Fast tidal cycling and the origin of life

Richard Lathe [a,b]

[a] *Department of Biomedical Sciences, University of Edinburgh, George Square, Edinburgh EH8 9XD, UK*
[b] *Pieta Research, PO Box 27069, Edinburgh EH10 5YW, UK*

Abstract

Replicating prebiotic polymers are thought to predate the emergence of true life-forms. The initial mode of replication, a prerequisite for Darwinian selection, is unknown, but demands an explanation based on local physicochemistry. Dual consideration of the conditions of the early terrestrial surface, with the unusual physicochemical properties of nucleic acids like DNA, could explain the emergence of nucleic acids as key biomolecules. The early impact that produced the Moon, and fast terrestrial rotation, subjected coastal areas 3.9 Ga ago to rapid tidal flooding (dilution) and drying (concentration), with a likely periodicity in the range of 2–6 h, and could have provided a driving force for cyclic replication of early biomolecules. Such a mechanism applies only to molecules capable of association/polymerization at high salt concentration, and of dissociation at low salinity. Nucleic acids meet these criteria. It is suggested that tidal cycling, resembling the polymerase chain reaction (PCR) mechanism, could only replicate and amplify DNA-like polymers. This mechanism suggests constraints on the evolution of extra-terrestrial life.
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Keywords: Origin; Life; DNA; Nucleic acid; PCR; Moon; Tide; Cycling; Salinity

1. Introduction

One broadly-accepted view of the origin of life at -3.9×10^9 yr (Ga) is that replicative molecules emerged through chemical polymerization of precursors in the prebiotic 'soup' of the early sea (Haldane, 1929; Oparin, 1957; Miller, 1953; Miller and Urey, 1959; Orgel, 1982). In vitro, under conditions intended to resemble the early terrestrial surface, non-enzymatic polymerization of amino acids or nucleotides can take place (Fox and Harada, 1958; Schramm et al., 1962; Naylor and Gilham, 1966; von Kiedrowski et al., 1989; Ferris et al., 1996; Li and Nicolaou, 2002; Luther et al., 1998). A favored scenario is that one polymer strand directed the synthesis of a complementary strand, as in modern DNA. Two areas remain problematic. First, directed polymerization is compatible with diverse chemical structures; it is not known why nucleic acids like DNA (Watson and Crick, 1953) took on a central role. Second, in any duplex, the new complementary strand blocks further polymerization (Blum, 1957; Szathmary and Gladkih, 1989). In the absence of an energy-dependent mechanism

for dissociation, non-enzymatic copying is a dead-end: further synthesis cannot take place. This paper examines the early Earth environment, the peculiar structure of nucleic acids, and proposes a 'nucleic acid only' replicative mechanism based on fast tidal cycling and salt-dependent association/dissociation.

2. Analogy with the Polymerase Chain Reaction (PCR)

The ideas presented here draw on a conceptual analogy with PCR amplification. A common technique in biomedical laboratories, PCR involves repetitive cycling of a DNA sample, in the presence of a thermostable polymerase enzyme and monomeric precursors, between two temperatures.

At low temperature (e.g., 50 °C) single DNA strands direct the synthesis of complementary strands, doubling the total number of molecules.

At high temperature (e.g., 100 °C) the paired strands dissociate to permit the next round of synthesis.

Multiple cycling leads to exponential amplification, converting a single starting DNA molecule, in vitro, into 10^{15} identical molecules over 40 cycles (Mullis et al., 1986).

E-mail address: rlathe@pieta-research.org.

3. Fast tidal cycling at the early terrestrial surface

At the origin of life (-3.9 Ga) the rotation rate of the Earth was far faster than at present. Rapid rotation has been ascribed to the impact event that produced the Moon ~ 5 Ga years ago (Hartmann and Davis, 1975; Hartmann et al., 1986; Benz, 1986; Newsom and Taylor, 1989; Hartmann, 1999).

This idea is far from new: G.H. Darwin speculated in 1878 that the rotation period of the Earth was ~ 5 h at the time of formation of the Moon (Brush, 1986).

Faster early rotation has been empirically confirmed. Modern microscopic inspection of early shell fossils and sedimentary layers has revealed regular laminar periodicities that demonstrate significantly more days per year than at present (Panella, 1975). If the time taken to revolve about the Sun has not changed substantially, as seems likely (Scrutton, 1978), accumulated data from fossil corals, bivalves, and stromatolites, as well as from tidal deposits, argue that early daylength was shorter (Panella, 1975; Scrutton, 1978; Lambeck, 1978, 1980; Vanyo and Awramik, 1982; Sonett et al., 1996). For the purpose of illustration, a plot of these estimated values points to daylength at -3.9 Ga, close to 2 h. This plot cannot place error limits on the early rotation rate, the individual values plotted are estimates, and linear extrapolation unsatisfactory (Scrutton, 1978). The only reliable conclusion is that early rotation may have been rapid, according to previous views (e.g., Hartmann, 1999). (See Fig. 1.)
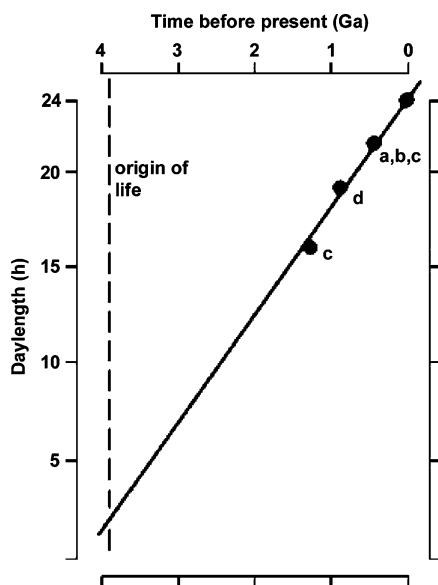

Fig. 1. Illustrative extrapolation of the Earth's rotation rate retropredicting an early day length in the range of hours. Data sources as follows: a (Lambeck, 1978, Fig. 2, p. 151); b (Scrutton, 1978, Fig. 8, p. 184); c (Lambeck, 1980, Fig. 11.5, p. 360; *N*, curve [$\varepsilon = 6°$], values at -0.4 and -1.2 Ga); d (Sonett et al., 1996, Table 2, p. 103); representative figures are given. The plot approximates to a straight line but a linear relationship between the two parameters is implausible.

Therefore, when terrestrial surface structures were first able to persist, the oceans formed, and life evolved at -3.9 Ga (Hartmann, 1980) the Earth's rotation may have been accompanied by rapid thermal (day/night) cycling with a periodicity under 6 h.

Now at 380,000 km, the early Moon was much closer to the Earth, perhaps only 200,000 km away 3.9 Ga ago (Kuala and Harris, 1975; Lambeck, 1980; Brush, 1986). Therefore tidal forces were correspondingly greater than today. Tidal areas could have extended several 100 km inland. Life evolved shortly after the oceans formed (surface temperature $< 100\,°$C). We may infer that, at the origin of life, large coastal areas ago were subject to hot and fast (perhaps every 2–6 h) cycles of flooding and drying. This would produce large local fluctuations in both salinity and in the concentration of prebiotic precursor molecules. These could have provided a driving force for life's emergence.

4. Tidal cycling may retropredict the structure of nucleic acids

A chemical polymer capable of replicating with tidal cycling is subject to physicochemical constraints.

4.1. Polymerization during the drying phase

Concentrations of polymer precursors in the primordial soup (Oparin, 1957; Miller, 1953; Miller and Urey, 1959), possibly including phosphate-activated nucleosides (Gulick, 1955; Schramm et al., 1962), were limiting (Hull, 1960; Bernal, 1960). Alignment of precursors opposite a parental strand is favored by high precursor concentrations, during the drying phase, and impaired at low concentrations, during dilution. Therefore, copying must take place during the drying phase; partially anhydric conditions also favor nonenzymatic polymerization through dehydration condensation (Schramm et al., 1962; Calvin, 1969; Weber et al., 1977).

Drying concentrates both precursors and dissolved minerals (principally NaCl); the polymerization phase is accompanied by elevated [NaCl].

4.2. A mechanism for complementary strand removal: dissociation on dilution

When a chemical polymer directs the synthesis of a complementary strand, e.g., during drying, further synthesis is blocked (Blum, 1957; Szathmary and Gladkih, 1989). For replication to proceed, dissociation must take place. A driving force is provided by tidal dilution, and concomitant reduction in salt concentration. Therefore, the only molecules capable of tide-driven replication are those that can dissociate at reduced salt concentration.

Only nucleic acids fulfill these two criteria. Biological polymers generally show the reverse behavior: for instance,
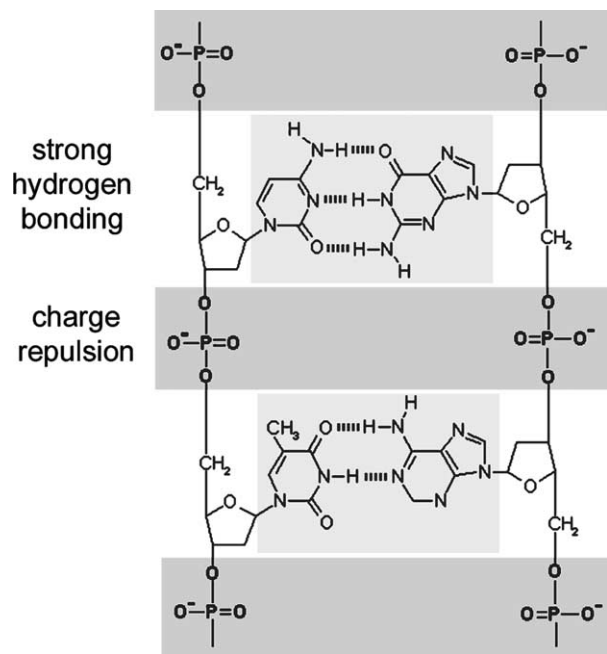
Fig. 2. Structure of DNA; robust interstrand hydrogen bonding (⫶) alternates with repulsion between opposing phosphate groups. Elevated [NaCl] neutralizes charge repulsion and promotes association; at low [NaCl] the two strands dissociate.

polypeptides associate at low salt (and precursor) concentration but dissociate in high, and therefore cannot replicate by tidal cycling.

Polynucleotides have two unique structural features (Fig. 2). First, robust pairing between the two strands, due to precise hydrogen-bonding between the bases, promotes association. Second, charge repulsion between opposing phosphate groups that separate each sugar-nucleotide monomer (Watson and Crick, 1953) promotes dissociation.

Polynucleotide association/dissociation is therefore critically dependent on soluble cation concentration. At elevated [NaCl], phosphate charges are neutralized, and inter-strand hydrogen bonding promotes association of the two polymer strands (Schildkraut and Lifson, 1965). Conversely, at room temperature, in distilled water, the phosphate charges repel, and the two strands of DNA spring apart (Schildkraut and Lifson, 1965).

Therefore, simultaneous tidal cycling of salinity and precursor concentrations would favor the replication of DNA-like molecules that can form complementary strand polymers on salinity and precursor concentration increase (drying), but then dissociate at low ionic strength (dilution).

Mineral surfaces could favor this process (Bernal, 1949, 1967). Surface association facilitates polymerization (Ferris et al., 1996; Luther et al., 1998); silicates can contribute to both alignment and polymerization of early biomolecules (Cairns-Smith, 1982, 2001; Ferris et al., 1983). Crucially, surface association is also salt-dependent. Nucleic acids adsorb to clays/silicates at high salt concentration, facilitating polymer synthesis, but not at low, permit-

ting dissociation on dilution (Vogelstein and Gillespie, 1979; Mitzutani and Narihara, 1982).

5. Early temperature and salinity

The origin of life followed closely behind the emergence of the oceans, when surface temperatures fell below 100 °C. At life's origin, temperatures in the 50–100 °C range are not implausible. Dissolution of salts only commenced on condensation of the oceans, pointing to a possible [NaCl] value at −3.9 Ga very much lower than at present (now ∼ 460 mM; compare blood salinity in vertebrates, ∼ 155 mM, popularly said but not confirmed to be a relic of life's emergence from the sea). Though ocean [NaCl] is thought to have remained fairly constant over the last 1 Ga (Knauth, 1998), at the emergence of life NaCl concentrations may have been in the low mM range.

Salt (NaCl) is not the only variable: trace divalent ions including Mg^{2+} can stabilize nucleic acid duplexes to a far greater extent than the same concentration of Na^+ (Williams et al., 1989), though Mg^{2+} is not abundant in seawater (presently ∼ 40 mM) and, paralleling [NaCl], early concentrations may have been very much lower. A role for divalent cations is questionable.

NaCl concentrations in the low mM range permit dissociation of nucleic acids during the dilution phase. A standard DNA 60-mer oligonucleotide duplex dissociates, in 10 mM NaCl, at 55–70 °C (Schildkraut and Lifson, 1965; Thomas and Dancis, 1973; Lathe, 1985; Rose et al., 2002); dissociation of a perfectly-matching 169 nucleotide DNA duplex in 10 mM NaCl at 61.5 °C has been empirically demonstrated (Rose et al., 2002). Conditions permitting dissociation of even relatively long DNA duplexes are likely to have been achieved in the early ocean.

However, DNA may not have been the earliest polynucleotide. RNA may have preceded DNA (Gilbert, 1986; Lamond and Gibson, 1990), potentially taking advantage of catalytically-active folded RNA molecules (Altman, 1990; Lamond and Gibson, 1990) to enhance polymerization: increased monovalent counter-ion concentrations accompanying evaporative concentration favor the folding and activity of catalytic RNA molecules (e.g., Takagi and Taira, 2002).

The melting temperature of double-stranded RNA molecules can be 10–30 °C higher than cognate DNA at the same salt concentration (e.g., Steger et al., 1980), approaching the limits of dissociation by tidal dilution, and perhaps arguing against an 'RNA alone' world at the origin of life. However, the RNA before DNA contention has not gone unchallenged (Dworkin et al., 2003) and others have argued that simpler and less highly-structured proto-nucleic acids preceded both RNA and DNA (Joyce et al., 1987; Wachtershauser, 1988). Therefore, association and dissociation could have taken place at lower temperatures than for either DNA or RNA. Thus, temperature/salinity conditions in the early ocean are likely to have permitted dissociation

of nucleic acids or proto-nucleic acids, and reversed by the [NaCl] elevation that accompanies drying.

Slow ocean [NaCl] elevation, combined with surface cooling, would be expected to impair such cycling progressively, perhaps driving a transition to cellular life.

6. Caveats

The emergence of replicating biopolymers within a prebiotic soup is predicated upon the availability of precursor monomers. Despite many indications that precursors including nucleosides may have been present, Shapiro (1995) has argued that prebiotic concentrations of adenine, a critical component of both DNA and RNA, may have been insufficient to support the formation of nucleic acids. Similar cautions apply to both ribose (Shapiro, 1988) and cytosine (Shapiro, 1999). This is a key point, because lack of precursors would block nucleic acid assembly by whatever route, perhaps pointing to an earlier replicator, constructed from simpler and more abundant precursors, that preceded RNA- or DNA-like substances in the origin of life (Shapiro, 1988, 1995, 1999).

Nevertheless, the chemistry accompanying tidal cycling and repetitive drying has not been fully explored. Such conditions might favor the accumulation of nucleic acid precursors, with catalytically-active mineral surfaces (Cairns-Smith, 1982, 2001; Ferris et al., 1983) potentially playing an important role.

Further, the inferred primitive and more flexible proto-nucleic acids may, like RNA (Altman, 1990), have displayed catalytic activity. Such activity is markedly enhanced by elevated temperature and cation concentrations (e.g., Peracchi, 1999; Takagi and Taira, 2002) that accompany drying: this could reinforce a role for catalytic nucleic acids at the origin of life. Precursor assembly offers a plausible target for such catalytic activity.

7. Discussion

The possibility deserves consideration that the formation of the Moon, with consequent rapid tidal cycling, provoked the origin of life on Earth. At the terrestrial surface, rapid salinity and temperature cycling produced by the event could only amplify polymers with a specific type of chemical structure—duplex structures with salt-dependent association and dissociation. Replication of differently structured prebiotic polymers could not take place.

This analysis agrees with Bernal (1961) who pointed to the importance of coastal regions for life's emergence, and with both Blum (1957, 1962) and Bernal (1967) who suggested that evaporative drying played a role.

Other strong candidate scenarios for the origin of life include submarine hot springs and seeding. Despite favorable present-day chemistry, the physical nature of such hot springs at −3.9 Ga remains to be evaluated. The hypothesis of seeding is not excluded but appears unnecessary.

Fast tidal cycling provides a mechanism for the amplification, and thereby Darwinian selection, of DNA-like molecules. The proposed mechanism requires rapid planetary rotation, and exploits tidal flooding, both being consequences of the early collision that produced the Moon.

If such cycling contributed to the emergence of life, it would follow that the likelihood of such emergence might be only be significant on planets, like the Earth, with appropriate surface temperature, rapid rotation, and a large close satellite.

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