

PTEE

aula 05

roteiro

- seminário
- endossimbiose
- discussão e ensaios

endossimbiose

- proposta original e evidências
- propostas modernas e evidências

proposta original

- fundamentalmente ligada a origem de Eukarya e divisão celular

On the Origin of Mitosing Cells

LYNN SAGAN

*Department of Biology, Boston University
Boston, Massachusetts, U.S.A.*

(Received 8 June 1966)

A theory of the origin of eukaryotic cells ("higher" cells which divide by classical mitosis) is presented. By hypothesis, three fundamental organelles: the mitochondria, the photosynthetic plastids and the (9+2) basal bodies of flagella were themselves once free-living (prokaryotic) cells. The evolution of photosynthesis under the anaerobic conditions of the early atmosphere to form anaerobic bacteria, photosynthetic bacteria and eventually blue-green algae (and protoplastids) is described. The subsequent evolution of aerobic metabolism in prokaryotes to form aerobic bacteria (proto-flagella and protomitochondria) presumably occurred during the transition to the oxidizing atmosphere. Classical mitosis evolved in protozoan-type cells millions of years after the evolution of photosynthesis. A plausible scheme for the origin of classical mitosis in primitive amoeboid flagellates is presented. During the course of the evolution of mitosis, photosynthetic plastids (themselves derived from prokaryotes) were symbiotically acquired by some of these protozoans to form the eukaryotic algae and the green plants.

The cytological, biochemical and paleontological evidence for this theory is presented, along with suggestions for further possible experimental verification. The implications of this scheme for the systematics of the lower organisms is discussed.

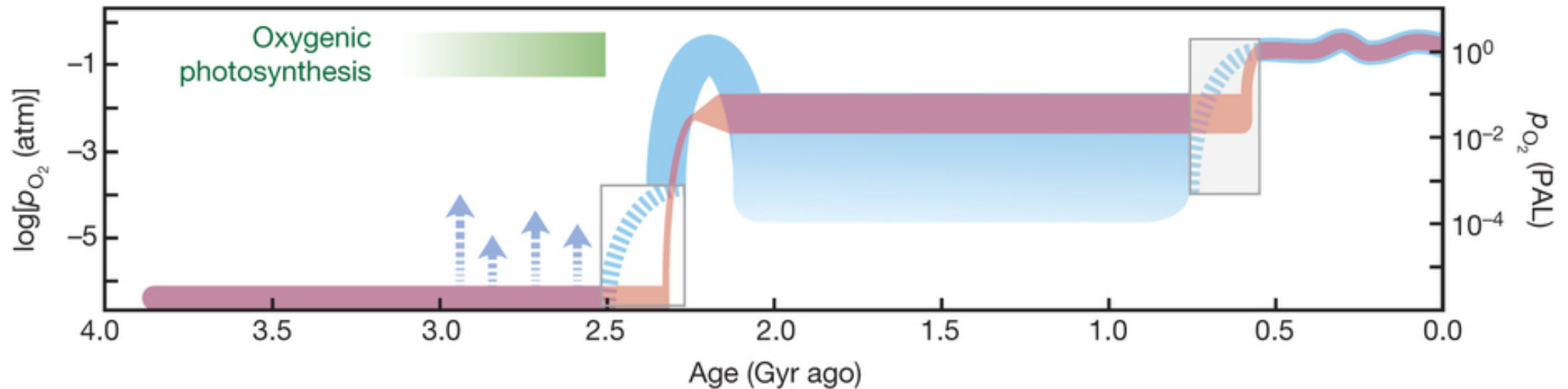
proposta original

- fundamentalmente ligada a origem de Eukarya e divisão celular
- explicação para origem de mitocôncrias, plastídeos e flagelos
- “cenário” evolutivo

proposta original

- surgimento de organismos fotossintetizantes
- aumento da pressão parcial de oxigênio na atmosfera

proposta original



The faded red curve shows a 'classical, two-step' view of atmospheric evolution⁹⁵, while the blue curve shows the emerging model (p_{O_2} , atmospheric partial pressure of O_2). Right axis, p_{O_2} relative to the present atmospheric level (PAL); left axis, $\log p_{O_2}$. Arrows denote possible 'whiffs' of O_2 late in the Archaean; their duration and magnitude are poorly understood. An additional frontier lies in reconstructing the detailed fabric of 'state changes' in atmospheric p_{O_2} , such as occurred at the transitions from the late part of the Archaean to the early Proterozoic and from the late Proterozoic to the early Phanerozoic (blue boxes). Values for the Phanerozoic are taken from refs 96 and 97.

Lyons, Timothy W., Christopher T. Reinhard, and Noah J. Planavsky. 2014. "The Rise of Oxygen in Earth's Early Ocean and Atmosphere." *Nature* 506 (7488): 307–15. doi: 10.1038/nature13068.

proposta original

- surgimento de organismos fotossintetizantes
- aumento da pressão parcial de oxigênio na atmosfera
- oxigenação de carbono inorgânico
- endossimbiose de aeróbio por um anaeróbio heterotrófico
- primeiro aeróbio, amitótico, ameboide

proposta original

- herança de material genético é central
- poliploidia solução inicial para divisão
- parasita espiroqueta e habilidade de 9+2
- centríolos e centrômeros

TABLE 2

*Taxonomic criteria in the formation of a natural phylogeny for microbes
(listed roughly in order of relative importance)*

Criterion	Techniques by which measured
Total homology of DNA base pairs	Direct DNA nucleotide sequence data Agar-gel technique for DNA homologies Ability to genetically recombine (i.e. classical genetic techniques) DNA base ratios on CsCl density gradient DNA denaturation (melting point) determinations
Homologous metabolic pathways	Classical biochemistry
Homologous cistrons, same "genetic code letters"	Homologous messenger RNA's (DNA-RNA homologies). Identity of individual transfer RNA's for specific amino acids
Ultrastructural morphology	Electron microscopy
Morphology and life cycle	Light microscopy, classical cytology
Single biochemical pigments, enzymes, etc., in common	Spectroscopy, classical biochemistry
Molecular structure of single pigment, or enzyme	Classical chemistry
Common phenotypic traits	Ability to grow on same carbohydrate, production of same end product, motility, etc.

corolários

- simbionte origina: DNA, mRNA, máquina de síntese protéica, fonte de moléculas pequenas, maquinaria de síntese de membrana
- redundâncias se tornarão obsoletas
- herança do simbionte depende de mecanismo de transmissão
- aquisição de segundo endossimbionte semelhante é implausível
- perda e reaquisição extremamente implausível
- dever ser possível encontrar o grupo-irmão do endossimbionte

TABLE 3

Cytological mechanisms for retention of organelles throughout life cycle

Organisms	Mechanism
A. Mitochondria	
Many plants and animal cells; dividing germ cells of vertebrates; cleavage stages	Many mitochondria randomly distributed throughout cell (Wilson, 1925, p. 712)
Spermatocytes of some scorpions, such as <i>Opisthancanthus</i> , <i>Hadrurus</i> , etc.	Primary spermatocytes: small and numerous mitochondria join together to form 24 spheroids Secondary spermatocytes: 12 spheroids are segregated to each daughter cell. Spermatids: six spheroids are segregated to each pole; thus six mitochondrial spheroids are present in each sperm cell (Wilson, 1925, p. 163)
Spermatocytes of scorpion, such as <i>Centrurus</i>	Primary spermatocytes: mitochondria aggregate into ring-shaped body, oriented on spindle, is cut transversely by division of cell into two half rings; each half ring forms a rod. Secondary spermatocyte: each rod is carried on spindle and cut by cell division into a half rod (Wilson, 1925, p. 365)
Spermatocytes of worm such as <i>Ascaris</i>	Mitochondria are oriented on spindles toward centrioles. They do not divide but are segregated to daughter cells by virtue of their orientation (Wilson, 1925, p. 163)
Some insects, such as <i>Hydrometra</i>	Elongate rods of mitochondria are oriented on spindles; some of these mitochondrial rods are cut by cell equator (Wilson, 1925, p. 164)
Some ciliates	Mitochondrial divisions of numerous mitochondria synchronous with nuclear division (Wilson, 1925, p. 13)
<i>Vicia</i> , a bean	Two groups of mitochondria orient at opposite poles at division (Wilson, 1925, p. 163)

predições

Analogous to the quantitative relationship between DNA and ploidy, satellite DNA correlated specifically with the various organelles should be found in cells in direct proportion to the number of organelles in these cells. No eukaryotic cell having flagellar basal bodies, cilia, centrioles, centromeres, or any other of the homologues can lack (9+2) homologue-specific DNA. It is likely that this DNA has evaded detection because it has very little metabolic responsibility and needs to be only a few cistrons long to code for its few specific proteins. Identification of (9+2) homologue-specific DNA and a complete characterization of its RNA and of its limited biochemical functions should eventually be possible. This is true of mitochondrial and plastid DNA as well.

In keeping with the hypothesis, the following organisms should have evolved: a free-living complex flagellar counterpart; a free-living mitochondrion counterpart; and a heterotrophic prokaryote capable of ingesting cells.

resumo

- bactéria heterotrófica anaeróbia, com sistema endomembranas, engole bactéria aeróbia
- endossimbiose mitocondrial inicial, depois (9+2) homólogo – pressão era oxigênio

constatações

- mitocôndria vem de bacterias aerobias (alphaproteo)
- maquinaria replicativa de arqueia

MAS

- existem muitos outros genes bacterianos e arqueanos no genoma de eucariontes....

hipótese do hidrogênio

- alphaproteo engolida por archaea (ou próxima)
- MAS ap era anaeróbia, excretando H₂ e CO₂
- archaea usava H₂ e CO₂ para energia (metanogênica)
- na ausência de H₂, o hospedeiro ficou dependente

hipótese do hidrogênio

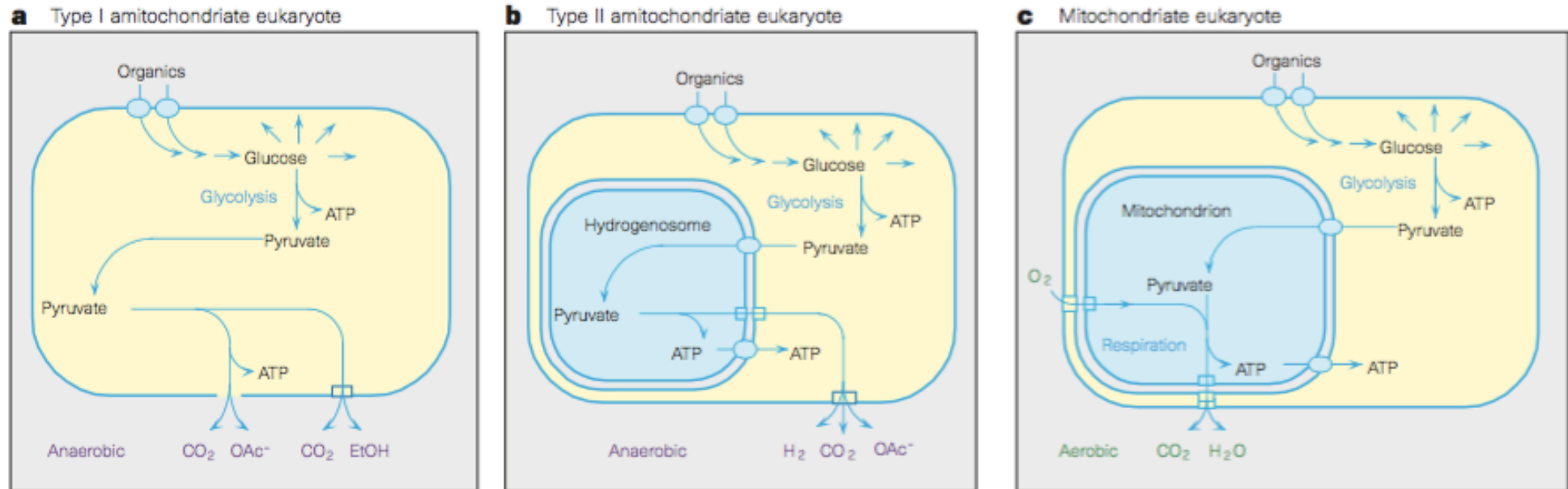
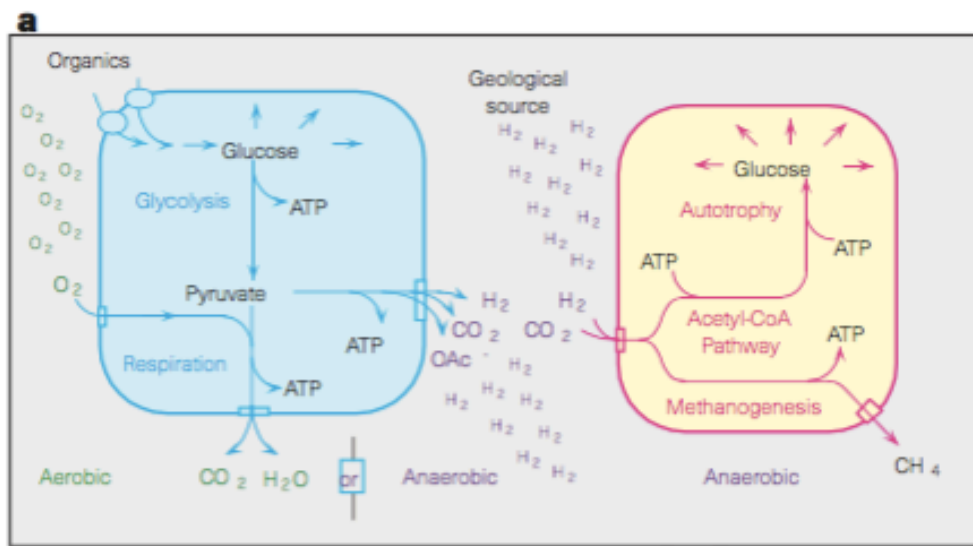


Figure 1 Schematic summary of forms of energy metabolism among heterotrophic eukaryotes (see refs 18 and 19 for details). OAc⁻, acetate; EtOH, ethanol; ATP, adenosine triphosphate. Respiration in the figure designates the combination of oxidative decarboxylation by PDH, Krebs cycle (also known as citric acid

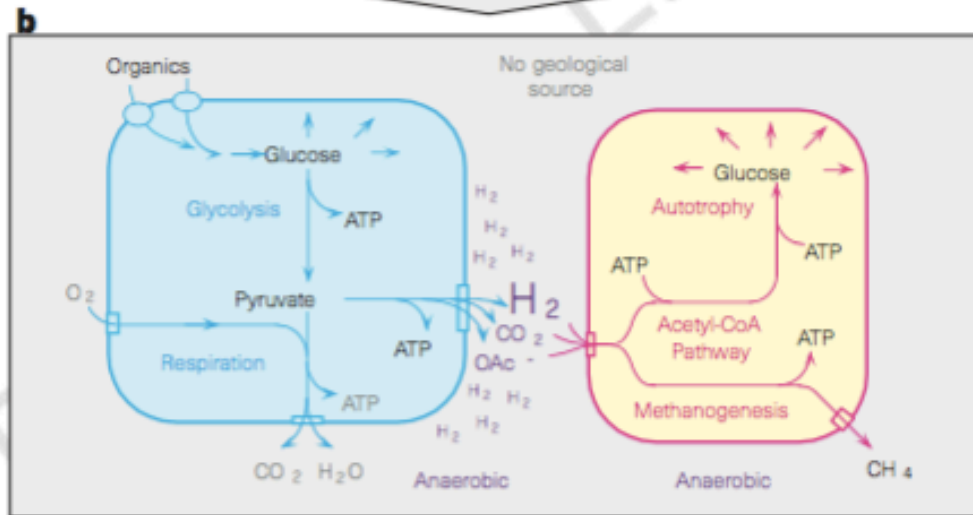
cycle, tricarboxylic acid cycle, TCA cycle) to produce NADH + H⁺ and FADH₂, and the respiratory electron transport chain that donates electrons and protons to O₂, yielding ATP through oxidative phosphorylation.

hipótese do hidrogênio

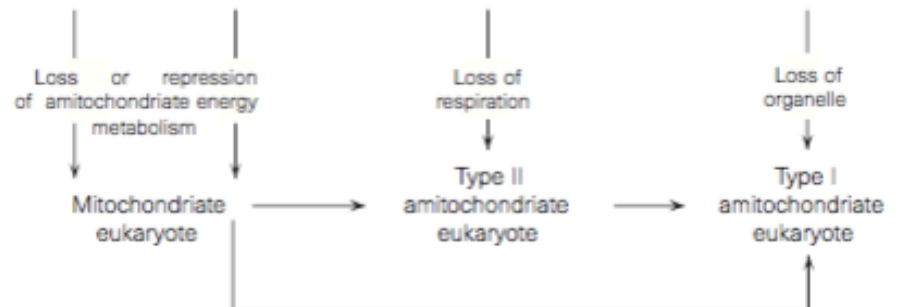
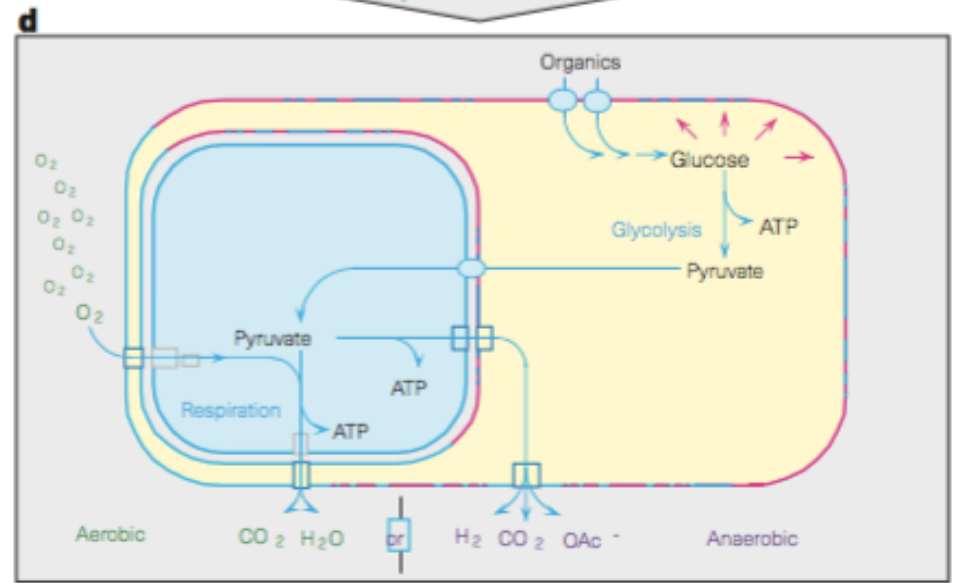
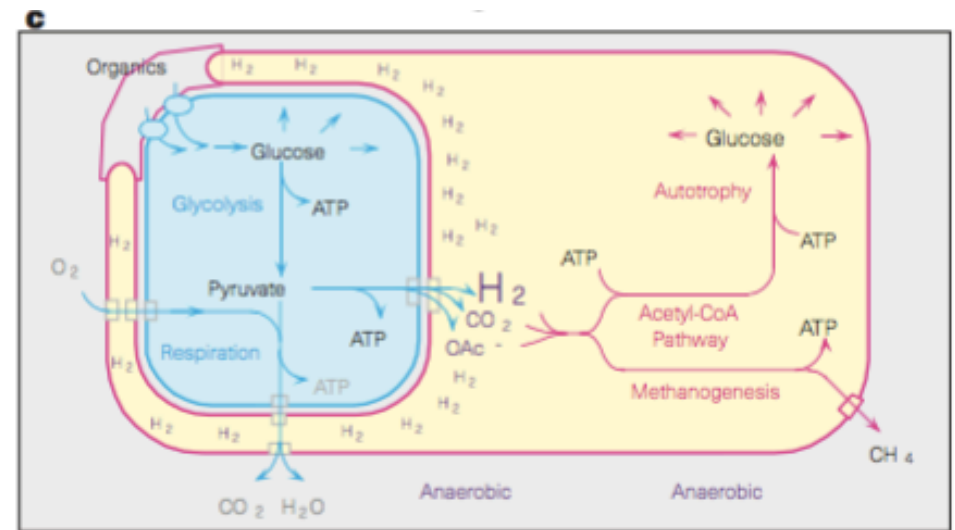
- LGT de genes de proteínas de membrana permitindo importação de substratos e enzimas de glicólise,
- permitem o hospedeiro “envolver e alimentar” o simbionte, pois agora pode usar moléculas mais complexas. Não mais autótrofo
- simbionte é então perdido, vira um hidrogenossomo, ou mitocôndria



Anaerobic syntrophy



Host dependence



hipótese do hidrogênio

Figure 2 Hypothetical model to derive the ancestral state of eukaryotic energy metabolism put forward here, invoking strict dependence of the host upon waste products of the symbiont's anaerobic heterotrophy (see text). Host components are shaded red (cytosol yellow), symbiont components are shaded blue. The composite nature of membranes in **d** symbolizes the process of replacement of archaeobacterial lipids (glycerol ethers of isoprenes) with eubacterial lipids (glycerol esters of fatty acids) through loss of the host's lipid biosynthetic pathway. For an alternative explanation of the origin of eubacterial lipids in eukaryotes, see ref. 6. Anaerobic substrates and end products are indicated in purple, aerobic substrates and end products are indicated in green. Substrates and end products, the non-availability of which for a given step underly ecological factors, are indicated in grey.