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Estimating LUCA's Population in Hadean Oceans

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Abstract

Recent studies leveraging both the physiology of LUCA (Last Universal Common Ancestor) and molecular dating methods suggest that this ancestral cell emerged very early in Earth's history, enduring a hostile environment characterized by intense cosmic bombardment. This investigation estimates LUCA's population size by assuming a metabolism akin to the methanogen *Methanocaldococcus jannaschii*, which thrives on H_2 and CO_2-one of the oldest known metabolic pathways. For an estimated cell mass of approximately 530 fg and an energy requirement of ~2.7 × 10^{-13} W/cell for metabolism and growth and further supposing that LUCA was sustained by chemical energy from submarine hydrothermal vents, we estimate a Hadean Ocean population of ~1.8 × 10^{24} cells. This value is roughly five orders of magnitude lower than the estimated population of extant marine prokaryotes. Investigating LUCA's physiology has the potential to reveal fundamental biochemical processes that might be universal to extraterrestrial life, thereby guiding the search for biosignatures on other planets.

Keywords: LUCA metabolism, Primitive life, Cell population evolution

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Introduction

Recent studies have revisited the characteristics of LUCA (Last Universal Common Ancestor) [1], corroborating earlier findings [2-4]. LUCA was likely an anaerobic, thermophilic, autotrophic and chemotrophic organism inhabiting hydrothermal vent environments. These recent analyses suggest a more complex LUCA than previously envisioned, with an estimated genome size of approximately 2.5 Mb and ~ 2600 protein-coding genes, a substantial increase from the 355 [3] or 572 [2] inferred in prior phylogenetic studies. It is important to note that the estimated gene number is uncertain because most bacteria and archaea have undergone horizontal gene transfer since LUCA's existence. Despite these uncertainties, the consensus remains that LUCA could produce proteins and conserve energy via ATP. These studies suggest that LUCA likely depended on abiotic and spontaneous synthesis of organic compounds from H_2 and CO_2, highlighting the importance of methyl groups in LUCA's metabolism. Two modern microbes exhibit lifestyles reminiscent of LUCA: clostridia (anaerobic bacteria) and methanogens (hydrogen-consuming, methane-producing archaea) [3]. These organisms may provide insights into LUCA's nature and potentially that of even earlier ancestors.

Molecular dating techniques place LUCA's emergence approximately 4.2 billion years ago [1], significantly earlier than previous estimates [see also 5]. The early Earth presented a particularly hostile environment, yet life managed to develop near hydrothermal vents. Evidence

supporting the early emergence of life comes from analyses of graphite inclusions in a 4.1 Gyr zircon crystal [6], revealing a $^{13}C/^{12}C$ isotopic ratio consistent with a biogenic origin. Although chemical and physical fractionation processes can alter carbon isotopic ratios, electron microscopy revealed a polygonal structure in the included graphite, contrasting with the porous morphology typically observed in abiotic graphite. Consequently, the biogenic origin of this inclusion is currently favored. Furthermore, the emergence of life ~ 450 Myr after Earth's formation aligns with the discovery of microfossils in sedimentary ferrous rocks dated between 3.77 and 4.28 Gyr, potentially originating from submarine hydrothermal sources [7].

This early emergence of life reinforces the hypothesis that key molecules for abiogenesis, such as amino acids, arrived from space via impacts from remnant planetesimals or comets during Earth's formation. While it was previously suggested that such bombardment would have completely sterilized Earth's surface, current interpretations of the impact timeline on the inner solar system differ. Lunar rocks from Apollo missions reveal evidence of impact shocks ~ 3.9 Gyr ago, a period termed the "late heavy bombardment" (LHB) [8]. Some researchers propose that the near absence of impact signatures older than 3.9 Gyr implies that the LHB was simply a peak in the impact rate [9]. Others contend that impacts have decayed monotonically since the formation of the inner rocky planets, with the apparent LHB peak resulting from sampling biases [10, 11]. More recently, a hybrid scenario has been proposed involving two bombardment phases: an early phase ending around 4.4 Gyr ago, caused by leftover planetesimals and a second phase initiated by late giant planet migration starting ~ 4.0-4.2 Gyr ago [12]. This model includes a long bombardment tail, consistent with dynamical models of the solar system.

The survival of life on Earth during the Hadean eon has been investigated through impact simulations [13], suggesting that only deep-marine life could survive after 150 Myr. This was bolstered by numerical simulations [14] indicating that complete sterilization of Earth's habitable zone due to impacts is unlikely. More recent impact simulations, guided by the age distribution of terrestrial zircons and lunar rocks, concluded that Earth's surface was significantly reprocessed by planetesimal bombardment [15]. These findings suggest that early life likely possessed resistance to high temperatures and the capacity to spread from stable, deep-marine niches. These niches were examined in [16], utilizing a refined bombardment timeline and more precise thermal models to assess impact consequences. They determined that the habitable marine volume continuously expands due to rapid heat dissipation compared to collision frequency, implying that global sterilization could only occur with an impact rate increased by at least one order of magnitude. This suggests that the Hadean bombardment did not sterilize the oceans, reinforcing the possibility that life emerged very early in Earth's history and survived these bombardment events.

This work explores the potential energy sources that fueled LUCA's metabolism and population growth. To model LUCA's metabolism, we assume that the ancestor cell behaved similarly to the methanogen archaeon *Methanocaldococcus jannaschii*, which thrives optimally at temperatures of ~ +85°C [17, 18] and pressures of ~250 atmospheres [19], conditions found near hydrothermal vents. *M. jannaschii* derives energy exclusively from H_2 and CO_2 to produce methane, representing one of Earth's oldest metabolisms. The present estimates suggest that the majority of chemical energy from hydrothermal vents was utilized for cell population growth and basal metabolism. The estimated number of LUCA cells is approximately five orders of magnitude smaller than the present prokaryote cell population in marine habitats. These aspects are crucial for understanding the early emergence of life on Earth and for speculating on similar processes in exoplanets featuring CO_2-rich atmospheres and tectonic activity-characteristics that could define habitable environments elsewhere in the universe. Analyzing LUCA's metabolic pathways can reveal fundamental biochemical processes potentially common to extraterrestrial life, guiding the search for biosignatures on other planets. The paper is organized as follows: Section 2 discusses LUCA's metabolism and the chemical energy sources related to hydrothermal vents; Section 3 presents a model for the evolution of LUCA's population; Section 4 estimates carbon productivity and compares it with modern prokaryotes; and Section 5 summarizes the main conclusions.

The Metabolism of LUCA

Cells are inherently out-of-equilibrium structures requiring a constant energy supply to maintain their state. Quantifying the energy required to sustain a cell or the heat produced during its metabolic processes is experimentally challenging. Beyond these challenges, there are various plausible definitions for a cell's rate of energy usage, complicating a rigorous discussion. During cellular growth, energy is needed to produce proteins, nucleic acids, and other components for cell division, derived mainly from metabolic pathways that convert nutrients into usable forms of energy, like ATP. Cell population growth depends on nutrient availability, environmental conditions, and the cell's efficiency in utilizing energy.

Once a cell population reaches a quasi-steady state, the energy used is primarily divided into two components [20]: (1) maintenance energy, or basal metabolism, sustaining basic cellular functions like ion transport, protein turnover, and cell integrity without necessarily promoting growth; (2) growth energy, fueling cell division. Maintenance energy, or basal metabolism (B), is measured in Watts per cell. Earlier studies

suggested that the metabolic rate (B) increased with organism size (or mass) following a scaling law of $B \propto m^{3/4}$, known as Kleiber's law [21]. However, more recent research [22, 23] indicates that Kleiber's scaling is not universally applicable. Metabolic rates increase with body size across different taxa, with each taxon exhibiting a distinct scaling relationship [23] found that prokaryote metabolism scales as $B \propto m^{2.52}$. Other investigations [24, 25] corroborated these results, demonstrating that the specific metabolic rate Q = B/m increases with size for different taxa. In particular [25] analyzed 173 prokaryotes with masses ranging from 10^{-14} to 10^{-11} g, finding that specific metabolic rates vary from 0.32 W/kg to 68.0 W/kg - a difference of more than two orders of magnitude.

The minimum energy required to construct a new cell represents the sum of energy needed to assemble its main components into biomolecules, including the genome, proteome, transcriptome and lipid bilayer [26], revisited earlier estimates of the minimum energy per-gram needed to form a new cell, conducting calculations at temperatures from 275 to 400 K for four cell models. The synthesis cost per gram of biomass was remarkably similar across species, indicating a fundamental floor in per-gram cost. While the lipid bilayer constitutes only 9% of a cell's mass, it accounts for 21% of total synthesis energy [26], calculated that the average specific energy for cell creation does not strongly depend on temperature and can be expressed as:

$$\varepsilon = 330\left(\frac{T}{300K}\right)^{1/3} J/g \qquad (1)$$

The maximum growth rate (r_m) of a cell population is also important, providing a standardized estimate of population-level biomass production and evolution. Maximal population growth rates under optimal conditions have been extensively studied in microbiology. Under these conditions, the total energy rate (P) required by the cell to maintain its metabolism and cell division is:

$$P = B + r_m \varepsilon m \qquad (2)$$

LUCA likely possessed a primitive metabolism involving sequences of chemical reactions yielding free energy, which the organism used to perform work or produce new cells. The specific metabolic strategies used depend on environmental constraints. LUCA's physiology suggests adaptation to hydrothermal vents, indicating a high-pressure, sulfur-rich environment with temperatures around 350 K or higher. In modern times, thermophilic methanogens thrive in deep-sea hydrothermal vents, using H_2 as an electron donor [27].

Deep-sea hydrothermal vents are located along mid-ocean ridge systems near volcanically active areas. Seawater penetrating fissures in the volcanic bed is heated by magma and expelled as mineral-rich water, providing energy and nutrients to chemoautotrophic organisms like LUCA. Currently, there are ~ 200 known hydrothermal fields near subduction oceanic zones at depths up to 5000 m. Gases and fine metallic particles emitted from these sources are rich in Fe, H_2S, CO_2 and H_2, among other inorganics. Many thermophilic, hyperthermophilic bacteria and archaea live within or near these vents, adapting through modifications to their proteins, membranes and nucleic acids. Hydrothermal vents create chemically reactive environments, far from equilibrium, with temperature, redox and pH gradients. Unicellular organisms consume chemical energy through the oxidation of reduced mineral compounds via an electron transfer chain coupled to a Calvin-Benson cycle for carbon fixation and ATP production [28] proposed that the first organisms were chemoautotrophs utilizing the oxidative formation of pyrite as the most likely energy source.

$$FeS + H_2S \rightarrow FeS_2 + 2H^+ + 2e^- + \Delta G \qquad (3)$$

Here, the Gibbs energy is ΔG ~ -38.4 kJ/mol. Other relevant pathways can be found in [29, 30-32]. The released chemical energy can be used by the organism to drive an uphill reaction or directly perform cellular work. Reaction (3) describes the oxidative formation of pyrite from hydrogen sulfide, likely serving as the reducing power source for chemoautotrophic organisms [28, 29]. The released Gibbs energy could drive an archaic CO_2 fixation cycle similar to the reductive citric-acid cycle. Pyrite could serve as a matrix for the growing pool of organic reactants [28]. For details on the reaction chain, see [33] or [29]. LUCA likely used chemical energy by translocating protons across its membrane and synthesizing ATP from ADP and orthophosphate (PO_4^{3-}), costing ~ 35 kJ/mol [26]. The ATP molecule's stored energy could be released via hydrolysis for cell maintenance and reproduction. Consequently, LUCA would have been unable to survive far from hydrothermal sources, lacking the ability to pump ions across its membrane to make ATP, a capability present in modern organisms.

LUCA obtained energy from inorganic compounds and likely built complex organic molecules from carbon dioxide and hydrogen in its environment. If LUCA was a chemoautotroph acetogenic organism, which is another possibility raised by Moody ERR, et al. [1], a possible

reaction leading to acetate formation is:

$$2CO_2 + 4H_2 \rightarrow CH_3COO^- + 2H_2O + H^+ + \Delta G \quad (4)$$

Here, the Gibbs energy is ΔG ~ -95 kJ/mol. The acetogenesis process in reaction (4) catalyzes the H_2-dependent reduction of carbon dioxide to acetate, as observed in *Clostridium aceticum* [34]. For a more detailed analysis of acetogenic pathways, see [32, 35].

Energetics of hydrothermal vents

If LUCA used hydrothermal vent chemical energy for metabolism and growth/reproduction, it is pertinent to ask: What is the total chemical energy available and what population size could such a source sustain? Hydrothermal vents contribute significantly to Earth's chemical and thermal energy budgets, both currently and in its early history. However, quantifying the exact energy input involves several variables, including the number of active vents, their temperatures, the chemical composition of vent fluids, and the rate of fluid discharge.

The total heat flux from modern hydrothermal vents is estimated to be 2-5 TW, representing ~12% of the radiogenic heat generated in Earth's core. During the Hadean, the heat flux from hydrothermal vents is believed to have been significantly greater due to geothermal gradients and intense volcanic activity, potentially reaching 20-50 TW [36, 37]. The chemical energy input is more difficult to quantify, depending on the specific reactions within vent fluids and the surrounding environment. Life near hydrothermal vents relies on abiotic sources of chemical energy in the form of disequilibrium concentrations of redox reactants driven by hydrothermal activity, primarily in the form of electron donors created through fluid-rock interactions, including H_2S, H_2, CH_4, and dissolved Fe^{2+} [38]**.** Detailed estimates by Hoehler TM, et al. [38] indicate that these chemical species provide ~26 GW of energy. Reduced chemicals like hydrogen and methane were likely more abundant on the early Earth. Combined with a more reducing atmosphere and ocean chemistry, this would have resulted in greater chemical energy availability, potentially in the range of 1-10 TW or more, depending on vent system conditions [39, 40]. To illustrate, we assume that the chemical energy output available in Hadean oceans was ~5 TW, with 10% efficiency in energy use for cell growth and maintenance. Therefore, the effective energy rate available to microorganisms was L_Q = 500 GW.

The Cell Population of LUCA

To understand and predict the dynamic evolution of a cell population, models describing the entire population are more valuable than approaches considering only a single cell. Cellular growth is affected by nutrient availability and fluctuations in cell density [41] provides a recent review of cell population growth models. This analysis will use a simplified approach to estimate the order of magnitude of LUCA's population.

The simplest population model assumes that the growth rate is proportional to the number of cells, implying exponential growth. This exponential phase is commonly used as a measure of fitness; however, it is short-lived and does not describe late evolutionary stages.

A more realistic "logistic model" considers the role of nutrients and can be described by the following set of differential equations [41]:

$$\frac{dN}{dt} = aCN - \frac{N}{\tau} \quad (5)$$

and

$$\frac{dC}{dt} = -\beta aNC \quad (6)$$

Here, N and C represent the number of cells and nutrient concentration at a given time, τ is the cell's lifetime and α and β are constants representing the growth rate per nutrient concentration and the amount of nutrient required to produce a new cell, respectively. The first term on the right side of equation (5) indicates that the growth rate is proportional to both cell number and nutrient concentration, while the last term represents the death rate. Equation (6) describes the decrease in nutrient concentration as it is consumed. If the death rate is neglected in equation (5), the remaining equations can be combined as

$$\frac{dC}{dN} = -\beta \qquad (7)$$

whose integration is trivial

$$C(t) = C_0 - \beta\left[N(t) - N_0\right] \qquad (8)$$

where C_0 and N_0 represent the initial nutrient concentration and cell population, respectively. Substituting the equation above into equation (5) yields:

$$\frac{dN}{dt} = aN(C_0 + \beta N_0 - \beta N) \qquad (9)$$

This indicates the existence of a critical cell population value, $N_{crit} = (C_0 + \beta N_0)/\beta$ corresponding to nutrient exhaustion and a steady population size, or a zero-growth rate. Without nutrients, the population decreases.

To describe LUCA's population, the "nutrients" must be replaced by chemical energy. Since the hydrothermal sources continuously replenish the energy, the consumption of energy by the cells does not represent a decrease of its value. In this case, equation (5) can be recast as:

$$\frac{dN}{dt} = r\left(1 - \frac{P}{L_Q}N\right)N - \frac{N}{\tau} \qquad (10)$$

where P is the energy rate required to form and maintain cells as discussed in section 2 (see equation 2) and L_Q is the available chemical energy. The solution of this equation is

$$N(t) = \frac{r_* k_1 Exp(r_* t)}{\left[1 + \lambda k_1 Exp(r_* t)\right]} \qquad (11)$$

where k_1 is an integration constant, $r_* = (r - 1/\tau)$ and $\lambda = r(P/L_Q)$. Assuming that at t = 0 only one cell is present and that λ << 1, equation (11) can be rewritten as:

$$N(t) \cong \frac{r_* Exp(r_* t)}{r_* + \lambda Exp(r_* t)} \qquad (12)$$

When $r_* > 0$, equation (12) indicates an initial exponential growth followed by a stable phase attained when $r_* t \gg 1$, with a number given by:

$$N_\infty \cong \frac{r_*}{\lambda} = \frac{L_Q}{P}\left(1 - \frac{1}{r\tau}\right) \qquad (13)$$

Therefore, LUCA's population can be computed from the equation above if adequate estimates of P, r, and τ can be obtained. The relevant quantity is P since, in general, $1/r\tau \ll 1$.

Currently, it is difficult to reliably estimate either the metabolic or energy rate required to form a cell in order to compute the quantity P. Studies of modern prokaryote cells indicate an important variation of P as a function of the cell mass [42]. According to these authors, the

median of the distribution is P = 3.6 × 10^{-13} W/cell while the median of the cell mass distribution is m = 1.2 × 10^{-12} g.

Since the majority of modern prokaryotes are heterotrophs, the analysis of a methanogen autotroph could be valuable once these archaea have similarities with the expected metabolism of LUCA [3]. An example is the *Methanocaldococcus jannaschii*, a hyperthermophilic archaeon that thrives in extreme environments like hydrothermal vents. This methanogen has an optimum growth at +85° C, a proteinic envelope cell, a genome size of about 1.74 Mb and an estimated wet mass of 1.8 × 10^{-13} g. Specifically, *M. jannaschii* uses CO_2 as a carbon source and H_2 as an electron donor, converting these into methane and water via the reaction [17]:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O + \Delta G \qquad (14)$$

Here, the Gibbs energy is ΔG = -131 kJ/mol. This reaction is part of the methanogenesis pathway, which is less energy-efficient than aerobic respiration but allows the organism to thrive in anaerobic, high-temperature environments. Cultures in the laboratory permit measurements of methane production rates and the metabolic energy involved in the process. However, the resulting rates depend on various factors such as: a) growth conditions like temperature and pressure; b) the substrates used, e.g., hydrogen and carbon dioxide that are used in the methanogenesis; c) the phase of growth (exponential or stationary). Laboratory studies were performed by Miller JF, et al. [19] at high temperatures and when the culture was pressurized with a 4:1 mix of H_2 and CO_2. High pressures favored methanogenesis but cell growth was quenched for temperatures above +90° C. However, even if cell growth decreased at a temperature of +95° C, substantial methane production was still observed for pressures of about 25 MPa but not at values around 0.8 MPa. From methane production fluxes provided by Miller JF, et al. [19], we have estimated a growth energy for *M. jannaschii* as P = 1.96 × 10^{-13} W/cell.

Cultures of *M. jannaschii* were also investigated by Tsao JH, et al. [43], who confirmed the fact that if the cell growth is inhibited at high temperatures, the methane production can be maintained at a relevant level by increasing the pressure. From methane production rates estimated by Tsao JH, et al. [43], the growth energy of *M. jannaschii* was estimated as P = 3.54 × 10^{-13} W/cell. These two investigations show clearly that metabolic and growth rates are not necessarily coupled and values of P derived from methane production rates must take into account the conditions in which they were obtained. The average from these two experiments will be considered here as representative of LUCA's metabolism. Notice that the mean value, that is P = 2.7 × 10^{-13} W/cell, is close of the median value reported by Lane N, et al. [42] for modern prokaryote cells.

Replacing the estimated value of P in equation 13, one obtains for the LUCA's population number N ~ 1.8 × 10^{24} cells. This number is about five orders of magnitude less than the present population of prokaryotes living in oceans [44].

Recalling that ATP is the "currency" used by cells in their metabolic pathways, the energetic balance involving ADP ↔ ATP reactions permit an alternative derivation of the cell population. This procedure requires a previous estimate of the cell mass and here we rely on the fact that different investigations have shown that correlations either between the genome size or the cell size and the number of genes are weak for eukaryotes but significant for prokaryotes [45]. The analysis by DeLong JP [23] provides a robust correlation between the cell mass and the number of genes N_{gen}, that is

$$\log m = -21.725 + 2.759 \log N_{gen} \qquad (15)$$

where the cell mass is given in grams. Using the number of genes estimated by Moody ERR, et al. [1], the expected mass of LUCA from equation 15 is about 5.3 × 10^{-13} g or 530 fg, corresponding to a size of about 0.50 μm for an equivalent spherical cell.

According to Ortega-Arzola E, et al. [26], the production of one mole of ATP needs an effective energy of 35 kJ. Then, the available chemical energy from hydrothermal vents leads to a production rate of 1.43×10^{7} ATP mol/s. Again, according to [26], the production of one gram of cells needs 9.2 mmol of ATP. From the estimated mass of the LUCA's cell and the calculated ATP production rate, one obtains a cell production rate of 2.92 × 10^{21}δ cell/s, where δ = 0.30 is the fraction of the released ATP energy by hydrolysis used to form new cells and the remaining fraction is used to drive the basal metabolic pathway of the organism. The ratio between the cell production rate and the maximum growth rate r_m = 1.6 h^{-1} [46] provides an additional estimate of the cell population, that is N = 2.0 × 10^{24}, in agreement with the previous calculation.

Carbon Productivity

Once the number of LUCA cells was estimated, the carbon productivity rate can be evaluated if the population turnover time is known. In

general, turnover timescales derived from laboratory cultures are higher than those estimated in natural habitats. As discussed in the previous section, if the death rate is small, the population size grows until the metabolism decreases to a minimum value required for maintenance. At this point, the population size is balanced against the available energy flux.

Modern prokaryote cells have turnover times ranging from one day up to several years, depending on the habitat [38,44,47]. Moreover, these values vary according to the environment temperature and the amount of nutrients [20]. For marine heterotrophic prokaryotes, reference [44] estimated turnover times ranging from 16 days up to 300 days, depending on the depth of the habitat. In general, higher is the depth, longer is the turnover timescale. For marine autotrophs that would correspond to a "modern LUCA", the turnover time is only of the order of 1.5 days [44], a value that will be adopted here. In this case, the carbon productivity rate is given by

$$P_C = N_{cel} f_C m / t_* \qquad (16)$$

where *fc* = 0.15 is the mass fraction of carbon present in the cell [38] and t_* is the turnover time. Using the numbers derived previously, one obtains Pc = 3.9×10^{10} C kg/yr. This value is in good agreement with the rate reported by Moody ERR, et al. [1], supporting the present estimate of LUCA's cell population.

Final Remarks

The new study of LUCA by ERR, et al. [1] suggests an early emergence of life on Earth, just 400-500 Myr after its formation, in agreement with previous investigations. LUCA lived probably in the vicinity of hydrothermal vents in niches that were protected from the bombardment suffered by the primitive Earth. Face to the hostile environment present in the Hadean Ocean, an estimation of the size of LUCA's population is an interesting parameter for our understanding of the early-life evolution.

The present analysis of LUCA's physiology was guided by our knowledge of modern prokaryotes, which are basically heterotrophic microorganisms, obtaining carbon from organic compounds. However, similarly to modern thermophilic prokaryotes, LUCA was probably able to develop features that allow him to thrive in high-temperature niches due to specialized enzymes, structural adaptations and thermodynamic advantages.

LUCA's metabolism and growth needs were fed by redox reactions that occur in the vicinity of hydrothermal vents. We have assumed that 10% of the total chemical energy present in the Hadean Ocean was used to feed the cells, representing an energy rate of about 500 GW.

The new estimate of the possible number of protein-coding genes characterizing the LUCA's cell by Moody ERR et al. [1] permitted a rough evaluation of its mass by using a tight relation with the gene number [23], that is m = 530 fg. The specific energy required to form a new cell was recently reconsidered by Ortega-Arzola E [26] and using their results as well as the maximum growth rate measured for the thermophilic methanogen *M. Jannaschii*, we have estimated that the energy rate to form a new LUCA cell is about 8.2×10^{-14} W/cell and that the total growing energy, including the basal metabolism is P = 2.7×10^{-13} W/cell. According to Lane N , et al. [42], the mean value of P for modern prokaryotes is about 3.6×10^{-13} W/cell, approximately 30% higher than the rate estimated for LUCA, a difference that can be explained by the fact that the mean mass listed in reference [42] is about 2.3 times the LUCA's estimated mass.

In order to estimate the LUCA's population, a modified logistic model was adopted in which nutrients were replaced by the chemical energy provided by redox reactions. After a short quasi-exponential phase of growth, the cell population number stabilizes and is approximately given by $N = L_Q/P = 2 \times 10^{24}$. Small corrections depending essentially on the ratio between the growth and mortality rates were neglected. The derived cell population is about five orders of magnitude smaller than the present estimated number of prokaryote cells in the oceans and three orders of magnitude smaller than the autotroph population [44].

The carbon productivity resulting from LUCA population is about 3.9×10^{10} C_kg/yr, consistent with the value estimated by Moody ERR et al. [1]. Notice that the present marine productivity is estimated to be 5.2×10^{13} C kg/yr, which is due essentially to prokaryotes, since plants contribute only with 2.4% of such a rate [48].

In astrobiology, one of the primary challenges is the identification of biosignatures, or signs of life on other planets. Understanding the molecular and biochemical pathways of primitive forms of life can help astrobiologists to develop more accurate models for detecting life beyond Earth. Metabolic processes of these organisms might produce gases or chemical compounds that could be detected by probes or telescopes scanning the atmospheres or surfaces of distant planets and moons. Additionally, studying their extremophilic properties could

expand our understanding of what constitutes a habitable zone.

Thermophilic prokaryotes are of particular interest when considering the possibility of life in the subsurface oceans of icy moons, such as Europa and Enceladus. Both moons are believed to have internal heat sources, possibly from hydrothermal vents at the ocean floor, similar to those found on Earth. These deep-sea environments, isolated from sunlight, are inhabited by thermophiles on Earth, which use chemosynthesis instead of photosynthesis to produce energy.

The study of primitive thermophilic micro-organisms offers crucial insights into the resilience, adaptability, and diverse biochemistry of life under extreme conditions. These lessons are invaluable in the ongoing search for extraterrestrial life, particularly in the exploration of planets and moons that present similarly hostile environments. Understanding how life emerged on Earth broadens our understanding of how life might evolve and persist in similarly extreme environments elsewhere in the Galaxy.

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