentiated into a metallic core, silicate mantle, and a substantial water-ice ocean (Anderson et al. 1997), while Callisto may be only partially differentiated, with a water-ice shell which may be liquid below the frozen cover (Sohl et al. 2002). Equilibrium models of thermal conductivity predict that the ice shell of an ocean that is 95% H_2O and 5% NH_3 will be around 60 to 80 km thick atop oceans that may be 200 to 350 km deep (Spohn and Schubert 2003).

All that was said above about the plausibility of life on Europa applies to Ganymede and Callisto, with one caveat. While the subsurface ocean on Europa is thought to be in direct contact with the underlying rocky mantle, the oceans of Ganymede and Callisto are likely sandwiched between two layers of ice, which would make hydrothermal vents as they exist on Earth and possibly on Europa difficult to envision. Also, the stability of their surfaces indicates that the two larger moons have been subjected to much less tidal flexing than Europa, so forms of energy derived from gravitational forces, such as kinetic energy from ocean currents, may be less in play. A stable surface also may make migration of oxidants into the subsurface ocean more difficult. Another consideration derives from models that suggest that Ganymede and Callisto formed at lower temperatures than Europa (Consolmagno and Lewis 1976), which could have had a bearing on the ease with which life may have originated there. With those possibly limiting factors in mind, the plausibility of life on Ganymede and Callisto appears less than for Europa, but still well above negligible.

11.2.5 Enceladus

Enceladus is a small moon, 512 km in diameter, that orbits Saturn just 4 Saturnian diameters from the surface of the gas giant. The much larger moon Titan (5150 km in diameter) orbits Saturn at a distance of just under 20 Saturnian diameters. Periodic gravitational pull from two directions, therefore, has a strong effect on Enceladus.

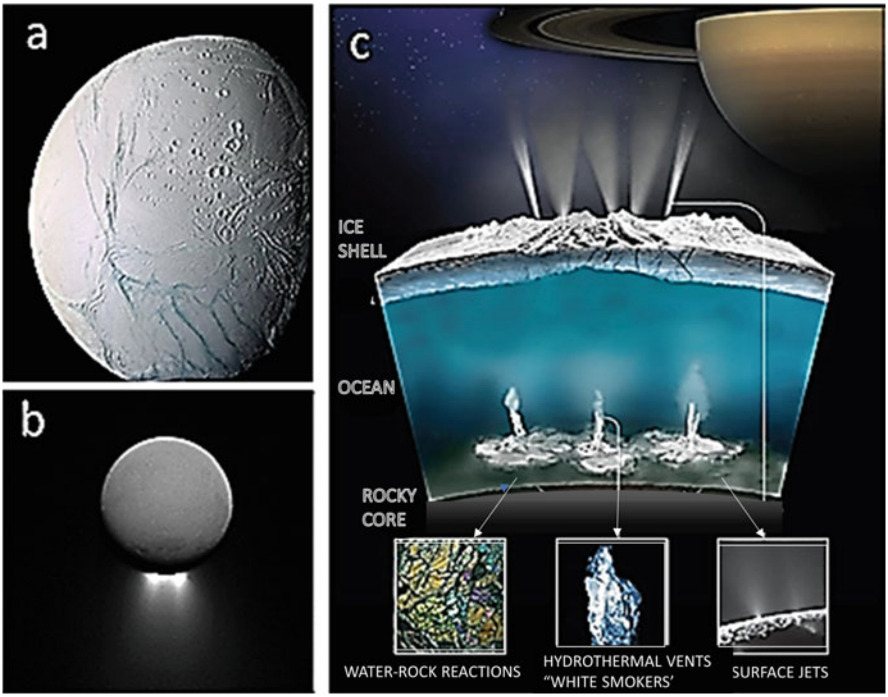


Fig. 11.4 Volatile activity on Enceladus. (**a**) View of Enceladus showing "tiger stripes" at the south pole; (**b**) Distant view of Enceladus showing ejection of vapor-granular composite; (**c**) artist's conception of how volatiles are created and ejected from the ocean floor through the "tiger stripe" ruptures on Enceladus. *Credit: NASA/JPL/Photojournal*

The southern polar region of Enceladus is characterized by a relatively smooth surface, indicative of resurfacing, broken by linear gashes referred to as "tiger stripes" (Fig. 11.4a). Gaseous and granular material is ejected at a high velocity (Fig. 11.4b) in volumes sufficient to account for the E ring around Saturn (Hansen et al. 2006; Spahn et al. 2006). These ejections are likely correlated with tidally controlled periodic rifts in the ice shell (Hurford et al. 2007). Energy driving the ejections could come from shear heating by tidally driven lateral (strike-slip) fault motion associated with the tiger stripes (Nimmo et al. 2007), hydrothermal vents beneath the ice (Hsu et al. 2015; Postberg et al. 2016), or aqueous ammonia methane clathrate decomposition (Kieffer et al. 2006; Shin et al. 2012).

Evidence for a subsurface ocean of liquid water is now strong (Schmidt et al. 2008). Gravitational field measurements suggest a regional south polar subsurface ocean of about 10 km thickness located beneath an ice crust 30–40 km thick (Iess et al. 2014; Hsu et al. 2015) at higher latitudes, but as little as 5 km thick at the south pole (Postberg et al. 2016).

Plumes ejected from Enceladus include organic carbon, biologically available nitrogen, redox energy sources, and inorganic salts (Postberg et al. 2009; McKay et al. 2014). Cassini's Cosmic Dust Analyzer picked up nanoparticles of ice with silica inclusions consistent with origin from ocean floor vents (Postberg et al. 2016).

Molecular hydrogen in the plumes ejected from Enceladus signals a hydrothermal interaction of water with rock that signals thermodynamic disequilibrium which would favor the formation of methane from CO_2 (Waite et al. 2017). The prebiotic constituents of life and the potential of a redox chemical as well as a thermal source of energy thus are present in a marine environment on Enceladus.

While the chemical, solvent, and energetic requirements of life are potentially met beneath the surface of Enceladus, the question remains of whether life could have originated there. Since it seems unlikely that a surface with standing liquid water ever existed for very long if at all on Enceladus, life would either have to have been generated at the water rock interface—likely at hydrothermal vents—or been delivered to Enceladus from another point of origin. To the extent that either of those possibilities is real, Enceladus could be one of the most promising places to search for life beyond Earth in the Solar System (McKay et al. 2008, 2014, Deamer and Damer 2017)—rivaled recently only by the dwarf planet Ceres (see Sect. 11.1.5 above). Thus, Enceladus has advanced to becoming a prime target for astrobiology and astrobiology-related missions (Porco 2017; Mathies et al. 2017)

11.2.6 Titan

While every planetary body in the Solar System has turned out to be unique, Saturn's largest moon, Titan, is more unique than most. Enshrouded in a dense atmosphere of nitrogen and volatile organic compound, obscured by a thick layer of larger organic molecules (tholins), the surface features of Titan were not revealed until the Huygens lander descended through its thick atmosphere for a soft landing on 14 January 2005 (Fig. 11.5).

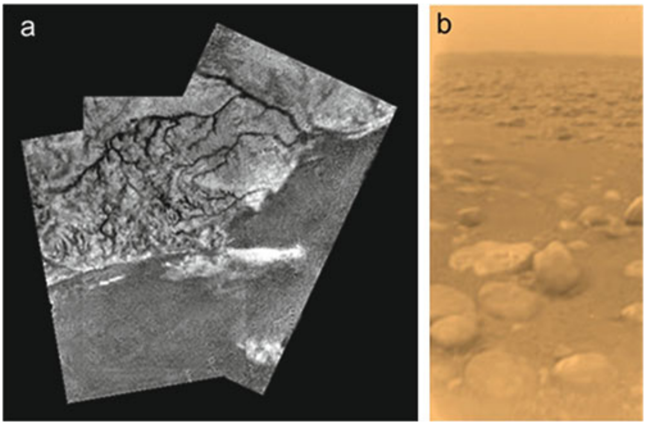


Fig. 11.5 The surface of Titan, revealed as the Huygens Probe (**a**) descended below its opaque atmosphere, and (**b**) landed on a substrate with the consistency of wet sand, provoking a brief expulsion of methane gas. *Credit: NASA/JPL/Caltech*

Subsequent investigations have disclosed a world with a surface so cold that water ice is frozen solid, but holds ponds and lakes of liquid hydrocarbons, charged by ethane rain precipitated from the skies and methane released at the surface (Raulin 2008; Moskowitz 2014). Channels apparently cut by flowing liquids, and other depressed areas, are coated with a dark substance thought to consist of tholins. There is now good evidence of a global layer of a water-ammonia mix beneath the frozen crust (Lorenz et al. 2008; Kerr 2012). Tidal stresses may be responsible for cryovolcanic activity, and provide possible pathways for liquid water-ammonia outbursts on Titan's surface, and the release of methane in its atmosphere (Sohl et al. 2014).

The most plausible reconstruction of planetesimal history for Titan is that it emerged from the generative stages of the Saturnian system, warm enough initially to hold oceans of liquid water (Schulze-Makuch and Grinspoon 2005) and massive enough to retain an ammonia-rich atmosphere with increasing amounts of methane and ethane (Coustenis and Lorenz 1999). As the satellite cooled, the aqueous ocean froze and became submerged by an ethane/methane-drenched surface of silica and tholins, as radiolytic conversion of the carbon compounds turned them into more complex organic polymers (Waite et al. 2006), and radiolysis dissociated the ammonia into hydrogen which escaped, leaving the N_2-rich atmosphere that exists today (Irwin and Schulze-Makuch 2011).

These events left Titan with two distinct habitats: a subsurface aquatic domain, and a scatter of hydrocarbon ponds, lakes, and seas on the surface (Fig. 11.6). The subsurface aquatic habitat could in principle be similar to that of Europa, except for probably being highly alkaline because of the ammonia content of the ocean. Anaerobic methane thiol degradation has been observed in highly alkaliphilic (pH 10) communities collected from several alkaline sediments on Earth, though growth required mesophilic (30 °C) conditions (van Leerdam et al. 2008), so applicability to Titan is questionable. Organisms on Earth are known to exist in highly alkaline environments, so that alone would not preclude the possibility of a subsurface aquatic biosphere.

Our ability to speculate about the possibility of a biosphere inhabiting the hydrophobic liquids on the surface is challenged by the fact that no such life exists to our knowledge on Earth. Microbes are known that can digest hydrocarbons at mesophilic temperatures (Prince 1993; Marcano et al. 2002; Wang et al. 2009a), but again, applicability to Titan is questionable. More problematic is envisioning how an organism could maintain structural integrity in a highly hydrophobic solvent, though a new type of membrane composed of small organic nitrogen compounds capable of forming and functioning in liquid methane at cryogenic temperatures has been proposed (Stevenson et al. 2015a, b), and additional adaptations have been noted for the fungus, *Fusarium alkanophyllum*, which can grow in saturated hydrocarbons with little or no oxygen or water requirements (Marcano et al. 2002). That hydrocarbon-dwelling organisms could exist, therefore, cannot be excluded.

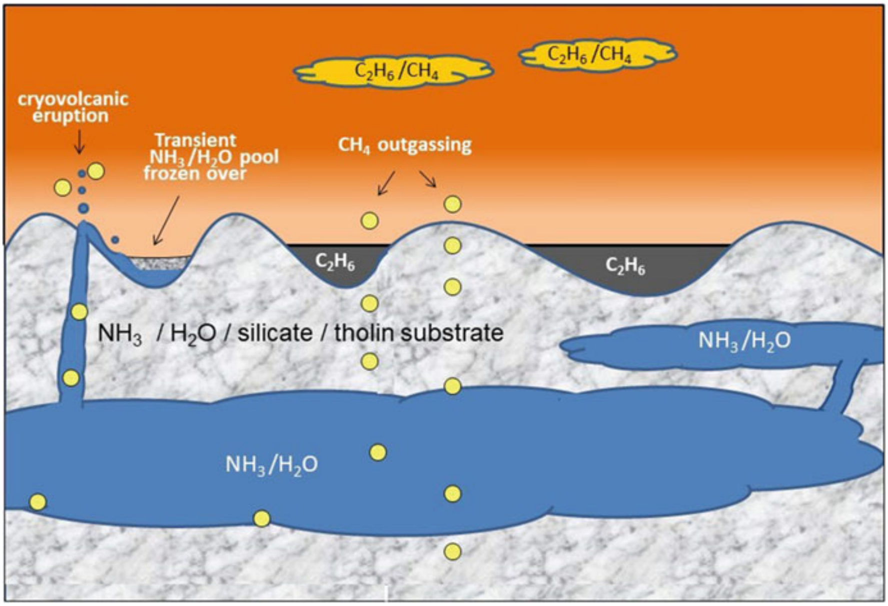


Fig. 11.6 Two possible biospheres on Titan. Circumstantial evidence supports the existence of an underground hydrosphere of NH_3 and H_2O, while pools of C_2H_6 and CH_4 constitute a liposphere on the surface. Occasional cryovolcanic eruptions disgorge the H_2O/NH_3 onto the surface where it quickly freezes over. *Credit: Art by Louis Irwin, from Irwin and Schulze-Makuch (*2011*), with permission*

A particularly suitable habitat for microorganism may lie at the bottom of the hydrocarbon lakes and seas, especially if heated ammonia-water is infiltrating from beneath (Schulze-Makuch and Grinspoon 2005). An analog for this scenario might be Pitch Lake in Trinidad, a natural asphalt lake which contains infiltrated droplets of salt water. Microbes within these droplets were found degrading hydrocarbons (Meckenstock et al. 2014).

Energy is another potential barrier for the support of life on Titan. Sunlight diminished to 1–2% of its intensity on Earth, and extremely frigid temperatures of <100 K (-173 °C) limit the availability of energy from those sources at the surface. A number of suggestions for chemical sources of energy have been offered, from photochemically produced organics, particularly acetylene, in Titan's atmosphere that could be reduced with atmospheric hydrogen (McKay and Smith 2005; McKay 2016), to recombination of radicals created in the atmosphere by ultraviolet radiation (Schulze-Makuch and Grinspoon 2005). Though Titan has an abundance of organic molecules for fuel, it has very little oxygen or other obvious oxidizing agents, so it could be simply a world with an abundance of potential chemical energy, but with no way to release it.

Beneath the surface, potential energy sources would be the same as on Europa, though kinetic energy generated by tidal excursions would presumably be less. Evidence of cryovolcanic activity on Titan suggests the release of energy from the interior, either from radiogenic heating (Kerr 2005), the release of methane from clathrates (Grasset and Pargamin 2005; Tobie et al. 2009), or other unknown sources.

We have repeatedly stressed, as have others, that the absence of Earth-like conditions on other worlds does not mean that forms of life unknown to us cannot exist there (Schulze-Makuch 2002; Benner 2002; Grinspoon 2003; Schulze-Makuch and Irwin 2004, 2006; Ward 2005; Baross et al. 2007; Irwin and Schulze-Makuch 2011). This is particularly true when a trajectory for the evolution of exotic forms from more familiar ancestral forms can be traced at least in theory (Schulze-Makuch et al. 2015a, b). We have done this in detail for Titan, showing how two diversified biospheres could exist in principle in both the hydrospheric and lipospheric habitats there, respectively (Irwin and Schulze-Makuch 2011). Nonetheless, until analog organisms can be shown to exist under the conditions on Titan, or at least until models of such organisms can be envisioned to a credible degree, a skeptical assessment of the possibility of life on Titan is not unreasonable.

11.2.7 Triton

Triton is the largest moon of Neptune—larger even than Pluto—with which it most likely shared an origin as a Kuiper Belt planetesimal at the outer edge of the Solar System. Most astronomers believe that Triton was captured by Neptune, as evidenced by the former's retrograde rotation and its orbital plane highly inclined to the ecliptic. Like most of the outer Solar System satellites, it consists of a rocky core encased in a shell of water frozen rock solid, along with other frozen volatiles (Fig. 11.7). In fact, Triton is so cold—38 K (−235 °C)—that even N_2 is frozen on its surface (Abelson 1989; McKinnon and Kirk 1999).

Fig. 11.7 Complex topography of Triton. The southern hemisphere's surface is relatively young, lacking extensive cratering. Wispy streaks of grey material extruded from the interior show a consistent downwind scatter to the northeast, amid light-colored nitrogen frost. The cantaloupe features perhaps related to diapirism of softer subsurface matter are visible in the mid-latitudes. *Credit: NASA/JPL-Caltech*

Models of Triton's capture by Neptune, which may well have involved tearing it away from a co-rotating twin (Agnor and Hamilton 2006), suggest that its initial orbit would have been highly elliptical, with radical gravitational excursions sufficient to heat Triton enough to keep water liquid for millions of years, even if the surface froze quite soon. If accurate, Triton can be presumed to have followed a trajectory that took it through a Europa-like stage to something like Titan. The youth of Triton's surface, indicated by visible evidence of cryovolcanic eruptions and the lack of much cratering, suggests that internal energy still drives its geological activity, supplemented by explosive outgassing of N_2 from the polar regions that alternate facing the Sun (Abelson 1989; McKinnon and Kirk 1999). The peculiar cantaloupe topography of Triton's mid-latitudes may be evidence of diapir-driven activity by softer material below the surface, and the orange-pink coloration may be indicative of organic compounds generated by radiation-driven interactions in its upper tenuous atmosphere (Thompson and Sagan 1990).

If Triton indeed evolved as Europa did, first covered with liquid water that froze on top, then progressed through a phase like Titan with some mix of precipitated organics, and proceeded beyond that to an even colder world with solidified N_2 at its surface, then Triton could harbor not just two, but three putative habitats for life (Irwin and Schulze-Makuch 2011): (1) a subsurface marine habitat, (2) inclusions of H_2O (or mix of H_2O and NH_3) at water-ice interfaces or in channels encased in ice, and (3) inclusions of liquid N_2 at interfaces with solid N_2 or in liquid channels encased within frozen N_2. If water really did stay liquid for hundreds of millions of years on Triton's surface, life would have had time to originate and begin evolving. As Triton cooled, directional selection could have led to microorganisms that occupied the more constricted habitats of ice-water and nitrogen inclusions or interfaces (Irwin and Schulze-Makuch 2011).

Triton is intriguing as probably the only sizable body in the Solar System where N_2 conceivably could be a solvent, and silicon in the form of silanes could possibly serve as a building block for living systems. Nitrogen is liquid between $-210°$ and -196 °C (Fig. 7.4), a thermal range that must occur at some depth beneath the surface. Si theoretically could replace C as a building block for biomolecules in conditions of extreme cold, high pressure, lack of oxygen and liquid water, and the presence of compatible organic solvents like methane and ethane (see Sect. 6.4.4.1). The presence of silicon-based life sequestered in layers or microchannels of liquid N_2 beneath the surface of Triton, while highly speculative, can therefore not be precluded.

11.2.8 Dwarf Planets of the Outer Solar System

The Pluto-Charon couple and Eris are the two largest known dwarf planets in the outer Solar System. Eris is the largest by mass (1.27 times that of Pluto) and most distant from the Sun. It has a highly elliptical orbit that varies from roughly 40 to 97 AU. At such a distance, it is very poorly characterized, but reasonably could be assumed to resemble Pluto in composition, as both are presumed (along with Triton) to have originated in the Kuiper Belt. Pluto and Charon form a double-planet pair that was visited by the *New Horizons* space craft.

Pluto's diameter is about two-thirds that of Earth's moon, but is much less dense, suggesting a rocky core encased in a substantial shell or frozen water and other volatile compounds—especially nitrogen and methane. It has a highly elliptical orbit which brings it close enough to the Sun at perihelion to sublimate its volatile compounds into a thin atmosphere of N_2 and CH_4, while at its maximum distance from the Sun of 49 AU, the atmosphere likely freezes back onto the surface.

Images taken from the *New Horizon* spacecraft's closest approach to Pluto in July 2015 reveal a surprisingly complex topography (Fig. 11.8). Pluto contains expansive, smooth plains—features suggestive of active geological processes (Stern et al. 2015). There are high jagged mountains, long rifts, troughs, and valleys, and peculiar "snakeskin" contours on the surface somewhat reminiscent of the cantaloupe regions of Triton. Sputnik Planitia—a prominent tear-drop-shaped depression approximately 1000 km in diameter—is characterized by a smooth, craterless plain 3–4 km beneath the surrounding rugged uplands. The floor appears to be the surface of a massive block of actively convecting volatile ices of N_2, CH_4, and CO, which may float above a subsurface ocean (Bertrand and Forget 2016; Keane et al. 2016). The age of Sputnik Planitia's surface has been estimated at only about 10 million years (Trilling 2016). Elsewhere on Pluto, evidence of cryovolcanism and dark areas suggestive of tholins are present (Shekhtman et al. 2018).

Pluto's smaller (about half-sized) companion, Charon, shows evidence of the presence of water-ammonia ice, which often is associated with flow like features on many icy satellites (Brown and Calvin 2000). It appears to have been geologically active in the past like Pluto, but currently may be less so, perhaps owing to its smaller size.

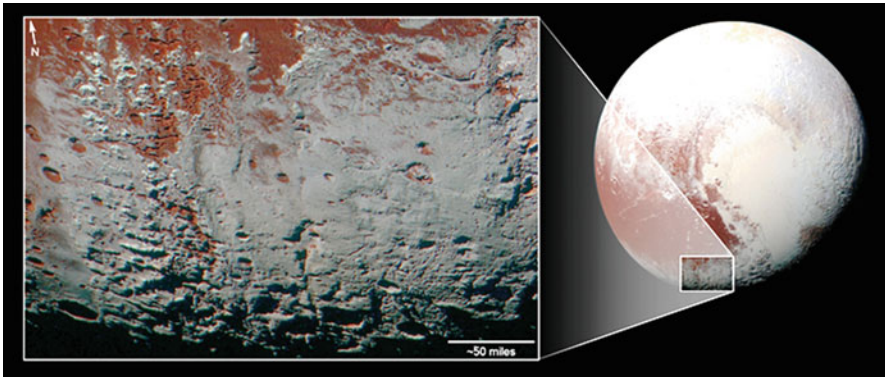


Fig. 11.8 Complex topography near Pluto's south pole. The close-up image reveals many troughs and scarps, elongated valleys, as well a smooth plains. Only a few craters are visible, indicative of a relatively young surface. Much of the surface is covered by nitrogen and methane snow. *Credit: NASA/Johns Hopkins University Applied Physics Laboratory/Southwest Research Institute*

The chance that these extremely frigid Kuiper Belt planetary bodies could harbor aquatic-based life as we know it seems extremely small. In their composition and characteristics, they resemble Triton, and Titan to a lesser extent. Inasmuch as exotic forms of life unknown to us could exist on those larger bodies, as discussed above, the possibility that life could exist in the Kuiper Belt as well cannot be totally dismissed.

11.3 Small Bodies

Billions of bodies smaller than dwarf planets swirl about within and around the Solar System. As potential habitats for life, they seem unlikely in the extreme. But they have turned out to be a surprisingly rich reservoir of chemicals that may have contributed the building blocks of biomolecules that took hold on larger, more stable planets and moons where life had a better chance to unfold.

11.3.1 Asteroids

Asteroids are the remnants of rocky accretions that failed to form planets before multiple collisions and the gravitational stress of other planets (especially Jupiter) tore them apart. Most asteroids orbit the Sun in the main asteroid belt between Mars and Jupiter, though some have orbits closer to Earth, outside the main belt, and others, called Trojans, occupy the same orbit as Jupiter either 60° behind or ahead of the huge planet. The largest asteroid by far is Ceres, now designated a dwarf planet, as discussed above.

The complex chemistry and water discovered on Ceres (Sect. 11.1.5) may not be unusual for asteroids. For example, gullies possibly cut by water were also found on Vesta, the second largest object in the asteroid belt (Scully et al. 2015). Evidence increasingly indicates that complex organic molecules and even amino acids are ubiquitous on small bodies in the Solar System (Cronin et al. 1988; Anders 1989; Chyba et al. 1990a, b; Küppers 2017). Asteroid impacts could also influence the genesis and trajectory of life by promoting the formation of certain biomolecules (Mimura and Toyama 2005), by melting ice to provide transient liquid habitats, and by affecting the ecology of planets where life may exist by opening new niches into which life can expand, as in the case of the evolutionary radiation of mammals after the Cretaceous-Tertiary (K-T) boundary caused by a major asteroid strike on Earth (Cockell and Bland 2005).

There is thus far no evidence for any form of life on an asteroid, though Ceres is close and accessible enough for a sample return mission that could investigate the possibility of life on that dwarf planet.

11.3.2 Comets

Comets are smaller bodies that orbit the Sun in highly irregular orbits. Most come from the Oort Cloud, a spherical conglomerate of residues from the early formation of the Solar System that has a radius of about 1.6 light years and contains trillions of small objects akin to rocky, dusty snowballs that become visible as they near the Sun and their volatile compounds sublimate away.

Like asteroids, comets contain biomolecular precursors (Greenberg 2000; Sandford 2008; Bockelee-Morvan and Biver 2017). A diverse suite of organic molecules was captured in dust from the comet 81P/Wild 2 by the Stardust spacecraft (Sandford et al. 2006). The recent Rosetta mission to the comet 67P/Churyumov-Gerasimenko detected volatile glycine accompanied by methylamine and ethylamine (Altwegg et al. 2016), consistent with data from the Stardust mission, despite previous concerns about contamination (Spencer and Zare 2007). The discovery of these molecules has been accompanied by the demonstration of plausible pathways to the creation of nucleosides (Nuevo et al. 2009; Becker et al. 2016). Some of the chemical ingredients for living systems would thus appear to be present in comets. However, the low-temperature extremes, the absence of liquid, and the lack of consistent sources of energy on comets render the chances that they could harbor living organisms extremely remote.

11.4 Metrics for the Plausibility of Life in the Solar System

We will now summarize what we think about the possibility of life throughout our Solar System in terms of metrics proposed as systematic and quasi-quantitative approaches to assessing the plausibility of life on other worlds. One of the first metrics proposed was our Plausibility of Life (POL) index (Irwin and Schulze-Makuch 2001; Schulze-Makuch and Irwin 2008). The POL index is based on criteria for the existence of life such as the presence of (1) a fluid medium, (2) a source of energy, and (3) constituents and conditions compatible with polymeric chemistry under the key assumptions that (a) life arises quickly under appropriate formative conditions and (b) remains static in stable environments or adapts to changing environments. We assigned a POL rating for each major planetary body in our Solar System, while pointing out that the rating must be regarded as a dynamic value consistent with the information currently available. Though quantitative, it should not be viewed as a measure of probability that life exists on the body in question, but only a relative measure of the plausibility that life could exist there, given the planetary history of the body and its past and current conditions. An updated definition of the POL categories with some examples are given in Table 11.1. An updated POL rating for all planets and major satellites in our Solar System consistent with knowledge at the time of this writing is provided in Tables 11.2 and 11.3.

Table 11.1 Astrobiology plausibility categories (modified from Irwin and Schulze-Makuch 2001)

Category	Definition	Examples
I	Presence of liquid water, available energy, organic compounds, atmospheric or surface shielding, and strong evidence of biogenic processes.	Earth
II	Evidence for past or present liquid water, availability of energy, inference of organic compounds, and planetary history favorable for genesis of life.	Mars, Europa, Enceladus, Ceres
III	Physically extreme conditions, but with evidence of energy sources and complex chemistry possibly suitable for life forms unknown on Earth	Titan, Venus
IV	Persistence of life very different from on Earth conceivable in isolated habitats, or reasonable inference of past conditions suitable for the origin of life prior to the development of conditions so harsh as to make its perseverance at present unlikely but conceivable in isolated habitats	Triton, Io
V	Conditions so unfavorable for life by any reasonable definition that its origin or persistence cannot be rated a realistic probability	Giant planets, Sun, Moon

Table 11.2 Plausibility of Life (POL) index for planets in our Solar System

Body	POL index	Reasoning for rating
Mercury	IV	Intense solar radiation; little if any geological cycling and no atmosphere, but thermal gradients at terminator and water ice at poles,
Venus	III	Extreme heat at surface and highly caustic atmosphere; but primordial ocean likely, water vapor in atmosphere, minute amounts of organic compounds, active geology with chemical recycling likely, and moderate temperatures in lower atmosphere
Earth	I	Salt water oceans, fresh water on surface, plate tectonics provide geological recycling, and oxygen-rich atmosphere with protective ozone layer. Life is present.
Mars	II	Oxidized surface, thin atmosphere, and some geological cycling in recent planetary history, but ample evidence for liquid water on surface in the past and subsurface water now; surface temperatures sometimes above freezing point of water, polar ice caps with some water ice, and evidence for presence of organic compounds~~.~~
Ceres	II	Salty water beneath ice cap; cryovolcanism and possible subsurface heat; clay minerals and organic compounds in ejecta from interior
Jupiter Saturn Uranus Neptune	V	Giant planets with indistinct physical transitions; temperature and pressure extremes; abundant energy and presence of organic and nitrogen compounds, but lack of solid substrates except at core.
Pluto/ Charon	IV	Extreme cold, density ~2.1 implies rock/ice composition; mix of light and dark features implies complex chemistry, and tidal flexing could provide energy, but likely origin as asteroids makes genesis of life improbable.

Table 11.3 Plausibility of Life (POL) index for major satellites in our Solar System

Body	POL index	Reasoning for rating
Moon	V	Extremely dry, no protective atmosphere, water ice at poles but no geological cycling.
Io	IV	Sharp thermal gradients and geochemical cycling; volcanic activity generates thin atmosphere and liquid sulfur compounds near surface for some time periods; coloration implies complex chemistry; but temperature fluctuations and radiation doses are extreme.
Europa Ganymede	II	High radiation and extremely low temperature at surface, but planetary ocean likely beneath ice shell. Surface coloration implies complex chemistry and frequent resurfacing implies geological activity.
Callisto	III	High radiation and extremely low surface temperature; possible subsurface liquid water, but little energy flux.
Tethys Dione Rhea	IV	Little evidence for liquid water at present; very low density and high albedo imply mostly water-ice composition; high radiation environment; extremely cold.
Enceladus	II	High radiation environment, extremely cold, and too small for significant radiogenic heating; but extensive resurfacing with evidence of ice geysers suggest geological activity, subsurface liquid water, and energy from tidal flexing
Iapetus	IV	High radiation environment, extremely cold, with no evidence for liquid water at present; low density and moderate albedo imply mostly ice composition; but dark leading edge suggests possible hydrocarbon chemistry.
Titan	III	Dense, colored atmosphere implies complex organic (reducing) chemistry; liquid hydrocarbons present on surface with possible water-ammonia liquid beneath surface; density of ~1.8 implies organic liquids and/or water-ice with solid core.
Titania	IV	Possible subsurface or recent surface liquid with evidence of liquid flow in canyons; relatively small for radiogenic heating, but tidal flexing could provide energy; extremely cold at surface.
Ariel Miranda Umbriel Oberon	IV	Small size and insufficient evidence of energy gradients; high albedo and density of ~1.5–1.7 imply rock/ice composition; extremely cold.
Triton	IV	Coloration implies complex chemistry; tidal flexing, radiogenic heating, or chemistry could provide energy; possible subsurface liquid water or water-ammonia mixes; density of ~2 implies rocky core with water/ice surface; but has coldest surface recorded in solar system.
Comets	V	Extreme cold, no atmosphere, no persistent internal energy source, rock/ice mixtures in composition, abundant water ice with possible hydrothermal alteration in parent bodies

Earth is the only body in our Solar System that qualifies for the highest POL rating. Based on information from recent robotic probes, the following planets and satellites now meet the criteria for Category II: Mars, Ceres, Europa, Ganymede, and Enceladus. Category III bodies consist of Callisto, Titan and Triton—exotic worlds with characteristics amenable to life in forms yet unknown to us. Based on our knowledge at this time, these eight worlds are the most likely, and perhaps the only likely habitats for life beyond Earth in our Solar System.

In the next chapter, we consider several other metrics for assessing the plausibility of life on other worlds. Different assumptions underlying each metric lead to slightly different plausibility estimates. For example, newer data used to recalculate the Planetary Habitability Index (Schulze-Makuch et al. 2011) result in the highest ratings after Earth for Mars, Titan, Europa, and Enceladus, in that order. If sample return missions in the future bring back more information from Ceres and the clouds of Venus, those two bodies could be added as higher possibilities for life elsewhere in the Solar System.

The only realistic chances for the evolution of multi-tiered biospheres consisting of organisms larger and more complex than microbes extant today would appear to be on bodies with sizeable subsurface oceans in contact with rocky cores: Europa foremost, with Enceladus, Ceres, Titan, Triton, and Pluto as distant possibilities. Mars and Venus may have harbored conditions sufficient and long enough for the origin and diversification of complex biospheres at one time. There appears to be no chance that such forms of life survive on Venus today; and on Mars, the habitat possibilities for life more complex than microbes are likely restricted to extreme niche environments such as lava tubes near the surface. For that reason, lava tubes on Mars should be a priority for future missions.

11.5 Chapter Summary

Conditions for the origin of life were probably good in the early history of four planetary bodies in the inner Solar System: Venus, Earth, Mars, and Ceres. Microbial life conceivably could still exist in the clouds of Venus, and beneath or near the surface of Mars. Organisms more complex than microbes could even persist in sequestered habitats, like lava tubes, on Mars. If Ceres does contain an extended body of salty water beneath its icy shell, some forms of complex life could even exist there as well.

The outer Solar System is dominated by giant planets and their satellites. While the gas (Jupiter and Saturn) and ice (Uranus and Neptune) giants provide no credible habitats for life, some of their satellites do. At Jupiter, Europa consists of a massive, global ocean with several putative energy sources beneath a frozen surface. It holds perhaps the greatest promise of any body in the Solar System beyond Earth of harboring a multi-tiered ecosystem. Recent evidence from Saturn's small satellite, Enceladus, reveals many characteristics similar to Europa, so it too along with Ceres, should be given serious astrobiological attention.

Saturn's large moon, Titan, and Neptune's sizable captured satellite, Triton, are both exotic worlds with abundant organic chemistry and probably aquatic-ammonia-salt habitats beneath their surfaces. If life exists on those worlds, it could be fragmented into different forms according to the habitat in which it thrives; and in any case would almost surely include forms totally unlike any living system on

Earth. The Pluto-Charon pair of dwarf planets resemble Triton. Like Titan and Triton, their planetary histories may have taken them from a Europa-like origin to their current state, where remnants of life from an earlier biosphere conceivably could persist.

By various metrics, the most likely habitats for life beyond Earth are near-surface and sequestered spaces on Mars, and sub-surface aquatic habitats on Europa, Ceres, and Enceladus. More speculative but distinct possibilities lie in the clouds of Venus and various habitats on Titan, Triton, and Pluto.

Chapter 12
Exoplanets and Exomoons

The study of exoplanets has revolutionized the scientific field of planet formation and changed scientific and public views on the possible frequency of life in the Universe. This has been motivated, at least to some extent, by the search for a second Earth. It started slowly with the first unambiguous evidence for an extrasolar planet announced by Alexander Wolszczan and Dale Andrew Frail (1992), and later confirmed by Wolszczan (1994). In 1995, Michel Mayor and Didier Queloz in Geneva reported that they had found a planet at least half the size of Jupiter rapidly orbiting the star 51 Pegasi (Mayor and Queloz 1995) in a 4 day orbit. Geoff Marcy and his colleagues at the University of California, Berkeley soon confirmed this finding (Marcy and Butler 1996, 1998), and Marcy's group has gone on to discover over 100 additional extrasolar planets. Since these initial findings, a flood of discoveries has brought the number of reported extrasolar planets to over 3800 as of this writing (for an update see https://exoplanets.nasa.gov/).

12.1 Methods for Detecting Planetary Bodies Outside the Solar System

The underlying problem of detecting exoplanets is that the host star is far brighter than the planet—the brightness ratio depending on the type of star, the planet, and the wavelength of observation. The factor is usually in the range of 1000 to 10 billion. Nevertheless, there are a few methods that not only can detect the presence of an exoplanet, but also obtain some additional information about it. The three most common methods for detecting exoplanets are detailed below.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_12

12.1.1 Radial Velocity

This method, pursued with vigor since the 1960s, is based on perturbations in the star's motion (wobble) due to interaction with one or more nearby planets. The difference in mass ratios between the star and a planet is in the order of 1000 to 100,000 (Sasselov 2008). Due to the gravitational pull of the exoplanet on the star, the star-planet(s) system rotates around its center of mass causing the star to wobble. This wobble can be measured through the Doppler Effect by a shift in wavelength in the visible spectrum of the star, which is proportional to the planet's mass. Many of the exoplanets have been found using this method, but its usefulness is limited by the determination of only a lower limit for the mass of the orbiting exoplanet. Also, at least one full orbit has to be observed to confirm that the wobble is actually caused by an exoplanet. Because larger planets and planets with a close orbit can induce larger wobbling amplitudes, this method is more efficient at finding larger planets in short period orbits.

12.1.2 Transit Photometry

The transit photometry method is based on the degree to which light is dimmed when a planet fortuitously passes nearly edge-on across the disk of its central star as seen from Earth. This method employs the difference in diameter between the star and its orbiting planet, which is typically a factor on the order of 10–100 (Sasselov 2008). If a Jupiter-size planet transits in front of a Sun-type star, a dimming of about 1% in the overall brightness of the Sun-planet system would be observed. However, the observation of a transit is exceedingly rare. For example, the transit of Venus across our Sun can be observed not more than twice within a century. Thus, thousands of stars have to be monitored simultaneously just to catch a few of those transits. If such an event can be observed, however, information about the planet's size and temperature can be determined, and in some cases major atmospheric constituents as well (Cowan 2014). Since planets that orbit closely to their central star can be detected more easily, this method is biased toward short-period planets.

12.1.3 Astrometry

Astrometrical measurements rely on very precise observations of star positions, their movements, and the cosmic background. One example is the technique of gravitational microlensing, which occurs if two stars are aligned in the line of sight from Earth so that the gravitational field of the front star acts as a magnifying lens for the light coming from the star behind it. If the star in the front has an orbiting planet, this will significantly alter the lensing effect with a rhythm that gives information about the orbiting planet. Unlike the radial velocity method and transit photometry, gravitational lensing is more sensitive to planets further away from their central star (1 to 10 AU for a Sun-like star). A disadvantage of the method is that only the mass of the exoplanet can be determined and that no follow-up observations are possible, because the chance alignment, which made the gravitational lensing event possible, will never occur again. Other astrometrical methods rely on very precise observations of star positions and their movements which have recently been made possible by space-based satellites and telescopes such as the European Space Agency's Gaia mission.

12.2 Detection Limits, or What We Know Now and What We Need to Learn

Currently only remote sensing provides a viable option for obtaining information about exoplanets. The distances are just too large. Only for the closest exoplanets such as Proxima b would a site visit with a robotic probe be a possible option (Schulze-Makuch and Bains 2017), but such a mission to the closest planetary system beyond our own probably lies at least 50 years in the future. It is sobering that the best resolution we can obtain with current technology is an unresolved dot of the observed exoplanet.

12.2.1 The One-Pixel Problem

Due to the great distances that lie between an exoplanet and Earth, only a few photons from the exoplanet will reach Earth. The photons are coming from both the central star and the planet, so the next challenge is to distinguish between the light coming from the star and the exoplanet. This can be done with interferometry to eliminate photons from the star, by physically blocking photons from the star with an occulter such as a starshade (Fig. 12.1) far from the telescope, or with a coronagraph within the telescope (Cowan 2014). The result in either case would be that the glare of the star is diminished, and the planet can be directly imaged as one dot. Once this is achieved, other parameters such as global mean temperatures might be determined, and possibly also processes that may affect the global character of the planet, especially its atmosphere and surface. For example, once the planet appears as a single dot, that dot would change brightness and color as it rotated and orbited its star. If conditions are favorable, this information could be used to get a crude map of the distribution of color on its surface, perhaps including ice caps and major continents (Bains and Schulze-Makuch 2017). Indeed, when the same single-pixel observations are applied to Earth, the analysis produced a coarse two-dimensional map of the continents and oceans, an estimate of the planetary obliquity, and

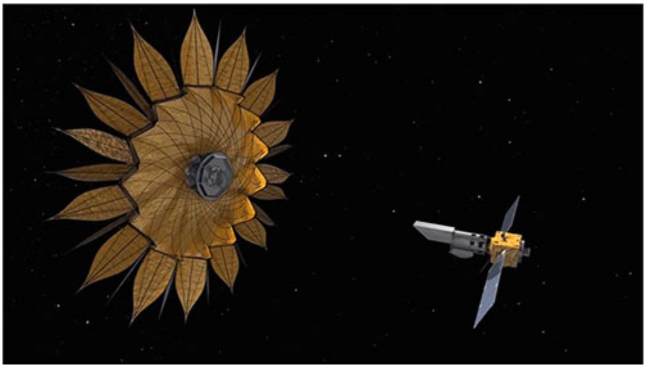


Fig. 12.1 The starshade has to be tens of meters across and fly in exact formation with a space telescope that is several tens of thousands of kilometers away. Compared to previously used technologies, much more information could be obtained regarding the planet's atmosphere and whether an observed exoplanet is potentially habitable. *Credit: NASA*

low-resolution spectra of clouds, land, and oceans (Cowan and Strait 2013). Certainly, this approach would be much more challenging to apply on an exoplanet as we have no means to verify the interpretations.

However, other interpretations may be more straightforward. If we can observe the exoplanet on both the dayside and the nightside, the measured temperature difference can inform us whether the planet is tidally locked and whether there is atmospheric exchange between the two sides. Further information might be obtained about atmospheric composition, vertical temperature profiles, and the presence of clouds using emission spectroscopy (Burrows 2014). A particularly promising approach might be to observe a planet as it disappears behind a star and then reappears (Majeau et al. 2012).

12.2.2 Technologies Becoming Available in the Near Future

The technological challenges brought on by the discovery of exoplanets require sophisticated instrumentation. Important orbital and physical properties of exoplanets can already be provided with some current instrumentation, such as HARPS (High Accuracy Radial velocity Planet Searcher), HIRES (HIgh Resolution Echelle Spectrometer), and telescopes such as Keck and Gaia. However, a new generation of instruments, particularly instruments deployed in space, is needed for detecting environmental conditions on an exoplanet, particularly one with Earth-like chemical, thermal, and atmospheric characteristics (Schulze-Makuch and Guinan 2016). Space missions planned to address this objective include the JWST (James Webb Space Telescope), PLATO (PLAnetary Transits and Oscillations of stars), WFIRST (Wide Field Infrared Survey Telescope), TESS (Transiting Exoplanet Survey Satellite), and the New Worlds Mission (NWM).

Ground-based telescopes are under construction, including the TMT (Thirty Meter Telescope) and the 39-m E-ELT (European-Extremely Large Telescope) and should be operational within a decade. The expectation is that these huge telescopes will return spectra and images of nearby potentially habitable planets and measure parameters that are relevant for assessing the planet's habitability (Table 12.1). One of the exciting possibilities is to deploy a large occulting "Star shade" in combination with either JWST or WFIRST (or a dedicated 4-m class space telescope). This would allow planets to be observed as one pixel, separated from the light from their host stars (Fig. 12.1). Ideally, this technology might allow determination of the chemical composition of the planet's atmosphere and the detection of oceans, continents, polar caps, and clouds.

12.2.3 An Outlook of What Might Be Possible in the Next Decades

There are several chemical features of life that could be detected using some of the advanced methods described above. For example, the presence of a gas in an atmosphere likely produced by life but not given off by volcanoes or other, non-living processes, could be detected. Single gases are unlikely to be definitive markers of life, though. Even oxygen can be generated by some astronomical and geological processes as pointed out in Chap. 9 (Sect. 9.1.1). Thus, the objective would be to detect a combination of gases, such as oxygen and methane together, which would only co-exist if continually produced.

Another often cited and potentially detectable biosignature is the Vegetation Red Edge effect (Seager et al. 2005). The chlorophyll pigment in green plants absorbs much visible light, but reflects almost all light at wavelengths longer than about 750 nm. This results in a sharp "edge"—a sudden dip in the absorption spectrum (or sharp increase in the reflectance spectrum)—at longer wavelengths beyond about 750 nm. The absence of such a sharp change in absorbance properties at this wavelength is not seen for other natural materials, so is taken to be characteristic of phototrophic life on Earth. On other worlds, however, the Red Edge effect may not necessarily occur. Bains et al. (2014) showed that plants would not exhibit a Red Edge if they use light on a world with an atmosphere consisting mostly of hydrogen. Also plants on Earth under water have a much reduced Red Edge, when observed from space. If an exoplanet with a "Red Edge" could be observed, then the conclusion might be that life was or is there, but seeing no Red Edge does not prove the opposite (Schulze-Makuch and Bains 2017).

The challenges of detecting any signature of life on an exoplanetary body are formidable, and will remain so for the foreseeable future, especially when relying on remote sensing methods only. An even harder challenge is detecting whether that life is macroscopic, as opposed to solely microbial. Bains and Schulze-Makuch (2017) tried to tackle this question and concluded that this would be possible in principle:

Table 12.1 Some examples of planetary parameters of terrestrial extrasolar planets that can be observed directly by current or proposed space missions, and their astrobiological significance (modified from Schulze-Makuch and Guinan 2016)

	Parameter	Example of missions and methods	Astrobiological significance
Orbital	Semi-Major Axis	Kepler, Gaia, TESS, PLATO via RV (e.g., HARPS) and TP from Kepler's 3rd law and estimated mass-spectral type relations	Surface temperature
	Eccentricity	HARPS, Keck-HIRES (via RV) or Gaia, JWST (via DI)	Seasonal variations
	Obliquity	Kepler, Gaia, TESS, PLATO (combined with RVs)	Seasonal variations
	Orbital Period	Kepler, Gaia, TESS, PLATO, HARPS, HIRES (most methods except GM)	Seasonal variations
Physical	Mass	HARPS, HIRES, ESPRESSO, HST, JWST, Gaia (best via combination of RV and TP, though AM or GM possible)	Surface pressure
	Radius	Kepler, Gaia, TESS, PLATO (via TP)	Surface gravity, pressure and temperature
	Density	Computed from mass and radius determined from missions above	Composition, Internal structure with models
	Habitability Parameters (mean surface temp., ocean areas, atmosph. composition, biosignatures, vegetation-red-edge, land-ocean ratio, etc.)	JWST, WFIRST, and TMT and E-ELT (latter two approved and being built with adaptive optics (AO) and chronographic capabilities to be able to measure exoplanet properties directly at least for nearby planets once planned for TPF. In proposal stage is NWM—a large occulter in space, designed to block the light of nearby stars to observe their hosted planets (returns spatially resolved images and spectroscopy)	Stability of liquid solvent (water?) cycle, bio-elements, plant-type life, habitat distribution

Notes: Planet detection methods are direct imaging (DI), astrometry (AM), radial velocity (RV), transit photometry (TP), gravitational microlensing (GM), Adaptive Optics (AO). Missions are TESS (Transiting Exoplanet Survey Satellite), PLATO (PLAnetary Transits and Oscillations of stars), HARPS (High Accuracy Radial velocity Planet Searcher), HIRES (HIgh Resolution Echelle Spectrometer), *ESPRESSO* (Echelle SPectrograph for Rocky Exoplanet- and Stable Spectroscopic Observations), HST (Hubble Space Telescope), JWST (James Webb Space Telescope), WFIRST (Wide Field Infrared Survey Telescope), TMT (Thirty Meter Telescope), E-ELT (European-Extremely Large Telescope), NWM (New Worlds Mission), and TPF (Terrestrial Planet Finder)

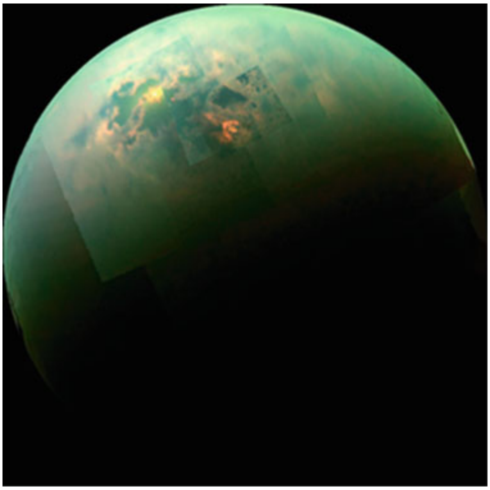


Fig. 12.2 The Sun glinting off Titan's north polar seas based on a near-infrared, color mosaic from NASA's Cassini spacecraft. The specular reflection is the bright area near the 11 o'clock position at the upper left. *Credit: NASA*

(1) If the planet can be mapped remotely in a way that differences on its surface can be analyzed.

(2) If land can be distinguished from seas. This may be accomplished by detecting the "glint" of sunlight reflected off the seas, just as the Cassini orbiter detected the glint of sunlight off the polar lakes on Titan (Fig. 12.2).

(3) If a distinctive spectral feature attributed to life on the land can be mapped, and it can be ensured that strangely colored rocks, dust clouds or other features are not detected instead, by mistake.

Condition (1) is extremely hard. Condition (2) is beyond any present planned capability, but possible. Condition (3) we do not know how to do yet, but ideas abound. For example, land plants have a substantial local effect on climate. Due to evapotranspiration and the release of aromatic chemicals into the air, plants increase rainfall over large forests, especially in the tropics. This changes the pattern of rainfall on Earth, alters the global cloud distribution, and cools the land. Trees can do this because they have a very large surface area, much larger than the ground they are growing on. In theory, this effect could be detected on another world as has been shown from modeling of "Desert world" planets and "Green planets" (Kleidon et al. 2000).

There is one other proposed method with enormous theoretical potential. It uses gravitational microlensing (see Sect. 12.1.3 above) by a star mid-way between Earth and an observed star-planet system. This method has already revealed intriguing exoplanets such as Kepler 452b that are hundreds or thousands of light years away from Earth. The advantage of the method is its high sensitivity to planets that are at about the same distance to their central star as Earth, thus being not biased toward planets that are very close to their star (hence less likely to be habitable) as the other observational methods are. However, the observed star-planet system, the mid-way star, and Earth have to be exactly aligned in order to use gravitational lensing. This is

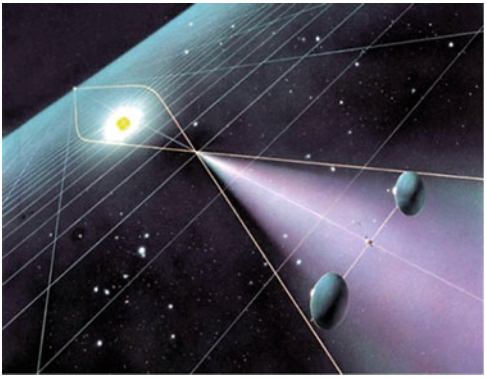


Fig. 12.3 A gravitational lens telescope, as envisioned by Claudio Maccone in his 2009 book Deep Space Flight and Communications

a major disadvantage of the method, because confirmation and follow-up of the planet once it moves out of that rare alignment is not possible. A variation to this method using our Sun as the mid-way star around which the light beams are gravitationally bent rather than a far-away star was proposed originally by Maccone (2009) and further developed by Alkalai et al. (2017). Using the Sun as a focal lense would be much more powerful, and it would allow the imaging of the exoplanet not just as a single pixel, but at 1000 × 1000 pixels, meaning a resolution of about 10 km on its planetary surface. This would enable visualization of surface features at a higher resolution than the Hubble space telescope provides for the imaging of Mars. It would also allow spectroscopic detection of atmospheric gases. Exoplanetary science would take a giant leap forward, as habitable planets, and perhaps even signs of life, could be detected by this method. Against these advantages, however, is the daunting disadvantage that the observing telescopes would have to be at least at a distance of 550 AU from the Sun, so they would have to be placed in interstellar space (Fig. 12.3). While the technological feasibility of accomplishing such a feat can be envisioned (Alkalai et al. 2017), another formidable challenge is that the telescopes would have to be aligned exactly with the Sun and the exoplanet, possibly with an accuracy of less than a meter. These mind-boggling challenges, along with a cost quite likely prohibitive, render such an effort highly implausible; but were it carried out, the results would be nothing less than revolutionary. We have described it here to illustrate that theoretical means for overcoming the limitations of current technology for revealing the nature of exoplanets lie well within the scope of human imagination.

12.3 Taxonomy of Exoplanets

12.3.1 General Categorization of Exoplanets

There are no widely accepted definitions for the different types of exoplanets, and assigning a given exoplanet to a particular category would be challenging even if such a classification did exist. The reason is that even for many of the exoplanets, we can't even determine for sure whether they are terrestrial planets or gas giants. In practice, any planet the size of Earth or smaller is assumed to be a terrestrial planet with a mainly rocky composition. Any planet more than ten times the mass of Earth is assumed to be a Neptune-type ice giant, while one at least 30 times the mass of the Earth is assumed to be a Jupiter-type gas giant. That leaves the so-called Super-Earths with several times up to ten times the mass of Earth. Since our Solar System has no terrestrial planet more massive than Earth, we do not have a well-studied analogue for this category. There is no physicochemical reason why a terrestrial planet cannot be more massive than Earth, but it is unclear what the limit might be.

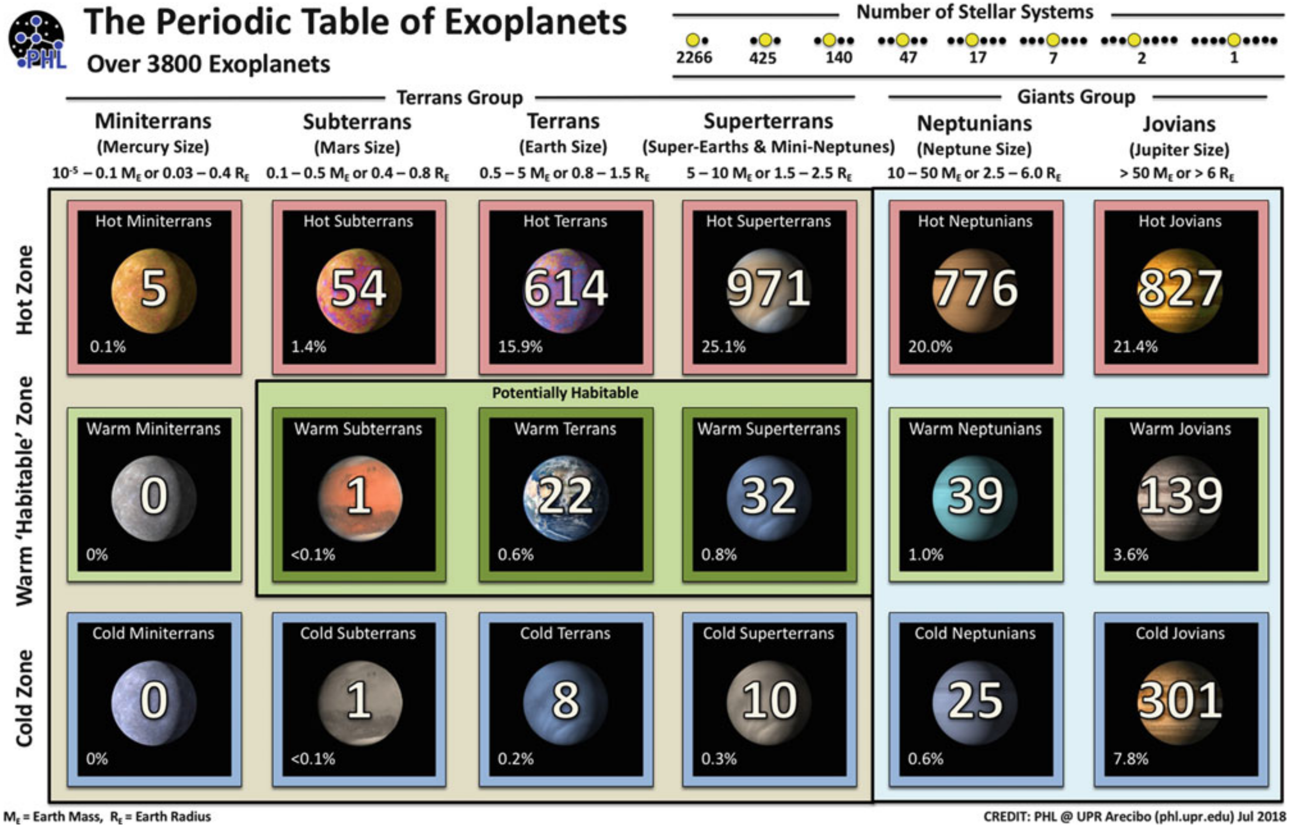
The categorical definitions used by the Planetary Habitability Laboratory at the University of Puerto Rico–Arecibo (http://phl.upr.edu/) provide a logical system for classifying exoplanets as they are discovered. Any planet at least five times the mass of Earth is defined as a Super-Earth or Superterran, while planets at least 10 times the mass of Earth are defined as Neptune-like. The breakdown of terrestrial planets versus gas giants, as interpreted by the Planetary Habitability Laboratory at the University of Puerto Rico—Arecibo, is shown in Fig. 12.4.

12.3.2 Categorization of Earth-size Exoplanets

If we don't yet know the full diversity of exoplanets that might exist, how can we understand the possible diversity of Earth-size exoplanets? For example, might an Earth-sized planet with an iron core, a very small or non-existing rocky mantle, and otherwise only gases be possible? While not indicated by current planet formation theory, Titan in our Solar System gives us a glimpse of the diversity that might be possible among rocky planetary bodies. Titan is the only icy moon with a significant atmosphere—1.5 bar of nitrogen gas and methane—and the only body in the Solar System other than Earth that has stable liquids on its surface, albeit in the form of hydrocarbon lakes. One can only wonder what other strange worlds may exist if we consider the whole Universe.

Unfortunately we do not yet have evidence for the existence of any of these strange worlds, but some scientific speculations have been put forward. One idea reminiscent of Titan would be a "carbide world," covered with oceans and atmospheres of hydrocarbons (Gaidos 2007). The underlying idea is that the initial carbon to oxygen ratio during planetary formation can vary widely and with it the amount of water that can be incorporated into a planet (Gaidos 2000). In an extreme case, silicate minerals could be replaced by silicon carbides.

A few attempts have been made to classify Earth-like planets according to the distribution and availability of water, and how these parameters are thought to be related to habitability. Schulze-Makuch et al. (2017) assigned such planets on the basis of whether water could exist (a) in the atmosphere, (b) on the surface, or (c) in the subsurface. Habitability in any of those environments was assumed to depend on temperature, liquid state, and energy source. Some planets, such as Venus, are



	Miniterrans (Mercury Size) $10^{-5} - 0.1\ M_E$ or $0.03 - 0.4\ R_E$	Subterrans (Mars Size) $0.1 - 0.5\ M_E$ or $0.4 - 0.8\ R_E$	Terrans (Earth Size) $0.5 - 5\ M_E$ or $0.8 - 1.5\ R_E$	Superterrans (Super-Earths & Mini-Neptunes) $5 - 10\ M_E$ or $1.5 - 2.5\ R_E$	Neptunians (Neptune Size) $10 - 50\ M_E$ or $2.5 - 6.0\ R_E$	Jovians (Jupiter Size) $> 50\ M_E$ or $> 6\ R_E$
Hot Zone	Hot Miniterrans 5 0.1%	Hot Subterrans 54 1.4%	Hot Terrans 614 15.9%	Hot Superterrans 971 25.1%	Hot Neptunians 776 20.0%	Hot Jovians 827 21.4%
Warm 'Habitable' Zone	Warm Miniterrans 0 0%	Warm Subterrans 1 <0.1%	Warm Terrans 22 0.6%	Warm Superterrans 32 0.8%	Warm Neptunians 39 1.0%	Warm Jovians 139 3.6%
Cold Zone	Cold Miniterrans 0 0%	Cold Subterrans 1 <0.1%	Cold Terrans 8 0.2%	Cold Superterrans 10 0.3%	Cold Neptunians 25 0.6%	Cold Jovians 301 7.8%

Fig. 12.4 Breakdown of terrestrial planets vs gas giants and projected temperature ranges. Figure is based on more than 3800 confirmed exoplanets as of July 2018, courtesy of the Planetary Habitability Laboratory and Prof. Abel Mendez of the University of Puerto Rico–Arecibo

presumed to hold liquid water only in certain cloud layers, representing the only possible abode for life, while others, such as Mars, hold substantial amounts of subsurface water but (today, at least) no long-standing bodies of liquid water on the surface. If life exists on planets such as Mars, it is likely to be sequestered beneath the surface or confined to specialized physical compartments like ice wedges or lava tubes with some amount of liquid water available, and therefore most likely microbial only. Ocean planetary bodies, on the other hand, could be covered with water, or some combination with or without ice, that could enable the existence of macroorganisms and more complex ecosystems, depending on the liquidity of water, its temperature, and available energy sources. Earth represents a planet on which many different categories are found locally, resulting in a highly diverse biosphere overall.

Lammer et al. (2009) classified four planetary types: (1) planets where only microscopic forms of life are possible, as on Venus and probably Mars; (2) planets that allow the evolution of complex multi-cellular life; (3) ocean-planets, with large bodies of water in contact with a silicate surface; and (4) ocean-planets with water not in contact with a silicate substrate.

Noack et al. (2016) focused on the classification of ocean-planets, where the H1 type hosts a single ocean layer in contact with a silicate surface, an H2 type has two ocean layers where the lower one is in contact with the silicate surface, and an H3 type with only one ocean that is not in direct contact with a silicate surface due to a high-pressure water-ice layer at the bottom.

It has to be emphasized that these schemes are based on life as we know it, which particularly applies to the nature of the solvent and energy source utilized. If life's biochemistry is or can be markedly different, for example, as a result of the utilization of a different type of solvent or energy source, this will also alter the results of the habitability assessment. A solvent with a lower liquidity range such as ammonia or an ammonia-water mixture would significantly decrease the temperature range at which life might be viable. If life can utilize a different source of energy such as magnetic fields, heat, or osmotic gradients (Chap. 5), then this could open up new habitats that would otherwise not be viable. Thus, the schemes outlined above should be understood as a first attempt to generalize some of the habitats on Earth-like planetary bodies that could possibly support life.

12.4 Examples of Some Intriguing Exoplanets

At the time of this writing we know of more than 3800 exoplanets that are confirmed and more than 5000 additional exoplanet candidates waiting for confirmation. Below are three exoplanets selected on the basis of their intriguing nature or location, to serve as examples of the diversity of planets existing in the Galaxy.

12.4.1 Proxima b

Proxima Centauri b is the closest exoplanet to Earth yet found, and the closest that *can* be found outside of our Solar System, give or take a few million kilometers (Anglada-Escudé et al. 2016). Obtained measurements indicate that the planet is nearly the size of our own planet, with about 1.3 Earth masses. It orbits its red dwarf or dM star, Proxima Centauri, in 11.2 days. Given its orbital location, liquid water could be present on its surface. Modelling by Ribas et al. (2016) indicated that Proxima Centauri b appears to have lost no more water than the volume of an Earth's ocean over its history, but it is not clear what the initial water endowment might have been. Thus, if Proxima b originally received around the same amount of water that Earth did, there should still be sufficient water remaining on the surface for the planet to harbor life. On the other hand, the planet might also be a Mercury- or Venus-type planet rather than Earth-like. Proxima Centauri, like other M stars, emits strong solar flares and X-ray emissions that would make the origin of life challenging on the surface of a nearby planet. It is also unknown whether the planet has a geomagnetic field to protect its surface from Proxima Centauri's extreme radiation, which would be a particular challenge for the survival of any non-aquatic organisms, given how closely the planet orbits its star. Other parameters necessary for life to originate and evolve include the availability of organic compounds and the presence of an effective mechanism for recycling key elements and compounds, such as plate tectonics. Nevertheless, even with these unknowns, it is intriguing to find that there is an Earth-sized exoplanet so close to us, in our neighboring solar system. Even if Proxima b is not habitable, which based on current knowledge appears to be the case, other exoplanets orbiting dM stars, such as GJ 667Cc, might be.

12.4.2 Kepler 452b

Kepler 452b is a planet orbiting a star similar in size to our own Sun, just 4% larger and 10% brighter (Jenkins et al. 2015). However, Kepler 452b, detected by the Kepler Space Telescope, is a so-called "Super Earth" with five times the mass of Earth and a 60% larger diameter. Kepler 452b has a similar orbital period to Earth with 385 days to complete one orbit. It is not the first earth-size planet found in the conventional habitable zone (where we would expect liquid water to be present on the planet's surface), but it is the first such exoplanet found that orbits a G2 star like our Sun rather than a common M star. The Kepler 452 system is estimated to be 1.5 billion years older than our own Solar System, which brings up the intriguing possibility that if life exists there, it has had longer to evolve than on Earth. Kepler-452b was detected by the gravitational microlensing method and is 1400 light years from Earth. We don't know whether Kepler 452b has an atmosphere, and if so of what composition and thickness; and we won't know any time soon. It might, though, be a suitable target for a SETI initiative or the Breakthrough Listen project (see also Chap. 15).

12.4.3 Kapteyn b

Two planets were discovered in orbit around Kapteyn's Star, which is only about 13 light years away in the southern constellation of Pictor (Anglada-Escudé et al. 2014). Both of the new planets are "Super Earths" with at least five times the mass of Earth. While Kapteyn c is considered to be too cold for life because of its distance from the star, Kapteyn b is within the zone where liquid water could be stable on the planet's surface. If its atmosphere were like Earth's, surface temperatures would be slightly cooler than ours. But given that it is more massive than Earth, it probably has a thicker atmosphere, and thus would likely be at least as warm as our own planet. The most intriguing fact about Kapteyn's Star and its planetary system, however, is its estimated age, which is 11.5 billion years old—two and a half times older than Earth and only about two billion years younger than the Universe itself. Despite being only 13 light years away from Earth, the Kapteyn system is thought to be part of a dwarf galaxy that was disrupted and absorbed by the Milky Way. The remnant of this dwarf galaxy is likely Omega Centauri, a globular cluster 16,000 light years from Earth that contains many similarly old stars. If life exists on one of the Kapteyn planets, it would likely be much older than life on Earth. On the other hand, since the metallicity content in the early days of the Universe was very low, it could be that the Kapteyn system may never have had the elementary chemistry needed for the origin of life.

12.5 Extrasolar Moons

Exoplanets appear to be extremely frequent and so should be extrasolar moons or exomoons, based on analogy with our own Solar System, where more than a hundred different moons are known to exist. Although no exomoon has been unequivocally confirmed, theoretical and technological requirements are now on the verge of being mature enough for such discoveries (Heller 2018). It is expected that most exomoons will be discovered by dynamical effects of the transiting host planet or by direct photometric transits of exomoons. Other promising techniques include direct imaging (Marois et al. 2008), microlensing (Han and Han 2002), pulsar timing variations (Lewis et al. 2008), and modulations of radio emissions from giant planets (Noyola et al. 2014).

Discoveries of several exomoons have already been claimed (Bennett et al. 2014; Ben-Jaffel and Ballester 2014; Hippke 2015), although alternative interpretations of the data have been suggested in some cases (Heller 2018). By the time this book is printed, however, the first detection of an exomoon will probably have been confirmed, some of which may potentially be habitable.

12.6 Habitability Metrics

Habitability can be defined as the extent to which a global or local environment, as the case may be, is suitable for the existence of life. If and when mechanical forms of life appear in this world or are found on another world (see Chap. 2), the criteria for habitability will need to be broadened considerably; but in practice at the present time, suitability for life is taken to mean suitability for the existence of organic life.

On Earth, the habitability of an environment is affirmed by the presence of life, but this cannot be the case for other theoretically habitable planets in the Universe. There might be many planets that are habitable in principle, but uninhabited since the conditions for the origin of life are expected to be more constrained than for the persistence of life once it has originated (see Chap. 3). On the other hand, the detection of presumed biosignatures on a non-habitable planet could be interpreted as a false-positive, or suggest a type of life with which we are not familiar, among other explanations. Thus, quantitative measures of habitability are valuable for properly assessing not only the distribution of potentially habitable worlds, but also the significance of any biosignature detections (Méndez et al. 2017).

Several approaches to assessing habitability in an astrobiological context have been proposed. They vary according to the aspect and nature of life for which suitability is being evaluated: whether energy is the primary criterion for survivability (Hoehler 2007; Shock and Holland 2007); whether moons are the primary targets of evaluation (Heller et al. 2014); similarity to Earth as an a priori criterion for suitability (Franck et al. 2001; Schulze-Makuch et al. 2011; Heller and Armstrong 2014); whether it is carbon-based life evolved in an aqueous medium, or organisms with more exotic chemistries and solvent requirements (Schulze-Makuch and Irwin 2006; Schulze-Makuch et al. 2011; Irwin et al. 2014); whether it resembles the biosphere on Earth (Schulze-Makuch et al. 2011; Heller and Armstrong 2014); and whether the life is likely to be complex and macroscopic or microbial only (Bounama et al. 2007; Irwin et al. 2014).

Similarity indices provide a powerful tool for categorizing and extracting patterns from large and complex data sets. They are relatively quick and easy to calculate and provide a simple quantitative measure of departure from a reference state, usually on a scale from zero to one. They are used in many fields, including mathematics (e.g., set theory and fuzzy logic), ecology (e.g., Sorensen similarity index), computer imaging (e.g., structural similarity index), chemistry (e.g., Jaccard-Tanimoto similarity index), and many others.

12.6.1 Habitat Suitability Index

The basis for defining and measuring habitability was established more than three decades ago by ecologists, who developed the Habitat Suitability Index (HSI) as part of their Habitat Evaluation Procedures (www.fws.gov/policy/ESMindex.html). The goal of the HSI was to assess the biological value of habitat resources under the assumption that habitat quantity and quality can be numerically described. The HSI value provided an index of relative carrying capacity with a range between zero and one. While the spatial and temporal scale as well as the specific organisms under consideration made the application to astrobiology difficult (Méndez et al. 2017), the HSI was the first habitability index developed, thus inspiring later indices such as the Earth Similarity Index (ESI), the Planetary Habitability Index (PHI), and the Biological Complexity Index (BCI) discussed below.

12.6.2 Earth Similarity Index (ESI)

The Earth Similarity Index (ESI) provides a metric for the extent to which another planetary body is similar to Earth. It is broadly used as it requires only a few physical parameters, which can readily be determined for most exoplanets. The generic equation is constructed from a weighted reformulation of the Bray-Curtis Similarity Index.

$$\mathrm{ESI_x} = \left[1 - \left|(\mathrm{x} - \mathrm{x_o})/(\mathrm{x} + \mathrm{x_o})\right|\right]^{\mathrm{w}} \tag{12.1}$$

where x is the planetary property, $\mathrm{x_o}$ is a terrestrial reference value, w is a weight exponent, and $\mathrm{ESI_x}$ is the similarity measure with a number between zero (no similarity) and one (identical to Earth). The weight exponent is adjusted in a way that planetary bodies similar to Earth have an $\mathrm{ESI_x}$ equal to or above 0.8.

The ESI for each planetary body is then combined into a single ESI value by determining the geometric mean from all component values. Properties used for these calculations usually include radius, mass, and temperature.

Schulze-Makuch et al. (2011) found it most instructive to distinguish among interior, surface, and global similarities. The interior similarity is a measure of the extent to which a planet has a rocky interior, while the surface similarity is a measure of the ability to hold a moderate temperature like that of the surface on Earth. These values can be determined by

$$\mathrm{ESI_i} = \left(\mathrm{ESI_r} \times \mathrm{ESI_\rho}\right)^{0.5} \tag{12.2}$$

where $\mathrm{ESI_i}$ is the interior similarity and calculated from the similarity of the mean radius and the bulk density, and

$$\mathrm{ESI_S} = \left(\mathrm{ESI}_{ve} \times \mathrm{ESI}_{TS}\right)^{0.5} \tag{12.3}$$

where $\mathrm{ESI_S}$ is the surface similarity and is determined from the similarity of the escape velocity *ve* and the mean surface temperature *TS*.

The global ESI is then computed by the geometric mean of the interior and surface ESI. It has to be emphasized that the ESI refers only to the similarity to

Earth, but holds no generic information as to whether a planet is habitable or even inhabited by life (Schulze-Makuch and Guinan 2016), since habitability does not have to be Earth-like in all respects. For example, Earth's Moon has a relatively high global ESI of 0.56, because it is a large rocky body with a mean surface temperature of 220 K, yet no one would suggest the Moon as a favorable habitat for life. On the other hand, Titan has a much lower global ESI of 0.24, given its extremely low temperatures, yet does have liquid hydrocarbon lakes on its surface, possibly a subsurface ammonia-water ocean, an atmosphere of 1.5 bar, and available energy sources; thus it could constitute a different type of habitat and might even harbor the presence of life (Shapiro and Schulze-Makuch 2009). Factors which are important for habitability and the presence of life such as the presence of a magnetic field, internal differentiation, and plate tectonics could in principle be included into an expanded ESI formulation. That hasn't been done, but reference to other factors relevant to the possibility of a habitat conducive for life has been addressed through the Planetary Habitability Index (PHI) described below.

12.6.3 Planetary Habitability Index (PHI)

If the objective is to assess the habitability of life in any form on other worlds, the Planetary Habitability Index (PHI) is a much better tool than the Earth-centric ESI. Based on what are thought to be essential requirements for any form of life, the PHI is calculated as follows:

$$\mathrm{PHI} = (\mathrm{S} \times \mathrm{E} \times \mathrm{C} \times \mathrm{L})^{1/4} \tag{12.4}$$

where the PHI is the geometric mean of separate values related to the presence of a stable substrate (S), available energy (E), appropriate chemistry (C), and a liquid solvent (L) on the planetary body of interest. Each of these parameters is divided into subcategories, and assigned a value proportional to the compatibility of that property with the presence of living organisms. For example, the substrate (S) category is subdivided into topography (solid or frozen = 1, no solidity = 0), atmosphere (dense = 1, thin = 0.5, trace = 0.1, absent = 0), and magnetosphere (strong = 1, moderate = 0.5, little or none = 0). See Schulze-Makuch et al. (2011) for details of how the other parameters are valued. Within each parameter category the values are summed and substituted into Eq. (12.4), then normalized to the maximum possible value to result in a rating on a scale of 0 to 1:

$$\mathrm{PHI}_{\mathrm{rel}} = (\mathrm{PHI}/\mathrm{PHI}_{\mathrm{max}}) \tag{12.5}$$

Note that the PHI is calculated from chemical and physical parameters conducive to life in general. For example, the solvent for life does not necessarily have to be water (Chap. 7). It is based on factors that, in principle, will be detectable at the distance of exoplanets from Earth with currently available and planned future space instrumentation.

12.6.4 Biological Complexity Index (BCI)

If the objective is not only to elucidate whether a particular planet or moon is habitable generically, but also whether it likely contains complex, macroscopic life, then the Biological Complexity Index (BCI) would be the most appropriate metric (Irwin et al. 2014). It differs from the PHI by including, not just the parameters thought to be minimal requirements for habitability, but additional factors most likely to be amenable to the evolution of a higher degree of biological complexity. For example, length of time over which a planet has to stay habitable is critical for the evolution of a higher degree of biological complexity. By calculating the geometric mean of relevant parameters, the BCI uses the same calculation strategy as that for the PHI, but adds thermal (T), geophysical (G), and age (A) characteristics presumed to favor the evolution of complex life (Irwin et al. 2014). The resulting equation for calculating the absolute BCI for any planetary body is thus as follows:

$$\mathrm{BCI}_{\mathrm{abs}} = (\mathrm{S} \times \mathrm{E} \times \mathrm{T} \times \mathrm{G} \times \mathrm{A})^{1/5} \tag{12.6}$$

where S is a measure of substrate complexity (a function of planetary composition and number of substrate layers plus an index of atmospheric complexity), E is a measure of available energy (summing values for solar flux and redox chemistry), T is the sum of estimates of the degree to which subsurface and surface temperatures approach an optimum, G is a measure of geophysical complexity (density plus orbital eccentricity), and A is the relative age of the planetary system. As for the PHI, the absolute BCI is finally normalized by dividing the $\mathrm{BCI}_{\mathrm{abs}}$ by the maximum possible BCI value, to yield a measure between 0 and 1.

All three metrics—the ESI, PHI, and BCI—are open to modification and/or expansion, as more data become available, or consensus develops around additional or other parameters considered relevant to the objective of the particular index. For calculating the PHI and BCI, in particular, the information required is not yet available for the vast majority of exoplanets and exomoons. However, these indices provide valuable templates for how information from the growing datasets on other worlds can be used in a systematic and objective way.

12.7 Chapter Summary

Exoplanets are the latest frontier in the field of astrobiology. In just a few decades, the number of confirmed planets outside our Solar System has jumped from a handful to several thousand, and the discovery of moons outside our Solar System will surely follow eventually. Exoplanets currently are detected mainly through one of three mechanisms. *Radial velocity* is based on perturbations in the star's motion (wobble) due to interaction with one or more nearby planets. *Transit photometry* is based on the degree to which light is dimmed when a planet fortuitously passes through the view of its central star as seen from Earth. *Gravitational lensing* occurs if two stars are aligned in the line of sight from Earth so that the gravitational field of the front star acts as a magnifying lens to a variable degree depending on the presence of an orbiting planet. Other methods include astrometrical measurements that rely on very precise observations of star positions and their movements in relation to the cosmic background. Detection by all these methods is currently subject to severe technological limitations, but prospects for heightened resolution with a new generation of space-based instruments and telescopes are promising.

From an astrobiological perspective, the habitability of planetary bodies, including those with the capacity for biospheres as complex as ours on Earth, are of greatest interest. Current technologies do not allow us to distinguish between habitable and non-habitable exoplanets, let alone to single out those that may host life. All we can say is that some exoplanets may be more suitable for life than others based on a set of measurable physical parameters. Various indices have been proposed for objectively assessing those planetary bodies that may be (a) more similar to Earth, (b) more likely to host life in any form, or (c) more likely to support the evolution of complex life. These indices, while open to adjustment as new information comes in, will enable us to better focus our resources on investigating those exoplanets and exomoons of greatest astrobiological interest.

Chapter 13
Ideas of Exotic Forms of Life

Science and speculation have converged at the boundaries of human imagination to conceive of some very exotic states of matter and/or energy that have been claimed by their authors to represent alternative forms of life or to exhibit life-like characteristics. Those ideas have been advanced by serious thinkers and thus deserve to be evaluated in the context of our assumptions about the fundamental nature of life. We will briefly mention some of the most important ideas proposed and critically examine them in light of our proposed definition advanced in Chap. 2 that a living entity (1) is a self-sustaining bounded local environment in disequilibrium with its surroundings, (2) consumes energy to maintain its high level of internal organization, carry out intrinsic activity, and adjust to its environment, and (3) is autonomously generated from or fabricated by antecedent (parental) entities that transmit information to the descendant (offspring) entities sufficient for the autonomous generation or fabrication of an indefinite succession of offspring. Only if all three criteria are met, does the proposed idea constitute a viable alternative form of life in our view.

13.1 Life Based on Spin Configurations

In Sect. 5.2.9 we discussed the possibility of obtaining energy from spin configurations. Feinberg and Shapiro (1980) took this idea a step further and speculated on the possibility of life based on spin configurations of p-hydrogen and o-hydrogen (Fig. 5.7). They suggested an organism with a helium interior, an inner o-hydrogen layer and an outer p-hydrogen layer, which would be capable of controlled processes and obtaining energy by the process described in Sect. 5.2.9. The living environment envisioned was a very cold and dark planet, just a few 10s of degrees above absolute zero. In this type of environment solid hydrogen would be floating in a sea of liquid hydrogen. An input of energy, most suitably from a faint star with emissions in the weak infrared and microwave wavelengths, would be

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_13

absorbed by hydrogen, thereby transferring some of the hydrogen into the energy-rich ortho-hydrogen state. The energy stored in the o-hydrogen state would then be released when the atoms are transformed into the p-hydrogen state. Feinberg and Shapiro (1980) suggested that for such life to form, a precise arrangement of o- and p-hydrogen would need to be established.

However, it is difficult to envision how such an organism could perform work efficiently without chemical reactions. Second, the force that would hold the unbounded organism together against the tendency toward entropy is unclear. Specifically the inner energy-rich o-hydrogen molecules would have to be kept apart from each other to avoid catalyzing their own destruction. The function of the helium interior is unclear as well.

Feinberg and Shapiro (1980) do address the issue of replication (though not in direct association with the proposed organism). Information encoding and transmission would not need to occur chemically, but rather could be based on magnetic orientation (Fig. 13.1). The starting point would be a chain of atomic magnets with their magnetic moments aligned in variable directions. A randomly directed magnet approaching the chain would line up with its direction parallel to that of the nearest magnet. If that process were continued for many magnets, a new chain would eventually be formed that duplicates the original chain in the directional arrangement of its magnets. If the magnets in place along the chain retained their alignment and could be protected, for example from re-magnetization from an exterior field, then

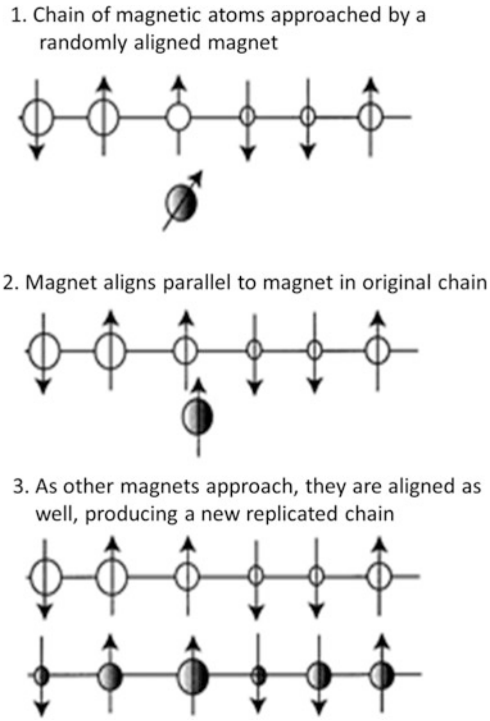


Fig. 13.1 Hypothetical replication mechanism of an ordered chain of magnets. Notice that identical components are replicated rather than complimentary and that the chain of magnets is only sensitive to the direction of magnetization, not to magnet size (modified from Feinberg and Shapiro 1980)

such an informational string would be a realistic possibility for replication and transmission of biological information. However, for such a code to be consistent with our definition of life, the code-bearing material would need to be distinct from the living entity that harbors it. Such a distinction is not made, nor is it clear how the information in such a magnetic string would be transformed into physical or chemical operations associated with living processes.

Thus, while this is a stimulating and intriguing idea for an exotic form of life, especially under conditions of extreme cold, which are common in the Universe, we consider the existence of such an organism as extremely unlikely.

13.2 Fred Hoyle's Black Cloud and Similar Ideas

The Black Cloud organism envisioned by Hoyle (1959) is portrayed as a formless mass living in space, obtaining energy from the light of stars, and communicating with itself and other forms of life by radio waves. It has an organization analogous to that of complex terrestrial animals, such as gas that has the function of blood, an electromagnetic heart and kidneys, and a complex neurological system that can be understood as a brain. In his novel Fred Hoyle entertains the fiction that a gaseous being in the Universe would have definite advantages compared to organisms living on a planetary surface, because it (1) would be free of constraints from large gravitational forces, and (2) would be able to absorb much more energy from starlight than the minute amount harvested by organisms confined to a planetary surface.

An organism like this is imaginable in principle (Goldsmith and Owen 2003). However, while such an amorphous and anthropomorphic creature is a worthy character of fiction, its potential for scientific credibility is severely limited. The major problem with this idea is the difficulty of envisioning how it could arise from an inanimate origin in the space environment. Being unbounded, the "protoorganismic" matter would have a low density, and be exposed to cosmic radiation. Low density and radiation would counteract any tendency for the matter within such an organism to become organized. Furthermore, no mechanism of replication is envisioned.

A somewhat similar concept was proposed by Arvidas Tamulis and co-workers (Tamulis et al. 2001, 2003), in the form of a molecular quantum computing cloud that could absorb magnetic and light energy from planets and stars, compute information, and move in space by using light pressure. Tamulis et al. (2003) pointed out the similarity to molecular quantum computers that use photoactive molecules converting light energy to magnetic flops interacting and controlling the central generating element of 10 quantum bits. An essential requirement for quantum computing life would be long lasting coherent quantum states, which would only be possible at extremely low temperatures found in interstellar dust clouds and on very cold planets. Basically, this idea suffers from the same problems as Hoyle's

Black Cloud—an intriguing idea, but it lacks key fundamental characteristics of living systems.

13.3 Life on a Neutron Star

Life based on the strong interaction (strong nuclear force) rather than electromagnetic energy has been suggested as a possible basis for life as well (Feinberg and Shapiro 1980; Goldsmith and Owen 2003). The strong interaction affecting quarks, antiquarks and gluons (carrier particle of the strong interaction) holds together the nuclei of atoms, but it is a force that is only strong at extremely short distances. Thus, if atoms are (for us) in their usual state with electrons orbiting the nucleus, the individual nuclei are too far apart for the strong atomic force to result in significant interactions between different nuclei. However, given the situation that electrons are ripped off from their nuclei, protons and neutrons from various nuclei come into close proximity. This requires immense gravitational forces, and occurs naturally in neutron stars, which have one to two solar masses concentrated in a body with a diameter of 10–20 km and a magnetic field of about 10^{12} gauss. Given the high density and temperatures, interactions between protons and neutrons occur much more frequently than electromagnetic force interactions. These interactions occur because of incredible gravitational and magnetic forces present on the surface of a neutron star. Ruderman (1974) pointed out that the magnetic forces would reshape the "normal" atoms into strange configurations exhibiting long polymer-like chains in which the nuclei lie along a central line and the electrons in elongated bands. Magnetically formed polymers could then even align to form larger structures.

Life on a neutron star based on the strong interaction is one of the most extreme applications of energy in a conceivably biological context. The idea provides some conceptualization of how dynamic complexity can be established, but falls far short of constituting a comprehensive model of a living system, including any meaningful definition of life such as the one offered in Chap. 2. Neutron stars, however, might have planets, and possible life on such a planet could use the extremely strong magnetic field of their star as a primary energy source (see Sect. 5.2.5). In fact, the first extrasolar planets were discovered around a neutron star, the pulsar PSR 1257+12 (Wolszczan 1994; see also Chap. 12).

13.4 Life on a Brown Dwarf

Brown dwarfs are accumulations of gas that have not been able to increase their mass and temperature sufficiently to sustain hydrogen fusion and become a star. Low-mass brown dwarfs may contain liquid water, and could possibly be capable of supporting life (Shapley 1958). Energy on a brown dwarf could be provided from the body's own intrinsic infrared spectrum, though this form of energy is much weaker than light in the visible and near-infrared spectrum. If life could adapt to use the low infrared spectrum to obtain energy instead of the visible and near-infrared spectrum as used on Earth, organisms relying on photosynthesis would have a nearly unexhaustible supply of energy. Such organisms, however, would have to adapt to the strong gravitational field of brown dwarfs, perhaps 100 times stronger than on Earth. That may not be a problem though. Mastrapa et al. (2001) tested *Deinococcus radiodurans* and *Bacillus subtilis* by exposing them to extreme acceleration (4.5×10^6 m/s^2) and jerks (1.5×10^{11} m/s^3) in a compressed-air pellet rifle and noted survival rates between 40 and 100%. Also, Sharma et al. (2002) observed physiological and metabolic activity of *Shewanella oneidensis* strain MR1 and *Escherichia coli* strain MG1655 at pressures of 68 to 1680 MPa in diamond anvil cells. However, other major problems would include the lack of available surfaces for chemical reactions, suitable temperatures, and the relative lack of heavier elements such as potassium, calcium, and iron, which are necessary for living processes with which we are familiar. A more conventional possibility would be life on planets that are orbiting brown dwarfs. Andreyeschchev and Scalo (2002), for example, modeled habitable distances and time scales for planets orbiting brown dwarfs. Near-infrared observations indicate that young brown dwarfs probably possess protoplanetary disks (Muench et al. 2001; Testi et al. 2002), thus life could conceivably exist on a planet in a brown dwarf system.

13.5 Life on a Rogue Planet

Rogue planets are planets that have been ejected from their parent stars soon after accretion (Stevenson 1999). Bada (2001) pointed out that many of these rogue planets could be Earth-like with an inventory of radioactive elements sufficient to heat and melt their interiors. These worlds could have retained their initial dense hydrogen atmosphere, thus the heat leaking out from their interiors would not be rapidly lost into space, but instead water could condense and oceans could form (Bada 2001). With a highly reducing atmosphere which would likely include methane and ammonia, these planets could be a laboratory for prebiotic chemistry. It is even imaginable that primitive life could form under these conditions. Abbot and Switzer (2011) suggested that a rogue planet with an Earth-like composition and age could maintain a subglacial liquid ocean if it were a Super-Earth planet with about 3.5 earth masses, corresponding to an ice layer with a thickness of about 8 km. Even planets with a significantly lower mass could maintain liquid water if the rogue planet would have a large complement of water, was overlain by a layer of frozen gas, or if the water melting point would be suppressed by salts or other compounds. Perhaps, rogue planets could constitute a universal mechanism for spreading prebiotic molecules or even primitive life from one Solar System to another. Unfortunately, rogue planets are very difficult to detect. The first one detected was a gas giant about six times the mass of Jupiter (Liu et al. 2013). Rogue planets ought to be very common on theoretical grounds, and some estimates are as high as 100,000 rogue planets for each star of our Galaxy (Strigari et al. 2012). A high number of rogue planets (but perhaps not that high) is also supported by the history of our own Solar System, in which Pluto, Charon, and Triton arguably represent captured rogue planetesimals.

13.6 Some Other Ideas on Forms of Exotic Life

Some other ideas of exotic life have been proposed in the past, ranging from crystalline life (Brandstetter 2012) to speculations of plasma life inside a star, which was first advanced by Maude (1963) and later elaborated on by Feinberg and Shapiro (1980). The idea is based on replication of certain patterns of magnetic force and the dynamic activities within a star. The idea was revived more recently by Lozneanu and Sanduloviciu (2003), who created blobs of gaseous plasma that replicated by splitting into two, grew by taking up neutral argon atoms and splitting them into ions and electrons to replenish their boundary layers, and "communicated information" by emitting electromagnetic energy, which made the atoms within the other spheres vibrate at a particular frequency. Vidal (2016) has speculated that some binary stars might actually constitute forms of intelligent life. Since these hypothetical entities would feed on other stars, he named them "stellivores," and presented a thermodynamic argument for their existence, with a metabolic interpretation of their binary interactions.

We consider these possible interactions as interesting examples of dynamic complexity arising from relative chaos similar to forest fires and hurricanes on Earth, but do not consider them alive by any meaningful definition of the term. Other speculations of exotic biology include suggestions of the possibility of dark matter life (Randall 2015), life based on pure energy, and life based on topological effects in quantum space rather than atoms as suggested in a novel by Egan (2002). As intriguing as these speculations are, any ideas not involving known atomic matter are farfetched and must remain in the realm of science fiction for now. Further, unlike matter, where two atoms or two planets affect each other's behavior through collisions, two independent flows of radiation will usually pass through each other without having any significant effect on each other. Thus, these ideas are imaginative examples of exotic physics, but, in our view, do not have a recognizable relationship to any meaningful definition of life.

13.7 Chapter Summary

We have given these brief examples of other, more exotic notions about forms of life that transcend even the basic chemical and physical laws that operate within usual planetary dimensions, because they have been advanced by serious thinkers who force us to critically examine our assumptions about the fundamental nature of life.

Recent insights would indicate that rogue planets could indeed harbor habitable conditions or even life. Conceivably that could also be the case for planets in orbit around brown dwarfs, or even neutron stars. In the other cases, however, we do not feel that the more exotic examples of life as proposed in this chapter constitute a plausible argument for an alternative form of life. They embody some imaginative alterations of state, matter, and energy, and bear some resemblance to some characteristics of life—particularly those having to do with the organizing capacity of energy flow and the tendency to create low-entropy states of disequilibrium. But in their totality, they do not come close to meeting the criteria for living systems set forth in Chap. 2. They do not prescribe bounded environments, nor specify a mechanism for reproduction, nor identify informational storage mechanisms that persist in unitary form from one generation to another. It perhaps could be argued that the flaw in our analysis lies in the definition of life, rather than its application. In other words, perhaps we lack the imagination to envision all the possibilities by which living systems could be manifested. However, we believe that in this book we have already pushed the limits of what it means to be alive, and to push beyond those limits at this point in our understanding would take us into the realm of a speculative physics that has no recognizable relationship to life in the Universe.

Chapter 14
The Future and Fate of Living Systems

The future of life on Earth and elsewhere in the Universe is the least studied of the three fundamental questions posed by NASA's Astrobiology Roadmap (Des Marais and Walter 1999; Des Marais et al. 2003, 2008). A lack of focus on this question raises two concerns. First, in a sense, the future of life is the question that has the greatest practical significance, since an ability to anticipate the consequences of human actions for the biosphere on Earth and wherever humans may come in contact with alien life in the future, should be a critical consideration in formulating policies for human activities on Earth at present and exploratory strategies for the future. The only one of the Roadmap's seven Goals and Objectives (#6) that relates to the future of life focuses narrowly on the fate of ecosystems and the evolution of microbes on Earth and in alien environments. The biosphere is now being changed so rapidly by anthropogenic forces, though, that the bigger and more immediate question is the general fate of groups of organisms, including especially those with the greatest environmental impact (Tong 2000; Woodruff 2001). This might also include an alteration of the genetic code (Xue and Wong 2017), intended or unintended. Secondly, on planetary systems older than the Solar System, there is little reason to doubt that life has emerged in some cases, and therefore had longer to evolve than on Earth. The question may then be asked whether the history of life on Earth provides insights into the fate of living systems that have had longer to unfold.

14.1 Evolutionary Alternatives

We propose that the history of life on Earth reveals consistent patterns that can be grouped as a working formalism into one of three scenarios: taxonomic groups either (1) reach a stable *plateau* from which they do not deviate for a long to indefinite period of time; (2) they *collapse* into near or total extinction; or (3) they undergo *transition* to a form of life with dramatically new features—after which a new round of evolution radiates into new forms, each of which again follows one of the three

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_14

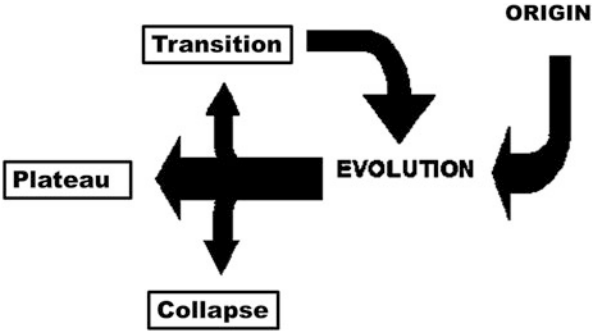


Fig. 14.1 Generic scheme for the cycle of evolution. The point at which life begins is a matter of definition. Once underway, life diversifies through evolution, with different taxa progressing ultimately to either collapse and extinction, a plateau phase leading to prolonged stability, or a radical transition to a new precursor that itself then radiates into a variety of forms, each with the same set of potential fates

scenarios. These interrelated possibilities are shown in Fig. 14.1. Each of these scenarios is considered below, with examples from the history of life as we know it.

14.1.1 Plateau

Organisms that occupy stable environments are subjected to stabilizing selection, which minimizes variation and optimizes adaptation over time (Campbell 1996). So long as the environment remains constant, form and function persist relatively unchanged. Hence, over geological time spans characterized by relatively constant environmental conditions, organisms tend to show little modification from the ancestral forms that emerged when they first arose. If that origin occurred as the consequence of punctuated equilibrium (Eldredge and Gould 1972), emphasis over the vast majority of the taxon’s life span will be on equilibrium. Even in changing environments, highly successful and robust biological features may be retained. Evolutionary plateaus are the result.

The most obvious examples of the plateau scenario are life’s most ancient surviving organisms, the bacteria and Archaea (Altermann and Kazmierczak 2003). Many microbes are likely unchanged from very early in their history. Cyanobacteria, though doubtlessly possessing a more elaborate photosynthetic machinery than the earliest versions, have remained virtually unchanged ecologically and morphologically for over two billion years (Altermann and Schopf 1995). A particularly good example is sulfur-cycling fossil bacteria from Western Australia, which are markedly similar in microbial morphology, habitat, and organization to their modern counterparts (Schopf et al. 2014). Among the plants, once they invaded the land, bryophytes quickly developed a morphology and physiology that has remained constant for at least 360 million years (Hueber 1961; Karssilov and Schuster 1984).

Among the invertebrates notable for their evolutionary longevity are crustaceans such as the horseshoe crab (Xia 2000), insects such as ants (Grimaldi and Agosti 2000), and mollusks such as the nautilus (Landman 1987). Among the vertebrates, the sharks emerged during the early Devonian and developed some unusual physiological features that have remained relatively stable for 400 million years (Lisney and Collin 2006; Miller et al. 2003; Speers-Roesch et al. 2006). Likewise, the turtles emerged in the late Triassic with a highly successful defensive morphology that has preserved them relatively unchanged for 200 million years (Krenz et al. 2005; Pritchard 1979).

The history of life on Earth leaves several unanswered questions about the Plateau scenario. First among them is whether evolutionary plateaus remain stable indefinitely as long as the environment does not change. Can genetic drift give rise to change even in unchanging environments? What are the critical factors that promote survival of some forms through global catastrophes, such as the persistence of bryophytes and sharks through the Paleozoic-Mesozoic (P-M) boundary, and the survival of turtles through the Cretaceous-Tertiary (K-T) transition?

14.1.2 Collapse

Biologists have long recognized that most taxa have finite life spans; hence the majority of species that have ever lived have become extinct (Eldredge 1985; Woodruff 2001). Collapse, therefore, is the ultimate fate of most forms of life. This presumably reflects the fact that even optimal adaptations are essentially irreversible, and sooner or later circumstances will change to the point that the basis for past evolutionary success becomes maladaptive. Alternatively, previously well-adapted forms may simply be displaced by more highly adapted competitors. Or, precipitous events may lead to a relatively sudden collapse, as in the global catastrophes that mark several prominent paleobiological boundaries.

The stromatolites dominated the biosphere for three billion years, but disappeared at the end of the Proterozoic (Cowen 1995) except in a few scattered niche environments such as Shark Bay, Australia. The Ediacaran fauna provided numerous experiments in animal morphology over a 40 million year period just prior to the Cambrian, but few representatives survived into the Paleozoic (Cowen 1995). With the advent of the jawed fishes, the placoderms came to dominate the early Devonian seas, but were displaced entirely by unarmored but more resilient competitors by the end of the Devonian. Dinosaurs rose to prominence during the Mesozoic but were exterminated precipitously by the K-T catastrophe. It has been estimated that extinction is now occurring on an unprecedented scale, accelerated by the impact of human activity on the biosphere (Tong 2000; Woodruff 2001; Braje and Erlandson 2013). The relatively sudden disappearance of the mammalian megafauna in North America has been attributed to the arrival of humans, though the precise role played by human-megafaunal interactions remains controversial (Barnosky et al. 2004; Brook and Bowman 2002; Diniz-Filho 2004; Johnson 2002; Remmert 1982). And the human species itself is the lone survivor of a number of hominids that appear to have been unable to compete with *Homo sapiens* during the late Pleistocene and early Holocene (Kaifu et al. 2005; McBrearty and Brooks 2000).

The question of causation is the one most relevant to the Collapse scenario. What is the relative importance of maladaptation and competition in precipitating extinction? Does collapse ever occur due to genetic drift, absent precipitating competition or abiotic changes? How common is Collapse, even in relatively stable environments?

14.1.3 Transition

According to the punctuated equilibrium model of the origin of species (Eldredge and Gould 1972), most new taxa come into existence through relatively rapid transitions from ancestral forms. The power of directional selection to drive adaptive change when either the biological or abiotic environment is altered compels often drastic and rapid evolutionary changes (Eldredge 1985; Elena and Lenski 2003; Reznick and Ghalambor 2001). Transition thus represents a third scenario among the fates that befall life.

Major transitions in the history of life that emphasize information transfer and hierarchical organization have been outlined by Szathmáry and Smith (1995). Highlights that affect the nature and biodiversity of life on Earth include the emergence of a metabolic machinery for photosynthesis, the endosymbiotic creation of eukaryotic cells, the origin of calcified exoskeletons, and reproductive innovations that drove protistan diversification in the late Proterozoic (Cowen 1995; Margulis and Sagan 1995). The Cambrian explosion generated several major transitions, the most successful of which appear to have been the origin of the arthropods and mollusks. The vertebrates represent a somewhat later but equally successful transition. Among the vertebrates, transitional innovations include the development of jaws, leading to the formulation of more complex food webs with larger and more active animals; the evolution of lungs, leading ultimately to the colonization of terrestrial niches by organisms with higher metabolic rates supported by the richer supply of oxygen; development of the amniotic egg that freed reproduction from restriction to aquatic habitats; and endothermy, which enlarged the range of climates and niches which animals could occupy.

The Transition scenario raises questions as well. Is transition inevitable, given enough time under hospitable conditions? Is transition even possible for most forms of life, especially for macrobiota, if the environment changes radically over a short time span, as appears to be occurring now in the global biosphere? A study of the survivors of past mass extinction events may lead to instructive insights in that regard (Ward 2001).

In rare cases, the transitions have been great enough to transcend biology. The evolution of photosynthesis altered the global atmosphere, while redirecting the course of evolution itself. Multicellularity transformed life from an exclusively microscopic domain, to macroscopic and megascopic dimensions (Beck and Irwin 2016; Schulze-Makuch and Bains 2017). The evolution of nervous systems gave rise to "neural individuals" (Jablonka and Lamb 2006), which evolved intelligence to varying degrees. The combination of intelligence and sophisticated communication with manual dexterity enabled humans to develop technology, which has so amplified biological capabilities that the Earth in its entirety is being transformed.

14.2 Evolution of Intelligence

Intelligence has evolved independently several times during the evolution of life on Earth (Irwin and Schulze-Makuch 2008, 2011). Four specific examples of the independent evolution of a transforming degree of intelligence are provided by the social insects, cephalopods, cetaceans, and primates.

Insects evolved on land during the Silurian, though the eusocial ants, wasps, and bees apparently did not diversify until the Mesozoic, $\sim$150 million years ago (Moreau et al. 2006; Schultz 2000; Wilson 1980). Biologists do not rate the social insects as intelligent in the conventional sense, and as individual organisms they certainly do not meet the usual criteria for intelligence. But in the aggregate, they display some of the features that would suggest intelligence, were they a single organism. They build elaborate housing, divide labor, communicate symbolically (in the case of bees), radically modify their microenvironment, grow food (in the case of fungal cultivating ants), domesticate other species, wage war, and cooperate for the good of the whole (Brady 2003; Mueller et al. 1998; Wilson 1980). As such, they represent a case of social intelligence, which obviously has been subject to strong group selection.

Cephalopods have achieved the pinnacle of intelligence among all the invertebrates (Young 1964). They diverged from other mollusks in the late Cambrian, became numerous in the Ordovician, and suffered a cataclysmic decline during the Permian crisis, with only the octopi, squids, cuttlefish and a few nautiloids surviving to the present day (Cowen 1995; Landman 1987). Those forms, however, are active benthic foragers and predators, with highly developed tactile and visual sensory abilities, and elaborate motor systems for the control of jet-like propulsion, complex mouth part movements, and fine manipulation of each of their eight appendages.

The Cetaceans probably diverged from their terrestrial ancestors near the start of the Cenozoic 65 million years ago, since the oldest fossil whale has been dated from the early Eocene, $\sim$55 million years ago (Bajpai and Gingerich 1998). Whales have the largest brains that have ever evolved, the brain of the blue whale measuring nine times the size of the human brain. By the Miocene ($\sim$20 Ma), cetacean brains had achieved essentially their modern size (Jerison 1973). Most of the enlargement of the brain in cetaceans reflects a huge elaboration of the neocortex beyond the sensorimotor primary projection areas (Hof et al. 2005; Lilly 1978). While cetaceans have essentially lost their olfactory sense, the pyriform cortex has not been reduced, perhaps reflecting compensatory enhancement of their gustatory sense. Anatomical changes have enabled the sound production that forms the basis of a sophisticated echolocating capability and a communication system whose full complexity is not yet known (Herman 1986).

Primates diverged from ancestral insectivores early in the great mammalian radiation at the start of the Cenozoic, about 65 million years ago (Cowen 1995). The evolution of hominids shows a relentless increase in brain size, characterized mainly by expansion of the neocortex, and in humans by increase in the prefrontal lobes in particular (Byrne 1995). The evolutionary acceleration in brain size occurred in the anthropoids much more recently than in the cetaceans—the qualitative expansion of the human brain over that of the chimpanzee occurred within the last 6 million years, while neocortical expansion in the Cetacea exceeded that of humans probably 20 Ma earlier (Jerison 1973). The acceleration of neural complexity in these two very distantly related mammals has thus been a completely independent event. By 4 million years ago, humans had split from chimpanzees, and begun to diversify into a number of species (Cowen 1995). *Homo sapiens* is the sole survivor of several competing human lineages, achieving modern morphology and brain size $\sim$200,000 years ago (Jerison 1973; McBrearty and Brooks 2000).

From an astrobiological perspective, the relative infrequency with which intelligence has arisen is noteworthy. Even among those species that have developed the capacity for insight such as chimpanzees, that ability appears to be underutilized in their natural habitat (Byrne 1995). It may be that high intelligence has sufficient negative attributes that its evolution is not commonplace. Thus, if and when complex living entities are found on other worlds, it should not be taken for granted that intelligent forms will be among them.

14.3 The Rise of Technological Competence and Its Fate

An equally compelling though lesser mystery is why technology has developed so rarely among species that have the intellectual capacity for it. Technology (the use of energy, tools, material, and information to amplify the impact of a species on its environment) has emerged fully in only the human species. Crude prototypes can be seen in other species, particularly among the primates and some birds. The social insects show limited forms of technology, in the construction of elaborate housing and limited domestication of other species. But only humans have fully exploited technology to the point of significantly changing their environment beyond their purely biological impact. A particularly pertinent issue raised by the human example is whether any technologically capable form of life will inevitably metamorphose into something else—perhaps (a) custom-designed, genetically engineered organic beings, (b) totally mechanized forms with artificial intelligence, or even (c) virtual (non-material) entities.

Technology for the first alternative is advancing rapidly. The pace at which humans create genetically modified species (Xue and Wong 2017), perhaps to the point of giving rise to new species, and/or enabling their own custom-designed genetic transformation, at this time appears to be constrained more by social, political, and moral attitudes than by technological capabilities. Inasmuch as social, political, and ethical views change over time, the trend to engineer new organic beings—non-human, human, or both—is likely to continue if not accelerate.

The second alternative leads to the question of the relationship between evolving machines and their human innovators. A symbiotic fusion is one possibility, and is already in the early stages of occurring (Clark 2003). Artificial limbs, sensory aids, and implanted mechanical devices such as pacemakers reflect this trend. An alternative relationship would be an ongoing co-evolution of humans and machines, with increasingly comparable capabilities of organic and mechanical forms but without significant fusion between the two. The advancement of robotic technology illustrates this trend. In this case, the ultimate possibility of replacement of organic by mechanical beings clearly looms. How rapidly (and how peacefully) the mechanical entities will replace their organic predecessors, is clearly a compelling question. The ability of machines to compete with humans depends ultimately on the capacity of the former for feature extraction, abstract processing, and anticipation—in short, to be intelligent. While it is commonplace to argue that computer intelligence is merely decades away, fundamental arguments that digital computers can never be intelligent have been advanced (Chyba and McDonald 1995; Hawkins and Blakeslee 2005; Searle 1984).

The third possibility is reflected in the growing sophistication of human-engineered virtual reality. As human biology becomes increasingly dominated by and subservient to cognitive experience, the motivation to manipulate that experience by artificial means is likely to grow. Once the ability to create enriching and satisfying virtual realities becomes feasible, and the logistical problems of sustaining sufficient other (social, economic, and political) requirements of the material world to support the virtual world are solved, organic humans would become progressively superfluous. The argument has been pushed even further by Bostrom (2003), who suggested that humans may have reached a “posthuman” stage capable of running a significant number of simulations of their own evolutionary history (or variations thereof), and that we might already be living in one such simulation.

In the event that technologically-capable species spawn mechanical adjuncts to their own biology, the nature of life and the forces that influence its evolution may be radically altered. In such cases, depending on the nature of the descendent forms, an adjustment in those definitions of life that emphasize organic complexity and evolution by natural selection may be required (Grinspoon 2003; Lwoff 1962, see also Chap. 2), as indicated in Fig. 14.2.

The benefits of considering the fate of life in a formal way may thus be not only to determine whether the scenarios observed over the course of life on Earth represent exhaustive examples of the fate that can befall living organisms anywhere, but to reexamine clearly the definition of life itself.

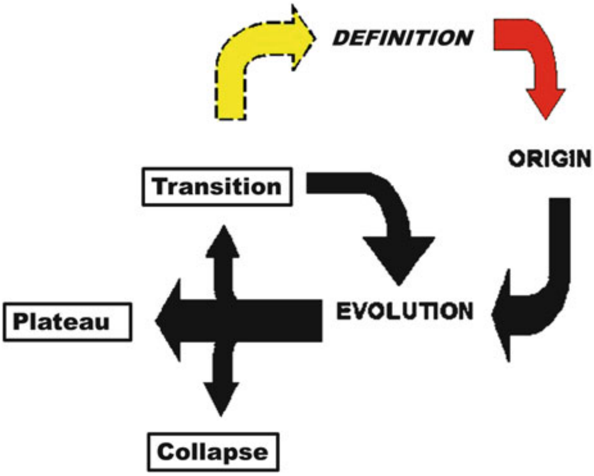


Fig. 14.2 The cycle of evolution with a redefinition of life. In the case where life evolves technological capabilities, the prospect of non-organic organisms and artificial intelligence requires a reconsideration of the definition of life

14.4 Application to the Possibility of Life on Other Worlds

We and others have argued previously that if life exists elsewhere in our Solar System—and we rate the probability that it does so moderately high (Irwin and Schulze-Makuch 2001; Irwin et al. 2014)—it almost surely exists in a microbial to small and relatively ancestral form. This is because conditions on the surfaces of all the other planets and satellites, with the possible exception of Titan (Campbell 1996; McKay and Davis 1999; Schulze-Makuch and Grinspoon 2005), are not favorable for complex liquid-based biochemistry. Whatever life may have arisen on (or been transported to) them, it would be expected to have become sequestered in stable, environments once life on the surface became untenable. Since subsurface habitats favor small organisms (Sect. 8.2), life on such bodies would likely be microbial to small, and probably near its ancestral state, or whatever state it was in when subsurface existence became mandatory.

Lack of knowledge about the nature of planetary bodies in other Solar Systems that could harbor life severely constrains informed speculation about the nature of living systems beyond our own Solar System. Of the over 3800 extrasolar system planets confirmed to exist as of this writing, most are giant planets orbiting near their central stars (Méndez 2015), presenting formidable challenges to the existence of life. Because there are also solar systems with planets more distant from their central stars (and more will be discovered in the future), many of them perhaps containing water or other liquids at temperatures where complex biochemical reactions can proceed, the chances are greater on bodies such as those that complex ecosystems could develop, leading to multiple trophic levels, hence complex macrobiota. To the extent that many planetary bodies resemble the cold arid surface of Mars, or the icy satellites of the outer planets, life on them would likely be subterranean, rendering the plateau scenario most likely.

If the conditions that enabled the evolution of complex life on Earth are indeed as rare throughout the Universe as they are in our own Solar System, so too might be the prevalence of complex life. However, we do not yet know that complex life *cannot* arise under conditions exotic by Earth standards (Schulze-Makuch and Irwin 2006), so a generalization about the rarity of complex life throughout the Universe (Ward and Brownlee 2000) is not yet justified.

We have previously defined life in a way that avoids limitation to the carbon-based, water-borne form of living organisms that currently inhabit Earth (Schulze-Makuch 2002). At the same time, our analysis of physicochemical constraints suggests that carbon-based, water-born life is by far the most likely form for life to take (Chaps. 6 and 7). In as much as numerous planetary bodies in our Solar System have, or have had, conditions for the origin and evolution of life as we know it (Irwin and Schulze-Makuch 2001), we suggest that planning continue for ~~space~~ exploratory missions ~~continue~~ to aquatic subsurface habitats on Mars, Ceres, Europa, and the other satellites of the outer planets, where ecosystems may be found to persist largely in a plateau stage of evolution. At the same time, the atmosphere of Venus (Grinspoon 1997; Schulze-Makuch et al. 2004) and the surface or subsurface of Titan (McKay and Smith 2005; Schulze-Makuch et al. 2005a, b) may offer habitats for forms of life quite unknown to us.

Where extreme geophysical transformations have occurred over the history of a planetary body, as on Venus and Titan, forms of life quite different from those known on Earth could be the outcome. Thus, the definition of life that guides our search for it needs to be generic enough to consider all the possibilities, including those difficult to envision by analogy with life on Earth.

14.5 Chapter Summary

With robotic missions to Mars and the outer planets increasing our knowledge of other potential habitats for life, and with astrobiology becoming an institutionalized interdisciplinary field of study, the time has come to formalize models for the life history of biospheres in their entirety. We propose a generic framework for considering the history and fate of life wherever it occurs in the Universe. Using analogs from the history of life on Earth, we extrapolate to a variety of circumstances likely to be encountered by life on other planetary bodies. The most common fate of life is evolution to a “plateau” state in which life stabilizes into forms optimally suited for persistently unchanging environments. Assuming that life on other worlds is most often microbial and ancestral, this is likely the most widespread scenario. “Collapse” occurs when evolutionary changes produce forms incapable of adapting to altered biotic or abiotic conditions. Total extinction is a special case of collapse, but near extinction leading to survival of only a few, significantly altered descendent forms is another, perhaps more common outcome of the collapse scenario. “Transition” occurs when evolution leads to biotic or environmental changes sufficient to generate radical transformations. The climactic evolution of neural complexity and manual dexterity, leading to symbolic language and technology in humans raises the question of whether any technologically capable form of life will inevitably be transformed through codependency with machines and external data processing and storage, into entities that require a redefinition of life. If the fate of living systems as we propose here holds generally for other worlds, it is most reasonable to expect that life will be found to be simple and near its ancestral state on worlds that solidified into a constant, constraining physical condition early in their history, such as the icy satellites in our Solar System. The transition to complex life, with the possible evolution of intelligence and rise of technology, is likely to be found only on worlds which have experienced a history of multiple physical transformations and persist in a heterogeneous state.

Chapter 15
The Search for Extraterrestrial Intelligent Life

The Search for Extraterrestrial Intelligence, or SETI, has traditionally been conducted and coordinated by the SETI Institute[1], based in Mountain View, California (USA). The SETI institute is a non-profit organization, which carries out not only research associated with possible extraterrestrial intelligent life, but also research related to planetary science, the origin of life, cultural evolution, and other topics. However, other initiatives are becoming increasingly visible, such as the Breakthrough Listen Project[2] and research associations in other countries including the United Kingdom SETI Research Network[3], the Forschungsnetzwerk Extraterrestrische Intelligenz in Germany[4], SETI.Austria[5], the SETI Australia Centre[6], and the Italian Radioastronomy Institute[7]. These organization are now conducting much of the research related to the search for extraterrestrial intelligent life.

15.1 Traditional SETI

The interest in extraterrestrial intelligent (ETI) life is probably as old as human civilization, but has been heightened in modern times by the discovery of radio waves from outside the Solar System. Cocconi and Morrison (1959) discussed the

---

[1] http://www.seti.org/)

[2] https://breakthroughinitiatives.org/initiative/1

[3] https://uksetiresearchnetwork.wordpress.com

[4] http://www.eti-research.net/personen.html#ds,

[5] http://www.setiaustria.at

[6] http://seti.uws.edu.au

[7] http://www.seti-italia.cnr.it

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_15

suitability of radio waves for communication between stars, and suggested as an optimum frequency for monitoring radio signals emanating from extraterrestrial civilizations the 21-centimeter line of neutral hydrogen, corresponding to a frequency of 1420 MHz. Electromagnetic radiation at this frequency can pass through large clouds of interstellar dust (optical light cannot) and also pass easily through Earth's atmosphere with little interference. Shortly afterwards, Frank Drake started the first observational SETI program, searching for microwave radio signals from other solar systems at that particular frequency (Project Ozma). The search remained unsuccessful, but sparked interest and other observation projects in the former Soviet Union and the United States. With time the efficiency of the search increased by orders of magnitude and included some additional radio wave frequencies on which extraterrestrials might transmit (such as the tritium line at 1516 MHz).

In principle, it is unclear at which frequencies a technologically advanced civilization would transmit a signal if it chose to do so. Radio waves between 1 GHz to 10 GHz are one obvious choice, because much of the signal would be strongly absorbed by interstellar gas and dust at lower frequencies, and by Earth's atmosphere, as well as presumably the atmosphere of any other habitable planet, at higher frequencies. The so-called "Water Hole"—a frequency range between 1420 MHz and 1720 MHz—has received particular attention, because of the emission of hydrogen and hydroxyl molecules within this frequency range. A hydrogen atom plus a hydroxyl molecule combine to make water, which is, at least for life as we know it, essential; thus, the preference for frequencies within the "Water Hole." Whether an alien civilization would follow the same logic is certainly unclear. Whatever frequency might be used for long-range communication, an artificial signal would be expected to be a transmission at a very narrow frequency window to maximize the signal with the least amount of energy. In contrast to an artificial signal, nearly all natural sources have a rather broadband emission pattern.

After NASA discontinued the High Resolution Microwave Survey in 1993 due to termination of US government funding for that program, the SETI institute continued the search for ETI life in the Universe, and has been, together with the Breakthrough Listen Project, the main institution for this research ever since. Despite that termination, the SETI institute has received renewed funding from US government agencies such as NASA, the National Science Foundation, and the Department of Energy. A continuation of traditional SETI efforts has also included a targeted search by Project Phoenix that has screened the regions around 1000 nearby Sun-like stars. The search for clever life, as Seth Shostak (2015) terms it, is still on, and even expanded by including disciplines such as life and cognitive sciences, and incorporating advancements in communication theory, bioneural computing, machine learning, and big data analysis in the search for alien life (Cabrol 2016). However, no clear signs of an extraterrestrial communication from any of these efforts have been received thus far. This non-observation has also been referred to as the Great Silence, and its possible implications are discussed in Sect. 15.6.

Traditional SETI-efforts continue with Project SERENDIP conducted by the University of California, Berkeley, in the form of piggy-back searches operating alongside conventional radio astronomy observations. This is being done, for example, at the Arecibo telescope in Puerto Rico and also at the Parkes radio telescope in Australia. In connection with the SERENDIP Project, a screensaver program (SETI@home) for personal computers was developed by the University of California-Berkeley to assist with the data analysis and search for signs of an extraterrestrial civilization in the collected data. In addition, the Allen Telescope Array, built with the goal of conducting SETI-dedicated searches at centimeter wavelengths, has been in operation since 2007. This project's objective is to use an array of 350 small dishes to provide the equivalent resolution of a 100-meter radio telescope, and thus be able to detect not only an extraterrestrial signal targeted at Earth, but even leaking radio and television signals from another planet—similarly to Earth, where this has been occurring for many decades. However, due to budget issues and other problems, only 42 of the dishes have been built and are in operation at the time of this writing, thus limiting the goal as originally envisioned.

15.2 Optical SETI

The idea of using visible and infrared spectra rather than radio waves for the search of extraterrestrial intelligent life was suggested only a year after the maser was invented and Frank Drake started to use radio waves to explore the skies (Schwartz and Townes 1961). This strategy includes the search for both continuous and pulsed signals that might originate from an extraterrestrial beacon in the visible and infrared spectrum. However, since radio technology was more advanced in 1961, efforts were focused on the 21 cm neutral hydrogen line, rather than the use of optical methods. The strategy of optical SETI is based on the assumption that an extraterrestrial civilization would want to optimize the signal-to-noise ratio and that this could best be accomplished with a well-designed laser, which could be aimed accurately at a target enabling the best use of the transmitted energy (Darling and Schulze-Makuch 2016). Also, optical signals are not produced as noise from quasars, pulsars, or black holes, and thus are highly distinctive (something not known at the time when the first radio wave surveys were done). An extraterrestrial civilization may thus want to transmit a signal outside of the natural noise environment, although it would be difficult to speculate exactly at what frequency. Also, a transmission with a laser could easily be blocked, for example, by clouds of interstellar dust in the line of transmission.

Several optical SETI efforts are currently in progress. One effort is piggy-backed on Harvard's 155 centimeter optical telescope, which is otherwise used for more conventional star surveys. The SETI effort searches for laser signals coming from nearby Sun-like stars, but also any signals coming from globular clusters and sources outside our Galaxy. Also, optical searches are ongoing as part of the SERENDIP project and SETI@home, and at the Optical SETI Observatory at Boquete, in Panama. However, nothing has been detected to date that could be associated with an ETI civilization.

15.3 The Search for Extraterrestrial Artifacts (SETA)

The possibility of using interstellar messenger probes as artifacts in the search for extraterrestrial intelligence was first suggested by Bracewell (1960). Freitas (1980) advanced this argument by proposing that physical space probes would be superior to radio signals as a way of communicating between civilizations on different planets, as they would allow a true conversation between the extraterrestrial civilizations, including an almost instantaneous interchange and interweaving of cultures. Also, based on our own record of space exploration, probes may be sent out within other solar systems all the time, and even into interstellar space, such as the Voyager probes. Beyond the search for space probes, SETA also includes the search for possible remains and artifacts of ETI on other planets and moons, including possible constructions by an extraterrestrial civilization, or robotic probes left over from early exploratory efforts. One example of such a possible construction is a Dyson Sphere (Dyson 1960), which could potentially be detected by emanating infrared radiation (Brooks and Schulze-Makuch 2010). Another example is the search conducted by Valdes and Freitas (1983) for possible extraterrestrial interstellar probes in the vicinity of the Earth-Moon Lagrange points, where any such hypothetical probe would not have to expend any energy to maintain a stable position for a long period of time.

15.4 False Positives, or How Do We Know a Signal Is Coming from ETI?

False positives or false alarms are obviously a big problem for SETI initiatives. There have been quite a few in the past. One outstanding example was CTA-102 in 1963, which was claimed by Soviet astronomers to be evidence for a highly advanced extraterrestrial civilization (Kardashev 1964). It turned out to be a quasar. Another well-known false alarm was the recording of a regularly pulsating signal using a radio telescope in Cambridge, England, by Jocelyne Bell in 1967. Early interpretations included the suggestion that the pulses might come from an interstellar beacon, but it turned out that they could be explained naturally coming from a rotating neutron star (Hewish et al. 1968). At the beginning of the radio observations, it was still challenging to determine whether a specific signal had a terrestrial or extraterrestrial source. Technological advances and protocols that in the case of a positive detection also have other telescopes observing the same target area of sky have made this less of a problem. However, this still remains problematic for optical SETI searches to some degree, because in addition to the photons of the observed central star, other starlight, cosmic rays, muon showers, and radioactive decays can trigger the sensitive light detectors. The general approach for a remedy to this problem is the use of three instead of two light detectors for optical SETI experiments. This has reduced the number of false alarms from one per day to one per year.

Also, in 2005 the International Academy of Astronautics established the SETI Post-Detection Science and Technology Task Group, which is charged “to act as a Standing Committee to be available to be called on at any time to advise and consult on questions stemming from the discovery of a putative signal of extraterrestrial intelligent (ETI) origin.”

It is interesting to note that the Wow! signal (see Sect. 15.5 below), probably the most promising of all recorded SETI signals as having an ETI source, is not recognized by SETI as being of extraterrestrial origin, because it could not be independently verified. Another example of the scrutiny with which SETI tries to analyze and verify any putative detection is the signal that was received at a frequency of 1420 MHz from the radio source SHGb02+14a in March 2003. It was a weak signal observed in a direction where no stars seem to be present, and the signal had a rapid drift corresponding to a rotation rate 40 times faster than Earth. Puzzlingly, for each detection the signal was at a frequency of 1420 MHz, at the original frequency before any drift and without the expected Doppler shift. Thus, the signal has been interpreted to be an artifact of cosmic noise, random chance, or a glitch in technology.

15.5 The Wow! Signal

A strong narrowband radio signal was detected at the Big Ear radio telescope located in Delaware, Ohio, on the 15th of August 1977. Jerry Ehman, who volunteered in the SETI program, discovered the radio signal a few days later, and wrote the comment “Wow!” next to it. The signal apparently originated from a location in the constellation Sagittarius, but many attempts by Ehman and others to receive the signal again were unsuccessful. The entire signal sequence lasted for 72 seconds and remains to date the most widely discussed possible signal deriving from a non-natural extraterrestrial source (Fig. 15.1).

The signal was received at a frequency of 1420.4556 MHz, within 10 kHz of the neutral hydrogen line. It appeared to be an unmodulated, continuous wave signal, with the sequence *6EQUJ5* simply representing the Gaussian distribution of signal intensity with respect to time. Several human- and Earth-based sources have been suggested (Ehman 2010; Gray 2012), but have not provided a satisfactory explanation. Thus, an extraterrestrial source from an ETI civilization cannot be excluded. However, why could it then not be detected anymore despite so many attempts? A possible explanation was provided by Bains (2015), who suggested that this signal may have represented a communication from one extraterrestrial civilization to another; or perhaps more likely, a signal from an extraterrestrial spacecraft back to its origin. Earth might have been simply in the way. Especially in the latter case the transmission target would be moving, so it would be very unlikely that the same signal would be picked up by an observer on Earth again. The same observation could apply to a hypothetical extraterrestrial observer with a sufficiently powerful detector who by chance intercepted the signals from Voyager 2 on 1 January 2015.

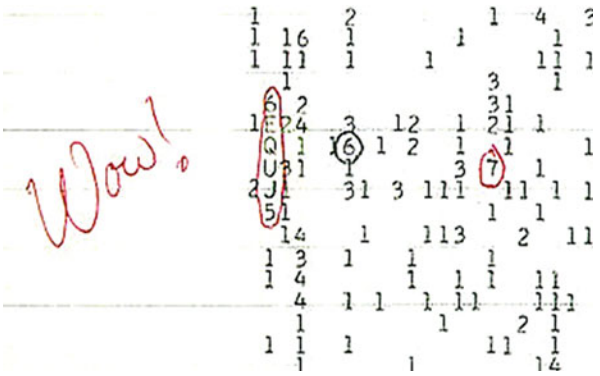


Fig. 15.1 The circled sequence *6EQUJ5* indicates the variation in intensity of the radio signal over time. It is measured as a unitless signal-to-noise ratio with the noise being averaged over the previous few minutes. Each character corresponds to the received signal, with a blank space denoting an intensity between 0 and 1; the numbers *1* to *9* denoting the correspondingly numbered intensities, and letters denoting an intensity of 10 and above, where *E,Q,U,J* correspond an intensity of 14–15, 26–27, 30–31, and 19–20, respectively

The observer might wrongfully conclude that humans live somewhere close to Eta Ophiuchi (Bains 2015). As Voyager is still moving, our hypothetical observer will never detect a signal from that region of the sky again, because both the Voyager spacecraft and its transmission target, the Earth, would have moved away. However, there is no evidence for this speculation nor that the received signal is from an extraterrestrial civilization.

Many signals received in the past have turned out to derive from natural phenomena of either terrestrial or extraterrestrial sources. One of the most recent examples is the detected signal apparently coming from the star HD 164595, which is a G-type star about 94 light years away with one known Neptune-size planet. It was detected by a RATAN-600 radio telescope in Russia in 2015, but couldn't be confirmed later on and might have been due to a Russian military satellite.

15.6 Messaging to Extraterrestrial Intelligence (METI)

Messaging to Extraterrestrial Intelligence (METI), also known as Active SETI, consists of sending signals into space with the expectation that they might be received by an ETI. Sending out interstellar messages continues to be highly controversial and several prominent scientists, including the late Stephen Hawking, have warned that we might just be inviting unfortunate consequences of an alien encounter.

Shuch and Almár (2007) described the divisions within the scientific establishment, particularly within the SETI Permanent Study Group of the International Academy of Astronautics, and summarized the most prevalent points they felt valid: "…no matter what positive motives we might ascribe to our cosmic companions, no matter how altruistic we may believe our neighbors to be, or no matter how unlikely we may consider it that we would encounter malevolent extraterrestrials, even the most ardent proponents of transmission from Earth, and other forms of Active SETI, must honestly concede that the probability of negative consequences from terrestrial transmission is non-zero…." Musso (2012) agreed that METI is very unlikely to be dangerous for the human population on Earth, but, that at present, such a possibility cannot be completely excluded. Haqq-Misra et al. (2013) attempted to put forward a balanced view of both the benefits and harm of transmitting into space. In their advisory capacity to such policy-making bodies such as the United Nations Committee for the Peaceful Uses of Outer Space (COPUOS), the SETI Permanent Study Group struggled for a long time to find a consensus, with one subset of the group even urging a total moratorium on any transmissions. The discord has continued. Many members of that group signed a statement in 2015 that a worldwide scientific, political and humanitarian discussion must occur before any message is sent.

The opposing position was taken by Vakoch (2016), who argued that human nature tends to overrate fear and underrate the potential benefit of a contact. Altruistic aliens might, for example, be able to help guide humans on a path to environmental sustainability, and by reaching out to them, humanity may actually avoid its own annihilation. He also made the point that even a slightly advanced extraterrestrial civilization would already know of our existence through TV and other emissions that have been leaking into space for decades. If we would really have been in danger of an invasion, it would already be too late since they would know where we are. On the other hand, if we are just now being discovered, either by chance or due to our METI efforts, we can look to historical precedent on Earth for how such an encounter might play out. There is hardly any case in human history in which contact between a technologically more advanced and less advanced civilization has not ended badly for the latter.

Both sides seem to agree that there should be international protocols established for interstellar communication, including simple messages. But what should those protocols look like? There is some guidance available under the SETI charter in its "Declaration of Principles Concerning Sending Communications with Extraterrestrial Intelligence." However, this is an issue the United Nations needs to address. Meanwhile, messages continue to be sent into space, like the Arecibo Message in November 1974, which was sent towards the globular cluster M13, 25,000 light-years from Earth. More recently, in October 2016, an interstellar transmission was sent in the direction of the North Star (Polaris) by the nonprofit group "A Simple Response," using the European Space Agency's deep space antenna at the Cebreros ground station in Spain. Of greater concern because of the nearness of its target is a more scientifically informed transmission by METI sent from the Eiscat transmitter in Tromsø, Norway in October 2017 toward GJ 273, also known as Luyten's star, for a time period of 3 days. Luyten's star is a red dwarf (dM) about 12 light years from Earth with two confirmed planets, one of them a potentially habitable Super-Earth planet with about three times the mass of Earth.

15.7 The Fermi Paradox

In 1950, the physicist Enrico Fermi allegedly asked his co-workers over lunch: "Where are they?" meaning where are the intelligent extraterrestrials? If there are billions of stars and even more planets, chances should be good that ETIs have evolved on some of them. Traditionally the so-called Drake equation has been used to provide some kind of estimate of how many ETIs might be in our Galaxy (Eq. 15.1). If any of the factors in the Drake Equation are very low, the number of expected civilizations (N) in the Galaxy would be dramatically reduced

$$N = R^* \bullet f_p \bullet n_e \bullet f_l \bullet f_i \bullet f_c \bullet L \tag{15.1}$$

where R^* is the average rate of star formation in our galaxy,

f_p is the fraction of formed stars that have planets,
n_e is the average number of planets per star that can potentially support life,
f_l is the fraction of those planets that actually develop life,
f_i is the fraction of planets bearing life on which intelligent, civilized life has developed,
f_c is the fraction of these civilizations that have developed communications, e.g., technologies that release detectable signals into space,
L is the length of time over which such civilizations release detectable signals.

A more recent approach is the one by Irwin et al. (2014) who estimated that the number of planets with biological complexity could exceed 100 million in our Galaxy alone. If we assume that on 1% of those planets a species would evolve with a high enough level of advanced technology to transmit messages through space, then there could be a million radio-emitting planets in our Galaxy. So why have we not already been in contact with them? This problem has been known for decades, and is called the Fermi Paradox. According to Gray (2015), a better term would be "the Great Silence," since despite the vastness of the universe we still do not have any evidence of intelligent extraterrestrial life.

Historically, two camps emerged to explain the Great Silence. One group argued that the absence of any evidence for ETI means that there is no such life in the Galaxy. Hanson (1998) suggested that the number of ETI civilizations capable of deep space travel and communication might be drastically limited by a "Great Filter" located somewhere along the timeline between the origin of planets and the evolutionary culmination of a technological civilization. That filter could, in principle, be located at the origin of life, or could yet lie ahead of our current evolutionary stage, if technologically advanced civilizations have a tendency to self-destruct within a very short life time. If another ETI has never arisen, or has never survived long enough to search for other ETIs or advertise its own existence, SETI is a pointless exercise (Tipler 1981). The other group favored the likelihood of technologically advanced life elsewhere in the Galaxy, and came up with several explanations for why none has been detected so far. An extensive list of possible solutions to the so-called Fermi

Paradox can be found in Webb (2015). One of the most popular explanations is that Earth serves as something like a nature preserve for an alien ETI. Another is that some of the unexplained UFO observations are actually caused by extraterrestrial visitations, but that the aliens do not want to reveal themselves. Shostak (2015) argued that any intelligent biological life might rather quickly be replaced by machines, if the ETI is capable of fabricating them, and that therefore we should be prepared to communicate with machines instead of the life forms themselves. However, we don't know whether the presumably more advanced machines would be interested in communicating with us.

Perhaps the solution to the Fermi Paradox—or better, the Great Silence—is rather mundane. The distances between stars and their planetary systems are vast, so the challenge of finding an extraterrestrial civilization at or beyond our technological level is a matter of diminishing probability. We have previously argued that the likelihood of intelligible contact between another ETI and us is limited by three factors: (1) the remote distances between Earth and any planetary system that could harbor an ETI; (2) the small time window—only about a century—in which humans have had the ability to send radio signals into space and receive them from outer space; and (3) the questionable ability for us and a remote ETI to communicate in a way that we both would understand. For the detailed argument, see Irwin and Schulze-Makuch (2011). As Beck and Irwin (2016) noted, "…the problem is akin to detecting short flickers of light at great distances within the brief time span of a camera's open shutter, having to look in precisely the right direction, and being able to understand the significance of the signal."

15.8 Chapter Summary

The search for extraterrestrial intelligence has fascinated humans since ancient times, with serious efforts being ongoing since the second half of the twentieth century. Early efforts focused on detecting the 21 cm neutral hydrogen line in the microwave spectrum, but were later expanded to other frequencies, including optical wavelengths. In addition, searches for ETI artifacts have been conducted, but no firm evidence for the existence of any ETI civilization has been found to date. A number of possible explanations for this Great Silence—popularized commonly as the Fermi Paradox—have been offered. The absence of evidence for ETI may be surprising, given the large number of planetary systems known to exist, but even large numbers can be so diluted by the vastness of space and time, that the probability of contact within the infinitesimally small period that humans on Earth have been able to transmit and receive signals through space, is vanishingly small.

Chapter 16
Optimizing Space Exploration

Both robotic and human missions into space are necessary for an effective program of space exploration. For the nations that have sent humans into space (Russia, China, and the United States) the competition for limited budgets between human and robotic exploratory strategies is inevitable. Yet, the two strategies are complimentary and mutually supportive. Robotic missions are much cheaper than human missions. A major breakthrough in cost are so-called CubeSats—small spacecrafts generally of 10 × 10 × 10 cm dimensions with scaled-down miniaturized payloads (Loff and Dunbar 2017). Robotic missions will remain the best if not only way to investigate difficult to reach planetary bodies and to explore hostile environments such as the radiation-intense surfaces of the Jovian moons. Also, any initial mission to a planetary body will have to be robotic to understand the planetary environments, avoid unnecessary risks, and conduct space exploration in a cost-efficient way. However, eventually human missions are warranted on philosophical grounds and necessary on practical grounds.

The urge to explore is a fundamental drive in human nature, and history shows that new worlds present an irresistible attraction to this urge. "When ships to sail the void between the stars have been invented," wrote Johannes Keppler centuries ago, "there will also be men who come forward to sail them." The first steps have already been taken with human visits to the Moon. Mars is the next inevitable destination, with NASA having held a first human landing site workshop in 2015. Humans will go there for a variety of reasons, not the least of which is simply that it is there. A more sophisticated treatment of the philosophical basis for human exploration of space is beyond the scope of this book, but we would note that the human condition on Earth, especially in the face of rapid climate change, continued population growth, and strife from many sources, will likely affect the urgency with which humans spread onto neighboring worlds in our Solar System within the coming century.

As a practical matter, human exploration has the advantage over machines at our current state of robotic technology of being much more maneuverable, with a much greater capacity to analyze complex information and make decisions locally and in

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7_16

real time. Collection of productive and appropriate samples, problem troubleshooting, astute evaluation of immediate and long-term environmental challenges, anticipation of pitfalls, and complicated physical manipulations are among the many advantages that a human explorer has over a robot. While a rover can cover square meters in a day with the risk of becoming stuck in a trivial depression for days at a time, a human can cover square kilometers in a day and avoid getting stuck in the first place. Thus, while human exploration is vastly more expensive, the payback is vastly greater.

The Lunar Apollo program carried humans to the Moon on six occasions, then suspended the effort. Such a program of human exploration which only visits a certain planetary body and then abandons it is neither cost-effective nor scientifically very valuable. With NASA now committed to a human return to the Moon and eventually also to Mars, and with China and possibly Russia and other nations joining the effort to transport humans beyond the Earth, the time to start planning a more extensive and systematic exploration of our nearest planetary neighbors is at hand. Humans and machines will increasingly be used in tandem to explore and ultimately colonize some of those worlds. Below, we enumerate a general strategy for the near-term exploration of our Solar System and beyond.

16.1 Mars

Mars is our second closest planetary neighbor (after Venus) and is a dynamic water-rich planet similar in many respects to Earth. It is the only planet in the Solar System similar enough to Earth to provide limited habitability to terrestrial organisms including humans. However, surface conditions on Mars are challenging due to cold temperatures averaging about −65 °C and ranging from about −140 °C to +35 °C, the lack of an ozone layer and magnetospheric shielding, and the absence of liquid water on the surface. Mars has a thin but substantial atmosphere mostly consisting of carbon dioxide (95%). A trip to Mars at the most favorable launch option takes about 6 months with present chemical rocket technology. Although Mars is currently cold, it once was apparently warmer and more humid, with running water producing floodplains and carving canyons and valleys. It probably harbored a large ocean in its northern hemisphere long ago (Fairén et al. 2004). Although at most locations on Mars today, liquid water is not stable and would turn to vapor within a very short time, there is substantial evidence suggesting the presence of water beneath the surface and possibly in caves (Boston 2003; Boynton et al. 2002; Feldman et al. 2002; Malin et al. 2006; Mitrofanov et al. 2002).

16.1.1 Robotic Missions to Mars

Prior robotic missions to planetary bodies such as Mars have focused either on exploration of a single site with a single lander or rover, or on global mapping from an orbiter. Several of these missions are still active on or at Mars. The lander/rover missions analyze a confined, readily accessible site in detail, but lack the capacity to achieve a regional overview, while orbiter missions return immense data sets that are global in scope but provide limited local detail. The first test of a combined approach will be taken by the Mars InSight Mission, launched on 5 May 2018. The mission consists of a lander with a drill, accompanied by two CubeSats for relaying communication between the Mars Reconnaissance Orbiter and Earth. A bolder approach has been suggested, using a hierarchical mission design that includes spaceborne (orbital), atmospheric (airborne), surface (mobile such as rover, and stationary such as lander or sensor), and subsurface (ground-penetrating radar, drilling, etc.) agents working in concert to allow for sufficient mission safety and redundancy, to perform extensive and challenging reconnaissance, and to lead to a thorough search for evidence of life and habitability (Fink et al. 2005). This is especially warranted for sites of astrobiological interest such as (1) canyons (e.g., Valles Marineris on Mars and chasms on Venus), (2) mountain ranges (e.g., Thaumasia highlands on Mars and Isthar Terra on Venus), (3) sites of suspected magmatic-driven uplift and associated tectonism and possible hydrothermal activity (e.g. the Warrego Valles rise on Mars and Maxwell Montes on Venus), (4) polar ice caps on Mars, (5) ice deposits within impact basins (Mercury and Mars), (6) volcanoes of diverse sizes and shapes (e.g., Apollinaris Patera on Mars and Beta Regio on Venus), (7) putative ancient accreted terrains and associated volcanism on Mars, (8) regions indicating potential recent hydrologic activity such as spring-fed seeps and recurrent slope lineae (RSL) on Mars, and (9) chaotic terrain, such as the source areas of the circum-Chryse outflow channel system on Mars (Schulze-Makuch et al. 2005a, b).

A sample return mission and a life detection mission (see Chap. 12) would be the next logical steps in the robotic exploration of Mars. A region of high astrobiological interest for such missions would be a site where water may be present at or near the surface. A priority of putative hydrothermal target areas has been proposed by Schulze-Makuch et al. (2007), which could serve as a baseline for further site selection efforts. After the sample return mission, which could be conducted with a life detection component, a permanent robotic station would be the next step in robotic exploration and an intermediate goal in a combined robotic-human exploration effort for Mars. A more thorough investigation of specific localities of interest (such as those described above) would be aided by a permanent robotic base. For example, any drilling investigation to probe the Martian deep subsurface for microbial life beneath the permafrost would mean energy requirements and an infrastructure that could only be met with permanent equipment on Mars. A permanent robotic base would not have to be very elaborate, but could simply consist of a communication relay and a power generator, perhaps together with a remotely operated telescope. The power generator could produce energy using solar panels that are laid out in a suitable location protected from wind-blown dust with wipers to remove any dust if needed. Alternatively, nuclear fuel (e.g., a plutonium rod) could be considered as well, especially if the robotic spacecraft that brought the equipment used one in the first place. The most straightforward strategy might be to land a spacecraft designed to be used as a permanent station, and have later equipment brought by other robotic missions with the capability to hook up to the base station. Even now such a limited base would be useful if it were located close to one of the rovers that is still operating on the surface of Mars. The battery of a rover could be recharged, and minor mechanical repairs could be made.

16.1.2 Human Missions to Mars

No destination in our Solar System offers a more enticing target for human mission exploration than Mars. The detection of methane via remote sensing (Formisano et al. 2004; Krasnopolski et al. 2004; Mumma et al. 2004) and by the Curiosity rover (Webster et al. 2015), and the discovery of abundant water ice (Boynton et al. 2002; Feldman et al. 2002; Mitrofanov et al. 2002) on the Red Planet elevates it to one of the highest priority targets for both robotic and human exploration. Mars is also the most Earth-like planet in our Solar System and offers various resources, including shelter, minerals, water, limited oxygen, and a tenuous atmosphere, that make its colonization a possibility, in principle (Davila et al. 2015). Observations from Earth-based telescopes and various robotic missions have provided some initial understanding about Mars and its current and past environments. NASA's goal as stated during the First Human Landing Site Workshop held in 2015 was to conduct a series of human missions to Mars, which would also include the establishment of a human base and an exploration zone. The selection of the exploration zone is prioritized for both high scientific value (including astrobiological considerations) and high engineering merit (for example, access to water ice from which liquid water and spacecraft fuel could be produced). The discussed timeline for a human mission and human base on Mars was set for the 2030s, but budget problems and uncertainty about NASA's vision for the next 50 years may push this goal further into the future.

Based on the discussions at that workshop, it became clear that many extensive robotic missions would be needed to prepare a human mission to Mars, and we consider a robotic base station as described above as a minimum requirement for a successful human mission. However, the mission should entail more than just a walk on Mars and the return of some environmental samples, as done by the Apollo missions to the Moon. Rather, a long-lived program should be envisioned as discussed during the First Human Landing Site Workshop in 2015. Otherwise, the science objective could be as easily achieved with a robotic mission at a much lower cost. The minimum goal should be to have the crew stay for an extended period of time, to explore interesting sites and conduct research on various aspects of habitability on Mars.

Resources on Mars itself could aid in such an extended stay. Instead of building radiation-protected shelters, astronauts could simply use natural shelters such as caves that would provide shelter from the intense ionizing radiation and strong ultraviolet light (Davila et al. 2015). Most of the natural caves appear to be lava tubes, and some of them are located at a low elevation in close proximity to the former northern ocean (Fairén et al. 2004), which means that they could harbor ice deposits similar to many ice caves on Earth (Boston 2000). If ice caves are found, they would also partially meet the needs of a human mission or future settlement for water and oxygen. Caves on Mars are likely to be much larger than on Earth due to the lower gravity on Mars ($0.38g$), which allows larger spans of unsupported rock to exist. Mars with its thin atmosphere has no ozone layer and no magnetospheric shielding; thus some natural or artificial shielding from ionizing and ultraviolet radiation will be required. The damage to DNA on the surface of Mars may be as much as a thousand times higher than on Earth under the worst case scenario, such as dust free skies (Cockell et al. 2000; Patel et al. 2003). However, a layer of 1 mm or less of Martian analog soil was shown to protect microorganisms sufficiently to prevent loss of viability (Cockell et al. 2005; Mancinelli and Klovstad 2000; Schuerger et al. 2003), thus a protective spacesuit or a cave could certainly provide sufficient protection for humans. Some of the caves may even hold water in the frozen form (Cousins and Crawford 2011), but even if no ice caves are found, evidence is accumulating that water is present in the subsurface. Although at most surface locations on Mars today, liquid water is not stable and would sublimate within short time frames into the atmosphere, evidence indicates that there is water beneath the surface (Boynton et al. 2002; Feldman et al. 2002; Malin and Edgett 2000a; Malin et al. 2006; Mitrofanov et al. 2002) and possibly in caves (Boston et al. 1992; Zubrin and Wagner 1996), but definitely present in the highly visible polar areas. Since temperatures on Mars can be extremely low, sometimes dipping below -100 °C, the use of natural caves would be a further asset by providing more temperate environments. Mars was and possibly still is a site of substantial volcanic activity with the episodically active Tharsis magmatic complex being the dominant release point for the internal heat energy of the planet (Dohm et al. 2001). Thus the presence of liquid water in caves associated with Tharsis is not unthinkable. Numerous igneous flow features, including lava tubes (Fig. 8.1), have been identified on Mars (Boston 2003).

16.1.3 A Vision for Mars Exploration

A far-reaching vision would be to establish human settlements on Mars. Natural caves could again be the focal point of those settlements with greenhouses extending out of them. In principle, plants could be grown in the greenhouses outside of the caves while affording some UV protection and enrichment of soil, thus providing the inhabitants of the cave with food and an additional supply of oxygen. Microbes could be used to break down and recycle wastes; thus each cave settlement would constitute its own independent biosphere with some additional resources provided by the Martian environment. Several of these cave-centered biospheres could be created, each being in constant communication with the others to share experiences on which technological approaches are working best. It would take a tremendous effort to establish such substantial settlements on Mars, but they are technologically achievable, in principle. Mars can provide some essential resources such as water and shelter, which would not need to be brought in from Earth or be constantly recycled, making such an endeavor more likely to succeed. While some robotic missions would need to re-supply the human outpost periodically, becoming as self-sufficient as possible would obviously be desirable. The ultimate goal of Martian exploration efforts should be a scientific station for maximum scientific return, including the in-situ analysis of Martian environmental samples. The logistics of implanting a persistent human presence on Mars are challenging, hence a substantial amount of further research on the feasibility of enclosed self-sustaining habitats needs to be carried out and successfully demonstrated under harsh conditions as analogous to those on Mars as possible, such as in Antarctica, prior to the attempt to establish such bases on Mars. Also, planetary protection issues are a major concern for any human mission (see below, Sect. 16.4), especially if indigenous life exists on Mars. So this possibility should be investigated prior to a human mission to the extent possible. Since a human mission will necessarily involve the transport of microbial hitchhikers from Earth, a great deal of care would have to be exercised in the establishment of the first scientific field stations on Mars. Whether a permanent station can ever be taken off Earth's "life support" is an open question, but the establishment of such a station provides a suitable vision for future exploration of the Red Planet. Without such a vision, humans will likely visit Mars, but with no further goals or lasting achievements.

How could a permanent human settlement on Mars be achieved? Keeping costs as low as possible is critical, as high projected costs have already delayed NASA's plan for a series of human missions, originally planned to start in the 2030s. Davies and Schulze-Makuch (2008) suggested a series of one-way missions to initiate the human exploration of Mars. Eliminating the need for returning early settlers to Earth would cut the costs several fold, while ensuring a continuous commitment to the exploration of Mars and space in general. Hardware being developed for the Moon program could be adapted for settlements on Mars. The colonists would be resupplied on a constant basis from Earth with elemental necessities, but otherwise would harvest resources available on Mars. Once the outpost was established and mostly self-sufficient, it could serve as a hub for the arrival of more personnel brought in to expand the colonization effort. With time and advancing technology, two-way travel between Mars and Earth would eventually be established, but a series of one-way human missions to Mars would represent a continuing commitment to explore and colonize the planet in the first stages of human progression to another world. Clearly, such a strategy would require a return to the exploratory spirit of the Vikings and the age of Columbus, but the appeal of space and the lure of adventure inherent in the human spirit would almost surely generate an abundance of volunteers.

16.2 The Moon

Many astrobiologists consider the Moon as a dry and dead rock in space. However, it is not as a dry as once thought. More recent mission data reveal a noticeable absorption signal for water across much of the lunar surface (Pieters et al. 2009; Clark 2009), even with some variability of water abundance observed over the course of the lunar day (Sunshine et al. 2009). Also, the Moon may have been relatively wet shortly after its formation, containing at least 0.3 to 1.7% of water at the time liquid magma covering its surface crystallized (Lin et al. 2017a, b). And about 3.5 billion years ago, gases deriving from huge lava outpourings are thought to have built up an atmosphere of about 10 mbar, nearly 1.5 times thicker than the atmosphere currently existing on Mars (Needham and Kring 2017). This atmosphere may have lasted for millions of years, and habitable conditions may have prevailed on the Moon during that brief time period (Schulze-Makuch and Crawford 2018). Nevertheless, even at this time oceans are not likely to have existed, particularly if the Moon was already tidally locked to Earth, meaning that any liquid water could have existed only in a relatively narrow area of benign temperatures, at the slowly moving terminator between the very hot side of the Moon facing the Sun and the shaded extremely cold side. Thus, if liquid water was present, it is not expected to have remained for very long. Aside from the possibility of liquid water on the Moon sometime in its history, there is another reason the Moon is of high astrobiological interest. It may hold evidence of the origin and early evolution of life on Earth, since meteorite impacts on Earth may have delivered biogenic material to the surface of the Moon. Thus, organic macromolecules or even fossilized early life forms could be recovered from ice-regolith mixtures, particularly near the south pole, and reveal critical clues for the origin of life on Earth (Armstrong et al. 2002; Schulze-Makuch 2013; Matthewman et al. 2015).

The Moon has also drawn renewed attention as a target for space exploration. The objective for further exploration of the Moon should be centered on a permanent human presence. As a large body, the Moon provides a solid surface to meet any structural requirements. The gravitational force is about 1/6 of that of Earth, but humans and other organisms should be able to adapt better to a fractional gravity environment than to the microgravity experienced in space. However, today the Moon is devoid of an atmosphere. Lacking an atmosphere or other protective shielding, the Moon is susceptible to an enormous amount of irradiation from the solar wind. Thus, any settlement would have to be shielded from radiation either by thick surface structures, by artificial subsurface structures, or by one of the numerous natural lunar lava tube caves that have been recognized since the Apollo era. Long-term survival is difficult on the Moon due to the apparent lack of oxygen and scarce resources of water. But water ice intermixed with lunar regolith at the south pole of the Moon could serve as a relatively accessible reservoir for analyzing cometary ice and provide water and oxygen for the possible future human habitation of the Moon. However, the ice would have to be extracted from the subsurface as the surface ice has been altered by radiation. About 2–3 m of lunar soil cover is required to protect surface ice from radiation damage (Schulze-Makuch et al. 2005b). Challenges for human habitation of the Moon, including long-term exposure to radiation and limited gravity such as on a lunar station at the south pole, have been described by Horneck et al. (2003). A thorough exploration of the Moon would be greatly aided if nuclear fusion becomes a viable alternative for producing energy on Earth. Helium-3, a helium isotope rare on Earth but deposited on the Moon by the solar wind, could then be harvested on the Moon as a fuel for nuclear fusion reactors in the future (although this is controversial). The refocus of NASA on human colonization of the Moon and missions to Mars, and Chinese interest in the same direction, should accelerate the development of technology for sustaining long-term human habitations in hostile environments.

16.3 Venus

As discussed in Sect. 8.3, microbial life could exist in the lower Venusian atmosphere. Therefore, a sample return mission from the lower cloud layer of Venus should be considered. Schulze-Makuch et al. (2002b) contemplated various mission options and concluded that a sample return mission involving a Parachute Drop—Balloon Floatation Mission, designed to return astrobiologically relevant material for analysis to the International Space Station, would be the most preferable option.

The relative ease of reaching Venus and returning to Earth, and the availability of appropriate existing technology, makes such a mission feasible in the near term. For example, a blimp/balloon could be deployed, which would be able to hover at an altitude of 51 km or descend to lower altitudes, where it could collect samples of cloud particles with aerogels similar to the Stardust and Genesis missions. Knollenberg and Hunten (1980) reported a cloud particle density of 10–100 particles per cm^3 at about 50 km altitude. These cloud particles, once obtained by the blimp/balloon, could be transported into orbit, and from there to the International Space Station or Earth for analysis. Even if the promising mode 3 particles in the Venusian atmosphere turn out not to be biological, a sample return mission would significantly increase our knowledge about the composition and dynamics of the atmosphere of Venus.

16.4 Other Exploration Targets

There are many other potential targets of astrobiological interest in our Solar System and beyond. Titan is of special interest because of its atmosphere uniquely rich in organic compounds and because of its potential to harbor alien life of a separate origin (Baross et al. 2007; Shapiro and Schulze-Makuch 2009). Others, such as Iapetus and Triton, appear to harbor complex chemistry as well. The icy satellites of the giant gas planets (Europa in particular) are prime targets because of their abundance of water, which are liquid beneath the surface in some cases, and their dynamic gravitational perturbations and/or geothermal activity. As the list and variety of extrasolar planets grows, so does the motivation to develop the technologies necessary for determining their possible suitability for life.

The Cassini-Huygens mission to Titan, Saturn's largest moon and the second largest satellite in the Solar System, transmitted stunning images from Titan that revealed a world where an ethane/methane mixture instead of water acts as the main surface transforming agent (Faulk et al. 2017). The presence of methane rain inferred from modeling (Toon et al. 1988) has been supported by observations from the Cassini-Huygens mission (Griffith et al. 2005). Lakes of liquid ethane/methane have been confirmed (Stofan et al. 2007), and methane aquifers are thought to exist in Titan's subsurface (Mitri et al. 2007). The possibility of life on Titan has been suggested (McKay and Smith 2005; Schulze-Makuch and Grinspoon 2005). But even if life is not present on Titan, its rich organic inventory makes it the closest analog to early Earth conditions that we can study. Thus, a follow-up mission to Titan should be launched, for a more close-up and detailed study of its surface. Titan's dense atmosphere is ideally suited for exploration by balloon-type vehicles. Particularly efficient would be an aerorover that uses a hot air balloon concept and is supported by an orbiter (Sittler et al. 2006).

Another target of great astrobiological importance is Europa. The presence of an ocean beneath its icy crust has been inferred from the observations of (1) magnetic fields induced by eddy currents in a mobile conducting medium within the body of the satellite (Khurana et al. 1998), (2) asynchronous rotation of Europa that implies subsurface generation of friction (Geissler et al. 1998), and (3) surface fracture features consistent with mobile icebergs driven by subsurface liquid (Carr et al. 1998; Hoppa et al. 1999). Doppler tracking by the Galileo spacecraft suggested that Europa has a differentiated internal structure, which includes a dense core of metal or metal sulfides, a rocky mantle, and a low-density ice crust or ice-crusted ocean with a thickness of 80–170 km (Anderson et al. 1998). A metallic core may provide internal heat through radioactive decay, subjecting the ocean floor to volcanic eruptions. Volcanic activity would also be expected since Europa's neighbor Io is volcanically the most active planetary body of the Solar System, and planetary evolution theories assume a roughly similar initial composition of Io and Europa (Consolmagno and Lewis 1976). The deep ocean environment on Europa may thus resemble that on Earth where hydrothermal discharge areas on the aphotic ocean bottom support hydrothermal vent communities (Amend and Shock 1998; Vinogradov et al. 1996). Irwin and Schulze-Makuch (2003) estimated that an ecosystem consisting of reasonably dense populations of macroorganisms could be supported by energy from plausible estimates of methanogenesis in the subsurface liquid ocean of Europa. Using similar modeling techniques, other estimates of potential biomass have been both higher, based on radiolytic generation of O_2 (Chyba 2000), and lower, based on sulfate reduction (Zolotov and Shock 2003).

Because of Jupiter's intense radiation environment, Europa most likely is suitable only for robotic exploration. A robotic mission should be launched that includes an orbiter and probes that sample the surface ice of Europa below the radiation-reworked upper 1 meter or so. Criteria for selecting landing sites of astrobiological interest have been suggested by Figueredo et al. (2003). If samples can be retrieved from suitable locations beneath the uppermost layer of ice, they may contain organisms, since frozen ice would preserve them very well. A life detection component is considered as part of the payload for NASA's planned "Europa Clipper" mission to Europa in the 2020s.

Other icy satellites of astrobiological interest include Ganymede, the largest satellite in the Solar System, which also shows evidence of surface remodeling and likewise is thought to contain a subsurface liquid ocean, and the Saturnian moons, Enceladus and Tethys. Enceladus, in particular, has moved to the forefront of astrobiological interest, due to its geyser-like eruptions into space from a liquid reservoir beneath its south polar region. Several missions to Enceladus are currently being proposed, including some with a life detection component. Observations from the Cassini orbiter strongly suggested geothermal activity also on Tethys; and Titania, the largest moon of Uranus, shows abundant evidence of surface resculpturing. Though small, remote, and therefore logistically difficult to explore, these smaller icy satellites should yield sufficiently important clues about the evolutionary history of the Solar System, whether or not they harbor life, to justify efforts to explore them.

Other intriguing targets for space exploration include comets and asteroids, which are important for sampling early Solar System material, and the Sun and its cycles, which directly affect every organism on Earth, as well as the planetary environment at least as far out as Saturn. Efforts to detect Earth-like planets in other Solar Systems, as discussed in Chap. 12, also need to continue. Further, many fundamental constants necessary for a full understanding of the physical Universe and the biology contained within it, can be measured by both space probes and ground-based telescopes. Thus, there is no lack of intriguing and significant targets for space exploration. The challenge will be to fit them into budgets that able governments are willing to appropriate. With intense competition for funds from the cost of persisting human conflicts and compelling social needs, perhaps the greatest hope for sustained space exploration lies within the private sector. The ability to finance relatively uncomplicated robotic missions appears to be within the reach of the world's wealthier individuals and corporations. Some of them, such as SpaceX, seem to be on the verge of being able to send a mission to the Moon or Mars. Harvesting planetary resources, such as Helium-3 on the Moon, may prove financially lucrative in time. And, while still in its infancy, space tourism may make travel at least to our nearest neighbor(s) a more common endeavor in the future. The history of human nature shows little evidence that the urge to go forth to other worlds, both in person and by robotic extension, will be stifled indefinitely.

16.5 Planetary Protection Considerations

Planetary protection is a serious consideration for both robotic and human missions. Protective measures are needed to preserve Solar System bodies from contamination by terran life, and to protect life on Earth from possible forms of life that may be returned from other Solar System bodies. The rationale is to preserve our ability to study other worlds as they exist in their natural states and to avoid contamination that would obscure our ability to find life elsewhere. Also, if we find life on other planetary bodies, we need to ensure that prudent precautions are taken to protect Earth's biosphere. In order to achieve this, spacecrafts and their components need to meet stringent cleanliness requirements. Specific planetary protection requirements for each mission and target body are based on the scientific advice of the Space Studies Board and on NASA or international policy guidelines. For example, a spacecraft destined for Mars with the objective of detecting life would have to meet the highest possible level of cleanliness, and some specific operating restrictions would be imposed.

The Committee on Space Research (COSPAR) implements planetary protection policy for the reference of spacefaring nations, both as an international standard on procedures to avoid spreading organic constituents and biological contamination through space exploration, and to provide accepted guidelines for complying with the wording of the UN Space Treaty and other relevant international agreements. For example, so-called Special Regions have been defined for Mars in which Earth organisms could potentially survive and thus pose a risk to the forward contamination of Mars (Special Regions Science Analysis Group 2006, 2007). These special regions would not be off limits for future space exploration, but any spacecraft intended to land there would have to undergo state-of-the-art sterilization procedures. This, however, would increase the costs for such a mission dramatically, which was suggested to be part of the reason why no mission has explored these astrobiologically interesting regions to date (Fairén and Schulze-Makuch 2013).

There is no known technique that would sterilize a spacecraft completely, and the microbial survivors of the sterilization procedure would also be those microbes more likely to survive on Mars or some other extrasolar body. One fall-out of the current policy was that the Curiosity Rover was not allowed to go near newly discovered recurrent slope lineae (RSL) in Gale Crater, because the rover was not sterilized sufficiently. RSL are dark markings on steep slopes, interpreted as seasonally briny water flows and thus of high astrobiological interest. A recent scientific discussion became heated, with scientists on one side arguing that the current planetary protection protocols for forward contamination should be relaxed (Fairén et al. 2017), while others vehemently denied the need to do so (Rummel and Conley 2017). Both sides agreed, however, that this is a discussion that needs to be held, and a workshop dealing with this controversy is scheduled for Stockholm, Sweden, in November 2018. A rethinking of some of the policies on planetary protection is timely because of planned human missions to Mars by NASA and possibly private enterprises.

16.6 Chapter Summary

Robotic and human exploration should proceed together to meet the challenges of discovery on other worlds. The history and characteristics of Mars make it the most suitable target for human exploration. With orbiters and rovers already there, the next goal should be to assemble a permanent robotic station, which would aid in the systematic exploration of Mars. Such a station on Mars, with experimental human colonization on the Moon, can serve as building blocks for an extended human mission and eventual human settlement on Mars. It should be emphasized that this long-range vision should not be implemented by ignoring other goals in space exploration that promise to provide a significant scientific return. Among others, these include the further robotic exploration of the outer Solar System, Venus, our Sun, the detection of extrasolar planets, and measurements of the fundamental constants of the Universe.

References

Abelson, P. H. 1989. Voyager 2 at Neptune and Triton. *Science* 246: 1369.

Abbas, O., and D. Schulze-Makuch. 2002. Acetyle-based pathways for prebiotic evolution on Titan. pp. 349-352. *2nd European Workshop on Exo-Astrobiology (EANA/ESA)*, Graz, Austria.

Abbot, D.S. and E.R. Switzer. 2011. The Steppenwolf: a proposal for a habitable planet in interstellar space. *Astrophys. J. Lett.* 735: 2, L27 (doi: https://doi.org/10.1088/2041-8205/735/2/L27).

Abe, F., C. Kato and K. Horikoshi. 1999. Pressure-regulated metabolism in microorganisms. *Trends Microbiol.* 7: 447-453.

Acevedo-Rocha, C.G. and D. Schulze-Makuch. 2015. How many biochemistries are available to build a cell. *ChemBioChem* 16: 2137-2139.

Aekesson, S., J. Morin, R. Muheim, et al. 2001. Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic North Pole. *Proc. Roy. Soc. Lond., Series B: Biological Sciences* 268: 1907-1913.

Agnor, C. B., and D. P. Hamilton. 2006. Neptune's capture of its moon Triton in a binary-planet gravitational encounter. *Nature* 441: 192-194.

Air-Liquide. 2003. www.airliquide.com/en/business/products/gases/gasdata.

Akasofu, S. 1999. Auroral spectra as a tool for detecting extraterrestrial life. *EOS Transactions AGU* 80: 397.

Alkalai, L., N. Arora, M. Shao, S. Turyshev, and S. L. Friedman et al. 2017. Mission to the solar gravity lens focus: natural highground for imaging Earth-like exoplanets. In *Planetary Science Vision 2050 Workshop 2017*: Lunar Planetary Institute (Contrib. #1989).

Altermann, W., and J.W. Schopf. 1995. Microfossils from the Neoarchean Campbell Group, Griqualand West Sequence of the Transvaal Supergroup, and their paleoenvironmental and evolutionary implications. *Precambrian Res.* 75: 65-90.

Altermann, W., and J. Kazmierczak. 2003. Archean microfossils: a reappraisal of early life on Earth. *Res. Microbiol.* 154: 611-617.

Altwegg, K., H. Balsiger, A. Bar-Nun, J. J. Berthelier, et al. 2016. Prebiotic chemicals-amino acid and phosphorus-in the coma of comet 67P/Churyumov-Gerasimenko. *Sci Adv* 2: e1600285.

Amend, J.P., and E.L. Shock. 1998. Energetics of amino acid synthesis in hydro-thermal ecosystems. *Science* 281: 1659-1662.

Amend, J.P., and E.L. Shock. 2001. Energetics of overall metabolic reactions of thermophilic and hyperthermophilic Archaea and bacteria. *FEMS Microbiol. Rev.* 25: 175-243.

Anders, E. 1989. Prebiotic organic matter from comets and asteroids. *Nature* 342: 255-257.

Anders, E., and N. Grevesse. 1989. Abundances of the elements; meteoritic and solar *Geochim. Cosmochim. Acta* 53: 197-214.

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7

Anderson, J. D., E. L. Lau, W. L. Sjogren, G. Schubert, and W. B. Moore. 1997. Gravitational evidence for an undifferentiated Callisto. *Nature* 387: 264-6.

Anderson, J.D., G. Schubert, R.A. Jacobson, et al. 1998. Europa's differentiated internal structure: inferences from four Galileo encounters. *Science* 281: 2019-2022.

Andes-Koback, M. and C.D. Keating. 2011. Complete budding and asymmetric division of primitive model cells to produce daughter vesicles with different interior and membrane compositoions. *J. Am. Chem. Soc.* 133: 9545-9555.

Andreyeschchehev, A., and J. Scalo. 2002. Duration of habitability of brown dwarf planets. *Bioastronomy 2002: Great Barrier Reef Conference Proceedings*.

Anglada-Escudé, G., P. Arriagada, M. Tuomi, M. Zechmeister, and J.S. Jenkins et al. 2014. Two planets around Kapteyn's star: a cold and a temperate super-Earth orbiting the nearest halo red dwarf. *MNRAS* 443 L89-L93.

Anglada-Escudé, G., P.J. Amado, J. Barnes, Z.M. Berdinas, et al. 2016. A terrestrial planet candidate in a temperate orbit around Proxima Centauri. *Nature* 536: 437-40.

António, M.R.S., and D. Schulze-Makuch. 2012. Toward a new understanding of multicellularity. *Hypoth. Life Sci.* 2:4-14.

Ardell, D.H. and G. Sella. 2001. On the evolution of redundancy in genetic codes. *J. Molec. Evol.* 53: 269-281.

Armstrong, J., L. Wells and G. Gonzalez. 2002. Rummaging through Earth's attic for remains of ancient life. *Icarus* 160: 183-196.

Arrhenius, S. 1903. Die Verbreitung des Lebens im Weltenraum. *Umschau* 7: 481-485.

Arrhenius, S. 1908. *Worlds in the Making*. Harper Collins, London.

Ashton, D., and D. Bernard. 1992. Thermophilic anaerobic sporeformers. pp. 309-316 in C. Vanderzant and D.F. Splittstoesser, eds. *Compendium of Methods for the Microbiological Examination of Foods*. American Public Health Association, Washington, DC.

Aspinall, G.M., Copsey M.C, A.P. Ledham, et al. 2002. Imido analogues of p-block oxoanions. *Coord. Chem. Rev.* 227: 217-232.

Attwater, J., A. Wochner, and P. Holliger. 2013. In-ice evolution of RNA polymerase ribozyme activity. *Nature Chem.* 5: 1011–1018.

Azam, F., B.B. Hemmingsen, and B.E. Volcani. 1974. Role of silicon in diatom metabolism. V. Silicic acid transport and metabolism in the heterotrophic diatom. *Nitzschia alba*. *Arch. Microbiol.* 97: 103-114.

Bachofen, R. 1986. Microorganisms in extreme environments: introduction. *Experientia* 42: 1179-1182.

Bada, J.L. 2001. State-of-the-art instruments for detecting extraterrestrial life. *Proc. Natl. Acad. Sci. USA* 98: 797-800.

Bada, J.L., and A. Lazcano. 2002a. Miller revealed new ways to study the origins of life. *Nature* 416: 475.

Bada, J.L., and A. Lazcano. 2002b. Some like it hot, but not the first biomolecules *Science* 269: 1982-1983.

Bada, J.L. 2004. How life began on Earth: a status report. *Earth Planetary Sci. Lett.* 226: 1-15.

Bain, J.D., E.S. Diala, C.G. Glabe, et al. 1989. Biosynthetic site-specific incorporation of a non-natural amino acid into a polypeptide. *J. Am. Chem. Soc.* 111: 8013-8014.

Bains, W. 2004. Many chemistries could be used to build living systems. *Astrobiology* 4: 137-167.

Bains, W. 2015. The WOW! Signal: an alternative hypothesis and search strategy for the WOW! origin. Paper read at Astrobiology Science Conference 2015, Chicago, USA, Abstract # 7157. [http://www.hou.usra.edu/meetings/abscicon2015/pdf/7157.pdf].

Bains, W. and S. Seager. 2012. A combinatorial approach to biochemical space: description and application to the redox distribution of metabolism. *Astrobiology* 12: 271-281.

Bains, W., S. Seager, and A. Zsom, A. 2014. Photosynthesis in hydrogen-dominated atmospheres. *Life* 4: 716-744

Bains, W., and D. Schulze-Makuch. 2017. Rare Earth or Cosmic Zoo: testing the frequency of complex life in the universe. In *Planetary Science Vision 2050 Workshop*. NASA Headquarters, Washington DC, USA.

Bajpai, S. and P.D. Gingerich. 1998. A new Eocene archaeocete (Mammalia, Cetacea) from India and the time of origin of whales. *Proc. Natl. Acad. Sci. USA* 95: 15464-15468.

Baker, V.R., J.M. Dohm, A.G. Fairén, P.A. Ferre, J.C. Ferris, H. Miyamoto, and D. Schulze-Makuch. 2005. Extraterrestrial hydrogeology. *Hydrogeol. J.* 13:51-68.

Baker, B.J., G.W. Tyson, R.I. Webb, et al. 2006. Lineages of acidophilic archaea revealed by community genomic analysis. *Science* 314: 1933-1935.

Balashova, V.V., and G.A. Zavarzin. 1980. Anaerobic reduction of ferric iron by hydrogen bacteria. *Microbiology* 48: 635-639.

Ball, R. and J. Brindley, J. 2015. The life story of hydrogen peroxide II: a periodic pH and thermochemical drive for the RNA world. *J. Roy. Soc. Interface* 12: 20150366.

Ballou, E.V., P.C. Wood, T. Wydeven, et al. 1978. Chemical interpretation of Viking lander 1 life detection experiment. *Nature* 271: 644-645.

Banathy, B.A. 1998. An information typology for understanding living systems *Biosystems* 46: 89-93.

Bandfield, J. L. 2007. High-resolution subsurface water-ice distributions on Mars. *Nature* 447: 64-67.

Barber, D.J., and E.R.D. Scott. 2002. Origin of supposedly biogenic magnetite in the martian meteorite Alan Hills 84001. *Proc. Natl. Acad. Sci. USA* 99: 6556-6561.

Barnosky, A.D., P.L. Koch, R.S. Feranec, et al. 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306: 70-75.

Baross, J.A., S.A. Benner, G.D Cody, S.D. Copley, N.R. Pace, and et al. 2007. *The Limits of Organic Life in Planetary Systems*. Washington, D.C.: National Academies Press.

Barrell, B.G., A.T. Bankier, and J. Drouin, J. 1979. A different genetic code in human mitochondria. *Nature* 282: 189-194.

Bartlett, D.H., and K.A. Bidle. 1999. Membrane-based adaptations of deep-sea piezophiles. pp. 503-512 in J. Seckbach, ed. *Enigmatic Microorganisms and Life in Extreme Environments*. Kluwer, Dordrecht.

Bartlett, D.H. 2002. Pressure effects on in vivo microbial processes *Biochim. Biophys. Acta* 1595: 367-381.

Bastian, H.C. 1914. Experimental data in evidence of the present-day occurrence of spontaneous generation *Nature* 92: 579-583.

Baumstark-Khan, C., and R. Facius. 2002. Life under conditions of ionizing radiation. pp. 261-284 in G. Horneck and C. Baumstark-Khan, eds. *Astrobiology: The Quest for the Conditions of Life*. Springer, Berlin.

Beatty, J.K., and A. Chaikin. 1990. *The new solar system.* Sky Publishing Corporation, Cambridge, Massachusetts.

Beatty, J.T., J. Overmann, M.T. Lince, et al. 2005. An obligately photosynthetic bacterial anaerobe from a deep-sea hydrothermal vent. *Proc. Natl. Acad. Sci. USA* 102: 9306-9310.

Beaulieu, J.P., D.P. Bennett, P. Fouque, et al. 2006. Discovery of a cool planet of 5.5 Earth masses through gravitational microlensing. *Nature* 439: 437-440.

Beck, C.H.M. and L.N. Irwin. 2016. *The Evolutionary Imperative: Why Change Happens, Where It Leads, and How We Might Survive*. Vancouver, B.C.: CCB Publishing. [https://www.amazon.com/Evolutionary-Imperative-Change-Happens.../B01NGZ8ZJF]

Becker, S., I. Thoma, A. Deutsch, T. Gehrke, P. Mayer, H. Zipse, and T. Carell. 2016. A high-yielding, strictly regioselective prebiotic purine nucleoside formation pathway. *Science* 352: 833-836.

Beeby, M., B.D. O'Connor, C. Ryttersgaard, et al. 2005. The genomics of disulfide bonding and protein stabilization in thermophiles. *PLOS Biology* 3: 1549-1558.

Bell, E.A., P. Boehnke, T.M. Harrison, and W.L. Mao. 2015. Potentially biogenic carbon preserved in a 4.1 billion-year-old zircon. *Proc. Natl. Acad. Sci. USA* 112: 14518-14521.

Ben-Jaffel, L. and G.E. Ballester. 2014. Transit of exomoon plasma tori: new diagnosis. *Astrophys. J.* 785: L30.

Benner, S.A., K.G. Devine, L.N. Matveeva, et al. 2000. The missing organic molecules on Mars. *Proc. Natl. Acad. Sci. USA* 97: 2425-2430.

Benner, S.A. 2002. Weird life: chances vs. necessity (alternative biochemistries). In “Weird Life” Planning Session for the Committee on the Origins and Evolution of Life, at Washington, DC, USA.

Benner, S.A., A. Ricardo and M.A. Carrigan. 2004. Is there a common chemical model for life in the universe? *Curr. Opin. Chem. Biol.* 8: 672-689.

Benner, S.A., W. Bains, and S. Seager. 2013. Models and standards of proof in cross-disciplinary science: the case of arsenic DNA. *Astrobiology* 13: 510-513.

Benner, S.A. and H.-J. Kim. 2015. The case for a Martian origin for Earth life. *SPIE Proc* 9606: doi: https://doi.org/10.1117/12.2192890.

Benner, S.A. 2017. Detecting Darwinism from molecules in the Enceladus plumes, Jupiter´s moons, and other planetary water lagoons. *Astrobiology* 17: 840-851.

Bennett, D.P., V. Batista, L.A. Bond, C.S. Bennett, and D. Suzuki et al. 2014. MOA-2011-BLG-262Lb: a sub-Earth-mass moon orbiting a gas giant primary or a high velocity planetary system in the galactic bulge. *Astrophys. J.* 785: 155-168.

Bennett, J., S. Shostak and B. Jakosky. 2003. *Life in the Universe*. Addison-Wesley, San Francisco.

Bennett, R.H., and M.H. Hulbert. 1986. *Clay microstructure* International Human Resource Development Corporation, Boston.

Bernal, J.D. 1967. *The origin of life*. World Publ., Cleveland.

Bertrand, T., and F. Forget. 2016. Observed glacier and volatile distribution on Pluto from atmosphere-topography processes. *Nature* 540: 86-89.

Biemann, K. 1979. The implications and limitations of the findings of the Viking organic analysis experiment. *J. Molec. Evol.* 14: 65-70.

Birchall, J.D. 1995. The essentiality of silicon in biology. *Chem. Soc. Rev.* 24: 351-357.

Blake, R.E., J.C. Alt and A.M. Martini. 2001. Oxygen isotope ratios of PO_4: an inorganic indicator of enzymatic activity and P metabolisms and a new biomarker in the search for life. *Proc. Natl. Acad. Sci. USA* 98: 2148-2153.

Blakemore, R.P. 1982. Magnetotactic bacteria. *Annu Rev Microbiol* 36: 217-238.

Bockelee-Morvan, D. and N. Biver. 2017. The composition of cometary ices. *Philos. Trans. A Math Phys. Eng. Sci.* 375.

Böttger, U., J.-P. de Vera, J. Fritz, L. Weber, H.W. Huebers, et al. 2012. Optimizing the detection of carotene in cyanobacteria in a Martian regolith analogue with a Raman spectrometer for the ExoMars Mission. *Planet. Space Sci.* 60: 356-362.

Bond, D.P.G. and S.E. Grasby. 2017. On the causes of mass extinctions. *Paleogeogr. Paleoclimatol. Paleoecol.* 478: 3-29.

Borucki, J.G., B. Khare and D.P. Cruikshank. 2002. A new energy source for organic synthesis in Europa’s surface ice. *JGR-Planets* 107: Art. no 5114.

Boss, A.P. 2006. Rapid formation of super-Earths around M dwarf stars. *Astrophys. J.* 644: L79-L82.

Boston, P.J. 2000. Bubbles in the rocks: Natural and artificial caves and cavities as life support structures. pp. 9-17 in R.M. Wheeler and C. Martin-Brennan, eds. *Mars Greenhouses: Concepts and Challenges*. NASA Tech. Mem 2000-208577, Kennedy Space Center, Florida.

Boston, P.J. 2003. Extraterrestrial Caves. pp. 355-358. *Encyclopedia of Cave and Karst Science*. Fitzroy-Dearborn Publishers, Ltd., London.

Boston, P.J., and C.R. Stoker. 1983. Microbial metabolism of organic molecules produced by chemical synthesis in a reducing atmosphere: implications for the origin of life. in R. Pepin and O’Connell, eds. *Planetary Volatiles, Lunar and Planetary Institute*. Lunar and Planetary Institute, Houston, pp 31-39.

Boston, P.J., M.V. Ivanov and C.P. McKay. 1992. On the possibility of chemosynthetic ecosystems in subsurface habitats on Mars. *Icarus* 95: 300-308.

Boston, P.J., M.N. Spilde, D.E. Northup, L.A. Melim, and D.S. Soroka, et al. 2004. Cave biosignature suites: microbes, minerals, and Mars. *Astrobiology* 4: 25-55.

Bostrom, N. 2003. Are you living in a computer simulation? *Philosoph. Quart.* 53: 243-255.

Bottke, W. F., R. J. Walker, J. M. Day, D. Nesvorny, and L. Elkins-Tanton. 2010. Stochastic late accretion to Earth, the Moon, and Mars. *Science* 330: 1527-30.

Boulange, B., J.-P. Ambrosi and D. Nahon. 1997. Laterites and bauxites. in P. H and N. Clauer, eds. *Soil and Sediments: Mineralogy and Geochemistry*. Springer-Verlag Berlin.

Bounama, C, W Von Bloh, and S Franck. 2007. How rare is complex life in the Milky Way? *Astrobiology* 7: 745-755.

Bowden, S., R. Wilson, J.M. Cooper, and J. Parnell. 2008. Surface enhanced Raman spectroscopy as a tool for characterizing pigments in the extracts of living organisms and sediments. *Astrobiology* 8: 302.

Bowen, T.C., R.D. Noble, and J.L. Falconer. 2004. Fundamentals and applications of pervaporation through zeolite membranes. *J. Memb. Sci.* 245: 1-33.

Boynton, W.V., W.C. Feldman, S.W. Squyres, et al. 2002. Distribution of hydrogen in the near surface of Mars: Evidence for subsurface ice deposits. *Science* 297: 81-85.

Bracewell, R.N. (1960) Communications from superior galactic communities. *Nature* 186: 670-671.

Bradley, J.P., R.P. Harvey and H.Y. McSween. 1996. Magnetite whiskers and platelets in the ALH84001 martian meteorite: evidence of vapor phase growth. *Geochim. Cosmochim. Acta* 60: 5149-5155.

Bradley, J.P., R.P. Harvey and H.Y. McSween. 1997. No 'nannofossils' in martian meteorite. *Nature* 390: 454-456.

Brady, S.G. 2003. Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proc. Natl. Acad. Sci. USA* 100: 6575-6579.

Bragger, J.M., R.V. Dunn and R.M. Daniel. 2000. Enzyme activity down to -100^{o}C. *Biochim. Biophys. Acta* 1480: 278-282.

Braje, T.J. and J.M. Erlandson. 2013. Human acceleration of animal and plant extinctions: A Late Pleistocene, Holocene, and Anthropocene continuum. *Anthropocene* 4: 14-23.

Branscomb, E. and M.J. Russell. 2012, Turnstiles and bifurcators: the disequilibrium converting engines that put metabolism on the road. *Biochim. Biophys. Acta* 1827: 62-78.

Brandstetter, T. 2012. Life beyond the limits of knowledge: crystalline life in the popular science of Desiderius Papp (1895-1993). *Astrobiology* 12: 951-95.

Brasier, M.D., O.R. Green, A.P. Jepherat, et al. 2002. Questioning the evidence for Earth's oldest fossils. *Nature* 416: 76-81.

Brasier, M.D., R. Matthewman, S. McMahon, and D. Wacey. 2011. Pumice as a remarkable substrate for the origin of life. *Astrobiology* 11: 725-735.

Bräucker, R., A. Cogoli and R. Hemmersbach. 2002. Graviperception and graviresponse at the cellular level. pp. 287-296 in G. Horneck and C. Baumstark-Kahn, eds. *Astrobiology: The Quest for the Conditions of Life*. Springer Publ, Berlin

Brillouin, L. 1956. *Science and Information Theory*. Academic Press, New York.

Brock, T.D., and J. Gustafson. 1976. Ferric iron reduction by sulfur and iron-oxidizing bacteria. *Appl. Environ. Microbiol.* 32: 567-571.

Brook, B.W., and D.M. Bowman. 2002. Explaining the Pleistocene megafaunal extinctions: models, chronologies, and assumptions. *Proc. Natl. Acad. Sci. USA* 99: 14624-14627.

Brooks, D.R., and D.A. McLennan. 1991. *Phylogeny, Ecology, and Behavior* University of Chicago Press, Chicago.

Brooks, H. and D. Schulze-Makuch. 2010. The solar wind power satellite as an alternative to a traditional Dyson Sphere and its implications for remote detection. *Int. J. Astrobiology* 9: 89-99.

Brown, R.D. 1984. Prebiotic matter in interstellar molecules. pp. 123-137 in Papagiannis MD, ed. *The Search for Extraterrestrial Life: Recent Development.* D. Reidel Publishing Company, Dordrecht.

Brown, M. E., and W. M. Calvin. 2000. Evidence for crystalline water and ammonia ices on Pluto's satellite Charon. *Science* 287: 107-9.

Buczkowski, D. L., B. E. Schmidt, D. A. Williams, S. C. Mest, et al. 2016. The geomorphology of Ceres. *Science* 353: 1004., doi: https://doi.org/10.1126/science.aaf4332

Budavari, S., M.J. O'Neill, A. Smith, et al., eds. 1996. *The Merck Index*. Merck and Co., Whitehouse Station, NJ.

Budisa, N. 2005. *Engineering the Genetic Code: Expanding the Amino Acid Repertoire for the Design of Novel Proteins*. New York, NY USA: John Wiley.

Budisa, N. and D. Schulze-Makuch. 2014. Supercritical carbon dioxide and its potential as a life-sustaining solvent in a planetary environment. *Life (Basel)* 4: 331-340.

Budisa, N., V. Kubyshkin, and D. Schulze-Makuch. 2014. Fluorine-rich planetary environments as possible habitats for life. *Life (Basel)* 4: 374-85.

Burrows, A.S. 2014. Spectra as windows into exoplanet atmospheres. *Proc. Natl. Acad. Sci. USA* 111: 12601-12609.

Buratti, B. 1999. Outer planet icy satellites. pp. 435-455 in P.R. Weissman, L.-A. McFadden, and T.V. Johnson, eds. *Encyclopedia of the Solar System*. Academic Press, New York.

Burnham, A. D. and A. J. Berry. 2017. Formation of Hadean granites by melting of igneous crust. *Nature Geosci.* 10: 457–461.

Burton, F.G., R. Lohrmann and L.E. Orgel. 1974. On the possible role of crystals in the origins of life. VII. The adsorption and polymerization of phosphoramidates by montmorillonite clay. *J Mol Evol* 3: 141-150.

Byrne, R. 1995. *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford Univ. Press, New York.

Byrne, J. M., N. Klueglein, C. Pearce, K. M. Rosso, E. Appel, and A. Kappler. 2015. Redox cycling of Fe(II) and Fe(III) in magnetite by Fe-metabolizing bacteria. *Science* 347: 1473-1476.

Cabral, J.M.S. 2001. Biotransformations. pp. 471-502 in C. Ratledge and B. Kristiansen, eds. *Basic Biotechnology*. Cambridge University Press, Cambridge, UK.

Cabrol, N. 2016. Alien mindscapes – a perspective on the search for extraterrestrial intelligence. *Astrobiology* 16: 661-676.

Cairns-Smith, A.G. 1982. *Genetic Takeover*. Cambridge University Press, London.

Cairns-Smith, A.G. 1985. *Seven clues to the origin of life.* Cambridge University Press, Cambridge.

Cairns-Smith, A.G., and H. Hartman. 1986. *Clay minerals and the origin of life* Cambridge University Press, UK.

Calvin, M. 1969. *Chemical Evolution: Molecular Evolution Towards the Origin of Living Systems on the Earth and Elsewhere*. Oxford University Press, New York.

Campbell, N.A. 1996. *Biology* Benjamin/Cummings, Menlo Park, CA.

Campen, R.K., T. Sowers and R.B. Alley. 2003. Evidence of microbial consortia metabolizing within a low-latitude mountain glacier. *Geology* 31: 231-234.

Cano, R.J., and M. Borucki. 1995. Revival and identification of bacterial spores in 25 to 40 million year old Dominican amber. *Science* 268: 1060-1064.

Cardona, T. 2016. Origin of bacteriochlorophyll a and the early diversification of photosynthesis. *PLoS ONE Biol* 11: e0151250.

Carlisle, E.M. 1981. Silicon in bone formation. pp. 383-408. in Simpson and Volcani, eds. *Silicon and Siliceous Structures in Biological Systems* Springer Verlag, New York.

Carlson, R. W., M. S. Anderson, R. E. Johnson, W. D. Smythe, et al. 1999. Hydrogen peroxide on the surface of Europa. *Science* 283: 2062-2064.

Carr, M.H. 1986. Mars: A water rich planet. *Icarus* 56: 187-216.

Carr, M.H. 1996. *Water on Mars*. Oxford University Press, Oxford.

Carr, M.H., M.J. Belton, C.R. Chapman, et al. 1998. Evidence for a subsurface ocean on Europa. *Nature* 391: 363-365.

Carrea, G., G. Ottolina and S. Riva. 1995. Role of solvents in the control of enzyme selectivity in organic media. *Trends Biotechnol.* 13: 63-70.

Carl Sagan, W. Reid Thompson, Bishun N. Khare. 1992. Titan: a laboratory for prebiological organic chemistry. *Accounts of Chemical Research* 25(7): 286–292.

Carter, C.W. 2015. What RNA world? Why a peptide/RNA partnership merits renewed experimental attention. *Life (Basel)* 5*:* 294-320.

Cassen, P.M., and D.S. Woolum. 1999. The origin of the solar system. pp. 35-63 in P.R. Weissman, McFadden L.-A. and T.V. Johnson, eds. *Encyclopedia of the Solar System*. Academic Press, New York.

Cavicchioli, R. 2002. Extremophiles and the search for extraterrestrial life. *Astrobiology* 2: 281-292.

Cech, T.R. 1985. Self-splicing RNA: implications for evolution. *Int. Rev. Cytol.* 93: 3-22.

Chaisson, E.J. 2013. Using complexity science to search for unity in the natural sciences. In *Complexity and the Arrow of Time*, edited by C. H. Lineweaver, P. C. W. Davies and M. Ruse. Cambridge University Press, Cambridge.

Chakrabarty, A.N., S. Das and K. Mukherjee. 1988. Silicon (Si) utilisation by chemoautotrophic nocardioform bacteria isolated from human and animal tissues infected with leprosy bacillus *Indian J. Exp. Biol.* 26: 839-844.

Chan, S., J. Orenberg and N. Lahav. 1987. Soluble minerals in chemical evolution. II. Characterization of the adsorption of 5’-AMP and 5’-CMP on a variety of soluble mineral salts. *Orig. Life Evol. Biosph.* 17: 121-134.

Chang, S. 1993. Prebiotic synthesis in planetary environments pp. 259-300 in J.M. Greenberg, C.X. Mendoza-Gomez and V. Pirronello, eds. *The Chemistry of Life’s Origins*. Kluwer Academic Publishers, Dordrecht.

Chaplin, M.F. 2003. http://www.sbu.ac.uk/water/phase.html, web site accessed 22 May 2003. School of Applied Science, London South Bank University.

Chaput, J.C., and J.W. Szostak. 2003. TNA synthesis by DNA polymerases. *J. Am. Chem. Soc.* 125: 9274-9275.

Chargaff, E., R. Lipshitz, C. Green, et al. 1951. The composition of the deoxyribonucleic acid of salmon sperm. *J Biol Chem* 192: 223-230.

Charlier, D., and L. Droogmans. 2005. Microbial life at high temperatures, the challenges, the strategies. *Cell. Mol. Life Sci.* 62: 2974-2984.

D. E. Canfield, S. W. Poulton, G. M. Narbonne, (2007) Late-Neoproterozoic Deep-Ocean Oxygenation and the Rise of Animal Life. Science 315 (5808):92-95

Chen, C.A., S.M. Sieburth and A.G.e. al. 2001. Drug design with a new transition state analog of the hydrated carbonyl: silicon-based inhibitors of the HIV protease. *Chemistry and Biology* 8: 1161-1166.

Chen, S., N. Gollop and I. Glazer. 2005. Cross-stress tolerance and expression of stress-related proteins in osmotically desiccated entomopathogenic *Steinernema feltiae* IS-6. *Parasitology* 131: 1-9.

Chen, B., C. Stoker, N. Cabrol, and C.P. McKay. 2008. Detecting life on Mars: Raman spectra identifications of mineral and organic constituents. *Astrobiology* 8: 303.

Chevaldonne, P., D. Desbruyeres and J. Childress. 1992. Some like it hot . . . and some even hotter. *Nature* 359: 593-594.

Chièze, J.P. 1994. The interstellar medium. in J. Audouze and G. Israël, eds. *The Cambridge Atlas of Astronomy*. Cambridge University Press., UK.

Christen, H.R. 1984. *Chemie* Verlag Diesterweg/Salle – Sauerlaender, Frankfurt, Germany.

Christensen, P.R., J.L. Bandfield and J.F. Bell et al. 2003. Morphology and composition of the surface of Mars: Mars Odyssey THEMIS results. *Science* 300: 2056-2061.

Chyba, C.F. 1997. Life on other moons. *Nature* 385: 201.

Chyba, C.F. 2000. Energy for microbial life on Europa. *Nature* 403: 381-382.

Chyba, C.F., and G.D. McDonald. 1995. The origin of life in the solar system: current Issues. *Ann. Rev. Earth Planet. Sci.* 23: 215-249.

Chyba, C. F. and C. B. Phillips. 2001. Possible ecosystems and the search for life on Europa. *Proc. Natl. Acad. Sci. USA* 98: 801-804.

Chyba, C., and C. Sagan. 1991. Electrical energy sources for organic synthesis on the early Earth. *Orig. Life Evol. Biosph.* 21: 3-17.

Chyba, C., and C. Sagan. 1992. Endogenous production, exogenous delivery and impact-shock synthesis of organic molecules: an inventory for the origins of life. *Nature* 355: 125-132.

Chyba, C. F., P. J. Thomas, L. Brookshaw, and C. Sagan. 1990. Cometary delivery of organic molecules to the early Earth. *Science* 249: 366-373.

Ciftçioglu, N., and E.O. Kajander. 1998. Interaction of nanobacteria with cultured mammalian cells *Pathophysiology* 4: 259-270.

Ciftçioglu, N., M. Björklund, K. Kuorikoski, et al. 1999. Nanobacteria: an infectious cause for kidney stone formation. *Kidney Intl.* 56: 1893-1898.

Clancy, R.T., B.J. Sandor, and G.H. Moriarty-Schieven. 2004. A measurement of the 362 GHz absorption line of Mars atmospheric H2O2. *Icarus* 168: 116-121.

Clark, A. 2003. *Natural-Born Cyborgs: Minds, Technologies, and the Future of Human Intelligence*. Oxford Univ Press, New York.

Clark, B. 2001. Planetary interchange of bioactive material: probability factors and implications *Orig. Life Evol. Biosph.* 31: 185-197.

Clark, R.N. 2009. Detection of adsorbed water and hydroxyl on the Moon. *Science* 326: 562-564.

Clark, M.V., J. Heinz, J. Schirmack, S.P. Kounaves, and D. Schulze-Makuch, D. 2017. Unambiguous in-situ life detection using a microbial growth sensing array. Astrobiological Science Conference (AbSciCon), Mesa, Arizona, USA, 24-28 April 2017.

Clarke, A. 2014. The thermal limits to life on Earth. *Int. J. Astrobiol.* 13: 141-154.

Clarke, A., G.J. Morris, F. Fonseca, B.J. Murray, E. Acton, and H.C. Price. 2013. A low temperature limit for life on Earth. *PLoS ONE Biol* 8: e66207.

Cleaves, C., G. Cody, J.P. Dworkin, M. Fogel, and R.M. Hazen. 2008. Recent insights into the prebiotic chemistry of HCN. *Astrobiology* 8: 3.

Clegg, J. 2001. Cryptobiosis - a peculiar state of biological organization. *Compar. Biochem. Physiol.* 128: 613-624.

Cleland, C., and S. Copley. 2005. The possibility of alternative microbial life on Earth. *Int. J. Astrobiol.* 4: 165-173.

Cloney, R. 2016. Synthetic biology: Automating genetic circuit design. *Nat. Rev. Genet.* 17: 314-5.

Cocconi, G. and P. Morrison. 1959. Searching for interstellar communications. *Nature* 184: 844-846.

Cockell, C. S., and P. A. Bland. 2005. The evolutionary and ecological benefits of asteroid and comet impacts. *Trends Ecol. Evol.* 20: 175-179.

Cockell, C.S., D. Catling, W.L. Davis, et al. 2000. The ultraviolet environment of Mars: biological implications past, present and future. *Icarus* 146: 343-359.

Cockell, C.S., and F. Westall. 2004. A postulate to assess habitability. *Int. J. Astrobiol.* 3: 157-163.

Cockell, C.S., A.C. Schuerger, D. Billi, et al. 2005. Effects of a simulated martian UV flux on the cyanobacterium, *Chroococcidiopsis* sp 029. *Astrobiology* 5: 127-140.

Cockell, C.S., T. Bush, C. Bryce, S. Direito, et al. 2016. Habitability: A Review. *Astrobiology* 16: 89-117.

Combe, J. P., T. B. McCord, F. Tosi, E. Ammannito, et al. 2016. Detection of local H_2O exposed at the surface of Ceres. *Science* 353 (doi:https://doi.org/10.1126/science.aaf3010)

Connerney, J.E.P., M.H. Acuna and P.J.W.e. al. 1999. Magnetic lineations in the ancient crust of Mars. *Science* 284: 794-798.

Consolmagno, G.J., and J. Lewis. 1976. Structural and thermal models of icy Galilean satellites. pp. 1035-1051 in T. Gehrels, ed. *Jupiter*. Univ. of Arizona Press, Tucson.

Costanzo, G., S. Pino, F. Ciciriello, and E. Di Mauro. 2009. Generation of long RNA chains in water. *J. Biol. Chem.* 284: 33206-16.

Cousins, C. R. and I. A. Crawford. 2011. Volcano-ice interaction as a microbial habitat on Earth and Mars. *Astrobiology* 11: 695-710.

Coustenis, A., and R.D. Lorenz. 1999. Titan. pp. 377-404 in P.R. Weissman, L.-A. McFadden and T.V. Johnson, eds. *Encyclopedia of the Solar System*. Academic Press, New York.

Couzin, J., 2002. Weight of the world on microbes' shoulders. *Science* 295: 1444-1445.

Cowan, N.B. 2014. The exoplanet opportunity: top-down planetary science. *EOS, Trans. Am. Geophys. Union* 95: 209-210.

Cowan, N.B. and T.E. Strait, T.E. 2013. Determining reflectance spectra of surfaces and clouds on exoplanets. *Astrophys. J. Lett.* 765: L17.

Cowen, R. 1995. *History of life.* Blackwell, Boston.

Cox, M., and J. Battista. 2005. *Deinococcus radiodurans* - the consummate survivor. *Nature Rev. Microbiol.* 3: 882-892.

CRC. 2001. *Handbook of chemistry and physics.* CRC Press, Boca Raton, FL.

Creamer, J.S., M.F. Mora, and P.A. Willis. 2017. Enhanced resolution of chiral amino acids with capillary electrophoresis for biosignature detection in extraterrestrial samples. *Anal. Chem.* 89: 1329–1337.

Crick, F.H.C. 1968. The origin of the genetic code. *J. Molec. Biol.* 38: 367-379.

Crick, F.H.C., and L.E. Orgel. 1973. Directed panspermia. *Icarus* 19: 341-345.

Cronin, J.R., S. Pizzarello and D.P. Cruikshank. 1988. Organic matter in carbonaceous chondrites, planetary satellites, asteroids and comets. pp. 819-857 in K. JF and M. MS, eds. *Meteorites and the Early Solar System* Univ. of Arizona Press, Tucson.

J H Crowe, F A Hoekstra, L M Crowe, (1992) Anhydrobiosis. Annual Review of Physiology 54 (1):579–599

Cuntz, M., L. Gurdemir, E.F. Guinan, and R.L. Kurucz. 2006. Astrobiological effects of stellar radiation in circumstellar environments. p. #AP1.004. *Texas Section of the APS Joint Fall Meeting*. American Physical Society.

Curtis, H., and N.S. Barnes. 1986. *Biology*. Worth, New York.

Dahn, J.R., B.M. Way, E. Fuller, et al. 1993. Structure of siloxene and layered polysilane (Si6H6). *Phys. Rev. B* 48: 17872-17877.

Daniel, R.M., J.L. Finney and M. Stoneham. 2004a. Introduction to discussion meeting issue on "The molecular basis of life: Is life possible without water?" *Phil. Trans. Roy. Soc. Lond. B* 359: 1143.

Daniel, R.M., J.F. Holden, R. van Eckert, et al. 2004b. The stability of biomolecules and the implications for life at high temperatures. pp. 25-39 in W. Wilcock, E. DeLong, D. Kelley, J. Baross and S. Cary, eds. *The Subseafloor Biosphere at Mid-Ocean Ridges*. American Geophysical Union, Washigton DC.

Danovaro, R., A. Dell'Anno, A. Pusceddu, C. Gambi, I. Heiner, and R. M. Kristensen. 2010. The first metazoa living in permanently anoxic conditions. *BMC Biol* 8: 30 (doi:https://doi.org/10.1186/1741-7007-8-30)

Darley, W.M., and B.E. Volcani. 1969. Role of silicon in diatom metabolism. A silicon requirement for deoxyribonucleic acid synthesis in the diatom Cylindrotheca fusiformis *Exp. Cell Res.* 58: 334-342.

Darling, D. and D Schulze-Makuch. 2016. In *The Extraterrestrial Encyclopedia*. Sarasota, FL, USA: First Edition Design Publishing.

Dartnell, L. R. 2011. Ionizing radiation and life. *Astrobiology* 11: 551-82.

Dartnell, L.R., T.A. Nordheim, M.R. Patel, J.P. Mason, and A.J. Coates, et al. 2015. Constraints on a potential aerial biosphere on Venus: I. cosmic rays. *Icarus* 257: 396-405.

Das, S., S. Mandal, A.N. Chakrabarty, et al. 1992. Metabolism of silicon as a probable pathogenicity factor for Mycobacterium and Nocardia *Indian J. Med. Res.* 95: 59-65.

Davila, A.F. and C.P. McKay. 2014. Chance and necessity in biochemistry: Implications for the search for extraterrestrial biomarkers in Earth-like environments. *Astrobiology* 14: 534-540.

Davila, A.F., A.G. Fairén, A.P. Rodríguez, D. Schulze-Makuch, J. Rask, et al. 2015. The Hebrus Valles Exploration Zone: Access to the Martian surface and subsurface. First Landing Site/Exploration Zone Workshop for Human Missions to the Surface of Mars. Houston, Texas, USA, 26-30 October 2015.

Davila, A.F., and D. Schulze-Makuch. 2016. The Last Possible Outposts for Life on Mars. *Astrobiology* 16: 159-68.

Davies, P. 2005. A quantum recipe for life. *Nature* 437: 819.

Davies, P., and C. Lineweaver. 2005. Finding a second sample of life on Earth. *Astrobiology* 5: 154-163.

Davies, P.C.W. 1996. The transfer of viable microorganisms between planets. *Ciba Foundation Symposium 202 (Evolution of hydrothermal ecosystems on Earth (and Mars?)*. Wiley, Chichester.

Davies, P.C.W. 2012. Footprints of alien technology. *Acta Astronautica* 73: 250-257.

Davies, P., and D. Schulze-Makuch. 2008. A one-way human mission to Mars. *Astrobiology* 8: 310.

de Duve, C. 1995. *Cosmic Dust: Life as a Cosmic Imperative*. Basic Books, New York.

De Maayer, P., D. Anderson, C. Cary, and D.A. Cowan. 2014. Some like it cold: understanding the survival strategies of psychrophiles. *EMBO Rep.* 15: 508-517.

Deamer, D. 2017. The Role of Lipid Membranes in Life's Origin. *Life (Basel)* 7: doi:https://doi.org/10.3390/life7010005.

Deamer, D. and B. Damer. 2017. Can life begin on Enceladus? A perspective from hydrothermal chemistry. *Astrobiology* 17: 834-839.

Deamer, D., J.P. Dworkin, S.A. Sandford, et al. 2002. The first cell membranes. *Astrobiology* 2: 371-381.

Deamer, D. W. and C. D. Georgiou. 2015. Hydrothermal conditions and the origin of cellular life. *Astrobiology* 15: 1091-1095.

Deamer, D.W., and R. Pashley. 1989. Amphiphilic components of the Murchison carbonaceous chondrite: surface properties and membrane formation *Orig. Life Evol. Biosph.* 19: 21-38.

DeLeeuw, B.J., R.S. Grev and H.F. Schaefer. 1992. A comparison and contrast of selected and unsaturated hydrides of group 14 elements. *J. Chem. Ed.,* 69: 441-444.

Des Marais, D.J., and M.R. Walter. 1999. Astrobiology: Exploring the origins, evolution, and distribution of life in the Universe. *Annu. Rev. Ecol. Syst.* 30: 397-420.

Des Marais, D. J., M. O. Harwit, K. W. Jucks, J. F. Kasting, et al. 2002. Remote sensing of planetary properties and biosignatures on extrasolar terrestrial planets. *Astrobiology* 2: 153-81.

Des Marais, D.J., L. Allamandola, S. Benner, A. Boss, J.R. Cronin, et al. 2003. The NASA Astrobiology Roadmap. *Astrobiology* 3: 219-235.

Des Marais, D.J., J.A. Nuth, L.J. Allamandola, A.P. Boss, J.D. Farmer, et al. 2008. The NASA Astrobiology Roadmap. *Astrobiology* 8: 715-730.

De Sanctis, M.C., E. Ammannito, A. Raponi, S. Marchi, T.B. McCord, et al. 2015. Ammoniated phyllosilicates with a likely outer Solar System origin on Ceres. *Nature* 528: 241-244.

De Sanctis, M. C., A. Raponi, E. Ammannito, M. Ciarniello, et al. 2016. Bright carbonate deposits as evidence of aqueous alteration on (1) Ceres. *Nature* 536: 54-57.

De Sanctis, M.C., E. Ammannito, H.Y. McSween, A. Raponi, S. Marchi, et al. 2017. Localized aliphatic organic material on the surface of Ceres. *Science* 355: 719-722.

Dessey, R. 1998. Posted in Scientific American Ask the Expert.

Di Achille, G. and B.M. Hynek. 2010. Ancient ocean on Mars supported by global distribution of deltas and valleys. *Nature Geosci.* 3: 459–463.

Di Giulio, M. 2005. The ocean abysses witnessed the origin of the genetic code. *Gene* 346: 7-12.

Diaspro, A., M. Bertolotto, L. Vergani, et al. 1991. Polarized light scattering of nucleosomes and polynucleosomes--in situ and in vitro studies, IEEE Trans. *IEEE Trans. Biomed. Eng.* 670 - 678: 670-678.

Diaz, B., and D. Schulze-Makuch. 2006. Microbial survival rates of *E. coli* and *D. radiodurans* under single and combined stresses of temperature, pressure, and UV radiation, and its relevance to Martian environmental conditions. *Astrobiology* 6: 332-347.

Dieter, W.R., R.A. Lodder and J.E. Lumpp. 2005. Scanning for Extinct Astrobi-ological Residues and Current Habitats (SEARCH). pp. 234-245. *Aerospace IEEE Conference*.

Dietrich, W.E., and T. Perron. 2006. The search for a topographic signature of life. *Nature* 439: 411-418.

Dimmick, R.L., H. Wolochow and M.A. Chatigny. 1979. Evidence for more than one division of bacteria within airborne particles. *Applied Environmental Microbiology* 38: 642-643.

Diniz-Filho, J.A. 2004. Macroecological analyses support an overkill scenario for late Pleistocene extinctions. *Braz J Biol* 64: 407-414.

Dinwiddie, R., D. Hughes, and C. Stott. 2008. The solar system. In *Universe*, edited by P. Frances. New York: DK Publishing.

Dobzhansky, T. 1951. *Genetics and the Origin of Species.* Columbia University Press, New York.

Dodd, M.S., D. Papineau, T. Grenne, J.F. Slack, M. Rittner, *et al.* 2017. Evidence for early life in Earth's oldest hydrothermal vent precipitates. *Nature* 543: 60-64.

Doelle, H.W. 1969. *Bacterial metabolism.* Academic Press, New York.

Dohm, J.M., R.C. Anderson, V.R. Baker, et al. 2000. System of gigantic valleys northwest of Tharsis, Mars; latent catastrophic flooding, northwest watershed, and implications for northern plain ocean. *Geophys. Res. Lett.* 27: 3559-3562.

Dohm, J.M., J.C. Ferris, V.R. Baker, et al. 2001. Ancient drainage basin of the Tharsis region, Mars: Potential source for outflow channel systems and putative oceans or paleolakes. *J. Geophys. Res.* 106: 32943-32958.

Domagal-Goldman, S. D., V. S. Meadows, M. W. Claire, and J. F. Kasting. 2011. Using biogenic sulfur gases as remotely detectable biosignatures on anoxic planets. *Astrobiology* 11: 419-441.

Dorn, E. D., K. H. Nealson, and C. Adami. 2011. Monomer abundance distribution patterns as a universal biosignature: examples from terrestrial and digital life. *J. Mol. Evol.* 72: 283-295.

Drinkwater, L., and J. Crowe. 1991. *Bid. Bull.* 180: 432-439.

Duckworth, A., W. Grant, B. Jones, et al. 1996. Phylogenetic diversity of soda lake alkaliphiles. *FEMS Microbiol. Ecol.* 19: 181-191.

Dunford, W. et al. 2017. *Ceres - In Depth*. NASA 2015b [cited 27 June 2018]. Available from https://solarsystem.nasa.gov/planets/ceres/indepth.

Dyson, F.J. 1960. Search for artificial stellar sources of infrared radiation. *Science* 131: 1667-1668.

Dyson, F. J. 1982. A model for the origin of life. *J. Molec. Evol.* 18: 344-350.

Dyson, F. J. 1999. *Origins of Life*. Cambridge University Press, Cambridge, U.K.

Edwards, H.G.M., and E.M. Newton. 1999. Application of Raman spectroscopy to exobiological prospecting. pp. 83-88 in J.A. Hisox, ed. *Search for Life on Mars*. British Interplanetary Society, London.

Edwards, K., P. Bond, T. Gihring, et al. 2000. An archael iron-oxidizing extreme acidophile important in acid mine drainage. *Science* 287: 1796-1799.

Egan, G. 2002. *Schild's Ladder*. Eos, New York.

Ehrenfreund, P., and K.M. Menten. 2002. From molecular clouds to the origin of life. pp. 1-23 in G. Horneck and C. Baumstark-Khan, eds. *Astrobiology – the Quest for the Conditions of Life* Springer Publ., Berlin.

Ehman, J.R. 2010. *The Big Ear Wow! Signal (30th Anniversary Report).* Big Ear Radio Observatory and North American AstroPhysical Observatory. 28 May 2010 [retrieved 20 June 2018] http://www.bigear.org/Wow30th/wow30th.htm.

Eigenbrode, J. L., R. E. Summons, A. Steele, C. Freissinet, et al. 2018. Organic matter preserved in 3-billion-year-old mudstones at Gale crater, Mars. *Science* 360: 1096-1101.

Eiler, J.M., J.W. Valley, C.M. Graham, et al. 2002. Two populations of carbonate in ALH84001: geochemical evidence for discrimination and genesis. *Geochim. Cosmochim. Acta* 66: 1285-1303.

Eisch, J.J., P.R. Munson, and J.N. Gitua. 2004. The potential of photochemical transition metal reactions in prebiotic organic synthesis. I. Observed conversion of methanol into ethylene glycol as possible prototype for sugar alcohol formation *Orig. Life Evol. Biosph.* 34: 441-454.

Eiseley, L. 1946. *The Immense Journey*. Random House, New York.

Eldredge, N., and S.J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. pp. 82-115 in T.J.M. Schopf, ed. *Models in Paleobiology.* Freeman, Cooper, and Co., San Francisco.

Eldredge, N. 1985. *Time Frames: The Rethinking of Darwinian Evolution and the Theory of Punctuated Equilibrium.* Simon and Schuster, New York.

Elena, S.F., and R.E. Lenski. 2003. Evolution experiments with microorganisms: The dynamics and genetic bases of adaptation. *Nature Rev. Genet.* 4: 457-469.

Elsila, J.E, D.P. Glavin, and J.P. Dworking. 2009. Cometary glycine detected in samples returned by Stardust. *Meteoritics Planet. Sci.* 44: 1323-1330.

Epstein, E. 1994. The anomaly of silicon in plant biology. *Proc. Natl. Acad. Sci. USA* 91: 11-17.

Erb, T.J., P. Kiefer, B. Hattendorf, D. Gunther, J.A. Vorholt. 2012. FGAJ-1 is an arsenate-resistant, phosphate-dependent organism. *Science* 337: 467-470

Erdman, S, B. Tschitschko, L. Zhong, M.J. Raftery. 2017. A plasmid from an Antarctic haloarchaeon uses specialized membrane vesicles to disseminate and infect plasmid-free cells *Nature Microbiol. (doi:* https://doi.org/10.1038/s41564-017-0009-2*).*

Eschenbach, D.A., Davick, P.R., Williams, B.L., Klebanoff, S.J., Young-Smith, K., Critchlow, C. M., and Holmes, K.K. 1989. Prevalence of hydrogen peroxide-producing *Lactobacillus* species in normal women and women with bacterial vaginosis. *J. Clin. Microbiol.* 27: 251-256.

Fairén, A.G. 2010. A cold and wet Mars. *Icarus* 208:165-175.

Fairén, A.G., J.M. Dohm, V.R. Baker, M.A. de Pablo, et al. 2003. Episodic flood inundations of the northern plains of Mars. *Icarus* 165: 53-67.

Fairén, A.G., J.M. Dohm, T. Öner, et al. 2004. Updating the evidence of oceans on early Mars. *Early Mars 2004 Conference*, Jackson, Wyoming.

Fairén, A.G., D. Schulze-Makuch, A.P. Rodríguez, W. Fink, et al. 2009. Evidence for Amazonian acidic liquid water on Mars - A reinterpretation of MER mission results. *Planet. Space Sci.* 57: 276-287.

Fairén, A.G., A.F. Davila, D. Lim, N. Bramall, et al. 2010. Astrobiology through the ages of Mars: the study of terrestrial analogues to understand the habitability of Mars. *Astrobiology* 10: 821-43.

Fairén, A.G. and D. Schulze-Makuch. 2013. The overprotection of Mars. *Nature Geosci.* 6: 510-511.

Fairén, A.G., V. Parro, D. Schulze-Makuch, and L. Whyte. 2017. Searching for life on Mars before it is too late. *Astrobiology* 17: 962-970.

Farkas, I. 1935. *Orthohydrogen, parahydrogen, and heavy hydrogen.* Cambridge University Press, Cambridge.

Farrimond, P., H.M. Talbot, D.F. Watson, et al. 2004. Methylhopanoids: molecular indicators of ancient bacteria and a petroleum correlation tool. *Geochim. Cosmochim. Acta* 68: 3873-3882.

Faulk, S.P., J.L. Mitchell, S. Moon, and J.M. Lora. 2017. Regional patterns of extreme precipitation on Titan consistent with observed alluvial fan distribution. *Nature Geosci.* doi:https://doi.org/10.1038/ngeo3043.

Fegley Jr. B. 1987. Carbon chemistry and organic compound synthesis in the solar nebula. *Meteoritics* 22: 378.

Feher, F.J. 2000. Polyhedral oligosilsesquioxanes and heterosilsesquioxanes. pp. 43-59. *Silicon, Germanium and Tin Compounds, Metal Alkoxides, Metal Diketons and Silicones*. Gelest Inc., Tullytown, PA.

Feinberg, G., and R. Shapiro. 1980. *Life beyond Earth: The Intelligent Earthling's Guide to Life in the Universe*. William Morrow and Company, Inc, New York.

Feldman, W.C., W.V. Boynton, R.L. Tokar, et al. 2002. Global distribution of neutrons from Mars: Results from Mars Odyssey. *Science* 297: 75-78.

Feldman, W.C., S. Maurice, A.B. Binder, B.L. Barraclough, R.C. Elphic, and D. J. Lawrence. 1998. Fluxes of fast and epithermal neutrons from Lunar Prospector: evidence for water ice at the lunar poles. *Science* 281: 1496-5000.

Feller, G. 2017. Cryosphere and psychrophiles: insights into a cold origin of life? *Life (Basel)* 7: 25 (doi:https://doi.org/10.3390/life7020025).

Ferguson, B.A., T.A. Dreisbach, C.G. Parks, et al. 2003. Coarse-scale population structure of pathogenic Armillaria species in a mixed-conifer forest in the Blue Mountains of northeast Oregon. *Canad. J. Forest Res.* 33: 612-623.

Fernandez-Remolar, D., N. Rodriquez and F. Gomez. 2003. Geological record of an acidic environment driven by iron hydrochemistry: The Tinto River system. *J. Geophys. Res.* 108: 5080.

Ferris, J.P. 1993. Prebiotic synthesis on minerals: RNA oligomer formation. In *The Chemistry of Life's Origins*, edited by J. M. Greenberg, C. X. Mendoza-Gómez and V. Pirronello: Kluwer Acad. Publ.

Ferus, M., D. Nesvorny, J. Sponer, P. Kubelik, et al. 2015. High-energy chemistry of formamide: a unified mechanism of nucleobase formation. *Proc. Natl. Acad. Sci. USA* 112: 657-62.

Figueredo, P.H., R. Greeley, S. Neuer, et al. 2003. Locating potential biosignatures on Europa from surface geology observations. *Astrobiology* 3: 879-897.

Fink, W., J.M. Dohm, M.A. Tarbell, et al. 2005. Next-generation robotic planetary reconnaissance missions: a paradigm shift. *Planet. Space Sci.* 53: 1419-1426.

Firsoff, V.A. 1963. *Life beyond the Earth*. Basic Books, Inc., New York.

Fisk, M.R., R. Popa, O.U. Mason, et al. 2006. Iron-magnesium silicate bioweathering on Earth (and Mars?). *Astrobiology* 6: 48-68.

Fleischaker, G.R. 1990. Origins of Life - an Operational Definition. *Orig. Life Evol. Biosph.* 20: 127-137.

Fliegel, D., J. Kosler, N. McLoughlin, A. Simonetti, and M.J. de Wit. 2010. In-situ dating of the Earth's oldest trace fossil at 3.34 Ga. *Earth Plan. Sci. Lett.* 299: 290-298.

Foley, W.T., and P.A. Giguère. 1951. Hydrogen peroxide and its analogues: II. Phase equilibrium in the system hydrogen peroxide-water. *Can. J. Chem.* 29: 123-132.

Folk, R.L. 1993. SEM imaging of bacteria and nannobacteria in carbonate sediments and rocks. *J. Sediment. Res.* 63: 990-999.

Folk, R.L. 1999. Nannobacteria and the precipitation of carbonate in unusual environments. *Sedimentary Geology* 126: 47-55.

Forget, F., and R.T. Pierrehumbert. 1997. Warming early Mars with carbon dioxide clouds that scatter infrared radiation. *Science* 278: 1273-1274.

Formisano, V., S. Atreya, T. Encrenaz, et al. 2004. Detection of methane in the atmosphere of Mars. *Science* 306: 1758-1761.

Forterre, P. 2006. The origin of viruses and their possible roles in major evolutionary transitions. *Virus Res.* 117: 5-16.

Fortes, A.D. 2000. Exobiological implications of a possible ammonia-water ocean inside Titan. *Icarus* 146: 444-452.

Fox, S.W., and K. Dose. 1977. *Molecular Evolution and the Origin of Life*. Marcel Dekker, New York.

Fox, S. and H. Strasdeit. 2017. Inhabited or Uninhabited? Pitfalls in the Interpretation of Possible Chemical Signatures of Extraterrestrial Life. *Front. Microbiol.* 8: 1622.: doi: https://doi.org/10.3389/fmicb.2017.01622. eCollection 2017.

Franchi, M., E. Bramanti, L.M. Bonzi, et al. 1999. Clay-nucleic acid complexes: characteristics and implications for the preservation of genetic material in primeval habitats. *Orig. Life Evol. Biosph.* 29: 297-315.

Franck, S., A. Block, W. von Bloh, C. Bounama, I. Garrido, et al. 2001. Planetary habitability: is Earth commonplace in the Milky Way? *Naturwissenschaften* 88: 416-426.

Frankel, R.B., R.P. Blakemore and R.S. Wolfe. 1979. Magnetite in freshwater magnetotactic bacteria. *Science* 203: 1355-1356.

Fraser, C. M., J. D. Gocayne, O. White, M. D. Adams, et al. 1995. The minimal gene complement of *Mycoplasma genitalium*. *Science* 270: 397-403.

Freissinet, C., D.P. Glavin, P.R. Mahaffy, K.E. Miller, J.L. Eigenbrode, et al. 2015. Organic molecules in the Sheepbed Mudstone, Gale Crater, Mars. *JGR-Planets* 120: 495-514.

Freitas, R.A. 1980. Interstellar probes: a new approach to SETI. *J. Brit. Interplanet. Soc.* 33: 95-100.

Frey, H.U., and D. Lummerzheim. 2002. Can conditions for life be inferred from optical emissions of extra-solar-system planets. pp. 381-388. *Atmospheres in the Solar System: Comparative Aeronomy. Geophysical Monograph 130*. American Geophysical Union.

Friedmann, E.I. 1982. Endolithic microorganisms in the Antarctic cold desert. *Science* 215: 1045-1053.

Friedmann, E.I., J. Wierzchos, C. Ascaso, et al. 2001. Chains of magnetite crystals in the meteorite ALH84001: evidence of biological origin. *Proc. Natl. Acad. Sci. USA* 98: 2176-2181.

Friedmann, E.I., and H.J. Sun. 2005. Communities adjust their temperature optima by shifting producer-to-consumer ratio, shown in lichens as models: 1. Hypothesis. *Microb. Ecol.* 49: 523-527.

Fujino, M. 1987. Photoconductivity in organopolysilanes. *Chem. Phys. Lett.* 136: 451-453.

Furnes, H., N.R. Banerjee, K. Muehlenbachs, et al. 2004. Early life recorded in Archean pillow lavas. *Science* 304: 578-581.

Furusawa, K. 1994. Protection of nucleosides using bifunctional sully reagents. *Journal of the National Institute of Materials and Chemical Research* 2: 337.

Fütterer, O., A. Angelov, H. Liesegang, G. Gottschalk, C. Schleper, et al. 2004. Genome sequesce of *Picrophilus torridus* and its implications for life around pH 0. *Proc. Natl. Acad. Sci. USA* 101: 9091-9096.

Fuzzi, S. 2002. Organic component of aerosols and clouds. *EUROTRAC-2 Symposium 2002: Transformation and Chemical Transformation in the Troposphere*, Garmisch-Partenkirchen, Germany.

Gaidos, E.J. 2000. A cosmochemical determinism in the formation of Earth-like planets. *Icarus* 145: 637-650.

Gaidos, E.J. 2007. New worlds on the horizon: earth-sized planets close to other stars. *Science* 318: 210-213.

Gaill, F., K. Mann, H. Wiedemann, et al. 1995. Structural comparison of cuticle and interstitial collagens from annelids living in shallow seawater and at deep-sea hydrothermal vents. *J. Mol. Biol.* 246: 284-294.

Garcia-Ruiz, J.M., E. Nakouzi, E. Kotopoulou, L. Tamborrino, and O. Steinbock. 2017. Biominetic mineral self-organization from silica-rich spring water. *Sci. Adv.* 3: e1602285.

Geissler, P.E., R. Greenberg, G. Hoppa, et al. 1998. Evidence for non-synchronous rotation of Europa. Galileo Imaging Team. *Nature* 391: 368-370.

Gel-Mann, M. 1994. *The Quark and the Jaguar*. W.H. Freeman & Co., New York.

Georgiou, C.D. and D.W. Deamer. 2014. Lipids as universal biomarkers of extraterrestrial life. *Astrobiology* 14: 541-9.

George Cooper, Novelle Kimmich, Warren Belisle, Josh Sarinana, Katrina Brabham, Laurence Garrel, (2001) Carbonaceous meteorites as a source of sugar-related organic compounds for the early Earth. Nature 414 (6866):879-883

Gervin, J.C., A.G. Kerber, R.G. Witt, et al. 1985. Comparison of level I land cover accuracy for MSS and AVHRR data. *International Journal of Remote Sensing* 6: 47-57.

Gibard, C., S. Bhowmik, M. Karki, E.-K. Kim and R. Krishnamurthy. 2017. Phosphorylation, oligomerization and self-assembly in water under potential prebiotic conditions. *Nature Chem.* doi:https://doi.org/10.1038/nchem.2878.

Gibson, E.K., D.S. McKay, K.L. Thomas-Keprta, et al. 2006. Life on Mars: evaluation of the evidence within martian meteorites ALH84001, Nakhla, and Shergotty. *Precambrian Res.* 106: 15-34.

Giguère, P.A., and E.A. Secco. 1954. Hydrogen peroxide and its analogues: V. Phase equlibria in the system D_2O-D_2O_2. *Can. J. Chem.* 32: 550-556.

Gislén, T. 1948. Aerial plankton and its condition of life. *Biological Reviews* 23: 109-126.

Gladstone, G.R., K.M. Towe and J.F. Kasting. 1993. Photochemistry in the primitive solar nebula; discussions and reply *Science* 261: 5124.

Glavin, D.P., J.L. Bada, O. Botta, et al. 2001. Integrated micro-chip amino acid chirality detector for MOD. p. abstract #1442. *32nd Lunar and Planetary Science Conference*, Houston, Texas.

Glavin, D.P., C. Freissinet, K.E. Miller, J.L. Eigenbrode, A.E. Brunner, et al. 2013. Evidence for perchlorates and the origin of chlorinated hydrocarbons detected by SAM at the Rocknest aeolian deposit in Gale Crater. *JGR-Planets* 118: 1955-1973.

Glavin D.P., C. Freissinet, J. Eigenbrode, K. Miller, M. Martin, et al. 2014. Origin of chlorobenzene detected by the Curiosity Rover in Yellowknife Bay: evidence for Martian organics in the Sheepbed mudstone? 45th Lunar and Planetary Science Conference, abstract # 1157.

Gold, T. 1992. The deep, hot biosphere. *Proc. Natl. Acad. Sci. USA* 89: 6045-6049.

Golden, D.C., D.W. Ming, C.S. Schwandt, et al. 2001. A simple inorganic process for formation of carbonates, magnetite, and sulfides in martian meteorite ALH84001. *Amer. Mineralog.* 86: 370-375.

Goldsmith, D., and T. Owen. 2003. *The Search for Life in the Universe* University Science Books, Sausalito.

Gonzalez-Partida, E., P. Birkle and I.S. Torres-Alvarado. 2000. Evolution of the hydrothermal system at Los Azufres, Mexico, based on petrologic, fluid inclusion and isotopic data. *Journal of Volcanology and Geothermal Research* 104: 277-296.

Gonzalez, G., D. Brownlee, and P.D. Ward. 2001. The Galactic Habitable Zone: Galactic chemical evolution. Icarus 152: 185-200.

González-Pastor, J.E., E.C. Hobbs and R. Losick 2003. Cannibalism by sporulating bacteria *Science* 301: 510-513.

Goodwin, B. 1994. *How the Leopard Changed Its Spots: The Evolution of Complexity*. Charles Scribner's Sons, New York.

Goordial, J., A. Davila, D. Lacelle, W. Pollard, et al. 2016. Nearing the cold-arid limits of microbial life in permafrost of an upper dry valley, Antarctica. *ISME J.* 10: 1613-24.

Gorbushina, A.A., W.E. Krumbein and M. Volkmann. 2002. Rock surfaces as life indicators: new ways to demonstrate life and traces of former life. *Astrobiology* 2: 203-213.

Gordon, H.R., D.K. Clark, J.L. Mueller, et al. 1980. Phytoplankton pigments from the Nimbus-7 coastal zone color scanner – comparison with surface measurements. *Science* 210: 63-66.

Goudge, T.A., J.W. Head, L. Kerber, D.T. Blewett, B.W. Denevi, et al. 2014. Global inventory and characterization of pyroclastic deposits on Mercury: New insights into pyroclastic activity from MESSENGER orbital data. *JGR-Planets*, doi: https://doi.org/10.1002/2013JE004480

Gould, S.J. 1981. G. G. Simpson, paleontology, and the modern synthesis. pp. 153-172 in M. E and P. WB, eds. *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Harvard Univ. Press, Cambridge, MA.

Grant, W.D. 2004. Life at lower water activity. *Philos. Trans. Roy. Soc. Lond. Biol.* 359: 1249-1267.

Grasset, O., and J. Pargamin. 2005. The ammonia-water system at high pressures: Implications for the methane of Titan. *Planetary Space Sci.* 53: 371-384.

Gray, R.H. 2012. *The Elusive WOW: Searching for Extraterrestrial Intelligence*. Chicago: Palmer Square Press.

Gray, R.H. 2015. The Fermi Paradox is neither Fermi's nor a paradox. *Astrobiology* 15: 195-199.

Greeley, R. 1987. Release of juvenile water on Mars – estimated amounts and timing associated with volcanism. *Science* 236: 1653-1654

Greenberg, J. M. 2000. The secrets of stardust. *Sci. Am.* 283 (6):70-75.

Greenberg, R. 2010. Transport rates of radiolytic substances into Europa´s ocean: implications for the potential origin and maintenance of life. *Astrobiology* 10: 275-283.

Greenberg, R. 2011. Exploration and protection of Europa's biosphere: implications of permeable ice. *Astrobiology* 11:183-191.

Greenwood, N.N., and A. Earnshaw. 1984. *Chemistry of the Elements* Pergamon Press, Oxford, Great Britain.

Griffith, C.A., T. Owen and R. Wagener. 1991. Titan's surface and tropossphere, investigated with ground-based near-infrared observations. *Icarus* 93: 362-378.

Griffith, C.A., P. Penteado, K. Baines, P. Drossart, J. Barnes, et al. 2005. The evolution of Titan's mid-latitude clouds. *Science* 310: 474-477.

Grimaldi, D., and D. Agosti. 2000. A formicine in New Jersey cretaceous amber (Hymenoptera: formicidae) and early evolution of the ants. *Proc. Natl. Acad. Sci. USA* 97: 13678-13683.

Grinspoon, D.H. 1997. *Venus Revealed: A New Look Below the Clouds of Our Mysterious Twin Planet.* Perseus Publishing, Cambridge, Massachusetts.

Grinspoon, D.H. 2003. *Lonely Planets: The Natural Philosophy of Alien Life*. HarperCollins, New York.

Grosch, E.G. and N. McLoughlin. 2014. Reassessing the biogenicity of Earth's oldest trace fossil with implications for biosignatures in the search for early life. *Proc. Natl. Acad. Sci. USA* 111: 8380–8385.

Gross, W. 1999. Revision of Comparative Traits for the Acido- and Thermophilic Red Algae Cyanidium and Galdieria. In Enigmatic Microorganisms and Life in Extreme Environments, edited by J. Seckbach. Dordrecht: Springer Netherlands.

Guillemin, J.-C. 2000. Organic photochemistry in the atmosphere of Jupiter and Saturn - The role played by H_2S, PH_3 and NH_3 *Orig. Life Evol. Biosph.* 30: 236.

Guinan, E.F., S.G. Engle, L.E. DeWarf, D. Schulze-Makuch, M. Cuntz, et al. 2007. Living with a red dwarf: Evolution over time of dynamo generated X-ray – UV emissions and effects on hosted planets. p. Abstract # 04. *Amer. Astronomical Society General Meeting*, Seattle, WA.

Gull, M, M.A. Mojica, F.M. Fernandez, D.A. Gaul, and T.M. Orlando, et al. 2015. Nucleoside phosphorylation by the mineral schreibersite. *Sci. Repts.* 5: #17198; doi: 10.1038/srep17198.

Gundersen, J.K., B.B. Jørgensen, E. Larsen, et al. 1992. Mats of giant sulphur bacteria on deep-sea sediments due to fluctuating hydrothermal flow. *Nature* 360: 454-456.

Gusev, V.A. 2002. Chemical and prebiotic synthesis in the droplets of thunderstorm cloud. pp. 205-208. *2nd European Workshop on Exo-Astrobiology*.

Gusev, V.A., and D. Schulze-Makuch. 2005. Low frequency electromagnetic waves as a supplemental energy source to sustain microbial growth. *Naturwissenschaften* 92: 115-120.

Haqq-Misra, J., M.W Busch, S.M. Som, and S.D. Baum. 2013. The benefits and harm of transmitting into space. *Space Policy* 29: 40-48.

Haas, J.R. 2010. The potential feasibility of chlorinic photosynthesis on exoplanets. *Astrobiology* 10: 953-963.

Hadorn, M. and P. Eggenberger Hotz. 2010. DNA-mediated self-assembly of artificial vesicles. *PLoS One* 5: e9886.

Hagemann, M., A. Schoor, S. Mikkat, et al. 1999. The biochemistry and genetics ofthe synthesis of osmoprotective compounds in cyanobacteria. pp. 177-186 in Oren A, ed. *Microbiology and Biogeochemistry of Hypersaline Environments.* CRC press, New York.

Haldane, J. 1929. The origin of life. *Rationalist Annual* 148: 3-10.

Haldane, J.B.S. 1954. *The origin of life* Penguin Books, Harmondsworth.

Hall, D.T., D.F. Strobel, P.D. Feldman, et al. 1995. Detection of an oxygen atmosphere on Jupiter's moon Europa [see comments]. *Nature* 373: 677-681.

Hammel, H.B., I. dePater, S.G. Gibbard, G.W. Lockwood, and K. Rages. 2005. Uranus in 2003: Zonal winds, banded structure, and discrete features *Icarus* 275: 534-535.

Hammond, C., R.L. Jenkins, N Dimitratos, J.A. Lopez-Sanchez, et al. 2012. Catalytic and Mechanistic Insights of the Low-Temperature Selective Oxidation of Methane over Cu-Promoted Fe-ZSM-. *Chemistry* 518: 15735-15745.

Han, C. and W. Han. 2002. On the feasibility of detecting satellites of extrasolar planets via microlensing. *Astrophys. J.* 580: 490-493.

Han, T.-M., and B. Runnegar. 1992. Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee Iron-Formation, Michigan. *Science* 257: 232-235.

Hand, E. 2011. Venus scientists fear neglect. *Nature* 477: 145.

Hanon, P., M. Chaussidon and F. Robert. 1996. The redox state of the solar nebula; C and H concentrations in chondrules. *Meteoritics & Planetary Science* 31: 57.

Hansen, C. J., L. Esposito, A. I. Stewart, J. Colwell, A. Hendrix, W. Pryor, D. Shemansky, and R. West. 2006. Enceladus' water vapor plume. *Science* 311: 1422-1425.

Hanson, R. 1998. *The great filter: are we almost past it?* [Available from http://hanson.gmu.edu/greatfilter.html].

Harrison, P.G. 1977. Silicate cages: precursors to new materials. *J. Organometal. Chem.* 542: 141-184.

Harrop, B.L. and D. Schulze-Makuch, 2010. The Solar Wind Power Satellite as an alternative to a traditional Dyson Sphere and its implications for remote detection. *Intl. J. of Astrobiol.* 9: 89-99.

Hartman, H. 1998. Photosynthesis and the origin of life *Orig. Life Evol. Biosph.* 28: 515-521.

Harvey, R.P., and H.Y. McSween. 1996. A possible high-temperature origin for the carbonates in the martian meteorite ALH84001. *Nature* 382: 49-51.

Hawkins, J., and S. Blakeslee. 2005. *On Intelligence*. Henry Holt, New York.

Hazen, R.M. and J.H. Ausubel. 2016. On the nature and significance of rarity in mineralogy. *Am. Minerol.* 101.

Head, J.W., D. Smith and M. Zuber. 1998. Mars; assessing evidence for an ancient northern ocean with MOLA data. *Meteoritics & Planetary Science* 33: 66.

Heath, M.J., L.R. Doyle, M.M. Joshi, et al. 1999. Habitability of planets around red dwarf stars. *Orig. Life Evol. Biosph.* 29: 405-424.

Hecht, M.H., S.P. Kounaves, R.C. Quinn, S.J. West, S.M.M. Young, et al. 2009. Detection of perchlorate and the soluble chemistry of Martian soil at the Phoenix Lander site. *Science* 325: 64-67.

Heller, R. 2018. The nature of the giant exomoon candidate Kepler-1625 b-i. *Astron. Astrophys.* 610: https://doi.org/10.1051/0004-6361/201731760.

Heller, R. and J. Armstrong. 2014. Superhabitable worlds. *Astrobiology* 14: 50-66.

Heller, R., D. Williams, D. Kipping, M.-A. Limbach, E. Turner et al. 2014. Formation, habitability, and detection of extrasolar moons. *Astrobiology* 14: 798-835.

Henderson, M.E.K. and R.B. Duff. 1965. The release of metallic and silicate ions from mineral rocks and soils by fungal activity. *J. Soil Sci.* 14: 236-246.

Herlihy, L.J., J.N. Galloway and A.L. Mills. 1987. Bacterial utilization of formic and acetic acid in rainwater. *Atmos. Environ.* 21: 2397-2402.

Herman, L. 1986. Cognition and language competencies of bottlenosed dolphins. pp. 221-252 in R. Schusterman, J. Thomas and F. Wood, eds. *Dolphin Cognition and Behaviour: A Comparative Approach*. Lawrence Erlbaum Associates, Hillsdale, NJ.

Heron, N. 1989. Toward Si-based life: zeolites as enzyme mimics *Chemtech Sept.* September: 542-548.

Hewish, A., S.J. Bell, J.D.H. Pilkington, P.F. Scott, and R.A. Collins. 1968. Observation of a rapidly pulsating radio source. *Nature* 217: 709-713.

Hiesinger, H., S. Marchi, N. Schmedemann, P. Schenk, et al. 2016. Cratering on Ceres: Implications for its crust and evolution. *Science* 353: 1003 (doi:https://doi.org/10.1126/science.aaf4759).

Higgs, P. G. and R. E. Pudritz. 2009. A thermodynamic basis for prebiotic amino acid synthesis and the nature of the first genetic code. *Astrobiology* 9: 483-490.

Hippke, M. 2015. On the detection of exomoons: a search in Kepler data for the orbital sampling effect and the scatter peak. *Astrophys. J.* 806: 51-74.

Hoehler, T. M. 2007. An energy balance concept for habitability. *Astrobiology* 7: 824-38.

Hoehn, A., K. Lynch, J. Clawson, J. Freeman, J. Kapit, et al. 2007. Microbial Detection Array (MDA), a novel instrument for unambiguous detection of microbial metabolic activity in astrobiology applications. SAE Technical Paper 2007-01-3190, https://doi.org/10.4271/2007-01-3190.

Hoesl, M.G., Oehm, S., Durkin, P., Darmon, E., Peil, L., et al. 2015. Chemical evolution of a bacterial proteome. *Ang. Chem.*: doi:https://doi.org/10.1002/anie.201502868.

Hof, P.R., R. Chanis and L. Marino. 2005. Cortical complexity in cetacean brains. *Anat Rec A Discov Mol Cell Evol Biol* 287: 1142-1152.

Hoffman, P.F., A.J. Kaufman, G.P. Halverson, et al. 1998. A neoproterozoic snowball Earth. *Science* 281: 1342-1346.

Hohsaka, T., and S.M. Masahiko. 2002. Incorporation of non-natural amino acids into proteins. *Curr. Opin. Chem. Biol.* 6: 809-815.

Holden, J.F., and J.A. Baross. 1995. Enhanced thermotolerance by hydrostatic pressure in the deep-sea marine thermophile *Pyrococcus* strain ES4. *FEMS Microbiol. Ecol.* 18: 27-34.

Holm, N. G., C. Oze, O. Mousis, J. H. Waite, and A. Guilbert-Lepoutre. 2015. Serpentinization and the formation of H2 and CH4 on Celestial Bodies (Planets, Moons, Comets). *Astrobiology* 15: 587-600.

Hoppa, G.V., B.R. Tufts, R. Greenberg, et al. 1999. Formation of cycloidal features on Europa. *Science* 285: 1899-1902.

Horikawa, D.D., J. Cumbers, I. Sakakibara, D. Rogoff, S. Leuko, and et al. 2013. Analysis of DNA repair and protection in the tardigrade *Ramazzottius varieornatus* and *Hypsibius dujardini* after exposure to UVC radiation. *PLoS ONE* 8 (6):e64793.

Horneck, G. 1981. Survival of microorganisms in space: a review. *Adv. Space Res.* 1: 39-48.

Horneck, G. 1993. Responses of *Bacillus subtilis* spores to the space environment: results from experiments in space *Orig. Life Evol. Biosph.* 23: 37-52.

Horneck, G., H. Buecker, and G. Reitz. 1994. Long-term survival of bacterial spores in space. *Adv. Space Res.* 14: 41-45.

Horneck, G., R. Facius, M. Reichert, et al. 2003. HUMEX, a study on the survivability and adaptation of humans to long-duration exploratory missions, part I: lunar missions *Adv. Space Res.* 31: 2389-2401.

Horneck, G., D. Stöffler, S. Ott, U. Hornemann, C.S. Cockell, et al. 2008. Microbial rock inhabitants survive hypervelocity impacts on Mars-like host planets: first phase of lithopanspermia experimentally tested. *Astrobiology* 8: 17-44.

Horneck, G., R. Moeller, J. Cadet, T. Douki, et al. 2012. Resistance of bacterial endospores to outer space for planetary protection purposes--experiment PROTECT of the EXPOSE-E mission. *Astrobiology* 12: 445-456.

Horowitz, E. D., A. E. Engelhart, M. C. Chen, K. A. Quarles, et al. 2010. Intercalation as a means to suppress cyclization and promote polymerization of base-pairing oligonucleotides in a prebiotic world. *Proc. Natl. Acad. Sci. USA* 107: 5288-93.

Horowitz, N.H., G.L. Hobby and J.S. Hubbard. 1977. Viking on Mars: The Viking carbon assimilation experiments. *J. Geophys. Res.* 82: 4659-4662.

Hose, L.D., A.N. Palmer, M.V. Palmer, et al. 2000. Microbiology and geochemistry in a hydrogen-sulphide-rich karst environment *Chem. Geol.* 169: 399-423.

House, K.Z., D.P. Schrag, C.F. Harvey, et al. 2006. Permanent carbon dioxide storage in deep-sea sediments. *Proc. Natl. Acad. Sci. USA* 103: 12291-12295.

Houtkooper, J.M. and D. Schulze-Makuch. 2007. A possible biogenic origin for hydrogen peroxide on Mars: the Viking results reinterpreted. *Int. J. Astrobiol.* 6: 147-152.

Houtkooper, J.M. and D. Schulze-Makuch. 2010. Do perchlorates have a role for Martian life? *J. Cosmol.* 5: 930-939.

Hovis, W.A., D.K. Clark and F. Anderson et al. 1980. Nimbus-7 CZCS coastal zone color scanner – system description and early imagery. *Science* 210: 60-63.

Hoyle, F. 1959. *The black cloud.* Signet, New York, USA.

Hoyle, F. 1983. *The intelligent universe* Michael Joseph, London.

Hsu, H.W., F. Postberg, Y. Sekine, T. Shibuya, et al. 2015. Ongoing hydrothermal activities within Enceladus. *Nature* 519: 207-210.

Huber, C., and G. Wächtershäuser. 1998. Peptides by activation of amino acids with CO on (NiFe)S surfaces. *Science* 281: 670-672.

Huber, H., M.J. Hohn, R. Rachel, et al. 2002. A new phylum of Archaea represented by a nanosized hyperthermophilic symbiont. *Nature* 417: 63-67.

Hueber, F.M. 1961. *Hepaticites devonicus*: a new fossil liverwort from the Devonian of New York. *Annals Missouri Bot. Garden* 48: 125-132.

Hurford, T. A., P. Helfenstein, G. V. Hoppa, R. Greenberg, and B. G. Bills. 2007. Eruptions arising from tidally controlled periodic openings of rifts on Enceladus. *Nature* 447: 292-294.

Hutchison, C. A., R. Y. Chuang, V. N. Noskov, N. Assad-Garcia, et al. 2016. Design and synthesis of a minimal bacterial genome. *Science* 351: 1414-U73; doi: https://doi.org/10.1126/science.aad6253

Ibrahim, A.I., J.H. Swank and W. Parke. 2003. New evidence of proton-cyclotron resonance in a magnetar strength field from SGR 1806-20. *Astrophys. J. Lett.* 584: L17-L21.

Iess, L., D.J. Stevenson, M. Parisi, D. Hemingway, R.A. Jacobson, J.I. Lunine, F. Nimmo, J.W. Armstrong, S.W. Asmar, M. Ducci, and P.Tortora. 2014. The gravity field and interior structure of Enceladus. *Science* 344: 78-80.

Ikushima, Y. 1997. Supercritical fluids: an interesting medium for chemical and biochemical processes. *Adv. Colloid Interface Sci.* 71-72: 259-280.

Inagaki, F., M.M.M. Kuypers, U. Tsunogai, J.-I. Ishibashi, K.-I. Nakamura, et al. 2006. Microbial community in a sediment-hosted CO2 lake of the southern Okinawa through hydrothermal system. *Proc. Natl. Acad. Sci. USA* 103: 14164-14169.

Ioale, P., A. Gagliardo and V.P. Bingman. 2001. Further experiments on the relationship between hippocampus and orientation following phase-shift in homing pigeons. *Behavioural Brain Research* 108: 157-167.

Irwin, L.N. 2018. Exotic forms of life on other worlds. In *Handbook of Exoplanets*, edited by H. J. Deeg and J. A. Belmonte. Cham: Springer International Publishing, pp. 1-13; https://doi.org/10.1007/978-3-319-30648-3_161-1

Irwin, L.N., and D. Schulze-Makuch. 2001. Assessing the plausibility of life on other worlds. *Astrobiology* 1: 143-160.

Irwin, L.N., and D. Schultze-Makuch. 2003. Modeling putative multilevel ecosystems on Europa. *Astrobiology* 3: 813-821.

Irwin, L.N., and D. Schulze-Makuch. 2005. Prebiotic evolution of riboglycopeptides: bridging the entropy gap at the dawn of life on earth. *International Conference on the Origin of Life*, Beijing, P.R.C.

Irwin, L.N. and D Schulze-Makuch. 2008. Inferences from the independent, infrequent, and underutilized evolution of intelligence on Earth. *Astrobiology* 8: 391.

Irwin, L.N., and D. Schulze-Makuch. 2011. *Cosmic Biology: How Life Could Evolve on Other Worlds*. New York: Praxis.

Irwin, L.N., A. Méndez, A.G. Fairén, and D. Schulze-Makuch. 2014. Assessing the possibility of biological complexity on other worlds, with an estimate of the occurrence of complex life in the Milky Way galaxy. *Challenges* 214 (5): 159-174.

Ishii, Y., and T. Yanagida. 2000. Single molecule detection in life science. *Single Mol.* 1: 5-16.

Isken, S., and J.A.M. de Bont. 1998. Bacteria tolerant to organic solvents. *Extremophiles* 2: 229-238.

Islam, M.R., and D. Schulze-Makuch. 2007. Adaptation mechanisms of multicellular extremophiles. *Int. J. Astrobiol.* 6: 199-215.

Jablonka, E., and M.J. Lamb. 2006. The evolution of information in the major transitions. *J. Theor. Biol.* 239: 236-246.

Jakosky, B. 1998. *The search for life on other planets* Cambridge University Press.

Jannasch, H.W. 1995. Seafloor hydrothermal systems: physical, chemical, biological and geological interactions. American Geophysical Union, Washington DC, USA.

Jenkins, J.M., P. G. Steffes, D.P. Hinson, J.D. Twicken, and G.L. Tyler. 1994. Radio Occultation Studies of the Venus Atmosphere with the Magellan Spacecraft. *Icarus* 110: 79-94.

Jenkins, J.M., J.D. Twicken, N.M. Batalha, D.A. Caldwell, W.D. Cochran, et al. 2015. Discovery and validation of Kepler-452b: a 1.6 RÅ Super Earth exoplanet in the habitable zone of a G2 star. *Astronom. J.*: 150: 56-75

Jerison, H. 1973. *Evolution of the Brain and Intelligence*. Academic Press, London.

Jim P. Williams, John E. Hallsworth, (2009) Limits of life in hostile environments: no barriers to biosphere function?. Environmental Microbiology 11 (12):3292-3308

Johnson, C.N. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc Biol Sci* 269: 2221-2227.

Johnson, H.P., and t.L.S. Party. 2003. Probing for life in the ocean crust with the LEXEN program. *EOS Trans. AGU* 84: 109-112.

Jolivet, E., E. Corre, S. L'Haridon, et al. 2004. Thermococcus marinus sp. nov. and Thermococcus radiotolerans sp. nov., two hyperthermophilic archaea from deep-sea hydrothermal vents that resist ionizing radiation. *Extremophiles* 8: 219-227.

Jönsson, K.I., E. Rabbow, R.O. Schill, M. Harms-Ringdahl, and P. Rettberg. 2008. Tardigrades survive exposure to space in low Earth orbit. *Curr. Biol.* 18: R729-R731.

Junge, K., C. Krembs, J. Deming, et al. 2001. A microscopic approach to investigate bacteria under in-situ conditions in sea-ice samples. *Annals Glaciol.* 33: 304-310.

Junge, K., J.W. Deming and H. Eicken. 2004. Bacterial activity at -2 to -20 °C in Arctic wintertime sea ice. *Appl. Environ. Microbiol.* 70: 550-557.

Junge, K., H. Eicken, B.D. Swanson, et al. 2006. Bacterial incorporation of leucine into protein down to -20°C with evidence for potential activity in subeutectic saline ice formations. *Cryobiology* 52: 417-429.

Juhas, M. 2016. On the road to synthetic life: the minimal cell and genome-scale engineering. *Crit. Rev. Biotechnol.* 36: 416-23.

Kaifu, Y., H. Baba, F. Aziz, et al. 2005. Taxonomic affinities and evolutionary history of the Early Pleistocene hominids of Java: dentognathic evidence. *Am J Phys Anthropol* 128: 709-726.

Kajander, E.O., I. Kuronen, K. Akerman, et al. 1997. Nanobacteria from blood, the smallest culturable autonomously replicating agent on Earth. *Proc. SPIE* 3111: 420-428.

Kajander, E.O., and N. Ciftçioglu. 1998. Nanobacteria: an alternative mechanism for pathogenic intra- and extracellular calcification and stone formation. *Proc. Natl. Acad. Sci. USA* 95: 8274-8279.

Kajander, E.O., N. Ciftcioglu, M.A. Miller-Hjelle, et al. 2001. Nanobacteria: controversial pathogens in nephrolithiasis and polycystic kidney disease. *Current Opinion in Nephrology and Hypertension* 10: 445-452.

Kan, S. B., R. D. Lewis, K. Chen, and F. H. Arnold. 2016. Directed evolution of cytochrome c for carbon-silicon bond formation: Bringing silicon to life. *Science* 354: 1048-1051.

Kardashev, N. 1964. Transmission of information by extraterrestrial civilizations. *Soviet Astron.* 8: 217-221.

Kargel, J.S., J.Z. Kaye, J.W. Head, et al. 2000. Europa's crust and ocean: origin, composition, and the prospects for life. *Icarus* 148: 226-265.

Karssilov, V.A., and R.M. Schuster. 1984. Paleozoic and Mesozoic fossils. pp. 1172-1193 in R.M. Schuster, ed. *New Manual of Bryology*. The Hattori Botanical Garden.

Kashefi, K., and D. Lovley. 2003. Extending the upper temperature limit for life. *Science* 301: 934.

Kasting, J. F. 1988. Runaway and moist greenhouse atmospheres and the evolution of Earth and Venus. *Icarus* 74: 472-494

Kasting, J.F., D.P. Whitmere and R.T. Reynolds. 1993. Habitable zones around main sequence stars. *Icarus* 101: 108-128.

Kasting, J.F., and L.L. Brown. 1998. The early atmosphere as a source of biogenic compound. pp. 35-56 in B. A., ed. *The Molecular Origins of Life*. Cambridge University Press, Cambridge, UK.

Kasting, J.F. 2006. Ups and downs of ancient oxygen. *Science* 443: 643-645.

Kato, C., L. Li, Y. Nogi, et al. 1998. Extremely barophilic bacteria isolated from the Mariana Trench, Challenger Deep, at a depth of 11,000 meters. *Appl. Environ. Microbiol.* 64: 1510-1513.

Kattenhorn, S.A. and L.M. Prockter. 2014. Evidence for subduction in the ice shell of Europa. *Nature Geosci.* 7: 762-767.

Kauffman, S.A. 1995. *At Home in the Universe: The Search for Laws of Self-Organization and Complexity*. Oxford Univ Press, Oxford.

Keane, J. T., I. Matsuyama, S. Kamata, and J. K. Steckloff. 2016. Reorientation and faulting of Pluto due to volatile loading within Sputnik Planitia. *Nature* 540: 90-93; doi:https://doi.org/10.1038/nature20120.

Keilin, D. 1959. The problem of anabiosis or latent life: history and current concept. *Proc. Roy. Soc. Lond. B* 150: 149-191.

Keim, C.N., F. Abreu, U. Lins, et al. 2004. Cell organization and ultrastructure of a magnetotactic multicellular organism. *J. Struct. Biol.* 145: 254-262.

Keller, M. A., D. Kampjut, S. A. Harrison, and M. Ralser. 2017. Sulfate radicals enable a non-enzymatic Krebs cycle precursor. *Nat. Ecol. Evol.* 1: 0083; doi https://doi.org/10.1038/s41559-017-0083.

Kelley, D.S., J.A. Karson, G.L. Früh-Green, D.R. Yoerger, T.M. Shank, et al. 2005. A serpentinite-hosted ecosystem: the lost city hydrothermal field. *Science* 307: 1428-1434.

Kent, A.J.R., I.D. Hutcheon, F.J. Ryerson, et al. 2001. The temperature of formation of carbonate in martian meteorite ALH84001: constraints from cation diffusion. *Geochim. Cosmochim. Acta* 65: 311-321.

Keosian, J. 1968. *The Origin of Life*. Reinhold, New York.

Keppler, F., D.B. Harper, M. Greule, U. Ott, T. Sattler, et al. 2014. Chloromethane release from carbonaceous meteorite affords new insight into Mars lander findings. *Sci. Rept.* 4: 7010.

Kerr, R.A. 2005. Icy volcanism has rejuvenated Titan. *Science* 308: 193.

Kerr, R.A. 2009. Planetary science. Yes, there's ice on the moon--but how much, and what use is it? *Science* 326: 1046.

Kerr, R.A. 2010. Planetary science. How wet the moon? Just damp enough to be interesting. *Science* 330: 434.

Kerr, R.A. 2012. Planetary science. Cassini spies an ocean inside Saturn's icy, gassy moon Titan. *Science* 336: 1629.

Khanna, M., and G. Stotzky. 1992. Transformation of Bacillus subtilis by DNA bound on montmorillonite and effect of DNase on the transforming ability of bound DNA. *Applied Environmental Biology* 58: 1930-1939.

Khurana, K.K., M.G. Kivelson, D.J. Stevenson, et al. 1998. Induced magnetic fields as evidence for subsurface oceans in Europa and Callisto. *Nature* 395: 777-780.

Kiang, N.Y., A. Segura, G. Tinetti, et al. 2007a. Spectral signatures of photosynthesis. II. Coevolution with other stars and the atmosphere on extrasolar worlds. *Astrobiology* 7: 252-274.

Kiang, N. Y., J. Siefert, Govindjee, and R. E. Blankenship. 2007b. Spectral signatures of photosynthesis. I. Review of Earth organisms. *Astrobiology* 7: 222-251.

Kieffer, S.W., R. Lopes-Gautier, A. McEwen, et al. 2000. Prometheus: Io's wandering plume. *Science* 288: 1204-1208.

Kieffer, S.W., X. Lu, C.M. Bethke, J. R. Spencer, S. Marshak, and A. Navrotsky. 2006. A clathrate reservoir hypothesis for Enceladus' south polar plume. *Science* 314: 1764-6.

Kirkland, B.L., F.L. Lynch, M.A. Rahnis, et al. 1999. Alternative origins for nannobacteria-like objects in calcite. *Geology* 27: 347-350.

Kirschvink, J.L., A.T. Maine and H. Vali. 1997. Paleomagnetic evidence of a low-temperature origin of carbonate in the martian meteorite ALH84001. *Science* 275: 1629-1633.

Kirschvink, J.L., E.J. Gaidos, L.E. Bertani, et al. 2000. Paleoproterozoic snowball Earth; extreme climatic and geochemical global change and its biological consequences. *Proc. Natl. Acad. Sci. USA* 97: 1400-1405.

Kis-Papo, T., A. Oren, S.P. Wasser, et al. 2003. Survival of filamentous fungi in hypersaline Dead Sea water. *Microb. Ecol.* 45: 183-190.

Kivelson, M.G., K.K. Khurana, C.T. Russell, et al. 2000. Galileo magnetometer measurements: a stronger case for a subsurface ocean at Europa. *Science* 289: 1340-1343.

Kleidon, A., K. Fraedrich, and M. Heimann. 2000. A green planet versus a desert world: estimating the maximum effect of vegetation on the land surface climate. *Climatic Change* 44: 471-493.

Klein, F., S. E. Humphris, W. Guo, F. Schubotz, E. M. Schwarzenbach, and W. D. Orsi. 2015. Fluid mixing and the deep biosphere of a fossil Lost City-type hydrothermal system at the Iberia Margin. *Proc. Natl. Acad. Sci. USA* 112: 12036-12041.

Klein, H.P. 1977. The Viking biological investigation: general aspects. *J. Geophys. Res.* 82: 4677-4680.

Klein, H.P. 1978. The Viking biological experiments on Mars. *Icarus* 34: 666-674.

Klein, H.P. 1999. Did Viking discover life on Mars? *Orig. Life Evol. Biosph.* 29: 625-631.

Klibanov, A.M. 2001. Improving enzymes by using them in organic solvents. *Nature* 409: 241-246.

Kminek, G., and J.L. Bada. 2006. The effect of ionizing radiation on the preserva-tion of amino acids on Mars. *Earth Planet. Sci. Lett.* 245: 1-5.

Knoll, A.H. 1999. A new molecular window on early life. *Science* 285: 1025-1026.

Knollenberg, R.G., and D.M. Hunten. 1980. The microphysics of the clouds of venus: results of the pioneer venus particle size spectrometer experiment. *J. Geophys. Res.* 85: 8038-8058.

Koerner, D., and S. LeVay. 2000. *Here Be Dragons: The Scientific Quest for Extraterrestrial Life* Oxford University Press, New York.

Koike, J., T. Oshima, K.A. Koike, et al. 1991. Survival rates of some terrestrial microorganisms under simulated space conditions. *Adv. Space Research* 12: 274.

Kolb, V. 2007. On the applicability of the Aristotelian principles to the definition of life. *Int. J. Astrobiology* 6: 51-57.

Kompanichenko, V.N. 1996. Transition of precellular organic microsystems to a biotic state: environment and mechanism. *Nanobiology* 4: 39-45.

Koshland, D.E. 2002. The seven pillars of life *Science* 295: 2215-2216.

Krasnopolski, V.A., J.P. Maillard and T.C. Owen. 2004. Detection of methane in the martian atmosphere: evidence for life? *Icarus* 172: 537-547.

Krenz, J.G., G.J.P. Naylor, H.B. Shaffer, et al. 2005. Molecular phylogenetics and evolution of turtles. *Molecular Phylogenetics and Evolution* 37: 178-191.

Kreuzwieser, J., J.-P. Schnitzler, R. Steinbrecher, (1999) Biosynthesis of Organic Compounds Emitted by Plants. Plant Biology 1 (2):149–159.

Kröger, N., S. Lorenz, E. Brunner, et al. 2002. Self-assembly of highly phosphorylated silaffins and their function in biosilica morphogenesis *Science* 298: 584-586.

Krulwich, T.A., M. Ito, D.B. Hicks, et al. 1998. pH homeostasis and ATP synthesis: studies of two processes that necessitate inward proton translocation in extremely alkaliphilic *Bacillus* species. *Extremophiles* 2: 217-222.

Kuchner, M.J. 2003. Volatile-rich Earth mass planets in the habitable zone. *Astrophys. J.* 596: L105

Küppers, M. 2017. Dwarf planet Ceres and the ingredients of life. *Science* 355: 692-693.

Küppers, M., L. O'Rourke, D. Bockelee-Morvan, V. Zakharov, et al. 2014. Localized sources of water vapour on the dwarf planet (1) Ceres. *Nature* 505: 525-527.

Kushner, D. 1981. Extreme environments: Are there any limits to life? pp. 241-248 in C. Ponnamperuma, ed. *Comets and the Origin of Life*. D. Reidel Publishing Co., Dordrecht.

Lahav, N. 1991. Prebiotic co-evolution of self-replication and translation or RNA world? *J Theor Biol* 151: 531-539.

Lahav, N. 1994. Minerals and the origin of life: Hypotheses and experiments in heterogeneous chemistry. *Heterogeneous Chem Rev* 1: 159-179.

Lahav, N., and S. Nir. 1997. Emergence of template-and-sequence-directed (TSD) syntheses: I. A bio-geochemical model. *Orig. Life Evol. Biosph.* 27: 377-395.

Lahav, N. 1999. *Biogenesis: theories of life's origin.* Oxford University Press.

Lammer, H., J.H. Bredehöft, A. Coustenis, M.L. Khodachenko, L. Kaltenegger, et al. 2009. What makes a planet habitable? *Astron. Astrophys. Rev.* 17: 181-249

Landman, N. 1987. *Nautilus: The Biology and Paleobiology of a Living Fossil.* Plenum Press, New York.

Larsen, H. 1967. Biochemical aspects of extreme halophilism. *Adv. Microb. Physiol.* 1: 97-132.

Lathe, R. 2004. Fast tidal cycling and the origin of life. *Icarus* 168: 18-22.

Lattimer, J.M., and M. Prakash. 2004. The physics of neutron stars. *Science* 304: 536-542.

Lauwers, A.M. and W. Heinen. 1974. Biodegradation and utilisation of silica and quartz *Arch. Microbiol.* 95: 67-78.

Lazard, D., N. Lahav and J.B. Orenberg. 1987. The biogeochemical cycle of the adsorbed template. I: Formation of the template. *Orig. Life Evol. Biosph.* 17: 135-148.

Lazard, D., N. Lahav and J.B. Orenberg. 1988. The biogeochemical cycle of the adsorbed template. II: Selective adsorption of mononucleotides on adsorbed polynucleotide templates. *Orig. Life Evol. Biosph.* 18: 347-357.

Lazcano, A. 1994. The RNA world, its predecessors and descendants. pp. 70-80 in B. S, ed. *Early life on Earth*. Columbia University Press, New York.

Lazcano, A., and S.L. Miller. 1994. How long did it take for life to begin and evolve to cyanobacteria? *J. Molec. Evol.* 39: 549-554.

Lazcano, A. 2004. An answer in search of a question. *Astrobiology* 4: 469-471.

Le Rudulier, D., and L. Boillard. 1983. Glycine Betaine, an osmotic effector in *Klebsiella pneumonia* and other members of the Enterobacteriaceae. *Appl. Environ. Microbiol.* 46: 152-159.

Lee, M. S. and S. Scandolo. 2011. Mixtures of planetary ices at extreme conditions. *Nat. Commun.* 2:185.

Leger, A., M. Pirre and F.J. Marceau. 1993. Search for primitive life on a distant planet: relevance of O_2 and O_3 detections. *Astron. Astrophys.* 277: 309-313.

Leger, A., F. Selsis, C. Sotin. T. Guillot, D. Despois, et al. 2004. A new family of planets? “ocean planets.” *Icarus* 169: 499-504.

LeGrand, A.P. 1998. *The Surface Properties of Silicas.* John Wiley and Sons, New York.

Leliwa-Kopystyński, J., M. Maruyama, and T. Nakajima. 2002. The water-ammonia phase diagram up to 300 MPa: application to icy satellites. *Icarus* 159: 518-528.

Leshin, L.A., K.D. McKeegan, P.K. Carpenter, et al. 1998. Oxygen isotopic constraints on the genesis of carbonates from martian meteorite ALH84001 - evidence from stable isotopes and mineralogy. *Geochim. Cosmochim. Acta* 62: 3-13.

Leslie, J. 1996. *Universes*. Routledge, London.

Levin, G.V. 1998. The future search for life on Mars: an unambiguous Martian life detection experiment. *Workshop on the Issue of Martian Meteorites*. Lunar and Planetary Institute, Houston, Texas.

Levin-Zaidman, S., J. Englander, E. Shimoni, et al. 2003. Ringlike structure of the Deinococcus radiodurans genome: A key to radioresistance?. *Science* 299: 254-256.

Levin, G.V., and P.A. Straat. 1977. Recent results from the Viking Labeled Release Experiment on Mars. *J. Geophys. Res.* 82: 4663-4667.

Levin, G.V., and P.A. Straat. 1981. A search for a nonbiological explanation of the Viking Labeled Release Life Detection Experiment. *Icarus* 45: 494-516.

Levin, G.V. and P.A. Straat. 2016. The case for extant life on Mars and its possible detection by the Viking Labeled Release Experiment. *Astrobiology* 16: 798-810.

Levison, H. F., K. A. Kretke, K. J. Walsh, and W. F. Bottke. 2015. Growing the terrestrial planets from the gradual accumulation of submeter-sized objects. *Proc. Natl. Acad. Sci. USA* 112: 14180-5.

Lewin, J.C. 1954. Silicon metabolism in diatoms. I. Evidence for the role of reduced sulfur compounds in silicon utilization *J. Gen. Physiol.* 37: 589-599.

Lewis, J.S. 1995. *Physics and chemistry of the solar system. Academic Press, San Diego, California.* Academic Press, San Diego, California.

Lewis, K.M., P.D. Sackett, and R.A. Mardling. 2008. Possibility of detecting moons of pulsar planets through time-of-arrival analysis. *Astrophys. J.* 685: L153-L156.

Lilly, J. 1978. *Communication between Man and Dolphin: The Possibilities of Talking with Other Species*. Crown Publishers, New York.

Limaye, S. S., R. Mogul, D. J. Smith, A. H. Ansari, G. P. Slowik, and P. Vaishampayan. 2018. Venus’ Spectral Signatures and the Potential for Life in the Clouds. *Astrobiology* 18: doi:https://doi.org/10.1089/ast.2011.9270.

Lin, X., A. C. Yu, and T. F. Chan. 2017. Efforts and challenges in engineering the genetic code. *Life (Basel)* 7: doi:https://doi.org/10.3390/life7010012.

Linde, A.D. 1986. Eternally existing self-reproducing chaotic inflanationary universe. *Physics Lett B* 175: 395-400.

Lineweaver, C.H., and T.M. Davis. 2002. Does the rapid appearance of life on Earth suggest that life is common in the universe? *Astrobiology* 2: 293-304.

Lineweaver, C.H., Y. Fenner and B.K. Gibson. 2004. The galactic habitable zone and the age distribution of complex life in the Milky Way. *Science* 303: 59-62.

Linn, N. 2001. Molecular visualization using methods of computational chemistry. *Summer Ventures in Science and Mathematics*. University of North Carolina at Charlotte.

Lipps, J.H., G. Delory, J. Pitman, and S. Rieboldt. 2004. Astrobiology of Jupiter's icy moons. *SPIE USE* 2: 5555-5510.

Lipps, J., and D. Schulze-Makuch. 2008. Origin of life in ice: prospects for the solar system and beyond. *Astrobiology* 8: 345.

Lisney, T.J., and S.P. Collin. 2006. Brain morphology in large pelagic fishes: a comparison between sharks and teleosts. *Journal of Fish Biology* 68: 532-554.

Liu, M.C., E.A. Magnier, N.R. Deacon, K.N. Allers, T.J. Dupuy, et al. 2013. The extremely red, young L dwarf PSO J318.5338–22.8603: a free-floating planetary-mass analog to directly imaged young gas-giant planets. *Astrophys. J. Lett.* 777: 2, L20; doi: https://doi.org/10.1088/2041-8205/777/2/L20.

Liu, R., and L.E. Orgel. 1997. Oxidative acylation using thioacids. *Nature* 389: 52-54.

Liu, S., Y. Zhao, J.W. Parks, D. Deamer, A.R. Hawkins, et al. 2014. Correlated electrical and optical analysis of single nanoparticles and biomolecules on a nanopore-gated optofluidic chip. *Nano Lett.* 14: 4816–4820.

Llorca, J. 1998. Gas-grain chemistry of carbon in interplanetary dust particles; kinetics and mechanism of hydrocarbon formation. p. 29. *29th Lunar and Planetary Science Conference*.

Loeffler, M. J., and R. L. Hudson. 2015. Descent without modification? The thermal chemistry of H_2O_2 on Europa and other icy worlds. *Astrobiology* 15: 453-61.

Loff, S and B. Dunbar. 2017. *CubeSats*. NASA, 3 Aug 2017 [cited 17 Jan 2018]. Available from https://www.nasa.gov/mission_pages/cubesats/index.html.

Lofftus, K.D., M.S. Quinby-Hunt, A.J. Hunt, et al. 1992. Light scattering by Prorocentrum micans: a new method and results. *Applied Optics* 31: 2924-2931.

Long, D.A. 2002. *The Raman Effect: A Unified Treatment of the Theory of Raman Scattering by Molecules*. John Wiley and Sons Ltd, Chichester, U.K.

Lopez-Archilla, A.I., I. Marin and R. Amils. 2001. Microbial community composition and ecology of an acidic aquatic environment: The Tinto River, Spain. *Microbiol. Ecol.* 41: 20-35.

Lorenz, M.G., and W. Wackernagel. 1987. Adsorption of DNA to sand and variable degradation rates of adsorbed DNA. *Applied Environmental Microbiology* 53: 2948-2952.

Lorenz, R.D. 1993. The surface of Titan in the context of the ESA Huygens probe. *ESA J* 17: 275-292.

Lorenz, R.D., and J.I. Lunine. 1997. Titan's surface reviewed: the nature of bright and dark terrain. *Planet. Space Sci.* 45: 981-992.

Lorenz, R.D. 2000. Post-Cassini exploration of Titan: science rationale and mission concepts. *JBIS* 53: 218-234.

Lorenz, R.D., E. Kraal, E. Asphaug, et al. 2003. The seas of Titan. *EOS Transactions AGU* 84: 131-132.

Lorenz, R.D., B.W. Stiles, R.L. Kirk, M.D. Allison, et al. 2008. Titan's rotation reveals an internal ocean and changing zonal winds. *Science* 319: 1649-1651.

Lovelock, J.E. 1965. A physical basis for life detection experiments. *Nature* 207: 568-570.

Lovelock, J.E. 1979. *Gaia: A New Look at Life on Earth*. Oxford University Press, Oxford.

Lovelock, J.E. 1995. New statements on the Gaia theory. *Microbiologia*. 11: 295-304.

Lovelock, J.E. 2000. The Gaia hypothesis in L. Margulis, C. Matthews and A. Haselton, eds. *Environmental Evolution*. MIT Press, Cambridge, Massachusetts, pp. 1-28.

Lovley, D.R., E.J.P. Philipps and D.J. Lonergan. 1989. Hydrogen and formate oxidation coupled to dissimilatory reduction of iron or manganese by Alteromonas putrefaciens. *Appl. Environ. Microbiol.* 55: 700-706.

Lovley, D.R. 1991. Dissimilatory Fe(III) and Mn(IV) reduction. *Microbiol. Rev.* June: 259-287.

Lowenstein, T. 2006. Tracking changes in the chemistry of ancient seawater: mammal blood, salt, and sea shells. Presentation at the University of Idaho, Moscow, ID.

Lozneanu, E., and M. Sanduloviciu. 2003. Minimal-cell system created in laboratory by self-organization. *Chaos, Solitons and Fractals* 18: 335-343.

Luef, B., K. R. Frischkorn, K. C. Wrighton, H. Y. Holman, et al. 2015. Diverse uncultivated ultra-small bacterial cells in groundwater. *Nature Commun.* 6: 6372; doi: https://doi.org/10.1038/ncomms7372.

Luisi, P.L. 1979. Why are enzymes macromolecules? *Naturwissenschaften* 66: 498-504.

Luisi, P.L. 2003a. Autopoiesis: a review and a reappraisal. *Naturwissenschaften* 90: 49-59.

Luisi, P.L. 2003b. Contingency and determinism. *Philos Transact A Math Phys Eng Sci* 361: 1141-1147.

Luisi, P.L., F. Ferri and P. Stano. 2006. Approaches to semi-synthetic minimal cells: a review. *Naturwissenschaften* 93: 1-13.

Lunine, J.I., D.J. Stevenson and Y.L. Yung. 1983. Ethane ocean on Titan. *Science* 222: 1229-1230.

Lunine, J.I., Y.L. Yung and R.D. Lorenz. 1999. On the volatile inventory of Titan from isotopic substances in nitrogen and methane. *Planetary Space and Science* 47: 1291-1303.

Lwoff, A. 1962. *Biological Order*. M.I.T. Press, Cambridge.

Maccone, C. 2009. *Deep Space Flight and Communications: Exploiting the Sun as a Gravitational Lense.* Springer-Praxis.

MacKenzie, A.S., S.C. Brassell, G. Eglinton, et al. 1982. Chemical fossils: the geological fate of steroids. *Science* 217: 491-504.

Madigan, M.T. and B.L. Marrs. 1997. Extremophiles. *Sci. Am.* 276: 82-87.

Madigan, M.T. and A. Oren. 1999. Thermophilic and halophilic extremophiles. *Curr. Opin. Microbiol.* 2: 265-269.

Madigan, M.T., J.M. Martinko and J. Parker. 2000. Brock Biology of Microorganisms. Prentice Hall, Upper Saddle River, NJ

Madison, L.L. and G.W. Huisman, 1999. Metabolic engineering of poly (3-hydroxyalkanoates): from DNA to plastic. *Microbiol. Mol. Biol. Rev*. 63: 21-53.

Majeau, C., E. Agol, and N.B. Cowan. 2012. A two-dimensional infrared map of the extrasolar planet HD 189733b. *Astrophys. J. Lett.* 747: L20.

Malin, M.C., and K.S. Edgett. 2000a. Evidence for recent groundwater seepage and surface runoff on Mars. *Science* 288: 2330-2335.

Malin, M.C., and K.S. Edgett. 2000b. Sedimentary rocks of early Mars. *Science* 290: 1927-1937.

Malin, M.C., K.S. Edgett, L.V. Posiolova, et al. 2006. Present-day impact cratering rate and contemporary gully activity on Mars. *Science* 314: 1573-1577.

Malyshev, D. A., K. Dhami, T. Lavergne, T. Chen, et al. 2014. A semi-synthetic organism with an expanded genetic alphabet. *Nature* 509: 385-388.

Mancinelli, P.L., and M. Klovstad. 2000. Martian soil and UV radiation: microbial viability assessment on spacecraft surfaces. *Planet. Space Sci.* 48: 1093-1097.

Mancinelli, R.L. 1989. Peroxides and the survivability of microorganisms on the surface of Mars. *Adv. Space Res.* 9: 6191-6195.

Mandell, A.M., S.N. Raymond, S. Sigurdsson. 2007. Formation of Earth-like planets during and after giant planet migration. *Astrophys. J.* 660: 823-844.

Manuel A.S. Santos, Mick F. Tuite. 1995. The CUG codon is decoded in vivo as serine and not leucine in Candida albicans. *Nucleic Acids Research* 23(9): 1481–1486.

Marcano, V., P. Benitez and E. Palacios-Pru. 2002. Growth of a lower eukaryote in non-aromatic hydrocarbon media > C-12 and its exobiological significance. *Planet. Space Sci.* 50: 693-709.

Marchant, J., A.T. Da Vison and G.J. Kelly. 1991. UV-B protecting compounds in the marine alga *Phaeocystis pouchetti* from Antarctica. *Marine Biol.* 109: 391-395.

Marcy, G.W., and R.P. Butler. 1996. A planetary companion to 70 Virginis. *Astrophysical Journal* 464: L147-L151.

Marcy, G.W., and R.P. Butler. 1998. Detection of extrasolar giant planets. *Annu. Rev. Astron. Astrophys.* 36: 57-97.

Margulis, L., and D. Sagan. 1995. *What Is Life?* Simon & Schuster, New York.

Margulis, L. 1998. *Symbiotic planet.* Sciencewriters, Brockman, Inc., Amherst, Massachusetts.

Marion, G., and D. Schulze-Makuch. 2006. Astrobiology and the search for life in the universe. pp. 351-358 in C. Gerday and N. Glansdorff, eds. *Physiology and Biochemistry of Extremophiles, Ch. 26.* ASM Press.

Marion, G.M., C.H. Fritsen, H. Eicken, et al. 2003. The search for life on Europa: Limiting environmental factors, potential habitats, and Earth analogues. *Astrobiology* 3: 785-811.

Marois, C., B. Macintosh, T. Barman, B. Zuckerman, et al. 2008. Direct imaging of multiple planets orbiting the star HR 8799. *Science* 322: 1348-1352.

Marshall, C.R. 2006. Explaining the Cambrian "explosion" of animals. *Ann. Rev. Earth Planet. Sci* 34: 355-384.

Martin, W., J. Baross, D. Kelley, and M. J. Russell. 2008. Hydrothermal vents and the origin of life. *Nat. Rev. Microbiol.* 6: 805-814.

Martin D. Brasier, Richard Matthewman, Sean McMahon, David Wacey, (2011) Pumice as a Remarkable Substrate for the Origin of Life. Astrobiology 11 (7):725–735

Martins, R.F., W. Davids and W.A. Al-Sond et al. 2001. Starch-hydrolyzing bacteria from Ethiopian soda lakes. *Extremophiles* 5: 135-144.

Mastrapa, R.M.E., H. Glanzberg, J.N. Head, et al. 2001. Survival of bacteria exposed to extreme acceleration: implications for panspermia. *Earth Planet. Sci. Lett.* 189: 108.

Mastrobuono-Battisti, A., H. B. Perets, and S. N. Raymond. 2015. A primordial origin for the compositional similarity between the Earth and the Moon. *Nature* 52: 212-215.

Mathies, R.A., M.E. Razu, J. Kim, A.M. Stockton, P. Turin, et al. 2017. Feasibility of detecting bioorganic compounds in Enceladus plumes with the Enceladus Organic Analyzer. *Astrobiology* 17: 902-912.

Matthew O. Schrenk, K. J. Edwards, Robert Hamers, Jillian F. Banfield, (1998) Distribution of thiobacillus ferrooxidans and leptospirillum ferrooxidans: implications for generation of acid mine drainage. Science 279: 1519-22.

Matson, D.L., and D.L. Blaney. 1999. Io. pp. 357-376 in P.R. Weissman, McFadden L.-A. and T.V. Johnson, eds. *Encyclopedia of the Solar System.* Academic Press, New York.

Matthewman, R., R.W. Court, I.A. Crawford, A.P. Jones, K.H. Joy, et al. 2015. The Moon as a recorder of organic evolution in the early Solar System: a lunar regolith analog study. *Astrobiology* 15: 154-168.

Matthews, C.N., and R.E. Moser. 1966. Prebiological protein synthesis. *Proc. Natl. Acad. Sci. USA* 56: 1087-1094.

Mattimore, V., and J.R. Battista. 1996. Radioresistance of *Deinococcus radiodurans*: Functions necessary to survive prolonged desiccation. *J. Bacteriol.* 178: 633-637.

Maturana, H.R. and F.J. Varela. 1981. Autopoiesis and cognition: the realization of the living. *Boston Studies in the Philosophy of Science*. D. Reidel, Boston.

Maude, A.D. 1963. Life in the Sun. in I.J. Good, ed. *The Scientist Speculates*. Basic Books, New York.

Maurer, S. E., D. W. Deamer, J. M. Boncella, and P. A. Monnard. 2009. Chemical evolution of amphiphiles: glycerol monoacyl derivatives stabilize plausible prebiotic membranes. *Astrobiology* 9: 979-987.

Maurer, S. E. and G. Nguyen. 2016. Prebiotic vesicle formation and the necessity of salts. *Orig. Life Evol. Biosph.* 46: 215-22.

Maxka, J., L.M. Huang and R. West. 1991. Synthesis and NMR spectroscopy of per-methylpolysilane oligomers Me(SiMe2)10Me, Me(SiMe2)16Me, and Me(Me2Si)22. *Organimetallics* 10: 656-659.

Mayor, M., and D. Queloz. 1995. A Jupiter-mass companion to a solar-type star. *Nature* 378: 355-359.

Mazur, P. 1980. Limits to life at low temperatures and at reduced water contents and water activities. *Orig. Life Evol. Biosph.* 10: 137-159.

McBrearty, S., and A.S. Brooks. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J Hum Evol* 39: 453-563.

McClendon, J.H. 1999. The origin of life *Earth Science Rev* 47: 71-93.

McCollom, T.M. 1999. Methanogenesis as a potential source of chemical energy for primary biomass production by autotrophic organisms in hydrothermal systems on Europa. *J. Geophys. Res.-Planets* 104: 30729-30742.

McCord, T. B., G. B. Hansen, F. P. Fanale, R. W. Carlson, D. L. Matson, T. V., Granahan, et al. 1998. Salts on Europa's surface detected by Galileo's near infrared mapping spectrometer. The NIMS Team [see comments]. *Science* 280: 1242-1245.

McCubbin, F. M., A. Steele, E. H. Hauri, H. Nekvasil, S. Yamashita, and R. J. Hemley. 2010. Nominally hydrous magmatism on the Moon. *Proc. Natl. Acad. Sci. USA* 107: 11223-8.

McEwen, A. S., L. Keszthelyi, J. R. Spencer, G. Schubert, et al. 1998. High-temperature silicate volcanism on Jupiter's moon Io. *Science* 281: 87-90.

McKay, C. P. 2016. Titan as the Abode of Life. *Life (Basel)* 6 (1): doi https://doi.org/10.3390/life6010008.

McKay, C.P. and W.L. Davis. 1999. Planets and the origin of life. pp. 899-922 in P.R. Weissman, McFadden L.-A. and T.V. Johnson, eds. *Encyclopedia of the Solar System*. Academic Press, New York.

McKay, C.P., C.C. Porco, T. Altheide, W.L. Davis, and T.A. Kral. 2008. The possible origin and persistence of life on Enceladus and detection of biomarkers in the plume. *Astrobiology* 8: 909-919.

McKay, C.P. and H.D. Smith. 2005. Possibilities for methanogenic life in liquid methane on the surface of Titan. *Icarus* 178: 274-276.

McKay, D.S., K.G. Everett, K.L. Thomas-Keprta, et al. 1996. Search for past life on Mars: possible relic biogenic activity in Martian Meteorite ALH84001. *Science* 273: 924-930.

McKay, D.S., S.J. Clemett, K.L. Thoomas-Keprta, et al. 2006. Analysis of in situ carbonaceous matter in martian meteorite Nakhla. *Astrobiology* 6: 184.

McKay, C.P., A.D. Anbar, C. Porco, and P. Tsou. 2014. Follow the plume: the habitability of Enceladus. *Astrobiology* 14: 352-355.

McKinnon, W., and R.L. Kirk. 1999. Triton. pp. 405-434 in P.R. Weissman, McFadden L.-A. and T.V. Johnson, eds. *Encyclopedia of the Solar System*. Academic Press, New York.

McMahon, S., J. Parnell, and N.J. Blamey. 2016. evidence for seismogenic hydrogen gas, a potential microbial energy source on Earth and Mars. *Astrobiology* 16: 690-702.

Meckenstock, R.U., F. von Netzer, C. Stumpp, T. Lueders, A.M. Himmelberg, et al. 2014. Water inclusions in oil are microhabitats for microbial life. *Science* 345: 673–676.

Mee, A.J. 1934. *Physical chemistry*. William Heinemann, London, UK.

Meech, K.J., R. Weryk, M. Micheli, J.T. Kleyna, et al. 2017. A brief visit from a red and extremely elongated interstellar asteroid. *Nature* 552: 378-381.

Mehard, C.W., C.W. Sullivan, F. Azam, and B.E. Volcani. 1974. Role of silicon in diatom metabolism. IV. subcellular localization of silicon and germanium in Nitzschia alba and Cylindrotheca fusiformis. *Physiol. Plant.* 30: *265-272.* 30: 265-272.

Melim, L.A., K.M. Shinglman, P.J. Boston, et al. 2001. Evidence for microbial involvement in pool finger precipitation, Hidden Cave, New Mexico. *Geomicrobiol. J.* 18: 311-329.

Melosh, H.J. 1988. The rocky road to panspermia. *Nature* 332: 687-688.

Melosh, H.J. 2003. Exhange of meteorites (and life?) between stellar systems. *Astrobiology* 3: 207-215.

Méndez, A. 2015. Exoplanets Catalogue - Planetary Habitability Laboratory: University of Puerto Rico at Arecibo.[http://phl.upr.edu/projects/habitable-exoplanets-catalog/stats].

Méndez, A., D. Schulze-Makuch, and G. Nery. 2017. Habitability metrics for astrobiology. In *Astrobiological Science Conference (AbSciCon)*. Mesa, Arizona, USA, 24-28 April 2017.

Merck-Research-Labs. 1996. *The Merck index*. Whitehousestation, New Jersey.

Mileikowsky, C., F.A. Cucinotta, J.W. Wilson, et al. 2000. Risks threatening viable transfer of microbes between bodies in our solar system. *Planetary Space and Science* 48: 1107-1115.

Miller, P.S., K.B. McParland, K. Jayaraman, et al. 1981. Biochemical and biological effects of nonionic nucleic acid methylphosphonates. *Biochemistry* 20: 1874-1880.

Miller, R.F., R. Cloutier and S. Turner. 2003. The oldest articulated chondrichthyan from the Early Devonian period. *Nature* 425: 501-504.

Miller, S.L. 1953. A production of amino acids under possible primitive earth conditions. *Science* 117: 528-529.

Miller, S.L., and L.E. Orgel. 1974. *The Origins of Life on the Earth*. Prentice-Hall.

Miller, S.L., and A. Lazcano. 1996. The origin and early evolution of life: prebiotic chemistry, the pre-RNA world, and time. *Cell* 85: 793-799.

Mimura, K. and S. Toyama. 2005. Behavior of polycyclic aromatic hydrocarbons at impact shock: Its implication for survival of organic materials delivered to the early Earth. *Geochimic. Cosmochim. Acta* 69: 201-209.

Mischna, M.A., J.F. Kasting, A. Pavlov, et al. 2000. Influence of carbon dioxide clouds on early martian climate. *Icarus* 145: 546-554.

Mitchell, F.J., and W.L. Ellis. 1971. Surveyor III; bacterium isolated from lunar-retrieved TV camera. *Geochimica et Cosmochimica Acta* 2: 2721-2733.

Mitri, G., A.P. Showman, J.I. Lunine, et al. 2007. Hydrocarbon lakes on Titan. *Icarus* 186: 385-394.

Mitrofanov, I., D. Anfimov, A. Kozyrev, et al. 2002. Maps of subsurface hydrogen from the high-energy neutron detector, Mars Odyssey. *Science* 297: 78-81.

Mittlefehldt, D.W. 1994. ALH84001, a cumulate orthopyroxenite member of the Martian meteorite clan. *Meteoritics* 29: 214-221.

Miura, Y.N., K. Nagao, N. Sugiura, et al. 1995. Orthopyroxenite ALH84001 and shergottite ALH77005: Additional evidence for a martian origin from noble gases. *Geochim. Cosmochim. Acta* 59: 2105-2113.

Mix, L.J. 2015. Defending definitions of life. *Astrobiology* 15: 15-19.

Moeller, T. 1957. *Inorganic chemistry*. Wiley, New York.

Mojzsis, S.J., G. Arrhenius, K.D. McKeegan, et al. 1996. Evidence for life on Earth before 3,800 million years ago. *Nature* 384: 55-59.

Monnard, P.A., C.L. Apel, A. Kanavarioti, et al. 2002. Influence of ionic solutes on self-assembly and polymerization processes related to early forms of life: implications for a prebiotic aqueous medium. *Astrobiology* 2: 139-152.

Monnard, P.-A., C.L. Apel, A. Kanavarioti, and D.W. Deamer. 2004. Influence of ionic inorganic solutes on self-assembly and polymerization processes related to early forms of life: implications for a prebiotic aqueous medium. *Astrobiology* 2: 139-152.

Monnard, P.A., A. Kanavarioti and D.W. Deamer. 2003. Eutectic phase polymerization of activated ribonucleotide mixtures yields quasi-equimolar incorporation of purine and pyrimidine nucleobases. *J Am Chem Soc* 125: 13734-13740.

Monod, J. 1971. *Chance and Necessity*. Alfred A. Knopf, New York.

Morawietz, T., A. Singraber, C. Dellago, J. Behler. 2016. How van der Waals interactions determine the unique properties of water. *Proc. Natl. Acad. Sci. USA* 113: 8368-8373.

Moreau, C.S., C.D. Bell, R. Vila, et al. 2006. Phylogeny of the ants: diversification in the age of angiosperms. *Science* 312: 101-104.

Moreno, A., A. Fernandez and A. Etxeberria. 1990. Cybernetics, autopoiesis and definition of life. pp. 357-364 in Trappl. R, ed. *Cybernetics and Systems'90. pp 357-364*. Singapur: World Scientific, Singapur.

Moreno, M.A. 1988. Microorganism transport from Earth to Mars *Nature* 336: 209.

Morgan, T.H. 1915. Localization of the Hereditary Material in the Germ Cells. *Proc. Natl. Acad. Sci. USA* 1: 420-429.

Moriyama, Y., S. Hiyama and H. Asai. 1998. High-speed video cinematographic demonstration of stalk and zooid contraction of *Vorticella convallari*. *Biophys. J.* 74: 487-491.

Morowitz, H.J. 1968. *Energy Flow in Biology*. Academic Press, New York.

Morowitz, H. 2011. Life on Venus. *Astrobiology* 11: 931-932.

Morowitz, H. and C. Sagan. 1967. Life in the clouds of Venus? *Nature* 215: 1259-1260

Morris, R. V., S. W. Ruff, R. Gellert, D. W. Ming, et al. 2010. Identification of carbonate-rich outcrops on Mars by the Spirit rover. *Science* 329: 421-424.

Moskowitz, C. 2014. Surf's up on Titan. *Sci. Am.* 310 (6): 20.

Mueller, U.G., S.A. Rehner and T.R. Schultz. 1998. The evolution of agriculture in ants. *Science* 281: 2034-2038.

Mueller, V., R. Spanheimer and H. Santos. 2005. Stress response by solute accumulation in Archaea. *Curr. Opinion Microbiol.* 8: 729-736.

Muench, A.A., J. Alves, C.J. Lada, et al. 2001. Evidence for circumstellar disks around young brown dwarfs in the Trapezium cluster. *Astrophys. J.* 558: L51-54.

Muller, A.W.J. 1985. Thermosynthesis by biomembranes: energy gain from cyclic temperature changes. *J. Ther. Biol.* 115: 429-453.

Muller, A.W.J. 1993. A mechanism for thermosynthesis based on a thermotropic phase transition in an asymmetric biomembrane. *Physiol. Chem. Phys. Med. NMR* 25: 95-111.

Muller, A.W.J. 1995. Were the first organisms heat engines ? - a new model for biogenesis and the early evolution of biological energy conversion. *Prog. Biophys. Molec. Biol.* 63: 193-231.

Muller, A. W. 2003. Finding extraterrestrial organisms living on thermosynthesis. *Astrobiology* 3: 555-564.

Muller, A.W.J., and D. Schulze-Makuch. 2006a. Thermal energy and the origin of life. *Orig. Life Evol. Biosph.* 36: 177-189.

Muller, A.W.J., and D. Schulze-Makuch. 2006b. Sorption heat engines: simple inanimate negative entropy generators. *Physica A* 362: 369-381.

Muller, T., W. Zilche and N. Auner. 1998. Recent advances in the chemistry of Si-heteroatom multiple bonds. pp. 857-1062 in Z. Rappoport and Y. Apeloig, eds. *The Chemistry of Organic Silicon Compounds*. John Wiley & Sons, Chichester, UK.

Mumma, M.J., R.E. Novak, M.A. DiSanti, et al. 2004. Detection and mapping of methane and water on Mars. *Bull. Amer. Astronom. Soc.* 36: 1127.

Munsell, K. and K. Erickson. 2017. *InSight . . . into the early evolution of terrestrial planets*, 3 Nov 2017 [cited 17 Jan 2018]. Available from https://insight.jpl.nasa.gov/home.cfm.

Musso, P. 2012. The problem of active SETI: an overview. *Acta Astronautica* 78: 43-54.

Mykytczuk, N.C.S, S.J. Foote, C.R. Omelon, G. Southham, C.W. Greer, et al. 2013. Bacterial growth at -15°C; molecular insights from the permafrost bacterium *Planococcus halocryophilus* Or1. *ISME J.* 7:1211-1226.

Nadeau, J., C. Lindensmith, J. W. Deming, V. I. Fernandez, and R. Stocker. 2016. Microbial morphology and motility as biosignatures for outer planet missions. *Astrobiology* 16: 755-774.

Nakasone, K., A. Ikegami, C. Kato, et al. 1998. Mechanisms of gene expression controlled by pressure in deep-sea microorganisms. *Extremophiles* 2: 149-154.

Narita, N., T. Enomoto, S. Masaoka, and N. Kuskabe. 2015. Titania may produce abiotic oxygen atmospheres on habitable exoplanets. *Sci. Repts.* 5: #13977.

Navarro-González, R., K.F. Navarro, J. de la Rosa, E. Iñiguez, P. Molina, et al. 2006. The limitations on organic detection in Mars-like soils by thermal volatilization-gas chromatography-MS and their implications for the Viking results. *Proc. Natl. Acad. Sci. USA* 103: 16089-16094.

Navarro-González, R., E. Vargas, J. de la Rosa, A.C. Raga, and C.P. McKay. 2010. Reanalysis of the Viking results suggests perchlorate and organics at midlatitudes on Mars. *JGR-Planets* 115: E12, doi: https://doi.org/10.1029/2010JE003599.

Nealson, K. 2006. Lakes of liquid CO_2 in the deep sea. *Proc. Natl. Acad. Sci. USA* 103: 13903-13904.

Nealson, K.H. 1997. The limits of life on Earth and searching for life on Mars. *J. Geophys. Res.* 102: 23675-23686.

Needham, D.H. and D.A. Kring. 2017. Lunar volcanism produced a transient atmosphere around the ancient Moon. *Earth Planet. Sci. Lett.* 478: 175-178.

Neidhardt, F.C., J.L. Ingraham and M. Schaechter. 1990. *Physiology of the bacterial cell. A molecular approach. Sinauer Associates, Inc. Sunderland, Mass.* Sinauer Associates, Inc., Sunderland, Mass.

Neubauer, R.L. 2012. *Evolution and the Emergent Self: The Rise of Complexity and Behavioral Versatility in Nature.* New York: Columbia University Press.

Newcomb, T.G., and L.A. Loeb. 1998. Oxidative DNA damage and mutagenesis. pp. 65-68 in J.A. Nickoloff and M.F. Hoekstra, eds. *DNA Repair in Prokaryotes and Lower Eukaryotes*. Humana, Totowa, NJ.

Nicholson, W. L., K. Krivushin, D. Gilichinsky, and A. C. Schuerger. 2013. Growth of *Carnobacterium* spp. from permafrost under low pressure, temperature, and anoxic atmosphere has implications for Earth microbes on Mars. *Proc. Natl. Acad. Sci. USA* 110: 666-671.

Nicholson, W.L., N. Munakata, G. Horneck, et al. 2000. Resistance of Bacillus endospores to extreme terrestrial and extraterrestrial environments. *Microbiol. Molec. Biol. Rev.* 64 548-572.

Nicolini, C., A. Diaspro, M. Bertolotto, et al. 1991. Biochemical and Biophysical Research Communications *Biochemical and Biophysical Research Communications* 177: 1313-1318.

Nielsen, P.E. 1993. Peptide nucleic acid (PNA): a model structure for the primordial genetic material *Orig. Life Evol. Biosph.* 23: 323-327.

Nilsson, A. and L. G. Pettersson. 2015. The structural origin of anomalous properties of liquid water. *Nat. Commun.* 6: 8998; doi: https://doi.org/10.1038/ncomms9998.

Nilsson, G.E., and P.L. Lutz. 2004. Anoxia tolerant brains. *J. Cerebral Blood Flow Metabol.* 24: 475-486.

Nimmo, F., J. R. Spencer, R. T. Pappalardo, and M. E. Mullen. 2007. Shear heating as the origin of the plumes and heat flux on Enceladus. *Nature* 447: 289-291.

Nisbet, E.G., and N.H. Sleep. 2001. The habitat and nature of early life. *Nature* 409: 1083-1091.

Noack, L., D. Höning, A. Rivoldini, C. Heistracher, N. Zimov, et al. 2016. Water-rich planets: how habitable is a water layer deeper than on Earth? *Icarus* 277: 215-236.

Noffke, N., D. Christian, D. Wacey, and R. M. Hazen. 2013. Microbially induced sedimentary structures recording an ancient ecosystem in the ca. 3.48 billion-year-old Dresser Formation, Pilbara, Western Australia. *Astrobiology* 13: 1103-1124.

Noffke, N. 2015. Ancient sedimentary structures in the < 3.7 Ga Gillespie Lake Member, Mars, that resemble macroscopic morphology, spatial associations, and temporal succession in terrestrial microbialites. *Astrobiology* 15: 169-192.

Noren, C.J., S.J. Anthony-Cahill, M.C. Griffith, et al. 1989. A general method for site-specific incorporation of unnatural amino acids into proteins. *Science* 244: 182-188.

Noyola, J.P., S. Satyal, and Z.E. Musielak. 2014. Detection of exomoons through observation and radio emissions. *Astrophys. J.* 791: 25-47.

NRC. 2007. *The Limits of Organic Life in Planetary Systems*. National Research Council, National Academies Press, Washington, D.C.

Nuevo, M., S. N. Milam, S. A. Sandford, J. E. Elsila, and J. P. Dworkin. 2009. Formation of uracil from the ultraviolet photo-irradiation of pyrimidine in pure H2O ices. *Astrobiology* 9: 683-695.

Nussinov, M.D., Y.B. Chernyak and J.L. Ettinger. 1978. Model of the fine-grain component of martian soil based on Viking lander data. *Nature* 274: 859-861.

O'Brien, D. P, B. J. Travis, W. C. Feldman, M. V. Sykes, P. M. Schenk, S. Marchi, C. T. Russell, and C. A. Raymond. 2015. The potential for volcanism on Ceres due to crustal thickening and pressurization of a subsurface ocean. In *46th Lunar and Planetary Science Conference, p. 2831*.

Obe, G., C. Johannes and D. Schulte-Frohlinde. 2001. DNA double-strand breaks induced by sparsely ionizing radiation and endonucleases as critical lesions for cell death, chromosomal aberrations, mutations and oncogenic transformation. *Mutagenesis* 7: 3-12.

Ojha, L., M.-B. Wilhelm, S.L. Murchie, A.S. McEwen, J.J. Wray, et al. 2015. Spectral evidence for hydrated salts in recurring slope lineae on Mars. *Nature Geosci.* 8: 829-832.

Olive, K.A., and Y.-Z. Quian. 2004. Were fundamental constants different in the past? *Physics Today*: 40-45.

Olsen, T.M., and J.G. Duman. 1997. Maintenance of the supercooled state in the gut fluid of overwintering pyrochroid beetle larvae, *Dendroides canadensis*: role of ice nu-cleators and antifreeze proteins. *J. Comp. Physiol. B* 167: 114-122.

O'Malley-James, J.T., Raven, J.A., Cockell, C.S., and Greaves, J.S. 2012. Life and light: exotic photosynthesis in binary and multiple-star systems. *Astrobiology* 12: 115-124.

Onstott, T.C., T.J. Phelps, F.S. Colwell, et al. 1999. Observations pertaining to the origin and ecology of microorganisms recovered from the deep subsurface of Taylorsville Basin, Virginia. *Geomicrobiology Journal* 14: 353-383.

Oparin, A.I. 1938. *Origin of Life*. Dover reprinted 1953, New York.

Orenberg, J.B., S. Chan, J. Calderon, et al. 1985. Soluble minerals in chemical evolution. I. Adsorption of 5'-AMP on CaSO4--a model system. *Orig. Life Evol. Biosph.* 15: 121-129.

Orgel, L.E. 1998. The origin of life – a review of facts and speculations. *Trends Biochem. Sci.* 23: 491-495.

Oro, J., T. Mills and A. Lazcano. 1992. Comets and the formation of biochemical compounds on the primitive Earth--a review. *Orig. Life Evol. Biosph.* 21: 267-277.

Orton, G.S. and P.A. Yanamandra-Fisher. 2005. Saturn's temperature field from high-resolution middle-infrared imaging. *Science* 307: 696-698.

Oyama, V.I. 1972. The gas exchange experiment for life detection: the Viking Mars lander. *Icarus* 16: 167-184.

Oyama, V.I., and B.J. Berdahl. 1977. The Viking gas exchange experiment results from Chryse and Utopia surface samples. *J. Geophys. Res.* 82: 4669-4676.

Oyama, V.I., B.J. Berdahl and G.C. Carle. 1977. Preliminary findings of the Viking gas exchange experiment and a model for Martian surface chemistry. *Nature* 265: 110-114.

Pace, C.N., S. Treviño, E. Prabhakaran, et al. 2004. Protein structure, stability and solubility in water and other solvents. *Phil. Trans. Roy. Soc. Lond. B.* 359: 1225-1235.

Paget, E., L. Jocteur-Monrozoir and P. Simonet. 1992. Adsorption of DNA on clay minerals: protection against DNaseI and influence on gene transfer *FEMS Microbiol. Lett.* 97: 31-40.

Palmer, M. Y., M. A. Cordiner, C. A. Nixon, S. B. Charnley, et al. 2017. ALMA detection and astrobiological potential of vinyl cyanide on Titan. *Sci. Adv.* 3: e1700022.

Pappalardo, R. T., J. W. Head, R. Greeley, R. J. Sullivan, C. Pilcher, G. Schubert, W. B. Moore, M. H. Carr, J. M. Moore, M. J. Belton, and D. L. Goldsby. 1998. Geological evidence for solid-state convection in Europa's ice shell. *Nature* 391: 365-368.

Parkinson, S.M., M. Wainwright and K. Killham. 1989. Observations on oligotrophic growth of fungi on silica gel. *Mycol. Res.* 93: 529-534.

Parnell, J., D. Cullen, M.R. Sims, S. Bowden, C.S. Cockell, et al. 2007. Searching for life on Mars: selection of molecular targets for ESA's Aurora ExoMars mission. *Astrobiology* 7: 578-604.

Parro, V., J.A. Rodríguez-Manfredia, C. Brionesa, C. Compostizob, P.L. Herrerob, et al. 2005. Instrument development to search for biomarkers on Mars: terrestrial acidophile, iron-powered chemolithoautotrophic communities as model systems. *Planet. Space Sci.* 53: 729-737.

Parro, V., G. de Diego-Castilla, J.A. Rodriguez-Manfredi, L.A. Rivas, Y. Blanco-Lopez, et al. 2011. SOLID3: a multiplex antibody microarray-based optical sensor instrument for in situ life detection in planetary exploration. *Astrobiology* 11: 15-28.

Pasek, M. A., J. P. Harnmeijer, R. Buick, M. Gull, and Z. Atlas. 2013. Evidence for reactive reduced phosphorus species in the early Archean ocean. *Proc. Natl. Acad. Sci. USA* 110: 10089-94.

Pasteris, J.D., B. Wopenka, J.W. Schopf, A.A. Kudryavtsev, G. David, et al. 2002. Images of Earth's earliest fossils? discussion and reply. *Nature* 420: 476-477.

Patel, M.R., A. Bérces, C. Kolb, et al. 2003. Seasonal and diurnal variations in Martian surface ultraviolet irradiation: biological and chemical implications for the Martian regolith. *Int. J. Astrobiology* 2: 21-34.

Patel, B. H., C. Percivalle, D. J. Ritson, C. D. Duffy, and J. D. Sutherland. 2015. Common origins of RNA, protein and lipid precursors in a cyanosulfidic protometabolism. Nat Chem 7: 301–7

Pawlenko, S. 1986. *Organosilicon Chemistry*. De Gruyter, Berlin.

Pedersen, K., and S. Ekendahl. 1990. Distribution and activity of bacteria in deep granitic groundwaters of southeastern Sweden. *Microb. Ecol.* 20: 37-52.

Pedersen, K. 2000. Exploration of deep intraterrestrial microbial life: current perspectives. *FEMS Microbiol Lett* 185: 9-16.

Pedersen, K., E. Nilsson, J. Arlinger, et al. 2004. Distribution, diversity and activity of microorganisms in the hyper-alkaline spring waters of Maqarin in Jordan. *Extremophiles* 8: 151-164.

Perakis, F., K. Amann-Winkel, F. Lehmkuhler, M. Sprung, et al. 2017. Diffusive dynamics during the high-to-low density transition in amorphous ice. *Proc. Natl. Acad. Sci. USA* 114: 8193-8198.

Perez, N., R. Cardenas, O. Martín, and M. Leiva Mora. 2013. The potential for photosynthesis in hydrothermal vents: A new avenue for life in the Universe? *Astrophys. Space Sci.* 346: 327-331.

Peters, K.E., C.C. Walters and J.M. Moldowan. 2004. *The Biomarker Guide, Vol. 1.* Cambridge University Press, Cambridge, U.K.

Peterson, K.J., J.B. Lyons, K.S. Nowak, et al. 2004. Estimating metazoan divergence times with a molecular clock. *Proc. Natl. Acad. Sci. USA* 101: 6536-6541.

Petit, C., and A. Sancar. 1999. Nucleotide excision repair: from *E. coli* to man. *Biochimie* 81 15-25.

Pfeffer, C., S. Larsen, J. Song, M. Dong, et al. 2012. Filamentous bacteria transport electrons over centimetre distances. *Nature* 491: 218-221.

Philip, G.K. and S.J. Freeland. 2011. Did evolution select a nonrandom "alphabet" of amino acids? *Astrobiology* 11: 235-240.

Phillips, T. 2014. Water Detected on Dwarf Planet Ceres. In *Science@NASA*, edited by T. Phillips.

Phoenix, V.R., K.O. Konhauser, D.G. Adams, et al. 2001. Role of biomineralization as an ultraviolet shield: Implications for Archean life. *Geology* 29: 823-826.

Pick, U. 1999. *Dunaliella acidophila* - a most extreme acidophilic alga. pp. 467-478 in J. Seckbach, ed. *Enigmatic Microorganisms and Life in Extreme Environments*. Kluwer, Dordrecht.

Pickett-Heaps, J., A.A.A. Schmid and L.A. Edgar. 1990. pp. 1-169 in F.E. Round and D.J. Chapman, eds. *Progress in Phycological Research 7*. Biopress, Bristol, UK.

Pierson, B.K., A. Oesterle and K. Murphy. 1987. Pigments, light penetrations, and pho-tosynthetic activity in the multi-layered microbial mats of Great Sippewissett Salt Marsh, Massachusetts. *FEMS Microbiol. Ecol.* 45: 365-376.

Pieters, C.M., J.N. Goswami, R.N. Clark, M. Annadurai, J. Boardman. 2009. Character and spatial distribution of OH/H_2O on the surface of the Moon seen by M3 on Chandrayaan-1. *Science* 326: 568-572.

Pitman, J., A. Duncan, D. Stubbs, R. Sigler, R. Kendrick, et al. 2004. Planetary remote sensing science enabled by MIDAS (Multiple Instrument Distributed Aperture Sensor). abstract #1454. *35th Lunar and Planetary Science Conference*, Houston, Texas.

Plaxco, K.W. and S.J. Allen. 2002. Life detection via tetrahertz circular dichroism spectroscopy. p. p. F6. *American Geophysical Union Fall Meeting* American Geophysical Union.

Pledger, R.J., B.C. Crump and J.A. Baross. 1994. A barophilic response by two hyperthermophilic, hydrothermal vent Archaea: an upward shift in the optimal temperature and acceleration of growth rate at supra-optimal temperatures by elevated pressure. *FEMS Microbiol. Ecol.* 14: 233-242.

Popa, R., A. R. Smith, R. Popa, J. Boone, and M. Fisk. 2012. Olivine-respiring bacteria isolated from the rock-ice interface in a lava-tube cave, a Mars analog environment. *Astrobiology* 12: 9-18.

Porco, C.C. 2017. A community grows around the geysering world of Enceladus. *Astrobioloy* 17: 815-819.

Porco, C.C., P. Helfenstein, P.C. Thomas, A.P. Ingersoll, J. Wisdom, et al. 2006. Cassini observes the active South Pole of Enceladus. *Science* 311: 1393-1401.

Potts, M. 1994. Desiccation tolerance of prokaryotes. *Microbial. Rev.* 58: 755-805.

Postberg, F., S. Kempf, J. Schmidt, N. Brilliantov, A. Beinsen, B. Abel, U. Buck, and R. Srama. 2009. Sodium salts in E-ring ice grains from an ocean below the surface of Enceladus. *Nature* 459: 1098-101.

Postberg, F., G. Tobie, T. Dambeck. 2016. Under the sea of Enceladus. *Sci. Am.*315 (4): 38-45.

Prat, L., I. U. Heinemann, H. R. Aerni, J. Rinehart, P. O'Donoghue, D. Soll. 2012. Carbon source-dependent expansion of the genetic code in bacteria. *Proc. Natl. Acad. Sci. USA* 109: 21070-21075.

Preiss, L., D. Hicks, S. Suzuki, T. Meier, and T. Krulwich. 2015. Alkaliphilic bacteria with impact on industrial applications, concepts of early life forms, and bioenergetics of ATP synthesis. *Front. Bioengin. Biotechnol.* 3: 75.

Price, P.B., and T. Sowers. 2004. Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proc. Natl. Acad. Sci. USA* 101: 4631-4636.

Price, P.B. 2010. Microbial life in Martian ice: a biotic origin of methane on Mars? *Planet. Space Sci.* 58: 1199-1206.

Prince, R. C. 1993. Petroleum spill bioremediation in marine environments. *Crit Rev. Microbiol.* 19 (4): 217-42.

Pritchard, P. 1979. *Encyclopedia of Turtles*. T.F.H., Jersey City, NJ.

Pross, A. 2004. Causation and the origin of life. Metabolism or replication first? *Orig. Life Evol. Biosph.* 34: 307-321.

Purves, W.K., G.H. Orians, H.C. Heller, et al. 1998. *Life: The science of biology*. Sinauer Associates, Sunderland, MA.

Qiao, Y., M. Li, R. Booth, and S. Mann. 2016. Predatory behaviour in synthetic protocell communities. *Nature Chemistry*: doi:https://doi.org/10.1038/nchem.2617.

Quinn, R.C., and A.P. Zent. 1999. Peroxide-modified titanium dioxide: a chemical analog of putative Martian soil oxidants. *Orig. Life Evol. Biosph.* 29: 59-72.

Rahm, M., J. I. Lunine, D. A. Usher, and D. Shalloway. 2016. Polymorphism and electronic structure of polyimine and its potential significance for prebiotic chemistry on Titan. *Proc. Natl. Acad. Sci. USA* 113: 8121-8126.

Randall, L. 2015. *Dark Matter and the Dinosaurs; The Astounding Interconnectedness of the Universe*. 1st ed. New York: Harper Collins.

Raulin, F. 2008. Planetary science: Organic lakes on Titan. *Nature* 454: 587-589.

Raulin, F., and A. Bossard. 1985. Organic synthesis in gas phase and chemical evolution in planetary atmospheres. *Adv. Space Res.* 4: 75-82.

Raulin, F., P. Bruston, P. Paillous, et al. 1995. The low temperature organic chemistry of Titan's geofluid. *Adv. Space Res.* 15: 321-333.

Raveendran, P., Y. Ikushima and S.L. Wallen. 2005. Polar attributes of super-critical carbon dioxide. *Acc. Chem. Res.* 38: 478-485.

Raven, P.H., and G.B. Johnson. 1999. *Biology*. McGraw-Hill, Boston.

Reddy, P.M., and T.C. Bruice. 2003. Solid-phase synthesis of positively charged deoxynucleic guanidine (DNG) oligonecleotide mixed sequences. *Biorg. Med. Chem. Lett.* 13: 1281-1285.

Rees, M. 2001. *Our Cosmic Habitat*. Princeton University Press, Princeton, NJ.

Rein, H., Y. Fujii, and D.S. Spiegel. 2014. Some inconvenient truths about biosignatures involving two chemical species on Earth-like exoplanets. *Proc. Natl. Acad. Sci. USA* 111: 6871-6875.

Reinhard, C. T., S. L. Olson, E. W. Schwieterman, and T. W. Lyons. 2017. False negatives for remote life detection on ocean-bearing planets: lessons from the early Earth. *Astrobiology* 17: 287-297.

Remmert, H. 1982. The evolution of man and the extinction of animals. *Naturwissenschaften* 69: 524-527.

Rettberg, P., and L.J. Rothschild. 2002. Ultraviolet radiation in planetary atmospheres and biological implications. pp. 233-243 in Horneck G and Baumstark-Khan C., eds. *Astrobiology: the quest for the conditions for life.* Springer Publ., Berlin, Germany.

Reynolds, J.E. 1906. Recent advances in our knowledge of silicon and its relation to organised structures *Proc. R. Inst. GB* 19: 642-650.

Reznick, D.N., and C.K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution *Genetica* 112: 183-198.

Ribas, I., E. Bolmont, F. Selsis, A. Reiners, J. Leconte, et al. 2016. The habitability of Proxima Centauri b. *Astron. Astrophys.*596: A111.

Ricardo, A., M. A. Carrigan, A. N. Olcott, and S. A. Benner. (2004) Borate minerals stabilize ribose. Science 303 (5655):196-196

Richter, O. 1906. Zur Physiologie der Diatomeen. *Sitzber. Akad. Wiss. Wien, Math.-Naturw. Kl.* 115: 27-119.

Rios, A. C. and Y. Tor. 2012. Refining the genetic alphabet: a late-period selection pressure? *Astrobiology* 12: 884-91.

Rivkina, E.M., E.I. Friedmann, C.P. McKay, et al. 2000. Metabolic activity of permafrost bacteria below the freezing point. *Appl. Environ. Microbiol* 66: 3230-3233.

Roadcap, G.S, R.A. Sanford, Q. Jin, J.R. Pardinas, and C.M. Bethk. 2006. Extremely alkaline (pH > 12) ground water hosts diverse microbial community. *Ground Water* 44: 511-517.

Robbins, E.I., T.M. Rodgers, C.N. Alpers, et al. 2000. Ecogeochemistry of the subsurface food web at pH 0-2.5 in Iron Mountain, California, U.S.A. *Hydrobiologia* 433: 15-23.

Robinson, J.M. and J.A. Mikucki. 2016. Occupied and empty regions of the space of extremophile parameters. In *Habitability of the Universe Before Earth*, edited by R. Gordon. London, UK. Imperial College Press.

Rohde, R.A., and P.B. Price. 2007. A new habitat in glacial ice: metabolism by solid-state diffusion to isolated microbes. *Proc. Natl. Acad. Sci. USA* 104: 16592-16597.

Romanek, C.S., M.M. Grady, I.P. Wright, et al. 2002. Record of fluid-rock interactions on Mars from meteorite ALH84001. *Nature* 372: 655-657.

Romero, A. 2009. *Cave Biology: Life in Darkness*. Cambridge University Press.

Roth, L., J. Saur, K.D. Retherford, D.F. Strobel, P.D. Feldman, et al. 2014. Transient water vapor at Europa's south pole. *Science* 343: 171-174.

Rothschild, L.J. 1999. Microbes and radiation. pp. 551-562 in J. Seckbach, ed. *Enigmatic Microorganisms and Life in Extreme Environments*. Kluwer, Dordrecht.

Rothschild, L.J., and R.L. Macinelli. 2001. Life in extreme environments. *Nature* 409: 1092-1101.

Rothschild, L.J. 2007. Extremophiles: defining the envelope for the search for life in the universe. in R.E. Pudritz, P. Higgs and J. Stone, eds. *Planetary Systems and the Origins of Life*. Cambridge University Press.

Roya Saffary, Renu Nandakumar, Dennis Spencer, Frank T Robb, Joseph M Davila, Marvin Swartz, Leon Ofman, Roger J Thomas, Jocelyne DiRuggiero, (2002) Microbial survival of space vacuum and extreme ultraviolet irradiation: strain isolation and analysis during a rocket flight. FEMS Microbiology Letters 215 (1):163-168

Ruderman, M. 1974. Physics of dense matter. in C. Hansen, ed. Reidel Publiching Co., Dordrecht, The Netherlands.

Ruf, A., B. Kanawati, N. Hertkorn, Q. Z. Yin, et al. 2017. Previously unknown class of metalorganic compounds revealed in meteorites. *Proc. Natl. Acad. Sci. USA* 114: 2819-2824.

Ruff, S. W. and J. D. Farmer. 2016. Silica deposits on Mars with features resembling hot spring biosignatures at El Tatio in Chile. *Nat Commun* 7: 13554. doi: https://doi.org/10.1038/ncomms13554.

Rugnetta, M. 2016. Synthetic biology. *Encyclopedia Britannica Online*, https://www.britannica.com/science/synthetic-biology.

Rummel, J.D. and C.A Conley. 2017. Four Fallacies and an oversight: searching for Martian life. *Astrobiology* 17: 971-974.

Rumpho, M. E., J. M. Worful, J. Lee, K. Kannan, et al. 2008. Horizontal gene transfer of the algal nuclear gene psbO to the photosynthetic sea slug *Elysia chlorotica*. *Proc. Natl. Acad. Sci. USA* 105: 17867-17871.

Russell, M.J., and A.J. Hall. 1997. The emergence of life from monosulfide bubbles at a submarine hydrothermal redox and pH front. *J. Geol. Soc. London* 154: 377-402.

Russell, M.J., W. Nitschke, and E. Branscomb. 2013. The inevitable journey to being. *Phil. Trans. R. Soc. B* 368: 20120254.

Russell H. Vreeland, William D. Rosenzweig, Dennis W. Powers, (2000) Isolation of a 250 million-year-old halotolerant bacterium from a primary salt crystal. Nature 407 (6806):897-900

Ryan, C.S., and I. Kleinberg. 1995. Bacteria in human mouths involved in the production and utilization of hydrogen peroxide. *Arch. Oral. Biol.* 40: 753-763.

Rzonca, B., and D. Schulze-Makuch. 2002. Investigation of hydrothermal sources in the Rio Grande rift region. pp. 319-324. *53rd Field Conference, Geology of White Sands*. New Mexico Geological Society Guidebook.

Sagan, C. 1961. The planet Venus. *Science* 133: 849-858.

Sagan, C., E.R. Lippincott, M.O. Dayhoff, et al. 1967. Organic molecules and the coloration of Jupiter. *Nature* 213: 273-274.

Sagan, C., and E.E. Salpeter. 1976. Particles, environments, and possible ecologies in the jovian atmosphere. *Astrophys. J. Suppl. Ser.* 32: 624.

Sagan, C. 1994. The search for extraterrestrial life. *Sci. Am.* 271: 92-99.

Saeidi, N., C. K. Wong, T. M. Lo, H. X. Nguyen, et al. 2011. Engineering microbes to sense and eradicate *Pseudomonas aeruginosa*, a human pathogen. *Mol. Syst. Biol.* 7: 521; doi https://doi.org/10.1038/msb.2011.55.

Saladino, R., C. Crestini, S. Pino, G. Costanzo, and E. Di Mauro. 2012. Formamide and the origin of life. *Phys. Life Rev*. 9: 84-104.

Salama, F., L. J. Allamandola, F. C. Witteborn, D. P. Cruikshank, S. A. Sandford, and J. D. Bregman. 1990. The 2.5-5.0 micrometers spectra of Io: evidence for H_2S and H_2O frozen in SO_2. *Icarus* 83: 66-82.

Salama, F., L. J. Allamandola, S. A. Sandford, J. D. Bregman, F. C. Witteborn, and D. P. Cruikshank. 1994. Is H_2O present on Io? The detection of a new strong band near 3590 cm-1 (2.79 micrometers). *Icarus* 107: 413-7.

Salzman, G.C., J.K. Griffith and C.T. Gregg. 1982. Rapid identification of microorganisms by circular-intensity differential scattering. *Appl Environ. Microbiol.* 44: 1081-1085.

Samuels, A.L., and A.D.M. Glass. 1991. Distribution of silicon in cucumber leaves during infection by powdery mildew fungus (Sphaerotheca fulginea) *Can. J. Bot.* 69: 140-146.

Sandford, S. A. 2008. Terrestrial analysis of the organic component of comet dust. *Annu. Rev. Anal. Chem.* 1:549-78.

Sandford, S. A., and L. J. Allamandola. 1993. The condensation and vaporization behavior of ices containing SO_2, H_2S, and CO_2: implications for Io. *Icarus* 106: 478-88.

Sandford, S. A., J. Aleon, C. M. Alexander, T. Araki, et al. 2006. Organics captured from comet 81P/Wild 2 by the Stardust spacecraft. *Science* 314: 1720-4.

Sangster, A.G., and D.W. Parry. 1981. Ultrastructure of silica deposits in higher plants. pp. 383-408 in Simpson and Volcani, eds. *Silicon and Siliceous Structures in Biological Systems.* Springer Verlag, New York.

Sasselov, D.D. 2008. Astronomy: extrasolar planets. *Nature* 451: 29-31.

Sattler, B., H. Puxbaum and R. Psenner. 2001. Bacterial growth in supercooled cloud droplets. *Geophys. Res. Lett.* 28: 239-242.

Scharf, C., Virgo, N., Cleaves, J., Aono, M., Aubert-Kato, N., et al. 2015. A strategy for origins of life research. *Astrobiology* 15: 1031-1042.

Shekhtman, L., E. Landau, and C. Hoang. 2018. *Pluto - In Depth*. NASA 2018 [cited 27 June 2018]. Available from https://solarsystem.nasa.gov/planets/pluto/indepth.

Schenk, P. M. 2002. Thickness constraints on the icy shells of the galilean satellites from a comparison of crater shapes. *Nature* 417: 419-421.

Schidlowski, M., J.M. Hayes and I.R. Kaplan. 1983. Isotopic inferences of ancient biochemistry: carbon, sulfur, hydrogen, and nitrogen. pp. 149-186 in J.W. Schopf, ed. *Earth's earliest biosphere: its origin and evolution.* University Press, Princeton, NJ.

Schidlowski, M. 1988. A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* 333: 313-318.

Schieber, J., and H.J. Arnott. 2003. Nannobacteria as a by-product of enzyme-driven tissue decay *Geology* 31: 717-720.

Schleper, C., G. Pühler, B. Kühlmorgen, et al. 1995. Life at extremely low pH. *Nature* 375: 741-742.

Schlesinger, W.H. 1997. *Biogeochemistry*. Academic Press, New York, USA.

Schmidt, J., N. Brilliantov, F. Spahn, S. Kempf. 2008. Slow dust in Enceladus' plume from condensation and wall collisions in tiger stripe fractures. *Nature* 451: 685-8.

Schmidt-Nielsen, K., C.R. Taylor and A. Shkolnic. 1971. Desert snails: problems of heat, water and food. *J. Exp. Biol.* 55: 385-398.

Schmidt-Nielsen, K. 1990. *Animal Physiology: Adaptation and Environment*. Cambridge Univ. Press, p. 51, Cambridge, UK.

Schmitt, H. H. 2006. Ch. 4. Moon's origin and evolution: Alternatives and implications. In *Solar System Update*, edited by P. Blondel and J. W. Mason: Springer-Verlag.

Schoffstall, A.M., R.J. Barto and D.L. Ramo. 1982. Nucleoside and deoxynucleoside in formamide solutions. *Orig. Life Evol. Biosph.* 12: 143-151.

Schoffstall, A.M., and E.M. Liang. 1985. Phosphorylation mechanisms in chemical evolution. *Orig. Life Evol. Biosph.* 15: 141-150.

Schöning, K.-U., P. Scholz, W. Guntha, et al. 2000. Chemical etiology of nucleic acid structure: The alpha-threofuranosyl-(3'2') oligonucleotide system. *Science* 290: 1347-1351.

Schopf, J.W., and B.M. Packer. 1987. Early Archean (3.3 billion to 3.5 billion-year-old) microfossils from Warrawoona Group, Australia. *Science* 237: 70-73.

Schopf, J.W. 1993. Microfossils of the early Archean Apex Chert; new evidence of the antiquity of life. *Science* 260: 640-645.

Schopf, J.W. 1994. The oldest known records of life: early Archean stromatolites, microfossils, and organic matter pp. 193-206 in S. Bengtson, ed. *Early life of Earth.* Columbia Univ. Press, New York.

Schopf, J.W. 1999. *Cradle of Life: The Discovery of Earth's Earliest Fossils*. Princeton University Press, Princeton NJ.

Schopf, J. W., J. D. Farmer, I. S. Foster, A. B. Kudryavtsev, V. A. Gallardo, C. Espinoza. 2012. Gypsum-permineralized microfossils and their relevance to the search for life on Mars. *Astrobiology* 12: 619-33.

Schopf, J.W., A.B. Kudryavtsev, M.R. Walter, M.J. Van Kranendonk, K.H. Williford, et al. 2014. Sulfur-cycling fossil bacteria from the 1.8-Ga Duck Creek Formation provide promising evidence of evolution's null hypothesis. *Proc. Nat. Acad. Sci. USA* 112: 2087–2092.

Schreiber, U., O. Locker-Grütjen, and C. Mayer. 2012. Origin of life in deep-reaching tectonic faults. *Orig. Life Evol. Biosph.*: doi https://doi.org/10.1007/s11084-012-9267-4.

Schrenk, M.O., D.S. Kelley, J.R. Delaney, et al. 2003. Incidence and diversity of microorganisms within the walls of an active deep-sea sulfide chimney. *Appl. Environ. Microbiol.* 69: 3580-3592.

Schrödinger, E. 1944. *What is Life? The Physical Aspect of the Living Cell*. University Press, Cambridge.

Schuerger, A.C. and W.L. Nicholson. 2016. Twenty species of hypobarophilic bacteria recovered from diverse soils exhibit growth under simulated Martian conditions at 0.7 kPa. *Astrobiology* 16: 964-976.

Schuerger, A.C., R.L. Mancinelli, R.G. Kern, et al. 2003. Survival of *Bacillus subtilis* on spacecraft surfaces under simulated Martian environments: implications for the forward contamination of Mars. *Icarus* 165: 253-276.

Schultz, T.R. 2000. In search of ant ancestors. *Proc. Natl. Acad. Sci. USA* 97: 14028-14029.

Schulze-Makuch, D. 2002. At the crossroads between microbiology and planetology: a proposed iron cycle could sustain life in an ocean – and the ocean need not be on Earth. *ASM News* 68: 364-365.

Schulze-Makuch, D. 2003. Chemical and microbial composition of subsurface-, surface-, and atmospheric water samples in the southern Sacramento Mountains, New Mexico. p. 62. *New*

Mexico Geological Society Annual Spring Meeting. New Mexico Geological Society Socorro, New Mexico.

Schulze-Makuch, D. 2010. Io: Is Life Possible Between Fire and Ice? *Cosmology* 5: 912-919.

Schulze-Makuch, D. 2013. Organic molecules in lunar ice: a window to the early evolution of life on Earth. In *Habitability on other Planets and Satellites* edited by J. Seckbach and J.-P. d. Vera. Dordrecht, The Netherlands: Springer.

Schulze-Makuch, D. 2014. 100 million planets in our galaxy may harbor complex life. *Air & Space Smithsonian*, http://www.airspacemag.com/daily-planet/100-million-planets-our-galaxy-may-harbor-complex-life-180951598/#ixzz3904nYVjj.

Schulze-Makuch, D., and D.H. Grinspoon. 2005. Biologically Enhanced Energy and Carbon Cycling on Titan? *Astrobiology* 5: 560-567.

Schulze-Makuch, D. and L.N. Irwin. 2001. Alternative energy sources could support life on Europa. *EOS, Trans. Am. Geophys. Union* 82: 150.

Schulze-Makuch, D. and L.N. Irwin. 2002a. Energy cycling and hypothetical organisms in Europa's ocean. *Astrobiology* 2: 105-121.

Schulze-Makuch, D. and L.N. Irwin. 2002b. Reassessing the possibility of life on Venus: proposal for an astrobiology mission. *Astrobiology* 2: 197-202.

Schulze-Makuch, D., L.N. Irwin and H. Guan. 2002a. Search parameters for the remote detection of extraterrestrial life. *Planet. Space Sci.* 50: 675-683.

Schulze-Makuch, D., L.N. Irwin and T. Irwin. 2002b. Astrobiological relevance and feasibility of a sample collection mission to the atmosphere of Venus. pp. 247-250. *2nd European Workshop on Exo-Astrobiology (EANA/ESA)*,

Schulze-Makuch, D., Guan, H., Irwin, L.N., and Vega, E. 2002c. Redefining life: an ecological, thermodynamic, and bioinformatic approach. *Fundamentals of Life*. Elsevier SAS, Amsterdam, pp. 169-179.

Schulze-Makuch, D., O. Abbas, L.N. Irwin, et al. 2003. Microbial adaptation strategies for life in the Venusian atmosphere. *Astrobiology* 2: 506-507.

Schulze-Makuch, D. and L. N. Irwin. 2004. *Life in the Universe: Expectations and Constraints*: Springer-Verlag, 1st edition.

Schulze-Makuch, D., D.H. Grinspoon, O. Abbas, et al. 2004. A sulfur-based UV adaptation strategy for putative phototrophic life in the Venusian atmosphere. *Astrobiology* 4: 11-18.

Schulze-Makuch, D., L.N. Irwin, J.H. Lipps, D. LeMone, J.M. Dohm, and A.G. Fairén. 2005a. Scenarios for the evolution of life on Mars. *J. Geophys. Res. - Planets* 110:E12S23.

Schulze-Makuch, D., J.M. Dohm, A.G. Fairén, et al. 2005b. Venus, Mars, and the ices on Mercury and the moon: astrobiological implications and proposed mission designs. *Astrobiology* 5: 778-795.

Schulze-Makuch, D. and L.N. Irwin. 2006. Exotic forms of life in the universe. *Naturwissenschaften* 93: 155-172.

Schulze-Makuch, D., J.M. Dohm, C. Fan, et al. 2007. Exploration of hydrothermal targets on Mars. *Icarus* 189: 308-324.

Schulze-Makuch, D. and L. N. Irwin. 2008. *Life in the Universe: Expectations and Constraints*: Springer-Verlag, 2nd edition.

Schulze-Makuch, D., C. Turse, J.M. Houtkooper, et al. 2008. Testing the H_2O_2-H_2O hypothesis for life on Mars with the TEGA instrument on the Phoenix Lander. *Astrobiology* 8: 205-214.

Schulze-Makuch, D., A. Mendez, A. G. Fairén, P. von Paris et al. 2011. A two-tiered approach to assessing the habitability of exoplanets. *Astrobiology* 11:1041-1052.

Schulze-Makuch, D, B. Laval, and L.N. Irwin. 2012a. The rise of complexity: Pavilion Lake microbialites suggest a pathway toward macroorganismic communities. *Hypoth. Life Sci.* 2:55-59.

Schulze-Makuch, D., J.N. Head, J.M. Houtkooper, M. Knoblauch, R. Furfaro, et al. 2012b. The Biological Oxidant and Life Detection (BOLD) Mission: a proposal for a mission to Mars. *Planet. Space Sci.* 67: 57-69.

Schulze-Makuch, D. and J. Seckbach. 2013. Tardigrades, an example of multicellular extremophiles. In *Polyextremophiles*, edited by J. Seckbach, A. Oren and H. Stan-Lotter. Berlin: Springer.

Schulze-Makuch, D., A.G. Fairén, A. Davila. 2013a. Locally targeted ecosynthesis: a proactive in situ search for extant life on other worlds. *Astrobiology* 13: 774-778.

Schulze-Makuch, D., L. N. Irwin, and A. G. Fairén. 2013b. Drastic environmental change and its effects on a planetary biosphere. *Icarus* 225:275–280.

Schulze-Makuch, D. and J. M. Houtkooper. 2015. Is methanol the missing ingredient for the origin of life? In *EANA Astrobiology Meeting*. ESTEC, Netherlands.

Schulze-Makuch, D., A. Schulze-Makuch, and J. M. Houtkooper. 2015a. The physical, chemical and physiological limits of life. *Life (Basel)* 5: 1472-86.

Schulze-Makuch, D., J. Rummel, S. Benner, G. Levin, V. Parro, et. al. 2015b. Nearly forty years after Viking: Are we ready for a new life detection mission? *Astrobiology* 15: 413-419.

Schulze-Makuch, D. and E. Guinan. 2016. Another Earth 2.0 – Not so fast. *Astrobiology* 16: 817-821.

Schulze-Makuch, D., and W. Bains. 2017. *The Cosmic Zoo: Complex Life on Many Worlds*. Chichester, U.K.: Springer Praxis.

Schulze-Makuch, D., A. Airo, J. Schirmack, et al. 2017. The adaptability of life on Earth and the diversity of planetary habitats. *Front. Microbiol.* 8: 2011 (doi.org/10.3389/fmicb.2017.02011).

Schulze-Makuch, D., D. Wagner, S. P. Kounaves, K. Mangelsdorf, et al. 2018. Transitory microbial habitat in the hyperarid Atacama Desert. *Proc. Natl. Acad. Sci USA* 115: 2670-2675.

Schulze-Makuch, D. and I. Crawford. 2018. Was there an early habitability window for our Moon? *Astrobiology* 18: 985-988.

Schwartz, A.W. 1993. Biology and theory: RNA and the origin of life. pp. 323-344 in J.M. Greenberg, C.X. Mendoza-Gomez and V. Pirronello, eds. *The chemistry of life's origins.* Kluwer Acad. Publ.

Schwartz, R.N. and C.H. Townes. 1961. Interstellar and interplanetary communication by optical masers. *Nature* 190: 205-208.

Scully, J.E.C., C.T. Russell, A. Yin, R. Jaumann, E. Carey, et al. 2015. Geomorphological evidence for transient water flow on Vesta. *Earth Planet. Sci. Lett.* 411: 151-163.

Seager, S., W. Bains, and J. J. Petkowski. 2016. Toward a List of Molecules as Potential Biosignature Gases for the Search for Life on Exoplanets and Applications to Terrestrial Biochemistry. *Astrobiology* 16: 465-85.

Seager, S., E.L. Turner, J. Schafer, and E.B. Ford. 2005. Vegetation's Red Edge: a possible spectroscopic biosignature of extraterrestrial plants. *Astrobiology* 5: 372-390.

Searle, J. 1984. *Minds, Brains, and Science*. Harvard University Press, Cambridge, MA.

Segre, D. and D. Lancet. 2000. Composing life. *EMBO Rept.* 1: 217-222.

Segre, D., D. Ben-Eli, and D. Lancet. 2000. Compositional genomes: prebiotic information transfer in mutually catalytic noncovalent assemblies. *Proc. Natl. Acad. Sci. USA* 97: 4112-7.

Sekiguchi, A., R. Kinjo and M. Ichinohe. 2004. A stable compound containing a silicon-silicon triple bind. *Science* 305: 1755-1757.

Sellberg, J. A., C. Huang, T. A. McQueen, N. D. Loh, et al. 2014. Ultrafast X-ray probing of water structure below the homogeneous ice nucleation temperature. *Nature* 510: 381-384.

Sesselov, D.D. 2008. Extrasolar planets. *Nature* 451: 29-31.

Shapley, H. 1958. *Of Stars and Men*. Beacon Press, Boston.

Sharma, A., J.H. Scott, G.D. Cody, et al. 2002. Microbial activity at gigapascal pressures. *Science* 295: 1514-1516.

Sharma, H.K., and K.H. Pannell. 1995. Activation of the Si-Si bond by transition metal complexes. *Chem. Rev.* 95: 1351-1374.

Sharp, T.G., A.E. Goresy, B. Wopenka, et al. 1999. A post-stishovite SiO2 polymorph in the meteorite Shergotty: implications for impact events. *Science* 284: 1511-1513.

Shapiro, R.S. and D. Schulze-Makuch. 2009. The search for alien life in our solar system: strategies and priorities. *Astrobiology* 9: 335-343.

Sharp, Z. D., C. K. Shearer, K. D. McKeegan, J. D. Barnes, and Y. Q. Wang. 2010. The chlorine isotope composition of the moon and implications for an anhydrous mantle. *Science* 329: 1050-3.

shCherbak, V.I. and M.A. Makukov. 2013. The "Wow! signal" of the terrestrial genetic code. *Icarus* 224: 228-242.

Shihira-Ishikawa, I., and T. Nawata. 1992. The structure and physiological properties of the cytoplasm in intact Valonia cell. *Jpn. J. Phycol. (Sorui)* 40: 151-159.

Shin, K., R. Kumar, K. A. Udachin, S. Alavi, and J. A. Ripmeester. 2012. Ammonia clathrate hydrates as new solid phases for Titan, Enceladus, and other planetary systems. *Proc. Natl. Acad. Sci. USA* 109: 14785-14790.

Shkrob, I.A., and M.C. Sauer. 2001. Solvent anions in supercritical carbon dioxide: formation of complexes with polar solutes. *J. Phys. Chem. B* 105: 7027-7032.

Shock, E. L. and M. E. Holland. 2007. Quantitative habitability. *Astrobiology* 7: 839-851.

Shostak, S. 2015. Searching for clever life. Astrobiology 15: 949-950.

Showman, A.P., and R. Malhotra. 1999. The Galilean satellites. *Science* 286: 77-84.

Showstack, R. 1998. Lunar prospector finds signature for water ice on Moon, NASA announces *EOS, Trans. Am. Geophys. Union* 79: 138 -144.

Shuch, H.P. and I. Almár. 2007. Shouting in the jungle: the SETI transmission debate. *J. Brit. Interplanet.* Soc. 60: 142-146.

Sieger, M. T., W. C. Simpson, and T. M. Orlando. 1998. Production of O2 on icy satellites by electronic excitation of low-temperature water ice. *Nature* 394: 554-556.

Sittler, E.C., J.F. Cooper, P. Mahaffy, J. Esper, D. Fairbrother, et al. 2006. Titan Orbiter with Aerorover Mission (TOAM). *Proceedings of the 4th International Planetary Probe Workshop*, Pasadena, CA.

Slade. 1992. Mercury radar imaging: Evidence for polar ice. *Science* 258: 635-640.

Sleep, N.H. 1994. Martian plate tectonics. *J. Geophys. Res.* 99: 5639.

Sleep, N.H., and K. Zahnle. 1999. Vestiges of living at ground zero. *Abstracts with Programs – Geological Society of America* 31: 239-240.

Smith, B.A., and R.J. Terrile. 1984. A circumstellar disk around Beta-Pictoris. *Science* 226: 1421-1424.

Smith, D. J. 2013. Microbes in the upper atmosphere and unique opportunities for astrobiology research. *Astrobiology* 13: 981-990.

Smith, D.W. 1982. Extreme natural environments. pp. 555-574 in R.G. Burns and H.J. Slater, eds. *Experimental Microbial Ecology*. Blackwell Scientific Publications, Oxford.

Smith, K.C. 2004. Recombinational DNA repair: the ignored repair systems. *BioEssays* 26: 1322-1326.

Smith, D. J., D. A. Jaffe, M. N. Birmele, D. W. Griffin, et al. 2012. Free tropospheric transport of microorganisms from Asia to North America. *Microb. Ecol.* 64: 973-85.

Smrekar, S.E., E.R. Stofan, N. Mueller, A. Treiman, L. Elkins-Tanton, et al. 2010. Recent hotspot volcanism on Venus from VIRTIS emissivity data. *Science* 328: 605-608.

Sohl, F., A. Solomonidou, F. W. Wagner, A. Coustenis, H. Hussmann, et al. 2014. Structural and tidal models of Titan and inferences on cryovolcanism. *J. Geophys. Res. Planets* 119: 1013–1036.

Sohl, F., T. Spohn, D. Breuer, K. Nagel. 2002. Implications from Galileo observations on the interior structure and chemistry of the Galilean satellites. *Icarus* 157: 104-119.

Sojo, V., B. Herschy, A. Whicher, E. Camprubi, N. Lane. 2016. The Origin of Life in Alkaline Hydrothermal Vents. *Astrobiology* 16: 181-197.

Sowers, T. 2001. N_2O record spanning the penultimate deglaciation from the Vostok ice core. *J. Geophys. Res. Atmosph.* 106: 31,903-931,914.

Spahn, F., J. Schmidt, N. Albers, M. Horning, et al. 2006. Cassini dust measurements at Enceladus and implications for the origin of the E ring. *Science* 311: 1416-1418.

Sparks, W. B., J. Hough, T. A. Germer, F. Chen, et al. 2009. Detection of circular polarization in light scattered from photosynthetic microbes. *Proc. Natl. Acad. Sci. USA* 106: 7816-7821.

Special Regions Science Analysis Group. 2006. Findings of the Mars special regions science analysis group. *Astrobiology* 6: 677-673.

Special Regions Science Analysis Group. 2007. COSPAR Colloquium on Mars Special Regions held from September 11-13, Rome, Italy.

Speers-Roesch, B., J.W. Robinson and J.S. Ballantyne. 2006. Metabolic organization of the spotted ratfish, Hydrolagus colliei (Holocephali: Chimaeriformes): insight into the evolution of energy metabolism in the chondrichthyan fishes. *J. Exp. Zool. A Comp. Exp. Biol.* 305: 631-644.

Spencer, M. K. and R. N. Zare. 2007. Comment on "Organics captured from comet 81P/Wild 2 by the Stardust spacecraft". *Science* 317: 1680; author reply 1680.

Spencer, J.H. 1940. *Life on Other Worlds.* Hodder and Stoughton, London, UK.

Spencer, J.R., L.K. Tamppari, T.Z. Martin, et al. 1999. Temperatures on Europa from Galileo photopolarimeter-radiometer. *Temperatures on Europa from Galileo photopolarimeter-radiometer.* 284: 1514-1516.

Spencer, J.R., J.A. Rathbun, L.D. Travis, et al. 2000. Io's thermal emission from the Galileo photopolarimeter-radiometer. *Science* 288: 1198-1201.

Spencer, J.R., T.Z. Martin, J. Goguen, et al. 2001. Galileo PPR observations of the Galilean satellites. pp. 105-106. *Jupiter: Planets, Satellites & Magnetosphere*, Boulder Colorado.

Spohn, T., and G. Schubert. 2003. Oceans in the icy Galilean satellites of Jupiter? *Icarus* 161: 456-467.

Srivatsan, S.G. 2004. Modeling prebiotic catalysis with nucleic acid-like polymers and its implications for the proposed RNA world. *Pure Appl. Chem.* 76: 2085-2099.

Steele, A., D.S. McKay, C.C. Allen, K. Thomas-Keprta, D. Warmflash, et al. 2001. Mars Immunoassay Life Detection Instrument for Astrobiology (MILDI). *32nd Lunar and Planetary Science Conference, abstract # 1684*, Houston, Texas.

Steinbeck, C., and C. Richert. 1998. The role of ionic backbones in RNA structure: an unusual stable non-Watson-Crick duplex of a nonionic analog in an apolar medium. *J. Am. Chem. Soc.* 120: 11576-11580.

Stern, S. A., F. Bagenal, K. Ennico, G.R. Gladstone, et al. 2015. The Pluto system: Initial results from its exploration by New Horizons. *Science* 350: aad1815. (doi:https://doi.org/10.1126/science.aad1815).

Stetter, K.O. 1985. *Thermophilic archaebacteria occurring in submarine hydrothermal areas.* Van Nostrand Reinhold Co., New York.

Stetter, K.O. 1998. Hyperthermophiles and their possible role as ancestors of modern life pp. 315-335 in B. A., ed. *The Molecular Origins of Life.* Cambridge University Press.

Stetter, K.O. 1999. Extremophiles and their adaptation to hot environments. *FEBS Lett.* 452: 22-25.

Stevens, T.O., and J.P. McKinley. 1995. Lithoautotrophic microbial ecosystems in deep basalt aquifers. *Science* 270: 450-454.

Stevenson, A., J. Burkhardt, C.S. Cockell, J.A Cray, J. Dijksterhuis, et al. 2015a. Multiplication of microbes below 0.690 water activity: implications for terrestrial and extraterrestrial life. *Environ. Microbiol.* 17:257-277.

Stevenson, J., J. Lunine, and P. Clancy. 2015b. Membrane alternatives in worlds without oxygen: Creation of an azotosome. *Sci. Adv.*1 (1): e1400067.

Stevenson, D.J. 1999. Life-sustaining planets in interstellar space? *Nature* 400: 32.

Stofan, E.R., C. Elachi, J.I. Lunine, R.D. Lorenz, B. Stiles, et al. 2007. The lakes of Titan. *Nature* 445: 61-64.

Stoker, C.R., P.J. Boston, R.R. Mancinelli, et al. 1990. Microbial metabolism of tholin. *Icarus* 85: 241-256.

Stoker, C.R., and M.A. Bullock. 1997. Organic degradation under simulated Martian conditions. *J. Geophys. Res.* 102: 10881-10888.

Stolz, J.F., and R.S. Oremland. 1999. Bacterial respiration of arsenic and selenium. *FEMS Microbiology Reviews* 23: 615-627.

Stone, F.G.A., and R. West. 1994. *Advances in organometallic chemistry.* Academic Press, New York.

Stone, E.C. and E. D. Miner. 1989. The Voyager 2 Encounter with the Neptunian System. *Science* 246: 1417-1421.

Storm, A.J., C. Storm, J. Chen, H. Zandbergen, J.F. Joanny, et al. 2005. Fast DNA translocation through a solid-state nanopore. *Nano Lett.* 5: 1193–1197.

Stribling, R., and S.L. Miller. 1991. Template-directed synthesis of oligonucleotides under eutectic conditions. *J. Mol. Evol.* 32: 289-295.

Strigari, L., M. Barnabè, P. Marshall, and R Blandford. 2012. Nomads of the Galaxy. *Monthly Notices Royal Astron. Soc.* 423: 1856-1865.

Stringer, C. 2012. *Lone Survivors*. New York: St. Martin's Press.

Stüeken E.E. 2016. Nitrogen in ancient mud: a biosignature? *Astrobiology* 16: 730-735.

Sullivan, R., R. Greeley, K. Homan, J. Klemaszewski, M. J. Belton, M. H. Carr, C. R. Chapman, R. Tufts, J. W. Head, 3rd, R. Pappalardo, J. Moore, and P. Thomas. 1998. Episodic plate separation and fracture infill on the surface of Europa. Galileo Imaging Team. *Nature* 391: 371-373.

Summers, Z.M., J.A. Gralnick, and D.R. Bond. 2013. Cultivation of an obligate Fe(II)-oxidizing lithoautotrophic bacterium using electrodes. *mBio* 4: e00420-12.

Sun, H.J., and E.I. Friedmann. 1999. Growth on geological time scales in the Antarctic cryptoendolithic microbial community. *Geomicrobiology Journal* 16: 193-202.

Sunshine, J.M., T.L. Farnham, L.M. Feaga, O. Groussin, F. Merlin, et al. 2009. Temporal and spatial variability of lunar hydration as observed by the Deep Impact spacecraft. *Science* 326: 565-568.

Susskind, L. 2005. *The Cosmic Landscape: String Theory and the Illusion of Intelligent Design*. Little, Brown, Boston.

Szathmary, E., and J.M. Smith. 1995. The major evolutionary transitions. *Nature* 374: 227-232.

Szent-Györgyi, A. 1972. *The Living State, with Observations on Cancer.* Academic Press, New York.

Tacke, R., and U. Wannagat. 1979. *Syntheses and Properties of Bioactive Organo-Silicon Properties*. Springer-Verlag, Berlin.

Tajika, E., and T. Matsui. 1993. Degassing History and Carbon-Cycle of the Earth - from an Impact-Induced Steam Atmosphere to the Present Atmosphere. *Lithos* 30: 267-280.

Takai, K., K. Nakamura, T. Toki, U. Tsunogai, M. Miyazaki, et al. 2008. Cell proliferation at 122 degrees C and isotopically heavy CH4 production by a hyperthermophilic methanogen under high-pressure cultivation. *Proc. Natl. Acad. Sci. USA* 105:10949-10954.

Tamulis, A., J. Tamuliene, M.L. Balevicius, et al. 2001. Ab initio quantum chemical search of per linear transition state of azo-dye molecules and design of molecular logical machines. *Nonlinear Optics* 27: 481-488.

Tamulis, A., J. Tamuliene, V. Tamulis, et al. 2003. Quantum mechanical design of molecular computer elements suitable for self-assembling to quantum computing living systems. *6th International Conference on Self-Formation, Theory and Applications*, Vilnius, Lithuania.

Tanenbaum, S.W. 1956. The metabolism of *Acetobacter peroxidans*. I. Oxidative enzymes. *Biochim. Biophys. Acta* 21: 335-342.

Tang, B.L. 2007. A case for immunological approaches in detection and investigation of alien life. *Int. J. of Astrobiology* 6: 11-17.

Tang, Y., Q. Chen, and Y. Huang. 2006. Early Mars may have had a methanol ocean. *Icarus* 180: 88-92.

Tapponnier, P., and P. Molnier. 1977. Active faulting and tectonics in China *J. Geophys. Res.* 82: 2905-2930.

Tarter, J.C., P.R. Backus, R.L. Mancinelli, et al. 2007. A reappraisal of the habitability of planets around M dwarf stars. *Astrobiology* 7: 30-65.

Taylor, D.J., M.J. Ballinger, S.M. Bowman, and J.A. Bruenn. 2013. Virus-host coevolution under a modified nuclear genetic code. *PeerJ* 1: e50; doi: https://doi.org/10.7717/peerj.50.

Testi, L., A. Natta, E. Oliva, et al. 2002. A young very low mass object surrounded by warm dust. *Astrophys. J.* 571: L155-159.

Thomas-Keprta, K.L., D.A. Bazylinski, J.L. Kirschvink, et al. 2000. Elon-gated prismatic magnetite crystals in ALH84001 carbonate globules: potential martian magnetofossils. *Geochim. Cosmochim. Acta* 64: 4049-4081.

Thomas-Keprta, K.L., S.J. Clemett, D.A. Bazylinski, et al. 2001. Truncated hexa-octahedral magnetite crystals in ALH84001: presumptive biosignatures. *Proc. Natl. Acad. Sci. USA* 98: 2164-2169.

Thomas-Keprta, K.L., S.J. Clemett, D.A. Bazylinski, et al. 2002. Magnetofossils from ancient Mars: a robust biosignature in the martian meteorite ALH84001. *Appl. Environ. Microbiol.* 68: 3663-3672.

Thompson, W. R. and C. Sagan. 1990. Color and chemistry on Triton. *Science* 250: 415-418.

Tiago, I., A.P. Chung, and A. Verissimo. 2004. Bacterial diversity in a nonsaline alkaline environment: heterotrophic aerobic populations. *Appl. Environ. Microbiol.* 70: 127378-127387.

Tice, M.M., and D.R. Lowe. 2006. Hydrogen-based carbon fixation in the earliest known photosynthetic organisms. *Geology* 34: 37-40.

Tipler, F.J. 1981. Extraterrestrial intelligent beings do not exist. *Quart. J. Roy. Astronom. Soc.* 21: 267-281.

Tivey, M.K., A.M. Bradley, T.M. Joyce, et al. 2002. Insights into tide-related variability at seafloor hydrothermal vents from time-series temperature measurements. *Earth Planet. Sci. Lett.* 202: 693-707.

Tobie, G., M. Choukroun, O. Grasset, S. Le Mouelic, J. I. Lunine, C. et all. 2009. Evolution of Titan and implications for its hydrocarbon cycle. *Philos. Transact. A Math Phys. Eng. Sci.* 367 (1889):617-31.

Tokito, N., and R. Okazaki. 1998. Polysilanes: Conformation, chromotropism and conductivity. pp. 1063-1104 in Z. Rappoport and Y. Apeloig, eds. *The Chemistry of Organic Silicon*. John Wiley and Sons, Chichester, UK.

Tong, S. 2000. The potential impact of global environmental change on population health. *Australian New Zealand J. Med.* 30: 618-625.

Toon, O.B., C.P. McKay, R. Courtin, et al. 1988. Methane rain on Titan. *Icarus* 75: 255-284.

Torrella, F., and R.J. Morita. 1981. Microcultural study of bacterial size changes and microcolony and ultramicrocolony formation by heterotrophic bacteria in seawater. *Appl. Environ. Microbiol.* 41: 518-527.

Tribe, H.T., and S.A. Mabadje. 1972. Growth of moulds on media prepared without organic nutrients *Trans Br. Mycol. Soc.* 58: 127-137.

Trilling D.E. 2016. The surface age of Sputnik Planum, Pluto, must be less than 10 million years. PloS one 11(1):e0147386 (doi:https://doi.org/10.1371/journal.pone.0147386).

Trinks, H., W. Schroder and C.K. Biebricher. 2005. Ice and the origin of life. *Orig. Life Evol. Biosph.* 35: 429-445.

Tucker, C.J., J.R.G. Townshend and T.E. Goff. 1985. African land-cover classification using satellite data. *Science* 277: 369-375.

Turian, G. 2003. Biogenic bipolarity - A new approach to the origin of life. *Arch. Sci.* 56: 155-182.

Turse, C., D. Schulze-Makuch, D. Lim, et al. 2008. The rise of complexity: Evidence from cell signaling compounds for Pavilion Lake microbialites and temperate zone microbial community ecosystems. *Astrobiology* 8: 383.

Tyrell, R.M. 1991. UVA (320-380 nm) radiation as an oxidative stress. pp. 57-83 in H. Sies, ed. *Oxidative Stress: Oxidants and Antioxidants*. Academic Press, London.

Udry, S., X. Bonfils, X. Delfosse, et al. 2007. The HARPS search for southern extra-solar planets XI. Super-Earths (5 & 8 Earth masses) in a 3-planet system. *Astron. Astrophys.* 469: L43-L47.

Vakoch, D.A. 2016. In defence of METI. *Nature Physics* 12: 890 (doi:https://doi.org/10.1038/nphys3897).

Valdes, F. and R. A. Freitas. 1983. A search for objects near the Earth-Moon Lagrangian points. *Icarus* 53: 453-457.

Valley, J.W., J.M. Eiler, C.M. Graham, et al. 1997. Low-temperature carbonate concretions in the martian meteorite ALH84001: evidence from stable isotopes and mineralogy. *Science* 275: 1633-1638.

Van Dover, C.L., J.R. Cann, C. Cavanaugh, et al. 1994. Light at deep sea hydrothermal vents. *EOS Trans. AGU* 75: 44-45.

Van Dover, C.L., and R.A. Lutz. 2004. Experimental ecology at deep-sea hydrothermal vents: a perspective. *J. Exp. Marine Biol. Ecol.* 300: 273-307.

Van Holde, K.E., W.C. Johnson and P.S. Ho. 1998. *Principles of Physical Biochemistry*. Prentice Hall, Upper Saddle River, NJ.

van Leerdam, R.C., M. Bonilla-Salinas, F.A. de Bok, H. Bruning, P.N. Lens, et al. 2008. Anaerobic methanethiol degradation and methanogenic community analysis in an alkaline (pH 10) biological process for liquefied petroleum gas desulfurization. *Biotechnol. Bioeng*. 101: 691-701.

Van Zuilen, M., C. Thomazo, B. Luais, and P. Phillippot. 2008. Photosynthesis in a 3.5 Ga old shallow marine depositional environment: clues from carbon and iron isotope systematics. *Astrobiology* 8: 325.

Varela, M.E., and N. Metrich. 2000. Carbon in olivines of chondritic meteorites. *Geochim. Cosmochim. Acta.* 64: 3433-3438.

Vercoutere, W., S. Winters-Hilt, H. Olsen, D.W. Deamer, D. Haussler, et al. 2001. Rapid discrimination among individual DNA molecules at single nucleotide resolution using a nanopore instrument. *Nature Biotech.* 19: 248-250.

Vernadsky, I.V. 1997. *The Biosphere*. Springer-Verlag, Copernicus, New York.

Vidal, C. 2016. Stellivore extraterrestrials? Binary stars as living systems. *Acta Astronautica* 128: 251-256.

Vidal-Madjar, A., J.-M. Désert, A. Lecavelier des Etangs, G. Hébrard, G.E. Ballester, et al. 2004. Detection of oxygen and carbon in the hydrodynamically escaping atmosphere of the extrasolar planet HD 209458b. *Astrophys. J.* 604: L69-L72.

Vinogradov, M.E., A.L. Vereshchaka and E.A. Shushkina. 1996. Vertical structure of the zooplankton communities in the oligotrophic areas of the northern Atlantic, and influence of the hydrothermal vent. *Okeanologiya* 36 71-79.

Viswanath, V., G.M. Story, A.M. Peier, et al. 2003. Opposite thermosensor in fruitfly and mouse. *Nature* 423: 822-823.

Vlassov, A.V., B.H. Johnston, L.F. Landweber, et al. 2004. Ligation activity of fragmented ribozymes in frozen solution: implications for the RNA world. *Nucleic Acids Res* 32: 2966-2974.

Voet, D., and J. Voet. 2004. *Biochemistry*. Wiley and Sons, Hoboken, N.J.

von Bloh, W., C. Bounama, M. Cuntz, and S. Franck. 2007. The habitability of super-Earths in Gliese 581. *Astron. Astrophys.* 476: 1365-1371.

Vornanen, M., and V. Paajanen. 2006. Seasonal changes in glycogen content and Na-K-ATPase in the brain of crucian carp. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 291: R1482-1489.

Wächtershäuser, G. 1988. Before enzymes and templates: theory of surface metabolism. *Microbiol Rev* 52: 452-484.

Wächtershäuser, G. 1994. Vitalists and virulists: a theory of self-expanding reproduction. pp. 124-132 in S. Bengtson, ed. *Early life on Earth.* Columbia University Press, New York.

Wächtershäuser, G. 2007. On the chemistry and evolution of the pioneer organism. *Chem Biodivers* 4: 584-602.

Wackett, L.P., A.G. Dodge and L.B.M. Ellis. 2004. Microbial genomics and the periodic table. *Appl. Environ. Microbiol.* 70: 647-655.

Wainwright, M. 1997. The neglected microbiology of silicon - from the origin of life to an explanation for what Henry Charlton Bastian saw. *Society General Microbiology Quarterly,* 24: 83-85.

Wainwright, M., K. Al-Wajeeh and S.J. Grayston. 1997. Effect of silicic acid and other silicon compounds on fungal growth in oligotrophic and nutrient-rich media *Mycological Research* 101: 8.

Waite, J.H., Jr., M.R. Combi, W.H. Ip, et al. 2006. Cassini ion and neutral mass spectrometer: Enceladus plume composition and structure. *Science* 311: 1419-1422.

Waite, J. H., C. R. Glein, R. S. Perryman, B. D. Teolis, et al. 2017. Cassini finds molecular hydrogen in the Enceladus plume: Evidence for hydrothermal processes. *Science* 356: 155-159.

Walker, J.C.G. 1977. *Evolution of the atmosphere* Macmillan, New York.

Wallis, J.N., C. Wickramasinghe, D.H. Wallis, N. Miyake, M.K. Wallis, et al. 2012. Possible biological structures in the Tissint Mars meteorite. *Proc. SPIE 8521, Instruments, Methods, and Missions for Astrobiology* XV, 852110R.

Walsh, R. 1981. Bond dissociation energy values in silicon-containing compounds and some of their implications. *Accounts Chem. Res.* 14: 246-252.

Wang, Q., A.R. Parrish, L.Wang. 2009. Expanding the genetic code for biological studies. *Chemistry & Biology* 16: 323–336.

Ward, P. 2001. *Future Evolution*. W. H. Freeman.

Ward, P.D. 2005. *Life As We Do Not Know It: The NASA Search for (and Synthesis of) Alien Life.* 1st ed: Viking.

Ward, P.D., and D. Brownlee. 2000. *Rare Earth: Why Complex Life Is Uncommon in the Universe*. Springer-Verlag, New York.

Warren, P.H. 1998. Petrologic evidence for low-temperature, possibly flood-evaporitic origin of carbonates in the ALH84001 meteorite. *JGR-Planets* 103: 98E01544.

Waters, C. N., J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, et al. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351: 137 (doi: https://doi.org/10.1126/science.aad2622).

Watson, J. and F. Crick. 1953. A structure for deoxyribose nucleic acid. *Nature* 171: 737-738.

Way, M.J., A.D. Del Genio, N.Y. Kiang, L.E. Sohl, et al. 2016. Was Venus the first habitable world of our solar system? *Geophys. Res. Lett.* 43: 8376-8383.

Webb, S. 2015. *If the Universe is Teeming with Aliens… Where is Everybody?: Seventy-Five Solutions to the Fermi Paradox and the Problem of Extraterrestrial Life.* Springer, Berlin.

Webster, C.R., P.R. Mahaffy, S.K. Atreya, G.J. Flesch, M.A. Mischna, et al. 2015. Mars methane detection and variability at Gale crater. *Science* 347: 415-417.

Webster, G., and J. Cruz. 2009. NASA Phoenix results point to M3artian climate cycles. https://www.jpl.nasa.gov/news/phoenix/release.php?ArticleID=2210.

Wehner, R. 1989. Strategien gegen den Hitzetod. Thermophilie und Thermoregulation bei Wüstenameisen (*Cataglyphis bombycina*). *Acad. Wiss. Lit., Mainz, Germany*: 101-112.

Weiss, B.P., S. Sam Kim, J.L. Kirschvink, et al. 2004. Magnetic tests for magnetosome chains in martian meteorite ALH84001. *Proc. Natl. Acad. Sci. USA* 101: 8281-8284.

Weiss, M. C., F. L. Sousa, N. Mrnjavac, S. Neukirchen, et al. 2016. The physiology and habitat of the last universal common ancestor. *Nat. Microbiol.* 1: 16116.

Werner, D. 1967. Untersuchungen ueber die Rolle der Kieselsaeure in der Entwicklung hoeherer Pflanzen. I Analyse der Hemmung durch Germaniumsaeure. *Planta (Berlin)* 76: 25-36.

Wernet, P., D. Nordlund, U. Bergmann, M. Cavalleri, et al. 2004. The structure of the first coordination shell in liquid water. *Science* 304: 995-999.

West, R. 1986. The polysilane high polymers. *J. Organometallic Chem.* 300: 327-346.

West, R. 1987. Chemistry of the silicone-silicone double bond. *Angew. Chem. Int. Ed.,* 26: 201-1211.

West, R. 2001. Polysilanes: Conformation, chromotropism and conductivity. pp. 541-563 in Z. Rappoport and Y. Apeloig, eds. *The Chemistry of Organic Silicon*. John Wiley and Sons, Chichester, UK.

Westall, F., M.J. de Wit, J. Dann, et al. 2001. Early Archean fossil bacteria and biofilms in hydrothermally-influenced sediments from the Barberton greenstone belt, South Africa. *Precambrian Research* 106: 93-116.

Westheimer, F.H. 1987. Why nature chose phosphates. *Science* 235: 1173-1178.

Wettergreen, D., N. Cabrol, V. Baskaran, F. Calderón, S. Heys, et al. 2005. Second experiments in the robotic investigation of life in the Atacama desert in Chile. *Proceedings of the ISAIRAS Conference*, Munich, Germany.

Wharton, D.A. 2002. *Life at the Limits-Organisms in Extreme Environments*. Cambridge University Press, New York.

White, R.H. 1984. Hydrolytic stability of biomolecules at high temperatures and its implication for life at 250 degrees C. *Nature* 310: 430-432.

White, S.N., A.D. Chave, G.T. Reynolds, et al. 2002. Ambient light emission from hydrothermal vents on the Mid-Atlantic Ridge *Geophys. Res. Lett.* 29: 1744.

Whitman, W.B., D.C. Coleman and W.J. Wiebe. 1998. Prokaryotes: the unseen majority *Proc. Natl. Acad. Sci. USA* 95: 6578-6583.

Wilhelm, R. C., K. J. Radtke, N. C. Mykytczuk, C. W. Greer, L. G. Whyte. 2012. Life at the wedge: the activity and diversity of arctic ice wedge microbial communities. *Astrobiology* 12: 347-360.

Williams, D.M., and J.F. Kasting. 1997. Habitable planets with high obliquities. *Icarus* 129: 254-267.

Williams, D. R. 2016. Venus fact sheet: NASA (https://nssdc.gsfc.nasa.gov/planetary/factsheet/venusfact.html).

Williams, J.P., and J.E. Hallsworth. 2009. Limits of life in hostile environments: no barriers to biosphere function? *Environ. Microbiol.* 11: 3292-3308.

Wilmer, P., G. Stone and I. Johnston. 2000. *Environmental physiology of animals*. Blackwell Science, Oxford., Blackwell Science, Oxford.

Wilson, E. 1980. *Sociobiology*. Harvard Univ Press, Cambridge.

Winebrenner, D. 2008. Detection of biogenic molecules by means of circular polarized light scattering. *Astrobiology* 8: 305.

Woese, C. 1979. A proposal concerning the origin of life on the planet Earth. *J Molec Evol* 13: 95-101.

Wolf, E.T. and O.B. Toon. 2013. Hospitable Archean climates simulated by a general circulation model. *Astrobiology* 13: 656-673.

Wolfe-Simon, F., P.C.W. Davies, and A.D. Anbar. 2008. Did nature also choose arsenic? *Astrobiology* 8: 360.

Wolfe-Simon, F., J. Switzer Blum, T. R. Kulp, G. W. Gordon, et al. 2011. A bacterium that can grow by using arsenic instead of phosphorus. *Science* 332: 1163-1166.

Wolszczan, A. 1994. Confirmation of Earth-mass planets orbiting the millisecond pulsar Psr B1257 +12. *Science* 264: 538-542.

Wolszczan, A. and D.A. Frail. 1992. A planetary system around the millisecond pulsar PSR1257 +12. *Nature* 355: 145-147.

Woodruff, D.S. 2001. Declines of biomes and biotas and the future of evolution. *Proc. Natl. Acad. Sci. USA* 98: 5471-5476.

Wordsworth, R., F. Forget, E. Milloura, J.W. Head, J.-B. Madeleine, and B. Charnay. 2013. Global modelling of the early martian climate under a denser CO2 atmosphere: Water cycle and ice evolution. *Icarus* 222: 1-19.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proceedings of the Sixth International Congress of Genetics. pp. 356-366. *Sixth International Congress of Genetics*.

Wrights, D.Y., and A. Oren. 2005. Nonphotosynthetic bacteria and the formation of carbonates and evaporates through time. *Geomicrobiol. J.* 22: 27-53.

Wynn-Williams, D.D., and H.G.M. Edwards. 2000. Proximal analysis of regolith habitats and protective biomolecules in situ by laser Raman spectroscopy: overview of terrestrial Antarctic habitats and Mars analogs. *Icarus* 144: 486-450.

Wynn-Williams, D.D., H.G.M. Edwards, E.M. Newton, et al. 2002. Pigmentation as a survival strategy for ancient and modern photosynthetic microbes under high ultraviolet stress on planetary surfaces *Int. J. Astrobiology* 179: 174-183.

Xia, X. 2000. Phylogenetic relationship among horseshoe crab species: effect of substitution models on phylogenetic analyses. *Syst Biol* 49: 87-100.

Xie, J. and P. G. Schultz. 2005. Adding amino acids to the genetic repertoire. *Curr. Opin. Chem. Biol.* 9: 548-554.

Xu, J., G.J. Ramian and J.F. Galan et al. 2003. Terahertz circular dichroism spectroscopy: a potential approach to unbiased, in situ life detection. *Astrobiology* 3: 489-504.

Xue, H. and T.-F. Wong. 2017. Future of the genetic code. *Life* 7: 10, doi:https://doi.org/10.3390/life7010010.

Yamamoto, K., Y. Sakata, Y. Nohara, et al. 2003. Organic-inorganic hybrid zeolites containing organic frameworks *Science* 300: 470-472.

Yamao, F., A. Muto, Y. Kawauchi, M. Iwami, S. Iwagami, et al. 1985. UGA is read as tryptophan in *Mycoplasma capricolum*. *Proc. Natl. Acad. Sci USA* 82: 2306-2309.

Yancey, P.H., M.E. Clark, S.C. Hand, et al. 1982. Living with water stress: evolution of osmolyte systems. *Science* 217: 1214-1216.

Yang, Z., F. Chen, J.B. Alvarado, and S.A. Benner. 2011. Amplification, mutation, and sequencing of a six-letter synthetic genetic system. *J. Am. Chem. Soc.* 133: 15105–15112.

Yasui, A., and S.J. McCready. 1998. Alternative repair pathways for UV-induced DNA damage. *BioEssays* 20: 291-297.

Yayanos, A.A. 1995. Microbiology to 10,500 meters in the deep sea. *Annu. Rev. Microbiol.* 49: 777-805.

Yen, A.S., S.S. Kim, M.H. Hecht, et al. 2000. Evidence that the reactivity of the martian soil is due to superoxide ions. *Science* 289: 1909-1912.

Yeung, L. Y., J. L. Ash, and E. D. Young. 2015. Isotope geochemistry. Biological signatures in clumped isotopes of O_2. *Science* 348: 431-434.

Yoshino, T. 1990. Growth accelerating effect of silicon on Pseudomonas aeruginosa. *J. Saitama Med. Sch. (in Japanese).* 17: 189-198.

Young, J. 1964. *A Model of the Brain*. Oxford Univ Press, London.

Zhang, Y., P.V. Baranov, J.F. Atkins, and V.N. Gladyshev. 2005. Pyrrolysine and selenocysteine use dissimilar coding strategies. *J. Biol. Chem.* 280: 20740-20751.

Zahradka, K., D. Slade, A. Bailone, et al. 2006. Reassembly of shattered chromosomes in *Deinococcus radiodurans*. *Nature* 443: 569-573.

Zamudio, G.S. and M.V. José. 2017. On the uniqueness of the standard genetic code. Life 7: doi: https://doi.org/10.3390/life7010007.

Zeigler, J.M., and F.W.G. Fearon. 1989. *Silicon-based polymer science: a comprehensive resource* American Chemical Society, Washington, DC.

Zent, A.P., and C.P. McKay. 1994. The chemical reactivity of the martian soil and implications for future missions. *Icarus* 108: 146-157.

Zimmer, C., K.K. Khurana and M.G. Kivelson. 2000. Subsurface oceans on Europa and Callisto: contraints from Galileo magnetometer observations *Icarus* 147: 329-347.

Zolotov, M.Y., and E.L. Shock. 2003. Energy for biologic sulfate reduction in a hydrothermally formed ocean on Europa. *Journal of Geophysical Research-Planets* 108: art. no.-5022.

Zubrin, R., and R. Wagner. 1996. *The Case for Mars: The Plan to Settle the Red Planet and Why We Must*. The Free Press, New York, N.Y.

Index

A
Acetylene, 29, 142, 219
Acidophiles, 66
Adaptation
  to chemical extremes, 62, 71
  to desiccation, 61, 67, 70, 71
  to extreme cold, 62, 65
  to extreme heat, 64, 67
  to low nutrient availability, 61, 71
  to low oxygen availability, 62, 68–69
  to pH extremes, 61, 62, 65–66
  to pressure extreme, 61, 62, 69–70
  to radiation, 61, 62, 70–71
  to temperature extremes, 61–65
Adenosine triphosphate (ATP), 11, 38, 39, 68, 75, 79, 80, 82, 86–88, 120, 141, 171, 172
  phosphate in, 38, 80, 120
Aerobes, 61, 68, 76, 103, 110, 133, 186
Alcohol, 101, 105, 143
Aldehyde, 101, 105
Algae, 62, 63, 65, 213
ALH8400
  argument for fossil-like structures in, 196–197
  carbonate globules in, 195
  formation temperatures of, 195–196
  magnetite crystals in, 197, 198
Alkaliphiles, 66
Alpha Centauri, 161
Aluminum oxide, 10
Amino acids, 16, 29, 30, 32, 33, 40, 46–50, 52, 64, 72, 101, 102, 105, 106, 108, 127, 130, 132, 133, 135, 141, 171, 186, 200, 201, 223
  canonical, 46, 48, 106
  non-canonical, 46, 48–49, 106
Amino (NH_2) groups, 101, 133
Ammonia, 29, 119, 120, 124, 127, 131–136, 140, 144, 146, 147, 153, 167, 178, 210, 211, 216–218, 239, 251
Amniotic egg, 258
Amphiphilic molecules, 24, 36, 37, 43
Anaerobes, 52, 62, 68, 69, 76, 184, 186, 218
Anhydrobiosis, 67
Anoxia, 68, 69
Anoxybiosis, 68
Antarctica, 62, 149, 186, 193, 194, 199, 280
Archaea, 12, 30, 42, 48, 61, 62, 64–67, 69, 153, 197, 256
Ariel, 180, 226
Armadillos, 55
Arsenic, 71, 76, 120
Asteroids, 159, 173, 180, 193, 195, 196, 209, 223, 225, 284
Astrobiological potential
  asteroids, 223
  Callisto, 215
  Ceres, 209–210
  comets, 224
  Earth-Moon, 205–206
  Enceladus, 215–217
  Eris, 221
  Europa, 212–215
  Ganymede, 215
  gas giants, 210–212
    opposing arguments, 211
  Io, 212
  Jupiter, 210
  Mars, 207–209, 263

D. Schulze-Makuch, L. N. Irwin, *Life in the Universe*, Springer Praxis Books,
https://doi.org/10.1007/978-3-319-97658-7

Astrobiological potential (*cont.*)
        InSight Mission, 277
    Mercury, 203–204
    Neptune, 211
    Pluto-Charon, 221–223
    Saturn, 210
    Titan, 217–220
    Triton, 220–221
    Uranus, 210
    Venus, 204–205, 282
Atmospheres
    composition of, 166–168, 232
    composition of, as biosignature, 166–168
    distinct gas mix on Mars, 193
    motion of, 177
    neutral, 29
    pressure gradients in, 94, 99, 177
    reducing, 28, 29, 251
Atmospheric habitats
    advantages of, 154
    challenges of, 155, 156
    prototypical, 154
    on Venus, 57, 154, 156, 174
ATP, *see* Adenosine triphosphate (ATP)
Autopoiesis, 13, 15

B

Bacillus subtilis, 60, 157, 158, 251
Bacteria
    iron-oxidizing, 76, 78
    iron-reducing, 76
    metal-oxidizing, 78
    sulfur-cycling, 256
Banded iron formation (BIF), 166, 168
Bilaterians, 52
Biodiversity, 2, 4, 59–60, 204, 258
Bioenergetics, 3, 66, 93, 98
Biofilms, 170, 196
Biogenic heat, 172
Biomembranes
    for encapsulation, 20
    as energy transducers, 20, 36
    exchange of materials across, 54
    for excitation, 20
    fluidity, 61, 63
Biominerals, 170
Biosignature, 165–173, 179, 181, 183, 197–198, 200, 203, 233, 234, 242
Biosignatures
    atmospheric, 168
    gases, 167
    isotope ratios, 170
    minerals as, 168
    nitrogen abundance, 169
    polarization spectroscopy, 171
    reliability of, 166, 169
    technological, 173
Biosphere, 4, 7, 13, 17, 57, 64, 160, 163, 168, 176, 202, 204, 209, 214, 218–220, 227, 228, 239, 242, 246, 255, 257, 258, 263, 280, 285
Boehmite, 10
Bombardment
    cometary, 28
    great, 2, 51, 53, 54
Boron, 71, 106, 119, 120
Brine shrimp, 68

C

Cadmium, 71, 186
Calcite, 9, 196
Calcium, 43, 71, 186, 194, 196, 251
Calcium chloride, 66
Callisto, 99, 174, 180, 212, 213, 215, 226
Cambrian
    explosion, 52, 258
    oxygen level during, 68
Cambrian explosion, 52, 258
Carbon
    ability to form double and triple bonds, 107, 108, 121
    ability to form long-chain polymers, 103, 105
    bond energies with other elements, 103
    C-C bond, 103, 105–108, 113, 119, 131
    complexity and versatility of, 107
    compounds of, in Murchison meteorite, 105
    cosmic abundance, 100
    C–Si bond, 107
    favorable for redox reactions, 75, 103
    in the interstellar medium, 104, 108
    physical properties, 104, 105
    range of redox states, 103
Carbon dioxide, 22, 28, 30, 38, 39, 43, 51, 61, 63, 75, 77, 81, 103, 108, 130, 143, 154, 156, 161, 174, 184, 186, 189–191, 195, 205, 212, 214, 215, 217, 276
Carbon monoxide, 30, 63, 154, 184, 212, 222
Carboxyl groups, 101, 105, 109, 132
Carboxylic acid, 101, 105, 109
Carotene, 170
Carp, 62, 68, 69
Cephalopods, 58, 259

Charon, 180, 222, 225, 252
Chemoautotrophy, 38, 89, 94, 98
Chemoheterotrophy, 75
Chemolithotrophy, 8, 75
Chemoorganotrophy, 9
Chirality, 102, 170–171, 201
Chlorine, 81, 87, 168
Chlorophyll, 61, 79, 81, 111, 166, 170, 200, 233
Clams, 55
Clay, 9–11, 14, 21, 40, 41, 50, 112, 118, 191, 209, 225
Cockroaches, 55, 62, 71
Comets, 78, 114, 134, 135, 140, 173, 180, 224, 226, 284
Copper, 71, 76, 140
Corals, 20, 22, 24, 59, 60, 168
Cretaceous-Tertiary boundary, 57
Cretaceous-Tertiary (K-T) transition, 223, 257
Crocodiles, 55
Cryptoendoliths, 63
Crystals, 9, 11, 14, 16, 61, 70, 90, 93, 109, 112, 118, 129, 132, 138, 157, 158, 194, 197, 198
CubeSats, 275, 277
Cyanobacteria, 66–68, 81, 86, 170, 184, 256
Cytosine, 47, 102

D
Definition of life
  capacity for evolutionary change, 13, 14, 16–17, 24
  ecological perspective, 13
  as global phenomenon, 13, 17, 24
  historical views, 12–13
  implications for remote detection, 24–25
  redefinition, 262, 264
  as reproductive potential, 15–16
  as self-sustaining autoregulation, 15
  semantic ambiguity of, 17, 19
Dehydration, 10, 29, 32, 45, 67, 127, 130
Deinococcus radiodurans, 62, 67, 70, 96, 158, 251
Denitrification, 76, 78
Deoxyribonucleic acid (DNA), 3, 9, 18, 23, 25, 28, 39, 41, 42, 49, 61, 64, 65, 67, 70, 80, 102, 105, 111, 120, 127, 158, 171, 196, 197, 200, 279
  phosphate in, 120
Diatoms, 3, 110, 111
Dinitrogen, 139, 140, 146
Dione, 180, 226
DNA, *see* Deoxyribonucleic acid (DNA)
DNA-RNA-protein world, 35
Doppler imaging, 176, 177
Dwarf stars, 80, 162, 163, 240, 253, 271
Dyson Sphere, 173, 268

E
Earth
  appearance of first life, 51
  early atmosphere, 51, 52
  formation of, 51
Ediacaran fauna, 257
Eelworm, 66
Electromagnetic radiation, 29, 70, 79, 96, 169, 266
Emergent properties, 8, 22
Enceladus, 98, 99, 152, 165, 173–176, 179, 180, 210, 215–217, 225–228, 284
Energy
  availability on early Earth, 29
  chemical, 3, 24, 38, 39, 75, 79–82, 92, 95, 98, 118, 151, 219
  from convection currents, 84
  exotic forms of, 3, 100
  geothermal, 98–100, 176
  from gravitational forces, 92–93, 215
  ionotrophic, 3, 85–88
  isothermal, 2
  kinetic, 79, 81, 84–85, 93, 96, 98, 100, 129, 177, 180, 214, 215, 219
  kinetotrophic, 85
  from magnetic induction, 88–92
  magnetotrophic, 90
  osmotrophic, 3, 85–88, 98–100
  from oxidation-reduction chemistry, 76–78
  photoautotrophic, 15, 75, 79, 81, 86, 89, 94, 97, 98, 167
  piezoelectric, 93
  from pressure gradients, 94, 99
  from radioactivity, 96
  from radiogenic heating, 98, 153, 174, 219, 226
  remote detection of gradients, 176
  from spin configurations, 94–95
  from tectonic stress, 93–94, 98
  thermal, 29, 81–84, 97, 98, 177
  from tidal flexing, 82, 92, 98–100
Energy consumption
  to maintain low entropy, 12, 20–22
  to organize materials, 21, 75
  to perform work, 15, 21–22, 26, 75
  to sustain complexity, 22
Energy gradients, 20, 24, 32, 50, 176, 179, 226

Entropy, 12–14, 20–22, 26, 75, 97–98, 118, 173, 248, 253
Enzyme induction, 10, 11
Enzymes, 10, 11, 15, 40, 61, 63, 66, 71, 103, 119, 134, 142, 190, 200
Erosion, 99, 166, 169
Escherichia coli (E. coli), 70, 251
Ethane, 4, 109, 112, 139, 140, 142, 146, 147, 162, 174, 178, 217, 218, 221, 283
Eukaryotes, 41, 52, 62, 64, 72
Europa, 57, 78, 81, 84, 88, 91, 96, 98, 99, 147, 152, 160, 165, 167, 174–178, 180, 205, 210, 212–215, 218, 219, 221, 225–228, 263, 282–284
Evaporates, 62, 168, 196
Evolution
  accelerated by environmental change, 57–58
  collapse trajectory, 255–258
  plateau trajectory, 256–257
  simplicity favored over complexity, 58
  static under constant conditions, 55, 57
  transitional trajectory, 258–259
Exoplanets, 5, 160, 167, 168, 229–246
  confirmed number, 5, 238, 239
  detection method
    astrometry, 230–231
    emerging technologies, 232
    gravitational microlensing, 231, 235, 240
    limits to, 231
    radial velocity, 230
    red edge effect, 233
    transit photometry, 230
  observable parameters, 234
  taxonomy of, 236–239
Exoskeleton, 3, 258
Exotic forms of life
  Hoyle's Black Cloud, 249–250
  on a neutron star, 250
  quantum computing cloud, 249
  on a rogue planet, 251–252
  spin configurations, 247–249
Extrasolar planets, 160, 161, 167, 229, 234, 250, 283, 286
Extraterrestial intelligence
  artifacts of (SETA), 268
  messaging to (METI), 270–271
  search for (SETI)
    false positives, 268–269
    Institute, 265, 266
    optical, 267
    Permanent Study Group, 270, 271
    Project BAMBI, 265
    Project SERENDIP, 266, 267
    traditional, 265–267
    the "Wow!" signal, 269–270
Extremophiles, 61, 62, 68, 205

F
Fermi Paradox, 272–273
Fluorescence, 9, 200
Folk, Bob, 194
Formaldehyde, 28, 29
Formamide, 128, 131, 139–141
Fossil remnants, 169
Fossils, 1, 25, 51, 52, 58, 165, 169–170, 196, 200, 201, 256, 259
Fungi, 42, 48, 62, 63, 65–67, 110, 150, 152

G
Gaia Hypothesis, 17
Galactic habitable zone (GHZ), 161, 164
Ganymede, 98, 99, 152, 174, 178, 180, 212, 213, 215, 226, 284
Gas chromatograph mass spectrometer (GC-MS), 184, 185, 188, 189, 191, 192
Gas giants, 45, 57, 92, 98, 99, 119, 145, 146, 154, 155, 159, 161, 174, 176, 177, 210–212, 215, 237, 238
GC-MS, *see* Gas chromatograph mass spectrometer (GC-MS)
Genetic code, 9–11, 17, 23, 30, 35, 46–50, 105, 255
  flexibility of, 48–49
  non-canonical amino acids, 48–49
  standard, 46–48
Genetic drift, 56, 58, 257, 258
Geoindicator, 98, 165, 167, 173–181, 183, 206
Geosignature, 165–167, 169, 179, 203
Gibbsite, 10
Gravity, 3, 43, 79, 92–94, 152, 159, 193, 210, 234, 279, 281, 282
  tidal flexing from, 215
Green sulfur bacteria, 39, 77, 81
GTP, 11
Gypsum, 9, 169

H
Habitability
  atmospheric, 156
  definition of, 160, 242

  - distinction from inhabited, 164
  - on Earth-sized planets, 162
  - metrics, 242
    - Biological Complexity Index (BCI), 245
    - Earth Similarity Index (ESI), 243–244
    - Habitat Suitability Index, 242–243
    - Planetary Habitability Index (PHI), 244–245
- Habitable zone
  - classical description of, 160
  - limitations of, 160
- Habitable zone (HZ), 156, 160, 161, 163, 164, 240
- Habitat(s)
  - fractionation of, 60
  - subsurface, 150, 152, 153, 174, 262, 263
  - subsurface of the ocean, 53, 160
  - subterranian, 94
- Habitats for life
  - atmospheric, 153–157
  - space, 157–159
  - subsurface, 4, 149–153, 155, 160, 164
  - surface, 149–153
- Halobacteriaceae, 67
- Halophiles, 62, 66, 86, 110
- Heterotrophy, 15, 39, 78, 184
- *Homo sapiens,* 17, 258, 260
- Horowitz, Norman, 184
- Hoyle, Fred, 42, 159, 249
- Human exploration
  - advantages of, 275, 276
  - of Mars, 276–280
  - of the Moon, 281–282
- Humans, 1, 2, 5, 17, 48, 58, 61, 163, 183, 190, 196, 236, 247, 255, 257–261, 264, 265, 269–271, 273, 275–282, 284–286
- Hydrazine, 120, 131, 139
- Hydrocyanic acid, 124, 134–136, 144, 147, 162
- Hydrofluoric acid, 136, 144
- Hydrogen, 15, 29, 30, 37–39, 41, 50, 65, 66, 71, 76–78, 80, 90, 94–96, 101, 103, 104, 108, 112, 113, 115–117, 119, 123, 125–127, 129, 130, 133, 137, 141, 142, 167, 170, 186, 210, 211, 214, 217, 218, 233, 247, 248, 250, 251, 266, 267, 269, 273
  - cosmic abundance of, 90, 95
- Hydrogen cyanide, 35, 135, 141
- Hydrogen peroxide, 40, 77, 81, 125, 137–138, 188, 190–192, 208, 214
- Hydrogen sulfide, 35, 38, 39, 136–137, 144, 147, 178
- Hydrothermal vents
  - alkaline, 30, 66
  - photosynthesis at, 81
- Hyperthermophiles, 42, 64, 70

I

- Iapetus, 100, 152, 175, 176, 179, 180, 226, 282
- Ice shield, 174–175, 180, 181
- Infopolymers, 28
- Information
  - chemical basis of, in living systems, 13
  - encoding and transmission of, 13, 23–24, 50
  - persistence through successive generations, 23
- Instrumentation for life detection
  - Astrobiological Residues and Current Habitats (SEARCH), 201
  - Mars Immunoassay Life Detection Instrument (MILDI), 200
  - Mars Organic Detector (MOD), 200
  - Multiple Instrument Distributed Aperture Sensor (MIDAS), 201
  - single molecule detector (SMD), 200
  - Viking landers, 183–185, 188, 200
- Intelligence
  - evolution of, in cephalopods, 259
  - evolution of, in cetaceans, 259
  - evolution of, in primates, 259, 260
  - evolution of, in social insects, 259
- Internal differentiation, 174–176, 180, 244
- Io, 56, 82, 92, 98, 99, 119, 137, 145–147, 153, 175–178, 180, 212, 213, 225, 226, 283
- Iron, 38, 44, 71, 76–78, 90, 116, 140, 168, 170, 186, 194, 214, 237, 251
- Ironstones, 168
- Isotopic fractionation, 142, 169

J

- Jaws, 258
- Jellyfish, 55
- Jupiter, 43, 45, 82, 89, 91–93, 98, 99, 108, 131, 135, 154, 160, 167, 176–178, 180, 209, 210, 212, 213, 223, 225, 227, 229, 230, 237, 251, 283

K

- Kapteyn b, 241
- Kepler 452b, 235, 240–241
- Keppler, Johannes, 275

Kinetotrophy, 85
Klein, Harold (Chuck), 184

L
Language, 58, 264
Lava tube caves, 152, 170, 209, 281
Lederberg, Joshua, 184
Levin, Gilbert, 184, 187–189
Lichen, 63, 169
Life
  as adaptation, 9, 163
  artificial, 17–19
  based on spin configurations, 247–249
  biological, 8, 14, 18, 273
  biosignatures of, 165–173, 179, 181, 183
  as black cloud, 249, 250
  on a brown dwarf, 250–251
  as collection of attributes, 8
  definition of, 2, 7–27, 106, 249, 250, 252, 253, 261–264 (*see also* Definition of life)
  detection of, 24–26, 165, 166, 173, 183, 189, 202
    metabolic approach, 202
    novel approaches, 201
    by Phoenix mission, 190
    by Viking mission, 183–192
  fossilized in Martian meteorite, 5, 183, 193–195
  future of, 255
  gases produced by, 168
  geoindicators for, 98, 165, 167, 173–174, 179–180, 183, 206
  geosignatures of, 165–167, 169, 179, 203
  as a global community, 17
  as growth, 7, 9, 24
  instruments for detection of, 200–202
  macrobiological, 163
  as matter gone wild, 7
  mechanical, 8, 14, 16, 18–19, 242
  microbial, 25, 52, 61, 91, 110, 129, 133, 150–152, 156, 168, 173, 174, 203–205, 282
  on a neutron star, 92, 250
  origin of, 12, 18, 25, 27–50, 112, 117, 118, 120, 129, 133, 142, 155, 160, 163, 164, 168, 225, 240, 242, 265, 272, 281 (*see also* Origin of life)
  as planetary exuberance, 7
  as plasma inside star, 252
  plausibility of
    metrics for, 224–227
    on rogue planets, 253
  as reproduction, 9, 14, 16
  resilience of, 60
  on a rogue planet, 251–253
  seven pillars of, 13
  signatures of advanced forms, 173
  statistical probability of, 54
  synthetic, 18, 46–49
  tendency to remain relatively unchanged, 53
  tendency to stay small and simple, 55
  tendency toward increasing complexity, 53
  terran, 46, 50, 75, 76, 81, 97, 103, 120, 130, 140, 141, 153, 167, 171, 285
  time required to emerge, 25
  transfer by asteroid, 159
  virtual, 18
Limestones, 168, 194
Liquid medium
  advantages for living processes, 123, 178
  as geoindicator for life, 174
Living entities
  alive but not reproducing, 16
  bioinformatic criteria, 13
  as bounded environments, 19–21
  as bounded local environments, 19, 24, 25, 247
  distinct from being alive, 16
  evolutionary criteria, 16–17
  as low entropy states, 12, 21–22
  as self-organizing, 11
  that convert free energy and materials, 14
  that reproduce frow raw materials, 16
  that reproduce functional capability, 16
  thermodynamic criteria, 14–15
  in thermodynamic disequilibrium, 19–21
  thermodynamic improbability of, 13
Living entity, 8, 12, 19, 22, 23, 249
Living systems, 1, 3, 7, 10, 13–15, 17, 18, 20–23, 25, 27, 28, 45, 55, 75, 76, 79, 80, 86, 91, 93, 97, 103, 105, 117, 118, 121, 123, 125, 130, 134, 135, 146, 152, 157, 164, 165, 172, 175, 181, 205, 214, 221, 224, 227, 250, 253, 255–264
  future and fate of, 255–264
Lobsters, 55
Lorentz force, 88–91
Luminescence, 9, 11, 20
Lungs, 258

M

Macromolecules, 13, 15, 20, 21, 31, 35, 36, 39, 43, 50, 61, 68, 78, 84, 102, 103, 106, 116, 118, 123, 127, 130, 132, 133, 135, 137, 141, 142, 162, 166, 170–172, 178, 200, 211, 281
Macroorganisms, 52, 283
Magnesium, 71, 186, 196, 213
Mammals, 48, 58, 64, 223, 260
Manganese, 71, 76, 78
Manual dexterity, 58, 259, 264
Marcy, Geoff, 229
Mars
  human settlements on, 279, 280, 286
  lava caves on, 152, 208, 227
  one-way human mission to, 280
  robotic exploration of, 277
  sample return from, 205
Mayor, Michel, 229
McKay, David, 25, 49, 169, 170, 190, 192–197, 199, 216, 217, 219, 262, 263, 283
Melanin, 170
Membrane, 20, 21, 27, 30, 35–37, 39, 41, 43, 52, 54, 61, 63, 69, 75, 79, 82, 84, 86–88, 93, 101, 118–120, 127, 129, 130, 138, 141, 142, 158, 197, 218
  cellular, 27, 36–37, 61, 120, 127, 129, 138, 142
Membranes
  phosphate in, 120
Mercury, 57, 71, 93, 99, 153, 176, 180, 203–204, 225, 277
Metabolic rates, 258
Metabolism, 8, 10, 11, 14–16, 27, 28, 35–39, 45, 52, 63, 66, 68, 69, 75–78, 82, 84, 89, 103, 110, 111, 121, 130, 131, 133, 137, 153, 162, 167, 170, 186, 189–191, 205, 211, 212
Metal oxide, 9, 10
Meteorite
  heavy bombardment of, 31
Methane, 4, 29, 38, 77, 81, 101, 103, 108, 109, 116–118, 121, 124, 134, 139, 140, 142, 146, 147, 162, 167, 174, 178, 184, 186, 201, 202, 205, 206, 208, 210, 211, 214, 216–222, 233, 237, 251, 278, 283
Methanogenesis, 38, 76, 77, 103, 142, 214, 283
Methanol, 63, 121, 131, 139–141, 144, 147
Methyl chloride, 167
Methyl iodide, 167
Micelles, 28, 36, 109
Microbialites, 55, 169
Microfossils, 169
Microorganisms, 31, 42, 46, 49, 63, 64, 66, 69, 70, 153, 196, 212, 219, 221, 279
Microwave radiometry, 176
Miller, Stanley, 12, 29, 31, 44, 52, 53, 78, 105, 257
Mineralogy, 10–12
Minerals
  as catalysts, 28
  as templates, 40
Miranda, 180, 226
Mission
  Cassini-Huygens, 142, 283
  ExoMars, 179, 201
  Galileo, 177–179, 283
  Genesis, 282
  Kepler, 251, 253, 258
  Lunar Apollo, 293
  Mars Express, 179
  Mars Global Surveyor, 179
  Mars Odyssey, 207
  Mars Odyssey Orbiter, 207
  Mars Reconnaissance Orbiter, 179, 277
  Mars Science Laboratory, 179
  Pathfinder, 179
  Phoenix, 179, 190–192, 266
  Russian Mars '96, 190
  Spirit and Opportunity, 179
  Stardust, 224, 282
  Terrestrial Planet Finder, 234
  Viking, 21, 179, 183–193, 202
Missions
  robotic *vs.* human, 5, 275, 278, 285, 286
  sample return, 156, 157, 205, 223, 277, 282
Mollusks, 58, 72, 257–259
Molybdenum, 71
Monomers, 28, 31, 32, 44, 171, 201
Montmorillonite, 40, 118
Moon, 15, 22, 24, 25, 32, 56, 91–94, 98, 99, 115, 117, 119, 131, 142, 149, 151, 153, 160, 162, 165, 167, 168, 174, 177, 179, 180, 183, 186, 202, 203, 205, 206, 212, 215, 217, 220, 222, 223, 225–227, 237, 241, 242, 244, 245, 268, 275, 276, 278, 280–284, 286
Multicellular, 16, 20, 23, 52, 54, 55, 58, 61, 63, 66, 68, 71, 72, 129, 133, 150
Murchison meteorite, 105

N
Nakhla, 199
Nanobacteria, 42, 194, 196, 197
NASA, 179, 184, 185, 192, 194, 198, 205, 208, 235, 255, 266, 275, 276, 278, 280, 282, 284, 285
Natural selection
  directional, 58, 156, 205, 207, 208, 221, 258
  stabilizing, 4, 55–58, 73, 153, 256
Nematode, 67, 68
Neptune, 1, 99, 174, 177, 178, 180, 210, 211, 220, 221, 225, 227
Nervous systems, 58, 68, 259
Nitriles, 29, 143
Nitrogen, 3, 8, 15, 32, 41, 71, 78, 101, 103, 104, 106, 109, 113, 119, 120, 131, 133, 134, 136, 139–141, 162, 169, 170, 174, 184, 186, 216–218, 220–222, 225, 237
  abundance of, 131

O
Oberon, 180, 226
Oligonucleotide, 28
Origin of life
  benthic thermophilic, 30–31
  chemo-autotrophic, 30
  conditions for, 227, 242
  constraints on, 160
  on differentiated, heterogeneous worlds, 40, 45
  failure of quantum mechanics to predict, 27
  first cellular membranes, 27, 36–37
  first metabolism, 27, 36–39
  first replication mechanism, 27, 39–41
  first replication mechanisms, 39–41
  in ice water, 31
  implications for life on other worlds, 45
  iron-sulfur world, 30, 44
  lukewarm marine, 29–30
  on Mars, 42, 141
  medium for, 43–44
  meteorites and, 31, 32, 44
  minerals and substrates for, 44–45
  requirements for, 35–36
  sparking experiments, 29
  in tide pools, 32
Orphan planets, 161
Osmolarity, 67
Osmotic stress, 67, 151
Osmotrophy, 87
Oxidation
  of carbon, 121
  of hydrogen, 38, 39, 50, 76–78, 80
  of hydrogen sulfide, 38
  of minerals, 52
  of organic sources, 78
  of sulfur, 77, 78
Oxygen
  abundance of, 121
  as geosignature of life, 166
Oyama, Vance, 184, 186, 189, 191
Ozone, 43, 129, 166, 167, 201, 225, 276, 279

P
Paleozoic-Mesozoic (P-M) boundary, 257
Panspermia, 27, 28, 42, 158, 159, 211
Peptide bonds, 30, 102, 130, 132, 141
Peptide nucleic acids (PNA), 40
Peptides, 31, 40, 111, 127, 130, 141, 200, 201
Permian-Triassic boundary, 57, 259
Perovskite, 93
Phospholipids, 36, 37, 170
Phosphonic acid, 105
Phosphorus, 71, 103–106, 109, 120, 121
  abundance of, 120
Photoautotrophy, 15, 75, 79, 81, 89, 94, 98, 167
Photooxidation, 77
Photosynthesis, 8, 11, 21, 22, 29, 38, 39, 52, 63, 76, 79, 81, 91, 97, 104, 109, 150, 153, 156, 167, 168, 176, 184, 207, 251, 258, 259
  animal, 76
  chlorinic, 81, 168
  oxygenic, 76, 81
  spectral signature of, 167
Planetary protection, 280, 285
Plate tectonics, 82, 93, 175, 213, 225, 244
Plausibility of life (POL) index, 155, 215, 224–227
Pluto, 1, 100, 180, 220–222, 225, 227, 228, 252
Polychaetes, 65
Polycyclic aromatic hydrocarbons (PAHs), 104, 193, 200, 201, 204
Polymeric chemistry, 3, 4, 107, 109, 112–114, 144, 165, 173, 175, 180, 181, 206, 224
Polymerization, 29, 32, 40
Polymers, 3, 4, 28, 46, 66, 103, 105–107, 109, 113–118, 121, 175, 201, 218, 250
Potassium, 67, 71, 135, 251
Prebiotic molecules, 120
  on Titan, 162
Prebiotic soup, 29

Precambrian, 52, 168
Pressure, 3, 4, 39, 43, 44, 46, 56, 61–66, 69–70, 72, 79, 82, 85–87, 93, 94, 98, 99, 104, 107, 113, 116, 118, 121, 123, 125–128, 131, 133, 134, 138, 140, 143, 144, 146, 147, 151, 155–157, 159, 176, 177, 180, 191, 207, 208, 210, 221, 225, 234, 239, 249, 251
  hydrostatic, 63, 69
Primates, 58, 259, 260
Primordial soup, 29
Prokaryotes, 68, 79, 150, 151
Protein, 9, 15, 16, 18, 23, 28, 30, 35, 39, 40, 46, 47, 49, 50, 61, 63–68, 75, 80, 86, 101, 103, 104, 106, 107, 110, 111, 121, 127, 130–133, 135, 142, 170, 200, 201
Protists, 62, 84, 258
Protometabolism, 45
Protoplasm, 15
Protopolymers, 33
Proxima b, 231, 240
Proxima Centauri, 161, 240
Psychrophily, 62–64
Punctuated equilibrium, 58, 256, 258
Purines, 105, 135
Pyrimidines, 105, 135

Q
Quartz, 93, 190
Queloz, Didier, 229

R
Radar interferometry, 177
Radiation
  alpha particles, 70, 96
  beta particles, 70, 96
  cosmic rays, 70, 175, 268
  gamma, 62, 70, 96, 196, 200
  infrared, 81, 176, 177, 205, 268
  ionizing, 43, 70, 71, 96, 156, 279
  radioactive decay, 70, 96, 175, 268, 283
  solar, 98–100, 227
  ultraviolet, 9, 70, 80, 113, 129, 205, 206, 219
  x-ray, 70
Radiowaves, 166, 173
Red dwarfs, 162, 163, 240, 271
Red edge effect, *see* Exoplanets
Reduction
  of carbon dioxide, 38, 39, 77
  of iron, 77, 78, 214
  of manganese, 76, 78
  of sulfur, 76–78
Replication, 16, 23, 26–28, 31, 33–35, 39–41, 50, 70, 96, 111, 112, 248, 249, 252
Respiration, 111
  aerobic, 68, 76, 103
Rhea, 180, 204, 226
Rich, Alexander, 184
RNA, 9, 10, 25, 28, 31, 34, 35, 39–42, 105, 120, 130, 200
  phosphate in, 120
  self replication of, 31
RNA world, 28, 31, 34, 40
Rochelle salt, 93
Rogue planet, 251–252
Rotifers, 62, 66, 67
Rovers on Mars
  Pathfinder, 179
  Spirit, 179

S
Salinity, 61, 67, 72, 87
Sand, 41, 65, 190, 217
Saturn, 45, 89, 92, 98, 99, 142, 154, 162, 174, 178–180, 210, 215–217, 225–227, 283, 284
Selection, 4, 36, 55, 56, 58, 72, 153, 256, 259, 277, 278
  See also Natural selection
Selenium, 71, 76
SETI, 173, 241, 265–272
Sharks, 55, 257
Shewanella oneidensis, 251
Silanols, 140
Silicon
  bond energies with other elements, 103, 107, 112
  C–Si bond, 107
  physical properties, 107–109
  polymeric chemistry of, 112–114
  Si-O bond, 113
Sodium, 67, 93, 213
Sodium chlorate, 93
Sodium chloride, 67
Solvents
  cosmic abundance, 136, 144, 145
  dipole moment, 93, 124–126, 128, 132, 134, 136, 137, 139, 141, 144, 145
  distance distribution from Sun, 138

Solvents (*cont.*)
  enthalpy of vaporization, 125
  inorganic non-polar, 139–140
  local abundance, 144, 145
  organic non-polar, 127, 141–142
  organic polar, 140–141
  physical properties of, 124, 125, 128, 139
  suitability for different planets, 242
  thermal range, 131, 145, 147
Space habitats
  challenges of, 156
  microbial survival in, 158
SpaceX, 284
Stars
  brown dwarfs, 161, 250–251, 253
  G, 162
  M, 162–164, 240
  red dwarf (dM), 162, 163, 240, 271
Stromatolites, 20, 22, 24, 52, 166, 168, 169, 257
Sturgeons, 55
Subcellular specialization, 41, 52
Subsurface habitats
  advantages of, 150
  caves, 152, 174
  challenges of, 150
  on icy satellites, 152
  macroscopic life in, 152
  on Mars, 152
  on Mercury and Venus, 153
  on the Moon, 153
Sulfide, 30, 35, 36, 38, 39, 62, 77, 136–137, 144, 147, 170, 178, 193, 194, 283
Sulfonic acid, 105
Sulfur, 38, 39, 44, 71, 76–78, 81, 84, 101, 104, 106, 109, 113, 119, 120, 137, 146, 167, 168, 170, 178, 211, 226
  abundance of, 104
Sulfur dioxide, 136–137, 178
Sulfuric acid, 130, 136–137, 204, 205
Sun, 7, 52, 63, 70, 79–81, 92, 96, 104, 137, 149, 151, 156, 161, 162, 176, 203–207, 221–225, 230, 235, 236, 240, 281, 284, 286
Supercritical fluids, 143, 197
Surface habitats
  advantages of, 150
  challenges of, 150
Survival
  anoxic, 69
  hypobaric, 70
  maximum acidity for, 65
  maximum alkalinity for, 66
  maximum temperature for, 64
  minimum water activity for, 66–68
Symbolic language, 264

T
Tardigrades, 63, 67, 71, 126
Technology, 18, 157, 165, 166, 168, 171–174, 200–203, 231–233, 236, 246, 259–261, 264, 267, 269, 272, 275, 276, 280, 282
TEGA instrument, 190
Teleonomy, 13
Teleosts (bony fishes), 86
Tethys, 180, 226, 284
Thermal radiometry, 176, 177
Thermophiles, 30–31, 64–65, 158, 204
Thermosynthesis, 82, 97
Thermotrophs, 82–84
Threose nucleic acids (TNA), 40
Tidal flexing, 82, 92, 98–100, 152, 153, 213, 215, 225, 226
Tide pools, 32
Titan, 22, 24, 37, 56, 57, 93, 98, 100, 117, 121, 134, 135, 139, 140, 142, 145, 146, 153–155, 162, 172, 174, 176–180, 183, 215, 217–221, 223, 225–228, 235, 237, 244, 262, 263, 282, 283
Titania, 152, 179, 180, 226, 284
Transition metals, 28
Triton, 34, 57, 98, 100, 139, 140, 146, 152, 174–177, 179, 180, 220–223, 225–227, 252, 282
Tropical forests, 59
Troposphere, 62, 63, 210
Turtles, 55, 62, 68, 257

U
Ultraviolet radiation, 9, 70, 113, 129, 205, 206, 219
Umbriel, 180, 226
Uranus, 99, 178, 180, 210, 211, 225, 284
Urey, Harold, 29

V
Vascular plants, 64
Venus, 56, 57, 98, 99, 130, 137, 143, 150, 153–157, 160, 165, 173, 174, 176, 177, 179–181, 204–205, 225, 227, 228, 230, 237, 239, 263, 276, 277, 282, 286
Vertebrates, 55, 61, 68, 84, 110, 257, 258

Viking landers
  Gas Exchange Experiment, 184, 186, 187, 189, 191
  Labeled Release Experiment, 184, 185, 187–189, 191, 192, 201
  mission preparation, 185–186
  Pyrolytic Release Experiment, 184, 187–189, 191
Virtual reality, 261
Virus, 10, 12, 48
Vishniac, Wolf, 184
Vitalism, 12

W
Water
  activity of, 67
  as climatic stabilizer, 128
  cosmic abundance, 136, 144, 145
  dissociation of, 104, 133
  as heat insulator, 127, 144
  high surface tension of, 129
  as source of oxygen and ozone, 190
  triple point of, 126
  as universal solvent for life, 45, 125–130
  unusual properties of, 129
Water-hydrogen peroxide (H_2O–H_2O_2), 190, 192

Z
Zinc, 71