



THE EUKARYOTE ENDOSYMBIOTIC ORIGIN: A CONSTRUCTAL THEORY-BASED EXPLANATION

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The origin of eukaryotes is understood as one of the most important issues in the history of living beings. There are several points of view to seek a broad understanding of the eukaryote origins, which encompass paleontological data, energetics, eukaryote-particular characteristics origins or the connections among dissimilar eukaryotic groups. Many proposals of endosymbiotic theory have been presented to explain the origin of eukaryotes and their mitochondria. Only recently, energy and the energetic constraints started to be considered by endosymbiotic theory to understand the contribution of prokaryotic cell organization to cell history, acknowledging that only cells that possessed mitochondria had the bioenergetic assets to achieve eukaryotic cell complexity, which explains why no in between beings existed in the prokaryote-to-eukaryote transition. This study attempts to approach the eukaryote origins from the standpoint of constructal theory, i.e., “For a flow system to persist in time (to survive), it must evolve in such a way that it provides easier and easier access to the currents that flow through it.” Therefore, the explanation is based on the direction of evolution in time, in which it has been introduced the thought that system structure should morph freely towards the optimal architecture and flow organization that minimize resistances to the internal flows (exergy losses) that are required for the system existence, which is proposed as the origin of eukaryotes, mitochondria, chloroplasts, and for the origin of the eukaryotic nucleus.

Keywords: Exergy destruction; Nucleus; Archaeobacterium; Evolutionary design.

1. INTRODUCTION

The formation process of the eukaryotic cell with all its contents (nucleus, membrane encapsulated organelles, cytoskeleton and endomembrane system) is still enigmatic. Most likely, the process started from a prokaryote cell, which are known to be the first living cells in the planet, to the first eukaryotic common ancestor (FECA). Such innovatory cellular structure and the symbiotically acquired mitochondria allowed for broader ecological participation, and eventually originated the last eukaryotic common ancestor (LECA), which evolved and diverged to form the successful origins of the current uni and multicellular eukaryotes' lineages [1, 2]. Figure 1 shows the main steps of cellular evolution on Earth [3].

There are several models that propose to explain the evolutionary path of the modern eukaryotic cell. The evolution of the nucleus is based: (i) on prokaryote plasma membrane invaginations or (ii) on archaeon endosymbiosis in a prokaryote host, or (iii) on a membrane system autogenous origin with the nuclear

component in an archaeal host after mitochondria incorporation. The assumption that an endosymbiont (protomitochondria) entered an archaeal cell host through phagocytosis and united to form the first eukaryotic common ancestor (FECA) is the fundamental basis for the symbiogenic models, that are currently the most accepted theories [1, 2]. Recently, because of experimental evidence gathered from cultivation, genomics, and literature data interpretations, an alternative eukaryogenesis theory has been proposed, namely, the entangle–engulf–endogenize (E^3) model [4]. All such perspectives comprise the so-called *outside-in* models, which have been questioned by the fact that archaea are known to produce extracellular protrusions but typically do not carry out endocytosis or phagocytosis [5]. Hence, the *outside-in* perspective has been challenged by suggesting that a prokaryotic cell generated protrusions beyond its surrounding membrane, aggregating to form the endomembrane and cytoplasm system. According to this *inside-out* model, the nucleus would be the first and oldest part of the eukaryotic cell, which was kept unaltered. In contrast, the cell organization changed from prokaryotic to eukaryotic [5]. The natural question is: Which of these two models best represents what happened during the evolution of eukaryotic cells?

This study invokes the Constructal law to provide a possible answer: “For a finite-size flow system to persist in time, it must evolve with freedom such that it provides greater and easier access to its flows” [6,7]. One way to figure out which of the two unsteady processes led to the most negligible resistances to the flows required for the system to exist is to estimate the total entropy generated (or exergy destruction) in each process.

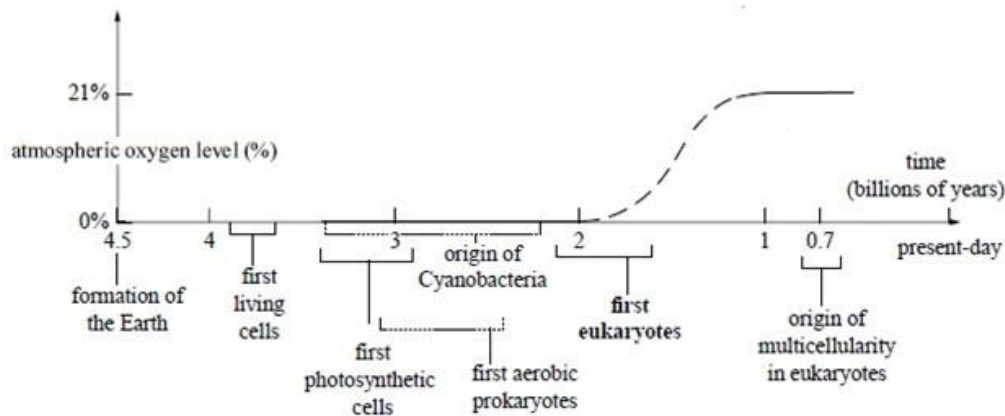


Fig. 1 – The currently accepted eukaryotic cellular evolution steps [3].

2. MATERIALS AND METHODS

The schematic diagram of the *inside-out* and *outside-in* models is shown in Fig. 2, where 1 and 2 are the start and finish of the process, respectively. Consider the resulting eukaryotic cell ancestor as an open system in Fig. 2 – right. The system has inlet and outlet ports through the permeable boundary, and the system's operation is unsteady. Mass conservation, the 1st and 2nd law of thermodynamics, and the *quasi-steady* assumption for crossflow pumping state at any instant that [7]:

$$\frac{dM}{dt} = \dot{m}_{in} - \dot{m}_{out}; \quad \frac{dU}{dt} = \dot{Q} + \frac{dM}{dt} h_{in} + \underbrace{\dot{m}_{out}(h_{in} - h_{out})}_{=0} - \dot{W}, \quad (1)$$

$$\dot{S}_{gen} = \frac{dS}{dt} + \dot{m}_{out} s_{out} - \dot{m}_{in} s_{in} - \frac{\dot{Q}}{T_0} \geq 0, \quad (2)$$

where M is the mass, \dot{m} the mass flow rate, U is the internal energy, \dot{Q} the heat transfer rate, h is the specific enthalpy, \dot{W} the work transfer rate, \dot{S} the entropy rate, s is the specific entropy, T is the temperature, and subscripts in, out, 0, and gen the inlet, outlet, environment, and generation, respectively.

Next, the *quasi-steady* assumption will be adopted, and eqs. (1) and (2) will be integrated from states 1 to 2:

$$Q_{1-2} = -(M_2 - M_1) v_0 p_0 = -\Delta M v_0 p_0 = -p_0 \Delta V; \quad S_{gen,1-2} = p_0 \Delta M v_0 / T_0, \quad (3)$$

where v is the specific volume, p is the pressure, Δ the variation, and V is the volume.

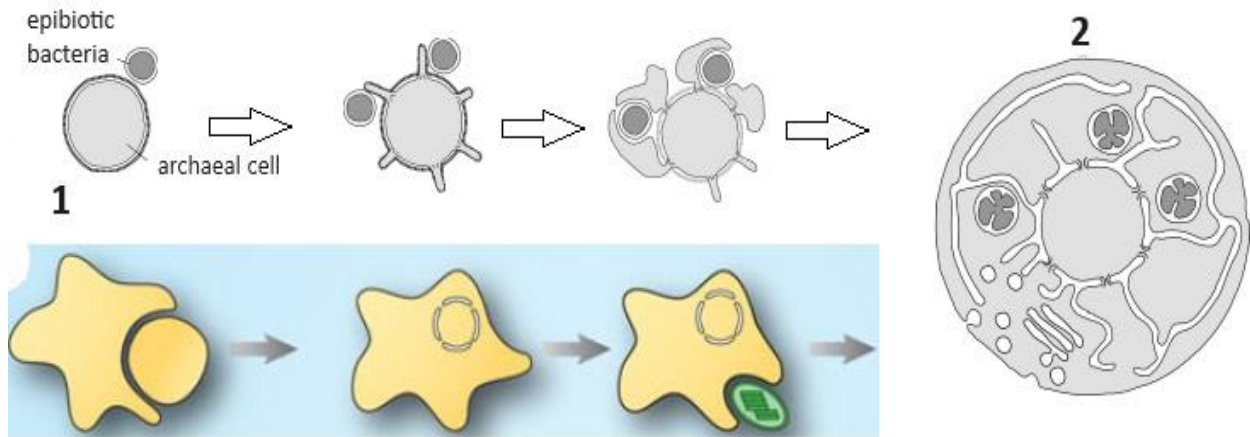


Fig. 2 – Top left: the *inside-out* model evolution path; Bottom left: the *outside-in* model evolution path, and Right: the resulting eukaryotic cell ancestor (adapted [1, 5]).

From Fig. 2 and Eq. (3), the archaeal cell is only the nucleus for the *inside-out* model, so $M_{1,oim} > M_{1,iom}$, $\Delta M_{oim} < \Delta M_{iom}$ and $S_{gen,1-2,iom} > S_{gen,1-2,oim}$, in which subscripts “oim” and “iom” refer to the outside-in and inside-out models, respectively.

3. DISCUSSION AND CONCLUSIONS

The total entropy generated with the *inside-out* process was more significant than that with the *outside-in* process. Hence, based on Constructal law, the *outside-in* process is expected to be the actual direction of eukaryotic cell evolution over time.

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