The Origin of Life

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Introduction

Biological evolution begins with the origin of life, but the subject is the perhaps the most interdisciplinary of any in science. Understanding how life began on Earth requires knowledge of the astronomical, geological, and atmospheric settings. However, those settings are in turn dependent on knowing the time period when life arose, which comes from the fossil and molecular records, including molecular clocks based on genetic mutations. Interrelated with the setting is the chemistry that generates the organic molecules used to assemble the first cells and carry the genetic information to successive generations of cells. But holding the chemical reactions and products together in a cell requires a membrane, and the assembly of that involves biophysics. Thus, we have all of the fields of science coming together to understand a single event that happened about four billion years ago and initiated the Tree of Life on Earth. Because little evidence of anything has remained from this early time, there have been enormous amounts of published speculation on this subject. Narratives on how life originated can be grouped by location (surface versus submarine hydrothermal vents), temperature (cold versus hot), source of energy (heterotrophic versus autotrophic), and evolutionary order (genetics-first versus metabolism-first). I use the last dichotomy here, only because it has a long history and renewed focus in recent years. Currently there is no consensus on any one theory for the origin of life, but this is an active field that has made great strides in recent decades.

General Overviews

There have been many general overviews of the origin of life but few that are updated, do not espouse one particular theory or another, and are written by someone with intimate knowledge of the material. Two works come closest to this ideal. Hazen 2012 is a short adaptation of Hazen 2005 and would be a good place to gain a quick overview. Lazcano 2011, with an emphasis on the history of the field, is another excellent starting place to gain an overview. Gesteland, et al. 2006 and Deamer and Szostak 2010 are edited books on the RNA World and Origins of Life, respectively. They are more technical and mostly written to be understood by graduate students or scientists with some background in the field. Among the shorter, technical reviews, Hedges 2009 takes the perspective of the molecular record, Zahnle, et al. 2007 addresses early Earth geology and atmosphere, and Szostak, et al. 2001 covers the polymerization of nucleotides and cell formation.

Deamer, David W., and Jack W. Szostak, eds. 2010. *The Origins of Life*. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

This is a nicely integrated collection of separate articles written by experts in those areas, on cohesive themes rather than specific research projects.

Gesteland, Raymond F., Thomas R. Cech, and John F. Atkins, eds. 2006. *The RNA World*. 3d ed. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

An edited volume of chapters written by experts on different aspects of RNA, biochemistry, and how RNA figures in the origin of life. It is not an overview of the origin of life but rather of RNA research bearing on the genetics-first theories.

Hazen, Robert H. 2005. *Gen-e-sis: The scientific quest for life's origin*. Washington, DC: Joseph Henry.

A good, even-handed overview of research on the origin of life, written by an astrobiologist.

Hazen, Robert H. 2012. Geochemical origins of life. In *Fundamentals of geobiology*. Edited by Andrew H. Knoll, Donald E. Canfield, and Kurt O. Konhauser, 315–332. Chichester, UK: Wiley.

A shortened adaptation of the author's 2005 book *Gen-e-sis: The Scientific Quest for Life's Origin* but with some new references. One of the best overall reviews of this field in concise form.

Hedges, S. Blair. 2009. Life. In *The timetree of life*. Edited by S. Blair Hedges and Sudhir Kumar, 89–98. New York: Oxford Univ. Press.

Reviews the origin and early evolution of life, including the astronomical and physical setting, with respect to organisms, relationships, rooting the tree, terminology, and especially the timing from molecular clocks.

Lazcano, Antonio. 2011. Origin of life. In *Encyclopedia of astrobiology*. Edited by Muriel Gargaud, 1183–1190. Berlin: Springer-Verlag.

An excellent general overview of the field, appropriate for undergraduates, graduate students, and scientists.

Szostak, Jack W., David P. Bartel, and P. Luigi Luisi. 2001. Synthesizing life. *Nature* 409:387–390.

An essay on advances in membrane biophysics and cell formation, pointing out the importance of evolution and natural selection at an early stage in the origin of life.

Zahnle, Kevin, Nick Arndt, Charles Cockell, et al. 2007. Emergence of a habitable planet. *Space Science Reviews* 129:35–78.

A comprehensive treatment of the atmospheric, geological, and astronomical setting during the first 300 million years of Earth history.

Journals

Articles touching on the origin of life are found in many scientific journals, including those with the broadest readership such as Science and Nature as well as the best journals in physics, chemistry, geology, and biology. Early volumes of the Journal of Molecular Evolution contain many relevant articles and an increasing number are in Molecular Biology and Evolution. With the recognition of astrobiology as a field in itself in recent years, most articles on the origin of life now can be found in the astrobiological journals, including one focused mostly on space science, Icarus, and several others that are more general in scope: Astrobiology, Origins of Life and Evolution of Biospheres, and the International Journal of Astrobiology.

Astrobiology.

Associated with the Astrobiology Society and initiated in 2001. The field of astrobiology is broad and covers many topics besides the origin of life.

Icarus.

Devoted to the publication of original contributions in the field of solar system studies, including much on the origin of life.

International Journal of Astrobiology.

Also covers the broad field of astrobiology, which includes research into the origin of life. The journal was started in 2002.

Journal of Molecular Evolution.

Established in 1971, this journal published a significant number of articles related to the origin of life in its first three decades. In more recent years, the journal has shifted direction, and fewer such articles have been published.

Molecular Biology and Evolution.

Publishes research at the interface of molecular and evolutionary biology, including studies on the origin of life, mostly involving DNA and protein sequence analyses. It was started in 1983 and is now linked with the Society for Molecular Biology and Evolution.

Nature.

A general journal of science that publishes articles of wide interest, occasionally including those on the origin of life.

Origins of Life and Evolution of Biospheres.

This journal of the International Astrobiology Society, started in 1968, is the one most dedicated to research on the origin of life. The society was previously known as the International Society for the Study of the Origin of Life.

Science.

Another general journal of science that publishes articles of wide interest, including those on the origin of life.

Definitions

One might suppose that a definition of life is needed to study the origin of life, but that is not the case. Like art, life has proven to be a challenge to define, and the most influential articles on the subject are usually the ones concluding that a definition is not possible. These include Cleland and Chyba 2002, Lazcano 2010, and Tirard, et al. 2010, which are all well-written and understandable by scientifically literate readers. On the other hand, one can find a diversity of definitions of life in the literature. For example, Walker and Davies 2012 defines life as a shift in “causal structure” whereas Ruiz-Mirazo, et al. 2004 emphasizes “autonomy and open-ended evolution.”

Cleland, Carol E., and Christopher Chyba. 2002. Defining “Life.” *Origins of Life and Evolution of Biospheres* 32:387–393.

No definition is provided, but rather a discussion of the challenges faced in developing a definition.

Lazcano, Antonio. 2010. Which way to life? *Origins of Life and Evolution of Biospheres* 40:161–167.

Concludes that life is a continuum of steps between the non-living and living, and that it may be meaningless to draw a strict line between them.

Ruiz-Mirazo, Kepa, Juli Pereto, and Alvaro Moreno. 2004. A universal definition of life: Autonomy and open-ended evolution. *Origins of Life and Evolution of Biospheres* 34:323–346.

Besides qualities noted in the title, they propose, as a definition, the presence of a semi-permeable membrane, an energy transduction apparatus, and at least two types of “functionally interdependent macromolecular components.”

Tirard, Stephane, Michel Morange, and Antonio Lazcano. 2010. The definition of life: A brief history of an elusive scientific endeavor. *Astrobiology* 10:1003–1009.

Probably the most comprehensive article on this topic. The authors review previous definitions of life and where, in their opinion, they fail.

Walker, Sara I., and Paul C. W. Davies. 2012. The algorithmic origins of life. *Interface* 10.

The informational aspect of life is considered key, and life is defined as a shift in “causal structure.”

History

The concept of evolution by natural selection begins with Darwin 1859, but in it there is almost no mention of the origin of life. As discussed in Lazcano 2010, Charles Darwin later speculated on the topic in a famous letter to his colleague Joseph Hooker in 1871, about a “warm little pond” where a protein molecule was “chemically formed” from light, heat, electricity, etc., only to undergo further “complex changes.” This short letter represents the beginnings of modern thought on the origin of life. The classical works in the field appeared in the 20th century. Haldane 1929 and Oparin 1938 discuss the formation of organic molecules, and Urey 1952 elaborates further on the need for an atmosphere low in oxygen. Miller 1953 is the classic work describing how organic molecules can be produced in the laboratory under early Earth conditions, and Bada and Lazcano 2003 offers additional historical insights on that experiment. Müller 1961 expounds on the importance of genetics over metabolism, in the origin of life.

Bada, Jeffrey L., and Antonio Lazcano. 2003. Prebiotic soup: Revisiting the Miller experiment. *Science* 745–746.

A short account of the famous experiment of Stanley Miller, published in the same journal in 1953 that simulated early Earth conditions in the laboratory and produced amino acids.

Darwin, Charles. 1859. *On the origin of species by means of natural selection*. London: John Murray.

One of the most influential books in science, where the correct mechanism for biological evolution is first described. He only briefly touches on the origin of life, but his private letters, now public, reveal that he thought seriously about it.

Haldane, J. B. S. 1929. The origin of life. *Rationalist Annual* 148:3–10.

A short paper suggesting that organic molecules could have been synthesized in an early atmosphere of carbon dioxide.

Lazcano, Antonio. 2010. Historical development of origins research. In *The origins of life*. Edited by David Deamer and Jack W. Szostak, 5–20. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Focuses on the history of research in the field.

Miller, Stanley L. 1953. A production of amino acids under possible primitive Earth conditions. *Science* 117:528–529.

The first study to demonstrate synthesis of organic molecules under early Earth conditions.

Müller, Hermann J. 1961. Genetic nucleic acid: key material in the origin of life. *Perspectives in Biology and Medicine* 5:1–23.

One of the earliest proponents of a genetics-first theory for the origin of life. Here he develops further ideas that he laid out in works on the primacy of the gene, four decades earlier.

Oparin, Alexander I. 1938. *The origin of life*. New York: Macmillan.

This is the English translation of the major work of Oparin, laying out his ideas on how the first organic molecules formed on early Earth, in a reducing atmosphere, and aggregated into colloidal droplets.

Urey, Harold C. 1952. *The planets: Their origin and development*. Chicago: Univ. of Chicago Press.

The author develops his concept, like that of Oparin, of a highly reducing terrestrial atmosphere.

Astronomical Setting

Ciesla 2008 describes how Earth and the rest of the solar system formed from a protoplanetary disk of dust and gas 4.6 billion years ago. Ehrenfreund and Cami 2010 reviews what is known about organic (carbon) molecules that have been detected in interstellar clouds. The presence of such a large diversity indicates that these molecules are among the easiest to form naturally, in part explaining why our life is carbon-based. The habitable zone of solar systems, where a planet can support liquid water on its surface, is reviewed and characterized in a technical but readable account in Kasting, et al. 1993 and updated in Kopparapu, et al. 2013. Solar luminosity was only 70 percent of current levels during the Hadean, some four billion years ago, which should have frozen the Earth but did not. This Faint Young Sun Paradox has posed the greatest scientific challenge for this area of origins research in the late 20th and early 21st centuries, and Feulner 2012 gives a comprehensive review of the problem. Wordsworth and Pierrehumbert 2013 presents yet another possible solution for the paradox. In a key research paper, Gomes, et al. 2005 provides an elegant explanation, based on orbital dynamics, for the Late Heavy Bombardment, which was a surge in large impact events on Earth and the moon at approximately 3.8 billion years ago. Large impact events at that time may have challenged any life that had evolved earlier, in the Hadean.

Ciesla, Fred J. 2008. Observing our origins. *Science* 319:1488–1499.

Perspective on an article about protoplanetary disks that describes the origin of stellar systems like our own.

Ehrenfreund, Pascale, and Jan Cami. 2010. Cosmic carbon chemistry: From the interstellar medium to the early Earth. In *The origins of life*. Edited by David Deamer and Jack W. Szostak, 21–34. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

A review of what is known about organic material found in interstellar space.

Feulner, Georg. 2012. The faint young sun problem. *Reviews in Geophysics* 50:RG2006.

Reviews the complex problem of why the oceans of the early Earth were not frozen over, a dilemma that has challenged researchers for decades.

Gomes, R., H. F. Levison, K. Tsigani, and A. Morbidelli. 2005. Origin of the cataclysmic Late Heavy Bombardment period of the terrestrial planets. *Nature* 435:466–469.

A model is proposed for a surge in large impacts on the Earth and moon at 3.8 billion years ago, involving rapid migration of the giant planets.

Kasting, James F., Daniel P. Whitmire, and Ray T. Reynolds. 1993. Habitable zones around main sequence stars. *Icarus* 101:108–118.

The classic paper that laid out the dimension of the habitable zone and inspired a large number of astrobiologists and research.

Kopparapu, Ravi K., Ramses Ramirez, James F. Kasting, et al. 2013. Habitable zones around main-sequence stars: New estimates. *Astrophysical Journal* 765:131.

Updated estimates, from Kasting, et al. 1993, for water loss and maximum greenhouse limits.

Wordsworth, Robin, and Raymond Pierrehumbert. 2013. Hydrogen-nitrogen greenhouse warming in Earth's early atmosphere. *Science* 339:64–67.

Proposed as yet another solution for the faint-young sun paradox, to warm the otherwise cold early Earth.

Geological Setting

The solar system and Earth formed 4.57 billion years ago, and a relatively short time later (approximately fifty million years) an impact with a Mars-sized object created the Moon. Zahnle, et al. 2007 focuses on this Moon-forming impact and the effect it had on shaping the early Earth environment. This is also one of the best sources for a review of the early impact history of Earth, and likelihood of ocean-boiling impacts (see also Gomes, et al. 2005, cited under Astronomical Setting). Sleep, et al. 2012 points out that an ocean and continental crust were already present 4.4–4.2 billion years ago and highlights the importance of the Earth's mantle in retaining a record of the early environment and possibly signatures of life. Kranendonk 2011, Shirey and Richardson 2011, and Dhuime, et al. 2012 cover the origin of plate tectonics, driven by the subduction of plates, and evidence that it did not get going fully until about three billion years ago. Two other geology-based reviews touch more on the relationship with early life. Sleep and Bird 2008 discusses rock formations, especially black shales, that are robust biosignatures of early life, and Sleep, et al. 2011 focuses on rocks that may have been useful in prebiotic chemistry, such as serpentinite, and their abundance on the early Earth.

Dhuime, Bruno, Chris J. Hawkesworth, Peter A. Cawood, and Craig D. Storey. 2012. A change in the geodynamics of continental growth 3 billion years ago. *Science* 335:1334–1336.

Oxygen isotopes in zircons reveal a major change 3 billion years ago, interpreted by these authors as the onset of plate tectonics and building of continents.

Kranendonk, Martin J. Van. 2011. Onset of plate tectonics. *Science* 333:413–414.

Perspective, presenting additional insights, on the article by Shirey and Richardson in the same issue, reporting analysis of diamond inclusions showing that plate tectonics began 3 billion years ago.

Shirey, Steven B., and Stephen H. Richardson. 2011. Start of the Wilson Cycle at 3 Ga shown by diamonds from subcontinental mantle. *Science* 333:434–436.

Continental crust began forming soon after the Earth formed, but that analysis of diamond inclusions showed that subduction-drive plate tectonics began much later, 3 billion years ago.

Sleep, Norman H., and Dennis K. Bird. 2008. Niches of the pre-photosynthetic biosphere and geological preservation of Earth's earliest ecology. *Geobiology* 5:101–117.

Organic carbon burial was rare before photosynthesis. Black shales are biosignatures of photosynthesis, both anoxygenic and oxygenic. These facts should continue to guide exploration of early Earth sediments, and their metamorphosed remnants, for signs of life.

Sleep, Norman H., Dennis K. Bird, and Emily Pope. 2011. Serpentine and the dawn of life. *Philosophical Transactions of the Royal Society B* 366:2857–2869.

Hydrogen gradients, attractive for life processes, may have formed in association with serpentinite and hydrothermal vents in the Hadean.

Sleep, Norman H., Dennis K. Bird, and Emily Pope. 2012. Paleontology of Earth's mantle. *Annual Review of Earth and Planetary Sciences* 40:277–300.

Inclusions in the Earth's mantle can still tell us a lot about the Hadean environment when life began.

Zahnle, Kevin, Nick Arndt, Charles Cockell, et al. 2007. Emergence of a habitable planet. *Space Science Reviews* 129:35–78.

A comprehensive treatment of the atmospheric, geological, and astronomical setting during the first three hundred million years of Earth history.

Atmospheric Setting

Kasting and Catling 2003, and more recently Zahnle, et al. 2010, are good places to start for an overview of research in this area. Of more historical value are three earlier reviews of this subject, all still quite useful. Walker 1977 laid out some of the groundwork and was the first to establish the low levels of oxygen in the early Earth atmosphere. This was important for the origin of life because an atmosphere low in oxygen would have facilitated the formation of organic molecules. Kasting 1993 is less technical than others and therefore could provide a good entry point for students into this literature. Pavlov, et al. 2001 discusses simulation results of a methane-rich Archean atmosphere and touches on implications for the Earth's atmosphere at the time of the origin of life. The Faint Young Sun Paradox also is a major focus of research into the early Earth atmosphere. The absence of evidence for early global glaciations is unexpected based on the low solar luminosity of that time period, and this continues to be a challenge to explain (see Feulner 2012 and Wordsworth and Pierrehumbert 2013, both cited under Astronomical Setting).

Kasting, James F. 1993. Earth's early atmosphere. *Science* 259:920–926.

Review paper describing the early evolution of Earth's atmosphere.

Kasting, James F., and David Catling. 2003. Evolution of a habitable planet. *Annual Review of Astronomy and Astrophysics* 41:429–463.

A review of the early atmosphere and of planetary habitability issues.

Pavlov, Alexander A., James F. Kasting, and Lisa L. Brown. 2001. UV-shielding of NH_3 and O_2 by organic hazes in the Archean atmosphere. *Journal of Geophysical Research* 106:23267–23287.

A still reasonably up-to-date simulation of the photochemistry of a methane-rich Archean atmosphere, with some implications for atmosphere at the time of the origin of life.

Walker, James C. G. 1977. *Evolution of the atmosphere*. New York: Macmillan.

First work to correctly estimate the low concentration of oxygen in the prebiotic atmosphere. This low level was important for the formation of organic molecules needed in the origin of life.

Zahnle, Kevin, Laura Schaefer, and Bruce Fegley. 2010. Earth's earliest atmospheres. In *The origins of life*. Edited by David Deamer and Jack W. Szostak, 49–65. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

The focus here is on the moon-forming impact that occurred 4.5 billion years ago and the effect of that event on Earth's atmosphere, and especially how it may have influenced the origin of life.

Fossil Record

The earliest fossils are important for research on the origin of life because they establish a minimum time for that event. Knoll 2012 is the best entry point into this body of literature. Mojzsis, et al. 1996 describes the earliest evidence of life, albeit controversial, which are chemical fossils from the oldest known sedimentary rocks, the 3.8 billion-year-old Isua formation in Greenland. See also Sleep, et al. 2012 (cited under Geological Setting) for discussion of the importance of this evidence. Graphitic carbon from that formation is depleted in carbon-13 apparently because of biological action, which molecular clocks now tell us could not have been from cyanobacteria and oxygenic photosynthesis (see Molecular Record). Brasier, et al. 2002 offered up a critical analysis of the earliest microfossils, from 3.5 billion-year-old rocks in Australia, and concluded that they were most likely artifacts. This was taken as a call-to-arms by the deep time paleontologists and resulted in greater scrutiny of the fossil record of early life. Nonetheless, the take home message has not changed appreciably, because results of the scrutiny yielded the same date (3.5 billion years ago) for the earliest non-controversial evidence of life. For discussion of this see the technical report in Schopf, et al. 2002, presenting analysis of Laser-Raman images, and several reviews: Brasier, et al. 2006, Schopf 2006, and Knoll 2012.

Brasier, Martin D., Owen R. Green, Andrew P. Hephcoat, et al. 2002. Questioning the evidence for Earth's oldest fossils. *Nature* 416:76–81.

Reinterpretation of some famous 3.5-billion-year-old fossils as artifacts, not life at all.

Brasier, Martin D., Nicola McLoughlin, Owen Green, and David Wacey. 2006. A fresh look at the fossil evidence for early Archean cellular life. *Philosophical Transactions of the Royal Society B* 361:887–902.

A review of the microfossil evidence for the earliest life on Earth, concluding that life was probably present by about 3.5 billion years ago. In that sense, there is agreement with Schopf 2006.

Knoll, Andrew H. 2012. The fossil record of microbial life. In *Fundamentals of geobiology*. Edited by Andrew H. Knoll, Donald E. Canfield, and Kurt O. Konhauser, 297–314. Chichester, UK: Wiley.

A comprehensive and critical review of the microbial fossil record, including discussion of geochemical evidence and the debate surrounding the earliest evidence of life.

Mojzsis, S. J., G. Arrhenius, K. D. McKeegan, T. M. Harrison, A. P. Nutman, and C. R. L. Friend. 1996. Evidence for life on Earth before 3,800 million years ago. *Nature* 384:55–59.

Report of the Isua sedimentary formation in West Greenland, containing isotopically light carbon, interpreted (and contested) to be the oldest evidence of life.

Schopf, J. William. 2006. Fossil evidence of Archean life. *Philosophical Transactions of the Royal Society B* 361:869–885.

A comprehensive review of the fossil and geochemical evidence for the earliest life on Earth, concluding that life was present at least by 3.5 billion years ago. This date is in agreement, more or less, with Brasier, et al. 2006.

Schopf, J. William, Anatoliy B. Kudryavtsev, David G. Agresti, Thomas J. Wdowiak, and Andrew D. Czaja. 2002. Laser-Raman imagery of Earth's earliest fossils. *Nature* 416:73–76.

The earliest microfossils are reported to be carbonaceous, and not graphite inclusions, and thus disagreeing with Brasier, et al. 2002.

Molecular Record

The genomes of organisms provide us with an extensive molecular record of the history of life, but complex analyses are required to reveal this history. Hedges 2009 (cited under General Overviews) reviews the current evidence of the early history of life, including the phylogeny, the root, and the timescale from molecular clocks. Because the DNA composition of genes in living organisms can reflect temperatures that their ancestors were exposed to in the past, several studies have examined this question, with somewhat different results. Gaucher, et al. 2008 focuses on the gene for elongation factor, where they found that the last common ancestor of life was a thermophile, preferring high temperatures. However, the reports of Boussau, et al. 2008 and Groussin and Gouy 2011, using multiple genes, concluded that the last common ancestor was a mesophile, preferring moderate temperatures, and that optimal growth temperature subsequently increased and then decreased to the present. These results are relevant for the early evolution of life because of the possibility of ocean-boiling impacts selecting for species preferring high temperatures (see Geological Setting). Battistuzzi and Hedges 2009 presents genomic evidence for a large group of prokaryotes, Terrabacteria, adapted to land and infers a time of 3 billion years ago for the colonization of land, consistent with the origin of subduction-driven plate tectonics (see Geological Setting).

Battistuzzi, Fabia U., and S. Blair Hedges. 2009. A major clade of prokaryotes with ancient adaptations to life on land. *Molecular Biology and Evolution* 26:335–343.

An update of a 2004 study by these authors, estimating the time of the earliest splits in life. Here they added more data from additional genomes, still inferring an origin of life before four billion years ago, colonization of land at three billion years ago, and an origin of cyanobacteria at 2.6 billion years ago.

Boussau, Bastien, Samuel Blanquart, Anamaria Necsulea, Nicolas Lartillot, and Manolo Gouy. 2008. Parallel adaptations to high temperatures in the Archaean eon. *Nature* 456:942–946.

Analysis of multiple genes showed that the last common ancestor was a mesophile and that temperature increased in parallel in the two domains, before decreasing toward the present time.

Gaucher, Eric A., Sridhar Govindarajan, and Omjoy K. Ganesh. 2008. Palaeotemperature trend for Precambrian life inferred from resurrected proteins. *Nature* 451:704–707.

The optimal growth temperature of elongation factor at earlier times in history was estimated in a phylogenetic tree. The authors concluded that the last common ancestor was a thermophile and that temperature has since decreased through time.

Groussin, Mathieu, and Manolo Gouy. 2011. Adaptation to environmental temperature is a major determinant of molecular evolutionary rates in Archaea. *Molecular Biology and Evolution* 28:2661–2674.

Following previous work on the history of optimal growth temperature across all of life, this study focuses on the archaebacteria. The authors found that it is more complex than previously thought and that shifts in optimal temperature throughout the history of this group likely affected evolutionary rates.

Formation of Organic Molecules

Bada and Lazcano 2003 provides a good, yet brief, introduction to this topic. Lazcano 2013 offers a more detailed introduction and is more up-to-date. Of historical value, Haldane 1929 and Oparin 1938 lay out early ideas on this subject. Miller and Urey 1959 discusses the first syntheses of organic molecules under early Earth conditions and is also worth reading from a historical perspective. Subsequent work has shown that the specific composition of the gases used in laboratory synthesis experiments is not critical for producing organic molecules. Several of those studies stand out. Ferris, et al. 1978 shows the potential importance of hydrogen cyanide in forming nucleotides on early Earth, which would facilitate a genetics-first origin of life. Oro, et al. 1990 shows how a great diversity of molecules has been created in these laboratory experiments simulating early Earth conditions. Finally, Cleaves, et al. 2008 is important because it shows that organic molecules can form in atmospheric conditions that are neutral, challenging the dogma that reducing atmospheres are required.

Bada, Jeffrey L., and Antonio Lazcano. 2003. Prebiotic soup: Revisiting the Miller experiment. *Science* 745–746.

A short account of the famous experiment of Stanley Miller, published in the same journal in 1953 that simulated early Earth conditions in the laboratory and produced amino acids.

Cleaves, H. James, John H. Chalmers, Antonio Lazcano, Stanley L. Miller, and Jeffrey L. Bada. 2008. Prebiotic organic synthesis in neutral planetary atmospheres. *Origins of Life and Evolution of Biospheres* 38:105–155.

Demonstration that organic molecules can form in atmospheric conditions that are neutral, such as with nitrogen and carbon dioxide. This challenged the dogma in the field that reducing atmospheres are needed for the formation of organic molecules.

Ferris, James P., P. C. Joshi, E. H. Edelson, and J. G. Lawless. 1978. HCN, a plausible source of purines, pyrimidines, and amino acids on the primitive Earth. *Journal of Molecular Evolution* 11:293–311.

Evidence that hydrogen cyanide was likely an important gas for the formation of biological molecules on early Earth, including nucleotides and amino acids.

Haldane, J. B. S. 1929. The origin of life. *Rationalist Annual* 148:3–10.

Suggests that organic molecules could have been synthesized in an early atmosphere of carbon dioxide.

Lazcano, Antonio. 2013. How did life originate? In *Evolution from the Galapagos two centuries after Darwin*. Edited by Gabriel Trueba and Carlos Montfar, 17–32. New York: Springer-Verlag.

Covers the history of the field, including the opinions of Darwin through his published works and letters, as well as 20th-century discoveries.

Miller, Stanley L., and Harold C. Urey. 1959. Organic compound synthesis on the primitive Earth. *Science* 130:245–251.

A review article by Miller and Urey that discusses implications of their work to understanding the origin of life.

Oparin, Alexander I. 1938. *The origin of life*. New York: Macmillan.

This is the English translation of the major work of Oparin, laying out his ideas on how the first organic molecules formed on early Earth, in a reducing atmosphere, and aggregating into colloidal droplets.

Oro, J., Stanley L. Miller, and Antonio Lazcano. 1990. The origin and early evolution of life on Earth. *Annual Review of Earth and Planetary Sciences* 18:317–356.

Includes a review of studies that have synthesized organic molecules, under early Earth conditions, since the time of the first study by Stanley Miller.

Formation of Cells

The chemical reactions of life are contained by the cell membrane, and the isolation itself is also important for evolution and natural selection. The best and most accessible introduction to this topic is Ricardo and Szostak 2009, while Szostak, et al. 2001 provides a more detailed and more technical review. Of historical value are Bangham, et al. 1965 and Singer and Nicolson 1972, which report that cell membranes are able to self-assemble from simple fatty acids, and that nucleotides can move across primitive membranes. Two articles bear on potential extraterrestrial sources for amphiphilic compounds capable of self-assembly into membranes. Deamer 1985 reports the finding of such compounds on a meteorite, and Deamer, et al. 2001 shows that those compounds can be synthesized in a simulated interstellar molecular cloud. Finally, two articles on protocell assembly stand out as important reading. Walde, et al. 1994 shows how a functional enzyme can be encapsulated in a protocell and then synthesize internal RNA, and Hanczyc, et al. 2003 demonstrate other properties required of a protocell, which is a step toward a primitive version of life.

Bangham, A. D., M. M. Standish, and J. C. Watkins. 1965. Diffusion of univalent ions across the lamellae of swollen phospholipids. *Journal of Molecular Biology* 13:238–252.

First demonstration that phospholipids spontaneously form membrane-bounded vesicles by self-assembly. The vesicles, often referred to as liposomes, are able to maintain concentration gradients of solutes, and we presume that the first forms of cellular life needed to have some sort of boundary structure.

Deamer, David W. 1985. Boundary structures are formed by organic components of the Murchison carbonaceous chondrite. *Nature* 317:792–794.

First demonstration that a mixture of organic material synthesized in the early solar system contained amphiphilic compounds capable of self-assembling into membranes.

Deamer, David W., Jason P. Dworkin, Scott A. Sandford, Max P. Bernstein, and Louis J. Allamandola. 2001. The first cell membranes. *Astrobiology* 2:371–381.

Shows that the organic compounds synthesized in a simulated interstellar molecular cloud were amphiphilic and could assemble into membranes. It makes sense that this material accumulates into the dust particles of a nascent solar system and is then delivered to planetary surfaces during accretion.

Hanczyc, Martin M., Shelly M. Fujikawa, and Jack W. Szostak. 2003. Experimental models of primitive cellular compartments: Encapsulation, growth, and division. *Science* 302:618–622.

Demonstration of properties required of a protocell, defined as a complex system of molecules enclosed in a membrane-bounded compartment.

Ricardo, Alonso, and Jack W. Szostak. 2009. Life on Earth. *Scientific American* 301:54–61.

An article for the scientifically literate public on a possible genetics-first scenario for the origin of life, formation of cells, and synthesis of nucleic acid chains.

Singer, S. J., and Garth L. Nicolson. 1972. The fluid mosaic model of the structure of cell membranes. *Science* 175:720–731.

Argued that all biological membranes were composed of fluid lipid bilayers containing integrated proteins. Early cellular life must have had similar membranous boundaries.

Szostak, Jack W., David P. Bartel, and P. Luigi Luisi. 2001. Synthesizing life. *Nature* 409:387–390.

An essay on advances in membrane biophysics and cell formation, pointing out the importance of evolution and natural selection at an early stage in the origin of life.

Walde, Peter, Ayako Goto, Pierre-Alain Monnard, Michaela Wessicken, and P. Luigi Luisi. 1994. Oparin's reactions revisited: Enzymatic synthesis of poly(adenylic acid) in micelles and self-reproducing vesicles. *Journal of the American Chemical Society* 116:7541–7547.

Demonstration that an enzyme can be encapsulated in a membrane-bounded compartment and then synthesize internal RNA. This same result was independently reported in the same year by Ajoy C. Chakrabarti, et al. in *Journal of Molecular Evolution*, 39:555–559.

Metabolism-first Theories

As the name implies, these models for the origin of life begin with metabolism and focus on how protein catalysts are synthesized. The ideas of Haldane 1929 and Oparin 1938 (both cited under History) nearly a century ago could be placed in this group. Wächtershäuser 1988 proposes a metabolism-first model that relies on submarine hydrothermal systems (SHSs), where protein synthesis occurs on the iron-sulfur mineral pyrite. Wächtershäuser 2002, a short and readable essay, is a good place to start, followed in Wächtershäuser 1988 for those wanting more details. Synthesis on a mineral surface plays a major role in this model, and an accessible background article on that topic is Hazen and Sverjensky 2010. Simulations have been conducted to see just how easily peptide chains can be synthesized under SHS conditions. Two of those articles are recommended here, because of their different conclusions despite having similar results. Both found that polymerization of glycine was difficult, yielding oligopeptides only several subunits long. Yet Imai, et al. 1999 sees this as a positive result, supporting SHS-based models for the origin of life, whereas Cleaves, et al. 2009 takes a more sobering viewpoint that SHSs are not "robust sources of even simple peptides."

Cleaves, H. J., A. D. Aubrey, and J. L. Bada. 2009. An evaluation of the critical parameters for abiotic peptide synthesis in submarine hydrothermal systems. *Origins of Life and Evolution of Biospheres* 39:109–112.

A simulation similar to that of Imai, et al. 1999, but with conditions altered to be more realistic of early Earth conditions. Oligopeptides several subunits long were synthesized, which demonstrated polymerization, but the authors concluded that this was not sufficient to figure into origin-of-life scenarios.

Hazen, Robert M., and Dimitri A. Sverjensky. 2010. Mineral surfaces, geochemical complexities, and the origins of life. In *The origins of life*. Edited by David Deamer and Jack W. Szostak, 157–177. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

A review of a key aspect of modern theories for the origin of life: how the first molecules were able to polymerize without a biological catalyst.

Imai, Ei-ichi, Hajime Honda, Kuniyuki Hatori, and Andre Brack. 1999. Elongation of oligopeptides in a simulated submarine hydrothermal system. *Science* 283:831–833.

A polymerization experiment designed to test a metabolic theory for early life, under deep-sea hydrothermal vent conditions. Oligopeptides several subunits long were synthesized, which demonstrated polymerization, although see Cleaves, et al. 2009 for a similar study but with different conclusions.

Wächtershäuser, Günter. 1988. Before enzymes and templates: Theory of surface metabolism. *Microbiological Reviews* 52:452–484.

This long, technical review is Wächtershäuser's original proposal that life started in an autotrophic, metabolic state, prior to any genetic mechanism for replication.

Wächtershäuser, Günter. 2002. Life as we don't know it. *Science* 289:1307–1308.

Provides the best introduction to the topic, useful for students and scientists. See Wächtershäuser 1988 for more details.

Genetics-first Theories

These models for the origin of life start with replication and now focus primarily on how nucleotides are synthesized. The earlier ideas of Müller 1961 (cited under History), in a general sense, fall into this group. For short and readable essays, accessible to students, and covering the modern scenarios, the best place to start is with Bada and Lazcano 2002, and Ricardo and Szostak 2009 (cited under Formation of Cells). As with the metabolism-first theories, synthesis on a mineral surface plays a major role in genetics-first models as well, and an accessible background article on that topic is Hazen and Sverjensky 2010 (cited under Metabolism-first Theories). The concept of an "RNA World" fits squarely in the realm of genetics-first theories, and Gesteland, et al. 2006 (cited under General Overviews) covers that area thoroughly. Separately, Orgel 2004 focuses on the early steps and a proposed scenario. The efficiency of polymerization has been a focal point in research here, as it has with metabolism-first models, but researchers working with genetics-first models have had more success. Ferris, et al. 1996 explains how exceptionally long oligomers of up to fifty-five subunits, including both nucleotides and amino acids, long enough to catalyze reactions, have been generated at cool, surface conditions. Joshi, et al. 2009 provides details on the catalytic process involved in making RNA oligomers on montmorillonite. Schrum, et al. 2010 comes closest to putting together an up-to-date genetics-first scenario, while at the same time discussing challenges involved in current research at each step of the way.

Bada, Jeffrey L., and Antonio Lazcano. 2002. Some like it hot, but not the first biomolecules. *Science* 296:1982–1983.

Provides the best introduction to this topic. Good for students and scientists.

Ferris, James P., Aubrey R. Hill, Jr., Rihe Liu, and Leslie E. Orgel. 1996. Synthesis of long prebiotic oligomers on mineral surfaces. *Nature* 381:59–61.

Report of long oligomers (up to fifty-five subunits) of amino acids and nucleotides that were synthesized on mineral surfaces in the laboratory at room temperature or cooler. Oligomers of that length are able to catalyze reactions.

Joshi, Prakash C., Michael F. Aldersley, John W. Delano, and James P. Ferris. 2009. Mechanism of montmorillonite catalysis in the formation of RNA oligomers. *Journal of the American Chemical Society* 131:13369–13374.

Reports on experiments that provide additional insights into the catalytic process that yields RNA oligomers on montmorillonite.

Orgel, Leslie E. 2004. Prebiotic chemistry and the origin of the RNA World. *Critical Reviews in Biochemistry and Molecular Biology* 39:99–123.

Focuses on the difficult early steps necessary in the RNA World, before the first cell.

Schrum, Jason P., Ting F. Zhu, and Jack W. Szostak. 2010. The origins of cellular life. In *The origins of life*. Edited by David Deamer and Jack W. Szostak, 245–259. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Breakdown of the steps involved in going from organic molecules to a functioning cell containing replicating genetic information.

Panspermia

Panspermia is the theory, not widely supported, that life on Earth originated somewhere else and arrived here as living cells in comets or on extraterrestrial dust grains—asteroids and meteorites would have been less efficient. This concept should not be confused with the transport to Earth of organic molecules (non-living), which is less controversial. Kamminga 1982 reviews the long history of panspermia, and Hoyle and Wickramasinghe 2000 would be a good source for current ideas in this area. Crick and Orgel 1973 goes a step further and proposes that intelligent life seeded Earth from another planet. Kirschvink and Weiss 2001 gives a scientific argument why Mars should be considered as a likely place for the origin of Earth life. Melosh 2003 approaches the question of exchange inside rock bodies (e.g., asteroids) statistically, concluding that it is highly unlikely that life could be seeded from another stellar system, but that exchange among planets within our solar system was possible. Hedges 2009 (cited under General Overviews) points out the necessity of comparing early Earth with the early history of other planets and showing a distinct advantage for panspermia before the latter theory can be supported.

Crick, F. H. C., and L. E. Orgel. 1973. Directed panspermia. *Icarus* 19:341–346.

A provocative suggestion, by distinguished scientists, that life on Earth was seeded by intelligent life from another planet.

Hoyle, Fred, and N. Chandra Wickramasinghe. 2000. *Astronomical origins of life*. Dordrecht, The Netherlands: Kluwer Academic.

Diverse aspects of panspermia are considered in a collection of papers, with emphasis on delivery of cells by comets.

Kamminga, Harmke. 1982. Life from space: A history of panspermia. *Vistas in Astronomy* 26:67–86.

A review of the historical development of the theory of panspermia.

Kirschvink, Joseph L., and Benjamin P. Weiss. 2001. Mars, panspermia, and the origin of life: Where did it all begin? *Palaeontologica Electronica* 4.2.

An argument for why life on Earth probably began on Mars and was transported here.

Melosh, H. J. 2003. Exchange of meteorites (and life?) between stellar systems. *Astrobiology* 3:207–215.

A statistical argument against the exchange of life between stellar systems that leaves the possibility open for exchange among planets in our solar system.

LAST MODIFIED: 01/13/2014

DOI: 10.1093/OBO/9780199941728-0045

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