Estimates of the magnitude of the global NPP may improve as better knowledge of algal physiology and ecology is incorporated into the computations. In contrast, the spatial and temporal evolution of the ocean productivity is already described with a tremendous wealth of detail. The synergistic use of modeling and data from various sensors (for ocean color, temperature, clouds, wind, surface height) is the recipe for future progress. An international strategy for the implementation of a global-scale, internally consistent, temporally uninterrupted set of such data is imperative (*19*).

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PERSPECTIVES: ORIGIN OF LIFE

Some Like It Hot, But Not the First Biomolecules

Jeffrey L. Bada and Antonio Lazcano

Ever since the pioneering work of Aleksandr Oparin and John Haldane nearly a century ago, the prebiotic soup theory has dominated thinking about how life emerged on Earth (*1*, *2*). According to the modern version of this theory, organic compounds accumulated in the primordial oceans and underwent polymerization, producing increasingly complex macromolecules that eventually evolved the ability to catalyze their own replication (see the figure). But is this really how life originated? And what were the conditions that favored its emergence?

Experimental support for the prebiotic soup theory was first provided in 1953 by Stanley Miller, who demonstrated that important biomolecules such as amino acids could be synthesized under simulated early-Earth conditions. The discovery of extraterrestrial amino acids in the Murchison meteorite in 1970 showed that reactions like those in Miller's experiment (involving ammonia, hydrogen cyanide, and aldehydes or ketones) occurred on meteorite parent bodies early in the history of the solar system.

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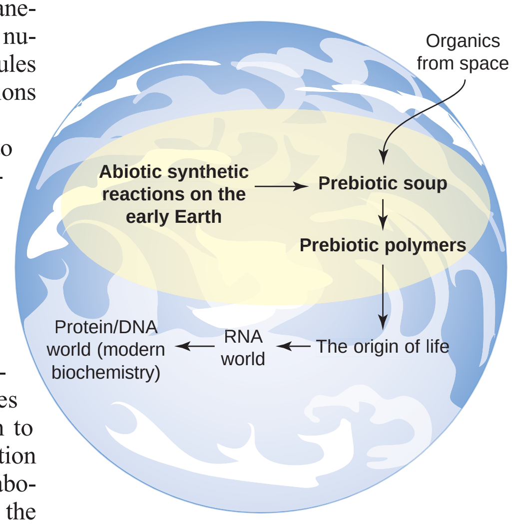
The inventory of organic compounds on the early Earth may thus have been derived from a number of sources: Earth-based syntheses, asteroid and comet impacts, and the accretion of meteorites and interplanetary dust particles. These abiotic, monomeric organic compounds would have accumulated in the early oceans, providing the raw material for subsequent reactions. Eventually these reactions would have led to life as we know it: membrane-enclosed systems of polymers such as nucleic acids and proteins, the core molecules involved in the central biological functions of replication and catalysis.

For monomers in the early oceans to undergo polymerization, a thermodynamically unfavorable process, concentration of the soup constituents, would have been required. Experimental evidence suggests that clays, metal cations, and imidazole derivatives, among others, may have catalyzed prebiotic reactions, including polymerization. Selective absorption of molecules onto mineral surfaces has been shown to promote concentration and polymerization of various activated monomers in the laboratory (*3*). Because absorption involves the formation of weak noncovalent bonds, mineral-based concentration would have been most efficient at low temperatures (*4*). Other processes such as evaporation of tidal lagoons and eutectic freezing of dilute aqueous solutions may also have assisted concentration. The latter process is particularly effective in the nonenzymatic synthesis of oligonucleotides (*5*).

As polymerized molecules became larger and more complex, some of them began to fold into configurations that could bind and interact with other molecules, expanding the list of primitive catalysts that could promote nonenzymatic reactions. Some of these catalytic reactions, especially those involving hydrogen-bond formation, may have assisted in making polymerization more efficient. As the variety of polymeric combinations increased, some polymers may have developed the ability to catalyze their own imperfect self-replication and that of their molecular



How did life emerge? Various steps thought to be involved in the origin of life on Earth. The shaded area represents the contribution from the metabolist theory to the overall scheme.

SOURCE: JEFFREY L. BADA, ILLUSTRATION: PRESTON MORRIGHAN/*SCIENCE* kin. This would have marked the appearance of the first molecular entities capable of multiplication, heredity, and variation, and thus the origin of both life and evolution.

This scheme is necessarily speculative but has an intrinsic heuristic value: Experimental models can be developed to construct a coherent narrative of this evolutionary sequence. The chemical nature of the polymers used by the first self-replicating entities remains uncertain, but threose-based RNA analogs and peptide nucleic acid molecules are possible contenders (*6–8*). It is generally thought that the first living molecular entities evolved into the RNA world, which was in turn a stepping stone to the DNA/protein world of modern biochemistry.

Low temperatures are the most favorable for the long-term survival of organic compounds (*9*), especially those carrying genetic information, and for the stability of catalytic polymer configurations. Studies of fossils have shown that ancient DNA is preserved for ~100,000 years in cool, high-latitude environments, compared with only 1000 to 10,000 years in warmer, lower latitude environments (*10*, *11*). RNA is much more fragile (*12*). Although the survival of nucleic acids may be extended by encapsulation into hydrocarbons, such as amberlike resins (*10*), it is unknown whether this would have been important in enhancing the stability of genetic molecules in early biotic systems.

The prebiotic soup scenario thus suggests that the first living entities appeared, and evolved through the RNA world to DNA/protein biochemistry, when Earth was cool rather than boiling hot. Because of the reduced luminosity of the young Sun, Earth may indeed have been completely covered with ice during its early history (*13*). The first self-replicating molecular entities may have developed under these conditions from the prebiotic organic ingredients.

In the last decade, the validity of the prebiotic soup theory has been questioned, particularly with respect to the robustness of polymer synthesis. An alternative "metabolist" theory has been proposed (*14–16*), although it is not a new idea (*17*). According to this theory, the first living system on Earth was a primitive metabolic life characterized by a series of self-sustaining reactions based on monomeric organic compounds made directly from simple constituents (CO_2, CO) in the presence of metal sulfide catalysts. A primitive type of reductive citric acid cycle is often cited as a model. According to this theory, life in its beginning was nothing more than a self-sustaining chain of chemical reactions associated with mineral surfaces, with no requirement for genetic information. Metabolic life is thus rightfully referred to as "life as we don't know it" (*18*).

Self-sustaining autotrophic chemical reactions could have arisen in any environment, as long as the reactant/product molecules survived long enough to continue to be part of the reaction chain. Proponents of this scenario, however, generally favor hydrothermal environments [for example, see (*19*)]. Various metabolic reaction schemes have been proposed and investigated, but none have been demonstrated to be autocatalytic. Nor are there any empirical indications that this is even possible in a prebiotic context (*20*).

Furthermore, most of the proposed reactions are probably not unique to hydrothermal settings and would also occur at lower temperatures, albeit at slower rates (*21*). Exceptions may include the formation of short peptides from amino acids. This reaction becomes thermodynamically more favorable with increasing temperature, but peptide bonds are also rapidly hydrolyzed at elevated temperatures (*22*). The steady-state concentration of peptides under hydrothermal conditions is therefore problematic.

If self-sustaining reaction chains did arise on early Earth, they could have played an important role in enriching the prebiotic soup in molecules not readily synthesized by other abiotic reactions or derived from space. The metabolist theory can thus be viewed as a component of the prebiotic soup theory (see the figure). But regardless of its initial complexity, autocatalytic chemical-based metabolic life could not have evolved in the absence of a genetic replication mechanism ensuring the maintenance, stability, and diversification of its components. In the absence of hereditary mechanisms, autotrophic reaction chains would have come and gone without leaving any direct descendants able to resurrect the process.

Life as we know it consists of both chemistry and information. If metabolic life existed on the early Earth, converting it to life as we know it would have required the emergence of some type of genetic information system. Polymer stability would have been critical as an autocatalytic reaction system advanced to the point of synthesizing information-carrying molecules, such as nucleic acids, which deteriorate rapidly at elevated temperatures (*10*, *12*). As metabolic life evolved closer to modern biochemistry, it would likely only have been feasible in cool environments.

Proponents of a high-temperature transition from purely chemical reactions to the first autonomous self-replicating entities and their evolution into cellular organisms often assert that the universal tree of life appears to be rooted in hyperthermophilic (high-temperature) organisms. However, this argument is flawed. First, there is disagreement about whether the deepest branches in the tree of life are indeed occupied by heat-loving organisms (*23*). Second, primitive stages of life that may have existed before protein biosynthesis was invented are not amenable to molecular phylogenetic analysis. Finally, alternative mechanisms can explain the early emergence of heat-loving organisms. For example, they may have been the survivors from early Archean high-temperature regimes generated by severe impact events (*24*).

If the transition from abiotic chemistry to the first biochemistry on the early Earth indeed took place at low temperatures, it could have occurred during cold, quiescent periods between large, sterilizing impact events (*13*). But regardless of how the first life arose, it may not have survived subsequent impacts. Life may have originated several times before surface conditions became tranquil enough for periods sufficiently long to permit the survival and evolution of the first living entities into the prokaryotic microbes whose remnants may be present in ~3.5-billion-year-old rocks (*25*).

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