

## A roadmap to eukaryogenesis

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Biologists had long accepted that there are two morphologically distinct types of cells. It was in 1962, however, that Stanier and van Neil formally classified them into “prokaryotes” and “eukaryotes”. Eukaryotes were thought to be the product of gradual Darwinian-like evolution from prokaryotes, until the endosymbiotic theory for the origin of plastids and mitochondria was re-popularized in 1967 by Lynn Margulis. In order to reconcile endosymbiotic theory with the origin of eukaryotes, the “*Archezoa hypothesis*” was put forth, which posits an amitochondriate eukaryote phagocytosed the mitochondrial ancestor. The “*Archaezoa hypothesis*” has since then been disproven by the phylogenetic presence of mitochondrial genes in amitochondriate eukaryotes and the fact that they have diverged mitochondria instead of classical aerobic forms. The competing hypothesis envisages a symbiogenic origin of eukaryotes where endosymbiosis of the mitochondrial ancestor by an archaeon precipitates eukaryote origin (mitochondria early), contrary to gradualistic theories where the mitochondria completes eukaryogenesis (mitochondria late). With the discovery that eukaryotes emerge from within the archaea, the phagocytosing host was reimagined as a complex archaeaon instead of an “archezoan”. While the debate on the nature of the host continues feverishly today, a strategic time-out to understand the problem of eukaryogenesis is prudent. The ability to phagocytose is crucial for mitochondria late scenarios, however the complexity required for phagocytosis is underappreciated. Here we take a comprehensive approach to understand the problem of eukaryogenesis and present a concise list of challenges that evidently were solved by evolution during eukaryogenesis. Comparing the existing theories and the extent to which they are able or unable to explain these challenges will allow future research to focus on aspects of eukaryogenesis that remain unaddressed. While a definitive answer to eukaryogenesis might be impossible, a scientifically plausible scenario should undoubtedly be preferred over fantasy.