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Physiology, anaerobes, and the origin of mitosing cells 50 years on

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Abstract.

Endosymbiotic theory posits that some organelles or structures of eukaryotic cells stem from free-living prokaryotes that became endosymbionts within a host cell. Endosymbiosis has a long and turbulent history of controversy and debate going back over 100 years. The 1967 paper by Lynn Sagan (later Lynn Margulis) forced a reluctant field to take endosymbiotic theory seriously and to incorporate it into the fabric of evolutionary thinking. Margulis envisaged three cellular partners associating in series at eukaryotic origin: the host (an engulfing bacterium), the mitochondrion (a respiring bacterium), and the flagellum (a spirochaete), with lineages descended from that flagellated eukaryote subsequently acquiring plastids from cyanobacteria, but on multiple different occasions in her 1967 account. Today, the endosymbiotic origin of mitochondria and plastids (each single events, the data now say) is uncontested textbook knowledge. The host has been more elusive, recent findings identifying it as a member of the archaea, not as a sister group of the archaea. Margulis's proposal for a spirochaete origin of flagellae was abandoned by everyone except her, because no data ever came around to support the idea. Her 1967 proposal that mitochondria and plastids arose from different endosymbionts was novel. The paper presented an appealing narrative that linked the origin of mitochondria with oxygen in Earth history: cyanobacteria make oxygen, oxygen starts accumulating in the atmosphere about 2.4 billion years ago, oxygen begets oxygen-respiring bacteria that become mitochondria via symbiosis, followed by later (numerous) multiple, independent symbioses involving cyanobacteria that brought photosynthesis to eukaryotes. With the focus on oxygen, Margulis's account of eukaryote origin was however unprepared to accommodate the discovery of mitochondria in eukaryotic anaerobes. Today's oxygen narrative has it that the oceans were anoxic up until about 580 million years ago, while the atmosphere attained modern oxygen levels only about 400 million years ago. Since eukaryotes are roughly 1.6 billion years old, much of eukaryotic evolution took place in low oxygen environments, readily explaining the persistence across