

CHEMICAL EVOLUTION AND ORIGIN OF LIFE

Ganga Shy Meena

Assistant Professor, Chemistry, S.C.R.S. Govt. PG College, Sawai Madhopur, Rajasthan, India

ABSTRACT: Chemical evolution and the origins of life is a topic that spans and transcends many domains: all disciplines of science, eras, cultures, and even space. (1,2) It is a topic that enduringly captures the imagination of scientists and the general public alike. (3–5) Understanding how life arose on the Earth and elsewhere is a historical and reconstructive endeavor, but it is also very much a contemporary and ever-refreshing scientific undertaking. (6) These efforts have rich histories and have been driven by competing ideas ranging from protein-, RNA-, metabolism-, and lipid-world hypothesis to “far-out” ideas such as panspermia. (7–12) From the perspective of chemists this pursuit is focused on understanding how elements and molecules that accumulate on a young planet can transform—under the abiotic geochemical constraints—into self-assembling, self-sustaining interactive systems with emerging patterns and behavior, and begin to evolve into what could be considered as living entities. (13)

KEYWORDS: chemical evolution, origin of life, chemistry, earth, geochemical, endeavor, abiotic

I.INTRODUCTION

From the viewpoint of astrochemistry, prebiotic-chemistry, and biochemistry, this thematic issue covers our current understanding of a spectrum of topics associated with the chemical origins of life. Along with their compilations of impressive advances, each contribution also acknowledges remaining unsolved problems and challenges that are to be faced as we aspire to address the grand question “Can the origins of life be demonstrated or understood experimentally?” While answering that question in a historically accurate context may be not possible, it is indeed within the grasp of chemists (with guidance from observations in astrochemistry, geological constraints of early Earth and its atmosphere, prebiotic organic chemistry and extant biochemistry) to demonstrate in the laboratory the transformations of molecules—by chemical reactions—to systems that approximate the behavior/phenomenon observed in biology. (14) Although this may fall short of “recreating life in a test tube”, it surely would be a more modest—but still a powerful—substantiation of the emergence and evolution of chemical processes that can lead to the origins of life.

This thematic issue begins with Sandford and colleagues describing the Prebiotic Astrochemistry and the Formation of Molecules of Astrobiological Interest in Interstellar Clouds and Protostellar Disks, where planetary systems form, thus laying the foundation for chemical species that are available for processes leading to the origins of life on planets. If this process is indeed “universal” then questions arise about the possibility of extraterrestrial life elsewhere in the universe, and Sandford and colleagues suggest that life may be common where local conditions favor these chemical processes. With Earth being our only current example of a planet harboring life to guide our search for life elsewhere, there must be a set of criteria for life detection missions using our understanding of the essence and uniqueness of biology and its processes. (15) One such singularity of biology on the Earth is homochirality, including the use of L-amino acids and D-sugars of single-handedness. (16) However, using chiral asymmetry as a definitive biosignature is complicated by nonbiological processes that can interfere. Glavin et al. review the enantiomeric and isotopic compositions and distributions of molecules found in meteorites and propose a set of criteria for The Search for Chiral Asymmetry as a Potential Biosignature in our Solar System. These authors also present arguments for “sample return missions” that may represent our best chance to establish firmly the origins of chiral asymmetry as a potential biosignature of life elsewhere in our solar system.

Once source molecules, such as amino acids, nucleobases, and sugar building blocks have been deposited (or formed in situ) on the early planet (e.g., Earth), the ensuing interactions and reactions between them leading to more complex molecules are hypothesized to be a natural part of the processes under geochemical constraints. (17) For example, phosphorylation, a central reaction in the metabolic, structural, and replicative processes in biology, is also widely assumed

to have played an important role in jumpstarting chemical evolution toward life on the early Earth. (18) As Pasek points out, the Thermodynamics of Prebiotic Phosphorylation can be used to evaluate the likelihood of various sources, processes, and geochemical environments that enabled the conversion of inorganic phosphorus compounds to organic phosphates for further processing. Amino acids are prebiotically plausible compounds of the early Earth and are the building blocks of peptides and proteins, which are the catalytic engines of extant biology. (19) Prior to the emergence of coded protein enzymes, noncovalent interactions of prebiotic peptides could have played a key role in the emerging interconnected molecular networks. Ashkenasy, Lemán and colleagues summarize mechanisms of how amino acids (and coexisting molecules) were transformed into peptides and protopeptides and discuss the early roles of Prebiotic Peptides as Molecular Hubs in the Origin of Life. Furthermore, they review the plausible interactions of prebiotic peptides (and protopeptides) with other classes of molecules, thereby emphasizing a systems chemistry approach (20) for synergistic interactions in chemical evolution.

Another crucial class of molecules in life are nucleotides, the monomers of RNA and DNA, whose prebiotic availability is more challenging when compared to amino acids. (21) Nevertheless, the central role played by RNA in extant biology, especially of the ribosome in peptide synthesis, has forced the reckoning with an RNA world scenario on early Earth. (22) This powerful impetus has resulted in intensive efforts to fashion plausible prebiotic synthesis of canonical nucleotides. Krishnamurthy and colleagues review the current status the Chemistry of Abiotic Nucleotide Synthesis in a prebiotic context and point to the remaining challenges in elucidating pathways to the building blocks of RNA and DNA that are universally acceptable as prebiotically plausible in an early Earth geochemical context. The plethora of noncanonical products that are formed in many of the reactions that produce the canonical sugars (ribose) and nucleobases (A, U, G, and C), raises the question: Were alternative nucleosides and nucleotides involved in chemical evolution and the origins of life? (23) Hud et al. point out in their review, Prebiotic Syntheses of Noncanonical Nucleosides and Nucleotides, that alternative nucleobases, sugars, backbone linkers, and nucleosides/-tides would have been formed by similar or competing chemistries. More than the four canonical nucleotides for RNA, these alternative building blocks have the potential to give rise to self-assembling/functional alternative proto-RNA or pre-RNA candidates, whose roles need to be given serious consideration and evaluated in the chemical evolutionary processes and transitions leading to extant biopolymers on the early Earth. (24,25)

In all of the above scenarios, the chirality of the building blocks must be considered, especially as one proceeds toward polymeric and supramolecular assemblies. How homochirality or one-handedness manifested in biology as D-sugars and L-amino acids is an extremely important, but far from understood, phenomenon. (26) Blackmond tackles this question by considering Autocatalytic Models for the Origin of Homochirality and discusses the Soai reaction (the only known example of an amplifying autocatalytic reaction) in depth as a model to examine whether a prebiotically plausible variant would be feasible. Increasingly, it appears that the emergence of homochirality is not determined by a single event but rather by a series of synergistical and sustained chemical and physical processes.

II.DISCUSSION

While the historical details are still unclear, at some point evolution, chemical or biological, sorted out all that was necessary to make ribozymes, catalytic molecules encoded in RNA—as epitomized by the ribosome, which is responsible for coded-protein synthesis in all living systems. (25) Williams and colleagues, in their review, Root of the Tree: The Significance, Evolution, and Origins of the Ribosome, argue that ribosome complexity is a molecular fossil that has implied information about ancient biological processes, which allows for a reconstruction of how the proteins and RNA coevolved—as the ribosome became a ribozyme (24) possessing the exquisite specific activity of peptide synthesis. One might surmise that the earliest ribozymes would have been crude constructs possessing not-so specific activities, molecules with rather promiscuous activities, catalyzing a range of reactions. However, Chen et al. examine the evidence and discuss the Promiscuous Ribozymes and Their Proposed Role in Prebiotic Evolution. Their review suggests that the *de novo* ribozymes are not more promiscuous than their evolved counterparts pointing to the advantage of being promiscuous under selective pressures for prebiotic chemical evolution. In the final article, Maurel and associates consider the function of ribozymes under high pressure, examining the structure–function relationship of the self-cleaving hairpin and hammerhead ribozymes. What they describe in Ribozyme Chemistry: To Be or Not To Be under High Pressure suggests that such activities of these ribozymes are slowed down by increase in pressure. They examine plausible mechanisms to

account for this behavior, which they discuss in the context of the extreme conditions that can occur in deep-sea vents or hydrothermal surfaces.

Through the various articles in this thematic issue on Chemical Evolution and the Origins of Life we hope the reader will see how this collective scientific endeavor is making meaningful progress on multiple fronts and offering plausible alternative solutions to long-standing problems for which once attractive and popular solutions have not held up to experimental scrutiny. The intent of this special issue is not to make the claims that specific problems have been solved, but to highlight the progress made so far and to emphasize that there are still problems that are (and may be) unsolved. (23) This special issue should be construed as an open invitation and a call for more chemists to get involved in this fascinating and enigmatic journey (22)—of developing a systematic understanding of the origins of life from a chemical perspective: the chemical-beginning, chemical-evolution, and chemical-life.

III.RESULTS

The solar system formed about 5.5 Ga, and took a billion or so years to cool. From that point on the environment was probably set to allow the chemistry to get going. But where exactly might this have occurred—can we identify candidates for the role of Darwin's 'warm little pond'? Sleep et al. [1] (Stanford) argue that a suitable environment might have been provided at submarine hydrothermal vents above serpentinite rocks, where chemical gradients of dissolved hydrogen gas and hydrogen ions could have provided a source of chemical free energy. Primitive life might have been established in pores contained within vent chimneys.

What kind of chemistries might have generated the building blocks on which the earliest life forms might have been based? Everyone knows the early experiments of Stanley Miller showing that subjecting a gaseous chemical mixture that might resemble the early Earth's atmosphere to electrical discharge could produce relatively complex compounds such as amino acids. But if we make the assumption for now that nucleic acids were required at an early stage, can we construct a plausible scenario that could have led to prebiotic synthesis of nucleosides, the basic building blocks of RNA? While it was previously assumed that nucleosides would be made by joining pre-assembled ribose and nucleobase entities, Powner & Sutherland [2] have shown that a complete pyrimidine nucleoside can be built in a single entity beginning with a reaction between cyanamide and glycolaldehyde. Of course, an important aspect of all biological macromolecules is that they are constructed from chiral monomers, and the possible origins of enantiomerically pure amino acids and ribonucleotides are discussed by Blackmond [3] (Scripps).

We next consider how self-assembling systems could have arisen at the early stages of life. This would require some kind of compartmentalization to form protocells, possibly involving lipid membranes. Hanczyc [4] (Odense) shows how self-assembled oil droplets can move around, powered by the hydrolysis of oleic anhydride, exhibiting a kind of chemotaxis sensitive to pH gradients. Szostak [5] (Harvard Medical School) discusses membrane self-assembly, and the advantages of mixtures over single compounds and systems chemistry in general.

At this point, we must address one of the main themes of the discussion meeting, the proposed central role of RNA. In all living cells in the present biological world, there is a marked division of labour between the macromolecules used to store and transmit genetic information (nucleic acids) and those that perform the processing (proteins). Proteins are the chemical workhorse of the cell that keeps its metabolism running along. They are well suited to the role of chemical catalysis, being able to bring a range of side chains with different chemical structures to bear on this task. The nucleic acids seem indispensable, because without their capacity to store information there can be no evolution, and without that there can be no refinement of primitive organisms. But a massive chicken and an egg problem emerges in thinking about how all this got started. In contemporary biology, nucleic acids require enzymes to make their precursors and for replication, and proteins require nucleic acids to provide the information for their synthesis. It is hard to imagine how this complicated interwoven system began. On the other hand, if one type of molecule carried out all the required functions, informational and catalytic, then this would simplify the process greatly. So it was proposed many years ago that perhaps an early form of self-replicating life was based solely on RNA, with no proteins involved. RNA contains information in the order of its

nucleotide bases, and could specify its own replication. But could it also act as a primitive enzyme? For a long time, there was very little precedent for the idea. However, the discovery of the group I intron [6] and ribonuclease P [7] ribozymes, and perhaps the lead ion-induced cleavage reaction of tRNA [8] provided that precedent, increasing the possibility of RNA-based life existing approximately 3.6 Ga. This has been called the RNA World hypothesis, as elegantly set out recently by Mike Yarus (Boulder) [9].

RNA occupies a small fraction of the chemical space that proteins cover, consisting of ribose-phosphate and four rather similar heterocyclic bases. Unlike proteins, RNA is a poly-anion, and will be associated with metal ions to neutralize charge. A few ribozymes can be found in contemporary cells, including the above-mentioned RNase P and self-splicing introns—in addition, mRNA splicing in eukaryotes is probably catalysed at least in part by the U2 : U6 small nuclear RNA. What is arguably the most important reaction in the cell, the condensation of amino acids to form polypeptides, is also RNA catalysed. Thus, the ribosome is a ribozyme, and ancient. RNase P is present in all domains of life, and Altman [10] (Yale) argues persuasively that this is also an ancient RNA.

Peptidyl transferase aside, all the remaining ribozymes we find catalyse phosphoryl transfer reactions, either hydrolysis or transesterification. Precedent from the protein world suggests that there are two ways to achieve this, using either metal ions or general acid–base catalysis. Lilley [11] argues that all the nucleolytic ribozymes use variations on the theme of general acid–base catalysis, predominantly using nucleobases. Catalytic efficiency is inherently limited by the unfavourable pK_a values of these, but if this is factored out then these ribozymes are potentially almost as good as a protein like ribonuclease A. As we move to the larger ribozymes, such as RNase P and the self-splicing introns, we seem to switch mechanisms to metal ion-based catalysis.

GlmS provides a fascinating glimpse into how the limitations of chemical functionality in the nucleobases could be expanded by recruitment of a small-molecule cofactor. Here, the role of the general acid in cleavage is taken by glucosamine-6-phosphate, as shown in the crystal structures of Hiller & Strobel [12] (Yale) and Ferré-D'Amaré [13] (National Institutes of Health). The role of guanosine in the group I intron ribozyme is another pointer, although this is not catalytic. This extension of ribozyme activity might also suggest that there could be other ribozymes using cofactors in modern cells. These might be using quite different chemistry, and so have escaped detection to this point.

However, for now, the range of chemistry employed by the known ribozymes is really quite limited, and a workable RNA-based metabolism would have required a much wider range of ribozyme activity. One way to address this is to use in vitro selection to isolate activities that might have been essential to the viability of such life. Demonstration of the feasibility of such ribozymes offers a kind of proof of principle of an RNA world. RNA catalysts that accelerate radically different reactions have been isolated, including Diels-Alder pericyclic reactions [14] and Michael addition [15]. Clearly, a fundamental requirement would be a ribozyme that can replicate RNA, and the related ligase, and these have been isolated in the Bartel laboratory [16,17]. Piccirilli & Koldobskaya [18] (Chicago) present the structure of the Bartel ligase RNA, arguing for a two-metal ion mechanism. Would such ribozymes have been efficient enough to support self-sustaining RNA-based organisms? One essential requirement would have been a polymerase activity that could replicate at least a few hundred nucleotides with reasonable accuracy, and this has not yet been achieved by in vitro selection, although progress continues to be made. On the other hand, chemists have only been doing this for a few years, while nature had millions of years to experiment, so perhaps we must keep an open mind.

But ultimately, the clear advantages offered by proteins as the cell's chemical engine had to win out, perhaps leaving only the remnants of RNA catalysis in a few remaining ribozymes and coenzymes like NAD. The RNA world might only have lasted a relatively short period of time, and may always have had amino acids and short non-coded peptides associated with it because of concurrent prebiotic chemical synthesis. GlmS may suggest how this transition might have started. Perhaps similar ribozymes recruited amino acids or short peptides to augment their function, and from that point it is a fairly short step conceptually at least to the point at which the protein tail wagged the RNA dog. But the essential requirement of a transition to protein-based life is the creation of some kind of translation system.

The first requirement of translation is to link together the RNA components and the protein building blocks. Yarus [19] discusses some very basic reactions carried out by short oligonucleotides with aminoacyl adenylate, a kind of primitive aminoacylation reaction, and using in vitro selection Suga et al. [20] (Tokyo) have isolated RNA species that carry out amino acid charging reactions on tRNAs. Convincing thermodynamic arguments made by Pascal & Boiteau [21] (Montpellier) point to a crucial early role for aminoacyl adenylates. These would be synthesized by chemical aminoacylation of ribonucleotides with high free energy amino acid derivatives such as N-carboxyanhydrides, rather than by reaction of amino acids with ribonucleoside triphosphates. With 20 different amino acids in contemporary biology, the fidelity of aminoacylation is a challenge, discussed by Schimmel [22]

IV. CONCLUSIONS

Using aminoacylated RNA molecules, the final requirement in the transition to the protein world is a translation apparatus. In our cells, this is of course the ribosome. But how did this emerge from the RNA world? The ribosome must carry out two functions, decoding the genetic code of the RNA, and catalysing the condensation of the amino acids to form the polypeptide. These functions are the responsibility of the small and large subunits, respectively. The RNA world hypothesis would require that the components of the translation apparatus would have to be made of RNA initially at least, and remarkably this is still true. Twenty years ago, Noller et al. [23] showed that a ribosome severely depleted of protein could still carry out peptidyl transfer, suggesting that perhaps the catalytic component was RNA rather than a protein enzyme. This was confirmed when Steitz et al. [24] solved the structure of the large ribosomal subunit, showing that there was no protein within 20 Å of the peptidyl transferase centre. Krupkin et al. [25] (Rehovot) have now identified a symmetrical core element in the rRNA that might be a vestige of that primitive peptidyl transferase centre. It is hard not to be impressed by the thought that this could be a 3.6 billion-year old molecular fossil from an earlier RNA world lying at the heart of our most basic systems for gene expression! Finally, Wohlgemuth et al. [26] (Göttingen) bring us to the present day, describing how the modern ribosome achieves high fidelity of translation.

REFERENCES

1. Sleep N. H., Bird D. K., Pope E. C. 2011. Serpentinite and the dawn of life. *Phil. Trans. R. Soc. B* 366, 2857–2869 10.1098/rstb.2011.0129 (doi:10.1098/rstb.2011.0129) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
2. Powner M. W., Sutherland J. D. 2011. Prebiotic chemistry: a new *modus operandi*. *Phil. Trans. R. Soc. B* 366, 2870–2877 10.1098/rstb.2011.0134 (doi:10.1098/rstb.2011.0134) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
3. Blackmond D. G. 2011. The origin of biological homochirality. *Phil. Trans. R. Soc. B* 366, 2878–2884 10.1098/rstb.2011.0130 (doi:10.1098/rstb.2011.0130) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
4. Hanczyc M. M. 2011. Metabolism and motility in prebiotic structures. *Phil. Trans. R. Soc. B* 366, 2885–2893 10.1098/rstb.2011.0141 (doi:10.1098/rstb.2011.0141) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
5. Szostak J. W. 2011. An optimal degree of physical and chemical heterogeneity for the origin of life? *Phil. Trans. R. Soc. B* 366, 2894–2901 10.1098/rstb.2011.0140 (doi:10.1098/rstb.2011.0140) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
6. Grabowski P. J., Zaug A. J., Cech T. R. 1981. The intervening sequence of the ribosomal RNA precursor is converted to a circular RNA in isolated nuclei of *Tetrahymena*. *Cell* 23, 467–476 10.1016/0092-8674(81)90142-2 (doi:10.1016/0092-8674(81)90142-2) [PubMed] [CrossRef] [Google Scholar]
7. Guerrier-Takada C., Gardiner K., Marsh T., Pace N., Altman S. 1983. The RNA moiety of ribonuclease P is the catalytic subunit of the enzyme. *Cell* 35, 849–857 10.1016/0092-8674(83)90117-4 (doi:10.1016/0092-8674(83)90117-4) [PubMed] [CrossRef] [Google Scholar]
8. Brown R. S., Hingerty B. E., Dewan J. C., Klug A. 1983. Pb(II)-catalysed cleavage of the sugar–phosphate backbone of yeast tRNAPhe—implications for lead toxicity and self-splicing RNA. *Nature* 303, 543–546 10.1038/303543a0 (doi:10.1038/303543a0) [PubMed] [CrossRef] [Google Scholar]
9. Yarus M. 2010. *Life from an RNA world*, pp. 1–198 Cambridge, MA: Harvard University Press [Google Scholar]
10. Altman S. 2011. Ribonuclease P. *Phil. Trans. R. Soc. B* 366, 2936–2941 10.1098/rstb.2011.0142 (doi:10.1098/rstb.2011.0142) [PMC free article] [PubMed] [CrossRef] [Google Scholar]

11. Lilley D. M. J. 2011. Mechanisms of RNA catalysis. *Phil. Trans. R. Soc. B* 366, 2910–2917 10.1098/rstb.2011.0132 (doi:10.1098/rstb.2011.0132) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
12. Hiller D. A., Strobel S. A. 2011. The chemical versatility of RNA. *Phil. Trans. R. Soc. B* 366, 2929–2935 10.1098/rstb.2011.0143 (doi:10.1098/rstb.2011.0143) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
13. Ferré-D'Amaré A. R. 2011. Use of a coenzyme by the glmS ribozyme-riboswitch suggests primordial expansion of RNA chemistry by small molecules. *Phil. Trans. R. Soc. B* 366, 2942–2948 10.1098/rstb.2011.0131 (doi:10.1098/rstb.2011.0131) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
14. Seelig B., Jäschke A. 1999. A small catalytic RNA motif with Diels-Alderase activity. *Chem. Biol.* 6, 167–176 10.1016/S1074-5521(99)89008-5 (doi:10.1016/S1074-5521(99)89008-5) [PubMed] [CrossRef] [Google Scholar]
15. Sengle G., Eisenfuh R. A., Arora P. S., Nowick J. S., Famulok M. 2001. Novel RNA catalysts for the Michael reaction. *Chem. Biol.* 8, 459–473 10.1016/S1074-5521(01)00026-6 (doi:10.1016/S1074-5521(01)00026-6) [PubMed] [CrossRef] [Google Scholar]
16. Johnston W. K., Unrau P. J., Lawrence M. S., Glasner M. E., Bartel D. P. 2001. RNA-catalyzed RNA polymerization: accurate and general RNA-templated primer extension. *Science* 292, 1319–1325 10.1126/science.1060786 (doi:10.1126/science.1060786) [PubMed] [CrossRef] [Google Scholar]
17. Bagby S. C., Bergman N. H., Shechner D. M., Yen C., Bartel D. P. 2009. A class I ligase ribozyme with reduced Mg²⁺ dependence: selection, sequence analysis, and identification of functional tertiary interactions. *RNA* 15, 2129–2146 10.1261/rna.1912509 (doi:10.1261/rna.1912509) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
18. Piccirilli J. A., Koldobskaya Y. 2011. Crystal structure of an RNA polymerase ribozyme in complex with an antibody fragment. *Phil. Trans. R. Soc. B* 366, 2918–2928 10.1098/rstb.2011.0144 (doi:10.1098/rstb.2011.0144) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
19. Yarus M. 2011. The meaning of a minuscule ribozyme. *Phil. Trans. R. Soc. B* 366, 2902–2909 10.1098/rstb.2011.0139 (doi:10.1098/rstb.2011.0139) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
20. Suga H., Hayashi G., Terasaka N. 2011. The RNA origin of transfer RNA aminoacylation and beyond. *Phil. Trans. R. Soc. B* 366, 2959–2964 10.1098/rstb.2011.0137 (doi:10.1098/rstb.2011.0137) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
21. Pascal R., Boiteau L. 2011. Energy flows, metabolism and translation. *Phil. Trans. R. Soc. B* 366, 2949–2958 10.1098/rstb.2011.0135 (doi:10.1098/rstb.2011.0135) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
22. Schimmel P. 2011. Mistranslation and its control by tRNA synthetases. *Phil. Trans. R. Soc. B* 366, 2965–2971 10.1098/rstb.2011.0158 (doi:10.1098/rstb.2011.0158) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
23. Noller H. F., Hoffarth V., Zimniak L. 1992. Unusual resistance of peptidyl transferase to protein extraction procedures. *Science* 256, 1416–1419 10.1126/science.1604315 (doi:10.1126/science.1604315) [PubMed] [CrossRef] [Google Scholar]
24. Nissen P., Hansen J., Ban N., Moore P. B., Steitz T. A. 2000. The structural basis of ribosome activity in peptide bond synthesis. *Science* 289, 920–930 10.1126/science.289.5481.920 (doi:10.1126/science.289.5481.920) [PubMed] [CrossRef] [Google Scholar]
25. Krupkin M., Matzov D., Tang H., Metz M., Kalaora R., Belousoff M. J., Zimmerman E., Bashan A., Yonath A. 2011. A vestige of a prebiotic bonding machine is functioning within the contemporary ribosome. *Phil. Trans. R. Soc. B* 366, 2972–2978 10.1098/rstb.2011.0146 (doi:10.1098/rstb.2011.0146) [PMC free article] [PubMed] [CrossRef] [Google Scholar]
26. Wohlgemuth I., Pohl C., Mittelstaet J., Konevega A. L., Rodnina M. V. 2011. Evolutionary optimization of speed and accuracy of decoding on the ribosome. *Phil. Trans. R. Soc. B* 366, 2979–2986 10.1098/rstb.2011.0138 (doi:10.1098/rstb.2011.0138) [PMC free article] [PubMed] [CrossRef] [Google Scholar]