Rev. Roum. Sci. Techn.– Électrotechn. et Énerg.
Vol. **70**, *2*, pp. 259–262, Bucarest, 2025

Thermotechnique et thermoénergétique
Thermal engineering and thermal energy

THE EXPLANATION OF THE EUKARYOTE ENDOSYMBIOTIC ORIGIN BY THE CONSTRUCTAL LAW

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

The origin of eukaryotes is regarded as one of the most significant issues in the history of life. Various perspectives aim to provide a comprehensive understanding of eukaryote origins, drawing on paleontological evidence, energetics, the unique characteristics of eukaryotes, and the relationships between different eukaryotic groups. Several versions of the endosymbiotic theory have been proposed to explain the emergence of eukaryotes and their mitochondria. Only recently have energy and energetic constraints been integrated into this theory, recognizing that the prokaryotic cell structure played a crucial role in the development of eukaryotic complexity. Specifically, cells with mitochondria possess the bioenergetic capabilities necessary for this complexity, which explains the absence of transitional forms between prokaryotes and eukaryotes. This study explores eukaryotes' origins through the lens of constructal theory, which posits that "for a flow system to persist over time (to survive), it must evolve to facilitate easier and more efficient flow." In this context, the theory suggests that the evolution of systems is driven by a need for optimal architecture and flow organization, reducing resistance to internal flows (exergy losses) that sustain the system. This framework is proposed as the underlying principle behind the origin of eukaryotes, mitochondria, chloroplasts, and the eukaryotic nucleus.

1. INTRODUCTION

One of the most significant events in the evolution of Earth's organisms is the emergence of eukaryotic cells**.** This event represents a transition from simpler organisms (archaea and bacteria) to more complex life forms. The origin 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, known as the first living cell on the planet, and evolved into the first eukaryotic common ancestor (FECA). The innovative cellular structure and mitochondria acquired through symbiosis enabled greater ecological involvement, ultimately leading to the emergence of the last eukaryotic common ancestor (LECA). From there, it evolved and diversified, giving rise to the successful lineages of both unicellular and multicellular eukaryotes [1,2]. Figure 1 illustrates the key stages of cellular evolution on Earth [3].

Several models have been proposed to explain the evolutionary development of the modern eukaryotic cell. The evolution of the nucleus is thought to have occurred in one of three ways: (i) through invaginations of the prokaryotic plasma membrane, (ii) via endosymbiosis between an archaeon and a prokaryote host, or (iii) through the autogenous origin of a membrane system with the nuclear component emerging in an archaeal host following the incorporation of mitochondria. The central idea behind the symbiogenic models—currently the most widely accepted theories—is that an endosymbiont (protomitochondria) entered an archaeal cell via phagocytosis and merged to form the first eukaryotic common ancestor (FECA) [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 to that question: "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 resistance to the flows required for the system to exist is to estimate the total entropy generated (or exergy destruction) in each process.

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 last eukaryotic common ancestor (LECA), state 2, 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,

$$\frac{dM}{dt} = \dot{m}_{in} - \dot{m}_{out} \tag{1}$$

The 1st law of thermodynamics, and eq. (1) state at any instant that [7]:

$$\frac{dU}{dt} = \dot{Q} + \frac{dM}{dt} h_{in} + \underbrace{\dot{m}_{out}(h_{in} - h_{out}) - \dot{W}}_{=0} \tag{2}$$

in which the third and fourth terms on the right-hand side add up to zero. This results from assuming a *quasi*-steady process for the mass of incompressible liquid that flows in and out of

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DOI: 10.59277/RRST-EE.2025.2.18

the eukaryotic cell annular space (the region between the external boundary and the nucleus) in the open system in Fig. 2 – right $\dot{m}_{out}$. Note also that the archaeal cell (nucleus) rejects the metabolic heat rate, $\dot{Q}$, to the annular space, which rejects the same heat rate to the environment through the external boundary. Therefore, for any time interval of the *quasi*-steady process in the eukaryotic cell annular space, the 1st law of thermodynamics states that [7]:

$$0=\dot{Q}-\dot{Q}+\dot{m}_{out}(h_{in}-h_{out})-\dot{W}. \qquad (3)$$

Next, the 2nd law of thermodynamics, and eq. (1), state that [7]:

$$\begin{aligned}\dot{S}_{gen}&=\frac{dS}{dt}+\dot{m}_{out}s_{out}-\dot{m}_{in}s_{in}-\frac{\dot{Q}}{T_0}\\&=\frac{dS}{dt}+\dot{m}_{out}s_{out}-\left(\frac{dM}{dt}+\dot{m}_{out}\right)s_{in}-\frac{\dot{Q}}{T_0}\ge 0\end{aligned} \qquad (4)$$

in which $\frac{dS}{dt},\ \frac{dM}{dt} << \frac{dS_{gen}}{dt}$, assuming a *quasi*-steady process $s_{out}-s_{in}=\int_{T_{in}}^{T_{out}}\frac{c}{T}dT=0$, with $T_{in}=T_{out}=T_0$ and acknowledging that the external boundary (control surface) is at the environment temperature. As a result, for the open system in Fig. 2 – right, the entropy generation rate is given by:

$$\dot{S}_{gen}=\frac{dS_{gen}}{dt}=-\frac{\dot{Q}}{T_0}>0. \qquad (5)$$

In eq. (1) to (5), M is the mass, $\dot{m}$ the mass flow rate, U is the internal energy, $\dot{Q}$ the metabolic 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.

3. RESULTS AND DISCUSSION

Integrating eq. (2) and (5) from states 1 to 2, the result is:

$$\begin{aligned}Q_{1-2}&=(U_2-U_1)-h_{in}(M_2-M_1)\\&=M_2u_0-M_1u_0-(u_0+p_0v_0)\underbrace{(M_2-M_1)}_{\Delta M_{1-2}},\end{aligned} \qquad (6)$$

$$Q_{1-2}=-(M_2-M_1)\,p_0v_0=-p_0v_0\Delta M_{1-2}, \qquad (7)$$

where U is the internal energy, u is the specific internal energy, v is the specific volume, p is the pressure and Δ the variation.

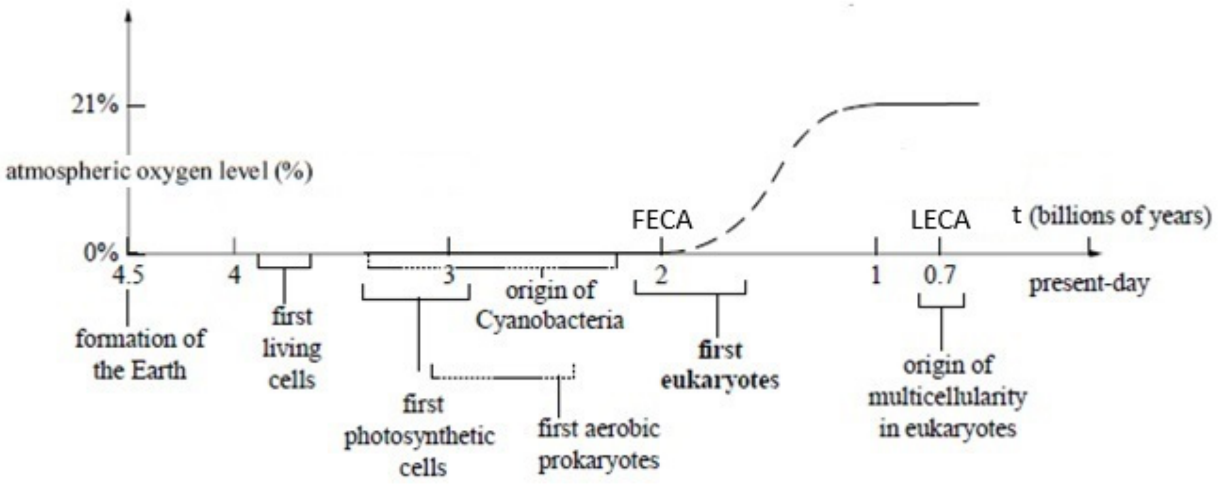

Fig. 1 – The currently accepted eukaryotic cellular evolution steps [3,8].

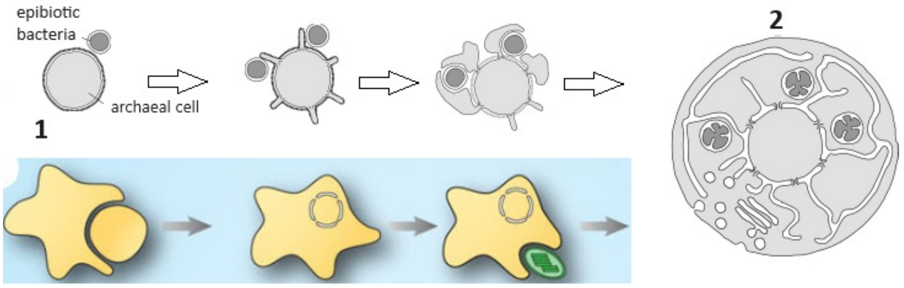

Fig. 2 – Top left: the *inside-out* model evolution path; Bottom left: the *outside-in* model evolution path, and Right: the resulting eukaryotic cell ancestor (adapted [1,5,8]).

$$S_{gen,1-2} = p_0 \Delta M_{1-2}\, v_0 / T_0 = \gamma\, \Delta M_{1-2}, \tag{8}$$

in which, for simplicity, the constant $\gamma = p_0 v_0 / T_0$ was defined.

From Fig. 2, the archaeal cell is only the nucleus for the *inside-out* model, so $M_{1,oim} > M_{1,iom}$, $\Delta M_{1-2,oim} < \Delta M_{1-2,iom}$ and from Eq. (8), $S_{gen,1-2,iom} > S_{gen,1-2,oim}$, in which subscripts "oim" and "iom" refer to the *outside-in* and *inside-out* models, respectively.

It is instructive to visualize graphically the entropy generated by the process concerning evolution time. For that, two essential points in the eukaryotic cell evolution are utilized, i.e., the appearance of the first eukaryotic common ancestor (FECA) and the last eukaryotic common ancestor (LECA), that allowed for the formation of the current uni and multicellular eukaryotes' lineages [1, 2].

Figure 3 was built schematically to provide a representation of the total entropy generated from the formation of the earth $t = 0$ (state 1) to the appearance of the FECA (state FECA) and of the LECA $t \cong 3.8$ billion years (state 2 or LECA), based on Fig. 1 [3]. Conceptually, it is reasonable to assume that most of the entropy generation occurred during the process from 1 to FECA, since it was the process in which most of the morphological changes happened (mass increase). Fewer structural modifications took effect from FECA to 2 (or LECA). Based on eq. (8), the entropy generated in each process is proportional to ΔM, i.e., the cell mass variation. Since $\Delta M_{oim} < \Delta M_{iom}$ in both processes, based on Fig. 2, and the discussion right after Eq. (8), $S_{gen,1-FECA,iom} > S_{gen,1-FECA,oim}$, and $S_{gen,FECA-2,iom} > S_{gen,FECA-2,oim}$. The vertical axis shows the total entropy generation $S_{gen} = \gamma\, \Delta M$, and the horizontal axis the evolution time, t, in billions of years, according to Fig. 1 [3]. For clarity, the oim and iom S_{gen} states 1, FECA, and 2 were curve-fitted with solid (oim) and dashed (iom) lines.

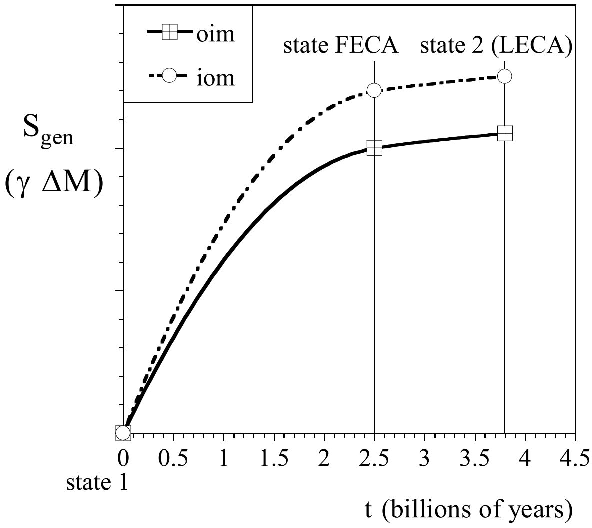

Fig. 3 – The total entropy generated by the iom and oim processes concerning Earth's evolution time.

As a result of the theoretical analysis and the schematic evolution of the two proposed processes, the total entropy generated with the *inside-out* process was more significant than that with the *outside-in* process. Hence, based on the Constructal law, the *outside-in* process is expected to be the actual direction of eukaryotic cell evolution over time.

The analysis relied on the fact that any system or process in the universe complies with the mass and energy conservation principles (1st Law) that determine the thermodynamic states visited by the system. Next, based on those states, the 2nd Law of thermodynamics determines the entropy the system generates so that $S_{gen} > 0$, with no exceptions. Consequently, such laws are related to the Constructal law since knowledge of the dynamic flow system morphology and operational change is required for the analysis. However, all laws are different and independent principles [9].

The entropy generation minimization (EGM) method can predict the optimal structural design and energy flow organization of any system for minimizing losses at any given time, depending on its geometry, materials, environment, and other process variables. Hence, the dynamic design phenomenon could be modeled by a succession of periods (time steps) where, in each of them, the optimal design remains practically unchanged, "…like the images in a movie at the cinema…" [6]. Any system or process optimization study represents one of those images, thus included in the Constructal law.

Each time step duration is much shorter than the evolution timescale since evolution never ends [6], which justifies the quasi-steady assumption in the analysis presented herein. The changing rate of optimal designs indicates the direction of system/process evolution over time, *i.e.*, the Constructal design [6, 9]. This line of thought seeks to demonstrate that all systems and processes in the universe evolve according to the Constructal law with no exceptions.

4. CONCLUSIONS

This study investigated two proposed models to explain the possible origin of eukaryotic cells. A thermodynamic analysis was conducted based on the Constructal Law.

During the eukaryotic cell evolution, a 2nd law analysis demonstrated that the *outside-in* model provided easier access to the currents that flow through the system than the *inside-out* model. As a result, based on the constructal law, the *outside-in* model is the most probable explanation for the origin of eukaryotic cells.

NOMENCLATURE

c	specific heat, J kg^{-1} K^{-1}
h	specific enthalpy, kJ kg^{-1}
$\dot{m}$	mass flow rate, kg s^{-1}
M	mass, kg
p	pressure, N m^{-2}
Q	heat transfer, J
$\dot{Q}$	heat transfer rate, W
s	specific entropy, J kg^{-1} K^{-1}
S	entropy, J K^{-1}

$\dot{S}$	entropy rate, W K^{-1}
t	billions of years
T	temperature, K
u	specific internal energy, kJ kg^{-1}
U	internal energy, J
v	specific volume, m^3 kg^{-1}
$\dot{W}$	work transfer rate, W

Greek letters

Δ	variation
γ	constant, $p_0 v_0 / T_0$

Subscripts

FECA	first eukaryote common ancestor
gen	generation
in	inlet
iom	inside-out model
LECA	last eukaryote common ancestor
oim	outside-in model
out	outlet
0	ambient

ACKNOWLEDGEMENTS

J.V.C. Vargas acknowledges the support of the Brazilian National Council of Scientific and Technological Development, CNPq (projects 430986/2016-5, 443823/2018-9, 313646/2020-1, 446787/2020-5, 408073/2021-7, 405864/2022-1, and 408080/2022-1), CAPES, Ministry of Education, Brazil (project CAPES-PRINT-UFPR-88881.311981/2018-01), Araucaria Foundation of Parana, Brazil (project 115/2018, no. 50.579 – PRONEX).

The paper was initially published in the proceedings of 14th Constructal Law Conference, CLC 2024 [8].

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Vanessa Kava: Conceptualization, Investigation, Methodology, Writing. José Vargas: Conceptualization, Investigation, Methodology, Writing-Original draft preparation. Juan Ordonez: Visualization, Investigation, Methodology, Writing- Reviewing and Editing. A. B. Mariano: Writing-Reviewing and Editing.

Received on 15 February 2025

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