The Emergence of Organizations and Markets

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Autocatalysis in Chemistry and the Origin of Life

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The purpose of this chapter is to provide background to social scientists on the concept of autocatalysis, drawn from chemistry and the literature on the origins of life. More comprehensive, though less focused, reviews of the early history of life from different theoretical perspectives are provided in Eigen, in Maynard Smith and Szathmáry, and in Margulis and Sagan.[1] The literature on the origin of life is tumultuous, much like the history of biological life itself. The placid and comforting image of Darwin's warm tidal pool as the physical locus for the first emergence of chemical life has been partly replaced (or at least challenged) in the current literature by violent volcanoes and thermal vents. The even more violent crashing of Venus- and Mars-sized proto-planets to create our Earth and its moon lies in the background of these early crescive volcanoes, which may have helped power early evolution. Obviously academic disputes do not compare in degree of violence to this, but much heat and constructive energy has been generated by an ongoing theoretical struggle between the RNA-first position, which places all its explanatory emphasis on the self-organization of nucleic acids, and the metabolism-first position, which focuses on the self-organization of simpler energy-processing chemistries that RNA and DNA later regulated and reproduced. A minority position insists that lipid cell vesicles came first, which both types of chemistry came to inhabit.

[1] Eigen 1992; Maynard Smith and Szathmáry 1995; Margulis and Sagan 1995. Perhaps the best popular treatment is Capra 1996.

This literature review chapter cannot adjudicate these highly technical disputes, even though its assumption will be that all three contending positions have something valuable to contribute. Its purpose is more modest: to point out that the concept of autocatalysis lies at the foundation of all of these positions. The three schools of thought do not dispute the foundational importance of the concept of autocatalysis to the definition and emergence of life. They just dispute exactly which were the primary chemicals and chemical reactions involved in early autocatalysis. If the concept of autocatalysis ever succeeds in its transposition to the social sciences, we likewise can anticipate fruitful contention about exactly which types and combinations of autocatalysis are applicable to which historical episodes of organizational transformation.

This chapter proceeds in four sections: first, a definitional overview of the problem; second, a selective review of the current chemical literature on the origin of life; third, a brief review of formal modeling in this area; and finally a section on autopoiesis, the first not entirely successful attempt to transpose the concept of autocatalysis to the social sciences. I conclude with some remarks about Harrison White and William Sewell Jr., on whose work we build.

DEFINITIONS OF CHEMICAL AUTOCATALYSIS AND LIFE

The motivating puzzle for everyone who studies the origin of life on earth is that life arose very quickly, in geological time. The core facts, as described by Martin and Russell,[2] are these:

> The Earth is 4.5 billion years (Gyr) old, and the first ocean had condensed by ca. 4.4 Gyr. There are good reasons to believe that life arose here by ca. 3.8 Gyr, because carbon isotope data provide evidence for biological CO_2 fixation in sedimentary rocks of that age. By 3.5 Gyr, stromatolites were present, preserved microbial mats indicative of deposition by photosynthetic prokaryotes.[3] By ca. 1.5 Gyr, so-called acritarchs became reasonably abundant, microfossils of unicellular organisms that are almost certainly eukaryotes and are probably algae because of an easily preserved cell wall. By 1.2 Gyr, spectacularly preserved multicellular organisms appear that were very probably red algae.

In other words, as measured directly by fossils, life emerged about 20 percent of the way into the history of the earth. As measured indirectly by chemical traces, life emerged 15 percent of the way into the history of the earth. In such an early epoch, the originally molten earth was still quivering with volcanoes, left over from the giant collision of its birth and subsequent meteor bombardments. Life emerged so early in the history of the earth that the history of the earth itself is shaped by the history of life upon it—for example, the earth's atmosphere of oxygen, not to mention soil and oil.

The definition of life is contested but only in the sense that authors differ as to how many of the following list of items to include in the definition:

1. Thermodynamic throughput of energy
2. Autocatalysis or self-reproduction
3. Cellular enclosure
4. Evolution

This list is almost hierarchical, in the natural-science sense of that term:[4] namely, items lower in the list are included within and presuppose items higher in the list.

Throughput of energy is required not just as fuel for chemical reactions but also for self-organization of any kind, defined thermodynamically as a decrease in entropy. Maximal entropy is defined as randomness in an ensemble; hence decrease in entropy means increase in nonrandomness or order.[5] The Second Law of Thermodynamics states that any ensemble that is energetically isolated will gradually decay into complete randomness and that any ensemble that is energetically coupled to only one reservoir will gradually increase in entropy, going to equilibrium with its environmental reservoir. Material ensembles, in other words, gradually disintegrate and "die." The reason that living systems, which increase in order over developmental and evolutionary time, appear to violate the Second Law of Thermodynamics is throughput of energy. Here ensembles are attached to two reservoirs—an energy source from which order is drawn and an energy sink into which disorder is deposited.[6] Throughput of energy in physical and chemical ensembles induces alignment, patterning, or order into the elements of those ensembles. The earth itself is an ensemble experiencing a throughput of energy, since light from the sun during the day is radiated away as heat into outer space during the night.

Prigogine has done mathematically the most to analyze these "far-from-equilibrium" throughput systems, which he has labeled "dissipative systems."[7] Morowitz added the important addendum that cycling is part of the "pattern" produced by steady-state energy throughput.[8] All authors treat the throughput of energy as

[2] Martin and Russell 2003, 59–60 include citations for each of their numbers. To place these numbers in comparative perspective, the universe is 13.7 billion years old (Weintraub 2011); the sun is 4.6 Gyr; the Cambrian explosion, from which all animal phyla descend, is 0.53 Gyr (Gould 1989; Morris 1998); and humans (i.e., homo sapiens) arose .0002 billion years ago.

[3] Prokaryotes are simple single-celled bacteria, with no internal compartmentalization. Eukaryotes are complex and larger single-celled bacteria with extensive internal differentiation, including mitochrondria and a nucleus. Once aggregated, eukaryotes became cells in higher-level multicellular organisms.

[4] Simon 1969.

[5] The formula for entropy—namely, $S = -k\Sigma_i p_i \ln_e p_i$—is almost identical to that for information in Shannon-type information theory—namely, $I = -\Sigma_s p_s \ln_2 p_s$. Hence many authors equate entropy with information, even though Morowitz (1992, 74, 126) warns against such switching between interpretative contexts.

[6] No system violates the Second Law if both source and sink are included in the definition of "ensemble." Intermediate ensembles "defeat" the Law only through degrading the order in source into the disorder in sink.

[7] Prigogine [1955] 1967; Nicolis and Prigogine 1977, 1989. Prigogine won the Nobel Prize in 1977. The phrase *far from equilibrium* is potentially confusing for social scientists. In this context, it refers to thermodynamic equilibrium or disordered "death." *Steady state* is the term physicists use instead of equilibrium when referring to stable and reproducible patterns generated by throughput.

[8] Morowitz 1966; Morowitz 1968, 29–33.

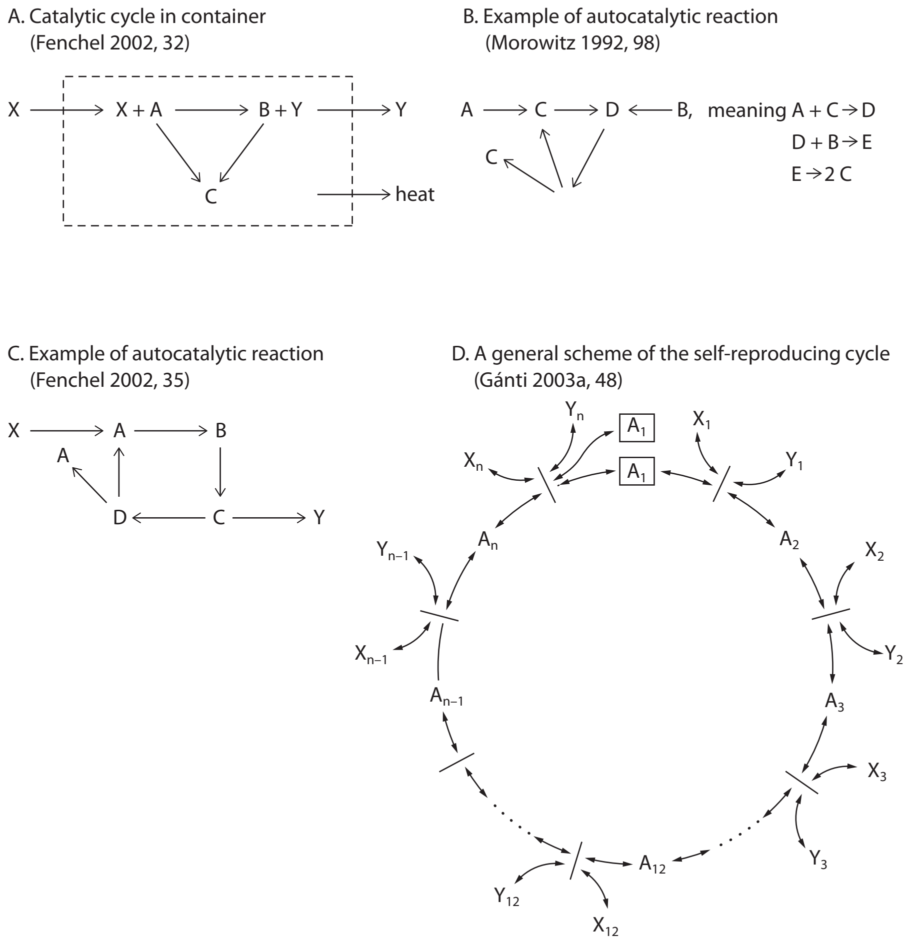


Figure 2.1 Examples of catalytic and autocatalytic chemical cycles.

a necessary precondition to life, but only a few of them treat this criterion as sufficient.[9] As Prigogine made clear, physical thermal convection systems are ordered dissipative systems, without being alive.

Autocatalytic systems are chemical dissipative systems with the criterion of self-reproduction added. The word *chemical*, unlike the word *physical*, implies transformation: elements interact not only by aligning with each other but also by changing each other. The most general definition of self-reproduction is that which was discussed in the introductory chapter to this book: "A set of nodes (in this case chemicals) whose transformational interaction reproduces the nodes in the set." In the face of inevitable dissipation and random decay in constituent chemical elements, chemical systems with the topology of autocatalysis have the potential (realized under favorable kinetic circumstances) to reconstruct their own lost components. In the steady-state case where energetic input equals energetic output, autocatalysis implies self-maintenance of the chemical network as a whole. At the micro level of individual chemicals, however, system self-maintenance is only achieved by the continual regeneration of the constituent chemicals to replace those that have been lost. Simple examples are given in figure 2.1. Self-repair of the system against perturbations that are not too severe is one corollary. If energy input exceeds energy

[9] See Schrödinger [1944] 1967 for a prescient analysis, before DNA was discovered, based on thermodynamics.

Chemical autocatalysis when coupled with a powering energy source and cellular enclosure leads naturally to cells that physically grow and eventually divide. Add a finite resource constraint to growing and dividing cells, and Darwin's natural selection is induced. All then that is missing for evolution is variation, which could be random or could be structured. Evolution, while not part of my and others' definition of life, easily grows out of the lower items on the list, once a few auxiliary features are added.

Speed of evolution, however, is another matter. It took about 70 percent of the earth's history before the early single-celled bacteria ever assembled into multicelled algae. And it took about 88 percent of the earth's history before anything as recognizable as organized critters with body plans emerged. If we were reasoning halfway into the history of the earth, I'm not sure that the concept of evolution would have entered our minds. The inventions of sex and cell death[20] were late arrivals in the history of evolution, which sped up biological evolution enormously, perhaps analogous to the invention of language in human evolution. None of these later steps is explained by autocatalysis alone, but autocatalysis remains a critical processual building block in higher-order explanations of evolutionary and historical transformations.

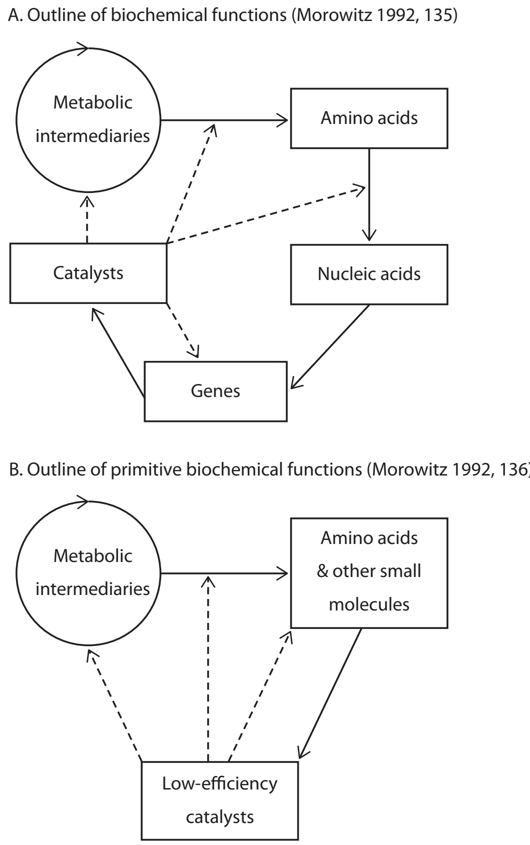


Figure 2.3 Simplified chemistry of life.

THE CHEMICAL ORIGIN OF LIFE

The details of biochemistry are incredibly complicated, even at the level of bacteria. Fortunately social scientists (who deal with enough complexity already) do not need to know those details in order to appreciate the structure and topology of the issues involved in the study of biological genesis. The questions asked in origins-of-life research are more useful to social scientists than are the specific answers generated in that subfield because social scientists have their own versions of these issues. The intellectual objective is to engage in interdisciplinary dialogue about challenging topics of interest to multiple disciplines, not to copy or mimic in either direction.[21]

Again Morowitz is useful to cut to the chase. Figure 2.3 reproduces two of his diagrams, which lay out in schematic overview the chemical structures both of currently living biochemistries and of posited primitive biochemistries. The generality is such that contending RNA-first and metabolism-first positions both can be accommodated. In currently living biochemical systems, metabolism generates amino acids and nucleobases (among other things), which are

of Species: "It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us" (Darwin [1859] 1993, 648). Competitive natural selection lies at the heart of Darwin's laws, to be sure, but intraspecies competition is structured within a tangled web of interspecies ecological and chemical flows that in ensemble more accurately warrant the label of (interdependent) co-evolution than of (autonomous) evolution.

[20] Bacteria can be killed, but they do not die if fed. Left to their own, they are immortal. Programmed death was an historical invention that imposed cell turnover and thus speeded evolution.

[21] Thanks again are due to the Santa Fe Institute, in particular Ellen Goldberg, Erica Jen, and Walter Fontana, for encouraging interdisciplinary dialogue across unusually distant disciplines.

assembled into nucleic acids, which are assembled into genes, which produce protein enzymes that control metabolism, as well as regulate other production links in the grand cycle.[22] The origin problem for this or any other autocatalytic cycle in equilibrium is that each step presupposes previous steps. How can anything be jump-started without the products produced by it? In particular protein enzymes are very complicated macromolecules that control virtually all chemistries in living organisms, and these are created by even more complex strings of genes in DNA. Did Deus ex machina do all this?

The second diagram in figure 2.3, representing primitive biochemistry, simplifies the autocatalysis problem without resolving it. Instead of complicated macromolecules like DNA and protein enzymes, researchers currently imagine "low-efficiency catalysts" to get the earliest autocatalytic chemical system moving. A variety of candidates for the very first iterations of this primitive cycle have been proposed, but nearly everyone now agrees that sooner or later those low-efficiency catalysts were primitive, short-stringed RNA. This is called the "RNA world" hypothesis.[23]

This hypothesis has become hegemonic in the field not because it solves everything but because it allows the simplification of the intractable top diagram in figure 2.3 into the "easier" bottom one. Prior to this simplification, DNA and protein enzymes both were considered enormously complicated macromolecules with various versions of RNA (tRNA, rRNA, mRNA, etc.)[24] serving only the intermediating function of translating between these complex worlds.[25] That is because this is what they do today. But focusing on complicated DNA and proteins directly makes their emergence seem virtually impossible. In the simplified RNA world of the alleged past, however, plastic and multifunctional RNA molecules did double duty: both as DNA inheritance machines and as protein catalysts of chemical reactions in cells. That doesn't mean that they did this very well, but over evolutionary time the "Darwin-Eigen Cycle" kicked in to induce greater specialization and genome precision.[26] This positive feedback loop, which generates genome complexity, is the following: "selection increases [RNA reproduction] fidelity → larger genome size → new functionality evolving → selection increases fidelity." As my first item of business in the formal-modeling section of this chapter, I will review Eigen's hypercycle and quasi-species models, which are referenced here. Molecular-Darwinian conceptual frameworks like these tell us not much in detail about how evolution did it, but they give contemporary biochemists confidence (justified or not) that the transition from the bottom diagram in figure 2.3 to the top one is "just" a matter of Darwinian engineering. Most evolutionary biochemists think they understand that, in principle at least.[27]

The hegemonic RNA-world hypothesis leaves open the question of how the bottom chemical structure in figure 2.3 evolved. To their credit, both of the contending RNA-first and metabolism-first positions have been motivated by exciting empirical findings. Simultaneous with the discovery of DNA,[28] the famous experiments by Stanley Miller,[29] way back in the 1950s, set the origin-of-life agenda for the next thirty years. Those experiments surprisingly generated amino acids just by sending electric sparks, which simulated lightning, through a gaseous mixture of methane, ammonia, hydrogen, and vaporized water. These gases simulated the ideas of Oparin and of Urey (Miller's teacher) about the presumed reductive atmosphere of early earth. Those experiments, together with laboratory syntheses of nucleobases,[30] gave

[22] Food energy inputs and outputs are implicit but not shown.

[23] The phrase is from Gilbert (1986), who suggestively drew attention to and labeled path-breaking experiments by Altman and Cech, which demonstrated catalytic production capacity for transfer RNA (tRNA) and ribosomal RNA (rRNA), respectively. Thereby ribosomes became "ribozymes." Two decades of experimental research on the RNA world since then are reviewed in Orgel 2004 and Penny 2005. I agree with Martin and Russell (2003, 64) that the label "RNA era" would have been more felicitous than "RNA world," in order to eliminate the connotation of a world being self-contained. But it is too late for linguistic corrections like this.

[24] http://en.wikipedia.org/wiki/List_of_RNAs.

[25] Woese (2002, 8745) suggestively emphasizes this "symbolic" or "linguistic" translation function of RNA between the DNA and protein worlds. He provocatively interprets the move from the bottom to the top diagrams in figure 2.3 as "The evolution of modern cells, then, had to begin with the onset of translation."

[26] Poole, Jeffares, and Penny 1998; Poole, Jeffares, and Penny 1999, 881; Penny 2005, 641.

[27] Margulis 1967, 1970, Marulis and Sagan 1995, and Margulis and Dolan 2002; Woese 1998, 2002; and Shapiro 2011 inject informed and healthy doses of skepticism into this consensus. I discuss their views at the end of this section.

[28] Watson and Crick 1953. One of the more famous conclusions in science is their comment, "It has not escaped our notice that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material."

[29] Miller 1953, 1955, 1957.

[30] Two decades of experiments are reviewed in Miller and Orgel 1974, 83–117. Oró and Kimball (1960) were the

empirical support to early pre-DNA hypotheses by Oparin and Haldane,[31] and by Darwin himself,[32] about life emerging from a "prebiotic soup." Another glance at the bottom diagram in figure 2.3 illustrates why all of this experimental ferment consolidated the RNA-first theoretical position:[33] primitive biochemical catalysts might have polymerized spontaneously out of amino-acid (→ protein) and/or nucleobase (→ RNA) components, which then could have triggered metabolism in nearby energy-rich chemicals.[34]

Alas, the exciting RNA-first position has confronted so far insuperable empirical difficulties, one of which is that no geochemist believes anymore the original assumption of Oparin-Urey-Miller about the highly reductive atmosphere of early earth, which made the amino-acid experiments work so well. The consensus now is that the atmosphere on early earth was composed mostly of nitrogen, carbon dioxide, and water vapor with a little bit of chemically more active carbon monoxide and methane possibly thrown in as non-steady-state transients from the moon-forming impact.[35] For a couple of decades, this stubborn fact about the early atmosphere threw into question the optimistic assumption of the RNA-first school that synthesizing amino-acid and nucleobase components of proteins and RNA, respectively, was easy.[36]

This empirical barrier to the RNA-first school of thought no longer seems as daunting as it once did. For one thing, Miller and his colleagues, right before he died, added a little iron to their previous neutral-atmosphere experiments, which seemed to solve the problem.[37] More significant, numerous amino acids and even nucleobases have been discovered on meteors from outer space, dating to the beginning of the solar system.[38] Whatever the chemical synthesis details, in other words, it once again seems a safe assumption that amino acids and nucleobases were there virtually from the beginning, not just on earth but all over the solar system. The emergence of life might not be just an earthly phenomenon.[39]

A second empirical problem has proved to be more recalcitrant. It has so far proven impossible to synthesize RNA in the lab from its nucleobase, ribosome (sugar), and phosphate components. This is the lower-right arrow in the bottom diagram of figure 2.3. Rather than review all the experimental difficulties, which I frankly do not understand, the conclusion of the most prominent RNA-first advocates in the field will be cited:

> A robust, prebiotically plausible synthesis of RNA, if achieved, will dramatically strengthen the case for the RNA world hypothesis. Despite nearly a half a century of effort, however, the prospects for such a synthesis have appeared somewhat remote.[40]

first to synthesize nucleobases. The Miller and Orgel book reported with considerable optimism on the state of the field and hopes of researchers in 1974. Even in 1974, however, everything was not rosy: "Nucleoside synthesis under plausibly prebiotic conditions has proved to be unexpectedly difficult, so much so that no really satisfactory method has been reported" (ibid., 112). See Oró, Miller, and Lazcano 1990 for an updated review.

31 Oparin [1924] 1938; Haldane 1929.

32 "It is often said that all the conditions for the first production of a living organism are now present, which could ever have been present. But if (and oh what a big if) we could conceive in some warm little pond with all sorts of ammonia and phosphoric salts,—light, heat, electricity &c. present, that a protein compound was chemically formed, ready to undergo still more complex changes, at the present day such matter wd be instantly devoured, or absorbed, which would not have been the case before living creatures were formed." Darwin to Joseph Hooker, February 1, 1871, http://bevets.com/equotesd.htm.

33 The first to articulate this position was Muller (1926, 1966). See Lazcano 2010 for history.

34 Indeed the hope was that ATP itself might also have been so catalyzed.

35 Zahnle, Shaefer, and Fegley 2010; Zahnle et al. 2007; Sleep 2010.

36 "A number of experiments were later carried out using CO and CO_2 model atmospheres. However, the synthesis of organic compounds by the action of electric discharges on neutral gas mixtures is much less efficient than when reduced model atmospheres are used. As the gas mixture becomes less reducing (less H_2, CH_4 or NH_3), the yields of organic compounds decrease drastically, with glycine being the only major amino acid synthesized. The presence of methane and ammonia appears to be especially important for the formation of diverse mixtures of amino acids. The main problem in the synthesis of amino acids and other biologically relevant organic compounds with non-reducing atmospheres appears to be the limited amount of hydrogen cyanide that is formed, which is a central intermediate in the Strecker amino acid synthesis and an important precursor for the synthesis of nucleobases" (Cleaves et al. 2008, 106). I have deleted numerous citations, present in the original, from this quote.

37 Cleaves et al. 2008.

38 Chyba et al. 1990; Chyba and Sagan 1992; Cronin and Chang 1993; Ehrenfreund et al. 2002; Martins et al. 2008.

39 All along it has been recognized in the origin-of-life literature that so-called *Panspermia*—the importation into earth of spores of extraterrestrial organisms—cannot definitively be ruled out by our current evidence, especially in light of the enormous shower of meteors carrying organic compounds that descended upon the earth in its early years. However, no complicated macromolecules like nucleic acids and proteins have been found in meteors. An interesting new "aromatic world" hypothesis about the origin of life (Ehrenfreund et al. 2006; Ehrenfreund and Cami 2010) seeks to integrate the extraterrestrial influx of organic materials from early meteors into the existing theories. Moving out even beyond the solar system, Kuan et al. (2003) document the presence of glycine, the most common amino acid, in the Orion galaxy.

40 Anastasi et al. 2008, 273.

> From our discussion of prebiotic chemistry we will conclude that the abiotic synthesis of RNA is so difficult that it is unclear that the RNA World could have evolved *de novo* on the primitive Earth. . . . The polymerization of nucleotides in aqueous solution is an uphill reaction and does not occur spontaneously to a significant extent. . . . Consequently, attempts to polymerize nucleotides from aqueous solution must necessarily make use of external activating agents. . . . It is possible that all of these, and many other difficulties will one day be overcome and that a convincing prebiotic synthesis of RNA will become available. However, many researchers in the field, myself included, think that this is unlikely and that there must be a different kind of solution to the problem of the origin of the RNA World.[41]

An uncharitable way of describing decades of hard experimental work is this:

> The notion of Hadean oceans chock-full of Oparin's prebiotic soup still enjoys some popularity, but the question remains of how a solution at equilibrium can start doing chemistry. Put another way, once autoclaved, a bowl of chicken soup left at any temperature will never bring forth life.[42]

In the language of autocatalysis, all the pieces of RNA seem to be there in the chicken soup. But there is something missing that turns those pieces into a cyclical chemistry that reproduces. For a while, porous clay seemed to be a promising spatial array within which nucleobases could self-organize.[43] But "there is as yet no experimental support for the idea of a self-replicating, informational clay mineral."[44] This is the unfortunate dead-end in which the RNA-first school of thought currently finds itself. The evolutionary road leading out from RNA seems clear, but the evolutionary road leading up to RNA is enshrouded in fog.[45]

The metabolism-first school of thought is a second crack at the origin-of-life problem. This theoretical position goes back to Oparin, but it received a large boost in popularity from the dramatic discovery of life in the late 1970s at the very bottom of the ocean around thermal vents oozing from deep inside the earth.[46] It was not so much the waving tube worms or giant clams that fascinated origin-of-life researchers but the thermal bacteria emerging from within the volcanic vents that provided the worms and the clams their food. This was not a warm tidal pond fueled by photosynthesis; this was life based on sulfur and iron.[47] Thermal vents reminded geochemists of early conditions on earth when volcanoes interacted chemically with oceans with much greater frequency than they do today.[48] This discovery, moreover, dovetailed nicely with the earliest application of genome sequencing to evolutionary questions, which placed thermal archaebacteria at or near the root of the evolutionary tree.[49] Far-from-equilibrium energy throughput obviously is not a problem with thermal vents.

On a basic level, the metabolism-first position and the RNA-first position both agree that autocatalysis in the form of Morowitz's second diagram in figure 2.3 must kick in for chemical life as we know it to emerge. The difference between these positions lies on the emphasis of the metabolism-first school on metallic surface catalysts, which are regarded as having jump-started cyclical metabolism before RNA evolved to do that job more efficiently.[50] Thermal vents are perfect for that job because they are porous rock funnels consisting largely of iron, sulfur, and nickel, arranged in tiny 3D compartments.[51] Thermal vent theory has been criticized because RNA is not stable at the high temperatures (~300° C) of "black smoker" cones.[52] But laterally away from the central rift, the temperature of thermal vents is not too high (~50–60° C), and mixture of magma material with convective seawater is more thorough.[53] In addition, many

[41] Orgel 2004, 100, 109, 114.
[42] Martin and Russell 2003, 62.
[43] Cairns-Smith 1982; Ferris 2002; Huang and Ferris 2003.
[44] Orgel 2004, 114. Orgel (1998) and Shapiro (2006, 107–17) provide more details on this negative assessment.
[45] Not everyone has given up. Anastasi et al. (2008) outline an experimental search procedure to exhaustively explore all the synthesis options involving compounds similar to RNA that have not been tried over the last fifty years.

[46] Corliss et al. 1979.
[47] Wächtershäuser 1992.
[48] Baross and Hoffman 1985, 329; Sleep 2010.
[49] Woese and Fox 1977; Woese, Magrum, and Fox 1978; Woese 1981, 1982, 1987; Achenbach-Richter et al. 1987; Iwabe et al. 1989; Woese, Kandler, and Wheelis 1990; Stetter 1996, 151; Woese 2000.
[50] Wächtershäuser 1988.
[51] Vivid pictures of what thermal-vent precipitates look like up close today, in laboratories, and 3.6 billion years ago (two fossils from Ireland) are shown in Martin and Russell 2003, 63 and Martin and Russell 2007, 1914. Thermal vents structurally have not changed over time.
[52] Miller and Bada 1988; Bada and Lazcano 2002.
[53] Russell et al. 1988; Corliss 1990; Martin and Russell 2007, 1914.

contemporary archaebacteria live in high temperatures (~80–110° C).[54]

Morowitz reminds us that "the chart of metabolic pathways is an expression of the universality of intermediary metabolism. The reaction networks of all extant species of organisms map onto a single chart, the great unity within diversity of the living world."[55] The metabolic network is far too complicated to reproduce in this chapter, but a wall-sized version of it, simplified, has been produced by the Roche pharmaceutical corporation.[56] At the core of this vast chemical network are a set of autocatalytic cycles: the Krebs or citric-acid cycle, which creates numerous biochemical components (like precursors to amino acids) out of food inputs (like carbohydrates, fats, and proteins); the Calvin or pentose-phosphate cycle, which fixes carbon in photosynthesis; the formose cycle, which processes sugars; the fatty-acid cycle, which makes lipids for cell walls; and the uric-acid cycle, which eliminates nitrogen waste. These core autocatalytic cycles are interlinked through metabolic pathways that lead from one to another through chemical-reaction chains. This whole multiple-network metabolic apparatus is regulated by protein enzymes, created by DNA and RNA in response to chemical feedbacks from the operation of the metabolic networks. In this sense, DNA and RNA function not only as inheritance machines for Darwinian evolution but also as chemical components within metabolism, which regulate it.

The metabolism-first school's approach to the origin of life is to shrink this vast metabolic system down to its minimal core and then to imagine chemical ways to construct that. A number of "minimal cores" have been proposed,[57] but the most popular has been the reductive or reverse citric-acid cycle (and components thereof). The reductive citric-acid cycle is the oxidative or regular citric-acid cycle run in reverse: "Where the Krebs cycle takes complex carbon molecules in the form of sugars and oxidizes them to CO2

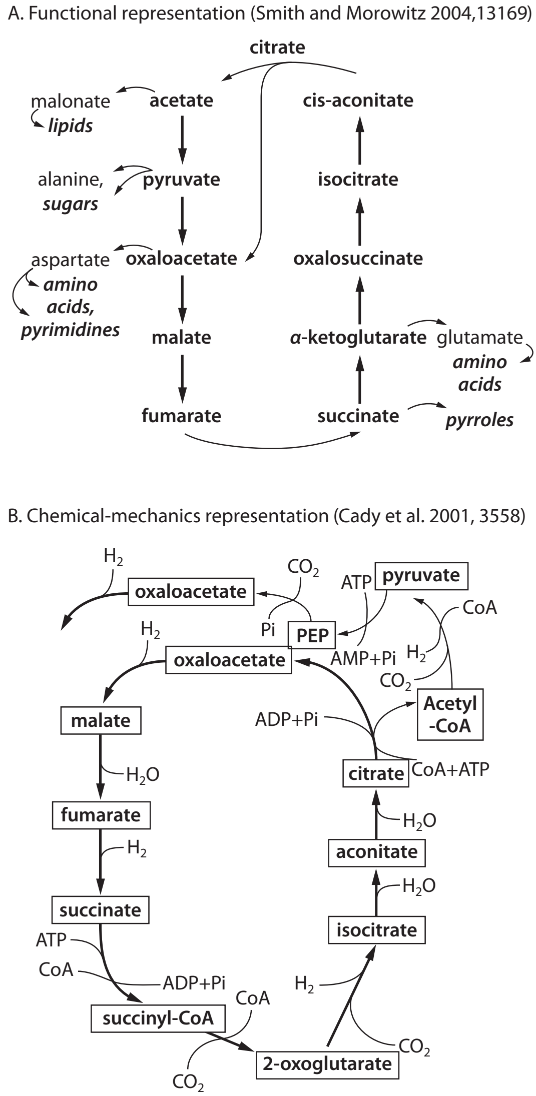


Figure 2.4 Reductive citric-acid cycle.

and water, the reverse cycle takes CO2 and water to make carbon molecules."[58] The reductive citric-acid cycle is described in terms of both chemical outputs and chemical mechanics in figure 2.4. The reason for the metabolism-first school's substitution of reverse citric-acid cycle for normal (oxidative) citric-acid cycle is that the normal cycle requires biochemical input from the Calvin cycle, whereas the reductive citric-acid cycle can process primitive chemicals directly.[59]

[54] Stetter 1996. Recently subterranean archaebacteria also have been discovered deep inside thermal hot springs in Idaho (Chappelle et al. 2002), far removed from any organic food other than primitive CO_2 and H_2. The authors speculate that if life exists on Mars, it will be of this form.

[55] Morowitz et al. 2000, 7704.

[56] See Dagley and Nicholson 1970, which breaks this into manageable pieces.

[57] A creatively "out of the box" suggestion by Jalbout (2008) is that the formose cycle, which makes sugars, formed in the gases of outer space. Formaldehyde and glycoaldehyde, key chemicals in that cycle, have been detected there by radio telescope. The formose cycle is the one metabolic cycle that is known to be possible without enzymes.

[58] http://en.wikipedia.org/wiki/Reverse_Krebs_cycle.

[59] Morowitz 1999; Smith and Morowitz 2004.

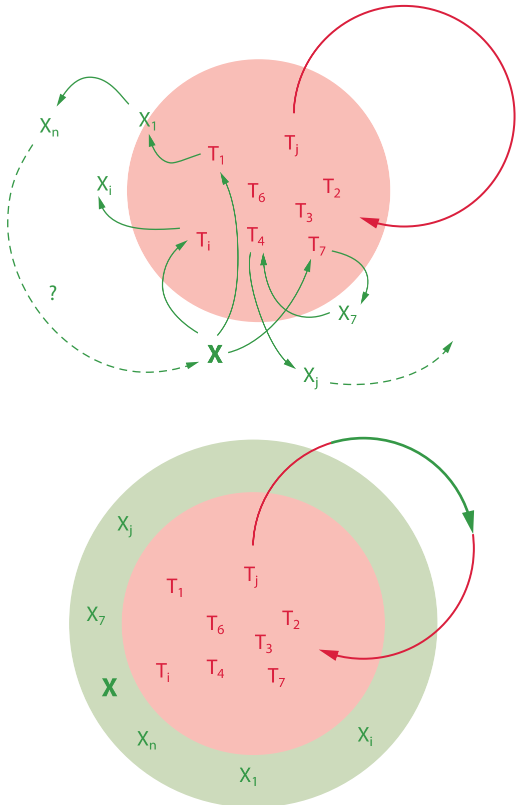


Figure 2.10 Fontana's λ-calculus model of autocatalysis (Fontana 2003, 26). The extension of a self-maintaining organization: A self-maintaining organization is schematically represented by a red set containing "red" components. The autocatalytic "red" organization is perturbed by a "green" component X, spawning a trail of consequences X_i. If that trail gives rise to a pathway that loops back to reproduce the original perturbing agent X, the "red" organization is extended in a self-maintaining fashion by a "green" layer (bottom).

transform concepts into other concepts—even better than it does chemistry. λ-calculus, after all, is symbolic logic at its base. If this proves to be the case, then this computer-science modeling framework might prove to be just as suggestive for the autocatalytic emergence of language as it is for the autocatalytic emergence of life.

All the formal models of autocatalysis reviewed in this section are by definition toy models. Whether their findings carry over into the real world of chemistry requires experimental and paleontological verification. Apart from the details of their individual fates, however, in ensemble they offer the promise that there are general principles about the emergence of life, which are there to be found underneath the enormous variety of particular histories of life forms. The models themselves are the "glue" that might be able to connect the biochemical sciences and the social sciences into symbiosis—or if not they themselves, then others like them. It is at least worth a try. Biochemists and social scientists both study "life" in its different manifestations. That doesn't mean that the word means exactly the same thing in its different realms. But it does mean that the two realms overlap, with evolutionary consequences for both sides.

AUTOPOIESIS

Social scientists are likely to have encountered the chemical concept of autocatalysis through the almost identical philosophical concept of "autopoiesis," invented by the Chilean biologists Maturana and Valera[129] and imported into sociology by the German social theorist Niklas Luhmann.[130] This pre-history and connotation are, from my perspective, most unfortunate. The concept of autopoiesis, unlike the concept of autocatalysis, was invented with no reference whatsoever to the extensive literature on the origin of life.[131] Its intellectual roots lay instead in cybernetic systems theory.[132] Because of this intellectual heritage, autopoiesis emphasizes autonomy and self-control, not interdependence; systems and subsystems, not self-organizing flux; and static equilibrium, not evolutionary dynamics. The concept of autopoiesis itself is fine, but what it is used for is not—at least not if the topic of interest is emergence and the production of novelty. In my opinion, Maturana-Varela and

[129] Varela, Maturana, and Uribe 1974; Maturana 1975, 1981; Maturana and Varela 1980; Varela 1979. Their label "autopoiesis," invented by them, derives from αὐτόσ = self, and ποιειυ = to make.

[130] Luhmann 1982, 1986a, 1989, 1990, [1984 in German] 1995.

[131] The papers by Maturana and Valera, just cited, contain remarkably few non-self citations: 4, 0, z, 23 citations, respectively. Only Varela (1979) makes a serious effort to engage with the field. That book is the only writing to cite Eigen and Schuster, who first published on hypercycles in 1971, but even its references to them are perfunctory.

[132] The first English translation of their 1973 Spanish book—eventually to become Maturana and Varela 1980—was published as a preprint (Maturana and Varela 1975) in the research center on cybernetics at the University of Illinois established by Heinz von Foerster.

APPENDIXES: TRANSACTIONS FROM PAPAL REGISTERS AND ENGLISH LIBERATE ROLLS

Appendix A. Bonsignori Company (Siena): 1250–89

Table 5A.1.
Bonsignori Company Members and Their Transactions, 1250–56

Bonsignori company (Siena)	1250	1251	1252	1253	1254	1255	1256
Bonsignore di Bernardo (1203: salt)							
Bonifacius Bonsignoris	4815		5608, 6777a	L/6264,6386, 6381,6861, 6878	7342,7406, 7489,7980,	8034	XXVIII
Orlandius Bonsignoris	4815		5608	L/6264,6386, 6446,6861	7197,7406	Ch (dir.)	1148
Orlando Bartolomei Malavolti		L/5469		6381		Ch	
Aldebrandinus Bartholomei				6381			
Hugolinus Belmontisb		L/5469		L/6264,6386	7197,7489	165	1148
Capitino Buctin/ Capucino Buccic						165	1148
Bartholomeo Guidii Ciabacte						165	1148
Andrea Iacobi						Ch	
Facius Juncte				L/6264			
Bartholomeo Christophori				6861,6878			
Theobaldum Thebalducii		L/5469					
Rainerium Tetii		L/5469					
Albizo Deuteaute					7342		
Bernardino Prosperini Cendonazi				XXIII,XXV,XXIV	8034		
Bonaventure Bernardini				6381, 6446	7980	Ch,165, XXVIII	1148
Aldebrando Aldebrandini				XXIII,XXV		XXVII, XXVIII	
Ruskitello Cambiid				XXIII			
Amanatto Spinetti5				XXIII			

Notes:

[a]First mention as campsor domini papae (actually campsoris nostri).

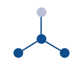
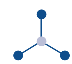
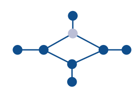
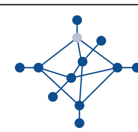
[b]This reorganization (initiation?) of company connected to Sicilian venture (see Chiaudano 1935, 114). Scali also mobilized as campsors papae at this time.

[c]In June 1255, part of Tolomei company (English 1988, 15).

[d]In June 1255, part of Tolomei company (English 1988, 15).

[e]Part of Scali company (though not really consolidated yet).

Table 12.5.
Local Network Positions

Network position		*N*	Percentage of nonisolate	Means of ego network statistics	Graph illustration[a]
I.	Isolate	12,378	-	Size: 0.00 Alters' size: 0.00 Cohesion: 0.00 Alters' cohesion: 0.00	
D.	Dyad member	1,260	22.12%	Size: 1.00 Alters' size: 1.00 Cohesion: 0.00 Alters' cohesion: 0.00	
P.	Small star periphery	1,985	34.86%	Size: 1.22 Alters' size: 3.34 Cohesion: 0.00 Alters' cohesion: 0.00	
L.	Large star periphery	280	4.92%	Size: 1.05 Alters' size: 12.10 Cohesion: 0.00 Alters' cohesion: 0.00	
S.	Star center	543	9.53%	Size: 3.37 Alters' size: 1.35 Cohesion: 0.00 Alters' cohesion: 0.00	
C.	Cohesive cluster member	899	15.79%	Size: 2.84 Alters' size: 6.82 Cohesion: 0.46 Alters' cohesion: 1.20	
G.	Strongly cohesive group member	728	12.78%	Size: 2.71 Alters' size: 9.91 Cohesion: 2.40 Alters' cohesion: 8.55	
Total		18,073	100.00%		

[a] Gray node indicates local network position in graph illustrations.

strongly cohesive group (G). In 1998 the firm becomes a small star periphery again (P). At the end of the period, from 2000, the star shrinks into a dyad (D).

On this basis, we have 1,696 such network histories—sequences of positions—for each of the firms in our population. Some firms' histories, of course, are likely to resemble each other (not because they are tied to each other but because they have similar sequences of network positioning) while differing from others. Using an optimal matching algorithm modified from the analysis of gene sequencing, we construct a matrix of pairwise distances between each of the sequences.

Optimal matching of sequences is a method that historical sociology borrowed from the natural sciences. The use of optimal matching in the natural sciences typically does not involve temporality; instead, the sequences are typically spatial. One important area in the natural sciences in which optimal matching is used is DNA analysis. DNA molecules are considered to be very similar even when large chunks of the molecular sequence are in reverse order (Sankoff and Kruskal 1999). Unlike measures based on vector similarities, optimal matching has some advantages for historical application; but it has been justifiably criticized by Wu (2000) and others (Levine 2000) for its lack of sensitivity to the directionality of time. For example, a firm that is an isolate for eight years and then becomes a small star periphery in 1995 for the next

Table 12.6.
Pathways' Typical Sequences of Network Positions

Pathways	*N*	Typical sequence of network positions[a]															Share in categories of capital in 2001 (%)	
		87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	All	Networked-foreign
Star-periphery recombinants																		
1	34	I	I	I	S	S	S	S	S	S	S	S	S	S	S	S	7.1	1.4
2	106				P	P	P	P	P	P	P	P	P	P	P	P	3.8	3.0
Cohesive recombinants																		
3	70		I	I	P*	P	C	C*	C	C	C	C	C	P	P	P	18.2	36.1
4	44			C	C	C	G	G	G	G*	G	C	C	C	C	C	4.9	12.2
5	65			C	C	C	G	G	G	G	G	G*	G	I	I	I	3.6	0.6
6	56	I	I	I	I	I	I	I	I	L	L	C	C	G	G	G	7.0	6.7
Start-ups																		
7	63			P	P*	P	P	P	P	P	I	I	I	I	I	I	3.4	0.0
8	97				D	D*	D	D*	I	I	I*	I	I	I	I	I	4.2	0.3
9	70				P*	P	P	P	P	D	D*	D	D	D	D	D	3.9	8.6
Second wave networks																		
10	136	I	I	I	I	I	I	I	I	D*	D	D	D	P	P	P*	9.1	21.6
11	101											D*	D*	P	P	P	3.3	8.7
Isolates																		
12	854						I	I	I	I	I	I	I*	I	I	I	30.7	0.0
Total	1,696																100.0	100.0

Notes: I = Isolate, D = Dyad member, P = Star periphery, L = Large star periphery, S = Star center, C = Cohesive cluster member, G = Strongly cohesive group member. Asterisked figures represent surges in foreign investment when new foreign capital amounted to at least 20 percent of the total capitalization of the pathway in that year.

[a]Cells indicate network positions from table 12.2.

Table 12.7.
Sizable Foreign Ownership in 2001: Logistic Regression Estimates

	Sizable foreign ownership in 2001 (Yes = 1)	
Independent variables	1	2
Pathways[a]		
Star-periphery recombinants		
1(I-S)	−5.513**	−5.781**
2(P)	−.422**	−.785**
Cohesive recombinants		
3(I-P-C-P)	−.065**	.622**
4(C-G-C)	.485**	1.112**
5(C-G-I)	1.327**	2.047**
6(I-L-C-G)	−1.091**	−1.341**
Start-ups		
7(P-I)	1.565**	2.087**
8(D-I)	.342**	1.076**
9(P-D)	1.419**	2.756**
Second wave networks		
10(I-D-P)	1.218**	1.752**
11(D-P)	1.184**	1.717**
Industry[b]		
Agriculture		−2.973**
Food industry		2.779**
Energy and mining		.996**
Chemical industry		4.756**
Heavy industry		1.768**
Light industry and textiles		.378**
Construction		−.517**
Wholesale		.391**
Retail		3.695**
Finance		.359**
Local network position in 2001[c]		
D (Dyad member)	−.720**	
P (Small star periphery)	−.097**	
L (Large star periphery)	1.892**	
S (Star center)	.140**	
C (Cohesive cluster member)	−.039**	
G (Strongly cohesive group member)	−2.737**	
Early foreign ownership (1990)		4.326**
Constant	.205**	−.935**
N	1286.........	1286.........
-2LL	1709.03....	1326.78....
R-squared	.249...	.498...
Percentage correctly classified 74.8......		66.7......
X^2 (df)	302.45 (11)	684.71 (28)
p-value	.000...	.000...

Notes: I = Isolate, D = Dyad member, P = Star periphery, L = Large star periphery, S = Star center, C = Cohesive cluster member, G = Strongly cohesive group member.

[a]Pathway 12 (Isolates) is the omitted category.

[b]Services and transportation is the omitted category.

[c]Local network position 1 (Isolate) is the omitted category.

** $p < .05$