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Membranes as the earliest entropy resisting structures in the origin of life

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Abstract

The origin of life remains among the most compelling and debated scientific mysteries. Traditional hypotheses, such as the RNA World and Metabolism-First models, emphasize nucleic acids or metabolic cycles as life's earliest foundations. However, both approaches inherently assume the existence of structured, stable compartments to maintain molecular interactions; yet do not fully explain their emergence. In this paper, we propose the Membrane-First Hypothesis, asserting that a plausible pathway toward life may have begun with spontaneously forming amphiphilic boundaries that enabled protocellular microenvironments that actively resisted entropy, maintained stable internal environments, and provided primitive localized gradients that bias reaction fluxes. Other prebiotic organizing structures, such as mineral surfaces and coacervate-like droplets, are considered alongside membranes, and their respective advantages and limitations are evaluated. Drawing insights from systems science, including dissipative structures, autopoiesis, hierarchical complexity, and cybernetics, we argue that membranes were not passive containers, but the drivers of differential persistence ('proto-selection') and complexity. By systematically comparing existing origin-of-life theories, we propose that membrane-based compartments uniquely integrate metabolic and genetic emergence, offering robust experimental pathways for validation. This systems-science-informed model fundamentally reshapes our understanding of life's defining origin. We argue that membranes represent one plausible route by which localized, energy-coupled protocellular systems could have emerged prior to fully Darwinian evolution.

1 Introduction

The origin of life is probably the most profound question in science. Competing theories have explored how molecular complexity emerged from a primordial environment, leading to the first self-sustaining biological systems. Two prominent frameworks, i.e., the RNA World [25] and Metabolism-First models [63], have focused on genetic replication and catalytic cycles as the foundations for early life. Many contemporary versions of these perspectives, however, invoke some form of sustained localization or confinement in which key reactions could persist. If so, what physical conditions first enabled molecular systems to remain together long enough for cumulative change to take hold?

The importance of spatial organization in prebiotic chemistry has been recognized since early origin-of-life theorists such as Bernal [7], who emphasized the role of structured environments in stabilizing and concentrating reactive molecules.

Defining life remains contested, and proposed criteria vary across disciplines and historical periods. For this reason, several authors argue that definitions should be judged by explanatory usefulness rather than by identifying a single essential property, and they caution against projecting modern cellular organization directly onto prebiotic contexts [37, 59]. In this spirit, we adopt a minimal operational framing that keeps metabolism, heredity, and compartmentalization in view, while asking which physical structures could first support persistence, coupling, and individuation under prebiotic conditions.

A growing body of research suggests that a near-universal feature of extant life is compartmentalization, i.e., the presence of boundaries that help sustain internal chemistry, enable selective exchange with the environment, and support energy transduction [12, 17, 36, 57]. Biological membranes play this role by establishing the boundary conditions under which biochemical processes occur and by shaping molecular traffic. Yet, in many origin-of-life narratives, membranes are treated as late "packaging" relative to genetic and metabolic considerations. Although earlier hypotheses such as the 'Lipid World' [53] and the nanocell model proposed by Trevors and Psenner [60] emphasized the possible role of lipid membranes in early life, they primarily emphasized encapsulation rather than regulatory or selective roles of membranes. These models did not articulate the systemic, thermodynamic, or evolutionary implications of membrane formation. Our approach builds upon these insights by framing membranes as active, entropy-resisting structures that initiate regulatory and selective dynamics. In this systems-science-grounded perspective, we argue that membranes were not just passive enclosures but might have enabled early persistence, coupling, and proto-selective dynamics under prebiotic conditions.

A question that has preoccupied the author for years found clarity when he began to view the challenge through a systems science lens - and ultimately shaped the ideas presented in this paper. In contemplating themes of longevity, overcoming death, or even returning from death, he encountered a key observation that became central to his argument: once a cell's membrane is irreversibly damaged, life cannot return.

While proteins, genetic material, and even entire metabolic cycles can persist after cell death, the destruction of membrane integrity marks the definitive transition from living to non-living. This prompted the author to speculate that membranes, which formed much earlier than other organic tissues, may have offered the mechanism that triggered the emergence of biological complexity.

Here, we explore the hypothesis that membranes, probably being the first entropy-resisting structures on Earth, initiated processes that eventually led to life.

Definition (thermodynamic sense) In this paper, "entropy-resisting" does not imply a violation of the second law. Rather, it denotes localized order formation and persistence in an open system driven by environmental free-energy gradients and dissipation (non-equilibrium thermodynamics). Amphiphile self-assembly can generate order at equilibrium, but our stronger claim concerns the capacity of membrane-bounded compartments to sustain chemical differentiation over time under flux (e.g., cycling, gradients), thereby creating the preconditions for continued organization and selection-like persistence.

Terminology note (chemical evolution vs. Darwinian evolution) In this paper, we use "chemical evolution" to refer to pre-genetic transformations and selection-like processes (e.g., differential persistence and compositional inheritance) operating prior to templated genetic replication. We reserve "Darwinian evolution" for systems in which heritable variation is mediated by genetic polymers and selection acts on replicating lineages.

1.1 The transition from life to death: the role of membranes

One of the most distinctive features of living systems is their ability to maintain a low-entropy state in an open environment. Unlike inanimate systems, living cells sustain intricate molecular organization by constantly exchanging energy and materials with their surroundings [52]. This capacity depends critically on the integrity of biological membranes, which regulate the selective transport of molecules, maintain ion gradients, and provide a controlled reaction space for biochemical processes [4].

When an organism dies, a cascade of events unfolds at the cellular level. The first significant disruptions include loss of homeostasis, cessation of metabolic activity, and breakdown of genetic control mechanisms [30]. However, these events are not immediately irreversible—specific proteins remain functional, and in some cases, post-mortem gene transcription has been observed hours after death [47]. What, then, marks the final, irrevocable threshold between life and death?

Although many of the best-characterized death pathways derive from eukaryotic systems, analogous loss of membrane integrity, dissipation of electrochemical gradients, and failure of permeability control are also central to cell death in prokaryotes, underscoring the universal role of membranes in maintaining cellular viability across all domains of life.

In the following sections, we will explore how membranes could have formed before genetic or metabolic systems, how they may have driven prebiotic evolution, and why they remain life's most fundamental feature.

1.2 Membrane formation as the first entropy-resisting process

As already mentioned above, biological membranes create and sustain localized order, enabling the emergence of controlled biochemical processes, thus maintaining a state of low entropy in an open environment. While various hypotheses propose that genetic self-replication [25] or metabolic autocatalysis [63] initiated life, these processes typically require some form of localization (whether on surfaces, within pores, droplets, or compartments) that counteracts dilution and preserves reaction continuity. Deamer has long argued that boundary formation is not a late "packaging step," but a physically enabling condition that makes protocellular evolution experimentally tractable in plausible early-Earth settings [16–18]. We therefore propose that membranes were among the earliest self-organized structures capable of supporting local order under far-from-equilibrium conditions, and that they may have provided a critical scaffold for subsequent genetic and metabolic emergence.

We do not suggest that all early prebiotic organization required membranes; mineral surfaces, porous geological structures, and coacervate-like systems could also have supported localized chemistry prior to cellular life. Rather, we argue that membranes represent a particularly robust route to sustained compartmentalization once amphiphilic boundaries became available.

1.3 The thermodynamics of membrane self-assembly

In aqueous environments, amphiphilic molecules, such as fatty acids and phospholipids, spontaneously form bilayers, micelles, or vesicles due to hydrophobic interactions [19]. These formations are driven by the minimization of free energy, resulting in a stable yet dynamic boundary that separates an "inside" from an "outside." The self-assembly of membranes reduces local entropy, even though it occurs within a broader thermodynamic system in which energy dissipation still follows the Second Law of Thermodynamics [52].

We must, nonetheless, be cautious, because the spontaneous formation of an ordered structure does not, by itself, constitute life. The key transition from chemistry to biology occurs when a membrane stabilizes its structure long enough to regulate the flow of molecules. Living systems cope with complexity by maintaining integrity, which in systems science denotes wholeness [51]. To survive and develop, "wholes" must achieve autonomy, i.e., responsibility for their own regulation ([6], p. 103). This autonomic control is essential for a system to maintain a stable internal milieu, but also for efficient adaptation to changes in the external environment. This ability to selectively exchange energy and matter with the environment enables a primitive system to remain in a non-equilibrium state, which is a prerequisite for biological complexity [49].

In contrast to crystalline structures, which also exhibit low entropy, but fall short on the aspect of adaptability, membranes are uniquely both stable and dynamic. They allow for the continuous exchange of energy, a property seen in all living organisms. This provides a first hint that membranes could have been the first self-sustaining, entropy-resistant structures on early Earth.

1.4 Membrane-driven energy regulation and entropy dissipation

A critical feature of biological membranes is their ability to store and channel free energy via electrochemical gradients. Even primitive membranes formed from prebiotic amphiphiles could have developed proton gradients, an essential precursor to ATP-driven bioenergetics [39]. This ability to regulate ion flow represents the earliest known example of an energy-processing system that resists entropy by maintaining a non-equilibrium state, thus adding to our argument.

Modern cells utilize proton motive force (force that drives protons across a membrane generated by the difference in proton concentration between two compartments) to drive ATP synthesis [35], but even before enzymatic ATP production, protocellular membranes could have established rudimentary ion gradients due to natural pH and redox fluctuations in the prebiotic environment [31]. These gradients would have facilitated selective molecular absorption from the surrounding medium, chemical energy storage, allowing longer stability of enclosed reactions, and increased complexity over time, as more effective membranes persisted through selection.

1.5 Prebiotic selection: why membranes came before genetics

This section consolidates and extends earlier arguments concerning molecular stability and prebiotic selection, focusing specifically on how membranes could have served as substrates for selection prior to genetic inheritance.

If membranes were the first structures to locally resist entropy, then they likely provided the first selective pressures in prebiotic evolution. While RNA-world theories

propose that self-replicating genetic molecules initiated selection [57], such molecules would have rapidly degraded or diffused in the absence of a stabilizing enclosure.

Instead, selection could have first acted on membranes themselves, favoring those that (a) maintained structural integrity longer in fluctuating environments, (b) incorporated amphiphiles that enhanced permeability for nutrient intake, and (c) regulated energy gradients more effectively, enabling early metabolic-like reactions. The above perspective does not imply that membranes constituted fully living or autocatalytic systems, as lipid assemblies cannot catalyze the synthesis of their own components and therefore lack catalytic closure. Rather, membranes are treated here as physical scaffolds whose persistence depended on environmental lipid availability and whose evolutionary relevance emerged only through coupling with catalytic networks and, later, genetic inheritance.

This perspective reframes the origin of natural selection itself. Rather than genetic molecules serving as the first replicators, the first entities to undergo selection were prebiotic membranes competing for stability and energy efficiency, rendering them the first "holons" using Koestler's [29] language (i.e., a nodal point in a hierarchy that describes the relationship between entities that are self-complete wholes and entities that are seen to be other dependent parts.

This paper will explore how concepts from systems science, such as dissipative structures, autopoiesis, and cybernetics, further support the Membrane-First hypothesis, integrating a systemic viewpoint rarely applied explicitly to origin-of-life questions.

2 Membrane-driven evolution and the emergence of complexity

The ability of membranes to resist entropy and regulate energy flow not only provided a structural foundation for life but also established the first conditions necessary for evolutionary selection. While traditional views of evolution focus on genetic inheritance, the principles of prebiotic selection suggest that membranes themselves underwent a form of evolution long before nucleic acids emerged. In this section, we propose that membrane dynamics served as the first evolutionary system, allowing increasingly stable and functional compartments to emerge, ultimately paving the way for cellular complexity.

2.1 Early membranes as the first selective units (pre-genetic chemical evolution)

Darwinian evolution requires variation, selection, and inheritance. In this section, we use "selection" in a qualified, pre-Darwinian sense to refer to differential persistence and proliferation of compartments under environmental cycling, rather than to genetic inheritance in replicating lineages. In other words, the dynamics discussed here fall within a phase of chemical evolution (in Oparin's, 1957 sense) [44], where physical–chemical constraints shape which structures persist long enough to accumulate functional coupling. The central claim is therefore not that membranes were sufficient for life, but that they could have provided a comparatively persistent and scalable context in which metabolic and genetic systems later became evolutionarily decisive. While genetics is now the primary mechanism for these processes, early membrane vesicles could have undergone a primitive pre-genetic selection based on their physical and chemical stability. We discuss below how likely key factors could have influenced membrane survival and proliferation in prebiotic environments:

2.1.1 Structural integrity

Membranes with more robust lipid compositions would have been more resistant to mechanical stress, extreme temperatures, and osmotic pressure. Certain amphiphilic molecules may have conferred greater longevity, outcompeting vesicles that degraded more quickly.

2.1.2 Selective permeability

Early membranes with spontaneous pores or embedded mineral complexes may have facilitated nutrient uptake while preventing the loss of crucial molecules. Experimental work with fatty-acid vesicles suggests that such compartments can exhibit limited, condition-dependent permeability to small solutes while retaining larger or more highly charged molecules, especially under environmental cycling or in the presence of mineral interactions ([27, 32]). Selective retention of charged or catalytic molecules inside vesicles would have given them an energetic advantage over unstructured molecular assemblies. While this permeability is modest and far less specific than modern protein-mediated transport, it is sufficient to support differential molecular retention under plausible prebiotic conditions.

2.1.3 Energy gradients and proto-metabolism

Membranes capable of maintaining proton gradients [39] could have stored and harnessed energy, a precursor to the development of primitive metabolic cycles. We do not suggest that such gradients enabled ATP synthesis or modern chemiosmotic energy conversion in the absence of transporters or pumps; rather, early gradients may have biased local reaction environments, influenced molecular retention, and provided energetically favorable microconditions before the evolution of protein-mediated coupling mechanisms. Some vesicles may have adsorbed catalytic molecules (such as metal ions or peptides), leading to the emergence of membrane-associated chemical networks. While some models (e.g., Mulkidjanian et al., [40] suggest that early cells possessed leaky membranes and depended on external ion gradients, such views do not contradict the Membrane-First Hypothesis. On the contrary, they underscore the role of membranes in enabling spatial and energetic compartmentalization, even prior to the evolution of ion-tight structures and internal energy metabolism. Selective permeability, even if imperfect, represents a crucial first step toward functional complexity and thermodynamic regulation.

2.1.4 Growth and division

Membranes that could spontaneously grow by incorporating free amphiphiles from the environment would have expanded more efficiently than static structures. Under fluctuating conditions, vesicles reaching a certain size could have divided due to mechanical stress or lipid redistribution, leading to an early form of non-genetic replication [27]. A key constraint, however, is supply: in a pre-metabolic stage, membrane growth presupposes an environmentally sustained availability of amphiphiles [17, 27]. The Membrane-First hypothesis therefore assumes that early vesicles drew on exogenous lipid sources produced through plausible prebiotic pathways (e.g., abiotic synthesis under hydrothermal or photochemical conditions) and/or delivered by meteoritic infall, rather than on endogenous lipid biosynthesis requiring enzymes. This framing does not resolve the

origin of amphiphiles, but makes explicit that membrane persistence and proliferation depend on a continuing environmental flux of membrane-forming molecules.

The above characteristics justify our positing that prebiotic evolution may have first occurred at the level of membranes, with genetic replication emerging later as a refinement mechanism rather than a prerequisite for selection.

2.2 The Role of Membranes in the Transition to Cellular Life

In this section, we discuss how primitive membranes might have set the stage for the emergence of cellular complexity by becoming increasingly selective and energy-efficient. The progression from simple vesicles to proto-cells is marked by the transitions elaborated below.

2.2.1 Encapsulation of catalytic networks

As membranes stabilized, they likely trapped prebiotic catalysts such as ribozymes, peptides, and metal cofactors [8, 27, 57]. This provided a concentrated reaction space, allowing chemical cycles to persist and refine. Therefore, membrane-bound chemical networks may have preceded full-fledged metabolism, leading to proto-metabolic cycles.

A complementary terrestrial scenario emphasizes fluctuating hydration conditions in which membranes and polymers could have co-developed. In the "hot spring / wet–dry cycling" framework, dehydration concentrates solutes and can promote polymerization, while rehydration yields protocell populations in which compartment properties influence which chemistries persist across cycles [13]. This perspective strengthens the plausibility of membranes as early enabling structures while avoiding the assumption that fully developed genetics or metabolism had to predate compartment formation.

2.2.2 Emergence of membrane-embedded functions

The incorporation of hydrophobic peptides into membranes may have altered membrane permeability and facilitated rudimentary, nonspecific molecular translocation. We do not imply the existence of genetically encoded transporters at this stage; rather, such peptide–membrane interactions are understood as physicochemical effects that preceded, and potentially scaffolded, the later evolution of gene-encoded transport proteins. These early interactions may have produced transient or weakly selective conduits rather than true ion channels, with increasing specificity and regulation emerging only after the appearance of ribozymes, peptides, and eventually genetically encoded transporters.

2.2.3 Co-evolution of membranes and genetic systems

Once nucleic acid replication emerged, membranes provided a selective advantage by preventing the dilution of genetic material. This created an interdependent system where membranes protected genetic molecules, and genetic molecules coded for membrane-associated proteins (e.g., lipid biosynthesis enzymes). This feedback loop solidified the membrane-genome relationship, transitioning from membrane-driven selection to fully integrated cellular life. Thus, rather than serving as a passive structure, membranes were the primary architects of life's emergence, creating the conditions necessary for genetic evolution to take hold.

Experimental work on model protocells increasingly indicates that the emergence of genetic polymers and membrane-bounded compartments need not be strictly

sequential, but could have proceeded through coupled constraints and mutual accommodation. A central challenge has been the incompatibility between the ionic conditions required for RNA catalysis and replication—particularly the need for divalent cations such as Mg^{2+}—and the structural fragility of simple fatty-acid membranes. However, multiple studies have demonstrated plausible routes around this tension. For example, chelation strategies and mixed amphiphile compositions can stabilize membranes while preserving ribozyme activity [1, 2], and selective permeability of simple vesicles allows uptake of activated nucleotides and short oligomers without catastrophic leakage [43]. More recently, RNA-catalyzed RNA ligation has been demonstrated within vesicle-based protocells under conditions compatible with membrane stability, further supporting the feasibility of membrane–genetic co-development rather than a strict "genetics-first" chronology [14]. Together, these findings suggest that early membranes could have acted as enabling constraints, shaping the chemical conditions under which genetic polymers became functionally relevant, rather than merely encapsulating already autonomous replicators.

2.3 Experimental evidence for membrane-driven complexity

To strengthen our argument, we now highlight recent studies which have demonstrated that prebiotic vesicles can undergo selection and functional adaptation in environments mimicking early Earth conditions. Key findings include:

Membrane self-replication without genetic instructions: Fatty acid vesicles spontaneously divide under pH fluctuations, mimicking primitive cell division [27].

Membrane-permeable proton gradients enabling energy storage: Experiments show that lipid vesicles can harness proton gradients, suggesting an early mechanism for primitive energy processing [39].

Encapsulation of catalytic molecules enhances vesicle survival: Studies demonstrate that vesicles trapping simple catalysts exhibit greater structural longevity, supporting the idea of membrane-driven prebiotic selection [8].

Together, these findings support our hypothesis that membranes were not passive enclosures but active participants in early evolution.

3 Discussion

In this Perspective, the author presented an alternative hypothesis to explain how life might have begun. Rather than viewing membranes as secondary facilitators of prebiotic chemistry, it is suggested they were the first structures defining life. Membranes created the first self-sustaining systems capable of increasing complexity, thereby setting the stage for evolutionary selection by resisting entropy and interacting selectively with the environment.

The new perspective has far-reaching implications for diverse scientific disciplines. However, several critical questions remain unanswered, offering avenues for future research. To better present and elaborate on the various angles, the discussion begins with a critique of competing hypotheses, frames the Membrane-First hypothesis within systems and complexity science, highlights theoretical and experimental challenges, and proposes future directions and implications for Astro- and Evolutionary biology.

3.1 Competing Hypotheses for the Origin of Life

3.1.1 RNA world and metabolism-first models

RNA world and metabolism-first models and the question of early spatial organization

As we have already elucidated in the introduction, various scientists have theorized about the origins of life. Two of the most influential models are the RNA World hypothesis [25] and the Metabolism-First hypothesis [63]. In the following paragraphs, we examine how these influential frameworks conceptualize early organization and highlight areas that remain actively debated in contemporary research. While both models offer powerful accounts of how biological complexity might emerge, they often invoke some form of localized or structured environment in which key chemical processes could persist. What remains less clearly specified in many versions of these models is how such persistent organization initially arose under prebiotic conditions.

The RNA world model often requires sustained localization

Contemporary RNA-world research has significantly refined the mechanistic plausibility of RNA-centered early evolution, including clearer articulation of biochemical constraints, plausible transitional stages from RNA to mixed RNA/DNA systems, and evolutionary feasibility under realistic chemical conditions [10, 11, 41, 61]. These developments strengthen RNA-first scenarios as serious mechanistic frameworks rather than purely speculative narratives. At the same time, many RNA-world pathways still rely, explicitly or implicitly, on some form of sustained localization (e.g., adsorption to surfaces, confinement within pores, association with films or droplets, or encapsulation in protocellular compartments) to mitigate dilution, stabilize reactive intermediates, and maintain reaction continuity over time [10, 61]. It is this recurring need for persistent organized space, rather than the plausibility of RNA catalysis per se, that motivates our emphasis on boundary formation as a primary enabling condition.

The RNA World hypothesis posited that RNA molecules, which were capable of self-replication, were responsible for the development of early life. These molecules had the potential to serve as both genetic carriers and catalysts (ribozymes) simultaneously. This model can elucidate the potential initiation of genetic replication; however, it does not directly address the manner in which RNA molecules were able to remain stable and localized in a prebiotic environment.

RNA molecules are chemically fragile and susceptible to hydrolysis, especially in aqueous environments. Thus, RNA would have required some form of containment or stabilization to persist long enough for selection to act.

Other researchers have later proposed diverse mechanisms to overcome the impasse.

While Ferris [22] proposed that RNA could polymerize on mineral surfaces, Martin and Russell [33] and Russell and Hall [50] explored how hydrothermal vents might provide confinement. However, these models do not fully explain how RNA remained stable in the long term. Oparin, [45] suggested that coacervates could offer encapsulation, whereas Deamer [17] highlighted the potential role of membranous compartments formed by lipid-like molecules. However, the persistence of both types of encapsulation under realistic prebiotic conditions remains uncertain. While membranes may have coexisted with mineral- or coacervate-based organizing structures, their distinctive contribution lies in enabling persistent, self-maintained boundaries that couple energy gradients with internal chemistry across environmental cycles.

Even accounting for such stabilization mechanisms, the RNA World model does not explain how such prebiotic compartments formed and remained stable over time. This raises the question: if RNA molecules could replicate, how did they avoid immediate degradation or dispersal in a chaotic environment?

Metabolism-first model and the problem of persistence

Metabolism-first frameworks conceptualize life's emergence as a process of free-energy–driven self-organization, in which chemical reaction networks arise and persist in far-from-equilibrium environments sustained by geochemical gradients. Such models emphasize the thermodynamic grounding of early evolution, the continuity between planetary chemistry and biochemistry, and the plausibility of network-level self-organization in settings such as alkaline hydrothermal systems, mineral-catalyzed surfaces, and redox interfaces [21, 38, 62]. In this respect, metabolism-first approaches provide some of the most detailed energetic accounts of how prebiotic chemistry might have escaped equilibrium and achieved sustained reaction fluxes long before the appearance of genetic polymers.

At the same time, important questions remain regarding how such open reaction networks could achieve long-term persistence, individuation, and continuity in highly dynamic geochemical settings. In particular, metabolism-first scenarios continue to debate how early systems acquired heritable identity, resisted dispersal, and transitioned toward bounded evolutionary units in the absence of durable compartments—or when confined only by transient, highly permeable boundaries.

From this perspective, the Membrane-First hypothesis is not positioned as a replacement for metabolism-driven models but as a complementary and discriminating framework. By introducing semi-stable boundaries capable of regulating fluxes, sustaining localized free-energy gradients, and coupling internal chemistry to growth and division, membranes may have supplied the missing physical scaffold required for metabolic networks to persist as selectable individuals. The key distinction therefore concerns not whether metabolism preceded genetics, but when and how boundary formation became essential for evolutionary continuity—a question that can be addressed empirically by comparing reaction persistence and adaptive behavior inside and outside protocellular compartments.

The Metabolism-First hypothesis suggests that life began with autocatalytic chemical cycles before genetic systems evolved. Unlike the RNA World model, it does not require self-replicating molecules at the outset but rather assumes that life emerged from self-sustaining metabolic networks that gradually increased in complexity. The problem is that such metabolic cycles would still require a localized environment to function. Supporters of the Metabolism-First model made different assumptions as to where that spatial organization came from.

Wächtershäuser, [63] proposed that mineral surfaces, particularly iron-sulfur clusters, provided catalytic platforms for early metabolic cycles. Martin and Russell, [33] and Sojo et al., [46] extended this by demonstrating how alkaline hydrothermal vents might have sustained metabolic reactions through chemical gradients. Meanwhile, lipid-based vesicles facilitated by mineral surfaces [27] may have offered compartments for primitive reaction networks, but the long-term stability of such structures remains a subject of debate.

Recent syntheses have sharpened what "geochemical continuity" could mean by tracing plausible connections between prebiotic reaction spaces and reconstructed metabolic architectures, rather than treating early metabolism as a black box that simply appears [9]. At the same time, these analyses underscore how difficult it remains to explain the emergence of biosynthetic routing and sustained chemical organization without additional mechanisms that stabilize intermediates and preserve reaction context over time [42]. In this respect, membrane-bounded compartments remain a plausible candidate: they can provide persistent individuation and repeated microenvironments in which reaction networks are not only energized but also retained, coupled, and selectively stabilized.

Despite these containment mechanisms, this model still assumes a stable and structured chemical environment that allows prebiotic reactions to persist. It does not provide a clear explanation of how such stable compartments emerged in the first place.

3.2 Expanding the Landscape: Competing Hypotheses for the Origin of Life

While the RNA World and Metabolism-First models have dominated origin-of-life discussions, numerous other hypotheses attempt to explain this fundamental question. In Table 1 below, we compare several contemporary theories, highlighting their strengths and limitations relative to the Membrane-First Hypothesis.

It is important to emphasize that both RNA-first and metabolism-first frameworks have matured into detailed research programs with substantial mechanistic development. In particular, RNA-world scholarship has advanced beyond early formulations by addressing evolutionary feasibility, biochemical constraints, and plausible transitions from RNA- to DNA-based heredity [10, 11, 41, 61]. Accordingly, our comparison does not treat these models as lacking mechanisms; rather, it highlights where different hypotheses place the earliest requirements for persistence, localization, energy coupling, and selection.

While each of these hypotheses offers valuable insights, the Membrane-First model addresses several critical challenges in the origin-of-life debate:

- Stable, self-sustaining compartmentalization: Unlike mineral surfaces, vent pores, or transient coacervates, membranes provide a long-term, dynamically regulated boundary for molecular interactions.
- Energy regulation from the start: Membranes can help sustain ion or chemical gradients, which are precursors to ATP-driven metabolism, whereas other models assume energy sources but do not actively regulate them.
- Selective molecular exchange: Unlike free-solution chemistry, membranes allow for concentration and retention of key biomolecules, preventing dilution.
- Bridging the metabolism-genetics divide: Membranes create an environment where prebiotic chemistry and replication could co-evolve, resolving a key weakness in competing theories.

3.3 The need for an intrinsic self-organized space: the membrane-first hypothesis

The RNA World and Metabolism-First models both rely on some form of spatial stability but do not explain how such stability initially arose. What we propose is that membranes, among several possible organizing structures, may have been the first self-organized spaces capable of sustaining life's essential chemistry over extended timescales. Other

Table 1 Comparative synthesis of representative RNA-first, metabolism-first, and membrane-first frameworks across organizational criteria relevant to persistence, compartmentalization, energy coupling, inheritance, and selection

Criterion	RNA-First Models	Metabolism-First Models	Membrane-First Hypothesis
Primary organizing principle	Catalytic and replicating RNA polymers	Autocatalytic reaction networks driven by geochemical energy	Self-assembling amphiphilic boundaries enabling localized systems
Source of compartmentalization	Surface adsorption, pores, droplets, or protocells	Mineral surfaces, vent micropores, emulsions	Spontaneously forming vesicles and films
Persistence mechanism	Replication of polymers	Continuous free-energy flow through networks	Boundary-mediated retention + growth/division
Energy coupling	Often external (UV, chemistry); weak internal regulation	Strong geochemical gradients	Gradients sustained across semi-permeable boundaries
Stability challenges	RNA hydrolysis, dilution	Network dispersal, instability	Amphiphile fragility; permeability control
Inheritance prior to genes [a]	RNA sequence replication	Network recurrence	Compositional inheritance of membranes/catalysts
Unit of selection [b]	RNA molecules	Reaction networks	Vesicle-bounded protocells
Key strengths	Information storage; catalysis	Thermodynamic grounding; geochemical continuity	Boundary-driven individuation; proto-bioenergetics
Open questions	Sustained localization; coupling to metabolism	Individuation; heredity	Emergence of selective permeability; robustness
Discriminating predictions [c]	Polymer persistence vs. dilution	Network stability without compartments	Vesicle persistence, permeability optima, gradient coupling

Entries in the RNA-first column synthesize representative discussions from Gilbert [25], Cech [10], Cojocaru and Unrau [11], Vázquez-Salazar and Lazcano [61], and Muñoz-Velasco et al., [41]. Entries in the metabolism-first column synthesize representative discussions from Wächtershäuser [63], Martin and Russell [33], Morowitz and Smith [38], Fani and Fondi [21], Sojo et al., [46], Carbonell and Peretó [9], and Negrón-Mendoza et al., [42]. Entries in the membrane-first column synthesize representative discussions from Segré et al., [53], Trevors and Psenner [60], Deamer ([16–18]), Damer and Deamer ([12, 13]), Hanczyc et al., [27], Budin and Szostak [8], Mulkidjanian et al., [39], and related sources discussed in the text. The table is intended as an interpretive comparative synthesis rather than a one-to-one historical attribution of each cell to a single source.

[a] "Inheritance prior to genes" refers to sequence inheritance in RNA-first models, network recurrence in metabolism-first models, and compositional inheritance or compartment-level persistence in membrane-first models.

[b] "Unit of selection" is used comparatively and includes pre-Darwinian differential persistence where explicitly indicated in the text.

[c] "Discriminating predictions" summarizes experimentally testable contrasts proposed in this Perspective.

non-cellular organizing structures, such as mineral surfaces and coacervate-like droplets, have also been proposed as early stabilizing environments for prebiotic chemistry. Recent work has directly addressed a key limitation of coacervate compartments—rapid fusion and loss of compositional identity—by demonstrating conditions under which coacervate droplets can suppress fusion and maintain RNA compartmentalization over longer timescales [3]. However, such systems remain highly sensitive to environmental perturbations and lack intrinsic boundary persistence, highlighting an important contrast with membrane-bounded compartments.

To make this distinction concrete, Fig. 1 schematically contrasts uncontained prebiotic chemistry with membrane-bounded systems and illustrates how self-assembled amphiphilic boundaries could concentrate reactants, regulate exchange, and support localized energy gradients.

Amphiphilic molecules in prebiotic environments spontaneously assemble into bilayer vesicles that partially isolate internal chemistry from the external milieu. Semi-permeable boundaries concentrate reactants, reduce dilution, and allow the establishment of

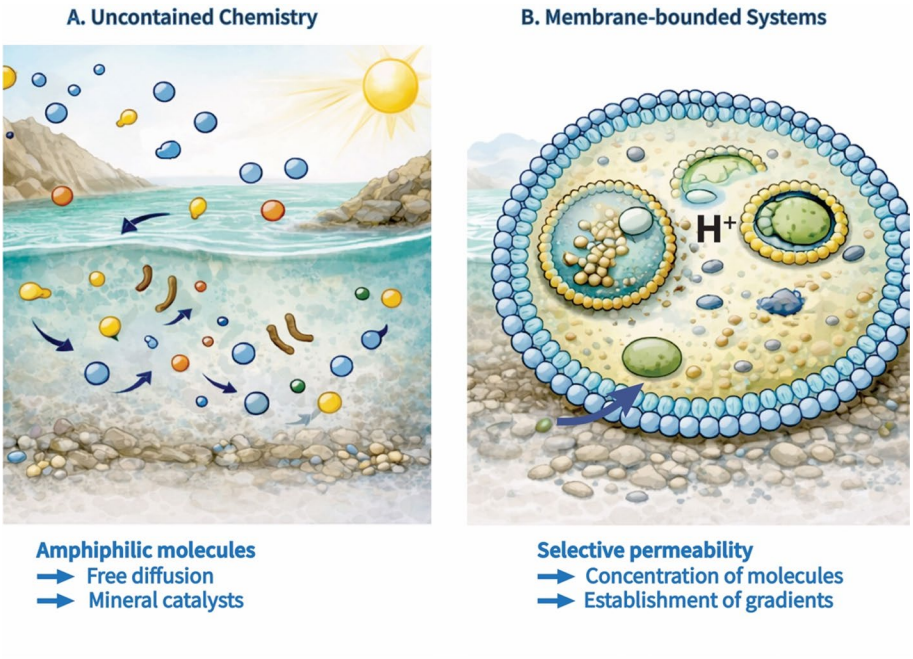

Fig. 1 Prebiotic membrane self-assembly and boundary-mediated organization

chemical or ionic gradients across the membrane. Mineral catalysts or redox couples at the membrane interface may further bias reaction fluxes. The diagram contrasts uncontained chemistry (left) with membrane-bounded systems (right), highlighting how boundaries could promote persistence and proto-selection.

Deamer, [17] argues that amphiphilic molecules in prebiotic conditions could spontaneously form vesicles, providing a naturally occurring compartment for early molecular systems. Furthermore, Mulkidjanian et al., [39] highlight how prebiotic membranes could have supported primitive ion gradients, laying the groundwork for later bioenergetic processes.

Membranes offer a distinct solution to the problem of early molecular stability by providing (1) a self-assembled and adaptable boundary rather than relying solely on external surfaces; (2) partial regulation of molecular exchange, reducing dilution and degradation of key biomolecules; and (3) the capacity to sustain local energy gradients, thereby enabling proto-metabolic reaction networks.

If early membranes formed spontaneously from amphiphilic molecules, they would have provided the first stable compartments in which life's chemistry could develop. Unlike RNA molecules or metabolic cycles, which depend on external stabilization, membranes create their own dynamic yet persistent boundaries. This reframes the emergence of life: rather than assuming an already organized space, life may have begun when membranes first created one.

3.4 Revisiting earlier membrane-based hypotheses

Several earlier hypotheses have hinted at the central role of lipid membranes in the origin of life. The Lipid World hypothesis [53] proposed that amphiphilic molecules could form vesicular structures capable of primitive selection and inheritance. Similarly, Trevors and Psenner , [60] discussed nanocells as membrane-bound microstructures capable of encapsulating early biochemical processes. Garwood, [23] outlined how liposomes

may have preceded genetic molecules, aiding the transition to replication-capable systems.

While valuable for their early focus on compartmentalization, these models generally portray membranes as passive containers. They lack an integrated systems perspective and fail to capture how membranes could actively regulate molecular traffic, mediate energy flow, or sustain complexity over time. Moreover, they do not compare their models against competing hypotheses or articulate broader theoretical implications.

In contrast, the Membrane-First Hypothesis posits that membranes are not just boundary structures but the earliest active systems capable of resisting entropy, establishing internal order, and mediating prebiotic selection. By enabling stable, self-sustaining compartmentalization, membranes allowed for prolonged molecular interactions shielded from environmental disruption. Their capacity to form and maintain ion gradients introduced primitive energy regulation mechanisms, which are precursors to later bioenergetic systems like ATP synthesis. Selective permeability helped retain beneficial molecules and exclude harmful ones, enhancing the potential for localized evolutionary processes.

Membranes also bridge a critical divide in origin-of-life research: the gap between metabolism-first and replication-first models. They offer an organized, enclosed space where both prebiotic chemistry and primitive genetic systems could emerge and co-evolve. This integrative potential uniquely positions membranes as the foundation upon which more complex biological systems were built.

This view gains further depth when examined through the lens of systems science, which is explained in the next section.

The membrane-centered progression proposed here is summarized schematically in Fig. 2.

Conceptual timeline illustrating a membrane-centered pathway toward cellular life: (1) Abiotic amphiphiles assemble into vesicles. (2) Vesicles encapsulate mineral catalysts and simple reaction networks. (3) Energy gradients across membranes bias internal chemistry, producing proto-metabolic cycles. (4) Membrane-embedded functions and compositional inheritance emerge through growth and division. (5) Genetic polymers later co-evolve with boundaries, producing fully cellular systems.

In sum, the Membrane-First Hypothesis does more than extend previous lipid-centric ideas. It reframes them within a systemic paradigm, articulating a coherent, multi-level account of how life could originate from the bottom up—not through molecules alone, but through the formation of structured, adaptive systems capable of evolution.

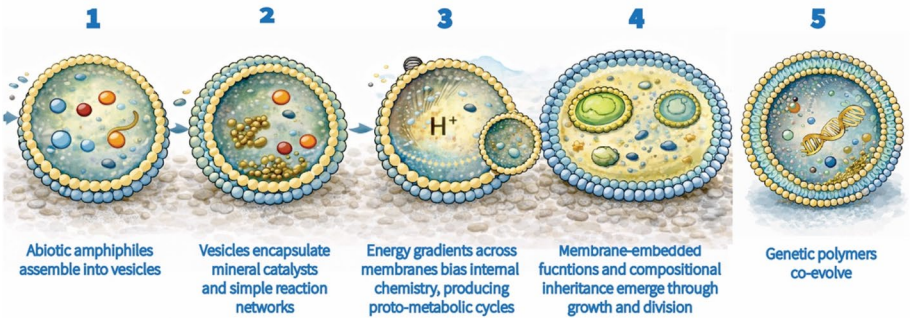

Fig. 2 Proposed staged progression from amphiphilic vesicles to protocells

3.5 Justifying the membrane-first hypothesis utilizing systems and complexity science and implications derived

In this section, we frame our thesis within the context of systems and complexity science. We propose that the Membrane-First hypothesis aligns better than competing hypotheses with non-equilibrium thermodynamics and far-from-equilibrium systems theory, emphasizing self-maintaining (autopoietic) organization, hierarchical structure, and other systems-science principles essential to life's emergence [48]. They exhibit features of autopoiesis, enabling the system to self-produce and maintain its boundary conditions [34]. By providing a hierarchical structure with nested levels of organization, membranes lay the groundwork for increasing complexity [55]. Through feedback regulation and control over internal dynamics, they fulfill basic principles of cybernetics [5]. And critically, they serve as the earliest units of selection, subject to environmental pressures long before the advent of nucleic acids (Szathmáry & Smith, [54, 58]).

3.5.1 Thermodynamic systems & nonequilibrium dynamics

Prigogine's dissipative structures theory suggests that self-organized complexity arises in far-from-equilibrium conditions [48]. Life is an open system. Living systems import energy, export entropy, and maintain order. We propose that membranes create the first dissipative structures. They form stable compartments that resist entropy by maintaining ion gradients and energy flux.

The Membrane-First hypothesis aligns with the emergence of dissipative structures as a necessary precursor to life. In contrast, other hypotheses (e.g., RNA World, Metabolism-First) assume chemical reactions happened first, but without containment, such reactions would dissipate before sustaining complexity.

3.5.2 Autopoiesis: self-maintaining systems

A system is autopoietic if it continuously regenerates itself while maintaining its boundaries [34]. Membranes enable the first autopoietic processes, because they maintain structure while allowing selective exchange. They create a stable environment for reactions, allowing internal molecular processes to self-organize. RNA or metabolism-first models, on the other hand, lack self-maintaining organization—they require external scaffolds (minerals, vents) to persist. Membrane-enclosed compartments could have evolved into fully autopoietic systems before genetic encoding emerged.

3.5.3 Systems hierarchies & complexity growth

Simon's Near-Decomposability Principle (1962) states that complex systems evolve from simpler, hierarchically structured units. Membranes provide the first hierarchical structures in prebiotic evolution, because their role begins with supporting molecular interactions inside simple vesicles, i.e., the lowest level of structure, and evolve at higher levels, where membrane-enclosed protocells interacting with the environment. Prebiotic systems needed hierarchy to scale complexity over time and membranes create the necessary modularity that is essential for evolutionary adaptability.

3.5.4 Synergetics: self-organization in complex systems

Synergetics studies how systems self-organize into higher-order structures through internal interactions [26]. Membranes facilitate synergetic interactions by creating

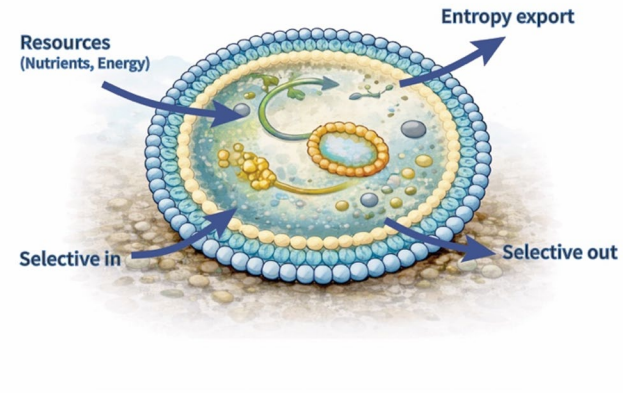

Fig. 3 Membranes as dissipative, self-maintaining systems

chemical reaction networks, stabilizing prebiotic systems into emergent complexity, and enabling cooperative molecular processes. The Membrane-First model aligns with synergetics because prebiotic molecules self-organize into structured enclosures before genetic information appears. No other hypothesis explicitly accounts for self-organization within a defined boundary.

3.5.5 Evolutionary systems & cybernetics

Ashby's Law of Requisite Variety [5] states that a system must have internal complexity (referred to here as "variety") at least as great as its external challenges to survive. Membranes can increase internal variety because they enable selective exchanges with the outside world, leading to increasing reaction diversity inside the vesicle. More importantly, membranes create a dynamic equilibrium, which allows internal processes to adapt. Therefore, in contrast, RNA and metabolism-first models do not explain how systems regulate external complexity. Membranes, on the other hand, introduce an embryonic kind of cybernetic control, enabling selection before information-based systems emerge.

These systems-level dynamics are illustrated schematically in Fig. 3, which depicts membrane-bounded protocells as dissipative, feedback-coupled structures maintaining local order through energy and material fluxes.

Systems-level representation of membrane-bounded protocells as dissipative structures. Resource fluxes across the boundary drive internal reactions, which in turn stabilize or modify membrane composition, creating feedback loops linking boundary maintenance, metabolism, and growth. Entropy is exported to the environment while local order is sustained. Such feedback-coupled systems provide the physical basis for early selection prior to genetic replication.

This systems-level coupling between boundary maintenance, internal chemistry, and emergent selection has been anticipated in earlier integrative framings of life's origins. Dyson, [20], for example, emphasized the interdependence of metabolism, replication, and compartmentalization in early evolution, while Kaneko [28] explored how hierarchical self-organization and compositional diversity can arise in complex chemical systems prior to fully developed genetic control. We build on these insights but shift the analytical focus to membranes as the earliest persistent boundary structures capable of sustaining individuated, energy-coupled protocellular systems. In this framing, compartments

are not merely supportive contexts but candidate primary loci of pre-genetic persistence and selection-like dynamics under far-from-equilibrium conditions.

3.5.6 Multi-level selection

According to Smith and Szathmáry [56], life evolves through selection across multiple levels: from molecules → protocells → cells. Membranes introduce the early selection-like sorting among compartments as some vesicles last longer due to better molecular retention, and over time, selection favors more robust membranes. Few origin-of-life models explicitly specify a selection unit prior to genetic replication. Membranes create the first entity subject to evolutionary selection.

Grounding our thesis on the above arguments, we therefore suggest that the Membrane-First model is not just about chemistry but represents a systems-level transition where (a) the laws of thermodynamics are considered in the sense that membranes are viewed as the first entropy-regulating structures in open systems. (b) The concept of Autopoiesis is at play, as membranes enable self-maintaining organization prior to genetic inheritance. (c) They create the first nested modular system in compliance with the principles of hierarchy and complexity. (d) draws from cybernetics as they introduce internal regulation and early selection pressures, and (e) membranes define the first proto-selection evolutionary unit, before molecular replication emerges, setting the ground for evolutionary systems.

3.5.7 Systems-science claims translated into testable predictions

A central aim of the Membrane-First hypothesis is not merely to reframe the origin of life conceptually, but to generate experimentally tractable expectations that distinguish boundary-driven scenarios from alternatives centered primarily on metabolism or genetic polymers. Systems-science principles such as dissipative organization, feedback regulation, and organizational closure imply specific physical and chemical behaviors that can be evaluated in laboratory models of protocells.

First, if membranes constituted early selectable units, then populations of prebiotic vesicles exposed to fluctuating environmental stresses (e.g., changes in salinity, pH, temperature, hydration cycles) should display differential persistence and growth depending on boundary composition and stability. This predicts measurable distributions of vesicle lifetimes and division frequencies, with certain amphiphile mixtures becoming enriched over time.

Second, semi-permeable boundaries are expected to exhibit a trade-off between molecular influx and internal retention. Systems-level reasoning predicts that protocells with intermediate permeability will outperform both highly leaky compartments (which cannot maintain internal reaction networks) and overly impermeable ones (which starve internal chemistry). This trade-off can be quantified experimentally by relating membrane composition to reaction yields, concentration gradients, and long-term persistence.

Third, the Membrane-First framework implies that energy transduction need not await complex protein machinery. Primitive membranes interacting with mineral catalysts or redox couples should, under suitable conditions, sustain localized ion or chemical gradients that bias reaction fluxes inside vesicles relative to the surrounding medium.

Detecting persistent gradient-coupled reaction rates would provide support for boundary-mediated proto-bioenergetics.

Fourth, in the absence of nucleic-acid replication, selection would have operated on compositional states of protocells. Systems models therefore predict forms of "compositional inheritance," whereby vesicles that grow and divide while maintaining characteristic lipid or catalyst mixtures bias the properties of their progeny. Such effects could be tested by tracking vesicle lineages in microfluidic or cycling environments and quantifying whether chemical compositions persist across multiple growth–division cycles.

Finally, systems theory suggests that the emergence of evolutionary individuality should display threshold-like behavior. Once boundary stability, resource flux, and internal reaction coupling exceed critical values, protocells should transition sharply from transient chemical assemblies to long-lived, self-maintaining units. Experimental systems exploring broad parameter spaces may therefore reveal phase-transition-like regimes in which persistence, internal organization, and adaptive responses increase non-linearly.

Together, these predictions recast the Membrane-First hypothesis as a program for empirical investigation rather than solely a conceptual framework. By specifying measurable observables—such as vesicle persistence distributions, permeability–function trade-offs, gradient-coupled reaction yields, compositional inheritance metrics, and threshold dynamics—the model invites direct experimental comparison with RNA-first and metabolism-first scenarios.

3.6 Future research directions: theoretical and experimental challenges

Boundary conditions and key uncertainties: A Membrane-First route requires (i) plausible persistence of amphiphile assemblies across realistic environmental cycling (e.g., ionic strength, pH fluctuations, temperature, UV exposure), and (ii) an environmentally sustained flux of membrane-forming amphiphiles sufficient to support repeated growth and re-compartmentalization. While these requirements are consistent with existing experimental protocell work, they remain central uncertainties that should be treated as testable constraints rather than assumed resolutions. We therefore treat membrane persistence and prebiotic amphiphile availability as explicit boundary conditions for the hypothesis.

To validate the hypothesis that membranes were indeed the first step toward the emergence of life, future research needs to address many questions, some of which are discussed here. The first question is whether membranes are able to sustain long-term prebiotic chemistry. Walde et al., [64] demonstrated that fatty acid vesicles could persist under prebiotic conditions. Their work supports the idea that primitive membranes were indeed viable. While lipid bilayers can encapsulate molecules, more research is needed to find out how long early membranes could have persisted under prebiotic conditions. Additionally, Budin and Szostak , [8] showed that encapsulated catalysts within vesicles could enhance reaction efficiency, reinforcing the idea that membranes were integral to early metabolic-like processes. Future experiments should assess membrane durability in fluctuating environments that mimic early Earth conditions.

A second important question is whether primitive membranes can support catalytic organization and selection-like dynamics in the absence of fully developed genetic systems. If membranes preceded metabolism, it is reasonable to ask whether they facilitated

the concentration and stabilization of catalytic molecules, thereby increasing the persistence of localized reaction networks under environmental cycling. Future research should investigate whether prebiotic vesicles containing simple catalysts can exhibit differential persistence and proliferation in laboratory simulations. Experimental protocell studies such as Mansy & Szostak [32] have shown that vesicle growth, division, and competition can be strongly influenced by encapsulated contents, highlighting how compartment-level differences can affect persistence; however, such work should not be taken to imply that membrane competition alone constitutes a complete pre-genetic evolutionary mechanism. Future experiments should therefore explore whether vesicle-encapsulated catalytic networks can be maintained and iterated across cycles in ways that plausibly bridge toward self-sustaining protocells.

A third interesting and more challenging question is whether membrane selection could have occurred before genetic replication. Assuming that early membranes competed for survival in prebiotic environments, can we identify processes that facilitated or led to the eventual emergence of genetic encoding? Maybe computational models could simulate membrane evolution to determine whether physical stability alone is sufficient to drive complexity before genetic inheritance.

The fourth and probably the most exciting question is whether Membrane-First models could help us create synthetic life. If membranes were indeed responsible for the emergence of life, then we should be able to develop synthetic protocells that exhibit self-sustaining behaviors without nucleic acids. If research can prove this, we would have compelling evidence that membranes are indeed the fundamental requirement for life's origin.

Future work should:

- Conduct experiments simulating early Earth conditions to test the durability and evolution of primitive membranes.
- Explore whether vesicle-encapsulated metabolic networks can evolve into self-sustaining protocells. Future experimental work might specifically leverage laboratory-based vesicle evolution experiments under controlled prebiotic simulation conditions to rigorously test the predictive power of the Membrane-First hypothesis.
- Investigate how membrane-bound compartments could have guided the emergence of genetic material.

By addressing these questions, we can refine the understanding of how life truly began—not in unstructured chemistry, but within stable, evolving membranes that defined the boundary between life and non-life.

4 Implications for astrobiology and molecular biology

4.1 Astro-biological implications: searching for membrane-like structures in space

If membranes are the earliest and most foundational features of living systems, then the search for extraterrestrial life should not focus only on genetic material, but also on membrane-like structures. This perspective complements earlier proposals that lipid hydrocarbon patterns may serve as universal biosignatures for life detection [15, 24]. Our contribution is not to claim novelty in lipid-based biosignatures per se, but to provide a systems-science rationale for why boundary-forming amphiphiles—and the

capacity to sustain individuated, energy-coupled compartments—are privileged markers of persistent organization across environments. Such a shift would have several implications for astrobiology and planetary exploration. For example, exoplanets and moons with environments favorable to amphiphilic self-assembly (e.g., persistent liquid phases such as water-rich oceans or hydrocarbon lakes) could be prioritized for study. This does not exclude targets such as Enceladus and Europa, where subsurface oceans and possible hydrothermal activity could support prebiotic compartmentalization, or Titan, whose hydrocarbon lakes may permit alternative amphiphile self-assembly pathways. Furthermore, amphiphilic molecules have been reported in some meteorites [17], suggesting that membrane formation may not be unique to Earth. Future missions could analyze extraterrestrial lipids for signs of self-assembly and molecular organization.

4.2 Implications for evolutionary biology

If our hypothesis is correct and membranes played a primary role in early evolution, then we can deduce that the observed complexity of life could not have been driven by genetics alone. Instead, we could at least consider a two-stage model of evolution. In stage I, early membranes were formed, they competed, and diversified based on their capabilities of stability and energy regulation. In other words, prebiotic vesicles evolved before genetic replication mechanisms. Once genetic molecules emerged, membranes assumed a new role. They provided protection, thus enhancing stability. The first protocells could have emerged when membranes and genetic systems became interdependent. If this conjecture is true, it would challenge our traditional RNA World models and suggest that selection pressure existed before the appearance of hereditary information. An interesting line of possible future work would be to explore whether and how membranes and genetic encoding systems co-evolved to shape modern biology.

5 Conclusion: membranes as life's defining feature

This paper has explored the hypothesis that membranes, rather than genetic or metabolic systems, were among the earliest organized structures capable of resisting entropy and supporting selection-like processes. The argument rests on three central points:

1. Membranes were among the earliest organized structures to resist entropy, providing a self-sustaining organization in an otherwise chaotic prebiotic world.
2. Selection-like sorting among compartments may have preceded genetic evolution, with vesicles competing for stability, permeability, and energy efficiency long before nucleic acids emerged.
3. Irreversible membrane failure marks a decisive threshold in extant cellular life. If irreversible membrane breakdown marks a decisive threshold in extant life, then the emergence of membranes may also have marked a critical step in life's origin.

Through a systems science lens, this paper has highlighted membranes not merely as passive containers, but as the earliest active, entropy-resisting structures capable of selection-like persistence and differential stabilization; a strong candidate for an early enabling condition for persistent, individuated protocellular organization.

This perspective suggests that membranes are the universal feature of life, whether on Earth or beyond. The work has implications in our search for extraterrestrial life, synthetic biology, and the origin of life. Entropy-resistant Membrane-based models should

be prioritized, as they may hold the key to understanding how living systems emerge from non-living chemistry.

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Data availability
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