National Aeronautics and Space Administration

ASTROBIOLOGY STRATEGY

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EXECUTIVE SUMMARY

NASA's strategic objective in planetary science is to determine the content, origin, and evolution of the Solar System and the potential for life elsewhere (*2014 NASA Science Plan*). Astrobiology research sponsored by NASA focuses on three basic questions: How does life begin and evolve? Does life exist elsewhere in the Universe? What is the future of life on Earth and beyond? Over the past 50 years, astrobiologists have uncovered a myriad of clues to answering these Big Questions.

Since the astrobiology community published its last roadmap in 2008, research in the field has focused more and more on the link between the "astro" and the "bio" in astrobiology—that is, what makes a planetary body habitable. "Habitability" has become a major buzzword in astrobiology as researchers have learned more about extraterrestrial environments in our Solar System and beyond and deepened their understanding of how and when the early Earth became habitable.

Why is Earth habitable? How, when, and why did it become habitable? Are, or were, any other bodies in our Solar System habitable? Might planets orbiting other stars be habitable? What sorts of stars are most likely to have habitable planets? These are just a few of the questions that astrobiologists are trying to answer today.

In preparing this new science strategy, hundreds of members of the astrobiology community collaborated in an intensive process of defining goals and objectives for astrobiology research moving forward. The community identified six major topics of research in the field today:

- Identifying abiotic sources of organic compounds
- Synthesis and function of macromolecules in the origin of life
- Early life and increasing complexity
- Co-evolution of life and the physical environment
- Identifying, exploring, and characterizing environments for habitability and biosignatures
- Constructing habitable worlds

This science strategy identifies questions to guide and inspire astrobiology research on each of these topics—in the lab, in the field, and in experiments flown on planetary science missions—over the next decade. The strategy also identifies major ongoing challenges that astrobiologists tackle as they attempt to answer these universal questions.

Progress and accomplishments in each of these areas of research over the past ten years are detailed in each of the successive chapters of this document.

What follows is a brief summary of the topics described in depth in Chapters 1–6 of this strategy.

Identifying Abiotic Sources of Organic Compounds

Where did the building blocks of life come from? A major goal of research on this topic in astrobiology is to understand how the abiotic (non-biological) production of small molecules led to the production of large and more complex molecules, prebiotic chemistry, and the origin of life on Earth. This line of research also aims to understand what roles primitive icy bodies (asteroids and comets) play in the origin of life on habitable planets and whether life or prebiotic chemistry could or did evolve on differentiated (altered) icy worlds such as Enceladus, Europa, and Titan. Understanding the production of molecules in various endogenous (planetary) environments, as well as in exogenous (space) environments with the associated delivery of extraterrestrial molecules to planetary surfaces, is critical for establishing the inventory of ingredients from which life originated on Earth.

Synthesis and Function of Macromolecules in the Origin of Life

On Earth, macromolecules—specifically, proteins and nucleic acids—form the catalytic and genetic means for life to sustain itself. Macromolecules evolve—that is, they change over time—thus meeting another criterion for recognizable life.

The macromolecules (large, complex molecules, or polymers) of Earth-based life are composed of a small subset of all potential chemical building blocks (smaller organic molecules, or monomers). It is likely that the exact components of these macromolecules are accidental. It also is possible that macromolecules formed from different selections of smaller molecules could characterize other living systems. Thus, it is crucial to characterize the overall chemical underpinnings of the processes that lead to the function and persistence of evolvable macromolecular systems. As part of this effort, it is necessary to identify interactions, intermediary structures and functions, energy sources, and environmental factors that contributed to the diversity, selection, and replication of these systems.

These macromolecules are uniquely capable of the structural, catalytic, and genetic functions required for life. The diverse chemical alphabet of 20 amino acids found in Earth life leads to protein architectures that are capable of structural transitions essential to catalytic functioning. Catalysis can be carried out by nucleic acids and proteins. In general, protein catalysis is more efficient than nucleic acid catalysis. Nucleic acid catalysts found in life today are thought to be “living fossils” of an earlier system.

From a broader perspective, these polymers can be seen not only as the information- and function-carrying molecules in life on Earth but also as information- and function-carrying molecules for life on any planet. As such, questions of whether and how polymers transmit information and fold to generate function are of interest.

To further refine understanding of life’s origins and early chemical evolution, researchers must continue to map the chemical landscape of potential primordial informational polymers. The advent of polymers that could replicate, store genetic information, and exhibit properties subject to selection likely was a critical step in the emergence of prebiotic chemical evolution. Astrobiologists thus must focus on developing an understanding of macromolecule synthesis, stability, and function in the context of plausible prebiotic conditions and environments.

Early Life and Increasing Complexity

Understanding the history of life on Earth is key to a full understanding of what life is and how it works. Over four billion years, life on Earth has generated an extraordinary range of organizational plans, creating the immense variety that operates on Earth today. Astrobiologists face the challenge of deciphering overarching rules for evolutionary processes, drawing on theory and observation to make a general model of life.

Recognizing life on other planets depends on how scientists define life. However, defining life has proved problematic because it is unclear where to draw the boundary between living and non-living entities, or whether drawing such a boundary is the best way to frame the issue. For example, self-replicating RNA, viruses, and prions are alive by some definitions but not by others. The lack of a precise boundary between living and non-living entities today mirrors a similarly fuzzy divide at the origin of life. Identifying which attributes of life are likely to be common to all origins, and which are context-dependent, will enable better predictions about the possible nature of life on other planets.

Co-Evolution of Life and the Physical Environment

Life affects its environment. At the same time, the environment affects life. Astrobiologists are focused on understanding the relationship between life and environment well enough to inform the search for potentially habitable environments beyond Earth. Examples of major transitions in biological evolution that affected our planet include the origins of photosynthesis, multicellularity, and intelligent life. Major changes in the physical state of the planet that have affected biology include the emergence of plate tectonics and continents, as well as climatic transitions such as "Snowball Earth" episodes.

Studying the co-evolution of life and environment informs other lines of research in astrobiology in three major ways. First, the delivery of abiotic organic compounds to Earth and the development of prebiotic chemistry on Earth can be thought of as the first environmental influences on life. Second, as early life evolved increasing complexity, its interactions with the planet would have increased in diversity, eventually developing into complex feedback systems. Studying Earth's co-evolutionary past can improve understanding of habitability on Earth and Earth-like planets. Third, studies of other planets—both real and hypothetical—inform and benefit from work on the intimate interactions between life and its physical environment.

Identifying, Exploring, and Characterizing Environments for Habitability and Biosignatures

Identifying and characterizing habitable or inhabited environments requires the synthesis of information from a large range of spatial scales. Astrobiologists are focused on the goal of determining whether a particular environment was or is presently habitable and whether it was or is able to generate and support life. Habitability indicators, including biosignatures, must be interpreted within a planetary and environmental context. The aim is to understand how habitable worlds and environments form and evolve, better understand the range of parameters that influence habitability, and determine how to detect, confirm, and characterize habitable environments.

The development of new tools for determining the relative habitability of either present or ancient environments within the Solar System will facilitate target selection for future planetary missions. These tools also will enable researchers to prioritize exoplanets for targeted follow-up observations of potential habitability.

Constructing Habitable Worlds

Earth is the only inhabited world we know thus far. Missions to explore other worlds are searching for others. In addition to Solar System bodies, astrobiologists now have a growing catalogue of planets orbiting other stars to explore as potentially habitable, all with diverse and potentially exotic chemistries and environments. They now face the challenge of determining whether limited experience with habitability, on Earth alone, has limited understanding of the basic set of requirements for a habitable world or whether this experience serves as a helpful guide for the search for life beyond Earth.

Habitability has been defined as the potential of an environment (past or present) to support life of any kind. Liquid water is a necessary but not sufficient condition for life as we know it. Habitability is a function of a multitude of environmental parameters whose study is biased by the effects that biology has on these parameters. Habitability may be a matter of degrees, depending on how much diversity, productivity, or spatial cover of life that an environment supports.

A habitable environment is one with the ability to generate life endogenously—solely using available resources—or support the survival of life that may arrive from elsewhere. Whether a planet will emerge as habitable depends on the sequence of events that led to its formation—which could include the production of organic molecules in molecular clouds and protoplanetary disks, delivery of materials during and after planetary accretion, and the orbital location in the planetary system. Habitability provides the context for understanding possible signs for life. A deeper understanding of habitability provides context for interpreting the significance of presumed biosignatures, or their absence.

Conclusion

Given NASA's focus on the search for planets and life, astrobiology will be the focus of a growing number of Solar System exploration missions. Astrobiology research sponsored by NASA will continuing pushing science closer to answering the Big Questions in space science: Where did we come from? Where are we going? And are we alone?

INTRODUCTION

JOHN BAROSS

The first astrobiology roadmap (Des Marais et al., 2008) served as a guideline to advance research on three basic questions: how does life begin and evolve? does life exist elsewhere in the universe? and what is the future of life on Earth and beyond? The roadmap identified seven goals that expanded on these three basic questions while maintaining life as the driving theme. Thus, the life sciences became a central component of future missions to planetary bodies in our Solar System and beyond and in theories and models of the origin of the universe. It also advocated research to better understand life on Earth: its origin, evolution, history, diversity, and limits, with the primary goal of increasing the probability for detecting life elsewhere. The scientific discoveries that were part of the backdrop of the first roadmap were also implicit in pointing out one of the guiding principles of astrobiology: it involves questions and issues that are multidisciplinary and that require an interdisciplinary approach to address.

The new *NASA Astrobiology Strategy* document is a reflection of the many science advancements during the past seven years. These include advancements in our understanding of the potential habitability of planets and moons in our Solar System and beyond and a deepened understanding of how, when, and under what environmental conditions the early Earth became habitable. These, along with new advancements, will help address many key questions including: Are, or were, any other bodies in our Solar System habitable? Might planets orbiting other stars be habitable? What sorts of stars are most likely to have habitable planets? These are just a few of the questions that astrobiologists are trying to answer today. The advancement of research addressing these and other habitability questions is part of NASA's ongoing exploration of our stellar neighborhood and the identification of biosignatures for in situ and remote sensing applications.

While astrobiology at NASA is a research and analysis activity, rather than mission development and operations, the advancements made in astrobiology have resulted in an inseparable link to planetary exploration missions. This is due to the continuing expansion of knowledge about life, habitability, and the co-evolution of life and its environments. Consequently, astrobiology will have a greater focus on such missions. This is already evident in current and planned missions to Mars and icy moons of Saturn and Jupiter. The spectacular accomplishments of the Mars rovers have greatly advanced our understanding of the geological and geochemical history of Mars and in the selection of sites for future missions that have the greatest potential for past or present habitability. The *Mars Atmospheric and Volatile Evolution* mission (*MAVEN*) that commenced in September 2014 is providing insight into the history of climate change on Mars. The data generated will provide astrobiologists with a glimpse of Mars' past when there were bodies of liquid water and potential habitable environments. Astrobiologists are also involved in planning for NASA's next Mars Lander mission, *Mars 2020*, and the European Space Agency's *ExoMars* mission. Both missions have the goal of searching for biosignatues of life by exploring martian environments including its subsurface.

Similarly, spectacular discoveries have and are still being made by *Cassini-Huygens* mission to Saturn's moons, Titan and Enceladus. Both moons offer astrobiologists the opportunity to explore the possibility of habitability in liquid bodies that include hydrocarbon lakes on Titan and a salty, liquid subsurface ocean on Enceladus. *Cassini* captured water-ice crystals erupting from Enceladus' surface plumes for chemical analysis. The presence of a wide range of organic compounds and ammonia indicates their source may be similar to the water/rock reactions known to occur on Earth and that are known to support life. These water/rock reactions, which may be the result of tidal-heating, may also be occurring on Jupiter's moon Europa. Future astrobiology-led missions will further explore the potential for these and other icy moons to support life, as we know it, while increasing our understanding of the diversity of potential geophysical processes that might be linked to chemical steps involved in the origin of life.

Beyond our Solar System, thanks to observations by NASA's *Kepler* planet-hunting spacecraft, an astrophysics mission launched in 2009, astrobiologists now have an exploding tally of exoplanets to study and characterize, many within their star system's habitable zone. (While the habitable zone is currently defined as the region around a star in which a planet could sustain liquid water on its surface, it is worth noting that astrobiologists are debating whether this definition should be updated based on what they have learned in the last few years.) Present and future research will focus on new instrumentation and models to further characterize Earth-like exoplanets including a broader spectrum of gases and particles in the atmosphere as well as an assessment of important geological properties including volcanism and the potential for plate tectonics.

The origin and early evolution of life is another exciting key focus of astrobiology research. There are three components of these research efforts which include (1) understanding the sources of the organic building blocks of life and how they react to form the canonical macromolecules of life including nucleic acids, proteins, and lipid membranes; (2) taking advantage of advancements in molecular biology and biochemistry to better understand the diversity and evolutionary history of extant microbes as a window into better understanding the physiologies, including metabolisms, of the earliest organisms; and (3) merging the results from (1) and (2) to better constrain the environmental conditions that can spawn life. Astrobiology is also committed to understanding the boundary conditions for life on Earth and whether or not those boundary conditions can be expanded to include extraterrestrial environments not found on Earth. While considerable emphasis in astrobiology has been on the detection of microbial life on planets and moons in our solar system, the search for life on exosolar planets has the additional focus to better understand the origin and evolution of complex life and its co-evolution with the environment throughout Earth's history. It is possible that an Earth-like exoplanet will be discovered that is in some transition period similar to one of those that Earth experienced during its four billion year history. It also follows that astrobiology is interested in the future of life on Earth and beyond.

Below is a list of goals for the astrobiology-community that will help us meet the challenges we face over the coming decade. If we meet these goals, the impacts will be profound. Most directly, this will improve our research products on the origins, evolution, and future of life on Earth and on the abundance of habitable and inhabited environments beyond our home planet. Additionally, the individuals that lead us past these obstacles will take on other challenges in other disciplines and, as they do so, will bring with them the successful strategies they develop for communicating across disciplinary boundaries and at the forefront of knowledge of humanity's place in the cosmos.

Foster Interdisciplinary Science. Astrobiology is multidisciplinary in its content and interdisciplinary in its execution. Its success depends critically upon the close coordination of diverse scientific disciplines and programs, including space missions.

- Understand linkages between geology, climate and life
- Coordinate field/mission observations, laboratory experimentation and theory
- Enhance effective communication between scientists and technologists
- Promote collaborations between government offices and agencies
- Enhance the ability of society to address important challenges that require interdisciplinary approaches.

Enhance NASA's Missions. Astrobiology research and technology programs help NASA's missions determine the distribution of habitable environments and life in the Universe and thereby deepen our understanding of the origins, evolution, and fundamental nature of life.

- Research analog environments to understand processes underlying habitability
- Develop more effective proxies for life (biosignatures) and environments ("envirosignatures").

Promote Planetary Stewardship. Astrobiology encourages planetary stewardship through an emphasis on understanding relationships between life and its environment, protections against forward and back biological contamination, and recognition of ethical issues associated with exploration.

- Understand interactions between biological activity and environmental change at several spatial scales (e.g., has synergy with other government, etc. programs on the anthropocene)
- Support planetary protection efforts (comply with international agreements)
- Constrain human exploration (minimize adverse impacts on other planetary environments).

Enhance Societal Interest and Relevance. Astrobiology recognizes a broad societal interest in its endeavors, especially in areas such as achieving a deeper understanding of life, searching for extraterrestrial biospheres, assessing the societal implications of discovering other examples of life, and envisioning the future of life on Earth and in space.

- Act upon the public interest to understand our place in the Universe and broaden understanding of life

- Sustain the human imperative to explore the unknown.

Inspire Future Generations. The intrinsic public interest in astrobiology offers a crucial opportunity to educate and inspire future generations of scientists, technologists, and informed citizens. Thus, a strong emphasis upon education and public outreach is essential.

- Enhance the interest in science and technology to the benefit of our society
- Enhance critical and creative thinking in all fields of inquiry.

NASA continues to be the lead agency of astrobiology research in the United States. In addition, NASA collaborates with other agencies such as the National Science Foundation and with the growing number of nations that are engaging in planetary exploration and the search for evidence of life beyond Earth. Looking into the future, astrobiology will be the focus of a growing number of Solar System exploration missions, as astrobiologists keep finding new potentially habitable environments inside and outside our Solar System.

Research accomplishments over the past five years have guided the astrobiology community in developing a new science plan for the field, detailed in this report. What follow is a series of discussions of recent astrobiology research accomplishments and a vision for research over the next decade. Major discoveries in science are typically the result of a long line of seemingly small but significant findings. Over the past five years, astrobiologists have produced a rich array of findings that, ultimately, will help to answer the big questions in the field.

UPDATES TO THE ROADMAP

FRANK ROSENZWEIG

SUMMARY

Over the past year, NASA Astrobiology Mission Directorate has sponsored a grass-roots effort to develop a decadal Strategic Plan that is aspirational, inspirational, and inclusive. The path toward this goal has now passed through four stages: public review of the 2008 Roadmap, formulation of concept papers describing science that astrobiologists “would like to write or to read about 10 years from now,” public discourse on these concept papers, and integration of concept papers into six thematic documents: *Identifying abiotic sources of organic compounds; Synthesis and function of macromolecules in the origin of life; Early life and increasing complexity*; *Co-evolution of life and the physical environment*; *Identifying, exploring, and characterizing environments for habitability and biosignatures*; and *Constructing habitable worlds*. The final stage in developing the new *Astrobiology Strategic Plan* will be to assemble these thematic documents into a draft Roadmap that will be revised following review by NASA Advisory Council. Because achievement of this goal has been a community effort, the process of creating the new decadal Plan embodies the proverb, “Art is I, Science is We.”

Astrobiology Strategic Plan: Updating the Astrobiology Roadmap

The 2008 Astrobiology Roadmap has brought clarity to the scientific scope and mission of NASA’s Astrobiology Program, and has guided principle investigators along the path toward answering fundamental questions such as: How did life on Earth emerge and how did early life evolve with its changing environment? What are the environmental limits of life as we know it? By what evolutionary mechanisms does life explore the adaptive landscape shaped by those limits? What principles will shape life in the future? Do habitable environments exist elsewhere in the Universe? and By what signatures may we recognize life on other worlds as well as on early Earth? Programmatic output can be measured in terms of new knowledge, human resources, public outreach, and intellectual property. Over the past Roadmap cycle NASA’s Astrobiology Program teams have generated more than 5,000 original peer-reviewed publications and trained hundreds of graduate and post-graduate students in core STEM disciplines: Physics, Chemistry, Biology, Mathematics, and Computer Science. NASA’s Astrobiology Program teams have projected NASA-sponsored research into the nation’s K–12 schools, have stimulated public awareness of and interest in science by circulating hundreds of press releases, blogosphere entries, and tweets and have served as the focus of dozens of reports in mainstream media outlets such as the *BBC, New York Times, Discover,* and *National Geographic*. Finally, NASA Astrobiology funding has spawned a dozen invention disclosures and patents and catalyzed at least one new start-up company. By all these metrics, NASA's Astrobiology Program can be accounted as a resounding success, a testament to the utility of constructing and implementing a Strategic Plan as well as to the energy and ingenuity of NASA PIs.

Over the past year, NASA Mission Directorate has promoted a grass-roots effort to envision a new Strategic Plan for the coming decade. To ensure that this Plan be aspirational, inspirational, and inclusive, NASA contracted *KnowInnovation* (http://knowinnovation.com/), consultants who facilitated comparable activities at NSF, AAAS, and the American Mathematical Society. The *2015 Astrobiology Strategic Plan* has been developed in five stages, each meticulously recorded and made accessible for public review and comment. The first stage was launched in May 2013 and consisted of five hour-long, NASA PI-led webinars that were broadly focused on topics related to the 2008 Roadmap but also aimed at astrobiology's future: Early Evolution of Life and the Biosphere, Planetary Conditions for Life, Evolution of Advanced Life, Prebiotic Evolution, and Astrobiology for Solar Systems Exploration (https://astrobiologyfuture.org/). Following each webinar, members of the astrobiology community engaged in a spirited week-long, on-line debate that produced a rich record of controversy and critical knowledge gaps. This ground-breaking activity drew over 500 participants whose research interests spanned the entire range of our community.

The second stage of Strategic Plan-making was launched in mid-June 2013. Under the auspices of the National Research Council, 60 scientists gathered for four days at the Wallops Flight Facility in Wallops Island, VA. In keeping with the broad scope and interdisciplinary nature of astrobiology research, the Strategic Plan Working Group consisted of biochemists, physicists, evolutionary biologists, applied mathematicians, and paleontologists, both actually and virtually present. Working group members shared a record of scholarship attesting to their ability to work across disciplinary boundaries and to think critically about astrobiologically significant targets of planetary exploration, essential attributes needed to engage in the organic process envisioned by *KnowInnovation* facilitators.

The goal of the Wallops Island gathering was to build by brainstorming, argument, and consensus a set of working documents, each focused on a broad research theme that could be easily explained and justified. Each working document contained a set of sub-questions that were framed to provoke further community input about potential research projects. The first step in the path toward this goal was for participants to pose questions, the answers to which would be "the paper s/he would like to write or to read in 10 years' time." These were debated by the group as a whole, reduced to several dozen questions recorded on sticky notes, posted, then iteratively grouped into broad categories. Relative interest in these categories was then assayed by forming "chains of interest" among participants. Focus groups nucleated around categories that attracted the interest of five or more participants, who then worked to define a category with an overarching question. These "big questions" led to the creation of a set of twenty-six concept documents, accessible at https://astrobiologyfuture.org/. Although very different types of science are represented among these documents, the paths that led to each shared four features: first, each focus group included investigators whose research specialty lay in that category and others who held a keen interest; second, focus group membership was fluid, with participants freely moving among and contributing to different groups; third, the "big questions," their explanations and justifications, as well as each subsidiary question were iteratively vetted by the Strategic Plan team as a whole through a series of poster sessions, each of which was succeeded by additional focus group meetings; and finally, each working document was composed in Google.docs via real-time collaboration among focus group members and, until the last day, the Strategic Plan team as a whole. Thus, genesis and refinement of each concept document progressed via argument and consensus, in keeping with the goal of envisioning a new Astrobiology Roadmap that is aspirational and inclusive.

The third stage of Strategic Plan-making was launched September 19 with a three-part Kick-off webinar led by participants Eric Smith and Frank Rosenzweig, Program Officer Michael New, and NASA Postdoctoral Management Program Fellow Lindsay Hays. This webinar laid out the ground rules and objectives for the next five months. The concept documents, which had been further refined over the summer, were now open to discussion by the community at large. Beginning on September 25 with *How might the evolution of the atmosphere through Earth's history, including its interactions with the solid Earth and biosphere, inform our exploration of habitable worlds?* and ending on January 30 with *What was the origin and early evolution of photosynthesis?* each concept document was presented as a single-question public webinar with virtual Q&A, followed by a week-long open forum. These webinars remain part of the public record of how the astrobiology community has created its new Strategic Plan (http://www.youtube.com/view_play_list?p=PL2vV9BqKn2ze3RuPly6UCkkshnVynpVoY). Commentary and debate following each webinar engaged astrobiology researchers as well as interested lay persons, and was notably incisive and collegial. The concept documents and webinars remained open for viewing and commentary at https://astrobiologyfuture.org/ through mid-February. Altogether, nearly 250 individuals participated in the Astrobiology Future webinars in real time; 30 individuals (other than the paper authors themselves) registered a total of over 80 comments on the white papers in the week-long follow-ups. Public commentary was instrumental in helping Wallops Island focus group co-authors to refine their documents into a set of white papers, which served as the starting point for the next Strategic Plan-making activity.

The fourth stage in creating our new Strategic Plan was undertaken at the Astrobiology Integration Workshop convened in Washington, DC March 21–24, 2014. Twenty-five representatives from the Astrobiology community, all current or past NASA PIs, joined with NASA Astrobiology Program Officers, NPMP Lindsay Hays, *Astrobiology Magazine* editor Leslie Mullen, *KnowInnovation* staff, and *Gizmo the Goldendoodle* to merge the twenty-six white papers into a set of six thematic documents. As at each prior stage, the process by which this was achieved was collaborative and iterative and subject to debate with each iteration. While membership in a particular thematic writing group was fixed, each group designated ambassadors to communicate with other groups working on conceptually related documents. Also, every day, Workshop participants gathered as one body in morning and in evening sessions to report on progress toward integrating "their" white papers as well as on thorny issues that had emerged as barriers to integration. At the conclusion of the workshop, participants discussed the research implications raised by questions identified in each document, in particular, how research carried out under one theme might overlap with and support research carried out under others. The March Integration Workshop produced six thematic documents that broadly encompass all of Astrobiological science: (1) *Identifying abiotic sources of organic compounds*, (2) *Synthesis and function of macromolecules in the origin of life*, (3) *Early life and increasing complexity*, (4) *Co-evolution of life and the physical environment*, (5) *Identifying, exploring, and characterizing environments for habitability and biosignatures*, and (6) *Constructing habitable worlds.* These six themes are being assembled to create a new decadal Strategic Plan, which will lead to the final stage of the process. The first draft will be reviewed by the Planetary Science Subcommittee of the NASA Advisory Council and by an *ad hoc* committee of the National Research Council. Following the consideration of comments arising from these reviews, a final draft will be published in fall 2015.

Claude Bernard, the father of physiology, famously remarked, “Art is I, Science is We.” The grass-roots effort that has created the new Strategic Plan embodies this concept. The astrobiology community will have produced a document that is at once aspirational, inspirational, and inclusive, a Roadmap with which the NAI can navigate toward even greater success in the coming decade.

1 IDENTIFYING ABIOTIC SOURCES OF ORGANIC COMPOUNDS

INTRODUCTION

The organic molecules of life span a wide range of molecular weights and constitution: from the small molecules of metabolic cycles (e.g., citric acid) and the monomers of polymers (e.g., amino acids) to the macromolecular polymers (e.g., proteins, nucleic acids, polysaccharides). The small molecules of metabolic cycles and the monomers of biopolymers are often considered the "building blocks" of living organisms.

These molecules are necessary for the abiotic synthesis of the larger molecules (e.g., functional polymers) and chemical systems (e.g., metabolic cycles) that constitute life. Understanding how the abiotic production of molecules (including what is commonly referred to as prebiotic molecules) led to the origin of life on the early Earth and on other potentially habitable planets is a major goal of the research.

Abiotic molecules include those that are not directly involved in the origin of life, as well as molecules that are used in life. For example, abiotic chemical reactions can produce a wide range of amino acids; however, only a small subset of possible amino acids is used in life. In model prebiotic reactions and/or meteorites, a good number of amino acids are formed.

An important step in the process that led to the origin of life was the formation of simple organic compounds that became the molecules of early life. In some cases, the molecular species that initiated life may still be in use today. Alternatively, modern biomolecules may retain structural features of earlier ancestral molecules, or differ from them substantially. While the astrobiology community generally favors a catabolic origin of life, some researchers in the microbiological community consider an autotrophic origin more likely.

Many biological organic molecules are found universally across the Tree of Life (e.g., the 20 amino acids, the nucleobases of RNA), whereas the polymers synthesized from these small molecules can vary tremendously in structure and sequence, even between closely related organisms. The monomers of biopolymers tend to be more chemically stable than their associated polymers, with biopolymer degradation occurring more easily than monomer degradation. The prebiotic reactions that produced the first small organic molecules of life could be distinct temporally, spatially, and mechanistically from the prebiotic reactions that gave rise to the first polymers and metabolic cycles of life.

One hypothesis promotes a “smooth continuum” of functional molecules, from the origin of life to those active today. If a smooth continuum occurred, it may well be that a predecessor of RNA (pre-RNA) was similar enough to have enabled the transfer of nucleobase sequence information, such as we see today. Another possibility is that the precursor to RNA was a quite different functional molecule. We must therefore consider alternative chemical pathways for the origin of life. Investigating such alternative chemistries could then inform our understanding of the ways that life could arise and evolve elsewhere.

The formation of the original molecules of life may have occurred in a wide variety of environments, through both endogenous (on Earth) and exogenous (external to Earth) processes. Endogenous environments could have included the planetary atmosphere, bodies of water (e.g., lakes, oceans, tidal pools, and hydrothermal vents), and exposed continental landmasses. Exogenous environments could have included the interstellar medium (e.g., via catalysis on interstellar dust particles), protoplanetary disks, comets, and asteroids.

The accumulation and concentration of organic molecules on a planetary surface is also considered an essential early step for the origin of life. In the case of endogenous molecule production, mechanisms for transport from the point of synthesis to environments that favor subsequent steps in the emergence of life (e.g., initiation of metabolic cycles and biopolymer formation) are important considerations. In the case of exogenous molecule production, transport to the planet by a mechanism that preserves an appreciable amount of intact organic materials is an added challenge that must be considered.

1.1 WHY IS THIS TOPIC IMPORTANT?

> Identifying and understanding the mechanisms that led to the production of prebiotic molecules in various environments is critical for establishing the inventory of ingredients from which life originated on Earth, assuming that the abiotic production of molecules ultimately influenced the selection of molecules from which life emerged.

Researchers have compiled inventories of likely prebiotic molecules on the early Earth and hypothesized their sources, relative production, and contribution to the total prebiotic carbon available for the origin of life. The relative importance of varied sources of organic molecules during the origin of life on Earth is not yet known, and could depend both on the abundances produced by different sources and whether any source produced unique compound distributions.

Identifying the sources of prebiotic molecules on the early Earth may aid our understanding of where life can be found in the Universe. This in turn may help us discriminate between biosignatures and abiotic chemistry as we look for signs of life on other planets.

1.2 WHAT DOES THIS RESEARCH ENTAIL?

Life arose on Earth around 4 billion years ago, but under conditions that are strikingly different from those on Earth today. The Earth has changed dramatically over time due to geologic and biological activity (see Figure 1-1). The terrestrial atmosphere is now rich in molecular oxygen, but that was not the case before the biological invention of oxygenic photosynthesis. As a consequence of the rise of molecular oxygen, soluble Fe(II) was oxidized to insoluble Fe(III) and was precipitated from oceans, rivers, and lakes. Thus, the chemistries possible at the time that life began cannot be assumed to occur spontaneously on Earth today, nor can chemistry that happens spontaneously today be expected to have been favored 4 billion years ago. It is therefore important to understand what abiotic chemistries were possible in the context of the early Earth environment. It should also

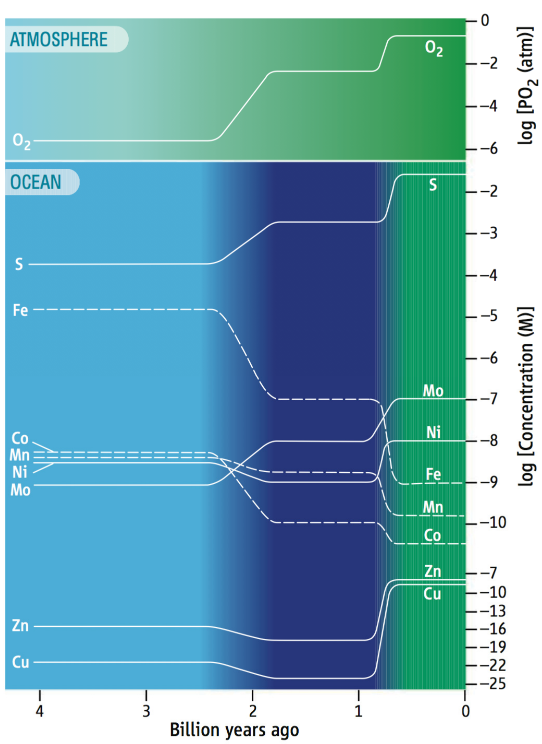

FIGURE 1-1. Changes in element abundances through time. These histories are approximate, based on simple geochemical models and inferences from ancient sediments. An expansion in H_2S-rich ocean regions after 2.4 billion years ago is assumed (2, 5). Color gradations indicate a transition from anoxic, S-poor oceans before 2.4 billion years ago (light blue) to H_2S-rich oceans between 1.8 billion and 800 million years ago (dark blue), subsequently giving way to complete ocean oxygenation (green). Different line styles are for clarity only; dashed lines are for elements with falling concentrations. [Adapted from (26), based on data from (2, 5, 9, 10)]. *Source:* Image from Anbar 2008. Reprinted with permission from AAAS.

be noted that early Earth chemistry may be occurring today on places like Jupiter's moon Europa or Saturn's moon Enceladus, and, therefore, exploration of those environments could provide insight into prebiotic chemistry.

Abiotic chemical reactions typically produce a diverse array of molecules, whereas life utilizes only a small subset of possible organic compounds (see Figure 1-2). It is not yet understood how or why biology specifically selected certain molecules from the larger set that was likely available on the early Earth. This selection may have occurred at the small-molecule, polymer, and cellular levels. It is therefore important to consider how properties of certain molecules or their formation pathways in particular environments could have influenced their incorporation into biology.

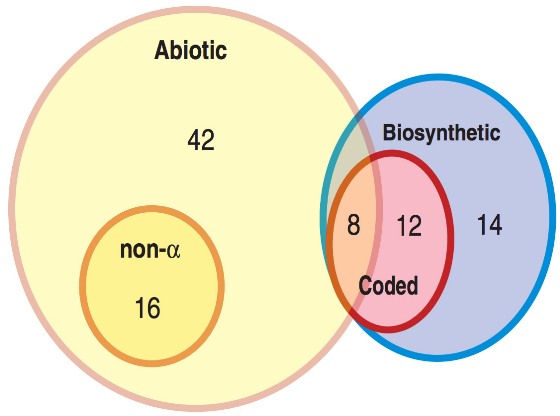

FIGURE 1-2. Venn diagram showing the number of amino acids represented in different categories of chemical space. *Abiotic* refers to the 66 amino acids reported in the Murchison meteorite (included 8 members of the standard alphabet). Non-α refers to the 16 amino acids reported from the Murchison meteorite that have longer carbon "backbones" than those used in genetic coding. *Coding* refers to the 20 amino acids used within the standard genetic code. *Biosynthetic* refers to the additional 12 members of the standard alphabet and a further 14 amino acids that are produced as intermediates in their production. Color images available online at www.liebertonline.com/ast. *Source:* Image from Philip and Freeland 2011. The publisher for this copyrighted material is Mary Ann Liebert, Inc. publishers.

Many molecules of life have molecular weights usually less than 250 amu (atomic mass units) (e.g., amino acids, nucleobases, monosaccharides). In contrast, biopolymers are big, with molecular weights up to millions of amu. Polymers are composed of monomers held together by covalent bonds and/or non-covalent bonds. The polypeptides, for example, are polymers of amino acids joined by peptide (or amide) bonds. Cell membranes are multimolecular assemblies, held together by hydrogen bonding, dipoles, and van der Waal forces. Within the membrane structure, lipid molecules are covalently bound to oligomer components including glycerol, choline, phosphate, and fatty acids.

The reactions and environments that resulted in the production of the small molecules of life were not necessarily the same as those that resulted in the production of the first biopolymers and cells. Thus, the thermodynamic and kinetic stability of small, prebiotic molecules must be considered when discussing the possible sources of organic monomers. Both formation and degradation must be understood in order to evaluate the expected steady-state concentrations. Determining where life may have originated depends on the sources of prebiotic molecules, the rates of their formation and degradation, the benefits and deficits of these syntheses, the relative production rates of these processes, and the organization of these molecules into higher-order structures/systems (i.e., polymers, biochemical cycles, cells).

Because organic molecules can occur in many environments, it is important to know the degree to which the products formed in different environments could have ultimately accumulated on the early Earth or on other habitable planets. Different formation pathways exist in each of these environments, and will produce different organic compounds with varying relative distributions. Understanding these pathways and the steady state distributions of compounds sheds light on the inventory of available prebiotic organic compounds. There may be characteristic signatures in the distributions and types of organic molecules produced by specific formation mechanisms and environments. For example, carbonaceous chondrites are well known to have a rich inventory of organics. Analyses of organic content of meteorites and other extraterrestrial samples for comparison with the distribution of organics in laboratory reactions could have important implications regarding the reactions that produced the organics on the early Earth, either by endogenous or exogenous processes.

The Murchison meteorite, a carbonaceous chondrite, fell in Murchison, Australia in 1969. Many organic molecules, including biological building blocks (e.g., amino acids), have been isolated from the Murchison meteorite. The fragment shown is at the National Museum of Natural History, Washington D.C.

FIGURE 1-3. Carbonaceous chondrites are well known to have a rich inventory of organics. *Source:* Image from Basilicofresco 2008, Wikipedia.

Finally, the introduction of exogenous material to a planetary surface, or the gradual accumulation of endogenous material (e.g., in an evaporating pool), can result in a disequilibrium system that could provide energy or a local environment that facilitates the further synthesis and polymerization of organics (e.g., condensation reactions), alteration of the organics (e.g., oxidation, reduction), and solubilization of the organics (e.g., by increased cosolvent concentrations). Quantification of these processes could provide valuable insight regarding the organic inventory of the early Earth, as well as possible local environments for the formation of larger and more complex prebiotic molecules (e.g., early biopolymers).

1.3 PROGRESS IN THE LAST TEN YEARS

Observational

The advent of a new generation of telescopes, including the interferometer *ALMA* (Atacama Large Millimeter Array) and the European Space Agency's far-infrared space telescope *Herschel*, has enabled scientists to study the distribution of abiotic organic molecules in star-forming regions to a much greater extent with the potential to reveal more about the relationship of these molecules to prebiotic chemistry. The number of known so-called "Super Earth" planets continues to grow, and their atmospheres are just starting to be probed chemically. Although one comet (103P/Hartley 2) was found to have a deuterium-to-hydrogen (D/H) elemental ratio that mirrors that of Earth's oceans, other studies of comets have not found a match. In contrast, the D/H ratio of meteorites originating from the Asteroid Belt suggest that, despite their lower water content, most of Earth's water could have come from asteroids. The *Stardust* comet sample return mission shows that the early Solar System was a much more chaotic place than formerly envisaged. The abiotic inventory of meteorites has been better defined, constraining the isotopic, enantiomeric excess (unequal handedness), and structural characteristics of organic molecules, including amino acids and nucleobases. The meteorite organic inventory serves to check abiotic synthetic pathways and may have provided sources of abiotic molecules on the early Earth, presuming their survival on atmospheric entry.

Rock Record

The impact history of the early Earth is more constrained both by models and by the geologic record. Although Earth endured frequent and large-scale asteroid strikes 4.1 to 3.8 billion years ago (a period known as the "Late Heavy Bombardment"), these events would not have necessarily eradicated all life. Significant progress has been achieved in recovering samples from Earth's oldest (>4 billion year old) crust, which, when coupled with advances in analytical methods and interpretation, offers new insights into the earliest stages of the evolution of the planet. For example, multiple lines of evidence from natural samples, combined with laboratory experiments (e.g., oxygen isotopes, Ti in zircon thermometry) point to a rapidly cooled planet, with a liquid water ocean, and a felsic continental crust capable of supporting life less than a few hundred million years after Earth's accretion.

Laboratory Experiments

The abiotic production of molecules in laboratory experiments is critical for understanding the chemistry leading to prebiotic chemistry and the subsequent origin of life. These experiments have a long history, starting with the results of the Miller-Urey experiments published in 1953. Recent work focused on the production of prebiotic molecules on Earth has included further exploration of Miller-Urey synthesis, with advanced analysis of the resultant product mixtures and with more current models of early Earth atmospheres.

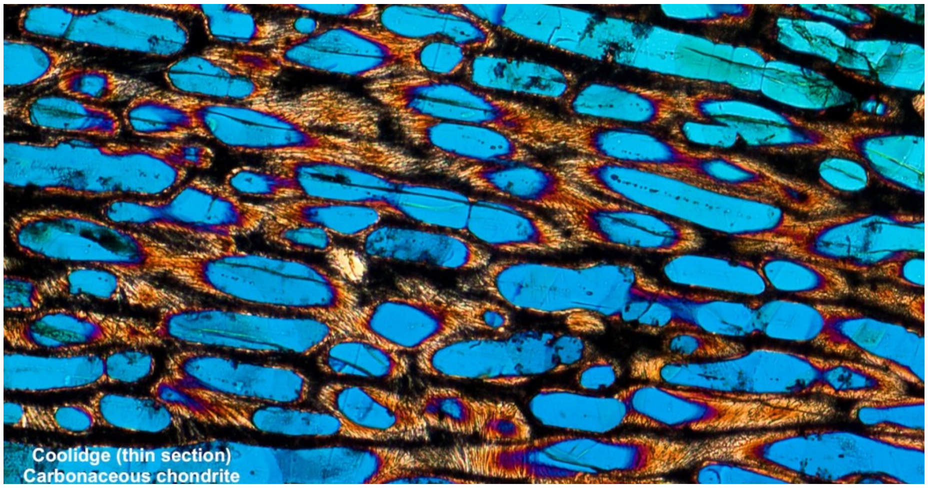

FIGURE 1-4. Thin section of carbonaceous chondrite. *Source:* Photo by L. Garvie/ASU. Courtesy of the Center for Meteorite Studies.

Numerous experiments on cold mixed ices have shown that photolysis can lead to the production of a variety of basic organic molecules including alcohols, esters, aldehydes, etc., which are also found in regions of star formation. The observation of organic molecules in interstellar space that are known to produce biological molecules by abiotic reactions (e.g., formamide) increases the relevance of laboratory experiments to understanding the potential breadth of compounds that can be produced in space.

Experiments from the last ten years have shown that abiotic syntheses can produce a large suite of compounds, that the products of some abiotic reactions can be directed by inorganic cofactors toward molecules that are found in existing life, and that interstellar space is likely rich in the molecules that were important for the emergence of life. These results suggest that abiotic mechanisms that lead to the selection, stabilization, and accumulation of certain organic molecules were important contributors to prebiotic chemistry. Additionally, synthetic organic research has shown that molecules not found in life today might have originally served in place of those that do, such as a different sugar in the backbone of RNA. These results illustrate the potential importance of non-biological molecules for the origin of life on Earth as well as the emergence of life in non-Earth environments.

Computer Modeling Experiments

An emerging frontier is the use of computer science to explore why life on our planet evolved to use particular molecules—for instance, the 20 amino acids used by the time of the last universal common ancestor (LUCA). Although this approach cannot replace laboratory experiments, it complements such work by providing a guide for investigations into interesting chemical spaces and, in some cases, by providing a way to test a hypothesis that would be impossible or too expensive to test by experiment.

1.4 AREAS OF RESEARCH WITHIN ABIOTIC SOURCES OF ORGANIC COMPOUNDS

I. What Were the Sources, Activities, and Fates of Organic Compounds on the Prebiotic Earth?

II. What is the Role of the Environment in the Production of Organic Molecules?

III. What is the Role of the Environment on the Stability and Accumulation of Organic Molecules?

IV. What Constraints Can the Rock Record Place on the Environments and Abiotic Reactions of the Early Earth?

I. What Were the Sources, Activities, and Fates of Organic Compounds on the Prebiotic Earth?

Modern life is based on surprisingly few small molecules relative to the number of possible compounds of similar molecular weights that can be created using the elements carbon, hydrogen, nitrogen, oxygen, phosphorus, and sulfur (CHNOPS). The molecular “building blocks” that initially started life were undoubtedly influenced by availability, since molecules that were not present in the prebiotic chemical inventory could not have played a role in the earliest stages of life. The functionality of available molecules was also important, as molecules lacking properties conducive to the emergence of life would not have been directly involved in the origin of life even if they were present.

It is also possible that extant life contains “frozen accidents”—that is, molecules (or a particular isomer/handedness of some molecules) that were originally incorporated by chance, but could not be changed after chemical evolution had progressed beyond a certain point (e.g., the emergence of coded proteins, or a complex metabolism). Another possibility is that apparent frozen accidents may not have been accidental at the time, but instead may have been highly advantageous under the environmental conditions faced by early life, and then could not easily be altered when those conditions later changed.

The principal biopolymers of life are nucleic acids, proteins, polysaccharides, and lipid membranes. The abiotic production, accumulation, stability, and overall availability of the monomers that make up these polymers are therefore of interest for understanding the emergence of life. These monomers include the nucleobases, ribose, the canonical amino acids, lipids, and sugars found in nucleic acids and polysaccharides. The small organic molecules that are currently found in metabolic cycles (e.g., organic acids) and as cofactors (e.g., flavins) are also of interest.

The aforementioned molecules are by no means the only molecules that should be considered as potentially important for the emergence of life. There may have been other organic molecules, generated by abiotic reactions, which are no longer found in life but were essential for the emergence of life. In particular, the structure and constitution of the biopolymers and metabolic cycles may have evolved considerably since the origin of life. Thus, organic molecules in the “chemical space” around the small molecules of extant life may be of great importance for understanding the origin of life. For example, there may have been pre-RNA polymers with different nucleobases and different sugars before the emergence of RNA. The proteins also may have evolved from polymers that did not contain our current set of twenty L-alpha-amino acids; pre-protein polymers may have utilized a set of amino acids that included a racemic mixture of alpha, beta, and gamma-amino acids, or even hydroxy acids. Moreover, life on planets with environments different from those that existed on Earth at the origin of life (e.g., different temperature range, different redox state) might start and evolve from a different set of monomers than those utilized by life on Earth, producing so-called “Weird Life.” Thus, the production of molecules by abiotic reactions that could lead to functional polymers or metabolic cycles in different environments could be of importance regarding the molecules that are necessary for life in alternative environments.

A substantial number of the monomers found in life today are relatively stable organic molecules that have already been produced by one-pot, abiotic reactions. These include several of the amino acids in the Miller-Urey experiment from a model Hadean atmosphere, the nucleobases from HCN-based chemistry, and many sugars by the formose reaction (i.e., from formaldehyde) and related reactions. Nevertheless, there is still a need to demonstrate reactions that provide more efficient abiotic routes to organic molecules of interest and by reactions that are compatible with the most current data on the nature of the early Earth environment.

Some biopolymers are made from monomeric units that are more stable than the over-all biopolymers, but do not appear to be made from a single starting material or class of molecules. The mononucleotides, which are the monomeric units of RNA, are a much-discussed example of this class of monomers. From a chemical perspective, the mononucleotides are a composite of a nucleobase, a sugar, and a phosphate group. Lipid molecules, some of which are composites of fatty acids, glycerol, phosphate, and an amino acid, are another example of biomolecules that appear to be made from small molecules that are themselves the products of more than one starting material and chemical reaction. The abiotic reactions that could have first produced the building blocks of more complex biological molecules, or their predecessors, are of great interest to understanding the origins of life.

Just as life currently utilizes small molecule cofactors (e.g., flavins, NADH), early life may have as well for a range of functions, acting as catalysts, as electron donors/acceptors in redox reactions, and even as important components of the solvent milieu (e.g., solubilizing agents). Thus, small molecules produced in abiotic reactions that can facilitate the production of biological molecules are potentially important for understanding the emergence of life on Earth and on other habitable planets.

The emergence of life would have been greatly facilitated by abiotic mechanisms that locally concentrate and increase the chemical activities of the molecules necessary for life. Concentration mechanisms include, but are not limited to, molecular associations, differential solubility, and selective affinity for particular surfaces. Thus, physical and chemical processes that provide a feasible mechanism for the robust concentrating of molecules of interest on the early Earth are of potential interest for understanding early stages of chemical evolution.

Key Research Questions about Molecules and Chemistry

What is the connection between the organic monomers produced in various environments and those used in terrestrial biology?

Abiotic chemistry typically produces a diverse array of isomers, whereas life utilizes a subset of the available compounds. It is not yet understood the extent to which the subset of molecules used in life today was defined by the environments in which abiotic compounds were produced that gave rise to life.

What properties of certain molecules, their formation pathways, or their environments, led to these molecules being used by the first forms of life?

Organic molecules are formed in a variety of environments and by many diverse reaction pathways. It is possible that the physical and chemical properties of certain abiotic compounds, in addition to availability, influenced their participation in the emergence of life. These properties could include, but are not limited to, solubility, pKa, participation in molecular recognition, and the ability to form reversible covalent bonds.

What are plausible geochemical sources of CHNOPS compounds?

The formation of organic molecules relies on the availability of one-carbon molecules (e.g., CO_2, CH_4). These molecules may originate from a variety of geochemical processes, or they may be primordial volatiles present in planetary environments. The transformation of one-carbon molecules to abiotic molecules can occur by many geochemical processes and often result in vastly different final products.

In addition, nitrogen and phosphorus are elements with a substantial inorganic reservoir. Both are critical as part of the chemistry of life (CHNOPS). However, both show little reactivity toward abiotic organic compounds when in their dominant geochemical reservoir (N_2 in the atmosphere, and phosphate in minerals). How these elements became reactive enough to form new abiotic compounds is an open question.

Learning how the CHNOPS elements became reactive in various environments, as well as their delivery by extraterrestrial materials to planetary surfaces, is critical for establishing the inventory of ingredients from which life originated. This information is, in turn, useful for the search for life elsewhere, because this knowledge can focus attention on environments in which the organic chemicals needed for life can be found. Importantly, we only know that life was able to originate on Earth under the conditions that existed about 4 billion years ago (assuming that there was no panspermia), but we do not know whether life could originate under other planetary conditions.

II. What is the Role of the Environment in the Production of Organic Molecules?

Many environments contain organic molecules produced by abiotic reactions. Such environments include, but are not limited to, planetary surfaces, planetary atmospheres, comets, and asteroids. One challenge for chemists is to formulate models for the production of organic molecules in these environments, and to use such models to advance theories for the origin of life. A long history of abiotic chemistry experiments has demonstrated that the early Earth had a substantial organic inventory. Furthermore, organic molecules formed in space could have been delivered to the early Earth and to other potentially habitable planets.

Key Research Questions about the Production of Organics

What are the primary mechanisms for organic formation in planetary environments, and what relative abundances of organics are produced?

Organic synthesis may have occurred in a variety of environments on Earth. Determination of the sources and rates of formation and degradation of these organics, geologic locations of these environments, benefits and deficits of these syntheses, and relative production rates of these processes are critical to determine where life might have originated.

A specific branch of prebiotic chemistry focuses on organic formation in the early atmosphere. Prior to the origin of life, the atmosphere was potentially a major source of organic and inorganic compounds that were either used without modification as precursors to more complex molecules, or participated in reactions leading to such precursors. Constraining the redox state of the atmosphere, as well as the composition and partial pressures of gases such as N_2, CO_2, H_2, CH_4, NH_3, CH_2O and O_2, allows for an understanding of the availability and stability of prebiotically relevant compounds. For example, the redox state of the atmosphere would directly influence the relative ratios of fixed (prebiotically useful) to unfixed biogenic elements such as nitrogen (e.g., NO_3- or NH_3 versus N_2) or carbon (e.g., CH_4 or CO versus CO_2). Other planetary environments are also possible locations for the production of organic compounds, including on the surface of the planet, in bodies of water, near volcanoes, and in hydrothermal vents. Likewise, the potential relevance of these environments as possible locations for the abiotic production of molecules requires an understanding of the mechanisms for molecule formation and degradation in these environments.

A related question is whether different formation mechanisms and environments have characteristic signatures reflected in the types of organic molecules produced and their planetary distribution. If so, we may be able to determine how the diversity of molecules produced in exogenous locations compares to the diversity of molecules created in different environments on the early Earth and other potentially habitable planets. Such information could reveal the relative importance of exogenous and endogenous reactions to the creation of the chemical inventory necessary for the emergence of life.

What is the probability that organic molecules produced in exogenous environments, like interstellar space, are delivered intact to planetary surfaces?

Organic molecule formation can occur in extraplanetary environments, including star-forming regions, interstellar matter, protoplanetary disks, and parent bodies. Different formation pathways exist in each of these environments, producing different organic compounds with varying distributions. Understanding these pathways and the distributions of compounds formed sheds light on the inventory of organics in space. Potential factors that could influence organic production include the density and temperature of pre-stellar sources, their location in the galaxy, and time of formation (which can affect total availability and metallicity of elements). The relevance of such molecules to the origin of life depends on their ability to be delivered to an environment that is suitable for life. Evaluating the relative importance of different kinds of impactors and their contents, their relative fluxes, and their survivability could answer questions about the organic and volatile inventory on planets.

Questions for future research include how the complexity, diversity, and quantity of organics produced differ between exogenous environments. How does delivery to a planetary surface alter the original diversity and quantity of molecules that are present prior to delivery? Was the delivery of organics to the early Earth associated with the delivery of water?

What is the relative importance of exogenous and endogenous sources of organic compounds?

Can all organic molecules necessary for the emergence of life arise *in situ*, or must some species be delivered by impact? As mentioned above, numerous environments and reactions on the early Earth are likely to have contributed organic molecules to the prebiotic chemical inventory. Additionally, impactors may have been responsible for delivering biogenic elements (e.g., phosphorus) and small molecules (e.g., formaldehyde, HCN, nucleobases) to the early Earth or to other planetary surfaces. Such impactors include material deriving from comets or asteroids, and it may be that particular materials or classes of materials are unique to a particular formation mechanism or environment. The relative importance of exogenous and endogenous sources of materials for the emergence of life remains an open question, and could depend both on the abundances produced in these sources and whether any source produced unique compounds necessary for life.

How do different energy sources result in different organic production?

Production of organics can take place through thermodynamic and kinetic drivers. Low-temperature reactions within molecular clouds, high-energy modification of carbon molecules near star-forming regions, and aqueous alteration on asteroids all affect organic synthesis and complexity. Energy sources for molecular transformations on Earth and other terrestrial bodies include high-energy discharge, UV radiation, heat, radiation bombardment, hydrothermal energy, and serpentinization. If the relative importance of these energy sources for the production of organic molecules necessary for the origin of life can be understood, this information could provide insight on the probability of various locations for the origin of life or source materials as well as the respective roles of endogenous and exogenous material.

Part of this area of research includes determining how important secondary chemical and physical processes that alter organic molecules (e.g., radiation-induced chemistry, impacts, heating) are to the generation of molecules that are key to the origin of life. Given the same precursor material, do different thermodynamic and kinetic drivers in different environments lead to distinct product distributions? Refer to Chapter 2: Synthesis and Function of Macromolecules in the Origin of Life.

III. What is the Role of the Environment on the Stability and Accumulation of Organic Molecules?

The accumulation and differential survival of chemical compounds is likely an important factor in the evolution of the matter that gives rise to life. Stabilization and accumulation of abiotic materials can occur by reaction with the environment (e.g., accumulation on mineral surfaces), by specifics of chemistry (e.g., reactions of formaldehyde), and by physicochemical changes (production of condensed compounds via dehydration).

The last 60 years of prebiotic laboratory and sample studies have shown that the abiotic production of many molecules (particularly small organic molecules) is easily achieved if low yields are sufficient. However, it is expected that some processes key to the origin of life, such as polymer formation, required particular molecules at sufficient local concentrations that bimolecular (and polymerization) reactions became favorable. An important part of abiotic chemistry is therefore the identification of environments that lead to accumulation of abiotic molecules, either by selection from a mixture, or by preferential production of key precursors.

The ubiquity of selective and accumulative environments could directly inform the search for biosignatures. Since abiotic synthesis of organic compounds must occur prior to life's emergence, recognition of those environments where these processes can occur is critical to origins of life studies. Conversely, environments that enhance the abiotic accumulation and stability of organic compounds must be identified to avoid misinterpreting abundant abiotically generated compounds as a true biosignature.

Key Research Questions about the Stability and Accumulation of Organics

What is the survivability of small, organic molecules in their formation and reaction environments?

Not only must organic molecules be produced before protobiopolymers and proto-metabolisms can emerge, but these building blocks of life also must accumulate to sufficient concentrations to allow for further reactions (e.g., polymerization). Thermodynamics must be considered when discussing sources of small, organic molecules; both formation and degradation must be understood in order to evaluate expected steady-state concentrations. Constraints on the rates of production and degradation of these organics in their formation environments can also help determine how critical environmental change would have been to the use of these molecules in a subsequent stage of chemical evolution. Compounds may change environments after formation (e.g., an abiotic organics formed on a mineral surface or in the atmosphere may dissolve in water), and it is therefore important to understand the stability and subsequent reactivity of these molecules in environments where life might originate.

What changes take place to these organics over time in the environments of terrestrial planets?

Introduction of exogenous material to planetary surfaces can result in a disequilibrium system that may provide energy for further synthesis and alteration of the organics (e.g., oxidation, reduction). Quantification of these processes can provide insights regarding the organic inventory of a planet. The interaction between dynamic environments on Earth (or other planetary surfaces) and the synthesis/alteration of molecules that become part of a self-replicating/self-sustaining process is important for understanding the emergence of life.

What is the survivability of organic molecules during delivery to planets with differing atmospheres and differing asteroidal or cometary sources?

Planetary atmospheres influence material delivery through ablation and deceleration of meteors, which in turn influences total organic inventory. The source material for exogenous organics includes parent bodies with varying material strengths, organic content, and composition. Again, thermodynamics and degradation pathways and rates play an important role in determining the final monomer concentrations and relative abundances.

Comets and carbonaceous meteorites deliver organic molecules to planets, and the delivery of such material may have contributed to the inventory of ingredients required for life’s origins. The surviving icy bodies and carbonaceous meteorites of the Solar System contain an array of molecules whose chemical and isotopic compositions and petrographic characteristics provide a record of their origins. These bodies provide insights into the nature and abundance of organic material, which could inform us about processes that may influence similar evolutionary sequences during the formation and evolution of exoplanetary systems.

Current predictions suggest that small abundances of gas-phase organics in protoplanetary disks do exist and should be detectable by the *ALMA* interferometer. The organics in disks can be both remnants of molecules found in hot cores and molecules produced during the disk stage. Chemical simulations show that both sources lead to the production of terrestrial-type organic molecules. As the dust particles coated with ices of water and organics coagulate into larger bodies, it is possible that these bodies retain much of the organic material, whether they are primitive, such as comets, or possibly undergo further chemical processes, such as asteroids.

How do enantiomeric excesses at the monomer level arise, and were those processes important for determining biological homochirality?

Certain compounds of terrestrial life are homochiral (e.g., amino acids, sugars), whereas abiotic chemistry tends to produce racemic mixtures. Enantiomeric excesses have been observed for some compounds in some carbonaceous chondrites. It is not clear how these enantiomeric excesses were produced, whether the conditions that produced them were widespread, or if they exerted any influence on the emergence of biological homochirality. Further research may reveal how enantiomeric excesses observed in certain meteoritic amino acids were produced and/or amplified, and whether similar processes existed in planetary environments or are unique to the meteoritic parent bodies.

IV. What Constraints Can the Rock Record Place on the Environments and Abiotic Reactions of the Early Earth?

Earth's mineral and rock record preserves a limited selection of materials older than 4 billion years, constituting a record of conditions near the time of life's origin that is incomplete, but nonetheless the best available. The rock record holds invaluable clues for understanding how life came about on Earth by constraining the phase space of chemical processes of early Earth environments. For instance, the earliest rock record provides constraints on atmospheric composition (e.g., redox) and physical conditions (e.g., temperature and pressure), constraints that can be used by experimentalists and theoreticians to provide refined models of the possible environments on the early Earth available for chemical synthesis.

Earth's oldest rocks may also tell us about the composition and physical characteristics of the earliest ocean. We do not know whether life first emerged in freshwater or saline conditions or, for that matter, under deep or shallow conditions or on exposed land. Conditions of water available at Earth's surface ultimately influenced the prebiotic physicochemical environment. Finally, the onset of plate tectonics may have been associated with the appearance of new environments to concentrate and cycle early abiotic materials and mixtures.

Key Research Questions about the Environment of Early Earth

What was the nature of Earth's early atmosphere, oceans, and crust?

Earth's atmosphere has responded to events and processes (e.g., impacts, onset of plate tectonics, advent of photosynthesis) and gradually changed its physical and chemical characteristics such as pressures and mixing ratios of its constituent gases. The composition of the early ocean (e.g., acidity [pH], Mg, Ca, Fe, total dissolved solid content) and physical properties (e.g., temperature) would have significantly influenced the abiotic processes that might have occurred. Increasing salinity results in the precipitation of several elements, which may have promoted organic degradation or synthesis, and could have changed redox characteristics of organic solutes. Changes in pH and temperature affected chemical syntheses and rates of formation and degradation of potentially important prebiotic molecules. The development of continental crust is tied to the onset of plate tectonics. Differentiation of felsic rocks from mafic material formed new minerals and new environments, including environments with low water activity in contact with the atmosphere. Additionally, continental crust significantly altered oceanic and atmospheric composition.

The lithosphere has the potential to record atmospheric evolution through direct rock-atmosphere interactions, or indirectly by changing the composition of the hydrosphere. Such changes can be, for example, recorded in mineral assemblages (e.g., magnetite, hematite), redox-sensitive elements (e.g., Mo, Re), or isotopic signatures. The oceanic composition modified and was modified by reaction with the crust and atmosphere. These conditions can be reflected in the major and trace element geochemical parameters of sedimentary rocks in contact with or precipitated from the ocean.

What was the bombardment history of the Earth?

The bombardment of Earth by extraterrestrial material delivers both disequilibrium material and energy to the surface. Current theories suggest that much of Earth's water ultimately originated from extraterrestrial material. Surface bombardment can provide unique thermal and chemical environments and may have been a source of abiotic synthesis. The bombardment history may be extracted from the rock record using platinum-group elements or trace element isotope systematics. In addition to the geologic record, studies of planetary formation and orbital dynamics can provide insights regarding the nature of impacts on the early Earth.

Are there still undiscovered Archean and older rocks, and what could they tell us about the environment of the early Earth?

Rocks from the early Archean are sparse, and rocks from the earlier Hadean are virtually nonexistent. Sedimentary and metasedimentary rocks from these times can provide information on the environmental conditions that produced the molecules from which life emerged on the early Earth. A systematic search for early Archean and Hadean formations (or rocks derived from weathered samples of these materials) could provide new information on these environments.

1.5 CHALLENGES FOR THE NEXT TEN YEARS

How do environments drive organic molecule production?

Laboratory investigations can determine organic molecule production in a variety of simulated environments including but not limited to interstellar objects, planetary atmospheres, planetary surfaces, and hydrothermal environments. Thus, future studies should identify effects of variables such as temperature, pH, density, energy source, and starting material composition on product distributions and identify distinct signatures of formation processes.

Were meteorites and comets relevant to organic inventories on prebiotic Earth? Were all molecules required for the emergence of life on Earth generated endogenously, or were some necessarily provided from exogenous sources?

Better models of Earth's early atmosphere would help answer this question, as it may have affected the delivery of exogenous materials as well as the efficiency of endogenous production. Overall, the astrobiological relevance of cometary and meteoritic organic matter should be investigated further. In addition to the refractory presolar materials found in meteorites, we should determine whether any of the icy or volatile material in the Solar System has a presolar origin. Additional questions include: were water and organic molecules delivered together to Earth and other terrestrial planets, or did they come from different sources?

What were the sources of the molecules that became the building blocks of life?

By understanding which molecules could be made endogenously on prebiotic Earth, which could be delivered from exogenous sources, and which were unique to these sources, it may be possible to determine the sources of the molecules that became the building blocks of life. Answering this question requires continued investigations to determine the molecules and processes required for the emergence of life.

What compounds derived from abiotic synthesis are characteristic of their sources?

In order to interpret potential chemical biosignatures, it is essential to first determine the molecules that can be produced abiotically and the signatures of various formation mechanisms and environments. Refer to Chapter 2: Synthesis and Function of Macromolecules in the Origin of Life.

How did prebiotic organics become narrowed to the biotic chemistry in life today?

There should be studies aimed at understanding the selectivity of biology (or prebiotic chemistry) in using certain subsets of molecules out of the diverse prebiotic (or abiotic) inventory. Refer to Chapter 2: Synthesis and Function of Macromolecules in the Origin of Life.

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2 Synthesis and Function of Macromolecules in the Origin of Life

Introduction

A fundamental property of life on Earth is likely common to all living systems, regardless of their chemistry: life is based on polymers. Owing to the vast combinatorial space that results from polymerizing just a few monomeric building blocks, polymers can aptly serve both catalytic and genetic roles. One of the most widely shared definitions of life is that it is a self-sustaining system capable of Darwinian evolution. Macromolecules—specifically, proteins and nucleic acids—form the catalytic and genetic species that allow system self-sustenance. Also, macromolecules evolve—in other words, change over time—thus fulfilling a criterion for recognizable life.

FIGURE 2-1. Synthesized from a limited set of monomers through a limited set of reaction types, polymers efficiently serve as functional and informational macromolecules. *Source:* Image modified from Kyle Schneider (2009), Wikipedia Commons.

2.1 WHY IS THIS TOPIC IMPORTANT?

> The macromolecules of Earth-based life are composed of a small subset of all potential chemical building blocks. It is likely that macromolecules formed from different monomers would share many characteristics with modern biopolymers. Thus, it is crucial to characterize the overall chemical underpinnings of the processes that lead to the persistence and function of evolvable macromolecular systems. As part of this effort, it is necessary to identify interactions, intermediary structures and functions, energy sources, and environmental factors that contributed to their diversity, selection, and replication.

Polymers are well-suited for the structural, catalytic, and genetic functions required for life. In modern biology, linear polymers, generated by the condensation of relatively simple monomers, have unparalleled non-covalent assembly properties. These properties lead to two- and three-dimensional structures that are essential for functioning and regulation. Vital elements of life, including structure, energy storage, catalysis and information transfer, are all carried out by polymers. Information storage and transfer by nucleic acids depend on the linear assembly of a small chemical alphabet of four nucleotides linked by a self-repulsive polyanionic backbone (phosphodiesters). The diverse chemical alphabet of 20 amino acids, linked by an adhesive polyamide backbone, leads to protein architectures that are capable of structural transitions essential for their catalytic function.

Catalysis can be carried out by both nucleic acids and proteins. Protein enzymes have access to a wide array of functional groups, including acids/bases/nucleophiles/electrophiles and redox-active moieties, and thus are generally considered to have a greater potential for catalysis than nucleic acid ribozymes; however, proteins do not carry genetic information in organisms that we can observe. The nucleic acid catalysts that remain in contemporary biology are thought to be “living fossils” of an earlier system. Beyond chemical specialization, there may be additional selective pressures favoring multiple polymeric systems. For example, the interdependence of separate genetic and catalytic polymers may provide opportunities for enhanced feedback mechanisms unavailable to single polymeric systems.

Protein and nucleic acid biopolymers may be the products of evolutionary processes that acted on protobiopolymers that no longer exist in biology. These precursor protobiopolymers would likely have achieved informational competency and catalytic ability by employing assembly strategies that are similar to those of contemporary macromolecules. Non-covalent assembly of proto-monomers and polymers likely drove further polymerization, which in turn autocatalytically enhanced assembly. Properties such as solubility, solvation (dissolution), hydrophobicity, reactivity, and, ultimately, assembly were characteristics critical to primitive function. The processes of early macromolecular chemical evolution were intrinsically linked to energy transduction and to the environment.

It is notable that some short, relatively simple polymers have been shown to engage in chemical processes that could lead to sustained amplification and natural selection. For instance, certain peptides can self-replicate or catalyze the synthesis of other peptides in symbiotic or parasitic fashion. Likewise, certain oligonucleotides can self-replicate and undergo self-sustained exponential amplification.

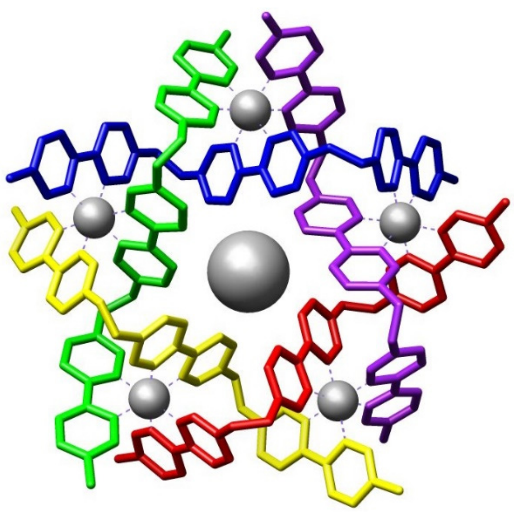

FIGURE 2-2. Non-covalent assemblies may have preceded the formation of protobiopolymers. *Source:* Image from Stone 2007, Wikipedia.

Whether and how polymers transmit information and fold to generate function are of interest, irrespective of whether those questions are posited on a particular environment. Indeed, by answering the more general question of how polymers might support function, and what the sequence, structure, and function spaces that attend to different chemistries may be, we may constrain environments that are conducive to life, on Earth or otherwise. In such scenarios, polymer function can be "unmoored" from the necessity of recapitulating Earth-like prebiotic synthesis. Parallel efforts to determine the molecular phylogeny of modern life will help to determine whether our biopolymers are a small subset of potentially life-supporting polymers, or represent a singular or near-singular solution. Such analyses would inform the likely abundance and locations of life in the Universe.

2.2 WHAT DOES THIS RESEARCH ENTAIL?

To further refine the understanding of life's origins and early chemical evolution, researchers must continue to map the chemical landscape of potential primordial informational oligomers. Considering the central role of biopolymers in modern biology, there is no doubt that a critical step in the emergence of chemical evolution was the advent of polymers that could replicate, store genetic information, and exhibit phenotypic properties capable of Darwinian evolution. Therefore, a central effort in origin-of-life research must be to develop an understanding of macromolecule synthesis, stability, folding, and function in the context of plausible prebiotic conditions and environments.

Overcoming Kinetic and Thermodynamic Hurdles

There exist both kinetic and thermodynamic hurdles to the prebiotic synthesis of biopolymers. For example, oligopeptides, oligonucleotides, and oligosaccharides are formed by the dehydrative polymerization of monomers in water, which are thermodynamically disfavored reactions in aqueous solution (i.e., it is difficult to make polymers even at high concentrations of monomers). Conversely, the polymers must be kinetically stable long enough for them to replicate, even though their hydrolysis is thermodynamically favored. In modern biology, hydrolysis of nucleoside triphosphate is the energetic driver of these condensation-coupling reactions.

The Role of Catalysts

The kinetics of uncatalyzed condensation polymerization reactions in abiotic systems are also problematic. The slow rates of uncatalyzed coupling between amino (peptide) and hydroxyl (nucleotide) reactants with electron-rich carboxylate (peptide) and phosphate ester (nucleotide) electrophiles are unlikely to support metabolism.

In the absence of modern biology's ATP-driven condensation processes, prebiotic polymerization must have been enabled by suitable environments containing abiotic reagents and catalysts. Experiments have demonstrated that condensation polymerization can be facilitated by simple chemical coupling agents, for example: carbodiimides, polyphosphates, and carbonyl sulfide. However, the abiotic source of these agents and their kinetic resistance to hydrolysis in aqueous environments awaits more complete demonstration. Alternatively, dynamic polymerization and depolymerization, and assembly and disassembly, may have been driven by water activity or temperature oscillations commanded by planet rotation, tides, seasons, tectonic phenomena, or other periodic energy fluxes. Compartmentalization or encapsulation could help to extend these periods of disequilibrium.

Catalysis of monomer-coupling reactions by Brønsted and mineral Lewis acids has been demonstrated both in solution and on surfaces. Additional mechanisms to concentrate and orient monomers, and thus enhance polymerization rates, include surface adsorption and co-localization within compartments bounded by either organic molecules or minerals. The templated or untemplated non-covalent assembly of monomers prior to polymerization provides a further mechanism to increase the effective concentration of substrates. A potentially powerful early function for polymers would be to drive the assembly of monomers, thus enhancing the rate of polymerization and resulting in the further assembly of monomers.

The Selection of Homochirality

It is also conceivable that homochirality was selected for at an early stage of chemical evolution. Abiotic synthesis such as the Miller-Urey experiment are generally not stereospecific; however, contemporary biopolymers are formed from single stereoisomers, e.g., L (S) - amino acids. Because there is little if any intrinsic chemical difference between two stereoisomeric forms of a compound, it is likely that homochirality is the result of selection. It is necessary to determine plausible mechanisms by which stereospecific polymers could be achieved, either through selection of one stereoisomeric form of the precursor and polymerizing it preferentially, or by selection of oligomers that are enriched for one form rather than another. This selection need not be an all-at-once event. Experiments have shown that some functionality can be retained in RNA polymers containing mixed 2′–5′ and 3′–5′ phosphodiester bonds, suggesting that selection may have occurred by repeated action over time.

The Role of the Planetary Environment

The near ubiquity of condensation polymerization in modern biology may inform the conditions of early geological and biological processes. Low water activity, even for short periods, may have allowed polymerization to proceed without activation groups such as carbonyl sulfide or polyphosphates. Environments of low water activity may have included hydrothermal vents, icy bodies, tidal zones, evaporative surfaces, and many more, but likely rule out environments such as the open ocean or other large bodies of water. Alternative solvents may also be prebiotically plausible. Non-aqueous or mixed-aqueous solvents, including formamide, urea, hydrocarbons, and a multitude of eutectics, may help resolve the energetic constraints to condensation polymerization.

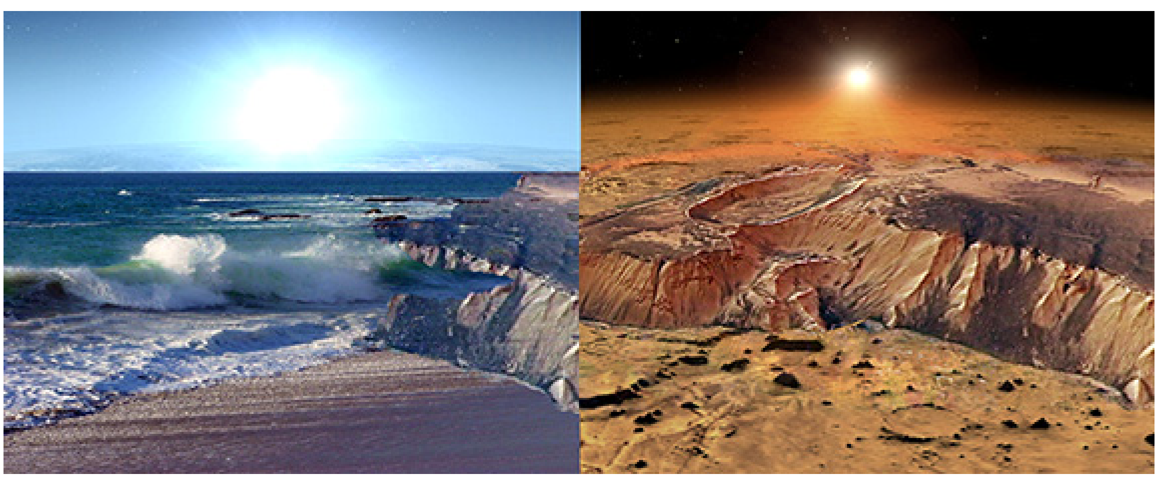

FIGURE 2-3. Planetary environments may have fostered condensation of monomers to polymers. *Source:* Modified images from NASA GSFC SVS.

Concentration of Reactants

It is important also to consider plausible mechanisms of polymer synthesis other than condensation polymerization of activated monomers. For instance, one alternative mechanism could involve the anchoring of nucleobase or protein side-chain units onto simple, independently formed backbone structures or surfaces. Another mechanism could involve dynamic polymerization and depolymerization resulting from stringing together monomers via kinetically reversible covalent bonds (such as disulfide bonds). The earliest polymers may have been structurally related to, but different from, current oligonucleotides and proteins. Further experimental studies of such systems are needed to identify the polymer structures and mechanisms of assembly that could have been compatible with chemical evolution in the origin of life.

Pathways of Evolution

It will be necessary to define plausible pathways by which protobiopolymers could have been supplanted by contemporary biopolymers. One possibility is that the stereo- and regio-homogeneity of modern biopolymers allows greater functionality than could occur in heterogeneous proto-biopolymers. Early selected functions of protobiopolymers likely included increased resistance to hydrolysis. A major question that would need to be addressed is whether the genetic information of a "protobiopolymer world" became useless in the transition from protobiopolymers to biopolymers.

The evolution of polymer backbones is intrinsically linked to the evolution of folded structures. Regular hydrogen bonds along peptide backbones stabilize protein secondary structures crucial to the stability of modern enzymes. It is likely that an evolution from early heterogeneous oligomers to modern homochiral proteins with regular polyamide backbones was accompanied by large gains in folding competence, solubility, and catalytic efficiency.

It is important to consider the role of nucleotide cofactors and metal clusters in augmenting or even initiating advanced polymer functions such as electron transfer. Nucleotide cofactors are clearly crucial to current biology. Studying their ancestry may enable us to identify and demonstrate their role in early metabolism. It seems reasonable to assume that early biological catalysts were more promiscuous, with lower substrate selectivity and product purity, than modern enzymes.

The Question of Polymer Function

The question of polymer function is intrinsically tied to the origin of life. As far as current science understands, life as we know it cannot exist without catalysis and genetics. Most broadly, the former allows energy transduction and the latter allows evolution; both are essential for life. In modern biology, proteins and nucleic acids fill these dual roles. A similar central question pertains to the capabilities of polymers to perform a range of different functions. We know many functions that current proteins and RNAs can accomplish; however, we do not know if the list is exhaustive. It will be important to determine whether these or other polymers could perform as yet unknown functions that can inform plausible pathways to life.

Cooperation

The establishment of a cooperative relationship between polypeptides and nucleic acids was a fundamental threshold in the evolution of life. These two polymers, with distinct structures and functions, became codependent. A division of major roles was achieved, with a nexus at the translation system. The origin of translation is a key process in the evolution of life. In modern biology, the translational system synthesizes all mRNA-coded protein using near-universal codes, similar structures of the ribosome core, similar biopolymer sequences of RNA that form the ribosome, and similar chemical processes. The translation system is ancient and highly conserved, and is a source of deep phylogenetic, structural, and catalytic information that extends from modern life to before the Last Universal Common Ancestor (LUCA). The common core of the ribosome was complete at LUCA. Information from the translational system generates the canonical Tree of Life, containing bacterial, archaeal, and eukaryotic branches.

The ubiquity, conservation, and importance of the translation system offer a window to understanding how nucleic acids and peptides gained mutual dependence. This relationship places fundamental constraints on the evolutionary pathway of life. In understanding the relationship between polypeptide and polynucleotide, it is of interest how the interactions between other polymeric systems could have benefited early life forms or might benefit alternative life forms.

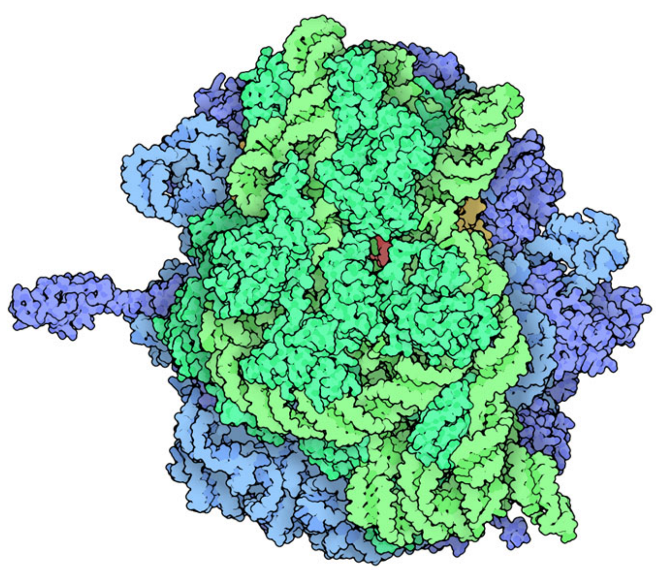

FIGURE 2-4. The ribosome is the nexus of codependence between modern peptide and nucleic acid biopolymers. In this image, the small subunit is in green and the large subunit is in blue. *Source:* Image from Goodsell 2010. Reprinted with permission from RCSB.

2.3 PROGRESS IN THE LAST TEN YEARS

Macromolecule Formation

The oligomerization of monomers such as nucleotides, saccharides, or amino acids likely preceded the emergence of evolving biochemical systems. However, monomer coupling by condensation is thermodynamically and kinetically disfavored in dilute aqueous media. Proposed solutions to augment monomer condensation in potential prebiotic environments include dehydration agents, reversible linkers, monomer co-location, and water-activity cycling. Potential drivers of non-equilibrium water cycling include daily and seasonal variations in solar and tidal forces.

Carbonyl sulfide and isocyanic acid are strong electrophiles with plausible prebiotic availability. These dehydration agents have been employed to transform amino acids into reactive cyclic anhydrides (termed Leuchs anyhydrides or N-carboxyanhydrides). Further peptide oligomerization occurs as the growing polymer reacts with additional equivalents of anhydride. Mineral Lewis acids continue to be employed to enhance and/or direct coupling reactions in dry and high-salt reaction environments. Hot non-aqueous polar solvents have also been used to drive oligomerization. Organization and co-location of monomers by adhesion to mineral or lipid membranes also have been shown to enhance polymerization rates both in the presence of and without dehydrating agents.

Prebiotic Models for Macromolecular Synthesis and Replication

Nucleotides found in RNA and DNA are difficult to synthesize abiotically, although progress has been made. This suggests that other backbone structures may have served as genetic polymers prior to the emergence of RNA. Nucleic acids containing different backbones have been shown to serve as templates for contemporary polymerase enzymes. Potential pre-RNA supra-molecular assemblies can be formed from prebiotic compounds, and they assemble through rules similar to those used by DNA and RNA. The polyphosphate trimetaphosphate can be used by catalytic RNAs to generate RNA 5'-triphosphates, demonstrating that polyphosphates could have been used as activation agents during the RNA world.

RNAs containing both 2' and 3' phosphodiester bonds instead of only a 3' phosphodiester linkage can be copied by contemporary polymerase enzymes *in vitro*. This suggests that the original RNA world tolerated structural ambiguity that was then refined by evolution. This ambiguity may have been both regio- and stereochemical. Prior to the evolution of competent polymerases, template-guided RNA ligation and recombination reactions may have been driven by highly-active dehydrating reagents.

Macromolecular Function

Work by synthetic biologists has indicated that contemporary biochemistry is considerably more plastic than would have been predicted. The genetic code has been expanded by reallocating specific codons to novel amino acids. Orthogonal pairs of tRNA and tRNA synthetase have been generated by directed evolution and shown to be effective and selective *in vivo*. For example, a variety of xenobiotic amino acids can be incorporated into proteins by ribosomes *in vitro* and *in vivo*. Computational modeling supports significant optimization of the genetic code prior to LUCA.

Understanding of the chemical basis of ribosome function has expanded, guided by available three-dimensional structural information. Ribozymes have been shown in the lab to be capable of catalyzing a wide array of chemical transformations including isomerizations, redox reactions, hydrolyses, phosphodiester exchange, aminoacylation, pericyclic reactions, conjugate additions, and many other extremely important reactions.

The kinetic properties of RNA catalysts can be enhanced in vesicles, pointing to the involvement of protocells in the origin of life. RNA can participate in regulatory processes, similar to those that characterize contemporary biological networks. Examples include metabolite-binding riboswitches, which alter gene expression and regulate metabolite biosyntheses. Riboswitches are found in all three domains of life and may be analogues of early regulatory systems. The multitude of artificial riboswitches generated in the last decade is evidence of their regulatory potential.

2.4 AREAS OF RESEARCH WITHIN SYNTHESIS AND FUNCTION OF MACROMOLECULES IN THE ORIGIN OF LIFE

I. Paths to Today’s DNA/RNA/Protein-Dominated World

A. Big Picture Questions

B. Key Research Questions

I. Paths to Today’s DNA/RNA/Protein-Dominated World

A broadly accepted group of models presupposes that the number of polymeric components of biology increased over time. Variations of the RNA world are the predominant models of this kind. These models are appealing in part because of the apparent simplicity of a single polymer world, which takes on the dual role of storing genetic information and catalyzing chemical transformations. RNA is the only polymer known to possess both of these abilities in Nature.

RNA is an informational molecule, as indicated by messenger RNAs and by viruses with RNA genomes. RNA is also catalytic, as demonstrated by both *in vivo* examples and *in vitro* experimental selections. In some variations of these models, RNA self-replication and catalysis benefited from non-coded peptides and other non-RNA cofactors. In RNA world models, metabolic catalysis and information processes were handed from RNA to proteins, driven by the superior catalytic capabilities of the latter. In this model, ribosomal translation was a late acquisition, and the central informational enzymatic system of early life, an RNA-based RNA polymerase, went extinct.

In an alternative model of the path from prebiotic chemistry to early life, polynucleotide and polypeptide backbones co-evolved. In this model, nucleic acids and proteins were interdependent even in ancestral forms. This model has the advantage of simplicity in that mature biological systems did not need to undergo disjunctive processes such as inventing new polymer backbones, incorporating new biosynthetic pathways and information transduction mechanisms. This model would not require prebiotic systems to withstand wholesale disappearance of prior informational molecules, and could also favor exaptation, where a selected molecule could be used for another function.

It is unclear how the fidelity of information transfer affected the interplay between RNA and peptides. While the universal genetic code has barely changed since LUCA, it clearly is the result of evolutionary changes over time. Numerous traces of this process can be found in today's biology. Nevertheless, to understand the early stages of protein-based life, the history and origin of the genetic code must be unraveled. Additionally, the ribosome can synthesize peptide bonds using a variety of non-natural amino acids; perhaps this plasticity is a remnant of earlier systems.

It is possible that many different sets of amino acids and nucleotides might function as effectively as the ones used by life today, indicating that the convergence of the universal genetic code was a local solution to environmental constraints rather than a global solution maximizing catalytic and genetic efficiency. Alternatively, the code may have undergone significant evolution both in codon usage and monomer identities prior to LUCA. The order found in the modern genetic code, for example the assignment of similar codons to similar or identical amino acids, suggests some level of functional evolution before convergence.

The co-evolution of a symbiotic relationship between multiple polymeric systems could be facilitated by encapsulation, possibly in protocells or membrane vesicles, allowing retention of successful outcomes and separation from competitors. The self-organization of systems into hypercycles could facilitate these processes.

Although it is generally agreed that there once was an RNA World, it is not clear if RNA was the first genetic macromolecule or if it was preceded by a simpler polymeric structure or surface. The study of nucleic acid analogs as potential precursors to RNA is an area of active research in the origin of life. In considering the importance that a proposed polymer structure might have had in early evolution, one must assess several different characteristics and functions.

A. Big Picture Questions

Are there straightforward routes for the prebiotic synthesis and coupling of the monomeric building blocks of the polymer?

Does the polymer offer advantages in comparison to RNA in terms of chemical stability?

Can the polymer convey and transmit sequence information, such as by a hybridization process, to itself or to other nucleic acids?

Does the polymer have the capacity to catalyze reactions of importance to early chemical evolution?

Can the polymer self-replicate or template the synthesis of other sequences with good fidelity?

Is any genetic information retained during the transition from the polymer to the RNA World?

B. Key Research Questions

What is the chemistry of macromolecular formation reactions?

Was polymerization driven by chemical coupling agents? What is the source and persistence of these agents? What was the source of energy and pathway of energy utilization?

How is the hydrolytic instability of chemical coupling agents managed in water? By brute force? By removing the water? By making a coupling reaction different from a hydrolysis reaction?

What mechanisms promote high effective concentrations of monomers (thermal convection, surface adsorption/permeability, etc.)?

Did non-covalent assembly drive early polymerization? How can supramolecular assemblies transition to covalently-linked polymer systems?

If the polymerization of building blocks present at low concentration are thermodynamic-unfavorable, how high a concentration is needed to overcome that problem? What kinds of concentration would not only raise the concentration of the species, but also raise their chemical activity? How can molecular species be pre-organized to create effectively higher concentrations? What system would not make the problem worse?

If no single set of conditions solves the problem of polymerization of building blocks at low concentrations, what sort of prebiotic geological scenarios are plausible? Does that scenario involve dry land? a surface exposed to different intensities of ultraviolet light? a particular inventory of water on Earth? What about the environment of Mars, where the surface of dry land was always more abundant than on Earth?

How does information transmission and chemical evolution occur?

What chemical mechanisms allow for information replication and mutation?

What kinds of molecules can be replicated with errors, where the errors themselves are replicable?

What physical parameters of pre-RNAs and pre-proteins influence kinetics and the accuracy of replication?

Can nontemplated production of informational polymers be demonstrated?

What are the chemical alternatives? How and why do they occur?

What alternative backbones and side chains exist for functional and informational macromolecules, and what are their properties? What is the size of the chemical space for these alternative chemistries?

Did homochirality arise during polymerization/assembly rather than during monomer synthesis? What degree of homochirality is necessary or optimal?

What is the role of phosphate in early condensation polymerization?

What is the role of environment?

What does the mechanism of polymerization in modern biology (primarily condensation polymerization and aldol reactions) tell us about the environment in which the polymers evolved?

Was polymerization driven by cyclic conditions (e.g., water activity, temperature, tidal, convection)?

Is there a role for non-aqueous solvents and environments (formamide, hydrocarbons, deep eutectic solvents, micelles, etc.) in condensation polymerization?

How do non-standard solvents and environments (formamide, hydrocarbons, deep eutectic solvents, micelles, etc.) affect activity of functional macromolecules?

Macromolecular function: how did physicochemical effects develop over time?

What other chemical linkages exhibit the simultaneous thermodynamic instability and kinetic stability that characterize phosphate diesters?

What role does polymer solubility/solvation/hydrophobicity play in the origin of function?

What types of rudimentary functions promote polymer persistence, assembly, and growth?

Which folding properties are sufficient for function to arise, and which properties (such as specific binding and catalysis) are optimal for function?

What are the advanced steps of macromolecular function?

What functions are most likely to emerge early?

What range of chemical functions besides the ones in contemporary biology could proteins and/or RNA accomplish?

What biological and proto-biological functions can be accomplished by non-natural polymers?

What led to macromolecular complexity?

How did polypeptides and polynucleotides begin to cooperate? How did the genetic code originate?

What forces select for regulatory processes in the prebiotic world?

2.5 CHALLENGES FOR THE NEXT TEN YEARS

To understand the origin of current biology, we must investigate possible evolutionary paths from earliest macromolecular assemblies and polymers to contemporary DNA/RNA/protein-dominated life. Discontinuities in the pathway to contemporary life that are the consequence of these models must be addressed. Models must be validated by molecular experiments where they are experimentally tractable. Models need to be evaluated statistically as well to provide an estimate of their plausibility—we need to show not only that certain things can happen, but evaluate how likely it is they will occur in an abiotic environment. Hypothesis-driven research should shift from what is possible to what is likely. Modern methods of analysis must be employed to evaluate and extend current and proposed models.

Sequence and structure analysis of nucleic acids and proteins has been a cornerstone of our ability to recapitulate earlier forms of life. These efforts can be expanded to analyze higher levels of biopolymer history. Structures of modern biomolecules at all levels, from the primary to the tertiary, when viewed in their phylogenetic context, can inform us about biopolymer history. Understanding hetero- and homochiral assemblies of RNA, protein, metals, and cofactors can tell us about ways in which biopolymer structure is constrained by energetics and the environment. Similarly, the functional consequences of contemporary modified nucleotides, and of various orthogonal nucleotides, when present in RNA or other polymers, might help to understand potential pre-RNA building blocks. Functions of modern non-coding RNA might indicate how they could have functioned in early forms of life. The full catalytic power of RNA or proto-RNA polymers in the context of size, metal and protein cofactors, and sequence space poses many important questions.

In the search for simple replicating systems of catalytic polymers that have the potential to evolve into more complex systems, a variety of different monomers warrant consideration, including those that could arise in environments unlike Earth's. Separation of template and daughter molecules in the absence of evolved enzymes such as DNA or RNA polymerase remains a challenge.

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3 EARLY LIFE AND INCREASING COMPLEXITY

INTRODUCTION

Over the span of four billion years, living systems have generated an extraordinary range of organizational plans, creating the immense variety present in the modern biosphere. We are faced with the challenge of deriving overarching rules for evolutionary processes on the basis of empirical observations and theoretical frameworks and using them to develop a general model of life from which predictions can be made.

This chapter addresses the inception and subsequent development of life on Earth since its origin. The history of life should be understood in the context of two fundamental observations: first, increasingly complex living systems have arisen over time, and, second, despite these innovations, the different branches of life have retained many traits in common for both contingent and deterministic reasons.

3.1 WHY IS THIS TOPIC IMPORTANT?

> The history of life on Earth is the only example of life that we know of so far and, therefore, the only example from which we are able to derive general principles of what life is and how it works. A growing understanding of the origin and history of life on Earth contributes to astrobiological goals in a basic way: better data leads to better theory and, thus, to better predictions regarding the prerequisites for the evolution and characteristics of life elsewhere in the Universe.

Observations of present-day life provide the best ecological, behavioral, morphological, and molecular data. Successful interpretation of patterns exhibited by existing life depends, in turn, on understanding the geologic context in which that subset of life originated and how it fared through a succession of challenges and opportunities. Plate tectonics, long-term climate fluctuations, asteroid impacts, and other large-scale Earth processes have contributed to the origin and diversification of complex life.

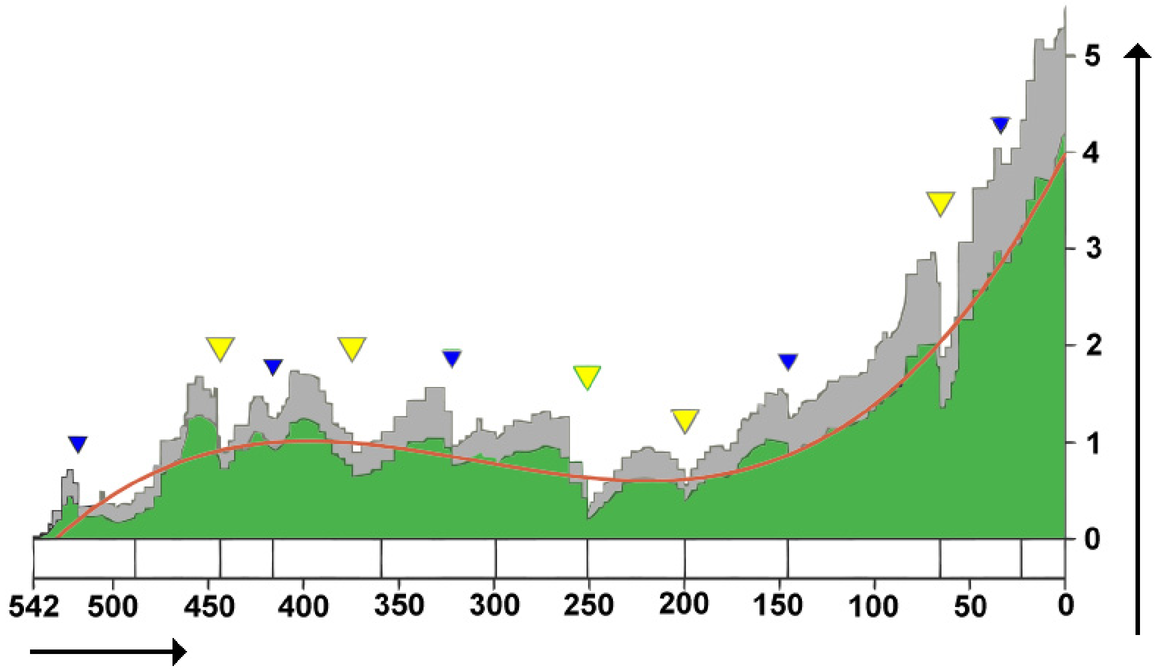

FIGURE 3-1. A history of extinction through the Phanerozoic. The green and grey represent thousands of well-defined genera and total genera, respectively, averaged into the red trend line. The yellow triangles represent the five major mass extinctions and the blue triangles represent several smaller events. Along the bottom, time is represented in millions of years before present day. *Source:* Image modified from Albert Mestre 2005, Wikipedia.

3.2 WHAT DOES THIS RESEARCH ENTAIL?

How we understand and recognize life will guide our search for life on other planets. On Earth, the transition from non-living to living entities was not a single event but a process of increasing complexification. Living systems on other planets may prove difficult to recognize if the discovered organic system is a transitional form.

Here, we adopt the definition that life is a chemical system capable of Darwinian evolution and focus specifically on the emergence of the first evolving organisms and subsequent elaborations of living systems. Although there is no commonly held definition of life, all life shares attributes which may be inherent in living states everywhere. Thus, identifying which attributes of life are likely to be common to all origins and which are context-dependent will allow us to better predict the nature of life on other planets.

Life’s Origin

One of the major questions we are trying to answer is: how does life begin? Every model that has been proposed so far for life’s origins on Earth involves a prebiotic chemical system that achieves a level of complexity which allows replication and natural selection. The models for the emergence of the first Darwinian evolving system involve, for example, the origin of genes and gene transfer mechanisms, translation, metabolic networks, cellular boundary control, and cell division. The transition to organismal individuality and increasingly vertical inheritance from earlier states is not well understood, but may have been a prerequisite for the subsequent evolution of ecological complexity and the metabolic diversity from which Earth’s biosphere is constructed. Detectable biosignatures require the proliferation of living systems, and therefore may depend on the occurrence of these transformations.

The Evolution of Complexity

A number of lineages of life on Earth represent innovations that further increased complexity and altered the nature of information transfer among individuals and across generations. These innovations include, for example, eukaryotic cell organization, endosymbiosis, photosynthesis and other metabolic innovations, multicellularity, cell differentiation, ecological diversification, ecosystem formation, and eusociality. These major transitions, along with their environmental context, must be identified and described empirically. In addition, these observations should be used to construct general theories of processes that promote or reduce complexity, and the accumulation or loss of diversity at a given level of complexity, which can then be applied to unique, non-Earth contexts.

Universal Traits of Life

The exact nature of life on other planets most likely depends on the historical context specific to each world, just as the nature of life on Earth is the product of contingent events here. Yet, life on Earth also displays remarkable similarities among lineages, not all of which can be explained by common descent. Evolution has produced convergent solutions in unrelated taxa. For example, multicellularity has evolved independently many times, and now characterizes many eukaryotic species. Multicellularity might thus be expected to evolve in living organisms elsewhere, perhaps with a different probability of doing so depending on the specific genetic architecture of the extra-terrestrial form of life. A robust accounting of the universal traits of life, and the degree to which their appearance reflects contingency or inevitability, should be pursued as a means to help predict the attributes of life on other planets. In addition, an understanding of how different types of complex life respond to environmental perturbations, including the evolution of interacting lineages, can help predict the dynamics, deployment, and fate of life on other planets.

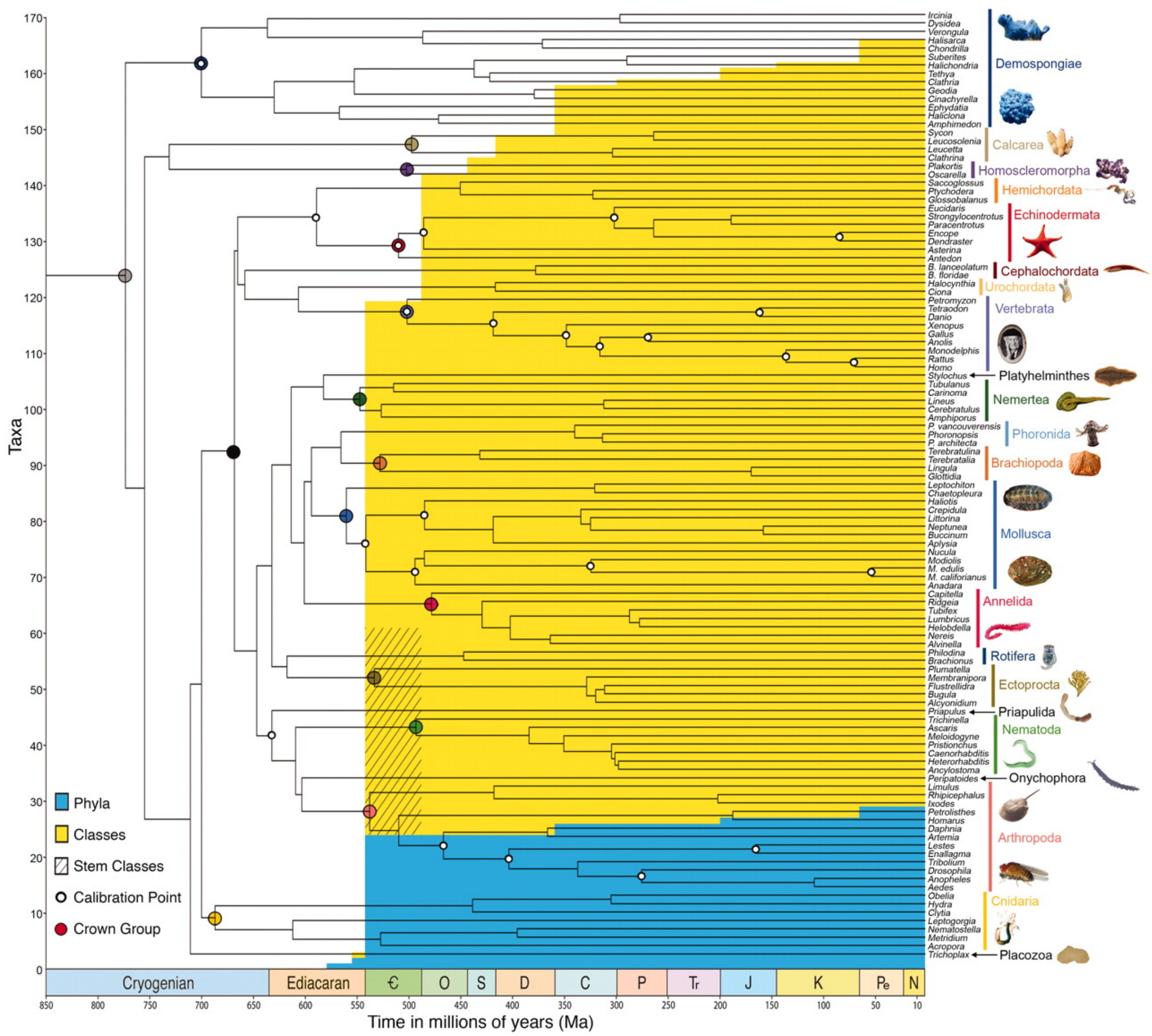

FIGURE 3-2. The origin and diversification of animals as inferred from the geologic and genetic fossil records. The dramatic rise in the number of animal fossils (see scale on left) in the Cambrian relative to the Ediacaran conveys the impact of the Cambrian explosion of animal life. Little high-level morphological innovation occurred during the subsequent 500 million years in that much of animal disparity, as measured by the Linnean taxonomic ranking, was achieved early in the radiation. Overlying the geologic record is the pattern of animal origination as inferred from the molecular clock. Twenty-four calibrations (open circles) were used and treated as soft bounds. There is general concordance of bilaterian phylum-level crown groups (colored circles; the color of each circle is the same as the corresponding taxonomic bar and label on the far right), with the first appearance of most animal groups at the Ediacaran-Cambrian boundary. In contrast, the origins of the demosponge (dark blue) and cnidarian (yellow) as well as the bilaterian (black) and metazoan (gray) crown groups are deep in the Cryogenian. Geological period abbreviations: Є, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pe, Paleogene; N, Neogene. A high-resolution image is available in the SOM. *Source:* Image from Erwin et al. 2011. Reprinted with permission from AAAS.

3.3 PROGRESS IN THE LAST TEN YEARS

The following are a few examples of research in the past ten years that have advanced our understanding about early life and increasing complexity.

1. New pathways for prebiotic synthesis have been discovered. Investigations have delved into the relationship between life and energy availability, a topic relevant to understanding habitability in subsurface environments. Research has revealed that certain peptides (compounds containing two or more amino acids) can achieve prebiotically relevant enzymatic activity, a finding which aids our understanding of the transition from prebiotic chemistry to life.

2. In an effort to explore possible first steps toward the origin of life, researchers have constructed a continuous flow reactor to simulate the interaction of hydrothermal fluids and ocean waters with submarine crust on early Earth. They are using this reactor to investigate the theory that life could have originated around deep-sea vents at high pressure. Another project has produced a fuel-cell model of the origin of metabolism on the early Earth or any wet terrestrial world. Further research into the submarine hydrothermal theory of the origin of life has shown that the first biological waste product of life originating in this sort of environment would be acetate, making this organic compound a target for life detection.

3. Toward understanding how life originated, astrobiologists are analyzing the oldest remaining evidence of earliest life that preceded the “last common ancestor.” This evidence lies in the core mechanisms of cellular machinery. It is expressed not only in the structure and function of individual biomolecules, but also in their interactions and dependencies within the cell. Research conducted over the past 50 years has started to reveal that the genetic code is more likely an evolved construct than a “frozen accident.” Research conducted by astrobiologists in recent years considerably strengthens the case for an evolved genetic code.

4. Astrobiologists have conducted the first digital life simulation capable of open-ended growth of complexity (i.e., arbitrarily high complexity over time). The standard conception of evolution shows how the fitness of the organism is maximized in a given ecosystem, but does not explain how complex life emerges or whether such life is generic or peculiar to Earth. Among insights derived from this work was that horizontal gene transfer and gene duplication are two operations that enable the evolution of open-ended complexity.

5. *In vivo* studies of the evolution of open-ended biocomplexity have been driven by advances in both experimental and comparative genomics. These studies, including real-time laboratory experiments using microbes, have deepened our understanding of the genetic and ecological mechanisms that drove major evolutionary transitions in the history of life on Earth. These transitions include the evolution of cooperation,

which leads to syntrophic communities as well as to a variety of symbiotic associations that range along the continuum from mutualism to parasitism. Other transitions in complexity whose mechanistic bases have been illuminated by *in vivo* studies include the evolution of differentiated multicellularity and speciation itself.

6. Ancestral sequence reconstruction has proven to be a powerful tool for studying ancient cellular life. Reconstruction of the ancestral sequences of ancient gene families has been used to infer the original functions in the ancestral members of these families or the conditions under which they had evolved. The synthesis of proteins from ancestral amino acid sequences has been used to measure the conditions under which these proteins optimally functioned, a credible proxy for the environmental conditions in which the ancestral population lived.

7. Work on synthetic biology in the field of astrobiology has focused on building “life” from scratch in the lab. Their aim is to assemble a self-replicating protocell under realistic early Earth conditions. While the transition from non-living to living matter remains unexplained, research has advanced in many productive directions. Most advances have been made toward hypothetical RNA world organisms, specifically the non-enzymatic synthesis of RNA polymers, the development of catalytic RNAs, and possible compartments such as lipid vesicles.

8. Some of the oldest sedimentary rocks in the world—the 3.5-billion-year-old Strelley Pool Formation in Western Australia—provide the best evidence to date for the earliest life on Earth. This formation contains a reef-like assembly of laminated sedimentary carbonate accretion structures, called “stromatolites,” that were created in part by photosynthetic microbes. Recent work on these ancient stromatolites suggests that an important photosynthetic pathway in the ancient oceans may have been anoxygenic photosynthetic iron oxidation.

9. Recent research has explored the role of anaerobic methanotrophic microbes in regulating Earth’s climate. Such methane-consuming organisms may have been an important part of early Earth’s ecosystem, and astrobiologists speculate that this type of metabolism might be possible on Mars. Astrobiologists are also advancing understanding of chemolithoautotrophs—microorganisms that live on inorganic energy sources such as minerals. Such organisms provide another model of the type of microbial life that might be able to thrive on Mars, or other rocky planets.

   The development of photosynthetic fixation of carbon has been long regarded as one of the most important biological innovations on the early Earth, setting the stage for heterotrophic respiration pathways such as bacterial sulfate and iron reduction. Astrobiologists have recently compared the isotopic record for carbon, sulfur, and iron in 3.8-billion to 1.5-billion-year-old marine sedimentary rocks. They found that expansion of bacterial iron reduction occurred after the carbon isotope record indicates development of photosynthesis but before the major expansion of bacterial sulfate reduction. A well-known major excursion, or deviation, in carbon isotope compositions at about 2.7 billion years ago coincides with a major excursion in iron isotope compositions. These coincidental deviations may be an indicator of the development of a complex ecosystem on Earth that included photosynthesis, bacterial iron reduction, and methanotrophy.

10. Today, Earth's first-order biodiversity pattern is a diversity gradient with maximum richness in the tropics, and this pattern has been shown to be closely associated with variations in temperature and other physical variables in time and space, many of which can be accessed by remote sensing in the present day and estimated using geochemical and other proxies in the geologic past. The dynamics of these spatial diversity trends have been quantified and modeled, and the fossil record shows that the steep gradients seen today were often shallower, and perhaps even absent, under different global climate states of the geologic past. Research has shown that ecological communities have responded to these past climate changes by disassembling, with species moving individualistically along temperature and other environmental gradients, rather than shifting as cohesive units. These results have provided insights into the general mechanisms that may generate and maintain biodiversity in non-Earth systems.

11. The explosion of complex animal life in the Cambrian has been shown, by integrating paleontological, geochemical, and molecular-phylogenetic data, to be a genuine biological phenomenon, and not simply a preservational artifact as many had suspected. The late pre-Cambrian fossil record was found to contain a few complex fossils, many of which are now considered to represent an early extinct experiment in multicellularity, but the precursors to the major bilaterian groups such as arthropods, mollusks, echinoderms, and vertebrates were simple, small, and homogeneous in form until the Cambrian explosion. Comparative analyses of later diversifications that resulted in new higher taxa have shown that the Cambrian radiation was unique in its magnitude, but that some other evolutionary explosions, such as those associated with the invasion of land by plants and animals, show a similar "early burst" of biological form followed by a slowdown, rather than a steady accumulation of novel morphologies.

12. The history of complex life on Earth provides information about how life may have evolved elsewhere. Many aspects of this history are captured in the fossil record, and the first and last occurrences of many species and higher taxa have now been placed in a temporal and spatial framework that permits quantitative analyses. These analyses have confirmed that the trajectory of biodiversity over the past 600 million years has been extremely unsteady and episodic. Five major mass extinctions and several smaller events have been confidently detected, and in at least two cases found to permanently shift the composition, evolutionary rates, and direction of life on Earth. Geochemical and sedimentary evidence has shown that at least one of these

events, the end-Cretaceous extinction 66 million years ago, is associated with an asteroid impact that had a devastating effect on the global biota.

Progress toward a general understanding of life in the Universe has been achieved by studies conducted at multiple scales and using multiple methodologies. Next, we outline a research agenda that likewise embraces broad approaches, including evolutionary theory, the emergence and function of the fundamental molecules of life, and the drivers of evolutionary dynamics at ecological and geologic timescales.

3.4 AREAS OF RESEARCH WITHIN EARLY LIFE AND INCREASING COMPLEXITY

I. **Origin and Dynamics of Evolutionary Processes in Living Systems: Theoretical Considerations**

II. **Fundamental Innovations in Earliest Life**

III. **Genomic, Metabolic, and Ecological Attributes of Life at the Root of the Evolutionary Tree**

IV. **Dynamics of the Subsequent Evolution of Life**

V. **Common Attributes of Living Systems on Earth**

I. Origin and Dynamics of Evolutionary Processes in Living Systems: Theoretical Considerations

We are working to generate a general understanding of life in the Universe on the basis of life on Earth. In order to make this step, we must start with a theoretical framework that captures the general features of life on Earth. Two approaches to life—as composed of interacting networks and evolving lineages—allow us to think of life in broad terms. They provide important insights into what it means to be “alive,” but also challenge us to be more precise about how we think about individuals and groups in the context of life.

Life on Earth began with the origin of the earliest metabolic and evolutionary network and then diversified into an astonishing array of life forms across the surface of the planet. As the process unfolded, new selective pressures arose as the biosphere became a larger actor within the environment. The emergence of interacting networks allows for more complex functions than those of the individual alone (e.g., molecules to genes, genes to genomes, cells to colonies, etc.). The new relations effect new mechanisms of variation and selection and give rise to new levels and forms of individuality. Such interactions appear to be crucial for understanding the properties of life. The evolution of sequences (e.g., polymers, metabolic chains) and networks (e.g., metabolic, ecological) provides a major source of biological change and innovation. Understanding the dynamics of these transitions is, therefore, a crucial prerequisite to understanding the origin and development of life.

Life is characterized by exquisitely coordinated metabolic and information-processing mechanisms. Because these are prone to degradation and decay, Darwinian evolution is required to preserve and stabilize out-of-equilibrium structures: if the metabolic and information processing mechanisms are not present in the daughter cells, then the cell dies out and is replaced by other cells that have these mechanisms.

Similarly, organisms coordinate with other organisms. Microbes form associations with one another and with complex macroorganisms, and these associations vary from incidental interactions on ecological time-scales to seemingly permanent relationships that endure over geologic time-scales. Over short time-scales, microbes can opportunistically use waste products produced by other organisms as sources of energy. More stable and finely tuned interactions may give rise to syntrophies, where certain processes in one organism require close interaction with another organism, and vice versa. The associations among or between microbes, or among microbes and their macrobial partners, may become so interdependent that one cannot exist without the other, as in symbiosis, or that neither can exist without the other, as in mutualism. Perhaps the most striking examples of the latter are those associations that gave rise to two of the most significant innovations in the eukaryotic lineage: the mitochondrion and the chloroplast. All of these associations, from the incidental and opportunistic to the enduring and obligate, challenge the definition of what is an individual, and present interesting problems for evolutionary theory.

One example presently of interest, which explores how something as general as spatial geometry can constrain quite sophisticated systems, comes from scaling relations originating in metabolism. Many biological variables (mass, metabolic rate, longevity, structure of circulatory system, etc.) are related to one another “allometrically;” that is, the relationship can be described by a power law in which the typical exponent is some multiple of 0.25. These allometric relationships constrain the morphological and functional states occupied by organisms, species, and ecosystems and may influence patterns in the evolution of complex life. They are thus likely to be universal constraints that will apply to life anywhere. The evolutionary dynamics of such allometric processes have not been fully explored.

Key Research Questions about Origins and Dynamics of Evolutionary Processes

Evolutionary Context

Both the environmental conditions and genetic context of a genotype can heavily influence its phenotype. Their interactions are unclear and unpredictable but absolutely crucial for understanding evolution and the emergence of innovations. These considerations beg the questions:

1. How do environmental conditions affect and constrain evolutionary pathways, influencing, for example, the types of mutations and the rates at which they arise?

2. How do prior genetic context and history affect and constrain future evolution and, for example, the emergence of metabolic and organizational innovations?

3. Are there universal principles related to the origin of selection?

4. Is there directionality in the evolution and elaboration of complexity?

Evolvability

The ability to innovate is perhaps the most exciting feature of biological systems. Biology has demonstrated this ability in myriad ways, but we do not yet understand how to manipulate or analyze it. We may therefore ask:

1. How do evolutionary innovations originate?

2. What are the advantages and disadvantages of modularity, and how does modularity arise?

3. What is evolvability, and what are good metrics for evolvability of different chemical systems?

4. How do evolvable chemical systems arise from non-evolvable chemical systems?

5. Are there characteristic time-scales of evolution?

6. What properties are required for open-ended evolution?

Structure of Networks

Interaction networks are central to life. Molecular interactions, genetic interactions, epistasis, metabolic networks, and ecological networks are all examples of the importance of network structure and architecture in living systems. While we may understand the "parts" of life, we know relatively little about their interactions. Therefore, we ask:

1. What is an individual?

2. How did/do individuals emerge?

3. How did/does the network structure of molecular or organismal interactions affect evolution?

4. What network architectures support survival and evolution?

Evolutionary Landscapes

The importance of evolutionary landscapes has spawned much theoretical work, but comparatively little experimental work has been done due to technical difficulty. Recent developments in biotechnology now enable quantitative study of these crucial issues.

1. How reproducible and diverse are evolutionary pathways, given the same or different conditions?

2. How does evolutionary history constrain future evolutionary pathways?

3. What do fitness landscapes look like? Which landscapes are characterized by neutral networks, and why?

4. How do evolutionary landscapes in sequence space translate into landscapes in structure and function space, both at the molecular level and at the supramolecular level?

Modularization of Living Functions and Levels of Selection

1. How do mechanisms of evolution change at greater levels of complex organization?

2. How does selection relate to individuality, and how far down (atoms, molecules, proteins) and how high up (communities, symbioses, ecosystems) can the individual extend?

3. Is it inevitable that units of selection cluster into forms that act as higher level units of selection?

Physical, Developmental, and Chemical Constraints on Selection

1. What are the constraints on the evolution of developmental complexity? What are the constraints on the chemical pathways for metabolisms and organisms to emerge and evolve? Is the evolution of complexity inevitable, and does it require eukaryotic

architecture? What are the modes of developmental complexity (life history, cell associations, tissue types)? What processes were essential in episodes when complexity increased?

2. What are the allometric laws constraining the evolution of life, and under what conditions are they obeyed or violated?

3. Is life a generic outcome of the laws of physics, an inevitable planetary phenomenon if certain conditions of disequilibrium are met?

II. Fundamental Innovations in Earliest Life

Life on Earth displays a wide variety of complex structures and operations, such as cells, RNA, proteins, lipid bilayers, metabolic networks, information systems, and so on. Understanding the emergence of these traits will require both reductive and synthetic approaches.

Reductive approaches are those that identify traits by scaling down existing living systems. Synthetic approaches are those that identify traits by building models up from plausible prebiotic components, linking environmental chemistry to the formation of the earliest life. Both approaches are needed because reductive approaches have the difficult task of tracing evolutionary steps backwards, and much of the information (i.e., genes and gene domains) was almost certainly lost, and therefore is not present in any living organism. Synthetic approaches, meanwhile, can generate an array of plausible scenarios that can be difficult to narrow to specific historical pathways.

These approaches are particularly useful in considering alternative solutions to those that appeared on Earth. We do not know, for example, whether alternative modes of inheritance would yield patterns or processes of evolution that would differ significantly from those observed in Earth's biota. Research using both reductive and synthetic approaches will lead to a better understanding of how early life formed, and the sequence and dates that particular traits were acquired.

Neither the existence or functioning of living systems can be understood outside the context of the conditions in which they exist. These conditions include physical aspects of the environment, such as chemistry and energetics, and also inherently biological aspects such as co-evolved interdependencies among members of communities. Therefore, an essential part of identifying plausible models for earliest life also includes identifying relevant contexts, and the ways living systems embed within them.

Key Research Questions about Innovations in Earliest Life

How do the essential traits of life arise from the geochemical environment, and what factors do we consider essential for the most basic living system?

1. What are the relevant spatial and temporal scales for the origin of life?

2. Is life a necessary consequence of certain environmental conditions?

3. What is a minimal energetic source/mechanism?

4. What environmental pressures applied to the earliest life on Earth?

5. What evolutionary pressures applied to the earliest life?

6. How do the conditions for the origin of life differ from conditions for sustaining life? What does this tell us about the “habitable zone”?

7. Are there adaptations and selections preserved within reconstructions of the LUCA genome that would indicate its origin?

8. If Earth organisms exist that represent a second origin of life, how would we recognize and differentiate them?

What was the history and order of biological innovations associated with the emergence of life?

1. What are the simplest structures we think of as having a biological “function” (e.g., enzymes, genes)?

2. What are the simplest structures that could have been the first life forms, or contributed to the origin of life? (e.g., viruses, prions)? Put another way, what are the simplest structures that could undergo Darwinian evolution, with self-replication, selection, and mutagenesis, which would then have evolved into more complex life forms and cells?

3. Are viruses good models for the earliest life?

4. Can we date important metabolic innovations (e.g., chemiosmosis, chemoautotrophy, phototrophy)?

5. Can we date important structural innovations (e.g., chromosomes, organelles, flagella)?

6. What does phylogenetics tell us about the oldest/most common genetic components of life?

7. Can we make progress toward constructing life capable of Darwinian evolution from atoms?

8. Can we make progress toward constructing life capable of Darwinian evolution from components of living cells?

9. Are endosymbionts good models for the earliest cellular life?

10. What was the relative timing of an RNA-to-DNA genome transition, if such an event occurred?

11. How did life make the transition from a communal or collective phase, where it is the community that varies in descent, to the present epoch, where there is vertical descent of individual organismal lineages?

Is there a minimal set of vital requirements for life?

1. How is life/metabolism determined by structure, energetics, and information content?

2. Which components of a membrane are important for establishing cellular individuality?

3. Is it helpful to think of the earliest life as a “self-sustained chemical system capable of undergoing Darwinian evolution”?

4. How did the sharing of genes (or information molecules) through lateral gene transfer affect the results of evolution by natural selection (i.e., “Darwinian evolution”) in the first replicators, and afterward?

5. How are lineages defined with respect to the “lateral transfer” of genes (or other information molecules), and how should the concept of selection be applied to lineages with high levels of such mixing?

6. Can studies of living bacteria and microbial organisms indicate whether evolutionary dynamics are different when lateral variation is common or uncommon?

Experimental model systems

1. Which molecules are necessary to obtain a self-replicating system capable of open-ended Darwinian evolution?

2. How do physical and chemical properties of biopolymers affect evolution and evolvability?

3. What can we learn about the evolution of early life from experimental systems of molecular networks and cycles?

4. What can we learn about the evolution of early life from long-term experimental evolution of microbes?

5. What can we learn about the evolution of early life from artificial life?

6. Is there any genomic evidence for interplanetary panspermia (e.g., Mars to Earth)?

7. How do new forms of selection (i.e., starting from strictly abiotic environments and evolving into ecological interactions) and, consequently, drift and neutrality arise? How important are these new mechanisms for stabilizing and filtering diversity for the elaboration of biological complexity?

8. What processes drive unassociated microorganisms toward interactions of increasing connectivity with other organisms, such as syntrophy and symbiosis?

III. Genomic, Metabolic, and Ecological Attributes of Life at the Root of the Evolutionary Tree (LUCA)

Present-day organisms share a number of foundational commonalities that testify to a last universal common ancestor (LUCA) by which they are all related. The sequencing of genomes from across the Tree of Life has enabled comparison-based studies, which so far reveal that the organisms represented by LUCA were likely cellular and contained many of the genes, proteins, and biological functions present within modern lineages (LUCA may well be not a single organism but many, perhaps thousands, of different organisms or populations).

This minimalist reconstruction lacks the resolving power to discriminate among competing hypotheses about prebiotic chemistry and early life, the relative timing of LUCA, the origin of cellularity and Darwinian selection, and other issues critical for placing the emergence of life on Earth within an astrobiological context. Advances in genomics, bioinformatics, and computational biology, paired with increasingly sophisticated techniques in molecular evolutionary biology, will enable descriptions of LUCA that are more detailed and more accurate than previously have been possible.

The recent growth of bioinformatics databases, the sophistication of evolutionary and ecological models, the availability of high-performance computing resources, and the emerging capabilities of synthetic biology permit new investigations of life at this stage of evolution with greater detail and greater confidence than has been previously attempted or even considered possible. This transition, the timing and nature of LUCA, and the emergence of the first branches on the Tree of Life can, therefore, be understood in mutual context.

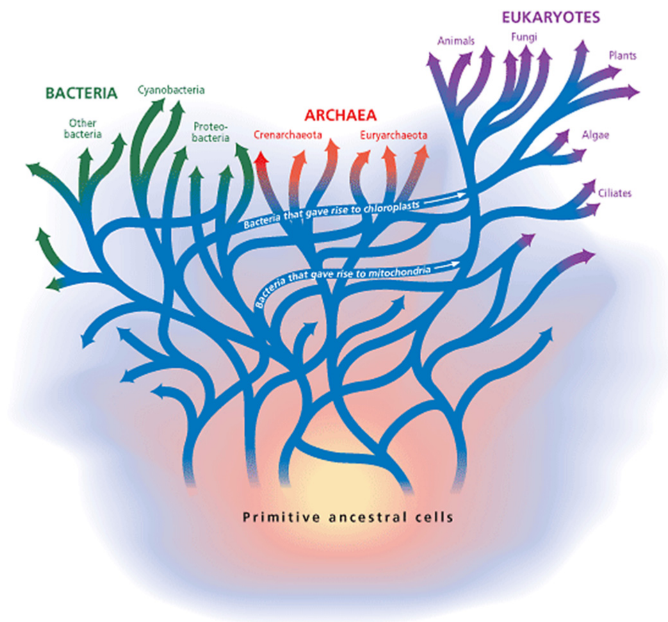

FIGURE 3-3. Uprooted Tree of Life, where LUCA is a population of organisms. *Source:* From Teske and Edwards 2005. Illustration by Jayne Doucette, WHOI.

The root of the Tree of Life identifies the ancestral, organismal point of coalescence of all life known to have existed on Earth. This ancestral state marks a horizon at which the structure of evolutionary dynamics altered due to changes in the composition, integration, and transmission of cellular components. LUCA presumably encompasses periods during which multiple innovations in molecular biology occurred, possibly including the roles and relations of macromolecules and the nature of cellular memory and control systems, including translation.

The nature of life prior to LUCA is of particular importance because it provides a window into the changes in modes of individuality that led gradually to vertical descent as the dominant mode of gene transmission. This transition made possible the appearance of discrete organismal lineages, and therefore initiated the characteristic branching nature of the Tree of Life. As such, understanding life just prior to the first branch can inform our expectations for whether and how this same transition might take place throughout the Universe.

Key Research Questions about Attributes of LUCA

The evolutionary history and ecological context of LUCA

A popular evolutionary model for the earliest life is that it was dominated by horizontal gene transfer (HGT) to a sufficient degree that individual lineages cannot be distinguished from one another. A transition from this regime to one of vertical inheritance and the establishment of distinct lineages would, in retrospect, result in the apparent detectability of LUCA. Alternatively, this transition could have occurred earlier, with vertical inheritance, speciation, and distinct microbial lineages existing before the time of LUCA. In this schema, pre-LUCA lineages still could have acquired many genes via HGT, in the same way that organismal lineages do today.

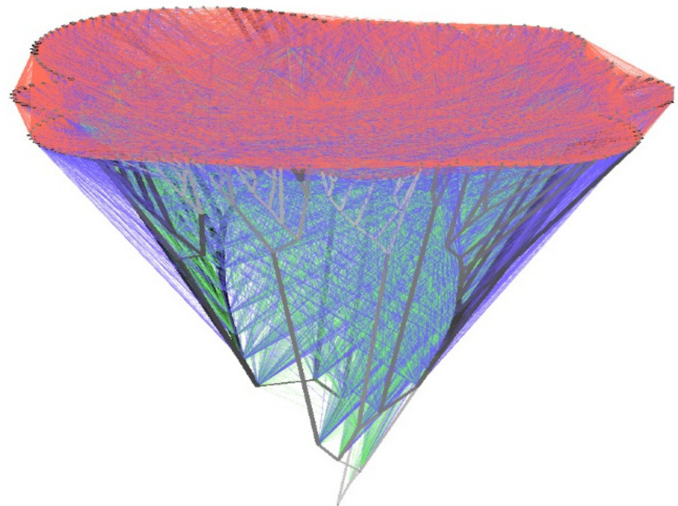

FIGURE 3-4. Phylogenetic tree showing horizontal gene transfers, indicated in green and blue, between different vertical lines representing genetic descent. On the top surface, the pink web shows the interconnectedness of the modern community. *Source:* Image from Dagan et al. 2008. Copyright 2008 National Academy of Sciences, U.S.A.

1. How much time and evolution occurred between the origin of life and LUCA?

2. Do genomic, proteomic, or metabolic features at the root of the Tree of Life suggest even earlier stages of evolution that can be characterized?

3. Does the root of the Tree of Life represent a single individual, a species, or a population of species?

4. What is the role of HGT in the coalescence of the last common gene ancestors, and how does this relate to the last common organismal ancestor? Did HGT from extinct lineages contribute to the coalescence of LUCA?

5. What selection regimes could have driven life toward organismal individuality and gene transmission through vertical inheritance?

LUCA as a window into early cellular life

A minimal LUCA genome can be, and has been, computed by comparing the gene complements of modern species across the evolutionary tree. In some cases, the emergence of certain gene families prior to LUCA can be ordered. Further refinement of these techniques is required, however, to achieve higher-confidence predictions of LUCA's genome and pre-LUCA gene evolution, and to possibly infer other biological properties that may not have endured to be present in modern lineages. Important membrane-related protein families were present in LUCA, including those responsible for inserting other proteins into the membrane. The ability of LUCA to use the membrane as a controlled boundary may reveal characteristics pertaining to organismal individuality and its

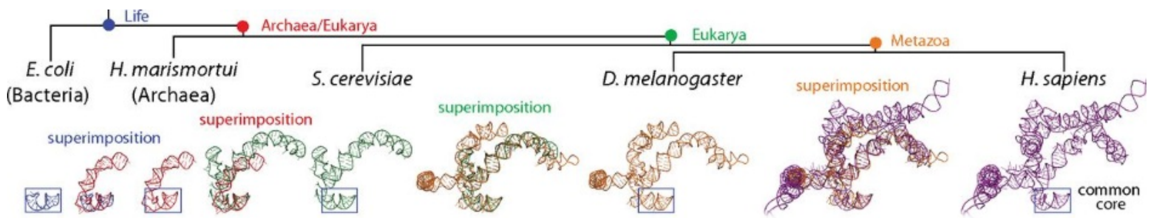

FIGURE 3-5. The evolution of helix 25/ES 7 shows serial accretion of rRNA onto a frozen core. This image illustrates at the atomic level how helix 25 of the large subunit rRNA grew from a small stem loop in the common core into a large rRNA domain in metazoans. Each accretion step adds to the previous rRNA core but leaves the core unaltered. Common Ancestors are indicated. Pairs of structures are superimposed to illustrate the differences and to demonstrate how new rRNA accretes with preservation of the ancestral core rRNA. Each structure is experimentally determined by X-ray diffraction or Cryo-EM. *Source:* Image from Petrov et al. 2014. Reprinted with permission from PNAS.

relationship to the environment and other organisms within it. In addition, the growth of metabolic databases and metabolic pathway prediction based on organismal gene complements permits the prediction of metabolic pathways in modern organisms. This same approach could be applied to LUCA gene complements, which should constrain possible biological environment(s) for life at the root of the evolutionary tree.

1. Which gene families had evolved by the time of the root of the evolutionary tree? In what order did these earliest functions emerge?

2. Which metabolic networks existed at the root of the evolutionary tree, and can we use that information to constrain the surrounding chemical environment?

3. What was the nature of cellular membranes at the root of the Tree of Life?

4. Was DNA the genetic material of LUCA, or could it have been RNA or some other genetic polymer?

5. When was the timing of LUCA with respect to the geologic and geochemical record?

IV. Dynamics of the Subsequent Evolution of Life

The biological innovations that have shaped the history and breadth of life on Earth have been mediated by changes in their physical and biological environments. Thus, a simple way to organize the drivers of evolutionary dynamics is in terms of intrinsic and extrinsic factors. Intrinsic factors involve the origin and consequences of evolved traits, from the appearance of fundamental traits like complex cells to the development of clade-specific traits such as limbs or flowers. Extrinsic factors are the environmental factors that drive evolutionary innovation. They may operate on time scales ranging from abrupt events, such as asteroid impacts and major volcanic eruptions, to longer-term shifts, such as changes in seawater chemistry. Understanding these factors and their interactions will enable us to better use Earth systems to estimate probabilities and evaluate biosignatures of complex life on other planets, and to predict where on other planets life is likely to be most abundant and diverse.

Intrinsic Factors

Evolutionary lineages appear to differ in their ability to generate evolutionary novelties, but the differences are poorly understood. Intrinsic factors such as the configuration of developmental pathways or background levels of metabolic activity may be involved, but these are open questions. Further, the origin and success of evolutionary innovations might primarily represent necessary biological responses to the local environment. Alternatively, they could mainly represent chance events frozen into the biosphere by history and unusual events. The investigation of habitability and extrapolation from Earth life to life elsewhere should explore the relationship between necessary and chance events in the history of life. Analyses of the evolutionary and environmental context in which microbial and metazoan/metaphyte innovations arise (including such “late” innovations as flight, limbs, flowers, and metazoan photo- and chemosymbioses) can contribute to a predictive theory of evolutionary novelty that extends beyond contingency to large-scale generalization.

As examples, we focus here on three innovations of particular interest to astrobiology. The first is the evolution of complex biological systems from simple ones, a process that includes genealogical, functional, and morphological aspects. Events that represent increasing complexity include the origins of chemotrophy and autotrophy, metabolisms active in chemical cycles (such as the nitrogen cycle), intracellular structure, regulation of internal conditions, and multicellularity. The second innovation is the acquisition of energy by living systems. Like the first innovation, this affects geologic and atmospheric chemistry, the incorporation of energy as biological information, and the diversity of life. The third innovation, phototrophy, stands out for its contribution to the global energy budget and atmospheric composition of Earth.

Intrinsic Factor: The Evolution of Complexity

Some evolutionary innovations represent increases in complexity, although complexity trends are not universal across lineages or through time. Certain increases in complexity are the raw material for generating new levels of organization that represent major evolutionary transitions, such as from prokaryotes to eukaryotes. Moreover, certain classes of innovation seem to characterize certain time intervals; for example, during the Cambrian explosion of multicellular life. Some of these pulses of innovation also appear to be related to environmental change. Evolutionary rates might be linked to complexity, but this effect may be more evident in comparing single cells to multicellular organisms than in analyses within single groups, such as mammals or echinoderms.

Intrinsic Factor: Energy Acquisition in Living Systems

The conversion of environmental energy to biological maintenance and work is central to our understanding of life on Earth and our expectations for life elsewhere. Phototrophs convert sunlight into biologically useful energy in the form of chemical gradients and reduced molecules (notably adenosine triphosphate [ATP] and nicotinamide adenine dinucleotide [NADH]). This process is complex, suggesting that simpler forms of energy acquisition developed first. Chemotrophy involves the generation of biologically useful energy from local chemicals rather than light. Chemoautotrophs take energy from inorganic molecules, while chemoheterotrophs take energy from organic molecules, often the byproducts of other organisms. Mechanisms for energy acquisition have a profound impact on chemical cycles on Earth. They inform our understanding of the boundary between living systems and their environments as well as our expectations for geologic processes on inhabited worlds.

Intrinsic Factor: The Origin and Early Evolution of Phototrophy

Life on present-day Earth is largely dependent on the products of oxygenic photosynthesis. A major question, therefore, is how did photosynthesis originate and evolve? The geologic record of sulfur isotopes, red beds, and detrital uraninites and pyrites are consistent with the presence of oxygenic photosynthesis since at least 2.4 billion years ago (Ga). The geologic record of carbon isotopes in sedimentary carbonates and organics displays a relative difference in $\delta^{13}C$ of ~20–30% from the present-day to ~3.5 Ga. This is consistent with some form of carbon fixation, including photosynthesis or chemoautotrophy. Possible microfossils with cyanobacteria-like morphologies and stromatolites of probable biogenic origin are present at 3.5 Ga, and may offer additional indirect evidence for the presence of photosynthesis. The meta-sedimentary rocks of Akilia, which are older than 3.85 Ga, contain apatite with graphitic inclusions with $\delta^{13}C$ values consistent with some form of carbon fixation. The entire record of life on early Earth appears to be a record of carbon fixation, and quite possibly photosynthesis specifically.

Extrinsic Factors

The diversity of life on Earth at any point in time is a function of environmental gradients (temperature, moisture, redox potential, light spectra and intensity, nutrients, etc.) and how those gradients have developed through time. Plate tectonic processes control the distribution of land masses and topography through time, which in turn has significant influence on sea-level and climate. On shorter timescales, planetary climate also responds dramatically to astronomical forcing and perturbation to the ocean-atmosphere system. These relatively continuous processes are critical to understanding the evolution of complex life, but must be viewed in concert with short term, global scale perturbations of the planet such as bolide impacts, massive volcanic eruptions, or geochemical cycle changes that have generated mass extinctions. Despite several decades of intensive, multidisciplinary study of mass extinctions, a full understanding of the causes and consequences of these events remains elusive. Because similar events also may occur on other planets, we seek a general understanding of how organisms, species, and ecosystems respond to perturbations, including the rate and mode of recovery from mass extinctions. This understanding must encompass the components of biodiversity beyond numbers of taxa, including ecological, functional, and morphologic disparity, among others. Understanding how the various processes on Earth, including biological interactions, regulate the many components of biodiversity is essential for identifying the principles involved in the generation and maintenance of the diversity of complex life on other planetary bodies.

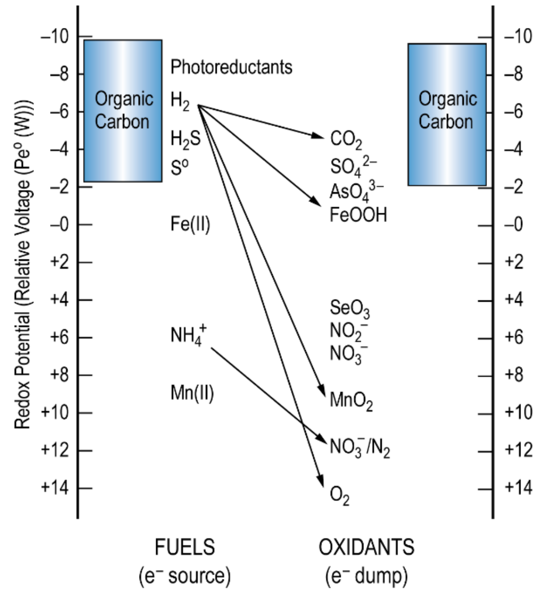

FIGURE 3-6. Redox potentials and life. Energy produced by reactions between a reductant and an oxidant can be used for growth or reproduction. *Source:* Image from Mix, L.J. et al. 2006.

Composite Events: Intrinsic plus Extrinsic Factors

Many evolutionary events reflect both intrinsic and extrinsic factors. The Cambrian explosion of animal life, as currently understood, is a good example. The explosion drew on intrinsic evolutionary innovations in the developmental regulation of organismic anatomy, yielding the relatively sudden appearance or elaboration of the major metazoan body plans, and was evidently promoted (directly or indirectly) by increasing oceanic/atmospheric oxygen. The evolutionary interplay and feedbacks between organisms and their environment is typified by multiple independent origins of mineralized skeletons, presumably in response to ecological pressures such as predation and competition, which further affected global carbon, phosphorous, and other nutrient budgets. As another example, complex organisms modify their environment in ways that affect the evolution of their own and other species. Although many such changes are ephemeral, other changes are sufficiently persistent in time or space to influence evolutionary trajectories of the modifying species or other taxa. These modifications, often produced by complex communities of intimately interacting organisms, can affect both the physical and chemical environments, e.g., formation of reefs, which allow colonization by organisms that prefer this substrate. Such ecosystem engineering can be an important driver of evolution, and is also likely to occur during the evolution of life beyond Earth.

Key Research Questions about the Dynamics of the Subsequent Evolution of Life

Intrinsic Factors: Complexity

1. What are the different modes of complexity, and how can they be quantified?
2. Why do complexity trends appear in some lineages and not others?
3. Why do certain classes of innovation characterize certain time intervals?
4. What are the pressures and mechanisms for the increase in complexity?
5. What might drive a lineage to reduce complexity once achieved?
6. What can account for variations in the rate of evolution at different levels of complexity?
7. Are more complex organisms more prone to extinction than simpler ones?
8. Do mechanisms of evolution change at greater levels of complex organization?

Intrinsic Factors: Energy Acquisition

1. Can we propose minimal energy requirements for life, both in terms of availability and efficiency?
2. How are trophic pathways related to other metabolic processes historically, energetically, and organizationally?
3. What trophic mechanisms were present in the last common ancestor?
4. What is the role of trophism and other metabolic processes in starting and maintaining chemical cycles on Earth?
5. Can we discern isotopic signatures of early chemotrophic processes?
6. What energy sources are available in Earth environments, and what environments were available for early life?
7. What potential electron sources and sinks exist that are not utilized by known metabolisms?

8. What electron sources and sinks are available in non-Earth environments? How does their abundance inform our expectations for the existence, diversity, and range of life in those environments?

9. How will biosignatures vary as a function of the metabolisms of the organisms that produce them?

Intrinsic Factors: Phototrophy

1. How soon after the origin of life did phototrophy arise?

2. How does phototrophy impact the way life interacts with the surrounding geochemistry, and to what extent does this relationship provide biosignatures?

3. What did the earliest forms of phototrophy look like?

4. What photoreactive chemicals were available in the environment of early life?

5. Was phototrophy adapted from simpler forms of light-driven energy transduction, UV protection mechanisms, trophic mechanisms, or some other process?

6. When did organisms evolve oxygenic photosynthesis, what were its evolutionary precursors, and how is this innovation related to the general oxidation of the Earth's crust and atmosphere?

7. How much biologically useful energy is produced by bacteriorhodopsin and other photoreactive biochemistries? Is this enough to sustain an organism?

8. Are there undiscovered types of phototrophy present on Earth today?

9. What types of light can be biologically useful and how does the range of phototrophy constrain our concept of habitable planets?

10. How will the biosignatures of pigments differ for different atmospheric compositions and parent stellar type?

Extrinsic Factors

1. What are the planetary controls resulting in taxonomic, ecological, metabolic, functional, and morphological biodiversity?

2. Are there general principles underlying mass extinctions and recoveries?

3. How does the rate or spatial scale of a perturbation determine its evolutionary consequences?

4. How can we predict the consequences of a perturbation, depending on whether it occurs in different planetary states (e.g., greenhouse vs. glaciated worlds)?

5. How does the construction and modification by organisms of complex environments affect the evolution of complex life?

V. Common Attributes of Living Systems on Earth

Identifying the major drivers of planetary-scale patterns and trends in biodiversity, with the goal of differentiating between those mechanisms likely to be present wherever complex life exists and those specific to the evolution of life on Earth, will contribute to our understanding. To that end, particular attention must be paid to the environmental context and the tempo, mode, and direction of that evolution.

Shared attributes of living systems on Earth may reflect constraints of physical or chemical law, features that are historically contingent but shared due to common descent, or results of convergence from ancestral states that were more or less divergent. Some inherent confounds exist between features reflecting absolute constraint and others reflecting universal common ancestry, as commonality alone is not sufficient to distinguish the two as causes. In addition to the problem of confounded chance and necessity, further distinctions may exist between attributes that would be necessary under general conditions, and others that may be strongly determined and yet sensitive to fine details of environmental conditions. Features shared only within clades are more readily interpreted as having a common ancestry rather than strict constraint, while convergences are more readily interpreted as reflections of shared conditions of life.

Examples of universal or near-universal features include the genetic code, chirality, sugar metabolism, and the lipid bilayer structure of cell membranes. As examples of commonality within single evolutionary branches, vascular plants have inherited photosynthetic mechanisms, vertebrates have inherited calcium phosphate skeletons, and mammals have inherited digits from ancestral forms near the inception of those lineages. A recent study has suggested that the direction of the proton gradient across cellular membranes might be the result of the life originating at alkaline hydrothermal vents.

Shared traits due to convergence result when taxa independently arrive at similar solutions to similar problems. These solutions are the outcomes of repeated experiments conducted in very different environmental contexts and by forms of life that are phenotypically very distinct. The generality of a solution might be estimated from the number of times a similar adaptation arose in strongly disparate lineages; the more readily acquired it is by evolutionarily divergent lineages, the more likely it is to appear on another planet in response to a similar problem. For example, highly integrated multicellularity arose independently in animals, land plants, two groups of algae, and two groups of fungi, and colonization arose independently in taxa as varied as marine invertebrates, freshwater algae, and social insects.

TABLE 3-1. Extremophile and tolerance tables.

The Limits of Known Life on Earth*			
Factor		**Environment/Source**	**Limits**
High Temperature		Submarine Hydrothermal Vents	110 to 121°C
Low Temperature		Ice	-17 to -20°C
Alkaline Systems		Soda Lakes	pH > 11
Acidic Systems		Volcanic Springs, Acid Mine Drainage	pH -0.06 to 1.0
Ionizing Radiation		Cosmic Rays, X-rays, Radioactive Decay	1,500 to 6,000 Gy
UV Radiation		Sunlight	5,000 J/m^2
High Pressure		Mariana Trench	1,100 bars
Salinity		Low Temperature Systems	αH_20 ~ 0.6
Desiccation		Atacama Desert (Chile), McMurdo Dry Valleys (Antarctica)	~60% relative humidity
Extremophiles**			
Factor	**Class**	**Defining Growth Condition**	**Example Organisms**
High Temperature	Hyperthermophile Thermophile	> 80°C 60 to 80°C	*Pyrolobus fumarii*
Low Temperature	Psychrophile	< 15°C	*Synechococcus lividis*
High pH	Alkaliphile	pH > 9	*Psychrobacter, Vibrio, Anthrobacter*
Low pH	Acidophile	pH < 5 (typically much less)	*Natronobacterium, Bacillus, Clostridium paradoxum*
Radiation	–	High ionizing and UV radiation	*Deinococcus radiodurans, Rubrobacter, Pyrococcus furiosus*
High Pressure	Barophile Piezophile	High weight High pressure	Unknown *Pyrococcus* sp.
Salinity	Halophile	2 to 5 M NaC1	*Halobacteriaceae, Dunaliella salina*
Low Nutrients	Oligotroph	e.g., <1 mg L^{-1} dissolved organic carbon	*Sphingomonas alaskensis, Caulobacter* spp.
Oxygen Tension	Anaerobe Microaerophile	Cannot tolerate O_2 Tolerates some O_2	*Methanococcus jannaschii* *Clostridium*
Chemical Extremes	–	Tolerates high concentrations of metal (e.g., Cu, As, Cd, Zn)	*Ferroplasma acidarmanus* *Ralstonia* sp. CH34

* Table adapted from Marion et al. 2003. Reprinted with permission from Elsevier.

** Table adapted from Mancinelli and Rothschild 2001. Reprinted with permission from Macmillan Publishers Ltd.

It is important to understand how, within the last half-century, our expanded understanding of terrestrial environments that harbor life has changed our understanding of the limits within which life is not only definable, but still is capable of sharing many features. The discovery of life outside Earth could further change the ways we understand what is necessary and what is contingent upon environment.

Key Research Questions about the Common Attributes of Living Systems

Are common attributes of life on Earth due to common ancestry (homology) or limited solutions to common problems (convergence)?

1. Which common attributes - molecular, organismal, and ecological - are shared by distantly related organisms?

2. What attributes of organisms, species, ecosystems, etc., have repeatedly originated in distantly related organisms?

3. Under what evolutionary and environmental context(s) did analogous traits appear?

4. What role did chance and necessity play in the origin of analogous traits (i.e., which were deterministic, and which were contingent)?

5. To what extent does convergence depend on the initial conditions or starting point of the evolutionary lineages involved?

Which common attributes of life on Earth are likely to arise?

1. On another planet, how likely are events which precipitate the appearance of a common solution?

2. How likely is it that a given biosignature will be produced by extraterrestrial life in similar environments?

3. From common features related to Earth's chemical composition and geo-energetics, how do we extrapolate our understanding of these commonalities to other locations of astrobiological interest that have different chemical compositions and energetics?

4. To what extent is the diversity of environments on Earth representative of the diversity that can be expected elsewhere?

5. When does the diversity of terrestrial environments afford experimentally accessible analogues to smaller astronomical bodies?

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4 Co-Evolution of Life and the Physical Environment

Introduction

Life affects its environment; at the same time, the environment affects life. This give-and-take is often expressed in feedback loops within planetary systems—that is, responses to change that either resist or enhance the perturbation and tend to stabilize an environment at a particular state, transition it to a different stable state, or send it into a runaway state.

Life forms complex relationships with its environment on all spatial scales. Ultimately, we wish to understand these relationships well enough for them to be useful in looking at other planets and environments. The overarching theme, then, is how does life modify its environment while environmental change is mediating the distribution of life over a range of scales in time and space? We break up this question based on various spatial or temporal divisions: past/future life, subsurface/atmospheric processes, microbial/planetary scales, and chemical/physical environmental parameters.

One approach to studying these feedbacks is through analysis of Earth's past and present, which informs our predictions about Earth's future. This combined perspective gives us many examples and possible scenarios that lead to testable hypotheses. Examples of past scenarios include how major transitions in biological evolution, such as the origins of photosynthesis, multicellularity, and intelligent life, affected the planet. Major changes to the physical state of a planet that have influenced biology include the emergence of plate tectonics and continents, as well as climatic transitions and extremes such as the global-scale glaciations known as "Snowball Earth" episodes. Mass extinctions have been triggered by both planetary processes and feedbacks initiated by biological processes.

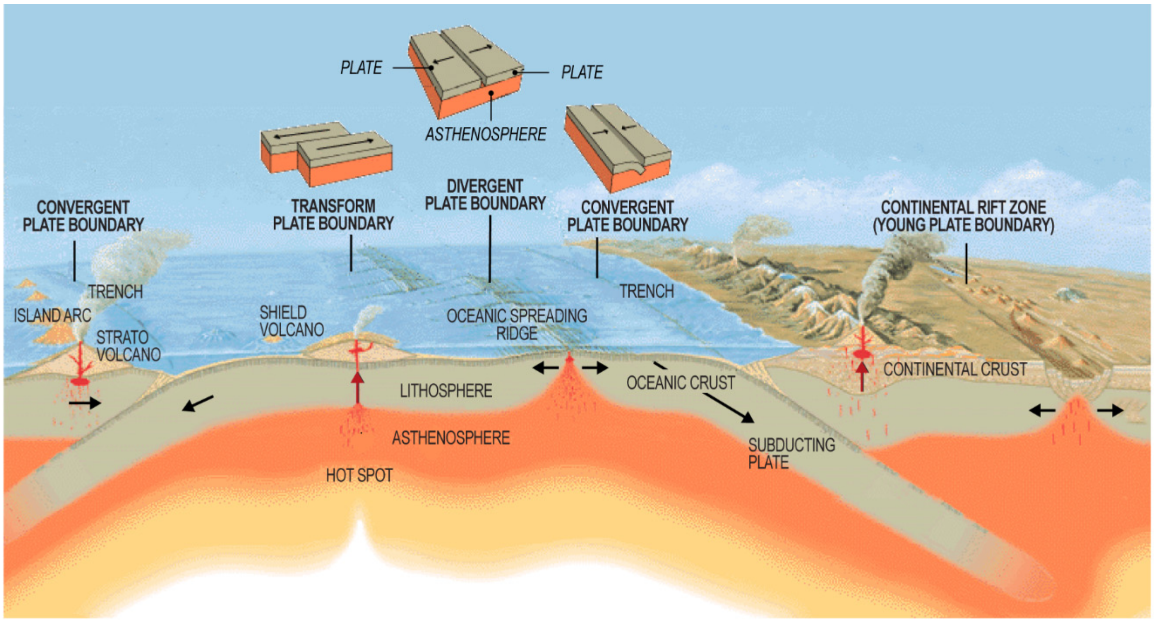

FIGURE 4-1. Major geological processes that have shaped and altered the mineralogical and physical landscapes of Earth. Dynamic processes, such as weathering, erosion and plate tectonics, have helped insure the habitability of Earth for billions of years. *Source:* Modified from images from Submarine Ring of Fire 2002 (NOAA/OER) and José F. Vigil and Robert I. Tilling (U.S. Geological Survey).

4.1 WHY IS THIS TOPIC IMPORTANT?

> Environmental change has accompanied every major event in the history of life—as either a cause or an effect. This relationship is the most compelling argument for co-evolution of life and the physical environment. It follows that the collective mechanisms, feedbacks, tipping points, contingencies, and intrinsic and extrinsic drivers that define this co-evolution must be understood to explain billions of years of sustained habitability on Earth—and likely elsewhere. It is our good fortune that this relationship manifests in diagnostic fingerprints, including diverse geochemical markers, which can be read in the geologic record as evidence of the combined factors that sustain habitable worlds under dynamic conditions and can be detected as such, even on extraterrestrial hosts.

Co-evolution of life and the environment ties into and informs other themes in this document in three major ways. First, the processes that led to life on Earth are inherently environmental phenomena. Abiotic delivery of organic compounds and prebiotic chemistry can be regarded as the first environmental influences on life. Second, as early life evolved increasing complexity, its interactions with the planet increased in diversity, eventually developing into complex feedbacks. By studying this co-evolutionary past, we deepen our understanding of habitability and learn about significant branch points in the history of the habitability of Earth-like planets. Finally, studies of other planets—both real and hypothetical—inform and benefit from work on the intimate interactions between life and its physical environment. Observations of specific habitable environments in planets and moons in our Solar System can illuminate the properties of Earth that permitted life to flourish here, suggest the potential for life on other bodies in our Solar System, and provide a foundation to model rocky planets in other planetary systems. Furthermore, as we explore planets in and beyond our Solar System, we must develop the capacity to assess the habitability of these environments and to recognize and characterize signatures of life—from the microscopic to the planetary scale. These efforts to identify and characterize biosignatures are necessarily informed by close examination of Earth's past, present, and future.

4.2 WHAT DOES THIS RESEARCH ENTAIL?

We wish to understand how life and biological communities respond to changes in their environment, and in turn alter the environment. This effort requires a fundamental understanding of the diversity of life on Earth today—genomic, physiological, and metabolic—along with an understanding of how life diversifies to occupy its multitude of ecological niches. The resulting models would not only predict the most likely early life-sustaining metabolic strategies, but also their distribution along various dimensions of geochemical variation. This framework could then guide strategies to detect life as well as inform our understanding of Earth's past.

Within the general theme of biological-environmental interactions, many of the divisions we have drawn are artificial and were made to serve the organization of this document. In reality, the interactions on different temporal scales can inform each other—studying processes on one scale can provide insight into processes on a different scale.

One such approach to studying the mechanisms by which living systems interact with the environment is at the microbial scale. Life on other worlds is most likely to include microbes, and any complex living system elsewhere is likely to have arisen from and be founded upon microbial life. Important insights on the limits of microbial life can be gleaned from studies of microbes on modern Earth, as well as their ubiquity and ancestral characteristics.

On a planet-wide scale, each of the different habitable states evidenced in Earth's history represents a potential test case for life on other planetary bodies. Exoplanet discovery and observation is proceeding rapidly, with thousands of worlds discovered in the last few years alone. The difficulty of characterizing the diversity of these worlds can be alleviated by a better understanding of the range of habitable states over Earth's history. There is a need to use properties measured for an exoplanet (such as atmospheric composition or surface temperature) to infer habitability. The early Earth provides a way of calibrating this approach, whereby we can infer or model a given composition for the ancient atmosphere as the sum total of specific physical and biological processes on and within Earth, and how and why those interacted and co-evolved over time.

Further, a major aspect of studying the co-evolution of life and Earth is to utilize our understanding of modern Earth, as a potential analog, to inform our understanding of Earth's past. Linking the modern to the past, however, is limited by inherent biases and gaps in the Tree of Life, therefore requiring a robust and intricate understanding of the feedbacks between modern life and their environments.

By reconstructing the Earth system at different stages of its evolution, we can build a catalog of properties and biosignatures on Earth, had it been viewed remotely at different stages of its ~4.5-billion-year existence. Thus, efforts to understand our own origin, evolution, and future also provide critical and complementary data to exoplanet research, including distinct glimpses of habitable worlds that all offer opportunities to understand how we would recognize and characterize a habitable planet.

Over the past ten years, we have made major strides in our understanding with the advent of genomics, proteomics, metallomics, etc. These advances have dramatically expanded our ability to study the diversity of life on present-day Earth, to elucidate the history of diversity through time, and to propose linkages between biological diversity and environmental parameters. Meanwhile, the use of new geochemical tools has uncovered or clarified pages in the history of Earth and highlighted times when the planet underwent transitions between different states—such as from an oxygen-poor to oxygen-rich ocean/atmosphere system. Many of these transitions have been driven by biological activity, presenting us with new examples of the intricate and complex relationships between life and the planet it inhabits.

4.3 PROGRESS IN THE LAST TEN YEARS

The following are a few examples of research in the past ten years that have advanced our understanding about the co-evolution of life and the environment.

1. Mineralogy, one the oldest subfields of Earth sciences, has long relied on categorization without the context of planetary evolution. Recent work on analyzing mineral evolution in the framework of planetary processes, including the evolution of life, has opened up a new way of studying planetary systems. This reframing of mineralogy in the context of "deep time" has been characterized by *Science* magazine as "the first paradigm shift in mineralogy in 200 years."

2. Significant progress has been made in our understanding of the interplay between surface life and the evolution of Earth's interior, showing that, through the subduction of deep-sea sediments, biological processes strongly influence mantle concentrations of nitrogen, carbon, and even uranium.

3. Understanding the history of Earth's biosphere involves understanding physical conditions on the early Earth, when the Sun was up to 30 percent dimmer than it is today. With that much less energy delivered to it, early Earth theoretically should have been encased in ice. However, new research has found that an abundance of greenhouse gases most likely kept Earth warm during the geologic eon preceding the proliferation of complex life. Understanding the changing composition of those atmospheric gases and their relationships with the ocean, solid Earth, and life is a critical area of inquiry related to sustained and dynamic habitability on and beyond Earth.

4. Biofilms are microbial communities linked together by sticky extracellular materials produced by the microbes. Astrobiologists have shown for the first time that biofilms may have a number of evolutionary advantages including protection from harmful radiation in the absence of an ozone shield and against toxicity of specific minerals in the environment.

5. Astrobiologists have identified a method of tracing the history of large impacts with the early Earth by studying impact-shocked zircons. Furthermore, analysis of 2.5-billion to 4.4-billion-year-old zircons indicates that weathering was intense on the early Earth and strengthens the hypothesis that a differentiated crust formed on Earth as early as 4.4 billion years ago, that liquid water oceans formed before 4.3 billion years, and that Earth became habitable as much as 800 million years before the oldest known microfossils.

6. Banded iron formations appear to reflect a time in Earth's past when iron was cycled quite differently than it is today. Recent research shows that these ancient iron-rich rocks were formed by microbial processes and also that the inventory of these rocks may be much larger than previously thought. These findings indicate that virtually all of the iron in use today was processed by microbes billions of years ago.

FIGURE 4-2. Banded iron formation (BIF) from Australia. *Source:* Image from Zamora 2015.

7. In recent years, astrobiologists have been deepening their understanding of a period in early Earth's history long known for oceans rich in dissolved iron. Studies suggest

that Earth's oceans were nearly or completely devoid of oxygen and rich in hydrothermally derived dissolved iron for at least the first 1 billion to 2 billion years (and potentially the first 4 billion years) of the planet's history. Recent analyses point to a new understanding of how life evolved to incorporate iron into the intracellular metabolic processes known in all modern day life forms. Recent research is also leading to an emerging understanding of the potential antiquity of the utilization of iron as a source of extracellular chemical energy (that is, food), as well as for intracellular metabolism, in microbial life.

8. Studies of some of the oldest sedimentary rocks in the world—the 3.5-billion-year-old Strelley Pool Formation in Western Australia—provide the best evidence to date for the earliest life on Earth. This formation contains a reef-like assembly of laminated sedimentary carbonate accretion structures known as stromatolites. Given the evidence for photosynthetic life provided by ancient stromatolites (fossil microbial communities), recent work suggests that an important photosynthetic pathway in the ancient oceans may have been anoxygenic photosynthetic iron oxidation. Also, while it is generally assumed that life on Earth around 3 billion years ago consisted of simple single-celled archaea and bacteria, astrobiologists have recently found evidence of 3-billion-year-old microfossils of plankton that inhabited the early oceans, suggesting that life diversified very quickly.

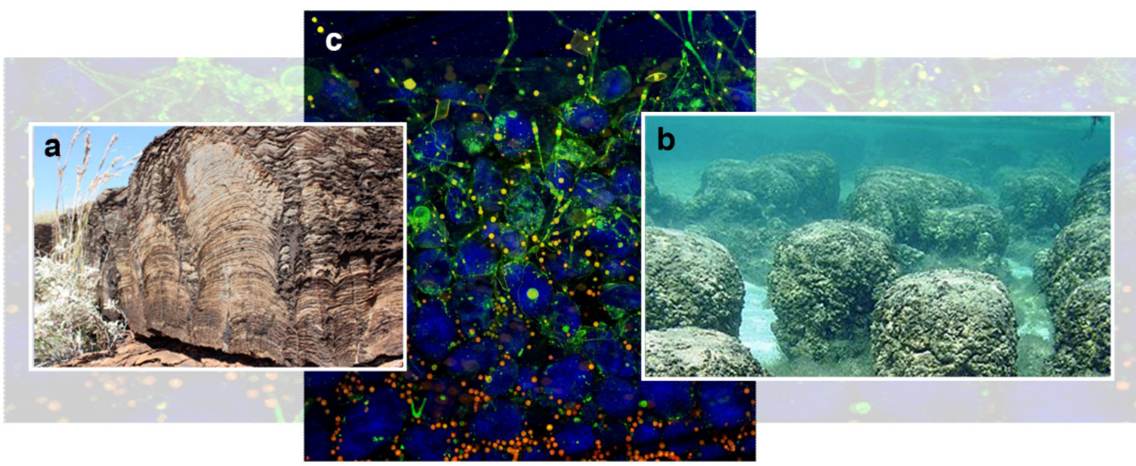

FIGURE 4-3. Representative images of stromatolites, the oldest known ecosystem on Earth. (a) Ancient stromatolites from the 2.72 Ga Meentheena Member, Tumbiana Formation, Fortescue Group, Western Australia. Photo by David Flannery. (b) Living stromatolites from Carbla, Hamelin Pool, Western Australia. Photo Credit Jamie Foster and Pam Reid. (c) Confocal micrograph of living stromatolite community from Highborne Cay, The Bahamas. Photo credit Jonathan Franks and John Stolz.

9. Recent research aimed at unraveling the details of the so-called "Great Oxidation Event" (GOE) on the early Earth, around 2.4 billion years ago, provides evidence for local, shallow oxygen oases before the atmosphere became "oxic". New work also

indicates that this “event” was not a simple process or a single dramatic rise. Studies have elucidated the biological impact of this event, examining the evolutionary history and the metabolic and biosynthetic pathways of extant microorganisms and exploring the fossil record of the evolution of cyanobacteria and the first appearance of microbes that utilize aerobic metabolisms. Progress has been made in understanding the controls and delays behind the timing of oxygen accumulation in the atmosphere and oceans and their associations with the evolution of life. In addition, much attention has turned to the interval between the GOE and the much later rise of animals and other diverse complex life. This period is marked by the development of eukaryotic organisms, but at generally low abundances and diversity relative to the major events that followed just before, during, and after the Snowball Earth glaciations. New models are emerging for the throttles and tipping points in biotic and environmental co-evolution, including extreme climatic and atmospheric change.

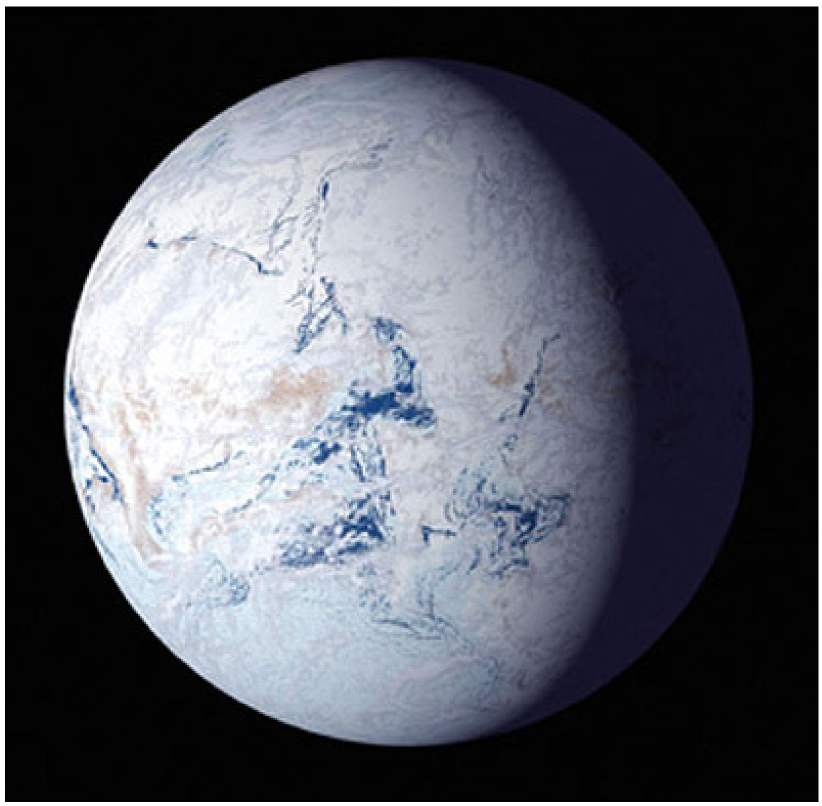

FIGURE 4-4. An artist’s rendering of Snowball Earth, which are theorized periods of Earth’s past where Earth’s surface was mostly, or entirely, frozen. These proposed global ice ages represent one of the most extreme climactic changes in Earth’s history. *Source:* Image from Hadhazy 2015, NSF.

10. Astrobiology research has continued to expand the limits of life. Recent discoveries of microbial life existing, and potentially even thriving, in rarified atmospheres under intense radiation, turbulent flow, dry freezing cold, and ultra-low pressure extend the

boundaries of where to look for evidence of life (existing or extinct) beyond Earth, and also point to the possibility of a wider variety of mechanisms for the distribution of life in the Universe.

4.4 AREAS OF RESEARCH WITHIN CO-EVOLUTION OF LIFE AND THE PHYSICAL ENVIRONMENT

> **I. How Does the Story of Earth—Its Past, Present, and Future—Inform Us about How the Climates, Atmospheric Compositions, Interiors, and Biospheres of Planets Can Co-Evolve?**
>
> **II. How Do the Interactions between Life and Its Local Environment Inform our Understanding of Biological and Geochemical Co-Evolutionary Dynamics?**
>
> **III. How Does Our Ignorance about Microbial Life on Earth Hinder Our Understanding of the Limits of Life?**

I. How Does the Story of Earth—Its Past, Present, and Future—Inform Us about How the Climates, Atmospheric Compositions, Interiors, and Biospheres of Planets Can Co-Evolve?

Earth's history comprises a series of discrete states of habitability. Viewed along the axis of time, the Earth has effectively been many habitable planets, each characterized by different internal feedbacks and external forcings. Understanding how each of these states was initiated and maintained, as well as the processes that governed the transitions into succeeding states, will form an important constraint on understanding habitable states on other planets.

Key Research Questions

How do interactions between life and its environment affect Earth's ability to retain habitability?

Earth has remained a continuously-inhabited planet despite extreme and sometimes rapid changes to Earth's surface chemistry and physical processes, as well as singular events such as large impacts, changing solar luminosity, a fundamental shift from a reducing to an oxidizing world, changing plate tectonics and continental expressions, and the progressive emergence of biological innovation. However, this continuity belies a long evolution through a series of discrete states of habitability across wide-ranging redox and climatic conditions, nutrient cycling, etc. Each state, although an independent window of persistent habitability, is a legacy of previous conditions and precursor of those to follow, and much of the story lies with the tectonic, climatic, and evolutionary drivers that tip Earth from one stable state to the next.

Systems evolve from state to state under the influence of internal feedbacks and external forcings. This evolution is tracked by measuring state variables (e.g., atmospheric composition, the compositions of sediments and sedimentary rocks, the presence or absence of key metabolic processes, etc.). States that persist over time may be inherently stable or may simply represent long-term transitions between stable states. Understanding the processes that move complex systems between states is important for developing and testing hypotheses about complex cause-and-effect relationships (e.g., the timing of the oxygenation of the atmosphere and the evolution of oxygen production). Characterizing and quantifying the diverse states that the atmosphere/biosphere/solid Earth system has occupied, and determining the critical processes that governed its evolution will need to be coupled with mechanistic modeling to better understand how state variables measured on other planets may reflect their evolution and habitability.

How have processes in Earth's interior and their surface manifestations shaped habitability, and how does life affect these physical processes?

The trajectory of Earth as a habitable—and inhabited—world is strongly shaped by the evolution of its interior, and the same will be true of all rocky planets. Heat dissipating from Earth's interior drove the prebiotic chemistry that may have set the stage for life's beginnings in deep sea hydrothermal systems and enables its persistence in the deep sea and deep crust. Once established, the co-evolution of Earth and life was fundamentally shaped by plate tectonics—a manifestation of the cooling and chemical differentiation of the planet—which regulates the larger-scale recycling of the bio-essential elements (e.g., C, S, O, N, P, and Fe), the nature and formation of the crust, and the exchange of volatiles between Earth's interior and surface. Conditions at the surface are also modified by Earth's magnetic field—driven by the dynamics in the core—which shields the atmosphere from charged particles. The emergence and expansion of an extensive biosphere is therefore intimately linked to the physics and chemistry of Earth's accretion and differentiation; to the physicochemical dynamics of the core, mantle, and crust; and to the evolving internal inventory of radiogenic and volatile elements.

Despite the centrality of plate tectonics, there is much debate about when it began and how its initiation was affected by the conditions set during accretion, great uncertainty about its drivers, and more questions than answers about its relationship to major changes in the biosphere. Provocative new theories even postulate that plate tectonic processes do not simply place boundary conditions on surface habitability, but are themselves affected by life-driven processes such as Earth's surface oxygenation, which modifies the composition of materials that subduct back to the interior. As we deepen our understanding of these issues on Earth, we will derive general principles that can be extrapolated to understand the prospects for life on rocky worlds that differ from Earth in mass, elemental composition, and volatile inventories.

Full exploration of these topics requires integration across a range of disciplines and techniques, including perspectives and approaches from planetary science, deep Earth geophysics, and biogeochemistry, combined with better empirical constraints on heat flow evolution, properties of mantle materials, tectonic dynamics, more advanced quantitative models of early planet evolution, and explicit linking between evolutionary models of geodynamics, tectonics, atmospheric chemistry, and biological evolution through time.

How have climate and atmospheric processes shaped habitability, and how does life affect these physical relationships?

The oldest signs of animal life appear in the geologic record between about 600 and 700 million years ago. For the four billion years prior to this milestone, our planet experienced dramatic change that paved the way for the early animals—and our own existence.

One such transformation was the first significant increase in atmospheric oxygen roughly two-and-a-half billion years ago, perhaps the single most important environmental change in Earth's history. This oxygenation, triggered by the advent of oxygenic photosynthesis by cyanobacteria, and balanced with reduced gas fluxes from Earth's interior, may have spawned global glaciation through destabilization of a greenhouse climate linked to methane and other reduced compounds. This climatic extreme, along with intense oxidative weathering of the continents, likely spurred enhanced nutrient delivery to the ocean that furthered the process of oxygenation and the eventual appearance and diversification of eukaryotic organisms. Almost two billion years later, oxygen rose again coincident with the formation and break-up of a supercontinent, another episode of global Snowball Earth glaciation, dramatic diversification among eukaryotic organisms, and the emergence and diversification of animals.

The cause-and-effect relationships among these first-order tectonic, climatic, and evolutionary controls, including dramatic shifts in the way carbon is cycled at Earth's surface, are at the heart of our understanding of the nature and persistence of habitability of Earth and the value of Earth's history in providing analogs for life elsewhere. Important research opportunities lie with our need to unravel these coupled relationships, and specifically their timings. Basic questions such as the detailed relationships between animal life and the rise of oxygen and specific triggers of global climatic events remain unresolved. What is known, however, is that biology is essential in both the stabilizing feedbacks that have dominated over the long-term, and in runaway feedbacks that have caused rapid, short-term changes.

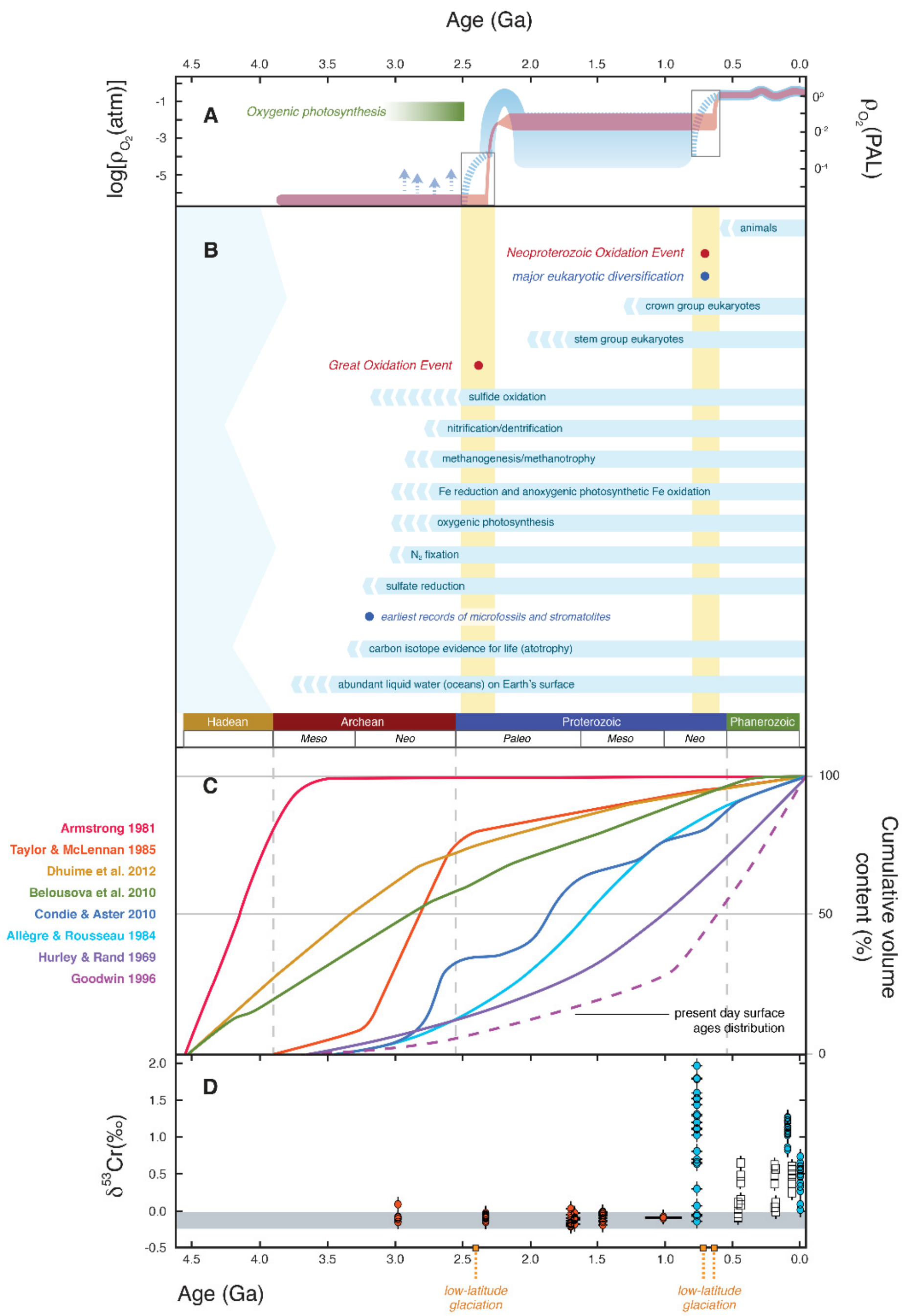

FIGURE 4-5. Summary of trends and milestones in the biotic and abiotic evolution of the Earth surface system: a) Earth's atmospheric oxygen content through time [from Lyons et al, 2014; faded red curve shows classic 'two-step' model; blue curve depicts emerging model with a more dynamic pattern of rising and falling oxygen levels; PAL = Present Atmospheric Level]; b) historical record of microbial metabolisms and key environmental events captured in paleontological, isotopic, elemental, and organic geochemical data [after Lyons et al., 2015]; c) diverse models for crustal growth compared to age distribution of crust preserved today [after Cawood et al., 2013]; d) summary of chromium isotope data as a proxy for evolving atmospheric oxygen content—largely unfractionated early values relative to high-temperature Cr sources [gray bar] suggest a predominance of low atmospheric oxygen levels prior to ~0.8 to 0.75 billion years ago, a milestone marked also by dramatic diversification among complex life. *Source:* Image modified from Planavsky et al. 2014. Reprinted with permission from AAAS.

Recent analytical developments, novel geochemical tracers, sophisticated numerical approaches, and greatly improved age control are allowing us to explore the dynamic compositions of the early atmosphere and oceans and their cause-and-effect relationships with climate and life in unprecedented ways. Recent work shows, for example, that the initial rise of oxygen may have occurred in fits and starts rather than in a single step—and that once it was permanently present in the atmosphere, oxygen likely rose to high levels and then plummeted. One-and-a-half billion years of oxygen-free conditions in the deep ocean followed and set a challenging course for the simple microscopic inhabitants. This is a story of first-order (large-scale, long-term, easily sensed) transitions in climate and atmospheric composition reflecting first-order tectonic and climatic drivers, and the best understandings lie with the feedbacks and tipping points that bind biospheric oxygenation, climate regulation, and evolving life.

Within this framework, we must also consider the potentially deleterious relationships between changing environments and life. For example, the advent and proliferation of methanogenesis could have had an impact on the concentrations of multiple greenhouse gases, including carbon dioxide, hydrogen, and methane. Higher rates of organic material production from photosynthesis could have intensified methane production, and may have even led to the formation of a sunlight-blocking organic haze. Conversely, the advent of methanotrophy, and the increasing importance of this process during the oxidation of the surface environment, would have consumed methane and lessened the effects atmospheric organics had on climate. The Snowball Earth event that coincided with the rise of oxygen may have been triggered by this collapse of atmospheric methane. This climate extreme, including associated positive albedo feedbacks, could have driven life to its limits were it not for stabilizing carbon dioxide feedbacks that involve the atmosphere, oceans, and solid Earth. Similarly, fundamental shifts in the redox state of Earth's atmosphere, from reducing to oxidizing, changed ecosystems profoundly.

How do studies of Earth's deep history inform our understanding of future changes to Earth's environment?

Just as "the present is the key to the past" in considerations of Earth's future, the past also is key in these considerations. Meaningful extrapolations of future processes can be made based on the rich record of coupled changes in Earth systems, combined with well-understood future changes in solar luminosity and Milanković (orbital) forcings, in addition to less well-understood but physically-modeled changes in systems such as future magnetic field reversals and long-term cooling of Earth's interior. Among the questions in this area that could benefit from future research are perturbations to the carbon cycle due to changes in the amount of radiation received from the Sun and adaptations in photosynthesis in response to altered atmospheric composition.

Study of past responses of the Earth system to environmental perturbations can help us predict the response to ongoing and anticipated anthropogenic changes. For example, among the major concerns on the current list of global change linked to human activities is decreasing oxygen content in the ocean. In part, this process is tied to accelerated nutrient delivery to river systems through urban runoff and agriculture. Also critical, and related, is decreasing oxygen solubility in seawater under rising sea-surface temperatures. Studies of the past, now with increasing accuracy, are showing the range of possibilities for oxygen deficiency in the ocean and allow studies of the full redox landscape (from oxygen-rich to oxygen-poor to oxygen-free and hydrogen-sulfide-containing). The landscapes include quantitative estimates of the global distributions of specific redox conditions in the ocean, including those during the so-called Mesozoic Oceanic Anoxic Events and during the generally oxygen-lean Precambrian. Most importantly, the mechanistic underpinnings of those conditions and the transitions among changing redox states are emerging. Key factors reflecting a changing climate include evolving nutrient delivery to the ocean and the feedbacks that control distributions in time and space of primary production in the ocean, such as long-term phosphorus inputs and internal nitrogen cycling and its ties to essential micronutrients. From this platform, we can predict what is possible in the future ocean, relationships to specific drivers of change, and the positive and negative feedbacks that can both accelerate and temper oxygen loss.

Ongoing changes to the oxygen content of the modern ocean highlight an important facet of using Earth as a natural laboratory for exploring habitable planets—the importance of considering the future of the biosphere and the duration over time of terrestrial habitability. Is the accumulation of significant quantities of molecular oxygen and ozone an inexorable process on a planet with oxygenic photosynthesis? If so, what does this require/imply about the early inventory of reducing volatiles on Earth and their atmospheric escape mechanisms, and how broadly applicable can we expect such features to be? Is such a process necessarily unidirectional—in other words, how much longer into Earth's future will the atmosphere be strongly oxidizing, and by what mechanisms could Earth's surface become reducing again? Conversely, is it possible that hydrogen escape through the top of the atmosphere could lead to further oxidation of the surface and near-surface parts of the Earth system? Are there asymmetries in the relative stabilities of either of these states, and to what extent does such stability rely on initial conditions?

How do modeled or hypothesized future Earth states inform our understanding of habitability?

Some portion of the nearby exoplanets observed in the future will likely be considerably older than our Solar System and/or have biospheres where complex life arose earlier than on Earth. To the extent that we can constrain possible future states of Earth, we will be better able to recognize and characterize Earth-like exoplanets at analogous evolutionary stages. Thus, the study of future-Earth states expands the range of likely exoplanet evolutionary stages that can be linked to the more accessible story of our home world. For these reasons, it is important to know how continued changes will impact the future habitability of the planet, alter geochemical cycles, and change atmospheric gas concentrations.

Broadly speaking, there are two aspects to this question. We can focus on the long-term evolutionary changes that would befall Earth, and similar planets, in the absence of human influences. Additionally, we can look at anthropogenic changes that increasingly dominate Earth, and ask whether this defines a separate significant category of change that might be key in determining the future habitability of Earth and the later stages of some planets with complex life.

Over hundreds of thousands or even millions of years, Earth's climate will be greatly influenced by increases in solar luminosity as the Sun continues its main-sequence evolution. Research should consider what other factors can influence the future climate system, such as biogenic gases and geochemical cycles. In particular, we need to evaluate the effect of feedback cycles operating on long timescales. It is also important for such work to evaluate how universal such climate evolution might be before we use the future Earth as a proxy for older, evolved, habitable planets.

It will also be important to consider how changes to Earth's biosphere, induced by increased solar luminosity, will impact biogeochemical cycles absent human interference. For example, future evolution may alter fluxes of greenhouse gases to the atmosphere or shift rates of organic carbon burial. Also, when solar luminosity has substantially increased, it is likely that the temperature-CO_2-weathering feedback will reduce CO_2 to extremely low levels, possibly driving evolution of new photosynthetic systems, which, in turn, will feedback into an altered atmospheric composition.

Looking at the increasingly dominant role of human industrial activities in altering the atmosphere, climate, biodiversity, and the hydrological and geochemical cycles of Earth, we must consider the role of humanity in the future of Earth's habitability. In the near term, anthropogenic release of CO_2 into the atmosphere is a significant driver of climate change. Given the size of hydrocarbon reservoirs that might be oxidized by humans, future work should consider the impact of possible future fossil fuel use on Earth's habitability by looking, for example, at an expected climate and geochemical cycling under a 4,000 parts per million CO_2 atmosphere (which is consistent with the most extreme scenarios presented by the Intergovernmental Panel on Climate Change). It might also be possible to understand at what point in the future short-term CO_2 increases can push the Earth into a moist or runaway greenhouse condition.

As astrobiology concerns itself with the relationship between planets and life, the anthropogenic transition, and the possibility of an analogous transition on other planets with complex life, is of obvious importance to our field. If anthropogenic influence becomes a long-term factor (in the geologic sense) in Earth's evolution, then this is likely to dominate over all other physical considerations discussed earlier in this section. Therefore, over the coming decades as we develop the ability to discern the nature of exoplanets and examine them for anomalous properties which might be biosignatures, we should also be aware of the possibility of planets with anomalies that are the result of technological activities. Much attention has focused on which qualities of terrestrial life might be universal, and therefore relevant to the search for biosignatures; similarly, it is worth considering which aspects of technological civilization might be universal, how such qualities should be expected to affect the observable aspects of a planet, and how they might be discernible from other biosignatures.

II. How Do the Interactions between Life and Its Local Environment Inform Our Understanding of Biological and Geochemical Co-Evolutionary Dynamics?

Biodiversity is a consequence of the myriad interactions between life and its environment that have played out over geologic time. Such timescales are inaccessible for direct observation, which hampers efforts to understand the causative linkages between biological and geologic change. Geologists often utilize comparative analyses of spatial variations to test ideas about temporal changes that occur over inaccessible (i.e., geologic) timescales. This approach can be taken to examine the links between biology and environment to reconstruct how evolution responds to environmental pressure to yield biodiversity.

A more complete understanding of the extent of life on Earth today, together with the development of a mechanistic understanding of how life diversified to occupy its multitude of ecological niches, will lead to more robust proxies and models to predict how ecosystems have responded to environmental change in the past and how they might respond in the future.

Key Research Questions

How do geochemical variations in space and time affect biological diversity?

The interaction between cellular life and its environment is mediated by highly specialized biomolecules that function in conserving energy, maintaining cytoplasmic homeostasis, and numerous other critical functions. The genomic variation of today's biome provides a record of the historical environmental and/or interspecies interactions that precipitated the emergence of biomolecules, which shaped their evolutionary history. This genomic record can be mined for clues that inform our understanding of the mechanisms that underpin gene loss, acquisition, and evolution through geologic time. By combining molecular, biological, and geochemical analyses within a robust theoretical framework, we can take advantage of variation within the present—the distribution of metabolic strategies in different geologic and geochemical environments—to recognize the extent of diversity and the reasons that it exists.

Phylogenetic reconstructions of genes or proteins suggest that taxa and/or their constituent genes and proteins evolve at variable rates. This variable rate of evolution across life is acknowledged but is poorly understood, and this severely impedes efforts aimed at understanding the co-evolution of Earth and its biosphere over geologic timescales. There are many processes that contribute to the variable rates of evolution observed across microbial life, including differences in doubling times and chromosomal replication as well as variation in the efficacy of DNA replication enzymes. However, it is becoming increasingly clear that some environment types, most notably “extreme” environments, constrain or filter evolutionary divergent phenotypes, while other environmental types are less constrictive, and thereby promote evolutionary change. The rate of variation of the environment and how strong those fluctuations are may also be critical components in increasing diversity. It is also possible that adaptation to the conditions of a particular environment that is stable (e.g., anoxic subsurface sediments) does not promote diversification due to the lack of expandable ecological niche space. However, ecologists over the last ten years have documented that the statistical measures of ecosystem abundance and diversity are remarkably insensitive as to whether the environment contains strong selective niches or none at all. Thus, neutral drift must also be considered as a potential component of evolutionary change. Understanding whether organisms that inhabit certain environments undergo more or less evolutionary change is critical to accurately mapping the co-evolution of the biosphere and geosphere and for predicting ecological properties of ancestral organisms.

In addition, microbial populations that have a strong tendency to live together in the same geochemical gradients can be expected to interact at some level, and they are likely to have co-evolved. How these populations organize within a space, divide resources, communicate, and ultimately assemble into complex communities are fundamental questions in astrobiology, with direct relevance to the evolution of complex forms of life from their more primitive single-celled ancestors. Overlays of geochemical data on the network analyses can identify geochemical components that are indicative of the specific points of interaction between populations (e.g., CH_4 availability and two populations involved in anoxic CH_4 production and oxidation). Such interactions can be further examined by analyzing meta-omic data (e.g., genomic, transcriptomic, proteomic data) for functional processes associated with populations that are likely to interact with a given environmental component. The information gleaned from such studies is fundamental to improving our understanding of how complex life evolved on Earth.

How have ecosystems been structured through time?

Ecosystems are structured compositionally, geographically, and temporally by a variety of processes, both environmentally controlled and intrinsically biological. To understand how habitable states have evolved through time and, by extrapolation, their relevance to other planetary systems, we must determine how those processes have varied, the distinct types of ecosystems they have produced, and their effects on biogeochemical exchanges with the larger Earth system. Critical questions focus on the development and spread of new biological processes, the environmental gradients that developed in response to and supported distinct biological communities, and the rates at which biological communities exchanged materials with their environments.

Metabolic activity catalyzes the flow of energy and mass through ecosystems, and metabolic innovations as well as novel syntrophic associations between organisms have invented or significantly modified geochemical cycles and shaped the overarching environmental conditions on Earth through time. Constraining the timing of key biological innovations such as the emergence of photosynthesis (both anoxygenic and oxygenic), biological nitrogen fixation, multiple pathways of carbon fixation, and the development of other metabolisms and their adaptation to and co-evolution with our Sun's spectral radiation and with the atmospheric and oceanic composition, as well as documenting the spread of these metabolisms into new environments through pioneering organisms, will be critical to characterizing states of the biosphere.

How have changing patterns of life through time impacted the environment?

Detailed studies of microbial interactions on the present and past Earth are vital, because they highlight the web of essential feedbacks that drive the overall biogeochemical cycling of elements and their impact on developing and sustaining habitability.

For example, the emergence of oxygen-producing photosynthesis led to a fundamental shift in the redox state at Earth's surface and opened up new opportunities for biological innovation, including the emergence of eukaryotes and, ultimately, animals, while also providing organic substrates that drove other steps in the global biogeochemical cycles. With the rise of oxygen in the atmosphere, pathways of microbially-mediated oxidation of sulfide minerals on the continents arose and flourished, increasing the flux of sulfate and essential trace metals to the ocean—with the later likely regulating enzymatic pathways as cofactors required in nitrogen and methane cycling, among other processes. Sulfate in the ocean would stimulate bacterial sulfate reduction, which, when coupled to archaeal anaerobic oxidation of methane, has important climatic implications. Similarly, the resulting hydrogen sulfide would impact, as a feedback, the availability of redox-sensitive trace metals that may ultimately control the pathways and magnitudes of carbon cycling in the ocean, and thus redox conditions in the ocean and atmosphere. Anoxygenic photosynthesis linked to sulfide oxidation in the water column would produce organic matter that could foster loss of respiratory oxygen in the deep ocean without a naturally accompanying release of oxygen. Sustained low oxygen in the deep ocean could, at the same time, enhance release of essential phosphorus while leading, in an offsetting way, to loss of important fixed nitrogen through, for example, denitrification.

In the realm of exciting speculation, all of these processes, through crustal recycling in subduction zones, might have impacted the deep Earth through fundamental compositional shifts. The surface tectonic manifestations of those deep-seated processes, such as the emergence of continents and mountain building and subsequent erosion would, in turn, drive biogeochemical cycles at the surface through nutrient reprocessing, shifting patterns of volcanism and organic burial, etc. With increasing confidence we are now able to identify and quantify the evolutionary, interactive nature of these pathways and their associated couplings through diagnostic fingerprints expressed in distinctive organic biomarkers, elemental mass balance relationships, and novel isotopic systems and applications. This perspective, when coupled to numerical models for the ocean and atmosphere, allow us to predict fundamental state shifts and their interrelationships, through feedbacks, to life on Earth and, by analogy, elsewhere.

How do we measure the co-impacts of life and the environment?

Biological interactions with the atmosphere, hydrosphere, and solid Earth are ultimately quantifiable in terms of mass fluxes of various biological substrates and waste products. Determining how these fluxes have changed over time, especially in comparison to abiotic fluxes, will be critical to a detailed modeling of the Earth as an integrated biogeochemical system and, thus, for understanding the various states that system has occupied.

The biosphere also mediates the energy balance of the Earth, through the interception and reflection of solar radiation by photosynthetic organisms in the ocean and on land. In the ocean, radiative transfer influences by phytoplankton are of sufficient magnitude to affect temperature stratification and ocean circulation patterns. On land, vegetation cover is critical to the partitioning of latent and sensible heat. In the early ocean particularly, could energy balance influences have driven the evolution of ocean chemistry, climate change, and the timing of critical geologic-scale events?

Among the exciting frontiers in studies of Earth history are developments in our ability to fingerprint specific organismal groups and/or metabolic processes through organic and inorganic geochemical proxies, and thus assess their environmental interactions. These methods include organic (molecular) biomarker records, which are now collected and interpreted with increasing attention to the possibility of contamination and other overprints during burial and subsequent analysis. We can also infer historical patterns and even quantify the impacts of these metabolisms via independent characterization of the ambient chemical environments, such as the availability of enzymatically key trace metals essential in processes that include nitrogen fixation (Mo, V, Fe) and methanogenesis (Ni). With increasing sophistication, isotopic systematics defined and refined in modern natural and experimental systems are allowing us to fingerprint wide-ranging metabolisms and their implicit connections to environmental parameters, including ocean redox and availability of diverse electron acceptors. Further, we can link growing genomic databases and improving molecular clocks (i.e., phylogenomic predictions tied to the geologic record, calibrated by fossils) to independently-constrained ancient environments—for example, bridging estimates for biological metal utilization through time to our predictions for temporally varying metal concentrations in the ocean. However, it should be noted that this is very challenging to do credibly beyond a certain amount of time without calibration by specific and unique biomarkers tied to the rock record.

Major advances include recent studies of microbial sulfur cycling, explored using all four of sulfur's stable isotopes, and nitrogen and carbon isotope analyses that include measurements at the level of individual compounds. Novel metal isotope methods are asserting themselves as new ways to fingerprint metabolisms, and mass-independent fractionations among sulfur isotopes are allowing us to track oxygen accumulation in the atmosphere at unprecedented resolution. At the same time, other emerging isotopic systems, such as chromium, are delineating our earliest records of oxygenic photosynthesis and helping us delineate oxygen's accumulation in the atmosphere. Overall, details about the metabolic and biogeochemical landscape of the early ocean and its relationship to the atmosphere are becoming clearer, particularly in light of improved numerical approaches to atmospheric modeling. The net result is that the composition of an atmosphere detected remotely might provide biosignatures and illuminate the broad complement of biogeochemical processes that define that composition, as calibrated through early Earth studies.

An important part of this story is that the co-evolution of life and the environment is not limited to the microbial world. The origins and diversification of multicellularity, and animals more specifically, are also products and drivers of environmental change. The first appearance of animals in the geologic record roughly 700 to 600 million years ago is widely heralded as a major milestone in the history of life, and it was most likely caused by a significant rise in the oxygen content of the atmosphere and ocean. Other claims, however, have challenged this simple cause-and-effect relationship, suggesting that animals may have facilitated oxygen increases during the later chapters of Earth history via their role in processing organic compounds. These contributions to the carbon cycle include repackaging of fine-grained organic particulates into larger fecal material, and removal of organic compounds from the water column through benthic filter feeding. Other cause-and-effect relationships among animals and their environments include initial and pervasive/deep colonization of the subsurface seafloor through burrowing, organic ballasting effects and elemental cycling tied to the emergence of mineral skeletons, and, in general, production of larger and potentially more recalcitrant organic material. At the same time, weathering of continents facilitated by the development of land plants must be considered. While the details remain fodder for future research, the essential message again is that life and the environment co-evolve.

III. How Does Our Ignorance About Microbial Life on Earth Hinder Our Understanding of the Limits to Life?

Just as on Earth, most life on other worlds is likely to be microbial. Although it is difficult to predict what that life might look like and how it might exploit the available resources for growth and replication, understanding the limits of life on Earth, both in the present and the past, is critical for where and how we should search for life elsewhere.

To address this issue, insights can be gleaned from studies of microbes on Earth. Past and present studies of extremophiles from environments with elevated salt concentrations, variable temperatures, acidic or basic conditions, or toxic heavy metals have revealed numerous microbial strategies for survival. Therefore, it is critical to understand the full complement of microbial and metabolic diversity on Earth, even in communities considered non-extreme. However, achieving this goal presents a challenge, as most of the microbes on Earth remain unknown to the scientific community. Most microbes cannot yet be cultured and are only represented as ribosomal gene sequences. These unknown organisms and their undescribed physiologies might play a significant role in influencing and changing their surrounding environments, or even represent the vast majority of the life within an ecosystem,

The limitation of microbe culturing means that an enormous amount of information regarding microbial physiology, microbe-mineral interactions, and the formation of biosignatures is missing. Studies of both single species and communities are required to provide insights into the specific processes or pathways that microbes use to interface with their local environment. Natural communities have many characteristics that are not well represented in the strain-isolation model. Indeed, certain functional properties, such as mineral precipitation and light harvesting, may only occur when the relevant community members are grown together. Furthermore, the ecological significance of rare organisms within communities remains an important unanswered issue. These rare organisms may become drivers of ecosystem function over time and may not function on the same timescales. The competition or facilitation for physical or chemical niches may drive interactions between microbes and their environment.

Expanding the current database of life and developing novel strategies for analyzing these organisms in their natural habitats is critical to understanding biogeochemistry, the assembly and function of microbial communities, and the co-evolution of ecosystems with their environment. This increased knowledge of microbial and functional diversity will need to be coupled with experimental validation of the environmental tolerance and metabolic capabilities of microbes. Together, these complementary approaches will enable us to understand the impact on ecological stability, regime shifts, and biosignatures—and may reveal novel ways to search for and detect life on other worlds.

Over the past decade, researchers have made large advances in our ability to access high-level functional and evolutionary information about uncultured organisms (e.g., metagenomics, metatranscriptomics, and single-cell genomics), as well as culturing new organisms with previously unfathomed functions (e.g., NC10, which produces molecular oxygen as an intermediate in the nitrate-dependent oxidation of methane). These advances have illustrated new roles for microbes in the environment, and highlighted how much still remains to be discovered. Despite these rapid advances, comprehensive genome sequencing and detailed functional studies have been completed for only a small fraction of Earth's microbes. Even in the best-studied organisms, such as *Escherichia coli*, we understand perhaps half of what their genomes encode. Moreover, although the analysis of organisms in single-species culture can provide important insights into the molecular mechanisms supporting specific processes or pathways, these studies may poorly reflect on how these processes support the viability of a species in its natural environment. For each new environment, molecular analyses reveal unexplored microbial and metabolic diversity, emphasizing that uncharacterized taxa remain in the great majority.

Key Research Questions

How can we reduce bias derived from current methodologies and database limitations?

Despite the enormous amount of molecular information that has recently emerged over the past few decades, there are inherent biases that can limit our understanding of microbial and functional diversity. These biases can arise because primers for gene amplification are often targeted toward previously known organisms; genome and metagenome annotations are derived from databases comprised mainly of cultured organisms; and genes that are more evolutionarily conserved tend to be targeted as significant to physiology. Using methods that do not rely on DNA amplification, such as metagenomic and metatranscriptomic sequencing, require no prior knowledge of or previous selection for specific groups of organisms. Additionally, developing new methods for annotating the uncharacterized regions of genomes without depending on homology to cultured organisms will be essential for discovering new microbial functions in currently uncharacterized organisms.

These methodology-based biases can also be subject to sampling and temporal biases, since populations in nature may turn over on the experimentally intractable timescales of hundreds to thousands of years. Accessing certain biomes on Earth, such as the deep ocean, polar regions, and the continental subsurface can prove difficult and skew our understanding of microbial diversity in these remote habitats. For example, the largest biome on Earth is the marine subsurface, yet this biome has been very poorly sampled. It is prudent to target these understudied systems, however difficult and costly this may be, to ensure a balanced and complete view of the full complement of microbial life. Further, there is very little uniformity in providing ecological context in the annotations of –omics data. This is a huge issue in understanding the importance of functional diversity in genomes or metagenomes, since a gene that is insignificant in one context could be hugely important in another. It is necessary to improve the way in which databases of biological data and databases of ecological context are linked and integrated so that we may have a predictive science of the co-evolution of biology and the environment.

How can we best identify the physiological characteristics of uncultured organisms and link newly discovered genomes to the functional roles the microbes play in a community and/or environment?

Ecologically remote habitats tend to be populated with strains whose nearest known relatives are genetically distant, and thus provide little insight into likely metabolisms and other behaviors. Metagenomics, or the extraction and sequencing of DNA *en masse*, provides extensive information on the functional complexity of microbial communities. Metagenomic analyses can produce community gene catalogs and deep sequencing that will increasingly allow assembly of complete or nearly complete genomes from many samples. Despite this rich source of information, its interpretation can be compromised by difficulties in assigning function for the many protein-encoding genes. Propagation of errors from computational annotations throughout the database makes it difficult to be confident about annotations, particularly for members of superfamilies in which a basic scaffold is conserved but functional specificity has diverged.

Therefore, experimental and *in situ* characterization of an organism's physical and chemical environment is critical to complement various molecular approaches to understand the physiology of microbes in the context of their native environment. Innovative methods of culturing, gene probes, and better annotations will serve to improve interpretation of functionality and delineate the actual roles of organisms and their functions within microbial communities. Useful approaches might include cloning and purification of proteins for *in vitro* assays, CARD-FISH (catalyzed reporter deposition-fluorescent *in situ* hybridization) to examine the abundance and associations of particular microbes, methods for extraction of living microbes or consortia from complex environments, and probing the evolutionary response of microbial communities to environmental perturbations in micro-fabricated environments. Interdisciplinary approaches such as direct assays for specific metabolic or biogeochemical functions, targeting analyses of molecules other than DNA or RNA (e.g., fatty acid methyl esters [FAME]), innovative attempts at culturing, and various microscopic methods from scanning electron microscopy (SEM) to X-ray Absorption Near Edge Structure (XANES) will be required.

How can we explain undiscovered catabolic strategies that may be used by organisms in largely unexplored environments?

Chemotrophic organisms obtain energy by catalyzing disequilibrium redox reactions. All redox disequilibria may represent potential catabolisms. However, only a subset of these reactions are currently known to support life, including a wide variety of carbon, sulfur, and nitrogen redox couples, as well as Fe and Mn redox, hydrogen utilization, and more.

Until anammox organisms were discovered, the reaction of nitrite-plus-ammonia to generate nitrogen gas was not among the list of catabolic strategies. Methane-plus-sulfate in the anaerobic oxidation of methane is also relatively new to our understanding of catabolism. There are undoubtedly many more such examples of currently unknown catabolic strategies.

If a redox reaction is exergonic (energy-yielding) in a particular environment, cultivation and molecular-based experiments can be designed to target that particular potential catabolism. Additionally, mineralogical consequences or products visible in habitats of at least some of these potential catabolisms might be able to point to an unsuspected organism or organisms responsible for producing such a mineralogical indicator of catabolism.

How can we assess previously unknown areas of microbial diversity using a fundamental physics and chemistry approach to define habitable phase space?

If we combine all of the known parameters that affect an organism's survival and behavior, it may be possible to formulate predictions regarding previously unknown habitats. Constructing a multi-dimensional database of a range of physical and chemical parameters (e.g., temperature, pH, salinity, light, availability of reduced iron) and populating it with known organisms that fit within the given space, we can begin to assess phase space to look for previously unknown areas of habitability. Such information could guide us to select from the wide variety of unexplored/poorly explored environments, and focus greater efforts to determine whether previously undiscovered organisms exist under those conditions.

A similar exploration strategy could map known gene functions, superimposing those metabolic networks on relevant-condition phase space, and be used for a similar guidance purpose. These efforts may enable us to use studies of Earth's varied environments as a test bed for remote sampling of other worlds and enhance capabilities for measuring process rates *in situ,* help overcome changes to the ecosystem upon sample retrieval (e.g., depressurization of deep ocean organisms), or to study potential ecosystems where samples cannot yet be retrieved.

4.5 CHALLENGES FOR THE NEXT TEN YEARS

How do the different worlds of the past, present, and future Earth inform our understanding of exoplanets?

The differences among various worlds will be apparent in the spectral appearance of the planet, which, in the context of exoplanets, is our primary avenue for determining whether or not a planet is habitable and/or inhabited. Future work on Earth's spectral appearance through time falls into two categories: (1) remote characterization of the planetary environment and (2) biosignatures and related false positives. In the first category, we seek to understand how to use remote sensing techniques to determine Earth's habitability at different stages in its evolution. The second category seeks to not only identify the biosignatures for Earth throughout its history, but to understand how these would be recognized in the spectrum of a distant world and whether such signatures might be obscured on planets with physicochemical characteristics slightly different from Earth's.

How can we better understand the constraints on the timing and tempo of surface evolution and processes?

To better understand the co-evolution of life and the environment, and specifically the rates and timing of change, we need well-dated and well-preserved archives of the rock record. Extending to older periods of time where the rock record is non-existent will require study of detrital minerals or indirect inferences, such as mantle history or ancient isotopic systems. In addition, drill core samples drilled cleanly and tied to detailed geologic maps, as well as an understanding of local sequence stratigraphy, should provide our best continuous records. Although more survey work may be needed, we have the possibility of filling many, if not most, of the existing stratigraphic gaps through coordinated multi-core drilling campaigns to provide an integrated proxy perspective in full stratigraphic and paleoenvironmental context. However, the need for excellent samples is not enough. Robust dating is also necessary to define rates of processes at high resolution, and to place the inferred environmental details within a broad temporal framework. New isotopes techniques, such as 187Re-187Os systematics in black shales, are broadening the range of materials that can be dated. Further, reliable dating will also quantitatively link geologic observations to phylogenetic trees and molecular clocks.

What is the fidelity of proxies of biology and environment over long and complex geologic histories?

The sedimentary record of Earth's four billion years of habitability offers much potential for informing our understanding of other habitable worlds. However, the stratigraphic record is incomplete and has undergone substantial alteration over various timescales. Experiments that seek to better understand the transformations undergone by mineralogical, geochemical, and organic materials as they are subjected to changing temperatures, pressures, and chemical regimes can inform our interpretation of the record of Earth's habitation and suggest lithologic targets for additional study. Such experiments range from better constraining low-temperature authigenic mineral production to alteration at substantially elevated temperature and pressure conditions, all guided by the wide range of metamorphic grades captured in the rock record. Additionally, investigation of unconformities (e.g., gaps in the stratigraphic record) provide context for understanding the completeness of the stratigraphic record as well as providing a better understanding of the processes of weathering and erosion that are critical elements of biogeochemical cycles. Finally, studies aimed at understanding the various physiological aspects and isotopic fractionation patterns of geologic proxies in modern organisms are necessary to better assess the robustness of various biosignatures in the rock record.

How can biological data and geologic data be integrated through evolutionary time?

Another area of needed improvement is to find ways of reducing the gap in temporal resolution provided by the geochemical and genomic records of major events in the history of life. Recent studies have begun to provide a potential framework for the integration of biological and geologic data through evolutionary time. In particular, the reconstruction of the phylogenetic history of sequenced genomes—phylogenomics—-coupled to time calibration with the rock record has been utilized to infer relationships between biological and geological evolution. However, using sequenced genomes to infer such relationships often ignores the *in situ* ecology of an organism. Thus, future work must integrate information recovered from natural environments that span geochemical gradients using single-cell genomic and metagenomic approaches to provide new and more robust models of the relationship between the distribution of encoded proteins, their geochemical environment, and, thus, the co-evolution of the geosphere and the biosphere.

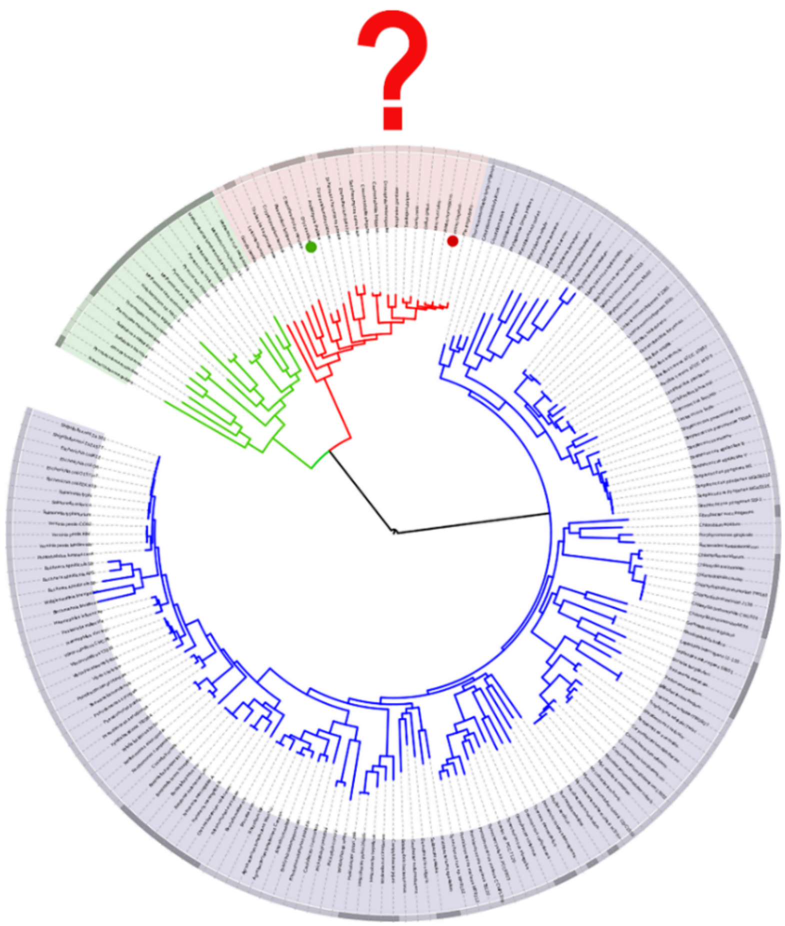

FIGURE 4-6. A highly resolved tree of life based on completely sequenced genomes. However, this view of the tree of life is incomplete, as the majority of microbial organisms are not yet cultured in the lab making it difficult to fully assess the full diversity and metabolic complexity of Earth's microbes. This microbial "dark matter", as represented by the question mark, reflects an important area of future research. *Source:* Image from Ciccarelli et al. 2006. Reprinted with permission from AAAS

How can we develop new approaches or modifications of current approaches to enrich and ultimately isolate organisms currently known only by their DNA sequences?

Traditional microbial cultivation approaches often isolate the fastest growing or most numerically dominant organisms in a community. However, the cultivation of most of the organisms in a community, especially in poorly characterized environments, may require much more careful mimicry of the organism's ecosystem. These targeted parameters may include the aqueous and solid phases, the trace elements, redox disequilibria, nutrient flux, organic speciation, spectral irradiance enrichment, and more. Measurements of microbial activity, especially very low activity, may be possible with new techniques, including micro-calorimetry and single-cell approaches. Additionally, with organisms from habitats that are very low in energy sources, the inherent pace of growth may be exceedingly slow. Efforts to enhance our ability to deal with very slow-growing and even more slowly replicating organisms are essential to develop a full picture of the microbial world.

What are the methodological challenges coordinating and synthesizing *in silico* data?

With the recent massive outputs of metaomic data (e.g., metagenomic, metatranscriptomic, and metaproteomic), integrating and translating this information into a comprehensive understanding of organism physiology and emergent behaviors requires a larger systems approach to assess complex biological processes. Developing this systems-level understanding of the organisms present on Earth requires not only an identification of genes and the proteins they encode, but also knowledge of how they work together to give rise to that biological process. This systems biology approach of integration and synthesis of large-scale high-throughput functional genomics techniques will be necessary to assess how organisms can interact amongst themselves, respond to, and alter their environment.

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5 Identifying, Exploring, and Characterizing Environments for Habitability and Biosignatures

Introduction

Habitability has typically been defined as the potential for an environment to support life, be it on planet-wide or microscopic scales. Assessment of this potential has focused to a very large degree on determining whether liquid water was or is present. Such an assessment constitutes an inherently "binary" approach to habitability—liquid water was either present or was not; life could either be supported or could not—that has served to identify a wide spectrum of apparently water-bearing (nominally habitable) planetary environments. Reference to life on Earth, with habitats that exhibit a continuum from sparsely to densely inhabited, suggests that significant variation in the degree of habitability could likewise exist within the set of water-bearing environments on other planetary objects.

The main purpose of habitability investigations in the context of astrobiology is to narrow and prioritize the search space for life detection efforts. Investigations and methodologies capable of resolving "more habitable" environments from "less habitable" environments will enable the identification of worlds or locations that are more likely to show signs of past or present life. Thus, a key challenge for the coming decades of exploration is to augment the liquid water metric that has served as a guide to habitability with additional metrics that will aid in target prioritization. Major goals are to develop ideas and techniques for determining the relative habitability of an environment, to understand how the signatures of life are generated and preserved in different environments, and to study how non-biological processes can generate the signatures of life and habitability. These new approaches will need to incorporate a variety of parameters that underpin habitability and life, including the presence and persistence of liquid water, potential free energy sources, physical and chemical environmental factors, and the presence of bio-essential elements.

5.1 WHY IS THIS TOPIC IMPORTANT?

The search for life in the Solar System and beyond is guided by our quest to find habitable environments, and is essential to our understanding of the distribution of life in the Universe. Within the Solar System, an improved understanding of the environmental requirements for habitability, the development of tools for either detecting life or determining the relative habitability of either present or ancient environments, and the exploration of analog environments on Earth will facilitate target selection for spacecraft, lander, and rover missions. Beyond the Solar System, improving techniques and ideas for discovering and characterizing habitable and/or inhabited environments, coupled with an understanding of the potential false positives for habitability or life, will enable us to efficiently prioritize exoplanets for targeted follow-up observations.

5.2 WHAT DOES THIS RESEARCH ENTAIL?

Identifying and characterizing habitable or inhabited environments synthesizes information from a large range of spatial scales and across the electromagnetic spectrum. The goal is to determine the likelihood that a particular environment was or is presently habitable or inhabited, and to understand how the physical and chemical conditions relevant to habitability and life in that environment have varied through time. By studying preserved or current evidence, investigations can discern whether or not an environment was able to generate and support life, noting that conditions for the latter may be quite distinct from the former. Habitability indicators and biosignatures must be interpreted within a planetary and environmental context, recognizing that relevant data may be corrupted, incomplete, or unavailable.

5.3 PROGRESS IN THE LAST TEN YEARS

The following are a few examples of observations, measurements, and theoretical research in the past ten years that have advanced our ability to identify, explore, and characterize habitable environments.

Exoplanets

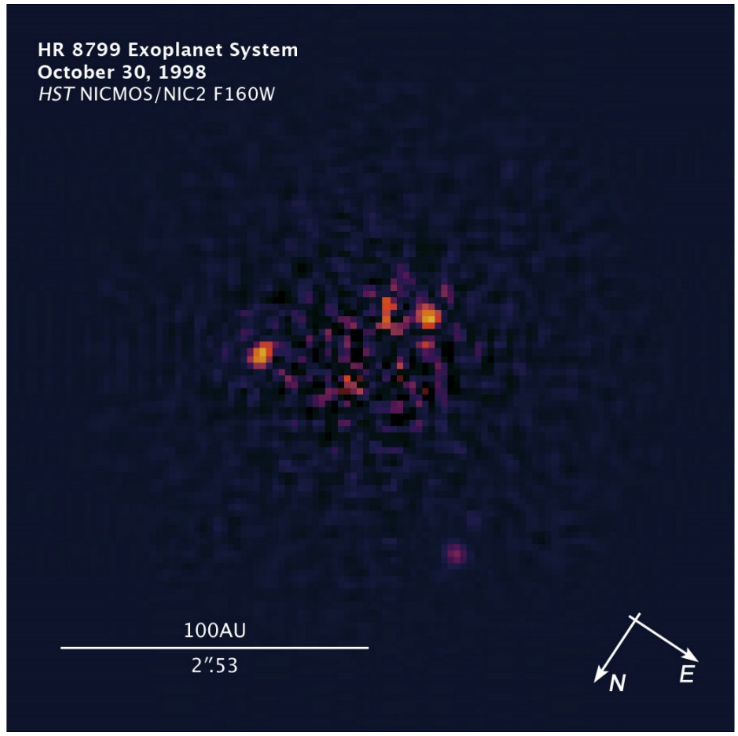

FIGURE 5-1. A directly-imaged planet taken from the Hubble Space Telescope. *Source:* Hubblesite.org, courtesy of NASA, ESA, and R. Soummer (STScI); modified with callouts for reuse.

In the last decade, observations have revealed that Earth-like planets are common around low-mass stars. Astronomers using data from NASA's *Kepler* mission have now detected enough small planets in the habitable zone of their parent stars to make preliminary estimates of the fraction of stars that likely have Earth-size planets in their habitable zones. Current estimates are that about half of Sun-like stars in the Milky Way may have Earth-like terrestrial planets, with more low-mass planets around lower-mass stars. Approximately 50% of M-dwarf stars and 20% of Sun-like stars, may have Earth-size planets in their habitable zones. Two of the most promising planets discovered in the habitable zone are Kepler-62f and Kepler-186f, at 1.4 and 1.1 times the size of the Earth, respectively. The masses of these two planets are not yet known—so determining their bulk composition using density measurements is not yet possible—but recent observations and theoretical models both suggest that planets smaller than 1.5 times the Earth are more likely to be made of rock, rather than ice or gas.

Research over the past ten years has shown how both radiative and gravitational interactions with the star can affect planetary habitability, the likely position of the habitable zone, and a planet's spectrum. This research includes using models to explore the effects of stellar activity on atmospheric chemistry and surface ultraviolet flux, how interactions between the host star's radiation and clouds and ice on the planet can impact planetary climate, and the effects of planetary obliquity and orbital evolution on habitability. Research into interactions between the longer-term evolution of planet and star have also helped to identify situations in which a planet is more likely to lose its habitability, either via atmospheric loss or from tidal interaction with the star, and become thereby a lower-priority target for additional observation. New techniques have been proposed to probe the pressure and temperature of terrestrial exoplanet atmospheres and understand the effects of hazes on exoplanet observations. Significant improvements also have been made in developing techniques to retrieve information about a planet's atmospheric composition and physical state from spectral and/or photometric observations. These new retrieval techniques have been used to improve our understanding of planets many times the mass of Jupiter, down to planets with masses lower than Neptune, in anticipation of data of more Earth-like planets in the next decade.

Icy Bodies

Astrobiologists have significantly advanced our understanding of the potential habitability of subsurface liquid water oceans on icy worlds in the outer Solar System, including Jupiter's moons Europa and Ganymede, Saturn's moons Titan, Enceladus, and Dione, and Neptune's moon Triton.

Continued analysis of data from NASA's *Galileo* mission, in addition to data from the *Hubble Space Telescope* and ground-based telescopes, have yielded new discoveries and theories relevant to the habitability of Europa and Ganymede. Researchers proposed that hydrothermal vents at the bottom of Europa's ice-covered liquid water ocean could create conditions conducive to the origin and sustenance of chemosynthetic microbial life (i.e., depending on chemicals rather than sunlight for energy). Very recently, observations by the *Hubble Space Telescope* provided evidence that Europa may have large plumes of water vapor erupting from its surface. If confirmed, this would be a significant finding as it would provide strong evidence for liquid water and also allow for the possibility of detecting biosignatures on or above the surface of the moon.

NASA's *Cassini* mission to the Saturn system continues to observe plumes of water ice crystals erupting from the surface of Enceladus, providing a rich new source of data. Astrobiologists have

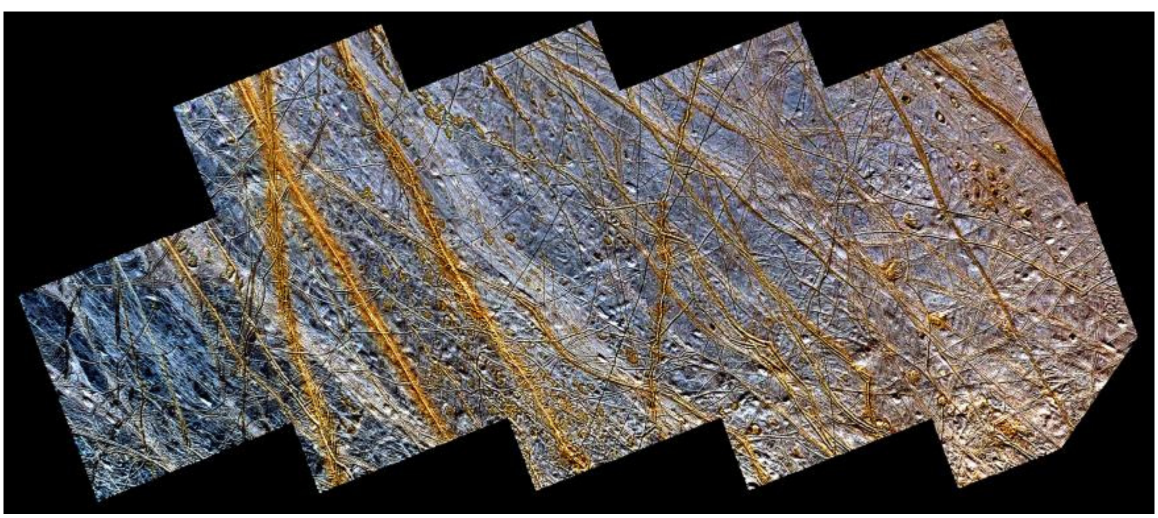

FIGURE 5-2. The picture above is a mosaic of images from Europa's southern hemisphere. The brown, linear ridges extending across the scene are thought to be frozen remnants of cryovolcanic activity. "Cryovolcanoes" (cold volcanoes) occur when liquid or partially frozen water erupts onto the Europan surface, freezing instantly in the extremely low temperatures so far from our Sun. *Source:* Image from Science@NASA Headline News 1998.

determined the chemical makeup of the plumes, and amassed increasingly compelling evidence for a subsurface ocean there. Analysis of Titan's electric field recorded by the *Huygens* probe during its descent indicates that this moon likely has a salty subsurface sea, covered by an ice crust that is several tens of kilometers thick. Astrobiologists are intently studying the ever-present haze on Titan as an analog for the prebiotic organic chemical environment of early Earth, and have recently reported evidence for photochemical activity in Titan's lower atmosphere. *Cassini* observations have helped to better understand Titan's surface lakes of liquid ethane, methane, and propane, and laboratory simulations are being used to gain insight into these environments. Observations of Saturn's moon Dione indicate an active surface, with particles streaming off its surface and fractures in its ice similar to those seen on Enceladus. Scientists now think this moon may harbor a liquid water or slush layer underneath an outer icy shell.

Research over the past decade shows evidence that the surface of Neptune's moon Triton may be as young as Europa's. And, similar to Europa, tidal heating may be maintaining an ocean within Triton today.

Mars

The last few years have yielded a boom in astrobiological investigations of the past and present habitability of Mars due to the simultaneous operation of multiple missions in orbit around, and on the surface of, the Red Planet. For example, using data collected by the *Mars Exploration Rovers*, astrobiologists made the first *in situ* identification of a hydrothermal system on another planet. The

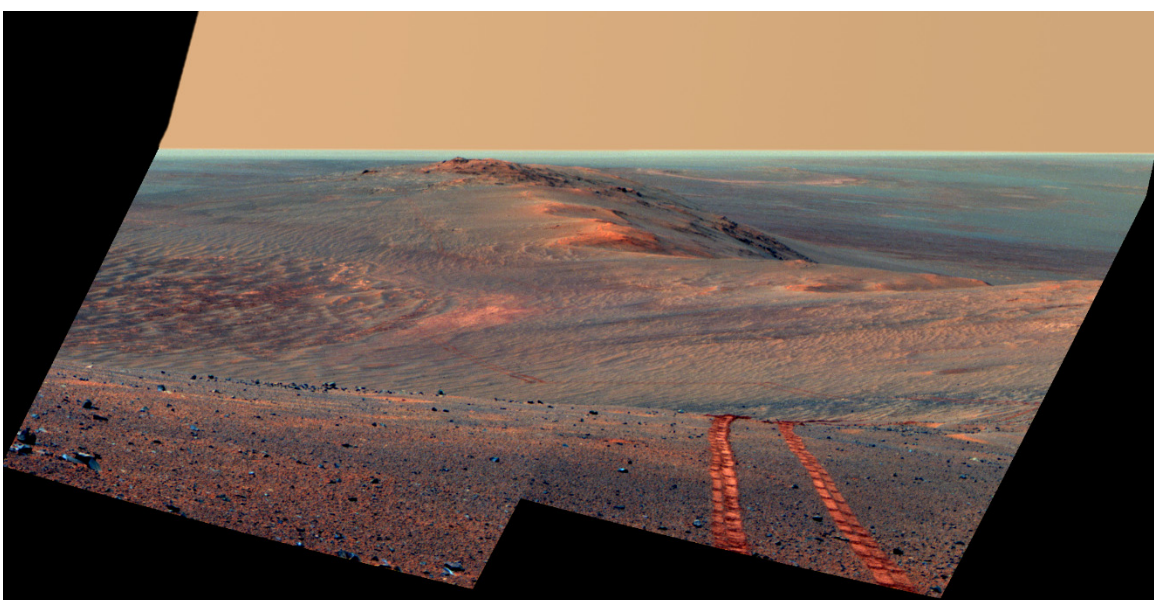

FIGURE 5-3. This scene from the panoramic camera (Pancam) on NASA's Mars Exploration Rover Opportunity looks back toward part of the west rim of Endeavour Crater that the rover drove along, heading southward, during the summer of 2014. *Source:* Image from NASA/JPL-Caltech/Cornell Univ./Arizona State Univ.

discovery by NASA's *Mars Science Laboratory* rover *Curiosity* of sediments in the Gale Crater region of Mars offers evidence of abundant freshwater during the early history of the planet, although the debate continues over whether early Mars was cold and dry or warm and wet.

NASA's *Curiosity* rover has detected methane in the martian atmosphere, suggesting that either serpentinization or life processes have occurred recently on Mars, as methane has a relatively short lifetime in the martian environment (lasting only several hundred years). Early claims of detection of martian atmospheric methane occurred more than a decade ago. Nevertheless, methane on Mars remains a topic of great interest as well as controversy to astrobiologists, since living systems on Earth produce more than 90% of atmospheric methane, with the balance produced by geochemical processes. Astrobiologists are now studying possible mechanisms for the production, release, and destruction of methane on Mars.

Earth

Our planet will always be the best-studied habitable world, and serves as a testing ground for theories and techniques relevant to the origin of life and for the remote study of potentially habitable exoplanets. Astrobiologists continue to study the process of serpentinization in Nature and in the lab to better under its possible role in prebiotic chemistry and the origin of life. Space-based observations of the distant Earth and ground-based observations of Earthlight scattered from the Moon's surface have provided critical new data that have been leveraged in a number of recent studies aimed at understanding photometric and spectral signatures of habitability. These signatures include the "glint" phenomenon which is seen when a planet nears crescent phase, and which may reveal the presence of a surface liquid. The ultimate goal of this line of research is to develop techniques for characterizing potential Earth-like planets around distant stars.

Biosignatures

The identification of biomarkers in the rock record of a planet remains a central research area. Although debate continues over the origin of nanometer-scale magnetite crystals in the martian meteorite ALH84001, progress has been made to understand the significance of magnetite as a potential inorganic biomarker in the rock record. In addition, confocal laser scanning microscopy and Raman spectroscopy have been powerful tools for investigating ancient microfossils, yielding evidence of the three-dimensional form, cellular anatomy, and the molecular structure of rock-embedded microscopic fossils and of the minerals in which they are entombed. Another recently developed technique is deep ultraviolet native fluorescence, which is used to detect microbes, organics, and key biosignatures with greater precision and has been critical in detecting life in a deep borehole in the ocean crust. In recent years, these techniques have been used to examine microbial fossils from numerous ancient geological formations on Earth and offer a way to distinguish bona fide fossils from inorganic "look-alikes."

In looking for life beyond the Solar System, exoplanet biosignature research has focused on improving our understanding of photosynthetic biosignatures, the dominant biosignature on our planet, as well as providing an initial exploration into the types of biosignatures that might exist on non-Earth-like planets. Work on photosynthetic atmospheric biosignatures—such as abundant oxygen and ozone—has made significant progress in understanding whether or not planetary processes can produce similar signatures in the absence of life. Theoretical models suggest that in fact at least four planetary processes may produce false positives for atmospheric oxygen and/or ozone, including atmospheric loss and photochemistry. These studies are identifying which planetary properties and host star characteristics are more likely to lead to false positive signatures. In the quest for non-photosynthetic life biosignatures, researchers have explored alternative surface reflectivity signals from different organisms that may dominate a global ocean, such as halophiles, and have looked at the generation, atmospheric lifetimes, and end products of alternative metabolic gases. Work has been done to explore possible biosignatures for life in hydrogen-rich atmospheres, an atmosphere type that may be more common on larger, super-Earth planets. Novel ways to detect biosignatures on exoplanets have also been proposed. These include looking for planetary disequilibrium signals that take into account atmosphere-ocean interactions, and the use of pairs of oxygen molecules that can produce stronger signals in higher density atmospheres.

5.4 AREAS OF RESEARCH WITHIN IDENTIFYING, EXPLORING, AND CHARACTERIZING ENVIRONMENTS FOR HABITABILITY AND BIOSIGNATURES

- **I. How Can We Assess Habitability on Different Scales?**
- **II. How Can We Enhance the Utility of Biosignatures to Search for Life in the Solar System and Beyond?**
- **III. How Can We Identify Habitable Environments and Search for Life within the Solar System?**
- **IV. How Can We Identify Habitable Planets and Search for Life Beyond the Solar System?**

I. How Can We Assess Habitability on Different Scales?

A number of observable components of planets and planetary systems can be used to help assess habitability. For additional explanation of many the factors that affect habitability, refer to Chapter 6: Constructing Habitable Worlds.

Planetary systems: In general, the galactic environment influences prospects for long-term habitability. The birth environment of the parent star of planetary systems will impose constraints on the history of habitability of any specific system through the early radiation environments, dynamical history, and chance events such as proximity to nearby supernovae.

The prospects for habitable environments for any specific planetary architecture are constrained by the type of parent star. Planets are also found in multi-star systems, and such multiple star systems are common and may not preclude habitability. Further constraints are imposed by the age and metallicity (elemental composition) of the parent star.

FIGURE 5-4. This is an artist's impression of a young star surrounded by a protoplanetary disc in which planets are forming. Using ALMA's 15-kilometre baseline astronomers were able to make the first detailed image of a protoplanetary disc, which revealed the complex structure of the disc. Concentric rings of gas, with gaps indicating planet formation, are visible in this artist's impression and were predicted by computer simulations. Now these structures have been observed by ALMA for the first time. *Source:* Image from almaobservatory.org, ESO/L. Calçada.

Habitability is also influenced by the architecture of the planetary system around a star. The evolution and stability of these systems are determined by gravitational dynamics, which drive the orbital evolution of terrestrial planets, shaping our understanding of planetary habitability. The presence of satellites and neighboring planets provide opportunities to drive the thermal evolution of a planet via tidal forces or could allow for habitable exomoons.

With the discovery of a large number of exoplanetary systems has come the realization that the planets of the Solar System are representative of only a fraction of the range of the possible types of planets. Individual systems may have environments with specific properties unlike any found in the Solar System, and yet may show both indicators of habitability and signatures of life. We need to recognize, model, and explore the full range of potentially habitable environments and sites of life over the full range of exoplanetary properties. A key tradeoff in the discovery space is between finding the best nearby habitable exoplanet environments and having a range of diverse potentially habitable exoplanets. Recent discoveries indicate we can be highly optimistic of finding a selection of diverse potentially habitable observing targets in the solar neighborhood.

Planet-wide: A number of bulk or planet-scale properties influence the potential habitability of an individual world (be it a planet or moon). Of central importance are size, mass, and composition. For example, it is clear that terrestrial planets that form with little or no water are less habitable (or are not habitable), and the potential habitability of terrestrial planets larger than Earth (so-called "super-Earths") remains an open question. The planetary rotational period, obliquity (i.e., tilt of the rotational axis), radiation environment, and tectonic activity are further examples of key planet-scale properties that influence habitability.

The atmospheric properties of exoplanets are of particular importance, as atmospheres provide the most likely astrobiologically-relevant exoplanet observables for the near future, including habitability indicators and biosignatures. The atmospheric composition, circulation, and climate of the various types of exoplanets need to be observed, modeled, and understood in the context of potential habitability, opportunity for the origin of life, and signatures of life or prebiotic chemistry.

Within the Solar System, icy bodies such as Europa or Enceladus present some of the clearest evidence for liquid water on large or global scales, and challenge direct analogy to planet-wide ocean processes on Earth. If water is indeed necessary for life, these bodies represent attractive targets to search for signs of biologically-relevant chemicals and/or life, especially if essential elements and nutrients can be delivered to oceans on these worlds, perhaps from a rocky interior. As the solar flux is typically quite small at the orbital distances of icy bodies, internal mechanisms such as tidal or radiogenic heating are key for maintaining subsurface oceans. While the dynamics and extent of internal processes on icy worlds remain controversial, these processes are well-suited to observation by flyby missions, orbiters, and landers. Additionally, fluxes of ocean material toward the surface, either by ice transport or plume eruption, could allow for the direct detection of organic material, thereby providing insight into subsurface conditions for either originating and/or supporting life.

For all of the above, we also need to understand the evolution over time and the stability of each of the extensive properties of the worlds and their environments, including secular (non-periodic) and stochastic (random) variations and potential internal feedback cycles driven by biological and abiological processes. In many cases, the current habitability of a system may be contingent not just on its current state but also its history. Some of the processes affecting current habitability also may be dependent on its past environment, and, if so, any one-time remote observation would provide only an estimate of the likelihood of that specific environment being habitable.

Regional: Planetary surfaces typically embody diverse features that may vary widely in the type, abundance, and quality of evidence of habitability and potential biosignatures that might be present or preserved. The targeting of life-detection investigations can be strongly informed by an assessment of both how habitable an environment may have been—and therefore how much evidence of life could have been produced—as well as the biosignature-preservation potential of that environment. Specific issues in these areas are the nature and abundance of the life supported by the environment, its likely signatures, levels of accumulation and preservation, and what information may have been lost. Understanding the processes of alteration and preservation related to a given environment and for specific types of biosignatures is therefore essential.

Local: Landers, rovers, or human investigators can conduct observations at spatial scales from that of a geologic field site down to the microscopic. *In situ* investigations can constrain current or prior water availability with respect to duration, extent, and chemical activity, and can characterize past or present physical and chemical environments, emphasizing temperature, pH, water activity, and chemical composition. These studies can also constrain energy availability with respect to type (e.g., light, specific redox couples), chemical potential (e.g., Gibbs energy yield), and flux, as well as measure the abundance and characterize potential sources of bio-essential elements. *In situ* studies also can determine the major processes that degrade or preserve complex organic compounds and other features that might represent examples of potential biosignatures.

Subsurface: Conceivably, if life exists (or existed) on Mars, an icy moon, or some other planetary body, evidence of that life could be found, or is best preserved, in the subsurface, away from present-day harsh surface processes. Key questions still exist with regard to the properties, extent, and stability of subsurface environments, and whether or not such environments are amenable to the origin and maintenance of life. Studies of analog subsurface ecosystems on Earth, including certain aqueous and icy environments, can provide a wealth of information about how organisms survive seemingly stressful conditions for hundreds or even millions of years. Such timescales are impossible to replicate in the laboratory. Field investigations of subsurface environments (including sub-ice environments) must devise ways to overcome challenges that include, but are not limited to, fieldwork, site characterization, sample collection, geologic complexity, methodological biases, biosignature recognition, and in many cases low biomass and activity.

Temporal: Habitable, or inhabited, environments can exist at the spatial scales outlined above for a wide range of timescales. However, all else being equal, environments that are persistently habitable are more relevant to studying the potential for originating and sustaining life. Thus, in addition to expanding and refining methods for detecting current or past habitable environments, techniques should be developed to diagnose the duration of habitability in an environment. Ideas related to the duration and intermittency of habitability apply at all spatial scales, both within and outside the Solar System, and can be used to highlight and rank worlds or locations for targeted follow-up observations.

Key Research Questions about Assessing Habitability

How do habitable worlds and environments form and evolve?

Habitability can be defined on a range of spatial and temporal scales. Additionally, the conditions required for originating life might be distinct from those required for maintaining life. Thus, as our understanding of life's origins grows (see Chapters 3: Early Life and Increasing Complexity and 4: Co-Evolution of Life and the Physical Environment), so shall our understanding of the evolution of environments—from those capable of forming life to those capable of supporting life. Thus, what measurements and studies are needed to improve our definitions of habitability, what are the uncertainties in how habitability is defined, and how can we understand the evolution of habitable environments through time?

How can we better understand the range of parameters that influence habitability?

The relative habitability of an environment will depend on its history of available physical and chemical states, which will vary both in time and space. Thus, can we define a habitability "profile" for an environment that takes into consideration the full range of characteristics, both spatially and temporally, that determine habitability? How might habitability be unevenly distributed over a planet or throughout an environment?

How will we detect, confirm, and characterize habitable environments?

What instruments and measurements are needed to confirm past or present habitability? For worlds in the Solar System, what can be gained by *in situ* studies? For past habitable environments, how will we recognize signatures of habitability, and what are the conditions under which these signatures are preserved?

II. How Can We Enhance the Utility of Biosignatures to Search for Life in the Solar System and Beyond?

A biosignature is an object, substance, and/or pattern whose origin specifically requires a biological agent. Such signatures are, by definition, an indication of habitability. The usefulness of a biosignature is determined not only by the probability of life creating it, but also by the improbability of non-biological processes producing the signature (i.e., a false positive). Thus, investigations into biosignatures generated by modern organisms must also consider how such signatures could be generated, preserved, and/or detected within the context of other environments or worlds. The types of biosignatures that are accessible for exoplanets are more limited than those that can be used in the Solar System and in terrestrial analog environments. In general, biosignatures and habitable environment signatures can be grouped into ten broad categories:

1. *Stable isotope patterns*: Isotopic evidence or patterns that require biological processes.

2. *Chemistry*: Chemical features that require biological activity.

3. *Organic matter*: Organics formed by biological processes.

4. *Minerals*: Minerals or biomineral-phases whose composition and/or morphology indicate biological activity (e.g., biomagnetite).

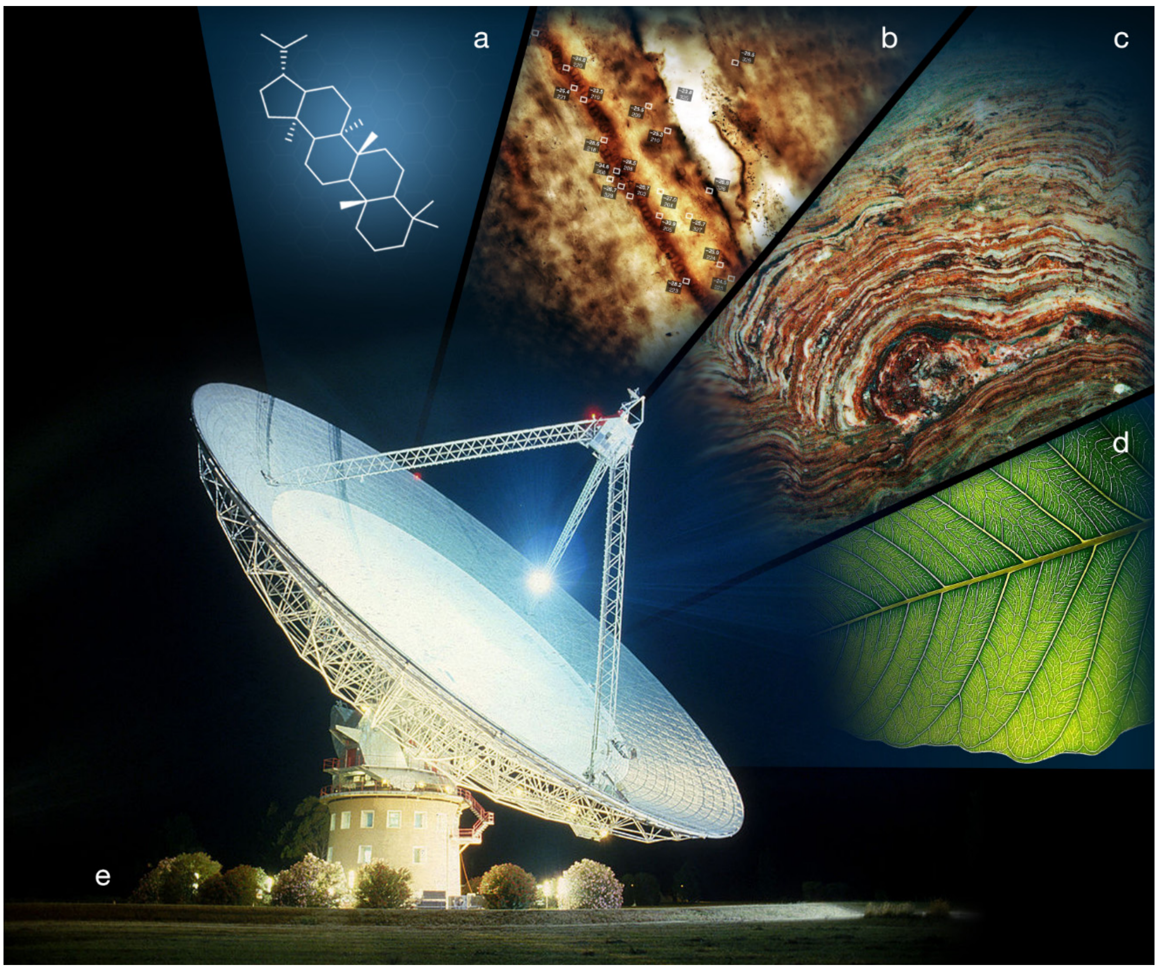

FIGURE 5-5. A variety of biosignature types, including (a) hopane, a lipid that can be preserved in rocks and is indicative of past biological activity, (b) a magnified view of chert, which contains microfossils, (c) a section of a stromatolite, which shows macroscopic layering due to microbial mat activity, (d) a plant leaf, whose characteristic reflectance suggests the complex process of photosynthesis, and (e) a radio telescope, as might be used to detect technosignatures from advanced civilizations. *Source:* (a) Image courtesy Toney 2015, with permission; (b) Image from Williford et al. 2013, with permission from Elsevier; (c) Image courtesy James St. John, Flicker; (d) Image courtesy Fasaxc 2010, Wikipedia. (e) Image courtesy of Kerton 2000, CSIRO.

5. *Microscopic structures and textures*: Biologically formed cements, microtextures, microfossils, and films.

6. *Macroscopic physical structures and textures*: Structures that indicate microbial ecosystems, biofilms (e.g., stromatolites), or fossils of larger organisms.

7. *Temporal variability:* Variations in time of atmospheric gases, reflectivity, or macroscopic appearance that indicate the presence of life.

8. *Surface reflectance features:* Large-scale reflectance features due to biological pigments, which could be detected remotely.

9. *Atmospheric gases*: Gases formed by metabolic and/or aqueous processes, which may be present on a planet-wide scale, and thus relevant to exoplanets.

10. *Technosignatures:* Biosignatures that indicate a technologically advanced civilization.

Future biosignature research will enhance the utility of these signatures so that they can be exploited effectively as tools for astrobiological investigation. Biosignature utility depends on: (1) prior awareness of the type of biosignature in at least a broad or hypothetical sense, so that it can be recognized when encountered; (2) the availability of techniques and measurements to detect potential examples of the biosignature; and (3) the ability to confidently interpret the origin of the potential biosignature once detected. To enhance the utility of biosignatures as astrobiological tools therefore requires expanding the array of known possible biosignatures, constraining their variability, expanding and improving the available detection methods, and increasing the robustness of methods and approaches for biosignature interpretation.

The venue of exploration fundamentally determines the perspective taken to biosignature research. Mars and the early Earth are prominent venues for biosignature exploration, and a significant proportion of biosignature research focuses on detecting signs of past life embedded in the rock record of these planets. Earth's earliest geologic record is the key to determining the antiquity of life on Earth, and rocks from geological epochs through the Proterozoic (depending on preservation state and history) can be useful analogues for searching for ancient biosignatures and habitability signatures on other rocky bodies. The significance of Mars arises from the relative similarity of Mars and Earth among the planets of the Solar System, as well as the relative accessibility of the martian geologic record. Exploration of the martian geologic record provides an opportunity to determine whether life ever arose beyond Earth.

The search for life in unexpected terrestrial settings focuses on direct detection of life or life byproducts in extreme settings such as the deep crust, caves, extremely arid locations, permanently icy bodies, etc. The search for life elsewhere in the Solar System has a variety of potential targets, foremost of which are Jupiter's moon Europa, Saturn's moon Enceladus, and Mars. The search for biosignatures beyond the Solar System currently focuses mainly on spectroscopic measurements of exoplanet atmospheres to search for signs of biogenic gases. It remains unclear if temporal variations in biologically-mediated gases, while compelling, could represent an unambiguous biosignature. Finally, spectroscopic characterization of a planet's surface for biological reflectance features is an important goal for which techniques are being investigated.

Key Research Questions about Biosignatures

What are the processes influencing biosignature formation, preservation, and destruction?

While we understand that certain types of processes play a critical role in biosignature preservation or destruction, there is significant scope for improvements. Studies focusing on the chemical and biological processes involved in how biosignatures are formed, altered, preserved, and destroyed are critical in allowing us to confidently interpret the occurrence of biosignatures in the search for life—be it in the rock and ice record, other planets in our Solar System, or beyond.

How are habitability and biosignatures interrelated?

The extent to which a world or environment is habitable will likely affect the prevalence and/or detectability of biosignatures. Additionally, detecting potential life signatures in an environment that lacks signs of past or present habitability could help indicate a false positive for life detection. Thus, how might changes to our understanding of habitability influence our interpretation of potential biosignatures (and their associated false positives)?

What is the influence of variations in habitability on biosignature formation?

An environment that is highly favorable for habitation enables life to gain a firm foothold, leading to well-established communities, greater productivity, more biomass, and consequently a greater likelihood that life will leave a detectable imprint on the environment and in the fossil record. How the varying degrees of habitability affect specific biosignature formation are unknown; therefore, studies of analog environments will be critical in understanding these aspects of biosignature formation and preservation.

What are the fundamental characteristics of life (even as we do not know it) that may translate into biosignatures?

Because life on Earth shares some common attributes, including complex interacting physical and chemical structures, utilization of free energy, homochirality of certain key molecular structures, the production of biomass (both organic structures and inorganic mineral phases), and phenomena that can be sustained through self-replication and evolution, studies are needed to determine what the fundamental attributes of life are that may result in unique but as-yet unrecognized biosignatures or biosignature assemblages.

What are the abiotic mimics of biosignatures?

When evidence of life is discovered in a setting where life's existence was previously unknown, a key focus will be determining whether the evidence could be produced by abiotic mechanisms. This work can be conducted on a continuous, preemptive basis in order to be best prepared when such discoveries are made. Such a preemptive approach is especially relevant in the context of Solar System exploration and exoplanet observations, where mission constraints require long-term planning, and yet may permit only short windows of opportunity to make observations. Investigations may involve exploring the fundamental physiological and chemical processes involved in producing the signature, with direct comparison of "equivalent" biological and abiotic systems.

What new types of biosignatures can we identify and how can they be detected?

Our ability to detect life improves as the variety of potential biosignatures increases. Expanding the catalogue, figuratively speaking, is a work in progress as researchers continue to examine the way biology influences its environment. New biosignatures may arise from laboratory experimentation or observation of the natural world, and experiments and modeling may reveal a uniquely biogenic trait of an existing category of a potential biosignature. Of course, biosignatures become interesting only when all abiotic sources can be ruled out, as evidenced by the chemical and physical patterns that indicate the presence of life in Earth's earliest rock record. Some categories of biosignatures can be detected with the same instruments that are used for assessment of past habitability. These categories include types of gases, gases that vary in concentration over time, mineral and ice compositions, stable isotopes, and organic compounds. Sediment features, surface reflectance, micro-scale morphologies, and signs of active metabolism can be measured with *in situ* tests, including spectroscopy, imaging, and other detectors.

What contextual information is required to enhance the confidence in interpretation of biosignatures?

The importance of context for interpreting biosignatures has become increasingly apparent in recent years, but "context" is a broad term that can mean many different things, from a high level interpretation of the paleoenvironment that hosts an ancient potential biosignature to detailed measurements of dozens to hundreds of features associated with the potential biosignature. Understanding exactly what contextual information is required depends on many factors specific to the type of biosignature. Some biosignature measurements are suggestive but not definitive. Other measurement types provide greater confidence as to whether the feature under investigation has been produced by biological activity. When multiple types of measurements are combined, the ability to establish the presence of any potential biosignature improves. Our knowledge in this area of the key contextual questions that relate to different biosignatures, and how they can be measured adequately to resolve the origin of a potential biosignature, has significant room to grow.

III. How Can We Identify Habitable Environments and Search for Life within the Solar System?

Our understanding of the habitability of some of our neighboring worlds has dramatically changed in the last decade. Mars, Europa, and Enceladus show different kinds of evidence that liquid water was once present at or just under the surface—or may even persist today. Of course, duration and intermittency are key factors that influence our understanding of the quality of the potentially habitable environments on these worlds, either past or present.

The 1976 *Viking* landers revealed that the surface of Mars is highly oxidizing, making its uppermost surface hostile to the existence of organic markers of life. At the same time, internal heating around volcanic sources mobilizes liquids and drives water-rock chemistry conducive to supporting life. Finding anomalous heat signatures on Mars would thus point to places we might investigate for signs of life or habitability.

Investigations that emphasize liquid water and the chemical elements relevant to life have clear analogies beyond Mars, as shown by the discovery and characterization of plumes at the south pole of Enceladus, indicating that liquid water may persist in the present day at some depth below the surface. High temperatures along cracks where plumes originate indicate relevant geophysical processes. The presence of salt and silica in the plumes suggests that the water results from direct water-rock interactions, which may be analogous to those that are known to support life on Earth. Europa and other icy worlds may contain vast oceans larger than Earth's, and thus constitute habitable environments. Searching for habitable environments in the Solar System necessitates innovation in our thinking of possible settings for life's origins, and designing experiments to explore these settings in the face of planetary evolution and degradational processes (e.g., erosion). This search will involve a combination of investigation from space, *in situ* exploration, and modeling, which will all make use of ever-improving techniques for geologic characterization, assessing geophysical processes, and organic/inorganic chemical analysis.

Once the drivers of planetary- or local-scale habitability dissipate, the imprint of the environment and/or life on the geologic record begins to fade. However, on icy worlds like Europa, radiation from Jupiter may cause indicators to fade essentially as fast as they emerge. Understanding the processes of alteration and preservation related to a given environment, and for specific types of environmental indicators, is therefore essential. This is true not only in the search for traces of ancient habitable environments, but also for currently existing habitable environments. Degradation and/or preservation of physical, biogeochemical, and isotopic biosignatures is controlled by a variety of chemical and physical factors, and the combination of factors that would best preserve one class of features may not be favorable for another. These factors include heat, pressure, radiation and chemical degradation, physical destruction by impact shock, wind and liquid agitation and fragmentation, abrasion, and dissolution.

Ongoing research and reconnaissance on Earth in extreme or analog environments informs our understanding of the limits of habitability. These studies are important to planetary exploration, as they help to ensure that we ask the right questions of new extraterrestrial environments and bring with us the right tools for investigation.

Planetary exploration is a highly resource-limited endeavor, so making the most of a given mission will be essential. Learning from previous missions and connecting processes across targets of investigation is critical. The long list of past, ongoing, and future missions provide (and will provide) data sets that may hold key chemical or geophysical clues to habitability.

Earth's Analog Environments

A number of habitable environments on Earth remain poorly understood, yet some offer us the opportunity to study extraterrestrial habitable environments by analogy. For example, the subsurface biosphere on Earth is large, persistent, heterogeneous, relatively stable, and mostly unexplored. Some icy environments, such as the North and South Poles, are difficult to reach. Other environments (e.g., the Atacama Desert) are easier to access and help us understand the limits of habitability.

Subsurface: If life exists (or existed) on Mars or other planetary bodies like the icy moons, it probably would be best maintained in the subsurface away from harsh surface conditions and processes. Studies of Earth's deep biosphere are likely to provide insights about the nature and persistence of any subsurface life elsewhere. Earth-based subsurface ecosystems can indicate how organisms survive long-term starvation or otherwise stressful conditions for hundreds or even millions of years. These timescales are impossible to replicate in the laboratory, but the deep subsurface of Earth provides a kind of laboratory where Nature has already "performed" these experiments. Studies of the subsurface biosphere inform our understanding of how organisms might persist over long periods of time in the subsurface of planetary bodies, or during long trips between celestial bodies on debris or spacecraft.

FIGURE 5-6. The Atacama desert (left) and Antarctica (right) are Earth analog environments that can be studied to understand how terrestrial life adapts to extremes of low humidity and temperature, and provide data for potential extraterrestrial habitable environments. *Source:* (left) image courtesy ESO/S. Guisard; (right) image courtesy Mandemaker 2006, Wikipedia.

Marine and terrestrial subsurfaces represent two of the largest biomes on Earth, yet we have only a limited understanding of these vast environments. New research can address challenges related to fieldwork, site characterization, sample collection, geologic complexity, methodological biases, and in many cases low biomass and activity. Work should be aimed at a diversity of subsurface environments in order to better understand the global distribution of microbial groups and the geochemical processes that they mediate. A combination of new methods and established approaches will be needed to overcome the specific challenges of subsurface research and to ensure that microbiological investigations acquire a sufficient breadth of data types. In the absence of direct subsurface samples, it could be possible to analyze emissions from fracture zones and other outflows for chemical and isotopic evidence of active processes in subsurface environments. This approach may be particularly relevant to the exploration of Mars, Europa, and other planetary bodies. In addition, sub-ice environments have their own particular set of challenges, and new methods should therefore be developed to improve our exploration and enable further research within these important locations.

In many subsurface environments, cellular resources are limited, yet organisms have high energetic needs to deal with the stresses of temperature, pressure, pH, and toxic compounds. Organisms in the deep subsurface therefore may function at lower activities than life in areas with abundant resources, so detecting their activity levels can be very challenging. Fortunately, techniques are available to detect organisms with very low metabolic activities at the single cell level. However, no technology currently quantifies the metabolic rate of an individual low-activity cell of a known identity. Such an advance would be ideal for determining how processes are divided among individuals in a diverse community, and how each cell uses those processes to meet the basic requirements for life. Future experimental, field, and modeling studies of subsurface microorganisms on Earth could map out the diverse range of limiting factors that ultimately constrain the limits of this life.

Additionally, it is not currently well understood how organisms, biosignatures, and other bio-relevant chemicals cycle between surface and subsurface environments via sedimentation, fluid or diffusive transport, and tectonic processes. By characterizing the impact of the deep microbial biosphere on surface processes, biosignatures can be identified for use in detecting analogous effects on other planetary bodies. For instance, there appears to be a systematic decrease with depth in the population of microbes in sediments deep beneath the seafloor. This decrease is poorly understood, but may be related to allometric scaling. Understanding the scaling of population sizes and metabolic rates with depth might help predict biogenic gas fluxes at the surface.

Surface: Surface analog environments are easier to study than the subsurface, but each presents unique challenges and opportunities. It is the nature of analog research that each site will only represent a subset of conditions to describe a particular extraterrestrial environment. Examples of this are the Mars analogs, where a site on Earth may be very dry but the temperature is too warm, the geology may be very relevant but the sites are also covered in terrestrial life, or the sites are cold and dry but have a different geology to Mars and are hard to reach. A diverse program that tackles specific questions in each terrestrial environment is necessary to build a complete picture of terrestrial equivalents to extraterrestrial bodies. Europa’s sub-ice oceans, the Mars subsurface, and Enceladus' briny lakes all may be environments that could support a subset of terrestrial life in one form or another, at least at some time in their history. It is important to understand the context of the terrestrial environment as an analog, since currently there are over 200 proposed sites for analog research around the globe. The emphasis on these sites must "follow the science" to be conducted by plausible mission scenarios. The choice of an ideal analog must primarily be decided by the science justification. However, other important considerations are ease of access, local logistics, safety, national park status, transport of samples and equipment, and weather/operating conditions.

Analog research addresses core ideas and questions related to how environments maintain (or preserve) signatures of habitability and life. Fundamentally, research at analog sites traces the boundaries of life on our planet, with implications for where life might be found elsewhere. By understanding the complex interplay between life and non-life processes in analog environments, and how these processes relate to survival, diagenesis, and preservation of biosignatures (as well as signatures of habitability), we can better inform our exploration of potentially life-bearing environments in the Solar System. Ideas formulated in analog environments can then be used as constraints and tests for mission designs and strategies that aim to explore astrobiologically relevant worlds in the Solar System.

TABLE 5-1. Extremophiles on Earth, with similar environments in the Solar System.

Extremophile	Conditions	Earth Habitat	Relevant Environment(s)
Psychrophiles	Low temperature	Snow, ice, sediment	Ice shells of Europa and Enceladus; poles of Mars
Halophiles	High salinity	Sea ice inclusions, saline lakes, evaporation ponds	Subsurface oceans of Europa, Titan, and Enceladus
Piezophiles	High pressure	Hydrothermal vents of the ocean floor	Ocean floors of Europa (hydrothermal?)
Xerophiles	Low water activity	Atacama desert, rock surface	Surface of Mars
Radiation-tolerant microorganisms	High radiation	Nuclear reactor water, cores	Surface of Europa
Chemolithotrophs	Liquid hydrocarbon matrix	Pitch Lake, oil seeps	Hydrocarbon lakes of Titan

Key Research Questions about Earth Analog Environments

How can the exploration of extreme environments on Earth reveal the presence (or absence) of life under stress?

How can we expand and enhance our capabilities to explore and characterize extreme environments, and how can we improve our abilities to detect life in these conditions? Are organisms present in extreme environments truly "alive," and what can they tell us about life's origins and/or the potential for life in extraterrestrial environments? How is life in extreme environments coupled to the larger Earth system, and on what timescales is this coupling relevant? By characterizing the impact of extreme microbial ecosystems on surface processes, candidate biosignatures can be identified for detecting analogous life forms on other planetary bodies.

How does environmental stress influence the persistence and activity of life?

How do organisms survive in long-term starvation/stress conditions, and how active are these organisms? What are the limiting factors to life in extreme environments? Future experimental, field, and modeling studies could map out the diverse limiting factors of life.

What are the potentials for preserving the signatures of life in extreme environments?

Research on the identification and preservation of life's signatures in extreme environments will enhance our ability to identify and interpret biosignatures in similar environments elsewhere.

Mars

Mars has emerged as a prime target in the cosmic search for evidence of habitable environments and life. Earth and Mars may have hosted relatively similar environments during their early histories, and life emerged relatively early on Earth. Life-related investigations have become a unifying theme for Mars system science.

Understanding the interplay of factors ranging from geophysical to climatological is an essential part of the search for evidence of life on Mars. Habitability and the potential emergence and fate of life are intimately linked to the evolving planetary environment.

Finding evidence of either past or present life on Mars would be a watershed event. However, significant differences exist in the strategies, technologies, target environments, and forms of evidence that are most appropriate in searching for ancient versus current life. For example, it is generally thought that definitive evidence of life in ancient samples might only be obtained through return of samples from Mars to Earth, whereas some investigations for life must be, or may best be, conducted *in situ*. Likewise, it may be necessary to access the martian subsurface to find currently habitable environments, while a variety of sites that are presently accessible at the surface of Mars exhibit evidence of previously habitable conditions. Missions to the surface that are ongoing or being developed target ancient systems, because deposits formed in various ancient habitable environments are presently more accessible to characterization at the level of detail needed to constitute a viable search for any evidence of life. However, recent findings—for example, sporadically buried ice deposits in tropical regions on Mars caused by microclimates, and, on Earth, an expanding understanding of the potential for currently-existing photosynthesis-independent subsurface life—emphasize the significance of potential subsurface habitats on Mars.

Mars presents a diverse array of environments that may vary widely in the type, abundance, and quality of biosignature evidence they might preserve. The targeting of potential life-detection missions should thus be strongly informed by assessment of (a) habitability (i.e., how much and what sorts of evidence of life a given environment could be expected to have accumulated when/if it was inhabited), and (b) biosignature preservation potential (i.e., what sorts of evidence of life could have accumulated, how well differing lines of evidence could have been preserved, and what information may have been lost at a definable point in space and time).

Multiple metrics are required to resolve habitability as a continuum (i.e., more habitable, less habitable, uninhabitable). The past presence of liquid water, albeit essential for habitability, is not solely sufficient. Thus, the principal determinants of habitability for life on Mars include the following: 1) the presence, persistence, and chemical activity of liquid water; 2) the presence of thermodynamic disequilibria (i.e., suitable energy sources); 3) the presence of bio-essential elements, principally C, H, N, O, P, S, and a variety of metals; and 4) environmental factors (e.g., temperature, pH, salinity, radiation) that bear on the stability of covalent and hydrogen bonds in biomolecules.

Understanding the processes of alteration and preservation of evidence of past environments, and of specific types of biosignatures, is essential. Degradation and/or preservation of physical, chemical, and isotopic biosignatures or environmental indicators is controlled by a combination of biological, chemical, and physical factors; a combination that would best preserve one class of features may not be favorable for another. These factors might have varied substantially from one potential landing site to the next, even among sites that had been habitable at some time in the past. Characterization of the environmental features and processes on Mars that preserve specific lines of biosignature evidence is a critical prerequisite in the search for life.

Key Research Questions about Mars

Where, when, and for how long were habitable conditions maintained on the surface of early Mars?

Can we use the rock record to distinguish sites that were more habitable from those that were less habitable? What other pieces of geochemical evidence (e.g., indicators of pH or temperatures) might address the potential for ancient Mars to harbor life? Can we constrain the abundances of bio-essential elements in ancient martian environments? Can we use the polar ice record to identify relatively warm periods in more recent Mars history?

Are there habitable environments on Mars at present?

How can we identify and characterize locations where liquid water currently exists? Are there near-surface habitable environments on Mars? What types of life, and associated metabolisms, might exist in these environments?

What major processes on Mars work to either degrade or preserve signatures of habitability and life?

What role do oxidation, metamorphism, and other key geochemical processes play in obscuring or preserving isotopic and chemical information?

How can ongoing and future missions to Mars help to constrain its past and present habitability and advance our search for life?

What kinds of evidence for habitable environments and life can be obtained from remote observations? To what extent are *in situ* and/or sample return missions necessary for constraining Mars' past or present habitability and its potential for life?

Icy Worlds in the Solar System

Icy worlds present some of the clearest evidence for liquid water on a global scale. If water is necessary for life, then these bodies represent attractive targets to search for life. Whether the results are positive or negative, testing for the presence of life on icy worlds may prove to be transformative in establishing the bounds for life beyond Earth. Further, detection of prebiotically-relevant chemistry will also contribute materially to the context in which we view a potential intensive search for existing or extinct organisms on such bodies. Any indicators of life on such bodies could also shed light on fundamental questions about the origin of life on Earth. For example, is a "little warm pond" where life could originate likely on an icy body, or could a model like a hydrothermal ocean vent more clearly fit circumstances for the origin of life on a body like Europa or Enceladus? If water is the overarching requirement for life, then the presence or absence of life on water-rich icy bodies will provide insight into other requisite conditions. As our catalog of exoplanets increases, the potential habitable space of icy moons around gas giants of both Jovian and Neptunian classes is also anticipated to expand. Thus, the number of habitable icy moons may exceed that of rocky terrestrial primary planets like Earth, and be an extremely important—albeit very difficult to characterize—planetary class when considering the distribution of habitable environments in our galaxy.

Habitability of icy worlds is naturally a prerequisite for the emergence and maintenance of life, but it is poorly assessed to date. Any life present on icy worlds could have originated *in situ*, or it could have come from elsewhere, e.g. via lithopanspermia (transported on meteors). There are profound differences in the astrobiological implications stemming from these two cases. Even if no life is found to be present, the detection of organic compounds produced on an icy body by intrinsic processes (physical processes native to the body), or sequestered and concentrated from outside sources, will inform us about prebiotic processes on Earth and elsewhere.

Sunlight is typically very minimal at the orbital distances of these bodies from the Sun; however icy bodies may possess interior heat sources derived from a rocky core, or be internally heated by tidal resonances with fellow moons and the planet they orbit. Heating from naturally-occurring radioactive elements was more important in the early history of these moons, and depends on how much rock comprises each body. Tidal heating allows for the variety of activity we see on icy satellites today (such as the volcanism on Jupiter's moon Io). Heating from meteor or comet impacts also may have been important in the early history of icy satellites, and may have consequences for the internal evolution of these bodies. Modeling studies are increasing our understanding of how these processes have developed through time, driving geophysical and geochemical evolution, and thus influencing habitability.

Many icy worlds have surfaces that are geologically very young, indicating resurfacing processes that either are ongoing or have occurred recently. These processes may cycle material from potentially habitable (or life-bearing) subsurface environments to the surface, which could be detected with remote or *in situ* techniques. Additionally, the processes that drive resurfacing may maintain chemical gradients in water environments that could be utilized by organisms for energy. We are just beginning to understand how geophysical processes on icy bodies transport chemicals and biosignatures, and how these signatures are preserved over the range of relevant timescales.

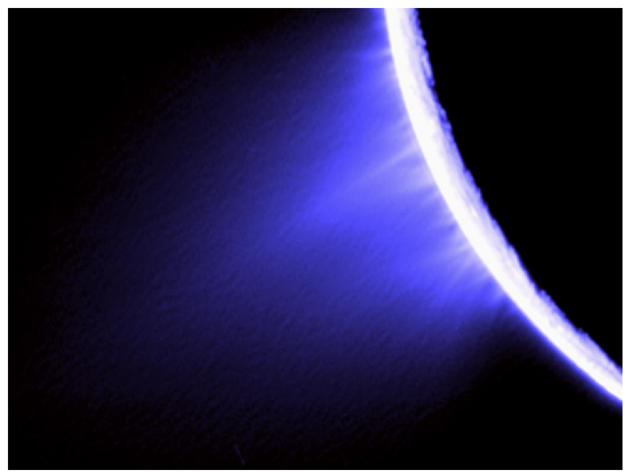

FIGURE 5-7. Cassini imaging scientists used views like this one to help them identify the source locations for individual jets spurting ice particles, water vapor, and trace organic compounds from the surface of Saturn's moon Enceladus. *Source:* Image courtesy NASA/JPL/Space Science Institute.

Finally, icy moons present opportunities for testing chemistry relevant to prebiotic processes and the origin and early evolution of life. The role of meteors and comets delivering materials to these bodies should be investigated. The synthesis of organic molecules that occurs through atmospheric or geologic processes (e.g., via chemical interactions in Titan's atmosphere or in potential hydrothermal systems at the base of Europa's ocean) needs to be studied with regard to, for example, what chemical pathways exist, what prebiotic compounds are created and in what quantity, and what processes may exist for concentrating these compounds.

Key Research Questions about Icy Worlds

How can we better understand processes related to subsurface oceans using past, present, and future spacecraft observations?

What observations might indicate the histories of oceans on icy worlds?

What are the key energy sources for icy worlds, and how do these evolve in time?

What is the potential for hydrothermal activity and water-rock interactions, and how could we remotely detect evidence for these processes? What are the implications for the origin and maintenance of life on these worlds?

What role do interior and/or atmospheric chemical processes play in the development of prebiotic compounds on icy worlds?

Which cycles (e.g., freeze-thaw) might lead to the evolution of complex organic molecules and, potentially, life? Can strong evidence for complex organics or life be established only by *in situ* and/or sample return investigations?

IV. How Can We Identify Habitable Planets and Search for Life beyond the Solar System

A habitable exoplanet is typically defined as a world able to maintain liquid water on its surface—a characteristic that depends on the planet's surface temperature and pressure. Exoplanetary science is a rapidly growing and evolving field of study, and with the accelerating rate of discovery, we need to make it a priority to observe planets that are most likely to harbor liquid water and, potentially, life. However, observations will provide only limited glimpses into the atmospheric and surface environments of exoplanets, thereby challenging our ability to constrain the likelihood of surface liquid water and/or life.

The development of a habitable planet follows a complex sequence of events, beginning with the conditions inside the protoplanetary disk, and ending with the formation of a water-bearing planet in the habitable zone. Atmospheric and surface conditions on this world will then evolve with time, subject to a number of physical process, such as atmospheric loss, outgassing from the planetary interior, the potential emergence of life and subsequent onset of biogeochemical cycles, and the brightening of its host star with time.

Information provided by current exoplanet detection techniques and available (or near-future) instrumentation can begin to address the likelihood that a certain exoplanet is habitable. Of central importance is the planet's orbital distance, its mass and/or radius, and the host star's spectral energy distribution. Other factors, such as planetary system architecture, can also influence our interpretation. The ultimate determination of whether or not a planet has surface liquid water and/or life will require detailed follow-up observations from future telescopes. To guide the design of such instruments and to help prioritize targets for characterization, we must develop a detailed understanding of the information content of the spectra of habitable and inhabited exoplanets.

Characterizing Potentially Habitable Exoplanets

Whether a planet will emerge as habitable depends on the set of events that led to its formation, including the production of prebiotic molecules in the natal molecular cloud, the accretion of the planet such that it contains the proper mix of key volatile species, and the orbital evolution of the planet that delivers it to the star's habitable zone.

The astrophysical processes that govern planet formation appear to be universal, with planets being recognized as a natural byproduct of star formation. How these processes shape the properties of the planets that form depends on factors such as the stellar mass and metallicity (elemental composition), the carbon-to-oxygen ratio of the system, and the stellar environment in which the planetary system forms. In the near future, it may be possible to begin assessing a planetary system's habitability on the basis of such compositional measurements. Similarly, bulk chemical properties of exoplanets relevant to habitability may be determined from the standard methods used to detect exoplanets (radial velocity and/or transit techniques), and other techniques could be devised to begin to understand planetary interior structure.

A long-term goal would be to define a habitability "profile" that encompasses planetary characteristics to inform the chances that the planet is habitable. For example, what radiative and gravitational interactions between the planet and star will affect its habitability? Did this planet likely form with abundant water? What are its orbital characteristics and history of orbital evolution?

In the future, we will be required to estimate or infer the key quantities of habitability from exoplanet spectra, which provide information about the atmospheric state and, possibly, surface properties. In preparation, we must explore and validate techniques for characterizing exoplanet spectra, and we must understand how these techniques perform when confronted with noisy, sparse, and incomplete data. The detection of habitable exoplanets is key in our search for life beyond the Solar System, since it flags worlds as important for follow-up observations meant to characterize potential biosignatures. Furthermore, in the event that we detect worlds that are demonstrably habitable but not inhabited, we will begin to understand the likelihood of the independent origins of life.

Searching for Life on Exoplanets

Exoplanet environments will likely be extremely diverse, with environmental parameters that exceed those known in our Solar System. To determine the best targets for the remote-detection of life and to choose the best measurements to characterize a planet sufficiently to detect life's effect on its environment, we will need to obtain a comprehensive understanding of the range of potential biosignatures beyond the classic photosynthetic biosignatures of modern Earth. Without this comprehensive knowledge, our search for life will be narrowly constrained to the search for modern Earth-twins.

Detecting the presence of life on extrasolar planets requires understanding life's global impact on its environment for a variety of different metabolisms and planetary environments. To do this, we need to improve our understanding of potential biosignatures and determine a way to predict dominant metabolisms based on a planet's atmospheric and surface composition and parent star. We also need to be able to infer metabolisms from observations of the planet's atmosphere and surface, and to be able to identify false-positive biosignatures for different planetary environments. These metabolisms include systems driven by both photochemical and/or redox geochemical processes as distinct schemes for acquiring energy and producing biosignatures.

The search for life—whether *in situ* or remote—requires prioritization. This prioritization typically occurs along two axes: (1) the accessibility/observability of the environment and (2) the likelihood of that environment to produce and support life. The second of these is driven by habitability. Habitability has traditionally been defined with a "follow the water" approach, with searches for evidence of water inside the Solar System, and exoplanet habitability defined by the potential to harbor surface water. Meanwhile, water may be a necessary but not sufficient condition for life; therefore, searches for habitable environments must go beyond a "follow the water" approach to examine a multi-parameter space governed by the interaction of components of the planet's environment, as well as interaction with the parent star and other elements of the planetary system. Better defining these other conditions that support life will improve our understanding of local-to-global habitability, and through that improve our prioritization of future exoplanet observations and planetary missions.

Despite the understanding of the diversity of planets and planetary systems from recent discoveries, we are still biased to consider current Solar System habitable environments as "normal." It is possible that there are qualitatively different habitable environments—for example terrestrial planets with significant H_2 atmospheres, water worlds, and free-floating planets. We need to consider whether certain other planetary systems may be more "normal," such that the Solar System is actually an outlier. Thus, it is necessary to understand the possibilities for novel habitable environments and biosignatures for exoplanets that may be radically different from worlds in the Solar System. Of course, any such endeavors must weigh the likelihood that the proposed worlds exist, but these estimates will evolve as the field of exoplanetary science develops.

Key Research Questions about Exoplanets

How can we observe and characterize potentially habitable exoplanets?

What observation methods can be used to constrain planetary (and planetary system) characteristics relevant to habitability? Can habitability profiles, which consider the spatial and temporal distribution of habitable environments, be constructed for individual exoplanets? Can habitability profiles be used to rank targets for follow-up observations?

What is the diversity of biosignatures that might be expected for habitable exoplanets?

How will the parent star's spectral energy distribution influence potential metabolisms on an exoplanet? How will we recognize atmospheric biosignatures and distinguish them from potential false positives?

What future technologies must be developed in order to best characterize exoplanets for habitability and life?

Which wavelength ranges and spectral resolutions will best enable characterization? How might astrophysical processes (e.g., debris disks) affect our attempts to find and characterize habitable exoplanets?

Current Techniques and Strategies for Life Detection

The search for life elsewhere has motivated planetary exploration since its inception. But how should we look for this life? And where? Narrowing the scope to a few planetary bodies is not sufficient, especially for landed *in situ* missions. Should we search for evidence of extinct or existing life? What about "weird" life? How do we mitigate the possibility of contamination?

A unique metric should be established for each target of astrobiological interest. Life detection technologies are constantly improving; the planetary science community must carefully consider where and how to implement them with a full understanding of the limitations and risks inherent in each technique.

Thus far, all life detection strategies have focused on life "as we know it": organisms that are carbon-based, using RNA and DNA, with L-amino acids, D-sugars, and water as the solvent. However, this constitutes only a small part of the chemical spectrum, and many solutions could exist for life outside this specific set of reactions. For instance, we may find life that started out with similar building blocks, but evolved to operate with the opposite enantiomer set of D-amino acids. Such evidence would be a "smoking gun" for extraterrestrial life, or at least life that branched off of our Tree of Life very early.

We must consider the possibility of life that is much more exotic than our own. Life certainly needs a solvent to facilitate molecular interactions, but water may not be the only liquid capable of performing this role. Ammonia and hydrocarbons like methane and ethane are abundant in the

Universe, and could serve as alternative solvent systems. Any life found in such environments would be quite different, as molecules will have different reactivities, solubilities, and stabilities in these solvents. The theories on how to search for this “weird” life are diverse, though development of a more universal protocol might be possible.

A concise, and likely incomplete, listing of techniques and strategies for life detection are provided below. The indicators discussed span from direct to circumstantial evidence for the presence of life. The strongest evidence would be the detection of living cells or organisms. Biochemicals, fossil biochemicals, fossilized cells, and atmospheric chemical disequilibrium remains represent increasingly indirect forms of evidence for past or present life.

Remote Detection

Remote detection is exemplified by methane on Mars. Earth-based telescopes and the *Mars Express* orbiter have detected low but measurable (parts per billion) levels of methane in the martian atmosphere (*Curiosity* rover later detected spikes of atmospheric methane at 7 parts per billion.) At present it is unknown whether martian methane is from biological or abiotic sources, but there are reports that methane emissions display seasonal hotspots. Remote detection has several advantages; for example, orbiters tend to be less expensive than landers, and a greater surface area of the planet or moon can be investigated with a given technique. However, for many remote sensing instruments, the limits of detection for biomarkers are poor and resolution may be insufficient to allow for unequivocal detection of life. The best example portraying the difficulties of life detection may be the search for life on Earth by the *Galileo* spacecraft. At a distance of 1000 km, *Galileo* was able to identify molecules out of thermodynamic equilibrium (e.g., molecular oxygen and methane), in addition to water vapor and red-absorbing pigment (chlorophyll). However, no single observation alone could unequivocally prove the existence of life on our home planet.

Direct Detection

Direct detection is exemplified by sampling the south polar geyser of Saturn’s moon Enceladus by a series of *Cassini* spacecraft fly-bys. The onboard mass spectrometer instrument detected 91% water vapor, 4% nitrogen, 3.2% carbon dioxide, and 1.7% methane. *In situ* techniques have many benefits, such as sensitive limits of detection for biomarkers like amino acids, nucleotides, and fatty acids. Further, a lander or rover can potentially move rocks or drill holes, accessing areas less likely to be sterilized by ultraviolet radiation or other surface weathering effects. However, *in situ* detection strategies are more susceptible to contamination, and must carry appropriate controls to mitigate false positives. Planetary protection technology and procedures (e.g., organic contamination control, or the development of blanks and other controls) should be further developed to avoid false positives and to ensure the scientific integrity of direct detection missions.

Detection strategies for extinct life include focusing on the following:

- Fossils, microfossils, stromatolites (fossilized microbial mats)
- Chemical signatures (hopanoids, sterols, cyclic alkanes, isoprenoids, carotenoids)
- Isotopic fractionation (carbon, sulfur, etc.)

Best places to look: Aqueous sedimentary rocks, carbonates, evaporites, silica-rich precipitates (cherts), siliciclastic minerals (clays); thermal spring deposits.

How to look: Start with infrared reflectance measurements using remote sensing to identify the right sort of rocks, then send a lander and use *in situ* techniques to look for fossils, chemical signatures and isotopic fractionation.

Common techniques: Extraction of rocks with organic solvents (dichloromethane, methanol) followed by liquid chromatography (bitumen) and demineralization (kerogen). Then use one or more techniques to identify the isotopic abundances (high-resolution mass spectrometry), chemical species (GC-MS, NMR, or FTIR spectroscopy) and/or elemental composition (inductively coupled argon plasma mass spectrometry).

Detection strategies for existing life include searching for the following:

- Biomolecules (amino acids, nucleotides, proteins, DNA, RNA, ATP, NAD+, PLFA)
- Byproducts of life (methane, N_2O)
- Disequilibria (redox, chemical, mineralogical, thermal, etc.)
- Chiral excess (i.e., more D-amino acids than L-amino acids)

Best places to look: Follow the water; areas of disequilibrium (redox, thermal gradients).

How to look: Use remote sensing to select targets (ices, lakebeds, cryovolcanic flows, impact melts), then send a lander and use *in situ* techniques.

Common techniques: Melting and filtration of ice (or extraction of cells/organics from soil or some other matrix), followed by ultra-sensitive analysis using various chemical techniques. These include, but are not limited to, PCR and phylogenetic analyses, immunoassays, lab-on-a-chip methods using capillary electrophoresis and laser-induced fluorescence, and ultra-sensitive mass spectrometry.

We note that, for the search of both extinct and existing life, the general protocol is the same: start with remote sensing to select promising targets, then implement *in situ* detection strategies at those sites.

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6 CONSTRUCTING HABITABLE WORLDS

INTRODUCTION

We have only one example of an inhabited world: Earth. In the past few decades our definition of habitability has expanded with the discovery of life in extreme environments, but now using Earth as our reference to determine habitability has been challenged by the explorations of other worlds.

In addition to the worlds in our own Solar System, we now have a growing catalogue of worlds around other stars, all with diverse and potentially exotic chemistries and environments. So, the question arises: has our limited experience of habitability on Earth distorted our understanding of the basic set of requirements for a habitable world? and how does our experience serve as a helpful guide for the search for life beyond Earth?

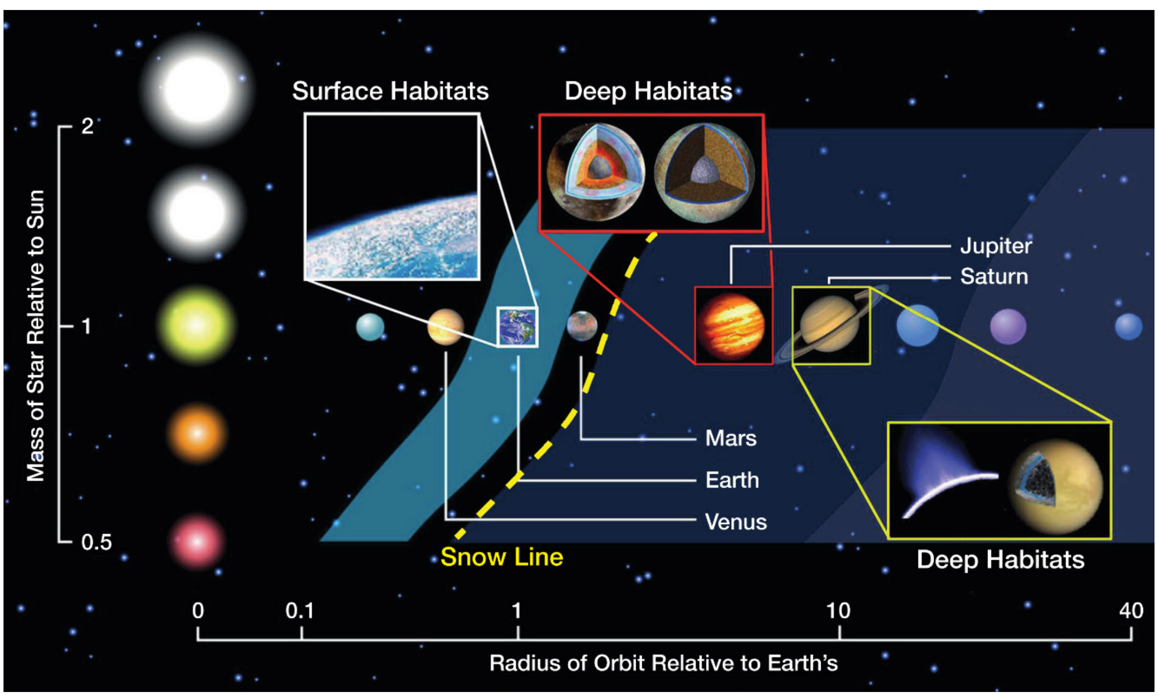

FIGURE 6-1. The original model of the habitable zone (in light blue) used the relative size of the host star and the distance of the planet from this star to model where water could be present in surface environments. As the icy moons of the outer planets (such as Europa, Ganymede or Enceladus) have been studied, the potential for deep liquid water habitats on these bodes has broadened the diversity of habitable worlds. *Source:* Image reprinted from Grasset et al. 2013, with permission from Elsevier.

Earth presents our best clues to life's origin since it has the only known example. The ingredients for life were brought together in such a way that allowed the transition from chemistry to biology, but we still don't know how this happened. We don't know exactly what materials were required, nor what scales of space and time were involved. We do know that water and rock were involved, and we have some sense of the conditions that were present at the time that life emerged. Life's imprint is present in the oldest rocks available, going back almost 4 billion years.

However, we believe life originated before the earliest fossils, because evidence suggests that organisms at this time resemble those near the root of the phylogenetic tree. That is, life had already evolved most of the important features of modern cells—in particular translational machinery. There are two implications to this. First, that life originated close to the time of the formation of the Earth. Second, that the early evolution of life was much faster than its subsequent evolution. The leading theories postulate that life's early evolution is a product of massive horizontal gene transfer and highly fluctuating environments.

The question of where else life may exist in the Solar System (or may have existed in the past) necessarily includes places where Earth-like conditions may occur. We have good evidence that other bodies in the Solar System may have had conditions similar to the early Earth. Such conditions include places where liquid water exists in contact with rocks that contain the essential combinations of elements and molecules, and where there is sufficient input of energy from geophysical processes such as hydrothermal activity or solar irradiation. These parameters probably were also present on Mars and very likely on Venus, and today may be present on the larger icy moons orbiting the large planets in the outer Solar System. There are good reasons to believe that these parameters also occur on worlds around other stars. The distribution of watery worlds in our Solar System and beyond challenges our limited understanding of life's emergence on Earth and encourages us to think about the environmental conditions amenable to life. For instance, Saturn's moon Titan, an active world sculpted by hydrocarbons, causes us to wonder if liquid water is the only possible solvent for life. Such examples lead us to think about the concept of habitability in the broadest possible terms.

6.1 WHAT MAKES AN ENVIRONMENT HABITABLE?

Habitability has been defined as the potential of an environment (past or present) to support life of any kind. Liquid water is a necessary but not sufficient condition for life as we understand it—habitability is more complex than just the presence of liquid water; habitability is a function of a multitude of environmental parameters whose study is biased by the effects biology has on these parameters. A habitable environment is one with the ability to generate life endogenously (using local resources) or support the survival of life that may arrive from elsewhere (exogenous). That ability may depend on inputs such as radiation energy, the generation of chemical disequilibria from geologic processes, or the delivery and accumulation of volatiles and nutrients by meteors and other exogenous sources.

Inhabited environments are habitable settings that are currently occupied by living organisms. Habitability may imply degrees of being habitable and inhabited, reflecting how much diversity, productivity, or spatial cover of life an environment supports. The degree of habitability is important for the detectability of life, whether locally or at the planetary scale. We should also consider that environments evolve, allowing for successive processes to transform a planet between different epochs of habitability. Studies of extreme environments on Earth (see Chapter 5: Identifying, Exploring, and Characterizing Environments for Habitability and Biosignatures) inform our concepts of how life might adapt to transitions between such epochs.

Whether a planet emerges as habitable depends on the sequence of events that led to its formation—which could include the production of organics in molecular clouds and protoplanetary disks, delivery of materials during and after planetary accretion, and the orbital location of planetary bodies in the Solar System.

The astrophysical processes that govern planet formation appear to be universal, with planets being recognized as natural byproducts of star formation. How these external processes operate and shape the properties of the planets that form depends on such factors as stellar size and composition, elemental composition of the system, and stellar environment in which the planetary system forms. Understanding how these factors influence the properties of the planets that have emerged around a star will allow us to evaluate which stars are likely to harbor habitable planets.

The geophysical evolution of a planet or moon controls its climate, atmospheric composition, and surface volatile inventory. Planets are expected to range in size, composition, and orbital elements, all of which can affect interior processes that are known or thought to influence their potential habitability, as well as the length of time they remain habitable. A more thorough understanding of geophysical processes in our Solar System can illuminate the properties of Earth that permitted life to flourish here and the potential for life on other bodies in our Solar System, as well as provide a foundation to predict the physical properties and potential environmental conditions for planets in other planetary systems.

Understanding how Earth has maintained habitability on timescales of many billions of years may provide insight into how habitable worlds may evolve through time. Furthermore, Earth's past, present, and future represent distinct glimpses of different kinds of habitable worlds, providing us with opportunities to understand how we would recognize and characterize a habitable planet at different stages in its evolution. Factors that may control habitability include surface water and continents, a strong magnetic field, and a convective mantle which drives plate tectonics and the carbon cycle as well as planetary heat flow. Are these all critical features of habitability, or are they merely the special properties of our own planet? We know that life on Earth depends on these properties, but there may be other ways to construct a biosphere that would be equally effective in maintaining habitability on another planet.

Habitable settings providing the best chance of detecting life are those where communities of organisms might leave a detectable imprint, or biosignature, in preserved geology. The availability of minerals and maintenance of chemical gradients determine the potential biomass and metabolic strategies of life. The biochemistry of life on Earth requires specific organic compounds that exceed the diversity of organic molecules found in non-living environments. What role did the environment play in selecting these compounds? This influence might have included promoting the formation of organics, providing energy gradients, templating organics and catalyzing key molecule formation, and separating chemical mixtures from other chemical mixtures.

6.2 WHY IS THIS TOPIC IMPORTANT?

> This field is the starting point for deciding where to look for life beyond Earth, and how. If we know what makes a planet habitable, we can go look for it; if we know what conditions preclude habitability, we can limit our targets.

Habitability provides the context for understanding possible signs for life. To enhance the utility of astrobiological tools, we must expand the array of known possible biosignatures—understanding how they relate to the environments from which they are derived—and develop approaches to describe signatures of habitable environments. A deeper understanding of habitability provides context for interpreting the significance of putative biosignatures, or their absence.

Multiple worlds in our Solar System have enough energy for life and for the possible geologic and geochemical precursors to life. We can gain insight by comparing Earth's development through time with the other terrestrial planets, Venus and Mars, which may have had environments comparable to Earth—including oceans and continents—billions of years ago, but have since lost these Earth-like environments for various reasons. The myriad of icy worlds orbiting the Sun and the giant planets includes many that have vast oceans under their icy surfaces. The giant planets themselves inform our understanding of how large atmospheres work.

The diversity of worlds in our Solar System is a small subset of the diversity of worlds in the Universe. As we begin to explore exoplanetary systems that are unlike anything humanity has encountered, we must draw upon our knowledge of Earth and the other planets (and their moons) in our Solar System to develop a theoretical basis for identifying habitable planets elsewhere. We must be open to a wide range of possibilities if we are to understand how life forms, evolves, and can be remotely detected throughout the Universe.

It is important to determine the critical elements of habitability in order to develop a basic understanding of the range of potentially interesting worlds beyond Earth. We must consider alternatives to a terrestrial planet with liquid water at its surface and converge on an answer or strategy for exploration that couples our musings with observations, models, and theories. Our definition of habitability thus defines where and how we will search for life beyond Earth.

6.3 WHAT DOES THIS RESEARCH ENTAIL?

Earth is the only inhabited planet we know of, but it is only one example of how a habitable world may work. The habitability of Earth and other worlds depends on their composition and geophysical evolution. Comparative planetology helps us understand processes that led the Solar System's planets to their current diverse states over time, and provides a template that should be extended to exoplanetary systems. Our emerging understanding of the degree of habitability of bodies in our Solar System may be at least as important as models of Earth's development for building realistic pictures of potentially habitable worlds.

Studies of the habitability of Earth are benefitting from access to new and better locations of study and improved geochronologies and analytical techniques. These provide an unprecedented view of early environmental conditions on Earth that inform our understanding of habitability. In addition, diverse environments on Earth reproduce or inform conditions on other potentially habitable worlds, providing opportunities for *in situ* study that complement other suites of observations of those distant worlds.

Studies of planetary formation are an important part of understanding habitability. For example, icy bodies were scattered throughout the early Solar System, contributing materials to accreting planets and through later bombardment events. The delivery of such material may have contributed to the inventory of ingredients available for prebiotic and biological processes. The surviving small bodies in planetary systems (bodies that are not planets, satellites, or dwarf planets) contain an array of volatiles and other materials, chemical and isotopic compositions, and petrographic characteristics indicative of early Solar System conditions. These bodies provide a record of their interstellar and protoplanetary disk origins, and provide insights into the nature and abundance of different materials. This, in turn, informs us about the starting ingredients for planet formation and evolution.

Questions to address include:

- What ingredients are necessary for life to arise? How do those ingredients come together with planetary-scale processes?
- How do local factors affect global conditions? How do smaller-scale niches—environments that cover less than the planetary surface or subsurface—support the development or evolution of life?

FIGURE 6-2. Dead trees in the terraces of Mammoth Hot Springs, Yellowstone National Park, Montana, US. These trees grew during inactivity of the mineral-rich springs, and were killed when calcium carbonate carried by spring water clogged the vascular systems of the trees. The same process also effectively preserves the trees by preventing decay. *Source:* Image from Brocken Inaglory 2008, Wikipedia.

- What external factors, if any, are crucial to the determination of a world's habitability?
- Are Earth's characteristics and processes for the basic requirements of habitability extendable to other worlds? or is there a way to understand what role and function they play that challenges our assumptions about the habitable zone and the conditions of a habitable planet?
- Are alternatives possible, and might they in fact be more prevalent in other worlds?

To understand how habitability arises and to select targets for potential life-detection missions calls for additional metrics. In addition to searching for liquid water, we may also ask:

- What is the inventory of inorganic compounds and energy sources that affect habitability, and how do these change over time and space?

- What are the thermodynamic constraints on where life forms arise?
- Is life an inevitable physical phenomenon which can be confidently predicted to arise when planetary environments are, for example, far from equilibrium?
- How can we infer habitability in the atmospheres of exoplanets?
- What are the uncertainties in our measurements and models of habitability? How can we reduce these uncertainties?

6.4 PROGRESS IN THE LAST TEN YEARS

The following are a few examples of research in the last ten years that have advanced our understanding about what makes a planet habitable.

Identifying Habitable Zones

While the habitable zone is currently defined as the region around a star where a rocky planet could sustain liquid water on its surface, astrobiologists debate whether this definition should be updated based on what we have learned in the last few years. Recent studies have focused on how star-planet interactions affect the limits of habitable zones and overall planetary climate conditions. For example, M-type stars have generated great interest among exoplanet researchers, as most of the stars in our Milky Way galaxy are M-types and many planets have been detected orbiting them. However, stellar flaring and tidal locking may pose a threat to atmospheres, because a planet must orbit such a cool star at close range for water to remain as a liquid on its surface. Recent theoretical research suggests that planetary habitability should be extended to accommodate non-Earth-like planets, such as desert planets, ice-covered worlds, and even planets with hydrogen-dominated atmospheres.

Revealing the Formation of Planetary Systems

Models and understanding of planet-formation processes have improved markedly in the last decade, due to both observational and theoretical work. Observations spanning a wide range of wavelengths have helped to reveal structure in the distribution of gas and dust in a number of protoplanetary disks, hinting at the formation processes occurring in them. The measurement of the oxygen isotopic composition of the Sun and confirmation of molecular self-shielding in protoplanetary disks has provided invaluable context for the meteorite record and for telescopic data that reveal processes occurring around young stars. Development of the so-called “Nice Model,” a scenario for the orbital evolution of the Solar System which proposes that gas giant planets migrate, has provided insight into the late stages of planet formation around the Sun. Advancements in modeling planetary accretion have made large steps in understanding the timescales and, thus, potential material reservoirs involved in the construction of planets. Similarly, modeling of terrestrial planet formation around other stars suggests that habitable planet formation is possible, if not probable, over a wide range of conditions.

The Important Role of Small Bodies in Forming Habitable Worlds

Studies of comets and asteroids are providing new evidence that may shed light on the role of small bodies in delivering water as a key ingredient in constructing habitable worlds. The similarity of hydrogen isotopes in lunar volcanic materials and terrestrial water to that in some carbonaceous-chondrite meteorites provides evidence that such meteorites delivered water to the Moon and the Earth early in the evolution of both bodies. Researchers also have detected Earth-ocean-like deuterium concentrations in the Jupiter-family comet 103P/Hartley 2. The recent detection and measurement of water in the Oort-cloud comet 8P/Tuttle is consistent with independent measurements in five other Oort-cloud comets. Discoveries of main belt comets—small bodies with main belt orbits that produce dust tails near their perihelion—suggests that asteroid water may be an important part of the volatile story in the inner Solar System. Amino acids have been found to be common in carbonaceous chondrite meteorites, pointing to prebiotic processes on these bodies. Both water ice and organics have been discovered on the surfaces of several asteroids, including 24 Themis, parent body of many of the main belt comets. These findings provide context for establishing the fraction of Earth's oceans and other prebiotic materials that could have been delivered from impacts of asteroids and comets early in its formation, as well as important processes occurring within the inner Solar System.

Understanding the Diversity of Habitable Worlds

The past decade of Solar System exploration provides needed perspective for understanding the construction of habitable worlds. Chemolithotrophs found living under Earth's glaciers, in its caves, and in its deep crust point to a host of potential analogues for environments on other planets (see Chapter 5: Identifying, Exploring, and Characterizing Environments for Habitability and Biosignatures). Signs of active geology on Mars, the dwarf planet Ceres in the asteroid belt, Jupiter's moon Europa, and the Saturn moons Enceladus and Titan reveal that these worlds have sustained geological activity over long time periods. Mars and Titan have been revealed as worlds with complex geochemistry influenced by liquids flowing on their surfaces.

Mars looks increasingly like it was once an Earth-like world with all of the ingredients for life. The *Mars Exploration Rovers* revealed mineral deposits strikingly similar to salts found on Earth in extinct lakebeds in the Atacama Desert and Death Valley. Potential methane was detected in the atmosphere of Mars in *Keck* and *Mars Express* telescopic spectra, raising the possibility for present day water-rock chemistry beneath the surface of Mars. This is supported by the detection of methane made by the *Mars Science Laboratory* (aka *Curiosity* rover). *Curiosity* rover also discovered signs that water once flowed extensively in Gale crater, creating an environment that could have supported microbial life. Serpentinite minerals—seen in *Mars Reconnaissance Orbiter* spectra across the surface of Mars—suggest that activity known to support chemolithotrophic organisms on Earth might have once taken place there.

Titan now is clearly a place of rich chemical diversity that includes the basic elements of life (C,H,N,O,P,S), and yet this moon of Saturn is a place to consider as hosting life that might differ from life on Earth. The *Cassini-Huygens* spacecraft found lakes of liquid methane and ethane on Titan, fed by hydrocarbon rains. Saturn's largest moon contains more hydrocarbon reserves than all of those existing on Earth, and *Cassini* results strongly suggest there is a vast subsurface ocean of liquid water beneath Titan's surface.

Observations in the last decade support the likelihood of past or present day subsurface oceans in icy moons and dwarf planets, many of which could contain vastly more water than in all of Earth's oceans. Observations of Ceres revealed a shape and density that indicates it has a large hydrosphere and could have maintained an ocean.

Europa's icy surface geology remains mysterious, but further interpretation of specific features suggests liquids just beneath the surface at the time of the *Galileo* mission, and plate-tectonic-like cycling of oxidized surface materials into the interior. We currently have no way of knowing whether this activity has any connection with recently observed water vapor emission from the southern region of Europa, a potential indicator of a plume like the one emanating from the south pole of Enceladus. At least, a localized south polar ocean in Enceladus is also strongly suspected, based on multiple investigations by *Cassini/Huygens*.

Achievements in Earth System Science

The study of the habitability of planets continues to rely on major advances in understanding the processes on our own inhabited planet Earth. Sophistication in measuring and modeling complex interactions among atmospheric, surface, subsurface, and ocean processes on Earth has led to fundamental shifts in understanding the rise of life, mass extinction events, major climate events, and how this couples to the geologic record. Improvements in understanding tectonic processes on Earth, including how plate tectonics arose and the planetary characteristics that were present during Earth's tectonic evolution, inform models of tectonic evolution on other planets.

Ocean and atmospheric models have provided insight into how changes in greenhouse gases, aerosols, obliquity, and other factors influence planetary habitability. Extensive work on how the environment and biology interact within individual systems, such as within sea ice, below glaciers, and within deep ocean crust, continues to reveal the underlying requirements and processes within a habitable world. This work influences our understanding of possible strategies of organisms that thrive in such extremes, which in turn bounds our perspective on the limits of life on other planets. It also informs our search for life on other worlds—including placing limits on the remote detectability of life based on atmospheric signatures—by constraining the many biotic and abiotic drivers of chemical equilibrium and disequilibrium.

6.5 AREAS OF RESEARCH WITHIN CONSTRUCTING HABITABLE WORLDS

I. What are the Fundamental Ingredients and Processes That Define a Habitable Environment?

II. What are the Exogenic Factors in the Formation of a Habitable Planet?

III. What Does Earth Tell Us about General Properties of Habitability (and What is Missing)?

IV. What are the Processes on Other Types of Planets That Could Create Habitable Niches?

V. How Does Habitability Change Through Time?

I. What are the Fundamental Ingredients and Processes That Define a Habitable Environment?

The principal determinants of habitability may be the presence, persistence, and chemical activity of liquid water; the presence of thermodynamic disequilibria providing suitable energy sources; physicochemical environmental factors that bear on the stability of covalent and hydrogen bonds in biomolecules (e.g., solar input, subsurface heating, temperature, pH, salinity, irradiation); and the presence of bio-essential elements, principally C, H, N, O, P, S, and a variety of metals on the periodic table. These factors couple to the timescale over which these conditions have existed, because the origin and evolution of a biosphere, particularly a detectable one, will not be instantaneous.

Endogenic factors include considerations of the presence of atmospheres, continents, and oceans, and associated outgassing rates and geochemical cycles. Additional laboratory experiments on material properties can produce vital input for modeling efforts (e.g., thermal conductivity, viscosity, density). Geophysical, geochemical, and material science research on Earth-centric processes is relevant to such questions, and can be extended to the broader range of environmental parameters on other worlds.

In addition to composition, a world's energy budget provides critical information relevant to its evolution and habitability. Internal heat can be thought of as the engine for geodynamics and an important factor for determining where liquid water occurs. For Earth, energy flux through the surface is well known, but the relative importance of the sources of the energy is not. Approaches to exploring tectonic systems very different from Earth's will be crucial for delineating the general "habitable space" within a tectonic context and how it will evolve over time. This will again necessitate understanding the initial chemical inventories and formation mechanisms of a variety of potential planets and planetary systems, and a focus on whether different drivers (e.g., radiogenic or tidal heat, etc.) or styles of tectonics (e.g., stagnant lid or plate-driven, depth and chemical integration of subducting crust into the mantle, etc.) promote or inhibit the emergence and maintenance of habitable environments.

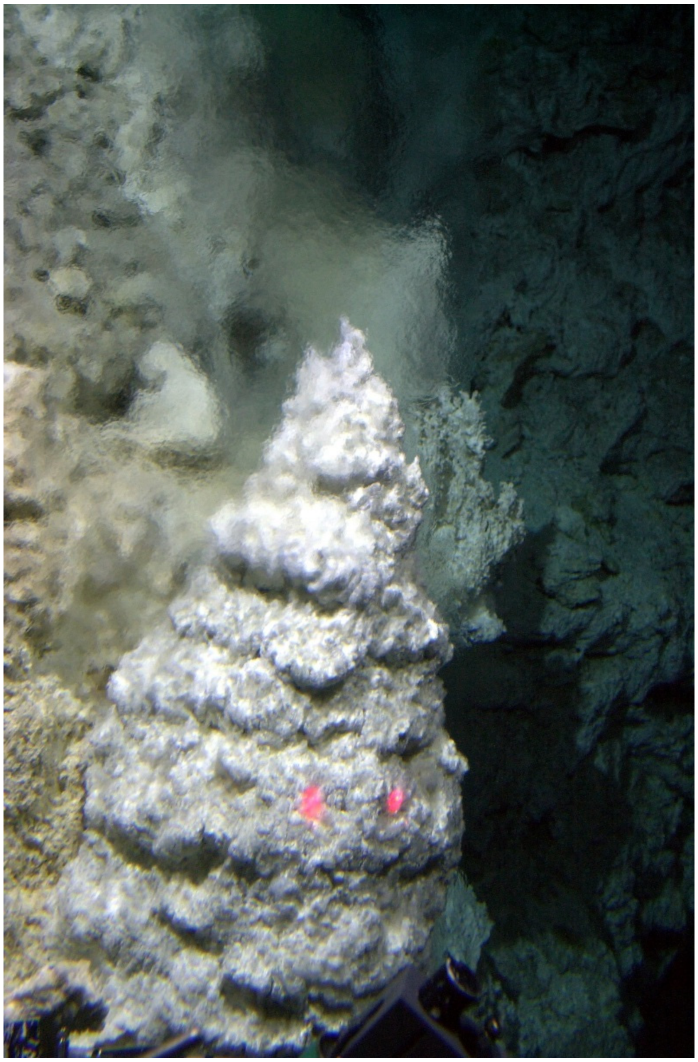

FIGURE 6-3. This small Beehive structure vents the highest temperature (91°C), highest pH fluids (11) at Lost City. This image was taken with Alvin in 2003 during the NSF-funded expedition. Lasers are 10 cm apart. *Source:* Image reprinted with permission from D. Kelley, University of Washington and NSF.

Energy is also a requirement for magnetic-field generation, which may be critical for atmospheric retention in the face of strong stellar activity and/or high-energy radiation. Earth's dynamo is primarily a product of convection in its outer core. Earth's magnetosphere protects life from damaging solar radiation, but without convection, dynamos may be too weak to support a magnetic field. It is therefore crucial to understand the origin and evolution of magnetic fields as an important part of the geophysics of all planets. Differentiation and core crystallization depend on composition and initial energy, neither of which is possible to observe but may be deduced. New insights into constraining the energy budget of planets, or the relative importance of a planet's thermal evolution, will be vital toward assessing the habitability of planetary bodies in the Solar System and beyond.

Key Research Questions for Ingredients and Processes

What is the effect of the size of the planet?

How does habitability relate to the inventory, distribution, and role of critical elements and minerals within the planet's interior: radiogenic nuclides, water, C, H, N, O, P, S?

What is the role of core formation in habitability; e.g., separation of Fe/H, Mg/Si, C/O, generating a magnetic field, separating siderophile elements?

What governs the geophysical evolution of a world's interior and what are its effects on habitability: heat budget, rate of mantle-surface exchange, the manner of that exchange, redistribution of bio-relevant compounds and energy sources?

What are the sources of planetary-scale energy available to drive active processes on the planet: radiogenic, accretionary, tidal, differentiation, tectonism, convection/conduction, exothermic/endothermic reactions (e.g., serpentinization)?

What is the function of plate tectonics in habitability, and can other processes reflect its impact: redox state of the mantle and crust, source of energetic disequilibrium, inventory of bio-available minerals, evolution of the planet's mineralogy, recycling of atmospheric constituents, coupling to environmental factors, erosion and sedimentation, influence on ocean or atmospheric composition?

What is the role of geochemical processes on habitability: serpentinization or other relevant water-rock interactions and their dependence/impact upon environmental factors, such as tectonics?

What environmental conditions provided energy for prebiotic processes? The utilization of energy is a fundamental property of all life. Given that geologic environments also produce energy, what are the elements of these environments that might be used by life? Similarly, what are unlikely ways for the environment to supply energy to life?

II. What are the Exogenic Factors in the Formation of a Habitable Planet?

Planets will be affected by the environment where they form and the conditions of the neighborhood in which they exist. These can include the age of the host star and its mass and stellar type, the number, class, and orbits of other planets and stars in the system, the radiation environment, and the accretionary/bombardment environment, including the oxidation state, temperature, timescales of formation, and volatility of the protoplanetary disk. This is true of planets within and outside of the Solar System.

Accretionary heat depends on the timing and physics of formation as well as any final massive collisions. The distribution of radiogenic isotopes in the galaxy is unknown, and for a given system likely depends on the location of the host star relative to massive stars that manufacture elements like uranium and thorium.

A planet's composition can influence its radius, which is observable in planetary transit; several studies have predicted how the radius can indicate different compositions. However, with current astronomical precision, most planetary compositions are uncertain, and progress in this area likely requires significant technological improvement in observational capabilities, or reliance on other approaches.

Key Research Questions for Exogenic Factors

How is habitability influenced by the initial inventory and distribution of volatiles and the oxidation state of the disk?

How do protoplanetary disk processes influence formation (e.g., accretion, migration, stellar activity) and maintenance of life?

What are the properties of the host star that are conducive to or prevent the formation of a habitable world: age, size and elemental composition of the star, its activity, and the properties of nearby stars?

When does the stellar environment become suitable for the formation of and preservation of stable environments: ocean, atmosphere, and shielding from solar radiation?

What were the abundant elements and molecules in the protoplanetary disk and their effects on planet formation: e.g., Mg/Si ratio, C/O ratio, Fe/H ratio, radiogenic isotopes?

Was the dynamical environment of the planet conducive to habitability: system architecture, obliquity, tidal and resonant effects, spin-orbit coupling, satellite systems, impactors, primary and late accretion, bombardment(s), volatile delivery?

How can we test our models of protoplanetary disk evolution and chemical evolution? D/H measurements will inform our understanding of how water is processed—from its origin in the molecular cloud to its processing in and dynamical evolution within protoplanetary disks. Can we hope to achieve the same type of insight with organic molecules or other species?

How can we constrain the masses of protoplanetary disks with greater certainty? Disk mass estimates, which tell us about the amount of raw material available for planet formation and how that evolves with time, are dependent on a number of uncertain assumptions (typically a uniform dust-to-gas mass ratio). How can we detect variations and probe the distribution to greater sizes?

What molecules can be best used to trace the chemical evolution of protoplanetary disk interiors? Molecular emission features allow us to probe the chemical compositions of protoplanetary disk surfaces, where the molecular abundances are affected by cosmic rays, energetic photons, and energetic particles from the young star. Given that planet formation occurs deeper within these disks, how can certain species be identified that provide a record of chemistry and transport from the disk's mid-plane?

What molecules can be used to trace planet formation processes in protoplanetary disks, e.g., spiral arms and standing shock waves, or disk gaps driven by embedded protoplanets? Understanding the scale and distribution of these features, which previously have been too small to resolve spatially, will provide important constraints on how planets form and interact with their protoplanetary disks. Such constraints would serve to improve our understanding of these processes that are key to determining the architectures of planetary systems.

How can exoplanet census data be used to constrain models for the accretion of terrestrial planets? What is the number of planets in the habitable zones of their host stars? Are they rocky or gas giants? Knowing where planets are will serve to test our models and provide opportunities to better identify those which may be habitable.

III. What Does Earth Tell Us about General Properties of Habitability (and What is Missing)?

Lithosphere-surface-atmosphere exchanges and the abundance and spatial distribution of resources are critical to the productivity, diversity, extent, and persistence of life. Replenishment and recycling of resources is an important aspect of this. This may occur on small scales through cycling in ecosystems and geochemical processes, at intermediate scales through spatial heterogeneity (i.e., the distribution of water bodies and land masses) that concentrate resources and maintain gradients, at the planetary scale through plate tectonics maintaining atmosphere-lithosphere redox gradients, and at the planetary-system scale through delivery of matter and stellar radiation.

By building a detailed knowledge of Earth's history, we can enrich our understanding of the possible range of habitable cases we may expect elsewhere. Our planet has undergone marked redox variations throughout its history, with dramatic consequences for the biosphere. As a result, Earth's rock record contains important information about environments that are habitable and yet quite distinct from recent Earth environments. The earliest rock record holds our best available constraints on atmospheric composition and pressure. Life today operates symbiotically with the atmosphere, but this may not always have been true. Earth's oldest rocks also tell us about the composition of the earliest ocean, which may have been more saline than the present-day ocean. We don't know whether the first life operated in freshwater or saline conditions, or for that matter, whether in deep or shallow conditions. We don't know whether the average temperature of the ancient ocean was high, medium, or low. Earth's diverse habitats and their co-evolution with life (see Chapter 4: Co-Evolution of Life and the Physical Environment) provide important clues to life's robustness, and thereby to the degree of its influence on the Earth system.

Key Research Questions for General Properties of Habitability on Earth

To what extent does Earth's rock record inform us about the conditions and processes present when life emerged (e.g., atmospheric and oceanic conditions and composition, tectonic processes, redox state, strategies employed, abundance and diversity of life across various niches)?

How do geophysical cycles and surface processes influence the availability of bio-relevant compounds in terrestrial systems: weathering, erosion, tectonism, interaction with water and the atmosphere, (bio)geochemical cycles, crust and surface reservoirs, potential for surface/subsurface recycling of materials?

What does the nature of Earth's atmosphere tell us about habitability: primary atmosphere, atmospheric loss, composition, geologic fluxes, surface pressure, temperature, aerosols, clouds, or hazes?

How has the pressure and composition of Earth's atmosphere changed over time? How would we determine whether it has changed, and if it has, what does that imply about the evolution of our planet and of life?

How do we determine whether an intrinsic magnetic field is necessary for habitability on the surface of a planet?

What is the habitability of Earth's interior?

IV. What Are the Processes on Other Types of Planets That Could Create Habitable Niches?

Our Solar System contains a multitude of ice-covered worlds, and there may be many that have more water than is contained in the oceans of Earth. In Earth's history there may have been epochs of near-complete ice cover, so-called "Snowball Earth" epochs.

Another consideration for habitable world alternatives to Earth is for "water worlds"— those worlds with oceans and no continents at their surfaces. Water worlds may be very similar to icy worlds in some aspects, but there will be important differences. Internal pressure, especially in its effect on the existence of high-pressure ices, is a key factor to explore in these planets. Such worlds ask us to determine the basic set of processes that govern habitability, and to seek examples of how processes within alternate planetary systems might behave and function. Is geologic activity a proper proxy or sufficient enough to determine habitability? How do geologic and geochemical processes work on water worlds? What niches for life exist over evolutionary timescales within such worlds? Do higher-pressure phases of ice have any effect on the habitability of a certain environment? How does sedimentation operate in such worlds? What other factors might icy worlds or icehouse epochs of a planet be hospitable for life? Can life even begin there?

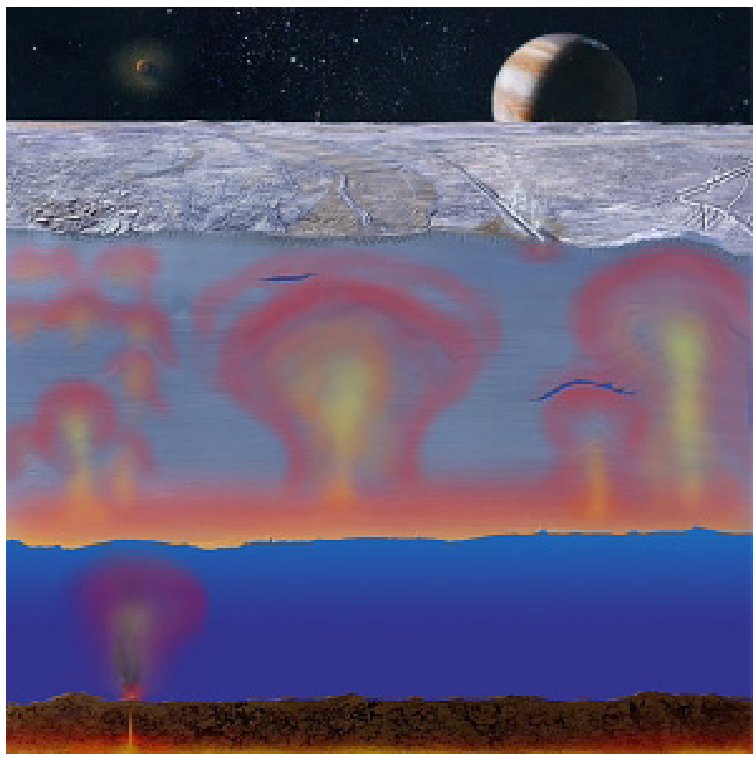

FIGURE 6-4. Artist's representation of the "thick shell" model for Europa's icy surface and subsurface ocean. *Source:* NASA/JPL-Caltech.

An additional source of energy on some planets will be tidal heating, as occurs on Jupiter's volcanic moon Io and in neighboring moons Europa and Ganymede. For planets orbiting low-mass stars, the habitable zone is close enough to the star that tidal effects can be important and tidal heating could be significant. In extreme cases, this additional heat could trigger a runaway greenhouse, but more likely it contributes some or most of the internal energy in a planet. In some cases, tidal heating can be time-variable if the orbit is evolving due to gravitational perturbations from other planets (heating scales as orbital eccentricity squared). Thus, tidal heating not only changes the energy budget, but the thermal profile of the planet. Energy deposited near the surface of the planet could quench plate tectonics and the geodynamo by limiting solid state convection. (This is the problem for Venus, where high surface temperature results in a flat geothermal gradient and little or no mantle convection.) The role of tidal heating in the habitability of planets orbiting low mass stars (as well as brown dwarfs and white dwarfs) or exomoons orbiting exoplanets, requires further attention.

Key Research Questions for Habitability on Other Planets

How might processes on other worlds mimic those on Earth or a terrestrial planet to sustain habitability: how does the geology work, and does the ice act as an atmosphere? What are the influences from very large or very sparse atmospheres?

What is the nature of the hydrosphere on icy, ocean, or water-poor planets, and how does it affect where habitable conditions may occur: high-pressure ices, oceanic composition and circulation (mixing, heat transfer, etc.), interaction with the atmosphere, presence/absence/depth of oceans?

How is the heat budget related to creating habitable conditions?

What are the ways that very large planets with extended oceans or atmospheres, or planets with little water or volatile content, interact with their interiors, and how does this affect the habitability?

What is the effect on the habitability of a planet if there is no rock-atmosphere cycle? What is the effect if the rock-atmosphere-ocean cycle is significantly altered?

What are potential reservoirs of prebiotic, bio-relevant or biological materials (and processes): e.g., reactions between ocean and seafloor, hydrocarbon reservoirs, ocean circulation, ice overturn, sputtering, liquid alkane solvents, methane abundance, stable volatiles, other ices, or surface processes?

What might a biochemical system on other planets look like: available polymers, metabolic pathways, compartmentalization, solvents?

How do volatile-rich/potentially habitable moons form around giant planets?

What is the probability of measuring habitability indicators and what are the relative uncertainties in these measurements in the context of stasis, extremes, and variability?

V. How Does Habitability Change Through Time?

Viewed along the axis of time, the Earth has effectively been many habitable planets, each characterized by different internal feedbacks/couplings and external forcings. Understanding how each of these states was maintained and the processes that governed the transitions into succeeding states provides opportunities for understanding habitable states on other planets.

This evolution of a planet can be tracked by measuring state variables (e.g. atmospheric composition, the composition of sediments and sedimentary rocks, the presence or absence of key metabolic processes, etc.). States that persist over time may result from occupation of stable equilibria or may simply represent long-term transients between equilibria. Understanding the processes that move complex systems between states is important for developing and testing hypotheses about complex cause and effect relationships (e.g., the timing of the oxygenation of the atmosphere and the evolution of oxygen production). Characterizing and quantifying the diverse states that the Earth system has occupied, and determining the critical processes that governed its evolution, will need to be coupled with mechanistic modeling to better understand how state variables measured on other planets may reflect their evolution and states of habitability.

Inquiries into epochs and duration of change in planetary cycles are important because the chemical systems that preceded the emergence of life needed time to form. Such systems depended upon a sort of “stable disequilibrium” to drive electron transfer, as well as produce polymers such as proteins and other prebiotic molecules. Thus, there must be a timescale over which the environment and its planetary host could provide such uniform, or at least hospitable, conditions for these early systems of life.

Key Research Questions for Changes in Habitability through Time

How does the volatile inventory evolve after formation and formation-like impact events?

How do the evolution and variation of the host star affect a world’s habitability through time?

What is the timescale over which an environment must persist to be conducive to the emergence of life?

What defines the timescale over which a planet may be inhabited: climate stability, internal heat budget, internal heat, chemical inventory, tectonic regime?

How might environmental fitness be determined in part by changes in planetary cycles?

How can planetary orbital dynamics affect the habitability of a planet over time (e.g. spin-orbit coupling, stabilization from satellites, changing semi-major axis, eccentricity, etc.)?

How does the movement of the host star through the galaxy affect the habitability of its planets?

6.6 QUESTIONS AND CHALLENGES FOR THE NEXT TEN YEARS

The next decade of exploring Solar System bodies and exoplanets will help us refine our definition of habitability. In order to determine the relevance and relationship of these environments to the concept of habitability, and thus the likelihood that life has originated there, it will be critical to address what utility and limitations exist in our exploration of potentially habitable planets.

Each of the following five major questions provides an outlook for how to frame the study of habitability, and thus inspires directions for research and measurements that should define the next decade of progress.

1. How do we constrain the fundamental ingredients and processes that define a habitable environment?

2. How can we model, measure, or eliminate exogenic factors that result in or destroy habitable worlds?

3. What new lessons can we draw from Earth to inform us about how terrestrial planets evolve? What critical points are we missing from our understanding of the Earth system?

4. What might new measurements of the diversity of worlds tell us about how habitability works on these planets? What measurements have we not considered that could revolutionize our perspective on how these worlds may support life?

5. What processes are occurring in different worlds and distant systems that give us perspective on how habitability evolves? Can we measure a range of states that complete our picture of habitability?

In short, we must enable a "planetary systems science" approach that mimics the integrated approach of Earth systems science. This will require the study of the broad questions posed here in great enough detail to form a larger understanding of how different processes interact across the parameter space represented by known and hypothesized worlds. Given the scale of many of the observations in the next ten years, a systems science approach seems to suggest a hierarchy of inquiry that connects across many scales: systems biology → environmental systems science → Earth systems science → planetary systems science.

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7 CHALLENGES AND OPPORTUNITIES IN ASTROBIOLOGY

INTRODUCTION

Scientific research, by definition, constantly pushes against the limits of human knowledge. These limits encompass not only what humans know, but also how we know, and must go beyond technical and scientific challenges (like those discussed in other chapters). This tension creates challenges for our pre-existing set of standards, practices, and language that developed alongside our current knowledge base, and these challenges in turn erect barriers that could prevent us from declaring success, even if we successfully pursue all the research goals outlined in those chapters.

Many of the challenges and opportunities on astrobiology's horizons arise from the interdisciplinary nature of astrobiological research. The search for our origins as well as signs of life on other worlds requires that we consider the broadest possible signatures of life, together with the myriad processes that could mimic those signatures. We must continually refine our concept of life in order to improve our criteria for successful detection and question the boundaries we historically have set between living and non-living systems, recognizing the possibility that "weird life" might exist with signatures dissimilar from those produced on present-day Earth. It also requires us to breach traditional boundaries between the physical sciences and other areas of human inquiry such as history, theology, philosophy, and linguistics. With each of these challenges lies the opportunity for the field to advance our ability to conduct research as a highly interactive community and for astrobiology to become an example for other fields facing similar challenges.

We discuss here many of the challenges our community will face over the next decade. Many have overlapping themes, both in the disciplines involved and in the anticipated strategies needed to meet these challenges. However, each challenge is sufficiently significant to warrant a brief discussion.

7.1 WHERE ARE WE NOW?

I. What is Life?

First, comprehending life is a conundrum. Clearly, we need to develop a working concept of the entity whose origins and cosmic distribution we seek to determine. This will help to identify the "services" that an environment must provide in order to sustain life, and it helps to identify and interpret any signatures that might indicate its presence. This, in turn, will help to identify past or present planetary environments as promising candidates for exploration. However, without at least a second known, independent example of life it is probably not possible to determine with great certainty the characteristics that are unique to terrestrial life and those that are truly universal for all life. We have little choice but to begin by identifying attributes of life that are universal among living systems as we know them and that are relatively less likely to reflect adaptations specific to the historical trajectory of habitable environments on Earth.

Recent studies (e.g., Baross et al., 2007) have proposed the following necessary set of universal attributes of life: (1) life must exploit thermodynamic disequilibrium in the environment in order to perpetuate its own disequilibrium state; (2) life most probably consists of interacting sets of covalently bonded molecules that include a diversity of heteroatoms (e.g., N, O, P, S, etc. as in Earth-based life) that promote chemical reactivity; (3) life requires a liquid solvent that supports these molecular interactions; and (4) life employs a molecular system capable of Darwinian evolution. These attributes imply the following basic universal functions: (1) life harvests energy from its environment and converts it to forms of chemical energy that directly sustain its other functions, and thus, life requires useable sources of energy; (2) life sustains "metabolism," namely a network of chemical reactions that synthesize all of the key chemical compounds that are required for maintenance, growth, and self-replication, and, thus, life needs chemical "building blocks" and an appropriate solvent to host these reactions; and (3) life sustains an "automaton," a multi-component system that is essential for self-replication and self-perpetuation (Von Neumann, 1966), and, thus, life needs information-rich chemical compounds and favorable environmental conditions in order to sustain this complex machinery.

The above thoughts might be just a starting point in our pursuit of a universal concept of life. Clearly we must identify and pursue a path that leads from our Earth-centric thoughts ultimately to a concept that is truly universal.

Key Research Questions for Defining Life

> **Can we agree on a definition of life that is sufficiently broad to include all known living systems and exclude non-living systems?**
>
> **How do we evaluate systems in the "grey area" between living and non-living, such as viruses?**
>
> **How do we envision life in a way that takes into account living systems we have yet to discover?**
>
> **How do we apply our concepts of life to the development of measurements and experiments to conduct on other worlds?**
>
> **What characteristics of a planet are essential for a *de novo* origin of life and for life to diversify and increase complexity? Is a rocky planet with water and plate tectonics necessary for a *de novo* origin of life?**

II. How Will We Know When We Have Found Life?

This is an absolutely critical question for astrobiology, but it is fraught with difficulty. As addressed in more detail in other chapters, the standards that the community traditionally uses to determine if a feature is evidence for life are based on observations of life on modern Earth. The indicators we have used to know when we have found evidence of past life include: fossils created in the rock record that preserve the physical forms of individual organisms or communities of microorganisms; the molecular constituents of life, i.e., specific organic compounds, or a suite of such molecules; the by-products of biological processes, in particular the waste products of the reactions life uses to obtain energy; and the effects life has on the isotopic composition of its environment. However, some of these features might be specific to biological properties or processes of modern Earth-based life.

Additionally, there is the daunting challenge of ruling out false positives for life. Even if we have a well-defined signal for life, we must also rule out the ways in which non-biological processes could mimic that signal. This challenge has been demonstrated in past biosignature searches. Abiotic mechanisms have been proposed to explain data that had previously been used to claim the presence of life on the surface of Mars, in martian meteorites collected from the surface of Earth, and in Earth's most ancient rocks. This history has sent the astrobiology community two clear messages: (1) context is key, and (2) multiple signals of life are preferred. We must understand the chemical and physical context of any single biosignature to estimate the probability that non-biological processes could have created it. Further, we should always attempt to increase the fidelity of our conclusions by detecting multiple, unrelated signatures from biota.

Key Research Questions for Knowing When We Have Found Life

How do we develop and utilize biosignatures—signs of life—on other worlds?

- How do these biosignatures map onto our concepts of life?
- How to we measure these biosignatures, and what instruments are required to make the measurements?
- What is the size of the signal we might expect, as a function of different life forms or of life forms within the context of different environments?

How can we rule out non-biological processes as a source of a purported biosignature?

- What are the non-biological processes that can mimic a particular biosignature? Do these processes carry their own signals or contextual constraints?
- What specific measurements are needed to eliminate these non-biological processes?
- How can we increase the fidelity of a biosignature?

If life is about information in all its many expressions from molecular, to cellular, to organismal and societal, we need biosignatures and ways of looking for all of these forms.

III. Can We Draw the Boundary Between Prebiotic Chemistry and Life?

A working concept of life affects not only our criteria for identifying life beyond Earth but also our research on the origins and early evolution of life on Earth. This is in part a by-product of the different approaches taken to the origins of life, which either can attempt to create the molecular constituents and chemical networks observed in biological systems or back out the properties of early organisms by attempting to “rewind the tape” of life. These so-called bottom-up and top-down approaches leave a gap between them, which includes the transition between non-living and living systems (Goodwin and Lynn, 2014). This is further complicated by the possibility that the transition may not even be a single moment, or event, but rather a gradual shift in organization and complexity. Finally, life might have begun more than once on Earth or arose in multiple locations.

Key Research Questions for the Possible Boundary between Prebiotic Chemistry and Life

How do we explore the fertile area where the “top-down” and bottom-up” approaches meet, namely a “golden spike” where the processes of life take form (Goodwin and Lynn, 2014)?

Was there only a single origin of life, or did multiple events occur where life arose from chemical systems?

Was the origin of life an “event”? Or was it more of a gradual transition of a chemical system that increased in complexity, organization, and the tendency to reproduce and evolve?

What forms of and support for interdisciplinary research at the boundaries of prebiotic, inanimate chemistries and living matter will guide our search for and identification of life or its precursors’ chemistries elsewhere in the universe?

IV. How Can We Account for “Weird Life” That May Have Alternative Biochemistry or Alternative Habitability Constraints?

Astrobiology has involved exhaustive study of past and present life on Earth, providing lessons that can be extrapolated to environments on other worlds. This helps focus the community on the environments most likely to harbor Earth-like life and will translate into spaceflight exploration strategies such as “follow the water.” It is also at the heart of how we plan to search those environments for signs of Earth-like life; for example, by looking for the chemistry based on organic carbon.

Conceivably, some of our most fundamental concepts of life might still be too Earth-centric to capture the full diversity of life elsewhere. An alien biochemistry might not have the same chemistry exhibited in Earth-based life; for example, it might not have molecular backbones composed primarily of reduced carbon atoms. Solvents other than water might be capable of supporting an alien biochemistry. Some of the specific features we look for, such as the by-products of life's energy-obtaining strategies, may be different elsewhere. Any of these possibilities could expand the diversity of environments and planets on which life could exist and, therefore, modify the array of techniques we would utilize to search for life on those worlds.

Our understanding of what is possible will need to be continually refined in response to both laboratory and field investigations. Past discoveries of life in what were previously "extreme" environments have expanded our definitions of habitability, and similar shifts in our expectations may be expected in the future. Further, progress in the research of "synthetic life" could also expand the set of known conditions for life. This work could include the insertion of novel bases into bacterial chromosomes that code for amino acids other than the conical 20+1 amino acids. It is also possible that this research can produce organisms that could live under different environmental conditions not found on Earth, and perhaps organisms that utilize use novel energy sources other than light and chemicals. The existence of such organisms—even if they were created by human experiments—would have implications for the possibilities for life elsewhere.

The hypothesis that carbon commonly plays prominent roles in the chemistry of life in the Universe remains quite strong, principally because of its seemingly unique capacity to form stable, complex, chemically-reactive molecules that are essential components of a molecular automaton (Des Marais, 2013). Water meets all of the key requirements of an excellent solvent for life as we now understand it (Pohorille, 2012). A few alternative solvents have been identified that also might meet many of these requirements; however, none of these could approach the sheer abundance and broad distribution of water in the known Universe. Thus, even if alternative solvents support exotic examples of life in some cosmic niches, water might still be the solvent of choice for the vast majority of extraterrestrial life. Therefore, the search for life based on carbon chemistries and water as a solvent should play a major role in near-term exploration strategies.

Accordingly, those who propose to search for "weird life" must start by developing viable working models of such life. These models will be essential for developing strategies to investigate the origins and distribution of any "weird life" in the Universe.

Key Research Questions for Potential "Weird Life"

How do we expand and elaborate the nascent search underway to catalog and characterize more fully the diversity of biochemistries that exist on Earth?

How do we improve our appreciation for and understanding of complexities rooted in extant biochemistries, building from simplifying and reductionist concepts and

research, and then leverage that understanding toward the search for alternative biochemistries?

Can alternative biochemistries exist, such that we need broader or separate tests to search for life that might utilize them?

- What are the properties of Earth-based biochemistry that are absolutely essential to life of any kind?
- Of the properties that are essential, are there alternative biochemistry networks that also have those properties?
- In what environments are these alternative biochemistries relevant? Do they require a liquid water or another solvent?
- What are the by-products of those alternative chemistries that we could search for in order to identify them?

Is it possible for life to exist in solvents other than water?

- Under what physical and chemical conditions are these solvents stable, and are there specific environments that have these conditions?
- What are the signatures of these potentially habitable environments?
- What are the implications of the biochemistries that might exist in those solvents?

Do we actually know the limits of carbon-based life that might persist outside the bounds of habitable Earth environments?

V. How Should Astrobiology Approach Perturbations to Planetary Biospheres by Technological Civilizations on Earth and Elsewhere in the Universe?

Astrobiology concerns itself with the interaction between living systems and planetary environments, and with the future of life. It is clear that Earth – the one example we have of an inhabited planet – is currently being severely perturbed by forces that are neither geological nor strictly biological but are the result of the actions of human industrial civilization.

This has led to the proposal, currently under review by the stratigraphy community, of formally naming the current geological epoch as the “Anthropocene.” It is important for astrobiology to understand how our planet is being perturbed now by human technology, since we use Earth as a baseline in so many ways for comparative planetology. When we project the future of Earth’s environment on different timescales, we cannot ignore the growing, dominant influence of human civilization. On the timescale of decades to centuries, Earth’s climate, atmospheric composition, ocean pH, ice coverage and land use are changing rapidly. On the timescale of millennia, there is the possibility that the natural cycles (Milanković cycles) will bring changes to atmospheric composition. Over much longer timescales, when we model the future habitability of Earth and chart the eventual runaway greenhouse destruction of Earth's biosphere, we should also consider whether this process might ultimately be either hastened or delayed/prevented by the actions of reckless or wise civilizations. Members of our community may also feel obligated to spread knowledge of emerging threats to future habitability or to the "comfort range" for human civilization. This raises challenging issues that the Earth Science community has had to confront—of ethics and the boundary between science communication and activism.

Additionally, there is the question of technological civilizations elsewhere. Complex life may evolve into cognitive systems that can employ technology in ways that may be observable. Nobody knows the probability, but we know that it is not zero. As we consider the environments and biospheres of other planets, this is among the type of developments we could anticipate. While traditional Search for Extraterrestrial Intelligence (SETI) is not part of astrobiology, and is currently well-funded by private sources, it is reasonable for astrobiology to maintain strong ties to the SETI community. There are also other ways not included in contemporary SETI that astrobiology can contribute to the search for technological life. Chief among these is the search for "technosignatures". As we explore the exoplanets and search for biosignatures, we should also be aware of the possibility that technological life could also perturb atmospheric composition, or other planetary qualities, in observable ways. Rather than argue for or against the likelihood of finding such a signature, or attempt to describe specifically what such a signature would look like, we should be sure to include it as a possible kind of interpretation we should consider as we begin to get data on the exoplanets.

Key Research Questions for Astrobiology's Approach to Perturbations to Planetary Biospheres by Technological Civilization

How are humanity's current actions affecting the long-term climate of the planet? How does this impact our thinking of planetary habitability?

How does our understanding of the long-term co-evolution of Earth's climate and biosphere give context and understanding to modern changes to Earth's climate?

How might civilizations affect their planets – intentionally or unintentionally – in ways that could be detectable by space-based telescopes that plan to search for signs of life and habitability on exoplanets?

VI. How Does Astrobiology Relate to Other Fields, and How Does It Operate in the Context of Those Other Efforts?

One of the greatest challenges — and greatest opportunities — faced by the astrobiology community is the need for collaborative, interdisciplinary research. The challenge comes in the form of different technical standards and terminology, different sets of expectations for behavior, and sometimes conflicting stakeholder interests. It is notable that these types of challenges are common to all interdisciplinary research. Research that mixes traditional disciplines often viewed as failing to adhere to the standards of those disciplines by their practitioners. This tendency requires at least a subset of the astrobiology community to be intentional in its approach to overcoming these barriers when input is required from multiple disciplines. Key by-products of this type of boundary-blurring are scientists and a community whose skills transfer to other settings. For example, the community's demand for cross-disciplinary communication skills has caused it to discover and nurture strong science communication skills. Similarly, the challenges in forging and strengthening our interdisciplinary collaborations can transfer to other similar endeavors in related fields. Astrobiology, because it seeks to scientifically address deep questions that are at the heart of the quest for human self-understanding, also presents opportunities and challenges for collaboration with scholars from fields within the humanities. There is growing interest in developing these interdisciplinary studies within the "astrobiological humanities."

Key Research Questions for Astrobiology's Relationship with Other Fields

What role does planetary protection play in astrobiology?

- How do we mitigate the bias in our search for life on other worlds that would be introduced if we – either accidentally or through human exploration – brought Earth-based life with us to other planets?
- If astrobiological research requires samples to be returned to Earth from potentially habitable environments, how do we protect Earth life from competition or invasion from alien organisms?

What is the relationship between astrobiology and human spaceflight?

- How does astrobiology research help motivate human spaceflight?
- How does human spaceflight enable future astrobiological investigations?

What is the relationship between astrobiology and planetary science?

- How can we leverage the exploration of these other worlds to better inform our understanding of planetary processes that affect life?

- How can we leverage the astrobiology community to motivate and improve science investigations of these other worlds?
- How can astrobiology's commitment to planetary stewardship be reconciled with human exploration of Mars?

What is the relationship between astrobiology and Earth systems science research?

- How can we leverage state-of-the-art Earth systems models to inform questions about the habitability of other worlds and detectability of their biosignatures?
- How can our simulations of other worlds help validate the "tuning" of Earth-based climate models?
- How can we leverage lessons from deep Earth time to give us differing examples of how planetary climate systems might act?

What is the relationship between astrobiology and heliophysics?

- How can we improve our detailed understanding of the Sun-Earth system to better understand how other planets have to "live with another star."
- How can we leverage current and future observations of other planetary systems to improve our understanding of the history of the Sun-planet interactions in our home system?

What is the relationship between astrobiology and astrophysics?

- How can we leverage the experience astrobiologists have at looking for habitable environments and developing biosignatures for future observations of extrasolar planets?
- How have observations of exoplanets expanded our expectations for planetary processes, and how can we maximize our future observations to place our own system in a more complete context?

More broadly, how do we overcome issues that arise in interactions among disciplines?

- How do we deal with the different standards in different disciplines, for publication of data, for professional development, and for interactions between colleagues?

7.2 CONFRONTING THESE CHALLENGES CREATES ADDITIONAL BENEFITS

If we overcome the challenges presented above, the impacts will be profound. Most directly, this will improve our research products on the origins, evolution, and future of life on Earth and on the search for habitable and inhabited environments beyond our home planet. Additionally, the individuals that lead us past these obstacles will take on other challenges in other disciplines, and as they do will bring with them the successful strategies they develop for communicating across disciplinary boundaries and at the forefront of knowledge of humanity's place in the cosmos. This can place astrobiologists at the forefront of a growing trend in the sciences—to produce advances by collaborating across disciplines and by incorporating the knowledge and skillsets of diverse communities.

FURTHER READING

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APPENDICES

Beyond Natural Sciences: Humanities and Social Science Contributions to Astrobiology

Lucas Mix and Connie Burtka

Introduction

Astrobiology addresses questions about the past, future, extent, and interconnection of living things in the universe. The breadth of the astrobiology endeavor makes it both popular and unwieldy as astrobiologists explore questions that incorporate data from a wide variety of scientific fields. The expansive nature of these questions also results in their intersection with questions about life that arise in other fields. Answers to these questions have implications for a broad range of stakeholders. Awareness of the dynamics between natural sciences and related fields will prove critical to the generation, integration, and dissemination of scientific understanding.

The results of astrobiology research will have broad societal impact, affecting the way we think about life in the context of ethics, law, philosophy, theology, and a host of other issues. Our place in the universe, as a species and as a planet, speaks to our fundamental understanding of ourselves. There was not space in this format to comprehensively address the breadth of research possible or currently available on these topics. We felt it important, however to comment briefly on the range of humanities and social sciences that contribute to the central goals of astrobiology. The following list sketches out some of the issues that arose in discussions around the strategy process.

While the primary focus of astrobiology lies within the natural sciences, a number of questions from other disciplines have proved essential to creating a common framework for understanding life in the universe. In particular, philosophical and sociological questions inform the way we collaborate and integrate data. Definitions of “life,” “function,” and “evidence,” for example, shape our research. Best practices in collaboration shape our research teams. Meanwhile, issues related to astrobiology in ethics, history, law, communications, and education impact our ability to share discoveries so that they can inform decision-making and inspire future research. Resources are already available that could be of use to investigators. Further research along the following lines could aid and be aided by the science objectives of astrobiology.

A. What Is the Role for Epistemology in Astrobiology?

Astrobiologists address many issues at the edges of current disciplines, even at the edges of science, as we know it. Questions of how we generate knowledge and reach consensus inform how we collaborate and design experiments. Interdisciplinary teams will be most productive when thought has been given to how integration of data from multiple labs will occur. Missions will be most informative when interpretation of outcomes is considered during the design phase.

What are the comparative standards of evidence in astrobiology-related fields?

- Should there be a common standard in astrobiology?
- What can we learn from Viking labeled release experiment and other cases of epistemological goalpost shifting?

Is a definition of life necessary to the pursuit of astrobiology?

- What are the hallmarks of a successful definition of life?
- Are there meaningful distinctions to be made between synthetic life, engineered life (including GMOs), “artificial life,” and “natural life”?

B. What Is the Role for Social Science in Astrobiology?

Astrobiology receives public and governmental support in part due to common enthusiasm for the exploration of life and space. This leads to unique opportunities for scientific education and outreach, but also calls for critical assessment of whether and in what ways astrobiologists answer the questions the public is asking. In addressing these questions, astrobiology attempts to integrate knowledge from diverse areas both inside and outside the natural sciences. Social science can help monitor and optimize that integration.

Who is doing astrobiology and what professional and personal motivations encourage their work?

- What level of inter-field collaboration have astrobiologists achieved, and has there been progress since NAI was founded?

What is the range of interest in and attitudes toward astrobiology?

- Why and to what end is the public interested?
- What is the range of interest in and attitudes toward astrobiology by scientists not personally engaged with the subject?

- What is the range of interest in and attitudes toward astrobiology by scholars in the humanities?

What tools are available to assess and facilitate research collaborations?

- What technologies and interfaces provide the best environment for innovation and communication?
- What organizational structures are most useful for astrobiology research, collaboration, and education?

C. What Is the Role for Ethics in Astrobiology?

Interest in the history, character, and extent of life is intimately tied to questions of value. Astrobiological questions impact public thinking about our ethical obligations toward living entities. Legal and ethical limitations on experiments, particularly those traveling to other planets, shape the science we do.

What role do definitions of life play in ethical typologies?

- What role do definitions of life play in cultural and religious cosmologies?
- What resources are available within various cultural and religious traditions for the incorporation of non-Terran life into worldviews?
- To what extent is human exceptionalism and/or Terran exceptionalism necessary or desirable?

Do humans have non-Terran ethical obligations?

- Can they be agreed upon in a socially plural fashion?

Does Astrobiology have implications for Terran environmental ethics?

D. What Is the Role for History in Astrobiology?

Interest in the distribution of life in the universe has been a popular topic for scientists and philosophers throughout recorded history. Records of speculation and reasoning about non-Terran life extend back at least to the time of Democritus in the 5th century BCE. We also have excellent records for the rise of exobiology and astrobiology over the last century. Historical awareness, over short and long time-scales, can provide perspective into how we frame questions and reach conclusions. Specific historical knowledge of astrobiology can tell us which questions our current theories were designed to answer as well suggest new avenues of research.

Who has speculated on non-Terran life historically? What methods have they used and what theories have they proposed?

What theories and perspectives have been considered historically? Why were they accepted or excluded from future research?

How have technologies shaped our expanding knowledge of life in the cosmos?

E. What Is the Role for Law in Astrobiology?

Astrobiology research takes place in an environment of diverse and evolving laws regarding both exploration and technology. Laws regarding space and biotechnology, in particular, are rapidly changing. Astrobiologists should be informed about the relevant laws and treaties, while lawyers and policy makers should be informed about the current state of the art and potential developments in astrobiology.

What are the costs and benefits associated with compliance measures for the Outer Space Treaty and Planetary Protection Protocols?

- How do they shape the types of research that can be done?
- How effective are they in preserving environments for astrobiological research

How do discoveries in astrobiology impact the formation and implementation of laws?

- How did scientific understanding in the 20th century shape the formation of space law?
- How is current scientific understanding integrated into policy decisions, particularly implementation of the Outer Space Treaty and associated policies (i.e., forward and backward contamination protocols)?
- How would strong evidence of non-Terran life and/or intelligence change the legal framework in which astrobiologists operate?

Have astrobiology issues had an impact on other areas of law?

How can NASA's relationship to government, education, and industry be leveraged to create dialogue among stakeholders around issues of law, policy, and compliance with regard to space law, both nationally and internationally?

F. What is the Role for Communications in Astrobiology?

Throughout the strategy process, a number of terms came up that highlighted challenges for communication. In some cases the words have different meanings for different fields or sub-fields. In other cases, they came with semantic baggage from outside the natural sciences.

What are the best ways to communicate time points in the development of life on Earth while remaining open to alternative theories? How do these terms represent or misrepresent consensus: origin of life, proto-cell, pre-biological, RNA world, LUCA, … ?

What are the best ways to communicate when a single word has entrenched meaning in multiple fields (for example, stellar, chemical, or Darwinian "evolution")?

What are the best ways to communicate about emerging technical terms, which do not yet have a consensus definition in the field (for example, habitable, biosignature, and complexity)?

G. What Is the Role for Astrobiology in Education?

Excitement about astrobiology opens opportunities for engaging younger students in science, technology, engineering, and mathematics. It also opens pathways for upper-level students to practice shaping complex questions in answerable ways and integrating data from across fields.

Is there a role for astrobiology in K-12 education?

Is there a role for astrobiology in general college education?

How do we foster astrobiology-related thinking/research at the graduate student level?

- Is there benefit to having astrobiology specific graduate programs?

Things to Work on in the Coming Ten Years

Over the last 15 years, astrobiology has developed into a radically interdisciplinary community with common standards, common journals, and a clearer sense of common questions. Concrete progress toward scientific objectives over the next decade will be aided by critical and comparative assessment of research and exploration programs, with an eye toward what does and does not work when collaborating across fields. Which projects have produced significant contributions to our knowledge and why were they successful? Which philosophical and communications barriers have been successfully overcome, both inside and outside the scientific community, and which still represent challenges? Further, as astrobiology continues to play an ever-larger role in the broader scientific, academic, and public discussion, it will be important to regularly assess the impact of that discussion on the science and the import of the science for the discussion. Encouragement of independent work in the humanities and social sciences on these topics will aid astrobiology immensely. Opportunities for junior and senior scientists to engage with that work will also be important.

Further Reading

The literature on these subjects, even when narrowed to astrobiological interests are too extensive to list; however, we can recommend a few documents that will provide an entry into the literature.

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Glossary

A

AAAS: American Association for the Advancement of Science

Abiotic: refers to the absence of life.

Chapters 1, 2, 3, 4, 5

Ablation: the removal of material from the surface of an object by vaporization, chipping, or other erosive processes.

Chapter 1

Accretion: the growth of a massive object by gravitationally attracting more matter, typically gaseous matter in an accretion disk. The model for Earth's formation posits that clumps of minerals and gas and dust came together by gravitational attraction as they swirled around the young Sun. This "accretion" process caused the planet to gradually grow larger and larger.

Chapters 1, 4, 6, 5

Adenosine triphosphate (ATP): coenzyme used as an energy carrier in the cells of all known organisms.

Chapters 2, 3, 5

Akilia meta-sedimentary rocks: Akilia is an island in southwestern Greenland that has a rock formation proposed to contain the oldest known sedimentary rocks on Earth (>3.85 Ga), and perhaps the oldest evidence of life on Earth.

Chapter 3

Albedo: a measure of how much light a surface reflects.

Chapter 4

Aldol reaction: when the enolate of an aldehyde or a ketone reacts at the α-carbon with the carbonyl of another molecule under basic or acidic conditions to obtain β-hydroxy aldehyde or ketone. "Aldol" is an abbreviation of aldehyde and alcohol.

Chapter 2

Allometric scaling: Allometry is how characteristics of living creatures change with size. The term originally referred to the scaling relationship between the size of a body part and the size of the body as a whole, as both grow during development. However, the meaning of the term has been modified and expanded to refer to biological-scaling relationships in general. This includes morphological traits (e.g., the relationship between brain size and body size among adult humans), physiological traits (e.g., the relationship between metabolic rate and body size among mammal species), and ecological traits (e.g., the relationship between wing size and flight performance in birds).

Chapter 5

ALMA: Atacama Large Millimeter Array

Amide bond (or peptide bond)**:** a covalent bond between two molecules when the carboxyl group of one molecule reacts with the amino group of the other molecule, causing the release of a molecule of water (H_2O); hence, the process is a dehydration synthesis reaction (or condensation reaction). The bonds that connect amino acids within a protein are amide bonds (or peptide bonds).

Chapter 1

Anammox: an abbreviation for anaerobic ammonium oxidation, it is a microbial metabolism in which nitrite and ammonium are directly converted to dinitrogen (N_2) gas.

Chapter 4

Animals: multi-celled eukaryotes (i.e., the nucleus in their cells is enclosed in a membrane). Generally they are mobile and heterotrophic, meaning they must obtain organic molecules from the environment rather than create it from inorganic molecules (like autotrophic plants do).

Chapter 4

Annotation: part of genome analysis in which gene sequences are identified by their particular biological functions.

Chapter 4

Anthropogenic changes: changes that originate through human activity (chiefly relating to environmental pollution and pollutants).

Chapter 4

Archaea: single-celled organisms that have traits of both bacteria and eukaryotes.

Chapters 2, 4

Archaean era: era that lasted from 4 billion to 2.5 billion years ago.

Chapter 1

Astronomical forcing: describes how changes in Earth′s orbit—its eccentricity, axial tilt, and precession—affect climatic patterns. (See also: Milanković cycles.)

Chapter 3

ATP: adenosine triphosphate

Authigenic: a mineral or sedimentary rock deposit that was generated in the location where it is found.

Chapter 4

Autocatalytic reaction: when the reaction product is the same as the catalyst for that reaction.

Chapter 2

Autotroph: an organism that ″fixes″ carbon, forming covalent bonds between inorganic molecules to form organic molecules. Plants and algae are photosynthetic autotrophs (or photoautotrophs), using sunlight as an energy source to drive the process.

Chapter 3

B

Bacteriorhodopsin: a protein used by Archaea. It captures light energy and uses it to move protons across the membrane out of the cell.

Chapter 3

Ballast: material that is used to provide stability to a structure.

Chapter 4

Banded iron formations: alternating layers of iron-poor rock and iron-rich rock. The rock containing iron is often red in color due to oxidation.

Chapter 4

Benthic: the ecological region at the lowest level of a body of water, including the sediment surface and some subsurface layers.

Chapter 4

Biofilms: a group of microorganisms in which cells stick to each other on a surface. These adherent cells are frequently embedded within a self-produced matrix of extracellular polymeric substance (EPS), which can also trap and bind sediments.

Chapter 5

Biogenic: something that is produced or brought about by living organisms.

Chapter 5

Biological communities: groups of organisms whose composition and characteristics are determined by the environments they inhabit and the relation of the organisms to each other.

Chapter 4

Biomarker: a substance that indicates the existence of a living organism, either currently living or long deceased.

Chapters 4, 5, 5

Biomes: contiguous areas with similar climatic conditions, defined by the communities of plants, animals, and soil organisms that inhabit them. They are often referred to as “ecosystems.”

Chapter 4

Biopolymers: a polymer (see below) that is produced by living organisms.

Chapter 3

Biosignature: a detectable sign of life. This could include a molecule that would persist only thanks to the influence of life or a phenomenon that would occur only if life were present.

Chapters 1, 3, 4, 5, 6

Blanks: Scientific controls act as comparison standards for an experiment. A “blank” does not contain any of the substance being tested, whereas other controls may contain a known amount of the substance.

Chapter 5

Bolide: either a large comet or asteroid that impacts the Earth.
Chapter 3

Brønsted acid: acid that donates a proton to a base, creating a reaction. (Related: Lewis acid.)
Chapter 2

Brown dwarfs: stellar objects that are too low in mass to sustain hydrogen fusion in their cores.
Chapter 6

C

Cambrian explosion: based on the fossil record, a huge array of diverse animal lifeforms appeared over a relatively short time period approximately 540 million years ago. When this was discovered, scientists labeled this sudden diversity the Cambrian explosion. We now know that animals had evolved before this time, so one explanation could be that they developed hard parts for the first time, leading to better preservation of fossils.
Chapter 3

Capillary electrophoresis: an analytical technique that separates ions based on their electrophoretic mobility with the use of an applied voltage.
Chapter 5

Carbonaceous chondrites: the most primitive types of meteorites. In addition to carbon, silicates, oxides, and sulfides, most contain water or minerals that have been altered in the presence of water and some contain organic compounds.
Chapters 1, 6

Carotenoids: organic pigments found in plants as well as in some photosynthetic bacteria and fungi.
Chapter 5

Catabolism: the set of metabolic pathways that breaks down molecules into smaller units to release energy.
Chapters 1, 4

Catalysis: to cause or accelerate; to drive forward. Catalysis is the increase in the rate of a chemical reaction of one or more reactants due to the participation of an additional substance called a catalyst.
Chapters 2, 6, 4

Catalyst: substance that increases the rate of a chemical reaction of one or more reactants. Catalysts are not altered in the reaction they accelerate.
Chapter 1

Chemical differentiation: as a planet cools from its molten state at formation, different elements sink or rise depending on their density, leading to distinct planetary layers. However, the chemical differentiation of the planet is not strictly tied to density. Because some elements are bound to other compatible elements, very dense elements can be found in the crust rather than the core, for instance.

Chapter 4

Chemiosmosis: the movement of ions across a semi-permeable membrane from a solution of high concentration to one of low concentration; more specifically, it refers to the movement of protons used to generate ATP (adenosine triphosphate) in cellular respiration.

Chapter 3

Chemoautotrophs: organisms that derive energy from chemical reactions of inorganic molecules in their environments. Most are bacteria or archaea that live in hostile environments such as deep sea vents.

Chapter 3

Chemolithotrophs: organisms that obtain their energy from chemical reactions—such as the oxidation of reduced inorganic compounds like sulfide, ammonia, and hydrogen—and use carbon dioxide as a carbon source. They are also known as chemoautotrophs.

Chapter 6

Chiral: a type of molecule that has a non-superposable mirror image, like right and left hands.

Chapters 3, 5

Chloroplasts: structures in plant and algal cells that conduct photosynthesis.

Chapter 3

CHNOPS: the most common elements for life: carbon, hydrogen, nitrogen, oxygen, phosphorus, and sulfur.

Chapter 6

Chromatography: the collective term for a set of laboratory techniques for the separation of mixtures.

Chapter 5

Clade: a group consisting of an ancestor and all its descendants, a "branch" on the "Tree of Life." The ancestor may be an individual, a population, or even a species.

Chapter 3

Cloning: the process of making genetically identical copies of DNA, cells, or entire organisms.

Chapter 4

Coalescence: the point of origin where all branches on the tree of life come together into a single common ancestor

Chapter 3

Codon: a sequence of three DNA or RNA nucleotides that corresponds with a specific amino acid or stop signal during protein synthesis.

Chapter 2

Cofactor: a non-protein chemical compound needed for a protein's biological activity. Cofactors are "helper molecules" for proteins (commonly enzymes), assisting in biochemical transformations.

Chapters 1, 2, 4

Complex living systems: refers to a system with more parts, and more interactions among parts, than a less complex system.

Chapter 3

Concretion: a compact mass within sedimentary rock, usually round or oval in shape, and usually formed from the same material as the rock plus the cementing mineral. Microbial activity can often be the trigger for the mineral cements, and such concretions can have fossils in the middle.

Chapter 5

Condensation: a chemical reaction where molecules are joined together to form larger, more complex molecules, usually through the elimination of a simple molecule (usually water).

Chapters 1, 2

Confound: In statistics, a confound (or confounding variable) is an extraneous variable that correlates (directly or inversely) with both the dependent and independent variable.

Chapter 3

Controls: Scientific controls act as comparison standards for an experiment. A ″blank″ does not contain any of the substance you are testing for, whereas other controls may contain a known amount of the substance.

Chapter 5

Convection: the motion of a fluid (such as water or air) caused by heating, where the fluid carries energy with it as it moves away from the heat source.

Chapter 6

Convergent: process whereby organisms not closely related, independently evolve similar traits as a result of having to adapt to similar environments.

Chapter 3

Co-solvent: a second solvent added to an original solvent, creating a mixture that has a greater ability to dissolve other substances.

Chapter 1

Covalent bond: involves the sharing of electrons between atoms, creating a stable balance of attractive and repulsive forces.

Chapters 1, 2, 5, 6

Cryovolcano: colloquially known as an ice volcano, a cryovolcano erupts volatiles such as water, ammonia, or methane instead of molten rock.

Chapter 5

Cyclic alkanes: hydrocarbon compounds.

Chapter 5

Cytoplasmic homeostasis: the mechanisms and properties by which the cytoplasmic environment of a cell is regulated to maintain stable and relatively constant conditions.

Chapter 4

D

Deep sequencing: when the same nucleotide is sequenced multiple times (in which the depth refers to the number of times it has been sequenced).

Chapter 4

Denitrification: a microbially facilitated process of nitrate reduction that may ultimately produce molecular nitrogen (N_2).

Chapter 4

Detritus: particles of rock derived from preexisting rock through processes of weathering and erosion. Uraninites and pyrites readily weather when oxygen is present.

Chapters 3, 4

D/H: the ratio of deuterium (2H) to hydrogen (H) in water.

Chapter 6

Diagenesis: the change of sedimentary rock during and after rock formation at temperatures and pressures less than what is required for the formation of metamorphic rocks but excludes surface alteration (weathering).

Chapter 5

Diesters: a class of organic compounds, corresponding to inorganic salts, that form from an organic acid and an alcohol.

Chapter 2

Disequilibrium: A system in equilibrium has properties that do not change over time. It is thought life on Earth depends on the energy of our planet being in disequilibrium (i.e., experiencing earthquakes, turbulence, heating, etc.)

Chapters 2, 3, 4, 5, 6

DNA: deoxyribonucleic acid

Doubling time: the period of time required for a quantity to double in size or value.

Chapter 4

Drift: refers to random fluctuations in gene variants within a population, which over time can lead to the loss of genes.

Chapter 3

D-sugars, L-amino acids: The L and D prefixes refer to the two types of chiral compositions.

Chapter 5

Dynamo: theory that describes how an interior rotating, convecting, and electrically conducting fluid generates a magnetic field. Earth's dynamo (also called the "geodynamo") is generated by molten iron circulating at Earth's core.

Chapter 6

E

Ecological niche: the space in which an organism or community lives, uses resources, competes with other life forms, and has other behaviors related to the specific aspects of that environment.

Chapter 4

Electrophiles: positively charged species that are attracted to an electron-rich center.

Chapter 2

Enantiomers: molecules that are chiral. A chiral molecule has a non-superposable mirror image, like right and left hands (thus, chiral molecules are often referred to as "handed").

Chapters 1, 5

Encapsulation: when one molecule becomes contained within a larger molecule, such that it is prevented from contacting other molecules it otherwise would react with.

Chapter 2

Endosymbiosis: when one organism lives inside another, each conveying benefits from the cooperative system. The endosymbiotic theory states that several key structures of eukaryotes originated through bacteria or other single-celled organisms being taken inside another cell.

Chapter 3

Enzymatic activity: a measurement of how effectively an enzyme can catalyze a given reaction.

Chapter 3

Enzymes: metabolic catalysts responsible for many life processes, including DNA synthesis and food digestion. Most enzymes are proteins.

Chapters 2, 3, 4

Epistasis: refers to genes at multiple locations whose effects interact, often through one activating, suppressing, or modifying the expression of another.

Chapter 3

Equilibrium: a system whose properties do not change over time. It is thought that life on Earth depends on the energy of our planet being far from equilibrium, i.e., experiencing earthquakes, turbulence, heating, etc.

Chapter 6

Eukaryote: an organism whose cells contain a nucleus and other structures that are enclosed within membranes. Animals, plants, and other complex life forms are eukaryotes.

Chapters 2, 3, 4

Eusociality: defined by the following characteristics: cooperative care of offspring, overlapping generations within a colony of adults, and a division of labor into reproductive and non-reproductive groups. Often observed in insects (ants, wasps, bees), eusociality is distinguished from all other social systems because individuals of at least one group lose the ability to perform at least one behavior characteristic of individuals in another group.

Chapter 3

Eutectic: a mixture of chemical compounds or elements that have a single chemical composition that solidifies at a lower temperature than any other composition made up of the same ingredients.

Chapter 2

Evolutionary landscape: a construct to think about and visualize how evolution has affected different aspects of life (including genes, species, populations, etc.)

Chapter 3

Exaptation: a shift in the function of a trait during evolution. For instance, a trait that evolved because it served one particular function subsequently comes to serve another function.

Chapter 2

Exoplanet light curve: When exoplanets pass in front of the star they orbit (as seen from Earth), they block a portion of the starlight. Telescopes measuring this dip in light over the course of the planet's orbit provide data points for a light curve (where the two variables on the graph are time and total numbers of photons). Fitting models to the light curve, various planetary characteristics can be determined.

Chapter 5

Exoplanets: planets outside our Solar System (i.e., planets that orbit other stars).

Chapters 4, 5, 6

Extremophiles: an organism that thrives in environments considered extreme or detrimental to most life on Earth.

Chapter 5

F

Felsic: igneous rocks enriched in lighter elements (e.g., silicon, oxygen, aluminum, sodium, and potassium) that form feldspar and quartz.

Chapter 1

Flagellum: a lash-like appendage protruding from certain cells. The primary role is locomotion but it also functions as a sense organ, being sensitive to chemicals and temperatures outside the cell.

Chapter 3

FTIR: Fourier transform infrared spectroscopy is an efficient method for processing spectra data obtained using interferometers.

Chapter 5

G

Ga: billion years

GC–MS: Gas chromatography-mass spectrometry combines the features of gas-liquid chromatography and mass spectrometry to identify different substances within a test sample.

Chapter 5

Gene amplification (also known as gene duplication)**:** a process in which multiple copies of a gene are produced. The result is an amplification of the phenotype, or expressed trait, associated with the gene.

Chapter 2

Genome annotation: part of genome analysis in which gene sequences are identified by their particular biological functions.

Chapter 4

Genotype: the complete set of genetic information of an individual.

Chapter 3

Geochemical proxies: elemental, isotopic, and molecular properties of the rock that allow us to fingerprint a particular transient feature or process on Earth's surface in the distant past that cannot be observed directly. These tracers include inherited, well-preserved chemical records of the composition and temperature of the ocean and the gas content of the ancient atmosphere, or evidence for a particular organism or metabolic process (such as oxygen-producing photosynthesis).

Chapter 4

Geochronology: determining the age of rocks, sediments, and fossils by measuring features within these structures, such as radioactive isotopes.

Chapter 6

Gibbs free energy: a measure of the maximum available work that can be derived from any system under conditions of constant temperature and pressure.

Chapter 5

GOE: Great Oxidation Event

Greenhouse: energy from the Sun heats the Earth's surface, and some of that energy reflects back into space. However, atmospheric gases such as water vapor and carbon dioxide can act like the glass roof of a greenhouse, trapping the outgoing energy and causing the climate to be warmer than it would be otherwise.

Chapters 3, 4, 6

H

Habitability: potential for an environment to support life, be it on planet-wide or microscopic scales.

Chapter 5

Habitable niche: the space in which an organism or community lives, uses resources, competes with other life forms, and has other behaviors related to the specific aspects of that environment.

Chapter 6

Habitable zone: traditionally defined as the orbital region around a star where water can exist as a liquid on an object's surface.

Chapters 3, 5, 6

Hadean: the first geologic eon on Earth, lasting from the planet's formation 4.540 billion years ago to 4 billion years ago.

Chapter 1

Halophiles: organisms that thrive in salty environments.

Chapter 5

Handedness: refers to molecular chirality; a chiral molecule has a non-superposable mirror image, like right and left hands. A chiral object and its mirror image are called enantiomorphs or, when referring to molecules, enantiomers.

Chapter 1

Heterogeneous: when a structure is diverse in character and content.

Chapters 2, 5, 6

Heterotrophs: organisms that cannot synthesize their own food and rely on other organisms for nutrition (versus autotrophs that can produce food from their surroundings via photosynthesis (light) or chemosynthesis (chemicals).

Chapter 3

HGT: horizontal gene transfer

Homochirality: A substance is homochiral if all the constituent units are molecules of the same chiral form (enantiomer). A chiral molecule has a non-superposable mirror image, like right and left hands.

Chapters 1, 2, 5

Homology: the existence of shared ancestry between a pair of structures, or genes, in different species.

Chapter 4

Hopanoids: compounds found in bacteria and other primitive organisms (but not in archaea).

Chapter 5

Horizontal gene transfer (also known as lateral gene transfer)**:** refers to the transfer of genes between organisms in a manner other than traditional reproduction. It contrasts with vertical transfer, the transmission of genes from the parental generation to offspring via sexual or asexual reproduction.

Chapters 3, 6

Hydrolysis: the cleavage of chemical bonds by the addition of water.

Chapters 1, 2

Hydrophobic molecules: non-polar molecules that cluster together in solution and do not interact with water molecules. The mixing of oil and water is the classic example of a hydrophobic interaction.

Chapter 2

Hydrosphere: all the water on a planet—on the surface, in the air, and underground.

Chapters 1, 4, 6

Hydrothermal: refers to the activity of heated water in a rocky planet's crust.

Chapters 1, 3, 4, 5, 6

Hypercycle: a new level of organization whereby self-replicative units are connected in a cyclic, autocatalytic manner.

Chapter 2

I

Icehouse: another name for Ice Age, it is a period when Earth is broadly covered by sheets of ice and temperatures are low.

Chapter 6

Immunoassay: a test that measures the presence or concentration of a macromolecule in a solution through the use of an antibody or immunoglobulin.

Chapter 5

In silico: studies performed as part of a computer simulation.

Chapter 4

In situ: Latin for "in place." In biology, it means examining a phenomenon exactly where it occurs without moving it to another medium.

Chapters 4, 5, 6

Interferometer: many telescopes or mirrors linked together. The greater area of the linked telescopes provides a higher resolution of astronomical targets than what a single telescope can observe.

Chapter 1

In vitro: Studies that are done in a laboratory environment using test tubes, petri dishes, etc.

Chapter 2

***In vitro* assays:** scientific tests performed in a test tube or other sterile container, rather than in a living organism. The test measures the activity of a drug on a sample of organic tissue.

Chapter 4

In vivo: studies in which the effects of various biological entities are tested on whole, living organisms, as opposed to partial or dead organisms.

Chapters 2, 3

Isomerization: the process by which one molecule is transformed into another molecule through the rearrangement of atoms.

Chapter 2

Isomers: molecules with the same molecular formula but different chemical structures.

Chapter 1

Isoprenoids: lipids found in all living things.

Chapter 5

Isotope: a version of an element with different numbers of neutrons in the atom. This affects the mass of the element. For example, carbon-12, carbon-13 and carbon-14 are three isotopes of the element carbon (with mass numbers 12, 13, and 14.)

Chapters 1, 3, 4, 5, 6

Isotopic fractionation: the enrichment of one isotope—an element that varies in the number of neutrons in the atom—relative to another isotope. This usually occurs with the same element, such as the isotopes Carbon-14, Carbon-13, and Carbon-12.

Chapters 4, 5

K

Kinetics: the rate at which chemical reactions occur as well as the energy required for reactions to proceed.

Chapters 1, 2

L

L and S amino acids: the “L” and “S” refer to the configuration of the amino acid molecule. In the “L” form, the hydroxyl group is on the left side of the molecule. (Amino acids in proteins are all the “L” form.) “S” indicates that the molecular form is arranged counterclockwise.

Chapter 2

Lab-on-a-chip: a device that integrates one or several laboratory functions on a single electronic circuit chip only millimeters to a few square centimeters in size.

Chapter 5

Lamination: thin sedimentary layers, typically one centimeter or thinner.

Chapter 3, 4

L-amino acids, D-sugars: The L and D prefixes refer to the two types of chiral compositions.

Chapter 5

Laser-induced fluorescence: a spectroscopic method used for studying the structure of molecules, detection of selective species, and flow visualization and measurements. The species to be examined is excited with a laser, and then will de-excite and emit light at a wavelength longer than the excitation wavelength.

Chapter 5

Latent heat: a type of energy released or absorbed in the atmosphere. Latent heat is related to changes in phase between liquids, gases, and solids (as opposed to sensible heat, which is related to changes in temperature of a gas or object with no change in phase.)

Chapter 4

Lateral gene transfer: see horizontal gene transfer.

Lewis acid: when this acid reacts with a base, it doesn’t involve the transfer of a proton, but instead accepts a pair of electrons. (Related: Brønsted acid)

Chapter 2

Ligation: the covalent linking of two ends of DNA or RNA molecules, usually with the enzymes DNA ligase or RNA ligase.

Chapter 2

Linear polymer: a polymer where the molecules form long chains, without branches or cross-linked structures.

Chapter 2

Lithosphere: the outermost shell of a rocky planet. On Earth, the lithosphere is the crust and the relatively elastic portion of the upper mantle.

Chapters 1, 6

LUCA: stands for last universal common ancestor.

Chapter 3

M

M-dwarf stars: also known as red dwarfs, M-dwarf stars are smaller, cooler, and less luminous than our Sun.

Chapters 5, 6

Macromolecules: large molecules (polymers) composed of many repeated subunits (monomers). Nucleic acids, proteins, carbohydrates, and lipids are all essential macromolecules of life.

Chapters 2, 3

Macroorganisms: lifeforms large enough to be seen with an unaided eye; i.e., without a microscope.

Chapter 3

Mafic: rocks that are igneous silicate characterized by a more magnesian and ferrous (iron with a +2 oxidation state) composition, with fewer alkali elements.

Chapter 1

Mantle: of a rocky planet, the region between the crust and the outer core. Earth′s mantle is a silicate solid that, over geological time, acts like a viscous liquid.

Chapters 4, 6

Mass-independent isotope fractionation: refers to any chemical or physical process that acts to separate isotopes, where the amount of separation does not scale in proportion with the difference in the masses of the isotopes.

Chapter 4

Mass spectrometry: an analytical technique that produces spectra of the masses of the atoms or molecules comprising a sample of material.

Chapter 5

Mesozoic oceanic anoxic events: episodes of widespread oxygen deficiency in the deep ocean on timescales of hundreds of thousands of years, during the Mesozoic era (252 to 66 million years ago).

Chapter 4

Messenger RNA: see mRNA.

Metabolism: a set of chemical reactions that all life needs to grow, reproduce, maintain structure, and respond to the environment. Metabolic pathways involve one chemical being transformed into another chemical.

Chapters 1, 2, 3, 4, 5, 6

Metabolite: a product necessary for metabolism or a product of metabolism. The term usually refers to small molecules.

Chapter 2

Metagenomics: the study of genetic material recovered directly from environmental samples.

Chapter 4

Metallicity: in astronomy, refers to an object's composition of chemical elements other than hydrogen or helium.

Chapter 1

Metallomics: the comprehensive analysis of metal and metalloid species within a cell or tissue type.

Chapter 4

Metamorphic: rock that has been transformed by heat or pressure.

Chapters 4, 5

Metaphytes: multi-cellular plants.

Chapter 3

Metasedimentary rocks: sedimentary rocks that have been altered by metamorphism.

Chapter 1

Metatranscriptomics: the study of actively expressed genes within a multi-species community over space and time.

Chapter 4

Metazoans: multi-cellular animals.

Chapter 3

Methanogenesis: the formation of methane by microbes.

Chapter 4

Methanotrophy: the process whereby microbial organisms are able to metabolize methane (with and without oxygen) as a source of carbon and energy.

Chapter 4

Micelle: an aggregation of molecules in water that have both polar or charged groups and non-polar regions (amphiphilic molecules).

Chapter 2

Milanković cycles: predictable, periodic variations in Earth′s orbital properties—on timescales of tens to hundreds of thousands of years—linked specifically to the tilt and wobble of Earth′s axis and the shape of Earth′s orbit around the Sun. These parameters impact the flux of solar radiation to Earth′s surface and, thus, climate. (See also: astronomical forcing.)

Chapters 4, 3

Miller–Urey experiment: originally simulated the conditions thought (at the time) to represent the atmosphere of the early Earth and tested for the production of molecules that may have played a role in the origin of life. More than 20 types of amino acids were produced in this experiment. It is also known as a “spark discharge” experiment because the energy for chemical reactions is often provided by the spark between two high-voltage electrodes. The results of this experiment were published in 1953.

Chapters 1, 2

Mineral skeletons: During the Cambrian period (540–485 million years ago), animals first developed skeletons made from minerals such as calcite, magnesian calcite, aragonite, apatite, and opal.

Chapter 4

Mitochondrion: a structure within cells that generates most of the cell's supply of energy in the form of ATP (adenosine triphosphate). In addition, mitochondria are involved in cellular signaling, differentiation, control, growth, and death.

Chapter 3

Mixing ratio: the amount of one component of a mixture, relative to the total amount of all other components. For example, the mass of water vapor to the mass of dry air.

Chapter 1

Modularity: a property of system architecture in which complex structures or functions are divided into simpler and weakly linked components. Modularity has been observed in all model systems and can be studied at nearly every scale of organization (molecular interactions up to the whole organism).

Chapter 3

Moiety: a well-defined part of a larger molecule.

Chapter 2

Moist greenhouse: a hot climate that is caused by an abundance of water vapor in the atmosphere of a planet.

Chapter 4

Molecular clouds: Sometimes called stellar nurseries because they are where stars are born, molecular clouds are collections of gas that are dense enough to permit the formation of molecules (most typically hydrogen [H_2]).

Chapters 1, 5, 6

Molecular emission features: on the spectrum of frequencies of electromagnetic radiation, these are emitted by atoms or molecules as they transition from a higher-energy to a lower-energy state. Because each element's emission spectrum is unique, spectroscopy can be used to identify them.

Chapter 6

Monomer: a molecule that can form a chemical bond with other molecules that are similar or identical to form a polymer. For example, amino acids are the monomers of proteins.

Chapters 1, 2

mRNA (messenger RNA)**:** conveys genetic information from DNA to the ribosome.

Chapter 2

N

NAD+: Nicotinamide adenine dinucleotide (NAD+) is a coenzyme found in all cells. Also NADH.

Chapter 5

NAI: NASA Astrobiology Institute

NC10: a recently discovered phyla that is only represented by recovered DNA sequences; no member of this phyla has yet been cultured. The presence of NC10 seems to be associated with nitrite- and methane-rich freshwater environments.

Chapter 4

Network analysis: study of graphs as a representation of either symmetric relations or, more generally, of asymmetric relations between discrete objects.

Chapter 4

Neutral drift: evolutionary change at the molecular level that is caused by random drift of neutral mutant alleles rather than by natural selection.

Chapter 4

Neutrality: At the molecular level, random genetic mutations can occur that have no effect (i.e., are neutral).

Chapter 3

NMR: Nuclear magnetic resonance spectroscopy exploits the magnetic properties of certain atomic nuclei to determine the physical and chemical properties of atoms or the molecules in which they are contained.

Chapter 5

Non-covalent bonds (or non-covalent interactions)**:** weak interactions between ions, molecules, and parts of molecules. These bonds are essential for determining the three-dimensional shape of large molecules (e.g., proteins) but are weak enough to be continually broken and reformed at room temperature. Biologically important non-covalent bonds are 10 to 100 times weaker than covalent bonds.

Chapters 1, 2

NSF: National Science Foundation

Nucleobase: see Watson-Crick nucleobases.

Nucleophile: a reactant that provides a pair of electrons to form a new covalent bond.

Chapter 2

Nucleoside triphosphates: used as a source of chemical energy to drive a variety of biochemical reactions, they also serve as the activated precursors of DNA and RNA synthesis. (Nucleotides may have one, two, or three phosphate groups covalently linked at the 5' hydroxyl of ribose. These are referred to as nucleoside mono-, di-, and triphosphates, respectively.)

Chapter 2

Nucleotide: composed of a nucleobase (adenine, thymine, cytosine, guanine, or uracil), a five-carbon sugar, and one or more phosphate groups. Nucleotides serve as subunits (monomers) of nucleic acids like DNA or RNA.

Chapters 1, 2

Nuclide: an atom or ion that is characterized by the contents of the nucleus.

Chapter 6

O

Obligate: a necessary quality, e.g., obligate aerobes need oxygen in order to survive.

Chapter 3

Obliquity: In astronomy, obliquity (or axial tilt) is the angle between an object's rotational axis and its orbital axis; i.e., the angle between its equatorial plane and orbital plane.

Chapters 5, 6

Oligomer: a molecular complex that consists of several monomer units, typically larger than dimers or trimers, but smaller than polymers. For example, a DNA molecule 10 nucleotides in length is considered an oligomer, whereas a gene-length molecule is considered a polymer.

Chapters 1, 2

Oligonucleotides: short, single-stranded DNA or RNA molecules.

Chapter 2

Oligopeptides: peptides that have between 2 and 20 amino acids.

Chapter 2

Oligosaccharide: a polymer containing a small number (typically 3 to 9) of simple sugars (monosaccharides).

Chapter 2

One-pot reaction: in chemistry, a strategy to improve the efficiency of a chemical reaction, whereby a reactant is subjected to successive chemical reactions in just one reactor without isolation or purification between reactions.

Chapter 1

Orbital eccentricity: the amount by which an orbit deviates from a perfect circle.

Chapter 6

Organelle: a specialized subunit within a cell that has a specific function; it is usually separately enclosed within its own lipid bilayer.

Chapter 3

Organic: molecules that contain carbon atoms. The distinction from “inorganic” is historically arbitrary; some carbon-containing molecules such as carbides, or simple carbon-oxygen combinations (like CO_2), are considered inorganic.

Chapters 1, 2, 3, 4, 5, 6

Orthogonality: refers to the possibility of two or more supramolecular, often non-covalent interactions being compatible, reversibly forming without interference from the other.

Chapter 2

Overprint: (also known as imprint) development or superposition of structures on original formations. Examples include contamination, thermal breakdown of organic matter, and extreme metamorphism.

Chapter 4

Oxidation: the loss of electrons or an increase in degree of oxidation. Oxidation is usually combined with reduction—the gain of electrons or a decrease in the degree of oxidation—in so-called “redox” reactions that change the oxidation state of atoms or molecules.

Chapter 1

P

Panspermia: the hypothesis that life exists throughout the Universe and is distributed by meteors, asteroids, and comets. For Earth, it presumes that life originated elsewhere and was transported here.

Chapters 1, 3

PCR: The polymerase chain reaction is a biochemical technology used to amplify a single or a few copies of a piece of DNA, generating thousands to millions of copies of a particular DNA sequence.

Chapter 5

Peptide bond: see amide bond.

Peptides: short chains of amino acid monomers linked by peptide (amide) bonds. Peptides are distinguished from proteins on the basis of size, and contain 70 or fewer amino acids.

Chapter 2

Perihelion: the point of an orbit when the object (planet, comet, asteroid) is closest to its star.

Chapter 6

Petrography: the detailed study of rock features to determine their origin, distribution, and structure.

Chapters 1, 6

Phase space: represents all possible states of a system, with each possible state corresponding to one unique point in the phase space.

Chapter 4

Phenotype: the composite of an organism′s observable traits (body shape, behavior, etc.). A phenotype results from the expression of an organism's genes as well as the influence of environmental factors.

Chapters 3, 4

Phosphodiester bond: a group of strong covalent bonds between a phosphate group and two 5-carbon ring carbohydrates (pentoses) over two ester bonds. Phosphodiester bonds are central to most life on Earth, as they make up the backbone of the strands of DNA.

Chapter 2

Photolysis: when a chemical compound is broken down by light.

Chapter 1

Photometry: the measurement of the brightness or intensity of light, as perceived by the human eye.

Chapter 5

Photosynthesis: the process of converting energy from sunlight into chemical energy. In oxygenic photosynthesis, water (H_2O) is split, carbon dioxide (CO_2) is fixed to make a sugar, and oxygen is released as a waste product.

Chapters 1, 3, 4, 5

Phototrophs: organisms that capture photons to acquire energy, using the energy from light to carry out various cellular metabolic processes.

Chapter 3

Phylogenetics: the study of evolutionary relationships among groups of organisms, which are discovered through molecular sequencing data and morphological data matrices.

Chapters 2, 3, 4

Phylogenetic tree: a diagram that shows the evolutionary relationships of different species based on their genes.

Chapter 6

Physicochemical: relating to physics and chemistry.

Chapters 2, 6

PI: Principal Investigator

Piezophiles: an organism that can grow and reproduce at high pressures.

Chapter 5

pKa: a measurement of the strength of an acid. The larger the value of pKa, the weaker the acid. For a given chemical group, the pKa is the solution pH at which one half of these groups will be protonated and one half will be ionized (i.e., lost a proton to solution).

Chapter 1

Planetesimals: when cosmic dust grains in protoplanetary disks collide and stick together, planetesimals form. When the bodies reach sizes of approximately one kilometer, they can attract each other through their mutual gravity, aiding further growth into moon-sized protoplanets.

Chapter 1

Plate tectonics: the movement of the outer layer of our planet (the lithosphere) that is broken into several plates. The movement is driven by geological processes in the layer below (i.e., in the mantle).

Chapters 1, 3, 4, 5, 6

Platinum-group elements: the six elements platinum (Pt), palladium (Pd), rhodium (Rh), iridium (Ir), osmium (Os), and ruthenium (Ru). They are the rarest metals on Earth but five of them are more plentiful in meteorites and can therefore indicate when a crater was made by an impact.

Chapter 1

PLFA: Phospholipid-derived fatty acids are used in microbial ecology as chemotaxonomic markers of bacteria and other organisms.

Chapter 5

Polar solvent: a liquid with molecules that have a slight electrical charge.

Chapter 2

Polyamide: a macromolecule with repeating units linked by amide bonds. Proteins are polyamides.

Chapter 2

Polyanion: an anion (negatively charged ion) that has more than one negative charge.

Chapter 2

Polymer: a large molecule (or “macromolecule”) composed of many repeated subunits (monomers). A protein, for instance, is made up of many amino acid monomers.

Chapters 1, 2

Polynucleotide: a polymer or chain of nucleotides. DNA is a pair of polynucleotides. RNA is also a polynucleotide.

Chapter 2

Polypeptide: a long, continuous, and unbranched peptide chain.

Chapter 2

Prebiotic: refers to chemistry or processes that eventually led to the origin of life.

Chapters 1, 2, 3, 4, 5, 6

Precambrian: this time covers the vast bulk of Earth's history, starting with the planet's creation about 4.5 billion years ago and ending with the emergence of complex, multi-cellular life forms during the Cambrian period, 540 million years ago.

Chapter 4

Primers for gene amplification: A scientific technique called polymerase chain reaction (PCR) combines primers (short DNA fragments) and DNA polymerases (enzymes that build DNA from nucleotides) to generate thousands to millions of copies of a DNA sequence, thereby ″amplifying″ the genes.

Chapter 4

Prion: an infectious agent composed of a misfolded protein; it acts as a template, causing existing, properly folded proteins to also misfold.

Chapter 3

Prokaryotes: a group of organisms whose cells lack a membrane-bound nucleus.

Chapter 3

Proteome: refers to the complete set of proteins within an individual.

Chapter 3

Proteomics: the large-scale study of proteins, particularly their structures and functions.

Chapter 4

Protobiopolymers: polymers that may have preceded RNA, proteins, and/or DNA.

Chapter 2

Protocells: the evolutionary precursors to the first cells and thought to be self-ordered spherical collections of lipids.

Chapter 2

Protoplanetary disk: a flattened dense cloud of gas and dust rotating around a newly formed star. Protoplanetary discs are thought to evolve into planetary systems. Gravity causes dust and gas to clump together to form protoplanets. Protoplanets eventually accumulate enough material to become planets.

Chapters 1, 5, 6

Psychrophiles: an organism that can grow and reproduce at low temperatures.

Chapter 5

R

Racemic: a mixture with equal amounts of left- and right-handed enantiomers (chiral molecules).

Chapter 1

Radiative transfer: the physical phenomenon of energy transfer in the form of electromagnetic radiation.

Chapter 4

Radiogenic: formed by radioactive decay.

Chapters 4, 5, 6

Raman spectroscopy: provides information about molecular vibrations that can be used for sample identification. The technique involves shining a light source (laser) on a sample and detecting the scattered light.

Chapter 5

Rarified: atmospheres that are less dense and compressed. Due to gravitation, Earth′s atmosphere at higher elevations is more rarified than the atmosphere closer to the ground.

Chapter 4

Reagent: a substance that is added to a system to create a chemical reaction.

Chapter 2

Recalcitrant: compounds that are resistant to being broken down through chemical processes.

Chapter 4

Red beds: sedimentary rocks typically consisting of sandstone, siltstone, and shale. They are predominantly red in color due to the presence of iron oxides.

Chapter 3

Redox: Reduction and oxidation, or “redox” reactions, are chemical reactions in which the oxidation state of atoms or molecules change. Oxidation is the loss of electrons, or an increase in degree of oxidation. Reduction is the gain of electrons, or a decrease in the degree of oxidation.

Chapters 1, 2, 3, 4, 6

Redox couple: a reducing species and its corresponding oxidized form, e.g., Fe^{2+}/Fe^{3+}. See Redox.

Chapter 5

Redox state: a measure of the balance of redox, or reduction-oxidation, reactions in a system. These reactions are characterized by a transfer of electrons, which is often facilitated by microbiological activity.

Chapter 4

Reduced gas: a gas with a low oxidation number (or ″high reduction″), which is usually hydrogen-rich. Strongly reduced gases include methane, ammonia, and hydrogen sulfide. Such gases are strongly associated with the origin of life.

Chapter 4

Reduction: the gain of electrons, or a decrease in the degree of oxidation. Reduction is usually combined with oxidation—the loss of electrons, or an increase in degree of oxidation—in so-called "redox" reactions which change the oxidation state of atoms or molecules.

Chapters 1, 3

Refractory: materials that remain a solid until exposed to high temperatures. (The opposite term is "volatile.")

Chapter 1

Regio-specific chemical reaction: when one structural isomer is produced exclusively, when other isomers are also theoretically possible.

Chapter 2

Replication: the process of generating identical copies of a DNA molecule. This occurs in all forms of life and is the basis for biological inheritance.

Chapter 2

Respiration pathways: on a cellular level, respiration refers to the biochemical pathway by which cells release energy from the chemical bonds of food molecules and then provide that energy for the essential processes of life.

Chapter 3

Respiratory oxygen: Just as animals need oxygen in the atmosphere to breathe, sea creatures need dissolved (or respiratory) oxygen in the ocean. The amount of dissolved oxygen in the ocean depends on temperature and salinity.

Chapter 4

Ribosomal gene sequences: Ribosomes link amino acids together, in the order determined by messenger RNA, to build proteins. A major part of ribosomes is ribosomal RNA (rRNA). All organisms have rRNA, and the gene sequences are of ancient origin, so it is used to determine evolutionary relationships.

Chapter 4

Ribosome: a large and complex molecular machine found within all living cells that serves as the primary site of protein synthesis (translation).

Chapter 2

Riboswitches: ribonucleic acid sequences encoded within messenger RNA that perform a regulatory function, directly affecting the function of genes.

Chapter 2

RNA: ribonucleic acid

RNA polymerase: an enzyme necessary for constructing RNA chains using DNA genes as templates, a process called transcription. RNA polymerase enzymes are essential to life and are found in all organisms and many viruses.

Chapter 2

RNA world: hypothesis that proposes that self-replicating ribonucleic acid (RNA) molecules were precursors to current life, which is based on deoxyribonucleic acid (DNA), RNA, and proteins.

Chapter 2

Runaway greenhouse: when the atmosphere is such that sunlight cannot escape back into space and temperatures continue to rise until the oceans boil away.

Chapter 6

Runaway state: a system beyond a certain “tipping point,” where feedbacks push a system so far in one direction there is no going back to the previous state. The most commonly cited example of this effect is a “runaway greenhouse” climate, where atmospheric carbon dioxide and other greenhouse gases raise the global temperature and cause other events to occur that also raise the global temperature (e.g., ice sheet disintegration and melting of methane hydrates).

Chapter 4

S

S and L amino acids: the “S” and “L” refer to the configuration of the amino acid molecule. In the “L” form, the hydroxyl group is on the left side of the molecule. (Amino acids in proteins are all the “L” form.) “S” indicates the molecular form is arranged counterclockwise.

Chapter 2

Sedimentary rocks: rocks that form by the deposition of sediment, usually in lakes or other bodies of water.

Chapters 1, 3, 4, 5

Sedimentation: the deposition of sediment, usually in lakes or other bodies of water, forming sedimentary rocks.

Chapter 6

Semi-major axis: that part of a planet's orbital ellipse that is the radius of the orbit at the two most distant points.

Chapter 6

Sensible heat: a type of energy released or absorbed in the atmosphere. Sensible heat is related to changes in temperature of a gas or object with no change in phase (as opposed to latent heat, which is related to changes in phase between liquids, gases, and solids).

Chapter 4

Serpentinization: a reaction between water and mantle material (usually mafic rock), whereby water is added to the mineral structure of the rock and heat and hydrogen (H_2) are released.

Chapters 1, 5, 6

SETI: Search for Extraterrestrial Intelligence

Siderophile: elements, such as iridium or gold, that tend to bond with metallic iron; they are "iron-loving" elements.

Chapter 6

Solar flare: a sudden, rapid, and intense variation in brightness of the Sun (or other star). This occurs when magnetic energy that has built up in the star's atmosphere is suddenly released. Radiation is emitted across virtually the entire electromagnetic spectrum, from radio waves at the long wavelength end, through optical emission, to x-rays and gamma rays at the short wavelength end.

Chapter 6

Solid-state convection: a complicated phenomenon in the Earth's mantle that causes various tectonic activities, especially magmatism and plate tectonics, and makes the mantle evolve over geologic time.

Chapter 6

Solubilization: to bring a substance into solution, i.e., dissolve in a liquid state.

Chapters 1, 2, 4

Solvation (also known as dissolution)**:** the interaction of a solute with a solvent, which leads to stabilization of the solute in the solution, such as sodium in water.

Chapter 2

Spectra: refers to the range of frequencies of electromagnetic radiation. Humans see the visible light portion of the electromagnetic spectrum.

Chapters 3, 4, 5, 6

Sputtering: occurs when a substance with high moisture is heated, resulting in explosive loss of material.

Chapter 6

Stellar flare: see solar flare.

STEM: science, technology, engineering, and mathematics

Stereochemistry: the study of the relative spatial arrangement of atoms that form the structure of molecules. An important branch of stereochemistry is the study of chiral molecules. Stereochemistry is also known as 3D chemistry because the prefix "stereo" means “three-dimensionality.”

Chapter 2

Stereoisomers: isomeric molecules that have the same molecular formula and sequence of bonded atoms (constitution) but that differ only in the three-dimensional orientations of their atoms in space.

Chapter 2

Stereospecificity: the property of a reaction mechanism that leads to different stereoisomeric reaction products from different stereoisomeric reactants.

Chapter 2

Sterols: organic molecules found in plants, animals, and fungi.

Chapter 5

Stratigraphy: a branch of geology which studies rock layers (strata) and layering (stratification).

Chapter 4

Stromatolites: layered structures formed by the trapping, binding, and cementation of sedimentary grains by microbial mats, especially cyanobacteria. Stromatolites provide the most ancient records of life on Earth, with fossil remains that date from more than 3.5 billion years ago.

Chapters 3, 4

Subduction: the process in plate tectonics where one plate slips under another and melts into the mantle.

Chapters 4, 6

Substrates: substances that an organism can consume and metabolize for growth.

Chapter 4

Supercontinent: a collection of most of the world’s land mass into a single continent. Due to tectonic activity, supercontinents have assembled and then broken apart several times throughout Earth’s history. The most recent supercontinent (Pangea) existed 300 million years ago.

Chapter 4

Super Earth: a planet generally defined as having a mass between 2 and 10 times that of our planet.

Chapters 1, 5

Superfamilies: large groups of closely related proteins or other molecules.

Chapter 4

Symbiotic: a close association between two or more organisms of different species. This association is often, though not necessarily, beneficial for each member.

Chapters 2, 3, 6

Synthetase: an enzyme that catalyzes the linking together of two molecules, usually using the energy derived from the concurrent splitting off of a pyrophosphate group from a triphosphate.

Chapter 2

Syntrophic: communities where one organism relies on another for nourishment (or they each rely on the other). This type of symbiosis is important for key biochemical transactions on Earth, such as the microbially mediated cycling of carbon.

Chapters 3, 4

T

Taxa: groups of organisms that are genetically related or otherwise have characteristics that differentiate them from other groups.

Chapters 3, 4

Tectonism (tectonics): see plate tectonics.

Template: a structure that acts as a "mold," directing the pattern of a second structure. In biology, this usually refers to a strand of DNA directing the creation of a complementary DNA strand.

Chapters 2, 6

Terrestrial: planets that are solid (as opposed to gaseous planets like Jupiter) and, like Earth, are usually composed of silicate rocks.

Chapters 3, 4, 5, 6

Thermodynamic disequilibria: chemical systems that undergo reactions in which the overall number of particular molecules in the system changes.

Chapters 5, 6

Thermodynamics: the energy of a system (often heat/temperature) or the process by which reactions occur.

Chapters 2, 6

Thermodynamic stability: a system in its lowest energy state, or in chemical equilibrium with its environment. Chemical reactions may occur, but the overall number of molecules in their particular form remains the same.

Chapter 1

Tidal force: the gravitational influence one body has on another, where the side nearest is affected more strongly than the far side. The tidal force exerted by our Moon causes tides in Earth's ocean.

Chapters 2, 5

Tidal heat: a gravitational effect where a less massive object orbits a more massive one (such as the moon Europa orbiting the gas giant planet Jupiter). In non-circular (eccentric) orbits, the less massive body becomes distorted or "squeezed," and this change in shape causes friction between the rocks, generating internal heating.

Chapters 5, 6

Tidal locking: when an orbiting body always faces the same side to the body it orbits.

Chapter 6

Ti in zircon thermometry: measuring the titanium content in zircon crystals can indicate the temperature under which the crystals formed.

Chapter 1

Trace element isotope systematics: the process of calculating the radioactive decay of isotopes in order to determine the date when something was alive (for organisms) or when it formed (for features such as impact craters).

Chapter 1

Transduction: in biophysics, the conveyance of energy from one electron (a donor) to another (a receptor) at the same time that the class of energy changes.

Chapter 2

Transit: when a celestial body appears to move across the face of another celestial body, hiding a small part of it, as seen from the observer's vantage point.

Chapter 6

Translation: the process in which ribosomes "read" messenger RNA base pairs in order to assemble the amino acid chains that form proteins.

Chapters 2, 6

Tree of Life: a way to describe the evolutionary relationships of all life on Earth. Early diagrams of the interconnected nature of life, such as from Charles Darwin's *On the Origin of Species*, appeared tree-like, with branches depicting the divergence of species.

Chapters 1, 2, 3, 4, 5

tRNA: an RNA molecule that serves as the physical link between the nucleotide sequence of nucleic acids (DNA and RNA) and the amino acid sequence of proteins. Aminoacyl-tRNA is tRNA to which its cognated amino acid is chemically bonded (charged). The aa-tRNA deliver the amino acid to the ribosome for incorporation into the polypeptide chain that is being produced.

Chapter 2

Trophism: refers to feeding and nutrition; e.g., chemotrophy, phototrophy, etc.

Chapter 3

V

Vertical inheritance: the transmission of genes from the parental generation to offspring via sexual or asexual reproduction.

Chapter 3

Vesicle: an assembly of lipid molecules, such as a cell membrane.
Chapter 2

Viscosity: a measure of a fluid's resistance to flowing. Whether a fluid has a high or low viscosity depends on the internal friction caused by the fluid's molecular structure.
Chapter 6

Volatile: a substance that easily evaporates at normal temperatures.
Chapters 1, 4, 6

W

Watson-Crick nucleobases: the heterocycles (i.e., ring structures made of two elements) guanine, cytosine, adenine, and thymine that form the base pairs between the two polymers of a DNA double helix.
Chapter 1

Weathering: the process by which rocks are broken down by chemical reactions. Different types of chemical weathering caused by exposure to water, oxygen, carbon dioxide, and acids can alter the minerals found in rocks.
Chapter 4

White dwarf: a stellar remnant of high density composed mainly of electron-degenerate matter. A white dwarf has the mass of our Sun but the volume of Earth. Our Sun will become a white dwarf after it goes through its red giant phase.
Chapter 6

X

Xenobiotic: a form of biology that is not familiar to science or is not found in nature, i.e., synthetic biological systems and biochemistries that differ from the DNA/RNA/20 amino acid system.
Chapter 2

Xerophiles: an organism that can grow and reproduce in conditions with a low availability of water.
Chapter 5

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$\delta^{13}C$: an isotopic signature, a measure of the ratio of stable Carbon 13 to Carbon 12 isotopes, in parts per thousand.
Chapter 3

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