"Evolution of biological innovations in early complex cells: insights from the fossil record"

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Considerable debates still exist regarding the origins of the three domains of life (Archaea, Bacteria, Eucarya), their relationships and relative order of branching, as well as the evolution of cellular life before LUCA, and between FECA and LECA (first and last eukaryotic common ancestors). Molecular and ultrastructural analyzes provide insights on the evolution of crown groups of the 3 domains back to their respective last common ancestors. The geological record preserves both part of Earth and life history further back in time, including evidence for early (chemical and morphological) traces of life that pass the tests of endogenicity, syngenicity and biogenicity. Some of these Precambrian biosignatures, from 3.5 to 0.5 Ga, may be related to modern metabolisms or modern clades, but most cannot. Regardless of taxonomy, the microfossil record can provide direct evidence for extinct clades and/or for the minimum age of evolution of biological innovations.

Population of large (up to 300 µm in diameter) organic hollow vesicles occur in 3.2 Ga marine shallow-water shales of South Africa (Javaux et al, Nature 2010). Up to 100 µm long, spindle-shaped, flanged, and sometimes hollow vesicles may form chains and are preserved in 3.45 Ga shallow-water marine cherts of Australia (Sugitani et al, Geobiology 2015). These large and sometimes complex microfossils cannot be placed with confidence in known clades, and could be early prokaryotes (or akaryotes), early eukaryotes (between FECA and LECA), or remnants of another domain of life, before LUCA or contemporaneous of the three domains. Whichever their interpretation, these Archean microfossils illustrate the fact that, on the contrary to traditional views, early cells or vesicles do not need to be small and simple.

Microfossils become more common in Proterozoic rocks and some of them can be related with confidence to (stem or crown group) eukaryotes, based on a combination of characters unknown so far in prokaryotes, including complex morphology, wall ornamentation, wall ultrastructure, recalcitrant chemistry, excystment structures, division pattern, and complex multicellularity (Javaux et al, OLEB 2003). Most of the time however, phylogenetic placement within the Eukarya is difficult, and molecular clock estimates suggest that preserved unambiguous eukaryotic microfossils (since 1.7 Ga) may belong to stem group eukaryotes (before LECA) or stem or crown lineages within major clades of the eukaryotic crown groups (after LECA). Anyhow, Proterozoic fossils provide direct or inferential evidence for many basic and important features of eukaryotic biology, including the synthesis of recalcitrant biopolymers in ornamented walls, a dynamic cytoskeleton and endomembrane system that enables cells to change shape (and, in some taxa, to synthesize and emplace plates making up walls), life cycles that include vegetative cells and resting cysts with different types of excystment structures, reproduction by budding and binary division, osmotrophy, photosynthesis, predation, biomineralization, and different grades of multicellularity (reviews in Javaux, 2011 In: Gargaud, M, et al (Eds): Origins and Evolution of Life: an astrobiology perspective. *Cambridge Univ. Press.*; Knoll et al, Proc. Roy Soc. 2006; Knoll, CSPH persp. 2014; Butterfield, J of Paleontology 2015).