

*Letter to the Editor***Biogenesis as an Evolutionary Process**Harold J. Morowitz,¹ David W. Deamer,² and Temple Smith³¹ Biology Department, George Mason University, Fairfax, VA 22030, USA² Department of Zoology, University of California, Davis, CA 95616, USA³ MBCRR/DFCI, Harvard University, Boston, MA 02115, USA

Summary. The earliest fossil stromatolites present evidence of a complex ecosystem of photosynthetic organisms. Because the origin of present life can be dated within a few hundred million years prior to these fossils, their complexity poses a problem. A heuristic model outlines the first radiation leading to the universal ancestor.

Key words: Evolution — Vesicle — Biogenesis

A recent paper (Sleep et al. 1989) bracketed the appearance of life between the globally sterilizing asteroid impacts on the earth and the oldest microfossil record preserved in stromatolites and suggested by the C_{13}/C_{12} ratio found in even more ancient rocks. It was concluded that at most a few hundred million years (4.0–3.8 Ga) separated the last major impact and the appearance of an ecosystem of photosynthetic, phototactic, mat-forming, walled microorganisms. Because biogenesis must have moved from simplicity to complexity, it is puzzling that the earliest archean fossil organisms appear so like contemporary forms. The ancestor of the stromatolite organisms, which was presumably the universal ancestor, must have developed from unorganized material in the window of time mentioned above. The notion of the universal ancestor derives from the universality of core biochemical pathways of all extant species.

We are here concerned with the process by which the earliest protobiontes may have formed and given rise to the universal ancestor. The chief heuristic tool is the principle of continuity that looks for those prebiotic processes and structures that show the greatest analogy and homology with subsequent bi-

otic processes and structures. This is to be contrasted with attempts to identify rare later processes (such as RNA self-splicing) as major prebiotic steps.

By postulating vesicles of amphiphilic bilayers to be primitive structures and competition and selection for fitness as operative processes, we can form a plausible scenario leading to the universal ancestor. We thus assume that the first post-asteroid sterilization protocells formed spontaneously from amphiphilic bilayers made of primitive phospholipids that were either of terrestrial or meteoritic origin (Folsome and Morowitz 1969; Hargreaves et al. 1977; Deamer and Pashley 1989). Vesicles of this type have the following properties, each of which has been experimentally demonstrated in model systems.

1) The bilayer is a barrier to free diffusion of polar solutes, permitting concentration gradients to develop and be maintained with decay half-times measured in minutes to hours.

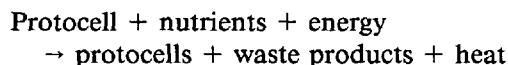
2) The lipid phase provides an environment in which nonpolar solutes can partition and concentrate. If such molecules are chromophores, light energy can be captured and transduced into forms capable of performing useful chemical, electrical, or osmotic work.

3) Given a source of chemical free energy, there are several potential reactions by which vesicles could accumulate nonpolar "nutrients" and form amphiphilic molecules. This process would result in growth of a given vesicle as amphiphiles are added to its membrane.)

4) There is a size range within which vesicles are optimally stable at a given level of thermal or mechanical agitation. Any vesicles growing beyond this size will tend to break into smaller vesicles.

5) Conversely, vesicles smaller than the optimal size will tend to fuse upon collision.

Properties 3 and 4 establish the process of self-replication of vesicles. This can be represented as:



In a previous paper (Morowitz et al. 1988) we have discussed several simple chemical embodiments of this process. This process requires vastly fewer components in the environment than the "chicken soup" that has been postulated in chemical evolution.

Proto-cells can vary in a population by chemical composition, chemical reactivity, and structural components. If these differences persist through proto-cell division, then we have a type of pre-genetic memory that allows us to consider "species" of proto-cells. We consider three modes of achieving memory.

In the first a molecule arises as the result of a random event that has a low probability in the system as constituted. Assume that this molecule, either in solution or more likely adsorbed on the vesicle membrane, can act as a catalyst for reactions that are possible for protocellular components. If the catalyst leads to reaction sequences that result in the enhanced synthesis of the catalytic molecule, we have the process of reflexive autocatalysis (Ycas, personal communication). If the rate of synthesis of catalyst is equal to or greater than the average proto-cell division rate plus the rate of loss, then memory of the initial event persists and a kind of genetics arises that does not require macromolecules.

In the second process the original random event leads to enhanced energy transduction such as might occur with a membrane-dissolved chromophore. If the transduced energy increased the probability of synthesis of the transducer such that the formation occurs at a rate equal to or greater than the rate of division plus the rate of loss, then the same conditions exist as before and "genetic memory" of the transducer persists.

In the third type of process the rare event leads to a molecule that adsorbs on or in the membrane and so alters transport as to admit precursors to its own synthesis. If the rate of synthesis of the transport molecule follows the criteria given above it will become a characteristic component of that strain of vesicle.

This type of memory allows for the partitioning of the world of vesicles into competing species defined by the distributed properties of the reaction networks rather than reified into macromolecules or protogenes. Some species of vesicles will replicate

faster than others, and in an environment of limited resources, either nutrient or energy, a Darwinian-type competition will ensue. Even in the absence of resource limitation a distribution of populations will result and the fastest growing species will eventually force a limitation.

Occasional vesicle fusion can bring together favorable metabolic properties and, in the cases where these are synergistic, greater competitive advantages follow. The fusion between two species of vesicles will likely be proportional to the product of their concentrations, so the most successful features have a high probability of clustering.

This model provides the earliest proto-cells with the potential to "evolve" via selection into complex self-reproducing objects without requiring macromolecular genetics at the earliest stages. It is clearly a system on the way to metabolic sophistication and one that provides a milieu for the development of larger and larger molecules with ever more specific functional roles. In addition the model explains the combining of successful, even if quite weak, chemical feedback network providing the advantages of genetic combination long before the emergence of sex and the exchange of macromolecular genes.

The possibility that a single molecular event could lead to protocellular memory and speciation offers a possible solution to the chirality problem by providing amplification of single molecule random events that may be optically asymmetrical.

In summary, we postulate a protocellular evolutionary radiation leading from vesicles to a universal ancestor. Vesicles and the associated chemical processes and energy transduction mechanisms possess the requisite properties to amplify and select for advantageous molecular accidents, even though information is not yet embodied in a macromolecular genetic apparatus. The special feature of the model is that it allows macromolecules to be a consequence of evolutionary processes rather than requiring that they be prerequisite to such processes!

References

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