An Estimate of LUCA's Population in Hadean Oceans

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Article

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Abstract: Recent studies on the physiology of LUCA (Last Universal Common Ancestor) associated to molecular dating methods suggest that the ancestor cell appeared very early in the history of the Earth, in a hostile environment, consequence of an intense cosmic bombardment occurred at that time. In the present investigation, the population size of LUCA was estimated by assuming that the ancestor cell had a metabolism similar to the methanogen *M. jannaschii* fed essentially by H_2 and CO_2, one of the oldest known metabolism. The cell (wet) mass was evaluated to be approximately 530 fg and the energy per cell required to drive its metabolism and growth was estimated to be around 2.7×10^{-13} $W/cell$. If LUCA was fed by the chemical energy available from submarine hydrothermal vents, then its cell population in the Hadean oceans was expected to be around 1.8×10^{24}. Such a value corresponds to approximately five orders of magnitude less than the present estimated number of prokaryote cells in the Earth's oceans. The study of LUCA's physiology can reveal essential biochemical processes that might be common in extraterrestrial life, guiding the search for biosignatures on other planets.

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1. Introduction

Recently, the characteristics of LUCA (Last Universal Common Ancestor) have been revisited by [1], who confirmed some past results obtained by [2–4]. LUCA was an anaerobic, thermophilic, autotrophic, and chemotrophic organism that lived probably in the environment of hydrothermal vents. This new investigation suggests that LUCA was more sophisticated than previously imagined, having an estimated genome size of about 2.5 Mb and approximately 2600 protein-coding genes, instead of 355 [3] or 572 [2] derived in precedent phylogenetic studies. Notice that the estimation of the gene number is quite uncertain because most bacteria and archaea have experienced horizontal gene transfer since the time of LUCA. All these investigations agree that LUCA was able to produce proteins and save energy through ATP. These investigations concluded that LUCA was probably dependent on abiotic and spontaneous synthesis of organic compounds from H_2 and CO_2 , emphasizing the importance of methyl groups in the development of LUCA metabolism. Two modern microbes were identified with lifestyles resembling LUCA: clostridia, a class of anaerobic bacteria, and methanogens, a group of hydrogen-eating, methane-producing archaea [3]. They may offer a living hint not just of what LUCA was like, but possibly even on earlier ancestors.

According to [1], the application of molecular dating methods makes it possible to go back to an age of 4.2 billion years, significantly earlier than previous assessments (see also [5]). At that time, the terrestrial environment was particularly hostile, but life was able to develop in the vicinity of hydrothermal vents. Previously, evidence for an early emergence of life came from analyses of graphite inclusions in a zircon crystal with an age of 4.1 Gyr [6], having an isotopic ratio $^{13}C/^{12}C$ consistent with a biogenic origin. Chemical and physical fractioning processes can modify the carbon isotopic ratio, but further electronic microscopy indicated a polygonal structure of the included graphite in the zircon crystal while, in general, abiotic graphite has a porous morphology. Hence, for the moment, the biogenic origin of such an inclusion is favored. It should be emphasized that the emergence of life very early in the history of the Earth, that is about 450 Myr after its formation, is also consistent with the discovery of microfossils in sedimentary ferrous rocks with ages between 3.77 and 4.28 Gyr, probably originated in submarine hydrothermal sources [7].

This early emergence of life reinforces the scenario in which the main molecules required for abiogenesis like amino acids, came from space as a consequence of impacts either with remnant

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planetesimals or comets during the formation of the primitive Earth. Past studies suggested that at the same time such a bombardment could maintain the Earth's surface completely sterilized. Presently, there are two interpretations concerning the timeline of impacts suffered by the inner planets of the solar system just after their formation. Lunar rocks collected by the Apollo missions carry evidence for impact shocks that occurred approximately 3.9 Gyr ago (see, for instance [8]). This period of an apparent intense bombardment is known in the literature as the "late heavy bombardment" (LHB). In the one hand, since impact signatures older than 3.9 Gyr are practically absent from lunar rocks data, some authors suggest that the LHB was simply a prominent spike in the impact rate curve [9]. On the other hand, other authors support the view that the impacts decayed monotonically since the formation of the inner rocky planets and that the apparent spike is a consequence of sampling biases [10,11]. More recently, the authors in reference [12] described the possibility of a hybrid scenario where two bombardment phases took place; an early one ending around 4.4 Gyr produced by leftover planetesimals, and a second one initiated by late giant planet migration that started near 4.0 - 4.2 Gyr ago. In this model, there is a long bombardment tail, consistent with existing dynamical models of the solar system.

The presence of life on Earth during the Hadean eon was investigated by different impact simulations. A past study by [13] led to the conclusion that after 150 Myr only deep-marine life survives. This result was reinforced by numerical simulations performed by [14], who have shown that there is no plausible situation in which the habitable zone was fully sterilized on Earth as a consequence of impacts. More recent impact simulations, guided by the age distribution of terrestrial zircons and lunar rocks data, were performed by [15], who concluded that the Earth's surface was strongly reprocessed by the bombardment of planetesimals. Their conclusions are not radically different from previous studies or, in other words, life emerging in this period was probably resistant to high temperatures and capable of spreading from stable deep-marine niches. These niches of life were investigated in [16], who used a revised bombardment timeline, and more accurate thermal models to describe the consequences of the impacts. They found that the habitable marine volume grows continuously because the heat generated during impacts dissipates rapidly in comparison with the collision frequency. Hence, global sterilization can only be achieved by increasing the impact rate at least by one order of magnitude. This implies that the Hadean bombardment would not sterilize the oceans as claimed in the past, reinforcing the scenario in which life could have emerged very early in the history of Earth, surviving these bombardment episodes.

In this work, the possible energy sources feeding either the metabolism or the population growth of LUCA are discussed. In order to model the metabolism of LUCA, we have supposed that the ancestor cell behaves like the methanogen archaeon *Methanocaldococcus jannaschii*, which has an optimal growth at a temperature of about $+85^{o}C$ [17,18] and at pressures around 250 atmospheres [19] that represent physical conditions found in the vicinity of hydrothermal sources. *M. jannaschii* derives energy solely from H_2 and CO_2 in order to produce methane, which is one of the oldest metabolisms on Earth. The present estimates suggest that most of the available chemical energy from hydrothermal vents was used for the cell population growth and the basal metabolism. The derived number of LUCA cells is about five orders of magnitude less than the present number of prokaryote cells in marine habitats. These aspects are relevant for the understanding of the early emergence of life on Earth and possibly to speculate about the development of similar processes in exoplanets having CO_2 rich atmospheres and tectonic activity, criteria that could constitute habitable environments elsewhere in the universe. Analyzing the metabolic pathways of LUCA can reveal essential biochemical processes that might be common in extraterrestrial life, guiding the search for biosignatures on other planets. The paper is organized as follows: in section 2 the metabolism of LUCA is discussed as well as the possible sources of chemical energy related to hydrothermal vents; in section 3 a toy model for the evolution of the LUCA's population is presented; in section 4 the carbon productivity is estimated and compared with that of modern prokaryotes and finally, in section 5, the main conclusions are summarized.

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2. The Metabolism of LUCA

Cells are out-of-equilibrium structures and require a constant supply of energy to remain in that privileged state. Measuring how much power is required to run a cell or the heat produced as it goes through its normal metabolic operations is experimentally challenging. Beyond the challenges associated with actually measuring cellular power consumption, there are several plausible definitions for a cell's rate of energy usage, making a rigorous discussion of the problem extremely complex. During cellular growth, energy is needed to produce proteins, nucleic acids, and other cell components required for cell division. This energy is mainly derived from metabolic pathways that convert nutrients into usable forms of energy, such as ATP. The growth of the cell population depends on the nutrient availability, environmental conditions, and the cell's efficiency in utilizing energy.

Once the cell population attains a quasi-steady situation, the energy used by the cells is constituted essentially by two distinct terms [20] : 1) the maintenance energy or basal metabolism that is required to sustain basic cellular functions such as ion transport, protein turnover, and cell integrity without necessarily growing. It tends to be a low, constant energy expenditure; 2) growth energy, used for cell division. The maintenance energy or the basal metabolism B is given in Watts per cell. Past investigations on the metabolic rate B suggested an increase with the size of the organism and the scaling $B \propto m^{3/4}$, where m is the cell mass, is known as the Kleiber's law [21]. However, more recent studies [22,23] indicate that the Kleiber's scaling does not apply universally across different organisms. According to those authors, metabolic rates increase with body size across different taxa but each taxon is characterized by a distinct scaling relationship. In fact, [23] found that the metabolism of prokaryotes scales as $B \propto m^{2.52}$. These results were corroborated by the studies of [24,25], who have shown that, in fact, the specific metabolic rate Q ($Q = B/m$) increases with the size for different taxa (notice that according to Kleiber's scaling Q should decrease with size). From the analysis of 173 prokaryotes with masses in the range $10^{-14} - 10^{-11}$ g , the authors in [25] found that the specific metabolic rate varies from 0.32 W/kg up to 68.0 W/kg, that is by more than two orders of magnitude.

The minimum energy needed to build a new cell is essentially the sum of the energy required to assemble all its main components into their biomolecules, that is the cell's genome, the proteome, the transcriptome, and lipid bilayer. The authors in [26] revisited the past estimates of the minimum energy per-gram required to form a new cell. Their calculations were made at temperatures ranging from 275 to 400 K and for four different cell models. The synthesis cost of a gram of biomass of each of the species is remarkably similar, indicating a consistent fundamental floor in the per-gram cost of biomass synthesis. Despite the lipid bilayer accounting for only 9% of the cell's mass fraction, it is the second most energy-intensive component, requiring 21% of the cell's total synthesis energy. According to the calculations by [26], the average specific energy required to create a cell does not depend critically on the temperature. Using their results, the specific creation energy can be expressed as

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

It is also important to introduce the maximum growth rate of the cell population r_m that provides a standardized estimate of the population-level rate of biomass production and evolution. Maximal population growth rates under optimal conditions have received considerable attention in both basic and applied studies of microorganisms. Under these conditions, the total energy rate P required by the cell to maintain its metabolism and cell division is

$$P = B + r_m \varepsilon m \tag{2}$$

LUCA had a primitive metabolism that can be envisioned as sequences of chemical reactions yielding free energy. Once produced, the energy can be used by the organism to do work or to produce new cells as discussed above. The nature of the metabolic strategies employed depends largely upon the environmental constraints that affect the organism. The physiology of LUCA indicates that he was

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adapted to live in the vicinity of hydrothermal vents, that is in a high-pressure environment rich in sulfur compounds, having temperatures around $350K$ or even higher. In modern times, thermophilic methanogens are common in the environment of deep-sea hydrothermal vents, using H_2 as donor of electrons [27].

Deep sea hydrothermal vents are located along the mid-ocean ridge system, near volcanically active areas. Sea water penetrating the fissures of the volcanic bed is heated by the magma, and the expelled heated water flow is rich in minerals, which provide a source of energy and nutrients to chemoautotrophic organisms like LUCA. Presently, about 200 hydrothermal fields are known near subduction oceanic zones and down to 5000 m of depth. Gaseous and fine metallic particles are emitted from these hot sources, rich in Fe, H_2S, CO_2 and H_2, among other inorganics. Many thermophilic, hyperthermophilic bacteria and archaea live inside or in the vicinity of these vents, and the adaptation of these microorganisms to such environments implies modifications of their proteins, membranes and nucleic acids. Hydrothermal vents revealed chemically reactive environments, far from equilibrium conditions, as well as temperature, redox and pH gradients. Unicellular organisms living in such environments are able to consume chemical energy from the oxidation of reduced mineral compounds. This process involves an electron transfer chain associated to a Calvin-Benson cycle for carbon fixation and ATP production. It was proposed more than thirty years ago that the first organisms were chemoautotrophs and the most probable chemical energy source was the oxidative formation of pyrite [28], represented by the reaction

$$FeS + H_2S \rightarrow FeS_2 + 2H^+ + 2e^- + \Delta G \tag{3}$$

where the Gibbs energy is $\Delta G \simeq -38.4\ kJ/mol$. Other relevant pathways can be found in [29–32]. The released chemical energy can be used by the organism to drive an uphill reaction or it may be directly utilized to perform cellular work. Reaction (3) describes the oxidative formation of pyrite from hydrogen sulfide, the most plausive source of reducing power for chemo autotrophic organisms [28,29]. The released Gibbs energy is sufficient to drive an archaic CO_2 fixing cycle similar to the reductive citric-acid cycle of contemporary organisms. Pyrite formed by this process could serve as a matrix for the growing pool of organic reactants [28]. A detailed discussion on the reaction chain can be found in [33] or in [29]. According to [1], LUCA was able to use chemical energy by translocating protons outside of the cell's membrane and synthesizing adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and the orthophosphate ion (PO_4^{3-}), with a cost of about 35 kJ/mol [26]. The energy stored by the ATP molecule can be released by hydrolysis and used for cell maintenance and reproduction. As a result, LUCA would have been unable to survive away from the neighborhood of hydrothermal sources, because it would not have been able to pump ions across its membrane to make ATP, a feat that every organism can do in the present days.

LUCA obtained energy from inorganic compounds and probably built complex organic molecules to grow from carbon dioxide and hydrogen present in its environment. If LUCA was a chemoautotroph acetogenic organism, which is another possibility raised by [1], then a possible reaction leading to acetate formation is

$$2CO_2 + 4H_2 \rightarrow CH_3COO^- + H^+ + 2H_2O + \Delta G \tag{4}$$

with a Gibbs energy of about $\Delta G \simeq -95\ kJ/mol$. The acetogenesis process described by reaction (4) catalyzes the H_2-dependent reduction of carbon dioxide to acetate as it can be observed in the microorganism *Clostridium aceticum* [34]. A more detailed analysis of these acetogenic pathways can be found in references [32,35].

2.1. Energetics of Hydrothermal Vents

If LUCA used the chemical energy from hydrothermal vents to drive metabolism and growth/reproduction finalities, one may ask what is the total available chemical energy and what is the cell population that can be sustained by such a source. Hydrothermal vents contribute significantly to the chemical and

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thermal energy budgets of the Earth, both today and in its early history. However, quantifying the exact energy input from these vents involves several variables, including the number of active vents, their temperatures, the chemical composition of the vent fluids, and the rate of fluid discharge.

In the one hand, the total heat flux from modern hydrothermal vents is estimated to be in the range of $2-5$ TW. This heat flux represents the amount of heat released from Earth's interior through hydrothermal systems, which includes both high-temperature and low-temperature vents, representing about 12% of the radiogenic heat generated in the core of the Earth. During the Hadean, the heat flux from hydrothermal vents is believed to have been significantly higher due to significant geothermal gradients and more intense volcanic activity. Estimates suggest that the heat flux could have been as much as 10 times greater than today, potentially reaching $20-50$ TW [36,37]. On the other hand, the chemical energy input from hydrothermal vents is more difficult to quantify, as it depends on the specific reactions occurring within the vent fluids and the surrounding environment. Life in the vicinity of hydrothermal vents depends on abiotic sources of chemical energy in the form of disequilibrium concentrations of redox reactants driven by the hydrothermal activity. This energy is primarily in the form of electron donors created through fluid-rock interactions and the main contributors are H_2S, H_2, CH_4 and dissolved Fe^{2+}. Detailed estimates by [38] indicate that these chemical species provide an amount of energy of about 26 GW. In the early Earth, the availability of reduced chemicals like hydrogen and methane was likely much higher. This, combined with a more reducing atmosphere and ocean chemistry, would have resulted in greater chemical energy availability. The chemical energy input could have been several times higher, though specific estimates are less certain. Some studies suggest that it could have been in the range of $1-10$ TW, possibly more, depending on the local conditions and the nature of the vent systems [39,40]. In order to fix ideas, let us assume that the chemical energy output available in the Hadean oceans was about 5 TW, and assume further a 10% efficiency for the energy effectively used in the growth and maintenance of the cells. Hence, the effective energy rate available for the needs of the microorganisms was $L_Q = 500\ GW$.

3. The Cell Population of LUCA

In order to understand and predict the dynamical evolution of a cell population, models describing the whole population are more useful than approaches considering just a single cell. The evolution of cellular growth is affected not only by the nutrient availability but also by fluctuations of the cell density. A recent review on different cell population growth models can be found, for instance, in [41]. Here, a simple approach will be considered since we aim to have only an order of magnitude estimate of the LUCA's population.

The simplest population model assumes that the rate of growth is proportional to the number of cells, implying an exponential growth. This exponential phase is commonly used as a measure of "fitness" in experimental microbiology studies. However, in realistic biological scenarios, this phase is short-lived and does not describe late evolutionary stages of the cell population.

A more realistic picture, the so-called "logistic model", includes the role of nutrients in the evolution of the cell population and can be described by the following set of differential equations [41]

$$\frac{dN_c}{dt} = \alpha C N_c - \frac{N_c}{\tau} \tag{5}$$

and

$$\frac{dC}{dt} = \beta \alpha C N_c \tag{6}$$

In these equations N_c and C are respectively the the number of cells and the concentration of nutrients in a given instant of time, τ is the life-time of a cell, α and β are constants that can be interpreted respectively as the rate of growth per nutrient concentration and the amount of nutrient needed to produce a new cell. The first term on the right of equation 5 says that the growth rate of cells is proportional not only to the number of cells but also to the concentration of nutrients, while the

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last term is the rate of death. Equation 6 describes the decrease of the nutrient concentration as it is consumed by cells. If the death rate is neglected in equation 5, the remaining equations can be combined as

$$\frac{dC}{dN_c} = -\beta \tag{7}$$

whose integration is trivial, that is

$$C(t) = C_0 - \beta[N_c(t) - N_0] \tag{8}$$

where C_0 and N_0 are respectively the initial nutrient concentration and the cell population. Replacing the equation above into equation 5 gives

$$\frac{dN_c}{dt} = \alpha(C_0 + \beta N_0 - \beta N_c)N_c \tag{9}$$

This equation indicates the existence of a critical cell population value given by $N_{crit} = (C_0 + \beta N_0)/\beta$, which corresponds to the exhaustion of nutrients and a steady population size or, in other words, the growth rate is zero. In fact, in the absence of nutrients the population must decrease, which is the role of the neglected death rate term.

In order to describe LUCA's population by the logistic model, the "nutrients" must be replaced by the chemical energy. The consummation of this energy by the cells does not represent a decrease of its value because there is a continuous replenishment by the hydrothermal sources. In this case, equation 5 can be recast as

$$\frac{dN_c}{dt} = r\left(1 - \frac{P}{L_Q}N_c\right)N_c - \frac{N_c}{\tau} \tag{10}$$

where r is the growth rate, P is the energy rate required to form and to maintain the metabolism of a cell as discussed in Section 2, and L_Q is the available chemical energy. The solution of this equation is

$$N_c(t) = \frac{r_* k_1 Exp(r_* t)}{1 + \lambda k_1 Exp(r_* t)} \tag{11}$$

where k_1 is an integration constant and we have introduced $r_* = (r - 1/\tau)$, $\lambda = r(P/L_Q)$. In order to estimate the integration constant, we have assumed that at $t = 0$ only one cell is present in the medium and that the condition $\lambda << 1$ is satisfied. In this case, equation 11 can be rewritten as

$$N_c(t) \simeq \frac{r_* Exp(r_* t)}{r_* + \lambda Exp(r_* t)} \tag{12}$$

When $r_* > 0$, equation 12 indicates an initial exponential growth of the cell population number, followed by stable phase attained when $r_* t >> 1$ and whose number is given by

$$N_c \simeq \frac{r_*}{\lambda} = \frac{L_Q}{P}\left(1 - \frac{1}{r\tau}\right) \tag{13}$$

Hence, the LUCA's population can be computed from the equation above if adequate estimates of the parameters P, r and τ can be obtained. In fact, the relevant quantity is P since, as we shall see later, the term $1/r\tau << 1$ does not significantly affect the population number.

Presently, it is difficult to have a reliable estimate either of the metabolic or the energy rate required to form a cell in order to compute the quantity P according to equation (2). 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 $P = 3.6 \times 10^{-13}\ W/cell$ while the median of the cell mass distribution is $1.2 \times 10^{-12}\ g$.

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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 $+85^o\ C$, a proteinic envelope cell, a genome size of about 1.74 Mb, and an estimated wet mass of $1.8 \times 10^{-13}\ g$. 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]

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O + \Delta G \tag{14}$$

where the Gibbs energy is $\Delta G = -131\ kJ/mol$. 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 [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 $+90^o\ C$. However, even if cell growth decreased at a temperature of $+95^o\ C$, 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 [19], we have estimated a growth energy for *M. jannaschii* as $P = 1.96 \times 10^{-13} W/cell$. Cultures of *M. jannaschii* were also investigated by [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 [43], the growth energy of *M. jannaschii* was estimated as $P = 3.54 \times 10^{-13}\ W/cell$. 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 $P = 2.7 \times 10^{-13} W/cell$, is close of the median value reported by [42] for modern prokaryote cells.

Replacing the estimated value of P in equation 13, one obtains for the LUCA's population number $N_c \simeq 1.8 \times 10^{24}$ 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 $ADP \leftrightarrow ATP$ reactions permits 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 [23] provides a robust correlation between the cell mass and the number of genes N_{gen} , that is

$$\log m = -21.725 + 2.759 \log N_{gen} \tag{15}$$

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

According to [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 $1.43 \times 10^7\ ATP\ mol/s$. 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 $2.92 \times 10^{21} \alpha\ cell/s$, where α = 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.

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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 $N_c = 2.0 \times 10^{24}$, in agreement with the previous calculation.

4. 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

$$P_C = \frac{N_c m f_C}{\tau_*} \tag{16}$$

where f_C = 0.15 is the mass fraction of carbon present in the cell [38] and τ_* is the turnover time. Using the numbers derived previously, one obtains $P_C = 3.9 \times 10^{10}\ C\ kg/yr$. This value is in good agreement with the rate reported by [1], supporting the present estimate of LUCA's cell population.

5. Final Remarks

The new study of LUCA by [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 use to feed the cells, representing an energy flux of about 500 GW.

The new estimate of the possible number of protein-coding genes characterizing the LUCA's cell by [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 [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 $P = 2.7 \times 10^{-13}$ W/cell. According to [42], the mean value of P for modern prokaryotes is about 3.6×10^{-13} W/cell, approximately 30% higher than the rate derived 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-

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exponential phase of growth, the cell population number stabilizes and is approximately given by $N_c = L_Q/P = 2 \times 10^{24}$. 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 [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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