



## Macroevolution in early eukaryotes

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The origin of the domain Eucarya is not constrained and might be an Archean event. However, the Archean eukaryotic record is much discussed and limited to biomarkers, possibly indicating the presence of cells able to synthesize eukaryotic sterols in their flexible membranes. Large organic-walled microfossils have been recently discovered in archean shales and cherts and might reveal new information regarding early life diversity, but their biological affinities remain unknown at present.

A hypothesis is proposed to offer a new reading of the diversification pattern of early eukaryotes, divided into three steps involving different taxonomic levels.

During Period I (?Archean-1.8 to 1.2 Ga), moderately diverse stem (and possibly but not necessarily crown-group) eukaryotes appeared. These early eukaryotic cells had a flexible lipidic membrane, a cytoskeleton and associated endomembrane system, and a nucleus. The diversity of organic-walled microfossils was moderate and included smooth and ornamented sphaeromorphs, and vesicles with asymmetrically distributed processes and one species with symmetrically distributed processes. Macroscopic compressions (interpreted as macroalgae) include few taxa.

During Period II (1.2-0.63 Ga), a major diversification occurred at the supergroup level. Members of all extant supergroups: the Opisthokonts, the Amoebozoa, the Archaeplastida, the chromalveolates, and the Rhizaria, except the Excavates, are recorded in the fossil record. The diversity of protists and of macroalgae increases gradually. Major biological innovations such as multicellularity, sex, biomineralisation, heterotrophy and eukaryotic photosynthesis appeared, and possibly the first appearance of animals, leading to ecological tiering and complex food webs and interactions. Recent discoveries suggest protists also invaded freshwater lakes at that time.

During Period III, the Ediacaran (0.63–0.55 Ma), a second diversification, this time within the supergroups, occurred and left more preservable parts and more morphological diversity, but within clades. After a drop in diversity (of which the timing and intensity are discussed), the Ediacarian (635–555 Ma) starts with a low-diversity assemblage of leiospheres and rare acanthomorphs, then records a burst in diversity of acritarchs with symmetrically distributed processes, microscopic early animals, macroalgal compressions and the macroscopic Ediacara fauna (including possible cnidarians and bilaterians). Florideophytes and brown algae are documented. The late Ediacarian (555–542 Ma) yields the first mineralized metazoans, and mostly large microscopic smooth vesicles, with rare acanthomorphs. Complex multicellularity (tissue-grade then organ-grade organization), and animal biomineralization and predation evolved during the Ediacaran, leading to more complex ecosystems and diversification within supergroups. A transient shallow-water anoxia and animal predation might have caused the extinction of the Ediacara biota, prior to a Cambrian radiation of much smaller, diverse ornamented and process-bearing acritarchs.

The diversification of eukaryotic supergroups occurred early during Period II, and coincided with major environmental changes, with Rodinia amalgamation and breakup, progressively spreading oxygenated shallow-water niches above declining euxinic conditions, and transient anoxia followed by two glaciations at the end of the Period. Although the direct role of these geological events on eukaryotic evolution is not clear yet, they contrast sharply with the quiet times of Period I.