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Dynamics of the osmotic lysis of mineral protocells and its avoidance at the origins of life

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Abstract

The osmotic rupture of a cell, its osmotic lysis or cytolysis, is a phenomenon that active biological cell volume regulation mechanisms have evolved in the cell membrane to avoid. How then, at the origin of life, did the first protocells survive prior to such active processes? The pores of alkaline hydrothermal vents in the oceans form natural nanoreactors in which osmosis across a mineral membrane plays a fundamental role. Here, we discuss the dynamics of lysis and its avoidance in an abiotic system without any active mechanisms, reliant upon self-organized behaviour, similar to the first self-organized mineral membranes within which complex chemistry may have begun to evolve into metabolism. We show that such mineral nanoreactors could function as protocells without exploding because their self-organized dynamics have a large regime in parameter space where osmotic lysis does not occur and homeostasis is possible. The beginnings of Darwinian evolution in proto-biochemistry must have involved the survival of protocells that remained within such a safe regime.

KEYWORDS
chemical gardens, chemobrionics, hydrothermal vents, origin of life

1 | INTRODUCTION

If a cell explodes it dies, and its genetic material is lost. Cells generally live within an aqueous medium in which they must take account of osmotic forces acting owing to the semipermeable form of their membrane and the different solutes within and without the cell wall. Therefore, cells have, over millions of years, developed exquisite mechanisms of active biological control over the cell membrane in order to determine what comes in and what goes out and hence to regulate their volume (Hoffmann et al., 2009). Some of the first active mechanisms in the cell wall would surely have evolved to regulate the osmotic pressure to avoid osmotic explosions. But what about at the origin of life, when these active mechanisms had not been developed? If complex chemistry gave way to metabolism within some abiotic membrane, then at this first stage all pressure regulation mechanisms would have to have been self-organized, later to be supplemented and supplanted by active mechanisms as the first protocells evolved. Here, we analyse a fluid-mechanical model that represents the completely abiotic, self-organized case.

Compartmentalization plays a multiple and fundamental part in the origins of life (Caliari et al., 2021). A compartment is a chemical reaction vessel that prevents dilution and protects against changes in the external environment, but beyond these two factors, the wall or membrane of such a compartment needs to possess a degree of selective permeability, or semipermeability, to control the intake and expulsion of chemical species in order to maintain homeostasis (Engelhart et al., 2016), and to enable the persistence of chemical and other gradients in order to drive reactions; to create a metabolism (Noireaux & Libchaber, 2004). The elaborate volume regulation mechanisms present in today's cells would not have existed in

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the earliest protocells. In the earliest compartmentalization, membrane permeability would have to balance potential bottlenecks for metabolism within the protocell, the accessibility of chemical nutrients or fuel and the disposal of internal waste products (Chen & Walde, 2010; Maurer & Monnard, 2011; Szathmáry et al., 2005; West et al., 2017). Hence, early protocells must have been rather susceptible to volume and pressure changes under osmosis, and ultimately to the possibility of osmotic rupture: to cytolysis or osmotic lysis (Bigan et al., 2015; Chabanon et al., 2017; Idiart & Levin, 2004; Koslov & Markin, 1984; Morris, 2002).

There is great interest in the influence of osmotic pressure on vesicles and protocells. In biomolecular systems the influence of osmotic pressures on the stability, structure and also reactivity are well-recognized (Knop et al., 2022). Oscillations in pH and proton gradients are shown to arise from microscale heat flow (Keil et al., 2017). Such flow is through diffusiophoresis, the physical process through which molecules or larger particles may drift along a solute concentration gradient owing to osmotic pressure differences on their interface (Bocquet & Palacci, 2021). Kinetic restrictions can lead to osmotic stability of protocellular metabolism (Olasagasti et al., 2007). Protocell filamentation may be a growth mode stemming from osmotic pressure (Bigan et al., 2015). Vesicle shape oscillations can be induced by osmotic alterations from protein concentration changes (Litschel et al., 2018). In addition, osmotic shocks in lipid vesicles are shown to lead to engulfing of external material into inner compartments and bursting events (Vanhille-Campos & Šarić, 2021).

Membranes play a significant role in both natural and industrial settings. In nature, they can be observed in hydrothermal vent structures and biological cell walls, and in industry in porous materials utilized for water treatment. The most rudimentary of membranes, referred to as permeable membranes, are porous sheets that enable chemical exchange in both directions between two separate compartments. More elaborate flow control is possible with semipermeable membranes that permit the passage of certain chemical species while impeding others. This regulation may typically be due to size limitations—small solvent molecules may pass through the pores, while larger solutes are rejected—electrical charge effects or chemical affinities. Semipermeable membranes are particularly interesting for selectivity in processes of transportation. Only the most intricate of membranes, such as those found in biological organisms, exhibit selective transport in both directions.

Chemical gardens are complex laboratory systems in which chemistry, fluid and solid mechanics and osmotic forces combine to produce membranes with complex structures that can often appear plantlike. The membranes of chemical gardens are semipermeable. They typically allow water molecules across but rebuff larger ions. Recent work on chemical gardens has been performed in three- (Kaminker et al., 2014; Pantaleone et al., 2008, 2009; Stone & Goldstein, 2004; Thouvenel-Romans & Steinbock, 2003), two- (Cartwright et al., 2002; Haudin et al., 2014), and even one-dimensional (Batista & Steinbock, 2015; Ding et al., 2016) configurations and has shown that the complex interaction of chemistry and fluid mechanics can form a panoply of spatial structures. However, few studies have concentrated on the natural ensuing flow through the membrane. A principal theory for the origins of life on Earth hypothesizes that it occurred at hydrothermal vents emitting alkaline waters that are found on the ocean floor (Cartwright & Russell, 2019; Martin et al., 2008; Martin & Russell, 2007; Sojo et al., 2016). There, mineral-rich waters emerging into the ocean deposit their mineral loads in mineral structures that can be tens of metres in size (Kelley et al., 2005). Some of these vent structures, it is argued, would have possessed the ideal conditions under which complex chemistry could get started. Moreover, these structures, natural geological analogues of chemical garden structures in the laboratory, possess a complex morphology involving mineral membranes that form natural nanoreactors (Ding, Cartwright, & Cardoso, 2019) in which osmosis across a mineral membrane plays a fundamental role. Such systems form part of a new area of study named chemobrionics (Barge et al., 2015).

Here, we bring to bear the mathematical modelling that we have developed to the case of mineral protocells and the question of lysis at the origins of life. We demonstrate that such natural nanoreactors could function as protocells because their self-organized dynamics contains a large regime in parameter space where osmotic lysis does not occur. We focus on the self-driven flow across a semipermeable membrane of precipitate. A dual-permeability structure develops. In the regions of low permeability, the small solvent molecules flow under osmotic forces; solute ions are carried along with solvent under gradients of pressure in wider pores (Ding, Cartwright, & Cardoso, 2019). This system can hold an exchange flow using chemical potential energy and exhibits a variety of dynamical regimes: stable but also oscillatory and unstable. The self-organized control of micro- to nanoscale pumping by the associated chemistry can avoid osmotic lysis.

2 | FLOW ACROSS A CHEMICAL-GARDEN MEMBRANE

In previous work, we developed a theoretical model to describe a chemical nanopump (Ding et al., 2020). This may be applied to natural compartments within a hydrothermal vent; Figure 1. The evolution of relative pressure within the membrane, p, and product concentration at the interface of two reacting fluids, c, may be given.

$$\frac{dc}{dt} = \left(u_{\text{in}}\frac{c_{\text{o}}}{L_{\text{r}}} - u_{\text{out}}\frac{c}{R}\right)H\left[u_{\text{out}}\right], \tag{1a}$$

$$\frac{dp}{dt} = \gamma\left(u_{\text{in}}A_{\text{in}} - u_{\text{out}}A_{\text{out}}\right). \tag{1b}$$

Here, u_{out} and u_{in} are radial speeds of internal fluid on the outer membrane border and external fluid toward the membrane. When internal fluid leaves the membrane, it produces fingers of the pore radius scale R. Chemical reaction takes place on a lengthscale L_{r} over the finger surface. The Heaviside step function $H\left[u_{\text{out}}\right]$ indicates that

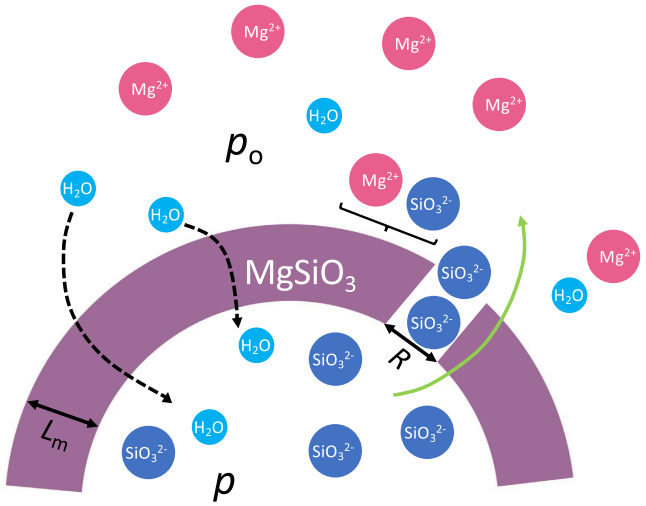


FIGURE 1 The geometry of our model; the membrane and the two solutions for the example case of magnesium and silicate ions.

product forms solely with an outflow of reacting ions. Coefficient $\gamma = (\partial p/\partial V)_T = 2L_m E/(R_p V_p)$ describes deformation of a thin—thickness L_m—cylindrical membrane, where V_p and R_p are volume and radius for the membrane; E is the membrane material Young's modulus. The surface area of inward osmotic flow A_{in} and outward flow A_{out} are supposed constant. Thus, the first equation gives a balance of the ion supply for reaction for the build-up of product and product spreading due to the outflow. Pressure change due to alterations of volume in fluid enclosed by the membrane within the cell is given by the second equation.

The radial outward and osmotic speeds are:

$$u_{in} = \frac{k_{in}}{\mu}\frac{p_o - p}{L_m}, \tag{2a}$$

$$u_{out} = \frac{k_{out}}{\mu}\frac{p}{L_m}\left(1 - \frac{c}{c^*}\right)H\left[1 - \frac{c}{c^*}\right]. \tag{2b}$$

Here, k_{out} and k_{in} are membrane permeabilities (Cardoso & Cartwright, 2014; Kedem & Katchalsky, 1958; Turcotte & Schubert, 2002) in zones of outflow and inflow, and μ is the fluid viscosity without product. As product concentration rises at the outer–inner fluid interface, the speed of outflow fingers declines; motion stops above a critical concentration of product c^*. Wagatsuma et al. (2017) first proposed that the growth speed of a precipitate filament depend in this way on concentration. We use $H[1 - c/c^*]$, the Heaviside step function, to assure that $c \le c^*$ and $u_{out} \ge 0$. In both laboratory chemical garden experiments and geological vent systems, osmosis and overpressure both drive the flow. Osmotic flow comes from differing ion concentrations in both cases. In the laboratory, the overpressure stems from the volume within the chemical garden; in the hydrothermal vent, it develops in regions with restricted convective flow within the porous structure. Exact values of the concentrations used, and thus the osmotic and inside pressures are not important, given that all our conclusions are based on non-dimensional considerations.

Substituting (2a) and (2b) into the governing Equations (1a) and (1b), noting that $p_o \gg p$ for this system, non-dimensionalizing with time $t_s = \mu R_p V_p/(2EA_{out}k_{out})$, pressure $p_s = 2EL_m A_{out} R/(V_p R_p)$ and concentration scales $c_s = c^*$, gives coupled simplified equations

$$\frac{d\hat{c}}{d\hat{t}} = \left(M + \left(-\hat{c}\hat{p} + \hat{c}^2\hat{p}\right)\right)H[1 - \hat{c}], \tag{3a}$$

$$\frac{d\hat{p}}{d\hat{t}} = N + \left(-\hat{p} + \hat{c}\hat{p}\right)H[1 - \hat{c}], \tag{3b}$$

where the hats denote the nondimensionalized versions of the variables of concentration and pressure. Here, $N = p_o k_{in} A_{in} V_p R_p/(2EL_m k_{out} A_{out}^2 R)$ and $M = N[(c_o A_{out} R)/(c^* A_{in} L_r)]$. Thus, the evolution of the non-dimensional concentration of solid $\hat{c}$ and pressure inside the cell $\hat{p}$ depends solely on two dimensionless groups: M is the ratio of the timescales for accumulation of solid and outflow; N is the timescale ratio of osmotic pumping and outflow. In the simplified limit of $A_{out} \sim A_{in}$ and $R/L_r \sim 1$, then $M \approx Nc_o/c^*$.

3 | CHEMICAL PRECIPITATION AND OSMOTIC ADVECTION

In the early ocean, mineral precipitation at hydrothermal vents must have produced porous membranes having osmotic properties, like those found today in the Strytan field off northern Iceland (Marteinsson et al., 2001); Figure 2. In the above model, we are considering a two-dimensional geometry representing the transport of ions through the porous vent structure in a horizontal cross-section. Our laboratory experiments have shown that osmosis pushes water containing small ions inwards through the vent wall at the same time as interior pressure of fluid expels water containing both large and small ions via pores and channels of larger size (Ding et al., 2020; Ding, Gutiérrez-Ariza, et al., 2019). The balance between osmotic and internal pressures sets circulation in–out and accordingly growth of the vent membrane.

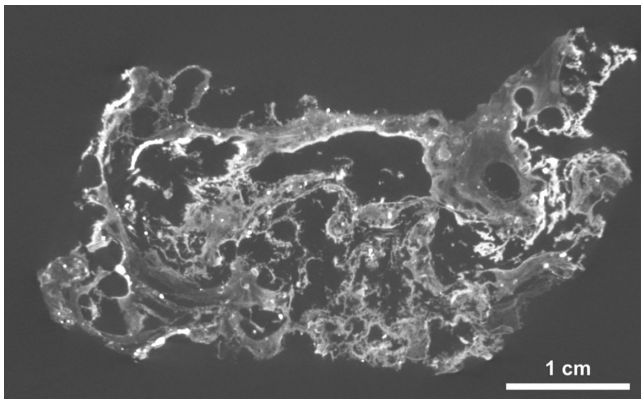


FIGURE 2 Microcompartments in a hydrothermal vent. Micro CT slice showing microcompartments in material mainly composed of magnesium silicates from Strytan hydrothermal field, Akureyri, Iceland.

At Strytan, for example, the mineral membrane grows by reaction of an outer solution containing cation Mg^{2+} and an inner solution containing anion SiO_3^{2-} (Price et al., 2017) as depicted in Figure 1, which shows a sample collected by breaking it off from the vent cone. The Strytan chimney precipitates are composed of magnesium silicates, together with calcium carbonates and calcium sulphates (Gutiérrez-Ariza et al., 2024). The membrane is semipermeable, so that there develops across it an osmotic pressure p_o. The pressure gradient p_o / L_m, where L_m is the membrane thickness, pushes water into the volume enclosed by the membrane from the exterior environment, increasing the internal pressure p. In turn, this pressure increase pumps fluid outwards across the membrane through the pores. On the membrane outer surface, the chemical reaction

$$Mg^{2+}(aq) + SiO_3^{2-}(aq) \rightarrow MgSiO_3(s)$$

at the fluid interface forms a layer of precipitate of growing thickness over time. The nucleation-precipitation process is fast (Hirsch-Ayalon, 1961, 1973), so that product formation is limited only by ion supply. Imaging and speed measurements from laboratory chemical-garden experiments show that there are distinct outflow and inflow regions of the membrane (Ding, Cartwright, & Cardoso, 2019), and the outflow permeability is much greater than that for the inflow, $k_{out} \gg k_{in}$; the complex structure permits the membrane to auto-regulate the two flows. In a simplified treatment, this system is describable with a reaction–advection equation for formation of precipitate and chemical transport, coupled with a volume–pressure balance, as we have discussed above. Scaling of these governing equations shows that system evolution is dependent solely on two dimensionless groups:

$$N = \frac{p_o k_{in} A_{in} V_p R_p}{2 E L_m k_{out} A_{out}^2 R},$$

proportional to osmotic pressure, and so the inner ion concentration, is the timescale ratio for outflow and for the inward osmotic pumping;

$$M = \frac{c_o A_{out} R}{c^* A_{in} L_r}$$

is proportional to the concentration of outer ions and represents the timescales ratio for accumulation of solid and for outflow. Here, A_{in} and A_{out} are surface areas of inward and outward flow. Reaction takes place on a lengthscale L_r at the membrane surface and the outflow pore radius scale is R. The radius and volume of the membrane, which is cylindrical, are R_p and V_p; E is Young's modulus of the material of the membrane. The outward motion stops above a critical product concentration c^*, at which the exit pores of the membrane become blocked.

Linear stability analysis of equations (3) about the steady-state (ss) concentration of product $\hat{c}_{ss} = M / N$ and interior pressure $\hat{p}_{ss} = N^2 / (N - M)$ permits identifying different dynamical behaviour for varying concentrations of anion and cation. When the initial conditions correspond to any particular M and N we find that there are stable, oscillatory and explosive regimes, illustrated in Figure 3. For a given concentration of the cation, at low M, corresponding to small concentration of anion, the system remains stable: concentration

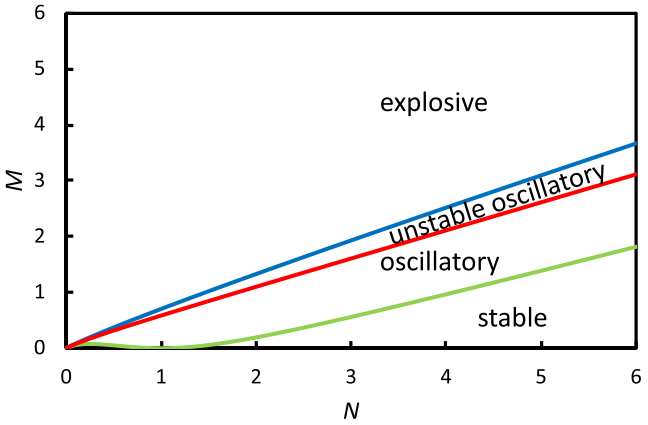


FIGURE 3 Stability regimes of Equations (3). M is the ratio of the timescales for accumulation of solid and outflow; N is the timescale ratio of osmotic pumping and outflow. For a mineral protocell to survive it should remain below the red line in the parameter space.

of product and the internal fluid pressure decrease over time. The system oscillates, showing damped, then stable and then growing oscillations of concentration and pressure for increasing concentration of anion. The system has a fast—explosive—increase of pressure at even greater concentrations of anion (high M). These regimes of behaviour and the ranges of parameters for which they occur are non-dimensional, so the behaviour is applicable to other chemical systems having an osmotic membrane with these same mechanisms of transport.

4 | STABILITY OF A MINERAL PROTOCELL AT THE EMERGENCE OF LIFE

The model we have presented is for a fixed membrane thickness. In other work, we have explored a mathematical model that shows the longer-time evolution with increasing membrane thickness (Ding, Gutiérrez-Ariza, et al., 2019). Laboratory experiments we have performed with different metal salts show how precipitate growth varies for different metal salts, magnesium chloride, manganese chloride and cobalt chloride reacting with sodium silicate solution (Figure 4). All these ions are found in hydrothermal vent systems and have been chosen as illustrative of various possible vent chemistries. We may compare precipitate growth velocity against the growing membrane model (Ding, Gutiérrez-Ariza, et al., 2019) for different types of behaviour. Figure 5 displays a comparison of theory with experiment for (a) stable growth, (b) oscillatory growth and (c) unstable growth behaviour. Figure 5d shows the influence of the width of the experimental cell on growth velocity and compares this to the variable-thickness model. In 2D, such growing membranes eventually explode (Ding, Gutiérrez-Ariza, et al., 2019). Single chemical-garden membranes, then, grow with time, and the present model is the short-time behaviour, with membrane thickness frozen, of these regimes.

This analysis may be compared to the rate at which geological hydrothermal precipitates develop. In previous work, we showed

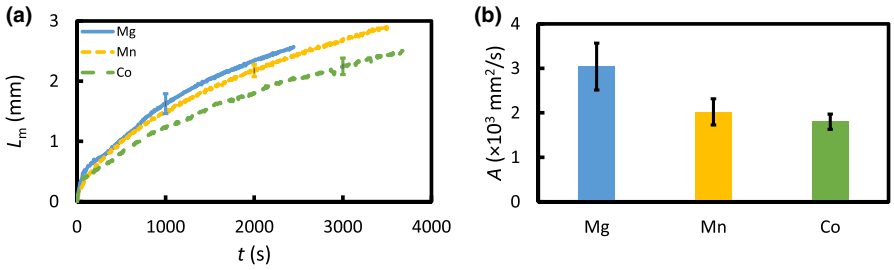
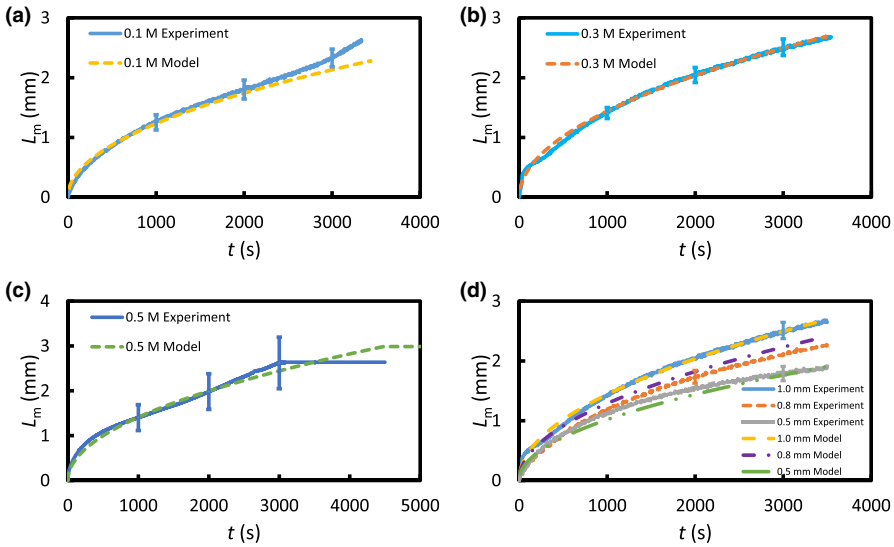


FIGURE 4 Chemical garden membrane growth in laboratory experiments. Magnesium chloride, manganese chloride and cobalt chloride, reacting with sodium silicate solution. (a) Time evolution of the membrane thickness. (b) Slopes of the squared $L_m - t$. In all cases, c_{Si} was maintained at 0.30 M.

FIGURE 5 Growth of chemical garden membrane thickness for stable (a), oscillatory (b) and unstable (c) behaviours. (d) Growth of the thickness of the membrane in Hele-Shaw cells of different gap widths.



that black smoker and Lost City-type hydrothermal vent precipitates, which grow at very different speeds, have differing fluid-dynamical growth mechanisms (Cardoso & Cartwright, 2017). Most recently, we have compared these classes of vent to the predominantly magnesium silicate hydrothermal vents at Strytan in Iceland (Gutiérrez-Ariza et al., 2024). Fluid mechanics predicts that there is a vast range of time-scales, with black smokers growing rapidly by thermal diffusion over time-scales of years; Lost City-type vents grow by chemical diffusion over tens of thousands of years; and Strytan has an intermediate growth rate. Clearly it is difficult to reproduce such slow geological growth rates in the laboratory and so mathematical modelling becomes an essential tool when combined with experiments that use higher ion concentrations to give faster growth suitable for analogue laboratory experiments.

In a geological hydrothermal vent, there is not one single membrane, but a complicated maze of microchannels and microcompartments, as shown in Figure 2. Material is added at the edge of the existing material. In this case, in the inner microcompartments we may encounter constant-thickness membranes where growth has ceased. In addition, it is in the membranes and vesicles of some of these microcompartments that complex chemistries may have developed on the road to life. Consider that at very low concentrations, the explosion time increases to infinity; and cells have very low concentrations. Intermediate concentrations exhibit longer-lived membranes; they allow a robust membrane to form, and diminished clogging of the pores, compared to higher concentrations. There is a balance; the membrane needs to keep its pores open or it ruptures, so it has a lifetime, which is much more optimized and complex in biological cells. The dimensionless results from our analysis show that any protocell has to control permeability to have stable membrane conditions at ion concentrations it finds itself at. There has to start to be a control over growth and over permeability in order not to rupture. That control is the beginnings of a cell metabolism, as in order for there to exist any of the processes of life, there must be control over what enters and leaves the system. The membrane does not increase in thickness with time in a biological cell, and the cell controls inflows and outflows. This control must have started right at the beginnings of life.

In terms of the emergence of life, any complex chemistry taking place within a mineral micro-compartment must initially have functioned under the parameters set by its mineral environment. But if the chemistry could influence those parameters (Borrego-Sánchez et al., 2022), through adding material to the membrane, then we have a mechanism through which Darwinian evolution could act. The most successful protocell will be one that has, by takeover of the mineral membrane, N and M stay within the stable regime. Within the stable region of Figure 3 there is a regime with a stable fixed point and another with stable oscillations. There are advantages

to oscillations in protocells (Ding, Cartwright, & Cardoso, 2019). Osmotic pressure oscillations in giant lipid vesicles have been found to induce phase separation in lipid mixtures (Oglecka et al., 2014). In chemical gardens, slight alterations in membrane thickness and a porous gel layer produce a varying flow velocity component and this waviness provides achieves enhanced transport across abiotic hydrothermal vent membranes (Ding et al., 2016).

A self-organized semipermeable mineral membrane is able to auto-regulate the outward and inward fluid flow to be similar in magnitude by forming zones of two different permeabilities: low permeability pushes osmotic flow of water in one sense, while greater permeability permits the flow of ions in solution in the other. The quasi-balance of these flows allows an in–out ion circulation across the membrane wall to persist. In laboratory experiments we have performed (Ding et al., 2020), the flux of ions being driven by osmosis and flowing through the porous membrane is estimated as $F = u_{out}c_{Co} \sim 10^{21}$ m^{-2} s^{-1}. The flow is $\sim 10^{15}$ ions s^{-1} across one single pore $R = 4.5 \times 10^{-4}$ m in radius. For lower solute concentrations in today's cells of the order of $\sim 10^{-3}$ M, (Milo & Phillips, 2015), flow in a single pore is $\sim 10^{9}$ ions s^{-1}. As the membrane becomes obstructed, this flow falls to zero. Our maximum pore flows are much greater than those measured in one ion channel in a modern living cell, of $\sim 10^{7}$ ions s^{-1} (Milo & Phillips, 2015), thus suggesting that in a less-efficient prebiotic cell proto-biological processes might be maintained by osmotic flow. This is consistent with the bioenergetic requirement for 'leakiness' in protocells prior to the Last Universal Common Ancestor, LUCA (Ding et al., 2016; Sojo et al., 2014; Weiss et al., 2016).

5 | CONCLUSIONS

The emerging dynamical regimes seen in laboratory experiments and which correlate to mineral precipitates at hydrothermal vents can be described by the minimum physical model given here. The goal has been to simplify the complex interaction between chemical reaction and osmotic flow in the membrane from the self-assembling precipitate's myriad physical and chemical processes. The process is an exquisite illustration of active fluid dynamics in which chemistry regulates flow that affects in succession the pattern of membrane creation.

Chemical energy from concentration gradients can cause substantial flows across a developing mineral membrane, such as a hydrothermal vent structure and potentially trigger its disruption. Such fluxes favour additional processes by carrying ions over the barrier, especially tiny ones. A source of chemical energy, particularly concentration gradients, generates fluxes of chemical and kinetic energies across the porous membrane, which in turn could energetically favour other chemical reactions occurring within its pores. The vision for the origins of life at such a hydrothermal vent is of an incipient complex chemistry within such structures that led to the first protocells under a gradual chemical and then biochemical takeover of the mineral membrane. Such a protocell would clearly be most successful when away from the lysis region. That is to say that maintaining itself without exploding from osmotic lysis, hence being able to pass on that chemical recipe for stable existence to daughter protocells, long before the evolution of today's sophisticated active mechanisms for osmotic pressure regulation, is a first instance of the survival of the fittest.

6 | EXPERIMENTAL METHODS

The experimental procedures have been documented in detail in our previous research (Ding, Cartwright, & Cardoso, 2019; Ding, Gutiérrez-Ariza, et al., 2019). The experiments were carried out in a horizontal Hele-Shaw cell with different gap widths of 0.5, 0.8 and 1.0 mm; Figure 6. The Hele-Shaw cell consisted of a pair

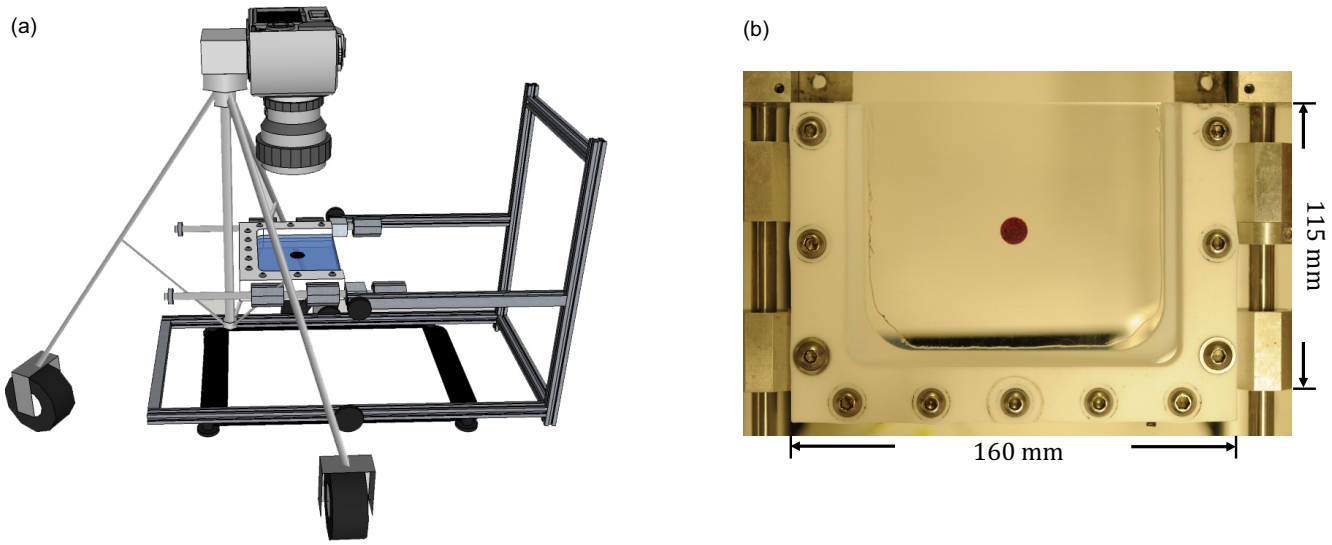


FIGURE 6 (a) Schematics of the experimental setup: The camera, horizontal Hele-Shaw cell and light source; (b) photograph of the horizontal Hele-Shaw cell with a metal-salt pellet inserted.

of transparent perspex plates (130×100×6 mm) and was fitted to stainless steel back frames with underlying uniform lighting from a LED lightbox. Sodium silicate (Na_2SiO_3, Honeywell Fluka) solutions with different concentrations were prepared by dilution of a commercial concentrated solution of 6.25 M with respect to silica. Different metal salt crystals, including cobalt(II) chloride hexahydrate ($CoCl_2 \cdot 6H_2O$, ACROS Organic), manganese(II) chloride tetrahydrate ($MnCl_2 \cdot 4H_2O$, Sigma Aldrich) and magnesium chloride hexahydrate ($MgCl_2 \cdot 6H_2O$, Sigma Aldrich), were pressed into pellets with a diameter of 10 mm by a KBR Port-A-Press™ Kit (International Crystal Laboratories) under a pressure of 110 MPa. To start an experiment, a metal salt pellet with a thickness the same with the gap width of the Hele-Shaw cell was firstly placed in the middle of the cell. Na_2SiO_3 solution with a concentration of c_{si} was injected into the Hele-Shaw cell by a syringe. The dynamics of each experiment was recorded by a Nikon D300s digital single-lens reflex (DSLR) camera (4288 × 2848 pixels) with a Hoya circular polarizing lens filter from above the cell. At each concentration condition, at least 5 runs of experiments were conducted.

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CONFLICT OF INTEREST STATEMENT

None of the authors has a conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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REFERENCES

Barge, L. M., Cardoso, S. S. S., Cartwright, J. H. E., Cooper, G. J. T., Cronin, L., De Wit, A., … Thomas, N. L. (2015). From chemical gardens to chemobrionics. *Chemical Reviews*, *115*, 8652–8703.

Batista, B. C., & Steinbock, O. (2015). Growing inorganic membranes in microfluidic devices: Chemical gardens reduced to linear walls. *Journal of Physical Chemistry C*, *119*, 27045–27052.

Bigan, E., Steyaert, J.-M., & Douady, S. (2015). Filamentation as primitive growth mode? *Physical Biology*, *12*, 066024.

Bocquet, L., & Palacci, J. (2021). Life on the osmotic slopes. *Nature Physics*, *17*(7), 763–764.

Borrego-Sánchez, A., Gutiérrez-Ariza, C., Sainz-Díaz, C. I., & Cartwright, J. H. E. (2022). The effect of the presence of amino acids on the precipitation of inorganic chemical-garden membranes: Biomineralization at the origin of life. *Langmuir*, *38*(34), 10538–10547.

Caliari, A., Xu, J., & Yomo, T. (2021). The requirement of cellularity for abiogenesis. *Computational and Structural Biotechnology Journal*, *19*, 2202–2212.

Cardoso, S. S. S., & Cartwright, J. H. E. (2014). Dynamics of osmosis in a porous medium. *Royal Society Open Science*, *1*, 140352.

Cardoso, S. S. S., & Cartwright, J. H. E. (2017). On the differing growth mechanisms of black-smoker and Lost City-type hydrothermal vents. *Proceedings of the Royal Society A*, *473*(2205), 20170387.

Cartwright, J. H. E., García-Ruiz, J. M., Novella, M. L., & Otálora, F. (2002). Formation of chemical gardens. *Journal of Colloid and Interface Science*, *256*, 351–359.

Cartwright, J. H. E., & Russell, M. J. (2019). The origin of life: The submarine alkaline vent theory at 30. *Interface Focus*, *9*, 20190104.

Chabanon, M., Ho, J. C. S., Liedberg, B., Parikh, A. N., & Rangamani, P. (2017). Pulsatile lipid vesicles under osmotic stress. *Biophysical Journal*, *112*, 1682–1691.

Chen, I. A., & Walde, P. (2010). From self-assembled vesicles to protocells. *Cold Spring Harbor Perspectives in Biology*, *2*, a002170.

Ding, Y., Batista, B., Steinbock, O., Cartwright, J. H. E., & Cardoso, S. S. S. (2016). Wavy membranes and the growth rate of a planar chemical garden: Enhanced diffusion and bioenergetics. *Proceedings of the National Academy of Sciences USA*, *113*, 9182–9186.

Ding, Y., Cartwright, J. H. E., & Cardoso, S. S. S. (2019). Intrinsic concentration cycles and high ion fluxes in self-assembled precipitate membranes. *Interface Focus*, *9*, 20190064.

Ding, Y., Cartwright, J. H. E., & Cardoso, S. S. S. (2020). Convective flow driven by a chemical nanopump. *Physical Review Fluids*, *5*, 082201.

Ding, Y., Gutiérrez-Ariza, C. M., Sainz-Díaz, C. I., Cartwright, J. H. E., & Cardoso, S. S. S. (2019). Exploding chemical gardens: A phase-change clock reaction. *Angewandte Chemie*, *131*(19), 6273–6279.

Engelhart, A. E., Adamala, K. P., & Szostak, J. W. (2016). A simple physical mechanism enables homeostasis in primitive cells. *Nature Chemistry*, *8*(5), 448–453.

Gutiérrez-Ariza, C., Barge, L. M., Ding, Y., Cardoso, S. S. S., McGlynn, S. E., Nakamura, R., Giovanelli, D., Price, R., Lee, H. E., Huertas, F. J., Sainz-Díaz, C. I., & Cartwright, J. H. E. (2024). Magnesium silicate chimneys at the Strytan hydrothermal field, Iceland, as analogues for prebiotic chemistry at alkaline submarine hydrothermal vents on the early Earth. *Progress in Earth and Planetary Science*, *11*, 11.

Haudin, F., Cartwright, J. H. E., Brau, F., & De Wit, A. (2014). Spiral precipitation patterns in confined chemical gardens. *Proceedings of the National Academy of Sciences USA*, *111*, 17363–17367.

Hirsch-Ayalon, P. (1961). Precipitate impregnated membranes: II. *Recueil des Travaux Chimiques des Pays-Bas*, *80*, 365–375.

Hirsch-Ayalon, P. (1973). Precipitation Membranes. *The Journal of Membrane Biology*, *12*, 349–360.

Hoffmann, E. K., Lambert, I. H., & Pedersen, S. F. (2009). Physiology of cell volume regulation in vertebrates. *Physiological Reviews*, *89*, 193–277.

Idiart, M. A., & Levin, Y. (2004). Rupture of a liposomal vesicle. *Physical Review E*, *69*, 061922.

Kaminker, V., Maselko, J., & Pantaleone, J. (2014). The dynamics of open precipitation tubes. *The Journal of Chemical Physics*, *140*, 244901.

Kedem, O., & Katchalsky, A. (1958). Thermodynamic analysis of the permeability of biological membranes to non-electrolytes. *Biochimica et Biophysica Acta*, *27*, 229.

Keil, L. M., Möller, F. M., Kieß, M., Kudella, P. W., & Mast, C. B. (2017). Proton gradients and pH oscillations emerge from heat flow at the microscale. *Nature Communications*, *8*(1), 1897.

Kelley, D. S., Karson, J. A., Früh-Green, G. L., Yoerger, T. M., Shank, D. R., Butterfield, D. A., Hayes, J. M., Schrenk, M. O., Olson, E. J., Proskurowski, G., Jakuba, M., Bradley, A., Larson, B., Ludwig, K., Glickson, D., Buckman, K., Bradley, A. S., Brazelton, W. J., Roe, K., … Sylva, S. P. (2005). A serpentinite-hosted ecosystem: The Lost City hydrothermal field. *Science*, *307*, 1428–1434.

Knop, J.-M., Mukherjee, S., Jaworek, M. W., Kriegler, S., Manisegaran, M., Fetahaj, Z., Ostermeier, L., Oliva, R., Gault, S., Cockell, C. S., & Winter, R. (2022). Life in multi-extreme environments: Brines, osmotic and hydrostatic pressure? A physicochemical view. *Chemical Reviews*, *123*(1), 73–104.

Koslov, M. M., & Markin, V. S. (1984). A theory of osmotic lysis of lipid vesicles. *Journal of Theoretical Biology*, *109*, 17–39.

Litschel, T., Ramm, B., Maas, R., Heymann, M., & Schwille, P. (2018). Beating vesicles: Encapsulated protein oscillations cause dynamic membrane deformations. *Angewandte Chemie International Edition*, *57*(50), 16286–16290.

Marteinsson, V. T., Kristjánsson, J. K., Kristmannsdóttir, H., Dahlkvist, M., Sæmundsson, K., Hannington, M., Pétursdóttir, S. K., Geptner, A., & Stoffers, P. (2001). Discovery and description of giant submarine smectite cones on the seafloor in Eyjafjordur, northern Iceland, and a novel thermal microbial habitat. *Applied and Environmental Microbiology*, *67*(2), 827–833.

Martin, W., Baross, J., Kelley, D., & Russell, M. J. (2008). Hydrothermal vents and the origin of life. *Nature Reviews Microbiology*, *6*, 805–814.

Martin, W., & Russell, M. (2007). On the origin of biochemistry at an alkaline hydrothermal vent. *Philosophical Transactions of the Royal Society B*, *362*, 1887–1926.

Maurer, S. E., & Monnard, P.-A. (2011). Primitive membrane formation, characteristics and roles in the emergent properties of a protocell. *Entropy*, *13*, 466–484.

Milo, R., & Phillips, R. (2015). *Cell biology by the numbers*. Taylor & Francis.

Morris, C. E. (2002). How did cells get their size? *The Anatomical Record*, *268*, 239–251.

Noireaux, V., & Libchaber, A. (2004). A vesicle bioreactor as a step toward an artificial cell assembly. *Proceedings of the National Academy of Sciences USA*, *101*(51), 17669–17674.

Oglecka, K., Rangamani, P., Liedberg, B., Kraut, R. S., & Parikh, A. N. (2014). Oscillatory phase separation in giant lipid vesicles induced by transmembrane osmotic differentials. *eLife*, *3*, e03695.

Olasagasti, F., Moreno, A., Peretó, J., & Morán, F. (2007). Energetically plausible model of a self-maintaining protocellular system. *Bulletin of Mathematical Biology*, *69*, 1423–1445.

Pantaleone, J., Toth, A., Horvath, D., McMahan, J. R., Smith, R., Butki, D., Braden, J., Mathews, E., Geri, H., & Maselko, J. (2008). Oscillations of a chemical garden. *Physical Review E*, *77*, 046207.

Pantaleone, J., Toth, A., Horvath, D., RoseFigura, L., & Maselko, J. (2009). Pressure oscillations in chemical gardens. *Physical Review E*, *79*, 056221.

Price, R., Boyd, E. S., Hoehler, T. M., Wehrmann, L. M., Bogason, E., Valtỳsson, H. T., Örlygsson, J., Gautason, B., & Amend, J. P. (2017). Alkaline vents and steep Na^+ gradients from ridge-flank basalts—Implications for the origin and evolution of life. *Geology*, *45*(12), 1135–1138.

Sojo, V., Herschy, B., Whicher, A., Camprubi, E., & Lane, N. (2016). The origin of life in alkaline hydrothermal vents. *Astrobiology*, *16*, 181–197.

Sojo, V., Pomiankowski, A., & Lane, N. (2014). A bioenergetic basis for membrane divergence in archaea and bacteria. *PLoS Biology*, *12*, e1001926.

Stone, D. A., & Goldstein, R. E. (2004). Tubular precipitation and redox gradients on a bubbling template. *Proceedings of the National Academy of Sciences USA*, *101*, 11537–11541.

Szathmáry, E., Santos, M., & Fernando, C. (2005). Evolutionary potential and requirements for minimal protocells. In *Prebiotic chemistry* (pp. 167–211). Springer.

Thouvenel-Romans, S., & Steinbock, O. (2003). Oscillatory growth of silica tubes in chemical gardens. *Journal of the American Chemical Society*, *125*, 4338–4341.

Turcotte, D., & Schubert, G. (2002). *Geodynamics*. Cambridge University Press.

Vanhille-Campos, C., & Šarić, A. (2021). Modelling the dynamics of vesicle reshaping and scission under osmotic shocks. *Soft Matter*, *17*(14), 3798–3806.

Wagatsuma, S., Higashi, T., Sumino, Y., & Achiwa, A. (2017). Pattern of a confined chemical garden controlled by injection speed. *Physical Review E*, *95*, 052220.

Weiss, M. C., Sousa, F. L., Mrnjavac, N., Neukirchen, S., Roettger, M., Nelson-Sathi, S., & Martin, W. F. (2016). The physiology and habitat of the last universal common ancestor. *Nature Microbiology*, *1*, 16116.

West, T., Sojo, V., Pomiankowski, A., & Lane, N. (2017). The origin of heredity in protocells. *Philosophical Transactions of the Royal Society B*, *372*, 20160419.

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